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Phylogeny of the tribe Sciophilini (Diptera: Mycetophilidae: Sciophilinae)

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Abstract. The monophyly and phylogenetic relationships within the species rich Sciophilini (Diptera: Mycetophilidae) were analysed, based on 96 adult morphological characters. The cladistic analysis included 80 Sciophilini exemplar species (representing all but 1 of the 36 genera placed previously in the Sciophilini) and 11 outgroup taxa of other mycetophilid tribes. The monophyly of Sciophilini was supported in the parsimony analysis by four synapomorphies. The tribe now contains 34 genera: Acnemia Winnertz, Acomoptera Vockeroth, Adicroneura Vockeroth, Afrocnemia Matile, Allocotocera Mik, Anaclileia Meunier, Aneura Marshall, Austrosciophila Tonnoir, Azana Walker, Baeopterogyna Vockeroth, Cluzobra Edwards, Drepanocercus Vockeroth, Duretophragma Borkent gen.n., Eudicrana Loew, Leptomorphus Curtis, Loicia Vockeroth, Megalopelma Enderlein, Monoclona Mik, Morganiella Tonnoir & Edwards, Neoallocotocera Tonnoir, Neoaphelomera Miller, Neotrizygia Tonnoir & Edwards, Neuratelia Rondani, Paramorganiella Tonnoir, Paratinia Mik, Paratrizygia Tonnoir, Parvicellula Marshall, Phthinia Winnertz, Polylepta Winnertz, Sciophila Meigen, Stenophragma Skuse, Tasmanina Tonnoir, Taxicnemis Tonnoir & Edwards, and Trizygia Skuse. Four genera placed previously in Sciophilini (Coelophthinia Edwards, Impleta Plassmann, Speolepta Edwards and Syntemna Winnertz) are transferred to the Gnoristini. Neoneurotelia Shinji and Neoparatinia Shinji are considered **nomina dubia**. Diagnoses are given for all genera in the tribe. Duretophragma gen.n. is described for the following species (all of which are comb.n.): Duretophragma andina (Duret), Duretophragma argentina (Duret), Duretophragma glabanum (Johannsen), Duretophragma fusca (Edwards), Duretophragma humeralis (Edwards), Duretophragma intermedia (Edwards), Duretophragma longifurcata (Freeman) (type species), Duretophragma morigenea (Edwards), Duretophragma naumanni (Duret), Duretophragma nigricauda (Edwards), Duretophragma obscura (Duret), Duretophragma ochracea (Freeman), Duretophragma pleuralis (Edwards) and Duretophragma similis (Johannsen). Other new generic combinations include: Trizygia albidens (Oliveira & Amorim) comb.n., Trizygia alvesi (Oliveira & Amorim) comb.n., Trizygia balbi (Oliveira & Amorim) comb.n., Trizygia camargoi (Oliveira & Amorim) comb.n. and Afrocnemia stellamicans (Chandler) comb.n.

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Introduction

The Mycetophilidae are a ubiquitous and diverse component of the dipteran fauna of forest ecosystems worldwide, where their larvae feed on fungal fruiting bodies, hyphae or spores. The family currently includes approximately 4100 described species in 180 genera (Pape et al., 2011). Traditionally three subfamilies Sciophilinae, Manotinae, and Mycetophilinae are recognized although only the latter two are thought to be monophyletic (Søli, 1997b; Hippa et al., 2004; Rindal & Søli, 2006). These subfamilies are further divided into four, one and two tribes, respectively (Edwards, 1925; Tuomikoski, 1966). Recent phylogenetic work on the subfamily Mycetophilinae has further clarified the limits of each of its two tribes and supports the monophyly of each tribe and the subfamily (Rindal & Søli, 2006; Rindal et al., 2007, 2009a,b). The five tribes within Sciophilinae (Gnoristini, Leiini, Metanepsiini, Mycomyiini and Sciophilini) are less well defined, with only Sciophilini and Mycomyiini apparently monophyletic (Søli, 1996, 1997b; but see Rindal et al., 2009b). The lack of phylogenetic resolution of tribal relationships in Sciophilinae (Søli, 1997b; Rindal et al., 2009b) particularly between the Gnoristini and Sciophilini, led us to start with a traditional tribal classification of the Sciophilinae (Edwards, 1925; Søli, 1997b; Vockeroth, 2009) in this study, rather than raising the tribes to subfamily level as some authors have done (e.g. Matile, 1991; Amorim et al., 2008).

The Sciophilini contains more than 520 extant species in 38 genera, and is an ancient group known to have occurred in the lower Cretaceous (Blagoderov, 1995). It is one of the four tribes described originally by Edwards (1925) within Sciophilinae and was defined as containing those genera with macrotrichia on the wing membrane and bristles on the mediotergite. However, the limits of Edwards' tribes are less than clear, as indicated by his frequent use of 'nearly', 'generally' and 'usually' in his descriptions (Edwards, 1925). Søli (1997b) suggested that Sciophilini was monophyletic based on an analysis of the Mycetophilidae that included 13 genera assigned to this tribe (from which two were removed by Søli (1997b): Paratinia Mik and Syntemna Winnertz). The clade with the remaining 11 genera was supported by 12 unambiguous character state changes (primarily characters involving presence/absence of setae on wings and legs). However, the genera included in the analysis represented only a third of the genera placed in this tribe and all were Palaearctic.

The Australasian/Oceanian region contains seven endemic Sciophilini genera. Although this might reflect divergence during the long isolation of the Australasian fauna from those of other regions, it may derive from the taxonomic approach of Tonnoir (1929). The six new genera described from Australia were not compared with the types of genera described previously from the region by Skuse (Tonnoir, 1929). The expectation was that future workers would compare this work to previous types and synonymize where needed. Unfortunately, this has not happened.

Other than Søli (1997b) most systematic studies on this tribe have been in the context of regional revisions, with no phylogenetic study of the relationships. Notable exceptions include a preliminary study of Sciophilini genera with a reduced posterior wing vein fork by Matile (1998) who suggested that these ten genera formed a monophyletic group, although no phylogenetic analysis was undertaken, and phylogenetic studies of *Cluzobra* Edwards (Matile, 1996), *Leptomorphus* Curtis (Borkent & Wheeler, 2012) and the Afrotropical species of *Sciophila* Meigen (Søli, 1997a).

We conducted a generic-level phylogenetic analysis of Sciophilini, using 80 exemplar species representing 35 of the 38 previously and currently included genera. The taxonomic limits of Sciophilini and the relationships between the genera are determined based on this analysis and new generic diagnoses are provided, including the description of a new genus. This analysis provides a classification and phylogenetic framework for future generic revisions and phylogenies within the tribe.

Materials and Methods

Specimens of Sciophilini and outgroup mycetophilid genera were obtained from the following collections (including acronyms used in the text): Australian National Insect Collection, CSIRO, Canberra, Australian Capital Territory, Australia (ANIC); Bernice P. Bishop Museum, Honolulu, HI, USA (BPBM); California Academy of Sciences, San Francisco, CA, USA (CAS); Canterbury Museum, Christchurch, New Zealand (CMNZ); Canadian National Collection, Ottawa, ON, Canada (CNC); Iowa State University Insect Collection, Ames, IA, USA (ISUI); Lyman Entomological Museum, McGill University, Ste-Anne-de-Bellevue, QC, Canada (LEM); Muséum National d'Histoire Naturelle, Paris, France (MNHN); New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand (NZAC); National Museum of Natural History, Washington DC, USA (USNM).

Exemplars of 35 of the 38 genera assigned previously to the Sciophilini were obtained. No specimens of the monotypic genera Neoneurotelia Shinji and Neoparatinia Shinji could be located; the types apparently have been lost or were never deposited in a collection. No known specimens from Japan, the type locality for both genera, fit either genus description (Shinji, 1938, 1939; T. Saigusa, personal communication). These two names are therefore considered nomina dubia. All specimens identified as Neoallocotocera Tonnoir that we examined were misidentified, and we were unable to obtain other specimens of this monotypic genus. Exemplar species for the remaining 35 genera included the type species, whenever possible, and additional exemplar species from additional biogeographic regions in which a genus occurs, for a total of 80 ingroup species (Table S1). Exemplar species are listed after each generic diagnosis, along with the known distribution of the species. The following general regions, with abbreviations, were used for the distributions: Afrotropical (AF), Australasian/Oceanian (AU), Nearctic (NE), Neotropical (NT), Oriental (OR), and Palaearctic (PA). Eleven exemplar species representing all other mycetophilid

subfamilies/tribes except Metanepsiini, were selected as outgroups: Gnoriste bilineata Zetterstedt, G. macra Johannsen (Gnoristini); Allactoneura obscurata Walker, Leia oblectabilis (Loew), Tetragoneura pimpla Coquillett (Leiini); Mycomya marginata (Meigen) (Mycomyiini); Manota sp.n. (Manotinae); Exechia attrita Johannsen, E. fusca (Meigen) (Mycetophilinae: Exechiini); Mycetophila exstincta Loew, M. fungorum (de Geer) (Mycetophilinae: Mycetophilini) (Table S1).

Morphological terminology follows Cumming & Wood (2009) in general and Søli (1997b) for some genitalic interpretations. The posterior wing veins CuA₁ and CuA₂ of Cumming & Wood (2009) are interpreted here as veins M₄, and CuA, respectively (Blagoderov & Grimaldi, 2004; Saigusa, 2006; Amorim & Rindal, 2007). Cuticular projections are referred to as a variety of setae/bristles (articulating projections with a basal membranous socket (alveolus)) or as micro- and macrotrichia (immovable projections). The distinction between micro- and macrotrichia on the wing membrane is determined principally by the length (macro-> width of an average wing vein; micro- < 1/2 width of wing vein).

Genitalia were prepared by first removing the genitalia along with the posterior three to four segments of the abdomen from a specimen. These were then cleared in 85% lactic acid heated for three to five 15-s intervals in a microwave oven, each separated by cooling periods of 1-2 min. The cleared material was then immersed in two washes of glycerin before being placed on a microscope slide for detailed observation, or being stored in glycerin in a plastic vial pinned below the specimen.

Phylogeny

A matrix of characters was constructed using Mesquite v2.74 (Maddison & Maddison, 2011) and a parsimony analysis was performed using TNT v1.1 (Goloboff et al., 2003). An heuristic search was run with 500 replicates, saving 100 trees per replicate. The MaxTrees limit was set to 50 000 trees. Tree Bisection Reconnection (TBR) branch swapping was used for the search and branches were collapsed when the maximum length was zero. Characters were treated as unordered. Several characters have states recorded as present or absent, in some cases causing interdependent characters. However, we retain these characters as separate, as this is the only way to extract some pertinent phylogenetic data from the observed differences in morphology (Lee & Bryant, 1999; Strong & Lipscomb, 1999). Bremer support (Bremer, 1994) and Bootstrap (Felsenstein, 1985) values were calculated using TNT. Suboptimal trees with 1-20 extra steps were used to calculate Bremer support values. Bootstrap values were calculated using the same parameters as in the heuristic search.

Characters

The phylogenetic analysis was based on 96 characters (62 binary, 34 multistate). The plesiomorphic state (0) is given for each character (based on results of the analysis), followed by

the apomorphic states (1, 2, 3) and, in parentheses, by the consistency index and retention index for each character. As discussed above, the morphological terminology used follows Søli (1997b), and many of the character states given below can be seen clearly in illustrations in that paper.

- Head shape (anterior view, eye width and height from bottom margin of eyes to peak of occiput): wider than tall (0), subequal (1), taller than wide (2) (0.1, 0.44).
- 2. Medial eye margins: farther apart dorsally than ventrally (0), parallel or closer together dorsally than ventrally (1) (1, 1).
- Antennal eye notch: deep, angular, at least two to three ommatidia deep (0), slight, margin concave at antenna no more than one to two ommatidia deep and not angular (1), absent or eye flattened adjacent to antenna (2) (0.13, 0.59).
- Interommatidial setae: present between all ommatidia (0), sparse (1), absent (2) (0.15, 0.39).
- 5. Ocelli number: 3 (0), 2 (1) (0.11, 0.5).
- 6. Ocelli arrangement: triangular (0), median ocellus just anterior (1), linear (2) (0.13, 0.44).
- 7. Lateral ocelli distance from eye margin: at least $1.5 \times$ ocellar diameter from eye margin (0), $<0.5 \times$ to $<1.5 \times$ diameter from eye margin (1), at eye margin (2) (0.12, 0.69).
- Lateral ocelli distance from median ocellus: 0.5–1× diameter of lateral ocellus) (0), >1–2.5× diameter of lateral ocellus (1), >2.5× diameter of lateral ocellus (2). If two ocelli present, half the distance between them was used to approximate the location of the median ocellus (0.13, 0.56).
- 9. Median ocellus: on raised base (0), flat or sunken (1) (0.14, 0.54).
- Median ocellus orientation facing: anteriorly (0), anterodorsally (1), dorsally (2) (0.33, 0.5).
- 11. Straight line between lateral ocelli touches eye margin: no (0), yes (1) (0.08, 0.73).
- 12. Lateral ocelli on raised base: yes (0), no (1) (0.17, 0.69).
- 13. Ocellar triangle colour (around ocelli): darker than background (0), same as background (1) (0.07, 0.54).
- Frontal cleft (Søli, 1997b: Figs 1, 2): absent (0), from lateral ocelli to eye margin (ocelli touching eye margin are included here) (1), from frontal furrow to eye margin (2) (0.11, 0.51).
- 15. Frontal furrow (median ocellus to apex of frons): complete (0), partial (1), absent (2) (0.08, 0.51).
- 16. Occipital furrow (median ocellus to occipital foramen): present (0), absent (1) (0.17, 0.64).
- 17. Setae on frons: absent (0), present on entire frons (1), present ventrally (2) (0.22, 0.87).
- 18. Length of scape setae relative to length of scape: $0.5-1 \times (0)$, $>1 \times (1) (0.08, 0.5)$.
- 19. Length of pedicel setae relative to length of pedicel: 0.5−1 (0), 1.1−2 (1), >2 (2) (0.1, 0.59).
- Flagellomere 1 basal stalk: uniformly tapering (0), slightly offset (1), distinctly offset towards dorsal margin (2) (0.18, 0.7).

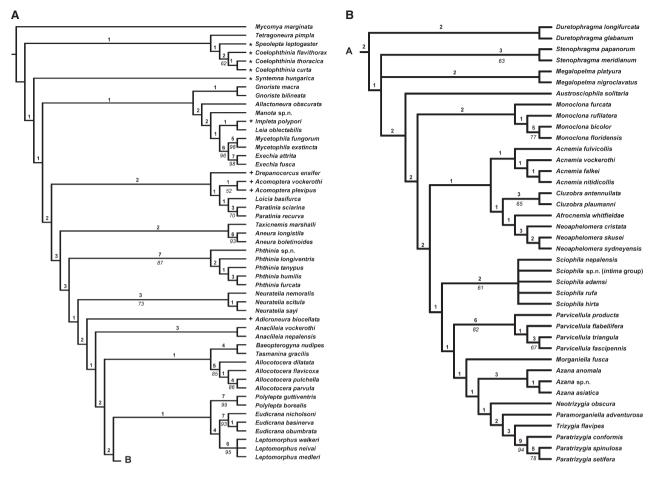


Fig. 1. (A) Base of strict consensus tree of 12 equally parsimonious trees found in the phylogenetic analysis. Bremer support values are above the branches in bold; bootstrap values >50% are in italics below the branches. Taxa included previously in Sciophilini are noted with an '*' and new additions with a '+'. (B) Apex of strict consensus tree of 12 equally parsimonious trees found in the phylogenetic analysis. Bremer support values are above the branches in bold; bootstrap values > 50% are in italics below the branches. Taxa included previously in Sciophilini are noted with an '*' and new additions with a '+'.

- 21. Flagellomeres: cylindrical (0), slightly laterally compressed (1), strongly laterally compressed (1) (0.4, 0.57).
- 22. Flagellomere 6 shape: longer than wide (0), subequal (1), wider than long (2) (0.14, 0.4).
- 23. Face length relative to clypeus length: $0.3-1 \times (0)$, $1.1-2 \times (1)$, $>2 \times (2) (0.15, 0.69)$.
- 24. Face and clypeus: >1/3 of margin fused (0), <1/3 of margin fused (1), separate (2) (0.18, 0.64).
- 25. Acrostichal setae: present (0), absent (1) (0.5, 0.67).
- 26. Anepisternal bristles: absent (0), present (1) (0.25, 0.86).
- 27. Anepisternal bristle location: bare (0), up to dorsal half covered (1), more than half covered (2) (0.33, 0.8).
- 28. Anepisternal trichia: present (1), absent (0) (0.17, 0.55).
- 29. Anterior basalare: bare (0), with many bristles (1) (0.2, 0.6).
- 30. Anapleural suture: single (0), double (1), absent (2) (0.4, 0.67).
- 31. Anapleural suture: complete (0), reduced (1), absent (2) (0.5, 0.5).

- 32. Anterior end of (upper) anapleural suture relative to posterior end: dorsal (0), subequal (1), ventral (2) (0.13, 0.63).
- 33. Mediotergite bristles: absent (0), present (1) (0.33, 0.92).
- 34. Mediotergite with macrotrichia (hairs): absent (0), present (1) (0.33, 0.75).
- 35. Mediotergite trichia placement: absent (0), anteriorly (1), central patch (2) (0.67, 0.86).
- 36. Laterotergite with bristles: absent (0), present (1) (0.25, 0.83).
- 37. Laterotergite with trichia: absent (0), present (1) (0.33, 0.6).
- Laterotergite shape (Søli, 1997b: fig. 14): evenly rounded (0), protruding with keel (1) (0.25, 0.5).
- 39. Metepisternum: bare (0), with several setae, usually posteriorly (1) (0.13, 0.71).
- 40. Bristle(s) on metanotal membrane just posteromedially of halter base: present (0), absent (1) (0.25, 0.8).
- 41. Wing membrane macrotrichia: present (0), absent (1) (0.5, 0.95).

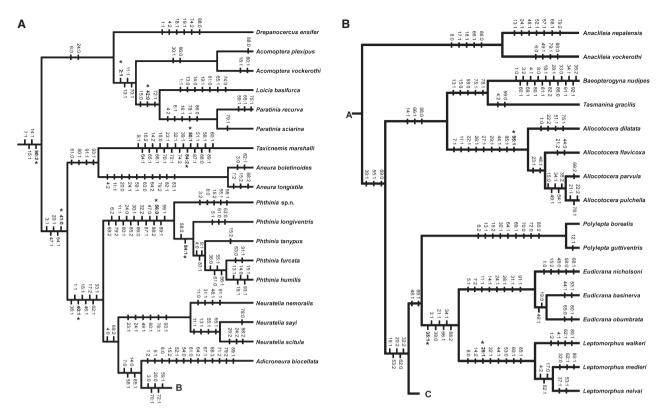


Fig. 2. (A) One of 12 equally parsimonious trees showing relationships at the base of the tree (*Drepanocercus – Adicroneura*). Character state changes are indicated by black bars. Uniquely derived synapomorphies are in bold with an asterisk. (B) Continuation of 1 of 12 equally parsimonious trees showing relationships from *Eudicrana* to *Polylepta*. Character state changes are indicated by black bars. Uniquely derived synapomorphies are in bold with an asterisk. (C) Continuation of 1 of 12 equally parsimonious trees showing relationships from *Stenophragma* to *Monoclona*. Character state changes are indicated by black bars. (D) Continuation of 1 of 12 equally parsimonious trees showing relationships from *Stenophragma* to *Monoclona*. Character state changes are indicated by black bars. (D) Continuation of 1 of 12 equally parsimonious trees showing relationships within the *Acnemia* clade (*Acnemia–Neoaphelomera*) and *Sciophila*. Character state changes are indicated by black bars. Uniquely parsimonious trees showing relationships at the apex of the tree (*Parvicellula – Paratrizygia*). Character state changes are indicated by black bars. Uniquely derived synapomorphies are in bold with an asterisk.

- 42. Wing membrane setae: present (0), absent (1) (1, 1).
- 43. Wing macrotrichia orientation: absent or decumbent to wing tip (0), reflexed (1) (0.5, 0.75).
- 44. Wing membrane microtrichia: present (0), absent (1) (0.11, 0.43).
- 45. Microtrichia arrangement on wing membrane: irregular or appearing absent (only present near wing veins) (0), parallel lines (1) (1, 1).
- 46. Distal median plate (Fig. 3B): bare (0), setose (1) (0.25, 0.89).
- 47. Humeral vein: oblique (0), curved (1) (0.5, 0.96).
- 48. Dorsal humeral setae: absent (0), present (1) (0.1, 0.65).
- 49. Ventral humeral setae: absent (0), present (1) (0.11, 0.74).
- 50. Subcostal vein: ending in C (0), free beyond sc-r (1), ending in sc-r (i.e. Sc ending in R) (2), free at wing base (3) (0.38, 0.55).
- 51. Subcostal vein: long (>1/3 wing length) (0), short (1) (0.11, 0.74).
- 52. sc-r: present (sometimes reported as Sc ending in R) (0), absent (1) (0.14, 0.68).

- 53. sc-r ending: before Rs or Sc ending near level of Rs if sc-r absent (0), at or very near Rs (1), beyond Rs (2) (0.14, 0.45).
- 54. Ventral surface of subcostal vein: bare (0), setose (1) (0.33, 0.91).
- 55. Ventral base of subcostal vein: bare (0), setose (1) (0.17, 0.83).
- 56. Dorsal surface of subcostal vein: bare (0), setose (1) (0.33, 0.88).
- 57. Dorsal base of subcostal vein: bare (0), setose (1) (0.17, 0.82).
- 58. bM dorsally: bare (0), setose (1) (0.13, 0.81).
- 59. bM ventrally: bare (0), setose (1) (0.09, 0.73).
- 60. C ending: beyond R₅ (0), at R₅ (1) (0.13, 0.5).
- 61. R₁ ventrally: bare (0), setose (1) (0.14, 0.57).
- 62. R₄: present (0), absent (1) (0.08, 0.65).
- 63. R₅ ventrally: bare (0), setose (1) (0.17, 0.55).
- 64. M_{1+2} length relative to anterior fork: shorter or absent (M_1 and M_2 joining at r-m) (0), subequal (1), longer or reaching wing margin (fork absent) (2) (0.25, 0.67).
- 65. M_{1+2} dorsally: bare (0), setose (1) (0.08, 0.68).
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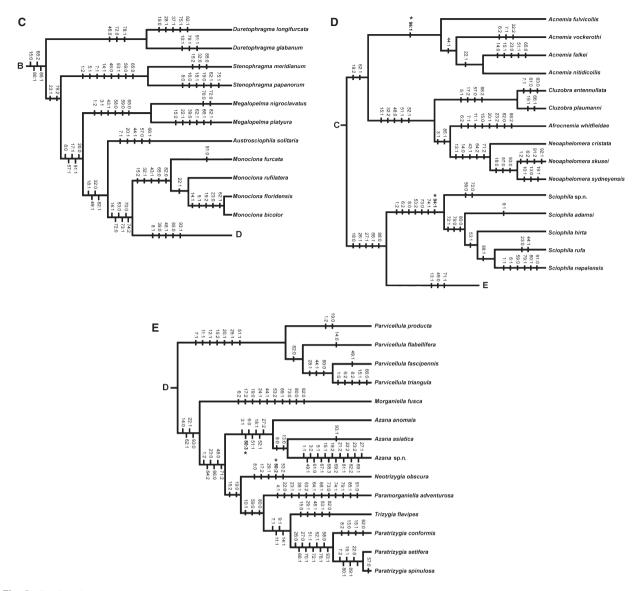


Fig. 2. Continued.

- 66. M_{1+2} ventrally: bare (0), setose (1) (0.1, 0.71).
- 67. Anterior fork $(M_1 + M_2)$: present (0), absent (1) (0.5, 0).
- 68. Anterior fork origin: arising after posterior fork (0), subequal to posterior fork (1), before posterior fork or posterior fork absent (2), absent (M_{1+2} reaching wing margin) (3) (0.3, 0.82).
- 69. Base of M_1 : strong (reaching M_{1+2} as thick as medial portion of M_2) (0), weak (reaching M_{1+2} as thinning vein (<0.5× medial thickness), crease, or setae) (1), free or absent (2) (0.18, 0.31).
- 70. M₁ ventrally: bare (0), setose (1) (0.14, 0.78).
- 71. Base of M_2 : strong (reaching M_{1+2} as thick as medial portion of M_2) (0), weak (reaching M_{1+2} as thinning vein (<0.5× medial thickness), crease, or setae) (1), free or absent (2) (0.33, 0.78).
- 72. M₂ ventrally: bare (0), setose (1) (0.13, 0.75).

- 73. Posterior fork (M_4 and CuA): present (0), absent (M_4 missing) (1) (0.25, 0.88).
- 74. M₄ extent: joining bM (0), joining CuA (1), free or absent (2) (0.25, 0.8).
- 75. M₄ dorsally: bare (0), setose (1) (0.2, 0.2).
- 76. M₄ ventrally: bare (0), setose (1) (0.5, 0.5).
- 77. CuA dorsally: bare (0), setose (1) (1, 1).
- 78. CuA ventrally: bare (0), setose (1) (0.14, 0.4).
- 79. A_1 extent: ending after posterior fork (0), ending at posterior fork (1), ending before posterior fork, or posterior fork absent and A_1 short (2) (0.15, 0.7).
- Halter knob color: same as stalk (0), darker than stalk (1) (0.06, 0.63).
- 81. Hind coxa, row of strong erect setae from base to apex on posterior margin: present (0), absent (1) (0.25, 0).



Fig. 3. Duretophragma glabanum. (A) Male habitus. (B) Wing, ventral view. Wing length is 4.5 mm in both figures. A_1 , A_2 , anal veins; C, costa; CuA, anterior branch of cubitus; CuP, posterior branch of cubitus; dmp, distal median plate; h, humeral crossvein; M_1 , M_2 , M_4 , branches of the media; r-m, radial-medial crossvein; Rs, radial sector vein; R_1 , R_4 , R_5 , branches of the radius; Sc, subcosta; sc-r, subcostal-radial crossvein.

- 82. Extent of strong setal row on hind coxa: complete (0), partial (1), none (2) (0.13, 0.68).
- 83. Hind coxa, apical patch of setae: present (0), absent (1) (0.17, 0.58).
- 84. Arrangement of vestiture of tibia (excluding large setae): irregular (0), apical portion with parallel lines (1), all in parallel lines (2) (0.33, 0.6).
- 85. Mid tibial organ: absent (0), weak bare line dorsally or posterodorsally (1), present (2) (0.18, 0.71).
- 86. Base of hind tibial bristles placed: on level surface (0), at base of short depression/groove (1) (0.14, 0.63).
- 87. Vestiture arrangement on tarsomeres (dorsal view): irregular (0), in parallel lines (1) (0.2, 0.67). Note: some when viewed laterally appear to be in helical parallel lines.
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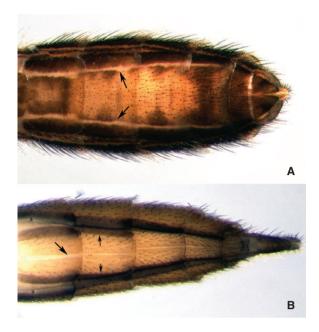


Fig. 4. Abdomens, ventral view showing main inwardly folding lines on sternites (large arrows) and outward folding lines (small arrows). (A) *Sciophila* sp. female. (B) *Mycetophila* sp. female.

- 88. Foretarsomere I length relative to foretibia length: <0.9 (0), 0.9–1.1 (1), >1.1 (2) (0.12, 0.67).
- Empodium: well-developed (0), reduced/absent (1) (0.11, 0.65).
- Abdominal sternite fold lines (Fig. 4): absent (0), one (sometimes appearing as three, see discussion below) (1), two (2) (0.5, 0.87).
- 91. Male segment 7: >0.5× length of segment 6 (0), ≤0.5× length of segment 6 (1), reduced/not visible (sternite 7 sometimes visible, tergite 7 always reduced (2) (0.13, 0.65).
- 92. Male segment 7: not retractable (0), retractable (1) (0.2, 0.6).
- 93. Sternite 8: <2× length of tergite 8 (0), >2× length of tergite 8 and partially covering genitalia (1) (0.08, 0.65).
- 94. Gonostylus with apically-feathered, spatulate, megasetae (i.e. Søli, 1997a, fig. 17): absent (0), present (1) (1, 1).
- 95. Male genitalia: visible beyond segment 8 (not strongly retracted) (0), completely or almost completely (90%) retracted within segment 7 (1) (1, 1).
- 96. Base of gonostylus: single lobe (0), thick lobe accompanied by one to three partially articulating, thinner processes (Fig. 5), each usually bearing a variety of trichia and/or setae (1) (1, 1).

Results and Discussion

Monophyly of the Sciophilini

The phylogenetic analysis resulted in 12 equally parsimonious trees (length = 777, C.I. = 0.17, R.I. = 0.68). Tree

support values (Bremer (Br) and bootstrap >50%) are shown on the branches of the strict consensus tree (Fig. 1). The 12 trees varied principally in the arrangement of species within *Leptomorphus* and *Sciophila*. Ignoring arrangement within genera, the two different trees (six of each), vary in the arrangement of *Stenophragma* (s.s.) and *Megalopelma* in the middle of the tree. One arrangement places *Stenophragma* (s.s.) as sister group to the remaining genera and the other puts *Megalopelma* + *Stenophragma* (s.s.) as the sister. We took a conservative approach (not inferring sister taxa relationship where there might not be one) and chose one of the 12 equally parsimonious trees with the former arrangement as the basis for classification. Character state changes are shown on this tree (Fig. 2).

Exemplars of four genera placed previously by some authors within Sciophilini (*Coelophthinia* Edwards, *Impleta* Plassmann, *Speolepta* Edwards and *Syntemna* Winnertz) were placed consistently outside the tribe (Fig. 1). Søli (1997b) found a similar result, although *Impleta* was not included in his analysis. These four genera therefore are assigned to the Gnoristini as suggested by Vockeroth (1980), Väisänen (1986) and Søli (1997b).

The monophyly of Sciophilini is supported (Br = 2;Fig. 1A) by one uniquely derived synapomorphy (Fig. 2A): at least several adjacent sternites with two mediolateral inwardly folding lines (Fig. 4A; character 90: state 2, hereafter 90:2), and by three homoplasious character states: lateral ocelli $0.5-1.5\times$ their own diameter from eye margin (7:1), frontal cleft running from lateral ocelli to eye margin (14:1), and frontal furrow only running part of the distance to apex of frons (15:1). These sternite fold lines are unique within the Mycetophilidae. Rindal & Søli (2006) considered this character state present in most Mycetophilinae; however, in the Mycetophilinae we examined there was a single medial inward folding line sometimes accompanied by a pair of thinner lateral outwardly folding lines (Fig. 4B). Rindal and Søli appear to have mistaken these outward folding lateral lines as homologous with the inwardly folding lines of the Sciophilini. Therefore, all other groups of Mycetophilidae have either no fold lines or a medial inward fold line, with or without outwardly folding lateral lines. Sciophilini is the only group to possess only two, inwardly folding, mediolateral lines.

Relationships within Sciophilini

Although the general structure of the Sciophilini phylogeny is mostly pectinate, there are six monophyletic groups containing two or more genera. These clades are referred to as the *Acomoptera* Vockeroth, *Aneura* Marshall, *Allocotocera* Mik, *Leptomorphus* Walker, *Cluzobra* Edwards and *Parvicellula* Marshall clades. Further details and discussion of characters supporting individual genera is given in the generic diagnoses.

The Acomoptera clade is placed as the sister group to the remaining Sciophilini (Figs 1A, 2A). Of the four included genera, two were included previously in Gnoristini (*Drepanocercus* Vockeroth, and Acomoptera) as they lacked macrotrichia or setae on the wing membrane. This clade

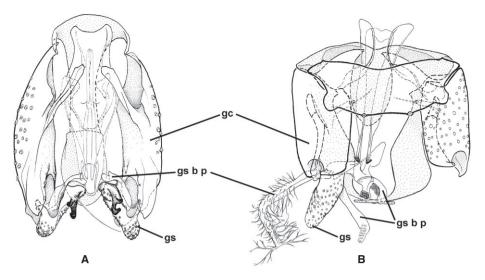


Fig. 5. Male genitalia of Acnemia, showing presence of gonostylar basal processes (after Søli, 1997b). (A) A. longipes. (B) A. nitidicollis. gc, gonocoxite; gs, gonostylus, gs b p, gonostylar basal process.

is supported by two homoplasious character states. The *Acomoptera* clade retains several plesiomorphic character states and should be included as an outgroup in future phylogenetic studies of the Sciophilinae, particularly with regards to generic relationships within the Gnoristini.

The monotypic genus *Drepanocercus* is sister to all remaining members of the *Acomoptera* clade and is supported by six homoplasious character states (Fig. 2A). The remaining three genera form a clade supported by one uniquely derived synapomorphy: medial eye margins parallel or closer together dorsally than ventrally (2:1), and three homoplasious character states. The genus *Acomoptera* is weakly supported by two homoplasious character states (Figs 1A, 2A). The double anapleural suture is found in only two other genera within Sciophilini, *Phthinia* Winnertz and *Polylepta* Winnertz.

Loicia Vockeroth and *Paratinia* Mik are sister genera (Figs 1A, 2A) supported by a synapomorphy: wing membrane with setae (with a clear socket/ring at the base of the seta) (42:0), and two homoplasious character states, and the two genera are monophyletic, each supported by multiple character states (Figs 1A, 2A). The remaining Sciophilini genera form a clade supported by one unique synapomorphy: wing membrane macrotrichia (no visible socket/ring at trichia base) present (41:0) and four homoplasious character states.

The Aneura clade, containing Aneura and Taxicnemis Tonnoir & Edwards, is supported by four homoplasious character states. Taxicnemis is supported by 21 character states (Fig. 2A) including two unique synapomorphies: subcostal vein ending free beyond sc-r (50:1) and arrangement of vestiture of tibia (exclusive of large setae) in parallel lines (84:2). Aneura is supported also by multiple character states.

The remainder of the Sciophilini form a well-supported monophyletic group based on eight character state changes including one unique synapomorphy: bristle(s) just posteromedial of halter base absent (40:1) (Figs 1A, 2A). All genera in the previous two clades have one or more bristles present on the metanotal membrane just posteromedially of the halter base, a state that is common in the outgroup and clearly is plesiomorphic. This clade corresponds closely to Edwards' (1925) concept of the Sciophilini, as all the members have bristles on the mediotergite (except *Baeopterogyna* Vockeroth, which has trichia) (33:1) and macrotrichia on the wing (41:0). Outside Sciophilini mediotergite bristles are found only in some *Coelophthinia* and *Mycomya* Rondani. All members of this clade, except *Duretophragma* gen.n. and *Stenophragma* Skuse, also have the distal median plate of the wing (Fig. 3B) setose (46:1), a state found only within two tribes of Mycetophilidae – the Sciophilini and Mycetophilini.

Phthinia is supported by 16 character states including one unique synapomorphy: dorsal surface of subcostal vein bare (56:0) (Figs 1A, 2A). Another unique synapomorphy occurs within some of the *Phthinia* included in the analysis: apical vestiture of tibia (exclusive of large setae) in parallel lines (84:1). *Phthinia* is sister to the remaining genera, which are united by two homoplasious character states (Figs 1A, 2A).

Neuratelia is the sister group to the remaining Sciophilini and the monophyly of the genus is supported by six character states (Figs 1A, 2A).

The clade above *Neuratelia* is united by four homoplasious character states (Figs 1A, 2A). This clade includes *Adicroneura* Vockeroth, previously included in the Gnoristini. *Adicroneura* is the sister genus to the remaining genera (Fig. 2A). The monophyly of the remaining Sciophilini genera is supported by five character states (Figs 1A, 2A).

Anaclileia is supported by five homoplasious character states and is the sister group to the remaining Sciophilini, which are supported by three character states (Figs 1A, 2B).

The three genera in the *Allocotocera* clade are united by three homoplasious character states (Figs 1A, 2B). *Allocotocera* is the sister group to the remaining two genera and is supported by nine character states including one unique

synapomorphy: male genitalia completely or almost completely (90%) retracted within segment 7 (95:1) (Figs 1A, 2B). The remaining two genera, *Baeopterogyna* and *Tasmanina* Tonnoir, share five homoplasious character states. *Baeopterogyna* is supported by 17 homoplasious character states and *Tasmanina* in a is supported by two (Fig. 2B).

The *Allocotocera* clade is sister to the remaining genera, which form a monophyletic group supported by five homoplasious character states (Figs 1A, 2B).

The *Leptomorphus* clade is supported by two character states (Figs 1A, 2B). *Polylepta* is the sister group to the other two genera and is supported by nine character states (Figs 1A, 2B). *Eudicrana* and *Leptomorphus* are sister genera, supported by seven character states including one unique synapomorphy: mediotergite with trichia placed anteriorly (35:1). *Eudicrana* is supported by eight character states and *Leptomorphus* by eight including one unique synapomorphy: acrostichal setae absent (25:1).

Above the *Leptomorphus* clade the remaining Sciophilini genera are united (Figs 1B, 2C) by four homoplasious character states. *Duretophragma* gen.n. is the sister group to the remaining genera and is supported by three character states. The remaining genera are supported by two homoplasious character states.

In the strict consensus tree (Fig. 1B) a tritomy is formed by *Stenophragma* Skuse, *Megalopelma* Enderlein and the remaining genera. For our discussion of character state placement we have chosen one of the 12 most parsimonious trees that places *Stenophragma* as sister to the remaining genera. This placement occurs in 50% of the trees, with the alternative being a monophyletic *Stenophragma* plus *Megalopelma* that is sister to the remainder. *Stenophragma* is supported by eight homoplasious character states (Figs 1B, 2C). The remaining genera are a monophyletic group supported by five homoplasious character states.

The sister group to the remaining genera is *Megalopelma* Enderlein which is supported by six homoplasious character states (Figs 1B, 2C). The other Sciophilini genera are united by four character states (Figs 1B, 2C).

The monotypic genus *Austrosciophila* Tonnoir is sister to the remaining genera and is supported by five character states (Fig. 2C). The clade of remaining genera is supported (Figs 1B, 2C) by six homoplasious character states. This apical clade contains all but one (*Adicroneura*) of the genera of the Sciophilini that have strong reduction or loss of longitudinal wing veins. This group corresponds to the expanded view of Matile's (1998) '*Azana* group' suggested by Amorim *et al.* (2008).

Monoclona Mik is sister to the remaining genera and is supported by five homoplasious character states (Figs 1B, 2C). The remaining clade is supported by five character states.

The *Cluzobra* clade (*Acnemia* Winnertz, *Cluzobra*, *Afrocnemia* Matile, *Neoaphelomera* Marshall) is sister to the remaining genera and is supported by two character states (Figs 1B, 2D). *Acnemia* is the sister group to the other three genera based on one unique synapomorphy: base of gonostylus a thick lobe accompanied by one to three short to long, partially articulating, thinner processes, each usually bearing a variety of trichia and/or setae (Fig. 5, 96:1) (Figs 1B, 2D).

The monophyly of the remaining three genera is supported by five homoplasious character states (Figs 1B, 2D). *Cluzobra* is the sister group to *Afrocnemia* and *Neoaphelomera*, and is supported by four character states. The remaining two genera are united by two homoplasious character states. *Afrocnemia* is supported by eight character states and *Neoaphelomera* by five (Figs 1B, 2D).

The remaining genera of the Sciophilini (*Sciophila* Meigen + *Parvicellula* clade) form a monophyletic clade supported by four homoplasious character states (Figs 1B, 2D). *Sciophila* is monophyletic based on seven character states, including one unique synapomorphy: gonostylus with apically-feathered, spatulate, megasetae (94:1).

The monophyly of the *Parvicellula* clade is supported by three homoplasious character states (Figs 1B, 2D). *Parvicellula* is the sister group to the remainder of the clade and is supported by seven character state changes (Figs 1B, 2E). The monophyly of remainder of the clade is supported by four character states.

The monotypic genus *Morganiella* is sister to the remaining genera and is supported by ten homoplasious character states (Fig. 2E). The remainder of the clade is supported by six character states (Figs 1B, 2E). *Azana*, sister group to the remaining genera is supported by seven character states (Figs 1B, 2E), including one unique synapomorphy: subcostal vein ending free at wing base (50:3).

The remaining genera in the *Parvicellula* clade are supported by two character states (Figs 1B, 2E). The monotypic genus *Neotrizygia* is sister to the remaining three genera and is supported by five character states (Fig. 2E), including one unique synapomorphy: subcostal vein ending in sc-r. The rest of the genera form a monophyletic group supported by three character states (Figs 1B, 2E).

Paramorganiella, a monotypic genus, is the sister group to *Trizygia* plus *Paratrizygia*. The genus is supported by 12 character states (Fig. 2E). *Trizygia* and *Paratrizygia* are monophyletic, supported by four character states (Figs 1B, 2E). *Trizygia* is supported by five character state changes. *Paratrizygia* is supported strongly by ten character states. This justifies retaining *Paratrizygia* as a separate genus from *Trizygia* (Oliveira & Amorim, 2010; Amorim *et al.*, 2011).

Although the above unweighted parsimony analysis produced the preferred tree, we explored the data using implied weighting in a parsimony analysis in TNT (using the same parameters). This type of analysis gives higher weight to characters with lower homoplasy when choosing between conflicting arrangements. The weight is determined by the constant of concavity values (K) with lower values giving higher weights to fewer characters (Goloboff, 1993). We used K values of 6–20 which all supported the majority of Sciophilini genera being monotypic. The only exception to this was *Stenophragma* or *Megalopelma*, both of which were problematic also in the unweighted analysis (*Duretophragma* still was considered monotypic). The overall arrangement and order of genera from base to apex generally was similar as well,

though a few of the larger clades were broken up in some results, and a few genera placed in slightly different relationships (e.g. *Polylepta* removed from *Leptomorphus* clade and united with *Phthinia*; *Baeopterogyna* and *Tasmanina* forming their own clade and *Allocotocera* placed individually; movement of a couple of genera between the *Cluzobra* and *Parvicellula* clades). The other noticeable difference under implied weighting when K < 16, was the removal of the *Aco-moptera* clade from the Sciophilini to the Gnoristini and the accompanying placement of *Syntemna* as the sister group to the remainder of the Sciophilini. This was not unexpected, based on the plesiomorphic nature of the *Acomoptera* clade, as discussed above.

Generic diagnoses

The following generic diagnoses are based principally on the characters used in the phylogenetic analysis, with a few additional characteristics in some cases. Most of the genera are in need of revision which, when undertaken, will further clarify generic limits. Major works on individual genera, when available, are given at the end of the diagnosis.

Acnemia Winnertz

Acnemia Winnertz, 1863: 798. Type species: *Leia nitidicollis* Meigen, 1818: 255 (subsequent designation by Johannsen, 1909).

Diagnosis. Macrotrichia decumbent, wing membrane without microtrichia in some species, sc-r placed before origin of Rs, R₄ absent, anterior fork present and complete, posterior fork absent (M₄ missing), male abdominal segment 7 less than $0.5 \times$ length of segment 6, and base of gonostylus a thick lobe accompanied by one to three short to long, partially articulating, thinner processes, each usually bearing a variety of trichia and/or setae (Zaitzev, 1982a,b).

Distribution. AF (Uganda, 1 sp.), NE (13 spp.), NT (5 spp.), OR (Sri Lanka, 1 sp.), PA (14 spp.). Three fossil species.

Species examined. Acnemia falkei Matile & Vockeroth; Acnemia fulvicollis (Philippi); Acnemia nitidicollis (Meigen); Acnemia vockerothi Zaitzev.

Acomoptera Vockeroth

Acomoptera Vockeroth, 1980: 534. Type species: Eudicrana plexipus Garrett, 1925: 4 (original designation).

Diagnosis. Medial eye margins closer together dorsally than ventrally, frons bare, mediotergite and laterotergite bare, bristle(s) present just posteromedially of halter base, wing membrane without macrotrichia, sc-r placed before origin of Rs, R₄ present and forming a cell $\sim 3 \times$ as long as tall, anterior and

posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, origin of anterior fork after origin of posterior fork, M_4 always joined to CuA (though sometimes a small spur continuing beyond junction towards wing base,) and male abdominal segment 7 more than $0.5 \times$ length of segment 6 (Kerr, 2011).

Distribution. NE (7 spp.), PA (2 spp.).

Species examined. Acomoptera plexipus (Garrett); Acomoptera vockerothi Kerr.

Adicroneura Vockeroth

Adicroneura Vockeroth, 1980: 535. Type species: *Adicroneura biocellata* Vockeroth, 1980: 536 (original designation).

Diagnosis. The only genus in Sciophilini with wing vein M_{1+2} not forking and a complete posterior fork (M₄ and CuA). Two or three ocelli, wing membrane with microtrichia and macrotrichia present (macrotrichia sometimes sparse and difficult to discern), sc-r and R₄ absent, and male abdominal segment 7 more than $0.5 \times$ length of segment 6 (Matile, 1995).

Distribution. NE (western, 1 sp.), NT (Chile, 2 spp.).

Species examined. Adicroneura biocellata Vockeroth.

Afrocnemia Matile

Afrocnemia Matile, 1998: 390. Type species: Afrocnemia whitfieldae Matile, 1998: 391 (original designation).

New combinations. Afrocnemia stellamicans (Chandler) **comb.n**.

Diagnosis. Macrotrichia decumbent, wing vein sc-r present or absent, sc-r placed before origin of Rs when present, R₄ absent, anterior fork present, posterior fork absent (M₄ missing), stem of anterior fork (M₁₊₂) shorter than fork, foretarsomere I longer than foretibia, and male abdominal segment 7 less than $0.5 \times$ length of segment 6.

Distribution. AF (3 spp.), PA (Israel, 1 spp.).

Species examined. Afrocnemia whitfieldae Matile.

Comments. Based on the description and the figures of the genitalia (Chandler, 1994) *Acnemia stellamicans* belongs to this genus, though sc-r is present, unlike the remaining species.

Allocotocera Mik

Eurycera Dziedzicki, 1885: 166. Type species: *Eurycera flava* Dziedzicki, 1885: 167 [= *Leia pulchella* Curtis, 1837], (monotypy) [preoccupied de Laporte, 1833.]

Allocotocera Mik, 1886: 102 (nom.n. for Eurycera).

Euryceras Marshall, 1896: 291. Type species: *Euryceras* anaclinoides Marshall, 1896: 291 (monotypy).

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Diagnosis. Anepisternum setose, anterior basalare setose, metepisternum setose, wing membrane without microtrichia in some species, sc-r placed before origin of Rs, R₄ absent, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than or equal to fork length, base of M_1 usually strong but sometimes weak or free, origin of anterior fork after origin of posterior fork, foretarsomere I shorter than foretibia, male abdominal segment 7 more than $0.5 \times$ length of segment 6, and male genitalia completely or almost completely (90%) retracted within segment 7.

Distribution. AU (NZ, 4 spp., undescribed species in Australia (Tonnoir, 1929)), NE (2 spp.), NT (4 spp.), PA (3 spp.). Two fossil species.

Species examined. Allocotocera dilatata Tonnoir; Allocotocera flavicoxa Freeman; Allocotocera parvula (Coquillett); Allocotocera pulchella (Curtis).

Anaclileia Meunier

Anaclileia Meunier, 1904: 146. Type species: *Anaclileia anacliniformis* Meunier, 1904: 146 (subsequent designation by Johannsen, 1909).

Paraneurotelia Landrock, 1911: 161. Type species: *Paraneurotelia dziedzickii* Landrock, 1911: 161 (original designation).

Diagnosis. Wing vein sc-r present or absent, sc-r placed before origin of Rs when present, R₄ absent, anterior and posterior fork present, stem of anterior fork (M₁₊₂) shorter than fork, base of M₁ free, origin of anterior fork same as or after origin of posterior fork, and male abdominal segment 7 more than $0.5 \times$ length of segment 6 (Bechev, 1990a; Coher, 1995).

Distribution. NE (4 spp.), OR (1 spp.), PA (3 spp.). One fossil species.

Species examined. Anaclileia nepalensis Bechev; Anaclileia vockerothi Bechev.

Aneura Marshall

Aneura Marshall, 1896: 287. Type species: Aneura boletinoides Marshall, 1896: 288 (monotypy).

Diagnosis. No interommatidial setae present, frons bare, mediotergite and laterotergite bare, bristle(s) present just posteromedially of halter base, sc-r placed before origin of Rs, R₄ present or absent, when present forming a cell that is $\sim 3 \times$ as long as tall, anterior and posterior fork present, stem of anterior fork (M₁₊₂) longer than fork, origin of anterior fork after origin of posterior fork, and male abdominal segment 7 less than 0.5× length of segment 6 (Duret, 1975; Zaitzev, 2001).

Distribution. AU (NZ, 13 spp.), NT (Patagonia, 4 spp.). One fossil species.

Species examined: Aneura boletinoides Marshall; Aneura longistila Freeman.

Austrosciophila Tonnoir

Austrosciophila Tonnoir, 1929: 604 (Sciophila subg). Type species: Sciophila (Austrosciophila) solitaria Tonnoir, 1929: 604 (original designation).

Diagnosis. Metepisternum setose, wing membrane without microtrichia, sc-r placed well after origin of Rs, R₄ present, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, origin of anterior fork before origin of posterior fork, and male abdominal segment 7 less than $0.5 \times$ length of segment 6.

Distribution. AU (Australia, 1 spp.).

Species examined. Austrosciophila solitaria (Tonnoir).

Azana Walker

Azana Walker, 1856: 26. Type species: *Azana scatopsoides* Walker, 1856: 26 (monotypy) [= *anomala* (Staeger)].

Diagnosis. Two or three ocelli, anepisternum setose, subcostal vein ending free at wing base (unique in the Sciophilini), sc-r absent, R_4 absent, anterior fork usually present (M_{1+2} running to wing margin in NT species) but incomplete (M_2 free in apical portion of wing), posterior fork absent (M_4 missing), and male abdominal segment 7 less than $0.5 \times$ length of segment 6 (Kerr, 2010).

Distribution. AF (2 spp.), NE (3 spp.), NT (1 sp.), OR (3 spp.), PA (5 spp.). One fossil species.

Species examined. Azana anomala (Staeger); *Azana asiatica* Senior-White; *Azana* sp. (Ecuador).

Baeopterogyna Vockeroth

Baeopterogyna Vockeroth, 1972: 1529. Type species: *Baeopterogyna nudipes* Vockeroth, 1972: 1532 (original designation).

Diagnosis. Mediotergite bare of setae but with macrotrichia, metepisternum setose, sc-r placed before origin of Rs, C not produced beyond the apex of R₅, R₄ absent, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, base of M_1 weak, origin of anterior fork after origin of posterior fork, foretarsomere I shorter than foretibia, and male abdominal segment 7 less than $0.5 \times$ length of segment 6 and retractable.

Distribution. NE (northern, 1 sp.), PA (western, 1 sp.).

Species examined. Baeopterogyna nudipes Vockeroth.

Cluzobra Edwards

Cluzobra Edwards, 1940: 463. Type species: *Acnemia binocellaris* Edwards, 1934: 362 (original designation).

Diagnosis. Two or three ocelli, sc-r absent, R_4 absent, anterior fork present, posterior fork absent (M_4 missing), stem of anterior fork (M_{1+2}) shorter than fork, and male abdominal segment 7 less than 0.5× length of segment 6 (Matile, 1996; Coher, 1997; Amorim & Oliveira, 2008).

Distribution. NE (southern, 1 sp.), NT (40 spp.).

Species examined. Cluzobra antennullata Coher; Cluzobra plaumanni Edwards.

Drepanocercus Vockeroth

Drepanocercus Vockeroth, 1980: 538. Type species: *Drepanocercus ensifer* Vockeroth, 1980: 539 (original designation).

Diagnosis. No interommatidial setae present, frons bare, mediotergite and laterotergite bare, bristle(s) present just posteromedially of halter base, wing membrane without macrotrichia, distal median plate bare, sc-r placed before origin of Rs, R₄ present and forming a cell $\sim 3 \times$ as long as tall, anterior and posterior fork present, stem of anterior fork (M₁₊₂) shorter than fork, origin of anterior fork after origin of posterior fork, M₄ almost reaching wing base before ending free, foretarsomere I shorter than foretibia, male abdominal segment 7 more than 0.5× length of segment 6, female cerci forming an elongate blade-like structure (Vockeroth, 1980: fig. 11).

Distribution. NE (eastern, 1 sp.).

Species examined. Drepanocercus ensifer Vockeroth.

Duretophragma Borkent

Duretophragma Borkent gen.n. Type species: Stenophragma longifurcata Freeman, 1951: 57 (present designation).

Included species. Duretophragma andina (Duret) comb.n., Duretophragma argentina (Duret) comb. n., Duretophragma fusca (Edwards) comb.n., Duretophragma glabanum (Johannsen) comb.n., Duretophragma humeralis (Edwards) comb.n., Duretophragma intermedia (Edwards) comb.n. Duretophragma longifurcata (Freeman) comb.n., Duretophragma morigenea (Edwards) comb.n., Duretophragma naumanni (Duret) comb.n., Duretophragma nigricauda (Edwards) comb.n., Duretophragma obscura (Duret) comb.n., Duretophragma ochracea (Freeman) comb.n., Duretophragma pleuralis (Edwards) comb.n., Duretophragma similis (Johannsen) comb.n.

Diagnosis. Flagellomere 1 with a distinctly offset basal stalk, frontal cleft absent, metepisternum setose, wing hyaline or with light shading on apical $\frac{1}{4}$, distal median plate bare, bM and CuA ventrally setose, M₁₊₂ dorsally setose, M₂ ventrally bare, sc-r placed well after origin of Rs (at least halfway along cell created by R₄), R₄ present forming a rectangular cell longer than wide, anterior and posterior fork present, stem of anterior fork (M₁₊₂) much shorter than fork (sometimes missing), origin of anterior fork before origin of posterior fork, male abdominal segment 7 more than 0.5× length of segment 6, and gonocoxites bearing apicolateral projection (with one to several apical long setae) (Duret, 1976, 1979).

Distribution. NE (2spp.), NT (12 spp.).

Species examined. Duretophragma glabanum (Johannsen); Duretophragma longifurcata (Freeman); Duretophragma ochracea (Freeman).

Generic description. Figure 3, see also figures in Duret (1976, 1979)

Total length: 5–6.5 mm. Wing length: 4–5 mm.

Color. Head brown to black, mouthparts and palps yellow to brown, antenna mostly dark brown with scape and pedicel yellow to brown. Thorax yellow to dark brown, scutum sometimes with two to three darker longitudinal stripes. Legs yellow to dark brown. Abdomen brown, tergites sometimes with light brown or yellow patches or bands anteriorly and posteriorly on each tergite. Genitalia light to dark brown.

Head. Circular in anterior view. Pedicel and scape bearing several bristles. Flagellomere 1 with a distinct, offset, basal stalk. Flagellomeres at least $1.5 \times$ longer than wide. Face and clypeus separate and subequal in length. Frons with ventral bristles, frontal furrow present, frontal cleft absent. Palpus with five segments, typically increasing in length from base to apex, segment 1 small and often hidden behind eye.

Compound eye with indentation (two to three ommatidia deep) on medial margin just above level of antennae; interommatidial setulae present on entire eye surface. Three ocelli present on a dark background and almost in a straight line (median slightly in front of lateral ocelli), with lateral ocelli $1-1.5\times$ own diameter from eye margin and $1.5\times$ own diameter from median ocellus.

Thorax. Scutum with acrostichal and dorsocentral setae present and covered with small setae. Scutellum with large

and small setae. Mediotergite with several bristles posteriorly and sometimes with small setae or appressed hairs medially. Laterotergite with several bristles and setae, sometimes with trichia as well. Anepisternum bare or with small dorsal patch of short trichia, metepisternum with several setae posteriorly. Anterior basalare bare. Anapleural suture with slight ventral curve on anterior portion.

Legs. Coxae with setae on dorsal margin, hind coxa with complete or partial row of strong setae on posterior margin. Tibiae with bristles and irregularly arranged, small, setae. Tibial spurs 1:2:2. Foretibia with anteroapical depressed area present. Midtibia with weak dorsal or posterodorsal bare line. Tarsi covered with irregularly arranged macrotrichia. Foretarsomere I subequal in length to foretibia. Empodium present.

Wing. (Fig. 3B) Hyaline, rarely with apical ¹/₄ lightly shaded. Membrane with both irregularly arranged microtrichia and macrotrichia, macrotrichia sparser near wing base and dense near apex. C extending barely beyond R₅. Humeral vein joining C close to wing base. Sc ending in C. sc-r present and joining R1 just before or after R4. R4 present and forming rectangular cell longer than broad.M₁₊₂ forking into M₁ and M₂ immediately after origin at r-m (sometimes M₁₊₂ absent). Origin of posterior fork (M₄ and CuA) after origin of anterior fork. Petiole of posterior fork (bCuA) shorter or longer than either M₄ or CuA. A₁ ending at or beyond origin of posterior fork. A1 absent to faintly present as crease. Distal median plate bare. Dorsal surfaces of Sc, R1, R5, all M veins, CuA, and A1 setose. Dorsal and ventral surface of humeral vein bare. Ventral surface of Sc, R1, R5, M1, CuA setose, and of M2, bare. M4 bare or setose ventrally. Halter stem yellow, knob dark.

Abdomen. Abdominal segments 1–6 unmodified, segment 1 $\sim \frac{1}{2}$ size of remainder. Segment 7 0.5–0.7× length of segment 6 and not retractable. Segment 8 reduced in size and at least partially retracted inside segment 7.

Male genitalia. Sternite 9 setose or bare, ranging from small (> $\frac{1}{4}$ length of gonocoxite) triangular sclerite at base of genitalia, to thin oval or rectangular sclerite as long as medial length of gonocoxites, posterior margin concave, rounded or with medial point. Tergite 9 prominent, at least as long as rest of genitalia (often extending beyond), composed of two parts: basal rectangular or oval component, covered with sparse setae, making up $\sim \frac{3}{4}$ of length, and apical component (may be a remnant of tergite 10) densely covered in both small and long setae (concentrated on the apex) and frequently rectangular but sometimes tapering to a point. Gonocoxites large and setose, forming largest portion of genitalia and with an apicolateral protrusion ventrally, bearing one to several long apical setae. Gonostylus with two to three broad lobes, bearing one to several combs of medially directed setae, as well as a group of short, thick, setae. Several long setae usually also present on medial margin. Aedeagus variable though apodemes appearing to fuse with gonocoxal apodemes.

Female genitalia. Tergite 9 lightly sclerotized. Sternite 9 bearing gonopore subapically, apical margin sclerotized. Tergite 10 a thin band at base of cerci. Sternite 10 sclerotized, setose and extending at least $\frac{1}{2}$ length of cerci I. Cerci I large, cerci II usually small (although almost as long as cerci I in some species).

Etymology. The genus is named for Dr. José Pedro Duret (1913–2007) in recognition of his legacy of studies on the Mycetophilidae, including members of this new genus. The suffix indicates the close relationship between this genus and *Stenophragma*.

Comments. This genus is in need of revision. Some species have been assigned to *Duretophragma* based solely on published descriptions and examination of material is recommended to confirm their placement.

Eudicrana Loew

Eudicrana Loew, 1870: 142. Type species: *Eudicrana* obumbrata Loew, 1870: 141 (monotypy).

Pareudicrana Tonnoir, 1929: 600. Type species: Pareudicrana monticola Tonnoir, 1929: 600 (original designation).

Diagnosis. Two ocelli, flagellomere 1 with a distinctly offset basal stalk, R₄ present, wing membrane without microtrichia in some species, sc-r placed near or well after origin of Rs, C not produced beyond the apex of R₅, R₄ present and forming a cell $\sim 3 \times$ as long as tall, anterior and posterior fork present, stem of anterior fork (M₁₊₂) shorter than fork, origin of anterior fork after or at origin of posterior fork, foretarsomere I longer than foretibia, and male abdominal segment 7 < 0.5× length of segment 6.

Distribution. AU (Australia, 3 spp.), NE (1 sp.), NT (7 spp.), PA (2 spp.).

Species examined. Eudicrana basinerva Freeman; Eudicrana nicholsoni (Tonnoir); Eudicrana obumbrata Loew.

Leptomorphus Curtis

Leptomorphus Curtis, 1831: 365. Type species: Leptomorphus walkeri Curtis, 1831: 365 (monotypy).

Diomonus Walker, 1848: 87 Type species: Diomonus nebulosus Walker, 1848: 87 (monotypy).

Gymnoscutum Matile 1977: 144 (subgenus of *Leptomorphus*). Type species: *Leptomorphus obscurus* Matile 1977: 152 (original designation).

Austroleptomorphus Matile 1977: 145 (subgenus of Leptomorphus). Type species: Leptomorphus grjebinei Matile 1977: 154 (original designation).

Diagnosis. Interommatidial setulae absent or very sparse and short, frons bare or with a few setae ventrally, flagellomere 1 with a distinctly offset basal stalk, flagellomeres slightly

laterally compressed, an epimeron and preepisternum II bare, antepronotum and proepisternum setose, acrostichal bristles absent, wing membrane without microtrichia, sc-r (when present) placed before or at origin of Rs, C not produced beyond the apex of R_5 , R_4 present or absent, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, base of M_1 complete, origin of anterior fork after origin of posterior fork, tibial bristles short, no more than half thickness of tibia in length, and male abdominal segment 7 more than 0.5× length of segment 6. (Papp & Ševčík, 2011; Borkent & Wheeler, 2012).

Distribution. AF (12 spp.), AU (Only in NW, not reaching Australia, 2 spp.), NE (8 spp.), NT (8 spp.), OR (11 spp.), PA (7 spp.). Three fossil species.

Species examined. Leptomorphus medleri Matile; Leptomorphus neivai Edwards; Leptomorphus walkeri Curtis; most other described species in this genus were also studied, see Borkent & Wheeler (2012).

Loicia Vockeroth

Loicia Vockeroth, 1980: 530. Type species: *Loicia basifurca* Vockeroth, 1980: 531 (original designation).

Diagnosis. Medial eye margins parallel, frons bare, mediotergite and laterotergite bare, bristle(s) present just posteromedially of halter base, wing membrane without macrotrichia but with setae (having a basal alveolus), distal median plate bare, sc-r placed before origin of Rs, R₄ present and forming a cell $\sim 3 \times$ as long as tall, anterior and posterior fork present, stem of anterior fork (M₁₊₂) shorter than fork, origin of anterior fork after origin of posterior fork, M₄ joining bM near wing base, and male abdominal segment $7 > 0.5 \times$ length of segment 6.

Distribution. NE (British Columbia, 1 sp.).

Species examined. Loicia basifurca Vockeroth.

Megalopelma Enderlein

Megalopelma Enderlein, 1910: 165. Type species: Megalopelma planiceps Enderlein 1910: 166 (original designation).

Diagnosis. Metepisternum setose in some species, wing membrane macrotrichia reflexed towards wing base, sc-r placed well after origin of Rs, R₄ present or absent, anterior and posterior fork present, stem of anterior fork (M₁₊₂) shorter than fork, origin of anterior fork before origin of posterior fork, and male abdominal segment 7 < 0.5× length of segment 6.

Distribution. NE (2 spp.), NT (3 spp.), PA (1 sp.).

Species examined. Megalopelma nigroclavatus (Strobl); Megalopelma platyura Edwards.

Monoclona Mik

Staegeria van der Wulp, 1876: xlix (preoccupied Rondani, 1856). Type species: *Sciophila halterata* Staeger, 1840: 275 (monotypy) [= *rufilatera* (Walker)].

Monoclona Mik, 1886: 279 (nom.n. for *Staegeria* Wulp).

Diagnosis. Two or three ocelli, metepisternum setose, wing membrane macrotrichia reflexed towards wing base, sc-r placed before origin of Rs, R_4 present or absent, anterior fork present, posterior fork absent (M₄ missing), and stem of anterior fork (M₁₊₂) shorter than fork (Zaitzev, 1983).

Distribution. NE (4 spp.), NT (7 spp.), OR (1 sp.), PA (6 spp.).

Species examined. Monoclona bicolor (Enderlein); Monoclona floridensis Fisher; Monoclona furcata Johannsen; Monoclona rufilatera (Walker).

Morganiella Tonnoir & Edwards

Morganiella Tonnoir & Edwards, 1927: 817. Type species: Morganiella fusca Tonnoir in Tonnoir & Edwards, 1927: 817 (original designation).

Diagnosis. An episternum setose, wing membrane without microtrichia, sc-r placed well after origin of Rs, R₄ absent, anterior and posterior fork present but posterior fork incomplete (M₄ free in apical portion of wing), stem of anterior fork (M₁₊₂) shorter than fork, base of M₁ and M₂ weak, and male abdominal segment 7 < 0.5× length of segment 6.

Distribution. AU (NZ, 1 sp.).

Species examined. Morganiella fusca Tonnoir.

Neoallocotocera Tonnoir

Neoallocotocera Tonnoir, 1929: 601. Type species: *Neoallocotocera fusca* Tonnoir, 1929: 601 (original designation).

Diagnosis (Based on Tonnoir, 1929). Eyes with numerous interommatidial setae, antennal segments wider than long and somewhat laterally compressed, anepisternum with bristles, anterior basalare bare, sc-r absent, R_5 sinuous, anterior and posterior wing forks complete, stem of anterior fork (M_{1+2}) shorter than fork, anterior fork origin just before origin of posterior fork, and male abdominal segment 7 long.

Distribution. AU (Tasmania, 1 sp.).

Species examined. None.

Neoaphelomera Miller

Aphelomera Skuse, 1888: 1206. Type species: *Aphelomera sydneyensis* Skuse, 1888: 1207 (monotypy) [preoccupied Stephens, 1833].

Neoaphelomera Miller, 1945: 72 (nom.n. for Aphelomera).

Diagnosis. Wing membrane macrotrichia reflexed towards wing base, sc-r absent, R_4 absent, anterior fork present but incomplete (M_2 free in apical portion of wing), posterior fork absent (M_4 missing), stem of anterior fork (M_{1+2}) weak or free at base, and male abdominal segment 7 < 0.5× length of segment 6.

Distribution. AU (9 spp.), NT (southern, 4 spp.).

Species examined. Neoaphelomera cristata Freeman; Neoaphelomera skusei (Marshall); Neoaphelomera sydneyensis (Skuse).

Neotrizygia Tonnoir & Edwards

Neotrizygia Tonnoir & Edwards, 1927: 816. Type species: *Neotrizygia obscura* Tonnoir *in* Tonnoir & Edwards, 1927: 816 (original designation).

Diagnosis. Anepisternum setose, anterior basalare setose, subcostal vein ending in sc-r (sometimes referred to as ending in R, unique character state in the Sciophilini), sc-r placed well after origin of Rs, R₄ absent, anterior fork present but incomplete (M_2 free in apical portion of wing), posterior fork absent (M_4 missing), male abdominal segment 7 < 0.5× length of segment 6.

Distribution. AU (NZ, 1 sp.).

Species examined. Neotrizygia obscura Tonnoir.

Neuratelia Rondani

Neuratelia Rondani, 1856: 195. Type species: Mycetophila nemoralis Meigen 1818: 265 (original designation).

Anaclinia Winnertz, 1863: 770. Type species: Mycetophila nemoralis Meigen 1818: 265 (monotypy).

Odontopoda Aldrich, 1897: 187. Type species: *Odontopoda sayi* Aldrich 1897: 187 (monotypy).

Diagnosis. Flagellomere 1 with a distinctly offset basal stalk in some species, sc-r placed before origin of Rs, C not produced beyond the apex of R₅, R₄ absent, R₅ sinuous, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, base of M_1 free, and origin of anterior fork after origin of posterior fork. Distribution. NE (13 spp.), NT (1 sp.), OR (India, 1 sp.), PA (14 spp.). Three fossil species

Species examined. Neuratelia nemoralis (Meigen); Neuratelia sayi (Aldrich); Neuratelia scitula Johannsen.

Paramorganiella Tonnoir

Paramorganiella Tonnoir, 1929: 606.

Type species: *Paramorganiella adventurosa* Tonnoir, 1929: 606 (original designation).

Diagnosis. Anepisternum setose, metepisternum setose, sc-r placed well after origin of Rs, R₄ absent, anterior and posterior fork present, but anterior fork incomplete (M₂free in apical portion of wing), and male abdominal segment $7 > 0.5 \times$ length of segment 6. Males of *Paramorganiella* are the only Mycetophilidae with strongly modified palpi (see Jaschhof *et al.*, 2010).

Distribution. AU (Australia, 1 sp.).

Species examined. Paramorganiella adventurosa Tonnoir.

Paratinia Mik

Paratinia Mik, 1874: 333. Type species, *Paratinia sciarina* Mik 1874: 331 (monotypy).

Diagnosis. Medial eye margins parallel, frons bare, mediotergite and laterotergite bare, bristle(s) present just posteromedially of halter base, wing membrane without macrotrichia but with setae (having a basal alveolus), distal median plate bare, sc-r placed before origin of Rs, R₄ present and forming a cell $\sim 3 \times$ as long as tall, anterior and posterior fork present, stem of anterior fork (M₁₊₂) shorter than fork, origin of anterior fork after origin of posterior fork, and male abdominal segment 7 > 0.5× length of segment 6.

Distribution. NE (1 sp.), PA (3 spp.).

Species examined. Paratinia recurva Johannsen; Paratinia sciarina Mik.

Paratrizygia Tonnoir

Paratrizygia Tonnoir, 1929: 605. Type species: Paratrizygia conformis Tonnoir, 1929: 605 (original designation).

Diagnosis. An episternum bare, wing vein sc-r absent, R₄ present or absent, anterior fork present but incomplete (M₂ free in apical portion of wing), posterior fork absent (M₄ missing), Humeral vein dorsally setose, bM dorsally bare, M₁₊₂, M₁, M₂ and CuA ventrally setose, male abdominal segment $7 < 0.5 \times$ length of segment 6, and setae scattered on apicoventral surface of male tergite nine.

Distribution. AU (Australia, 1 sp.), NT (4 spp.).

Species examined. Paratrizygia conformis Tonnoir; Paratrizygia setifera Freeman; Paratrizygia spinulosa Freeman.

Comments. Amorim *et al.* (2011), in redescribing the holotype of *P. conformis*, retained their recently described *Paratrizygia* species (Oliveira & Amorim, 2010) in this genus, based on the presence of parallel rows of spines on the ventral apex of tergite nine. Unfortunately the genitalia of the holotype are permanently mounted in lateral view. We have studied other material of *P. conformis* in which the genitalia in lateral view correspond to those of the holotype. However, in ventral view it is clear that the setae present on the ventral apex of tergite nine are not in parallel rows but are scattered, as in Freeman (1951: fig. 123). The arrangement of setae seen in the holotype is apparently coincidental due to the aspect of preservation. Based on this observation as well as other characteristics (i.e. anepisternum setose) the *Paratrizygia* species described from Brazil are transferred to *Trizygia* (see below).

Parvicellula Marshall

Parvicellula Marshall, 1896: 284. Type species: *Parvicellula triangula* Marshall, 1896: 284 (monotypy).

Diagnosis. Anepisternum setose, anterior basalare setose, wing membrane without microtrichia in some species, sc-r placed before origin of Rs, R₄ present, anterior fork present, posterior fork absent (M₄ missing), stem of anterior fork (M₁₊₂) shorter than fork, base of M₂ weak, male abdominal segment 7 < $0.5 \times$ length of segment 6, and male with one to two pairs of processes arising from the distal margin of tergite nine and each bearing a comb of setae on apical margin.

Distribution. AU (NZ, 9 spp.), NT (4 spp.).

Species examined. Parvicellula fascipennis Edwards; Parvicellula flabellifera Freeman; Parvicellula producta Freeman; Parvicellula triangula Marshall.

Phthinia Winnertz

Phthinia Winnertz, 1863: 779. Type species: *Phthinia humilis* Winnertz, 1863: 780 (subsequent designation by Johannsen, 1909: 83).

Diagnosis. Two or three ocelli, dorsal surface of subcostal vein bare, sc-r placed before origin of Rs, R₄ absent, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, origin of anterior fork before origin of posterior fork, foretarsomere I longer than foretibia, mid tibial organ (sensory groove) clearly present, and tarsomeres with vestiture in parallel lines when viewed dorsally, (Zaitzev, 1984).

Distribution. AU (1 sp.), NE (6 spp.), NT (4 spp.), PA (15 spp.). One fossil species.

Species examined. Phthinia furcata Freeman; Phthinia humilis Winnertz; Phthinia longiventris Tonnoir; Phthinia sp.n.; Phthinia tanypus Loew.

Polylepta Winnertz

Polylepta Winnertz, 1863: 745. Type species: *Polylepta undulata* Winnertz, 1863: 746 (subsequent designation by Johannsen, 1909: 43) [= *guttiventris* (Zetterstedt)].

Diagnosis. Flagellomere 1 with distinctly offset basal stalk, metepisternum setose, sc-r placed well after origin of Rs, R₄ present, R₅ sinuous, anterior and posterior fork present, stem of anterior fork (M₁₊₂) equal to fork length, base of M₁ weak, origin of anterior fork after origin of posterior fork, mid tibial organ (sensory groove) clearly present, and male abdominal segment $7 > 0.5 \times$ length of segment 6 (Bechev, 1990b; Kurina, 2003).

Distribution. NE (2 spp.), OR (1 sp.), PA (5 spp.). Two fossil species.

Species examined. Polylepta borealis Lundström; Polylepta guttiventris Winnertz.

Sciophila Meigen

Sciophila Meigen, 1818: 245. Type species: *Sciophila hirta* Meigen, 1818 (subsequent designation by Curtis, 1837: 641).

Lasiosoma Winnertz, 1863: 748. Type-species: *Sciophila pilosa* Meigen, 1838: 42 (subsequent designation by Coquillett, 1910: 558) [= *hirta* Meigen].

Diagnosis. Anepisternum setose, wing membrane without microtrichia in some species, sc-r placed at or well beyond origin of Rs, R₄ present, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, origin of anterior fork before origin of posterior fork, and gonostylus bearing apically-feathered, spatulate, megasetae (Zaitzev, 1982c; Søli, 1995, 1997a).

Distribution. AF (20 spp.), NE (52 spp.), NT (22 spp.), OR (12 spp.), PA (56 spp.). Eleven fossil species.

Species examined. Sciophila adamsi Edwards; Sciophila hirta Meigen; Sciophila sp.n. (intima group); Sciophila nepalensis Zaitzev; Sciophila rufa Meigen.

Stenophragma Skuse

Homaspis Skuse, 1888: 1191. Type species: *Homaspis meridiana* Skuse, 1888: 1192 (monotypy) [preoccupied Förster, 1869].

Stenophragma Skuse, 1890: 612 (nom.n. for Homaspis).

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Diagnosis. Two or three ocelli, flagellomere 1 with a distinctly offset basal stalk, frontal cleft running from lateral ocelli to eye margin, metepisternum setose, wing with three to four ~parallel grey stripes (Matile, 1991, fig. 12), distal median plate bare, bM and CuA ventrally bare, M_{1+2} dorsally bare, M_2 ventrally setose, sc-r placed near Rs, R₄ present or absent, anterior and posterior fork present, stem of anterior fork (M₁₊₂) missing (M₁ joining r-m), and origin of anterior fork before origin of posterior fork.

Distribution. AU (Australia, New Caledonia, 4 spp.), OR (undescribed species from Indonesia, Malaysia; C. Borkent, personal observation).

Species examined. Stenophragma meridianum (Skuse); Stenophragma papanorum Matile.

Tasmanina Tonnoir

Tasmanina Tonnoir, 1929: 602. Type species: Tasmanina gracilis Tonnoir, 1929: 603 (original designation).

Diagnosis. No interommatidial setae present, metepisternum setose, sc-r placed before origin of Rs, R₄ absent, anterior and posterior fork present, stem of anterior fork (M₁₊₂) shorter than fork, origin of anterior fork after origin of posterior fork, foretarsomere I shorter than foretibia, and male abdominal segment $7 > 0.5 \times$ length of segment 6.

Distribution. AU (Australia, 1 sp.).

Species examined. Tasmanina gracilis (Tonnoir).

Taxicnemis Tonnoir & Edwards

Taxicnemis Tonnoir & Edwards, 1927: 805. Type species: *Sciophila hirta* Marshall, 1896: 283 (original designation) [pre-occupied Meigen, 1818 = *Taxicnemis marshalli* Matile, 1989].

Diagnosis. Frons bare, mediotergite and laterotergite bare, metepisternum setose, bristle(s) present just posteromedially of halter base, distal median plate bare, subcostal vein ending free beyond sc-r (unique in the Sciophilini), sc-r placed before origin of Rs, C not produced beyond the apex of R₅, R₄ present and forming a cell $\sim 3 \times$ as long as tall, anterior and posterior fork present, stem of anterior fork (M₁₊₂) equal to fork length, origin of anterior fork after origin of posterior fork, M₄ almost reaching wing base before ending free, foretarsomere I shorter than foretibia, vestiture of the tibia and tarsomeres arranged in parallel lines, and male abdominal segment 7 < 0.5× length of segment 6.

Distribution. AU (NZ, 3 sp.).

Species examined. Taxicnemis marshalli Matile.

Trizygia Skuse

Trizygia Skuse, 1888: 1204. Type species: *Trizygia flavipes* Skuse, 1888: 1205 (monotypy).

New combinations: Trizygia albidens (Oliveira & Amorim) comb.n., Trizygia alvesi (Oliveira & Amorim) comb.n., Trizygia balbi (Oliveira & Amorim) comb.n., Trizygia camargoi (Oliveira & Amorim) comb.n.

Diagnosis. An episternum setose, anterior basalare setose, sc-r placed near Rs when present, R₄ absent, anterior fork present but incomplete (M₂ free in apical portion of wing), posterior fork absent (M₄ missing), humeral vein dorsally bare, bM dorsally setose, M₁₊₂, M₁, M₂ and CuA ventrally bare, male abdominal segment 7 < 0.5× length of segment 6, and 2–4 parallel lines of thick setae present on ventral apex of tergite 9.

Distribution. AU (Australia, 1 sp.), NT (5 spp.).

Species examined. Trizygia flavipes Skuse.

Comments. As discussed above, the *Paratrizygia* species described by Oliveira & Amorim (2010) belong in this genus based on the presence of a setose anepisternum and the parallel rows of strong setae present ventrally on tergite nine.

Conclusions

Here we provide the first phylogeny to include all genera of Sciophilini, revise the tribal limits and clarify the placement of several genera placed previously both in the Sciophilini and Gnoristini. The tribe now includes 34 genera and over 520 described species. This phylogeny lays the foundation for future taxonomic and phylogenetic work within the tribe.

Much of the world's mycetophilid fauna remains to be discovered and described (Pape et al., 2009), and genera of the Sciophilini and other tribes continue to be found in regions from which they were unknown previously (e.g. Azana, Amorim et al., 2008; Leptomorphus, Papp & Ševčík, 2011), particularly in the Afrotropical, Australasian and Oriental regions. None-the-less, some general comments on biogeographic patterns of the Sciophilini can be made. The tribe is cosmopolitan except for Antarctica. Most genera have either a principally Holarctic or Gondwanan distribution, sometimes with dispersal into adjacent regions. Acomoptera, Baeopterogyna, Drepanocercus, Loicia, and Paratinia are exclusively Holarctic. Acnemia, Anaclileia, Azana, Monoclona, Neuratelia, Phthinia, Polylepta and Sciophila are most species-rich in the Holarctic but have a few representatives in other regions. Genera that are found exclusively in the southern hemisphere include: Afrocnemia, Aneura, Austrosciophila, Morganiella, Neoaphelomera, Neotrizygia, Paramorganiella, Paratrizygia, Parvicellula, Tasmanina, Taxicnemis and Trizygia.

Allocotocera, Eudicrana and Stenophragma are most speciesrich in the southern hemisphere but also have several species elsewhere. Adicroneura, Cluzobra and Duretophragma are restricted to the New World; all are most species-rich in South America, with one species present in the southern or western Nearctic. Megalopelma has equal numbers of described species from the Holarctic and Neotropical regions. Leptomorphus is the only genus known from all regions, although in the Australasian region it is restricted to the islands of the northwest of the region, and is not present in Australia or New Zealand. Further generic and species-level phylogenies within Sciophilini are required before robust hypotheses about historical dispersal and vicariance within the tribe can be proposed.

Most genera of Sciophilini are in need of revision, particularly outside the Holarctic region, and these studies, when undertaken, will almost certainly reveal finer details of the relationships both within and between genera. Collection and description effort should be concentrated particularly in the Oriental, Afrotropical and Australasian regions because of likely high diversity there. Genera in particular need of revision to resolve the polytomy in the strict consensus tree are *Duretophragma, Megalopelma* and *Stenophragma* (Fig. 1B). Most Australasian genera would benefit from revisionary work as they have a greater diversity than is described (see comments in Tonnoir & Edwards, 1927; Tonnoir, 1929).

More information is needed on the morphology and habits of immature stages of this and other tribes to test the current hypotheses of relationships between genera and to allow the study of associations with their fungal hosts. This may, in turn, contribute to Mycetophilidae being used as a proxy for the diversity of fungi in a forest.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12002

Table S1. Data matrix (nexus file).

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