A new genus of Helicoboscinae from the Himalayas (Diptera: Calliphoridae), with emended genus and subfamily concepts

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The male, female and larva I (uterine) of Gulmargia angustisquama gen. n., sp. n. are described from northern India (Kashmir and Uttar Pradesh). The female is macrorlarviporous. Gulmargia and the western Palearctic Eurychaeta Brauer & Bergenstamm are vicariant sister groups which together form the subfamily Helicoboscinae of the Calliphoridae. Revised definitions of Helicoboscinae and Eurychaeta are provided. The monophyly of all taxa involved is established on the basis of several synapomorphies. It is suggested that the Helicoboscinae is an ancient clade of the Calliphoridae.

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Introduction

An undescribed species of Calliphoridae from North-West and West Himalayas (Kashmir and Uttar Pradesh provinces of northern India) has been examined. This appears to be more closely related to the western Palearctic Eurychaeta Brauer & Bergenstamm (Helicobosca Bezzi) than to any other genus on the basis of synapomorphic agreement in several adult and larval features. It differs sufficiently from members of that genus, however, to justify the erection of a new genus for it. The purpose of the present paper is to describe the new taxa and to revise earlier concepts of both the subfamily Helicoboscinae and the genus Eurychaeta (Rognes 1986; 1991) in consequence of the new discovery. The papers of Verves (1990) and Shewell (1991) challenging the view of Helicoboscinae as a calliphorid taxon (Rognes 1986; 1991) are commented upon.

Material and terminology

The study is based upon material of Calliphoridae in Universitetets Zoologiske Museum, Copenhagen (ZMUC). Females of Brachicoma devia (Fallén), Sarcophila lutfrons (Fallén) and Wohlfahrtia magnifica (Schiner) (all Sarcophagidae) from my own collection were dissected for examination of internal reproductive organs and uterine larvae. The morphological terms and abbreviations follow Rognes (1991).

Family CALLIPHORIDAE

Subfamily HELICOBOSCINAE


Helicoboscina Verves, 1980: 1477 (as subtribe of tribeParamacronychiini of subfamily Paramacrionychinae of family Sarcophagidae); Verves 1982: 258.

Helicoboscinae; Rognes 1986: 75 (as subfamilty of the family Calliphoridae); Rognes 1991: 140.

Helicoboscini; Verves 1990: 25, 27 (as tribe of subfamily Paramacronychinae of family Sarcophagidae).

Description. – The discovery of the new genus (described below) makes my earlier diagnoses of this hitherto monogenic subfamily (Rognes 1986, 1991) obsolete. An emended description of the subfamily is therefore given below.

Adults. – Colour. Black ground colour and silvery white microomentum, sometimes with additional bluish (Eurychaeta) or brownish (Gulmargia) hue. Palp yellow (Eurychaeta) or black (Gulmargia). Abdominal tergites T1–5 with median black stripe.
and black hindmargins, otherwise mostly with more or less shifted pattern of microomentum according to angle of view.

Head. Setae and ground setulae black. Facial carina absent. Antennal scapes close together. Arista plumose (Gulmargia) or pubescent (Eurychaeta).

Male always with laterocline orbital seta (though very fine in Gulmargia). Parafacial setose for whole length, lower setae enlarged, though sometimes only very slightly so. Intrapostocular cilia absent. Palp long, slightly widened distally. Occiput convex.

Thorax. Proepisternal depression, pronotum and metasternal area densely setose. Outer ph outside of prs seta or in line with it (some Eurychaeta). 2 np1 setae, with or without a supplementary seta in between. Prepst strong and surrounded by 4–6 subequal additional setae. One strong anepimeral seta among the hairs. Greater ampulla, lesser ampulla, anterior half of anepimeron, and katatergite bare. Anatergite with numerous short hairs below lower calyptr. Katepisternum sparsely setose or bare along a broad zone anterodorsally of mid coxa. 1+1+1 or 2+1+1 kepst setae. Katepimeron with some hairs. Postalar wall and supraquamal ridge bare. Coxopleural streak present. Metathoracic spiracle rather small for a calliphorid with anterior lappet smaller than posterior one. Metakatepisternum bare. Subscutellum slightly swollen (Eurychaeta) or not (Gulmargia).

Wing. Tegula and basiconsta black. Stem vein bare on both sides of wing. Second costal sector setulose below (between exits of Sc and R4), costa bare below beyond junction with R4. No or only a very small costal spine. Node at base of R2+3 and R4+5 with 3–5 setae on both sides of wing. Both calypet,es white, bare on disc. Haltere dark brown (Eurychaeta) or pale yellow (Gulmargia).


Preabdom. T1–2 excavated to hind margin, without median marginals but with 1–3 lateral marginal setae. T3 with 2–4 median marginals and with 2–3 lateral marginals on each side well separated from the median group. T4–5 with 10–16 strong erect and evenly spaced marginals. No discal setae on any tergite. ST1 hairy. ST2–4 broadly exposed, usually without alpha–setae (trichoid sensilla) (a pair present between ST1 and ST2 in Gulmargia). Margins of sternites overlapped by margins of corresponding tergites.

Postabdomen of ♂. ST5 with short bare basal part and large posterior lobes, without alpha–setae at fore margin. T6 a narrow sclerite. Spiracle 6 in membrane, spiracle 7 in STST7 + 8. Sturysyllus well developed. Bacilliform sclerites well developed, separate. Hypandrium with posterior arms free, not united behind basiphallicus. Pregonite simple (Eurychaeta) or bilobate (Gulmargia).


Internal reproductive organs of ♀. Uterus large, simple and cylindrical, projecting anteriorly beyond entrance of common oviduct as a blind pouch. 3 oval spermathecae. Spermathecal ducts entering uterus by a common unsclerotized duct which is either very short (Eurychaeta) or rather long (Gulmargia).

Immaturestages. – First instar larva. Cuticular spines short and strong or elongate and filiform, black. Labrum very large, hook-shaped. Mandibles with a strong, tooth-like projection. Ten- toropharyngeal sclerite with slender posterior arms (very short in Gulmargia); anterior projections absent. Posterior spiracular field can be hidden completely by transverse folding and apposition of dorsal and ventral halves. Posterior spiracle bilobate (see Rognes 1986: 81, fig. 21).

Third instar larva and puparium. Known only for Eurychaeta. Salient features described by Rognes (1986).

Reproductive habit. – All species exhibit macrolarviparous reproduction, i.e. large larvae are being born singly at considerable time intervals. The larae of Eurychaeta feed on dead or dying snails. Larval habits are unknown for Gulmargia, but to judge from the very strong labrum, these do not differ from Eurychaeta.

Monophyly of the Helicoboscinae. – The following features are possibly apomorphic relative to the groundplan of the Calliphoridae as defined by Rognes (1991) and support the monophyly of the Helicoboscinae (assumed groundplan states of the Calliphoridae are given in parentheses):

1. black and silvery white sarcophagid–like non–metallic colour (metallic);
2. postalar wall bare (setulose);
It is possible that the corresponding groundplan states for Calliphoridae are non-metallic body colour (cf. Rognes 1986) and bare postalar wall. If so items (1) and (2) are plesiomorphies and uninformative at this level.

(3) middle katepisternal setae present (absent);

The presence of a middle katepisternal seta in both Gulmargia (pattern 1+1+1) and Eurychaeta (pattern 2+1+1) is unique among Calliphoridae, even though freak specimens from other subfamilies occasionally may show it (cf. Rognes 1986: 88). Rognes (1991) assumed that the groundplan state of Calliphoridae is 2 anterior and 1 posterior katepisternal setae, i.e. a 2+1 pattern, with no middle setae in between. If this is true, the 2+1 pattern of Eurychaeta is most likely the groundplan state of the Helicoboscinae and the 1+1+1 pattern of Gulmargia derived from this (see below).

(4) katepisternum with sparse cover of ground setulae along a broad 'path' anterodorsally of mid coxa (Eurychaeta) or setulae absent from this area (Gulmargia) (this area with full cover of setulae);

Some Rhiniinae (Calliphoridae) and Paramacronychiinae (Sarcophagidae) also have this character state.

(5) outer ph outside a line through prs seta (on line with prs seta);

This character state is widespread in the Calliphoridae but does not occur elsewhere among the Oestroidea. I have used it to define several monophyletic groups of the interrelationships of which are obscure (homoplasies) (Rognes 1991). However, it may be a groundplan state of the Calliphoridae and the plesiomorphic position of the seta in some calliphorid groups secondary reversals (pseudoplesiomorphy) (cf. Rognes 1986). In this case item (5) is uninformative at the level under consideration.

(6) uterus very large and cylindrical, serving macrolarviparous birth to single, very large, first instar larvae at long time intervals (uterus small, serving oviparous reproduction);

Macrolarviparous reproduction also occurs in other calliphorid groups (Ameniinae, Mesembrinellinae, Euphmosia Malloch, Dyscritomyia Grimshaw) but apparently of independent origin. It is unknown elsewhere in the Oestroidea (cf. Rognes 1986).

(7) first instar larva with hypertrophied labrum (labrum small);

This state does not occur elsewhere in the Calliphoridae, but may occur among other Oestroidea (homoplasies).

(8) tentoropharyngeal sclerite of first instar larva when seen in profile connected (fused or articulating) directly to the labrum, no anterior projections present on the tentoropharyngeal sclerite (tentoropharyngeal sclerite connected through long slender anterior ventral projections to the labrum);

The apomorphic state does not occur elsewhere among the Oestroidea. In all other first instar larvae the tentoropharyngeal sclerite has a long anterior ventral process on each side connecting it to the labrum.

(9) posterior segments of first instar larva with strikingly long and slender cuticular spines (only short spines);

I know of no other Calliphoridae with similar filiform cuticular spines on the hind segments of the first instar larva.

(10) third instar larva with posterior spiracular plates completely and evenly sclerotized, no peritreme or separate slit sclerotizations distinguishable (Eurychaeta, third instar of Gulmargia unknown) (spiracular plate consisting of separate peritreme and slit sclerotizations);

I know of no other Oestroidea with this type of posterior spiracle in third instar.

Distribution. - The subfamily contains 2 genera with vicariant distribution, one in the western Palaearctic and one in the north-western Oriental Region.

Genus Eurychaeta Brauer & Bergenstamm

*Theria* Robineau-Desvoidy, 1830 (preocc.); *Eurychaeta* Brauer & Bergenstamm, 1891; *Helicobosca* Bezzi, 1906 (details of synonymy and type-species as well as key to species are given by Rognes 1991).

This genus has recently been treated by Rognes (1986, 1991) who provided diagnoses and numerous figures of salient features.

*Emended diagnosis.* - *Eurychaeta* is a member of the subfamily Helicoboscinae as defined above with the following additional characters:

Eye bare. All setae strikingly strong. Very strong setae in lower part of parafacial. Male always with strong laterocline orbital seta. Arista strongly pubescent in basal half. Scape erect and projecting. Palp yellow. 5–7 h. 3–4 ph, outer ph in line with prs or rarely slightly exterior to it. 5+3 acr. 4+4 dc. 0–1+3 ia. 2+1 npl. 1 pra. 2–3 sa of equal size. On each side of anterior slope of thorax at level with anteriormost acr seta a transverse row of about 4–6 setae much stronger than normal thoracic vestiture. 2+1+1 kepst setae. Scutellum with 2 pairs of discal setae and 5–7 marginal pairs. Subscutellum slightly swollen. Halteres dark brownish. Lower calyptra with inner edge backwards converging with longitudinal axis of fly. Front tibia with 3–5 pd and 2 p setae. Mid tibia with 3–5 ad, 3–5 pd and 2–3 p setae.
Figs 1–5. *Gulmargia angustisquama*: (1) head in profile (holotype); (2) left part of thorax, dorsal view (♀); (3) upper posterior corner of left katepisternum (♀); (4) area around coxopleural streak (♀); (5) scutellum (♀). Scale 1 mm (1–3, 5), 0.5 mm (4). (In 2–4 only bases of strong setae are shown.)

Hind tibia with strong *ad*, *a*, *pd* preapical setae; *pv* preapical seta as strong as *av* preapical seta. Pregonite simple. Distiphallus straight. Acrophal- lus armed with minute denticles. Apical opening of the ejaculatory duct very large. T6 of ovipositor divided in midline. Male and female terminalia else as described by Rognes (1986, 1991), except that reexamination of the course of the spermathecal ducts has shown that a very short common duct is present.
First instar larva with tentoropharyngeal sclerite separate from labrum; its posterior arms at least as long as, usually much longer than labrum (Rognes 1991: fig. 22).

Monophyly. -- The following apomorphies relative to the groundplan of the Helicoboscinae support the monophyly of Eurychaeta (assumed helicoboscine groundplan states are given in parentheses):

1) main setae very strong (normal);
2) arista pubescent (plumose);
3) very strong setae in lower part of parafacial (at most weak setae differentiated in lower part of parafacial);
4) inner ph seta in line with prs (outside prs);
5) transverse row of strong setae present on each side of anterior slope of thorax at level with anteriormost acr setae (absent);
6) 2+1 npt setae (2);
7) 5-7 pairs of scutellar marginal setae (3 pairs);
8) 2 pairs of discal setae (1 pair);
9) subscutellum slightly swollen (not swollen);
10) many pd and p setae on front and mid tibiae (few).

Distribution. -- Western Palearctic Region east to the Altai Mountains in Central Asia. 3 species.

Genus Gulmargia gen. n.

Type species: Gulmargia angustisquama sp. n.

Etymology. -- From the name of the locality in Kashmir (India) where the dissected female was captured.

Diagnosis. -- Gulmargia is a member of the subfamily Helicoboscinae as defined above with the following additional characters: Eye with small short hairs, widely apart (careful observation necessary). Main setae normal, not strikingly strong. At most weak setae in lower part of parafacial. Male with a laterocline orbital seta that is very fine. Arista plumose in basal 0.66 to 0.75. Palp black. 3-5 h, 2 ph, outer ph well outside of prs seta. 4+3 acr. 3+3 dc. 0+2 ia (occasionally small accessory ia seta between the suture and the first large seta, and also between the first and second large ia seta). 2 npt. 1+1+1 kepst setae. 1 pra. 2 sa, hind-

most about as strong as pra, much weaker than anterior one. No transverse row of strong setae at anterior slope of thorax at level of anteriormost acr seta. Scutellum with 1 pair of discal setae, 3 marginal pairs of normal size, 1 small prebasal pair. Subscutellum not swollen. Haltere pale yellow. Lower calyptral tongue-like with inner edge backwards diverging from longitudinal axis of fly. Front tibia with 1 p. Mid tibia with 1-2 ad, 1 pd and 2 p setae. Hind tibia with ad and d preapical setae, pd preapical seta absent; pv preapical seta about half as long as av preapical seta. Pregonite bilobate. Distiphallus strongly bent. Acrothallus unarmed, no minute denticles on the aedeagal wall except a few along the hypophalic ridges. Apical opening of the ejaculatory duct very narrow. T6 of ovipositor undivided, evenly sclerotized, also in midline. Spermathecal ducts entering uterus by a long common duct.

First instar larva with tentoropharyngeal sclerite fused with the labrum and its posterior arms very much shorter than labrum; the whole structure working as one piece.

Monophyly. -- The following apomorphies relative to the groundplan of the Helicoboscinae support the monophyly of Gulmargia (plesiomorphic condition in parentheses):

Fig. 6. Gulmargia angustisquama, Q: area around wing base. bc – basicosta; l cal – lower calypter; sc – scutellum; w – wing. Scale 1 mm.
(1) lower calypter narrow with inner edge backwards diverging from long axis of fly (broad, inner edge backwards converging);

(2) acrofllus unarmed, no minute denticles on the aedeagal wall except for the hypophallic ridges (armed);

(3) katepisternal setae 1+1+1 (2+1+1);

(4) male pregonite bilobate (simple);

(5) first instar larva with labrum broadly fused with tentoropharyngeal sclerite (separate);

(6) first instar larva with arms of the tentoropharyngeal sclerite short (long).

**Distribution.** - Oriental Region: southern slopes of Western Himalayas in Northern India. 1 species, described below.

**Gulmargia angustisquama** sp. n.

(Figs 1-22)

*Type material.* - Holotype ♂, INDIA: Uttar Pradesh, Mussoorie, 1500–2200 m, 3–14.viii.1978 (ZMUC exp.: V. Michelsen & P. Nielsen) (dissected; dissected parts in glycerol in vial on pin). Paratypes: 1 ♀, same data as holotype; 4 ♀, INDIA: Kashmir, Gulmarg 2600–3000 m, 17.viii–5.ix.1978 (ZMUC exp.: V. Michelsen & P. Nielsen) (1 ♀ dissected; ovipositor slide G. pr. 328; uterus, spermathecae with ducts, and uterine first instar larva in glycerol in vials on pin). All material in ZMUC.

*Etymology.* - From the Latin *angustus* = narrow, and *squamata* = scale, referring to the shape of the lower calyp-ter.

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**Fig. 7. Gulmargia angustisquama,** ♀: posterior apical part of wing. Scale 1 mm.

**Fig. 8. Gulmargia angustisquama** (holotype): ST2 −5. Scale 1 mm.
Figs 9–11. Gulmargia angustisquama (holotype), ♀ terminalia: (9) cerci, surstyli and epandrium, posterior view; (10) cerci, surstyli, epandrium and bacilliform sclerite, lateral view; (11) bacilliform sclerites (‘x’ – attachment to hypandrial arms). Scale 0.2 mm.

Description

Male and female. – Fronto-orbital plate with white microtomentum, frontal vitta black when seen from above. Parafacial with white microtomentum, almost as wide as first flagellomere (both compared in widest aspect). Setae in lower part of parafacial only very slightly enlarged. Antenna black, a slight reddening at junction of pedicel and first flagellomere. First flagellomere 3.5–4.0 times longer than wide. Arista plumose. Vibrissa strong, about as long as distance from its base to lunula, close to lower facial margin. Supravibrissal setulae ascending 0.25 towards lunula. Facial plate with thin white microtomentum. Occiput with white microtomentum, shifting according to angle of view. Paravertical setae 1 pair, postocellar setae 2 pairs. Palp black, slender, about as long as first flagellomere. Premen- tum about as long as palp, shining, thinly microtomentose.

Thorax. Mesonotum with three vittae, variable in appearance according to angle of view. When seen from behind in low tangential view it can be described as follows. Median vitta situated between the acr setae. In front of suture rather broad, reaching the bases of the prst acr setae, its anterior end behind anterior slope of mesonotum. In its post- sutural part much narrower and not reaching the bases of the post acr, ending posteriorly at level of hindmost acr pair of setae. Lateral vittae interrupt- ed at suture. Presutural part broad and situated be- tween the prst dc setae and the outer ph and prs setae, enclosing the base of the inner ph seta, but
not the other setae. Behind the suture a narrow stripe between the post dc and the post ia setae. Anterior half of anepimeron bare. Meron with 4–8 strong setae in a row, some additional setulae present.

Wing. Cell r4+5 widely open. Node at base of R2+3 and R4+5 with 1 short seta intermingled with 2–4 setulae on each side of wing. First anal vein (A1+CuA2) not reaching wing margin. Subcostal sclerite with microtrichiae only, no setae. Bend of M rather sharp, a very short appendix present in 2 specimens. Distance from bend of M to wing margin is about 2 times distance from bend to dm–cu if measured along imagined continuation of M towards wing margin. Haltere yellow.

Legs. t1 with row of 4–7 ad setae, 1 p seta. f2 with a preapical seta and without preapical comb of short setae. t2 with 1–2 ad setae, 1 pd, 2 p and 1 v setae. t3 with 2–3 short av setae and rows of erect ad and pd setae, 3–5 larger setae intermingled with small ones in each row; ad and d preapical setae present, no pd preapical seta. pv preapical seta half as long as av preapical seta.

Abdomen without discal setae. Lateral marginal setae on all tergites. A pair of median marginal setae on T3. On T4 and T5 the median and lateral marginals tend to form uninterrupted marginal rows of setae.

**Male.** Length 8 mm. Frons at narrowest 0.193 times head width (n=1). Frons length (distance from lunula to anterior ocellus) 1.682 times frons
width. Inner vertical seta strong, outer vertical seta absent. Fronto-orbital plates half as wide as frontal vitta at level of tip of ocellar triangle. 6–7 frontal setae, antennomost at level of junction of scape and pedicel. 1 very slender and weak lateroclnate seta present. No proclinate orbital setae. Height of genal dilation 0.16 x eye height in profile. Cerci narrow, converging gradually toward apex, separate for a little less than apical half. Surstylus broadly triangular in lateral view, narrow in dorsal view. Bacilliiform sclerites separate, with median extensions that do not reach each other. Epiphallus originating from distal half of basiphallus. Distiphallus bent at middle forming an angle of about 120°. Paraphallic processes apically dentate. Aedeagal wall devoid of armature except for the short ventrolateral hypophallic ridges each carrying about 5 teeth. Ejaculatory apodeme with sclerotizations around its base. Pregonite bilobate, anterior lobe with 1–2 setae, posterior lobe with about 5 setae. Postgonite without strong basal seta.

Female. – Length 8.0–9.2 mm. Frons at narrowest 0.292–0.333 times head width (mean 0.318, n = 5). Frons length (distance from lunula to anterior ocellus) 0.895–1.029 times frons width (mean 0.949, n = 5). Outer vertical seta present, about half as long as inner vertical. Fronto-orbital plate half as wide as frontal vitta at level of tip of ocellar triangle. 6–7 frontal setae, antennomost at level of junction of scape and pedicel. 1 lateroclnate and 2 proclinate orbital setae. Height of genal dilation about 0.25 x eye height in profile. T6 narrow, undivided. T7 divided. T8 undivided. T6, T7 and T8 invaded from behind by microtrichiae. Epiproct with 2 large and 1 small setae. Cerci setose only in distal half, without microtrichiae. ST6 and ST7 very large, both invaded by microtrichiae on about the posterior two thirds. ST8 small, without microtrichiae, with about 7 large setae set transversely across disc and numerous sensillae. Hypoproct sclerotized apically, where it carries setae. A narrow weakly sclerotized strip in middle. Uterus large and cylindrical. Entrance of common oviduct some distance behind apex on dorsal surface of uterus. A short distance further back a small thick-walled protuberance into which structure open the ducts of the accessory glands and the common spermhecal duct. 3 oval spermhecae present, each with a duct opening into the distal end of the common spermhecal duct. The common spermhecal duct unsclerotized.

Fig. 15. Gulmargia angustisquama, ♀ (G. pr. 328): ST1–5. Scale 1 mm.

First instar larva. – Length 3 mm (not fully outstretched). Posterior end facing genital opening. Dorsally segments 2–5 carry only anterior spine bands (spines directed backwards). Segments 6–9 have dorsally both anterior and posterior spine bands. Segments 10–11 dorsally have only posterior spine bands (spines directed forwards). (In the drawings the spines seem to point in directions opposite to those just described, since the segments are not fully outstretched, and one segment is telescoped partially into the neighbouring segment). Ventrally there are double belts of short stubby spines behind segment 4 or 5. More or less separate spined areas are present laterally behind segment 5. Segment 12 has a transverse opening bordered by bands of filiform spines. This leads into a chamber.
Fig. 16. G. angustisquama, ♀ terminalia (G. pr. 328): dorsal sclerites of ovipositor (stipple indicates extent of microtrichiae). Insets: microtrichiae of intersegmental membranes (upper); sensillae on apical part of cerci (lower) (both in high magnification). Scale 0.5 mm.

carrying the posterior spiracular openings. These are identical to those of Eurychaeta palpalis (Robineau-Desvoidy) (Rognes 1986: 81, fig. 21).
The labrum is a large, strongly sclerotized hook. The mandibles are situated towards the apex of the labrum, each shaped as a well sclerotized rod, carrying a tooth in its anteriormost half. The tentoropharyngeal sclerite is fused with the labrum, and its posterior arms greatly shortened.

Second and third instar larvae, puparium. - Unknown.

Biology. - Unknown. The substrate for larval development is probably dying or dead snails as in Eurychaeta to judge from the size and shape of the first instar mouthparts.

Distribution. - At present only known from NW and W Himalayas (Kashmir and Uttar Pradesh provinces of northern India).

Discussion
In previous papers I have argued that the Helicoboscinae is a calliphorid and not a sarcophagid taxon. There is no need to repeat the arguments of my 1986–paper concerning the postabdominal and aedeagal structure of the adult male and the uterine structure of the adult female, all of which speak decisively against a classification with the paramacronychiine or other Sarcophagidae (cf. also Pape 1989: 14–15). These and other arguments
have not only retained their validity with the discovery of *Gulmargia*, but have received added support with the establishment of at least one new ground-plan feature of the Helicoboscinae: the lateral position of the outer ph seta. Such a position is not found outside the Calliphoridae and it may be a groundplan state of this family.

Recently Verves (1990) and Shewell (1991) have restated their opposition to this classification and reaffirmed that *Eurychaeta* belongs in the sarcophagid subfamily Paramacronychiinae. Verves (1990) seems to believe that I (Rognes 1986) included *Eurychaeta* in the Calliphoridae because of a free male abdominal sclerite T6 and an aedeagus with an acrophallus and an apical ejaculatory opening. This may be based on an inaccurate reading of my paper. Rather, these and other primitive features were discussed because they showed that *Eurychaeta* could not belong in the Paramacronychiinae as this group is usually defined. Quite different arguments were used for assigning it to the Calliphoridae. Unfortunately neither of these are addressed by Verves (1990).

Further, Verves (1990) must have misunderstood my description of the posterior spiracle of the third instar larva of *Eurychaeta* (Rognes 1986) when claiming that it has an interrupted peritreme and when using this error of fact as evidence for classifying the genus with the Paramacronychiinae. He also considers that the helicoboscine male postabdomen with a free and narrow T6 of ordinary calliphorid type and an acrophallus with an apical
sible to consider the presence of a primitive free and narrow T6 in the male postabdomen as an argument for treating *Eurychaeta* (or Helicoboscinae) as the sister group to all other Paramacronychiinae. However, this requires that *Eurychaeta* (or Helicoboscinae) shares synapomorphies with the Paramacronychiinae that are not at the same time shared with the Calliphoridae. Verves does not demonstrate the existence of any such synapomorphies in his paper.

Shewell (1991), hoping I would change my mind concerning the systematic position of *Eurychaeta*, emphasizes that the immature stages should weight heavily when phylogeny of groups is in question and states that 'at the beginning of its ontogeny, *Eurychaeta* resembles a Paramacronychiine Sarcophagid, but at its end it has apparently a mixture of Sarcophagid and Calliphoridae characters'. Unfortunately, Shewell does not explicitly provide any synapomorphic character states in support of his classification.

The relationship of the Helicoboscinae to the other subfamilies of the Calliphoridae is still obscure. Three features of the Helicoboscinae: i.e. lack of metallic colour, bare postalar wall, and a rather small metathoracic spiracle with an anterior lappet much smaller than the posterior one, may all be


The ejaculatory opening is compatible with an inclusion of *Eurychaeta* with the Paramacronychiinae, which he, in the same paper, explicitly redefines as comprising taxa with a full reduction of T6 in the male postabdomen and a ventrally situated acrophallus. This paradox is resolved by assuming that *Eurychaeta* separated off early from the main paramacronychiine stem, before the T6 was 'lost' [actually it is fused with the TST7 + 8, but this appears not to be Vordes' present opinion] and before the acrophallus shifted ventrally. It is of course pos-

primitive at this level (partly opposite my views in Rognes 1991). They may therefore indicate that the Helicoboscinae is the sister group of all other Calliphoridae, or at least that it is an ancient clade of this family.

The acrophallus of Gulmargia is without minute denticles on its outer surface. This unarmed condition is most likely a secondary reduction from the groundplan state of the Helicoboscinae (shown by Eurychaeta) since presence of denticles is the condition in most Calliphoridae (where the outgroup is to be found). Absence of armature of the acrophallus also occurs in the Melanomyinae and Polleniinae (Rognes 1991), here evidently of independent origin.

An interesting feature of the internal reproductive organs of the female Gulmargia angustisquama is the system of spermathecal ducts, with three ducts entering the internal end of a long unscleroidized common duct attached to the uterus via a thick-walled (muscular?) organ. The long narrow acrophallus is possibly inserted into the common duct during copulation. This duct system differs from the one present in its sister group Eurychaeta
where only a very short common duct is present. A system with three ducts joining the inner end of an unsclerotized canal is known in the calliphorid *Angioneura acera* (Meigen) (Melanomyiinae) (Rognes 1991: 190, fig. 500). According to unpublished data, such a system is also present in the calliphorids *Phumosis imitans* (Villeneuve) (Phumosinae) and *Sarconesia magellanica* (Le Guillou) (Toxotarsinae). In a species of *Hemigynnochaeta* Corti (Auchmeromyiinae) the spermathecal ducts enter the uterus directly through three separate openings. A common duct arrangement resembling the one in *Gulmargia* is also found in various sarcophagine and paramacronychiine Sarcophagidae (see figures published by Lopes 1941, 1981, and discussion in Rognes 1991). However, the common spermathecal duct in *Wohlfahrtia magnifica* and *Sarcophila latifrons* (both Paramacronychiinae) is long and strongly sclerotized and basally fused with a smooth concave sclerotized plate (signum) in the dorsal wall of the uterus. In *Wohlfahrtia magnifica* the common sclerotized duct is even distally trifurcating into very short branches receiving the spermathecal ducts. In *Brachicoma devia* (Paramacronychiinae) there is a small sclerotized plate in the dorsal wall of the uterus carrying the spermathecal ducts, but no long common sclerotized duct. In *Parasarcophaga crassipalpis* (Sarcophaginae) there has been found a sclerotized hollow plate or short common stalk (signum) carrying three small sclerotized tubes, one medial (cephalad) and two lateral (caudal), receiving the spermathecal ducts (unpublished drawing received by B. A. Holloway, New Zealand) (cf. also Lopes 1941; Hori 1961). No trace of a signum is found in *Gulmargia*. Possibly a sclerotized signum plate and a common sclerotized duct are further synapomorphies corroborating the clade Paramacronychiinae + Sarcophaginae in addition to those suggested by Pape (1989).

Unfortunately the spermathecal duct system is at present insufficiently known among the Oestroidea to be used with much confidence to resolve problems regarding the phylogeny of the Calliphoridae. However, one may hypothesize that the helicoboscean system with all spermathecal ducts arising from the same point is a primitive one taken over from the ancestors of a more inclusive group comprising the Sarcophagidae and possibly other groups. This implies that the system of a single duct successively sending off two branches, a system assumed to be present in most calliphorids (cf. Rognes 1991), has descended from this.

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