

A study of the male abdomen of *Gyrostigma rhinocerontis* Hope (Diptera: Gasterophilidae), the stomach bot of the African rhinoceroses, with notes on the ground plan and affinities of Gasterophilidae

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Our knowledge of the anatomy of the male abdomen of *Gyrostigma rhinocerontis* Hope is reviewed. A description of the male abdomen of this species is given, and by means of a comparison with *Gasterophilus* (esp. *Gasterophilus pecorum* (Fabricius)), a list of the more fundamental characters of Gasterophilidae is produced. Several features in the list suggest that Ephydroidea could be the area of origin for Gasterophilidae, as well as what are here regarded as that family's closest relatives, namely Glossinidae-Hippoboscidae and Oestridae.

KEYWORDS: Phylogenetics, *Gyrostigma*, Gasterophilidae, Oestridae, Ephydroidea, Calyptratae, genitalia.

Introduction

Through the kindness of the Director, Natal Museum, Pietermaritzberg, South Africa, and Dr D. A. Barraclough, I received from the Museum a specimen of a male *Gyrostigma rhinocerontis* Hope, to assist in the study of the male genitalia of this interesting fly, the stomach bot fly of the African rhinoceroses. It was hoped that the anatomy would, taken in conjunction with what is known concerning the better researched *Gasterophilus* spp., throw light on the ground plan and affinities of gasterophilid flies. Zumpt (1962) mentioned that the segmentation of the abdomen and the hypopygial structure of *Gyrostigma* Brauer were as in *Gasterophilus*, citing the work of Patton (1935) in respect of the latter genus; he provided figures of the anal cerci and parolobi (postsurstyli of the present paper) of the male *Gyrostigma rhinocerontis* (under the synonym of *G. pavesii* (Corti)), and of the aedeagus. These appear to be the only published figures concerning the male abdominal anatomy of *Gyrostigma*, and there is certainly a large gap in our knowledge of such anatomical details. In the course of the present work it was found that indeed the anatomy of *Gyrostigma rhinocerontis* did resemble that of a large *Gasterophilus*, and the anatomical concordance between the two genera, *Gasterophilus* and *Gyrostigma*, makes a listing of ground plan features of the family quite straightforward. However, the

conclusions that we should draw from this proposed ground plan are very much open to debate.

The overall view taken here is that the clade Gasterophiloidea (i.e. Gasterophilidae + Glossinidae-Hippoboscidae) is the sister group of Oestridae (comprising Oestrinae, Hypodermatinae, the anomalous oestrids such as *Cobboldia* and *Ruttenia*, and Cuterebrinae), and that this whole complex, Gasterophiloidea-Oestridae, derives from ephydroid roots. Two parts of this working hypothesis are already in place: (i) presentation of the evidence that Gasterophilidae, *Glossina* and Hippoboscidae form a monophyletic group (Pollock, 1971, 1973) and (ii) a description of the brood pouch of *Cyrtona*, Curtonotidae (Ephydroidea) (Pollock, 1996), that is regarded here as homologous to the more elaborated brood pouch of *Glossina*, Hippoboscidae and Oestrinae. The present paper, besides describing the *Gyrostigma rhinocerotis* male genitalia, is a preliminary examination of a third part of this working hypothesis, namely that the gasterophilid ground plan reveals links with Ephydroidea.

Material

The specimen studied carried on the pin, three labels hand-written in black ink, as follows: Top label 'Ex *Diceros simus*'; middle label 'Umfolozu G. R. Zululand 29.11.67'; bottom label '*Gyrostigma*♂ *pavesii* (Corti) det. Zumpt 69'.

Terminology

Dealing with the male terminalia of *Diastata* (Diastatidae, Ephydroidea), Chandler (1987) made a useful distinction between an inner pair of articulating claspers, normally larger and broader, inserted near the anal cerci, and an outer pair that was rounded, elongate or spatulate, and always with a brush of long bristles, apically. Both types of claspers stood on the ventral lateral margin of the epandrium. A similar distinction is made in the present paper, in respect of the male appendages in gasterophilids, but here these appendages are termed postsurstyli and presurstyli, respectively. The presurstyli in gasterophilids are often reduced to a ridge of long hairs lying within the genital cavity.

The dorsal sclerotization following the sixth abdominal tergite is here regarded as tergite 7. It is symmetrical, and there are no vestigial sutures present indicating a condensation of the sclerite in question from two or more pre-existing sclerites; a simple serial numbering of the dorsal abdominal sclerites 1–7 will therefore be followed. This nomenclature will facilitate the longer term aim of the present study to clarify suspected links between Gasterophilidae and Ephydroidea. A potential criticism is that this terminology assumes an origin for the sclerite that is convenient for supporting the ephydroid link hypothesis: however, there is no intrinsic evidence that the sclerite in question is anything but tergite 7. The only reason for calling it a 7–8 syntergosternite, in the manner of McAlpine (1989), is the fact that the sclerite following tergite 6 in most Calyptratae (Scathophagidae, Anthomyiidae, Muscidae and the calliphorid-sacrophagid-tachinid block) is such a compound sclerite. There is no reason in logic, however, when exploring the possibility that gasterophilids have ephydroid origins, to make such an assumption. Having said that, the sclerite could ultimately prove to be a compound one, once the origins of Ephydroidea are better understood. Such an eventuality is still distant, but even if it should occur, it would make little difference to the present inquiry.

Description

The shape of the male abdomen is shown in figures 1 and 2. Abdominal segments 2–5 show, in that order, a slight progressive reduction in width, but the shape of the tergites of segments 6 and 7, together with that of the epandrium, give a rounded posterior end to the abdomen. The male genitalia are somewhat hidden, being housed at the level of segments 5 and 6, partially tucked under the large trapezoidal sternite 5. Externally visible features of the male abdomen at rest, are symmetrical.

Seven pairs of abdominal spiracles are present, and all are in the membrane: they are symmetrically arranged (figures 1, 2, 3, 5).

Tergites 1 and 2 are fused in the mid-dorsal areas, but show some separation laterally. Tergites 2–5 are all large, and almost equal in size; tergites 6 and 7 are fused, with a symmetrical suture visible marking the union. Tergite 6 is larger than

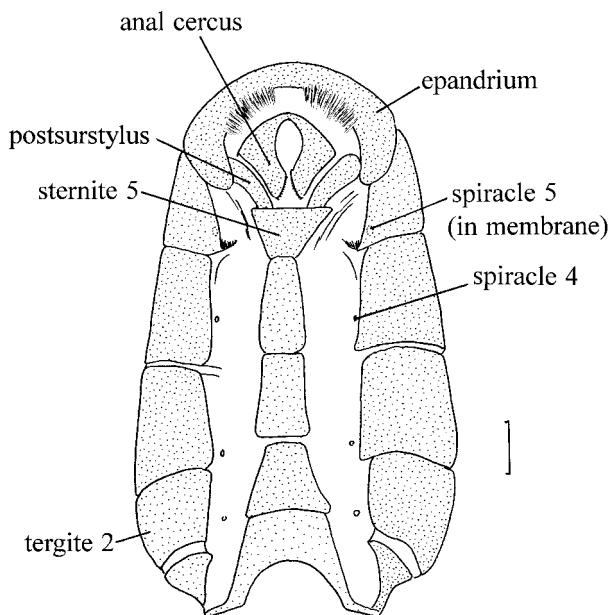


FIG. 1. Male abdomen of *Gyrostigma rhinocerontis*, ventral view. Scale bar 2 mm.

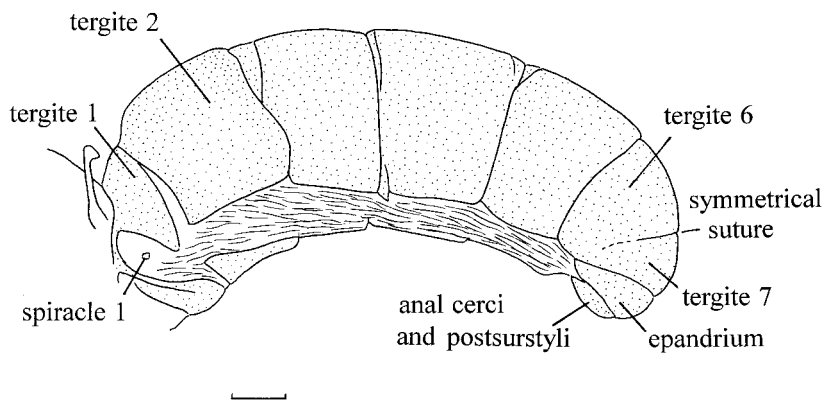


FIG. 2. Male abdomen of *Gyrostigma rhinocerontis*, left lateral view. Scale bar 2 mm.

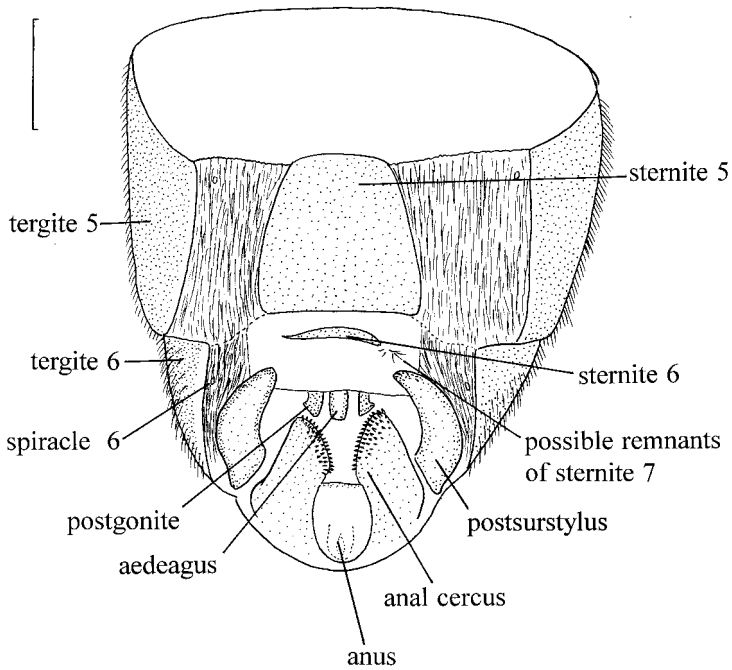


FIG. 3. Male postabdomen of *Gyrostigma rhinocerontis*, ventral view; showing the asymmetrically placed possible remnant of the seventh abdominal sternite. Scale bar 2 mm.

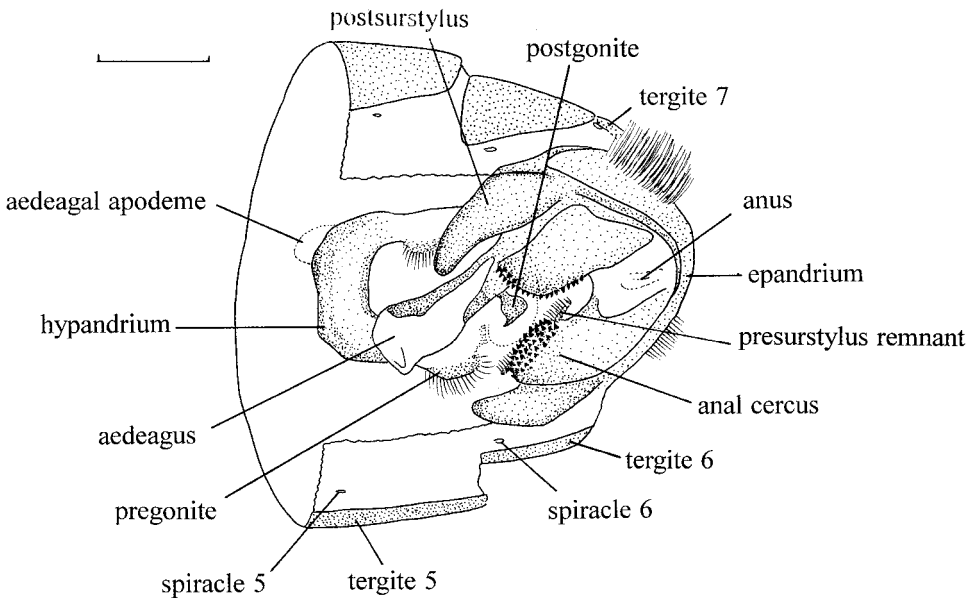


FIG. 4. Male postabdomen of *Gyrostigma rhinocerontis*, left lateroventral view, after removal of the sternites; showing the hook-like process by which the epandrium makes contact with the hypandrium. Scale bar 2 mm.

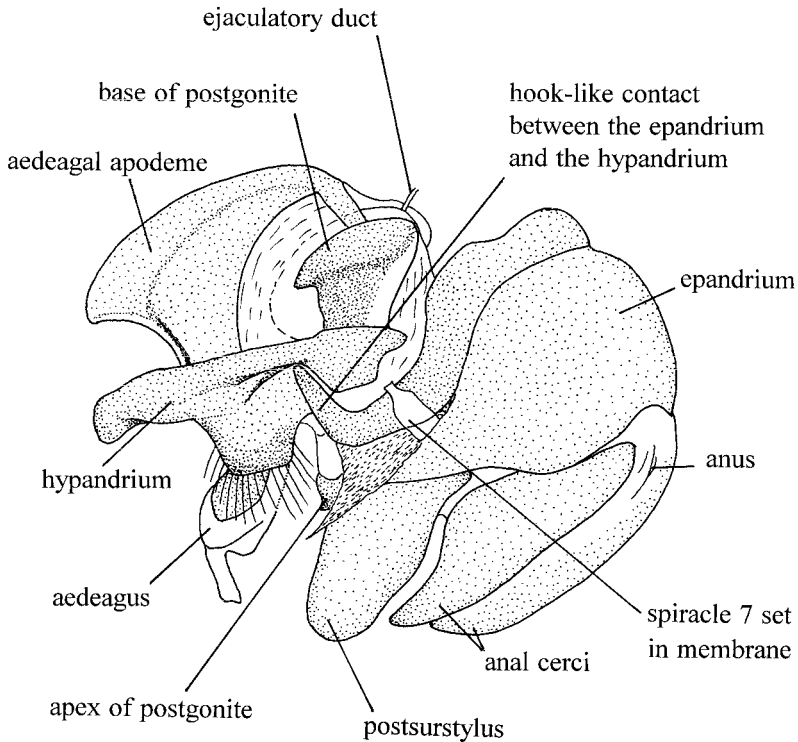


FIG. 5. Male genitalia of *Gyrostigma rhinocerontis*, left lateroventral view, partially dissected by removal of all tergites to tergite 7, and of all sternites to sternite 7. Scale bar 2 mm.

tergite 7, and both are larger than the epandrium. The lateral extremities of the epandrium are produced into strong hook-like structures that articulate with the corners of the hypandrium (figure 5). The morphologically posterior margin of the epandrium carries the robust anal cerci (figure 4). The anus is lodged between the bases of the cerci. Each cercus is specialized by being armed with numerous short spines mainly on the inner face, as is well shown in Zumpt's (1962) figure. The cerci do not fuse ventrally to the anus, but lie close together. Flanking the cerci is a pair of strongly built appendages, the postsurstyli; these appendages were referred to as paralobi by Zumpt (1962).

Sternite 1 is large and robust, and the series of sternites 1–4 have a decreasing width. Sternite 5 is wider than sternite 4 particularly at its posterior margin. There is a relatively small, nearly symmetrical sternite 6, and an asymmetrically placed tuft of setae (in the left ventral station, near the left extremity of sternite 6) which may possibly represent a reduced sternite 7 (figure 3). This area is one that is likely to show considerable variation from specimen to specimen, if experience with *Gasterophilus pecorum* (Fabricius) is any guide. In this species, I have seen specimens with no sign of the sternite 7 in the male abdomen, and one with clear indications of this sclerite (Pollock, 1973).

The *Gyrostigma rhinocerontis* hypandrium is strongly built, and forms three sides of a roughly rectangular structure (figures 4, 7), open at the posterior

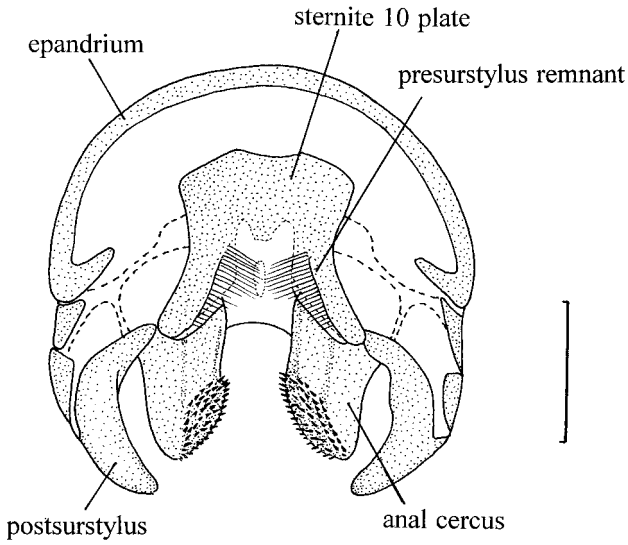


FIG. 6. Male genitalia of *Gyrostigma rhinocerontis*; elements forming the posterior wall of the genital pouch; appearance after removal of the hypandrium. Scale bar 2 mm.

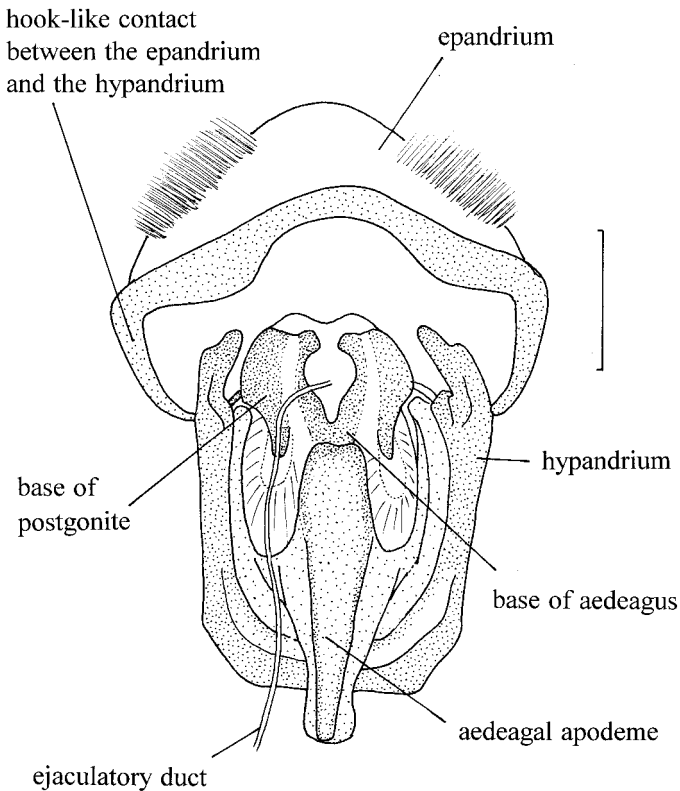


FIG. 7. Male genitalia of *Gyrostigma rhinocerontis*; view from the antero-dorsal angle (from within the fly), of the hypandrium, aedeagal apodeme and associated structures. Scale bar 2 mm.

(morphologically the dorsal) end. To each side, the hypandrium bears one of a pair of haired structures, the pregonites (gonopods *auct.*). These are broadly fused to the hypandrium, not articulated.

The aedeagus was also figured by Zumpt (1962). The point of attachment to the rest of the body is at the top of his figure. My preparation indicates a small tubular appendage at the distal end (figure 5); however, the gonopore could not be identified with certainty. The aedeagus is flanked by two strongly constructed postgonites or parameres (corresponding to the posterior parameres of *Gasterophilus*, in Pollock (1973)), which are hooked. The aedeagal apodeme is a curved structure looping from the posterior margin of the hypandrium, to the base of the aedeagus (figure 5). There is a relatively small anterior prolongation or flange to the aedeagal apodeme. Leading to the base of the aedeagus is the ejaculatory duct; this can be easily traced even in a macerated specimen (figure 7). No sign of an ejaculatory pump or sclerite could be found (as is the case in *Gasterophilus*), at least up to the base of the aedeagus.

The posterior wall of the genital chamber has a large plate (representing the 10th sternite; in Pollock (1973), the corresponding structure in *Gasterophilus* was termed the editum plate) carrying a pair of hairy processes or ridges (figure 6); the latter are the presurstyli. In *Gasterophilus pecorum* the corresponding structures are particularly prominent, taking the form of hairy, inwardly pointing finger-like processes. They have earlier (Pollock, 1973) been termed edita, to emphasize their homology with the edita of *Glossina*; this homology is again endorsed, but given the wider context, these appendages are now better termed presurstyli. A more conventional interpretation has been offered by Wood (1987), who regarded the postsurstyli (of *Gasterophilus intestinalis*) as surstyli, but unfortunately he does not mention or figure the paired structures on the lateroposterior wall of the genital chamber, nor does he consider *G. pecorum*, in which the presurstyli are better developed, making a comparison of viewpoints more difficult.

Status of Gasterophilidae

Zumpt (1957) presented a summary of the way in which the status of Gasterophilidae has varied in the treatments given by different authorities. He noted that Hennig (1952) regarded Oestridae as a monophyletic entity, comprising five groups of genera, arranged mainly on larval morphology: (i) *Gasterophilus*-group; (ii) *Cephenomyia*-group; (iii) *Oestrus*-group; (iv) *Hypoderma*-group; and (v) *Cuterebra*-group. He remarked that 'Hennig's *Gasterophilus*-group is certainly not related to the Oestridae s.str., but this author is also right, I believe, in rejecting the opinion of van Emden, who transfers the genera *Gasterophilus* and *Gyrostigma* to the Acalyptrata. The short cleft of the second antennal segment, the structure of the hypopygium and other features, indicate that they belong to the Calyptrata too...' Zumpt's manner of treatment is unsatisfactory, because such an antennal structure is equally consistent with an acalyptrate (ephydroid) origin for this group, and the comparative anatomy of the hypopygium is very complex, and one has to state precisely which aspect one is considering. Later in this paper, I present evidence that the comparative anatomy of the male postabdomen of Gasterophilidae, when considered in detail, also indicates an ephydroid origin for the family.

Rohdendorf (1974) also, in his very tentative arrangement, placed Gasterophilidae within the Acalyptrata, in an area completely distinct and well separated from the Oestridae. This approach (the profound separation of Gasterophilidae

from Oestridae) also has its major problems, because it leaves unexplained the important similarities between gasterophilids and oestrids; these include the location of abdominal sclerites in the membrane, vein 1 long, veins 2 and 3 long, close and parallel, and larval parasitism. Rohdendorf drew attention to the work of Chereshev (1951, 1953) who observed that the eggs of *Gasterophilus pecorum* were laid on fodder, rather than directly on the host animal; the matter will be referred to later. This work extended an earlier report by Dinulescu (1929).

Grunin (1969) regarded *Gasterophilus* and *Gyrostigma* as the sole members of the Gasterophilidae; this is in accord with the view taken in the present paper. Recognizing the proper scope of Gasterophilidae is essential for further progress in this field.

Zumt and Wetzel (1970) extended Gasterophilidae further, covering not only *Gasterophilus* and *Gyrostigma*, but also the oestrid genera *Cobboldia* Brauer (including *Platycobboldia* Townsend and *Rodhainomyia* Bequaert), *Ruttenia* Rodhain and *Neocuterebra* Grunberg. While many would dispute the utility of splitting these anomalous oestrid flies into five genera, as Zumt (1965) does, the main point in the present context is that the forward swing of vein 4 (M1) shows that the genera *Cobboldia*, *Platycobboldia*, *Rodhainomyia*, *Ruttenia* and *Neocuterebra* are oestrids and not gasterophilids; the primitive retention of slits in the posterior spiracular plate (whether vertically, diagonally or horizontally arranged), indicates that this group split off at an early stage from the oestrine/hypodermatine line of oestrid evolution, before the porous plate of the posterior spiracles developed. *Dermatobia* Brauer (Cuterebrinae, Oestridae) shows a similar retention of slit-like apertures in the larval posterior spiracular plate, while having a venation of the familiar oestrid type, with vein 4 swinging forward: this example shows again that at the differentiation of Oestridae the bending forward of vein 4 preceded the transformation of the spiracular plate bearing three simple slits into the type bearing highly sinuous slits, characteristic of most cuterebrines.

Pollock (1971, 1973) identified Gasterophilidae as the sister group of Glossinidae-Hippoboscidae, citing as evidence the comparative anatomy of the male abdomen, the wing venation, and the absence of the tergal branch of the depressor muscle of the mid-trochanter (TDT muscle) from all three families (Smart, 1958). The term Gasterophiloidea was used to refer to the superfamily containing these three families. Griffiths (1976) disagreed with this concept, repeating the traditional view of that time that gasterophilids belong to Oestridae *s.l.*, and that '*Glossina* + *Pupipara*' was monophyletic, ignoring contrary evidence such as the distribution of the TDT muscle (Schlein, 1970) and important features of the male postabdomen. He also pointed to areas in which Gasterophilidae resembled Oestridae, as evidence against the concept of Gasterophiloidea, disregarding the possibility that Gasterophiloidea and Oestridae might be sister groups, with many shared features. The matter has not been reinvestigated by any further studies directed specifically at resolving the questions raised. However, Wood (1987) and McAlpine (1989) subordinated Gasterophilidae to Oestridae *s.l.*, in their reviews.

Wood (1987) treated Oestridae as having four subfamilies, of which two, Oestrinae and Hypodermatinae, were sister groups, of uncertain relationship to the other two, namely Gasterophilinae (consisting of *Gasterophilus*, *Gyrostigma* and *Cobboldia*) and Cuterebrinae. His account did not explicitly consider the origin of the straight condition of vein 4 (M1) in *Gasterophilus* and *Gyrostigma*, and the distribution of the TDT muscle was not mentioned.

McAlpine (1989) generally followed the lead provided by Wood (1987), concerning Oestridae *s.l.* McAlpine allowed that Glossinidae was the sister group of Hippoboscidae (rather than of 'Pupipara'), and even cited the absence of the TDT muscle from the two families as a 'synapomorphy', but unfortunately did not explore the implications of this for the status of *Gasterophilus*, which also lacks that muscle.

Pape (1992) studied the relationships of oestroid flies in the context of the so-called Tachinidae family group; his views are noted below, in the discussion of wider relationships.

Ground plan of Gasterophilidae

The following remarks arise out of the observations made in the present paper, and from the earlier work concerning the male abdominal structure of *Gasterophilus* (Patton, 1935, 1937; Pollock, 1973). *Gyrostigma rhinocerontis* is morphologically fairly typical of Gasterophilidae, for instance in the presence of a readily identifiable tergite 7 in the male abdomen (fused with tergite 6, but with the symmetrical line of join still apparent), the symmetry of all sclerites in the male abdomen with the possible exception of the seventh sternite, the curved aedeagal apodeme, with only a minor anterior extension, the presence of a nearly symmetrical sternite 6 and the location of all the abdominal spiracles in the membrane. However, *Gasterophilus pecorum* shares these features (except that the aedeagal apodeme has a larger anterior projection) but has a wider representation of fundamental characters in other respects, for example the large, hairy, inwardly projecting presurstyli (= edita) in that species, and the unspecialized form and location of the cerci (Patton, 1937; Pollock, 1973). The presurstyli of *Gyrostigma rhinocerontis* take the form of haired ridges hidden within the genital pouch, and the anal cerci are very robust, set close together ventral to the anus, and armed with a group of spinules on the inner (medial) surface. It is very likely that the habit of *G. pecorum* of laying its eggs on fodder (Chereshnev, 1951, 1953) is also a basic (primitive) feature of Gasterophiloidea-Oestridae; cuterebrines (regarded here as components of Oestridae) also lay their eggs away from the hosts, in places frequented by a given host species (Catts, 1982).

However, further anatomical studies on the one other *Gyrostigma* species known from the adult form, the poorly known *G. conjugens* Enderlein, might be sufficient to modify these interim conclusions.

The following characters of the male abdomen are shared by *Gasterophilus* (especially *G. pecorum*) and *Gyrostigma rhinocerontis*, and form part of the ground plan of the Gasterophilidae:

- (1) abdomen almost completely symmetrical, externally, the only exception being the possible rudimentary seventh sternite*;
- (2) seven pairs of spiracles present, symmetrically arranged;
- (3) all abdominal spiracles in the membrane*;
- (4) tergites 6 and 7 fused, with a symmetrical suture marking the line of union*;
- (5) sternite 6 relatively unmodified, remaining a symmetrical (or nearly symmetrical) plate*;
- (6) pregonites (= gonopods) not articulated*;
- (7) ventral corners of the epandrium developed into strong hook-like processes, linking the epandrium to the sides of the hypandrium;
- (8) aedeagus flanked by two robust postgonites (parameres);

- (9) pair of haired structures (presurstyli) present, articulating with the 10th sternite plate (editum plate) that forms the inner wall of the genital pouch, and with the margin of the epandrium;
- (10) no ejaculatory pump free in the body cavity.

The presumed common ancestor of the two constituent genera of Gasterophilidae, *Gasterophilus* and *Gyrostigma*, can be described in the following way, the description being supplementary to the ground plan features of the male abdomen already mentioned, and numbered accordingly:

- (11) bristling normally to be found in schizophoran flies, to a greater or lesser degree replaced by a pile composed of fine hairs;
- (12) eggs laid away from the host (this is inferred from the biology of *Gasterophilus pecorum*, and that of cuterebrines);
- (13) larvae parasitic in the alimentary canal of perissodactyls;
- (14) mouthparts greatly reduced, and no food taken by the adult stage (also to be seen in oestrids, as a parallel or convergent development);
- (15) male dichoptic*;
- (16) thoracic transverse dorsal suture incomplete*;
- (17) TDT of the mid-trochanter absent (condition in *Gyrostigma* not known);
- (18) wings at rest with the leading edges held parallel;
- (19) squamae relatively small, not fully covering the halteres*;
- (20) vein 1 (R1) long, ending in the distal half of the wing;
- (21) veins 2 (R2+3) and 3 (R4+5) long, sub-parallel and close, not further apart (or scarcely so) than the length of the anterior cross vein (r-m);
- (22) posterior cross vein (dm-cu) well away from the trailing wing margin;
- (23) vein 4 (M1) not sharply bent forward, but proceeding in a nearly straight path to the trailing wing margin;
- (24) anal cerci small and unspecialized, not heavily sclerotized or armed, and not strongly contiguous with the opposite partner (based on condition in *Gasterophilus pecorum*)*.

The significance of the asterisk symbol is explained below.

Discussion of wider relationships

It should not be assumed, just because the gasterophilids are large, stout-bodied flies, with a parasitic life history, that they are calyptrates closely allied to calliphorids, sarcophagids and tachinids. Affinities between Gasterophilidae and Calliphoridae, sometimes mentioned in passing in the literature (see, for instance, Zumpt, 1957) but seldom properly tested, are unsustainable. Pape (1992) has examined the possible sister group relations between members of what he termed the Tachinidae family-group (i.e. Oestridae *s.l.*, Rhinophoridae, Sarcophagidae, Tachinidae, Calliphoridae). His analysis is potentially useful, but was hampered by several assumptions that I regard as erroneous: (i) that Gasterophilidae falls within Oestridae as a constituent subfamily; (ii) that the Tachinidae-family group is a valid monophyletic entity; and (iii) that Calyptratae is also a valid monophyletic entity. These unexamined assumptions seriously blunt the impact of his analysis. More specifically, Glossinidae and Hippoboscidae were not covered, and his work therefore unfortunately provides few data immediately relevant to Gasterophiloidea. However,

Pape found that there was no conclusive evidence of sister group relationships at the family level within his Tachinidae family-group.

Exactly how one should place the ground plan features (1)–(24) listed above into primitive and derived categories would partly depend on one's view of these wider relationships. Some, such as (11), (13), (14), (17), (20) and (21), are clearly specializations, often to do with the parasitic habit. Other features contrast with the so-called Calyptratae ground plan (McAlpine, 1989), and have more in common with the ground plan of the Ephydroidea; this is especially true of the asterisked features (1), (3)–(6), (15), (16), (19) and (24), above. These early gasterophilid flies, that had all the abdominal spiracles in membrane, the male postabdomen nearly symmetrical in its external features, including a symmetrical suture between tergites 6 and 7, with sternite 6 free, well formed and symmetrical, the pregonites broadly attached to the hypandrium and non-articulated, the anal cerci unspecialized and not strongly contiguous ventral to the anus, the males dichoptic and the thoracic dorsal suture incomplete, are better regarded as involving directly from acalyptrate antecedents, in particular from the ephydroids. This helps to explain why some earlier workers sensed an affinity between Gasterophilidae and 'Acalyptratae'. According to McAlpine (1989), the ground plan of the Calyptratae includes abdominal spiracles in the tergites, the male abdomen strongly asymmetrical in its external features, sternite 6 reduced and shifted to the left side, sternite 6 fused with tergite 6 on the left side, pregonites articulated, anal cerci contiguous below the anus or fused, and the male fly holoptic. On this basis, clearly, gasterophilids have to be excluded from the Calyptratae. The ephydroids are well qualified to play an ancestral role to Oestridae and Gasterophiloidea in other respects: one branch at least (*Cyrtona*: Curtonotidae) possesses a brood pouch (Pollock, 1996), here seen as the homologue of similar but more elaborated structures in *Glossina*, Hippoboscidae and Oestrinae. We may also recall that the ephydroid pattern of antennal structure is essentially the same as the calyptrate one, with a dorsal seam to the pedicel, and the arista arising dorsally from the base of the decumbent first flagellomere.

As stated in the introduction, Gasterophiloidea is regarded here as the sister group of Oestridae. The evidence for this lies in the absence of the TDT muscle from the thorax of Gasterophiloidea, matched against its extreme reduction in Oestridae (Smart, 1958); in the basic venation plan for both groups that has vein 1 long and veins 2 and 3 long and close together; and in larval parasitism. Other shared features such as the presence of abdominal spiracles in the membrane, not in the tergites, are seen as carried over from the ephydroid root; the lack of fully functional mouthparts in the adult stage is seen as a convergent (parallel) feature of the two groups. A fuller treatment of this proposed sister group relationship will be presented elsewhere.

The claim that Gasterophilidae and the whole Gasterophiloidea-Oestridae complex have ephydroid origins has many aspects which should be examined further in subsequent studies.

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