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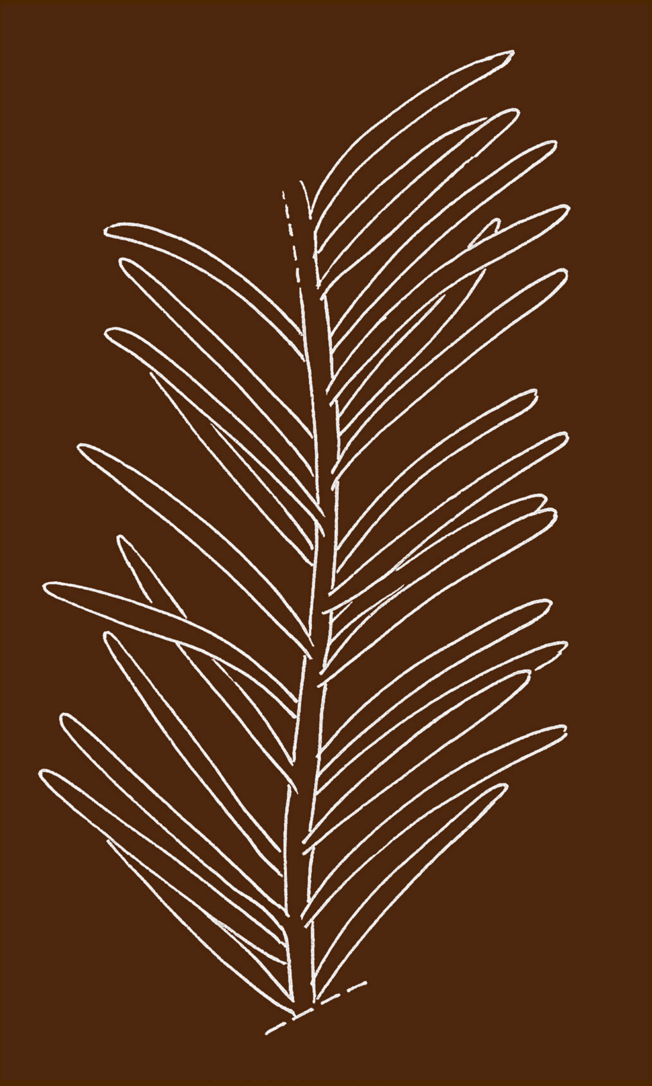
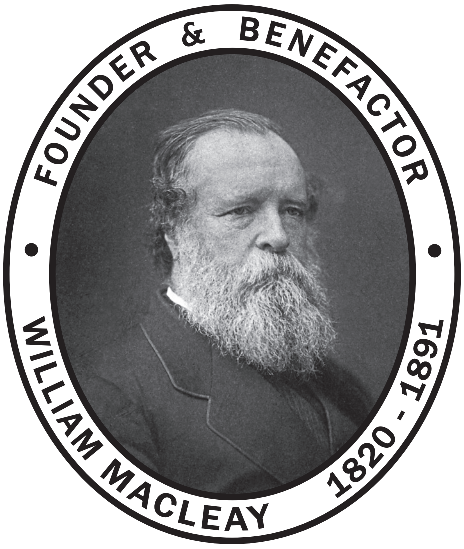
VOLUME 135



NATURAL HISTORY IN ALL ITS BRANCHES

THE LINNEAN SOCIETY OF NEW SOUTH WALES

ISSN 1839-7263



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Cover motif: Sketch of the *Rissikia media* fossil shown in Figure 6B in the paper by W.B.K. Holmes and H.M. Anderson, pages 55-76, this volume

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VOLUME 135
December 2013

Silurian Brachiopods from the Cappanana Formation East of Cooma, Southern New South Wales

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Strusz, D.L. (2012). Silurian brachiopods from the Cappanana Formation east of Cooma, southern New South Wales. *Proceedings of the Linnean Society of New South Wales* **135**: 1-17.

A collection of strongly tectonically distorted fossils from the Cappanana Formation east of Cooma, NSW, is treated using digital imagery and computer software to restore the better-preserved specimens to an approximation of their original shape and size, using previously published principles. The fauna is dominated by brachiopods, all as dissociated valves, but also includes some encrinurid trilobites and a few corals. Ten brachiopod species are recognised, of which seven - *Mesopholidostrophia bendeninensis, Morinorhynchus oepikensis*, cf. *Apopentamerus clarkei, Atrypa* cf. *duntroonensis, Atrypoidea australis, Howellella* aff. *elegans* and *Spirinella caecistriata* - are identical to, or closely comparable with, published species of late Wenlock to Ludlow age. Three taxa (*Coelospira* sp., a leptaenine and an eospiriferine) are very rare and could be new, but the material is insufficient, and restored images as obtained by the methods used here should not be used to erect new taxa. The fauna is enclosed in mudstone, probably a current-winnowed slump deposit, so the original environment cannot be determined.

Manuscript received 26 October 2012, accepted for publication 20 February 2013.

KEYWORDS: *Apopentamerus, Atrypa, Atrypoidea,* brachiopods, Cappanana Formation, distortion digitally removed, *Howellella*, Ludlow, *Mesopholidostrophia, Morinorhynchus* , *Spirinella*, Silurian, Wenlock.

INTRODUCTION

In 1999 the residents of ‘Lara’ property, 15 km east of Cooma, advised ANU geologists that abundant fossils had been turned up during regrading of the road west of the homestead. Dr Tim Munson (the then collections manager) and I visited the spot, and made a collection of the better preserved material, overwhelmingly brachiopods. Fossils in the Early Palaeozoic of southeastern New South Wales between Canberra and the Victorian border are generally moderately to strongly distorted. As many are in shales and thinly bedded muddy limestones, part of this distortion is a result of compaction, but the major component is tectonic, the result of at least one major compressional phase with consequent strong folding and faulting. In Canberra this distortion is much less, insufficient to make recognition of taxa difficult (see, e.g., Strusz 1984, 1985). This cannot be said of the region around Cooma, some 100 km to the south, an area further complicated by the formation of the Cooma Gneiss (part of the Murrumbidgee Batholith). Consequently, there have been very few taxa described from that region, and the ages of the various stratigraphic units are not well constrained. Distortion of the collected specimens is strong, as is weathering, but at the time of collecting the fauna was recognised as being clearly Silurian, and several taxa were considered comparable with those known from Canberra. The collection was therefore set aside until more was known of the better-preserved Silurian faunas in the Canberra - Yass region.

MATERIALS

The topographic map available to us at the time of collecting was the first edition Cooma 1:100 000 sheet of 1969, and this did not show ‘Lara’ homestead or all of its access road, so our estimate of the position was very approximate. Satellite imagery is now readily available, as is a more detailed topographic map (the Numeralla 1:25,000 sheet of 2001), and this allows

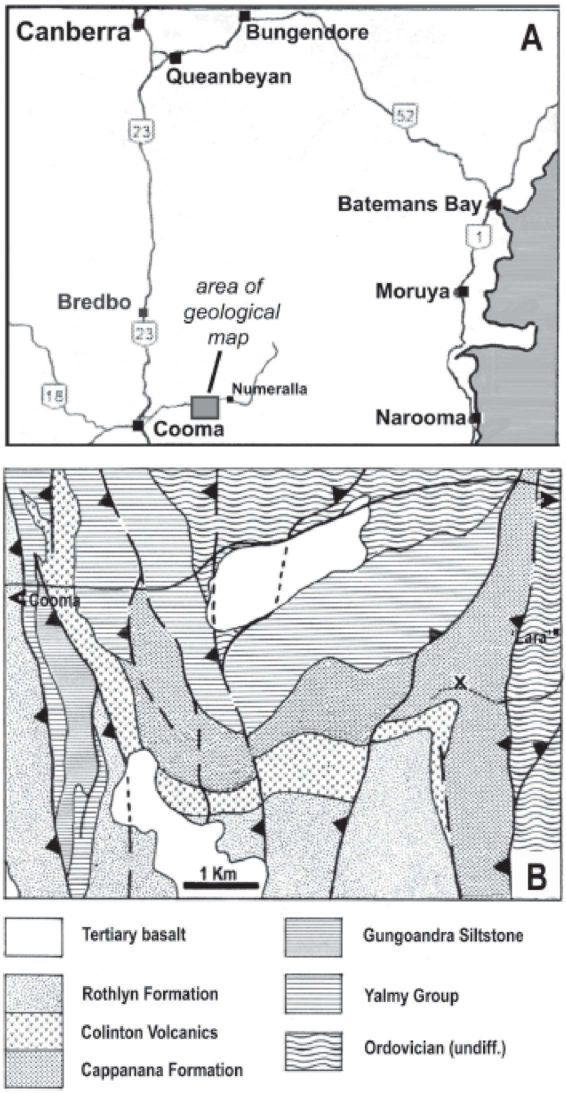

Figure 1. Location of the collection from near 'Lara' homestead, east of Cooma. A: regional map. B: geology in the vicinity of 'Lara' (derived from Lewis and Glen, 1995). The approximate position of the locality is marked by x. The undifferentiated Yalmy Group is considered to be laterally equivalent to the whole Bredbo Group (Cappanana Formation to Rothlyn Formation).

greater precision. The material came from the north side of the road on a curve, and is at approximately GA065.907. On the second edition of the Bega-Mallacoota 1:250 000 geological sheet (Lewis and Glen, 1995) this locality lies in a folded and faulted area within the Cappanana Formation (see Fig. 1). The fossils are preserved as moulds in soft, yellow- to buff-weathering pale olive-green mudstone; the extensive weathering has partly to completely obliterated fine detail. Some of the moulds are lined with clusters of small crystals of iron oxide - possibly derived from the overlying Colinton Volcanics - and limonitisation is heavy in some specimens. All the brachiopods occur as dissociated valves, the trilobites as detached parts (moults?). The valves of strophomenide and orthotetide taxa are generally parallel to the original bedding, but the more strongly biconvex atrypide and spiriferide valves can lie at moderate angles to that bedding. This means that initial compaction has had only a minor effect on the shape of the strophomenides and orthotetides, but more on the others. The appearance of the material - flat-lying weakly convex valves, more randomly oriented strongly convex valves, often in discrete layers - suggests current winnowing of soft, slumped sediment, and so the original depth inhabited by the fauna is uncertain.

PROCEDURES

Important in making reliable identifications of such strongly distorted fossils is a means to reconstruct their original appearance. Because of the fragility of the specimens from 'Lara' even after impregnation with acetone-diluted adhesive ('Tarzan's Grip' in this case), no attempt has been made to obtain latex casts, but the natural moulds, when carefully prepared, were generally quite sufficient. Specimens were photographed using a digital camera with x3 optical zoom, under a mix of natural and artificial light, without whitening. For the purposes of this paper, as fine detail is generally poorly preserved, colour has been retained. Removal of the effects of distortion followed methods outlined by Cooper (1990) and Rushton and Smith (1993), taking advantage of the digital tools available in Adobe Photoshop. In essence, the procedure is to determine the extent of distortion by determining the strain ellipse (i.e. a distorted initial circle), then calculate the factors to be applied to return that ellipse to circularity. These factors are then applied to images of individual fossils to restore their original shape.

Strain ellipse

Several slabs containing a number of fossils with unambiguous traces of their original hinge line and longitudinal axis of symmetry (or the equivalents in the case of trilobite cranidia) were photographed, taking care to include a linear scale. The images were then oriented with the trace of lineation horizontal. Prints were then used to analyse strain following Wellman's method (see Cooper 1990, pp. 323-324), with the 'control line' parallel to the lineation. The

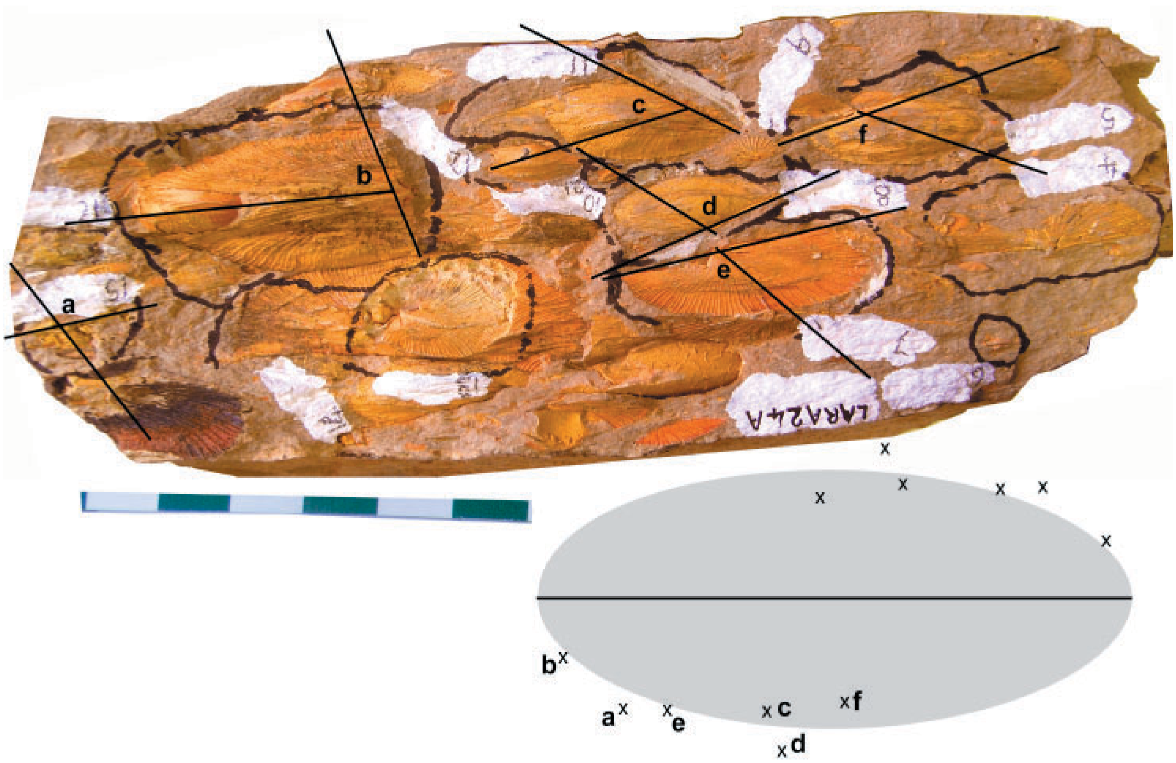

Figure 2. Specimen Lara 24A (containing MMF45320-45334) with symmetry axes (see text) superimposed on individuals labelled a to f. Scale is in centimetres. Lower right: a control line 80 mm in length is drawn parallel to the direction of maximum extension, its ends forming the control points referred to by Cooper (1990). For each individual, lines drawn through these control points, parallel to the two marked axes of symmetry, intersect at the labelled points (and their diagonally opposite counterparts). The shaded area is the ellipse which appears to best fit these intersections.

resulting points, to be used to estimate the strain ellipse, were then plotted on a millimetre grid in Photoshop. In a separate layer, an ellipse was drawn through them using the ellipse tool, adjusting the shape of the ellipse until it was seen to be a best fit for the plotted points (see Fig. 2). For each slab, the correction factors needed to restore the ellipse to circularity (on the assumption that the contained area within the original circle remained constant) were then calculated, again following the methods described by Cooper (1990).

There are steps in this procedure by which inaccuracies are inevitably introduced - determining the original axis of symmetry (not easy if ornament is uniform or internal structures are subdued or diffuse), fitting an ellipse to the plotted points, and the assumption of unchanged area occupied by the fossil during distortion. Added to these is the likelihood for the 'Lara' specimens that not all individuals were equally affected by compaction (see below) or lay precisely on the original bedding plane. Consequently, the calculated correction factors for the selected slabs varied significantly. There were insufficient suitable slabs for a calculated mean to be useful. Many fossils were on pieces with too few suitable individuals for the above procedure to be appropriate. Therefore it was decided to use correction factors rounded from the median, and see how well they worked for the majority of specimens - a potentially iterative process, but fortunately the chosen factors (reduction in the direction of lineation x0.6, extension at right angles to that of x1.4) worked well in nearly all cases, so did not need changing.

Application to individual fossils

Inevitably most of the fossils on the photographed slabs were not well oriented relative to the direction of lighting, and there were numerous fossils, not on those slabs, which were needed for reliable taxonomy. Therefore chosen fossils were photographed either individually or in small groups of similar orientation, again with the inclusion of a scale - in this case, a 6 mm diameter disc of graph paper (meaning that one diameter would always be oriented correctly relative to the direction of photography, and could be used to determine magnification during processing of the image). Care was taken to save a fresh file for each image at each step in the subsequent process. Each image was brought to an appropriate magnification, then rotated to bring the traces of lineation to either horizontal or vertical orientation. The correction factors were then applied, and their effectiveness checked. Errors arose because the direction of lineation was not always easily seen (meaning orientation of the image could be not quite right), or in the case of taxa such as globose atrypides or spiriferides because orientation before compaction was not always parallel to bedding before compaction, so that the resulting distortion was uneven. This second source of error also made orientating small specimens for photography uncertain. Where the 'restored' images were not quite symmetric, the process was repeated using the saved files, with slightly changed orientation, until an optimum result was obtained. The second source of error mentioned above meant that full symmetry could not always be attained even with several attempts. The final 'restored' images were then cropped to remove surplus background (and significantly reduce file size), and adjustments made to colour balance (the artificial light used was a 'white' LED, which resulted in very blue-biassed images), to bring the images as close as possible to the originals. Images of very dark brown fossils were made more useful by changing brightness and contrast. These images were then used for systematic study of the fauna.

Limitations

As can be seen from the above discussion, this is not a precise procedure. Provided strain was uniform across the outcrop, a fair approximation to the original proportions of symmetric fossils can be obtained. However, in most cases the strain will vary from bed to bed, depending on variations in lithology and distance from the nearest fold axis. In the case of the material from 'Lara', nearly all the specimens were loose, the result of grading of strongly weathered rock, and little bedding (let alone folding) could be seen in the road-bed, so this limitation certainly applied!

Original size is not restored using this methodology - again, because of the uncertainties in orientation and strain analysis - but the images will be a reasonable approximation of that size. Restoration of proportions (such as length to width ratio) is more accurate, but still not perfect.

As shown by Hughes and Jell (1992), and Rushton and Smith (1993), this is a very useful tool in assessing the relationships of taxa which have been described from strongly distorted specimens, particularly when there are many individuals available. As in the current case, it is also useful when dealing with a distorted fauna in which many of the taxa have been previously described from good material from other localities. Known taxa can often be identified with confidence. However, it is not reasonable to base new taxa just on images from which distortion has been removed. This is particularly so when trying to discriminate between species of the same genus, where size and proportions are often critical and not infrequently overlap.

RESULTS

Ten brachiopod species have been recognised, of which four can be confidently identified with known taxa; another three are closely comparable with known taxa but because of insufficient material cannot be identified with certainty. One species can be placed in a known genus but not species, and the final two (represented by only a few specimens) can be assigned to subfamilies. The fauna also contains encrinurid trilobite fragments, mostly librigenae, and a few moulds of rugose corals, including (Fig. 3) a small syringaxonid with a massive columella.

The fauna of the Cappanana Formation farther north, near Bredbo, has been listed previously, mostly at the generic level, but the only species described from the formation is the rugose coral *Rhizophyllum interpunctatum* de Koninck, 1876, from Rock Flat Creek southeast of Cooma. Richardson and Pickett (p. 61 in Pickett 1982) commented that 'precise correlation is not possible until identifications have been carried to specific level for as many forms as possible, but the overall aspect of the fauna resembles most closely that of the Canberra Group, and it is most likely to be of Late Wenlockian or Ludlovian age.'

Of the brachiopods described here, the known species elsewhere range in age from mid-Wenlock to

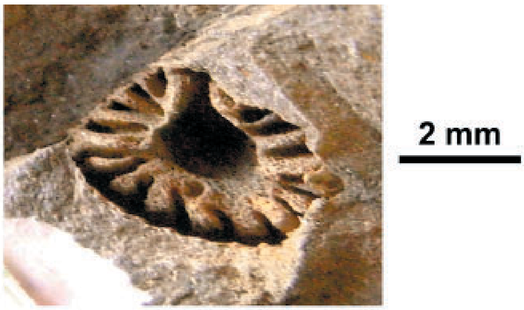

Figure 3. MMF45247, calical mould of an undetermined syringaxonid rugose coral.

early Ludfordian, with several known from Wenlock rocks in Canberra but not above, and only one not previously known below the Ludlow (it enters at Yass at about the Wenlock-Ludlow boundary). This is not enough for a definitive determination of the age of the Cappanana Formation, but a Wenlock age is more likely than not.

SYSTEMATIC PALAEONTOLOGY

Classification follows that in the six volumes of the revised Treatise on Invertebrate Paleontology, part H (Williams et al. 1997-2007). References to suprageneric taxa can be found in the relevant parts of that work.

The specimens used in this study have been lodged with the Geological Survey of New South Wales, their catalogue numbers being prefixed with MMF. Other depositories cited are the Research School of Earth Sciences, Australian National University (ANU), the Commonwealth Palaeontological Collection held by Geoscience Australia (CPC), and the Australian Museum (AMF). The dimensions quoted are for specimens as digitally restored, and are at best only a reasonable estimate of the dimensions of the original undistorted valves.

Abbreviations used are:

Ls - length of shell (normally the ventral valve)
Ld - length of dorsal valve
Lwmax - length to position of maximum width
Ws - shell width (except for alate species)
Wc - width of corpus (i.e. of the main body of alate taxa)
Wh - width of hinge (including alae where relevant) in strophic shells
CM - width of cardinal margin in nonstrophic shells

In lists of dimensions, italicised numbers indicate estimated values (e.g. doubled from measured half-width).

Class STROPHOMENATA Williams et al., 1996
Order STROPHOMENIDA Öpik, 1934
Superfamily STROPHOMENOIDEA King, 1846
Family RAFINESQUINIDAE Schuchert, 1893
Subfamily LEPTAENINAE Hall and Clarke, 1894

Leptaeninae, gen. et sp. indet.

Fig. 4

Material.

MMF45315 - ventral internal and dorsal external moulds.

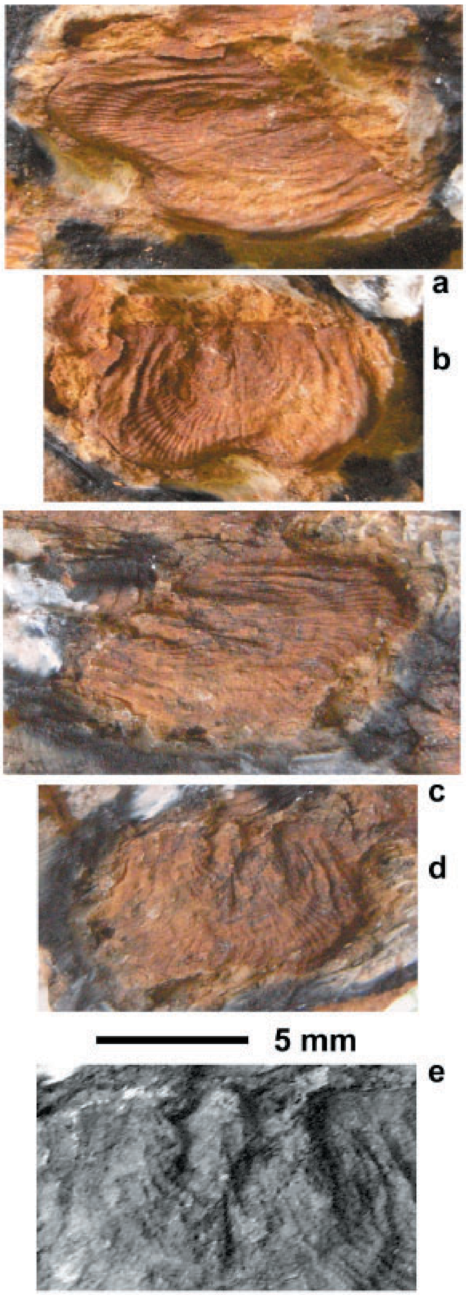

Figure 4. Leptaeninae, gen. et sp. indet., MMF 45315; a, b, dorsal external mould as collected, and restored; c, d, ventral internal mould as collected, and restored; e, posteromedian area of 4d, in grey-scale with increased contrast, enlarged to show the unusually shaped ventral muscle field.

Description.

Outline transverse, subquadrate with rounded margins, concave anteromedially; maximum width at about 2/3 length. Ventral valve convex, dorsal valve gently resupinate, with abrupt dorsal geniculation; trail short. Dorsal surface radially ribbed, relatively irregularly rugate; ribs rounded, 4-5 per mm marginally. Ventral beak broad, fairly low; interarea narrow, concave; delthyrium triangular, open, pseudodeltidium obscure; foramen not seen.

Teeth narrow, diverge from median line at about 50°. Muscle field subquadrate, with strong anterior and lateral reentrant, extends to about 1/3 valve length; in cross-section trough-shaped, gently impressed medially and moderately raised laterally. Adductor scars small, elongate elliptical, smooth. Floor of field not strongly ridged. Low, narrow myophragm starts at mouth of anterior reentrant in muscle field, extends to a little beyond mid-length. No other details visible. Dorsal interior unknown.

Dimensions Ls 5.0 mm, Ws 9.5 mm, Wh c. 8.6 mm, Ls/Ws 0.53, Wh/Ws c. 0.9.

Remarks

This single individual cannot be easily assigned to a leptaenine genus, particularly in the absence of details of the dorsal interior. It does not closely resemble any described species of *Leptaena*. A weakly concave anteromedian margin is unusual but not unknown in *Leptaena* - see Hoel (2005, Figs 2K, P). The Siluro-Devonian leptaenine *Glossoleptaena* Havlíček, 1967, has a concave anterior margin, but this is associated with a distinct sulcus; also it has much weaker shell ornament. The outline of the ventral muscle field in the 'Lara' specimen is quite distinctive (see Fig. 4e), perhaps approached only by that of *Glossoleptaena pixis* (Kelly, 1967).

Very few leptaenids have been described from the Australian Silurian, none being similar to the present species. An indeterminate *Leptaena* from the Walker Volcanics in Canberra was figured by Strusz (1982, p. 119). The single ventral internal mould has a semi-oval outline and a small subtriangular ventral muscle field. *Bracteoleptaena pannucea* Rickards and Wright, 1997 has a weakly developed trail, and a fairly large cordate ventral muscle field with evenly curved muscle-bounding ridges to either side of but not anterior to the field. The valve floors are noticeably papillate. *Leptaena compitalis* Strusz, 2003 has a fairly strong trail, and the ventral muscle field is small, rhomboid in outline with a concave front contained within the well developed muscle-bounding ridges.

Family EOPHOLIDOSTROPHIIDAE Rong and Cocks, 1994

Genus MESOPHOLIDOSTROPHIA Williams, 1950

Type species

Pholidostrophia (*Mesopholidostrophia*) *nitens* Williams, 1950. Wenlock, Gotland.

Mesopholidostrophia bendeninensis (Mitchell, 1923)
Fig. 5

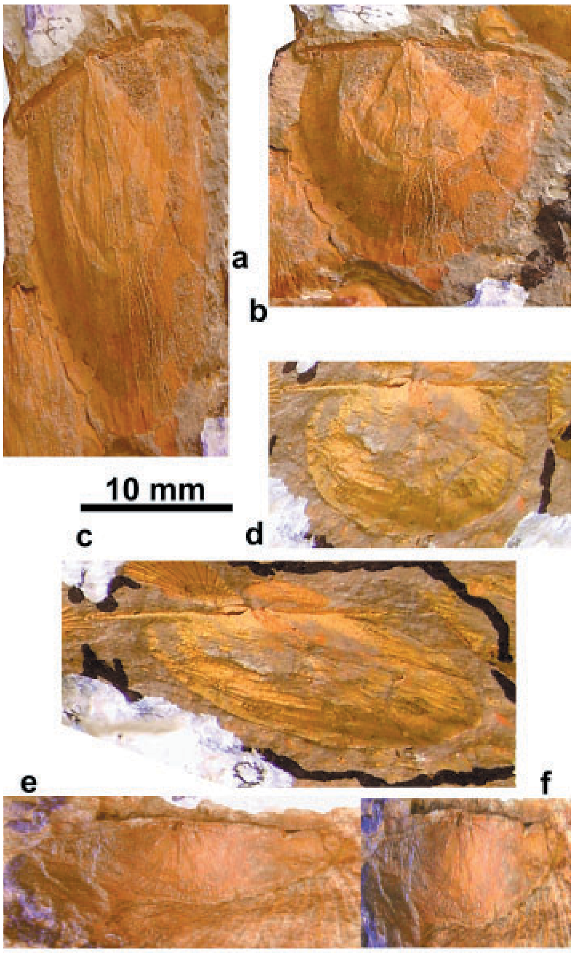

Figure 5. *Mesopholidostrophia bendeninensis* (Mitchell, 1923); a, b, MMF45238, ventral internal mould with well defined muscle field, as collected, and restored; c, d, MMF45329a, ventral internal mould with poorly defined muscle field, distinct ventral process, and strong reentrants in front of narrow alae, as collected, and restored; e, f, MMF45250, incomplete dorsal internal mould as collected, and restored.

Synonymy

Mesopholidostrophia bendinensis (Mitchell, 1923); Strusz, 2003, pp. 10-17, figs 7-10, cum syn.; Strusz, 2010b, pp. 149-150, figs 3Q-S..

Type material

Lectotype AM F28789. Bowning Creek, near Bowning, NSW. "Lower Trilobite Bed" = Black Bog Shale; Ludfordian (Upper Silurian).

New material

MMF45233, 45236-45238, 45243, 45244, 45250, 45260-45262, 45273, 45303, 45310-45314, 45329-45331.

Description

Outline weakly to moderately transverse, semi-oval, alate; alae narrow, reentrant at junction with corpus of shell shallow or absent. Largest shell 16.3 mm long. Greatest width at 0.35-0.4 Ls. Profile concavo-convex, ventral valve moderately to strongly convex, dorsal valve weakly to moderately concave. Ornament absent, or weak with moderately irregular rounded ribs, and sometimes sparse, irregular, weak concentric wrinkles. Ventral interarea low, flat, apsacline; dorsal interarea not seen. Delthyrium open; notothyrial structures not seen. Cardinal margin on both valves denticulate to 0.4-0.5Wc.

Ventral muscle field variably well expressed, moderately to strongly impressed into valve floor posteriorly, extends to about 0.4Ls; outline anteriorly poorly defined, subtriangular to bilobed. Adductor scars obscure, or weak, small, elongate, subparallel. Muscle-bounding ridges divergent, straight, faintly to moderately tuberculate, little if at all raised above posterolateral valve floor. Ventral process small, divided by shallow triangular furrow. Myophragm fine to obscure. Valve floor outside muscle field variably tuberculate.

Cardinal process lobes elongate, narrowly triangular, nearly parallel, separated by narrow slot and supported by small, low notothyrial platform; other details obscure. Notothyrial platform continuous with socket ridges, muscle-bounding ridges and myophragm. Inner socket ridges low, slightly curved, tuberculate, weakly divergent from cardinal margin. Muscle-bounding ridges curved, initially fairly strongly divergent then anteriorly only moderately so (at about 25-30°), tuberculate. Myophragm long, narrow, may be slightly swollen anteriorly. Notothyrial platform, muscle-bounding ridges and myophragm combine to form anchor-shaped structure posteriorly enclosing moderately divergent, oval, smooth adductor scars. Remainder of valve floor moderately tuberculate.

Dimensions

specimen	Ls	Wc	Wh	Ls/Wc	Ls/Wh	Wh/Wc
MMF45311	16.3	17.3	≥21	0.94	≤0.78	≥1.2
MMF45329	10.5	14.5	16.3	0.72	0.64	1.12
MMF45238	15.0	16.3	≥16.7	0.92	≤0.9	≥1.02

Remarks

There are three fairly similar species of 'stropheodontid' brachiopods in the Silurian of southeastern Australia which had to be considered when identifying this form: *Mesoleptostrophia* (*Mesoleptostrophia*) *quadrata* (Mitchell, 1923), *Mesoleptostrophia* (*M.*) *oepiki* Strusz, 1985, and *Mesopholidostrophia bendeninensis* (Mitchell, 1923). The first of these (from the Ludlow of Yass) is fairly small, and can be recognised externally by its subquadrate outline and the usually strong reentrants where the relatively short alae join the sides of the shell corpus; its ribs are fine and subdued. Internally it has a large, triangular, posteriorly impressed ventral muscle field bounded by straight tuberculate muscle-bounding ridges. The notothyrial platform, inner socket ridges, dorsal muscle-bounding ridges, and myophragm are all well developed. *Mesoleptostrophia* (*M.*) *oepiki* (Wenlock, Canberra) can be distinguished from it by its longer, thinner alae separated from the valve corpus by weaker reentrants, coarser ornament, a fine ventral myophragm, and curved dorsal muscle-bounding ridges. It also tends to be larger. *Mesopholidostrophia bendeninensis* is closer to the latter in size, and in having long slender alae and weak reentrants. It differs from both species of *Mesoleptostrophia* in its very weak external ornament, a ventral muscle field which is less obviously triangular and is often bilobed, weak ventral myophragm and muscle-bounding ridges, weak inner socket ridges, notothyrial platform and muscle-bounding ridges, and a longer myophragm which may expand slightly anteriorly.

The material from 'Lara', where many features are not well preserved, is so similar to both *Mesoleptostrophia* (*M.*) *quadrata* and *Mesopholidostrophia bendeninensis* that it is very unlikely to be a new species of either genus. The very weak external ornament and often significant convexity alone suggest the latter, and internal features, particularly the form of the ventral muscle field and the relatively weak dorsal structures, confirm the specific identity.

Since the revision of this species was published, a locality low in the Bowspring Limestone Member at Yass (locality GOU57 - see Strusz 2005) yielded a few specimens. This locality is below the *Ancoradella ploeckensis* zone, and could be either earliest Ludlow or latest Wenlock.

Order ORTHOTETIDA Waagen, 1884
Suborder ORTHOTETIDINA Waagen, 1884
Superfamily CHILIDIOPSOIDEA Boucot, 1959
Family CHILIDIOPSIDAE Boucot, 1959
Subfamily CHILIDIOPSINAE Boucot, 1959
Genus MORINORHYNCHUS Havlíček, 1965

Type species

Morinorhynchus dalmanelliformis Havlíček, 1965. Ludlow, Bohemia.

Morinorhynchus oepiki Strusz, 1982
Fig. 6

Synonymy

Morinorhynchus oepiki Strusz, 1982; Strusz 2003, pp. 31-33, figs 20-21, cum syn.; Strusz, 2010b, pp. 140-150, figs 3K'-M'.

Type material

Holotype CPC20987, paratypes CPC20415-20419, 20988-20994. Molonglo Valley, Canberra, ACT. Walker Volcanics; probably Homerian, Wenlock.

New material

MMF45234, 45240, 45246, 45249, 45252-45255, 45264-45267, 45271, 45274, -45277, 45298-45302, 45304, 45320-45327, 45335-45340, 45348-45353, 45355.

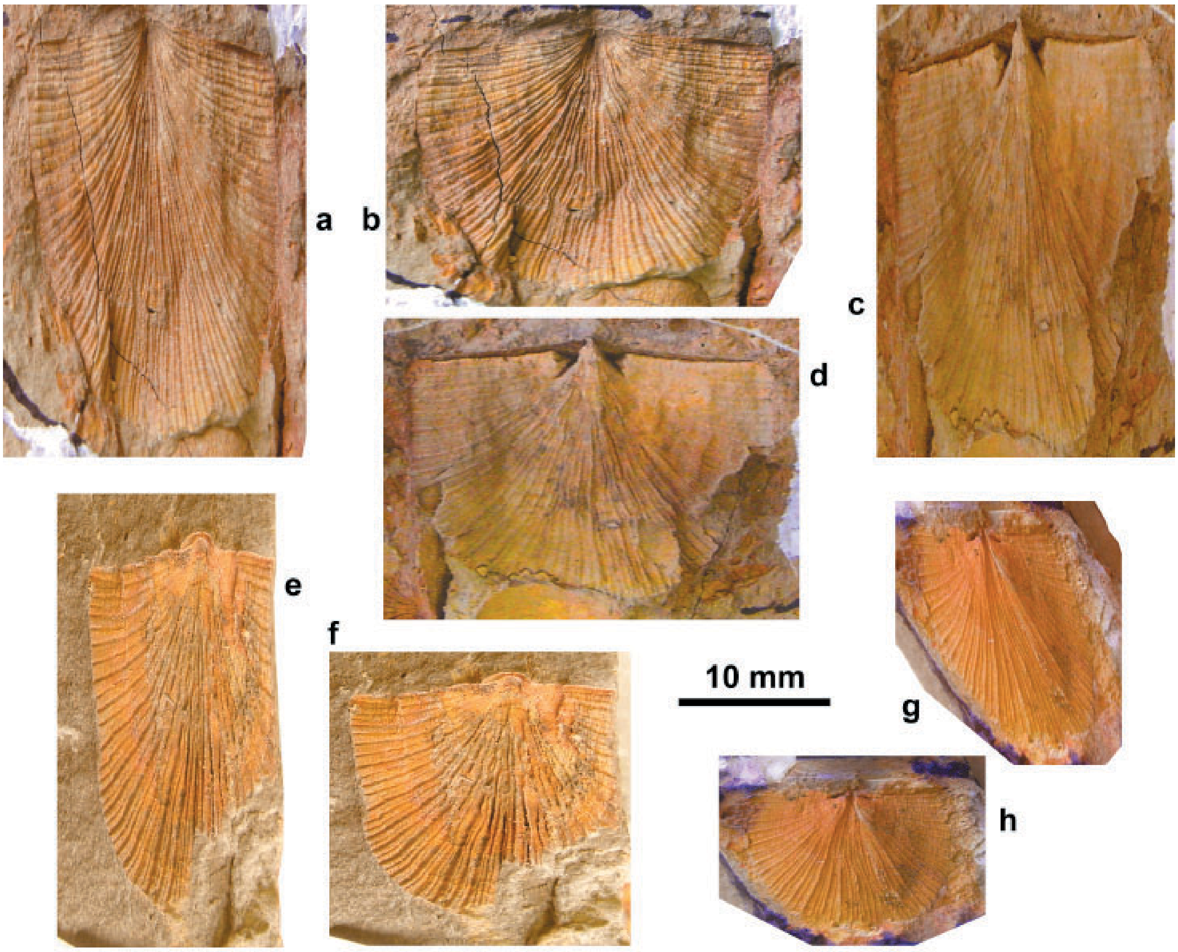

Figure 6. *Morinorhynchus oepiki* Strusz, 1982; a-d, MMF45298, a, b, ventral external mould as collected, and restored; c, d, ventral internal mould as collected, and restored; e, f, MMF45255, incomplete dorsal external mould showing large chilidium extending posterior to hinge line, as collected and restored; g, h, MMF45264b, dorsal internal mould as collected, and restored.

Description

Shell gently to moderately biconvex, ventral valve moderately more convex than dorsal valve; outline semi-elliptical, Wh ca 0.95Ws, Ls ca 0.75Ws but very variable, greatest width at about 0.4Ls. Anterior margin rectimarginate to moderately sulcate, dorsal sulcus most prominent in large shells. Ventral umbo low, interarea low, flat, strongly apsacline; pseudodeltidium large, moderately convex; foramen small, apical. Dorsal umbo low, interarea very low, chilidium broad, convex, projects posteriorly. Ornament unequally parvicostellate, with strong, rounded ribs separated by wider flat-bottomed interspaces crossed by fine growth lines; at 5 mm radius, at least 20 ribs in 5 mm.

Teeth small, dental plates well developed, upright, gently curved outward, divergent at about 90°. Muscle field obscure. Socket plates well developed, curved outwards, strongly divergent, fused with bilobed cardinal process; myophragm weak, broad. Further details obscure.

Dimensions

specimen	Ls	Ws	Wh	Ls/Ws	Wh/Ws
MMF45266	11.5	18.0	17.5	0.64	0.97
MMF45298	17.5	23.5	22.8	0.74	0.97
MMF45326	22.0	25.0	23.0	0.88	0.92
MMF45353	15.8	20.5	18.8	0.77	0.92

Remarks

The specimens from east of Cooma are morphologically (allowing for the poorer preservation) the same as Wenlock specimens from the Canberra Formation (Strusz, 1985) and those from the Ludlow of Yass (Strusz, 2003). As noted by Strusz (2003), *M. oepiki* is now known to reach a larger size than the type specimens from the Walker Volcanics indicated. The largest new specimen is MMF45326, with Ls 22 mm, Ws 25 mm, comparable with MMF610 (Ls 17 mm, Ws 26.1 mm) from Bowning. Rib spacing is on the low side, but within the previously known range.

Unlike elsewhere, where *Morinorhynchus oepiki* is a minor part of the fauna, the collection from 'Lara' is dominated by this species.

Class RHYNCHONELLATA Williams et al., 1996
Order PENTAMERIDA Schuchert and Cooper, 1931
Suborder PENTAMERIDINA Schuchert and Cooper, 1931
Superfamily PENTAMEROIDEA M'Coy, 1844
Family PENTAMERIDAE M'Coy, 1844
Genus APOPENTAMERUS Boucot and Johnson, 1979

Type species

Apopentamerus racinensis Boucot and Johnson, 1979. Wenlock, Wisconsin.

cf. *Apopentamerus clarkei* Strusz, 2011
Fig. 7

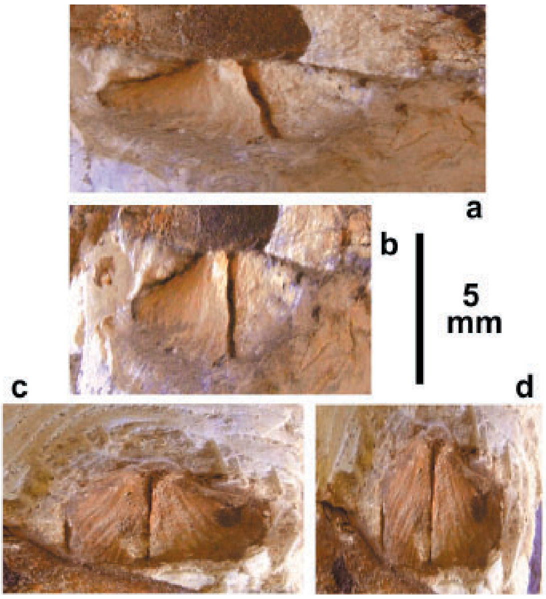

Figure 7. cf. *Apopentamerus clarkei* Strusz, 2011; a, b, MMF45256, ventral internal mould as collected, and restored; c, d, MMF45305, ventral internal mould as collected, and restored.

Synonymy

cf. *Apopentamerus clarkei* Strusz, 2011, pp. 36-39, fig. 5.

Material

MMF45256, 45305, 45306, 45328.

Discussion

These four small shells are clearly a smooth pentameroid, but only the exterior (completely lacking ribs, but one has a few concentric wrinkles) and the ventral interior are known. The ventral median septum is very long, and supports a narrow and upwardly flaring spondylium. There is considerable similarity with smaller specimens of *Apopentamerus clarkei*, recently described from the Canberra Formation, although the specimens from 'Lara' are even smaller (compare especially MMF45305 with Strusz 2011, figs 5e, h, and MMF45256 with fig. 5c). I am reasonably confident that this is the same species, but the material from 'Lara' is insufficient for certainty.

Order ATRYPIDA Rzhonsnitskaya, 1960
Suborder ATRYPIDINA Moore, 1952
Superfamily ATRYPOIDEA Gill, 1871
Family ATRYPIDAE Gill, 1871
Subfamily ATRYPINAE Gill, 1871
Genus ATRYPA Dalman, 1828
Subgenus ATRYPA Dalman, 1828

Type species

Atrypa reticularis Linnaeus, 1758. Ludlow, Gotland.

Atrypa (Atrypa) sp. cf. *duntroonensis* Mitchell and Dun, 1920
Fig. 8

Synonymy

cf. *A. (Atrypa) duntroonensis* Mitchell and Dun, 1920; Strusz, 2011, pp. 39-44, figs 6-9, cum syn.

Material

MMF45269, 45281, 45302, 45318, 45319.

Discussion

Available material is very limited, with no well preserved ventral valves. Until the recent redescription of *A.* (*Atrypa*) *duntroonensis* by Strusz (2011), based on abundant new material from the Wenlock of Canberra, only one species of *Atrypa* was reasonably well known from the Silurian of southeastern Australia: *A.* (*A.*) sp. cf. *dzwinogrodensis* Kozłowski, 1929 of Strusz (1984, 2007) from the Late Wenlock? to Ludlow of Yass. The two highly variable species are very similar externally, *A.* (*A.*) *duntroonensis* tending to be somewhat more elongate, with the dorsal valve more often anteromedially extended as a broad ventrally directed tongue. Rib shape, density and mode of increase are the same in the two species. In the dorsal valve, *A.* (*A.*) *duntroonensis* has a deeper cardinal pit, the sockets have distinct median ridges, and diverge at about 110-120°, and the myophragm is less prominent than in *A.* (*A.*) sp. cf. *dzwinogrodensis*. MMF45318 is the only available dorsal internal mould, and has a broad but rather low myophragm. The socket plates are short but robust, and the sockets (whose finer details are obscure) diverge at more than 140°. On this basis, the few specimens from 'Lara' are most comparable with *A.* (*A.*) *duntroonensis*, but specific identity must remain uncertain.

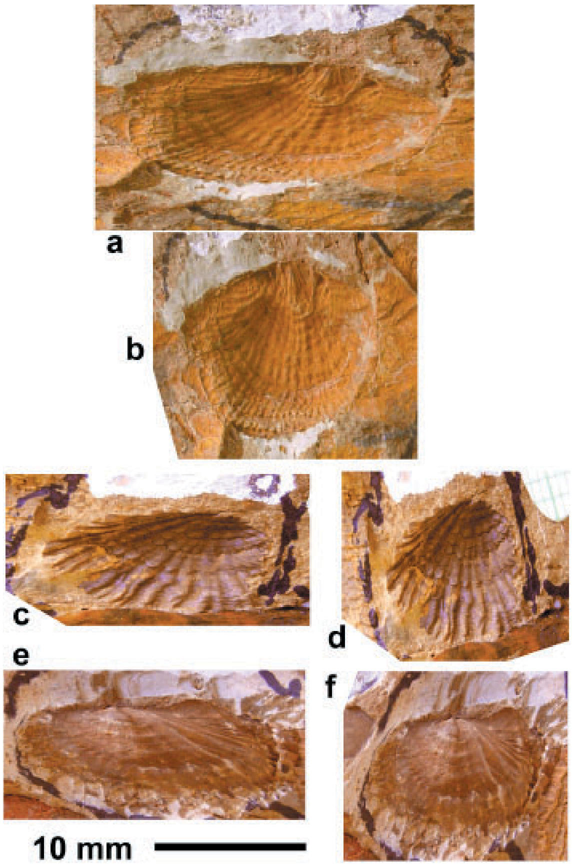

Figure 8. *Atrypa* (*Atrypa*) sp. cf. *duntroonensis* Mitchell and Dun, 1920; a, b, MMF45302b, dorsal external mould as collected, and restored; c-f, MMF45318, c, d incomplete dorsal external mould as collected, and restored, e, f, dorsal internal mould as collected, and restored.

Suborder LISSATRYPIDINA Copper, 1996
Superfamily LISSATRYPOIDEA Twenhofel, 1914
Family LISSATARYPIDAE Twenhofel, 1914
Genus ATRYPOIDEA Mitchell and Dun, 1920
Subgenus ATRYPOIDEA Mitchell and Dun, 1920

Type species

Meristina (?) *australis* Dun, 1904. Ludlow, Molong, NSW.

Atrypoidea (*Atrypoidea*) *australis* (Dun, 1904)
Fig. 9

Synonymy

Atrypoidea (*Atrypoidea*) *australis* (Dun, 1904); Strusz 2007, pp. 322-331, figs 16-21, cum syn.

Material

MMF45258, 45263, 45270, 45272, 45280, 45307-45309, 45232, 45233.

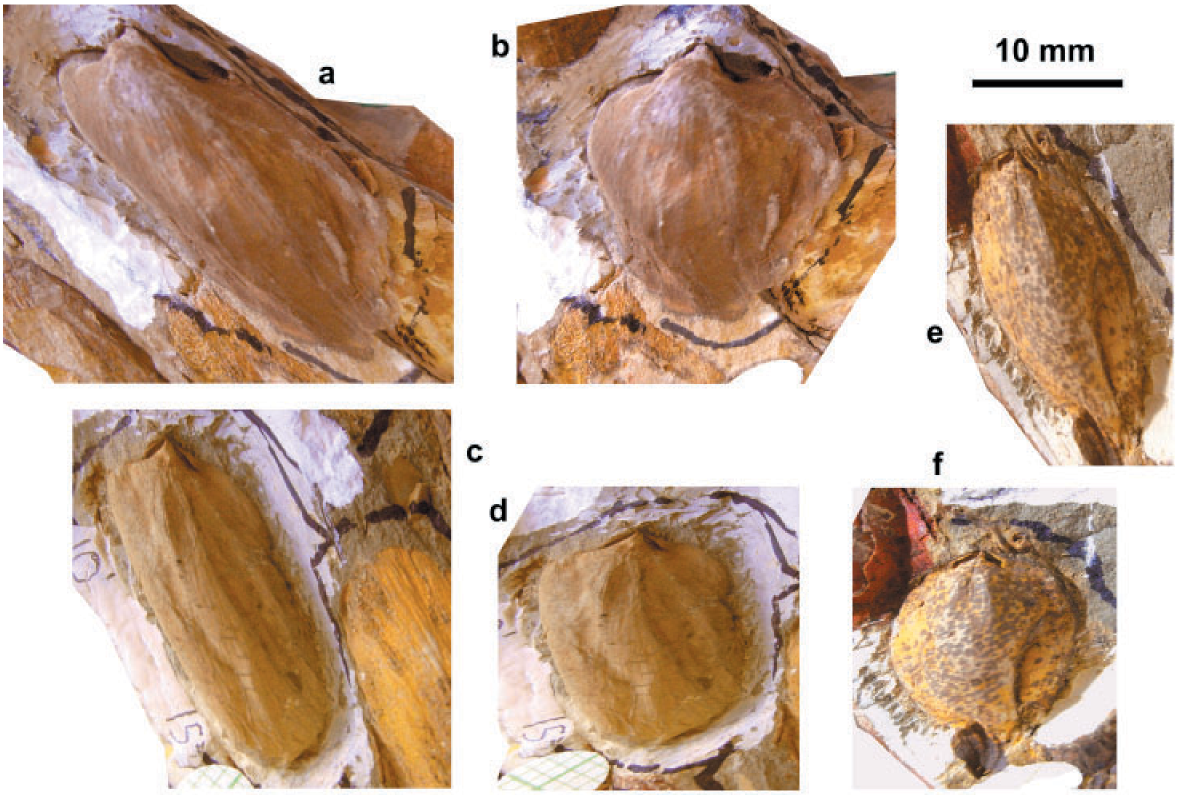

Figure 9. ***Atrypoidea* (*Atrypoidea*) *australis* (Dun, 1904); a, b, MMF45263, ventral internal mould as collected, and restored; c, d, MMF45308a, dorsal internal mould as collected, and restored; e, f, MMF45309, dorsal internal mould as collected, and restored.**

Discussion

The limited available material is mostly not well preserved, but fits well within the morphological limits of this highly variable species, and there can be little doubt of its identity. The one good ventral internal mould, MMF45263, is very like AMF17432 (Strusz 2007, Fig. 18C) in outline. With Ls = 18.5 mm, Ws = 17.0 mm, CM = 10.5 mm and Lwmax ≈ 7mm, it fits well within the published plots of Ls: Ws and CM:Ws, and differs only in the relatively posterior position of maximum width (it is just within the limits of the published plot of Lwmax: Ls). Its internal structures are also quite comparable with the few known interiors (e.g. ANU9736, Strusz 2007, fig. 17L). The same can be said of the dorsal valves - MMF45308 is close to the dorsal valves of AMF29186 and 29195 (Strusz 2007, figs 17G,19C), and MMF45309 to AMF29183, 29184 (Strusz 2007, figs 17E, F) and 29188 (fig. 18B).

Order ATHYRIDIDA Boucot, Johnson and Staton, 1964
Suborder Incertae Sedis

Superfamily ANOPLOTHECOIDEA Schuchert, 1894
Family ANOPLETHECIDAE Schuchert, 1894
Subfamily COELOSPIRINAE Hall and Clarke, 1895
Genus COELOSPIRA Hall, 1863

Type species

Leptocoelia concava Hall, 1857. Lochkovian, New York.

Coelospira sp. indet.
Fig. 10

Material

MMF45317, 45334.

Discussion

The two diminutive specimens are damaged and incomplete ventral valves of undoubted anoplothecid morphology. Both show strong curved ribs flanking a more finely ribbed fold. The one internal mould is not well enough preserved to show details. Nevertheless the basic morphology indicates this form could only belong to *Coelospira*.

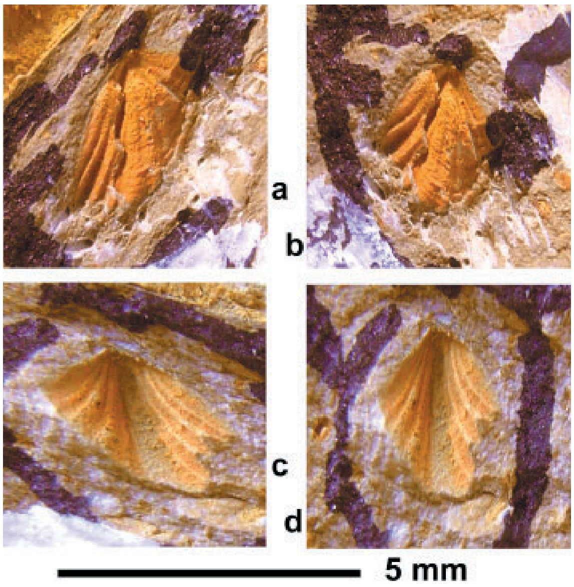

Figure 10. *Coelospira* sp. indet.; a-d, MMF45334, a, b, incomplete ventral internal mould as collected, and restored, c, d, incomplete ventral external mould as collected, and restored.

Coelospira has been recorded from the late Wenlock to early Ludlow of the Yass-Canberra region (*C. cavata* Strusz, 1982), and Cadia in central NSW (*Coelospira* sp. Percival in Rickards et al., 2001). The one incomplete ventral valve from Cadia differs from those of *C. cavata* only in having fewer, stronger ribs on the fold. In this respect the specimens from 'Lara' more closely resemble the Cadia form, but lack of material displaying the range of morphological variability means the specific relationships of the Cadia and 'Lara' forms remain unknown.

Order SPIRIFERIDA Waagen, 1883
Suborder SPIRIFERIDINA Waagen, 1883
Superfamily CYRTIOIDEA Frederiks, 1924
Family CYRTIIDAE Frederiks, 1924
Subfamily EOSPIRIFERINAE Schuchert, 1929

Eospiriferinae gen. et sp. indet.
Fig. 11

Material

MMF45282-45286.

Description

Only ventral valves are known, represented by relatively small external and internal moulds. Outline transverse spiriferoid, length 3/4 - 7/8 width, with

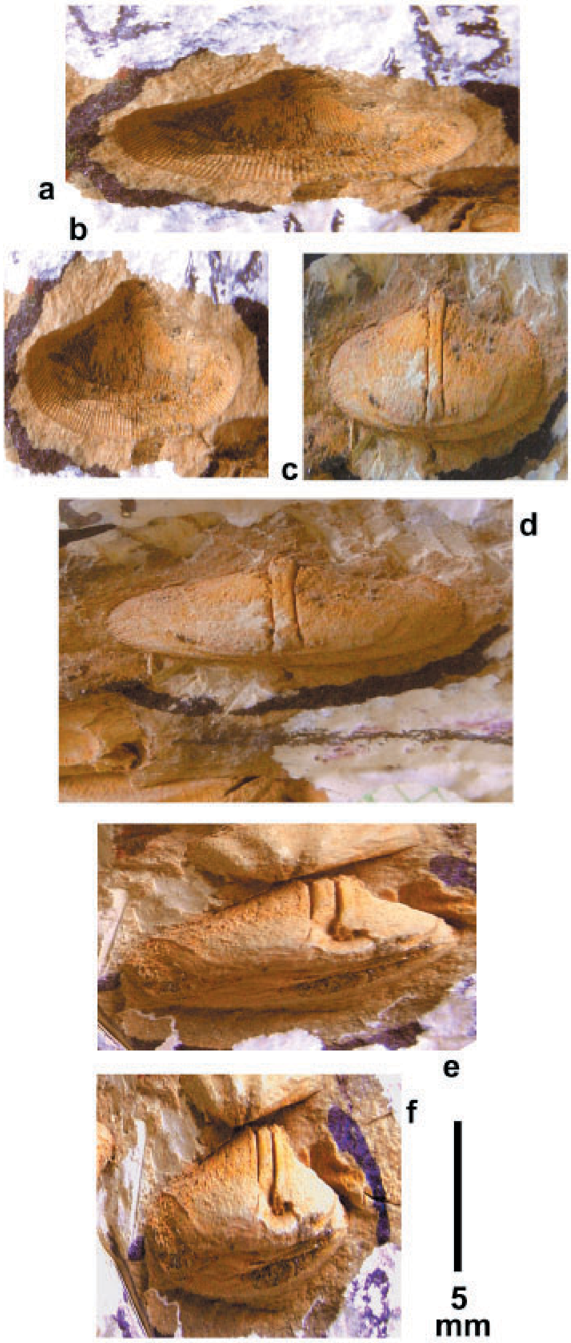

Figure 11. Eospiriferinae gen. et sp. indet.; a-d, MMF45285, a, b, ventral external mould showing well developed capillate ornament, as collected, and restored, c, d, ventral internal mould with very long parallel dental plates, restored, and as collected, e, f, MMF45284a, damaged ventral internal mould with shorter parallel dental plates, as collected, and restored.

prominent umbo, incurved beak, rounded lateral and anterior margins; greatest width somewhat anterior to mid-length. Valve strongly convex, without sulcus or ribs; anterior margin rectimarginate. Micro-ornament of rounded capillae separated by somewhat wider interspaces, *Eospirifer*-like, increasing by intercalation. Concentric micro-ornament absent or too fine to be preserved.

Dental plates parallel, long, extending to or beyond mid-length. Muscle field obscure, but weak myophragm between dental plates in some specimens, starting anterior to apex. Teeth small, triangular. One internal mould shows a small delthyrial plate. No visible pallial markings.

Dimensions

specimen	Ls	Ws	Ls/Ws
MMF45284	6.0	*6.8*	*0.88*
MMF45285	5.3	7.2	0.74
MMF45286	*6.5*	*8.4*	*0.77*

Discussion

In the absence of dorsal valves the generic identity of this form cannot be determined, but it is clearly a smooth eospiriferine. It is close to *Eospirifer* Schuchert, 1913, especially in the form of the micro-ornament, but species of that genus generally have robust divergent extrasinal dental plates, and usually have at least a shallow sulcus. In the absence of a sulcus, it cannot be said whether the dental plates in the 'Lara' form are intrasinal or extrasinal. Moreover, *Eospirifer* lacks a delthyrial plate or deltidium. Close to *Eospirifer* is *Endospirifer* Tachibana, 1981, which is known from the Silurian of Canberra and Yass, differing in having a well developed deltidium. It has fairly long and only moderately divergent dental plates which, however, lie outside a narrow but generally well developed sulcus. *Nurataella* Larin, 1973 (= *Baterospirifer* Rong, Su and Li, 1984) lacks a sulcus and has a rudimentary delthyrial plate, but the dorsal valve is of low convexity, and there are short extrasinal dental plates. Moreover, its capillae are more like those of *Myriospirifer* Havlíček, 1978, which are broadly rounded to flattened, and increase exclusively by splitting. The only eospiriferine known to me with parallel dental plates is the diminutive *Nanattegia* Strusz, 2010a, from the Silurian of Yass, but that has concave flanks on the very convex ventral valve, a deep, narrow sulcus, and no apical delthyrial structures.

Suborder DELTHYRIDINA Ivanova, 1972
Superfamily DELTHYRIDOIDEA Phillips, 1841
Family DELTHYRIDIDAE Phillips, 1841
Subfamily HOWELLELLINAE Johnson and Hou, 1994
Genus HOWELLELLA Kozłowski, 1946

Type species

Terebratula crispa von Hisinger, 1826. Wenlock, Gotland.

Howellella sp. aff. *elegans* (Muir-Wood, 1925)
Fig. 12

Synonymy

Howellella sp. aff. *elegans* (Muir-Wood, 1925); Strusz, 1982, pp. 132-134, figs 27A, C-E; Strusz, 1985, p. 117, figs 12A, 13; Strusz 2010b, figs 6, 8A-C

Material

MMF45239, 45241, 45242, 45259, 45279, 45287-45297, 45341-45344, 45345-45347.

Description

Ventral valve fairly strongly convex, outline spiriferoid, umbo wide and fairly prominent, lateral and anterior margins rounded; Ls/Ws and Wh/Ws both about 0.8. Ventral sulcus well developed, defined by two strong, sharply rounded ribs; At most, one pair of subdued lateral ribs arises anterior to beak. Dorsal valve moderately convex; beak low, fold prominent, rounded to slightly flattened medially, flanked by strong furrows. Inner pair of lateral ribs lower but well developed, rounded, slightly curved laterally. Outer pair of lateral ribs low, developed only anterolaterally; there can be a very faint third pair of ribs developed only marginally. Ventral interarea concave, apsacline; delthyrium open - structures otherwise obscure. Dorsal interarea very low, weakly anacline. Micro-ornament of fimbriate growth lines.

Teeth small, dental plates robust, upright, divergent forward, extra-sulcal, extend forward to 0.3-0.4Ls. Myophragm low, commences at about level of cardinal margin, extends forward to about mid-length. Muscle field obscure. Sockets small, widely divergent; inner socket ridges well developed, outer hinge plates narrow, steep, crural bases short, supported by triangular crural plates convergent on low notothyrial platform. Cardinal process small, its ventral face bilobed (MMF45290, 45341, 45346) or trilobed (MMF45342). Myophragm weak or absent; muscle scars obscure.

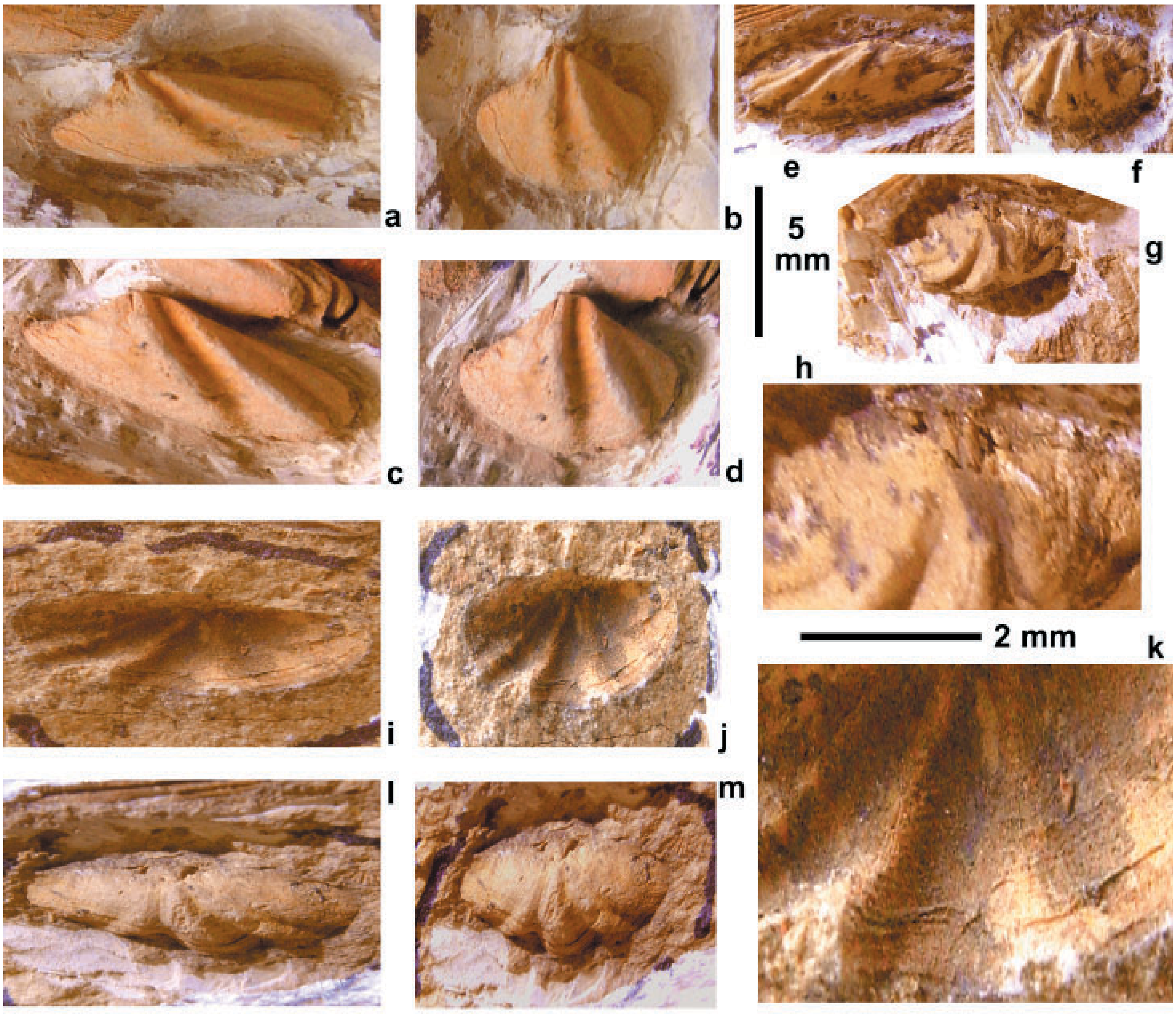

Figure 12. ***Howellella*** **sp. aff.** ***elegans*** **(Muir-Wood, 1925) Strusz, 1982; a, b, MMF45287a, ventral internal mould as collected, and restored; c, d, MMF45288a, ventral internal mould as collected, and restored; e-h, MMF45342a, dorsal internal mould, e, f, as collected, and restored, g, tilted posteriorly (restored) to show cardinalia, enlarged in h; i-m, MMF45344, i, j, dorsal external mould as collected and restored, and k, enlargement showing fimbriate ornament, l, m, dorsal internal mould as collected, and restored; 5 mm scale bar applies to a-g, i, j, l, m, 2 mm scale bar applies to h, k.**

Discussion

While preservation of detail in these small specimens is rather poor, in all that can be seen they are the same as the material from the Walker Volcanics and Canberra Formation of Canberra .

Superfamily RETICULARIOIDEA Waagen, 1883
Family RETICULARIIDAE Waagen, 1883
Subfamily RHENOTHYRIDINAE Gourvennec, 1994
Genus SPIRINELLA Johnston, 1941

Type species

Spirinella caecistriata Johnston, 1941. Late Wenlock, Yass, NSW.

Spirinella caecistriata Johnston, 1941
Fig. 13

Synonymy

Spirinella caecistriata Johnston, 1941; Strusz 2011, pp. 45-46, fig. 12, cum syn.

Material

MMF45245, 45248, 45268, 45278, 45316, 45354, 45356, 35357.

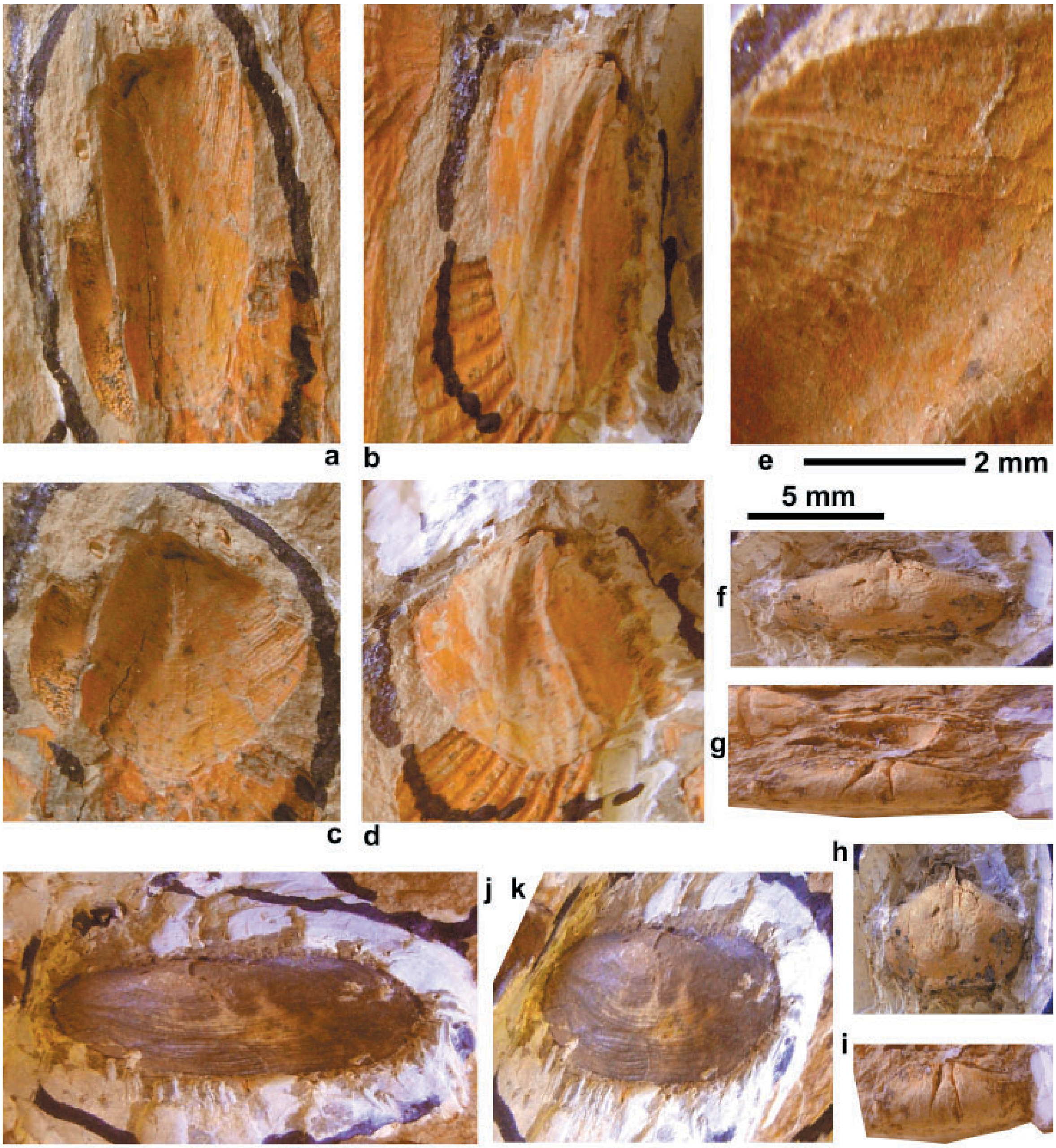

Figure 13. ***Spirinella caecistriata*** **Johnston, 1941; a-e, MMF45278, ventral valve external and internal moulds, a, b, as collected, c, d restored, e portion of c reoriented and enlarged to show fimbriate ornament; f, h, MMF45354a, incomplete ventral internal mould as collected, and restored; g, j, MMF45357, incomplete ventral mould with large apical callist, viewed postero-ventrally, as collected and restored; j, k, MMF45316a, dorsal internal mould as collected, and restored; 5 mm scale bar applies for all except e, to which 2 mm scale bar applies.**

Remarks

These few small specimens are not well preserved, most showing evidence of post-burial compaction prior to tectonic distortion. Nevertheless they show all the characteristics of the species, and the proportions fit well within the limits of variability reported by Strusz (2010a). Ventral valves have a weak ventral sulcus, fairly prominent beak, fimbriate micro-ornament, strong, divergent dental plates and a weak myophragm; two internal moulds show a well-developed apical callist - e.g. compare MMF35357 with Strusz (2010a, fig. 18G). The one dorsal internal mould is damaged by compaction, so no useful comparison can be made.

Dimensions

specimen	Ls	Ws	Wh	Ls/Ws	Wh/Ws
MMF45278	9.0	*12.0*	*11.5*	*0.75*	*0.96*
MMF45354	4.8	*5.5*	4.5	*0.87*	*0.82*

ACKNOWLEDGEMENTS

This paper was prepared in the Research School of Earth Sciences (ANU) in my capacity as a School Visitor, and also as a Research Associate of the Australian Museum, Sydney, and is a contribution to IGCP591. I would like to thank Dr T. Munson (now with the Northern Territory Geological Survey) for his assistance in collecting the material, Dr I. Percival and Dr R.A. Glen (New South Wales Geological Survey) for assistance in sourcing an appropriate geological map of the area, and Dr J. Laurie (Geoscience Australia) for his careful review of the first draft of the paper.

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The Spider Genus *Toxopsoides* (Araneae: Desidae: Toxopinae): New Records and Species from Australia

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Smith, H.M. (2013). The Spider Genus *Toxopsoides* (Araneae: Desidae: Toxopinae): New Records and Species from Australia. *Proceedings of the Linnean Society of New South Wales* **135**, 19-43.

Toxopsoides huttoni Forster and Wilton from New Zealand has not been recorded since its description in a monotypic genus in 1973. Here, the species is recorded from south-eastern Australia. Additional descriptive notes and figures are provided for comparison with three new species of *Toxopsoides* that are described from the same area. *Toxopsoides erici* sp. nov. is from higher altitudes of north-eastern New South Wales and south-eastern Queensland, *T. kathleenae* sp. nov. is from the Sydney Basin and lower areas to the north-east, and *T. macleayi* sp. nov. is from the Blue Mountains to the west of Sydney. Characters are discussed pertaining to the continuing placement of the genus within family Desidae.

Manuscript received 15 November 2012, accepted for publication 24 July 2013.
urn:lsid:zoobank.org:pub:5A9ADFDA-8CE4-47C5-8571-248BC654D60F

KEYWORDS: Australia, Australasia, Desidae, grate-shaped tapetum, new species, New Zealand, Toxopinae, *Toxopsoides*.

INTRODUCTION

The family Toxopidae was erected by Hickman (1940) for the Tasmanian genus *Toxops* Hickman. Forster (1964) subsequently revised and relimited the family Toxopidae to include *Laestrygones* Urquhart, *Cycloctenus* L. Koch, *Plectophanes* Bryant and *Toxopsiella* Forster. In the course of writing his iconic series on New Zealand Spiders, Forster (1970) reconsidered both the family status and generic composition of the group, placing Toxopinae as a subfamily of Desidae and removing all genera except *Toxops* and *Laestrygones* and the smaller species formerly in *Toxopsiella*, which were transferred to the new genus *Hapona* Forster.

The monotypic genus *Toxopsoides*, with type species *T. huttoni* Forster and Wilton, 1973 was the final genus to be added to the subfamily. Placed at the end of the fourth part of the New Zealand series, Forster and Wilton (1973: 309) wrote: “In general appearance this genus is similar to *Toxops* from Tasmania, but it does not seem to be closely related”.

Toxopsoides has turned out to be rather an enigma. The type locality of *Toxopsoides huttoni*, Waitetola in Hawkes Bay, has subsequently proven to be an incorrect transliteration for Waitetoko, near Lake Taupo (Vink et al. 2011). The type locality remains the only published locality for this species (Vink et al. 2011), although I have not searched for further unidentified New Zealand specimens in collections. Perhaps the observation that the species was presumably a vagrant was true in more ways than apparently intended by Forster and Wilton (1973: 309).

In Australia, to my knowledge there have been no specifically identified records of *Toxopsoides* species, however, the presence of spiders referrable to the genus has been recognised for some time, having been figured by Davies (1986: 42, figs 67, 67a) under family Toxopidae. Twenty-four toxopid species from the north-east forests of New South Wales were also listed by Gray and Cassis (1994), most of which were referred to the genus *Toxopsoides* in the Australian Museum databases, although not in the report.

In this paper, I provide the first records for *T. huttoni* since its description. These new records are from south-eastern Australia, where the species appears to be widespread. Three new Australian species are described, all are clearly related to *T. huttoni* in their male and female genitalic morphology:

T. erici sp. nov. from higher altitudes of north-eastern New South Wales and south-eastern Queensland, *T. kathleenae* sp. nov. from the Sydney Basin and lower areas to the north-east, and *T. macleayi* sp. nov. from the Blue Mountains to the west of Sydney.

METHODS

Specimen examinations, measurements and drawings were made using an Olympus SZ16 microscope, fitted with graticule and camera lucida. Photographs in several focal planes (usually 15-40) were taken using a ColorViewI camera mounted on the Olympus SZ16 and layers combined using HeliconFocus software. Plates were composed using Adobe Photoshop. Diagrammatic figures were prepared using Inkscape v.0.45.1. Specimen preparations for scanning electron microscopy were passed through an alcohol series (75–100%), critical point dried and mounted on stubs before coating with gold and viewing using a Zeiss Evo LS15 SEM incorporating a Robinson backscatter detector. Internal details of female genitalia were drawn from an excised epigynum cleared in lactic acid. Eye measurements are taken in dorsal view except MOQL, which is measured from the same plane as the eye bases. Caput width is measured at the posterior edge of posterior lateral eyes.

In this paper I use the term '*Toxopsoides* group' to refer to toxopine relatives of *T. huttoni* that as yet are of unassessed generic status. I use the term '*T. huttoni* group' to refer to species with similar morphology to those treated herein, which are undoubtedly congeneric.

Abbreviations

Specimens with numbers prefixed KS are in the Australian Museum, Sydney, Australia; ANIC denotes the Australian National Insect Collection, Canberra, Australia. Abbreviations are used in reporting some measurements and general text, as follows: AME, anterior median eye(s); ALE, anterior lateral eye(s); EGW, eye group width; MOQAW, median ocular quadrangle anterior width; MOQL, median ocular quadrangle length; MOQPW, median ocular quadrangle posterior width; PME, posterior median eye(s); PLE, posterior lateral eye(s), SEM scanning electron micrograph or microscope.

TAXONOMY

Family Desidae Pocock

Toxopsoides Forster and Wilton, 1973

Toxopsoides Forster and Wilton 1973: 309. Type species *Toxopsoides huttoni* Forster and Wilton by original designation.

Diagnosis

From other Toxopinae genera by double row of trichobothria on metatarsi and tarsi; additionally, from *Toxops* by distinctly narrowed caput in dorsal view and male palp with median apophysis, from *Laestrygones* and *Hapona* by chelicerae with lateral boss, by absence of denticulate ventral abdominal plate present in *Laestrygones*, from *Hapona* by apical insertion of embolus of male palp.

The following combination of non-genitalic characters quickly separate *Toxopsoides* group species from the Cycloctenidae, Ctenidae and Zoridae—where they are most commonly misplaced in collections: eyes PLE>PME≥AME>ALE; ALE positioned c. half way between AME and PLE; at least 6 pairs of erectable ventral macrosetae on tibia one and two (rather long in females—see Fig. 2b, usually shorter in males, Fig. 2d); paturon with a single anteriorly projecting macroseta from basal third (Figs 1d, 2a); abdomen tapering posteriorly with spinnerets usually visible in dorsal view (Figs 1a, 1c); three claws without claw tufts; abdominal setae not modified, similar in size over whole dorsum.

Description

This description is based on the detailed description (= diagnosis) of Forster and Wilton (1973) with some refinements and additions. Body length up to c. 5.5 mm; laterigrade; ecribellate. Carapace highest at fovea (Fig. 1d); chilum broad, single; paturon with single anteriorly projecting macroseta at c. 1/3 length; eye group occupying most of head width; two rows of four eyes, both strongly recurved; PLE>PME≥AME>ALE; ALE positioned c. half way between AME and PLE; PME separation less than diameter of one eye; posterior eyes with open grate-shaped tapetum (similar to that figured for a borraline stiphidiid by Gray and Smith (2008 fig. 4g). Legs strongly spined, with double row of long spines along ventral surfaces of tibiae and metatarsi of legs 1 and 2; 4123 or 4(12)3 or 4(123); trichobothria long and numerous, in double row on tibiae and tarsi (longest distally); tarsal organ present; superior claws with four teeth, similar; inferior claw with two or three teeth; claw tufts, tenent hairs and scopulae lacking; pretarsus (onychium) present; trochanters shallowly notched (Fig. 2c). Epigynum weakly sclerotised; paired fovea, each with small posteriorly pointing

Figure 1. ***Toxopsoides huttoni*** **Forster and Wilton. a, b, Female (KS.49670): a, habitus, dorsal; b, habitus, ventral; c, male (KS.120530), habitus, dorsal; d, male (KS.45210), carapace profile. Scale bar: d, 0.5 mm.**

projection on ventral lip; internally, copulatory ducts initially pass anteroventrally then loop one or more times to receptacula. Colulus undivided; spinnerets with anterior and posterior pairs similar in size; distal segment short. Anal setae long and thick. Male pedipalp without locking tegular/subtegular lobes; with apically arising filiform embolus curving anticlockwise down the prolateral margin, basally enclosed within membranous tegular outgrowth or envelope (Fig. 4c), which is continuous with sclerotised conductor (Fig. 5a, b); radix absent; median apophysis arising retrolaterally, an elongate, folded plate, rounded distally, with folded edges (Fig. 5d); tibia with retrolateral tibial apophysis and elongate plate. Pedipalp of female with trichobothria on tibia and tarsus; claw smooth.

Figure 2. ***Toxopsoides huttoni*** **Forster and Wilton. a, Female (KS.49670), eyes, frontal; b, c, female (KS.45210), right leg one, prolateral; c, mouthparts and anterior coxae; d, male (KS.120530), right leg one, prolateral. Scale bars b, 0.5 mm, c, 0.5 mm, d, 1.0 mm.**

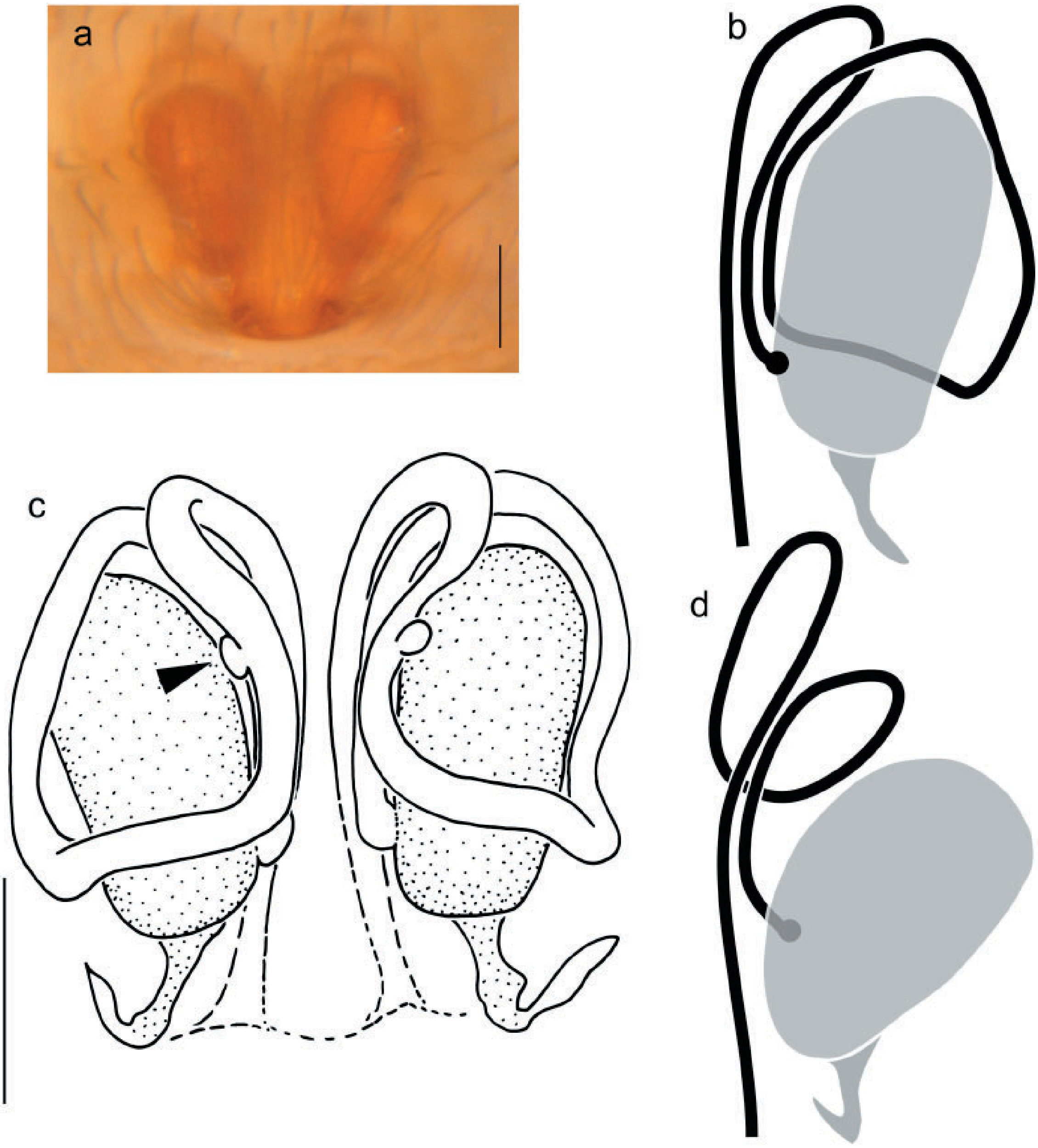

Figure 3a-c. *Toxopsoides huttoni* Forster and Wilton, female genitalia. a, Ventral photograph (KS.45210); b, diagrammatic ventral view of left spermatheca and duct based on Fig. 3c; c, dorsal (internal) cleared (KS.108220), pointer indicates nodule. d, *T.* ?*huttoni* South Australia, left spermatheca and duct, ventral diagrammatic. Scale bars 0.1 mm.

Comments

Forster and Wilton's figure of the internal genitalia of *T. huttoni* (Forster and Wilton, 1973: fig. 1088) shows a small glandular structure or caecum on each copulatory duct (unlabelled). The present study has confirmed that these were not artefacts and similar structures are found in all species detailed here (pointers in Figs 3c, 14c). Their detailed structure has not been probed.

The male pedipalp of *T. huttoni* group spiders have a general structure as described below for *T. huttoni*. Some other *Toxopsoides* group species lack long convoluted epigynal ducts, have short embolus and differ in other aspects of genitalic morphology; they also differ in behaviour. These species await further analysis as to generic placement.

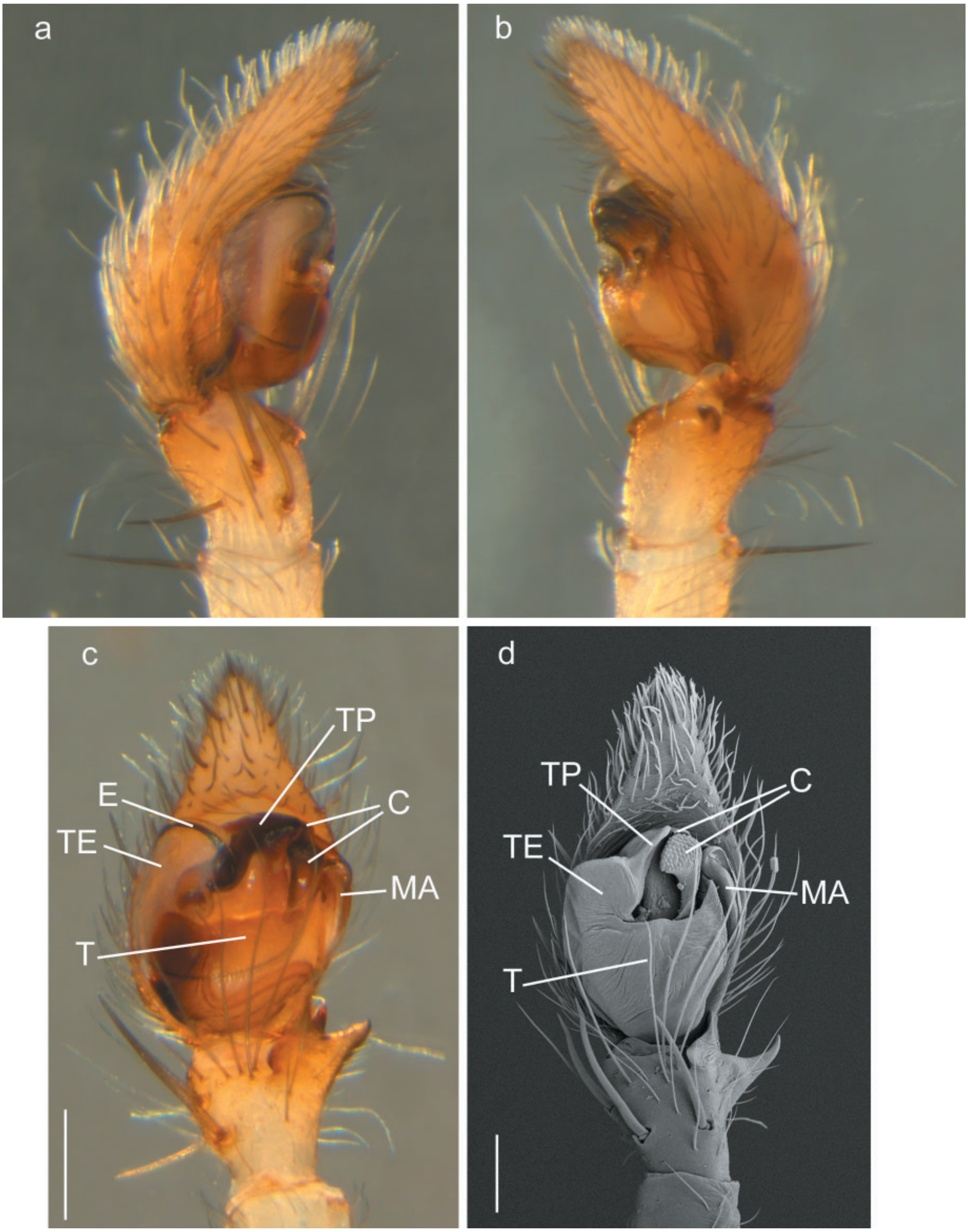

Figure 4. ***Toxopsoides huttoni*** **Forster and Wilton, male pedipalps. a-c, Left pedipalp, prolateral, retrolateral and ventral (KS.108220, Gulaga NP, NSW); d, ventral (right, image reversed) SEM (KS.45210, Macedon, Vic). Scale bars 0.2 mm. Labels: E, embolus (inside TE); C, conductor; MA, median apophysis; T, tegulum; TE, tegular envelope; TP, tegular envelope process.**

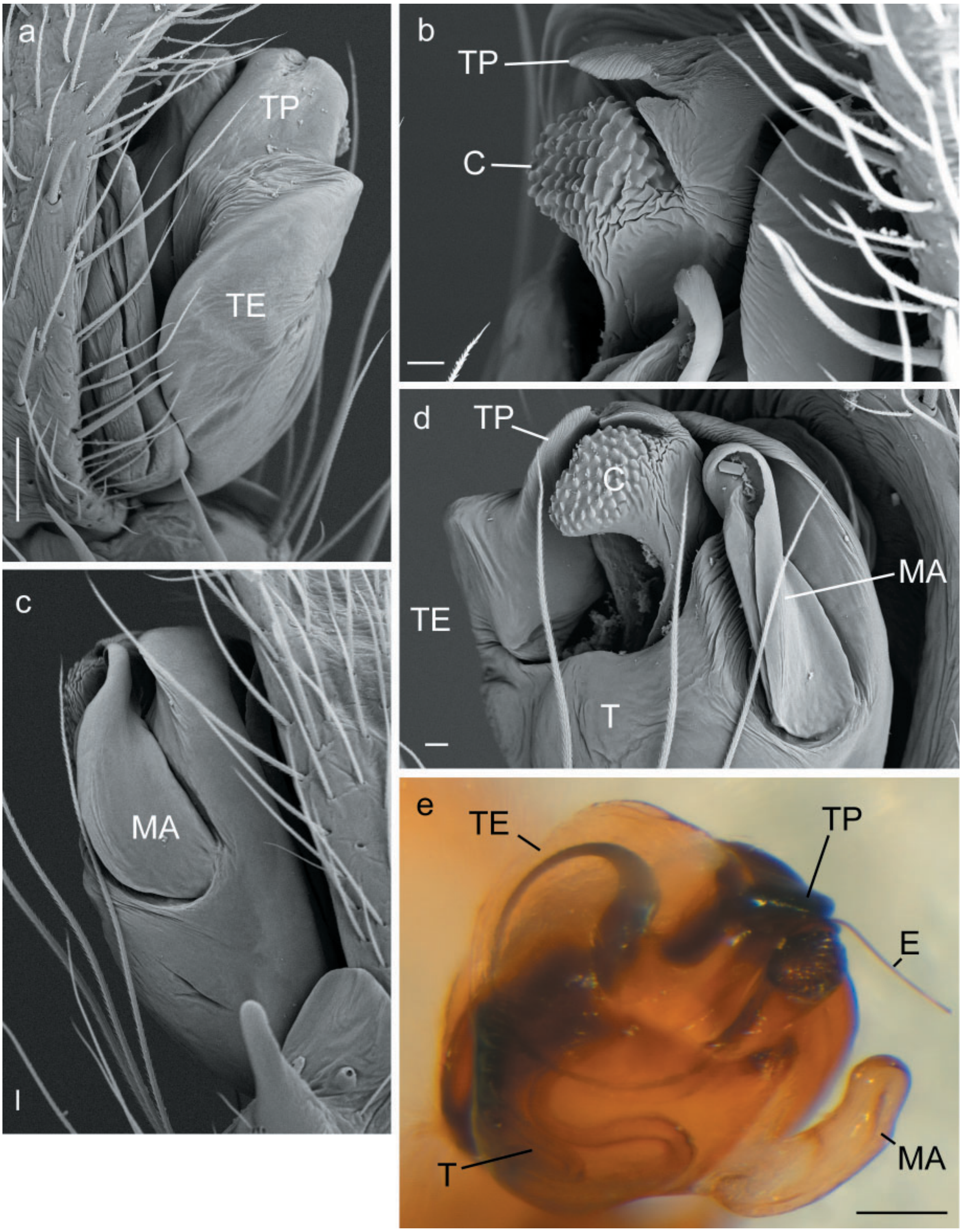

Figure 5. ***Toxopsoides huttoni*** **Forster and Wilton, male pedipalp. a-d, SEM details (KS.45210, right, images reversed): a, prolateral; b, retroapical; c, retrolateral; d, retroventral; e, expanded left bulbus, proapical (KS.120530). Scale bars: a, e, 0.1 mm; b-d, 20 µm. Labels: E, embolus; C, conductor; MA, median apophysis; T, tegulum; TE, tegular envelope; TP, tegular envelope process.**

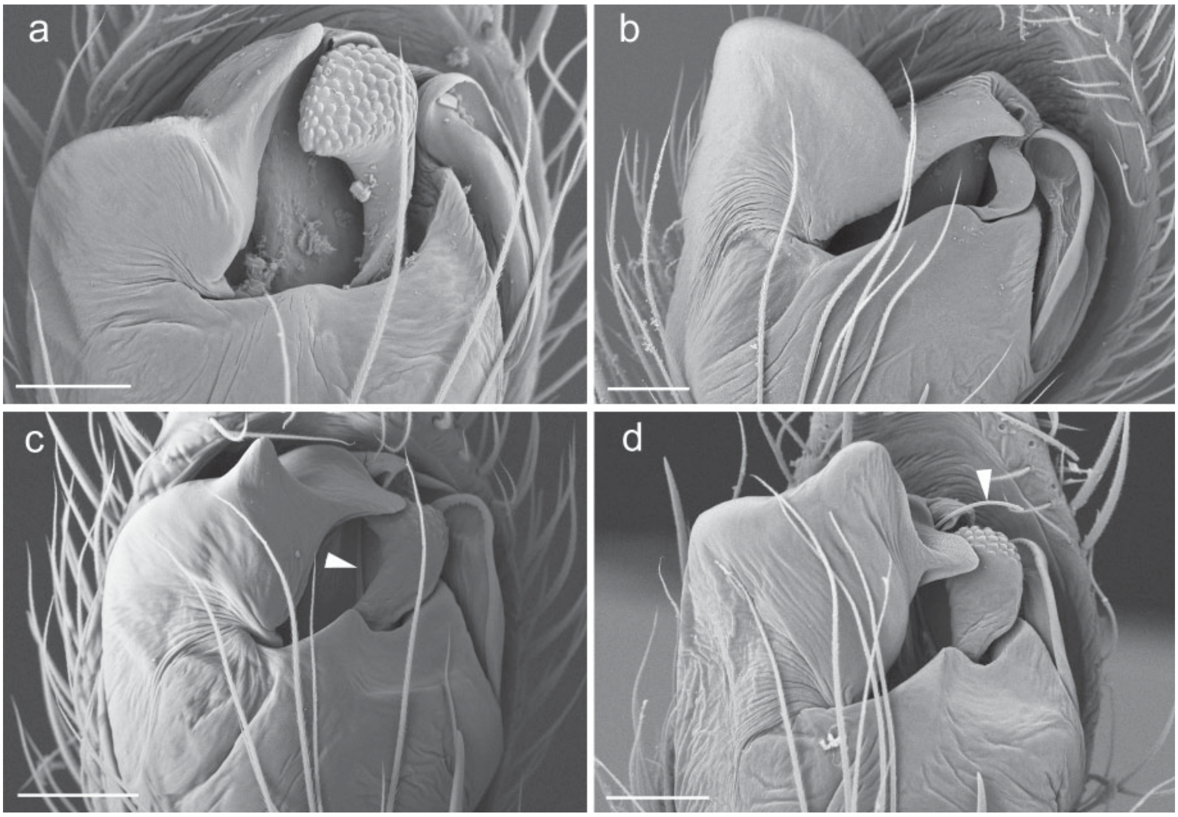

Figure 6. *Toxopsoides* species, male pedipalps, comparison of apical half of left bulbus, ventral. a, *T. huttoni* Forster and Wilton (KS.45210, right, image reversed); b, *T. erici* sp. nov. (KS.103221); c, *T. kathleenae* sp. nov. (KS.118808); d, *T. macleayi* sp. nov. (KS.115589). Scale bars 0.1 mm. Pointers indicate visible embolus.

Included species

Toxopsoides huttoni Forster and Wilton, 1973 (North Island of New Zealand, Victoria to south-east New South Wales, Australia); *T. erici* sp. nov. (Barrington Massif and Great Dividing Range to south-east Queensland, Australia); *T. kathleenae* sp. nov. (Sydney Basin and Hunter region, Australia); *T. macleayi* sp. nov. (Blue Mountains, Australia).

Biology

Toxopsoides huttoni group species are primarily tree trunk dwellers, hiding under loose bark by day and moving out from cover at night. The spiders drop as bark is removed. Specimens have also been found under logs and are occasionally caught in pitfall traps. It is not known where spiders reside at times of the year when trees have shed their loose bark. Adults of *T. erici*, probably the most collected species, have been recorded in every season, *T. huttoni* from January to July, and the other two species have been collected in every season except summer. To some extent this is likely to reflect collector bias, for instance there may be a bias away from the hottest (and therefore most uncomfortable) seasons, and towards the south later in the year, northwards earlier.

The only definite record of a *Toxopsoides* egg sac of which I am aware (from one of the wider *Toxopsoides* group species) is in the Australian Museum collections. The data indicate that the female was guarding a plano-convex egg sac attached to a surface under a rock overhang (orientation not specified); the egg sac was disguised with sand. I have seen this specimen and the embryos are well developed and close to eclosion. This might suggest some level of parental care in the group. However, despite extensive hand collecting and an attempt to keep spiders in captivity, egg sacs remain unrecorded for any species in the *T. huttoni* group.

***Toxopsoides huttoni* Forster and Wilton, 1973**

(Figs 1-5, 6a, 16)

Toxopsoides huttoni Forster and Wilton 1973: 309, figs 1084-1088

Type Material

Holotype ♀, allotype ♂, New Zealand, North Island, "Hawkes Bay, Waitetola, R. W. Hutton" (as given by Forster and Wilton 1973); label data "Waitetola, 7.V.1966" according to Vink et al. (2011) this locality should be Waitetoko, near Lake Taupo. Otago Museum, not examined.

Diagnosis

Strongly striped leg femora (in both sexes but especially obvious in females Fig. 1a, even old faded specimens) distinguish *T. huttoni* from *T. macleayi* and *T. kathleenae*. Female: from *T. erici* by pear-shaped spermathecae in uncleared ventral view (Fig. 3a), and lacking sinuous ventral loop of copulatory ducts usually visible through the cuticle in *T. erici* (cf. Fig. 3a and Fig. 8a, b). Male: from *T. erici* by more robust ventral conductor with rugose knob-like end (Figs 4c, d, 6a), and embolus base occupying c. 1/2 height of tegular extension (1/3 in *T. erici*); males with faded leg stripes from *T. macleayi* and *T. kathleenae* by lack of anterior prong from tegular extension (cf. Fig. 6a with Figs 6c, d, 12d).

Supplementary description

Forster and Wilton (1973) give a detailed description, which fits most aspects of Australian specimens except as follows. Female. Colour: dorsal pigmentation varies (that recorded by Forster and Wilton was quite dark overall), patterns illustrated (Fig. 1) typical for Australian specimens in alcohol. Eyes (Fig. 2a), in particular anterior eyes, larger than shown by Forster and Wilton (fig. 1086), eyes overall somewhat variable. Sternum slightly longer than wide (Fig. 1b); tip narrowing abruptly between fourth coxae, width similar to length to region of narrowing. Labium wider than long, basal notches present (Fig. 2c). Legs: tarsal organ at 3/4 length of segment on leg four, 5/6 on legs one to three; spination (variable) many specimens with prolateral macroseta on anterior femur. Epigynum. Posteriorly pointing foveal teeth small, blunt. Copulatory ducts, in ventral uncleared view, proximal duct usually not visible except briefly anteriorly (Fig. 3a), with single complete loop dorsally leading directly into spermatheca (Figs 3b, c). Male. Carapace broadens level with posterior eyes, making caput slightly shorter than in female, carapace slightly broader than female. All legs longer than female in proportion to carapace width. Male pedipalp (Figs 4, 5). Basal part of curving, filiform embolus (E) enclosed in translucent tegular envelope (TE). A retrolaterally directed process (TP) arises from anteroretral margin of TE; process extends dorsad, wrapping around towards tegulum and fusing with conductor (C). Embolus curves behind (or possibly through) ventral tegulum (T), to enter complex of TE and conductor; embolus of expanded palpus exits through a narrow fold (top centre, Fig. 6a). Conductor with rugose knob ventrally (C, Fig. 5d). Cleft between tegulum and tegular process broad and tall (Fig. 6a). Dorsal cymbium with trichobothria and weak terminal scopula (Figs 4a, b).

Measurements of Australian specimens (in mm). Female. Carapace length range, 1.50 to 2.13. (KS.45210): Total length, 5.31; carapace length, 2.13; width, 1.69; height, 0.80; caput width, 0.95; clypeus height, 0.10; abdomen length, 3.35; width, 2.10; labium length, 0.26; width, 0.33; sternum length, 1.05; width (max), 0.93; Eyes: AME, 0.16; PME, 0.19; ALE, 0.14; PLE, 0.21; EGW, 0.83 MOQAW, 0.34; MOQPW, 0.44; MOQL, 0.40. Limbs (femur + (patella-tibia) + metatarsus + tarsus = total): pedipalp, 0.68 + 0.85 + + 0.75 = 2.28; leg I, 1.72 + 2.44 + 1.24 + 0.64 = 6.04; leg II, 1.76 + 2.12 + 1.36 + 0.64 = 5.88; leg III, 1.68 + 1.88 + 1.24 + 0.68 = 5.48; leg IV, 2.00 + 2.48 + 2.00 + 0.84 = 7.32. Ratio leg I / carapace width: 3.57. Male. Carapace length range, 1.56 to 2.13. (KS.45210): Total length, 4.60; carapace length, 2.10; width, 1.70; height, 0.85; caput width, 1.00; clypeus height, 0.08; abdomen length, 2.55; width, 1.35; labium length, hidden; width, hidden; sternum length, 1.15; width (max), 0.98; Eyes: AME, 0.16; PME, 0.19; ALE, 0.14; PLE, 0.21; EGW, 0.78 MOQAW, 0.35; MOQPW, 0.45; MOQL, 0.40. Limbs (femur + (patella-tibia) + metatarsus + tarsus = total): pedipalp, 0.80 + 0.73 + + 0.88 = 2.40; leg I, 2.28 + 3.08 + 1.80 + 0.80 = 7.96; leg II, 2.36 + 2.96 + 1.80 + 0.80 = 7.92; leg III, 2.20 + 2.52 + 1.92 + 0.76 = 7.40; leg IV, 2.48 + 3.16 + 2.64 + 0.96 = 9.24. Ratio leg I / carapace width: 4.68.

Comments on description

Some aspects of this description of Australian specimens are at variance with that given by Forster and Wilton. Discrepancies in eye measurements and relative positions may be accounted for by non inclusion of lenses (e.g. apparently omitted in Forster and Wilton fig. 1086). Sclerites of the male pedipalp are here reinterpreted. Forster and Wilton use the term radix for a projection arising near the base of the embolus and (in the generic description) describe the conductor as membranous. Because the figure is not labelled it is not clear what part is intended for either appellation.

The term tegular envelope has been coined based on the observation that the embolus is free to move laterally within the enclosing structure. This is evidenced by inducing expansion of the pedipalp, which causes rotation of the basal embolus anticlockwise, tightening the radius of curvature and partially expelling the embolus from the conductor groove (Fig. 5e). Fusion of the tegular process with conductor is evidenced by lack of seam under SEM (Fig. 5b) and non separation in an expanded preparation.

Material Examined

Australia. AUSTRALIAN CAPITAL TERRITORY: 1 ♂ (ANIC), Blundells Creek, 3 km E of Picadilly Circus, 35°22′S, 148°50′E, 850 m, Jun 1984, Weir, Lawrence, Johnson. 1 ♂ (ANIC), Wombat Creek, 6 km NE Picadilly Circus, 35°19′S, 148°51′E, 750 m, Jul 1984, Weir, Lawrence, Johnson. NEW SOUTH WALES: 1 ♀ (KS.113028), Coolangubra State Forest, near Waratah Creek, 37°00′30″S, 149°23′32″E, Jan 1984, pitfall trap, G.A. Webb. 1 ♂, 1 ♀ (KS.108220), Gulaga National Park, road to Mt Dromedary, 36°17′13″S, 150°02′24″E, 224 m, 22 May 2009, beat/sweep and hand collecting, G.A. Milledge, H.M. Smith. 1 ♂, 1 ♀ (KS.108153), Meroo National Park, 0.4 km N on Lake Rd, 35°23′52″S, 150°25′02″E, 27 m, 19 May 2009, beat/sweep and hand collecting, G.A. Milledge, H.M. Smith. VICTORIA: 1 ♂ (KS.48877), 7.5 km SE of Woodend, 37°28′S, 144°37′E, 4 Apr 1978, M.R. Gray. 1♂, 1 ♀ (KS.45210), 1 ♂, 2 ♀ (KS. 120530), Mt Macedon Forest Park, 37°25′S, 144°38′E, 5 Apr 1978, M.R. Gray, in curled bark. 1 ♂ (KS.118807), Otway Ranges, 1 mile E of Beech Forest, 38°38′S, 143°34′E, 7 Apr 1973, M.R. Gray, on bark. 1 ♂ (KS.105878), Silverband Rd, nr Halls Gap, 37°08′S, 142°31′E, 21 Mar 1974, M.R. Gray. 1 ♀ (KS.49670), Wonderland Rd, Halls Gap, 37°08′S, 142°31′E, 1 May 1973, M.R. Gray. 1 ♂ (KS.105895), Zumsteins, The Grampians, 37°06′S, 142°25′E, 18 Mar 1974, hand collected, M.R. Gray.

Discussed specimens of uncertain status: SOUTH AUSTRALIA: 2 ♂, 1 ♀ (KS.76384), Cleland Conservation Park, 34°58′40″S, 138°41′59″E, 18 Mar 2002, hand, G.A. Milledge and H.M. Smith.

Distribution

New Zealand: North Island, Waitetoko, near Lake Taupo. Australia: South-eastern states and the Australian Capital Territory (Fig. 16). Specimens from South Australia need confirmation (see below).

Comments

The distribution of *T. huttoni* in New Zealand requires further investigation. If the species truly has a limited distribution it could be an accidental introduction from Australia, where it is widespread in south-eastern states. However, the *T. huttoni* group of species are often poorly represented in collections unless appropriate collecting techniques have been used. Until New Zealand collections have been examined and suitable techniques have been used to search loose bark habitats, it is not possible to draw firm conclusions.

In general males from NSW have the longest embolus for the species, and females have longest ducts (measured by the size of the dorsal loop). In specimens from further south and west, the embolus or ducts become slightly shorter, the examined female from western Victoria approaching the duct configuration of *T. kathleenae*; these specimens are accepted as *T. huttoni*. In South Australia, the two male specimens currently available from the Adelaide area are within the range of variation seen in other areas. However, the single female has the duct loop in a quite different position, as if unwound and stretching anteriorly (Fig. 3d). Conspecificity of males and female requires confirmation and the status of this population awaits assessment.

***Toxopsoides erici* sp. nov.**

(Figs 6b, 7-9, 16)

Type Material

Australia, NEW SOUTH WALES. Holotype ♀ (KS.118803), Barrington Tops Reserve, Polblue Picnic Area, Barrington Trail, 31°56′57″S, 151°26′38″E, 1537 m, 5 Dec 2006, beat, sweep, under bark and logs, G.A. Milledge, H.M. Smith. Paratypes: 1 ♂ (KS.118804), 2 ♂ (KS.98543), data as holotype. 2 ♀ (KS.101478), Coneac State Conservation Area, 31°51′47″S, 151°48′03″E, 1 Jun 2007, H.M. Smith. 1 ♀ (KS.101473), Barrington Tops National Park, Gloucester Tops Rd, 32°02′49″S, 151°37′46″E, 30 May 2007, H.M. Smith. 1 ♂ (KS.98587), Barrington Tops National Park, Gloucester Tops, gate on Kerripit Rd, 32°03′43″S, 151°34′39″E, 1253 m, 6 Dec 2006, beat, sweep, under bark and logs, G.A. Milledge, H.M. Smith.

Etymology

This species is named in memory of my father, Eric Smith who always encouraged my interests in natural history.

Diagnosis

Strongly striped leg femora (in both sexes but especially obvious in females, Fig. 7a) distinguish specimens from *T. macleayi* and *T. kathleenae*. Female: from all other species by elongate spermathecae and distal dorsal loop of copulatory duct (Fig. 8d, pointer);

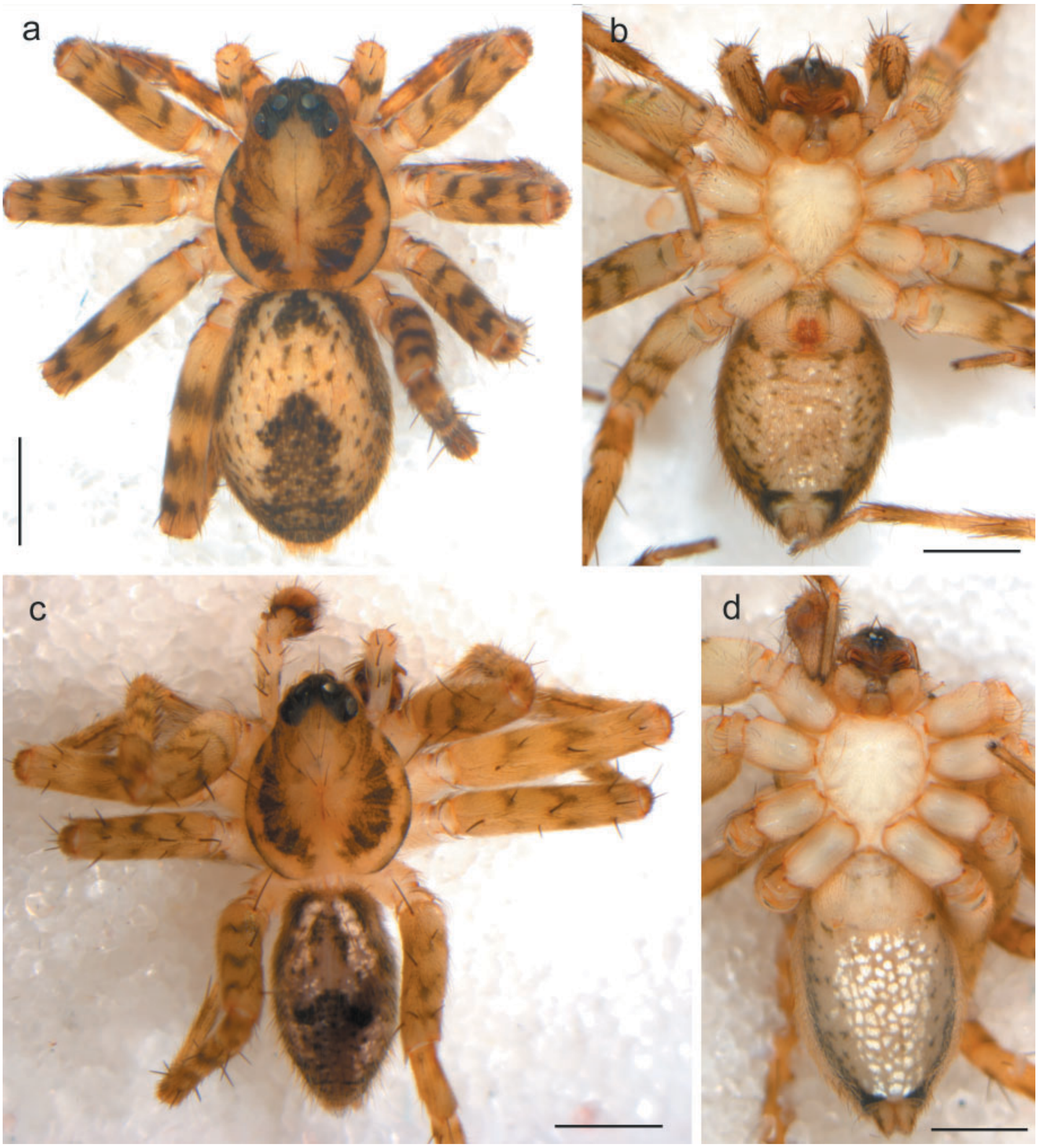

Figure 7. ***Toxopsoides erici*** **sp. nov. a, Female (KS.101478), habitus, dorsal; b, female (holotype), habitus, ventral; c, male (KS.103286), habitus, dorsal; d, male (KS.118804), ventral sternum and abdomen. Scale bars: 1.0 mm.**

a sinuous loop of copulatory duct across spermatheca in ventral view (Figs 8a-c, pointer in 8b) is diagnostic if visible but may be unclear, and is reduced or absent in northern specimens. Male: from *T. macleayi* and *T. kathleenae* by lack of anterior prong from tegular extension (cf. Fig 6b with Figs 6c, d); from *T. huttoni* by finely curved conductor without pronounced knob (Fig. 6b cf. Fig. 6a), and embolus base occupying c. 1/3 height of tegular extension (1/2 in *T. huttoni*).

Description

Generally similar to *T. huttoni* except in genitalia, as follows. Female. Epigynum with posteriorly pointing foveal teeth, similar size to those of *T. kathleenae* (Fig. 11b). Spermathecae long; in ventral view copulatory duct loops sinuously across spermatheca (Figs 8a, b) (southern specimens); ducts pass anteriorly three times connected by broad lateral loop and distal dorsal loop (Figs 8c, d); ventral duct

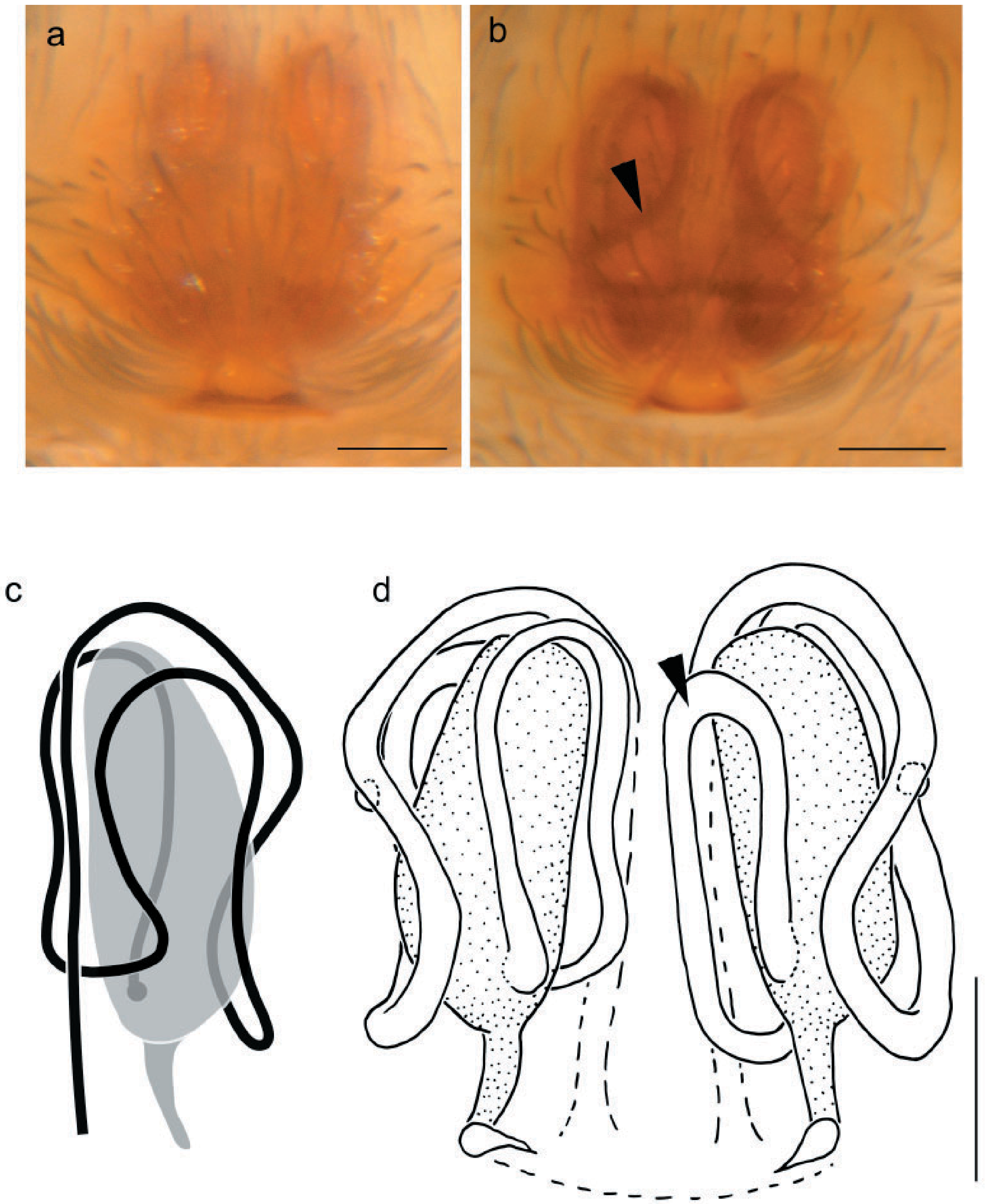

Figure 8. *Toxopsoides erici* sp. nov., female genitalia. a, Ventral photograph (holotype); b, ditto (KS.101472), pointer indicates sinuous ventral duct not present in northern specimens; c, diagrammatic ventral view of left spermatheca and duct based on Fig. 8d; d, dorsal (internal) cleared (KS.101478), pointer to distal dorsal duct loop. Scale bars 0.1 mm.

of northern specimens may lack sinuosity, but distal loop present (pointer, Fig. 8d). Male. Embolus longer than in *T. huttoni*, with correspondingly greater area of tegular envelope (Figs 9a, c), and more elongate path across dorsal tegulum. Conductor slim and sinuous, without enlarged rugose knob (Figs 6b, 9c, d). Cleft between tegulum and tegular process long and narrow (Fig. 6b).

Measurements (in mm). Female. Carapace length range, 1.70 to 2.40. Specimen KS.118803. Total length, 5.10; carapace length, 2.40; width, 1.95; height, 0.94; caput width, 1.15; clypeus height, 0.10;

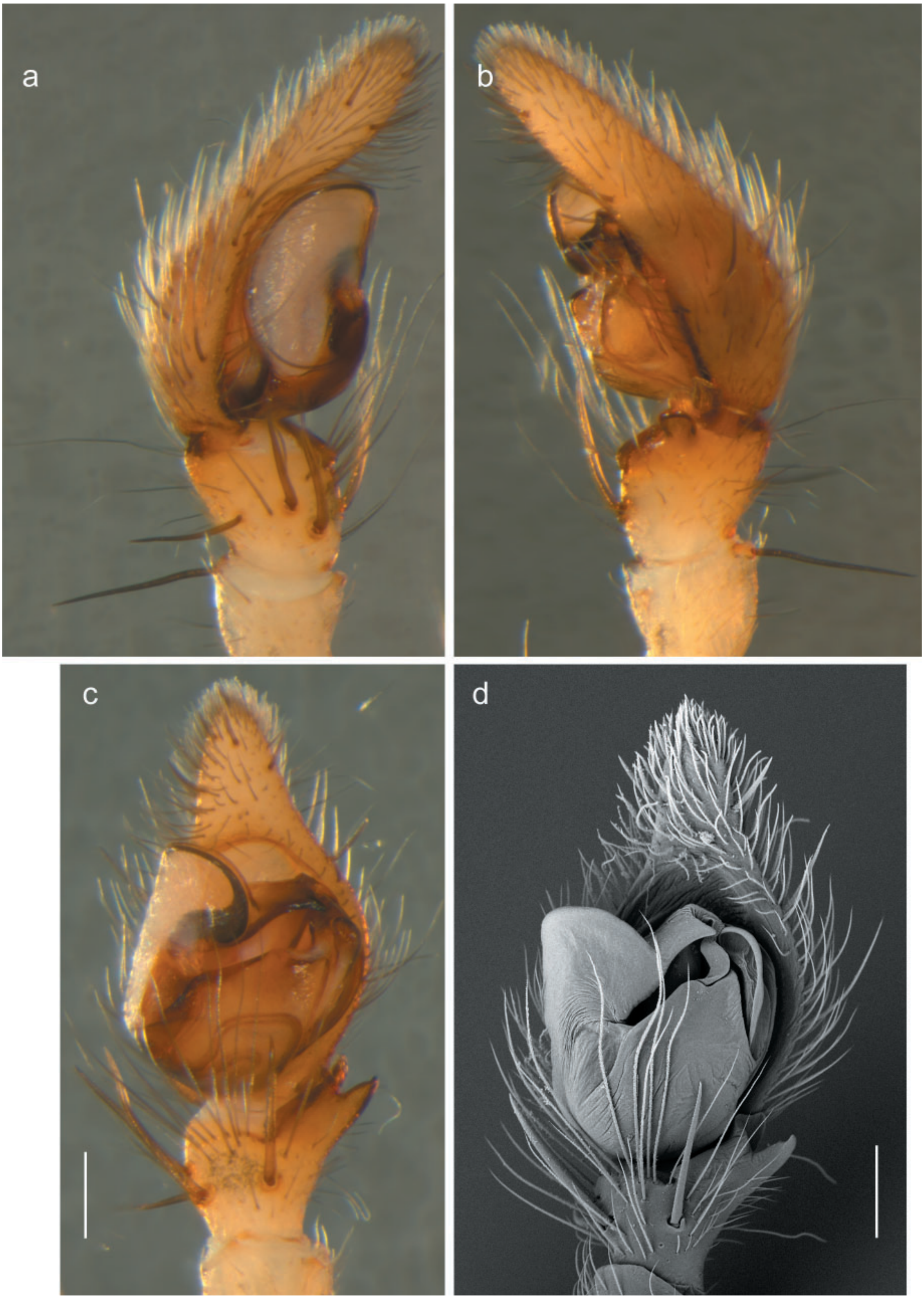

Figure 9. ***Toxopsoides erici*** **sp. nov., male left pedipalps. a-c, Prolateral, retrolateral and ventral (KS.118804); d, ventral SEM (KS.103221). Scale bars 0.2 mm.**

abdomen length, 2.90; width, 1.85; labium length, 0.31; width, 0.35; sternum length, 1.25; width (max), 1.10; Eyes: AME, 0.19; PME, 0.23; ALE, 0.13; PLE, 0.24; EGW, 1.00 MOQAW, 0.44; MOQPW, 0.54; MOQL, 0.48. Limbs (femur + (patella-tibia) + metatarsus + tarsus = total): pedipalp, 0.93 + 0.98 + + 0.85 = 2.75; leg I, 2.10 + 2.80 + 1.65 + 0.65 = 7.20; leg II, 2.15 + 2.65 + 1.70 + 0.65 = 7.15; leg III, 2.05 + 2.50 + 1.70 + 0.75 = 7.00; leg IV, 2.50 + 3.05 + 2.50 + 0.95 = 9.00. Ratio leg I / carapace width: 3.69.
Male. Carapace length range, 1.50 to 2.50. Specimen KS.118804. Total length, 5.19; carapace length, 2.38; width, 2.10; height, 0.80; caput width, 1.05; clypeus height, 0.08; abdomen length, 3.05; width, 1.65; labium length, 0.30; width, 0.36; sternum length, 1.30; width (max), 1.16; Eyes: AME, 0.21; PME, 0.21; ALE, 0.15; PLE, 0.25; EGW, 0.93 MOQAW, 0.44; MOQPW, 0.50; MOQL, 0.49. Limbs (femur + (patella-tibia) + metatarsus + tarsus = total): pedipalp, 0.95 + 0.75 + + 1.08 = 2.78; leg I, 2.55 + 3.30 + 1.95 + 0.90 = 8.70; leg II, 2.60 + 3.20 + 2.00 + 0.90 = 8.70; leg III, 2.45 + 2.80 + 2.15 + 0.95 = 8.35; leg IV, 2.80 + 3.40 + 2.85 + 1.15 = 10.20. Ratio leg I / carapace width: 4.14.

Material Examined

Australia, NEW SOUTH WALES. 1 ♀ (KS.101476), Barrington Tops National Park, Gloucester River Campground, 32°03′38″S, 151°41′13″E, 30 May 2007, H.M. Smith. 1 ♀ (KS.104156), Barrington Tops National Park, [as previous], 30 Jan 2008, beat/sweep and hand collecting, G.A. Milledge, A.D. Hegedus. 1 ♀ (KS.101474), Barrington Tops National Park, Gloucester Tops, Antarctic Beech walk, 32°05′19″S, 151°35′43″E, 30 May 2007, H.M. Smith. 1 ♀ (KS.103238), Barrington Tops National Park, Honeysuckle Picnic Area, 31°54′03″S, 151°32′01″E, 1300 m, 18 Mar 2008, night collecting, G.A. Milledge, A.D. Hegedus. 2 ♀ (KS.102237), 1 ♂, 1 ♀ (KS.103289), 1 ♂, 3 ♀ (KS.104160), Barrington Tops Reserve, Barrington Trail, 31°56′37″S, 151°26′53″E, 1350 m, 30 Apr 2008, 19 Mar 2008, 31 Jan 2008, beat, sweep, litter and under bark, G.A. Milledge, A.D. Hegedus. 1 ♂ (KS.103286), Barrington Tops Reserve, Gummi Rd, Manning River crossing, 31°51′41″S, 151°33′07″E, 1109 m, 19 Mar 2008, beat, sweep and under bark, G.A. Milledge, A.D. Hegedus. 1 ♀ (KS.118802), Barrington Tops Reserve, Nth Branch Rd. 0.4 km from Pheasant Ck Rd, 31°52′41″S, 151°29′32″E, 1225 m, 18 Mar 2008, beat/sweep and hand collecting, G.A. Milledge, A.D. Hegedus. 1 ♀ (KS.101692), Barrington Tops State Forest, Cobark Lookout rest area, 31°53′45″S, 151°36′06″E, 25 Sep 2007, G.A. Milledge. 1 ♀ (KS.101472), Barrington Tops State Forest, Dilgry Circle, Dilgry River crossing, 31°53′20″S, 151°32′19″E, 1189 m, 29 May 2007, H.M. Smith. 4 ♀ (KS.101477), Barrington Tops State Forest, 31°54′01″S, 151°37′49″E, 29 May 2007, H.M. Smith. 1 ♂ (KS.40379), Barrington Tops State Forest, Tugalow Creek, eastern side of Barrington Trail, 31°54′41″S, 151°26′38″E, 1370 m, 4 Feb-9 Apr 1993, pitfall, M.R. Gray, G.A. Cassis. 1 ♂ (KS.115449), Carrai State Forest, 30°54′35″S, 152°16′26″E, 1090 m, 3-8 Dec 1997, sticky trap, E. Tasker. 2 ♀ (KS.101475), Copeland Tops State Forest, near Sleepy Hollow Trail, 31°58′30″S, 151°47′49″E, 28 May 2007, H.M. Smith. 1 ♀ (KS.43759), Mt Allyn nr Barrington Tops, 32°08′S, 151°26′E, Sep 1993, G.S. Hunt, Bark scraped from *Nothofagus* trunks. 1 ♀ (KS.101652), Stewarts Brook State Forest, Polblue Ridge Rd, 0.4 km N of Barrington Tops Forest Rd, 31°56′54″S, 151°23′46″E, 25 Sep 2007, under bark and logs, sclerophyll. 1 ♀, 1 ♂ (KS.103221), Stewarts Brook State Forest, [as previous], 15 Nov 2007, under bark and logs, G.A. Milledge, A.D. Hegedus, L. Kampen. 1 ♂ (KS.65898), Toonumbar National Park, 5 km S Hanrahans, Murray Scrub Rd, 28°28′S, 152°43′E, 350 m, 17-18 Dec 1998, yellow pans, D. Bickel. 1 ♀ (KS.9235), Washpool State Forest, Coobadjah Ck, 0.6 km from Moongem Rd, 29°16′S, 152°22′E, 13 Feb 1982, C. Horseman. 1 ♂ (KS.115467), Werrikimbe National Park, 31°11′56″S, 152°10′23″E, 1025 m, 1 Dec 1997, sticky trap, E. Tasker. 1 ♀ (KS.66689), Werrikimbe National Park, [as previous], 9-14 Apr 1998, sticky trap, E. Tasker, on *E. cameronii*. 1 ♂ (KS.66670), Werrikimbe National Park, 31°10′23″S, 152°09′45″E, 1060 m, 3-8 Jul 1998, sticky trap, E. Tasker, on *E. divea*. 1 ♂ (KS.66672), Werrikimbe National Park, 31°11′24″S, 152°09′39″E, 1030 m, 3-8 Jul 1998, sticky trap, E. Tasker, on *E. cameronii*. 1 ♀ (KS.66688), Werrikimbe National Park, 31°16′50″S, 152°03′19″E, 1045 m, 29 Jan-4 Feb 1998, sticky trap, E. Tasker, on *E. campanulata*. 2 ♂, 1 ♀ (KS.115440), Werrikimbe National Park, Gunny Bag, 31°16′42″S, 152°05′05″E, 1040 m, 1-7 Dec 1997, sticky trap, E. Tasker. QUEENSLAND. 1 ♀, 1 ♂ (KS.103220), Tingalpa Creek, Buhot Creek Reserve, 27°35′27″S, 153°10′19″E, 17 Feb 2008, beat, sweep and under bark, H. Smith, G. Anderson. Lamington [SEM of male palp from Lamington specimen sent by R.J. Raven, actual specimens not examined].

Discussed specimens of uncertain status: NEW SOUTH WALES. 2 ♂ (KS.31719, KS.31742), ‘Scalloway’, Willowvale, 34°44′11″S, 150°47′23″E, 6 Dec 1986 and 11 Mar 1987, in pool, G. Wishart; 1 ♂ (KS.119166), 1 ♀ (KS.119075), Mount Gibraltar Reserve, S of Mittagong, 34°27′59″S, 150°25′48″E, 17 Sep 2012, under bark, G. Milledge, H. Smith, female adult at collection, male matured c. 1 Oct 2012.

Distribution

Australia: Great Dividing Range from Barrington area of New South Wales to south-eastern Queensland (Fig. 16, includes Lamington record). Three males from the Illawarra area south of Sydney, show very slight variations in the pedipalp; however, the only co-collected female has quite different duct configuration (looking more like a banded-legged *T. macleayi*). Further males and females are required to assess this population.

Comments

The northern females have shorter, more tightly looped, copulatory ducts and the sinuous path of the ventral duct may be straightened. As in other species, there is considerable variation in size and colour. In *T. erici* the northern specimens are smallest by far (the large female holotype is typical of Barrington specimens). When alive, some specimens have a bright white terminal spot on the dorsal abdomen.

Toxopsoides kathleenae **sp. nov.**

(Figs 6c, 10-12, 16)

Type Material

Australia, NEW SOUTH WALES. Holotype ♀ (KS.118805), Watagans National Park, Watagans Forest Rd, 33°02′17″S, 151°22′27″E, 20 Mar 2012, beat/sweep and hand collecting, G.A. Milledge, H.M. Smith. Paratypes: 1 ♂ (KS.118806), 2 ♂, 1 ♀ (KS.118165), data as holotype. 1 ♀ (KS.74975), Hornsby, Waitara Creek, 33°42′52″S, 151°05′22″E, 28 Oct 2001, G.A. Milledge, H.M. Smith. 1 ♀ (KS.100617), 1 ♂ (KS.100621), Hornsby, Waitara Creek, [as previous], 29 Apr 2007, G.A. Milledge, H.M. Smith.

Etymology

This species is named in honour of my mother, Kathleen Smith, for her encouragement of independent thought.

Diagnosis

Leg femora darkening distally but without, or with only vague, banding distinguishes specimens from *T. huttoni* and *T. erici* (Fig. 10a,b). Female: from all other species by short, broad area of spermatheca and ducts in ventral view (broader than long, or subequal) and prominent, broad ventral distal loop (Fig. 11a). Male: from faded *T. huttoni* and *T. erici* by presence of anterior prong from tegular extension (pointer Fig. 12d); from *T. macleayi* by short embolus, visible over c. 1/2 height of bulbus in prolateral view (Fig. 12a, cf. 2/3 in *T. macleayi*, Fig. 15a).

Description

Generally similar to *T. huttoni* except in coloration and genitalia, as follows. Female. Carapace with similar patterning but suffused dark brown overall (Fig. 10a); abdomen generally dark dorsally with paler patterning of variable extent along midline; legs without strong dark markings. Epigynum with strong posteriorly pointing foveal teeth (Fig. 11b). Spermathecae rounded; in ventral uncleared view copulatory duct visible looping around anterior spermatheca and passing posteriorly medially (Fig. 11a); ducts relatively broad. Male. Colour similar to female but legs usually paler (Figs 10b-d). Tegular envelope with anterior prong (Figs 6c, 12c, d); embolus shorter than most *T. huttoni*. Conductor comma-shaped, with small rugose prominence and cup-like hollow separating fold enclosing embolus (embolus just visible in cleft between tegulum and tegular process in Fig. 6c). Cleft between tegulum and tegular process narrower than in *T. huttoni* and shorter than in *T. erici*.

Measurements (in mm). Female. Carapace length range, 1.65 to 2.10. Specimen KS.118805. Total length, 5.31; carapace length, 2.10; width, 1.70; height, 0.95; caput width, 1.03; clypeus height, 0.06; abdomen length, 3.05; width, 2.05; labium length, 0.28; width, 0.35; sternum length, 1.10; width (max), 1.00; Eyes: AME, 0.18; PME, 0.20; ALE, 0.13; PLE, 0.24; EGW, 0.86 MOQAW, 0.36; MOQPW, 0.48; MOQL, 0.44. Limbs (femur + (patella-tibia) + metatarsus + tarsus = total): pedipalp, 0.75 + 0.88 + + 0.78 = 2.40; leg I, 1.80 + 2.64 + 1.44 + 0.60 = 6.48; leg II, 1.84 + 2.40 + 1.40 + 0.64 = 6.28; leg III, 1.76 + 2.16 + 1.56 + 0.48 = 5.96; leg IV, 2.08 + 2.68 + 2.08 + 0.92 = 7.76. Ratio leg I / carapace width: 3.81. Male. Carapace length range, 1.35 to 2.20. Specimen KS.118806. Total length, 4.31; carapace length, 2.10; width, 1.80; height, 0.83; caput width, 0.98; clypeus height, 0.05; abdomen length, 2.35; width, 1.40; labium length, 0.25; width, 0.35; sternum length, 1.15; width (max), 1.03; Eyes: AME, 0.19; PME, 0.19; ALE, 0.10; PLE, 0.21; EGW, 0.81 MOQAW, 0.39; MOQPW, 0.44; MOQL, 0.44. Limbs (femur + (patella-tibia) + metatarsus + tarsus = total): pedipalp, 0.78 + 0.68 + + 0.88 = 2.33; leg I, 2.28 + 3.08 + 1.80 + 0.76 = 7.92; leg II, 2.40 + 3.00 + 1.76 + 0.80 = 7.96; leg III, 2.24 + 2.72 + 1.88 + 0.76 = 7.60; leg IV, 2.52 + 3.20 + 2.60 + 1.00 = 9.32. Ratio leg I / carapace width: 4.40.

Figure 10. ***Toxopsoides kathleenae*** **sp. nov. a, Female (holotype) habitus, dorsal; b, d, male (KS.118806), habitus, dorsal, ventral; c, male (KS.118808), live (photo Carl Bento, Australian Museum).**

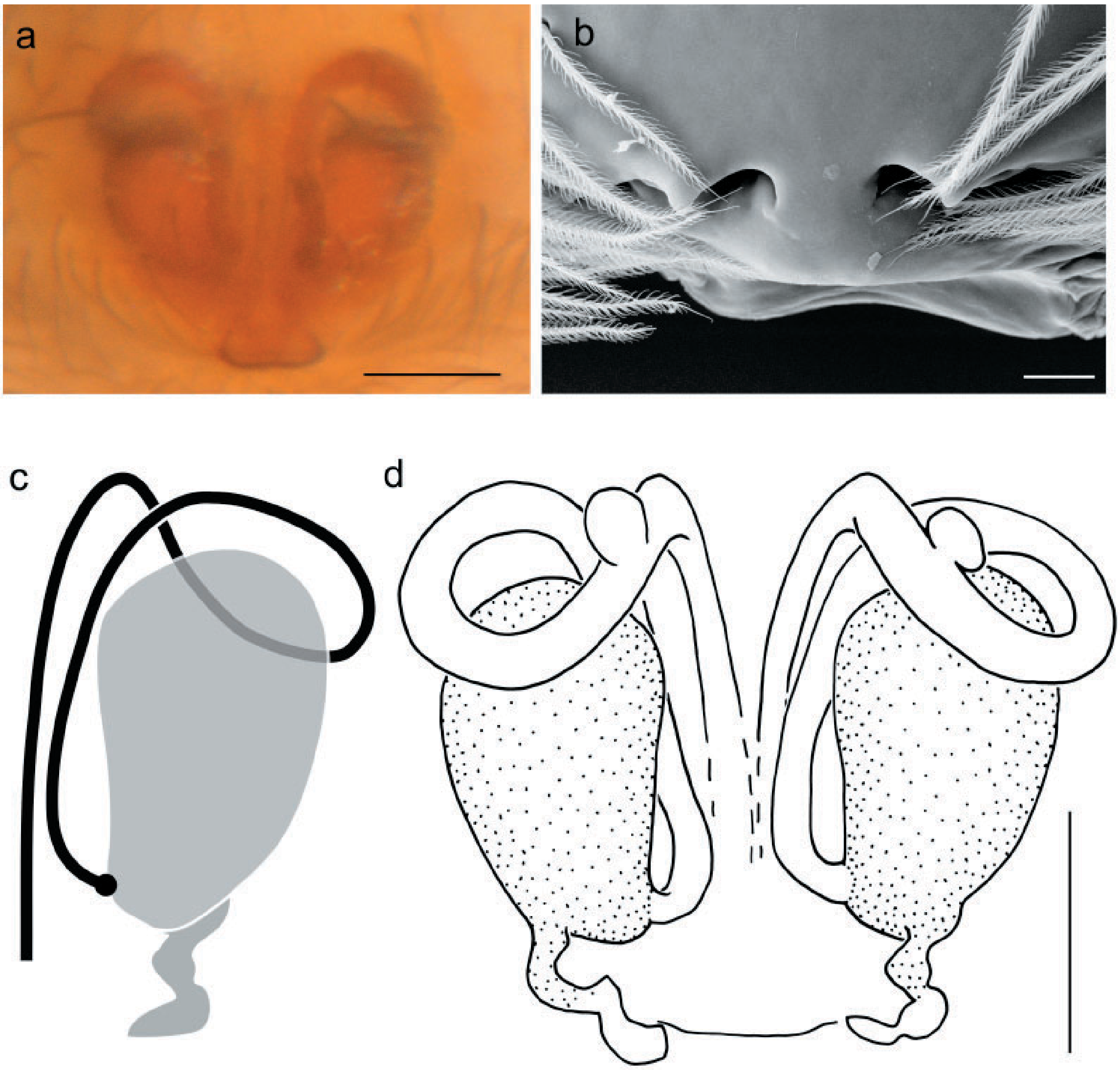

Figure 11. ***Toxopsoides kathleenae*** **sp. nov., female genitalia. a, Ventral photograph (KS.74975); b, epigyne detail of foveae (unregistered specimen, The Glen); c, diagrammatic ventral view of left spermatheca and duct based on Fig. 11d; d, dorsal (internal), cleared (KS.118222). Scale bars a, d, 0.1 mm; b, 20 µm.**

Material Examined

Australia, NEW SOUTH WALES. 3 ♂ (KS.115756), Berowra Valley Regional Park, fire trail, 33°39′25″S, 151°06′51″E, 1 May 2011, beat/sweep and hand collecting, G.A. Milledge, H.M. Smith. 1 ♂ (KS.118234), Heaton State Forest, Macleans Lookout, 32°57′27″S, 151°25′03″E, 463 m, 21 Mar 2012, beat, sweep, litter and hand collecting, G.A. Milledge, H.M. Smith. 1 ♀ (KS.100618), 1 ♂ (KS.100619), 1 ♂ (KS.100622), 2 ♂, 1 ♀ (KS.101480), 1 ♀ (KS.79603), Hornsby, Waitara Creek, 33°42′52″S, 151°05′22″E, 29 Apr 2007 (2), 22 Apr 2007, 11 Jun 2007, 20 Jul 2002, G.A. Milledge, H.M. Smith. 3 ♂, 1 ♀ (KS.118808), Hornsby, [as previous], 20 May 2007, under bark (1 ♂ on SEM stubs s/684, s/685). 1 ♀ (KS.49770), Jamieson Park Narrabeen, 33°43′S, 151°18′E, 5 m, 6-20 Nov 1995, pitfall trap, M.R. Gray, H.M. Smith, *Eucalyptus botryoides* - *Allocasuarina torulosa* open forest. 1 ♂ (KS.69222), Kirkconnell, 33°27′S, 149°51′E, 13 Apr 1972, G.S. Hunt. 1 ♀ (KS.111113), Mount Colah, Berowra Valley Regional Park, 33°39′29″S, 151°06′50″E, 4 Apr 2010, hand collected, G.A. Milledge, H.M. Smith. 1 ♂ (KS.87619), Rookwood Cemetery, 33°52′S, 151°04′E, 13 Jul 1969, D. Grant. 1 ♂, 1 ♀ (KS.101490), 2 ♂ (KS.104129), 1 ♂ (KS.104130), 1 ♀ (KS.104131), 1 ♂ (KS.104132), 1 ♀ (KS.104133), The Glen Nature Reserve, Etheridges Rd, off Glen

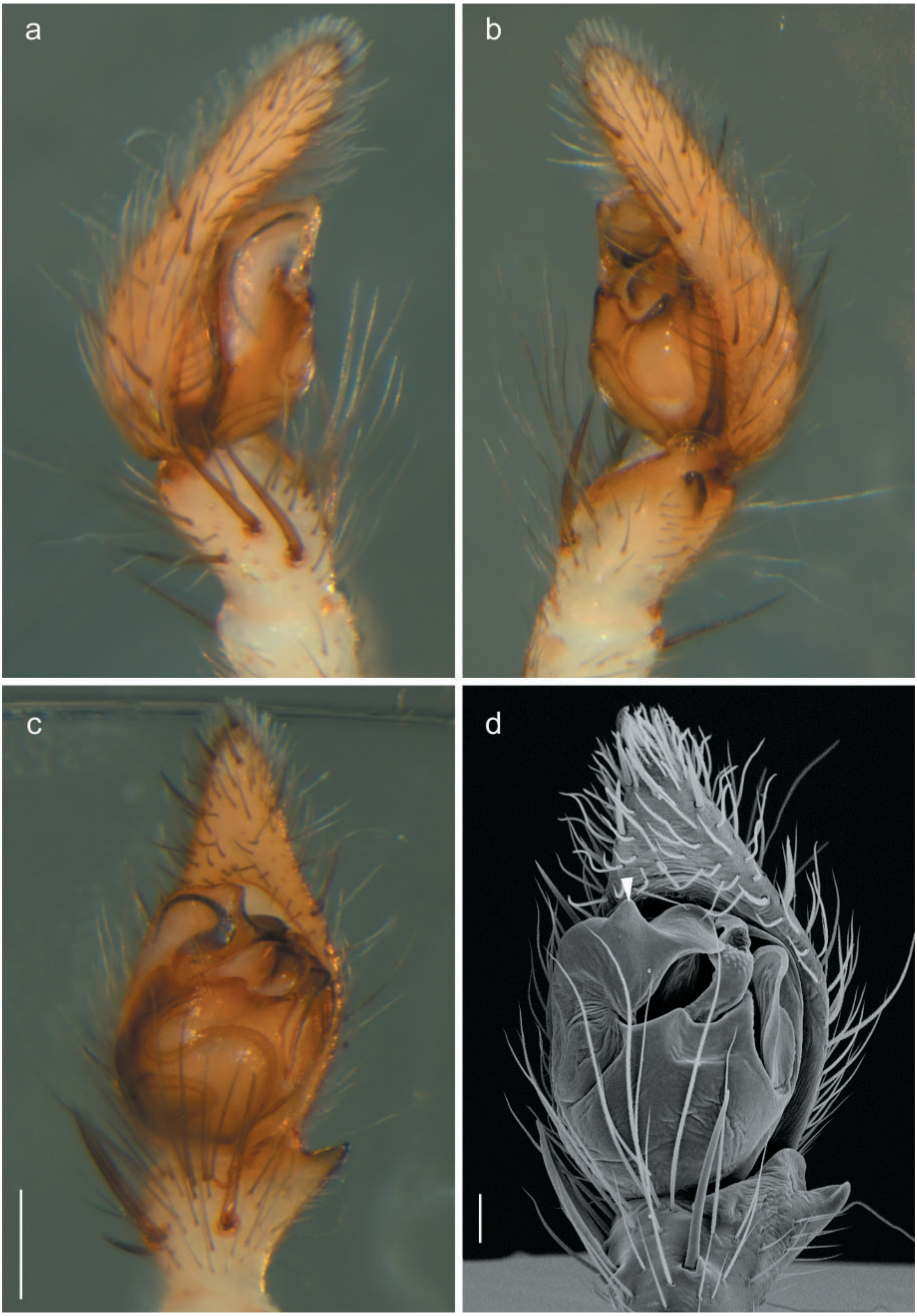

Figure 12. ***Toxopsoides kathleenae*** **sp. nov., male left pedipalps. a-c, Prolateral, retrolateral and ventral (KS.118806); d, ventral SEM (KS.118808), pointer indicates anterior prong. Scale bars: c, 0.2 mm; d, 60 µm.**

Figure 13. ***Toxopsoides macleayi*** **sp. nov. a, b, Female (KS.106059): a, habitus, dorsal; b, habitus, ventral; c, male (KS.119067), habitus, dorsal.**

Rd, 32°09′56″S, 152°00′16″E, 2 Jun 2007, H.M. Smith. 1 ♂, 1 ♀ (KS.101488), 1 ♂, 1 ♀ (KS.101489), The Glen Nature Reserve, junction of Glen Rd and McKays Trail, 32°09′59″S, 152°00′06″E, 2 Jun 2007, H.M. Smith. 1 ♀ (KS.118298), Watagans National Park, fire trail near Sandy Knob, 33°02′42″S, 151°21′56″E, 492 m, 22 Mar 2012, beat/sweep and hand collecting, G.A. Milledge, H.M. Smith. 1 ♂, 3 ♀ (KS.118222), Watagans National Park, Georges Rd, 1 km W of Heaton Rd, 32°58′12″S, 151°23′26″E, 415 m, 21 Mar 2012, beat/sweep and hand collecting, G.A. Milledge, H.M. Smith. 2 ♂, 1 ♀ (KS.118283), Watagans National Park, Watagans Forest Rd, Jilliby State Conservation Area, 33°03′01″S, 151°20′07″E, 398 m, 22 Mar 2012, G.A. Milledge, H.M. Smith. 1 ♂ (KS.118181), Watagans National Park, Watagans

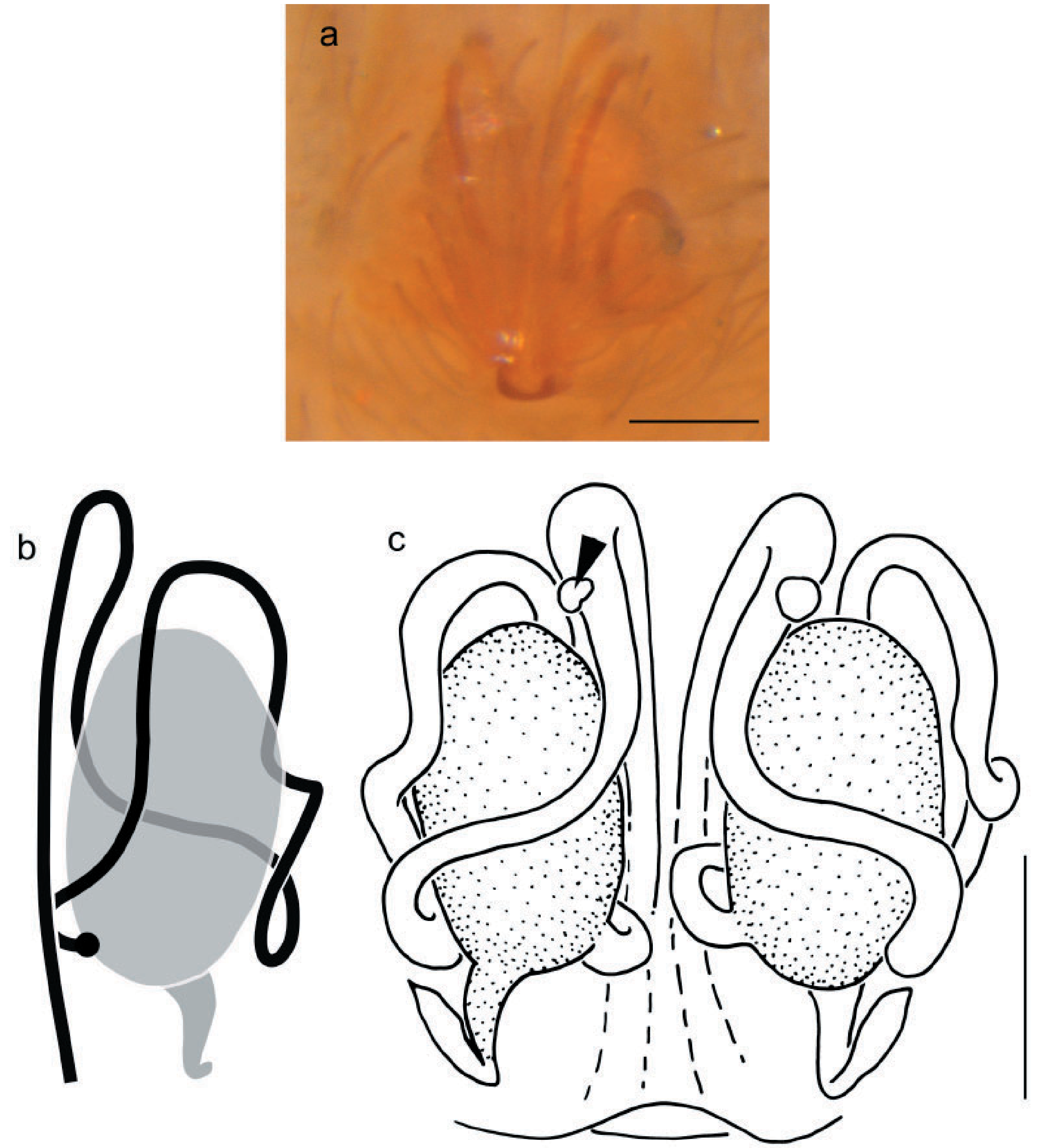

Figure 14. *Toxopsoides macleayi* sp. nov., female genitalia. a, Ventral photograph (KS.119069); b, diagrammatic ventral view of left spermatheca and duct based on Fig. 14c; c, dorsal (internal), cleared (KS.106059). Pointer indicates nodule. Scale bars 0.1 mm.

Forest Rd, near old quarry, 33°00′32″S, 151°23′43″E, 20 Mar 2012, beat/sweep and hand collecting, G.A. Milledge, H.M. Smith.

Distribution

Australia: Sydney Basin and Hunter region (Fig. 16). A possible distribution west of the Blue Mountains indicated by the single male from Kirkconnell (KS.69222) requires further specimens for confirmation.

Comments

Specimens from the Sydney Basin are almost all smaller than those from further north. The single male from west of the Blue Mountains is similar to those from the northern populations. Some Sydney specimens were noted to have a bright yellow-orange terminal spot on the dorsal abdomen when alive. Specimens almost devoid of paler markings are quite common in this species and *T. macleayi*.

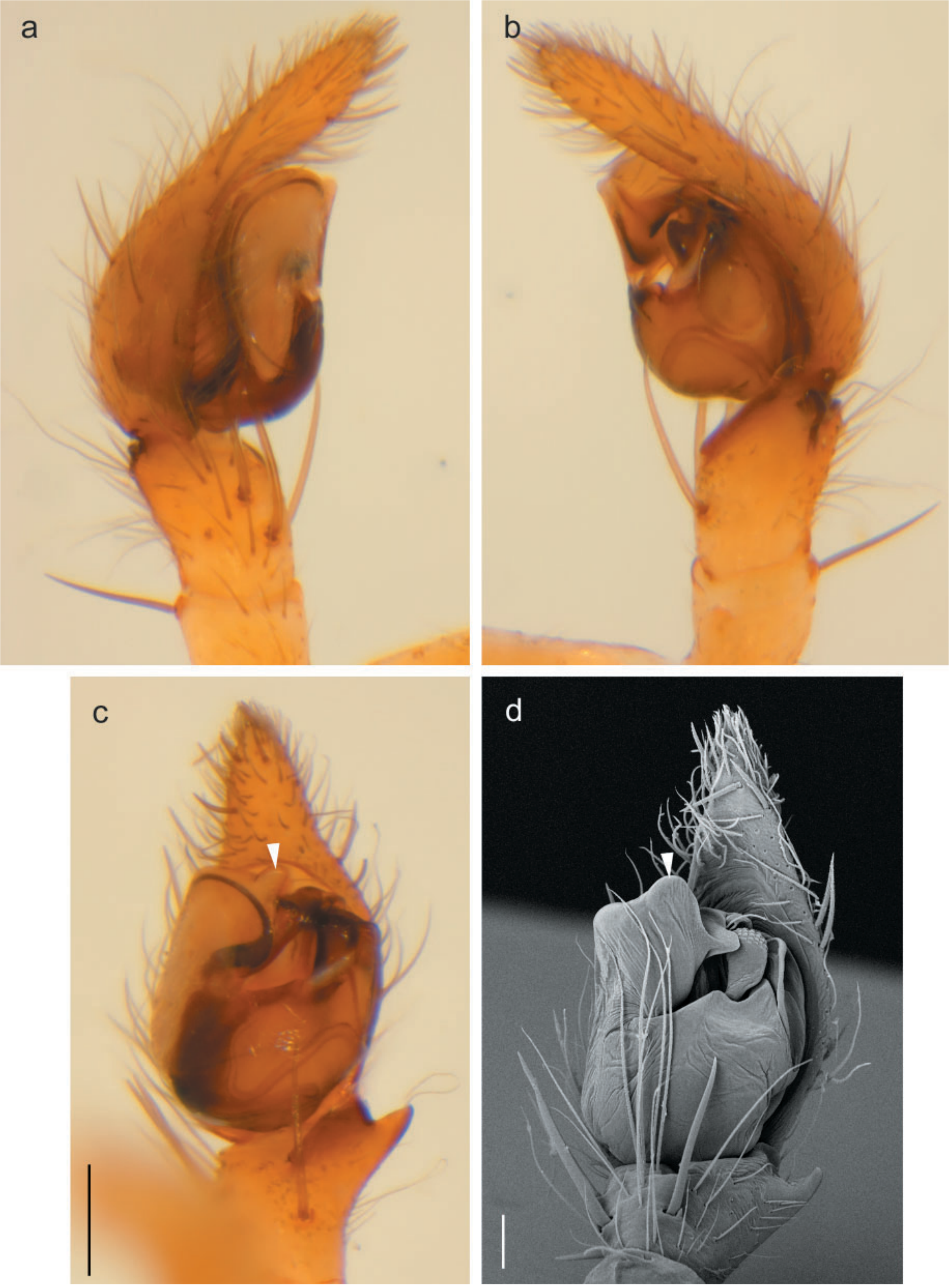

Figure 15. ***Toxopsoides macleayi*** **sp. nov., male left pedipalps. a-c, Prolateral, retrolateral and ventral (KS.119067); d, ventral SEM (KS.115589). Scale bars: c, 0.2 mm; d, 0.1 mm. Pointers in c, d indicate anterior prong.**

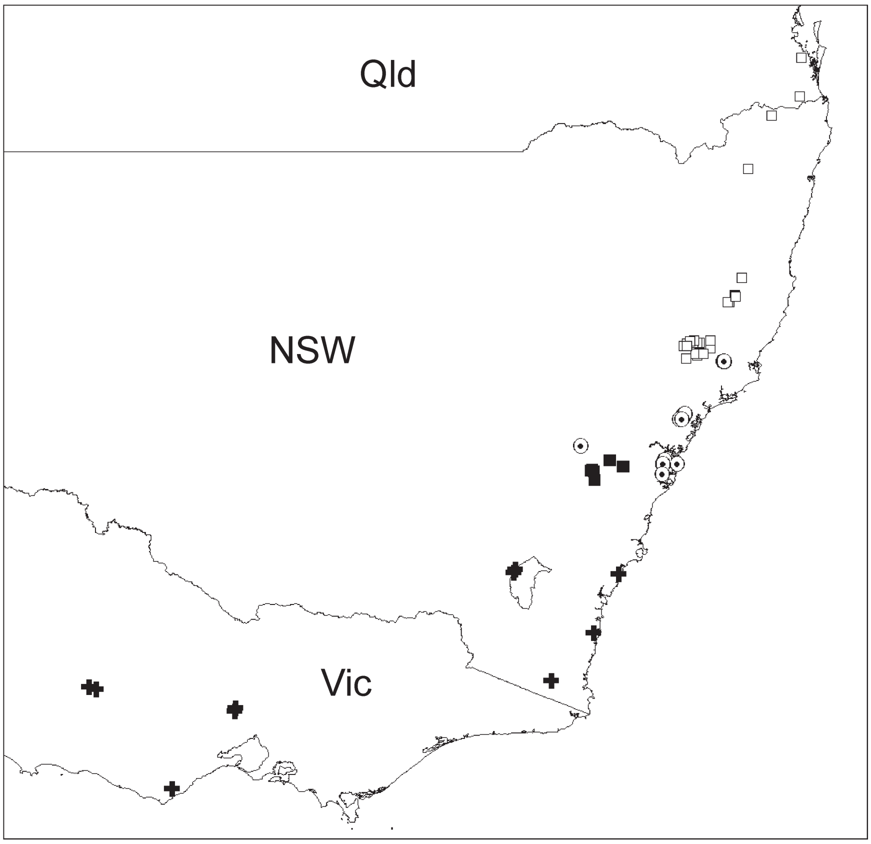

Figure 16. Map of south-eastern Australia, showing the Australian distributions of the four *Toxopsoides huttoni* group species. [+] *T. huttoni* Forster and Wilton; [unfilled square] *T. erici* sp. nov.; [circle/dot] *T. kathleenae* sp. nov.; [filled square] *T. macleayi* sp. nov.

***Toxopsoides macleayi* sp. nov.**

(Figs 6d, 13-16)

Type Material

Australia, NEW SOUTH WALES. Holotype ♀ (KS.119277), Blue Mountains National Park, Murphy's Glen camping area, S of Woodford, 33°46′07″S, 150°29′11″E, 3 Nov 2008, night collecting, G.A. Milledge, H.M. Smith. Paratypes: 2 ♀ (KS.106059), data as holotype. 1 ♂, 1 ♀ (KS.119067, KS.119069), Medlow Bath, 33°41′S, 150°17′E, under bark on gum tree, M. Ward colln. 1 ♂ (KS.22538), Jenolan Caves Area, Southern Limestone Area, 33°49′S, 150°02′E, 14 Aug 1989, pitfall trap, G.S. Hunt.

Etymology

This species is named for the Macleay Museum in The University of Sydney. Several specimens were unearthed as a result of work carried out under the Macleay Miklouho-Maclay Fellowship.

Diagnosis

Leg femora mottled or darkening distally but without distinct banding distinguishes specimens from *T. huttoni* and *T. erici* (Fig. 13a). Female: from all other species by narrow posterior plate and three narrow loops of copulatory ducts in ventral view, including one lateral loop (Fig. 14a, b). (See comment about similar undescribed female, below). Male: from faded *T. huttoni* and *T. erici* by presence of anterior prong from tegular extension (Figs 15c, d); from *T. kathleenae* by long embolus, visible over c. 2/3 height of bulbus in prolateral view (Fig. 15a, cf. 1/2 in *T. kathleenae*, Fig. 12a).

Description.

Generally similar to *T. kathleenae* except in genitalia, as follows. Female. Epigynum with long thin posteriorly pointing foveal teeth. Spermathecae long ovoid; in ventral uncleared view (Fig. 14a) copulatory ducts often visible from fovea onwards; three separate loops visible, including small lateral loops; ducts rather narrow. Male. Pedipalp: similar to *T. kathleenae*, with anterior tegular prong and similar conductor shape, but embolus long, as in *T. erici* (Fig. 15a, c). Cleft between tegulum and tegular process similar to *T. kathleenae*.

Measurements (in mm). Female. Carapace length range, 1.85 to 2.30. Specimen KS.119277. Total length, 4.65; carapace length, 1.85; width, 1.53; height, 0.84; caput width, 0.94; clypeus height, 0.06; abdomen length, 2.90; width, 2.05; labium length, 0.23; width, 0.29; sternum length, 1.00; width (max), 0.88; Eyes: AME, 0.14; PME, 0.19; ALE, 0.13; PLE, 0.23; EGW, 0.80 MOQAW, 0.34; MOQPW, 0.44; MOQL, 0.40. Limbs (femur + (patella-tibia) + metatarsus + tarsus = total): pedipalp, 0.68 + 0.80 + + 0.70 = 2.18; leg I, 1.68 + 2.28 + 1.32 + 0.60 = 5.88; leg II, 1.60 + 2.12 + 1.28 + 0.60 = 5.60; leg III, 1.60 + 1.92 + 1.24 + 0.64 = 5.40; leg IV, 1.92 + 2.44 + 1.88 + 0.80 = 7.04. Ratio leg I / carapace width: 3.84. Male. Carapace length range, 1.95 to 2.25. Specimen KS.119067. Total length, 4.30; carapace length, 1.95; width, 1.72; height, 0.72; caput width, 0.97; clypeus height, 0.04; abdomen length, 2.45; width, 1.30; labium length, n/a; width, 0.30; sternum length, 1.13; width (max), 0.98; Eyes: AME, 0.16; PME, 0.18; ALE, 0.11; PLE, 0.21; EGW, 0.79 MOQAW, 0.34; MOQPW, 0.43; MOQL, 0.39. Limbs (femur + (patella-tibia) + metatarsus + tarsus = total): pedipalp, 0.78 + 0.68 + + 0.88 = 2.33; leg I, 2.20 + 3.08 + 1.76 + 0.76 = 7.80; leg II, 2.16 + 2.92 + 1.80 + 0.76 = 7.64; leg III, 2.20 + 2.68 + 1.92 + 0.76 = 7.56; leg IV, 2.56 + n/a + n/a + n/a = n/a. Ratio leg I / carapace width: 4.53.

Material Examined

Australia, NEW SOUTH WALES. 1 ♀ (KS.106075), Blue Mountains National Park, Murphy's Glen camping area, S of Woodford, 33°46′07″S, 150°29′11″E, 4 Nov 2008, night collecting, G.A. Milledge, H.M. Smith. 2 ♀ (KS.119068, KS.119070), Medlow Bath, 33°41′S, 150°17′E, under bark on gum tree, M. Ward colln. 1 ♀ (KS.30002), Kanangra-Boyd National Park, Blood Filly Creek near Jenolan Caves, 33°51′S, 150°03′E, 27 Mar 1976, in logs, M.R. Gray, G.S. Hunt, J. McDougall. 1 ♀ (KS.106136), Kanangra-Boyd National Park, Boyd River campsite, 33°58′18″S, 150°03′21″E, 5 Nov 2008, night collecting, G.A. Milledge, H.M. Smith. 1 ♂ (KS.115589), Mt Edwards, Boyd Plateau, 33°50′S, 150°00′E, 15 May 1971, under log, M.R. Gray.

Distribution

Australia: Great Dividing Range to the west and south-west of Sydney (Fig. 16).

Comments

None of the three males known for this species is in perfect condition, but the one used for measurements represents the only one to be from the same locality as the females of the species. The male specimen used for SEM (KS.115589) has a rather broader anterior tegular prong than the other two males (and this part of the palp has warped in SEM preparation), but appears to agree otherwise. The described male has eight pairs of ventral tibial macrosetae on left leg one, i.e. one more than other described specimens of the *T. huttoni* group; on the right are seven large and one small macrosetae on the prolateral side (matching the left) but one large macroseta is missing from the retrolateral sequence; here macrosetae spread out to fill the space, so they are no longer paired (offset visible in Fig. 13c).

A female from the Illawarra area south of Sydney, discussed under *T. erici*, has superficially similar epigynum and ducts to *T. macleayi* in ventral view (although the lateral loops are more anterior); however the legs of that specimen (like *T. erici*) are strongly banded, and the course of the copulatory ducts can be seen to be quite dissimilar when traced in the excised epigynum. Very darkly coloured specimens were found in Blue Mountains specimens of this species and in *T. kathleenae*.

DISCUSSION

Toxopsoides is a rather a mysterious element of the New Zealand fauna. The male and female spiders later described as *Toxopsoides huttoni* were either overlooked or were not available to Ray Forster at the time of writing his Desidae volume (III) on New Zealand spiders (Forster 1970) and the species was added, under subfamily Toxopinae, in the final pages of Volume IV. The original description remains the only published record of the species, indeed the genus, in New Zealand (Vink et al. 2011: 35).

In Australia, the genus *Toxopsoides* has been recognised for many years (Davies 1986) but no specific name has been used. Based on material in the Australian Museum collections, I can report that *Toxopsoides* relatives can be found in all temperate forested areas of Australia, including Tasmania and the south-west of Western Australia, and northwards into the subtropics of south-east Queensland. The species that are most common in survey collections are from pitfall traps, which probably explains why it has taken so long to recognise *T. huttoni* itself, which is primarily a tree-trunk dweller.

Of the 22 *Toxopsoides* species tentatively identified under 'Toxopidae genus 1' in Gray and Cassis (1994) from the north-east forests of New South Wales, only one, *T. erici*, is described here; the other species belong among the relatives I have termed the *Toxopsoides* group. I have seen many more species belonging in these as yet undefined groups from southern NSW, from other states and the ACT. In several species I have examined in any detail the specific boundaries were unclear and there may be complexes. Even within the *T. huttoni* group, specific boundaries need much more work to fully comprehend. In many cases, populations from physically separated areas show slight, but consistent differences—or one sex appears identical whilst the apparently corresponding partner is different. Some examples are discussed under their relevant species entries above.

Not all *T. huttoni* group species known to me have been included here, but all species known from both sexes and paired with reasonable certainty have been described. Although many *Toxopsoides* specimens would no doubt be available through the other Australian museums, it is not the intention of this paper to thoroughly investigate species boundaries and variation. Rather, I wish to take the first steps to tie *T. huttoni* firmly to Australia and demonstrate that further closely related species occur here.

The final note here concerns the familial placement of *Toxopsoides*. The suite of characters listed in the generic diagnosis for species of the *T. huttoni* group do not fit neatly into any current family definition. Whilst some male palpal characters, such as the broad median apophysis and membrane-enclosed embolus, at least superficially resemble those seen in other taxa of Desidae (e.g. *Badumna* Thorell or *Phryganoporus* Simon), the grate-shaped tapetum is not currently recorded within that family—nor from any of the 'fused paracribellar clade' that otherwise held all the desid taxa tested by Griswold et al. (2005). Although the grate-shaped tapetum originally defined the Lycosoidea (Homann 1971), Gray and Smith (2002, 2008) substantiated the occurrence of the character in the non lycosoid family Stiphidiidae. Reviewing their own results (Griswold 1993, Griswold et al. 1999), and those of Silva Dávila (2003) and Raven and Stumkat (2005), Griswold et al. (2005) have concluded that the grate-shaped tapetum appears to have little phylogenetic value, and they no longer recover a monophyletic 'lycosoid' clade. Despite this, the combined characters of *Toxopsoides* (three claws, two rows of tarsal trichobothria lengthening distally, grate-shaped tapetum, pretarsus, strongly recurved eye rows, multiple paired macrosetae on venter of anterior tibiae and metatarsi, absence of locking tegular/subtegular lobes) appear to fit within a loose concept of Lycosoidea slightly better than the clades entirely lacking a grate shaped tapetum. However, with no satisfactory alternative at the present time, I leave *Toxopsoides* in the Desidae pending further research—a decision supported by researchers working on the higher systematics of Lycosoidea and related taxa (C.E. Griswold pers. comm.).

ACKNOWLEDGMENTS

I am grateful to Sue Lindsay for scanning electron microscopy; Carl Bento for the photograph of a live *T. kathleenae*, and Graham Milledge for assistance with field work and Australian Museum collection management matters. Mike Gray and Graham Milledge made helpful comments on earlier drafts and referees Mark Harvey and Robert Raven made useful suggestion for improvement. I also thank Charles Griswold and Robert Raven for discussions on the potential placement of the genus. This work was begun under an award from the Australian Museum and this publication has been prepared with support from the Australian Museum and Macleay Museum, University of Sydney through the author's Macleay Miklouho-Maclay Fellowship (2011-2012).

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Temporal changes in the Macroinvertebrate Fauna of two Glacial Lakes, Cootapatamba and Albina, Snowy Mountains, New South Wales

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Timms, B.V., Morton, J. and Green, K. (2013). Temporal changes in the Macroinvertebrate Fauna of two Glacial Lakes, Cootapatamba and Albina, Snowy Mountains, New South Wales. *Proceedings of the Linnean Society of New South Wales* **135**, 45-54.

Before 2003, unique assemblages of aquatic invertebrates in Lake Cootapatamba and Lake Albina lived in a fishless environment. A sequence of events in 2003 following a large-scale bushfire in the area allowed the native Mountain Galaxias *Galaxias olidus* to enter Lake Cootapatamba. This study determines the extent of any temporal changes in the invertebrate assemblages of each lake and whether the introduction of fish into Lake Cootapatamba affected these assemblages. The littoral and benthic fauna of both lakes were found to have changed since the earliest studies of these lakes in 1997/1998 and 1976, respectively. In particular, there has been a large decrease in the abundance of the isopod *Metaphreatoicus australis* and planarians, and the gastropod *Glacidorbis hedleyi* and amphipod *Neoniphargus* sp. have apparently disappeared. The effect is greatest in the benthos and in Lake Cootapatamba, so while fish seemed to have affected some invertebrates in some habitats, other factors may be acting. Sometime since 1976, the exotic worm *Lumbriculus variegatus* arrived into Lake Albina. Shifts in the representation of other taxa, such as ephemeropterans, plecopterans, tricopterans, dipterans and coleopterans, are thought to reflect natural year-to-year fluctuations but more data are needed.

Manuscript received 9 March 2013, accepted for publication 24 July 2013

KEY WORDS: benthos, fish predation, *Galaxias olidus,* littoral rocks, *Lumbriculus variegatus, Metaphreatoicus australis, Neoniphargus* sp.

INTRODUCTION

The five lakes (i.e. Lake Cootapatamba, Lake Albina, Blue Lake, Club Lake and Hedley Tarn) of the Snowy Mountains alpine area (sensu Costin 1957) support a unique assemblage of invertebrates (Bayly 1970; Timms 1980a; Benzie 1984; Hancock et al. 2000; Suter et al. 2002), with a few species endemic to these lakes (e.g. *Daphnia nivalis*) and others to alpine regions (e.g. *Tillyardophlebia alpina*) (Benzie 1984; Dean 1999). Before 2003, the two west draining lakes, Lake Cootapatamba and Lake Albina, did not contain fish and as a result had a different assemblage of invertebrates, both in species composition and relative numbers, compared to other alpine lakes in the region (Bayly 1970; Timms 1980a; Hancock et al. 2000). Specifically the isopod *Metaphreatoicus australis* and amphipod *Neoniphargus* sp. were more common in the fishless lakes, particularly in the benthos, while the chironomid *Chironomus oppositus*? was only common in two lakes with fish. The summer zooplankton was dominated by the conspicuous *Daphnia nivalis* and *Boeckella montana* in the two fishless lakes, but both were absent in Blue Lake with fish (Timms 1980a; Hancock et al. 2000).

With global warming already affecting the Snowy Mountains alpine area and its lakes (Green and Osborne 2012), it is important that biodiversity is monitored over time and that the possible influence of other extraneous environmental factors is also investigated. Following the landscape scale fires of January-February 2003, log jams formed pools beneath waterfalls in many creeks throughout the Snowy Mountains (Ken Green unpublished data). The native Mountain Galaxias *Galaxias olidus* (previous identified as *G. findlayi*), possibly utilized such pools beneath previously un-scalable waterfalls in the outflowing creek to gain access to Lake Cootapatamba (Green 2008). These fish are known to prey on various terrestrial and aquatic invertebrates (reviewed in Green and Osborne 2012) and it was assumed that by 2012 any influence these predatory fish had on the invertebrates of Lake Cootapatamba would have had time to be expressed. It is fortunate that Lake Cootapatamba had been part of a 'biodiversity blitz' ten years earlier (Timms 2002) so, together with Timms (1980a) and Hancock et al. (2000), baseline data were available previous to the fish invasion. At that time both Lake Cootapatamba and the nearby Lake Albina had a similar assemblage of invertebrates with high abundances of isopods and amphipods (Hancock et al. 2000), which are known prey items of *G. olidus* (reviewed in Green and Osborne 2012).

This study aimed to reassess Lake Cootapatamba and Lake Albina to determine temporal changes in their invertebrate assemblages and whether the introduction of fish into the former lake has affected these assemblages. It was assumed that the invertebrate assemblages in Lake Cootapatamba would have changed significantly since the arrival of *G. olidus*, notably with expected reductions in the abundance of isopods and amphipods, but this would not have occurred in Lake Albina over the same timeframe since it remains inaccessible to fish.

METHODS

The littoral fauna of Lake Cootapatamba and Lake Albina (Fig. 1) were sampled on two occasions in 2012 (14 February and 3-4 December). Established sampling protocols used by Timms (1980a) and Hancock et al. (2000) were employed including, where possible, the same sites used in these previous studies to allow temporal comparisons (Fig. 1). The effect of season on comparing the results of the present and past studies was minimised by all sampling occurring within the summer months of December to February. Littoral fauna were sampled at each site using cobble picks and net sweeps in waters of approximately 10-50 cm depth. Cobble picks consisted of selecting ten cobbles of approximately 20-40 cm diameter. A net was used to capture escapees when each cobble was overturned and these along with all invertebrates picked from the under-surface of the cobble were combined into a single replicate. Cobbles resting on other cobbles were selected as those resting on sediment were found not to have epifauna beneath them. The area of the under-surface of each cobble was estimated by measuring perpendicular diameters and counts were converted to abundances per m^2. Net sweeps consisted of a single 'kick' sample at each site where a net, mesh size 0.5 mm, was immediately swept through the water above sediment that was disturbed over a 10 x 1 m area and abundances were recorded as individuals per m^2. Benthic fauna to a depth of 5 cm were sampled at each site (Fig. 1) with four replicate Birge-Ekman grabs of 225 cm^2 gape in shallow (0.5 m) and deep (2-3 m) water depths. Collected sediment was passed through a 0.4 mm sieve and the remaining benthos was sorted live and preserved in 70% alcohol for later counts and identification in the laboratory. Benthic fauna were collected on a single occasion at Lake Cootapatamba (14 February) and Lake Albina (3-4 December). In March 2013 a household sieve, mesh size ca. 1 mm, was used to check for the presence of *Lumbriculus variegatus* in the littoral of the other lakes. Biomasses were estimated by blotted wet weights using a Sartorius top loading electronic balance (±0.001 g). The shells of molluscs and cases of caddis fly larvae were removed before weighing.

Assemblages associated with littoral cobbles, littoral sweeps and benthic fauna were compared with past studies, namely Timms (1980a), Hancock et al. (2000) and Timms (2002), and differences were visualised separately for each habitat using non-metric multidimensional scaling (nMDS) ordination plots in PRIMERv6 (Clarke and Gorley 2006). Separate nMDS plots for littoral cobbles and sweeps were also used to visualise differences in assemblages among sites at Lake Albina and Lake Cootapatamba for each sampling occasion in 2012. Before analyses, data for littoral sweeps and cobbles were square-root transformed, and data for benthic fauna were fourth-root transformed to reduce the influence of numerically abundant species and increase the importance of rare species. For littoral cobbles and sweeps, a two-way nested ANOSIM (Analysis of Similarities) (Clarke and Gorley 2006), with sampling occasions nested within lakes, was used to test the null hypotheses that assemblages did not differ between Lake Albina and Lake Cootapatamba in 2012, and that assemblages in each lake did not differ between the February and December sampling occasions. In ANOSIM tests, the magnitude of the associated *R*-statistic value was used to offer an absolute measure of difference between paired groups. In general, if $R>0.75$, groups

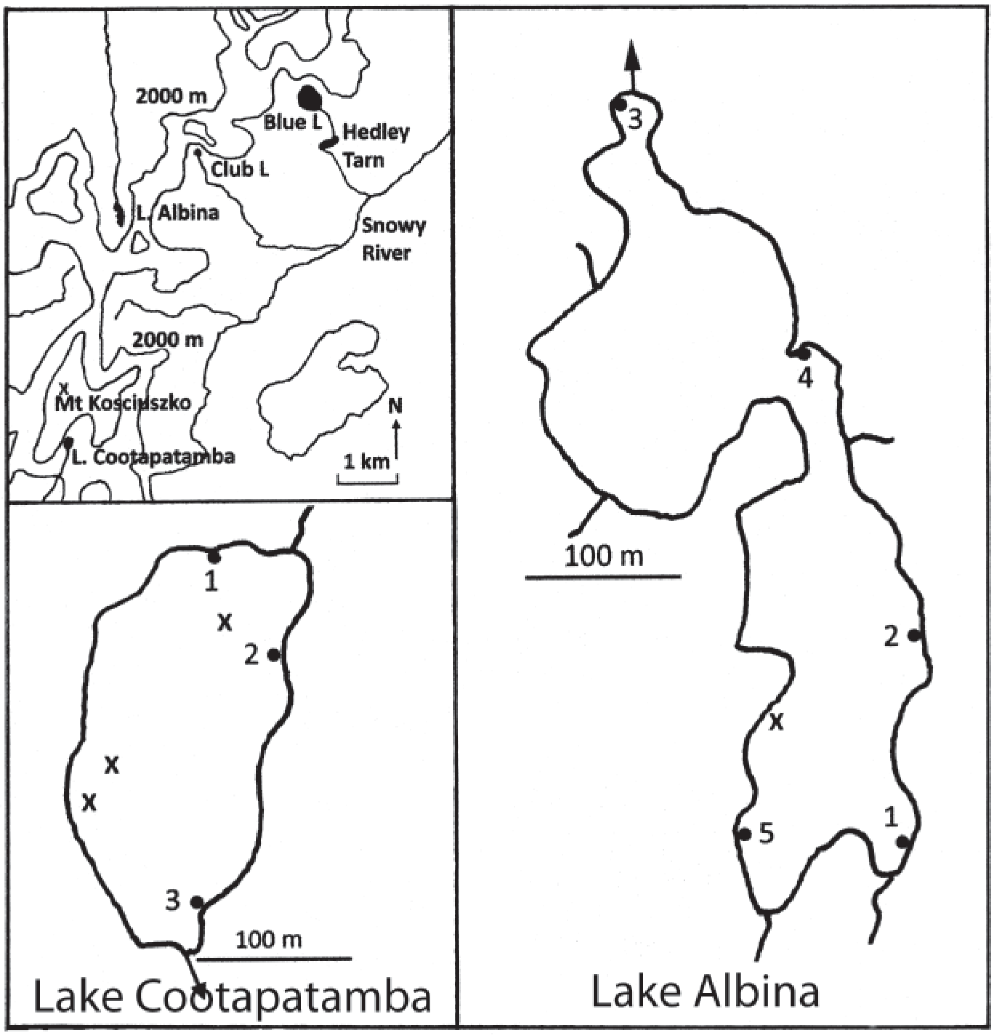


Figure 1: Index map of part of the Snowy Mountains region showing the locale of the five alpine lakes, including Lake Cootapatamba and Lake Albina. Littoral sites in these are marked with an ● and benthic sites with an x.

are clearly distinguishable, if R>0.5, groups overlap but are clearly different, and if R<0.25, groups are typically indistinguishable (Clarke and Gorley 2006). Generated p-values for comparing assemblages between lakes were not useful in the two-way nested ANOSIM design due to an insufficient number of permutations (i.e. 3), so a one-way ANOSIM was used instead. Both tests produced comparable R-statistic values but a sufficiently high number of permutations (i.e. 999) in the one-way ANOSIM provided for meaningful interpretations of p-values.

RESULTS

Littoral fauna

In total thirty-five taxa were found in the littoral of Lake Cootapatamba and Lake Albina with twenty-one of these occurring in both cobbles and sweep samples (Tables 1 and 2). In the littoral cobbles of both lakes there has been a substantial reduction in the abundance of platyhelminths and the isopod *Metaphreatoicus australis* since 1997-98, and the gastropod *Glacidorbis hedleyi* and the amphipod *Neoniphargus* sp., which were once especially abundant in Lake Cootapatamba, are now apparently absent from both lakes. In Lake Cootapatamba, the abundance of the trichopteran *Archeophylax ochreus* has increased and the trichopteran *Economus* sp. is now present but was not reported in previous studies (Tables 1a and 2a). In Lake Albina, plecopterans, tricopterans and dipterans have become especially abundant since Dec 97/Mar 98, and the oligocheate *Lumbriculus variegatus* is now common despite not being present in previous surveys (Tables 1b and 2b).

Table 1: Abundance of littoral fauna under cobbles in Lake Cootapatamba and Lake Albina over several years represented as numbers/m^2.

		a) Lake Cootapatamba				b) Lake Albina		
		Dec 97/ Mar 98$^{\#}$	Jan 02*	Feb 12	Dec 12	Dec 97/ Mar 98$^{\#}$	Feb 12	Dec 12
Platyhelminthes	Unidentified planarians	55.1	69	3.8	0.2	21.1		2.2
	Temnosewellia sp.		3					
Oligochaeta	Various tubificids[1]	1.5	5		0.2	3.5	2.1	
	Lumbriculus variegatus						2.1	16.7
Mollusca: Bivalva	*Pisidium kosciusko*		6			1.3		4.0
Mollusca: Gastropoda	*Glacidorbis hedleyi*	32.9	3			10.6		
Crustacea: Isopoda	*Metaphreatoicus australis*	19.6	61	0.7		61.6	3.3	2.2
Crustacea: Amphipoda	*Neoniphargus* sp.	128	107			0.9		
Insecta: Ephemeroptera	*Ameletoides lacusalbinae*	1.5	3		0.2	26.6	18.7	7.5
	Other Ephemeroptera[2]	31.5		20.2	14.1	11.4	4.0	18.5
Insecta: Plecoptera	*Eusthenia venosa*						1.1	0.5
	Notonemourid nymph			4.3	1.5		26.2	22.0
Insecta: Trichoptera	*Ecnomus* sp.			16.9	14.5	7.5	30.0	32.2
	Plectrocnemia sp.	5.4	2	4.1		4.3	15.5	15.4
	Austrorheithrus sp.						1.2	23.6
	Leptocerid larvae							0.1
	Archaeophylax ochreus	38.3	11	53.5	100	0.9		
	Triplectides varius		2					
Insecta:Diptera	*Procladius viliosimanus*		19			4		
	Other Chironomidae[3]					2.6	0.5	
	unidentified ceratopogonid				0.05			
Insecta: Coleoptera	*Sternopriscus* adults					1.3	1.1	4.2
	Sternopriscus larvae					5.3		
	Sclerocyphon sp.			0.7				
	Elmid adults (2 spp)					7.1		
	wet biomass (g/m^2)	3.9	n/a	5.9	1.2	3.9	4.6	19.4

from Hancock et al. (2000);
* from Timms (2002)
1 includes *Antipodrilus davidis, Antarctodrilus proboscidea* and *Dero furcatus*
2 includes *Nousia* sp., *Tasmanophlebia lacuscoerulei* and *Tillyardophlebia alpina*;
3 includes *Tanytarsus* sp.

Table 2: Abundance of littoral fauna in sweeps in Lake Cootapatamba and Lake Albina over several years represented as numbers/m^2.

		a) Lake Cootapatamba				b) Lake Albina		
Taxa	Species (if known)	Dec 97/ Mar 98#	Jan 02*	Feb 12	Dec 12	Dec 97/ Mar 98#	Feb 12	Dec 12
Platyhelminthes	Unidentified planarians		1		0.4	1.5		0.2
Oligochaeta	Various tubificids[1]	0.3	3	3.4	0.7	0.2	5	7.3
	Lumbriculus variegatus						12.4	18.4
Mollusca: Bivalva	*Pisidium kosciusko*	0.2	2	6.2	0.2	10.7	4.3	0.2
Mollusca: Gastropoda	*Glacidorbis hedleyi*					5.4		
Crustacea: Isopoda	*Metaphreatoicus australis*	16.8	25.4	4	1.3	32.1	2.3	10.3
Crustacea: Amphipoda	*Neoniphargus* sp.	11	5.2			0.3		
Insecta: Ephemeroptera	*Ameletoides lacusalbinae*	0.2			0.8	1.7	1.3	11.8
	Other Ephemeroptera[2]	0.5	1	0.4		1.1		16.4
Insecta: Plecoptera	Notonemourid nymph	0.05		1.3	0.2	0.1	0.8	3.2
Insecta: Hemiptera	*Micronecta* sp.						1	
	Sigara sp.	0.05						
Insecta: Trichoptera	*Ecnomus* sp.			0.13	0.4	0.2	0.6	7.9
	Plectrocnemia sp.	0.1		0.23		0.3	1.3	4.1
	Austrorheithrus sp.	0.05				0.1		
	Kosreithrus sp.		1					
	Leptocerid larvae					0.1	0.5	6.4
	Archaeophylax ochreus		1					
Insecta:Diptera	*Procladius villosimanus*		2	2.3	1.4	0.5	22	12.5
	Polypedilum sp.	0.1			0.1	0.2		3.2
	Chironomus sp.		1	10.3	0.3			1
	Other Chironomidae[3]					0.4	49	15.7
	Tipulid larvae					0.05		
Insecta: Coleoptera	*Antiporus femoralis*	0.05	1	0.05	0.2			
	Unidentified Scirtid larvae	0.05						
	Unidentified Curculionid		1					
	Sternopriscus adults					0.2	2.5	1
	Sternopriscus larvae					2.6		1
	Elmid adults (2 spp)					0.4		
	Elmid larvae					0.2		
	wet biomass (g/m^2)	2.6	n/a	3.6	1.8	7.8	5.3	7.6

from Hancock et al. (2000); * from Timms (2002)
1 includes *Antipodrilus davidis, Antarctodrilus proboscidea* and *Dero furcatus*
2 includes *Nousia* sp., *Tasmanophlebia lacuscoerulei* and *Tillyardophlebia alpina*;
3 includes *Tanytarsus* sp.

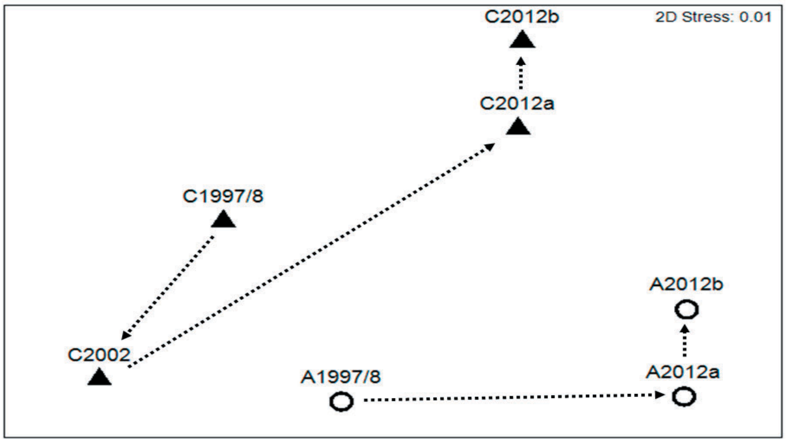
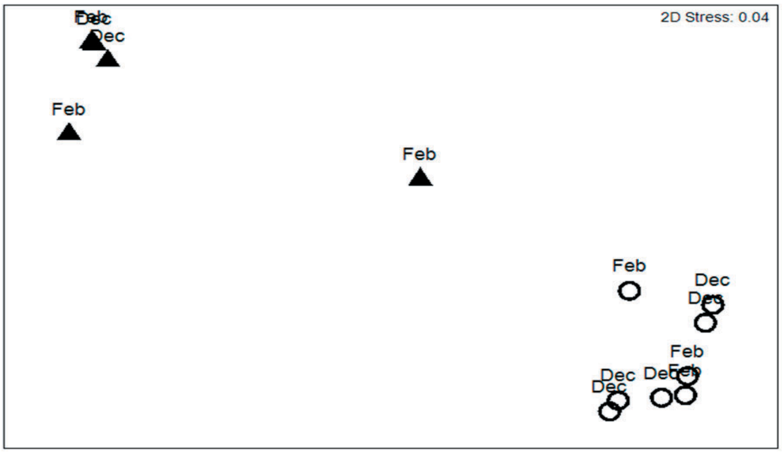


Figure 2: Assemblages associated with littoral cobbles in Lake Cootapatamba (▲) and Lake Albina (○) comparing: [a, left] previous overall assemblages (i.e. 1997/98 and 2002) with those in the present study and [b, below] site assemblages in both lakes on the two sampling occasions in 2012. In Fig. 2a, the February and December surveys in 2012 are represented as 2012a and 2012b, respectively, and arrows show progression through time.



These shifts in littoral cobble and sweep assemblages are illustrated in figures 2a and 3a, respectively, where points representing assemblages in Dec 97/Mar 98 are located toward the left of each plot and those for 2012 are located toward the right.

Proximity of points on the nMDS plot of Figure 2a revealed that the cobble assemblages of Lake Cootapatamba and Lake Albina have not diverged since Dec 97/Mar 98, as indicated by these lakes remaining a similar distance apart on the nMDS in 2012, suggesting that the magnitude of changes in the overall assemblages of one lake is reflected in the other (Fig. 2a). Assemblages collected from sweeps did reveal a divergence of points for each lake since Dec 97/Mar 98 (Fig. 3a). This divergence reflects the occurrence of taxa in Lake Albina since Dec 97/Mar 98 that are not in Lake Cootapatamba (e.g. *Lumbriculus variegatus*) and high abundances in Lake Albina of ephemeropterans, trichopterans and various dipterans in 2012 which did not occur in Lake Cootapatamba (Table 2).

The nMDS showing sampled sites at both lakes in 2012 revealed the points representing littoral assemblages in Lake Cootapatamba were located on the left side of the plot and separated from those of Lake Albina on the right for both the cobble and sweep samples (Figs 2b and 3b). ANOSIMs revealed the cobble and sweep assemblages to be different between lakes with Global R-values of 0.984 and 0.951 (both p=0.1%), respectively, and differences occurred between the February and December 2012 samples in both lakes for cobbles and sweeps with Global R values of 0.491 (p=1.8%) and 0.525 (p=0.3%), respectively.

Whilst all species are unevenly distributed around the shores associated in part with the variation in rock size and nature of the substrate (Hancock et al. 2000), numbers of *Lumbriculus variegatus* were particularly variable. It was most common along the southern shores of the Lake Albina (sites 1, 2, and 5 in Fig. 1) and almost absent for the more wave washed rocks of the northern shore and peninsula (sites 3 and 4 in Fig. 1).

Littoral biomasses in Lake Cootapatamba have remained about the same before (3.9 g/m^2) and after (1.2-5.9 g/m^2) fish gained access, with the losses due to the lower numbers of isopods and amphipods made up by increases in trichopterans and chironomids (Table 1). The same applies in Lake Albina, though in some cases values are much higher (to 19.4 g/m^2), due to many more trichopterans and *Lumbriculus variegatus* (Table 1).

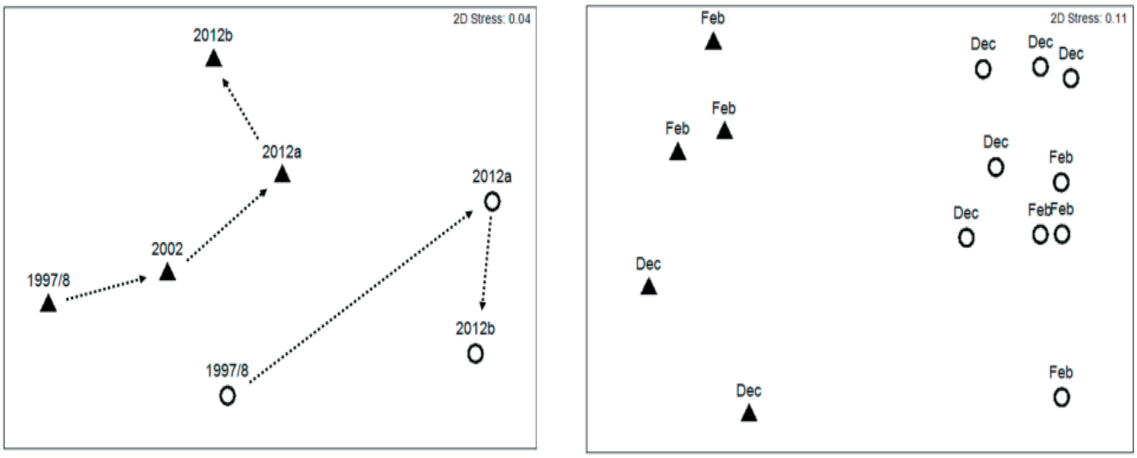


Figure 3: Assemblages associated with littoral sweeps in Lake Cootapatamba (▲) and Lake Albina (○) comparing: [a, left] previous overall assemblages (i.e. 1997/98 and 2002) with those in the present study and [b, right] site assemblages in both lakes on the two sampling occasions in 2012. In Fig. 3a, the February and December surveys in 2012 are represented as 2012a and 2012b, respectively, and arrows show progression through time.

Benthic fauna

A total of fourteen taxa was found in the benthos of Lake Cootapatamba and Lake Albina with only six shared by both lakes (Table 3). Since 1976 there has been a substantial reduction in the abundance of tubificid worms in both lakes and amphipods, which were present in previous studies, were absent from both lakes in 2012. Lake Cootapatamba had a higher abundance of chironomids in 2012 comparable with previous studies, but some of the changes (fewer tubificids and more *Procladius villosimanus*) occurred by 2002 before fish entered (Table 3). In Lake Albina the chironomid *Procladius villosimanus* and the oligochaete *Lumbriculus variegatus* are now common, the latter not being a component of the benthic fauna in 1976. Despite these changes, the nMDS plot for benthic fauna showed that overall there has been little change in the assemblages within Lake Albina since 1976 (Fig. 4). This is due largely to the presence of similar taxa in 1976 and 2012, and little change occurring in the abundance of most of these taxa (Table 3b). Major shifts have occurred in the assemblages within Lake Cootapatamba since 2002 (Fig. 4) as there has been a substantial change in the representation of taxa and in the abundance of most taxa (Table 3a).

DISCUSSION

Fish have an important role in structuring communities in lakes, none more so than changes effected by the introduction of non-native fish into naturally fishless mountain lakes (Knott et al. 1978; Donald et al. 2001; Parker et al. 2001). Historically, the three lakes in the Snowy Mountains with a long history of fish occupation (i.e. Blue Lake, Club Lake and Hedley Tarn) lack large zooplankton such as *Daphnia nivalis*, and the isopod *Metaphreatoicus australis* and amphipod *Neoniphargus* sp. are uncommon whilst the chironomid *Chironomus oppositis*? is more abundant than in Lake Cootapatamba and Lake Albina (Bayly 1970; Timms 1980a; Benzie 1984; Hancock et al. 2000). The absence of *Neoniphargus* sp. and reduced numbers of *M. australis* in Lake Cootapatamba in the present study could be attributed to fish being present post 2003 but, surprisingly, both species have suffered a similar fate in Lake Albina which still lacks fish. However, changes in *Metaphreatoicus australis* are more pronounced in the benthos where there is a major decrease in Lake Cootapatamba and none in Lake Albina. Also the change in *Neoniphargus* sp. is from a much lower number in Lake Albina and is too small to be of significance. Changes in the littoral fauna of *M. australis* in Lake Albina could have other causes: one is the additional presence of the worm *Lumbriculus variegatus* which is also a detritus feeder and another is a change in littoral aquatic plants. The latter are thought to be favoured by *M. australis* and it is possible littoral plants are less common in Lake Albina since the removal of the Albina hut and its septic system, thus reducing nutrient input (B. Timms pers. obs).

Despite evidence that the Mountain Galaxias, *G. olidus*, eats isopods and amphipods (reviewed in Green and Osborne 2012) and despite abundant evidence

Table 3: Abundance of benthic fauna in Lake Cootapatamba and Lake Albina over several years represented as numbers/m^2.

		a) Lake Cootapatamba			b) Lake Albina	
Taxa	Species (if known)	Feb 76# (0.5-3 m)	Jan 02* (0.3-3 m)	Feb 12 (0.3-3 m)	Feb 76# (3 m)	Dec 12 (2 m)
Platyhelminthes	Unidentified platyhelminthes				11	
Oligochaeta	Tubificid worms[1]	1096	258	274	344	110
	Lumbriculus variegatus					886
Mollusca: Bivalvia	*Pisidium kosciusko*	236	253	340	732	440
Mollusca: Gastropoda	*Glacidorbis hedleyi*				22	
Crustacea: Isopoda	*Metaphreatoicus australis*	355	704	174	444	555
Crustacea: Amphipoda	*Neoniphargus* sp.	275	11		11	
Insecta:Plecoptera	Unidentified notonemourid			7		
Insecta:Tricoptera	*Austreithus* sp.	11				
Insecta:Diptera	*Procladius villosimanus*	45	582	573	211	1100
	Chironomus ?oppositus	5	11	136		
	Chironomus sp.				33	44
	Other chironomids[2]		5	2111	322	180
Nematomorpha	Unidentified nematomorphian			22		
	wet biomass (g/m^2)	9.1	14.8	7.4	7.3	10.1

from Timms (1980a); * from Timms (2002)
1 includes *Antipodrilus davidis, Antarctodrilus proboscidea* and *Dero furcatus*;
2 includes *Tanytarsus* sp.

that introduced fish in overseas mountain lakes reduce the diversity of aquatic insects, amphipods and other crustaceans (Hannelly 2009; Messner, 2013), it cannot be stated for certain that fish predation is responsible for the changes observed in Lake Cootapatamba because of some similar changes in Lake Albina. However, severe reductions in Lake Cootapatamba in the abundance of the amphipod *Neoniphargus* sp., which were historically rare in Lake Albina (Hancock et al. 2000), and the reduction of *M. australis* in the benthos of Lake Cootapatamba where they are most easily preyed upon are likely to be attributed to the introduction of *G. olidus*. Similarly, in keeping with numerous observations that large zooplankton species suffer from the introduction of fish in mountain lakes (Donald et al. 2001; Parker et al. 2001), there is strong evidence to suggest that the abundance of the large plankter *Daphnia nivalis* has been severely adversely affected in Lake Cootapatamba by the predatory activities of *G. olidus* (T. Kobayashi pers. comm.). However, in the absence of this predator, *D. nivalis* is still abundant in Lake Albina (B. Timms pers. obs.).

Surprisingly, the snail *Glacidorbis hedleyi* has apparently disappeared from both Lake Cootapatamba and Lake Albina in recent years. It is unlikely this is due to fish predation, as this snail historically occurred in fish and fishless lakes alike (Hancock et al. 2000), and also it is not a recorded prey item of *G. olidus* (Green and Osborne 2012). Numbers could be fluctuating naturally or possibly this is an expression of climate change, but data are needed on other Snowy Mountain lakes to confirm this. Given it occurs in upland areas of New South Wales and Victoria and so is a coldwater species (Ponder and Avern 2000), it is a likely candidate to be affected by climate change.

Chironomids have increased in recent years in Lakes Cootapatamba and Albina. Some of the increase occurred before the fish reached Lake Cootapatamba, but *Chironomus* sp. (it may be *C. oppositus*) has definitely increased in Lake Cootapatamba since fish

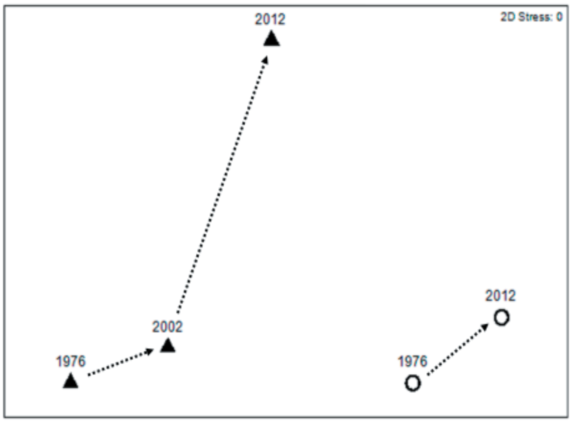


Figure 4: Assemblages of benthic fauna in Lake Cootapatamba (▲) and Lake Albina (○) comparing previous overall assemblages (i.e. 1976 and 2002) with those in the present study. Arrows show progression through time.

arrived. Given its abundance in Club and Blue Lakes with fish, this is expected. Increases in other species, largely unidentified, are not so easily explained. Neither is the reduction in planarians on cobbles in both lakes. Some invertebrates such as the caddises *Ecnomus* sp. and *Plectrocnemia* sp. had increased numbers in 2012 compared to previous studies. The reason for these changes is not currently known but it is likely to represent natural fluctuations in the abundances of these taxa.

There is no doubt that the exotic worm *Lumbriculus variegatus*, which is still absent from Lake Cootapatamba, and also Club and Blue Lakes and Hedley Tarn, is a recent immigrant to Lake Albina. It has a widespread distribution occurring in many Australian urban ponds and streams largely due to thoughtless disposal by aquarists (A. Pinder pers. comm.), but this is the first record of its presence in the benthos of an Australian lake (Timms 1980b). *L. variegatus*, which is common in many New Zealand lakes where it often dominates (Timms 1983), is not yet abundant throughout Lake Albina, but it could well be in time. Future studies are needed to determine how this species interacts with other lake inhabitants; for instance it could be at least partly responsible for some of the changes observed in other species in Lake Albina.

Besides some major changes in abundances of some taxa over the fourteen years that sampling has occurred in Lake Cootapatamba and Lake Albina, some species appear sporadically. Such species include *Eusthenia venosa, Micronecta* sp., limnephid larvae, *Chironomus* sp., tipulid larvae and elmid beetles in Lake Albina, and *Temnoswellia* sp., *Sigara* sp., *Austrorheithrus* sp., *Kosrheithrus* sp., *Triplectides varius*, *Polypedilum* sp., a ceratopogonid, *Sclerocyphon* sp., and a curculionid in Lake Cootapatamba. Intensive sampling is needed to establish more reliable data on these species.

Whilst seasonal changes in the abundance of various invertebrates occurred in Lake Cootapatamba and Lake Albina in the present study and in the study by Hancock et al. (2000), seasonal effects on results between previous years and 2012 have been minimised by sampling at almost the same times. Assuming littoral ice is injurious to most littoral inhabitants, differential timing of winter ice breakup is likely to be important in timing the occurrence of littoral fauna. However, in the years that Lake Cootapatamba and Lake Albina have been studied this affect is probably minimal. Although the dates of ice breakup has been collected irregularly for these lakes, ice break up on the regularly monitored Blue Lake occurred within the same 7 day period in late October (Ken Green, unpublished data). However, in 1905 ice break up in Blue Lake has been calculated to have been in mid December, it was recorded in early to late November in the 1970s and now usually occurs in October (Green, 2011); these long term changes could well have affected the littoral and benthic communities. With the ice-free period increasing in the lakes with climate change (Green 2011), and with greater input of spring solar radiation into extremely clear waters unprotected by a cover of ice and snow, invertebrate life cycles and abundances could be changing, but there are no long term data to show this.

It was the aim of this study to reassess Lake Cootapatamba and Lake Albina to determine temporal changes in their invertebrate assemblages and whether the introduction of fish into Lake Cootapatamba in 2003 has since affected these assemblages. The littoral fauna and benthic fauna of both lakes was found to have changed since the earliest studies of these lakes in 1997/1998 and 1976, respectively, with increases in the abundance of some taxa, decreases in others, the apparent disappearance of some taxa and the addition of *Lumbriculus variegatus*. None of these changes can be unequivocally attributed solely to the arrival of fish into Lake Cootapatamba as the fishless Lake Albina has experienced some similar trends. However, it is likely *M. australis* and *Neoniphargus* sp. have been adversely affected, especially in habitats of simple structure where they would be more susceptible to predators. Other factors could be operating, including effects associated with warming waters and changes to ice formation/melting cycles in association with climate change, so future monitoring of these lakes is of great importance.

ACKNOWLEDGEMENTS

We thank Caleb Rankin for able assistance in the field, and Adrian Pinder of DEC, WA who identified *Lumbriculus variegatus* for this study and John Bradbury, David Cartwright, Peter Cranston, Jenny Davis, John Dean, Winston Ponder, Ros St. Clair, Chris Watts and George Wilson who helped with identifications in previous studies on these lakes

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The Middle Triassic Megafossil Flora of the Basin Creek Formation, Nymboida Coal Measures, New South Wales, Australia. Part 9. The Genera *Heidiphyllum, Voltziopsis, Rissikia* and affiliated cones, and ?*Yabeiella.*

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Leaves from the coniferophyte genera *Heidiphyllum, Voltziopsis* and *Rissikia* with its associated fertile cones *Rissikistrobus* (female) and *Rissikianthus* (male) and simple leaves provisionally placed in *Yabiella brachesbuschiana* are described from two quarries in the Middle Triassic Nymboida Coal Measures of the Nymboida sub-Basin in northern New South Wales, Australia. Leaves of *Heidiphyllum* and *Rissikia* form monotypic assemblages on certain bedding planes and are amongst the most common fossils found at Nymboida.

Manuscript received 7 December 2012, accepted for publication 24 July 2013.

KEYWORDS: Middle Triassic flora, Nymboida Coal Measures, palaeobotany, *Heidiphyllum*, *Voltziopsis*, *Rissikia*, *Rissikistrobus, Rissikianthus, Yabeiella.*

INTRODUCTION

This is the ninth paper of a series describing the early-middle Triassic Nymboida flora. Part 1 of this series (Holmes 2000) described the Bryophyta and Sphenophyta; Part 2 (Holmes 2001) the Filicophyta; Part 3 (Holmes 2003) fern-like foliage; Part 4 (Holmes and Anderson 2005a) the genus *Dicroidium* and its fertile organs *Umkomasia* and *Pteruchus*; Part 5 (Holmes and Anderson 2005b) the genera *Lepidopteris, Kurtziana, Rochipteris* and *Walkomiopteris*; Part 6 (Holmes and Anderson 2007) the Ginkgophyta; Part 7 (Holmes and Anderson 2008) the Cycadophyta; Part 8 (Holmes et al. 2010) the genera *Nillsonia, Taeniopteris, Linguifolium* and *Gontriglossa* together with the enigmatic lobed leaf *Scoresbya carsburgii*. In this paper the coniferophyte vegetative genera *Heidiphyllum, Voltziopsis* and *Rissikia* together with its affiliated fertile cones (strobili) *Rissikistrobus* (female) and *Rissikianthus* (male) are described. Also included are a cluster of incomplete leaves attributed to the genus *Yabeiella* which occur on a slab with other leaves and dispersed male cones.

A description of the Coal Mine and Reserve Quarries, the source localities of our described material together with a summary of the geology of the Basin Creek Formation, the Nymboida Coal Measures and the Nymboida Sub-Basin were provided in Holmes (2000).

METHODS

The material described in this paper is based mainly on collections made over a period of forty years by the senior author and his family from two then-active Nymboida quarries (Coal Mine Quarry and Reserve Quarry; abbreviated below as CM and RES respectively). The specimens noted in Flint and Gould (1975), Retallack (1977) and Retallack et al (1977) were examined in the collections of the Australian Museum, Sydney, the Department of Geology and Geophysics of the University of New England, Armidale and the Queensland Museum, Brisbane.

SYSTEMATIC PALAEOBOTANY

The classification follows that used by Anderson et al (2007) for all higher groups from Class to Family. As mentioned in previous Nymboida papers (Holmes et al 2010) cuticles are not preserved. However in most specimens the preservation of gross morphology is excellent.

Class PINOPSIDA Burnett 1835

Family *Voltziaceae* Arnold 1947

Genus *Heidiphyllum* Retallack 1981

Type species

Heidiphyllum elongatum (Morris 1845) Retallack 1981

Heidiphyllum elongatum (Morris 1845) Retallack 1981

Figures 1A–E, 2A, 3A

Selected references

1845 *Zeugophyllites elongatus,* Morris fig. 6(5)
1958 *Phoenicopsis elongatus,* de Jersey p. 84
1965 *Phoenicopsis elongatus*, Hill et al. Pl.T 9(1)
1975 *Phoenicopsis elongatus,* Flint and Gould Pl. 2, fig. 6b
1977 *Phoenicopsis elongatus,* Retallack et al fig. 10A
1978 *Podozamites elongatus*, Anderson Pl. 1, 6–9
1981 *Heidiphyllum elongatum,* Retallack p182, fig.6B
1982 *Phoenicopsis ?elongatus,* Holmes, fig. 11D
1989 *Heidiphyllum elongatum,* Anderson and Anderson p.432, Pls 249–263
2000 *Heidiphyllum elongatum,* Troncoso et al. pp 121–122, figs 3A,B, 3 E–G
2003 *Heidiphyllum elongatum,* Anderson and Anderson pp 90–91

Description

Leaves individually dehisced; simple, linear, elliptic or oblanceolate; length and width variable within assemblages; from 100mm to 200mm, average c. 160 mm in length; from 10mm to 30 mm, average c. 15 mm in width; base narrow to broadly sessile, apex rounded to broad acute; veins dividing near the base then straight and parallel throughout the lamina (c. 10 per 10 mm) and conjoining close to the apex.

Material

AMF137589 (and counterpart) CM; AMF137590 RES; AMF137591 RES; AMF137592 RES; AMF137593 CM.

Discussion

The genus *Heidiphyllum* was erected by Retallack (1981) for simple Gondwana leaves previously placed in the genera *Phoenicopsis* or *Podozamites* on the basis of their close association with the distinct female strobilus *Telemachus* (Anderson 1978). Anatomically preserved leaves described from Antarctica under *Notophytum krauselii* (Axsmith et al 1988b) are probably the permineralised equivalent of *Heidiphyllum.* Compared with the four species described and illustrated in Anderson and Anderson (1989) the Nymboida leaves (Figs 1–3) clearly belong in *H. elongatum*.

Within assemblages the leaves in the Nymboida collection are somewhat variable in length and width. We consider they all belong to a single species complex that is distinguished by its parallel venation and the presence of inter-veinal striae. However this latter feature may not be obvious due to varying forms of preservation. These inter-veinal striae are clearly evident in cuticular studies of the South African Molteno material (Anderson and Anderson 1989, Pl. 252). They are not to be confused with leaf mining (Anderson and Anderson 1989, Pl. 254) which is common in *Heidiphyllum* leaves in the Molteno and was first recorded from the Ipswich C.M. (Rozefelds 1985). At Nymboida distal linear fragments of *Sphenobaiera* leaves may be confused with *Heidiphyllum* but can be separated by their clearly etched veins and the lack of inter-veinal striae.

Specimens of *Heidiphyllum elongatum* account for c. 1% of the Nymboida catalogued collection. On certain bedding planes their massed leaves form monotypic assemblages (Figs 2, 3). During working operations at the Reserve Quarry one such bedding plane of over 300 square metres was exposed. However individual leaves often occur in mixed assemblages (Figs 7D, 8D). Monotypic occurrences of *H. elongatum* are recorded from the Molteno Formation of South Africa (Anderson and Anderson 1989, Cairncross et al 1995) and are considered by those authors to indicate growth in areas of high water table in the floodplain or on channel sandbars. Retallack *et al* (1977) concluded for the Nymboida

Colliery locality that *H. elongatum* occurred as the dominant plant in levee and point bar scrub or woodland. Such a monotypic mass of *H. elongatum* leaves may also be suggestive of an Autumnal leaf fall. Bomfleur et al (2011a) regarded *Heidiphyllum* as 'seasonally deciduous'. Anderson and Anderson (2003) wrote 'whether *Heidiphyllum* leaves were deciduous or evergreen is unknown but we regard them as having probably been evergreen'.

Based on Molteno specimens bearing attached leaves, Anderson and Anderson (2003) envisaged *H. elongatum* in life as an erect woody shrub to small tree bearing leaves in dense pseudo-whorls on short shoots. From their Antarctic material Bomfleur et al (2011a) suggest that it is a 15–20 m forest tree and note that 'the largest axes known exceed 20 cm in diameter'. Both reconstructions could be valid with young trees colonising the water's edge and floodplain and then mature trees becoming forests on drier ground as water courses and tables change over time.

The female and male organs *Telemachus* and *Odyssianthus* respectively that are affiliated with *Heidiphyllum elongatum* in the Molteno of southern Africa (Anderson 1978, Anderson and Anderson 2003) have not been recorded from Nymboida or other Australian localities despite the prevalence of preserved leaves. The female cone *Telemachus* associated with *Heidiphyllum* has also been described from New Zealand (Retallack 1981), South America (Spalletti et al 1991) and Antarctica (Axsmith et al 1998a). However the male cone *Odyssianthus* has been recorded only from the type locality, Telemachus Spruit (Tel 111) which is also the type locality for the female cone. Based on their Antarctic collection from Mt Falla locality Bomfleur et al (2011a) suggest that *Switzianthus* is the male cone of *Heidiphyllum* rather than *Dejerseya* which is also common at the site. In the Molteno of southern Africa *Switzianthus* (Anderson and Anderson 2003) was affiliated with the leaf *Dejerseya* based on closely similar cuticles and their mutual occurrence at two localities (with a possible third). In the Ipswich Coal Measures at Dinmore *Dejerseya* was found as a monodominant leaf on some bedding planes together with numerous *Switzianthus* and a possible *Matatiella* megasporophyll (Anderson and Anderson 2003). The affiliation of organs will always be uncertain short of finding direct attachment. In another paper Bomfleur et al (2011b) reconstructed *Dejerseya* as having the pollen organ *Townrovia* based on slim evidence (a single specimen with uncertain generic identification) and no reference was made to the *Switzianthus* affiliations described from other localities in Gondwana. Another puzzle is the apparent affiliation of *Heidiphyllum* with the cone *Dordrectites* bearing T-shaped ovulate scales at numerous Molteno localities. This affiliation is also recorded by Anderson and Anderson (2003, p. 63) from the Moolayember Formation, Australia and in the Los Rastros Formation of South America. A single specimen of *Dordrectites* sp. was found at Nymboida by us (23.5.2002) associated with *Heidiphyllum* leaves but unfortunately the specimen has subsequently been misplaced.

Genus *Voltziopsis* Potonié 1899

Type Species

Voltziopsis africana Seward 1934

Voltziopsis sp. A

Figures 4A–F, 5A–D

Description

Branching foliar shoots; length incomplete, as preserved 80 mm; width c. 7 mm wide; leaves closely spaced on stem, c. 3mm wide and to 7 mm long, attached at c. 30º–45º, concave, thicker near base, ovate with acuminate apex.

Material

AMF137594 and counterpart AMF137595, RES.

Discussion

This taxon is based on one slab and its counterpart showing two foliar shoots (the larger shoot marked 'x' and the smaller 'y') each with a lateral branch (Figs 4A–F, 5A–D). Details of the leaves are illustrated (Fig. 5D) and an arrow indicates the acuminate apex of a leaf.

The coniferophyte genus *Voltziopsis* is known from five species ranging from Upper Permian to Early Triassic (Townrow 1967b, Anderson and Anderson 1989). The species are differentiated essentially on both gross morphological and cuticular features of the foliar shoots and female cones. In the absence of cuticle and cones the Nymboida material is placed with reservation in *Voltziopsis*. Similar sterile material can occur in various families with very specific cones and in the absence of fertile material is often placed in the form genus *Brachyphyllum*, eg. the Nymboida specimens are similar in gross morphology to *B. crucis* (Barbacka et al. 2006, Pl 2, fig. 5). We prefer to place it in *Voltziopsis* as the genus is well documented in Gondwana (Townrow, 1967b; Holmes and Ash 1979, Anderson and Anderson 1989) and furthermore the Nymboida material is similar to the shoots of *Voltziopsis angusta* (Townrow, 1967b) first described by Walkom (1925) as *Brachyphyllum angustum*.

?*Voltziopsis* sp.

Figure 5E, F

A small narrow linear fragment of a foliage stem with alternate triangular bract-like leaves c. 1.5 mm long (AMF137622, CM) is illustrated (Figs. 5E, F) but is too poorly preserved to allow closer identification and is referred to ?*Voltziopsis* sp.

Family Podocarpaceae Endlicher 1847

Genus *Rissikia* Townrow 1967a

Type species

Rissikia media (Tenison Woods 1883) Townrow 1967a

Rissikia media (Tenison Woods 1883) Townrow 1967a

Figures 6A–G, 7A–D, 8A–D

Selected references

1883 *Taxites medius,* Tenison-Woods Pl. 9(3)
1965 *Elatocladus* sp., Hill et al. Pl. T 8 (7)
1967a *Rissikia media,* Townrow; fig.1E–I
1975 *Rissikia media,* Flint and Gould fig. 6a
1977 *Rissikia media,* Retallack et al. fig. 10F
1982 *Rissikia media,* Holmes, fig. 11E
1989 *Rissikia media*, Anderson and Anderson, p. 453, Pls 265–273
2000 *Rissikia media*, Troncoso et al. p.122, fig 3D
2003 *Rissikia media*, Anderson and Anderson, p. 113

Description

Foliage shoot, narrow to broadly elliptical from 70–100 mm average c. 85 mm in length and from 20–50 mm average c. 25 mm in width; leaflets from 20 to 65 average c. 45, helically attached from 45º to 80º to rachis but appearing pinnate as preserved; linear to linear elliptic; single median vein.

Material

AMF137596 CM; AMF137597 RES; AMF137598 CM; AMF137599 RES; AMF137600 RES; AMF137601 RES; AMF137602 RES; AMF137603 CM; AMF137604 CM; AMF137605 CM; AMF137606 CM; AMF137607 CM; AMF137619 RES.

Discussion

While the individual leaves at Nymboida show some variation in length, width and density of the leaflets, we regard them all as forming a single species complex (Figs 6, 7). Leaflet attachment varies from fairly closely spaced (Fig. 6D) to more widely spaced (Fig. 6C). Absent from our collections are the narrow shoots with shortened leaflets that occur in some Molteno assemblages (e.g. Umk111 and Hla213) and were described as *R. apiculata* by Townrow (1967a). Based on their extensive collections Anderson and Anderson (1989) showed that *R. media* and *R. apiculata* formed a continuous range of variation and synonymised the latter forms with *R. media.* Occasional leaves from Nymboida with more closely spaced and broader leaflets approach *R. eskensis* as described by Webb (1980) from the Esk Formation of Australia and the Molteno Formation of southern Africa by Anderson and Anderson (1989).

At both Nymboida localities foliage shoots of *Rissikia media* are very common and found together with other fossils on the same slabs (Figs 6A–C, 7D). They also occur as massed monotypic assemblages on certain bedding planes (Fig. 8A–C) or in association with *Heidiphyllum elongatum* (Figs 7D, 8D) which suggests autumnal leaf falls from a woodland comprising these two species. From occurrences in the Molteno Retallack and Dilcher (1988) visualised *Rissikia* as a tree in the *Dicroidium odontopteroides* dominated deciduous floodplain woodlands. However at Nymboida *Dicroidium* leaves are absent from autochthonous *Rissikia* leaf assemblages but often occur together in allochthonous deposits (Fig. 6A, B).

We follow Townrow (1967) in the placement of *Rissikia* and its associated female and male cones in the family Podocarpaceae. However this placement is not secure as was discussed in detail by Anderson and Anderson (2003, p. 105) and in the more recent synthesis of the gymnosperms by Anderson et al (2007). While extant members of the Podocarpaceae are evergreen this does not exclude ancient members from being deciduous.

Genus *Rissikistrobus* Anderson and Anderson 2003

Type species

Rissikistrobus plenus Anderson and Anderson 2003

Rissikistrobus sp. A

Figures 9A–C, 10A–G, 11A

Description

Linear female cone, longer than 50 mm, 5 mm wide with bract/scale complexes bearing ovules.

Material

AMF137613 CM; AMF137614 CM; AMF137615 RES; AMF137624 CM; AMF137625a,b RES; AMF137626 CM.

Discussion

Eight specimens of female cone occur in the collection (Figs 9, 10, 11A). Slab AMF137613 bears three individuals (Fig. 9) and shows two longer sections 'x', 'y' and one small portion of cone 'z'. The longest cone 'y' as preserved is 50 mm long and 5 mm wide with basal and distal sections missing. The bract/scale complex are closely spaced and attached at c. 30º–45º to the axis, 2 mm wide and 4 mm long, ovate with acute apex. They appear to show ovules (visible at high magnification with suitable light), mainly in lateral view (a possible one is marked by an arrow in Fig. 9C) but the presence of the diagnostic paired arrangement of the ovule/seed on the cones is not apparent probably due to the high rank coalification of the specimens. The cone AMF137626 (Figs 10D–G) is broken at the upper end and shows a group of *Rissikia* leaflets at a slightly lower level. It is uncertain whether they may belong together or are a chance alignment during preservation. The unusual female cone (Fig. 11A, 't', AMF 137615) occurring close to some male cones of *Rissikianthus* (AMF 137608) shows simple ovuliferous scales and along the distal portion the longer scales look more like leaves. Slab AMF137613 showing three cones closely aligned. (Fig. 9) may be the chance preservation or indicate that these cones occurred on a common axis as is found in some modern genera e.g. *Taxodium mucronatum*. On the same surface occur three clear portions of *Rissikia* leaves and other fragments. The slab is irregular and has no clear bedding plane probably indicating that these fossils were deposited quickly in a high energy environment.

The Nymboida specimens are placed in *Rissikistrobus* with confidence. However, from the absence of specific characters in the bract/scale complex due to the high rank coalification of the cones they are here referred to as *Rissikistrobus* sp. The small portion of a cone as drawn by Retallack et al (1977) shows pairs of ovules but the ovuliferous scales are not clear enough to determine the species. These specimens and the one mentioned above from Cloughers Creek Fm., also in the Nymboida C.M. are the only other records of *Rissikistrobus* in the Gondwana Triassic apart from the Molteno, southern Africa where three species are described from seven localities with a total of 85 individuals by Anderson and Anderson (2003).

A female cone possibly similar to *Rissikistrobus* was described from the Jurassic Nambour Basin (Loc. 4) by Pattimore and Rigby (2005, pl. 78). The material is poorly preserved. However it is associated with male cones and leaves assigned to *Rissikia*.

Genus *Rissikianthus* Anderson and Anderson 2003

Type species

Rissikianthus townrovii Anderson and Anderson 2003

Rissikianthus sp. A

Figures 11A–D, 12A–G, 13A–C, 14A, B

Description

Ovate male cone 7–15 mm long, 5–7 mm wide; microsporophyll triangular, c. 1.5 mm in width, with acuminate apex.

Material

AMF137608, RES; AMF137610 RES; AMF137611 and counterpart AMF137612 CM; AMF137616 RES; AMF137621 RES.

Discussion

Twelve cones are present in the collections from Nymboida. On three slabs the cones occur in groups with four cones (w, x, y, z) close together on AMF137608 (Fig. 11A.B); three cones (x, y, z) on AMF137611 (Figs 12C–G) and three cones (x, y, z) on AMF137616 (Figs 13A–C,14A, B). On the latter slab are portions (AMF137618) of the cycad *Pseudoctenis nymboidensis* (Holmes and Anderson 2008) and numerous fragmentary leaves (AMF137617) described below as ?*Yabeiella brackebushiana*. The specimens AMF137621 (Figs 11C,D) and AMF137610 (Figs 12A,B) each bear a single *Rissikianthus* cone.

The high rank coalification of the cones has obscured specific details and makes comparison with described species difficult. Microsporangia have not been observed. On a number of cones the microsporophyll is visible in side view (e.g. Fig. 11D, AMF137621) and on AMF137610 it is visible in outer view (Fig. 12B). From the Molteno Flora Anderson and Anderson (2003) have described four species of *Rissikianthus* based on 79 individuals and including some very clearly preserved cones especially from the Peninsula (Pen321) locality. The Nymboida material is closest in gross morphology to the microsporophyll of *R. concavus* Anderson and Anderson (2003).

Pattemore and Rigby (2005, Pl. 8B,C) described a group of conifer cones attached to a stout stem from the Jurrasic Nambour Basin, Queensland. The cones are very similar superficially to *Rissikianthus* but differ from material described from the Molteno (Anderson and Anderson, 2003, p.110) of cones being attached to a gracile axis.

Class GNETOPSIDA Eichler ex Kirpotenko 1884

Family Fraxinopsiaceae Anderson and Anderson 2003

Genus *Yabeiella* Oishi 1931

?*Yabeiella brackebushiania* (Kurtz 1921) Oishi 1931

Figures 13A–C, 14A, B

Description

Leaves linear, longer than 43 mm, width 4–6 mm, venation fine (25 per 10 mm) forking close to midrib, mostly parallel with occasional anastomoses and faint marginal vein.

Material

AMF137617 RES, numerous incomplete leaves.

Discussion

A cluster of sixteen linear leaf fragments are preserved at various orientations and alignment on a single slab (Figs 13,14). The longest leaf portion preserved (marked as 'w') is 43 mm. The width of the leaves is fairly constant at 4-6 mm. Venation is very fine and sometimes difficult to decipher. There are at least 25 veins per 10 mm and on some leaves seem to be even denser. Each lateral vein divides close to the midrib and then runs straight and parallel at c. 80º towards the margin; sometimes dichotomising again mid way or near the margin. Occasionally the veins appear to coalesce and form areoles. There is a suggestion of a marginal vein on the longest leaf and possibly on some of the other leaves.

On this slab there is a mixed plant assemblage containing three male cones of *Rissikianthus* sp. A and two portions of the cycad leaf (AMF137618) *Pseudoctenis nymboidensis* (Holmes and Anderson 2008) together with numerous linear leaf fragments identified here as ?*Yabeiella brackebushiania*. The presence of the marginal vein is the main character of the genus *Yabeiella* that distinguishes it from leaves in the genus *Taeniopteris*. However, in *Yabeiella* leaves this feature is not always obvious and is only clearly evident in well preserved material. The marginal vein on one of the leaflets from Nymboida (Fig 14A'w') is similar to that preserved in *Yabeiella brackebushiania* from Konings Kroon (Anderson and Anderson 1989, Pl. 280 figs 10, 14). Some of the Molteno leaves have similar fine venation as in the Nymboida material but most leaves have much more widely spaced venation. The width of the Nymboida leaves (4–6 mm) is consistently narrower than the populations of *Yabeiella brackebushiania* from the Molteno (mainly 8–14 mm) and may indicate a separate species. However as the Nymboida leaves are so incomplete we are reluctant to place it in a new species.

Yabeiella is clearly affiliated with the winged seed *Fraxinopsis* in South America (Jain and Delevoryas 1967), Southern Africa (Anderson and Anderson 2003) and Australia (Oishi 1931, Jones and de Jersey 1947). At Nymboida *Fraxinopsis* is as yet unknown.

If one disregards the presence of the indistinct marginal vein then the dense venation of these leaves is similar to certain species in the genus *Taeniopteris*. For example *T. cylomeiformis* Anderson and Anderson (1989, p. 372) has similar dense venation but the veins fork once only. *T. densinervis* Menendez (1951) from Argentina and from Chile (Gnaedinger and Herbst, 2004) has similar dense venation but the leaves are three times as broad as the Nymboida material. The venation of *T. parvilocus* (Anderson and Anderson (1989, p.373) is similar in also forking twice and occasionally anastomosing but the venation is more widely spaced (13/10 mm) and the leaf width is generally much wider (20 mm). The *Taeniopteris* species described from Nymboida (Holmes and Anderson 2010) differ from the above fragmentary leaves by their much larger size and coarse venation. These leaves are thus unlike any known *Taeniopteris* from Gondwana.

ACKNOWLEDGEMENTS

WBKH deeply appreciates the assistance provided by his daughters Marnie and Netta and late wife Felicity in collecting from the Nymboida localities over many years. HMA values the patient guidance of son-in-law Hannes du Plessis with the digital preparation of this paper.

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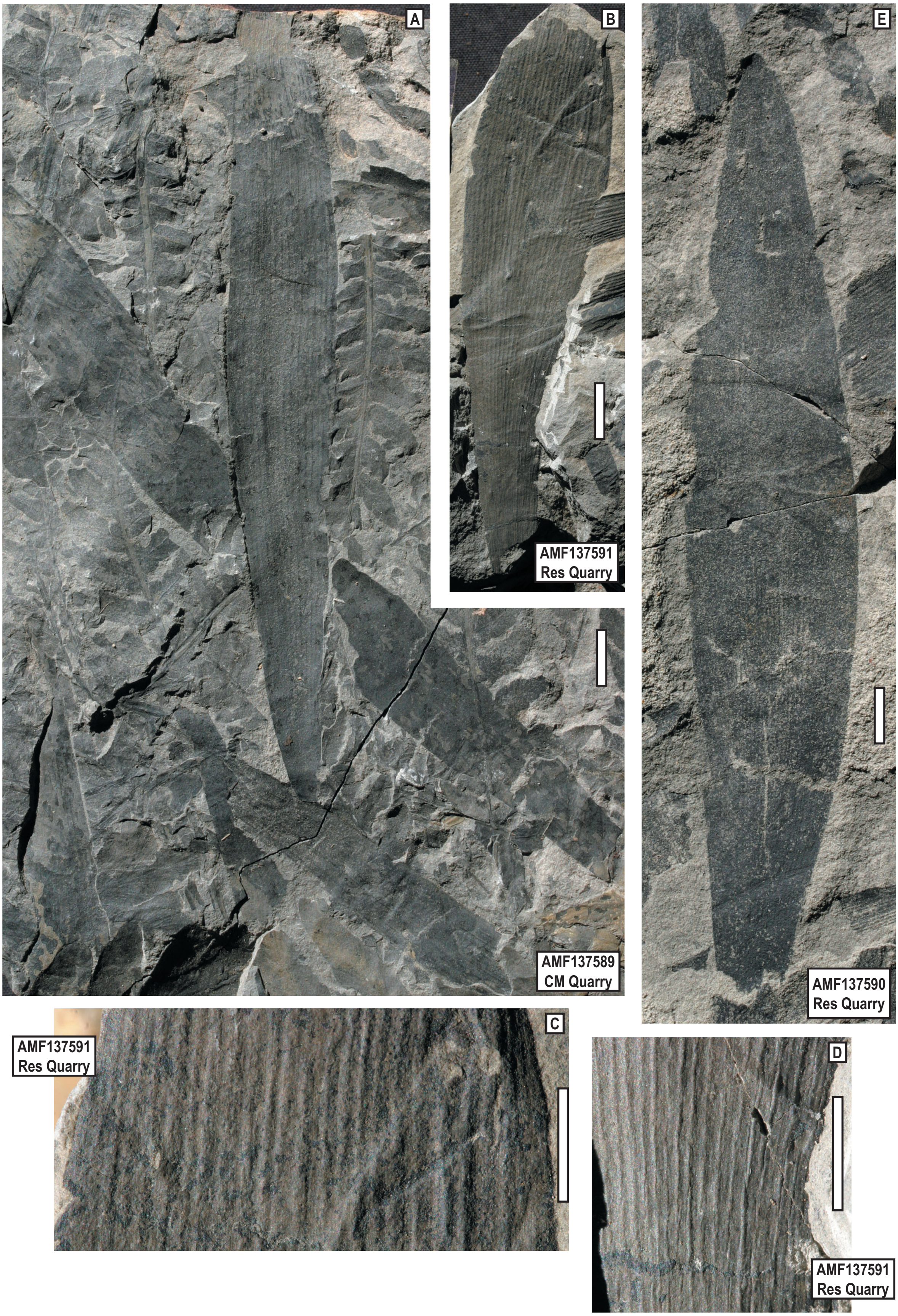

Figure 1. A–E. *Heidiphyllum elongatum* Retallack (scale bar = 10 mm).

Figure 2. A. *Heidiphyllum elongatum* Retallack (scale bar = 50 mm).

Figure 3. A. *Heidiphyllum elongatum* Retallack (scale bar = 10 mm).
AMF 137593. CM Quarry.

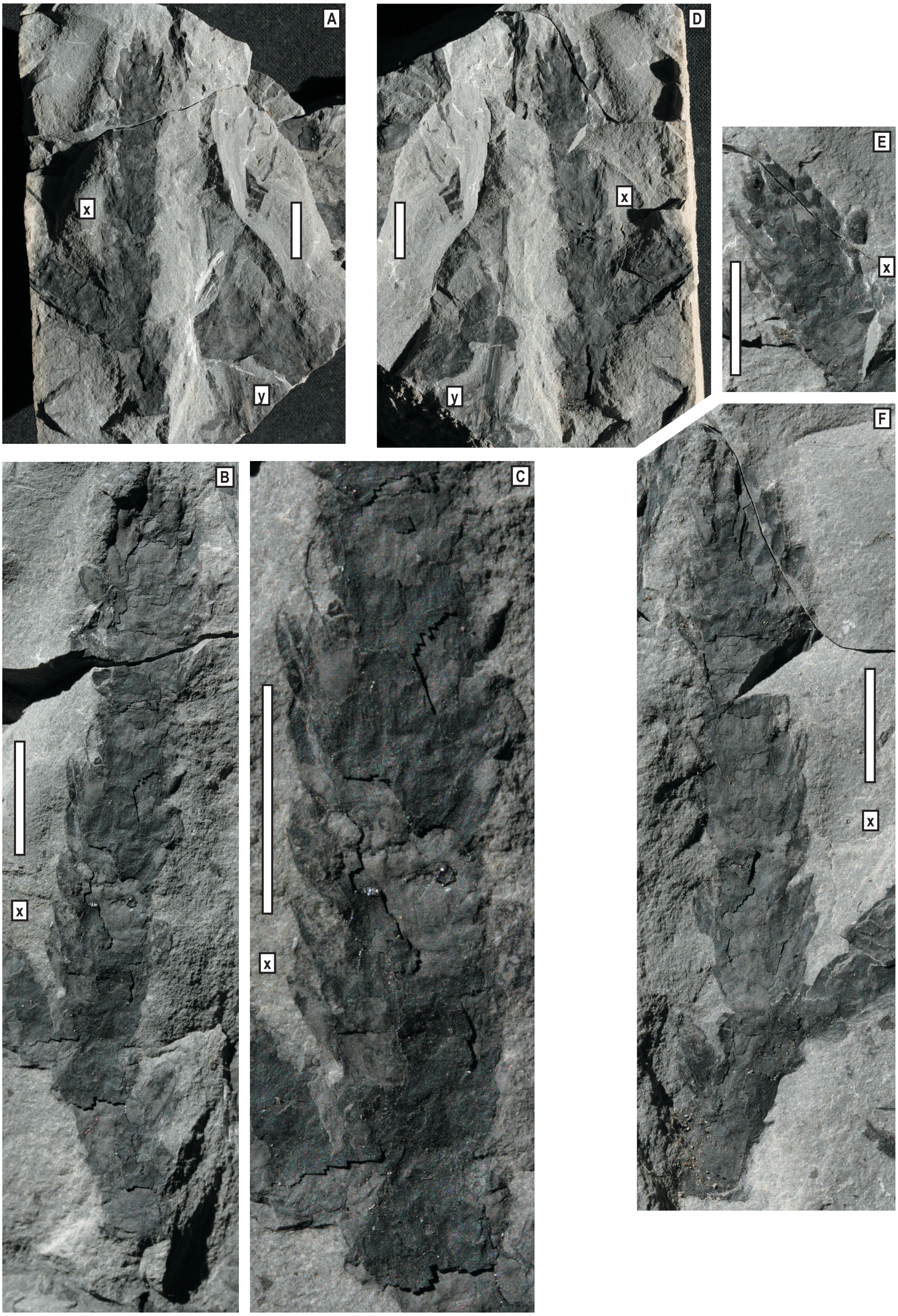

Figure 4. *Voltziopsis* sp. A., A–C AMF137595; D–F AMF137594, Res. Quarry (scale bar = 10 mm).

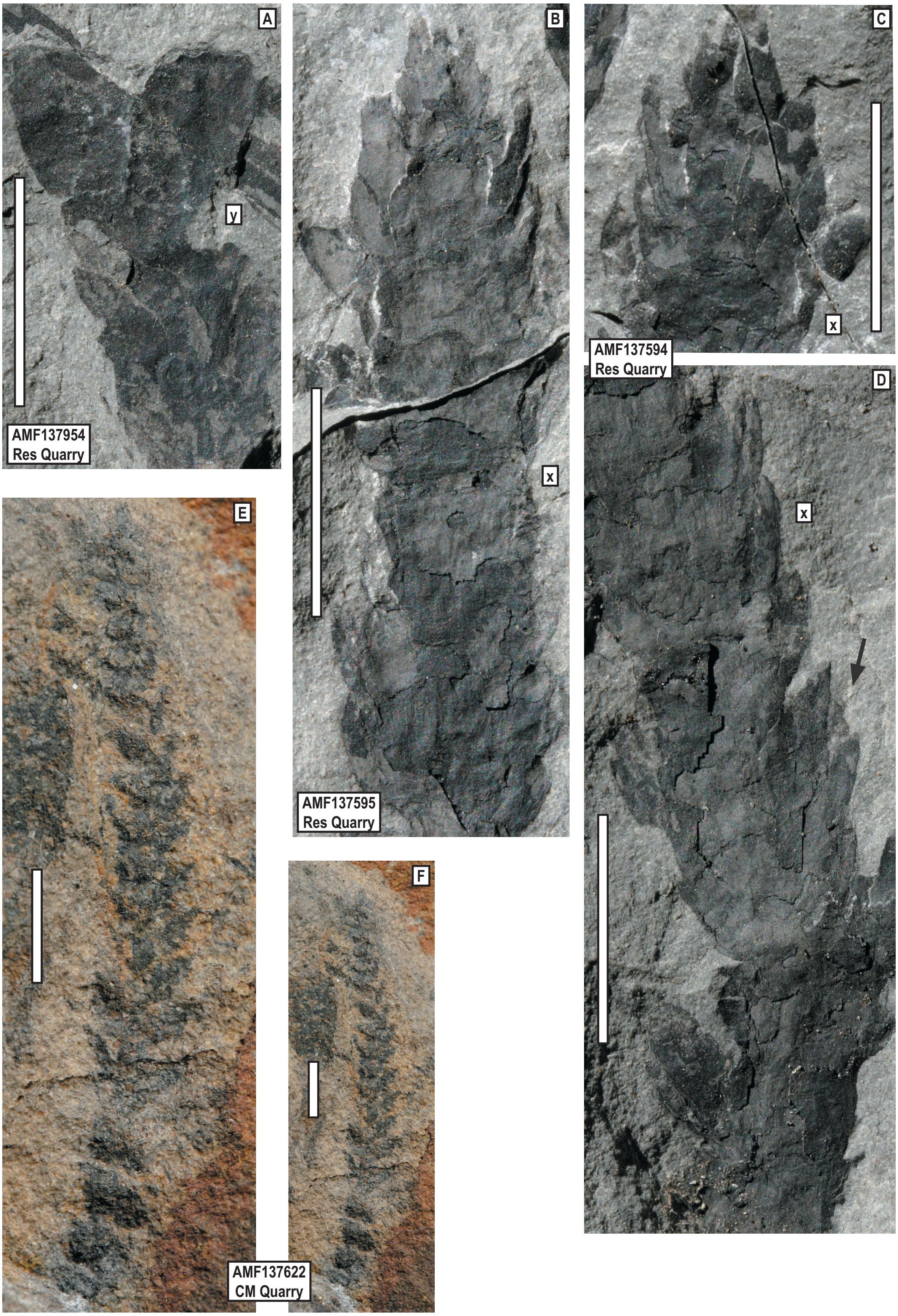

Figure 5. A–D *Voltziopsis* sp. A., E, F ?*Voltziopsis* sp. (scale bar = 10 mm).

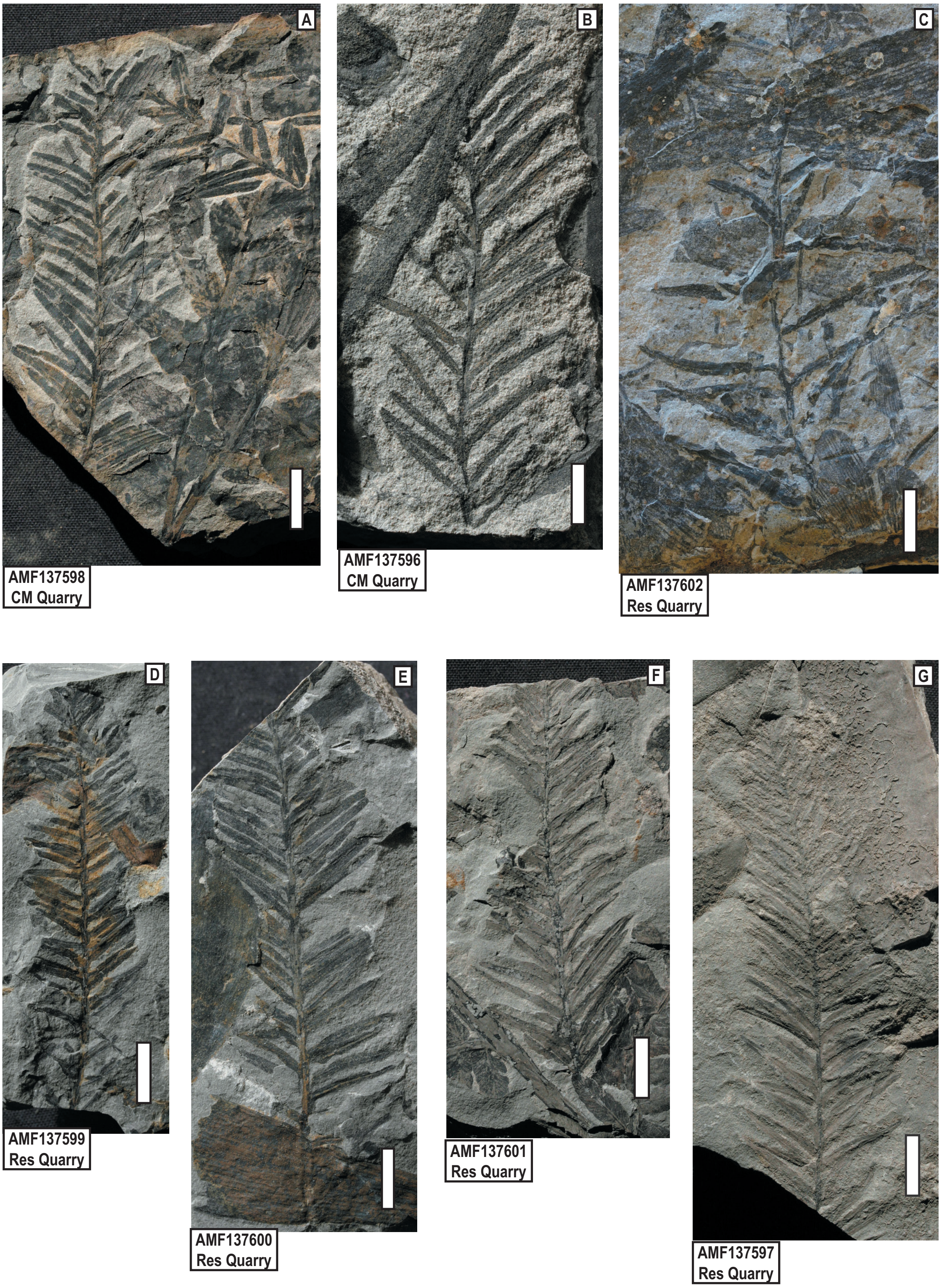

Figure 6. A–G *Rissikia media* Townrow (scale = 10 mm).

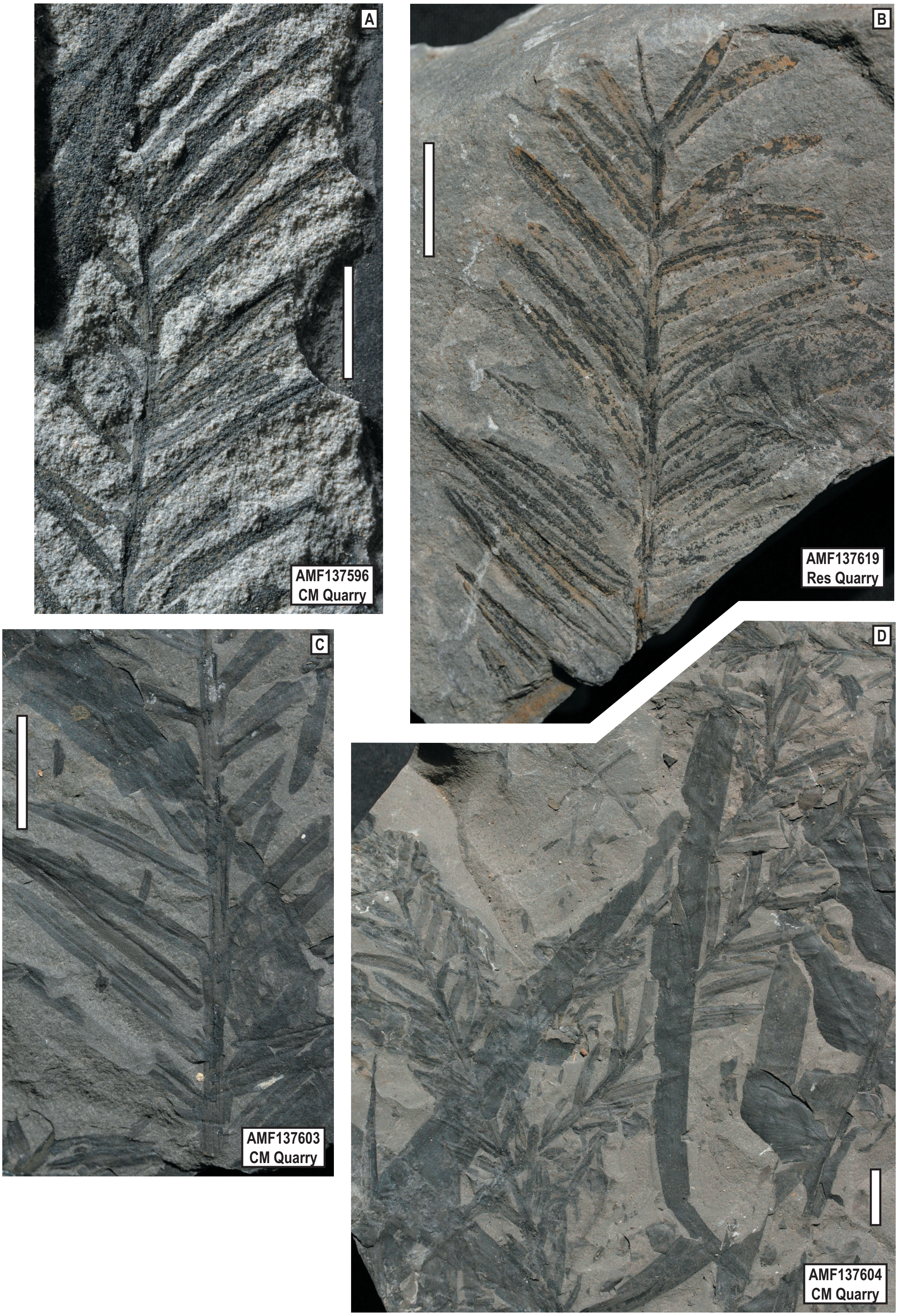

Figure 7. A–C *Rissikia media*Townrow. D *R. media* and *Heidiphyllum elongatum* Retallack (scale = 10 mm).

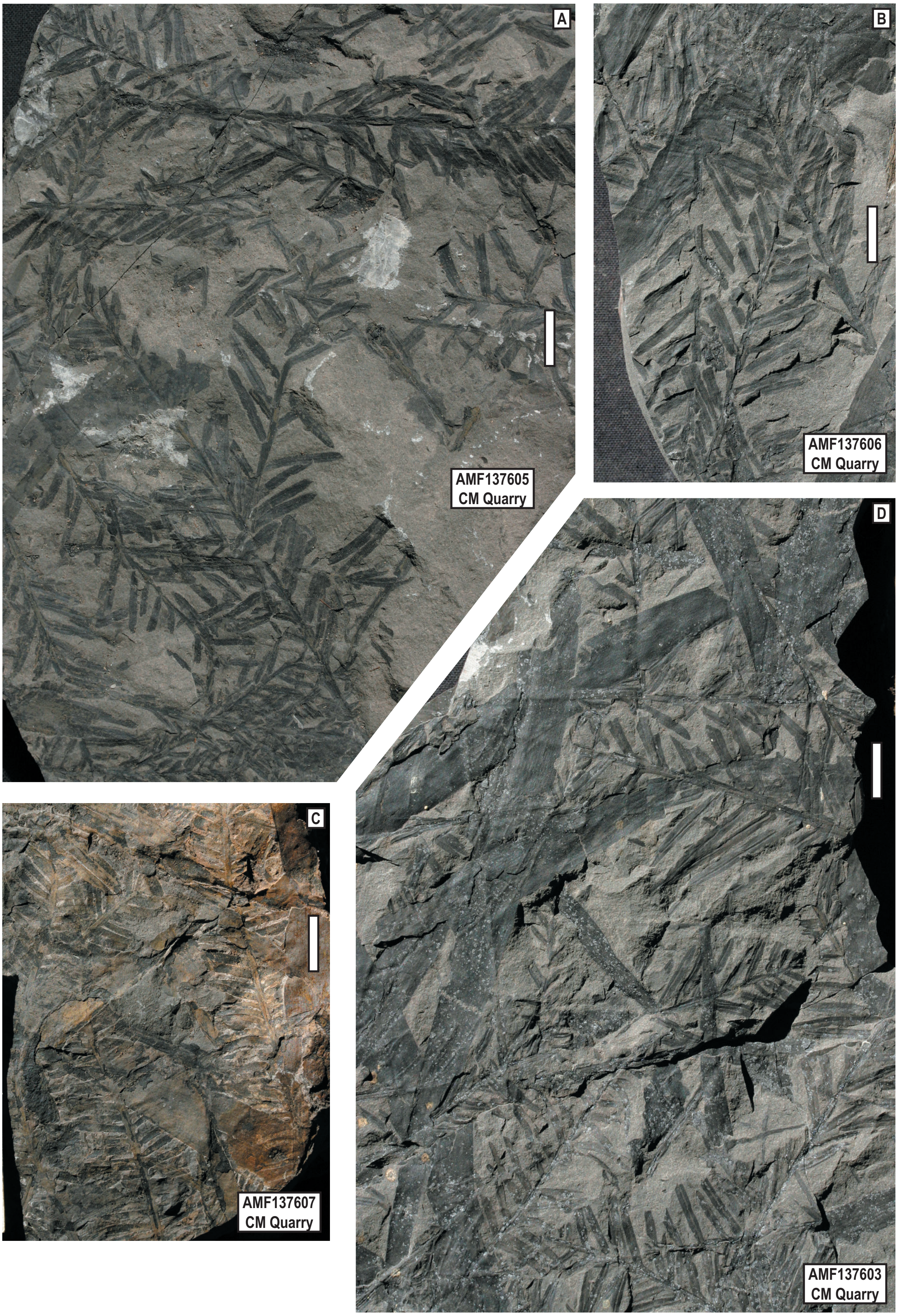

Figure 8. A–D *Rissikia media* Townrow (scale = 10 mm).

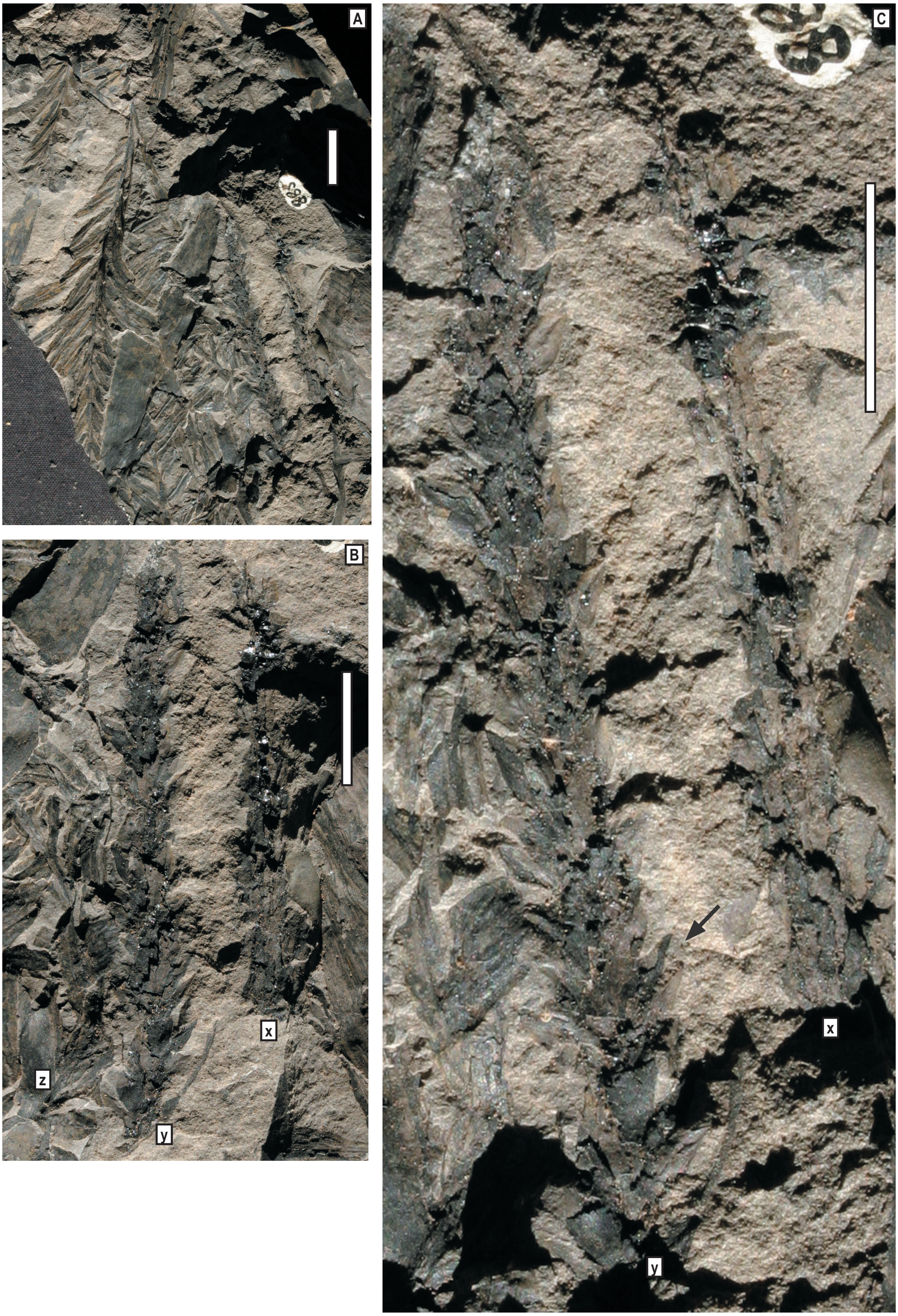

Figure 9. A–C *Rissikistrobus* sp. A (3 cones x, y, z). Arrow shows tips of two scales and an ovule to lower left. AMF 137613, Coal Mine Quarry (scale = 10 mm).

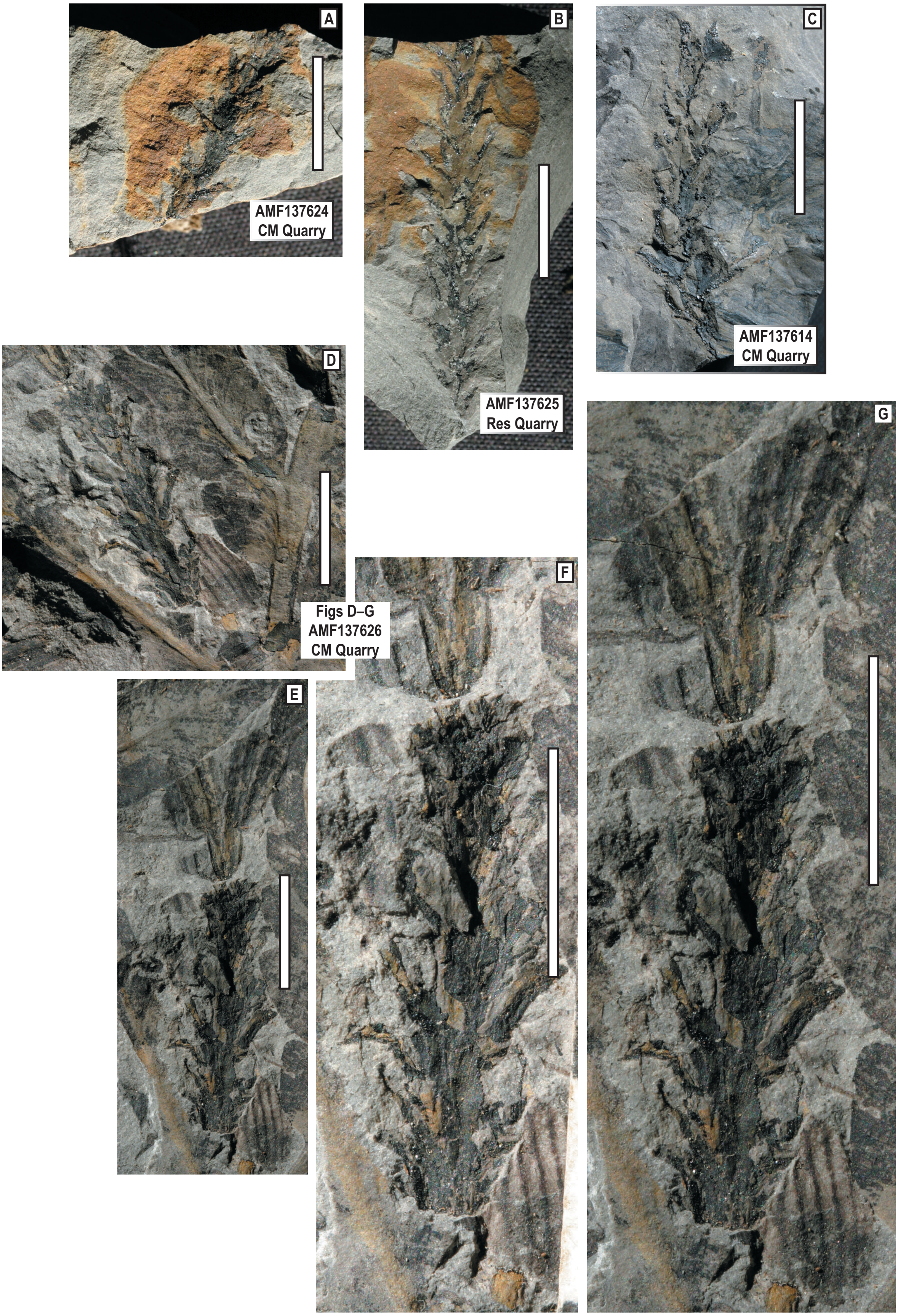

Figure 10. A–G *Rissikistrobus* sp. A (scale = 10 mm).

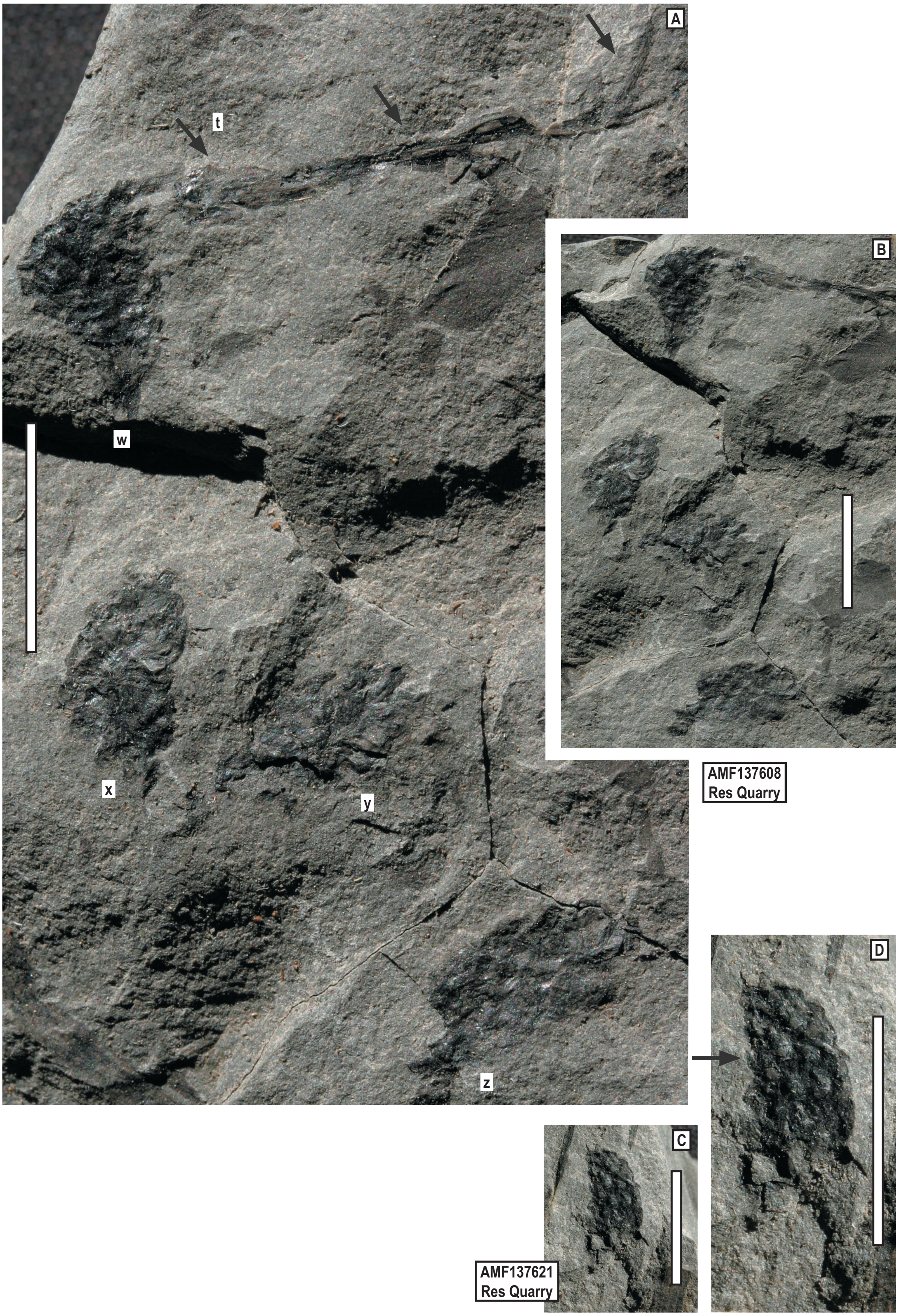

Figure 11. *Rissikianthus* sp. A. A,B has four male cones in close proximity marked as 'w, x, y ,z' AMF 137608 with a female cone marked 't' (see 3 arrows) AMF 137615. C,D a single male cone with a scale in side view (see arrow) (scale = 10 mm).

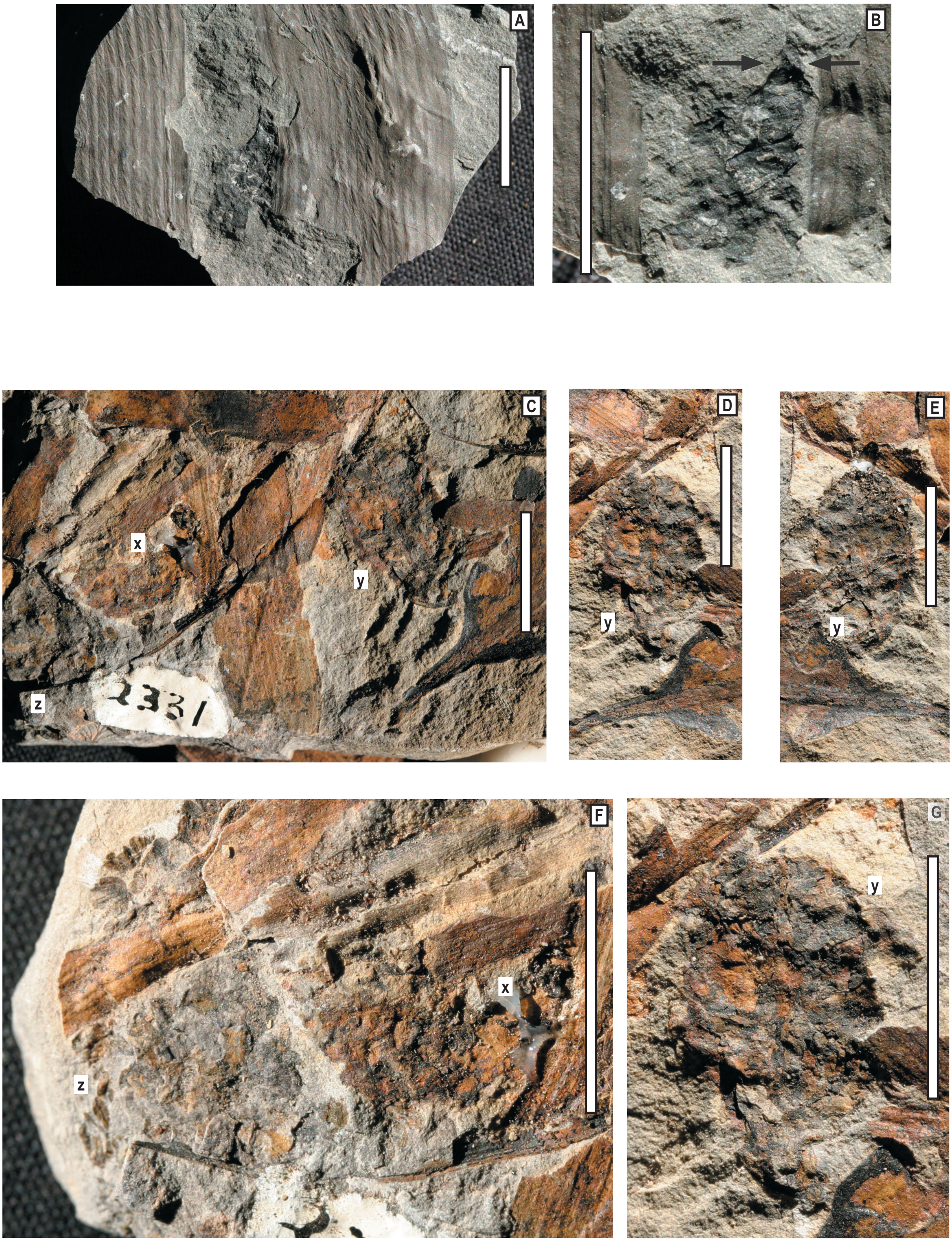

Figure 12. *Rissikianthus* sp. A. A,B Single incomplete cone with a good scale indicated by arrow, Reserve Quarry, AMF 137610; C–G Three cones in close proximity ‘x, y, z’, Coal Mine Quarry, C,D,F,G AMF 137611, E AMF 137612 (counterpart) (scale = 10 mm).

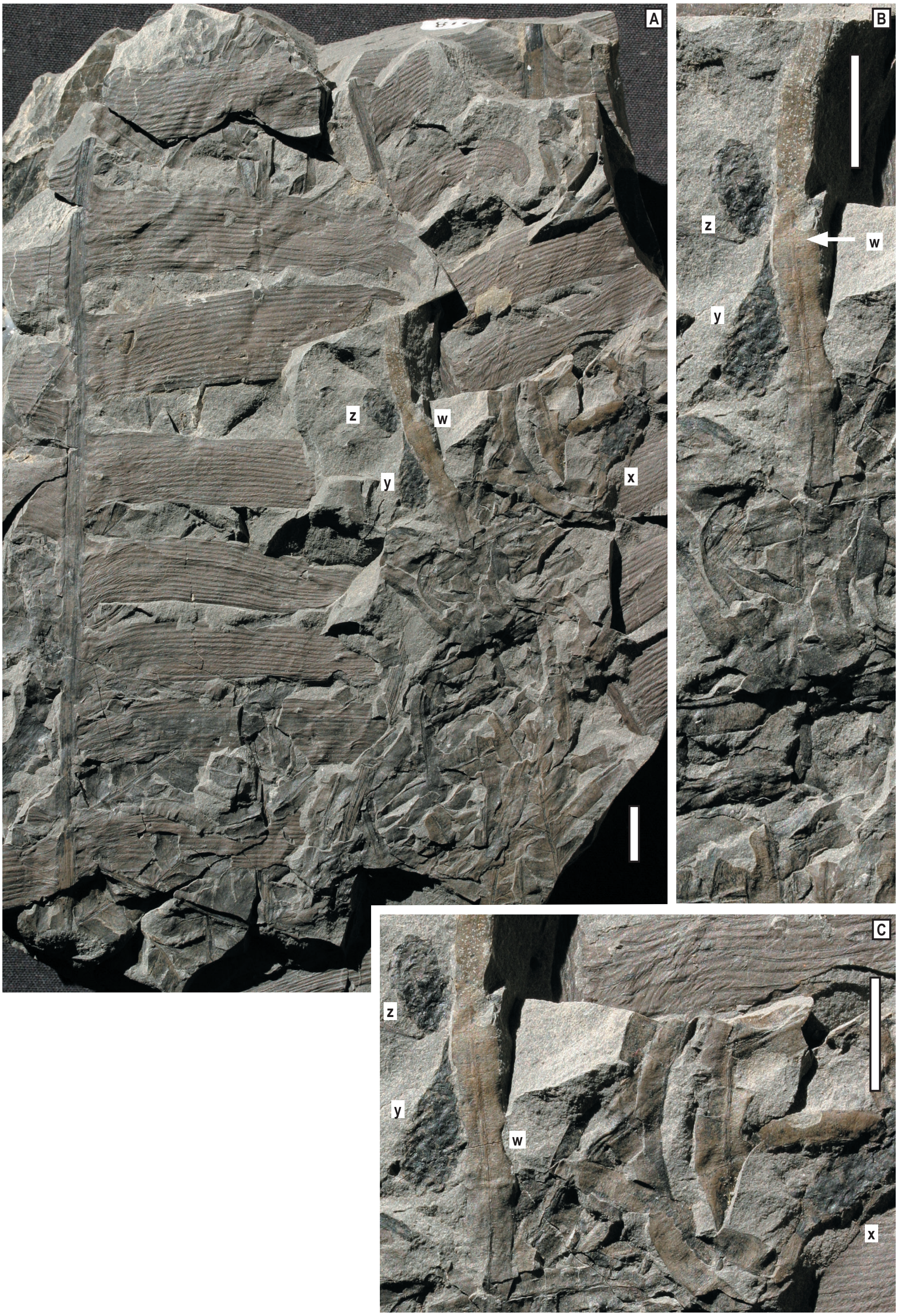

Figure 13. A–C One large slab with: *Rissikianthus* sp. A (3 male cones x, y, z) AMF 137616; ?*Yabeiella brackebushiania* (numerous leaf fragments, longest indicated as w) AMF 137617; *Pseudoctenis nymboidensis* (cycad leaf on LHS) AMF 137618. Reserve Quarry (scale = 10 mm).

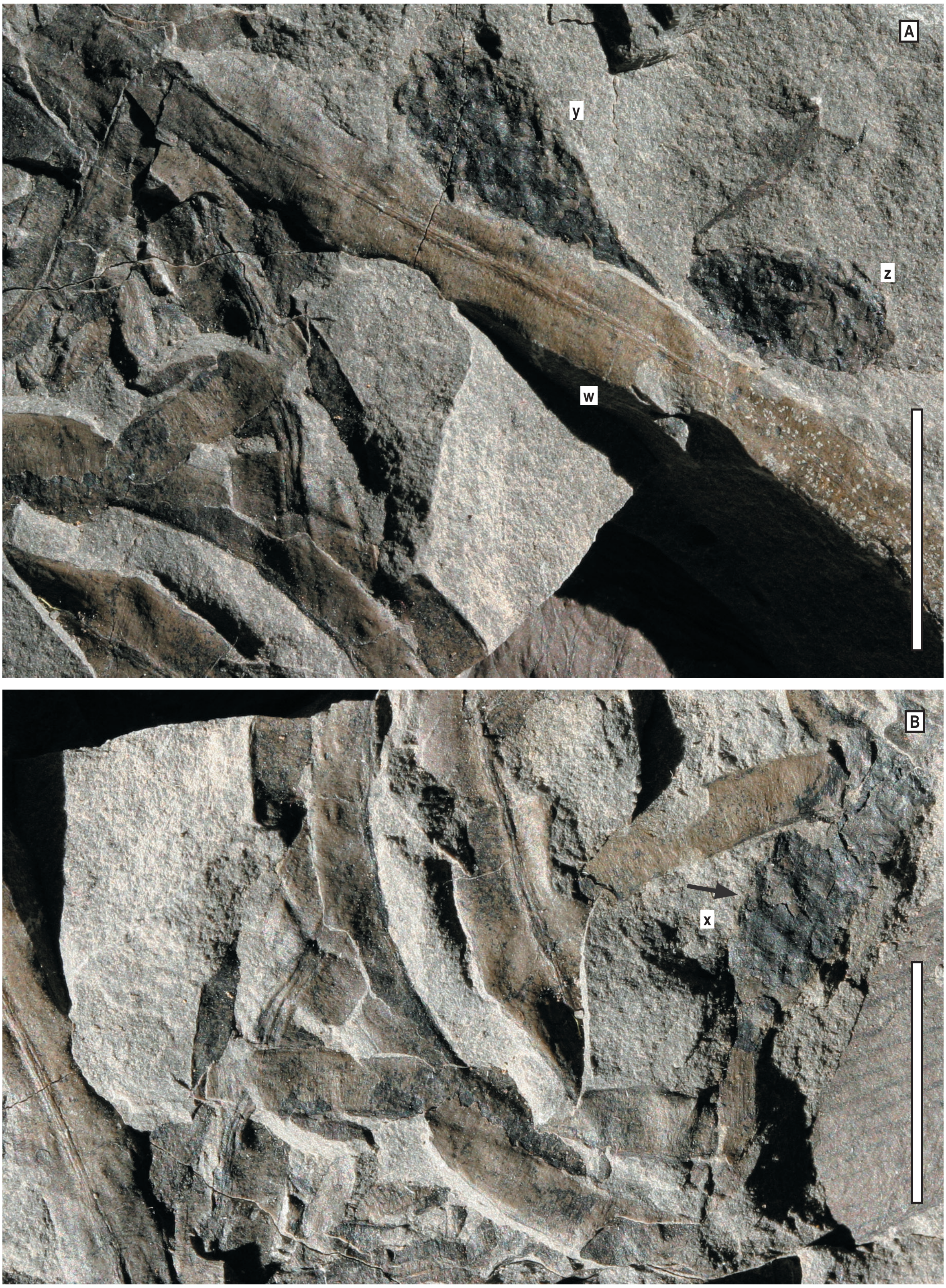

Figure 14. A,B *Rissikianthus* sp. A (3 male cones x, y, z) AMF 137616, ?*Yabeiella brackebushiania* (numerous leaf fragments, longest indicated as w) AMF 137617. Reserve Quarry (scale = 10 mm).

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