

***Prochetostoma*, a New Genus Proposed as a Basal
Group of the Subtribe Chetostomatina (Diptera:
Tephritidae)**

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ABSTRACT

A new genus, *Prochetostoma* Han, is proposed based on two tephritid species: *P. bhutanicum*, n. sp., and *P. contemnens* (Hering). A cladogram of these species and representative species of all the other genera of the subtribe Chetostomatina (Tribe Trypetini) is presented in discussion of the phylogenetic position of the new genus. *Prochetostoma* is recognized as a basal group within the subtribe, but its monophyly is neither supported nor rejected. A tentative phylogeny of the whole Chetostomatina is also suggested based on the present analysis and data from the literature.

INTRODUCTION

As a result of examination of more than 200 species of the tribe Trypetini, I recognized a monophyletic subtribe (Han, 1992, Ph.D. dissertation) and later formally named it as the subtribe Chetostomatina of the tribe Trypetini (Han, 1999). This classification was also supported by the mitochondrial 16S ribosomal DNA sequence data (Han and McPheron, 1997, 1999; Han, 2000; Han and Ro, 2002). In my recent morphological study (Han, 1999), a new genus was included in a cladistic analysis of the Trypetini, and was suggested as a sister-group of the *Chetostoma* group within Chetostomatina. Since this new genus was neither formally named nor described at that time, I here describe it as *Prochetostoma* based on *P. bhutanicum* n. sp. (type species) and *P. contemnens* (Hering). In addition, the phylogenetic position of *Prochetostoma* within the Chetostomatina is reanalyzed using 22 representative species of all seven genera of the subtribe.

MATERIALS AND METHODS

The terminology and morphological interpretations used in this paper follow White et al. (1999). In addition, the following eight ratios are used in the descriptions: frons-head ratio = width of frons / width of head in dorsal view; eye ratio = shortest eye diameter / longest eye diameter; gena-eye ratio = genal height / longest eye diameter (genal height is the distance between ventral eye margin and ventral genal margin immediately anterior to genal seta); arista-antenna ratio = length of arista / length of antenna excluding arista; vein R_{4+5} ratio = distance along vein R_{4+5} between crossvein R-M and wing tip / distance between crossvein R-M and basal node of vein R_{4+5} ; vein M ratio = distance along vein M between crossveins R-M and DM-Cu / distance between crossveins R-M and BM-Cu; subcosta-costa ratio = length of subcostal cell / length of costal cell, both measured on vein C; wing-thorax ratio = wing length / thorax length. The cladistic methods used to infer interspecific relationships of *Prochetostoma* are described in the appropriate section.

Acronyms of depositories, and the curators who kindly made the specimens available for this study, are as follows:

BMNH—The Natural History Museum, Department of Entomology, London, England (I. White)
 NRS—Swedish Museum of Natural History, Section for Entomology, Stockholm, Sweden (P.I. Persson)
 USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA
 (A.L. Norrbom).

TAXONOMY

Prochetostoma Han, n. gen.

Prochetostoma Han. Type species: *Prochetostoma bhutanicum* Han, n. sp., by present designation.

Prochetostoma Han 1992: 62, nomen nudum (Ph.D. thesis, unavailable for zoological nomenclature).

Unnamed new genus; Han 1999: 290.

Diagnosis

The two recognized species of *Prochetostoma* can be distinguished from other species of the Trypetini by the following combination of characters: (1) wing with narrow, unbroken C-shaped apical band from crossvein DM-Cu through anteroapical wing margin, ending before

apex of vein M; (2) ocellar setae at most 2.2 times as long as ocellar triangle; (3) eversible membrane smooth and cylindrical; and 4) apex of aculeus flattened dorsoventrally.

Description

Body. yellow brown to dark brown with dark brown setae; wing length 4.2-5.1 mm; thorax length 1.5-2.2 mm.

Head. Yellow brown to orange brown. Frons-head ratio 0.36-0.37; eye ratio 0.74-0.84, and gena-eye ratio 0.15-0.18; 1 medial vertical, 1 lateral vertical, 1 postocellar, 1 paravertical, 1 ocellar, 2 orbital, 3 frontal, 1 genal, 1 postgenal setae; ocellar seta 1.5-2.2 times as long as ocellar triangle; arista almost bare with microscopic setulae; parafacial less than 0.4 times as wide as flagellomere 1; genal seta strong, dark brown; postgena strongly swollen with long dark setulae; postgenal seta strong, dark brown; mouth parts short, palpus with dark brown setulae.

Thorax. Yellow brown to dark brown, with 1 postpronotal, 2 scapular, 1 acrostichal, 1 dorsocentral, 1 intra-alar, 1 presutural supra-alar, 1 postsutural supra-alar, 1 postalar, 2 notopleural, 2 scutellar, 2 anepisternal, 1 anepimeral, 1 katepisternal setae; dorsocentral setae aligned at 0.5-0.8 distance from level of intra-alar setae to postsutural supra-alar setae; apical scutellar setae parallel, 0.8-0.9 times as long as basal scutellar setae; proepisternum densely covered by long setulae; anepisternum with 2 strong setae of similar length. Wing hyaline with brown to yellow brown pattern; with unbroken C-band from posterior wing margin across crossvein DM-Cu through anteroapical wing margin, ending before apex of vein M; vein R₄₊₅ dorsally with 4-6 tiny setulae between node and crossvein R-M; subcosta-costa ratio 0.5-0.6; vein R₄₊₅ ratio 2.4-3.8; vein M ratio 0.7-1.4; posterodistal lobe of cell bcu short.

Male Terminalia. Lateral surstylus apically rounded in profile; lateral preniseta as long as or slightly shorter than medial preniseta; both prenisetae apically blunt; acrophallus of glans (dorsal sclerite of Han, 1999) heavily sclerotized with pattern of numerous hexagonal cells, each cell with tiny round granules inside; distinct subapical lobe present.

Female Terminalia. Oviscape with 1 (pair) strong apicoventral setae and 1-2 (pairs) apicodorsal setae; eversible membrane cylindrical without any strong teeth, but with tiny scales; dorsal and ventral taeniae extending almost entire length of eversible membrane; aculeus elongated without serration, dorsoventrally flattened; 3 ovate spermathecae with one much smaller than other two, yellow brown to brown with transverse spinular patterns, apical portion of spermathecal duct slightly swollen.

Etymology

The generic name originates from the Latin *Pro* (earlier, ancestral) prefixed to the generic stem *Chetostoma*, in reference to its phylogenetic position among the genera of the subtribe Chetostomatina. It is neuter in gender.

Biology

Unknown for the two included species of *Prochetostoma*. A possible third species of *Prochetostoma* was bred from the fruits of *Ilex integra* Thunberg in Japan (Sueyoshi and Han, in preparation).

Distribution

Burma, Bhutan, China.

Comments

Prochetostoma was included in the key to the genera of Trypetini (Han, 1999) as “Unnamed New Genus.” It is interesting to note that the only other tephritid associated with *Ilex* spp. is the genus *Parastenopa*, which appears to be another basal group within the subtribe Chetostomatina (see Phylogenetic Relationships section).

Key to the species of *Prochetostoma*

1. Scutum entirely yellow brown; crossvein R-M situated slightly distal to mid-point of cell dm ***P. bhutanicum*, n. sp.**
- . Scutum dark brown; crossvein R-M situated distinctly proximal to mid-point of cell dm ***P. contemnens* (Hering)**

***Prochetostoma bhutanicum* Han, n. sp.**

(Figs. 1-13)

Prochetostoma bhutanicum Han 1992: 62, nomen nudum (Ph.D. thesis, unavailable for zoological nomenclature).

Pseudospheniscus desperatus Hering, 1938: 18 (in part, see Material Examined section).

Diagnosis

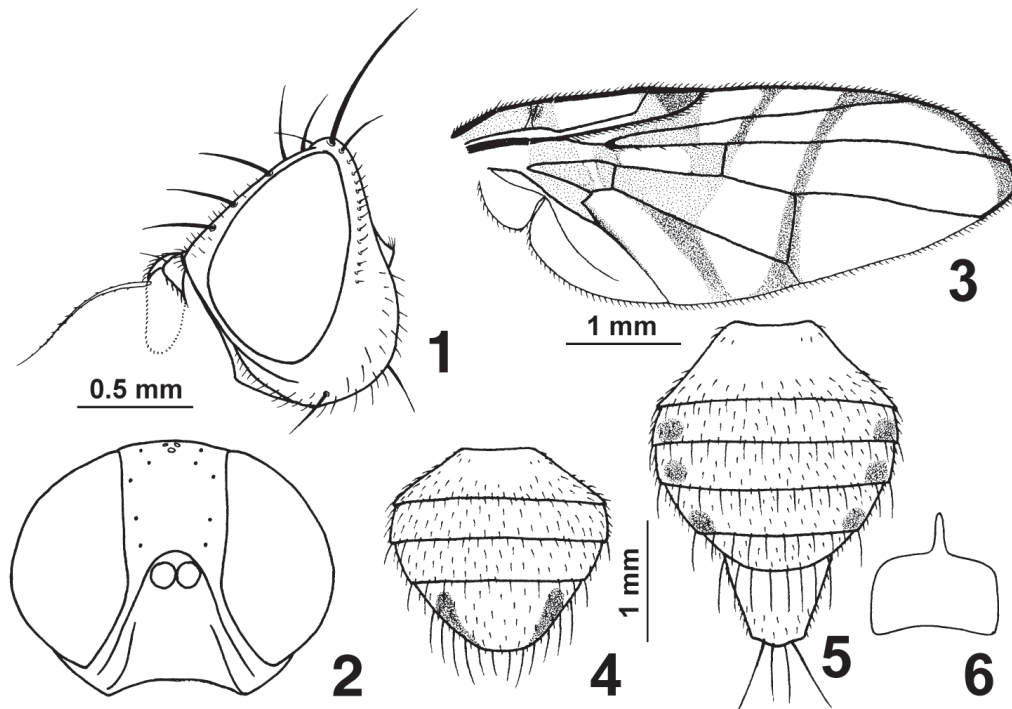
Prochetostoma bhutanicum is similar to yellow brown species of *Philophylla* Rondani, which is the most diverse genus within the tribe Trypetini. Nevertheless, *P. bhutanicum* can be distinguished by its rather peculiar wing pattern (Fig. 3): a dark brown accessory costal band merged with yellowish discal band. This species can also be readily separated from its congener, *Prochetostoma contemnens*, in having an entirely yellow brown scutum and the crossvein R-M situated beyond mid-point of cell dm (Figs. 3 vs. 16).

Description

Body. almost entirely yellow brown with dark brown setae and setulae; wing length 4.9-5.1 mm.

Head (Figs. 1, 2). Entirely yellow brown. Frons-head ratio 0.37, eye ratio 0.74 and gena-eye ratio 0.15-0.18; medial vertical seta 0.6 times as long as longest diameter of eye; lateral vertical seta 0.6 times as long as medial vertical seta; postocellar seta half as long as medial vertical seta; paraverticilar seta half as long as postocellar seta; ocellar triangle dark brown; ocellar seta hair-like, 1.5 times as long as ocellar triangle; frons yellow brown with sparse, fine dark brown setulae; 2 orbital setae; 3 frontal setae; antenna with arista-antenna ratio 1.60-1.63; scape and pedicel with dark brown setulae; arista dark brown except yellowish basal area, almost bare with microscopic setulae; ventral part of face slightly projecting beyond anterior margin of parafacial and facial ridge in profile; parafacial about 0.3 times as wide as flagellomere 1; facial ridge with fine dark brown setulae; genal seta strong, dark brown; postgena swollen with long dark brown setulae; postocular setae extended to 0.7 distance from dorsal eye margin to ventral eye margin.

Thorax. Entirely yellow brown with dark brown setae and setulae; scutum shiny with dorsocentral seta about half distance from level of intra-alar seta to postsutural supra-alar seta; basal scutellar seta 2.2 times as long as scutellum and apical scutellar seta twice as long as



Figs. 1-6. *Prochetostoma bhutanicum* Han, n. sp. 1. Head, lateral view. 2. Head, frontal view. 3. Wing. 4. Male abdomen, dorsal view. 5. Female abdomen, dorsal view. 6. Female abdominal sternite 6.

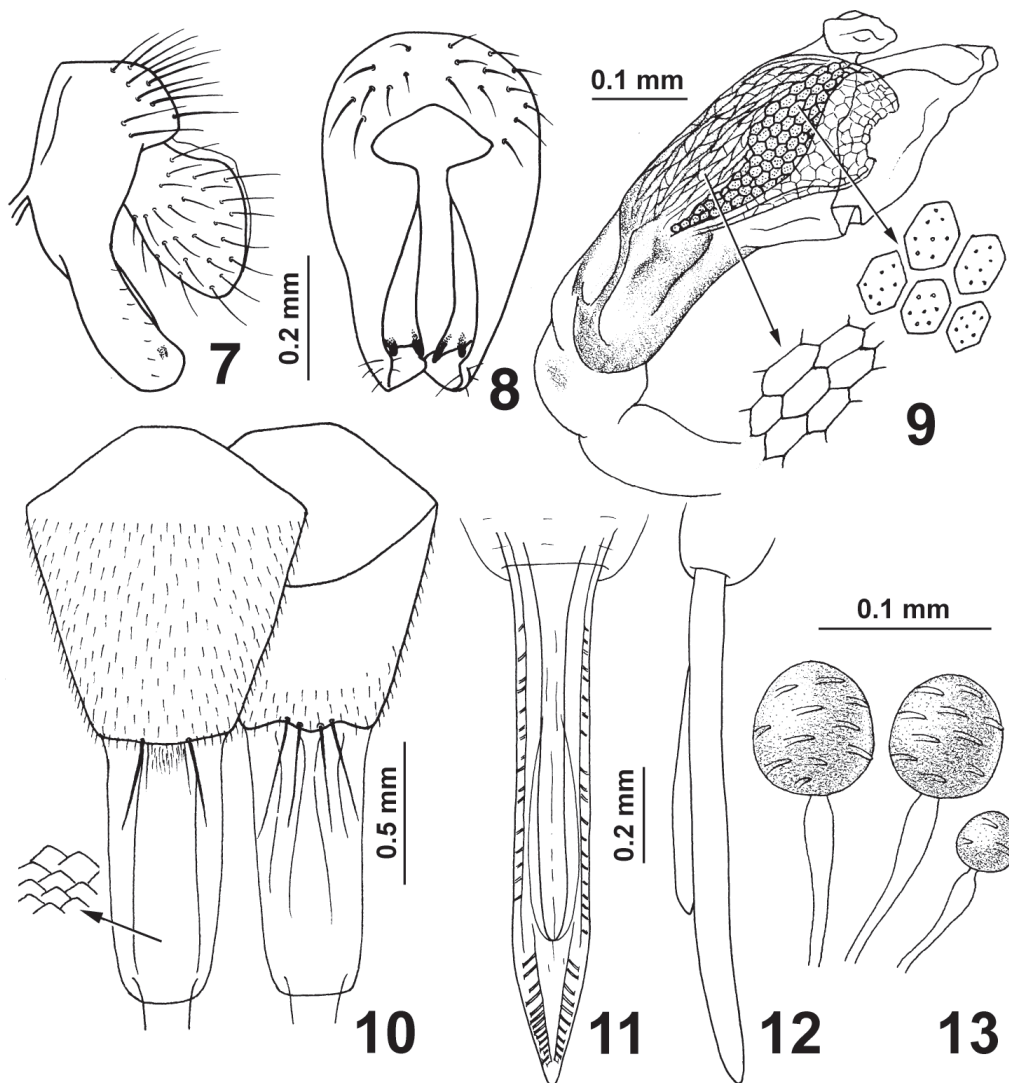
scutellum, apical scutellar setae more or less parallel; proepisternum densely covered with dark brown setulae; anepisternum with 2 setae of similar length; mediotergite shiny yellow brown with broad dark brown longitudinal band (in female paratype, band separated by median yellow area resulting in pair of dark brown longitudinal bands). Legs yellow brown with dark brown setae and setulae; forefemur with 6 posteroventral setae; midtibial spur 1.3 times as long as tibial width. Wing (Fig. 3) hyaline with dark brown to yellow brown pattern including: cell bc, basal 0.25 of cell c, basal half of pterostigma, cell r_1 posterior to vein R_1 , basal 0.2 of cell r_{2+3} , cell br distal to level of crossvein H, proximal to level of crossvein BM-Cu, and distal to level of apex of vein R_1 and over crossvein R-M, cell bm, cell bcu, basal half of cell dm yellow brown; distal half of pterostigma dark brown; brown radial medial band across cells r_1 and r_{2+3} but not reaching crossvein R-M; narrow brown anal streak; brown discal band in cell cu_2 ; narrow brown C-band from posterior wing margin over crossvein DM-Cu through anterior apical wing margin to slightly before apex of vein M. Wing-thorax ratio 2.31-2.46, vein R_{4+5} ratio 2.08-2.53, and vein M ratio 0.65-0.75; vein R_{4+5} with 6 tiny setulae between node and crossvein R-M.

Male abdomen (Fig. 4). Slightly longer than wide, almost entirely shiny yellow brown with dark brown setae and setulae; tergite 5 with pair of dark brown lateral longitudinal specks; epandrium and surstylus yellow brown; lateral surstylus rounded apically in lateral view (Fig. 7); medial surstylus with medial preniseta slightly larger than lateral preniseta (Fig. 8); glans

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(Fig. 9) with distinct trumpet-shaped subapical lobe; large and heavily sclerotized acrophallus basally with pattern of closely approximated fusiform cells and apically with pattern of honeycomb-shaped hexagonal cells, each cell with tiny granules inside.

Female abdomen (Fig. 5). Almost entirely yellow brown, tergites 3-6 each with pair of round dark brown posterolateral specks; sternite 6 with long anteromedial apodeme (Fig. 6);



Figs. 7-13. *Prochetostoma bhutanicum* Han, n. sp. 7. Epandrium, surstyli, and proctiger, lateral view. 8. Epandrium and surstyli, posterior view (proctiger removed). 9. Glans, dorsolateral view (insets at 7x main figure). 10. Oviscape and eversible membrane, ventral and dorsal view (insets at 10x main figure). 11. Aculeus, ventral view. 12. Aculeus, lateral view. 13. Spermathecae.

preceding sternites without apodeme; oviscapae (Fig. 10) shiny yellow brown, densely covered by fine yellow brown setulae, with 1 (pair) strong apicoventral setae and 2 (pairs) strong apicodorsal setae; eversible membrane cylindrical without any strong teeth, but with scale-like pattern; taeniae as long as eversible membrane; aculeus (Figs. 11, 12) long, parallel-sided, apical 0.25 tapering toward apex, dorsoventrally flattened; 3 ovate spermathecae (Fig. 13) with one much smaller than other two, yellow brown with transverse spinular patterns, apical portion of spermathecal duct slightly swollen.

Material Examined

Holotype ♂, BHUTAN, 12.VI.1985, also written on label as “Tephritidae, Potato Rukubji, T162” (BMNH).

Paratypes: CHINA: Hanchow, 8.V.1931 (1 ♀; USNM); BURMA: Kambaiti, 2000 m, 30.V.1934, Malaise (1 ♀; NRS; previously labeled as paratype of *Pseudospheniscus desperatus*); INDIA: United Provinces, Naini Tal. 6600 ft, 2.V.1934, J.A. Graham (1 ♂; BMNH).

Etymology

The specific epithet is derived from Bhutan, the type locality.

Distribution

China, Burma, Bhutan, India.

Prochetostoma contemnens (Hering), n. comb.

(Figs. 14-24)

Euleia contemnens Hering 1938: 45 (original description); Chen 1948: 76 (Chinese list); Han 1999: 290 (unnamed new genus).

Myoleja contemnens; Hardy 1977: 110 (Oriental catalog); Kapoor et al. 1980: 51 (distribution); Norrbom et al. 1999: 169 (world catalog).

Prochetostoma contemnens; Han 1992: 63 (nomen nudum).

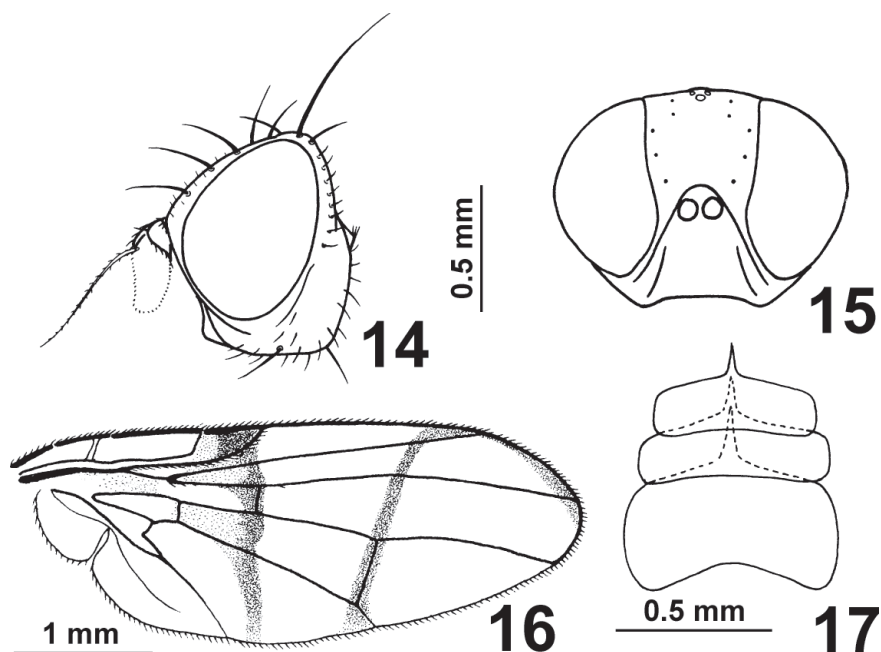
Diagnosis

Prochetostoma contemnens is superficially similar to some species of *Phylophylla* Rondani and *Anomoia* Walker, but can be easily distinguished by its proximal position of crossvein R-M (situated well proximal to the mid-point of cell dm). This species can also be separated from its congener, *P. bhutanicum*, in having a dark brown scutum and the proximal position of crossvein R-M (Figs. 3 and 16).

Description

Body. dark brown to yellow brown, mostly with dark brown setae and setulae; wing length about 4.2 mm.

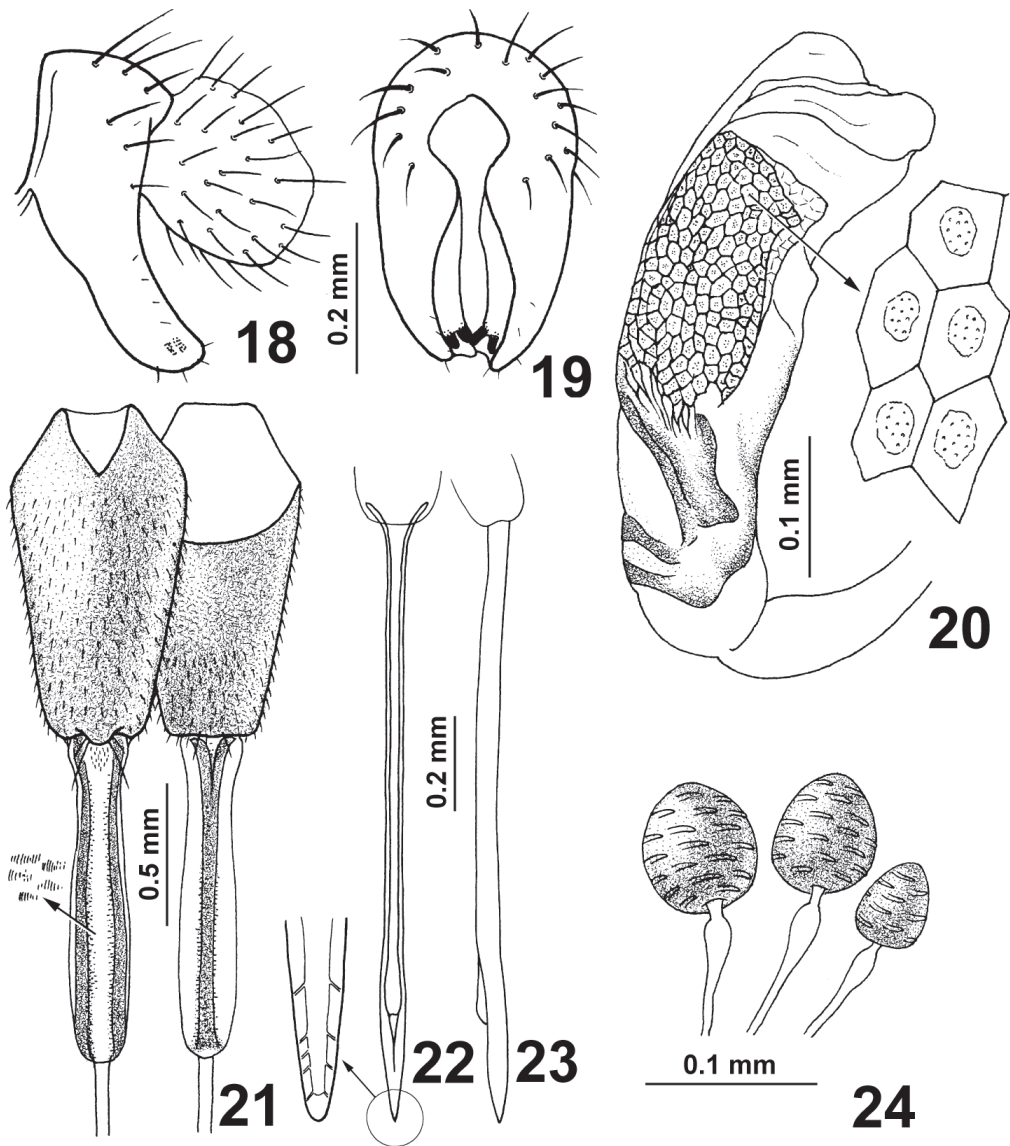
Head (Figs. 14, 15). Orange brown. Frons-head ratio 0.36, eye ratio 0.76-0.84 and gena-eye ratio 0.15-0.17; medial vertical seta 0.6 times as long as longest diameter of eye; lateral vertical seta 0.5-0.7 times as long as medial vertical seta; postocellar seta 0.4-0.5 times as long as medial vertical seta; paraverticilar seta half as long as postocellar seta; ocellar triangle dark brown; ocellar seta hair-like, 2.0-2.2 times as long as ocellar triangle; frons orange brown, with sparse, fine dark brown setulae; 2 orbital setae; 3 frontal setae; antenna with arista-antenna ratio 1.37-



Figs. 14-17. *Prochetostoma contemnens* (Hering). 14. Head, lateral view. 15. Head, frontal view. 16. Wing. 17. Female abdominal sternites 4-6.

1.39; scape and pedicel with dark brown setulae; flagellomere 1 orange brown in ground color, tinged with dark brown anteroapically; arista brown, almost bare, with microscopic setulae; ventral part of face slightly projecting beyond anterior margin of parafacial and facial ridge in profile; parafacial about 0.2 times as wide as flagellomere 1; facial ridge with fine dark brown setulae; genal seta strong, dark brown; postgena swollen with long dark brown setulae; postocular setae extended 0.7 distance from dorsal eye margin to ventral eye margin.

Thorax. Orange brown to dark brown with dark brown setae and setulae; postpronotal lobe orange brown; scutum subshiny dark brown with moderately microtrichose, with very fine setulae; dorsocentral seta slightly posterior to level of postsutural supra-alar seta; notopleuron dark brown; scutellum with basal scutellar seta 2.5 times as long as scutellum and apical scutellar seta twice as long as scutellum, apical scutellar setae more or less parallel; proepisternum orange brown, densely covered by orange brown setulae; proepimeron orange brown; anepisternum shiny dark brown, with 2 setae of similar length; katepisternum, anepimeron, katepimeron, meron, katatergite, anatergite and mediotergite shiny dark brown. Legs orange brown with dark brown setae and setulae; forefemur with 5 posteroventral setae; midtibial spur twice as long as tibial width. Wing (Fig. 16) hyaline with dark brown to yellow brown pattern including: basal 0.4 of pterostigma, basal 0.17 of cell r_1 , basal 0.33 of cell dm yellow brown; dark brown to brown discal band from distal 0.6 of pterostigma over crossvein R-M, reaching posterior wing margin; narrow C-band from posterior wing margin over crossvein DM-Cu through anterior apical wing margin, ending before apex of vein M. Wing-



Figs. 18-24. *Prochetostoma contemnens* (Hering). 18. Epandrium, surstyli, and proctiger, lateral view. 19. Epandrium and surstyli, posterior view (proctiger removed). 20. Glans, dorsolateral view (insets at 7x main figure). 21. Oviscape and eversible membrane, ventral and dorsal view (insets at 10x main figure). 22. Aculeus, ventral view. 23. Aculeus, lateral view. 24. Spermathecae.

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thorax ratio 2.48-2.71, vein R_{4+5} ratio 3.60-3.79 and vein M ratio 1.39; vein R_{4+5} with 4 tiny setulae between node and crossvein R-M.

Male abdomen. As long as wide, almost entirely shiny dark brown with dark brown setae and setulae; epandrium and surstylus yellow brown with yellow brown setae; lateral surstylus rounded apically in lateral view (Fig. 18); medial surstylus with medial preniseta slightly larger than lateral preniseta (Fig. 19); glans (Fig. 20) with subapical lobe not clearly distinguished in lateral view; large and heavily sclerotized acrophallus almost entirely with pattern of honeycomb-shaped hexagonal cells, each cell with tiny granules.

Female abdomen. Almost entirely shiny dark brown; sternites 4-6 each with long anteromedial apodeme; oviscape (Fig. 21) shiny dark brown, densely covered by fine dark brown setulae, with 1 (pair) relatively strong apicoventral seta and 1 (pair) much shorter apicodorsal seta; eversible membrane cylindrical without any strong teeth, but with scale-like pattern; taeniae dark brown, as long as eversible membrane; aculeus (Figs. 22, 23) very long, parallel-sided, with apex clearly dorsoventrally flattened; 3 ovate spermathecae (Fig. 24) with one much smaller than other two, brown with transverse spinular patterns, apical portion of spermathecal duct slightly swollen.

Material Examined

Holotype ♂, BURMA: Kambaiti, 2000 m, 12.IV.1934, Malaise (NRS).

Paratype ♀, Kambaiti, 2000 m, 27.III.1934, Malaise (BMNH).

Distribution

Known only from the type locality in Burma.

PHYLOGENETIC RELATIONSHIPS

The new genus, *Prochetostoma*, undoubtedly belongs to the subtribe Chetostomatina of the tribe Trypetini in having smooth eversible membrane and long taeniae (Figs. 10, 21), which are the synapomorphies of the subtribe (Han, 1999). Within this subtribe, Han and Freidberg (1994) and Han (1996) previously recognized a monophyletic group of five genera (the *Chetostoma* group: *Chetostoma* Rondani, *Paramyiolia* Shiraki, *Myoleja* Rondani, *Anomoia*, and *Montiludia* Ito) based on the following two synapomorphies: (1) aculeus tip flattened in sagittal plane; and (2) acrophallus with extensive pattern of hexagonal cells (Figs. 9, 20). The two species of *Prochetostoma* do not have the former synapomorphy, while clearly sharing the latter. Therefore, it is possible that *Prochetostoma* is the sister group of the *Chetostoma* group.

A cladistic analysis was conducted to clarify the above hypothesis and further test the monophyly of *Prochetostoma*. For this analysis, a sister group relationship between the subtribes Trypetina and Chetostomatina was assumed a priori based on the previously published information (Han, 1992, 1996, 1999, 2000). From the numerous characters surveyed, only those showing small to no variation within the previously recognized monophyletic groups, such as *Chetostoma*, *Paramyiolia*, *Anomoia* s. str., and *Parastenopa* s. str., were used. Only 17 characters were selected (Appendix 1) after comparing 20 representative species of all seven recognized genera of the Chetostomatina. In order to minimize the risk of introducing unexamined character states to the analysis, only the species with both sexes available were included. The polarity for each character was determined by an outgroup comparison with the Trypetina. State 0 is considered plesiomorphic.

The character matrix of 21 species (including a hypothetical ancestor) and 17 characters is shown in Table 1. All characters were treated as unordered. The branch-and-bound search procedure of PAUP* (Swofford, 2001) initially recovered 87 most parsimonious (MP) trees, but the successive weighting by maximum values of rescaled consistency indices subsequently recovered 37 MP trees (strict consensus tree shown in Fig. 25A). The successive weighting procedure put low weights to characters 2 (weight 0.38), 5 (weight 0.11) and 9 (weight 0.17). I also selected one MP tree identical to the 50% majority rule consensus tree, where the character state changes are plotted using the fast and slow optimization options (Figs. 25B and 25C respectively) of Winclada (Nixon, 1999). The following discussions are based on a hypothesized character evolution in this MP tree (Figs. 25B, C):

1. Grouping of the two *Prochetostoma* species was shown in 84% of the MP trees recovered after successive weighting (e.g. Figs. 25B, C). This is based on character state 9-1 as a synapomorphy (as in Fig. 25C), but, in this case, three parallel evolutions of same apomorphy should be hypothesized. I believe that this is highly unlikely (see following paragraph for alternative interpretation). Therefore, I considered that monophyly of *Prochetostoma* is not supported based on any convincing synapomorphy. Even though this analysis failed to prove the monophyly of the new genus, recognizing a single genus rather than two genera is preferred for the stability of nomenclature. Therefore, the genus *Prochetostoma* could be either a paraphyletic group or a monophyletic group that did not evolve any recognizable morphological synapomorphy.
2. The cladogram with the fast optimization option (Fig. 25B) suggests *Prochetostoma* as a sister group based on the pattern of hexagonal cells on the acrophallus (character state 9-1). However, this hypothesis only holds true if this state truly did not exist in both the genus *Parastenopa* and its ancestor. I believe that the apomorphic state of character 9 is such a complex structure that is unlikely to have evolved more than once, but possibly could have been lost more than once. In other words, character 9 appears to be highly prone to reversals (three times within the *Chetostoma* group, Fig. 25B). It is therefore possible that the hexagonal pattern may be a synapomorphy of the subtribe Chetostomatina but reversed in *Parastenopa*. If we do not include this particular character in the cladistic analysis, the most ancient lineage could be either Neotropical *Parastenopa* or Oriental *Prochetostoma*. Since *Parastenopa* is a clear monophyletic group while *Prochetostoma* is not, a more rigorous phylogenetic approach is necessary to clarify their relationships. Recently, a possible third species of *Prochetostoma* was bred from the fruits of *Ilex integra* Thunberg in Japan (Sueyoshi and Han, in preparation). The only other tephritid taxon associated with species of *Ilex* is the genus *Parastenopa* (Han 1998, 1999). Analysis of all the known *Parastenopa* and *Prochetostoma* may result in finer resolution near the basal branches of the chetostomatine phylogeny.
3. A sister-group relationship between *Paramyiolia* and two *Myoleja* species is rather strongly supported. This is based on two unequivocal synapomorphies (Characters 8, 16). The sharply pointed lateral prensiseta and striate spermatheca are rather unusual, and thus support their close relationships. The concept of the genus *Myoleja* has been highly arbitrary in the past, but recently narrowed down substantially (Han 1999). Nevertheless, it is still non-monophyletic as shown in the cladograms (Figs. 25, 26).

A tentative phylogeny of the whole Chetostomatina is suggested based on the present

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Table 1
Character state distribution of characters used in the cladistic analysis of the subtribe Chetostomatina (0 = plesiomorphy, 1 = apomorphy, ? = uncertain state)

Taxa / Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Hypothetical Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Parastenopa guttata</i> Aczél	0	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1
<i>Parastenopa elegans</i> (Blanchard)	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1
<i>Parastenopa fallax</i> (Johnson)	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	?	1
<i>Parastenopa limata</i> (Coquillett)	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1
<i>Prochetostoma bhutanicum</i> n. sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Prochetostoma contemnens</i> (Hering)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Montiludia nemorivaga</i> Ito	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
<i>Montiludia fucosa</i> Ito	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
<i>Anomoia permunda</i> (Harris)	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0
<i>Anomoia apicalis</i> Ito	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0
<i>Anomoia vulgaris</i> (Shiraki)	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
<i>Myoleja lucida</i> (Fallén)	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	0
<i>Myoleja sinensis</i> (Zia)	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	0
<i>Myoleja boninensis</i> (Ito)	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
<i>Paramyiolia takeuchii</i> Shiraki	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0
<i>Paramyiolia nigricornis</i> (Doane)	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0
<i>Paramyiolia rhino</i> (Steyskal)	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0
<i>Chetostoma curvinerve</i> Rondani	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0
<i>Chetostoma californicum</i> Blanc	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0
<i>Chetostoma rubidium</i> (Coquillett)	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0

analysis plus data from the literature (Fig. 26). It shows the current status of our still poor knowledge on this group of flies. I believe this situation can be improved through an on-going effort to introduce more comparative data from their morphology, biology and other non-conventional sources, such as molecular sequences, as demonstrated by Han (1999, 2000).

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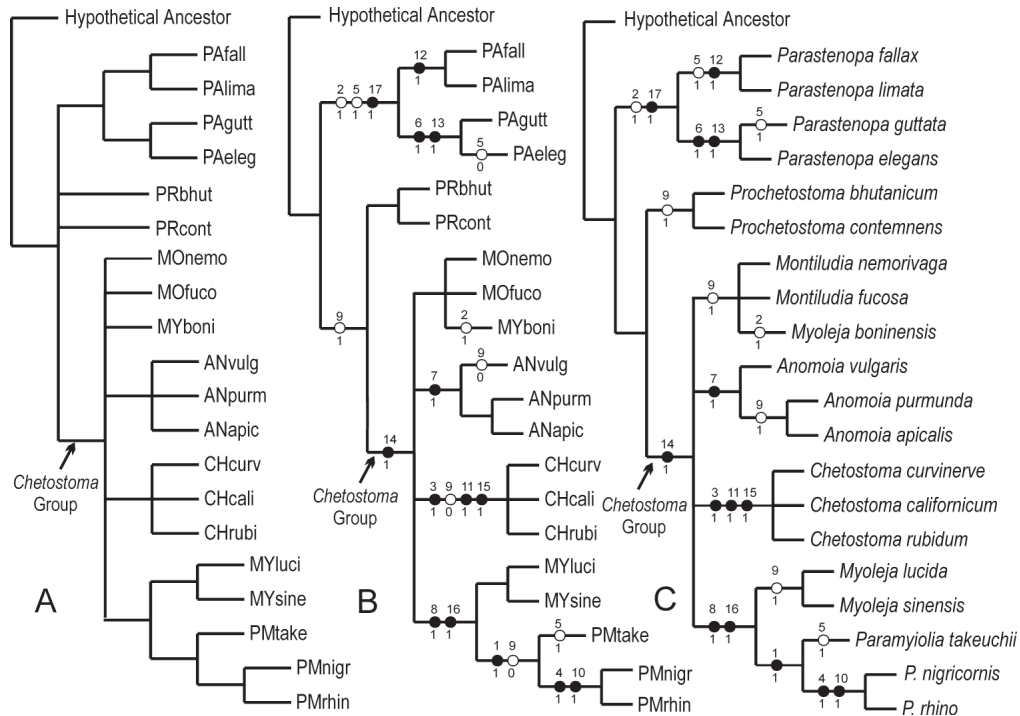


Fig. 25. Possible phylogenetic relationships of representative species of Chetostomatina. (A) Strict consensus tree of 37 most parsimonious (MP) trees recovered after successive weighting. (B) One of 37 MP trees (identical topology as 50% majority rule consensus tree). All character state changes are plotted using fast optimization option (Winclada software). (C) Same tree as (B) except based on slow optimization option. ● = forward changes without homoplasy; ○ = changes with homoplasy.

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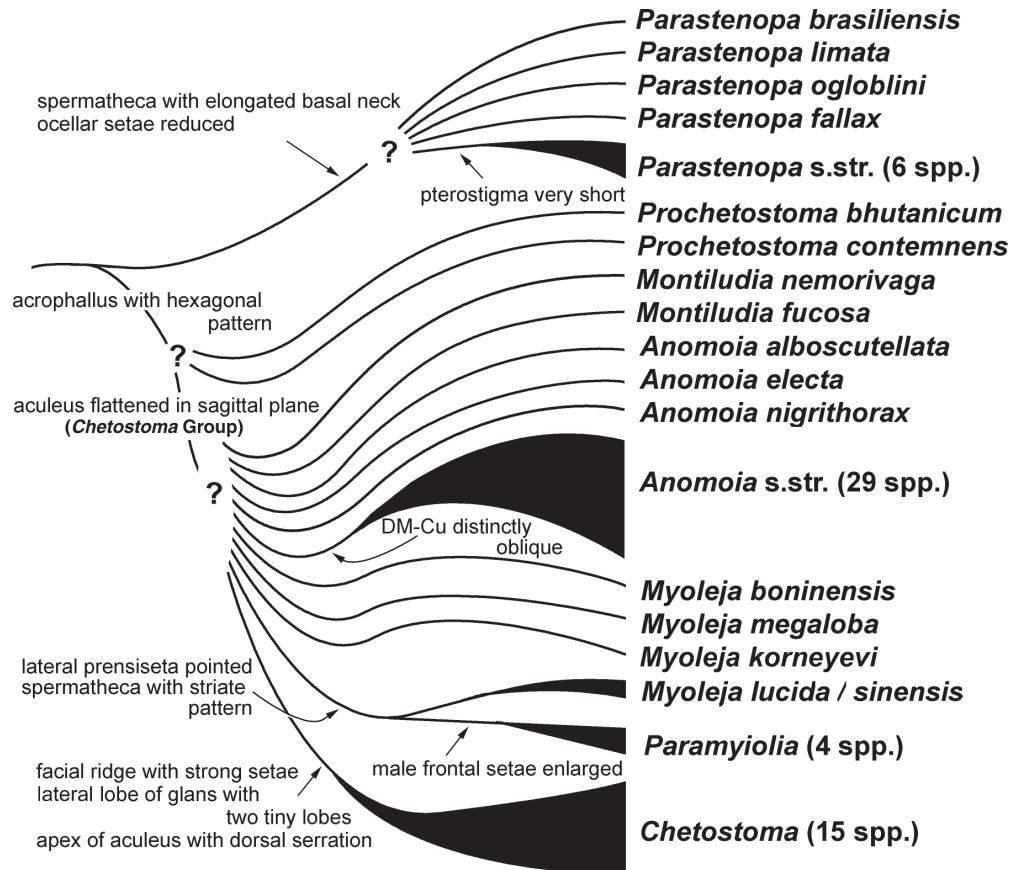


Fig. 26. Preliminary cladogram showing possible phylogenetic relationships among genera and species of the subtribe Chetostomatina. Hypothesized synapomorphies are shown on the internal branches.

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APPENDIX 1

Morphological characters used for cladistic analysis of the subtribe Chetostomatina

Head

1. Male frontal setae: 0) not modified; 1) enlarged with first one largest and sharply pointed. This peculiar sexually dimorphic structure is only found in *Paramyiolia* within the Chetostomatina. Enlargement of the male frontal setae also occurs in several genera of the outgroup, Trypetina, but the shape of the setae, their arrangement, and even which particular setae are modified differ among these genera.
2. Ocellar setae: 0) at least 1.5 times as long as ocellar triangle; 1) reduced or at most as long as ocellar triangle. The reduction of the ocellar seta is considered apomorphic because it is less common in the outgroup. Since both states also occur outside of the tribe Trypetini, this character appears to have evolved independently numerous times.
3. Facial ridge: 0) only with short fine setulae in both sexes; 1) anteroventrally with strong setae, especially pronounced in males. The apomorphic state is a unique condition not found in any other tephritid taxa or other tephritoid families.

Thorax

4. Apical scutellar setae: 0) at least 0.8 times as long as basal scutellar setae; 1) shorter than 0.6 times as long as basal scutellar setae. The plesiomorphic state is consistently found within the outgroup.
5. Anepisternal setae: 0) ventral seta at least 0.6 times as long as dorsal seta; 1) ventral setae reduced or at most half as long as dorsal seta. The plesiomorphic state is more consistently found within the outgroup.

Wing

6. Pterostigma: 0) normal (subcosta-costa ratio larger than 0.5); 1) very short (subcosta-costa ratio smaller than 0.3). The plesiomorphic state is more consistently found within the outgroup.
7. Crossvein DM-Cu from vein CuA_1 : 0) more or less right-angled; 1) distinctly oblique. The plesiomorphic state is consistently found within the outgroup.

Abdomen

8. Apex of lateral preniseta: 0) blunt; 1) sharply pointed. The plesiomorphic state is consistently found within the outgroup.
9. Acrophallus of glans: 0) without pattern of hexagonal cells; 1) with pattern of hexagonal cells. The apomorphic state is a unique condition not found in any other tephritid taxa or other tephritoid families.
10. Subapical lobe of glans: 0) present; 1) reduced. The reduction of the subapical lobe is considered apomorphic because it is less common in the outgroup. Since both states also occur outside of the tribe Trypetini, this character appears to have evolved independently numerous times.
11. Apex of subapical lobe of glans: 0) without two tiny lobes; 1) with two tiny lobes. The apomorphic state is a unique condition not found in any other tephritid taxa or other tephritoid families.
12. Dorsal taeniae: 0) as long uninterrupted medial pair; 1) clearly divided into two pairs. The apomorphic state is a unique condition not found in any other tephritid taxa.

BIOTAXONOMY OF TEPHRITOIDEA

13. Ventral taeniae: 0) as long uninterrupted lateral pair; 1) basal portion separated into pair of basal sclerites. The apomorphic state is a unique condition not found in any other tephritid taxa.
14. Aculeus tip: 0) dorsoventrally flattened; 1) flattened in sagittal plane with ventral serration. The apomorphic state is a unique condition not found in any other tephritid taxa or other tephritoid families.
15. Aculeus tip: 0) without dorsal serration; 1) with dorsal serration. The apomorphic state is a unique condition not found in any other tephritid taxa or other tephritoid families.
16. Spermatheca: 0) with spinular pattern; 1) with striate pattern. The plesiomorphic state is consistently found within the outgroup.
17. Spermatheca: 0) without elongated basal neck; 1) with elongated basal neck. The plesiomorphic state is much more commonly found within the outgroup.