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Acraspisoides gen. nov. (Diptera: Therevidae: Agapophytinae): a new genus of stiletto-flies from Australia

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Abstract

A new Australian genus of Therevidae, *Acraspisoides* **gen. nov.**, comprising a single species (*A. helviarta* **sp. nov.**) is described and illustrated. This new genus is placed within the subfamily Agapophytinae based on the presence of velutum patches on the fore and hind femora. *Acraspisoides* is easily separated from other agapophytine genera by the combination of characters: large ventral lobe on aedeagus, multiple rows of postocular setae in both sexes, antennae positioned low on frons, and wing cell m_3 closed. Cladistic analyses using all genera of Agapophytinae (including *Acraspisoides***)** based on adult morphological characters and sequence data of the protein-encoding gene, elongation factor-1α (EF-1α), were performed to determine the phylogenetic placement of *Acraspisoides* **gen. nov.** in the subfamily. Analysis of the combined morphological and molecular matrices produced two most parsimonious trees, placing *Acraspisoides* **gen. nov.** as the most basal genus of Agapophytinae.

Key words: Diptera, Asiloidea, Therevidae, Agapophytinae, *Acraspisoides*, taxonomy, phylogenetic, EF-1α, Australia

Introduction

Stiletto-flies (Diptera: Therevidae) are of virtually worldwide distribution, occurring in all geographical regions with the exception of Antarctica (Irwin & Lyneborg 1989). Therevids occur in a multitude of habitats including rainforests, coastal dunes, and deserts, with greatest diversity apparent in arid environments where the sandy, friable soils provide a suitable habitat for the soil-dwelling larvae (Irwin 1976; Winterton *et al.* 2001).

Adult stiletto-flies are similar in appearance to robber flies (Diptera: Asilidae) but the mouthparts and fore legs are rather weak and without the predatory characteristics of robber flies. Also, most therevids lack a mystax and a vertex that is indented or depressed

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between the eyes. The face of stiletto-flies is deeply excavated below the antennae and the proboscis is curved upwards and mostly concealed within this hollow (Majer 1997).

Stiletto-fly larvae differ from other fly larvae in their secondarily segmented abdomen and apically spatulate tentorial rod (Irwin & Lyneborg 1981a, 1981b). The larvae are rapacious, fossorial predators of soil arthropods, and thus abundance of adult therevids could be considered a reasonable indirect indicator of underground productivity (Irwin 2001).

Therevidae, along with Asilidae, Apioceridae, Apsilocephalidae, Bombyliidae, Mydidae, and Scenopinidae, form the superfamily Asiloidea based on the apomorphic position of the larval posterior spiracles in the penultimate abdominal segment (Woodley 1989; Yeates 1994, 2002). Historically, therevids were considered to be most closely related to the scenopinids based on the secondary segmentation of the larval abdomen, which gives the appearance of 17 abdominal segments (Irwin & Lyneborg 1981b). Yeates (2002) suggested that Apsilocephalidae is the sister-group to Therevidae based on the presence of a distinct knob on the anterior surface of the hind coxa, a structure not found in most scenopinids. Interestingly, the larvae of apsilocephalids are unknown and thus, it is not known whether the larvae have secondary segmentation (Yeates 2002).

Approximately 1000 species of therevids have been described thus far, and this is thought to be just a fraction of the actual therevid diversity (Irwin pers. com.). Species of Therevidae are presently divided into three subfamilies: Phycinae, Therevinae (Lyneborg 1976; Irwin & Lyneborg 1981a) and Agapophytinae (Winterton *et al*. 2001). Phycinae have been divided into two tribes, Phycini and Xestomyzini (Lyneborg 1976), but a complete tribal-level classification has not been proposed for Therevinae and Agapophytinae. A fourth group, the endemic Australasian *Taenogera* genus-group, is a putative sister-group to Agapophytinae, although its monophyly is uncertain (Winterton *et al.* 1999b, 2001). The majority of papers on Australasian Therevidae were published during the first half of the last century by White (1915), Kröber (1912a–f, 1913, 1928, 1929, 1932), Mann (1928, 1929, 1933). More recent efforts include those of Winterton & Irwin 1999; Winterton *et al.* 1999a,b, 2000 and 2001; Lyneborg 1992, 2001.

The subfamily Agapophytinae was proposed by Winterton *et al*. (2001) for a diverse and species-rich lineage of Australasian therevids presently consisting of ten genera: *Acatopygia* Kröber, *Acraspisa* Kröber, *Acupalpa* Kröber, *Agapophytus* Guérin, *Belonalys* Kröber, *Bonjeania* Irwin & Lyneborg, *Laxotela* Winterton & Irwin, *Parapsilocephala* Kröber, *Patanothrix* Winterton, and *Pipinnipons* Winterton. The genera within Agapophytinae are a monophyletic group defined by the presence of elongate velutum patches on the ventral surfaces of the fore and hind femora and the presence of a velutum patch on the posteroventral surface of the gonocoxites (Winterton *et al*. 2001). The majority of agapophytine genera are endemic to Australia (Winterton *et al*. 2001), although three species of *Agapophytus* are recorded from Papua New Guinea (Winterton and Irwin 2001) and a single species of *Acraspisa* is recorded from Indonesia (Frey 1934).

A genus-level cladistic analysis of Agapophytinae was rendered using 21 ingroup taxa from the ten genera, based on 68 adult morphological characters and approximately 1000 base pairs of the protein-encoding gene, elongation factor-1α (EF-1α) (Winterton *et al*. 2001). They found that the subfamily can be divided into two clades based on the presence/absence of a posteromedial atrium between the gonocoxites of the male.

To continue the most recent efforts to document the Australian therevid diversity, we herein describe a new genus of Therevidae from Australia. The presence of elongate velutum patches on the fore and hind femora clearly places this new genus in Agapophytinae (Winterton *et al*. 2001). Diagnostic characters are discussed and illustrations of significant characters are provided. A cladistic analysis of the same 68 adult morphological characters and EF-1α used by Winterton *et al.* (2001) was performed with the addition of sequence data and morphological character scorings for this new genus to determine its placement within Agapophytinae.

Materials and Methods

Methodology and terminology follows that of Winterton *et al*. (2001). Genitalia were placed in a 10% KOH solution at 40–50°C for one hour to remove soft tissue, then rinsed and dissected in 80% ethanol. Female reproductive organs were stained with a saturated solution of Chlorazol Black in 40% ethanol. Preparations were then placed into glycerine gel and figures were drawn with the aid of the Olympus SZX12 and the MTI digital camera. Images produced from the camera were then traced with the aid of a lightboard. Internal membranous structures of the female reproductive system were figured in ethanol to prevent collapsing of the structures and optical distortion by glycerine gel. Genitalia preparations are stored in glycerine and/or glycerine gel in a genitalia vial mounted on the pin beneath the specimen.

Abbreviations for scutal chaetotaxy are as follows: *dc*, dorsocentral setae; *np*, notopleural setae; *pa*, postalar setae; *sa*, supra-alar setae; *sc*, scutellar setae. Abbreviations for genitalic structures are as follows: *d*, distiphallus; *da*, dorsal apodeme of parameral sheath; *ea*, ejaculatory apodeme; *ga*, gonocoxal apodeme; *gs*, gonostylus; *h*, hypandrium; *igp*, inner gonocoxal process; *lea*, lateral ejaculatory apodeme; *ogp*, outer gonocoxal process; *va*, ventral apodeme of parameral sheath; *vl*, ventral lobe; *ac*, accessory gland duct; *f*, furca; *ss*, spermathecal sac; *ssd*, spermathecal sac duct; *s*, spermatheca; *sd*, spermathecal duct. Other abbreviations used are as follows: A1, acanthophorite setae; t8, tergite 8.

Specimens examined in this study are deposited at the Australian National Insect Collection, CSIRO Entomology, Canberra (ANIC) and the Michael Irwin Collection, University of Illinois, Champaign (IRWC).

Taxonomy

Acraspisoides helviarta, gen. *et* sp. nov. (Figs. 1A–B; 2A–I)

Type species. *Acraspisoides helviarta*, **sp. nov.**, by monotypy.

Etymology. The generic name is derived from the therevid genus name *Acraspisa* Kröber; and the Latin- *oides*, resembling, referring to its morphological similarity to *Acraspisa*. The specific epithet is derived from the Latin- *helvus*, yellow; and *artus*, limb, referring to the yellow colouration of the legs.

Type material: Holotype male, AUSTRALIA: New South Wales: Warrumbungles [=Warrumbungle] National Park, Brownes Cr. [creek] nr. Wombelong Cr., 12–16.xii.1995, M.E. Irwin, 31°16'24''S, 148°57'38''E, Malaise [trap] nr. cliff overhang at waterhole (MEI#050798) (ANIC). Paratypes, AUSTRALIA: New South Wales: 2 females, Warrumbungle N.P., Buckleys Ck., 1.7 km N Camp Blackman, 480 m., 2.i.1993, M.E. Irwin (MEI#025320-1) (IRWC); female, Warrumbungle N.P., Buckleys Ck., 1.5 km NE Camp Blackman, 17.xii.1995, M.E. Irwin (MEI#051080) (IRWC), 1 male (MEI#140272), 10 females (MEI#140273-282) Warrumbungle N.P., nr. Woolshed; 31-x-7.xi. 1997; S.L. Winterton & J.H. Skevington; Malaise trap (ANIC).

Diagnosis. Antenna positioned very low on frons; antenna length shorter than head; male frons narrow (Fig. 1A), female frons relatively wide (Fig. 1B); male and female with multiple, poorly defined rows of postocular setae; palp spatulate apically; pleuron glossy black with horizontal stripe of silver velutum; wing banded, cell m_3 closed; velutum patches on ventral surface of fore femur, and posteroventral surface of hind femur; numerous stiff pale setae along posterior and dorsal surfaces of hind femur; velutum patch on ventral surface of gonocoxite barely evident; aedeagus with large globose bulb ventrally (Fig. 2C); female with three spermathecae (Fig. 2H); spermathecal sac small, rounded.

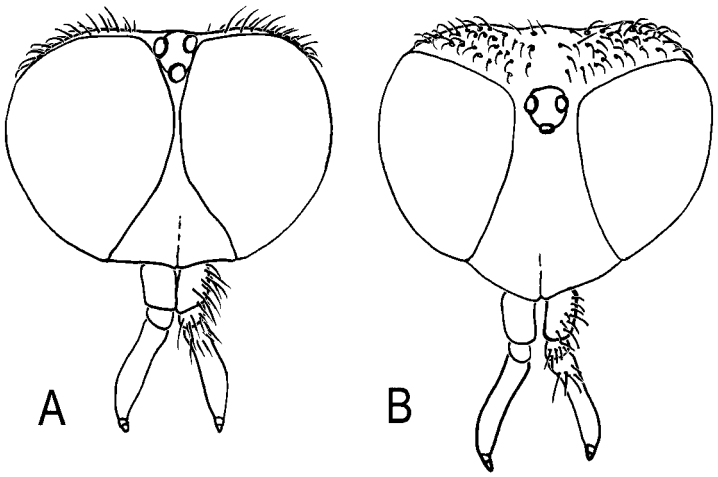

FIGURE 1. *Acraspisoides helviarta* gen. *et* sp. nov. (A) head, holotype male, dorsal view. (B) head, female, dorsal view. Scale line = 0.5mm.

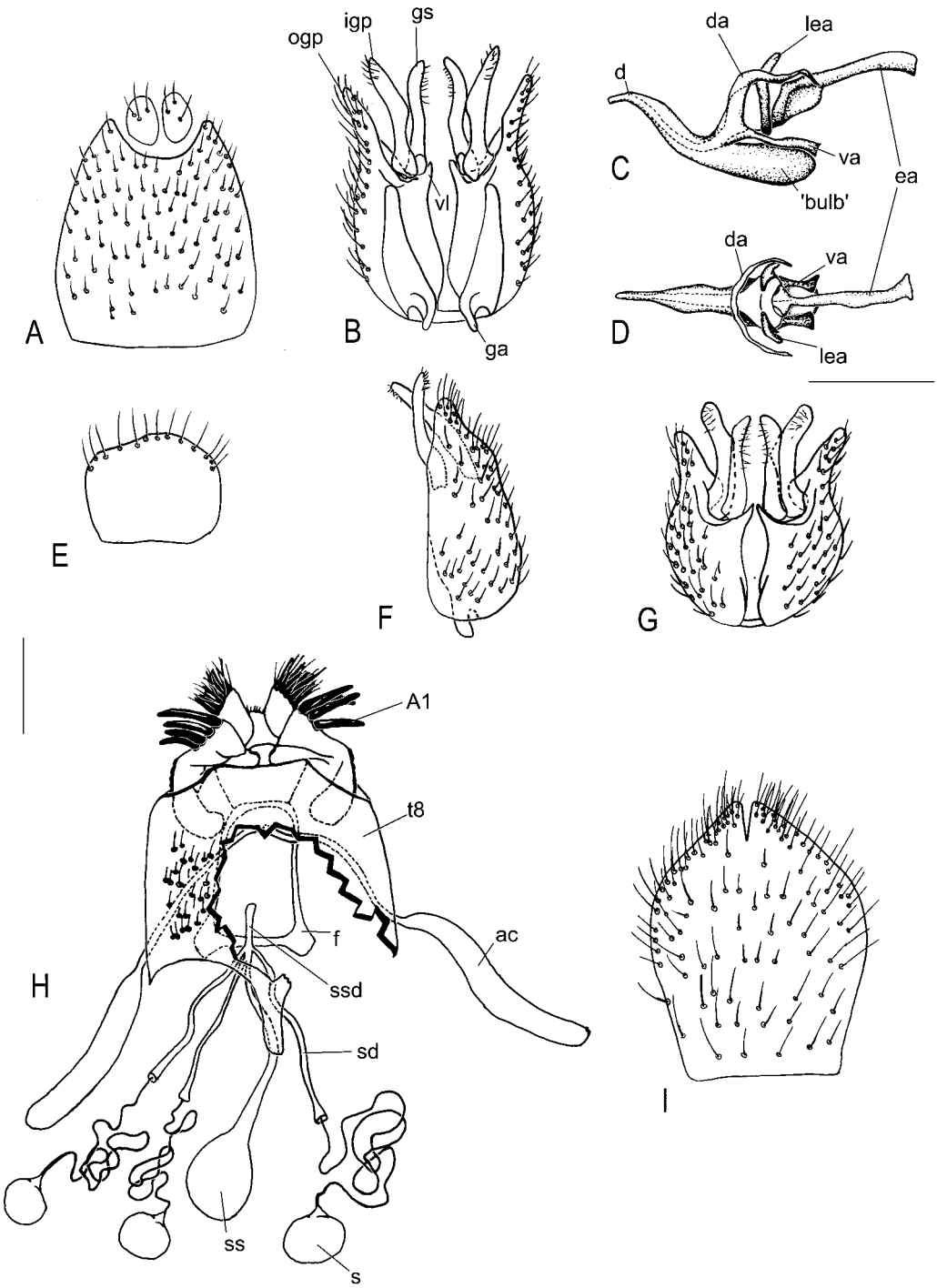

FIGURE 2. *A. helviarta* sp. n., male. (A) Epandrium, dorsal view. (B) Gonocoxite, dorsal view. (C) Aedeagus, lateral view. (D) Same, dorsal view. (E) Sternite 8, ventral view. (F) Gonocoxite, lateral view. (G) Same, ventral view. (H) Female terminalia, dorsal view, tergite 8 partially cut away to show spermathecal sac complex and accessory glands. (I) Sternite 8, ventral view. Scale line = 0.3mm.

Description. Head. Body length: 10.0 mm (male), 8.0–12.0 mm (female). Antennae very low on frons; head slightly longer than high; male eye with dorsal facets large; frons black, covered with sparse gray pruinescence interspersed with short black setae, setae more numerous in female, male frons very narrow dorsally such that eyes almost meet below ocellar tubercle (Fig. 1A), frons broadened above antennal tubercle, subtriangular, female frons wider than ocellar tubercle along entire length (Fig. 1B); ocellar tubercle black, overlain with sparse gray pruinescence, flattened in female; occiput concave in male, flattened to broadly convex in female, overlain with gray pruinescence, 2–3 poorly defined rows of black postocular setae; gena rounded, gena with sparse, long, dark, setae; mouthparts orange to pale brown, apical segment of palp spatulate; antennae orange to yellow, covered with pale pruinescence, short dark setae on scape, pedicel and base of flagellum; scape darker than rest of antennae in some specimens; flagellum ovoid shaped, longer than scape and pedicel combined, style two-segmented, scape 2.5–3.0x length of pedicel, flagellum conical, 2.0–2.5x length of scape, all segments with short, black setae except distal 4/5 of flagellum.

Thorax. Scutum glossy black with sparse gray pruinescence admixed with dark setae, setae much longer in male; pleuron glossy black, distinct silver longitudinal stripe of velutum running from proepimeron, dorsal half of katepisternum to katepimeron and meron; ventral half of katepisternum and meron overlain with sparse gray pruinescence; fore and mid coxae yellow to pale brown, hind coxae dark brown, all coxae with velvety silver pruinescence (denser on coxa 3) admixed with pale setae; legs dark yellow, male femora 2 and 3 with proximal 1/2–3/4 brown, hind femur and tibia with brown stripe dorsally, setae absent at apex of hind femur; patch of pale velutum on ventral surface of fore femur and posteroventral surface of hind femur; hind femur distinctly longer than fore and mid femora; wing hyaline with distinctive bands, venation dark, cell m_3 closed; haltere black, distal half of knob white; scutal chaetotaxy: np, 4; pa, 1; sa, 1; dc, 3–4 [rarely fewer]; sc, 1.

Abdomen. Glossy black, sparsely overlain with silver-gray pruinescence, brown-bronze pruinescence on tergites 1–5, long pale setae laterally on tergites 1–4, longer in male, margin of tergites 2–3 (sometimes 4) with white band, bands more pronounced in male; terminal segments yellow to pale brown.

Male genitalia (Figs 2A–G). Epandrium elongate, flattened, narrowed posteriorly; cerci relatively small, ovate (Fig. 2A); tergite 8 greatly emarginated medially such that the lateral surfaces are joined by a dorsal bridge, spiracular pore absent, 10–15 short to medium length setae along posterior margin of lateral lobe; sternite 8 broad (Fig. 2E), quadrangular, elongate setae along posterior margin; gonocoxites (Figs 2B, F, G) elongate and relatively shallow, hypandrium barely distinct, outer gonocoxal processes large and acuminate, not projecting past inner gonocoxal process; inner gonocoxal process narrow, slightly elbowed laterally at midpoint, several apical setae present; gonostylus narrow, setae present on inner surface; ventral lobe very small and acuminate; velutum patch on ventral surface of gonocoxite barely evident; gonocoxal apodemes relatively short; aedeagus (Figs

2C, D) with narrow, slightly dorsally recurved distiphallus, ventral surface of parameral sheath with large anteriorly directed globose bulb, dorsal apodeme forked, arcuate in dorsal view; ventral apodeme forked, similar length to dorsal apodeme; lateral ejaculatory apodeme distinct, band-like; ejaculatory apodeme narrow, extending well beyond dorsal and ventral apodemes.

Female genitalia (Figs. 2H, I). Acanthophorite (A1) setae large, 6–8 in number; tergite 8 with narrow anterior process; sternite 8 ovate, narrowed posteriorly; furca rectangular in shape with anterolateral processes; accessory glands with separate ducts leading to bursa copulatrix; spermathecal sac single lobed, relatively small and ovate, spermathecal ducts joined to spermathecal sac duct close to bursa copulatrix; spermathecae x3, membraneous, spherical.

Comments. A single species is included in *Acraspisoides*; *A. helviarta* from New South Wales. *Acraspisoides* can be readily recognized from non-agapophytine genera by the presence of femoral and gonocoxite velutum patches. *Acraspisoides* appears superficially similar to *Acraspisa*, with similarities in general body shape, and the shape of the male gonocoxites and aedeagus. It can be distinguished from other genera of Agapophytinae (including *Acraspisa*) by the globose ventral lobe on the aedeagus, a characteristic not found in any other species in that subfamily. Both sexes of *Acraspisoides* have multiple rows of postocular setae, a character shared with *Laxotela* and some *Agapophytus* species. The pleural stripe of silver velutum on the thorax is shared with *Parapsilocephala* and *Acraspisa*. *Acraspisoides* has a closed wing cell $m_{3,}$ which is the most common state in Agapophytinae. This character is shared with all genera in the subfamily except *Belonalys* and *Laxotela*. The hind femur is slightly longer than the fore and mid femora in *Acraspisoides*, a character also shared with *Acraspisa* and *Acatopygia*. To identify *Acraspisoides* the following couplet may be inserted (as triplet 6) into the key to genera of Agapophytinae in Winterton *et al.* (2001):

6(3). Male with single row of postocular setae; gonocoxites widely separated medially to form atrium; ventral lobe directed medially; velutum patch present on gonocoxites or on membrane across gonocoxal atrium; ventral apodeme of parameral sheath without ventral lobe; scutellum always rounded; body size from 6–15 mm 7

- Male with single row of postocular setae; gonocoxites not widely separated medially; ventral lobe never directed medially; velutum patch on gonocoxites greatly reduced; ventral apodeme of parameral sheath without ventral lobe; scutellum dorsally acuminate or rounded; body size < 8 mm ..... *Acraspisa*
- Male with multiple rows of postocular setae; gonocoxites not widely separated medially; ventral lobe never directed medially; velutum patch on gonocoxites greatly reduced; ventral apodeme of parameral sheath with large globose ventral lobe; scutellum rounded, not dorsally acuminate; body size = or > 8 mm .... *Acraspisoides* gen. nov.

Phylogenetic placement of *Acraspisoides*

Cladistic analyses including *A. helviarta* were performed to determine the phylogenetic placement of *Acraspisoides* in the subfamily Agapophytinae. *Acraspisoides* is superficially similar in appearance to *Acatopygia* and *Acraspisa*. *Acatopygia* is placed in the *Parapsilocephala* group due to the presence of a medial atrium in the male gonocoxites; *Acraspisoides* and *Acraspisa* lack this character. All described species of *Acraspisa* have a scutellum with a conical dorsal projection, a characteristic lacking in *Acraspisoides*.

Morphological character scoring

Sixty-eight adult morphological characters were scored from the character list provided in Winterton *et al.* (2001: Appendix 1: p.209; herein in Appendix 1). These character scores for *A. helviarta* were added to the matrix provided in Winterton *et al.* (2001: Table 3: p.178; reproduced in Table 1), which previously included 21 ingroup taxa representing all genera of Agapophytinae and five outgroup genera representing major therevid clades. Character state scoring for Character 40 was corrected in the morphological matrix presented in Winterton *et al.* (2001); in this case the three species of *Acraspisa* included in the matrix are scored as State 1, representing an elongate hind femur length, rather than State 0, representing a hind femur only slightly longer than the other femora.

S*equencing methodology and alignment*

Gene sequence of the nuclear, protein-encoding gene EF1-α was generated for *A. helviarta* using the DNA amplification and sequencing methods described in Winterton *et al.* (2001). Approximately 1.1 kb of EF1-α was sequenced and aligned manually with sequences already aligned in the matrix used previously by Winterton *et al.* (2001) comprising the aforementioned set of exemplars. EF1-α sequence for *A. helviarta* is deposited in Genbank (Accession number AY138981; MEI#140283). The EF1-α sequence for *A. helviarta* is unique in the alignment because it is the only member of Agapophytinae so far sequenced to contain an intron (65 bp at position 428 in this alignment). A homologous intron of similar size is also recorded in EF1-α for three other Therevidae (*Efflatouniella* Kröber, *Megalinga* Irwin & Lyneborg, *Orthactia* Kröber) (Yang *et al.* 2000), but this is the first recorded for agapophytines.

Phylogenetic analyses

The expanded nucleotide and morphological datasets of Agapophytinae genera with *Acraspisoides* included was combined in a simultaneous ('total evidence') analysis, in PAUP* version 4.0 (Swofford 2002) under parsimony criterion and using a heuristic search protocol (20 random addition sequences). Bremer support values were calculated for branches on the phylogenetic tree using TreeRot ver.2 (Sorenson 1999).

TABLE 1: Morphological character set matrix.

	0	10	20	30	40	50	60
Phycus niger	0000200000	0100000000	0000000000	0000000000	0000000000	0000000000	00000000
Anabarhynchus sp.	0110010000	0101000000	0000110011	1001100000	0000000040	1311000000	14001111
Ectinorhynchus sp. 1	0130011200	0011010010	1000001021	1001000000	0010000120	0200100100	03101111
Taenogerella elizabethae	0110000011	0001010010	1000000011	1001000000	0000000120	0200100100	03101111
Nanexila gracilis	0110000011	0000000010	1000100001	1001000000	0000000020	0400100100	03101111
Acraspisa sp. 2	0123100011	0010000010	1000001120	1010000011	0000000020	0202100200	01001211
Acraspisa sp. 3	0133100011	0010000010	1000001020	1010001011	0000000020	0202100200	01001211
Acraspisa sp. 1	0123100011	0010000010	1000001020	1010000011	0000000020	0202100200	01001211
Parapsilocephala sp. 1	0133010001	0020000011	1000001000	1010000000	0000002140	0202120211	01001211
Parapsilocephala sp. 2	0130010001	0020000011	1000001000	1010000000	0000012140	0202120211	01001211
Laxotela whitei	0130000000	0101000000	0000001021	1110000010	0000001010	0400100200	02001211
Bonjeania clamosis	0130000001	0020000010	1000001000	1010010100	0120012141	0102121320	31001211
Patanothrix skevingtoni	0130000001	0000000011	1000001000	1010000100	0100003130	0400100210	01001211
Patanothrix wilsoni	0130000001	0000000011	1000001000	1010000100	0100003130	0400100210	01001211
Acupalpa fascipennis	0031202212	1010100011	1000000020	1010011110	0110001020	0200100100	02001211
Acupalpa kroeberi	1031202212	1010100011	1000000000	1010011110	0110001020	0200100100	02001211
Acupalpa divisa	0031202212	1110111011	0010000020	1010000110	0010001020	0200100100	02011211
Acupalpa albitarsa	0031212212	1110111011	0010000020	1010000110	0010001020	0200100100	02011211
Agapophytus pallidicornis	1032213112	2110001000	0100000020	1010011010	1000001020	0200100100	02011211
Agapophytus australasiae	1032213112	2110000000	0100000020	1010011010	1000001020	0200110100	02011211
Agapophytus queenslandi	0031213112	2110100010	1000000020	1010011110	0000001020	0100120100	02001211
Agapophytus aterrimus	0031213112	2110101010	1001001020	1010010110	0010001020	0200110100	02001211
Agapophytus albobasalis	0032213112	2110111010	1000001020	1010010110	0000001020	0200110100	02001211
Agapophytus bicolor	0031203112	2110100000	0000001020	1010000000	0000001020	0200120100	02022211
Belonalys obscura	0130000001	0100000011	2000001011	1110000110	0100001010	0400130100	02001211
Acatopygia paradoxa	1130001000	0001000110	1000000020	1010001111	0011113140	0002110200	01001211
Acraspisoides helviarta	0033100001	0011000000	1000001020	1010001011	0000100020	0202120201	31001211

Results: Phylogenetic position of Acraspisoides

Analysis of the combined morphological and molecular matrices produced two most parsimonious trees (length= 964; CI=0.46; RI=0.54). A strict consensus tree is presented in Figure 3. *Acraspisoides* is placed as the most basal genus of Agapophytinae. The next node on the strict consensus tree is a polytomy between *Acraspisa*, the *Parapsilocephala* clade, and the rest of the agapophytines. Application of successive weighting to the combined matrix produced a single minimum-length tree identical in topology to one of the most parsimonious trees in the equally weighted analysis. This tree (not shown) places *Acraspisa* as the next most basal genus of Agapophytinae next to *Acraspisoides*. *Acraspisoides* is similar in appearance to *Acraspisa*, and while the phylogenetic analysis clearly places the two genera close to each other, it does not place them as sister genera. The basal position of *Acraspisoides* in Agapophytinae was not expected (but we have no prior evidence to suggest that this is not the case) and awaits verification with more extensive taxon sampling using more characters (e.g. morphology and genes).

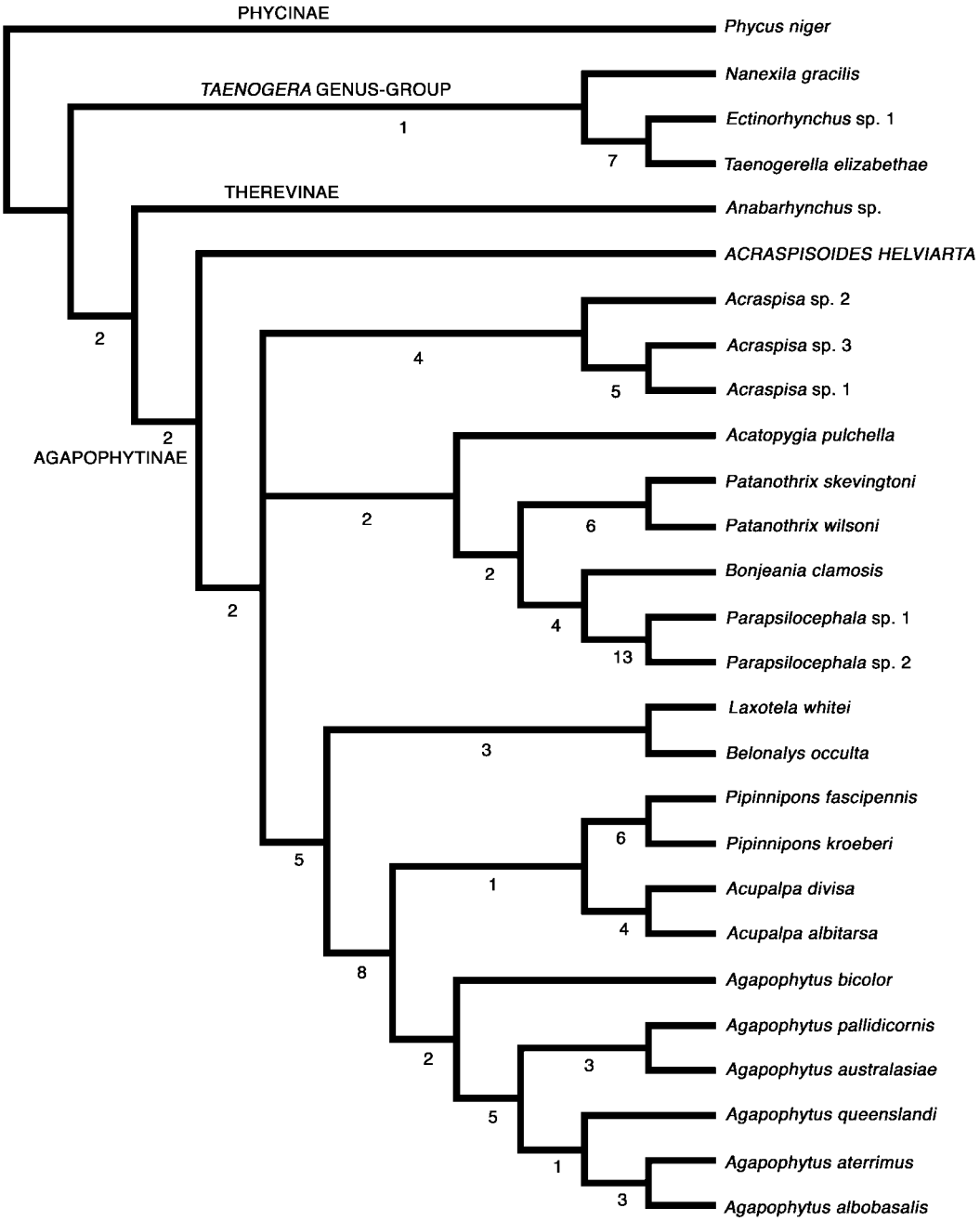

FIGURE 3. Phylogenetic relationships within the Agapophytinae. Strict consensus of two most parsimonious trees produced from analysis of expanded morphological and molecular dataset (length= 964; CI=0.46; R.I.=0.54). Numbers below branches represent Bremer support values.

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Appendix 1. Character descriptions of adult morphological characters used in the analysis of Agapophytinae (from Winterton *et al.* 2001).

1. *Antennae*: (0) drab coloured; (1) brightly coloured.
2. *Flagellum length to pedicel length*: (0) 3:1; (1) greater than 6:1.
3. *Shape of second flagellar segment*: (0) quadrangular; (1) tapered gradually; (2) inverted cup-shaped; (3) rounded and abruptly tapered.
4. *Flagellum with setae*: (0) present at base; (1) present on basal half; (2) present along entire length; (3) absent.
5. *Flagellum shape*: (0) tapered, onion-shaped; (1) "leaf"-shaped; (2) elongate.
6. *Flagellum segments (excluding style)*: (0) 2; (1) 3.
7. *Scape length to pedicel length ratio*: (0) 2:1; (1) 3:1; (2) 4:1; (3) greater than 4:1.
8. *Scape length*: (0) shorter than flagellum; (1) longer than flagellum; (2) approximately equal to flagellum.
9. *Scape width*: (0) wider than pedicel; (1) narrower than or equal to width of pedicel.
10. *Length of setae on scape and pedicel*: (0) long; (1) long, admixed with shorter setae; (2) all very short.
11. *Position of antennae on frons*: (0) low, closer to mouthparts; (1) equidistant from ocellar tubercle and mouthparts; (2) high, closer to ocellar tubercle.
12. *Frons width in male*: (0) narrower than ocellar tubercle; (1) wider than or equal to ocellar tubercle width.
13. *Frons shape*: (0) flat or broadly rounded; (1) antenna slightly raised on tubercle; (2) rounded with distinct glossy tubercle immediately dorsal to antennae.
14. *Male frons*: (0) with enlarged setae absent; (1) present.
15. *Upper frons profile*: (0) rounded or flat; (1) concave so that antennae appear raised.
16. *Upper frons*: (0) smooth; (1) striated.
17. *Lower frons*: (0) without setae below antennae; (1) with setae below antennae.
18. *Transverse furrow across eye*: (0) absent; (1) present.
19. *Number of rows of postocular setae in male*: (0) 2 or more; (1) one.
20. *Number of rows of postocular setae in female*: (0) 2 or more; (1) one.
21. *Shape of dorso-lateral region of male occiput*: (0) convex; (1) concave; (2) highly concave and deflexed medially.
22. *Lower margin of gena*: (0) narrow; (1) broad.
23. *Palp shape*: (0) apically spatulate; (1) apically acuminate.
24. *Thorax with white scale-like setae*: (0) absent; (1) present.
25. *Number of supra-alar setae*: (0) 1; (1) 2.
26. *Number of post-alar setae*: (0) 1; (1) 2.
27. *Number of dorso-central setae*: (0) 1–2; (1) 3–8.
28. *Scutellum*: (0) rounded; (1) acuminate dorsally.
29. *Wing*: (0) hyaline; (1) smoky infuscate; (2) banded.

30. *Wing cell m_3*: (0) open; 1, closed.
31. *Wing R_1 vein*: (0) setose; (1) glabrous.
32. *Base of costal margin*: (0) with small setae; (1) with enlarged flattened setae.
33. *Fore and hind femur*: (0) without velutum; (1) velutum present.
34. *Hind femur with anteroventrally directed, apical seta*: (0) absent; (1) present.
35. *Femora vestiture*: (0) single, erect type; (1) multiple types, appressed elongate setae admixed with erect short setae.
36. *Fore tibia and fore basitarsus*: (0) narrow; (1) broad.
37. *Fore tarsi coloration*: (0) contrasting to other tarsi; (1) all tarsi concolourous.
38. *Femora with long pale setae admixed with short dark setae*: (0) absent; (1) present.
39. *Hind coxa*: (0) with large ventrolaterally directed seta on outer surface of hind coxa; (1) without large seta(e).
40. *Hind femur length*: (0) slightly longer than other femora; (1) much longer than other femora.
41. *Scutum coloration with posterolateral white patches*: (0) absent; (1) present.
42. *Abdominal tergite 2 with posteromedial patch of short modified setae*: (0) absent; (1) present.
43. *Male abdomen*: (0) without velutum; (1) with velutum; (2) velutum present as thickened bands.
44. *Epandrium*: (0) narrow, flattened; (1) anterior corners expanded laterally to partially conceal gonocoxites.
45. *Epandrium*: (0) short; (1) long.
46. *Male cerci*: (0) short; (1) long.
47. *Gonocoxites with velutum*: (0) absent or greatly reduced; (1) present as rounded patch on sclerite; (2) present as raised, cup or plate-like patch; (3) present on atrium membrane between sclerites.
48. *Gonocoxites*: (0) not widely spaced medially; (1) widely separated posteriorly to form a medial atrium.
49. *Ventral lobe of gonocoxite*: (0) reduced or absent; (1) broad, paddle-shaped; (2) small, paddle-shaped, shorter than gonostylus; (3) narrow and elongate, medially directed apically, as long as gonostylus; (4) narrow but shorter than gonostylus, medially directed apically.
50. *Gonocoxal apodeme length*: (0) shorter than length of gonocoxites; (1) much longer than gonocoxite length.
51. *Dorsal apodeme of parameral sheath*: (0) connected to gonocoxal apodeme by a sclerotised bridge; (1) separate from gonocoxal apodeme.
52. *Dorsal apodeme of parameral sheath*: (0) greatly reduced; (1) poorly sclerotised, narrow T-shaped; (2) strongly sclerotised T-shaped; (3) broad, plate-shaped; (4) elongate, sclerotised.
53. *Ventral apodeme of parameral sheath*: (0) forked; (1) simple.

54. *Ventral apodeme*: (0) small; (1) greatly reduced or absent; (2) elongate.
55. *Inner gonocoxal process*: (0) absent or reduced; (1) well developed.
56. *Distiphallus*: (0) narrow apically, straight or ventrally directed apically; (1) straight, broad and cylindrical; (2) narrow along length, reflexed dorsally; (3) broad, spinose flanges laterally.
57. *Distiphallus length*: (0) short; (1) long.
58. *Lateral ejaculatory apodeme*: (0) absent; (1) present but reduced; (2) enlarged; (3) extremely enlarged.
59. *Ejaculatory apodeme*: (0) small; (1) large; (2) greatly enlarged.
60. *Male sternite 8*: (0) elongate or width equal to length; (1) length much shorter than width.
61. *Number of spermathecae*: (0) 3; (1) 2; (2) 1.
62. *Spermathecal sac*: (0) absent; (1) rounded; (2) elongate with parallel lobes; (3) trilobate with lobes of equal size; (4) T-shaped.
63. *Female accessory gland ducts*: (0) separate along entire length; (1) fused to form common duct before joining to bursa copulatrix.
64. *Female sternite 8*: (0) with uniform short setae; (1) with ornate patterning of thickened setae; (2) with uniform elongate setae.
65. *Acanthophorites*: (0) absent; (1) present; (2) reduced.
66. *Anterior process of female tergite 8*: (0) absent; (1) broad; (2) narrow.
67. *Female tergite 8*: (0) separate from tergite 9+10; (1) connected to tergite 9+10 by sclerotised bridge.
68. *Tergite 9+10*: (0) separate from furca; (1) joined to furca by narrow sclerotised bridges laterally.

