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A Revision of the Genus *Minibiotus* (Tardigrada: Macrobiotidae) with Descriptions of Eleven New Species from Australia

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ABSTRACT. The genus *Minibiotus* is redefined and the type species, *Minibiotus intermedius* (Plate, 1889) is redescribed. Eleven new species of *Minibiotus* are diagnosed and described, and three are transferred from the genus *Macrobiotus* using a range of qualitative and quantitative characters of adults and eggs. Keys are provided to the adults of the 22 reported species in the genus and to the eggs of the 20 species for which eggs have been described. Characters useful in discriminating species with very similar morphology are noted. The difficulties inherent in taxonomic studies of small animals such as many of those in the genus *Minibiotus* are discussed as are the problems of recognition of species in groups where both the adult form and sometimes also the egg are very similar. The examination and description of the eggs is important in tardigrade taxonomy.

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Minibiotus Schuster *et al.*, 1980 is a genus of terrestrial tardigrades found commonly in mosses and lichens. The type species *Minibiotus intermedius* (Plate, 1889) remained the only species in the genus until *M. maculartus* was described by Pilato & Claxton in 1988. The adults of this species closely resembled *M. intermedius* but the eggs were 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. *Minibiotus fallax* was described by Pilato *et al.* in 1989. This species had few adult characters similar to those of *M. intermedius* apart from the presence around the mouth of papulae (Fig. 1a) rather than the lamellae present in the closely related genus *Macrobiotus*. Miller *et al.*, (1994) transferred *Macrobiotus weinerorum* Dastych,

1984 to the genus *Minibiotus* while Dastych & Drummond (1996) attributed *Macrobiotus stuckenbergi* Dastych *et al.*, 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). One of the aims of this paper is to provide a more precise definition of the genus.

Minibiotus intermedius (Plate, 1889) 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. Another 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.

The work presented here is part of a study of the Australian terrestrial tardigrade fauna and it has been found that specimens with the characteristic appearance of *M. intermedius* are frequently encountered and abundant in mosses and lichens. Close examination of these and careful collection of eggs with specimens have revealed that although many could be mistaken on adult morphology for *M. intermedius* as described by Thulin (1911), they have very different egg types. In this paper eleven new species are described and three are transferred from the genus *Macrobiotus* based on a character set which includes new quantitative and qualitative characters of adults and eggs. Keys are provided to the adults and to the eggs of these and the eight previously described species in the genus.

Materials and methods

Tardigrades were extracted from mosses and lichens from many localities in Australia. The sample of cryptogam was placed in about 750 ml of tap water in a beaker and left to soak for about eight hours or overnight. The sample was agitated and then squeezed over the beaker and removed. Water and sediment were poured through a coarse sieve (about 2 mm mesh) and then through a fine sieve $(40 \ \mu m)$ using boiling water in the latter case. The sediment on this mesh was washed into a Petri dish and individual animals and eggs removed to mounting medium with an Irwin loop. Individual specimens were mounted in Hoyer's medium on microscope slides and the coverslip sealed with epoxy paint after three weeks drying. Measurements were made at the highest power (×1250) using an Olympus BH microscope equipped for oil immersion phase contrast microscopy, an eyepiece micrometer and a drawing tube. Some specimens were examined using Nomarski (or DIC) microscopy. Other specimens were gold coated for scanning electron microscopy studies.

Body lengths were measured from the mouth to the end of the body, not including the back legs. Buccal tube lengths were measured from the stylet sheaths to the base of the tube. Buccal tube widths were measured as the external diameters of the buccal tubes at the level of the stylet support insertion point. In all species the buccal tube walls were found to be 0.5 μ m thick. Lengths of claws were measured from the base of the claw to the top of the main 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. Abbreviations used in tables include: BT—buccal tube, m—macroplacoid, MPR—macroplacoid row, PH—pharyngeal bulb, PR—placoid row, SI—stylet support, and VS—ventral support.

Eggs were ascribed to new species only after observation of an embryonate egg. A "specimen" in the text below implies an adult specimen.

All holotypes and some paratypes are deposited in The Australian Museum, Sydney. Other paratypes and other material are in the author's collection (SKC). Other material (slide mounted specimens) was borrowed from a number of institutions and private collections. These are listed below and referred to in the text by their abbreviations:

- AM Australian Museum, Sydney
- BG collection of Mr B. Grabowski, Marburg, Germany
- BMD Bohart Museum, University of California, Davis, USA MM Macleay Museum, University of Sydney
- 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, Universita di Catania, Catania, Italy
- UMI Dipartimento di Biologia Animale, Universita 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, Kansas, USA
- ZIM Zoologisches Institut und Museum, Hamburg University, Hamburg, Germany

Systematic account

Genus Minibiotus Schuster et al.

Minibiotus Schuster, Nelson, Grigarick & Christenberry, 1980: 294.

Type species. Macrobiotus intermedius Plate, 1889: 535.

Diagnosis. Macrobiotidae with ten peribuccal papulae, no peribuccal lamellae. Antero-ventral mouth; teeth in oral cavity absent or strongly reduced. Buccal tube short, rigid; 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.



Figure 1. a, papulae of *Minibiotus hufelandioides* SEM; b, suboral pores of *Minibiotus aculeatus* SEM. (Scale bars = $1 \mu m$).

Keys to species of *Minibiotus* Key to adults

1	two macroplacoids	
	- three macroplacoids	
2	cuticle with dorsal tubercles especially towards rear	M. fallax
	- cuticle without dorsal tubercles	M. scopulus
3	cuticle with pores	
	- cuticle without pores	
4	pores in rows	
	- pores randomly distributed	9
5	cuticle thickened in caudal region	M. ethelae
	- no caudal thickening	
6	pores irregular in size and shape	7
	- pores small and round	
7	no granulation around claws	M. furcatus
	- granulation around claws	M. bisoctus
8	eight rows of small (0.5 µm) pores	M. poricinctus
	- ten rows (1.0 μm) pores	M. keppelensis
9	soft spines above leg IV, or above legs II, III and IV	M. aculeatus
	- no soft spines	
10	granulation on fourth pair of legs only	M. asteris
	- granulation on all legs	
11	dorsal crest in oral cavity fragmented into teeth	M. vinciguerrae
	- no teeth in oral cavity	

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12	teeth on lunules of fourth pair of legs	M. stuckenbergi
	- no teeth on lunules of fourth pair of legs	
13	long macroplacoid row; short, low accessory claws	M. ramazzottii
	- short macroplacoid row; very high accessory claws	M. weinerorum
14	cuticle with transverse rows of wrinkles	M. pilatus
	- cuticle smooth	
15	granulation around claws absent or very sparse	M. intermedius
	- granulation around all claws	
16	macroplacoid row length long (pt greater than 36)	
	- macroplacoid row length short (pt less than 35)	
17	stylets inserted at pt 73	M. milleri
	- stylets inserted at <i>pt</i> less than 73	
18	ventral reinforcing bar long (pt 53), claws long (pt IV pair 34.6)	M. aquatilis
L	- ventral reinforcing bar short (pt 46), claws short (pt IV pair 29.3)	M. hufelandioides
19	toothed lunules on IV claws, short high accessory claws	M. maculartus
	- smooth lunules on IV claws	
20	stylets inserted at pt 60.3; short, low accessory claws	M. taiti
	- stylets inserted at <i>pt</i> greater than 60.3	
21	claws long (pt IV pair 34.0), high accessory claws	M. floriparus
	- claws short (pt IV pair 28.1), low accessory claws	M. hispidus

Key to eggs

1	processes with membrane	
	- processes without membrane or with partial membrane	
2	membrane covering thin nail-like processes	M. taiti
	- membrane enclosing each process separately	
3	processes shaped like short-stemmed flowers	M. floriparus
	- processes shaped like screw-heads	
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	
6	processes long, javelin-shaped, protruding through membrane and arranged in rings, others short rods	M. pilatus
	- processes cone-shaped	
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	
9	distal disk of processes with smooth or slightly notched margin, shell dotted	M. hufelandioides
	- distal disk of processes with 6-8 distinct arms, shell smooth	M. asteris

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10	processes hemispherical, shell surface smooth	M. weinerorum
	around base	
11	processes conical or hemispherical with longitudinal ridges around base	M. maculartus
	- processes elongated cones	
12	processes fine and close; shell reticulate	M. hispidus
	- processes with conical or swollen base; shell smooth or dotted	
13	smooth egg shell	
	- dots on egg shell	
14	processes base smooth, processes 3.5-5.5 µm long	M. ramazzottii
	- processes base indented	
15	processes 8 µm long	M. vinciguerrae
	- processes 9–11 μm long	M. aculeatus
16	processes base indented; processes 11-12 µm long	M. aquatilis
	- processes base smooth	
17	processes with round base rising rapidly to fine filamentous tip	
	- processes strap-like variable in length, slightly swollen at base	
18	processes 5-6 µm long	M. furcatus
	- processes 12–23 μm long	M. ethelae
19	processes 6-11 µm long, rarely up to 16 µm	M. scopulus
	- processes 12–16 μm long, rarely up to 22 μm	M. fallax

Species descriptions

Minibiotus intermedius (Plate, 1889)

Figs. 2, 18a; Table 1

Macrobiotus intermedius Plate, 1889: 535.

Type material examined. NEOTYPE in AM (AM KS41463): **Germany**: Marburg, 27 August 1994, B. Grabowski, moss on oak bark. SYNTYPES (3 specimens on 2 slides in AM): same data as neotype, AM KS41464–KS41465.

Material examined. AUSTRALIA: New South Wales: Cambewarra Mountain, 34°48'S 150°35'E, 625 m, 9 May 1993, S.K. Claxton, mosses and lichens on sandstone rock in cool temperate rain forest, 8 specimens, 20 eggs. Burragorang, 34°04'S 150°26'E, 29 July 1990, R. Siebels, moss and lichen on rock in open forest, 5 specimens, 3 eggs. Blue Mountains, 33°43'S 150°20'E, 1200 m, 26 December 1993, S.K.C., moss and leaf litter in closed forest, 1 specimen. Douglas Park, 34°11'S 150°43'E, 110 m, 9 March 1986, 17 May 1986, 19 July 1986, 13 September 1986, 15 November 1986, 11 January 1987, S.K.C., mosses and lichens on sandstone in open forest, 60 specimens, 16 eggs. Barrengarry, 34°40'S 150°30'E, 26 December 1993, S.K.C., leafy liverwort on tree in cool temperate rainforest, 1 specimen. Wederburn, 34°10'S 150°50'E, 23 March 1993, lichen on rock in open forest, 1 specimen; ditto but collected 7 August 1993, S.K.C., moss on rock, log in sheltered gully, 2 specimens. Wombeyan, 34°19'S 149°58'E, 8 March 1992, S.K.C., moss and lichens on sandstone in open forest, 3 specimens, 2 eggs. Fitzroy Falls, 34°38'S 150°30'E, 26 January 1986, S.K.C., moss

and lichens on dead trees in open forest, 2 specimens. New England National Park, 30°30'S 152°30'E, 1200 m, 20 April 1995, moss on rock in subalpine heath, 3 specimens; ditto but collected 7 January 1996, moss and lichen on rock in subalpine heath and open forest, 55 specimens, 7 eggs; ditto but collected 18 December 1994, S.K.C., moss and lichen on rock in open field, 15 specimens. Queensland: Cunningham's Gap, 28°03'S 152°25'E, 3 September 1985, liverwort on twigs in temperate rainforest, 3 specimens; ditto but collected 10 January 1996, S.K.C., lichen and leafy liverwort on branches, logs, rocks in temperate rainforest, 14 specimens, 1 egg. (All Australian specimens in SKC). NEW ZEALAND: North Island: Pilbrows Hill, 16 May 1971, D.S. Horning Jr, 1 specimen (NZ642); Rangatira Island, 25 August 1971, D.S. Horning Jr, 1 specimen (NZ893). (NZM). UNITED KINGDOM: 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). NORTH AMERICA: Alaska, Denali National Park, P. Marley, 5 specimens. (PM). Michigan, Schoolcraft County, 14 August 1978, T. Hounseal, moss from base tree in virgin forest, 4 specimens. Tennessee, Henderson County, 2 August 1980, C.W. Beasley, lichen from tree, 4 specimens. Missouri, Carter County, 1 August 1980, C.W. Beasley, lichen on oak tree and rock, 4 specimens. (MUT). SOUTH AMERICA: Venezuela, Obispos, Barrinas, 6 July 1979, R.W. Brooks, A.A. Grigarick, J. McLaughlin and R.O. Schuster, 4 specimens. Pedraza, Barinas, 4 July 1979, Brooks et al., 9 specimens. Liberatador, Merida, 3 July 1979, Brooks et al., 32 specimens. Girardot, Aragua, 14 July 1979, Brooks et al., 2 specimens. Perija, Zulia, 24 June 1979, Brooks et al., 1 specimen. (BMD). SOUTH AFRICA: Natal Midlands, Geckies Farm, 4 December 1988, P. Croeser, moss and fern in indigenous forest, 10 specimens and 1 egg. (NMP). ITALY: Sardegna, Caprera, 21 March 1974, R. Bertolani, lichen, 4 specimens. (UMI).



Figure 2. Taxonomic details of *Minibiotus intermedius*: **a**, habitus; **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

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 μ m 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 μ m. 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 main 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 μ m, with processes 45–52 μ m. About 30 processes around circumference, about 130 in hemisphere. Processes nail-like, each surrounded by membrane; height 2.5–3.5 μ m, base 0.5–1.5 μ m, top 2.5–3.5 μ m, 3–4 μ m apart. The top on each process appears to consist of a ring of tiny pores visible only under the highest power of magnification.

Table 1. Measurements (in µm) of adults of Minibiotus intermedius.

Character	No.	Range	Mean	SD	SE N	eotype
body length	20	195-270	219.4	21.1	4.7	250
BT length	20	22.7-27.6	24.7	1.3	0.3	23.8
BT width	20	1.4 - 2.2	1.7	0.2	0.04	1.6
SI length	20	12.4–14.9	13.6	0.7	0.2	13.0
VS length	20	8.7 - 10.8	9.2	0.5	0.1	8.1
PR length	20	6.2-8.1	7.2	0.5	0.1	7.6
MPR length	20	5.7-7.0	6.5	0.3	0.07	6.5
m1	20	1.4 - 2.2	1.6	0.2	0.04	1.6
m2	20	1.1–1.9	1.6	0.2	0.04	1.6
m3	20	1.1–1.9	1.6	0.2	0.04	1.6
microplacoid	20	0.4–0.8	0.5	0.1	0.02	0.5
PH length	20	20.0-27.0	23.6	2.2	0.5	23
PH width	20	21.0-28.0	23.4	2.3	0.5	27
claw I	20	4.3-6.0	5.0	0.4	0.09	4.9
claw II–III	20	4.9-6.5	5.5	0.4	0.09	5.4
claw IV	20	5.47.0	6.1	0.4	0.09	6.0

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 & 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 the new species, *Minibiotus poricinctus*, is very similar. It has not been included in this paper as embryonate eggs have not been observed by this author.

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.

Minibiotus taiti n.sp.

Figs. 3, 18b; Table 2

Type material. HOLOTYPE in AM (AM KS41430): Australia, New South Wales: Ryde, 33°48'S 151°04'E, 500 m a.s.l., 16 June 1993, S.K. Claxton, foliose lichen and leaf litter on asphalt. PARATYPES (7 specimens, 3 eggs in AM [AM KS41431–41440]; 31 specimens, 2 eggs in SKC): same data as holotype but collected on 3 May 1985 and 1 February 1992.

Additional material examined. New South Wales: Appin, 34°12'S 150°47'E, 29 August 1985, P.D. Claxton, weft moss on rock in open sclerophyl forest, 10 specimens, 3 eggs. Sandy Hollow, 32°22'S 150°34'E, 20 March 1993, S.K. Claxton, weft moss on rock in open sclerophyl forest, 22 specimens, 5 eggs. Queensland: Eumundi, 26°28'S 152°27'E, 20 December 1986, D.S. Horning, fruticose lichen on old bridge timber, wind exposed, 6 specimens, 3 eggs. Great Keppel Island, 23°10'S 150°58'E, 14 July 1993, P.D. Claxton, foliose lichen on rock, wind exposed, 3 specimens, 1 egg. Australian material in SKC. NEW ZEALAND: Snares Islands, Ho Ho Creek, 23 October 1972, D.S. Horning, 2 specimens (SA301). Mollymawk Bay, 30 January 1971, D.S.H., 2 specimens (SA26). Seal Point, 2 March 1972, D.S.H., 2 specimens (SA216). Broughton Island, 18 February 1971, D.S.H., 4 specimens (SA60). (NZM). CHINA: Quingdao, October 1994, N. Marley, moss, 6 specimens in NM. USA: Texas, Taylor County, 27 December 1989, C.W. Beasley, leaf litter on soil, 2 specimens in 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



Figure 3. Taxonomic details of *Minibiotus taiti* n.sp.: **a**, habitus (holotype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

to main branch. Lunules smooth on all claws.

Eggs colourless, round, diameter without processes 54 μ m, with processes 64 μ m. About 48 processes around circumference, about 160 in a hemisphere. Processes like thin nails, 3.2–5.4 μ m high, base diameter 1–1.5 μ m, top

diameter $2-3 \ \mu\text{m}$. 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.

Table 2. Measurements (in μ m) of adults of *Minibiotus taiti* n.sp.

Character	No.	Range	Mean	SD	SE H	lolotype
body length	20	176–297	248	31.4	7.0	277
BT length	20	21.6-27.6	25.2	1.6	0.4	27.0
BT width	20	1.6-2.4	2.0	0.2	0.04	2.2
SI length	20	13.0-16.8	15.2	1.0	0.2	16.2
VS length	20	8.7-11.4	10.2	0.7	0.2	10.8
PR length	20	7.6-10.8	9.5	1.0	0.2	10.8
MPR length	20	6.5-9.2	8.1	0.9	0.2	9.2
m1	20	1.6-3.0	2.4	0.4	0.1	2.7
m2	20	1.6-2.7	1.9	0.3	0.1	2.2
m3	20	1.6 - 2.7	2.2	0.3	0.1	2.2
microplacoid	20	0.4 - 1.1	0.8	0.2	0.1	0.8
PH length	15	23.0-30.0	26.0	2.3	0.6	27
PH width	15	22.0-30.0	25.0	2.2	0.6	27
claw I	20	6.5-8.1	7.2	0.4	0.1	7.6
claw II–III	20	7.0-8.7	7.7	0.4	0.1	8.1
claw IV	20	7.6–9.2	8.4	0.6	0.1	9.2

Etymology. The species is named after Dr N.N. Tait of Macquarie University.

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 *Macrobiotus acontistus* 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.

Habitat. 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 poricinctus n.sp.

Figs. 4, 18c; Table 3

Type material. HOLOTYPE in AM (AM KS41585): Australia, Tasmania: Mount Cameron West Aboriginal Site, 41°52'S 144°42'E, 9 January 1996, A. Moscal, moss on rock. PARATYPES (10 specimens, 3 eggs in AM [AM KS41586–41595]; 50 specimens, 5 eggs in SKC) same data as holotype.

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 μ m, colourless. Eye spots large in posterior position. Cuticle with eight bands of small, round (0.5 μ m) 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 main 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 μ m, with processes 60 μ m. 18–20 processes around circumference, 50 in hemisphere. Processes screw-like, each surrounded by a membrane, height 6.5–7 μ m, base 1.5 μ m, top 5.5 μ m, 6–8 μ m apart. Small dots visible on shell surface around each process where membrane appears to reach the surface.

Etymology. Latin, *porus*, masculine, hole and *cinctus*, Latin noun, girdle, belt.

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.

Habitat. The type material was found in a single mixed sample of two mosses (*Lembophyllum divulsum* and *Thuidium furfurosum*) and a liverwort (*Cheilolejeunea mimosa*) on a sandstone boulder in a littoral flat with low shrubs and herbs.

Table 3. Measurements (in μ m) of adults of *Minibiotus* poricinctus n.sp.

Character	No.	Range	Mean	SD	SE H	lolotype
body length	20	174-290	240.3	30.0	6.7	270
BT length	20	20.5 - 28.1	24.7	1.6	0.4	26.0
BT width	20	1.5 - 2.2	1.9	0.2	0.04	2.1
SI length	20	12.2-16.8	14.7	1.0	0.2	15.4
VS length	20	7.6-10.3	8.8	0.6	0.1	9.2
PR length	20	7.0-10.0	8.7	0.7	0.2	8.7
MPR length	20	6.0-8.9	7.6	0.7	0.2	7.6
m1	20	1.6-2.5	2.1	0.2	0.04	2.2
m2	20	1.4 - 2.4	1.9	0.3	0.1	1.9
m3	20	1.4-2.4	1.9	0.3	0.1	1.9
microplacoid	20	0.5 - 1.0	0.6	0.2	0.1	0.5
PH length	15	20.0-27.0	24.0	1.9	0.4	25.0
PH width	15	20.0-26.0	22.7	1.8	0.4	24.0
claw I	20	4.3-6.2	5.6	0.5	0.1	6.0
claw II–III	20	5.1-6.8	6.2	0.4	0.1	6.5
claw IV	20	5.7–7.6	6.8	0.5	0.1	7.0



Figure 4. Taxonomic details of *Minibiotus poricinctus* n.sp. **a**, habitus (holotype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.



Figure 5. Taxonomic details of *Minibiotus floriparus* n.sp. **a**, habitus (holotype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

Minibiotus floriparus n.sp.

Figs. 5, 18d; Table 4

Type material. HOLOTYPE in AM (AM KS41441): Australia, New South Wales: Camden, 34°04'S 150°42'E, 120 m a.s.l., 4 April 1994, S.K. Claxton. PARATYPES (7 specimens, 5 eggs in AM [AM KS41442–KS41451]; 36 specimens, 8 eggs in SKC): same data as holotype. **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 main 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

Character	No.	Range	Mean	SD	SE H	olotype
1 1 1 4	10	170 400	200.2	(1.0	14.0	005
body length	19	170-420	300.2	64.9	14.9	285
BT length	19	20.0-33.5	27.1	3.6	0.8	27.6
BT width	19	1.6 - 2.7	2.1	0.4	0.1	2.1
SI length	19	13.0-21.6	17.5	2.4	0.6	17.8
VS length	17	9.2-16.2	12.5	1.7	0.4	13.0
PR length	19	7.6–14.1	10.7	1.9	0.4	11.4
MPR length	19	6.5–11.9	9.0	1.6	0.4	9.7
m1	19	1.9-3.8	2.7	0.5	0.1	2.7
m2	19	1.6-3.2	2.3	0.4	0.1	2.4
m3	19	1.6-3.8	2.6	0.5	0.1	2.7
microplacoid	19	0.4 - 1.5	0.8	0.3	0.1	0.8
PH length	17	21.0-32.0	26.9	3.4	0.8	27.0
PH width	15	22.0-38.0	27.5	5.0	1.3	24.0
claw I	19	5.4-10.3	7.8	1.4	0.3	7.6
claw II–III	19	6.0-10.8	8.3	1.3	0.3	8.1
claw IV	19	6.5–11.9	9.2	1.4	0.3	9.2

Table 4. Measurements (in μ m) of adults of *Minibiotus floriparus* n.sp.

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 main 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 μ m, with processes 70 μ m. 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 μ m, base diameter 2–3 μ m, distal disc diameter 6–7 μ m. Each process surrounded by a membrane. Shell surface smooth.

Etymology. Latin, *floriparus*, bearing flowers, describing the egg and its processes.

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.

Habitat. The species was found only in crustose and foliose lichens on the branch of a species of *Eucalyptus* in open woodland.

Minibiotus aquatilis n.sp.

Figs. 6, 18e; Table 5

Type material. HOLOTYPE in AM (AM KS41452): Australia, Australian Capital Territory: Coppin's Crossing, 35°16'S 149°05'E, 1750 m a.s.l., 4 September 1993, S.K. Claxton. PARATYPES (7 specimens, 5 eggs in AM [AM KS41453–KS41462]; 23 specimens, 34 eggs in SKC): same data as holotype.

Additional material examined. NEW SOUTH WALES: Narrandera, 34°45'S 146°33'E, 19 March 1994, S.K. Claxton, lichen on rock in open forest, 22 specimens, 14 eggs. TASMANIA: King River, 42°00'S 145°32'E, June 1989, J. Lake, moss on rock, 3 specimens, 3 eggs. Mount Montgomery, 41°09'S 146°03'E, 21 October 1994, A. Moscal, moss on soil, 1 specimen. All SKC.

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

Table 5. Measurements (in μ m) of adults of *Minibiotus aquatilis* n.sp.

Character	No.	Range	Mean	SD	SE H	olotype
body length	16	182-399	309.8	55.6	13.9	354
BT length	16	21.6-36.8	31.0	4.1	1.0	35.7
BT width	16	1.8-3.5	2.8	0.4	0.1	3.2
SI length	16	14.6-24.9	21.2	2.9	0.7	24.9
VS length	15	11.4-20.0	16.6	2.3	0.6	18.9
PR length	16	8.7-19.8	14.0	2.0	0.5	16.8
MPR length	16	7.6–14.6	11.8	0.7	0.2	14.1
m1	16	2.2-4.3	3.5	0.7	0.2	3.8
m2	16	1.6-3.9	3.1	0.7	0.2	3.8
m3	16	2.2-4.3	3.4	0.7	0.2	4.3
microplacoid	16	0.6-1.9	1.3	0.4	0.1	1.6
PH length	11	22.0-43.0	33.0	5.4	1.6	36.0
PH width	11	22.0-43.0	33.0	6.1	1.9	35.0
claw I	16	6.0-10.3	8.9	1.2	0.3	9.7
claw II–III	16	6.5-10.8	9.4	1.2	0.3	10.3
claw IV	16	7.6–12.4	10.7	1.5	0.4	11.9



Figure 6. Taxonomic details of *Minibiotus aquatilis* n.sp. **a**, habitus (holotype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

branch. Accessory claws short and lie close to main branch. Lunules on first three pairs of legs smooth and distinct. Lunules on fourth pair of legs toothed.

Egg round, diameter without processes $60-70 \mu m$, with processes $80-93 \mu m$. Thirty-six processes around circumference, about 100 in hemisphere. Processes long

cones tapering from hemispherical base (diameter 4–4.5 μ m) 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 μ m (two eggs with processes 16–21 μ m long), about 2 μ m apart. Each process with indentations around the base. Shell

surface with large round dots around each process which may be difficult to see in some preparations.

Etymology. Latin, *aquatilis*, living near water, describing the type locality.

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 μ m long with base diameter 3–3.5 μ m) and a little further apart (3 μ m). However this is variable, one egg had process height 9–10 μ m, base diameter 2–2.5 μ m; two eggs had process height 5–7 μ m, base diameter 3 μ m. 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* n.sp., 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.

Habitat. 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 hispidus n.sp.

Figs. 7, 18f; Table 6

Type material. HOLOTYPE in AM (AM KS41467): Australia, Queensland: Crow's Nest, 27°16'S 152°03'E, 3 September 1985, S.K. Claxton. PARATYPES (6 specimens, 4 eggs in AM [AM KS41468–KS41477]; 24 specimens, 5 eggs in SKC): same data as holotype.

Additional material examined. AUSTRALIA, New South Wales: Appin, 34°12'S 150°47'E, 29 June 1985, P.D. Claxton, moss and lichen on sandstone rock in open forest, 30 specimens, 5 eggs. Queensland: North Stradbroke Island, 27°30'S 153°30'E, 19 February 1996, R.M. Kristensen, soil under *Eucalyptus* tree, 10 specimens. Isla Gorge, 25°10'S 149°56'E, 7 March 1996, R.M. Kristensen, moss on rock, 8 specimens, 1 egg. Bribie Island, 27°30'S 153°08'E, 16 April 1995, S.K. Claxton, leaf litter and sand in *Banksia* heath, 21 specimens, 1 egg. Western Australia: John Forest National Park, 31°53'S 116°05'E, 22 November 1994, P.D. Claxton, moss and lichen on rock in open forest, 27 specimens, 1 egg. (All SKC). NEW ZEALAND: South Island, (NZ526) Canaan Rd, Abel Tasman National Park, 9 April 1971, D.S. Horning, 2 specimens in 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 μ m, colourless. Eye spots in posterior position. Cuticle smooth, coarse

Table 6. Measurements (in μ m) of adults of *Minibiotus* hispidus n.sp.

Character	No.	Range	Mean	SD	SE H	olotype
body length	10	234-300	274.1	21.8	6.9	263
BT length	10	26.5-29.7	28.3	1.0	0.3	28.1
BT width	10	2.2 - 2.4	2.3	0.1	0.03	2.2
SI length	10	17.3–19.5	18.4	0.7	0.2	18.4
VS length	10	12.4–14.1	12.9	0.6	0.2	12.4
PR length	10	9.7-11.4	11.0	0.6	0.2	11.4
MPR length	10	8.7–9.7	9.4	0.4	0.1	9.5
m1	10	2.0 - 2.7	2.3	0.2	0.06	2.4
m2	10	1.6 - 2.2	2.0	0.3	0.09	2.2
m3	10	2.0 - 2.7	2.3	0.2	0.06	2.2
microplacoid	10	0.5 - 1.1	0.8	0.2	0.05	0.8
PH length	10	27.0-31.0	28.5	1.4	0.5	27.0
PH width	10	26.0-30.0	28.1	1.5	0.5	27.0
claw I	10	6.2–7.0	6.6	0.3	0.1	6.5
claw II–III	10	6.8–7.6	7.2	0.4	0.1	7.0
claw IV	10	7.3-8.7	8.0	0.4	0.1	8.1

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 main branch. Lunules on all claws small and smooth, somewhat thickened on fourth pair.

Eggs round, colourless, diameter without processes 59 μ m, with processes 72 μ m. 48 processes around circumference, about 340 in hemisphere. Processes small cones with fine tips, height 6.5–8.4 μ m, base diameter 2.8 μ m and 1–2 μ m apart. Ring of very small pores around base of each process. Shell appears to be covered with very small pores of uniform size.

Etymology. Latin, *hispidus*, bristly, prickly, describing the appearance of the egg.

Remarks. The population from Appin, NSW is smaller than the type population from Crow's Nest (mean body length 213.6 μ m, SD 41.5 μ m, n = 15) as is that from Perth (mean body length 196.9 μ m, SD 36.4 μ m, n = 16) but otherwise the adults are the same. Egg processes from the Appin population are slightly longer (10 μ m) and further apart (3.3 μ m) than those of the type population. The single egg from Perth has quite narrow processes (1.5–2 μ m base diameter).

The species is very similar to *Minibiotus maculartus* but has a shorter ventral support and smooth lunules on



Figure 7. Taxonomic details of *Minibiotus hispidus* n.sp. **a**, habitus (holotype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

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.

Habitat. 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 in leaf litter and sandy soil. The species can cope with high temperatures and drying.

Minibiotus pilatus n.sp.

Figs. 8, 17b, 19a; Table 7

Type material. HOLOTYPE in AM (AM KS41478): Australia, New South Wales: Cambewarra Mountain, 34°48'S 150°35'E, 625 m a.s.l., 9 May 1993, S.K. Claxton. PARATYPES (3 specimens, 2 eggs in AM [AM KS41479–KS41483]; 3 specimens, 2 eggs in SKC): same data as holotype.

Additional material examined. QUEENSLAND: Cunningham's Gap 28°03'S 152°25'E, 10 January 1996, S.K. Claxton, lichens on branches on ground in cool temperate rainforest, 8 specimens in SKC.

Diagnosis. Cuticle with a wrinkled pattern on the dorsum (Fig. 17b) 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 main 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 μ m, with processes 68 μ m. Fifty-six processes around circumference. Processes of two types; first javelin-shaped (Fig. 19a), height 5.5–8 μ m, base 1–1.6 μ m joined by a membrane where they are expanded in the middle. Second type of process a short rod, about 2 μ m high. Javelin-shaped processes form circles about 10 μ m 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.

Etymology. Latin, *pilatus*, armed with a javelin, which describes the egg, and in addition the species is dedicated to Dr G. Pilato in appreciation of his assistance.

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.

Table 7. Measurements (in µm) of adults of *Minibiotus pilatus* n.sp.

Character	No.	Range	Mean	SD	SE H	olotype
body length	7	150-290	234.7	53.2	20.1	264
BT length	7	20.0 - 28.1	25.0	2.9	1.1	26.0
BT width	7	1.4 - 2.2	2.0	0.3	0.1	2.1
SI length	7	13.5-19.2	17.0	2.0	0.8	17.6
VS length	7	9.7-13.5	12.0	1.3	0.5	12.4
PR length	7	5.4 - 10.8	8.8	1.8	0.7	9.7
MPR length	7	4.9–9.2	7.7	1.4	0.5	8.1
m1	7	1.1 - 3.2	2.5	0.7	0.3	2.7
m2	7	1.0 - 2.4	2.0	0.5	0.2	2.2
m3	7	1.1 - 2.7	2.3	0.6	0.2	2.7
microplacoid	7	0.5 - 1.1	0.8	0.3	0.1	1.1
PH length	7	18.0-29.0	24.7	4.0	1.5	27.0
PH width	7	18.0-30.0	25.4	4.5	1.7	30.0
claw I	7	5.1 - 7.0	6.3	0.7	0.3	6.5
claw II–III	7	5.7-7.6	6.9	0.7	0.3	7.0
claw IV	7	6.2-8.1	7.4	0.7	0.3	7.6

Habitat. The species was found in temperate rainforest at both localities; in foliose lichens on rock at the type locality and in foliose lichens on tree branches at Cunningham's Gap.

Minibiotus ethelae n.sp.

Figs. 9, 19b; Table 8

Type material. HOLOTYPE in AM (AM KS41484): Australia, New South Wales: Cobbitty, 34°01'S 150°40'E, 90 m a.s.l., 20 March 1994, E.S. Siebels. PARATYPES: same data as holotype but collected on 8 November 1985, 11 May 1991, 29 August 1992 and 20 March 1994, 7 specimens, 3 eggs in AM (AM KS41485–KS41494); 50 specimens, 19 eggs in SKC; 1 specimen, 1 egg in collection of Binda and Pilato (UCI).

Additional material examined. SOUTH AFRICA: Lydenberg, Transvaal, 2250 m, 6 May 1988, M. Filmer, lichens, 11

Table 8. Measurements (in μ m) of adults of *Minibiotus* ethelae n.sp.

Character	No.	Range	Mean	SD	SE H	Iolotype
body length	8	311-412	362.9	34.4	12.2	368
BT length	8	33.0-35.7	34.7	1.0	0.3	34.1
BT width	8	2.6 - 2.7	2.7	0.04	0.01	2.7
SI length	8	21.1-23.5	22.5	1.0	0.4	21.6
VS length	7	17.8–18.9	18.0	0.4	0.2	17.8
PR length	8	11.9–13.5	12.8	0.5	0.2	12.4
MPR length	8	10.3-11.4	11.2	0.4	0.2	10.8
m1	8	3.2-3.8	3.5	0.3	0.09	3.2
m2	8	2.4-2.7	2.7	0.1	0.04	2.7
m3	8	2.7 - 3.2	3.1	0.2	0.06	3.2
microplacoid	8	0.5 - 1.1	0.9	0.3	0.09	0.7
PH length	8	31.0-35.0	33.1	1.6	0.6	32.0
PH width	8	30.0-35.0	34.1	1.7	0.6	35.0
claw I	8	10.8–11.9	11.4	0.5	0.2	11.4
claw II–III	8	11.4–12.4	12.0	0.4	0.2	11.9
claw IV	8	12.4–13.5	13.0	0.5	0.2	13.0



Figure 8. Taxonomic details of *Minibiotus pilatus* n.sp. **a**, habitus (holotype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

specimens, 2 eggs in NMP. Natal, Drakensberg, Cathedral Rock Area, 30 May 1988, H. Dastych, moss on rock in Indumeni forest, 4 specimens in NMP. Rus-Te-Winter National Reserve, 1500 m, 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 in ZIM. Hendriksdaal, Palmers Creek, 1400 m, July 1971, A. Szeptycki, rock, 1 specimen in 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.



Figure 9. Taxonomic details of *Minibiotus ethelae* n.sp. **a**, habitus (holotype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

Description. Body length $175-480 \mu m$, 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 $32 \mu m$ 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 main branch. Lunules small, smooth and thin on all claws.

Eggs colourless, round, diameter without processes 67–70 μ m, with processes 90–100 μ m. 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 μ m, on three others 14.5–19 μ m and on another 19–22.5 μ m. Base diameter of processes 2.7–3.8 μ m (on egg with longest processes 4.3–4.9 μ m), about 5 μ m apart. Shell surface dotted, SEM shows these to be bumps (Fig. 19b).

Etymology. The species is named after Ethel Siebels who kindly assisted in the collection of the specimens.

Remarks. The species is similar to *Minibiotus furcatus* 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.

Habitat. 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.

Minibiotus keppelensis n.sp.

Figs. 10, 19c; Table 9

Type material. HOLOTYPE in AM (AM KS41495): Australia, Queensland: Great Keppel Island, 23°10'S 150°59'E, 14 July 1993, P.D. Claxton. PARATYPES (4 specimens, 2 eggs in AM [AM KS41496–KS41501]; 13 specimens, 4 eggs in SKC) same data as holotype.

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 μ m, colourless, some specimens with red pigment granules. Eye spots large, in posterior position. Cuticle smooth with round (1 μ m) 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 (27×30 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 main branch on all claws. Lunules small, smooth on all claws.

Eggs colourless, round, diameter without processes $45-55 \mu m$, with processes $65-85 \mu m$. Eleven processes around circumference and 24 in hemisphere. Processes short cones with pointed apices $11-16 \mu m$ high, base diameter $9-12 \mu m$ and $4-6 \mu m$ -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.

Etymology. The species is named after the type locality, Great Keppel Island.

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.

Habitat. The species was found in foliose lichen on rock and in crustose lichen on a dead tree in open woodland.

Table 9. Measurements (in μ m) of adults of *Minibiotus* keppelensis n.sp.

Character	No.	Range	Mean	SD	SE H	Holotype
body length	12	200–287	259.4	25.4	7.3	270
BT length	12	24.9-28.4	26.9	1.2	0.3	27.0
BT width	12	1.4 - 1.7	1.6	0.08	0.02	1.5
SI length	12	15.1-17.3	16.3	0.8	0.2	16.2
VS length	12	9.7–11.9	10.9	0.7	0.2	10.8
PR length	12	7.6-8.7	8.1	0.4	0.1	8.1
MPR length	12	7.0-7.6	7.2	0.2	0.07	7.0
m1	12	1.6 - 2.7	2.2	0.3	0.08	2.2
m2	12	1.6 - 2.2	1.8	0.2	0.06	1.9
m3	12	1.6 - 2.2	2.0	0.3	0.08	2.2
microplacoid	12	0.5-0.8	0.6	0.1	0.03	0.5
PH length	11	24.0-30.0	26.7	2.2	0.7	27.0
PH width	11	23.0-31.0	27.6	2.9	0.9	30.0
claw I	12	6.0 - 7.0	6.7	0.4	0.1	7.0
claw II–III	12	6.5–7.6	7.3	0.4	0.1	7.6
claw IV	12	7.0-8.6	8.1	0.6	0.2	8.6



Figure 10. Taxonomic details of *Minibiotus keppelensis* n.sp. **a**, habitus (holotype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

Figs. 11, 19d; Table 10

Type material. HOLOTYPE in AM (AM KS41502): Australia, Tasmania: O'Neill's Creek, Mount Roland Protected Area, 41°29'S 146°15'E, 680 m a.s.l., 21 May 1996, A. Moscal. PARATYPES (5 specimens, 3 eggs in AM [AM KS41503–KS41510]; 80 specimens, 17 eggs in SKC) same data as holotype.

Additional material examined. AUSTRALIA TASMANIA: Mount Montgomery 41°09'S 146°47'E, 470 m, 20 October 1994, A. Moscal, moss on rock in low woodland, 11 specimens in SKC. Hartz Mountains, 43°25'S 146°47'E, 4 December 1988, A.J. Downing, moss on mudstone in Eucalyptus/Myrtle forest, 6 specimens, 3 eggs in SKC. VICTORIA: Melba Gully, Otway Ranges, 38°40'S 143°20'E, 4 May 1997, S.K. Claxton, leafy liverwort, moss and lichen on fallen branches in Nothofagus forest, 33 specimens, 2 eggs (SKC). MACQUARIE ISLAND: Scobie Lake, 400 m, 9 December 1977, D.S. Horning, 26 specimens. Gadget's Gully, 220 m, 25 November 1977, D.S.H., 17 specimens. Lusitania Bay, 400 m, 1 December 1977, D.S.H., 7 specimens. Mount Hamilton summit, 433 m, 17 January 1978, D.S.H., 8 specimens. Mount Waite summit, 452 m, 29 December 1977, D.S.H., 11 specimens. Mount Fletcher summit, 428 m, 17 February 1978, D.S.H., 8 specimens. All Macquarie Island specimens in WM. NEW ZEALAND, SOUTH ISLAND: Temple Basin Lower Ski Huts, Arthur's Pass National Park, 19 May 1970, D.S. Horning, 2 specimens (NZ186, 188). Pegley Flat, Arthur's Pass National Park, 18 May 1970, D.S.H., 1 specimen (NZ170). Fox Glacier Valley, 28 March 1970, D.S.H., 3 specimens (NZ23) in 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 μ m) 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 is 28% of buccal tube length) with small refractive zone at base and long secondary branch; accessory claws short and rising well clear of main branch. Lunules small and smooth on all claws.

Eggs colourless, round, diameter without processes 54–67 μ m, with processes 64–85 μ m. 20–28 processes around circumference, 75–90 in a hemisphere. Processes like those

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Table 10. Measurements (in μ m) of adults of *Minibiotus asteris* n.sp.

Character	No.	Range	Mean	SD	SE H	olotype
body length	20	155-368	259.7	62.8	14.0	274
BT length	20	21.6-30.8	26.7	3.0	0.7	28.1
BT width	20	1.6 - 2.8	2.1	0.3	0.07	2.2
SI length	20	13.5-19.5	17.0	2.0	0.5	18.1
VS length	20	9.7–14.1	12.0	1.4	0.3	12.4
PR length	20	7.0–11.9	9.4	1.4	0.3	9.2
MPR length	20	6.0-10.3	8.0	1.2	0.3	8.1
m1	20	1.6-3.2	2.4	0.5	0.1	2.4
m2	20	1.6 - 2.7	2.2	0.4	0.09	2.4
m3	20	1.6 - 2.7	2.2	0.4	0.09	2.4
microplacoid	20	0.7 - 1.4	1.1	0.2	0.04	0.8
PH length	20	22.0-33.0	26.7	3.5	0.8	27.0
PH width	20	22.0-36.0	26.5	3.6	0.8	27.0
claw I	20	4.9–7.6	6.3	0.9	0.2	7.0
claw II–III	20	5.4-8.2	6.9	0.9	0.2	7.6
claw IV	20	6.0-8.9	7.5	1.0	0.2	8.1

of *Macrobiotus hufelandi* but with distal disk consisting of about six (up to eight) distinct arms like those of a starfish. Process height 5–10 μ m, base diameter 4.3–7.0 μ m and disk diameter 4.3–5.4 μ m. Processes are 2–4 μ m apart. 12–14 small pores around the base of each process. Egg shell surface smooth or lightly striated.

Etymology. Latin *aster* with masculine ending *is*, star, describes the appearance of the distal end of the egg processes.

Remarks. This species is probably most closely related to *Macrobiotus 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.

Habitat. 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 milleri n.sp.

Figs. 12, 16b, 19e; Table 11

Type material. HOLOTYPE in AM (AM KS41599): Australia, New South Wales: New England National Park, 30°30'S 152°24'E, 1450 m a.s.l., 18 December 1994, S.K. Claxton. PARATYPES (7 specimens, 4 eggs in AM [AM KS41600–KS41608]; 56 specimens, 4 eggs in SKC) same data as holotype but some also collected on 20 April 1995 and 7 January 1996.

Additional material examined. NEW SOUTH WALES: Cambewarra Mountain, 34°48'S 150°35'E, 625 m, 9 May 1993, S.K. Claxton, moss and lichen on rocks and trees in cool temperate rainforest, 14 specimens in SKC.



Figure 11. Taxonomic details of *Minibiotus asteris* n.sp. **a**, habitus (holotype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

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 μ m, 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 μ m diameter) containing small apophyses, three macroplacoids and a microplacoid. Macroplacoid row long (37%)



Figure 12. Taxonomic details of *Minibiotus milleri* n.sp. a, habitus (holotype); b, egg; c, ventral view of the buccal armature; d, claws of the first pair of legs; e, claws of the fourth pair of legs; f, detail of eggshell.

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 main branch. Lunules on first three pairs of legs very small, smooth; on fourth pair smooth.

Table 11. Measurements (in μ m) of adults of *Minibiotus milleri* n.sp.

Character	No.	Range	Mean	SD	SE H	lolotype
body length	20	182–398	272.6	60.2	13.5	349
BT length	20	24.3-35.1	29.1	3.3	0.7	31.9
BT width	20	2.3-3.5	2.8	0.4	0.09	3.2
SI length	20	17.3-26.0	21.2	2.5	0.6	23.0
VS length	20	8.7-12.7	10.6	1.3	0.3	11.9
PR length	20	10.8-15.7	12.9	1.5	0.3	14.1
MPR length	20	8.7-13.0	10.8	1.3	0.3	11.4
m1	20	2.2-3.2	2.7	0.3	0.07	3.0
m2	20	2.4-3.5	2.9	0.3	0.07	3.2
m3	20	2.7 - 4.1	3.4	0.5	0.1	3.5
microplacoid	20	0.8-1.9	1.4	0.3	0.07	1.6
PH length	20	23.0-35.0	27.7	2.8	0.6	29.0
PH width	20	23.0-33.0	26.8	2.7	0.6	27.0
claw I	20	4.9–7.6	6.4	0.9	0.2	7.0
claw II–III	20	5.4-8.7	7.0	0.9	0.2	7.6
claw IV	20	6.5–9.7	7.7	1.0	0.2	8.7

Eggs round, diameter without processes $68-74 \mu m$, with processes $90-98 \mu m$. 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 $10-14 \mu m$, base diameter 3 μm arranged evenly about 3 μm apart. Shell surface faintly striated.

Etymology. The species is named after Dr William R. Miller, friend and colleague.

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.

Habitat. 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 hufelandioides (Murray, 1910) n.comb.

Figs. 1a, 13, 19f; Table 12

Macrobiotus hufelandioides Murray, 1910: 138–139, pl. XVIII, figs. 29a-c.

Material examined. Australia: NEW SOUTH WALES: Kosciusko (type locality), Digger's Creek, 36°20'S 148°30'E, 1500 m, 1 October 1992, P.D. Claxton, moss and lichen on rock in open alpine area, 58 specimens, 16 eggs. Thredbo Creek, 36°27'S 147°55'E, 1200 m, 1 October 1992, P.D.C., moss and lichen on rock in open alpine area, 10 specimens, 1 egg. Waste Point, 36°20'S 148°36'E, 1000 m, 1 October 1992, P.D.C., moss and lichen on rock, 4 specimens, 1 egg. Lake George, 35°04'S

149°23'E, 27 March 1992, P.D.C., moss and lichen on rock in open forest, 29 specimens, 24 eggs. Galore, 35°07'S 146°47'E, 340 m, 19 March 1994, S.K.C., moss and lichen on rocks on summit of monolith in open forest, 19 specimens, 1 egg. All SKC.

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 pearshaped 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 main 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 μ m, with processes 65–75 μ m. 20–26 processes around circumference. Processes conical with expanded discoid tops, distal disk smooth or lightly notched; process height 5.5–6.5 μ m, base diameter 5.5–7 μ m, disk diameter 4.5– 6.5 μ m. 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.

Table 12. Measurements (in μ m) of adults of *Minibiotus* hufelandioides.

Character	No.	Range	Mean	SD	SE
body length	16	240-378	315.2	43.0	10.8
BT length	16	24.9-34.6	28.9	2.6	0.7
BT width	16	2.0 - 3.1	2.5	0.3	0.08
SI length	16	16.8-23.7	19.5	1.8	0.5
VS length	16	10.8 - 16.2	13.3	1.5	0.4
PR length	16	10.8-16.2	13.0	1.4	0.4
MPR length	16	9.2-13.5	11.0	1.1	0.3
m1	16	2.7 - 3.5	3.0	0.3	0.07
m2	16	2.2 - 3.0	2.6	0.2	0.06
m3	16	2.7 - 3.8	3.1	0.4	0.09
microplacoid	16	0.8-1.6	1.2	0.3	0.08
PH length	16	28.0-41.0	32.1	3.4	0.9
PH width	16	26.0-42.0	32.3	4.7	1.2
claw I	16	6.0-8.7	7.3	0.8	0.2
claw II–III	16	6.5–9.2	7.8	0.8	0.2
claw IV	16	7.0–9.7	8.5	0.9	0.2



Figure 13. Taxonomic details of *Minibiotus hufelandioides* **a**, habitus; **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

Although Murray's description lacks detail such as the granulation around the claws and the toothed lunule 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.

Habitat. 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.

Minibiotus aculeatus (Murray, 1910) n.comb.

Figs. 1b, 14, 16a, 17a, 20a; Table 13

Macrobiotus aculeatus Murray, 1910: 139–140, pl. XVIII, figs. 27a-e.

Macrobiotus intermedius subjulietae Horning, Schuster & Grigarick, 1978: 237, figs. 117-120.

Material examined. AUSTRALIA: NEW SOUTH WALES: Kosciusko (type locality), Digger's Creek, 36°20'S 148°30'E, 1500 m, 1 October 1992, P.D. Claxton, moss on rock, 1 specimen. Thredbo Creek, 36°27'S 147°55'E, 1200 m, 1 October 1992, P.D.C., lichen on rock, 7 specimens, 1 egg. Waste Point, 36°20'S 148°36'E, 1000 m, 1 October 1992, P.D.C., lichen on rock, 1 egg. New England National Park, 30°30'S 152°30'E, 1400 m, 18 December 1994, S.K. Claxton, moss and lichen on rocks and trees in Banksia heath, 36 specimens, 2 eggs; ditto but collected 20 April 1995, S.K.C., moss and lichen on rock in heath, 13 specimens, 1 egg; ditto but collected on lichen on tree in Nothofagus forest, 1 specimen; ditto but collected 7 January 1996, S.K.C., moss and lichen in heath, 91 specimens, 4 eggs. Jenolan, 33°49'S 150°02'E, 14 December 1986, S.K.C., moss on trees and rocks in sheltered valley, 22 specimens, 6 eggs. Barrington Tops, 31°59'S. 151°30'E, 8 February 1993, D. Clark, moss on branch on ground in closed forest, 1 specimen. Mount Wilson, 33°30'S 150°23'E, 27 October 1991, S.K.C., moss on tree in cool temperate rainforest, 1 specimen, 1 egg. QUEENSLAND: Ravensbourne, 27°22'S 152°08'E, 3 September 1985, S.K.C., moss on tree in closed forest, 5 specimens. LORD HOWE ISLAND, D.S. Horning, 6 specimens. TASMANIA: Mount Pedder, Maria Island National Park, 42°38'S 148°05'E, 620 m, 20 April 1995, A. Moscal, moss on rock in heath, 7 specimens. All SKC.

NEW ZEALAND: 16 paratypes of *Macrobiotus intermedius* subjulietae: NORTH ISLAND: Waimaua Gorge, 17 May 1971, C.J. Horning, 1 specimen (NZ650). Grays Bush, 19 May 1971, C.J.H., 1 specimen (NZ672). Bruce Park Scenic Reserve, 21 May 1971, D.S. Horning, 3 specimens (NZ705). Taumarunui, 15 July 1970, B.J. Donovan, 2 specimens (NZ279, NZ281). Norsewood, 20 May 1971, D.S.H., 1 specimen (NZ687). Mount Egmont National Park, 23 May 1971, D.S.H., 1 specimen (NZ753). Morere Hot Spring Scenic Reserve, 19 May 1971, D.S.H., 1 specimen (NZ674). SOUTH ISLAND: Abel Tasman National Park,

Table 13. Measurements (in μ m) of adults of *Minibiotus* aculeatus.

Character	No.	Range	Mean	SD	SE
body length	7	210-350	290.6	43.8	16.6
BT length	7	24.9-32.4	29.1	2.5	1.0
BT width	7	1.9-2.5	2.3	0.2	0.08
SI length	7	15.7-20.8	18.5	1.7	0.7
VS length	7	13.0-16.8	15.0	1.4	0.5
PR length	7	9.7-12.2	11.1	0.9	0.4
MPR length	7	7.3-10.5	9.4	1.1	0.4
m1	7	2.2 - 3.2	2.8	0.4	0.1
m2	7	1.6 - 2.7	2.3	0.4	0.1
m3	7	1.6-3.0	2.4	0.5	0.2
microplacoid	7	0.6-1.1	1.0	0.2	0.08
PH length	7	27.0-34.0	29.6	2.7	1.0
PH width	7	27.0-38.0	31.1	3.4	1.3
claw I	7	4.3-6.0	5.6	0.6	0.2
claw II–III	7	4.7-6.5	6.1	0.7	0.3
claw IV	7	5.4–7.0	6.6	0.6	0.2

9 April 1971, D.S.H., 1 specimen (NZ538). Cowper's Knob, 9 April 1970, D.S.H., 1 specimen (NZ86). West Harper Hut, 12 April 1971, H.A. Best, 1 specimen (NZ544). CHATHAM ISLAND: Waterfall Creek, 31 August 1971, D.S.H., 2 specimens (NZ932, NZ924). THREE KINGS ISLAND: Summit Ridge, 28 November 1970, G.W. Ramsey, 1 specimen (NZ479). All NZM

Diagnosis. Smooth cuticle with pores of variable size and shape and three pairs of soft spines (Fig. 17a) over legs II, III and IV (or one pair over leg IV); 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 $(27 \times 30 \ \mu m)$ containing well developed, granular apophyses, three macroplacoids and a microplacoid. Macroplacoid row short (32.2% of buccal tube length); first macroplacoid pearshaped 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 is 22.8% of buccal tube length) with no refractive zone at the base; accessory claws long and rising well clear of main branch. Lunules very small.



Figure 14. Taxonomic details of *Minibiotus aculeatus* **a**, habitus; **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

Eggs colourless, round, diameter without processes 54 μ m, with processes 65 μ m. 24–30 processes around circumference, 100 in hemisphere. Processes long cones with attenuated, areolated tips, 9–11 μ m long, base diameter 3–5 μ m, processes 3–4 μ m 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).

Habitat. 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.

Minibiotus scopulus n.sp.

Figs. 15, 20b; Table 14

Type material. HOLOTYPE in AM (AM KS41511): Australia, New South Wales: Galore, 35°07'S 146°47'E, 340 m a.s.l., 19 March 1994, S.K. Claxton, moss and lichen on dead trees, rock and soil in dense dry woodland. PARATYPES (7 specimens, 5 eggs in AM [AM KS41512– KS41521]; 39 specimens, 40 eggs in SKC): same data as holotype.

Additional material examined. AUSTRALIA, Western Australia: Ravenswood, 32°33'S 115°43'E, 18 February 1993, P.D. Claxton, crustose lichen on tree, 1 specimen in SKC. NEW ZEALAND: North Island, Tikitiki, 18 May 1971, D.S. Horning, 1 specimen in 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 main branch. Lunules very small.

Eggs colourless to pale brown, often found in pairs, round, diameter without processes 60 μ m, with processes 70 μ m. Thirty-six processes around circumference and 120 in hemisphere. Processes long, thin, apparently flattened at least along the distal half. Processes mostly 6–11 μ m long with a few on each egg up to 16 μ m and then often bent at an acute angle; base diameter 2–3 μ m and 4–6 μ m between them. Shell surface dotted.

Etymology. Latin *scopulus* (masculine), observation point, projecting rock, which describes the type locality, a large

Table 14. Measurements (in μ m) of adults of *Minibiotus* scopulus n.sp.

Character	No.	Range	Mean	SD	SE H	olotype
body length	15	165–428	328.9	81.4	21.0	423
BT length	15	22.2-35.1	30.9	4.1	1.1	35.1
BT width	15	1.6-3.2	2.7	0.5	0.1	3.2
SI length	15	14.6-23.2	20.4	2.8	0.7	22.7
VS length	15	11.4–18.9	16.5	2.3	0.6	18.9
PR length	15	7.0-15.1	11.9	2.4	0.6	15.1
MPR length	15	6.0-13.0	10.3	2.1	0.5	13.0
m1	15	3.2-7.6	5.9	1.3	0.3	7.6
m2	15	2.2-4.3	3.4	0.7	0.2	4.3
microplacoid	15	0.5-1.6	1.2	0.4	0.1	1.6
PH length	12	25.0-42.0	34.8	5.4	1.4	38.0
PH width	12	27.0-38.0	35.1	3.9	1.1	38.0
claw I	15	7.0–11.9	10.2	1.8	0.5	11.9
claw II–III	15	7.6-12.4	10.8	1.7	0.5	12.4
claw IV	15	8.7–14.1	12.2	1.9	0.5	14.1

monolith on the plains of western New South Wales.

Remarks. The species is similar to *Minibiotus fallax* Pilato *et al.*, 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.

Habitat. 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 fallax Pilato, Claxton & Binda, 1989

Fig. 20c

Minibiotus fallax Pilato, Claxton & Binda, 1989: 23-26, fig. 2A-E.

Type material examined. HOLOTYPE in MM (1139-38): Australia, New South Wales, Douglas Park, 34°11'S 150°43'E, 11 January 1987, S.K. Claxton, moss and lichen on rock in open forest. PARATYPES (13 specimens, 1 egg in MM; 18 specimens, 2 eggs in SKC): same data as holotype but some also collected on 9 March 1986, 14 September 1986, 15 November 1986.

Additional material examined. NEW SOUTH WALES: Barrengarry, 34°40'S 150°30'E, 26 January 1986, S.K.C., moss on rock, cool temperate rainforest, 2 specimens. Blue Mountains, 33°43'S 150°20'E, 1000 m, 26 December 1993, 8 August 1995, 26 November 1995, S.K.C., moss on trees and rocks in closed forest, 16 specimens. New England National Park, 30°30'S 152°30'E, 1200 m, 18 December 1994, 20 April 1995, 7 January 1996, S.K.C., moss and lichen on rocks and trees in subalpine heath, 21 specimens. Jenolan, 33°49'S 150°02'E, 14 December 1986, 26 December 1992, S.K.C., moss and lichen on trees in open forest, 7 specimens. Fitzroy Falls, 34°38'S 150°30'E, 26 January 1986, S.K.C., moss and lichen in open forest, 2 specimens. Crookwell, 34°28'S 149°29'E, 29 August 1992, J. Lloyd, lichen on tree open trees, 15 specimens, 37 eggs. Taralga, 34°24'S 149°49'E, 26 April 1996, S.K.C., lichen on tree on street, 6 specimens, 1 egg. Apsley Falls, 31°03'S 151°46'E, 6 February



Figure 15. Taxonomic details of *Minibiotus scopulus* n.sp. **a**, habitus (paratype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

1993, D. Clark, lichen on tree, 3 specimens, 1 egg. Kosciusko, 36°30'S 148°19'E, 1 October 1992, P.D. Claxton, moss and lichen on rock, 3 specimens. QUEENSLAND: Cunninghams Gap, 28°03'S 152°25'E, 3 September 1985, S.K.C., moss and lichen on trees in closed forest, 3 specimens. Ravensbourne, 27°22'S 152°08'E, 3 September 1985, S.K.C., moss and lichen on trees in open forest, 8 specimens. Crows Nest, 27°15'S 152°05'E, 3 September

1985, S.K.C., moss on rock in open forest, 3 specimens. Eumundi, 26°28'S 152°57'E, 20 December 1986 [D.S. Horning], 18 March 1994 [S.K.C.], fern on soil, moss and lichen on trees in urban park, 7 specimens. Yarraman, 26°20'S 151°58'E, 3 September 1985, S.K.C., lichen on trees in open forest, 11 specimens. Cania Gorge, 24°40'S 150°58'E, 1 April 1997, S.K.C., lichen on rock, 1 specimen. Cammoo Caves, 23°10'S 150°27'E,



Figure 16. a, buccal apparatus of *Minibiotus aculeatus* DIC; b, buccal apparatus of *Minibiotus milleri* DIC. (Scale bars = $10 \mu m$).



Figure 17. a, dorsal cuticle of *Minibiotus aculeatus* Phase; b, dorsal cuticle of *Minibiotus pilatus* DIC. (Scale bars = $10 \mu m$).

1 September 1985, S.K.C., lichen on tree open field, 14 specimens. Capricorn Caves, 23°10'S 150°27'E, 2 April 1997, S.K.C., leaf litter on rock open forest, 1 specimen. All SKC.

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.



Figure 18. Eggs of a, Minibiotus intermedius DIC; b, Minibiotus taiti DIC; c, Minibiotus poricinctus Phase; d, Minibiotus floriparus Phase; e, Minibiotus aquatilis Phase; f, Minibiotus hispidus DIC. (Scale bars = $10 \mu m$).

Emended description. Eggs colourless, found singly, in pairs and sets of four; 59–80 μ m in diameter without processes, 80–100 μ m 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 μ m but may reach 22 μ m, these longer processes often swollen or bent at an acute angle near distal end, processes 3–4 μ m base diameter and 2–4 μ m 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.

Habitat. The species occurs frequently but rarely in abundance. It seems to prefer lichens on trees in dry environments.



Figure 19. Eggs of **a**, *Minibiotus pilatus* DIC; **b**, *Minibiotus ethelae* SEM; **c**, *Minibiotus keppelensis* DIC; **d**, *Minibiotus asteris* Phase; **e**, *Minibiotus milleri* DIC; **f**, *Minibiotus hufelandioides* SEM. (Scale bars $a-e = 10 \mu m$, scale bar $f = 1 \mu m$).

Minibiotus maculartus Pilato & Claxton, 1988

Minibiotus maculartus Pilato & Claxton, 1988: 86-88, figs. 3A-D.

Type material examined. HOLOTYPE in MM (1019-39): Australia, New South Wales Douglas Park, 34°11'S 150°43'E, 9 March 1986, S.K. Claxton, moss and lichen on rock in open forest. PARATYPES (7 specimens, 3 eggs in MM; 61 specimens, 11 eggs in SKC) same data as holotype but some also collected on 17 May 1986, 19 July 1986, 13 September 1986, 15 November 1986 and 11 January 1987.

Additional material examined. AUSTRALIA, New South Wales: Jenolan, 33°49'S 150°02'E, 14 December 1986, S.K.C., moss and lichen on rock in open forest, 8 specimens, 8 eggs. New England National Park, 30°30'S 152°30'E, 18 December 1994, 20 April 1995, 7 April 1996, S.K.C., moss, lichen and liverwort on trees in closed forest, 26 specimens, 5 eggs. Montague Island, 36°15'S 150°14'E, 22 January 1993, D. Clark, lichen on rock exposed to salt spray, 28 animals, 3 eggs.



Figure 20. Eggs of a, Minibiotus aculeatus Phase; b, Minibiotus scopulus DIC; c, Minibiotus fallax DIC. (Scale bars = $10 \mu m$).

All SKC. NEW ZEALAND: Weka Island, East Coast, 28 November 1971, G.I. Wilson, 3 specimens in NZM (NZ1136).

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.

Emended description. Re-examination of the type material revealed the presence of tiny teeth on the lunules of the fourth pair of claws which are 29% of the length of the buccal tube (measurement in the original description included the accessory claw).

Eggs may be quite variable in shape of the processes. In the population from Montague Island, the processes are rounded not pointed.

Minibiotus bisoctus (Horning et al., 1978) n.comb.

Macrobiotus bisoctus Horning, Schuster & Grigarick, 1978: 236–237, figs. 114–116.

Type material examined. PARATYPE: New Zealand: Snares Islands, Penguin Rookery, 9 October 1972, D.S. Horning, 1 specimen (SA255) in NZM.

Diagnosis. Smooth cuticle with pores of irregular size and shape arranged in transverse bands, granulation on all legs; three round granular macroplacoids and an indistinct microplacoid; long robust claws with short, high accessory claws and smooth lunules.

Emended description. Body length up to 305 µm, colourless. Eyespots absent. Cuticle smooth with transverse bands of pores of irregular shape and size and granulation in small patches on outside of first three pairs of legs above claws and around claws on fourth pair of legs. Buccal tube narrow (8.3% of buccal tube length). Stylet supports inserted at 60.3% of buccal tube length, ventral support short (42% of buccal tube length). Pharyngeal bulb round containing large granular apophyses, three granular macroplacoids and one microplacoid. Macroplacoid row short (31% of buccal tube length); first macroplacoid round partly obscured by apophysis, which is about same size, second macroplacoid small, granular, and third macroplacoid granular with slight caudal bulb, which curves towards the midline. Microplacoid indistinct, lying very close to third macroplacoid. Claws long, robust (fourth pair of claws is 31% of buccal tube length). Accessory claws short, rising high above main branch. Lunules very small and smooth on all claws.

Eggs unknown.

Minibiotus furcatus (Ehrenberg, 1859)

Macrobiotus furcatus Ehrenberg, 1859: 452, fig. III. [Type locality: Monte Rosa, Italy]
Minibiotus furcatus.-Binda & Pilato, 1992: 113-115, figs. 1A,B.

Material examined. None

Emended diagnosis. Yellow body cells, smooth cuticle with variably shaped pores arranged in rows; long ventral reinforcing bar and long macroplacoid row, small indistinct microplacoid; long slender claws with short, high accessory claws and lightly toothed lunules on fourth pair of legs.

Minibiotus ramazzottii Binda & Pilato, 1992

Minibiotus ramazzottii Binda & Pilato, 1992: 115–117, fig. 1C– F. [Type locality: Rancagua, Chile].

Material examined. None

Emended diagnosis. Yellow body cells, smooth cuticle with small round pores, granulation on all legs; long ventral reinforcing bar and long macroplacoid row, distinct microplacoid; very long slender claws with short, low accessory claws and smooth lunules.

Minibiotus stuckenbergi (Dastych et al., 1990)

- *Macrobiotus stuckenbergi* Dastych, Ryan & Watkins, 1990: 61–65, figs. 6–10. [Type locality: western Dronning Maud Land, Antarctica].
- Minibiotus stuckenbergi.-Dastych & Drummond, 1996: 114.

Material examined. None.

Emended diagnosis. Cuticle with small oval and large irregular pores, granulation around all claws; single dorsal transverse thickening in oral cavity; long ventral support, 3 round macroplacoids and indistinct microplacoid; slender claws with short high accessory claws and lunules with a few jagged teeth on fourth pair of claws.

Minibiotus vinciguerrae Binda & Pilato, 1992

Minibiotus vinciguerrae Binda & Pilato, 1992: 117–120, figs. 2A–E. [Type locality: Victoria Land, Antarctica].

Material examined. ANTARCTICA: Victoria Land, Pilato, 1 specimen, 1 egg in UCI.

Emended diagnosis. Smooth cuticle with variably shaped pores and fine granulation around claws on all legs; dorsal crest in oral cavity broken into teeth, long ventral reinforcing bar and long macroplacoid row, distinct microplacoid; slender claws with short, high accessory claws and smooth lunules.

Minibiotus weinerorum (Dastych, 1984)

Macrobiotus weinerorum Dastych, 1984: 400–402, fig. 14, photographs 21–25. [Type locality: Enderby Land, Antarctica].

Minibiotus weinerorum.–Miller, Heatwole, Pidgeon & Gardiner, 1994: 152–155, figs. 3A–C.

Material examined. None.

Emended diagnosis. Smooth cuticle with randomly distributed pores and granulation around claws on all legs; small round macroplacoids and indistinct microplacoid; slender claws with very high accessory claws and small, smooth lunules.

Discussion

It has become clear during this study that there are several species in the Australian fauna which may well have been identified as *Minibiotus intermedius* on the basis of older, imprecise descriptions. In order to differentiate these species a range of qualitative and quantitative characters of adult specimens were examined. Because of the small size of most of these species, observation of these characters required the highest usable power of light magnification.

Oualitative 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 have been 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 15) 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 the processes.

Table 15. Number of observations (n), mean and standard deviation (SD) of pt values for some characters of *Minibiotus* species with three macroplacoids. SIL—stylet support insertion level; VS—ventral support length; BTW—external buccal tube width; MPRL—macroplacoid row length; and CLIV—claw length on fourth pair of legs excluding or including (*) accessory claw.

species	n	SIL mean	SD	VS mean	SD	BTW mean	SD	MPRL mean	SD	CLIV mean	SD
M. intermedius	20	55.0	0.9	37.3	2.0	6.8	0.5	26.5	1.5	24.8	1.8
M. taiti	20	60.3	0.3	40.3	0.7	8.0	0.3	32.1	1.6	33.2	0.8
M. poricinctus	20	59.5	0.4	35.8	0.9	7.6	0.4	30.9	1.4	27.3	0.7
M. floriparus	19	64.4	0.7	46.1	3.8	7.6	0.7	33.1	1.9	34.0	1.6
M. aquatilis	16	68.3	0.2	53.0	0.8	9.0	0.4	37.9	1.9	34.6	2.2
M. hispidus	10	65.2	0.5	45.7	1.5	8.0	0.2	33.2	1.1	28.1	0.8
M. pilatus	7	67.9	0.5	48.1	0.4	7.9	0.4	30.4	2.7	29.7	0.8
M. ethelae	8	64.9	1.2	51.4	1.2	7.6	0.2	32.3	0.8	37.6	0.7
M. keppelensis	12	60.6	0.9	40.4	1.6	5.8	0.2	26.6	1.0	30.1	1.2
M. asteris	20	63.8	0.7	44.8	0.9	8.0	0.5	30.0	1.8	28.1	0.9
M. milleri	20	73.0	0.7	36.4	1.0	9.7	0.3	37.0	1.1	26.5	0.8
M. hufelandioides	16	67.4	0.5	45.9	2.0	8.6	0.4	38.2	1.1	29.3	1.2
M. aculeatus	7	63.7	1.1	51.4	1.5	7.8	0.3	32.2	2.0	22.8	0.9
M. maculartus	14	64.4	0.6	53.0	1.3	8.1	0.6	31.5	1.8	29.2	1.3
M. bisoctus	1	60.3		42.0		8.3		31.0		31.0	
M. furcatus		68.4		62.0		7.9		36.5		38.6*	
M. ramazzottii		68.2		61.5		11.6		42.4		48.1*	
M. vinciguerrae		67.4		59.0		9.9		37.3		41.6*	

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 marcusi De Barros, 1942. Seventy four slide mounted specimens from Venezuela labelled Minibiotus intermedius and deposited in the Bohart Museum were examined. Forty nine of those specimens conform to the description of M. intermedius supplied in this paper. Five specimens appear to belong to the taxon M. marcusi and 11 specimens to M. acontistus. These have not been described in this paper 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 not to have a curve in the buccal tube as it enters the pharyngeal bulb. 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 16. 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 16. Length or 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.

	Minibiotus (18 species)	Macrobiotus (19 species)
stylet insertion length	≤ 73	≥ 74
ventral support length	≤ 62	≥ 65
buccal tube width	≤ 12	≥ 13
macroplacoid row length	≤ 42	≥ 42

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