

**Taxonomic limits, phylogeny and higher classification
of Anthomyzidae (Diptera), with special regard to fossil record**

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Abstract. Taxonomic limits of the family Anthomyzidae are prescribed. Two fossil genera are affirmed, viz. *Protanthomyza* Hennig, 1965 (Baltic amber) and *Grimalantha* gen. n. (type species: *G. vulnerata* sp. n.) described from Dominican amber. Fourteen extant genera are recognized, including *Chamaebosca* Speiser, 1903 (= *Penquistus* Kieffer, 1906 syn. n.) and *Apterosepsis* Richards, 1962. New diagnoses of the latter two genera and redescrptions of their type species are given and their relationships are discussed. *Chamaebosca cursor* (Kieffer, 1906) becomes a new combination. The monotypic genus *Echidnocephalodes* Sabrosky, 1980 is removed from Anthomyzidae, newly diagnosed and its type species *E. barbatus* (Lamb, 1914) redescrbed and a lectotype designated. *Echidnocephalodes* is considered to be related to Periscelididae and/or Aulacigastridae, particularly to those genera with symmetrical male postabdomen. The inferred phylogeny of the Anthomyzidae, based on cladistic analysis, is presented. The Opomyzidae are confirmed as a sister-group of the Anthomyzidae, while *Protanthomyza* is found to be the most primitive anthomyzid genus forming a sister-group to all recent genera plus the fossil *Grimalantha* gen. n. The monophylies of the latter group of genera, and of the Anthomyzidae as a whole, are demonstrated. The genus *Protanthomyza* is classified in a new subfamily Protanthomyzinae, and all remaining genera are placed in the subfamily Anthomyzinae Frey, 1921. An annotated world checklist of the family Anthomyzidae is appended.

INTRODUCTION

The relationships and taxonomic limits of the family Anthomyzidae have most recently been discussed by J.F. McAlpine (1989). He summarized changes in the concept of the family since Hennig's (1971, 1973) delimitation and rejected the majority of problematic extant genera which Hennig (l.c.) considered to be related or possible members of the Anthomyzidae, e.g. *Waterhouseia* Malloch, 1936, *Melanthomyza* Malloch, 1933, *Nothoasteia* Malloch, 1936, *Paraleucopis* Malloch, 1913, *Gayomyia* Malloch, 1933 and *Schizostomyia* Malloch, 1933. The remaining genera which J.F. McAlpine (l.c.) retained in the family, seem to form a compact, well-defined group, if three of them, viz. *Chamaebosca* Speiser, 1903, *Apterosepsis* Richards, 1962 and *Echidnocephalodes* Sabrosky, 1980, which were not seen by J.F. McAlpine (l.c.), are excluded.

Of the three fossil genera from Baltic amber which were tentatively assigned by Hennig (1965, 1967, 1969) to the Anthomyzidae, only *Protanthomyza* Hennig, 1965 is now regarded as affiliated to that family (see J.F. McAlpine, 1989). The genus *Anthoclusia* Hennig, 1965, with the species *A. gephyrea* Hennig, 1965 and *A. remotinervis* Hennig, 1969, was transferred by D.K. McAlpine (1978) to a new family Neurochaetidae and the genus *Xenanthomyza* Hennig, 1967, with one species, *X. larssoni* Hennig, 1967, was associated with the Clusiidae by Hennig (1971: 46) and confirmed by J.F. McAlpine (1989).

Two years ago I attempted to clarify the above problem with some preliminary results of my studies on the family Anthomyzidae, which were presented in a lecture at the 3rd International Congress of Dipterology, Guelph, 1994, and summarized in an abstract (Roháček, 1994). Since then further progress has been made and the results can now be presented in full, including new taxonomic, nomenclatural and phylogenetic data. Based on cladistic analysis of fossil and recent genera the relationships of the family Anthomyzidae are discussed and a new higher classification of the family is proposed.

MATERIAL AND METHODS

Numerous specimens of Anthomyzidae and other families of Opomyzoidea were examined during this study, but only the types and comparative material of taxa dealt with here are listed. Standard methods of examination were used, including the study of the male and female postabdominal structures (cf. Roháček, 1983).

The presentation of label data is strictly verbatim for type specimens but standardized for other material examined. Abdomens of some specimens were detached and genitalia dissected. After examination, all dissected parts were put into plastic tubes containing glycerine and pinned below the respective specimens; this is indicated by the abbreviation "genit. prep." in the text.

Morphological terminology essentially follows that used in my recent papers (e.g. Roháček, 1996) except for some terms of the male hypopygium. The "hinge" hypothesis of the origin of the eremoneuran hypopygium, re-discovered and documented recently by Zatwarnicki (1996), was accepted in this study and, therefore, the following alterations of terms of the male genitalia against my previous papers need to be listed (new term first): ejacapodeme = ejaculatory apodeme, epandrium = periandrium, medandrium = intraperiandrial sclerite, phallapodeme = aedeagal apodeme, transandrium = posterior hypandrial bridge.

Abbreviations of morphological terms used in text and figures: A_1 – anal vein; ac – acrostichal (seta); afa – aedeagal part of folding apparatus; ag – accessory gland; bm – basal membrane; C – costa; ce – cercus; CS_3 , CS_4 – 3rd, 4th costal section; ct – ctenidial spine; CuA_1 – cubitus; dc – dorsocentral (seta); dm – discal medial cell; dm-cu – discal medial-cubital (= posterior, t_p) cross-vein; dp – distiphallus; ea – ejacapodeme; ep – epandrium; f – filum of distiphallus; f_1 , f_2 , f_3 – fore, mid, hind femur; fc – fulcrum of phallapodeme; gs – gonostylus; hu – humeral (= postpronotal) (seta); hy – hypandrium; in – internal sclerite(s); M – media; ma – medandrium; mspl – mesopleural (= anepisternal) (seta); mt_1 – fore basitarsus; npl – notopleural (seta); oc – ocellar (seta); occe – external occipital (seta); ors – orbital (seta); ov – ovipositor; pa – postalar (seta); pg – postgonite; pha – phallapodeme; pk – preapical kink on R_1 ; pp – phallophore; ppl – propleural (= proepisternal) (seta); pr – process of phallapodeme; prg – pregonite; prs – presutural (seta); prsc – prescutellar acrostichal (seta); pvt – postvertical (seta); R_1 – 1st branch of radius; R_{2+3} – 2nd branch of radius; R_{4+5} – 3rd branch of radius; r-m – radial-medial (= anterior, t_a) cross-vein; s – saccus of distiphallus; S2–S10 – abdominal sterna; sa – supraalar (seta); sc – scutellar (seta); Sc – subcosta; sp – spermatheca; stpl – sternopleural (= katepisternal) (seta); sTS – syntergosternum; T1–T10 – abdominal terga; t_1 , t_2 , t_3 – fore, mid, hind tibia; ta – transandrium; vi – vibrissa; vr – ventral receptacle; vte – outer vertical (seta); vti – inner vertical (seta).

COMPOSITION OF THE FAMILY ANTHOMYZIDAE

During the past five years I have had opportunities to examine representatives of almost all the genera included in the family Anthomyzidae by J.F. McAlpine (1989), with the sole exception of *Penquistus* Kieffer, 1906. I also thoroughly studied Hennig's (l.c.) descriptions of fossil genera and the original description of the above-mentioned genus where no material is available, re-examined the holotype of *Protanthomyza collarti* Hennig, 1965 and investigated a new fossil genus from Dominican amber (see below) with the aim to re-define taxonomic limits of the family and to better understand its relationships.

FOSSIL GENERA

Only two fossil genera (and species) of Anthomyzidae are known: the older *Protanthomyza collarti* Hennig, 1965 from Baltic amber (probably Eocene-Oligocene, 35–55 million years old – Larsson, 1978) and the younger, described here as a new genus and species from Dominican amber (Oligocene–Miocene, 15–40 million years old – Poinar, 1992). A new diagnosis, based on the study of the holotype of *Protanthomyza collarti*, is prepared with respect to character set used recently to characterize genera of Anthomyzidae (see Roháček, 1992, 1993, 1996; Roháček & Freidberg, 1993) to be comparable with those of extant genera and commensurate with phylogenetic considerations.

Genus *Protanthomyza* Hennig, 1965

Protanthomyza Hennig, 1965: 169. Type species: *Protanthomyza collarti* Hennig, 1965 (by monotypy).

MATERIAL EXAMINED: Holotype ♂ labelled: "Fam. Anthomyzidae, *Protanthomyza collarti* Hennig, Holotypus" (Baltic amber, Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium).

DIAGNOSIS. (1) Head higher than long (Fig. 2). (2) Eye large, suboval, convex; its longest diameter vertical (Fig. 2). (3) Frons relatively narrow (Fig. 3) because of large eyes. (4) Ocellar triangle protruding; ocelli large (Figs 2–3). (5) Occiput slightly concave behind pvt. (6) Antenna relatively porrect (Fig. 2) with suboval, laterally compressed (Fig. 3) 1st flagellomere. (7) Arista dorsobasal, shortly ciliate (Fig. 2). (8) Palpus small, with several setulae (Fig. 2). Cephalic chaetotaxy (Figs 2–3): (9) pvt short, convergent; (10) vte and vti long, longer than oc; (11) 3 subequal ors (or the posterior slightly longer) and 4 microsetulae on orbits (2 in front of the foremost ors) (Fig. 2); (12) postocular setulae in a long (partly double) row; (13) 1 relatively short vi; (14) peristomal setulae medium long.

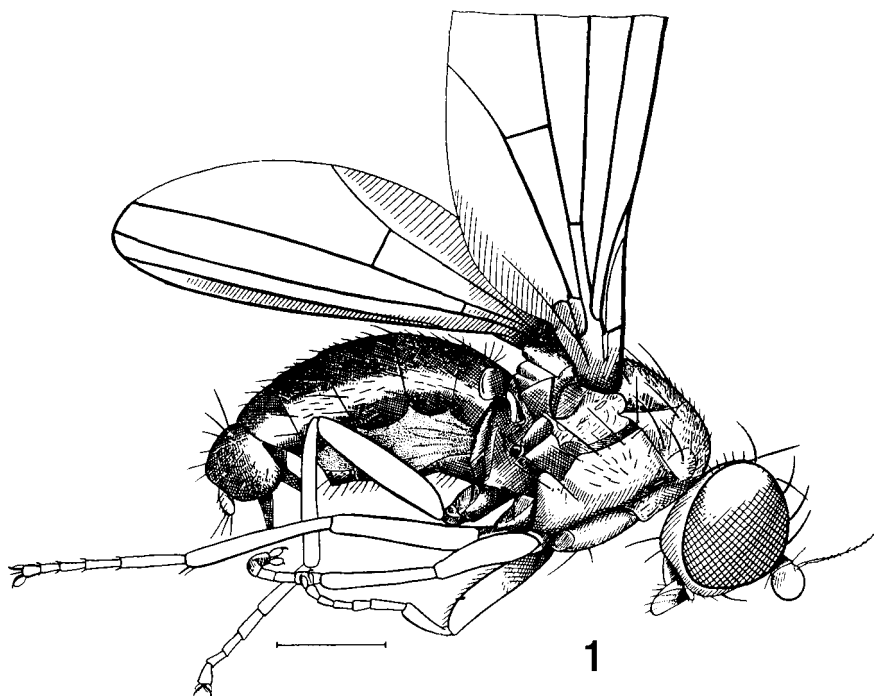


Fig. 1. *Protanthomyza collarti* Hennig, male holotype laterally (after Hennig, 1965). Scale = 0.5 mm.

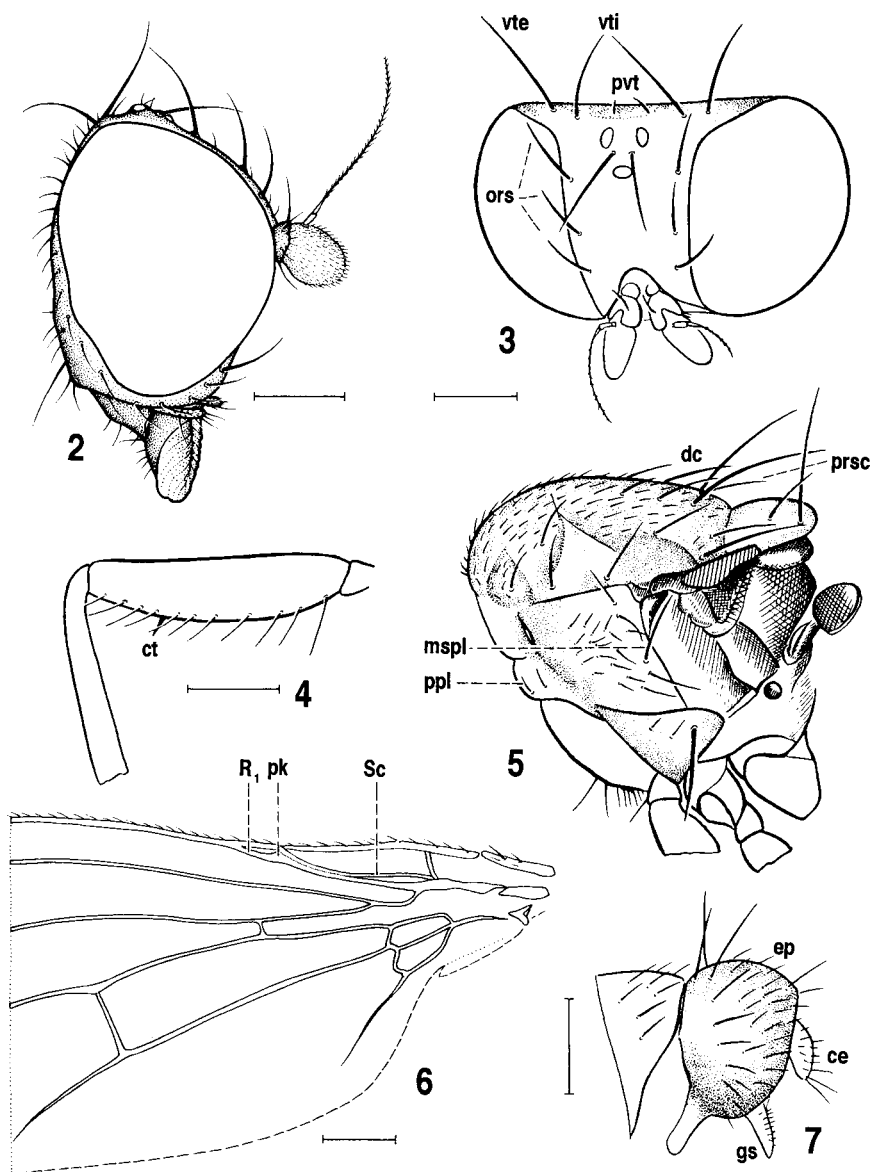
(15) Thorax slightly narrower than head. Thoracic chaetotaxy (Figs 1, 5): (16) 1 long hu, 2 long (subequal) npl; (17) 1 long prs; (18) 1 sa, 2 long pa; (19) 3 dc (all postsutural) becoming shorter anteriorly, the posterior much longer than others; (20) ac microsetae relatively dense (number of rows could not be observed); 1 long prescutellar ac (Fig. 5); (21) 2 sc, apical long, laterobasal short; (22) 2 small but distinct ppl; (23) mesopleuron setose, with a row of longer setae at posterior margin, including 1 particularly long seta (Fig. 5); (24) 1 long stpl and 2 short in front of it. (25) f_1 with short but distinct ctenidial spine (Fig. 4). (26) t_2 with distinct ventroapical seta (Fig. 1). (27) Male f_3 simply uniformly setulose. (28) Wing (Figs 1, 6) not particularly narrow, unicolorous. (29) C without costal break but attenuated at apex of Sc (Fig. 6); no enlarged setulae on C. (30) Sc distinct along its entire length but fused to R_1 in its terminal half; preapical kink on R_1 present in its simplest form. (31) R_{2+3} long, subparallel with C and almost straight apically; (32) R_{4+5} parallel with apical part of M. (33) Cell dm medium-sized, not very narrow. (34) CuA_1 almost reaching wing margin; A_1 ending far from it. (35) Alula indistinct, apparently small and narrow.

Male abdomen (Fig. 1): (36) T1 and T2 probably (at least partly) coalesced; (37) preabdominal terga large and wide; (38) preabdominal sterna much narrower than associated terga. Male postabdomen: (39) T6 not visible (hidden below T5 or absent); (40) S6 not visible (hidden ventrolaterally below T5 and S5); S7 clearly asymmetrical, on left side of postabdomen (visible as a narrow stripe behind left posterior corner of T5); (41) S8 situated dorsally (Fig. 7), rather symmetrical (= "pregenital Tergite" of Hennig 1965: 173).

Male genitalia (Fig. 7): (42) epandrium dorsobasally with 2 pairs of longer setae; (43) epandrium with an anteroventral finger-like projection on each side (Fig. 7); (44) gonostylus discrete, small, narrow, pointed (Fig. 7); (45) male cercus well developed, discrete (Fig. 7).

Female unknown.

DISCUSSION. The genus *Protanthomyza* is here considered a true, although very primitive, member of the family Anthomyzidae (see below). It bears a number of plesiomorphic characters (e.g. characters no. 8, 12, 18, 22, 23, 29, 30) which are unknown in extant genera as well as in the other fossil genus, *Grimalantha* gen. n., described below. As it also possesses several distinct autapomorphies (e.g. 4 – enlarged ocelli and protruding ocellar triangle, 20 – long prescutellar ac setae, 43 – epandrial anteroventral projections), it appears to be very different from all other known genera of Anthomyzidae and is, therefore, placed in a new subfamily of its own (see below). Some of the features used in the above diagnosis need special comments. The large eyes with vertical longest diameter (no. 2), porrect antenna (6), complete cephalic chaetotaxy (9–14) and comparatively broad wings (28) also belong to plesiomorphic characters but these (or some of them) were also found in certain recent genera. The formation of subcosta (no. 30) of *Protanthomyza* is particularly interesting. It is not free as Hennig described and illustrated (Hennig, 1965: Figs 260–261; Fig. 1 in this paper) although well discernible along its entire length (see Fig. 6); actually it is fused to R_1 in its terminal half (not coalesced with it as in more advanced Anthomyzidae) and forms with R_1 a distinct preapical kink so characteristic for the Opomyzidae and Anthomyzidae. Consequently, this condition is regarded as the first stage of transformation series to typical, apically reduced Sc and compact R_1 kink in recent anthomyzids.



Figs 2–7. *Proanthomyza collarti* Hennig, male. 2 – head laterally (holotype); 3 – head frontodorsally (paratype); 4 – fore leg (without apex of tibia and tarsus) posteriorly; 5 – thorax laterally; 6 – proximal part of left wing; 7 – external genitalia and S8 laterally (all based on holotype). Figs 3–5, 7 after Hennig (1965). Scales = 0.2 mm.

Genus *Grimalantha* gen. n.

Type species: *Grimalantha vulnerata* sp. n.

ETYMOLOGY. An abbreviated conjunction of Grimal[di] + Anth[omyz]a. Named in honour of the well-known dipterist Dr. David Grimaldi (New York), who discovered the holotype of the type species in Dominican amber. Gender feminine.

DIAGNOSIS. (1) Head as long as high. (2) Eye large, convex; its longest diameter oblique (Fig. 9). (3) Frons comparatively narrow (Fig. 8). (4) Ocellar triangle and ocelli normal. (5) Occiput relatively deeply concave (Fig. 8). (6) Antenna geniculate between pedicel and 1st flagellomere, the latter suboval and laterally compressed. (7) Arista dorsobasal, short, with short cilia. (8) Palpus slender, pale, with 1 longer setula (Fig. 9). Cephalic chaetotaxy (Figs 8–9): (9) pvt well developed, crossed; (10) vte longest of cephalic setae, vti short, oc rather weak; (11) 3 ors becoming shorter anteriorly and 1 microsetula in front of the foremost ors; (12) postocular setulae in a single, medium-long, row; (13) 1 rather short vi and 1 distinct subvibrissa; (14) peristomal setulae short and sparse.

(15) Thorax distinctly narrower than head (Fig. 8). Thoracic chaetotaxy (Figs 8–9): (16) 1 long hu, 2 npl; (17) 1 small prs; (18) 1 sa, 1 pa; (19) 2 dc (all postsutural) plus 1 enlarged dc microseta in front of them; (20) ac microsetae in 4 rows; no prescutellar ac enlarged; (21) 2 sc, apical very long, also laterobasal relatively long; (22) 1 very minute ppl; (23) mesopleuron bare; (24) 2 stpl, only posterior long. (25) f_1 with reduced ctenidial spine (Fig. 11). (26) t_2 with 1 ventroapical seta (Figs 11, 12). (27) male f_3 unknown. (28) Wing long and narrow (Fig. 10), unicolorous. (29) Costal break at apex of Sc (Fig. 10) present; C with distinct spinulae between apices of R_1 and R_{4+5} . (30) Sc apically coalesced with R_1 and producing a distinct preapical kink on R_1 . (31) R_{2+3} long, subparallel with C, sinuately bent subapically; (32) R_{4+5} almost parallel with apical part of M. (33) Cell dm relatively long and narrow. (34) CuA_1 almost reaching wing margin; A_1 ending in front of it. (35) Alula normal, small and narrow.

Female abdomen (Figs 11, 12): (36) T1 and T2 fused together; (37) preabdominal terga large and wide; (38) preabdominal sterna (S2–S6) unusually broad (Fig. 12).

Female postabdomen (Fig. 12): (39) T7 extended lateroventrally but S7 discrete; (40) S8 narrow, medially divided; (41) cercus small and relatively short, with rather small setulae (Figs 11, 12).

Male unknown.

DISCUSSION. *Grimalantha* gen. n. is clearly more closely related to extant Anthomyzidae than to the fossil genus *Protanthomyza* Hennig, 1965. The following features are particularly significant: 2, 5, 6, 8, 17–24 (thoracic chaetotaxy), 29, 30, 40. However, the new genus differs from all recent and fossil genera of Anthomyzidae in having (10) short vti (yet shorter than in *Amygdalops* Lamb, 1914) and (38) unusually broad female preabdominal sterna. The combination of visible characters of the female postabdomen also is highly diagnostic; while the discrete sclerites of the 7th abdominal segment belong to plesiomorphic features, the narrow, longitudinally divided S8 and short cerci appear to be rather advanced characters. The shape of S8 resembles closely that of *Anthomyza* Fallén, 1810, but the latter genus differs from *Grimalantha* by the shape of head (occiput not concave), long prs, usually fused female T7 and S7 (to form tergosternum) and by long, long-haired female cerci. The head of *Grimalantha* is rather similar to that of *Amygdalops* (cf.

Roháček & Freidberg, 1993); however, no other characters were found to support the relationship of these two genera.

The most important character of *Grimalantha*, viz. the broad preabdominal sterna, is difficult to interpret. The fossil genus *Protanthomyza* has narrow sterna, as also have all extant anthomyzids known to me. Consequently, it seems reasonable to consider broad sterna an apomorphic condition.

In spite of several modern characters shared by *Grimalantha* gen. n. and extant genera, no distinct sister-group of *Grimalantha* was recognized among known genera (including those described from the New World). It could not be ascertained whether *Grimalantha* forms a sister-group to all recent genera of Anthomyzidae, chiefly because of the lack of information on the male postabdominal and genital features of *Grimalantha*.

Grimalantha vulnerata sp. n.

(Figs 8–12)

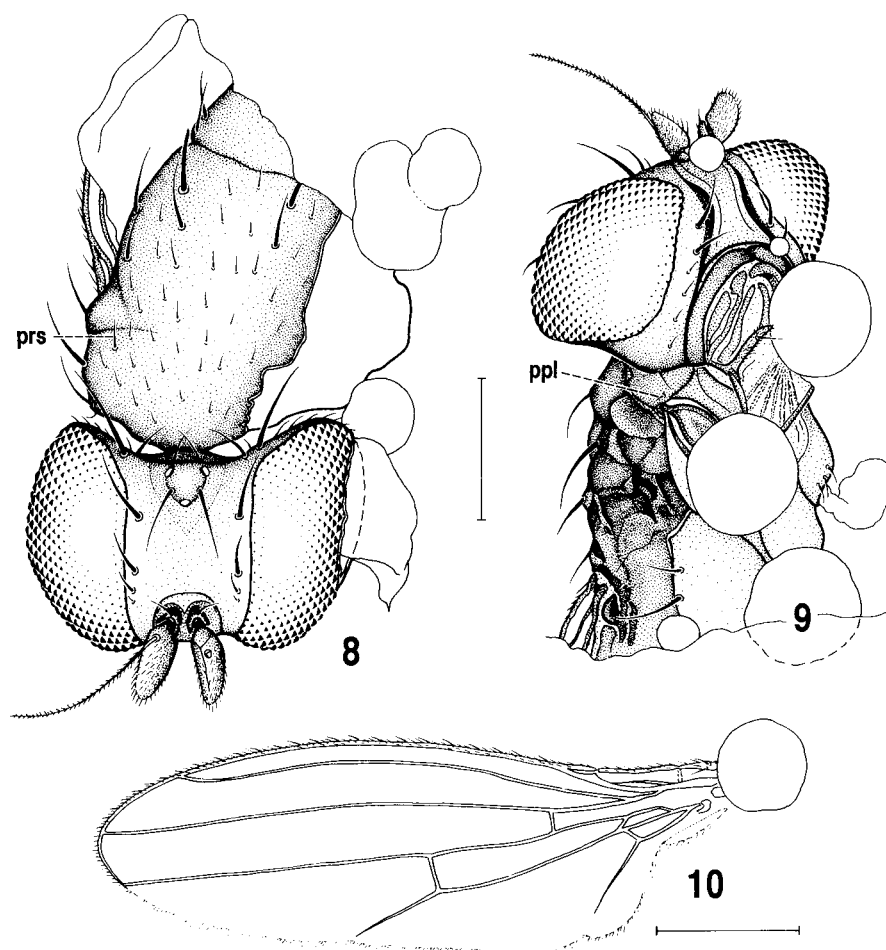
TYPE MATERIAL: Holotype ♀ labelled: "Amber: Oligo-Miocene, Dominican Republic, AMNH no. DR-10-1448, Locality:" and "*Grimalantha vulnerata* sp. n. ♀, J. Roháček det. 1996, Holotype" (red label). Deposited in the American Museum of Natural History, New York. The specimen is partly damaged and covered by numerous small air pockets obscuring the body surface.

ETYMOLOGY. The name "vulneratus" (= injured) refers to the damaged left side of the thorax of the holotype.

DESCRIPTION. Male unknown. Female. Total body length 2.0 mm. Body bicoloured, blackish brown and yellow. Head about as long as high but broad (broader than thorax), with strongly convex eyes, relatively narrow frons and distinctly excavated occiput (Figs 8, 9). Frons dark brown posteriorly, paler anteriorly, with brown, poorly defined frontal triangle (Fig. 8) and pale, yellowish brown orbits. Occiput and ocellar triangle blackish brown. Gena narrow, shifted ventrally below bulging eye, ochreous, with narrow dark brown anterior margin. Face (prefrons) ochreous brown. Cephalic chaetotaxy: see generic diagnosis and Figs 8, 9; all setae on frons relatively short; vti only slightly longer than pvt, also oc relatively short; 3 ors becoming shorter anteriorly and 1 microseta in front of the shortest (foremost) ors; occiput with a series of setulae behind eye margin; vi well developed although relatively short, subvibrissa about half length of vi and twice as long as sparse peristomal setulae (Fig. 9). Eye large, convex (Fig. 8); its longest diameter about 1.5 times as long as the shortest. Palpus yellow, of medium length and slender, with 1 longer subapical setula. Antenna ochreous to pale brown, with genicular articulation between pedicel and 1st flagellomere, the latter suboval and strongly laterally compressed (cf. dorsal view in Fig. 8), with pale, medium long cilia on apex. Arista relatively short (less than twice as long as antenna), inserted dorsobasally, shortly ciliate.

Thorax narrower than head; mesonotum blackish brown; pleura dorsally (pro-, meso- and pteropleuron) dark brown, sternopleuron and hypopleuron pale ochreous to yellow. Thoracic chaetotaxy as described in generic diagnosis. Not more than 4 rows of ac microsetae anteriorly (only 2 posteriorly – Fig. 8).

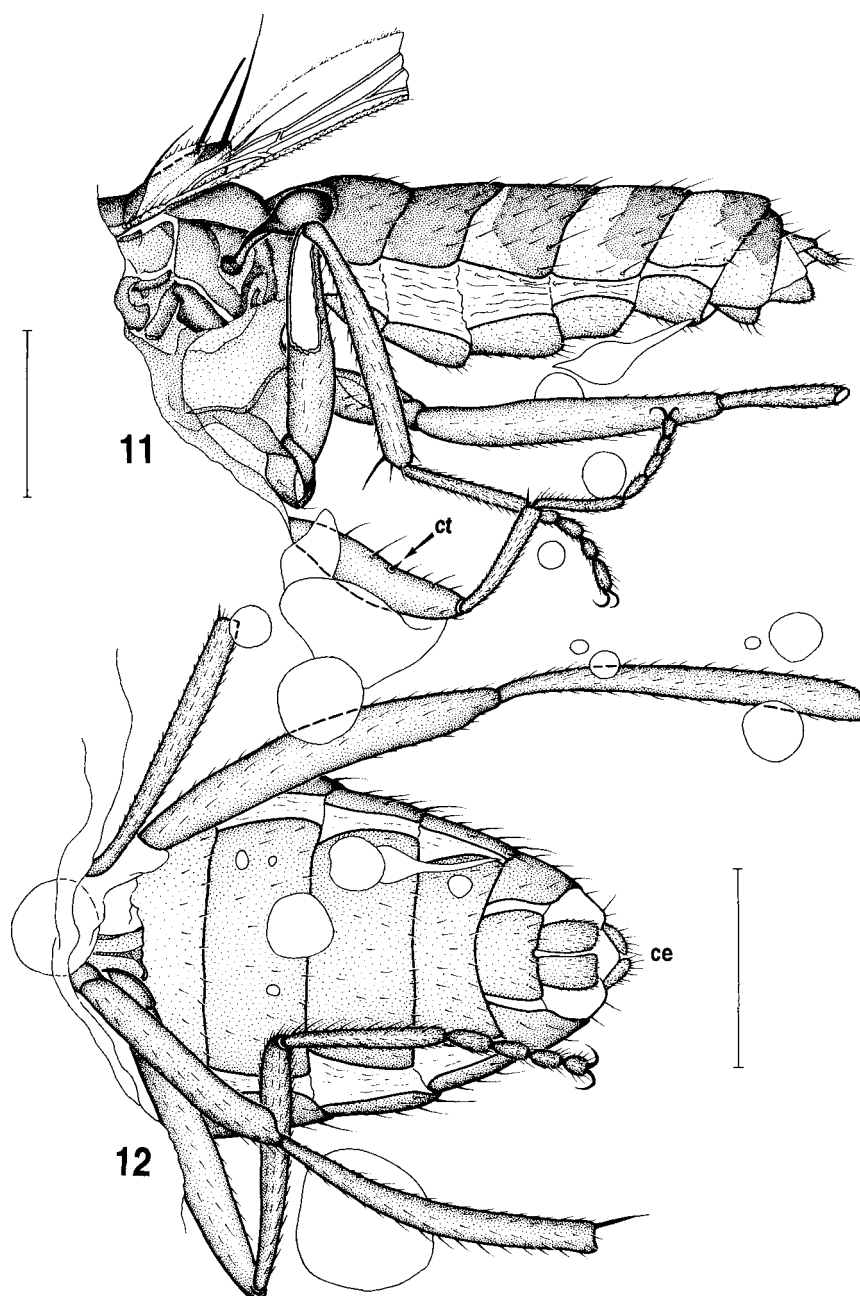
Legs slender, ochreous to yellow. f_1 with distinct but reduced ctenidial posteroventral spine (Fig. 11); t_1 with a short ventroapical seta; t_2 with usual longer ventroapical seta; f_3 and t_3 without long setae; posterior basitarsus with a ventral row of longer setulae. Tarsal claws relatively long (Figs 11, 12).



Figs 8–10. *Grimalantha vulnerata* sp. n., female holotype. 8 – head and thorax frontodorsally; 9 – ditto ventrolaterally; 10 – left wing. Scales: Fig. 10 = 0.5 mm, others = 0.3 mm.

Wing (Fig. 10) similar to that of most recent Anthomyzidae, long, narrow, with membrane hyaline, pale ochreous. Wing venation as described in generic diagnosis. R_{4+5} slightly bent and almost parallel to M. Cross-vein r-m in medium distance from wing base. Alula about twice as wide as that in Fig. 10 because folded upwards. The basal lobe near apex of A_1 (see Fig. 10) obviously is an artefact or damaged wing margin. Wing measurements: length 2.3 mm, width 0.7 mm, C-index ($Cs_3 : Cs_4$) = 1.6, $r-m \backslash dm-cu : dm-cu$ = 3.2. Haltere with pale brown stem and darker brown and large knob (Fig. 11).

Abdomen with large terga and unusually broad preabdominal sterna (Fig. 12). T1+2 and T3 dark brown, T4–T7 ochreous to yellow, each with a posterior transverse dark brown band-like spot (Fig. 11). S3–S6 (Fig. 12) pale ochreous and very broad, sparsely setulose. T7 extended on ventral side of abdomen but S7 discrete, not fused with T7 to form tergosternal sclerite. S7 pale and very shortly setulose, with a small posteromedial



Figs 11–12. *Grimalantha vulnerata* sp. n., female holotype. 11 – posterior half of thorax and abdomen laterally; 12 – abdomen and some legs ventrally. Scales = 0.3 mm.

incision. T8 and T10 not properly visible. S8 (Fig. 12) narrow, distinctly divided medially, similar to that of *Anthomyza* species. S10 poorly visible, pale. Cerci small, relatively short, each with several subequal (rather short) setulae.

DISCUSSION. *G. vulnerata* sp. n. can be easily recognized from all known anthomyzids by unusually large and broad abdominal sterna. Judging from additional differences (see under generic diagnosis) no extant species can be considered its close relative.

EXTANT GENERA

Genus *Chamaebosca* Speiser, 1903

Chamaebosca Speiser, 1903: 65. Type species: *Chamaebosca microptera* Speiser, 1903 (by monotypy).

Penquistus Kieffer, 1906: 349 syn. n. Type species: *Penquistus cursor* Kieffer, 1906 (by monotypy).

DIAGNOSIS. (1) Head longer than high. (2) Eye oval, of medium size; its longest diameter oblique. (3) Frons relatively broad (Fig. 15). (4) Ocellar triangle normal. (5) Occiput very slightly concave. (6) Antenna geniculate, 1st flagellomere rather long-oval, laterally compressed. (7) Arista dorsobasal, shortly ciliate. (8) Palpus relatively long, with several weak setulae. Cephalic chaetotaxy (Fig. 15): (9) pvt small, convergent; (10) vte, vti and oc and posterior ors subequal in length; (11) 2 ors (anterior short) and 1 microsetula in front of the anterior ors; (12) postocular setulae few and weak, in a short row; (13) 1 long vi and 1 subvibrissa well developed; (14) peristomal setulae small and sparse.

(15) Thorax substantially narrower than head (Fig. 15). Thoracic chaetotaxy (Fig. 15): (16) 1 small hu, 2 npl; (17) prs absent; (18) 1 sa; pa absent (?) or reduced; (19) 2 postsutural dc, anterior unusually long; (20) ac microsetae sparse, in 4 rows; (21) 2 usual sc; (22) 1 very minute ppl; (23) 2 stpl, only posterior long. (24) f_1 with distinct ctenidial spine (Fig. 13). (25) t_2 with normal ventroapical seta. (26) male f_3 ventrally simply setulose. (27) Wing (Fig. 16) shortened and narrowed. (28) C somewhat produced beyond apex of R_{4+5} but not reaching M. (29) Costal break at apex of Sc present, C uniformly setulose. (30) Sc fused apically with R_1 and forming a typical kink (Fig. 16). (31) R_{2+3} short, not reaching C; (32) R_{4+5} slightly divergent from M. (33) M reaching wing margin. (34) cells bm, cup, dm and vein CuA_1 absent; (35) A_1 strongly reduced; (36) alula small but well developed.

Male abdomen: (37) T1 separated from T2; (38) preabdominal terga large and wide (Fig. 15); associated sterna narrow. Postabdomen: (40) T6 absent (?); (41) S6 and S7 short, strongly asymmetrical; S8 also relatively short but slightly asymmetrical.

Male genitalia (Figs 14, 17–22): (42) epandrium without long setae (Figs 14, 22); (43) gonostylus partly (posteriorly) fused with epandrium (Figs 14, 22); (44) gonostylus without micropubescence (Fig. 17); (45) medandrium medium-sized (Fig. 14); (46) transandrium simple (without caudal process), fused with hypandrial arms (Fig. 20); (47) hypandrium (Figs 20, 21) fused with low, inconspicuous pregonites; (48) folding apparatus posteriorly with basal membrane provided with teeth (Figs 19–21), anterolaterally (aedeagal part) with flat tubercles (Fig. 19); (49) postgonite short, with 1 setula (Fig. 19); (50) phallapodeme with usual ventral fulcrum; (51) phallophore small, connected by ventral band-like sclerites with distiphallus (Fig. 19); (52) saccus of distiphallus without spines or similar armature; (53) filum of distiphallus rather compact, with a preapical projection and teeth on apex (Figs 18, 19); (54) ejacapodeme probably small (not observed).

Female unknown.

DISCUSSION. The affiliation of the genus *Chamaebosca* Speiser, 1903 with Anthomyzidae has been in much doubt up to the present (cf. J.F. McAlpine, 1989). Only the revision of its type species, *Ch. microptera* Speiser, 1903, revealed that it really belongs to the family, and that it is closely allied to the Holarctic genus *Stiphrosoma* Czerny, 1928. Moreover, the comparison of the redefined *Chamaebosca* with the original description of *Penquistus* Kieffer, 1906 resulted in finding that the latter genus is a new junior synonym of *Chamaebosca*. Both *Chamaebosca* and *Penquistus* are monotypic genera based on brachypterous species originating from Chile (*Ch. microptera* Speiser, 1903 from Valdivia, *P. cursor* Kieffer, 1906 from Penco nr. Concepcion; distance between these localities is only about 340 km). These species have both shortly ciliate arista, the same cephalic and thoracic chaetotaxy and armature of fore femur (ctenidial spine arising close to longest posteroventral seta) and similarly shortened and narrowed wings with reduced venation. Actually, the holotype of *P. cursor* has only left wing similar to that of *Chamaebosca microptera*; its right wing is much smaller and without venation – see Kieffer (1906: Fig. 1). However, these unevenly developed wings could be either a teratological monstrosity (as Kieffer, 1906: 349 suggested) or a case of wing polymorphism similar to that found in *Stiphrosoma sabulosum* (Haliday, 1837) (cf. Roháček, 1996: 101). It is even possible that *Ch. microptera* and *P. cursor* are conspecific but their synonymy cannot be demonstrated without revision of the holotype (or topotypic specimens) of *P. cursor*.

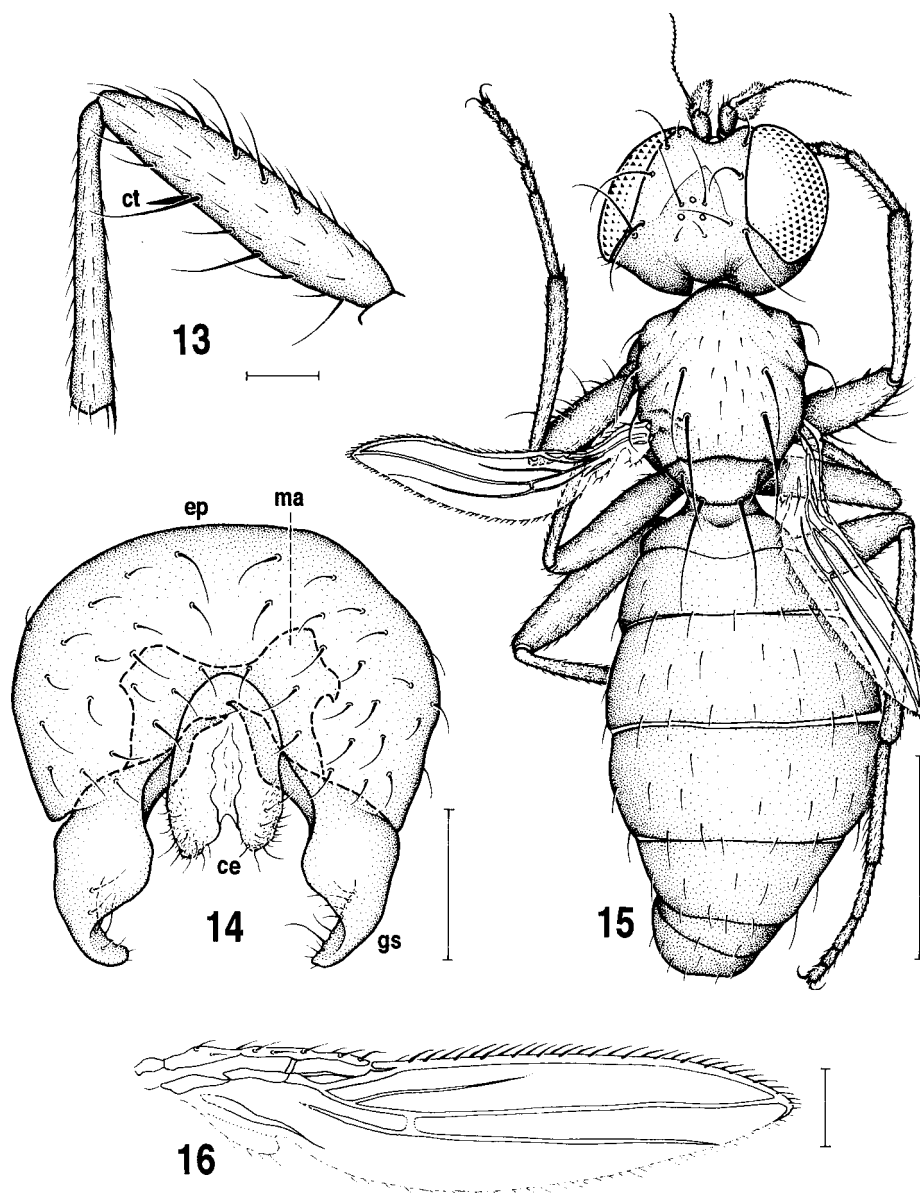
Formerly, *Penquistus* was synonymized under *Anthomyza* Fallén, 1810 (see Malloch, 1933) and this was followed also recently (e.g. Andersson, 1984). Roháček (1994), without knowing the genus *Chamaebosca*, considered *Penquistus* a distinct Neotropical genus different from *Anthomyza*.

The genus *Chamaebosca* clearly is the closest relative of the genus *Stiphrosoma*, as demonstrated by the following shared characters: 15, 17, 27, 37, 46–49, 51, 53. The structure of the male internal genitalia (features 46–49, 51, 53) is really highly similar in both genera and demonstrate, in my opinion, their sister-group relationships. Because the female of *Chamaebosca* is unknown (and female characters are very important in the diagnosis of *Stiphrosoma* – cf. Roháček, 1996: 94) and because of a number of distinct differences (see below) these genera cannot be united into a single genus for the time being. *Chamaebosca* differs from *Stiphrosoma* chiefly in having (7) short-haired arista, (8) palpus with several setulae, (26) male f_3 simply setulose ventrally, (41) shorter male S6–S8, (42) epandrium without longer setae, (43) gonostylus partly fused with epandrium and (52) saccus of distiphallus lacking spines or tubercles. Of these at least characters 41 and 43 are autapomorphic for *Chamaebosca*.

Chamaebosca microptera Speiser, 1903
(Figs 13–22)

Chamaebosca microptera Speiser, 1903: 67.

TYPE MATERIAL: Holotype ♂ labelled: “*Chamaebosca microptera* P. Speiser, Type, Berl. ent. Ztschr. 1903” (pencil writings on white label), “79, A/241/NMW, Ephydriidae, *Chamaebosca microptera*” (type-writing on white label) and “*Chamaebosca microptera* Speiser ♂, J. Roháček rev. 1996, Holotypus” (red label). The specimen originates from Chile: Valdivia (see Speiser, 1903: 67). It is very faded because originally preserved in ethanol, with tarsi of most legs lost and with a number of bristles broken off. It was dissected for this study and placed in glycerine in three plastic tubes (with wings, dissected abdomen and genitalia and with the rest of specimen). Deposited in the Naturhistorisches Museum, Wien (examined).



Figs 13–16. *Chamaebosca microptera* Speiser, male holotype. 13 – fore femur and tibia posteriorly; 14 – external genitalia caudally; 15 – specimen dorsally; 16 – right wing. Scales: Fig. 15 = 0.5 mm, others = 0.1 mm.

REDESCRIPTION. Female unknown. Male (Fig. 15). Total body length 2.1 mm. Colour characters are taken from the original description, the specimen being faded by long preservation in alcohol. General colour dark brown, only legs pale yellow and membranous pleural part of abdomen yellowish white. Head distinctly longer than high. Frons wide. Frontal triangle well discernible, darker than rest of frons and reaching anterior half of frons. Ocellar triangle normal; occiput very slightly concave behind pvt. Cephalic chaetotaxy (Fig. 15): all setae on frons relatively weak; pvt convergent but short and weak; vte, vti and oc subequal and together with posterior ors longest of cephalic setae; 2 ors (anterior about half length of posterior) and 1 microsetula in front of anterior ors on orbit; postocular setulae small, in a short row; vi and subvibrissa (the latter about half length of vi) well developed; peristomal setulae few (about 4) and weak. Eye oval, with longest diameter oblique and about 1.5 times as long as the shortest. Gena very low anteriorly (only about 0.07 times as long as shortest eye diameter) but strongly extended posteriorly. Palpus slender, relatively long, subapically somewhat dilated and bearing several weak setulae. Antenna comparatively small, geniculate between pedicel and 1st flagellomere, the latter relatively long-oval and laterally compressed; arista with enlarged basal segment, about 1.6 times as long as antenna and, like 1st flagellomere, shortly ciliate.

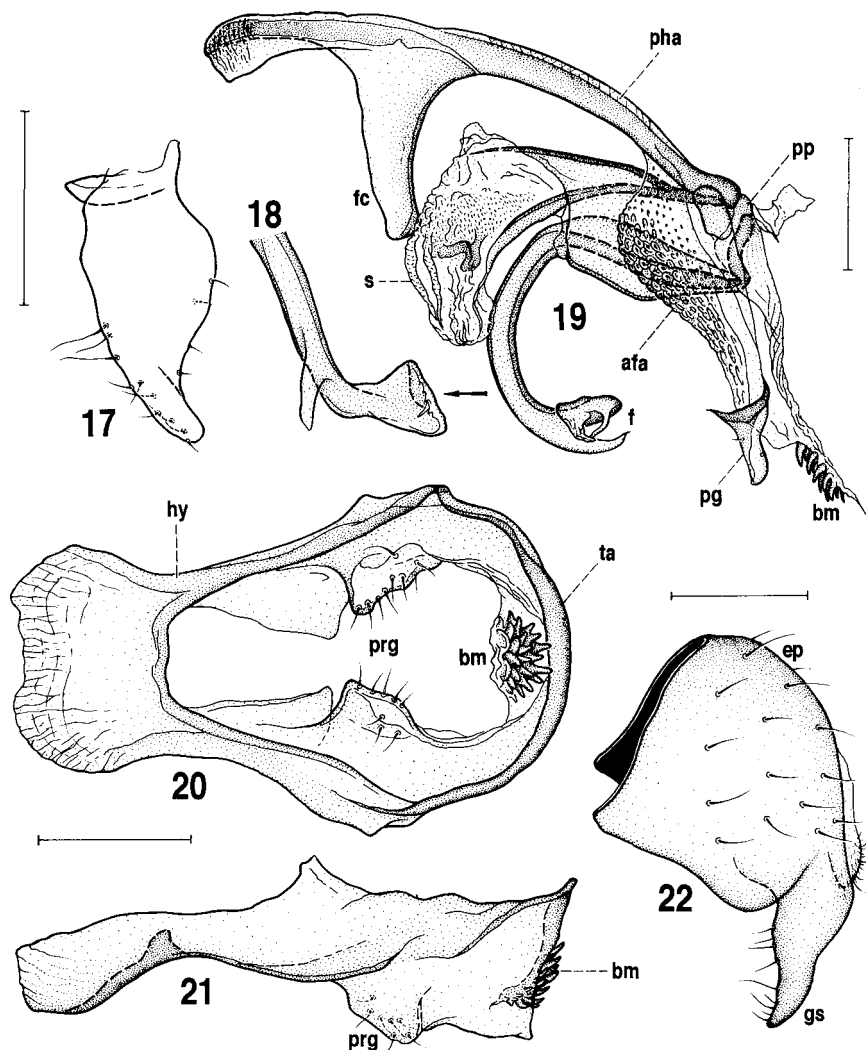
Thorax somewhat reduced, considerably narrower than head (see Fig. 15), unicolorous, brown. Thoracic chaetotaxy: 1 weak hu; no prs; 2 npl; 1 sa; no pa (reduced or broken off ?); 2 dc (both postsutural but unusually anteriorly situated), also the anterior very long, about as long as apical sc; ac microsetae very sparse, at most in 4 incomplete rows between anterior dc; 2 sc, laterobasal about one-third of apical; 2 stpl, posterior about twice as long as anterior; 1 very minute ppl. Scutellum short, rounded triangular.

Legs yellow, only femora somewhat darkened. f_1 (Fig. 13) with short but distinct ctenidial spine and a row of posteroventral and posterodorsal setae. t_1 with short, slightly curved ventroapical seta; t_2 with usual longer ventroapical seta; f_3 ventrally uniformly haired; t_3 with minute ventroapical setula; mt_3 with a row of subequal ventral setulae.

Wing (Fig. 16) reduced and narrowed, similar to that of the brachypterous form of *Stiphrosoma sabulosum* (Haliday, 1837). C thick, twice as thick as R_{4+5} and reaching somewhat beyond apex of R_{4+5} , relatively strongly setulose. Sc apically fused with R_1 and preapical kink on R_1 distinct. R_{2+3} short, not reaching C. R_{4+5} almost straight, ending near the apex of wing. M complete, slightly divergent from R_{4+5} . Cross-vein r-m preserved; discal (dm) cell, CuA_1 , cells bm and cup absent; A_1 strongly shortened. Anal lobe reduced, alula narrow but well developed. Wing measurements: length 0.90 mm, width 0.18 mm, $Cs_3 : Cs_4 = 3.20$. Haltere very reduced, short.

Abdomen. Terga large and broad, dark brown, sparsely setose, with longest setae mainly at posterior margin; T4 is the broadest tergum. T1 short, distinctly separated from T2 (Fig. 15). T6 not observed (absent or very faded and hence invisible). Preabdominal sterna (S2–S5) narrow, pale, becoming only slightly broader posteriorly. Pleural membranous part of abdomen large. S6 and S7 short, strongly asymmetrical, situated sinistrally; S8 relatively short (much shorter than in *Stiphrosoma*), slightly asymmetrical, positioned dorsally.

Genitalia. Epandrium (Figs 14, 22) relatively long, with short and weak setae. Gonostylus (Fig. 17) partly fused with epandrium (cf. Figs 14, 22), apically tapered and its apex curved inwardly. Outer side of gonostylus bare (without micropubescence); setae thin,



Figs 17–22. *Chamaebosca microptera* Speiser, male holotype. 17 – gonostylus laterocaudally (widest extension); 18 – apex of filum of distiphallus ventrally; 19 – aedeagal complex laterally; 20 – hypandrium and associated structures ventrally; 21 – ditto laterally; 22 – external genitalia laterally. Scales = 0.1 mm.

sparse and concentrated at anterior inner margin (Fig. 17). Medandrium (Fig. 14) pale, not very large, connected with dorsointernal projection of gonostylus; it is poorly visible. Hypandrial complex (Figs 20, 21) with simple transandrium (without caudal process) being fused with posterior arms of hypandrium; pregonite short, bent internally and bearing several (8–9) weak setulae; anterior inner lobes of hypandrium small and weakly sclerotized. Basal membrane (posterior part of folding apparatus connecting transandrium with

aedeagal complex) armed with a group of strong teeth (Figs 20, 21). Aedeagal complex (Fig. 19). Phallapodeme of usual shape, with robust but weakly sclerotized ventral fulcrum. Phallosphore small, poorly defined. Distiphallus with basal portion highly similar to that of *Stiphrosoma* species; saccus of distiphallus without special armature, membranous, with some microtomentum. Filum of distiphallus generally resembling that of *Stiphrosoma*, with a strong ventral preapical projection and its apex provided with several small processes and fine teeth (cf. also Fig. 18). Aedeagal part of folding apparatus (Fig. 19, afa) covered with dense flat tubercles. Postgonite (Fig. 19, pg) relatively small, simple, with posteriorly rounded apex and a minute setula at anterior margin. A ventral part of basal membrane (bent unnaturally downwards) with sclerotized teeth is also visible in Fig. 19. Ejacapodeme not observed, probably lost during preparation of the inner genitalia. Cercus (Fig. 14) rather small and shortly setulose.

DISCUSSION. As stated above, *Chamaebosca microptera* Speiser, 1903 obviously is very similar to *Penquistus cursor* Kieffer, 1906. Differences between these two taxa (based on Kieffer's very imperfect description, after elimination of apparent errors, e.g. overlooked or misinterpreted setae etc.) are small and can be summarized as follows: *P. cursor* has the right wing reduced to a minute, veinless stump (possibly teratological), body colour yellow (possibly faded) and only 1 pair of (apical) sc setae (small laterobasal pair possibly overlooked). Because the genus *Penquistus* is here synonymized under *Chamaebosca* (see above), *P. cursor* has to be treated as *Chamaebosca cursor* (Kieffer, 1906) comb. n.

The brachypterous form of *Stiphrosoma sabulosum* (Haliday, 1837) resembles *Chamaebosca microptera* but is easily distinguished by the absence of ctenidial spine on fore femur and in having distinctly pectinate arista and incomplete vein M, besides differences in the male genitalia (cf. Roháček, 1996).

Genus *Apterosepsis* Richards, 1962

Apterosepsis Richards, 1962: 466. Type species: *Apterosepsis basilewskyi* Richards, 1962 (original designation).

DIAGNOSIS. (1) Head higher than long (Fig. 23). (2) Eye not very large, with longest diameter slightly oblique. (3) Frons wide; frontal triangle long (Fig. 24). (4) Ocellar triangle not developed; ocelli very reduced (Fig. 24). (5) Occiput dorsally convex. (6) Antenna small, geniculate between pedicel and 1st flagellomere, the latter rounded and laterally compressed. (7) Arista dorsobasal, short, with short ciliation. (8) Palpus small, with 1 longer subapical setula. Cephalic chaetotaxy (Figs 23, 24, 26): (9) pvt very reduced, parallel, situated far behind posterior ocelli (Fig. 24); (10) vte half length of vti, the latter longest of cephalic setae; (11) only 1 or; (12) oc long and situated in front of anterior ocellus (Fig. 24); (13) postocular setulae reduced both in size and number, forming a short row; (14) 1 long vi and 1 subvibrissa of almost the same length; (15) only 2–3 short peristomal setulae (Fig. 23).

(16) Thorax (Figs 23, 24) reduced, considerably narrower than head. (17) Mesopleuron with elevated posterior margin (Fig. 23). Thoracic chaetotaxy (Figs 23, 24): (18) 0 hu, 1 (posterior) npl, anterior npl reduced to microsetula; (19) 0 prs; (20) 1 extremely enlarged sa, 1 ?pa reduced to microsetula; (21) 0 dc; (22) ac microsetae very sparse; (23) only 1 (apical) sc, reduced to microsetula; (24) 0 ppl; (25) 3 mspl microsetulae at posterior

margin of mesopleuron; (26) 0 stpl. (27) f_1 with distinct ctenidial spine (Fig. 25). (28) t_2 with a short ventroapical seta. (29) Wings and halteres absent.

Female abdomen: (30) T1 partly fused with T2, extremely narrowed and forming an abdominal petiole (Figs 23, 24); (31) preabdominal terga T2–T5 enlarged and strongly convex; (32) preabdominal sterna S2–S5 narrow but strongly sclerotized (Fig. 27); (33) abdominal spiracles 2–6 situated in ventrolateral margins of T2–T6 (Fig. 27).

Female postabdomen: (34) postabdomen short and relatively wide (Figs 27, 30–32); (35) T6 large and covering all following postabdominal segments; (36) T7 and S7 fused to form a complete tergosternal ring (Figs 27, 30–32); (37) T8 plate-shaped, transverse (Fig. 30); (38) S8 relatively short, medially longitudinally divided (Fig. 32); (39) internal sclerotization of female genital chamber consisting of 2 pairs of flat posterior sclerites and 1 anterior ring-shaped sclerite (Figs 31, 32); (40) ventral receptacle small, short subcylindrical (Fig. 29); (41) spermathecae (1+1) globular with distinct sclerotized cervix and several microglobuli on smooth surface (Fig. 28); (42) T10 short, transverse, with 1 pair of posteromedial setae (Fig. 30); (43) S10 simple, not wider but considerably longer than T10 (Figs 31, 32); (44) cerci short, laterally compressed, with rich but short setulae (Fig. 31).

Male unknown.

DISCUSSION. The position of the apterous, ant-mimicking, acalyprate genus *Apterosepsis* Richards, 1962 has been uncertain up to the present. It was originally placed in the Sepsidae (Richards, 1962), later in the Anthomyzidae (D.K. McAlpine, 1978) and Chloropidae (Sabrosky, 1980). Unfortunately, only two females of this peculiar species are known. I examined the paratype and found many characters very unusual for Anthomyzidae. Only the examination of the postabdominal structures convinced me that it really belongs to this family as D.K. McAlpine (1978, 1990) suggested.

Apparently, the majority of morphological peculiarities of *Apterosepsis* are due to its terricolous habits [e.g. loss of wings and halteres, minute ocelli, reduced thorax (owing to minimization of wing muscles), loss or reduction of cephalic (pvt, postocular and peristomal setae) and, particularly, thoracic (hu, npl, pa, dc, sc, ppl, stpl) setae, heavy body sclerotization (including abdominal sterna)] and/or due to the adaptation to ant-mimicry (e.g. abdominal petiole formed by constricted 1st segment or strikingly dilated abdomen). All these characters are highly adaptive and hence can hardly be used for an evaluation of the relationships of the genus.

On the contrary, the general structure and chaetotaxy of the head (although only 1 ors), form of antenna and palpus (6, 7, 8), presence of the ctenidial spine (27) on f_1 (hitherto unknown in Afrotropical Anthomyzidae!), annular 7th abdominal tergosternum (36), shape of S8 (38), internal sclerotization of female genital chamber (39) or shape of ventral receptacle (40) showed the real affinity of *Apterosepsis* to modern Anthomyzidae.

However, there are several conspicuous features requiring special comment: (25) 3 microsetulae at posterior ridge-like margin of mesopleuron might represent a remnant of true mesopleural setae, known in Anthomyzidae only in the fossil *Protanthomyza*. Microtomentose ventral portion of pleura (see redescription of *A. basilewskyi* below) is reminiscent of that of Sepsidae but probably it is only a restriction of the originally more extensive (covering entire pleura) microtomentose area – a similar (but greater) reduction of microtomentum occurs in *Paranthomyza* Czerny, 1902. The enormous sa seta (20) really is a unique feature in the family and its purpose is difficult to interpret. Abdominal

spiracles 2–6 embedded in tergal margins (33) – this character has not been found in Anthomyzidae or Opomyzidae until now but was considered a synapomorphy of Teratomyzidae, Xenasteiidae and Asteiidae by J.F. McAlpine (1989). The condition found in *Apterosepsis* certainly does not demonstrate its relationships to the above group of families but was plausibly caused by the secondary extension of terga in consequence of the ant-mimicry.

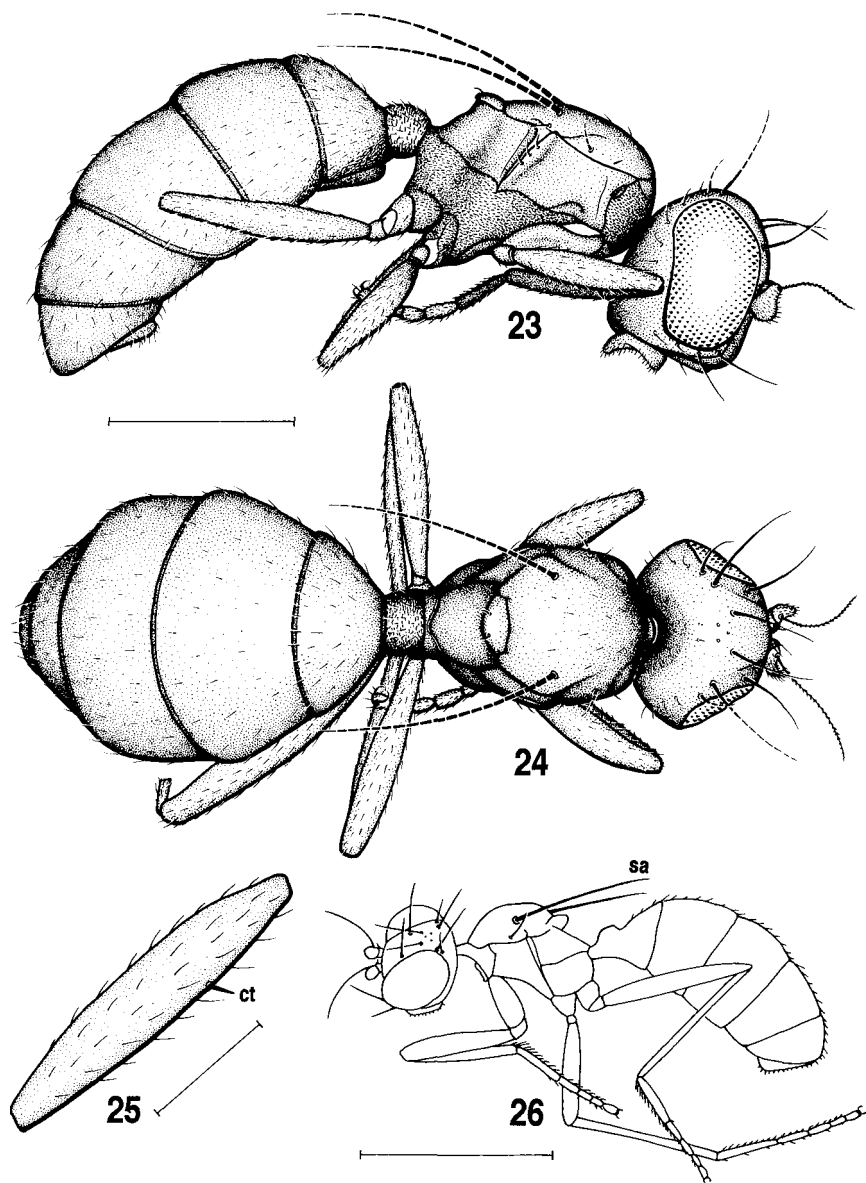
Apterosepsis basilewskyi Richards, 1962
(Figs 23–32)

Apterosepsis basilewskyi Richards, 1962: 467.

TYPE MATERIAL: Holotype ♀ (not examined), Mt. Meru, Olkokola, N.W. Slope, 2,750 m, tête de source de la Latia, 30.vi.1957 (in alcohol; deposited in the Musée Royal de l'Afrique Centrale, Tervuren, Belgium). Paratype ♀ labelled: "Para-type" (circular label with yellow margin), "tête de source de la Latia" (pale blue label), "Coll. Mus. Congo, Tanganyika Terr.: Mt Meru, Olkokola, versant N.O., 2750 m, 30-VI-1957", "Mission Zoolog. I.R.S.A.C. en Afrique orientale (P. Basilewsky et N. Leleup)", "*Apterosepsis basilewskyi* ♀ paratype Rich." (handwritten by O.W. Richards). The paratype is gummed on a small card; it has some legs or their parts broken off; genit. prep.; deposited in The Natural History Museum, London (examined).

REDESCRIPTION. Male unknown. Female apterous, of ant-like appearance (Figs 23, 24). Total body length 2.1 mm; general colour dark brown and shining, only legs yellow. Head distinctly higher than long, much broader than thorax, brown. Frons unusually wide (Fig. 24). Frontal triangle long and shining, almost reaching anterior margin of frons, separated from glabrous orbits by finely striated and somewhat microtomentose stripes. Ocellar triangle not developed, ocelli reduced and very minute (Fig. 24). Occiput dorsally convex, somewhat concave only around occipital foramen. Cephalic chaetotaxy (Figs 23, 24): pvt reduced to minute, pale, parallel setulae situated far behind posterior ocelli; vte only half length of long vti; oc situated unusually anteriorly, slightly in front of anterior ocellus and far from each other; only 1 or about as long as oc; a few microsetulae at anterior margin of frons above antennae; several minute and pale postocular setulae dorsally behind eye; 1 long vi and 1 subvibrissa of almost the same length; only 2–3 short peristomal setulae. Palpus reduced, with 1 longer subapical setula. Face (prefrons) sclerotized and medially somewhat convex, only lateroventrally shining, medially and dorsally somewhat microtomentose. Eye oval, its longest (slightly oblique) diameter about 1.7 times as long as the shortest. Gena very narrow, its shortest height only 0.05 times as long as longest eye diameter. Frontal lunule not observed. Antenna small (Fig. 23), slightly but distinctly geniculate between pedicel and 1st flagellomere. Scape very minute; pedicel dorsally distinctly incised; 1st flagellomere rounded, laterally compressed, with long apical cilia. Arista about 2.05 times as long as antenna, arising dorsobasally, with shorter cilia than those on 1st flagellomere.

Thorax reduced, narrow. Mesonotum, metanotum and dorsal half of pleuron shiny; propleuron, sternopleuron and hypopleuron densely grey microtomentose (Fig. 23). Postpronotal lobe (humeral callus) strongly reduced; mesopleuron with posterior margin produced, keel-like. Thoracic chaetotaxy (see Figs 23, 24): 0 hu; 1 (posterior) npl and 1 anterior npl microseta; 1 pa microseta; 1 extremely robust and long sa; 0 dc, only several scattered pale microsetae in ac, dc and intra-alar rows; only 1 minute and pale apical sc; a short row of 3 pale microsetae on posterior elevated margin of mesopleuron; 0 stpl; 0 ppl.



Figs 23–26. *Apterosepsis basilewskyi* Richards, female paratype. 23 – specimen laterally; 24 – ditto dorsally (both with some setae reconstructed); 25 – fore femur posteriorly; 26 – holotype laterally (after Richards, 1962). Scales: Figs 23, 24 = 0.5 mm, Fig. 25 = 0.2 mm, Fig. 26 = 1.0 mm.

Legs yellow to ochreous, only mid coxa, t_1 and mt_1 brown, the latter contrasting with whitish yellow rest of fore tarsus. f_1 (Fig. 25) with distinct ctenidial spine but without any other long setae; t_2 with 1 short, somewhat curved ventroapical seta; rest of legs uniformly shortly setulose, only mid coxa with a few longer hair-like setae. Wings and halteres absent.

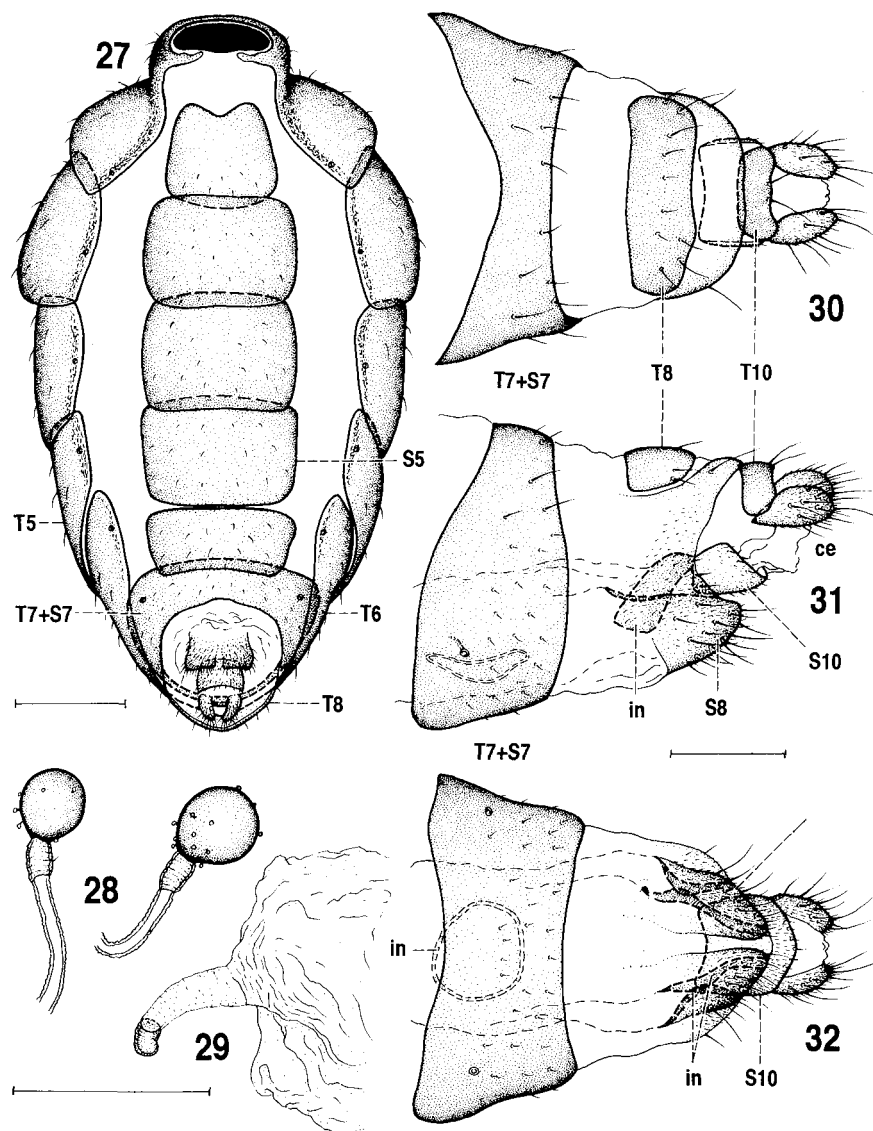
Abdomen highly distinctive (Figs 23, 24, 27), strongly constricted basally, forming (T1) a narrow petiole, dilated and very convex in the middle. Preabdominal terga large and extended laterally, dark brown, shining, with sparse pale setulae. T1–T6 with finely wrinkled lateral margins; T1 with the same microsculpture also dorsally. T3–T5 are the largest abdominal sclerites. Spiracles 2–6 embedded in lateral margins of T2–T6 (Fig. 27). Preabdominal sterna narrow, dark brown, glabrous and unusually strongly sclerotized (like preabdominal terga), S3 and S4 being the widest.

Postabdomen small, short, completely hidden under large T6 (Fig. 27). T7 and S7 forming a complete ring-shaped tergosternum being shortest dorsomedially (Fig. 30), longest laterally (Fig. 31). T8 short, transverse, relatively dark, sparsely setulose. Pleural part of 8th segment distinctly sclerotized, particularly dorsolaterally behind posterior corners of T8 (Fig. 31). S8 relatively short, medially longitudinally divided, with poorly defined anterior margin and rich setae and micropubescence (Figs 27, 32). Internal sclerotization of female genital chamber formed by 2 pairs of posterior sclerites (both attached to posterior margin of S8) and 1 anterior ring-shaped sclerite on ventral wall of vagina (Figs 31, 32). Anterior part of uterus (Fig. 29) with small subcylindrical (apically rounded) ventral receptacle resembling that of *Stiphrosoma* species (cf. Roháček, 1996: Fig. 34) on a broad short duct. Spermathecae 1+1 (Fig. 28), medium-sized, globular, with distinct (although less sclerotized) cervix and several stalked microglobuli on surface. T10 small, transverse (Fig. 30), with a pair of posteromedial setae. S10 more than twice as long as T10, pale, covered by fine micropubescence. Cerci short (Figs 30, 31), somewhat laterally compressed, with numerous, although rather short and fine setae.

DISCUSSION. This species superficially resembles a small shiny ant. It is characterized by some extraordinary features previously unknown in the family Anthomyzidae (see generic diagnosis). *Apterosepsis basilewskyi*, together with recently described Afrotropical species of the genera *Amnonthomyza* Roháček, 1993 and *Barbarista* Roháček, 1993, demonstrate an unexpected morphological diversity of the family being formerly considered a rather uniform group of acalyprate Diptera.

Other extant genera

More than ten years ago, when I began to work on the Palaearctic genera of Anthomyzidae, I found that some were not monophyletic, e.g. *Anthomyza* Fallén, 1810. To gain a better homogeneity of that particular genus it was necessary to transfer some species into two new genera, *Santhomyza* Roháček, 1984 and *Typhamyza* Roháček, 1992, and others to the genus *Stiphrosoma* Czerny, 1928 whose limits were considerably extended (Roháček 1996). Similarly, *Cercagnota* Roháček & Freidberg, 1993 was established to accommodate a species from the genus *Anagnota* Becker, 1902. Two remarkable Afrotropical genera, *Barbarista* and *Amnonthomyza* were recently discovered (Roháček, 1993) as a result of the revision of *Amygdalops* Lamb, 1914. My studies on the extant genera can be summarized as follows.



Figs 27–32. *Apterosepsis basilewskyi* Richards, female paratype. 27 – abdomen ventrally; 28 – spermathecae; 29 – ventral receptacle laterally; 30 – postabdomen (without 6th segment) dorsally; 31 – ditto laterally; 32 – ditto ventrally. Scales: Fig. 27 = 0.2 mm, others = 0.1 mm.

(1) All 14 described genera are undoubtedly related and form, together with the fossil *Grimalantha* gen. n., a monophyletic group (see below). These are: *Amnothomyza* Roháček, 1993 (Madagascan), *Amygdalops* Lamb, 1914 (circumtropical to subtropical), *Anagnota* Becker, 1902 (Palearctic), *Anthomyza* Fallén, 1810 (Holarctic, ?Oriental), *Apterosepsis* Richards, 1962 (Afrotropical), *Barbarista* Roháček, 1993 (Afrotropical), *Cercagnota* Roháček & Freidberg, 1993 (Palearctic), *Chamaebosca* Speiser, 1903 (= *Penquistus* Kieffer, 1906) (Neotropical), *Ischnomyia* Loew, 1863 (Nearctic), *Mumetopia* Melander, 1913 (New World), *Paranthomyza* Czerny, 1902 (Palearctic), *Santhomyza* Roháček, 1984 (southern Palearctic), *Stiphrosoma* Czerny, 1928 (Holarctic) and *Typhamyza* Roháček, 1992 (Palearctic).

(2) Besides the described taxa (see Appendix 1) I have examined numerous (about 40) unnamed species partly belonging to known genera, partly to 4–5 undescribed (mostly Afrotropical) genera. However, all these taxa are definitely allied to genera discussed above and belong to the same monophyletic group.

ECHIDNOCEPHALODES EXCLUDED FROM THE ANTHOMYZIDAE

The genus *Echidnocephalodes* Sabrosky, 1980 (new name for the preoccupied name *Echidnocephalus* Lamb, 1914) was tentatively included in Anthomyzidae by Hennig (1971, 1973), Sabrosky (1980) and J.F. McAlpine (1989) although it was originally described in Asteiidae. Recently, Roháček (1994) proposed to exclude it from the family Anthomyzidae. To support this action, it is necessary to redescribe the genus in detail and discuss its affinities on the basis of the whole set of characters including those from the male and female postabdominal structures which is done below.

Genus *Echidnocephalodes* Sabrosky, 1980

Echidnocephalus Lamb, 1914: 351. Type species: *Echidnocephalus barbatus* Lamb, 1914 (original designation). [Preocc. by *Echidnocephalus* Mark, 1858 (see Sabrosky, 1980: 650).]

Echidnocephalodes Sabrosky, 1980: 650 (nom. n.).

DIAGNOSIS. (1) Head broad, dorsoventrally flattened, longer than high. (2) Eye elongately oval and strongly bulging laterally, sparsely pilose. (3) Frons narrow compared to broad occiput. (4) Ocellar triangle normal, ocelli relatively large. (5) Occiput deeply excavated. (6) Antenna somewhat geniculate between pedicel and 1st flagellomere, the latter laterally compressed; pedicel slightly cap-like. (7) Arista dorsobasal, entirely bare. (8) Palpus extremely slender, finely haired. (9) Mouth cavity very large. Cephalic chaetotaxy (Lamb, 1914: Pl. 21, Figs 41–43): (10) pvt minute, divergent; (11) vte, vti and oc long, subequal; (12) 1 inclinate occe present; (13) 3 reclinate ors becoming somewhat shorter anteriorly; (14) postocular setulae numerous, particularly ventrally; (15) vi well developed, 1 distinct subvibrissa; (16) peristomal setae very long.

(17) Thorax considerably narrower than head. Thoracic chaetotaxy: (18) 1 small hu, 2 npl (posterior longer); (19) 0 prs, 1 long sa, inserted unusually anteriorly and dorsally; (20) 2 pa, posterior reduced to microseta; (21) 2 long and 1 short dc (all postsutural); (22) ac microsetae in 1–2 short, anterior rows; (23) 2 sc, apical long, laterobasal short; (24) 0 ppl; (25) mesopleuron bare; (26) 1 distinct pteropleural (anepimeral) seta; (27) 2 short stpl. (28) Subscutellum strikingly projecting posteriorly. (29) f_1 without ctenidial spine. (30) t_2 with normal ventroapical seta. (31) f_3 with a strong dorsal preapical seta. (32) Wing long

and very narrow (Lamb, 1914: Fig. 34). (33) C only attenuated in front of apex of R_1 , without spinulae, ending at apex of M. (34) Sc apically vanishing, not reaching R_1 or C; R_1 without preapical kink. (35) R_{2+3} long, parallel with C, terminated near apex of wing; (36) R_{4+5} almost straight, M slightly sinuate. (37) Cell dm very short and narrow; (38) cell bm coalesced with dm. (39) CuA_1 almost reaching wing margin. (40) Cell cup narrowed and open distally, A_1 reduced to a minute process. (41) Alula extremely narrow.

Male abdomen: (42) T1 separated from T2; (43) preabdominal terga dark, large and wide; associated sterna pale, relatively broad. Male postabdomen (Figs 33, 34): (44) T6 present and large; (45) S6 similar to S5, simple and large; (46) pregenital sclerite (probably syntergosternum 7+8) symmetrical, large; (47) abdominal sclerites 2–6 in pleural membrane, spiracle 7 in syntergosternum 7+8 (Fig. 33).

Male genitalia: (48) epandrium simple, uniformly setose (Figs 33–34); (49) gonostylus not developed; (50) medandrium absent; (51) hypandrium open posteriorly, without transandrium (Figs 35–36) and its lateral arms connected with dorsobasal projections of phallapodeme; (52) pregonite enlarged, projecting posteriorly and obviously substituting the lost gonostylus; (53) no folding apparatus developed; (54) postgonite slender, inserted between base of phallapodeme and arm of hypandrium; (55) phallapodeme plate-shaped, posteriorly expanded and forming dorsal processes being fused with hypandrial arms; (56) aedeagus simple and mostly membranous; phallopore poorly defined; (57) distiphallus simple, with 2 inner rod-like sclerites and its surface densely spinose, only apical gland bare; (58) ejacapodeme very small; (59) cercus weakly sclerotized, with rich setosity.

Female abdomen: (60) preabdominal terga broader and more transverse than in male, sterna narrower and pale; (61) spiracles 2–7 in pleural membrane.

Female postabdomen (Figs 39–41): (62) T7 normal, narrower than T6; S7 also similar to S6 but slightly narrower; (63) T8 reduced to a weakly sclerotized, transverse band; (64) 8th segment with membranous ovipositor; (65) no internal sclerites in genital chamber; (66) no ventral receptacle; (67) spermathecae (1+1) reduced or (?) absent; (68) T10 bare and fused with cerci; (69) S10 small, narrow, with projecting anterior corners; (70) cercus short but robust, with short setae.

DISCUSSION. The genus *Echidnocephalodes* Sabrosky, 1980 combines a number of plesiomorphic (in the framework of Opomyzoidea) and highly derived features. The formation of its postabdominal structures definitely excludes it from the Anthomyzidae or Opomyzidae (cf. characters 45–47, 49–53, 55–57, 63–69). Moreover, there are numerous considerable differences also on the head (1, 2, 7, 10, 12, 16), thorax (20, 24, 26, 28), legs (31) and wing (34, 37, 38, 40) which also preclude its placement in the Anthomyzidae. Apparently, many superficial similarities of *Echidnocephalodes* to Anthomyzidae (or to some of its genera), e.g. 3 ors, long flattened head with excavated occiput, geniculate antenna, mesonotal chaetotaxy, narrow elongate wings with reduced anal lobe and alula, long R_{2+3} and M) are either plesiomorphic groundplan characters of Opomyzoidea, or evolved in consequence of convergence and/or parallelism (e.g. shape of head, antenna, wing). It is beyond doubt that *Echidnocephalodes* is a member of Opomyzoidea sensu J.F. McAlpine (1989) but its relatives should be sought among families of the subgroup 1 of his suprafamily Asteioinea.

In my opinion, *Echidnocephalodes* is most closely allied to Periscelididae and Aulaci-gastridae. Unfortunately, concept and taxonomic limits of both these families are unstable

and differently treated even by recent authors (J.F. McAlpine, 1989; Colless & D.K. McAlpine, 1991; Baptista & Mathis, 1994).

Even the most recent definition of Periscelididae by Baptista & Mathis (1994) is poorly substantiated by only two very weak synapomorphies (cap-like pedicel, venal fold in cell dm). It is to be noted that the capiform pedicel probably is a homoplasy widely distributed also in Neurochaetidae, Neminidae and even in certain genera (e.g. *Anagnota* Becker, 1902; *Cercagnota* Roháček & Freidberg, 1993) of the more distantly related Anthomyzidae.

Echidnocephalodes possesses a mixture of features which resemble those of different genera of the Aulacigastridae and Periscelididae. Its symmetrical male postabdomen (syntergosternum 7+8) resembles that of Periscelidinae (true Periscelididae) and *Aulacigaster* Macquart, 1835, large T6 and phallapodeme fused with hypandrium those of Periscelidinae. Consequently, it seems to be more related to this group of genera than to those with asymmetrical postabdomen and placed in the subfamily Stenomicrinae (or family Stenomicridae), although the wing venation of *Echidnocephalodes* resembles most that of certain species of *Stenomicra* Coquillett, 1900 (cf. characters 34–41). General structure of the female postabdomen is similar to that of *Aulacigaster*; dorsal preapical seta on f_3 to that in the genus *Planinasus* Cresson, 1914 (placed in Periscelididae by Baptista & Mathis, 1994); large mouth cavity and enlarged peristomal setae to Periscelidinae, etc. On the other hand, *Echidnocephalodes* has several characters unique within the whole Opo-myzoidea or at least Asteioinea, e.g. completely bare arista, well developed inclinate occe, gonostylus and medandrium absent, female T8 strongly reduced, ventral receptacle undeveloped and spermathecae practically absent.

The association of the *Echidnocephalodes* with Periscelididae or Aulacigastridae would considerably increase their morphological diversity. However, the classification of both the families seems far from definitive. Although I am not familiar enough with these (predominantly exotic) groups, the placement of the family Stenomicridae (having a quite different type of the male postabdomen and hypopygium than other Periscelididae and Aulacigastridae) as a subfamily under Periscelididae (cf. Baptista & Mathis, 1994) seems to me rather unnatural. Characters hitherto used to diagnose Periscelididae and allies appear to be overvalued and often a subject of homoplasy. Characters of the male and female terminalia of all genera of these groups need to be examined and used in phylogenetic considerations (they are often based on complex structures and, consequently, of high phylogenetic significance).

Echidnocephalodes barbatus (Lamb, 1914)

(Figs 33–42)

Echidnocephalus barbatus Lamb, 1914: 352.

Echidnocephalodes barbatus: Sabrosky, 1980: 650 (catalogue).

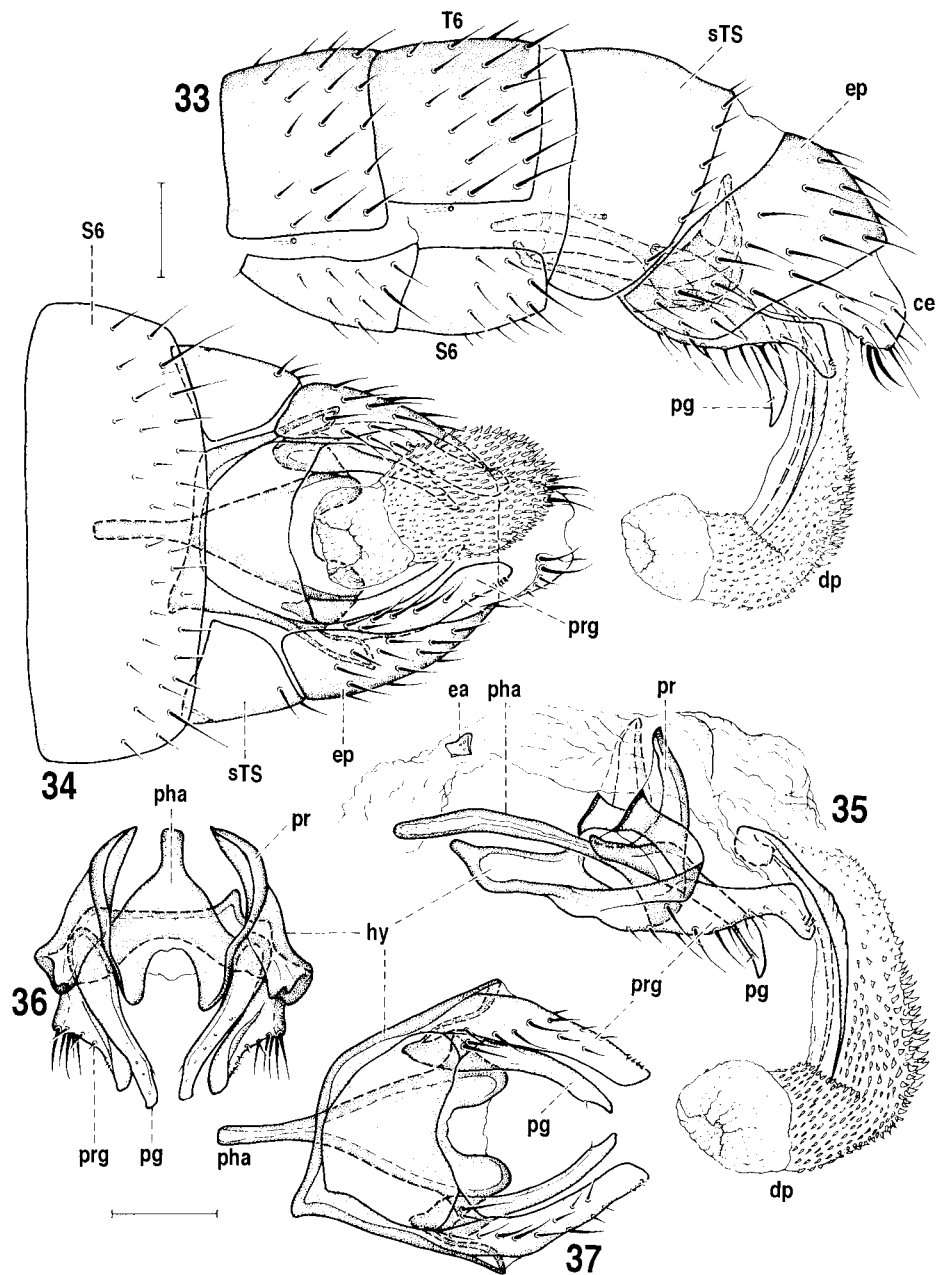
TYPE MATERIAL: Lectotype ♀ (designated herewith) labelled: "Felicite, '08. Seychelles Exp.", "Seychelles Is., Prof. J.S. Gardiner 1914-537", "Type H.T." (circular label with red margin), "Type (blue) barbata. CGL", "Lectotypus ♀, *Echidnocephalus barbatus* Lamb, J. Roháček des. 1996" (red label). Paralectotype ♀ labelled: "Mahe '08-9, Seychelles Exp.", "Seychelles Is. Prof. J.S. Gardiner 1914-537", "Paratype (blue) barbata. CGL", "Paralectotypus ♀, *Echidnocephalus barbatus* Lamb, J. Roháček des. 1996", both type specimens labelled "*Echidnocephalodes barbatus* (Lamb) ♀, J. Roháček det. 1996" and deposited in The Natural History Museum, London (examined). Paralectotype with genit. prep.

OTHER SPECIMENS EXAMINED: Madagascar S: 10 km North Fort Dauphin, 4♂, 18.iv.1991; Madagascar NW: Nosy Be, Beach Ambatoloaka, 2♂ 1♀, 4, 7.iv.1991, A. Freidberg & Fini Kaplan leg. (1♂ 1♀ with genit prep.; deposited in the Zoological Museum of the Tel Aviv University, Tel Aviv and [2♂] in the Slezské zemské muzeum, Opava); Madagascar: Maroantsetra, 1♀, 18–26.x.1987, SFMcE. JRD.SA leg. (deposited in The Australian Museum, Sydney).

REDESCRIPTION. Male. Total body length 2.10–2.27 mm; general colour pale brown, orange and yellow. Head brownish orange, twice as broad as long and strongly dorsoventrally flattened, with deeply excavated occiput (cf. Lamb, 1914: Pl. 21, Fig. 41; Hennig, 1971: Fig. 107). Frons narrow, only about half of the occiput width. Frontal triangle poorly delimited, reaching anterior half of frons, paler ochreous than rest of frons. Ocellar triangle brownish, ocelli relatively large. Frontal lunule reduced, hardly visible. Cephalic chaetotaxy (cf. Lamb, 1914: Pl. 21, Figs 41–43; Hennig, 1971: Figs 107, 108): pvt minute, divergent; vte and vti subequal, long; convergent occe about half length of vte inserted just behind the latter; oc as long as vti, subparallel or slightly divergent; 3 ors, all reclinate and becoming shorter anteriorly, the hindmost ors as long as vti; a pair of minute parallel setae situated above antennal bases; postocular setulae numerous, shorter dorsally, longer and more numerous ventrally; vi well developed, inclinate; a row of 4–6 unusually long peristomal setae (each three-fourths of vi length), the foremost (subvibrissa) being dark as vi, others strikingly pale; postgena and lateroventral portion of occiput with a group of longer setulae. Face ochreous, very low (broader than high), concave. Gena shifted on ventral side of head owing to strongly convex eyes, anteriorly very narrow, posteriorly expanded, i.e. almost triangular. Mouth cavity extremely wide. Palpus very slender, yellow, with fine hairs along its entire length. Eye elongately oval and produced laterally; its longest diameter about 1.68–1.83 times as long as the shortest. Eye surface not bare as Lamb (1914) described but sparsely finely pilose. Antenna small, orange-ochreous. Scape reduced, pedicel small but slightly cap-like (with dorsal cleft reduced); 1st flagellomere laterally compressed, directed ventrally and densely pale ciliate on apex. Arista about 2.27 times as long as antenna, completely bare.

Thorax considerably narrower than head. Mesonotum and scutellum orange to pale brown, sometimes with a darker wide stripe between dc rows and extended also on entire scutellum. Pleura yellowish white except for dark brown stripe running across anterior spiracle and dorsal margin of mesopleuron and pteropleuron to base of haltere. Thoracic chaetotaxy: 1 small hu; 2 npl (posterior longer); 1 long sa situated more anteriorly and more dorsally than usual; 2 pa but posterior reduced to microseta; 2 long and 1 short post-sutural dc and a row of dc setulae in front of suture; ac microsetae in only anterior third of mesonotum forming 1 medial row posteriorly and 2–3 rows anteriorly; 2 sc, basal weak, apical as long as hindmost dc; 0 ppl; 2 short, subequal stpl and 1 setula under the anterior stpl in addition; 1 distinct pteropleural seta. Scutellum distinctly triangular. Subscutellum (postnotal mediotergite) protruding posteriorly, more pointed than scutellum; stripe separating scutellum and subscutellum whitish yellow.

Legs yellow. f_1 with posterodorsal and posteroventral row of long setae, the latter being longer; t_1 uniformly shortly haired; f_2 with a posteroventral row of longer setae in proximal three-fifths; t_2 with usual ventroapical seta. f_3 with a similar row of posteroventral setae as on f_2 and with a strong dorsal preapical seta in addition; t_3 with a short ventroapical setula. All tarsi relatively short; all basitarsi about as long as the rest of relevant tarsus.



Figs 33–37. *Echidnocephalodes barbatus* (Lamb), male, Madagascar. 33 – end of male abdomen laterally; 34 – postabdomen ventrally; 35 – internal genitalia laterally (right pregonite and postgonite omitted); 36 – internal genitalia dorsocaudally (aedeagus removed); 37 – ditto ventrally. Scales = 0.1 mm.

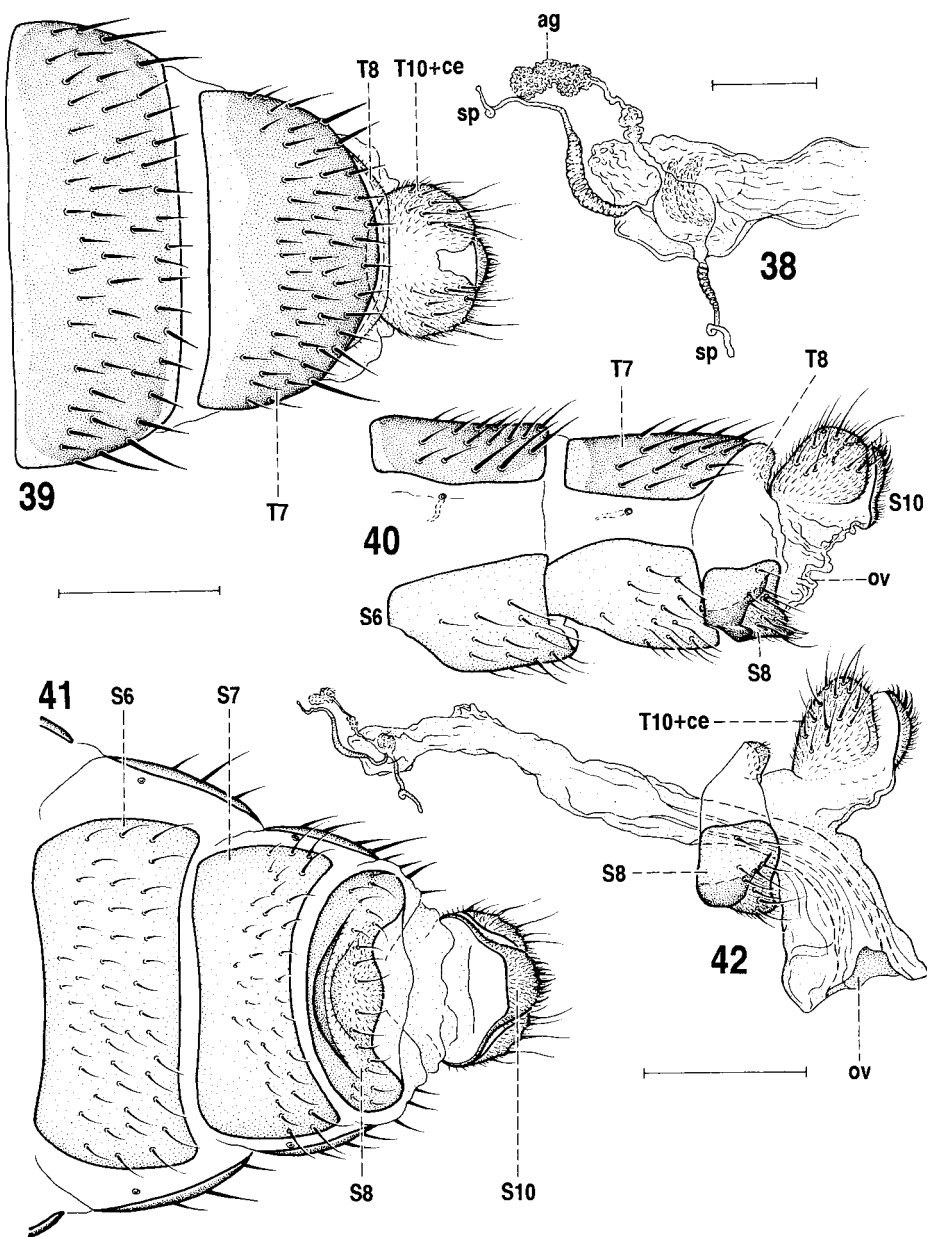
Wing (see Lamb, 1914: Fig. 34; Hennig, 1971: Fig. 106) distinctive, very narrow, with brownish membrane, particularly darkened at anterior margin. C only attenuated in front of apex of R_1 (without distinct costagial break), running to apex of M and uniformly setulose. Sc incomplete, vanishing in apical two-thirds of costal cell; R_1 short, without preapical kink; R_{2+3} very long, bent parallel to C and ending close to apex of wing; R_{4+5} almost straight or indistinctly bent, terminating in apex of wing; M long, basally somewhat divergent, apically slightly convergent to R_{4+5} . Cell dm very short and narrow, coalesced with cell bm (only a minute projection of cross-vein bm-cu is present) and with indistinct longitudinal fold. CuA_1 almost reaching wing margin. Anal (cup) cell much narrowed and open; A_1 reduced to a minute process. Alula very narrow but its margin long-haired; anal lobe strongly reduced. Wing measurements: length 2.02–2.15 mm, width 0.63–0.68 mm, $Cs_3 : Cs_4 = 0.66–0.85$, $r-m \backslash dm-cu : dm-cu = 3.33–4.60$. Haltere pale brown, with large knob being darker than stem.

Abdomen. Terga brown to dark brown, with short, dark setae. Sterna ochreous to yellowish ochreous, with finer setosity. T1 separated from T2. T2–T6 subequal in length, becoming narrower posteriorly. Preabdominal sterna (S2–S5) relatively broad, S2 narrowest, S5 broadest. T6 well developed, similar to but narrower than T5. S6 also similar to preceding sternum, only slightly narrower than T6. Pregenital sclerite (termed syntergosternum 7+8) wholly symmetrical. Abdominal spiracles 2–6 lying in membrane below lateral margins of relevant terga, spiracle 7 situated in syntergosternum 7+8 (see Figs 33, 34).

Genitalia highly characteristic (Figs 33–37). Epandrium simply arch-shaped and uniformly setose (Figs 33–34). Medandrium and gonostylus absent, the latter substituted by posteriorly projecting pregonite. Cercus pale, weakly sclerotized, with 2–3 thicker and curved ventral setae besides fine setosity. Internal genitalia (Figs 35–37). Hypandrium (Figs 35, 36) posteriorly open (without transandrium), slightly asymmetrical, with projecting right anterior corner. Basally it is firmly connected (via arched sclerites) with dorsobasal projections of phallapodeme. Pregonite arising from posterior arm of hypandrium, unusually large and projecting posteriorly, setose ventrally, with shoe-shaped apex (see Fig. 35). Postgonite simple, slender, apically pointed, inserted between base of phallapodeme and hypandrial arm (see Figs 36, 37). Phallapodeme forming an anteriorly projecting plate (anteriorly rod-like, see Fig. 37), posteriorly broadened and complex, with robust ventral and, particularly, dorsal subtriangular processes (Figs 35, 36) which are firmly fused with hypandrial arms. Aedeagus (Fig. 35) rather simple, with membranous and poorly delimited phallosophore; distiphallus supported by paired inner rod-like sclerite, densely spinose on entire surface except for apical gland. Basal part of aedeagus running between dorsal processes of phallapodeme (forming an aedeagal guide). Ejacapodeme very small and short (Fig. 35).

Female similar to male unless mentioned otherwise. Total body length 2.18–2.42 mm. Wing measurements: length 2.10–2.38 mm, width 0.67–0.70 mm, $Cs_3 : Cs_4 = 0.73–0.79$, $r-m \backslash dm-cu : dm-cu = 3.50–4.11$. Abdomen broader than in male; terga more transverse. Sterna narrow compared to associated terga. Spiracles 2–7 in pleural membrane near lateral margins of terga.

Postabdomen (Figs 39–42). T6 simple, dark, densely shortly setose, similar to T5. S6 relatively broad, pale and weakly sclerotized, finely setose. T7 longer and narrower than T6, semicircular, with pale anterior margin, similarly setose as is T6. S7 resembling S6 but narrower, shorter and posteriorly shallowly emarginate (Fig. 41). T8 (Figs 39, 40)



Figs 38–42. *Echinoccephalodes barbatus* (Lamb), female, Madagascar, only Figs 38 and 42 based on female paralectotype. 38 – apex of female genital chamber laterally; 39 – postabdomen dorsally; 40 – ditto laterally; 41 – ditto ventrally; 42 – end of postabdomen, with genital chamber and extruded ovipositor laterally. Scales: Fig. 38 = 0.05 mm, others = 0.2 mm.

extremely reduced, membranous, forming a small transverse, caudally oriented stripe. S8 (Figs 40–42) smaller than S7, with distinctive pigmentation and sinuate posterior emargination. 8th segment with protrusible membranous ovipositor (see Fig. 42). Genital chamber narrow, without internal sclerotization (Fig. 42). End of genital chamber without ventral receptacle (Fig. 38). Spermathecae 1+1 (Fig. 38), extremely reduced or wholly absent and their function probably substituted by dilated ringed ducts. Only one accessory gland observed (Fig. 38) although probably two exist. T10 (Figs 39, 40) bare, completely fused with cerci. S10 (Figs 40, 41) forming a small plate with projecting anterior corners and thicker setulae at posterior margin. Cercus fused with T10, short but robust, pale, with short fine setae (Figs 39, 40, 42).

PHYLOGENY AND CLASSIFICATION

THE OUTGROUP AND THE SISTER-GROUP OF THE ANTHOMYZIDAE

The family Opomyzidae has usually been considered a sister-group of the Anthomyzidae, chiefly because of the similar biology and wing venation. Hennig (1971, 1973) and particularly J.F. McAlpine (1989) supported this hypothesis by a number of synapomorphies. The latter author assembled these two families in a separate suprafamily Opomyzoinea of the superfamily Opomyzoidea. Colless & D.K. McAlpine (1991), on the contrary, placed Anthomyzidae in their superfamily Asteioidea, comprising Neurochaetidae, Periscelididae, Teratomyzidae, Aulacigastridae and Asteiidae, while Opomyzidae were united with Clusiidae, Acartophthalmidae, Odiniidae, Agromyzidae, Fergusoninidae, Xenasteiidae and Carnidae in the superfamily Opomyzoidea. Therefore I tested all synapomorphic characters of Opomyzoinea given by J.F. McAlpine (1989: 1460), those used by Colless & D.K. McAlpine (1991) to delimit Asteioidea and many others (see above generic diagnoses), when I compared the recent members of the Anthomyzidae with both fossil taxa, *Protanthomyza* Hennig, 1965 and *Grimalantha* gen. n., as well as with the families of the superfamily Opomyzoidea sensu J.F. McAlpine (1989). However, a large number of these characters had to be eventually excluded from further consideration because of high degree of their homoplasy within the Opomyzoidea and even acalyprates as a whole. No distinct outgroup of Anthomyzidae + Opomyzidae was revealed among families of the Opomyzoidea and, therefore, a hypothetical outgroup was established which accumulates plesiomorphic characters. Such an outgroup was subsequently found to be very similar to Clusiidae, i.e. to the most generalized group of the Opomyzoidea (see J.F. McAlpine, 1989).

My results are shown as a cladogram (Fig. 43). The fossil genus *Protanthomyza* bears a number of features occurring partly in the Opomyzidae, partly in the Anthomyzidae. Indeed, the genus *Protanthomyza* exhibits most of the plesiomorphic features of both these families. As it simultaneously also shares some apomorphic characters with the recent Anthomyzidae, I believe it is their sister-group and, therefore, a true, although rather primitive, anthomyzid. Some of the ancestral characters of *Protanthomyza* (17–21 in the cladogram) are retained in recent Opomyzidae but not in recent Anthomyzidae, e.g. 2 ppl (= proepisternal) setulae, setose mesopleuron (anepisternum), only 1 strong stpl (katapisternal) bristle and 2 pa. The somewhat intermediate position of *Protanthomyza*, together with distinct synapomorphies (1–6; 4 and 6 being particularly significant because unique

in the whole superfamily) of the Opomyzidae and Anthomyzidae (Fig. 43), demonstrate sister-group relationships of these two families. The discovery of a primitive preapical kink on R₁ (synapomorphy 4) in *Protanthomyza* (see above under that genus) strongly supports the above conclusion. Unfortunately, the features of the male genitalia cannot be tested in *Protanthomyza*, but also this genus supposedly had the complex distiphallus and the distinctive folding apparatus between hypandrium, transandrium and phallophore. Leaving the folding apparatus aside, the general structure of the male genitalia of both the Anthomyzidae and Opomyzidae resembles most those of the Clusiidae. I therefore presume that the sister-pair Opomyzidae-Anthomyzidae was most probably derived from a clusiid-like ancestor. It seems that Opomyzidae (characterized by synapomorphies 7–11, see Fig. 43) are now the more specialized group, particularly because of their phytophagy. Obviously, the ancestor of both families was saprophagous; the recent species of Anthomyzidae seem to form a transition stage from phytosaprophagy to phytophagy.

THE MONOPHYLY OF THE ANTHOMYZIDAE

The monophyly of the family Anthomyzidae is evidenced by synapomorphies 12–16 in the cladogram (Fig. 43), i.e. convergent postverticals, absence of pteropleural (anepimeral) setulae and presence of the ctenidial spine on fore femur. Because it is found in the genus *Protanthomyza*, the latter character (14) is considered to belong to the ground-plan of the Anthomyzidae, in spite of the fact it was secondarily lost in a number of recent genera (e.g. *Amnonthomyza*, *Amygdalops*, *Anagnota*, *Barbarista*, *Cercagnota*, *Santhomyza*, *Typhamyza*). The most distinctive synapomorphies of Anthomyzidae are found in the male and female terminalia. Unfortunately these cannot be verified in the fossil genera *Protanthomyza* and *Grimalantha* and, consequently, they are only presumed to occur in these taxa.

The main synapomorphic characters of Anthomyzidae can be found in the male internal genitalia. The most important are: (15) phallapodeme with single, robust ventral fulcrum connected with hypandrium (it is a modified aedeagal guide of other Muscomorpha); (16) bifid aedeagus having a slender sclerotized filum and voluminous membranous saccus. Other, less important, synapomorphies are: the sclerites of the 7th female abdominal segment tending to form a syntergosternum (this feature evolved independently also in a few other families of the Opomyzoidea); female genitalia provided with internal sclerites (may be secondarily lost in some genera).

The extant taxa of Anthomyzidae plus *Grimalantha* form a monophyletic sister-group of the genus *Protanthomyza* characterized by 5 apomorphic characters (17–21): postocular setulae reduced to a single row; only 1 ppl (proepisternal) setula; mesopleuron (anepisternum) bare or only with a few microsetulae (*Apterosepsis*), 2 stpl (katapisternal) setae (secondarily absent in *Apterosepsis*); only 1 (or 0) pa seta. The plesiomorphic states of these characters occur both in the Opomyzidae and *Protanthomyza* as emphasized above (see Fig. 43).

PHYLOGENETIC POSITION OF FOSSIL GENERA

While the older (Baltic amber) fossil genus *Protanthomyza* accumulates a number of plesiomorphic features and cladistic analysis links it as a sister-group to all other known genera of Anthomyzidae (it is characterized by autapomorphies 22–24 in the cladogram),

the position of *Grimalantha* has not been explicitly determined. Based on available features (see its above diagnosis) it indubitably belongs to a monophyletic unit formed by recent known genera (cf. Fig. 43). However, it is highly probable that unnamed anthomyzids allied to *Grimalantha* will be found in the Neotropical Region whose fauna of Anthomyzidae is the least known. Only then, when the postabdominal characters of its relatives are known, will it be possible to define the affinity of *Grimalantha* more precisely.

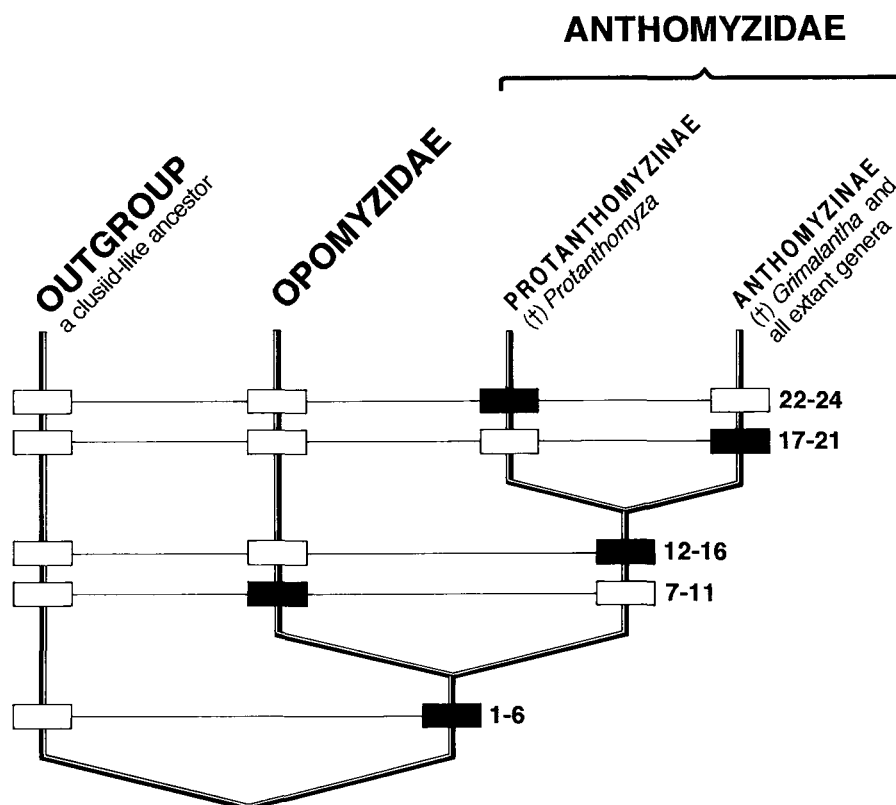
HIGHER CLASSIFICATION OF THE ANTHOMYZIDAE

The new subfamily classification proposed below has resulted from the above cladistic analysis. A new subfamily is established for the fossil genus *Protanthomyza*, forming a sister-group to all other known Anthomyzidae:

Subfamily Protanthomyzinae subfam. n.

Type genus: *Protanthomyza* Hennig, 1965.

DIAGNOSIS: Head with large eye having its longest diameter vertical (Fig. 2), frons narrow, ocellar triangle protruding, ocelli large (Figs 2–3), antenna relatively porrect (Fig. 2), arista dorsobasal. Cephalic chaetotaxy complete, pvt convergent, postocular setulae numerous. Thoracic chaetotaxy (Figs 1, 5) rich, with all usual macrosetae (see diagnosis of *Protanthomyza*), but with 2 pa, 1 long prescutellar ac (Fig. 5), 2 small ppl, mesopleuron with numerous setae (Fig. 5), and only 1 long stpl. f₁ with 1 ctenidial spine (Fig. 4). Wing



(Fig. 6) relatively broad, Sc distinct along its entire length but apically fused to R_1 and preapical kink on R_1 present in its simplest form. Epandrium with an anteroventral digitate projection on each side (Fig. 7), gonostylus discrete, small, pointed. The autapomorphic features of the subfamily are listed in the discussion under the genus *Protanthomyza* and in cladogram (Fig. 43).

Fig. 43 (opposite page). Cladogram showing the inferred relationships between the families Opomyzidae, Anthomyzidae and its subfamilies.

Characters mentioned in the cladogram:

plesiomorphic condition (white rectangles)	apomorphic condition (black rectangles)
1. wing broader	1. wing narrow
2. A_1 longer although not reaching wing margin	2. A_1 abruptly abbreviated
3. alula larger	3. alula reduced, narrowed
4. Sc free and complete, R_1 without preapical kink	4. Sc apically fused to or coalesced with R_1 and preapical kink on R_1 developed
5. arista apical	5. arista dorsobasal
6. no folding apparatus between phallopore, hypandrium and transandrium	6. phallopore linked to hypandrium and transandrium by a folding apparatus ¹
7. 3–4 ors setae but some may be reduced to microsetae	7. only 1 ors
8. vi distinctly developed	8. vi absent
9. prosternum bare	9. prosternum setulose
10. gonostylus discrete	10. gonostylus fused with epandrium
11. female 7th abdominal spiracle present	11. female 7th abdominal spiracle absent
12. pvt divergent ²	12. pvt convergent ²
13. pteropleural (anepimeral) setulae present	13. pteropleural setulae absent
14. f_1 without ctenidial spine	14. f_1 with 1 ctenidial spine ³
15. phallapodeme simple	15. phallapodeme with robust ventral fulcrum ¹
16. distiphallus unforked apically	16. distiphallus bifid apically, with membranous sacculus and more sclerotized filum ¹
17. postocular setulae in long, at least partly double row	17. postocular setulae in single short row
18. 2–3 ppl (proepisternal) setulae	18. only 1 ppl setula
19. mspl (anepisternal) setae present, at least 1 strong	19. mspl setae absent or reduced (cf. Fig. 23)
20. only 1 long stpl (katepisternal) seta	20. 2 long stpl setae
21. 2 pa setae	21. only 1 pa seta
22. ocelli small and ocellar triangle flat	22. ocelli enlarged and ocellar triangle protruding
23. at most small ac microsetae in prescutellar position	23. 1 long prescutellar ac seta ⁴
24. epandrium simple	24. epandrium with anteroventral projections

¹ These characters are only presupposed in the fossil genera of Anthomyzidae.

² Pvt may be secondarily absent in both groups.

³ Ctenidial spine is secondarily lost in several genera of Anthomyzidae.

⁴ Prescutellar ac are considered secondarily prolonged.

All other described genera and species of Anthomyzidae (including the fossil *Grimalantha* gen. n.) form a monophyletic group (see Fig. 43) and are assigned to the subfamily Anthomyzinae Frey, 1921. A complete checklist of described taxa of Anthomyzidae, arranged according to the new classification, is presented in Appendix 1. It includes also known synonyms and nomenclatural and distributional data. Taxonomic papers cited in the checklist are quoted in full in References.

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APPENDIX 1. A checklist of the world species of Anthomyzidae (Diptera).

Family **Anthomyzidae** Frey, 1921

Subfamily †**Protanthomyzinae** subfam. n.

Genus †**Protanthomyza** Hennig, 1965: 169 (feminine). Type species: *Protanthomyza collarti* Hennig, 1965, monotypy.

collarti Hennig, 1965: 169 (*Protanthomyza*). Palearctic: Baltic sea shores (amber).

Subfamily **Anthomyzinae** Frey, 1921

Genus **Amnonthomyza** Roháček, 1993: 180 (feminine). Type species: *Amnonthomyza regina* Roháček, 1993, original designation.

deplanata Roháček, 1993: 187 (*Amnonthomyza*). Afrotropical: Madagascar.

regina Roháček, 1993: 182 (*Amnonthomyza*). Afrotropical: Madagascar.

Genus **Amygdalops** Lamb, 1914: 357 (masculine). Type species: *Amygdalops thomasseti* Lamb, 1914, original designation.

geniculatus de Meijere, 1916: 207 (*Amygdalops*). Oriental: Java.

lineola de Meijere, 1916: 208 (*Amygdalops*). Oriental: Java.

rufior Roháček & Freidberg, 1993: 96 (*Amygdalops*). Palearctic: Israel.

thomasseti Lamb, 1914: 358 (*Amygdalops*). Afrotropical: Oman, Seychelles. Palearctic: Canary Is., Egypt, Israel, Greece, Spain.

trivittatus Frey, 1958: 32 (*Amygdalops*). Afrotropical: Cape Verde Is.

Genus **Anagnota** Becker, 1902: 309 (feminine). Type species: *Opomyza bicolor* Meigen, 1838, monotypy.

bicolor (Meigen, 1838): 380 (*Opomyza*). Palearctic: Czech Republic, Germany, Great Britain, Hungary, Italy, Poland, Slovakia, Sweden, The Netherlands.

coccinea Roháček & Freidberg, 1993: 79 (*Anagnota*). Palearctic: Israel.

major Roháček & Freidberg, 1993: 75 (*Anagnota*). Palearctic: Czech Republic, Hungary, Slovakia, ?Germany or Poland.

Genus **Anthomyza** Fallén, 1810: 20 (feminine). Type species: *Anthomyza gracilis* Fallén, 1823, designated by Westwood (1840: 152).

=*Leptomyza* Macquart, 1835: 580 (feminine). Type species: *Anthomyza gracilis* Fallén, 1823, designated by Coquillett (1910: 560).

=*Anthophilina* Zetterstedt, 1837: 55 (feminine). Type species: *Anthomyza gracilis* Fallén, 1823, monotypy.

albimana (Meigen, 1830): 107 (*Opomyza*). Palearctic: Austria, Belgium, Bulgaria, Czech Republic, Estonia, France, Germany, Great Britain, Hungary, Italy, Poland, Russia [Central European territory of

Russia (CET), North European territory of Russia (NET)], Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland, The Netherlands, Turkey.

=*glabra* (Meigen, 1838): 380 (*Opomyza*).

=*nigrimana* (Meigen, 1838): 400 (*Agromyza*).

=*armillaris* (Rondani, 1875): 4 (*Anthophilina*).

=*rufa* Czerny, 1928: 3 (*Anthomyza*).

anderssoni Roháček, 1984a: 388 (*Anthomyza*). Palaearctic: Bulgaria, Czech Republic, Italy, ?Switzerland.

bellatrix Roháček, 1984a: 385 (*Anthomyza*). Palaearctic: North Korea.

collini Andersson, 1976: 49 (*Anthomyza*). Palaearctic: Austria, Belgium, Czech Republic, Estonia, Germany, Great Britain, Ireland, Latvia, Poland, Russia [CET, NET, West Siberia (WS)], Slovakia, Spain, Sweden, Switzerland.

concolor (Thomson, 1869): 596 (*Piophila*). Nearctic: USA (California).

cuneata Roháček, 1987: 48 (*Anthomyza*). Oriental: Nepal.

dissors Collin, 1944: 271 (*Anthomyza*). Palaearctic: Czech Republic, Estonia, Finland, Great Britain, Latvia, Poland, Russia (NET), Slovakia, Sweden.

dorsata Collin, 1944: 271 (*Anthomyza*, as var. of *A. dissors*). Palaearctic: Great Britain, Russia (NET), Sweden.

elbergi Andersson, 1976: 47 (*Anthomyza*). Palaearctic: Estonia, Great Britain, Latvia, Lithuania, North Korea, Russia (NET), Sweden.

gracilis Fallén, 1823: 8 (*Anthomyza*). Palaearctic: Austria, Belgium, Bulgaria, Czech Republic, Denmark, Estonia, Finland, France, Germany, Great Britain, Hungary, Iceland, Ireland, Italy, Latvia, Lithuania, Poland, Roumania, Russia (CET, NET, WS), Slovakia, Slovenia, Serbia, Sweden, Switzerland, The Netherlands, Ukraine. Nearctic: ?Canada, ?USA.

=*sordidella* (Zetterstedt, 1848): 2695 (*Anthophilina*).

=*trojani* Elberg, 1968: 630 (*Anthomyza*).

macra Czerny, 1928: 4 (*Anthomyza*). Palaearctic: Austria, Czech Republic, ?Germany, Great Britain, Roumania, Slovakia, Sweden, Switzerland.

neglecta Collin, 1944: 269 (*Anthomyza*). Palaearctic: Czech Republic, Germany, Great Britain, Slovakia, Sweden, Switzerland.

pallida (Zetterstedt, 1838): 785 (*Anthophilina*). Palaearctic: Austria, Czech Republic, Estonia, Finland, Germany, Great Britain, Norway, Poland, Russia [NET, South European territory of Russia (SET)], Slovakia, Sweden, Switzerland, The Netherlands. Nearctic: ?Canada, ?USA.

=*unguicella* (Zetterstedt, 1838): 753 (*Sapromyza*).

paraneglecta Elberg, 1968: 629 (*Anthomyza*). Palaearctic: Czech Republic, Denmark, Germany, Great Britain, Slovakia, Sweden.

pleuralis Czerny, 1928: 4 (*Anthomyza*). Palaearctic: Estonia, Finland, Germany, Great Britain, ?Poland, Roumania, Russia (CET, SET), Slovakia, Switzerland, Sweden.

receptrix Roháček & Freidberg, 1993: 105 (*Anthomyza*). Palaearctic: Israel.

setiplanta Roháček, 1987: 54 (*Anthomyza*). Oriental: Nepal.

socculata (Zetterstedt, 1847): 2534 (*Geomyza*). Palaearctic: Czech Republic, Estonia, Finland, Great Britain, ?Hungary, Norway, Poland, Russia [NET, WS, East Siberia (ES)], Sweden, Switzerland.

=*ungulata* Loew, 1873: 301 (*Anthomyza*).

tenuis (Loew, 1863): 324 (*Anthophilina*). Nearctic: Canada (Quebeck), USA (Alaska, Minnesota, New Hampshire, Virginia, Washington).

variegata (Loew, 1863): 324 (*Anthophilina*)*. Nearctic: USA (California, District of Columbia, Georgia, Maine, New York, Virginia, Washington).

Genus **Apterosepsis** Richards, 1962: 466 (feminine). Type species: *Apterosepsis basilewskyi* Richards, 1962, original designation.

basilewskyi Richards, 1962: 467 (*Apterosepsis*). Afrotropical: Tanzania.

Genus **Barbarista** Roháček, 1993: 159 (feminine). Type species: *Barbarista guttata* Roháček, 1993, original designation.

* The species probably belongs to the genus *Stiphrosoma*.

brachycera Roháček, 1993: 173 (*Barbarista*). Afrotropical: Nigeria.
brevifrons Roháček, 1993: 170 (*Barbarista*). Afrotropical: Uganda.
davidi Roháček, 1993: 177 (*Barbarista*). Afrotropical: Zimbabwe.
guttata Roháček, 1993: 162: (*Barbarista*). Afrotropical: Kenya.
pauperis Roháček, 1993: 168 (*Barbarista*). Afrotropical: Cameroon.

Genus *Cercagnota* Roháček & Freidberg, 1993: 83 (feminine). Type species: *Anagnota collini* Czerny, 1928, original designation.
collini (Czerny, 1928): 7 (*Anagnota*). Palearctic: Great Britain (England), Israel, Malta, Spain, Uzbekistan.

Genus *Chamaebosca* Speiser, 1903: 65 (feminine). Type species: *Chamaebosca microptera* Speiser, 1903, original designation.
= *Penquistus* Kieffer, 1906: 349 (masculine), syn. n. Type species: *Penquistus cursor* Kieffer, 1906, monotypy.
cursor (Kieffer, 1906): 350 (*Penquistus*), comb. n. Neotropical: Chile.
microptera Speiser, 1903: 67 (*Chamaebosca*). Neotropical: Chile.

Genus †*Grimalantha* gen. n. Type species: *Grimalantha vulnerata* sp. n., present designation.
vulnerata sp. n. (*Grimalantha*). Neotropical: Dominican Republic (amber).

Genus *Ischnomyia* Loew, 1863: 325 (feminine). Type species: *Ischnomyia vittula* Loew, 1863, monotypy.
albicosta (Walker, 1849): 1113 (?*Diastata*). Nearctic: USA (New York, North Carolina, Pennsylvania, Wisconsin).
= *vittula* Loew, 1863: 325 (*Ischnomyia*).
spinosa Hendel, 1911: 45 (*Ischnomyia*). Nearctic: USA (Michigan, New Hampshire, North Carolina, Wisconsin).

Genus *Mumetopia* Melander, 1913: 293 (feminine). Type species: *Mumetopia occipitalis* Melander, 1913, original designation.
nigrimana (Coquillett, 1900): 264 (*Anthomyza*). Nearctic: USA (Florida). Neotropical: Puerto Rico. Oceanian: Hawaii (introduced).
occipitalis Melander, 1913: 294 (*Mumetopia*). Nearctic: Northern Mexico, USA (Bermuda, Florida, Georgia, Louisiana, Massachusetts, South Dakota, Texas).
terminalis (Loew, 1863): 324 (*Anthophilina*). Nearctic: Canada (Quebec), USA (New Hampshire, Massachusetts, Michigan, Virginia).
= *nitens* Melander, 1913: 294 (*Mumetopia*).

Genus *Paranthomyza* Czerny, 1902: 254 (feminine). Type species: *Opomyza nitida* Meigen, 1838, monotypy.
nitida (Meigen, 1838): 380 (*Opomyza*). Palearctic: Austria, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Germany, Great Britain, Hungary, Ireland, Poland, Roumania, Russia (CET, NET), Slovakia, Sweden, Switzerland, The Netherlands.
= ?*asteia* (Haliday, 1833): 177 (*Opomyza*).
= *flavipes* (Zetterstedt, 1848): 2696 (*Anthophilina*).

Genus *Santhomyza* Roháček, 1984b: 532 (feminine). Type species: *Santhomyza inermis* Roháček, 1984, original designation.
bezzii (Czerny, 1902): 252 (*Anthomyza*). Palearctic: Italy.
biseta Roháček & Báez, 1988: 296 (*Santhomyza*). Palearctic: Canary Is.
inermis Roháček, 1984b: 534 (*Santhomyza*). Palearctic: Egypt, France, Greece, Israel, Spain.

Genus *Stiphrosoma* Czerny, 1928: 6 (neuter). Type species: *Stiphrosoma oldenbergi* Czerny, 1928, designated by Enderlein (1936: 167) by elimination.
= *Ptenotaenia* Enderlein, 1936: 167 (feminine). Type species: *Opomyza (Geomyza) sabulosa* Haliday, 1837, monotypy.
cingulatum (Haliday, 1855): 64 (*Geomyza*). Palearctic: Czech Republic, Great Britain (England), Ireland, Russia (CET, ES), Slovakia.

fissum Roháček, 1996: 101 (*Stiphrosoma*). Palaearctic: North Korea.
laetum (Meigen, 1830): 111 (*Opomyza*). Palaearctic: Czech Republic, Finland, Germany, Great Britain, North Korea, Poland, Russia (NET), Slovakia, Sweden.
sabulosum (Haliday, 1837): 151 [*Opomyza* (*Geomyza*)]. Palaearctic: Austria, Czech Republic, Denmark, Estonia, Finland, France, Germany, Great Britain, Hungary, Ireland, Poland, Russia (CET, NET), Slovakia, Switzerland, Sweden, The Netherlands. Nearctic: Canada, USA (?introduced).
 = *brevipennis* (Zetterstedt, 1852): 4335 (*Geomyza*).
 = *saliens* (Loew, 1866): 5 (*Anthomyza*).
 = *apterina* (Ruthe in Czerny, 1902): 251 (*Opomyza*).
 = *oldenbergi* Czerny, 1928: 6 (*Stiphrosoma*).
 Genus **Typhamyza** Roháček, 1992: 188 (feminine). Type species: *Anthomyza bifasciata* Wood, 1911, original designation.
bifasciata (Wood, 1911): 40 (*Anthomyza*). Palaearctic: Czech Republic, Finland, Germany, Great Britain, Hungary, Kazakhstan, Poland, Slovakia, Sweden, The Netherlands, Ukraine.
 = *fasciipennis* Oldenberg, 1927: 118 (*Anthomyza*).

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