



Description of adults and immature stages of *Antipodoecia* Mosely from Australia and synonymy of the families Antipodoeciidae and Anomalopsychidae (Insecta: Trichoptera)

ROSALIND M. ST CLAIR^{1,3}, JOHN C. DEAN¹ & OLIVER S. FLINT, Jr.²

¹Museums Victoria, GPO Box 666, Melbourne, Vic. 3001, Australia.

²Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 USA.

³Corresponding author. E-mail: rstclair@museum.vic.gov.au

Abstract

The female, larva, and pupa of *Antipodoecia* Mosely from Australia are described, males re-examined and briefly described. Similarities with other trichopteran families are discussed. Based on morphological synapomorphies of males, females, pupae, and larvae, we infer that the genera *Antipodoecia*, *Anomalopsyche*, and *Contulma* share an immediate common ancestor, although relationships among these genera remain unresolved. Consequently, the Neotropical family Anomalopsychidae is a junior synonym of Antipodoeciidae from Australia.

Key words: Caddisflies, Sericostomatoidea, South America, phylogeny, COI gene

Introduction

The family Antipodoeciidae is endemic to Australia and is monotypic. Its relationship to other families in the Sericostomatoidea has proved problematic. Here we examine the family in Australia more closely and its relationship with closely related families using predominantly morphological methods.

Since the initial description of *Antipodoecia turneri* Mosely 1934, many specimens have been collected but no additional species described. The current range of the family is the entire east coast of Australia, from far north Queensland to Tasmania. A distribution over several thousand kilometres and across different biogeographical subregions seems unlikely for a single species. Recognition of only one species can be attributed to the remarkably uniform male genitalia over this large geographical area and the lack of information on other life stages. The female has not been described but was figured by Neboiss (1986). Some information on larvae was provided by Neboiss (1991, partly incorrect) and Dean (2000).

Our examination of museum specimens and additional material has revealed only subtle differences in male genitalia but has found variation in other male and female characters which indicates the presence of additional species. Larvae were separated into three distinct morphospecies by Dean (2000), again indicating the presence of additional species. However, a lack of material associating larvae and adults has prevented us from resolving this subtle morphological variation into defined species. Recent limited genetic analysis using the COI gene is suggesting far more species than indicated by our morphological analysis. A detailed review of this genus is now a far larger undertaking than anticipated and will not be attempted here.

When the family Antipodoeciidae was established by Ross (1967) a formal diagnosis was not provided. Since then several family diagnoses have been provided by Neboiss, the most detailed by Neboiss (1991). This information has primarily been based on adult males, with only limited information on other life history stages. An error was made by Neboiss (1991) in the number of teeth on the larval anal claw, and this misinformation was subsequently used for investigations into higher taxonomy and family relationships within the Sericostomatoidea (e.g., Scott & de Moor 1993; Holzenthal & Flint 1995; Neboiss 2002). The Neotropical Family Anomalopsychidae was established by Flint (1981) who noted the close similarity with Antipodoeciidae from Australia. Examination of immatures shows that the two families are remarkably similar.

A recent study of the phylogeny of the Sericostomatoidea (Johanson *et al.*, 2016) summarised previous studies and provided a large amount of molecular data to develop a proposed phylogeny. However, the position of Antipodoeciidae within the superfamily remains a little uncertain.

We think that, for Antipodoeciidae at least, previous difficulties in understanding relationships with other families can be attributed to the lack of complete morphological information for all life stages, particularly adult females and immatures. The provision here of additional information should enable a better understanding of relationships. While some additional information is provided for males, we are unable to define taxa at species level.

Materials and methods

Most specimens were examined using a Leica MZ 12.5 stereo microscope. Due to the very small size of the specimens, many adult, pupal, and larval characters were examined on a cavity slide under a compound microscope. While characters such as the tentorial pits on the heads of pupa and larvae can be observed, with care, under a high-resolution stereo microscope, others such as the delicate multibranched secondary setae on the head and pronotum of the larva require examination using a compound microscope. Male and female genitalia were cleared in KOH and figures based on these or montaged photos of non-cleared specimens. Montage photos were produced from images taken with a Leica DFC320 camera, mounted on a Leica MZ16 microscope.

Terminology for wing venation follows Holzenthal *et al.* (2007).

All type material of *Antipodoecia turneri* is lodged in the British Museum of Natural History, London, United Kingdom (BMNH). Specimens that we examined are lodged in the Museum of Victoria, Australia. Abbreviations used in the material examined section are: M, male; F, female; P, pupa; L, larva. Examined larval and pupal specimens of *Anomalopsyche minuta* (Schmid 1957) and *Contulma penai* Holzenthal & Flint 1995 are lodged in the National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, United States of America.

Specimens were submitted to The Barcode of Life Data Systems (BOLD) for sequencing of the CO1 gene. These sequences are available at <http://www.boldsystems.org>.

Taxonomy

Genus *Antipodoecia* Mosely 1934

(Figs 1–24, 27)

Diagnosis. The following combination of characters is unique in Trichoptera: The small pointed forewings each have no discoidal cell and forks I, II, and V only, and an unusual notch in the anterior margin at about 2/3 length. On the head, ocelli are absent; the male maxillary palps are held in front of the face and each have two to four segments. The female is distinctive with a very broad and posteriorly projected abdominal sternite VIII, which is heavily setose and has strong, prominent, anterolaterally projected apodemes. In the pupa, the mandibles have an unusual apical whip-like filament and there are no swimming fringes on the legs. The larval head has a strong, beaded carina which almost encircles the head, and multibranched, very short and fine secondary setae. The presence of paired tentorial pits on the frontoclypeus is unusual. The mandibles are scoop-shaped, each with a brush of long setae mesally. The pronotum also has a strong, beaded carina like that on the head and a strong projection on each anterolateral corner. The anal claws each have a dorsal comb of 5 to 9 teeth. A lateral row of about 10 bifid processes is present on each side of abdominal segment VIII. The larval case has a posterior closure membrane which includes an aperture overhung by a dorsally protruding canopy of silk.

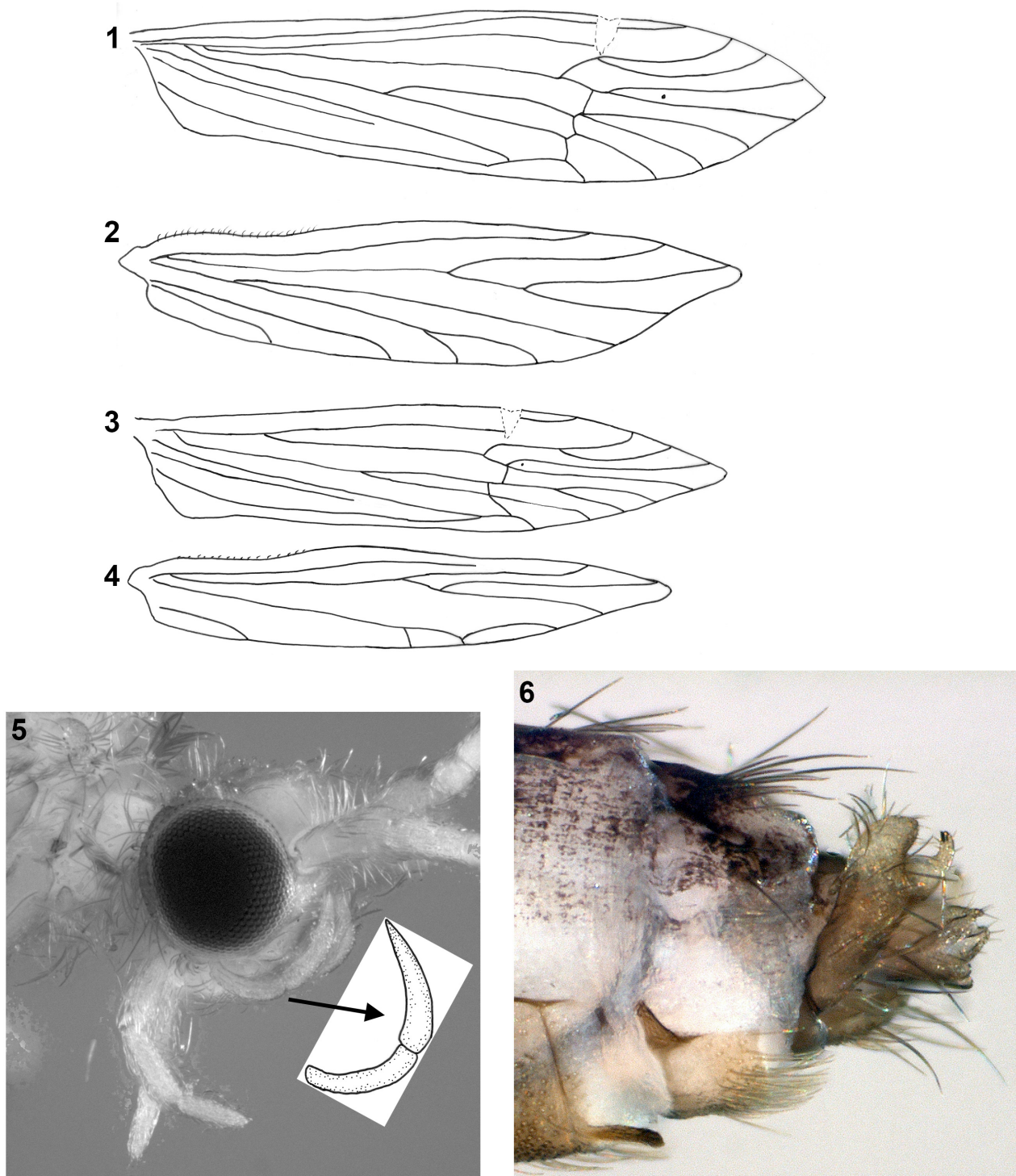
Description. Adult. Small, length of each forewing 2.9 to 4 mm. Head with ocelli absent; antennae about as long as forewings, scape cylindrical, about twice as long as wide; frontal setal warts large, ovoid; anteromesal warts separate, subtriangular; posterior setal warts large, oval; male maxillary palps each 2-, 3-, or 4-segmented (3-segmented most common), palps curved and held in front of face (Fig. 5), female maxillary palps each 5-segmented; labial palps each 3-segmented in both sexes. Thorax with pronotal warts transversely elongate, extending almost to lateral margin; mesoscutal setal warts small and indistinct or absent; scutellum with single,

large dome-shaped wart. Forewings pale brown, sometimes with pale patches; slender, apically pointed, each with distinct notch at about 2/3 length, paler opaque area immediately posterior to notch extending to vein R; forks I, II, and V present, sessile or with footstalks; thyridial cell present, discoidal and median cells absent (Figs 1, 3). Hind wings more slender, apically pointed, each with fringe of setae on posterior margin, length of setae about equal to width of wing; wing venation reduced, no cells present, forks II and V present (Figs 2, 4). Wings similar in both sexes, fewer complete veins in specimens from far northern Queensland (Figs 3, 4). Tibial spurs 2:2:4; mid legs each with row of short, dark, relatively evenly spaced spines on femur and tibia, first 4 segments of tarsus each with 3 short, dark, apical spines; fore- and hind legs with short, dark spines on tarsi only, arranged as on mid leg. Abdomen with sternite VII bearing sclerotised medial projection on posterior margin, projection shorter in females, size and shape possibly species specific. Male segment X broad, apically excised, with pair of narrow finger-like lateral projections near base (absent from some specimens in southern NSW); phallus slightly bifurcate apically; superior appendages absent; inferior appendages broad and bifurcate, upper branch broad with flat surface facing lower branch, lower branch narrow with distinctive dark tip, apparently articulating with upper branch (Fig. 6). Female abdominal sternite VIII broad, posteriorly projected, heavily setose, with strong anterolateral sclerotised apodemes, probably used as support when carrying egg mass (Figs 8, 9, 10). Tergite IX with sclerotisation variable, strongest on anterior margin and posterolateral projections and their basal depressions, membranous ventrally, numerous short pale setae posteriorly, longer on projections, dense in depressions; with small dorsal pleurites close to anterior margin of tergite IX, (Figs 7, 8, 9, 10). Sternum IX membranous with numerous small setae near dorsal margin. Tergite IX displaced under tergite VIII after deposition of egg masses (Fig. 10). Vaginal apparatus highly membranous with thin, twisted, and bifurcate sclerite, the prongs deeper ventrally (Fig. 11). Vaginal apparatus uniform (though small number of specimens examined).

Pupa. Labrum semicircular with 3 dorsal setae in each of anterolateral and basolateral corners (Fig. 12); pair of strongly developed tentorial pits posterior to labrum; mandibles broad and deep basally, each narrowing and dorsoventrally flattened in apical half, inner margin without teeth but very finely serrate, apex attenuate, slender and whip-like (Fig. 13); antennae reaching apex of abdominal segment VII. Wing pads reaching apex of abdominal segment VI; legs without swimming fringes. Abdomen (Fig. 14) without gills or setal fringe; anterior hook plates on segments III–VI (each plate usually with 2 hooks) and posterior hook plates on segment V (each plate rectangular, usually 2 hooks adjacent to posterior margin); anal processes long, slender and recurved, each with single long seta just before midlength; very small spicules apparently present over much of body surface but difficult to see when body darkly pigmented.

Larva. Small, length of final instar 5 mm or less (Fig. 15). Head round in dorsal view (Fig. 17) with strongly developed carina almost encircling head (Fig. 27); carina strongly beaded, particularly anterior to eyes; antennae very small, each located below carina about halfway between eye and anterior margin of head capsule (Figs 18, 27); frontoclypeus variable in shape; paired tentorial pits on frontoclypeus (Fig. 20); head sculptured with numerous small round tubercles; very short and delicate multibranched secondary setae interspersed between tubercles, setae longer in tubercle-free area toward anterior margin (Fig. 21); robust unbranched secondary setae along front margin of frontoclypeus; ventral apotome short equilateral triangle, extending to occipital margin; ventral apotome and abutting margins of genae very short relative to dorsal length of head capsule (Fig. 18). Pronotum heavily sclerotised; each lateral margin with strong, beaded carina extending from midline near posterior margin and terminating in long, apically acute anterolateral projection somewhat flattened dorsoventrally (Figs 15, 27); many short unbranched secondary setae, mostly lateral and along carina and anterior margin; tubercles and delicate multibranched secondary setae also present. Mesonotum moderately sclerotised with numerous short secondary setae (Fig. 17). Metanotum weakly sclerotised bearing few short setae (Fig. 17). Legs moderately setose, midleg slightly longer than foreleg, hind leg clearly longer than midleg (Fig. 16). Abdominal segment I with dorsal hump low; lateral humps inconspicuous, each bearing narrow oblique pad of very short modified setae (Figs 15, 22). Abdomen without gills or lateral setal fringe; lateral row of about 10 bifid spicules on each side of abdominal segment VIII (Fig. 15); tergum IX without sclerite, with 4 long and 6–8 fine short setae; anal claws, ventral sole plate, and lateral sclerite all small, with long thin sclerite extending ventrally from near base of each sole plate (Fig. 15); anal claw each with series of 5 to 9 accessory dorsal teeth (Fig. 19).

Case. Constructed of sand grains, cylindrical, gently tapered and slightly curved (Fig. 23); posterior end with silk closure membrane including aperture overhung dorsally by protruding canopy of silk (Fig. 24).



FIGURES 1–6. *Antipodoecia* sp. 1–4, adult female: 1, right forewing, dorsal, Leura, NSW; 2, right hind wing, dorsal, Leura, NSW; 3, right forewing, dorsal, North Queensland (NQ); 4, right hind wing, dorsal, NQ. 5–6, adult male: 5, head, right lateral, right maxillary palp enlarged, NQ; 6, adult male, genitalia, left lateral, NE New South Wales.

Type material. Holotype: male, New South Wales, Ebor, 10 & 12 Jan. 1916, R. J. Tillyard (BMNH, balsam preparation). Paratypes: 3 males, collected with holotype (BMNH) (Types not examined).

Material Examined. *Queensland.* 2F, Carron Ck, Kirrama State Forest, Apr 1993, G. Theischinger; 3M, 4F, Camp Creek tributary, Mt Spec State Forest, five dates 12 Dec 1993 to 23 Apr 1994, A.L.Sheldon; 1M, 5F, un-named creek Paluma Dam Rd, Mt Spec State Forest, 31 Oct 1993 and 17 Apr 1994, A.L. Sheldon; 1F, un-named creek “cascade”, Mt Spec State Forest, 17 Mar 1994, A.L. Sheldon; 1M, 4F, Birthday Ck below falls, Mt Spec State Forest, 17 and 23 Mar 1994, A.L. Sheldon; 1F Birthday Ck 3.5 km WNW of Paluma, 17 Feb 1990, R. St Clair; 1M, 1F, Dalrymple Ck, near Eungella, 3 Apr 1993, G. Theischinger; 1F, Carnarvon Gorge, 12 Nov 1990, G. Theischinger ; 1F, Brown Falls, Killarney, 13 Oct 1973, A. Neboiss; 7M, 3F, Queen Mary Falls, Killarney, 12 Oct 1973, A. Neboiss; 1M, 1F, Brown River at Falls, near Killarney, 25 Oct 1981, A. Wells and Carter; 197L, Dawson Creek, Mount Nebo, 2 Mar 1973, collector unknown; 2L, Purlingbrook Falls, Springbrook, 8 Feb 1973, collector unknown; 3L, Mt Barney Creek, Mount Barney Nat Park, 13 Jun 1997, J. Jackson; 7L, Stony Creek, Conondale Ranges, 11 Jun 1997, J. Jackson; 1M, 6F Girraween National Park, near Wyberba, 10 Oct 1973, A. Neboiss. *New South Wales.* 1M, Boonoo Boonoo R, upstream of Falls, 11 Oct 1973, A. Neboiss; 2M, 1P, Korrumbyn Ck, eastern slopes of Mt Warning, 29 Jul 1988, A. Neboiss; 1M, 6F, Terania Ck, N of Lismore, 21 Jan 1986, G. Theischinger; 1F, Dawson Springs, Mt Kaputar National Park, 9 Oct 1973, A. Neboiss; 3L, Upper Styx River, 21 Feb 1966, E.F. Riek; 1L, Upper Allyn River, 16 Feb 1966, E.F. Riek; 2L, Platypus Creek, site BELL16, 11 Oct 1995, Monitoring River Health Initiative (MRHI); 2L, Manning River, Henrys Bridge, 8 Apr 1998, MRHI; 7L, Manning River, Pheasant Creek Road, 3 Dec 2007, A. Glaister, J. Dean & R. St Clair; 6L, Allyn River, 0.6 km u/s Ladies Well, 28 Nov 2007, A. Glaister, J. Dean & R. St Clair; 2M, Gloucester Tops, 19 Nov to 4 Dec 1988, D. Bickel; 1F, Jerusalem Falls, near Karuah, 6 Dec 1988, G. Theischinger; 2L, Caparra Creek, Caparra Hut, 14 Oct 1998, MRHI; 1L, Brindle Creek, Brindle, 9 Oct 1998, MRHI; 10L, tributary of Forbes River, South Plateau Rd, 3 Oct 1995, MRHI; 1F, Blue Mountains, Leura, Leura Cascades, 1 Jan 1979, A. Wells; 13M, Blue Mountains, Leura, Leura Cascades, 12 Dec 1984, A. Wells; 3M, Blue Mountains, Leura, Lyre Bird Dell, 12 Dec 1984, A. Wells; 10M, Blue Mountains, Leura below falls, 13 Dec 1984, A. Wells; 2P, 14L, Blue Mountains, Bridal Veil Falls, 27 Dec 1978, A. Wells; 5L, Blue Mountains, Wentworth Falls, 31 Dec 1984, A. Wells; 1M, 1F, Undercliffe Falls, 25 km E of Stanthorpe, 11 Nov 1973, A. Neboiss; 9M, 3F, Undercliffe Falls, 12 km E of Liston, 24 Oct 1981, A. Wells and ?. Carter, 24 Oct 1981; 5L Wentworth Falls, 31 Dec 1978, A. Wells; 1F, Apsley R, 29 Oct 1981, A. Wells and Carter; 1F, Coombadja Ck, Washpool State Forest, 5 Jan 1986, G. Theischinger; 6M, 5F, Bargo R, 10 km SW of Picton, 31 Dec 1971, A. Neboiss; 1M, Bundanoon, Sep 1983, G. Theischinger. *Victoria.* 1M, Erskine Falls, 18 Feb 1984, G. Theischinger; 20M, 1F, 8P, 18L, Steavensons Falls, Upper Gellibrand River, Otways, 20 Jan 1982, A. Neboiss and A. Wells; 3M, 1F, Carisbrook Falls, Otways, 23 Jan 1953, A. Neboiss; 4M, 4F, Masons Falls, Kinglake National Park, 15 Feb 1953, A. Neboiss; 1M, Toorong Falls, 7 km NE of Noojee, 27 Nov 1981, J. Morse and A. Neboiss; 1L, Fork Ck, Mt Stirling, 16 Apr 1985, R. Morely; 1L, Falls Ck, Mt Stirling 7 Apr 1987, collector unknown; 1F, Mt Feathertop, 12 Feb 1984, G. Theischinger; 1F, Falls Creek, Bogong High Plains, 26 Jan 1960, A. Neboiss; 3M, 4F, Winnots Ck, Cann Valley, 21 Mar 1977, A. Neboiss. *Tasmania.* 4L, near Lake Gordon, 12 Nov 1987, J. Jackson; 2L, Scotts Peak Dam Rd, 6 Oct 1987, J. Jackson.

Genetic results. In September 2018, data were available on BOLD (<http://www.boldsystems.org>) for 14 specimens of Antipodoeciidae. Nine different Barcode Index Numbers (BINs) were assigned by BOLD. Specimens are assigned a unique BIN number for clusters considered to represent a single species. The neighbour-joining, taxon ID tree produced on the BOLD website showed genetic distances between these BIN numbers were very large (Fig. 30). Two pairs of BIN numbers were separated by just under 5% but most were 10% to 30% different. Such distances are generally indicative of different genera and yet the morphology of the males is almost uniform. These distances between BIN numbers are similar to distances between different species of *Contulma*.

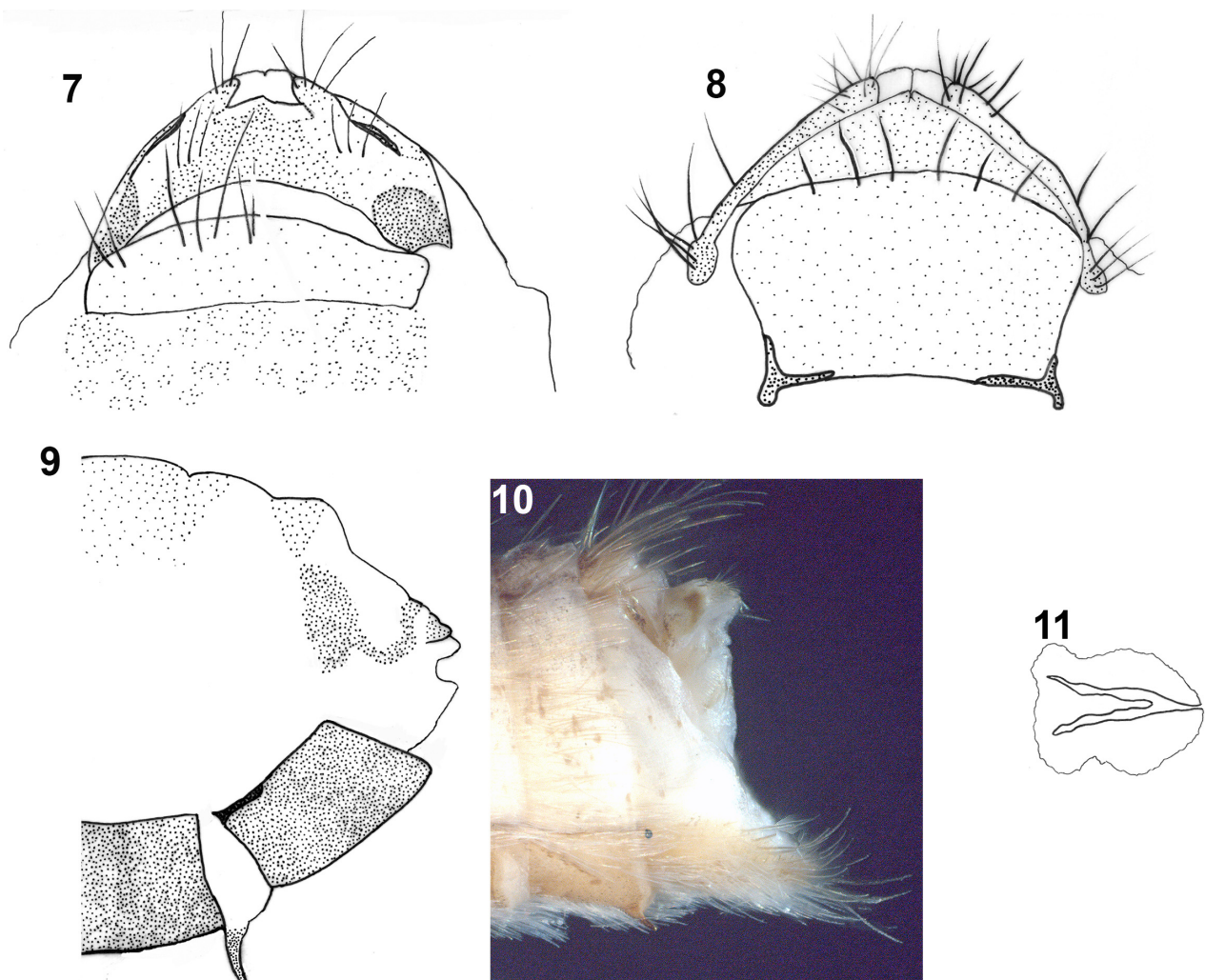
The type locality of *Antipodoecia turneri* is listed as “Ebor, New South Wales”. As none of the specimens with barcodes were collected near the type locality, we have not identified any of our specimens as *A. turneri*. Three specimens are labelled *A. turneri* in Fig. 30, but are unlikely to be that species.

Discussion

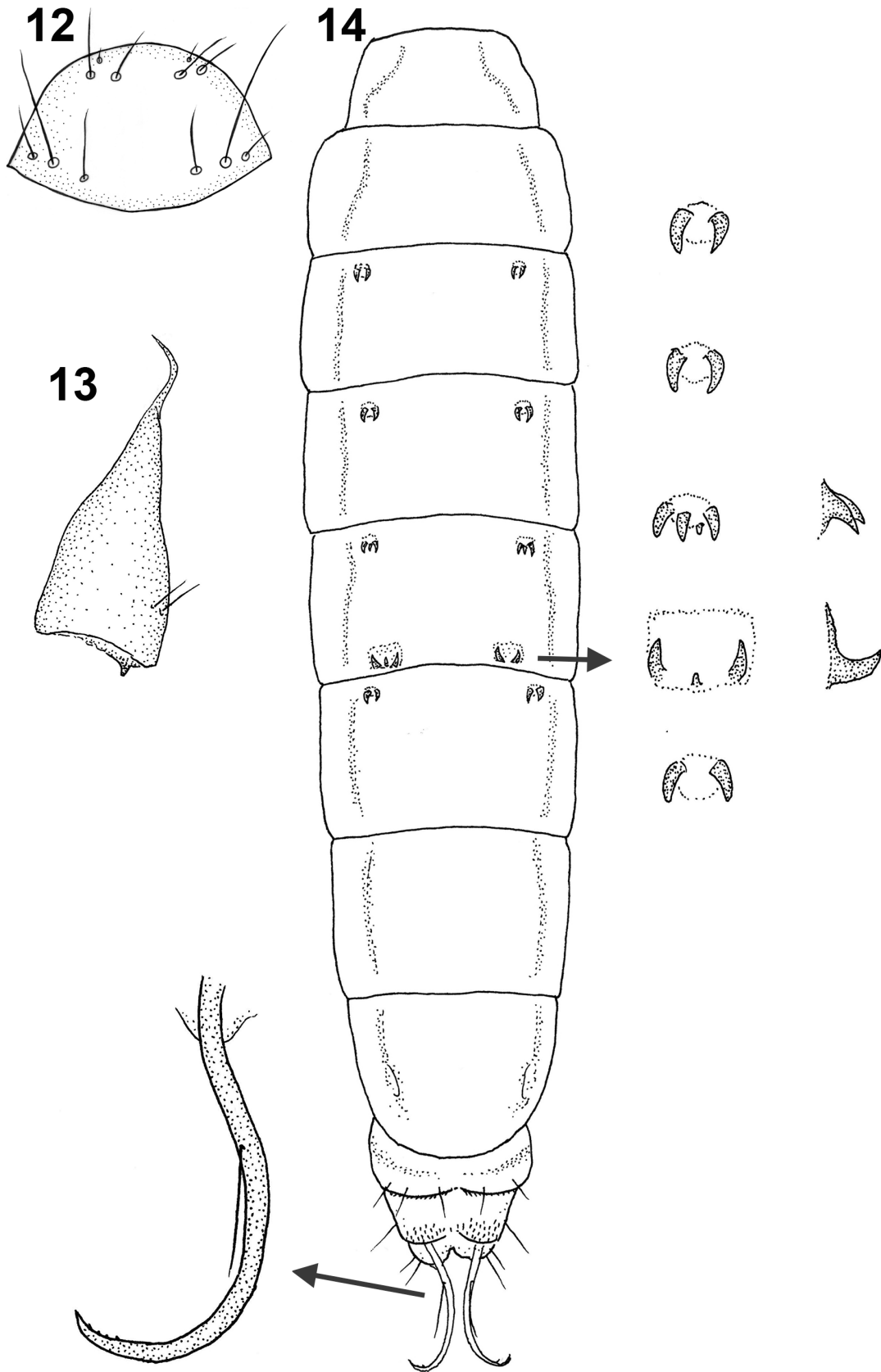
Status of *Antipodoecia turneri*. Subtle morphological variations in the male genitalia is a feature of the monotypic genus *Antipodoecia*. Morphological differences in females and larvae, together with large genetic differences in the COI gene, are clearly indicative of multiple species. The generic description given above applies to all specimens;

those morphological characters which are variable, and therefore potentially of value for species-level taxonomy, are reported as a range of values to include all examined specimens. These characters include the shape and venation of the adult wings, the number of maxillary palp segments in the male, subtle differences in male genitalia, the shape of the process on abdominal sternum VII of the male, the shape of female sternite VIII, the shape of the larval frontoclypeus and the number of accessory teeth on the anal claws of the larva. A full taxonomic revision of the genus will require a search for co-occurring variations of morphological and other organismal characters, possibly supported by DNA studies, research that is beyond the scope of the present work.

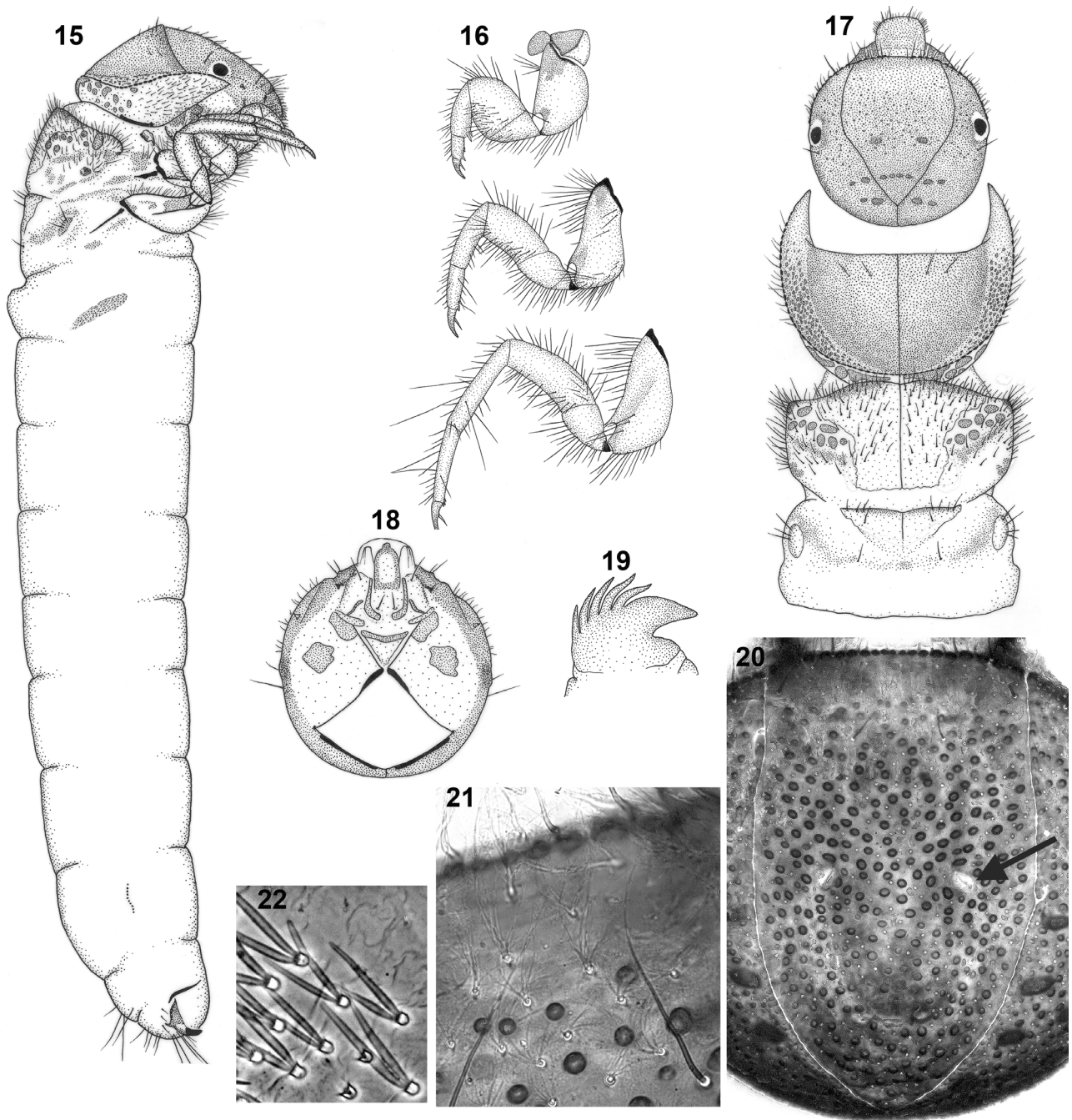
Phylogenetic position of *Antipodoecia*. Previous phylogenetic analyses of the Sericostomatoidea were reviewed by Johanson *et al.* (2016). Many did not include Antipodoeciidae and some, unfortunately, have used the limited and partially incorrect data provided by Neboiss (1991). The detailed genetic analysis of Johanson *et al.* (2016) provided two outcomes for Antipodoeciidae. A reduced data set of 90 taxa with sequences for 5 different genes identified Antipodoeciidae as a sister group to the Family Beraeidae. This was their preferred hypothesis. Using a data set of 149 taxa with sequences available for between 1 and 5 genes for each taxon, Antipodoeciidae and Anomalopsychidae were identified as sister groups. While improvements are constantly being made in the interpretation of DNA information, understanding of the relationships within the Sericostomatidae is not yet fully resolved. The combination of morphological and genetic data should help resolve the relationships better than either method on their own. We provide data for females and immatures of Antipodoeciidae. The striking morphological similarity, particularly of the immature stages, is compelling. Calor and Holzenthal (2008) gave an example of the difference that incorporating larval data can have on the results of phylogenetic analysis.



FIGURES 7–11. *Antipodoecia* sp. 7–9, adult female genitalia before deposition of eggs, NQ: 7, dorsal; 8, ventral 9, lateral. 10, adult female genitalia lateral after carrying egg mass, Victoria. 11, adult female vaginal apparatus ventral, NQ.



FIGURES 12–14. *Antipodoecia* sp. 12–14, pupa, Leura, NSW. 12, labrum, dorsal; 13, right mandible, dorsal; 14, abdomen, dorsal, hook plates and left anal process enlarged.

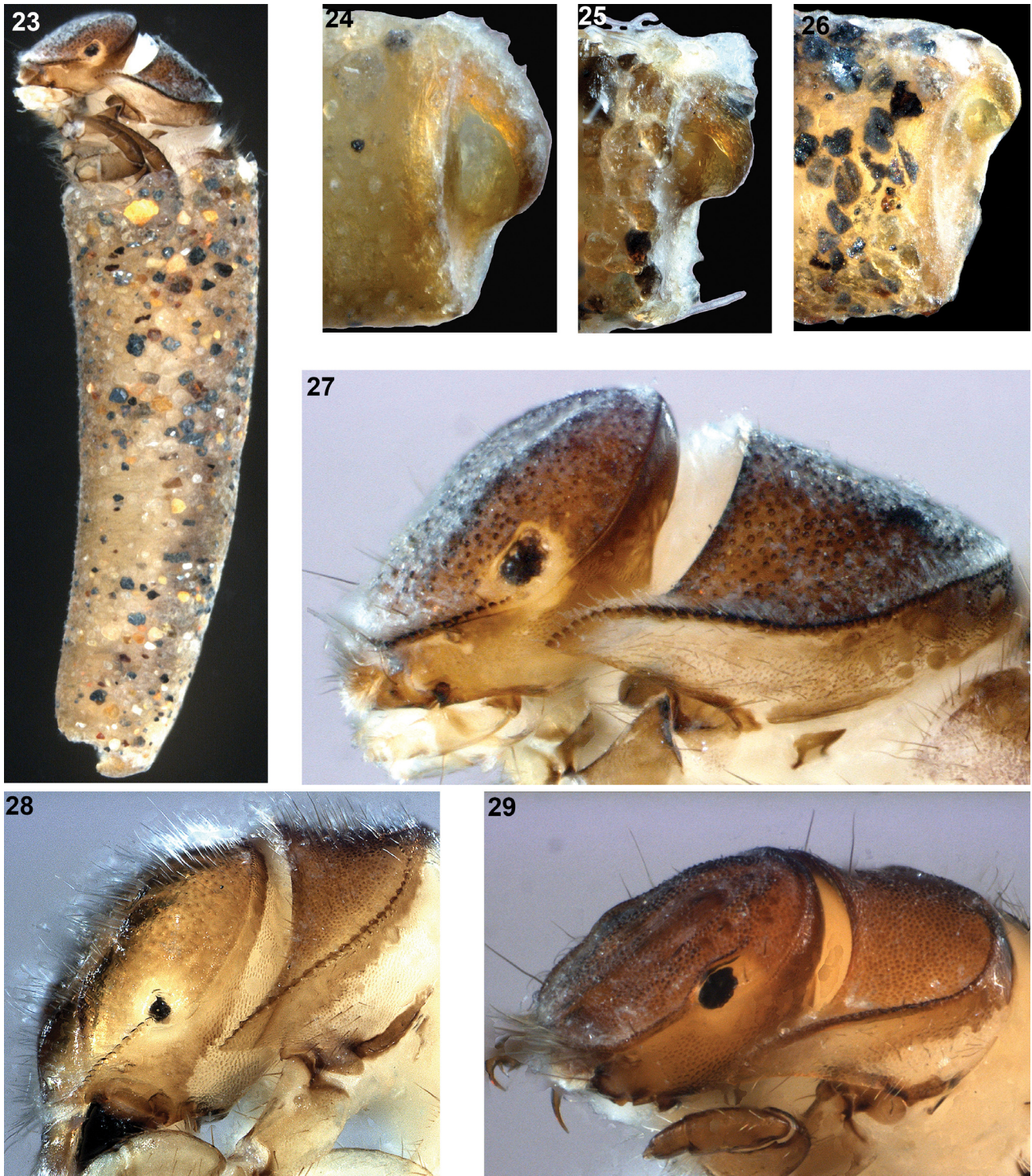


FIGURES 15–22. *Antipodoecia* sp. larva. 15, habitus, right lateral; 16, left legs, posterior (lateral); 17, head and thorax, dorsal; 18, head, ventral; 19, right anal claw, mesal; 20, frontoclypeus, dorsal, showing tentorial pits; 21, secondary setae on frontoclypeus, dorsal; 22, modified setae of friction pad of right lateral hump on abdominal segment I, right lateral. 15–19: Leura, New South Wales (NSW); 21, 22: NE NSW.

Flint (1981), when describing *Anomalopsyche*, suggested that it was most closely related to the families Beraeidae and Helicophidae and possibly also Antipodoeciidae, based on adult male morphology. At that time, he had information available only on the adult males of *Antipodoecia*, so that while he could recognise that the two genera were possibly closely related he had no reason to place them in the same family. We concur that Anomalopsychidae is closely related to both Beraeidae and Helicophidae (and other Sericostomatoidea) but believe that there is an even stronger relationship with Antipodoeciidae. The family Anomalopsychidae is restricted to the Neotropics and includes two genera, *Anomalopsyche* and *Contulma*, while *Antipodoecia* is the only genus in the family Antipodoeciidae and is restricted to Australia.

An obvious difference between the two families is the presence of ocelli in Anomalopsychidae. This is the only

family within the Sericostomatoidea which possesses ocelli, although Flint (1981) indicated that the “superfamily is primitively ocellate.” Flint (1981) also acknowledged that ocelli have been commonly lost in evolution and that it would not be surprising if the closest relatives of Anomalopsycheidae were without ocelli. We suggest that this is a generic character. The unrelated family Hydroptilidae includes ocellate and non-ocellate genera so it is possible for a family to show both character states.



FIGURES 23–29. Antipodoeciidae gen. spp. larvae and cases. 23, species of *Antipodoecia* Mosely 1934, Leura, New South Wales (NSW), larva and case, left lateral. 24–26, posterior closure membranes of larval cases, left posterolateral oblique: 24, *Antipodoecia* sp., Leura, NSW; 25, *Contulma penai* Holzenthal & Flint 1995, Ecuador; 26, *Anomalopsyche minuta* Schmid 1957, Argentina. 27–29, larval head and prothorax, left anterolateral oblique: 27, *Antipodoecia* sp., Leura, NSW; 28, *Contulma penai*, Ecuador; 29, *Anomalopsyche minuta*, Argentina.

Flint (1981) also highlighted the reduction in the number of maxillary palp segments and the more complete wing venation of *Anomalopsyche*. Maxillary palp segments are also reduced in *Antipodoecia* but not *Contulma*. Adults of *Anomalopsyche* and *Contulma* differ from *Antipodoecia* in having a discoidal cell and forks I, II, III, and V in the forewing (*Antipodoecia* has no discoidal cell and forks I, II, and V only). We interpret the venation differently from Mosely and Kimmins (1953), who described the forewing as having forks I, II, and III. In the hind wing, *Antipodoecia* is similar to *Contulma* in that veins R₂, R₃, and R₄ are fused and only forks II and V are present. This contrasts with *Anomalopsyche* where veins R₃ and R₄ are fused and forks I, II, and V are present.

The females also give a strong indication that the three genera share a common ancestor. The reduced and simple structure of the female genitalia and the enlarged, heavily setose sternum VIII have been identified as a synapomorphy for the family Anomalopsychidae (Flint 1981; Holzenthal & Flint 1995). In the South American genera, sternum VIII is large with prominent anterolaterally directed apodemes, there is a membranous connection to sternum IX, and the membranes of the pleural region are large. The abdomen is capable of distending greatly to accommodate the egg sac. Females of *Antipodoecia* also have reduced genitalia and an enlarged, setose sternum VIII with strongly developed anterolateral apodemes. The shape of sternum VIII in *Antipodoecia* is quite variable and appears to be an important species-specific character. In *Contulma* females, internal sclerites are complex and species specific. The equivalent in Antipodoeciidae are not particularly complex or variable, possibly related to the low degree of variation in male genitalia.

Pupae of *Antipodoecia* also show a close relationship with Anomalopsychidae. All three genera lack both a lateral fringe of setae on the abdomen and also a fringe of swimming hairs on the legs. The only other family with some species lacking fringes on both the abdomen and the legs is Beraeidae, although there are an additional 2 or 3 families which lack fringes at one or the other of these locations. The highly unusual whip-like attenuate apex of the mandible of *Antipodoecia* previously has been recorded only in the family Anomalopsychidae and the unrelated families Psychomyiidae and Odontoceridae. The pupa of *Antipodoecia* also has numerous minute spicules on the dorsal surface of much of the abdomen, a feature which is shared with species of Anomalopsychidae. The slender apical appendages, which curve upwards and bear one or several long setae in the basal third, are also distinctive and very similar to those of *Contulma*.

The larva of *Antipodoecia* is highly unusual and shares many oddities with larvae of the Anomalopsychidae. Particularly striking is the combination of strongly developed carinae on the head and pronotum, the strong anterolateral projections of the pronotal carinae, and the row of sclerotised protuberances, or beads, aligned along each carina (Figs 27–29). This synapomorphy appears to be unique to *Antipodoecia* and the two anomalopsychid genera *Anomalopsyche* and *Contulma*. The three genera exhibit, in addition, close similarities in their head capsules: the upper surface, including the frontoclypeus, is sculptured with small protuberances and bears numerous secondary setae (which are small and inconspicuous in *Antipodoecia* and *Anomalopsyche* and usually quite long in *Contulma*); the anterior margin of the frontoclypeus and the anterolateral margins of the head capsule bear a relatively dense row of long secondary setae (a feature which, as far as we are aware, is found elsewhere in the Sericostomatoidea only in several genera of Calocidae and Conoesucidae); the ventral apotome is an equilateral triangle, often weakly sclerotised, the distance from the anterior margin of the apotome to the apex at the occipital margin is very short relative to the length of the head capsule. An additional larval character of *Antipodoecia*, the presence of a comb of dorsal teeth on the anal claw, has been recorded for larvae of only the families Antipodoeciidae, Anomalopsychidae, Helicopsychidae, Petrothrincidae and Barbarochthonidae. In addition, Antipodoeciidae and Anomalopsychidae share as a synapomorphy a larval case with a posterior silk closure membrane which has an oval dorsal aperture overhung by a protruding canopy of silk (Figs 24–26). Posterior closure membranes are rare in trichopteran larval cases. Larval cases of the family Helicophidae are somewhat similar, but the aperture in Helicophidae is overhung dorsally by the case material rather than a discrete silken canopy formed from the posterior closure membrane.

Due to the unusual and striking morphological similarities of females, pupa and larvae, we propose that the genera *Antipodoecia*, *Anomalopsyche*, and *Contulma* are a monophyletic group sharing an immediate common ancestor. This is evidenced by at least 5 uniquely shared synapomorphies and by other unusual similarities that have not been well recorded in the Sericostomatoidea and may eventually also prove to be synapomorphous.

Antipodoecia, *Anomalopsyche* and *Contulma* share the following synapomorphies: Female with reduced segments IX and X and an enlarged sternum VIII with prominent anterolaterally directed apodemes; pupal mandibles each tapering to a slender apical process; larva with strongly developed carinae on the head and

pronotum, strong anterolateral projections of the transverse pronotal carina and a row of sclerotised protuberances or beads aligned along each carina; larval frontoclypeus sculptured with small protuberances and bearing numerous secondary setae; larval case with its posterior closure membrane modified to form a silken canopy overhanging the oval aperture.

The following character states are shared by the three genera and either have not been well examined in other Sericostomatoidea or are shared with at least one other family: Surface of pupal abdomen with minute spicules; pupa with setal swimming fringes absent from body and all legs, anal processes with distinct shape and setation; larva with anterior margin of frontoclypeus and anterolateral margins of the head capsule bearing a relatively dense row of long secondary setae; larva with a comb of accessory teeth on each anal claw.

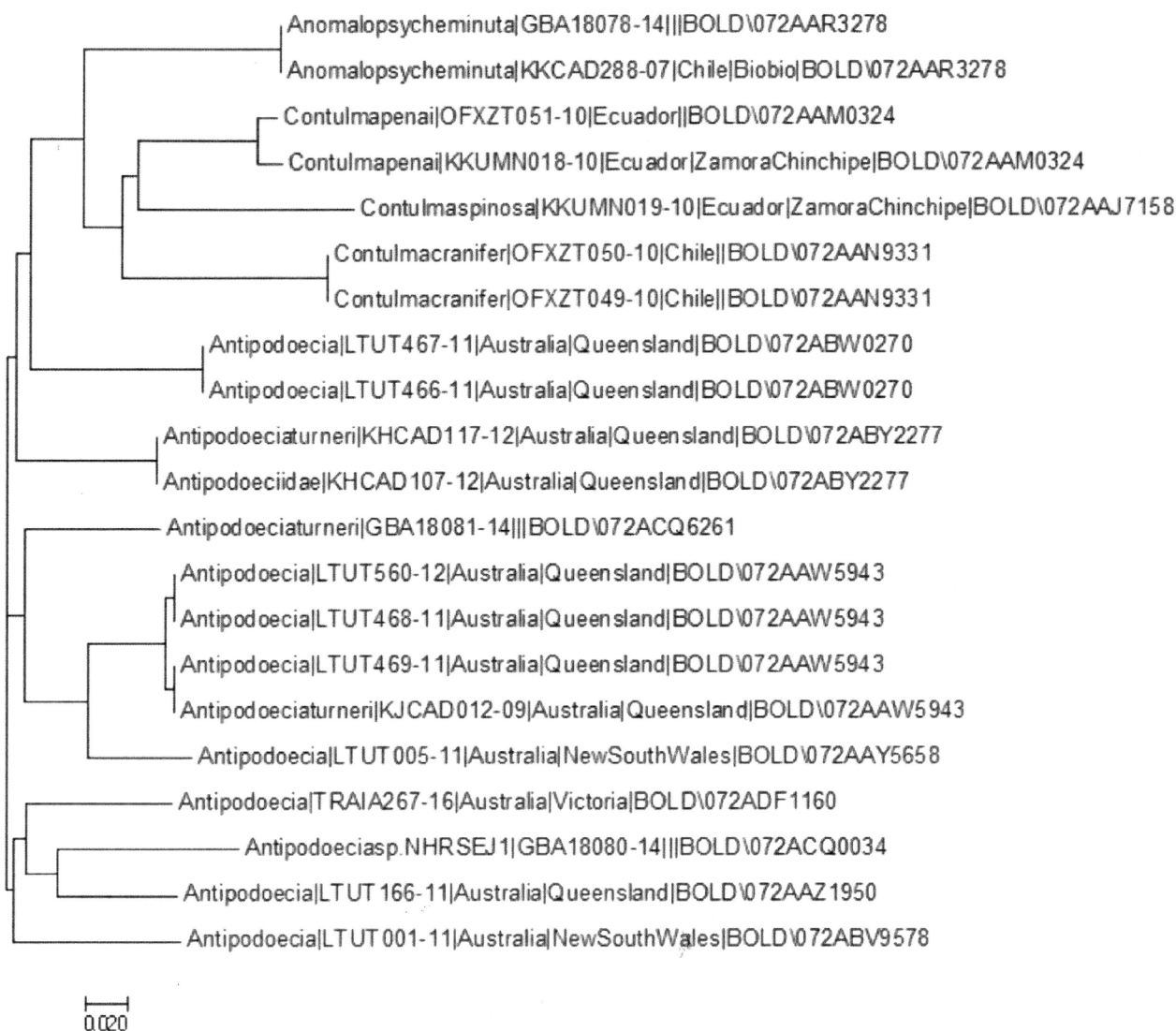


FIGURE 30. COI-5P Neighbour-joining tree for Antipodoeciidae and Anomalopsychidae using Kimura 2 Distance Model, with pairwise deletion and MUSCLE (Edgar 2004) alignment. Scale bar is a divergence in genetic distance of 0.02.

Although *Antipodoecia* shares some characters uniquely with *Anomalopsyche* and others uniquely with *Contulma*, monophyly of the three genera is clear. This hypothesis of monophyly leads to the conclusion that Anomalopsychidae **new synonym** is a junior synonym of Antipodoeciidae. The resulting revised family diagnosis for Antipodoeciidae is as follows: Adults with ocelli present or absent; male maxillary palps each 2- to 5-segmented, sometimes held in front of the face; forewings each with discoidal cell present or absent, forks I, II, and V present, fork III present or absent; hind wings each with vein R having 3 or 4 branches, vein M unbranched, vein Cu1 with 2 branches; tibial spurs 2,2,4; female with abdominal sternite VIII enlarged, strongly setose, with prominent anterolaterally directed apodemes; pupa with mandibles each tapering to a slender apical process, legs

without swimming fringes; minute spicules on at least part of the body surface; pupa with anal processes slender, shallowly curved, each with one to few fine setae; larva with weak to strong beaded carina on head, pronotum with anterolateral corners strongly projected and with a strong beaded transverse carina; abdomen without lateral fringe of setae; row of lateral spicules on segment VIII present or absent; anal claws each with row or comb of dorsal teeth; case closure membrane modified to form a silken canopy overhanging oval aperture.

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References

- Calor, A.R. & Holzenthal, R.W. (2008) Phylogeny of Grumichellini Morse, 1981 (Trichoptera: Leptoceridae) with the description of a new genus from southeastern Peru. *Aquatic Insects*, 30, 245–259.
<https://doi.org/10.1080/01650420802334087>
- Dean, J.C. (2000) *Preliminary keys for the identification of Australian caddisfly larvae of the families Antipodoeciidae, Atriplectididae, Limnephilidae and Plectrotarsidae. Identification guide No. 31.* Cooperative Research Centre for Freshwater Ecology, Albury, 16 pp.
- Edgar, R.C. (2004) MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32, 1792–1797.
<https://doi.org/10.1093/nar/gkh340>
- Flint, O.S. Jr. (1981) Studies of Neotropical caddisflies, XXVII: Anomalopsychidae, a new family of Trichoptera. In: Moretti, G.P. (Ed.), *Proceedings of the 3rd International Symposium on Trichoptera. Series Entomologica. Vol 20.* Dr. W. Junk Publishers, The Hague, pp. 75–85.
https://doi.org/10.1007/978-94-009-8641-1_11
- Holzenthal, R.W. & Flint, O.S. Jr. (1995) Studies of Neotropical Caddisflies, LI: Systematics of the Neotropical caddisfly genus *Contulma* (Trichoptera: Anomalopsychidae). *Smithsonian Contributions to Zoology*, 575, 1–59.
<https://doi.org/10.5479/si.00810282.575>
- Holzenthal, R.W., Blahnik, R.J., Prather, A.L. & Kjer, K.M. (2007) Order Trichoptera Kirby, 1813 (Insecta), caddisflies. *Zootaxa*, 1668, 639–698.
- Johanson, K.A., Malm, T. & Espeland, M. (2016) Molecular phylogeny of Sericostomatoidea (Trichoptera) with the establishment of three new families. *Systematic Entomology*, 42, 240–266.
<https://doi.org/10.1111/syen.12209>
- Mosely, M.E. (1934) A new Australian caddis-fly (Trichoptera). *Entomologist, London*, 67, 178–180.
- Mosely, M.E. & Kimmins, D.E. (1953) *The Trichoptera (Caddis-flies) of Australia and New Zealand.* British Museum (Natural History), London. 550 pp.
- Neboiss, A. (1986) Atlas of Trichoptera of the SW Pacific-Australian Region. *Series Entomologica. Vol 37.* Dr W. Junk Publishers, The Hague.
- Neboiss, A. (1991) Trichoptera. In: CSIRO (Ed.), *The Insects of Australia, Second Edition.* Melbourne University Press, Carlton, pp. 787–816.
- Neboiss, A. (2002) A family problem with placement of *Heloccabus buccinatus* gen. & sp. n., an Australian caddisfly (Insecta: Trichoptera). In: Mey, W. (Ed.), *Proceedings of the 10th International Symposium on Trichoptera. Nova Supplementa Entomologica. Vol 15.* Goecke & Evers, Keltern, pp. 195–204.
- Ross, H.H. (1967) The evolution and past dispersal of Trichoptera. *Annual Review of Entomology*, 12, 169–206.
<https://doi.org/10.1146/annurev.en.12.010167.001125>
- Schmid, F. (1957) Contribution à l'étude des Trichoptères néotropicaux II (Trichoptera). *Beiträge zur Entomologie*, 7, 379–398, pls. 7–10.
- Scott, K.M.F. & de Moor, F.C. (1993) Three recently erected Trichoptera families from South Africa, the Hydrosalpingidae, Petrothrincidae and Barbarochthonidae (Integripalpia: Sericostomatoidea). *Annals of the Cape Provincial Museums, Natural History*, 18, 293–354.