The systematic position of the genus *Helicobosca* Bezzi with a discussion of the monophyly of the calypterate families Calliphoridae, Rhinophoridae, Sarcophagidae and Tachinidae (Diptera)

KNUT ROGNES


The Western Palaearctic genus *Helicobosca* Bezzi, 1906 is described in detail and its systematic position discussed. The monophyly of the calypterate families Tachinidae, Rhinophoridae, Sarcophagidae and Calliphoridae is reviewed. *Helicobosca* is removed from its current position within the subfamily Paramacronychiinae of the Sarcophagidae and transferred to the Calliphoridae, where a new subfamily Helicoboscinae Verves, 1980, stat.n., is erected for its reception. The third stage larva of *H. palpa*i (Robineau-Desvoidy) is described for the first time.

K. Rognes, Havørnbrauten 7a, N-4040 Madla, Norway.

The genus *Helicobosca* Bezzi has been classified both in the Tachinidae (Villeneuve 1924, Lundbeck 1927) and in the Sarcophagidae (Stein 1924; Séguy 1941; Emden 1954; Venturi 1960; Rodendorf 1970; Mihályi 1979; Verves 1980, 1982; Lopes 1982). Current practice is to regard it as a member of the subfamily Paramacronychiinae (Agriniae) of the latter family (Verves 1980, 1982; Lopes 1982). The purpose of the present paper is to argue (1) that it does not belong in that subfamily, (2) that it does not belong in the Sarcophagidae, and (3) that its assignment to the Calliphoridae is the most natural one from a phylogenetic (cladistic) point of view. Furthermore, it is proposed that it should be placed in a new subfamily Helicoboscinae Verves, 1980, stat.n.

Material. The study is based on material of *Helicobosca palpalis* (Robineau-Desvoidy) (26 ♂, 20 ♀, 2 larva I, 1 larva III, 3 puparia), *H. muscari* (Meigen) (5 ♂, 5 ♀) and *H. nigropex* Villeneuve (2 ♂ 1 ♀) in Zoologisk Museum, Bergen (ZMB); Universitetets Zoologiske Museum, Copenhagen (ZMUC); British Museum (Natural History), London (BMNH); Zoologiska Institutionen, Zoologiska Museet, Lund (ZIL); Muséum National d'Histoire Naturelle, Paris (MHNP); and my own collection. Numerous Tachinidae, Rhinophoridae, Sarcophagidae and Calliphoridae and other calypterate groups (including Gasterophilidae, Hypodermatidae and Oestridae) have been available for comparison in ZMB; ZMUC; BMNH; Universitetets Zoologiske Museum, Oslo; Tromsø Museum, Tromsø, the private collection of T. R. Nielsen, Sandnes, and my own collection.

Family CALLIPHORIDAE

Subfamily HELICOBOSCINAE Verves, 1980, stat.n.


*Material.* The study is based on material of *Helicobosca palpalis* (Robineau-Desvoidy) (26 ♂, 20 ♀, 2 larva I, 1 larva III, 3 puparia), *H. muscari* (Meigen) (5 ♂, 5 ♀) and *H. nigropex* Villeneuve (2 ♂ 1 ♀) in Zoologisk Museum, Bergen (ZMB); Universitetets Zoologiske Museum, Copenhagen (ZMUC); British Museum (Natural History), London (BMNH); Zoologiska Institutionen, Zoologiska Museet, Lund (ZIL); Muséum National d'Histoire Naturelle, Paris (MHNP); and my own collection. Numerous Tachinidae, Rhinophoridae, Sarcophagidae and Calliphoridae and other calypterate groups (including Gasterophilidae, Hypodermatidae and Oestridae) have been available for comparison in ZMB; ZMUC; BMNH; Universitetets Zoologiske Museum, Oslo; Tromsø Museum, Tromsø, the private collection of T. R. Nielsen, Sandnes, and my own collection.

*Material.* The study is based on material of *Helicobosca palpalis* (Robineau-Desvoidy) (26 ♂, 20 ♀, 2 larva I, 1 larva III, 3 puparia), *H. muscari* (Meigen) (5 ♂, 5 ♀) and *H. nigropex* Villeneuve (2 ♂ 1 ♀) in Zoologisk Museum, Bergen (ZMB); Universitetets Zoologiske Museum, Copenhagen (ZMUC); British Museum (Natural History), London (BMNH); Zoologiska Institutionen, Zoologiska Museet, Lund (ZIL); Muséum National d'Histoire Naturelle, Paris (MHNP); and my own collection. Numerous Tachinidae, Rhinophoridae, Sarcophagidae and Calliphoridae and other calypterate groups (including Gasterophilidae, Hypodermatidae and Oestridae) have been available for comparison in ZMB; ZMUC; BMNH; Universitetets Zoologiske Museum, Oslo; Tromsø Museum, Tromsø, the private collection of T. R. Nielsen, Sandnes, and my own collection.

*Diagnosis.* As for the single included genus *Helicobosca*, see below.

Genus *Helicobosca* Bezzi

Figs. 1 – 28.


Description

ADULTS

Colour. Ground colour black with silvery or bluish white pollinosity. Palpi bright yellow. Thorax dorsally with three broad black stripes. Abdominal tergites T1–4 with narrow shining black hindmargins and median black stripe, otherwise silvery or bluish grey dusted with more or less shifting pattern according to angle of view. T5 dusted with narrow black hind margin and median black stripe or shining black all over. Wings hyaline or more or less infuscated.

Head. In profile as figured by Venturi (1960: 8) and Verves (1982: 258, 261). First antennal segment erect and projecting. Third antennal segment large and broad, 2.5–3 x as long as second. Arista strongly pubescent in basal half, longest hairs 1.5–3 x as long as width of arista itself at base. Facial carina absent. Parafacialia with an irregular row of hairs, in lower half also with 2–4 very strong setae near eye margin. Usually no minute intrapostocular cilia between posterior eye margin and postocular row of setae. Palpi long, distally widened.

Thorax. Prosternum, propleuron and basisternum (sclerite midventrally between middle and hind coxae) hairy. 5–7 h and 3–4 ph (Fig. 1). The most anterior and smallest h occasionally indistinguishable from the normal humeral vestiture or doubled. Outer ph in line with prst (Fig. 1), or more rarely, definitely exterior to it on one or both sides. 2 strong and 1 weaker npl, notopleuron hairy around bases of large setae. One strong pipl among the hairs. Subalar bulla and supraspiracular convexity (katatergit) bare. Coxopleural streak present. stpl 2+1+1 (Fig. 2). Hairs on surface below lower squama (anatergit). Postalar wall and suprasquamat ridge bare. Beret (katepimeron) hairy. Posterior spiracles operculate, posterior lappet larger than anterior one (Fig. 3). Lappets bare. No hairs along lower margin of spiracular opening. Area immediately above hind coxae (metakatepisternum) bare. acr 5+3, dc 4+4, ia 0–1+3, pra 1, sa 2 with 1–2 additional smaller setae between pra and first sa, pa 2 with a small seta medial to posterior one. On each side of anterior slope of thorax at level with anteriormost acr a transverse row of about 4–6 setae much stronger than normal thoracic vestiture. Scutellum with at least 2 pairs of discals and apical, subapical, lateral, basal and weak prebasal marginals (Fig. 4). Hindmost discals sometimes erect and spiny. Apicals crossed, only slightly shorter than the other marginals which are of uniform size and about 2 x as long as scutellum. Lateral sometimes doubled or tripled. Subscutellum slightly swollen and definitely convex with an even surface.

Wings. Vein pattern as figured by Ségy (1941: 175). Basiscosta black. Subcostal sclerite bare. Stem vein bare above and below. Node at junction of r2+3 and r4+5 with 3–5 setulose hairs above and below. Costa with hairs on ventral surface from base to junction with r1 or slightly beyond. No costal spine. Veins otherwise bare. Both squamae white, bare on disc, lower one broad distally with inner edge converging backwards with longitudinal axis of fly. Halteres dark.

Legs. Fore tibia with a row of strong ad in basal two thirds, 3–5 pd and 2 p on shaft, preapical ad of same size as or slightly longer than preapical d. Mid tibia with 3–5 strong ad, 3–5 pd, 2–3 p and 1 v. Med femur without a preapical and without pv preapical comb. Hind tibia with 2–4 av, rows of strong ad and pd, strong preapical ad, d and pd of uniform size, strong av and pv preapicals. Hind coxa bare behind. Hind metatarsus with short but conspicuous v near base.

Preabdomen. Relatively broad. T1–2 excavated to hind margin, without marginals. T3 with 2–4 strong erect median marginals and 2–3 lateral marginals on each side. T4 and T5 each with 12–16 very strong, erect and evenly spaced marginals.
Figs. 1–6. *Helicobosca palpata*; ♀. – 1. Left anterior corner of thorax, dorsal view. – 2. Upper posterior corner of left sternopleuron, lateral view. – 3. Left posterior thoracic spiracle, lateral view. – 4. Scutellum, dorsal view. – 5. ST5, ventral view. – 6. Postabdomen, left posterolateral view, epandrium removed. (In 1–4 only bases of strong setae are shown.)
No discals present on any tergite. ST1 hairy, ST2–4 widely exposed, margins overlapped by margins of corresponding tergites. ST5 in ♀ with prominent lobes with long setulose hairs (Figs. 5, 6). Sternites usually without alpha-setae on front margin, although a single alpha-seta was present on one side in a ♀ H. palpalis (4 dissections), and a pair on ST3 in a ♀ (3 dissections).

Postabdomen of ♀. As shown in Figs. 6–12. T6 free, rather narrow, T7+8 with 5–7 strong setae centrally on disc, spiracle VI in membrane, spiracle VII within T7+8.


Internal reproductive organs of ♀. As shown in Figs. 15–20 (cf. also Kholodkovskii 1907, 1908a, 1908b). Uterus large, simple and cylindrical, projecting anteriorly beyond entrance of common oviduct as a blind pouch, very well supplied with large calibre tracheae from the two spiracle pairs on T6. Ovaries strongly asymmetric, each apparently with a single ovariole. 2 accessory glands. 3 oval spermathecae. For some reason the figure given by Kholodkovskii (1908a: 117, 1908b: 373) shows the uterus not to project anteriorly beyond the entrance of the common oviduct to any significant extent, even though the uterus of the females he states to have examined contained either an embryo or a large larva.

IMMATURE STAGES

Eggs. Very large, rich in yolk (Figs. 16, 17).

Larva I. As figured by Nielsen (1917: XX), Thompson (1921a: plate XVII, figs. 124, 133) and Séguy (1941: 8). Cuticular spines black. Very large hook-shaped median hook, and two strong but smaller lateral hooks on each side, each with a ventral tooth at middle. Arms of pharyngeal
sclerite slender, no anterior process portion present. Posterior spiracular field can be hidden completely by transverse folding and apposition of dorsal and ventral halves. Posterior spiracles as shown in Fig. 21. I have not been able to find two slits in each spiracle as illustrated by Thompson (1921a: plate XVII, fig. 133).

* Larva II. Unknown.

* Larva III. As shown in Figs. 22-27. Size 14 mm (in alcohol). Cuticular spines small and unpigmented except those immediately behind anal aperture which are black. Pharyngeal sclerite weakly sclerotised only anterodorsally, without posterior incision in dorsal cornu. Salivary gland ducts sclerotised for a considerable distance. Posterior spiracular field encircled by 7 pairs of small papillae, somewhat depressed, and can be closed by transverse folding and bringing together of dorsal and ventral halves. Spiracular plates completely sclerotised, flush with surrounding surface of spiracular field. Slits straight, parallel and more or less horizontal. Button large and medial.

* Puparium. As shown in Fig. 28. Posterior spiracular field shallow.

**Reproductive habit**

The female deposits one larva at a time, which is a large larva I (5-7 mm), at intervals of about two weeks, on dying or dead snails. The following have been recorded as the substrate for larval development in *H. muscoria* and *H. palpalis*; *Theba pisana* (Müller, 1774), *Cepaea hortensis* (Müller, 1774), *Cepaea nemoralis* (Linnaeus, 1758).

---

Arianta arbustorum (Linnaeus, 1758), and Helix pomatia (Linnaeus, 1758) (Pulmonata, Helicidae) (names after Kerney & Cameron 1979) (Per- ris 1850; Schmitz 1910, 1917; Nielsen 1917; Keilin 1919; Lundbeck 1927). No records exist for H. nigrapex.

DISCUSSION

The problem of the current classification of Helicobosca

The subfamily Paramacronychiinae of the Sar- cophagidae is characterised by the following apo- morphies, all concerning the 5 postabdomen: (1) T6 and T7+8 fused into a single large sclerite in front of the epandrium, bearing at least a trans- verse row of strong setae near the fore margin and behind this row with a trace of a suture indicating the posterior border of the T6 part, (2) enclosure of spiracles VI and VII within this sclerite, (3) processi longi absent or very strongly reduced, (4) phallosome usually with various ventral appendages and a ventral opening of the ejaculatory duct (cf. Rodendorf 1950, 1957, 1962, 1967, 1969; Séguy 1941; Zumpt 1952, 1956b; Roback 1954; Kano, Field & Shinonaga 1967; Shewell 1971; Kurashashi 1972, 1975; Lopes 1982; Verves 1982). The absence in Helicobosca of all these apomorphies indicates that its current classification in the Paramacronychiinae is wrong.

The problem remains as to where it should be correctly classified. It is definitely a calyptrate genus and the presence of a row of strong setae on the hypopleuron and an undivided ST8 in the ovi- positore make Helicobosca a member of the group Calliphoroidea of Hennig (1958, 1973, 1976) (= Tachinidae s.lat. of Griffiths 1972) (= Oestroidea of McAlpine et al. 1981). According to Hennig (1976: VI–VII) this group probably consists of two monophyletic sister-groups, the group Calli- phoridae + Rhinophoridae + Sarcophagidae + Tachinidae on the one hand and Oestroidea s.lat. (= Cuterebridae + Gasterophilidae + Hypoder- matidae + Oestroidea s.str.) on the other, the latter being parasites of mammals in the larval stages. (Hennig also included Stackelbergomyiidae in the former group but the only included genus, Stackelbergomyia Rodendorf, has recently been transferred to the Tachinidae by Herting 1981).

However, a row of strong setae on the hypopleu- ron may be an autapomorphy of the group Calli- phoridae + Rhinophoridae + Sarcophagidae + Tachinidae only. In Oestroidea s.lat. the hypopleu- ron is usually bare or partly clothed with densely set long hairs (Grunin 1964–1969, 1966–1969, 1969). Both Griffiths (1972) and Hennig (1973) seem to regard this condition as derived from or similar in nature to the one in Calliphoridae + Rhinophoridae + Sarcophagidae + Tachinidae, but I consider this claim as unsubstantiated.

Helicobosca is definitely a member of the monophyletic group Calliphoridae + Rhinophoridae + Sarcophagidae + Tachinidae. The monophyly of the constituent families and the possibility of assigning Helicobosca to any particular one of them are discussed below.

Note on terminology: In the discussion to follow I have used the term apomorphous (without qualification) for derived characters in general. Those unique (inside Tachinidae + Rhinophoridae + Sarcophagidae + Calliphor- idae) for the group under consideration have in addition been qualified as autapomorphous. Features listed as apomorphous (without qualification) for the particular family under consideration occur, with varying frequency, in other families of the group Tachinidae + Rhinophoridae + Sarcophagidae + Calliphoridae also. Note that both terms are employed relative to the presumed conditions in the ancestor of the group Tachinidae + Rhinophoridae + Sarcophagidae + Calliphoridae. The corresponding primitive (plesiomorphous) i.e. ground-plan condition of the ancestor is implicit in the discussion and often not specified.

TACHINIDAE

Monophyly

The Tachinidae are probably a monophyletic group with the following apomorphies: (1) mouthparts of larva I with strongly developed median hook, paired mouth-hooks absent (presumed plesiomorphous condition: moderate sized median and paired mouth-hooks both present), (2) larva III without parastomal bar on the pharyngeal sclerite, (3) adult with strongly developed
subscutellum, (4) larvae parasitic, mostly in insect larvae (Herting 1960; Hennig 1973; Rikhter & Farinets 1983). Item (1) and (3) are probably autapomorphic, even though some Calliphoridae (Ameninae, Mesembrinellinae), Oestrata (Oestridae) and Gasterophilidae also have rather strongly developed subscutellum (cf. Hennig 1958, 1973; Crosskey 1965; Guimarães 1977).

Possibility of assigning Helicobosca to the Tachinidae

Helicobosca shows none of the apomorphies listed for Tachinidae and cannot be classified with that family.

RHINOPHORIDAE

Monophyly

The Rhinophoridae are probably a monophyletic group with the following apomorphies: (1) mouthparts of larva I without median hook (pleuron morphous condition: see above), (2) paired mouth-hooks of larva I each with 2 strong or several small teeth (pleuron morphous condition: only a single pointed projection present), (3) larva I with very elongate anterior process of the pharyngeal sclerite, (4) larva I with very characteristic external morphology, unique among calyptrates, (5) larva III without parastomal bar on the pharyngeal sclerite, (6) larvae normally parasitic in isopod crustaceans (I do not consider Angioneura Brauer & Bergenstamm, some species of which are recorded as parasite of snails, to be a rhinophorid genus, see discussion below under Calliphoridae), (7) adult with posterior thoracic spiracle small, subcircular and non-operculate with small subequal anterior and posterior fringes (probable pleuron morphous condition: posterior thoracic spiracle operculate with relatively large posterior and narrow anterior lappet, cf. discussion of this point below under Calliphoridae), (8) adult with lower squama small, tongue-like or subcircular, widely removed from scutellum (Bedding 1973; Crosskey 1977) (probable pleuron morphous condition: lower squama broad distally, inner edge following scutellar margin and converging backwards with long axis of fly). Items (2), (3), (4) and (6) are probably autapomorphous.

All rhinophorids have bare thoracic surfaces (propleuron, prosternum, postalar wall). This character is probably plesiomorphic and cannot be used to prove the monophyly of the group. Note, however, that if the group is regarded as a subfamily of the Calliphoridae (see discussion below under Calliphoridae), then the bare condition may represent reversal from the presumed hairy condition in the ancestral Calliphoridae (pseudoplesiomorphy). Note also that the immature stages and reproductive habit of the majority of rhinophorids are unknown.

Possibility of assigning Helicobosca to the Rhinophoridae

None of the apomorphies listed above for Rhinophoridae are present in Helicobosca and it cannot be classified with that family.

SARCOPHAGIDAE

Monophyly

The Sarcophagidae are probably a monophyletic group with the following apomorphies: (1) larva III usually with deeply recessed posterior spiracles, the cavity being retained in the puparium in the majority of forms, (2) larva III with slits of posterior spiracles parallel, proceeding more or less vertically from button which is ventral and often indistinct or absent (probable pleuron morphous condition: slits parallel, radiating more or less horizontally from button which is distinct and medial), (3) larva III usually with deep posterior incision in dorsal cornu of pharyngeal sclerite, (4) adult ♀ with heart-shaped, double-sac type of uterus, openings of common oviduct, accessory gland and spermathecal ducts close to external opening, (5) abdominal sternites without alphastae near anterior edge, (6) ovoviviparous or viviparous reproduction with several eggs or larvae I deposited at the same time (Thompson 1921a; Allen 1926; Maneval 1929; Cuthbertson 1939; Roback 1951; Arthur & Coppel 1953; Schuman 1954; Dowes 1955; Hori 1961; Zakharova 1966; Ishii 1967; Draber-Možko 1973; Day & Smith 1980; Teskey 1981a, 1981b). Items (1), (2) and (3) are probably autapomorphous. As the posterior spiracles do not appear to be very recessed in Miltogramminae or Macronychiinae and the posterior incision of the dorsal cornu of the
Pharyngeal sclerite is sometimes absent, items (1) and (3) may perhaps be more correctly interpreted as underlying synapomorphies in the sense of Sæther (1979, 1983).

Other characters used to diagnose the Sarcoptagradae (especially from the Calliphoridæ) such as lack of intrapostocular cilia (Hall 1948), position of outer ph seta (on line with or medial to a line through prst seta) (Mesnil 1944; Zumpt 1956a, 1956b), and black non-metallic colour are probably plesiomorphous and cannot be used to establish the monophyly of the group.

Possibility of assigning Helicobosca to the Sarcoptagradae

Helicobosca does not show apomorphies (1), (2), (3), (4) and (6) listed above for Sarcoptagradae and cannot be classified in that family. The adults usually lack alpha-setae on all abdominal sternites (item (5)) but this is insufficient evidence on which to base a classification in that family.

CALLIPHORIDÆ

Monophyly

The Calliphoridæ are probably a monophyletic group with the following apomorphies: (1) adults with thoracic surfaces prosternum, propleuron, postalar wall and basisternum hairy, (2) adult ♂ with distal end of each parapleural process well sclerotised, free from wall of distiphallus for a considerable distance and shaped as long narrow process, hook or denticulated or bare plate. Item (2) is probably autapomorphous.

Item (1) appears to apply to the majority of Calliphoridæ but not all genera have all these surfaces hairy. For example, Melanodexia Williston, Nepenthomyia Kurahashi & Beaver, Nesodexia Villeneuve, and most Pollenia Robineau-Desvoidy have only the postalar wall hairy, Eggitops Rondani only the propleuron, Rhyncomya Robineau-Desvoidy and Stomorhina Rondani only the prothorax, Opsodexia Towsend the propleuron, prosternum and basisternum but not the postalar wall, and Bengalia Robineau-Desvoidy only the prosternum and postalar wall. Onesioplisa umbrosa Villeneuve (cf. Zumpt 1956b) and Verticil Malloch (cf. Senior-White, Aubertin & Smart 1940; Tumrasvin, Kurahashi & Kano 1979) have all these surface bare. It is therefore possible that item (1) should be interpreted as an example of an underlying synapomorphy in the sense of Sæther (1979, 1983). Alternatively, absence of hairs on one or more of the surfaces may represent secondary losses.

Available information indicates that the ancestral Tachinidæ (cf. information in Crosskey 1973), Rhinophoridæ (Crosskey 1977) and Sarcoptagradae had all these surfaces bare. In the Tachinidæ only the Goniineæ regularly have the prosternum hairy, and the propleuron is only sporadically hairy throughout the family. In the Sarcoptagradae only the relatively apomorphic subfamily Sarcoptagrinae appears to have them regularly hairy (but the propleuron hairy only in some groups, cf. Rodendorf 1963, 1965). In its sistergroup, the subfamily Paramacronychineæ (cf. Rodendorf 1967), all genera have bare surfaces except Dexagria Rodendorf (propleuron hairy) (Rodendorf 1978; Verves 1982). All Macronychineæ have the thoracic surfaces bare (cf. Verves 1982, 1983). The same applies to the Mitogramminæ where the exceptions are also very few, e.g. Curranitopia Zumpt (cf. Zumpt 1961) (propleuron with dark setae).

Item (2) seems to be applicable to all calliphorids except e.g. Onesia Robineau-Desvoidy where the parapleural processes have been secondarily reduced in several species (cf. Schumann 1973). Illustrations of calliphorid phallosomes and their variously shaped parapleural processes can be found in e.g. Séguy (1928, 1941), Patton & Cushing (1934a, 1934b), Patton (1935, 1936), Hall (1948), Thomas (1951), Zumpt (1956a, 1956b, 1962), Crosskey (1965), Kano & Shinonaga (1968), Lehrer (1972), Dear (1977, 1979), Guimarães (1977), Kurahashi (1977, 1978), and Rognes (1985). No Tachinidæ (cf. Verbeke 1963) or Sarcoptagradae (cf. e.g. Rodendorf 1930, 1935, 1937; Verves 1982) appear to satisfy item (2). For Rhinophoridæ, see discussion below. Note that within Oestridae s.lat. two hook-shaped parapleural processes not unlike those in many Calliphoridæ are present in Hypodermatidæ but not in Gasterophilidæ or Oestridae s.str. (cf. figures in Grunin 1964–1969, 1966–1969, 1969). To judge from a dissected ♂ Oedemagenæ tarandi (Linnaeus), these processes are completely fused with the wall of the distiphallus, with at most their extreme tips free.
Further characteristics of the Calliphoridae

**Distiphallus.** Many calliphorids have a midventral mesohypophallic sclerotisation in the distiphallus which is usually articulated or fused basally with the pair of ventral projections from the basal part of the paraphallus (Salzer 1968; Rognes 1985). The ventral projections themselves also seem to be fused midventrally into a ring-shaped structure at the base of the distiphallus in numerous calliphorid groups. The nature and distribution of the mesohypophallic sclerotisation are still not known very well because most authors usually figure phallosomes only in profile. However, it is also present in all Rhinophorinae I have seen, and even in some Tachininae (Dexiosoma caninum (Fabricius), Tachina fera (Linnaeus)). I have never seen a similar structure in Sarcophagidae.

**Posterior thoracic spiracle.** Most adult calliphorids have a posterior thoracic spiracle with distinct anterior and posterior lappets. It may be rather small with lappets of about the same size (Eggisops), medium sized with anterior lappet narrower (shorter) than posterior one (Melanodexia, Nesodexia, Polenina, Rhycomyia, Stomorrhina, Verticia), or of varying size (often very large) with anterior lappet larger than posterior one (sometimes very much so). In some Sarcophagidae (Amobia Robineau-Desvoidy, Oeobalia Robineau-Desvoidy and Macrorychini) the posterior spiracle is as in Rhinophorinae, i.e. without lappets and only two subequal fringes present. In most Sarcophagidae and Tachinidae the posterior spiracle is of the type with large posterior and narrow anterior lappet. This is probably the type present in ancestral Calliphoridae and other types should be considered derived from this and therefore apomorphous.

**Intrapostocular cilia, position of outer ph, metallic colour.** Some characters used to diagnose the Calliphoridae such as presence of intrapostocular cilia (Hall 1948), position of outer ph seta, when present, outside of line through prst seta (Mesnil 1944), and metallic body colour, are probably apomorphous, but will not define the whole of Calliphoridae in the currently accepted sense (Zumpt 1956a; Crosskey 1965) nor as understood here. Intrapostocular cilia are absent in Rhiniinae (Hall 1948) and occasionally elsewhere, e.g. in Melanodexia (Hall 1948) and Ameniinae (Crosskey 1965). They are also absent in Eggisops pec-

chioli Rondani and Nesodexia corsicana Villeneuve. Note that such cilia are also present here and there in Tachinidae (e.g. Dexiosoma caninum, Tachina fera). There are also several undoubtedly calliphorid genera which have the outer ph seta in plesiomorphous position, e.g. Polenina, Melanodexia, Nesodexia and the majority of Ameniinae (Crosskey 1965). Finally, a number of calliphorids are non-metallic, e.g. Eggisops, Melanodexia, Nesodexia, Polenina (black ground colour) and Auchmeromyia Brauer & Bergenstamm, Bengalia, Cordylobia Grünberg, Tricycletia Wulp, Verticia (yellow ground colour). Whether absence of intrapostocular cilia, plesiomorphous position of the outer ph seta (in line with prst seta) and black non-metallic colour in these cases are primary or represent secondary reversals to ancestral conditions are questions that are very difficult to decide.

**Assignment of Helicobosca**

**General conclusion.** Helicobosca shows both apomorphies listed above for the Calliphoridae and should accordingly be classified in this family. It even has a mesohypophallic sclerotisation and the ventral projections from the basal part of the paraphallus fused midventrally into a ring-like structure at the base of the distiphallus. Moreover, as will be clear from the discussion given above, there is no real reason for rejecting this classification on the grounds of the primitive posterior spiracle, lack of intrapostocular cilia, primitive position of the outer ph seta and black non-metallic colour of the adult. However, certain features of the larval and adult morphology and the reproductive biology need some additional comments.

**Cephalopharyngeal skeleton of larva I.** The larva I of the Calliphoridae may have either a median hook and a pair of lateral hooks (plesiomorphous) or only a pair of lateral hooks (apomorphous) (Thompson 1921b; Schumann 1954, 1964, 1974; Guimarães 1977; Lopes 1982). Helicobosca fits into this pattern even though the mouth-hooks are enormously hypertrophied, particularly the median one. Some Paramacronychiinae also have strongly developed mouth-hooks reminiscent of those of Helicobosca (e.g. Nyctia halterata (Panzera), Paramacronychia flavipalpis (Girschner), cf. Thompson 1921a), but this must be due to convergence, an interpretation supported by discre-
pancies in several details of the morphology of the various parts of the cephalopharyngeal skeleton.

Posterior spiracular field of larva. The posterior spiracles of the larva I and III can be completely hidden by transverse folding of the spiracular field upon submergence of the larva into the substrate. The resulting depression does not appear to be homologous with the pit present in Sarcophagidae, which, according to Teskey (1981a), cannot be closed completely, and which is also retained in the puparium. A depression rather similar to that in the *Helicobosca* larva is present in the larva I and II of Ameniinae (Ferrar 1976) and in the larva III of *Cochliomyia hominivorax* (Coquerel) (Chrysomyiinae) (judged from puparium).

Slit pattern of posterior spiracles of larva III. This is similar to the pattern of most Calliphoridae, and the calliphorid pattern appears to be unique among the families of the Calliphoroidea (cf. Ishijima 1967; Oldroyd & Smith 1973; Teskey 1981b). Nevertheless, even though it is difficult to arrange slit patterns in a character transformation series, the calliphorid pattern may very well be plesiomorphous as rather similar arrangements also appear to be present in some members of Henning's (1973) group Muscoidae, viz. Scathophagidae, Anthomyiidae, Muscidae (cf. Thomson 1937; Roback 1951; Dušek 1971).

Humeral chaetotaxy. The high number (4-5 or more) of setae in *Helicobosca* is probably apomorphous. This is a rather common feature in Calliphoridae and Tachinidae, but very rare in Sarcophagidae, where most specimens seem to have 3 (I have only seen some specimens of the sarcophagine genus *Blaesoxipha* Loew with higher numbers). The normal number in Rhinophoridae also appears to be 3 (Herting 1961). However, a high number only occurs here and there in Calliphoridae, which indicates independent acquisition several times.

Scutellar chaetotaxy. The high number of marginal scutellar setae in *Helicobosca* is probably apomorphous. It is a common feature in Calliphoridae and Tachinidae. Most Sarcophagidae have only 3 pairs. Rhinophoridae also have a low number.

Notopleural chaetotaxy. The extra *npl* seta in *Helicobosca* is rather unusual. All Calliphoridae have 2, except some Phormiinae, where one or more extra *npl* may occur secondarily (cf. Rognes 1985). In Sarcophagidae the usual number is 2, but the subfamily Sarcophaginae have 4 except *Sarcophagula* Wulp which has 2 (Roback 1954). The most parsimonious character transformation would be the sequence 2-3-4, which would link *Helicobosca* with the Sarcophaginae. This appears quite improbable, and the extra seta must be an independent acquisition.

Abdominal sternites. Widely exposed abdominal sternites and a ST2 overlapped laterally by margins of T2 are rather unusual in Calliphoridae, but occur e.g. in *Eggisops pecchioli*, *Opsodexia flavipennis* (Coquillet) and in Ameniinae. This feature is of general occurrence in the Rhinophoridae (but apparently only in some species of *Mimodexia* Rodendorf) (note that *Mimodexia* has been transferred from the Sarcophagidae to the Rhinophoridae by Herting in his forthcoming contribution for the Catalogue of Palearctic Diptera, Herting in litt. 22.ii.1985; see also Rodendorf (1935, 1937, 1961), Lehrer (1972), and Lopes (1982) as to opinions on the systematic position of this genus). It is difficult to judge whether it is apomorphic or plesiomorphous, but most Calliphoridae and apparently all Sarcophagidae have a large ST2 covering margins of T2. Most Tachinidae have narrow ST2-4 all of which are overlapped and almost hidden by the ventral margins of the tergites (Villeneuve 1924; Lundbeck 1927; Mesnil 1944; Crosskey 1973).

Alpha-setae. In most Calliphoridae and several Rhinophoridae a pair of alpha-setae is present on the anterior edge of the abdominal sternites and this is apparently a primitive calyptrate feature (cf. Griffiths 1972). Their absence in most specimens of *Helicobosca* might be construed as indicating close relationship with the Sarcophagidae. However, this interpretation should not be accepted. It is easy to imagine independent loss of these setae, and in the Calliphoridae they are also absent in e.g. *Onesia sepulcralis* (Meigen), *Bengalia* and Ameniinae. Neither have I found them in any tachinid, but have not made extensive searches.

Viviparity. All Sarcophagidae are viviparous or ovoviviparous, producing a fairly large number of larvae I or eggs hatching into larvae I soon after being deposited. As most Calliphoridae are oviviparous, the ancestral Calliphoridae probably were
too. However, some calliphorid taxa are viviparous, e.g. *Bellardia* Robinieu-Desvoidy, *Eggisops*, *Onesia* (all giving birth to a large number of small larva I), *Euphemosia* Malloch (giving birth to a single large larva I or II), *Amenini* (giving birth to a single large larva II) and *Mesembrinellinae* (giving birth to a single large larva I). I consider this latter group as belonging to the Calliphoridae: see discussion below) (Thompson 1921b; Emden 1953; Schumann 1964, 1974; Crosskey 1965, 1969; Ferrar 1976, 1978; Guimarães 1977). These taxa do not compose a monophyletic group, and viviparity must therefore have been acquired independently several times in the Calliphoridae. It is an interesting point that so far no *Sarcophagidae* is known to be macrolarviporous (= unlarviparous) (Ferrar 1976). (Herting (1957: 444) reported *Nectia halterata* as macrolarviparous, but Thompson (1921a: 433) extracted several larvae from single females.) This is possibly a reflection of the uterine structure. It would not seem to “make sense” for an organism regularly to raise a single large larva in a double-sac heart-shaped type of uterus. A relatively primitive cylindrical uterus is present in all forms with macrolarviparous reproduction (Amenini, *Mesembrinellinae*, *Euphemosia*, *Helicobosca*, some *Musca Linnaeus*, *Glossinidae*, *Pupipara*) (Patton & Cragg 1913; Keilin 1916; Davey 1965; Ferrar 1976, 1978; Guimarães 1977) and may therefore have been a prerequisite for its development in calyptrate Diptera.

**Unique features.** *Helicobosca* has two features which appear to be unknown elsewhere in the Calliphoridae, i.e. very strong setae on the lower half of the parafacialia (which also occur here and there in *Rhinophoridae*, *Sarcophagidae* and *Tachinidae*), and a pattern of 2+1+1 stipl setae (which also occur here and there in *Sarcophagidae* and *Tachinidae*). (seen even in freak specimens of the calliphorids *Lucilia bufonivora* Moniez, *Pseudonota puberula* (Zetterstedt) and *Onesia sepulcralis* (Meigen)). As the genus does not fit particularly well into any of the currently recognised calliphorid subfamilies (Zumpt 1956a, 1956b; Crosskey 1965; Dear 1979) or other groups assignable to the Calliphoridae (Mesembrinellinae), I propose that a new subfamily, Helicobosca Verves, 1980, stat.n., be erected for its reception pending a phylogenetic analysis of the genera of the Calliphoridae on a world basis.

**Reclassification of other taxa**

The definition of the Calliphoridae proposed above has some consequences on the classification of other calyptrate taxa, as well as *Helicobosca*. These will be discussed below.

**MESEMBRINELLINAE**

This mainly Neotropical group satisfies both items in the list of calliphorid apomorphies and should therefore be classified as forming part of that family. (Guimarães 1977), apparently inspired by Crosskey (1965), ranked it as a separate family. Previously it had always been considered a subfamily of the Calliphoridae (Hall 1948; Hennig 1973).

**RHINOPHORIDAE**

According to material available to me, 4 genera currently placed in the Rhinophoridae (Crosskey 1977), viz. *Angioneura* Brauer & Bergenstamm, *Melanonyma* Rondani, *Morina* Robinieu-Desvoidy and *Phyto* Robineau-Desvoidy, have genitalia satisfying item (2) in the list of calliphorid apomorphies. This item also seems to apply to *Mimodexia* (cf. Rodendorf 1935: 99, fig. 81) (treated as a rhinophorid by Herting in his forthcoming contribution for the Catalogue of Palaearctic Diptera, Herting in litt. 22.ii.1985).

Nothing is known of the immature stages of *Mimodexia*, but its thoracic surfaces prolater, prothorax and postalar wall are bare (Herting in litt. 22.ii.1985).

As for *Phyto*, its immature stages are known (Thompson 1934; Bedding 1973). It is definitely a rhinophorid, and also fails to fulfil the other item in the list of calliphorid apomorphies.

**Angioneura**, two Nearctic and one Palaearctic species of which have been recorded as parasites of snails (Reinhard 1929; Downes 1965; Čepelák & Rozkošný 1968), was classified in the Calliphoridae by Downes (1965). The slits of the posterior spiracles of the larva III of *Angioneura cyrtoneura* (Zetterstedt) (figured by Čepelák & Rozkošný 1968) are arranged much as in calliphorids. The spiracles are not borne on a cylindrical protuberance at the end of the puparium (to judge from Čepelák & Rozkošný's figure) which is not agreement with known rhinophorid puparia (cf.
Systematic position of Helicobosca Bezzi 89

Abbreviations used in figures:
acc - accessory glands
com - common oviduct
hph - hypophallic lobes
molph - mesohypophallophic sclerotisation
pph - distal end of paraphallic process
re - rectum
sp - spermathoe
ut - uterus

Acknowledgements. I wish to thank the following colleagues for the loan or gift of material, helpful discussions, valuable information, comments on previous drafts of the manuscript and other assistance: O.A. Sether, ZMB; H. Schumann, Zoologisches Museum an der Humboldt-Universität zu Berlin; S. Andersen, L. Lynenborg, V. Michelsen, T. Pape, ZMUC; A. C. Pont, BMNH; R. Danielsson, ZIL; G. E. Shewell, Biosystematic Research Institute, Ottawa; L. Matile, MHN; T. R. Nielsen, Sandnes, and B. Herting and H. P. Tschorsnig, Staatliches Museum für Naturkunde, Stuttgart. Visits in 1984 to ZMUC and BMNH were made possible through a grant (D. 68.40-023) from Norges Almenviskapskapitalkasse Forskningsråd.

References
Cuthbertson, A. 1939. On the biology of Cricotylina tabaniformis F., (Diptera; Sarcophagidae) which

Thompson 1934). Angioneura acera (Meigen) has the prosternum and occasionally the basister- num hairy (and even odd hairs on the postalar wall in freak specimens), thus also (partly) satisfying item (1) in the list, an operculate posterior spiral, and a distally broad, calliphorid-like lower squama. The ovipositor, which is rather elongate and distally somewhat shovel-shaped, has the supra-anal plate (“Endtergite” of Herting 1957) fused with T8 and the cerci reduced to broad and low wart-like protuberances almost devoid of vestiture. In these respects it resembles the ovipositor of the calliphorid genera Melinda Robineau-Desvoidy and Eggisops, also known to parasite snails (Keilin 1921; Thompson 1921b).

Melanomya (monotypic) was also classified in the Calliphoridae by Downes (1965). It occasionally has some hairs on the prosternum (Crosskey 1977), thus (partly) satisfying item (1) in the list of calliphorid apomorphies. Its ovipositor is likewise elongate and has the same peculiarities as described above for A. acera (cf. Herting 1957). It is probably also a snail parasite. Furthermore, the posterior thoracic spiral of the adult is quite long anteroposteriorly and low dorsoventrally, rather different from the typical rhinophorid spiral.

As for Morinia, M. melanoepta (Fallén) has some rather strong hairs on the postalar wall, thus also (partly) satisfying item (1) in the list of calliphorid apomorphies. The phallosome structure is very similar to that of some Pollenia (triangular, distally pointed hypophallic lobes strengthened centrally by broad sclerotisation, long and slender paraphallic processes) (cf. also Khitsova 1983) (note that fig. 445 in Séguy 1941: 343 is definitely not M. melanoepta, but most probably Nyctia halterata). Its ovipositor, also very Pollenia-like, has a full length ST8 (cf. Herting 1957). Herting (1961) lists further peculiarities of this genus.

As long as the immature stages of these three genera are unknown a better case can be made for assigning them to the Calliphoridae rather than to the Rhinophoridae. However, the Rhinophoridae (deprived of Angioneura, Melanomya, Morinia) still remains a problematic group. The structure of the phallosome suggests that it may be a monophyletic subgroup within the Calliphoridae as defined here. I am therefore in favour of viewing it as a subfamily of the Calliphoridae. However, a full discussion of this problem is beyond the scope of this paper.


1919. On the life-history and larval anatomy of *Melinda cognata* Meigen (Diptera Calliphoridae) parasite in the snail *Helicella (Helionaneses) virgata* daCosta, with an account of the other Diptera living upon molluscs. — Parasitology 11: 430-455, pls. XXII-XXV.


Systematic position of Helicobosca Bezzi 91


Rikter, V. A. & Farinet, S. I. 1983. Lichinki I vozrasta takhmov podsem. Dexiniae (Diptera, Tachin-


1964. Revision derGattung Onesia Robineau-


— 1934. The tachinid parasites of woodlice. — Para-
sitology 26: 378–448, pls. XV–XXII.


Revised manuscript accepted September 1985.