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## Three New Species of *Heterotropus* Loew (Diptera: Bombyliidae) from South Africa with Descriptions of the Immature Stages and a Discussion of the Phylogenetic Placement of the Genus

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### ABSTRACT

Three new species of *Heterotropus* Loew, *H. gilvicornis* n. sp., *H. posthos* n. sp., and *H. stuckenbergi* n. sp., from western South Africa, are described. Adults were collected in sand dunes and the free-living larvae were sifted from sandy soil. A key to the South African species of the genus is presented. Little difference could be found between the cast larval exuviae and cast pupal cases of the three species. The larvae and pupae are described and illustrated. The phylogeny of the

genus is discussed in the light of evidence from the morphology and habits of the immature stages. Evidence is presented that the genus does not belong in the Bombyliidae. Adult morphology suggests that they are primitive members of the Asiloidea, and may be the sister group to the remaining asiloids. Larval morphology is discussed in relation to the synapomorphies of the Asiloidea.

### INTRODUCTION

The genus *Heterotropus* Loew (1873) currently contains 40 species, with all but four occurring in the Palearctic Region. They are

small flies with broad, hyaline wings and a distinctive yellow or cream-and-black color pattern. Previously, Africa was reported to

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have a total of nine species and all but one of these found in the northeast of the continent (Bowden, 1980). *H. munroi* Bezzi (1926) is the only previously described species in South Africa; it is also reported to occur in Botswana and Namibia (Bowden, 1980).

*Heterotropus* occupies an isolated position in the Bombyliidae. Becker (1913) proposed the new subfamily Heterotropinae for the genus alone. He considered it a transitional form between either the Therevidae or Empididae, and noted that the eye facets of the male were separated into smaller (lower) and larger (upper) facets by a horizontal division. Bezzi (1924), following Becker, placed the subfamily in the division Homoeophthalmae, consisting of all those subfamilies of Bombyliidae lacking an indentation on the posterior eye margin. Melander (1928) placed two additional Nearctic genera in the Heterotropinae: *Prorates* Melander and *Caenotus* Cole. *Prorates* was first described as an empidid and *Caenotus* as a therevid. Much later Melander (1950) added the monotypic Nearctic genus *Apystomyia* to the subfamily and described the first Nearctic *Heterotropus*, *H. senex*. This species was later removed to the new genus *Inyo* of the new subfamily Desmatomyiinae by Hall and Evenhuis (1987). Melander (1950) considered that the enlarged subfamily Heterotropinae could be separated from other Bombyliidae on the basis of the following characters: occiput flattened, eye facets of male separated into smaller (lower) and larger (upper) facets [but not indented behind as in Bezzi's (1924) Tomophthalmae], tibiae without seriate spines,  $R_{4+5}$  forked, cell  $r_5$  open and cell cup closed. Hull (1973) agreed with Melander (1950) regarding the genera of the Heterotropinae. Hall (1972) described the new genus *Caenotoidea*, added it to the Heterotropinae, and noted that the subfamily contained an anomalous group of small bombyliids. He amended the following details to the characterization of the subfamily: male usually holoptic, female dichoptic, inner margin of (male) eyes usually indented opposite antennal bases, anal lobe of wing greatly developed, and body not densely haired.

Hull (1973) further noted that many of the features used to differentiate the Heterotropinae were found in other bombyliids. He

also considered it possible that some of the constituent genera belonged in a separate family. None of the characters used to differentiate the subfamily is unique to it, and none could be considered as candidate apomorphies of the subfamily. Theodor (1983) suggested transferring *Prorates* from the Heterotropinae to the subfamily Proratinae of the Scenopinidae after noting similarities between *Prorates* and the Scenopinidae. Evenhuis (1991), in a catalog of genus names in the Bombyliidae, retained *Heterotropus* in the Heterotropinae of the Bombyliidae but removed the remaining genera to the Proratinae incertae sedis, citing Theodor (1983) for support. Nagatomi et al. (1991) treated *Heterotropus* as a bombyliid, citing similarities in male genitalia (which they do not elucidate).

One of us (MEI) collected adults and larvae of three new species of *Heterotropus* during fieldwork in western South Africa in September 1972. The larvae were taken by sieving sand, in the same way as therevid larvae are collected (Irwin, 1972), and are apparently free-living. We describe the adults of the three species and also describe the larvae and pupae. We review the morphology of the immature stages and the systematic placement of the genus in the light of Woodley's (1989) recent phylogenetic scheme of the Asiloidea.

#### METHODS

Genitalia were examined by soaking the terminal segments of the abdomen in cold 10 percent KOH overnight and dissecting out the relevant structures. Drawings were made using Zeiss binocular dissecting and compound microscopes with camera lucida attachments. Terminology for adults follows McAlpine (1981) except that the complex intromittent organ comprising the aedeagus and surrounding paramere sheath is here termed the phallus (Wood, 1990). Terminology for larvae follows Teskey (1981), and for the pupae follows Marston (1964). Larvae were kept in the laboratory according to the methods described in Irwin and Yeates (ms). The group of four numbers and two letters in the label data immediately following the date are map grid references (Stuckenberg and Irwin, 1972). Most specimens, including the holotypes,

have been deposited in the Natal Museum, Pietermaritzburg, South Africa; however, a few paratypes have been retained in the collection of the Illinois Natural History Survey (INHS) as indicated.

#### ACKNOWLEDGMENTS

This research was completed while DKY was in receipt of a Roosevelt Postdoctoral Fellowship from the American Museum of Natural History. We are grateful to Peling Fong of the AMNH for technical assistance with scanning electron microscopy. Drs. David Grimaldi (AMNH), Norm Woodley (USDA, Smithsonian Institution, Washington), Neal Evenhuis (B.P. Bishop Museum, Honolulu), Jeff Cumming, and Mr. Brad Sinclair (Biosystematics Research Centre, Agriculture Canada, Ottawa) provided helpful comments on the manuscript.

#### TAXONOMY

##### Genus *Heterotropus*

*Heterotropus* Loew, 1873: 180. Type species *H. albidipennis* Loew 1873: 180, by monotypy.

*Malthacotricha* Becker, 1907: 312. Type species *M. glauca* Becker, 1907, by monotypy.

*Heterotropus* is a monophyletic genus with the following diagnosis: small, rather bare flies with hyaline wings. Coloration of body with distinctive pale yellow or cream-and-black markings. Eye facets of male sharply divided into large facets dorsally and small facets ventrally. Antennae elongate; scape, pedicel, and flagellum of uniform thickness at their bases. Wing venation with cell cup closed with a short stalk, other marginal cells open; two branches of M, four branches of R, R<sub>4</sub> and R<sub>5</sub> fairly straight; anal cell broad. Legs lacking prominent setae. Male genitalia with large hypandrium; phallus strongly curved; distiphallus bifid or trifid. Gonostyli with dorsal lobe and median process or lobe. Aedeagal sheath extending anteriorly both lateral and ventral to ejaculatory apodeme. Female terminalia with three spermathecae and well-developed acanthoporphite spines. The dorsal processes of the gonocoxae, form of the gonostyli, and aedeagal sheath extending anteriorly lateral and ventral to ejaculatory apodeme provide apomorphies for the genus.

Previous authors have remarked on the sexual dimorphism in color pattern and the variability in color pattern within each sex exhibited by the different species (Efflatoun, 1945; Greathead, 1967). A revision of the genus will require the dissection and drawing of male genitalia of each species so that accurate comparisons can be made. With this in mind, the male genitalia of the three new species described here are illustrated in full. Comments regarding interspecific variability of color pattern notwithstanding, the species described below differ from all others found in Africa in color pattern. All the species described below have the entire scutum and scutellum black in both sexes and black bands on the abdominal tergites. *H. elephantinus* Seguy (1930) (known from two males from Egypt) has a completely yellow abdomen and the postpronotal lobes and postalar wall are reddish-brown. The other eight described African species (Bowden, 1980) have yellow markings on the scutum and scutellum, and parts of the pleurae yellow as well. The key provided below is only to those species known from South Africa.

Specific names proposed below are to be attributed to the first author.

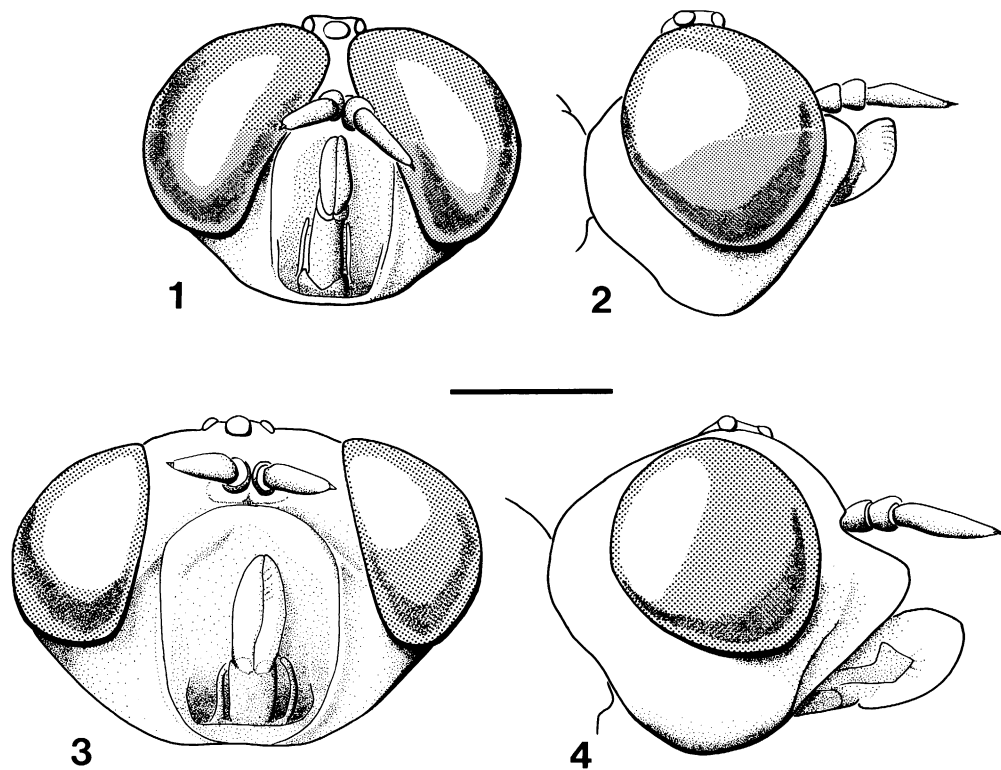
#### ADULTS

##### *Heterotropus gilvicornis*, new species

(Figures 1–18, 31, 32)

**DIAGNOSIS:** A small (3.4–3.7 mm body length) species with yellow antennae, shining black scutum and scutellum, yellow legs, and abdominal tergites mostly yellow with narrow black basal margins. Labium relatively short (length excluding labellum equal to ½ length of foretibia). Male tarsal claws reduced, short, and blunt. Phallus relatively short and gonocoxa with a dorsal process of distinctive shape (fig. 11).

**DESCRIPTION:** Male, *Head* (figs. 1, 2). Shining black-brown with sparse hyaline hairs except frons which is yellow and bare. Eyes separated by distance equal to ½ diameter of median ocellus. Ocellar tubercle broad with many hyaline hairs. Face rather protuberant, extended to apex of pedicel just below antennae. Labium relatively short (length excluding labellum equal to ½ length of foretibia), black. Palps narrow, about ¾ length of



Figs. 1-4. *Heterotropus gilvicornis* head, vestiture not shown. 1, Male anterior view; 2, male lateral view; 3, female, anterior view; 4, female, lateral view. Scale line 0.5 mm.

labium, curved upward and lying parallel to proboscis at rest in oral cavity, with shorter hyaline hairs. Dividing line between eye facets (fig. 6) horizontal, just ventral to bases of antennae. Genae produced below oral cavity. Occiput produced posteriorly behind greatest width of eye but narrow dorsally in lateral view. Antennae with scape and pedicel short, subcylindrical, slightly wider at apex than base; yellow with short, sparse, hyaline hairs. Flagellum yellow, base about  $\frac{1}{4}$  length, length

about twice that of scape and pedicel combined, tapered toward acute apex over distal half; apex with a single small segment (figs. 8, 9).

*Thorax.* Black with sparse, long, hyaline hairs. *Wings.* Venation typical for genus (fig. 5). Three branches of Rs, 2 branches of M, CuP and A<sub>1</sub> fused near wing margin, discal cell small, placed near middle of wing. Veins yellow-white. *Legs.* Coxae and trochanters black-brown, remainder of legs light yellow except tarsal segments 4 and 5 yellow-brown. Covered with white hairs, longer on posterior face of femora than anterior face. Tarsal claws reduced, blunt, about  $\frac{1}{4}$  length of pulvilli (fig. 7).

*Abdomen.* Tergite 1 yellow; tergites 2-8 mostly yellow with narrow black-brown basal margin, width of dark area narrowed on posterior segments until only a narrow strip on tergite 8. Sternites 1-4 black-brown; more posterior sternites with apical yellow margin, increased in width on more posterior seg-

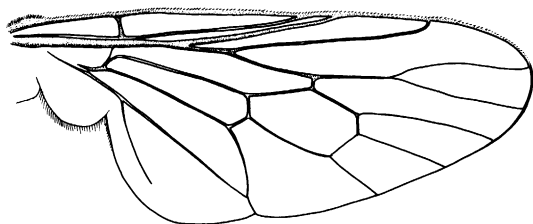
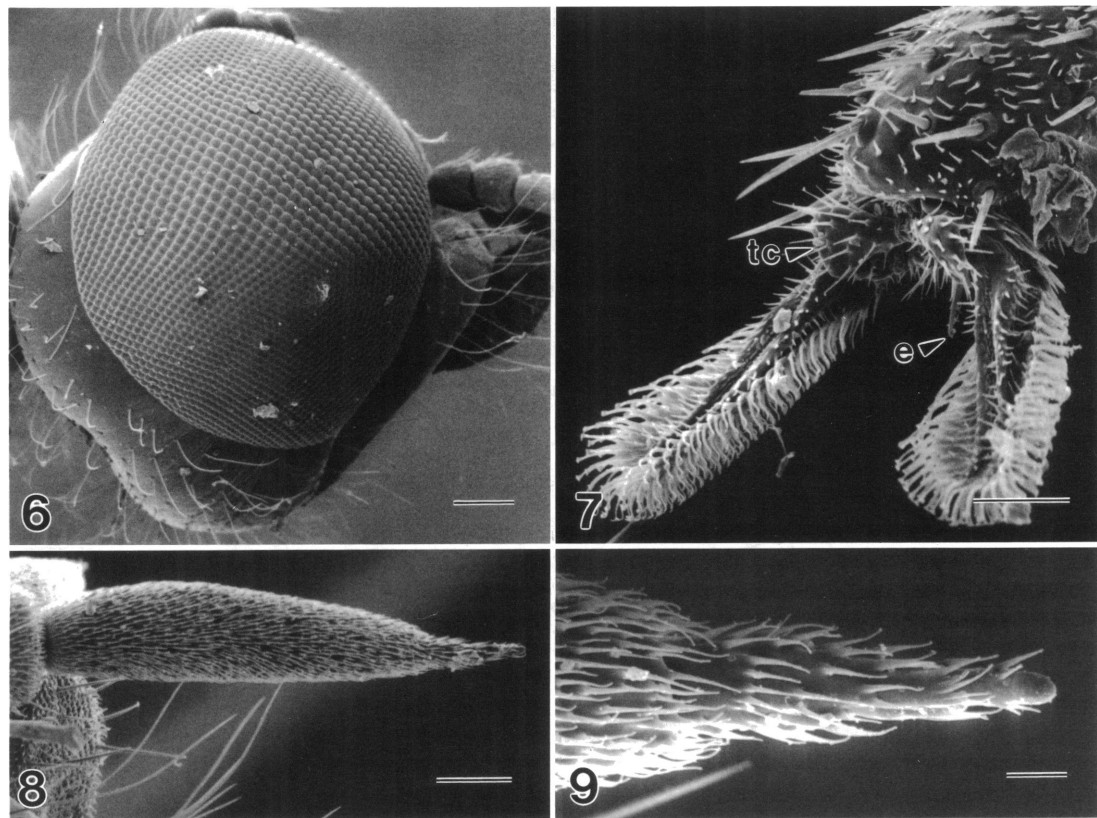


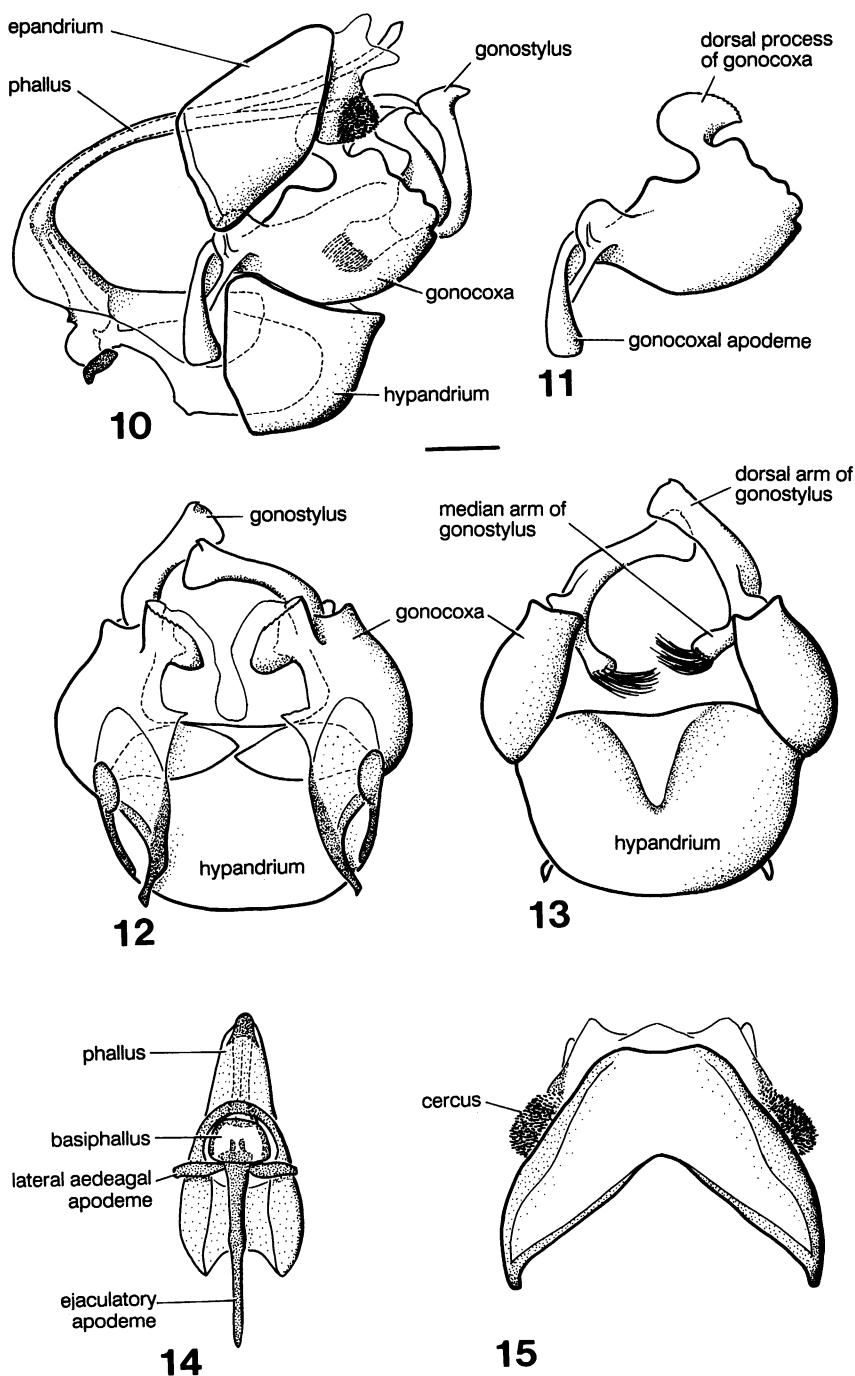
Fig. 5. *Heterotropus gilvicornis* male wing, right hand side.



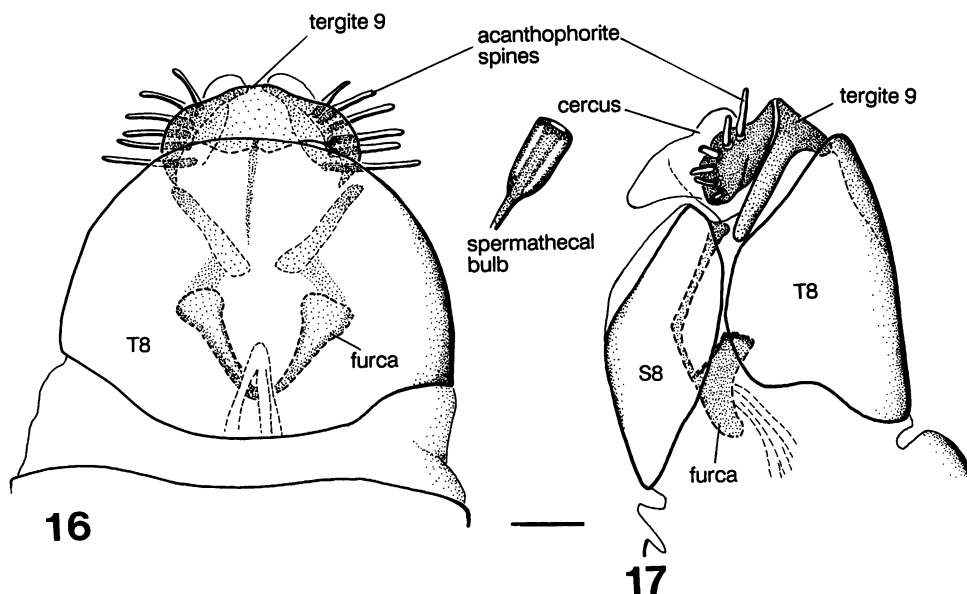
Figs. 6–9. Scanning electron micrographs of male *H. gilvicornis*. 6, Eye showing large facets dorsally and small facets ventrally; 7, tarsus showing reduced claws, tc = tarsal claw, e = empodium; 8, antennal flagellum; 9, detail of antennal flagellum showing apical segment. Scale fig. 6, 0.1 mm, fig. 7, 20  $\mu$ m, fig. 8, 50  $\mu$ m, fig. 9, 10  $\mu$ m.

ments. Terminalia black-brown. Tergites and sternites with long, sparse hyaline hairs. *Terminalia* (figs. 10–15). Epandrium whole, broad in dorsal view, narrowed apically with slight apical emargination (fig. 15). Cerci large, membranous posteriorly but each with distinctive sclerotized lateral lobe with dense pad of short brown hairs (fig. 15). Hypandrium large, deep (fig. 10). Gonocoxae small, separate, arising each side of hypandrium, leaving a large median cavity (fig. 13). Gonocoxae about as long as length of hypandrium, with well-developed gonocoxal apodemes curved ventrad (fig. 11). Dorsal process of gonocoxae just behind articulation of gonostyli with serrate dorsal margin (fig. 11). Gonostyli each with dorsal and median arms (fig. 13). Dorsal arms well developed, about as long as gonocoxae, small tooth laterally on

apex. Median arms slightly narrower than dorsal ones, extended mediad into cavity formed by separated gonocoxae. Apex with brush of long hairs. Phallus long, curved into inverted u shape (fig. 10). Ejaculatory apodeme large, laterally compressed, extended into hypandrium. Lateral aedeagal apodemes and basiphallus (fig. 14) small. Sheath of phallus extended ventrally under base of ejaculatory apodeme and curved dorsally on either side of it (fig. 14). Distiphallus swollen basally but abruptly narrowed along dorsal and posterior curve. Distiphallus divided into three distinct prongs about  $\frac{1}{3}$  distance from base. Each prong with an apical gonopore. Phallus prongs extended under epandrium with median prong dorsal to lateral ones. Apex of lateral prongs with small serrate spines ventrally. Phallus loosely connected through



Figs. 10–15. *Heterotropus gilvicornis* male genitalia, vestiture not shown except tuft of long hairs on gonostyli and short hairs on cerci. 10, Lateral view of genitalia with epandrium attached; 11, lateral view of gonocoxae showing dorsal process; 12, dorsal view of gonocoxae with epandrium and phallus removed showing ventral median space between gonocoxae; 13, ventral view of gonocoxae with epandrium and phallus removed showing dorsal and median arms of gonostyli; 14, anterior view of base of phallus showing lateral aedeagal apodemes and ejaculatory apodeme; 15, dorsal view of epandrium showing area of short setae on cerci. Scale 0.1 mm.



Figs. 16, 17. *Heterotropus gilvicornis* female genitalia, vestiture not shown. 16, Dorsal view; 17, lateral view; in between is detail of spermathecal bulb. Scale 0.1 mm.

membrane ventrally to gonocoxae and dorsally to sternite 10.

**Female.** Similar to male except: slightly larger, especially the head; hyaline hairs on body shorter and more sparse. Eyes widely separated (fig. 3) by almost half the head width in anterior view. Eye facets of similar size dorsally and ventrally (fig. 4). Head shining black except genae yellow and occiput yellow on ventral half. Some small yellow spots may be present on face on either side of oral cavity. Scape and pedicel yellow-brown. Tarsal claws of normal size, yellow at base, black at apex. Abdominal tergites and sternites yellow. **Terminalia** (figs. 16, 17). Well-sclerotized tergite 9 with long narrow lateral straps extended anteriorly almost to furca (fig. 17). Acanthophorites (tergite 10) well developed and separate from tergite 9, each with 6 large spines. Cerci with a large ventral lobe. Furca (sternite 9) u-shaped with arms thickening (fig. 16) posteriorly. Area between arms of tergite 9 and arms of furca weakly sclerotized. Three well-sclerotized spermathecae arising from separate, long spermathecal ducts; ducts extend into abdomen to level of 4th abdominal segment. Spermathecal ducts enter the genital chamber at a common opening (fig.

16). Spermathecal bulb about twice as long as wide and slowly widened toward apex.

**HOLOTYPE:** Male, SOUTH AFRICA, CAPE PROVINCE, top of Botterkloof Pass, Sept. 13, 1972, 3119Cd, 2230ft, M. E. and B. J. Irwin, white sand dune association.

**PARATYPES:** 7 males, 2 females, same data as holotype (2 males and 1 female in INHS); 1 female SOUTH AFRICA, CAPE PROVINCE, 11 miles NNE Hondeklip Baai, Sept. 8, 1972, 3017Ab, M. E. and B. J. Irwin, 200ft, reddish sand, shrubs.

**OTHER SPECIMENS EXAMINED:** 2 males, same data as holotype (one macerated and one coated for SEM study); 1 female, SOUTH AFRICA, Cape Province, Botterkloof Pass, Sept. 10, 1984, M.E. Irwin, white sand dune (last larval exuvium and cast pupal exuvium in microvial pinned underneath specimen).

**ETYMOLOGY:** The specific name refers to the pale yellow antennae and is derived from *gilvus*, meaning pale yellow, and *cornus*, meaning horn.

**REMARKS:** *Heterotropus gilvicornis* differs from the other species described here most noticeably in the yellow flagellum and the striking reduction of the tarsal claws of the male (fig. 7). The function of these reduced

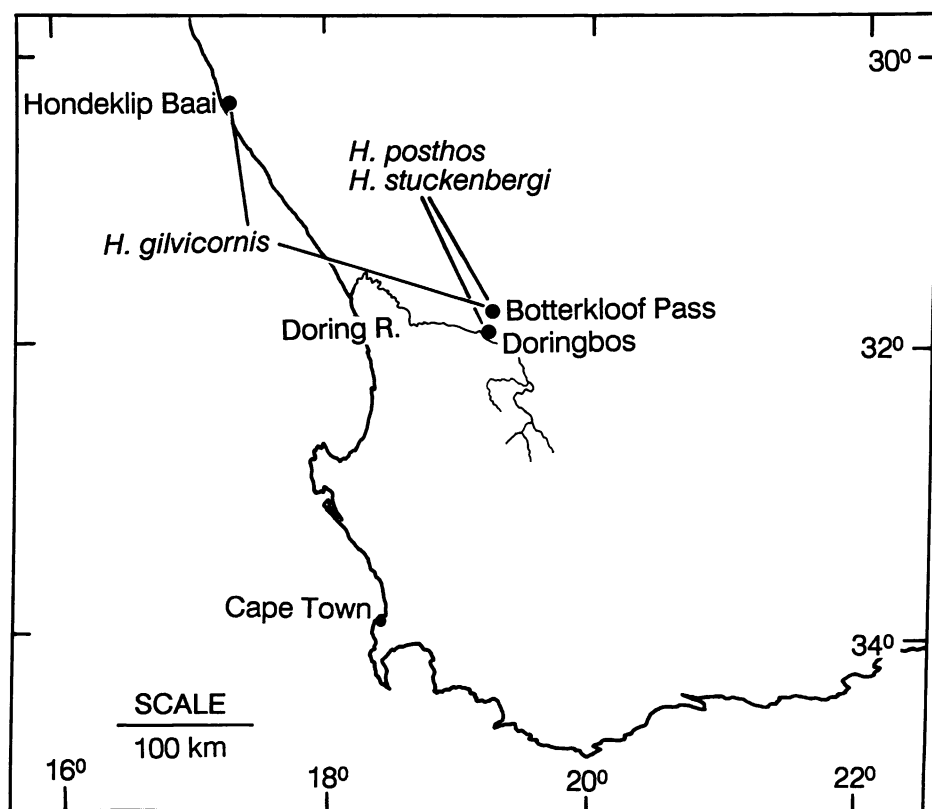


Fig. 18. Distribution of *H. gilvicornis*, *H. posthos*, and *H. stuckenbergi*.

tarsal claws is unknown, but their presence only in the male suggests that they may be concerned with mate recognition.

This species was collected by MEI first on the coast at Hondeklip Baai, then five days later at Botterkloof Pass (fig. 18). Adults were collected on sand dunes and could be seen walking around on the sand in preference to flying. One dipterous larva collected while sieving therevid larvae from loose sand at Botterkloof Pass on 10 September 1984 emerged as *H. gilvicornis*.

***Heterotropus posthos*, new species**

(Figures 18–25, 33–35)

**DIAGNOSIS:** A small (3.3–3.7 mm body length) species with black-brown antennae, shining black scutum and scutellum, yellow legs and abdominal tergites mostly black with narrow yellow apical margins. Labium is relatively long (length excluding labellum equal to length of foretibia). Male tarsal claws nor-

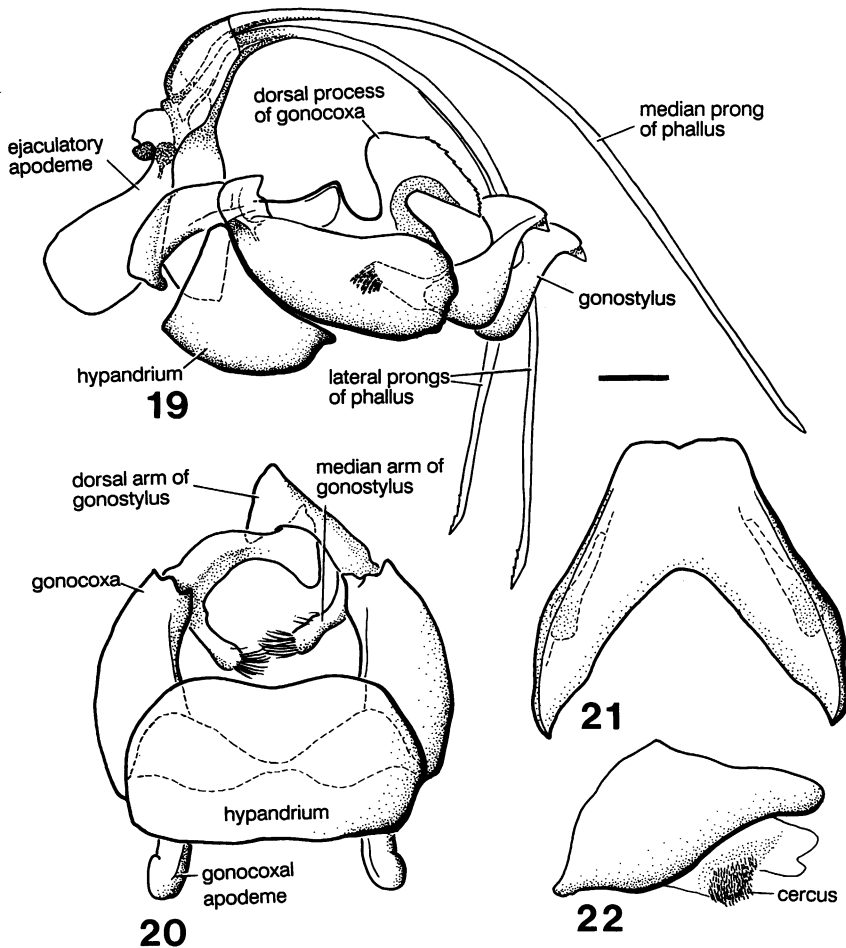
mal. Phallus relatively long and the gonocoxa has a dorsal process of characteristic shape (fig. 19).

**DESCRIPTION:** Similar to *H. gilvicornis* except as follows (unless otherwise stated, comparisons below are to *H. gilvicornis*). **Male, Head.** Frons yellow ventrally with small irregular yellow areas on genae at either side of oral margin. Eyes separated by distance equal to  $\frac{1}{3}$  diameter of median ocellus. Face extended to basal half of pedicel just below antennae. Labium relatively long (length excluding labellum equal to length of foretibia). Palps narrow, about  $\frac{1}{2}$  length of labium. Antennae with scape and pedicel brown. Flagellum brown.

**Legs.** Tarsal claws of normal size (length about  $\frac{1}{2}$  that of 5th tarsomere), as long as pulvilli, yellow at base but black at apex.

**Abdomen.** Tergites 2–8 mostly black with yellow basal margin, width of yellow area on tergite 2 covering about  $\frac{1}{3}$  of segment, narrowed on posterior segments until only a nar-





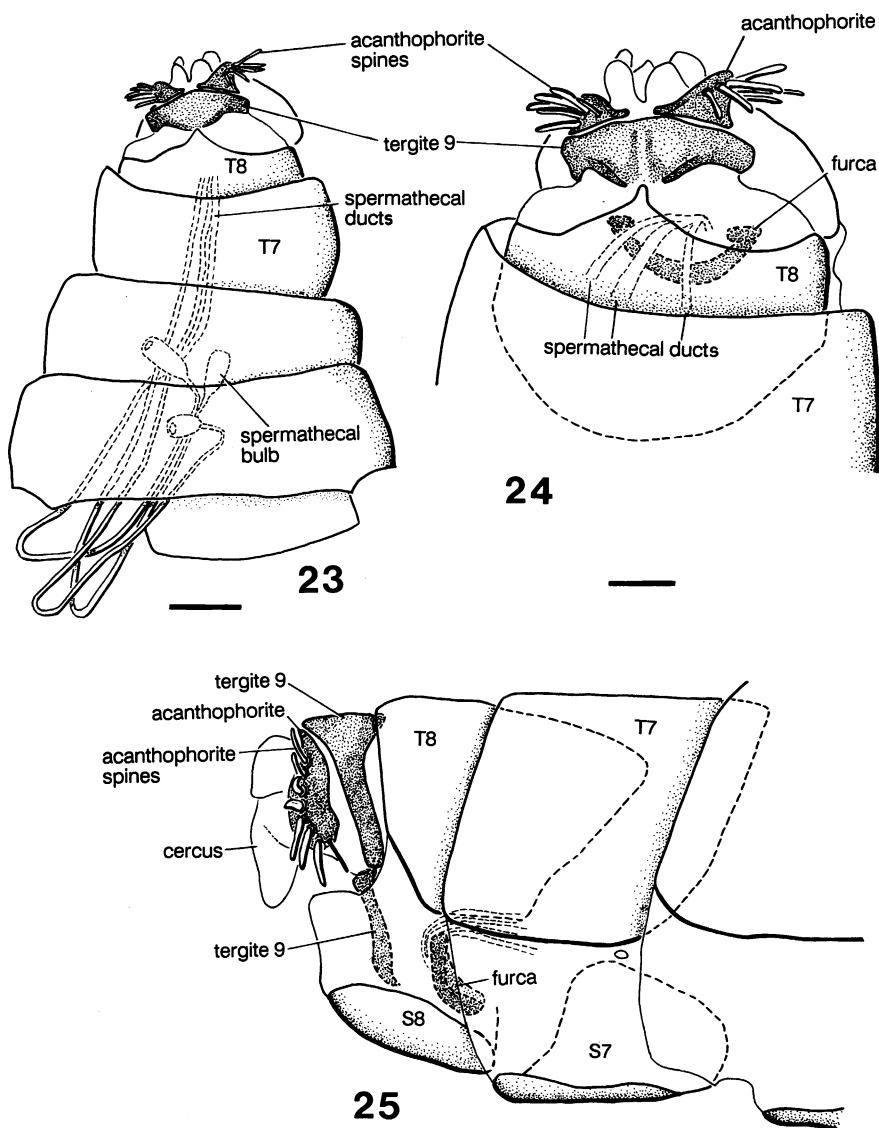
Figs. 19–22. *Heterotropus posthos* male genitalia, vestiture not shown except tuft of long hairs on gonostyli and short hairs on cerci. 19, Lateral view with epandrium removed; 20, ventral view; 21, dorsal view of epandrium; 22, lateral view of epandrium. Scale 0.1 mm.

row strip on tergite 8. Sternites 1–8 mostly black-brown with apical  $\frac{1}{4}$  yellow. Tergites and sternites with long, sparse hyaline hairs. *Terminalia* (figs. 19–22). Epandrium whole, more narrow in dorsal view. Cerci with hairs on lateral lobe longer (fig. 22). Dorsal process with larger posterior lobe (fig. 19). Dorsal arms of gonocoxae with apical tooth larger (fig. 19). Phallus long, about twice as long as phallus of *H. gilvicornis* and curved into an inverted u shape (fig. 19); tips of three aedeagal prongs ending well below gonocoxae. Distiphallus dividing into three distinct prongs close to basiphallus.

*Female*. Head shining black except wide yellow stripe on genae extended posteriorly

onto ventral half of occiput. A small yellow irregular area on frons ventrally around base of antennae and extended laterad to eye margins. Thorax black except dorsal margin of anepisternum narrowly yellow. Abdominal color pattern similar to that of male. *Terminalia* (figs. 23–25). Eight acanthophorite spines on each acanthophorite (fig. 25). Furca (sternite 9) in one piece, u-shaped with arms thickened posteriorly (fig. 24). Area between arms of tergite 9 and arms of furca not sclerotized (fig. 24). Furca with arms apically more narrow.

**HOLOTYPE:** Male, SOUTH AFRICA, CAPE PROVINCE, Doringbos on Doring River, Sept 14, 1972, 500ft, 3119Cc, M. E. Irwin,



Figs. 23–25. *Heterotropus posthos* female genitalia, vestiture not shown. 23, Dorsal view showing spermathecal ducts and bulbs, scale 0.2 mm; 24, dorsal view detail, scale 0.1 mm; 25, lateral view, scale 0.1 mm.

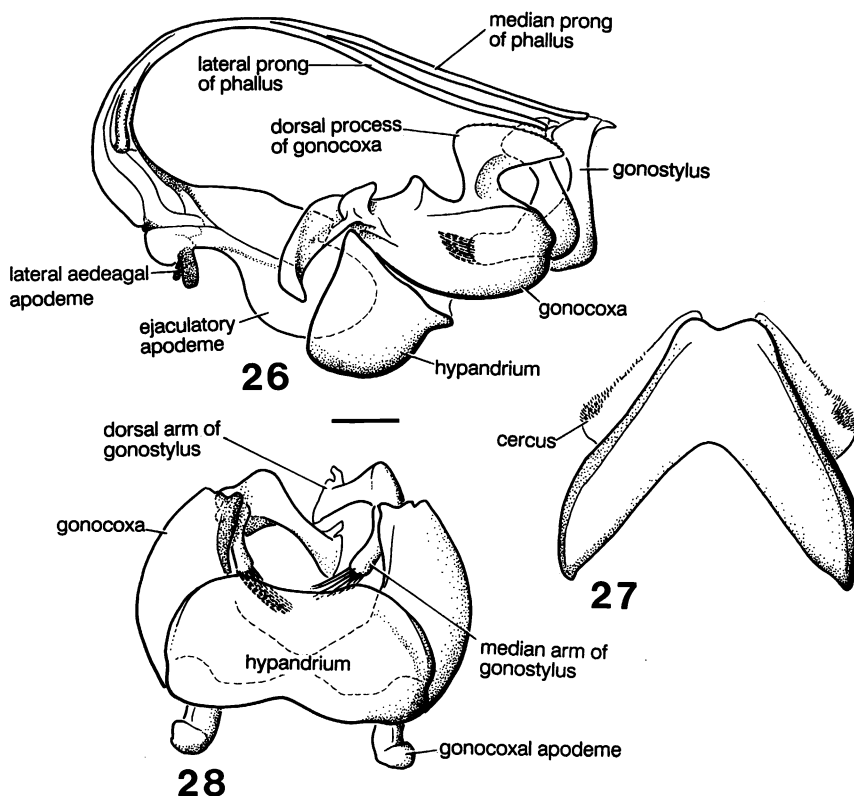
Riverbank sand dunes. Cast pupal exuvium in gelatin vial mounted on pin underneath specimen.

PARATYPES: 1 male, 1 female, same data as holotype (INHS); 2 males, SOUTH AFRICA, CAPE PROVINCE, top of Botterkloof Pass, Sept. 13, 1972, 3119Cd, 2230ft., M. E. and B. J. Irwin, white sand dune association. One male with pupal exuvium in glass vial mounted under specimen and the other male with last larval exuvium and pupal exuvium.

OTHER SPECIMEN EXAMINED: 1 female, same data as holotype (macrated).

ETYMOLOGY: The specific name refers to the long penis and is taken from *posthos* meaning one with large penis.

REMARKS: Two males were reared from larvae collected on 13 September 1972 at Botterkloof Pass. In addition, a male and two females were collected as adults at the Doringbos River on the next day, 14 September 1972. A male was also reared from a larva



Figs. 26–28. *Heterotropus stuckenbergi* male genitalia, vestiture not shown except tuft of long hairs on gonostyli and short hairs on cerci. 26, Lateral view; 27, dorsal view of epandrium; 28, ventral view. Scale 0.1 mm.

collected at the same locality on the 13 of September (fig. 18).

There is some variation in the yellow abdominal markings in the male. Some paratypes have black areas laterad on tergite 1 and yellow areas more narrow on other segments. This species shares more similarities with *H. stuckenbergi* than *H. gilvicornis* because of the normal male tarsal claws and black-brown flagellum.

***Heterotropus stuckenbergi*, new species**  
(Figures 18, 26–30, 36, 37)

**DIAGNOSIS:** A small (3.4–3.7 mm body length) species with brown antennae, shining black scutum and scutellum, yellow legs and abdominal tergites mostly yellow with narrow black basal margins. The labium is relatively short (length of labium excluding labellum equal to half length of foretibia). Male tarsal claws normal. Phallus intermediate in length between those of *H. gilvicornis* and *H.*

*posthos* and gonocoxa has a large dorsal process of characteristic shape (fig. 26).

**DESCRIPTION:** Similar to *H. gilvicornis* except as follows (unless otherwise stated, comparisons in description are to *H. gilvicornis*). **Male, Head.** Ventral half of frons bare, yellow. Eyes separated by distance equal to  $\frac{1}{4}$  diameter of median ocellus. Palps narrow, about half length of labium. Occiput not produced posteriorly behind eye as much. Antennae with scape, pedicel, and flagellum brown with short, sparse, hyaline hairs.

**Thorax.** Shining black with hairs more sparse. **Legs.** Similar to those of *H. posthos*.

**Abdomen.** Tergite coloration similar. Sternites black-brown with a narrow, apical, yellow margin, increasing in width in more posterior segments. **Terminalia** (figs. 26–28). Epandrium (fig. 27) whole, similar to that of *H. posthos* in dorsal view. Dorsal process of gonocoxa (fig. 26) larger, with posterior lobe directed posteriorly (not ventrally as in *H. posthos*). Dorsal arms of gonostyli each with

a large apical tooth (fig. 26). Phallus (fig. 26) intermediate in length between those of *H. gilvicornis* and *H. posthos*. Phallus prongs extended under epandrium with median prong almost in same plane as lateral ones.

*Female*. Description based on the only known female, teneral. Similar to male except: Head shining black with broad yellow stripe on genae and ventral half of occiput yellow. Scape and pedicel yellow-brown. Thorax black except dorsal  $\frac{1}{4}$  of anepisternum yellow. *Terminalia*. Not examined.

**HOLOTYPE**: Male, label data SOUTH AFRICA, CAPE PROVINCE, Doringbos on Doring River, Sept. 14, 1972, 500ft, 3119Cc, M. E. Irwin, Riverbank sand dunes.

**PARATYPES**: 1 male (INHS), 1 female, same data as holotype; female with cast pupal exuvium glued to mount.

**OTHER SPECIMENS EXAMINED**: 1 male, SOUTH AFRICA, CAPE PROVINCE, top of Botterkloof Pass, Sept. 13, 1972, 3119Cd, 2230ft, M. E. and B. J. Irwin, white sand dune association (teneral, associated with pupal exuvium).

**ETYMOLOGY**: This species is named in honor of Dr. Brian Stuckenberg, Director of the Natal Museum, Pietermaritzburg, South Africa, and accomplished dipterist.

**REMARKS**: This species has been collected at Doringbos and Botterkloof Pass (fig. 18). The male holotype and paratype were collected as adults and the female paratype and other male specimen were reared from larvae.

#### KEY TO SOUTH AFRICAN *HETEROTROPUS* ADULTS

1. Scutum entirely black ..... 2  
Scutum black with two mediolateral yellow stripes ..... *H. munroi* Bezzi
2. Antennal flagellum yellow; male tarsal claws reduced ..... *H. gilvicornis*, n. sp.  
Antennal flagellum black-brown; male tarsal claws normal ..... 3
3. Length of labium (excluding labellum) equal to length of foretibia; abdominal tergites mostly black-brown with narrow apical yellow border ..... *H. posthos*, n. sp.  
Length of labium (excluding labellum) equal to half length of foretibia; abdominal tergites mostly yellow with narrow basal black-brown bands ..... *H. stuckenbergi*, n. sp.

#### IMMATURES

Eleven mature larvae and 15 pupae were preserved, all with the label data: SOUTH AFRICA, CAPE PROVINCE, top of Botterkloof Pass, Sept. 13, 1972, 3119Cd, 2230 ft, M. E. and B. J. Irwin, white sand dune association. Adults of all the new species described here were found at this locality at this time; thus it is probable that more than one species was preserved as immatures.

#### IDENTIFICATION OF PUPAE

Three of the pupae (two males and one female) were preserved when the teneral adult was clearly visible inside. These adults were identified by labial length and flagellum color as follows: one *H. gilvicornis* male, one *H. posthos* female and one *H. stuckenbergi* male.

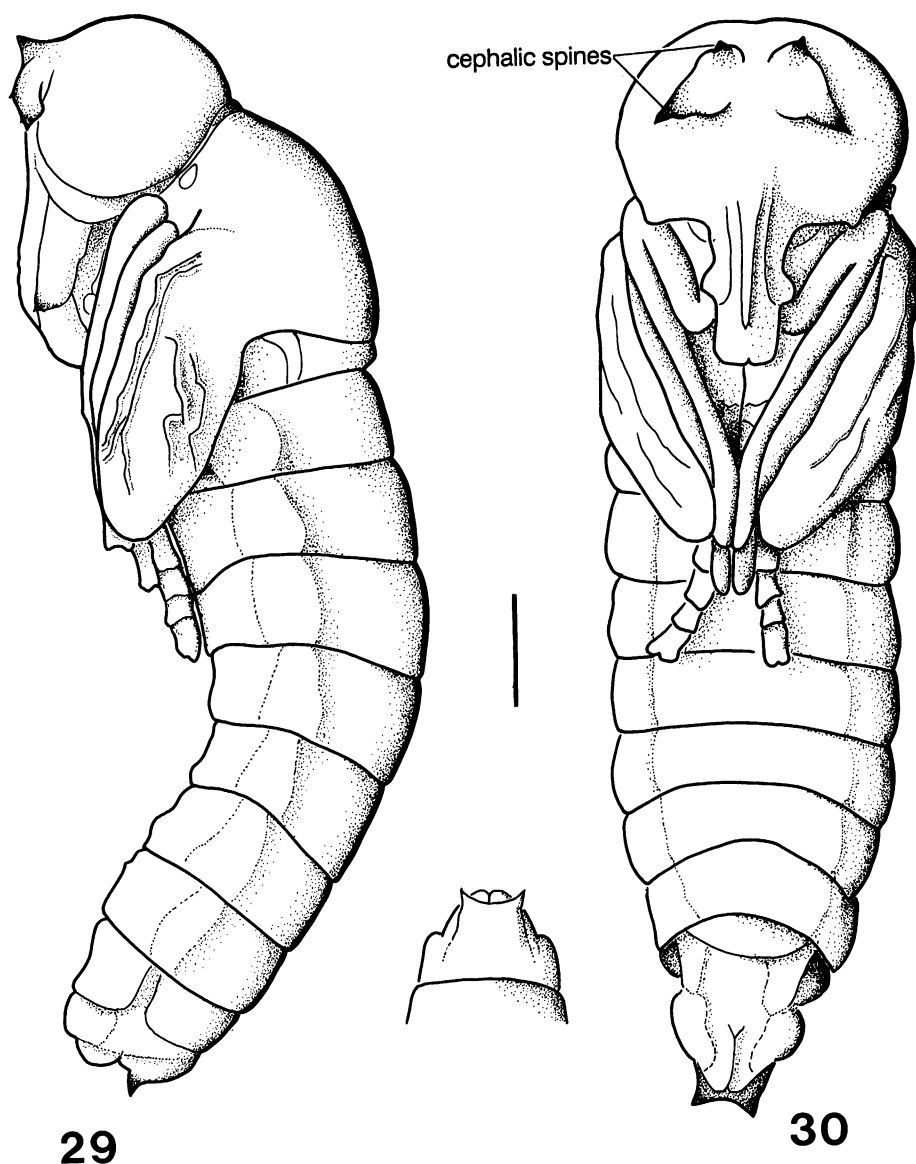
Cast pupal skins have been preserved for all three new species as follows: a single *H. gilvicornis* female; two male pupal skins of *H. posthos* and one female pupal exuvium of *H. stuckenbergi*. Initially it was hoped that specific pupal characters could be found on the adult-associated pupal skins which could then be used to identify the preserved pupae (figs. 31–37). The pupae of the three species are very similar in appearance. The shape of the cephalic spines varies, and it appears that *H. posthos* (figs. 33–35) and *H. stuckenbergi* (figs. 36, 37) each have the 2 posterior spines parallel, whereas *H. gilvicornis* (figs. 31, 32) has these posterior spines more divergent. Reliable characters could not be found to distinguish the pupae of *H. posthos* and *H. stuckenbergi*.

Because the pupae are so similar, only one, that of *H. stuckenbergi*, is fully described and illustrated.

#### DESCRIPTION OF PUPA OF *H. STUCKENBERGI*

This description is based on two cast pupal skins associated with eclosed adults and a pupa identified on the basis of the enclosed teneral adult (figs. 29, 30).

Overall length 4.9–5.2 mm, head width 1.2 mm, thorax width 1.3 mm, maximum abdominal width 1.2–1.3 mm, tapering to 0.5–0.6 mm maximum width of segment 8. Overall color light brown, slightly darker brown on the two most dorsal cephalic spines. Bare, with no hairs or spines except for the cephalic



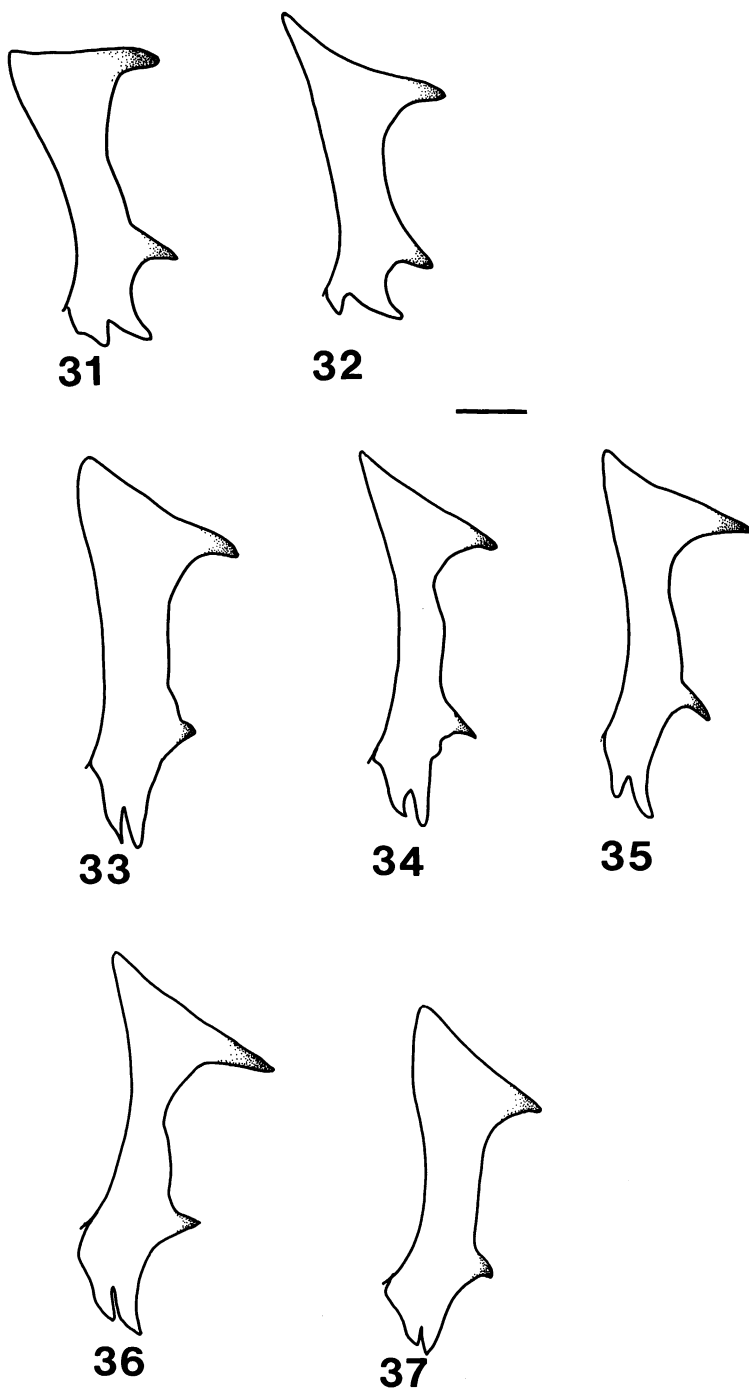
Figs. 29, 30. *Heterotropus stuckenbergi* pupa. 29, lateral view; 30, ventral view. Between them is dorsal view of apex of abdomen. Scale 0.5 mm.

spines and some smaller spines on the apex of the abdomen.

**Head.** Smooth, rounded; four cephalic spines each side of head, each group on raised base. Cephalic spines divided into single, prominent anterior spine and three smaller posterior spines (figs. 36, 37). The two posterior spines closest to thorax are subparallel. Proboscis sheath comprising median, raised

labral sheath, ventral labial sheath, and apical labellar sheath; extended just beyond forecoxal sheath.

**Thorax.** Scutum bare, rounded; prominent wing and leg sheaths present laterally and ventrally. Wing sheaths extended posteriorly to midway along abdominal segment 2. Fore-leg sheath extended to tip of wing sheath, midleg sheath extended to apical margin of



Figs. 31-37. *Heterotropus* pupae, cephalic spines, dorsal view. 31, Female *H. gilvicornis*; 32, male same; 33-35, male *H. posthos*; 36, female *H. stuckenbergi*; 37, male same. Scale 0.1 mm.

abdominal sternite 2; hindleg sheath reaching to apical margin of abdominal sternite 3.

**Abdomen.** Bare, tapering posteriorly; segments clearly visible. Caudal segment with two dorsal spines (fig. 30) in both sexes.

#### IDENTIFICATION OF LARVAE

In addition to the 11 preserved larvae, a single larval exuvium of both *H. gilvicornis* and *H. posthos* was preserved. The thorax and abdomen of both are severely crumpled, making comparison difficult; however the head capsules of the two specimens were compared. They were very similar, except that the apical antennal segment of *H. gilvicornis* is shorter than that of *H. posthos* (figs. 40–42). The head capsules of the preserved but unassociated larvae had long apical antennal segments similar to those of *H. posthos*. Thus the preserved larvae may be *H. posthos*; however, the morphology of *H. stuckenbergi* larvae is unknown, and that species could also be present in the sample. It is also possible that the apical antennal segments of the single *H. gilvicornis* larva were broken off in the substrate before or after the pupa was formed.

#### DESCRIPTION OF *HETEROTROPUS* LARVA

The following description is taken from one of the 11 preserved *Heterotropus* larvae collected at Botterkloof Pass. The head capsule of this specimen is identical to that of *H. posthos*. We regard its specific identity as uncertain, but it is undoubtedly one of the species described here.

Elongate (fig. 38), flattened dorsoventrally, tapered at both ends. Color pale cream with white fat body clearly visible through integument. Measurements (taken from all 11 preserved larvae): length 7.6–10.2 mm, maximum width of abdomen 0.7–1.1 mm.

**Head** (figs. 40–49). Head capsule tanish-brown, extended into prothorax as an elongate, posteriorly rounded, dorsal plate (fig. 42). More heavily sclerotized around lateral margins. Head somewhat swollen behind head capsule anterior to prothorax (fig. 42). Head capsule with mouthparts projecting anteriorly, sensory appendages laterally (fig. 43). Antennae and eyes arising on genae (figs. 40, 44). Antennae arising anterolaterally, two segmented with elongate, parallel-sided basal

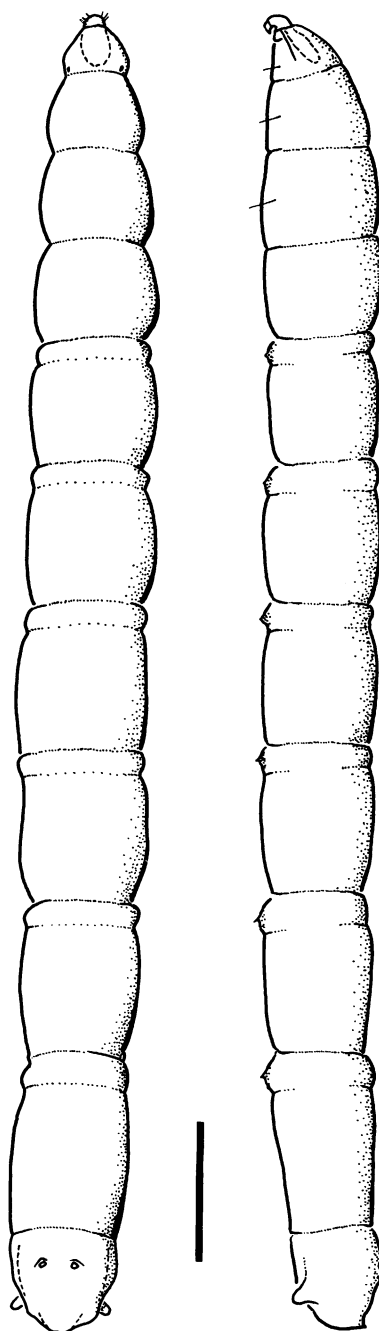


Fig. 38. *Heterotropus* mature larva, left dorsal view, right lateral view. Scale 1 mm.

segment and narrow apical segment about  $\frac{1}{2}$  length of basal segment (figs. 42, 47). Eyes immediately posterior to antennal bases (figs. 40, 42, 47). Two long, prominent, setae in



Fig. 39. *Heterotropus* larva, photographed in rearing medium. Specimen from Africa, Niger, 15 km west of Niamey, 17 July 1990, inland sand dunes, M. E. Irwin. Larva 10 mm long.

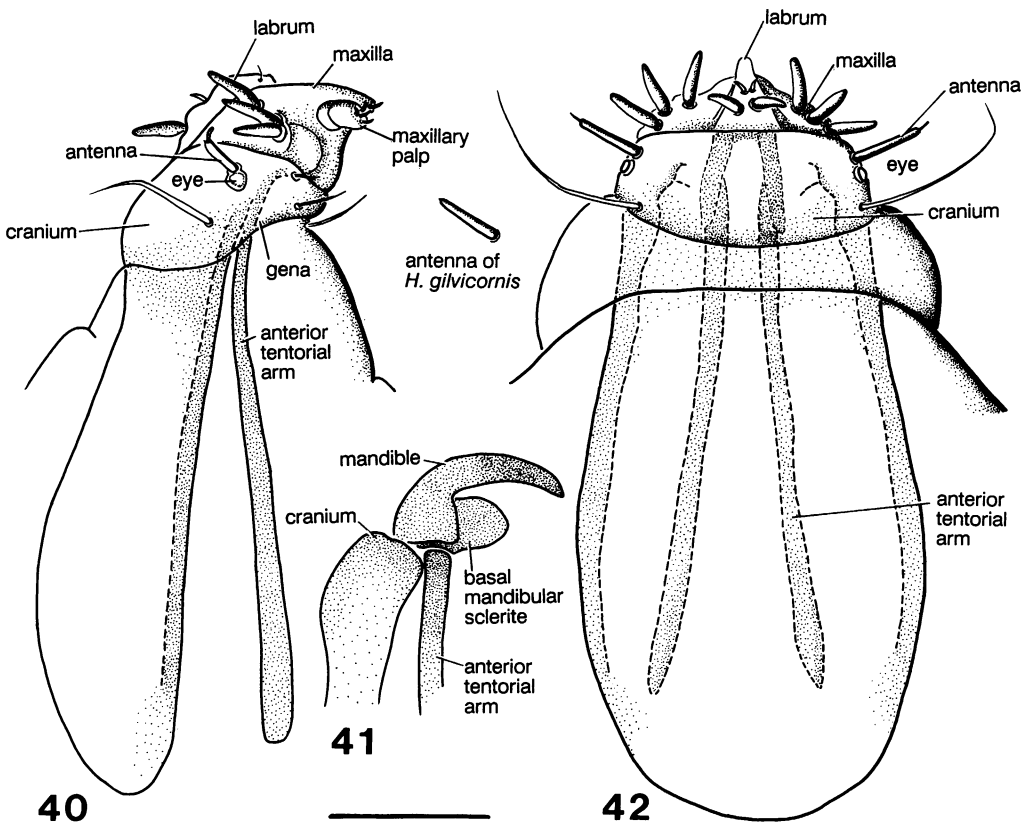
the posterolateral corner of the genae, extended anterolaterally (figs. 42, 44). Labrum distinct, extended anteriorly from head capsule between maxillae (figs. 42, 44). In lateral view labrum raised above maxillae (figs. 42, 44), with two pairs of stout bristles, a large basal pair and smaller apical pair (figs. 40, 45). Maxillae well developed, extended anteroventrally from head capsule (figs. 40, 42, 46). Basal cardo with three well developed, stout setae in a row (figs. 42, 47). Distal stipes bear two-segmented maxillary palps (figs. 40, 48). Apex of maxillary palp with central depression enclosing five setae (fig. 48). Stipes with small seta in small depression subapically on lateral surface (fig. 46), not divided into galea and lacinia. Mandibles narrow, sickle shaped, working in dorsoventral plane, wedged between labrum and maxillae (fig. 46). Basal mandibular sclerite visible at base of mandible, produced ventrally (fig. 41).

Small, narrow labium visible below tips of mandibles, armed with 6–7 anteriorly directed setae at apex (fig. 49). Ventral portion of head capsule narrower in lateral view than dorsal portion (figs. 40, 44), bearing two small setae ventrolaterally. Anterior tentorial arms extended posteriorly almost to posterior margin of head capsule (fig. 42). Poorly sclerotized, trough-shaped pharynx lying between anterior tentorial arms.

*Thorax.* Clearly divided into three segments, metathoracic segment wider than the previous two. Prothorax bearing small, simple spiracles in posterolateral corner of dorsal surface. Each thoracic segment with pair of setae ventrolaterally (fig. 38).

*Abdomen.* Eight segments, first segment simple; however segments 2–7 each with constriction (figs. 38, 51) near anterior end. Pair of ventral creeping welts borne just anterior to constriction (fig. 52) on these segments.





Figs. 40–42. *Heterotropus* larva, head capsule. 40, Lateral view; 41, detail of internal structures, lateral view; 42, dorsal view. Antenna of *H. gilvicornis* above figure 41. Scale 0.1 mm.

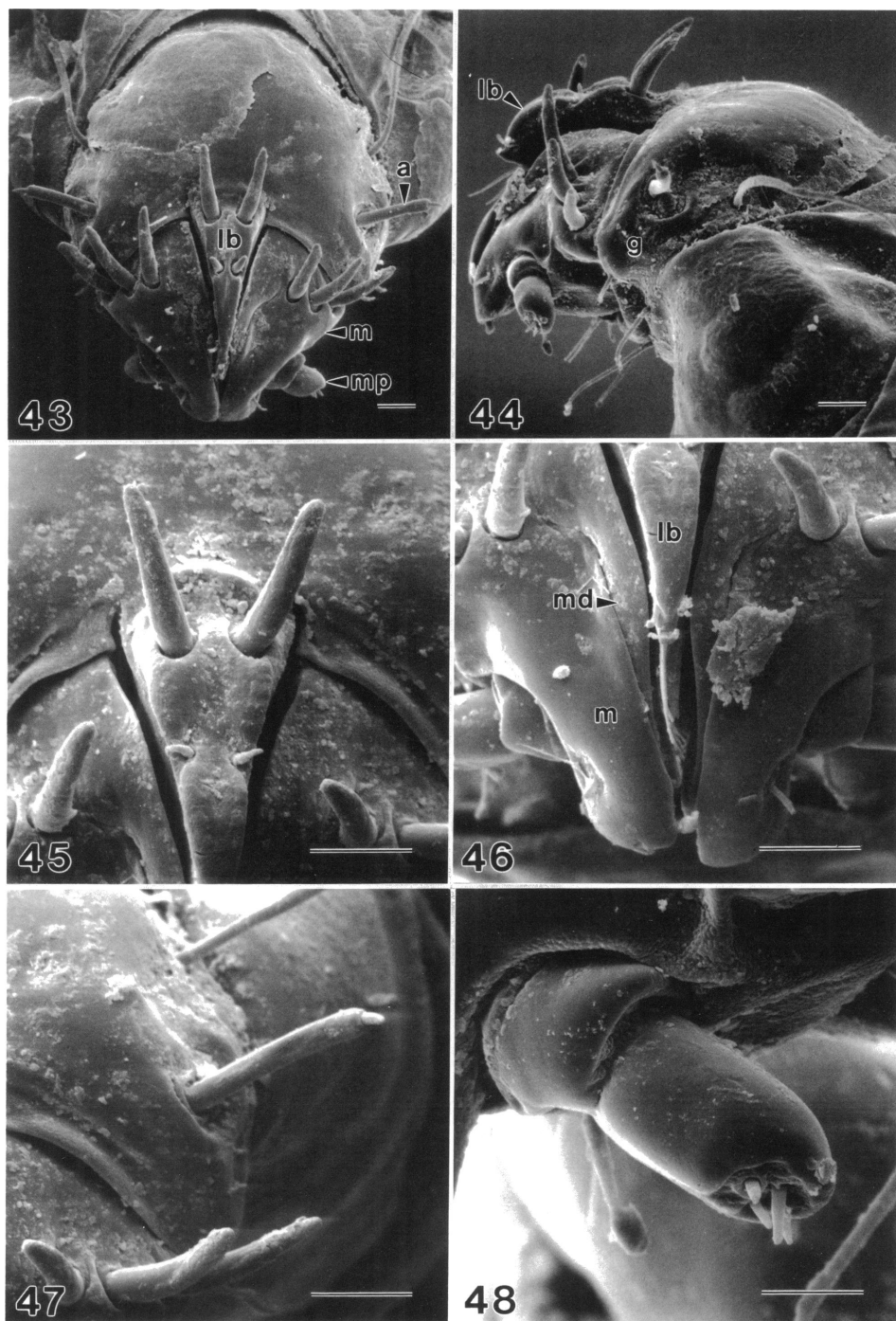
Segment 8 in dorsal view (fig. 53) with large posterior spiracles positioned anterodorsally. Caudal end with two small seta-bearing appendages (fig. 50) arising from median lobe. Segment 8 in ventral view with two posterolaterally directed anal papillae (fig. 54). Anal papillae composed of thick basal piece and narrow, domed apical piece; apical piece with small terminal slit. Raised ridge between anal papillae (fig. 54). Anus a short longitudinal slit posterior to raised ridge (fig. 54).

#### NOTES ON ADULT AND LARVAL BIOLOGY

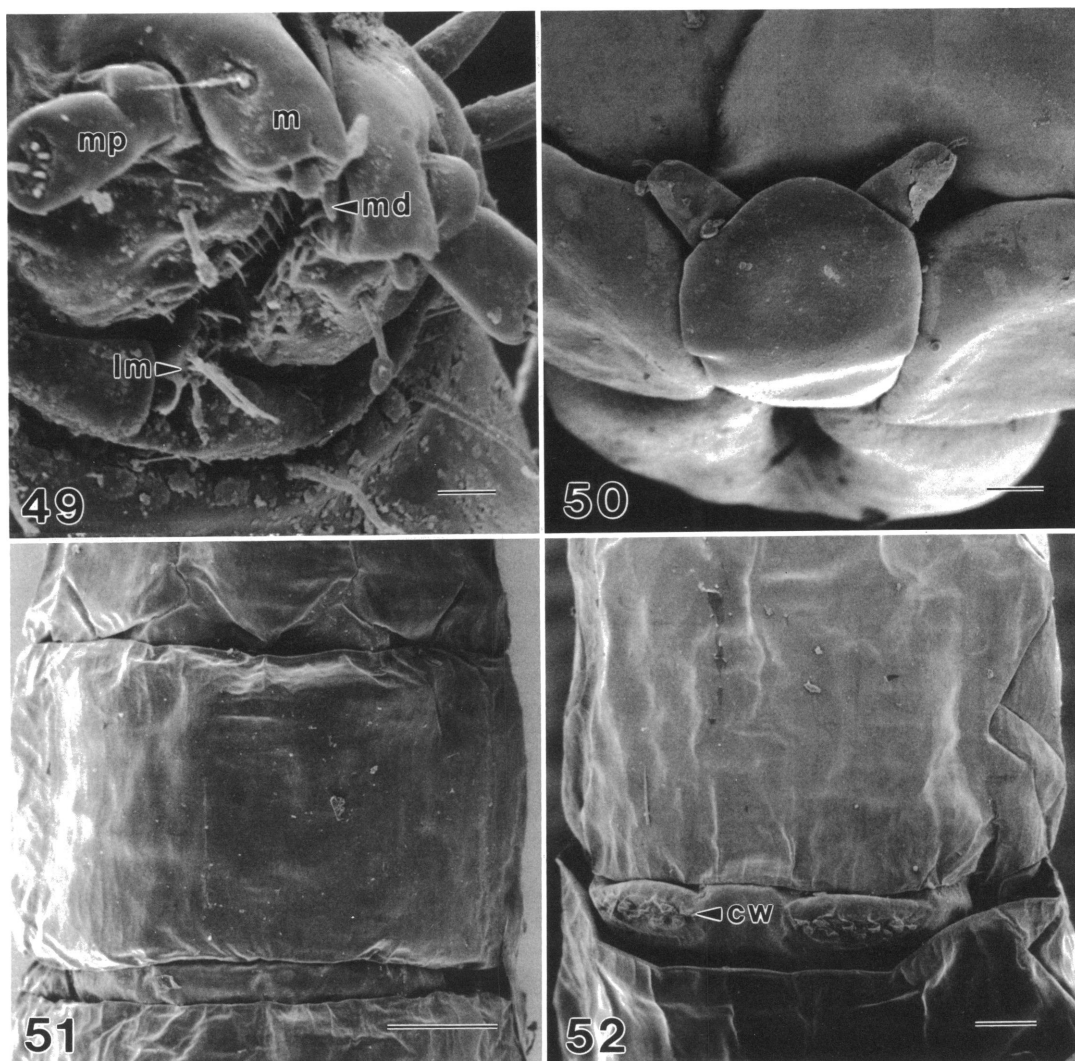
Adults of all three *Heterotropus* species were collected in sand dune associations with sparse herbaceous vegetation. Adults could be found walking on the surface of the sand and seemed unwilling to take flight. The three locations

where the new species were taken are in close proximity. Indeed, Doringbos and Botterkloof Pass are only about 10 km apart (fig. 18). All three species were collected at the top of Botterkloof Pass. Both *H. posthos* and *H. stuckenbergi* were taken at Doringbos on the Doring River and *H. gilvicornis* alone was taken at Hondeklop Baai, a coastal locality.

Larvae (fig. 39) were found while sieving the top few inches of sand to collect therevid larvae, as described by Irwin (1972). They were found alone, and their morphology does not suggest a parasitoid lifestyle, which is characteristic of almost all other known bombyliid larvae. It is most likely that they are predatory, like many other asiloid larvae. However, in the laboratory the *Heterotropus* larvae did not appear to eat *Tribolium* larvae offered them, and only the largest fly larvae successfully eclosed as adults.



Figs. 43–48. Scanning electron micrographs of *Heterotropus* larva. 43, Anterior view of head capsule, a = antenna, lb = labrum, m = maxilla, mp = maxillary palp; 44, lateral view of head, g = gena; 45, detail of setae on labrum; 46, detail of apex of labrum and mandibles, md = mandible; 47, detail of antenna and setae on cardo; 48, maxillary palp. Scale 10  $\mu$ m.



Figs. 49–52. Scanning electron micrographs of *Heterotropus* larva. **49**, View beneath maxilla showing labium, scale 10  $\mu$ m, lm = labium, m = maxilla, md = mandible, mp = maxillary palp; **50**, apex of abdomen showing small appendages each bearing a short seta, scale 20  $\mu$ m; **51**, dorsal view of abdominal segment 1, scale 0.2 mm; **52**, ventral view of creeping welts on segment 7, scale 0.1 mm, cw = creeping welt.

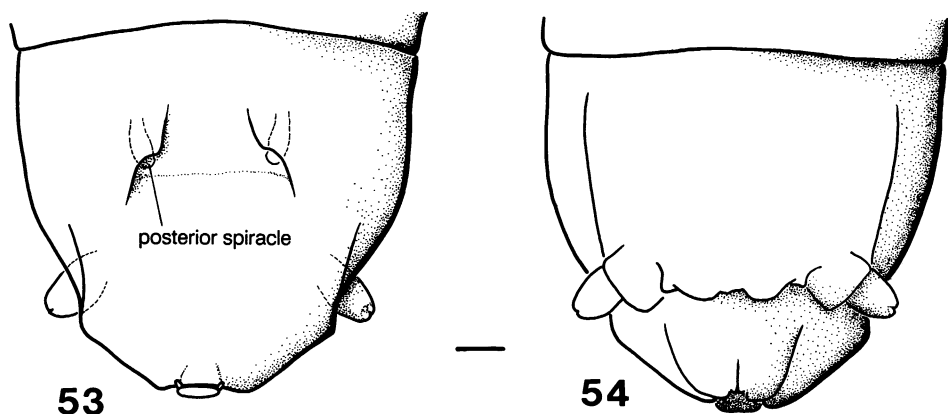
## DISCUSSION

### THE MORPHOLOGY OF *HETEROTROPUS*

This detailed examination of the morphology of the larvae, pupae, and adult of *Heterotropus* has highlighted many unusual, autapomorphic features which are not found in other Bombyliidae. In addition, *Heterotropus* exhibits some primitive features, as compared to other groups in the Bombyliidae and to the Asiloidea in general. These char-

acters will be discussed in the light of the known habits and morphology of the Bombyliidae and the characters used by Woodley (1989) in his cladistic analysis of the Asiloidea.

**Male Terminalia:** The phallus is long (especially so in *H. posthos*) and trifid with the lateral prongs bearing small ventral spines. Theodor (1983) reported that one undescribed species of *Heterotropus* has a bifid aedeagus. A trifid (or bifid) aedeagus is un-



Figs. 53–54. *Heterotropus* larva abdominal segment 8. 53, Dorsal view showing posterior spiracles; 54, ventral view showing anal papillae. Scale 0.1 mm.

known in the Bombyliidae except in some Mythicomysiinae (some species of *Paraconsors* Hall and Evenhuis 1987 and members of a new genus from Australia) but is common in the Scenopinidae (Kelsey, 1969) and Asilidae (Theodor, 1976) of the Asiloidea. The relatively small gonocoxae arise from a very large hypandrium and are widely separated medially, leaving a large central cavity. An apomorphic feature of other Bombyliidae is the medioventral fusion of the gonocoxae. In the *Heterotropus* specimens described in this work this large cavity is partially occupied by the peculiar median arms of the gonostyli, which have long apical setae. The gonocoxae bear large processes dorsally which have serrate dorsal margins. The shape of the dorsal process is different in each species examined. The dorsal processes of the gonocoxae and the dorsal and median arms of the gonostyli may be adaptations to guide the long phallus. On dissection, the phallus lies between these gonocoxal processes, then curves ventrally between the median and dorsal arms of the gonostyli. There is only a loose membranous connection of the phallus to the gonocoxae and to sternite 10. In Bombyliidae there is a stronger sclerotized connection between the phallus and the gonocoxae.

**Female Terminalia:** The female terminalia of *Heterotropus* are typical for asiloids in many respects. There are three spermathecae with well-sclerotized bulbs and the acanthophorite spines are well developed. Acantho-

phorite spines are considered to be a ground-plan feature of the Asiloidea (Adisoemarto and Wood, 1975; Woodley, 1989), and similar (?homologous) structures are also found in the Empidoidea. A plesiomorphic feature of the female terminalia is the separation of the acanthophorites from tergite 9. In other asiloids the acanthophorites have become more or less fused to tergite 9 (e.g., Irwin, 1976; Yeates, 1990).

**Pupa:** The pupa is immediately distinguished from those of other Bombyliidae (Hull, 1973) because it lacks a vestiture of long hairs. There are four pairs of cephalic setae on the head which are borne on the antennal sheaths. The anterior cephalic spine lies over the pedicel and the remaining three posterior spines lie over the apical half of the flagellum. Spine-bearing antennal sheaths are found in most Bombyliidae, and are probably a primitive feature of the family. They have been lost in a few disparate groups independently (Evenhuis, 1985). Cephalic spines are also found in all the related asiloid families: Asilidae (Hull, 1962), Therevidae (Irwin, 1972), Apioceridae (Peterson, 1981), Mydidae (Wilcox, 1981) and Scenopinidae (Krivoshchina, 1980). Almost all Bombyliidae pupae also possess rows of strong spines, called chitinous rods, on the abdominal tergites (Hull, 1973). These rods are often u-shaped in lateral view, with a spine at both the anterior and posterior ends. The only known Bombyliidae pupae lacking these chitinous rods belong to the Mythicomysiinae: *Glabel-*

*lula arctica* (Andersson, 1974), *Psiloderoides mansfieldi* (Hesse, 1967), and *Mythicomylia* sp. near *pusilla* (N.L. Evenhuis personal commun.). The pupae of all other asiloid families bear a row of stout spines on the abdominal tergites. However, the distinctive u-shaped spines appear to have arisen within the Bombyliidae.

**Larva:** Woodley (1989) used the parasitoid lifestyle and larval hypermetamorphosis as an apomorphy of the Bombyliidae. Our knowledge of the immature stages of the Bombyliidae is very limited but most are external parasitoids of other insects or egg predators. In the best-studied examples, the energetic first instar planidium larva has a very different morphology and habits from the largely sedentary mature parasitoid larva (e.g., Bohart et al., 1960). In most other cases, the presence (or absence) of hypermetamorphosis has been assumed after examination of the morphology of one larval instar. To date, there has been a single bombyliid recorded which does not appear to exhibit hypermetamorphosis. Andersson (1974) described the immature stages of *Glbellula arctica* Zetterstedt. Mature larvae of this species are very fast moving and live in ant nests, probably feeding on ant brood or other ant inquilines. Andersson (1974) assumed there is no hypermetamorphosis in this species because the final instar larva is similar to the planidium larvae of other species of Bombyliidae. This morphology and habit could be dismissed as a reversal except that the subfamily Mythicomylinae, to which *Glbellula* belongs, is primitive within the Bombyliidae and may be the sister group to the remaining members of the family (Yeates, in prep.). Thus it is possible that the most plesiomorphic larvae in the Bombyliidae are predatory and lack hypermetamorphosis.

*Heterotropus* larvae were found free-living in sandy soil, and are probably predatory there. In general body shape (fig. 39), the mature larva is similar to the predatory larvae of Asilidae (Melin, 1923; Musso, 1978) and Apioceridae (English, 1947). The morphology of *Heterotropus* mature larvae indicates that they do not undergo hypermetamorphosis, as do almost all other Bombyliidae.

The mouthparts of *Heterotropus* are similar to those of other asiloid families in basic

structure. The arrangement of large setae on the labrum and cardo appears to be peculiar to *Heterotropus*. B. J. Sinclair (personal commun.) considers that basal mandibular sclerite is present as a dorsal plate posterior to the mandible in the ground-plan of the Asiloidea. This plate is often mistaken for the cardo (e.g., Teskey, 1981: fig. 3.10), and is only poorly differentiated in *Heterotropus*. The segmentation of the abdomen is normal, the anterior constriction on segments 2–7 notwithstanding. This constriction may function to provide additional movement for the ventral creeping welts. *Heterotropus* larvae do not resemble the elongate, slender larvae of Therevidae and Scenopinidae which have the abdominal segments distinctly subdivided and thus appear to have 17 abdominal segments.

The retraction of the head capsule into the thorax and general reduction in extent of the cranium is a feature of larvae of the lower Brachycera (Teskey, 1981). Although the cranial reduction is variable, members of the Bombyliidae usually have one or two dorsal sclerotized plates remaining which extend into the prothorax. These plates are not articulated with the remainder of the cranium (Woodley, 1989). In other Asiloidea one or two metacephalic rods are present, which articulate with the remainder of the cranium. In the Therevidae and Scenopinidae only a slender metacephalic rod remains. *Heterotropus* is plesiomorphic among Bombyliidae in having a broad, well sclerotized dorsal cranium.

The single apomorphy for the Asiloidea used by Woodley (1989) was the division of the apical segment of the abdomen into two, with the posterior spiracle appearing in the apparent penultimate segment. This apomorphy holds true for all asiloid larvae we have examined except those of *Heterotropus*, where the abdomen is clearly eight-segmented with the posterior spiracles occurring in the ultimate segment. In this respect *Heterotropus* resembles the larvae of the lower Brachycera other than the Asiloidea.

#### PHYLOGENETIC POSITION OF *HETEROTROPUS*

After a consideration of the morphology of the adults and immature stages of *Heterotro-*

*pus*, it became obvious that they could only be placed in the Bombyliidae with the imposition of many (nonparsimonious) character state reversals. However, the presence of a bristleform empodium (fig. 7) and acanthophorite spines in the female suggests that they belonged within the Asiloidea. In an attempt to elucidate their phylogenetic position, we have placed *Heterotropus* in the context of the most recent cladistic analysis of the Asiloidea (fig. 55) (Woodley, 1989).

Woodley (1989) used 14 characters in his cladistic analysis of the families of Asiloidea. The higher Brachycera [Asiloidea, Empidoidea, and Muscoidea (= Muscomorpha or Cyclorrhapha of authors)] are characterized by a modified, bristleform empodium. These 15 characters were recoded into binary form for parsimony analysis using Hennig 86 (Farris, 1988). The Nemestrinidae were chosen as the outgroup, belonging to the sistergroup of the higher Brachycera (Woodley, 1989). *Heterotropus* was added as a terminal taxon and coded according to the character states found in this work. The characters used here correspond exactly to those of Woodley (1989); apomorphic states are noted here and the number in brackets refers to Woodley's character number. Character 3 (larvae parasitic with hypermetamorphosis) was coded 0 for Nemestrinidae because Woodley considered

the larval habits and morphology to be independently derived in the Nemestrinoidea and Asiloidea (Bombyliidae). Note that the advanced state of character 15 (palpal segment number) was used by Woodley as an apomorphy of Mydidae. Character 15 is coded here as the ground-plan state found in each family.

1. Empodium bristleform (32).
2. Larval posterior spiracle situated in apparent penultimate abdominal segment (33).
3. Larvae parasitic, with hypermetamorphosis (3.1).
4. Larval metacephalic rod hinged (3.2).
5. Larval abdominal segments secondarily segmented, the abdomen appearing to have 17 segments (3.3).
6. Larval metacephalic rod posteriorly spatulate (3.4).
7. Wing cell  $m_1$  strongly widened distally (3.5).
8. Wing with costal vein ending at  $M_1$  (3.6).
9. Adults with labellae of labium strongly reduced, fused with prementum (3.7).
10. Hypopharynx of adults strongly sclerotized, modified into a hypodermic, needlelike structure (3.8).
11. Adult face with vestiture of strong bristles (3.9).

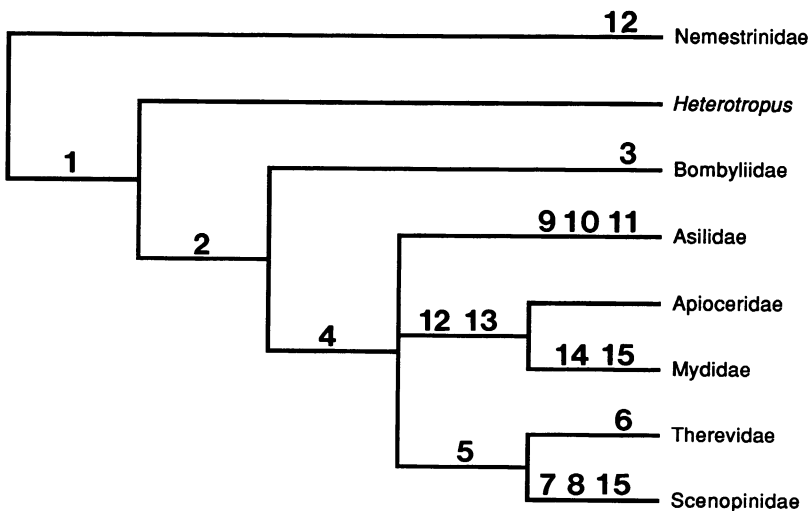


Fig. 55. Cladogram of relationships of asiloid families with *Heterotropus* included. Numbers indicate characters discussed in text changing from plesiomorphic state 0 to apomorphic state 1.

TABLE 1  
Data Matrix

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Nemestrinidae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Heterotropus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bombyliidae	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Asilidae	1	1	0	1	0	0	0	0	1	1	1	0	0	0	0
Apioceridae	1	1	0	1	0	0	0	0	0	0	0	1	1	0	0
Mydidae	1	1	0	1	0	0	0	0	0	0	0	1	1	1	1
Therevidae	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0
Scenopinidae	1	1	0	1	1	0	1	1	0	0	0	0	0	0	1

12. Wing with veins  $R_5$  and  $M_1$  strongly curved anteriorly, ending anterior to the wing tip (3.10).
13. Adult with supernumerary rectal papillae (3.11).
14. Hind femora with ventral armature of moderately to very stoutly thickened spinelike bristles (3.12).
15. Adult palpus one-segmented (3.13).

## RESULTS OF CLADISTIC ANALYSIS

Hennig 86 produced a single tree (fig. 55) 17 steps long. Not unexpectedly, the relationships of the asiloid families are as Woodley (1989) discussed. *Heterotropus*, however, is placed at the base of the tree, the sister group to the remaining Asiloidea. It lacks the apomorphy of the Bombyliidae (Character 3, larvae parasitic with hypermetamorphosis) and the apomorphy of the Asiloidea (Character 2, posterior spiracle in apparent penultimate abdominal segment of larva). Thus, under the current notion of the Asiloidea, the inclusion of *Heterotropus* in the Bombyliidae makes that family paraphyletic with respect to the remainder of the Asiloidea. The most acceptable solution would be to remove *Heterotropus* to a family of its own.

Woodley, Cumming and Sinclair (personal commun.) have suggested that a possible apomorphy of the Asiloidea is the anterodorsal position of the posterior spiracle on the eighth abdominal segment. *Heterotropus* has this putative apomorphy (fig. 53), and thus under this notion would be included in the Asiloidea. This suggestion will have to be tested taking into account the distribution of the character state in other Diptera and in

the light of other character systems. In particular, it appears that larvae of the Nemestrinoidea also have the posterior spiracle in an anterodorsal position on the eighth abdominal segment.

The paraphyly of the Bombyliidae has long been suspected (Hennig, 1952; Mühlenberg, 1971), and this study provides further evidence on that score. One of us (DKY) is currently studying the relationships of the Bombyliidae to other families of Asiloidea. This cladistic analysis, using many more characters than those of Woodley (1989) and including many more terminal taxa of asiloids, provides evidence that some genera of the Bombyliidae are more closely related to other families of the Asiloidea. Evidence is presented here that *Heterotropus* does not belong within the Bombyliidae and that it deserves status as a separate family. Rather than proceed in a piecemeal fashion, the formal erection of a new family to accommodate *Heterotropus* should properly wait until the results of DKY's more extensive analyses of Bombyliidae phylogeny are complete. At that time other genera will be removed from the family and placed in other asiloid families and putative synapomorphies of the remaining Bombyliidae will be discussed.

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