

THE TAXONOMY AND DISTRIBUTION OF AUSTRALIAN TERRESTRIAL TARDIGRADES

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LIST OF ABBREVIATIONS

AM	Australian Museum, Sydney, Australia
asl	Above sea level
AU	Australian
BG	Collection of Mr B. Grabowski, Marburg, Germany
BL	Body length
BMD	Bohart Museum, University of California, Davis, USA
BTL	Buccal tube length
BTW	Buccal tube width
CLIV	Length of fourth claw (excluding the accessory claw)
CO	Cosmopolitan
DIC	Differential interference contrast
<i>et al.</i>	<i>Et alia</i> (and others)
gen. n.	New genus
IVan	Anterior claw on fourth pair of legs
IVpo	Posterior claw on fourth pair of legs
m	Metre
m1, m2, m3	Macroplacoids 1, 2, and 3
MM	Macleay Museum, University of Sydney, Australia
MPRL	Macroplacoid row length
MUT	Department of Biology, McMurry University, Texas, USA
n	Number of observations
N-	New South Wales
nM	Nanometre
NM	Collection of Mr Nigel Marley, Bristol, United Kingdom
NMP	Natal Museum, Pietermaritzburg, South Africa
NZM	Museum of New Zealand, Wellington, New Zealand
OR	Oriental
PCA	Principal Component Analysis
PRL	Placoid row length
<i>pt</i>	Ratio of the length of a given structure to the length of the buccal tube expressed as a percentage (Pilato, 1981)

<i>ptd</i>	Ratio of the length of a structure to the length of the buccal tube from the anterior margin of the stylet sheath to the posterior end of the drop-shaped thickening, expressed as a percentage (Pilato & Binda, 1997/1998)
PVL	Polyvinyl lactophenol
Q-	Queensland
SD	Standard deviation
se	Septulum length
SEM	Scanning electron microscopy
SH	Southern hemisphere
SIL	Stylet insertion length
sp., spp.	Species, species
Sp. n.	New species
TA-	Tasmania
UCI	Dipartimento di Biologia Animale, Universita di Catania, Catania, Italy
µm	Micron
UMI	Dipartimento di Biologia Animale, Universita degli Studi di Modena, Italy
UNP	Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina
V-	Victoria
VB	Collection of Dr V.I. Biserov, Institute of Inland Water Biology, Yaroslav District, Russia
VS	Percent ratio of ventral support length with respect to buccal tube length
WM	Collection of Dr W.R. Miller, Philadelphia, USA
ZIM	Zoologisches Institut und Museum, Hamburg University, Hamburg, Germany – collection of Dr H. Dastych
ZMUC	Zoological Museum, University of Copenhagen, Denmark – collection of Dr R. Mobjerg Kristensen

SUMMARY

The terrestrial tardigrade fauna of Australia has been given scant attention in the past. This study was undertaken to collect and identify terrestrial tardigrade species from a wide variety of habitats in Australia. This new taxonomic data set was then used to explore zoogeographic patterns and processes in eastern Australia.

The first part of this study is concerned with the clarification of some taxonomic problems which arose during the course of the study, the solution of which was essential in order to delineate species boundaries. In the family Macrobiotidae, two genera, *Minibiotus* and *Calcarobiotus*, are remarkable for the high number of species recorded in Australia relative to other parts of the world. Within the genus *Macrobiotus* many new species within two groups, *hufelandi* and *harmsworthi*, are described and it is concluded that the nominal species in each case is not part of the Australian fauna. A new genus, *Haptobiotus*, is described in the family Macrobiotidae.

In order to clarify species within the *Diphascon* (*D.*) *pingue* group, populations were subjected to multivariate analysis. The analysis resulted in the conclusion that only two species in that group, *D. pingue* and *D. pinguiforme*, have so far been found in Australia. The study also resulted in the synonymisation with *D. pingue* and *D. pinguiforme* of two previously described species from Australia.

The discovery of a new genus, *Milnesioides*, provides an insight into the structure and function of the buccal apparatus of the rare monotypic genus *Limmenius* within the family Milnesiidae. A new genus, *Lexia*, is described in the subfamily Itaquasconinae along with other members of this group which has been under-recorded in Australia. The descriptions of three species in the genus *Antechiniscus* provides new morphological detail for this

genus and provides additional evidence that the genus is found only in cool temperate regions in the southern hemisphere.

The 161 species in 34 genera found in this study are described and line drawings provided. Of the 161 species, 59 are new to science and a further 16 have been published as new species during the course of the project. Also included are descriptions of an additional 21 species, recorded from Australia by other authors but not found in this study. Eleven of these species are probably misidentified. Keys to genera and species are supplied.

A small but revealing study provides some preliminary data on tardigrade species associated with cryptogams or leaf litter on soil and sand. The detection of a rich fauna suggests that such habitats need to be examined if the full tardigrade fauna of Australia is to be documented.

Data from 36 sites in eastern Australia containing 141 species were subjected to multivariate analysis in order to elucidate zoogeographic patterns of tardigrade communities. The study, although preliminary in many ways, showed a high correlation between tardigrade communities and core zoogeographic subregions in eastern Australia, e.g., a northern monsoonal, a nontropical south-eastern and a dry central-western subregion. Two distinct habitat types within the south-eastern subregion, cool temperate rainforest and limestone sites also support distinct species communities. Each tardigrade community consists of cosmopolitan, pantropical, oriental, southern hemisphere and Australian species. The degree to which each of these types contribute to each community is discussed in terms of the evolutionary history and the climatic regime (primarily temperature and length of dry periods) of each subregion and, to a limited extent by passive dispersal.

DECLARATION

This thesis contains no material that has been submitted for the award of a higher degree to any other university or institution.

Apart from the assistance listed in the acknowledgements, this thesis represents the original work of the author.

Sandra Kaye Claxton, BSc (Syd), BSc (Macqu), MSc (Macqu)

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CHAPTER 1. INTRODUCTION

Although this work deals with the taxonomy and distribution of Australian terrestrial species it is necessary to review some general issues regarding the phylum Tardigrada. Marine species will be mentioned only where relevant. Introductions to more specific aspects of this study are included in the appropriate chapters.

Tardigrades have been known and studied since 1773 when Goeze first described this freshwater invertebrate as a 'Kleiner Wasser Bär' or 'little water bear' (Goeze, 1773, cited in Ramazzotti & Maucci, 1982). Spallanzani (1776) named the group "Il Tardigrado", which means "the slow walkers" after the way most species move. Spallanzani was also the first to discover that terrestrial tardigrades have cryptobiotic stages. Tardigrades are, indeed, most famous for their capacity to enter an anhydrobiotic state and remain ametabolic for several years (Jönsson, 2001).

Tardigrades are essentially aquatic animals, being active only when surrounded by water. They occur in both marine and non-marine environments. In non-marine environments, the distinction has been made between freshwater species, those that inhabit sediments and bottom debris of permanent bodies of water and terrestrial species, those that inhabit the water-filled interstices of plants including cryptogams (liverworts, mosses, lichens and algae), leaf litter and soils, i.e., those that inhabit impermanent bodies of water. The distinction between terrestrial and freshwater species is not always clear-cut because some species may be found in both permanent water as well as in cryptogams (Bertolani, 1982). The term "semi-terrestrial" has been used to describe species that live in water films (e.g. Bertolani, 1987) but since the animals, although aquatic in their physiological

requirements, are living in a terrestrial environment, the term terrestrial seems to be more appropriate and will be used here.

Tardigrades may be found in a variety of extreme habitats, ranging from the deep sea (Bussau, 1992), to the highest elevations in the Himalayas (Dastyh & Kristensen, 1995), and from hot springs (Rahm, 1937) to cryoconite holes on the Greenland Ice Sheet (Grøngaard, Pugh & McInnes, 1999).

Although knowledge of these minute animals has advanced rapidly in recent years, largely because of the availability of improved extraction and microscopical techniques, they are still relegated, in the minds of even the most dedicated zoologists, to the “minor” phyla. Until recently, tardigrades have been regarded as a curiosity, probably because of their small size and the difficulty of studying them, and have been the object of study for a rather small group of dedicated “water bear” lovers.

Tardigrades have always been significant in our understanding of the origin of arthropods (see Plate, 1888, Richters, 1926, Marcus, 1929 and, more recently, Aguinaldo, Turbeville, Linford, Rivera, Garey, Raff & Lake, 1997). In addition, as one of the few micrometazoan organisms that have evolved a cryptobiotic capacity, tardigrades ought to take a prominent position in future research on the ecology and evolution of ametabolic states (Jönsson, 2001).

1.1 GENERAL CHARACTERISTICS OF TARDIGRADES

Tardigrades are amongst the smallest animals with 930 described species ranging in length from 100 to 500 μm . The adults of the smallest marine species are only 85 μm long but some terrestrial forms may reach 1200 μm (Ramazzotti & Maucci, 1983).

The body of a tardigrade is bilaterally symmetrical. It is generally cylindrical in shape and is covered with a relatively thick chitinous cuticle. The majority of species are white to translucent but some terrestrial species are strongly coloured - yellow, orange, green, red to olivine-black. This may be due to colouration of the intestinal contents, pigments in the haemolymph, haemocytes, epidermis or cuticle (Ramazzotti & Maucci, 1983). There are five distinct body segments including a cephalic segment and four trunk segments with the latter each bearing a pair of stumpy legs (Plate Ia). In terrestrial and freshwater forms, the legs bear two or four claws (Plate IIa-c) that may be missing in some soil inhabiting forms. Although tardigrades have no circulatory or respiratory structures, other systems, such as the digestive system, are quite complex.

1.2 HIGHER TAXONOMY OF TARDIGRADES

Diagnostic characters of higher classification categories of the Tardigrada are summarised in Table 1.1. Two classes are listed, Heterotardigrada and Eutardigrada. A third class, Mesotardigrada, was established on the basis of the description of a single species found in a hot spring in Japan (Rahm, 1937). The type material no longer exists and the species description has been criticized (Ramazzotti & Maucci, 1983). It will not be further discussed here. In the class Heterotardigrada (Table 1.1), consisting of two orders, Arthrotardigrada and Echiniscoidea, cephalic sensory structures are present (Plate Ib). The arthrotardigrades are marine (Table 1.2) as are the members of the family Echiniscoididae of the Echiniscoidea. These groups will, therefore, not be further discussed here. The family Carphanidae, represented by a single genus, has only been found in freshwater. The Echiniscidae are a successful group of twelve genera of armoured terrestrial species, whilst Oreellidae consists of a single terrestrial genus. The Eutardigrada consist mainly of unarmoured terrestrial and freshwater species and the class is divided into two orders, Parachela and Apochela. Cephalic sensory structures are absent in the former but present in

the latter but appear not to be homologous to those of the Heterotardigrada (Plate IIIa). The six families of Parachela are represented by forty-one genera of terrestrial and freshwater species and even a few marine species. The single family within the Apochela, Milnesiidae, is represented by three terrestrial genera.

1.3 PHYLOGENETIC RELATIONSHIPS

The phylum Tardigrada seems to be a monophyletic group of proarthropod origin. Most textbooks place them in their own phylum because the large commissure from the lateral protocerebral lobes to the first ventral double ganglion, the structure of the eyes and the formation of the claws and stylets in glands are unique (Greven, 1980; Ramazzotti & Maucci, 1983; Barnes, 1987). There are strong arguments, relating to the metameric segmentation of the nervous system and ultrastructure of the sense organs and cuticle, which suggest that they may have a close affinity to the arthropod complex (Marcus, 1929; Kristensen, 1981). Their small size and lack of some characters of their close relatives such as a dorsal heart, segmented coelomic cavities or metanephridia may be due to miniaturisation (Dewel & Dewel, 1996) although it is possible that small body size may be primary (Schmidt-Rhaesa, 2001). Nielsen (1995) included the tardigrades in a superphylum called Panarthropoda, which includes Onychophora, Tardigrada and Arthropoda.

Molecular evidence for a clade of moulting animals supporting the tardigrade/arthropod relationship and an explanation for the morphological characters shared by tardigrades and some aschelminths (Nematoda, Nematomorpha, Kinorhyncha and Pripulida) were presented by Garey, Krotec, Nelson & Brooks, 1996; Giribet, Carranza, Baguna, Riutort & Ribera, 1996, Aguinaldo *et al.*, (1997) and Schmidt-Rhaesa, Bartolomaeus, Lemberg, Ehlers & Garey (1998). However, Rebecchi, Guidi & Bertolani (2000) suggested that the spermatozoan ultrastructure of tardigrades was closer to that of Annelida than Arthropoda.

The Cambrian fossil evidence also supports an arthropod association (Mass & Waloszek, 2001). Heterotardigrades are considered to be the stem group from which other tardigrade groups evolved (Kristensen, 1976; Renaud-Mournant, 1982).

1.4 MORPHOLOGY

Electron microscope studies show that tardigrades, although small, are complex organisms (Kristensen & Neuhaus, 1999) and a number of recent review articles provide details of their biology (Nelson, 1982, 1991; Nelson & Higgins, 1990; Dewel, Nelson & Dewel, 1993; Kinchin, 1994; Eibye-Jacobsen, 1996; Wiederhoft & Greven, 1996, 1999). In the following sections, emphasis is placed on morphological features of non-marine species that are important in taxonomy and zoogeography.

1.4.1 The cuticle

The integument of tardigrades consists of a single layer of epidermal cells that secrete a cuticle extending into the fore- and hindgut. Although there is considerable variation between the cuticles of Heterotardigrada and Eutardigrada, a generalised cuticular structure has been proposed for tardigrades (Baccetti & Rosati, 1971; Greven, 1975; Kristensen, 1976; Wright, 1988a; Kristensen & Neuhaus, 1999). The basic pattern of the cuticle is seen in the very complex cuticle of arthrotardigrades. There are three main components to the cuticle; an outermost epicuticle composed of neutral polysaccharides, beneath which is a lipid-rich intracuticle and an innermost procuticle which contains chitin and protein (Greven & Peters, 1986).

The cuticle and its processes are taxonomically important in identifying genera and species as well as forming the basis for separating tardigrades into armoured and unarmoured groups (Nelson & Marley, 2000). The armoured tardigrades include terrestrial species of the family Echiniscidae and the marine Stygarctidae. In echiniscids, the sclerotised dorsal

plates (Plate Ia) are made up of a more elaborate epicuticle in which the pillars are fused and form an anastomosing lacunal system, which may be air-filled (Wright, 1988a), unlike the water-filled epicuticular space of marine tardigrades (Kristensen, 1976). The disposition of dorsal plates is a character useful at the generic level and the patterns of pores and papillae on the plates, as well as the position and size of spines and/or filaments on the plates, are highly species-specific and in a few cases are sexually dimorphic (Claxton, 1998).

The unarmoured tardigrades comprise the eutardigrades as well the heterotardigrade families Oreellidae and Carphanidae. The eutardigrade and unarmoured heterotardigrade cuticle may be smooth or covered with spines, tubercles, granulation, reticulation and/or pores. The size, shape and position of pores in the cuticle are species-specific and are, therefore, extremely useful taxonomic characters.

The cuticle is shed periodically in a moulting cycle in the typical arthropod fashion. When the new body cuticle is formed, the cuticle of the foregut, the buccal tube, the placoids, the peritrophic membrane and the cuticle in the hindgut are resynthesised. The claws of the legs are formed in the claw glands. The claw glands are homologous with the stylet glands (also called salivary glands) lying along the buccopharyngeal apparatus. The moulting process was recorded by Marcus (1929).

1.4.2 Limbs and claws

Tardigrades have four pairs of lateroventrally placed legs. They are cylindrical, non-articulated and carry, at their distal extremities, claws of varying shape, size and number.

In terrestrial heterotardigrades, juveniles and adults have four hooked claws (Plate IIb) on each leg whilst larvae have two. The inner claws of many species (and the outer claws of a few) have basal spurs (Plate IIb) whose shape and distance from the base of the claw are species specific. Although the claws of terrestrial heterotardigrades are rather conservative, the legs are often equipped with structures of taxonomic value. Many species have a sensory spine on the first pair of legs (rarely also on the second and third pair of legs) and a sensory papilla on the fourth pair of legs. The fourth pair of legs of many echiniscids also carries a plate equipped with a dentate collar (Plate Ia). A less well-defined plate may also be present on the other legs. Characteristics of the plates and the collar are species specific.

The systematic arrangement of families and genera in eutardigrades is primarily based on claw structure (Thulin, 1928, Pilato, 1982). The two double claws (diploclaws) on each leg of eutardigrades are differentiated into a primary and a secondary branch (Plate IIa) and the former is always equipped with a pair of accessory claws (Plate IIc). In Apochela, the primary branch is completely separate from the secondary branch which is two- or three-branched. In Parachela, the secondary branch is attached to the leg and the primary branch arises from it. The external claw may be very similar to the internal (e.g. family Macrobiotidae) or they may be very different (e.g. family Hypsibiidae). The sequence of claw branches, with respect to the midline of the leg is alternate (2-1-2-1) in some genera of Parachela whilst in other genera, the two primary branches are next to one another (2-1-1-2). In some eutardigrades, a cuticular thickening, called a lunule, surrounds the base of the diploclaw. Lunules vary in size and shape and may be smooth or dentate. A cuticular bar is often present below the claws, however, its taxonomic value is unknown as its presence both within and among populations has not been assessed.

1.4.3 Cephalic sensory structures

In heterotardigrades, the fine structure of all the cephalic sensory structures (cirri and clavae), the trunk setae (cirri) and leg sensory structures (spines or papillae) strongly resembles that of a single arthropod sensilla (Kristensen, 1981). The cirri are thought to be mechano-receptive and the clavae and papillae, with large terminal pores, are presumably chemo-receptive. The serial arrangement of the cephalic sensory structures follows that of the three-lobed brain. The plesiomorphic condition (found in a few Arthrotardigrada) is to have a single median cirrus, a pair of both clavae and cirri for each brain lobe, but the tertiary clavae are nearly always lacking and, in the Echiniscoidea, the median cirrus is so reduced that the structure can only be seen internally. The full set of cephalic appendages in Echiniscoidea (Plate Ib) consists therefore of 1) paired lateral cirri (cirri A) and primary clavae, 2) paired internal cirri and secondary clavae (cephalic papillae) and 3) paired external cirri. Characteristics of the cephalic cirri and clavae have been used to discriminate between genera of Echiniscidae. The morphology of the secondary clava was used by Kristensen (1987) to diagnose several new genera in that family.

In eutardigrades, the external part of the cephalic sensillae, as well as the trunk setae, are strongly reduced. In the Parachela, several sensory fields have been identified (Walz, 1978, 1979), e.g., a circumoral field. Sensory receptors are also found in anteriolateral sensory plaques or elliptical organs found in some eutardigrades (Dewel *et al.*, 1993). The six innervated peribuccal papillae of *Milnesium tardigradum* (Apochela, Plate IIIa) are probably homologous to the circumoral field in Parachela but not to the cephalic sensory organs of Heterotardigrada (Schuster, Nelson, Grigarick & Christenberry, 1980; Wiederhofs & Greven, 1999).

1.4.4 Eye spots

Both heterotardigrades and eutardigrades may have two eye spots, usually located inside the protocerebrum. These eye spots consist of a single cup-shaped pigmented cell, which encloses a few sensory cells which are ciliary (Kristensen, 1981) and microvillous or rhabdomeric (Dewel *et al.*, 1993). The colour of the eye spots was used by Kristensen (1987) to differentiate genera of echiniscids. Unfortunately, eye spots become invisible in many mountants. Hence, their presence or absence is considered to be an unreliable character, particularly for retrospective taxonomic studies.

1.4.5 Digestive tract

The digestive tract has three major sections: the foregut (ectodermal origin), the midgut (mesodermal origin) and the hindgut (ectodermal origin).

Foregut

The foregut (buccopharyngeal apparatus) is a very complex feeding structure and consists of a mouth surrounded by various labial structures, an oral (sometimes called a mouth or buccal) cavity, buccopharyngeal tube, pharynx and oesophagus all lined with cuticle.

Associated with the buccopharyngeal tube is a stylet mechanism, which in the plesiomorphic condition consists of a pair of calcium carbonate encrusted stylets and stylet supports. The stylets are quite delicate and dissolve rapidly under anoxic or slightly acid conditions, such as those found in some commonly used fixatives (Bird & McClure, 1997a) and mountants. They are absent in most fixed specimens and, hence, illustrations of them are commonly lacking. The other structures of the foregut are clearly visible in slide-mounted specimens, particularly of eutardigrades, and consequently are used extensively as taxonomic characters (Pilato, 1975, 1982; Schuster *et al.*, 1980; Guidetti & Bertolani, 2001a). They have been underutilised in Heterotardigrada (Kristensen, 1987), probably

because they are masked by the cuticular plates in slide preparations and because parts which are calcium carbonate encrusted rapidly dissolve in mountants.

During ecdysis, all the cuticular elements, including the stylet mechanism, are shed through the mouth opening and the mouth itself is subsequently closed by a cuticular membrane (Marcus, 1927). In this state the animal cannot feed and it is said to be in the simplex stage.

The structure of the foregut depends strongly upon the feeding habit of the tardigrade. In eutardigrades, the omnivorous and predatory species have a terminal mouth surrounded by large flap-like lamellae (Plate IIIb), while herbivorous and detritivorous species have a sub-terminal to ventral mouth surrounded by cuticular thickenings in the form of papulae (Plate IIIc) or lobes. The carnivorous eutardigrades (*Milnesium*, many *Macrobiotus* and *Amphibolus*) usually also have a very large oral cavity with strong buccal armature including cuticular ridges and teeth and a wide buccal tube. Hyvonen & Persson (1996) showed that some tardigrades are efficient predators of nematodes. The bacterivorous eutardigrades have a relatively small oral cavity and a narrow buccal tube. Some species of eutardigrades, e.g., *Diphascon* spp., and heterotardigrades, e.g., *Mopsechiniscus*, have the buccopharyngeal tube divided into a rigid anterior buccal tube and a flexible posterior pharyngeal tube the function of which is still unknown.

The majority of tardigrades feed on the fluids inside moss/algae or animals by piercing the wall with their paired stylets. The pointed ends of the stylets project into the anterior end of the buccal tube or oral cavity and, when protruded through the mouth, are used to pierce plant or animal tissues. Caudally, the stylets terminate in a furca, which, in most eutardigrades, rests on a stylet support that is inserted on the buccal tube. The calcium carbonate stylet support is present in many arthrotardigrades which makes the whole

mechanism into a rigid structure. The apomorphic condition is seen in nearly all echiniscoid and in stygarctid heterotardigrades. Here the stylet supports are absent (Kristensen 1987) and each stylet may be extruded separately out of the mouth for more than one third of its length. The mouth opening itself is located on a telescopic mouth cone.

The caudal extremity of the buccal tube penetrates into the pharynx and usually forms large apophyses for the pharyngeal muscles. The triradiate lumen of the pharynx is lined with cuticle and surrounded by myoepithelial cells containing radially arranged muscle filaments alternating with epidermal cells which form chitinous rods or placoids. The placoids are calcium carbonate encrusted in Arthrotardigrada and consist of three solid rods (fused placoids). In echiniscoid heterotardigrades, the encrustation may be lacking. In those eutardigrades with placoids, these are always flexible and unencrusted. Typically, they consist of six rows of chitinous macroplacoids often followed by smaller microplacoids (Eibye-Jacobsen, 2001). In some *Diphascon* species, a cuticular septulum is present posterior to, and in an alternating position with, the placoids. The number, size and shape of placoids are species specific and they may be lacking in some genera e.g. *Itaquascon*. The placoids provide attachment for the musculature and may also contribute to the mastication of food. The main function of the pharynx is to produce suction which permits the animal to attach itself for feeding, and to draw food into the gut.

The pharynx passes into a short tubular oesophagus lined with cuticle. The oesophagus is very metabolically active as indicated by the many mitoses occurring there. In eutardigrades, it forms the peritrophic membrane which covers the food and eventually the faecal pellet. Heterotardigrades do not form a peritrophic membrane and defaecate only into the old cuticle at each moult (Ramazzotti & Maucci, 1983).

Midgut

The larger species of eutardigrades (*Macrobiotus* and *Milnesium*) are carnivorous and may feed on prey such as rotifers, nematodes and other tardigrades and the pharyngeal structures of the prey can often be seen in the midgut of the predator. Many of the soil inhabiting eutardigrades (*Diphascon*, *Eohypsibius*), which feed on bacteria, have a whitish midgut content whilst detritivores (*Hypsibius*, *Isohypsibius*) will often contain small pieces of fungi and algae mixed with mineral particles so the midgut contents appear brown or green. The midgut is totally covered with microvilli and here digestion and absorption take place.

Hindgut

The hindgut or rectum is short and lined with cuticle. In eutardigrades, the plesiomorphic condition - a cloaca - is present, while in heterotardigrades the three-lobed anus is closed with cuticle so that defaecation can only take place at each moult. In the latter, the gonopore is separate from, and located anteriorly to, the anus.

1.4.6 Reproduction and Development

Reproduction is exclusively sexual and usually gonochoristic but hermaphroditism and parthenogenesis are common (Bertolani, 1987). These different reproductive modes are often environmentally determined (Bertolani, 2001).

The reproductive system is conservative in males and females and consists of a single gonad in the form of a dorsal sac (Bertolani, 1983a, b). The wall structure of the mature gonad is different in eutardigrades and heterotardigrades (Kristensen, 1979). All adult heterotardigrades have a separate gonopore and anus whilst eutardigrades have a cloaca. In heterotardigrades, the preanal gonopore is rosette-shaped in females and round in males (except for Renaudarctidae, Kristensen & Higgins, 1984) but is very similar among the various families (Pollock, 1970, 1975).

Marine species are almost always gonochoristic and sexual dimorphism occurs, at least, in the gonopore structure (Pollock, 1975). In non-marine species, gonochoristic reproduction is more often found in eutardigrades than in heterotardigrades with some species showing limited sexual dimorphism, expressed in some instances in the shape of the claws eg. *Milnesium* (see Bertolani, 1992). Rebecchi & Nelson (1998) showed, however, that the modified claw is not always present in males of *Milnesium tardigradum* so the sex ratio cannot be determined solely on the presence of the modified claw. Moss dwelling heterotardigrades (*Echiniscus*, *Pseudechiniscus*, *Hypechiniscus*, *Antechiniscus* and *Oreella*) have the same sexual dimorphism of the gonopore structure shown by marine species.

Until recently, males were unknown in the heterotardigrade genus *Echiniscus* (see Dastych, 1987) but have been found to be quite common in species of this genus found in Australia (Claxton, 1996). Sexual dimorphism of cuticular spines was described for some of these species. Stronger sexual dimorphism can be seen in some terrestrial echiniscoids, eg. males of *Antechiniscus lateromamillatus* are smaller and have larger primary and secondary clavae than the female.

Hermaphroditism has been reported to occur in most families of eutardigrades (Bertolani, 1979; Bertolani & Manicardi, 1986; Bertolani, Pilato & Sabatini, 1983) and a single dorso-caudal ovotestis is present (Rebecchi *et al.*, 2000). It is the least common type of reproduction in tardigrades but is adaptive for species occurring in low densities (Bertolani, Rebecchi & Beccaccioli, 1990). Self-fertilisation was reported in *Isohypsibius monoicus* by Rebecchi *et al.* (2000).

Parthenogenesis is widespread in non-marine tardigrades and is thought to be more frequent among heterotardigrades than eutardigrades. It takes place by a wide variety of

cytological mechanisms with the ameiotic type prevailing, where recombination does not occur (Bertolani, 1994; Rebecchi *et al.*, 2000). In eutardigrades, parthenogenetic populations often occur alongside amphimictic forms and are often indistinguishable (Bertolani, 1974). The implications for both taxonomic and distributional studies are not known because cytotaxonomic studies are generally not carried out. Evaluation of genome size has proven to be a useful cytotaxonomic tool by proving the existence of diploid and polyploid populations (Bertolani, Garagna, Monicardi, Rebecchi & Redi, 1994). With the evolution of cryptobiosis and passive dispersal, the reproductive strategies of parthenogenesis and self-fertilisation may have proven to be advantageous under unstable and isolated conditions because they permitted a single individual to colonise new habitats (Bertolani, 2001).

1.4.7 Eggs and moulting

In terrestrial and freshwater species, there is a correlation between egg maturation and moulting with many species laying eggs into the exuvium (Bertolani, 1983). Mating and egg-laying may occur at the time of the moult (Bertolani, 1975) with sperm being deposited into a recently shed female exuvium containing eggs. Marcus (1929) described internal fertilisation in eutardigrades. Sperm, deposited in the cloaca, may be stored in a single seminal receptacle or may directly fertilise eggs in the ovary. External fertilisation has been observed in one species of heterotardigrade (Kristensen, 1979) and inferred in most others from the morphology of the spermatozoa and the presence of external seminal receptacles in most arthrotardigrades (Jørgensen, Møbjerg and Kristensen, 1999; Rebecchi *et al.*, 2000). Seminal receptacles are also found in “primitive” tidal and terrestrial Echiniscoidea (*Anisonyches* and *Oreella*), but are lacking in advanced forms such as the family Echiniscidae (Kristensen, 1987). Mating behaviour is not well documented but the presence

of longer sensory structures in males of many species of heterotardigrades may be associated with finding females (Kristensen, 1981).

Eggs are round or oval and possess a smooth or ornamented shell. Ornamented eggs are generally laid free and are found in some eutardigrade genera (Plate IVa). Ornamented eggs may also be laid in an exuvium (Bird & McClure, 1997b). Free-laid, ornamented eggs are also present in the heterotardigrade genus *Oreella* (Bertolani, Rebecchi & Claxton, 1996) (Plate IVb). All other known terrestrial heterotardigrades lay smooth eggs either free or in an exuvium. Patterns of ornamentation of the egg shell, including size, shape and distribution of processes, are species-specific and therefore of considerable taxonomic significance.

Three eutardigrade species studied by Baumann (1961, 1964 and 1966) were found to be sexually mature after the second moult and all instars are morphologically similar to the adults. However, Bertolani *et al* (1984) concluded that heterotardigrades undergo indirect development and are characterised by two larval stages. The first larval stage has no anus or gonopore and has only two claws on each leg. The second larval stage (juvenile) has no gonopore but the anus is present and the same number of claws as in the adult is present. In some species, e.g. *Echiniscus curiosus*, the number of spines on the body increases with age (Claxton, 1996). A comprehensive review of the developmental biology of tardigrades is provided by Nelson (1982) and Eibye-Jacobsen (1996).

1.5 ECOLOGY

1.5.1 Habitats

Because of their small size, tardigrades are capable of very limited active dispersal (Kinchin, 1994). Only passive dispersal can account for the colonisation of isolated

terrestrial habitats (Bertolani, 2001). Cryptobiotic stages and eggs of non-marine species have been found as “aerial plankton” (Kristensen, 1987; Wright, 1987; McInnes, Chown, Dartnall & Pugh, 2001) although other studies (Maguire, 1963; Sudzuki, 1972) failed to observe tardigrades in air currents. Passive dispersal as an appreciable influence on tardigrade distribution over long distances is, therefore, still controversial.

Tardigrades are common in freshwater habitats, such as springs, rivers, ponds and lakes (Schuster, Tofner & Grigarick, 1978; Kristensen, 1982; Kathman & Nelson, 1987). In the heterotardigrade family Echiniscidae, a few species of *Echiniscus*, *Hypechiniscus* and *Pseudechiniscus*, are limnic (Nelson, 1991) and, especially from the Antarctic regions, several species of *Echiniscus* are found on benthic algal mats (McInnes & Ellis-Evans, 1987). The family Carphanidae (Echiniscoidea) (Binda, 1978) and the Mesotardigrada (Rahm, 1937) are only found in springs along with other very rare endemic eutardigrades (Kristensen, 1982). In the class Eutardigrada, three genera, *Dactylobiotus*, *Pseudobiotus* and *Thulinia* are said to be exclusively freshwater (Bertolani, 1982) but freshwater species also occur in other genera.

Among the Eutardigrada, two genera, *Halobiotus* (a Palearctic genus) and *Ramajendas* (found only in Antarctica and Subantarctica) are found in the marine environment (Ramazzotti, 1972; Kristensen, 1982). *Ramajendas heatwolei* was first recorded from the supralittoral zone on Macquarie Island (Miller, Horning & Dastych, 1995). *Isohypsibius itoi* (Tsurusaki, 1980) is a marine species found in an interstitial environment on a beach on Hokkaido, Japan (Tsurusaki, 1980).

Studies have described the tardigrade fauna of woodland epiphytes (Argue, 1971, 1972, 1974; Nelson, 1975), grasslands (Anderson, Ingham, Trofymow and Coleman, 1984;

Manicadi & Bertolani, 1987; Bertolani, Manicardi & Gibertoni, 1987), leaf litter in northern beech forests (Hallas & Yeates, 1972; Guidetti, Bertolani & Nelson, 1999) and coastal dunes (Bertolani, 1984). Tardigrade associations differ in different terrestrial habitats in Italy (Bertolani & Rebecchi, 1996), on Disko Island (Peters & Dumjahn, 1999) and in Japan (Ito, 1999).

The great success of tardigrades in the terrestrial environment seems to be correlated with the development of cryptobiosis (Kinchin, 1994). Even so, habitats of terrestrial tardigrades must provide sufficient aeration, alternate wet and dry periods and sufficient food (Nelson & Higgins, 1990) and each species will have its own optimum and range for each factor (Hofmann, 1987). Hofmann concluded that tardigrades are r-strategists, that is, adequate life conditions occur only in short periods of optimal humidity, so that the initial reproductive rate must be high enough to establish a population from a few individuals in a short space of time. Some authors have indicated that distribution and density of tardigrade populations are determined by microhabitat factors (Kathman & Cross, 1991; Grabowski, 1995; Romano, Barreras-Borrero & Nelson, 2001). Although some species are ecologically catholic (Wright, 1991), many others have very strict habitat requirements that may lessen the homogenising action of passive dispersal and therefore its effects on geographical distribution of species (Pilato & Binda, 2001).

Soil-inhabiting tardigrades are more prevalent in the upper porous strata and the species composition overlaps with that found in overlying leaf litter and even with that found in nearby moss and lichen (Guidetti, Bertolani & Nelson, 1999). A tendency to reduction in claw size, particularly of the fourth pair of claws, in soil inhabiting species in a number of genera has been noted (Dastyh & Alberti, 1990, Bertolani & Biserov 1996). This was interpreted as a convergent adaptation to living in soil.

1.5.2 Population studies

Production of eggs for many terrestrial species has been found to be a year-round occurrence in both xerophilic and temperate rainforest environments in Australia (Claxton, 1991). Dougherty (1964) found that an individual of *H. arcticus* under culture produced 84 progeny in eleven egg clutches.

Population densities are highly variable and changes in population densities have been correlated with a variety of environmental conditions, including moisture (Morgan, 1977) and food (Marcus, 1929) or the structure of the substrate (Horning, Schuster & Grigarick, 1978). Moss is believed to be the most favourable habitat for terrestrial tardigrades.

Morgan (1977) reported as many as 2,287,000 per square metre in two species of moss.

The study of tardigrade populations in mosses and lichens in a dry sclerophyll forest in NSW showed that high numbers of tardigrades could be found in cryptogams with apparently low moisture levels (Claxton, 1991). This environment, subject to frequent drying, provided stable and quite high populations throughout the year in contrast to a temperate rainforest where numbers showed a marked decline in the moist spring/summer period.

Few studies have been done on the life history of tardigrades and the literature is summarised by Altiero & Rebecchi (2001). These authors reared three species of eutardigrade in culture and confirmed an active life span of a little less than 9 months. The actual life span, including periods of cryptobiosis, will vary from individual to individual.

Tardigrades have no known economic significance although it is possible that they may be useful as bio-indicators of pollution (see Vargha, 1997, Hohl, Miller & Nelson, 2001). It

has been suggested that soil tardigrades control populations of pest nematodes (Sayre, 1969; Bird & McClure, 1997a).

1.5.3 Cryptobiosis

The term cryptobiosis was introduced by Keilin (1959) for a condition where metabolism is almost totally, but reversibly, suspended for variable periods in response to adverse abiotic changes in the environment. When the process is induced by dehydration it is called anhydrobiosis. Cold-induced cryptobiosis is called cryobiosis. Most anhydrobionts are capable of cryobiosis (Wright, 2001). This suggests a close homology between the biochemical mechanisms that underlie protection in each case.

Wright (2001) pointed out that the small size and limited mobility of interstitial organisms, such as tardigrades, impose unique stresses. The unavoidably high rates of dehydration in environments, such as the interstices of mosses, lichens or soil, require that the meiofauna either be restricted to permanently saturated microsites or they develop an anhydrobiotic capability. Freezing is also an unavoidable stress in subalpine, alpine or polar communities and demands similar adaptations. Species of tardigrades, rotifers and nematodes survive severe conditions, such as desiccation and freezing, by undergoing cryptobiosis (Crowe, 1971, 1975; Ramløv & Westh, 2001; Wright, Westh & Ramløv, 1992).

Tardigrades living in terrestrial environments, such as mosses and lichens, usually undergo anhydrobiosis as a normal part of their life cycle and many species cannot produce eggs if they are not rehydrated periodically. Movement of tardigrades in response to dehydration have been studied by several authors. Wright (1991) showed a pronounced vertical migration of two of three tardigrade species in response to dehydration of their moss cushion. However, no such response was noted by Nelson & Adkins (2001) and Greven &

Schüttler (2001). Wright (2001) postulated that the negative photokinesis observed by Beasley (2001) may serve to restrict animals to the base of a moss cushion.

The formation of the anhydrobiotic stage is a complex process including anatomical transformation into a resistant tun-state (Greven, 1971; Walz, 1979) as well as changes in the permeability of the cuticle (Wright, 1988b, 1989). Membrane protectants, such as trehalose and glycerol, are synthesised to preserve the fine structure of the cell organelles during anhydrobiosis (Westh & Ramløv, 1991). Jönsson & Rebecchi (2002) found that body size and energetic condition affected anhydrobiotic survival in the eutardigrade *Richtersius coronifer* and documented, for the first time, a decrease in the size of storage cells over a period of anhydrobiosis. Jönsson, Bosani & Rebecchi (2001) observed different survival rates between *Ramazzottius oberhaeuseri* and *R. coronifer* but not among geographically isolated populations of the same species. Anhydrobiotic tardigrades have been known to survive for up to 10 years (Guidetti & Jönsson, 2002). They can survive exposure to high and low hydrostatic pressure, cosmic and UV radiation and temperatures near absolute zero (-273°C). The extended longevity conferred by periods of anhydrobiosis has significant evolutionary consequences. Generation turnover may be reduced and hence the impact of drift and selection over time will be smaller (Wright, 2001).

Anoxybiosis and osmobiosis were excluded by Wright *et al.* (1992) from the categories of cryptobiosis in tardigrades, describing the former as a dormancy state and the latter as requiring more convincing evidence for its existence in these animals. Usually active tardigrades are very sensitive to low oxygen tension and they will respond by going into an inactive stage called asphyxia (Marcus, 1929). Asphyxia is not a cryptobiotic stage but represents a reduction in metabolism and a failure in osmoregulation so that the animal

becomes turgid with all the legs spread out. After about one or two days in asphyxia the animal dies (however, see Kristensen & Hallas, 1980).

1.5.4 Cyst formation

Terrestrial and freshwater tardigrades may form two kinds of cysts in response to unfavorable conditions (Murray, 1907a; Weglarska, 1957; Nelson & Higgins, 1990). White cysts are usually associated with freshwater species and seem to be initiated by low temperature (Westh & Kristensen, 1992). Red cysts are usually associated with soil species, but are also found in species inhabiting cryptogams. It seems that red cyst formation can be induced by gradual changes in abiotic factors such as low pH, lack of oxygen or desiccation. Red cyst formation is very dramatic. The claws and the entire digestive system, including stylets and placoids, are histolysed (Westh & Kristensen, 1992). The first ecdysis differs from that seen in the white cyst or in a normal moult. The old cuticle is tanned red to black and a new, very thin and translucent cuticle is formed around the animal which lacks legs and claws. When the animal excysts, a third cuticle is formed and normal legs developed, but with smaller claws (cyclomorphic type), and the buccal apparatus with stylets is regenerated. The red cyst is drought-resistant, but not anhydrobiotic, since significant metabolic activity is detectable in encysted tardigrades (Pigon & Weglarska, 1953).

1.5.5 Cyclomorphosis

Cyclomorphosis, or the cyclical change of form, is usually seasonal and has been reported in marine plankton and freshwater rotifers, cladocerans and copepods. A type of cyclomorphosis, characterised by changes in individuals, occurs in collembolans and tardigrades. Kristensen (1982) observed cyclomorphosis for the first time in *Halobiotus*, one of the few marine eutardigrade genera, in which a winter form and a sexually mature

summer form exist. He observed differences in the structure of the buccopharyngeal apparatus and in the claws. Cyclomorphosis has also been found in terrestrial and limnic eutardigrades. Rebecchi & Bertolani (1994) reported cyclomorphosis in the genus *Amphibolus* which is always associated with cyst formation. Dastych (1993a) reported cyclomorphosis in the cryoconite-dwelling tardigrade, *Hypsibius klebelsbergi*, and noted particularly differences in legs and claws. He suggested that cyclomorphosis may be a widespread phenomenon in tardigrades. Misunderstanding of cyclomorphosis may lead to false identification of species. The most obvious case of this is the single specimen of *Echinursellus longiunguis* which was believed to be a missing link between the two orders, Arthrotardigrada and Echiniscoidea (Iharos, 1968). Recent re-examination of the specimen (Kristensen, 1987) revealed it to be a cyst or an animal moulting to a different cyclomorphic stage of the freshwater eutardigrade genus *Pseudobiotus*.

1.5.6 Global distribution patterns

Tardigrades are found worldwide but their biogeography is relatively unknown and lack of a fossil record provides no additional information. The distribution of extant fauna is, therefore, the only tool available to explore tardigrade biogeography (McInnes & Pugh, 1998).

Some terrestrial species seem to have very broad ecological requirements and thus may be distributed worldwide. This apparent cosmopolitan distribution was thought to be related to the presence of passive dispersal mechanisms such as cryptobiotic tuns (Ramazzotti & Maucci, 1983), eggs, and cysts (Kristensen, 1987). Pilato (1979), however, stressed that 67% of the then known 481 species of non-marine tardigrades are present in only one biogeographical region and Pilato & Binda (2001) reaffirmed this finding. McInnes (1994)

recognised the sparseness of records of tardigrades for some areas of the world, such as Asia, Africa, South America and Australia.

The main difficulty in tardigrade biogeography (as it is with rotifers and nematodes) is the lack of accuracy in species differentiation (Pilato & Binda, 2001). In many cases, what was considered to be a cosmopolitan “species” has, on closer examination, been shown to be a complex of morphologically very similar species. Current research into the *Macrobiotus hufelandi* group (Bertolani & Rebecchi, 1993), the *Minibiotus intermedius* group (see Claxton, 1998) and the *Macrobiotus harmsworthi* group (see Pilato, Binda, Napolitano and Moncarda, 2000) has made it clear that within these groups only one or two species are cosmopolitan while a high proportion are limited to a single biogeographic region. Pilato & Binda (2001) and McInnes & Pugh (1998) hypothesised that each of these species groups has arisen from an ancestor that had a wide distribution throughout an earlier palaeo-biogeographical region. This interpretation is very speculative, however, as it does not consider the biological potential of such taxa (Dastyh, pers. comm.).

1.6 THE AUSTRALIAN TERRESTRIAL ENVIRONMENT

Much of Australia is arid or semi-arid and experiences seasonal drought. Despite this, the fringe areas of the continent support a diverse vegetation. The climate varies from moist tropical and monsoonal in the north to arid in the centre and west, Mediterranean in the south and southwest and cool temperate along the southeastern seaboard, grading to alpine at higher elevations. Accordingly, vegetation ranges from tropical to temperate rainforest through various forest and woodland types to savannah grassland and desert scrub (Heatwole, 1987). Any attempt to generalise on the geographic distribution of tardigrades in various natural regions (ie. combinations of vegetation associations, topography and climatic belts) must take into account the relative abilities of different species to withstand

desiccation as well as other aspects of their biology, such as their feeding biology and dispersal capability. In addition, all this must be considered in historical perspective:

- Gondwana was part of the super-continent Pangea prior to its break-up.
- Australia was once part of Gondwana and became completely isolated from other landmasses in the early Tertiary.
- Australia was isolated from the time it separated from Antarctica until collision with Asia in the Miocene. A dispersal route was thus opened up.
- During this isolation, populations of the original faunal elements evolved in response to changing environmental conditions. Australian climates commenced an arid deterioration which has continued to the present, subsequent to the establishment of a circumpolar current in the mid-Oligocene.

Thus it could be expected that both 'old' and 'new' distribution patterns will be revealed (Main, 1981). To date, no such patterns have been determined for tardigrades in Australia.

1.7 HISTORY OF DISCOVERY AND IDENTIFICATION OF TERRESTRIAL TARDIGRADES IN AUSTRALIA

Australian terrestrial tardigrades are poorly known with only fifty-three species recorded in the literature. There are no data at all on the freshwater or soil/ leaf litter tardigrades.

Richters (1908) was the first to record a tardigrade, *Macrobiotus hufelandi* (thought, until recently, to be a cosmopolitan species) from Australia. Murray (1910) reported 31 species of terrestrial tardigrades collected during the British Antarctic (Shackelton) Expedition in 1907-1909, from three sites on the east coast. Most of Murray's material has not survived but his descriptions of six new species and a new genus, *Oreella*, remain. A single slide labelled '*Echiniscus pulcher*' has been found in the archives of the Queckett Microscopical

Club and should provide a basis for comparison with more recently collected specimens of this rare species. A species of *Echiniscus* described, but not named, by Murray has been recollected at Mt. Kosciusko and given the name *Echiniscus jamesi* (see Claxton, 1996).

In the sixty-six years following Murray's paper, only a single reference was made to tardigrades found in Australia (Colledge, 1921). This small paper reported finding *Milnesium tardigradum* in a tuft of grass. Pilato & D'Urso (1976) recorded ten species, seven of which had not previously been recorded from Australia and two of which were new to science. The type material for these two species, *Macrobiotus santoroi* and *Macrobiotus australis*, is deposited in the Istituto Policattedra di Biologia Animale dell'Università, Catania as is that for *Doryphoribius macrodon*, an Italian species but recorded from Sydney by Binda, Pilato & Dastych (1980) and *Macrobiotus joannae* described by Pilato & Binda (1983).

Apodibius serventyi, an interesting clawless species, was described by Morgan & Nicholls (1986) and the types are deposited in the Western Australian Museum and ZMUC. Type material for the species described by Pilato & Claxton (1988) (*Macrobiotus hieronimi* and *Minibiotus maculartus*), Pilato, Claxton & Binda (1989a, b) (*Minibiotus fallax*, *Echiniscus marculsi* and *Macrobiotus peteri*) and Pilato, Claxton & Horning (1991) (*Diphascon (Adropion) gordonense*) are preserved in the Macleay Museum, University of Sydney. Types for the species *Echiniscus curiosus*, *E. jamesi* and *E. rodnae* (see Claxton, 1996) are preserved in the Australian Museum, Sydney. The type material for *Mopsechiniscus tasmanicus* is lodged in the Zoologisches Museum, University of Hamburg (Dastych & Moscal, 1992). *Macrobiotus cf pseudohufelandi*, a species transferred to the genus *Xerobiotus* (Bertolani & Biserov, 1996), was found in soil in South Australia and is the subject of a number of papers (Bird, 1996; Bird & McClure, 1997a, 1997b).

Recently, studies on the tardigrades of the Australian Antarctic Territories have appeared, Miller & Heatwole (1995); Miller, Heatwole, Pidgeon & Gardiner (1994); and Miller, Miller & Heatwole (1994). Two new species, *Echiniscus darienae* and *Ramajendas heatwolei*, were reported from Macquarie Island by Miller *et al.*, (1995). Miller, Claxton & Heatwole (1999) described the presence of males in populations of *Echiniscus* in the Australian Antarctic Territories and discussed the implications of these findings. Miller, Horning & Heatwole (2001) recorded 25 species from Macquarie Island.

1.8 AIMS OF THIS STUDY

This study was undertaken to establish a solid basis for the identification of tardigrade species found in a variety of habitats in Australia.

Specifically, the aims were

- To collect and identify terrestrial tardigrades from as wide a variety of habitats as possible, concentrating on those inhabiting mosses and lichens on rocks and trees and leaf litter, in order to gain a sound knowledge of the species found in Australia;
- To sample major vegetation types along the east coast of Australia to observe zoogeographic patterns of tardigrade communities;
- To estimate the level of endemism/cosmopolitanism in the Australian tardigrade fauna.

Table 1.1 Diagnostic characters of the higher divisions of the Phylum Tardigrada

Class Heterotardigrada Marcus, 1927

Cephalic sensory structures include cirrus A. Pharynx with continuous cuticular bands, no placoids. Claws not divided into primary and secondary branches.

Order Arthrotardigrada Marcus, 1927

Median cirrus usually present. Legs usually digitate or, if not, claws fixed directly onto ends of legs and not on papillae.

Order Echiniscoidea Marcus, 1927

Median cirrus absent. Legs non-digitate, claws inserted on minute papillae at ends of legs.

Family Echiniscoididae Kristensen & Hallas, 1980

Unarmoured. Cephalic papillae dome-shaped or indistinct, cephalic sensory structures reduced.

Family Oreellidae Ramazzotti, 1962

Unarmoured. Four claws on all legs. Ornamented eggs laid free.

Family Carphanidae Binda & Kristensen, 1986

Unarmoured. Two claws on first three pairs of legs, one claw on fourth pair.

Family Echiniscidae Thulin 1928

Armoured. Four claws on all legs. Smooth eggs laid in exuvium.

Class Eutardigrada Marcus, 1927

Cephalic sensory structures absent or, if present, papillate, cirrus A absent. Pharynx with cuticular bands or with separate placoids. Two diploclaws on each leg divided into primary and secondary branches.

Order Parachela Schuster, Nelson, Grigarick & Christenberry, 1980

Cephalic sensory structures absent. Primary and secondary branches of claws united or acting as a single unit.

Family Calohypsibiidae Pilato, 1969

Diploclaws on each leg asymmetrical with respect to the median plane of the leg; claws on each leg similar in size and shape. Two branches of the diploclaw fused together from the base which is not pedunculate.

Family Eohypsibiidae Bertolani, 1981

Diploclaws on each leg asymmetrical with respect to the median plane of the leg; claws on each leg similar in size and shape. Each claw consists of three distinct parts: basal part secondary branch and primary branch inserted linearly and separated by septa; internal claw can rotate on its base through 180°.

Family Hypsibiidae Pilato, 1969

Diploclaws on each leg asymmetrical with respect to the median plane of the leg; claws on each leg dissimilar in size and shape. Primary branch joined to secondary branch by a flexible connection. Claws reduced in size or absent in some taxa.

Continued

Subfamily Hypsibiinae Pilato, 1969

Claws of *Hypsibius*-type with secondary branch forming a continuous arc with base or *Isohypsibius*-type with secondary branch forming a right angle with base. Buccal tube rigid; apophyses for insertion of stylet muscles crescent-shaped.

Subfamily Diphasconinae Dastych, 1992

Claws of *Hypsibius*-type. Buccal tube with rigid and flexible parts; posterodorsal apodeme present or absent. Anterior apophyses shaped like blunt or semilunular hooks.

Subfamily Itaquasconinae Rudescu, 1964

Claws *Hypsibius*-type. Anterior apophyses in the shape of a wide flat ridge, symmetrical with respect to the frontal plane.

Family Macrobiotidae Thulin, 1928

Diploclaws on each leg symmetrical with respect to the median plane of the leg; claws on each leg similar in size and shape.

Subfamily Macrobiotinae Guidetti, Rebecchi & Bertolani, 2000

Claws Y-shaped with a tract common to the two branches connecting to the basal portion of the claw. No ventral hook on ventral support.

Subfamily Murrayinae Guidetti *et al.*, 2000

Claws V- or L-shaped with two branches diverging immediately after the basal portion. Ventral hook on ventral support.

Family Microhypsibiidae Pilato, 1998

Diploclaws on each leg asymmetrical with respect to the median plane; claws on each leg dissimilar in size, similar in shape. Claws with narrow basal part continuous with primary branch, secondary branch rigidly joined to primary branch.

Family Necopinatidae Ramazzotti & Maucci, 1983

Lacking claws on last three pairs of legs; first pair lacking or present as two sclerified pieces inserted on the median plane of the leg.

Order Apochela Schuster *et al.*, 1980

Cephalic sensory structures in form of ring of papillae around mouth and two lateral papillae. Primary branch of claws completely separate from secondary branch.

Family Milnesiidae Ramazzotti, 1962

As for Order.

Table 1.2 Subdivision of the Phylum Tardigrada

Class	Order	Family	Subfamily	Genus		
Heterotardigrada	Arthrotardigrada (m)					
	Echiniscoidea	Echiniscoididae (m)	2	<i>Echiniscoides, Anisonyches</i>		
		Oreellidae (t)	1	<i>Oreella</i>		
		Carphanidae (fw)	1	<i>Carphania</i>		
		Echiniscidae (ta)	12	<i>Antechiniscus, Bryochoerus, Bryodephax, Cornechiniscus, Echiniscus, Hypechiniscus, Mopsechiniscus, Novechiniscus, Parechiniscus, Proechiniscus, Pseudechiniscus, Testechiniscus</i>		
Eutardigrada	Parachela	Calohypsibiidae (t)	6	<i>Apodibius, Calohypsibius, Haplohexapodibius, Hapломacrobiotus, Hexapodibius, Parhexapodibius</i>		
		Eohypsibiidae (fw)	2	<i>Amphibolus, Eohypsibius</i>		
		Hypsibiidae (t, fw, m)	Hypsibiinae	11	<i>Acutuncus, Doryphoribius, Eremobiotus, Halobiotus, Hypsibius, Isohypsibius, Mixibius, Pseudobiotus, Ramajendas, Ramazzottius, Thulinus,</i>	
				Diphasconinae	3	<i>Diphascon, Hebesuncus, Paradiphascon</i>
				Itaquasconinae	5	<i>Astatumen, Itaquascon, Mesocrista, Platicrista, Parascon</i>
		Macrobiotidae (t, fw)	Macrobiotinae	8	<i>Adorybiotus, Calcarobiotus, Macrobiotus, Minibiotus, Pseudodiphascon, Pseudohexapodibius, Richtersius, Xerobiotus</i>	
				Murrayinae	3	<i>Dactylobiotus, Macroversum, Murrayon</i>
		Microhypsibiidae (t)		2	<i>Fractonotus, Microhypsibius</i>	
		Necopinatidae (t)		1	<i>Necopinatum</i>	
	Apochela	Milnesiidae (t)	3	<i>Limmenius, Milnesioides, Milnesium</i>		

(fw) = freshwater; (m) = marine; (t) = terrestrial; (ta) = terrestrial armoured; (t, fw) = terrestrial & freshwater; (t, fw, m) = terrestrial and freshwater, few marine species

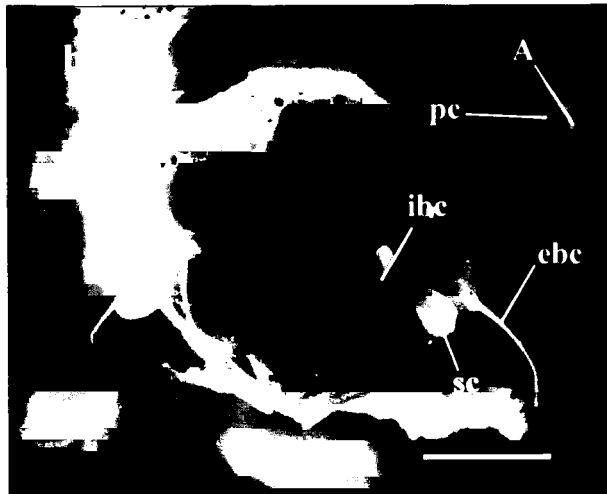
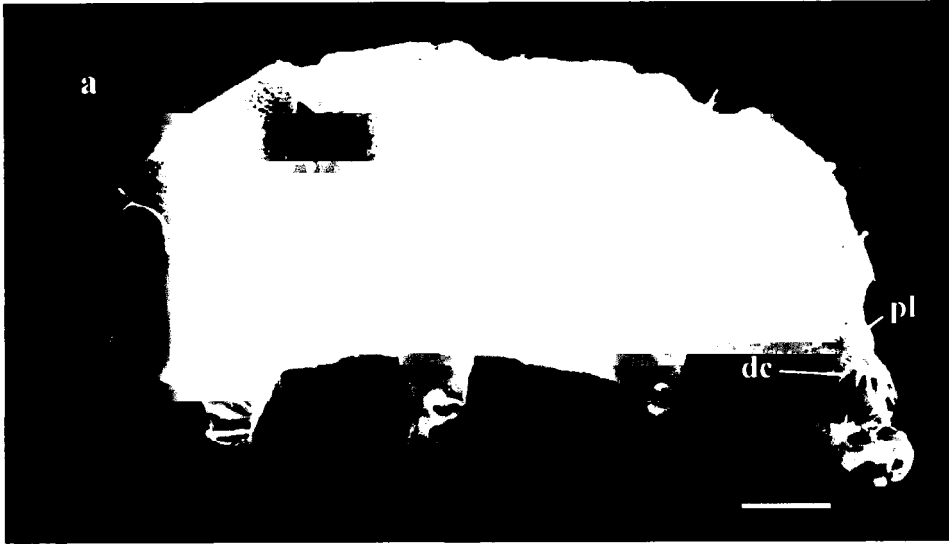


Plate I (a). Whole animal (*Echiniscus marcusii* Pilato, Claxton & Binda, 1989) showing five body segments, plate (pl), dentate collar (dc), SEM. (Scale bar = 20 μ m). (b). Head of *E. marcusii* showing cephalic sensory structures, cirrus A (A), primary clava (pc), external buccal cirrus (ebc), secondary clava (sc) and internal buccal cirrus (ibc), SEM. (Scale bar = 10 μ m)



Plate II. Claws of Tardigrada (a). Diploclaws on the leg of the eutardigrade *Macrobotus peteri* Pilato, Claxton & Binda, 1989, SEM. (b). Four claws on the leg of the heterotardigrade *Echiniscus marcusii* Pilato, Claxton & Binda, 1989, spur (sp), SEM. (c). Claws of the eutardigrade *Minibiotus milleri* Claxton, 1998 showing the accessory claws (ac) attached to primary branch (pb), secondary branch (sb) and lunule (lu), SEM. (Scale bars = 5 μm)

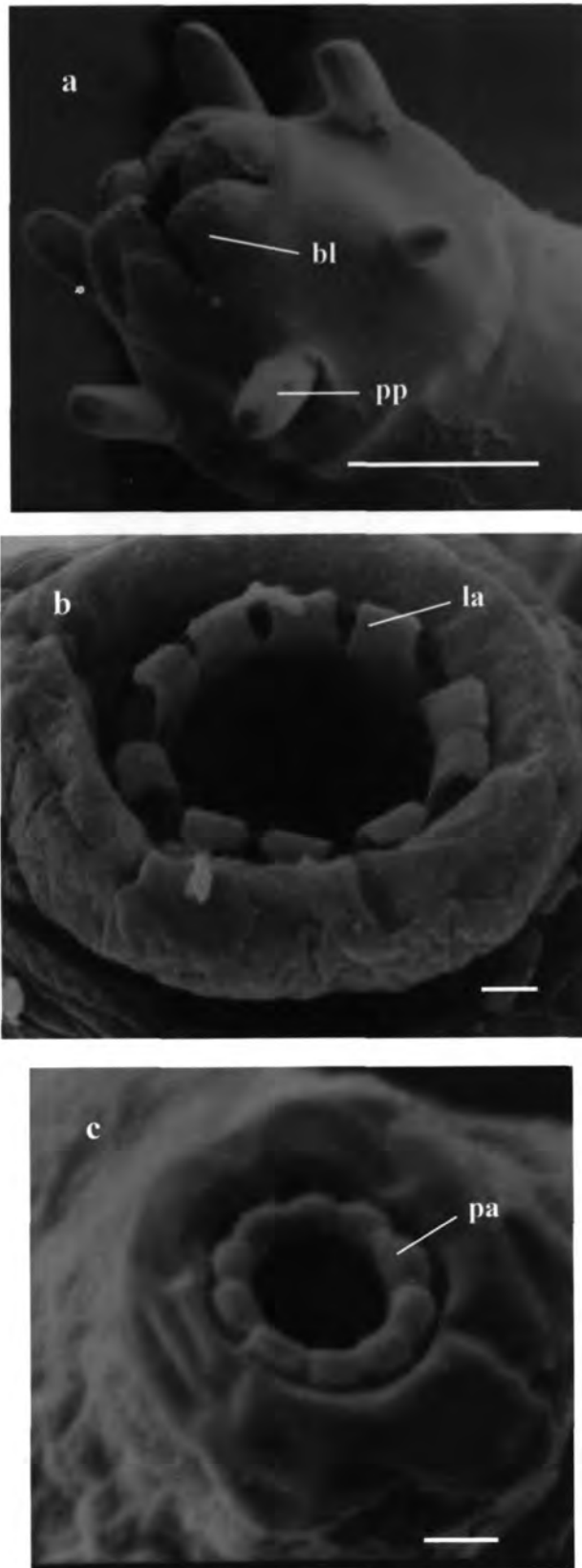


Plate III. (a). Cephalic sensory structures of the apochelan *Milnesium tardigradum* Doyere, 1840 showing buccal lamella (bl), peribuccal papilla (pp), SEM. (Scale bar = 10 μ m); of parachelans (b). *Macrobiotus* sp. showing lamella (la), SEM. (Scale bar = 1 μ m) and (c). *Minibiotus* sp. showing papula (pa), SEM. (Scale bar = 1 μ m).

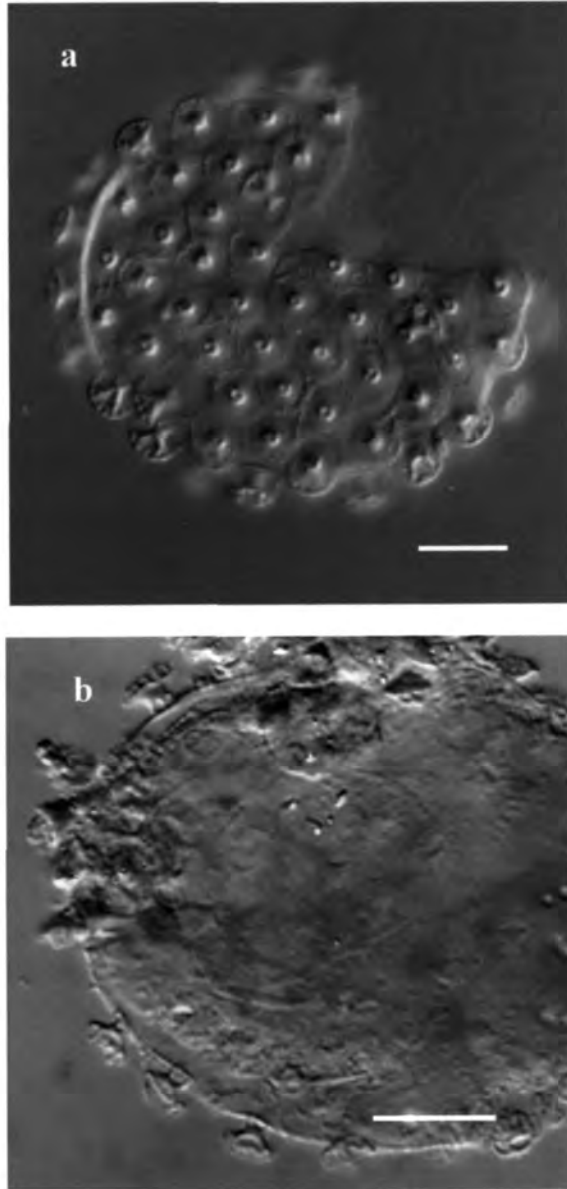


Plate IV. (a). Egg of *Minibiotus floriparus* Claxton, 1998, DIC. (b). Egg of *Oreella mollis* Murray, 1910, DIC. (Scale bars = 10 μ m)

CHAPTER 2. MATERIALS AND METHODS

2.1. MATERIAL EXAMINED

This study is based on tardigrade specimens extracted from cryptogams and leaf litter samples collected from 120 sites in Australia (Appendix 1) and on slide-mounted specimens obtained from museums and private collections. The Australian material consists primarily of collections from the eastern states. Some material was also collected in Western Australia and several new species from that region have been described in this work. However, Western Australia was not included in the distributional analysis (Chapter 6) because many of the specimens collected have still to be correctly identified. The material examined includes type material where available. Collection data for all identified species are listed with the respective species in Chapter 4.

The following abbreviations have been used:

Institutional and private collection acronyms used throughout this work are:

AM	Australian Museum, Sydney, Australia;
BG	Collection of Mr. B. Grabowski, Marburg, Germany;
BMD	Bohart Museum, University of California, Davis, USA;
MM	Macleay Museum, University of Sydney, Sydney, Australia;
MUT	Department of Biology, McMurry University, Texas, USA;
NM	Collection of Mr. N. Marley, Bristol, United Kingdom;
NMP	Natal Museum, Pietermaritzburg, South Africa;
NZM	Museum of New Zealand, Wellington, New Zealand;
UCI	Dipartimento di Biologia Animale, Università di Catania, Catania, Italy;
UMI	Dipartimento di Biologia Animale, Università degli Studi di Modena, Modena, Italy;

- UNP Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina;
- VB Collection of Dr. V.I. Biserov, Institute of Inland Water Biology, Yaroslavl District, Russia;
- WM Collection of Dr. W.R. Miller, Philadelphia, USA;
- ZMH Zoologisches Institut und Museum, Hamburg University, Hamburg, Germany;
- ZMUC Zoological Museum, University of Copenhagen, Denmark – collection of Dr. R. Mobjerg Kristensen.

2.2. SPECIMEN COLLECTION AND PRESERVATION

Samples of moss, lichen and leaf litter were placed in paper bags on which collection data was written. Specimens were extracted from these samples as described in Claxton (1998) and mounted on microslides in Hoyer's medium.

2.3. LIGHT MICROSCOPY AND PHOTOMICROGRAPHY

All examinations and measurements of slide-mounted specimens were done using an Olympus BH-2 microscope fitted with a halogen lamp, drawing tube, calibrated eyepiece micrometer and phase contrast optics up to 1000× magnification. The same microscope, fitted with Nomarski optics was used for some observations.

All microphotographs were taken with a Nikon E995 digital camera attached to the above microscope. The images were transferred as JPG files into a Pentium III computer and printed using ArcSoft Photostudio 2000, Adobe Pagemaker 6.5 and a Canon S800 printer. No images were altered during this process.

2.4. SCANNING ELECTRON MICROSCOPY (SEM)

Freshly killed specimens (specimens previously preserved in alcohol for some time were found not to be good subjects for SEM studies) and eggs were placed in a labeled filter paper envelope which was inserted into a modified BEEM capsule standing upright in absolute alcohol. The modified capsule was made by cutting the ends off a capsule and resealing the open ends using lids from which a central disc had been cut and replaced by wire mesh (less than 40 μm). The closed capsule was transferred to 70% acetone and then through a graded series of acetone to 100%, after which it was critical-point dried using carbon dioxide.

Individual animals or eggs were removed from the envelope and dropped onto double-sided sticky tape mounted on an aluminum stub. The specimens were then vacuum-coated with 10nm gold. A map of each stub was drawn for the location of each specimen.

Photographs were taken using a Jeol JSM-840 Scanning Electron Microscope.

2.5. STATISTICAL METHODS

For each species, the following statistics are given with descriptions:

- Body length - measured from the anterior tip of the body to the end of the body, excluding the fourth pair of legs.
- Buccal tube length - measured from the upper edge of the stylet sheaths (focusing on the dorsal face) to the posterior edge of the tube, not including the pharyngeal apophyses (Pilato, 1981).
- Buccal tube width - measured as the external diameter at the level of the stylet insertion point. I am aware that some studies (Bertolani & Rebecchi, 1993) measure the internal diameter of the buccal tube. However, the external diameter was chosen

in this study because the measurement error would be smaller the greater the width measurement taken. In species, such as many *Minibiotus*, this could be appreciable.

- Length of claw - measured from the base of the claw (not including the lunule) to the top of the main branch (excluding the accessory claws). In many other studies, the length of the claw is given as including the accessory claw. However, it seems to this author that the accessory claws of some species are rather flexible and therefore appear closer or farther from the primary branch in different specimens of the same species. The claws of species of *Doryphoribius* are often folded back on themselves so as to make consistent measurements of the whole claw, from base to the top of the primary branch, very difficult. In this study, therefore, for species of this genus measurements are given for the primary branch only (from its base to the top of the branch excluding the accessory claw).
- The *pt* ratio (Pilato, 1981) is the ratio of the length of a given structure to the length of the buccal tube expressed as a percentage.

Eggs are ascribed to new species only after the observation of an egg containing an embryo in an advanced state of development that diagnostic characters can be discerned. A “specimen” in the text implies an adult specimen.

The statistical package Minitab vers. 13 was used for various analyses including the multivariate analysis – Principal Components Analysis and Cluster Analysis.

2.6. ANALYSIS OF MOUNTANT DISTORTION

Forty randomly selected specimens were measured, first in water and then mounted in one of four mounting media – Hoyer’s, Faure’s, Gurr’s and Polyvinyl lactophenol. They were then measured after three weeks. The results are presented in Table 2.1. Hoyer’s medium

gave the best results, producing a slight increase in body length in most specimens but was, on the whole, the least variable of the media tested. PVL caused shrinkage in most specimens and, in some cases, this obscured valuable characters. However, the structure and shape of the pharynx remained more visible in this medium than in Hoyer's which tended to clear specimens. Where possible, especially for new species, live or asphyxiated specimens should be examined in a drop of water so as to observe some features, such as eye spots and stylets, which may be destroyed by mounting fluids. Ideally, wholemounts should be made using a variety of mountants such as Hoyer's medium, Polyvinyl lactophenol and, possibly, glycerin (Kristensen & Higgins, 1984) since they all produce variable results. The problem of excessive clearing of specimens by Hoyer's medium can be alleviated somewhat by the addition of Iodine. The vast majority of specimens examined for this study were mounted in Hoyer's medium to which Iodine had been added. Ramazzotti & Maucci (1983) give a lengthy discussion on the relative advantages and disadvantages of different mounting media and techniques.

2.7. MEASUREMENT ERROR ANALYSIS

When using a microscope, it is important to be aware of the magnitude of the random error associated with measurement. In order to evaluate this, measurements of the buccal tube length, the stylet support insertion length and the macroplacoid row length were taken on four different occasions one day apart on ten specimens of *Diphascon pingue* Marcus, 1936. The measurements were done at random and without observing the previously obtained measurements. The results are presented in Table 2.2. They show that the greatest degree of uncertainty is 0.5 μm , that is, a mean measurement of the buccal tube length of one specimen was 21.2 μm with a standard deviation of 0.5 μm (one eye-piece unit) and the standard error of the mean was low at 0.16 μm .

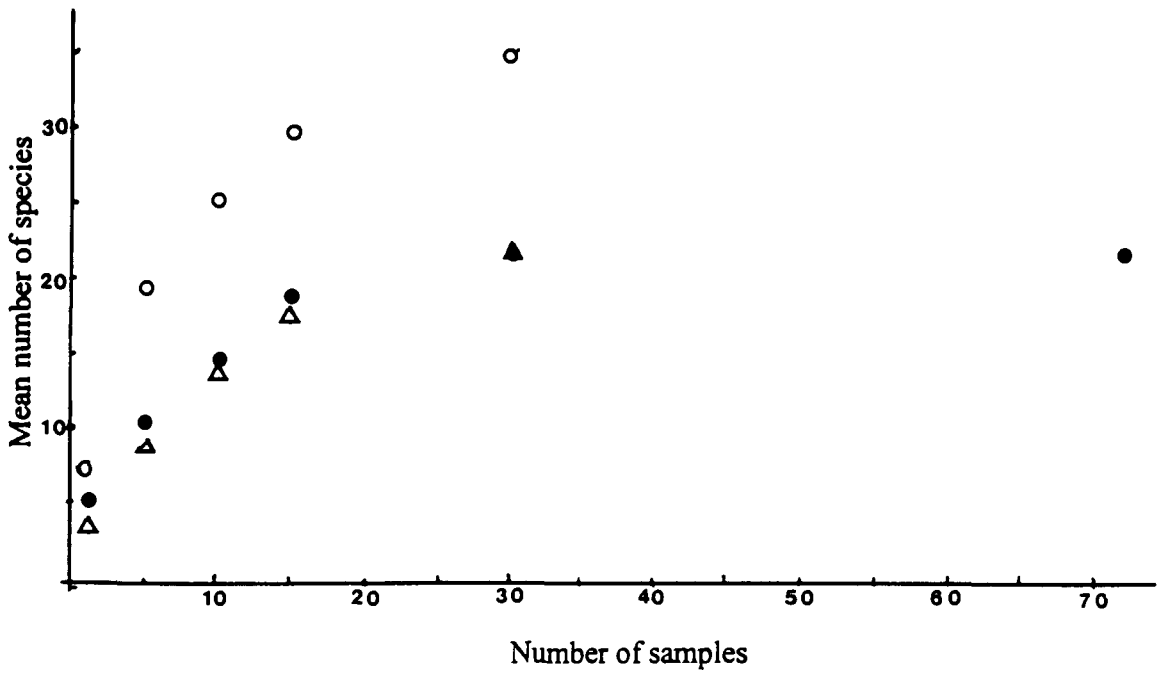
2.8. HOW MANY SAMPLES? – A RESAMPLING EXERCISE

Processing of cryptogam samples to extract tardigrades is time consuming and labor intensive. It is therefore important, when the main aim is to survey the tardigrade species in an area, to process as few samples as possible. A resampling exercise was therefore conducted on the sample data from three sites in order to arrive at a figure for the minimum number of samples that will contain the majority of species in a site. In the studies documented here a site is roughly 35m by 35m.

In the following analysis, 72 samples from Douglas Park, 30 from Wright's Lookout, New England National Park and 30 from the Gate, New England National Park, each with known species composition were used. For each site, samples (each sample represented by a card with the names of species that had been identified as occurring in that sample written on them) were drawn randomly in simulation of a field collection. One, five, 10 and 15 'samples' were drawn 10 times each. The number of species found in each 'collection' was noted and a mean value for 10 'collections' was obtained. The results were plotted (Fig. 2.1). Points showing the number of species found in all the samples taken from each site were also plotted on this figure, e.g., 21 species in 72 samples from Douglas Park.

The two dry sclerophyll sites (Douglas Park and the Gate) give very similar results, indicating that 86% of species will be found in 15 samples, 30 samples provide almost 100% of species that occur at a site as the same mean number of species per sample was obtained in 30 samples as were found in 72 samples from Douglas Park. The graph for Wright's Lookout (*Banksia* heath at 1300 m. asl.) also suggests that 15 samples is sufficient to recover 86% of species present and that the finding of 35 species in 30 samples has probably captured close to 100% of species.

Figure 2.1 Mean numbers of species collected in 1, 5, 10, 15 and 30 samples drawn in simulated field collections of cryptogams from three sites



- Wrights Lookout (New England National Park) (30 samples)
- △ The Gate (New England National Park) (30 samples)
- Douglas Park (72 samples)

Table 2.1. Body length measurements (in μm) of forty tardigrade specimens in water and in one of four different mounting media.

MOUNTANT															
PVL*				Faure				Gurr				Hoyer			
No	Body length (μm) in		%Diff	No	Body length (μm) in		%Diff	No	Body length (μm) in		%Diff	No	Body length (μm) in		%Diff
	Water	Mount			Water	Mount			Water	Mount			Water	Mount	
1	700	720	+2.8	11	325	375	+15.4	21	310	390	+25.8	31	445	450	+1.1
2	370	330	-10.8	12	220	180	-18.2	22	270	260	-3.7	32	430	440	+2.3
3	470	420	-10.6	13	210	190	-9.5	23	390	340	-12.8	33	500	507	+1.4
4	380	360	-5.3	14	440	430	-2.3	24	330	350	+6.1	34	335	337	+0.6
5	170	170	0	15	395	370	-6.3	25	465	437	-6.0	35	560	590	+5.4
6	360	370	+2.8	16	375	395	+5.3	26	237	240	+1.3	36	395	410	+3.8
7	380	350	-7.9	17	257	260	+1.2	27	270	285	+5.6	37	345	355	+2.9
8	400	380	-5.0	18	347	370	+6.6	27	610	605	-0.8	38	515	510	-1.0
9	500	471	-5.8	19	330	360	+9.1	29	360	330	-8.3	39	399	400	+0.3
10	350	320	-8.6	20	330	375	+13.6	30	465	475	+2.2	40	177	185	+4.5
Mean % Difference:			-4.8				+1.5				+0.9				+2.3
Maximum % Diff.			-10.8				-18.2				+25.8				+5.4
Minimum % Diff.			0.0				+1.2				-0.8				+0.3
% Diff. Range			+2.8				+15.4				+25.8				+5.4
			-10.8				-18.2				-8.3				-1.0

* Polyvinyl Lactophenol

Table 2.2 Repeat measurements (in μm) of three structures (buccal tube length, stylet insertion length and macroplacoid row length) of ten specimens of *Diphascon pingue* Marcus, 1936

Spec No.	BL (μm)	BTL (μm) repeat measurements				Mean	SD	SDOM
		1	2	3	4			
753-5	225	20.5	21.1	21.6	21.6	21.2	0.5	0.16
753-4	150	16.8	17.3	17.3	17.3	17.2	0.2	0.06
753-25	184	18.9	18.9	18.9	18.4	18.8	0.2	0.06
753-26	180	18.9	18.9	18.9	18.4	18.8	0.2	0.06
753-43	174	18.9	17.8	17.8	18.1	18.2	0.4	0.13
1097-18	215	20.5	20.5	21.1	21.6	20.9	0.5	0.16
1115-15	200	19.2	18.9	20.0	20.0	19.5	0.5	0.16
1069-6	237	18.9	18.9	18.9	18.9	18.9	0.0	0.00
1113-6	225	18.9	18.9	18.9	18.9	18.9	0.0	0.00
1137-6	212	19.5	19.5	20.0	20.0	19.8	0.3	0.10

Spec No.	SIL (μm) repeat measurements				Mean	SD	SDOM
	1	2	3	4			
753-5	12.4	13.0	13.0	13.0	12.9	0.3	0.10
753-4	10.3	10.3	10.3	10.3	10.3	0.0	0.00
753-25	10.8	11.1	10.8	10.8	10.9	0.1	0.03
753-26	10.8	11.4	10.8	11.4	11.1	0.3	0.10
753-43	10.8	10.5	10.5	10.8	10.7	0.2	0.06
1097-18	12.4	12.4	12.7	13.0	12.6	0.3	0.10
1115-15	11.9	11.4	11.9	11.9	11.8	0.3	0.10
1069-6	11.4	11.4	11.4	11.4	11.4	0.0	0.00
1113-6	11.6	11.4	11.6	11.4	11.5	0.1	0.03
1137-6	11.6	11.6	11.9	11.9	11.8	0.2	0.06

Spec No.	MPRL (μm) repeat measurements				MEAN	SD	SDOM
	1	2	3	4			
753-5	16.2	16.2	16.2	16.2	16.2	0.0	0.00
753-4	10.8	10.8	10.8	10.8	10.8	0.0	0.00
753-25	11.6	11.9	11.4	11.9	11.7	0.2	0.06
753-26	11.9	11.9	12.4	12.4	12.2	0.3	0.10
753-43	10.8	10.8	10.8	10.8	10.8	0.0	0.00
1097-18	11.4	11.4	11.4	11.4	11.4	0.0	0.00
1115-15	11.4	10.8	11.1	11.4	11.2	0.3	0.10
1069-6	10.3	9.7	10.3	10.0	10.1	0.3	0.10
1113-6	10.0	10.3	10.3	10.3	10.2	0.1	0.03
1137-6	10.8	10.3	10.8	10.8	10.7	0.2	0.06

BL Body length
 BTL Buccal tube length
 SIL Stylet support insertion length
 MPRL Macroplacoid row length
 SD Standard deviation
 SDOM Standard deviation of the mean

CHAPTER 3. TAXONOMIC STUDIES

3.1 INTRODUCTION

Tardigrades are a relatively small group of animals and their taxonomy is, at first glance, simple. Identification to the generic level is usually quite easy although the number of new genera added to the terrestrial tardigrades over the last 20 years has escalated. The last comprehensive monograph on the phylum Tardigrada was published 19 years ago (Ramazzotti & Maucci, 1983).

Identification of species is more difficult for a number of reasons. In many genera, e.g., *Minibiotus* and *Macrobiotus*, the species are extremely morphologically similar and identification is not easy. The problem is compounded by lack of type material for many species (Dastych, 1991) including those first described by two of the most prolific authors in the early 1900's – Richters and Murray. Many workers in the past did not make permanent slide preparations. In other cases, prepared slides have not survived and we are left with the descriptions and illustrations as the only record. Unfortunately, insufficient descriptions abound in the literature. An extreme example of this is the very perfunctory description of *Minibiotus intermedius* by Plate (1888). Subsequent authors compounded the perception that this is an extremely common and widespread species by simply assuming its presence based on an overall general impression of size and shape without actually giving precise measurements and details of their populations.

This chapter discusses a number of taxa that required a greater depth of investigation before species evaluation could be made. The actual species descriptions are included in Chapter 4.

Section 3.2 of this chapter describes a large number of species of *Minibiotus* found in Australia in this study. It is most likely that the genus also contains many undiscovered species in other countries. A similar situation, described by Bertolani & Rebecchi (1993), arose with *Macrobiotus hufelandi* Schultz, 1840. *M. hufelandi* is probably the most cited tardigrade species (after *Milnesium tardigradum*) but the more precise definition of this species by these authors has now placed all of these citations in doubt. The *hufelandi* group in Australia is discussed in section 3.3 along with other members of the Macrobiotidae.

In some tardigrade species, the above-mentioned problems are compounded by the problems associated with the small size of the adults. *Diphascon* species generally range from 140 μm to 300 μm in length, so measurement of structures such as macropylacoids (1-9 μm long) and claws (4-10 μm long), will always be subject to high error of measurement. Reliance on only a few such characters to identify species is therefore liable to be fraught with danger particularly when only a few specimens are used. Section 3.4 describes the utilisation of multivariate techniques on populations of specimens of the *Diphascon pingue* group in an attempt to arrive at a solution to the species problem in Australia.

The discovery of a new genus, *Milnesioides* Claxton, 1999, provided an insight into the structure and function of the buccal apparatus of the rare monotypic genus *Limmenius* within the family Milnesiidae. This work is described in section 3.5 along with a comparison of these two genera with the only other genus within that family, the very common and widespread *Milnesium*.

Section 3.6 describes three species in the rare genus, *Antechiniscus*, known only from the cool temperate rainforests of the southern hemisphere. This includes descriptions of a new

species from Tasmania, a New Zealand species now found in Australia and the redescription of a rare species known only from its original description by Murray (1910) from Mount Kosciusko, Australia.

Section 3.7 describes the members of three genera (including one new genus) within the subfamily Itaquasconinae. Only two members of this group have so far been recorded for Australia and this work indicates the existence of many new species.

Full descriptions of all Australian species mentioned in this chapter are provided in chapter 4 of this work.

3.2 THE GENUS *MINIBIOTUS*

3.2.1 Introduction

Minibiotus Schuster, Nelson, Grigarick & Christenberry, 1980 is a genus of terrestrial tardigrades found commonly in mosses and lichens. The type species *Minibiotus intermedius* (Plate, 1888) remained the only species in the genus until *M. maculartus* was described by Pilato & Claxton (1988). The adults of this species closely resembles *M. intermedius* but the eggs are quite dissimilar, having processes that lacked an enclosing membrane - a character suggested as definitive for the genus by its authors. Further species have since been described. *M. fallax* was described by Pilato, Claxton & Binda (1989a). This species had few adult characters similar to those of *M. intermedius* apart from the presence around the mouth of papulae (Plate 1c) rather than lamellae which are present in the closely related genus *Macrobiotus* (Plate 1b). Miller, Heatwole, Pidgeon & Gardiner (1994) transferred *Macrobiotus weinerorum* Dastych, 1984 to the genus *Minibiotus* while Dastych & Drummond (1996) attributed *Macrobiotus stuckenbergi* Dastych, Ryan & Watkins, 1990 to the genus *Minibiotus*. Binda & Pilato (1992) described two new species and transferred *Macrobiotus furcatus* to the genus *Minibiotus*. They suggested that the *Minibiotus* bucco-pharyngeal apparatus has a “characteristic appearance” which includes double curvature of the buccal tube, stylet supports inserted a considerable distance from the pharyngeal bulb and first macroplacoid situated very close to the apophysis. The genus *Minibiotus*, however, has not been uniformly accepted (Ramazzotti & Maucci, 1983) perhaps because of its unsatisfactory definition (Pilato, 1982).

M. intermedius, itself, is considered to be a cosmopolitan tardigrade, having been reported from many countries (McInnes, 1994). The original description of specimens from Chile and Marburg, Germany (the exact type locality was not noted), like most supplied in those

times, is inadequate by today's standards, lacking illustrations and mention of the egg. The species, however, seems to have been readily recognized by many workers even before Thulin (1911) provided a more complete description of the animal and its egg from material collected in Europe. A review of the extensive literature on this species, in which many authors cite its presence in many countries, reveals that most citations are based on the "characteristic appearance of the adults" usually with no reference to the egg. An aim of this work was to obtain specimens identified as *M. intermedius* from as many countries as possible to determine if there is a single cosmopolitan species which conforms to the description of this species and, more importantly, has a set of clearly definable characters.

It has been found in this study that specimens with the characteristic appearance of *M. intermedius* are very widespread and abundant in mosses and lichens in Australia. Close examination of these and careful collection of eggs with specimens have revealed that while many could be mistaken, on adult morphology, for *M. intermedius* as described by Thulin (1911), they have very different egg types.

Observations on 18 species in this genus provided the basis for a more precise definition of the genus (Claxton, 1998). In the following study these observations are discussed.

3.2.2 Results and Discussion

Diagnoses and descriptions for 18 species may be found in Chapter 4 of this work.

Because of the small size of most of these species, observations were made using the highest usable power of light magnification. Qualitative characters (such as the degree of granulation around the claws, presence or absence of teeth on the lunules, the nature of the microplacoid and the length of accessory claws and their proximity to the main branch)

have been shown to be important in the discrimination of species and have been included in the descriptions. It should be stressed, however, that these characters might not always be visible on all specimens. Quantitative characters (such as the lengths of structures of the buccal apparatus and of the claws) are given for the different populations of species and such measurements are considered to be essential for the description of any species in this genus. Ratios (*pt*) have been generated from these measurements (Table 3.2.1) and some of these are particularly effective in discriminating species, e.g. stylet support insertion point, ventral support length and claw length. Similar ratios have been used to discriminate species of the *hufelandi* group of the genus *Macrobiotus* (Bertolani & Rebecchi, 1993).

A group of species found in this study with very similar morphology (smooth cuticle and granulation around the claws) can be readily differentiated on the basis of the appearance of their distinctive eggs. However, when the egg cannot be found, as is often the case in the study of tardigrades, the use of a full range of adult characters becomes very important. Likewise, there is a group of species whose egg morphology is very similar (long thin processes) and it is important to report fully a range of qualitative and quantitative characters of the eggshell and its processes.

The description of *M. taiti* and *M. poricinctus* presented here and examination of specimens from a number of countries, suggests that there are many species in the *intermedius* group, that is, species in which the adult form is very similar and whose eggs bear processes which could be described as screw-shaped and are surrounded by a membrane. This work suggests that many reports of *M. intermedius* in the literature may be inaccurate. Bertolani & Rebecchi (1993) have described a parallel situation for the *Macrobiotus hufelandi* group.

A major difficulty in tardigrade taxonomy has been the lack of sufficient detail in older descriptions of species and the lack of type material for them. Consequently, it is almost impossible to decide on the correct identification for some species. As an example, the description of *Macrobiotus crassidens* Murray, 1907 suggests that it is very similar to *Minibiotus hispidus* although there appear to be sufficient differences to warrant the description of the latter as a new species. Other species of *Macrobiotus* almost certainly belong to the genus *Minibiotus* e.g. *Macrobiotus acontistus* De Barros, 1942 and *Macrobiotus marculsi* De Barros, 1942. Seventy four slide mounted specimens from Venezuela labelled *Minibiotus intermedius* and deposited in the Bohart Museum were examined. Forty nine of these specimens conform to the description of *M. intermedius* sensu Claxton (1998). Five specimens appear to belong to the taxon *M. marculsi* and 11 specimens to *M. acontistus*. These have not been described here because they are not from the type locality (both Sao Paolo, Brazil) of either species and there were no eggs accompanying them.

Of forty-four slide mounted specimens from New Zealand labelled *M. intermedius* and deposited in the Museum of New Zealand only two actually conform to the above description. The other specimens belong to seven other taxa including six Australian species and an unknown species. The last was not described here as there were no eggs included.

Binda & Pilato (1992) observed that all species of *Minibiotus* have double curvature of the buccal tube. However in this study, three species, *M. hufelandioides*, *M. aquatilis* and *M. milleri*, were found to have only a single curve in the buccal tube about one-third of the way along the tube from the mouth. Other characters considered by these authors to be generically significant are - stylet supports inserted a considerable distance from the

pharyngeal bulb, short reinforcing bar and the first macroplacoid always situated very close to the apophysis. With the examination of many more species in the present work it is possible to be more precise and to set out *pt* values which discriminate this genus from the closely related *Macrobiotus* as shown in Table 3.2.2. In addition, the following characters - antero-ventral mouth, teeth in the oral cavity absent or reduced, extra thickening of the buccal tube wall immediately below the point of insertion of the stylet supports have been found to be consistent among species of *Minibiotus*.

Table 3.2.1. Number of observations (n), mean and standard deviation (SD), of some characters of *Minibiotus* species with three macroplacoids.

SPECIES	n	SIL		VS		BTW		MPRL		CLIV	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>M. intermedius</i>	20	55.0	0.9	37.3	2.0	6.8	0.5	26.5	1.5	24.8	1.8
<i>M. taiti</i>	20	60.3	0.3	40.3	0.7	8.0	0.3	32.1	1.6	33.2	0.8
<i>M. poricinctus</i>	20	59.5	0.4	35.8	0.9	7.6	0.4	30.9	1.4	27.3	0.7
<i>M. floriparus</i>	19	64.4	0.7	46.1	3.8	7.6	0.7	33.1	1.9	34.0	1.6
<i>M. aquatilis</i>	16	68.3	0.2	53.0	0.8	9.0	0.4	37.9	1.9	34.6	2.2
<i>M. hispidus</i>	10	65.2	0.5	45.7	1.5	8.0	0.2	33.2	1.1	28.1	0.8
<i>M. pilatus</i>	7	67.9	0.5	48.1	0.4	7.9	0.4	30.4	2.7	29.7	0.8
<i>M. ethelae</i>	8	64.9	1.2	51.4	1.2	7.6	0.2	32.3	0.8	37.6	0.7
<i>M. keppeli</i>	12	60.6	0.9	40.4	1.6	5.8	0.2	26.6	1.0	30.1	1.2
<i>M. asteris</i>	20	63.8	0.7	44.8	0.9	8.0	0.5	30.0	1.8	28.1	0.9
<i>M. milleri</i>	20	73.0	0.7	36.4	1.0	9.7	0.3	37.0	1.1	26.5	0.8
<i>M. hufelandioides</i>	16	67.4	0.5	45.9	2.0	8.6	0.4	38.2	1.1	29.3	1.2
<i>M. aculeatus</i>	7	63.7	1.1	51.4	1.5	7.8	0.3	32.2	2.0	22.8	0.9
<i>M. maculartus</i>	14	64.4	0.6	53.0	1.3	8.1	0.6	31.5	1.8	29.2	1.3

SIL Percent ratio of stylet support insertion point with respect to buccal tube length
VS Percent ratio of ventral support length with respect to buccal tube length
BTW Percent ratio of buccal tube width with respect to buccal tube length
MPRL Percent ratio of macroplacoid row length with respect to buccal tube length
CLIV Percent ratio of fourth claw length (excluding the accessory claw) with respect to the buccal tube length

Table 3.2.2. Length and width ratios relative to length of the buccal tube expressed as a percentage (*pt*) for species in the genera *Minibiotus* and *Macrobiotus* with three macroplacoids.

Character	<i>pt</i> Ratio	
	<i>Minibiotus</i> (18 species)	<i>Macrobiotus</i> (19 species)
Stylet Insertion Length	≤ 73	≥ 74
Ventral Support Length	≤ 62	≥ 65
Buccal Tube Width	≤ 12	≥ 13
Macroplacoid Row Length	≤ 42	≥ 42

3.3 THE FAMILY MACROBIOTIDAE

3.3.1 Introduction

In the early systematic monographs on tardigrades (Thulin, 1928; Marcus, 1936 and Ramazzotti, 1962) all genera of eutardigrades, except *Milnesium*, were placed in the family Macrobiotidae. Within this family, all species with claws that are symmetric with respect to the median plane of the leg were assigned to the genus *Macrobiotus* Schultze, 1834. Pilato (1969a, 1969b) proposed the separation of eutardigrades into four families based on their claw structure. In this scheme, the family Macrobiotidae contained only those genera with symmetric claws that, at the time, included two genera, *Macrobiotus* and *Pseudodiphascon* Ramazzotti, 1964. Schuster *et al.* (1980) devised a classification of the eutardigrades based on characters of the buccopharyngeal apparatus and, secondarily, on claw characteristics. Aspects of this classification have been accepted, including the formation of two orders, Apochela and Parachela, and of several new genera, *Minibiotus*, *Dactylobiotus* and *Pseudobiotus*. Pilato (1982) argued that the systematic arrangement of the eutardigrades proposed by him in 1969 appears to be natural and in correspondence with the phylogenesis of the group. The placement and definition of genera within the eutardigrade families, for most workers, remains that proposed by Pilato (1969a).

Currently, there are 11 genera in the family Macrobiotidae, seven of which were created from existing species of *Macrobiotus*, e.g., *Minibiotus* (Schuster *et al.*, 1980) for *Macrobiotus intermedius* Plate, 1888; *Murrayon* (Bertolani & Pilato, 1988) for *Macrobiotus pullari* Murray, 1907 and *Xerobiotus* (Bertolani & Biserov, 1996) for *Macrobiotus pseudohufelandi* Iharos, 1966. Guidetti, Rebecchi & Bertolani (2000) hypothesised that two phyletic lines exist within the family Macrobiotidae and they created two subfamilies based on the shape of the claws and on the ultrastructure of the cuticle.

The subfamily Macrobiotinae is characterized by Y-shaped claws (*hufelandi*-type) with primary and secondary branches joined over some length and a pedunculate basal unit and a cuticle lacking pillars in the inner epicuticle. The subfamily Murrayinae is characterised by V-shaped claws (L-shaped or *echinogenitus*-type) with the branches diverging immediately after the basal unit and pillars in the inner epicuticle identified three genera within. A secondary character separating the subfamilies is the absence of a hook on the ventral margin of the ventral support of the buccal tube of all genera in the former group and its presence in genera in the latter.

In the early literature, the term *echinogenitus*-type was used for species with V-shaped claws. Twelve species were described as having *echinogenitus*-type claws by Ramazzotti & Maucci (1983). However, these authors stated that the term has very poor taxonomic value as *M. echinogenitus* has, in fact, *hufelandi*-type claws. Binda (1988), in her redescription of *M. echinogenitus*, reaffirmed the presence of *hufelandi*-type claws in that species. Four of the 12 species with *echinogenitus*-type claws have since been transferred to the genus *Murrayon* (Bertolani & Pilato, 1988). The term *pullari*-type (first proposed by Bertolani (1982) for claws of *Macrobiotus pullari*, the type species of the genus *Murrayon*) was used for the claws of these four species by Bertolani & Pilato (1988) and Guidetti (1998).

The confusion in terminology of claw types which is evident in the earlier literature has come about because there has been no attempt, until recently, to describe claws in detail. The much closer attention now being paid to structures, such as claws and buccopharyngeal apparatus, has done much to clarify evolutionary lineages within the family Macrobiotidae and has increased the awareness of all workers of the wide

heterogeneity still to be analysed within the group at the generic (Guidetti & Bertolani, 2001) and at the species level.

The genus *Macrobotus* is the most species rich genus of eutardigrades with, at present, about 140 species. The species within the genus display a high degree of morphological conservatism and many species descriptions are not sufficiently detailed to allow easy identification. Species of *Macrobotus* are very common in the moss/ lichen habitat. Often the eggs are rare and so it is important to be able to differentiate species on adult characters alone. Because of the high morphological conservatism, taxonomists in the past lumped species into species complexes or groups, e.g., the *hufelandi* group which are only now beginning to be resolved.

In the past, characteristics of eggs (which are laid free and have processes) were very important for identification of species. In the monograph of Ramazzotti & Maucci (1983), specimens that have two macroplocoids (the first with a median constriction and less than twice the length of the second) and a microplocoid and also have eggs with processes in the shape of an up-turned egg cup, key to the *hufelandi* group. The additional Key to species within the *hufelandi* group relies solely on egg characteristics. Only six species, including *M. hufelandi*, appear in that key. *M. hufelandi* was considered, at the time, to be one of the most cosmopolitan of species. More recent studies, using high power light and scanning electron microscopy have shown, however, that it is possible to differentiate species within this genus from characters of the adult specimens (Biserov, 1990a, 1990b; Bertolani & Rebecchi, 1993). These characters include, the number and type of teeth in the oral cavity, the size of the plocoids, presence or absence of granulation around the claws and the nature of the accessory claws. Bertolani & Rebecchi (1993) provided keys to adults as well as

their eggs to differentiate 17 species within the *hufelandi* group. They also redefined *M. hufelandi* itself.

Ramazzotti & Maucci (1983) included 15 species in the *harmsworthi* group within *Macrobiotus*. The common characters of the adults are – smooth cuticle with no pores, three macroplacoids with rounded ends arranged in a line concave towards the midline and a large microplacoid. Further differentiation of these species relied heavily on egg characteristics. Eggs of species placed in this group are morphologically very dissimilar. Pilato *et al.*, (2000) showed that there is a subset of species within this group (including *M. harmsworthi* itself) with the adult characters described above and with eggs having conical processes that taper distally and have a crown of dots around the base. This suggests that a reexamination of specimens identified as *M. harmsworthi* may also reveal new species and throws doubt on its cosmopolitan distribution.

Macrobiotus richtersi Murray, 1911 is another species that is considered, at present, to have a cosmopolitan distribution. Species with characters of both the adults and eggs very similar to *M. richtersi* have been described recently by Biserov (1996), Binda & Pilato (2001) and Binda, Pilato, Moncada & Napolitano (2001). This appears to be a situation similar to those described above for the *hufelandi* and *harmsworthi* groups.

The genus *Calcarobiotus* Dastych, 1993 is characterized by the presence of laterally protruding spurs on either side of the bases of all claws and the claws were described as V-shaped. The genus was considered, by its author, to be closely related to *Macrobiotus* because of the similarities in the type of buccal apparatus, claws and egg processes. Recently, Guidetti & Bertolani (2001b) revised the genus *Calcarobiotus* to include the species *Macrobiotus gildae* Maucci & Durante Pasa, 1980 because of the presence of a

laterally protruding spur on the outside of the external claw and on the inside of the internal claw of each leg. These authors described the claw more fully as having a distinct basal portion separated from the rest of the claw by a transverse septum and having a very short common tract with primary and secondary branches of similar length and size. They reported that the claws on the first three pairs of legs of *Macrobiotus eugranulatus* Maucci, 1993 and *Macrobiotus polygonatus* Binda & Guglielmino, 1991 were the same as those of *Calcarobiotus* except that they lacked the lateral basal spurs but that the claws of the fourth pair of legs were different in having a small basal portion and a long common tract. They, therefore, transferred these species to the genus *Calcarobiotus* and created a subgenus (*Discrepunguis*) for them. The subgenus *Calcarobiotus* was reserved for four species, *C. filmeri* Dastych, 1993, *C. occultus* Dastych, 1993, *C. imperialis* Abe & Takeda, 2000 and *C. gildae*. These species were said to have claws of similar shape on all legs, the basal portion of which had one or two basal claws.

Guidetti & Bertolani (2001b) noted an undescribed structure in *C. occultus* and in *C. gildae*. This involved three deep double-arched incisions in the end of the buccal tube within the pharyngeal bulb, in line with the three rows of placoids. They noticed the same arches in *C. eugranulatus* and in *C. polygonatus* and the lack of them in a neotype specimen of *M. hufelandi*.

In the present study, a large number of specimens belonging to the family Macrobiotidae have been identified and these constitute the majority of specimens examined from many sites. In order to correctly assess the taxonomic position of these specimens, it was necessary to analyze the structures of the claws and of the buccal apparatus. The findings are described in the following section.

3.3.2 Results and Discussion

Diagnoses and descriptions of the species mentioned in the following section are found in Chapter 4.

3.3.2.1 *The genus Macrobiotus*

3.3.2.1a *The hufelandi group of species*

Specimens conforming to the general description of this group, that is, adults with two macroplacoids and a microplacoid and eggs with processes in the shape of up-turned egg cups were found in 72% of the 108 sites at which tardigrades were collected in this study. After close examination, using the characteristics outlined by Bertolani & Rebecchi (1993), 12 species were found to fit within this group. Only two (*M. hibiscus* and *M. santoroi*) had previously been described and nine are new species (*M. albus*, *M. caniensis*, *M. clivus*, *M. guttus*, *M. hesperius*, *M. microcalix*, *M. purpureus*, *M. rigatus*, *M. saxatilis* and *M. torridus*). Three species – *M. hufelandi*, *M. joannae* and *M. persimilis* – have been described as occurring in Australia by other workers but were not identified in the collections examined in this study. The variation in appearance of the eggs of the 12 species found in this study can be seen in Plates V and VI and the variation in the claws in Plates VII and VIII. These comparative photomicrographs make it easier to observe subtle variation among species.

There is some evidence to suggest that the previous records of *M. hufelandi* in Australia by Murray (1910) and Pilato & D'Urso (1976) are incorrect. Murray collected the species at Mount Kosciusko, the Blue Mountains and Eumundi. In the present study, three species were found at three different sub-sites on Mount Kosciusko. At the highest sub-site (Digger's Creek 1500 m. asl.) *M. clivus* sp. n. was found. *M. rigatus* sp. n. (a species very

similar to *M. hufelandi*) was found at Wilson Valley at 1200 m. asl. and at the lower sub-site (Waste Point, 1000 m. asl.) *M. guttus* sp. n. was found. *M. rigatus* was also found in the Blue Mountains (as a common member of the fauna in the rainforest remnants) and Eumundi (in a rainforest remnant). *M. torridus* sp. n. was also found at both these sites. It is more than likely that Murray mistook *M. rigatus* for *M. hufelandi* because of the similarity of both adults and eggs of these two species. Pilato & D'Urso (1976) found *M. hufelandi* in moss from Wallacia. They stated that some of the eggs had a much reduced sculpture on the shell and compared them with those of *M. hibiscus*. However, the present study has demonstrated that the animals of the latter species have an antero-ventral mouth and are unlike those of *M. hufelandi*. A more parsimonious explanation is that the eggs found by the above authors belong to *M. torridus* which occurs commonly in and around dry sclerophyll areas like Wallacia. The adults are similar to those of *M. hufelandi* and the eggs have a shell with sculpture in which a clear mesh cannot be seen as it can in *M. hufelandi* (Plate VI f).

M. hibiscus appears, to this author, to be one of the most misidentified species of tardigrades. Bertolani & Rebecchi (1993) stated that the type material was not available and the measurements reported by de Barros (1942) were inconclusive. However, while the original description of de Barros (1942) gives very few measurements in the text, the drawings are supplied with scale bars, so it should be possible to obtain fairly accurate measurements of such parameters as the stylet insertion point and the length of the ventral support each as a ratio of the buccal tube length (not usually given in the early literature). In Fig 41 of the original description, the stylets are inserted on the buccal tube at about 70% (71% in Australian specimens) whilst in *M. hufelandi* they are inserted at about 80%. The diameter of the buccal tube is also quite different (8-9% in the former species and 13% in the later). The habitus figure of de Barros (Fig 40) indicates an antero-ventral mouth (as

is present in the Australian specimens) while *M. hufelandi* has the mouth in an anterior position. The egg of *M. hibiscus*, at 57 µm diameter (62 µm in the Australian specimens), is smaller than that of *M. hufelandi* (66.5-90.8 µm). The suggestion of Kathman (1990) that these two species be synonymised should be rejected and it seems probable that the species was not present in the Canadian material examined by that author. The description of *M. hibiscus* from New Zealand gives the stylet insertion point as 85% of the buccal tube length suggesting an erroneous identification. Durante Pasa & Maucci (1979), reporting material from Scandinavia, described the buccal armature of *M. hibiscus* as identical to that of *M. hufelandi* also suggesting an erroneous identification. Characters of both the adult and the egg of *M. humilis* described by Binda & Pilato (2001) from Sri Lanka appear to be extremely similar to those of *M. hibiscus*.

3.3.2.1b *The harmsworthi group of species*

Of the 16 species included in this group by Ramazzotti & Maucci (1983), four were found in this study (*M. furciger*, *M. orcadensis*, *M. montanus* and *M. australis*). According to these authors, these species could only be differentiated by observing the eggs, all quite different from each other and from *M. harmsworthi*. The present study indicates that adults can also be differentiated from each other. *M. australis* is easily identified by the presence of a band, rather than a single row, of teeth in the posterior position in the oral cavity. It also has a buccal tube which is wider relative to the length of the buccal tube (20%) than in the other three species (14-16%). The other three species are very similar having rather narrow buccal tubes, short macroplacoid row lengths and very high accessory claws on the main branches of claws on the fourth pair of legs. *M. orcadensis* has the shortest macroplacoid row length (36-38% of the buccal tube length), it has no teeth in the anterior position of the oral cavity and the granulation around the claws is clear and strong. *M. furciger* has teeth on the lunules of the fourth pair of legs, in which it differs from *M.*

montanus which has smooth lunules. These two species are very similar in most other characters although the macroplicoid row length of *M. furciger* is longer (42-45%) than that of *M. montanus* (40%).

In this study, two species of *Macrobiotus* were found which had very similar characteristics of both the adults and the eggs to those of *M. harmsworthi* sensu Pilato *et al.*, (2000). Since their characteristics were different from the five described species in the *harmsworthi* group (in the strictest sense), they were assigned to new species – *M. saltus* and *M. woodyi* (Plate Xa-d). No specimens or eggs conforming to the new description of *M. harmsworthi* were found in the current study leading to the suspicion that previous citations of this species in Australia (Murray, 1910 and Pilato & D’Urso, 1976) refer to other species. In fact, Murray identified the species from an egg containing an embryo found at Mount Kosciusko. In the present study, the eggs of *Calcarobiotus capricorniensis* sp. n. were found at that site. These eggs (Plate Xe) bear a strong resemblance to those of *M. harmsworthi* and could be confused with that species particularly if only embryos were examined. Murray (1910) was aware of the problems involved in identifying species in the *harmsworthi* group stating “not to be identified with certainty from the adult alone or from the egg alone”. It is not possible to assess the findings of Pilato & D’Urso (1976) as they only say that “all specimens lack eyes and have the buccal armature typical of that species”. (Pilato *et al.*, 2000 used the presence of eye spots as a distinct character of *M. harmsworthi*). The absence of full details of specimens collected in faunistic studies, such as that of Pilato & D’Urso (1976) is unfortunately, typical of many such reports and is one of the reasons why it is still not possible to give a true biogeographical account of tardigrades at the present time.

3.3.2.1c *Questionable Macrobiotus species*

Three species of *Macrobiotus* (*M. echinatus* sp. n., *M. galorensis* sp. n. and *M. sp. 3*) exhibit claws that have very long branches that arise from a swollen common tract (Plate IXa to c). The secondary branch appears to emerge from the common tract at the same level as the primary branch as in *Calcarobiotus* rather than arising from the primary branch itself as it appears to do in species of *Macrobiotus*. Clearly, the claw has the same elements (a pedunculate basal unit, a common tract and two branches, the primary branch of which carries accessory claws) as in these two genera but they are arranged differently and may even function differently, e.g., the secondary branch appears to be flexibly joined to the common tract.

These three species also share a number of other characteristics which would to differentiate them from other species of *Macrobiotus*, i.e., they have an antero-ventral mouth with very short lamellae, a narrow buccal tube with significant thickening below the level of insertion of the stylet supports, the furcae of the stylets are larger than is usual for this genus and what remains of the stylets above the furcae shows that they have a base that is expanded into two lobes just above the furcae. The oral cavity of these species is very simple, lacking teeth and with very weak crests, more like that found in species of *Minibiotus* than *Macrobiotus*.

It was extremely difficult to determine the number of lamellae in these three species. In the largest specimens of *M. galorensis* sp. n. there appeared to be about 16 very short lamellae. If that is the case (it could most likely be verified by SEM) then the four species most probably belong to a new genus and are provisionally placed here in the genus *Macrobiotus* until further studies can be made.

3.3.2.1d *Aberrant claws in Macrobiotus species*

In this study, specimens of three species of *Macrobiotus* were found with a spur at the base of the primary branch of some claws (Plate IXe, f). These specimens occurred at very low frequencies in the populations in which they occur as follows –

1. *M. galorensis* sp. n. One specimen in 40 from Galore, NSW. (No specimens in eight examined from Coppins Crossing, Australian Capital Territory). The aberrant spur was present on the single specimen only on some claws – both claws on the left first leg, both internal claws on the second pair of legs, both claws on the left third leg and the internal claw only on the right third leg, the internal claw of the right fourth leg.
2. *M. guttus* sp. n. Two specimens in 21 examined from Gama, Victoria. (No specimens in 150 examined from six other sites). The first specimen had a spur only on the internal claw of the left first leg; the second specimen had a spur only on the internal claw of the right fourth leg.
3. *M. saxatilis* sp. n. One specimen in 23 from Lake George, NSW. (No specimens in 90 examined from six other sites). The specimen had a spur only on the internal claw of the left fourth leg.

The spurs on these specimens are very similar to those described by Pilato & Binda (1996) as occurring on the claws of the first three pairs of legs of the single specimen used to describe a new species – *Macrobiotus armatus* Pilato & Binda, 1996. The above observations on Australian species strongly militate against describing new species on the basis of characters present on a single specimen.

3.3.2.2 *The genus Calcarobiotus*

Eight new species of *Calcarobiotus* are described in this study. All of these species have either one or both of the claws on the fourth pair of legs different from the claws on the other three pairs of legs (Plate XIa-f). This fact places all of these species into the subgenus *Discrepunguis* Guidetti & Bertolani, 2001. Three of the new Australian species also have hooks on the base of the claws which, according to Guidetti & Bertolani (2001), are absent from species belonging to that subgenus. Species of the subgenus *Calcarobiotus* have claws similar in shape on all legs and may have spurs on the basal unit. The Australian species do not fit well into these subgenera.

A large number of specimens of a doubled-spurred species of *Calcarobiotus* (*C. australis* sp. n.) were identified in this study. The claws of the first three pairs of legs (Plate XIe) are essentially as described by Dastych (1993b) and Guidetti & Bertolani (2001b). However, the posterior claws on the fourth pair of legs (Plate XI f) of this species are the same as those described, by the latter authors, for *C. eugranulatus* and *C. polygonatus*, i.e., there is a small basal part and a long common tract joining the primary and secondary branches. A single specimen of *C. occultus* Dastych, 1993 (Paratype, slide labeled No. 11 from Natal Drakensberg Cathedral Peak Area, South Africa) was examined and the posterior claws on the fourth pair of legs have the primary and secondary branches joined over a long distance (Plate XIIe). This is contrary to the evaluation of this species by Guidetti & Bertolani (2001b). This indicates that a reevaluation of the claw structure of *C. occultus* is necessary. Claw structure can be difficult to evaluate on many slide-mounted specimens because of poor orientation. In the present study, a large number of specimens of six of the eight species were available for study. It was possible to observe claws at many different angles in many different preparations. The eight species found in Australia, regardless of the presence or absence of basal spurs, have either one or both claws on the fourth pair of legs

different from those on the first three pairs. These species do not fit well within the two subgenera (*Calcarobiotus* and *Discrepunguis*), again suggesting that a reevaluation is necessary.

In this study, specimens of both *Calcarobiotus* and *Macrobiotus* have been observed with the double arch (Plate Xb, d, f) in the base of the buccal tube as described by Guidetti & Bertolani (2001b). Many were also found without such an arch. The double arch was observed in specimens with a wide buccal tube and in which the pharyngeal apophyses were separated from the tube. This suggests that excessive pressure on the coverslip has occurred. At the top of the pharyngeal apophyses in these specimens there is a bar which seems to fit well into the arched spaces on the base of the tube. The appearance (or non-appearance) of these arches may be a function of the mountant and the mounting process rather than a distinct character of the animal itself. The taxonomic value of this character would, therefore, seem to be in doubt and cannot be used to separate *Calcarobiotus* from *Macrobiotus* species as suggested by Guidetti and Bertolani (2001b).

3.3.2.3 *The genus Haptobiotus gen. n.*

The diagnostic character for this new genus is the distinctive claws. Clearly these animals belong to the family Macrobiotidae, having claws that are symmetrical with respect to the median plane of the leg and a *Macrobiotus*-type buccopharyngeal apparatus.

The claws (Plate XII) differ from those of *Macrobiotus* spp. by having both primary and secondary branches arising from a small triangular base. Although the branches are joined over much of their length, the vertical suture that separates them is quite clear. The bases of the branches are swollen and each branch tapers rapidly into a strong curved tip. The accessory claws are strong and rise high above the primary branch. The whole claw

appears to form a single robust functional unit, where neither branch seems to be able to move independently.

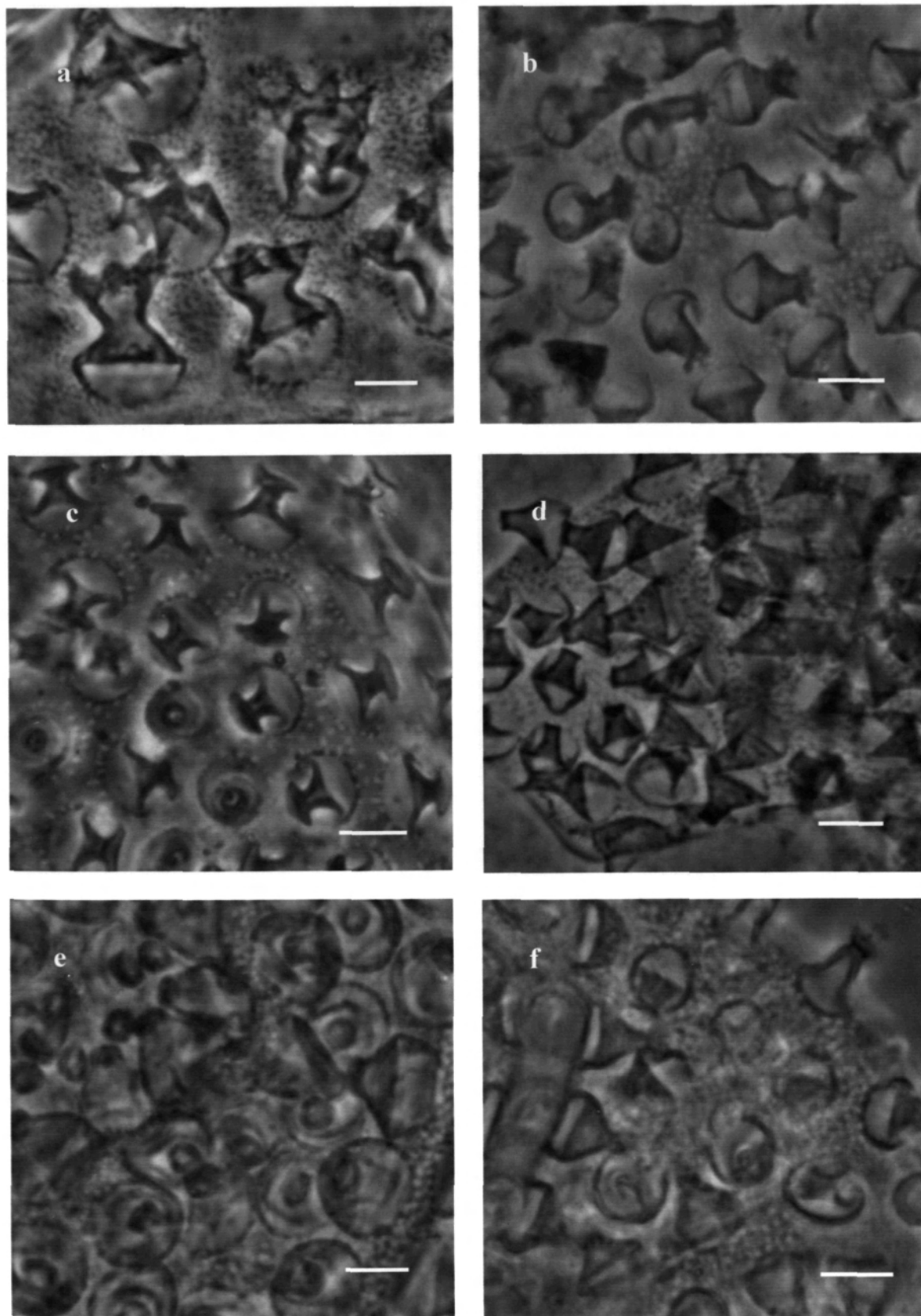


Plate V. Egg shell and processes of species of the *Macrobiotus hufelandi* group
 (a). *Macrobiotus albus* sp. n., (b). *M. caniensis* sp. n., (c). *M. clivus* sp. n.,
 (d). *M. guttus* sp. n., (e). *M. hesperius* sp. n., (f). *M. hibiscus* de Barros, 1942.
 Phase contrast. (Scale bars = 5 µm)

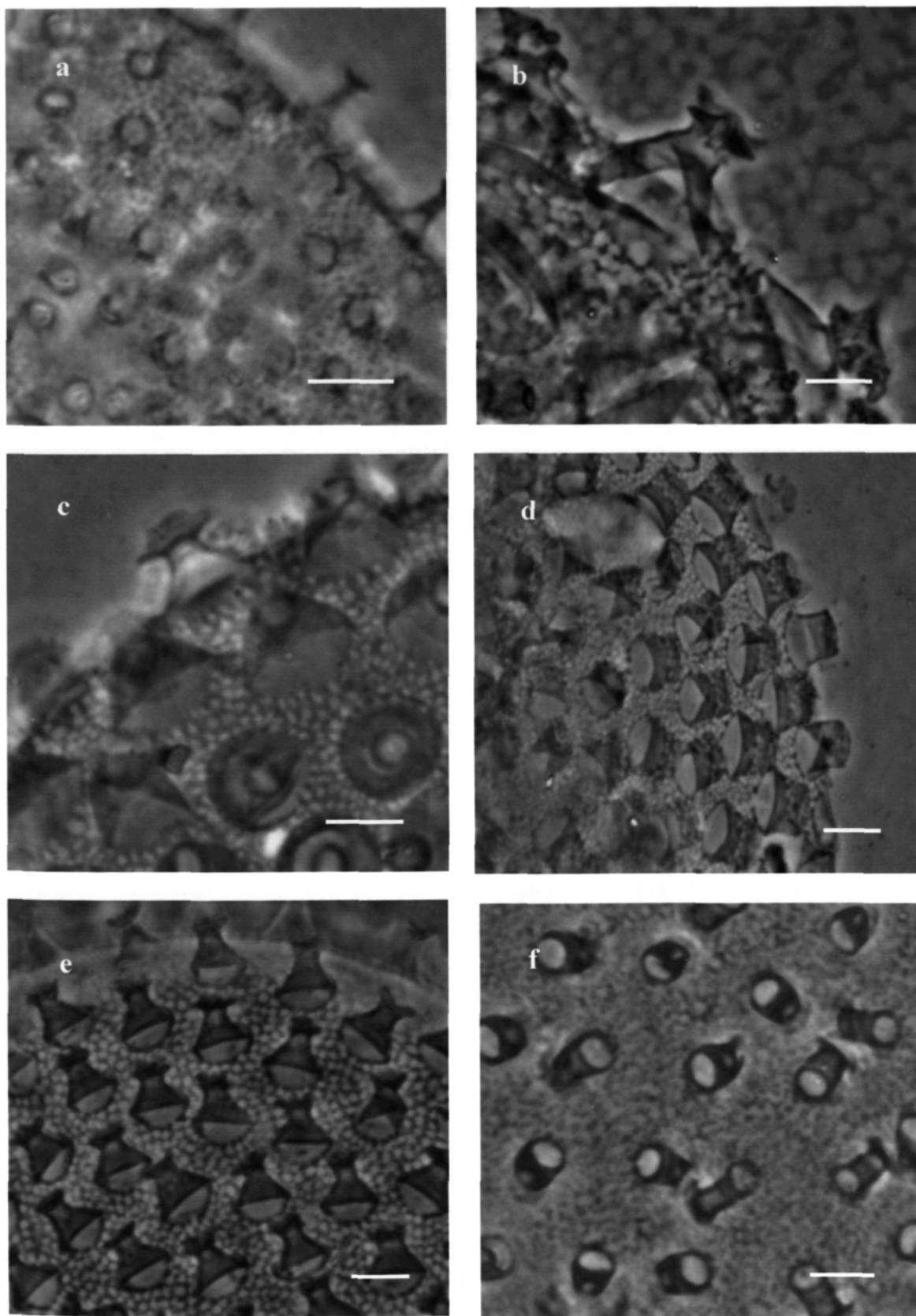


Plate VI. Egg shell and processes of species of the *Macrobiotus hufelandi* group
 (a). *M. microcalix* sp. n., (b). *M. purpureus* sp. n., (c). *M. rigatus* sp. n.,
 (d). *M. santoroi* Pilato & D'Urso, 1976, (e). *M. saxatilis* sp. n. (f). *M. torridus*
 sp. n. Phase contrast. (Scale bars = 5 µm)

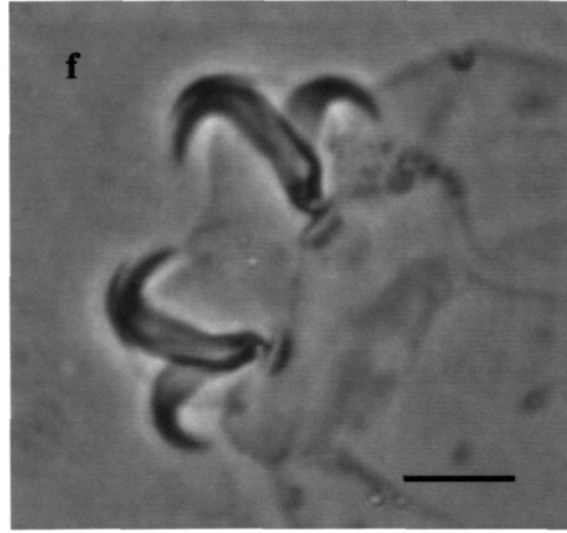
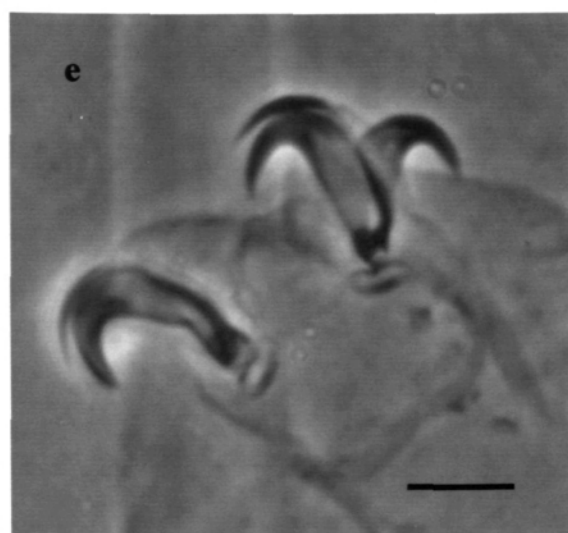
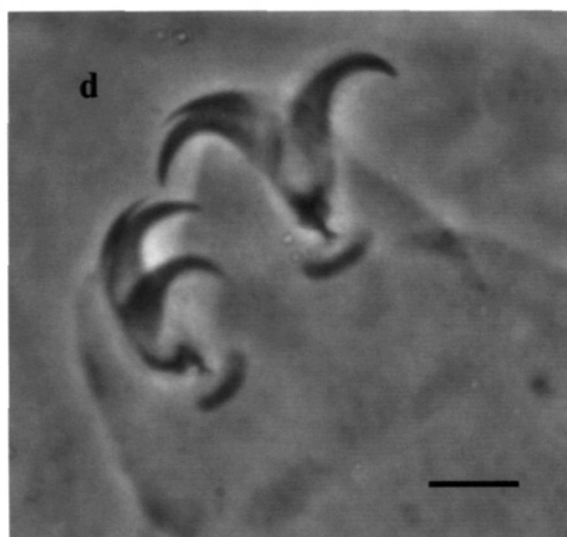
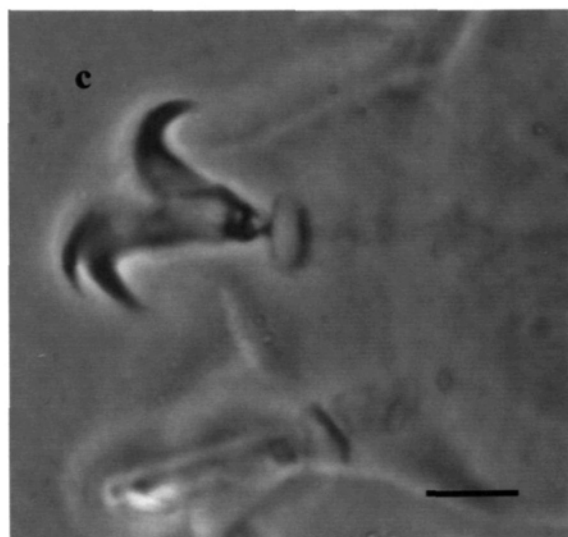
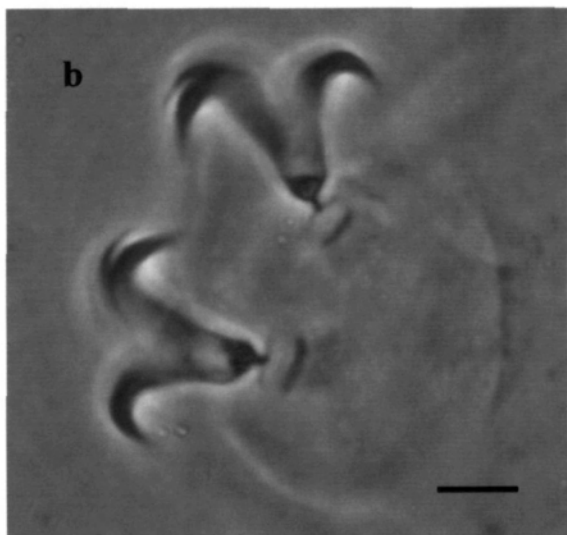
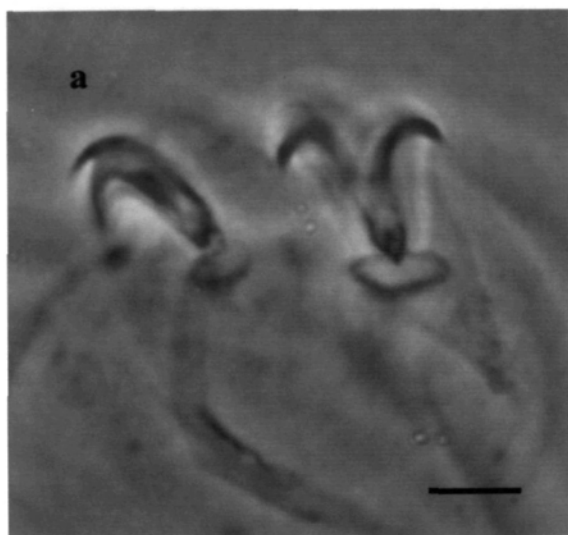


Plate VII. Claws of species of the *Macrobiotus hufelandi* group (a). *Macrobiotus albus* sp. n. , (b). *M. caniensis* sp. n., (c). *M. clivus* sp. n., (d). *M. guttus* sp. n., (e). *M. hesperius* sp. n., (f). *M. hibiscus* de Barros, 1942.
Phase contrast. (Scale bars = 5 μ m)

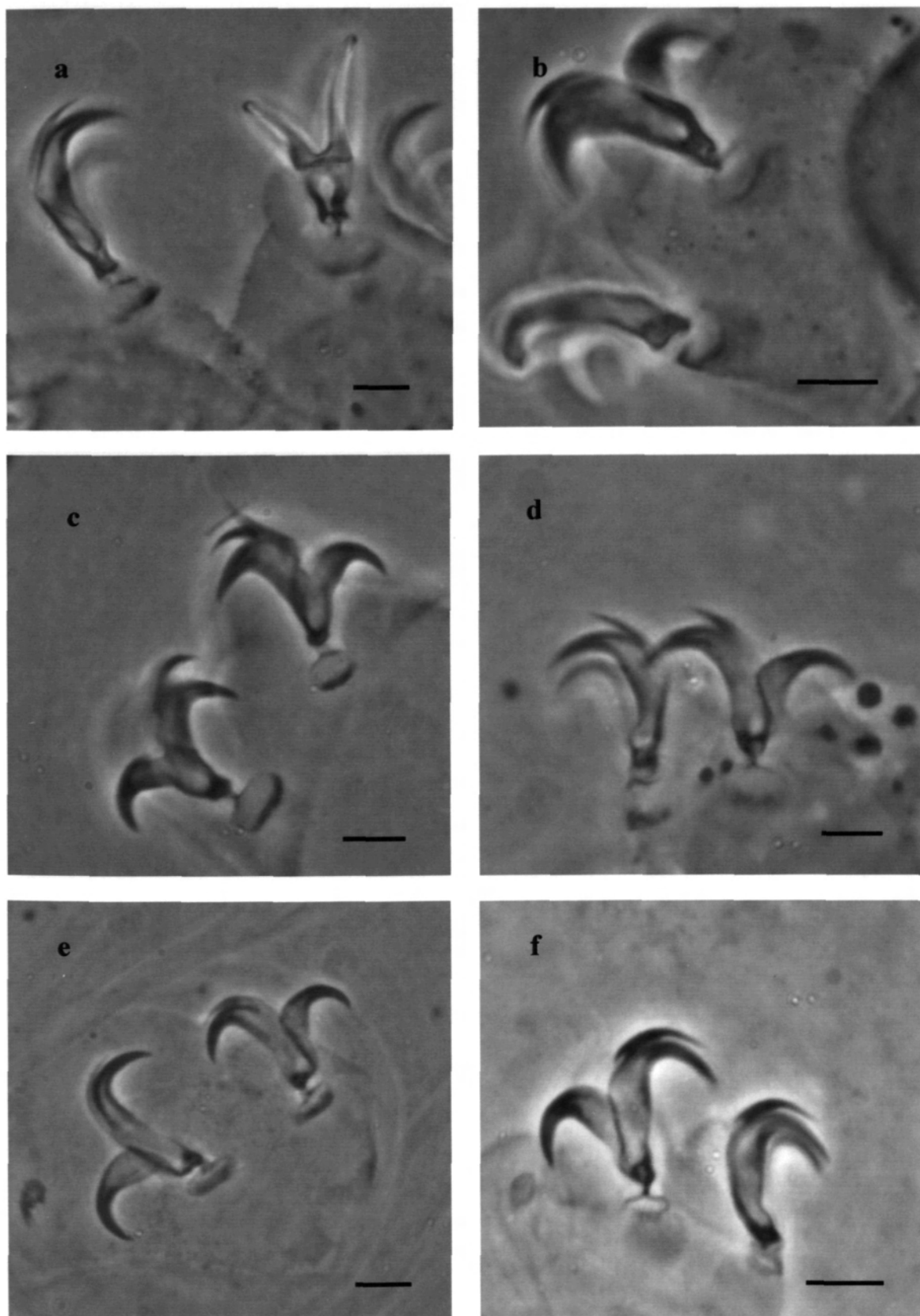


Plate VIII. Claws of species of the *Macrobiotus hufelandi* group (a). *M. microcalix* sp. n., (b). *M. purpureus* sp. n., (c). *M. rigatus* sp. n., (d). *M. santoroi* Pilato & D'Urso, 1976, (e). *M. saxatilis* sp. n., (f). *M. torridus* sp. n. Phase contrast. (Scale bars = 5 µm)

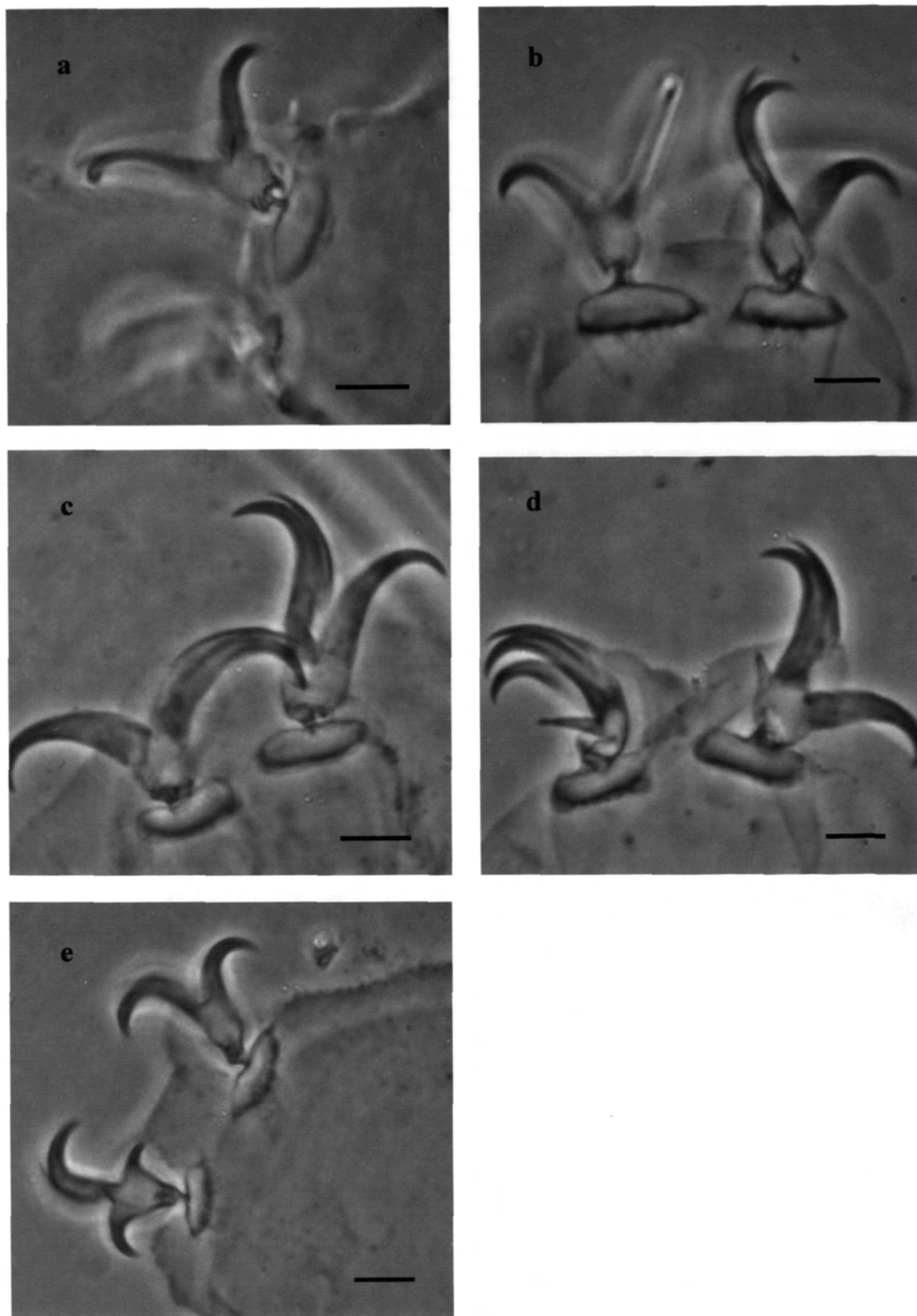


Plate IX. Claws of Macrobiotidae (a). *Macrobiotus echinatus* sp. n., (b). *M. galorensis* sp. n., (c). *Macrobiotus* sp. 3, (d). *M. galorensis* with aberrant spurs on both claws of right third leg, (e). *M. saxatilis* with aberrant spur on one claw of fourth leg. Phase contrast. (Scale bars = 5 μ m)

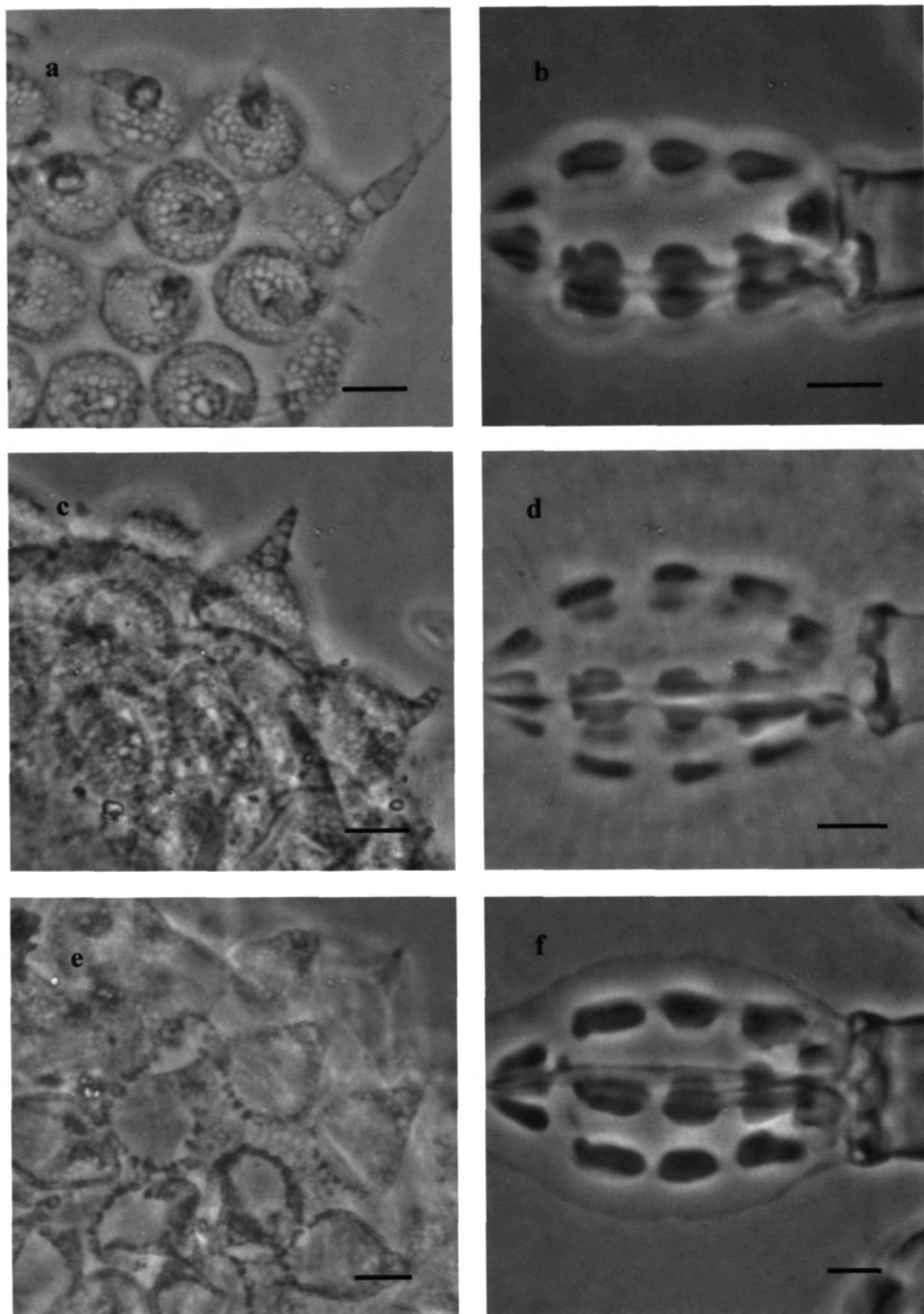


Plate X. Eggs and buccal tube double arches of some species of Macrobiotidae
Macrobiotus saltus sp. n. (a). egg, (b). arches and placoids; *M. woodyi* sp. n.
 (c). egg, (d). arches and placoids; *Calcarobiotus capricorniensis* sp. n.
 (e). egg; *Calcarobiotus maculatus* sp. n. (f). arches and placoids. Phase
 contrast. (Scale bars = 5 μ m)

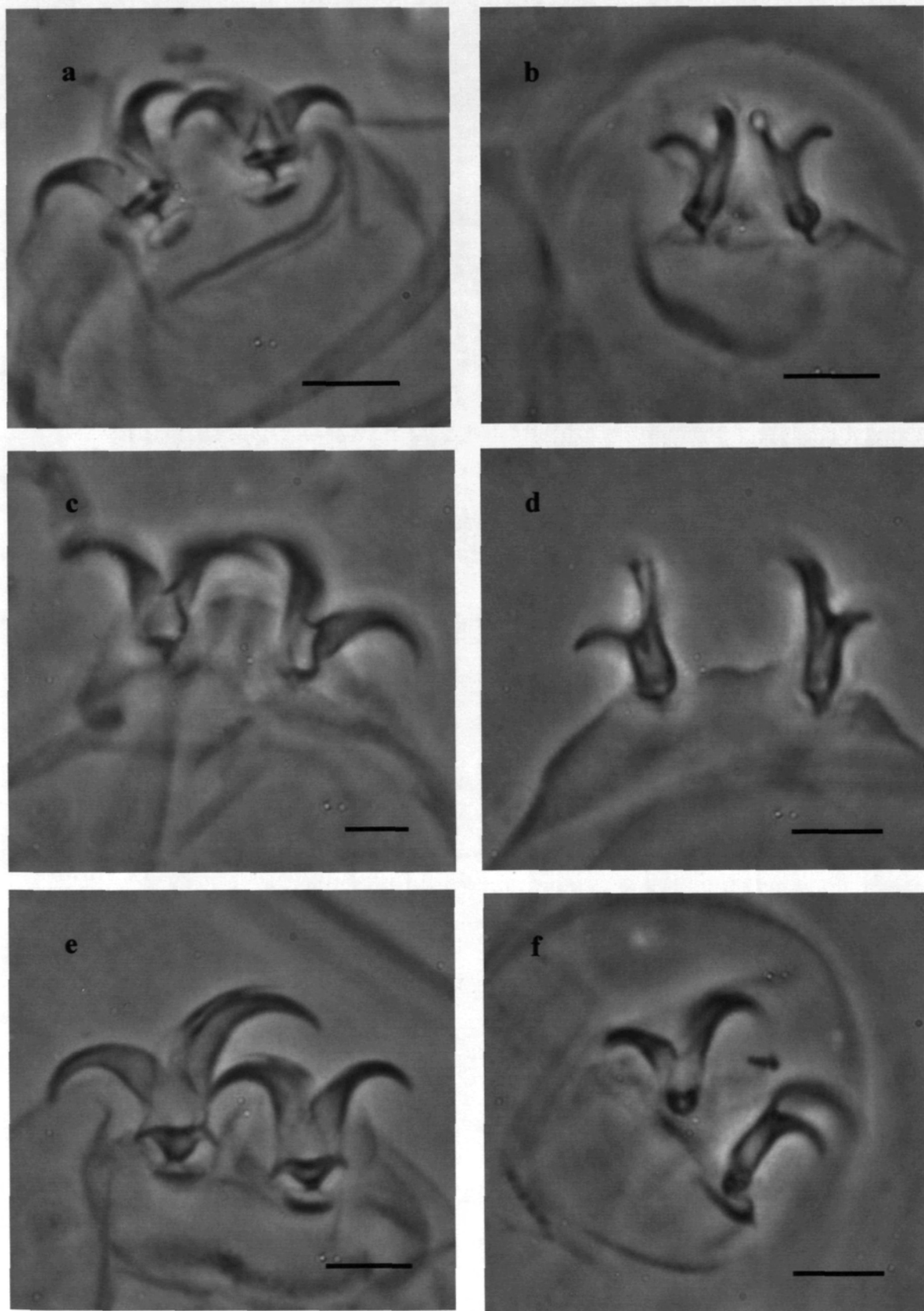


Plate XI. Claws of *Calcarobiotus* species *C. reticulatus* sp. n., (a). first leg, (b). fourth leg; *C. adunatus* sp. n., (c). first leg, (d). fourth leg; *C. australis* sp. n., (e). second leg, (f). fourth leg. Phase contrast. (Scale bars = 5 μ m)

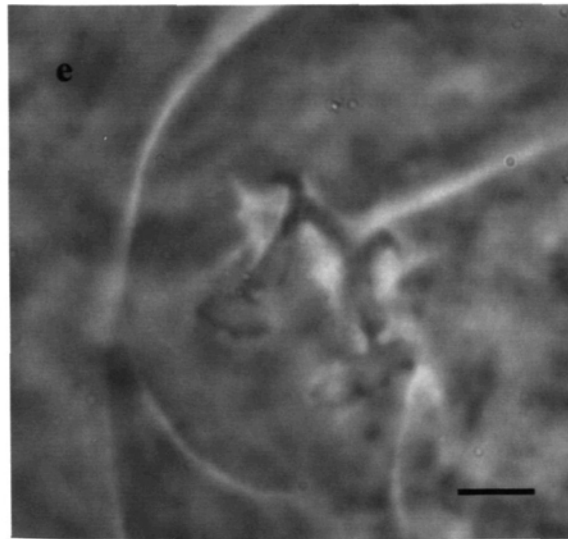
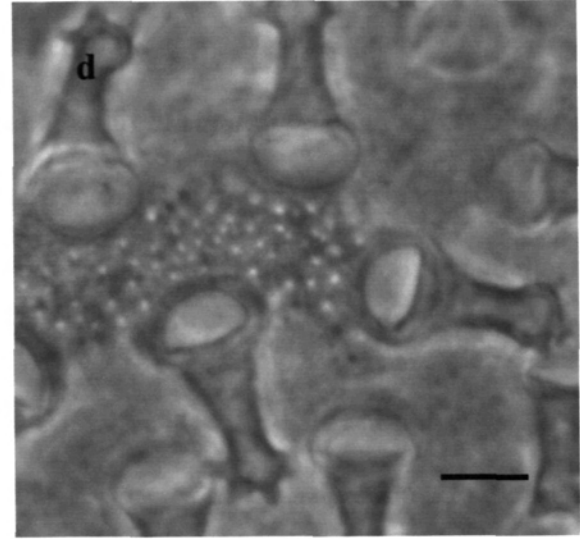
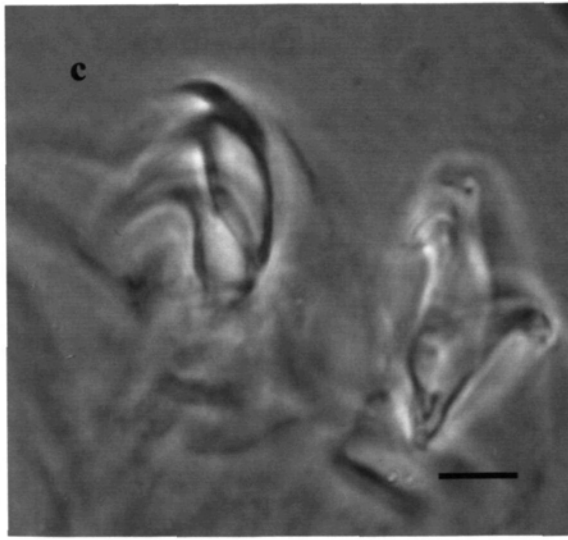
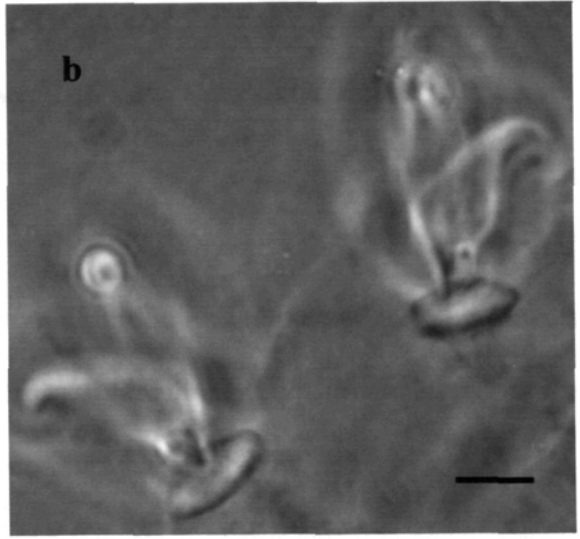
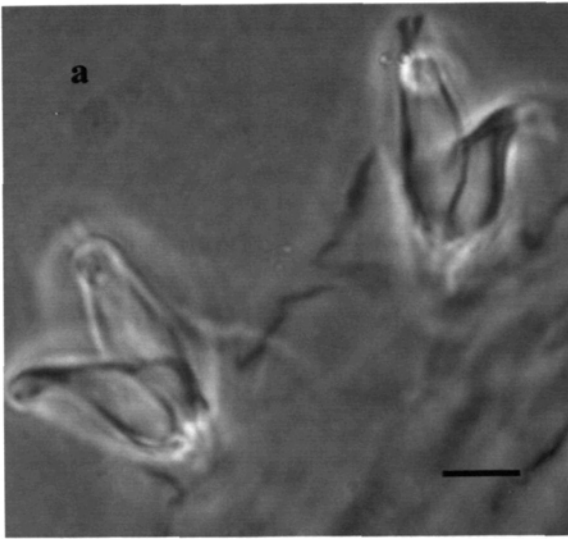


Plate XII. *Haptobiotus turritus* gen. n. sp. n.; (a-c). claws of fourth pair of legs, (d). egg processes. *Calcarobiotus occultus* Dastych, 1993. (e). claws of fourth pair of legs. Phase contrast. (Scale bars = 5 μ m)

3.4 A MULTIVARIATE MORPHOMETRIC ANALYSIS OF AUSTRALIAN SPECIMENS IN THE *DIPHASCON* (*DIPHASCON*) *PINGUE* GROUP

3.4.1 Introduction

Diphascon Plate, 1889 was one of the first genera of tardigrades to be recognised, probably because its members are widespread and numerous. In the family Hypsibiidae, it was separated from other genera by having the bucco-pharyngeal tube divided into a rigid anterior part (the buccal tube or mouth tube) and a flexible posterior part (the pharyngeal tube). In revising the genus, Pilato (1987) separated two genera *Mesocrista* and *Platicrista* (both with a rigid and flexible part in the buccal tube) from *Diphascon* on the basis of differences in the type of apophyses for the insertion of stylet muscles and on the shape of the stylet furcae. In *Diphascon*, the apophyses are shaped like “semilunar hooks” and the furcae have postero-lateral processes that are thickened at their apices. Pilato further divided *Diphascon* by the presence or absence of a drop-shaped structure at the junction of the buccal and the pharyngeal tubes. He placed those species without the drop into the subgenus *Adropion* and those with the drop into the subgenus *Diphascon*. One problem associated with this classification is that many of the older descriptions of species of *Diphascon* do not mention this character. Guidi & Rebecchi (1996) noted a greater similarity between the sperm of *Diphascon* (*Adropion*) and *Platicrista* than between *D. (Adropion)* and *D. (Diphascon)* suggesting that further inquiries may be needed into the relationships of these taxa.

Diphascon pingue Marcus, 1936 was quite well defined by its author, who provided a detailed illustration and measurements of placoids and claws. He did not, however, mention the drop-shaped structure which is now known to be present in this species (Pilato, 1987). The species has been reported from Europe, Asia, North and South

America, the Atlantic island of South Georgia and Antarctica (McInnes, 1994). Pilato & Binda (1997/1998) compared *D. pingue*, *D. alpinum* Murray, 1906 and *D. chilense* Plate, 1889 and discussed the confusion in the literature over their identification but reached the conclusion that the number of placoids in the pharynx is intraspecifically constant. Pilato & Binda (1997/1998) recognised that members of the subgenus *Diphascon*, with three rod-shaped macroplacoids, a microplacoid and a septulum, constituted a homogeneous group (the *D. pingue* group which, at that time, included only *D. pingue* and *D. pinguiforme* Pilato & Binda, 1997/1998). *D. pinguiforme* differed from *D. pingue* by having “clearly” longer placoids and “claws slightly more slender”. However, these authors have only provided measurements for the holotype (Pilato & Binda, 1997/1998) and for one additional specimen (Pilato & Binda, 1998).

Dastych (1984) reported that specimens of *D. pingue* from Antarctica could be divided into two populations, varieties “A” and “B”. Variety “A” had a short row of macroplacoids, longer and narrower buccal tube and “slightly less slender claws with slightly bigger accessory spines” than variety “B”. Summary data for 15 specimens of variety “A” and 26 specimens of variety “B” were provided. Pilato & Binda (1999) described three new species within the *pingue* group from Antarctica and provided a key to seven species (*D. pingue* and *D. pinguiforme*; *D. australianum* and *D. claxtonae* from Australia; *D. polare*, *D. dastychi* and *D. victoriae* from Antarctica). They assigned variety “A” of Dastych (1984) to *D. polare* and variety “B” to *D. dastychi*. The key relied heavily on macroplacoid row lengths to differentiate species.

The descriptions of the two Australian species, *D. (D.) australianum* and *D. (D.) claxtonae*, were based on five specimens from Blackheath and four specimens from Douglas Park, NSW, Australia (collected by Claxton) (Pilato & Binda, 1998). Examination

of approximately 200 specimens from Australia that conformed to the description of species within the *pingue* group revealed that the most obvious difference to be seen among populations was in the macroplacoid row length. However, in many cases it was impossible to identify specimens using the key provided by Pilato & Binda (1999). Consequently, the following study was undertaken to clarify the identity of the Australian fauna of the *pingue* group.

3.4.2 Materials and Methods.

Specimens belonging to the *pingue* group were collected from many sites along the east coast of Australia. For a number of sites, only one or two specimens were available, because few specimens were present and/or because few specimens were appropriately mounted for morphological analysis. However, four or more specimens from a single cryptogam sample were available for analysis from 13 sites (78 specimens). Included in this analysis were 14 specimens (population 1) from Blackheath (including the type material for *D. australianum*, measured before it was sent on loan) and nine specimens (population 2) from Douglas Park (including the type material for *D. claxtonae*, measured before it was sent on loan). Details of the 13 populations are given in Table 3.4.1.

For these 78 specimens, the following characters were measured (Table 3.4.2): body length (BL) (measured from the mouth to the end of the body, not including the fourth pair of legs), buccal tube length (BTL), buccal tube width (BTW), stylet support insertion length (SIL), pharyngeal tube length (PTL), placoid row length (PRL), macroplacoid row length (MPRL), lengths of macroplacoids 1, 2 and 3 (m1, m2 and m3), septulum length (se), length of posterior claw on fourth pair of legs (IVpo) and length of anterior claw on fourth pair of legs (IVan). Measurements of claws on the first three pairs of legs of a large number of specimens indicated that there was a distinct and consistent increase in size

from first to fourth. Therefore, only the lengths of the claws on the fourth pair of legs were included in the analysis. Pharynx length and width were measured where possible but this structure fades in Hoyer's medium and in many specimens, its dimensions were not clear. Consequently, these characters were not used in this study.

The *ptd* ratio (Pilato & Binda, 1997/1998) is defined as the ratio, expressed as a percentage, of the length of a structure to the length of the buccal tube from the anterior margin of the stylet sheaths to the posterior end of the drop-shaped thickening. *Ptd* ratios were calculated for buccal tube width, stylet support insertion length, placoid row length, macroplacoid row length, length of each of the macroplacoids, septulum and lengths of posterior and anterior claws on fourth pair of legs.

Statistical analyses, including Principal component analysis and Cluster analysis (standardised with complete linkage and using the Squared Euclidean method), were performed using the statistical package Minitab Version 13.

3.4.3 Results

3.4.3.1 *Macroplacoid row length ptd*

Both placoid (PRL) and macroplacoid (MPRL) row lengths and their *ptd* ratios have been reported for other species of *Diphascon* (Pilato & Binda, 1998; 1999). However, a regression plot of MPRL against PRL of the full data set in this study (Fig. 3.4.1) indicated an R^2 of 98%, so PRL *ptd* ratios were considered to be redundant and were not used in the following multivariate analyses.

Means, standard deviations and ranges for all structures and for their *ptd* ratios were calculated for each population. There were no obvious differences other than the MPRL

ptd ratios. When the mean MPRL *ptd* ratio for the 13 populations were plotted (Fig. 3.4.2), three subdivisions could be discerned -

Subdivision 1: Populations 7, 8, 9, 10, 11, 12 and 13 - with MPRL *ptd* <50%, according to Pilato & Binda (1997/1998) should be *D. pingue*.

Subdivision 2: Populations 2, 3, 4 and 5 - with MPRL *ptd* >50% <65%, should be *D. pinguiforme* or *D. claxtonae*.

Subdivision 3: Populations 1 and 6 - with MPRL *ptd* >70%, should be *D. australianum*.

MPRL *ptd* values for all 78 specimens were plotted (Fig. 3.4.3). Half of the specimens in population 1 had a MPRL *ptd* which placed them with Subdivision 2. Some specimens from populations 7, 9 and 11 also appeared in Subdivision 2 rather than Subdivision 3.

Several possibilities present themselves:

1. Some populations contain a mixture of species, eg., population 1 consists of specimens of *D. australianum* and *D. claxtonae* or *D. pinguiforme*
2. The populations consist of a single species but MPRL *ptd* is not a good indicator of species amongst these specimens
3. There is only one or perhaps two species amongst these specimens

In order to clarify this situation, that is, to look at the overall variation (not just the variation in the MPRL) amongst populations and amongst individuals, multivariate analyses were performed.

3.4.3.2 *Principal component analysis*

3.4.3.2a *On populations*

Principal component analysis (PCA) was carried out on the mean lengths of structures from the 13 populations (12 variables) (Fig. 3.4.4) and on the *ptd* ratios for these structures

(10 variables) (Fig 3.4.5). In both cases, two populations (Subgroup 3) clearly separated from the rest. The other populations formed 2 subgroups along the first principal axis but they contained different populations in each case (five populations in Subgroup 1 when the structure lengths were used and 3 populations in the same subgroup when *ptd* ratios of these lengths were used). The major contributors to variation along the first principal axis were the lengths of the macroplacoids, together and individually (MPRL, m1, m2 and m3) (Tables 3.4.3 and 3.4.4).

3.4.3.2b On individuals

PCA was also carried out on the lengths of structures of the 78 specimens (12 variables) (Fig. 3.4.6) and on *ptd* ratios of these structures for the 78 specimens (10 variables) (Fig. 3.4.7). In this analysis also, the major contributors to variation along the first principal axis were the lengths of the macroplacoids (Tables 3.4.5 and 3.4.6) but in both cases no distinct subgroups were formed.

3.4.3.3 Cluster analysis

Cluster analyses were performed on the same groups of data, first on the means of the 13 populations and then on the individual data for the 78 specimens.

3.4.3.3a On populations

Populations 1 and 6 clustered together (Subgroup 3) when the mean structure lengths (Fig. 3.4.8) and means of *ptd* ratios (Fig. 3.4.9) for the populations were used. In each case, populations 10, 12 and 13 also clustered together (Subgroup 1). However, the other clusters formed by the remaining populations do not support the formation of a single subgroup and suggest different combinations of populations in each case.

3.4.3.3b *On individuals*

Cluster analysis using the structure lengths of the 78 specimens (Fig. 3.4.10) produced clusters that did not support the subgroups found when MPRLs for individuals were plotted (Fig. 3.4.3). However, the dendrogram produced by analysing the *ptd* ratios for specimens (Fig. 3.4.11) produced three subgroups. The analysis retained all members of populations 10, 12 and 13 together in one subgroup (Subgroup 1 – specimens with the shortest macroplacoid row and probably equivalent to *D. pingue*). All members of populations 2, 3, 4 and 5 clustered in another subgroup (Subgroup 2 – specimens with intermediate length macroplacoid row, probably equivalent to *D. claxtonae* since they included all the type material for that species). Members of populations 1, 7, 8, 9 and 11 were split between subgroups. All members of population 6 were grouped with 10 of the 14 members of population 1 (Subgroup 3 – specimens with long macroplacoid row length and probably equivalent to *D. australianum* since they included all of the type material for that species).

3.4.3.4 *Analysis of subgroups*

The final subgroups (which replaced the subdivisions mentioned earlier) included all populations that the analyses suggested consist of only one species. Ten specimens from population 1 were included in Subgroup 3 because of the low numbers in that subgroup.

They are:

Subgroup 1 “*D. pingue*”: Populations 10, 12 and 13

Subgroup 2 “*D. claxtonae*”: Populations 2, 3, 4 and 5

Subgroup 3 “*D. australianum*”: Population 1 (10 specimens) and 6

These three subgroups were then treated as if they were separate entities (species?) and means, standard deviations and ranges for lengths and for *ptd* ratios of all structures were

obtained. A summary of the maximum and minimum dimensions of the structure lengths and their *ptd* ratios is presented in Table 3.4.7 together with ranges given by Pilato & Binda (1998) for apparently equivalent species.

3.4.3.5 *Regressions of structure lengths against body length*

Regression plots of structure lengths against body length were examined for any differences among groups. Very similar rates of increase in size of all structures was observed in the three groups except for macroplacoid row length of Subgroup 3 specimens which increased in length at a much greater rate than occurred in Subgroups 1 and 2 (Fig 3.4.12a, b and c). The macroplacoid row length as a percentage of body length lay between 6.2% and 7.5% for Subgroup 3 specimens (including all 14 specimens from population 1), between 4.4% and 5.4% for Subgroup 2 and between 3.5 % and 4.5% for Subgroup 1.

3.6.3.6 *Identification of single specimens*

Specimens belonging to the *pingue* group not included in this analysis (including those of populations 7, 8, 9 and 11) were examined using criteria established for the three subgroups (or species) in Table 3.4.7. Many specimens were impossible to place because of the overlap in the ranges of structure lengths among groups. The only definite character that could be used to separate specimens into either Subgroup 1 or Subgroups 2 and 3, was the macroplacoid row length to body length ratio, that is, those with a ratio of greater than 6.2% or those with a ratio of less than 5.4%.

3.4.4 Discussion

In taxonomic studies where there are obvious qualitative or quantitative differences, species identification can be relatively simple, but in situations, such as the one presented here, where differences are subtle, methods other than direct observation and measurement

may be necessary. In the case of the *pingue* group, Pilato & Binda (1997/1998, 1998) described seven species, only a few of which have clearly defined characters, eg., *D. polare* has a different drop-shaped thickening and *D. dastychi* has much longer claws than other species in the group. *D. victoriae* is difficult to assess as the authors use data from only three specimens. It appears to be very similar to *D. pinguiforme* but, as specimens have not been examined by this author, it was not considered in this study. Four species (*D. pingue*, *D. claxtonae*, *D. pinguiforme* and *D. australianum*) are extremely similar, varying only in lengths of the placoids and some subjective characters. Simple comparison of measurements of specimens with data supplied in the original descriptions produced no satisfactory identifications. Taxonomic research at the species level consists largely in the comparison of populations, or, more correctly, the comparison of samples from different populations (Mayr & Ashlock, 1991). The degree of difference among populations can only be ascertained with certainty when the amount of variation within the population has been determined. Unfortunately, in the case of many of the new species within the *pingue* group (*D. pinguiforme*, *D. claxtonae* and *D. australianum*), the amount of variation is very poorly estimated because of the low numbers of specimens used in the initial descriptions of these species.

The analyses presented here represent an attempt to more clearly define the limits of variation of the apparent subgroups within the Australian specimens belonging to the *pingue* group. Multivariate analyses have been used before in the analysis of populations of other genera of tardigrades (Bertolani & Rebecchi, 1993, Biserov, 1986, 1990b) but members of the genus *Diphascon* have not previously been analysed in this way.

The subgroups appear, at first glance, to be consistent with some of the currently described species within the group (possibly *D. pingue*, *D. claxtonae*, *D. pinguiforme* or *D.*

australianum). The presence of subgroups among populations was supported by all analyses performed here (plot of macroplacoid *ptd*, PCA and Cluster analysis). The major source of variation among subgroups was due to differences in the lengths of the macroplacoids.

Analysis of individuals, however, revealed that, at least for some populations, allocation of all specimens within a population to a single subgroup was not possible. When the questionable populations were removed from the analysis, it was reasonable to assume that the remaining populations which grouped together should display some clearly defined characters. In reality, however, the final subgroups demonstrated significant overlap in the ranges of values for all structures measured. In the absence of any defining qualitative characters, clearly defined quantitative characters were essential but not available. In particular, subgroups 1 and 2 of the Australian material were so similar that the observed differences would seem, to this author, to be more likely due to the presence of unisexual and bisexual strains of the same species or are even the result of some environmental factor rather than to the presence of separate species. Subgroup 2 contained the type specimens of *D. claxtonae*. Pilato & Binda (1998) described *D. claxtonae* as differing from *D. pingue* by having a slightly shorter buccal tube (untrue, Table 3.4.7); stylet supports inserted on buccal tube in more caudal position (untrue, Table 3.4.7); the second macroplacoid shorter than the first (untrue, in the type population (2) of 8 specimens the statement is true for only a single specimen, Table 3.4.2)); shorter septulum (untrue, Table 3.4.7); claws more slender (very subjective, not noted by this author for the type population for Subgroup 2 specimens). These considerations strongly suggest that *D. claxtonae* should be synonymised with *D. pingue*.

The use of ratios of structures to body length (introduced by Thulin, 1928) has fallen into disuse in favour of the *pt* ratio (Pilato, 1981) and *ptd* ratio Pilato & Binda (1997/1998). This is because changes in body length may occur when the specimens are placed in mounting medium and also body length is often altered by coverslip pressure. (An average increase in body length of 2.3% occurs in Hoyers Medium – see Chapter 2. Materials and Methods). In specimens of *Diphascon*, the deformation appears negligible (possibly because the specimens are smaller). In fact, the only character found that clearly separated Subgroup 3 specimens from specimens in other subgroups was the ratio of MPRL to body length (expressed as a percentage).

Because of the clear difference in MPRL to body length ratio and difference in the rate of increase in length of the macroplacoids of subgroup 3 from the other two subgroups, subgroup 3 was accepted as being a distinct species – *D. australianum*. Minimum and maximum dimensions of structures of *D. australianum* were originally given for only three specimens (Pilato & Binda, 1998), but the data provided here indicate a much greater range of values for all of these structures for this species. If these data are correct, then they also encompass the two specimens described by Pilato and Binda (1997/98) as *D. pinguiforme*. Since that species has precedence, *D. australianum* should be synonymised with *D. pinguiforme*.

The problems that have arisen in this study are not new to the study of taxonomy. The need for examination of populations rather than one, or a few, specimens is particularly important in the analysis of small animals where the impact of measurement error on small structures is great. The largest of the specimens examined measured 260 µm, with most being between 180 and 200 µm in length. The structures used for identification are correspondingly small – buccal tubes are around 20 µm long and claws 5-10 µm long. In

such cases, measurement error becomes a significant factor in the analysis. In the present study, it was estimated that measurement error was about 0.5 μm (see Chapter 2. Materials and Methods). Pilato (1981) stated that his error in measurement was “of the order of a tenth of a micron”. Differences in error measurement for different workers may become significant when one deals with such small organisms. A good example of this is shown in Table 3.4.8 which compares measurements of the holotypes of *D. australianum* and *D. claxtonae* provided by Pilato & Binda (1998) and by Claxton (this study). There are differences of 0.4 and 0.3 μm for *D. australianum* and 0.7 and 0.6 μm for *D. claxtonae* in the lengths obtained for the buccal tube and the stylet insertion lengths. This translates into differences of about 2% and 1.5% in the *ptd* ratios for that structure. Their measurements convinced Pilato & Binda that the differences were significant enough to erect two species. Measurements obtained in this study, however, were not considered to demonstrate a significant difference.

The difference in size of the first two macroplacoids was of major importance to Pilato & Binda (1998) who used this as a defining characteristic for both *D. claxtonae* and *D. australianum*. They were said to differ from others in the *pingue* group by having the second macroplacoid slightly longer than the first. Pilato & Binda (1998) measured the second macroplacoids of both the holotypes as being smaller than the first. Claxton (this study) measured them as the same length as the first (Table 3.4.8) and the difference is clearly due to measurement error inherent in microscopic work at high magnification. In addition, only two of the 14 specimens of population 1 (type population for *D. australianum*) and one of the eight specimens in population 2 (type population for *D. claxtonae*) had the first macroplacoid longer than the second. “Second macroplacoid shorter than first” cannot be used as a definitive character for these species.

In the light of the above discussion, it has been decided that the most parsimonious solution to the allocation of the Australian material is to accept two species, *D. pingue* and *D. pinguiforme*, since there is a distinct separation between those specimens with MPRL to body length percent ratio of less than 5.5 for the former and greater than 6 for the latter. All sites in which *D. pinguiforme* specimens were found were at high elevation or in rainforest or moist habitats. Other qualitative differences such as “slightly shorter claws” and “slightly shorter septulum” are impossible to evaluate effectively and it is the opinion of this author that *D. claxtonae* should be synonymised with *D. pingue* and *D. australianum* with *D. pinguiforme*.

Figure 3.4.1 **Regression plot of macroplacoid row length (MPRL) against placoid row length (PRL) for 78 specimens in the *pingue* group**

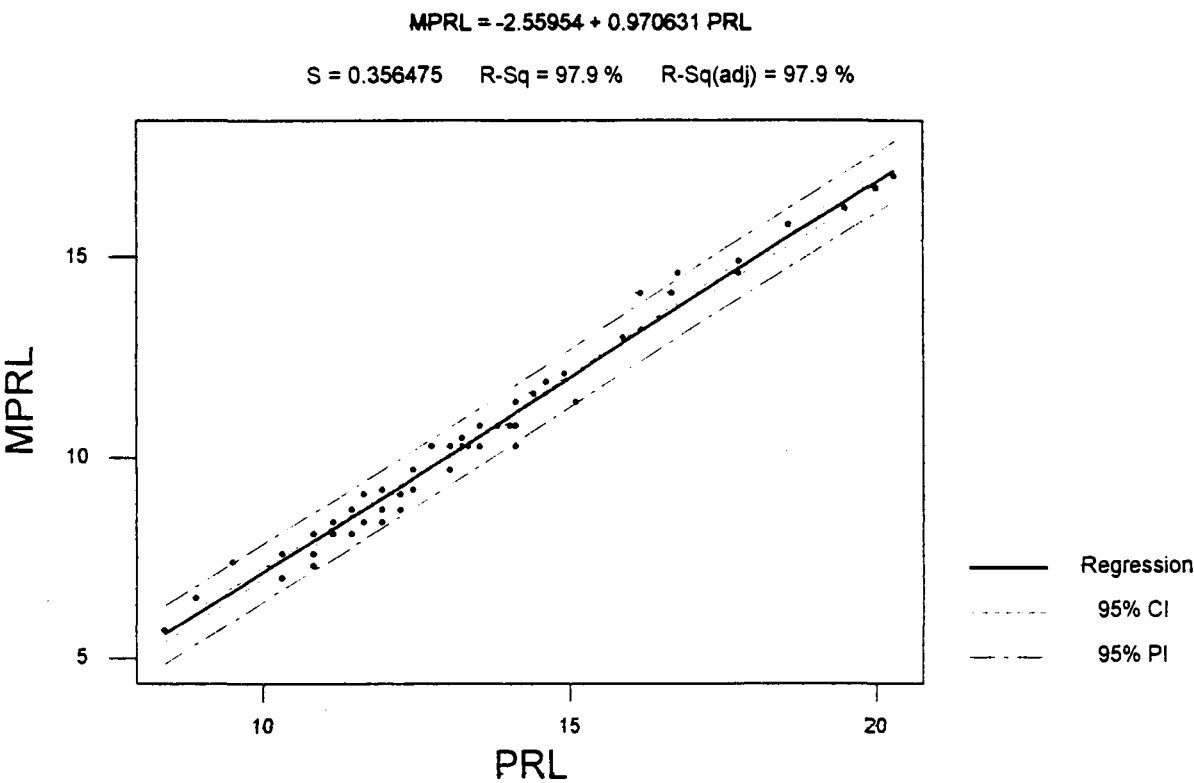


Figure 3.4.2 Plot of mean macroplacoid row length (MPRL) *ptd* ratios for 13 populations of the *pingue* group

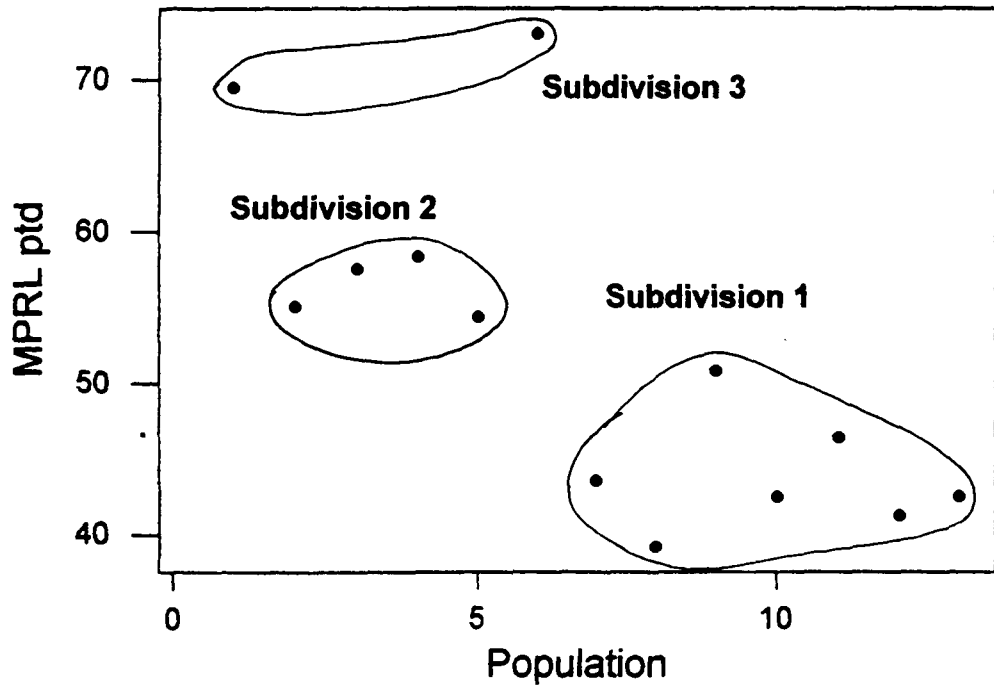


Figure 3.4.3 Plot of macroplacoid row length (MPRL) *ptd* ratios for 78 specimens in 13 populations of the *pingue* group

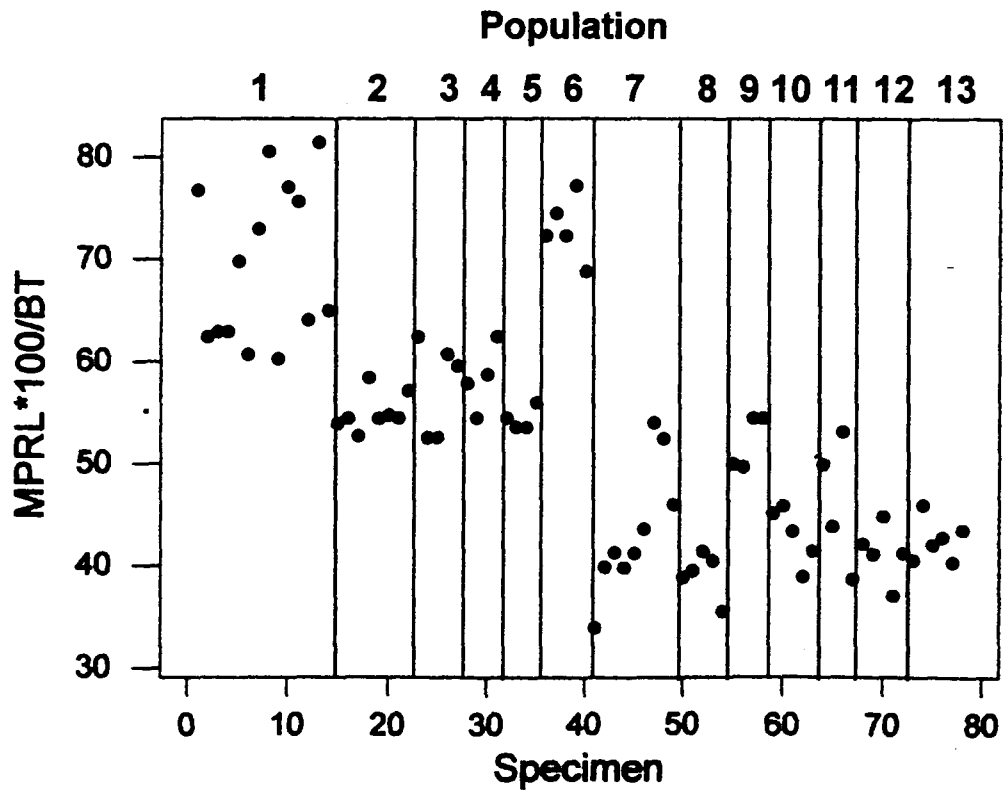


Figure 3.4.4 Principal component analysis score plot of 12 variables (mean lengths of structures) of 13 populations of the *pingue* group

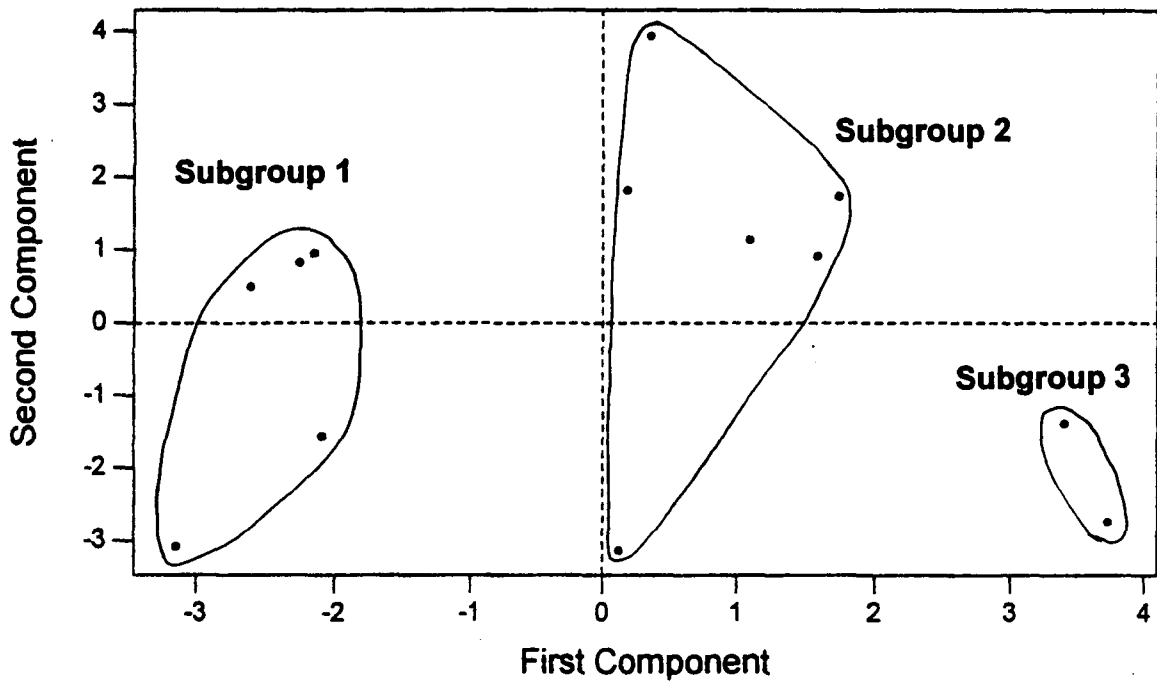


Figure 3.4.5 Principal component analysis score plot of 10 variables (mean *ptd* ratios of structures) of 13 populations of the *pingue* group

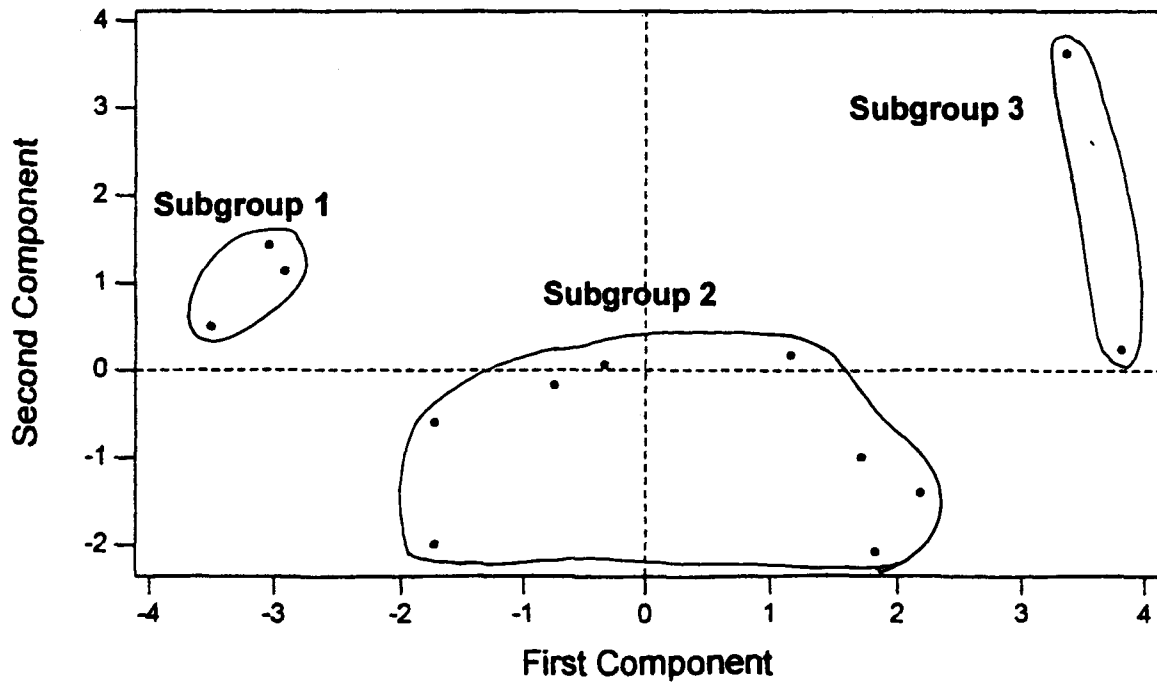


Figure 3.4.6 Principal component analysis score plot of 12 variables (lengths of structures) of 78 specimens of the *pingue* group

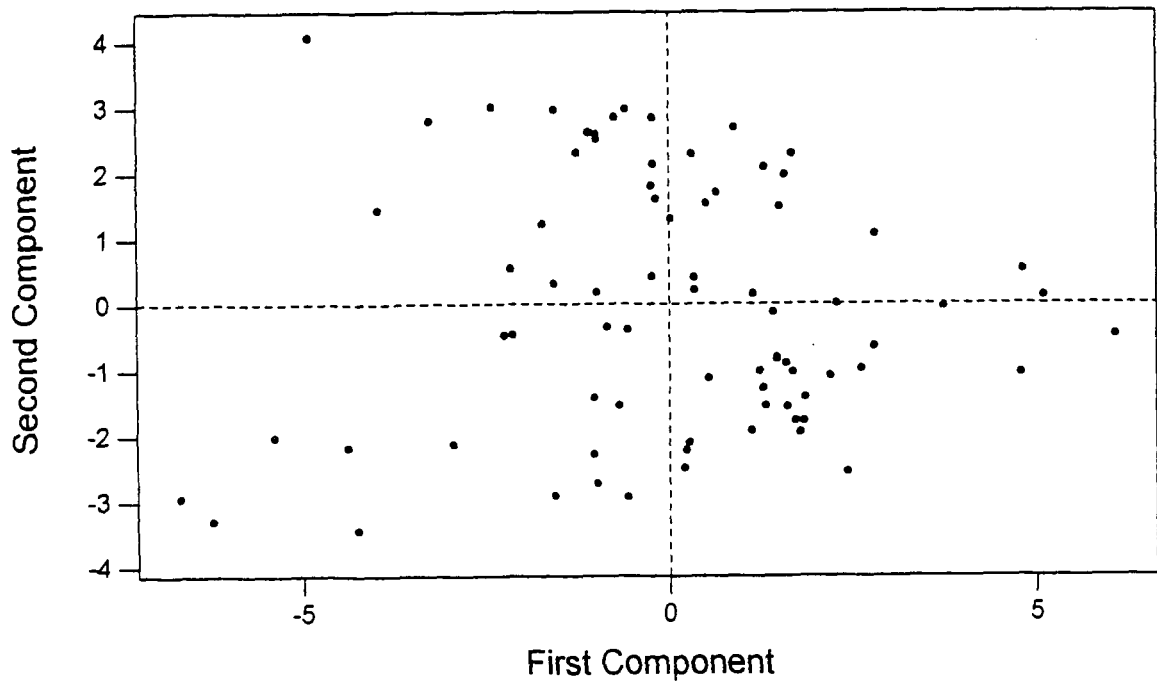


Figure 3.4.7 Principal component analysis score plot of 10 variables (*ptd* ratios of structures) of 78 specimens of the *pingue* group

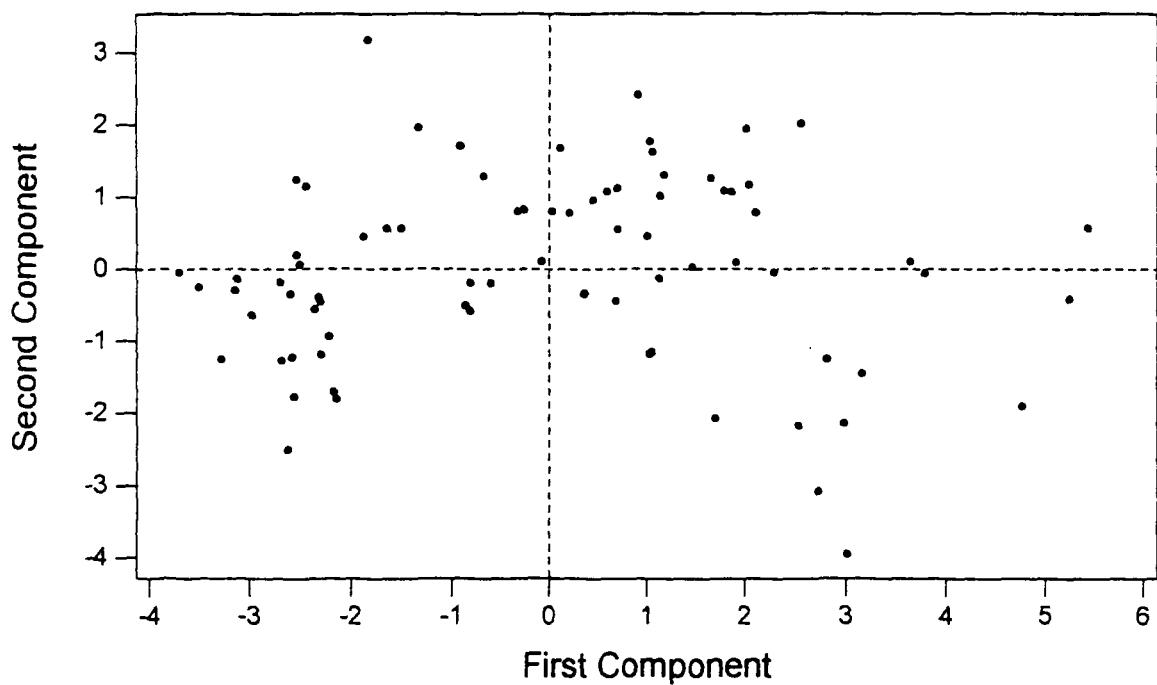


Figure 3.4.8 Cluster analysis dendrogram of 12 variables (mean lengths of structures) of 13 populations of the *pingue* group

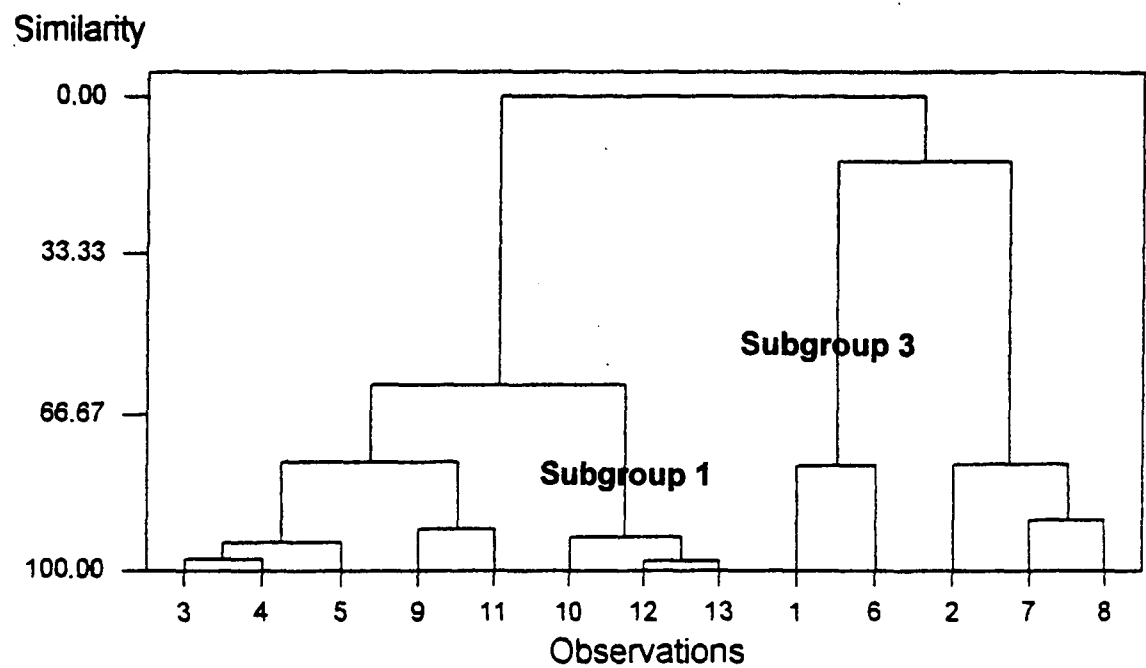


Figure 3.4.9 Cluster analysis dendrogram of 10 variables (mean *ptd* ratios of structures) of 13 populations of the *pingue* group

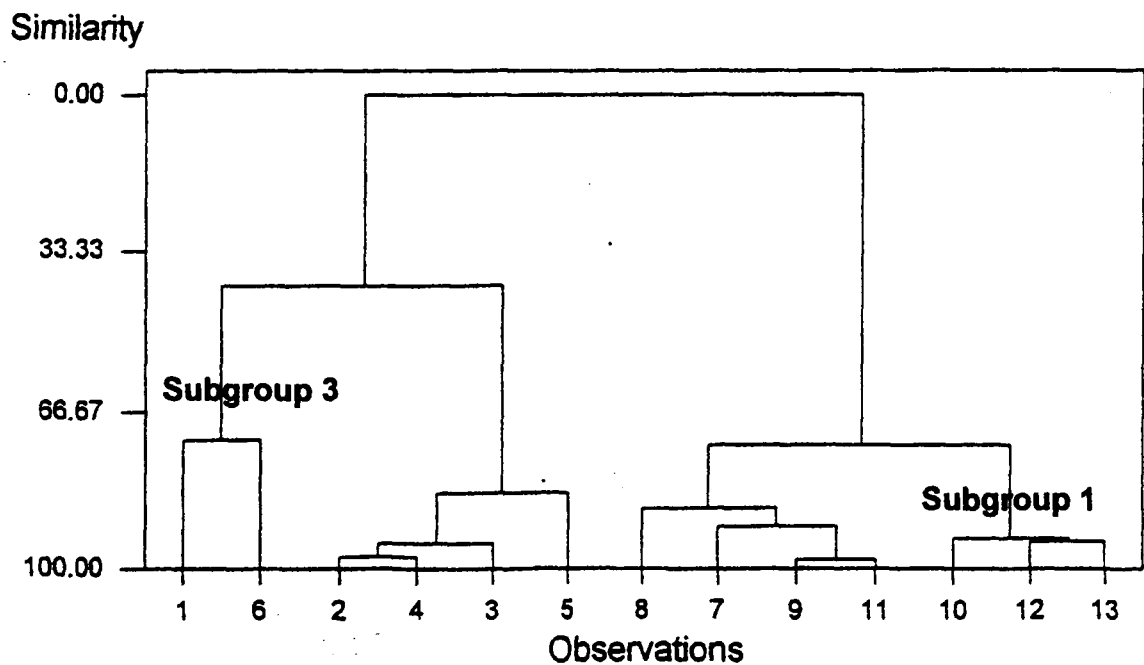


Figure 3.4.10 Cluster analysis dendrogram of 12 variables (lengths of structures) of 78 specimens of the *pingue* group

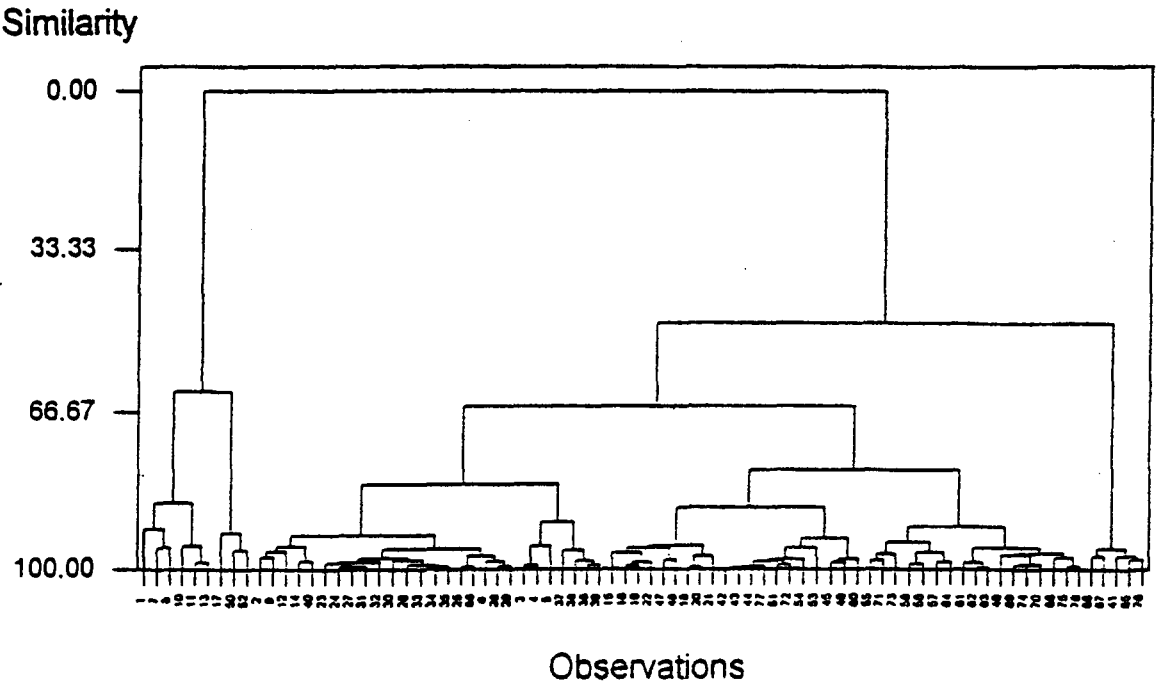


Figure 3.4.11 Cluster analysis dendrogram of 10 variables (*ptd* ratios of structures) of 78 specimens of the *pingue* group

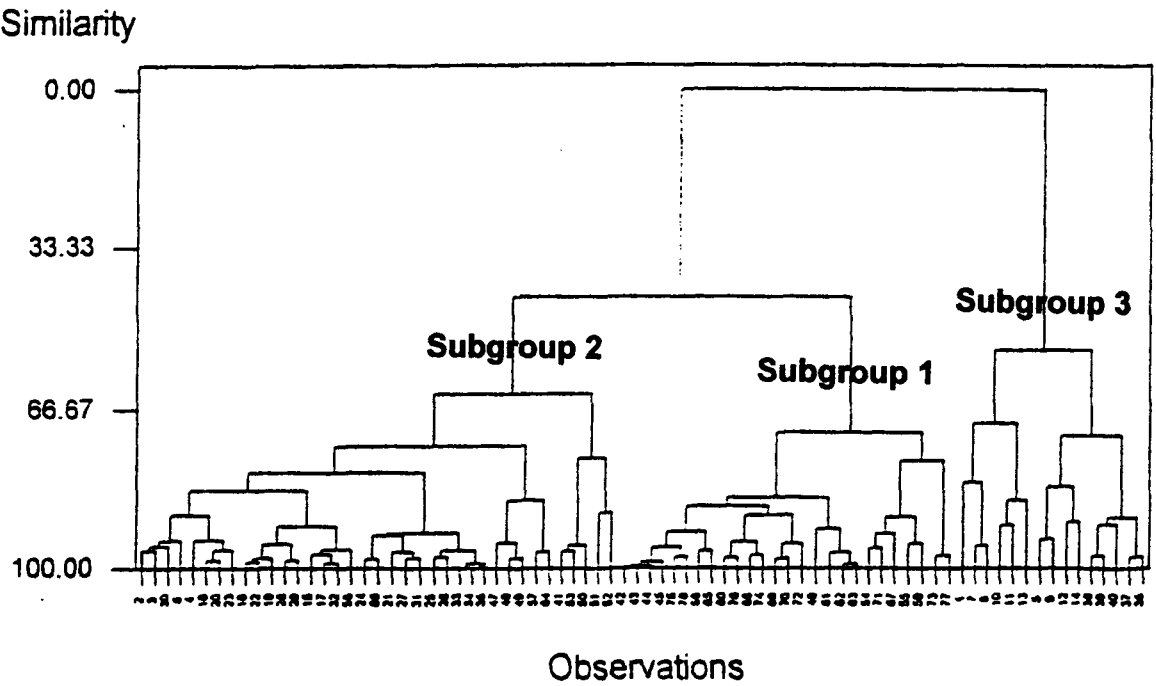
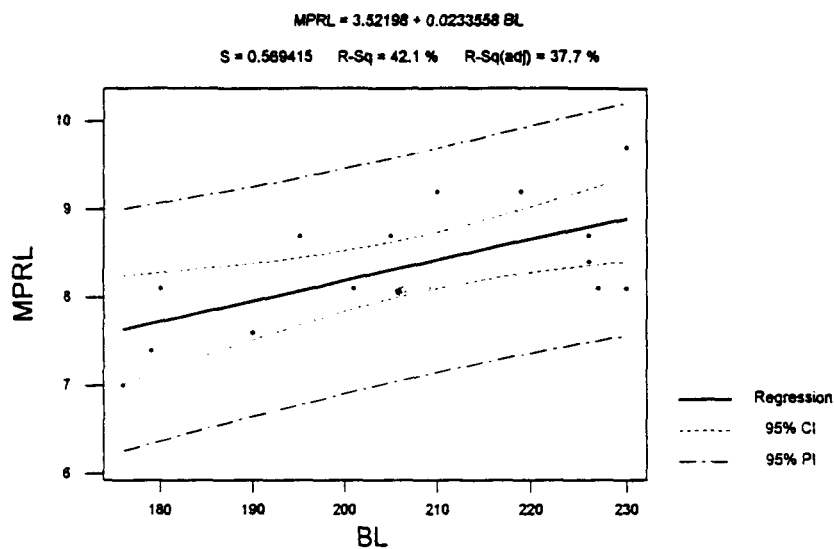
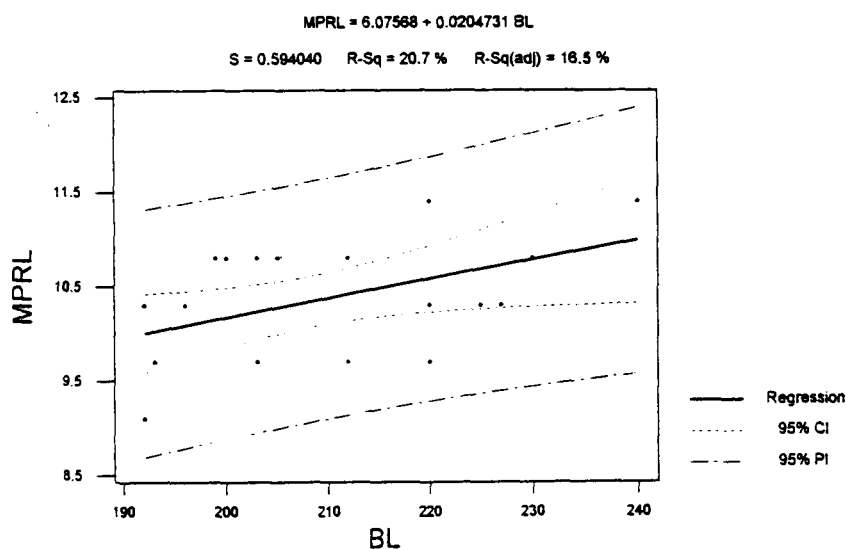


Figure 3.4.12 Plots of mean macroplacoid row length (MPRL) against mean body length (BL) for subgroups of the *pingue* group

a) Subgroup 1 (n=15)



b) Subgroup 2 (n=21)



c) Subgroup 3 (n=15)

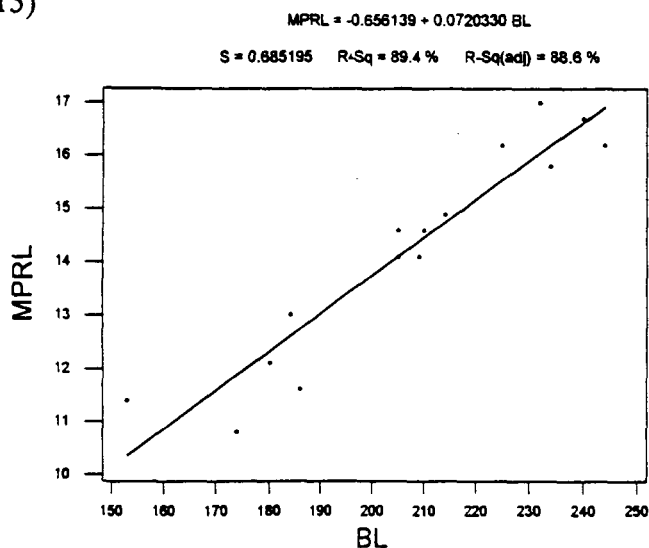


Table 3.4.1. Mean body lengths of 13 populations of specimens in the *pingue* group

POP'N	SITE HABITAT	NUMBER OF SPECIMENS	BODY LENGTH (μm)	
			Mean	SD
1	Evans Lookout, Blackheath, NSW (N14.1) Moss on rock open sclerophyll	14	198	32
2	Douglas Park, NSW (N27) Moss on rock open sclerophyll	8	218	10
3	King Island A, TAS (T 1) Moss on tree wet forest gully	5	190	20
4	Leura A, NSW (N14.2) Leaf litter on soil open sclerophyll	4	196	4
5	Yarrangobilly, NSW (N43) Moss on soil open forest	4	208	11
6	Leura B, NSW (N14.2) Moss on rock rainforest remnant	5	203	12
7	Wentworth Falls, NSW (N14.7) Moss on path moist forest	9	225	26
8	Leura C, NSW (N14.2) Moss on soil open sclerophyll	5	221	14
9	Crows Nest, QLD (Q21) Moss on rock open sclerophyll	5	183	20
10	Gordon Falls, NSW (N14.5) Lichen on tree open sclerophyll	4	199	22
11	Ryde, NSW (N8) Gumnuts on soil open sclerophyll	4	182	23
12	Mt Wilson, NSW (N11) Lichen on branches moist forest	5	216	20
13	King Island B, TAS (T1) Liverwort on log wet forest gully	6	216	25

Table 3.4.2 Measurements (in μm) of structures of specimens of the *pingue* group

Population	Specimen	BL	PT	BT	SIL	BTW	PRL	MPRL	m1	m2	m3	se	IVpo	IVan
1	1	225	29.7	21.1	12.4	1.6	19.5	16.2	3.8	3.8	7.0	2.2	9.7	6.5
1	2	150	30.8	17.3	10.3	1.4	13.5	10.8	2.7	2.7	4.6	1.8	8.1	5.4
1	3	184	36.8	18.9	11.1	1.8	14.6	11.9	2.7	2.7	4.9	1.9	8.7	8.0
1	4	180	35.7	18.9	11.4	1.8	14.6	11.9	2.7	2.7	4.9	1.9	8.7	8.0
1	5	178	28.7	18.9	11.4	1.8	18.2	13.2	2.7	3.0	5.4	1.8	8.1	6.0
1	6	174	31.4	17.8	10.5	1.6	13.8	10.8	2.4	2.2	4.8	1.6	8.1	5.4
1	7	210	36.2	20.0	11.9	1.9	17.8	14.6	3.2	3.2	8.0	1.9	8.7	8.0
1	8	232	35.1	21.1	12.4	2.1	20.3	17.0	3.7	3.7	7.0	1.9	9.7	6.5
1	9	153	30.2	18.9	11.4	1.5	14.1	11.4	2.7	2.4	4.8	1.8	8.7	5.4
1	10	234	38.1	20.5	12.1	1.6	18.6	15.8	4.2	4.2	7.0	1.9	8.7	8.0
1	11	244	42.3	21.4	13.0	1.9	19.5	16.2	4.7	4.7	7.0	1.9	9.8	6.1
1	12	186	27.4	18.1	10.9	1.3	14.4	11.6	2.8	2.8	5.1	1.4	8.4	5.7
1	13	240	42.0	20.5	12.1	1.9	20.0	16.7	4.7	4.7	7.0	1.9	9.7	8.5
1	14	180	36.3	18.6	11.4	1.4	14.9	12.1	3.0	3.0	4.9	1.5	8.4	5.7
2	15	212	34.6	20.0	12.2	1.7	14.1	10.8	2.7	2.2	4.3	1.9	9.7	6.0
2	16	227	37.9	18.9	11.4	1.8	14.1	10.3	2.4	2.4	3.5	1.7	9.2	6.0
2	17	240	40.1	21.6	13.2	1.8	15.1	11.4	2.4	2.7	4.3	1.9	10.3	6.5
2	18	220	39.5	19.5	11.8	1.8	15.1	11.4	2.7	2.7	4.3	1.9	9.2	6.0
2	19	205	35.1	18.9	11.4	1.7	13.5	10.3	2.2	2.2	3.5	1.6	9.2	6.0
2	20	230	40.0	19.7	11.8	1.7	14.0	10.8	2.7	3.0	4.4	1.9	9.2	8.0
2	21	220	41.2	18.9	11.4	1.5	13.3	10.3	2.4	2.6	4.3	1.7	9.2	8.0
2	22	200	37.8	18.9	11.4	1.7	14.1	10.8	2.6	2.6	3.8	1.6	9.2	6.0
3	23	205	35.1	17.3	10.3	1.5	13.5	10.8	2.7	2.7	4.3	1.6	8.5	5.4
3	24	192	34.6	17.3	10.3	1.4	12.2	9.1	2.2	2.2	3.8	1.6	8.5	5.4
3	25	192	32.4	17.3	10.5	1.3	11.6	9.1	2.2	2.2	3.8	1.5	8.5	5.4
3	26	203	33.5	17.8	10.8	1.3	13.5	10.8	2.4	2.4	4.9	1.5	8.5	5.4
3	27	196	34.8	17.3	10.5	1.4	13.0	10.3	2.7	2.2	3.8	1.5	8.5	5.4
4	28	192	35.7	17.8	10.8	1.6	13.2	10.3	2.2	2.4	3.8	1.6	8.1	5.4
4	29	193	32.4	17.8	10.8	1.6	12.4	9.7	2.2	2.2	3.8	1.6	8.1	5.4
4	30	200	35.1	18.4	10.8	1.5	14.1	10.8	2.4	2.4	4.9	1.6	8.5	6.0
4	31	199	34.1	17.3	10.5	1.4	13.5	10.8	2.4	2.4	4.3	1.6	8.1	5.4
5	32	220	33.0	17.8	10.8	1.4	13.0	9.7	2.2	2.4	3.8	1.6	8.5	5.4
5	33	212	35.1	18.1	10.8	1.3	13.0	9.7	2.2	2.2	4.3	1.6	8.7	5.4
5	34	203	35.0	18.1	10.8	1.3	13.0	9.7	2.2	2.2	4.3	1.6	8.7	5.4
5	35	196	36.2	18.4	11.1	1.3	13.5	10.3	2.2	2.4	4.3	1.6	8.7	5.4
6	36	205	40.5	19.5	11.4	1.5	16.2	14.1	2.7	3.0	5.7	1.6	8.7	5.4
6	37	214	35.1	20.0	11.6	1.5	17.8	14.9	2.7	4.3	6.0	1.6	8.6	5.4
6	38	209	36.8	19.5	11.4	1.4	16.7	14.1	2.7	3.8	6.0	1.6	8.7	5.4
6	39	205	36.8	18.9	11.1	1.4	16.8	14.6	3.0	3.2	6.0	1.6	8.6	5.4
6	40	184	32.4	18.9	11.1	1.4	15.9	13.0	3.0	3.2	5.1	1.6	9.2	5.4
7	41	166	28.7	16.8	10.1	1.3	8.4	5.7	1.4	1.4	1.9	1.6	8.1	4.9
7	42	212	34.6	21.1	12.4	1.6	11.6	8.4	1.9	2.2	2.4	1.7	10.3	6.5
7	43	220	34.1	21.1	12.4	1.6	11.9	8.7	1.9	2.2	2.4	1.7	10.3	6.5
7	44	226	35.1	21.1	12.4	1.6	11.6	8.4	1.9	2.2	2.7	1.6	10.3	6.5
7	45	250	35.1	21.1	12.4	1.6	12.2	8.7	1.9	2.2	2.7	1.6	10.8	6.5
7	46	240	37.3	21.1	12.4	1.6	12.4	9.2	2.2	2.2	3.2	1.7	11.4	7.0
7	47	241	36.2	20.0	11.9	1.6	13.5	10.8	3.0	3.0	4.1	1.8	10.3	6.5
7	48	234	39.5	20.0	11.9	1.6	13.2	10.5	2.2	2.4	4.1	1.6	10.3	6.5
7	49	230	36.8	18.9	11.4	1.5	11.4	8.7	2.2	2.2	3.0	1.5	10.0	6.2
8	50	223	36.8	21.6	13.0	1.9	11.9	8.4	2.2	2.2	2.7	2.2	10.8	6.5
8	51	212	31.9	20.5	12.4	1.7	10.8	8.1	1.9	2.2	2.4	1.6	10.8	6.5
8	52	243	37.3	22.2	13.3	1.9	12.4	9.2	2.2	2.4	2.7	2.2	11.9	7.8
8	53	205	33.5	20.0	12.0	1.5	11.1	8.1	1.9	2.2	2.7	1.9	10.3	6.0
8	54	224	35.1	20.5	12.4	1.6	10.8	7.3	1.6	1.9	2.2	1.6	10.3	6.0
9	55	180	31.4	18.4	11.1	1.4	11.9	9.2	1.6	2.2	3.2	1.6	9.2	5.2
9	56	180	33.5	19.5	11.4	1.6	13.0	9.7	2.4	2.4	3.2	1.6	9.7	8.0
9	57	198	29.7	18.9	11.4	1.6	12.7	10.3	2.2	2.4	3.2	1.4	9.2	5.7
9	58	204	33.5	18.9	11.4	1.6	13.0	10.3	2.2	2.2	3.8	1.8	9.7	5.7
9	59	152	32.4	16.8	10.0	1.2	10.8	7.6	1.9	1.9	2.6	1.4	8.1	4.9
10	60	230	35.1	21.1	12.4	1.4	13.0	9.7	2.2	2.2	2.7	1.7	10.5	6.5
10	61	195	35.1	20.0	11.6	1.5	11.4	8.7	1.6	1.6	2.2	1.3	10.5	6.5
10	62	190	34.3	19.5	11.4	1.5	10.3	7.6	1.6	1.6	2.2	1.3	10.3	6.0
10	63	180	33.0	19.5	11.4	1.5	11.4	8.1	1.6	1.9	2.2	1.4	10.3	6.0
11	64	210	33.5	18.4	11.1	1.6	11.9	9.2	2.2	2.2	3.2	1.4	8.7	5.4
11	65	175	28.1	17.3	10.3	1.4	10.3	7.6	1.6	1.9	3.0	1.5	8.7	5.4
11	66	185	32.4	17.3	10.3	1.4	11.9	9.2	1.9	2.2	3.2	1.5	8.7	5.4
11	67	155	27.0	16.8	10.0	1.2	8.9	6.5	1.4	1.6	2.4	1.2	7.6	4.9
12	68	230	29.7	19.2	11.4	1.4	10.8	8.1	1.9	1.9	2.4	1.4	10.3	6.0
12	69	227	33.0	19.7	11.4	1.4	11.4	8.1	2.2	2.2	2.7	1.4	10.3	6.0
12	70	219	35.1	20.5	11.9	1.5	11.9	9.2	2.2	2.2	3.2	1.4	10.3	6.0
12	71	176	29.7	18.9	11.4	1.3	10.3	7.0	1.6	2.2	2.7	1.4	9.7	5.4
12	72	226	31.4	21.1	12.2	1.6	11.4	8.7	1.6	2.2	2.7	1.5	10.8	6.5
13	73	201	29.1	20.0	11.4	1.4	10.8	8.1	1.6	2.0	2.7	1.6	9.2	6.0
13	74	210	31.5	20.0	11.9	1.4	11.9	9.2	2.2	2.4	2.7	1.4	10.3	8.0
13	75	226	32.4	20.0	11.6	1.5	11.1	8.4	1.7	1.7	2.7	1.6	9.7	8.5
13	76	179	27.0	17.3	10.3	1.1	9.5	7.4	1.4	1.6	2.2	1.4	8.7	5.4
13	77	205	35.1	21.6	12.4	1.6	11.4	8.7	1.9	2.2	2.7	1.6	10.3	6.5
13	78	226	33.5	20.0	11.6	1.5	11.4	8.7	1.9	2.2	2.7	1.6	10.3	6.5

BL Body length
PT Pharyngeal tube length
BT Buccal tube length
SIL Stylet support insertion length
BTW Buccal tube width
PRL Placoid row length
MPRL Macroplacoid row length
m1 Length of first macroplacoid
m2 Length of second macroplacoid
m3 Length of third macroplacoid
se Length of septulum
IVpo Length of posterior claw of fourth leg
IVan Length of anterior claw of fourth leg

Table 3.4.3 Principal component analysis – Eigenanalysis of the correlation matrix of 12 variables (mean lengths of structures) of 13 populations of the *pingue* group

Eigenvalue	5.2556	4.7454	0.8131	0.6017	0.2723	0.1913
Proportion	0.438	0.395	0.068	0.050	0.023	0.016
Cumulative	0.438	0.833	0.901	0.951	0.974	0.990
Eigenvalue	0.0740	0.0281	0.0152	0.0023	0.0010	0.0000
Proportion	0.006	0.002	0.001	0.000	0.000	0.000
Cumulative	0.996	0.998	1.000	1.000	1.000	1.000
Variable	PC1	PC2	PC3	PC4		
BL	-0.195	-0.322	-0.459	-0.198		
BT	-0.256	-0.326	-0.039	0.488		
PT	0.097	-0.349	-0.408	-0.502		
SIL	-0.245	-0.362	0.047	0.278		
BTW	-0.047	-0.361	0.601	-0.216		
MPRL	0.375	-0.199	-0.126	0.264		
m1	0.357	-0.245	0.087	0.116		
m2	0.350	-0.236	-0.122	0.309		
m3	0.410	-0.139	-0.145	0.079		
se	0.072	-0.389	0.248	-0.377		
IVpo	-0.397	-0.059	-0.333	0.047		
IVan	-0.320	-0.277	0.163	0.132		

Table 3.4.4 Principal component analysis – Eigenanalysis of the correlation matrix of 10 variables (mean *ptd* ratios of structures) of 13 populations of the *pingue* group

Eigenvalue	6.2407	2.3719	0.4822	0.4340	0.2111	0.1777
Proportion	0.624	0.237	0.048	0.043	0.021	0.018
Cumulative	0.624	0.861	0.909	0.953	0.974	0.992
Eigenvalue	0.0674	0.0119	0.0023	0.0008		
Proportion	0.007	0.001	0.000	0.000		
Cumulative	0.999	1.000	1.000	1.000		
Variable	PC1	PC2	PC3	PC4		
PT/BT	0.303	-0.193	-0.715	0.390		
SIL*100/BT	0.191	-0.519	-0.291	-0.403		
BTW*100/BT	0.221	-0.451	0.488	-0.147		
MPRL*100/BT	0.376	0.198	0.070	0.155		
m1*100/BT	0.383	0.051	0.167	0.173		
m2*100/BT	0.367	0.228	0.150	-0.064		
m3*100/BT	0.386	0.149	-0.032	0.121		
se*100/BT	0.305	-0.347	0.036	-0.256		
IVpo*100/BT	-0.360	-0.133	-0.183	-0.111		
IVan*100/BT	-0.165	-0.484	0.273	0.717		

Table 3.4.5 Principal component analysis – Eigenanalysis of the correlation matrix of 12 variables (lengths of structures) of 78 specimens in the *pingue* group

Eigenvalue	6.0139	3.6931	0.6679	0.6174	0.3079	0.2535
Proportion	0.501	0.308	0.056	0.051	0.026	0.021
Cumulative	0.501	0.809	0.865	0.916	0.942	0.963
Eigenvalue	0.1727	0.1132	0.0644	0.0604	0.0204	0.0152
Proportion	0.014	0.009	0.005	0.005	0.002	0.001
Cumulative	0.977	0.987	0.992	0.997	0.999	1.000
Variable	PC1	PC2	PC3	PC4		
BL	-0.309	0.173	-0.459	0.059		
PT	-0.283	-0.049	-0.645	-0.535		
BT	-0.330	0.254	0.110	0.281		
SIL	-0.342	0.238	0.131	0.163		
BTW	-0.333	0.040	0.283	-0.415		
MPRL	-0.261	-0.378	0.025	0.202		
m1	-0.274	-0.352	-0.019	0.125		
m2	-0.279	-0.338	-0.054	0.293		
m3	-0.208	-0.434	0.012	0.130		
se	-0.305	-0.061	0.504	-0.464		
IVpo	-0.209	0.417	-0.047	0.233		
IVan	-0.294	0.315	0.056	0.066		

Table 3.4.6 Principal component analysis – Eigenanalysis of the correlation matrix of 10 variables (*ptd* ratios of structures) of 78 specimens of the *pingue* group

Eigenvalue	5.1559	1.7375	0.9706	0.7215	0.5078	0.4471
Proportion	0.516	0.174	0.097	0.072	0.051	0.045
Cumulative	0.516	0.689	0.786	0.859	0.909	0.954
Eigenvalue	0.2663	0.0989	0.0728	0.0215		
Proportion	0.027	0.010	0.007	0.002		
Cumulative	0.981	0.991	0.998	1.000		
Variable	PC1	PC2	PC3	PC4		
IVpo*100/BT	-0.333	0.266	0.231	0.247		
IVan*100/BT	-0.115	0.520	0.608	-0.045		
BTW*100/BT	0.228	0.456	0.063	-0.389		
se*100/BT	0.281	0.326	-0.166	-0.440		
MPRL*100/BT	0.417	-0.130	0.171	0.023		
PT*100/BT	0.234	0.315	-0.015	0.741		
m1*100/BT	0.407	-0.005	0.208	0.078		
m2*100/BT	0.397	-0.173	0.174	0.088		
m3*100/BT	0.420	-0.123	0.102	0.046		
SIL*100/BT	0.130	0.429	-0.657	0.163		

Table 3.4.7 Maxima and minima of structure lengths (in μm) and of *ptd* ratios for three subgroups of *Diphascon pingue* from Australia given by Claxton (this thesis) and their equivalent species given by Pilato & Binda (1998)

Structure and <i>ptd</i>	Structure length (μm)											
	Subgroup 1 “ <i>D. pingue</i> ”				Subgroup 2 “ <i>D. claxtonae</i> ”				Subgroup 3 “ <i>D. australianum</i> ”			
	Claxton n=15		Pilato & Binda n=11		Claxton n=21		Pilato & Binda n=5		Claxton n=15		Pilato & Binda N=3	
	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
BL	176	230	127	254	192	240	175	304	153	244	210	222
BT+PT	44.3	56.7	40.4	56.4	49.7	62.8	53.2	61.7	45.2	63.7	58.9	61.0
BT	17.3	21.4	14.9	23.3	17.3	21.6	18.7	20.7	17.8	21.4	20.8	21.2
<i>BT/BT+PT</i>	36.3	40.7	37.8	39.5	31.5	36.6	32.1	35.1	32.5	41.5	34.5	35.3
SIL	10.3	12.4			10.3	13.2			10.5	13.0		
<i>ptd</i>	57.0	60.3	56.1	58.5	58.7	61.1	59.2	61.9	58.0	58.7	57.2	57.7
BTW	1.1	1.6	1.0	1.7	1.3	1.8	1.3	1.8	1.3	2.1	1.7	1.8
<i>ptd</i>	6.4	7.7	5.6	8.3	7.1	9.5	7.0	9.1	7.2	10.0	8.0	8.5
PRL	9.5	11.9	8.7	13.9	11.6	15.1	11.6	15.3	13.8	20.3	18.7	20.7
<i>ptd</i>	52.8	61.6	51.6	62.9	67.1	78.0	61.9	74.0	74.6	97.6	90.0	97.6
MPRL	7.0	9.7	6.7	10.7	9.1	11.4	9.3	12.3	10.8	17.0	15.9	17.6
<i>ptd</i>	37.0	46.0	40.2	49.0	52.6	62.4	49.9	59.3	60.3	81.5	76.4	83.0
m1	1.4	2.2	2.1	3.1	2.2	2.7	2.9	3.6	2.4	4.7	4.0	4.2
<i>ptd</i>	7.6	11.2	11.1	14.3	11.1	15.6	15.5	17.5	13.5	22.9	21.3	22.3
m2	1.6	2.4	2.2	3.2	2.0	3.0	2.7	3.6	2.2	4.7	4.0	4.2
<i>ptd</i>	8.5	11.6	12.7	15.6	11.0	15.6	14.5	17.5	12.4	22.9	19.2	20.2
m3	2.2	3.2	2.6	4.1	3.5	4.9	3.8	4.7	4.6	7.0	7.3	7.8
<i>ptd</i>	12.5	15.6	14.5	18.4	18.5	27.5	20.0	22.6	24.3	34.2	34.1	37.0
se	1.3	1.7	1.8	2.6	1.5	1.9	1.8	2.1	1.4	2.2	1.8	1.8
<i>ptd</i>	6.5	8.1	9.5	12.5	8.4	9.7	9.7	10.6	8.0	8.5	8.6	8.7
IVpo	8.7	10.8	9.3	12.0	8.1	10.3	8.3	10.8	8.1	9.8	8.6	9.0
<i>ptd</i>	46.0	53.7	46.6	57.2	45.5	48.7	43.9	52.2	42.4	48.7	41.2	42.6
IVan	5.4	6.5	6.6	7.5	5.4	6.5	6.0	6.9	5.4	6.5	6.0	6.6
<i>ptd</i>	28.6	32.5	31.1	35.9	29.4	32.6	31.3	33.5	27.0	28.6	28.8	31.2

ptd Ratio of length of structure to BT length, expressed as a percentage
n Number of specimens
BL Body length
BT Buccal tube
PT Pharyngeal tube
SIL Stylet insertion length
BTW Buccal tube width
PRL Placoid row length
MPRL Macroplacoid row length
m1, m2, m3 Length of macroplacoid 1, 2, 3
se Septulum
IVpo Posterior claw on 4th pair of legs
IVan Anterior claw on 4th pair of legs

Table 3.4.8. Dimensions (in μm) of holotypes of *D. claxtonae* and *D. australianum* given by Claxton (this thesis) and Pilato & Binda (1998)

Structure	<i>D. claxtonae</i>				<i>D. australianum</i>			
	Claxton		Pilato & Binda		Claxton		Pilato & Binda	
	μm	<i>ptd</i>	μm	<i>ptd</i>	μm	<i>ptd</i>	μm	<i>ptd</i>
BL	230.0		231.0		210.0		210.0	
BT+PT	59.7		61.7		58.6		58.9	
BT	19.7		19.8		20.5		20.8	
BT/BT+PT%		33.0		32.1		35.0		35.2
BTW	1.7		1.8		1.6		1.7	
		8.6		9.3		7.8		8.0
SIL	11.8		12.0		12.1		11.9	
		59.9		60.4		59.0		57.2
PRL	14.0		14.0		18.6		18.7	
		71.1		70.7		90.7		90.0
MPRL	10.8		11.0		15.8		15.8	
		54.8		55.3		77.1		76.4
m1	2.7		3.1		4.2		4.4	
		13.7		15.5		20.5		21.3
m2	3.0		2.9		4.2		4.0	
		15.2		14.5		20.5		19.2
m3	4.4		4.3		7.0		7.3	
		22.3		21.8		34.1		35.0
se	1.9		2.1		1.9		1.8	
		9.6		10.6		9.3		8.7
IVpo	9.2		9.0		8.7		8.7	
		46.7		45.4		42.4		41.6
IVan	6.0		6.2		6.0		6.0	
		30.5		31.3		29.3		28.9

ptd Ratio of length of structure to BT length, expressed as a percentage

BL Body length

BT Buccal tube

PT Pharyngeal tube

BTW Buccal tube width

SIL Stylet insertion length

PRL Placoid row length

MPRL Macroplacoid row length

m1, m2, m3 Length of macroplacoid 1, 2, 3

se Septulum

IVpo Posterior claw on 4th pair of legs

IVan Anterior claw on 4th pair of legs

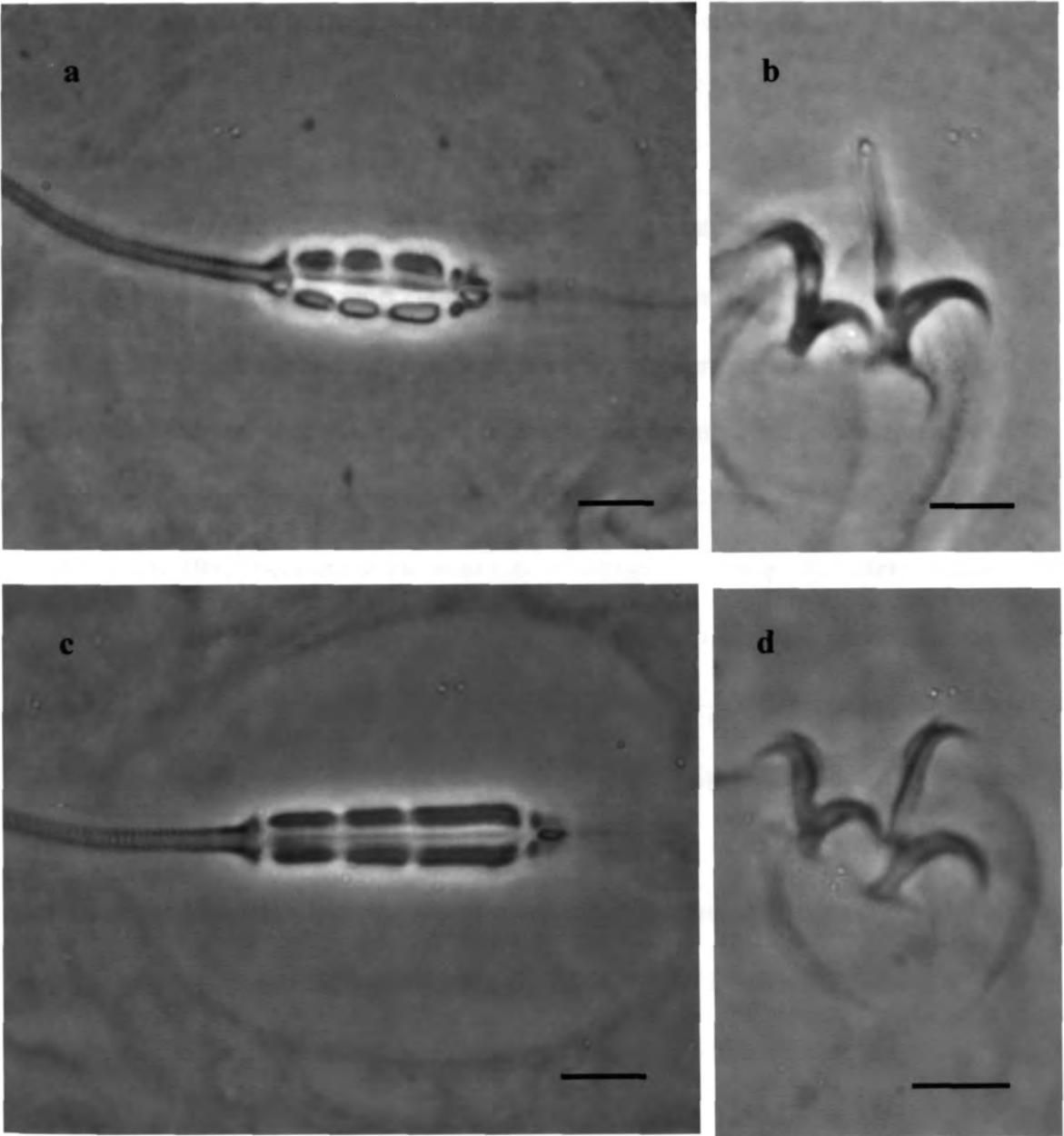


Plate XIII. *Diphascocon (D.) pingue* (Marcus, 1936) (a). pharynx and placoids, (b). claws of the fourth leg; *Diphascocon (D.) pinguiforme* Pilato & Binda, 1997/98, (c). Pharynx and placoids, (d). claws of fourth leg. Phase contrast. (Scale bars = 5 µm)

3.5 THE FAMILY MILNESIIDAE

3.5.1 Introduction

Milnesium tardigradum Doyère, 1840 was one of the first tardigrade species to be described and it remains the most commonly encountered and most often cited species. In Australia, specimens of this large carnivorous species can be found in a wide variety of habitats. The placement of the family Milnesiidae Ramazzotti, 1962 (represented by the single species *M. tardigradum*) in the class Eutardigrada has been questioned (Kristensen, 1981; Greven, 1982) because of the presence of somewhat aberrant characters. These include buccal and lateral papillae on the head, six triangular lamellae which close over the mouth and the complete separation of the primary and secondary branches of the claws. The latter character prompted the inclusion of the Milnesiidae in the order Apochela and the rest of the eutardigrades in the order Parachela (Schuster *et al.*, 1980). Molecular analysis using 18S rRNA sequences confirmed this phylogenetic relationship with the order Parachela (represented by *Thulinus*, *Hypsibius* and *Macrobiotus*) forming a monophyletic sister group to the Apochela (represented by *Milnesium*) (Garey *et al.*, 1996).

A new monotypic genus, *Limmenius porcellus* Horning, Schuster & Grigarick, 1978, was placed in the family Milnesiidae despite some characters such as “one or more membranous flaps around the mouth and peribuccal papillae, stylets and stylet supports absent” being at odds with this placement (Horning *et al.*, 1978). The claw structure and pharynx were described as being the same as in *M. tardigradum* but the buccal tube is elongate and without spiral thickening. The original description was later emended by Schuster *et al.* (1980) to include the presence of four rounded triangular buccal lamellae and long thin stylets with stylet supports unlike those of *M. tardigradum*. It is unclear

whether these authors still considered the species to have the membranous flaps. *L.*

porcellus was found in mosses in *Nothofagus* forests in New Zealand.

M. tardigradum remained the only species in the genus for 150 years. Recently, three new species have been described, *M. brachyungue* (Binda & Pilato, 1990) from Chile, *M. euryostomum* (Maucci, 1991) from South Greenland and *M. tetralamellatum* (Pilato & Binda, 1991) from Tanzania, Africa. All have the same claw structure as *M. tardigradum* but differ in some characters of the buccal apparatus.

During the course of this study, tardigrades resembling *M. tardigradum* in size and shape and in having the same claw structure were found. However, the very long narrow buccal tube and long mouth cavity enclosed in a “snout”, together with long thin stylets and small fine stylet supports suggested that this taxon was different from any previously described in the family Milnesiidae and a new genus, *Milnesioides*, was erected for it as *Milnesioides exsertum* Claxton, 1999. A large population of this tardigrade was found in mosses and lichens at New England National Park, NSW. Two other smaller populations were found in similar environments in Melba Gully, Victoria and Franklin River, Tasmania, with somewhat shorter and wider buccal tube than the New England population. In addition, a single specimen resembling *L. porcellus* was identified in a moss sample from Cradle Mt, Tasmania.

These findings prompted a morphological investigation of specimens of the new genus to compare it with other genera of Milnesiidae. Because of the similarities of the buccal apparatus of these specimens to that of *L. porcellus* a reinterpretation of the morphology of the buccal apparatus and an assessment of its function is presented. This work has been published (Claxton, 1999).

3.5.2 Materials and Methods

Fresh, asphyxiated specimens of *Milnesioides exsertum* Claxton, 1999 from New England National Park were mounted in water and observed for 10-15 minutes. Specimens from the three sites were measured and means and standard deviations of structures and their *pt* values calculated (Table 3.5.1).

In order to investigate the differences in morphology of the sexes, seven females and 11 males were chosen from the New England National Park population so that their mean body lengths were similar. Means and standard deviations of these groups were calculated (Table 3.4.2). (Only three males were found at Melba Gully and also at Franklin River so the numbers were insufficient to make comparisons).

Two paratypes of *L. porcellus* were obtained from The Museum of New Zealand, Wellington, New Zealand.

In order to make the differences between *Milnesioides*, *Milnesium* and *Limmenius* easier to observe, single individuals of about 500 μm body length were selected from each of *M. tardigradum*, *M. exsertum* from both New England and Melba Gully and the two New Zealand paratypes of *L. porcellus* and measurements and *pt* values of body structures were calculated and the figures drawn (Table 3.5.3 and Fig. 3.5.1).

The index *pt* is the ratio of the length of a structure to the length of the buccal tube expressed as a percentage (Pilato, 1981).

3.5.3 Results and Discussion

3.5.3.1 *Generic differences in the family Milnesiidae*

Diagnoses and descriptions of *M. exsertum*, *M. tardigradum* and *L. porcellus* can be found in Chapter 4 of this thesis. They show that all have flap-like lamellae which appear to close over the mouth like an operculum, peribuccal and lateral papillae and the same claw structure. In addition, all have a pear-shaped pharynx from which apophyses and placoids are absent. *Milnesioides* and *Limmenius* differ from *Milnesium* by having an elongated “snout” enclosing a long mouth cavity and by the having long thin stylets with short slender stylet supports. *Milnesioides* can be distinguished from *Limmenius*, by the absence of an annulated buccal tube, by the presence of a wide, rigid buccal tube and a large pharynx. These differences were considered to be sufficient to erect a new genus, *Milnesioides* within the family Milnesiidae (Claxton, 1999).

3.5.3.2 *Observations on fresh specimens of M. exsertum Claxton, 1999*

Live specimens of *M. exsertum* from New England were observed extending and retracting the elongated front part of the body. As the animal moved forward the extended “snout” (PlateXIVa, b) moved from side to side as if the animal was searching for food. The species is carnivorous as several preserved specimens displayed rotifer trophi in their gut. A few preserved specimens also displayed this extension but most of the mounted specimens have the “snout” partially or fully retracted (Plate XVa, b). An extendable “snout” is not unknown for tardigrades (Pollock, 1995) and is particularly well-developed in members of the marine subfamily Stygarctinae (Kristensen, pers. comm.). The “snout” in *Milnesioides* is taken up almost entirely by an elongated mouth cavity. The mouth cavity of the four known species of *Milnesium* is very short. *M. tardigradum* and, almost certainly, the other three species in the genus *Milnesium* are not able to extend and retract the front part of the body. On the other hand, the mouth cavity of *L. porcellus* is elongated

like that of *M. exsertum*. Comparison of a 500 µm long specimen showed that the mouth cavity was shorter than that in a specimen of the *Milnesioides* of similar dimensions and in all the mounted specimens observed the buccal apparatus was withdrawn well into the body (Plate XVIa, b) Comparison of these with a similar specimen of *Milnesioides* (Plate XVc) suggests that *L. porcellus* also has a protrusible “snout”.

3.5.3.3 *Analysis of populations of M. exsertum*

Three populations of *M. exsertum* were examined. All came from areas with high rainfall (over 2000 mm per annum) and all were either in or in close proximity to *Nothofagus* forests. All have a long mouth cavity with a protrusible “snout” and the stylet supports are inserted at nearly the same proportional length of the buccal tube (Table 3.5.1). The two south-eastern populations (Melba Gully and Franklin River) are very similar to each other but differ from the New England population by having a shorter, slightly wider buccal tube. Consequently the *pt* values for the buccal tube width (and indeed for other parameters) are different in the New England population and the south-eastern populations. This would be expected since *pt* values relate to the buccal tube length. However, when specimens of the same body length are compared (Table 3.5.3) it can be seen that they are similar in every respect save the buccal tube length. In specimens from the south-eastern populations, the cuticular sculpturing (Fig. 3.5.6) is stronger than in those from the New England National Park population and extends down onto the outer surface of the legs which is not the case in the New England population. The same sculpturing was found on the dorsum in some populations of *M. tardigradum* (from Great Keppel Island, Queensland and Bribie Island, Queensland). Ramazzotti (1962) described specimens of *M. tardigradum* from Chile with dorsal sculpturing as a variety, *M. tardigradum granulatum*. This sculpturing has also been noted to occur rarely in some populations of *M. tardigradum* from Europe (Maucci, 1986). With these considerations in mind, the

conservative approach was taken in deciding that the three populations were conspecific and the taxon was described as *M. exsertum* (Claxton, 1999).

3.5.3.4 *Sexual dimorphism in M. exsertum*

Males of *M. tardigradum* have long been recognized (Ramazzotti & Maucci, 1983) by the enlarged, modified secondary branch on the claws of the first pair of legs. This same modification (Fig. 158d, Chapter 4) was observed in 11 specimens of *M. exsertum* of the 76 from New England, three of the 14 from Melba Gully and three of the 26 from Franklin River. The specimens of *M. exsertum* with the modified claws on the first pair of legs were assumed to be males. Measurements were made on a set of individuals with (males) and without (females) the modified first claw (Table 3.5.2). The primary branch of the first pair of claws is longer in males than in females of the same size. The body length range is greater for females than for males (females 216-660 µm, males 345-418 µm). Males have a more delicate buccal apparatus (somewhat shorter, thinner buccal tube and oral cavity and smaller pharynx) than females of the same size.

3.5.3.5 *Reconsideration of L. porcellus*

Comparison of specimens of *M. exsertum* with two paratypes of *L. porcellus* revealed similarities. However, the buccal apparatus of *L. porcellus* had been incorrectly interpreted in the original description although a partial correction was offered by Schuster *et al.* (1980). They noted that the species has four rounded triangular peribuccal lamellae. However, six are visible on one of the paratypes examined (NZ373) (Plate XVIa). Peribuccal papillae were not described originally and were said to be absent by Schuster *et al.* (1980) but are visible on a paratype (NZ23) (Plate XVIb), although their number cannot be determined because the “snout” is withdrawn into the body (compare with Plate XVb). Schuster *et al.* (1980) also mentioned that the species has long thin stylets and stylet

supports but described the buccal tube as flexible without spiral thickenings. In the two paratypes examined, the stylets do appear to be very flexible as does the buccal tube. A faint annulation (similar to that seen on the flexible pharyngeal tube of *Diphascon*) can be seen on the buccal tube of both *L. porcellus* paratypes for almost its entire length (Plate XVIc).

The trend towards elongation and flexibility in the buccal tube occurs in other genera of tardigrades; in the Eutardigrada (Pilato, 1987) and in the Heterotardigrada (Kristensen, 1987). *Limmenius* is, however, unique in having the tube flexible, that is, annulated, above and below the point of insertion of the stylet supports. A reconstruction of *L. porcellus* and a comparison of it with similar sized specimens of *M. exsertum* and *M. tardigradum* are presented in Fig. 3.5.1 and Table 3.5.3. It is suggested that *L. porcellus* has the same ability to protrude and retract the “snout” although a live specimen of this species has not been observed. The single specimen of *Limmenius* found on Cradle Mountain, Tasmania (this is the first citation of this rare New Zealand species in Australia) was not sufficiently well preserved to shed more light on the morphology of the species. Its dimensions, however, were such that it is considered to almost certainly be *L. porcellus*. The diagnosis of the genus *Limmenius* has been emended on the basis of the above observations, Claxton (1999) and see Chapter 4 of this work.

Figure 3.5.1 Habitus of members of the Milnesiidae a) *Milnesium tardigradum*, b) *Milnesioides exsertum*, c) *Limmenius porcellus*. (Scale bar = 50 μ m)

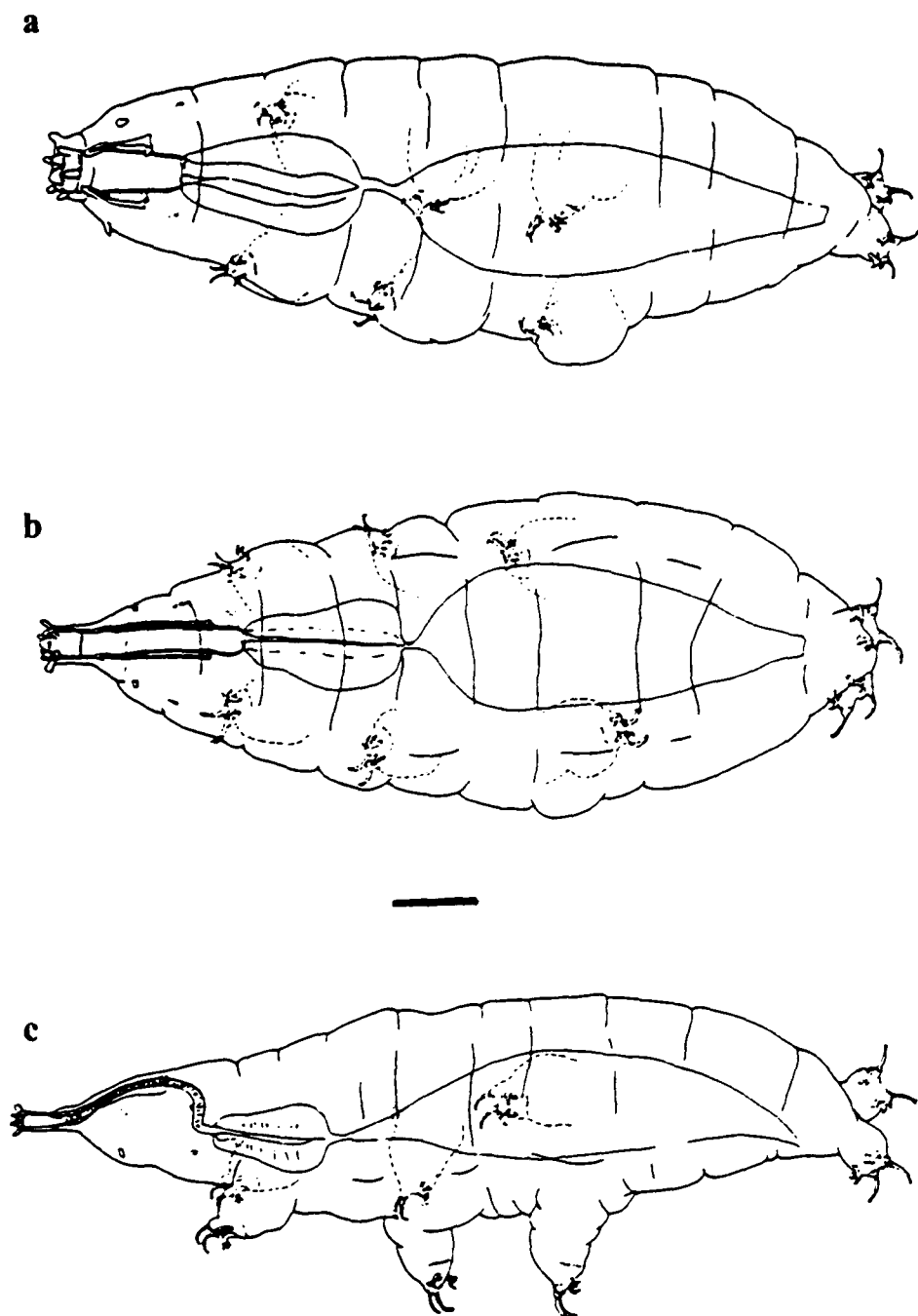


Table 3.5.1. Comparison of three populations of *Milnesioides exsertum* Claxton, 1999 (Measurements in μm).

Population Site Number of specimens Character	Mean Dimensions (μm) and <i>pt</i> values					
	New England (<i>N3</i>)		Melba Gully (<i>V3</i>)		Franklin River (<i>T12</i>)	
	24		13		15	
	Mean	SD	Mean	SD	Mean	SD
Body length	482.8	84.2	478.8	117.5	406.9	69.2
Buccal tube length	76.0	12.5	53.7	9.7	56.9	8.1
Stylet support insert. length	58.0	9.4	40.0	7.5	42.6	5.8
<i>pt</i>	76.3	0.8	74.4	1.5	74.9	1.2
Buccal tube width	12.4	2.3	13.6	3.5	13.2	2.1
<i>pt</i>	16.2	1.5	25.0	2.9	23.2	1.9
Mouth cavity length	18.8	6.5	17.8	3.1	17.2	2.6
Mouth cavity width	15.5	2.7	16.0	3.3	16.6	1.9
Peribuccal papilla	7.5	1.2	8.0	1.4	7.3	0.9
Lateral papilla	4.4	0.8	5.8	1.5	5.2	0.6
Pharynx length	81.7	12.4	78.6	18.5	79.8	14.6
Pharynx width	50.8	8.8	49.3	15.3	44.6	9.7
Claw I main branch	12.6	1.3	15.1	3.3	13.5	1.9
Claw I secondary branch	10.9	1.3	12.6	2.6	10.7	3.0
Claw IV main branch	14.8	1.9	16.6	3.5	15.2	2.6
Claw IV secondary branch	12.7	1.6	13.4	2.8	12.6	2.1

Table 3.5.2. Measurements (in μm) of some characters of males and females of *Milnesioides exsertum* Claxton, 1999

Gender Number of specimens Character	Mean Dimensions (μm) and <i>pt</i> values			
	Females		Males	
	7		11	
	Mean	SD	Mean	SD
Body length	381.6	38.2	379.6	24.7
Buccal tube length	65.2	9.8	53.8	4.3
Stylet support insert length	49.7	7.4	41.0	3.4
<i>pt</i>	76.2	0.3	76.2	0.6
Buccal tube width	9.8	1.7	7.7	0.7
<i>pt</i>	15.1	1.8	14.3	1.4
Mouth cavity length	16.2	1.7	14.0	1.0
Mouth cavity width	12.2	1.6	10.8	1.1
Peribuccal papilla length	6.3	0.9	5.8	0.5
Lateral papilla length	4.2	0.9	4.0	0.6
Pharynx length	68.0	7.3	56.9	6.4
Pharynx width	43.9	4.1	36.2	5.3
Claw I main branch	10.8	0.8	12.1	0.7
Claw I secondary branch	8.7	1.0	11.3	0.4
Claw IV main branch	12.4	1.0	13.0	0.8
Claw IV secondary branch	10.4	1.1	10.9	0.6

Table 3.5.3. Comparison of some characters (measurements in μm) of single specimens, of body length about 500 μm , of *Milnesium tardigradum*, *Milnesioides exsertum* and *Limmenius porcellus*

Character	Species	Dimensions (μm) and <i>pt</i> values				
	Site	<i>M. tardigradum</i>	<i>M. exsertum</i>	<i>M. exsertum</i>	<i>L. porcellus</i>	<i>L. porcellus</i>
		New England (N3)	New England (N3)	Melba Gully (V3)	New Zealand	New Zealand
Body length		500.0	493.0	500.0	513.0	500.0
Buccal tube length		47.0	86.5	57.8	173	118
Stylet support insert length		30.3	66.5	44.3	97.3	71.9
	<i>pt</i>	64.5	76.9	76.7	56.2	61.0
Buccal tube width		20.0	15.1	16.2	5.1	4.4
	<i>pt</i>	42.6	17.5	28.0	3.2	3.8
Mouth cavity length		6.5	20	20	12.4	12.4
Mouth cavity width		22.2	19.5	18.9	8.1	7.0
Peribuccal papilla		8.7	8.7	8.7	4.4	4.9
Lateral papilla		7.0	4.3	4.9	5.7	6.5
Pharynx length		100.0	92.0	87.0	68.0	68.0
Pharynx width		75.0	60.0	48.0	50.0	50.0
Claw I main branch		13.5	13.5	14.1	14.6	14.6
Claw I secondary branch		11.4	11.4	11.4	11.9	11.9
Claw IV main branch		16.2	16.2	16.2	16.2	16.5
Claw IV secondary branch		13.6	14.1	14.1	13.6	14.1

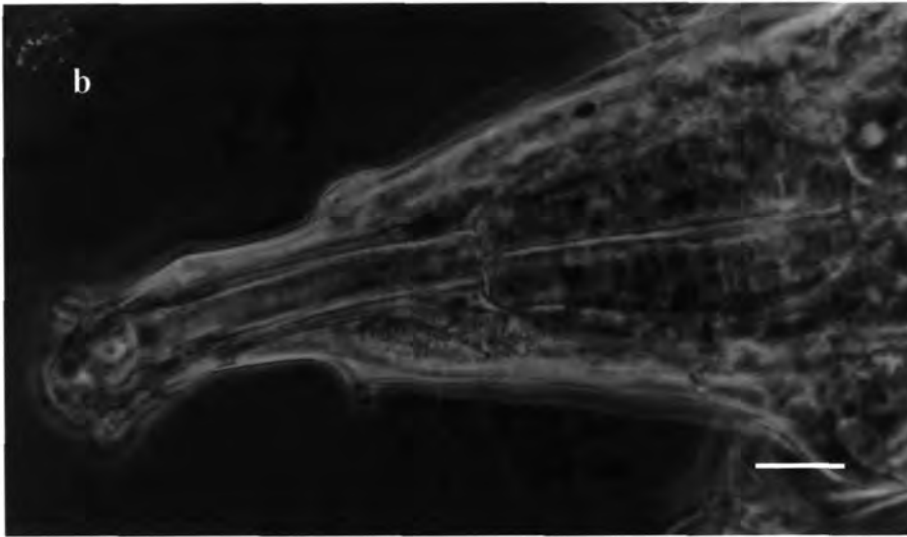
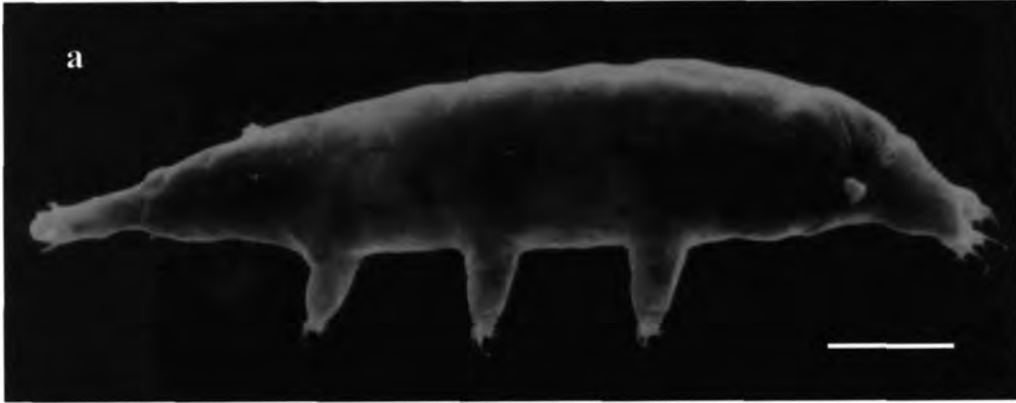


Plate XIV. *Milnesioides exsertum* Claxton, 1999 (a). Whole animal in lateral view, SEM. (Scale bar = 50 μ m). (b). Anterior of live animal with extended “snout”. Light microscopy. (Scale bar = 20 μ m)

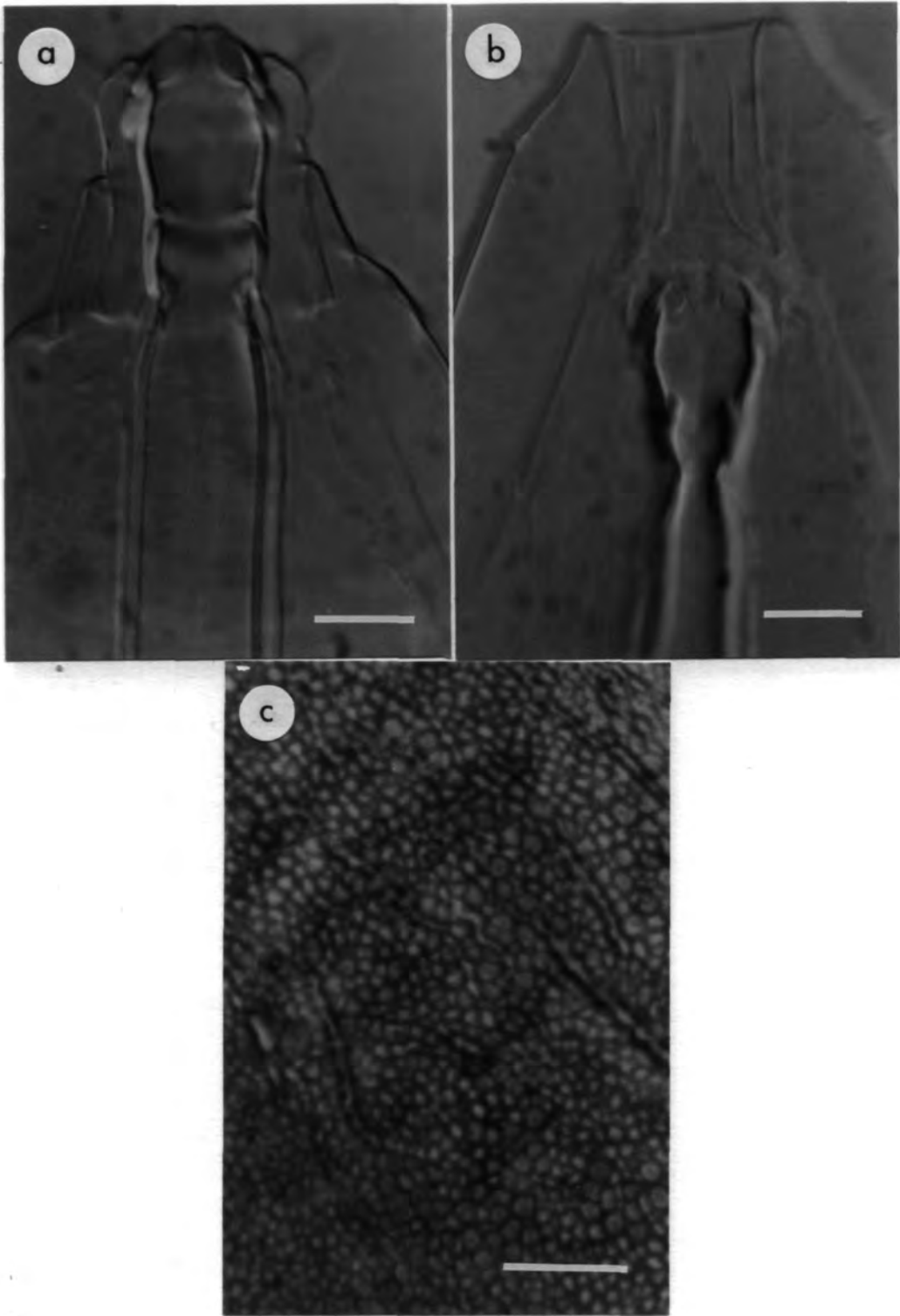


Plate XV. *Milnesioides exsertum* Claxton, 1999 (Paratypes). (a). Anterior of preserved specimen with partially retracted “snout”, DIC. (b). Anterior of preserved specimen with fully retracted “snout”, DIC. (c). Dorsal cuticle. Phase contrast. (Scale bars = 10 um)

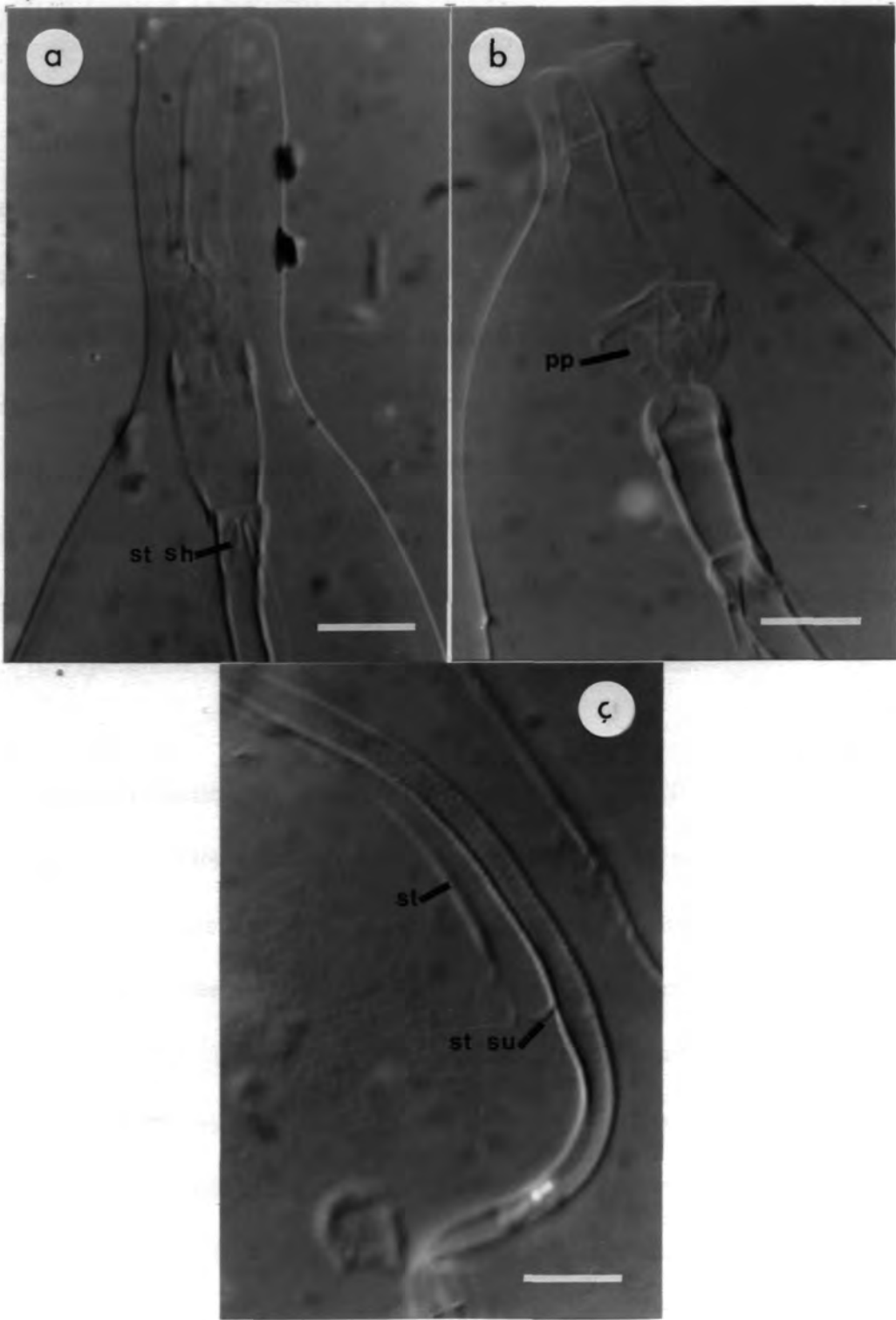


Plate XVI. *Limmenius porcellus* Horning, Schuster & Grgarick, 1978. (a). Anterior of preserved specimen (paratype NZ373) showing stylet sheath (st sh), DIC. (b). Anterior of preserved specimen (paratype NZ23) showing peribuccal papilla (pp), DIC. (c). Buccal tube of paratype NZ23 showing annulation, stylet (st) and stylet support (st su). DIC. (Scale bars = 10 μ m)

3.6 THE GENUS ANTECHINISCUS

3.6.1 Introduction

The genus *Antechiniscus* Kristensen, 1987 is, as presently known, confined to the *Nothofagus* rainforests of South America and New Zealand (Kristensen, 1987; Rossi & Claps, 1989). Five species have been described, two from South America and three from New Zealand. *Antechiniscus lateromamillatus* was described by Ramazzotti (1964) from Chile and *A. jermani* by Rossi & Claps (1989) from Argentina. The three New Zealand species, *Antechiniscus conversus* (Horning & Schuster, 1983), *A. perplexus* (Horning & Schuster, 1983) and *A. parvisentus* (Horning & Schuster, 1983) were described on the basis of few specimens and the descriptions are brief and inadequate.

Kristensen (1987) described the genus using *A. lateromamillatus* (Ramazzotti, 1964) as the type species. This species is identified by the presence of a lateral ridge with a triangular papilla running along the lower edge of each paired segmental plate. In defining the genus *Antechiniscus*, Kristensen also used the presence of pseudosegmental elements to place it in the *Pseudechiniscus* lineage. In *A. lateromamillatus*, large unpaired pseudosegmental plates occur along the posterior margin of each of the segmental plates. In *A. jermani* these plates are reduced to large triangles while in the three New Zealand species they appear as small triangles. An important generic character is the presence of additional pseudosegmental plates and a large median plate 3 that overlaps the pseudosegmental plate anterior to the caudal plate (Kristensen (1987). Other characters included in the generic diagnosis are black eye spots, a rigid buccal tube continuing inside the pharyngeal bulb and small males with enlarged primary and secondary clavae. Ventral plates were noted as being absent. The three New Zealand species were transferred from the genus

Pseudechiniscus although there was no information about eye spots, buccal apparatus or presence or absence of males in the original descriptions of these three species.

This work describes three species of *Antechiniscus* from Tasmania and New South Wales. The first, *Antechiniscus moscali* Claxton, 2001, is described here and the second, *A. parvisentus* was first recorded from New Zealand. *Antechiniscus pulcher* (Murray, 1910) is reported for the first time since its discovery on Mount Kosciusko (Murray, 1910). The work has been published (Claxton, 2001).

3.6.2 Materials and Methods

Material examined

Two live specimens of *A. moscali* were observed in a drop of water at 150× magnification using phase contrast. Other specimens were mounted in Hoyer's medium and measured at 1000× under oil immersion using phase contrast.

Dorsal plate terminology is that of Kristensen (1987).

Paratypes of *A. parvisentus* were borrowed from the Museum of New Zealand, Wellington, New Zealand.

3.6.3 Results

Details of the material examined, diagnoses and descriptions of the three species can be found in Chapter 4 of this work.

Examination of two live specimens of *A. moscali* in water under a coverslip brought the buccal apparatus into clearer view as the water evaporated. The pharynx was seen to move

dorso-ventrally, through an angle of about 15° with the flexion point just below the thickening on the buccal tube (Fig 3.6.1).

Ventral plates were observed on all specimens of the three species and their placement and number are discussed in the descriptions of the species, their arrangement can be seen in Figs 3.6.2, 3.6.3 and 3.6.4. Sexual dimorphism of the plates around the gonopore was observed in all species. However the number and placement of plates is conspecifically constant.

Sexual dimorphism was observed in the three species as follows –

1. Body length – in all species, males are on average shorter than females (see Species descriptions p. 175, 177 and 179)
2. Internal and external buccal cirri and primary and secondary clavae are longer in males than in females of the same size in all species (Table 3.6.1)
3. Claws are longer in males than in females of the same size only in *A. moscali* and *A. pulcher* (Table 3.6.1)
4. In *A. parvisentus*, males have a long filament at lateral position D while females have a triangular papilla
5. In all species, the number and distribution of ventral plates around the gonopore were different in females and males. In both *A. moscali* and *A. parvisentus* females have a podial plate on either side of the gonopore while the males have these plates and a small crescent shaped plate immediately anterior to the gonopore. In *A. pulcher*, females have a set of six plates arranged in a curve below the gonopore while males have a plate on either side of the gonopore.

3.6.4 Discussion

Placement of the three Australian species in the genus *Antechiniscus* is based on the following characters - the presence of lateral ridges along the lower edge of each segmental plate, presence of pseudosegmental plates and an overlapping median plate 3, black eye spots, and small males with enlarged clavae. Their presence in and around *Nothofagus* sites is additional supporting evidence for their inclusion in the genus. However, the presence of a buccal tube with a flexible element in *A. moscali* and, particularly, the presence of ventral plates in all species gives some room for doubt about their generic position, since both the structure of the buccal apparatus and the presence or absence of ventral plates were shown by Kristensen (1987) to be important diagnostic features at the generic level in the family Echiniscidae.

The presence of a flexion point in the buccal apparatus of *A. moscali* but apparently not in *A. parvisentus* or *A. pulcher* requires further investigation and serves to reinforce Kristensen's (1987) contention that characters of the buccal apparatus in Echiniscidae should prove as valuable taxonomically as they are in Eutardigrada and should therefore be examined fully.

The presence of ventral plates is one of the main characters separating *Testechiniscus* Kristensen 1987 from *Echiniscus* Schultze 1840. The ventral plates of *A. moscali* and *A. pulcher* are unique in the family Echiniscidae because of their large number and sexual dimorphism, however, they are similar in number to those of *Testechiniscus macronyx* (Richters, 1907) which was redescribed by McInnes (1994). The presence of ventral plates is considered to be a plesiomorphic character (Kristensen (1987)). They are present in the echiniscid *Bryodelphax* Thulin, 1928 and also in the primitive arthrotardigrade

Renaudarctus Kristensen & Higgins, 1984 and in *Halechiniscus* Richters, 1908

(Kristensen (1987). Their presence in the three species discussed here and their absence in *A. lateromamillatus* and *A. jermani*, suggests that further study is required.

Sexual dimorphism

Sexual dimorphism in body length and in size and shape of cephalic sensory structures and claws has been recorded in a number of genera within the family Echiniscidae (Kristensen, 1987). Males tend to be smaller and have longer buccal sensory structures and claws than females (Dastych, 1987, Kristensen, 1987 and Claxton, 1996). This is the first time, however, that sexual dimorphism of the ventral plates has been recorded.

Figure 3.6.1 *Antechiniscus moscali* Claxton, 2001. Lateral view showing buccal apparatus with buccal tube thickening (bt – buccal tube, ph – pharynx, s – stylet, ss – stylet support, th – thickening). (Scale bar = 20µm)

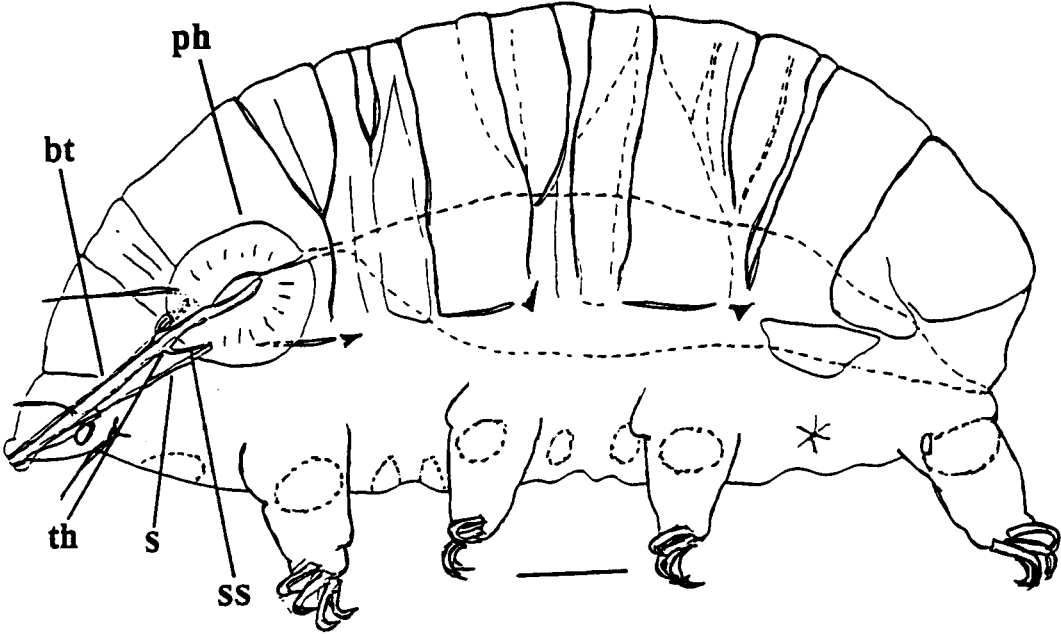


Figure 3.6.2 *Antechiniscus moscali* Claxton, 2001. Ventral view (a) Female, (b) Male (sc – subcephalic plates, pd1 – podial plates, gp – gonopore). (Scale bar = 20µm)

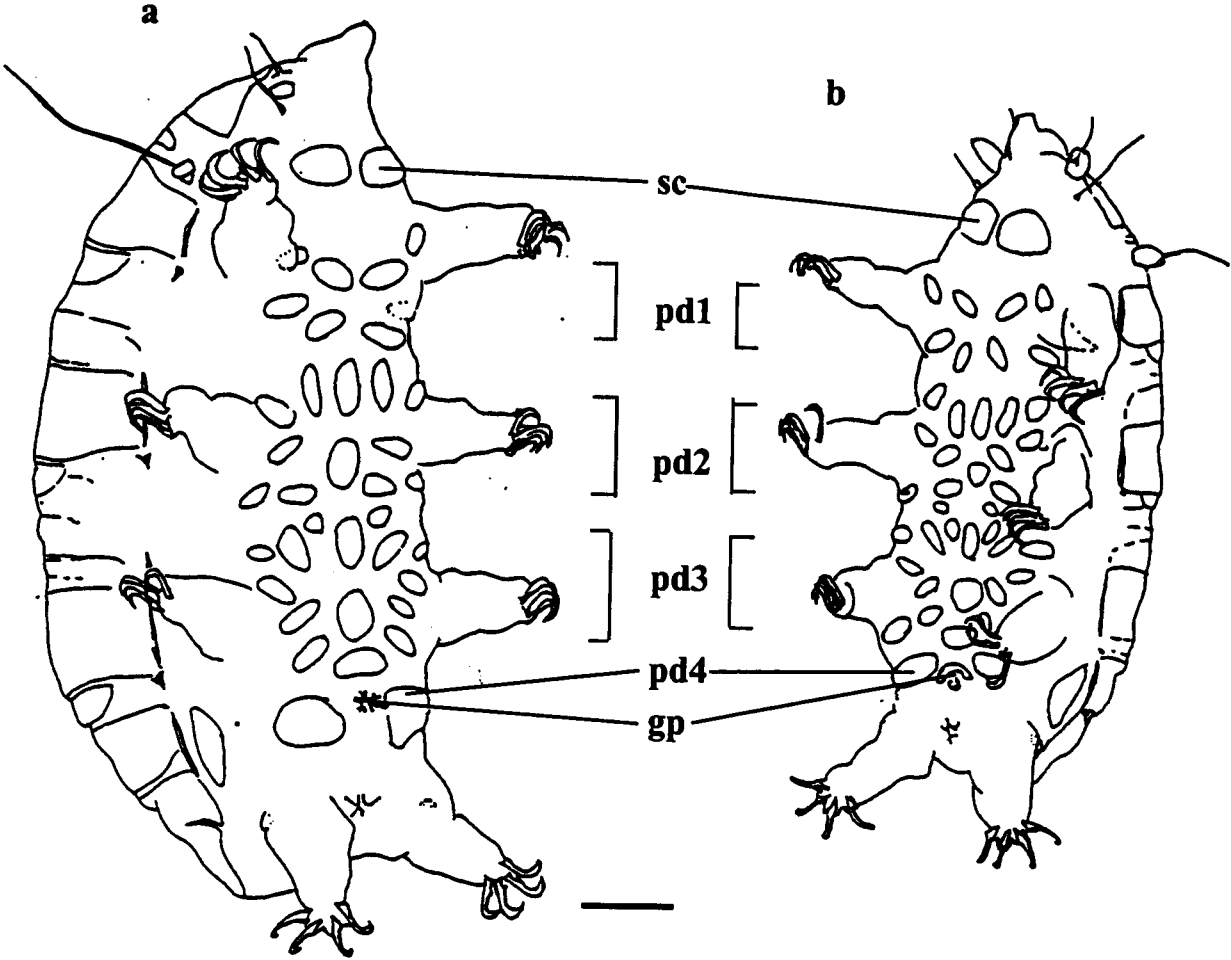


Figure 3.6.3 *Antechiniscus parvisentus* (Horning *et al.*, 1983). Ventral view (a) Female, (b) Male (sc – subcephalic plates, pd1 to 4 – podial plates, gp – gonopore). (Scale bar = 20µm)

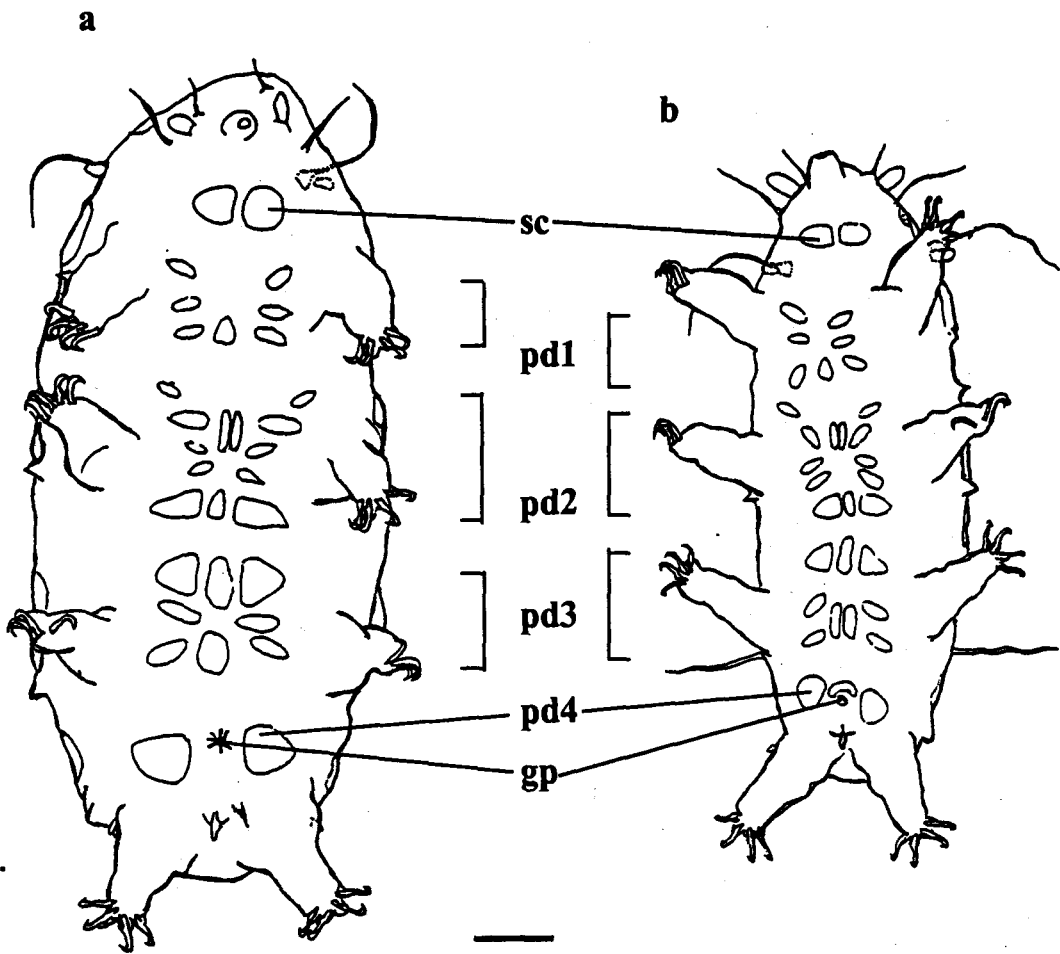


Figure 3.6.4 *Antechiniscus pulcher* (Murray, 1910). Ventral view (a) Female, (b) Male (sc – subcephalic plates, pd1 to 4 – podial plates, gp – gonopore). (Scale bar = 20µm)

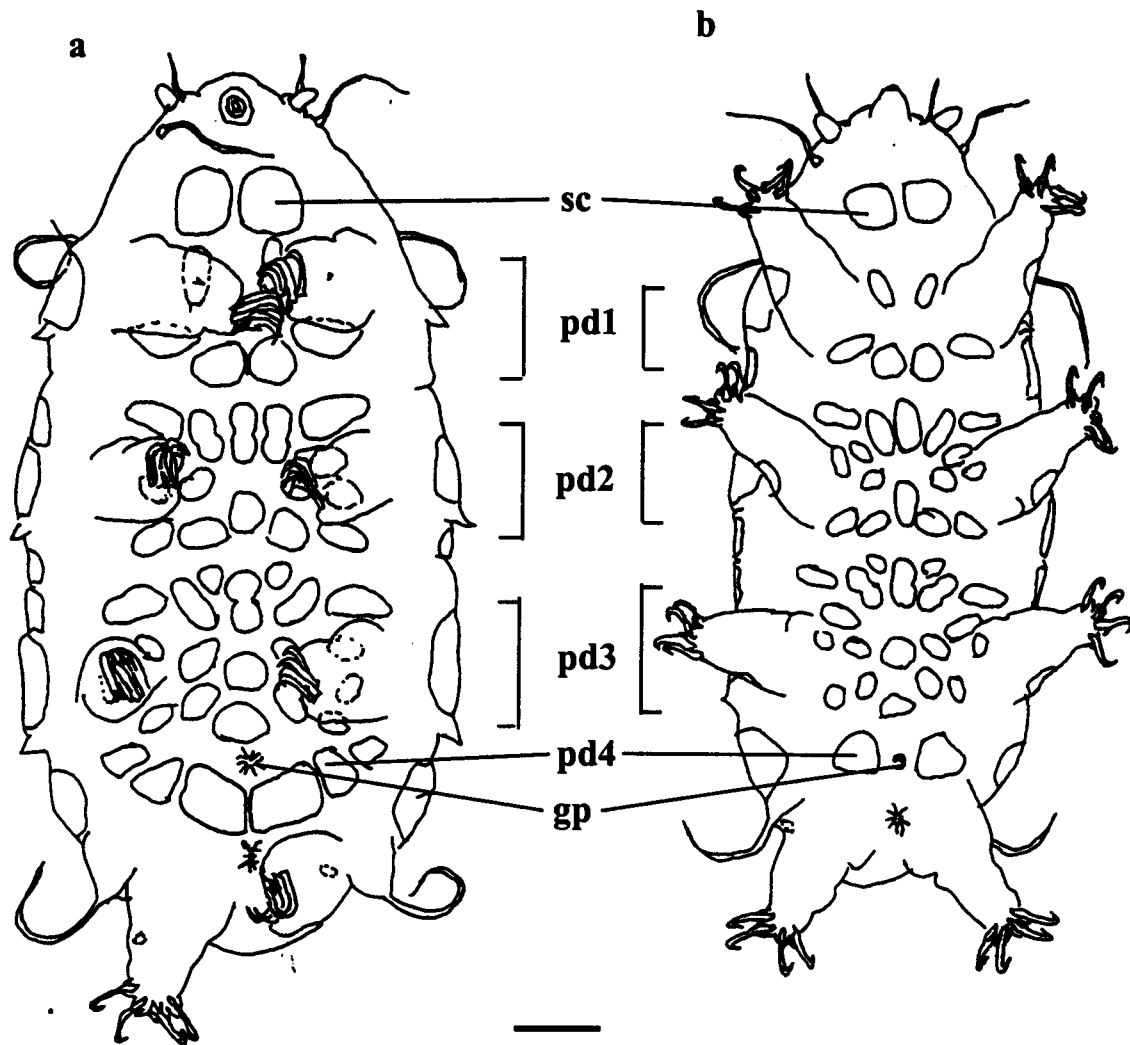


Table 3.6.1. Measurements (in μm) of a male and a female of similar size of three species of *Antechinus*.

Character	Species Gender	Measurement (μm)					
		<i>A. moscali</i>		<i>A. parvisentus</i>		<i>A. pulcher</i>	
		Female	Male	Female	Male	Female	Male
Body length		166.0	165.0	151.0	146.0	180.0	182.0
Internal buccal cirrus		12.4	15.7	7.6	9.7	12.4	15.1
Secondary clava		5.0	7.0	4.9	7.6	6.0	7.6
External buccal cirrus		14.6	19.6	16.2	17.8	24.3	27.0
Primary clava		5.0	6.5	4.9	6.5	6.0	7.6
Cirrus A		35.0	37.0	37.0	34.0	54.0	49.0
Appendage B		3.2	1.6	3.0	3.0	3.0	3.0
C		3.2	1.6	4.0	3.0	3.0	3.0
D		3.2	2.0	3.0	24.0	3.0	3.0
E		-	-	3.0	3.0	29.0	22.0
Claw I		9.1	9.7	7.6	7.6	9.7	10.8
Claw II-III		8.7	9.2	7.0	7.0	9.7	10.8
Claw IV		9.7	10.8	8.1	8.1	10.8	11.9

3.7 THE SUBFAMILY ITAQUASCONINAE RUDESCU, 1964 IN AUSTRALIA

3.7.1 Introduction

The family Hypsibiidae Pilato, 1969 is the richest family, in terms of genera, of the terrestrial Eutardigrada. Members are characterized by the presence of *Hypsibius*-type claws, i.e., the double claws of each leg are dissimilar in size and shape and the primary branch of the external claw is flexible at the junction with the secondary branch (Plate XVIIb). The subfamily Itaquasconinae Rudescu, 1964 contains few genera with few, rather rare, species. Only two species from this subfamily have been found in Australia (Pilato, Binda & Claxton, 2002). At present, there are five genera in this subfamily – *Itaquascon* de Barros, 1939, *Mesocrista* Pilato, 1987, *Platicrista* Pilato, 1987, *Parascon* Pilato & Binda, 1987 and *Astatumen* Pilato, 1997.

Pilato (1987) revised the definition of the subfamily and based it primarily on the nature of the apophyses for the insertion of muscles of the stylets which are “in the shape of a wide flat ridge” symmetrical with respect to the frontal plane. The caudal processes of these apophyses are “well developed and pointing backwards and sideways or slender and pointing sideways”. The furcae may have the postero-lateral processes thickened apically or they may be spoon-like and tapering or reduced while the placoids are long or absent and the pharyngeal apophyses absent. In describing the buccal apparatus of this subfamily, Pilato (1987) used the term “*Diphascon* model” but qualified it with the word “generally” because he noted that a bucco-pharyngeal tube with both a rigid anterior portion and a flexible posterior portion was to be found in a number of genera belonging to groups far removed from Hypsibiidae. Within the Hypsibiidae, this *Diphascon*-type buccal apparatus occurs in *Diphascon*, *Hebesuncus* (subfamily Diphasconinae) and in *Paradiphascon*, *Itaquascon*, *Mesocrista*, *Platicrista* and *Astatumen* (subfamily Itaquasconinae). The

qualification proved fortuitous when the genus *Parascon* was found in Tanzania (Pilato & Binda, 1987) without a flexible posterior portion to the bucco-pharyngeal tube but with the other characters required to place it within the subfamily Itaquasconinae.

Within the Itaquasconinae, *Mesocrista* and *Platicrista* can be identified by the presence of placoids in the pharynx (Pilato, 1987). *Astatumen* was created for those species of *Itaquascon* which lacked stylet supports (Pilato, 1997).

This section discusses species found in Australia of two existing genera in the subfamily Itaquasconinae, one species in the genus *Astatumen* and six in *Itaquascon*, and describes and discusses a new genus, *Lexia*, represented by three new species (*L. breviunguis*, *L. melbaensis* and *L. trihalicis*) found in southern Australia.

3.7.2 Materials and Methods

Specimens were obtained from leaf litter and cryptogam samples and were mounted in Hoyer's medium and measured at 1000× under oil immersion using phase contrast (Chapter 2, Materials and Methods). Several specimens of the new genus were examined in water under normal light at 400×.

Fig. 3.7.2 shows the buccopharyngeal apparatus of a specimen of *Lexia* gen. n. and indicates the points used for measurement of the various structures.

3.7.3 Results and discussion

Details of the material examined, diagnoses and descriptions of all the species discussed may be found in Chapter 4 of this work.

Amongst the six species of *Itaquascon* found in Australia, five are new to science. The only previously described species, *I. pawlowskii*, was redescribed by Dastych (1988). It is known from only a few sites in Europe (Dastych, 1988), one in Canada (Kathman, 1990) and one in Japan (Abe & Takeda, 2000a). The two Australian specimens were found at two different sites in the highlands of New South Wales. Of the other five species, four are very similar in overall appearance and in having stylet supports inserted at the junction of the buccal and pharyngeal tubes and in having very slender, S-shaped stylet supports (plate XVIIa). They are *I. brevitubulus*, *I. cambewarrensis*, *I. longitubulus* and *I. unguiculum*. *I. pseudotrinacriae* is very different in overall appearance, having a much wider buccal tube and a long oval pharynx. It is much more similar in appearance to *A. trinacriae* which, however, lacks stylet supports and has a very long pharyngeal tube which continues anteriorly well past the caudal ends of the stylets (Plate XVIIc).

I. pseudotrinacriae may prove to be the same species described by Bertolani (1982) and named *Itaquascon* cf. *trinacriae* by Manicardi & Bertolani (1987) since it was described as having annulation on the bucco-pharyngeal tube only below the level of the stylet furcae, i.e., much shorter than in specimens of *A. trinacriae*. Although there was no mention of stylet supports in either description of *I. cf. trinacriae*, these structures could be overlooked as they are very fine and hard to see in many specimens in the Australian material (Plate XVIIId). Both *I. pseudotrinacriae* and *I. cf. trinacriae* have cuticular bars only on the second and third pair of legs (*A. trinacriae* has bars on the first three pair of legs). Only three specimens of *A. trinacriae* were found in this study. It is considered to be a cosmopolitan species (McInnes, 1994) but because of the problems described above there is the possibility of misidentification in many of these citations.

***Lexia* gen. n.**

The *Hypsibius* type claws (Plate XVIIIb, d, f) place *Lexia* gen. n. in the family Hypsibiidae and these claws and the absence of placoids in the pharynx place it close to *Itaquascon*.

The size and shape of the bucco-pharyngeal apparatus, however, suggests that it is very close to the genus *Parascon*, although it differs from that genus by having spiral thickening around the tube below the insertion point of the stylet supports and by the shape and size of the stylet supports. The annulation around the pharyngeal tube of this new taxon was observed in fresh specimens mounted in water. In most of the specimens mounted in Hoyer's medium and examined at a later date, the annulation had faded considerably and, in many specimens, was not visible at all. This was also found to be a problem with many specimens of *Itaquascon*. It is, therefore, imperative that specimens of this whole group should be observed first in water before mounting. It is possible that the single specimen of *Parascon* used in the description of this genus has annulation that has faded with time in the mounting medium. In analyzing their data, Pilato & Binda (1987) give *pt* values for the claws of their specimen as the ratios of the claw length to the length of the buccal tube from the anterior apophyses to the point of insertion of the stylet supports. This implies that the tube is divided into a buccal tube and a pharyngeal tube at the level of the stylet insertion point. However, in the diagnosis for the genus, the authors state that the tube is rigid over the whole length and should, therefore, be considered to be a buccal tube in keeping with the terminology used for other genera with rigid tubes eg. *Hypsibius*. The *pt* ratio should, therefore, be relative to the entire length of the tube. Similar sized specimens of *Lexia* gen. n. were compared with the specimen of *Parascon schusteri* Pilato & Binda, 1987 in Table 3.7.1. The *pt* ratio (relative to the length of the tube from the anterior apophyses to the stylet insertion point) for *Parascon* was used to facilitate the comparison. The measurements of *P. schusteri* and the specimen of *Lexia melbaensis* sp. n. are similar in many measurements but the *pt* ratios are rather dissimilar.

In particular, the *pt* for the stylet insertion point is quite different and should be discriminatory at the species level. *Pt* values for the claws indicate considerable difference between *Parascon schusteri* and the two species of *Lexia* which have very similar values. This is misleading, as the posterior claws of the two species of *Lexia* are quite dissimilar in the length of the primary branch. A more discriminatory ratio might be, the length of the primary branch with respect to the length of the secondary branch.

There seems to be a distinct difference in the nature of the stylet supports between *Parascon* and *Lexia*. The buttressed stylet supports of *Lexia* (Plate XVIIIa, c, e) are unique in the Eutardigrada and are quite dissimilar to those of *Parascon*, which are described as being “slender”, and those of *Itaquascon*, which appear to be long slender rods often bent into an S-shape and without either proximal or distal thickening, at least in the six species found in Australia. The buttress of the stylet support of specimens of *Lexia* gen. n. (strongest in *L. melbaensis*) is clearly part of the support itself and not a thickening of the buccal tube as happens in other genera of eutardigrades, e.g., some species of *Minibiotus* and *Macrobiotus*. In addition, the distal end of the stylet support is a little narrower than the proximal end and does not have the leaf-like structure that is present on supports of other Hypsibiidae, e.g., *Diphascon* and *Isohypsibius*. *Lexia* gen. n. has no cuticular structures in the pharynx while *Parascon* is described as “lacking pharyngeal apophyses, placoids and septula but with cuticular bulbular bars as present in *Itaquascon trinacriae*” (Pilato & Binda, 1987).

An important character described by Pilato (1987) for Itaquasconinae is the shape of the apophyses, for the insertion of muscles of the stylets, as a “very flat ridge”. In *Lexia* gen. n., the whole buccal apparatus is reduced in size and, in all three species, the buccal tube is very narrow and the nature of the apophyses is very difficult to discern, even in the largest

specimens. If apophyses in the shape of a “very flat ridge” are present they are also very reduced.

Pilato & Binda (1987) gave a ratio of the length of the bucco-pharyngeal tube to the body length of 8.3% for *Parascon* and of 15.7% for *I. umbellinae*. *L. breviunguis* (5-6.3%) and *L. trihallicis* (6.3%) have a much shorter buccal tube relative to body length than any other species. *L. melbaensis* has a somewhat longer bucco-pharyngeal apparatus at 10.4%. A ratio of 9-10% is quite common amongst species of *Isohypsibius* and *Minibiotus* but tends to be higher in *Itaquascon* (15% for *I. brevitubulus*, 22% for *I. longitubulus*).

The reduction of the furcae of the stylets seen in species of *Itaquascon* is even more pronounced in *Lexia* gen. n. (Plate XVIIIa, c, e). The stylets do not have the two small branches seen in species of *Itaquascon* but appear to terminate in a single small knob.

Although the specimens under consideration here are similar to *Parascon* in a number of respects, the differences in the nature of the stylet supports and the presence of an annulated pharyngeal tube present sufficient grounds to institute a new genus for them.

Figure 3.7.1 Buccopharyngeal apparatus of *Lexia* gen. n. indicating points used for measurement of structures

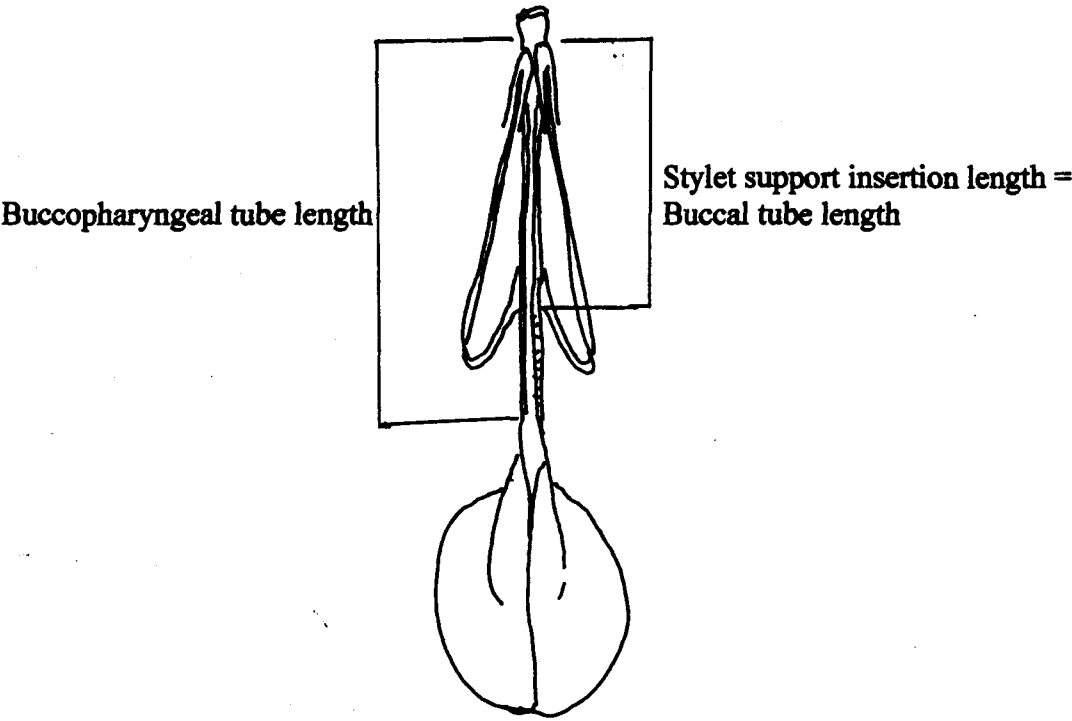


Table 3.7.1. Comparison of measurements (in μm) and pt values of some characters of single individuals of approximately the same body length of *Parascon schusteri* Pilato & Binda, 1987, *Lexia melbaensis* sp. n. and *Lexia breviunguis* sp. n.

Character	Species	Measurement					
		<i>Parascon schusteri</i>		<i>Lexia melbaensis</i>		<i>Lexia breviunguis</i>	
		μm	pt	μm	pt	μm	pt
Body length		320		308		322	
Buccopharyngeal tube length		26.5		31.9		20.5	
Buccal tube length		16.9		21.6		15.1	
Stylet support insertion length		16.9		21.6		15.1	
			63.9		67.7		73.7
Buccal tube width		1.6		1.9		1.5	
			9.5		8.9		7.3
Pharynx length		16.1		16		15	
Pharynx width		12.5		15		15	
Claw IV anterior		10.2		9.7		6.8	
			60.1		44.9		45.0
Claw IV posterior		17.7		17.3		12.4	
			104.7		80.1		82.1

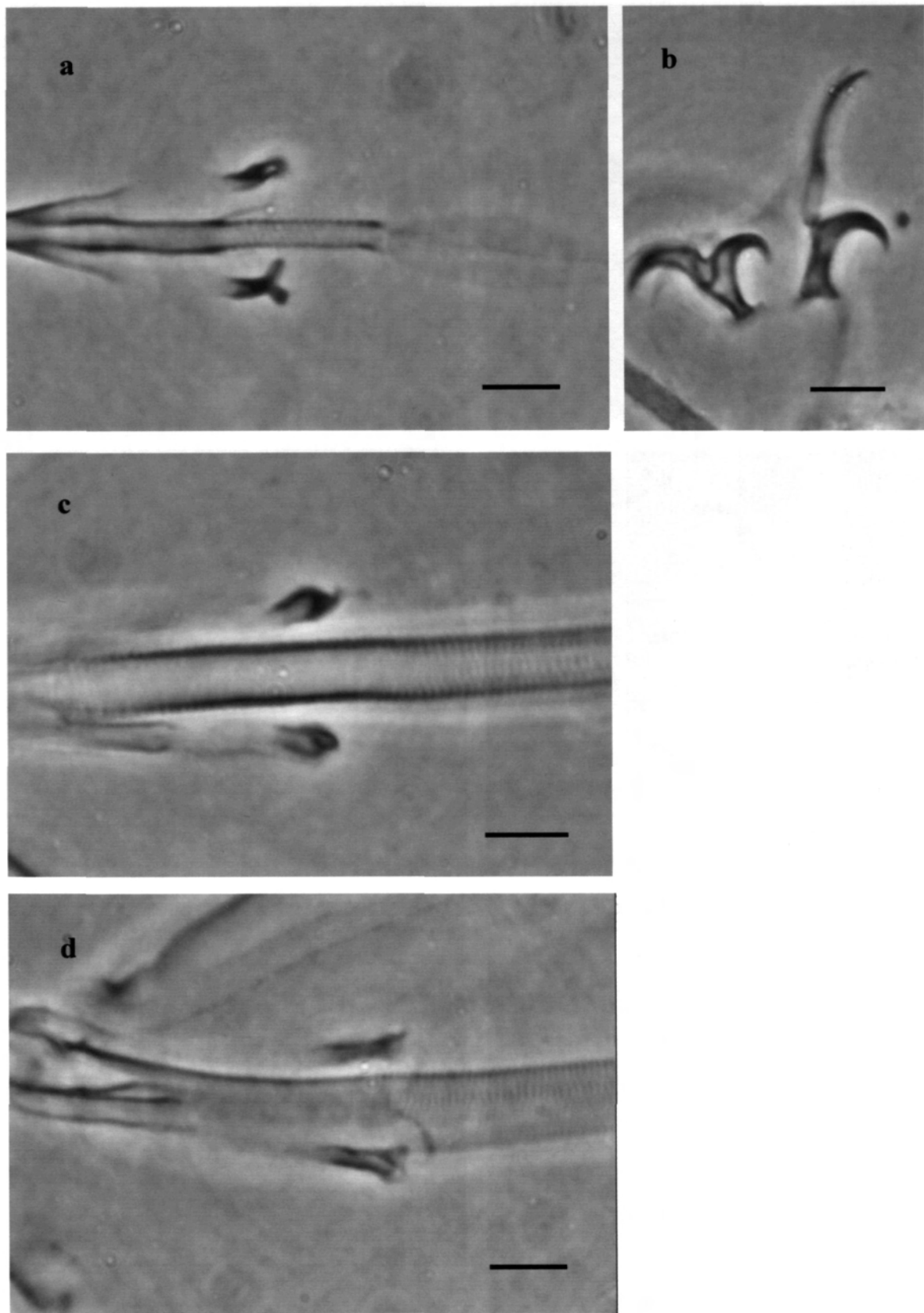


Plate XVII (a). Buccal tube and S-shaped stylet supports of *Itaquascon brevitubulus* sp. n., (b). claws of the fourth leg of Hypsibiidae, (c). Buccal tube and stylets of *Astatumen trinacriae* (Arcidiacono, 1962), (d). Buccal tube and stylet supports of *Itaquascon pseudotrinacriae* sp. n. Phase contrast. (Scale bars = 5 um)

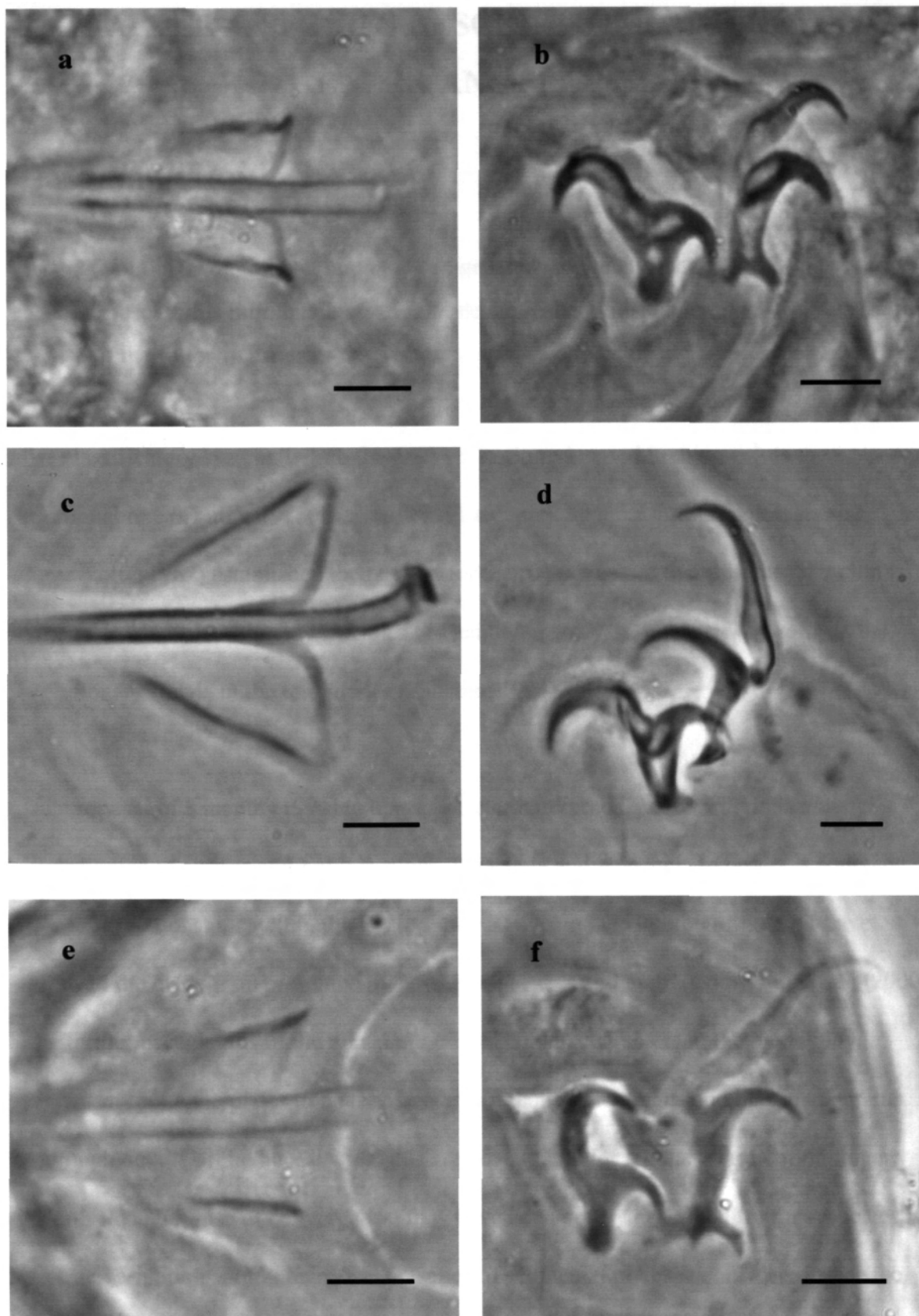


Plate XVIII. *Lexia* gen. n. sp. n. *Lexia breviunguis* sp. n. (a). buccopharyngeal tube, (b). claws of the third leg. *Lexia melbaensis* sp. n. (c). buccopharyngeal tube with buttressed stylet supports, (d). claws of the third leg. *Lexia trihallicis* sp. n. (e). buccopharyngeal tube, (f). claws of the third leg. Phase contrast. (Scale bars = 5 μ m)

CHAPTER 4. SPECIES DESCRIPTIONS AND KEYS TO GENERA AND SPECIES.

4.1 INTRODUCTION

A review of the taxonomic literature of tardigrades is found elsewhere in this thesis. The main purpose of this introduction is to provide the reader with some points of guidance for the use of the following species descriptions.

The classificatory system, within the phylum Tardigrada, used in this work is the traditional one (Thulin, 1928; Marcus, 1929) accepted by most tardigradologists since Ramazzotti (1962) established the phylum for them. I am aware that this classification is not constructed according to principles of Hennigian analysis, but it clearly reflects the evolutionary trends in the tardigrades (Kinchin, 1994).

The proposal of Kinchin (1994) to upgrade Heterotardigrada, Mesotardigrada and Eutardigrada to classes and Echiniscoidea, Parachela and Apochela to orders is followed here. For relationships within the family Echiniscidae in the Heterotardigrada, I have followed the cladogram presented by Kristensen (1987) and upgraded by Jørgensen (2000). The former used details of the dorsal plates as the main characters in the phylogeny. Jørgensen found the plates to be less convergent than sense organs and buccal apparatus. Although details of the buccal apparatus are not suitable for reconstruction of phylogeny in Echiniscidae because of convergence, they have been poorly described for most species so the true variation is not known. The presence of segmental plates is considered to be the plesiomorphic condition and the lack of plates the apomorphic condition found in all other heterotardigrade families and all eutardigrades.

The classification of Eutardigrada is a synthesis of the work of Pilato (1969a, 1987, 1998) and Schuster *et al.* (1980). These authors combined the evolutionary trends in the shape of the claws with the structure of the buccal apparatus. The shape of the claws has been especially conservative in the evolution of eutardigrades and has, therefore, been a key character in defining the seven eutardigrade families. Although the two orders (Parachela and Apochela) raised by Schuster *et al.* (1980) have been accepted, it is the families erected by Pilato (based on claw structure) which have gained widest acceptance and which are used here.

Pilato (1987) subdivided the genus *Diphascon* into four genera (*Diphascon*, *Hebesuncus*, *Mesocrista* and *Platicrista*) and provided evidence that the two latter genera shared a common origin with *Itaquascon*. He ascribed these three genera to the subfamily Itaquasconinae. *Diphascon* was split into two subgenera (*Diphascon* and *Adropion*) and these subgenera have been accepted in this work. However, Guidi & Rebecchi (1996) noted a greater similarity between the sperm of *Diphascon* (*Adropion*) and *Platicrista* than between *Diphascon* (*Adropion*) and *Diphascon* (*Diphascon*) suggesting that further inquiries into the relationships of these taxa are necessary.

The phyletic relationships within the most speciose family, the Macrobiotidae, have recently come under scrutiny (Guidetti *et al.*, 2000; Guidetti & Bertolani, 2001a). The former authors utilised the ultrastructure of the cuticle and details of the claws and buccopharyngeal apparatus to identify two subfamilies; Macrobiotinae and Murrayinae. The latter authors resolved the relationships among the genera of Murrayinae and identified, but did not resolve the relationships among the five main phyletic lines in the Macrobiotinae.

Pilato (1998) re-evaluated the claw structure of a number of species of eutardigrades and proposed the family Microhypsibiidae for two genera *Microhypsibius* and *Fractonotus*.

This chapter contains descriptions of 182 species of terrestrial tardigrades in 34 genera recorded in Australia in the present study and in other published works. Keys to these genera and species are provided. No single, up to date key to species of tardigrades is presently available. To determine the identity of the Australian species, the keys in Ramazzotti & Maucci (1983) were initially used. Other keys for specific genera were also used, e.g., Bertolani & Rebecchi (1993) for the *Macrobiotus hufelandi* group and Biserov (1997/98) for *Ramazzottius*. Reference is also made to the primary literature.

Several recently published works have addressed the problems of species identification in some taxonomically difficult species eg., the *Minibiotus intermedius* group (Claxton, 1998), the *Macrobiotus hufelandi* group (Bertolani & Rebecchi, 1993) and the *Macrobiotus harmsworthi* group (Pilato *et al*, 2000). However, although these have clarified the descriptions of some species, they have also thrown others into doubt. This account, therefore, provides as full a description as possible of the species found so far in Australia.

New species have been named and have the designation “sp. n.”. However, neither type material nor type localities have been included for these species in this thesis. Those will be designated in the appropriate publication with lodgement of type specimens in appropriate institutions.

Some “species” have not been formally named but have the suffix “sp.”, sometimes followed by a number. These are species for which there was insufficient material to determine if the specimens belonged to a known taxon or to a new species.

Descriptions of 21 species found in Australia by other workers, but not found in this study, have also been included for completeness. These descriptions have been derived from the original descriptions and/or from more complete descriptions in more recent publications. Figures are not included with these descriptions.

This chapter should be read in conjunction with Volume 2 that contains the relevant Figures and Plates and two Appendices. Figures constitute line drawings for each species found and identified in this study. Plates are provided for particular taxonomic features where greater clarity was deemed necessary.

Appendix 1 summarises the data for each of the sites at which tardigrades were found. Sites are referred to in the 'Material examined' sections for each species with, an italicised capital letter identifying the State in which the site is found, eg., *N*, for New South Wales, *Q*, Queensland, *V*, Victoria, *T*, Tasmania, *C*, Australian Capital Territory, *W*, Western Australia) followed by a number which is site specific, eg., "*N3*" is the site code for New England National Park.

Appendix 2 consists of a glossary of the terms used in the species descriptions with three figures (Figs. I-III).

For ease of use, all families in the Eutardigrada, genera in all families (Eutardigrada and Heterotardigrada) and all species within genera have been placed in alphabetical order. However, convention has been followed in placing the Heterotardigrada before the Eutardigrada and, within the Eutardigrada, Parachela is treated before Apochela.

McInnes (1994) was consulted for data on the distribution of known species. More recent publications supplied additional records for some species.

4.2 KEY TO GENERA

1.	Cirrus A present.....	2
	Cirrus A absent.....	10
2.	Cuticular plates on dorsum absent.....	<i>Oreella</i>
	Cuticular plates on dorsum present.....	3
3.	Pseudosegmental plates absent.....	4
	Pseudosegmental plates present.....	7
4.	Median plates 1 and 2 undivided.....	5
	Median plates 1 and 2 divided into anterior and posterior parts.....	6
5.	Plates strongly defined, leg plate on fourth pair of legs with dentate collar.....	<i>Echiniscus</i>
	Plates poorly defined, no leg plate on fourth pair of legs.....	<i>Hypechiniscus</i>
6.	Median plate 3 divided into anterior and posterior parts.....	<i>Bryochoerus</i>
	Median plate 3 undivided.....	<i>Bryodelphax</i>
7.	Cirrus A hair-like with short cirrophore.....	8
	Cirrus A different.....	9
8.	Pseudosegmental plates posterior to both paired plates.....	<i>Antechiniscus</i>
	No pseudosegmental plates posterior to paired plates.....	<i>Pseudechiniscus</i>
9.	Cirrus A horn-like with large cirrophore.....	<i>Cornechiniscus</i>
	Cirrus A long stiff spine without cirrophore.....	<i>Mopsechiniscus</i>
10.	Cephalic sensory structures present in the form of papillae..	11
	Cephalic sensory structures absent.....	13
11.	Oral cavity very short, buccal tube short, rigid, wide.....	<i>Milnesium</i>
	Oral cavity long, buccal tube long.....	12

- 12 Buccal tube long and annulated, stylets very long and flexible..... *Limmenius*
- Buccal tube not annulated, stylets long but not flexible..... *Milnesioides*
- 13 Claws absent..... *Apodibius*
- Claws present..... 14
- 14 Diploclaws similar in size and shape on each leg (except for fourth pair of legs where one or both claws may be different in shape from those on other three pairs of legs), symmetrical with respect to median plane of leg..... 15
- Diploclaws not similar in size and shape on each leg, asymmetrical with respect to median plane of leg..... 20
- 15 Basal parts of diploclaws on each leg joined by cuticular bar..... *Dactylobiotus*
- Basal parts of diploclaws on each leg not joined by cuticular bar..... 16
- 16 Claws with small thin basal part not separated from rest of claw by septum..... *Xerobiotus*
- Claws with basal part separated from rest of claw by septum..... 17
- 17 Mouth surrounded by 10 papulae..... *Minibiotus*
- Mouth surrounded by 10 lamellae..... 18
- 18 One or both claws on fourth pair of legs different from those on the other three pairs of legs, ie, with primary and secondary branches joined over a long distance..... *Calcarobiotus*
- Claws same on all pairs of legs..... 19
- 19 Claws short and thick, primary and secondary branches

- joined over much of their length with vertical suture and forming bulbous refractive unit, distal ends of primary and secondary branches diverging by 80° angle..... *Haptobiotus*
- Primary and secondary branches of claws not forming bulbous refractive unit at base..... *Macrobiotus*
- 20 Primary branch continuous with basal part of claw, secondary branch joined rigidly to primary branch either by vertical suture or at point just above base of claw..... 21
- Secondary branch continuous with basal part of claw, primary branch joined to secondary branch a considerable distance from base..... 24
- 21 Primary and secondary branches joined by vertical suture from base of claws..... 22
- Secondary branch joined to primary branch above a narrow basal portion continuous only with primary branch..... 23
- 22 Ventral support on buccal tube present..... *Parhexapodibius*
- Ventral support on buccal tube absent..... *Calohypsibius*
- 23 Paired elliptical organs present on head; on anterior of buccal tube, dorsal apophyses for insertion of stylet muscles split into two, anterior part a stumpy hook, posterior part a longitudinal thickening..... *Fractonotus*
- Paired elliptical organs absent; on anterior of buccal tube, dorsal apophyses for insertion of stylet muscles split into two, anterior part a “semilunar hook”, posterior part a small, short thickening..... *Microhypsibius*
- 24 Ventral support on buccal tube present..... *Doryphoribius*

	Ventral support on buccal tube absent.....	25
25	Buccopharyngeal tube divided into rigid anterior buccal tube and flexible posterior pharyngeal tube.....	26
	Buccopharyngeal tube rigid.....	30
26	Placoids present in pharynx.....	27
	Placoids in pharynx absent or reduced to single long slender rod.....	28
27	On anterior of buccal tube, apophyses for insertion of stylet muscles in shape of “semilunar hook”, symmetrical with respect to frontal plane.....	<i>Diphascon</i>
	On anterior of buccal tube, apophyses for insertion of stylet muscles in shape of “blunt hook”, asymmetrical with respect to frontal plane.....	<i>Hebesuncus</i>
28	Stylet supports absent, buccal tube very short.....	<i>Astatumen</i>
	Stylet supports present.....	29
29	Stylet supports fine and curved, no additional thickening on buccopharyngeal tube, stylets with furcae.....	<i>Itaquascon</i>
	Stylet supports with buttressed thickening on side of buccopharyngeal tube, stylets without furcae.....	<i>Lexia</i>
30	Six peribuccal papulae and 6 peribuccal lobes present, all diploclaws with primary and secondary branches diverging at 180° angle.....	<i>Eremobiotus</i>
	Peribuccal structures different, claws different.....	31
31	Six peribuccal lobes present.....	32
	Peribuccal lamellae present.....	34
32	Paired elliptical organs present; two claws on each leg very	

	different from each other.....	<i>Ramazzottius</i>
	Paired elliptical organs absent.....	33
33	On anterior of buccal tube, apophyses for the insertion of stylet muscles crest-shaped.....	<i>Isohypsibius</i>
	On anterior of buccal tube, apophyses for the insertion of stylet muscles hook-shaped.....	<i>Hypsibius</i>
34	30 small irregular sized peribuccal lamellae present.....	<i>Pseudobiotus</i>
	12 lamellae present.....	<i>Thulinus</i>

4.3 SPECIES DESCRIPTIONS AND KEYS TO SPECIES

Class Heterotardigrada Marcus, 1927

Suborder Echiniscoidea Marcus, 1927

Family Echiniscidae Thulin, 1928

Genus *Antechiniscus* Kristensen, 1987

Antechiniscus Kristensen, 1987: 269, Figs 6, 7, 15, 37, 45J.

Type species. *Pseudechiniscus lateromamillatus* Ramazzotti, 1964

Diagnosis. (Emended from Kristensen, 1987). Black eye spots. Rigid buccal tube. Cirrus A hair-like with short cirrophore. Unpaired pseudosegmental plates present posterior to all paired segmental plates. Small bar-shaped pseudosegmental plate IV' anterior to caudal plate; large undivided median plate 3. Ventral plates present.

Key to species of *Antechiniscus*

1. Spines or filaments at B, C and D..... *A. moscali*
 Spines or filaments at B, C, D and E..... 2
2. Long filament at E..... 3
 Short spine at E..... 4
3. Single ventral plate either side of gonopore..... *A. pulcher* male
 Three ventral plates either side of gonopore..... *A. pulcher* female
4. Long filament at D..... *A. parvisentus* male
 Short spine at D..... *A. parvisentus* female

Antechiniscus moscali Claxton, 2001

Figs 1, 3.6.1, 3.6.2; Tab. 3.6.1

Antechiniscus moscali Claxton, 2001: 282-286, Figs 1, 2, 4-10, Tab. 1.

Type locality. Pieman River, Tasmania.

Material examined: Australia: TASMANIA: *T10*, liverwort on tree in a riparian flat with regenerating rainforest including *Nothofagus*, 26 females, 19 males, 5 juveniles and 5 exuvia containing eggs (**Holotype**, allotype and paratypes).

Diagnosis: *Antechiniscus* with short broad-based spines at positions B, C and D. Broad pseudosegmental plate IV', narrow median plates. Ventral plates consisting of paired sub-cephalic plates and multiple plates on all trunk segments. Males smaller than females with relatively enlarged primary and secondary clavae.

Description: Yellow-green. Body length 122 (juvenile)-200 μm , females 166-200 μm , males 135-165 μm . Paired black eye spots present. In a 200 μm long specimen, cirrus A 43 μm long, primary clava 6 μm long, ovoid. Internal and external buccal cirri 13.5 and 17.8 μm long, with cirrophores, slender papillate secondary clava 5.4 μm long. Sculpture on plates double, consisting of uniformly distributed black dots and randomly distributed white spots. Head plate with median anterior notch and fine black dots only. Neck plate narrow with very fine black dots only. Scapular plate undivided, covered with black dots and small white spots. Paired segmental plates (II and III) wide, divided by a thin unsculptured band into an anterior third and posterior two thirds (with same cuticular pattern as scapular plate). Pseudosegmental plates II' and III' triangular. Pseudosegmental plate (IV') quite broad and with same sculpture as scapular plate. Median plate 1 small with convex posterior edge. Median plate 2 large with unsculptured band. Median plate 3 narrow. Lateral plate present below ventral margins of pseudosegmental plate IV' and caudal plate IV. Caudal plate with lateral indentations, sculpture of black dots and white spots larger than on other plates. Small, broad-based triangular spine present at the posterior edge of scapular plate, paired plates II and III (positions B, C and D) often missing in males.

Ventral plates present (Fig. 3.6.2). Pair of subcephalic plates below fused head segment. Trunk segment 1 with four lateral plates on each side, trunk segment 2 with two median plates and five lateral plates on each side, trunk segment 3 with two median plates and six lateral plates on each side. The number and grouping of these plates is the same in males and females. Trunk segment 4 with one plate on either side of the gonopore; males also have a crescent shaped plate immediately anterior to the gonopore.

First pair of legs with no sense organ, small papilla present on fourth pair. Patch of black dots above claws on outside of all legs, no dentate collar on fourth pair of legs. Claws long and slender, internal claws on all legs with fine recurved spur near base. Claws on first pair of legs slightly longer and more robust than those on second and third, those on fourth pair slightly longer than those on first pair. External claws of fourth pair of legs 11.3 μm long, internal 12 μm long (in 200 μm long specimen).

Five exuvia containing respectively 2, 2, 3, 3 and 3 smooth eggs were found.

Remarks. See Chapter 3, section 3.6

Distribution. The species was found in association with *Nothofagus*.

Antechiniscus parvisentus (Horning & Schuster, 1983)

Figs. 2, 3.6.3; Tab. 3.6.1

Pseudechiniscus parvisentus Horning & Schuster, 1983: 109-111, Figs 3, 4.

Type locality. Otepatotu Bush, Banks Peninsula, South Island, New Zealand

Material examined: **Australia:** NEW SOUTH WALES: *N3.2.b*, moss and lichen on rocks in subalpine heath, 26 specimens. *N3.3.a*, moss and lichen on trees in *Nothofagus* forest below escarpment lip, 34 specimens. *N3.4.a*, moss and lichen on trees, 1 specimen and *N3.4.b*, moss on trees and rocks in stand of *Nothofagus* on edge of escarpment, 3 specimens. *N3.5.a*, foliose lichens on trees in subalpine *Banksia* heath on escarpment top, 13 specimens. **New Zealand:** South Island, Otepatotu Bush, Banks Peninsula, in moss, 4 females (**holotype and paratypes**), 1 male.

Diagnosis. *Antechiniscus* with short broad-based spines at positions B, C, D and E. Males with spines at B, C and E, filament at D. Narrow pseudosegmental plate IV', large median plate 3. Ventral plates present but unclear. Males smaller than females with relatively enlarged primary and secondary clavae.

Description. Pale yellow-green. Body length 99 (larva)-212 μm , females 139-212 μm , males 131-149 μm . Black eye spots present. In 185 μm long female, cirrus A 40 μm long, primary clava 5.4 μm long. Internal and external buccal cirri 8.4 and 16.8 μm long, with cirrophores, secondary clava 5.4 μm long. Sculpture on plates double, consisting of uniformly distributed black dots and randomly distributed white spots. Head plate with median anterior notch, sculpture of black dots and white spots. Neck plate narrow, with very fine black dots only. Scapular plate undivided with uniform black dots (0.5 μm) becoming a little larger at the rear of the plate and with large white spots. Paired segmental plates (II and III) wide, divided by a unsculptured band. Pseudosegmental plates II' and III' large triangles. Caudal plate with large (0.8 μm) black dots and large white dots and with two lateral indentations. Short spine with very long base arises from within lateral incision of caudal plate. Pseudosegmental plate (IV') thin but ornamented with black dots and white spots, median plate 3, large overlapping pseudosegmental plate IV', covered with same sculpture as scapular plate. Median plates 1 and 2 with convex posterior edge, sculpture occurring only on posterior edge. Lateral plates present below ventral margins of pseudosegmental plate (IV') and caudal plate. Small broad based spines occur at postero-lateral point of scapular plate, and paired plates II and III (positions B, C and D). Spine at position D is replaced by filament (21-32 μm long) in males. In the single male specimen from New Zealand the filament was 15 μm long.

Ventral plates present (Fig. 3.6.3). Paired subcephalic plates and paired podial plates 4 are visible other plates are visible but not clear enough to count.

Measurements for the cephalic appendages of the Australian specimens agree with those given by Horning and Schuster (1983) for the New Zealand type material. Males have slightly longer primary and secondary papillae than females of the same size.

First pair of legs with long thin pointed papilla or spine and fourth pair with papilla about 3 μm long. Patch of black dots above claws on outer surface present on all legs, no dentate collar on fourth pair of legs. Claws robust, inner claw on all legs with short recurved spur near base. Claws on first pair of legs slightly longer than those on second and third. External claws on fourth pair of legs 7.5 μm long, internal 8 μm (in 185 μm female).

Larvae with two claws with spurs on each leg, otherwise similar to adults.

Two exuvia each containing 3 smooth orange eggs were found.

Remarks. See Chapter 3, section 3.6.

Distribution. Found in or near *Nothofagus* forests in Australia and New Zealand.

Antechiniscus pulcher (Murray, 1910)

Figs 3, 3.6.4; Tab. 3.6.1

Echiniscus pulcher Murray, 1910: 127, Pl. XVIII, Fig 34

Pseudechiniscus pulcher Marcus, 1928: 110, Fig 126

Type locality. Mount Kosciusko, NSW

Material examined. NEW SOUTH WALES: *N46.2* (type locality) moss on rock in subalpine open woodland, 1 specimen. Moss on rock collected by J. Murray, April, 1909, 5 specimens (syntypes). *N3.4.b*, moss on tree and rock in *Nothofagus* stand, 7 specimens, *N3.6.a*, moss and foliose lichen on rock in subalpine heath, 16 specimens.

Diagnosis. *Antechiniscus* with short broad-based spines B, C, D and long broad-based filament at E. Narrow pseudosegmental plate IV', narrow median plates. Ventral plates strong, consisting of paired subcephalic plates and multiple plates on all trunk segments. Females with 3 plates either side of gonopore, males with a single plate either side. Males smaller than females with relatively enlarged primary and secondary clavae.

Description. (Based on New England specimens) Orange-red. Body length 112(larva)-219 μm , females 180-219 μm , males 167-187 μm . Black eye spots present. In 184 μm long female, cirrus A 49 μm long, primary clava 6 μm long. Internal and external buccal cirri 13 and 26 μm long with small cirrophores, secondary clava slender, papillate and 6 μm long. Sculpture on plates double, consisting of uniformly distributed black dots and small randomly distributed white spots. Head plate with median incision and small black dots only. Neck plate narrow with very small black dots only. Scapular plate undivided, covered with double sculpture. Paired segmental plates (II and III) wide, with thickened bar on ventro-lateral edge, divided into an anterior third and posterior two-thirds by thin unsculptured band. Pseudosegmental plates II' and III' triangular. Pseudosegmental plate (IV') broad with double sculpture. All median plates with double sculpture and convex posterior edge. Median plate I small, median plate 2 large. Median plate 3 overlaps pseudosegmental plate IV'. Cushion-shaped lateral plate lies directly below ventral margins of pseudosegmental plate IV' and caudal plate IV. Small triangular spine present

at posterior edge of the scapular plate (position B), paired plate II (C) and paired plate III (D). Long broad-based filament at E.

Ventral plates present (Fig. 3.6.4). Paired subcephalic plates present. Trunk segment 1 with three lateral plates on each side, trunk segment 2 with two median plates and seven lateral plates on each side, trunk segment 3 with three median plates and eight lateral plates on each side. The number and grouping of these plates is the same in females and males.

Trunk segment 4 with three plates either side of the gonopore in females and one either side in males.

First pair of legs with sense organ in form of a spine and fourth pair of legs with small papilla. Patch of black dots present above claws on outside of all legs, no dentate collar on fourth pair of legs. Claws slender with fine recurved spurs on inner claws. Claws of first pair of legs slightly longer than those on second and third and those on fourth pair slightly longer than claws on first pair. External claws of fourth pair of legs 11.8 μm long, internal 12.4 μm long (in 184 μm female).

3 and 4 smooth orange eggs found in exuvia.

Remarks. See Chapter 3, section 3.6.

Distribution. Found near *Nothofagus* forest at New England. It occurs on Mt Kosciusko in the absence of *Nothofagus* but pollen of these trees has been found in soil cores from that mountain.

Genus *Bryochoerus* Marcus 1936

Bryochoerus Marcus 1936: 41, Fig. 47.

Type species. *Bryochoerus intermedius* (Murray, 1910)

Diagnosis. (Emended from Kristensen, 1987). Red eye spots. Rigid buccal tube with CaCO₃ encrusted stylet supports. Median plates 1, 2 and 3 divided. Pseudosegmental plates IV' absent. Lateral intersegmental plates present. Ventral plates absent.

***Bryochoerus intermedius* (Murray, 1910)**

Fig 4

Echiniscus intermedius Murray, 1910: 129-131, Pl XVI, Fig. 17

Bryodelphax intermedius Thulin, 1928: 221

Echiniscus (Bryodelphax) intermedius Marcus, 1929: 308-309, Fig. 142

Echiniscus (Bryochoerus) intermedius Marcus, 1936: 42-43, Fig. 48

Type locality. Eumundi, Queensland.

Material examined: NEW SOUTH WALES. *N43*, moss on rock in subalpine heath, 12 specimens.

Diagnosis. Head and neck plates well developed. Scapular plate with two anterior insertions. Segmental plates II and III paired. Caudal plate without notch or indentation but with indentation lines separating facets. Secondary clava bent latero-ventrally.

Description. Pale yellow. Body length 135-165 µm. Males not found. Red eye spots present. In 160 µm long specimen, cirrus A 35 µm long, primary clava 3.8 µm long.

Internal and external buccal cirri 5.4 and 8 μm long without cirrophores, secondary clava 4.9 μm long bent latero-ventrally. Sculpture double, fine uniformly distributed black dots and large coalescing white spots. Head plate with large anterior median incision. Neck plate narrow with very fine black dots only. Scapular plate narrow, with double sculpture and with white spots arranged in irregular rows. Paired segmental plates II and III with thin unsculptured band dividing plates in half. Lateral plates present at dorso-lateral edges of scapular plate and paired plates II and III. Median plate I narrow with rounded posterior edge; median plate 2 large with plain transverse band across middle; median plate 3 small with small triangular anterior part and narrow posterior part. Caudal plate without lateral indentations but with ridges dividing plate into facets.

Ventral surface with uniformly distributed black dots only, two round areas with more pronounced dots on either side of gonopore (they do not appear to be plates).

Sensory organ absent on first pair of legs and present, in form of a small papilla, on fourth pair. Sculptured leg plate with serrated but not dentate collar present on fourth pair of legs. Claws slender with fine recurved spur on the inner claws. Internal claw of fourth pair of legs 7 μm long, external claw 6.5 μm long (in 160 μm long specimen).

Eggs not found.

Remarks. The genus *Brychoerus* is dubious (Kristensen 1987).

Distribution. This species has been recorded from North and South America and the Pacific Islands as well as Australia. Two subspecies have been described, however,

considering the taxonomic problems associated with this species its distribution should be considered to be unknown.

***Bryodelphax* Thulin 1928**

Bryodelphax Thulin 1928: 220

Type species. *Bryodelphax parvulus* Thulin 1928

Diagnosis. (from Kristensen, 1987) Red eye spots. Rigid buccal tube with CaCO₃ encrusted stylet supports. Median plates 1 and 2 divided; median plate 3 undivided. Pseudosegmental plates IV' absent. Ventral plates present or absent.

***Bryodelphax australis* sp.n.**

Fig 5

Type material examined: Australia: NEW SOUTH WALES: *N1*, leafy liverwort on tree in garden, 3 specimens. QUEENSLAND. *Q1*, moss on rock in vine thicket, 15 specimens. *Q4*, moss/lichen on tree in shade, 2 specimens. *Q9*, lichen on tree close to sea, 13 specimens. *Q15*, moss and liverwort on tree in dry rainforest, 28 specimens. *Q18*, liverwort on tree in park, 2 specimens. *Q26*, liverwort on tree in rainforest remnant, 7 specimens.

Diagnosis. Paired plates II and III divided in half by unsculptured band. Caudal plate without incisions but with two lateral ridges which form facets. Median plates 1 and 2 divided into two parts, median plate 3 undivided. Ventral plates in 5 transverse rows, each plate made up of small granules.

Description. Pale yellow. Body length 90-140 μm . Males not found. Red eye spots present. Mouth antero-ventral, buccal tube short, stylet supports not visible. In 130 μm long specimen, cirrus A 29 μm long, primary clava 4 μm long. Internal and external buccal cirri 6.5 and 12.4 μm long without cirrophores, secondary clava 4.6 μm long. Sculpture double, with uniformly distributed black dots and of randomly distributed white spots which often appear to join. Head plate with anterior median incision. Narrow neck plate present. Scapular plate narrow. Paired plates II and III divided into two by thin unsculptured transverse band. Lateral plates absent, although small ridges apparent along lower edge of scapular and paired plates. Median plates I and 2 divided into two parts by plain transverse bands, median plate 3 undivided. Caudal plate without lateral indentations but with lateral ridges dividing plate into facets.

Ventral plates present in 5 transverse rows, each plate consisting of small granules. Paired subcephalic plates present. Trunk segment 2 lacking plates, trunk segments 3 and 4 with two round median plates and two elongated lateral plates, trunk segment 4 with an elongated plate either side of gonopore and one posterior to it.

Sensory organ absent on first pair of legs and present in the form of small papilla, on fourth pair of legs. Small unornamented leg plate with lightly serrated but not dentate collar on fourth pair of legs. Claws slender with fine recurved spur on the internal claws. Internal claws of fourth pair of legs 6 μm long, internal claws 5.4 μm long (in 130 μm specimen).

Eggs were not found.

Etymology. *L. australis*, southern

Remarks. This species differs from all other known species in the genus by the nature and number of the ventral plates.

Distribution. The species is widespread in Queensland.

Genus *Cornechiniscus* Maucci & Ramazzotti, 1981

Cornechiniscus Maucci & Ramazzotti 1981: 147-151

Type species. *Echiniscus cornutus* Richters 1906

Diagnosis. (from Kristensen, 1987) Black eye spots. Flexible buccal tube. Cirrus A horn-shaped with large cirrophore with primary clava rising from it. Secondary clava ovoid; internal and external cirri onion-shaped. Paired pseudosegmental plates IV' present.

***Cornechiniscus* sp**

Fig 6

Material examined: Australia: NEW SOUTH WALES: *N15*, weft moss on limestone rock in valley, 1 exuvium containing 4 smooth eggs.

Diagnosis. Yellow-red body cells. Strong W-shaped suture on scapular plate. Sculpture of evenly spaced black granules. Unpaired plates 1, 2, 3 undivided. Paired plates II and III with transverse fold. Caudal plate with long deep incisions.

Description. Yellow-red. Body length about 330 μm Eye spots unknown. Cirrus A 30 μm long, horn-shaped, rigid, rising from a conical base which it shares with an ovoid primary clava 8 μm long. Secondary clava dome-shaped 7.6 μm diameter. Internal buccal cirrus unknown, external buccal cirrus short, conical with flagellum 22 μm long. Sculpture composed of evenly spaced granules. Head plate with large W-shaped suture and fine even black dots. Neck plate narrow with very fine black dots. Scapular plate narrow with wide W-shaped suture, wide pseudosegmental plate I'. Paired segmental plates II and III very wide with pseudosegmental elements (II' and III') along posterior edges. Pseudosegmental plate IV' are very difficult to see on this specimen. Median plate I divided into two parts, median plate 2 divided into three parts? and median plate 3 undivided. Intersegmental plates present laterally to median plates 1 and 2. Caudal plate small without lateral indentations. Sense organs on legs unknown. Leg plate present on fourth pair of legs with smooth collar. Claws long and slender, spurs absent. Outer claw on first pair of legs 16.8 μm , on fourth pair 24.3 μm long.

One exuvium containing four smooth eggs found.

Remarks. The exuvium is not sufficiently well preserved to allow identification to species.

Distribution. This is the first record of the genus *Cornechiniscus* in the Southern hemisphere, and throws into doubt the contention of Kristensen (1987) that it is an exclusively northern genus. There is the possibility that the specimen has been imported from the northern hemisphere by people, because Jenolan Caves, where the specimen was found, is a busy tourist attraction.

Genus *Echiniscus* Schultze 1840

Echiniscus Schultze 1840:

Type species. *Emydium testudo* Doyère, 1840

Diagnosis. (after Kristensen 1987) Red eye spots. Rigid buccal tube. Primary and secondary clavae papillate. Median plates undivided, caudal plate notched.

Pseudosegmental plates IV' and ventral plates absent. Leg plate on fourth pair of legs with dentate collar.

Key to species of *Echiniscus*

- | | | |
|----|---|------------------------|
| 1. | Trunk appendages absent..... | 2 |
| | Trunk appendages present..... | 7 |
| 2. | Green body cells..... | <i>E. viridissimus</i> |
| | Red or yellow body cells..... | 3 |
| 3. | Cuticular sculpture of ridges and hemispherical knobs..... | <i>E. tessellatus</i> |
| | Cuticular sculpture different..... | 4 |
| 4. | Scapular and caudal plates with unsculptured bands, no
sensory organ on first leg, patch of sculpture on all legs..... | <i>E. vinculus</i> |
| | Scapular and caudal plates without unsculptured bands..... | 5 |
| 5. | Cirrus A short, dentate collar on fourth pair of legs with few
large teeth..... | <i>E. neowendti</i> |
| | Cirrus A long, dentate collar on fourth pair of legs with many
teeth..... | 6 |
| 6. | Cuticular sculpture, dense uniformly sized hexagonal dots, | |

	caudal plate facettèd.....	<i>E. arctomys</i>
	Cuticular sculpture of fine uniformly sized and shaped pores, caudal plate not facettèd.....	<i>E. kerguelensis</i>
7.	Large bulb on caudal plate.....	8
	No large bulb on caudal plate.....	9
8.	Long spines present at B, B ^d , C, C ^d , D, D ^d and E; sculpture of strong small round unevenly distributed black dots and large unevenly sized and distributed white spots; males present.....	<i>E. bulbulus</i>
	Short spines at C, C ^d , D, D ^d and E; sculpture of small evenly sized and distributed black dots and white spots; males present.....	<i>E. curiobulbus</i>
9.	Sensory spines present on first three pairs of legs, trunk appendages spines at positions C, D, D ^d and E.....	<i>E. perarmatus</i>
	Sensory spines only on first pair of legs.....	10
10.	Dorsal trunk appendages absent.....	11
	Dorsal trunk appendages present.....	12
11.	Trunk appendages long filaments at C, D and E.....	<i>E. jamesi</i>
	Trunk appendages short spines at C, D and E.....	<i>E. rodnae</i>
12.	Trunk appendages only at E, C ^d and D ^d	<i>E. aridis</i>
	Trunk appendages at lateral positions.....	13
13.	Sculpture polygonal.....	14
	Sculpture not polygonal.....	16
14.	Polygons solid.....	<i>E. virginicus</i>
	Polygons with round white centers.....	15
15.	Trunk appendages filaments at C, D and C ^d and spines at D ^d and E.....	<i>E. blumi</i>

Trunk appendages spines present or absent at B, always present at C, D, E, C ^d and D ^d	<i>E. pusae</i>
16. Trunk appendages only spines.....	17
Trunk appendage both spines and filaments.....	22
17. Trunk appendages spines only at C, D, C ^d and D ^d	<i>E. maculosus</i>
Trunk appendages spines at other positions.....	18
18. Trunk appendages spines at B, C, D, E, C ^d and D ^d all with serrated edge.....	<i>E. duboisi</i>
Trunk appendages spines smooth.....	19
19. Trunk appendages small spines (less than 15 µm long) at B, C, D, E, C ^d and D ^d ; patches of sculpture on all legs.....	<i>E. marcusii</i>
Trunk appendages long spines (greater than 20 µm long); no patch of sculpture on first three pairs of legs.....	20
20. Spurs on internal claws of all legs strong and very high on claw.....	<i>E. spiniger</i>
Spurs near base of internal claw on all legs.....	21
21. Caudal plate with dark areas in matrix of cuticle forming lines.....	<i>E. arboris</i>
Caudal plate with no pattern of lines.....	<i>E. curiosus</i>
22. Trunk appendage filaments at B, D, E and C ^d and spines at C and D ^d	<i>E. oihonnae</i>
Trunk appendages filaments at E and C ^d and spines at C, D and D ^d	<i>E. velaminis</i>

Echiniscus arboris sp. n.

Fig 7, Plate 1a

Material examined: Australia: NEW SOUTH WALES: *N14.7*, lichen on tree in garden, 1 specimen. *N15*, moss and lichen on tree in sheltered valley, 4 specimens. *N29*, lichen on tree in sheltered valley, 48 specimens, 5 exuvia containing 1, 2, 3, 4 and 6 orange eggs. *N37*, lichen and liverwort on tree beside road, 19 specimens, 1 exuvium containing 3 eggs. QUEENSLAND: *Q18*, lichen on tree beside road, liverwort on tree in rainforest remnant, 13 specimens.

Diagnosis. Orange-gold. Sculpture double, evenly distributed black dots and pores (0.5-1.5 μm); caudal plate with dark areas in matrix of cuticle forming lines. Spines present or absent at B, C, D, E, C^d and D^d. Collar on fourth pair of legs with faint patch of pores and blunt teeth. Spurs on internal claws close to base of claw.

Description. Orange-gold. Body length 110 (larva)-250 μm . No males found. Eye spots unknown. In 200 μm long specimen, cirrus A 32 μm long, primary clava 6 μm long, ovoid. Internal and external buccal cirri short, 14 and 16 μm long, secondary clava 7 μm long. Sculpture double, evenly distributed black dots over all surfaces and unevenly sized and spaced round white spots (0.5-1.5 μm) on all plates (Plate 1, fig a), matrix around spots often with dark areas particularly on terminal plate where they form lines giving the appearance of faceting. Head plate with median anterior notch. Neck plate narrow with very fine black dots only. Scapular plate, with small lateral plates without spots. Short spine (about 5 μm long) present at B in 9/13 specimens from Eumundi, absent in other populations. Paired segmental plates (II and III) wide, with narrow unsculptured band separating anterior third with very small spots from posterior two thirds with larger spots. Short spines present at C and D (2-8 μm), one or both may be missing particularly in small specimens; longer flat spines also present or absent at C^d and D^d (7 and 15 μm), C^d shorter

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and absent in some populations. Short spine present at E (9-14 μm). Median plate I triangular with pores; median plate 2 with smooth anterior one third and pores on posterior two thirds and median plate 3 small. Caudal plate with wide short lateral indentations; matrix of cuticle with dark areas, which form lines across plate. First pair of legs with small spine and small papilla present on fourth pair. Plate on fourth pair of legs a faint patch of pores, dentate collar with 10-14 narrow separate sharp teeth. Claws short and robust, internal claws with strong curved spur close to base of claw. Claws of first three pairs of legs equal in length, fourth pair longest, internal claws 12 μm long, external 11 μm (in 200 μm long specimen).

Exuvia containing up to 6 smooth eggs found.

Etymology. *L. arboris*, tree, as the species was only found on trees.

Remarks. There is considerable variation in presence or absence of spines at all lateral and both dorsal positions and in the presence or absence of additional spurs along the length of some or all of these spines. One large specimen from Wombeyan not only had no spines on the body but both cirri A were very short and spine-like. The three populations (Wombeyan, Hamden Bridge and Eumundi) are essentially the same except for the spine variation and are a good reminder of the importance of examining populations and not single specimens in describing species.

Distribution. The species was only found in cryptogams on trees at all sites at which it was found.

***Echiniscus arctomys* Ehrenberg, 1853**

Echiniscus Arctomys Ehrenberg, 1853: 530

Type locality. Monte Rosa Mt, Italy.

Material examined: Australia: None. Cited by Murray (1910) as occurring at Katoomba, Blue Mountains, NSW.

Diagnosis. Sculpture of dense and uniform punctuation which are true granules and which are closer to each other than their diameter. Lateral appendages absent. Median plate 3 absent.

Description. Body length 230-330 μm . Reddish eye spots. Cirrus A moderate length.

Sculpture of plates a dense and uniformly distributed and sized punctuation; distance between dots less than their diameter. Paired segmental plates II and III sometimes with an anterior zone finely punctuated. Caudal plate faceted and with lateral indentations.

Median plate 3 absent. Trunk appendages absent. Spine on first pair of legs and small papilla on fourth pair of legs. Internal claws with large robust strongly curved spur, outer claws smooth. Fourth pair of legs with dentate collar of many sharp, irregular teeth. (from Ramazzotti & Maucci, 1983)

Remarks. Murray (1910) cited this species from observations on a single specimen from Katoomba, Blue Mountains where, he states, it was fairly plentiful. However, he describes his specimen as having sculpture in which the dots appear to be pits (in other descriptions of this species the dots are said to be true polygonal granules (Maucci, 1986). As well, Murray's specimen had no dentate collar or spurs on the inner claws so his identification is

extremely doubtful. It must be said however, that there is much taxonomic confusion in the *arctomys* group of *Echiniscus* species (those that have no lateral appendages other than cirrus A) largely due to the very poor original descriptions of such species as *E. arctomys* and *E. kerguelensis* Richters, 1904.

Distribution. Said to be cosmopolitan and found, in Italy, only above 1500 m. altitude (Ramazzotti & Maucci 1983). Taxonomic confusion makes the true distribution of this species questionable.

Echiniscus aridus sp. n.

Fig. 8, Plate 1b

Material examined: Australia: NEW SOUTH WALES: N48, foliose lichen on sandstone rock in open sclerophyll forest, 11 specimens, 1 exuvium containing eggs.

Diagnosis. Yellow-gold. Sculpture double small evenly spaced pores and fine regular granulation. Spines at C^d and D^d, small spine at E present or absent. Leg plates on all legs.

Description. Yellow-gold. Body length 135(larva)-297 µm. No males found. Eye spots unknown. In 220 µm long specimen, cirrus A 34 µm long on large cirrophore, primary clava small (4.3 µm long) ovoid. Internal and external buccal cirri with large cirrophores (18 and 22 µm long), secondary clava large (7.6 µm long) ovoid. Sculpture double, small evenly sized and spaced black dots small randomly spaced round spots about 0.5-0.8 µm diameter and about 1-1.5 µm apart over all surfaces (Plate 1, fig. b). Head plate with anterior median incision and double sculpture. Neck plate narrow, with double sculpture. Scapular plate large, with narrow lateral plates and even double sculpture over whole plate.

Paired plates II and III with unsculptured transverse bands separating narrow sculptured anterior region from wide sculptured posterior region. Trunk appendages thick flat spines at C^d (20-28 µm long) and at D^d (7-20 µm long). Caudal plate large with wide lateral incisions and double sculpture. Trunk appendages at E small spines on 7 specimens, absent from one E position on one specimen and absent from both E positions on 3 specimens. Median plate I a large triangle, median plate 2 large with unsculptured anterior half and strongly sculptured posterior half, median plate 3 strongly sculptured. Leg plates with double sculpture present on all legs. Ventral surface with strong evenly sized and spaced black dots, pair subcephalic plates present. First pair of legs with small spine, small papilla present on fourth pair. Dentate collar on fourth pair of legs with about 10 long strong, sometimes multiple-cusped teeth. Claws robust, internal claws with strong, curved spur near, but not reaching, base of claw. Claws on first three pairs of legs equal in length, claws of fourth pair longest, internal 12.5 µm long, external 11.5 µm (in 220 µm long specimen).

One exuvium containing 4 smooth eggs found.

Etymology. *L. aridus*, dry, for the environment in which it was found.

Remarks. The arrangement of appendages makes this species different from all other species described to date.

Distribution. Found only at the one locality.

Echiniscus blumi Richters, 1903

Fig 9, Plate 1c

Echiniscus blumi Richters, 1903: 172

Type locality. Spitsbergen.

Material examined: **Australia:** NEW SOUTH WALES: *N40*, foliose lichen on rock in open sclerophyll forest, 14 specimens, 1 exuvium containing 2 eggs. *N46.1*, moss and foliose lichen on rock in open sclerophyll forest, 14 specimens, 1 exuvia containing 7 eggs; *N46.2*, moss and foliose lichen on rock in open sclerophyll forest, 6 specimens. *N48*, wet moss and foliose lichen on sandstone rock in open sclerophyll forest, 13 specimens. **Switzerland.** Klus, moss on roof, 6 specimens.

Diagnosis. Orange-gold. Sculpture double, uniform polygons with clear central pores on all plates and even black dots. Filaments at B, C, D, C^d and spines at D^d and E. Internal claws with large spur, external claws with small spine near base, at least on fourth pair of legs.

Description. Orange-gold. Body length 155(larva)-400 µm (Kosciusko). No males found. Eye spots red. In 300 µm long specimen, cirrus A 78 µm long, primary clava 7.5 µm long, ovoid. Internal and external buccal cirri short, 15 and 23 µm long with large cirrophores, secondary clava 8.5 µm long, ovoid. Sculpture double, evenly sized and distributed black dots and evenly distributed polygons with white central spots up to 3 µm diameter (Plate 1, fig. c). Head plate with median anterior notch with patch of large black dots anterior to it. Neck plate narrow, with polygons without white centres. Scapular plate large, with lateral plates not separated from main plate by deep groove. Filament at B (25-180 µm long) present in some specimens. Paired segmental plates (II and III) wide, with transverse band dividing plate into anterior third and posterior two thirds. Transverse band is actually a

trough in the plate with sculpture of polygons without white centres that often extends to the anterior part of the plate. Long filaments at C, C^d and D (75-21 µm) and short spine at D^d (12-16 µm). Median plates 1 and 2 triangular; median plate small poorly defined.

Showy plates with open polygons present on all legs Caudal plate with short lateral indentations. Very short spine present at E, sometimes absent. Ventral surface with strong black dots and with pair of stronger patches in subcephalic position. Small triangular spine present on first pair of legs and small papilla present on fourth pair. Dentate collar of fourth pair of legs with up to 16 large triangular teeth. Claws slender, internal claws with large curved spine near base, external claw of third pair of legs often also with straight spur. Claws of first and third pair of legs equal in length, of second pair slightly shorter, of fourth pair longest. Internal claw of fourth pair 20.5 µm long, external 19.5 µm (in 300 µm long specimen).

Exuvia containing 7 smooth eggs found.

Remarks. The species has been the object of considerable study in Europe because of the variability within and between populations in the presence or absence of lateral trunk appendages, for example, Maucci (1985). Within the '*blumi*' group Maucci considered *E. trisetosus* (with no lateral appendages at B) to be a doubtful species, but Dastych (1988) treated it as a proper species and distinct from *E. blumi*.

In the present study, three populations were observed, Kosciusko with 9 specimens with filament at B, 16 without; Lake George with 1 specimen with filament at B, 14 without and Darling Hill with no specimens with filament at B. Specimens with and without the B filament of the same body length were measured and compared. There were no other observable differences between them and so all of these specimens have been placed in the

taxon *E. blumi*. Any more detailed study would require the observation of more specimens than were available here.

Distribution. This species has been recorded from every continent except Antarctica.

Echiniscus bulbulus sp. n.

Fig. 10, Plate 1d

Material examined. Australia: TASMANIA: T3, moss on rock in low woodland on mountain summit at 470 m. asl., 2 specimens. T8, moss/lichen on skeletal soil humps in stunted *Athrotaxis* stand, 22 specimens.

Diagnosis. Yellow-orange. Sculpture double, small unevenly spaced black dots and large uneven white spots. Filaments at B, C, D, E, B^d, C^d and D^d. Caudal plate with long notches and a median bulb-like thickening in the cuticle. Males present.

Description. Yellow-orange. Body length 90(larva)-211 μ m, females 160-211 μ m, males 150-183 μ m. Eye spots absent. In 180 (160) μ m long female (male), cirrus A 49 (44) μ m long, primary clava 5.4 (7.5) μ m long, ovoid. Internal and external buccal cirri 16 (15) and 17 (16) μ m long, both with cirrophores, secondary clava 6 (8) μ m long, ovoid. Sculpture on plates double, consisting of minute unevenly spaced black dots and large white spots, uneven in shape and often running into one another (Plate 1, fig. d). Head plate with anterior median notch. Neck plate narrow. Scapular plate large with double sculpture, with very large pores (2-3 μ m) often particularly in band on posterior border, side plates with only minute black dots. Trunk appendages long strong filaments at positions B and B^d (35-50 μ m long). Paired segmental plates II and III divided by an unsculptured band into anterior third and posterior two thirds. In the lateral area of the anterior third sculpture is

very faint. Long strong filaments at C, D, C^d and D^d (30-50 µm long). Median plate I triangular with double sculpture, median plate 2 with small anterior sculptured area, wide transverse unsculptured band and wide posterior sculptured area, median plate 3 with double sculpture. Caudal plate with short, wide incisions and carrying round cuticular bulb-like structure in mid-line, present on all specimens. Long filament present at E (30-40 µm). Ventral surface smooth. Spine on first pair of legs and small papilla on fourth pair. Fourth pair of legs with plate with only fine black dots and dentate collar with 10-12 long slender teeth, uneven in length. Claws rather short and robust, internal claws with long strong curved spurs. Claws on second and third pair of legs slightly shorter than those on first, those on fourth pair longest. Internal claws 9.2 (9.2) µm long, external 8.7 (8.7) µm (in 180 (160) µm specimens).

No eggs found.

Etymology. *L. bulbulus*, a swelling, after the strange bulb on the caudal plate.

Remarks. The round bulb-like structure in the caudal plate of this species is unique amongst tardigrade species and is, at present, unexplainable. It is present on all the specimens of this species and all of the specimens of *E. curiobulbus*. It is also similar to that species in the general dimensions of the body and the cephalic appendages but differs from it by having a different sculpture and having filaments at all positions and particularly at B and Bd.

Sexual dimorphism is limited to the body length and size of the clavae, males are on average shorter and males have relatively larger primary and secondary clavae than females.

Distribution. Found only at the type locality.

Echiniscus curiobulbus sp. n.

Fig. 11, Plate 1e; 4c

Material examined. Australia: VICTORIA: *V2*, fruticose lichen on rock in subalpine heath, 7 specimens. *V3*, moss and liverwort on tree in cool temperate rainforest, 27 specimens. TASMANIA: *T2*, foliose lichen on rock in heath, 2 specimens. *T3*, moss and filmy fern on rock in stream in heath on mountain, 3 specimens. *T5*, liverwort on log in wet sclerophyll, 1 specimen. *T7*, moss and liverwort on rock in wet gully, 27 specimens. *T10*, liverwort on tree, moss on soil in cool temperate rainforest, 9 specimens. *T12*, liverwort, 2 specimens. *T17*, moss on dolerite at 620 m. asl., 3 specimens.

Diagnosis. Yellow-orange. Sculpture double, small evenly spaced black dots and large uneven white spots. Spines at C, D, E, C^d and D^d in females, C, D, E and C^d in males. Caudal plate with short wide notches and a median bulb-like thickening in the cuticle. Males present showing some sexual dimorphism.

Description. Yellow-orange. Body length 90(larva)-211 µm, females 150-211 µm, males 135-189 µm. Eye spots absent. In 160 (160) µm long female (male), cirrus A 38 (38) µm long, primary clava 4.9 (7.5) µm long, ovoid. Internal and external buccal cirri 13 (15) and 15 (16) µm long, both with cirrophores, secondary clava 5.4 (8) µm long, ovoid. Sculpture double, consisting of minute evenly spaced black dots and large white spots, uneven in shape and often running into one another (Plate 1, fig.e). Head plate with anterior median notch. Neck plate narrow. Scapular plate large with double sculpture, with spots (1-1.6 µm diameter) particularly in band on posterior border, side plates with only the minute black dots. Paired segmental plates II and III divided by an unsculptured band into anterior third

and posterior two thirds. In the lateral area of the anterior third the sculpture is very faint. Spines present at C, D, C^d and D^d (5-15 µm long) in females rather variable in length, D^d spine always longest; C, D, and C^d in males. Spine at E (17 µm long), usually longer than those at other positions. Median plate 1 triangular with double sculpture; median plate 2 with small anterior sculptured area, wide transverse unsculptured band and wide posterior sculptured area; median plate 3 with double sculpture. White spots on all median plates larger (1.6 µm) than those on other plates. Caudal plate with short, wide incisions and carrying round cuticular bulb-like structure (Plate 4, fig. c) in mid-line, present on all specimens. Ventral surface smooth, faint plate-like areas either side of gonopore, often very difficult to see and two in subcephalic area. First pair of legs with spine and small papilla present on fourth pair. Fourth pair of legs with plate with fine black dots only and dentate collar with 10-12 long slender teeth, uneven in length. Claws rather short and robust, internal claws with long strong curved spurs. Claws on second and third pair of legs slightly shorter than those on first, those on fourth pair longest; internal claws 8.7 (9.7) µm long, external 8.2 (9.2) µm (in 160 (160) µm long specimen).

No eggs found.

Etymology. *L. curio-*, strange; *L. bulbus*, a swelling, after the strange bulb on the caudal plate.

Remarks. The round bulb-like structure in the caudal plate of this species was present on all specimens found and is the same as that present in *E. bulbulus* sp. n. It is also similar to that species in the general dimensions of the body and the cephalic appendages but differs from it by having a different sculpture, having spines not filaments and having no appendages at B and Bd. It is also rather similar to *E. curiosus* Claxton, 1996, in the

cuticular sculpture and the nature of the sexual dimorphism. It differs from that species by having a bulb on the caudal plate and having much larger spurs on the internal claws of all legs.

The sexual dimorphism exhibited by this species is a little less complex than that shown by *E. curiosus*. Males are, on average, shorter than females as in that species. Males have relatively larger primary and secondary clavae than females and also have longer claws. In all populations, males lack a spine at the C^d position and all females have a spine there. The male to female ratio is high, about 50:50 in all the populations examined.

Distribution. Found in a number of mesic habitats in Tasmania, the species was also found in similar habitats in southern Victoria.

Echiniscus curiosus Claxton, 1996

Fig. 12, Plate 1f

Echiniscus curiosus Claxton, 1996: 21-23, Figs 3A-D, 4C, 5C, 10; Tabs 5-7

Type locality. Cambewarra Mountain, NSW.

Material examined. NEW SOUTH WALES: *N3.1*, moss and lichen on rock in open sclerophyll at 1500 m. asl., 7 specimens; *N3.3*, *N3.5*, moss and lichen on rock and trees in subalpine heath, 22 specimens; *N3.3*, *N3.4*, liverwort and lichen on trees in cool temperate rainforest, 2 specimens. *N11*, lichen on trees in warm temperate rainforest, 6 specimens. *N14*, moss, lichen and *Banksia* cones on rocks, trees and soil in open sclerophyll on cliff top at 1200 m. asl., and moss on rock in warm temperate rainforest pocket, 144 specimens. *N21*, foliose lichen on tree in urban backyard, 7 specimens. *N29*, lichens on rock in open sclerophyll, 28 specimens. *N31*, lichen on tree in cool temperate rainforest, 1 specimen. *N34*, lichen on tree

in sclerophyll forest, 2 specimens. *N35*, moss on tree in cool temperate rainforest, 1 specimen. *N39*, moss and lichen on rock in warm temperate rainforest, 176 specimens (**type material**).

Diagnosis. Yellow-gold. Sculpture double, small evenly spaced black granulation and large uneven white spots. Spines present at C, D, E, C^d and D^d in females; D^d or absent at both dorsal positions in males. Paired plates with wide unsculptured band. Median plate 3 present but poorly defined. Caudal plate with long narrow incisions. Spurs on internal claws close to base of claws. Males present.

Description. Yellow-gold. Body length 85(larva)-215 µm, females 112-215 µm, males 115-190 µm. Eye spots absent. In 180 (160) µm long female (male), cirrus A 45 (47) µm long, primary clava 4.6 (5.5) µm long, ovoid. Internal and external buccal cirri 16 (19) and 17 (21) µm long, both with cirrophores; secondary clava 5.5 (6.5) µm long, ovoid. Sculpture on plates double, consisting of minute black granulation and large white spots, uneven in shape and often running into one another (Pl. 1, fig. f). Head plate with anterior median notch. Neck plate narrow. Scapular plate large with double sculpture, side plates with minute black dots only. Paired segmental plates II and III divided by an unsculptured band into anterior third and posterior two thirds. In the lateral area of anterior third sculpture is very faint. Long fine spines at C, D (12-14 µm long in female, 23-33 µm in males); very short spines at C^d and D^d (2-3 µm long when present). Median plate I triangular with double sculpture, median plate 2 with small anterior sculptured area, wide transverse unsculptured band and wide posterior sculptured area, median plate 3 with double sculpture. Caudal plate with long, narrow incisions, with long spine at E (around 20 µm long in females, 30 µm in males). Ventral surface with very fine black granulation. First pair of legs with spine and small papilla present on fourth pair. Leg plate on fourth pair of legs with faint double sculpture, dentate collar on fourth pair of legs with 9-15

sharp, triangular separate teeth. Claws rather short and robust, internal claws with fine curved spurs. Claws on first three pairs of legs same length, those on fourth pair longest (internal claws 10.3 (9.7) μm long, external 9.7 (9.2) μm (in 180 (160) μm long specimens).

Exuvia containing up to 7 yellow eggs found.

Remarks. This species exhibits considerable sexual dimorphism a description of which can be found in Claxton (1996). It is similar to *E. curiobulbus* sp. n. in the general dimensions of the body and the cephalic appendages but differs from it by having no cuticular bulb on the caudal plate and having much finer spurs on the internal claws on all legs.

Distribution. Widespread in NSW in both dry and temperate habitats. This species is, so far, known only from Australia.

***Echiniscus cf duboisi* Richters, 1902**

Fig. 13, Plate 2a

Echiniscus duboisi Richters, 1902: 24, Plate 1, Fig 4

Type locality. Java.

Material examined: Australia: QUEENSLAND: *Q5*, moss on rotten log in warm temperate rainforest, 3 specimens. *Q8*, lichen on tree in park, 9 specimens. *Q14*, crustose lichen on tree on island, 2 specimens. *Q17*, moss and lichen on trees and logs in open sclerophyll forest, 8 specimens. *Q18*, lichen and liverwort on tree in park and liverwort on tree in remnant rainforest, 15 specimens. *Q22*, moss/lichen on tree in open sclerophyll forest, 14 specimens. *Q25*, moss, lichen and fern on trees, liverwort on rock in warm temperate

rainforest, 18 specimens, lichen/liverwort on tree in Box forest, 3 specimens. NEW SOUTH WALES: *N2*, foliose lichen on tree coastal roadside, 1 specimen. *N3.1*, lichens on rocks and trees in open sclerophyll forest, 39 specimens; *N3.3*, *N3.4*, moss and lichen on trees in cool temperate rainforest, 23 specimens; *N3.2*, *N3.5*, *N3.6*, moss and lichen on rocks and trees and in leaf litter in sub-alpine heath, 104 specimens. *N4*, moss and liverwort on tree in cool temperate rainforest, 2 specimens. *N6*, lichen on rock in forest, 4 specimens. *N11*, moss and lichen on tree in street, 7 specimens. *N14.1*, foliose lichen on rock in open sclerophyll forest on cliff top, 2 specimens; *N14.2*, moss and lichen on trees in warm temperate rainforest remnant, 2 specimens. *N15*, moss and lichen on limestone rock in closed forest, 5 specimens. *N19*, foliose lichen on branch on ground in open sclerophyll forest, 2 specimens. *N21*, foliose lichen on bark on ground in *Casuarina* grove, 3 specimens. *N27*, moss and lichen on rock in open sclerophyll forest, 185 specimens. *N29*, moss and lichen on rock and lichen on tree in open sclerophyll forest, 24 specimens. *N31*, lichen on tree in cool temperate rainforest, 7 specimens. *N35*, moss and liverwort on rock and moss and lichen on trees in cool temperate rainforest, 7 specimens. *N39*, moss and lichen on rock in warm temperate rainforest, 200 specimens.

Diagnosis. Red-gold. Sculpture double, evenly distributed black dots and large white spots (1.5 μm) on all plates. Serrated (along one edge only) spines at B, C, D, E, C^d and D^d. Median plate 3 present. Collar on fourth pair of legs with sharp teeth.

Description. Red-gold. Body length 100 (larva)-256 μm , females 140-256 μm , males 140-212 μm . Eye spots unknown. In 195 (190) μm long female (male), cirrus A 38 (40) μm long; primary clava 5 (6) μm long, ovoid. Internal and external buccal cirri 16 (17.8) μm and 20 (20) μm long, both with cirrophores; secondary clava 5.4 (7) μm long, ovoid. Sculpture on plates double with fine evenly sized and distributed black dots and large (1.5 μm) white spots (Plate 2, fig. a). Head plate with median incision. Neck plate narrow with very fine black dots and some spots. Scapular plate with lateral plate. Serrated (along one edge only) spines at B, 14 (27) μm long. Paired segmental plates (II and III) wide, divided into anterior third and posterior two thirds by wide unsculptured band. Serrated spines at

C, D, C^d and D^d, 14-20 (16-35) µm long. Caudal plate with long lateral indentations.

Serrated spine at E, 22 (32) µm long. Median plate I large, strongly sculptured; median plate 2 large with wide unsculptured transverse band separating narrow anterior part from wide posterior. Median plate 3 strongly sculptured. Ventral surface with even black dots. Small spine on first pair of legs, papilla present on fourth pair. Dentate collar on fourth pair of legs with 10-14 long strong narrow teeth. Claws short and robust, internal claws with long spur on inner claws reaching almost to claw base. Claws on second and third legs equal in length, slightly shorter than first, claws on fourth pair longest. Internal claw on fourth pair 11.4 (11.9) µm long, external claw 10.3 (10.8) µm (in 195 (190) µm long specimens).

Exuvia containing up to 6 smooth eggs were found.

Remarks. Differences between the specimens described here and the rather brief description of the species by Richters (1902) were discussed in Claxton (1996). Murray (1910) discussed two varieties that he found in Australia neither of which agreed closely with the type. The type, according to Richter's diagram has smooth dorsal trunk appendages. The presence of males in all the Australian populations examined in this study and their absence, presumably from other described populations of *E. duboisi*, also suggests that the Australian material may belong to a different taxon. A comparative study, using material from known sources of *E. duboisi* is necessary to resolve the question of how many species there are in the "*duboisi*" group.

Distribution. *E. cf duboisi* is very widespread and abundant in eastern Australia. *E. duboisi*, itself, has been reported from Indonesia, New Guinea and South America as well as from Africa.

***Echiniscus jamesi* Claxton, 1996**

Fig. 14, Plate 2b

Echiniscus jamesi Claxton, 1996: 15-20; Figs 1A-D, 4A, 5A, 6, 7, 8; Tabs 1, 2

Type locality. Mount Kosciusko, NSW

Material examined: Australia: NEW SOUTH WALES: *N46.3*, foliose lichen and moss on rock in low open woodland, 82 specimens, 1 exuvium containing 2 smooth eggs (**type material**).

Diagnosis. Red-gold. Sculpture double, fine evenly distributed black dots and large round (1-1.5 μm) uniformly distributed spots on all plates. Filaments at C, D, E often with small swelling at tip. Median plate 3 present. Males present.

Description. Red-gold. Body length 120 (larva)-257 μm (females 200-257 μm , males 182-230 μm). Black eye spots present. In 200 (200) μm long female (male), cirrus A long 65 (74) μm long, with large cirrophore; primary clava 6 (8) μm long, ovoid. Internal and external buccal cirri long 16.7 (20.5) and 17.2 (23.2) μm long with prominent cirrophores; secondary clava 6.8 (8.7) μm long, club-shaped. Sculpture double, fine evenly distributed black dots and large (1-1.5 μm) white uniformly distributed spots (Plate 2, fig. b). Head plate with median anterior notch. Patch of fine black dots immediately anterior to it. Neck plate very narrow. Scapular plate with very small lateral plates. Paired plates (II and III) with unsculptured transverse band, anterior band of sculpture narrow. Long filaments at C and D (60-80 μm long) sometimes with swollen tips. Median plates 1 and 2 large, median plate 3 present. Caudal plate with short wide lateral incisions, with slightly larger (1.5 μm) uniform spots. Long filament at E (80-130 μm) often with swollen tip. Ventral surface with

strong even black dots. First pair of legs with small spine and papilla on fourth pair. Faint spots on leg plate of fourth pair of legs above dentate collar with 8-9 triangular sharp separate teeth with broad bases. Claws robust, internal claws on all legs with short spurs near base of claw. Claws increasing in length from first to fourth, second and third equal in length. Internal claws of fourth pair of legs 12.4 (14.2) μm long and external claws 12 (13.5) μm (in 200 (200) μm long specimens).

One exuvium containing 2 smooth eggs found.

Remarks. Specimens were obtained from the site at which James Murray collected tardigrades in 1909. They are consistent with an unnamed species described by Murray (1910). Males for that species were not mentioned by Murray. Males are smaller than females and have longer primary and secondary clavae and longer claws than females of a similar size.

Distribution. The species was found only at elevations above 2000 m. in mosses and lichens subject to freezing during the winter months and to desiccation during summer months. It has only, so far, been recorded from Australia.

Echiniscus kerguelensis Richters, 1904

Echiniscus kerguelensis Richters, 1904: 239

Type locality. Kerguelen Islands

Material examined: Australia: None. Cited in Murray (1910) from Mount Kosciusko.

Diagnosis. Red. Sculpture more or less fine and regular pores on all plates. No trunk appendages. Median plate 3 absent.

Description. Red. Body length up to 270 μm . Red eye spots present. Cirrus A about 80 μm long, primary clava prominent and somewhat elongate. Internal and external buccal cirri normal, secondary clava normal. Plates coarsely punctate with pores more or less fine and regular. Paired plates (II and III) with plain transverse band, anterior band of pores narrow. Caudal plate with lateral incisions, not faceted. Median plates 1 and 2 present; median plate 3 absent. Dentate collar with narrow sharp teeth. Inner claws on all legs with spurs. Papilla on fourth pair of legs. (from Ramazzotti & Maucci, 1983)

Remarks. Murray (1910) stated that the identity of his specimens was not quite certain because of the absence of figures from the original description. Without type material, this species remains questionable.

Distribution. Murray stated “ the occurrence of this Kerguelen species in Australia, one of the nearest masses of continental land, is not at all surprising, and at the high elevation at which it lived the climatic conditions might approximate nearly to those of the bleak southern island”. It has also been reported from Scotland, South-West Africa, Greenland and Italy but these citations must be questionable given the problems with its identification.

Echiniscus maculosus sp. n.

Fig. 15, Plate 2c

Material examined: Australia: NEW SOUTH WALES: N29, foliose lichen on branch on ground in protected valley, 2 exuvia containing 2 smooth eggs each. SOUTH AUSTRALIA: foliose lichen on rock, 1 specimen.

Diagnosis. Orange-gold. Sculpture double, fine evenly distributed black dots on all surfaces and round (0.5-1.2 μm) uniformly distributed pores on all plates. Spines at B, C, D, C^d and D^d. Median plate 3 present but poorly defined.

Description. Orange-gold. Body length up to 250 μm . Males not found. Eye spots unknown. In 250 μm specimen, cirrus A 50 μm long, primary clava 5.4 μm , ovoid. Internal and external buccal cirri 14 and 16 μm long with prominent cirrophores; secondary clava 8 μm long, club-shaped. Sculpture double with tiny evenly distributed black dots over all surfaces and small (0.5-1.2 μm) randomly distributed white spots (Plate 2, fig. c). Head plate with median anterior notch. Neck plate with large spots. Scapular plate with lateral plates not heavily sculptured. Long spine at B (27 μm long). Paired plates (II and III) with unsculptured transverse band, anterior band of pores narrow. Long spines at C and D (32 and 46 μm long); long and flat spines at C^d and D^d (27 and 31 μm). Median plate 1 triangular; median plate 2 with anterior one third unsculptured, posterior two thirds sculptured; median plate 3 present but poorly defined. Caudal plate with lateral incisions and some unsculptured bands. Ventral surface with black dots. Small spine on first pair of legs and papilla on fourth pair of legs. Faint pores on leg plate of fourth pair of legs above dentate collar with 12 long uniform triangular teeth. Claws robust, internal claw on all legs with small spurs close to base of claw. Claws increasing in length from first to fourth,

internal claw of fourth pair of legs 14.6 μm long, external claw 14 μm (in 250 μm long specimen).

Two exuvia containing two smooth eggs each found.

Etymology. *L. maculosus*, spotted, describing the sculpture on all plates.

Remarks. This species is similar to *E. lichenorum* Maucci, 1984 in the size and placement of appendages. However, it differs from that species by having a sculpture of round pores, distinct black dots on the ventral surface and also by having no unsculptured bands on the scapular plate. The dorsal trunk appendages are smooth not rough as described for *E. lichenorum*. Median plate 3 is present in this species but absent in *E. lichenorum*.

Distribution. The species is rare but widespread in Australia.

Echiniscus marcus Pilato, Claxton & Binda, 1989

Fig.16, Plate 2d

Echiniscus marcus Pilato *et al.*, 1989: 43-45; Fig. 1A-E

Type locality. Douglas Park, NSW

Material examined. NEW SOUTH WALES: *N5*, foliose lichen on rock in open sclerophyll forest, 25 specimens, 2 exuvia containing 6 and 7 eggs. *N8*, lichen and gumnuts on asphalt in urban car-park, 39 specimens. *N14.1*, foliose lichen on rock in open sclerophyll forest, 8 specimens. *N21*, foliose lichen on branch on ground, 20 specimens. *N22*, foliose lichen on rock in open sclerophyll, 1 specimen. *N26*, moss and lichen on rocks in sclerophyll forest, 6 specimens. *N27*, foliose lichen and moss on rock in open sclerophyll forest, 89 specimens, 6 exuvia containing up to 7 smooth eggs (**type material**). *N28*, moss and lichen on

rock in open sclerophyll forest, 3 specimens. *N38*, foliose lichen on rock in open sclerophyll forest, 1 specimen. *N40*, foliose lichen on rock in open sclerophyll forest, 10 specimens. *N41*, moss and lichen on rock in open sclerophyll forest, 4 specimens. *N45*, foliose lichen on rock on island off coast, 11 specimens. *N46.1*, moss and lichen on rock in open sclerophyll forest, 22 specimens. QUEENSLAND: *Q4*, crustose lichen on tree on island, 3 specimens. *Q11*, crustose lichen on tree on beach, 12 specimens. *Q14*, foliose lichen on rock on island, 6 specimens. *Q15*, leaf litter and foliose lichen on rock in open sclerophyll, 6 specimens. *Q16*, moss on rock in open sclerophyll forest, 9 specimens. *Q21*, moss and lichen on rock in open sclerophyll forest, 24 specimens, 1 exuvium with 3 eggs. AUSTRALIAN CAPITAL TERRITORY: *A2*, foliose lichen on rock in open sclerophyll forest, 2 specimens. WESTERN AUSTRALIA: *W2*, foliose lichen on rock in open forest, 16 specimens.

Diagnosis. Yellow-gold. Sculpture double, fine evenly distributed black dots and small irregularly distributed spots on all plates. Short spines at B, C, D, E, C^d and D^d. Median plate 3 present. Patches of sculpture on all legs.

Description. Yellow-gold. Body length 110 (larva)-380 µm. Males not found. Eye spots absent. In 210 µm long specimen, cirrus A 40 µm long, primary clava 5.4 µm long ovoid. Internal and external buccal cirri short, 16 and 22 µm long, with cirrophores; secondary clava 6.5 µm long, club-shaped. Sculpture double, fine evenly distributed black dots on all surfaces and irregularly distributed white spots (0.5-1.2 µm) on a dark matrix on all plates (Plate 2, fig. d) except anterior areas of paired plates and median plate 2 where interpore area is darker. Head plate with median anterior notch. Patch of fine granulation immediately anterior to it. Neck plate very narrow. Scapular plate large with very narrow weakly sculptured lateral plate. Short (3-10 µm) sharp spines present at B. Paired plates (II and III) with wide unsculptured transverse band separating narrow anterior band and a wide posterior band. Short (6-15 µm) sharp spines present at C, D, C^d and D^d. Short (8-10 µm) sharp spines present at E. Median plates 1 triangular; median plate 2 subdivided by

unsculptured band into narrow anterior part and wide posterior part; median plate 3 strongly sculptured but poorly defined. Spines may be missing, particularly in small animals. Caudal plate with two short wide lateral incisions. Well developed spine on first pair of legs and papilla on fourth pair. Faint pores on leg plate of fourth pair of legs above dentate collar with 9 (up to 15) strong teeth, leg plates with faint pores also on first three pairs of legs. Claws robust, internal claws on all legs with strong, basally directed spurs better developed on hind legs. Claws on second and third pair of legs equal in length and slightly shorter than those on first pair, claws on fourth pair longest, internal claw 14 μm long, external 13.5 μm (in 210 μm long specimen). Larvae (110-150 μm long) with spines E and D^d only.

Exuvia containing up to 7 smooth eggs found.

Remarks. This species differs from *E. spinulosus* (Doyere 1840) in the characteristics of the sculpture, by having a strongly sculptured third median plate, by having two unsculptured bands on paired plates I and II and by having shorter lateral and dorsal appendages.

Distribution. The species was found only in dry sclerophyll forests and then primarily in foliose lichens subject to extreme desiccation during summer months (Claxton, 1991). it has , so far, only been recorded in Australia.

Echiniscus neowendti sp. n.

Fig.17, Plate 2e

Material examined: Australia: QUEENSLAND: Q7, moss on rock in open sclerophyll forest, 1 specimen.

Q21, moss and lichen on rock in open woodland, 11 specimens.

Diagnosis. Yellow-gold. Sculpture double, consisting of fine evenly distributed black dots and round dark areas surrounded by small light points. Trunk appendages absent. Median plate 3 absent.

Description. Yellow-gold. Body length 125(larva)-280 μm . Males not found. Eye spots unknown. In 220 μm long specimen, cirrus A 21 μm long, primary clava small, 4.3 μm long, ovoid. Internal and external buccal cirri with prominent cirrophores (13.5 and 17.8 μm long); secondary clava 6.5 μm long. Sculpture double, with fine evenly distributed black dots and large (1.5-2 μm diameter) round dark areas surrounded by small light spots (Plate 2, fig. e). Head plate small with median anterior notch. Neck plate absent. Scapular plate with same sculpture on lateral plate. Trunk appendages absent. Paired plates II and III with unsculptured band, anterior third with net-like sculpture, posterior part with same sculpture as scapular plate. Median plates 1 and 2 triangular with same sculpture as on head plate; median plate 3 absent. Caudal plate with short lateral incisions, sculpture double. Ventral surface with fine even black dots. Spine on first pair of legs and small papilla on fourth pair of legs. Areas of net-like sculpture (plates?) on all legs. Fourth pair of legs with dentate collar with about 7 large sparse triangular teeth with wide bases and often with 2 tips. Claws long and slender, internal claws on all legs with short fine spurs close to base. Claws increasing in length from first to fourth; internal claw of fourth pair of legs 14 μm and external 13.5 μm long (in 220 μm long specimen).

No eggs found.

Remarks. This species differs from *E. wendti* Richters, 1903 by having extremely short cirrus A and by the nature of the sculpture and from *E. pseudowendti* Dastych, 1984 also by the length of cirrus and the nature of the sculpture and, as well, by the size of the spurs on the internal claws.

Distribution. The species appears to be limited in distribution to southern Queensland.

Echiniscus oihonnae Richters, 1903

Echiniscus oihonnae Richters, 1903: 172

Type locality. Norway

Material examined: Australia: None. Described by James Murray (1910) as occurring in moss in the Australian Alps near the southern border of New South Wales, altitude 5000 to 6000 feet.

Diagnosis. Sculpture double, pores uniformly sized and regularly spaced on all plates. Filaments at B, D, E, and C^d. Long spines at C, D^d. Caudal plate divided into four facets of which the posterior one shows obscure subdivision into two. Median plate 3 absent.

Description. Body 250 µm. Males not mentioned. Eye spots unknown. Cirrus A long with large cirrophore, primary clava large. Internal and external buccal cirri long. Caudal plate with lateral incisions divided into four facets of which the posterior one shows obscure division into two. Filaments at B, D, E and C^d. Long spines at C and D^d. Dentate collar

with acute triangular teeth. Claws large. Inner claws on all legs with recurved spurs a little way from base.

Remarks. Murray was somewhat doubtful about his identification of this species because of the absence of spicules at the bases of appendages B, C, D and E and the reduction of C to a long spine and D^d to a sharp spine of moderate length.

Distribution. This species has been recorded from Europe, Asia (Japan), North America and Canada.

Echiniscus perarmatus Murray, 1907

Fig. 18, Plate 2f

Echiniscus perarmatus Murray, 1907: 519-520; Plate XVII, Figs 4a-4c

Type locality. Cape Territory, South Africa

Material examined: Australia: QUEENSLAND: Q5, algae on tree in warm temperate rainforest, 24 specimens. Q7, liverwort/lichen on tree in warm temperate rainforest, 3 specimens. Q15, moss on tree in dry rainforest, 1 specimen. Q25, liverwort on tree in warm temperate rainforest, 1 specimen. NEW SOUTH WALES: N27, moss and lichen on rock in open sclerophyll forest, 8 specimens.

Diagnosis. Yellow-gold. Sculpture double, uniform black hexagons and randomly distributed white spots on all plates. Spines at C, D and E sometimes at D^d. Median plate 3 absent. Subcephalic plates present. Sensory spines on first three pairs of legs.

Description. Yellow-gold. Body length 110(larva)-240 µm. Males not found. Eye spots unknown. In 200 µm long specimen, cirrus A 46 µm long, with large cirrophore, primary

clava, 6.5 μm long, ovoid. Internal and external buccal cirri (22 and 25 μm long) with prominent cirrophores; secondary clava 8 μm long, club-shaped. Sculpture double, evenly distributed black hexagons and small (1 μm diameter) white spots positioned randomly between hexagons (Plate 2, fig. f). Head plate with double sculpture and median anterior notch. Neck plate a thin line of black hexagons. Scapular plate without side plates and with double sculpture except for a thin band of black hexagons only on the caudal edge. Paired plates (II and III) with double sculpture over caudal half and with thin band of hexagons only on caudal edge. Short spines at C, D and at D^d (about 30 μm long) where they are very variable in size and may be missing in one or both positions. Long recurved spine at E (about 40 μm). Median plates 1 and 2 large triangular with double sculpture except for thin band of hexagons only on caudal edge; median plate 3 absent. Caudal plate with large lateral incisions, with double sculpture over whole surface, also with row of denticles on caudal edge (Plate 4, Fig. e). Ventral surface with very fine sculpture of hexagons; subcephalic plates present with double sculpture much finer than on dorsal plates. Spine on first three pairs of legs and papilla on fourth pair. Patch of black hexagons on leg plate of fourth pair of legs above dentate collar with 13-14 large triangular broad-based teeth; patch (plate?) also present on other three pairs of legs. Claws robust with “foot”, internal claws on all legs with long fine prominent spurs which stand out from the claw. Claws of second and third pair of legs slightly shorter than those on first pair, fourth pair longest, internal claw 13.8 μm long, external 12.4 μm (in 200 μm long specimen).

Eggs not found.

Remarks. The very distinctive characters of this species make its identification certain.

Distribution. The species was found only in rainforest areas in Queensland but in a single dry site in south-eastern Australia. This is the first record of its occurrence in Australia. It has been recorded also from Indonesia and North and South America as well as from the type locality in Africa.

Echiniscus pusae Marcus, 1928

Fig. 19, Plate 3a

Echiniscus pusae Marcus, 1928: 61; Fig. 68

Type locality. Lombok Island, Indomalaya

Material examined: Australia: QUEENSLAND: Q6, algae/crustose lichen on tree in rainforest remnant, 1 specimen. Q18, liverwort and foliose lichen on rotten log in park, 13 specimens, 1 exuvium containing 3 eggs. NEW SOUTH WALES: N31, weft moss on tree in temperate rainforest, 7 specimens, 1 exuvium containing 3 eggs.

Diagnosis. Yellow-orange. Sculpture double, fine evenly distributed black dots and large hexagons with round spots in centre on some plates, other plates with white spots with no hexagonal surround, joining one another. Spines at B, C, D and E (B spine missing in NSW population) and also at C^d and D^d. Median plate 3 present.

Description. Yellow-orange. Body length 130-185 µm. Males not found. Eye spots unknown. In 166 µm long specimen, cirrus A rather short, 32 µm long, primary clava 5.4 µm long, ovoid. Internal and external buccal cirri 11 and 12 µm long, with prominent cirrophores; secondary clava 6 µm long, club-shaped. Sculpture double and rather complex with fine evenly distributed black dots over all plates and ventral surface, large (3 µm) hexagons with white central spots particularly well-developed on scapular, terminal and

posterior parts of paired plates (Plate 3, fig a); median plates and anterior areas of paired plates with white spots joining one another and without the polygonal surround. Head plate well developed with median anterior notch. Neck plate very thin. Scapular plate with lateral plates with sculpture of small (0.5 μm) solid polygons. Spine present at B position, about 7 μm long, (may be absent). Paired plates II and III with narrow unsculptured transverse band. Spines present at C, D, C^d and D^d (19, 19, 6 and 10 μm long) Median plates 1 and 2 well developed; median plate 3 present. Caudal plate large and with short wide lateral incisions. Spine at E (27 μm long). Ventral surface with fine black dots. Spine on first pair of legs and papilla on fourth pair. Leg plate on fourth pair of legs with patch of small black dots and dentate collar with 10-12 small narrow even teeth. Claws slender, internal claws on all legs with strong fine spurs. Claws of second and third pair of legs equal in length and slightly shorter than those on first pair, claws on fourth pair longest, internal claw 10.8 μm long, external 9.7 μm (in 166 μm long specimen).

Two exuvia, each containing 3 smooth eggs, found.

Remarks. Specimens from Eumundi and Minnamurra were identical in every respect except for the presence or absence of the spine at B. Thirteen of the 14 specimens from Eumundi had a spine at B, one of 8 specimens from Minnamurra had the spine at B. The specimens agree well with the description of this species except that median plate 3 is said to be absent and the terminal plate faceted in *E. pusae*. Both of these characters could be confused, depending on the state of preservation of the specimens so these specimens were assigned to this taxon.

Distribution. This is the first record of this species in Australia. This species has been recorded from South Africa as well as Indonesia.

***Echiniscus rodnae* Claxton, 1996**

Fig. 20, Plate 3b

Echiniscus rodnae Claxton, 1996: 20-21, Figs. 2A-D, 4B, 5B, 9, Tabs 3, 4

Type locality. Burragorang, NSW

Material examined. NEW SOUTH WALES: *N13*, foliose lichen on rock in suburban street, 1 female, 1 male. *N14.3*, foliose lichen on rock in open sclerophyll, 12 specimens, 1 exuvium containinig 3 eggs. *N22*, lichen and moss on rock in open sclerophyll forest, 89 specimens, 2 exuvia containing 4 smooth eggs each (type material).

Diagnosis. Yellow-gold. Sculpture with fine evenly distributed black dots, very small (0.3 μm diameter) numerous spots and larger (0.6-1 μm) unevenly distributed spots. Spines at C, D, E. Median plate 3 present, poorly defined. Males present.

Description. Yellow-gold. Body length 110 (larva)- 216 μm , females 170-216 μm , males 150-210 μm . Eye spots absent. In 185 (185) μm long female (male), cirrus A short, 39 (37) μm long with large cirrophore; primary clava 5 (6.7) μm long, ovoid. Internal and external buccal cirri short 15 (16.7) μm and 16.7 (18.9) μm long, both with conical cirrophores; secondary clava 5.6 (7.6) μm long, ovoid. Sculpture with fine evenly distributed black dots and very small (0.3 μm) numerous white spots and larger (0.6-1 μm) white spots unevenly distributed and more prominent on some plates than on others (Plate 3, fig. b). Head plate with larger pores and median anterior notch. Patch of fine black granulation immediately anterior to it. Neck plate a thin band of larger spots. Scapular plate with very few large spots and with small side plates with small spots. Paired plates (II and III) with thin

unsculptured transverse band, narrow anterior band often with many large spots on median part, lateral part with faint sculpture; wide posterior band with very few large spots but covered with very small spots. Spines present at C and D (14-20 μm in females, 25-35 μm in males), rarely at Dd. Median plates 1 and 2 large with few large spots scattered anteriorly, median plate 3 with large spots. Caudal plate with lateral incisions and few large spots. Spine at E long and curved (20 μm in females, 40 μm in males). Ventral surface with fine even black dots. First pair of legs with small spine and papilla on fourth pair. Faint spots on leg plate of fourth pair of legs above dentate collar with up to 11 (usually 8-9) long thin sharp separate teeth with narrow bases. Claws robust, internal claws on all legs with short robust spurs close to claw base. Claws of first three pairs of legs same length, fourth pair longest, internal claw 12.7 (13.5) μm long, external 12.3 (12.7) μm (in 185 (185) μm long specimens). Larvae (110-116 μm long) and juveniles (130-165 μm) with reduced number of spines.

Two exuvia containing 4 smooth eggs each, were found.

Remarks. The species exhibits some sexual dimorphism and spine asymmetry described in Claxton (1996).

Distribution. The species was found only in the very xeric environment provided by patches of moss and lichen on rocks in open sclerophyll forests typical of the Australian east coast around Sydney. It has only, so far, been recorded from Australia

***Echiniscus cf spiniger* Richters, 1904**

Echiniscus spiniger Richters, 1904: 349

Type locality. Sweden.

Material examined: Australia: QUEENSLAND: Q22, moss on tree in open forest, 1 specimen. Reported from Eumundi, Queensland by Murray (1910).

Diagnosis. Red-gold. Sculpture double, large round (1 μm) uniformly distributed pores on all plates and fine regular granulation over all surfaces. Spines at B, C, D, E, C^d and D^d.

Description. Cirrus A long with large cirrophore, primary clava ovoid. Internal and external buccal cirri long with prominent cirrophores; secondary clava club-shaped. Sculpture of fine pellucid dots. Scapular plate large. Spines at B 8-10 μm long. Paired plates (II and III) with unsculptured transverse band. Spines at C and D (about 30 μm long) and at C^d and D^d (10-15 μm). Dorsal processes vary greatly in size and may be absent. Caudal plate with lateral incisions. Spines present at E, 30 μm long. Dentate collar of fourth pair of legs with obtuse teeth. Internal claws on all legs with very strong spurs placed far from base of claw.

Remarks. This species is very poorly described. Identifications probably involve many different species. This group requires a full comparative study.

Distribution. Unknown at present.

***Echiniscus tessellatus* Murray, 1910**

Fig. 21, Plate 3c; Plate 4d

Echiniscus tessellatus Murray, 1910: 129; Plate XVI, Fig. 15

Type locality. Eumundi, Queensland

Material examined: Australia: QUEENSLAND: *Q6*, liverwort on rock and tree, lichen on branch on ground in remnant rainforest, 5 specimens. *Q7*, moss on rock, liverwort on tree in remnant rainforest, 8 specimens. *Q18*, (**type locality**) liverwort on tree in suburban park, 18 specimens, 1 exuvium containing 2 eggs. *Q25*, liverwort on tree in rainforest remnant, 14 specimens. *Q26*, liverwort on tree in remnant rainforest, 23 specimens. NEW SOUTH WALES: *N10*, moss on log in temperate rainforest, 1 specimen. *N31*, moss/lichen on rock in temperate rainforest, 2 specimens.

Diagnosis. Yellow-gold. Sculpture of large round hemispherical knobs delineated by cuticular ridges which subdivide dorsal plates into subplates. Trunk appendages absent. Median plate 3 absent.

Description. Yellow-gold. Body length 90 (larva)-220 μm . Males not found. Eye spots absent. In 200 μm long specimen, cirrus A 70 μm long, with large cirrophore, primary clava 6.5 μm long, ovoid. Internal and external buccal cirri 17 and 20 μm long with prominent cirrophores, secondary clava 8 μm long, ovoid. Head plate consisting of two transverse oval areas delineated by raised ridge with faint sculpture of raised knobs. Neck plate absent. Scapular plate with 9 subplates consisting of raised knobs, about 2 μm diameter and surrounded by narrow ridges (Plate 3, fig. c). Bulb-like cuticular structure (Plate 4, fig. d) present just posterior to lateral margin of scapular and both paired plates very similar to those found in *E. vinculus*. Paired plates (II and III) with same organisation as scapular plate, that is, with subplates of raised knobs and delineated by narrow ridges.

Median plates 1 and 2 large with raised knobs; median plate 3 apparently absent, area between paired plates III and caudal plate with raised knobs but not separated from caudal plate by heavy line. Caudal plate with 7 subplates and with large lateral incisions. Ventral surface smooth. First pair of legs with spine and long papilla on fourth pair. Dentate collar with 5-6 wide based triangular teeth, no sculpture above, ie, no leg plate. Claws robust, internal claws on all legs with fine, downwardly directed spurs which lie close to claw; those on the fourth pair of legs somewhat better developed than those on the other three pairs. Claws on second and third pairs of legs slightly shorter than those on first pair, claws on fourth pair longest, internal 13 μm long, external 12 μm (in 200 μm long specimen).

Exuvium containing 2 smooth eggs found.

Remarks. The morphology of this species was discussed by Dastych (1997) using material from Hawaii. The description above is based on material obtained from the type locality, it confirms the yellow colour of the Australian specimens (as opposed to red colour of Indonesian specimens reported by Pilato & Binda (1990). It also confirms the presence of projecting flanges or bulbs, reported by Murray (1910) but dismissed by Dastych (*l. c.*) as probably an artifact. Two other characters, not mentioned by either of the above authors, are the lack of a strong line between median plate 3 and the caudal plate and the shorter length of claws of the second and third pair of legs.

Distribution. The species was reported from Indonesia (Pilato & Binda, 1990) from moss but no habitat data was given. Dastych (*l. c.*) reported it from moss from mesic environments in Hawaii. It is noteworthy that all sites in which the species was found in Australia, are rainforest sites and this report has markedly increased its range along the eastern coast of Australia.

***Echiniscus velaminis* Murray, 1910**

Fig. 22, Plate 3d; 4f

Echiniscus velaminis Murray, 1910: 112-113; Plate XV, Fig. 6

Type locality. Nun's Veil Mountain, New Zealand

Material examined: Australia: NEW SOUTH WALES: *N43*, moss at 1200 m. asl., 1 specimen. *N46.2*, moss and lichen on rock in subalpine forest, 15 specimens, 1 exuvium containing 3 eggs. TASMANIA: *T17*, moss on dolerite at 650 m. asl., 10 specimens.

Diagnosis. Orange-gold. Sculpture double with evenly distributed black dots and small clearly defined spots on all plates except terminal where they are large and indistinct. Appendages at C, D (short filaments) and E (very long filament), also C^d (filament) and D^d (spine).

Description. Orange-gold. Body length 140 (larva)-290 µm. Males not found. Eye spots unknown. In 270 µm long specimen, cirrus A 75 µm long with large cirrophore, primary clava 7 µm long, ovoid. Internal and external buccal cirri 20 and 30 µm long with prominent cirrophores, secondary clava 8 µm long, ovoid. Sculpture double, consisting of fine evenly distributed dots over every surface and clear white spots (pores), 0.5-1.5 µm, unevenly distributed over scapular (Plate 3, fig. d), paired and median plates; caudal plate also with white spots, 2-3 µm, and with indistinct edges (Plate 4, fig. f). Head plate with median anterior notch. Wide neck plate present. Scapular plate with lateral plates almost completely separated by a deep incision. Paired plates (II and III) with very narrow unsculptured band. Trunk appendages present at C and D (15-40 µm long) and at C^d (60-

90 μm) and D^d (15-40 μm). Median plates 1 a large triangle, median plate 2 with unsculptured anterior area smaller than posterior sculptured area; median plate 3 present. Caudal plate with long wide incisions. Long filament at E (150-200 μm). Ventral surface with 2 large patches of strong black granulation in subcephalic area and one patch either side of the gonopore. Spine on first pair of legs and papilla on fourth pair. Dentate collar with 5-10 wide based triangular teeth, patch of fine sculpture above dental collar and on first three pairs of legs. Claws robust, internal claws on all legs with strong, downwardly directed spurs which stand out from claw. On inner claw of fourth pair of legs and, sometimes, on inner claw of third and even first pair of legs a small straight spur present. Claws on second and third pairs of legs slightly shorter than those on first pair, claws on fourth pair longest, internal 16 μm long, external 15 μm (in 270 μm long specimen).

Exuvium containing 3 smooth eggs found.

Remarks. In his original description Murray described the claws of this species as without barbs and it is difficult to see how he could have missed them as they are quite well developed on these specimens. However the specimens described here, agree in all other respects with the description of the species. Horning, Schuster & Grgarick (1978) also described this species from cool temperate rainforest in the South Island but added nothing further to the description and expressed the opinion that the identity of their material was questionable. In the absence of type material the identification of the Australian material may also be questionable.

Distribution. The species has only been reported from New Zealand. This is the first report from Australia.

***Echiniscus vinculus* Horning, Schuster & Grigarick, 1978**

Fig. 23, Plate 3e

Echiniscus vinculus Horning *et al.*, 1978: 192-193; Figs, 16-18, 161 lower

Type locality. Chatham Islands, New Zealand

Material examined. **Australia:** QUEENSLAND: *Q5*, liverwort/moss/lichen on log, alga on tree in closed sclerophyll forest, 3 specimens. *Q6*, lichen on trees, remnant rainforest, 3 specimens. *Q15*, moss/liverwort on tree in dry rainforest, 2 specimens. *Q17*, lichen on tree in open sclerophyll forest, 6 specimens. *Q18*, liverwort on tree in park, 3 specimens. *Q20*, leaf litter/sand, crustose lichen on tree on a sand island, 6 specimens. *Q25*, moss/lichen/liverwort on trees in Box forest and in rainforest, 5 specimens. **NEW SOUTH WALES:** *N3.1*, moss and lichen on rocks, moss on trees in open sclerophyll forest, 3 specimens, *N3.3* and *N3.4*, moss and lichen on trees and moss on rocks in cool temperate rainforest, 10 specimens, *N3.2*, *N3.5* and *N3.6*, moss and lichen on trees and rocks in subalpine heath, 47 specimens. *N4*, liverwort on tree in cool temperate rainforest, 1 specimen. *N5*, lichen on rock and tree branch in open sclerophyll forest, 3 specimens. *N11*, lichen on tree branches and on tree fern in temperate rainforest, 13 specimens. *N14.1*, moss lichen on rock in open sclerophyll forest on cliff top, 2 specimens, *N14.2*, moss, lichen and liverwort on rock, moss and liverwort on trees in temperate rainforest, 20 specimens, *N14.3*, moss on rock in temperate rainforest, 2 specimens, *N14.4*, moss on tree and rock in temperate rainforest, 4 specimens, *N14.5*, foliose lichen on tree and leaf litter on soil in open sclerophyll forest, 2 specimens, *N14.6*, *Banksia* cone on tree and lichens on trees in open sclerophyll forest, 13 specimens. *N15.2*, foliose lichen on branch on ground in protected valley, 2 specimens, *N15.3*, moss and lichen on trees, lichen and liverwort on limestone rocks at caves entrance, 10 specimens. *N22*, moss and lichen on rock in open sclerophyll forest, 10 specimens. *N23*, moss and lichen on trees in open sclerophyll forest, 7 specimens, 2 exuvia containing 3 and 4 eggs. *N25*, moss/liverwort on rock in moist forest near falls, 1 specimen. *N27*, moss and lichen on rock in open sclerophyll forest, 25 specimens. *N31*, lichens on branches on ground in temperate rainforest, 6 specimens. *N34*, lichen and fungus on dead trees in closed woodland, 6 specimens. *N35*, moss and liverwort on rock, moss on tree in cool temperate rainforest, 6 specimens. *N39*, moss and lichen on rock in cool temperate rainforest, 30 specimens. *N46.2*, *46.3*, lichen on rocks and trees in open sclerophyll forest at high altitude, 10 specimens, 1 exuvium containing eggs. **TASMANIA:** *T3*, moss/lichen on gully slope, moss on log in closed tall scrub gully, 2

specimens. *T7*, moss on stream bank in wet forest gully, 1 specimen. *T8*, moss/liverwort/lichen on soil in heathland, 1 specimen. *T10*, liverwort on tree in regenerating cool temperate rainforest, 1 specimen. *T11*, moss in river gully, 6 specimens. *T12*, lichen, liverwort and moss on rock in river gully, 5 specimens. *T17*, moss on dolerite boulder in forest on island, 1 specimen. *T20*, moss on rock in tall closed forest, 1 specimen. LORD HOWE ISLAND: moss and lichen, 6 specimens. **New Zealand:** **Paratypes**, NZ859, Chatham Island, lichen on tree, 1 specimen; NZ932, Waterfall Creek, 1 specimen; NZ983, Three Kings Island, 1 specimen; NZ505, Three Kings Island, 1 specimen.

Diagnosis. Pale yellow-gold. Sculpture of unevenly sized and spaced pores with plain bands. Trunk appendages absent. Median plate 3 absent.

Description. Pale yellow-gold. Body length up to 260 μm . Males present. Eye spots absent. In 200 (200) μm long female (male) specimens, cirrus A 38 (35) μm long, with large cirrophore, primary clava ovoid, 5.5 (7) μm long. Internal and external buccal cirri short with prominent cirrophores (13.5 (15) and 16 (16) μm long), secondary clava 7 (9) μm long. Sculpture single, consisting of irregularly shaped and unevenly distributed spots (pores?), 1-3 μm diameter (Plate 3, fig. e). Head plate with median anterior notch. Neck plate absent. Scapular plate with same spots as on head plate but with unsculptured bands crossing plate. A bulb-like structure is present just posterior to lateral margin of scapular plate, similar bulbs present at dorso-lateral points of paired plates II and III. Paired plates (II and III) with narrow unsculptured transverse band (appearing white) close to anterior edge, otherwise with same sculpture as head plate with unsculptured bands primarily on the posterior edges of these plates. Median plates 1 and 2 triangular with same sculpture as on other plates and with unsculptured band along posterior edge; median plate 3 absent, area between plates III and caudal plate sometimes with a few pores. Caudal plate with lateral incisions, also with same sculpture as on other plates and with a pattern of transverse and vertical unsculptured bands which give the appearance of facetting. Ventral

surface smooth. First pair of legs with spine and small papilla on fourth pair. Dentate collar with 9-10 short blunt teeth often with multiple tips, area above collar with same sculpture as plates, patch of spots also on first three pairs of legs. Claws short and robust, internal claws on all legs with fine downwardly directed spurs which lie close to claw. Claws increasing in length from first to fourth, internal claws on fourth pair of legs 11.8 (12) μm long, external 13 (13) μm (in 200 (200) μm long specimens).

Exuvia containing up to 5 smooth eggs found.

Remarks. Males were not noted in the original description of this species but were found at almost every site in Australia at which the species was collected. The four New Zealand paratypes examined were females. The Australian specimens have been placed in this taxon because of the overall similarity in appearance and size of structures to the New Zealand specimens. However, there are some differences that should be noted. The most important is the presence of a spine on the first pair of legs in *E. vinculus* noted in the description but only seen on two of the four paratypes all of which were poorly preserved. The spine is absent in Australian specimens. Other minor differences are, much less extensive unsculptured areas, particularly on the scapular and caudal plates although this is very variable from specimen to specimen at a single site, and longer claws in the Australian specimens.

Distribution. The species is very widespread in eastern Australia but was rarely found in abundance, more often in low numbers with a second species of *Echiniscus* (often *E. cf duboisi*). It appeared to be eurytopic, occurring in cryptogams in dry sclerophyll as well as temperate rainforests. So far, it has only been reported from New Zealand and Australia.

Echiniscus virginicus Riggin, 1962

Fig 24, Plate 3f

Echiniscus virginicus Riggin, 1962: 31-32; Plate VI, Figs. 16, 17, 18

Type locality. John's Creek Mountain, Virginia, USA.

Material examined: **Australia:** QUEENSLAND: *Q19*, moss/liverwort on tree in closed forest, 6 specimens. *Q25*, turf moss on tree in temperate rainforest, 5 specimens. NEW SOUTH WALES: *N11*, turf moss on tree in temperate rainforest, 1 specimen. *N26*, moss/fruticose lichen on rock in sheltered gully, 1 specimen. *N27*, fruticose lichen on rock in open sclerophyll forest, 1 specimen. *N35*, weft moss on tree in temperate rainforest, 5 specimens. **Venezuela:** La Carbonera, Merida, 1 specimen.

Diagnosis. Yellow-gold. Sculpture of small black regularly spaced polygons and large coalescing pore-like areas on all plates; ventrally fine regular black dots with a showy patch on side of each leg and above dentate collar. Short spines at B, C, D and E; B often missing; spines at C^d and D^d. Median plate 3 poorly defined.

Description. Yellow-gold. Body length 120-190 µm. Males not found. Eye spots unknown. In 160 µm long specimen, cirrus A 31 µm long, primary clava 5.4 µm long, ovoid. Internal and external buccal cirri 11 and 15 µm long, with prominent cirrophores, secondary clava club-shaped, 6 µm long. Sculpture double, small evenly distributed black polygonal dots and large white irregularly shaped spots which often appear to join (Plate 3, fig. f). Head plate with median anterior notch and sculpture of black dots only. Neck plate narrow strip of black dots only. Scapular plate broad, with small lateral plates. Spine at position B (6-14 µm long) in about half the specimens. Paired plates II and III with narrow plain transverse band, anterior band narrow, posterior band wider, sculpture double. Spines at C and D (20-25 µm), shorter spine at C^d (4-7 µm) and heavy flat spine at D^d (11-16 µm).

Median plates 1 and 2 triangular, with double sculpture, median plate 3 poorly defined but area with very small faint black dots. Caudal plate with large lateral incisions; sculpture double. Spine at E (25 μm). Ventral surface smooth. Spine on first pair of legs and papilla on fourth pair. Dentate collar with 10-14 short wide triangular teeth of uneven size; area above with fine polygonal sculpture; patch also present on other three legs. Claws slender with long curved distal portion, internal claws on all legs with long downwardly pointing spurs placed well away from the base of the claw. Claws on second and third pair of legs equal in length, slightly shorter than those on first pair, claws on fourth pair longest, internal claw 9 μm long, external 11 μm (in 160 μm long specimen).

No eggs found.

Remarks. The original description was rather poor and did not describe the sculpture and showed the species without the spine at B. However, Ramazzotti & Maucci (1983) described new specimens from the USA with spine B and with the typical polygonal sculpture. The specimens described here from Australia are identical to a specimen from Venezuela examined in this study, except that it is missing the B spine. Specimens without the B spine, in this study, were all short (less than 150 μm body length). In their redescription of this species Christenberry & Mason (1979) noted that sub-adults (148 μm long) lacked the spine at B.

Distribution. The species has been found in Florida and Virginia in southern USA, in Dominican Republic (Central America) and in Venezuela (South America). It is a widely distributed and common species in Venezuela (Grigarick, Schuster & Nelson 1983) in subtropical and tropical rainforests and in mountain areas with high rainfall. In Australia the species is not abundant but is widespread in rainforest or temperate sheltered areas,

predominantly in moss on trees. The apparent disjunct distribution of this species may be due to lack of collection. This is the first report of its occurrence in Australia.

***Echiniscus viridissimus* Peterfi, 1956**

Fig. 25, Plate 4a and b

Echiniscus viridissimus Peterfi, 1956:

Type locality. Romania.

Material examined: Australia: NEW SOUTH WALES: N29, moss on limestone in protected valley, 36 specimens, 2 exuvia containing 1 and 3 eggs. North America: Johnson City, Tennessee, 1 specimen.

Diagnosis. Olive green. Sculpture with fine evenly distributed black dots and with small white spots and small regularly arranged hollows on some plates. Trunk appendages absent. Median plate 3 present.

Description. Olive green. Body length 125 (larva)-276 μm . Males not found. Eye spots unknown. In 205 μm long specimen, cirrus A long, 76 μm , primary clava 5.4 μm long. Internal and external buccal cirri 15 and 17 μm long with prominent cirrophores, secondary clava 6.5 μm long. Sculpture double, with evenly distributed black dots and unevenly distributed white spots and regularly arranged hollows on some plates. Head plate rather small with median anterior notch and sculpture of black dots only. Neck plate absent. Scapular plate wide, with double sculpture of uniform black dots and white spots (1.5-3 μm diameter) (Plate 4, fig. a). Trunk appendages absent. Paired plates II and III with anterior one third with sculpture of large (1.2-1.5 μm) black spots, posterior two thirds with double sculpture like that on scapular plate. Median plates 1 a small triangle with

sculpture the same as scapular plate. Median plate 2 with anterior part with same sculpture as anterior parts of paired plates (Plate 4, fig. b). Median plate 3 with same sculpture as anterior zones of paired plates. Caudal plate same sculpture as scapular plate, with two short lateral incisions. Ventral surface covered with strong black dots, with two patches of stronger dots present in subcephalic area. Spine on first pair of legs and short papilla on fourth pair of legs. Dentate collar with 8-9 sharp triangular teeth, area above collar with patch of strong black uniform dots, patch also present on all other legs. Claws robust, internal claws on all legs with fine short spurs close to claw base. Claws of second and third legs equal in length and slightly shorter than those on first pair of legs, claws on fourth pair of legs longest, internal 16.8 μm , external 15.1 μm (in 205 μm long specimen).

Two exuvia containing 1 and 3 smooth eggs found.

Remarks. The original description describes the species with spurs absent but all other species in the “*viridis*” group have very slender spurs visible only under oil immersion phase contrast. The specimen from the USA, examined here, has spurs and is very similar to the Australian material.

Distribution. The species has also been recorded from North and South America and Japan. This is the first record of its occurrence in Australia. Maucci (1987) found a rich population of this species in a moss sample on a concrete curbstone in Yellowstone National Park in USA suggesting that the species may have a preference for a calcareous substrate.

Genus *Hypechiniscus* Thulin, 1928

Hypechiniscus Thulin, 1928: 221, Fig 12.

Type species. *Echiniscus gladiator* Murray, 1905

Diagnosis. (From Kristensen, 1987) Black eye spots. Rigid buccal tube with cuticular bulb anterior to a small pharyngeal bulb, stylet supports absent. Cirrus A hair-like above cirrophore. Dorsal plates poorly defined, ventral plates absent. Head plate large with suture. Pseudosegmental plate IV' absent. All median plates undivided. No leg plates on fourth pair of legs.

Key to species of *Hypechiniscus*

1. Single trunk appendage at mid-dorsal point between median plate 2 and paired plate III, ventral surface with raised cuticular ridges..... *H. gladiator*
Trunk appendages absent, ventral surface with fine dotting. *H. exarmatus*

***Hypechiniscus exarmatus* (Murray, 1907)**

Fig. 26

Echiniscus gladiator Murray, 1907 var *exarmatus* Murray, 1907: 652; Plate 1, Figs. 5a-5b

Type locality. Scotland.

Material examined. Australia: QUEENSLAND: *Q18*, liverwort on rotting log in rainforest remnant, 16 specimens, 2 exuvia containing 3 eggs each. TASMANIA: *T12*, leafy liverwort and lichen in cool temperate rainforest, 18 specimens.

Diagnosis. Dorsal cuticular plates indistinct. Trunk appendages absent. Cirrus A rather long. Clavae short. Ventral surface with fine evenly distributed black dots.

Description: Pale yellow. Body length 124-226 μm (females 184-226 μm , males 169-184 μm). Black eye spots present. In 195 (185) μm long female (male), cirrus A 30 (31) μm long, primary clava small, 4.3 (5.4) μm long, ovoid. Internal and external buccal cirri 10 (15) and 21 (21) μm long, filiform, with large cirrophores, secondary clava 5.4 (6) μm , slightly longer and wider in males than in females. Dorsal cuticular plates indistinct. Sculpture a fine evenly distributed black dotting over the whole body. Large suture on head plate nearly dividing it into five pieces. Scapular plate rather narrow with faint mid-dorsal line. Lateral intersegmental plates between paired plates and median plates 1, 2 and 3. median plates 1 and 2 often with deep transverse fold. Caudal plate large with 2 long folds (not incisions) and two shorter folds. Ventral surface with very fine black dots. No sensory organ on first three pairs of legs, small papilla on fourth pair of legs. Plate-like areas of heavy black dots on exterior of all legs. Claws long slender and rather straight, internal claws on all legs with large curved spurs. Claws curved slightly at top, claws of second and third pair of legs equal in length slightly shorter than those of first pair, those of fourth pair longest. Internal claw of fourth pair of legs 11.4 (11.4) μm long, external 10.8 (10.8) μm (in 195 (185) μm long specimens).

No eggs found.

Remarks: See remarks for *H. gladiator*.

Distribution: The species is cosmopolitan and has been reported from the UK, Korea and New Zealand. This is the first record of this species in Australia.

Hypechiniscus gladiator (Murray, 1905)

Fig. 27

Echiniscus gladiator Murray, 1905: 683; Plate 1, Figs. 1a-c

Type locality. Scotland.

Material examined. Australia: NEW SOUTH WALES: *N3.2*, moss and lichen on rock in subalpine heath, 62 specimens, 2 exuvia containing 2 and 4 eggs; *N3.3* and *N3.4*, moss on rocks and trees in cool temperate rainforest, 5 specimens. *N4*, moss/liverwort on tree in cool temperate rainforest, 8 specimens, 1 exuvium containing 3 eggs.

Diagnosis. Dorsal cuticular plates indistinct; long spine mid-dorsally on thin triangular area of cuticle between median plate 2 and paired plate III. Short cirrus A. Long thin clavae especially in males. Cuticular ridges over ventral surface.

Description: Pale yellow. Body length 100-243 µm (females 145-243 µm, males 145-207 µm). Black eye spots present. In 195 (185) µm long female (male), cirrus A 23 (23) µm long, primary clava 5 (6) µm long, very long and slender in males, inserted very close to cirrus A. Internal and external buccal cirri 9 (11) and 16 (17) µm long, thin filiform with large cirrophores, secondary clava 6.3 (7.6) µm, very long and slender in males. Dorsal cuticular plates indistinct. Sculpture a fine evenly distributed black dots over whole body. Large suture on head plate nearly dividing it into five pieces. Scapular plate narrow,

unpaired. Lateral intersegmental plates between paired plates and median plates 1, 2 and 3. Long spine (about 40 μm long) mid-dorsally on thin triangular area of cuticle between median plate 2 and paired plate III. Median plates 1 and 2 often with deep transverse fold. Caudal plate with two long folds (not incisions) and two short folds. Ventral surface with faint raised cuticular ridges, seen at edge of body to be without internal structure and without black dots. No sensory organs on first three pairs of legs, small papilla on fourth pair. Plate-like areas of heavy black dots on exterior of all legs. Claws long and rather straight, curved slightly at top, internal claws on all legs with short very strong hook-like spurs. Claws of second and third legs slightly shorter than those of first, those on fourth pair longest. Internal claws of fourth pair of legs 9.7 (9.7) μm long, 9.1 (9.1) μm (in 195 (185) μm long specimens).

Exuvia containing 2, 3 and 4 smooth eggs found.

Remarks: Two specimens of the 67 examined from New England were missing the dorsal spine. A comparison of a similarly sized specimen of *H. exarmatus* from Tasmania and a specimen of *H. gladiator* with a spine showed that *H. gladiator* has shorter cirrus A, relatively longer and thinner primary and secondary clavae and shorter, thicker claws than *H. exarmatus*. Kristensen (1987) justified the elevation of *H. exarmatus* to species rank because it had different claws, that is, smaller spurs, than *H. gladiator*.

Distribution: The species is cosmopolitan and has been reported from Europe, Asia, North America and New Zealand. This is the first record of this species in Australia.

Genus *Mopsechiniscus* Du Bois-Reymond Marcus, 1944

Mopsechiniscus Du Bois-Reymond Marcus, 1944: 6 Fig 9A-C

Type species. *Pseudechiniscus imberbis* Richters, 1908

Diagnosis. (from Kristensen, 1987) Black eye spots. Flexible buccal tube without CaCO_3 . Cirrus A long stiff spine without cirrophore, primary clava bent backwards. Internal and external buccal cirri absent, secondary clava small ovoid dome-shaped in female, large round dome-shaped in male. Paired pseudosegmental plates IV', median plates undivided. Small rectangular plate with a "thorn" on either side of scapular plate.

***Mopsechiniscus tasmanicus* Dastych & Moscal, 1992**

Mopsechiniscus tasmanicus Dastych & Moscal, 1992: 222-224; Figs. 1-14

Type locality. Sandy Cape, Tasmania.

Material examined. Australia: TASMANIA: liverwort on tree in cool temperate rainforest, 1 specimen (Holotype).

Diagnosis. Trunk appendages present at E. Subcephalic plates present. Bases of cirrus A and appendage E with unique internal sculpture.

Description. Body length 291 μm , male. Red body cells. Dark brown eye spots present. Cirrus A very long, base with transverse thickenings interspersed with small granules and with internal lumen the whole surrounded by a transparent cuticular envelope. Short wide blunt primary clava inserted in small cavity beside cirrus A. Surface of cavity with fine

granulation. Internal and external buccal cirri absent; secondary clava dome-shaped. Sculpture of dorsal plates small hemispherical hollows which appear as dots sparse and irregularly distributed. Similar but much smaller dots on outside of legs. Subcephalic plates on chin. Head plate faceted. Scapular plate with small lateral plates. Paired plates I and II with lateral plates. Median plates undivided. Pseudosegmental plate large and divided. Spines or papillae absent on first three pairs of legs; papilla on fourth pair of legs. Leg plates and dentate collar absent. Inner claws with thin sharp downwardly directed spurs. (from Dastych & Moscal, 1992)

Eggs not found.

Remarks. The genus was revised by Dastych (2001).

Distribution. Members of the genus have only been reported from the southern hemisphere and then only in mountain and/or subpolar regions (Dastych, 2001).

Genus *Pseudechiniscus* Thulin, 1911

Pseudechiniscus Thulin 1911: 18, Fig 7-7a

Type species. *Echiniscus suillus* Ehrenberg, 1853

Diagnosis. (from Kristensen, 1987) Black eye spots. Rigid buccal tube, stylet supports may be present. All median plates present. Pseudosegmental plates IV' paired or unpaired. Males with enlarged secondary clavae.

Key to species of *Pseudechiniscus*

1. Claws without spurs..... 2
 - Claws with spurs..... 3
2. Strong even granulation on dorsal plates, long sharp spines on posterior margin of pseudosegmental plate..... *P. novaezeelandiae*
 - Fine uneven granulation on plates, short triangular projections on posterior margin of pseudosegmental plate... *P. longiunguis*
3. Secondary clava dome-shaped, posterior margin of scapular plate divided into four parts..... *P. jiroveci*
 - Secondary clava ovoid, posterior margin of scapular plate in one piece..... 4
4. Pseudosegmental plate with triangular projections on posterior margin..... *P. ficus*
 - Pseudosegmental plate with straight or slightly sinuous posterior margin..... 5
5. Head and caudal plates facettèd, males present..... *P. australis*
 - Head and caudal plates not facettèd, males absent..... *P. suillus*

Pseudechiniscus australis sp. n.

Fig. 28, Plates 5a; 6a

Material examined. Australia: QUEENSLAND: *Q4*, crustose lichen on dead tree on island, 1 specimen. *Q15.1*, foliose lichen and moss on rock, leaf litter in open sclerophyll forest, 13 specimens. *Q15.3*, moss on tree in dry rainforest, 1 specimen. *Q18*, liverwort on trees in park, 3 specimens. *Q25*, foliose lichen and fern on branches on ground in rainforest, 13 specimens. NEW SOUTH WALES: *N3.1*, moss and lichen on rock, moss on trees in open sclerophyll forest, 27 specimens; *N3.3* and *N3.4*, moss and lichen on trees in cool

temperate rainforest, 40 specimens; *N3.2*, *N3.5* and *N3.6*, moss, liverwort and lichen on rocks and trees in subalpine heath, 221 specimens. *N4*, moss on branch on ground in cool temperate rainforest, 1 specimen. *N10*, moss/lichen on rotten log in warm temperate rainforest, 4 specimens. *N11*, moss and lichen on trees, tree ferns and branches on ground in temperate rainforest, 12 specimens. *N14.1*, *N14.2.c*, *N14.2.e* and *N14.6*, moss and lichen on trees and rocks in open sclerophyll forest on cliff top, 113 specimens. *N14.2.d*, *N14.3* and *N14.4*, moss, liverwort and lichen on rock and trees, moss on soil, 65 specimens. *N15*, moss on limestone in sheltered valley, 1 specimen. *N27*, moss and lichen on rock in dry sclerophyll forest, 212 specimens, 5 exuvia containing 2 eggs each. *N29*, lichen on sandstone in open sclerophyll forest, 2 specimens. *N31*, moss and lichen on trees and rocks in cool temperate rainforest, 11 specimens, 1 exuvium containing 2 eggs. *N34*, moss and lichen on trees in closed woodland, 4 specimens. *N35*, moss and lichen on tree, moss/liverwort on rock in cool temperate rainforest, 7 specimens. *N36*, moss/lichen/fern on rock in open sclerophyll forest, 1 specimen. *N39*, moss and lichen on rock in temperate rainforest remnant, 393 specimens, 4 exuvia containing 2, 2, 2, 3 eggs. *N43*, moss on rock in open sclerophyll forest, 1 specimen. *N46.2*, moss on rock in subalpine open woodland, 1 specimen. TASMANIA: *T2*, moss on sandstone in heathland, 1 specimen. *T3*, moss on rock and logs, moss/liverwort on trees and stream bank in closed tall forest gully, 24 specimens. *T4*, moss on rock in closed forest, 3 specimens. *T7*, moss and liverwort on rock and soil in wet forest gully slope, 26 specimens. *T9*, moss and liverwort on limestone in wet sclerophyll forest, 5 specimens. *T10*, liverwort on tree in regenerating cool temperate rainforest, 3 specimens. *T12*, moss, 1 specimen. *T16*, moss on boulder on shaded slope, 1 specimen. *T17*, moss on boulder on island, 1 specimen. *T18*, moss on dolerite in dry sclerophyll forest, 14 specimens. *T21*, weft moss on rock in regenerating closed forest, 1 specimen.

Diagnosis. Cuticle with small evenly distributed black dots. Head and terminal plates faceted. Posterior margin of pseudosegmental plates straight. Claws robust, internal claws with strong spurs. Males present.

Description. Pale yellow. Body length 90 (larva) -190 μm . Females 120-187 μm , males 120-160 μm . Black eye spots present. In 158 (158) μm long female (male), cirrus A with cirrophore, 27 (26) μm long, primary clava 4.3 (5) μm long, ovoid. Internal and external

buccal cirri filiform, 8 (8) and 12 (14.5) μm long, secondary clava 5 (5.7) μm long, ovoid (Plate 6, fig a). Sculpture of small (0.5-0.8 μm) evenly distributed black dots joined by fine radiating lines (Plate 5, Fig a), dots largest on posterior edges of scapular plate, paired plates, on pseudosegmental plate and on caudal plate. Head plate strongly faceted with “W” shape. Scapular plate with longitudinal and transverse folds forming four facets. Paired plates II and III well developed. Median plate 1 undivided, median plates 2 and 3 divided transversely. Two lateral plates present on either side of median plates 1 and 2. Pseudosegmental plate weakly divided. Caudal plate with two long curved incisions. Ventral surface with bands of black dots in reticular pattern, stronger bands in subcephalic area and between each pair of legs (Plate 6, fig. c). Small sensory papilla on fourth pair of legs. Patches of black dots on exterior of all legs. Claws short and robust, internal claws of all legs with strong slightly curved spurs near base of claw. Claws of first pair of legs slightly longer than those of second and third pairs which are equal in length, claws of fourth pair longest. Internal claws of fourth pair of legs 7.6 (7.6) μm long, external 7 (7) μm (in 158 (158) μm specimens).

Exuvia containing 2 or 3 smooth eggs found.

Etymology. Named for Australia as this is the most common species within this genus in Australia.

Remarks. This species is rather similar to *P. suillus*, but differs from it by having a strongly faceted head plate, by being somewhat smaller, having shorter claws and by having males.

Distribution. The most widespread of species in this genus in Australia, it can be found in a wide variety of habitats from far north Queensland to Tasmania.

Pseudechiniscus ficus sp. n.

Fig. 29, Plate 5b

Material examined. Australia: QUEENSLAND: Q6, liverwort on rock in rainforest remnant, 3 specimens. Q7, liverwort on tree in rainforest remnant, 1 specimen.

Diagnosis. Cuticle with very small evenly distributed black dots. Posterior margin of pseudosegmental plates with very short triangular blunt processes. Claws short, internal claws with fine spurs.

Description. Yellow-orange. Body length 141-159 μm . Males not found. Eye spots absent. In 159 μm long specimen, cirrus A 40 μm long, with cirrophore, primary clava 4.3 μm long, ovoid. Internal and external buccal cirri short, 10 and 14 μm long, filiform, secondary clava 4.3 μm long, ovoid. Sculpture of evenly distributed but quite variable in size (0.3-1 μm) black dots (Plate 5, fig. b). Head plate with folds forming “W”-shape. Scapular plate without facets. Paired plates II and III large. Median plates 1 small and undivided; plate 2 divided by transverse fold and plate 3 undivided and poorly separated from pseudosegmental plate. One lateral plate present on either side of median plates 1 and 2. Pseudosegmental plate large with longitudinal division with a pair of short broad-based blunt spines on posterior edge. Caudal plate broad, faceted. Lateral and ventral surfaces with thick lines forming a reticular pattern. Sensory organs absent on first three pairs of legs, papilla on fourth pair. Patches of strong dots on exterior of all legs. Claws short and strongly curved distally, internal claws of all legs with fine spurs close to base of claw.

Claws of first, second and third pairs of legs equal in length, claws of fourth longest.

Internal claws of fourth pair of legs 8 μm long, external 7.6 μm (in 159 μm long specimen).

Etymology. *Ficus*, L. fig-tree, after the large fig tree at the type locality.

Remarks. There are, at present, 12 species described which have triangular projections on the posterior margin of the pseudosegmental plate. This species differs from *P. spinerectus* Pilato *et al.*, 2001 by having a longer cirrus A and having more poorly developed spines on the pseudosegmental plate. It differs from *P. asper* Abe *et al.*, 1998 by having a different division of the median plates and only one intersegmental plate either side of the median plates 1 and 2. It differs from *P. brevimontanus* Kendall-Fite & Nelson, 1996 by having small dot size on the cuticle and having normal shaped secondary clavae. Kendall-Fite & Nelson also outlined some significant characters of the other nine species with triangular projections and those differences hold true for *P. ficus* sp. n.

Distribution. Found at two rainforest sites rather close together in north Queensland.

Pseudechiniscus jiroveci Bartos, 1963

Fig. 30, Plates 5c; 6b and d

Pseudechiniscus jiroveci Bartos, 1963:

Type locality. China

Material examined. **Australia:** QUEENSLAND: Q6, liverwort on tree in rainforest remnant, 2 specimens. Q15, moss and liverwort on tree in dry rainforest, 19 specimens, 1 exuvium containing 2 orange eggs. Q25,

moss and liverwort on tree in rainforest, 2 specimens. NEW SOUTH WALES: *N1*, leafy liverwort on tree in yard, 3 specimens. *N14*, moss/lichen on path, 1 specimen. *N15*, moss and lichen on limestone and on tree in sheltered valley, 13 specimens. *N29*, moss on limestone and lichen on tree in sheltered valley, 19 specimens. *N39*, moss in gutter near rainforest, 3 specimens.

Diagnosis. Cuticle with evenly distributed black dots arranged in light and dark lines.

Secondary clava dome-shaped. Posterior margin of pseudosegmental plates rather sinuous.

Claws short, internal claws with strong spur near base.

Description. Yellow-orange. Body length 99(larva)-243 μm . Males not found. Black eye spots present. In 176 μm long specimen, cirrus A 25 μm long, with cirrophore, primary clava 3.2 μm long, ovoid. Internal and external buccal cirri 7 and 12 μm long, filiform, secondary clava 3.2 μm long and 2.8 μm wide, hemispherical (Plate 6, Fig. b). Sculpture of evenly distributed black dots forming a complex pattern of areas and lines on plates (Plate 5, fig. c). Head plate faceted with lines forming a “W” shape. Scapular plate also faceted. Anterior two-thirds faceted, posterior one third divided into four by three transverse lines. Paired plates II and III large. Median plates 1 and 2 divided transversely, 3 undivided. Two lateral plates on either side of median plates 1 and 2. Pseudosegmental plate divided longitudinally, with rather sinuous posterior edge. Caudal plate faceted. Ventral and lateral surfaces with lines of fine evenly distributed black dots in a reticular pattern (Plate 6, fig. d) and with stronger bands beneath chin, between pairs of legs and around gonopore. Sensory organs absent from first three pairs of legs, papilla on fourth pair. Patches (plates?) of heavier black dotting consisting of 6-8 large dots surrounded by much smaller dots, on exterior of all legs. Claws rather short and robust and curved strongly distally, internal claws of all legs with strongly curved spur near base. Claws of first pair of legs slightly longer than those of second and third pairs which are equal in length, claws of

fourth pair longest. Internal claws of fourth pair of legs 7.6 μm long, external 7 μm long (in 176 μm long specimen)

Exuvia containing 2 smooth orange eggs found.

Remarks. The Australian specimens agree very well with the redescription of this species by Binda (1984) although she suggested that the hemispherical appearance of the secondary clava described by Bartos (1963) was an artifact caused by coverslip pressure. In the Australian specimens, the hemispherical nature of the clava can be seen in many specimens which are unaffected by coverslip pressure and would seem to suggest that, in fact, an elongated appearance of this organ in this species is an artifact.

Distribution. The species has also been found in China and South Africa and Tanzania. This is the first record for Australia.

Pseudechiniscus longiunguis sp. n.

Fig. 31, Plates 5d; 6e

Material examined. Australia: NEW SOUTH WALES: N/5, moss on limestone in sheltered valley, 2 specimens, 1 exuvium containing 3 eggs.

Diagnosis. Cuticle with evenly distributed black dots rather variable in size across plates. Posterior margin of pseudosegmental plates with 2 small cone-like projections. Claws long slender without spurs.

Description. Yellow-orange. Body length 184-204 μm . Males not found. Eye spots absent. In 184 μm long specimen, cirrus A 38 μm long, with cirrophore, primary clava 6 μm long, ovoid. Internal and external buccal cirri short, 11 and 16 μm long, filiform, secondary clava large 7 μm long, ovoid. Sculpture of small (0.2-0.5 μm) black dots evenly distributed but variable in size (Plate 5, fig. d). Head plate with faint folds forming facets. Scapular plate wide with median fold. Paired plates II and III large. Median plates 1 small and undivided, plate 2 divided by transverse fold and plate 3 undivided and poorly separated from pseudosegmental plate. One small lateral plate present either side of median plates 1 and 2. Pseudosegmental plate large undivided with two small cone-like projections on posterior margin. Caudal plate two incisions not facetted. Lateral and ventral surfaces with fine broken lines forming a reticular pattern (Plate 6, fig e), with stronger patches of dots in subcephalic region. Sensory organs absent on first three pairs of legs, papilla on fourth pair. Patches of strong dots on outside of all legs. Claws long and slender not strongly curved distally, with pronounced “toe” on each claw, all claws without spurs. Claws increasing in length from first to fourth, second and third equal in length. Internal and external claws of fourth pair of legs 12.4 μm long (in 184 μm long specimen).

Exuvium containing 3 smooth eggs found.

Etymology. *Longus*, L, long; *unguis*, L, m. claw.

Remarks. This species is similar to *P. novaezeelandiae* in having 2 processes on the posterior edge of the pseudosegmental plate and in lacking spurs on all claws. However it has a very different cuticular pattern and much longer, more slender claws than that species.

Distribution. Found only at one site, Jenolan Caves, NSW.

Pseudechiniscus novaezeelandiae (Richters, 1908)

Fig. 32, Plates 5e; 6f

Echiniscus novaezeelandiae Richters, 1908: 205; Plate 17, figs. 3, 3a

Type locality. North Island, New Zealand.

Material examined. **Australia:** NEW SOUTH WALES: *N11*, weft moss on tree street, 1 specimen. *N14*, moss on tree, 8 specimens. *N15*, moss and liverwort on limestone, moss and lichen on tree in sheltered valley, 32 specimens. *N35*, weft moss on tree in warm temperate rainforest, 8 specimens. *N39.1.b*, moss on rock and log in temperate rainforest remnant, 6 specimens, 1 exuvium containing 3 eggs. **TASMANIA:** *T5*, moss and liverwort on tree in wet sclerophyll forest, 21 specimens. *T7*, moss on rock in wet forest gully slope, 8 specimens, 1 exuvium containing 3 eggs.

Diagnosis. Cuticle with evenly distributed black dots on dorsum and strong ventral pattern. Posterior margin of pseudosegmental plates a pair of broad-based, often bifid, spines. Claws robust, without spurs.

Description. Yellow-orange. Body length 104-220 μm . Males not found. Black eye spots present. In 180 μm long specimen, cirrus A 35 μm long, with cirrophore, primary clava 6.5 μm long, ovoid. Internal and external buccal cirri 14 and 19 μm long, filiform, secondary clava 5.4 μm long, ovoid. Sculpture of evenly distributed black dots, up to 1.5 μm diameter and joined by fine radiating lines (Plate 5, fig. e). Head plate faceted. Scapular plate rather narrow with one transverse and one longitudinal line forming four facets. Paired plates II and III large. Median plates 1 and 3 undivided, 2 divided by transverse line. One lateral plate present on either side of median plates 1 and 2. Pseudosegmental plate divided

longitudinally, with a pair of broad-based, often bifid, spines (about 10 μm long) on posterior edge. Caudal plate with two incisions, not faceted. Ventral surface with very fine evenly distributed black dots often exhibiting heavy lines in a reticular pattern and with particularly heavy bands beneath chin, between pairs of legs (Plate 6, fig. f) and around gonopore. Sensory organs absent from first three pairs of legs, papilla on fourth pair. Patches (plates?) of heavier black dotting on exterior of all legs. Claws rather short and robust and curved strongly distally, all claws without spurs. Claws of first and fourth pair of legs equal in length slightly longer than those of second and third pairs also equal in length. Internal claws of fourth pair of legs 9.7 μm long, external 9.2 μm long (in 180 μm long specimen).

Exuvia containing 3 smooth eggs found.

Remarks. The Australian specimens differ somewhat from descriptions of this species in the literature. Horning, Schuster & Grigarick (1978) and Miller, Heatwole, Pigeon & Gardiner (1994) mention the presence of a spine on the first pair of legs of specimens from New Zealand and Antarctica respectively. Grigarick, Schuster & Nelson (1983) found a basal spur on the inner claw of specimens from Venezuela. Both of these characters are species specific which suggests that there may be more than one species under consideration and that the Australian specimens may belong to a different taxon. A comparative study is necessary to clarify the situation.

Distribution. The species has also been found in the Pacific Islands, Central and South America and Antarctica. The record of this species in Poland by Weglarska (1959) is questionable (Dastyh, 1988) especially in view of the above discussion.

***Pseudechiniscus suillus* (Ehrenberg, 1853)**

Echiniscus suillus Ehrenberg, 1853: 530

Type locality. Mount Rosa, The Alps

Material examined. Australia: None. Described by Murray (1910) as occurring at Kosciusko, Blue Mountains and Eumundi.

Diagnosis. Cuticle with evenly distributed black dots. Head and caudal plates not faceted. Posterior margin of pseudosegmental plates straight. Internal claws with spurs.

Description. Body length up to 285 μm . Males not found. Black eye spots present. Sculpture of small evenly distributed black dots, especially fine on the head and scapular plates and on the three median plates, coarser on other plates and especially visible on terminal plate. Paired plates II and III may be divided longitudinally by a smooth fold. Pseudosegmental plate may be divided longitudinally by fold. Caudal plate two incisions not faceted. Patches of strong dots on outside of all legs. Sensory organs absent on first three pairs of legs, papilla on fourth pair. Claws robust. Internal claws with spurs. Exuvium containing 1 to 5 smooth eggs found. (Ramazzotti & Maucci, 1983).

Remarks. Ramazzotti & Maucci (1983) stated that “it is certain that many citations of *P. suillus* especially older ones do not refer to this species but to other close species”. This “*suillus*” group is in need of revision. It is most probable that the species which Murray described as *E. mutabilis* (later synonymised with *P. suillus* by Richters, 1911) from the three sites in Australia is in fact *P. australis* sp. n. which is similar in some respects.

Distribution. Unknown because of incorrect identifications.

Suborder Echiniscoidea Marcus, 1927

Family Oreellidae Puglia, 1959

Genus *Oreella* Murray, 1910

Oreella Murray, 1910: 135, Plate XVIII, Fig 26.

Type species. *Oreella mollis* Murray 1910

Diagnosis. (from Dastych, McInnes & Claxton 1998) Dorsal and ventral cuticular plates absent; short caudal median projection present. Primary and secondary clavae sexually dimorphic. Secondary clava located under the cuticular surface. Telescopic leg with four claws in adults, two claws in larvae. Female with pair of ductless seminal receptacles. Eggs ornamented and laid free.

Key to species of *Oreella*

1. Cuticle with small evenly arranged pillars and with larger
papillae..... *O. mollis*

Cuticle with small evenly arranged pillars only..... *O. reinhardti*

***Oreella mollis* Murray, 1910**

Fig. 33

Oreella mollis Murray, 1910: 135-137; Plate XVIII, fig. 26

Type locality. Katoomba, NSW

Material examined. **Australia:** NEW SOUTH WALES: N3.2, moss and fruticose lichen on rock in subalpine heath, 24 specimens, 5 eggs. N3.5, moss on trees in cool temperate rainforest, 8 specimens, 1 egg. N39, moss on rock in temperate rainforest, 49 specimens, 4 eggs (including one embryonate egg). **TASMANIA:** T3.2, moss on rock in low wood heathland at 470 m. altitude, 1 specimen. T12, foliose lichen in closed woodland, 3 specimens. T17, moss on dolerite boulder in heath on island mountain at 620 m. altitude, 1 specimen. **New Zealand:** 1 specimen. **Antarctica:** 1 specimen.

Diagnosis. Cuticle covered with small dots (“pillars”) arranged in hexagons also covered with larger, unevenly distributed papillae. Elongated, forward-pointing, cone-shaped secondary clava under thin layer of cuticle.

Description. White. Body length 84 (larva)-237 μm ; females 162-237 μm , males 155-205 μm . Eye spots absent. Cuticle covered with small dots (“pillars”) about 0.5 μm diameter, arranged in hexagons; also covered with larger, unevenly distributed papillae, 1.5-2.5 μm which increase slightly in size towards the posterior. Ventral papillae are smaller and more sparsely distributed towards the anterior. Mouth antero-ventral. In 203 (173) μm long female (male), buccal tube 19 (19) μm and 1.8 μm wide. Stylet supports inserted at 68% of buccal tube length. Pharyngeal bulb small round (about 15 μm diameter). Cirrus A 42 (40) μm long with large bell-shaped cirrophore; primary clava 5.4 (12) μm long and 1 (1.5) μm wide, arising from side of cirrophore. Internal buccal cirrus short, 3 (3.8) μm long and cone-shaped, external buccal cirrus 10 (11) μm long, seta-like, with small poorly defined

cirrophore. Secondary clava 4.3 (6) μm long and 3 (3.8) μm wide, arising under the cuticle, pointing forward and downward. In females, a pair of seminal receptacles, opening directly to the exterior, present caudo-laterally at the level of the genital papilla. Female genital papilla rosette-shaped with six lobes; male papilla a small, transversely directed oval structure. Slit-like anus located between two rounded anal plates. Short median caudal projection is located just behind anus between fourth pair of legs. Legs long, thin and retractable. First pair of legs with small spine-like sensory organ, fourth pair with small sensory papilla. Claws robust with distinct angle half way up, internal claws with strong spur standing well out from claw, inserted well above base with distal end almost reaching base. Claws of first three pairs of legs equal in length, those of fourth pair slightly longer. Internal claws on fourth pair of legs 5.4 (4.9) μm , external 4.9 (4.3) μm long (in 203 (173) μm long specimens).

Eggs laid free, round with processes. Diameter with processes 59-71 μm , without 50-63 μm . Processes thin-walled regularly distributed over surface, 16-20 around circumference. Process mushroom-shaped with strongly sclerotised and compartmentalised core; up to 6 μm high and 4-6 μm cap diameter and base diameter 3 μm . Egg processes appear very similar to those of *Minibiotus floriparus*.

Remarks. A more complete description of this species can be found in Dastych, McInnes & Claxton (1998). A discussion of the significance of the egg type in this genus may be found in Bertolani, Rebecchi & Claxton (1996).

Distribution. The genus *Oreella* (and *O. mollis*) are Gondwanan elements reported from Australia, New Zealand, Maritime Antarctic (Signey Island), South Georgia and South America.

***Oreella reinhardti* sp. n.**

Fig. 34

Material examined. Australia: NEW SOUTH WALES: N39, moss and lichen on rock in temperate rainforest, 79 specimens.

Diagnosis. Cuticle covered with small dots (“pillars”) arranged in hexagons. Elongated, forward-pointing, cone-shaped secondary clava between internal and external cirri. Legs long, thin. First pair of legs with small spine-like sensory organ, fourth pair with small sensory papilla. Claws short; inner claws with spur inserted well above base but distal end reaching almost to base.

Description. White. Body length 85-210 μm ; females 135-210 μm , males 125-170 μm . Cuticle covered with small dots (“pillars”) about 0.5 μm diameter, arranged in hexagons. Eye spots absent. Mouth antero-ventral. In 210 (167) μm long female (male), buccal tube 23.8 (21.6) μm long and 1.5 μm wide. Stylet supports inserted at 72% of buccal tube length. Pharyngeal bulb small round (about 15 μm diameter). Cirrus A 37 (34) μm long with large bell-shaped cirrophore; primary clava 6.5 (12) μm long and 1 (1) μm wide, arising from head beside cirrophore of cirrus A. Internal buccal cirri very short, 2.5 (2.5) μm long, and cone-shaped; external buccal cirri 8 (5) μm long, seta-like, without cirrophore. Secondary clava 6.5 (7.6) μm long by 2.7 (4.3) μm wide, arising under cuticle, elongated and pointing forward and downward. In females, a pair of seminal receptacles open directly to the exterior present caudo-laterally at the level of the genital papilla. Female genital papilla rosette-shaped with six lobes; male papilla a small, transversely directed oval structure. Slit-like anus located between two rounded anal plates. Short median caudal projection is located just behind anus between fourth pair of legs. Legs

long, thin and retractable. First pair of legs with small spine-like sensory organ, fourth pair with small sensory papilla. Claws robust, strongly curved, distally tapering to long fine points, internal claws with distinct spur inserted well above base with distal end almost reaching base. Claws of first three pairs of legs equal in length, those of fourth pair slightly longer. Internal and external claws on fourth pair of legs 5.4 (5) μm long (in 210 (167) μm long specimens).

Eggs not found.

Etymology. Named for Reinhardt Mobjerg Kristensen in appreciation of his friendship and assistance with these lovely beasts.

Remarks. This species differs from *O. mollis* by lacking papillae covering the dorsal cuticle, having secondary clavae not covered by cuticle and having primary clavae separate from the cirrophore of cirrus A.

Distribution. Found only at Cambewarra Mountain.

Class Eutardigrada Marcus 1927

Order Parachela Schuster et al 1980

Famliy Calohypsibiidae Pilato, 1969

Genus *Apodibius* Dastych, 1983

Apodibius Dastych: 1983: 1

Type species. *Apodibius confusus* Dastych, 1983

Diagnosis. (emended from Dastych, 1983) Six peribuccal lobes. Rigid buccal tube, ventral support present. Legs strongly reduced and without claws or sclerified structures.

Apodibius serventyi Morgan & Nicholls, 1986

Fig 35

Apodibius serventyi Morgan & Nicholls, 1986: 1-3, Figs 1-4

Type locality. Perth, Western Australia

Material examined. Australia: WESTERN AUSTRALIA: *W1*, moss on rock and footpath, leaf litter on soil under *Eucalyptus* tree in urban street, 9 specimens, 7 cysts. *W3*, moss on limestone wall urban park, 8 specimens.

Diagnosis. Cuticle smooth, no pores colourless. Six peribuccal lobes present. Pharynx with 3 macroplacoids, microplacoid absent. Claws absent.

Description. Colourless. Body length 166-411 μm . Eye spots present. Cuticle smooth, no pores. Mouth terminal, no teeth or ridges in oral cavity. Buccal tube 34 μm long in 320 μm long individual and 4.3 μm wide (12.7% of buccal tube length). Stylet supports inserted at 81% of buccal tube length, ventral support short 42%. Pharyngeal bulb pear-shaped (32 μm long by 28 μm wide) containing large triangular apophyses and 3 macroplacoids. Macroplacoids rounded rods increasing in length from first to third or first two same size (3, 3.2, 3.8 μm long). First and second macroplacoids connected by a narrow rod. Macroplacoid row length 37% of buccal tube length. Microplacoid absent. Legs without claws.

No eggs found. A number of black cysts were found including ones with fully developed individuals that were extruded from the cysts when mounted.

Remarks. The species is very similar to *Apodibius nuntius* Binda, 1984 but differs from it by having the stylets inserted more caudally (75.5-77% in *A. nuntius*) and a shorter ventral support (50% in *A. nuntius*). It differs from *A. confusus* Dastych, 1983 by having three macroplacoids.

Distribution. The species has only been reported from the type locality. Members of this genus have not been widely reported.

Genus *Calohypsibius* Thulin, 1928

Calohypsibius Thulin, 1928: 238.

Type species. *Macrobiotus ornatus* var *spinifer* Richters, 1900

Diagnosis. (emended from Pilato, 1998) Rigid buccal tube, ventral support absent.

Diploclaws on each leg similar in shape and size and asymmetrical with respect to median plane of leg. Diploclaws on each leg with branches rigidly connected by a vertical suture.

Calohypsibius ornatus (Richters, 1900)

Fig 36

Macrobiotus ornatus Richters, 1900: 40-42; Plate 6, figs 1, 4

Hypsibius ornatus var *spinifer* Thulin, 1911: 28; fig 13-13b

Hypsibius ornatus Marcus, 1928: 178; fig. 217

Calohypsibius ornatus Thulin, 1928: 238-239

Type locality. Taunus Mts, Germany.

Material examined. **Australia:** NEW SOUTH WALES: N3.5, moss on rock in subalpine hath, 1 specimen.

TASMANIA: T7, moss/liverwort on rock in wet forest gully, 1 specimen. T8, moss/liverwort/lichen on soil in wet forest, 7 specimens.

Diagnosis. Dorsal cuticle with 8 transverse rows of spines. Narrow buccal tube, pharynx with two small macroplacoids, microplacoid absent. Claws small slender, similar on each leg, primary and secondary branches joined, from the base by a vertical suture.

Description. Colourless. Body length 122-167 μm . Eye spots absent. Cuticle with 8 transverse rows of spines, the first row at the level of the first pair of legs, eighth row, above fourth pair of legs with very strong curved spines. Small papillae cover head region, and occur between rows of spines. Mouth antero-ventral. Buccal tube 19.5 μm long in 156 μm specimen and 1.6 μm wide (8.3% of buccal tube length). Stylet supports inserted at 55-

57% of buccal tube length. Pharyngeal bulb round (15 μm diameter) containing large apophyses and 2 granular macroplacoids. First macroplacoid largest (3.8 μm), second (1.6 μm). Macroplacoid row length very short (19% of buccal tube length). Claws short secondary branch joined to primary branch by vertical suture; primary branch with short low accessory claws. Internal claws slightly shorter than external claws. Claws increasing in length from first to fourth. Internal claws on first pair of legs 3.2 μm long (16.6% of buccal tube length), external 3.8 μm (19.4%); anterior claws of fourth pair of legs 4.3 μm long (22%), posterior 4.9 μm (25%). Lunules absent.

Smooth eggs laid in exuvium (not found in this study).

Remarks. Measurements of these specimens agree very well with those provided by Pilato, Claxton & Binda (1989a), for specimens of *C. ornatus* from Greenland and Italy.

Distribution. A cosmopolitan species reported from every continent (reported here for the first time for Australia). The habitats in which it was found in Australia agree with the findings of Dastych (1988) that this is a mountain species. This is the first record of its occurrence in Australia.

Genus *Parhexapodibius* Pilato, 1969

Parhexapodibius Pilato, 1969: 386

Type species. *Hexapodibius lagrecai* Binda & Pilato, 1969.

Diagnosis. Buccal tube rigid, ventral support present. Diploclaws on each leg rather similar in shape and size and asymmetrical with respect to median plane of leg. Diploclaws

on each leg with branches rigidly connected by vertical suture. Claws of fourth pair of legs shorter than those on the other three pairs of legs, sometimes reduced to single claw on each leg.

Key to species of *Parhexapodibius*

1. Single claw on each of the fourth legs..... 2
 - Two claws on each of the fourth legs..... 3
2. Two bulbs present on dorsum above fourth pair of legs, eye spots absent..... *P. australis*
 - Cuticle smooth, no dorsal bulbs, eye spots present..... *P. pilato*
3. Buccal tube narrow (11% of buccal tube length), eye spots present..... *P. ramazzotti*
 - Buccal tube wide (18% of buccal tube length), eye spots absent..... *P. lagrecai*

Parhexapodibius australis sp. n.

Fig. 37

Material examined. **Australia:** NEW SOUTH WALES: *N3.1*, leaf litter in dry sclerophyll forest, 8 specimens. QUEENSLAND: *Q15*, leaf litter on soil in dry sclerophyll forest, 20 specimens. *Q20*, leaf litter on sand in *Banksia* scrub, 10 specimens.

Diagnosis. Cuticle smooth, no pores; narrow buccal tube, pharynx with 2 macroplacoids, no microplacoid. Claws slender, similar on each leg; fourth leg with single claw.

Description. Colourless. Body length 150-237 μm . Eye spots absent. Cuticle smooth. Buccal tube 23.8 μm long and 2.1 μm (8.6% of buccal tube length) wide in 237 μm individual. Stylet supports inserted at 73-74% of buccal tube length, ventral support short (36%). Pharyngeal bulb oval (20 μm by 18 μm) containing large apophyses and 2 macroplacoids. First and second macroplacoids very close about same size (1.4 μm) third small round (2.2 μm). Claws slender with short secondary branch and short low accessory claws; inner shorter than outer (2.7 and 3.8 μm on first pair of legs). Single claw on each leg of fourth pair (4.3 μm long). Lunules absent.

No eggs found.

Etymology. Named for Australia as this is the first new species of this genus to be found on this continent.

Remarks. Differs from other species in the genus by having two dorsal bumps above the fourth pair of legs.

Distribution. The species occurs in similar conditions in the three sites at which it was found.

Parhexapodibius lagrecai (Binda & Pilato, 1969)

Fig. 38

Hypsibius (Calohypsibius) lagrecai Binda & Pilato, 1969: 176-179; Fig. 2, 3, 4A

Type locality. Ustica, Italy.

Material examined. Australia: WESTERN AUSTRALIA: *Q1*, leaf litter and moss on rock in dry sclerophyll, 7 specimens, 1 exuvium containing 6 eggs.

Diagnosis. Wide buccal tube, pharynx with 3 macroplacoids, no microplacoid. Claws slender, similar on each leg.

Description. Colourless. Body length 211-394 μm . Eye spots absent. Cuticle smooth. Mouth antero-ventral, no teeth in oral cavity. Buccal tube 40.5 μm long and 7.3 μm wide (18% of buccal tube length) in 394 μm individual. Stylet supports inserted at 73.4% of buccal tube length, ventral support 41%. Pharyngeal bulb round (32 μm diameter) containing small apophyses and 3 macroplacoids. First macroplacoid 4.6 μm long, second, 4.1 μm and third longest (5.4 μm) with slight median constriction. Claws with long slender primary branch and short fine secondary branch vertical suture between them very clear; accessory claws very fine and close to primary branch. Internal claw shorter than external on all legs (7.6 and 8.1 μm long on first three pairs, 7.0 and 7.6 μm long on fourth pair). Lunules absent.

One exuvium containing six smooth eggs found.

Remarks. The specimens described here have very similar dimensions to those given in the original description.

Distribution. The species has been reported only from Italy and North Africa (Algeria). This is the first report of its occurrence in Australia. The disjunct distribution is probably due to lack of collection of suitable habitats.

***Parhexapodibius pilatoi* (Bernard, 1977)**

Fig. 39

Hexapodibius pilatoi Bernard, 1977: 476-479; Figs. 1-3, 10-13

Type locality. Michigan, USA

Material examined. Australia: QUEENSLAND: Q20, leaf litter/sand in *Banksia* heath on sand island, 6 specimens.

Diagnosis. Large eyes. Cuticle smooth, no pores; narrow buccal tube, pharynx with 3 macroplacoids, no microplacoid. Claws small, single claw on each of fourth pair of legs.

Description. Colourless. Body length 246-315 μm . Large eye spots present. Mouth antero-ventral, no teeth in oral cavity. Buccal tube 33 μm long and 3.2 μm wide (9.8% of buccal tube length) in 315 μm individual. Stylet supports inserted at 76% of buccal tube length, ventral support 41%. Pharyngeal bulb oval to round (24 μm diameter) containing large apophyses and 3 macroplacoids. Macroplacoids increasing in length from first to third (2.7, 3.0, 3.6 μm). Claws slender with short secondary branch, accessory claws short fine but high at the tip on all claws. Internal claw shorter than external on first three pairs of legs (5.4 and 6.0 μm on first pair, 6 and 7 μm on second and third pair). A single claw (6.5 μm long) present on each leg of fourth pair. Lunules absent.

No eggs found.

Remarks. The specimens agree well with the description of this species.

Distribution. The species was found in soil at the type locality and in moss on soil in Georgia, USA. It has also been reported from soil under grass in Italy and from moss in Korea. This is the first report of its occurrence in Australia. The disjunct distribution of this species is most probably due to poor collection of its habitat.

Parhexapodibius ramazzotti Manicardi & Bertolani, 1987

Fig.40

Parhexapodibius ramazzotti Manicardi & Bertolani, 1987: 180-183; Fig. 2

Type locality. Northern Italy.

Material examined. **Australia:** NEW SOUTH WALES: *N47*, moss on soil near ocean, 8 specimens.

QUEENSLAND: *Q20*, leaf litter/sand near ocean beach, 2 specimens, 22 cysts.

Diagnosis. Cuticle smooth, no pores. Narrow buccal tube, pharynx with 3 macroplacoids, no microplacoid. Claws slender, similar on each leg. Claws of fourth pair of legs shorter than those of third pair.

Description. Colourless. Body length 196-315 μm . Large eye spots present. Cuticle smooth. Mouth terminal, no teeth in oral cavity; crests absent. Buccal tube 29.2 μm long and 3.1 μm wide (10.6% of buccal tube length) in 315 μm individual. Stylet supports inserted at 76.5% of buccal tube length, ventral support short (41%). Pharyngeal bulb oval (27 μm by 21 μm) containing large apophyses and 3 macroplacoids. Macroplacoids increasing in length from first to third (2.2, 2.7, 3.2 μm). Internal claws shorter than external (7.0 and 8.1 μm on first and third pair of legs), slightly longer on second pair (7.6

µm and 8.7 µm); fourth pair shortest (anterior 5.4 µm and posterior 6.5 µm). Secondary branch short and accessory claws short but well-developed. Lunules absent.

Remarks. The specimens described here agree well with the dimensions of the type material.

Distribution. This is the first report of this species apart from the original finding in soil under grass in Italy.

Family Hypsibiidae Pilato, 1969

Subfamily Diphasconinae Dastych, 1992

Genus *Diphascon* Plate, 1888

Diphascon Plate, 1888: 537, Fig. 25.

Type species. *Diphascon chilense* Plate, 1888

Diagnosis. (emended from Pilato, 1987) Buccopharyngeal tube with rigid anterior buccal tube and flexible posterior pharyngeal tube. Apophyses for insertion of stylet muscles in shape of “semilunar hook”, symmetrical with respect to frontal plane. Placoids present in pharynx. Diploc claws on each leg different in shape and size and asymmetrical with respect to median plane. Primary branch of each claw joined flexibly to secondary branch at a distance from base of claw.

Subgenus *Adropion* Pilato, 1987

Diagnosis. “Drop-like” thickening between buccal and pharyngeal tubes absent.

Key to species of the subgenus *Adropion*

1. Three macroplacoids, microplacoid and septulum in
pharynx..... *D. (A.) gordonense*
Three macroplacoids in pharynx..... *D. (A.) prorsirostre*

***Diphascon (Adropion) gordonense* Pilato, Claxton & Horning, 1991**

Fig. 41

Diphascon (Adropion) gordonense Pilato *et al.*, 1991: 157-160, Fig 1a-d

Type locality. Gordon Falls, Blue Mountains, New South Wales.

Material examined. Australia: NEW SOUTH WALES: *N14*, leaf litter on soil, moss and lichen on rock, 9 specimens. WESTERN AUSTRALIA: *W1*, lichen on rock in Jarrah forest, 2 specimens.

Diagnosis. Cuticle smooth. 3 macroplacoids, a microplacoid and a septulum in pharynx.

Claws slender, outer claw much longer than inner. Faint cuticular bars on legs I-III.

Description. Colourless. Body length 160-234 μm . Eye spots absent. Cuticle smooth.

Antero-ventral mouth. Buccal tube 20.9 μm in 210 μm specimen and 1.2 μm wide (5.9% of buccal tube length). Stylet supports inserted at 62.7% of buccal tube length. Pharyngeal tube 33.5 μm long (61.5% of buccopharyngeal tube length). Pharynx oval (23 μm by 16 μm), containing well developed apophyses, 3 macroplacoids, microplacoid and septulum.

Macroplacoid row length 36%. First macroplacoid 2.2 μm , second 2.2 μm , third 2.7 μm , microplacoid 0.6 μm and septulum 2.1 μm . Macroplacoid row length 8.1 μm (39% of buccal tube length. Claws well developed, slender, increasing in length from first to fourth, (second and third equal in length). Internal claws with long primary branch with thick accessory claws. External claw with long thin primary branch with fine short accessory claws. Anterior claw of fourth pair of legs 8.2 μm (39.2% of buccal tube length), posterior claws 13.3 μm (63.4%). Secondary branch of posterior claw 68% of length of primary branch. Lunules absent. Faint thickened bar present on first three pairs of legs near inner claw.

Eggs not found.

Remarks: This species differs from other species in the subgenus by having short placoids.

Distribution: A rare but widespread species in Australia. It was reported from Macquarie Island, sub-Antarctica by Miller, Horning & Heatwole (2001).

***Diphascon (A.) prorsirostre* Thulin, 1928**

Fig. 42

Diphascon prorsirostre Thulin, 1928: 256, Fig 27

Type locality. Sweden.

Material examined. NEW SOUTH WALES: *N14.2*, lichen and leaf litter on sandstone soil in open sclerophyll forest on escarpment top, 5 specimens. *N14.5*, moss, lichen and liverwort on rock in rainforest

remnant, 9 specimens. *N15*, moss on limestone, 1 specimen. *N46.2*, moss on rock in subalpine heath, 5 specimens. QUEENSLAND: *Q25*, moss on rock in Box forest, 2 specimens. LORD HOWE ISLAND: moss, 4 specimens.

Diagnosis. Smooth cuticle. Long thin buccopharyngeal tube. 3 rod-shaped macroplacoids in pharynx.

Description. Colourless. Body length 157-320 μm . Eye spots absent. Cuticle smooth. Buccal tube 23 μm long in 287 μm long specimen and 2.2 μm wide (9.4% of buccal tube length. Stylet supports inserted at 70% of buccal tube length. Pharyngeal tube 37.8 μm long (62.2% of buccopharyngeal tube length). Pharyngeal oval (32 μm by 26 μm) containing very small apophyses and three long rod-shaped macroplacoids. Macroplacoid row length 67% of buccal tube length. Macroplacoid length increasing from first to third (3.2, 3.8, 5.7 μm). Microplacoid and septulum absent. Macroplacoid row length 15.4 μm (67% of buccal tube length). Claws rather short and slender, increasing in length from first to fourth (second and third equal in length). Internal claws much shorter than external, with short secondary branch and short thick accessory points on primary branch. External claws short slender with short secondary branch and primary branch with refractory zone at base and short thick accessory points. Anterior claw of fourth pair of legs 6 μm long (50% of length of posterior claw), posterior claw 11.9 μm long. Secondary branch of posterior claws 70-71% of length of primary branch. Lunules and cuticular bars absent.

Eggs not found.

Remarks. Pilato (1987) gives the ratio of the pharyngeal tube to the buccopharyngeal tube as 59.4-62.1% and the ratio of the stylet support insertion length to the buccal tube length as 67-69.2%. The values obtained in the present study are close to these values.

Distribution. The species is widespread and has been found in Europe, North and South America and New Zealand. This is the first report of this species in Australia. Dastych (1988) considered it to be a geopolitan element which prefers soil mosses and occurs (in Poland) more frequently on carbonate bedrock.

Subgenus *Diphascon* Pilato, 1987

Diagnosis. “Drop-like” thickening between buccal and pharyngeal tubes present.

Key to species of the subgenus *Diphascon*

1. Cuticle smooth..... 2
 - Cuticle sculptured..... 9
2. Thickening between buccal and pharyngeal tubes a large drop..... 3
 - Thickening between buccal and pharyngeal tubes small and flat..... *D. (D.) higginsii*
3. Three macroplacoids and/or microplacoid and septulum in pharynx; cuticular bars on legs present or absent..... 4
 - Two macroplacoids and septulum in pharynx; cuticular bars on inside of internal claw on all legs and inside posterior claw of fourth pair of legs..... *D. (D.) brevipes*

4	Cuticular bars on legs absent.....	5
	Cuticular bars present on some legs.....	8
5	Microplacoid and septulum present.....	6
	Microplacoid or septulum present.....	7
6	Macroplacoid row length 37-60% of buccal tube length.....	<i>D. (D.) pingue</i>
	Macroplacoid row length 60-83% of buccal tube length.....	<i>D. (D.) pinguiforme</i>
7	Microplacoid present; macroplacoid row length 24% of buccal tube length.....	<i>D. (D.) langhovdense</i>
	Septulum present; macroplacoid row 52% of buccal tube length.....	<i>D. (D.) ongulense</i>
8	Cuticular bars at base of internal claw of first three pairs of legs and between claws on fourth pair; teeth on bases of all claws.....	<i>D. (D.) nobilei</i>
	Cuticular bars at base of internal and external claws on first three pairs of legs; bases of all claws smooth.....	<i>D. (D.) scoticum</i>
9	Cuticle sculptured, no gibbosities.....	10
	Cuticle with polygonal sculpture and gibbosities arranged two-by-two in 8 transverse rows.....	<i>D. (D.) bullatum</i>
10	Sculpture of wrinkles or thickenings on posterior half of dorsum.....	11
	Sculpture of polygonal granules over whole dorsum; 2 macroplacoids and septulum in pharynx.....	<i>D. (D.) rugosum</i>
11	Microplacoid present.....	<i>D. (D.) puniceum</i>
	Microplacoid and septulum present.....	<i>D. (D.) pannuceum</i>

***Diphascon (Diphascon) brevipes* (Marcus, 1936)**

Fig. 43

Hypsibius (Diphascon) brevipes Marcus, 1936: 302-303, Fig 284

Type locality. Hungary.

Type material examined. Australia: VICTORIA: VI, leaf litter and moss under mallee scrub, 10 specimens.

Diagnosis. Cuticle smooth. Large drop-shaped thickening between buccal and pharyngeal tubes. 2 macroplacoids and a septulum in pharynx. Cuticular bars on inside of internal claws on all legs and between claws on fourth pair of legs.

Description. Colourless. Body length 261-356 μm . Cuticle smooth. Eye spots present. Mouth antero-ventral. Buccal tube 23.2 μm long in 344 μm long specimen and 2.2 μm wide (9% of buccal tube length). Stylet supports 68.7% of buccal tube length. Pharyngeal tube 35.7 μm long (60.6% of buccopharyngeal tube). Large drop-shaped cuticular thickening between buccal and pharyngeal tubes on dorsal surface. Pharynx oval (30 μm by 34 μm) with small apophyses, 2 macroplacoids and a septulum. First macroplacoid 5.4 μm long, second 3.8 μm and septulum 1.6 μm . Macroplacoid row length 9.7 μm (42% of buccal tube length). Claws short and robust, increasing in length from first to fourth, second and third equal in length. Internal claw with short narrow base, short secondary branch and primary branch set at an angle of about 180° to secondary branch, short close accessory points. External claw with rather long narrow base, long hooked secondary branch and short primary branch with a long hooked distal part with short close accessory claws. Anterior claw of fourth pair of legs 6.5 μm (60% of length of posterior claw).

Posterior claw 10.8 μm . Secondary branch of posterior claw 64% of length of primary branch. Long sinuous cuticular bars (9.7 μm on first pair) arise from base of inner claw on first three pairs of legs, short bars (3-3.5 μm) arise from bases of both claws on fourth pair of legs. Lunules absent.

Eggs not found.

Remarks. These specimens agree well with the dimensions given by Biserov (1996) and the ratios for pharyngeal tube length to buccopharyngeal tube length and stylet support insertion length are similar to those given by Pilato (1987).

Distribution. This species has been reported from Europe (Hungary, Italy, Finland, Russia) and was considered to be a rare species by Maucci (1986). It was also reported from Argentina and North America. This the first report of the occurrence of this species in Australia. Its apparent rarity and disjunct distribution may be a result of its preference for a habitat that is not frequently studied.

***Diphascon (D.) bullatum* Murray, 1905**

Fig. 44

Diphascon bullatum Murray, 1905: 164, Fig 2a-f

Type locality. Scotland.

Material examined. **Australia:** NEW SOUTH WALES: *N14.2.b*, moss on tree on escarpment top, 5 specimens. *N25*, moss/liverwort on rock in closed forest, 1 specimen. *N27*, moss on rock in open sclerophyll forest, 7 specimens, 1 exuvium containing 4 eggs. *N48*, weft moss on rock in open sclerophyll forest, 3

specimens. QUEENSLAND: *Q25*, moss on rock in Box forest, 2 specimens. VICTORIA: *V3*, leaf litter in cool temperate rainforest, 12 specimens. WESTERN AUSTRALIA: *W1*, leaf litter after flood, 2 specimens.

Diagnosis. Cuticle with polygonal sculpture also gibbosities arranged two-by-two in 8 transverse rows on dorsum. Eye spots present. Large drop-shaped thickening between buccal and pharyngeal tubes. Two macroplacoids and a septulum in pharynx. Cuticular bars present at base of inner claw on first three pairs of legs, two small cuticular bars at base of each claw on fourth pair of legs.

Description. Colourless. Body length 157-340 μm . Eye spots present. Cuticle with polygonal sculpture and gibbosities arranged two-by-two in 8 transverse rows on dorsum. Mouth antero-ventral. Buccal tube 22.2 μm long in 250 μm long specimen and 1.6 μm wide (7.3% of buccal tube length). Stylets inserted at 68% of buccal tube length. Pharyngeal tube 32.4 μm long (59% of buccopharyngeal tube length). Large drop-shaped cuticular thickening between buccal and pharyngeal tubes on dorsal surface of tube. Pharynx oval (28 μm by 23 μm) with large apophyses, 2 macroplacoids and a septulum. First macroplacoid 4.7 μm long, with faint median constriction, second 3.8 μm and septulum 2.2 μm . Macroplacoid row length 9.7 μm (44% of buccal tube length). Claws short and robust. Internal claw with short narrow base, short secondary branch and long primary branch with short fine accessory claws. External claw with rather long base, long hooked secondary branch and short primary branch with a long hooked distal part with short fine accessory points. Anterior claw of fourth pair of legs 7 μm (68% of length of posterior claw), posterior claw 10.3 μm . Secondary branch of posterior claw 57% of primary branch. Long cuticular bars (7 μm on first pair of legs) at base of inner claw on first three pairs of legs, short bars (3-3.5 μm) at bases of both claws on fourth pair of legs. Lunules absent.

One exuvium containing 4 eggs found.

Remarks. Dastych (1988) suggested that this species is conspecific with *D. (D.) patanei* Binda & Pilato, 1971 but remarked that resolution of the matter was extremely difficult because the type material no longer exists (Van der Land, 1966). The specimens examined here were placed in this taxon because it has precedence over *D. (D.) patanei*.

Distribution. Reported for the first time for Australia, this species is rather rare but widely distributed. It has been reported from Europe, North and South America and New Zealand.

***Diphascon (D.) higginsii* Binda, 1971**

Fig. 45

Diphascon higginsii Binda, 1971: 761-764, Figs A, B

Type locality. Marrakech, North Africa.

Material examined. **Australia:** NEW SOUTH WALES: *N3.1*, leaf litter in open sclerophyll forest, 3 specimens; *N3.2*, moss and lichen on rock in *Banksia* heath, 9 specimens, 1 exuvium containing 2 eggs; *N3.5*, moss and lichen on trees in subalpine heath, 9 specimens. *N14*, moss on rock, on tree and on soil, leaf litter on soil, lichen on tree in open sclerophyll forest on escarpment top, 43 specimens; *N14.2 and 14.3*, moss and lichen on rock, liverwort on tree in rainforest pockets, 35 specimens, 1 exuvium containing 3 eggs. *N28*, moss on rock in sclerophyll forest, 1 specimen. *N29*, lichen on sandstone, 1 specimen. *N34*, moss and lichen on tree in sclerophyll forest, 17 specimens, 3 exuvia containing 1, 2 and 2 eggs. *N35*, moss on tree in rainforest pocket, 5 specimens. *N36*, moss on rock in open sclerophyll forest, 2 specimens, 1 exuvium containing 5 eggs. *N46.2, 46.3*, moss on rock in subalpine heath, 1 specimen, 1 exuvium containing 3 eggs. **QUEENSLAND:** *Q15.3*, liverwort on rock in dry rainforest, 1 specimen. **VICTORIA:** *V3*, moss/liverwort on

tree in *Nothofagus* forest, 2 specimens. TASMANIA: *T3*, moss on rock in coastal heath, 1 specimen. *T7*, moss on soil in wet forest gully, 4 specimens, 1 exuvium containing 3 eggs. *T18*, moss on dolerite in sclerophyll forest, 3 specimens. *T20*, moss on clay, 1 specimen. WESTERN AUSTRALIA: *W1*, leaf litter, 3 specimens.

Diagnosis. Cuticle smooth. Small flat thickening between buccal and pharyngeal tubes. 2 macroplacoids, microplacoid and septulum present in pharynx. Cuticular bars present on inside of internal claws of first three pairs of legs. Teeth on expanded base of posterior claw on fourth pair of legs.

Description: Colourless. Body length 144-453 μm . Eye spots absent. Cuticle smooth.

Mouth antero-ventral. Buccal tube 21.6 μm in 268 μm long specimen and 1.6 μm wide (7.5% of buccal tube length. Stylet supports inserted at 65% of buccal tube length.

Pharyngeal tube 40.5 μm long (65.3% of buccopharyngeal tube length). Small flat cuticular thickening between buccal and pharyngeal tubes on dorsal surface of tube.

Pharyngeal bulb oval (40 μm by 24 μm) containing small apophyses 3 rod-shaped macroplacoids, a microplacoid and septulum. First and second macroplacoids similar in length (5 μm), third longest (7.6 μm), microplacoid 1 μm and septulum 1.6 μm .

Macroplacoid row length 18.4 μm (85% of buccal tube length). Claws robust, outer claw much longer than inner claw; increasing in length from first to third, second and third equal in length. Internal claw with long strong branches, primary branch with fine short accessory claws. External claw with wide base and very long hooked secondary branch and rather short thick primary branch with short thick accessory claw. Base on posterior claw of fourth pair of legs with serrated edge. Anterior claw of fourth pair of legs 7.6 μm long (58.5% of length of posterior claw), posterior claw 13 μm long. Secondary branch of

posterior claw 71% of length of primary branch. Cuticular bar on leg near base of internal claw of first three pairs of legs (3 μm long on first pair). Lunules absent.

Exuvia containing up to 5 eggs found.

Remarks: The specimens described here differ somewhat from those described by other authors from Europe. Both anterior and posterior claws of the fourth pair of legs are shown to have teeth in the type material. Manicardi & Bertolani (1987) confirmed that this species has small indentations at the bases of the external claws on all legs. However, Dastych (1988) states that this species has spines on the bases of only both claws on the fourth pair of legs. The ratio of the stylet support insertion point to the length of the buccal tube is given by Pilato (1987) as 67.8-71.5%, a little greater than was obtained for the Australian species. However, the ratio of the length of the pharyngeal tube to the buccopharyngeal tube of the Australian specimens is within the range given by Pilato (1987), that is, 63.1-66.8%. It was decided that the differences observed could be more probably accounted for by geographic variation within the species and so these specimens are here identified as *D. higginsi*. However, the variability in descriptions of this species should be further investigated.

Distribution: The species has been reported from North Africa, Europe, New Zealand and North America (McInnes, 1994). It was found in leaf litter and surface soil in a bamboo forest in Japan (Abe & Takeda, 2000). It was described as a rare lowland species and a Palearctic element in Poland (Dastych, 1987). This is the first record of its occurrence in Australia.

***Diphascon (D.) langhovdense* (Sudzuki, 1964)**

Fig. 46

Hypsibius (D.) chilense (Plate, 1888) *langhovdense* Sudzuki, 1964: 13-14, Figs 1-8

Diphascon langhovdense (Sudzuki, 1964): Dastych (2002/2003)

Type locality. East Antarctica.

Material examined. Australia: NEW SOUTH WALES: *N3.3*, *N3.4*, moss, lichen and liverwort on tree in cool temperate rainforest, 52 specimens; *N3.5*, *N3.6*, moss and lichen on rock in subalpine heath, 45 specimens. *N4*, moss on tree in cool temperate rainforest, 4 specimens. *N39*, moss and lichen on rock in warm temperate rainforest, 3 specimens. *N44*, lichen on rock in subalpine heath, 4 specimens. *N46.2*, *46.3*, moss and lichen on rock in subalpine heath, 24 specimens. TASMANIA: *T2*, moss and lichen on rock on headland, 7 specimens. *T7*, moss/liverwort on rock on wet gully slope, 25 specimens. *T8*, moss/lichen/liverwort on soil in subalpine heath, 2 specimens. *T17*, moss on dolerite on wet gully slope, 7 specimens. LORD HOWE ISLAND: moss and liverwort, 20 specimens.

Diagnosis. Cuticle smooth or somewhat thickened and wrinkled on dorsum to rear of third pair of legs. large drop-shaped thickening between buccal and pharyngeal tubes. 3 small round macropiloids and a round micropiloid in pharynx. Claws very short. Cuticular bars absent.

Description. Colourless. Body length 122-225 μm . Eye spots absent. Cuticle thickened and wrinkled on dorsum to rear of third pair of legs. Mouth antero-ventral. Buccal tube 20 μm long in 215 μm long specimen and 1.1 μm wide (5.4% of buccal tube length). Stylet supports inserted at 51.3% of buccal tube length. Pharyngeal tube 64% of buccopharyngeal tube length. Large drop-shaped thickening between buccal and pharyngeal tubes on dorsal surface of tube. Pharynx round (about 20 μm diameter) with

small apophyses, 3 macroplacoids and a microplacoid. First and second macroplacoids equal in length (1.1 μm), third macroplacoid 1.4 μm and microplacoid 0.8 μm .

Macroplacoid row length 24% of buccal tube length. Claws short and stumpy, increasing in length from first to fourth. external claws not much longer than internal claws. Internal claws with short base and short, thick accessory claws. External claws with very short thick base, primary branch arising very close to base of claw with refractive zone at base and short fine accessory points. Anterior claw of fourth pair of legs 4.9 μm long (61% of length of posterior claw), posterior claw 8.1 μm . Secondary branch of posterior claw 78% of length of primary branch. Lunules and cuticular bars absent.

Egg not found.

Remarks. Dastych (1988) discussed the systematic vagueness concerning *D. chilense* Plate, 1889 and the subsequent confusion in the literature over its identity. Pilato & Binda (1997/98) redescribed that species indicating the presence of both a microplacoid and a septulum. The absence of a septulum in the specimens under consideration here would seem, to this author, to be sufficient grounds to place it a different species category. However, the specimens described here agree well with the description of the subspecies *D. chilense langhovdense* Sudzuki, 1964 provided by Dastych (1988) from Antarctic material. The Australian specimens differ in two significant characters, the presence of roughened cuticle at the rear and much shorter stumpier claws (posterior claw of fourth leg 8.5 μm in Antarctic specimen 170 μm long, 5.4 μm long in similar sized Australian specimen). The rough cuticle is not visible on many specimens and could possibly be overlooked or dismissed as an artifact. Differences in length of claws, *per se*, is not, in the opinion of this author, sufficient to designate a different taxon. In view of these reservations the Australian material was assigned to the taxon *D. langhovdense* (Sudzuki, 1964) as proposed by Dastych (2002/2003).

Distribution. The species is restricted to highland areas on the east coast and Tasmania suggesting that it requires a rather benign climate. It appears to be restricted to the southern hemisphere (Dastych, 2002/2003).

***Diphascon (D.) nobilei* (Binda, 1969)**

Fig. 47

Hypsibius (Diphascon) nobilei Binda, 1969: 630-631, Figs 2, 5, 6

Type locality. Sicily.

Material examined. Australia: WESTERN AUSTRALIA: *W1*, leaf litter after flood, 16 specimens. Also reported by Pilato & D'Urso (1976) as occurring at Moss Vale, NSW.

Diagnosis. Cuticle smooth. Large drop-shaped thickening between buccal and pharyngeal tubes. 3 macroplacoids and microplacoid in pharynx. Base of all claws expanded and toothed. Cuticular bars on inside of internal claw on first three pairs of legs and between claws on fourth pair of legs.

Description. Colourless. Body length 188-450 μm . Eye spots absent. Cuticle smooth. Mouth antero-ventral. Buccal tube 25.7 μm long in 320 μm long specimen and 2.7 μm wide (10.5% of buccal tube length. Stylet supports inserted at 65.2% of buccal tube length. Pharyngeal tube 27 μm long (51.2% of buccopharyngeal tube length). Large drop-shaped thickening between buccal and pharyngeal tubes on dorsal surface of tube. Pharyngeal bulb oval (38 μm by 30 μm) with very small apophysis, three rod-shaped macroplacoids and tear-drop shaped microplacoid. First and second macroplacoids about equal length (3.8 μm), third longest (5.7 μm) and terminating in caudal bulb; microplacoid small, 1.4 μm

long. Macroplacoid row length 63% of buccal tube length. Claws robust, increasing in length from first to fourth, second and third equal in length. Internal claw with refractive zones and very short fine accessory claws; external claws with long strong secondary branch, short primary branch with short fine close accessory claw. Base of all claws flared and with distinct teeth. Base of posterior claw of fourth pair of legs very wide and massive. Anterior claw of fourth pair of legs 10.8 μm long (62% of length of posterior claw), posterior claw 17.3 μm long. Secondary branch of posterior claw 87% of length of primary branch. Cuticular bars present beside inner claw of first three pairs of legs and between claws of fourth pair of legs. Lunules absent.

Eggs not found.

Remarks. As with *D. higginsii*, there is some variability in the reported presence of teeth on the base of claws (absent on first three pairs in the type material, present on all claws in specimens reported by Bertolani (1982). Both the ratio of the stylet support insertion point to the buccal tube length and that of the pharyngeal tube length to the buccopharyngeal tube length are different to those quoted for this species by Pilato (1987). These differences may be due to the difficulties associated with measuring *Diphascon* species so, in the case of the Australian material, a conservative approach was taken in identifying these specimens as *D. nobilei*.

Distribution. Originally found in moss on coastal dunes in Italy this species has been reported as a freshwater inhabitant by Bertolani (1982), Nelson, Kincer & Williams (1987) and Pilato, Catanzaro & Binda. (1989).

***Diphascon (D.) cf ongulense* (Morikawa, 1962)**

Fig. 48

Hypsibius (Diphascon ongulense) Morikawa, 1962: 4, Pl I, Figs 5, 6

Type locality. East Ongul Island, Antarctica.

Material examined. **Australia:** NEW SOUTH WALES: *N15*, lichen on tree branch in open woodland at 600m. asl., 13 specimens. *N46.3*, fruticose lichen on tree, moss on rock in subalpine heath at 1000 m., 5 specimens. **TASMANIA:** *T7*, moss/liverwort on rock in wet forest, 1 specimen.

Diagnosis. Cuticle smooth. Large drop-shaped thickening between buccal and pharyngeal tubes. 3 rod-shaped macroplacoids and septulum in pharynx. Cuticular bars absent.

Description. Colourless. Body length 250-350 μm . Eye spots absent. Cuticle smooth. Mouth antero-ventral. Buccal tube 21.6 μm long in 315 μm long specimen and 1.8 μm wide (8.5% of buccal tube length). Stylet supports inserted at 62.6% of buccal tube length. Pharyngeal tube 47.6 μm long (69% of bucco-pharyngeal tube length). Large drop-shaped thickening between buccal and pharyngeal tubes. Pharynx oval (26 μm by 20 μm) with small triangular apophysis, 3 macroplacoids and a septulum. First macroplacoid slightly longer than second (2.7 and 2.2 μm), third longest (4 μm); septulum a showy triangle 2.5 μm long. Macroplacoid row length 52.5% of buccal tube length. Claws large robust, increasing in length from first to fourth, second and third equal in length. Internal claw with short thick secondary branch and short primary branch with very thick accessory claw. External claw with short thick secondary branch, long thin primary branch with refractive zone at base and fine accessory claws which stand away from primary branch at tip. Flared base on posterior claw on fourth pair of claws. Anterior claws of fourth pair of

legs 17.8 μm long (49% of length of posterior claw), posterior claws 8.7 μm . Secondary branch of posterior claw 48% of length of primary branch. Lunules and cuticular bars absent.

Eggs not found.

Remarks. The specimens described here conform to the original description in some important respects, for example, there are three macroplacoids and a septulum and the macroplacoids increase in length from first to third. There is, however, no mention of the drop-shaped thickening between the buccal and pharyngeal tubes which, in the Australian specimens, is large and unlikely to be missed. Also, the pharyngeal tube is almost twice as long as the pharynx in the Australian specimens but is about the same length as the pharynx in *D. ongulense*. Unfortunately, the type material from that species cannot be traced (Dastych & McInnes, 1996).

Distribution. Dastych (1996) considered that reports of *D. ongulense* from Europe (Bertolani, 1982 and Biserov, 1991) referred to the species *D. recamieri* Richters, 1911 and also considered reports from Southern Argentina and from Antarctica by Utsugi & Ohyama (1989) to be doubtful because of the presence of microplacoids in the latter description.

***Diphascon (D.) pannuceum* sp. n.**

Fig. 49

Material examined. Australia: NEW SOUTH WALES: *N3.2*, *N3.5*, moss and lichen on rock, lichen on tree in subalpine heath, 8 specimens, 2 exuvia containing eggs; *N3.4*, moss and lichen on tree in cool temperate rainforest, 2 specimens. *N11*, foliose lichen on tree branch in suburban street at 1000m. asl, 31 specimens, 1

exuvium containing eggs. *N44*, foliose lichen on rock in subalpine heath, 7 specimens. *N46.3*, moss and lichen on rock in subalpine heath, 12 specimens, 1 exuvium containing eggs. VICTORIA: *V3*, liverwort/lichen on branch in cool temperate rainforest, 5 specimens.

Diagnosis. Cuticle wrinkled on dorsum below level of first pair of legs. Large drop-shaped thickening between buccal and pharyngeal tubes. 3 short round macroplacoids, a microplacoid and a conspicuous septulum in pharynx. Cuticular bars absent.

Description. Colourless. Body length 174-280 μm . Eye spots absent. Cuticle wrinkled, consisting of a system of interconnecting ridges about 8 μm long, extending over dorsum and sides and onto fourth pair of legs. Wrinkles become gradually less pronounced towards the anterior of the body and are not visible forward of the first pair of legs. Mouth antero-ventral. Buccal tube 22.2 μm long in 268 μm long specimen and 1.4 μm wide (6.3% of buccal tube length). Stylet supports inserted at 53.6% of buccal tube length. Pharyngeal tube length 42 μm (65.6% of buccopharyngeal tube length). Large drop-shaped thickening between buccal and pharyngeal tubes on dorsal surface of tube. Pharynx round (22 μm diameter) containing apophyses, three macroplacoids, microplacoid and conspicuous septulum. First and second macroplacoids same length (1.5 μm), third a little longer (1.9 μm), microplacoid small, and septulum 1.4 μm long. Macroplacoid row short, 27% of buccal tube length. Claws robust, increasing in length from first to fourth, second and third equal in length. Internal claws with long branches and thick high accessory claws on primary branch. External claws more slender than internal, with long curved secondary branch, primary branch with refractive zone at base and thick high accessory claws. Anterior claw of fourth pair of legs 8.1 μm (65% of length of posterior claw), posterior claw 12.4 μm . Secondary branch of posterior claw 51% of length of primary branch. Lunules and cuticular bars absent.

Four exuvia containing respectively 2, 2, 2 and 3 smooth eggs found.

Etymology: Latin, m, *pannuceus*, wrinkled.

Remarks. The species is distinguished by the wrinkled cuticle which is similar to that described for *Diphascon (Diphascon) burti* Nelson, 1991, however, it differs from that species in the number of placoids in the pharynx.

Distribution. The distribution of this species in eastern Australia suggests that it requires a benign environment not subject to extreme drying.

***Diphascon (D.) pingue* (Marcus, 1936)**

Fig. 50, Plate XIIIa and b

Hypsibius (Diphascon) pinguis Marcus, 1936: 308-309, Fig 289

syn. *Diphascon (D.) claxtonae* Pilato & Binda (1998)

Type locality. Hartz Mts, Germany.

Material examined. Australia: NEW SOUTH WALES: *N1*, liverwort on tree in garden, 1 specimen. *N3.2*, moss on rock and leaf litter in subalpine heath, 4 specimens; *N3.3*, moss on tree in cool temperate rainforest, 1 specimen; *N3.5*, moss/lichen on tree in subalpine heath, 1 specimen. *N4*, liverwort on tree in cool temperate rainforest, 1 specimen. *N8*, gumnuts on soil in urban car-park, 8 specimens, 2 exuvia containing eggs. *N11*, lichen and liverwort on tree in street, 5 specimens. *N14.2*, lichen on tree, moss, lichen, leaf litter and *Banksia* cone on soil in open sclerophyll forest on escarpment top, 13 specimens, moss and lichen on rock in rainforest remnant, 14 specimens; *N14.3*, moss and lichen on rock in rainforest remnant, 12 specimens, 2 exuvia containing eggs; *N14.5*, foliose lichen on tree in open sclerophyll, 4 specimens; *N14.6*, moss on tree in open sclerophyll, 3 specimens; *N14.7*, moss/lichen on path in yard, 9 specimens. *N26*, turf moss on rock in

closed forest gully, 3 specimens. *N27*, weft moss on rock in open sclerophyll, 9 specimens. *N31*, moss/lichen on rock and log in rainforest, 2 specimens. *N35*, weft moss on rock and leaf litter on soil in rainforest, 5 specimens, 2 exuvia containing eggs. *N39*, turf moss on rock in temperate rainforest, 3 specimens. *N43*, moss on soil in open forest, 4 specimens. *N46.2*, moss on soil in subalpine heath, 2 specimens; *N46.1*, moss on rock in open sclerophyll, 1 specimen. QUEENSLAND: *Q15*, leaf litter in dry rainforest, 6 specimens. *Q18*, leaf litter in rainforest remnant, 1 specimen. *Q20*, leaf litter on sand in *Banksia* scrub, 1 specimen. *Q21*, moss/lichen on rock in open sclerophyll, 5 specimens. *Q22*, weft moss in tall open forest, 1 specimen. *Q24*, liverwort on tree in subtropical rainforest, 1 specimen. *Q25*, weft moss on rock and lichen/liverwort on tree in Box forest, 2 specimens. VICTORIA: *V4*, moss on soil in open coastal scrub, 1 specimen. TASMANIA: *T1*, liverwort on log in wet forest gully, 12 specimens. *T5*, liverwort on tree in wet gully, 1 specimen. LORD HOWE ISLAND: moss, 2 specimens.

Diagnosis. Cuticle smooth. Large drop-shaped thickening between buccal and pharyngeal tubes. 3 macroplacoids, microplacoid and septulum in pharynx. Macroplacoid row length short (37-60% of buccal tube length). Cuticular bars absent.

Description. Colourless. Body length 150-264 μm . Eye spots absent. Cuticle smooth. Mouth antero-ventral. Buccal tube 21.4 μm long in 234 μm long specimen and 1.6 μm wide (7.7% of buccal tube length). Stylet supports inserted at 60.3% of buccal tube length. Pharyngeal tube 59.3% of buccopharyngeal tube length. Large drop-shaped thickening between buccal and pharyngeal tubes on dorsal surface of tube. Pharynx oval (32 μm by 24 μm) containing well-developed granular apophyses, three macroplacoids and a microplacoid. Macroplacoids similar in size (2.1, 2.2, 2.6 μm long), microplacoid small and round, septulum 1.7 μm . Macroplacoid row short (46% of buccal tube length, range 37-60%). Claws rather slender; increasing in length from first to fourth, second and third equal in length. Internal claw much shorter than external with accessory claws short and rising well clear of primary branch. External claw with long secondary branch and short low accessory claws on slender primary branch. Anterior claws of fourth pair of legs 6.0

µm long (55.5% of posterior claw), posterior claw 10.8 µm. Secondary branch of posterior claw 76% of primary branch. Lunules and cuticular bars absent.

Exuvia containing up to 5 eggs found.

Remarks. This species was the subject of a study to establish a range of measurements for it and other, possibly closely related species, such as *D. (D.) pinguiforme* (see Section 3.4).

Distribution. A widespread species that occurs in a wide variety of habitats in Australia and throughout the world although existing records need to be further examined. The species is recorded here for the first time in Australia.

***Diphascon (D.) pinguiforme* Pilato & Binda, 1997/98**

Fig. 51, Plate XIIIc and d

Diphascon (Diphascon) pinguiforme Pilato & Binda, 1997/1998: 184, Figs 1g, h

syn. *Diphascon (D.) australianum* Pilato & Binda (1998)

Type locality. Sibillini Mountains, Italy.

Material examined. **Australia:** NEW SOUTH WALES: *N14.1* moss, lichen on rock on escarpment top at 1200m. asl., 9 specimens, moss and lichen on rock in rainforest remnant, 14 specimens. QUEENSLAND: *Q6*, crustose lichen on tree in remnant rainforest, 1 specimen. VICTORIA: *V3*, liverwort on tree in cool temperate rainforest, 4 specimens. TASMANIA: *T3*, moss on soil in wet forest gully, 1 specimen.

Diagnosis. Cuticle smooth. Large drop-shaped thickening between buccal and pharyngeal tube. 3 long macroplacoids, microplacoid and septulum in pharynx. Macroplacoid row long (60-83% of buccal tube length). Cuticular bars absent.

Description. Colourless. Body length 150-250 μm . Eye spots absent. Cuticle smooth. Mouth antero-ventral. Buccal tube 21.1 μm long in 232 μm long specimen and 1.8 μm wide (8.5% of buccal tube length). Stylet supports inserted at 58.9% of buccal tube length. Pharyngeal tube 63.6% of buccopharyngeal tube length. Large drop-shaped thickening between buccal and pharyngeal tubes on dorsal surface of tube. Pharynx oval (37 μm by 26 μm) containing well-developed granular apophyses, three long macroplacoids and a microplacoid. First two macroplacoids similar in length, third longer (3.8, 3.8, 6.8 μm long), microplacoid small and round, septulum 1.6 μm . Macroplacoid row long (79% of buccal tube length, range 60-83%). Claws rather slender, increasing in length from first to fourth, second and third equal in length. Internal claw different in size from external. Internal claw with short high accessory claw on primary branch. External claw with long secondary branch and accessory claws short and rising well clear of primary branch. Anterior claw of fourth pair of legs 6.0 μm long (65% of length of posterior claw), posterior claw 9.2 μm . Secondary branch of posterior claw 78% of length of primary branch. Lunules and cuticular bars absent.

Eggs not found.

Remarks. This species was the subject of a study to determine the range of measurements (see Section 3.4).

Distribution. A rather rare but widespread species in Australia occurring in sheltered habitats. Because of taxonomic problems with this species its world distribution is not known. However, because of the similarity between the Australian specimens and those

from Italy it may be considered to be cosmopolitan. This is the first record of its occurrence in Australia.

***Diphascon (D.) puniceum* (Jennings, 1976)**

Fig. 52

Hypsibius (Diphascon) puniceus Jennings, 1976: 16, Fig 11

Type locality. Signy Island, South Orneys.

Material examined. **Australia:** NEW SOUTH WALES: *N3.2*, moss on tree and rock in subalpine heath, 3 specimens. *N11*, fruticose lichen on branch in street at 1000m asl., 3 specimens. *N14.2*, *N14.5*, lichen and leaf litter on soil on escarpment top (1000m), 9 specimens. *N35*, moss and lichen on branches on ground in cool temperate rainforest, 2 specimens. *N39*, moss and lichen on tree and rock in warm temperate rainforest, 138 specimens, 2 exuvia containing eggs. **WESTERN AUSTRALIA:** *W2*, lichen on branch on ground in Jarrah forest, 6 specimens (1 in black cyst). *W5*, lichen on tree in open, 6 specimens, 3 cysts.

Diagnosis. Colourless to pale pink. Cuticle with thickenings on dorsum towards the rump. Small flat cuticular thickening between buccal and pharyngeal tubes. 3 round macroplacoids and a round septulum in pharynx. Cuticular bars absent. External claws with refractive zone at base of primary branch.

Description. Colourless to pale pink. Body length 125-300 μm . Eye spots absent. Cuticle with thickenings on dorsum on rear half of body, more or less arranged in transverse rows, and on back of fourth pair of legs. Thickenings may be reduced so as to be barely visible on some specimens. Mouth antero-ventral. Buccal tube 20.5 μm long in 264 μm long specimen and 1.6 μm wide (7.8% of buccal tube length). Stylet supports inserted at 60.2% of buccal tube length. Pharyngeal tube 66.5% of buccopharyngeal tube length. Very small flat thickening between buccal and pharyngeal tubes on dorsal surface of tube. Pharynx

round (24 μm diameter) containing well-developed granular apophyses, three granular macroplacoids and large round septulum. First and third macroplacoids equal in length (1.8 μm), second macroplacoid smaller (1.5 μm); septulum short round distinct (0.8 μm). Macroplacoid row 30% of buccal tube length. Claws robust, increasing in length from first to fourth, second and third equal in length. Internal claw rather short with thick short accessory claws on primary branch. External claw with long strongly curved secondary branch and clear refractive zone at base of primary branch, accessory claws short and thick. Anterior claw of fourth pair of legs 6.5 μm long (52% of length of posterior claw), posterior claw 12.4 μm . Secondary branch of posterior claw 52% of length of primary branch. Lunules and cuticular bars absent.

Exuvia containing up to 3 eggs found.

Remarks. The specimens described here fit rather well with the description and measurements given for *D. puniceum* by Dastych (1984). Most of the Australian specimens examined were colourless. However, the colour exhibited by some species of tardigrades is influenced by the food that they consume and this may be different in different places. The dorsal thickening also appears to be somewhat different in the Australian specimens.

Distribution. This species has only otherwise been found in Antarctica.

Diphascon (D.) rugosum (Bartos, 1935)

Fig. 53

Hypsibius (Diphascon) rugosus Bartos, 1935: 258, Fig. 3

Type locality. Czechoslovakia.

Material examined. **Australia:** NEW SOUTH WALES: *N29*, moss on soil over limestone in sheltered valley, 13 specimens. *N43*, liverwort and moss on soil, lichen on branch on ground, 8 specimens. *N47*, moss on soil near coast, 2 specimens. **VICTORIA:** *V4*, moss on soil, 6 specimens.

Diagnosis. Cuticle with faint regular granules over dorsum. Eye spots present. Large drop-shaped thickening between buccal and pharyngeal tubes. 2 macroplacoids and septulum in pharynx. Cuticular bars near internal claw on first three pairs of legs and near both claws on fourth pair of legs.

Description. Colourless. Body length 188-315 μm . Eye spots present. Cuticle with small (1-1.5 μm) faint granular, regularly arranged over dorsum. Mouth antero-ventral. Buccal tube 23.2 μm long in 216 μm long specimen and 2.2 μm wide (9.5% of buccal tube length). Stylet supports inserted at 67.6% of buccal tube length. Pharyngeal tube 36.8 μm long (61.3% of buccopharyngeal tube length). Large drop-shaped cuticular thickening between buccal and pharyngeal surface on dorsal surface of tube. Pharynx oval (32 μm by 26 μm) containing well-developed apophyses, two macroplacoids and a septulum. First macroplacoid 5.4 μm long, with median constriction; second 3.8 μm , with a caudal constriction; septulum 2.2 μm . Macroplacoid row length 10.3 μm long (44.3% of buccal tube length). Claws robust, increasing in length from first to fourth, second and third equal in length. Internal claw with short secondary branch, long primary branch with very short, very fine accessory claws. External claw with long secondary branch, primary branch with clear zone at base and very short fine accessory claws. Anterior claw of fourth pair of legs 7.0 μm long (59% of length posterior claw), posterior claw 11.9 μm . Secondary branch of posterior claw 59% of length of primary branch. Cuticular bars present beside internal

claw on first three pairs of legs and beside both claws on fourth pair of legs. Lunules absent.

Eggs not found.

Remarks. The measurements for these specimens agree very well with those provided for this species by Dastych (1988) and Argue (1972).

Distribution. This is the first report of this species from Australia. It has been reported from Europe and Canada and was found to be widely dispersed but rare in Poland (Dastych, 1988). The disjunct distribution and rarity may be the result of infrequent sampling of its habitat.

Diphascon (D.) scoticum Murray, 1905

Diphascon scoticum Murray, 1905: 162, Fig. 1a-c

Type locality. Scotland

Material examined. Australia: None. Described by Murray (1910) as occurring frequently at Katoomba, Blue Mountains, NSW.

Diagnosis. Cuticle smooth. Small drop-shaped thickening between buccal and pharyngeal tubes. 3 long macroplacoids and microplacoid present in pharynx. Cuticular bar present at base of internal claw on first three pairs of legs and between bases of internal and external claws on all legs.

Description. White. Body length 180-370 μm . Eye spots absent. Cuticle smooth.

Buccopharyngeal tube 67 μm long in 320 μm long specimen, 2.5 μm wide. Pharynx oval (48 μm by 23 μm) containing small apophyses, three elongated macroplacoids and a microplacoid. Second macroplacoid shortest (7.5 μm), first macroplacoid 10 μm and third longest (12.5 μm). External claws robust with long primary branch and long accessory claws. Cuticular bars at base of internal claws on first three pairs of legs and between base of internal and external claw of each leg. Lunules absent. (Details from Dastych, 1988).

Distribution. The species is cosmopolitan having been reported from all continents.

Genus *Hebesuncus* Pilato, 1987

Hebesuncus Pilato, 1987: 351

Type species. *Diphascon conjungens* Thulin, 1911

Diagnosis. (from Pilato, 1987) Buccopharyngeal tube with rigid anterior buccal tube and flexible posterior pharyngeal tube. Apophyses for insertion of muscles of stylets in shape of “blunt hook”; asymmetrical with respect to frontal plane. Placoids present in pharynx. Diploclaws on each leg different in shape and size and asymmetrical with respect to median plane of leg. Primary branch of claw joined flexibly to secondary branch at a distance from base of claw.

***Hebesuncus conjungens* (Thulin, 1911)**

Fig. 54

Hypsibius (Hypsibius) conjungens Thulin, 1911: 37, Fig. 20-20b

Type locality. Sweden.

Material examined. **Australia:** NEW SOUTH WALES: *N3.5*, moss on rock in subalpine heath, 1 embryonate egg. *N43*, moss on rock in open sclerophyll forest, 6 specimens. *N46.1*, moss and lichen on rock in open sclerophyll forest, 18 specimens, 2 eggs (1 embryonate). **VICTORIA:** *V2*, fruticose lichen on rock in subalpine heath, 9 specimens. *V4*, moss on soil in closed forest, 9 specimens. **TASMANIA:** *T3*, moss on rock in low open woodland, 1 specimen.

Diagnosis. Cuticle smooth. Eye spots present. Two granular macroplacoids in pharynx, microplacoid absent. Short robust claws with high showy accessory claws.

Description. Colourless. Body length 124-288 μm . Eye spots present. Cuticle smooth. Buccal tube 22.7 μm long in 244 μm long specimen and 1.5 μm wide (6.6% of buccal tube length). Stylet supports inserted at 73% of buccal tube length. Pharyngeal tube 17.8 μm long (44% of buccopharyngeal tube length). Pharynx almost spherical (22 μm by 20 μm) containing well-developed granular apophyses and two granular macroplacoids. Microplacoid absent. Macroplacoid row short (26% of buccal tube length); first macroplacoid longest (2.4 μm) with faint median constriction, second macroplacoid granular (2.2 μm long). Claws short robust. Internal claw with long strong secondary branch and very thick strong accessory claws; external claws with short thick base, short primary branch with refractive zone at base and thick short accessory claws. Anterior claw of fourth pair of legs 6.0 μm (26%) and posterior claw 12.4 μm (54.6%). Lunules and cuticular bars absent.

Egg laid free, diameter without processes 60 μm , with processes 68 μm . About 32 around circumference and 100 in hemisphere. Processes are small cones tapering to fine point,

6.5-7 μm on egg from New England, 9-10 μm long in egg from Kosciusko, base diameter 2.5 μm and 4-5 μm , 2-3 μm apart, with pores around base. Shell surface smooth.

Remarks. Several authors have cited the presence of this species in the southern hemisphere (Horning, Schuster & Grigarick, 1978, Nelson & Horning, 1979 – New Zealand; Maucci, 1988 – Patagonia; Utsugi & Ohyama, 1991, 1993 – Antarctica; Rossi & Claps, 1989 – Argentina). However Dastych & Thaler (2002) questioned the distribution of this species in the southern hemisphere since none of these authors had found the distinctive eggs with specimens said to belong to this taxon. The present study reports the first instance of the eggs of this species being found in the southern hemisphere. The characteristics of both specimens and eggs conform well with the redescription of this species by Dastych & Thaler (2002).

Distribution. The present study confirms the eualpine and lithophilous distribution of this species as indicated by Dastych & Thaler (2002). Its presence in Australia is also consistent with a cosmopolitan distribution (McInnes, 1994) rather than an arctic-alpine distribution as originally suggested by Dastych (1988). This is the first record of its occurrence in Australia.

Subfamily Hypsibiinae Pilato, 1969

Genus *Doryphoribius* Pilato, 1969

Doryphoribius Pilato, 1969: 888.

Type species. *Hypsibius evelinae* Marcus, 1928

Diagnosis. Six peribuccal lobes present. Rigid buccal tube, ventral support present.

Diploclaws on each leg rather similar in shape and size and asymmetrical with respect to median plane of leg. Smooth eggs laid in exuvium in known species.

Key to species of *Doryphoribius*

1. Three macroplacoids..... *D. capricorniensis*
Two macroplacoids..... 2
2. Cuticle smooth..... 3
Cuticle sculptured..... 6
3. 2 round bumps on dorsum above fourth pair of legs..... *Doryphoribius* sp. 1
Dorsum without bumps..... 4
4. Cuticle with caudal undulations, yellowish, several teeth in
oral cavity..... *D. macrodon*
Cuticle without caudal thickenings..... 5
5. Cuticle smooth, claws of fourth pair of legs same length as
those of first pair..... *D. occidentalis*
Cuticle smooth, claws of fourth pair of legs longer than
claws on other legs..... *D. doryphorus*
6. Cuticle with reticulate sculpture and with 9 transverse rows
of gibbosities..... *D. zyxiglobus*
Cuticle with sculpture, no gibbosities..... 7
7. Sculpture of fine bumps, ventral tooth in oral cavity..... *D. obscurus*
Reticulate sculpture..... 8
8. Yellow, primary branch on posterior claw of fourth pair of
legs 36-37% of buccal tube length..... *D. australocitrinius*

Colourless, primary branch of posterior claw 31%..... *Doryphoribius* sp. 2

***Doryphoribius australocitrinus* sp. n.**

Fig. 55

Material examined. Australia: QUEENSLAND: *Q6*, liverwort on tree in remnant rainforest, 6 specimens. *Q7*, moss on tree and rock in open forest, 12 specimens. *Q9*, lichen on tree on beach, 2 specimens. *Q15*, moss and foliose lichen on rock in open sclerophyll forest, 40 specimens, 1 exuvium containing 3 eggs; *Q15.c*, leaf litter, liverwort on rock, moss, liverwort on trees in dry rainforest, 15 specimens, 1 exuvium containing 6 eggs. *Q18*, moss and liverwort on trees in street, 24 specimens, 4 exuvia containing 4, 5, 6 and 7 eggs. *Q24*, liverwort on tree in subtropical rainforest, 6 specimens. *Q25.a*, weft moss and liverwort/foliose lichen on trees in Box forest, 15 specimens, 1 exuvium containing 5 eggs. NEW SOUTH WALES: *N1*, leafy liverwort on tree in backyard, 9 specimens, 2 exuvia containing 2 and 3 eggs.

Diagnosis. Yellow. Cuticle covered with thickenings forming a reticular pattern on dorsum and sides, absent from legs. No teeth in oral cavity. Pharynx with 2 short macroplacoids. Claws large and robust, similar on each leg with very fine accessory claws. Lunules absent.

Description. Yellow body cells. Body length 155-534 μm . Eye spots present. Cuticle covered with thickenings forming a reticular pattern most prominent at rear and on top of legs. Mouth antero-ventral Oral cavity very short, no teeth present. Buccal tube 43.2 μm long in 360 μm long specimen and 5.4 μm wide (12.5% of buccal tube length). Stylet supports inserted at 71-73% of buccal tube length, ventral support long (67-69%). Pharynx oval (36 μm by 43 μm) containing large apophyses and 2 macroplacoids. First macroplacoid with median constriction 5.4 μm long, second bean-shaped (3.8 μm). Macroplacoid row length 26-28% of buccal tube length. Claws long and robust, similar in

size and shape on each leg; increasing in length from first to fourth, second and third equal in length. Internal claws with long secondary branch, primary branch strongly curved with short very fine, low accessory claws. External claw with flared base rising to massive distal part, long, relatively slender primary branch with fine short accessory claws. Primary branch of internal claw of first pair of legs 11.9 μm long (27.5% of buccal tube length, of external claw 13.5 μm (31.3%). Primary branch of anterior claw of fourth pair of legs 13.5 μm , of posterior claw 15.7 μm (36.3%). Lunules present on all claws.

Smooth orange eggs laid in exuvium, up to 6 in a single exuvium.

Etymology. *L. australis*, southern; *L. citrinus*, n. of citrus.

Remarks. The species is similar to *Doryphoribius citrinus* (Maucci, 1972) but differs from it in the nature of the cuticular sculpture, by having no sculpture on the legs and by having very fine short accessory claws.

Distribution. The species is quite widespread in Queensland and can be found in a wide range of habitats although most seem restricted to moister areas.

***Doryphoribius capricorniensis* sp. n.**

Fig. 56

Material examined. Australia: QUEENSLAND: *Q12*, *Nostoc* on limestone in protected crevice, 12 specimens (1 with 3 orange eggs).

Diagnosis. Bright orange. Cuticle covered with thickenings forming a reticular pattern over dorsum and sides. Ventral tooth in oral cavity. Pharynx with 3 macroplacoids. Claws very long and slender, very fine low accessory claws. Lunules present on all claws.

Description. Bright orange body cells. Body length 200-550 μm . Eye spots present.

Cuticle covered with thickenings forming a reticular pattern over the dorsum and sides, completely absent from all legs. Mouth antero-ventral. Single tooth ventrally in posterior part of oral cavity. Buccal tube 38.9 μm long in 380 μm individual and 3.2 μm wide (8.3% of buccal tube length). Buccal tube walls thick, particularly below the level of the insertion point of the stylet supports, inner diameter of tube 1.6 μm . Stylet supports inserted at 72-73% of buccal tube length, ventral support reaching point of insertion of stylet supports. Pharynx round (34 μm diameter) containing large apophyses and 3 macroplacoids. First macroplacoid (2.7 μm long) placed close to apophyses, slightly larger than second (2.5), third bean-shaped (3 μm). Macroplacoid row length 26-33% of buccal tube length. Claws long and slender, increasing in length from first to fourth, similar in size and shape on each leg. Internal claw with narrow base rising to thick distal part with strong refractive zones and long primary branch with very short very fine accessory claws. External claw with narrow slightly flared base rising to a thick distal part with strong refractive zones and long slender primary branch with very fine short accessory claws. Primary branch of internal claw of first pair of legs 10.8 μm long (27.8% of buccal tube length), of external claw 14.6 μm (37.5%). Primary branch of anterior claw of fourth pair of legs 13 μm (33.3%) and of posterior claw 16.8 μm (43%). Fine lunules present on all claws.

Eggs orange, one specimen still attached to old cuticle and containing 3 eggs was found.

Etymology. The species is named for the place in which it was found, Capricorn Caves.

Remarks. This species differs from other described species of *Doryphoribius* in the intensity of the colour of the cells in the body and the sculpture of the cuticle.

Distribution. Found only at the type locality.

Doryphoribius doryphorus (Binda & Pilato, 1969)

Fig. 57

Hypsibius (Hypsibius) doryphorus Binda & Pilato, 1969: 174-176, Fig. 1A-C

Type locality. Ustica, Italy.

Material examined. **Australia:** WESTERN AUSTRALIA: *W3*, moss on limestone wall suburban, 9 specimens, 1 cyst. *W4*, moss on limestone wall in suburban park, 2 specimens, 8 cysts.

Diagnosis. Colourless, cuticle smooth. No teeth in oral cavity. Pharynx with 2 macroplacoids. Claws very slender. Lunules absent.

Description. Colourless. Body length 155-280 μm . Eye spots present. Cuticle smooth. Antero-ventral mouth, no teeth in oral cavity. Buccal tube 27.6 μm long in 280 μm individual and 3.2 μm wide (11.8% of buccal tube length). Stylet supports inserted at 70% of buccal tube length, ventral support 60%. Pharynx round (24 μm diameter) containing large apophyses and 2 macroplacoids. First macroplacoid with deep median constriction 3.8 μm long, second bean-shaped (2.7 μm). macroplacoid row length 29% of buccal tube length. Claws very slender similar in length on each leg, increasing in length from first to third, second and third equal in length. Internal claw with narrow base rising to wide distal part, primary branch narrow with fine accessory claws rising clear of primary branch at

tips. External claw with flared base and very slender primary branch with fine short accessory claws rising well clear of primary branch at tips. Primary branch of internal claw of first pair of legs 6.5 μm long (23.5% of buccal tube length), of external claw 8.7 μm (31.3%). Primary branch of anterior claw of fourth pair of legs 7.6 μm long (27.4%), of posterior claw 9.7 μm (35.3%). Lunules absent.

No eggs but 7 black cysts found.

Remarks: Cyst formation has not before been reported for this species.

Distribution: The species has been reported from Italy, Libya, North Africa and Colorado, USA and all reports were from moss although no other habitat data has been supplied. It was reported from Australia by Pilato & D'Urso (1976) but the identification was later (Binda, Pilato & Dastych, 1980) changed to *Doryphoribius macrodon* Binda, Pilato & Dastych 1980.

***Doryphoribius macrodon* Binda, Pilato & Dastych 1980**

Doryphoribius macrodon Binda *et al.*, 1980: 23-26, Figs. 1, 2A-C

Type locality. Adrano, Sicily.

Material examined. Australia: None. Reported by Binda *et al.*, 1980 from moss in Sydney, NSW.

Diagnosis. Yellowish, cuticle smooth, with some caudal undulations. Pharynx with two macroplacoids. Tooth in oral cavity. Ventral support short (less than 50% of buccal tube length). Claws slender with thick accessory claws. Lunules present but small.

Description: Yellowish body cells. Body length up to 564 μm . Eye spots present. Cuticle smooth but may have some caudal undulations. Mouth antero-ventral. Teeth in posterior position in oral cavity, median dorsal a tooth. Buccal tube ventrally bent at about one third its length, 52 μm long in 564 μm long specimen and 4.8 μm wide (9.2% of buccal tube length). Stylet supports inserted at 71% of buccal tube length, ventral support less than half length of buccal tube. Pharyngeal bulb oval, containing apophyses and 2 macroplacoids. First macroplacoid largest with median constriction, second half length of first. Claws different on each leg, bases of claws expanded, basal part and secondary braches large and massive. Primary branches with strong accessory claws. Posterior claw on fourth pair of legs 34.7 μm long (67% of buccal tube length). Small lunules present. (From the original description).

Distribution: The species was reported from Europe (Spitsbergen as well as Italy) and from the USSR.

***Doryphoribius obscurus* sp. n.**

Fig. 58

Material examined. Australia: QUEENSLAND: *Q25.a*, weft moss on rock in Box forest, 14 specimens. NEW SOUTH WALES: *N19*, liverwort on rock near stream, 1 specimen. *N29*, moss on soil over limestone, 1 specimen. LORD HOWE ISLAND: lichen, 5 specimens.

Diagnosis. Colourless, cuticle with faint nodules on dorsum. Ventral tooth in oral cavity. Pharynx with 2 macroplacoids. Large claws with long primary branches. Lunules on all claws.

Description. Colourless. Body length 166-600 μm . Eye spots present. Cuticle of dorsum and legs with faint nodules 1-2 μm diameter. Antero-ventral mouth. Buccal tube bent ventally at one third its length. Single ventral median tooth in posterior position in oral cavity. Buccal tube 42.2 μm long in 490 μm long specimens and 6.1 μm wide (14.5% of buccal tube length). Stylet supports inserted at 70-71% of buccal tube length, ventral support 58%. Pharynx round (53 μm diameter) with large square apophysis, and 2 macroplacoids. First macroplacoid with faint median constriction, 7.6 μm long, second a short rod 4.9 μm . Macroplacoid row length 41% of buccal tube length. Claws long and slender, increasing in length from first to fourth. Large swelling on back of fourth leg. Internal claw with strong narrow base, primary branch with short fine accessory claw. External claw with slightly flared base, particularly on fourth pair of legs, rising to thick distal part; primary branch long and slender with short fine accessory claws. Primary branch of internal claw of first pair of legs 11.9 μm long (28% of buccal tube length), of external claw 16.2 μm (38.4%). Primary branch of anterior claw of fourth pair of legs 13.5 μm (32%), of posterior claw 18.4 μm (43.6%). Fine lunules present on all claws. Cuticular bars absent.

No eggs found.

Etymology. *L. obscurus*, obscure, referring to the dorsal cuticular pattern.

Remarks. This species differs from others in the genus with two macroplacoids and sculptured cuticle by having sculpture made up of fine bumps and also by having a ventral tooth in the oral cavity.

Distribution: Found only at the type locality.

Doryphoribius occidentalis sp. n.

Fig. 59

Material examined. Australia: WESTERN AUSTRALIA: *W1*, soil and leaf litter in street, 41 specimens, 5 black cysts.

Diagnosis. Colourless. Cuticle smooth. No teeth in oral cavity. Pharynx with 2 macroplacoids. Claws slender but short relative to the buccal tube length. Claws on fourth pair of legs same size as those on first, both slightly shorter than claws on second and third pair of legs.

Description: Colourless. Body length 122-420 μm . Cuticle smooth. Eye spots present. Antero-ventral mouth. No teeth in oral cavity. Buccal tube 30.3 μm long in 300 μm individual, 3.2 μm wide (10.7% of length of buccal tube). Stylet supports inserted at 71-73% of buccal tube length, ventral support 57%. Pharynx oval (34 by 28 μm) containing large apophyses and 2 macroplacoids. First macroplacoid with faint median constriction, 6 μm long, second bean-shaped, 4.3 μm long. Macroplacoid row length 39% of buccal tube length. Claws slender but small, first and fourth claws equal in length, slightly shorter than second and third claws, also equal in length. Internal claws with short secondary branch and very short very fine accessory claws on long slender primary branch. External claw similar to internal with slightly longer primary branch with very short very fine accessory claws. Five specimens with a single diploclaw on one or both of fourth legs. Claw length from base to top of primary branch very difficult to measure so primary branch, itself, was measured. Primary branch of internal claw of first and fourth legs (on 300 μm specimen) 5.4 μm long (17.8% of buccal tube length), of external claw 6.5 μm (21.5%). Primary branch of internal claw of second and third legs 6.5 μm long, of external claw 7 μm (23%). Lunules absent.

No eggs found but five black cysts were found in some cases with fully developed animal within.

Etymology. *L. occidentalis*, western, for the first species in the genus *Doryphoribius* to be found in Western Australia.

Remarks. This species demonstrates some of the typical adaptations to living in soil, that is, the legs and claws are reduced in size. They are not, however, reduced as far as those of *Doryphoribius pilatoi* Bertolani, 1984 which was found in moss on coastal dunes in Italy.

Distribution: Found only at the one locality.

***Doryphoribius zyxiglobus* (Horning, Schuster & Grigarick, 1978)**

Fig. 60

Macrobiotus zyxiglobus Horning *et al.*, 1978: 226, Figs. 96-98, 168 *upper*

Type locality. Chatham Island, New Zealand

Material examined. **Australia:** NEW SOUTH WALES: *N3.1*, moss on rock in open sclerophyll forest, 1 specimen; *N3.2*, *N3.5*, and *N3.6*, moss on trees and rocks, liverwort on tree in subalpine heath, 15 specimens, 1 cuticle containing eggs: *N3.3*, moss and lichen on tree in cool temperate rainforest, 4 specimens, 1 exuvium containing 5 eggs. *N4*, weft moss on branch on ground in cool temperate rainforest, 1 specimen. *N15*, moss and liverwort on limestone and moss on tree in sheltered valley, 7 specimens, 1 exuvium containing 3 eggs. *N29*, moss on limestone, 5 specimens. *N37*, lichen and liverwort on tree, 2 specimens. *N39*, moss on roadside gutter below cool temperate rainforest, 13 specimens, 3 exuvia containing 4, 5, 6 eggs. **QUEENSLAND:** *Q22*, weft moss on tree in tall open forest, 34 specimens, 1 exuvium containing 10 eggs. **New Zealand:** Chatham Island, 1 specimen. **South Africa:** Karkloof National Reserve, Natal, 1 specimen.

Diagnosis. Yellow-orange body cells. Cuticle reticulate and with 9 rows of gibbosities on dorsum comprising from the front 4, 6, 4, 6, 4, 6, 4, 4, 2 gibbosities per row. No teeth in oral cavity. Pharynx with 2 macroplacoids. Claws robust, rather similar on each leg. Lunules on all claws.

Description: Yellow-orange body cells. Body length 176-440 μm . Eye spots present.

Cuticle with fine reticulate sculpture and with 9 rows of gibbosities on dorsum comprising from the front, 4, 6, 4, 6, 4, 6, 4, 4, 2 gibbosities per row. Mouth antero-ventral. No teeth in oral cavity. Buccal tube 34.1 μm long in 350 μm individual and 4.2 μm wide (12.4% of length of buccal tube). Buccal tube with very thick walls, particularly below the level of insertion of stylet supports, internal diameter 2.2 μm). Stylet supports inserted at 70% of buccal tube length and ventral support long 68%. Pharynx oval (32 μm by 38 μm).

Pharynx containing square apophyses and 2 macroplacoids. First macroplacoid longest (5.4 μm) with faint median constriction, second bean-shaped (3.2 μm). Macroplacoid row length 30% of buccal tube length. Claws robust rather similar in size and shape, outer a little more slender than inner, increasing in length from first to fourth, second and third equal in length. Internal claw with slender base rising to very thick distal part, primary branch with very thick proximal part and short rather thick accessory claws. External claw with more slender and slightly longer primary branch with short thick accessory claws. Primary branch of internal claw of first pair of legs 8.1 μm long (23.8% of buccal tube length), of external claw 8.7 μm (25%). Primary branch of anterior claw of fourth pair of claws 8.7 μm (25%), of posterior claw 9.2 μm (27%). Lunules present on all claws. Cuticular bars absent.

Smooth orange eggs laid in exuvium, up to 10 eggs in a single exuvium found.

Remarks: There was no mention of colour in the original description of this species and there was no mention of the row of 4 gibbosities on the head. Gibbosities are sometimes very difficult to see particularly in smaller specimens on which they are poorly developed. However, there is little doubt about the identification of these specimens as they are extremely similar to the New Zealand specimen examined. Eggs have not been reported for this species before.

Distribution: This is the first report of this species from Australia and South Africa.

Doryphoribius sp. 1

Fig. 61

Material examined. Australia: QUEENSLAND: Q15, leaf litter, 1 specimen.

Diagnosis. Colourless, cuticle smooth but thickened and with two large bumps dorsally above the fourth pair of legs. Pharynx with 2 macroplacoids, no microplacoid. Claws slender, similar on each leg. Lunules only on internal claws.

Description: Colourless. Body length 350 μm . Eye spots absent. Cuticle smooth but with two large bumps dorsally above the IV pair of legs. Antero-ventral mouth, no teeth in oral cavity. Buccal tube 31.4 μm long and 6 μm wide (19% of buccal tube length). Stylet supports inserted at 75.5% of buccal tube length, ventral support 46.5%. Pharynx round (32 μm diameter) containing large apophyses and 2 macroplacoids. First macroplacoid with two constrictions 6.5 μm long, second bean-shaped (4.6 μm). Macroplacoid row length 40% of buccal tube length. Claws long and slender, similar in size and shape, increasing in length from first to fourth, second and third equal in length. Internal claw

slender with long secondary branch and short fine accessory claws on long slender primary branch. External claw with very long slender primary branch with fine accessory claws rising clear of primary branch for long distance. Primary branch of internal claw of first pair of legs 8.1 μm (25.8% of buccal tube length), of external claw 9.2 μm (29.3%). Primary branch of anterior claw of fourth pair of claws 9.2 μm , of posterior claw 11.4 μm (36.2%). Lunules present only on internal claws.

No eggs found.

Remarks: This appears to be a new species as there are no other described species with such a wide buccal tube. It was not deemed to be wise, however, to describe a new species on the basis of a single specimen.

Distribution: Unknown as a single specimen was found.

Doryphoribius sp. 2

Fig. 62

Material examined. Australia: NEW SOUTH WALES: N14.4, moss on rock in gully, 1 specimen.

Diagnosis. Colourless, cuticle with faint reticular sculpture over dorsum. No teeth in oral cavity. Pharynx with 2 macroplacoids. Claws robust with thick prominent accessory claws. Lunules absent.

Description: Colourless. Body length 277 μm . Eye spots absent. Cuticle of dorsum with faint reticular sculpture. Antero-ventral mouth, no teeth in oral cavity. Buccal tube short 28 μm long and 3.5 μm wide (12.5% of buccal tube length). Stylet supports inserted at 72% of

buccal tube length, ventral support 69%. Pharynx briefly oval (27 μm by 32 μm) containing large apophyses and 2 short macroplacoids. First macroplacoid with median constriction 3.8 μm long, second bean-shaped 2.7 μm . Macroplacoid row length 30% of buccal tube length. Claws robust, internal very similar to external, claws increasing in length from first to fourth, second and third equal in length. Internal claw with long curved secondary branch, primary branch with two distinct bends and fine accessory claws rising well clear of branch at the tip. External claw also with double bend in primary branch and with similar accessory claws. Primary branch of anterior claw of fourth pair of legs 7.6 μm (27% of buccal tube length), of posterior claw 8.7 μm (30.8%). Lunules absent.

No eggs found.

Remarks: This species differs from the other species with two macroplacoids and a reticulate sculpture (*D. australocitrinus*) by lacking the yellow colour of that species and by having a shorter primary branch on the claws.

Distribution: Found only at the one locality.

Genus *Eremobiotus* Biserov, 1992

Biserov, 1992: 108, figs 1,2 and 3.

Type species. *Eremobiotus ovezovae* Biserov, 1992:95, Figs 1-9, Tab 1.

Diagnosis. (from Biserov, 1992) Six peribuccal papulae and six peribuccal lobes present. Buccal tube rigid, ventral support absent. First three pairs of claws of similar size,

asymmetrical with respect to median plane of leg. Primary branch joined to secondary branch, very wide angle (about 180°) between primary and secondary branches.

***Eremobiotus alicatai* (Binda, 1969)**

Fig. 63

Hypsibius (Hypsibius) alicatai Binda, 1969: 627-629, Figs. 1, 3 and 4

Type locality. Gela, Sicily.

Material examined. NEW SOUTH WALES: N29, moss on soil over limestone in sheltered valley, 3 specimen.

Diagnosis. White, smooth cuticle. Mouth antero-ventral. Very long thin bucco-pharyngeal tube, short fine stylets.

Description. Body length 200-250 µm, white. Cuticle smooth. Eye spots absent. Mouth antero-ventral, no teeth in oral cavity. Buccal tube 27.7 µm long in 250 µm individual and 3 µm wide (11% of buccal tube length). Stylet supports inserted at 71.2%. Pharyngeal bulb oval (27 µm long by 22 µm wide) containing large apophyses and 2 macroplacoids. Macroplacoid row length 29%. First macroplacoid with median incision 4.4 µm long, second macroplacoid bean shaped 2.7 µm long. Claws of *Isohypsibius* type short, very similar in size and shape, with angle between primary and secondary branch about 170° on first three pairs of legs. Accessory claws on primary branches of both claws short and low. Claws of fourth pair of legs with primary and secondary branches at even more extreme angle (180°), primary branches with short high accessory points. Fourth pair of claws 6.7

μm and $7.0\ \mu\text{m}$ long. Lunules small and dentate on all claws; cuticular bars (about $10\ \mu\text{m}$ long) arise from base of inner claw on first three pairs of legs. Eggs not found.

Remarks. The Australian specimens agree in all respects with the original description of this species.

Distribution. This is the first report of this species in Australia. It was reported from Poland by Dastych (1988) who recorded it as a rare eucalciphilous upland species, collected mainly in rock mosses. He considered it to be a sub-Mediterranean element as it had only been collected in Italy (Binda & Pilato 1972, Bertolani, 1982, Bertolani, Guidetti & Rebecchi, 1993), North Africa (Pilato & Pennisi, 1976) and Russia (Biserov, 1991, 1996). Its appearance in Australia considerably widens its distribution.

Genus *Hypsibius* Ehrenberg, 1848

Hypsibius Ehrenberg, 1848: 381

Type species. *Macrobiotus dujardini* Doyère, 1840: 288.

Diagnosis. (emended from Schuster *et al.*, 1980) Six peribuccal lobes present. Buccal tube short and rigid, ventral support absent. Appendages for insertion of stylet muscles hook-shaped. Claws of each leg different in size and form, asymmetrical with respect to median plane of leg. Primary branch inserted by means of a flexible junction, secondary branch and base form a hooked curve:

Key to species of *Hypsibius*

1. Septulum present..... 3
Septulum absent..... 2
2. Cuticular bars present at base of posterior claw of fourth pair
of legs..... *H. convergens*
Cuticular bars absent on legs..... *H. arcticus*
3. Cuticular bars present only at base of posterior claw of fourth
pair of legs..... *H. dujardini*
Cuticular bars present at base of all internal claws and of
posterior claw of fourth pair of legs..... *Hypsibius* sp.

Hypsibius arcticus (Murray, 1907)

Macrobiotus arcticus Murray, 1907: 671, 672, 677, 680, Figs. 5a-f

Type locality. Franz Joseph Land

Material examined. Australia: None, recorded by Murray (1910) from Katoomba, Blue Mountains.

Diagnosis. Cuticle smooth. 2 macroplacoids in pharynx. Claws very different in length.

Description. Colourless. Body length 196-231 μm . Eye spots absent. Cuticle smooth.

Buccal tube 40 μm long in 278 μm long specimen and 3.3 μm wide (12% of buccal tube length). Stylet supports inserted at 67% of buccal tube length. Pharyngeal bulb (32 μm by 30 μm) containing large apophyses and two macroplacoids. First macroplacoid 6 μm long with slight median constriction, second 4.4 μm with constriction below middle. Claws

with pronounced internal sculpture. External claw of fourth pair of legs 16.5 μm (41% of buccal tube length), primary branch 11 μm . Lunules and cuticular bars absent.

Eggs oval covered with short round headed rods, may be deposited free or in exuvium.

Remarks. Murray admitted that his identification of his specimens was questionable since he collected no eggs. The specimens he examined from Australia probably belong to the taxon *H. antarcticus* (Richters 1904) for reasons discussed in Dastych (1991).

Distribution. Unknown for reasons discussed in Remarks for this species.

Hypsibius convergens (Urbanowicz, 1925)

Fig. 64

Macrobiotus convergens Urbanowicz, 1925: 136-139

Type locality. Vilnius, formerly Poland, now Lithuania.

Type material examined. **Australia:** NEW SOUTH WALES: *N43*, moss on limestone, 6 specimens. *N48*, moss on rock in open sclerophyll forest, 3 specimens.

Diagnosis. Cuticle smooth. Buccal tube narrow. Pharynx containing 2 macroplacoids, microplacoid and septulum absent. Claws very different in size on each leg. Lunules absent, cuticular bars present on inside of base of posterior claw of fourth pair of legs.

Description. Colourless. Body length 203-237 μm . Eye spots present. Cuticle smooth. Buccal tube 22.7 μm in 220 μm specimen and 1.6 μm wide (7% of buccal tube length). Stylet supports inserted at 61-63% of buccal tube length. Pharyngeal bulb almost round (25

µm by 24 µm) with apophyses and two macroplacoids. First macroplacoid with slight median constriction 3.2 µm long, second bean-shaped 2.4 µm. Macroplacoid row length 7.6 µm (33%). Claws different on each leg, increasing in length from first to fourth, second and third equal in length. Internal claws with long hooked secondary branch, primary branch with short low accessory claw. External claw with slightly flared base and long hooked secondary branch, primary branch with refractive zone at base and short fine accessory points. Anterior claw of fourth pair of legs 5.4 µm long (24% of buccal tube length), primary branch 5 µm; posterior claw 9.7 µm long (43%), primary branch 6.5 µm. Lunules absent, small cuticular bar at base of posterior claw on fourth pair of legs. No eggs found.

Remarks. Dastych (1988) described this species as one in need of revision because of the great variability he found in the shape and size of placoids and claws, and the existence, in some specimens of a very small “cuticular granule” in the microplacoid position. Specimens agreeing with this description were found among specimens with septula (*H. dujardini*) but the relative length of the claws suggested that they belonged to the latter taxon and not to *H. convergens*.

Distribution. Dastych (1988) found this species to be widely distributed in Poland, more frequently found on carbonate bedrock. It is considered to be cosmopolitan (but see remarks for this species) and this is the first report of this species from Australia.

Hypsibius dujardini (Doyère, 1840)

Fig. 65

Macrobotus Dujardin Doyère, 1840: 288

Type locality. Paris, France

Material examined. **Australia:** NEW SOUTH WALES: *N1*, leafy liverwort on tree, 1 specimen. *N3*, moss on tree in open sclerophyll, leaf litter on soil in subalpine heath, moss on tree in cool temperate rainforest, 10 specimens. *N8*, gumnuts on soil and asphalt, 11 specimens. *N9*, leaf litter on soil in rainforest, 1 specimen. *N11*, moss and lichen on tree sheltered, 14 specimens, 5 exuvia containing 2,4,4,5 and 7 eggs. *N14*, leaf litter on soil, moss on path in open sclerophyll forest, 7 specimens. *N15*, moss and lichen on limestone, 45 specimens, 3 exuvia containing 3,4 and 10 eggs. *N18*, moss on asphalt in suburb, 3 specimens, 1 exuvium containing 1 egg. *N27*, moss on rock in sclerophyll, 2 specimens. *N29*, leaf litter on soil, lichen on branches on ground, 14 specimens, 5 exuvia containing 2,3,3,7 and 7 eggs. *N32*, moss and lichen on tree roadside, 6 specimens. *N33*, lichen and moss on tree roadside, 6 specimens. *N34*, moss on tree in closed forest, 1 specimen. *N35*, leaf litter on soil in closed forest, 3 specimens. *N39*, moss on log in warm temperate rainforest, 7 specimens. *N43*, moss and lichen on soil, liverwort on soil near stream, 18 specimens. *N46.1*, *46.2*, moss and lichen on rock in subalpine heath, 32 specimens. *N48*, moss on rock, 1 specimen. QUEENSLAND: *Q15*, leaf litter in dry rainforest, 4 specimens. *Q22*, liverwort on tree in high forest, 1 specimen. *Q25*, leafy liverwort on rock in warm temperate rainforest, 2 specimens. AUSTRALIAN CAPITAL TERRITORY: *A1*, moss on rock and tree near river, 6 specimens. TASMANIA: *T1*, moss on tree in coastal scrub, 5 specimens. *T7*, moss on rock in wet gully forest, 8 specimens. *T10*, moss on soil in regenerating rainforest, 4 specimens, 2 exuvia containing 4 and 8 eggs. *T11*, moss, 4 specimens. *T15*, moss on rock in closed forest, 8 specimens. LORD HOWE ISLAND: 1 specimen.

Diagnosis. Cuticle smooth. Buccal tube short and narrow. Pharynx containing 2 macroplacoids and septulum. Claws different on each leg, cuticular bars present at base of posterior claw on fourth pair of legs.

Description. Colourless. Body length 138-414 μm . Eye spots present. Cuticle smooth. Mouth antero-ventral, no teeth in oral cavity. Buccal tube 22 μm in 220 μm specimen and 1.8 μm wide (8.2% of buccal tube length). Stylet supports inserted at 61-63% of buccal tube length. Pharyngeal bulb oval (24 μm by 21 μm) with apophyses, two macroplacoids

and septulum. First macroplacoid with slight median constriction 3 μm long, second bean-shaped 2.2 μm ; septulum 1 μm . Macroplacoid row length 6.5 μm (30%). Claws different on each leg, increasing in length from first to fourth, second and third equal in length. Internal claw with long hooked secondary branch, base small and straight, primary branch with short low accessory points. External claw long and slender, secondary branch long and hooked, base flared, primary branch with short fine accessory points. Anterior claw of fourth pair of legs 7 μm long (32% of buccal tube length), primary branch 5.4 μm . Posterior claw 13 μm (60%), primary branch 9.7 μm . Lunules absent, cuticular bar present at base of posterior claw on fourth pair of legs.

Up to 10 smooth eggs deposited in exuvium.

Remarks. The identity of this species is not absolutely definite. Dastych (1988) described the species as having a microplacoid, however, Bertolani (1982) found that his Italian specimens had a septulum and he suggested that this was a common source of error in the literature. Pilato & Binda (1997) stated that specimens (which they identified as *H. dujardini*) from New Zealand had a septulum. This difference is probably sufficient to nominate a second species.

Distribution. Widespread in rather moist habitats in Australia, this species has often been reported from aquatic habitats overseas. This is the first report of its occurrence in Australia.

Hypsibius sp.

Fig. 66

Material examined. Australia: NEW SOUTH WALES: N28, moss on rock in sclerophyll forest, 1 specimen.

Diagnosis. Cuticle smooth. Pharynx containing 2 macroplacoids and septulum. Cuticular bars at base of all internal claws and at base of posterior claw of fourth pair of legs.

Description. Colourless. Body length 290 μm . Eye spots absent. Cuticle smooth. Mouth antero-ventral, no teeth in oral cavity. Buccal tube 28 μm in 290 μm individual and 2.7 μm wide (9.6% of buccal tube length). Stylet supports inserted at 67% of buccal tube length. Pharyngeal bulb round (28 μm diameter) with small apophyses and 2 macroplacoids. First macroplacoid with slight median constriction (4.3 μm long) and second bean-shaped (3.5 μm); septulum 1.6 μm . Macroplacoid row length 9.7 μm long (34.6%). Claws robust, increasing in length from first to fourth, second and third equal in length. Internal claw with long secondary branch above thick mid-section flared at base, primary branch long and slender with short low accessory claws. External claw with long secondary branch with mid-section with flared base, primary branch long with short fine accessory points. Anterior claw of fourth pair of legs 8.1 μm long (29%), primary branch 9.2 μm ; posterior claw 19.5 μm (69%), primary branch 13.5 μm . Lunules absent, thick cuticular bars arising from inside base of internal claws on all legs and also base of posterior claw of fourth pair of legs.

No eggs found.

Remarks. Probably a new species but, as only a single specimen was found, it was thought premature to name it here.

Distribution. Unknown.

Genus *Isohypsibius* Thulin, 1928

Isohypsibius Thulin, 1928: 239

Type species. *Isohypsibius prosostomus* Thulin, 1928

Diagnosis. Six peribuccal lobes present. Rigid buccal tube, ventral support absent. Appendages for the insertion of stylet muscles crest-shaped. Diploclaws of each leg different in shape and size, asymmetrical with respect to median plane of leg. Primary branch of claws inserted on secondary branch at a distance from base of claw, secondary branch forming almost a right angle with base.

Key to species of *Isohypsibius*

- | | | |
|----|--|-----------------------|
| 1. | Cuticle smooth..... | 2 |
| | Cuticle not smooth..... | 4 |
| 2. | Microplacoid present..... | <i>I. prosostomus</i> |
| | Microplacoid absent..... | 3 |
| 3. | Two macroplacoids, bars on legs I-III..... | <i>I. aridus</i> |
| | Three macroplacoids, no bars on legs..... | <i>I. itoi</i> |
| 4. | Cuticle with mamillary gibbosities..... | <i>I. papillifer</i> |

Cuticle different.....	5
5. Cuticle with small tubercles.....	<i>I. cameruni</i>
Cuticle different.....	6
6. Cuticle without gibbosities.....	7
Cuticle with gibbosities.....	9
7. Claws without lunules or cuticular bars.....	<i>I. australogilvus</i>
Claws with lunules and cuticular bars.....	8
8. Cuticular bar crescent-shaped beneath inner claws I-III.....	<i>I. palmai</i>
Cuticular bars sinuous to side of inner claws I-III.....	<i>I. wilsoni</i>
9. Dorsum with at least 8 rows of 4-6 gibbosities each.....	<i>I. sattleri</i>
Different.....	10
10. Dorsum with 8 rows of gibbosities.....	11
Dorsum with 10 rows of gibbosities.....	12
11. Three macroplacoids, no cuticular bars on legs I-III.....	<i>I. heatwolei</i>
Two macroplacoids, cuticular bars on legs I-III.....	<i>I. peteri</i>
12. Cuticular bars on legs I-III.....	13
No cuticular bars on legs I-III.....	14
13. Three gibbosities in rows 1, 3, 5, 7, 9 and 10.....	<i>I. lunulatus</i>
Three gibbosities only in row 1.....	<i>I. elegans</i>
14. Three gibbosities in row 10.....	<i>I. bellus</i>
Two gibbosities in row 10.....	<i>I. cf bartosi</i>

***Isohypsibius aridus* sp. n.**

Fig. 67

Material examined. Australia: VICTORIA: *V1*, leaf litter under Mallee, 4 specimens.

Diagnosis. Cuticle smooth. Pharynx containing 2 macroplacoids, microplacoid absent.

Claws small, fourth pair almost same size, with 180° angle between primary and secondary branch, all with 5-6 small teeth around base. Lunules present, on fourth pair of claws round with small dot-like teeth. Long thin cuticular bars at base of internal claws on first three pairs of legs, short bars at base of each claw on fourth pair of claws.

Description. Body length 278-360 µm, colourless. Eye spots absent. Cuticle smooth.

Antero-ventral mouth, no teeth in oral cavity. Buccal tube 32.4 µm in 345 µm specimen and 4.3 µm wide (13.4% of buccal tube length). Stylet supports inserted at 71.5% of buccal tube length. Pharyngeal bulb oval (33 µm by 34 µm) containing small triangular apophyses and two macroplacoids. Macroplacoid row 33% of buccal tube length. First macroplacoid longest (6 µm) with deep median constriction, second macroplacoid (4.3 µm) bean-shaped. Claws dissimilar in size on first three pairs of legs, same size on fourth pair angle of about 180° between primary and secondary branches. Internal claw of first three pairs of legs with refractive zone where branches meet, very narrow basal part, short secondary branch and thick primary branch with short fine accessory claws; angle between primary and secondary branches approaching 180°. External claw of first three pairs of legs more slender than internal, with narrow base, long curved secondary branch and refractive zone at base of primary branch with short low accessory claws. Fourth pair of claws almost same size and dimensions, both with angle of 180° between primary and secondary branches, short straight basal part, thick short secondary branches and primary branches with refractory zones in each. Primary branches appear to be twisted outwards from claw, accessory points can be seen standing up like ears behind primary branch. Inner claw on first pair of legs 6 µm long (18.5% of buccal tube length, outer claw 10.3 µm (31.7%).

Anterior claw on fourth pair of legs 6 μm long (18.5%), posterior claw 7 μm long (20.5%). Lunules present on all claws, on first three pairs of legs small and smooth, on fourth pair of legs small round and with about 5-6 dot-like teeth, similar teeth were noted at base of each claw on fourth pair of legs. Long thin cuticular bar (11 μm long on first pair of legs) present near inner claw of first three pairs of legs, short anteriorly pointing cuticular bars (3 μm on posterior claws, 5 μm on anterior) present on all claws on fourth pair of legs.

No eggs found.

Etymology. *Aridus*, L., dry, for the environment in which the species was found.

Remarks. This species is very similar to *Isohypsibius bertolani* Manicardi 1989 in having rather short claws with a wide angle between the branches and a long sinuous cuticular bar on the first three pairs of legs. Both species have smaller cuticular bars below claws on the fourth pair of legs but *I. aridus* has small teeth at the base of those claws and on the lunules just below them that are absent on *I. bertolani*. *I. bertolani* has a finely dotted cuticle, *I. aridus* has smooth cuticle. The fact that the rear claws are significantly different from those on the other three legs may be strong grounds for the institution of a new genus for this species but as only 4 specimens were available for examination at this time it was decided not to do so at this time.

Distribution. The species was found at only one site and in a habitat which has not been widely sampled so its distribution at this point is unknown.

Isohypsibius australogilvus sp. n.

Fig. 68

Material examined. Australia: NEW SOUTH WALES: *N3.1*, lichen on rock in dry sclerophyll forest, 1 specimen; *N3.2* and *N3.5*, moss and lichen on rock and trees and leaf litter in subalpine heath, 21 specimens; *N3.3* and *N3.4*, moss, lichen and liverwort on trees and moss on rock in cool temperate rainforest, 9 specimens. *N14.1* and *N14.2*, moss on rock and soil, 4 specimens; *N14.4*, moss on rock in rainforest remnant, 1 specimen. VICTORIA: *V3*, liverwort on branches on ground in cool temperate rainforest, 9 specimens. TASMANIA: *T3*, moss on rock in closed forest gully, 1 specimen. *T7*, moss, liverwort on rock and soil, lichen on rock in wet forest gully, 13 specimens. *T9*, moss and liverwort on limestone on river cliff shelf, 26 specimens.

Diagnosis. Cuticle with reticular pattern over dorsum. 2 macroplacoids in pharynx. Claws similar in size on each leg. Lunules absent.

Description. Colourless. Body length 155-254 μm . Posterior eye spots present. Cuticle with reticular pattern over dorsum. Reticular pattern uneven in size because of variable thickness of raised ridges. On head ridges are small and enclose small (1.5 μm) hexagons, on dorsum hexagons are larger (3 μm); in caudal area ridges become more like series of bumps so that hexagonal pattern is obscured. On outside of legs – most noticeable on fourth pair – are small bumps, small bumps and ridges are also present on ventral surface. Antero-ventral mouth, no teeth in oral cavity. Buccal tube 24.1 μm long in 254 μm specimen, 2.2 μm wide (9 % of buccal tube length). Stylet supports inserted at 67.5% of the buccal tube length. Pharyngeal bulb oval to round (22 μm diameter) containing apophyses and two macroplacoids. Macroplacoid row short (28% of buccal tube length). First macroplacoid a short rod (3.2 μm long) with slight median constriction, second macroplacoid small (2 μm) granular. Claws long slender with very long secondary

branches and very slender basal part. Accessory claws on both internal and external claws short and rather thick but lie close to primary branch. Anterior claws of fourth pair of legs 8.1 μm long (33.6% of buccal tube length); posterior 9.7 μm (40.4%) Lunules absent.

A single smooth egg found in cuticle still attached to one individual.

Remarks. The sculpture appears to be very similar to that of *Isohypsibius gilvus* Biserov, 1986 but is not so clearly arranged in rows across the dorsum. *I. gilvus* has stylet supports much more posteriorly placed than in this species.

Distribution. The species appears to be limited in Australia to localities with a benign climate.

Isohypsibius cf bartosi (Iharos, 1966)

Fig. 69

Hypsibius bartosi Iharos, 1966: 77

Type locality. Hungary.

Material examined. Australia: QUEENSLAND: Q25, moss on rock in Box forest, 2 specimens. NEW SOUTH WALES: N48, moss on sandy soil near sea cave, 3 specimens.

Diagnosis. Dorsum with thickened cuticle with pores and 10 transverse rows of gibbosities. Two macroplacoids in pharynx. Robust claws with minute accessory claws. Lunules present on all claws.

Description. Colourless. Body length up to 320 μm . Eye spots absent. Cuticle on dorsum and back of fourth pair of legs thick with ridge-like areas separating lighter pits of very variable shape. Ten transverse rows of gibbosities. First to ninth with 4 gibbosities, tenth with 2. Mouth anterior, no teeth in oral cavity. Buccal tube 35.1 μm long in 256 μm specimen and 4.3 μm wide (12% of buccal tube length). Stylet supports inserted at 69% of buccal tube length. Pharyngeal bulb round (34 μm diameter) containing apophyses and two macroplacoids. Macroplacoid row 32% of buccal tube length. First macroplacoid longest (5.4 μm) with strong median constriction, second (4.1 μm) with caudal constriction. Claws robust rather short, similar in dimensions on each leg. Internal claw with short basal part and long secondary branch, primary branch with refractive regions and short very fine accessory claws. External claw with wider base, short secondary branch and rather short primary branch with very short very fine accessory claws. Anterior claw of fourth pair of legs 7.6 μm long (22% of length of buccal tube); posterior 9.7 μm (28%). Lunules large on all claws.

Eggs not found.

Remarks. The specimens described here have the same number and disposition of gibbosities as *I. bartosi* however that species was poorly described with no information about the buccal apparatus (which is not clear in the diagram reproduced from the original in Ramazzotti and Maucci (1983)). The cuticle of that species is given as “finely granulated” and that description could apply to the Australian specimens if viewed under low power. The only dimensions given for *I. bartosi* are the claws on the fourth pair of legs (7 μm and 10 μm) which are about the same as the Australian specimens. Because of the small number of specimens examined here it was thought best not to institute a new species at this time.

Distribution. *I. bartosi* has only been reported from Hungary and Greece and the latter record contained no additional information about the species.

Isohypsibius bellus sp. n.

Fig. 70

Material examined. Australia: NEW SOUTH WALES: *N31*, moss/fern/leaf litter in temperate rainforest, 1 specimen.

Diagnosis. Cuticle thick with strong reticulate pattern and 10 rows of gibbosities. Pharynx containing 2 macroplacoids, microplacoid absent. Lunules present on all claws. Claws similar in size, with very short fine accessory claws.

Description. Colourless. Body length 289 μm . Eye spots absent. Cuticle thick with reticular pattern (1 μm) on and between gibbosities also on sides and on back of fourth pair of legs. Dorsum with 10 rows of large gibbosities: first and second with 2 gibbosities, third to ninth with 4 and tenth with 3. Anterior mouth, no teeth in oral cavity. Buccal tube 35.7 μm long in 289 μm specimen, 3.8 μm wide (13.6% of buccal tube length). Stylet supports inserted at 66.6% of buccal tube length. Pharynx round (35 μm diameter) containing apophyses and two macroplacoids. Macroplacoid row 33% of buccal tube length. First macroplacoid longest (5.4 μm) with median constriction, second (3.8 μm) granular with median constriction. Claws rather short and slender, similar in size on each leg. Internal claw with narrow basal part short secondary branch, primary branch long with refractory zone at base and short fine accessory claws. External claw with expanded base and short secondary branch, primary branch long slender with short fine accessory claws. Anterior

claw of fourth pair of legs 9.2 μm (25.7% of buccal tube length); posterior 12.4 μm (35%).

Lunules present on all claws. Cuticular bars absent.

No eggs found.

Remarks. This species is rather similar to *I. silvicola* (Iharos, 1966) but that species has bars below the first three pairs of claws.

Distribution. Found only at the one locality.

Isohypsibius cameruni (Iharos, 1969)

Fig. 71

Hypsibius cameruni Iharos, 1969: 118, Fig. 2A-C

Type locality. Cameroun Mountains, (West Africa).

Material examined. QUEENSLAND: *Q18*, liverwort on tree in park, 2 specimens. *Q25*, foliose lichen/fern on tree in rain forest, 1 specimen. NEW SOUTH WALES: *N3.1*, moss and lichen on rocks and trees in dry sclerophyll forest, 11 specimens, 1 cuticle containing eggs; *N3.2*, *N3.5* and *N3.6*, moss, lichen and liverwort on rocks and trees also in leaf litter in subalpine heath, 57 specimens, 1 cuticle containing eggs; *N3.4*, moss on rocks and trees in cool temperate rainforest, 6 specimens. *N14.1*, moss and lichen on rock in dry sclerophyll forest, 17 specimens; *N14.2*, moss and lichen on rock, tree, on soil (1 specimen), liverwort on tree in open forest on escarpment top, 61 specimens, 1 cuticle containing eggs; *N14.3*, moss on tree and rock, liverwort on tree in remnant rainforest, 3 specimens; *N14.4*, moss on tree in dry sclerophyll forest on escarpment top, 1 specimen; *N22*, fruticose lichen on rock in dry sclerophyll forest, 2 specimens. *N25*, moss/liverwort on rock, 1 specimens. *N27*, moss and lichens on rocks in dry sclerophyll forest, 49 specimens, 8 cuticles containing eggs. *N28*, turf moss on rock in dry sclerophyll forest, 3 specimens. *N29*, fruticose lichen on tree in dry sclerophyll forest, 2 specimens. *N34*, foliose lichen on tree in closed forest, 1 specimen, 1 cuticle containing eggs. *N35*, moss on rock and tree in cool temperate rainforest, 2 specimens. *N39*, moss

and lichen on rock in temperate rainforest, 66 specimens, 6 cuticles containing eggs. VICTORIA: *V3*, liverwort on branch on ground in cool temperate rainforest, 3 specimens. TASMANIA: *T1*, fruticose lichen on soil in coastal scrub, 1 specimen. *T3*, moss on rock in closed forest gully, 4 specimens. *T6*, moss, 2 specimens. *T7*, moss/liverwort on rock in wet forest gully, 2 specimens. *T10*, liverwort on tree in regenerating temperate rainforest, 9 specimens. *T13*, moss, 1 specimen. *T17*, moss on dolerite at 620 m., 3 specimens. *T21*, wet moss on rock in closed forest, 2 specimens.

Diagnosis. Cuticle on dorsum, sides and back of fourth pair of legs with tubercles more or less arranged in rows; 8 rows each with 3 gibbosities each consisting of 20-30 tubercles, 1 dorso-medial and 2 lateral. Two macroplacoids in pharynx. Claws similar in size on each leg, lunules absent.

Description. Colourless. Body length 115-195 μm . Eye spots absent. Cuticle on dorsum, sides and back of fourth pair of legs with tubercles more or less arranged in rows; 8 rows each with 3 gibbosities (each consisting of 20-30 tubercles), 1 dorso-medial and 2 lateral. Mouth antero-ventral. Buccal tube 19 μm long in 180 μm individual and 1.6 μm wide (8.4% of buccal tube length). Stylet supports inserted at 60% of buccal tube length. Pharyngeal bulb round (18 μm diameter) with small triangular apophyses and 2 macroplacoids. Macroplacoid row length 32% of buccal tube length. First macroplacoid largest (2.7 μm long) with faint median constriction, second (2.2 μm) bean shaped. Claws robust and similar in size on each leg. Internal claws robust with long secondary branch and long low accessory points on primary branch, 72% of length of outer claws. External claws with long robust secondary branch and slender primary branch with long fine accessory points. Anterior claw of fourth pair of legs 5.4 μm long (28.4% of buccal tube length), posterior claw 7.6 μm long (40%). Cuticular bars absent. Lunules absent.

Exuvia containing 1 or 2 smooth eggs found.

Remarks. The species has a sculpture of small tubercles which distinguishes it from all other species in the genus.

Distribution. The species has only otherwise been recorded from Africa and New Zealand.

Isohypsibius elegans Binda & Pilato, 1971

Isohypsibius elegans Binda & Pilato, 1971: 903-906, Fig. 4A-C

Type locality. Catania, Sicily.

Type material examined. **Australia:** Reported from Stanmore, Sydney by Pilato & D'Urso (1976)

Diagnosis. Cuticle with polygonal sculpture over dorsum and sides. Gibbosities in transverse rows, up to 10; row 1 with 3 gibbosities, row 2 with 2, rows 3 to 9 with 4 and row 10 with 1 median gibbosity. Pharynx with 2 macroplacoids; microplacoid absent. Sinuous cuticular bars on first 3 pairs of legs; lunules on all claws, developed best on fourth pair.

Description. Colourless. Body length up to 400 μm . Eye spots present. Cuticle of dorsum and sides densely dotted, dots polygonal in shape (maximum diameter 1 μm generally smaller). 10-11 transverse rows of gibbosities from anterior 3, 2, 4, 4, 4, 4, 4, 4, 4, 1 becoming clearer caudally. Antero-ventral mouth, small teeth on medioventral and mediodorsal crests in posterior of oral cavity. Buccal tube long 39.5 μm in 400 μm specimen and narrow 3.6 μm wide (9% of buccal tube length). Stylet supports inserted at 72% of buccal tube length. Pharyngeal bulb briefly oval containing apophyses and two

macroplacoids. First macroplacoid longest and with strong median constriction, second with apical constriction. Claws robust with long secondary branch and a round refractive base; accessory claws short and close to main branch. Lunules present on all claws, better developed on fourth pair of legs. Sinuous cuticular bars present on inside of inner claw of first three pairs of legs.

Smooth oval eggs deposited in exuvium.

Remarks. This species differs from other Australian species in the genus with ten rows of gibbosities by having cuticular bars on the first three pairs of legs and three gibbosities only in the first row.

Distribution. Reported from Italy, Poland USSR, North Africa as well as Australia.

Isohypsibius heatwolei sp. n.

Fig. 72

Material examined. Australia: NEW SOUTH WALES: N3, moss on rock in cool temperate rainforest, 20 specimens, 1 exuvium containing eggs.

Diagnosis. Cuticle thickened into ridges arranged in a reticulate pattern over back and sides and tops of legs. Dorsum also with eight transverse rows of hemispherical gibbosities: two in rows one, three and five, four in rows two, four, six, seven and eight. Median gibbosities of row six reduced. 3 macroplacoids in pharynx. Claws robust similar in size on each pair of legs with short close accessory claws. Lunules present on all claws.

Description. Colourless. Body length 155-378 μm . Eye spots absent. Cuticle thickened into ridges arranged in a reticulate pattern over back and sides and top of fourth pair of legs. Dorsum also with eight transverse rows of hemispherical gibbosities: two in rows one, three and five, four in rows two, four, six, seven and eight. Median gibbosities of row six reduced. Mouth antero-ventral, a few teeth present in posterior of oral cavity. Buccal tube 30.3 μm long in 254 μm specimen and 2.4 μm wide (8% of buccal tube length). Stylet supports inserted at 71% of buccal tube length. Pharyngeal bulb almost round (31 μm by 27 μm) containing well-developed granular apophyses and three macroplacoids. Macroplacoid row 33% of buccal tube length; macroplacoids equal in length (2.7 μm). First macroplacoid pear-shaped, lying close to apophysis and partly obscured by it; second macroplacoid granular lying closer to first than third; third granular. Claws robust almost identical in size and shape on each leg with small refractive zone at base and long secondary branch; accessory claws short and rising well clear of main branch. Anterior claw of fourth pair of legs 15.7 μm long (51.7% of buccal tube length); posterior 19.5 μm (64.2%). Lunules thin and smooth on inner claws, thick and smooth on outer claws. One exuvium containing 3 smooth eggs found.

Remarks. This species differs from the other Australian species with eight rows of gibbosities (*I. peteri*) by having three macroplacoids and no cuticular bars on the first three pairs of legs.

Distribution. Found at only a single locality, its distribution appears to be limited.

Isohypsibius itoi (Tsurusaki, 1980)

Fig. 73

Hypsibius (Isohypsibius) itoi Tsurusaki, 1980: 281-283, Fig. 1

Type locality. Ishikari, Hokkaido, Japan.

Material examined. Australia: QUEENSLAND: Q20, leaf litter/ sand under *Casuarina* tree 100 m. from sea, 1 specimen.

Diagnosis. Cuticle smooth. Eye spots absent. Mouth tube short and thick. Pharynx containing 3 macroplacoids, microplacoid absent. Long slender claws.

Description. Colourless. Body length 193 μm . Eye spots absent. Cuticle smooth. Anterior mouth, no teeth in oral cavity. Buccal tube 26 μm long and 3.8 μm wide (14.6% of buccal tube length). Stylet supports inserted at 72.8% of buccal tube length. Pharyngeal bulb large oval (28 μm by 23 μm) containing well-developed granular apophyses and three macroplacoids. Macroplacoid row short (34.3% of buccal tube length) lying in anterior part of pharynx. Macroplacoids equal in length (2.7 μm); first macroplacoid pear-shaped, lying close to apophysis and partly obscured by it; second macroplacoid granular touching first, third granular. Claws long and slender with very fine short accessory claws. Anterior claw of fourth pair of legs 10.3 μm long (39.5% of buccal tube length). Lunules absent.

Remarks. Measurements for this specimen agree very well with those of a paratype given by Tsurusaki (1980). This specimen appears to have accessory claws on all primary branches which are so fine and close to the primary branch that they may be overlooked. They are stated as being absent in the original description of this species.

Distribution. This is only the second record of this species but its disjunct distribution (Japan and Australia) is probably not strange as this was found in intertidal sand in Japan.

Isohypsibius lunulatus (Iharos, 1966)

Fig. 74

Hypsibius (Isohypsibius) lunulatus Iharos, 1966: 116

Type locality. Hungary.

Material examined. **Australia:** NEW SOUTH WALES: *N15*, moss on soil over limestone in sheltered valley, 1 specimen. *N43*, moss on soil, 4 specimens, 2 exuvia containing eggs. **VICTORIA:** *V3*, leaf litter in cool temperate rainforest, 29 specimens, 1 exuvium containing eggs.

Diagnosis. Dorsum with thick cuticle with pores and transverse rows of gibbosities. Two macroplacoids in pharynx. Robust claws with minute accessory claws. Lunules present on all claws, cuticular bars on first three pairs of legs.

Description. Colourless. Body length 167-317 μm . Eye spots absent. Cuticle on dorsum, sides and back of legs thick with large pores (on the head about 1.5 μm , on the body and on gibbosities below first pair of legs about 2.5 μm). Ten transverse rows of gibbosities. First, third, fifth, seventh, ninth and tenth have 3 gibbosities and second, fourth, sixth and eighth have 4. Mouth anterior, no teeth in oral cavity. Buccal tube 27 μm long in 294 μm specimen and 3.2 μm wide (12% of buccal tube length). Stylet supports inserted at 71% of buccal tube length. Pharyngeal bulb oval (30 μm by 25 μm) containing apophyses and two macroplacoids. Macroplacoid row (34% of buccal tube length); first macroplacoid longest (4.9 μm) with strong median constriction, second (3.2 μm) with caudal constriction. Claws long, similar in dimensions on each leg. Internal claw with very narrow basal part and long secondary branch, primary branch with refractive regions and very short very fine accessory claws. External claw with wider base long strong secondary branch and rather short primary branch with very short very fine accessory claws. Anterior claw of fourth

pair of legs 8.1 μm long (30% of length of buccal tube); posterior 11.4 μm (42%). Lunules large and thick on all claws. Strong sinuous cuticular bars on first three pairs of legs arising from base of inner claw.

One exuvium containing 5 smooth eggs found.

Remarks. The specimens agree in almost all respects with the description of this species provided by Binda and Pilato (1969) except that they do not have eyes. However, the presence or absence of eyes is known to be variable within species of tardigrades and may depend on many factors including the nature of the mounting medium.

Distribution. The species is new for the Australian fauna. The species is widely distributed throughout Europe and has been reported also from Africa, North and South America.

Isohypsibius palmai Pilato, 1996

Fig. 75

Isohypsibius palmai Pilato, 1996: 69-70, Fig. 3A-E

Type locality. Piriaka, North Island, New Zealand.

Material examined. **Australia:** TASMANIA: 79, moss on limestone on cliff shelf in wet sclerophyll forest, 6 specimen, 4 black cysts.

Diagnosis. Cuticle with fine reticulate sculpture over back and sides, outside of legs I-III and on back and sides of fourth pair of legs. Mouth tube short and thick. Pharynx

containing 3 macroplacoids, microplacoid absent. Large robust claws. Lunules on all claws. Thick crescent-shaped bar below internal claw of first three pairs of legs.

Description. Colourless. Body length 222-294 μm . Eye spots in posterior position. Cuticle over dorsum and sides with reticulate sculpture (0.5 μm) also on outside of first three pairs of legs and back and sides of fourth pair. Antero-ventral mouth, no teeth in oral cavity. Buccal tube 35.1 μm in 290 μm specimen and 3.2 μm wide (9% of buccal tube length). Stylet supports inserted at 72% of buccal tube length. Pharyngeal bulb round (36 μm diameter) containing granular apophyses and three macroplacoids. Macroplacoid row long (43% of buccal tube length). First and third macroplacoids equal in size, granular, second macroplacoid granular slightly smaller than other two. Claws robust with thick common basal area, primary branches of all claws with large oval refractive zone at base. Internal claw with very narrow basal peduncle, long robust secondary branch, primary branch very robust with sharp right angled bend about half way up and thick low accessory claw. External claw with narrow base but flared on lower edge, secondary branch thick with refractive zones tapering rapidly to strong sharp point, primary branch rather short and robust with fine low accessory claws. Anterior claws of fourth pair of legs 14 μm long (40% of buccal tube length); posterior 16.5 μm (47%). Small lunules present on all claws. Crescent-shaped cuticular bar beneath internal claw on first three pairs of legs. No eggs found but fully developed specimens in black cysts were found.

Remarks. The species is rather similar to *I. wilsoni* but differs from it by having crescent shaped cuticular bars beneath inner claws of first three pairs of legs.

Distribution. So far this species has been recorded only from New Zealand (this is the first record from Australia).

***Isohypsibius papillifer* (Murray, 1905)**

Macrobiotus papillifer Murray, 1905: 692, Pl. 3, Fig. 15a-c

Type locality. Scotland

Material examined. Australia: None. Reported by Murray (1910) in moss from the Australian Alps, altitude 5000 feet.

Diagnosis. Cuticle covered dorsally and laterally and at base of legs with mammillary gibbosities Pharynx containing 3 macroplacoids, microplacoid absent. Claws similar in size on each leg.

Description. Colourless. Body length up to 250 μm . Eye spots present. Cuticle covered dorsally and laterally and on base of legs with isolated mamillary gibbosities with wide proximal parts, often hemispherical, and terminated in spines which are sometimes distally rounded. Pharyngeal bulb shortly oval containing apophyses and three macroplacoids. Macroplacoid row short; macroplacoids about equal in size, short rounded granules. Claws slender, about equal in size on each leg.

Remarks. This species differs from other Australian species in the genus by having distinctive mamillary-like gibbosities on the cuticle.

Distribution. Reported from many localities in Europe, from Brazil and New Zealand.

Isohypsibius peteri sp. n.

Fig. 76

Material examined. Australia: NEW SOUTH WALES: *N46.1*, moss and foliose lichen on rock in open sclerophyll forest, 13 specimens, 3 exuvia containing eggs. *N48*, weft moss on rock in open sclerophyll forest, 2 specimens.

Diagnosis. Cuticle with thickened areas separating pore-like spots about 1.5 μm diameter. Dorsally there are eight transverse rows of gibbosities; first to sixth with 4 gibbosities, seventh with 2 and eighth with 3. Pharynx containing 2 macroplacoids, microplacoid absent. Claws short robust, similar in length on each pair of legs. Sinuous cuticular bar near claws on first three pairs of legs. Lunules on all claws.

Description. Colourless. Body length 160-370 μm . Eye spots absent. Cuticle thick with pore-like spots about 1.5 μm diameter over dorsum and sides. Dorsally there are eight transverse rows of gibbosities: first to sixth with 4 gibbosities, seventh with 2 and eighth with 3. Antero-ventral mouth, no teeth in oral cavity. Buccal tube 33.5 μm in 370 μm specimen and 4 μm wide (12% of buccal tube length). Stylet supports inserted at 72% of buccal tube length. Pharyngeal bulb round (38 μm diameter) containing small apophyses and two macroplacoids. Macroplacoid row 30% of buccal tube length. First macroplacoid longest (5.4 μm long) with median constriction, second macroplacoid (3.8 μm) granular with slight caudal constriction. Claws robust, similar in size on each leg, with large refractory zones at base of primary branches on all claws. Internal claw with narrow base and robust secondary branch and primary branch with very short low accessory claws. External claw with thick secondary branch and primary branch with very short low accessory claws. Anterior claw on fourth pair of legs 8.7 μm long (26% of buccal tube

length) and posterior claw 13.5 μm (40%). Long sinuous bars (8.7 μm long on first pair of legs) on inside of leg below inner claw. Lunules present on all claws, large on fourth pair of legs.

3 exuvia containing 5, 5, 8 eggs were found.

Etymology. Named for Peter Claxton in appreciation for the specimens collected at the type locality.

Remarks. This species is most similar to *I. latiunguis* (Iharos, 1964) in having the same number of rows each with the same number of gibbosities. That species, however, does not have bars above the claws. It is rather similar to *I. heatwolei* amongst Australian species of this genus but differs from it by having two macroplacoids and cuticular bars on the first three pairs of legs.

Distribution. The species has a limited distribution in south-eastern Australia.

Isohypsibius prosostomus Thulin, 1928

Fig. 77

Isohypsibius prosostromus Thulin, 1928: 250-251

Type locality. Sweden.

Material examined. Australia: NEW SOUTH WALES: *N/S*, foliose lichen on tree branch in sheltered valley, 3 specimens.

Diagnosis. Cuticle smooth. Buccal tube short and wide. Pharynx containing 3 macroplacoids and microplacoid. Large robust claws with small lunules; cuticular bars on legs I-III.

Description. Colourless. Body length 268-415 μm . Eye spots in posterior position. Cuticle smooth. Terminal mouth; 3 rows small even denticles in posterior position in oral cavity. Buccal tube 28.1 μm in 304 μm specimen, 3.5 μm wide (12.5% of buccal tube length). Stylet supports inserted at 66% of buccal tube length. Pharyngeal bulb round (26 μm diameter) containing small granular apophyses, three macroplacoids and a microplacoid. Macroplacoid row 10.8 μm (38.5% of buccal tube length); first and third macroplacoids equal in length, second slightly smaller; first and second macroplacoids close; third has a slight bulb at the caudal end that curves towards the midline. Microplacoid short, distinct. Claws robust external much longer than internal. Internal claws with narrow basal peduncle rising to massive base of primary and secondary branches with large refractive areas; accessory claws fine and close to primary branch. External claws with flared basal peduncle rising to massive base of primary and secondary branches with refractive areas; primary branch long with large circular refractive area at base and fine low accessory claws. Anterior claw of fourth pair of legs 10.8 μm long (38.5%); posterior 19 μm (67.6%). Lunules small and smooth on all claws. Cuticular bars on first three pairs of legs.

No eggs found.

Remarks. These specimens agree well with the measurements provided by Dastych (1988).

Distribution. Widespread in Europe, it is considered to be a geopolitan species preferring carbonate bedrock but euryhydric and eurythermic by Dastych (1988). This is the first record of its occurrence in Australia.

Isohypsiobius sattleri (Richters, 1902)

Fig. 78

Macrobiotus sattleri Richters, 1902: 11, Fig. 1

syn. *Isohypsiobius bakonyiensis* Iharos, 1964: 65, Figs. 27-28

Type locality. Taunus Mts, Germany.

Material examined. **Australia:** QUEENSLAND: *Q6*, liverwort on rock and tree in rainforest remnant, 2 specimens. *Q7*, moss on rock in rainforest remnant, 1 specimen. *Q18*, moss on rock in rainforest remnant, 1 specimen (also recorded by Murray, 1910 from this locality). *Q21*, moss on rock in open woodland, 2 specimens. *Q22*, weft moss on tree in open woodland, 1 specimen. *Q25*, moss, foliose lichen and liverwort on trees and rocks in rainforest, 4 specimens, 1 exuvium containing eggs; moss on rock, lichen/liverwort on tree in Box forest, 4 specimens. **NEW SOUTH WALES:** *N3.1*, moss and lichen on tree, lichen on rock in open sclerophyll forest, 6 specimens; *N3.2*, leaf litter in subalpine heath, 2 specimens. *N5*, foliose lichen on rock in open woodland, 2 specimens. *N8*, gumnuts on soil and asphalt in car park, 24 specimens, 5 exuvia containing eggs. *N11*, weft moss on gutter, 1 specimen. *N14*, moss on rock and tree in rainforest remnant and escarpment top, 8 specimens, 1 exuvium containing eggs. *N15*, moss on trees in protected valley, 5 specimens, 1 exuvium containing eggs. *N27*, weft moss and lichen on rock in open sclerophyll forest, 34 specimens, 4 exuvia containing eggs. *N29*, moss on soil and limestone in sheltered valley, 10 specimens, 2 exuvia containing eggs. *N34*, moss, lichen and liverwort on trees in closed forest, 5 specimens. *N35*, moss/lichen on trees, leaf litter on rock, 3 specimens, 1 exuvium containing eggs. *N38*, moss on soil and rock in open sclerophyll woodland, 5 specimens. *N41*, moss and lichen on rock in open sclerophyll woodland, 2 specimens. *N46.2*, moss on rock in open subalpine woodland, 1 specimen. *N47*, moss on soil near ocean, 3 specimens. **VICTORIA:** *V3*, leaf litter in cool temperate rainforest, 1 specimen. *V4*, moss on soil in low scrub, 13 specimens. **TASMANIA:** *T1*, moss on tree in coastal scrub, 1 specimen. *T2*, moss on tree in coastal

heath, 5 specimens. *T3*, moss/liverwort on tree in closed forest, 1 specimen. *T7*, moss and liverwort on rock, moss on soil in wet forest, 6 specimens. *T11*, moss, 2 specimens. *T16*, moss on dolerite, 5 specimens, 2 exuvia containing eggs. WESTERN AUSTRALIA: *W1*, leaf litter on soil in suburban street, 16 specimens, 4 exuvia containing eggs. LORD HOWE ISLAND: moss and lichen, 13 specimens.

Diagnosis. Cuticle of dorsum and sides covered with net-like structure and with cone-like tubercles many of which terminate in spines. Tubercles arranged in at least 8 transverse rows of 4-6 in each row. Pharynx with two macroplacoids. Claws slender, similar in size on each leg; lunules present.

Description. Colourless. Body length 115-250 μm . Eye spots absent. Cuticle of dorsum and sides covered with net-like structure and with cone-like tubercles many of which terminate in spines. Mesh variable in size (0.6-1.2 μm), much smaller on tubercles. Lateral tubercles smaller and more pointed than dorsal ones. Tubercles arranged in at least 8 transverse rows: 6 in first, second, third and fifth rows, 4 in fourth, seventh, eighth and ninth rows and 2 in sixth row. Antero-ventral mouth. Buccal tube 18.9 μm long in 160 μm specimen and 1.6 μm wide (8.6% of buccal tube length). Stylet supports inserted at 64.5% of buccal tube length. Pharyngeal bulb oval (19 μm by 18 μm) containing apophyses and two macroplacoids. Macroplacoid row short (31% of buccal tube length). First macroplacoid (2.7 μm long) strongly constricted in middle, second macroplacoid (2.2 μm) granular. Claws slender. Internal claw with long secondary branch and short thick accessory claw on primary branch. External claw with long secondary branch and round refractive zone at base of primary branch, accessory claws short fine. Anterior claw of fourth pair of legs 6 μm long (31.5% of buccal tube length); posterior 8 μm (42.3%). Lunules on all claws.

Exuvia containing up to 5 smooth eggs found.

Remarks. This species was redescribed by Dastych (1990) on the basis of a single specimen of Richters because of the very poor original description and the confusion that subsequently arose in the literature regarding its identification. He also synonymised *Isohypsibius bakonyiensis* (Iharos 1964) with this species.

Distribution. Dastych (1990) described this species as a euryhygric form with a preference for wet habitats and for carbonate bedrock. It has a wide vertical range in central Europe (Dastych, 1988) although Guidetti *et al.*, (1999) found it to be rare above 1500m. asl. It is clearly widespread in a variety of habitats in Australia.

Isohypsibius wilsoni (Horning, Schuster & Grigarick, 1978)

Fig. 79

Hypsibius (Isohypsibius) wilsoni (Horning *et al.*, 1978: 217, Fig. 67-70)

Type locality. Open Bay Island, Taurmaka, South Island, New Zealand

Material examined. **Australia:** NEW SOUTH WALES: *N15.1*, moss on limestone and trees in sheltered valley, 24 specimens, 2 cuticles containing eggs; *N15.3*, moss and foliose lichen on limestone and moss on tree in sheltered valley, 31 specimens, 1 cuticle containing eggs. *N35*, moss on tree in temperate rainforest, 10 specimens. *N39*, moss on log in temperate rainforest, 1 specimen. **TASMANIA:** *T11*, moss, 3 specimens. **LORD HOWE ISLAND:** moss and lichen, 15 specimens. **New Zealand:** Bruce Park Reserve, 1 specimen.

Diagnosis. Cuticle with reticulate sculpture. Buccal tube short and wide. Pharynx containing 3 macroplacoids, microplacoid absent. Large robust claws, lunules present on all claws, small cuticular bars on first three pairs of legs.

Description. Colourless. Body length 170-350 μm . Eye spots absent. Cuticle of dorsum and sides of body caudally of first pair of legs and top of fourth pair of legs covered with a reticulate pattern (largest mesh about 2 μm diameter). Antero-ventral mouth, no teeth in oral cavity. Buccal tube 24 μm in 200 μm specimen and 3 μm wide (12% of buccal tube length). Stylet supports inserted at 65% of buccal tube length. Pharyngeal bulb round (25 μm diameter) containing small granular apophyses and three macroplacoids. Macroplacoid row short (34% of buccal tube length). Macroplacoids granular about equal in size (2.7, 2.7 and 3.2 μm long). Claws robust. Internal claw with refractive zone where branches meet, long robust secondary branch and thick primary branch with very fine accessory claws. Inner claw about 72% of length of outer claw. External claw more slender than inner with long robust secondary branch and large refractive zone at base of primary branch with short low accessory claws. Anterior claws on fourth pair of legs 12 μm long (49.3%); posterior 16.1 (66.1%). Small lunules on all claws. Short thin cuticular bar present near inner claw of first three pairs of legs.

Exuvia containing 1, 7 and 9 eggs found.

Remarks. The dimensions on the specimens described here are very similar to those given for this species by Pilato (1996). However, he mentioned indistinct protuberances on the caudal part of the body that were not observed in the Australian material nor in the specimen from New Zealand.

Distribution. The species has been found so far only in New Zealand and Australia.

Genus *Ramazzottius* Binda & Pilato, 1986

Ramazzottius Binda & Pilato, 1986: 164

Type species. *Macrobiotus oberhaeuseri* Doyère, 1840

Diagnosis. Six peribuccal lobes present. Elliptical sensory organs on either side of head. Rigid buccal tube, ventral support absent. Apophyses for insertion of stylet muscles in form of “a blunt hook” and asymmetrical with respect to frontal plane. Diploclaws of each leg different in shape and size, asymmetrical with respect to median plane of leg. Flexible primary branch of external claw inserted on secondary branch at distance from base and joined to it by a narrow sclerified part.

Key to species of *Ramazzottius*

1. Cuticle smooth..... *R. lacus*
Cuticle not smooth..... 2
2. Dorsum with seven rows of tubercles covered with polygonal
network..... *R. szeptycki*
Dorsum with small polygonal thickenings..... *R. oberhaeuseri*

***Ramazzottius lacus* sp. n.**

Fig. 80

Material examined. NEW SOUTH WALES: *N11*, moss on tree on street, 1 specimen. *N40*, weft moss and foliose lichen on sandstone in open sclerophyll forest beside large lake, 10 specimens.

Diagnosis. Smooth cuticle.

Description. Body length 200-510 μm . Eye spots absent, elliptical sense organs present. Adults pigmented with red-brown pigment spots (very small dots) not arranged in bands, cuticle smooth. Mouth antero-ventral. Buccal tube 36.8 μm long and narrow, about 3.1 μm wide (internal diameter 1.6 μm) in animal 420 μm long. Buccal tube wall thickened below stylet support insertion point. Stylet supports inserted at 60.5% of buccal tube length. Pharyngeal bulb almost spherical (about 40 μm diameter) containing large triangular apophyses and 2 macroplacoids, the first (4.5 μm long) with faint median constriction, a little longer and larger than the second (3.2 μm). Macroplacoid row length 9.5 μm (25.8%). Claws similar to those of *R. oberhaeuseri*, internal claws and base of external claws robust. Internal claw with narrow base rising to very thick mid region and rather short secondary branch, primary branch robust with thick accessory claw. External claw with long pillar-like base and short hooked secondary branch, primary branch long and very slender with accessory claws reduced to two minute points. Base of anterior claw of fourth pair of legs 7.6 μm long, primary branch 8.1 μm . Base of posterior claw of fourth pair of legs 14.6 μm , primary branch 19 μm ; total length of claw 29.7 μm (80%).

Eggs not found.

Etymology. Latin, m. *lacus*, body of standing water, after Lake George on the shores of which this species was found.

Remarks. Four species of this genus are known to have smooth cuticle, and in the key to this genus provided by Biserov (1997/98), separation of these species is primarily based on characteristics of the egg. However several characters separate this species from others

with smooth cuticle - the presence of a median constriction in the first macroplacoid, a different length of the posterior claw relative to the length of the buccal tube (66% in *R. velaamis* Biserov & Tumanov, 1993, 76% in *R. anomalus* (Ramazzotti, 1962), 73% in *R. subanomalus* (Biserov, 1985) and 86% in *R. caucasicus* Biserov 1997/98). In addition it has a longer macroplacoid row length than *R. anomalus* and *R. subanomalus* and a shorter one than *R. caucasicus* and *R. velaamis* and these two latter species have teeth in the oral cavity. For these reasons this species has been determined to be a new taxon.

Distribution. The species has limited distribution in eastern Australia.

***Ramazzottius oberhaeuseri* (Doyère, 1840)**

Fig. 81

Macrobiotus Oberhaeuser Doyère, 1840: 286, Pl. 14, Fig. 11

Type locality. Greifswald, Pomerania.

Material examined. NEW SOUTH WALES: *N8*, foliose lichen on asphalt, 1 specimen. *N11*, lichen on tree in street, 2 specimens. *N13*, moss and lichen on tree, 5 specimens, 1 egg. *N14.7*, moss and lichen on tree, moss on path, 3 specimens. *N15*, moss and lichen on tree in sheltered valley, 3 specimens, 2 eggs. *N18*, moss on asphalt, 1 specimen. *N20*, lichen on tree in street, 1 specimen. *N21*, lichen on roof and on branch on ground in open sclerophyll, 5 specimens, 3 eggs. *N23*, lichen on tree in open sclerophyll, 6 specimens, 3 eggs. *N27*, moss and lichen on rock in open sclerophyll, 7 specimens. *N29*, lichen on branches on ground and moss on limestone in sheltered valley, 11 specimens, 7 eggs. *N31*, lichen on branch on ground in temperate rainforest, 3 specimens. *N32*, lichen on tree beside road, 20 specimens, 1 egg. *N33*, lichen on tree beside road, 1 specimen, 1 egg. *N34*, moss on tree in forest, 1 specimen. *N35*, moss on tree in temperate rainforest, 1 specimen. *N37*, lichen on tree beside road, 5 specimens. AUSTRALIAN CAPITAL TERRITORY: *A1*, lichen on rock in river bed, 1 specimen. *A2*, lichen on rock in open sclerophyll, 3 specimens, 1 egg. TASMANIA: *T11*, moss, 1 specimen. WESTERN AUSTRALIA: *W1*, moss on soil in street, 1 specimen.

W3, moss on soil and limestone wall in park, 4 specimens, 1 egg. *W4*, moss on tree and limestone wall, 8 specimens, 2 eggs.

Diagnosis. Dorsal cuticle with small (2-3 μm) polygonal evenly spaced thickenings in 7 bands.

Description. Body length 175-380 μm . Eye spots absent, elliptical sense organs present. Adults pigmented with red-brown to violet colour with 5 longitudinal and 9 transverse colourless bands, cuticle with small (2-3 μm) polygonal evenly spaced thickenings in 7 bands across dorsum. Antero-ventral mouth. Buccal tube 34 μm long in 300 μm long specimen and 2.2 μm wide (internal diameter 1 μm). Buccal tube wall thickened below the insertion point of the stylet supports and bent ventrally. Stylet supports inserted at 58.5% of buccal tube length. Pharyngeal bulb round (30 μm diameter) containing large triangular apophyses and 2 granular macroplacoids, first 2.8 μm long, second 2.4 μm . Macroplacoid row length 6.7 μm (20%). Claws very different on each leg; internal claws and base of external claw robust. Internal claw with narrow base rising to thick mid section and long strongly curved secondary branch, primary branch robust with thick showy accessory claw. External claw with pillar-like base and strong curved secondary branch, primary branch slender with accessory claws reduced to two points which stand away from branch. Base of anterior claw of fourth pair of legs 9.2 μm long, primary branch 7 μm . Base of posterior claw of fourth pair of legs 10.8 μm , primary branch 17.3 μm ; total length of claw 24.3 μm (71%).

Eggs laid free, often occurring in two's and three's. Egg spherical with processes which are mostly dome-shaped but may sometimes be shaped like short cones or irregularly truncated cones or an hour glass. Base of each process with tiny pore-like indentations.

Diameter without processes 61 μm , with processes 70 μm . 26 processes around circumference, 70 in hemisphere. Processes 4-4.5 μm high and 7-8 μm diameter at base, distance between 2-4 μm . Shell surface smooth.

Remarks. The eggs of this species are rather distinctive and the specimens found in Australia comply with the characters of the adults given by Biserov (1997/98) namely, a narrow buccal tube (less than 2 μm inner diameter), claws 15-25 μm long and with weakly developed sculpture on the dorsum.

Distribution. *R. oberhaeuseri* is considered to be a cosmopolitan species but like many tardigrade species has probably been misidentified many times. In his taxonomic analysis of *Ramazzottius*, Biserov (1997/98) stated that it could easily be confused with a number of other species in the absence of eggs. This is the first record of its occurrence in Australia.

***Ramazzottius szeptycki* (Dastych, 1979)**

Fig. 82

Hypsibius szeptycki Dastych, 1979: 505-508, Figs. 1-5

Type locality. Hendriksdaal, South Africa.

Material examined. NEW SOUTH WALES: *N/4.7*, moss/foliose lichen on cement curb of footpath in suburban garden, 1 specimen.

Diagnosis. Elliptical sense organs present. Dorsum with 7 transverse rows of tubercles. Tubercles and sometimes surface between them covered with polygonal network; cuticle

smooth anterior of first pair of legs. Large triangular apophyses and two macroplacoids in pharyngeal bulb. Microplacoid absent.

Description. Pigmented with red-brown colour. Body length 420 μm . Eye spots absent, elliptical sense organs present. Dorsum with 7 transverse rows of tubercles. Tubercles and sometimes surface between them covered with a polygonal network; cuticle smooth anterior of first pair of legs. Buccal tube 35 μm long and narrow, about 3.5 μm wide (internal diameter 0.8 μm), wall strengthened below stylet support insertion point. Stylets furcae very pronounced. Stylets inserted at 21 μm (60% of buccal tube length). Pharyngeal bulb almost spherical (about 35 by 40 μm) containing large apophyses and 2 macroplacoids, the first, 4 μm long (11.2%) a little longer and larger than the second, 2.9 μm (8.2%) and with a slight median constriction. Macroplacoid row length 8.7 μm (24.6%). Claws similar to those of *R. oberhaeuseri*, internal claws and base of external claws very robust. Internal claw with short strong accessory points. External claw with long fine primary branch with very small accessory points; base of external claw with crest-like structures (Biserov, 1997/98). Base of anterior claw of fourth pair of legs 9.1 μm , primary branch 8.1 μm . Base of posterior claw 12.4 μm , primary branch 20.6 μm ; total length of claw 33 μm (94%). Lunules absent. A single tubercle present on dorso-lateral surface of legs IV.

Eggs not found.

Remarks. The specimen agrees well with the original description of this species.

Distribution. Only known from South Africa – a single specimen from the type locality found in moss on rock at 1400 m., and 2 specimens from moss from Tanzania. It was also reported from a river in a rainforest on Mount Kilimanjaro by Van Rompu, De Smet & Bafort (1991). This is the first record of this species in Australia.

Genus *Thulinus* Bertolani, 1981

Thulinia Bertolani: 1981: 249

Thulinus Bertolani: 2003: 1-4

Type species. *Isohypsibius stephaniae* Pilato, 1974

Diagnosis. (from Bertolani, 2003). Mouth opening with twelve small, partially fused peribuccal lamellae and six peribuccal lobes, sometimes subdivided into a larger number of irregular sublobes. Rigid buccal tube, ventral support absent. Buccal apophyses for insertion of stylet muscles crest-shaped. Diploclaws on each pair of legs different in shape and size, asymmetrical with respect to median plane of leg. Primary branch of claw inserted flexibly on secondary branch at distance from base, secondary branch forming curved hook with base.

Key to species of *Thulinus*

- 1. Lunules present, cuticular bars on first three pairs of legs..... *T. ruffoi*
Lunules absent, cuticular bars absent..... *T. augusti*

***Thulinus augusti* (Murray, 1907)**

Macrobiotus augusti Murray, 1907: 660, Pl. III, Fig. 22a-c

Hypsibius augusti (Thulin, 1911)

Pseudobiotus augusti (Schuster *et al.*, 1980)

Type locality. Scotland.

Material examined. None. Reported by Murray (1910) from ponds in Sydney.

Diagnosis. Pharynx with three macroplacoids. Two claws on each legs similar in appearance and dimensions. First three pairs of legs with lateral conical papilla.

Description. (from Bertolani 1981) Body length up to 750 μm , colourless. Eye spots present or absent. Cuticle smooth or a little rough. Anterior mouth; row of teeth, delimited on both sides by a triangular tooth, in posterior position of oral cavity; three transverse crests (median one short) below row of teeth. Buccal tube moderately wide. Pharynx round with apophyses and three long macroplacoids of which the second is smallest. Legs particularly slender, first three pairs with lateral conical papilla. Claws very long (50 μm in 705 μm specimen), rather similar in appearance and dimensions. Inner claw with narrow base and thick basal tract, primary branch with accessory tracts which are not detached from the primary branch at their distal ends. Outer claw with expanded base. No lunules or cuticular bars on legs.

Smooth eggs deposited in exuvium.

Remarks. This species differs from *T. ruffoi* by lacking lunules on the claws and from *T. stephaniae* (Pilato, 1974) by having much longer, thinner basal tracts on all claws.

Distribution. McInnes (1994) recorded this species as cosmopolitan but many of the records have not been verified (Bertolani *et al.*, 1999)

***Thulinus ruffoi* (Bertolani, 1981)**

Fig. 83

Thulinia ruffoi Bertolani, 1981: 55-57, Fig. 30

Type locality. Sesia River, Valsesia, Italy

Material examined. WESTERN AUSTRALIA: *W1*, wet willow leaves on ground after flood, 3 specimens.

Diagnosis. Lunules on all claws, cuticular bar below claw on first three pairs of legs.

Description. Colourless. Body length 426-436 μm . Eye spots absent. Oral cavity with row strong teeth in posterior position with row weaker teeth immediately anterior to it. Buccal tube 39 μm long in 432 μm specimen and 4.3 μm wide (11% of buccal tube length). Stylet supports inserted at 71-72% of buccal tube length. Pharynx round (38 μm diameter) with large apophysis and three rounded rod-shaped macroplacoids. First macroplacoid elongated, same length as third, 4.2 μm , second shortest, 3.1 μm , close to first. Claws very different on each leg. Internal claw robust with narrow base, strong secondary branch, primary branch robust with thick short accessory claws. External claw with narrow base thickening rapidly before tapering to a fine tip, primary branch long and slender with fine accessory claws. Claws of fourth pair of legs similar to those on other three legs. Small fine lunules present on all claws. Anterior claw on fourth pair of legs 11 μm long (28% of buccal tube length); posterior claw 19 μm (48.6%). Cuticular bar present below both claws on first three pairs of legs.

No eggs found.

Remarks. This species differs from *T. stephaniae* by having thinner claws, less marked cuticular thickenings on the legs and by having lunules (Bertolani, 1981). It differs from *T. augusti* by having lunules on the first three pairs of claws.

Distribution. This freshwater species has only otherwise been found in Italy, Turkey and Russia. This is the first record of the species and the genus in Australia.

Subfamily Itaquasconinae Rudescu, 1964

Genus *Astatumen* Pilato, 1997

Astatumen Pilato, 1997: 206.

Type species. *Itaquascon trinacriae* Arcidiacono, 1962.

Diagnosis. (from Pilato, 1997) Peribuccal lamellae and papulae absent. Bucco-pharyngeal tube subdivided into an anterior rigid buccal tube and a posterior flexible pharyngeal tube. Stylet supports absent. Buccal tube, without ventral lamina, very short. Apophyses for the insertion of stylet muscles in form of a wide flat ridge, symmetrical with respect to the frontal plane; caudal processes of these apophyses thin and pointing laterally. Pharyngeal bulb lacking apophyses and placoids or with a long undivided placoid. Diploclaws on each leg different in shape and size, asymmetrical with respect to median plane of leg. Primary branch of external claw inserted flexibly on secondary branch at distance from base. Eggs smooth and laid in exuvium in known species.

Astatumen trinacriae (Arcidiacono, 1962)

Fig. 84, Plate XVIIe

Itaquascon trinacriae Arcidiacono, 1962: 128-132, Figs. 3, 4

Type locality. Mount Nebrodi, Italy.

Material examined. **Australia:** NEW SOUTH WALES: *N14.2.b*, moss on tree in open forest, 3 specimens.

Diagnosis. Cuticle smooth, no pores; wide buccopharyngeal tube and very short buccal tube. Elongated pharynx. Claws very different on each leg, internal claw robust, main branch of external claw with refractive zone at base. Cuticular bars on legs II and III.

Description: Colourless. Body length 277-378 μm . Eye spots absent. Cuticle smooth. Anterior mouth. Buccal tube short 5.4 μm long in 378 μm long specimen (11% of buccopharyngeal tube length); pharyngeal tube 40.5 μm long, annulated and 3.7 μm wide. Stylets 21 μm long (in longest specimen) with short, rounded furcae. Pharyngeal bulb oval (29 μm long by 17 μm wide) with placoids 15 μm long. Internal claws robust, with short secondary branch and long high accessory claws (inner claws 45-48% of length of outer claws). External claw with slender primary branch with fine short accessory claws and refractive zone at base; short robust secondary branch (secondary branch 56-60% of length of main branch). Anterior claw of fourth pair of legs 7 μm long, posterior claw 15.1 μm long. Cuticular bars on inside of internal claw on legs II and III. Lunules absent.

No eggs found.

Remarks: The measurements obtained here are very similar to those given for this species from Poland (Dastyh, 1988) and Italy (Pilato, 1969c).

Distribution: The species has been reported from Italy, Poland and was considered to be widespread in Europe by Binda (1980). It was also reported from Tennessee, USA and North and South Africa. This is the first record of its occurrence in Australia.

Genus *Itaquascon* de Barros, 1939

Itaquascon de Barros, 1939: 108, Figs. 1, 2 and 3.

Type species. *Itaquascon umbellinae* de Barros, 1939

Diagnosis. Peribuccal lamellae and papulae absent. Buccopharyngeal tube divided into an anterior rigid buccal tube and a posterior flexible pharyngeal tube. Postero-lateral processes of furcae reduced. Stylet supports present. Pharyngeal bulb lacking apophyses and placoids or with a long undivided placoid. Diploclaws on each leg different in shape and size, asymmetrical with respect to median plane of leg. Primary branch of external claw inserted flexibly on secondary branch at distance from base. Eggs smooth and laid in exuvium.

Key to species of *Itaquascon*

- 1. Stylet supports inserted at junction of buccal and pharyngeal tubes..... 2
- Stylet supports not inserted at junction of buccal and

- pharyngeal tubes..... *I. pseudotrinacriae*
2. Buccal tube <35% of buccopharyngeal tube length..... 3
- Buccal tube >35% of buccopharyngeal tube length..... 4
3. Pharynx small round, buccal tube 21% of buccopharyngeal tube length..... *I. pawlowski*
- Pharynx oval, buccal tube 32% of buccopharyngeal tube length..... *I. longitubulus*
4. Buccal tube >35% and <50% of buccopharyngeal tube length 5
- Buccal tube 55% of buccopharyngeal tube length, claws slender, same length on all legs..... *I. brevitubulus*
5. Buccal tube 39% of buccopharyngeal tube length, claws short. *I. unguiculum*
- Buccal tube 46% of buccopharyngeal tube length, external claw long and slender..... *I. cambewarrense*

***Itaquascon brevitubulus* sp. n.**

Fig. 85, Plate XVIIa

Material examined. Australia: NEW SOUTH WALES: N3.2.a. turf moss on rock in open heath, 2 specimens.

Diagnosis. Cuticle smooth. Stylet supports inserted at junction of buccal and pharyngeal tubes. Stylet supports fine and S-shaped. Stylet furcae distinct branches, not swollen. Claws long and slender. Lunules and cuticular bars absent.

Description. Colourless. Body length 155, 189 μm . Cuticle smooth. Eye spots absent. Mouth antero-ventral. Buccopharyngeal tube 23.8 μm long in 189 μm specimen and 1.6

um wide. Stylet supports fine and S-shaped inserted at 55% of buccopharyngeal tube length at junction of buccal and pharyngeal tubes. Stylet furcae with long postero-lateral processes, ends not swollen. Rigid buccal tube longer than apophyses for insertion of stylet muscles, apophyses flat ridges symmetrical with respect to frontal plane; pharyngeal tube with spiral thickening. Pharyngeal bulb oval (about 16 µm long by 12 µm wide) without apophyses or placoids. Claws long and slender, same length on all legs. Internal claws with short secondary branch and short high accessory points, 52.6% of length of external claws. External claws long and slender, primary branch with fine accessory points. Secondary branch of outer claws 49.4% of length of primary branch. Anterior claw of fourth pair of legs 6 µm or 44.4% of length of buccal tube, posterior claw 11.4 µm or 84.4%. Lunules and cuticular bars absent. Eggs not found.

Etymology. *Brevis*, L. M. short; *tubulus*, L. m. tube, referring to the short buccopharyngeal tube.

Remarks. The unusually long buccal tube relative to the pharyngeal tube length (55% of the buccopharyngeal tube length) separates this species from *I. unguiculum* and *I. cambewarrense* in which the buccal tube is >35% but <50% of the buccopharyngeal tube length.

Distribution. Only found at the type locality.

Itaquiscon cambewarrense Pilato, Binda & Claxton, 2002

Fig. 86

Itaquiscon cambewarrense Pilato *et al.*, 2002: 90-93, Figs. 4, 5, 6F

Type locality. Cambewarra Mountain, NSW

Material examined. **Australia:** NEW SOUTH WALES: *N3.1.b*, leaf litter, moss and lichen on rock in open sclerophyll forest, 24 specimens; *N3.3.a*, liverwort on tree in *Nothofagus* forest, 2 specimens. *N14.2.c*, weft moss on soil in dry sclerophyll forest, 3 specimens; *N14.2.d*, moss on soil, rocks and trees, liverwort on trees in rainforest remnant, 12 specimens; *N14.2.e*, moss on rock in open sclerophyll forest, 13 specimens; *N14.2.a*, liverwort on tree in rainforest remnant, 10 specimens, 1 exuvium containing 3 eggs. *N39.2.b*, fruticose lichen on rock, 3 specimens; *N39.2.f*, weft moss on rock, 1 specimen; *N39.2.i*, fruticose lichen on tree in warm temperate rainforest, 1 specimen. **TASMANIA:** *T3*, filmy fern on rock in closed forest, 2 specimens.

Diagnosis. Cuticle smooth. Stylet supports inserted at junction of buccal and pharyngeal tubes. Stylet supports fine and S-shaped. Stylet furcae triangular with thickened apices. Inner claws robust, outer claws slender. Lunules and cuticular bars absent.

Description. Colourless. Body length 196-231 μm . Cuticle smooth Eye spots absent. Mouth antero-ventral. Buccopharyngeal tube 39.2 μm in 205 μm specimen and 2.3 μm wide (12.6% of buccal tube length). Stylet supports fine and S-shaped, inserted at 46.4% of buccopharyngeal tube length at junction of buccal and pharyngeal tubes. Stylet furcae triangular with apices thickened but not prolonged to form distinct postero-lateral processes. Pharyngeal bulb (20 μm long by 15 μm wide) without apophyses or placoids. Claws long, increasing in length from first to fourth. External claws longer and more slender than internal claws. Internal claws robust, 45-50% of length of external claws on first three pairs of legs, 42-48% on fourth pair. External claws long with rather robust secondary branch and long slender primary branch with fine accessory points. Secondary branch of outer claws 57-62% of length of primary branch. Anterior claw of fourth pair of

legs 5.8 μm or 31.9% of length of buccal tube, posterior 13.7 μm or 75.3%. Lunules and cuticular bars absent.

Smooth eggs laid in exuvium.

Etymology. Named after Cambewarra Mountain on which it was found.

Remarks. This species differs from other species in the genus in the shape of the furcae. It also differs from *I. unguiculum* by having the stylet supports inserted on the buccal tube in a more posterior position.

Distribution. Found only in highland areas of Tasmania suggests that this species requires a benign climate.

Itaquascon longitubulus sp. n.

Fig. 87

Material examined. Australia: NEW SOUTH WALES: Q5, liverwort on rotten log in closed *Eucalyptus* forest, 1 specimen.

Diagnosis. Cuticle smooth. Stylet supports inserted at junction of buccal and pharyngeal tubes. Stylet supports fine and S-shaped. Stylet furcae with small postero-lateral processes, not swollen. Claws short and robust. Lunules and cuticular bars absent.

Description. Colourless. Body length 247 μm . Cuticle smooth. Eye spots absent. Mouth antero-ventral. Buccopharyngeal tube 55.6 μm and 2.3 μm wide (7.9% of buccal tube

length). Stylet supports fine and S-shaped inserted at 32% of buccopharyngeal tube length at junction of buccal and pharyngeal tubes. Stylet furcae with small postero-lateral processes, not swollen. Pharyngeal bulb (about 17 μm by 14 μm) without apophyses or placoids. Claws increasing in length from first to fourth. Internal claws robust, external claws small and slender. Internal claws with short, thick accessory points, 52-55% of length of external claws on first three pairs of legs, 57% on fourth pair. External claws with short primary branch with refractive zone at base and short fine accessory points. Secondary branch of external claw 66% of primary branch. Anterior claw of fourth pair of legs 6.5 μm long or 36.5% of length of buccal tube, posterior claw 11.4 μm or 64%. Lunules and cuticular bars absent. Eggs not found.

Etymology. *Longus*, L. long; *tubulus*, L. m. tube, referring to the long buccopharyngeal tube.

Remarks. The unusual length of the buccopharyngeal tube separates this species from other known species in this genus. It is most similar to *I. globuliferum* Abe & Ito, 1994 but differs from it by having the stylet supports inserted at 32% of the buccal tube length (39% in *I. globuliferum*).

Distribution. Found only at the type locality.

Itaquiscon pawlowskii Weglarska, 1973

Fig. 88

Itaquiscon pawlowskii Weglarska, 1973: 153, Figs. 5, 6

Type locality. Tatra Mountains, Poland.

Material examined. NEW SOUTH WALES: *N3*, foliose lichen on branch in subalpine scrub, 1 specimen.

N14.2.c, fruticose lichen on soil in open forest, 1 specimen.

Diagnosis. Smooth cuticle. Very long thin buccopharyngeal tube, short fine stylets, buccal tube 21% of bucco-pharyngeal tube length. Pharynx small and round. Inner claws robust, outer claws with long slender main branches. Lunules and cuticular bars absent.

Description. Colourless. Body length 164, 238 μm . Cuticle smooth. Eye spots absent.

Anterior mouth. Buccopharyngeal tube 56.3 μm in 238 μm specimen and 1.1 μm wide (8% of buccal tube length). Stylets supports thickened where they join the buccopharyngeal tube then become fine as they loop down and then up to meet furcae of stylets. Furcae with two postero-lateral processes, not swollen. Stylet supports inserted at 21% of the buccopharyngeal tube length at junction of buccal and pharyngeal tubes. Pharyngeal bulb round (9 μm diameter) containing a single placoid 4 μm long. Internal claws robust, 63-65% of the length of external claws. Internal claws with short secondary branch and short rather high accessory points on primary branch. External claws short slender with short secondary branch and primary branch with refractory zone at base and short accessory points which rise high above branch. Secondary branch of external claws 70-71% of length of primary branch (claws of fourth pair of legs 4.3 μm and 6.5 μm long). Lunules and cuticular bars absent.

Eggs not found.

Remarks. The dimensions of the specimens reported here agree well with those supplied by Dastych (1988).

Distribution. The distribution of this species in Australia agrees with the contention of Dastych (1988) that this is a montane species. It is considered to be a rare species (Durante Pasa & Maucci, 1979 and Dastych, 1988) in Europe; it has also been reported from Canada, the Dominican Republic and Japan. This is the first record of its occurrence in Australia.

Itaquascon pseudotrinacriæ sp. n.

Fig. 89, Plate XVIIId

Material examined. NEW SOUTH WALES: *N14.2.a*, crustose and fruticose lichen on trees in open sclerophyll forest, 2 specimens; *N14.2.d*, weft moss on rock in remnant rainforest, 1 specimen; *N14.3.b*, weft moss on rock in remnant rainforest, 1 specimen; *N14.4*, lichen on tree in open sclerophyll forest, 17 specimens; *N14.5*, foliose lichen on trees in open sclerophyll forest, 6 specimens; *N14.7*, lichen on path in garden, 2 specimens, exuvium containing 12 embryonate eggs. *N11*, lichens on trees and weft moss on post at roadside, 8 specimens.

Diagnosis. Smooth cuticle. Buccal tube and pharyngeal tube about equal length, stylets as long as buccal tube. Pharynx oblong with placoids. Cuticular bars on second and third pairs of legs.

Description. Colourless. Body length 180-608 μm . Cuticle smooth. Eye spots absent. Mouth antero-ventral. Buccopharyngeal tube 44.4 μm long, buccal tube 22.2 μm long and 3.2 μm wide in 378 μm long specimen. Pharyngeal tube with spiral thickening. Stylet supports present in 14 of 37 specimens; very fine S-shaped and meeting at ventral mid-line

of the buccopharyngeal tube at junction of the buccal and pharyngeal tubes. Pharyngeal bulb elongate (27 μm long by 20 μm wide) with thin placoids 15 μm long. Claws short. Internal claws robust with short secondary branch and short low accessory points on primary branch, 45-48% of length of external claws. External claws with short robust secondary branch and slender primary branch with short fine accessory points. Secondary branch 56-60% of length of primary branch. Anterior claw of fourth pair of legs (in 378 μm individual) 8.7 μm long, posterior claw 18.9 μm long. Cuticular bars present beside inner claw of second and third pair of legs. Lunules absent.

Twelve smooth eggs laid in exuvium.

Remarks. This species has been placed in the genus *Itaquascon* because of the presence in some specimens of stylet supports. Their absence in 23 specimens is assumed to be due to poor preservation of many of the specimens, that is, they have faded rather badly and many have been squashed in preparation. All 37 specimens have been placed in the above taxon because all have a buccal tube which is 50% of the length of the buccopharyngeal tube, all have cuticular bars only on the second and third pair of legs and the size of claws is the same. All the specimens come from the same geographical area. It may well be that this is the same species as described by Manicardi & Bertolani (1987) with spiral thickening only on the lower half of the buccopharyngeal tube and cuticular bars only on the second and third pair of legs although they made no mention of stylet supports. The latter are, however, hard to see and, as mentioned above, cannot be seen at all in poor preparations.

Distribution. Limited to the Blue Mountains region (including Mount Wilson).

Itaquiscon unguiculum Pilato *et al.*, 2002: 87-89, Figs. 2, 3, 6B

Type locality. Douglas Park, NSW.

Material examined. **Australia:** NEW SOUTH WALES: *N3.1.a*, weft moss on tree open sclerophyll forest, 3 specimens. *N27.e*, *27.g*, *27.h*, weft moss on rock in open sclerophyll forest, 5 specimens. *N29.1.b*, leaf litter over limestone in protected valley, 1 specimen. QUEENSLAND: *Q15*, leaf litter in open sclerophyll, 1 specimen. VICTORIA: *V3*, leaf litter in *Nothofagus* forest, 1 specimen. *V5*, weft moss on rock in closed forest, 1 specimen.

Diagnosis. Cuticle smooth. Stylet supports inserted at junction of buccal and pharyngeal tubes. Stylet supports fine and S-shaped. Stylet furcae very small. Claws very short with respect to the body length. Lunules and cuticular bars absent.

Description. Colourless. Body length 195-381 μm . Cuticle smooth. Eye spots absent. Mouth antero-ventral. Buccopharyngeal tube 35.6 μm long (in 219 μm long specimen) and 2.3 μm wide (16.7% of buccal tube length). Stylet supports very fine and S-shaped (39-41% of length of buccopharyngeal tube) inserted at the junction of the buccal and pharyngeal tubes. Stylet furcae very small with branches not thickened. Rigid buccal tube longer than apophyses for insertion of stylet muscles, apophyses flat ridges symmetrical with respect to frontal plane; pharyngeal tube with spiral thickening. Pharyngeal bulb (17 μm long by 11 μm wide) without apophyses or placoids. Claws very short with respect to body length. Internal claws slender, 59-63% of the length of external claws on first three pairs of legs, 59-61% on fourth pair. External claws short slender with long fine secondary branch and short primary branch with fine accessory points. Secondary branch of external claws 72-76% of length of primary branch. Anterior claw of fourth pair of legs 5.8 μm or

42% of length of buccal tube, posterior claw of fourth pair 9.8 μm or 71%. Lunules and cuticular bars absent.

Eggs not found.

Etymology: *unguis* L. claw, stressing the small size of the claws.

Remarks. This species differs from other species in the genus from Australia by having the buccal tube 39% of the bucco-pharyngeal tube length and by having very short claws.

Distribution. A rare species from the east coast of Australia.

Lexia gen. n.

Type species. *Lexia melbaensis* sp. n.

Etymology. The genus is named after Lexie Nicholls who first collected the species.

Diagnosis. Peribuccal lamellae and papulae absent. Buccopharyngeal tube divided into a rigid anterior buccal tube and a flexible posterior pharyngeal tube. Stylet supports present, with buttressed attachment to sides of buccal tube. Stylets lacking furcae. Pharynx lacking apophyses and placoids. Diploclaws of each leg different in shape and size, asymmetrical with respect to median plane of leg. Primary branch of external claw inserted flexibly on secondary branch at distance from base. Eggs smooth and laid in exuvium.

Key to species of *Lexia*

1. Claws short, external claw with secondary branch as long as primary branch *L. breviunguis*
Claws long, external claw with secondary branch shorter than primary branch..... 2
2. Base of external claw with blunt “heel” and “toe” *L. melbaensis*
Base of external claw with “heel” and “toe” and additional “toe” between *L. trihallicis*

Lexia breviunguis sp. n.

Fig. 91, Plate XVIIIa and b

Material examined. **Australia.** VICTORIA: *V1*, leaf litter on soil under *Mallee* scrub, 8 specimens.
WESTERN AUSTRALIA. *W1*, leaf litter on soil under lilac tree in garden, 14 specimens, 3 exuvia containing 14, 24, 32 eggs. *W4*, moss on pine tree in park, 4 specimens.

Diagnosis. Cuticle rough. Buccopharyngeal tube about 5-6% of body length. Secondary branch of external claw same length as primary branch.

Description. Colourless. Body length 280-676 μm . Cuticle rough. Eye spots absent. Mouth antero-ventral. Buccopharyngeal tube 24.3 μm in 440 μm long specimen, buccal tube 17.8 μm long and 1.9 μm wide. Stylet supports inserted at 17.8 μm (73.3% of buccopharyngeal tube length). Pharyngeal bulb oval (19 μm long and 22 μm wide) lacking apophyses and placoids. Claws short and slender increasing in size from first to fourth. Internal claws with short secondary branch with refractive areas in basal part which has

straight sides on first three pairs but flared on fourth. Secondary branch about same length as primary which has close but prominent accessory claws. External claws with very robust thick secondary branch with refractive areas in basal part which has a foot with blunt ended “heel” and “toe”. Secondary branch about same length as primary branch. Primary branch thick with accessory claws short and close. Anterior claw on fourth pair of legs 9.2 μm long, posterior claw 16.2 μm . Lunules and cuticular bars absent.

Eggs colourless, round and smooth, diameter 62-68 μm , up to 32 deposited in exuvium.

Etymology: *brevi* L. short, *unguis* L. m. claw

Remarks. Differs from the other two species in the genus by having very short primary branches on all claws.

Distribution. The species was found in two areas subject to high temperatures and low rainfall.

***Lexia melbaensis* sp. n.**

Fig. 92, Plate XVIIIc and d

Material examined. Australia: NEW SOUTH WALES. *N4*, liverwort on tree in *Nothofagus* forest, 3 specimens. *N14*, leaf litter on soil in rainforest remnant, 1 specimen. *N36*, turf moss on rock in open sclerophyll, 1 specimen. VICTORIA. *V2*, fruticose lichen on rock in subalpine heath, 1 specimen. *V3*, liverworts, lichens and mosses on branches on ground and on trees also leaf litter in *Nothofagus* rainforest, 26 specimens, 8 exuvia containing 6, 6, 9, 10, 11, 20, 25 and 27 eggs.

Diagnosis. Cuticle smooth. Bucco-pharyngeal tube about 7-10.5% of body length.

Secondary branch of external claws about two thirds length of primary branch.

Description. Colourless. Body length 144-567 μm . Cuticle smooth. Eye spots absent.

Mouth antero-ventral. Buccopharyngeal tube 31.9 μm in 308 μm long specimen, buccal tube 21.6 μm long and 1.9 μm wide (8.8% of buccal tube length). Stylet supports long and extending up the side of the buccal tube wall like a buttress, inserted at 21.6 μm (67.7% of buccopharyngeal tube length). Pharyngeal bulb small round (about 16 μm diameter) lacking apophyses and placoids. Claws slender, increasing in size from first to fourth. Internal claws about half length of external, with short secondary branch same length as primary branch; base straight sided without “foot”. External claws with slender but strongly hooked secondary branch and long basal part terminating in a pointed “heel” and “toe”. Secondary branch about two thirds length of primary branch. Primary branch long and slender with short close accessory claws which rise clear of primary branch only at tip. Anterior claw on fourth pair of legs 9.7 μm long, posterior claw 17.3 μm . Lunules and cuticular bars absent.

Eggs colourless, round and smooth, diameter 54-65 μm , up to 27 deposited in exuvium.

Etymology. The species is named after the proposed type locality.

Remarks. Differs from *L. breviunguis* by having a longer buccopharyngeal tube relative to the body length and having claws with secondary branch shorter than the primary branch.

Distribution. The species is rather widespread but is largely restricted to localities with benign climates.

Lexia trihallicis sp. n.

Fig. 93, Plate XVIIIe and f

Material examined. Australia. WESTERN AUSTRALIA. *W1*, leaf litter on soil under lilac tree in garden, 1 specimen.

Diagnosis. Cuticle smooth. Buccopharyngeal tube 6% of body length. Secondary branch of external claw about two thirds length of primary branch, base with three blunt toe-like projections.

Description. Colourless. Body length 378 μm . Cuticle smooth. Eye spots absent. Mouth antero-ventral. Buccopharyngeal tube 23.9 μm , buccal tube 17.3 μm long and 1.9 μm wide (11% of buccal tube length). Stylet supports rather short and inserted at 17.3 μm (72.7% of buccopharyngeal tube length). Pharyngeal bulb round (15 μm diameter) lacking apophyses and placoids. Claws slender increasing in size from first to fourth. Internal claws with short secondary branch with refractive areas in basal part which has straight sides on first three pairs but flared on fourth. Secondary branch same length as primary which has close but prominent accessory claws. External claws with secondary branch with short hook and refractive areas in basal part which has a foot with blunt ended “heel” and “toe” and an additional “toe” between. Secondary branch about two thirds length of primary branch. Primary branch short and slender with accessory claws long and close except at the tips. Anterior claw on fourth pair of legs 8.1 μm long, posterior claw 21.1 μm . Lunules and cuticular bars absent.

Eggs not found.

Etymology: *tri*, three; *hallicis*, L. m. great toe.

Remarks: This species differs from the other known species in the genus by having a different base on the claws.

Distribution: only found at the one locality.

Family Macrobiotidae Thulin, 1928

Subfamily Macrobiotinae Guidetti, Rebecchi & Bertolani, 2000

Genus *Calcarobiotus* Dastych, 1993

Calcarobiotus Dastych, 1993: 175-176

Type species. *Calcarobiotus filmeri* Dastych, 1993

Diagnosis. (emended from Dastych, 1993b) Ten peribuccal lamellae present. Rigid buccal tube, ventral support present. Diploclaws on each leg similar in shape and size except on fourth pair of legs where one or both claws have primary and secondary branches joined over a considerable distance; symmetrical with respect to median plane of leg. Diploclaws with base attached to leg by fine peduncle and separated from branches by transverse septum. Eggs with processes on shell deposited freely.

Keys to species of *Calcarobiotus*

Key to adults

1. Only one of the two claws on the fourth pair of legs with
primary and secondary branches joined..... 2
Both claws of fourth pair of legs with branches 7
joined.....
2. Hooks present on bases of claws..... 3
Hooks absent on bases of claws..... 5
3. Hooks present on both sides of bases of all claws..... *C. australis*
Hooks present on only one side of claw..... 4

4. 4-5 rows of teeth in anterior of oral cavity..... *C. maculatus*
 No teeth in anterior of oral cavity..... *C. microaculeus*
5. One row of teeth and extra teeth ventrally above crests in
 posterior of oral cavity; accessory claws separated from
 primary branch over a considerable distance..... *C. erugatus*
 One row of teeth in posterior of oral cavity; accessory claws
 joined normally..... 6
6. Stylets inserted at 76-78% of buccal tube length,
 macroplacoid row short (38-41%)..... *C. capricorniensis*
 Stylets inserted at 79-81% of buccal tube length,
 macroplacoid row long (47-50%)..... *C. hesperius*
7. Cuticle with reticulate sculpture..... *C. reticulatus*
 Cuticle smooth..... *C. adunatus*

Key to eggs

1. More than 70 processes around circumference, more than 150
 in hemisphere..... *C. australis*
 Fewer than 70 processes around circumference, fewer than
 150 in hemisphere..... 2
2. Processes blunt cones..... 3
 Processes tapering cones..... 4
3. Processes 19-24 μm long and 24-27 μm base diameter, 22
 small pores around base..... *C. maculatus*
 Processes 9-14 μm long and 8-10 μm base diameter, more
 than 22 pores around base..... *C. reticulatus*

4. Process base diameter less than 9 μm , 16-18 pores with thickened vertical walls around base..... *C. microaculeus*
 Process base diameter greater than 9 μm 5
5. Six large pores around base each process, floor of each process striated..... *C. erugatus*
 Many small pores around base of each process, shell with pores with thin walls..... *C. capricorniensis*

***Calcarobiotus adunatus* sp. n.**

Fig. 94, Plate XIe, d

Material examined. Australia: NEW SOUTH WALES: *N29*, moss on soil over limestone, 19 specimens.

N48, soily moss on sandstone in open sclerophyll forest, 31 specimens.

Diagnosis. Short back legs, granulation over back and sides all legs. No teeth in anterior of oral cavity, single row teeth in posterior. Stylet supports 79-81% of buccal tube length. Basal part of all claws small and round; both claws of fourth pair of legs different from those on other three legs and similar to each other, that is, with branches joined of much of their length. Tiny teeth on lunules of fourth pair of legs.

Description. Colourless. Body length 264-507 μm . Anterior eye spots present. Cuticle smooth, fine granulation over back and sides above claws on all legs. Mouth terminal. No teeth in anterior of oral cavity, single row close to crests in posterior. Three ventral crests and 3 dorsal crests present. Buccal tube 38.7 μm long in specimen 400 μm long and 6.2 μm wide (16% of buccal tube length). Stylets inserted at 79-81% of buccal tube length and

ventral support 60%. Pharyngeal bulb round (40 μm diameter) containing large apophyses, three large granular macroplacoids and strong grape-seed-shaped microplacoid.

Macroplacoid row length 40-45% of buccal tube length; first macroplacoid same length as third (5 μm) which has a terminal bulb, second macroplacoid shortest (4.6 μm).

Microplacoid 3.5 μm . Claws on first three pairs of legs with a rather small rounded pedicelate base without hooks. Branches wide and strongly curved, deeply divided; secondary branch almost as long as primary branch. Primary branch with short low accessory claws. Internal claw similar in shape to, but slightly smaller than, external claw. Claws increasing in length from first to fourth, second and third equal in length. Both claws of fourth pair of legs different from those on other legs but similar to each other (Plate XIc, d). Branches of both claws joined over much of their length forming a single slender unit above a small rounded pedicelate base. All claws with short low accessory claws. Claws of fourth pair of legs 9.7 μm long (25% of buccal tube length). Lunules on first three pairs of legs large with thick smooth edge; on fourth pair of legs with toothed edge, posterior lunule larger than anterior.

Eggs not found.

Etymology. *Adunatus*, L. united, made one, describing the claws of the fourth pair of legs.

Remarks. The species is very similar in adult morphology to the other known species of *Calcarobiotus*. It differs from all except *C. reticulatus* in having both claws on the fourth pair of legs different from those on the other three pairs of legs. It differs from *C. reticulatus* by having smooth cuticle.

Distribution. This species was found only at a single locality.

***Calcarobiotus australis* sp. n.**

Fig. 95, Plate XIe, f

Material examined. Australia: NEW SOUTH WALES: *N8*, gumnuts and leaf litter on soil in garden bed in car park, 28 specimens, 1 egg. QUEENSLAND: *Q12*, leaf litter on limestone, 14 specimens, 1 egg; *Q15*, leaf litter in open sclerophyll and dry rainforest, 52 specimens, 7 eggs; *Q20*, leaf litter/sand, 58 specimens, 8 eggs (3 embryonate).

Diagnosis. Legs short, patch granulation above claws on first three pairs of legs, around claws on fourth pair. Strong band of teeth in anterior of oral cavity, single row close to crests in posterior. Stylet supports at 79-80% of buccal tube length. All claws with basal hooks on each side, thick accessory claws. Posterior claw only, different from those on first three pairs of legs. Lunules on fourth pair of claws toothed. Egg processes bell-shaped, shell surface with minute pores.

Description. Colourless or white. Body length 190 (embryo)-539 μm . Eye spots absent. Cuticle smooth, patch of faint granulation above claws on first three pairs of legs and extending over back and sides of fourth pair. Mouth terminal. Strong band of 5-6 rows of teeth in anterior of oral cavity, single row close to crests in posterior. Median ventral crest divided into up to 3 or 4 teeth, 3 dorsal crests. Buccal tube 45.4 μm long in specimen 375 μm long and 7.6 μm wide (15-17% of buccal tube length). Stylets inserted at 79-80% of buccal tube length and ventral support 62%. Pharyngeal bulb round to oval (40 by 37 μm) containing large apophyses, three large granular macroplacoids and strong pear-shaped microplacoid. Macroplacoid row length 38-39% of buccal tube length. First macroplacoid elongated anteriorly (5.4 μm long), second macroplacoid smallest (3.8 μm) and third macroplacoid longest (5.7 μm) with a slight caudal knob. Microplacoid large (3.8 μm). Claws on first three pairs of legs with long wide pedicelate base with a hook on either side (Plate XIe). Branches wide and strongly curved, joined by a triangular area above the base.

Primary branch with short high accessory claws. Internal claw similar in shape but slightly smaller than external claw on first three pairs of legs. Anterior claw 12.4 μm (27.3% of buccal tube length) and similar in shape and structure to those of first three pairs of legs. Posterior claws of fourth pair of legs different (Plate XI f). Posterior claw with wide base with lateral hooks but with primary and secondary branches joined for about half length of primary branch, 13 μm , long (28.6%). Accessory claws short and rise well above primary branch. Lunules on first three pairs of legs small round with thick smooth edge, on fourth pair of legs with toothed edge.

Eggs colourless, round, diameter without processes 75 μm , with processes 92 μm . About 75 processes around circumference and 160 in hemisphere. Processes are bell-shaped with rings of indistinct pores with thickened walls apparent along outline and on top of process; height 6 μm , base diameter 3.5-5 μm and 1.6-2.2 μm apart. Egg shell surface covered with tiny pores (0.3-0.5 μm) with thick walls.

Etymology. Named for Australia.

Remarks. The species is very similar in adult morphology to the other three known *Calcarobiotus* species and the eggs are the main source of differentiation of these species. It is most similar to *C. imperialis* Abe & Takeda 2000, although the Australian species has a longer buccal tube (for animals with the same body length) and the inner and outer claws of the first three pairs of legs are somewhat closer in size than in *C. imperialis*. The eggs differ by having processes twice the height of those of *C. imperialis* and the tops of the processes are not smooth as they are in the latter species.

Distribution. This species is quite widespread on the east coast of Australia and has a distinct preference for soil or soil associated substrates. Abe & Takeda (2000b) also noted this preference for all other species in this genus including an unidentified species from Central Japan.

Calcarobiotus capricorniensis sp. n.

Fig. 96, Plate Xe

Material examined. Australia: NEW SOUTH WALES: *N46.2*, moss on rock in subalpine heath, 4 eggs (1 embryonate). QUEENSLAND: *Q1*, moss on tree root in vine thicket, 19 specimens, 3 eggs (1 embryonate). *Q12*, moss on bark on soil, liverwort on limestone in an area protected by a rock outcrop, 4 specimens, 5 eggs (2 embryonate). *Q15*, leaf litter in dry rainforest, 18 specimens, 1 embryonate egg. *Q20*, leaf litter on soil on sand island, 11 specimens, 14 eggs (2 embryonate).

Diagnosis. Short legs, patch granulation on sides first three pairs legs back and sides of fourth pair. Strong band teeth in anterior of oral cavity, single row in posterior. Stylet supports inserted at 76-78% of buccal tube length. Claws with small rounded base and thin accessory claws. Posterior claw only, different from those on first three pairs of legs. Lunules on fourth pair of legs toothed. Egg processes cones with pointed tips. Shell surface with closely spaced minute pores.

Description. Colourless. Body length 185 (embryo)-547 μm . Eye spots absent. Cuticle smooth, patch of fine granulation above claws on first three pairs of legs and extending over back and sides of fourth pair. Mouth terminal. Strong band of teeth in anterior of oral cavity, single row close to crests in posterior. Three ventral crests, median ventral crest usually divided into 2 teeth; 3 dorsal crests present. Buccal tube 42.7 μm long in specimen 367 μm long and 6.8 μm wide (16-17% of buccal tube length). Stylets inserted at 76-78%

of buccal tube length and ventral support 60%. Pharyngeal bulb round (45 μm diameter) containing large apophyses, three large granular macroplacoids and strong pear-shaped microplacoid. Macroplacoid row length 38-41% of buccal tube length; first macroplacoid elongated anteriorly (5.2 μm long), second macroplacoid smallest (4.3 μm) and third macroplacoid longest (5.2 μm) with a slight caudal knob. Microplacoid large (4.6 μm long). Claws on first three pairs of legs with rather small rounded base without hooks, branches wide strongly curved and deeply divided. Claws increasing in length from first to fourth. Primary branch with short low accessory claws. Internal claw similar in shape but slightly smaller than external claw. Anterior claw of fourth pair of legs same as those on first three pairs, 10.9 μm long (25.5% of buccal tube length), Posterior claws of fourth pair of legs different. Posterior claw with primary and secondary branches joined for about half length of primary branch, 11.4 μm (26.6%). Accessory claws short and close to primary branch on all claws. Lunules on first three pairs of legs small round with thick smooth edge, on fourth pair of legs with toothed edge. Posterior lunule larger than anterior.

Eggs colourless, round, diameter without processes 54 μm , with processes 78 μm . About 14 processes around circumference and 32 in hemisphere. Processes (Plate Xe) are cones with attenuated tops covered with clear pores, bases ringed with vertical marks; height 16 μm , base diameter 10-11 μm and 1.5-2 μm apart. Egg shell surface covered with pores with thin walls.

Etymology. Named for the Capricorn Coast area of Queensland where it was found in abundance.

Remarks. The species is very similar in adult morphology to the other known *Calcarobiotus* species and the eggs are the main source of differentiation of these species.

It is most similar to *C. maculatus* sp. n., although that species has a wider buccal tube and shorter claws with a single small spine at the base of each claw. The eggs differ by having processes with attenuated ends whilst those of *C. maculatus* are blunt.

Distribution. This species is quite widespread along the east coast of Australia north of 27° longitude and has a preference for soil or soil associated substrates.

***Calcarobiotus erugatus* sp. n.**

Fig. 97

Material examined. Australia: NEW SOUTH WALES: *N38*, moss on soil and rock in open sclerophyll forest, 71 specimens, 16 eggs (1 embryonate). *N41*, moss and foliose lichen on rock at top monolith, 5 specimens, 1 egg. *N46.1*, moss on rock in dry sclerophyll, 1 specimen, 1 egg.

Diagnosis. Large animal with short back legs, no granulation around claws. Band of teeth in anterior of oral cavity, single row of long sharp teeth with few additional teeth above lateral crests in posterior. Stylet supports inserted at 75-77% of buccal tube length. Claws on all pairs of legs with accessory claw separated over long distance. Posterior claw only, different from other claws. Lunules on fourth pair of legs with thick jagged edge. Egg processes short areolated cones with 6 large pores around base, shell striated.

Description. Colourless. Body wide with short back legs, 190 µm (embryo) to 538 µm long. Eye spots present. Cuticle completely smooth with no granulation around claws. Mouth terminal. Band of four to five rows of small dot-like teeth in anterior of oral cavity, single row of sharp teeth above crests with a few additional teeth between row and lateral crests in posterior. Three ventral and three dorsal crests. Buccal tube 38.9 µm long in 408

µm specimen, with very thick wall, 6.2 µm wide (16% of buccal tube length). Stylets inserted at 75-77% of buccal tube length and ventral support 60-62%. Pharynx round (38 µm diameter) with large apophyses, three macroplacoids and a very large microplacoid. Macroplacoid row length 41% of buccal tube length. Macroplacoids rounded, first and third equal in length, 5 µm, second 4.3 µm. Microplacoid strong tear-drop shaped, 3.8 µm long. Claws on first three pairs of legs different from those on fourth pair, increasing in length from first to fourth. Both internal and external claws on first three pairs robust with very wide branches, secondary branch almost as long as primary; two branches joined by large triangular area, large oval base with pedicle below. Accessory claws short thick at base and separated from primary branch at the distal end for a considerable distance. Long prominent cuticular bar below both claws on first three pairs of legs. Anterior claw of fourth pair of legs similar to those of first three pairs of legs, 9.7 µm long (25% of buccal tube length) Posterior claw different, with two branches joined about two thirds of length of primary branch, both branches more slender than those on first three pairs of legs; same length as anterior claw. Accessory claw normally attached to primary branch over most of its length, fine short and close to main branch. Lunules small oval with thick smooth edges on first three pairs of legs. On fourth pair of legs lunules thick with jagged edge.

Eggs colourless, round, diameter without processes 67 µm, with processes 82 µm. 12-14 processes in optical section, 32 in hemisphere. Processes short areolated cones with pointed apices, 11-16 µm high, base diameter 11-13.5 µm, about 2 µm between processes. Six large pores around base of each process, floor of pores with random striations, struts between each process areolated.

Etymology. *Erugatus*, L. smooth, referring to the completely smooth cuticle.

Remarks. Differs from other species in the genus with no hooks on the claws by having a completely smooth cuticle.

Distribution. The species was found only at the type locality and a nearby locality.

Calcarobiotus hesperius sp. n.

Fig. 98

Material examined. Australia: WESTERN AUSTRALIA: *W1*, moss on path, 5 specimens. *W2*, moss on wall in open forest, 8 specimens.

Diagnosis. Large animal with smooth cuticle, very fine granulation around claws. Band of teeth in anterior of oral cavity, single row of long sharp teeth above crests in posterior. Stylet supports inserted at 79.5-81%. Claws on all pairs of legs with accessory claw joined normally to primary branch over most of its length. Posterior claw only different from other claws. Lunules on fourth pair of legs large with strong teeth.

Description. Colourless. Body length up to 587 μm . Eye spots present. Cuticle smooth except for patch faint granulation above external claw on first three pairs of legs and around claws on fourth pair. Mouth terminal. Band of four to five rows of small dot-like teeth in anterior of oral cavity, single row of sharp teeth just above crests in posterior. Two strong lateral crests and a median crest broken into 2-3 teeth ventrally and three dorsal crests. Buccal tube 44.9 μm long in 445 μm specimen, with thick wall, 8.7 μm wide (19.3% of buccal tube length). Stylets inserted at 79.5-81% of buccal tube length and ventral support 60-62%. Pharynx round (42 μm diameter) with large apophyses, three macroplacoids and a very large microplacoid. Macroplacoid row length 46-49% of buccal

tube length. Macroplacoids rounded, first and third equal in length (6 μm), second a little longer (6.5 μm). Microplacoid strong tear-drop shaped, 4.6 μm long. Claws on first three pairs of legs different from the posterior claw on fourth pair, increasing in length from first to fourth, second and third equal in length. External claw a little longer than internal. Both internal and external claws on first three pairs robust with very wide branches, secondary branch almost as long as primary; two branches joined by large triangular area, large oval base with pedicle below. Accessory claws short thick at base but with rather fine tip. Long prominent cuticular bar below both claws on first three pairs of legs. Anterior claw of fourth pair of legs similar to those of first three pairs of legs, 12.4 μm long (28% of buccal tube length). Posterior claw different, with two branches joined about two thirds of length of primary branch, both branches more slender than those on first three pairs of legs; 13 μm long (29%). Accessory claw normally attached to primary branch over most of its length, fine short and close to main branch. Lunules large oval with thick smooth edges on first three pairs of claws, thick with clear teeth around edge on fourth pair. Posterior lunule much larger than anterior.

No eggs found.

Etymology. *Hesperius*, L. western as the species was only found in Western Australia.

Remarks. Differs from other species of the genus with no hooks on the claws by having long claws and large thick, toothed lunules on the fourth pair of legs.

Distribution. There has been insufficient collecting of tardigrades in Western Australia to comment yet about the distribution of species found there.

Calcarobiotus maculatus sp. n.

Fig. 99, Plate Xf

Material examined. **Australia:** NEW SOUTH WALES: *N*8, leaf litter and gumnuts on soil in garden bed of carpark, 42 specimens, 13 eggs (8 embryonate). QUEENSLAND: *Q*7, liverwort/moss on rock in open sclerophyll, 2 specimens, 2 eggs. *Q*12, leaf litter over limestone rock in open woodland, 3 specimens. *Q*18, moss, leaf litter and pine cone on soil in rainforest remnant, 20 specimens, 3 embryonate eggs.

Diagnosis. Small back legs, patch granulation around claws of first three pairs of legs, around claws on fourth pair. Showy band of teeth in anterior of oral cavity, single row of long sharp teeth above crests in posterior. Stylet supports inserted at 76.5-78% of buccal tube length. Small spur on outside of base of external claw and inside of base of internal claw on all legs, short rather thick accessory claw. Posterior claw only, different from those on first three pairs of legs. Lunules on fourth pair of claws with thick jagged edge. Egg processes large areolated blunt cones with small pores surrounding base.

Description. Colourless. Body wide with short back legs. Body length 230 µm (embryo) to 740 µm. Eye spots absent. Cuticle smooth except for small patch of fine granulation on outside of leg near claws on first three pairs of legs, granulation extensive over back and sides and below claws on fourth pair of legs. Mouth terminal. Band of about five rows of teeth in anterior of oral cavity, single row of long sharp teeth above crests in posterior. Two strong ventro-lateral crests, median ventral crest two to four teeth; three dorsal crests. Buccal tube 49.7 µm long in 500 µm specimen, with very thick wall, 11.6 µm wide (23% of buccal tube length); stylets inserted at 78-81% of buccal tube length and ventral support 64-67%. Parynx oval (58 µm by 55 µm) with small apophyses, three macroplacoids and a very large microplacoid (Plate Xf). Macroplacoid row length 38-44% of buccal tube length.

Macropylacoids rounded, one and two about equal in length (6.5, 5.7 μm), third longer with caudal bulb (6.8 μm). Microplacoid very strong tear-drop shaped, 5.4 μm long. Claws on first three pairs of legs different from those on fourth pair, increasing in length from first to fourth, second and third equal in length. Internal and external laws on first three pairs robust with very wide branches, secondary branch almost as long as primary; two branches joined by large triangular area, large oval base with pedicle below. Accessory claws short but prominent, joined to primary branch over most of its length. Long prominent cuticular bar below both claws on first three pairs of legs. Anterior claw of fourth pair of legs similar to those on first three pairs of legs. Anterior claws of fourth pair of legs 13.5 μm long (27% of buccal tube length). Posterior claw different, with two branches joined about two thirds of length of primary branch, both branches more slender than those on first three pairs of legs, same length as anterior claw. Accessory claws normally attached to primary branch over most of its length, fine short and close to main branch. Lunules large oval with thick smooth edges on first three pairs of legs. On fourth pair of legs lunules thick with jagged edge, anterior lunule larger than posterior.

Eggs colourless, round, diameter without processes 100-108 μm , with processes 128-138 μm . 11-13 processes in optical section, 28-32 in hemisphere. Processes large cones with blunt apices areolated, 19-24 μm high, base diameter 24-27 μm . Each process with about 22 small pores around base which they share with adjacent processes.

Etymology. *Maculatus*, L. spot, for the extensive dotting around the back legs.

Remarks. The species is carnivorous, one specimen was found with rotifer trophi in the stomach. Two other species of *Calcarobiotus*, *C. gildae* and *C. microaculeus*, have a single hook on the outside of each claw. *M. maculatus* differs from both these species by having

4-5 rows of teeth in the anterior position of the oral cavity and from *M. microaculeus* by having jagged but not toothed lunules on the fourth pair of claws.

Distribution. In Australia, the species was found in a variety of habitats from dry to moist but appeared to favour leaf litter. It is quite widespread down the east coast.

Calcarobiotus microaculeus sp. n.

Fig. 100

Material examined. Australia: NEW SOUTH WALES: N3.2, moss/lichen on rock in subalpine heath, 1 egg. QUEENSLAND: Q7, moss and liverwort on sandstone by roadside, 2 specimens, 5 eggs (2 embryonate).

Diagnosis. Slender body with small legs. No teeth in anterior of oral cavity, single row teeth close to crests in posterior. Stylet supports inserted at 76-77% of buccal tube length. Claws with one small spur on outside of base of external claw and on inside of base on internal claw of all legs, thin accessory claw raised at tip. Posterior claw only, different from those on first three pairs of legs. Lunules of fourth pair of claws toothed. Processes of egg cones with long tapering distal ends with single row of “bubbles”, shell surface with pores with thick walls

Description. Colourless or white. Body length 290, 295 μm . Eye spots absent. Cuticle smooth, patch of faint granulation extending over back and sides of fourth pair of legs. Mouth terminal. No teeth in anterior of oral cavity, a single row of teeth close to crests in posterior. Median ventral crest 2 teeth or short bar, 2 ventro-lateral crests present, 3 dorsal crests. Buccal tube 34.6 μm long in specimen 295 μm long and 6.7 μm wide (19% of buccal tube length). Stylets inserted at 76.5% of buccal tube length and ventral support

62.5%. Pharyngeal bulb round (34 μm diameter) containing large apophyses, three large granular macroplacoids and a strong pear-shaped microplacoid. Macroplacoid row length 40% of buccal tube length; first macroplacoid slightly elongated anteriorly (3.2 μm long), second macroplacoid smallest (2.7 μm) same length as microplacoid and third macroplacoid longest (3.8 μm) with a slight caudal knob. Claws on first three pairs of legs with long wide pedicelate base with a small spur on outside of base of external claw and inside of base of internal claw. Branches wide and strongly curved, joined by a triangular area above the base. Primary branch with short high accessory claws. Internal claw similar in shape but slightly smaller than external claw. Cuticular bar present below claws of first three pairs of legs. Claws of fourth pair of legs different. Anterior claw of fourth pair of legs 8.7 μm long (25% of buccal tube length) similar in shape and structure to those of first three pairs of legs. Posterior claw with slender base but with primary and secondary branches joined for more than half length of primary branch, 9.2 μm long (26.6%). Accessory claws short and rise well above primary branch. Lunules on first three pairs of legs small round with thick edge, on fourth pair of legs with toothed edge.

Eggs colourless, round, diameter without processes 62 μm , with processes 90 μm . About 24 processes around circumference and 64 in hemisphere. Processes are cones with a long tapering distal end with single row of distinct pores terminating in one or more hairs; height 14-16 μm , base diameter 6.5-8 μm and 1.0 μm apart. Cone surface with indistinct pores and base of each process surrounded by 16-18 pores with thickened vertical walls. Egg shell surface probably smooth but difficult to see as all eggs recovered were dirty.

Etymology. *Micro*, small; *aculeus*, L. m. spur, for the small spur on each claw.

Remarks. The species is similar in adult morphology to *Calcarobiotus gildae* (Maucci & Durante Pasa, 1980), both having a very wide buccal tube and similar armature in the oral cavity. The processes of the eggs of these two species are of similar size and shape. The two species differ in the placement of the stylet supports (75% of buccal tube length in *C. microaculeus* sp. n. and 80% in *C. gildae*). The claws of *C. gildae* are much longer and more slender than those of the new species and it has no eye spots which are present in *C. gildae*.

Distribution. This species was found only at the type locality. The single egg found at New England National Park has also been attributed to this species but without specimens its identity remains somewhat questionable.

Calcarobiotus reticulatus sp. n.

Fig. 101, Plate XIa, b

Material examined. Australia: QUEENSLAND: *Q12*, leaf litter over limestone rock in open woodland, 5 specimens. *Q15*, leaf litter in open sclerophyll forest and in dry rainforest, 70 specimens, 47 eggs (10 embryonate).

Diagnosis. Large animal with fine polygonal sculpture over the whole cuticle, granulation around claws on all legs. Row fine teeth in anterior of oral cavity, strong row teeth with additional rows ventrally above two strong ventro-lateral crests in posterior. Stylet supports inserted at 78-80% of buccal tube length. Claws on first three pairs of legs with accessory claw separate from primary branch over almost the whole length of claw, accessory claws attached normally on fourth pair of legs. Both claws on fourth pair of legs different from those on first three pairs of legs. Lunules on claws of fourth pair of legs with

jagged edge. Egg processes blunt areolated cones, shell surface with small pores with unevenly thickened walls.

Description. Colourless. Body wide with short back legs, length 190 μm (embryo) to 600 μm . Eye spots absent. Cuticle with uniformly sized (0.5-0.8 μm) polygonal granules over the whole body surface including legs. Patch of fine granulation above claws on first three pairs of legs, granulation extensive over back and sides and below claws on fourth pair of legs. Mouth terminal. Row of fine teeth in anterior of oral cavity, single row of teeth with additional rows ventrally above two strong ventro-lateral crests in posterior. Median ventral crest may be one or two small teeth much lower in position than ventro-lateral crests; three dorsal crests. Buccal tube 51.4 μm long in 490 μm specimen with very thick wall, 8.1 μm wide (15.8% of buccal tube length); stylets inserted at 78-80% of buccal tube length and ventral support 52-59%. Pharynx round (55 μm diameter) with large apophyses, three macroplacoids and a very large microplacoid. Macroplacoid row length 34-44% of buccal tube length. macroplacoids rounded almost equal in length (6.5 μm , 6 μm , 7 μm), third macroplacoid with small caudal bulb; microplacoid very strong tear-drop shaped, about same length as second macroplacoid. Claws large robust, increasing in length from first to fourth, second and third equal in length. Internal and external claws on first three pairs robust with very wide branches, secondary branch almost as long as primary; two branches joined by large triangular area, large oval base with pedicle below (Plate XIa). Accessory claws short but prominent, joined only at base of primary branch. Long prominent cuticular bar below both claws on first three pairs of legs. Anterior and posterior claws of fourth pair of legs similar in shape and size, 15 μm long (28-30% of buccal tube length). Both claws different from those on the other three pairs of legs, with two branches joined about two thirds of length of primary branch, both branches more slender than those on first three pairs of legs (Plate XIb). Accessory claws normally attached to primary

branches of fourth pair of claws over most of their length, fine short and close to main branch. Lunules large oval with thick edges smooth on first three pairs of legs, on fourth pair of legs thick with jagged edge. Posterior lunule larger than anterior.

Eggs colourless, round, diameter without processes 97-101 μm , with processes 114-124 μm . 22-26 processes in optical section, 96-105 in hemisphere. Processes blunt areolated cones, 9-14 μm high, base diameter 8-10 μm , diameter at top 5-6 μm and 2-3 μm apart. Flat top of processes often with tuft of hairs of various lengths. Shell surface with small (0.5 μm) pores with thick uneven walls Shell surface looks very similar to the surface of the processes.

Etymology. *Reticulatus*, L. netlike, referring to the cuticular sculpture.

Remarks. This species is very similar to *Macrobotus polygonatus* Binda & Guiglielmino, 1991 from Africa, however that species has sculpture only on the dorsum, has 3-4 rows of teeth in the posterior position in the oral cavity and well developed accessory claws on the fourth claws. *M. polygonatus* was described from only five specimens and no eggs were reported. The Australian species is also very similar to *M. eugranulatus* Maucci, 1990 but that species has smooth legs and ventral surface, a very wide buccal tube (20.9%) and a single row of teeth in the posterior position of the oral cavity. This species was also described from five specimens and no eggs were found. The Australian species is carnivorous, one specimen was found with a nematode in its mouth.

Distribution. In Australia, the species was only found in leaf litter and in none of the moss and lichen samples collected from rock and trees at both sites. *M. polygonatus* was found in moss and lichen on trees and *M. eugranulatus* was found in moss on rocks.

Genus *Haptobiotus* gen. n.

Type species. *Haptobiotus turritus* sp. n.

Etymology. *Hapto*, Gr, join (emphasising the showy vertical suture joining the claw branches); *bios*, Gr, life

Diagnosis. Ten peribuccal lamellae present. Buccal tube rigid, ventral support present. Diploclaws on all legs similar in shape and size, symmetrical with respect to median plane of leg. Diploclaws with small basal piece shaped like an inverted triangle, connected to lunule by short peduncle. Primary and secondary branches joined over much of their length with conspicuous vertical suture, base of each branch swollen into bulbous refractive unit. Short upper parts of branches diverging by small angle (about 80°).

***Haptobiotus turritus* sp. n.**

Fig. 102, Plate XIIa-d

Material examined. **Australia:** TASMANIA: T8, moss/liverwort/lichen on skeletal soil hump in close forest, 37 specimens, 24 eggs (4 embryonate).

Diagnosis. Colourless, cuticle smooth no pores. Band of teeth around base of lamellae band of teeth in posterior position in oral cavity. Pharynx with two macroplacoids and a microplacoid. Claws short and robust, with prominent accessory claw on all legs. Fine granulation around all claws; lunules on all claws smooth round.

Description. Colourless. Body length 250 (embryo) - 822 μm . Eye spots present. Cuticle smooth except for small patch of fine granulation above claws on first three pairs of legs and back and sides on fourth pair of legs. Cuticle without pores. Anterior mouth. Long strongly reinforced oral cavity. Band of teeth on lower half of buccal lamellae, band of strong teeth present in posterior position in oral cavity. Three ventral and 3 dorsal crests present. Buccal tube 49.7 μm long (in 460 μm individual) and 7.3 μm wide (14.7% of buccal tube length). Stylet supports inserted at 81.5% of length of buccal tube. Ventral support long (63%). Pharynx oval (51 μm long by 59 μm wide) with large square apophyses, two macroplacoids and a microplacoid. Macroplacoid rounded rods, first with strong medial constriction (13 μm long), second about two thirds of length of first (8.7 μm). Macroplacoid row length 47% of buccal tube length. Microplacoid short (3.2 μm). Claws short and robust, increasing in length from first to fourth, all claws with small basal unit (Plate XIIa-c). Primary and secondary branches of all claws joined over much of their length by conspicuous vertical suture base of each branch swollen and highly refractive, particularly on fourth pair of legs. Upper parts of primary and secondary branches rather short but strongly curved. Accessory claws short and very thick and high above primary branch particularly on fourth pair of claws. Fourth pair of claws 11.4 μm (22.8%). Lunules round smooth on all claws.

Eggs white, round, laid free. Egg diameter with processes 158 μm , without 135 μm ; 30-36 processes around circumference, 200-250 in a hemisphere. Processes (Plate XIIId) like towers with rather straight sides surmounted by a ring of 6 blunt arms with convex centre. Processes 9-11 μm high, 6-7 μm base diameter, terminal disk 4.3-7 μm diameter, about 4-5 μm apart. Shell surface with pores (0.5 μm) irregularly distributed over surface in an irregularly thickened matrix.

Etymology. *Turritus*, L. with towers, castellated, referring to the egg processes.

Remarks.

Distribution. Found only at the type locality.

Genus *Macrobiotus* Schultze, 1834

Macrobiotus Schultze, 1834:

Type species. *Macrobiotus hufelandi* Schultze, 1834.

Diagnosis. Ten peribuccal lamellae present. Rigid buccal tube, ventral support present.

Diploclaws on each leg similar in shape and size, symmetrical with respect to median plane of leg. Diploclaws with small basal piece shaped like an inverted triangle and attached to leg by small peduncle, base separated from claw by a transverse septum. Eggs with processes on shell deposited freely.

Keys to species of *Macrobiotus*

Key to adults

- | | | |
|----|---|----|
| 1. | Two macroplacoids in pharynx..... | 2 |
| | Three macroplacoids in pharynx..... | 22 |
| 2. | Mouth antero-ventral..... | 3 |
| | Mouth terminal..... | 7 |
| 3. | Single row of teeth in posterior position of oral cavity, stylets | |

inserted at 71% of buccal tube length.....	<i>M. hibiscus</i>
No teeth in oral cavity.....	4
4. Lunules on fourth pair of claws smooth, stylets inserted at 77%, claws short.....	<i>M. albus</i>
Lunules on fourth pair of claws with teeth.....	5
5. Teeth also on lunules of first three pairs of claws.....	<i>M. echinatus</i>
Lunules on first three pairs of claws smooth.....	6
6. Stylet supports inserted at 72% of buccal tube length, claws of fourth pair of legs 33%.....	<i>M. galorensis</i>
Stylets inserted at 75%, anterior claw on fourth pair of legs 39%, posterior 45%.....	<i>Macrobiotus</i> sp. 3
7. Lunules on fourth pair of claws smooth.....	8
Lunules on fourth pair of claws ragged or toothed.....	10
8. Long rather straight claws, fourth pair $\geq 30\%$ of buccal tube length.....	9
Claws long but well curved, fourth pair 28%.....	<i>M. torridus</i>
9. Teeth in anterior of oral cavity, patch of granulation on first three pairs of legs.....	<i>M. santoroi</i>
No teeth in anterior of oral cavity, granulation over back and sides of first three pairs of legs.....	<i>M. microcalix</i>
10. Lunules on fourth pair of claws ragged with no true teeth.....	<i>M. caniensis</i>
Teeth on lunules of fourth pair of claws.....	11
11. No teeth in oral cavity, stylet supports inserted at 73-74% of buccal tube length.....	<i>Macrobiotus</i> sp. 2
Teeth in oral cavity, stylets inserted at $>75\%$	12
12. Claws short relative to buccal tube length, 22-23%.....	13

Claws longer relative to buccal tube length >27%.....	14
13. No teeth in anterior of oral cavity.....	<i>M. clivus</i>
Fine band of teeth in anterior of oral cavity.....	<i>M. rigatus</i>
14. No teeth in anterior of oral cavity.....	15
Teeth in anterior of oral cavity.....	20
15. Accessory claws thick and high above primary branch.....	16
Accessory claws thin and low.....	18
16. Stylet supports inserted at 81% of buccal tube length, 4 rows of teeth in posterior of oral cavity.....	<i>M. nemus</i>
Stylet supports inserted at 78-79%.....	17
17. Ventral crests with median tooth, fourth pair of claws 30% of buccal tube length.....	<i>M. persimilis</i>
Ventral crests bars, fourth pair of claws 27%.....	<i>M. hesperius</i>
18. Two rows of teeth in posterior of oral cavity, claws on fourth pair of legs 34% of buccal tube length.....	<i>M. saxatilis</i>
Band of fine teeth in posterior of oral cavity, fourth pair of claws <33%.....	19
19. Stylet supports inserted at 79-81% of buccal tube length, fourth pair of claws 27%.....	<i>M. guttus</i>
Stylet supports inserted at 78%, anterior claw of fourth pair of legs 31%, posterior 32.5%.....	<i>Macrobiotus</i> sp. 1
20. Posterior teeth in oral cavity a single row with a few ventrally, claws of fourth pair of legs 27% of buccal tube length.....	<i>M. purpureus</i>
Posterior teeth in oral cavity a band.....	21
21. Stylet supports inserted at 74-77% of buccal tube length,	

claws on fourth pair of legs 33-40%.....	<i>M. echinogenitus</i>
Stylet supports inserted at >77%, claws on fourth pair of legs >30%.....	22
22. Width of buccal tube 16-18% of buccal tube length, thin accessory claws.....	<i>M. joannae</i>
Width of buccal tube 13-14%, thick accessory claws.....	<i>M. hufelandi</i>
23. Cuticle of dorsum with reticulate pattern or with tubercles.....	24
Cuticle smooth.....	25
24. Cuticle of dorsum with reticulate pattern.....	<i>M. fuscus</i>
Cuticle of dorsum above fourth pair of legs with small tubercles.....	<i>Macrobiotus</i> sp. 4
25. No teeth in anterior of oral cavity.....	26
Teeth in anterior of oral cavity.....	27
26. Several rows of teeth in posterior of oral cavity, stylets inserted at 79-80% of buccal tube length, patch of granulation above claws on first three pairs of legs.....	<i>M. australoliviae</i>
One row teeth in posterior of oral cavity plus few ventrally, stylets inserted at 77%, strong granulation over back and sides of first three pairs of legs.....	<i>M. orcadensis</i>
27. Four rows small teeth in posterior of oral cavity, buccal tube width 20% of buccal tube length.....	<i>M. australis</i>
One row of teeth in posterior of oral cavity plus few ventrally.	28
28. Smooth lunules on fourth pair of claws.....	29
Toothed lunules on fourth pair of claws.....	33
29. Buccal tube wide, 19-20% of buccal tube length.....	30

Buccal tube narrower, 15-17%.....	32
30. Stylet supports inserted at 77% of buccal tube length.....	<i>M. saltus</i>
Stylet supports inserted at 80% or greater.....	31
31. Claws short relative to the buccal tube length (23%), no granulation around claws.....	<i>M. peteri</i>
Claws longer (27%), granulation around claws.....	<i>M. richtersi</i>
32. Very short claws 21% of buccal tube length, short macroplacoid row length (40%).....	<i>M. montanus</i>
Claws 25%, macroplacoid row 46%.....	<i>M. calcareus</i>
33. Thin short accessory claws.....	34
Thick high accessory claws.....	35
34. Slender claws, fourth pair 27.5% of buccal tube length, very weak microplacoid, often absent.....	<i>M. areolatus</i>
Robust claws, 24%; strong microplacoid.....	<i>M. woodyi</i>
35. Fourth pair of claws 21% of buccal tube length, buccal tube width 16%.....	<i>M. furciger</i>
Claws > 25%, buccal tube width >17%.....	36
36. Fourth pair of claws 25-27% of buccal tube length, single row of teeth in posterior of oral cavity.....	<i>M. hieronimi</i>
Claws >27%, single row of teeth plus some ventrally in posterior of oral cavity.....	37
37. Stylet supports inserted at 75-77% of buccal tube length.....	<i>M. harmsworthi</i>
Stylet supports inserted at 79-80%.....	<i>M. tasmanicus</i>

Key to eggs

1.	Processes <i>hufelandi</i> type, that is, in shape of upturned goblet...	2
	Processes not shaped like upturned goblet.....	15
2.	Processes small, height 4-5.5 µm, base 3-3.8 µm, dish 2-3 µm, and 2-3 µm apart.....	3
	Processes larger.....	4
3.	Process height 4 µm, 240-300 in hemisphere.....	<i>M. microcalix</i>
	Process height 5-5.5 µm, 140-180 in hemisphere.....	<i>M. hibiscus</i>
4.	Process distal dish with distinct arms.....	5
	Process distal dish without arms.....	6
5.	Processes with 4-6 spiny arms on distal dish, base diameter 9- 13 µm, 0.5-1 µm pores in shell.....	<i>M. albus</i>
	Processes with 5-6 smooth arms on distal dish, domed centre, 1.6-2 µm pores in shell with unevenly thickened walls.....	<i>M. purpureus</i>
6.	Smooth shell.....	<i>M. persimilis</i>
	Shell with pores.....	7
7.	Distinct circle of large pores on shell around each process, few others on shell.....	<i>M. clivus</i>
	Shell between processes covered with pores.....	8
8.	Distal dish very reduced, processes flask-shaped.....	9
	Distal dish larger with smooth or notched edge.....	11
9.	Distal dish 2 µm diameter, shell with small pores (0.5 µm) appears dotted.....	<i>M. guttus</i>
	Distal dish 3-3.5 µm diameter, shell with distinct pores.....	10
10.	Processes 4 µm high, 5-6 µm apart; shell with 0.5 µm pores	

with uniform walls.....	<i>M. torridus</i>
Processes 5.5 μm high, 2.5 μm apart; shell with 0.5 μm pores	
with unevenly thickened walls.....	<i>M. caniensis</i>
11. Shell with unevenly thickened walls around pores.....	12
Shell with walls of uniform thickness around pores.....	14
12. Process height 5.5-6 μm , base diameter 6 μm	<i>M. hesperius</i>
Process height >6 μm , base >6 μm	13
13. Large dish, 5.2-5.8 μm with strong teeth, processes 4 μm apart.....	<i>M. joannae</i>
Dish 4.5-5 μm with notched edge, processes 2-3 μm apart.....	<i>M. rigatus</i>
14. Pores around processes larger than those on shell.....	<i>M. hufelandi</i>
Pores around processes same size as those on shell.....	<i>M. saxatilis</i>
15. Processes thimble-shaped with ring of tiny teeth around top... Processes different.....	<i>M. santoroi</i> 16
16. Processes hemispherical, base with corona of lines..... Processes different.....	<i>M. montanus</i> 17
17. Processes long cones (12-38 μm high); shell smooth..... Processes different.....	<i>M. echinogenitus</i> 18
18. Processes cones (13.5 μm high) with blunt finger-like top with very fine short hairs..... Processes different.....	<i>M. galorensis</i> 19
19. Processes cones with pointed apices and smooth edge..... Processes different.....	20 21
20. Processes cones with smooth but wavy lower edge, shell with small striations.....	<i>M. australoliviae</i>

- Processes cones with smooth straight edge, shell with long
wiggly striations radiating from base each process..... *M. calcareus*
21. Processes short cones, 8 μm high, with dichotomously
branched top, base with corona of lines..... *M. furciger*
- Processes different..... 22
22. Processes long straight-sided areolated cones, 32-45 μm high,
12-14 pores around base each process..... *M. tasmanicus*
- Processes different..... 23
23. Processes 5-11 μm high, surface not areolated, pointed or
bifurcate, base surrounded by pores continuous with those on
shell surface with unevenly thickened walls..... *M. orcadensis*
- Processes different..... 24
24. Processes cones surrounded by corona of points..... 25
- Processes cones surrounded by large pores..... 28
25. Processes cones with large hemispherical base and very short
pointed tip..... 26
- Processes cones with small hemispherical base and long
pointed tips..... 27
26. Process surface strongly areolated, shell dotted..... *M. harmsworthi*
- Processes sparsely areolated, shell with small pores (0.5 μm)
with unevenly thickened walls..... *M. australis*
27. Processes narrow, 8 μm base diameter, few clear areolae in tip
otherwise sparsely areolated; shell with small indistinct pores. *M. saltus*
- Processes wide, 1-16 μm , surface uniformly areolated; shell
with tiny pores in thick matrix..... *M. woodyi*

28. Processes 20-34 μm high, pointed tip.....	29
Processes <20 μm high.....	30
29. Processes with 6-8 large pores around base, shell with fine striations.....	<i>M. hieronimi</i>
Processes with 10-12 pores around base, shell dotted.....	<i>M. nemus</i>
30. Processes 10-14 μm high, base diameter 9-12 μm , with branched tip, 6-7 pores around base.....	<i>M. peteri</i>
Processes larger with unbranched tips.....	31
31. Processes blunt cones with random areolation, 15-20 μm high	<i>M. fuscus</i>
Processes cones with areolation arranged in distinct rows around process.....	32
32. Processes with blunt tip, 10 large pores with wavy edges around base each process.....	<i>M. richtersi</i>
Processes with pointed tips, 10-11 pores with round appearance.....	<i>M. areolatus</i>

***Macrobotus albus* sp. n.**

Fig. 103, Plates Va, VIIa

Material examined. **Australia:** TASMANIA: *T7*, moss and liverwort on rock in wet forest gully, 4 specimens, 7 eggs. *T10*, moss on tree trunk in cool temperate rainforest, 28 specimens, 16 eggs (5 embryonate). NEW SOUTH WALES: *N3.6*, moss and lichen on rock in subalpine heath, 14 eggs.

Diagnosis. Antero-ventral mouth. 2 macropilacoids and a micropilacoid in pharynx. No teeth in oral cavity. Stylet supports inserted at 77% of buccal tube length. Claws short

robust, with thick high accessory claw on all legs. No granulation around claws; lunules on all claws smooth round.

Description. White. Body length 214 (embryo)-487 μm . Large eye spots present. Cuticle smooth, no granulation on legs. Cuticle with small round pores (1.2 μm) on all surfaces. Mouth antero-ventral, lamellae short. No teeth in oral cavity. Three ventral (median tooth) and 3 dorsal (median tooth) crests present. Buccal tube with very thick walls, 40.5 μm long (in 385 μm individual) and 4.3 μm wide (10.7% of buccal tube length). Stylet supports inserted at 77.4% of length of buccal tube. Ventral support long (60%). Pharynx oval (36 by 31 μm) with large apophyses, two macroplacoids and a microplacoid. Macroplacoids rounded rods, first (9.7 μm long) without medial constriction, second 5.6 μm . Macroplacoid row length 41% of buccal tube length. Microplacoid short blunt solid (2 μm). Legs long and slender. Claws short robust deeply divided, increasing in length from first to fourth, with long secondary branch (Plate VIIa). Accessory claws long fine and high above primary branch particularly on fourth pair of claws. Claws of fourth pair of legs 10.3 μm long (25.4%). Lunules small round with thick edge on all claws, small teeth on lunules of fourth pair of legs.

Eggs white, round, laid free. Egg diameter with processes 96-110 μm , without 80-85 μm ; 16-21 processes around circumference, 48-80 in a hemisphere. Processes like upturned goblets with swollen bases (Plate Va) with 4-6 thick ragged arms distally, which have blunt ends and thorny surfaces. Processes 10-11 and 12-13.5 μm high, 8-10 and 7-9 μm base diameter, distal dish with arms 9-10 and 9-13 μm diameter, about 5 and 4 μm apart. Shell surface with pores (0.5 and 0.8-1 μm) uniformly distributed over surface 4-5 rows between processes.

Etymology. *Albus*, L. white for the colour of the animal.

Remarks. The short lamellae, antero-ventral mouth and very narrow buccal tube suggest that the species is herbivorous rather than a carnivorous. These characters also differentiate this species rather clearly from all other *Macrobiotus* species with two macroplacoids and a microplacoid.

Distribution. Found only at the one locality.

Macrobiotus areolatus Murray, 1907

Fig. 104

Macrobiotus echinogenitus var. *areolatus* Murray, 1907: 675, Pl. II, Figs. 14a-d

Type locality. Spitzbergen

Material examined. **Australia:** NEW SOUTH WALES: *N3*, mosses on sandstone rock in cool temperate rain forest, 1 specimen, 1 embryonate egg. TASMANIA: *T5*, moss on soil in sclerophyll forest, 1 specimen. *T9*, moss/liverwort on limestone riparian cliff shelf, 3 specimens, 1 embryonate egg. **Italy:** Rossena, moss on rock, 2 specimens, 1 egg. **Russia:** Daghestan, Manaskent, moss on soil, 4 specimens, 1 egg.

Diagnosis. Terminal mouth. 3 long macroplacoids, microplacoid absent or small tick in pharynx. Strong row teeth in anterior of oral cavity, one row teeth in posterior. Stylets inserted at 78-80% of buccal tube length. Patch granulation above claws on first three pairs of legs. Claws long slender with short thin accessory claws and smooth lunules on claws I-III, minutely toothed lunules on IV claws.

Description. Colourless, body length up to 610 μm , colourless. Eyespots absent. Cuticle smooth, granulation present in patch above claws I-III and around claws on IV pair of legs. Mouth terminal. Row of strong teeth in anterior of oral cavity, single row of small teeth close to crests in posterior of oral cavity. Three ventral crests and three dorsal crests. Buccal tube 31.4 μm in 278 μm long specimen and 5.7 μm wide (18.2% of buccal tube length). Stylet supports inserted at 78% (up to 80%) of buccal tube length; ventral support 57%. Pharynx round (33 μm diameter), containing large triangular apophyses and three macroplacoids. Macroplacoid row 40% of buccal tube length; first macroplacoid (3.2 μm) elongated, second macroplacoid (3 μm) round, third macroplacoid (3.8 μm) with terminal bulb. Microplacoid absent, thin cuticular thickening in its place in some specimens. Claws long and slender with short secondary branch. Accessory claws short and close to primary branch. Fourth pair of claws 8.7 μm long (27.5% of length of buccal tube). Lunules small and smooth on first three pairs of claws, minutely toothed on fourth pair.

Eggs colourless round, diameter without processes 85 μm , with processes 107 μm . Eleven processes around circumference, about 24 in hemisphere. Processes cones with blunt points; height 15-19 μm , base 17-22 μm . The surface of each process has a reticular pattern in which the mesh is oriented towards the apices of the processes. Processes close together separated only by large pores, 10-11 around each process, the shell within pores smooth.

Remarks: Adult specimens from the European countries have a much longer placoid row length (around 50%, also see Pilato, 2000). Otherwise the characters are very similar, eg, long slender claws with short close accessory claws, short secondary branch and fine granulation above the claws. The lunules on the IV claws are more strongly toothed than on the Australian animals. Processes on the egg of the Russian material short (11-14 μm)

and have smaller diameter (11-13.5 μm) as are those on the eggs from Italy (height 15 μm , base 14-16 μm).

Distribution. This species is quite tolerant of both wet and dry conditions. Considered to be a mountain (characteristic of the alpine zone) species by Dastych (1988).

Macrobiotus australis Pilato & D'Urso, 1976.

Fig. 105

Macrobiotus australis Pilato & D'Urso, 1976: 137-140, Fig. 1A, A'

Type locality. Australia, Wallacia, NSW.

Material examined. Australia: NEW SOUTH WALES: *N3.1.b*, moss on tree in open sclerophyll forest, 2 specimens; *N3.2.b*, moss on rock in sub-alpine heath, 1 specimen, 2 eggs; *N3.3.a*, foliose lichen on tree in *Nothofagus* forest, 1 specimen. *N14.2*, fruticose lichen on soil in open sclerophyll forest, 6 specimens, 1 egg. *N24*, foliose lichen on rock in open sclerophyll forest, 1 specimen, 4 eggs. *N27*, moss and lichens on rock in sclerophyll forest, 7 specimens, 7 eggs. *N28*, lichen and moss on rock in sclerophyll forest, 5 specimens, 13 eggs. TASMANIA. *T12*, foliose lichen, 2 eggs.

Diagnosis. Terminal mouth. 3 round macroplacoids and a large microplacoid in pharynx. Anterior teeth a faint band, posterior teeth a wide band of about 4 rows of minute teeth. Stylet supports inserted at 78-80% of buccal tube length. Buccal tube 20%. Patch fine granulation above claws on first three pairs of legs. Strong, long claws with large refractive base and very high accessory claws. All lunules smooth.

Description. Colourless. Body length 220-580 μm . Eye spots present in anterior position. Cuticle smooth, patch of very fine granulation on the outside of first three pairs of legs

near claws, also on back and sides of fourth pair of legs. Mouth terminal. Row of very fine teeth in anterior position in oral cavity, band of several rows of fine teeth in posterior position. Three ventral and three dorsal crests present. Buccal tube 49.7 μm long in 430 μm long specimen and 10 μm wide (20% of buccal tube length). Stylet supports inserted at 78-80% of the buccal tube length, ventral support 62.5% of buccal tube length. Pharynx shortly oval, containing small granular apophyses, three macroplacoids and a microplacoid. Macroplacoid row 48-50% of buccal tube length; first macroplacoid slightly elongated anteriorly (7.0 μm long) where it lies under the apophysis, same length as third, second macroplacoid smallest (5.4 μm), third macroplacoid with a caudal bulb which curves towards midline. Microplacoid small (3.2 μm) and drop-like. Claws robust, with short, deeply divided secondary branch. Accessory claws rise high above primary branch particularly on fourth pair of claws. Fourth pair of claws 12.4 μm long (25% of length of buccal tube). Lunules small and round on first three pairs of legs, inner larger than outer on fourth pair and with thick but smooth edge.

Eggs colourless, round, diameter without processes 69-76 μm , with processes 95-99 μm . About 12 processes around circumference, about 43 in a hemisphere. Processes with conical base tapering to a single blunt point, very faint sparse pores over surface. Process height 10-16 μm , base diameter 10-16 μm , distance between 2-3 μm . Row of pores around base of each process and shell covered with small indistinct pores (0.5 μm) with unevenly thickened edges.

Remarks. In some populations (from New England and Leura) the egg processes have an elongated tip so processes reach up to 19 μm in height (types are 10-11 μm), otherwise the animals are the same.

Distribution. This rather rare but widespread species has, so far, been found only in Australia but occurs in dry and wet environments.

Macrobotus australoliviae sp. n.

Fig. 106

Material examined. Australia: NEW SOUTH WALES: *N3.4*, moss and lichen on trees in cool temperate rainforest, 20 specimens, 11 eggs (1 embryonate). VICTORIA: *V3*, moss/lichen on tree and leaf litter on soil in cool temperate rainforest, 6 specimens, 3 eggs.

Diagnosis. Terminal mouth. 3 macroplacoids and microplacoid in pharynx. Anterior teeth in oral cavity absent, posterior teeth a thick band of tiny denticles slightly larger and more showy ventrally. Stylet supports inserted at 79% of buccal tube length. Buccal tube width 14%. Patch granulation above claws on first three pairs of legs. Claws robust, lunules smooth on all claws.

Description. Colourless. Body length 189-560 μm . Eye spots absent. Cuticle smooth except for small patch of fine granulation above claws of first three pairs of legs and back and sides of fourth pair legs. Mouth terminal. Anterior teeth absent in oral cavity, posterior teeth a thick row of tiny denticles slightly larger and more showy ventrally. Three ventral and three dorsal crests present. Buccal tube 41.6 μm long (in 408 μm individual) and 5.7 μm wide (13.6% of buccal tube length). Stylet supports inserted at 79% of length of buccal tube. Ventral support long (65%). Pharynx large and round (43 μm diameter) with large apophyses, three macroplacoids and a microplacoid. Macroplacoid rounded rods, first and second similar in length (5.4 μm), second always smallest (4.3 μm); first and second very close. Macroplacoid row length (43%). Microplacoid large (3 μm). Claws robust, deeply

divided, with long secondary branch and a large refractive zone at base, increasing in length from first to fourth. Accessory claws short and high above primary branch particularly on fourth pair of claws. Claws on fourth pair of legs 10.3 μm (25%). Lunules round small smooth on first three pairs of legs; round smooth on fourth pair. Posterior lunule a little larger than anterior on fourth pair of legs.

Eggs white, round, laid free. Egg diameter with processes 144 μm , without 72 μm ; 8-10 processes around circumference. 13 in hemisphere. Processes are large cones, elongated to a fine tapering tip, with large areolations. Processes with smooth rounded margin around bases. Processes 30-45 μm high, 22-27 μm base diameter, 5-6 μm apart. Shell surface with small striations.

Etymology. *australis* L. southern; *liviae*, after the similar species *M. liviae*.

Remarks. This species is very similar to *M. liviae* Ramazzotti, 1962 by having a band of teeth in the posterior position of the oral cavity (Binda & Pilato, 1994) and having similar macroplacoids but the most significant similarity is in the eggs. However, there are some differences which make it clear that the Australian animal belong to a different taxon. *M. liviae* has “pearls” in the cuticle, has a wide buccal tube and claws which are much longer than those of the Australian species. It differs from *M. pseudoliviae* Pilato & Binda, 1996 by having no teeth in the anterior position in the oral cavity, a narrower buccal tube and no teeth on the lunules of the fourth pair of claws.

Distribution. Found only in association with cool temperate rainforest.

***Macrobiotus calcareus* sp. n.**

Fig. 107

Material examined. Australia: NEW SOUTH WALES: *N4*, moss on tree in cool temperate rainforest, 2 specimens, 2 eggs. *N15*, moss and lichen on limestone, 6 specimens, 21 eggs (2 embryonate).

Diagnosis: Terminal mouth. 3 granular macroplacoids and microplacoid in pharynx. 3 rows small dots in anterior of oral cavity, single row long teeth with few ventrally above crests present posteriorly. Stylet supports inserted at 75% of buccal tube length. Buccal tube width 15%. Patch granulation around claws of first three pairs claws. Claws robust, with thick accessory claws. Lunules thick and smooth on all claws.

Description: Colourless. Body length 190-430 μm . Eye spots absent. Cuticle smooth, fine granulation in small patch above claws on first three pairs of legs, back and sides of fourth pair of legs. Mouth terminal, anterior teeth in oral cavity three small rows dots, posterior teeth a single row of long sharp teeth with a few small round teeth ventrally between row and crests. Three ventral (median usually two teeth) and three dorsal crests. Buccal tube 54 μm long in 430 μm long specimen and 8 μm wide (14.7% of buccal tube length. Stylet supports inserted at 75% of buccal tube length, ventral support 64%. Pharynx oval (48 μm by 44 μm) containing rather small apophyses, three macroplacoids and a microplacoid. First and third macroplacoids same size (8.5 μm), second macroplacoid smallest (6 μm). Macroplacoid row length 46% of buccal tube length. Microplacoid 4.9 μm long. Claws robust with long secondary branch. Claws increasing in length from first to fourth. Fourth pair of claws 13.5 μm long (25% of buccal tube length). Accessory claws long thick on primary branch; lunules smooth and thick on all claws.

Eggs laid free, diameter without processes 74 μm , with processes 124 μm . 9 around circumference, 21 in hemisphere. Processes large areolated cones tapering to a fine point sometimes bifurcate. Processes 35-41 μm high, 18-25 μm base diameter, about 4 μm distance between. Shell surface between processes with wave-like striations across shell from one process to next, tiny pores visible around base of each process under SEM but not with phase microscopy.

Etymology: *calcareus* Latin f. of lime

Remarks: The adults of this species are very similar to those of *M. montanus* but differ from them by having claws and macroplacoid row longer relative to the length of the buccal tube.

Distribution: Found only at one locality.

***Macrobiotus caniensis* sp. n.**

Fig. 108, Plates Vb, VIIb

Material examined. **Australia:** QUEENSLAND: Q15.3, moss and liverwort on tree in dry rainforest, 10 specimens, 7 eggs (2 embryonate).

Diagnosis. Mouth terminal. Two macroplacoids and a microplacoid in pharynx. Anterior teeth in oral cavity absent, posterior teeth a band of very fine teeth. Stylet supports inserted at 78% of buccal tube length. Claws robust, with thick high accessory claw on all legs. No granulation around claws; lunules on first three pairs of claws smooth, on fourth pair ragged.

Description. Colourless, some specimens with clumps of red pigment under cuticle. Body length 140-480 μm . Posterior eye spots present. Cuticle smooth, no granulation around claws. Cuticle with round pores (1 μm) on all surfaces. Mouth terminal. Anterior teeth in oral cavity absent, several distinct rows of teeth in posterior position. Three ventral (median a tooth) and 3 dorsal crests present. Buccal tube 42.2 μm long (in 420 μm individual) and 5.6 μm wide (13.24.9% of buccal tube length). Stylet supports inserted at 78% of length of buccal tube, ventral support 62%. Pharynx round (41 μm diameter) with large apophyses, two macroplacoids and a microplacoid. Macroplacoid rod-shaped, first with median constriction, 8.7 μm long, second with weak terminal constriction, 6 μm . Macroplacoid row 37% of buccal tube length. Microplacoid 2 μm long. Claws robust (PLate VIIb), increasing in length from first to fourth. Secondary branch short and well curved, primary branch with thick strong accessory claws. Claws on fourth pair of legs 11.2 μm (27% of buccal tube length). Lunules small round smooth on first three pairs of legs; small (posterior slightly larger than anterior) and ragged but not toothed on fourth pair of claws.

Eggs white, round, laid free. Egg diameter with processes 84 μm , without 75 μm ; 24 processes around circumference, 140 in a hemisphere. Processes like upturned goblets (Plate Vb) with long neck and strongly notched distal dish (around 12 notches), each process base surrounded by pores which are continuous with pores on shell surface. Processes 6 μm high, 5.4 μm base diameter, distal dish 3.5 μm diameter, about 2.5 μm apart. Shell surface with pores (0.5 μm) uniformly distributed over surface, 3-4 between each process.

Etymology. *Caniensis*, named for the type locality, Cania Gorge.

Remarks. This species is similar to *M. torridus* in having no granulation around the claws, having lunules with a rather thin edge, however it differs from that species by having a much shorter macroplacoid row and narrower buccal tube. The lunules of *M. caniensis* have a jagged edge while those of *M. torridus* are smooth.

Distribution. Found only at the single locality.

Macrobotus clivus sp. n.

Fig. 109, Plates Vc, VIIc

Material examined. Australia: NEW SOUTH WALES: *N44*, lichen on rock in subalpine heath, 10 specimens, 1 egg embryonate. *N46.3*, moss and lichen on rock in subalpine woodland, 13 specimens, 7 eggs (1 embryonate).

Diagnosis. Terminal mouth. Two macroplacoids and a microplacoid in pharynx. Anterior teeth in oral cavity absent, posterior teeth a band of very fine teeth, difficult to see in all but largest specimens. Stylet supports inserted at 81% of buccal tube length. Claws robust, with thick high accessory claw on all legs. Granulation around all claws, patch on first three pairs of legs. Lunules on first three pairs of claws smooth round, with tiny teeth on fourth pair.

Description. Body length 240–450 μm , colourless. Cuticle smooth except for patch of granulation on back and sides of all legs around claws. Cuticle with large elliptical pores (up to 3.5 μm) on all surfaces. Posterior eye spots present. Mouth terminal. Anterior teeth in oral cavity absent, posterior teeth a band of fine dots. Three ventral and 3 dorsal crests

present. Buccal tube 48.7 μm long (in 447 μm individual) and 7.6 μm wide (15.5% of buccal tube length). Stylet supports inserted at 81% of length of buccal tube, ventral support long (66.6%). Pharynx oval (47 μm by 43 μm) with large apophyses, two macroplacoids and a microplacoid. Macroplacoid slender rods, first with median constriction 13.5 μm long, second with caudal bulb 8.7 μm . Macroplacoid row long (50% of buccal tube length). Microplacoid strong 3.2 μm long. Claws robust (Plate VIIc), increasing in length from first to fourth. Secondary branch short but well curved, primary branch with high accessory claws. Claws on fourth pair of legs 10.3 μm (22.3%). Lunules round smooth on claws of first three pairs of legs, tiny teeth on those of fourth pair.

Eggs white, round, laid free. Egg diameter with processes 90 μm , without 80 μm ; 22-24 processes around circumference, 75-90 in hemisphere. Processes shaped like upturned goblets (Plate Vc) with large conical base and wide flat very weakly notched (about 12) distal dish, base surrounded by about 15-20 large pores. Processes 6-8 μm high, 6.5-8 μm base diameter, 4.5-7 μm dish diameter and about 3 μm apart. Shell surface with very few large pores besides those around bases of processes.

Etymology. *Clivus*, L. m., elevation, hillside.

Remarks. The eggs are similar to those of *M. macrocalix* Bertolani & Rebecchi, 1993 and *M. denticulus* Dastych, 2002 in having a distinct ring of large pores around the base of each process with few pores in the inter-process shell surface. The animals of *M. macrocalix*, however, differ from those of *M. clivus* by having anterior teeth and large posterior teeth in the oral cavity, small oval pores in the cuticle and a long narrow microplacoid. The animals of *M. denticulus* have a unique tiny tooth-like structure in the

anterior part of the buccal tube and a much lower *pt* index for the stylet support insertion point (71-76.7%) than *M. clivus* (81%).

Distribution. This species was found at only two highland sites quite close to each other.

***Macrobiotus echinatus* sp. n.**

Fig. 110, Plate IXa

Material examined. **Australia:** NEW SOUTH WALES: *N48*, moss on sandstone in open sclerophyll forest, 2 specimens.

Diagnosis. Antero-ventral mouth. Two macroplacoids and a microplacoid in pharynx. No teeth in oral cavity. Stylet supports inserted at 76% of buccal tube length. Claws slender, with thin accessory claw on all legs. No granulation around claws. Lunules on all claws large round with long fine teeth.

Description. Colourless. Body length 460 μm . Large anterior eye spots present. Cuticle smooth, no granulation around claws. Cuticle with round to elliptical pores (0.5-2 μm) on all surfaces. Mouth antero-ventral, lamellae short. No teeth in oral cavity. Three weak ventral and 3 dorsal crests present. Buccal tube 54.1 μm long (in 460 μm individual) and 7 μm wide (13% of buccal tube length). Buccal tube wall thick, internal diameter 3.2 μm . Stylet supports inserted at 76% of length of buccal tube. Ventral support long (60%). Pharynx oval (38 μm long by 45 μm wide) with large apophyses, two macroplacoids and a microplacoid. Macroplacoid rounded rods, first with faint medial constriction (11.4 μm long), second 7.3 μm . Macroplacoid row length 37% of buccal tube length. Microplacoid short but solid (2.2 μm). Claws slender with broad rounded refractive base (Plate IXa),

with long slender secondary branch, increasing in length from first to fourth. Accessory claws short and thin and close to primary branch but separated from it over a long distance. Fourth pair of claws 19.5 μm (36%). Lunules round with long fine teeth on all legs.

Eggs not found.

Etymology. *Echinatus*, L, prickly, for the conspicuous teeth on the lunules on all the claws of this species.

Remarks. This species is similar to *M. galorensis* sp. n. and *M. ariekammensis* Weglarska, 1965 but differs from them by having teeth on the lunules of all claws.

Distribution. Found only at the one locality.

***Macrobiotus echinogenitus* Richters, 1904**

Macrobiotus echinogenitus Richters, 1904: 503, Pl. 16, Figs. 16, 24

Type locality. Tannaus, Austria.

Material examined. Australia: None. Cited by Murray (1910) occurring at Katoomba, NSW at 2-3000 feet..

Diagnosis. Terminal mouth. Two macroplacoids and microplacoid in pharynx. Band teeth in anterior of oral cavity, strong band in posterior. Stylet supports inserted at 74.4-76.4% of buccal tube length. Claws long slender with thick accessory claws. Lunules of first three pairs of legs smooth, of fourth pair toothed.

Description. Colourless or pigmented brown. Body length up to 750 μm . Posterior eye spots present. Cuticle with showy pores. Oral cavity with band of teeth in anterior position and a well-developed band in posterior position. Three ventral and a single dorsal crest present. Buccal tube moderately wide (about 15% of length of buccal tube). Stylet supports inserted at 74.4-76.4% of buccal tube length. Pharynx oval with apophyses, 2 macroplacoids and a microplacoid. Macroplacoids short rods. Claws normally developed, that is, Y shaped and not V shaped (Binda, 1988) as has been erroneously stated in some publications. Accessory claws well developed. Claws of fourth pair of legs 33-40% of buccal tube length.

Eggs spherical, laid free. Diameter including processes 65-160 μm , 14-32 around circumference. Processes conical with reticulate sculpture. Processes 12-38 μm high. Shell surface smooth. Descriptions of animals and eggs from Binda (1988).

Remarks. This species has been drastically taxonomically altered (Marcus 1936). Probably misidentified in much of the literature, the redescription of Binda (1988) was not comprehensive and did not include a description of the egg and was derived from a specimen which was not from the type locality. Murray's citation of this species from Katoomba contained no indication of the number of specimens or eggs that he collected. He figured only the egg.

Distribution. Unknown at present because of taxonomic confusion.

***Macrobiotus furciger* Murray, 1906**

Fig. 111

Macrobiotus furcatus Murray, 1906: 327, Pl. 2, Fig. 6a-d, Pl. 4, Fig. 13a-c

Macrobiotus furciger Murray, 1907: 852

Type locality. South Orkneys.

Material examined. Australia: NEW SOUTH WALES: *N3.2*, 3.5, moss and lichen on rock in subalpine heath, 181 specimens, 24 eggs; *N3.3*, 3.4, moss and lichen on rock in cool temperate rainforest, 43 specimens, 6 eggs. *N14.2*, moss and lichen on tree and lichen on soil and rock in open sclerophyll forest at 1200 m. asl., 33 specimens, 1 egg; *N14.5*, lichen and leaf litter on soil in open sclerophyll forest at 1200 m. asl., 28 specimens, 2 eggs. *N28*, fruticose lichen on tree in gully, 3 specimens, 1 egg. *N29*, moss and lichen on rock, lichen on tree in dry sclerophyll forest, 10 specimens, 6 eggs. *N39*, moss and lichen on rock in warm temperate rainforest, 266 specimens, 27 eggs. *N46.2*, moss on rock in subalpine heath, 3 specimens, 5 eggs; *N46.3*, moss and lichen on rock in subalpine heath, 12 specimens, 19 eggs. QUEENSLAND: *Q18*, fruticose lichen on tree in warm temperate rainforest remnant, 23 specimens, 1 egg. VICTORIA: *V2*, fruticose lichen on rock in subalpine heath, 15 specimens, 1 egg. *V3*, moss and lichen on tree in cool temperate rainforest, 43 specimens, 3 eggs. WESTERN AUSTRALIA: *W2*, foliose lichen on tree in forest, 20 specimens, 2 eggs. **Antarctica:** King George Island, (ZIM) 2 specimens. **New Zealand:** Haas Pass, South Island, (BMD), 1 egg. **Chile:** Aguas Callientes, (ZMUC), 1 specimen, 1 egg.

Diagnosis. Terminal mouth. Three macroplacoids and a microplacoid in pharynx, short macroplacoid row length. Anterior teeth in oral cavity a few neat rows, posterior teeth a single row with a few extra teeth above crests ventrally. Stylet supports inserted at 78-79% of buccal tube length. Buccal tube width 16%. Claws short robust with very thick high accessory claws. Granulation present around claws, patch above claws on first three pairs. Lunules of fourth pair of legs with tiny teeth.

Description. Colourless. Body length 150-565 μm . Eye spots large in anterior position. Cuticle smooth, granulation in patch on sides of first three pairs of legs above claws, granulation very fine on back and sides of fourth pair of legs. Mouth terminal; anterior teeth in oral cavity a thin band, posterior teeth a single row with a few extra teeth between row and median ventral crests. Three ventral crests (median crest often divided into 2-3 teeth) and 3 dorsal crests present. Buccal tube 51.4 μm long in 420 μm long specimen and 8.4 μm wide (16.3% of buccal tube length). Stylet supports inserted at 78-79% of buccal tube length and ventral support 60%. Pharynx round (54 μm diameter), containing large apophyses, three similar sized macroplacoids and a short microplacoid. Macroplacoid row short, 42-45% of buccal tube length. First and third macroplacoids about same size (7.2 μm long), second macroplacoid slightly smaller than other two (6 μm), third with slight caudal bulb, which curves towards the midline. Microplacoid short, 3.8 μm . Claws short with short thick accessory claws on first three pairs of legs, short and very high on fourth pair. Claws increasing in length from first to fourth. Posterior claw of fourth pair of legs 11.4 μm long (22% of length of buccal tube), anterior claws 10.8 μm (21%). Lunules small and smooth on first three pairs of legs; small with fine teeth on the fourth pair of legs, posterior slightly larger than anterior.

Egg colourless, laid free, round. Diameter without processes 69-70 μm , with processes 85-88 μm . 20-24 processes around circumference, 75-95 in hemisphere. Processes with conical base with top branching dichotomously sometimes 2 or 3 times, height 8 μm , base diameter 6.5-8 μm , distance between 1.5-2 μm . Each process with ring of pores with distinct vertical walls. Shell surface with reticulum of rather indistinct pores.

Remarks. The species was very poorly described by Murray (1906) but he did confess to basing the description on very poor specimens observed only at moderately low power. He gave no details of the egg shell surface. He later, (Murray, 1910), found it in New Zealand and wrote of its presence on a number of islands in the Cape Horn region and on the Antarctic continent. Binda (1984) clarified some points about the characters of the adults and about the surface of the egg, stating that there was a fine reticulation over the surface. Binda & Rebecchi (1992) more clearly defined some characters of the adult, for example, stylet insertion length, buccal tube width, and suggested that the presence of eyes and of anterior teeth in the oral cavity were important characters of this species.

Distribution. Binda & Rebecchi (1992) concluded that this species is common and widespread in the southern hemisphere. They determined that specimens obtained in Italy were the same as those described by Argue (1972) and that they belonged to a taxon other than *M. furciger*. This is the first record of its occurrence in Australia.

Macrobiotus fuscus sp. n.

Fig. 112

Material examined. TASMANIA: *T19*, moss on sandy soil on exposed cliff top, 18 specimens, 13 eggs (2 embryonate).

Diagnosis. Terminal mouth. Cuticle with faint reticular pattern, black pigment in body cells. Three round macroplacoids and large microplacoid in pharynx. Weak row anterior teeth, single row posterior teeth with small teeth ventrally above crests. Stylets inserted at 81% of buccal tube length. Buccal tube width 16%. Claws robust with short thin accessory

claws. No granulation around claws. Lunules smooth on first three pairs of claws and toothed on fourth pair.

Description: Fine evenly distributed black pigment in body cells. Body length 210-743 μm . Large anterior eye spots present. Cuticle with faint reticular pattern over dorsum only, no granulation around claws. Terminal mouth. Two rows small teeth in anterior of oral cavity, single row small teeth in posterior position with randomly disposed tiny teeth above ventral crests. Two strong ventro-lateral crests and two-four median teeth, three strong dorsal crests. Buccal tube 55 μm long in 540 μm long specimen and 8.7 μm wide (16% of buccal tube length). Stylet supports inserted at 80.9% of buccal tube length, ventral support 64%. Pharyngeal bulb round (30 μm diameter) containing large apophyses, three granular macroplacoids and a large microplacoid. Macroplacoid row 45% of buccal tube length; first and third macroplacoids almost equal in size (8.1 μm long), second macroplacoid smallest (6.5 μm), slightly longer than microplacoid (5.4 μm). Microplacoid strong, evenly spaced with macroplacoids. Claws robust, with long secondary branch. Accessory claws short and low on primary branch. Fourth pair of claws similar to those on other legs, 16.2 μm long (29.4 % of the length of the buccal tube). Lunules small and smooth on first three pairs of legs and lightly toothed on the fourth pair, posterior lunule larger than anterior.

Eggs round and colourless, diameter without processes 95-115 μm , with processes 125-149 μm . 8-11 processes around the circumference, about 18-22 in hemisphere. Processes areolated cones with flattened apex, height 15-20 μm , base diameter 22-27 μm . 14-18 ridges radiate from each process to meet ridges from other processes forming large pores. Shell surface between ridges finely striated.

Etymology. *Fuscus*, L, dark, swarthy, for the colour of the animals.

Remarks. The species may be distinguished from other species in the genus by the reticulate pattern on the cuticle.

Distribution: Found only at a single locality.

Macrobotus galorensis sp. n.

Fig. 113, Plate IXb, e)

Material examined. Australia: NEW SOUTH WALES: *N41.a*, moss on rock on top of monolith in open sclerophyll forest, 40 specimens, 4 eggs (1 embryonate). AUSTRALIAN CAPITAL TERRITORY: *A1*, moss on rock, 8 specimens.

Diagnosis. Antero-ventral mouth. Two macroplacoids and a microplacoid in pharynx. No teeth in oral cavity. Stylet supports inserted at 72% of buccal tube length. Claws long and slender with bulbous common tract, accessory claws on all legs short and thin. No granulation around claws. Lunules on all claws large, toothed on fourth pair.

Description. Colourless. Body length 287-574 μm . Large posterior eye spots present. Cuticle smooth with small (0.5 μm) round pores, no granulation around claws. Antero-ventral mouth, lamellae very short. No teeth in oral cavity. Two ventral crests present, dorsal crest a single thin bar. Buccal tube (thickened below level of insertion of stylet supports) 50.8 μm long (in 460 μm individual) and 4.9 μm wide (9.6% of buccal tube length). Stylet supports inserted at 72% of length of buccal tube. Ventral support medium length (55%). Pharynx large round with large apophyses, two macroplacoids and a microplacoid. Macroplacoid thick rounded rods, first without median constriction (10.8

µm long), second about three quarters the length of first (7.6 µm). Macroplacoid row length 36% of buccal tube length. Microplacoid short and faint (1.6 µm long). Claws long and slender deeply divided with bulbous common tract (Plate IXb), with long secondary branch, increasing in length from first to fourth. Accessory claws short and close to primary branch. Fourth pair of claws 16.8 µm (33% of buccal tube length). Lunules large rounded with smooth thick edge on first three pairs of legs, with thick toothed edge on fourth pair. Cuticular bars present on first three pairs of legs.

Eggs white, round, laid free. Egg diameter with processes 136 µm, without 111 µm; 52 processes around circumference, 240 in a hemisphere. Processes have conical base rising to a finger-like top often with fine hairs at tip, base with ring of pores. Processes 13.5 µm high, 5.5 µm base diameter about 1.5-2.5 µm apart. Shell surface with pores with very thick uneven walls.

Remarks. All eggs were very dirty. The species bears a resemblance to *M. ariekammensis* Weglarska, 1965 in characteristics of both the adult and the egg. The adult differs from it by having no granulation around the legs and the egg processes of this species are about half the size of those of *M. ariekammensis*.

A single specimen of this species shows an interesting aberration of the claws, that is, a spur arises from the base of the primary branch pointing towards the top of the claw (Plate IXe). The claw and spur closely resemble that of *Macrobotus armatus* Pilato & Binda, 1996. That species was described from a single specimen and the presence of the spur was used as the primary character in assigning it as a new species. In the population of *M. galorensis* only one specimen had spurs indicating that their presence is an aberration and

should not be considered to be a character defining the species. It may be that the same applies to *M. armatus*.

Distribution. Found at two localities in moss on rock.

***Macrobotus guttus* sp. n.**

Fig. 114, Plates Vd, VIId

Material examined. **Australia:** NEW SOUTH WALES: *N38*, moss and lichen on rock, moss on soil in open sclerophyll, 63 specimens, 15 eggs. *N41*, moss on rock and soil on monolith, 25 specimens, 4 eggs. *N46.1*, turf moss and foliose lichen on rock in open sclerophyll forest, 15 specimens, 17 eggs (1 embryonate). *N48*, moss on rock in open sclerophyll, 12 specimens, 1 egg. QUEENSLAND: *Q15.1*, moss on rock and leaf litter in open sclerophyll, 22 specimens, 6 eggs. VICTORIA: *V1*, leaf litter on soil in *Mallee* scrub, 21 specimens. *V4*, moss on soil in coastal heath, 13 specimens.

Diagnosis. Terminal mouth. Two macroplacoids and a microplacoid in pharynx. No teeth in anterior of oral cavity, band of fine dot-like teeth in posterior. Stylet supports inserted at 81% of buccal tube length. Claws slender, with short thin accessory claw on all legs. Granulation around all claws, patch on first three pairs of legs. Lunules on first three pairs of claws smooth round, toothed on IV pair.

Description. Colourless. Body length 253-574 μm . Posterior eye spots present.

Granulation over back and sides of all legs. Cuticle with small round pores (1-1.5 μm) on all surfaces, one large pore (2 μm) on outer surface of first three pairs of legs above claws surrounded by granulation. Mouth terminal. No teeth in anterior part of oral cavity, band of very fine teeth in posterior position. Three ventral and 3 dorsal crests present. Buccal tube 42 μm long (in 423 μm individual) and 6.8 μm wide (16% of buccal tube length). Stylet

supports inserted at 81% of buccal tube length, ventral support 59%. Pharynx round (43 μm diameter) with small apophyses, two macroplacoids and a microplacoid. Macroplacoid rounded rods, first 9.2 μm long with strong median constriction, second 6 μm with caudal bulb. Macroplacoid row short (42.4% of buccal tube length). Microplacoid 2.7 μm long. Claws long and slender (PLate VIIId), increasing in length from first to fourth. Branches joined in bulbous base, secondary branch long and curved, primary branch with short rather thin accessory claws. Claws of fourth pair of legs 10.8 μm (27% of buccal tube length). Lunules round smooth on claws on first three pairs of legs, toothed on fourth pair, posterior larger than anterior.

Eggs white, round, laid free. Egg diameter with processes 74-80 μm , without 66-74 μm ; 32-35 processes around circumference, 180 in a hemisphere. Processes shaped like flask (Plate Vd), that is, with very reduced distal dish. Processes 5.5-7 μm high, 4.5-5 μm base diameter, dish 2 μm diameter and about 2 μm apart. Shell surface with dots appearing in walls of small pores (0.5 μm) continuous with pores around base of each process.

Etymology. *Guttus*, L, m, narrow-necked flask, describing the processes of the egg.

Remarks. This species is rather similar to *M. serratus* Bertolani, Guidi & Rebecchi, 1995 in having a small distal disk, however, the adults differ by having the stylet supports inserted more caudally (76-78% in *M. serratus*), a shorter macroplacoid row length and more, smaller, teeth on the lunules of the fourth pair of legs.

Distribution. Clearly prefers a dry habitat and only found on rock or soil.

***Macrobiotus harmsworthi* Murray, 1907**

Macrobiotus harmsworthi Murray, 1907: 677, Pl. 1, Fig. 7a-d

Type locality. Cape Mary Harmsworth, Franz Joseph Land, Spitzbergen.

Material examined. **Australia:** None. Cited by Murray (1910) as occurring at Kosciusko, NSW and by Pilato & D'Urso (1976) as occurring at Gosford, Wallacia, Moss Vale and Peat Ridge, NSW. **Italy:** Lago Beccio, 3 specimens, 1 egg. **Russia:** Kostroma District, moss on soil, 1 specimen, 1 egg.

Diagnosis. Terminal mouth. Three macroplacoids and a distinct microplacoid in pharynx. Band of teeth in anterior of oral cavity, single row with a few ventrally above crests in posterior. Stylet supports inserted at 75-78% of buccal tube length. Buccal tube width 17-21%. Claws long with thick high accessory claws and toothed lunules on the fourth pair of claws.

Description. Body length up to 555 μm , colourless. Eye spots present. Cuticle smooth. Mouth terminal. Anterior teeth in oral cavity a band, posterior teeth a single row triangular teeth with additional teeth ventrally above crests. Three ventral crests and 3 dorsal crests present. Buccal tube 50.3 μm long (in 450 μm specimen) and 9 μm wide (17.9% of buccal tube length). Stylet supports inserted at 76% of buccal tube length. Pharynx oval, containing apophyses, three macroplacoids and a small microplacoid. Macroplacoid row length 43-55% of buccal tube length; macroplacoids long rods, first longest (8.5 μm), third (7.5 μm) with caudal bulb, second shortest (6.3 μm). Microplacoid small 4.2 μm long. Claws long robust with long secondary branch. Accessory claws thick and high above primary branch on all legs. Anterior claw of fourth pair of legs 15.2 μm long (30.2% of

buccal tube length), posterior claw 15.7 μm (31.2%). Lunules on first three pairs of legs small and smooth, toothed on fourth pair of legs.

Egg round, diameter without processes 69-84 μm , with processes 88-104 μm , 12 processes around circumference, about 28 in hemisphere. Processes short cones tapering to small point from hemispherical base. Surface of processes areolate. Process height 15-16 μm , base diameter 14.5-17.5 μm . Each process with a weak corona of striations around base. Shell surface dotted (after Pilato *et al.*, 2000).

Remarks. The above description is taken from data supplied by Pilato *et al.* (2000). *M. harmsworthi* was considered to be a cosmopolitan species until that work which places in doubt many of the citations including that of Pilato & D'Urso (1976) from Australia. The latter authors did not describe their Australian specimens, noting only that they lacked eyes and had the buccal armature typical of that species. Pilato *et al.* (2000), however, stressed that *M. harmsworthi* has eyes (although dependence on the presence or absence of eyes as a constant character in any species is fraught with problems). It is more likely that the specimens examined by Pilato & D'Urso belong to one of the new species described here – most likely *M. wilsonensis* – although both *M. saltus* and *M. woodyi* have similarities to *M. harmsworthi*. Although Murray (1910) found the eggs of *M. harmsworthi* on Mount Kosciusko, it was not found there in this study. However eggs (including one embryonate egg) of *Calcarobiotus capricorniensis* sp. n. were found there. These eggs are similar to those of *M. harmsworthi* in having areolate, cone-shaped processes with a corona of dots around the base and with faint dotting on the shell.

Distribution. Said to be cosmopolitan but this may not be so in view of the work of Pilato *et al.* (2000).

***Macrobotus hesperius* sp. n.**

Fig. 115, Plates Ve, VIIe

Material examined. WESTERN AUSTRALIA: W2, moss and lichen on tree in forest, 49 specimens, 24 eggs (2 embryonate).

Diagnosis. Terminal mouth Two macroplacoids and a microplacoid in pharynx. No anterior teeth in oral cavity, fine band teeth in posterior. Stylet supports inserted at 78-79% of buccal tube length. Claws robust with thick high accessory claws. Lunules of first three pairs of claws small smooth, on fourth pair with tiny teeth.

Description. Colourless. Body length 176-497 μm . Eye spots present. Cuticle fine granulation patch above claws of first three pairs of legs and around claws on fourth pair. Mouth terminal. No anterior teeth in oral cavity, posterior teeth a fine band. Three ventral and three dorsal crests present. Buccal tube 42.7 μm long in 430 μm individual and 6.8 μm wide (15.8% of the buccal tube length). Stylet supports inserted at 78-79% of buccal tube length, ventral support 57.5%. Pharynx round (38 μm diameter) containing large apophyses, two rod-shaped macroplacoids and a short sharp microplacoid. First macroplacoid with median constriction 9.7 μm long, second with faint subterminal constriction, 7.8 μm . Short pointed microplacoid 2.5 μm long. Macroplacoid row 38-43% of buccal tube length. Claws robust (Plate VIIe), increasing in length from first to fourth. Secondary branch long and curved, primary branch with thick high accessory claws particularly on the fourth pair of legs. Claws of fourth pair of legs 11.4 μm long (26.6% of length of buccal tube). Lunules on first three pairs of legs small, round and smooth, those on fourth pair also rather small but with tiny teeth.

Eggs round, colourless, diameter without processes 76 μm , with processes 80 μm . 28 processes around circumference, 100 in hemisphere. Processes flask with bulbous base (Plate Ve) and with notched distal dish. Process height 5.5-6 μm , base diameter 6 μm , dish diameter 4.5-5.5 μm and 3 μm apart. Shell with pores, 0.8-1 μm diameter, with irregularly thick walls continuous with ring of pores around base of each process.

Etymology. *Hesperius*, L, western, as the species was found only in Western Australia.

Remarks. The species is very similar to other species in the *hufelandi* group. It differs from *M. hufelandi*, *M. sandrae* Bertolani & Rebecchi, 1993 and *M. terminalis* Bertolani & Rebecchi, 1993 by having much a shorter macroplacoid row length. It differs from *M. guttus* sp. n. by having very thick high accessory claws and large elliptical pores.

Distribution. The species has, so far, only been found in Western Australia.

***Macrobotus hibiscus* de Barros, 1942**

Fig. 116, Plate Vf, VIIf

Macrobotus hibiscus de Barros, 1942: 383-384, Figs. 40-44

Type locality. Brazil, Casa Branca, Sao Paolo.

Material examined. NEW SOUTH WALES: *N3.6.a*, fruticose lichen on rock in sub-alpine heath, 1 specimen. QUEENSLAND: *Q1*, moss on rock and dead tree in vine thicket, 18 specimens, 5 eggs. *Q3*, liverwort/lichen on rotten log and moss on live tree in rainforest, 17 specimens. *Q4*, moss and lichen on trees in rainforest remnant on island, 5 specimens, 1 egg. *Q6*, liverwort on rock in rainforest remnant, 1 specimen. *Q7*, moss and liverwort on tree in rainforest remnant beside road, 27 specimens, 2 eggs. *Q12*, leaf litter on

limestone, 1 specimen. *Q15.3*, moss/liverwort on rocks and trees and in leaf litter in subtropical rainforest, 139 specimens, 17 eggs.

Diagnosis. Antero-ventral mouth. Two macroplacoids and a microplacoid in pharynx. No teeth in anterior of oral cavity, single row of teeth in posterior. Stylet supports inserted at 71% of buccal tube length. Claws long robust with thin accessory claws. Lunules on all claws small and smooth. Granulation on back and sides above claws on all legs.

Description. Body length 173-433 μm , colourless. Eye spots present. Cuticle smooth with round to elliptical pores (0.5-1.0 μm) with granulation on back and sides of all legs.

Antero-ventral mouth. No teeth in anterior of oral cavity, single row teeth in posterior.

Three ventral and one long fine dorsal crest. Buccal tube 32 μm long in 324 μm individual) and 3 μm wide (9.7% of the buccal tube length). Stylet supports inserted at 70.9% of buccal tube length, ventral support 57.5%. Pharynx round (30 μm diameter) containing granular apophyses, two rod-shaped macroplacoids and an indistinct microplacoid. First macroplacoid with weak median constriction 6.5 μm long, second with faint caudal knob turned towards the midline, 4 μm . Small, indistinct microplacoid 1.3 μm . Macroplacoid row 33% of buccal tube length. Claws robust (Plate VIIIf), increasing in length from first to fourth. Secondary branch long a well curved, primary branch with short thin accessory claw which rises well clear of branch at tip. Claws of fourth pair of legs 10.5 μm long (32.5% of length of buccal tube). Lunules on all claws small, round and smooth.

Eggs round, colourless, diameter without processes 62 μm , with processes 70 μm . 34-40 processes around circumference, 140-180 in hemisphere. Processes shaped like upturned goblets (Plate Vf) with notched distal dish and ring of 14-16 indistinct pores around base.

Process height 4.9-5.5 μm , base diameter 3.0-3.8 μm , dish diameter 3.0 μm and 2-3 μm apart. Shell with irregular pores with thick walls.

Remarks. Measurements of the Australian specimens described here, agree well with measurements taken from drawings and the few measurements given in the text in the original description by de Barros (1942). Both have stylets inserted at about 70% of the buccal tube length, ventral supports 58% and the buccal tube width is 8-9% of the buccal tube length. These values are very different to those of *Macrobotus hufelandi* (see Bertolani & Rebecchi, 1993) and the species should not be synonymised with *M. hufelandi* as suggested by Kathman (1990). It is probable that *M. hibiscus* was not present in the Canadian material described by Kathman. The description of *M. hibiscus* from New Zealand (Horning, Schuster & Grigarick, 1978) gives the stylet insertion length as 85% of the buccal tube length suggesting an erroneous identification. Durante Pasa & Maucci (1979) described the buccal armature of *M. hibiscus* as identical to *M. hufelandi* also suggesting an erroneous identification.

Distribution. In Australia this species is widely distributed in Queensland but has not been found south of New England National Park in NSW where only a single specimen was found. It appears to favour moist conditions or at least does not favour excessive drying. This is the first record of its occurrence in Australia.

Macrobotus hieronimi Pilato & Claxton, 1988

Fig. 117

Macrobotus hieronimi Pilato & Claxton, 1988: 83-86, Figs. 1, 2A-C

Type locality. Australia. Douglas Park, NSW.

Material examined. NEW SOUTH WALES: *N15.1.a*, weft moss on tree moss on roof, 9 specimens, 5 eggs; *N15.2.a*, lichens on trees and rocks, 10 specimens, 7 eggs; *N15.3.b*, foliose lichens on trees, 2 specimens, 2 eggs; *N15.4*, lichen on tree, 9 specimens, 2 eggs. *N21.b*, lichens on trees in sclerophyll forest, 31 specimens, 8 eggs. *N23.a*, lichens and bark on trees in open sclerophyll forest, 36 specimens, 14 eggs. *N25*, moss on rock, 1 egg. *N27*, moss and lichen on rock in dry sclerophyll forest, 36 specimens, 12 eggs (**type material**). *N37*, lichen/liverwort on tree open woodland, 6 specimens, 2 eggs. *N38*, lichens on rocks in open woodland, 32 specimens, 14 eggs. *N40*, foliose lichens on rock in open woodland, 5 specimens, 10 eggs. *N41*, foliose lichen on rock in open woodland, 22 specimens, 12 eggs. *N42*, moss and lichen on trees near sea, 10 specimens, 14 eggs. *N45*, foliose lichen on rock near sea, 4 specimens, 2 eggs. QUEENSLAND: *Q2*, weft moss on dead wood, 5 specimens, 1 egg. *Q7*, moss on rock in open sclerophyll forest, 3 specimens, 3 eggs. *Q11*, crustose lichen on tree on beach, 5 specimens, 1 egg. *Q15*, moss and lichens on rock in sclerophyll forest, 54 specimens, 15 eggs. *Q19*, moss/liverwort on tree in *Eucalyptus grandis* forest, 3 specimens, 1 egg. *Q20*, leaf litter/sand, *Banksia* cone on ground, lichens on trees, 56 specimens, 8 eggs. *Q21*, moss and lichen on rock in open woodland, 7 specimens, 9 eggs. *Q22*, moss/liverwort on tree in open forest, 2 specimens, 1 egg. *Q25*, lichen on branch on ground, liverwort on rock in warm temperate rainforest, 10 specimens, 4 eggs. TASMANIA. *T2.1*, moss on rock on headland, 18 specimens, 2 eggs. LORD HOWE ISLAND: moss and lichen, 30 specimens, 9 eggs.

Diagnosis. Mouth terminal. Three macroplacoids and a microplacoid in pharynx. Fine band teeth in anterior of oral cavity, single row in posterior. Stylet supports inserted at 75% of buccal tube length. Buccal tube width 17%. Claws robust, with thick high accessory claws. Lunules on first three pairs of claws smooth, on fourth pair with few small teeth. Granulation present on all legs, in patch on sides of first three pairs.

Description. Colourless. Body length 160-604 μm . Eye spots anterior. Cuticle smooth, granulation in a patch on outside of first three pairs of legs just above the external claw, also on back and sides of fourth pair of legs. Mouth terminal. Fine band of teeth in anterior of oral cavity, posterior teeth a single row triangular teeth. Three ventral (median crest

sometimes divided) crests, three dorsal crests. Buccal tube 59.5 μm long in 500 μm long specimen and 10.5 μm wide (17.7% of buccal tube length). Stylet supports inserted at 75% of buccal tube length and ventral support at 65%. Pharyngeal bulb round containing large, round apophyses, three macroplacoids and a microplacoid. Macroplacoid row 46% of buccal tube length; first macroplacoid longest or same length as third (7.6 μm), third with a caudal bulb which curves in towards the midline, second 7 μm long. Microplacoid long (5 μm) and thin. Claws robust (with long secondary branch. Accessory claws thick and high above primary branch. fourth pair of claws 15.7 μm long (26.4% of buccal tube length). Lunules on claws of first three pairs of legs small and smooth; on fourth pair of legs with a few small teeth.

Eggs colourless, round, diameter without processes 68 μm , with processes 114 μm . Eleven processes around circumference, 24 in hemisphere. Processes areolate, large cones with sharp tip often with small hairs arising from tip; height 22-34 μm , base diameter 16-21 μm . middle. Shell with about 6 large pores around base of each process, striations on shell surface within these pores. Eggs with smaller processes (19-22 μm high, 14 μm base diameter) were found at Bribie Island.

Remarks. The species is very similar to *Macrobiotus snaresensis* Horning et al 1978 and may be synonymous with it. A specific type locality was not designated for that species and there may in fact be two species, one found in New Zealand, Tasmania and the wetter, higher altitude areas of mainland Australia, the other common in the dryer areas. A comparative study of specimens from both countries is necessary to resolve this question.

In addition, some slight differences in adult characters have been noted in some populations in which the eggs have smaller processes. Adults from Bribie Island have

stylet supports inserted more caudally (78%) and have additional teeth in the posterior position in the oral cavity, between the single row of teeth and the transverse crests. these slight differences could be due to differences in the ploidy of the populations and in this study have been identified as *M. hieronimi*. Clearly further study is needed on this species.

Distribution. The species was recorded in New Zealand by Pilato & Binda (1996).

Macrobiotus hufelandi Schultze, 1834

Macrobiotus hufelandii Schultze, 1834: 5-7, Figs. 1-4

Type locality. Germany.

Material examined. Australia: None. Murray (1910) described this species as being “the commonest species here as in most other places”. He found it at Mount Kosciusko, the Blue Mountains and Eumundi. Pilato & D’Urzo (1976) reported the species from Wallacia, NSW.

Diagnosis. Mouth terminal. Two macroplacoids and a microplacoid in pharynx. Band teeth in anterior and posterior of oral cavity. Stylet supports inserted at 80-81% of buccal tube length. Claws slender with thick accessory claws. Lunules smooth on first three pairs of legs, weakly toothed on fourth pair.

Description. Body length 166-556 μm , Eye spots present. Cuticle with round and elliptical pores (up to 1.5 μm). Mouth terminal. Oral cavity with band teeth in anterior and posterior positions. Three ventral and three dorsal crests present. Buccal tube width 13% of buccal tube length. Stylet supports inserted at 80-81% of buccal tube length. Pharynx round containing small apophyses, two macroplacoids and a microplacoid. Macroplacoid row 54% of buccal tube length First macroplacoid with median constriction, second with slight

caudal bulb. Microplacoid long. Claws slender with secondary branch joined over a long distance; accessory claws on primary branch conspicuous. Claws of fourth pair of legs 28% of buccal tube length. Lunules small and smooth on first three pairs of legs, occasionally weakly toothed on fourth pair.

Eggs colourless, round, diameter 66.5-91 μm . 75-108 in hemisphere. Processes of *hufelandi* type with conical base and a distal dish with cog-shaped border. Process height 5.5-7.4 μm , base diameter 5.4-9.9 μm , dish diameter 3.9-5.2 μm . Shell surface with reticular uniform pores continuous with ring around processes where diameter of pores (1.2 μm) is slightly larger than intermediate pores. (Description of animals and eggs from Bertolani & Rebecchi, 1993)

Remarks. This species was recorded from Australia by Murray (1910) and Pilato & D'Urzo (1976). However, in view of the recent work of Bertolani & Rebecchi (1993) and the inability of this worker to find specimens fitting the description of *M. hufelandi*, it is probable that the two citations are erroneous and that *M. hufelandi* does not occur in Australia.

Distribution. The cosmopolitan distribution of this species is in considerable doubt since the redescription of Bertolani & Rebecchi (1993).

***Macrobiotus joannae* Pilato & Binda, 1983**

Macrobiotus joannae Pilato & Binda, 1983: 267-272, Pl. 1, Figs. 1-3, Pl. 2, Figs. 1-5

Type locality. Bright, Victoria.

Material examined. Australia: None. Reported from Bright, Victoria by Pilato & Binda (1983).

Diagnosis. Mouth terminal. Two macroplacoids and a microplacoid in pharynx. Band of teeth in anterior of oral cavity, showy band slightly narrower dorsally in posterior. Stylet supports inserted at 79-83% of buccal tube length. Claws slender, accessory claws thin. Lunules smooth on first three pairs of legs, toothed on fourth pair.

Description. Body length 227-540 μm , Eye spots present. Cuticle with round and elliptical pores. Mouth terminal. Oral cavity with anterior teeth a band of 3-4 rows, posterior teeth a showy band slightly narrower dorsally. Three ventral crests (median crest a tooth) and three dorsal crests present. Buccal tube width 20-21% of buccal tube length. Stylet supports inserted at 79-83% of buccal tube length. Pharyngeal bulb oval (45 by 36 μm in 400 μm specimen) containing apophyses, two macroplacoids and a microplacoid. Macroplacoid row 49% of buccal tube length; first macroplacoid long with median constriction, second with caudal bulb that curves towards midline. Microplacoid small, indistinct. Claws slender with secondary branch joined over a long distance; short accessory claws lie close to primary branch. Claws of fourth pair of legs 29% of buccal tube length. Lunules small and smooth on first three pairs of legs weakly toothed on fourth pair.

Eggs colourless, round, diameter without processes 86 μm , with processes 111 μm . 27-29 processes around circumference and 150 in hemisphere. Processes of *hufelandi*-type with conical base and a terminal disk with 12-14 strong teeth. Process height 6.5-8.0 μm . Base diameter of processes 6.8-7.2 μm , disk diameter 5.2-5.8 μm about 4 μm apart. Shell surface with reticular uniform pores thickened at the points. (Description of animals and eggs from Pilato & Binda, 1983).

Remarks. This species is most similar to *M. hufelandi* but differs from it by having a much wider buccal tube and thin accessory claws.

Distribution. At the type locality the species was found in moss on a tree. It has also been reported from Russia (Biserov, 1991, 1996a, b, 1998, 1999).

Macrobotus microcalix sp. n.

Fig. 118, Plates VIa, VIIIa

Material examined. Australia: NEW SOUTH WALES: *N21*, foliose lichen on roof, 14 specimens, 27 eggs (1 embryonate). *N41*, fruticose lichen on dead tree on side of monolith, 8 specimens, 9 eggs.

Diagnosis. Mouth terminal. Two macroplacoids and a microplacoid in pharynx. No teeth in anterior of oral cavity, band of fine teeth in posterior. Stylet supports inserted at 80% of buccal tube length. Claws long and robust, accessory claws thin. Granulation around all claws, over back and outside of first three pairs. Lunules large and smooth on all claws.

Description. Colourless. Body length 196-650 μm . Large eye spots present. Cuticle smooth with 3 μm elliptical pores, with fine granulation over back and outside above claws on first three pair of claws and back and sides of fourth pair. Mouth terminal. Oral cavity with no teeth in anterior position, band of fine teeth in posterior. Three ventral and three dorsal crests present. Buccal tube 47.6 μm long in 450 μm long specimen and 8 μm wide (17% of buccal tube length). Stylet supports inserted at 80% of buccal tube length, ventral support 57%. Pharynx round (48 μm diameter) containing small apophyses, two macroplacoids and a microplacoid. First macroplacoid 12.4 μm long with median constriction, second 8 μm with caudal bulb. Macroplacoid row 48% of buccal tube length.

Microplacoid 2.7 μm long. Claws long robust (Plate VIIIb), increasing in length from first to fourth. Secondary branch almost as long as primary, primary branch with short rather fine accessory claws. Claws of fourth pair of legs 14.6 μm long (31% of buccal tube length). Lunules large particularly on fourth pair and with thick smooth edge.

Eggs colourless, round, diameter without processes 79 μm , with processes 86 μm . 44-56 processes around circumference and 240-300 in hemisphere. Processes shaped like thin upturned goblets (Plate VIb) with distal dish with tiny teeth. Process height 4 μm , base diameter 3 μm , dish diameter 2-3 μm about 2 μm apart. Shell surface with small pores about 0.5 μm diameter continuous with pores around base of each process seen with difficulty and appearing as a series of points on the shell surface.

Etymology. *Micro*, Gr, little, *calix*, L, chalice, referring to the egg processes.

Remarks. This species is most similar to *M. santoroi* but differs from it by lacking teeth in the anterior of the oral cavity and by having only a patch of granulation around the claws of the first three pairs of legs.

Distribution. Found in two very xeric environments.

***Macrobiotus montanus* Murray, 1910**

Fig. 119

Macrobiotus montanus Murray, 1910: 116-117, Pl. XV, Fig. 10a-d

Type locality. Nun's Veil Mountain, South Island, New Zealand.

Material examined. **Australia:** NEW SOUTH WALES: *N3.1*, moss on rock and tree in open sclerophyll forest, 21 specimens, 2 eggs; *N3.5*, moss and foliose lichen on tree branch in subalpine heath, 31 specimens, 15 eggs (1 embryonate). **TASMANIA:** *T4*, moss on rock in wet sclerophyll forest, 4 specimens, 1 embryonate egg. **Norway:** Finse, 1 specimen, 1 egg.

Diagnosis. Mouth terminal. Three macroplacoids and a microplacoid in pharynx. Thin band teeth in anterior of oral cavity, posterior teeth a row of long sharp teeth with many teeth ventrally above crests. Stylet supports inserted at 77% of buccal tube length. Buccal tube width 13.7%. Claws short and robust, with very thick high accessory claws especially on fourth pair of legs. Granulation around all claws, patch on side of first three pairs of legs. Small smooth lunules on all claws.

Description. Colourless. Body length 203-540 μm . Anterior eye spots present. Cuticle smooth except for patch of faint granulation above claws on first three pairs of legs and back and sides on fourth pair of legs. Mouth terminal. Anterior teeth in large oral cavity a thin band, often hard to see; posterior teeth a row of long sharp teeth with more teeth ventrally between row and crests; 3 long ventral and 3 dorsal crests present. Buccal tube 46 μm long (in 420 μm individual) and 6.3 μm wide (13.7% of buccal tube length). Stylet supports inserted at 77% of length of buccal tube. Ventral support long (62%). Pharynx round (38 μm diameter) with rounded apophyses, three macroplacoids and a microplacoid. Macroplacoids short rounded rods, first and third about equal in length (6 μm), second shortest (4.3 μm), third with faint caudal bulb. Macroplacoid row length short (40%). Microplacoid small (3 μm) and compact. Claws short and robust, with long secondary branch. Accessory claws fine short and high above primary branch especially on fourth pair of claws. Claws of first three pairs of legs much shorter than on fourth pair; first pair

8.1 μm , second and third 8.6 μm and fourth 9.7 μm (21%). Lunules round small smooth on all claws.

Eggs white, round, laid free. Egg diameter with processes 78 μm , without 68 μm ; 19 processes around circumference, 66 in hemisphere. Processes round flat hemispheres with thick dome with a few pores, each process surrounded by about 16 striae. Processes 4-5.5 μm high, 6.5-7.5 μm base diameter, about 1 μm apart. Shell surface with faint markings (pores?).

Remarks. The original description is rather poor, containing few details of adults or eggs, however there are a few characters which agree with the specimens examined here—hemispherical processes on the egg which almost meet at their bases, three short macroplacoids and a “rather obscure” microplacoid and strong accessory claws. The egg from Norway had obvious pores on the shell surface but the specimen was extremely similar to those reported here from Australia. Adults of the species from Australia are very similar to *M. furciger* and *M. orcadensis*.

Binda & Pilato (1994) described a closely related species, *M. mottai*, from Antarctica. The specimens from Australia differ from *M. mottai* by having much shorter claws, small lunules on all claws and smooth lunules on the fourth pair.

Distribution. *M. montanus* has been reported from most continents – Europe, the Americas and Antarctica (McInnes, 1994) and, for the first time here, in Australia. Horning, Schuster & Grigarick (1978), in their survey of the New Zealand fauna, did not report collecting it. It was reported as being rather scarce by Mihelcic (1952a) and as a montaine species by Durante Pasa & Maucci (1979). Its occurrence at 1500 m. asl. at New

England National Park and also in Tasmania is in agreement with this suggested distribution. (The type locality in New Zealand was also at high elevation – 1850 m. asl.).

***Macrobiotus nemus* sp. n.**

Fig. 120

Material examined. **Australia:** NEW SOUTH WALES: *N34*, moss on tree in open forest, 3 eggs. *N35*, moss, lichen, liverwort and leaf litter on rock and moss/lichen on tree in *Ceratopetalom* forest glade, 33 specimens, 2 embryonate eggs.

Diagnosis. Mouth terminal. Two macroplacoids and a microplacoid in pharynx. No teeth in anterior of oral cavity, band of teeth in posterior. Stylet supports inserted at 81% of buccal tube length. Claws robust with thick high accessory claws. Granulation around all claws, patch above claws on first three pairs of legs. Lunules on smooth on first three pairs of legs, toothed on fourth pair.

Description. Colourless. Body length 245-622 μm . Posterior eye spots present. Cuticle smooth except for patch of granulation above claws on first three pairs of legs and back and sides on fourth pair of legs. Cuticle with large elliptical pores (1.5-2 μm) on all surfaces. Anterior mouth. No teeth in anterior part of oral cavity, band of 4 rows teeth in posterior part. Three ventral (median crest a tooth) and 3 dorsal crests present. Buccal tube 38.7 μm long (in 410 μm individual) and 6.7 μm wide (17.2% of buccal tube length). Stylet supports inserted at 81% of length of buccal tube, ventral support long (59%). Pharynx oval (42 μm long by 35 μm wide) with small apophyses, two macroplacoids and a weak microplacoid. Macroplacoids short rods; first with median constriction (8.7 μm long), second 5.7 μm). Microplacoid 3 μm long. Macroplacoid row 42% of buccal tube

length. Claws robust, with secondary branch almost as long as primary, increasing in length from first to fourth. Accessory claws short and high above primary branch particularly on fourth pair of claws. Claws on fourth pair of legs 10.3 μm long (26.5% of buccal tube length). Lunules small round smooth on first three pairs of legs, with fine teeth on fourth pair.

Eggs colourless, round, diameter with processes 130 μm , without 90 μm . 10 processes in optical section, 23 in hemisphere. Processes large, tapering areolated cones, sometimes with bifurcate tip. Processes 26 μm high, 19-22 μm base diameter, base surrounded by 10-12 large pores. Sheel within pores dotted.

Etymology. *Nemus*, L. forest, glade.

Remarks. The species is rather similar to *M. pallarii* Maucci, 1954 but differs from it by having teeth on lunules of the fourth pair of legs and having much larger eggs with much larger processes. The eggs are even more similar to those of *M. ragonesi* Binda, Pilato, Manicada & Napolitano, 2001, however, the adults of that species have teeth in the anterior part of the oral cavity and smooth lunules on the fourth pair of legs.

Distribution. Only found at the type locality.

***Macrobiotus occidentalis* Murray, 1910**

Macrobiotus occidentalis Murray, 1910: 169-171, Pl. XXI, Fig. 54a-e

Type locality. Canada. Victoria, British Columbia.

Material examined. None. Cited by Murray (1910) as occurring in the Australian Alps between 5000 and 6000 feet

Diagnosis. Orange-red body cells. Terminal mouth. Two macroplacoids and a microplacoid in pharynx. Claws slender, internal different in length from external. Lunules on fourth pair of claws toothed.

Description. Body length up to 800 μm , orange-red body cells. Eye spots present. Cuticle dotted (elliptical pores?) Double layer of cuticle enclosing a colourless fluid in which float many thin hyaline rectangular plates. Buccal tube 4 μm wide, narrow. Pharyngeal bulb round (42 μm), containing apophyses, two macroplacoids, microplacoid absent. First macroplacoid is about three times as long as broad, the second about twice as long as broad. Claws like those of *hufelandi* but more slender and united for half the length of the primary branch. Claws of each pair unequal in length. Lunules irregularly dentate. Eggs red round, diameter without processes 45-55 μm , with processes 65-85 μm . Thirty processes around circumference and 90 in hemisphere. Processes cones with slender tapering curved apices. Processes are separated by a distance greater than the diameter of their bases.

Remarks.

Distribution. The species was regarded by Murray as being very close to *Richtersius coronifer* (Richters, 1903) and there has been considerable confusion by many authors as to the characters of this species and it needs to be redescribed from material from the type locality (Dastych, 1988). Murray found *M. occidentalis* in the Australian Alps at an elevation of between 5000 and 6000 feet. The specimens had the double cuticle but

without the hyaline rectangular plates and they also had a microplacoid (not found in the type material).

***Macrobotus orcadensis* Murray, 1907**

Fig. 121

Macrobotus orcadensis Murray, 1907: 661-662, Pl. II, Fig. 10a-e

Type locality. Scotland. Orkney Islands.

Material examined. NEW SOUTH WALES: *N11*, lichen on tree in rainforest remnant, 5 specimens, 2 eggs. *N14.1*, foliose lichen on rock in open woodland at 1200 m. asl., 4 specimens; *N14.2*, Banksia cone on soil in dry sclerophyll forest at 1200 m. asl., 13 specimens, 3 eggs. *N14.5*, leaf litter on soil in dry sclerophyll, 12 specimens. *N15*, lichen on tree in open woodland, 18 specimens, 8 eggs. *N29*, foliose lichen on rock in open woodland, 4 specimens, 2 eggs. *N36*, foliose lichen on log in open woodland, 22 specimens. *N44*, lichen on rock in subalpine heath, 8 specimens, 2 eggs. *N46.2*, moss and lichen on rock in subalpine heath, 2 specimens, 5 eggs. **New Zealand:** Bluff Hill, South Island, 1 specimen, 1 egg. **Norway:** Finse, (BMD) 1 specimen, 1 egg.

Diagnosis. Terminal mouth. Three macroplacoids and a microplacoid in pharynx. No teeth in anterior of oral cavity absent, posterior teeth a single weak row with a few ventrally above crests. Stylet supports inserted at 77% of buccal tube length. Buccal tube width 16%. Claws long with thick very high accessory claws particularly on fourth pair. Strong granulation on all legs, on back and outside of first three pairs of legs. Lunules smooth on all legs.

Description. Body length up to 520 μm , colourless. Posterior eye spots present. Cuticle smooth with strong granulation on back and outside of first three pairs of legs and back

and sides of fourth pair. Mouth terminal, anterior teeth in oral tube absent, posterior teeth weak, an even row and some ventrally above crests, observable only in the larger specimens. Three ventral crests (median crest a tooth) and three dorsal crests present. Buccal tube 36.8 μm long in 430 μm specimen and 6 μm wide (16.2% of buccal tube length). Stylet supports inserted at 77% of buccal tube length, ventral support 62%. Pharynx oval (34 μm long by 32 μm wide) containing well-developed apophyses, three macroplacoids and a microplacoid. Macroplacoid row very short 36-38% of buccal tube length. First and third macroplacoids equal in size (4 μm long), second macroplacoid always smaller than other two (3.2 μm). Microplacoid short, distinct 2 μm long. Claws long and slender, main and secondary branch joined over half their length with thick high accessory claws, rising very high on fourth pair of legs. Claws increasing in length from first to fourth. Posterior claws on fourth pair of legs 10.3 μm long (27.9% of buccal tube length). Lunules small round and smooth on all claws.

Eggs colourless, laid free, round Diameter without processes 70 μm , with processes 81 μm . 21 processes around circumference, 90-112 in a hemisphere. Processes are cones with pointed apices often subdivided into two or three points; height 5-7 μm (8-11 μm in Kosciusko and Kiandra populations), base diameter 4 μm (6-7 μm) and distance between 3 μm (4 μm). Egg shell surface with pores with unevenly thickened walls, about 3-4 pores between each process.

Remarks. The differences in the egg processes at two sites (Kosciusko and Kiandra) from the other populations may be due to the presence of polyploid populations. Bertolani *et al.* (1987) showed that bisexual populations of *X. pseudohufelandi* Iharos had fewer processes that were longer and wider at the base than those of eggs from unisexual populations.

Distribution. In Australia the species was found only in areas of some elevation and rather benign climate. It has been reported from Europe, South America, Japan and New Zealand. It may be considered to be a cosmopolitan species.

Macrobotus persimilis Binda & Pilato, 1972

Macrobotus persimilis Binda & Pilato, 1972: 51-54, Fig. 3A-D

Type locality. Sicily.

Material examined. None. Cited by Pilato & D'Urso (1976) as occurring at Five Dock, Sydney, NSW.

Diagnosis. Mouth terminal. Two macroplacoids and a microplacoid in pharynx. No teeth in anterior of oral cavity, fine band in posterior. Stylet supports inserted at 79% of buccal tube length. Claws slender with thick accessory claws. Lunules on first three pairs of legs smooth, toothed on the fourth pair.

Description. Body length up to 400 μm , colourless. Eye spots present. Cuticle smooth, with sparse pores. Mouth terminal. No teeth in anterior of oral cavity, fine band teeth in posterior. Buccal tube 37 μm (in 400 μm specimen), 6 μm wide (16% of buccal tube length); stylet supports inserted at 73% of buccal tube length; ventral support very short (pr 36.4). Pharynx oval (43 by 38 μm) containing apophyses, three macroplacoids and a microplacoid. First macroplacoid deeply divided into two parts (6.4 and 5.3 μm) second 7.9 μm . Claws long and slender with prominent accessory claws. Fourth pair of claws 13 μm (35% of buccal tube length). Lunules on first three pairs of legs very small, smooth; on fourth pair smooth.

Eggs round, diameter without processes 68 μm , with processes 78 μm . 24-32 processes around circumference. Processes are *hufelandi*-type with a ring of small pores around the base of each. Shell surface smooth.

Remarks. The species is similar to *M. hesperius* but differs from it by having a median tooth in the ventral position of the crests and having claws which are longer relative to the length of the buccal tube.

Distribution. The type material was found in moss but no other data were given. The species has also been found in Greece, Turkey, Spain, Portugal, USSR, Africa, Greenland.

***Macrobotus peteri* Pilato, Claxton & Binda, 1989**

Fig. 122

Macrobotus peteri Pilato *et al.*, 1989: 45-47, Fig. 2A-E

Type locality. Cambewarra Mountain, NSW.

Material examined. NEW SOUTH WALES: *N10*, moss and lichen on log in forest, 3 specimens, 1 egg; *N11*, moss and lichen on trees in warm temperate rainforest, 6 specimens, 5 eggs. *N14*, moss on rock and soil in open forest, 22 specimens, 9 eggs; *N15.2*, moss on limestone in open woodland, 5 specimen, 2 eggs. *N22*, fruticose lichen on rock in open woodland, 1 specimen, 1 egg. *N27*, moss and lichen on rocks in open woodland, 170 specimens, 79 eggs. *N35*, moss and lichens on trees and rocks in warm temperate rainforest, 13 specimens, 9 eggs. *N39*, moss and lichen on rock in warm temperate rainforest, 144 specimens, 46 eggs (**type material**). QUEENSLAND: *Q24*, liverwort on tree in subtropical forest, 2 specimens, 1 egg. *Q25*, moss and lichen on trees in rainforest, 1 specimen, 3 eggs.

Diagnosis: Mouth terminal. Three long macroplacoids and a microplacoid in pharynx.

Band of teeth in anterior of oral cavity, single row teeth in posterior. Stylet supports inserted at 81-83% of buccal tube length. Buccal tube width 20%. Claws slender but short with thin accessory claws. No granulation around claws. Lunules smooth on all legs.

Description: Body length 170-690 μm , colourless. Eye spots absent. Cuticle smooth, no granulation on legs. Mouth terminal. Strong band of teeth in anterior part of oral cavity, single row triangular teeth in posterior position. Ventrally two strong lateral crests and median crest broken into 3 or 4 teeth, 3 dorsal crests. Buccal tube 54 μm long in 450 μm specimen and 10.8 μm wide (20% of buccal tube length). Stylet supports inserted at 81-83% of buccal tube length, ventral support 65%. Pharynx oval (48 by 43 μm) containing small apophyses, three macroplacoids and a microplacoid. Macroplacoid row long (55% of buccal tube length); first macroplacoid long (9.7 μm); second macroplacoid shortest (6 μm), third macroplacoid with distinct caudal bulb and longest of the three (10.8 μm). Microplacoid small (3.2 μm) and distant from the third macroplacoid. Claws slender (fourth pair of claws is 23% of buccal tube length) with small base and long secondary branch. Accessory claws rather short and close to primary branch on first three pairs of claws but high on fourth pair. Lunules small and smooth on all legs.

Eggs colourless, round, diameter without processes 56-72 μm , with processes 81-93 μm . 16-18 processes around circumference, 44 in hemisphere. Processes conical with apices subdivided into a number of points, surface with a dense reticular sculpture 6-7 clear areolae around base of each process. Process height 10-14 μm , base diameter 9-12 μm .

Remarks. The species is somewhat similar to *M. richtersi* in having a very wide buccal tube, long macroplacoids and a microplacoid placed far from the macroplacoids. The eggs

also bear a resemblance to those of *M. richtersi* in the way that the pores on the process surface are aligned.

Distribution. The species has also been found in Indonesia (Pilato & Binda, 1990) and the Seychelles (Binda & Pilato, 1995). In Australia it seems to be limited to the north easterly part of the mainland but occurs in both very dry and in moist areas.

***Macrobotus purpureus* sp. n.**

Fig. 123, Plates VIb, VIIIb

Material examined. Australia: TASMANIA: T22, moss on limestone and soil in dense woodland, 3 specimens, 6 eggs (1 embryonate).

Diagnosis: Fine purple pigment in body cells. Mouth terminal. Two macroplacoids and a microplacoid in pharynx. Band of fine teeth in anterior of oral cavity, single row small teeth in posterior. Stylet supports inserted at 77% of buccal tube length. Claws robust with thick very high accessory claws. No granulation around claws. Lunules smooth on first three pairs of legs, with very fine teeth on fourth pair.

Description: Cuticle purple. Body length 324-487 μm . Large eye spots present. Cuticle smooth with round to elliptical pores (1-1.6 μm). No granulation on legs. Mouth terminal. Band of fine teeth in anterior part of oral cavity, single row of small teeth with a few more ventrally between row and crests in posterior position. Three ventral and 3 dorsal crests present. Buccal tube 43.8 μm long in 487 μm specimen and 6.5 μm wide (14.8% of buccal tube length). Stylet supports inserted at 77% of buccal tube length, ventral support 61%. Pharynx round (36 μm diameter) containing large apophyses, two macroplacoids and a

microplacoid. Macroplacoid row 41% of buccal tube length; first macroplacoid 10.3 μm long with median constriction, second macroplacoid with subterminal constriction 6.5 μm . Microplacoid 2.2 μm . Claws robust (Plate VIIIc), increasing in length from first to fourth, second and third equal in length. Secondary branch strongly curved, primary branch with short thick very high accessory claws Claws of fourth pair of legs 11.9 μm long (27% of buccal tube length). Lunules small and smooth on first three pairs of legs, rather small but with very fine teeth on fourth pair.

Eggs colourless, round, diameter without processes 105 μm , with processes 120 μm . 15 processes around circumference, 29 in hemisphere. Processes shaped like large upturned goblets (Plate VIc) with 5-6 distinct arms around dish with distinctly domed centre.

Process height 11-13.5 μm , base diameter 11-13.5 μm , dish diameter 6-8 μm , about 3 μm apart. Shell surface with large (1.6-2 μm) pores with unevenly thickened walls continuous with pores around base of each process.

Etymology. *Purpureus*, L, purple, for the colour of the cuticle.

Remarks. This species may be distinguished from others with two macroplacoids and a microplacoid and toothed lunules on the fourth pair of legs by the presence, in the oral cavity, of anterior teeth and a single row in the posterior position with a few below.

Distribution. Only found at the single locality.

Macrobiotus richtersi Murray, 1911

Fig. 124

Macrobiotus richtersi Murray, 1911: 7

Type locality. Clare Island, Ireland.

Material examined. Australia: NEW SOUTH WALES: *N1*, leafy liverwort on tree in backyard, 1 specimen. *N3.2, 3.3*, moss on rocks and tree in subalpine heath, 20 specimens, 4 eggs. *N5*, moss on rock in open sclerophyll, 1 specimen, 2 eggs. *N8*, gumnuts on soil, 1 specimen. *N10*, moss on log in closed forest, 4 specimens. *N11*, moss on tree in street, 1 egg. *N15*, moss and soil over limestone in protected valley, 46 specimens, 24 eggs, moss and lichen on trees, 17 specimens, 8 eggs. *N24*, lichen on rock in open sclerophyll, 1 specimen. *N26*, moss on rock and tree in gully, 1 specimen, 1 egg. *N27*, moss and lichen on rock in open sclerophyll, 14 specimens, 11 eggs. *N28*, moss and lichen on rock in open sclerophyll, 10 specimens, 8 eggs. *N29*, moss and soil over limestone, 32 specimens, 11 eggs. *N32*, lichen on tree instreet, 11 specimens, 13 eggs. *N33*, lichen on tree in street, 1 specimen, 1 egg. *N34*, moss on tree in park, 2 specimens. *N35*, moss and lichen on tree in rainforest remnant, 3 specimens, 1 egg. *N39*, moss and lichen on rock in rainforest remnant, 4 specimens. *N40*, moss on rock in open sclerophyll, 3 specimens, 1 egg. *N43*, moss on rock and soil in subalpine heath, 12 specimens, 6 eggs. *N46.1*, moss on rock in open sclerophyll, 1 specimen, 8 eggs; *N46.3*, moss and lichen on tree in subalpine open woodland, 3 specimens. *N48*, moss on rock in open sclerophyll, 4 specimens. QUEENSLAND: *Q1*, moss on rock in vine thicket, 7 eggs. *Q6*, crustose lichen on fig tree in rainforest remnant, 2 specimens. *Q7*, liverwort and lichen on tree in rainforest remnant, 1 specimen. *Q12*, *Nostoc*, moss and leaf litter on limestone, 58 specimens, 14 eggs. *Q15.1*, leaf litter in open sclerophyll, 2 specimens, 1 egg; *Q15.3*, moss on tree, leaf litter, liverwort on rock, 22 specimens, 7 eggs. *Q18*, liverwort on tree, moss on soil in rainforest remnant, 1 specimen, 1 egg. *Q20.3*, leaf litter on sand in *Banksia* heath, 5 specimens, 3 eggs. *Q21*, moss and lichen on rock in open sclerophyll, 2 specimens, 1 egg. *Q22*, moss on tree in tall open forest, 1 specimen. AUSTRALIAN CAPITAL TERRITORY: *A1*, moss on rock in open sclerophyll, 1 egg. VICTORIA: *V4*, moss on soil in coastal heath, 13 specimens, 11 eggs. WESTERN AUSTRALIA: *W1*, moss and leaf litter on soil in street, 8 specimens, 9 eggs. *W3*, moss on tree, moss on limestone wall in park, 13 specimens, 16 eggs. TASMANIA: *T7*, moss on rock in wet sclerophyll, 3 specimens, 2 eggs. *T9*, moss on rock in wet sclerophyll, 4 specimens, 2 eggs. *T16*, moss on dolerite, 14 specimens, 2 eggs. *T18*, moss on dolerite, 9 specimens, 6 eggs. **Russia.** Archangel'sk District, moss on tree, 3 specimens, 1 egg.

Diagnosis. Mouth terminal. Three long macroplacoids and a remote microplacoid in pharynx. Strong band teeth in anterior of oral cavity, single row in posterior. Stylet supports inserted at 80-82% of buccal tube length. Buccal tube width 22-23%. Claws slender with thin accessory claws. Fine granulation above claws on all legs. Lunules small and smooth on all legs.

Description. Colourless. Body length 190 (embryo)-810 μm . Eye spots absent. Cuticle smooth, fine granulation on all legs. Mouth terminal Strong band of teeth in anterior part of oral cavity, single row thick blunt teeth in posterior position. Ventrally two strong lateral crests and 2 teeth in median position, 3 dorsal crests present. Buccal tube 50.3 μm long in 450 μm long specimen and 11.4 μm wide (22.6% of buccal tube length). Stylet supports inserted at 80-82% of buccal tube length, ventral support 60%. Pharynx round (50 μm diameter), containing small apophyses, three macroplacoids and a microplacoid joined to third macroplacoid by black line. First macroplacoid 7 μm long close to second 5.4 μm , third 8.7 μm , with caudal constriction, microplacoid 3.2 μm . Macroplacoid row 48% of buccal tube length. Claws long and slender, increasing in length from first to fourth. Secondary branch strongly curved, primary branch with short fine and low accessory claws. Claws of fourth pair of legs 13.5 μm long (27% of buccal tube length). Lunules small smooth and round on all legs.

Eggs colourless, round, diameter without processes 80 μm , with processes 110 μm . Eleven processes around circumference and 29 in hemisphere. Processes large areolated blunt cones base surrounded by about 10 large pores with characteristic wavy edge. Pores on the process surface more or less aligned along the long axis, processes 16 μm high, base diameter 19 μm .

Remarks. The specimens and egg from Russia are very similar to the Australian specimens. Recent work by Biserov (1996b), Binda & Pilato (2001) and Binda *et al.*, (2001) that there are many species in which both the adults and eggs bear a close resemblance to *M. richtersi* suggesting possible misidentifications in the literature.

Distribution. The species is cosmopolitan but should be the subject of closer examination.

Macrobotus rigatus sp. n.

Fig. 125, Plates VIc, VIIIc

Material examined. **Australia:** QUEENSLAND: *Q18*, moss and lichen on dead tree in park, 6 specimens. NEW SOUTH WALES: *N3.1*, moss on rock in open sclerophyll, 3 specimens; *N3.3*, *3.4*, moss on tree and rock in cool temperate rainforest, 121 specimens, 18 eggs; *N3.2*, *N3.5*, *N3.6*, moss and lichen on rocks and trees in subalpine heath, 176 specimens, 36 eggs. *N4*, moss and liverwort on tree in cool temperate rainforest, 4 specimens. *N11*, moss and lichen on tree in rainforest remnant, 3 specimens, 1 egg. *N14.1*, moss on rock in open sclerophyll, 1 egg; *N14.2* and *N14.3*, moss on trees, rocks and soil in rainforest remnant, 50 specimens, 4 eggs. *N39*, moss and lichen on rock in warm temperate rainforest, 52 specimens, 2 eggs. *N46.2*, moss and lichen on rock in subalpine open woodland, 7 specimens, 4 eggs. **TASMANIA:** *T1*, lichen on soil in remnant rainforest, 4 specimens. *T3*, moss on rock in heath-land, 14 specimens, 3 eggs. *T4*, moss on rock in wet forest, 6 specimens. *T7*, moss/liverwort/lichen on rock in wet forest, 38 specimens, 7 eggs. *T8*, moss/liverwort/lichen on soil in subalpine heath, 1 specimen. *T9*, moss on limestone in wet forest, 11 specimens. *T10*, liverwort on tree in cool temperate rainforest, 16 specimens, 2 eggs. *T16*, moss/lichen on dolerite on shaded slope, 9 specimens. *T18*, moss on dolerite, 1 specimen. *T20*, moss on rock in wet forest, 9 specimens, 14 eggs. *T21*, moss on rock in wet forest, 5 specimens, 14 eggs. **VICTORIA:** *V2*, lichen on rock in subalpine heath, 10 specimens, 2 eggs. *V3*, liverwort on tree in *Nothofagus* forest, 1 specimen.

Diagnosis. Mouth terminal. Two macroplacoids and a microplacoid in pharynx. Anterior teeth in oral cavity fine thin row, posterior teeth several rows strong teeth. Stylet supports

inserted at 81% of buccal tube length. Claws robust, with thick high accessory claw on all legs. Granulation around all claws, patch above claws on first three pairs. Lunules on first three pairs of claws smooth round, faintly toothed on fourth pair.

Description. Colourless. Body length 230-520 μm . Posterior eye spots present. Cuticle smooth except for patch of, granulation above claws on first three pairs of legs and back and sides on fourth pair of legs. Cuticle with round to elliptical pores (1-1.5 μm) on all surfaces. Mouth terminal. Anterior teeth in oral cavity a fine thin row, posterior teeth several rows strong teeth. Three ventral crests, median crest often rounded into a tooth) and 3 dorsal crests (median crest often a tooth) present. Buccal tube 40.5 μm long (in 420 μm individual) and 5.6 μm wide (13.9% of buccal tube length). Stylet supports inserted at 81% of length of buccal tube, ventral support long (62%). Pharynx round (43 μm diameter) with large apophyses, two macroplacoids and a microplacoid. Macroplacoid long rods, first with strong median constriction 10 μm long, second 8 μm . Macroplacoid row 48-55% of buccal tube length. Microplacoid 2.7 μm long, rather blunt. Claws robust deeply divided (Plate VIIIa), increasing in length from first to fourth. Secondary branch long and curved, primary branch with high accessory claws. Claws on fourth pair of legs 9.7 μm (23.5% of buccal tube length). Lunules round smooth on claws on first three pairs of legs, toothed on fourth pair.

Eggs white, round, laid free. Egg diameter with processes 86-97 μm , without 77-80 μm . 24 processes around circumference, 86 in a hemisphere. Processes shaped like upturned goblets (Plate VIa) with long neck and wide notched distal dish with cog-like arms. Processes 6-8.5 μm high, 6.5-8.5 μm base diameter, 4.5-5 μm dish diameter and 2-3 μm

apart. Shell surface with large 1 μm pores continuous with ring around base of each process.

Etymology. *Rigatus*, L., water, moisten, because this species was always found in mesic environments.

Remarks. The species is very similar to *M. hufelandi* but differs from it by always having teeth on the fourth pair of legs, by having strong granulation on the back and sides of the first three pairs of legs and by having shorter macroplacoid row length and claw lengths relative to the length of the buccal tube. This species is rather similar to *M. joannae* Pilato & Binda (1983) in details of the egg, however the adults have much shorter claws relative to the length of the buccal tube and a shorter macroplacoid row length.

Distribution. In Australia this species is restricted to the more mesic environments.

***Macrobotus rubens* Murray, 1907**

Macrobotus rubens Murray, 1907: 270-271, Pl. XIV, Fig. 5a-d

Type locality. Himalayas

Material examined. **Australia:** None. Cited by Murray (1910) as occurring at Katoomba, NSW.

Diagnosis. Reddish-brown body cells. Mouth terminal. Two macroplacoids and a microplacoid in pharynx. Stylet supports inserted at about 70% of buccal tube length.

Ventral support absent. Claws robust with thick accessory claws.

Description. Reddish, brown. Body length up to 450 μm . Eye spots present. Cuticle smooth. Mouth terminal. Buccal tube narrow. Stylet supports inserted at about 70% of length of buccal tube, ventral support absent. Pharynx round with small apophyses, two macroplacoids and a microplacoid. First macroplacoid longer than second. Claws robust deeply divided, increasing in length from first to fourth. Secondary branch long and curved, primary branch with high accessory claws. Claws on fourth pair of legs 9.7 μm (23.5% of buccal tube length). Lunules round smooth on claws on first three pairs of legs, lightly toothed on fourth pair.

Eggs smooth oval, deposited in exuvium.

Remarks. The absence of a ventral support on the buccal tube places this species in a genus other than *Macrobotus*. However, since no specimens were available for examination it was not transferred to another genus here.

Distribution. Known from North and South America, Ascension Island, East Africa, Himalayas, Australia and India.

***Macrobotus saltus* sp. n.**

Fig. 126, Plate Xa, b

Material examined. Australia: NEW SOUTH WALES: N4, liverwort and moss on trees in *Nothofagus* forest, 6 specimens, 3 eggs (1 embryonate). TASMANIA: T6, moss, 2 specimens, 1 embryonate egg.

Diagnosis. Mouth terminal. Three macroplacoids and a microplacoid in pharynx. Single row of teeth in anterior of oral cavity, one row and additional teeth ventrally in posterior.

Stylet supports inserted at 77% of buccal tube length. Buccal tube width 19%. Claws short and robust with short, thin accessory claws. Granulation around claws, if present very fine. Lunules on all legs smooth.

Description. Body length 150-430 μm , colourless. Eye spots absent. Cuticle smooth, granulation, if present, very fine and difficult to see. Mouth terminal. Row of dots in anterior of oral cavity, single row triangular teeth with additional teeth ventrally above crests in posterior. Three ventral crests, median usually broken into 2 teeth; 3 dorsal crests present. Buccal tube 48.7 μm long in 430 μm specimen and 9.2 μm wide (19% of buccal tube length). Stylet supports inserted at 77% of buccal tube length, ventral support 60-62%. Pharyngeal bulb round (38 μm diameter), containing large apophyses, three macroplacoids and a long microplacoid (Plate Xb). Macroplacoid row length 38-39% of buccal tube length; first macroplacoid long rod equal in length to third (5.4 μm) which has a terminal bulb, second always smallest (4.3 μm). Microplacoid 4.3 μm long. Claws short and robust with long secondary branch. Claws increasing in length from first to fourth. Accessory claws short and thin and lie close to primary branch on all legs. Anterior claw 10.8 μm long (22% of buccal tube length), posterior claw 11.3 μm (23%). Lunules on first three pairs of legs small round and smooth, with thick smooth edge on fourth pair of legs. Strong cuticular bars present on first three pairs of legs.

Egg round, diameter without processes 66 μm , with processes 100 μm , 24 processes around circumference, about 80 in hemisphere. Processes long finely tapering cones (Plate Xa), fine tip often bifurcate or trifurcate, often terminating in several fine hairs. Surface of processes areolate, narrow upper part with a few large clear pores, lower part with a few diffuse pores. Process height 13-15 μm , base diameter 8 μm , about 1-2 μm apart. Each process with corona of dark points around base. Shell surface with small indistinct pores.

Etymology. *Saltus* L. m., woodland

Remarks. This species is rather similar to *M. woodyi* sp. n. in the shape of the macroplacoids and in having eggs with processes with a corona of points around the base. That species, however, has the stylet supports inserted at 80% or greater of the buccal tube length whilst *M. saltus* has them inserted at 77%.

Distribution. Occurs infrequently, found only in two rainforest localities.

Macrobiotus santoroi Pilato & D'Urso, 1976

Fig. 127, Plates VIId, VIIId

Macrobiotus santoroi Pilato & D'Urso, 1976: 140-142, Fig. 1B, B'

Type locality. Australia. Wallacia, NSW.

Material examined. Australia: NEW SOUTH WALES: *N24*, foliose lichen on rock in open sclerophyll, 3 specimens, 3 eggs; *N27*, moss on rock, foliose lichen on soil in open sclerophyll, 21 specimens, 8 eggs. *N28*, moss on rock in open sclerophyll, 4 specimens, 1 egg. QUEENSLAND: *Q21*, moss and lichen on rock in open sclerophyll, 4 specimens, 1 egg.

Diagnosis. Mouth terminal. Two macroplacoids and a microplacoid in pharynx. No teeth in anterior of oral cavity, band small teeth in posterior. Stylet supports inserted at 78-79% of buccal tube length. Claws long slender, primary and secondary branches joined in bulbous base with thin accessory claws. Granulation on all legs, patch on outside of first three pairs of legs. Lunules large and smooth on all legs.

Description. Colourless. Body length 220-570 μm . Eye spots present. Cuticle covered with round to elliptical pores. Patch of fine granulation on outside of first three pairs of legs and round claws on fourth pair. Mouth terminal. No teeth in anterior of oral cavity and band small teeth in posterior. Three ventral crests (median crest a tooth) and three dorsal crests. Buccal tube 48.7 μm in 410 μm long specimen and 6.8 μm wide (14% of buccal tube length). Stylet supports inserted at 78-79% of buccal tube length, ventral support 62%. Pharynx oval (45 μm by 39 μm) containing small apophyses, two macroplacoids and a microplacoid. First macroplacoid with weak median constriction 9.7 μm long, second with weak caudal bulb 6.2 μm . Microplacoid distinct 2 μm long. Macroplacoid row 39% of buccal tube length. Claws slender (Plate VIII d) with secondary branch almost as long as primary, increasing in length from first to fourth. Accessory claws short and rather thin although higher on the fourth pair. Claws of fourth pair of legs 15 μm long (31.5% of buccal tube length). Lunules rather large, round and smooth on all legs.

Eggs colourless, round, diameter without processes 76 μm , with processes 85 μm . 38-43 processes around circumference, 110 in hemisphere. Processes shaped like small thimble with ring tiny teeth around top (Plate VI d). Processes 3.5-4 μm high, base diameter 3.5-4 μm , diameter at top 2 μm , 2 μm apart, base of each process indented. Egg shell with tiny pores (0.5 μm).

Remarks. This species differs from the two other species in the *hufelandi* group from Australia with smooth lunules on the fourth pair of legs by having the fourth pair of claws greater than 30% of the buccal tube length and having teeth in the anterior part of the oral cavity.

Distribution. The species was only found in dry sclerophyll sites. It was found in Indonesia by Pilato & Binda (1990).

Macrobotus saxatilis sp. n.

Fig. 128, Plates VIe, VIIIe, IXf

Material examined. **Australia:** NEW SOUTH WALES: *N14.7*, moss on path in garden, 8 specimens. *N15*, moss on limestone wall in sheltered valley, 15 specimens, 3 eggs. *N18*, moss on asphalt in suburban street, 15 specimens, 2 eggs. *N29*, moss on limestone in sheltered valley, 25 specimens, 14 eggs (2 embryonate). *N40*, moss and lichen on sandstone in open sclerophyll, 23 specimens, 3 eggs. **WESTERN AUSTRALIA:** *W4*, moss on limestone wall, 4 specimens.

Diagnosis. Mouth terminal. Two macroplacoids and a microplacoid in pharynx. No teeth in anterior of oral cavity, band of very fine teeth in posterior. Stylet supports inserted at 78% of buccal tube length. Claws long and slender, with thin accessory claw on all legs. Granulation around all claws, patch on outside of first three pairs of legs. Lunules on first three pairs of claws smooth, on fourth pair with strong teeth.

Description. Colourless. Body length 190-612 μm . Large eye spots present. Cuticle smooth except for patch of granulation above claws on first three pairs of legs and back and sides on fourth pair of legs. Cuticle with small round pores (0.5 μm) on all surfaces. Mouth terminal. No teeth in anterior position in oral cavity, 2 rows of teeth in posterior. Three ventral and 3 dorsal crests present. Buccal tube 41.6 μm long (in 400 μm individual) and 7 μm wide (17% of buccal tube length). Stylet supports inserted at 78% of buccal tube length, ventral support 58%. Pharynx round (40 μm diameter) with large apophyses, two macroplacoids and a microplacoid. First macroplacoid 9.7 μm long with strong median constriction, second 7 μm with slight subterminal constriction. Macroplacoid row 44% of

buccal tube length. Microplacoid 2.7 μm long. Claws long and slender (Plate VIIIe), outer slightly longer than inner on all legs; increasing in length from first to fourth, second and third equal in length. Secondary branch short and curved. Primary branch with short thin accessory claws. Anterior claws on fourth pair of legs 13.5 μm long (32.5% of buccal tube length), posterior 14.1 μm (33.8%). Lunules round with thick smooth edge on first three pairs of legs; large with strong teeth on fourth pair (posterior slightly larger than anterior).

Eggs white, round laid free. Egg diameter with processes 87 μm , without 77 μm . 20 processes around circumference, 110 in hemisphere. Processes shaped like upturned goblets (Plate VIe) with distal dish with cog-wheel appearance. Processes 5.5-6.5 μm high, 5-5.5 μm base diameter, dish 4 μm and about 3 μm apart. Shell surface covered with pores about 1 μm diameter with walls of uniform thickness continuous with pores around base of each process.

Etymology. *Saxum*, L. n, rock; *saxatilis*, found among rocks, named because this species was found only on rock or-rock-like substrate.

Remarks. The claws of this species are very similar to those of *M. galorensis*, *M. echinatus* and *M. santoroi*. It differs from *M. galorensis* in having teeth in the posterior part of the oral cavity, from *M. echinatus* by having smooth lunules on the first three pairs of legs and from *M. santoroi* by having teeth on the lunules on the fourth pair of legs.

Distribution. The species is widespread, found on the west coast as well as on the east coast.

***Macrobiotus tasmanicus* sp. n.**

Fig. 129

Material examined. **Australia:** TASMANIA: *T3.2*, moss and liverwort on rock in low wood heathland at 470 m., 36 specimens, 27 eggs. *T5*, moss on tree in wet forest gully, 2 specimens, 2 eggs. *T7*, moss, liverwort and lichen on rock and moss and liverwort on soil in wet forest gully slope, 87 specimens, 42 eggs (1 embryonate). *T10*, liverwort on tree in cool temperate rainforest, 2 eggs. *T16*, moss/lichen on dolerite on shaded slope, 21 specimens, 9 eggs. *T17*, moss on dolerite boulder at 620 m. on island, 23 specimens, 7 eggs (3 embryonate). *T18*, moss on dolerite in dry sclerophyll woodland, 9 specimens, 14 eggs (1 embryonate). *T21*, moss on rock in closed forest, 3 specimens, 7 eggs. NEW SOUTH WALES: *N44*, moss and lichen on rock in subalpine heath, 9 specimens, 18 eggs. *N46*, moss on rock in subalpine heath, 37 specimens, 28 eggs.

Diagnosis. Mouth terminal. Two macroplacoids and a microplacoid in pharynx. Thick band of teeth in anterior of oral cavity, row of strong triangular teeth with second row ventrally above crests in posterior. Stylet supports inserted at 79-80% of buccal tube length. Buccal tube width 17%. Claws robust with thick accessory claws. Granulation on all legs, patch above claws on first three pairs. Lunules on first three pairs of claws smooth, fine teeth on fourth pair.

Description. Colourless. Body length 189-743 μm . Anterior eye spots present. Cuticle smooth except for patch of granulation above claws on first three pairs of legs and back and sides on fourth pair legs. Mouth terminal. Strong thick band of teeth in anterior of oral cavity, single row of triangular teeth and, ventrally, a second row above crests in posterior. Three ventral (median often divided into two or three teeth) and three dorsal crests present. Buccal tube 44.3 μm long (in 395 μm individual) and 7.6 μm wide (17% of buccal tube length). Stylet supports inserted at 79-80% of length of buccal tube. Ventral support bar long (61%). Pharynx large and round (49 μm diameter) with large apophyses, three

macroplacoids and a large microplacoid. Macroplacoid rounded rods, first and third similar in length (6 μm), second usually slightly smaller (5.4 μm); macroplacoid row length (46%). Microplacoid large (3.8 μm). Claws robust with long secondary branch, increasing in length from first to fourth. Accessory claws short and thick and high above primary branch. Claws on fourth pair of legs long, 10.8 μm (29%). Lunules round small smooth on first three pairs of legs; finely toothed on fourth pair, posterior lunule larger than anterior on fourth pair of legs.

Eggs white, round, laid free. Egg diameter with processes 135 μm , without 78 μm ; 8-10 processes around circumference, 16-17 in hemisphere. Processes elongated straight-sided cones with areolate surface extending to struts joining processes but absent from tapering part of process in Tasmanian specimens. Processes 32-45 μm high, 16-30 μm base diameter often with small hairs around tip. Shell with 12-14 large pores around base of each process, surface within them smooth.

Remarks. Differs from *M. liviae* Ramazzotti 1962 by having smooth cuticle and different teeth in the oral cavity.

Distribution. Widely distributed in Tasmania.

***Macrobiotus torridus* sp. n.**

Fig. 130, Plates VI f, VIII f

Material examined. **Australia:** NEW SOUTH WALES: *N3.1*, moss and lichen on rock, leaf litter on soil in open sclerophyll, 27 specimens, 1 egg; *N3.2*, *N3.5*, moss on tree and moss and lichen on rock in subalpine heath, 36 specimens, 4 eggs. *N5*, lichen on rock in open sclerophyll, 2 specimens, 1 egg. *N8*, lichen on

asphalt, gumnuts on soil in urban carpark, 51 specimens, 7 eggs. *N9*, lichen on tree branch on ground, leaf litter on soil in temperate rainforest, 14 specimens, 3 eggs. *N11*, lichen on tree in street, 34 specimens, 14 eggs (4 in one cuticle). *N14.3*, moss on rock in remnant rainforest, 1 specimen. *N15.2*, foliose lichen on rock in closed valley, 12 specimens, 13 eggs (5 embryonate eggs in *Milnesium tardigradum* cuticle). *N20*, lichens on tree in street, 18 specimens, 8 eggs. *N21*, lichen on trees in street, 44 specimens, 13 eggs. *N24*, lichen on rock in open sclerophyll, 8 specimens, 6 eggs. *N27*, moss and lichen on rock in open sclerophyll, 16 specimens, 4 eggs. *N31*, lichen on tree in warm temperate rainforest, 22 specimens, 3 eggs. *N42*, lichen on tree in open forest near beach, 4 specimens, 3 eggs. QUEENSLAND: *Q8*, lichen on tree in park, 27 specimens, 13 eggs. *Q15*, moss on tree in dry rainforest, 10 specimens, 7 eggs. *Q17*, moss and lichen on tree in open sclerophyll, 10 specimens, 1 egg. *Q21*, moss and lichen on rock in open sclerophyll, 6 specimens, 1 egg. *Q25*, lichen on tree in warm temperate rainforest, 38 specimens, 5 eggs. LORD HOWE ISLAND: 22 specimens, 18 eggs. TASMANIA: *T2*, lichen and moss on rock on headland, 9 specimens, 2 eggs.

Diagnosis. Mouth terminal. Two macroplacoids and a microplacoid in pharynx Fine thin band of teeth in anterior of oral cavity, several rows strong teeth in posterior. Stylet supports inserted at 78% of buccal tube length. Claws robust, with thin accessory claws. Very fine faint granulation on all legs, in patch above claws on first three pairs of claws. Lunules on all claws smooth round.

Description. Body length 230-505 μm , colourless. Posterior eye spots present. Cuticle smooth except for patch of very faint (often not visible at all), granulation above claws on first three pairs of legs and back and sides on fourth pair of legs. Cuticle with large elliptical pores (1-1.5 μm) on all surfaces. Mouth terminal. Fine thin row teeth in anterior of oral cavity, several rows strong teeth in posterior. Three ventral crests (median one a tooth) and 3 dorsal (median crest often a tooth) crests present. Buccal tube 44.3 μm long (in 430 μm individual) and 8.1 μm wide (18.3% of buccal tube length). Stylet supports inserted at 78% of length of buccal tube, ventral support long (65%). Pharynx round to oval (45 μm by 42 μm) with large apophyses, two macroplacoids and a microplacoid.

Macroplacoid rounded rods, first with strong median constriction 9.7 μm long, second with faint caudal bulb 5.4 μm . Macroplacoid row short (42.7% of buccal tube length).

Microplacoid short, 2.2 μm long, rather blunt. Claws robust (Plate VIII f), deeply divided, increasing in length from first to fourth. Secondary branch long and curved, primary branch with short rather thin accessory claws. Claws on fourth pair of legs 12.4 μm (28% of buccal tube length). Lunules round smooth on claws on all legs.

Eggs white, round, laid free. Egg diameter with processes 92 μm , without 81 μm ; 22-25 processes around circumference, 90-100 in hemisphere. Processes shaped like small cylinders (Plate VI f) with rather straight sides and a small notched distal dish. Base of each process surrounded by small pores but not obviously indented by them, pores are continuous with other pores over shell surface. Processes 4.5-5.5 μm high, 4 μm base diameter, dish 3 μm diameter and about 5-6 μm apart. Shell surface with small pores with rather thick walls.

Etymology. *Torridus*, L, dry, parched, for the environment in which this species appears to be most common.

Remarks. The adults are similar to other species with *hufelandi* type buccal apparatus (with 2 macroplacoids and a microplacoid). This species differs from the other two species from Australia (*M. santoroi* and *M. microcalix*) with smooth lunules on the fourth pair of legs by having claws on the fourth pair of legs 28% of the buccal tube length.

Distribution. Widely distributed down the east coast, this species prefers dry environments.

***Macrobiotus virgatus* Murray 1910**

Macrobiotus virgatus Murray, 1910: 173-174, Pl. XXI, Fig. 55a-c

Type locality. Vancouver, Canada.

Material examined. **Australia:** None. The species was cited by Murray (1910) from Katoomba, Blue Mountains, NSW.

Diagnosis. Brown colour arranged in longitudinal bands. Mouth terminal. Three macroplacoids, no microplacoid in pharynx. Claws robust very unequal in size, united for half the length of the primary branch with thick accessory claws.

Description. Body length up to 750 μm , with brown pigmentation in three main longitudinal bands. Two lateral bands may be subdivided into narrower bands and there are some thin transverse bands. Eye spots present. Mouth terminal. Teeth in oral cavity unknown. Ventral and dorsal crests unknown. Buccal tube 9-10 μm wide. Three macroplacoids microplacoid absent. Macroplacoid rounded rods, first and third long, second a small nut. Claws robust of *hufelandi* type but unequal in size. Accessory claws thick.

Eggs unknown.

Remarks. The species is probably a member of the genus *Doryphoribius* but no species with these characteristics was found in this study.

Distribution. Found also in Europe and South America.

***Macrobotus woodyi* sp. n.**

Fig. 131, Plate Xc, d

Material examined. Australia: QUEENSLAND: *Q18*, fruticose lichen on tree in open woodland, 7 specimens, 4 eggs (1 embryonate). NEW SOUTH WALES: *N11*, moss on tree in rainforest remnant, 10 specimens, 1 egg. *N49*, moss on rotten log in temperate rainforest, 1 specimen, 1 egg.

Diagnosis. Mouth terminal. Three macroplacoids and a microplacoid in pharynx. Band of teeth in anterior of oral cavity, single row close to crests in posterior. Stylet supports inserted at 76-78% of buccal tube length. Buccal tube width 19%. Claws robust with short, thin accessory claws. Granulation on all legs, patch above claws on first three pairs of legs. Lunules smooth on first three pairs of claws, with tiny teeth on fourth pair.

Description. Colourless. Body length 170-450 μm . Eye spots absent. Cuticle smooth, patch of very fine granulation present above external claw of first three pairs of legs and over back and sides of fourth pair of legs. Mouth terminal. Band of tiny teeth in anterior of oral cavity, single row triangular teeth close to crests in posterior. Three ventral crests and 3 dorsal crests present. Buccal tube 42.7 μm long in 440 μm specimen and 8.1 μm wide (19% of buccal tube length). Stylet supports inserted at 76-78% of buccal tube length, ventral support 57-62%. Pharynx round (44 μm diameter), containing small apophyses, three macroplacoids and a rather short microplacoid (Plate Xd). Macroplacoid row length 41-45% of buccal tube length; first macroplacoid equal in length to third (4.2 μm) which has a terminal bulb, second always smallest (3.2 μm). Microplacoid 2.7 μm long. Claws robust with long secondary branch, external claw slightly longer than internal. Claws increasing in length from first to fourth. Accessory claws short and thin on first three pairs of legs, thin but raised at the tip on fourth pair. Anterior claw 10.3 μm long (24% of buccal

tube length), posterior claw 10.8 μm (25%). Lunules on first three pairs of legs small round and smooth, with tiny teeth on fourth pair of legs. Cuticular bars present on first three pairs of legs.

Egg round, diameter without processes 77-80 μm , with processes 106-110 μm , 15-25 processes around circumference, 34-80 in hemisphere. Processes long finely tapering areolated cones (Plate Xc), fine tip often terminating in several fine hairs. Process height 12 μm (in NSW populations) 14.6-19 μm , base diameter (8 μm) 11-16 μm , (2) 3 μm apart. Each process with corona of dark points around base. Shell surface with tiny pores in a thick matrix.

Etymology. The species is named for Dr. D.S. “Woody” Horning for his friendship and advice on the Tardigrada.

Remarks. This species is similar to *M. harmsworthi* and *M. saltus* sp. n. in the shape of the macroplacoids and in having eggs with processes with a corona of points around the base. It differs from the former by lacking eyes and having a much shorter macroplacoid row length. It differs from the latter by having teeth on the lunules on the fourth pair of claws.

Distribution. Rather widespread down the east coast but not abundant or frequent, this species was only found on trees in rainforest or similar habitats (Q18, Eumundi, has remnants of the once prolific rainforest in that area).

Macrobotus sp. 1

Fig. 132

Material examined. Australia: QUEENSLAND: Q7, moss/liverwort on rock in open forest, 1 specimen.

Diagnosis. Mouth terminal. Two macroplacoids and microplacoid in pharynx. No teeth in anterior of oral cavity, fine band in posterior. Stylet supports inserted at 78% of buccal tube length. Claws slender and long, accessory claws short and thin. Granulation around all claws, strong patch above claws on first three pairs of legs. Lunules on all claws toothed.

Description. Colourless except for patches of pigment below dorsal cuticle. Body length 460 μm . Eye spots present. Cuticle smooth except for strong patch of granulation above claws on first three pairs of legs and back and sides on fourth pair of legs. Mouth terminal. No teeth in anterior of oral cavity, faint band teeth in posterior. Three ventral and 3 dorsal crests present. Buccal tube 45 μm long (in 460 μm individual) and 6.5 μm wide (14.5% of buccal tube length). Stylet supports inserted at 78.3% of length of buccal tube, ventral support 60%. Pharynx round (50 μm) with small apophyses, two macroplacoids and a microplacoid. Macroplacoid long rods, first 11.4 μm long with weak median constriction, second 6 μm . Macroplacoid row length 48% of buccal tube length. Microplacoid 3.2 μm long thin faint. Claws long slender, external slightly longer than internal and increasing in length from first to fourth. Secondary branch long and curved, primary branch with short thin accessory claws. Anterior claws of fourth pair of legs 14 μm (31% of buccal tube length), posterior claws 14.6 μm (32.5%). Lunules large with small but sharp evenly spaced teeth on all legs, posterior larger than anterior on fourth pair of legs.

Eggs not found.

Remarks. This species differs from *M. hufelandi* by having no teeth in the oral cavity, it is most similar to *M. guttus* but differs by having stylet supports inserted more anteriorly and having longer claws relative to the buccal tube length and teeth on the lunules of all legs.

Distribution. Only found at one site.

Macrobotus sp. 2

Fig. 133

Material examined. Australia: QUEENSLAND: *Q18*, lichen on tree, pine cone in street, 7 specimens.

Diagnosis. Mouth terminal. Two macroplacoids and microplacoid in pharynx. No teeth in oral cavity. Stylet supports inserted at 73-74% of buccal tube length. Claws large robust with thick accessory claws high at tip. Granulation on all legs, in patch on side of first three pairs of legs. Lunules smooth on first three pairs of legs, toothed on fourth pair.

Description. Colourless, patches of red pigment below dorsal cuticle in some specimens. Body length 270-490 μm . Large eye spots present. Cuticle smooth with small round pores and patches of fine granulation above claws on first three pairs of legs and back and sides on fourth pair of legs. Mouth terminal. No teeth in oral cavity. Three ventral and 3 dorsal crests present. Buccal tube 40 μm long (in 490 μm individual) and 7 μm wide (17.5% of buccal tube length). Stylet supports inserted at 73-74% of buccal tube length, ventral support 56%. Pharynx oval (43 μm by 38 μm) with small apophyses, two macroplacoids and a microplacoid. First macroplacoid 9.2 μm long with very weak median constriction,

second 5.4 μm . Macroplacoid row length 45% of buccal tube length. Microplacoid 2 μm long, thin. Claws large robust, external slightly longer than internal and increasing in length from first to fourth, second and third equal in length. Secondary branch short and strongly curved, primary branch strongly curved with thick accessory claws that rise well above branch. Anterior claw of fourth pair of legs 13 μm (32% of buccal tube length), posterior claws 13.5 μm (33.8%). Lunules on first three pairs of legs smooth thick edge, on fourth pair large with strong teeth, posterior larger than anterior on fourth pair of legs.

Eggs not found.

Remarks. This species differs from *M. hufelandi* by having no teeth in the oral cavity and by having the stylet supports inserted much more anteriorly.

Distribution. Only found at on site.

***Macrobiotus* sp. 3**

Fig. 134, Plate IXc

Material examined. **Australia:** AUSTRALIAN CAPITAL TERRITORY: *AI*, moss on rock at edge of stream, 8 specimens.

Diagnosis. Mouth antero-ventral. Two macroplacoids and microplacoid in pharynx. No teeth in oral cavity. Stylet supports inserted at 75% of buccal tube length. Claws long with bulbous common tract, accessory claw on all legs thin. No granulation around claws. Lunules on first three pairs of legs smooth, on fourth pair toothed.

Description. Colourless. Body length 270-447 μm . Large eye spots present. Cuticle with pores (1-2 μm) on all surfaces. Mouth antero-ventral. No teeth in oral cavity. Ventro-lateral crests weak, median ventral tooth present, dorsal crests very weak. Buccal tube 48 μm long (in 420 μm individual) and 6.5 μm wide (13.5% of buccal tube length). Buccal tube walls thick particularly below the level of insertion of the stylet supports, internal diameter 3.2 μm . Stylet supports inserted at 74.7% of buccal tube length, ventral support 58%. Pharynx round (46 μm diameter) with large apophyses, two macroplacoids and a microplacoid. First macroplacoid 8.7 μm long with median constriction, second 5.4 μm with slight subterminal constriction. Macroplacoid row 34% of buccal tube length. Microplacoid 2.2 μm long, close to second macroplacoid. Claws long and slender with bulbous common tract (Plate IXc), outer slightly longer than inner on all legs; increasing in length from first to fourth, second and third equal in length. Secondary branch very long and curved strongly only at distal end, primary branch with long thin accessory claws; strongly refractive bulbous common base. Anterior claws on fourth pair of legs 18.9 μm long (39% of buccal tube length), posterior 21.6 μm (45%). Lunules large oval with thick smooth edge on first three pairs of legs; large with strong teeth on fourth pair (posterior slightly larger than anterior).

Eggs not found.

Remarks. The claws of this species are very similar to those of *M. adelges* Dastych, 1977 but it differs from that species by having pores in the cuticle, having shorter claws and having a thickened buccal tube wall. It is also similar to *M. galorensis* and *M. echinatus*. It differs from *M. galorensis* in having much longer claws and stylet supports inserted more caudally, from *M. echinatus* by having smooth lunules on the first three pairs of legs.

Distribution. Only found at one site

***Macrobotus* sp. 4**

Fig. 135

Material examined. **Australia:** NEW SOUTH WALES: *N3.2*, moss/lichen on rock in *Banksia collina* scrub, 2 specimens. *N46.3*, lichen on rock in subalpine heath, 3 specimens.

Diagnosis. Mouth terminal. Three macroplacoids and microplacoid in pharynx. No teeth in anterior of oral cavity, single row pointed teeth in posterior. Stylet supports inserted at 77.6% of buccal tube length. Claws robust, with thick accessory claw on all legs. Granulation around claws on all legs and small tubercles on dorsum above fourth pair of legs. Lunules smooth on all claws.

Description. Colourless. Body length up to 450 μm . Eye spots present. Cuticle with smooth in anterior part of body, with tubercles (1.5-2 μm diameter on dorsum above fourth pair of legs. Granulation present on back and outsides of first three pairs of legs, back and both sides of fourth pair. Mouth terminal. No teeth in anterior of oral cavity, single row pointed teeth in posterior. Three ventral and three dorsal crests present. Buccal tube 46 μm long (in 450 μm individual) and 5.4 μm wide (11.8% of buccal tube length). Stylet supports inserted at 77.6% of buccal tube length, ventral support 56.4%. Pharynx round (41 μm diameter) with large apophyses, three macroplacoids and a microplacoid. First macroplacoid 4.9 μm long, second 4.3 μm and third 5.4 μm with slight subterminal constriction. Macroplacoid row 35% of buccal tube length. Microplacoid 2.7 μm long large and drop-shaped. Claws robust, increasing in length from first to fourth, second and third equal in length, with large round refractive base. Secondary branch long and curved,

primary branch with short thick accessory claws. Claws on fourth pair of legs 10.8 μm long (23.5% of buccal tube length). Lunules small round with thin smooth edge on all claws.

Eggs not found.

Remarks. This species is very similar to *Macrobiotus arguei* Pilato & Sperlinga, 1975 which also has small tubercles on the dorsum above the fourth pair of claws. However this species differs from *M. arguei* by having the stylet supports inserted much higher up the buccal tube (77.6% of buccal tube length, 85% in *M. arguei*). *M. arguei* has anterior teeth in the oral cavity and the posterior teeth are very showy, it also has a small third macroplacoid.

Distribution. The two sites at which the species was found, although many hundreds of kilometres apart are very similar in altitude and vegetation type.

Genus *Minibiotus* Schuster, Nelson, Grigarick & Christenberry, 1980

Minibiotus Schuster, Nelson, Grigarick & Christenberry, 1980: 294.

Type species. *Macrobiotus intermedius* Plate, 1888: 535.

Diagnosis. Ten peribuccal papulae present. Mouth antero-ventral, teeth in oral cavity absent or strongly reduced. Buccal tube rigid, ventral support present. Buccal tube narrow (12% or less of buccal tube length); wall thickened below point of insertion of stylet supports; stylet supports inserted at 73% or less of buccal tube length; ventral support short (62% or less of buccal tube length) and macroplacoid row length 42% or less of buccal tube length. Diploclaws on each leg similar in shape and size, symmetrical with respect to median plane of leg. Diploclaws with small base attached to leg by narrow peduncle, separated from branches by septum. Eggs with processes on shell deposited freely.

Keys to species of *Minibiotus*

Key to adults

- 1. Two macroplacoids present..... 2
 - Three macroplacoids present..... 3
- 2. Cuticle with dorsal tubercles especially towards rear..... *M. fallax*
 - Cuticle without dorsal tubercles..... *M. scopulus*
- 3. Cuticle with pores..... 4
 - Cuticle without pores..... 9
- 4. Pores in rows..... 5
 - Pores randomly distributed..... 7
- 5. Cuticle thickened in caudal region..... *M. ethelae*

No caudal thickening.....	6
6. Eight rows of small (0.5 μm) pores.....	<i>M. poricinctus</i>
Ten rows (1.0 μm) pores.....	<i>M. keppelensis</i>
7. Soft spines above fourth leg, or above last three pairs legs.....	<i>M. aculeatus</i>
No soft spines.....	8
8. Granulation on fourth pair of legs only.....	<i>M. asteris</i>
Granulation on all legs.....	9
9. Cuticle with transverse rows of wrinkles.....	<i>M. pilatus</i>
Cuticle smooth.....	10
10. Granulation around claws absent or very sparse.....	<i>M. intermedius</i>
Granulation around all claws.....	11
11. Macroplacoid row length long (<i>pt</i> greater than 36).....	12
Macroplacoid row length short (<i>pt</i> less than 35).....	14
12. Stylets inserted at <i>pt</i> 73.....	<i>M. milleri</i>
Stylets inserted at <i>pt</i> less than 73.....	13
13. Ventral reinforcing bar long (<i>pt</i> 53), claws long (<i>pt</i> fourth pair 34.6).....	<i>M. aquatilis</i>
Ventral reinforcing bar short (<i>pt</i> 46), claws short (<i>pt</i> fourth pair (9.3).....	<i>M. hufelandioides</i>
14. Toothed lunules on fourth claws, short high accessory claws..	<i>M. maculartus</i>
Smooth lunules on fourth claws.....	15
15. Stylet supports inserted at <i>pt</i> 51.....	<i>M. arcanus</i>
Stylet supports inserted at <i>pt</i> greater than 51.....	16
16. Stylet supports inserted at <i>pt</i> 60.3; short, low accessory claws.	<i>M. taiti</i>
Stylet supports inserted at <i>pt</i> greater than 60.3.....	17

17. Claws long (*pt* fourth pair 34.0), high accessory claws..... *M. floriparus*
 Claws short (*pt* fourth pair 28.1), low accessory claws..... *M. hispidus*

Key to eggs

1. Processes with membrane..... 2
 Processes without membrane or with partial membrane..... 5
2. Membrane covering thin nail-like processes..... *M. taiti*
 Membrane enclosing each process separately..... 3
3. Processes shaped like short-stemmed flowers..... *M. floriparus*
 Processes shaped like screw-heads..... 4
4. Processes small, height 2.5-3.5 μm , top 2.5-3.5 μm , 3-4 μm
 apart..... *M. intermedius*
 Processes height 6.5-7 μm , top 5.5 μm , 6-8 μm apart..... *M. poricinctus*
5. Processes partially enclosed by membrane..... 6
 Processes without membrane..... 8
6. Processes long, javelin-shaped, protruding through membrane
 and arranged in rings, others processes short rods..... *M. pilatus*
 Processes cone-shaped..... 7
7. Processes short cones with large pores around wide base,
 membrane reaching only to top of pores..... *M. keppelensis*
 Processes long cones tapering to blunt tip, indented base
 enclosed in membrane..... *M. milleri*
8. Processes in form of inverted chalice..... 9
 Processes cone-shaped or hemispherical..... 10
9. Distal disk of processes with smooth or slightly notched

margin, shell dotted.....	<i>M. hufelandioides</i>
Distal disk of processes with 6-8 distinct arms, shell smooth...	<i>M. asteris</i>
10. Processes hemispherical, shell surface smooth.....	<i>M. cf weinerorum</i>
Processes conical or if hemispherical with longitudinal ridges around base.....	11
11. Processes conical or hemispherical with longitudinal ridges around base.....	<i>M. maculartus</i>
Processes elongated cones.....	12
12. Processes fine and close; shell reticulate.....	<i>M. hispidus</i>
Processes with conical or swollen base; shell smooth or dotted	13
13. Smooth egg shell.....	<i>M. aculeatus</i>
Dots on egg shell.....	14
14. Processes base indented; processes 11-12 µm long.....	<i>M. aquatilis</i>
Processes base smooth.....	15
15. Processes with round base rising rapidly to fine filamentous tip.....	16
Processes strap-like variable in length, slightly swollen at base	17
16. Processes 5-6 µm long.....	<i>M. furcatus</i>
Processes 12-23 µm long.....	<i>M. ethelae</i>
17. Processes 6-11 µm long, rarely up to 16 µm.....	<i>M. scopulus</i>
Processes 12-16 µm long, rarely up to 22 µm.....	<i>M. fallax</i>

***Minibiotus aculeatus* (Murray, 1910)**

Fig 136

Macrobiotus aculeatus Murray, 1910: 139-140, Pl. XVIII figs 27a-27e.

Macrobiotus intermedius subjulietae Horning, Schuster and Grigarick, 1978: 237, figs 117-120.

Type locality. Australia. Mount Kosciusko, NSW.

Material examined. Australia: NEW SOUTH WALES: *N3.5.a*, moss and lichen on rocks and trees in *Banksia* heath, 36 specimens, 2 eggs, *N3.6.a*, moss and lichen on rock in heath, 13 specimens, 1 egg; *N3.3.a*, lichen on tree in *Nothofagus* forest, 1 specimen; *N3.2.b*, moss and lichen in heath, 91 specimens, 4 eggs. *N15.1.a*, *N15.2.a*, , moss on trees and rocks in sheltered valley, 22 specimens, 6 eggs. *N4*, moss on branch on ground in closed forest, 1 specimen. *N11.a*, moss on tree in cool temperate rainforest, 1 specimen, 1 egg. *N46.1* (**type locality**), lichen on rock in open sclerophyll, 1 egg; *N46.2*, *46.3*, lichen on rock in subalpine open woodland, 7 specimens, 2 eggs. QUEENSLAND: *Q22*, moss on tree in closed forest, 5 specimens. *Q25.b.*, foliose lichen on tree branch in temperate rainforest, 1 specimen. LORD HOWE ISLAND, lichen, 18 specimens, 1 egg. TASMANIA: *T17*, moss on rock in heath, 7 specimens. (SKC) **New Zealand:** 16 paratypes of *Macrobiotus intermedius subjulietae*: NORTH ISLAND: (NZ650) Waimaua Gorge, 17 May 1971, C.J. Horning, 1 specimen; (NZ672) Grays Bush, 19 May 1971, C.J.H., 1 specimen; (NZ705) Bruce Park Scenic Reserve, 21 May 1971, D.S. Horning, 3 specimens; (NZ279, NZ281) Taumarunui, 15 Jul 1970, B.J. Donovan, 2 specimens; (NZ687) Norsewood, 20 May 1971, D.S.H., 1 specimen; (NZ753) Mount Egmont National Park, 23 May 1971, D.S.H., 1 specimen; (NZ674) Morere Hot Spring Scenic Reserve, 19 May 1971, D.S.H., 1 specimen. SOUTH ISLAND: (NZ538) Abel Tasman National Park, 9 Apr 1971, D.S.H., 1 specimen; (NZ86) Cowper's Knob, 9 Apr 1970, D.S.H., 1 specimen; (NZ544) West Harper Hut, 12 Apr 1971, H.A. Best, 1 specimen. Chatham Island: (NZ932, NZ924) Waterfall Creek, 31 Aug 1971, D.S.H., 2 specimens. Three Kings Island: (NZ479) Summit Ridge, 28 Nov 1970, G.W. Ramsey, 1 specimen. (NZM)

Diagnosis. Smooth cuticle with pores of variable size and shape and three pairs of soft spines (Fig. 17a) over last three pairs of legs (or one pair over fourth pair; three small round macroplacoids and a distinct microplacoid; short, robust claws with prominent accessory claws and very small refractive base and lunules.

Description. Body length 204-350 μm most specimens pink or pale brown in colour. Eyes in the posterior position. Cuticle covered with small (0.5 μm diameter) round pores and, more sparsely, large triangular or star-shaped pores; large pores often with thickened rims. A ring of about ten pores around the mouth below the sensory fields are visible only under the highest light magnification and appear as slits in specimens prepared for SEM (Fig 1b). The shape under SEM is probably due to distortion of the specimen during preparation. Three pairs of soft, conical spines (about 7 μm long) on body, one pair each above the last three pairs of legs. No teeth in oral cavity, buccal tube narrow 2 μm (*pt* 7.8). Stylet supports inserted at 63.7% of length of buccal tube, ventral reinforcing bar 51.4% of buccal tube length. Pharyngeal bulb oval (27 μm by 30 μm) containing well developed, granular apophyses, three macroplacoids and a microplacoid. Macroplacoid row short (32.2% of buccal tube length); first macroplacoid pear-shaped lying close to apophysis and partly obscured by it, second and third macroplacoids granular and similar in size. Microplacoid small, distinct and lies close to third macroplacoid. Claws short, robust (fourth pair of claws 22.8% of buccal tube length) with no refractive zone at the base; accessory claws long and rising well clear of primary branch. Lunules very small.

Eggs colourless, round, diameter without processes 54 μm , with processes 65 μm . 24-30 processes around circumference, 100 in hemisphere. Processes long cones with attenuated, areolated tips, 9-11 μm long, base diameter 3-5 μm , processes 3-4 μm apart, base of each process indented. Egg shell surface smooth.

Remarks. Type material could not be located (see remarks for *M. hufelandioides*) but because of the very characteristic soft spines and the description of the eggs, the identification is not in doubt. Murray's description did not include pores in the cuticle and they are difficult to discern at low magnification. They are mentioned as occurring in the

posterior region of the animal in the description of *Macrobiotus intermedius subjulietae*. However they are certainly present over the whole cuticle in the 16 paratypes examined as they are in the material from the type locality. Specimens from all sites agree well with the dimensions of that material including the five specimens from Ravensbourne and three from Lord Howe Island which had only one pair of spines above the fourth pair of legs. (Murray (1910) reported specimens with one pair of spines from Katoomba, NSW).

Distribution. The species can be found in mosses and lichens at sites from high altitudes and seems to have a preference for these substrates on rock rather than on trees. The species was reported from New Guinea by Iharos (1967) and from the Karpathians by Bartos (1941) but these reports should be considered to be questionable because of the state of the art of tardigrade taxonomy in those days.

***Minibiotus aquatilis* Claxton, 1998**

Fig 137

Minibiotus aquatilis Claxton, 1998: 136-138, Figs. 6, 18e

Type locality. Australia. Coppins Crossing, Australian Capital Territory.

Material examined. NEW SOUTH WALES: *N38*, lichen on rock in open woodland, 22 specimens, 14 eggs. AUSTRALIAN CAPITAL TERRITORY: *A1*, moss and lichen on rock at river side, 29 specimens, 37 eggs (**type material**). TASMANIA: *T11*, moss on rock, 3 specimens, 3 eggs; *T3.2*, moss on soil, 1 specimen.

Diagnosis. Smooth cuticle with granulation on all legs; 3 long macroplacoids and a distinct microplacoid; long, slender claws with short, low accessory claws and toothed lunules on the fourth pair of claws.

Description. Body length 185-399 μm , colourless. Eye spots in the posterior position, consisting of large granules. Cuticle smooth, coarse granulation over back and both sides around claws on all legs. Buccal tube narrow (9% of buccal tube length). Stylet supports inserted at 68.3% of buccal tube length, ventral reinforcing bar 53%. Pharyngeal bulb round (about 30 μm diameter), containing large granular apophyses, three macroplacoids and a microplacoid. Macroplacoid row long (37.9% of buccal tube length); first macroplacoid pear-shaped, lying close to apophysis and partly obscured by it, second macroplacoid granular, smaller than other two, third macroplacoid granular but with faint caudal knob turned towards midline. Microplacoid distinct, short and lies close to third macroplacoid. Claws long, slender (on fourth pair of legs, 34.6% of length of buccal tube) with large refractive zone at base and with short secondary branch. Accessory claws short and lie close to primary branch. Lunules on first three pairs of legs smooth and distinct. Lunules on fourth pair of legs toothed.

Eggs round, diameter without processes 60-70 μm , with processes 80-93 μm . Thirty-six processes around circumference, about 100 in hemisphere. Processes long cones tapering from hemispherical base (diameter 4-4.5 μm) to fine tip sometimes bifurcate, often terminating in several fine hairs. Tapering portion appears to have a single row of bubbles within it. Process height 11-12.5 μm (two eggs with processes 16-21 μm long), about 2 μm apart. Each process with indentations around the base. Shell surface with large round dots around each process that may be difficult to see in some preparations.

Remarks. The population from Narrandera differs from the type only by having more prominent eyes and shorter claws (relative to the length of the buccal tube). Eggs of the Narrandera population differ by having shorter, thinner processes than the type (8-9 μm long with base diameter 3-3.5 μm) and a little further apart (3 μm). However this is

variable, one egg had process height 9-10 μm , base diameter 2-2.5 μm ; two eggs had process height 5-7 μm , base diameter 3 μm . The dots around the processes are particularly clear in eggs from King River.

The species is similar to *Minibiotus maculartus* Pilato & Claxton, 1988 and *Minibiotus floriparus* Claxton, 1998, having a smooth cuticle and granulation around all claws but differs from them in the position of insertion of the stylet supports and by having longer macroplacoids as well as having different shaped egg processes.

Distribution. The species was found in short turf moss and foliose lichens on rocks close to the Molonglo River at the type locality. At Narrandera it was found in very dry foliose lichens on rock in an open woodland and at King River in fine moss on rock.

***Minibiotus arcanus* sp. n.**

Fig. 138

Material examined. Australia: QUEENSLAND: Q5, mixed liverwort/ moss/ crustose lichen on rotten log in rainforest, 9 specimens.

Diagnosis: Cuticle smooth, no pores; 3 granular macroplacoids, microplacoid absent; granulation around all claws, short robust claws, with high, short accessory claws and small smooth lunules.

Description: 158-234 μm colourless. Cuticle smooth; granulation in small patch above claws on first three pairs of legs, back and sides of fourth pair of legs. Buccal tube very narrow (5.3% of buccal tube length) diameter 1.5 μm . Stylet supports inserted at 51% of

buccal tube length, ventral support 32% of buccal tube length. Pharynx round (24 μm in 234 μm animal) containing large apophyses and three macroplacoids. Macroplacoids granular equal in size, the first slightly pear shaped and partly obscured by the apophyses, second and third round granules, microplacoid absent. Claws short, robust with long secondary branch (fourth pair of claws 25% of buccal tube length) and large refractive zone at base. Accessory claws short but high above primary branch; lunules small and smooth on all claws.

Eggs unknown.

Etymology: *Arcanus*, L., m, secret, mysterious.

Remarks: This species is similar to *M. floriparus* in lacking pores on the cuticle and having distinct granulation on all legs but it differs from that species by lacking a microplacoid and having the stylet supports inserted on the buccal tube much more anteriorly.

Distribution: Specimens found in a single cryptogam sample in rainforest.

Minibiotus asteris Claxton, 1998

Fig 139

Minibiotus asteris Claxton, 1998: 145, Figs. 11, 19d

Type locality. Australia. Mount Roland, Tasmania.

Material examined. TASMANIA: *T3.1*, moss on rock in low woodland, 11 specimens. *T7*, moss and liverwort on rock in wet forest, 87 specimens, 20 eggs (**type material**). *T21*, moss on mudstone in *Eucalyptus*/Myrtle forest, 6 specimens, 3 eggs. NEW SOUTH WALES: *N3.4.b*, 1 specimen. VICTORIA: *V3*, leafy liverwort, moss and lichen on fallen branches in *Nothofagus* forest, 33 specimens, 2 eggs. MACQUARIE ISLAND: Scobie Lake, 400m., 9 Dec 1977, D.S. Horning, 26 specimens; Gadget's Gully, 220m, 25 Nov 1977, D.S.H., 17 specimens; Lusitania Bay, 400m., 1 Dec 1977, D.S.H., 7 specimens; Mount Hamilton summit, 433m., 17 Jan 1978, D.S.H., 8 specimens; Mount Waite summit, 452m., 29 Dec 1977, D.S.H., 11 specimens; Mount Fletcher summit, 428m., 17 Feb 1978, D.S.H., 8 specimens (WM). **New Zealand:** SOUTH ISLAND: (NZ186, 188) Temple Basin Lower Ski Huts, Arthur's Pass National Park, 19 May 1970, D.S. Horning, 2 specimens; (NZ170) Pegley Flat, Arthur's Pass National Park, 18 May 1970, D.S.H., 1 specimen; (NZ23) Fox Glacier Valley, 28 Mar 1970, D.S.H., 3 specimens. (NZM)

Diagnosis. Cuticle smooth with irregularly shaped pores over the whole cuticle and granulation on fourth pair of legs only; 3 small round macroplacoids and a distinct microplacoid; short, robust claws with high accessory claws and smooth lunules.

Description. Body length 128-361 μm , colourless. Eye spots in posterior position. Cuticle over the whole body is covered with small round (0.5-0.7 μm) pores; larger pores (about 2 μm) with irregular shape rare but more common towards the rump. Fine granulation around claws on fourth pair of legs only. Buccal tube narrow (8% of buccal tube length). Stylet supports inserted at 63.8% of buccal tube length, ventral support short (44.8% of length of buccal tube). Pharyngeal bulb round (26 μm diameter) containing well-developed granular apophyses, three macroplacoids and a microplacoid. Macroplacoid row short (30% of buccal tube length); macroplacoids equal in size; first macroplacoid granular, lying close to apophysis and partly obscured by it; second macroplacoid granular as is third which has a slight bulb at the caudal end that curves towards the midline. Microplacoid short, distinct and lies close to third macroplacoid. Claws robust (fourth pair of claws 28% of buccal tube length) with small refractive zone at base and long secondary branch;

accessory claws short and rising well clear of primary branch. Lunules small and smooth on all claws.

Eggs colourless, round, diameter without processes 54-67 μm , with processes 64-85 μm . 20-28 processes around circumference, 75-90 in a hemisphere. Processes like those of *Macrobotus hufelandi* but with distal disk consisting of about six (up to eight) distinct arms like those of a starfish. Process height 5-10 μm , base diameter 4.3-7.0 μm and disk diameter 4.3-5.4 μm . Processes are 2-4 μm apart. 12-14 small pores around the base of each process. Egg shell surface smooth or lightly striated.

Remarks. This species is probably most closely related to *Macrobotus allani* Murray, 1913 as far as is possible to tell from the original description. It differs from that species by having eyes, pores in the cuticle, a strong microplacoid and by the nature and number of disk arms on the egg processes. The adults are very similar to those of *M. cf weinerorum* but differ from them by having irregularly shaped pores and granulation around the claws on the fourth pair of legs.

Distribution. At the type locality the species was found in mosses and liverworts on soil and rocks on a northwest gully slope in a wet *Eucalyptus delegatensis* forest.

Minibiotus crassidens (Murray, 1907)

Macrobotus crassidens Murray, 1907: 524, Pl. XVIII, Fig. 9a-c

Type locality. Cape Colony, South Africa.

Material examined. None. Observed by Murray (1910) in Blue Mountains, NSW

Diagnosis. Cuticle smooth? Large apophyses, Three (?) small round wide macroplacoids. Long slender claws with primary and secondary branches joined over a long distance.

Description. Body length about 250 μm . Eye spots absent. Cuticle smooth? Buccal tube narrow. Stylet supports inserted at 50-60% of buccal tube length. Pharyngeal bulb round containing large well-developed granular apophyses and “two free nuts and a large comma”. Macroplacoid row short. Claws slender primary and secondary branch united more than half way.

Eggs colourless, round, diameter without processes 50 μm , with processes 70 μm . 20-28 processes around circumference, 75-90 in a hemisphere. Processes close set on shell, almost touching at bases. Each with bulbous base surmounted by slender undulating seta. (Description of animal and egg taken from Murray, 1907b, 1913).

Remarks. This species is insufficiently described to be able to differentiate it from the other species found here. No species found in this study has eggs whose characters match those of *M. crassidens*.

Distribution. Has been found also in Hawaii and Angola.

***Minibiotus ethelae* Claxton, 1998**

Fig 140

Minibiotus ethelae Claxton, 1998: 140-143, Figs. 9, 19b

Type locality. Australia. Cobbitty, NSW.

Material examined. Australia: NEW SOUTH WALES: *N20*, in crustose and foliose lichens on a tree trunk, 57 specimens, 23 eggs (**type material**). South Africa: Lydenberg, Transvaal, 2250m. 6 May 1988, M. Filmer, lichens, 11 specimens, 2 eggs; Natal Drakensberg Cathedral Rock Area, 30 May 1988, H. Dastych, moss on rock in Indumeni forest, 4 specimens; Rus-Te-Winter National Reserve, 1500m., 30 May 1988, M. Filmer, bark of *Acacia*, 2 specimens, (NMP); Kruger National Park, 20 May 1988, S. Neses, lichens on dead twigs, 8 specimens; Hendriksdaal, Palmers Creek, 1400m, Jul 1971, A. Szeptycki, rock, 1 specimen, (ZIM).

Diagnosis. Pale yellow body cells and variably shaped pores in the cuticle, cuticle thickened in caudal region; 3 small round macroplacoids and an indistinct microplacoid; long, slender claws with low accessory claws and smooth lunules.

Description. Body length 175-480 μm , yellow body cells. Large, posterior eye spots present. Cuticle with nine transverse bands of large pores (round, elliptical, trifoliate and quadrifoliate) around the body; pores also on the legs. Cuticle thickened in the caudal region. Buccal tube narrow (7.6% of buccal tube length). Stylet supports inserted at 64.9% of buccal tube length and ventral support 51.4%. Pharyngeal bulb round (about 32 μm diameter) containing large round apophyses, three macroplacoids and a microplacoid. Macroplacoid row short (32.3% of buccal tube length); first macroplacoid pear-shaped and partly obscured by apophysis, second granular and smaller than the other two and third granular with caudal bulb that curves towards midline. Microplacoid small, indistinct and

lies very close to third macroplacoid. Claws slender (fourth pair of claws is 37.6% of length of buccal tube) with small but obvious refractive zone at base and long secondary branch; short but well developed accessory claws lie close to primary branch. Lunules small, smooth and thin on all claws.

Eggs colourless, round, diameter without processes 67-70 μm , with processes 90-100 μm . 28-34 processes around circumference and 120-160 in hemisphere. Processes are cones tapering rapidly to attenuated tip, often bifurcate. Process height variable, on one egg 12-14 μm , on three others 14.5-19 μm and on another 19-22.5 μm . Base diameter of processes 2.7-3.8 μm (on egg with longest processes 4.3-4.9 μm), about 5 μm apart. Shell surface dotted.

Remarks. The species is similar to *Minibiotus furcatus* (Ehrenberg, 1859) but differs from it by having the stylet supports inserted more anteriorly, by having a much shorter ventral support and shorter placoids, by having smooth lunules on all legs and having much longer egg processes and a dotted shell. It differs from *Minibiotus ramazzottii* Binda & Pilato, 1992 by having large showy pores in the cuticle and from *Minibiotus vinciguerrae* Binda & Pilato, 1992 by having no granulation around the claws and longer, thinner egg processes.

Distribution. At the type locality the species was found in crustose and foliose lichens on the trunk of a *Casuarina* tree and a peppercorn tree in a suburban street. The disjunct distribution (Australia and South Africa) can probably be explained in terms of paucity of collection.

***Minibiotus fallax* Pilato, Claxton and Binda, 1989**

Fig 141

Minibiotus fallax Pilato *et al.*, 1989: 23-26, Fig. 2A-E

Type locality. Australia. Barrengarry, NSW.

Material examined. NEW SOUTH WALES: *N3*, moss and lichen on rocks and trees in subalpine heath, 21 specimens. *N14.7*, *N14.3.b*, *N14.2.d*, moss on trees and rocks in closed forest, 16 specimens. *N15.1.a*, *N15.3.b*, moss and lichen on trees in open forest, 7 specimens. *N27*, moss and lichen on rock in open forest, 18 specimens, 2 eggs. *N32*, lichen on tree on street, 6 specimens, 1 egg. *N33.a*, lichen on tree open trees, 15 specimens, 37 eggs. *N34*, moss and lichen in open forest, 2 specimens. *N35.a*, moss on rock, cool temperate rainforest, 2 specimens (**type material**). *N43*, moss on soil, 1 specimen. *N46.2*, *N46.3*, moss and lichen on rock in subalpine open woodland, 3 specimens. QUEENSLAND: *Q12*, leaf litter on rock open forest, 1 specimen. *Q13*, lichen on tree open field, 14 specimens. *Q15*, lichen on rock, 1 specimen. *Q17*, lichen on trees in open forest, 11 specimens. *Q18.a*, *Q18.b*, fern on soil, moss and lichen on trees in urban park, 7 specimens. *Q21*, moss on rock in open forest, 3 specimens. ; *Q22*, moss and lichen on trees in open forest, 8 specimens. *Q25.a*, moss and lichen on trees in closed forest, 3 specimens. LORD HOWE ISLAND: lichen, 6 specimens.

Diagnosis. Cuticle with transverse bands of rounded gibbosities more prominent in posterior part of body, nine bands of pores around body; two macroplacoids and an indistinct microplacoid; long robust claws with high accessory claws and thin, smooth lunules.

Description. Body length up to 550 μm colourless or with irregular bands of red pigment. Eye spots present in anterior position. Cuticle with round pores and transverse bands of rounded (circular or elliptical) gibbosities that vary in size and shape and become more pronounced towards the posterior. There are one or two pores in each gibbosity. Buccal

cavity with tiny teeth in posterior position just above transverse ridges. Buccal tube width 9.2% of buccal tube length. Stylet supports inserted at 64% of buccal tube length and ventral support at 56%. Pharyngeal bulb oval (31 μm long by 23 μm wide) containing apophyses, 2 macroplacoids and a microplacoid. First macroplacoid rod-shaped with median constriction nearly twice the length of the second macroplacoid whose caudal bulb curves towards the midline. Microplacoid indistinct. Macroplacoid row length 40% of buccal tube length. Claws robust (fourth pair of claws 42% of buccal tube length) with very small refractive zone at base and long secondary branch; accessory claws short and rise high above primary branch. Lunules very small and smooth.

Eggs colourless, found singly, in pairs and sets of four; 59-80 μm in diameter without processes, 80-100 μm with processes; 28-30 around circumference, about 100 in hemisphere. Processes are strap-like with swollen bases the distal ends of which appear flattened, quite variable in height between eggs and over a single egg, most 12-16 μm long but may reach 22 μm ; these longer processes often swollen or bent at an acute angle near distal end, processes 3-4 μm base diameter and 2-4 μm between. Shell surface strongly dotted.

Remarks. The description of eggs is based on two egg shells found at the type locality and on eggs (including embryonate eggs) found at other localities.

Distribution: The species occurs frequently but rarely in abundance. It prefers lichens on trees in dry environments in Australia

Minibiotus floriparus Claxton, 1998

Fig 142

Minibiotus floriparus Claxton, 1998: 135-136, Figs. 5, 18d

Type locality. Australia. Camden, NSW.

Material examined. Australia: NEW SOUTH WALES: *N21.j*, foliose/ crustose lichens on tree in dry sclerophyll forest, 40 specimens, 12 eggs (**type material**).

Diagnosis. Smooth red-purple cuticle, granulation on all legs; three round macroplacoids of same size and a distinct microplacoid; long robust claws with short accessory claws which rise high above the primary branch only on the fourth pair of claws and smooth lunules.

Description. Body length 152-420 μm , all but the smallest specimens with red-purple cuticle, some specimens also with purple granules. Eye spots large in posterior position. Cuticle smooth. Granulation on sides and back of first three pairs of legs above claws, granulation fine and dense on fourth pair of legs. Buccal tube narrow (7.6% of buccal tube length). Stylet supports inserted at 64.4% of buccal tube length and ventral support long (46.1%). Pharyngeal bulb round (about 24 μm diameter) containing large granular apophyses, three granular macroplacoids and a microplacoid. Macroplacoid row short (33.1% of buccal tube length); macroplacoids round granules of about the same size, second macroplacoid slightly smaller than other two, third with slight caudal bulb, which curves towards the midline. Microplacoid distinct and short. Claws robust (fourth pair of claws is 34% of length of buccal tube) with small refractive zone at base and with long secondary branch. Accessory claws short and rise high above the primary branch on fourth

pair of claws only. Lunules small and smooth on first three pairs of legs, thick and smooth on the fourth pair of legs.

Egg colourless, round, diameter without processes 62 μm , with processes 70 μm . 20-22 processes around circumference, 60-75 in hemisphere. Processes screw-shaped with flared distal end with ring of 9-10 pores around a central area, height 5.5-6 μm , base diameter 2-3 μm , distal disc diameter 6-7 μm . Each process surrounded by a membrane. Shell surface smooth.

Remarks. The species is very similar to *Minibiotus maculartus* Pilato & Claxton, 1988, having a smooth cuticle and granulation around all claws but differs from it by having purple coloured cuticle, smooth lunules on the claws of the fourth pair of legs and also by having very different processes on the egg.

Distribution. The species was found only in crustose and foliose lichens on the branch of a species of *Eucalyptus* in open woodland.

***Minibiotus hispidus* Claxton, 1998**

Fig 143

Minibiotus hispidus Claxton, 1998: 138-139, Figs. 7, 18f

Type locality. Australia. Crows Nest, Queensland.

Material examined. NEW SOUTH WALES: *N28*, moss and lichen on sandstone rock in open forest, 30 specimens, 5 eggs. QUEENSLAND: *Q16*, moss on rock, 8 specimens, 1 egg; *Q20.a*, leaf litter and sand in *Banksia* heath, 21 specimens, 1 egg. *Q21*, moss and lichen on rock in open woodland, 27 specimens, 8 eggs (**type material**). *Q23*, soil under *Eucalyptus* tree, 10 specimens. WESTERN AUSTRALIA: *W2*, moss and

lichen on rock in open forest, 27 specimens, 1 egg. (SKC). **New Zealand:** SOUTH ISLAND, (NZ526)

Canaan Rd, Abel Tasman National Park, 9 Apr 1971, D.S. Horning, 2 specimens. (NZM)

Diagnosis. Smooth cuticle with granulation on all legs, 3 small round macroplacoids and an indistinct microplacoid; slender claws with short, low accessory claws and smooth lunules.

Description. Body length 160-350 μm , colourless. Eye spots in posterior position. Cuticle smooth, coarse granulation on top and sides of first three pairs of legs above claws and around claws on fourth pair of legs. Buccal tube narrow (8% of the buccal tube length). Stylet supports inserted at 65.2% of buccal tube length, ventral reinforcing bar very short, 45.7%. Pharyngeal bulb round (about 28 μm diameter) containing large granular apophyses, three granular macroplacoids and a microplacoid. Macroplacoid row short (33.2% of buccal tube length); macroplacoids almost equal in size, first somewhat pear-shaped, lying close to apophysis and partly obscured by it, second is granular and third granular with a faint caudal knob turned towards the midline. Small, indistinct microplacoid lies close to third macroplacoid. Claws slender (fourth pair of claws is 28.1% of length of buccal tube) with small refractive base and long secondary branch. Accessory claws short and rise high above primary branch. Lunules on all claws small and smooth, somewhat thickened on fourth pair.

Eggs round, colourless, diameter without processes 59 μm , with processes 72 μm . 48 processes around circumference, about 340 in hemisphere. Processes small cones with fine tips, height 6.5-8.4 μm , base diameter 2.8 μm and 1-2 μm apart. Ring of very small pores around base of each process. Shell appears to be covered with very small pores of uniform size.

Remarks: The population from Appin, NSW is smaller than the type population from Crow's Nest (mean body length 213.6 μm , SD 41.5 μm , n=15) as is that from Perth (mean body length 196.9 μm , SD 36.4 μm , n=16) but otherwise the adults are the same. Egg processes from the Appin population are slightly longer (10 μm) and further apart (3.3 μm) than those of the type population. The single egg from Perth has quite narrow processes (1.5-2 μm base diameter).

The species is very similar to *Minibiotus maculartus* but has a shorter ventral support and smooth lunules on the fourth pair of legs. It is perhaps most closely related to *Macrobiotus crassidens* Murray, 1907 (based on the somewhat inadequate description of that species) but differs from it by having eyes, by having a very indistinct microplacoid and by having egg processes that are narrower at the base, shorter and not touching.

Distribution. At the type locality the species was found in mosses and lichens on rocks and fallen logs in open woodland. At other Australian localities it was found in moss and lichen on rocks in open woodland but also can be found leaf litter and sandy soil. The species can cope with high temperatures and drying.

Minibiotus hufelandioides (Murray, 1910)

Fig 144

Macrobiotus hufelandioides Murray, 1910: 138-139, Pl. XVIII, Figs. 29a-9c

Type locality. Australia. Mount Kosciusko, New South Wales.

Material examined. Australia: NEW SOUTH WALES: *N40*, moss and lichen on rock in open forest, 29 specimens, 24 eggs; *N41.1*, moss and lichen on rocks, moss on soil, on summit of monolith in open forest, 19 specimens, 1 egg. *N46.1*, (**type locality**) moss and lichen on rock in dry sclerophyll, 4 specimens, 1 egg; *N46.2*, *46.3*, moss and lichen on rock, in subalpine open woodland, 68 specimens, 17 eggs.

Diagnosis: Smooth cuticle with granulation on all legs; three long macroplacoids and an indistinct microplacoid; robust claws with long, high accessory claws and toothed lunules on fourth pair of claws.

Description: Body length 149-419 μm , colourless. Eyes large, posterior. Cuticle smooth except for strong granulation over back and outside of all legs around claws. Buccal tube narrow (8.6% of buccal tube length). Stylet supports inserted at 67.4% of buccal tube length, ventral support short (45.9% of buccal tube length). Pharynx round (30 μm diameter) containing large apophysis, three macroplacoids and a microplacoid. Macroplacoid row long (38.2% of buccal tube length); first macroplacoid pear-shaped and partly obscured by apophysis; second macroplacoid round, slightly shorter than other two; third macroplacoid kidney-shaped and about same size or slightly longer than the first. Microplacoid indistinct and lies close to third macroplacoid. Claws long and robust (fourth pair of claws is 29.3% of buccal tube length) with large, clear refractive base and short secondary branch. Accessory claws long and high above primary branch. Lunules small and smooth on first three pair of legs, jagged or toothed on fourth pair.

Eggs colourless, round, diameter without processes 54-64 μm , with processes 65-75 μm . 20-26 processes around circumference. Processes conical with expanded discoid tops, distal disk smooth or lightly notched; process height 5.5-6.5 μm , base diameter 5.5-7 μm , disk

diameter 4.5-6.5µm. Each process with a ring of pores around the base; shell surface lightly granulated.

Remarks. The original type material was not located. The main repository of James Murray's permanent slides is the Royal Scottish Museum, Edinburgh (Morgan, 1977). No Australian tardigrades are represented in that collection. Although Murray's description lacks detail such as the granulation around the claws and the toothed lunules on the fourth pair of legs, the identification of these specimens and eggs is not in doubt. His description of the animal having "three rods in the pharynx of nearly equal size,...no comma or a very small and obscure one,...eggs with processes like those of the typical *hufelandi* egg,...processes taper from a broad base which is surrounded by a circlet of dots..." agrees with the specimens described here.

Distribution. Murray (1910) indicated that the species was found in mosses at the Hospice on Mount Kosciusko. The material obtained for this study was found in mosses, fruticose and foliose lichens on rocks at the site of the Hospice (Digger's Creek). This species was the most abundant of the 31 species collected at Kosciusko in October 1992. Murray (1913) also identified specimens with two macroplacoids and a microplacoid from Africa as *M. hufelandioides*. Current thinking in tardigrade taxonomy suggests that such variation is not intraspecific so the African specimens almost certainly belong to a different taxon..

***Minibiotus intermedius* (Plate, 1888)**

Fig 145

Macrobiotus intermedius Plate, 1888: 535

Type locality. Germany. Marburg

Material examined. Australia: NEW SOUTH WALES: *N3.2.a*, moss on rock in subalpine heath, 3 specimens, *N3.2.b*, moss and lichen on rock in subalpine heath and open forest, 55 specimens, 7 eggs, *N3.1.a*, moss and lichen on rock in open field, 15 specimens; *N14.2.b*, moss and leaf litter in closed forest, 1 specimen; *N26.a*, lichen on rock in open forest, 1 specimen, *N26.b*, moss on rock, log in sheltered gully, 2 specimens; *N27.f*, *N27.g*, *N27.h*, *N27.i*, *N27.j*, *N27.k*, mosses and lichens on sandstone in open forest, 60 specimens, 16 eggs; *N29.2*, moss and lichens on sandstone in open forest, 3 specimens, 2 eggs; *N35.b*, leafy liverwort on tree in cool temperate rainforest, 1 specimen; *N39.2.b*, mosses and lichens on sandstone rock in cool temperate rain forest, 8 specimens, 20 eggs; *N46.c*, moss and lichen on rock in open forest, 5 specimens, 3 eggs. QUEENSLAND: *Q24.a*, liverwort on twigs in temperate rainforest, 3 specimens, *Q24.b*, lichen and leafy liverwort on branches, logs, rocks in temperate rainforest, 14 specimens, 1 egg. LORD HOWE ISLAND: lichen, 8 specimens, 1 egg. **New Zealand:** NORTH ISLAND: (NZ642) Pilbrows Hill, 16 May 1971, D.S. Horning Jr., 1 specimen; (NZ893) Rangatira Island, 25 Aug 1971, D.S. Horning Jr., 1 specimen. (NZM) **Germany:** Marburg (**type locality**), moss on oak bark, 4 specimens. **UK:** SURREY: Bookham Common, P. Marley, 9 specimens; DEVON: Plymouth, P. Marley, moss and lichen on oak, 1 specimen; Morwelham, P. Marley, moss and lichen, 3 specimens. (PM). **USA:** ALASKA, Denali National Park, P. Marley, 5 specimens. (PM). MICHIGAN, Schoolcraft County, 14 Aug 1978, T. Hounseal, moss from base tree in virgin forest, 4 specimens. TENNESSEE, Henderson County, 2 Aug 1980, C.W. Beasley, lichen from tree, 4 specimens. MISSOURI, Carter County, 1 Aug 1980, C.W. Beasley, lichen on oak tree and rock, 4 specimens. (MUT) **South America:** VENEZUELA, Obispos, Barrinas, 6 Jul 1979, R.W. Brooks, A.A. Grigarick, J. McLaughlin and R.O. Schuster, 4 specimens; Pedraza, Barinas, 4 Jul 1979, Brooks et al., 9 specimens; Libertador, Merida, 3 Jul 1979, Brooks et al., 32 specimens; Girardot, Aragua, 14 Jul 1979, Brooks et al., 2 specimens; Perija, Zulia, 24 Jun 1979, Brooks et al., 1 specimen. (BMD). **South Africa:** Natal Midlands, Geckies Farm, 4 Dec 1988, P. Croeser, moss and fern in indigenous forest, 10 specimens and 1 egg. (NMP) **Italy:** Sardegna, Caprera, 21 Mar, 1974, R. Bertolani, lichen, 4 specimens. (UMI)

Diagnosis. Cuticle smooth, no pores; 3 small, granular macroplacoids and an indistinct microplacoid; short, robust claws with high prominent accessory claws and smooth lunules.

Description. Length 132-290 μm colourless. Eyespots large in posterior position. Cuticle smooth, granulation, if present at base of claws on fourth pair of legs, very sparse. Buccal tube very narrow (6.8% of buccal tube length), diameter 1.5 μm . Stylet supports inserted at 55% of buccal tube length; ventral support very short (37.3% of buccal tube length). Pharyngeal bulb round (23 μm diameter) containing large triangular apophyses, three macroplacoids and one microplacoid. Macroplacoid row short (26.5% of buccal tube length); first macroplacoid round, slightly elongated anteriorly where it lies very close to the apophysis, second and third macroplacoids round, same size as first. Microplacoid very small and indistinct, lying close to third macroplacoid. Claws robust but short with long secondary branch (fourth pair of claws is 24.8% of length of buccal tube) and large, round refractive zone at base. Accessory claws long, rising high above primary branch. Lunules small and smooth on all claws. Some sparse granulation found on fourth pair of legs on some specimens.

Eggs colourless round, diameter without processes 40-45 μm , with processes 45-52 μm . About 30 processes around circumference, about 130 in hemisphere. Processes nail-like, each surrounded by membrane; height 2.5-3.5 μm , base 0.5-1.5 μm , top 2.5-3.5 μm , 3-4 μm apart. The top on each process appears to consist of a ring of tiny pores visible only under the highest power of magnification.

Remarks. Many early reports recorded this species without observing eggs. The species seems to be most often confused with a very similar species, the adult of which has pores in the cuticle, described from Europe (Morgan and King, 1976, Maucci, 1986, McInnes, 1991), the Americas (De Barros, 1942, Beasley, 1978) and personally observed on slides from Italy, Russia and South Africa. This species has not yet been found in Australia although *Minibiotus poricinctus* Claxton, 1998 is very similar.

The above description of *M. intermedius* was not based on type material which probably no longer exists. There are no collections of tardigrades in institutions in Marburg (B. Grabowski, pers. comm.), and no slides of Plate in Frankfurt or Hamburg institutions (H. Dastych, pers. comm.). It is impossible to determine the type locality from the original description since Plate referred to material collected in both Chile and Marburg, Germany. It seemed expedient, therefore, to redescribe the species using material which is both cosmopolitan and which most closely resembles the original description and to erect a neotype from material from Marburg.

Distribution. This species is quite tolerant of both wet and dry conditions and is cosmopolitan.

Minibiotus keppelensis Claxton, 1998

Fig. 146

Minibiotus keppelensis Claxton, 1998: 143, Figs. 10, 19c

Type locality. Australia. Great Keppel Island, Queensland.

Material examined. Australia: QUEENSLAND: *Q14*, foliose lichen on rock and crustose lichen on dead tree, 16 specimens, 6 eggs (**type material**).

Diagnosis. Cuticle smooth with 10 transverse rows of round pores and granulation on all legs; 3 small round macroplacoids and an indistinct microplacoid; robust claws with long, low accessory claws and smooth lunules.

Description. Body length 180-287 μm , colourless, some specimens with red pigment granules. Eye spots large, in posterior position. Cuticle smooth with round (1 μm) pores arranged in ten distinct transverse bands around body and on legs. Fine granulation on top and both sides of claws on first three pairs of legs and on back and sides of fourth pair of legs. Buccal tube very narrow (5.8% of buccal tube length). Stylet supports inserted at 60.6% of the buccal tube length, ventral support short (40.4% of buccal tube length). Pharyngeal bulb oval to round (27 μm by 30 μm), placoids in anterior half; containing three macroplacoids and a microplacoid. Macroplacoid row short (26.6% of buccal tube length); macroplacoids small, granular as are apophyses which are about the same size as the first macroplacoid. First macroplacoid round, slightly elongated anteriorly where it lies beneath the apophysis; second macroplacoid granular smaller than other two; third macroplacoid granular but with slight caudal bulb which curves towards midline. Microplacoid small, indistinct and lies very close to third macroplacoid. Claws robust (fourth pair of claws is 30.1% of buccal tube length) with large refractive zone at base and with long secondary branch; long accessory claws lie close to primary branch on all claws. Lunules small, smooth on all claws.

Eggs colourless, round, diameter without processes 45-55 μm , with processes 65-85 μm . Eleven processes around circumference and 24 in hemisphere. Processes short cones with pointed apices 11-16 μm high, base diameter 9-12 μm and 4-6 μm apart. Base of each process surrounded by about ten pores. Membrane around each process reaching half way up the side and apparently supported in between processes by struts (4 μm high) so that the shell surface appears dotted.

Remarks. The egg processes of this species are very similar to those of *M. maculartus* but the adult differs from that species by having rows of large pores around the body.

Distribution. The species was found in foliose lichen on rock and in crustose lichen on a dead tree in open woodland.

Minibiotus maculartus Pilato & Claxton, 1988

Fig. 147

Minibiotus maculartus Pilato & Claxton, 1988: 86-88, Fig 3A-D

Type locality. Australia. Douglas Park, NSW.

Material examined. NEW SOUTH WALES: *N3.1.a*, moss on rock and tree in open sclerophyll woodland, 9 specimens, *N3.6*, liverwort on tree in subalpine heath, 1 specimen, 1 egg. *N15.2.a*, moss and lichen on rock in open forest, 8 specimens, 8 eggs. *N27*, moss and lichen on rock in dry sclerophyll forest, 68 specimens, 14 eggs (**type material**). *N45*, lichen on rock exposed to salt spray, 28 animals, 3 eggs. **New Zealand:** (NZ1136) Weka Island, East Coast, 28 Nov 1971, G.I. Wilson, 3 specimens.

Diagnosis. Cuticle smooth, granulation on all legs; 3 round macroplacoids and an indistinct microplacoid; robust claws with short, high accessory claws and toothed lunules on fourth pair of claws.

Description: Body length 140-350 μm , colourless. Eyespots present. Cuticle smooth, with granulation over back and sides of first three pairs of legs, and around claws on fourth pair of legs. Buccal tube 7% of buccal tube length. Stylet supports inserted at 64.4% of buccal tube length, ventral reinforcing bar 50%. Pharyngeal bulb oval (23 by 21 μm) containing large granular apophyses, three granular macroplacoids and a microplacoid. Macroplacoid row is short (27% of buccal tube length); macroplacoids almost equal in size. Small, indistinct microplacoid lies close to third macroplacoid. Claws slender (29 % of the length

of the buccal tube) with long secondary branch. Accessory claws short and rise high above primary branch. Lunules small and smooth on first three pairs of legs and toothed on the fourth pair.

Eggs round and colourless, diameter without processes 65 μm , with processes 85 μm . 10-15 processes around the circumference, about 18 in hemisphere. Processes pointed or round cones, height 6.5-11.9 μm , base diameter 8-10.8 μm . 8-9 longitudinal struts (4 μm long and 1 μm wide) join the base of each process to the surface which is dotted. In the population from Montague Island, the processes are rounded not pointed.

Remarks: This species is most similar to *M. taiti*. but differs from it by having toothed lunules on the fourth pair of claws.

Distribution: At the type locality the species had a marked preference for foliose lichens on rock. It occurs mostly in drier environments.

Minibiotus milleri Claxton, 1998

Fig. 148

Minibiotus milleri Claxton, 1998: 145-148, Figs. 12, 16b, 19e

Type locality. Australia. New England National Park, NSW.

Material examined. NEW SOUTH WALES: *N3.2, 3.3, 3.4, 3.5*, moss and lichen on trees, leaf litter in subalpine heath and cool temperate rainforest, 60 specimens, 8 eggs (**type material**). *N39.2.i*, moss and lichen on rocks and trees in cool temperate rainforest, 14 specimens. QUEENSLAND: *Q22*, foliose lichen on tree in open forest, 1 specimen. WESTERN AUSTRALIA: *W2*, foliose lichen on tree in Jarrah forest, 10 specimens, 2 eggs.

Diagnosis. Smooth cuticle with fine granulation near claws, long bean-shaped macroplacoids and a distinct microplacoid; robust claws with short, high accessory claws and smooth lunules.

Description. Body length 149-398 μm , colourless. Eye spots in the posterior position consisting of large granules. Cuticle smooth, fine granulation around claws on all legs. Oral cavity long with single tooth ventrally just above stylet sheaths in some larger specimens. Buccal tube narrow (*pt* 9.7); stylet supports inserted at 73% of buccal tube length; ventral support very short (*pt* 36.4). Pharynx round (27 μm diameter) containing small apophyses, three macroplacoids and a microplacoid. Macroplacoid row long (37% of buccal tube length); first macroplacoid smallest, somewhat pear-shaped, lying close to apophysis and partly obscured by it; second granular, slightly longer than first; third longest. Microplacoid long, distinct, lying close to third macroplacoid. Claws robust (fourth pair of claws is 26.5% of buccal tube length) with long secondary branch, well divided. Round refractive zone at base of claws well developed. Accessory claws short, raised high above primary branch. Lunules on first three pairs of legs very small, smooth; on fourth pair smooth.

Eggs round, diameter without processes 68-74 μm , with processes 90-98 μm . 20-30 processes around circumference, 80-120 in hemisphere. Processes long cones tapering to blunt tip, rarely bifurcate, lower part of each cone indented and enclosed in membrane. Tapering portion above with rough surface which appears as transverse lines. Process height 10-14 μm , base diameter 3 μm arranged evenly about 3 μm apart. Shell surface faintly striated.

Remarks. This species is similar to *M. hufelandioides* and *M. aquatilis* in having a long macroplacoid row, stylet supports inserted a long way down the buccal tube and no bend in the tube as it enters the pharynx but may be distinguished from these species by its very short ventral support.

Distribution. At the type locality, specimens were recovered from moss on rock, moss and lichen on tree trunks and branches in cool temperate rainforest and *Banksia collina* thickets.

Minibiotus pilatus Claxton, 1998

Fig. 149

Minibiotus pilatus Claxton, 1998: 140, Figs. 8, 17b, 19a

Type locality. Australia. Cambewarra Mountain, NSW.

Material examined. NEW SOUTH WALES: *N3.2*, lichen and liverwort on tree in cool temperate rainforest, 6 specimens. *N14.4*, weft moss on tree, 1 specimen. *N31*, lichens on tree in temperate rainforest, 1 specimen. *N39.2*, foliose lichen on rock in temperate rainforest, 6 specimens, 4 eggs (**type material**). QUEENSLAND: *Q25*, lichens on branches on ground in warm temperate rainforest, 8 specimens.

Diagnosis. Cuticle with a wrinkled pattern on the dorsum and granulation on all legs; 3 small round macroplacoids and an indistinct microplacoid; robust claws with long, low accessory claws and lightly toothed lunules on the fourth pair of claws.

Description. Body length 150-290 μm , colourless. Eye spots with small, sparse dots, posterior. Cuticle with wrinkled pattern in transverse rows on the dorsum, granulation in a patch on outside of first three pairs of legs just above the external claw, also on back and

sides of fourth pair of legs. Buccal tube narrow (7.9% of buccal tube length). Stylet supports inserted at 67.9% of buccal tube length and ventral support at 48.1%. Pharyngeal bulb round (about 28 μm diameter) containing large, round apophyses, three macroplacoids and a microplacoid. Macroplacoid row short (30.4% of buccal tube length); first macroplacoid round and granular and slightly elongated anteriorly where it is partly obscured by the apophysis; second macroplacoid granular and smaller than the others; third macroplacoid granular but with a caudal bulb which curves in towards the midline. Microplacoid very small, indistinct and close to third macroplacoid. Claws robust (fourth pair of claws is 29.7% of length of buccal tube) with long secondary branch and a round refractive base; accessory claws long and well developed close to primary branch. Lunules on claws of first three pairs of legs small and smooth; on fourth pair of legs with a few small teeth.

Eggs colourless, round, diameter without processes 54 μm , with processes 68 μm . Fifty-six processes around circumference. Processes of two types; first javelin-shaped (Fig. 19a), height 5.5-8 μm , base 1-1.6 μm joined by a membrane where they are expanded in the middle. Second type of process a short rod, about 2 μm high. Javelin-shaped processes form circles about 10 μm diameter on the egg surface, short rods are scattered within the circles. Short rods appear to rise to surface of the membrane but do not protrude through, as do the javelin-shaped processes.

Remarks. The species is very similar to other species of *Minibiotus* with three macroplacoids and granulation around the claws but differs from them by the transverse bands of sculpture on the cuticle, which is only visible at high magnification and by the distinctive egg.

Distribution. The species was found in temperate rainforest at all localities.

Minibiotus poricinctus Claxton, 1998

Fig. 150

Minibiotus poricinctus Claxton, 1998: 133, Figs. 4, 18c

Type locality. Australia. Mount Cameron, Tasmania.

Material examined. Australia: TASMANIA: T2, moss on tree on headland, 52 specimens, 8 eggs (type material).

Diagnosis. Cuticle with eight bands of small round pores and granulation on all legs; three round macroplacoids of the same size and an indistinct microplacoid; long slender claws with short, close accessory claws and thick smooth lunules.

Description. Body length 135-277 μm , colourless. Eye spots large in posterior position. Cuticle with eight bands of small, round (0.5 μm) pores around the body, sparse on the ventral surface and on the outside of all legs. Fine granulation on top and both sides of legs I-III just above claws, also around claws on leg IV. Buccal tube narrow (7.6% of buccal tube length). Stylet supports inserted at 59.5% of buccal tube length, ventral support very short (35.8% of buccal tube length). Pharyngeal bulb almost round (24 μm long by 22 μm wide) containing large, triangular apophysis, three macroplacoids and a microplacoid. Macroplacoid row short (30.9% of buccal tube length); first macroplacoid slightly elongated anteriorly where it lies very close to and partly obscured by the apophysis; second and third macroplacoids round, same size as first. Microplacoid small and indistinct, lying close to third macroplacoid. Claws slender (fourth pair of claws is 27.3%

of length of buccal tube) with long secondary branch and round refractive zone at base.

Accessory claws short, lying close to primary branch on all claws. Lunules small, smooth on first three pairs of legs, thick and smooth on fourth pair of legs.

Eggs round, diameter without processes 49 μm , with processes 60 μm . 18-20 processes around circumference, 50 in hemisphere. Processes screw-like, each surrounded by a membrane, height 6.5-7 μm , base 1.5 μm , top 5.5 μm , 6-8 μm apart. Small dots visible on shell surface around each process where membrane appears to reach the surface.

Remarks. The species is superficially very similar to *M. intermedius* and *M. taiti* but differs from them by the presence of bands of pores in the cuticle.

Distribution. The type material was found in a single mixed sample of two mosses on a sandstone boulder in a littoral flat with low shrubs and herbs.

Minibiotus scopulus Claxton, 1998

Fig. 151

Minibiotus scopulus Claxton, 1998: 152, Figs. 15, 20b

Type locality. Australia. Galore, NSW.

Material examined. NEW SOUTH WALES: *N41.2*, moss and lichen on dead trees, rock and soil in dense dry woodland, 43 specimens, 44 eggs (**type material**). WESTERN AUSTRALIA: *W5*, crustose lichen on tree, 1 specimen. (SKC) **New Zealand:** NORTH ISLAND, Tikitiki, 18 May 1971, D.S. Horning, 1 specimen. (NZM)

Diagnosis. Smooth cuticle, yellow body cells, nine bands of pores around the body; two macroplacoids and an indistinct microplacoid; long robust claws with fine low accessory claws and thin smooth lunules.

Description. Body length 165-428 μm , pale yellow body cells, many specimens with red pigment granules in irregular bands. Eye spots present in posterior position. Cuticle smooth with round to elliptical pores (about 1 μm diameter) extending around the body in nine bands, and also on legs, becoming sparser towards the head. Buccal tube narrow (8.6% of buccal tube length). Stylet supports inserted at 66.1% of buccal tube length and ventral support long (53.2%). Pharyngeal bulb round to slightly oval, containing apophysis, two macroplacoids and a microplacoid. First macroplacoid short, solid with slight middle indentation, second macroplacoid granular with caudal bulb curved towards midline. Microplacoid indistinct and lies close to second macroplacoid. Claws robust (fourth pair of claws is 39.6% of buccal tube length) with very small refractive zone at base and short secondary branch; accessory claws short, fine and lie close to primary branch. Lunules very small.

Eggs colourless to pale brown, often found in pairs, round, diameter without processes 60 μm , with processes 70 μm . Thirty-six processes around circumference and 120 in hemisphere. Processes long, thin, apparently flattened at least along the distal half. Processes mostly 6-11 μm long with a few on each egg up to 16 μm and then often bent at an acute angle; base diameter 2-3 μm and 4-6 μm between them. Shell surface dotted.

Remarks. The species is similar to *Minibiotus fallax* Pilato, Claxton & Binda, 1989 in having two macroplacoids, pores in the cuticle, no lunules and in the appearance of the egg. It differs from that species by not having gibbosities on the cuticle.

Distribution. The species was found in mosses and foliose lichens on rock in dense, dry woodland half way up Galore Hill but not in mosses and lichens from the top of the hill.

Minibiotus taiti Claxton, 1998

Fig. 152

Minibiotus taiti Claxton, 1998: 131-133, Figs. 3, 18b

Type locality. Australia. Ryde, NSW.

Material examined. NEW SOUTH WALES: *N8*, foliose lichen and leaf litter on asphalt, 35 specimens, 4 eggs (**type material**). *N28*, weft moss on rock in open sclerophyll forest, 10 specimens, 3 eggs, *N29*, weft moss on rock in open sclerophyll forest, 22 specimens, 5 eggs. QUEENSLAND: *Q18.a*, fruticose lichen on old bridge timber, wind exposed, 6 specimens, 3 eggs. 14, foliose lichen on rock, wind exposed, 3 specimens, 1 egg. **New Zealand:** Snares Islands, (SA301) Ho Ho Creek, 23 Oct 1972, D.S. Horning, 2 specimens; (SA26) Mollymawk Bay, 30 Jan 1971, D.S.H., 2 specimens; (SA216) Seal Point, 2 Mar 1972, D.S.H., 2 specimens. (SA60) Broughton Island, 18 Feb 1971, D.S.H., 4 specimens. (NZM) **China.** Quingdao, Oct 1994, N. Marley, moss, 6 specimens. (NM). **USA:** Texas, Taylor County, 27 Dec 1989, C.W. Beasley, leaf litter on soil, 2 specimens. (MUT).

Diagnosis. Smooth cuticle with no pores and granulation on all legs; 3 round macroplacoids and a distinct microplacoid; long slender claws with short, low accessory claws and smooth lunules.

Description. Body length 160-320 μm , colourless. Eye spots, when present, in posterior position. Cuticle smooth, patch of granulation on the outside of first three pairs of legs near claws, also on back and sides of fourth pair of legs. Buccal tube narrow (8% of buccal tube length). Stylet supports inserted at 60.3% of the buccal tube length, ventral support very

short (40.3% of buccal tube length). Pharyngeal bulb round (25 μm diameter) containing large, granular apophyses, three macroplacoids and a microplacoid. Macroplacoid row short (32.1% of buccal tube length); first macroplacoid round but slightly elongated anteriorly where it lies under the apophysis (which is about the same size), second macroplacoid small, granular; third macroplacoid granular but with a slight caudal bulb which curves towards midline. Microplacoid distinct, lying close to third macroplacoid. Claws long and slender (fourth pair of claws is 33.2% of length of buccal tube) with refractive zone at base and with short secondary branch. Accessory claws short and lie close to primary branch. Lunules smooth on all claws.

Eggs colourless, round, diameter without processes 54 μm , with processes 64 μm . About 48 processes around circumference, about 160 in a hemisphere. Processes like thin nails, 3.2-5.4 μm high, base diameter 1-1.5 μm , top diameter 2-3 μm . Top of each process appears to have a ring of very small circles around a central pore. A membrane surrounds each process but it is not clear if this is continuous over all the processes or if it reaches the shell surface between the processes.

Remarks. This species differs from *M. intermedius* described above, by having granulation around the claws, a wider buccal tube, stylet supports inserted lower down the buccal tube and by the slightly different structure of the processes of the egg. It differs from *Macrobotus acotistus* De Barros, 1942 by having a microplacoid, a narrower buccal tube, macroplacoids of similar size, the second never larger than the first and by having granulation around the claws.

Distribution. The type material was found in foliose lichens and *Eucalyptus* nuts on asphalt in the parking lot at Macquarie University. At other sites in NSW and in

Queensland the species was found in mosses and lichens in locations subject to drying and high temperatures.

Minibiotus cf wienerorum

Fig. 153

Material examined. VICTORIA: V2, fruticose lichen on rock in subalpine bush, 14 specimens, 8 eggs (2 embryonate).

Diagnosis. Cuticle smooth with small round and rarely oval pores over whole body, 3 small round macroplacoids and a small but distinct microplacoid; slender claws with long high accessory claws and small smooth lunules.

Description. Body length up to 311 μm , colourless. Eye spots in anterior position. Cuticle over whole body covered with small round (0.5-1.0 μm) randomly distributed pores. Few larger pores, 1.6 μm occur. Granulation around claws absent or very sparse and feint. Buccal tube narrow, 6-8% of buccal tube length (26 μm long and 2 μm wide in 240 μm long individual). Stylets inserted at 60-61% of buccal tube length, ventral support long, 47%. Pharyngeal bulb round (24 μm diameter) containing apophyses, three granular macroplacoids and a microplacoid. Macroplacoid row length 31-33% of buccal tube length; macroplacoids equal in size (2.2 μm), microplacoid short distinct and lies very close to the third macroplacoid.. Claws slender (fourth pair of claws 25-27% of buccal tube length) with long deeply divided secondary branch; accessory claws long and rising high above primary branch particularly on fourth pair of claws. Lunules small and smooth on all first three pairs of claws, with smooth, thick edge on fourth pair.

Eggs colourless, round, diameter without processes 58-60 μm , with processes 68-70 μm . 19-24 processes around circumference, 80 in hemisphere. Processes small domes with thick wall on top where there are up to 12 pores, the base of each process indented.. Process height 3.2-4.3 μm , base diameter 5.5-6.5 μm , distance between 1.5-2.5 μm . Egg shell surface smooth.

Remarks. The adult is similar to *M. weinerorum* (Dastych, 1984) in having a very narrow buccal tube and three macroplacoids which are equal in length and a small microplacoid. Pores in the cuticle were not mentioned in the original description of this species and the claws were much longer than those of this species. The processes of both species are dome shaped but those of *M. weinerorum* itself are twice the size of those of this species. A positive identification of these specimens will require a direct comparison with specimens of *M. weinerorum*. This species is also similar to *M. asteris* (for differences see Remarks for that species).

Distribution. Found only at one locality.

Genus *Xerobiotus* Bertolani & Biserov, 1996

Xerobiotus Bertolani & Biserov, 1996: 302.

Type species. *Macrobiotus pseudohufelandi* Iharos, 1966.

Diagnosis. (from Bertolani & Biserov, 1996) Ten peribuccal lamellae. Buccal tube rigid, ventral support present. Diploclaws on each leg similar in shape and size, symmetrical with respect to median plane of leg. Diploclaws with a small, thin basal tract attached to

leg by thin peduncle, not separated from the rest of the claw by septum. Eggs with processes deposited freely.

Xerobiotus pseudohufelandi (Iharos, 1966)

Fig. 154

Macrobiotus pseudohufelandi Iharos, 1966

Type locality. Austria.

Material examined. **Australia:** VICTORIA: *V1*, leaf litter on soil under Mallee scrub, 15 specimens.

SOUTH AUSTRALIA: Avon, 30° 14'S, 138° 19'E, A.F. Bird, soil, 5 specimens. WESTERN AUSTRALIA:

W1, moss on rock, soil and leaf litter on soil, 42 specimens, 4 eggs; *W3*, moss on limestone wall, 32

specimens, 4 eggs; *W4*, moss on limestone wall, 3 specimens. **Italy:** moss, 5 specimens, 1 egg.

Diagnosis. Animals with short legs and very small claws, the external one a little longer than the internal; without lunules on first three pairs of legs and asymmetrical lunulae on the fourth pair.

Description. Body length 220-530 μm (up to 667 μm in Victorian population), white.

Cuticle smooth. Large posterior eyes. Mouth subterminal, surrounded by ten lamellae. No teeth in oral cavity. Two ventro-lateral crests with one or two small median teeth in larger specimens. One single dorsal crest. Ventral reinforcing bar on buccal tube long and strong. Stylet supports inserted at 79-80% of length of buccal tube. Buccal tube thick walled, width about 14% of buccal tube length. Pharynx large and round with two macroplacoids and a microplacoid. First macroplacoid long, with median constriction, second with slight terminal constriction; microplacoid large and strong. Macroplacoid row length 42% of buccal tube length. Legs reduced in length. Claws short and fine; secondary branch joined

to primary over much of its length, more so in fourth pair of legs. Accessory claws very short and fine, lying very close to primary branch. External claws slightly larger than internal ones on each leg. First pair of claws shortest, fourth pair about same size as second and third (21 and 23% of the buccal tube length). Lunules absent on first three pairs of legs; asymmetrical in size and shape on fourth pair, large and indented on posterior claws, small and indented on anterior claws.

Eggs white, round, laid free. Surface covered with goblet-shaped processes, upper disk with about 12 notches. Egg diameter with processes 107-109 μm , without 90-92 μm . Base diameter of process 6.5-7 μm , height 7-8 μm , disk diameter 3.8-4.9 μm , distance between processes 2.7-3.2 μm . Shell surface with very small (0.2 μm) pores, a ring around base of each process and about 4 between each process.

Remarks. Specimens from Australia are very similar to those from Europe except that the claws are somewhat shorter (in a specimen 550 μm long from Australia the fourth pair are 10.3 and 10.8 μm , from Europe they are 13.5 and 14.1 μm), the accessory claws in the Australian specimens are shorter and finer than those on European specimens.

Bird & McClure (1997a) discussed the eggs of this species, found in soil in South Australia, and noted that eggs were laid in the exuvia as well as free. Only free-laid eggs were isolated from moss from Western Australia in the present study. Bird & McClure also discussed the appearance of two types of egg, one with short narrow processes with wide distal head, the other taller and wider at the base with a narrow distal head. These would seem to correspond to the descriptions of eggs from bisexual and unisexual populations of this species from Europe (Bertolani, Garagna, Manicardi & Redi, 1987).

Distribution. This species was the most abundant of species found in mosses on coastal dune in Italy (Bertolani, 1983c) and was found in moss and litter in Sardinia (Binda and Giglielmino, 1982) and in sand and gravel in Sicily (Pilato, Catanzaro & Binda, 1989). Dastych (1988) found it to be rare in Poland and considered it to be eucalciphilous and xerothermic, the latter is certainly substantiated by the Australian distribution. Its submediterranean distribution has been greatly extended by the Australian findings.

Subfamily Murrayinae Guidetti, Rebecchi & Bertolani 2000

Genus *Dactylobiotus* Schuster, Nelson, Grigarick & Christenberry 1980

Dactylobiotus Schuster *et al.*, 1980: 294

Type species. *Macrobiotus grandipes* Schuster, Toftner & Grigarick 1977.

Diagnosis. Ten peribuccal lamellae present. Buccal tube short rigid, ventral support present with anterior hook. Diploclaws on each leg similar in shape and size, symmetrical with respect to median plane of leg. Diploclaws with bases separated from branches by septum and structurally connected by cuticular bar. Eggs with processes deposited freely.

Dactylobiotus dispar (Murray, 1907)

Macrobiotus dispar Murray, 1907: 6-10, Figs. 1-5

Type locality. Scotland

Material examined. **Australia:** None. Murray (1910) reported finding this species in ponds in the Botanic Gardens, Sydney.

Diagnosis. Aquatic. Cuticle smooth with two dorsal gibbosities between third and fourth pair of legs. Pharynx with two macroplacoids. Claws very long and slender, primary branches with long straight accessory claws.

Description. Body length up to 1000 μm , colourless. Cuticle smooth. Large posterior eyes. Mouth subterminal, surrounded by ten lamellae. No teeth in oral cavity. Two ventro-lateral crests with one or two small median teeth in larger specimens. One single dorsal crest. Ventral support on buccal tube long and strong. Stylet supports inserted at 79-80% of length of buccal tube. Buccal tube thick walled, width about 14% of buccal tube length. Pharynx large and round with two macroplacoids and a microplacoid. First macroplacoid long, with median constriction, second with slight terminal constriction; microplacoid large and strong. Macroplacoid row length 42% of buccal tube length. Legs reduced in length. Claws short and fine; secondary branch joined to primary over much of its length. Accessory claws short and fine, lying very close to primary branch. External claws slightly larger than internal ones on each leg. First pair of claws shortest, fourth pair about same size as second and third (21 and 23% of the buccal tube length). Lunules absent on first three pairs of legs; asymmetrical in size and shape on fourth pair, large and indented on internal claws, small and indented on external claws.

Eggs white, round, laid free. Surface covered with goblet-shaped processes, upper disk with about 12 notches. Egg diameter with processes 107-109 μm , without 90-92 μm . Base diameter of process 6.5-7 μm , height 7-8 μm , disk diameter 3.8-4.9 μm , distance between processes 2.7-3.2 μm . Shell surface with small (0.2 μm) pores, a ring around base of each process and about 4 between each process.

Remarks.

Distribution. Found on every continent.

***Dactylobiotus* sp.**

Fig. 155

Material examined. Australia: NEW SOUTH WALES: N46.2, moss and foliose lichen on rock in subalpine open woodland, 2 specimens.

Diagnosis. Terrestrial. Cuticle smooth. Thin band of teeth in posterior position of oral cavity. Pharynx with two macroplacoids. Claws long and slender, primary branches with short fine accessory claws. Cuticular bars below both claws on first three pairs of legs.

Description. Colourless. Body length 320-380 μm . Large posterior eyes spots present.

Cuticle smooth. Mouth terminal; no teeth in anterior part of oral cavity, thin band of fine teeth in posterior position. Three ventral and three dorsal transverse crests. Buccal tube 46 μm long in 380 μm long specimen and 9 μm wide (15.3% of buccal tube length). Stylet supports inserted at 80% of length of buccal tube and ventral support 41%. Pharynx large and round with two macroplacoids. First macroplacoid 12 μm long with deep median constriction, second 7.6 μm . Macroplacoid row length 42% of buccal tube length.

Legs reduced in length. Claws long and slender; secondary branch joined to primary over much of its length. Accessory claws short and fine. Claws of first pair of legs 13.5 μm long (29%); fourth pair 17.8 μm (38.7%). Cuticular bar below both claws on first three pairs of legs.

Remarks. These specimens undoubtedly belong to the genus *Dactylobiotus*. However, members of this genus are usually aquatic so their presence here in moss and lichen on rock is atypical for members of the genus.

Distribution. Found at only one locality.

Family Microhypsibiidae Pilato, 1998

Genus *Fractonotus* Pilato, 1998

Fractonotus Pilato, 1998: 132-133

Type species. *Calohypsibius ornatus* (Richters 1900) *caelatus* (Marcus 1928).

Diagnosis. Paired elliptical organ present on head. Buccal tube rigid, ventral support absent. Ventral and dorsal apophyses for the insertion of the stylet muscles asymmetrical with respect to the frontal plane; ventral apophyses a ridge with no hook, dorsal apophyses split into two distinct portions. Walls of buccal tube thickened below the insertion point of the stylet supports. Diploclaws of each leg rather different in shape and size, asymmetrical with respect to median plane of leg. Diploclaws with narrow basal part continuous with primary branch, secondary branch joined rigidly to primary branch.

Fractonotus caelatus (Marcus, 1928)

Fig. 156

Hypsibius ornatus var. *caelatus* Marcus, 1928: 179, Fig. 219

Type locality. Ireland.

Material examined. NEW SOUTH WALES: *N3.3*, moss on tree in *Nothofagus* forest, 1 specimen; *N3.2*, moss/lichen on rock in subalpine heath, 6 specimens, 1 exuvium containing 2 eggs. *N14.2.d*, *N14.2.e*, foliose and fruticose lichens on rock in temperate rainforest remnant on escarpment rim, 15 specimens; *N39.2.e.*, moss on rock in cool temperate rainforest, 1 specimen. TASMANIA: *T3.1*, moss on riparian rock in closed forest gully slope, 3 specimens. *T7*, moss/liverwort on rock in wet forest gully, 1 specimen.

Diagnosis. Cuticle with rows of bumps on dorsum; 2 small granular macroplacoids, no microplacoid.

Description. Length 108-174 μm , white. Eye spots absent. Dorsum covered with blunt papillae arranged in 10 rows but with rows of smaller granules between them; rows of small granules on ventral surface also on back of all legs. Papillae gradually becoming smaller and less pronounced towards the head. Mouth antero-ventral. Buccal tube 18.1 μm long in 154 μm long specimen and 1.2 μm wide (6.9% of buccal tube length). Buccal tube walls thickened below the level of stylet support insertion. Stylet supports inserted at 56.7% of buccal tube length. Pharynx almost spherical (15 μm long by 12 μm wide) with granular apophyses and two granular macroplacoids. First macroplacoid longest (2 μm) second macroplacoid 1.2 μm long. Macroplacoid row short (24% of buccal tube length). Claws rather long with long secondary branch particularly on external claw. Claws with small basal unit with secondary branch attached to primary branch; primary branch with short close accessory claws. Internal claws shorter than external claws. Claws increasing in length from first to fourth. Internal claws of first pair of legs 3.8 μm long (20.9% of buccal tube length), external claw 5.4 μm (29.3%); anterior claws of fourth pair of legs 5.4 μm , posterior claws 6.5 μm (35.8%). Lunules absent.

One exuvium containing two smooth eggs found.

Remarks. This species was considered to be a variety of *Calohypsibius ornatus* until given species status by Pilato, Claxton and Binda (1989a).

Distribution. Found throughout Europe at high latitudes and also in West Africa at 2000 m. above sea level. The findings in Australia extends its range considerably and confirms its high altitude (or high latitude) presence.

Genus *Microhypsibius* Thulin, 1928

Microhypsibius Thulin, 1928: 239

Type species. *Microhypsibius truncatus* Thulin, 1928

Diagnosis. Cephalic elliptical organs absent. Buccal tube rigid, ventral support absent.

Ventral apophyses in the shape of a ridge with a blunt hook; dorsal apophyses split into two, the anterior a semilunar hook, the posterior a short thickening. Both dorsal and ventral apophyses with two very slender caudal processes pointing posteriorly and laterally.

Diploc claws on each leg rather similar in shape and size and asymmetrical with respect to median plane of leg. Diploc claws with narrow basal part continuous with primary branch, secondary branch rigidly joined to primary branch.

***Microhypsibius japonicus* Ito, 1991**

Fig. 157

Microhypsibius japonicus Ito, 1991: 35-37, Fig. 3

Type locality. Japan. Mt. Fuji, Central Japan.

Material examined. NEW SOUTH WALES: N3.2.b, moss on rock in *Banksia collina* thicket, 5 specimens.

Diagnosis. Cuticle smooth

Description. Length 110–160 μm , colourless. No eye spots. Cuticle smooth. Mouth antero-ventral; buccal tube (15.7 μm in 160 μm animal) very narrow (8.5% of buccal tube length). Stylet supports inserted at 65.4% of buccal tube length. Pharynx round to oval with small apophyses, three rod-shaped macroplacoids and a faint microplacoid. Macroplacoid row 34.4% of buccal tube length; macroplacoids increasing in length from first to third (1.1 μm , 1.2 μm and 1.6 μm). Claws short with strong, high accessory points; outer claw slightly longer than inner claw on all legs (on fourth pair of legs outer claw is 3.8 μm and inner claw is 3.2 μm) no suture between primary and secondary branches. Lunules absent.

Eggs not found.

Distribution. Found in mosses on rock, decaying logs and tree trunks at the type locality, the species was found in moss on rock in a sheltered position in the New England National Park. The present finding (a new record for Australia) considerably extends the range of this species.

Order Apochela Schuster, Nelson, Grigarick and Christenberry, 1980

Family Milnesiidae Ramazzotti, 1962

Genus *Limmenius* Horning, Schuster and Grigarick, 1978

Limmenius Horning *et al.*, 1978: 247

Type species. *Limmenius porcellus* Horning *et al.*, 1978.

Diagnosis. (emended from Horning *et al.*, 1978) Six buccal lamellae forming an operculum and 6 peribuccal papillae present. Two lateral papillae present. Mouth at anterior end of a long protrusible snout enclosing long mouth cavity. Buccal tube long, thin, flexible with annulations over its entire length. Stylets very long, fine, stylet supports long and thin.

Limmenius porcellus Horning, Schuster and Grigarick, 1978

Figs. 158, Fig. 3.5.1c, Plate XVIa-c

Limmenius porcellus Horning *et al.*, 1978: 249, Figs. 154-156

Type locality. New Zealand.

Material examined. TASMANIA: T8, A. Moscal, moss/liverwort/lichen on skeletal soil hump, 1 specimen.

New Zealand: SOUTH ISLAND. Arthurs Pass National Park, Halpins Creek, 42° 58'S, 171° 34'E, D.S.

Horning Jr, hepatics on *Nothofagus* sp., 1 specimen (NZ373)- **Paratype**; Fox Glacier Valley, lichen on rock, 1 specimen (NZ23) – **Paratype**.

Diagnosis. Mouth at anterior of long protrusible snout enclosing mouth cavity. Buccal tube long, thin flexible with annulations over its entire length. Stylets very long, fine, stylet supports long and thin.

Description. Single specimen 595 μm long, colourless. Eye spots present. Cuticle smooth. Peribuccal lamellae 4.5 μm long, mouth cavity 13.5 μm long by 8.1 μm wide. Buccal tube 197 μm long and 5.4 μm wide. Stylet supports short thin inserted at 55% of buccal tube length. Pharynx piriform 91 μm long and 47 μm wide. Claws with separate primary and secondary branches. Primary branch long (16.8 μm on fourth leg) with short accessory claws; secondary branch with three long branches (14.1 μm long on fourth leg).

Eggs unknown.

Remarks. This specimen is very similar to the New Zealand specimens.

Distribution. The species is rare, only five specimens were recovered in New Zealand and all from *Nothofagus* forests. This is the first record of its occurrence in Australia.

***Genus Milnesioides* Claxton, 1999**

Milnesioides Claxton, 1999: 184

Type species. *Milnesioides exsertum* Claxton, 1999

Diagnosis. Six buccal lamellae forming an operculum and 6 peribuccal papillae present. Two lateral papillae present. Mouth at anterior of long protrusible “snout” enclosing long

mouth cavity which is thick walled and has a cuticular ring at two thirds its length. Buccal tube long and rigid. Stylet long and fine, stylet supports short and flat.

***Milnesioides exsertum* Claxton, 1999**

Fig. 159, Fig. 3.5.1b, Plates XIVa, b; XVa-c

Milnesioides exsertum Claxton, 1999: 184-187, Figs. 1-6, 10B

Type locality. New England National Park, NSW.

Material examined. NEW SOUTH WALES: *N3.2.b*, in moss and fruticose lichens on trachyte rock in subalpine heath, 36 specimens, *N3.2.a*, 30 specimens, *N3.1.b*, moss and lichen on sandstone rock in dry sclerophyll forest, 10 specimens (**type material**). TASMANIA: *T12*, moss on tree, 26 specimens. VICTORIA: *V3*, liverwort, moss and lichen on fallen branches in *Nothofagus* forest, 14 specimens.

Diagnosis. Long protrusible “snout”; long mouth cavity and buccal tube; long fine stylets and short flat stylet supports.

Description. Body length 216-660 μm : females 216-660 μm , males 345-418 μm). Colourless, dorsal cuticle with even reticular pattern (1.0-1.5 μm) more pronounced in caudal region; ventral cuticle smooth. Eye spots present. Mouth terminal surrounded by six peribuccal papillae, 8.7 μm long in 493 μm long female and six triangular buccal lamellae. Lamellae with longitudinal striations at base. Two small vento-lateral papillae 4.3 μm long. Mouth cavity long (20.0 μm long in 493 μm long female), thick walled with cuticular ring about one third of its length from the stylet sheaths, 19.5 μm wide. Buccal tube 86.5 μm long and 15.1 μm wide (17.5% of length of buccal tube). Stylet supports short, flat inserted at 76.9% of length of buccal tube. Stylets long and fine and lie close to the buccal tube; furca small, triangular. Pharyngeal bulb elongated and piriform. Claws

with separate primary and secondary branches. Primary branch short and robust with strong, thick accessory claws; secondary branch with three long branches, two lower ones robust, upper one fine. Two cuticular bars below claws on first three pairs of legs; cuticular bar around back and sides of leg just below primary branch of claw on all legs. Males with modified secondary branches on first pair of legs, two cuticular bars below claws on first three pairs longer and thicker than in females.

Two exuvia containing 3 and 5 smooth eggs were found.

Remarks. Differences between the different populations of this species are discussed in Chapter 3, part 5 of this thesis as is a detailed comparison of the three genera of the family Milnesiidae.

Distribution. The species is limited in its distribution to three similar non-xeric habitats in eastern Australia.

Genus *Milnesium* Doyère, 1840

Milnesium Doyère, 1840: 282

Type species. *Milnesium tardigradum* Doyère, 1840

Diagnosis. Six buccal lamellae forming an operculum and 6 peribuccal papillae present. Two lateral papillae present. Anterior mouth, mouth cavity very short. Buccal tube short, rigid and wide. Stylets short, robust and bent towards the buccal tube a little more than half way down their length. Stylet supports very short, triangular and flat.

***Milnesium tardigradum* Doyerè, 1840**

Fig. 160, Fig. 3.5.1a

Milnesium tardigradum Doyerè, 1840: 283-284; Pl. 13, Fig. 1

Type locality. France.

Material examined. NEW SOUTH WALES: *N1*, liverwort on tree, 1 specimen; *N2*, foliose lichen on tree, 3 specimens; *N3.1.a*, lichen and moss on trees and rocks, 11 specimens; *N3.1.b*, leaf litter, moss and lichen on trees and rocks, 57 specimens; *N3.2.a*, moss on rock, 1 specimen, *N3.2.b*, moss and lichen on rock, 58 specimens, *N3.3*, moss and lichen on trees, 7 specimens; *N3.4.a*, moss and lichen on trees, 6 specimens, *N3.4.b*, moss on tree, 1 specimen; *N3.5.a*, moss and lichen on trees and rocks, 45 specimens, *N3.5.b*, moss on tree, 3 specimens, *N3.6*, moss and lichen on trees and rocks, 11 specimens; *N4*, moss on branch, 1 specimen; *N5*, moss and lichen on rock and branch, 11 specimens; *N8*, lichen on asphalt, gumnuts on soil, 18 specimens, *N11.1*, lichens on branches, 6 specimens, *N11.2*, lichens on branches and trunks, 6 specimens; *N12*, *Banksia* cones on sand, 3 specimens; *N13*, moss and lichen on tree, 2 specimens; *N14.1*, lichen on rock, 4 specimens, *N14.2.a*, lichen on rock, 1 specimen, *N14.2.c*, moss on tree, lichen on rock, lichen on soil, 5 specimens, *N14.2.d*, moss, lichen, liverwort on rock, foliose lichen on branch, 20 specimens, *N14.2.e*, moss on tree, rock and soil, lichen on tree, *N14.3.a*, moss on rock, *N14.5*, leaf litter on soil, 2 specimens, *N14.7*, moss on tree and path, 3 specimens; *N15.1.a*, moss on tree, 2 specimens, *N15.2.a*, foliose lichen on rock and branch, 4 specimens, *N15.2.b*, lichen on tree, 1 specimen, *N15.3.a*, lichen on tree, 3 specimens, *N15.3.b*, moss on rock, 2 specimens, *N15.4*, moss and lichen on tree, 6 specimens; *N16*, foliose lichen on branch, 1 specimen; *N18*, moss on asphalt, 1 specimen; *N20.a*, *N20.b*, *N20.c*, lichens and bracket fungus on tree, 10 specimens; *N21.a*, *N21.c*, *N21.d*, *N21.f*, *N21.g*, *N21.i*, lichen on trees, branches and house roof; 10 specimens; *N22.c*, *N22.d*, moss on rock, lichens on trees and rocks, 15 specimens; *N23*, lichen on trees, 10 specimens; *N27*, moss and lichen on rock, 20 specimens; *N28*, foliose lichen on rock, 1 specimen; *N29.1*, moss on limestone rock and foliose lichen on trees, *N29.2*, moss and lichen on sandstone rock; *N31*, lichen on branch, 4 specimens; *N32*, lichen and moss on branches, 7 specimens; *N34*, lichen on tree, 2 specimens; *N36*, lichen on rocks and logs, 5 specimens, *N37*, lichen and liverwort on tree, 8 specimens; *N38*, lichen on rocks and trees, 4 specimens; *N39*, moss and lichen on rock, 20 specimens; *N40*, lichen on rock, 16 specimens; *N41*, moss on rock and soil, lichen on rock and trees, 17 specimens; *N42*, lichen on *Casuarina*

trees near sea, 6 specimens; *N43*, moss on soil and lichen on branch, 3 specimens; *N44*, moss and lichen on rock, 2 specimens; *N45*, lichen on rock near sea, 3 specimens; *N46*, mosses and lichens on rocks in dry sclerophyll and subalpine open woodland, 20 specimens; *N48*, lichen on sandstone, 6 specimens.

QUEENSLAND: *Q3*, lichen on rotten log, 6 specimens; *Q4*, lichens on trees, 6 specimens; *Q5*, liverwort on rotten log, 1 specimen; *Q6*, liverwort on tree, 2 specimens; *Q7*, moss on tree, 1 specimen; *Q8*, lichens on trees, 9 specimens; *Q9*, lichen on tree, 2 specimens; *Q10*, lichen on tree, 2 specimens; *Q11*, lichen on tree, 1 specimen; *Q12*, moss on tree, leaf litter on soil, *Nostoc* on limestone rock, 22 specimens; *Q14*, lichen on rock and tree, 9 specimens; *Q15*, leaf litter, moss and lichen on rocks and trees, 36 specimens; *Q17*, lichen on tree, 1 specimen; *Q18*, moss, lichen and liverwort on trees, fern on soil, lichen on dead wood, leaf litter, pine cones, 44 specimens; *Q19*, moss on tree, 1 specimen; *Q20*, leaf litter, *Banksia* cone, lichen on trees, 20 specimens; *Q21*, moss lichen on rock, 4 specimens; *Q22*, moss and lichen on tree, 3 specimens; *Q25*, lichen on tree in Box forest, 2 specimens. AUSTRALIAN CAPITAL TERRITORY: *A1*, moss and lichen on rock, lichen on tree, 6 specimens; *A2*, lichen on rock, 1 specimen. VICTORIA: *V2*, lichen on rock, 1 specimen. TASMANIA: *T1*, moss on tree, 11 specimens; *T2*, lichen on sandstone on headland, 1 specimen; *T3*, moss/liverwort on soil, moss on decaying log, moss on rock, 3 specimens; *T4*, moss on rock, 2 specimens; *T5*, liverwort on decaying log, 1 specimen; *T7*, moss on stream bank, 1 specimen; *T16*, moss on dolerite, 2 specimens; *T18*, moss on dolerite, 3 specimens; *T22*, moss on soil, 1 specimen. WESTERN AUSTRALIA: *W1*, moss on rock, leaf litter, 2 specimens; *W2*, lichen on rocks, 6 specimens; *W3*, moss on limestone wall, 1 specimen; *W4*, moss and lichen on pine tree, 4 specimens; *W5*, lichen on tree, 3 specimens. LORD HOWE ISLAND: lichen, 2 specimens.

Diagnosis. Very short wide oral cavity, short rigid buccal tube. Stylets short with distinctive bend about half way, stylet supports triangular.

Description. Length 297-840 μm . Colourless, sometimes larger specimens have brown to orange coloured cuticle, cuticle smooth. Eye spots large. Mouth terminal, surrounded by 6 peribuccal papillae, with 6 triangular pereibuccal lamellae. Lamellae with longitudinal striations at base. Two ventro-lateral papillae. Mouth cavity very short (6.5 μm in 500 μm long female), thick walled, with cuticular ring just above stylet sheaths and 20 μm wide.

Buccal tube 47 μm long and 20 μm wide (42.6% of length of buccal tube). Stylet supports short, flat, triangular, inserted at 64.5% of buccal tube length. Stylets short thick with bend about half their length. Pharyngeal bulb elongated and piriform (100 μm long, 75 μm wide). Claws with separate primary and secondary branches. Primary branch short and robust with strong accessory claws; secondary branch with three long branches. Two cuticular bars below secondary branch of claws on first three pairs of legs; cuticular bar around back and sides of just below primary branch of each claw on all legs. Males with modified secondary branches on first pair of legs, two cuticular bars below claws on this pair of legs longer and thicker than in females.

Smooth eggs laid in exuvium.

Remarks. Two populations (Great Keppel Island, *Q14* and Ravensbourne, *Q22*) have cuticular patterning like that of *Milnesioides exsertum*. These populations are, otherwise, similar to other populations of *M. tardigradum* with smooth cuticle.

Distribution. This species is the most widespread of all tardigrades found in this study. It may be found in extremely dry environments and in very wet ones. It was also found in leaf litter and pine and *Banksia* cones. This eurytopic distribution in Australia is comparable with its distribution elsewhere.

CHAPTER 5. TARDIGRADES FROM CRYPTOGRAMS AND LEAF LITTER ON SOIL AND FROM A SAND ISLAND

5.1 INTRODUCTION

The terrestrial tardigrade literature deals predominantly with tardigrades from cryptogams on rocks and tree trunks and to a lesser extent with cryptogams associated with soil. A much smaller literature exists on tardigrades from leaf litter and from soil and an even smaller literature on tardigrades from non-inundated marine sand.

Although tardigrades from soil and leaf litter were reported a number of times in the early 1900's, Marcus (1936) considered them to be accidental occupiers of these habitats. However, later reports indicate that tardigrades occur in these habitats in much greater numbers and diversity than could be considered accidental (Franz, 1942, 1952; Mihelcic, 1952a, b; Iharos, 1963, 1975 and Hallas & Yeates, 1972).

Iharos (1975), in summarising nearly 40 years of his own research, noted that the two most important factors for soil tardigrades are the structure and microclimate of the soil, while the chemical nature of the soil and the availability of food are also important. Tardigrades feed on rotting plant fragments, algae, hyphae and bacteria as well as nematodes and rotifers, so a rotting layer of leaf litter on top of the soil probably provides the most suitable zone for tardigrades to thrive.

The presence of a layer of leaf litter, cryptogams or even grass turf on the soil surface would be expected to provide a habitat that is more suitable to some species of tardigrade than others.

Bertolani & Rebecchi (1996) examined differences between tardigrade communities in cryptogams on rock, freshwater moss and sediment, grass turf and beech leaf litter. They found that each of these habitats was characterised by very different species although species

overlapping did occur. Two of the overlapping species were *H. dujardini* (found in beech litter, stream moss and stream sediment) and *I. sattleri* (found in turf, beech litter and stream moss). Other species were more restricted in their habitat preferences. For example, *I. lunulatus* and *D. prosirostre* were found in grass turf only. Grass turf and leaf litter were found to be very rich in Itaquasconinae whilst the other microhabitats were depauperate in representatives of this subfamily. In a later study, *I. lunulatus* was found only in the deeper layer below the leaf litter itself (Guidetti & Bertolani, 2001). Very different species associations were found in cryptogams on the beech tree trunks in the leaf litter sampling area.

Guidetti *et al.*, (1999) found high numbers of tardigrades and high species diversity in leaf litter, especially in the upper layers (top 3-5 cm). In comparing the tardigrade fauna of beech leaf litter from two different continents, they found that American and Italian communities were made up of the same genera and had similar species associations. Beech litter is quite humid and the tardigrade communities are made up of hygrophilous and eurytypic eutardigrade species of the genera *Macrobiotus*, *Diphascon* and *Hypsibius*. The same genera were found in soil under grass by Ramazzotti (1959)

Ito (1999) paid particular attention to soil inhabiting tardigrades in his study of the ecology of tardigrades on Mt Fuji, Japan. He determined a distinct pattern of preference of particular species for certain habitats. *M. orcadensis* was placed in a group which occurred in all habitats but which preferred soil. *M. richtersi* and *M. intermedius* were included in the group of species which occurred in all habitats but preferred epiphytes. *D. pingue* was placed in the group of species which occurred mainly in mosses on logs and rocks. He concluded that, in general, *Macrobiotus* species were comfortable in a wide variety of habitats, *Diphascon* species preferred moist habitats like soil or moss on a forest floor while *Echiniscus* species preferred relatively dry tree habitats. He also concluded that tardigrade diversity in soil was as great as that in epiphyte habitats.

Ito & Abe (2001) examined tardigrades in 1 cm slices of 10 cm deep cylindrical podsol soil samples from Mt Fuji, Japan. They found that the shallow layers were frequently dominated by species of *Diphascon* but that species of *Macrobiotus* occurred at higher abundance at greater depths.

Bertolani & Biserov (1996) noted, in genera such as *Xerobiotus*, *Pseudohexapodibius* and *Parhexapodibius*, a tendency to reduction in claw size, particularly of the hind claw. They interpreted this as a convergent adaptation to living in soil. Species with this adaptation were absent from leaf litter (Guidetti *et al.*, 1999). Bertolani (1983c) found several species with reduced claws, including *X. pseudohufelandi* and *E. alicatai*, in moss on coastal sand dunes.

There are no data on tardigrades from leaf litter or cryptogams on soil or sand in Australia although Bird (1996) recorded *X. pseudohufelandi* from sandy loam in South Australia.

Although the major emphasis of this thesis was the collection of tardigrade species in cryptogams on rocks and trees, the opportunity was taken, at many of the sites, to collect leaf litter and/or cryptogams on soil. These data are summarised here with the aim of providing some initial information on species living in these habitats in Australia. This study also reports the findings from a single collection of tardigrades from a sand island.

5.2 MATERIALS AND METHODS

5.2.1 Samples of leaf litter and cryptogams on soil

Forty-six leaf litter samples from 11 sites were collected along with 63 samples of cryptogams on soil from 15 sites (Table 5.1). All site details are listed in Volume 2, Appendix 1. Each sample included the top thin layer (0.5-1 cm.) of humus lying below the leaf litter or cryptogam.

In order to assess the preferences of the tardigrade species recovered from either leaf litter or cryptogam on soil, their prevalence in these sites as a whole and also their presence in other material on other substrates in this study were taken into account before each species was placed into one of the following five categories –

Category

1. Found almost exclusively in cryptogams on rocks or trees, i.e., found either as single specimens or at single sites in leaf litter or cryptogams on soil.
2. Found more often in cryptogams on rock or trees but exhibiting some tolerance for the leaf litter/ cryptogam on soil environment, i.e., occurring in more than one or two samples or sites in leaf litter or cryptogams on soil.
3. Found only in leaf litter on soil.
4. Found only in both leaf litter and cryptogams on soil.
5. Found only in cryptogams on soil.

5.2.2 Samples from a sand island (Bribie Island - Q20)

Bribie Island is a sand island about 16 km long by 6.5 km wide (Fig. 5.1), 0.5 km off the mainland of the central east coast of Australia (see Volume 2, Appendix 1 for further details). Samples of leaf litter and the top 1 cm of sand were taken as well as samples of lichen on trees, as follows:

Subsite

Q20.1-20.2 Skirmish Point. 13 samples of leaf litter/sand were taken about 100 m. from the sea under isolated *Casuarina* sp. trees and 6 samples about 200 m. from the sea under *Eucalyptus* sp. on the ocean (eastern) side of the island.

Q20.3 Heath Walk. 12 samples of leaf litter/ sandy soil, two *Banksia* sp. cones on sandy soil and one sample of foliose lichen from a tree in heath/*Banksia* sp. scrub in the middle of the island (about 2-3 km from the ocean).

Q20.4 Buckley's Hole. 8 samples of foliose lichen from tree trunks in small rainforest remnant on the mainland (western) side of the island.

The Bribie Island samples and the tardigrade species present in them are discussed separately because the underlying substrate is marine sand whilst the other samples discussed in this chapter all relate to soil habitats. The species found are listed in Table 5.2.

5.3 RESULTS

5.3.1 Samples of leaf litter and cryptogams on soil

A total of sixty-three species were found in samples taken from leaf litter and/or cryptogams on soil. On the basis of other distributional data presented elsewhere in this thesis, 19 species were placed into category 1 (Table 5.1). They were considered to be accidental visitors to the leaf litter/soil environment in this study.

Nearly half the species found in these samples (25/63) clearly find that leaf litter or cryptogams on soil provide an environment in which they can thrive, although they are encountered more commonly in cryptogams on rocks or occasionally on trees (Category 2).

The following cosmopolitan species were found - *M. tardigradum*, *D. pingue*, *H. dujardini*, *M. richtersi*, *I. sattleri*, *D. prorsirostre*, *D. higginsii*, *D. bullatum* and *H. conjungens*.

The remaining nineteen species were found to occur only in leaf litter and/or cryptogams on soil. Of these, seven were confined to leaf litter (Category 3), three were found in both leaf litter and cryptogams (Category 4) and nine were found only in cryptogams (Category 5). Ten of these species are new to science (*I. cf bartosi* is also probably a new species). Two species, *D. gordonense* and *L. porcellus*, have been found in other southern hemisphere countries. *X. pseudohufelandi*, *I. lunulatus*, *D. brevipes*, *D. rugosum*, *P. ramazzotti* and *E. alicatai* have all been found overseas and are here reported in Australia for the first time. Two species of *Parhexapodibius* and three of *Calcarobiotus* were found in sufficient numbers to suggest preferences for this habitat. A single species of *Macrobiotus* (*M. fuscus*) was found but as it was recorded at only a single site more records are required to verify its substrate preferences.

5.3.2 Samples from a sand island

Table 5.2 indicates the species present at the three sub-sites and in different substrates on Bribie Island. No quantitative analyses were performed on the samples. Almost 75% of all leaf litter/sand samples were positive although they contained very few (12) species and specimens. Eight of the 13 samples from Skirmish Point (near the beach) contained tardigrades whilst 12 of the 14 from Heath walk were positive. All samples of lichen from trees (nine) contained tardigrades. The Heath Walk samples were the most species productive, yielding nine species, only two of which (*C. australis* and *M. tardigradum*) were also found at the Skirmish Point site. Five species were found at the latter site. Three species (*E. vinculus*, *M. hieronimi?* and *M. tardigradum*) were found in the lichens from trees on the island. A single specimen of *E. vinculus* was found in a leaf litter sample in the Heath Walk but was found in high numbers in lichen on the tree sampled at that sub-site. *M. hieronimi?* and *M. tardigradum* were found in abundance on trees in the rainforest remnant (Buckley's Head) and in the lichen on the single tree at the Heath Walk. Both species were also found in leaf litter and in *Banksia* sp. cones on the sand at the Heath Walk. *M. tardigradum* was found also in leaf litter on the sand near the ocean at Skirmish Point.

The sand/leaf litter fauna from the sub-sites investigated consisted of three species of *Parhexapodibius*, two *Calcarobiotus*, two *Macrobiotus* and one each of *Echiniscus*, *Diphascon*, *Isohypsibius*, *Minibiotus* and *Milnesium*. The single specimen of the marine species, *I. itoi*, was found in sand near the ocean.

5.4 DISCUSSION

5.4.1 Samples of leaf litter and cryptogams on soil

A considerable number of species found in this study may be considered to be accidental visitors to leaf litter and/or cryptogams on soil. However, whether they survive and reproduce there is a question for further research. An even greater number appear to be as comfortable in

leaf litter or cryptogams on soil as they are on other substrates. The extent to which many of these species are truly indifferent to their substrate would require further quantitative studies. The nine cosmopolitan species listed in category 2 have all been cited as occurring in soil or soil related habitats in Europe or Japan (Ramazzotti, 1959; Hallas & Yeates, 1972; Bertolani, 1983c; Ito, 1999; Guidetti *et al.*, 1999; Stark & Kristensen, 1999 and Ito & Abe, 2001). These records and the present work suggests that they are eurytopic species.

Six cosmopolitan species listed in categories 3, 4 and 5 have all been found in soil overseas as well as in soil related habitats in Australia. Leaf litter and cryptogams on soil are also a source of novel species in Australia e.g. *C. australis* and *C. maculatus*, as they are elsewhere. Since there are few or no records of tardigrades of soil or soil related habitats in southern hemisphere countries, a comparison of these new species with those found in such countries cannot be made. Two species, *D. gordonense* and *L. porcellus* may fit into the category of soil inhabiting southern hemisphere species although more records are required.

Because of the preliminary nature of this work, substrate preferences of most of the species found here should be considered to be provisional. Many more records of their occurrences will be necessary before their true preferences are determined. For example, *I. lunulatus*, was found only in grass turf in the study of Bertolani & Rebecchi (1996), whereas in this study it was found in leaf litter and moss on soil. *D. prosirostre* is a second species with an apparent shift in habitat preference. In this study, it was found to prefer moss on rock while in the Italian study of Bertolani & Rebecchi (1996) it was found only in grass turf.

These instances suggest that perhaps very fine distinctions in habitat type are not appropriate when speaking of tardigrade preferences and/or that the apparent difference in species found in leaf litter and cryptogams on soil observed here may be a reflection of the small sampling. Both the number of samples and the number of specimens of many of the species found in this study are too low for any definite conclusions to be drawn. One hundred and nine leaf

litter/cryptogam/soil samples were processed along with about 1600 cryptogam samples in this study. It is not known whether any of these species live in the soil layer beneath the leaf litter or cryptogam rather than in those layers themselves. A point, made by Stark & Kristensen (1999) and not fully taken into consideration in this study, is that tardigrades may adhere to soil particles. Consequently, some may not be washed down during routine processing and may therefore be unaccounted for in the analysis of data.

In this study, 3/14 species of *Diphascon*, *D. gordonense*, *D. brevipes* and *D. rugosum*, were found exclusively in the soil related environment and another three species, *D. pingue*, *D. higginsii* and *D. prosirostre*, were found to utilise the habitat rather frequently. This finding is to some extent consistent with the contention of Ito (1999) that *Diphascon* spp. prefer moist habitats like soil or moss on the forest floor. However, many of the samples in this present study were from dry environments yet still contained a high proportion of *Diphascon* spp., suggesting that the soil environment may be more important than the level of moisture.

The findings in this study agree with the generally held belief that heterotardigrades avoid soil habitats and that *Echiniscus* spp. prefer dry tree habitats. Only two (*P. australis* and *E. marcusii*) of the 40 species of heterotardigrades found in this study were found in soil habitats in numbers which suggest that they are comfortable in this environment.

All known species of *Calcarobiotus* from other parts of the world have been found to prefer living in soil or moss growing on soil (Abe & Takeda, 2000). However, three of the eight new species of *Calcarobiotus* described in this present study were found exclusively in leaf litter or cryptogams on soil, three other species may have a partiality for this environment but prefer cryptogams on rock and two other species were found only in cryptogams on rock. This suggests that this genus may have broader habitat preferences than the literature would suggest although a partiality for soil related habitats is indicated. In this study, very few species of *Macrobiotus* were found, although, as in European and Japanese studies, *M.*

richtersi was found to be a common component of the tardigrade fauna of leaf litter and cryptogams on soil. It may be that more species of *Macrobiotus* would have been found had deeper depths of soil been examined (Ito & Abe, 2001). It is also possible that some species identified as *Macrobiotus* may in fact belong to the genus *Calcarobiotus* because the two genera are rather similar. Both adults and eggs of *C. maculatus* are similar to those of *M. richtersi*.

It is noteworthy that, of the species in this study that seem to favour soil habitats, only a few exhibit the reduction of claw size reported to be an adaptation for inhabiting soil environments (Dastych & Alberti, 1990, Bertolani & Biserov, 1996). Species exhibiting this adaptation are *Parhexapodibius* spp., *D. brevipes*, *E. alicatai*, *I. aridus* and *L. breviunguis*. It would appear that, although a tendency to reduction in claw size, particularly of the hind claw, may well be a convergent adaptation to living in soil, it would not appear to be essential to a successful existence in this habitat.

It is also noteworthy that the vast majority of species in Category 2 prefer their cryptogams on rock. Of the five species which seem to be equally as comfortable on trees as on rocks, four (*H. dujardini*, *I. sattleri*, *M. richtersi* and *M. tardigradum*) would be considered to be eurytopic both in this study and in European studies (Dastych, 1987; Bertolani & Rebecchi, 1996), whilst the preferences of the fourth (*I. pawlowskii*) are inconclusive because of the very low numbers of specimens involved. The finding, in this study, that most of those species which tolerate soil habitats but favour a rock substrate over trees or logs, is perhaps to be expected since most patches of cryptogam on rock accumulate soil and/or organic matter beneath them.

5.4.2 Samples from a sand island

Although the Heath Walk site appeared to be far more productive of tardigrade species than the Beach site, it should be remembered that soil mesofaunal distribution within a particular

habitat is usually quite variable (Anderson *et al.*, 1984). Proctor & Marks (1974) (cited by Anderson *et al.*, *ibid*) suggested that at least 40 core samples are required to obtain population estimates of soil mesofauna within 20% of the true mean. The 12 and 13 samples, examined here, from the two sites probably contain only a small proportion of the real number of species existing in the sand on Bribie Island.

A single specimen of *E. vinculus* was found in a leaf litter/sand sample from the Heath Walk. Taking into account the mass of other collecting data for this species (Chapter 4, page 236) and the fact that it was common in lichen on the trees in the same area, it may be concluded that this specimen is an accidental visitor to this habitat.

A single specimen of *I. itoi* was found in sand near the ocean. It was also found in supralittoral and intertidal sand at the type locality (Ishikari, Hokkaido, Japan). Marine species of the eutardigrade genus *Isohypsibius* are known from the coasts of northern Europe and Japan (Tsurusaki, 1980) but this is the first record from Australia. The disjunct distribution of this species is not inconsistent with what is known about the distribution of marine species but may also reflect the paucity of collection.

P. ramazzottii was found in rather a different habitat here than the soil under grass at the type locality in Italy (Manicardi & Bertolani, 1987). Eighteen of the 22 specimens of this species found in the beach sand at Skirmish Point were encysted. Formation of red cysts, such as those found here, is regarded as an adaptation to a hostile environment. The beach sand leaf litter is dominated by large carnivorous tardigrades, *C. australis*, *C. capricorniensis* and *M. tardigradum*. The first two species were replaced by *M. richtersi* and *M. hieronimi*? in the leaf litter on soily sand further away from the beach. *M. tardigradum* clearly retains its position as the most eurytopic and widespread of all tardigrade species, occurring in all the habitats sampled in this study.

The specimens identified as *M. hieronimi*? here are questionable because of some slight differences from the type. The egg processes are smaller and in the adults the stylet supports are inserted more caudally and the claws are somewhat shorter. The identification is also rather questionable as this is the only site at which the species was found in leaf litter/soil. Elsewhere, it shows a preference for cryptogams on trees. It is acknowledged, however, that the differences in morphology and in habitat preference may be due to a difference in biotype of the populations. Bertolani *et al.*, (1990) found that differences and frequency of sexual and parthenogenetic strains of *Ramazzottius* on different substrates were mainly due to the different modes of reproduction. Bertolani, Garagna, Manicardi & Redi (1987) showed that bisexual and unisexual populations of *X. pseudohufelandi* laid eggs with processes of different size while adults exhibited no differences in morphology.

One habitat, not examined in this study, is the soil beneath grass tufts. In Europe, a number of studies have revealed a wealth of tardigrades in this habitat (Manicardi & Bertolani, 1987; Bertolani, Manicardi & Gibertoni, 1987 and Bertolani & Rebecchi, 1996). Of the eleven species isolated by Manicardi & Bertolani (1987) five, *P. ramazzottii*, *I. lunulatus*, *D. prosirostre*, *D. higginsi* and *M. richtersi*, were found in this study in soily habitats and *P. pilatoi* was found in sand on Bribie Island.

5.5 CONCLUSION

Considering the low number of samples processed, this study has provided considerable data on the nature of Australian soil tardigrades and suggests that further study would be very fruitful. The study has revealed similarities with the fauna found elsewhere but has also provided evidence of many new species.

Figure 5.1 Location of collection sites on Bribie Island (Q20)

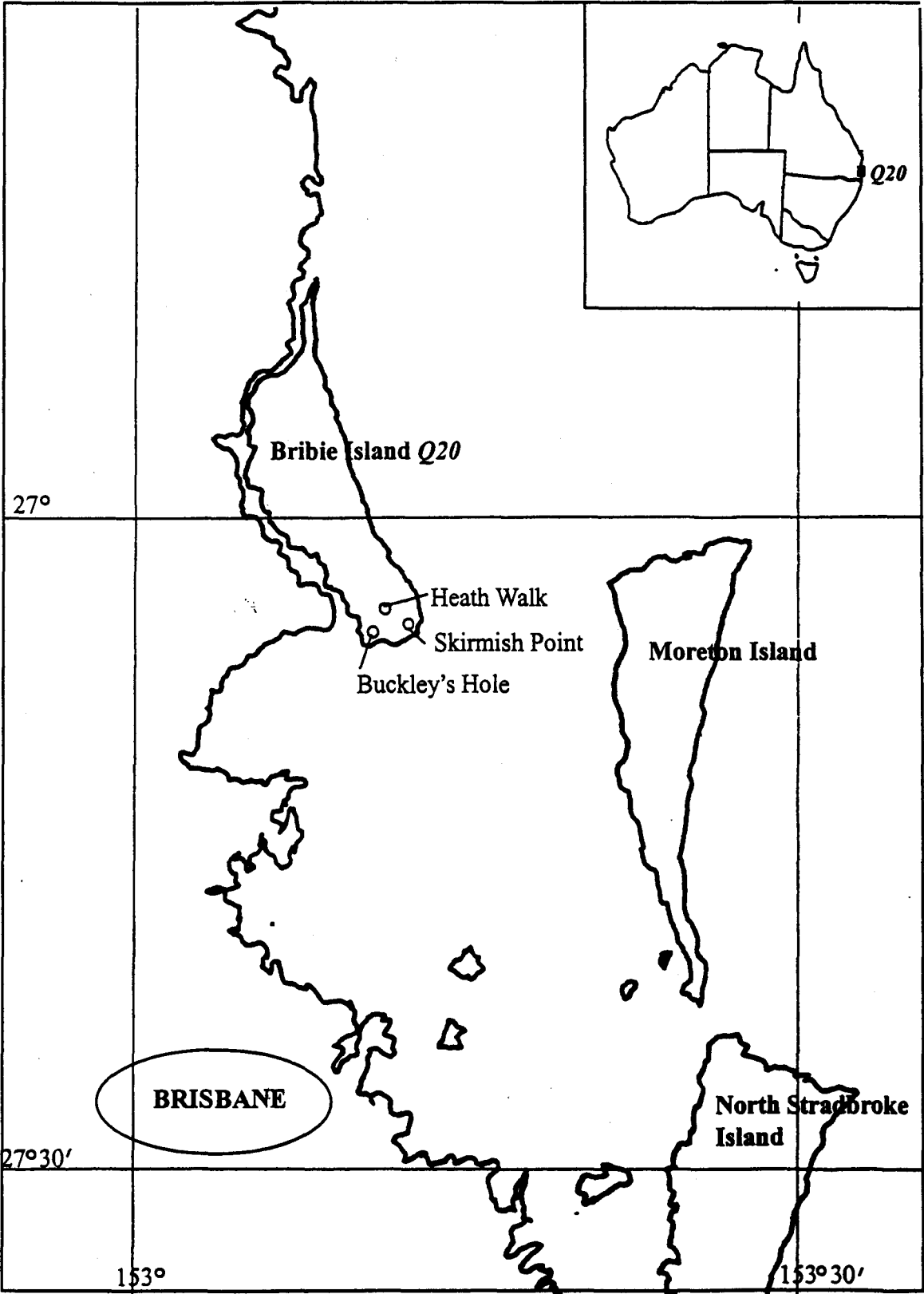


Table 5.1 Tardigrade species in leaf litter and cryptogams on soil

	Site/ Species	Leaf Litter											Cryptogams																
		N3	N8	N9	N14	N15	N35	Q12	Q15	Q18	V1	V3	N3	N8	N14	N15	N29	N31	N38	N41	N43	N47	Q18	Q26	V1	V4	TA		
1	<i>E. vinculus</i>				*										*												*		
	<i>I. cameruni</i>	*													*												*		
	<i>M. hibiscus</i>							*	*																		*		
	<i>M. orcadensis</i>				*										*												*		
	<i>M. intermedius</i>												*		*												*		
	<i>D. puniceus</i>				*										*												*		
	<i>E. curiobulbus</i>																										*		
	<i>M. tasmanicus</i>																										*		
	<i>M. aquatilis</i>																										*		
	<i>C. ornatus</i>																										*		
	<i>D. langhovdense</i>																										*		
	<i>D. pinguiforme</i>																										*		
	<i>M. hufelandioides</i>																			*							*		
	<i>L. melbaensis</i>				*																						*		
2	<i>E. cf duboisi</i>	*																									*		
	<i>M. milleri</i>	*																									*		
	<i>M. australoliviae</i>							*			*																*		
	<i>M. nemus</i>						*								*												*		
	<i>M. petersi</i>														*												*		
	<i>M. tardigradum</i>	*	*		*			*	*	*					*					*						*	*		
	<i>D. pingue</i>	*	*		*			*	*	*					*					*					*	*	*		
	<i>H. dujardini</i>	*	*	*	*	*	*	*	*	*		*		*	*		*	*	*	*		*			*	*	*		
	<i>M. richtersi</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
	<i>I. satleri</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
	<i>P. australis</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
	<i>M. guttus</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
	<i>M. furciger</i>	*	*	*	*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
	<i>M. torridus</i>	*	*	*	*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
3	<i>I. unguiculum</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
	<i>I. australogilvus</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
	<i>M. fallax</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
	<i>M. taii</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
	<i>D. higginsii</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
	<i>D. prorsirostre</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
	<i>M. rigatus</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
	<i>I. cambewarrense</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
	<i>E. marcusii</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
	<i>D. bullatum</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
	<i>H. conjungens</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
	<i>I. pawlowskii</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
	<i>E. bulbulus</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
	<i>C. adunatus</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*		
<i>C. erugatus</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*			
<i>C. capricorniensis</i>	*	*		*	*	*	*	*	*		*		*	*		*	*	*	*		*		*	*	*	*			
4	<i>P. australis</i>	*	*		*			*	*																				
	<i>C. australis</i> sp. n.	*	*		*			*	*																				
	<i>C. reticulatus</i> sp. n.	*	*		*			*	*																				
	<i>D. gordonense</i>	*	*		*			*	*																				
	<i>X. pseudohufelandi</i>	*	*		*			*	*																				
	<i>I. aridus</i>	*	*		*			*	*																				
5	<i>L. breviunguis</i>	*	*		*			*	*																				
	<i>C. maculatus</i>	*	*		*			*	*																				
	<i>I. lunulatus</i>	*	*		*			*	*																				
	<i>D. brevipes</i>	*	*		*			*	*																				
	<i>D. rugosum</i>	*	*		*			*	*																				
	<i>P. ramazzottii</i>	*	*		*			*	*																				
6	<i>I. cf bartosi</i>	*	*		*			*	*																				
	<i>E. alicatal</i>	*	*		*			*	*																				
	<i>I. bellus</i>	*	*		*			*	*																				
	<i>D. obscurus</i>	*	*		*			*	*																				
	<i>H. turritus</i>	*	*		*			*	*																				
	<i>M. fuscus</i>	*	*		*			*	*																				
	<i>L. porcellus</i>	*	*		*			*	*																				
	<i>Number of samples</i>	5	13	1	6	1	2	3	6	2	4	3	1	9	10	1	2	1	5	3	5	1	4	2	1	3	15		

**Table 5.2 Tardigrade species found on a sand island (Bribie Island), Queensland
Site Q20**

Species	Sub-site	Skirmish Point	Heath Walk			Buckley's Hole*
		Q20.1-2	Q20.3a	Q20.3b	Q20.3c	Q20.4
	Habitat	leaf litter/ sand	leaf litter/ sand	cone/ sand	lichen tree	lichen trees
<i>E. vinculus</i>			1		3	
<i>P. australis</i>			2			
<i>P. pilatoi</i>			2			
<i>P. ramazzottii</i>	1					
<i>D. pingue</i>			1			
<i>I. itoi</i>	1					
<i>C. australis</i>	4		1			
<i>C. capricorniensis</i>	2					
<i>M. hieronimi?</i>			3	3	3	4
<i>M. richtersi</i>			2			
<i>M. hispidus</i>			3			
<i>M. tardigradum</i>	2		2	2	3	4
Number of species		5	9	2	3	2
Number of samples		13	12	2	1	8
Number of pos samples		8	10	2	1	8
% Tardigrade Positive Samples		61.5	83.3	100	100	100
Average species per sample		1	1.7	2	3	1.6

- 1 – rare
2 – uncommon
3 – common
4 – abundant
* - rain forest remnant

CHAPTER 6. THE DISTRIBUTION OF TERRESTRIAL TARDIGRADES IN EASTERN AUSTRALIA

6.1 INTRODUCTION

The terrestrial habitat of tardigrades is difficult to define (Hofmann, 1987). Each species has its own requirements for many factors at the microhabitat level, such as humidity, insolation, mechanical and chemical properties of the substrate which may be moss, lichen or leaf litter on tree trunks, rocks or soil. Of all the possible factors, humidity and insolation are probably amongst the most important.

The classification of tardigrade species according to the hygrometric conditions in mosses is well documented (Bartoš, 1940, 1941; Ramazzotti & Maucci, 1983). Species are divided into four groups depending on the types of mosses which they find most favorable: xerophilous (typical of dry mosses), eurytopic (found in every type of moss), hygrophilous (characteristic of moist mosses) and hydrophilous (found in wet mosses and in water).

Other attempts to classify tardigrades (Mihelcic, 1954; Hofmann, 1987) using a complex of factors have been of limited value. In a general sense, it can be said that mosses (or lichens) that are well exposed to sunlight in open spaces will have a different suite of species to mosses in shady, rather moist places (Ramazzotti & Maucci, 1987). Such a general proposition does not necessarily assist in determining species assemblages in different macrohabitats because cryptogams housing tardigrades may be localised in a moist microhabitat within an otherwise dryer environment and vice versa. Consequently, it would be of little value to compare the tardigrade faunas of different regions by examining the species occurring at just one site within each region. Whilst single site studies may add considerably to our knowledge of tardigrade biodiversity they contribute little to our understanding of tardigrade communities and their patterns of distribution.

In some large scale studies (Horning *et al.*, 1978; Maucci, 1980) environmental factors such as altitude, substrate, insolation and sample moisture content were evaluated separately. Maucci (1980) also attempted to classify genera and common species according to their preference for a latitudinal band, 34-44°, 45-50° and 56-70°. He found some preferences amongst genera, e.g., *Diphascon* has a marked preference for higher latitudes and both *Echiniscus* and *Pseudechiniscus* a preference for lower latitudes and amongst species, e.g., *R. oberhaeuseri* a preference for low latitudes. He suggested that a study correlating these factors would require a far larger number of samples than the 2686 that he had analysed. Dastych (1988), in analysing 5261 samples from Poland, used similarity indices after first dividing his study area into geobotanical units. In addition, he provided evidence for the strong influence of the type of bedrock and of altitude on species distribution.

The study of tardigrade communities and their patterns of distribution, as with all animal communities, is complex. This complexity has resulted in only a small number of studies involving a limited range of statistically based analyses of distributional data. Multivariate techniques have rarely been used but could be of value in such studies.

Only a single, statistically based analysis of tardigrade distributional data has been published. Cluster and Principal component analyses of quantitative, replicated samples were undertaken by Kathman & Cross (1991). They failed to show that altitude is an important determinant of tardigrade distribution even though previous studies claimed this to be true (Rodriguez-Roda, 1951; Nelson, 1975; Bertrand, 1975; Beasley, 1988; Dastych, 1980, 1987, 1988).

Regional studies from Europe have stressed differences between the tardigrade fauna of mountainous regions and lowland areas, with higher altitude areas being richer in species (Morgan & King, 1976; Dastych, 1980, 1988 and Biserov, 1991). Dastych (1988) extended his examination of the Polish fauna with a detailed account of the zoogeographical implications of the species he found. He enumerated a number of difficulties that rendered his zoogeographical characterisations provisional. The main difficulty, apart from the lack of data from many areas, was the numerous taxonomic problems at the species level. Despite these difficulties, he provided an analysis of the species present in the geobotanical regions of Poland. He concluded that, while there is a clear difference in mountain and lowland fauna, probably related to glaciation, there are no distinctive tardigrade assemblages associated with either coniferous or deciduous forest associations.

Australia has a rich and highly endemic fauna and flora. It is well known that the Australian macrofauna and flora are unique, as exemplified by the diversity of marsupial mammals and plants of the family Myrtaceae. Many major groups of invertebrates are also richly developed in Australia, eg, Lepidoptera (Nielsen, 1999) and Onychophora (Briscoe & Tait, 1995). The distribution and abundance of Tardigrada in Australia is, at present, unknown.

To understand the present day composition and distribution of species within a taxon, one must consider the extent to which historical events, current physiogeographical factors and dispersal have moulded the patterns of occurrence.

The plate tectonic history of Australia has been summarised by Adam (1994) who described the separation of Australia from other Gondwanan land masses – Africa, Madagascar, India, South America and Antarctica. The important steps were –

- Africa and India separated from the rest of Gondwana in the late Cretaceous (around 70 million years ago).
- A connection or close proximity of Antarctica/ Australia/ New Zealand existed through most of the early Tertiary (55 MYA).
- Australia/New Zealand separated from Antarctica and moved north through 27° of latitude from the mid Eocene (45 MYA).
- The Australian plate became connected to south-east Asia by a chain of volcanics in the early Miocene (20 MYA). (Martin, 1984)

The movement of Australia from high latitudes 240 million years ago to its present position astride the tropic of Capricorn brought about enormous change in the climate of the continent, with a pronounced drying commencing about 15 million years ago. This brought about a general retreat of the, then, extensive rainforests eastward to refugia in the eastern highlands, while sclerophyllous derivatives of the rainforest came to occupy much of the rest of the continent.

The eastern highlands, known as the Great Dividing Range (Fig. 6.1), have been a major landmark feature for many millions of years (Adam, 1994). As the highest part of the continent and being situated close to the eastern seaboard, the highlands experience a relatively high rainfall. Rainfall decreases rapidly to the west of the Range and much of the continent is arid or semi-arid (annual rainfall less than 500mm). Higher annual rainfall (greater than 1000 mm) occurs along the eastern seaboard and in Tasmania. Along much of the east coast, rain occurs throughout the year but with seasonal maxima in summer in the north and winter in the south (Adam, 1994). However, there is considerable variability in rainfall from year to year in Australia.

The Great Dividing Range extends 2500 km along the eastern margin of the continent. It is elevated in the south-east as a region known as the Australian Alps at about 2000 m and contains the continent's highest mountain, Mt Kosciuszko (2228 m). Elsewhere along the Great Dividing Range only limited segments reach 1500 m. In the north, on Cape York, the range peters out into a series of low hills only a few hundred metres high. The watershed of the Great Dividing Range is not a dramatic feature, but the slopes to the east of the Divide are abruptly terminated by the Great Escarpment with rugged spurs and deep valleys that have provided opportunities for the development of numerous vegetation types including many types of rainforest. Areas of rainforest exist side by side with non-rainforest in harsh local environments such as steep, rocky north-facing slopes or nutrient-poor sites. Along the coastal plain, human impact has drastically reduced native vegetation. In the Sydney region, urbanisation and agriculture has increasingly fragmented what was originally continuous native vegetation (Benson & Howell, 1995). In the Blue Mountains (immediately to the west of Sydney, Fig. 6.1) outdated sewage outfalls have polluted many of the warm temperate rainforest pockets that occupy gorges (Wright, 1996).

There are almost as many ideas about biogeographic schemes for Australia as there are groups of organisms that have been studied (Archer & Fox, 1984). However, when considered over the full range of flora and fauna, there do appear to be a number of core subregions with each experiencing different climatic regimes. There is a northern monsoon subregion that supports a combination of sub-humid and semi-arid woodlands with a subtropical rainforest component in north-eastern Queensland. The central-western subregion supports grassland and semi-arid shrubland and the south-eastern subregion is typified by wet and dry sclerophyll forests and sub-humid woodlands as it is in the south-western subregion (Archer & Fox, 1984). Within these subregions, the ameliorating effects of topography provide conditions for intermingling of these major habitat types, e.g.,

stands of subtropical rainforest may occur as far south as Sydney. A significant habitat in the south-eastern region is the cool temperate rainforest, now reduced to isolated pockets along the great Dividing Range where rainfall exceeds 1200 mm pa. Extensive areas of Tasmania still retain these cool temperate elements. It may be that each of these geobotanical subregions contains members of the tardigrade fauna that reflect their different histories and climate regimes. To date, this idea has not been tested.

These geobotanical subregions correspond loosely with biogeographic elements proposed by MacKerras (1970) for Australian insects. His “Archaic” element consisted of species that have survived with little change since Paleozoic or early Mesozoic times. He described two Northern elements – an older one (Pantropical or northern Gondwanaland)) which had ancient affinities with India, Africa and Madagascar and even some neotropical relationships and a younger element (Oriental or Indo-Malayan) stemming back to the Holarctic Tertiary radiation whose main entry into Australia was via New Guinea. His Southern element, which he regarded as “antarctic” or southern Gondwanaland comprised a large part of the Australian invertebrate fauna. His endemic element represented species that have evolved within a particular geographical region of Australia.

Few data exist on the distribution of tardigrades in the different vegetation types in Australia, either at the broader scale of biogeographical subregions or in small scale studies. We may be led to believe, from the comments of Murray (1910), that there would be very few species living in the dry sclerophyll because of the lack of cryptogams (Murray only examined mosses) in that environment. Claxton (1991) found no lack of cryptogams in the dry sclerophyll forest at Douglas Park, NSW. This study showed that dry sclerophyll forest contained more tardigrade species in greater abundance than a warm temperate rainforest at Cambewarra Mountain, NSW and that there were differences in the

tardigrade assemblages in these two sites. All studies in Australia, to date, have dealt with species found in the moister eastern highlands and coastal region with only a single species having been described from Tasmania and one from Western Australia. There are no records of tardigrades from arid or semi-arid Australia. Although species of some key genera from the southern hemisphere *Nothofagus* forests, such as *Oreella* and *Mopsechiniscus*, have been found in similar habitats in Australia (Murray, 1910; Dastych & Moscal, 1996), there are no data on the tardigrade assemblages of these forests nor of other forest types in Australia.

The concept of cosmopolitanism amongst tardigrades is based on the presumed intercontinental distributions of many species as they are currently defined and on some evidence that their tuns can be transported passively (Kristensen, 1987). Other evidence, however, suggests that tardigrades are only transported very short distances by ‘rain-drop splash’ and strong winds (Sudzuki, 1972; Wright, 1987).

As taxa are being examined more closely, e.g., Bertolani & Rebecchi (1993), it is becoming evident that many of what we have been calling species up to now are, in reality, groups of closely related species. Pilato & Binda (2001) hypothesised that species “groups” have arisen from a very ancient ancestor that had a widespread distribution and that cosmopolitan components of such groups could be interpreted as being the more closely related descendants of the “group” ancestor. They summarised the limited fossil evidence and evidence from tardigrade biology to suggest that tardigrades evolve very slowly. These authors, together with McInnes & Pugh (1998) and Pugh & McInnes (1998) suggest that current biogeographical distribution patterns of non-marine tardigrades display evidence of paleogeographical events.

McInnes & Pugh (1998) claimed that 3% and Pilato & Binda (2001) 6.8% of tardigrade species are cosmopolitan. The degree of similarity of the Australian fauna to that of the rest of the world has not been investigated.

The aim of this section of the study was to determine if relationships exist between the distribution of tardigrade species and the major geobotanical subregions present along the eastern margin of Australia, including Tasmania, and to examine patterns of tardigrade distribution in relation to history, physiographical factors and dispersal. If such relationships exist the aim was also to identify the species associations which typify the different subregions. Because of the extensive species identifications which form the basis of a previous section of this study it may also be possible to investigate the relationship between the Australian fauna and that of other parts of the world.

6.2 MATERIALS AND METHODS

Species lists of tardigrades from cryptogams and leaf litter on a variety of substrates in 37 sites in eastern Australia including Tasmania were selected for multivariate analysis..

Tasmania is treated as a single site in this study. The 37 sites constitute a subset of the 110 sites listed in Appendix 1. In order to remove some bias from low yielding sites due to either low numbers of species or small numbers of samples, an arbitrary decision was made to remove from the analysis sites yielding less than seven species. Single sites representing an unusual environment, such as a sand island, were also removed.

Within each of the 37 sites, each species was scored on a five-point scale of abundance –

0-absent

1-rare

2-uncommon

3-common

4-abundant.

A total of 143 species were identified in 1198 samples from these sites.

In this study, a number of sites were sampled much more extensively than others. For the purposes of this section of the study, samples collected from sub-sites (listed in Appendix 1) within these large study sites were pooled. At some sites collections were made at a dry sclerophyll site close to the main study site. These are as follows -

1. New England National Park (*N3.1*) is the dry sclerophyll site near the main subalpine/cool temperate rainforest sub-sites (*N3.2*, *N3.3*, *N3.4*, *N3.5* and *N3.6*) the data from which were pooled to form New England National Park (*N3*).
2. Leura/Katoomba (*N14A*) consists of the pooled data from four collections (*N14.1*, *N14.2.e*, *N14.5* and *N14.6*) in dry sclerophyll in the Blue Mountains. Pooled data from six collections (*N14.2.a*, *N14.2.b*, *N14.3.a*, *N14.3.b*, *N14.4* and *N14.7*) from temperate rainforest constitute Leura/Katoomba (*N14*).
3. *N29.2* is the dry sclerophyll site on sandstone on Taralga Road a few kilometres away from the limestone site at Wombeyan Caves (*N29*).
4. On Mt Kosciusko, a dry sclerophyll site (*N46.1*) was chosen at 1000 m asl. Data from the two higher sites in subalpine woodland at 1200 and 1500 m asl (*N46.2* and *N46.3*) were pooled to form *N46*.
5. At Cania Gorge, Queensland, the dry sclerophyll site is *Q15.1*. Data from the Creek path (*Q15.2*) was pooled with that from the subtropical rainforest site (*Q15.3*) because of their proximity to each other and the similarity in vegetation as (*Q15*).

The sites/species data matrix was subjected to Agglomerative hierarchical cluster analysis with three types of linkage - Single, Average (McQuitty) and Complete using the statistical package Minitab vers. 13.32.

The 37th site, Barron Falls(Q5), appeared as an outlier and was removed from further analysis. The 141 species occurring in the remaining 36 sites in each resulting Cluster are identified in Table 6.1. Based on their frequency and abundance in each Cluster, species were grouped as follows –

Group 0 – species with no specific Cluster affiliation

Group 1 – species predominately or only occurring in Cluster 1 sites

Group 2 – species predominately or only occurring in Cluster 2 sites

Group 3 – species predominately or only occurring in Cluster 3 sites

Group 4 – species predominately or only occurring in Cluster 4 sites

Group 5 – species predominately or only occurring in Cluster 5 sites

Within each group the species were further divided according to their reported world distribution as follows –

CO – cosmopolitan, found in both northern and southern hemisphere land masses

PT – pantropical, found also in Africa and/or Central America and/or tropical Asia

OR – oriental, found also only in tropical Asia

SH – found only in the southern hemisphere

AU – found only in Australia

Species in the following text may be referred to according to this grouping and distribution, e.g., 0 CO refers to a species in Group 0 (Species occurring in all Clusters) with CO (cosmopolitan) distribution.

Both the groupings and the subdivisions are tentative and will almost certainly be subject to change with improved knowledge of tardigrade taxonomy and distribution. They should be seen as an attempt to place some structure on the data available, in order to provide an analysis of the zoogeography of tardigrades and the composition and evolution of their communities. Table 6.3 lists 30 species considered to be cosmopolitan in this study and identifies those that have been newly designated in that category in this study.

6.3 RESULTS

6.3.1 Site Clusters

The three dendrograms produced by Single, Average and Complete linkage are shown in Fig. 6.3. The Single linkage method produced no clear Clusters (Fig. 6.3a). The Complete and Average linkage dendrograms (Fig. 6.3b and 6.3c), however, suggest a main division of sites into two clusters with a further division of the larger cluster into a number of smaller clusters. Both dendrograms contain almost the same individual sites in each cluster suggesting that the data are robust. For clarity of discussion, however, the dendrogram produced by the Average linkage method was chosen in the following analysis.

Five Clusters of sites (Fig. 6.3b) were considered for further analysis.

6.3.1.1 Cluster 1 (6 sites)

The six sites that clustered together are quite distinct from all other sites. They are: *N3* (New England National Park), *N4* (Barrington Tops), *N46* (Mount Kosciusko national Park), *TA* (Tasmania), *V2* (Mt. William, The Grampians, Victoria), and *V3* (Melba Gully, Victoria).

All six sites are from cool temperate regions, either at more southerly latitudes (*TA*, *V2* and *V3*) or at high altitude (above 1200 m asl) at lower latitudes (*N3*, *N4* and *N46*) (Fig. 6.2a). *N3* and *N4* are in *Nothofagus* forests and *N3* consists of five sub-sites, two within *Nothofagus* stands and three in subalpine heath adjacent to *Nothofagus*. *N46* consists of two subalpine sites above 1200 m asl in Mount Kosciusko National Park. A high average annual rainfall (above 1300 mm) is characteristic of these sites although there is a summer rainfall pattern at *N3* and *N4* and winter rainfall in the more southerly sites *N46*, *V2*, *V3* and *TA*.

Tardigrades were recovered from 230 (86%) of the 268 samples examined.

Eighty-four species were identified (Table 6.2)

This Cluster could be classified as “Cool temperate” and is characterised by very short dry periods and relatively low temperatures. Cryptogams occur in large beds.

6.3.1.2 Cluster 2 (4 sites)

Four sites, *Q6* (Curtain Fig Tree), *Q7* (Mulgrave), *Q18* (Eumundi) and *Q15* (Cania Gorge), clustered together.

All four sites are from sub-tropical rainforests from 17°S to 26°S (Fig. 6.2b). The first two sites are rainforest remnants while *Q15* is subtropical rainforest in a largely untouched area and *Q18* is an urbanised site that includes rainforest remnants.

Tardigrades were recovered from 86 (86%) of the 100 samples examined. Forty-one species were identified (Table 6.2).

This Cluster could be classified as “subtropical” and is characterised by short dry periods and high temperatures. Cryptogams occur in isolated clumps.

6.3.1.3 Cluster 3 (10 sites)

Four sites clustered together, *N46.1* (Mount Kosciusko National Park), *N40* (Lake George Range), *N41* (Galore) and *N38* (Narrandera). At the next level of clustering (66% similarity), three sites, *N5* (Sandy Hollow), *N8* (Ryde) and *Q15.1* (Cania Gorge), also grouped with the first four sites. A further three sites, *Q21* (Crows Nest), *N28* (Appin) and *N48* (Darling Hill), clustered with lower similarity.

The four main sites in this group occur within a 250 km radius of each other at around 36-37°S latitude (Fig. 6.2c). All consist of dry open woodland with cryptogams more or less restricted to rocks and soil and with a winter rainfall pattern with little or no rain for about 8 months of the year. Both *N46.1* and *N40* occur above 600 m asl and the average annual rainfall is a little higher than that which falls at *N38* and *N41*. These latter sites are 20 km apart about 100 km inland of the first two sites. *N38* is an open woodland site in the Riverina area of NSW. *N41* consists of a large sandstone monolith and samples were taken from the top at about 600 m asl and half way down at 325 m asl. Extended dry periods are also characteristic of the two dry sclerophyll Queensland sites (*Q15.1* and *Q21*) that have a summer rainfall pattern. However the four sites around the

Sydney region (*N5*, *N8*, *N28*, *N48*) are all exposed to a non-seasonal rainfall pattern but have dry sclerophyll vegetation.

Tardigrades were recovered from 118 (93%) of the 127 samples examined. Forty-six species were identified (Table 6.2).

This Cluster could be classified as “Open dry woodland” and is characterised by long dry periods and high summer temperatures. Cryptogams occur mostly in isolated clumps.

6.3.1.4 Cluster 4 (11 sites)

Four sites, *N14* (Leura/Katoomba), *N14A* (Leura/Katoomba dry sclerophyll), *N39* (Cambewarra Mountain) and *N29.2* (Wombeyan dry sclerophyll) clustered at better than 84% similarity. An additional four sites, *N3.1* (New England National Park dry sclerophyll), *N31* (Minnamurra), *N27* (Douglas Park) and *Q25* (Cunningham’s Gap), clustered at 75% similarity with the first four sites. Two sites, *N11* (Mt Wilson) and *N35* (Barrengarry), clustered at 74%.

The sites in this interesting set come from an area of great ecological diversity that includes the Eastern Highlands, the escarpment and the coastal plain. Most came from the Blue Mountains region and the Sydney basin (Fig 6.2d) both of which are now heavily urbanised but once carried large areas of both temperate and subtropical rainforest of which *N31* is a remnant.

Two sites occur in the lower latitudes (*N3.1* at 30°S and *Q25* at 28°S) at altitudes of 600 and 1000 m respectively. Although the former site is in dry sclerophyll

forest and the latter in Box forest they both lie on the eastern edge of the escarpment, that is, have a climate rather similar to those of the temperate rainforest sites near Sydney. All but two sites (*N27* and *N31*) occur above 600 m asl. The Sydney sites occur in dry sclerophyll (*N14A*, *N29.1*, *N27* and *N22*) and in temperate rainforest remnants (*N14*, *N11*, *N39* and *N35*). *N31* occurs in a subtropical rainforest remnant close to the coast on the eastern escarpment. *N27* occurs at 125 m asl but is situated above a river cut deeply into sandstone. Rainfall is not seasonal and varies from below the average (1168 mm pa) to well above in some areas in the mountains. All of these sites have a climate moderated by their proximity to the coast and the nearby highlands.

Tardigrades were recovered from 464 (86%) of the 540 samples examined. Sixty-six species were identified (Table 6.2).

This Cluster could be classified as “Coastal warm temperate” and is characterised by short dry periods only occasionally becoming extensive and by moderate temperatures. Cryptogams occur in isolated clumps, rarely in beds.

6.3.1.5 Cluster 5 (5 sites)

Three sites, *N15* (Jenolan Caves), *N29* (Wombeyan Caves) and *N43* (Yarrangobilly Caves) clustered together at about 72% similarity. Two more sites, *N21* (Camden) and *Q22* (Ravensbourne), had some similarity to the first three sites (67%). The first three sites are on limestone and lie within a radius of about 200 km (Fig 6.2e). *N15* and *N29* are close to most of the Cluster 4 sites.

Half the samples from the first three sites were taken from trees and half from limestone. The samples from the last two sites (*N21* and *Q22*) were all taken from trees in open woodland. Like the Cluster 4 sites these sites have a climate moderated by proximity to the coast and the nearby range.

Tardigrades were recovered from 116 (85%) of the 137 samples examined. Forty-five species were identified (Table 6.2).

This Cluster could be classified as “Limestone/ coastal woodland” and is characterised by rare extensive dry periods and moderate temperatures.

Cryptogams occur primarily in isolated clumps.

6.3.2 Species occurrence in Site Clusters

Table 6.1 lists the sites grouped according to the Cluster analysis against species grouped according to a) their known distribution and b) their distribution and abundance in each site. The groups are somewhat arbitrary, e.g., *M. intermedius* is placed in the eurytopic group but is missing from some clusters. Its overall distribution does not suggest an affiliation with a particular Cluster so it was placed with the eurytopic species. Three Australian species, *P. australis*, *M. torridus* and perhaps *M. fallax* were found in every Cluster and so might be considered as eurytopic species. However, they show a very strong association with Cluster 4 and so were placed in that group. Since very infrequent species can contribute nothing to the overall pattern such species were removed from further discussion. Table 6.4 lists species that are considered to be significant members of the species assemblages of the Clusters.

6.3.2.1. Species with no Group affiliation (Group 0)

Eight species occurred frequently in all or most Clusters of sites (Group 0, Table 6.4). Six of these (0 CO) are eurytopic cosmopolitan species. Two species have a southern hemisphere distribution (0 SH) but both species require additional taxonomic work, so their distribution is still questionable.

6.3.2.2. Cluster 1 species (Cool temperate)

The six sites of Cluster 1 are very productive of species, with 84 species being identified. Thirty species occur in high frequency and abundance (Table 6.4). The sites are significant for the number of rare genera that occur only in them - *Milnesioides*, *Limmenius*, *Haptobiotus*, *Antechiniscus* and *Oreella*.

Of the 84 species that occur in Cluster 1 sites, 24 (29%) are cosmopolitan, one (1%) is pantropical, 18 (21%) are southern hemisphere and 41 (49%) are Australian (Table 6.5). It is significant that 86% of all southern hemisphere species found in this study were found in these sites and that no species from the oriental category and only a single species from the pantropical category were found (Table 6.6).

a) Cosmopolitan species

Twenty four (80%) of the 30 cosmopolitan species found in this study were also found in these sites (Table 6.6). The ten species set (1 CO, Table 6.4), is of particular interest because these species are found almost exclusively in these cool temperate sites. Some of these species also occur in sites in other Clusters but these occurrences are rare and are all in sites over 600 m. asl.

b) Pantropical species

A single specimen of *M. hibiscus* was found at New England National Park.

b) Southern Hemisphere species

Southern hemisphere species constitute a relatively high proportion (21%) of species found in these sites (Table 6.5).

Four southern hemisphere species occur with high frequency and abundance in these sites. They are, *M. furciger*, *D. langhovdense*, *M. aculeatus* and *M. asteris* (1 SH, Table 6.4). Other species of particular interest because they are known otherwise only from New Zealand are: *A. parvisentus*, *D. zyxiglobus*, *E. velaminis* and *L. porcellus* (1 SH, Table 6.4).

c) Australian species

Six of the 41 Australian species found in these sites, were found in abundance in these sites. They are: *M. rigatus*, *D. pannuceum*, *I. australogilvus*, *L. melbaensis*, *M. exsertum* and *E. curiobulbus* (1 AU, Table 6.4). Two Australian species of *Antechiniscus*, although not found in great numbers are significant members of the species assemblage of these sites. Other common species are *M. australis*, *M. australoliviae*, *M. tasmanicus* and *M. milleri*.

d) Similarity to other Clusters

Cluster 1 sites share a number of species with the sites of Cluster 4. Not only do many of the species strongly associated with Cluster 1 appear in highland Cluster 4 sites, e.g., *M. furciger*, *M. rigatus*, but, as well, many of

the most frequent and abundant species from Cluster 4 also occur in the cool temperate sites, e.g., *D. higginsii*, *I. cameruni* and *E. cf. duboisi*. Some southern hemisphere species found most commonly in Cluster 1 sites (1 SH) also occur in some highland Cluster 5 sites, e.g., the New Zealand species, *D. zyxiglobus*, is clearly a temperate species (Table 6.4).

Cluster 1 sites share very few species with Cluster 2 and 3 sites and when this occurs, it involves single occurrences of species in sites. For example, *M. furciger* was also found at *Q18*, an urbanised rainforest remnant site in southern Queensland, in Cluster 2 and at *N28*, a woodland site just south of Sydney, in Cluster 3 (Table 6.1).

6.3.2.3. Cluster 2 species (Subtropical)

Forty-four species were found in these sites. Twelve species occur in high frequency and abundance in these sites (Table 6.4). Species in two genera, *Doryphoribius* and *Calcarobiotus*, are more prevalent in these sites than in those from other Clusters (Table 6.1).

Of the 44 species found, nine (21%) are cosmopolitan and six are eurytopic species. Six species (14%) are pantropical, five species (11%) are southern hemisphere and 24 (54%) species are Australian (Table 6.5).

a) Cosmopolitan species

The cosmopolitan element is rather poorly represented at 21% of species found in the sites (Table 6.5). This constitutes only 30% of all cosmopolitan species found (Table 6.6). This element consists of six eurytopic species,

four of which are common or abundant (0 CO) as well as three other species that occur in very low frequency and abundance (Table 6.1).

b) Pantropical species

Sixty percent of all pantropical species found, occurred in these sites (Table 6.6). They represent a much higher percentage (14%) of species occurring in these sites than in other clusters of sites (1-10%) (Table 6.5). Three of the six pantropical species occur with high frequency and abundance in these sites. They are, *M. hibiscus*, *E. tessellatus* and *P. jiroveci* (2 PT, Table 6.4).

d) Southern Hemisphere species

The southern hemisphere element (11% of species found in Cluster 2 sites) is relatively small (Table 6.5). The five southern hemisphere species that do occur in these sites constitute only 24% of those found in the study (Table 6.6). Of these five species, two are eurytopic (*E. cf. vinculus* and *M. hieronimi*) and only the former occurs in an appreciable number (Table 6.1).

e) Australian species

Fifty four percent of the species found in these sites are Australian (Table 6.5). Only *D. australocitrinus* occurs in high frequency and abundance but *P. ficus* and *C. maculatus* are common (2 AU, Table 6.4).

f) Similarity to other Clusters

Cluster 2 sites share very few species with Cluster 1 sites, in most cases, involving occurrence at a single site, e.g., *M. hibiscus*, *C. microaculeatus* and *M. rigatus* (Table 6.1).

There is some overlap of species with Clusters 3 and 4. *C. maculatus* which is strongly associated with the subtropical sites of Cluster 2, occurs in abundance in the Cluster 3 site, *N8*. The pantropical species *E. tessellatus* (another species strongly associated with Cluster 2) and *E. pusae* are found as far south as 34°S in subtropical rainforest at Minnamurra (*N31*), a Cluster 4 site. Only *E. perarmatus* was found at the higher latitude of 34°S in a dry sclerophyll (Cluster 4) site above the Nepean River (*N27*). The Cluster 2 species, *D. australocitrinus*, was found only north of 28°S. Site *Q25*, the most southerly site from which this species was collected, is a rainforest site whose affinities lie with Cluster 4 (Table 6.1).

Cluster 2 sites have very few species in common with Cluster 5 sites except for the presence of *P. jiroveci* in both.

6.3.2.4. Cluster 3 species (Open dry woodland)

Forty-seven species were found in these sites. Fifteen species were found in high frequency and abundance (Table 6.4). The genus *Minibiotus* is well represented in the fauna of these sites.

Twelve species (26%) found in these dry woodland sites are cosmopolitan, one species pantropical (2%), one species (2%) is oriental, six (13%) are southern hemisphere and 27 (59%) are Australian (Table 6.5).

a) Cosmopolitan species

Twelve (40%) of the thirty cosmopolitan species found in this study were found in these sites (Table 6.6). The eurytopic cosmopolitan species, *M. intermedius* is absent from these sites. Two other cosmopolitan species, *M. taiti* and *E. blumi*, occur quite frequently and in abundance in these sites (3 CO, Table 6.4).

b) Pantropical species

Only one pantropical species, *M. hibiscus*, was found at a single site (*Q21*) in low numbers.

b) Oriental species

The oriental species, *M. santoroi*, was found in moderate frequency and abundance in two of these sites (3 OR, Table 6.4).

c) Southern Hemisphere species

Southern hemisphere species constitute a small percentage (13%) of the fauna of these sites (Table 6.5). The six species represent only 29% of all southern hemisphere species found in the study (Table 6.6). Three of these, *E. vinculus*, *M. furciger* and *I. cameruni*, occur at only one site each in low numbers. The eurytopic species, *M. hieronimi*, is common and abundant in these sites whilst two species of *Minibiotus*, *M. hispidus* and *M. scopulus*, were found only in these sites and in relatively high numbers (3 SH, Table 6.4).

d) Australian species

Members of the Australian component of the fauna of Cluster 3 sites (57% of the species found in these dry sites, Table 6.5) are rarely shared with sites from other Clusters. They constitute 34% of all Australian species found (Table 6.6). These sites are strongly characterised by four Australian species, *M. guttus*, *E. marculi*, *C. erugatus* and *M. hufelandioides* (3 AU, Table 6.4).

e) Similarity to other Clusters

The fauna of the Cluster 3 sites, even more so than that of Cluster 2, is distinguished by the low proportion of southern hemisphere species (13%) and also by a very high proportion of Australian species (57%) (Table 6.5).

There is very little overlap with other Clusters, particularly Cluster 1. There are isolated occurrences of some Cluster 2 species in these sites, e.g., *D. australocitrinus*, *B. australis* and *C. reticulatus* in Cluster 3 site, *Q15.1*, and conversely of Cluster 3 species in Cluster 2 sites, e.g., *M. guttus*, *E. marculi* and *C. australis* in Cluster 2 site, *Q15* (Table 6.1).

There are some co-occurrences with Cluster 4 and Cluster 5. *E. marculi* (a very strong indicator for the drier sites of Cluster 3) was found in three Cluster 4 and in one Cluster 5 dry sclerophyll sites. The Cluster 4 species, *M. torridus*, was found in high numbers in three Cluster 3 sites (Table 6.1).

6.3.2.5 Cluster 4 species (Coastal temperate vegetation)

Sixty-seven species were identified from these sites. Twenty-six species occur in high frequency and abundance in these sites. No single genus dominates the fauna.

Of the 67 species, 16 (24%) are cosmopolitan, seven (10%) are pantropical, one (2%) is oriental, 13 (19%) are southern hemisphere and 30 (45%) are Australian (Table 6.5).

a) Cosmopolitan species

All the eurytopic cosmopolitan species (0 CO) occur with high frequency and abundance in this Cluster along with several of the cool temperate species, *F. caelatus*, *I. pawlowski* and *M. montanus* in low frequency and abundance. 53% of the total number of cosmopolitan species found in the study, occur in these sites (Table 6.6) and they make up 24% of the species found in these sites (Table 6.5). *M. orcadensis* and *D. higginsii* are strongly associated with these coastal temperate sites (4 CO, Table 6.4).

b) Pantropical species

Seven of the ten species in this distribution group were found in these sites (Table 6.6) and they constitute 10% of the species found in these sites (Table 6.5). *E. tessellatus*, *P. jiroveci* and *E. perarmatus* (2 PT) and *E. virginicus* (4 PT) were found in rainforest sites in Cluster 4. The rare African species, *R. szeptycki*, was found in a rainforest environment in one Cluster 4 site. Two pantropical species, *E. virginicus* and *M. peteri* were found almost exclusively in these sites and in high frequency and abundance (4 PT, Table 6.4).

c) Oriental species

M. santoroi was found in low numbers in a dry sclerophyll site (N27) in this Cluster (Table 6.1).

d) Southern Hemisphere species

Southern hemisphere species represent a significant part of the fauna of these sites with 13 species (62% of all southern hemisphere species found, Table 6.6). Four of these species were found in high frequency and abundance (4 SH, Table 6.4) whilst the cool temperate species, *M. furciger*, *M. aculeatus*, *D. zyxiglobus* and *O. mollis* also occur in the upland sites of Cluster 4.

e) Australian species

The contribution of Australian species to the fauna in these sites is, at 45% (Table 6.5), somewhat lower than that for other Clusters. Nevertheless, five Australian species, *E. curiosus*, *P. australis*, *M. fallax*, *M. torridus* and *I. cambewarrense*, were found frequently and in abundance in Cluster 4 sites (4 AU, Table 6.4).

f) Similarity to other Clusters

These sites not only contain their own set of species but also share many species with all other Clusters, particularly with Cluster 1 (Table 6.1).

Many of the clearly cool temperate species of Cluster 1 sites such as the southern hemisphere species *I. cameruni*, *M. furciger*, *M. aculeatus*, *O.*

mollis and *D. zyxiglobus* are found in the highland sites of Cluster 4 as are a number of the Australian species from Cluster 1, for example, *M. rigatus*, *D. pannuceum*. Conversely, a number of the species assigned to Cluster 4 are also found in many cool temperate sites, for example, *D. higginsii*, *I. cameruni*, *P. australis* and *M. fallax*. Two species, *E. curiosus* and *I. cambewarrense* (strongly associated with Cluster 4 sites) also occur in cool moist Cluster 1 sites (Table 6.4).

Key species from the subtropical sites of Cluster 2 occur with some frequency in these Cluster 4 sites. The two Clusters share four pantropical species, *E. tessellatus*, *P. jiroveci*, *E. perarmatus* and *E. pusae* although three other pantropical species, *E. virginicus*, *M. peteri* and *R. szeptycki*, were found only in Cluster 4 sites (Table 6.1).

Cluster 4 sites share rather few species with Cluster 3 sites. Notable exceptions are the presence of *E. marcusii* (from Cluster 3) in three Cluster 4 sites and *M. torridus* (from Cluster 4) in abundance in three dry sclerophyll sites in Cluster 3. *M. torridus* (morphologically very similar to *M. hufelandi*) was also found in very low numbers in Clusters 1 and 2. It clearly prefers a dry habitat but is rather adaptable and widespread.

Cluster 4 sites and Cluster 5 sites share a number of species that occur commonly in Cluster 4, e.g., *E. cf duboisi*, *M. torridus* and *M. fallax* (Table 6.4).

6.3.2.6. Cluster 5 species (Limestone/ dry woodland)

Forty-five species of tardigrades were recovered from these sites. Fourteen species occur with reasonable frequency and abundance (Table 6.4). No single genus typifies these sites.

Fourteen species (31%) are cosmopolitan, four (9%) are pantropical, nine (20%) are southern hemisphere and 18 (40%) are Australian (Table 6.5). Species of two rare genera, *Eremobiotus* and *Cornechiniscus* were found in these sites.

a) Cosmopolitan species

The cosmopolitan component of 14 species includes five species (5 CO) found almost exclusively (except for the single occurrence of *I. lunulatus* at the Cluster 1 site, V3) in the three limestone sites of Cluster 5 (Table 6.1).

These are: *E. viridissimus*, *E. alicatai*, *I. lunulatus*, *D. rugosum* and *I. prosostomus* (5 CO, Table 6.4).

b) Pantropical species

Four pantropical species (9%) of all species found in these sites, (Table 6.5) occur in these sites. They are: *P. jiroveci*, *B. intermedius*, *M. peteri* and *M. ethelae*. *P. jiroveci*, although more clearly associated with the tropics, was found on limestone paths and gutters in other sites as well as on the limestone at Jenolan Caves (N15) and Wombeyan Caves (N29) and so appears to have a preference for a limestone substrate. The four species constitute 44% of all pantropical species found in the study (Table 6.6)

c) Southern Hemisphere species

The southern hemisphere component of nine species (20% of all species found in these sites, Table 6.5), apart from the two eurytopic species, consists of cool temperate species such as *D. zyxiglobus*, *M. aculeatus* and *E. velaminis* and of species found in abundance in nearby highland sites, e.g., *E. cf duboisi*, *P. novaezeelandi* and *I. wilsoni*.

d) Australian species

Amongst the Australian species only *M. saxatilis* could be considered to be strongly associated with limestone itself (it was also found on a limestone wall in Perth, Western Australia) although it was found in very low numbers on sandstone at one site (5 AU, Table 6.1). *E. arboris* was found at two of the limestone sites but always on trees so cannot be considered to be a limestone species. The most notable find amongst these sites was a specimen of a species of *Cornechiniscus* (5 AU Table 6.1). The single specimen came from limestone at Jenolan Caves (N15).

e) Similarity to other Clusters

This Cluster differs from all others in the distinctive set of limestone-loving cosmopolitan species. It shares only a few of the cool temperate southern hemisphere species, most notably, *D. zyxiglobus*.

This Cluster has little affinity with Cluster 2 sites although the two pantropical species, *P. jiroveci* and *B. intermedius* were found in these sites.

There are few shared species between Cluster 5 and Cluster 3 sites but these mostly involve the appearance of single species in single sites at rather low abundances (Table 6.1).

The Cluster 5 sites are geographically rather close to Cluster 4 sites and there is a relatively high frequency of occurrence of many of the species strongly associated with Cluster 4, *E. curiosus*, *P. australis*, *M. fallax* and *M. torridus*. The presence of some species usually found in cool temperate sites reflects the higher altitude, and therefore more benign climate, of the limestone sites.

6.4 DISCUSSION

6.4.1 Tardigrade species communities in geobotanical subregions in eastern Australia

Tardigrade communities in eastern Australia consist of a mosaic of cosmopolitan, pantropical, oriental, southern hemisphere and endemic species. The degree to which each of these types contribute to each assemblage is determined by the evolutionary history and the climatic regime of each region and, to a limited extent, by passive dispersal. Sixty-seven (48%) of the 141 species found in this study are strongly associated with one cluster or another (Table 6.4). This is the first study to reveal distinct species communities associated with different site groups in eastern Australia. The site groups are related primarily to the temperature regime and the length of dry periods that they experience and they can also be recognised as members of different geobotanical regions in Australia, e.g., subtropical rainforest sites form a single cluster.

The cool temperate forests (exemplified by Cluster 1) are characterised by high species diversity and abundance and, in this respect, are similar to high altitude regions elsewhere

in the world (Dastych, 1988). Some genera, unique to all southern hemisphere cool temperate rainforests, are present. A very high number (30) of species are strongly associated with these forests (Table 6.4). The tardigrade fauna is characterised by a high proportion of cosmopolitan montane species that are absent from lowland areas in Australia. It is also characterised by a high percentage of species found only in the southern hemisphere. The community associated with cool temperate areas in south-eastern Australia, is particularly different from assemblages from both dry and tropical subregions. Although it is clear that the cool temperate forest supports a very specific community of tardigrades it is also clear that species adapted to warm temperate upland areas may find, at times, suitable niches within the usually benign conditions of the cool temperate rainforests. Conversely, some of the cool temperate species may find their niche in other rainforest types on the eastern divide or even in subalpine heath now devoid of cool temperate rainforest vegetation.

Although the number of sites and samples from both subtropical (Cluster 2) and dry sclerophyll forests (Cluster 3) were much lower than those from other regions, there is clear evidence that each contains unique tardigrade species communities.

The subtropical forests (Cluster 2) of north-eastern Australia contain a high proportion of species otherwise found only in countries to the north and/or neotropical regions (pantropical) and these species are absent from the cool temperate rainforests and from the dry woodlands. A subtropical rainforest remnant as far south as 34°S (*N31*) still retains some of these species. Subtropical regions support very few species of southern hemisphere distribution and when they occur it is only in very low frequency and abundance. The regions do, however, support a high proportion of unique Australian species that rarely occur elsewhere in eastern Australia. Fewer species (12, Table 6.4)

occur in high frequency and abundance in the subtropical subregion than in other subregions, however, a greater sampling effort may reveal greater numbers.

Sites subjected to long dry periods, seasonal rainfall, high summer temperatures and with dry sclerophyll vegetation (Cluster 3) are characterised by a particularly high proportion of Australian species that rarely occur elsewhere in eastern Australia. A relatively large number of species (15) occurring in high frequency and abundance suggests that the aridification of Australia did not hinder the evolution of tardigrade species (Table 6.4). Like the subtropical rainforests, the dry sclerophyll forests contain very few species of southern hemisphere distribution but the pantropical species are also absent from these forests. The very low overlap of species with those from cool temperate sites is in keeping with statements suggesting that most tardigrade species have their own particular set of microhabitat requirements.

The coastal temperate sites on the mid-east coastal region of Australia (Cluster 4) have a rich mixture of species from all sources - cosmopolitan, southern hemisphere, pantropical, oriental and a set of endemic Australian species all of which occur in much greater numbers than in other habitats in Australia. Twenty-six species are strongly associated with these sites (Table 6.4). They also share other species that are more common in cool temperate, subtropical or dry areas. This mixture reflects the climatic conditions that provide this coastal region with a wide variety of niches (there are well over 40 distinct vegetation communities in the Blue Mountains alone, Wright, 1996), as well as the historical input of both the southern element and the tropical element as the continent moved through time and space to more northerly latitudes. It also reflects the human influence on tardigrade communities in some areas. The close similarity in species content of the temperate rainforests and the dry sclerophyll areas in the Blue Mountains west of

Sydney (*N14* and *N14A*) found in this study is almost certainly due to pollution and degradation of rainforest pockets so that only the most hardy species have now survived. *O. mollis* is one cool temperate species which was originally described by Murray (1910) from Leura/Katoomba (*N14*). However, the species could not be found at the type locality in this study despite the examination of 192 samples in seven different collections of cryptogams from the same area.

This analysis has provided some preliminary data on tardigrades in limestone areas in Australia (Cluster 5). The species assemblages differ from those found on sandstone with six species exhibiting a strong association with the limestone itself. Fourteen species may be found in high numbers in these sites (Table 6.4). These findings are consistent with those of Dastych (1980, 1988) for limestone communities in Poland. It is demonstrated most clearly at Wombeyan (*N29*) where a sandstone site (*N29.2*), close to the limestone, was sampled and can be seen to contain a very different suite of species. However, it must be said that the site data for Jenolan (*N15*) and Wombeyan (*N29*) in this analysis included species that also occur on trees in the vicinity of the limestone and this may account for their grouping with Camden (*N22*) and Ravensbourne (*Q22*) where collections were made largely from trees in open woodland. Dastych (1988) suggested that it is, perhaps, not just the pH of limestone that is important for tardigrades, but the sum of conditions, probably modified by the substrate. Limestone, for instance, reacts differently than other rock types to heating and cooling and this, in turn, modifies the moisture content and its rate of change. These conditions may possibly be duplicated on other substrates such as tree bark. At Jenolan Caves, in particular, many species occurred on both the limestone and the trees in the area. No tests were done on the acidity/alkalinity of the cryptogams sampled. It would, however, be instructive to do so in further studies.

6.4.2 Relationships of tardigrade species occurrences in geobotanical subregions to the climate and history of the subregions

The distribution patterns of organisms are responses to their environment and so reflect climatic factors. In Australia, clearly defined zoogeographic subregions with marked boundaries and distinctive characteristic faunas do not exist, but, when considered over the full range of flora and fauna there do appear to be a number of core subregions; a northern monsoonal, a nontropical south-eastern and a dry central-western subregion (Archer & Fox, 1984). The clusters of sites produced in this study by assemblages of tardigrade species correspond well to these broad-scale zoogeographic subregions. Cluster 2 represents subtropical rainforest of the northern subregion. Cluster 4 sites of the south-eastern subregion are moderated by proximity to a coast and a coastal range and typified by wet and dry sclerophyll forests. Cluster 3 sites are from the dry central-western subregion supporting dry sclerophyll to semi-arid shrubland and typified by high temperatures and long dry periods. Within the south-eastern region, clusters of sites representing two distinct habitat types have also emerged in this study. The first is cool temperate rainforest (Cluster 1) in areas of cool temperatures and high rainfall and the second is a set of limestone sites (Cluster 5).

Within the 36 sites involved in this analysis, eight of 141 species (6%) may be found in any Cluster (Group 0, Table 6.1). To this group of eurytopic species might be added the Australian species *P. australis* and *M. torridus* because both can be found in some sites in every Cluster. (Their subjective placement in Group 4 species reflects their occurrences in high numbers in many sites in Cluster 4.) The data suggest that a very low proportion of the tardigrade fauna (ten in 141 species, 6-7%) have broad habitat requirements. The distributions of other species (or at least those that occur in sufficient numbers that their preferences may be deduced) are clearly related to macroclimatic regimes although in most

cases individual environmental factors cannot be discerned. We can infer that, for example, species that are strongly associated with Cluster 3 sites (Table 6.4) are adapted to an environment dominated by high temperatures and long dry periods. Using the data from this study together with what is known from other overseas studies, a preference for a carbonate substrate may be deduced for some species, e.g., *Di. rugosum*. An interesting example is *E. marculsi* that can be found primarily in dry sites throughout the continent (it was also found in Western Australia). When the collection data are closely examined (Chapter 4 page 210) this species can be seen to be almost completely restricted to foliose lichens on non-carbonate rock.

Although it is admitted that analysis based on cosmopolitanism and endemism must contain a high level of speculation, such analysis, at this time, is justified because modern plate tectonics gives a fairly precise and rigid framework to which such speculations may be attached. The presence of a group of cosmopolitan species that may be found in any habitat (0 CO, Table 6.1) in Australia suggests that these species are eurytopic ones that, because of their adaptability, have survived on all continents since their origin when the continents formed a single unit, Pangea.

Another ancient set of cosmopolitan species (1 CO) has survived in a montane environment in Australia as they have in Europe. Five of the nine species (*M. areolatus*, *C. ornatus*, *H. conjungens*, *H. convergens* and *I. pawlowski*) are described as montane by Dastych (1988). *Microhypsibius japonicus* was found on Mount Fuji, Japan (Ito, 1991). The other four species have also been found primarily in highland areas in other countries. Two xerophilic cosmopolitan species, *M. taiti* and *E. blumi*, occur in Australia. The preferences of *Mi. taiti* elsewhere are still unrecorded. However Dastych (1980) recorded *E. blumi* as a xerophilic species in Poland. Most of the six cosmopolitan species that appear to have a preference for

temperate sites in Australia (4 CO) are problematic because of lack of detailed distributional data in some cases, e.g., *M. orcadensis*, or taxonomic problems in others, e.g., *D. higginsi*, *D. bullatum* and *D. pinguiforme*. Both *A. trinacriae* and *D. prosirostre* are widely distributed in Poland and are euryhydric (Dastych, 1988). This description fits their Australian distribution. The five cosmopolitan species (5 CO) found on limestone in Cluster 5 sites are found in this same habitat in Europe (Dastych, 1988). Of the 30 cosmopolitan species found in this study ten are recorded, for the first time, in this category (Table 6.3).

Pantropical species survive in Australia in warm moist habitats of subtropical (2 PT) and temperate areas (4 PT) of the east coast of Australia. This is consistent with their apparent origin at a time, about 135 million years ago, when Gondwana was still a single entity consisting of South Africa, South America, India and Australia.

The individuality of the tardigrade fauna of cool temperate sites (Cluster 1) is particularly significant, as these are remnants of a vegetation, once widespread in Australia and in other southern hemisphere countries (New Zealand, Antarctica and southern South America) when they formed a single continent lying at high latitudes 60-45 million years ago. Tardigrade species known only from cool temperate environments in other southern hemisphere countries occur here, not only in the same cool temperate environments but also in nearby high altitude areas, e.g., *Oreella mollis* can still be found in warm temperate rainforest on the east coast. It has also been recorded in New Zealand, Antarctica and South America (Dastych, McInnes & Claxton, 1998). This genus also contains another species, *O. reinhardti*, identified from the high altitude (670 m) forest at Cambewarra Mountain (N39) in New South Wales. Mount Kosciuszko (N46) which is now devoid of cool temperate rainforest still provides refuge for a species of *Antechiniscus*. Two species of that

genus occur in the cool temperate rainforest in New England National Park (N3) and also in the subalpine vegetation nearby. Even so, this study confirms the contention of Kristensen (1987) that *Nothofagus* (cool temperate) forests support specific communities of tardigrades. He stressed the presence of species of three genera - *Oreella*, *Mopsechiniscus* and *Antechiniscus* - all of which occur in cool temperate conditions in Australia. (Although no species of *Mopsechiniscus* were found in this study, a single species was described from cool temperate rainforest in Tasmania (Dastych & Moscal, 1992)).

At the species level, a set of southern hemisphere species (*M. furciger*, *O. mollis*, *Diphascon alpinum* and *M. intermedius*) is strongly associated with *Nothofagus* forests in Chile (Kristensen, 1987). *M. furciger* is an indicator species for cool temperate forests in Australia. Both *D. alpinum* and *M. intermedius* have undergone taxonomic revision since 1987 and it may be that *D. alpinum* is actually *D. langhovdense* (a species strongly associated with the cool temperate forests in Australia). *M. intermedius* was not found frequently in the cool temperate rainforests in this study but *M. aculeatus* and *M. asteris* were. Misidentification of *Minibiotus* species is possible or even likely (Claxton, 1998).

The Australian and Oriental regions are two of the great biogeographic regions of the globe and differences in the biota are profound (Keast, 1983). Opportunities for biotic interchange between these two regions arose during the Pleistocene about 15 million years ago. However, because there are so few studies describing the fauna of countries immediately to the north of Australia (McInnes, 1994), it is still too early to draw conclusions about the apparent lack of oriental tardigrade species in eastern Australia seen in this study. However, if the data presented here are any indication, the opening of a gateway to countries in the north by the northward movement of Australia had little effect on the distribution of tardigrade species in Australia.

The presence of a distinct suite of endemic species in each of the geobotanical regions, making up about fifty percent of the species in each subregion, suggests that 15 million years of isolation from other continents and aridification did not prevent the development of many new species.

6.4.3 Evidence for dispersal as a factor in tardigrade species occurrences in eastern Australia

The patterns of distribution of tardigrade species discussed above can be interpreted primarily as occurring through the influence of paleogeographical events and physiogeographical factors in eastern Australia. They support the contention of McInnes & Pugh (1998), Pugh & McInnes (1998) and Pilato & Binda (2001), that these events have a much greater influence on tardigrade distribution than long-range passive dispersal.

A model based on plate tectonics does imply that some species demonstrate an almost stagnant speciation with species ages of over 200 million years. Slow speciation is common in interstitial fauna (Sterrer, 1973; Pilato, 1979). The evolutionary conservatism of tardigrades is supported by a rare fossil of a 90 million year old *Milnesium* sp. that is remarkably similar to extant species in that genus (Bertolani & Grimaldi, 2000). The almost complete absence of Oriental species in eastern Australia suggests that tardigrades did not use the increasing proximity of Australia to the Orient over the last 50 million years as a pathway for dispersal.

There is some evidence in this study that tardigrades are capable of mid to short range dispersal. *M. hibiscus* is a species that is strongly associated with subtropical rainforests which evolved well after cool temperate rainforests in Australia. A few specimens were

found in the cool temperate rainforest at New England (Q3) and these specimens have most probably arrived by passive dispersal. *D. australocitrinus* is clearly a subtropical species which, at least at Cania Gorge, Queensland (Q15) can be found in dry sclerophyll woodland in the vicinity of the rainforest.

6.4.4 Comparison of the tardigrade fauna of eastern Australia with world fauna

The tardigrade fauna of eastern Australia is very rich and abundant judging by the 141 species obtained from 1185 samples in this study of which 88% contained tardigrades. This is more than comparable with other studies that provide similar statistics. Horning *et al.* (1978) found 58 species in 1354 samples from New Zealand of which only 42% contained tardigrades, Maucci (1980) reported 142 species from 2686 samples from Europe whilst Dastych (1988) found 95 species in approximately 48% of the 5261 samples examined in his study from Poland.

At the higher taxonomic levels, the Australian tardigrade fauna is comparable to that found elsewhere in the world. All genera and species found in this study fit into existing higher categories. This study reports the occurrence of a member of the family Microhypsibiidae in Australia for the first time, with members of all other families having been recorded previously in Australia.

Species from 34 genera are described in Chapter 4 of this work, three are new to science and 17 are recorded here in Australia for the first time. At the generic level, some similarities to, and some differences from, other faunas are apparent. The two most species-rich and most frequently occurring genera in Australia, *Macrobiotus* and *Echiniscus*, are also dominant elsewhere. Three genera, *Minibiotus*, *Calcarobiotus* and *Doryphoribius* are important contributors to the Australian fauna but appear to be less so elsewhere. The first

two genera were identified recently so their distribution is still to be determined. Maucci (1980) recovered specimens of *Doryphoribius* in only four of 2686 samples collected across Europe so it would appear to be much rarer there than in Australia. As a result of this study, sixteen existing genera, *Antechiniscus*, *Bryodelphax*, *Cornechiniscus*, *Hypechiniscus*, *Parhexapodibius*, *Hebesuncus*, *Doryphoribius*, *Eremobiotus*, *Ramazzottius*, *Thulinus*, *Astatumen*, *Calcarobiotus*, *Xerobiotus*, *Fractonotus*, *Microhypsibius* and *Limmenius*, can be added to the list of genera already known in Australia. Three new genera, *Lexia*, *Haptobiotus* and *Milnesioides* (9% of the total number of genera in Australia) are described here. Four other genera, *Oreella*, *Antechiniscus*, *Limmenius* and *Mopsechiniscus* (11% of genera) are known only from cool temperate rainforests in the southern hemisphere and their distribution in Australia confirms this habitat preference. *Cornechiniscus*, once thought to be a Palearctic species (Kristensen, 1987), is now recorded in Australia. Eighty percent of the genera now known in Australia are cosmopolitan.

Of the 141 species found in this study, 30 (21%) are cosmopolitan, ten (7%) have a pantropical distribution, one (1%) is known only from the oriental region, 21 (15%) have only been described from the southern hemisphere, and 79 (56%) have been described only from Australia. Some comparisons might be made with other faunistic studies although it must be remembered that they were completed prior to some new taxonomic studies that have altered the perception of cosmopolitanism for some species. Of the 95 species described by Dastych (1988) in Poland, 27% are present in Australia. Of the 170 species described by Maucci (1986) in Italy, 22% are present in Australia. Of the 68 species known from New Zealand, 71% are also present in Australia. These gross comparisons clearly indicate a high similarity of the New Zealand fauna with that of Australia.

The Australian tardigrade fauna described here is similar to the New Zealand fauna.

However, much of the material that forms the only large study of New Zealand tardigrades (Horning *et al.*, 1978) is in need of, and is undergoing, revision (Dastych, 1997, Pilato 1996; Pilato & Binda, 1997). The current perception of high similarity of the Australia fauna to that of New Zealand may change with close examination of New Zealand specimens, e.g., those identified as *M. harmsworthi*, *M. hufelandi* and *P. suillus*, for reasons discussed elsewhere.

Some tardigrade species, e.g., *D. pingue*, *H. dujardini*, *I. sattleri*, *R. oberhaeuseri*, *M. richtersi*, *M. intermedius* and *M. tardigradum*, have either remained essentially unchanged over very long periods of time or they have changed in different biogeographical regions but the change is not perceivable using present day techniques or they are efficient at long distance dispersal. The idea that species “groups” have arisen from a very ancient ancestor and that the cosmopolitan components of each group can be interpreted as being most closely related to descendants of the ancestor was considered by Pilato & Binda (2001) to be more plausible than the theory that widespread species have secondarily colonised all biogeographical regions. Their hypothesis is based on the presumed cosmopolitan nature of *M. harmsworthi*, *M. hufelandi*, *M. richtersi*, *D. pingue* and *M. tardigradum*. This study indicates that the first two to are absent from Australia and recent work (Bertolani & Rebecchi, 1993) suggests that all older records of these species should be re-examined. Records of *M. richtersi* may also need to be reviewed for the same reason.

The estimate of the percentage of cosmopolitan genera as 18% by McInnes & Pugh (1998) is inaccurate because genera such as *Cornechiniscus*, *Eremobiotus*, *Thulinia*, *Calcarobiotus* and *Xerobiotus* would not have been considered to be cosmopolitan in that study. In the

present study, 80% of genera found are considered to be cosmopolitan. Estimates of the percentages of cosmopolitan species are also very low in recent studies (3% in McInnes & Pugh, 1998 and 6.8% in Pilato & Binda, 2001). In this study, 21% (30 of 141) species are considered to be cosmopolitan. Ten of these species are recorded here as cosmopolitan for the first time (Table 6.3) but there are others e.g., *P. novaezeelandiae*, even though it has been recorded from Poland and other countries, it has been designated as a southern hemisphere species rather than cosmopolitan because of taxonomic problems (see Remarks p. 248). It is clear that accurate designation of genera and species as cosmopolitan awaits greater collecting effort and better taxonomic evaluation of existing records. The same might apply to estimates of endemism and this is not a problem restricted to tardigrades (Scott, 1988). This study has examined at a relatively small amount of material collected over a very large area in eastern Australia and there is still very little known about the tardigrade faunas of other southern hemisphere countries so the overall estimate of endemism is likely to be inaccurate.

There are at least three striking examples of genera and species found in this study which substantially alter world distribution records. The finding of a specimen of *Cornechiniscus* at Jenolan Caves in New South Wales tentatively removes this genus from a strictly northern hemisphere distribution to a cosmopolitan one. It is tentative because Jenolan Caves is frequented by tourists and there is the possibility that the specimen was accidentally introduced. Two species, *E. alicatai* and *I. pawlowski* are rare and known only from a few sites in the northern hemisphere and now found in a few sites in eastern Australia. Human introduction in these cases would seem to be rather improbable. Both were found in similar environments in Australia as they are overseas, the former on soily moss over limestone, the latter in mountain areas. These examples suggest that the absence of many species from the faunal lists of many countries, including Australia, may very

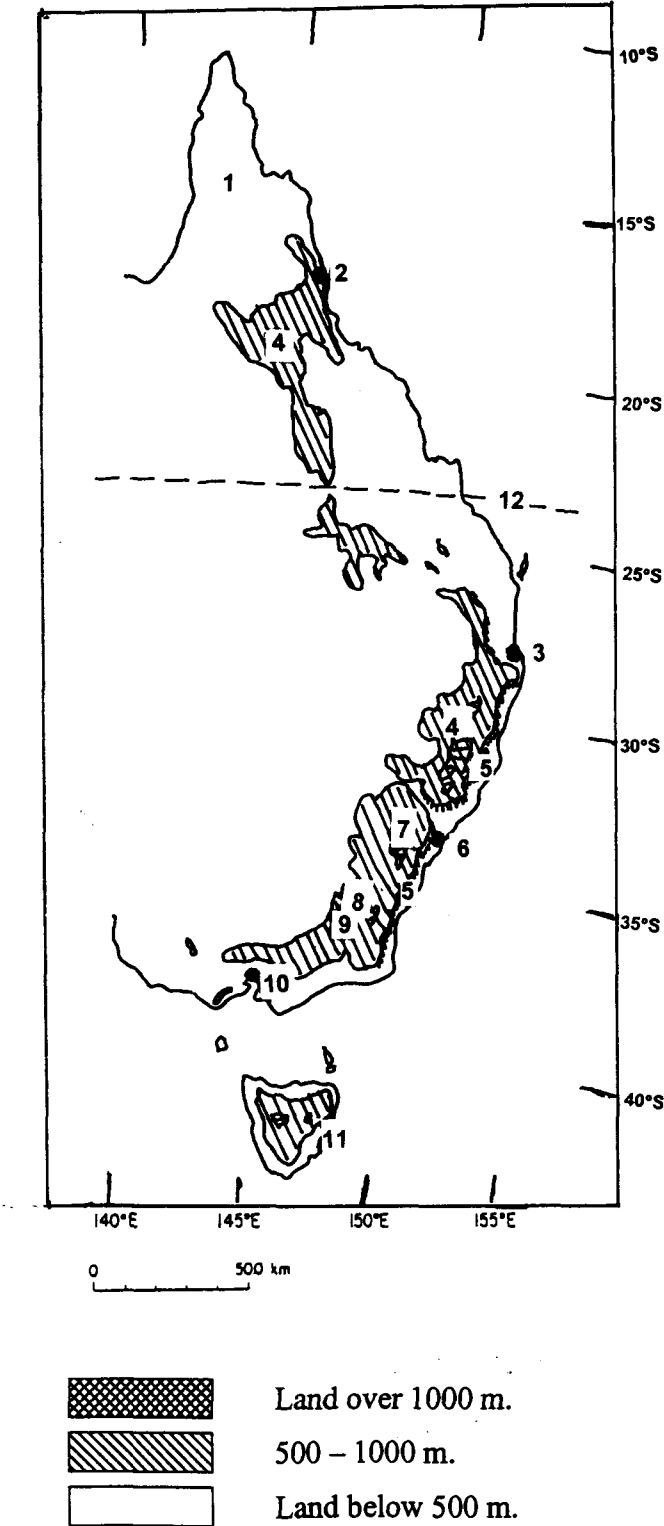
much be a function of the number of workers looking for tardigrades. Unfortunately there are very few tardigrade specialists in southern hemisphere countries.

6.4.5 Methodology

The method of Cluster analysis has been used in both plant and animal community analysis for many years. However, routine use of this and other multivariate analyses had to await the advent of development and availability of the computer and associated software packages.

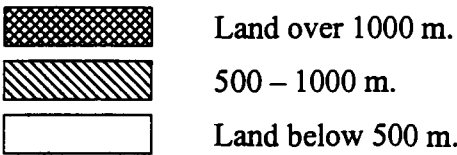
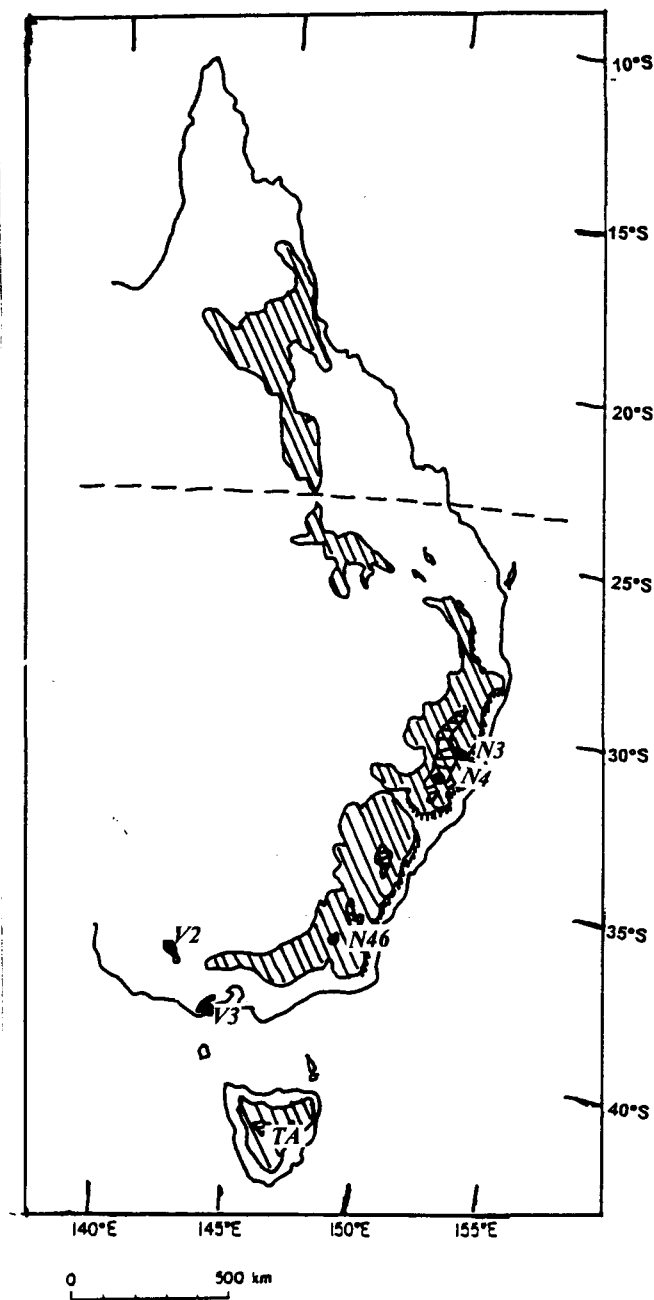
Despite the considerable number of problematic taxa and the very limited collecting in many areas, the analysis presented here has revealed some striking patterns of tardigrade species associations with zoogeographic subregions and the parts played by climatic and historical factors in the formation of these associations. The appearance of these patterns is impressive and suggests that multivariate analysis is a very useful tool for revealing such patterns in large-scale surveys when coupled with a sound systematic framework. The supposition of Maucci (1980) that more than 2000 samples would be necessary to assess the complex of factors affecting tardigrade species distribution is not supported by this study. It may be, however, that the distribution patterns in eastern Australia are unique in the world in that they reflect a past history that has seen the country move through a huge latitudinal, and therefore climatic, range.

Fig. 6.1 Major landscape features and cities of eastern Australia and places mentioned in the text



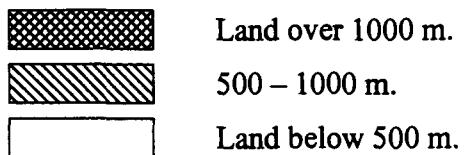
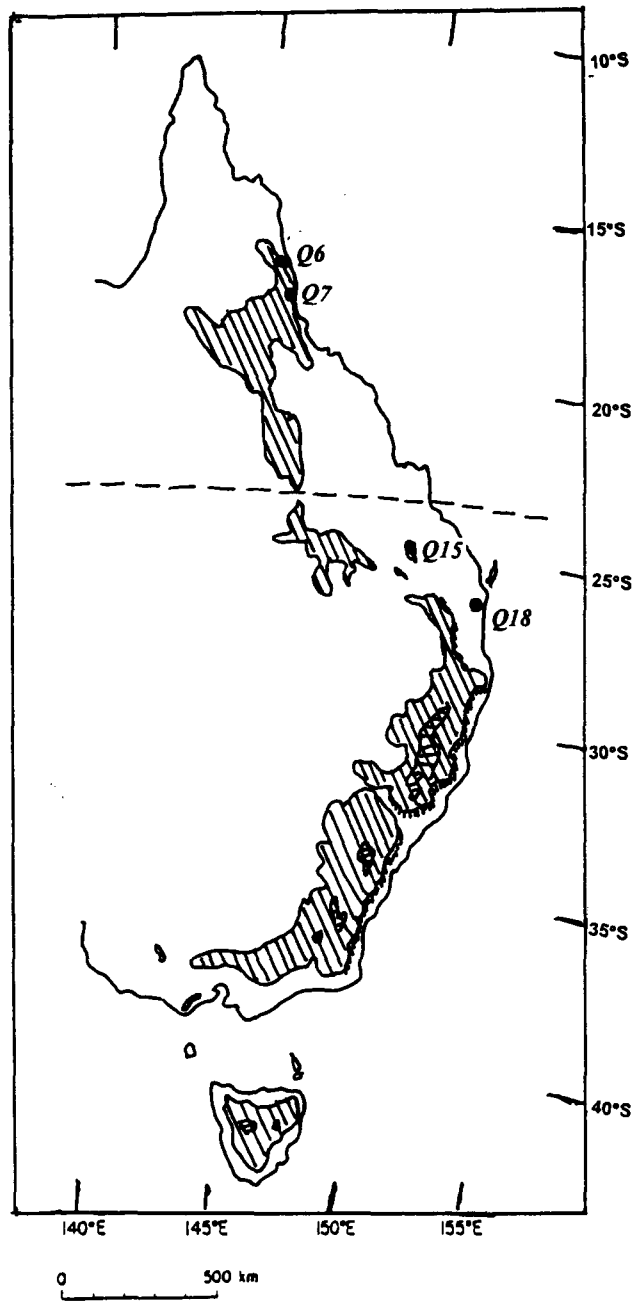
- | | |
|------------------------|------------------------|
| 1 Cape York | 7 Blue Mountains |
| 2 Cairns | 8 Australian Alps |
| 3 Brisbane | 9 Mount Kosciusko |
| 4 Great Dividing Range | 10 Melbourne |
| 5 Great Escarpment | 11 Tasmania |
| 6 Sydney | 12 Tropic of Capricorn |

Fig. 6.2a Cluster 1 (Cool temperate) sites



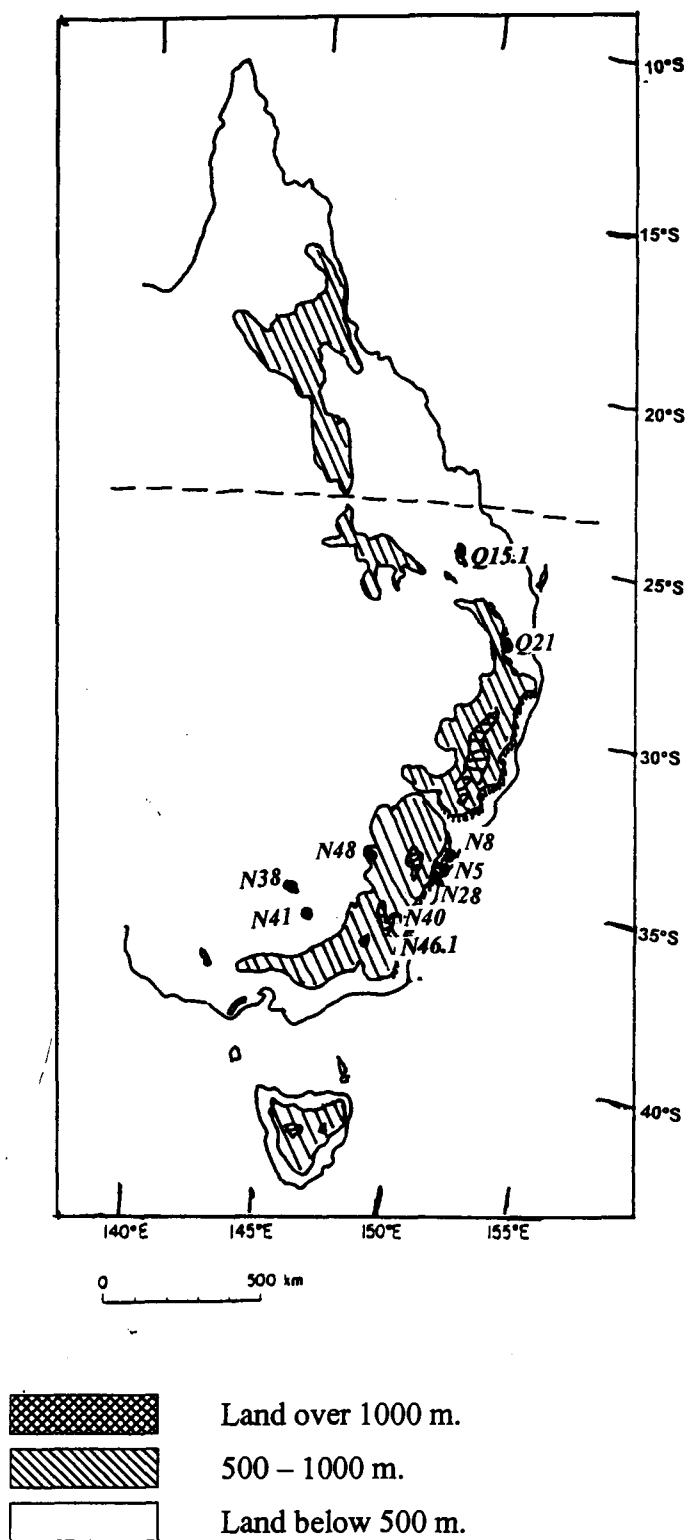
- N3 New England National Park
- N4 Barrington Tops
- N46 Mount Kosciusko
- V2 Mount William
- V3 Melba Gully
- TA Tasmania

Fig. 6.2b Cluster 2 (Tropical) sites



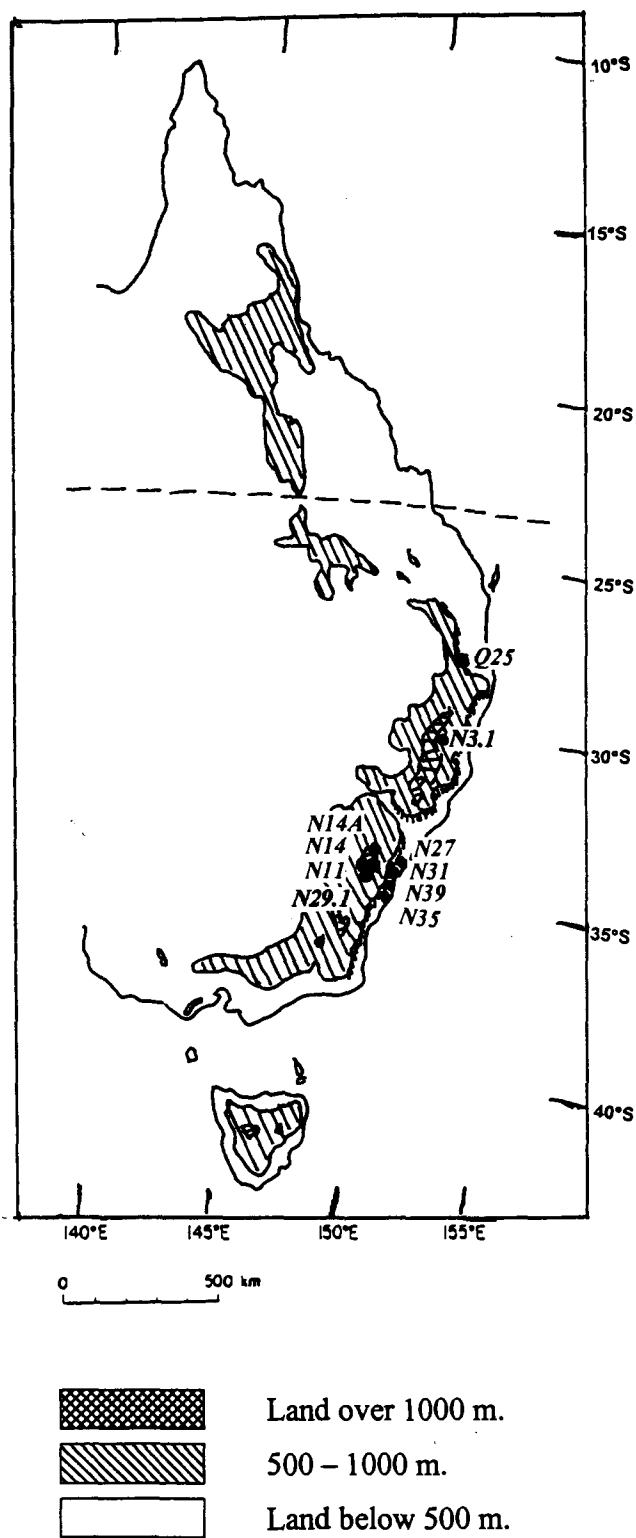
Q6	Curtain Fig Tree
Q7	Mulgrave
Q15	Cania Gorge
Q18	Eumundi

Fig. 6.2c Cluster 3 (Open dry woodland) sites



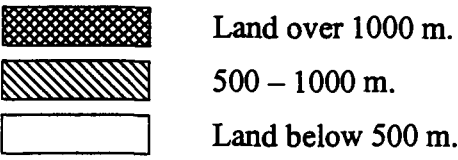
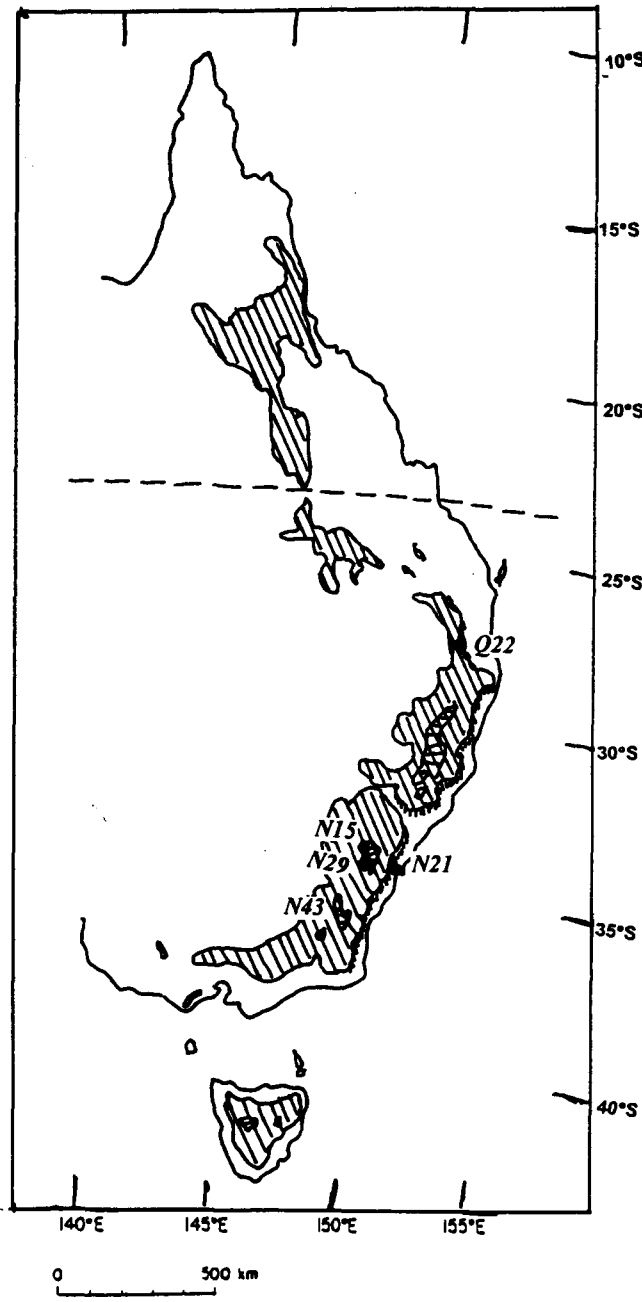
<i>Q15.1</i>	Cania Gorge (dry sclerophyll)	<i>N38</i>	Narrandera
<i>Q21</i>	Crows Nest	<i>N40</i>	Lake George Range
<i>N5</i>	Sandy Hollow	<i>N41</i>	Galore
<i>N8</i>	Ryde	<i>N46.1</i>	Mount Kosciusko (dry sclerophyll)
<i>N28</i>	Appin	<i>N48</i>	Darling Hill

Fig. 6.2d Cluster 4 (Coastal temperate) sites



<i>Q25</i>	Cunningham's Gap	<i>N27</i>	Douglas Park
<i>N3.1</i>	New England NP (dry sclerophyll)	<i>N29.2</i>	Wombeyan (dry sclerophyll)
<i>N11</i>	Mount Wilson	<i>N31</i>	Minnamurra
<i>N14</i>	Blue Mountains	<i>N35</i>	Barrengarry
<i>N14A</i>	Blue Mountains (dry sclerophyll)	<i>N39</i>	Cambewarra Mt
<i>N22</i>	Burraborang		

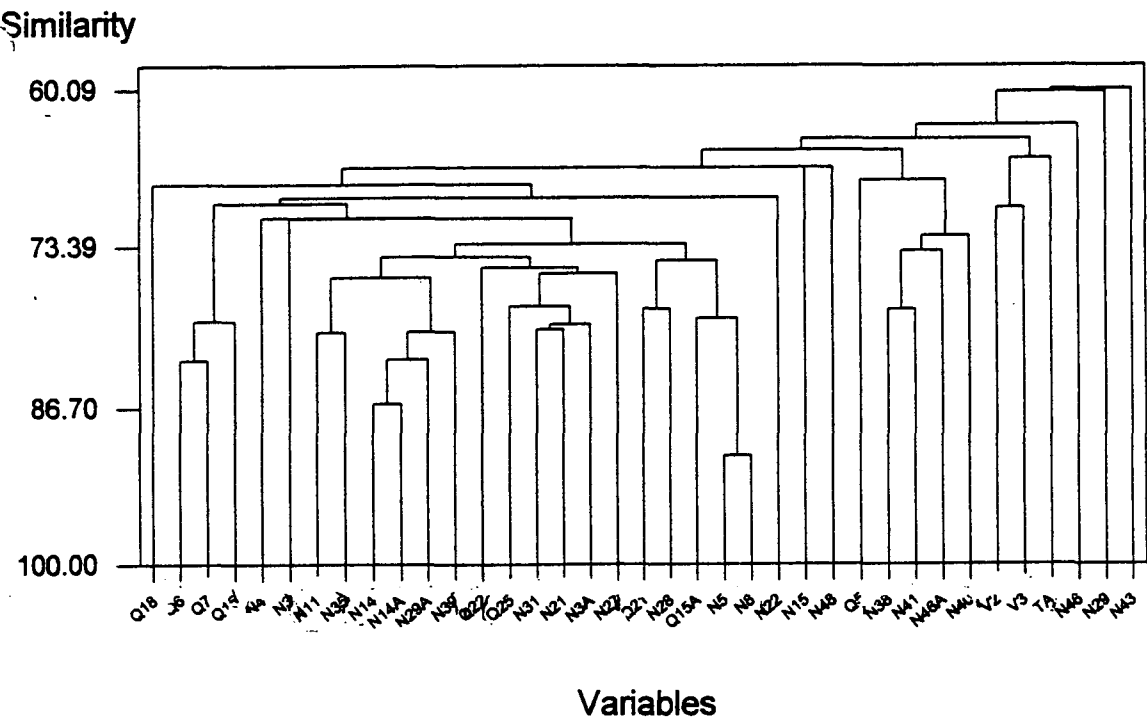
Fig. 6.2e Cluster 5 (Limestone/ dry woodland) sites



- | | |
|-----|---------------------|
| Q22 | Ravensbourne |
| N15 | Jenolan Caves |
| N21 | Camden |
| N29 | Wombeyan Caves |
| N43 | Yarrangobilly Caves |

Fig. 6.3 Cluster Analysis dendrograms of 37 variables (sites in eastern Australia) with 142 species

a) Single linkage



b) Average linkage

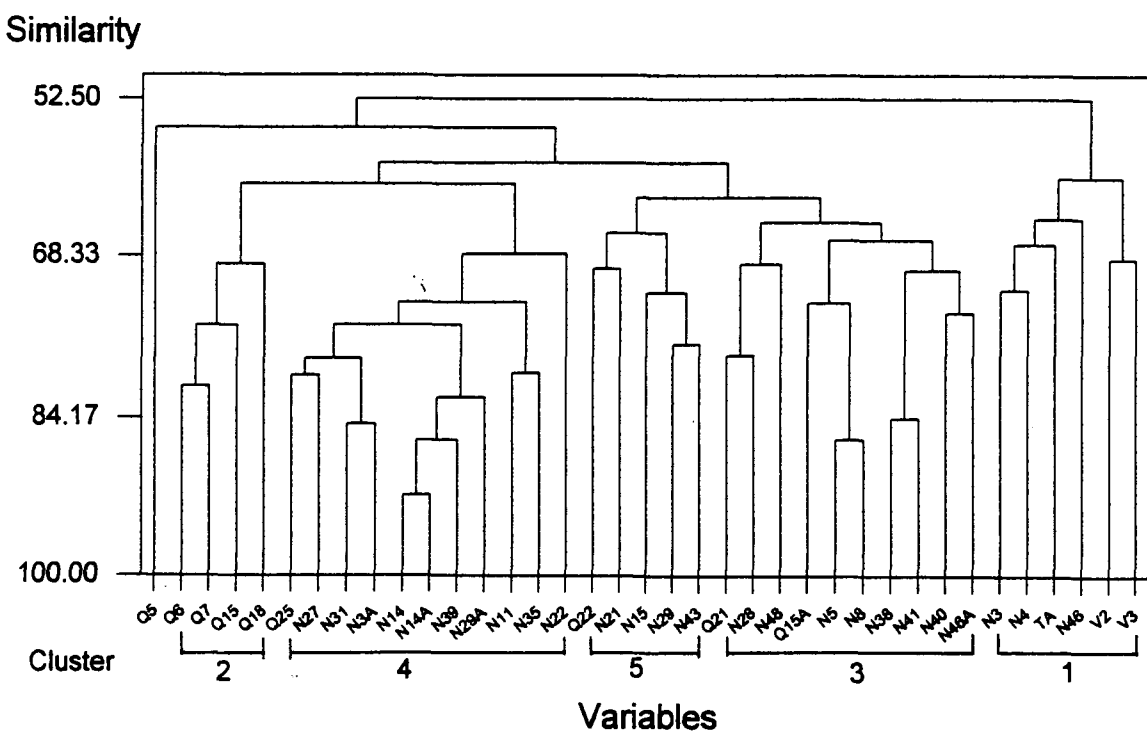


Fig. 6.3 Cluster analysis dendrograms of 37 variables (sites in eastern Australia) with 142 species

c) Complete linkage

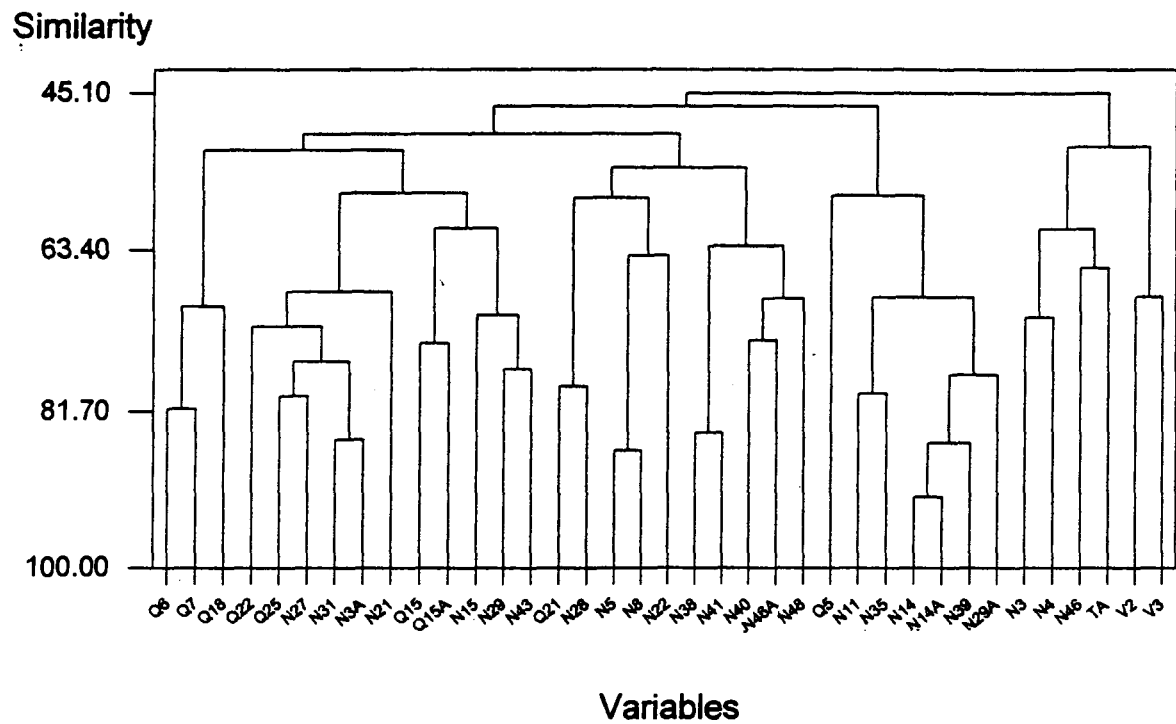


Table 6.1 Abundance of tardigrade species in five clusters of sites in eastern Australia

GROUP	DISTRIB	SPECIES SITES	Cluster 1							Cluster 2				Cluster 3								Cluster 4										Cluster 5							
			N3	N4	N46	V2	V3	T4	Q6	Q7	Q15	Q18	N46.1	N40	N38	N41	N5	N8	Q15.1	Q21	N28	N48	N14	N14A	N39	N29.2	N3.1	N31	N27	Q25	N11	N35	N22	N29	N43	N15	N21	Q22	
0	CO	<i>D. pingue</i>	1	1	1		2			1	1				1		2		1	1		3	1	1		1	1	1	1	1	1			1	1	1	1		
		<i>H. dujardini</i>	1		3		1	2			1		4					3				1	2	1		3	3	2			3	3	2			1			
1	CO	<i>I. saffordi</i>	1		1		1	3	2	1	1	1			2	2	2	3		1	2		2	1		2	1			3	1	1			1	1			
		<i>M. richersi</i>	1		1			2	1	1	3	1	2	3			2	1	2	2	3	1	3	3	4	3	3	1	3	4		2	2	4	2				
		<i>M. intermedius</i>	3						3	2		2	4	4	2	4	2	3	3	3	2	3	3	3	3	3	4	2	4	1	3		4	2	2	4	2		
		<i>M. tardigradum</i>	4	1	4	2		4	2	2	4	4	4	4	2	4	2	3	3	3	2	3	3	3	3	3	4	2	4	1	3		4	2	2	4	2		
		SH	<i>E. vincolus</i>	3	1	3			3			2	2					2						3	2	2	1	1		3	3	2	3		3	3	3	4	1
			<i>M. hirsutini</i>						3		2	1			4	3	4			4	3		4		1	1	1	1		3	3	1		3	3	3	4	1	
		SH	<i>H. conjugens</i>	1		1	3		1					3																									
			<i>H. exaratus</i>						1				1																										
			<i>H. gladiator</i>	3	2																																		
			<i>C. ornatus</i>	2					1																														
	<i>M. areolatus</i>		1					1																															
	<i>F. caelatus</i>		1					1																															
	<i>I. pavlovski</i>		1																																				
	<i>H. convergens</i>							1																															
	<i>M. montanus</i>		2					1																															
	<i>M. japonicus</i>		1																																				
	AU	<i>M. asteris</i>	1					3	3																														
		<i>M. fureiger</i>	4		4	3	3				3											2																	
		<i>M. aculeatus</i>	4	1	1			1																															
		<i>D. langhordense</i>	4	2	3			3																															
<i>O. mollis</i>		2					2																																
<i>E. velumitis</i>				3			1																																
<i>D. cycloglobus</i>		2	1								1																												
<i>A. parviventus</i>		3																																					
<i>D. cf. ongulense</i>				3			1																																
<i>I. palmar</i>							1																																
<i>L. porcellus</i>						1																																	
2	PT	<i>E. carlobulbus</i> sp. n.				3	3	4																															
		<i>M. rigatus</i> sp. n.	4	2	2	3	1	4			1																												
		<i>D. pannucens</i> sp. n.	2		3			2																															
		<i>I. australogilvus</i> sp. n.	2					2	2																														
		<i>L. melbaensis</i> sp. n.		1			2	4																															
		<i>M. exsertum</i>	2					3	1																														
		<i>M. australis</i>	2					1	1																														
		<i>M. milleri</i>	3					1																															
		<i>A. moscull</i>	2																																				
		<i>A. pulcher</i>	3					3																															
3	AU	<i>M. albus</i> sp. n.	1					1																															
		<i>M. tasmanicus</i> sp. n.			1			4																															
		<i>Macrobiotus</i> sp. 4	1		1																																		
		<i>E. bulbatus</i> sp. n.						1																															
		<i>M. tasmanicus</i>						1																															
		<i>H. turritus</i> sp. n.						1																															
		<i>I. heatwolei</i> sp. n.	1																																				
		<i>M. fuscus</i> sp. n.						1																															
		<i>M. purpureus</i> sp. n.						1																															
		<i>M. porleinctus</i>						1																															
4	CO	<i>E. Jamesi</i>			3																																		
		<i>M. cilius</i> sp. n.			3																																		

Table 6.2. Characteristics of the tardigrade fauna of five site Clusters in eastern Australia

	Cluster				
	1	2	3	4	5
Number of sites	6	4	10	11	5
Number of samples	268	100	127	540	137
Percent positive samples	86	86	93	86	85
Number of species	84	44	47	67	45

Table 6.3. Cosmopolitan tardigrade species found in the study of 36 sites in eastern Australia

No.	Species	Added this Study
1	<i>E. blumi</i> Richters, 1903	
2	<i>E. viridissimus</i> Peterfi, 1956	✓
3	<i>H. exarmatus</i> (Murray, 1907)	
4	<i>H. gladiator</i> (Murray, 1905)	
5	<i>C. ornatus</i> (Richters, 1900)	
6	<i>D. (A.) prorsirostre</i> Thulin, 1928	
7	<i>D. (D.) bullatum</i> Murray, 1908	
8	<i>D. (D.) higginsii</i> Binda, 1971	✓
9	<i>D. (D.) pingue</i> (Marcus, 1936)	
10	<i>D. (D.) pinguiforme</i> Pilato and Binda, 1997/98	✓
11	<i>D. (D.) rugosum</i> Bartos, 1935	✓
12	<i>H. conjungens</i> (Thulin, 1911)	✓
13	<i>E. alicatai</i> (Binda, 1969)	✓
14	<i>H. convergens</i> Urbanowicz, 1925	
15	<i>H. dujardini</i> (Doyere, 1840)	
16	<i>I. lunulatus</i> (Iharos 1966)	✓
17	<i>I. prosostomus</i> Thulin, 1928	
18	<i>I. sattleri</i> (Richters, 1902)	
19	<i>R. oberhaeuseri</i> (Doyère, 1840)	
20	<i>A. trinacriae</i> (Arcidiacono, 1962)	
21	<i>I. pawlowskii</i> Weglarska, 1959	✓
22	<i>M. areolatus</i> Murray 1907	
23	<i>M. montanus</i> Murray, 1910	
24	<i>M. orcadensis</i> Murray, 1907	
25	<i>M. richtersi</i> Murray, 1911	
26	<i>M. intermedius</i> (Plate, 1888)	
27	<i>M. taiti</i> Claxton, 1998	✓
28	<i>F. caelatus</i> (Marcus, 1928)	
29	<i>M. japonicus</i> Ito, 1991	✓
30	<i>M. tardigradum</i> Doyere, 1840	

✓ species determined to be cosmopolitan by this study

Table 6.4. Abundance of significant tardigrade species in five clusters of sites in eastern Australia

GROUP	DISTRIBUTION	SPECIES	CLUSTERS				
			1	2	3	4	5
0	CO	<i>D. pingue</i>	*	*	*	**	*
		<i>H. dujardini</i>	**	*	**	***	***
		<i>I. sattleri</i>	**	**	***	***	**
		<i>M. richtersi</i>	**	***	***	**	***
		<i>M. intermedius</i>	*	**		***	
		<i>M. tardigradum</i>	***	***	***	***	***
	SH	<i>E. vinculus</i>	**	**	*	***	*
		<i>M. hieronimi</i>	*	*	***	**	***
1	CO	<i>H. conjungens</i>	**		*		*
		<i>H. exarmatus</i>	*	*			
		<i>H. gladiator</i>	**				
		<i>C. ornatus</i>	**				
		<i>M. areolatus</i>	*				
		<i>F. caelatus</i>	*				
		<i>I. pawlowski</i>	*				
		<i>H. convergens</i>	*				
		<i>M. montanus</i>	*				
		<i>M. japonicus</i>	*				
	SH	<i>M. furciger</i>	***	*	*	**	
		<i>M. aculeatus</i>	***			*	*
		<i>D. langhovdensen</i>	***			*	
		<i>M. asteris</i>	**				
		<i>O. mollis</i>	**			*	
		<i>D. zyxiglobus</i>	**	*		**	**
		<i>E. velaminis</i>	**				*
		<i>A. parvisentus</i>	*				
		<i>L. porcellus</i>	*				
	AU	<i>M. rigatus</i> sp. n.	***	*		**	
		<i>D. pannuceus</i> sp. n.	***	*		*	
		<i>I. australogilvus</i> sp. n.	**			*	
		<i>L. melbaensis</i> sp. n.	***			*	
		<i>M. exsertum</i>	***			*	
		<i>E. curiobulbus</i> sp. n.	***				
		<i>M. australis</i>	**		*	*	
		<i>M. milleri</i>	**			*	
		<i>A. moscali</i>	*				
		<i>A. pulcher</i>	*				
2	PT	<i>M. hibiscus</i>	*	***	*		
		<i>E. tessellatus</i>		***		**	
		<i>P. jiroveci</i>		**		*	**
	AU	<i>D. australocitrinus</i> sp. n.		***	*	*	
		<i>P. ficus</i> sp. n.		**			
		<i>C. maculatus</i> sp. n.		**	*		
3	CO	<i>M. taiiti</i>	*	*	***		
		<i>E. blumi</i>			***		
	OR	<i>M. santoroi</i>			**	*	
	SH	<i>M. hispidus</i>			***		
		<i>M. scopulus</i>			**		
	AU	<i>M. guttus</i> sp. n.		*	***		
		<i>E. marcus</i>		*	***	**	*
		<i>C. erugatus</i> sp. n.	*		**		
4	CO	<i>M. orcadensis</i>	*			***	*
		<i>D. higgins</i>	**	*	*	**	
	PT	<i>M. peteri</i>				***	*
		<i>E. virginicus</i>				**	
	SH	<i>E. cf duboisi</i>	**			***	**
		<i>I. cameruni</i>	**	*	*	***	
		<i>P. novaezeelandiae</i>	*			**	*
		<i>D. puniceus</i>	*			**	
	AU	<i>E. curiosus</i>	*			***	*
		<i>P. australis</i> sp. n.	**	**	*	***	*
		<i>M. fallax</i>	**	*	*	**	**
		<i>M. torridus</i> sp. n.	*	*	**	***	**
		<i>I. cambawarens</i>	*			**	
5	CO	<i>E. viridissimus</i>					*
		<i>E. alicatai</i>					*
		<i>I. lunulatus</i>	*				*
		<i>D. rugosum</i>					**
		<i>R. oberhaeuseri</i>	*		*	*	**
		<i>I. prosostomus</i>					*
	AU	<i>M. saxatilis</i> sp. n.			*		**
		<i>E. arboris</i> sp. n.		*			**

AU – Australian; CO – cosmopolitan; OR – Oriental; PN – pantropical; SH – southern hemisphere
*** abundant; ** common; * rare

Table 6.5. Numbers and percentages of tardigrade species in five different distribution categories found in five site Clusters in eastern Australia

Cluster	Distribution categories					Total
	CO	PT	OR	SH	AU	
Cluster 1 - <i>Cool temperate</i>						
Number of species	24	1	0	18	41	84
<i>Percentage</i>	29	1	0	21	49	100
Cluster 2 – <i>Subtropical</i>						
Number of species	9	6	0	5	24	44
<i>Percentage</i>	21	14	0	11	54	100
Cluster 3 - <i>Open dry woodland</i>						
Number of species	12	1	1	6	27	47
<i>Percentage</i>	26	2	2	13	57	100
Cluster 4 - <i>Coastal/temperate</i>						
Number of species	16	7	1	13	30	67
<i>Percentage</i>	24	10	2	19	45	100
Cluster 5 - <i>Limestone</i>						
Number of species	14	4	0	9	18	45
<i>Percentage</i>	31	9	0	20	40	100

Distribution categories:

CO	Cosmopolitan
PT	Pantropical
OR	Oriental
SH	Southern Hemisphere
AU	Australian

Table 6.6. Numbers and percentages of total numbers of tardigrade species of each distribution category found in five site Clusters in eastern Australia

	Distribution categories				
	CO	PT	OR	SH	AU
Cluster 1 - Cool temperate					
Number of species	24	1	0	18	41
Percentage	80	10	0	86	52
Cluster 2 - Subtropical					
Number of species	9	6	0	5	24
Percentage	30	60	0	24	30
Cluster 3 - Open dry woodland					
Number of species	12	1	1	6	27
Percentage	40	10	100	29	34
Cluster 4 - Coastal/temperate					
Number of species	16	7	1	13	30
Percentage	53	70	100	62	38
Cluster 5 - Limestone					
Number of species	14	4	0	9	18
Percentage	47	44	0	43	23
Total number of species	30	10	1	21	79

Distribution categories: CO Cosmopolitan
PT Pantropical
OR Oriental
SH Southern Hemisphere
AU Australian

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