

Biology, affinity and description of an unusual aquatic new genus and species of Isotomidae (Collembola) from high altitude lakes in Tasmania

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Abstract. A new species of Isotomidae (Collembola) was collected from submerged stones on the edge of nine lakes on Tasmania's Central Highland Plateau. Because it did not comply fully with the characters of any existing genus, a new genus, *Chionobora* gen. n. is erected for it here. An Antarctic species, *Desoria klovstadi* (Carpenter), has characters which conform with the new genus so is formally transferred to the new genus here. The Antarctic Continent and Tasmania were last in proximity 60 million years b.p. so it is suggested both species are relicts persisting in probable ice-free refugia during glacial cycles. Gut contents of specimens of the new species exclusively contained diatoms in various stages of digestion and the species appears to graze on aquatic macrophytes, a feeding habit not recorded before for Collembola. We note the high numbers of endemic invertebrate taxa of restricted distributions in cold habitats of southern regions compared to warmer regions and stress their conservation values and threats to their populations.

INTRODUCTION

In 1988, numerous individuals of a previously unknown species of Collembola were collected by Tasmanian aquatic biologists during a survey of the littoral fauna of highland lakes on the Great Lakes Plateau. Superficially the species was similar in habitus and some characters to *Hydroisotoma schaefferi* (Krausbauer, 1898) from a similar habitat in North Hemisphere. Characters in common were cylindrical dens, claw and mucro as well as habitus, all of which are adaptations to an aquatic habitat (Deharveng & Bedos, 2004) however it lacked bothriotricha which are a diagnostic character for *Hydroisotoma*.

In order to demonstrate the phylogenetic and biogeographical affinities of the new species, a new genus is erected for it, is diagnosed and its affinities discussed. It was found that *Desoria klovstadi* complied with the characters of the new genus rather than with *Desoria* sensu stricto so it is transferred formally to the new genus, *Chionobora*, here.

We also here discuss the paleogeographic reasons why high generic and high taxon diversity in Collembola and other invertebrates is found in severe habitats in the extreme south including Tasmania.

METHODS

The specimens were collected by removing submerged pebbles from the edge of the lake, turning them over and washing any organism adhering to the surface through a sieve of mesh size 500 µm aperture, into a vessel containing 10% formalin and later preserved in 75% alcohol. A minimum of 20 rocks were sampled at each site.

ABBREVIATIONS: Abd – abdominal segments; Ant – antennal segments. PAO – post antennal organ, Th – thoracic segments. SAMA – South Australian Museum, Adelaide.

RESULTS

Chionobora gen. n.

Type species. *Chionobora amila* sp. n. by present designation.

Diagnosis. Ocelli 8 + 8, PAO present, simple. Ant 2 and 3 with many short, blunt, curved s chaetae both thick and thin. Subapical pin-chaeta of Ant 4 simple. Basomedian and proximal parts of labium polychaetotic. Maxillary head not modified, maxillary outer lobe with bifurcate palp and 2–4 sublobal hairs. Abd V and VI separate, Tibiotarsi with tenent hairs not clavate, T-chaetae partly lost. Furca long with many chaetae on anterior and posterior sides. Manubrium with ventroapical chaetae not differentiated. Dens regularly tapering, posterior side crenulate (*klovstadi*) or tuberculate (*amila*). Mucro slender, quadridentate.

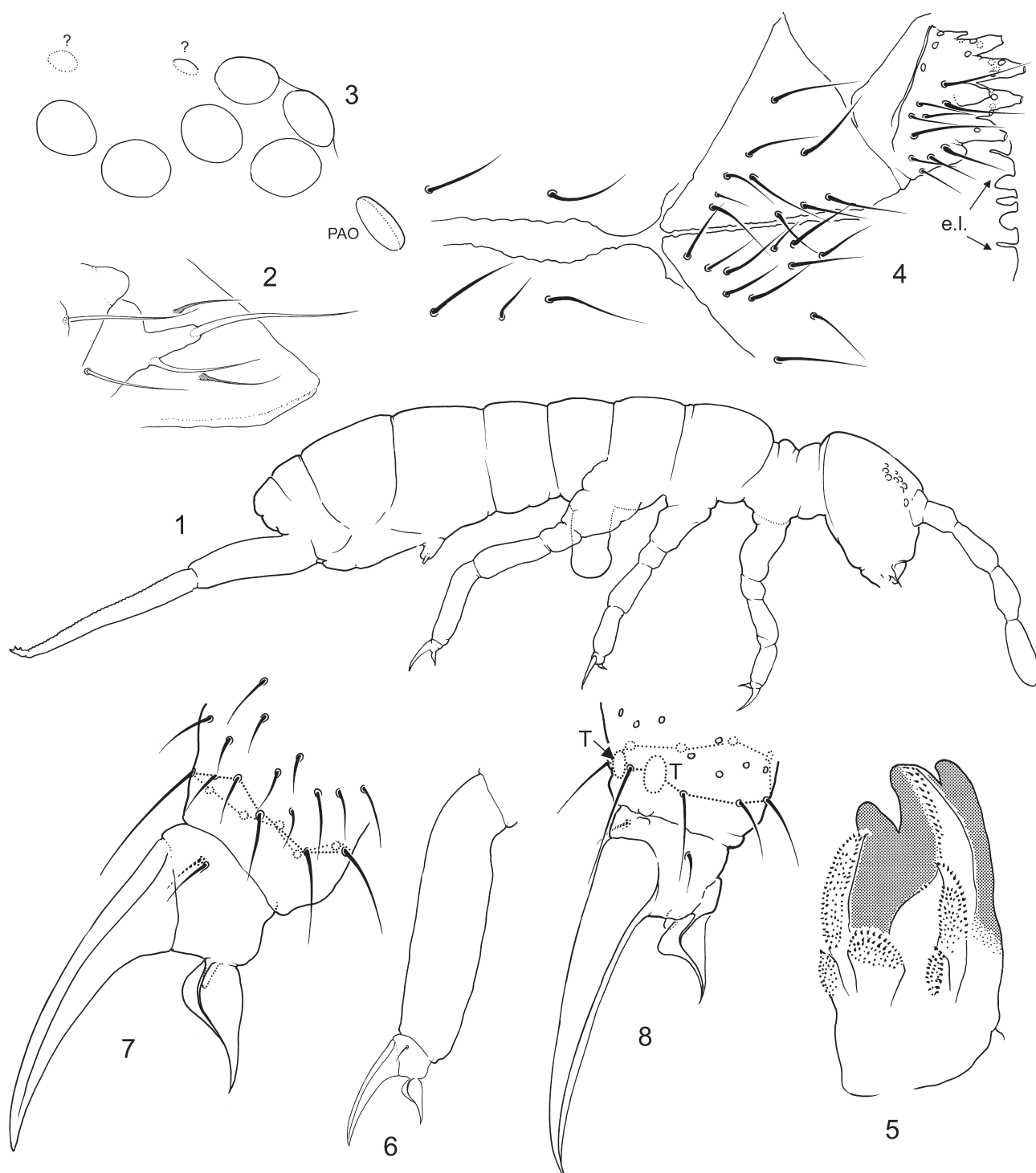
Body covered with fine smooth chaetae, macrochaetae short or hardly differentiated, smooth. Glands at base of chaetae absent. Bothriotricha absent. Accp-s chaetae positioned exactly in p-row of chaetae on body tergites.

Etymology. Chion – cold, bora – south (Greek roots). Feminine.

Chionobora amila sp. n.

Colour. Dark pigment in broad bands on body except for anterior part of abdomen VI.

Habitus. Head large, hypognathous, body stout (Fig. 1). Antennae about 1.5 times the diagonal of the head, ratio 5.5 : 3.5. Ratio of lengths of abdominal segments III to VI as 2.0–3.1 : 1.8–2.6 : 1.0–1.3 : 1.0 measured dorsally.

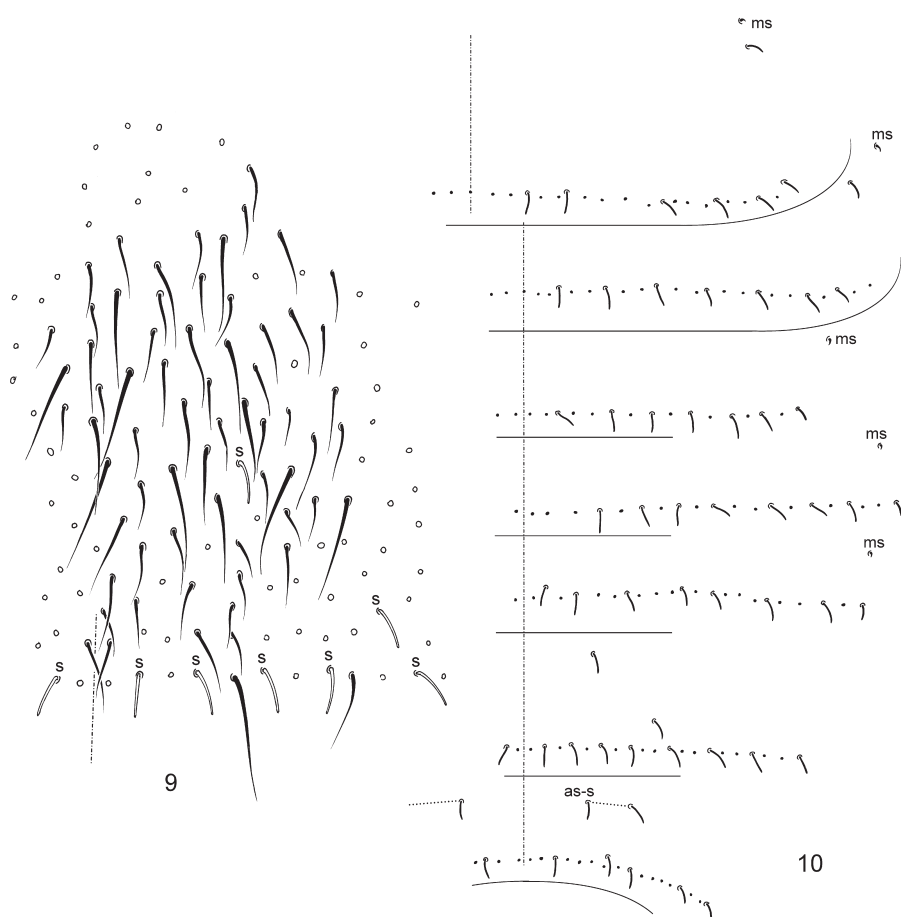


Figs 1–8: *Chionobora amila* sp. n. 1 – habitus; 2 – maxillary outer lobe; 3 – PAO and ocelli (the presence of ocelli G and H under question); 4 – ventral side of head, postlabial chaetae, labial palp and edge of labrum shown; 5 – maxillary head; 6–7 – distal half of leg 3; 8 – apical part of leg 2; e.l. – edge of labrum, T – T-chaetae.

Chaetotaxy. Plurichaetotic, body and appendages densely covered with short (but not equal), smooth, pointed chaetae (Fig. 9). Macrochaetae hardly developed, the longest chaetae of Abd V about 0.25 as long as this segment length. Bothriotricha absent; s chaetae well marked; shorter than common chaetae, number of s-chaetae in adult specimens on Th II–Abd V as 7–9 (6–8 accp + 1 al), 7–8 (6–7 accp + 1 al)/7 (accp), 7–8 (accp), 7–9 (7–8 accp + 0–1 as), 8–10 (7–9 accp + 1 as), 7 (5 accp + 2 as). Median s

chaetae (as) always present on Abd IV and V, often absent on Abd IV. Accp-s chaetae located in p-row (not anterior to it), very rarely with one or two s chaetae in a segment slightly displaced to a more anterior position (Figs 9–10). Laterally positioned accp s chaetae thicker and shorter than others. Micro s chaetae 1,1/1,1,1 from thorax to abdomen III inserted anteriorly on all segments (Fig. 10).

Head and antennae. Antennal organ III with 2 inner cylindrical s chaetae distally and 2 outer more basal s chaetae,



Figs 9–10: *Chionobora amila* sp. n. 9 – chaetal covering of median part of Abd IV; 10 – s chaetae chaetotaxy; as-s – as-s chaetae.

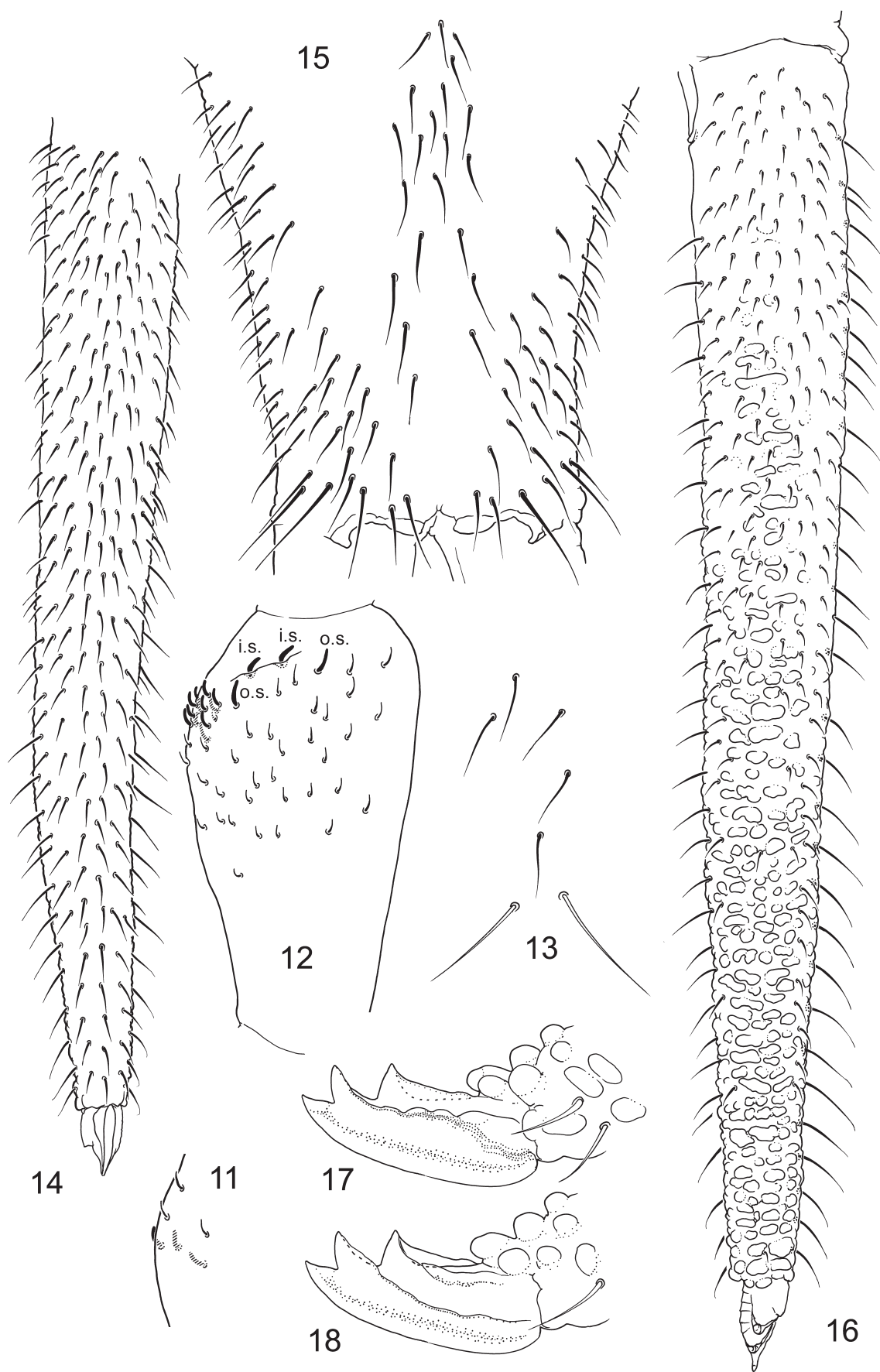
similar in shape. In addition, dorsal side of Ant III densely covered with numerous thin, short s chaetae in distal half; a compact group of thick cylindrical s chaetae inserted on outer edge (Fig. 12). Ant II with few both thin and thick s chaetae on outer edge (Fig. 11). Ant I with a group (about 4) of basal microchaetae and short and thick s chaetae at middle section (usually 4 in number). Antennal segment IV with simple knob at tip and simple (not bifurcate) subapical pin-chaeta. Subapical organite small, round. Many s chaetae with curved tips occur on all antennal segments distally, and numerous thinner s chaetae. Antenna of male without specialised chaetae. Clypeal field with about 65 chaetae. Prelabral chaetae 4; labral chaetae all spine-like particularly distally and set in papillae, 5,5,4 in number. Anterior margin of labrum with rather broad apical folds (Fig. 4). Ocelli 8 + 8, although G and H hardly visible. PAO small, simple, broadly oval, slightly longer than anterior ocelli. Maxilla not modified, with three teeth and six normal lamellae, not extending beyond the teeth, lamella 1 slender, with single row of cilia; other lamellae rather short (Fig. 5). Maxillary outer lobe with palp bifurcate, number of sublobal hairs varies from 2 to 3 (variant with 2 shown in Fig. 2). Labium with 8–11 basomedian, 8–11 proximal and 5 basolateral chaetae (Fig. 4). Labial palp unmodified, with full set of guards (16), lateral process small (Fig. 4).

Thorax. Tibiotarsus broad and flattened, shortest on leg 1 and 2 (Fig. 1). Claw long and thin, apparently without in-

ner tooth although minute lateral teeth sometimes visible. Tenent hairs not clavate (Figs 6–8). Empodial appendage with lobe at base, broad, with 3 lamellae and no teeth. Nomenclature of chaetae in tibiotarsal distal row of tibiotarsi uncertain as masked by polychaetosis (basal set is 7 A-chaetae and 4 T-chaetae, but some chaetae can be displaced to distal row from the main part of tibiotarsi). Distal row with from 8 to 11 (maximum primitive number 11) with at least T1 and T2 chaeta absent in some specimens (Fig. 8).

Abdomen. Abd V and VI separate dorsally. Ventral tube with 8–11 + 8–11 latero-distal chaetae and about 7 chaetae posteriorly, 2 in distal transversal row (Fig. 13). Anterior chaetae absent. Furca long. Medial cleft of manubrium fairly distinct. Dens thick, slightly tapering, tuberculated on posterior side, with numerous chaetae on posterior and anterior sides (Figs 14, 16). Chaetae of posterior side short, covering from 1/2 to 3/5 of its length. Mucro stout, lamellate, without chaeta, with three teeth evenly spaced, fourth tooth smallest, developed as projection of outer lamella of third tooth (Figs 16–18); both second and third teeth have outer and inner lamellae, inner lamella of second tooth with four scallops (Figs 17–18). Ratio manubrium : dens : mucro = 7–11 : 12–17 : 1; furcal subcoxae with about 32 and 100 chaetae respectively.

Female without spines on anal lobes, 2 + 2 fine chaetae on genital opening.



Figs 11–18: *Chionobora amila* sp. n. 11 – group of s chaetae in lateral part of Ant 2; 12 – s chaetae of Ant 3, dorsal view; 13 – chaetae of posterior side of ventral tube; 14, 16 – dens, anterior (14) and posterior (16) view; 15 – manubrium, anterior view; 17, 18 – mucro, inner (17) and outer (18) views; i.s. and o.s. – inner and outer s chaetae of antennal organ.

Type material. Holotype ♂: Tasmania, Central Plateau: Lake Meander, Central Plateau, 1306, GR577714, under submerged stones at edge of lake; RM, 4.ii.1988 (SAMA registration number

I22637). Paratypes: Four slides with single female each, one slide with three females; all paratypes with same collecting data as the holotype.

TABLE 1. Comparison of morphological characters of fifteen taxa of Isotominae.

Group / taxon	ocelli	slobals	anter-VT	basomed	proximal	bothriotricha	mucro	T-chaetae	clavatio	s-poster	fusAbd	mansp
<i>Isotoma</i> Bourlet, 1839 s. str.	0	0	0	1	0	0	1	0	0	1	0	1
<i>Desoria</i> spp. gr. <i>pjasini</i> (Martynova, 1974)	0	0	0	0	0	0	1	0	0	1	0	1
<i>Pseudoisotoma</i> Handschin, 1924	0	0	0	0	0	0	1	0	1	1	1	1
<i>Folsomotoma</i> Bagnall, 1949	1	0	0	0	0	0	1	0	0	0	1	1
<i>Parisotoma</i> Bagnall, 1940	1	0	0	0	0	0	1	0	0	0	0	0
<i>Desoria trispinata</i> (MacGillivray, 1896)	0	0	0	0	0	0	1	0	0	0	0	0
<i>Isotomurus</i> Börner, 1903 s. str.	0	0	0	1	1	1	0	0	0	1	0	0
<i>Isotomurus antennalis</i> Bagnall, 1940	0	0	0	1	1	0	0	0	0	1	0	0
<i>Desoria</i> Nicolet, 1941 s. str. 1	0	0	0	0	0	0	0	1	0	0	0	0
<i>Desoria</i> s. str. 2	0	0	0	0	0	0	0	1	0	1	0	0
<i>Vertagopus</i> Bagnall, 1939	0	0	0	0	0	0	0	1	1	0	0	0
<i>Azoritoma macquariensis</i> Greenslade & Potapov, 2008	1	1	0	0	0	0	0	0	0	0	0	0
<i>Chionobora amila</i> sp. n.	0	1	1	1	1	0	0	0	0	0	0	0
<i>Chionobora klovstadi</i> (Carpenter, 1902)	0	0	1	1	1	0	0	0	0	0	0	0
<i>Granisotoma</i> Cassagnau, 1957 s. str.	0	0	1	0	0	0	0	1	0	1	0	0

Character states used in phenetic analysis: 1. ocelli: number of ocelli: normal at 6–8 (0), reduced number at <5 (1). 2. slobals: number of sublobal hairs in maxillary outer lobe: normal number 4 (0), reduced number <4 (1). 3. anter-VT: chaetae on anterior side of VT: present (0), absent (1). 4. basomed: polychaetosis of basomedian group of chaetae in labium: 1 = absent (0), 2 = present (1). 5. proximal: polychaetosis of proximal group of chaetae in labium: absent (0), present (1). 6. ha: bothriotricha on body absent (0), present (1). 7. mucro: with 4 teeth (0), with 3 teeth (1). 8. T-chaetae: some of T-chaetae absent (0), all T-chaetae present (1). 9. clavatio: clavate tenent hairs absent (0), present (1). 10. s-poster: accp s chaetae on body tergites in p-row (0), in front of p-row (1). 11. fusAbd: Abd V and VI not fused (0), fused (1). 12. mansp: manubrial spines absent (0), present (1). *Desoria* s. str. 1 and 2 differ by accp s chaetae on body tergites situated in p-row or in front of p-row, respectively (see also Fig. 19).

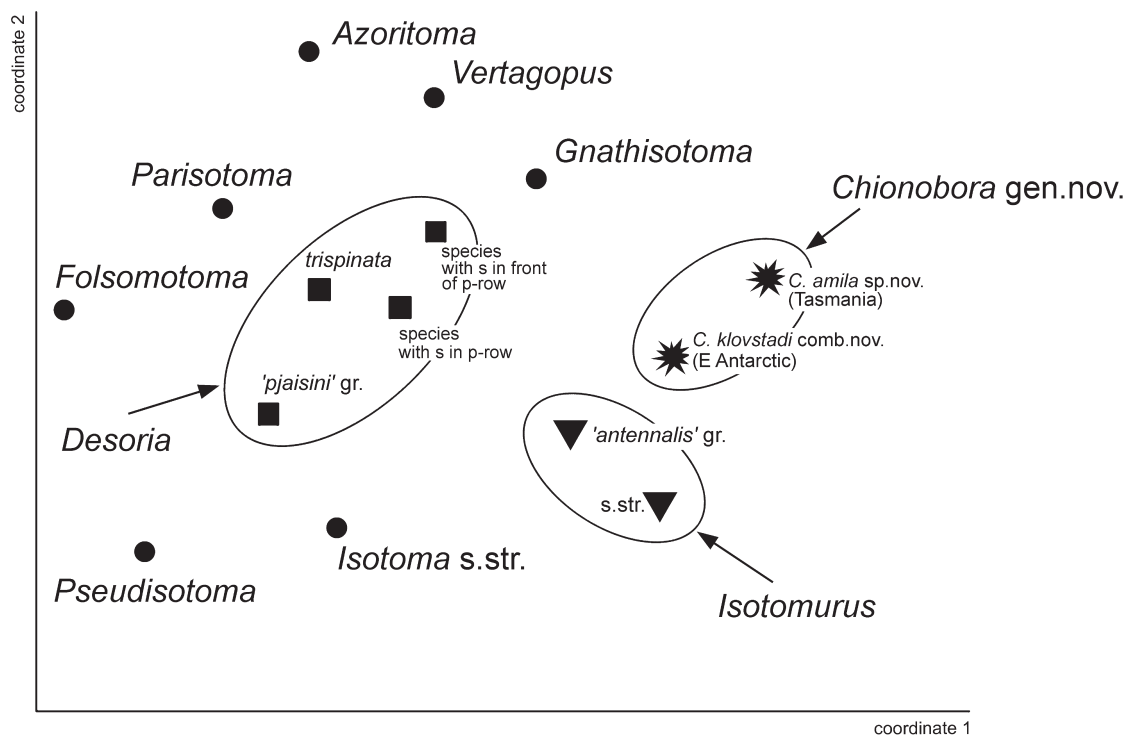


Fig. 19. Distance matrix of similarities between selected genera and southern species groups of Isotominae based on characters in Table 1. The programme PAST (Hammer et al., 2001) was used to perform non-metric multidimensional scaling basing on Euclidian distances matrix. The figure suggests that *Chionobora* gen. n. may be most closely related and sister group to *Isotomurus antennalis* group.



Fig. 20. Colour photograph of Long Tarns, taken by Karen Storey.

Other material examined (all Tasmania, SAMA). On slides: Lake Butters, 1240 m asl, GR483705, rock fauna, 6C/As, SC, 5.ii.1988 (1♂). In alcohol: Lake Toorah, 1170 m asl, GR393643 (5) RM; Lake Butters, GR483705 (7) SC; Triangle Lake, 1151 m asl, GR381585 (1) RM; Lake Naomi, 1015 m asl, GR476575 (1) RM; Lake Nive, 992 m asl, GR420499 (1) RM; Daisy Lake, 1270 m asl, GR452737 (1) SC; Lake Meander GR577714 (9+8 mounted) RM; Lunka Lake, 1200 m asl, GR507668 (1) SC; Long Tarns, 1270 m, GR463737 (4) PD. Collectors: R. McClaine (RM), S. Chilcott (SC), P. Davies (PD).

Etymology. Anagram of Alima (an Arabic word meaning water sprite or sea maiden).

Distribution. Only known from lakes on the Central Plateau of Tasmania.

Ecology. *Chionobora amila* sp. n. was collected by removing submerged or partially submerged stones from the

edges of lakes and washing the surfaces of the rocks. The habitat is illustrated in Figs 20 and 21.

The species is living in an aquatic medium which is confirmed by examination of gut contents of some individuals, each of which contained numerous diatoms belonging to the genera *Gomphonema*, *Navicola* and *Frustulia* (Fig. 22). *Gomphonema* species are epiphytic and *Frustulia* are acidophilic. The *C. amila* sp. n. specimens collected appeared to graze exclusively on diatoms growing on epiphytes and, as the species has a grinding molar plate, is probably able to penetrate the silicon coating of the diatoms.

Remarks. *Chionobora amila* sp. n. cannot be placed into any existing genus of Isotomidae but it shares characters with several genera of Isotominae. The genus to which the new species is most closely approximated is the Northern

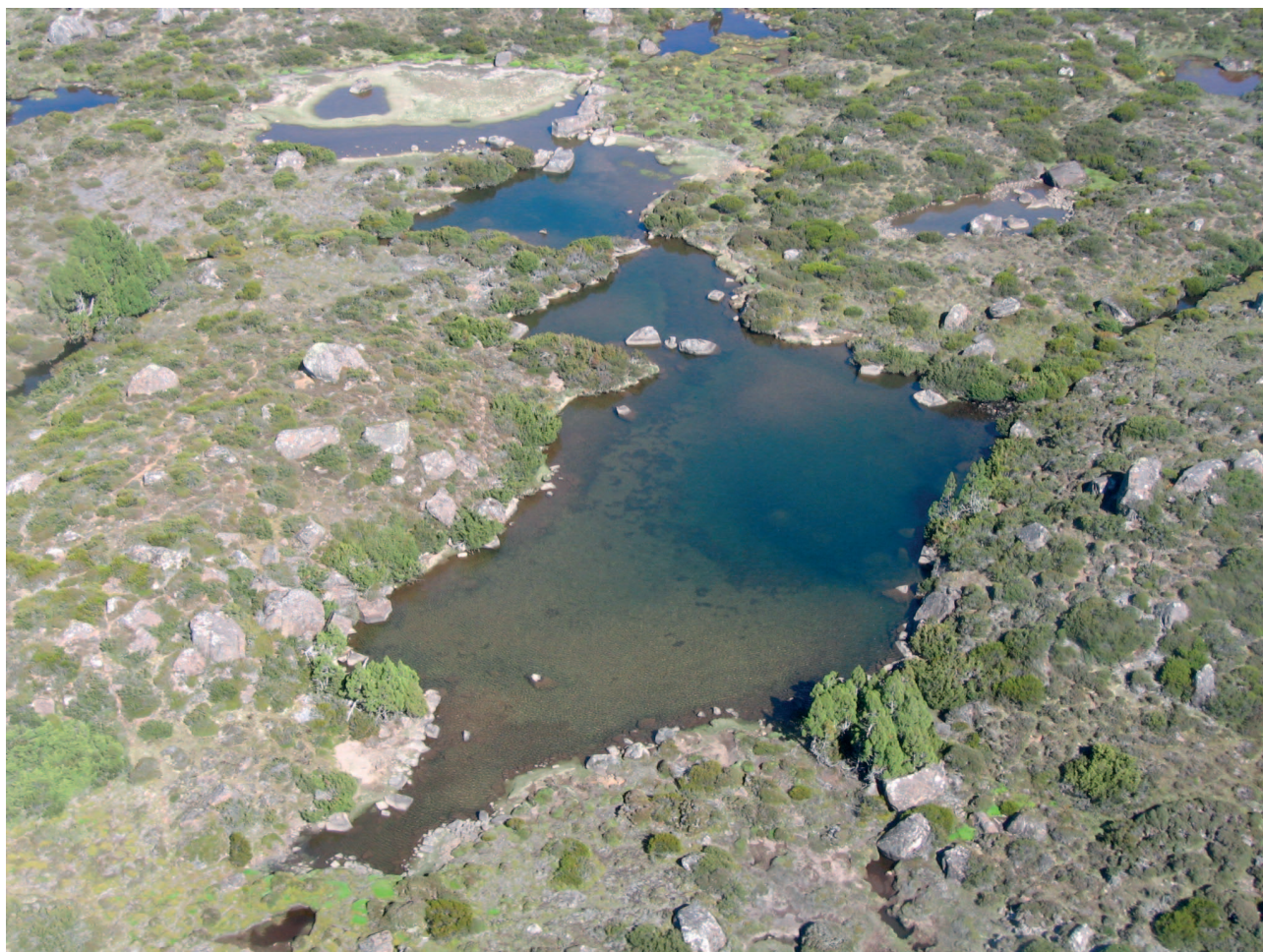


Fig. 21. Colour photograph of Daisy Lake, taken by Karen Storey.

Hemisphere *Desoria* Nicolet, 1841, although it differs in several diagnostic morphological characters for this genus. The only southern representatives of *Desoria* sensu stricto currently known from Australia are likely to be introduced. The exception is *Desoria klovstadi* (Carpenter, 1902) from the Antarctic, which was redescribed by Stevens et al. (2006) and noted as an aberrant member of the genus; it is herein transferred to the new genus *Chionobora* (see below). Significant characters can be grouped into three types as follows:

1. Characters that are adaptations to aquatic habitat. Subcylindrical tuberculated dens, massive lamellate mucro, slender claw, large hypognathous head, covering of short and numerous chaetae, flattened tibiotarsi and polychaetosis of labium (Deharveng & Bedos 2002). The new species is morphologically similar to *Hydroisotoma schaefferi* only in characters that are adaptations to an aquatic habitat. Characters in common are: lamellate mucro, reduced number of sublobal hairs (absent in *H. schaefferi*), increased number of chaetae on labial palp and form of dens. The new genus differs from *H. schaefferi* in the absence of bothriotracha, absence of mucronal chaetae, absence of spines on female anal valves and tubercles on dens. The four species of another Holarctic genus, *Granisotoma* Stach, 1947, live in contact with cold water, have long, cylindrical, tuberculated dens and lamellate mucro,

and manubrium in some species with numerous chaetae on anterior side (*G. danilevskyi* Martynova, 1968, *G. sadoana* Yosii, 1965) similar to the new genus. *Granisotoma* species, however, have chaetae on the mucro and labial baseis oligochaetotic. This last character has only been observed in the type species of the genus, *G. rainieri* (Folsom, 1937) but other species of *Granisotoma* are not well known so the position of the genus within Isotomidae is unclear. Two other semi-aquatic genera *Agrenia* Börner, 1906 (dens is always tuberculated) and *Isotomurus* Börner, 1903 (particularly species with tuberculated dens) have polychaetotic labia but both have other diagnostic differences, for example, a long subapical chaeta on dens and bothriotracha on body, respectively.

2. Characters showing affinities with Southern Hemisphere taxa. The presence of spiny or serrated chaetae on parts of furca and/or body is an important character in Isotominae genera of South Hemisphere. They are present in *Tomocerura* Wahlgren, 1901; *Procerura* Salmon, 1941; *Paracerura* Deharveng & Oliveira, 1994 and *Acanthomurus* Womersley, 1934 among others. The new genus lacks this character. Although the new genus differs in external appearance and ecology, it shares the rare character of two sublobal hairs with the monotypic euedaphic genus *Azoritoma* Greenslade & Potapov, 2008, described from within cushion plants on subantarctic Macquarie Island.

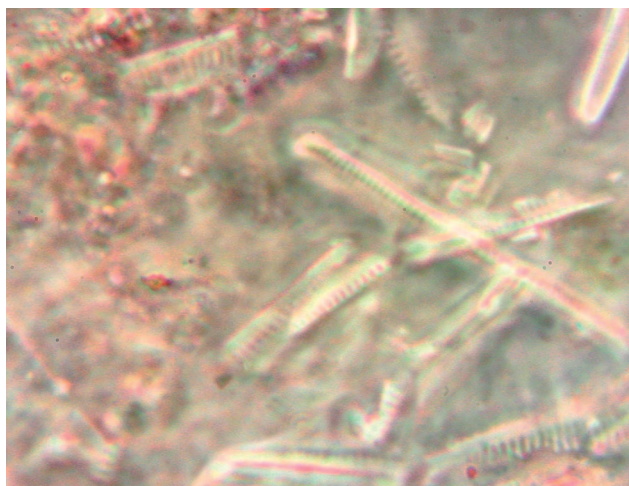


Fig. 22. Micrographs of gut contents of *Chionobora amila* sp. n. from Lake Meander, mid gut contents $\times 1000$, taken by I. Atazaheh.

Azoritoma possesses adaptations to an euedaphic way of life with loss of ocelli and pigment, as well as development of specialised s chaetae on Ant I and Abd V. Table 1 lists other characters that differ between these two genera. The unusual modification of mouthparts of *Azoritoma* is likely to be related to the specialised habitat in which it is found. The new genus also shows some morphological similarities with *Tibiolutra* Salmon, 1941, a genus living in a similar habitat in New Zealand, as both possess flattened tibiotarsi. However *Tibiolutra* has antennal segments III and IV subsegmented, is furnished with serrated chaetae on body and a dens with serrated spines.

3. Similarity to groups of Northern Hemisphere. The new taxon shows a few affinities with three, largely Northern Hemisphere, genera, *Isotoma*, *Desoria* and *Isotomurus* but it did not comply sufficiently to place the new species in any of the three. The relationships of these genera have been discussed in several papers (Deharveng, 1981; Potapov, 2002; Stevens et al., 2006). To graphically illustrate the currently known affinities of genera of Isotominae lacking dental spines, a phenetic scatter diagram is given in Fig. 19 using the characters listed in Table 1. The programme PAST (Hammer et al., 2001) was used to perform non-metric multidimensional scaling basing on Euclidian distances matrix. One hypothesis, based on a selection of characters, is that *Chionobora* gen. n. and *Isotomurus antennalis* group are possibly sister groups (Bagnall, 1940) (the group which has no bothriotricha).

***Chionobora klovstadi* (Carpenter, 1902) comb. n.**

Isotoma klovstadi Carpenter, 1902: 222.

Desoria klovstadi: Stevens in Stevens et al., 2006: 822.

Desoria klovstadi, from East Antarctica, is the most closely related species to *C. amila* and complies with the diagnosis of the new genus. Both species combine two rare characters: absence of anterior chaetae on ventral tube and strong polychaetosis of labium. Other characters in common are: position of accp-s chaetae in p-row, form of mucro, short and numerous smooth chaetae on body, general

shape of maxillary head rectangular and loss of some of T-chaetae on tibiotarsus. The Antarctic species however does not possess characters that are adaptations for species living in contact with water as does *C. amila*. The morphological characters of *Desoria klovstadi* placed the species in an intermediate position between the Northern Hemisphere *Isotoma* s. str. and *Desoria* s. str. Nicolet, 1841 (Stevens et al., 2006). Sequence data did not indicate a close relationship of *D. klovstadi* with existing Isotominae genera. Stevens et al. (2006) therefore provisionally placed the species in *Desoria*. The affinity of *D. klovstadi* with the new genus is demonstrated here; consequently it is hereby transferred to *Chionobora*.

Material examined. East Antarctic, Cape Jones, 11.ii.2009. Collector F. Frati (10 individuals in coll. M. Potapov).

Distribution. Patchily distributed in Northern Victoria Land, Antarctic Continent.

DISCUSSION

The new genus has the unique combination of characters in Isotominae of polychaetotic labium, lack of bothriotricha on body, no anterior chaetae on ventral tube and some T-chaetae on tibiotarsi lost. Two species, *C. amila* and *C. klovstadi* are known to possess these characters; both are restricted to high latitudes of the Southern Hemisphere. Sequence data for *C. klovstadi* did not resolve any affinity with Northern Hemisphere genera so it is possible that molecular analysis for *C. amila* might be similarly not illuminating. Ancient phylogenetic relationships may not always be revealed from sequence data. It may be significant that Tasmania was last adjacent to the part of North Victoria Land, where *C. klovstadi* occurs, 60 million years ago (Royer & Rollet, 1997).

The current climate of the Central Plateau is cold, windy and can be both wet and dry according to season. Annual rainfall here can vary from 3000 to 1000 mm from north-west to east. Average maximum temperatures are 18.7°C in summer and 5.5°C in winter while minimums are from -2°C in winter and 5.5°C in summer. (Storey & Comfort, 2007). Consequently both species of *Chionobora* live in extreme habitats, that is they are A- (adversity) selected and also possess a range of adaptive characters, typical for the habitat in which they are found. Correlates of adversity selection are given in Greenslade (1983) and include selection against dispersal if adapted to stable but predictably severe environments which may explain their restricted distributions. It is therefore most likely that vicariance and not dispersal is the cause of species divergence in this genus.

Glaciation on the plateau has occurred multiple times over the last two million years but it is believed the area west of Lake Augusta, where *C. amila* occurs, remained ice free and that alpine vegetation was present (Kieran, 1990; Colhoun et al., 1996; Kirkpatrick & Fowler, 1998). Shiel et al. (1998) note that at times these lakes "may have been refugia for aquatic species". Stevens et al. (2006) suggested that *C. klovstadi* is a relict persisting in Northern Victoria land (Eastern Antarctica) in refugia throughout glacial

periods and Stevens et al. (2006) detected multiple glacial refugia for *Chionobora* in Northern Victoria Land. This could also be proposed for *C. amila* with both *Chionobora* species surviving with limited change over a long period in extremely cold habitats in stasis. This proposes an alternative strategy to (Fraser et al., 2014) who suggested, based on biodiversity modelling, that geothermal sites allowed species to persist throughout glacial cycles.

The geological formation on which *C. amila* occurs is part of a large area of Jurassic dolerite over nearly half of Tasmania. This rock type cracks as it cools and later becomes eroded resulting in a plethora of crevices providing protected refuges for invertebrates.

There are over 3000 lakes and tarns in the Central Highlands. The survey during which *C. amila* was found, sampled 120 lakes (Fulton, 1998) but *C. amila* was only found on nine of them. These lakes are all fairly small, within 25 km of each other and at an altitude of between 1000 and 1200 m in the southern part of the Plateau. Two are shown in Figs 20 and 21. There appears to be no apparent reason for *C. amila* being only found in a few of the lakes surveyed but there are a number of possible reasons such as incomplete sampling, paleohistorical factors, fire both accidental and managed, algal composition, as well as past grazing by stock and road construction leading to erosion into the lake and recreation (Storey & Comfort, 2007). It is known that the Plateau lakes are heavily used for trout fishing and that trout have been introduced to most lakes with some lake levels manipulated for hydroelectric schemes (Anon., 2002; Storey & Comfort, 2007). Also trout are known to impact deleteriously on aquatic invertebrates (Cadwallader, 1996; Davies et al., 2002; Elvey, 2002), however all but one lake (Meander) contained trout at the time of sampling (S. Chilcott, pers. com.). Most individuals of *C. amila* were found in Lake Meander.

Other examples of invertebrate aquatic taxa with endemic species and genera in the Central Highlands region are the fresh water aquatic invertebrates of Rotifera (Shiel et al., 1998); Mollusca (Ponder et al., 1993), Annelida (Pinder & Brinkhurst, 2000), phreatoicoid Isopoda (Knott, 1975), Ephemeroptera (Campbell, 1988) (see Greenslade & New, 1991). An additional threat to this fauna is that it is predicted that the region will experience reduced rainfall with climate change. The preservation and protection of such faunas, that provide information on the palaeohistory of habitats and faunas present today is clearly of a high priority.

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