THE SYSTEMATICS AND PHYLOGENETICS OF THE SYCOECINAE (AGAONIDAE, CHALCIDOIDEA, HYMENOPTERA)

by
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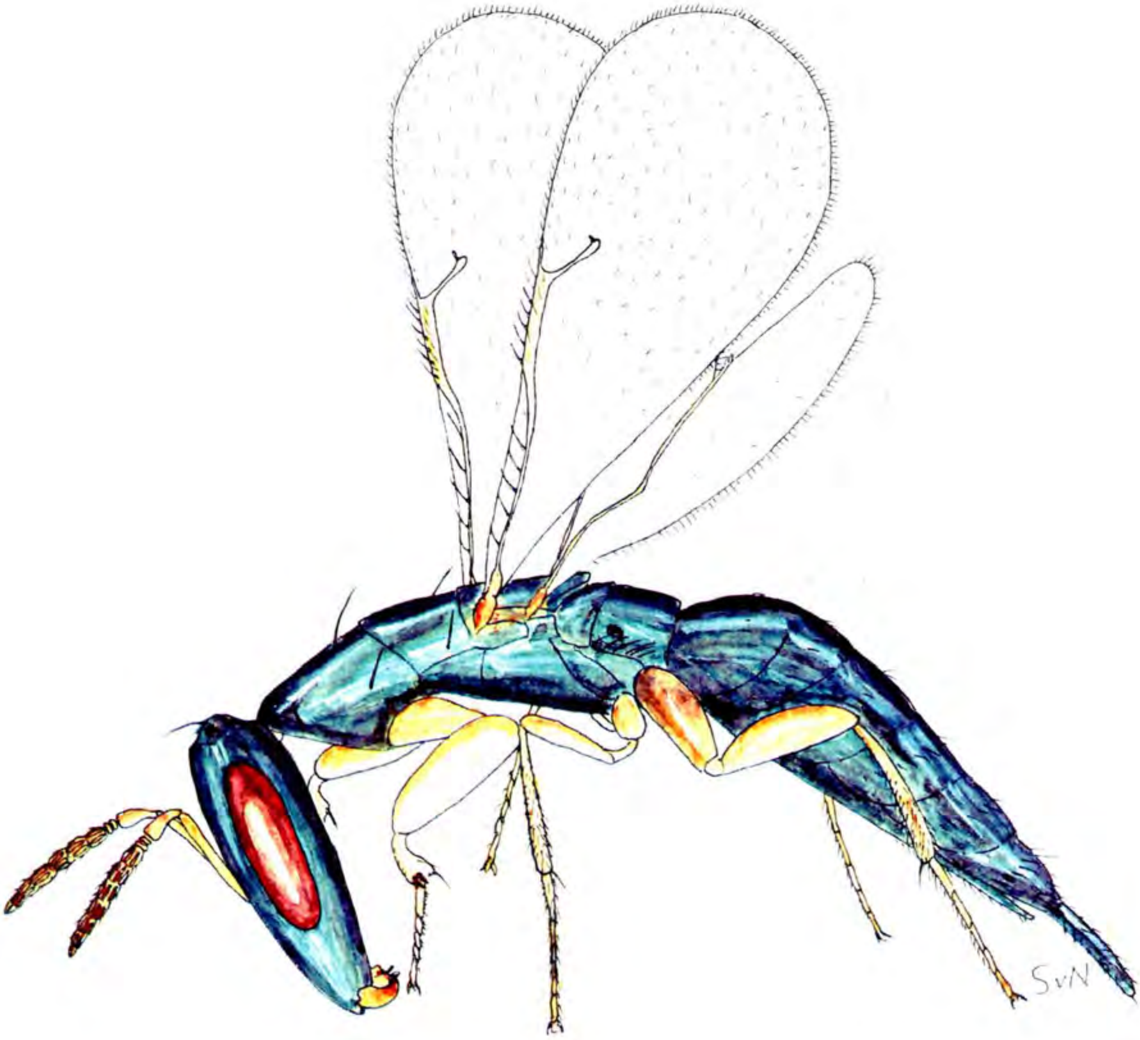

Philocaenus clairae sp. nov.

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ABSTRACT

The Sycoecinae are a distinct and well-defined subfamily of old world fig wasps (Agaonidae, Chalcidoidea, Hymenoptera), exclusively associated with the figs of *Ficus* species (Moraceae). The most likely sister group of the Sycoecinae was determined to be the Sycoryctini (Sycoryctinae) based largely on synapomorphies of the underside of the head. 67 sycoecine species and 3 subspecies were recognised and included in a phylogenetic analysis of the subfamily. This analysis clearly delimited six genera (four African and two extra-African), although the phylogenetic relationships between the genera were not strongly supported and remain flexible. Comparisons of the phylogeny of the Sycoecinae with the classifications of the Agaoninae and their host fig trees (*Ficus*, Moraceae) suggest a degree of cospeciation *sensu lato*.

Numerous homoplasies were detected within the Sycoecinae, some of which were shared with another group of fig wasps that also enter the fig to oviposit, the Agaoninae. The anatomy of the figs apparently provides strong selection pressures that have resulted in both parallelisms and convergences within and between the two subfamilies.

Among the 67 species and 3 subspecies that were recognised, 43 species and 2 subspecies are described as new. The males of three previously recognised species are also described for the first time. One generic and two specific synonyms are established, together with five new combinations. Keys are provided to the genera and species, for both sexes.

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INTRODUCTION

FIG WASP BIOLOGY

'Fig wasp' is a general term that encompasses all the chalcids (Hymenoptera, Chalcidoidea) that are associated with figs - the inflorescences of fig trees (*Ficus* spp., Moraceae). The majority of fig wasps have been placed in a single family the Agaonidae (Boucek, 1988). These include the subfamilies Agaoninae, Sycoecinae, Sycophaginae, Sycoryctinae, Otitesellinae, and Epichrysomallinae, all of which are hypothesised to have arisen from a common ancestor (Boucek, 1988). In addition there are fig wasps from other families that Boucek (1988) regards as later invaders of the fig wasp community, namely *Ormyrus* Westwood (Ormyridae), *Megastigmus* Dalman and *Physothorax* Mayr (Torymidae), and *Sycophila* Walker and related genera (Eurytomidae). There are also a few examples of fig wasps from the Pteromalidae and Eulophidae, which exploit hosts such as moth larvae and gall midges (Cecidomyiidae) feeding inside the figs.

The fig inflorescence is a closed receptacle with the reduced, morphologically or functionally unisexual, florets lining the inner cavity (Verkerke, 1989, Berg, 1990a). Most fig wasp larvae develop in galled ovules, either phytophagously, feeding on the galled endosperm, as parasitoids feeding on the phytophages, or as inquilines feeding initially on the phytophages and then on the galled plant tissue. There are two different strategies employed by fig wasp females to oviposit into the ovules. They either enter the fig through a narrow bract-lined opening called the ostiole (all Agaoninae; all Sycoecinae; *Sycophaga* Westwood from the Sycophaginae; *Grasseiana* Abdurahiman & Joseph, *Lipothymus* Grandi and *Eujacobsonia* Grandi from the Otitesellinae), or they oviposit through the fig wall from the exterior (all remaining fig wasps).

An obligate mutualism exists between species of the Agaoninae (the pollinating fig wasps) and their host fig trees, each needing the other for reproduction (Galil, 1977; Janzen, 1979). This relationship is characterised by an almost universal one-to-one host specificity within the Agaoninae (Ramirez, 1970; Wiebes, 1979b; Wiebes & Compton, 1990), although there are some well documented examples of exceptions to this rule, where two agaonines are associated with the same host (Galil & Eisikowitch, 1968; 1969; Ramirez, 1970; Michaloud *et al.*, 1985; Compton *et al.*, 1991), or where the same agaonine species is apparently associated with two or more different host species (Wiebes, 1989b; Wiebes & Compton, 1990). The degree of host specificity among non-pollinating fig wasps is largely undetermined, due to a lack of systematic studies undertaken on these groups. Gordh (1975) and Ulenberg (1985) in their revisions of *Idarnes* Walker and *Apocrypta* Coquerel respectively, nonetheless demonstrated extreme host specificity for the species in these genera. At the same time there are several instances of the same non-pollinating fig wasp recorded from different *Ficus* species (Hill, 1967b; Boucek, *et al.*, 1981; Wiebes, 1981). In Grahamstown, South Africa, for example, the *Sycoryctes* Mayr present in three local *Ficus* species appear to be morphologically inseparable and may be a single species (Compton, pers. comm.).

Within a population of fig trees the production of fig crops among the individual trees is asynchronous, whereas within a particular tree the figs are usually all at the same developmental stage (Ramirez, 1970; Janzen, 1979). The pollinators leaving their natal figs therefore often have to fly considerable distances to locate figs that are at the right stage of development. They accomplish this by homing in on host tree specific volatiles, produced by the figs when they are ready for pollination (van Noort *et al.*, 1989; Ware & Compton, in press a).

The ostiole is thought to act as a physical selective barrier, generally preventing wasps that are not adapted to the ostiolar morphology of a particular *Ficus* species from gaining entry into the fig (Janzen, 1979). The barrier provided by the ostiole may thus act as one of the mechanisms contributing towards the maintenance of host specificity (Ramirez, 1970; Galil, 1977; Janzen, 1979; Bronstein, 1987). In unusual circumstances some female wasps are nonetheless able to enter the figs of trees that are not their usual hosts (Ramirez, 1970; Compton, 1990; Ware & Compton, in press b). Style length may be another factor maintaining host specificity in internal ovipositing fig wasps, in that ovipositional success is limited by ovipositor length. Ovipositor length of both agaonines and sycoecines is strongly correlated with the mean style length of their associated *Ficus* species (Nefdt, 1989). Similarly ovipositional success in externally ovipositing species is limited by ovipositor length, in that these species need to penetrate the thick fig wall to reach the ovules. Some of the externally ovipositing species arrive at the fig well after the pollinators, so the same volatile cannot be used to home in on the fig. Notwithstanding these other factors, the major contributor to host specificity in the Agaoninae and the Sycoecinae is still probably specificity of the fig volatiles.

COEVOLUTION OF FIG WASPS AND FIGS

The term coevolution was introduced by Ehrlich & Raven (1964) in their study on butterflies and plants, but was not defined by them and subsequent usage became very broad. Janzen (1980) in his paper entitled 'When is it coevolution?' narrowed the application of the term by identifying three cases of misuse and provided a useful definition, which is basically the same as that subsequently advocated by Thompson (1982).

Coevolution as defined by Thompson is 'reciprocal evolutionary change in interacting species' such that both of the species involved in the interaction must evolve as a response to the interaction. This definition contrasts with Brooks' (1979) definition of cospeciation, in which cladogenesis of the parasite is considered to be a result of host cladogenesis. As Thompson (1982) points out, this is a definition of congruent phylogenies, but not necessarily of cospeciation. In such circumstances, although both of the partners may appear to have speciated in parallel, the selective forces provided by each partner have not necessarily resulted in evolution and speciation in the other. For example, parasites will often have coadapted in response to the evolution of their hosts, but their host's evolution was not affected by the parasites. Congruent phylogenetic trees therefore do not necessarily indicate cospeciation, and furthermore can be the outcome of sequential/radiating speciation (Jermy, 1976, Mitter *et al.*, 1991). Such sequential evolution has been proposed for insects on thistles (Straw, 1989) and lycaenids on *Eriogonum* (Shields & Reveal, 1988).

Thompson (1989) recognises five different modes of coevolution. The first three (gene-for-gene, specific, and guild coevolution) do not entail reciprocal speciation, only reciprocal evolutionary change. The fourth, diversifying coevolution (the allopatric cospeciation model of Wanntorp *et al.*, 1990), may result in reciprocal speciation caused by the interaction and is then termed cospeciation. Plant-pollinator interactions such as those of the fig-agaonine wasp, yucca-yucca moth, and globeflower *Trollius* - *Chiastocheta* fly, are included in this category. The fifth mode is escape-and-radiation coevolution (the exclusion model of Wanntorp *et al.*, 1990). This differs from diversifying coevolution in that host speciation occurs outside of the interaction and is thus not a direct result of the interaction, although the initiation of the new line of host speciation is in response to the interaction.

Sequential/radiating speciation (Jermy, 1976; 1984) (the colonisation model of Wanntorp *et al.*, 1990) is not an example of coevolution, because here the insects have radiated after the diversification of their host plants and consequently have had no effect on host speciation. Wanntorp *et al.* (1990) state that they would expect little or no phylogenetic congruence between insects and their host plants in this model. However, insects are still more likely to colonise closely related plants (Connor *et al.*, 1980) or chemically similar hosts (Futuyma & McCafferty, 1990) and subsequently speciate. Sequential evolution can therefore still result in congruent phylogenies. Determination of evolutionary ages and the biogeography and distribution of the two groups can help to elucidate whether such congruence is due to cospeciation or to sequential evolution (Farrell & Mitter, 1990).

The definition of coevolution as used by Thompson is a very precise one, to the extent that even if two organisms have speciated together it can not be called cospeciation unless the speciation event in each organism is a result of the interaction. For example, parallel cladogenesis between commensals and their hosts is not regarded as coevolution (Thompson, 1989). The interaction between non-pollinating fig wasps and their host fig trees cannot be termed cospeciation either, even if they have speciated together, as it is unlikely that the wasps have any effect on host speciation. Nevertheless, congruent phylogenies are still a desirable prerequisite for any hypotheses of cospeciation, even if cospeciation is not the only explanatory phenomenon for the congruence. Furthermore, cospeciation cannot be automatically rejected if phylogenies are not entirely parallel as colonisation and extinction events may have obscured congruence between the two phylogenies (Gould, 1988; Mitter *et al.*, 1991).

One of the primary prerequisites for cospeciation *sensu stricto* appears to be host specialisation or specificity, in combination with the gene flow of the host being limited by the symbiont (Thompson, 1982, 1989). Kiester *et al.* (1984) provide theoretical models for mutualistic coevolution in plants and their pollinators. The genetically effective population sizes and the selection intensity of the interaction are the two factors they maintain will influence reciprocal diversification in plants and their pollinators. The interaction between fig wasps and their hosts is extremely conducive for the coevolution of the two partners, due to the obligate, usually one-to-one host specific, mutualistic relationship.

Among fig wasps, the taxonomy and host relationships are best known for the Agaoninae, primarily owing to the extensive work of Prof. J.T. Wiebes. Those from the Afrotropical region have been the most comprehensively studied, with the pollinators known from 74 species and 8 subspecies of the 105 fig species and 21 subspecies occurring in the region (Wiebes & Compton, 1990). At a higher taxonomic level there is reasonable congruence between the wasp and the host tree classifications (Wiebes, 1973; Ramirez, 1977; 1978; Wiebes 1979b; Ramirez, 1980; Wiebes, 1982a). This led to the suggestion that the partners in the fig - fig wasp interaction may have coevolved with one another (Ramirez, 1974; Wiebes, 1979b, 1984; Thompson, 1989). Three other examples of specific plant - pollinator interactions that may be coevolved are the orchid - euglossine bee interaction (Sanford, 1974; Dodson, 1975; Dressler, 1982; Kiester *et al.*, 1984), although the interaction is not reciprocal as the orchids probably do not affect euglossine evolution (Feinsinger, 1983) and the interaction is therefore unlikely to be an example of cospeciation *sensu stricto*; the yucca - yucca moth interaction (Riley, 1892; Powell & Mackie, 1966; Addicott, 1986; Powell, 1992); and the *Trollius* - *Chiastocheta* interaction (Pellmyr, 1988).

Fig wasp diversity could be a result of their specificity, as specialists may have a higher speciation rate than generalists, since the former are probably more prone to isolation events (Eldredge & Cracraft, 1980; Mitter *et al.*, 1988). It is likely that the diversity of fig wasps and fig trees has been generated through allopatric speciation, as suggested by Janzen (1979). In this scenario a population of a fig species, its pollinator and the other associated fig wasps becomes geographically isolated from the parent population. This eventually leads to the speciation of the fig species and its pollinator and possibly also the other associated fig wasps. Alternatively Kiester *et al.* (1984), suggest that any small local population of figs within the broader population that become temporally isolated by differences in flowering time will restrict gene flow and result in possible diversification. They therefore believe that geographic isolation is not necessary for speciation. A weakness of this argument is the all-year-round breeding periods that seem to be typical of *Ficus* species (Windsor *et al.*, 1989; Addicott *et al.*, 1990).

THE SYCOECINAE

Distribution and host plant relationships

The Sycoecinae are a predominantly Afrotropical subfamily of non-pollinating fig wasps, with five of the seven described genera restricted to this region. All the Afrotropical Sycoecinae are associated with the *Ficus* subgenus *Urostigma*, section *Galoglychia*. Single outlying genera also occur in south-east Asia and Papua, New Guinea (Australasia). Twelve species belonging to the south-east Asian genus *Diaziella* Grandi have been described. Most were collected at light and thus their host relationships are unknown. The only exception is *Diaziella falcata* Wiebes which was reared from *Ficus (adamii) = F. glaberrima* Bl. var. *bracteata* Corner from subgenus *Urostigma*, section *Conosycea*. There are two described species in the Australasian genus *Robertsia* Boucek, both of which were reared from *F. xylosycia* Diels from subgenus *Urostigma*, section *Malvanthera*.

Biology of the Sycoecinae

The sycoecine fig wasps do not play an active role in the pollination process as they have no specific adaptations for carrying pollen, although Newton and Lomo (1979) nonetheless reported a case of accidental pollination by a sycoecine. Adult female sycoecines enter the fig for oviposition at approximately the same time as do the pollinators (pers. obs.). The larvae are probably phytophagous, feeding on the endosperm tissue of galled ovules (Verkerke, 1989; 1990). There is no evidence that any fig wasps are typical seed predators, requiring pollinated ovules (Compton *et al.*, 1991; Bronstein, 1991). Agaonine larval mortalities are nonetheless increased if they develop in unpollinated ovules (Galil & Eisikowitch, 1971), because the larvae are provided with better nutrition if the ovule has been fertilised (Verkerke, 1986). Pollination may therefore also influence sycoecine development, although *Sycoecus thaumastocnema* Waterston has been observed to oviposit before the associated pollinator *Agaon fasciatum* Waterston had entered the fig (J.-Y. Rasplus, pers. comm.). In addition, oviposition/galling by the sycoecines appears to be sufficient to prevent the figs from aborting, (at least with *Philocaenus barbarus* (Grandi) in *F. thonningii* Bl., pers. obs.), and from this point of view the sycoecines development is not reliant on pollination by the agaonine (Compton, pers. comm.). Some species of *Philocaenus* have been reported to be able to re-emerge through the ostiole after they have oviposited and enter further figs for oviposition, having retained their antennae and wings on initial entrance (G. Michaloud and R. Nefdt, pers. comm.). This is in contrast to the pollinating fig wasps associated with section *Galoglychia*, which usually loose part or most of their antennae and their wings on entering the ostiole, and which have not been reported to leave a fig once they have entered it.

Taxonomic history of the Sycoecinae

The sycoecines are a reasonably well defined group of fig wasps, but were only delimited as such by Hill (1967a, 1967b), eighty-two years after the first sycoecine genus, *Crossogaster*, was described by Mayr in 1885. Prior to this the genera were placed together with some current otiteselline genera, namely *Lipothymus* Grandi and *Eujacobsonia* Grandi, and a current sycophagine genus *Sycophaga* Westwood, in the Sycophagini of the then Agaoninae (Mayr, 1885; Grandi, 1916, 1928a, 1928b, 1952, 1955). This grouping of genera was based on what are now recognised to be parallel morphological adaptations of the females to enter the figs through the ostiole. The males of most genera were not known at the time, and subsequently were found to be quite different from each other.

The evolution of homoplastic morphological adaptations to enter the fig through the ostiole in the pollinators and sycoecines was recognised as early as 1914 by Waterston. These include the elongation and flattening of the head and thorax, and the presence of tibial and mandibular modifications. Wiebes (1961) concluded that this homoplasy was the reason that the Sycophaginae and the pollinating fig wasps (Agaoninae) had been placed together in the same family. On the grounds that the pollinators possessed synapomorphic mandibular and antennal characters, Wiebes suggested that the two groups should be separated and that the Sycophaginae should be classified with the Idarninae. He also suggested, based only on a knowledge of the females, that there were affinities between *Crossogaster*, *Phagoblastus*, *Seres*, and *Sycoecus*, but considered *Philocaenus* and *Diaziella* to be distinct. Based on Wiebes' suggestion, Joseph (1964) transferred the Sycophaginae to the subfamily Idarninae in the Torymidae, and lowered the group's status to tribal level. Wiebes (1964a) subsequently corrected Idarninae to Sycophaginae for reasons of priority.

Wiebes (1966) erected three new tribes for the Indo-Australasian sycophagine Torymidae based on the structure of the ovipositing organs, to accommodate genera that were unclassified in Joseph's (1964) division of the Sycophaginae. *Diaziella* was excluded from the Sycophagini and placed as *incertae sedis*, but at the same time Wiebes suggested that *Diaziella* warranted a tribe of its own.

Hill (1967a, 1967b) grouped *Sycoecus, Diaziella, Phagoblastus, Philocaenus, Seres* and *Crossogaster* to form the new tribe, Sycoecini. The main distinguishing features in his diagnosis of the Sycoecini were alate males, a thickened marginal vein just longer than the stigmal vein, and a postmarginal vein subequal in length to the stigmal, but very sharply tapering.

The phylogenetic relationship of the sycoecines with the rest of the fig wasps is uncertain, although they were used as a plesiomorphic sister group for the Agaonidae by Wiebes (1982a). Boucek in Boucek *et al.* (1981), while elevating the group to subfamilial status, listed the sycoecines as unplaced, but suggested they may belong in the Agaonidae (pollinating fig wasps as then defined). However, Wiebes (1981) retained the Sycoecinae as a torymid subfamily. Boucek (1988) later suggested that the Sycoecinae are closely related to the Otitesellinae, particularly *Grasseiana*. However he also believes, in contradiction to Wiebes (1981), that the mandibular form of the Sycoecinae suggests how the agaonine mandibular appendages could have evolved.

Boucek (1988) placed the majority of fig wasps in the Agaonidae and the Sycoecinae are thus currently given equal status with the Agaoninae (formerly Agaonidae), Epichrysomallinae and Otitesellinae (both formerly Pteromalidae), Sycophaginae and the Sycoryctinae (both formerly Torymidae). Boucek united the fig wasps into one family on the basis of the closing of the postgenal bridge anterior to the foramen magnum on the back of the head. He believes this may be a synapomorphy uniting the Agaonidae with the Torymidae and separating these two families from the Pteromalidae, in which the bridge is absent. He uses the presence of the occipital carina in combination with an elongate ovipositor as a practical means to separate the Torymidae from the Agaonidae. This is because some members of the Epichrysomallinae have retained the carina, but they then have short ovipositor sheaths.

SYSTEMATICS AND PHYLOGENETIC ANALYSIS

There are three basic schools of systematics: phenetic, cladistic and evolutionary (Mayr, 1974; 1982; Ridley, 1986). Pheneticists group organisms based on overall similarity, ignoring evidence based on descent, and therefore recognise paraphyletic groups (Sokal & Sneath, 1963; Simpson, 1964). In contrast, cladists only recognise monophyletic groups based on the possession of shared derived characters (Hennig, 1966; Wiley, 1981). Evolutionary systematics is the traditional approach to classification, taking into account both the branching of lineages as well as the amount of divergence after branching, divergence being measured by the number of autapomorphic characters that have evolved in each of the sister-groups. As a result, a group that has diverged far enough from its sister group is recognised as a distinct taxon on the same level as the sister group, even if it is paraphyletic. Consequently this approach does not define monophyletic groups in the Hennigian sense, in that not all the descendants of a common ancestor have to be included in the group (Simpson, 1961; Mayr, 1969; Bock, 1973; Ashlock, 1979). A further school, termed transformed cladistics or pattern cladistics, has arisen from within Hennigian cladistics. This school ignores evolutionary processes and simply concentrates on the patterns of nature, thereby simulating the phenetic school in its approach (Scott-Ram, 1990).

The cladistic approach is here considered to be the most appropriate, since the phylogeny of the Sycoecinae and hence the resulting classification can be based on the delimitation of natural groups. Natural groups are monophyletic (sensu Hennig 1966), whereas paraphyletic and polyphyletic groups are artificial groupings defined by primitive states (Hennig, 1966). Cladistics thus provides the best estimate of the evolutionary history of the Sycoecinae.

Perhaps the most biologically sound species concepts are the biological species concept (BSC) (Mayr, 1963, 1969, 1970), an extension of which is the evolutionary species concept (Simpson, 1961; Wiley, 1978), or the recognition species concept (RSC) (Paterson, 1978, 1980, 1981, 1982a, 1982b, 1985). These concepts define species on their potential to interbreed, which negates the need for a certain degree of morphological divergence to define a new species. However, there are both practical and theoretical problems associated with the BSC and RSC, as it is often difficult to define the limits of an interbreeding population (Mishler & Donoghue, 1982; Donoghue, 1985). From a strict phylogenetic point of view the BSC or the RSC are also not ideal because species defined on the potential to interbreed are not necessarily monophyletic. Monophyly is a criterion for the phylogenetic species concept advocated by de Quieroz & Donoghue (1988, 1990), in which species are defined by the possession of autapomorphies. However, other phylogenetic species concepts, such as that proposed by Nixon & Wheeler (1990), do not require monophyly of the species. Full discussions of the advantages and disadvantages of the different phylogenetic species concepts are presented by Eldredge & Cracraft (1980), Nelson & Platnick (1981), Wiley (1981), Mishler & Donoghue (1982), Nelson (1989), Wheeler & Nixon (1990) and Nixon & Wheeler (1990).

Out of necessity the species concept utilised here has had to be a morphological one. Phylogenetic species concepts could not been applied here, because the species recognised using morphological criteria were not necessarily defined by autapomorphies nor were they necessarily delimited "as the smallest aggregation of populations" as required by Nixon & Wheeler (1990). This latter requirement would result in an explosion of new species as all subspecific taxa would have to be elevated to species status.

The BSC or RSC could not be applied as the majority of the material was accessible only as preserved adult specimens. Logistics and the lifestyle of fig wasps prevented any significant first hand study of living material. Furthermore, many of the species are known from only a small number of collections or even a single collection. Consequently the range of morphological variation in the populations is unknown, and it is difficult to determine whether slight morphological variation warrants the designation of separate species status or is only indicative of geographical variation. As a consequence it is often tempting to take information on host tree relationships into account. This may be argued to be a realistic approach, as gene flow and thus interbreeding populations are likely to be delimited by host associations. However, there are dangers in this approach, as the identification of the host *Ficus* species may be inaccurate (and their taxonomy is still not finally settled) and there is not always a one-to-one host specific relationship of the fig wasps and the fig trees. Also, in unusual circumstances, such as when an isolated tree is on the edge of its range, the wasps can make mistakes and manage to breed in the incorrect host. For example, in an isolated tree of *F. turbinata* (Liebm.) in Venezuela a "strange" species of agaonine developed, but no viable seeds were produced (Ramirez, 1970) and in an isolated tree of *F. lutea* Vahl. in Grahamstown (South Africa) the sycoecine *Philocaenus barbarus* (Grandi) together with *Elisabethiella stuckenbergi* Grandi and *Otitesella tsamvi* Wiebes, all normally associated with *F. thonningii* Bl., managed to successfully reproduce (Compton, 1990; Ware & Compton, in press b).

The delimitation of species in this thesis is thus based on available morphological criteria, but at the same time geographical distribution and to a lesser degree host tree relationships are also taken into account, particularly in the case of subspecies. Subspecies have been designated when populations of the same species, that are geographically isolated, are recognised to be morphologically distinct and no knowledge of the morphology of interlinking populations is available. The populations are assumed to belong to the same species if they have the same host fig tree association. Consequently, these subspecies may turn out to be good species or alternatively may not warrant delimitation, as they may only represent the extremes of a morphological cline.

OBJECTIVES OF THIS STUDY

Prior to this study only twelve sycoecine species were described from the Afrotropical region, distributed among five genera - *Crossogaster*, *Phagoblastus*, *Philocaenus*, *Seres* and *Sycoecus*. Extensive collecting in southern Africa by Dr. S.G. Compton and colleagues produced a number of undescribed species. This prompted the initiation of the current study. The subsequent acquisition of more material from Prof. J.T. Wiebes, mainly collected in West Africa, and Dr. D.S. Hill, collected in East Africa, provided a strong base for the revision of the African members of the subfamily.

The systematic revision of the Sycoecinae was thus the initial purpose of this thesis, resulting in the description of 43 new species and two subspecies. To provide a natural classification, a phylogenetic analysis of the Sycoecinae was needed, which necessitated that the higher phylogenetic relationships of the Sycoecinae be determined in order to provide outgroups for the analysis. An understanding of the extent of parallelisms and convergences in the subfamily was also required. The phylogenetic analysis also enabled the comparison of sycoecine phylogeny with the current classification of the Agaoninae and their host *Ficus* species. This gave some idea of the type of evolutionary interactions the sycoecines have with their host fig trees and whether they were similar to those of the pollinating fig wasps.

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MATERIALS AND METHODS

MATERIAL

The majority of southern African sycoecines were obtained from collections of fig wasps made by Dr. S.G. Compton and his students over a period of seven years. During this period six extensive field trips in Southern Africa were made in order to collect specimens for this study. Material from the rest of Africa was kindly loaned by Prof. J.T. Wiebes and Dr. J.-Y. Rasplus (mainly west Africa) and Dr. D.S. Hill (mainly east Africa).

COLLECTION OF FIG WASPS

The collection of fig wasps can be more precise than for many other groups of insects, in that they can be obtained directly from a known source, their host fig tree. However, this is not always as simple as it sounds. Location of host trees is often difficult, especially for the rarer species. Often the fig tree will not be bearing fruit and even if the tree has a crop of figs, they may not be at the right stage of development for wasp emergence. It is estimated that in southern Africa less than one in thirty fig trees located will have a crop of figs at the correct stage of development (S.G. Compton, pers. comm.; pers. obs.). This stage, the D-phase of Galil (1977), can be recognised if the figs are slightly soft and yield to light pressure applied with the fingers. Figs with wasp emergence holes present on the same tree are also a good indicator.

The figs were placed in a plastic container with a gauze lid and the fig wasps allowed to emerge naturally over a period of 2-3 days, after which the figs were broken open to facilitate further emergence. The wasps were removed at regular intervals and killed with ethyl acetate. Specimens were preserved dry and not placed into alcohol. Alcohol acts as a decolouring and clearing agentover a period of time, and this is accelerated if the specimens are exposed to light and warmth. Even if the specimens are kept in the dark and at low temperatures they can become almost useless after only twenty years of storage (Noyes, 1982; pers. obs.).

Fig wasps were occasionally collected using other methods. Species in the genus *Diaziella*, for example, appear to be nocturnal fliers and are readily collected using light traps (Gardiner & Compton, 1987). Very occasionally specimens are obtained using the method of sweeping, whereby a net is systematically passed through vegetation.

MOUNTING OF SPECIMENS

Four females and four males (if available) of a sycoecine species were card mounted from each collection, following the method of Z. Boucek as described in Noyes (1982) and Boucek (1988). In addition two to six specimens of each sex for each species, depending on availability, were slide mounted using the following technique, which was modified after Prinsloo (1980) and Hawkes (1985).

Dry specimens.

1. The wings were removed and mounted in a drop of canada balsam on a glass slide.
2. The body was transferred to 10% KOH for 24-60 hours until cleared.
3. Transferred to 15% acetic acid for 15 minutes to prevent specimen bursting in step four.
4. Transferred to distilled water for 10 minutes.
5. Dehydrated through 30%, 50%, 70%, 90%, 100% (twice) for 10-15 minutes in each.
6. Transferred to a drop of terpineol and placed under an

electric lamp (60 watt bulb) for 20-30 minutes for final clearing and dehydration.

7. Specimen removed from under the lamp and allowed to cool before being transferred to a drop of canada balsam on the same glass slide as the wings.
8. Head removed from the body, antennae and mouthparts removed from the head and the legs removed from the thorax. Each part moved to its respective position on the slide (fig. 2.1).
9. All parts allowed to dry in a covered petri dish (to protect the slide from dust) for at least three days, before adding a small drop of canada balsam to each and covering with a 7mm coverslip. The drying period prevents the parts moving when the coverslip is applied.

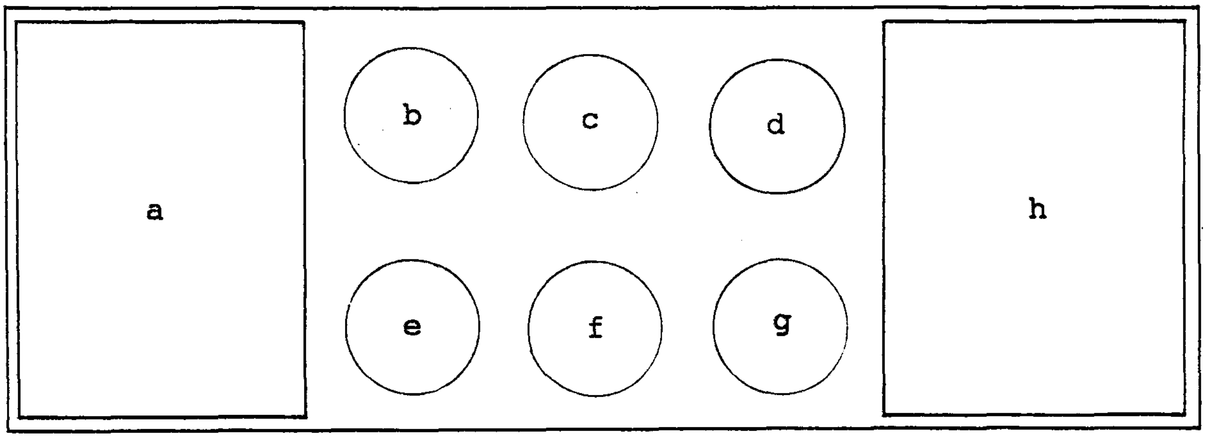


Fig. 2.1 Microscope slide showing the position of the labels and the six coverslips covering the different body parts a) locality and collection data b) fore and hind wings c) head d) antennae e) thorax and gaster f) legs g) mandibles h) identification data.

Specimens stored in alcohol.

1. Specimen placed on filter paper, which is in turn placed on cotton wool soaked in acetone in a glass dish with a lid.
2. Acetone allowed to gradually replace the alcohol present in the specimen for three hours, after which the specimen is removed and placed under an electric lamp for 30 minutes to evaporate the acetone.

3. Continued from step one of the procedure used for dry specimens.

The above heat assisted air drying from acetone (Trumen, 1968; Walpole, *et al.*, 1988) was utilised in preference to more conventional methods such as critical point drying (Gordh & Hall, 1979) or the direct slow drying of the alcohol (Noyes, 1982), because it is a simple and cost effective method which produces the same results (Ware & Cross, 1989). Furthermore, although a certain amount of collapse (particularly of the compound eyes) often occurs with all the above methods, it was found that acetone drying frequently produced specimens with no collapse. Whereas this is not important in specimens that are to be slide mounted, as they reconstitute themselves when placed in KOH, it is important in specimens that are to be subjected to scanning electron microscopy or are to be dry mounted on cards.

SCANNING ELECTRON MICROSCOPY

Specimens that were stored in alcohol were prepared using the heat assisted acetone drying procedure, as described above. Air dried specimens were mounted without prior treatment. Specimens were mounted on brass stubs using a chloroform based adhesive and sputter coated with gold, prior to observation and photography using a JEOL JSM 840 scanning electron microscope.

TERMINOLOGY

Morphological terminology generally follows that of Ulenberg (1983), except as noted below. The positional terms for the head (dorsal, ventral, anterior and posterior) are applied as if the head is in a prognathous position.

In the Sycoecinae there are varying degrees of closure of the postgenal bridge (*sensu* Boucek, 1988) on the ventral side of the head (fig. 2.2 c). The maximum closure is attained when the hypostomal sutures anterior to the tentorial pits have been compressed into a single medial suture. In the more derived *Crossogaster* species the hypostomal sutures appear to have secondarily separated, in combination with a widening of the hypostomal suture around the mouth parts, such that a portion of the hypostoma appears to have become detached from the postgenae. This detached portion of the hypostoma has become overlapped by the stipes. In *Apocrypta* Coquerel, where the hypostomal sutures are still separated, Ulenberg (1983) refers to the area between the sutures as the gula, on the grounds that the gular carina has no connection with the hypostomal suture. In the Sycoecinae, however, there is no gular carina and the hypostomal suture joins the post occipital carina, which surrounds the foramen magnum posteriorly and extends forwards past on either side of the tentorial pits (fig. 2.2 c). The medial portion anterior to the tentorial pits appears to be an extension of the hypostoma and for this reason is simply referred to as the hypostoma and not the gula.

In the Sycoryctinae and Torymidae there is a medial 'felt line' (new terminology) figured by Ulenberg (1983) but not described or named, extending between the oral cavity and the foramen magnum. This 'felt line' consists of a narrow band of numerous dense papillae. It is not present in the Sycoecinae.

The major sensilla type present on chalcid antennae has had various terms applied to it (rhinaria of authors; sensilla placodea of Snodgrass, 1926 & 1935 and Ulenberg, 1983; longitudinal sensilla of Boucek, 1988). Since the ultrastructure of this sensilla type was examined, it has received further descriptive names, such as thin walled sensilla (Slifer, 1970), multiporous pitted sensilla (Zacharuk, 1980), or multiporous plate sensilla (Barlin & Vinson, 1980). The term multiporous plate sensilla (MPS) appears to have become the most widely accepted and utilised and is therefore the term used in this thesis. MPS are often split into two distinct types, based on their degree of fusion to the flagellar segment and referred to as sensilla linearia and sensilla chaetica (Ware & Compton, in press). In the Sycoecinae both types of MPS are present, although the distinction between the two is often vague as there is a near continuum in the degree of fusion of the MPS to the antennal segments that bear them. Clearly the one type is simply a derived example of the other type. Here the two extremes of the range are referred to as placoid MPS and elongate MPS. Placoid MPS are plate-like and fused for at least three-quarters of their length to the surface with only the apical end free. They are shorter than or subequal to the length of the flagellar segment that bears them. Elongate MPS are free for at least fifty percent of their length, but are often completely free for their entire length and only attached at the base. They may be extremely elongate, up to 3 or 4 times as long as the flagellar segment from which they arise. However, they may also be only as long as the flagellar segment that bears them. The term sensilla chaetica is not recommended for elongate MPS, as Snodgrass (1926, 1935) defines the former sensilla type as being tactile, bristle or spine-like, whereas the elongate MPS of the Agaoninae and Sycoecinae are likely to have an olfactory function (Ware and Compton, in press; Ware and Compton, in press) and may be distinctly rod-like.

In the antennae the flagellum includes the anelli, the funicular segments and the club (fig. 2.3 b), following Boucek (1988). Anelli in female sycoecines can be defined by their general reduction in size in comparison to the funicle segments and by the absence of MPS (fig. 2.3 b). Anelli in the males can usually also be defined as they are in the females, except for *Crossogaster* where the MPS in males are reduced in number compared to the females. As a result they are absent on some of the funicle segments as well as on the anelli. Anelli in these males can therefore not be defined by the absence of MPS and the definition relies on the reduction in size of the segment in comparison to the size of the funicle segments.

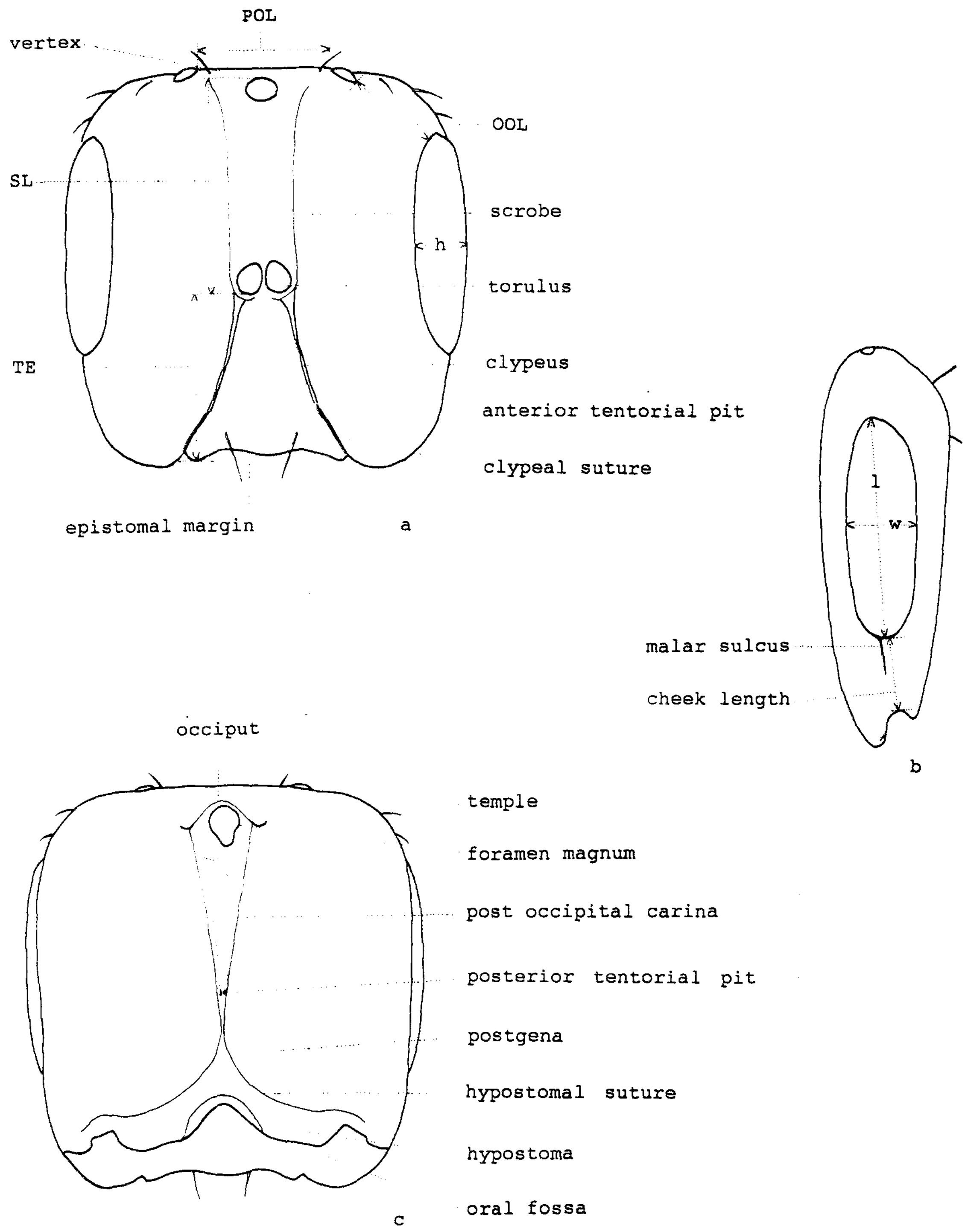
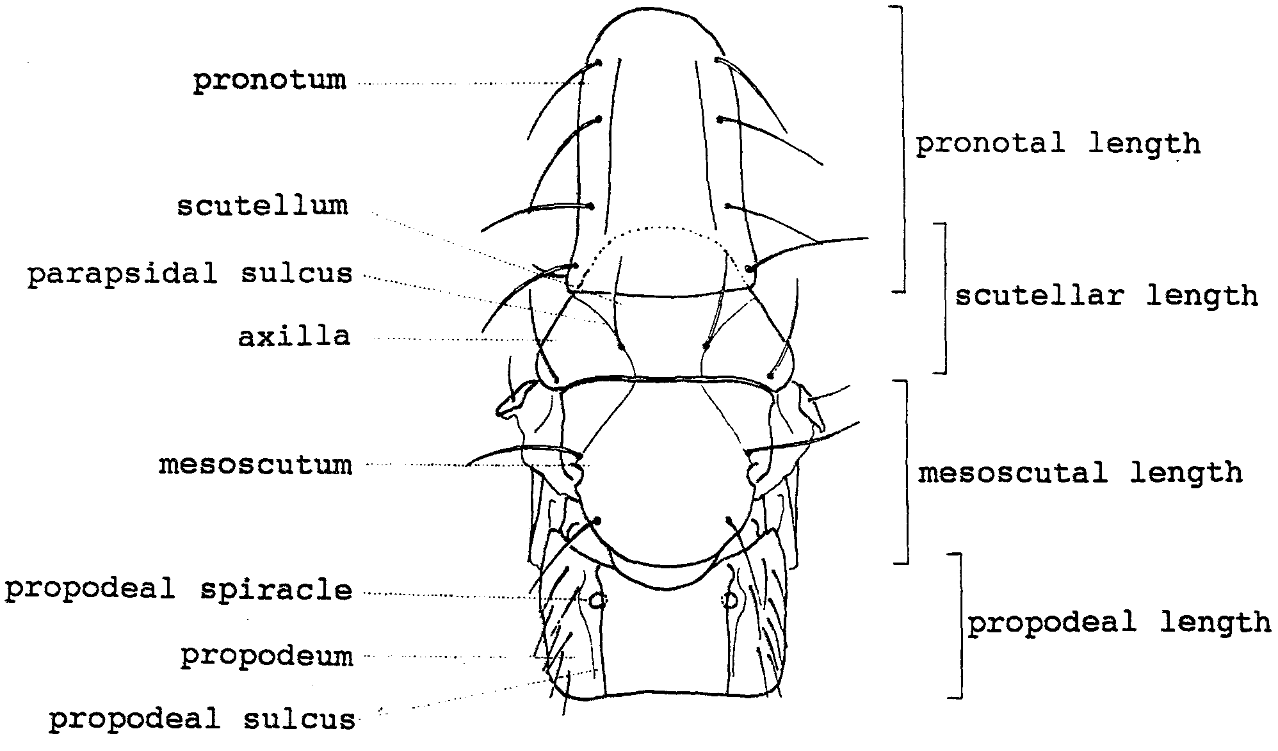
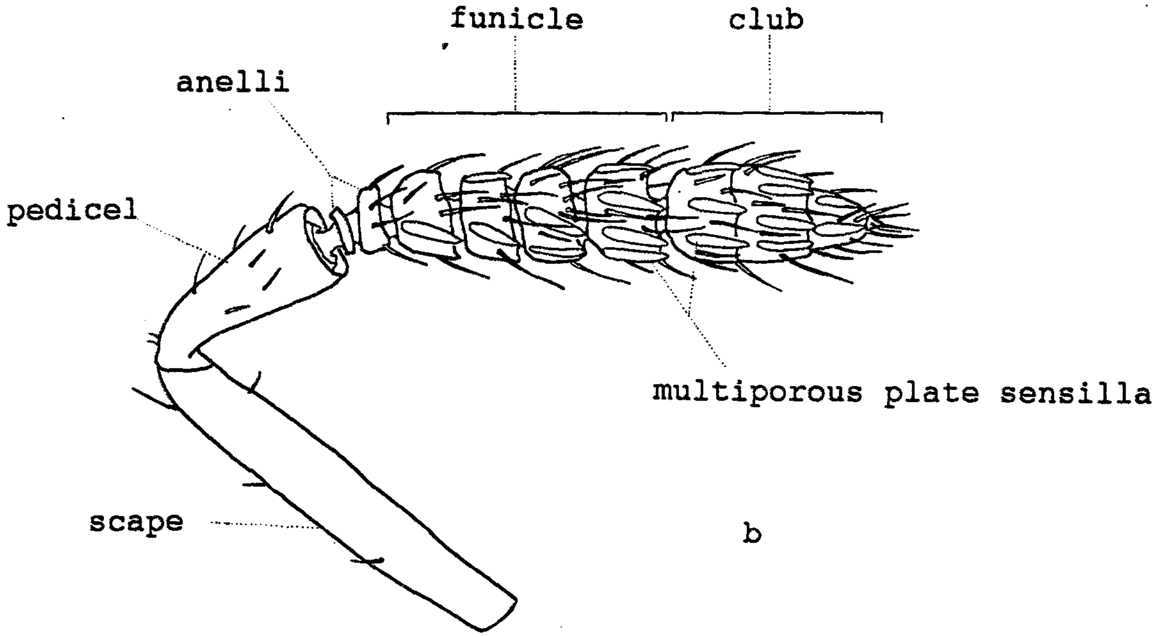


Fig. 2.2. Measurements and terminology associated with the head a) head in dorsal view b) head in lateral view c) head in ventral view. POL = posterior ocellar line. OOL = ocular ocellar line. TE = distance between the toruli and the epistomal margin. SL = scrobe length. h = eye height, l = eye length, w = eye width.



a



b

Fig. 2.3. Measurements and terminology associated with the thorax and the antennae a) thorax, dorsal view b) antenna.

The anterior margin of the clypeus is referred to as the epistomal margin (fig. 2.2 a), following Ulenberg (1983) and not the clypeal margin as in Boucek (1988). The sutures on the mesoscutum, termed notauli by Boucek (1988) are referred to as the parapsidal sulci (fig. 2.3 a) as in Ulenberg (1983). The propleura are the anterior ventral plates of the prothorax and may be extensively excavated in *Sycoecus*.

MEASUREMENTS

The majority of measurements were taken from slide mounted material. Additional measurements taken from card mounted material were the total length of the specimen, eye width, cheek length and head height (fig. 2.2 b). All measurements were taken using an ocular micrometer and care was taken to ensure that both ends of the part being measured were in the same focal plane, i.e. equidistant from the objective lens. All measurements were taken in millimetres, although they are not expressed as such in the descriptions.

The following definitions and abbreviations are used in the descriptions:

1. Head length: maximum distance from the anterior edge of the clypeus to the posterior edge of the vertex.
2. Head width: maximum distance across the compound eyes.
3. Head height: maximum distance between the dorsal and ventral surfaces.
4. Eye length: maximum distance between the anterior and posterior margins (fig. 2.2 b).
5. Eye height: maximum lateral projection from inner margin in dorsal view (fig. 2.2 a).
6. Eye width: maximum distance between the dorsal and ventral margins in lateral view (fig 2.2 b).
7. Ocular ocellar line (OOL): minimal distance between outer edge of lateral ocellus and inner eye margin (fig. 2.2 a).

8. Posterior ocellar line (POL): minimal distance between inner edges of the lateral ocelli (fig. 2.2 a).
9. Cheek length: distance between the anterior eye margin and the most posterior corner of the oral cavity, measured along the malar sulcus, or where the malar sulcus would be if it is absent (fig. 2.2 b).
10. Distance between the toruli and the epistomal margin (TE): distance between anterior margins of the toruli and most anterior margin of the epistomal margin (fig. 2.2 a).
11. Scrobe length (SL): distance between the anterior margin of the toruli and the posterior margin of the medial ocellus (fig. 2.2 a).
12. Distance between the toruli: minimum distance between the inner margin of each torulus.
13. Antennal flagellar length: maximum distance from the anterior edge of the pedicel to the tip of the club.
14. Pronotal length: maximum distance between the anterior and posterior margins (fig. 2.3 a).
15. Pronotal width: maximum width, which is usually posteriorad.
16. Mesoscutal length: maximum distance between the transscutal articulation posteriorly and the most anterior edge (covered by the posterior portion of the pronotum), but visible in slide mounted specimens (fig. 2.3 a).
17. Mesoscutal width: maximum distance across mesoscutum.
18. Scutellar length: maximum distance between the transscutal sulcus and the most posterior margin (fig. 2.3 a).
19. Scutellar-axillar width: maximum distance between outer axilla margins.
20. Propodeal length: maximum distance between the anterior and posterior margins measured along a line passing through one of the spiracles (fig. 2.3 a).
21. Propodeal width: maximum distance between lateral margins.
22. Wing venation: measurement of the submarginal vein (SM), marginal vein (M), postmarginal vein (PM) and stigmal vein (S) are as illustrated in Boucek (1988). The length of the submarginal vein is strictly the length of the costal cell, as

the distance is measured in a straight line and does not follow the curvature of the vein.

23. Fore leg components: maximum length of coxa (C), trochantellus (TR), femur (F), tibia (TI) and tarsus (TA).

24. Ovipositor length: maximum length from the anterior edge of the laminar falcata to the tip of the ovipositor.

25. Ovipositor valve length: maximum visible length of the valves.

26. Standard abbreviations are: l = length, w = width, h = height.

ILLUSTRATIONS

Drawings were made from slide mounted specimens, using a camera lucida mounted on a Nikon compound microscope. Scanning electron micrographs were used to supplement the slide mounted specimens.

3

OUTGROUP DETERMINATION

INTRODUCTION

A number of different methods can be utilised to ascertain the polarity, i.e. the evolutionary sequence, of the states displayed by a character. The most widely used method has probably been commonality, where the assertion is made that common equals primitive (Eldredge, 1979). However, common characters can also be derived and thus the credibility of this method is questionable (Watrous & Wheeler, 1981). The ontogenetic (De Queiroz, 1985; Kluge & Strauss, 1985) and palaeontologic methods may be useful in many animal groups, but cannot be applied to fig wasps, due to their almost non-existent fossil record and unstudied developmental processes. A fourth method, outgroup comparison is nevertheless applicable. Since this method is also considered to be the most reliable approach (Eldredge & Cracraft, 1980; Ridley, 1986), it is the method adopted here.

In order to determine which state of a character is derived (apomorphic) and which is primitive (plesiomorphic), within a monophyletic group under study (the "ingroup"), it is necessary to ascertain which state is also present in related plesiomorphic sister-groups (known as "outgroups") (Watrous & Wheeler, 1981; Maddison, *et al.*, 1984). To be able to do this, suitable outgroups need to be identified. Unfortunately, the higher phylogenetic relationships of groups such as fig wasps have often not been resolved, which makes the task of outgroup determination difficult. This is particularly so in insects such as fig wasps, where convergence and parallelism, as a result of their common life styles, often obscure relationships. One solution to this problem is to expand the investigation and carry out a full phylogenetic analysis at the higher level. However, besides the practical limitations, this also only moves the problem up a rank. A more practical solution is, in effect, to carry out aminiature analysis in order to identify one or more synapomorphies (shared derived characters) common to the ingroup and potential outgroups. These indicate commonality of descent and thus sister-group relationships. This is the methodology adopted in this chapter, where sister-groups of the Sycoecinae are identified using characters from the ventral surface of the head.

HIGHER RELATIONSHIPS AND MONOPHYLY OF THE AGAONIDAE

Fig wasp classification remains controversial. In contrast to previous classifications (Hill, 1967; Boucek *et al.*, 1981; Wiebes, 1981), Boucek (1988) united the majority of fig wasps, with the exception of those belonging to the Ormyridae, Eurytomidae, and to *Megastigmus* Dalman and *Physothorax* Mayr of the Torymidae, in one family, the Agaonidae. Boucek (1988) suggested that the closing of the postgenal bridge on the underside of the head anterior to the foramen magnum may link the Agaonidae and the Torymidae in a single monophyletic group, separating them from the Pteromalidae, where the oral fossa extends up to the foramen magnum as a broad channel. However, the closing of the postgenal bridge also occurs in *Sycophila* Walker (Eurytomidae) (fig. 3.1 a), *Ormyrus* Westwood (Ormyridae) (fig. 3.1 b) and in at least three genera of Pteromalidae (Grissell, 1991). This character may therefore be a wider synapomorphy than recognised by Boucek (1988) or alternatively it may be homoplasious, having evolved independently several times. Nevertheless, it may still be indicative of a relationship between the Torymidae and the Agaonidae, given that the monophyly of the Torymidae and Agaonidae is further supported by the shared presence of exserted cerci on the eighth urotergite (Grissell, 1991).

Boucek (1988) considered the presence of the occipital carina in the Torymidae to be a practical character for the separation of the Agaonidae from the Torymidae. The few agaonids, such as the primitive Epichrysomallinae, which also have an occipital carina, are separated from the torymids by the absence of a long exserted ovipositor. Boucek (1988) regarded the absence of the occipital carina in the Agaonidae as a reversal and not as the primitive state. This was supported by Grissell (1991), who regarded the presence of an occipital carina as the groundplan state for the Torymidae and thus as the primitive condition in the torymid/agaonid lineage. Additional support for this view is evident in the Sycoecinae if the thin carina present on the vertex (fig. 3.2 a) in most of the sycoecine genera is a remnant of the occipital carina. The presence of the carina on the sycoecine vertex appears to be a result of the occipital carina being forced towards the vertex by the posterior movement of the foramen magnum, with the simultaneous loss of the lateral arms of the carina. This loss is probably as a result of the overall smoothing and flattening of the ventral surface of the head which has taken place in order to facilitate ostiolar entry. Unfortunately the possession of the occipital carina by a few Epichrysomallinae and Sycoecinae means that its loss can not be used as a synapomorphy to define the Agaonidae and in the absence of other supporting evidence the monophyly of the group still remains questionable.

RELATIONSHIPS WITHIN THE AGAONIDAE

The relationships of the subfamilies within the Agaonidae are equally problematic and unresolved. The only general consensus is that the Agaoninae (the pollinating fig wasps) are probably the most derived group. Copland *et al.* (1973) in their studies of the female reproductive system of the Agaoninae suggested a common ancestry of the Agaoninae with the Sycophaginae and the Epichrysomallinae. They regarded the superficial resemblance of the Agaoninae to the Torymidae as convergent evolution. The Sycoecinae have been suggested as having some relationship with the Agaoninae, probably as a plesiomorphic sister-group (Boucek *et al.*, 1981), although in the same publication Boucek regarded them as "unplaced" taxonomically. Wiebes (1981) placed the Sycoecinae in the Torymidae, which at that stage also included the fig wasp subfamilies Sycophaginae and Sycoryctinae. The Sycoecinae were used as the outgroup by Wiebes (1982a) in his determination of agaonine phylogeny, and were therefore regarded as plesiomorphic to the Agaoninae. Boucek (1988) suggested that the form of the mandibles in some of the Sycoecinae "reflect a true relationship with the Agaoninae". Conversely Wiebes (1981) considered the similarity in their mandibles to be due to convergent evolution.

Although the above suggestions have been made regarding relationships within the Agaonidae, no substantial phylogenetic evidence has ever been forwarded. There was therefore no prior indication of a plesiomorphic sister-group for the Sycoecinae. This meant that in order to determine outgroups a search had to be made for synapomorphic characters to resolve the sister-group relationships of the Sycoecinae.

MORPHOLOGICAL EVIDENCE FOR SYCOECINE SISTER-GROUP RELATIONSHIPS

Chalcids in general have the foramen magnum situated centrally on the underside of the head, midway between the vertex and the oral fossa, with the tentorial pits in close proximity to the foramen magnum (Boucek, 1988). In all the agaonid subfamilies, other than the Epichrysomallinae, there is at least one genus where the foramen magnum has moved posteriorly towards the vertex. This movement has either been together with the tentorial pits or alternatively the tentorial pits have remained in their original position and have thus become separated from the foramen magnum. Whether the foramen magnum has moved or not, there may be a medial felt line (which is a narrow band of numerous, sometimes elongate papillae) (figs. 3.1 a-e, 3.3 a-f, 3.4 b-e) or a medial suture present between the foramen magnum and the oral fossa (figs. 3.2 c, e & f; 3.4 g-j). Alternatively both the medial suture and the medial felt line may be absent (fig. 3.4 f), with the hypostomal sutures sometimes laterally compressed to form what appears to be an analogous medial suture.

The undersides of the heads of 54 chalcid species were examined using scanning electron microscopy (Table 3.1). The chalcids can be divided into two groups depending on the position of the foramen magnum. The following range of variation was observed among those species where the foramen magnum was still situated in the centre of the head.

1. The tentorial pits are in close proximity to the foramen magnum and a medial felt line is present between the hypostomal sutures - *Sycophila* Walker (Eurytomidae) (fig. 3.1 a), *Ormyrus* Westwood (Ormyridae) (fig. 3.1 b) and *Apocrypta* Coquerel (Sycoryctinae) (fig. 3.3 a & 3.4 d).

2. The tentorial pits are slit-like grooves, sometimes almost extending from the foramen magnum to the oral fossa. A medial felt line is present between the hypostomal sutures - *Pseudotorymus* Masi (fig. 3.1 c), *Podagrion* Spinola (fig. 3.1 d & 3.4 b) (both Torymidae) and *Mesocomys* Cameron (Eupelmidae) (fig. 3.1 e).

3. The tentorial pits appear to be absent and a medial felt line is present - *Camarothorax* Mayr (Epichrysomallinae) (fig. 3.2 d & 3.4 c).

4. The tentorial pits are slit-like grooves extending from the foramen magnum to the oral fossa, but a medial suture is present between the hypostomal sutures, instead of a medial felt line - *Otitesella* Westwood (Otitesellinae) (fig. 3.2 c & 3.4 g).

5. The tentorial pits are situated on either side of the foramen magnum and a medial suture rather than a felt line is present - *Apocryptophagus* Ashmead and *Eukoebelea* Ashmead (*sensu* Wiebes,

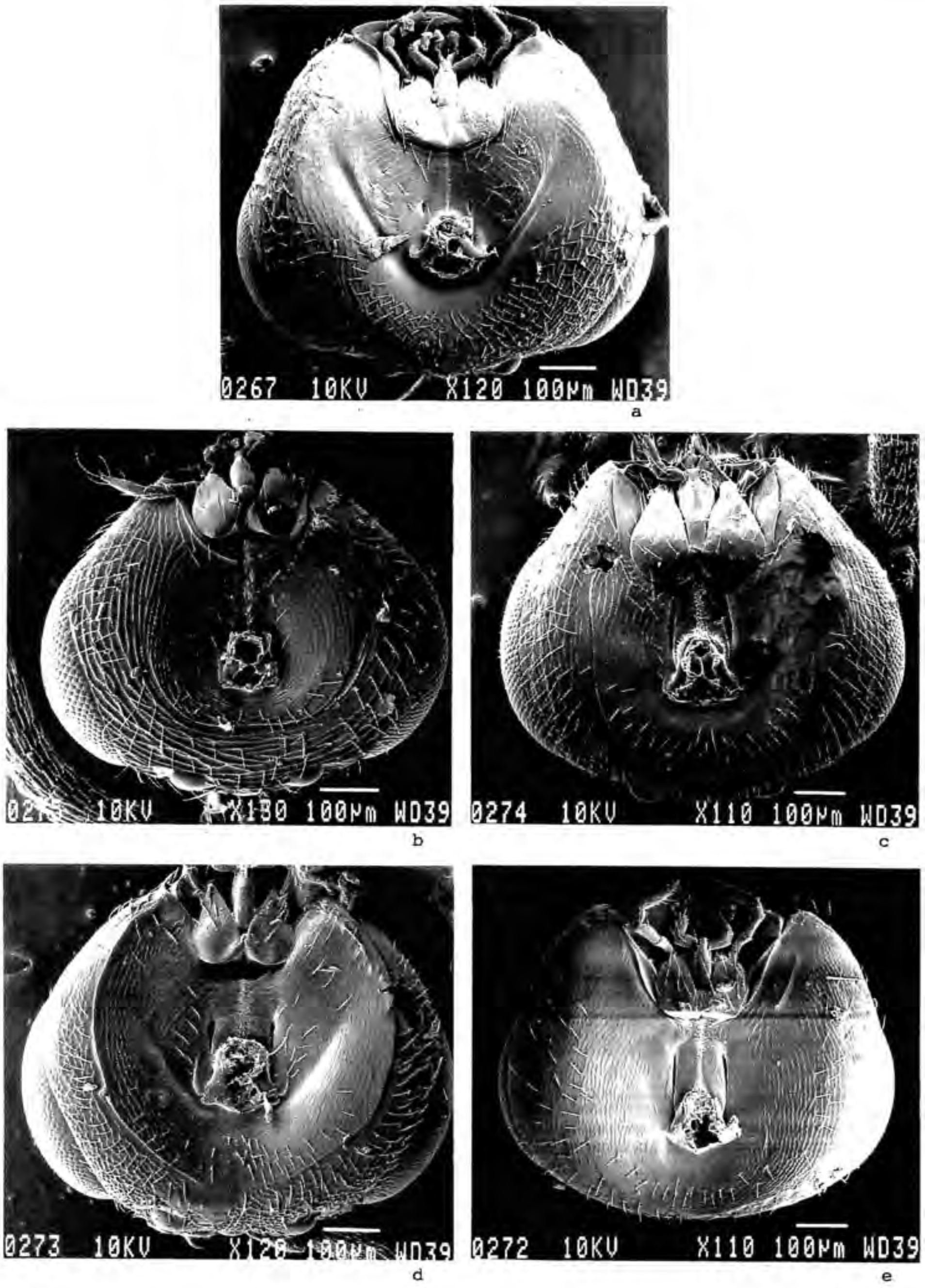


Figure 3.1 a-e: Scanning electron micrographs of the ventral surface of the head, which has been detached from the thorax. a) *Sycophila* sp. (Eurytomidae), ex. *F. thonningii*; b) *Ormyrus* sp. (Ormyridae); c) *Pseudotorymus* sp. (Torymidae); d) *Podagrion* sp. (Torymidae); e) *Mesocomys* sp. (Eupelmidae).

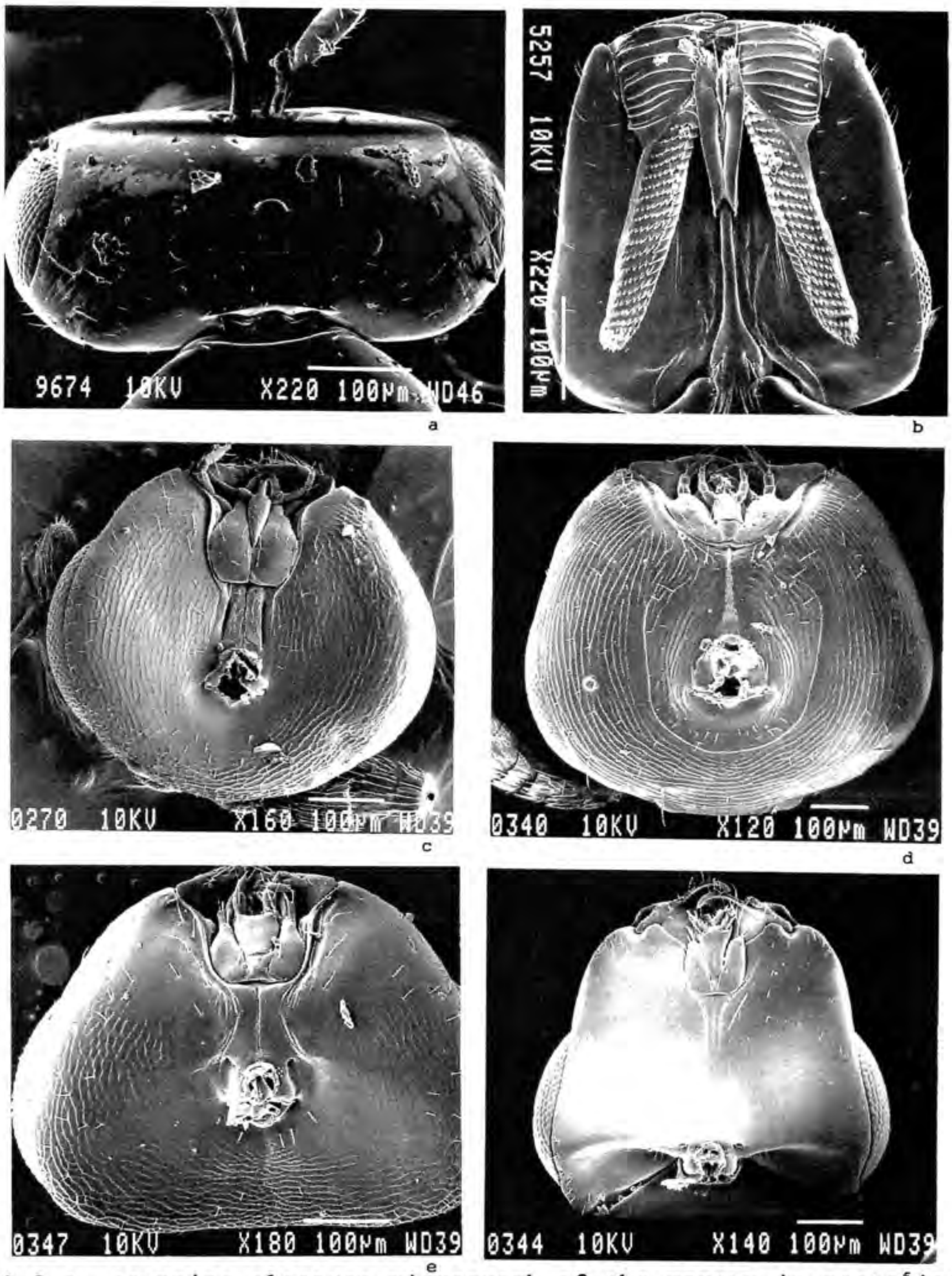


Figure 3.2 a: scanning electron micrograph of the vertex in posterior view; b-f: scanning electron micrographs of the ventral surface of the head, which has been detached from the thorax. All the species belong to the Agaonidae. a) *Philocaenus warei* sp. nov. (Sycoecinae); b) *Elisabethiella socotrensis* (Mayr) c) *Otitesella tsamvi* Wiebes, ex. *F. thonningii* (Otitesellinae); d) *Camarothorax* sp., ex. *F. thonningii* (Epichrysomallinae); e) *Apocryptophagus* sp., ex. *F. sur* (Sycophaginae); f) *Sycophaga* sp., ex. *F. sur* (Sycophaginae). SEM b) courtesy of A.B. Ware.

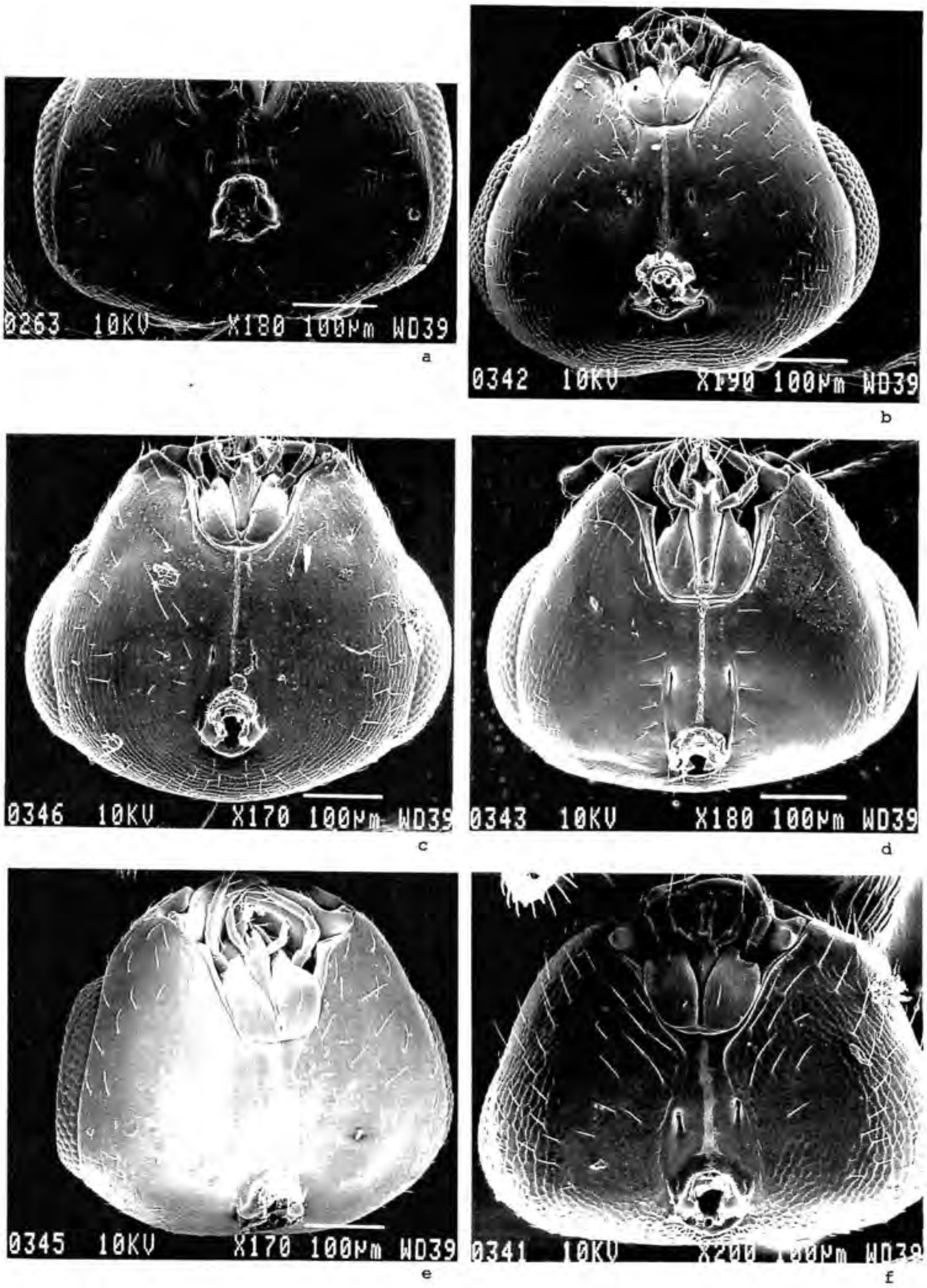


Figure 3.3 a-f: scanning electron micrographs of the ventral surface of the head, which has been detached from the thorax. All species are Sycoryctinae, Agaonidae. a) *Apocrypta longitarsus* (Mayr), ex. *F. sycomorus* (Apocryptini); b) *Sycoryctes* sp. (Sycoryctini), ex. *F. lutea*; c) *Watshamiella* sp. (Sycoryctini), ex. *F. sur*; d) *Philotrypesis* sp. (Sycoryctini), ex. *F. lutea*; e) *Sycoscapteridea* sp. (Sycoryctini), ex. *F. sur*; f) *Sycoscapter* sp. (Sycoryctini), ex. *F. lutea*.

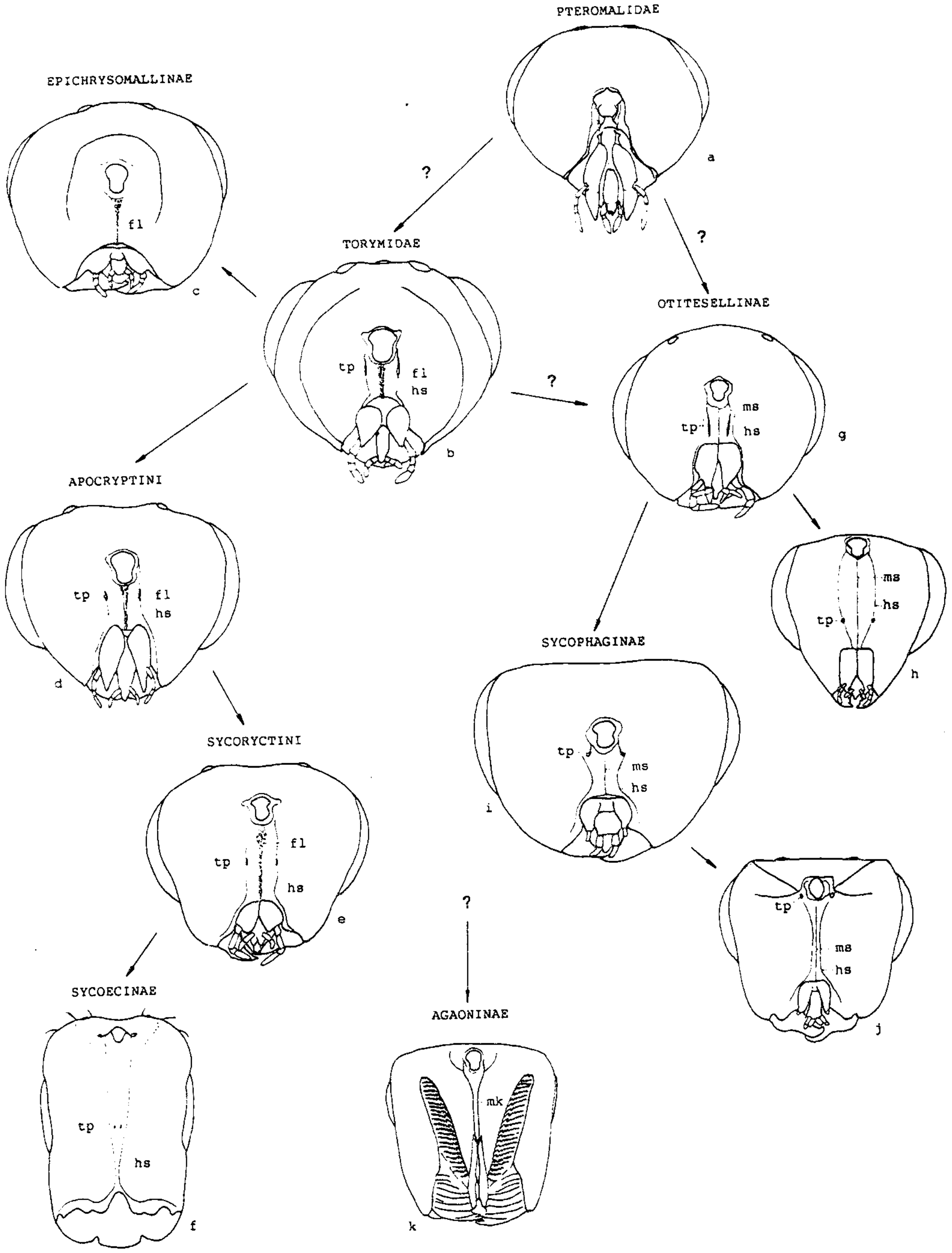


Fig. 3.4 Possible evolutionary relationships of the agaonid subfamilies and the Torymidae and Pteromalidae, based on the morphology of the underside of the head. a) *Stenomalina* (Pteromalidae) b) *Podagrion* (Torymidae) c) *Camarothorax* (Epichrysomallinae, Agaonidae) d) *Apocrypta* (Sycoryctinae, Agaonidae) e) *Sycoryctes* (Sycoryctinae, Agaonidae) f) *Philocaenus* (Sycoecinae, Agaonidae) g) *Otitesella* (Otitesellinae, Agaonidae) h) *Eujacobsonia* (Otitesellinae, Agaonidae) i) *Apocryptophagus* (Sycophaginae, Agaonidae) j) *Sycophaga* (Sycophaginae, Agaonidae). Fig. a) redrawn from Boucek (1988). **fl** = felt line; **hs** = hypostomal suture; **mk** = medial keel; **ms** = medial suture; **tp** = tentorial pit.

TABLE 3.1. Chalcidoid wasp species whose ventral head surfaces were examined using a scanning electron microscope.

SPECIES	HOST FIG SPECIES	LOCALITY
Sycoecinae		
Sycoecus oculabulbus sp.nov.	*F. cyathistipula pringsheimiana* (Braun & Schum.)	Cameroun
Sycoecus crinitus sp. nov.	*F. lyrata* Warb.	Ivory Coast
Sycoecus wiebesi sp. nov.	*F. cyathistipuloides* De Wild	Ivory Coast
Sycoecus lamtoensis sp. nov.	*F. sagittifolia* Berg	Ivory Coast
Seres wardi sp. nov.	*F. bubu* Warb.	South Africa
Seres a. armipes Waterston	*F. ovata* Vahl	Ivory Coast
Seres a. breviceps Wiebes	*F. ovata* Vahl	Uganda
Seres solweziensis sp. nov.	*F. s. sansibarica* Warb.	Zambia
Seres l. longivena sp. nov.	*F. s. sansibarica* Warb.	Zambia
Crossogaster inusitata sp. nov.	*F. s. sansibarica* Warb.	Zambia
Crossogaster rashbrooki sp. nov.	*Ficus* species	Uganda
Crossogaster ovata sp. nov.	*F. ovata* Vahl	Uganda
Crossogaster hilli sp. nov.	*Ficus* species	Uganda
Crossogaster r. robertsoni sp. nov.	*F. trichopoda* Baker	South Africa
Crossogaster rastellus sp. nov.	*Ficus* species	Uganda
Crossogaster praeacuta sp. nov.	*Ficus* species	Uganda
Crossogaster odorans sp. nov.	*F. thonningii* Bl.	South Africa
Crossogaster quadrata sp. nov.	*F. glumosa* Delile	South Africa
Crossogaster stigma sp. nov.	*F. glumosa* Delile	South Africa
Crossogaster lurida sp. nov.	*F. n. natalensis* Hochst.	South Africa
Philocaenus silvestrii (Grandi)	*F. lutea* Vahl	South Africa

Philocaenus barbarus Grandi	*F. thonningii* Bl.	South Africa
Philocaenus geminus sp. nov.	*Ficus* species	Uganda
Philocaenus jinjaensis sp. nov.	*Ficus* species	Uganda
Philocaenus insolitus sp. nov.	*F. craterostoma* Mildbr. & Burr.	Gabon
Philocaenus medius sp. nov.	*F. n. natalensis* Hochst.	South Africa
Philocaenus ugandensis sp. nov.	*Ficus* species	Uganda
Philocaenus hippopotomus sp. nov.	*F. trichopoda* Baker	South Africa
Philocaenus clairae sp. nov.	*F. t. tremula* Warb.	South Africa
Philocaenus warei sp. nov.	*F. glumosa* Delile	South Africa
Philocaenus liodontus (Wiebes)	*F. natalensis leprieurii* (Miq.) Berg	Gabon
Philocaenus quatuordentatus sp. nov.	*F. craterostoma* Mildbr. & Burr.	South Africa
Philocaenus rotundus sp. nov.	*F. abutilifolia* (Miq.) Miq.	South Africa
Sycoryctinae		
Sycoryctes remus Wiebes	*F. thonningii* Bl.	South Africa
Sycoryctes sp.	*F. lutea* Vahl	South Africa
Philotrypesis parca Wiebes	*F. thonningii* Bl.	South Africa
Philotrypesis sp.	*F. lutea* Vahl	South Africa
Watshamiella sp.	*F. sur* Forssk.	South Africa
Sycoscapter sp.	*F. sycomorus* L.	South Africa
Sycoscapter sp.	*F. lutea* Vahl	South Africa
Sycoscapteridea sp.	*F. sur* Forssk.	South Africa
Apocrypta longitarsus (Mayr)	*F. sycomorus* L.	South Africa
Sycophaginae		
Sycophaga sp.	*F. sur* Forssk.	South Africa
Eukoebelea sycomori Wiebes	*F. sycomorus* L.	South Africa
Apocryptophagus sp.	*F. sur* Forssk.	South Africa

Apocryptophagus gigas (Mayr)	*F. sycomorus* L.	South Africa
Agaoninae		
Ceratosolen arabicus Mayr	*F. sycomorus* L.	South Africa
Elisabethiella stuckenbergi (Grandi)	*F. thonningii* Bl.,	South Africa
Otitesellinae		
Otitesella tsamvi Wiebes	*F. thonningii* Bl.	South Africa
Epichrysomallinae		
Camarothorax sp.	*F. thonningii* Bl.	South Africa
Eurytomidae		
Sycophila sp.	*F. thonningii* Bl.	South Africa
Torymidae		
Podagrion sp.	Not associated with figs	South Africa
Pseudotorymus sp.	Not associated with figs	England
Ormyridae		
Ormyrus sp.	Aerial roots of *F. trichopoda* Baker	South Africa
Eupelmidae		
Mesocomys sp.	Not associated with figs	South Africa

1981) (Sycophaginae) (fig. 3.2 e & 3.4 i).

Four different morphological categories can be distinguished in those species where the foramen magnum has moved posteriorly:

1. The tentorial pits have moved posteriorly together with the foramen magnum. This condition is characteristic of the Agaoninae (where a medial keel is present) (fig. 3.2 b & 3.4 k) and *Sycophaga* Westwood (Sycophaginae, where a medial suture is present) (fig. 3.2 f & 3.4 j).

The fact that the tentorial pits have moved posteriorly with the foramen magnum in the Sycophaginae, suggests a possible relationship between this subfamily and the Agaoninae. In the Agaoninae the tentorial pits are not visible, but from internal dissection the tentorial beams appear to run along the internal ventral surface of the head posteriorly to the foramen magnum. Thus if the pits are present but not visible they appear to have moved with the foramen magnum rather than being hidden under the ventral medial keel.

2. The foramen magnum has moved posteriorly leaving the tentorial pits behind and still centrally situated between the vertex and the oral fossa. A distinct medial suture is present between the hypostomal sutures. This is characteristic of *Eujacobsonia* Grandi (Otitesellinae) (fig. 3.4 h).

Unfortunately, specimens of *Grasseiana* Abdurahiman & Joseph and *Lipothymus* Grandi, the two other otiteselline genera that enter figs to oviposit, were not available for examination. From observations of other Otitesellinae (for example fig. 3.2 c) the presence of a medial suture appears to be characteristic of the subfamily as a whole, whether or not the species enter the figs for oviposition.

3. The foramen magnum has moved posteriorly leaving the tentorial pits behind and still centrally situated between the vertex and the oral fossa. A medial felt line is present, between the hypostomal sutures, instead of the medial suture. This is characteristic of the Sycoryctini (figs. 3.3 b-f & 3.4 e).

4. The foramen magnum has moved posteriorly leaving the tentorial pits behind, centrally situated between the vertex and the oral fossa. No medial suture or medial felt line is present between the hypostomal sutures, although these may be

compressed together to form a medial suture. This fourth category is characteristic of the Sycoecinae (fig. 3.4 f).

Seres wardi sp. nov. has the hypostomal sutures laterally compressed to form a single medial suture between the tentorial pits and the oral fossa. The presence of a medial suture would seem to indicate a relationship with the Sycophaginae or *Eujacobsonia* (Otitesellinae). However, although *S. wardi* is one of the more primitive sycoecines, it is probably the most adapted to enter the fig ostiole, having an extremely compressed head. The lateral compression of the hypostomal sutures into a single suture therefore appears to be a derived condition. Furthermore the sycoecine species that have the hypostomal sutures still separated do not have a medial suture situated between them, as is the case in the Sycophaginae and Otitesellinae. It therefore appears that the presence of the medial suture in *S. wardi* is not homologous with the medial suture present in the Sycophaginae and the Otitesellinae.

The characteristics of the underside of the head provide information from which a tentative sister group of the Sycoecinae can be proposed. The separation of the tentorial pits from the foramen magnum as a result of the latter's posterior movement, in combination with the absence of a medial suture, is a synapomorphy that links the Sycoecinae with the Sycoryctini as a monophyletic group. Since the medial felt line is also present in plesiomorphic sister groups of the Agaonidae, such as the Torymidae, Ormyridae and Eupelmidae, the absence of the medial felt line in the Sycoecinae suggests that the loss of the medial felt line is a derived condition. That absence of the medial felt line is derived is also supported from a biological point of view. Selection would favour as smooth a surface on the head as possible to facilitate entry through the fig ostiole. In terms of the medial felt line, the Sycoecinae are therefore more derived than the Sycoryctini. Additional support for the plesiomorphy of the Sycoryctini is that the venation and segmentation of the antennae and mouthparts in the Sycoryctini are either primitive to those of the Sycoecinae (i.e. show less reduction) or possess the same primitive state as do the most plesiomorphic sycoecine species.

The condition of the underside of the head in the second tribe of the Sycoryctinae, the Apocryptini, where the foramen magnum must still be regarded as being medially situated, suggests that this tribe is primitive to the Sycoryctini. Boucek (1988) defined the Sycoryctinae by the possession of long ovipositors in combination with a lack of lateral grooves in the scutellum. This distinguished the Sycoryctinae from the Sycophaginae which also have long ovipositors. However, neither of these characters can be used to delimit the Sycoryctinae as a monophyletic entity, although the lateral grooves may be a synapomorphy uniting the Sycophaginae and the Agaoninae, as suggested by Boucek (1988). Thus there is no apparent synapomorphy characterising the Sycoryctinae and uniting the Apocryptini and the Sycoryctini. For this reason the Apocryptini are regarded as the plesiomorphic sister group of the Sycoryctini/Sycoecinae clade.

With the exception of the Sycoryctini, the females of the wasps, in which posterior movement of the foramen magnum has occurred, all enter the fig for oviposition. The movement of the foramen magnum is therefore clearly an adaptation allowing the head to be placed in a prognathous position, which is a prerequisite for entry through the fig ostiole. Why the foramen magnum has moved towards the vertex in the Sycoryctini is not clear, as there is seemingly no functional adaptation associated with the move. This may suggest that a common ancestor of the Sycoryctini and the Sycoecinae had a head adapted for entering the fig, with the implication that the ancestor of the Sycoryctini reverted to external oviposition.

This would mean the Sycoryctini are more derived than the Sycoecinae. However, parsimoniously this is not a very sound evolutionary hypothesis, and it also entails a reversal of selection pressures. It is more parsimonious to accept that some unknown factor resulted in the posterior movement of the foramen magnum in the common ancestor of the Sycoryctini and the Sycoecinae. This movement then preadapted the ancestor of the sycoecine lineage to enter the fig through the ostiole.

If the medial felt line and the medial suture are each synapomorphies, being two independent results of the closing of the postgenal bridge (*sensu* Boucek 1988), this then suggests that the Agaonidae are paraphyletic. The Otitesellinae/ Sycophaginae lineage and the Sycoryctinae/ Sycoecinae/ Torymidae lineage would therefore represent two independent derivations from within the Pteromalidae. The Epichrysomallinae, Eurytomidae and Eupelmidae would probably also belong to the torymid lineage. That the Eurytomidae and Eupelmidae have affinities with the Torymidae was also suggested by Copland & King (1972) in their study of the female reproductive system of the Torymidae.

Alternatively, the medial felt line may be a derived condition resulting from the total fusion of the medial suture. This would place the Otitesellinae and Sycophaginae as ancestral lineages to the Torymidae, Eurytomidae and Eupelmidae. Or, on the other hand, the suture may be a derived result of the compression of the medial felt line, which would support the current classification. Whichever is correct, the highly derived Agaoninae need further investigation in order to determine from which lineage they evolved.

CONCLUSIONS

From the above considerations the Sycoryctini are tentatively considered to be the most closely related plesiomorphic sister group to the Sycoecinae and are thus considered to be the immediate outgroup for the phylogenetic analysis of the Sycoecinae. This agrees with Boucek's (1988) view that the "plesiomorphic features of *Robertsia* suggest a relationship of the Sycoecinae with the Sycoryctinae". The Apocryptini are tentatively regarded as the sister group to the Sycoryctini/Sycoecinae and are therefore considered as the second outgroup. The Agaoninae are highly derived, quite different from the sycoecines and more likely to be an apomorphic sister group of the Sycophaginae than of the Sycoecinae/ Sycoryctinae lineage. The Otitesellinae and Sycophaginae together appear to be an independent lineage and are therefore not used as outgroups. The Torymidae, which Boucek (1988) and Grissell (1991) regard as the sister group of the Agaonidae, a view which is supported by the morphology of the underside of the head, are considered to be the wider third outgroup.

4

PHYLOGENETIC ANALYSIS

INTRODUCTION

Besides the determination of evolutionary relationships within the Sycoecinae, the results of a phylogenetic analysis of this group has two further uses. Firstly, it can act as the basis for the systematic revision of the subfamily, providing naturally delimited genera, based on synapomorphies. Secondly it enables the comparison of the sycoecine phylogeny with the corresponding phylogenies, or at least the current classifications, of the pollinating fig wasps (Agaoninae) and the host fig trees (*Ficus* species). This then allows a preliminary assessment of the extent and types of evolutionary interaction between these three groups to be formulated.

MATERIALS AND METHODS

Taxa

Seventy terminal taxa were included in the analysis, consisting of sixty-seven species and three subspecies. Fifty-three of the terminal taxa are Afro-tropical, of which forty-three are described in this thesis as new species and subspecies (Chapters 6-9). The fourteen extra-African taxa are divided between the south-east Asian *Diaziella* Grandi, and the Australasian *Robertsia* Boucek.

Computer software and options

Phylogenetic analyses were carried out on an IBM compatible microcomputer using the principle of maximum parsimony to select the tree best reflecting the true evolutionary relationships between the taxa. Hennig86 version 1.5 (released by Farris, 1988) was used for the phylogenetic analyses, rather than PAUP version2.4 (released by Swofford, 1985), because of its faster running speed and greater efficiency in calculating the most parsimonious solutions (Platnick, 1989; Sanderson, 1990). PAUP version 3.0 (released by Swofford, 1990) is comparable to Hennig86 in running time, but at present can be run only on a Macintosh computer, which was not available (Platnick, 1989; Sanderson, 1990).

The implicit enumeration (***ie***) options offered by Hennig86, are ideally the ones to use as they are exact algorithms and therefore certain to find all trees of minimal length (Farris, 1988). However, for this option data matrices have an effective size limit of approximately 15-25 taxa, unless the researcher is willing to wait geological time periods for a result (Platnick, 1989; Sanderson 1990). To confirm this limitation, preliminary investigations were carried out using the ***ie*** options on the current data matrix. The ***ie-*** sub-option, which is normally the fastest of the implicit enumeration options (Farris, 1988), did not produce a result after running for nine days on a computer with a 386 microprocessor. Implicit enumeration algorithms could therefore not be employed. Fortunately, for many data sets the ***bb*** options produce the same results as the ***ie*** options, at more practical speeds (Farris, 1988). Although there is no guarantee that heuristic algorithms will find all the shortest trees, they are the next-best option (Farris, 1988; Platnick, 1989).

The data set was therefore analysed using the ***mh**** option, followed by the ***bb**** option which uses the results produced by the ***mh**** option as the input data. The ***mh**** option "constructs several trees, each by a single pass [through the data], adding the terminals in several different sequences". Branch-swapping or branch rearrangement is then applied to each of these initial trees with only one tree being retained for each initial tree that was constructed (Farris, 1988). The ***bb**** option "applies extended branch-swapping" to these trees and produces all the equally most parsimonious trees it can find, the only limitation being the amount of storage space available (Farris, 1988). Tree storage was limited by the availability of 320 K bytes of memory, as Hennig86 was found to be unable to make use of expanded memory when this was provided. This limited the production of trees by the ***bb**** option to 1284 trees, which was achieved with overflow when this option was run. This meant that not all the possible most parsimonious trees were found.

Terminology

The term monophyly is used in this thesis in the restricted sense, *sensu* Hennig (1966), where a monophyletic group includes the most recent common ancestor and all the descendants of that ancestor. This is equivalent to the meaning of the term holophyly as proposed by Ashlock (1971), who considers the term monophyly to encompass both holophyly and paraphyly. The following definitions of paraphyly and polyphyly are adhered to: a paraphyletic group does not include all the descendant species of the most recent common ancestor while a polyphyletic group does not include the most recent common ancestor of the group (Hennig, 1966; Ashlock, 1984).

Characters and character states

Although there are numerous methods available for coding continuous data as discreet states (Thorpe, 1984; Archie, 1985; Goldman, 1988), there is doubt as to the justifiability of these arbitrarily created states (Pimentel & Riggins, 1987; Chappill, 1989; Farris, 1990). Specifically, Pimentel and Riggins (1987) maintain that very little confidence can be placed in the assumption that the same quantitative states are homologous, even if mutually exclusive states exist in the transformation series. This is because quantitative characters cannot be subjected to the homology-determination tests of similarity, congruence and conjunction as advocated by Patterson (1982). Also the presence of quantitative characters in the data matrix can result in distorted cladograms (Chappill, 1989). Consequently, quantitative data, in the strict sense of absolute and relative measurements, were expressly excluded from the analyses.

In cases where the state of a character could not be observed and recorded, as for example in species whose males where unknown, a ? was used to code for that state.

Multistate characters were treated as additive characters, to reflect relationships between the states (Mickevich, 1982). To treat multistate characters as non-additive, whereby each and every state can possibly be derived from all the other states, defeats the purpose of determining phylogenetic relationships and is invalid for cladistic analysis (Pimentel & Riggins, 1987; Mickevich & Weller, 1990). Multistate character complexes have been variously referred to as a transition series (Sokal & Sneath, 1963), a transformation series (Hennig, 1966), or a character state tree (Sokal & Sneath, 1963; Farris, 1970; Wiley, 1981).

For characters whose states followed in a linear sequence, a (0) coding was regarded as primitive and each increasing number as more derived than the last. Non-linear character transformation series were treated in two ways. When the character state tree (CST) was represented as a simple basal dichotomy the states were coded starting with a 0 for the most derived condition of one of the branches, and coded with consecutive numbers from there through the node to the most derived condition of the second branch. The primitive state was therefore coded by whatever number corresponded with the node (Farris, pers. com.; e.g. characters 0, 3, 19, 31 & 37, fig. 4.1). If the CST was multifurcating (e.g. characters 6 & 7, 8 & 9, 10-14, 16-18, 28 & 29, 38 & 39, figs. 4.1 & 4.2) the character states were coded using the ordinal coding method (Pimentel & Riggins, 1987; Mickevich & Weller 1990; Mickevich & Lipscomb, 1991), which is similar to the fewest variables coding method of Goldman (1989). In this method each of the linear paths or axes in the character state tree is assigned as a variable or character, hence the utilisation of a number of characters to describe a particular character state tree. The ordinal coding method was used as this method needs fewer characters or variables to describe the tree than the non-redundant linear coding method of O'Grady & Deets (1987) and O'Grady *et al.* (1989) (Mickevich & Weller, 1990).

Character weighting

Successive approximations character weighting (Farris, 1969; Carpenter 1988) was carried out to make a decision about which of the equally most parsimonious trees produced without weighting were supported by the more consistent characters. This reduces the number of trees produced and thereby improves the resolution of the resulting strict consensus tree (Carpenter, 1988; Farris, 1988). Through this method of weighting each character's weight was set according to the fit of that character, measured by the consistency index (CI), to the cladograms that had been previously generated without character weighting. As the CI is a measure of the fit of the character to the cladogram (Farris, 1989), homoplastic characters received low weights. The **mh*/bb*** sequence of options was then rerun using the new weights and the resultant CI of the characters on the new cladograms was used to reweight the characters. This iterative procedure was carried out until the weights no longer changed.

Outgroups and character state polarities

Outgroup comparison (Watrous & Wheeler, 1981; Maddison, *et al.*, 1984) was used to determine the polarities of the characters. Three outgroups were utilised (Chapter 3). The Sycoryctini (Sycoryctinae) were regarded as the plesiomorphic sister group of the Sycoecinae, with the Apocryptini (Sycoryctinae) as the sister group of this clade. The Torymidae were considered as the third outgroup. The determination of the outgroups is detailed in the preceding chapter. An hypothetical ancestor based on the three outgroups was used to root the cladograms. The hypothetical ancestor was therefore coded as possessing the most plesiomorphic character state present in all the outgroups and the ingroup for each character.

The relationships of states to one another within multifurcating CST's were determined by a combination of outgroup comparison and morphocline analysis. Morphocline analysis is a model of character evolution, whereby the states that are most similar morphologically are hypothesised to have a direct evolutionary relationship. This enables the ordering of the states in a sequence as a result of their similarity (Maslin, 1952; Hennig, 1966). Once the plesiomorphic state was identified by outgroup comparison, the remaining states were ordered by morphocline analysis.

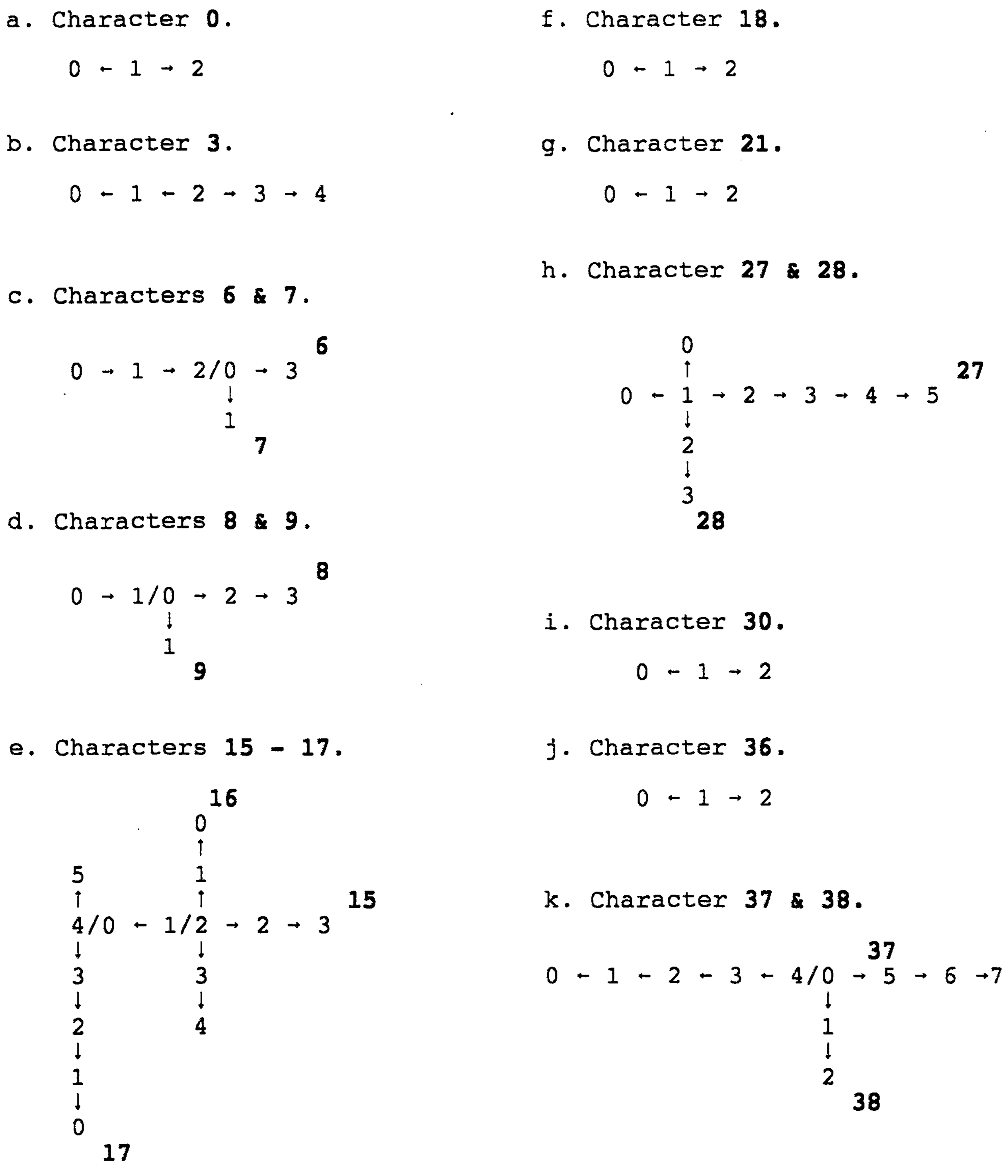
Using the three outgroups and morphocline analysis the following character state polarities and ordering, for the forty-four characters that were included, were arrived at. The character state trees for the non-linear multistate characters are illustrated in figs. 4.1 & 4.2. Unless otherwise stated (0) is the primitive state.

Character 0. Degree of sexual dimorphism: (0) male winged, head shape and mandible dissimilar to female; (1) male winged, head shape and mandible similar to female; (2) male apterous, head shape and mandible similar to female. State 1 is primitive (fig. 4.1 a).

Sexual dimorphism was regarded as being derived, with two degrees of dimorphism having evolved independently. Either the loss of the wings as in male *Robertsia* or divergence of the male head and mandibular form from that exhibited by the female.

Character 1. Female colour: (0) whole body metallic; (1) head only metallic, rest testaceous; (2) whole body testaceous.

Development of testaceous colouring was regarded as an apomorphy, which is apparently linked to nocturnal flight.



a. Character **0.**

b. Character **3.**

c. Characters **6 & 7.**

d. Characters **8 & 9.**

e. Characters **15 - 17.**

f. Character **18.**

g. Character **21.**

h. Character **27 & 28.**

i. Character **30.**

j. Character **36.**

k. Character **37 & 38.**

Fig. 4.1. Character state trees for the non-linear multistate characters used in the phylogenetic analysis of the Sycoecinae. Description of the characters numbered in the figure are provided in the text.

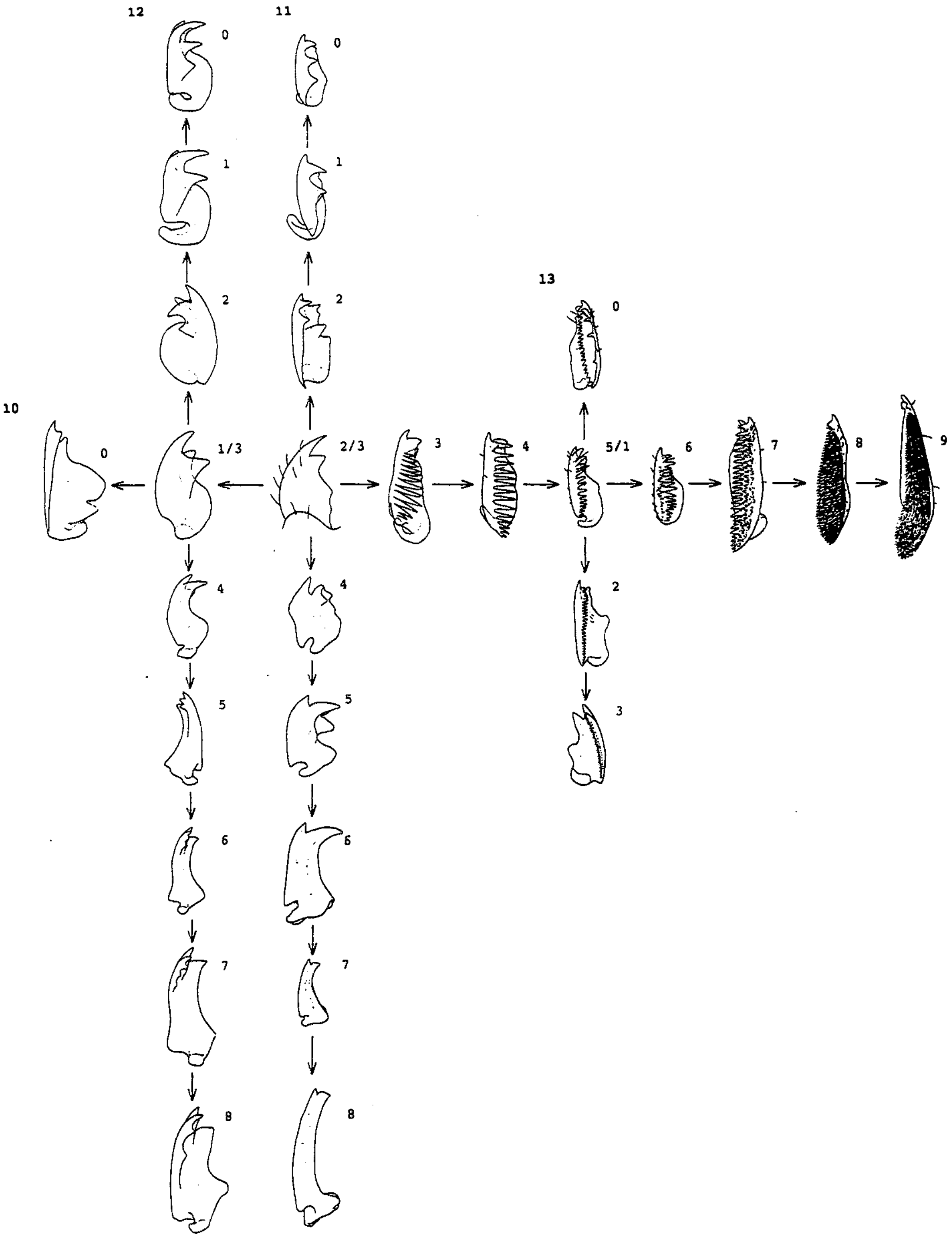


Fig. 4.2. Hypothesised character transformation series of the sycoecine mandibular character states, represented by characters 10-13 in bold lettering. Numbers in normal lettering represent the character states. Arrows depict the hypothesised evolutionary direction.

Character 2. Female occipital carina: (0) remnants present on the vertex below the ocelli; (1) absent.

Character 3. Female malar sulcus: (0) curves ventrad then dorsad half way down the cheek and immediately fades out; (1) present for full cheek length, sinusoidal - posteriorly curves ventrad, anteriorly curves dorsad; (2) present for full cheek length, gently curved dorsad; (3) present for posterior part of cheek length; (4) absent; (5) present for anterior part of cheek. State 2 is primitive (fig. 4.1 b).

State 5 appears to be a reappearance of the sulcus and is associated with the lengthening and modification of the anterior edge of the head capsule. This occurs in order to accommodate the extension of the mandible into a plate of fine teeth.

Character 4. Ventral tentorial pits in females: (0) well separated by as much as the width of the foramen magnum, situated half way between the oral fossa and the foramen magnum; (1) slightly separated by less than the width of the foramen magnum, situated half way between the oral fossa and foramen magnum; (2) in close apposition, situated half way; (3) in close apposition with a medial groove anteriorad, situated half way; (4) in close apposition, situated closer to the oral fossa; (5) widely separated, situated close to the oral fossa.

From the outgroups the positioning of the tentorial pits half way between the foramen magnum and the oral fossa is the primitive condition and the anterior movement of the pits is derived. The wide separation of the pits, present in some of the *Crossogaster* species is therefore regarded as a reversal.

This character could be construed as comprising two independent characters, namely the positioning of the tentorial pits and their degree of separation. However, coding them as two separate characters would result in a loss of information and false homology. The transformation series involving the positioning of the pits would not be altered, but the separation of the pits would, with the derived reversal of *Crossogaster* having to be coded as plesiomorphic. In contrast, by linking the degree of separation of the tentorial pits to their positioning, the condition in some of the *Crossogaster* species is recognised as being derived.

Character 5. Medial felt line on the ventral surface of the head in females: (0) present; (1) absent.

The following two characters (6 & 7) represent a single character state tree (fig. 4.1 c).
Character 6. Female hypostoma: (0) present for most of head width but thin; (1) very reduced; (2) present for most of head width, wide; (3) detached and overlapped by stipes medially.

Character 7. Female hypostoma: (0) present for most of head width, wide; (1) absent.

The following two characters (8 & 9) represent a single character state tree (fig. 4.1 d).
Character 8. Labial and maxillary palp segment numbers: (0) 2 & 4; (1) 2 & 3 - first maxillary palp segment the shortest; (2) 2 & 3 - proximal and distal maxillary palp segments subequal; (3) 2 & 3 - first maxillary palp segment longest.

Character 9. Labial and maxillary palp segment numbers: (0) 2 & 3 - proximal shortest; (1) 1 & 2.

The following five characters (10 - 13) represent a single character state tree (fig. 4.2).
Character 10. Female mandible: (0) with a single small ventral tooth at the apex extending into a longitudinal ridge; (1)

with a single large ventral medial tooth; (2) with no ventral teeth; (3) with a longitudinal row of ventral teeth: first tooth large in comparison to rest which are long and curved; (4) with a longitudinal row of many long, straight teeth; (5) with a longitudinal row of many short teeth; (6) with two longitudinal rows of teeth; (7) with ca. four rows; (8) with ca. six rows forming a plate of teeth extending posteriorly; (9) with a large plate of teeth extending posteriorly past the anterior eye margin. State 7 is primitive.

Character 11. Female mandible: (0) with three equal ventral teeth spread out, extending into a longitudinal ridge; (1) with two equal ventral teeth spread out, extending into a longitudinal ridge; (2) with two equal ventral teeth near the apex, extending into a longitudinal ridge; (3) with two apical and no ventral teeth; (4) with two apical, one subapical and a single small ventral tooth; (5) with two apical and one subapical tooth; (6) with two apical teeth, inner tooth longer and curved; (7) with only two apical teeth, mandible short; (8) with only two apical teeth, mandible elongate. State 3 is primitive.

Character 12. Female mandible: (0) with three large subequal ventral teeth spread out (proximal smallest); (1) with two large subequal (proximal smaller) ventral teeth spread out; (2) with two large subequal ventral teeth near apex, no ridge; (3) with a single large ventral medial tooth; (4) thin, curved with a single large ventral tooth extending into a slight longitudinal ridge; (5) with two small ventral teeth at apex; (6) with three small ventral teeth at apex; (7) with four small ventral teeth at apex; (8) with three larger ventral teeth spread out. State 3 is primitive.

Character 13. Female mandible: (0) with a longitudinal row of very short ventral teeth and small row of fewer ventral teeth anterior and parallel to the first row; (1) with a longitudinal row of very short ventral teeth; (2) with a longitudinal row of short, ventral teeth; (3) with a longitudinal row of short ventral teeth and four equally spaced ventral teeth anterior to the first row. State 2 is primitive.

Character 14. Female oral fossa: (0) narrow; (1) as broad as the head.

The following three characters (15-17) represent a single character state tree for the female antennae (fig. 4.1 e).

Character 15. Female antennae: (0) 1 anellus, 5 funicle segments, two integrated rows of MPS; (1) 2 anelli, 5 funicle segments, MPS single and close; (2) 1 anellus, 5 funicle segments, with stumpy free MPS; (3) 1 anellus, 5 funicle segments, with elongate, free MPS. State 1 is primitive.

The antennae comprise two separate characters, viz. the number of antennal segments and the MPS type. However, by considering these two characters together, far better resolution of the relationships between the different antennal types can be obtained. The coding of these two characters separately would result in homoplasy and lack of resolution.

Character 16. Female antennae: (0) 2 anelli, 4 funicle segments, MPS in a single row and widely spaced; (1) 1 anellus, 5 funicle segments, MPS in a single row and widely spaced; (2) 2 anelli, 5 funicle segments, MPS in a single row, close together; (3) 3 anelli, 4 funicle segments, MPS in a single row, close together; (4) 2 anelli, 4 funicle segments, MPS in a single row, close together. State 2 is primitive.

Character 17. Female antennae: (0) 1 anellus, 5 funicle segments, MPS in a single row but reduced; (1) 1 anellus, 5 funicle segments, MPS in a single row; (2) 1 anellus, 5 funicle segments, first funicle segment with two rows of integrated MPS; (3) 1 anellus, 5 funicle segments, first and second funicle segments with two rows of integrated MPS; (4) 1 anellus, 5 funicle segments, with two rows of integrated MPS on all funicle segments; (5) 2 anelli, 4 funicle segments, two rows of MPS integrated on all funicle segments. State 4 is primitive.

Character 18. Female antennal funicle segment expansion: (0) first segment expanded; (1) all segments normal; (2) second segment broadest, rest tapering to club. State 1 is primitive (fig. 4.1 f).

Character 19. Female antennal scrobe: (0) face immediately posterior to toruli excavated as scrobe, but scrobe not reaching the vertex; (1) face medially excavated as a distinct deep scrobe from the toruli to the vertex such that the medial ocellus is situated in the posterior end of the scrobe; (2) as in state 2, but the scrobe is shallow to indistinct; (3) face smooth, convex.

Character 20. Female antennal scape: (0) cylindrical, straight; (1) flattened, subclavate; (2) flattened, clavate.

Character 21. Female toruli: (0) touching; (1) separated; (2) separated by a narrow longitudinal carina. State 1 is primitive (fig. 4.1 g).

Character 22. Propodeal spiracle situation in females: (0) anterior; (1) medial.

The medial positioning of the spiracles was regarded as an apomorphy present in *Seres* (Sycoecinae) and also the Sycoryctini, because in the more primitive outgroups, Apocryptini and Torymidae the spiracles are anteriorly situated. This may be indicative of a relationship between

Seres and the Sycoryctini, but is probably homoplastic having evolved more than once.

Character 23. Propodeal plica: (0) extensive, present for most of propodeal length; (1) reduced, present for about half of propodeal length; (2) absent.

Character 24. Wing pilosity in females: (0) covered with numerous dense microsetae; (1) microsetae fewer and less dense.

Character 25. Female fore tarsi: (0) fore leg with five tarsal segments; (1) fore leg with four tarsal segments.

Character 26. Female fore tarsi: (0) first tarsal segment of fore leg smooth; (1) laminar projection on proximal part of first tarsal segment of fore leg.

The following two characters (27 & 28) represent a single character state tree (fig. 4.1 h).
Character 27. Female fore tibial armature: (0) double comb with a modified tibial spur; (1) bidentate; (2) tridentate; (3) comb of 4 to 6 teeth; (4) comb of 6 to 8 teeth with one or two teeth dorsad; (5) comb of nine teeth with two rows dorsad. State 1 is primitive.

Character 28. Female fore tibial armature: (0) plate of numerous fine teeth; (1) bidentate; (2) four teeth present along the circular apical edge; (3) six teeth present along the circular apical edge. State 1 is primitive.

Character 29. Presence of ventral tooth next to spur: (0) absent; (1) present as a tooth or cone.

Character 30. Shape of female fore femur: (0) elongate but laterally flattened; (1) subcylindrical, elongate; (2)

subtriangular, squat. State 1 is primitive (fig. 4.1 i).

Character 31. Female hind coxae: (0) smooth; (1) carina present on dorso-posterior margin.

Character 32. Female pronotum: (0) smooth; (1) sulci present.

Character 33. Female propleura: (0) smooth; (1) strongly excavated.

Character 34. Female gaster, posterior edge of tergites: (0) smooth with no incisions; (1) smooth with five incisions; (2) crenulated with three incisions.

Character 35. Female 8th urotergite spiracular peritremata: (0) normal; (1) expanded.

Character 36. Setation in males: (0) absent; (1) sparse and weak; (2) few strong setae on head and thorax, gaster without strong setae; (3) many strong setae present on head, thorax and gaster (setae on gaster as long as the setae on the thorax and head). State 1 is primitive (fig. 4.1 j).

The following two characters (37 & 38) represent a single character state tree (fig. 4.1 k).

Character 37. Male mandible: (0) elongate, apical teeth subequal, outer slightly longer; (1) elongate, outer apical tooth longer; (2) elongate, outer apical tooth longer with a small tooth present on the ventral margin at the base of the outer apical; (3) subelongate, outer apical tooth longer, with an apical ventral tooth extending as a ridge towards the base of the mandible; (4) broad, outer apical tooth longer, with a single ventral tooth; (5) inner tooth only slightly longer with a small ventral tooth; (6) inner tooth longer; (7) inner tooth longer with serrations on the inner margin. State 4 is primitive.

Character 38. Male mandible: (0) broad, outer longer, plus one ventral; (1) broad, outer longer, no ventral; (2) single apical.

Character 39. Toruli separation in males: (0) separated; (1) touching.

Character 40. Male flagellum: (0) normal; (1) compressed.

Character 41. Male thorax: (0) mesoscutum and scutellum normal; (1) mesoscutum and scutellum strongly reduced.

Character 42. Male ocelli: (0) normal; (1) reduced.

Conflicting character transformation series

An iterative procedure was adopted whereby character transformation series that conflicted with the cladogram topology were reassessed in terms of polarity and homology of the states. Occasionally errors in initial assessments were identified and these were adjusted. More often than not conflicting transformation series were accepted as such for two reasons. Firstly, there was confidence that the character transformation series determined by morphocline analysis, i.e. from biological information, were indicative of the real situation. Secondly, it was deemed to be quite plausible that those characters that did not fit the cladogram topology were homoplastic as a result of parallelism or reversal, and acceptable as such. For these reasons the more rigorous approach of transformation series analysis (Mickevich, 1982; Mickevich & Weller, 1990; Mickevich & Lipscomb, 1991), in which character transformations that disagree with the initial cladogram are recoded to fit the cladogram, was not adopted.

RESULTS

The distributions of the character states for the 74 taxa and the hypothetical ancestor used as the outgroup are listed in Table 4.1.

The 1339 cladograms obtained without character weighting each had a length of 190, a consistency index (CI) of 59, and a retention index (RI) of 92. The 1339 cladograms obtained after the successive approximations weighting procedure each had a length of 972, a CI of 73, and a RI of 95. The differential weighting of the characters results in an increased number of steps required to resolve the cladogram, hence the increased length values. The strict consensus tree (l = 210, CI = 53, RI = 90) of the cladograms without character weighting is depicted in fig. 4.3, and the strict consensus tree (l = 980, CI = 73, RI = 95) of the cladograms obtained after successive approximations weighting is depicted in fig. 4.4.

The justification for the running of the successive weighting option on the present data set was brought into question because only a subset of the possible equally most parsimonious trees could be utilised and this could produce a biased result (Schuh, 1991). However, the topology of the strict consensus tree obtained from the procedure of running the successive approximations weighting option on the ***mh**** option, which only produced 4 trees, was no different from the strict consensus tree obtained from the 1339 trees produced by successive weighting on the ***bb**** option. It is therefore unlikely that the strict consensus tree would be altered if all the possible most parsimonious trees were available. For this reason confidence can be placed in the results produced by successive weighting.

The synapomorphies defining each of the clades in figure 4.3 are listed in Table 4.2. The node numbers correspond with

TABLE 4.1. Character state distributions of the 43 characters for the 70 taxa used in the phylogenetic analysis.

		1111111111	2222222222	3333333333	444
Character No.	0123456789	0123456789	0123456789	0123456789	012
Hypothetical ancestor	1002000000	2332012410	0100000110	1000001400	000
D. falcata	0112212020	2532102112	1002111211	2000002?00	000
D. tumidigena	?112212020	2832102312	1002011111	200000????	???
D. pallidiceps	?212212020	2632102212	1002011111	200000????	???
D. retakensis	?112212020	2832102212	1002011111	200000????	???
D. longiceps	?112212020	2532102312	1002011111	200000????	???
D. laticeps	?112212020	2632102212	1002011111	200000????	???
D. latipennis	?112212020	2532102212	1002011111	200000????	???
D. alleni	?112212020	2532102112	1002011111	200000????	???
D. wiebesi	?112212020	2632102112	1002011111	200000????	???
D. bicolor	?112212020	2432102212	1002011111	200000????	???
D. macroptera	?112212020	2532102112	1002011111	200000????	???
D. philippinensis	?112212020	2432102412	1002011211	200000????	???
R. xylosyciae	2002210000	2332102013	2202100121	0000000410	011
R. mandibularis	2002210000	2332102013	2202100131	0000000420	011
C. odorans	0004513011	5332132411	0002100111	2000212700	000
C. quadrata	0004513011	5332132411	0002100111	2000212700	000
C. stigma	0004513011	5332132411	0002100111	2000212700	000
C. praeacuta	0000513011	5332132411	0002100111	2000212600	000
C. rastellus	0000513011	4332132411	0002100111	2000212600	000
C. oculagrandis	?104513011	5332132411	0002100111	200021????	???
C. lurida	0104513011	5332132411	0002100111	2000212700	000
C. vansomereni	?004513011	4332110411	0002100111	200021????	???
C. rashbrooki	?004513011	4332111411	0002100111	200021????	???
C. hilli	0004513011	4332110411	0002100211	2000212600	000
C. ovata	0004513011	4332111411	0002100211	2000212600	000
C. r. robertsoni	0004513011	4332110411	0002100111	2000212600	000
C. r. rasplusi	0004513011	4332110411	0002100111	2000212600	000
C. michaloudi	0001112011	3332112411	0002100110	1000112500	000
C. lachaisei	?001212111	4332112411	0002100210	100011????	???
C. inusitata	0004412011	4332122411	0002100211	1000112600	000
C. triformis	0004513011	4332111411	0002100211	2000212600	000
P. silvestrii	0002312020	5332110411	0002100121	2000203000	100
P. comptoni	0002412020	5330110411	0002100100	1000203000	100
P. cavus	0002412020	5331110411	0002100100	1000203000	100
P. liodontus	0004312030	1362110411	0002100211	2000202101	000
P. quatuordentatus	?004312030	1372110411	0002100311	200020????	???
P. warei	0004312030	1352110411	0002100211	2000202101	000
P. zambesiacus	0004312030	1382110411	0002100311	2000202101	000
P. rotundus	0004312030	1382110411	0002100311	2000202101	000
P. barbarus	0004312030	5332110411	0002100311	2000202101	000
P. bouceki	0004312030	5332110411	0002100211	2000202101	000
P. comorensis	0004312030	5332110411	0002100211	2000202101	000

P. geminus	?004312030	5333110411	0002100411	200020????	???
P. jinjaensis	0004312030	5333110411	0002100411	2000202101	000
P. insolitus	?004312030	6332110411	0002100211	200020????	???
P. ugandensis	0005312030	8332110411	0002100311	2000202101	000
P. medius	0005312030	7332110411	0002100311	2000202101	000
P. levi	?004312030	1342110411	0002100111	200020????	???
P. clairae	0004312030	1342110411	0002100111	2000202100	000
P. bakeri	?004312030	1332110411	0002100211	200020????	???
P. bifurcus	?004312030	1342110411	0002100211	200020????	???
P. barbatus	0005211020	9332110411	0002100111	2000202100	000
P. hippopotomus	0005212020	9332110411	0002100111	2000202100	000
S. longicalcar	?003211010	1322113411	0011100310	100010????	???
S. wardi	1003212110	0332113411	0011100100	1000101300	000
S. a. armipes	0004212020	1312114421	0011100510	1000102200	000
S. a. breviceps	0004212020	1312114421	0011100510	1000102200	000
S. solweziensis	0004212020	1312114421	0011100510	1000102200	000
S. l. longivena	0004212020	1302114421	0011100510	1000102200	000
S. l. bidens	0004212020	1312114421	0011100510	1000102200	000
S. oculabulbus	1002112000	2232102501	0000100010	1111102400	000
S. taylori	?00211??00	2232102501	0000100010	111110????	???
S. medleri	?002111000	2132102501	0000100010	111110????	???
S. bergi	1002111000	2032102501	0000100010	1111102400	000
S. ivoryensis	?002111000	2232102501	0000100010	111110????	???
S. lamtoensis	1002111000	2232102501	0000100010	1111102400	000
S. crinitus	1003111000	2232102501	0000100010	1111102400	000
S. wiebesi	1002111000	2232102501	0000100010	1111102400	000
S. thaumastocnema	1002111000	2032102501	0000100010	1111102400	000
S. nyassossoenis	1003111000	2032102501	0000100010	1111102400	000

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those represented on figure 4.4. The synapomorphies supporting the major clades are listed below. The first number in brackets is the character and the second the character state.

Node 1. The Sycoecinae are defined by the separation of the foramen magnum from the tentorial pits with the posterior movement of the former (4.1); the loss of the medial felt line on the underside of the head (5.1); and the broadening of the oral fossa (14.1).

Node 2. The monophyly of *Sycoecus* is supported by the ventral mandibular teeth extending into a longitudinal ridge (11.2); the presence of 2 anelli and 4 funicle segments with the MPS being in integrated rows on all the funicle segments (17.5); the expansion of the first funicle segment (18.0); modification of the tibial spur into a plate of fine teeth (27.0); presence of a carina on the dorso-posterior margin of the hind coxae (31.1); presence of sulci on the pronotum (32.1); and strongly excavated propleura (33.1).

Node 3. The rest of the sycoecines are indicated as a sister clade of *Sycoecus* by the close apposition or secondary widening of the ventral tentorial pits (4.2); the presence of a wide hypostoma (6.2); the reduction of the labial palp segments from four to three (8.1); and the reduction or absence of the propodeal plica (23.1).

Node 4. *Seres* is defined by the MPS on the antennae being in close apposition in a single row (16.3); and the medial positioning of the propodeal spiracles (22.1).

Node 5. The remaining members of the sycoecines are united by the following synapomorphies: absence of the propodeal plica (23.2); and the presence of a ventral tooth next to the fore tibial spur (29.1).

Node 6. The monophyly of *Diaziella* and *Robertsia* is supported by a shallow scrobe or smooth face (19.2); by a flattened, subclavate to clavate antennal scape (20.1); and a reversal to a smooth edge with no incisions on the posterior margin of the gasteral tergites (34.0).

Node 7. The monophyly of *Crossogaster* and *Philocaenus* is supported by their possession of a ventral longitudinal row of teeth (10.4).

Node 8. *Diaziella* is defined by the females having a metallic head, with the rest of the body being testaceous or the whole

Fig. 4.3. The strict consensus tree (l = 210, CI = 53, RI = 90) of the Sycoecinae, obtained from 1339 cladograms produced without character weighting.

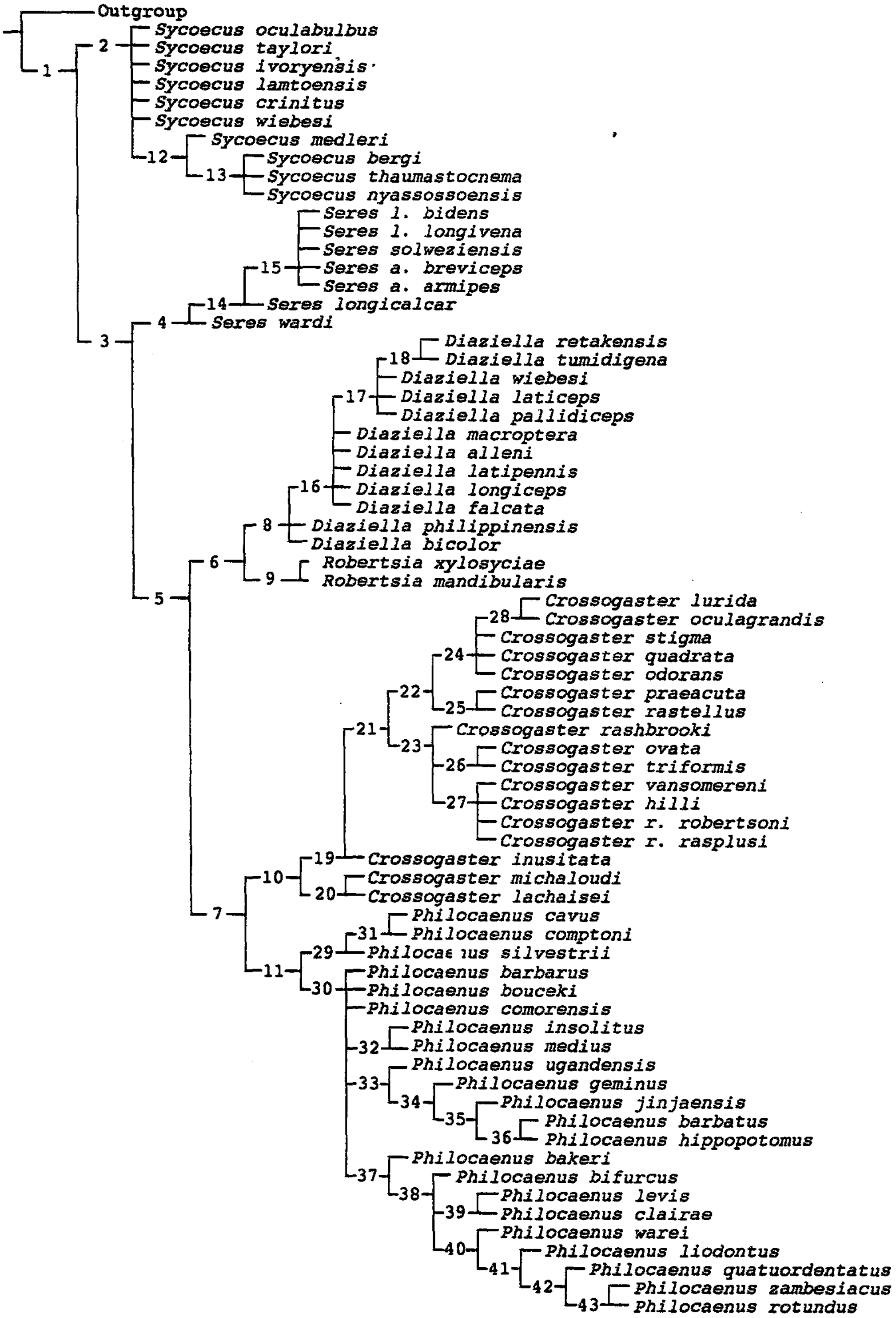

Fig. 4.4. The strict consensus tree (l = 980, CI = 73, RI = 95) of the Sycoecinae, obtained from 1339 cladograms produced with successive approximations weighting. Synapomorphies supporting the nodes numbered in the figure are detailed in the text and Table 4.2.

body including the head being testaceous. The last condition is homoplastic, having also evolved in *Crossogaster* (1.1); absence of remnants of the occipital carina (2.1); mandibular morphology (11.4); only four fore tarsal segments (25.1); and a laminar projection on the first fore tarsal segment (26.1).

Node 9. *Robertsia* is defined by a number of synapomorphies, including apterous males (0.2); a single anellus with 5 funicle segments in combination with reduced multiporous plate sensilla (17.0); a smooth face, without a scrobe (19.3); a flattened, clavate scape (20.2); the toruli separated by a narrow longitudinal carina (21.2); fore tibial teeth circularly positioned on the apical edge of the fore tibia (28.2); laterally flattened fore femur (30.0); absence of setae in the males (36.0); the reduction of the mesoscutum and the scutellum (41.1); and the reduction of the ocelli (42.1).

Node 10. *Crossogaster* is defined by the possession of a single labial palp segment and two maxillary palp segments (9.1); an expanded spiracular peritremata on the eighth urotergite (35.1); and the inner tooth of the male mandible being slightly to distinctly longer than the outer tooth (37.5).

Node 11. *Philocaenus* is defined by the possession of 2 anelli and 4 funicle segments with the MPS widely spaced in a single row [homoplastic apomorphy] (16.0); the posterior edge of the tergites of the female gaster are crenulated with three medial incisions [homoplastic] (34.2) and the outer apical mandibular tooth in the male being longer than the inner with the concurrent loss of the ventral tooth (37.1).

The successive weighting procedure increased the consistency index, which was to be expected as the homoplastic characters received the lowest weight. As far as could be ascertained, the number of equally most parsimonious trees appeared not to have been reduced, as the bb* option still produced more trees

TABLE 4.2. Synapomorphies (character number followed by state) defining the clades identified by node numbers (far left column) in fig. 4.4. Two states separated by a / are alternative most parsimonious resolutions on the cladogram, the numbers in brackets indicate at which node the alternative option is resolved. An (h) indicates that the state is homoplastic, and an (r) indicates that the state is a reversal.

NODES	**CHARACTER NUMBERS AND STATES**
1	4.1, 5.1, 14.1.
2	11.2, 17.5, 18.0, 27.0, 31.1, 32.1, 33.1.
3	4.2, 6.2, 8.1, 23.1.
4	3.3 (h), 16.3, 22.1, 37.3 (h).
5	23.2 29.1.
6	19.2, 20.1, 34.0 (r).
7	10.4.
8	1.1 (h), 2.1, 11.4, 25.1, 26.1.
9	0.2, 17.0, 19.3, 20.2, 21.2, 28.2, 30.0, 36.0, 38.1, 41.1, 42.1.
10	9.1, 35.1, 37.5.
11	8.2 (h), 16.0 (h), 34.2 (h), 37.1.
12	11.1.
13	11.0.
14	27.3 (h).
15	12.1, 16.4, 18.2, 27.5.
16	11.5.
17	11.6.
18	11.8.
19	37.6.
20	3.1.
21	4.5, 6.3, 34.2 (h).
22	10.4/5 (24) (h), 15.3.
23	16.1 (h).
24	10.5 (h), 37.7.
25	3.0.
26	27.2 (h).
27	16.0 (h).
28	1.1 (h).
29	36.3, 37.0, 40.1.
30	3.4 (h), 8.3, 27.2 (h), 39.1.
31	4.4 (h), 13.1, 28.0, 29.0 (r), 30.1 (r).
32	13.3, 27.4.
33	10.6.
34	3.5, 10.7.
35	10.8.
36	3.5 (h), 10.9.
37	10.1 (h).
38	12.4.
39	27.1 (r).
40	12.5.
41	12.6.
42	12.7.
43	12.8.

than could be stored in the computer memory.

Successive weighting produced no changes in the delimitation of the major clades and only a limited amount of further resolution within some of the clades such as *Diaziella*, the *Crossogaster triformis* species group, and the *Philocaenus barbarus* species group.

DISCUSSION

The cladogram supports the concept of the Sycoecinae as a monophyletic group, defined by two synapomorphies. The first synapomorphy is the loss of the medial felt line on the ventral surface of the head. However, as this involves the loss of a character state, less confidence can be placed in it being homologous than if the apomorphy had been the development of a complex character. Consequently this is not a strong synapomorphy. The second synapomorphic character is provided by the oral fossa, which has broadened to become almost as wide as the head. Once again this character is not unique to the Sycoecinae and appears to be homoplastic within the Agaonidae, having also evolved in the Agaoninae and some Otitesellinae.

All six of the sycoecine genera recognised are defined by the cladogram as good monophyletic groups, and agree with the intuitive taxonomic approach that was used for a preliminary designation of the genera. The delimitation of the genera remained constant from the first tentative analysis, through the subsequent reassessments of the characters and the character state polarities, to the final cladogram, further supporting the validity of the genera.

The description of 43 new species from the Afro-tropical region, often for both sexes, plus the description of males of characters may alter the position of the genera in the cladogram. The origination of *Robertsia* and *Diaziella* from within the African taxa also raises some difficult biogeographical and coevolutionary questions. A more complete discussion of this issue is given in Chapter 11.

A number of species groups can be recognised within *Crossogaster* and *Philocaenus* based on superficial morphology (Chapters 8 & 9). Many of these such as the *C. triformis* species group, the *C. odorans* species group, the *P. silvestrii* species group and the *P. liodontus* species group are supported by the cladogram and are thus monophyletic. The *P. barbarus* species group and the *P. levi* species group on the other hand are not strongly supported by the cladogram and are only recognisable using plesiomorphic characters. The species groups that are supported by synapomorphies are usually only distinguishable in the female sex. The *P. silvestrii* group, however, is exceptional as it is defined only by synapomorphies in the male sex. The raising of these species groups to generic status is therefore not supported.

Even after character weighting there are still many unresolved multifurcations in the cladogram involving closely related species. This is because quantitative data is often necessary to separate closely related species, and for the reasons outlined above, quantitative data was excluded from the analysis. The cladistic relationships between these species may be resolved in the future through the utilisation of new qualitative characters.

CONCLUSIONS

The cladogram generated by the phylogenetic analysis of the Sycoecinae supports the recognition of six monophyletic genera. The phylogenetic relationships between these six genera are less stable, in that the resolutions of the clades several described species previously only known from females, provided a vast increase in the knowledge of characters and character state distributions within the Sycoecinae. The increase in the knowledge of male morphology, in particular, has resulted in an improved conception of relationships between the species and genera. This has shown the existing classification of the Sycoecinae to be incorrect. The most striking result was the realisation that the conception of *Seres* was paraphyletic, with the true affinities of *Seres levi* lying with *Philocaenus*. *Crossogaster* as previously defined included a *Philocaenus* clade, the *P. silvestrii* species group, and was therefore also paraphyletic. *Phagoblastus* and *Philocaenus* were synonymised based on the acquisition of intermediate species and male morphology. The only African genus to retain its original delimitations was *Sycoecus*.

These taxonomic changes, detailed in the following chapters, were all supported by the cladogram. Most of the genera are defined by a suite of strong synapomorphic characters. *Philocaenus* however, is problematic in that it is not defined by any distinguishing female characters and is only weakly defined by a single male character state.

The cladogram suggests that *Sycoecus* is the most primitive genus within the Sycoecinae, and is thus the sister group of the rest of the sycoecines. *Robertsia* on the other hand, in contrast with Boucek's (1988) assessment of this taxon, appears to have more recent origins, diversifying relatively late within the sycoecines, along with the other extra-African genus *Diaziella*, as the sister group of *Crossogaster* and *Philocaenus*. This is contrary to the usual perceptions of *Diaziella* and *Robertsia* as being relatively primitive (Boucek, 1988). It needs to be reiterated, however, that the relationships between the genera in the cladogram are not stable, as they are only supported by a few, often weak characters. Consequently, the addition of newly discovered characters may alter the position of the genera in the cladogram. The origination of *Robertsia* and *Diaziella* from within the African taxa also raises some difficult biogeographical and coevolutionary questions. A more complete discussion of this issue is given in Chapter 11.

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CONCLUSIONS

The cladogram generated by the phylogenetic analysis of the Sycoecinae supports the recognition of six monophyletic genera. The phylogenetic relationships between these six genera are less stable, in that the resolutions of the clades are only supported by a few characters, but they suggest that the two extra-African genera may not be a sister group to the rest, as previously believed.

5

SYSTEMATICS OF THE SYCOECINAE

DELIMITATION OF THE SYCOECINAE

Although Hill (1967a; 1967b) provided a diagnosis of the sycoecine group when he created the new tribe Sycoecini, descriptions and addition of new species since then have broadened the limits of most of the delimiting characters and as a consequence these are now of no value. Such characters include, the antennal segmentation, the thickening of the marginal vein and the length of the postmarginal vein. Furthermore, one of the character states (the presence of alate males), that Hill used to define the sycoecines is primitive, and is consequently of no use as a defining apomorphy and in any case the recently described sycoecine genus *Robertsia* Boucek (1988) has apterous males, which makes the use of this plesiomorphic character invalid.

The synapomorphies defining both the Sycoecinae and their putative plesiomorphic sister group, the Sycoryctini, have arisen from adaptations related to their different modes of oviposition. The Sycoecinae are 'internal' ovipositors and have developed adaptations for entering the fig through the ostiole. The Sycoryctini are 'external' ovipositors and the ovipositor, ovipositor sheaths and terminal gastral segments have been adapted for penetration of the thick fig wall to reach the ovules.

Synapomorphies of the Sycoryctini

The structure of the ovipositing organs was used by Wiebes (1966) to define the new tribes Sycoryctini and Philotrypesini which have since been combined to form the Sycoryctini (Boucek, 1988). The tubular lengthening of either the ninth or both the eighth and ninth tergites to provide support for the ovipositor appears to be a synapomorphy supporting the monophyly of the Sycoryctini.

Synapomorphies of the Sycoecinae

The synapomorphies defining the Sycoecinae represent a suite of characters which have evolved as adaptations for the females to enter the figs. The Sycoecinae can be defined by the loss of the medial felt line on the ventral side of the head, probably as a result of the requirement for as smooth a surface as possible to facilitate entry through the ostiole. The foramen magnum is surrounded by, or is situated in, a slight to a very pronounced depression. This enables sycoecines to move their heads into a truly horizontal, prognathous position, streamlining the head and the body. The thickening of the fore femur and shortening of the fore tibia, the development of a row or a plate of teeth either on the mandibles or on the fore tibia (sometimes together with the modification of the fore tibial spur into a plate of teeth) and the dorso-ventral flattening of the head all separate the Sycoecinae from the Sycoryctini. At the same time many of these characters are homoplastic apomorphies that have convergently evolved in one or more of a number of other agaonid groups that also enter figs for oviposition. These include the Agaoninae; *Sycophaga* Westwood (Sycophaginae); *Grasseiana* Abdurahiman & Joseph and *Lipothymus* Grandi, (both Otitesellinae). However, the development of teeth on the mandible and the fore tibia are only broadly homoplastic in the sense of convergence, as their detailed morphology shows these structures to be nonhomologous across the groups. The specific type of teeth development in the Sycoecinae is therefore unique. Although, adaptations of the mandibles or tibiae are not consistent within the Sycoecinae and can therefore not be used as synapomorphies.

The sycoecine oral fossa is as broad as the head and can be used as an synapomorphy to distinquish the group from the Sycoryctini, where the oral fossa is rather narrow. This is probably an adaptation to accommodate the more powerful mandibles which have evolved to facilitate entry into the fig. It follows that the wide oral fossa would be expected to have evolved more than once among groups which enter the fig to oviposit. This is corroborated by *Grasseiana*, *Lipothymus*, *Sycophaga* and the Agaoninae.

Generally the wing venation of the Sycoecinae is distinctive, but as the venation is not consistent within the group it again cannot be used as a synapomorphy. The marginal vein is thickened in relation to the other veins, except in some *Crossogaster* species and in *Robertsia*, where the marginal vein is no thicker than the rest. The postmarginal vein is more or less subequal in length to the stigmal vein, but varies from distinctly longer to shorter than the stigmal. Despite the variation in the marginal vein thickness and postmarginal vein length, these two characters in combination can be used for the practical separation of the Sycoecinae from the Sycoryctinae, even though they do not represent synapomorphic characters for the Sycoecinae. Thus if in the Sycoecinae the marginal vein is not distinctly thickened then the postmarginal vein is always shorter than the stigmal vein. In the Sycoryctini the postmarginal vein is usually much longer than the stigmal vein and the marginal vein is never thickened.

The structure of the ovipositor can also be used for the practical separation of the Sycoecinae from the Sycoryctini. The condition in the sycoecines is probably plesiomorphic as none of the terminal gasteral segments are involved in the formation of the ovipositor sheath.

Sycoecine diversity

Sixty-seven sycoecine species in six genera are recognised. Together with their host *Ficus* and pollinating agaonine wasp associates they are listed in Table 5.1.

KEY TO THE SYCOECINE GENERA

FEMALES

1\. Tarsi four - segmented (fig. 5.1 c); laminar projection present on the proximal fore tarsal segment (fig. 5.1 c); clypeal sutures meet before the toruli (fig. 5.1 a) (south-east Asia) .... ***Diaziella***

\- Tarsi five - segmented; laminar projection absent; if the clypeal sutures are present then they are separate, or if they meet before the toruli then the clypeal margin is narrow (less than a third of the head width) 2

2\. No antennal scrobe; medial carina present between the toruli; clypeal sutures not defined (fig. 5.1 b) (Australasia) .... ***Robertsia***

\- Antennal scrobe present; no carina between the toruli; clypeal sutures present (Africa) 3

3\. Fore tibial spur expanded, plate-like, with many small teeth (fig. 5.1 d); propleura excavated (fig. 5.1 g); first funicle segment expanded antiaxially (fig. 5.1 e); 2 labial and 4 maxillary palp segments .... ***Sycoecus***

\- Fore tibial spur normal; propleura not excavated; first funicle segment not expanded; two or three maxillary palp segments 4

4\. Propodeal spiracles medially situated (fig. 5.2 a); propodeal plicae (sometimes weak) extend from the spiracles to the posterior propodeal margin (fig. 5.2 a) ...... ***Seres***

\- Propodeal spiracles anteriorly situated (fig. 5.2 b); propodeal plicae absent 5

5\. 8th urotergite spiracular peritremata expanded (fig. 5.1 i); marginal vein thin (more than 8X longer than wide); 1 labial, 2 maxillary palp segments; ventral tentorial pits usually distinctly and widely separated (fig. 5.1 f), or if in close apposition, then the toruli are situated more than their length below an imaginary line joining the base of the eyes and the head is elongate (more than 1.5X longer than wide) .... ***Crossogaster***

- 8th urotergite spiracular peritremata not expanded (fig. 5.1 h); marginal vein thickened (less than 8X longer than wide); 2 labial and 3 maxillary palp segments; ventral tentorial pits indistinquishable as separate, or in very close apposition; toruli usually situated between or in line with the base of the eyes, if below then a plate of teeth is present on the fore tibia and the head is less than 1.25X longer than wide .... ***Philocaenus***

MALES

1. Tarsi four - segmented (south-east Asia) .... ***Diaziella***
- Tarsi five - segmented 2

2. Apterous (Australasia) .... ***Robertsia***
- Fully winged (Africa) 3

3. Propodeal spiracles medially situated with a plica (which may be indistinct) present from the spiracle to the posterior propodeal margin .... ***Seres***
- Propodeal spiracles anteriorly situated 4

4. Two apical mandibular teeth and a single ventral tooth, mandible short and squat (fig. 5.2 c), head always testaceous; vertex produced medially between the lateral ocelli (fig. 5.2 d) .... ***Sycoecus***
- Mandible more elongate with two apical teeth and no ventral tooth, or if the ventral tooth is present then the head is metallic green; vertex evenly rounded 5

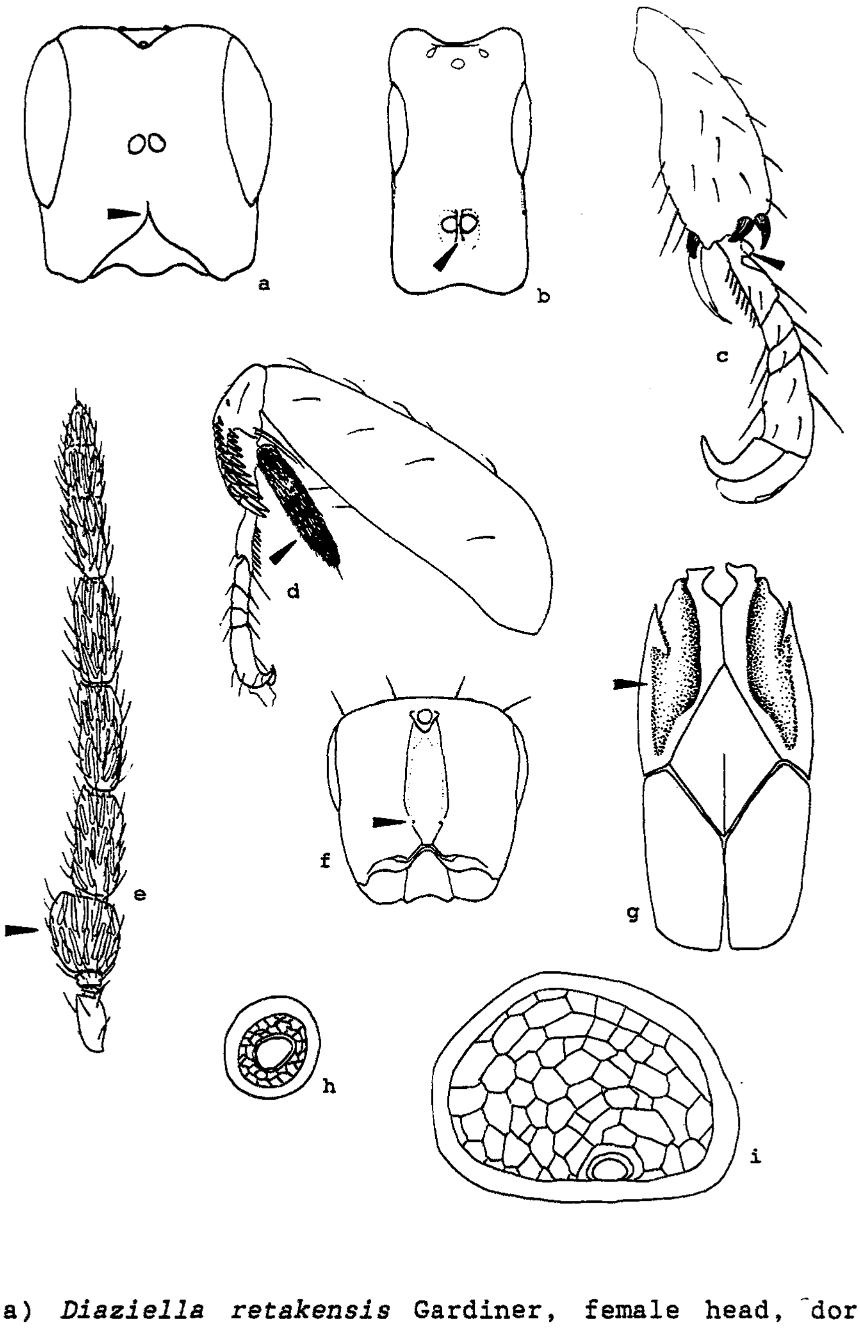


Fig. 5.1 a) *Diaziella retakensis* Gardiner, female head, dorsal view b) *Robertsia mandibularis* Boucek, female head, dorsal view c) *Diaziella wiebesi* Gardiner, female fore tibia and tarsus, antiaxial view d) *Sycoecus bergi* sp. nov., female fore coxa, tibia and tarsus, antiaxial view e) *Sycoecus crinitus* sp. nov., female antenna, dorsal view f) *Crossogaster stigma* sp. nov., female head, ventral view g) *Sycoecus wiebesi* sp. nov., female propleura, prosternum and fore coxae, ventral view h) *Philocaenus rotundus* sp. nov., female eighth urotergite spiracle i) *Crossogaster lurida* sp. nov., female eighth urotergite spiracle with expanded peritreme.

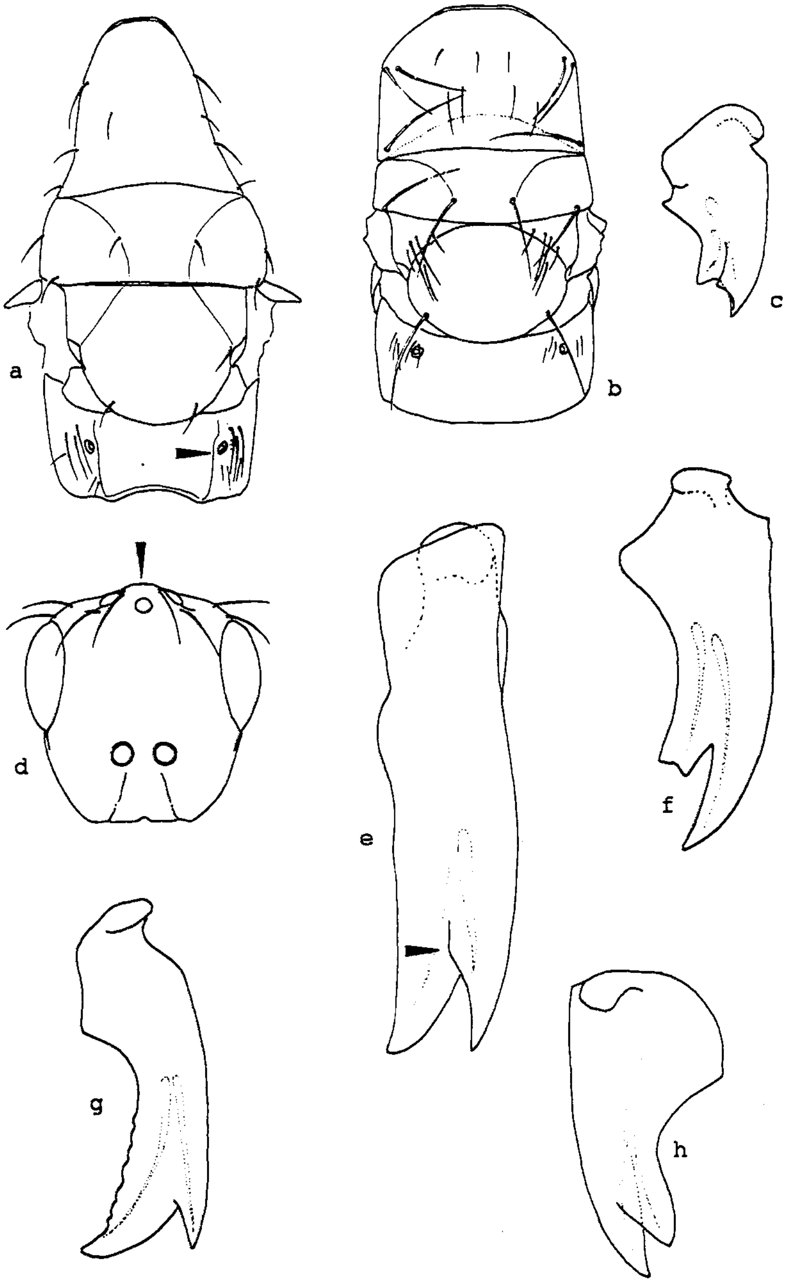


Fig. 5.2 a) *Seres armipes breviceps* Wiebes, female thorax, dorsal view b) *Crossogaster rastellus* sp. nov., female thorax, dorsal view c) *Sycoecus bergi* sp. nov., female mandible, ventral view d) *Sycoecus bergi* sp. nov., male head, dorsal view e) *Crossogaster michaloudi* sp. nov., male mandible, ventral view f) *Philocaenus comorensis* sp. nov., male mandible, ventral view g) *Crossogaster lurida* sp. nov., male mandible, dorsal view h) *Philocaenus comptoni* sp. nov., male mandible, dorsal view.

5. Inner mandibular apical tooth usually distinctly longer than the outer (fig. 5.2 g), or if only marginally longer then a small ventral tooth is present (fig. 5.2 e) and the toruli are separated by at least three-quarters of a torulus width .... ***Crossogaster***

- Outer mandibular apical tooth usually distinctly longer than the inner (fig. 5.2 f), or if only marginally longer then no ventral tooth is present (fig. 5.2 h) and the toruli are separated by less than a quarter of a torulus width .... ***Philocaenus***

EXTRA-AFRICAN SPECIES NOT REVISED IN THIS STUDY

Robertsia Boucek

Robertsia Boucek 1988, 178.
Type species: *Robertsia mandibularis* Boucek 1988.

R. mandibularis Boucek 1988, 179, figs. 277-280, ♀, ♂, New Guinea, ex *F. xylosycia* (Diels).
R. xylosyciae Boucek 1988, 179, figs. 281-282, ♀, ♂, New Guinea, ex *F. xylosycia* (Diels).

Key to *Robertsia* species:

FEMALES AND MALES

1. Mandible sickle-shaped without inner teeth; six teeth on the fore tibial apical margin, (♀ winged, ♂ apterous), ex *F. xylosycia* .... *R. mandibularis*

- Mandible broad, with a subapical inner tooth; four teeth on the fore tibial apical margin, (♀ winged, ♂ apterous), ex *F. xylosycia* .... *R. xylosyciae*

Diaziella Grandi

Diaziella Grandi 1928, 80-81.

Type species: *Diaziella bicolor* Grandi (designated by Grandi, 1935).

Wiebes 1974, 295-300 (revision, key to four species).

Gardiner & Compton 1987, 129-140 (key to females of all known species).

Boucek 1988, 177-178.

Catalogue of *Diaziella* species:

D. alleni Gardiner 1987, 139, figs. 53-60, ♀ Borneo, at light.

D. bicolor Grandi 1928, 81-86, figs. v-vi, ♀ Sumatra, at light. Boucek (1988), figs. 275-276.

D. falcata Wiebes 1974, 296-298, figs. 7-19, 29, ♀ ♂, Luzon, ex. *Ficus* probably *glaberrima* Bl. var. *bracteata* Corner.

D. laticeps Gardiner 1987, 137, figs. 43-44, ♀ Borneo.

D. latipennis Gardiner 1987, 137, 139, figs. 45-52, ♀ Borneo.

D. longiceps Gardiner 1987, 135-137, figs. 35-42, ♀ Borneo.

D. macroptera Grandi 1928, 86-89, figs. vii-viii, ♀ Sumatra. Wiebes, 1974, 296, ♀ Java.

D. pallidiceps Gardiner 1987, 133, figs. 12-18, ♀ Borneo.

D. philippinensis Wiebes 1974, 299-300, figs. 20-27, ♀ Mindanao and Palawan.

D. retakensis Gardiner 1987, 133, 135, figs. 19-26, ♀ Borneo.

D. tumidigena Gardiner 1987, 135, figs. 27-34, ♀ Borneo.

D. wiebesi Gardiner 1987, 139-140, figs. 61-68, ♀ Borneo.

The four African sycoecine genera - *Sycoecus*, *Seres*, *Crossogaster* and *Philocaenus* are dealt with individually in the following four chapters.

TABLE 5.1. Check list of the Sycoecinae with the host *Ficus* and pollinator (Agaoninae) associations.

SYCOECINAE	**HOST *FICUS***	**ASSOCIATED AGAONINAE**
Sycoecus		***Agaon***
1. *S. oculabulbus* sp. nov.	*F. c. pringsheimiana* (Braum & Schum.)	*A. kiellandi* Wiebes
2. *S. taylori* sp. nov.	*Ficus* sp.	
3. *S. ivoryensis* sp. nov.	*F. scott-elliotii* Mildbr. & Burr.	*Agaon* spec.
4. *S. lamtoensis* sp. nov.	*F. sagittifolia* Berg	*A. c. cicatriferens* Wiebes
5. *S. crinitus* sp. nov.	*F. lyrata* Warb.	*A. spatulatum* Wiebes
6. *S. wiebesi* sp. nov.	*F. cyathistipuloides* De Wild.	*A. obtusum* Wiebes
	F. subsagittifolia Berg	*A. c. multum* Wiebes
7. *S. medleri* sp. nov.	*F. "winkleri"*	*A. baliolum* Wiebes
8. *S. bergi* sp. nov.	*F. tesselata* Warb.	*A. taïense* Wiebes
9. *S. thaumastocnema* Waterston	*F. c. cyathistipula* Warb.	*A. fasciatum* Waterston
10. *S. nyassossoensis* sp. nov.	*Ficus* sp.	*Agaon* sp.
Seres		***Courtella***
11. *S. wardi* sp. nov.	*F. bubu* Warb.	*C. michaloudi* (Wiebes)
12. *S. longicalcar* sp. nov.	*F. artocarpoides* Warb.	*C. penicula* (Wiebes)
13. *S. a. armipes* Waterston	*F. ovata* Vahl	*C. h. hamifera* Kieffer
S. a. breviceps Wiebes	*F. ovata* Vahl	*C. h. modesta* (Wiebes)
14. *S. solweziensis* sp. nov.	*F. p. polita* Vahl	*C. b. bispinosa* (Wiebes)

	F. ovata Vahl	*C. h. modesta* (Wiebes)
	F. s. sansibarica Warb.	*C. armata* (Wiebes)
15. *S. l. longivena* sp. nov.	*F. s. sansibarica* Warb.	*C. armata* (Wiebes)
S. l. bidens sp. nov.	*F. s. macrosperma* (Mildbr. & Burr.)	*C. armata* (Wiebes)
Diaziella		***Waterstoniella***
16. *D. alleni* Gardiner	Host unknown	
17. *D. bicolor* Grandi	Host unknown	
18. *D. falcata* Wiebes	*F. glaberrima* Bl. var. *bracteata* Corner	*W. williamsi* Wiebes
19. *D. laticeps* Gardiner	Host unknown	
20. *D. latipennis* Gardiner	Host unknown	
21. *D. longiceps* Gardiner	Host unknown	
22. *D. macroptera* Grandi	Host unknown	
23. *D. pallidiceps* Gardiner	Host unknown	
24. *D. philippinensis* Wiebes	Host unknown	
25. *D. retakensis* Gardiner	Host unknown	
26. *D. tumidigena* Gardiner	Host unknown	
27. *D. wiebesi* Gardiner	Host unknown	
Robertsia		***Pleistodontes***
28. *R. mandibularis* Boucek	*F. xylosycia* Diels	*P. rieki* Wiebes
29. *R. xylosyciae* Boucek	*F. xylosycia* Diels	*P. rieki* Wiebes

Crossogaster		***Courtella*, *Elisabethiella*, *Alfonsiella***
30. *C. lachaisei* sp. nov.	*F. s. macrosperma* (Mildbr. & Burr.) Berg	*C. armata* (Wiebes)
31. *C. michaloudi* sp. nov.	*F. artocarpoides* Warb.	*C. penicula* (Wiebes) and *C. hladikae* (Wiebes)
32. *C. inusitata* sp. nov.	*F. s. sansibarica* Warb.	*C. armata* (Wiebes)
33. *C. rashbrooki* sp. nov.	*Ficus* sp.	-
34. *C. ovata* sp. nov.	*F. ovata* Vahl	*C. h. modesta* (Wiebes)
35. *C. triformis* Mayr	*F. vasta* Forssk	*E. socotrensis* Mayr
36. *C. vansomereni* sp. nov.	*Ficus* sp.	*E. stuckenbergi* Grandi
37. *C. hilli* sp. nov.	*F. "natalensis"*	*A. natalensis* Wiebes and *E. allotriozoonoides* (Grandi)
38. *C. r. robertsoni* sp. nov.	*F. trichopoda* Baker	*E. b. breviceps* Wiebes
C. r. rasplusi ssp. nov.	*F. trichopoda* Baker	*E. b. bergi* Wiebes
39. *C. rastellus* sp. nov.	*F. "natalensis"*	*A. natalensis* Wiebes and *E. allotriozoonoides* (Grandi)
40. *C. praeacuta* sp. nov.	*Ficus* sp. "K"	*E. hilli* Wiebes
41. *C. odorans* Wiebes	*F. thonningii* Bl.	*E. stuckenbergi* Grandi
	F. thonningii Bl.	*A. brongersmai* Wiebes
	F. stuhlmannii Warb.	*A. binghami* Wiebes
	F. "dekdeknena"	*A. fimbriata* Waterston
42. *C. quadrata* sp. nov.	*F. glumosa* Delile	*E. glumosae* Wiebes
43. *C. stigma* sp. nov.	*F. glumosa* Delile	*E. glumosae* Wiebes

44. *C. oculagrandis* sp. nov.	Host unknown	-
45. *C. lurida* sp. nov.	*F. n. natalensis* Hochst.	*A. longiscapa* Joseph
Philocaenus		***Allotriozoon***
46. *P. silvestrii* (Grandi)	*F. lutea* Vahl	*A. prodigiosum* Grandi
47. *P. comptoni* sp. nov.	*F. chlamydocarpa* Mildbr. & Burr.	*A. nigeriense* Wiebes
48. *P. cavus* sp. nov.	*F. saussureana* D.C.	*A. heterandromorphum* Grandi
		Elisabethiella, Alfonsiella, Courtella
49. *P. bouceki* Wiebes	*F. reflexa* Thunb.	*E. reflexa* Wiebes
50. *P. comorensis* sp. nov.	*F. antandronarum bernardii* (Perrier) Berg	*Elisabethiella* sp.
51. *P. barbarus* Grandi	*F. thonningii* Bl.	*E. stuckenbergi* Grandi
	F. thonningii Bl.	*A. brongersmai* Wiebes
	F. n. natalensis Hochst.	*E. socotrensis* (Mayr)
	F. stuhlmannii Warb.	*A. binghami* Wiebes
	F. "dekdeknena"	*A. fimbriata* Waterston
52. *P. geminus* sp. nov.	*F. "natalensis"*	*A. natalensis* Wiebes and
		E. allotriozoonoides (Grandi)
53. *P. jinjaensis* sp. nov.	*Ficus* sp. "K"	*E. hilli* Wiebes
54. *P. insolitus* sp. nov.	*F. craterostoma* Mildbr. & Burr.	*A. michaloudi* Wiebes
55. *P. medius* sp. nov.	*F. n. natalensis* Hochst.	*A. longiscapa* Joseph
	F. thonningii Bl.	*A. brongersmai* Wiebes
56. *P. ugandensis* sp. nov.	*F. "natalensis"*	*A. natalensis* Wiebes and

		E. allotriozoonoides (Grandi)
	F. "dekdeknena"	*A. fimbriata* Waterston
57. *P. barbatus* Grandi	*F. platyphylla* Delile	*Elisabethiella* near *pectinata*
58. *P. hippopotomus* sp. nov.	*F. trichopoda* Baker	*E. b. bergi* Wiebes
	F. trichopoda Baker	*E. b. breviceps* Wiebes
59. *P. bakeri* sp. nov.	*Ficus* sp.	*Courtella* sp.
60. *P. bifurcus* sp. nov.	*F. o. ulugarensis* (Mildbr. & Burr.)	*C. camerunensis* (Wiebes)
61. *P. levis* (Waterston)	*F. o. lucanda* (Ficalho) Berg	*C. scobinifera* (Waterston)
62. *P. clairae* sp. nov.	*F. t. tremula* Warb.	*C. wardi* Compton
63. *P. warei* sp. nov.	*F. glumosa* Delile	*E. glumosae* Wiebes
64. *P. liodontus* Wiebes	*F. n. leprieurii* (Miq.) Berg	*A. fimbriata* Waterston
	F. craterostoma Mildbr. & Burr.	*A. michaloudi* Wiebes
	F. l. lingua Wild. & Dur.	*A. michaloudi* Wiebes
	F. burtt-davyi Hutch.	*E. baijnathi* Wiebes
	F. thonningii Bl.	*A. brongersmai* Wiebes
	F. kamerunensis Mildbr. & Burr.	*A. fimbriata* Waterston
65. *P. quatuordentatus* sp. nov.	*F. craterostoma* Mildbr. & Burr.	*A. michaloudi*
66. *P. zambesiacus* sp. nov.	*F. bussei* Mildbr. & Burr.	*Elisabethiella* sp.
67. *P. rotundus* sp. nov.	*F. abutilifolia* (Miq.) Miq.	*E. comptoni* Wiebes

6

SYSTEMATICS OF *SYCOECUS*

INTRODUCTION

Sycoecus Waterston is the only African sycoecine genus to maintain its original delimitations in the current treatment and is probably the most distinctive genus found in the continent. Ten species are now known in this genus, nine of which are described here for the first time. The species are all associated with the *Ficus* subsection *Cyathistipulae* of section *Galoglychia*. As a result, *Sycoecus* is one of the two African sycoecine genera to be restricted to a single *Ficus* subsection and to be associated with a single agaonine genus, which in the case of *Sycoecus* is *Agaon* Dalman.

GENERIC DEFINITION

Sycoecus Waterston

Sycoecus Waterston 1914, 253. Type species: ***Sycoecus thaumastocnema*** Waterston 1914, by original designation.

FEMALE. Head elongate, dorso-ventrally flattened; smooth, no sculpture; clypeus narrow, produced at the epistomal margin, with a medial concavity of varying depth; toruli in close apposition; malar sulcus present, posteriorly as a fovea, but fading out or very indistinct towards the oral fossa. Compound eyes situated posteriorly on face, in proximation with the vertex. Vertex excavated laterally, excavation extending through the temples to the posterior eye margin. Lateral ocelli usually situated on the inside of the axial lip, and thus hidden or partially hidden from dorsal view, except in some species where the excavation is weak. Medially the vertex has a raised prominence between the lateral ocelli, on the posterior edge of which runs the occipital carina.

This carina encircles the top half of the foramen magnum, which is situated posteriorly in proximation with the vertex, such that the occiput is absent. Strong setae are present on the vertex. Ventral tentorial pits separated, situated about half way between the oral fossa and the foramen magnum. Hypostoma usually reduced, sometimes complete. Cardo reduced or absent, posterior portion of stipes overlaps hypostomal area. Four maxillary palp segments, proximal and third segments subequal, second slightly shorter and apical segment ca. twice as long as each of the first three; two labial palp segments, basal segment half to two-thirds as long as the distal. Mandible with two apical teeth, two or three ventral teeth, proximally the ventral edge is a sharp ridge; blunt lobe in molar region for muscle attachment; two glands, inner reduced and small. Dorsal tentorial pits situated on clypeal sutures, closer to the epistomal margin than to the toruli. Antenna eleven segmented, formula 1124(3), pedicel short, first anellus reduced in comparison to the second; first funicle segment expanded on the inner margin, lateral margins convex, about as long as wide, remaining funicle segments longer than wide; first three funicle segments dorso-ventrally flattened, fourth funicle segment subcylindrical, club segments cylindrical, tapering towards the apex. Multiporous plate sensilla (MPS) placoid, thin and elongate, present in alternating rows, absent or reduced on the ventral surface.

Thorax dorso-ventrally compressed; smooth, without sculpture; pronotum elongate, compressed laterally, with a carina on the dorso-anterior margin, two slight lateral depressions present for almost the length of the pronotum (inner margin of which is visible as a carina in slide mounts); the sides of the pronotum below the lateral depressions with broad concave excavations; mesonotum subtriangular, parapsidal sulci complete, straight; propodeal sulci well defined with a pronounced ridge defining the axial edge, spiracles anteriorly situated in the sulci. A few strong setae present. Propleura with pronounced excavations. General form of legs typical for sycoecines; fore femur stout, elongate, subcylindrical; adaxial face of fore tibia with two rows of stout teeth, inner row with fewer, stronger teeth. Fore tibial spur highly modified and expanded to form a plate of many teeth or spines on the antiaxial surface, axial surface smooth, articulation of spur more proximally situated on tibia than normal for the subfamily. Ventral tooth situated next to the spur insertion absent. Hind coxa usually with a medial posterior plica on axial face. Axial third of forewing glabrous, rest covered in microsetae; fringe present. Marginal vein thickened; postmarginal vein subequal to longer than the stigmal vein.

Gaster with five to seven evenly spaced slit-like incisions on the posterior edge of the tergites, otherwise edge smooth. Eighth urotergite spiracle normal, dorso-laterally situated, with a setal patch of variable density posteriorad. Ovipositor valves variable in length.

MALE. Head slightly elongate, narrowing anteriorly in dorsal view, not very compressed in lateral view, height about two-fifths of length; clypeus subtriangular in area, epistomal margin broader than in the females. Toruli always separated, situated below the eyes, closer to the epistomal margin than to the vertex. Antennal formula 1124(3), second anellus almost 3X the length of the first, and half the length of the funicle segments. MPS usually present as a single row, sometimes as two rows. Dorsal tentorial pits present on the lateral clypeal sutures closer to the epistomal margin than to the toruli. Malar sulcus present for the first quarter to two-thirds of the cheek length. Lateral ocelli usually situated in axial end of a shallow excavation on the vertex. Medial prominence present on the vertex between the lateral ocelli, with the occipital carina situated along the posterior edge, dorsal to the foramen magnum. Carina approximately straight. Eight to ten strong setae present on the vertex. Ventral tentorial pits separated, situated ca. half way between the foramen magnum and the oral fossa. Hypostoma present, hidden by stipes medially. Four maxillary palp segments, two labial palp segments, ratios much as in the females. Mandible with a single ventral tooth, short apical tooth and a shorter dorsal subapical tooth, two glands, subapical gland smaller.

Thorax. Pronotum subquadrate; mesonotum subtriangular, parapsidal sulci straight or slightly curved anteriorly. Axillae larger than in the females. Propodeal sulci present in varying degrees, spiracles anteriorly situated. Strong setae present on the thorax, positions much as in the females. No excavations on the propleura. Two strong dorso-apical teeth on the fore tibia, dorsal tooth twice as large; spur slightly modified and expanded, more proximally situated on the tibia as in the females; no ventral tooth. Wings pilose, axial third of fore wings bare, axial fifth to quarter of hindwings bare, rest of wings covered with microsetae, medial and anal setal tracts present, fringe present. Marginal vein thickened.

Gaster, posterior edge of tergites uniformally straight, with small setae along the edge. Aedeagus large.

Comments. *Sycoecus* is the most plesiomorphic genus of sycoecines with sexual dimorphism the least pronounced of any of the genera. Nonetheless the monophyly of this genus is strongly supported by a number of autapomorphies in the females. These include the fore tibial spur modified into a plate of many fine teeth; the axial expansion of the first funicle segment; excavation of the propleura and lateral depressions present on the pronotum. *Sycoecus* can also at once be distinguished by the plesiomorphic features of four maxillary palp segments in combination with two labial palp segments and by the pronounced propodeal plicae with the propodeal spiracles anteriorly situated in the sulci.

Most of the above autapomorphies have evolved as adaptations to facilitate ostiolar entrance by the female. The lateral depressions on the pronotum appear to have evolved to accommodate the flagellum, so as to prevent damage to the antennae and the MPS when they are folded back on entering the ostiole, much as the antennal scrobe protects the scape and pedicel or even the flagellum in genera where this is short. The *Sycoecus* flagellum is the longest amongst the sycoecine genera and this may explain why these pronotal depressions are not present in any of the other genera. The dorso-ventral flattening of the flagellum in combination with a lack of MPS on the ventral surface (which becomes the exposed dorsal surface when the antennae are folded back), must also facilitate the preservation of the antennae while the wasp is entering the ostiole. This either indicates that the antennae and MPS are necessary for the oviposition process or that *Sycoecus* also leaves a fig after oviposition and enters further figs, as do some of the *Philocaenus* species. If this were the case, the preservation of the antennae might be essential for the olfactory location of other figs that were ready for pollination.

The propleural excavations appear to be adaptations to accommodate the fore tibia and tarsi (the fore femur would still be pressed tightly against the side of the pronotum as in the other sycoecine genera) with the tibial plate closing off the excavation, such that only the tibial teeth and teeth on the tibial plate project from the flush surface. This presumably facilitates the streamlining required for ostiolar penetration.

KEY TO THE SPECIES OF *SYCOECUS*:

FEMALES

1. Tibial plate distinctly (more than 1.3X) longer than total fore tibial length (figs. 6.4 e & d; 6.7 b); epistomal margin indentation no deeper than the projection of the margin (figs. 6.3 a; 6.5 a; 6.6 a & g) 2

- Tibial plate subequal (less than 1.13X as long) to fore tibial length (figs. 6.2 c & d; 6.3 f); epistomal margin indentation deeper than the projection of the margin (figs. 6.3 c; 6.1 a, b & f) 7

2. Mandible with two ventral teeth (figs. 6.1 d; 6.2 a; 6.4 a & c; 6.5 e) 3
- Mandible with three ventral teeth (figs. 6.3 e; 6.6 e) . 6

3. Tibial plate more than twice as long as total fore tibial length 4
- Tibial plate less than twice as long as fore tibia 5

4. Cheek 1.6X longer than eye length (fig. 6.4 c); tibial plate 2.6X longer than fore tibia, ex *F. lyrata* .... *S. crinitus*
- Cheek at least twice as long as eye (fig. 6.7 a); tibial plate 2.35X longer than fore tibia, ex *F. cyathistipuloides* and *F. subsagittifolia* .... *S. wiebesi*

5. Tibial plate 1.3X as long as fore tibia; cheek 1.2X as long as eye, ex *F. sagittifolia* .... *S. lamtoensis*
- Tibial plate 1.8X as long as fore tibia; cheek 1.6X as long as eye, ex *F. scott-elliotii* .... *S. ivoryensis*

6. Epistomal margin indentation shallower than its width (fig. 6.6 g); cheek 1.76X longer than eye, ex *Ficus* sp. .... *S. nyassossoensis*
- Epistomal margin indentation deeper than its width, cheek 1.12X longer than eye, ex *F. c. cyathistipula* .... *S. thaumastocnema*

7. Mandible with three ventral teeth; cheek length 1.34X longer than eye length, ex *F. tesselata* .... *S. bergi*
- Mandible with two ventral teeth; cheek length either 1.46X, subequal or shorter than eye length 8

8. Cheek length 1.46X longer than eye, ex *Ficus* sp. .... *S. medleri*
- Cheek length shorter or subequal to eye length 9

9. Cheek length shorter than eye length (fig 6.2 a); indentation in epistomal margin as broad as the width of both toruli (fig. 6.1a), ex *F. cyathistipula pringsheimiana* .... *S. oculabulbus*
   - Cheek subequal to eye length; indentation narrower, width equivalent to the width of one torulus (fig. 6.1 f), ex *Ficus* sp. .... *S. taylori*

MALES*

1. Bilobed epistomal margin, with the medial concavity equivalent in size to each lateral convexity (fig. 6.1 c); vertex, mesoscutum and gaster dark brown, rest testaceous, ex *F. c. pringsheimiana* .... *S. oculabulbus*
   - Epistomal margin almost straight, with a medial concavity absent or minute; completely testaceous 2

2. Epistomal margin almost straight with no medial concavity (fig. 6.6 b), ex *F. cyathistipuloides* .... *S. wiebesi*
   - Epistomal margin with a medial concavity which may be very broad and shallow (fig. 6.3 b & d; 6.5 f) 3

3. Epistomal margin convex with a broad and very shallow medial concavity (fig. 6.5 f); toruli separated by a third of torulus width (fig. 6.5 f), ex *S. lyrata* ... *S. crinitus*
   - Distinct, small, medial concavity, ca. as deep as wide (figs. 6.3 b & d); toruli separated by more than half the width of a torulus 4

4. Head 1.16X longer than wide, eye length 1.2X longer than the cheek; toruli separated by less than the width of a torulus, ex *Ficus* sp. .... *S. nyassossoensis*
   - Head less than 1.09X longer than wide, eye more than 1.3X longer than the cheek; toruli separated by the width of a torulus 5

5. Eye length 1.47X longer than the cheek, ex *F. c. cyathistipula* .... *S. thaumastocnema*
   - Eye length 1.31X longer than the cheek 6

6. SL 2.4X longer than TE; head slightly elongate L:W = 1.08 (fig. 6.3 b), ex *F. sagittifolia* .... *S. lamtoensis*
   - SL 2.7X longer than TE; head ca. square L:W = 1.02 (fig. 6.3 d), ex *F. tesselata* .... *S. bergi*

* The males of *S. taylori*, *S. ivoryensis* and *S. medleri* are unknown.

SPECIES DESCRIPTIONS

Sycoecus oculabulbus sp. nov.

(figs. 6.1 a, c & e; 6.2 a-d)

Etymology: Ocula (latin) = eye, bulbus (latin) = bulb, referring to the large bulbous eyes.

Type material: Holotype ♀, allotype ♂, (slide mounted): Cameroun, SW Province, Bambili, 28 December 1981, leg. S.G. Compton & R.G.E. Baker, C1013, ex *F. cyathistipula pringsheimiana* (Braun & Schum.). Paratypes, 10 ♀, 3 ♂, (card mounted): same data as holotype.

FEMALE. Metallic black, legs (excluding hind coxae), and antennae testaceous. Total length with head in orthognathous position excluding ovipositor 2.7 mm.

Head (figs. 6.1 a & 6.2 a) elongate, parallel sided (l = 0.77, w = 0.54, h = 0.23), wedge shaped in lateral view, convex dorsally, flat ventrally. Eye elongate (l = 0.32, w = 0.18, h = 0.32), 0.41X as long as head. Cheek length 1.2X longer than eye. Malar sulcas present for most of cheek, fades out for last quarter, curves slightly dorsad. Lateral ocelli large, completely visible in dorsal view; lateral excavations on vertex very shallow; medial ocellus situated in posterior end of scrobe.

Occipital carina on the medial prominence broad and open, not extending in a tight U around the foramen magnum. Excavation around foramen magnum broad and shallow. POL = 0.14. OOL = 0.07. Toruli slightly separated, situated below the eyes; TE 0.7X as long as scrobe length (SL = 0.41). Clypeus trapezoid in area. Epistomal margin convex with medial indentation extending deeper than paraclypeal margins, three-tenths of head width. Hypostoma complete. Mandible with two ventral teeth close together, situated nearer the apex, proximally the ventral edge is a plain ridge (fig 6.2 a). Antennal flagellum (fig. 6.2 b) (l = 0.94) longer than head. Scape 6.8X longer than wide (l = 0.31). Pedicel a quarter of scape length. Multi-porous plate sensilla present as 3 to 4 alternating rows on funicle and first club segments, as two rows on penultimate and as one row on ultimate club segments (fig 6.2 b). MPS absent on ventral surface of first two funicle segments. Funicle segments subequal in length.

Thorax. Pronotum elongate (l = 0.43, w = 0.39), trapezoid. Propodeum l = 0.26, w = 0.43. Mesoscutum l = 0.36, w = 0.50. Scutellum, including axillae (l = 0.43, w = 0.42). Fore femur 4.2X longer than wide (l = 0.61), 1.5X longer than fore coxa (C = 0.40, TR = 0.13, TI = 0.22, TA = 0.35). Fore tibial plate same length as tibia, with few coarse teeth. Inner row of teeth on adaxial face of fore tibia with nine-eleven teeth, outer with six teeth (figs. 6.2 c-d). Hind coxal plica absent. Fore wing (l = 2.39, w = 1.04) very pilose, maximum fringe length = 0.08, anal and medial setal tracts present. Postmarginal vein longer than stigmal (SM = 0.79, M = 0.34, PM = 0.28, S = 0.25). Marginal vein 6.8X longer than wide. Hind wing 4X longer than wide (l = 1.68).

Gaster. Few setae present on hypopygium. Eighth urotergite spiracle l = 0.037. Ovipositor 6.3X longer than ovipositor valve, l = 0.20.

MALE. Testaceous, posterior half of head, flagella, eyes, mesoscutum, axilla and gaster dark brown. Total length with head in orthognathous position excluding ovipositor 2.34 mm.

Head (fig. 6.1 c) elongate (l = 0.59, w = 0.55), height normal (h = 0.25). Eye elongate (l = 0.27, w = 0.16), protrudes laterally (h = 0.10), 0.46X as long as the head. Cheek length 0.67X eye length. Malar sulcas present for first two-thirds of cheek. Lateral ocelli visible in dorsal view situated in very shallow depression. POL = 0.12, OOL = 0.08. Toruli separated by ca. half of torulus width, TE 0.50X as long as scrobe length, TE = 0.17, SL = 0.34. Width of clypeal margin 0.31X head width. Mandible (fig. 6.1 e). Antennal flagellum 5.6X pedicel length. Scape 4.5X longer than wide (l = 0.27). Pedicel 0.33X scape length. MPS present as two alternating rows with a total of 9, 9, 9 & 10 (starting at the proximal segment) sensilla on the funicle segments respectively and a single row of 7, 7 & 4 sensilla on the club segments respectively.

Thorax. Parapsidal sulci curved anteriorly. Propodeal plical furrows complete. Fore femur 3.8X longer than wide, l = 0.53. Fore tibia 1.5X longer than tarsus (C = 0.38, TR = 0.12, TI = 0.37, TA = 0.24). Fore wing 2.4X longer than wide, l = 2.25. Postmarginal vein same length as stigmal (SM = 0.73, M = 0.32, S = 0.26, PM = 0.26). Marginal vein 8X longer than wide. Hind wing 4.3X longer than wide, l = 1.56.

Gaster. Eighth urotergite spiracle small and round. Aedeagus large (l = 0.75). Four teeth on aedeagus claspers.

Comments. Most closely related to *S. taylori*, but *S. oculabulbus* has a longer cheek and a wider and broader medial indentation in the epistomal margin.

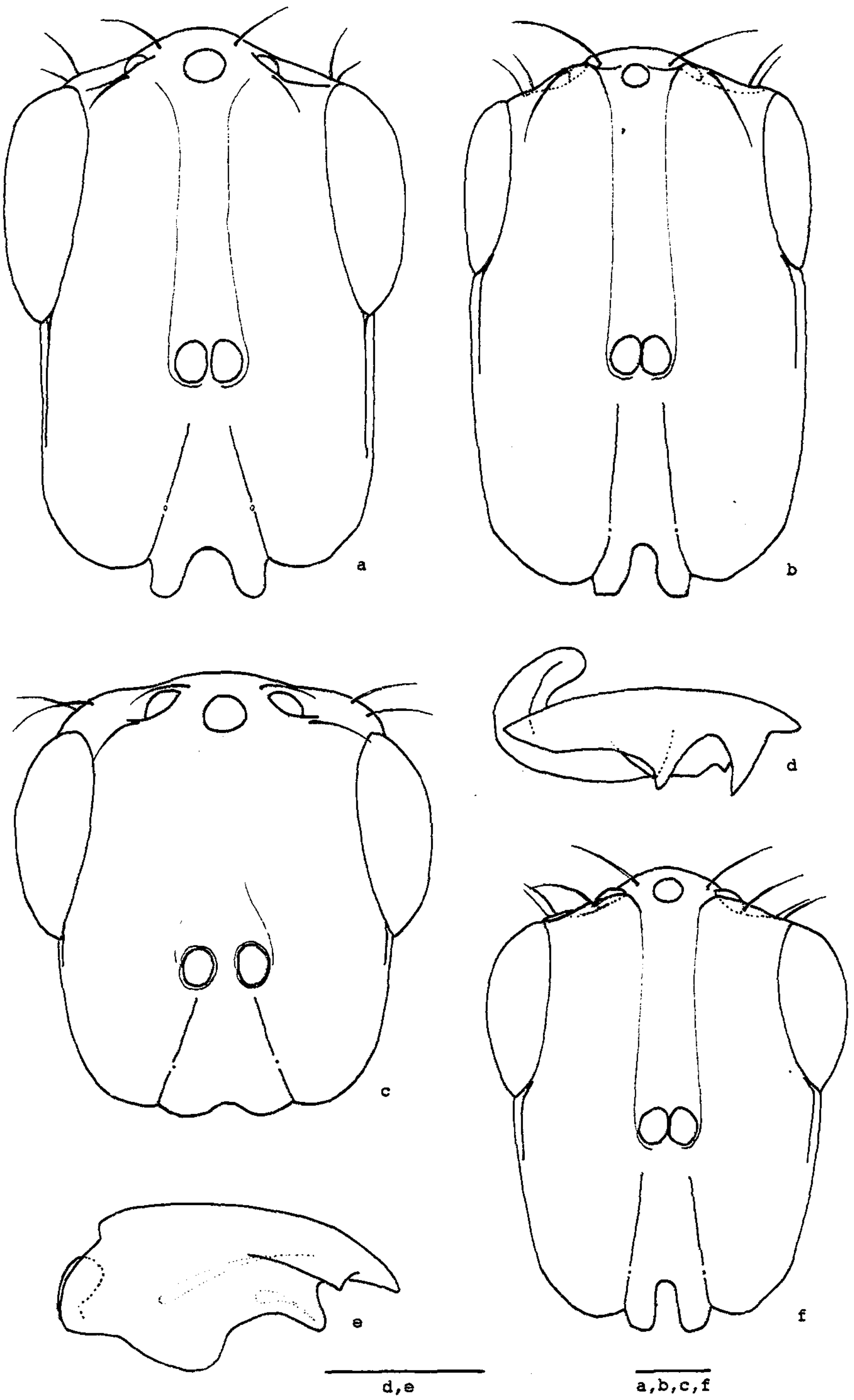


Fig. 6.1 a, c & e: *Sycoecus oculabulbus* sp. nov. a) female head, dorsal view c) male head, ventral view e) male mandible, ventral view; d-e: *Sycoecus medleri* sp. nov. b) female head, dorsal view; d) female mandible, ventral view; f: *Sycoecus taylori* sp. nov. f) female head, dorsal view. Scale bars = 0.1 mm.

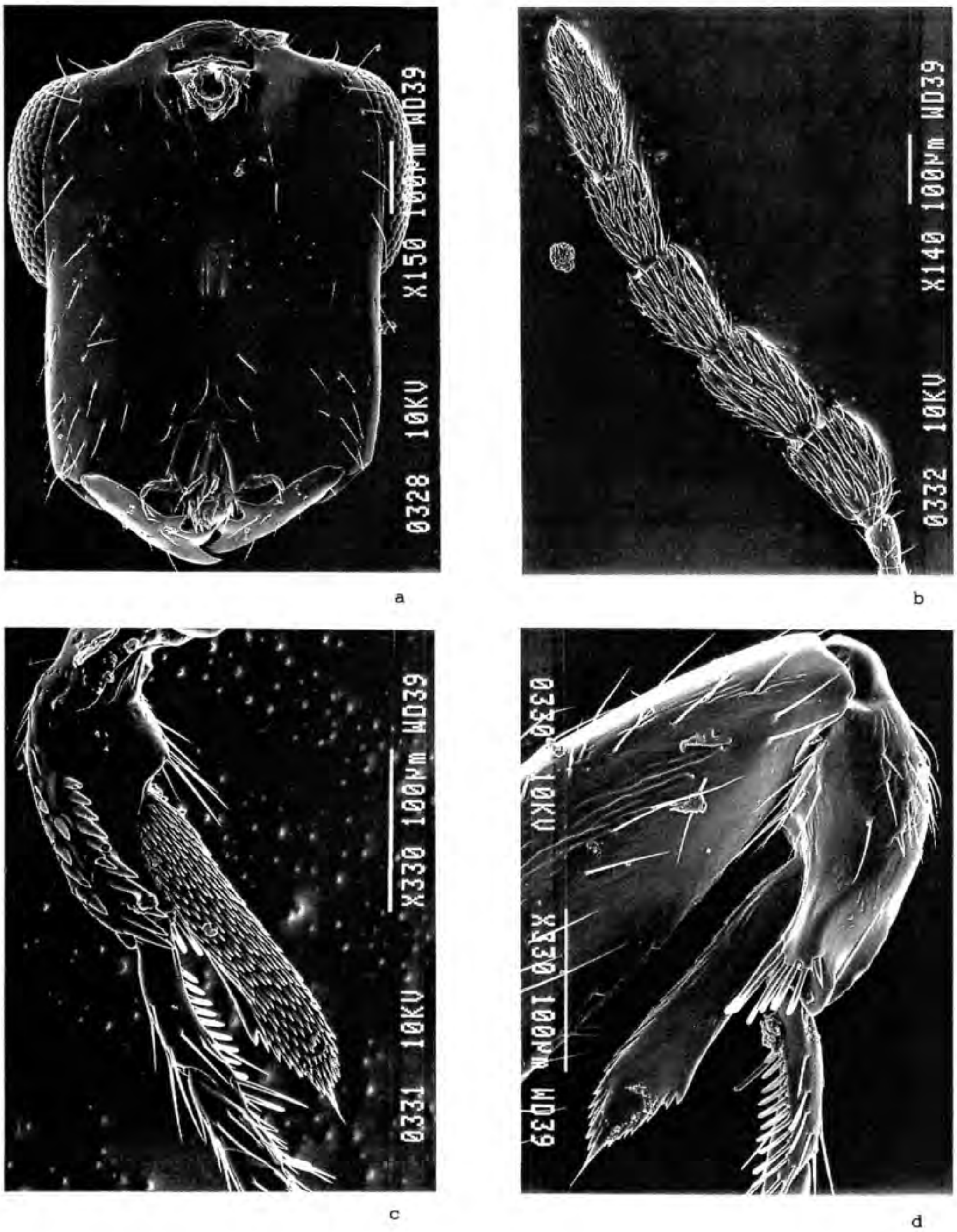


Fig. 6.2 a-d: *Sycoecus oculabulbus* sp. nov. a) female head, ventral view b) female antennae, dorsal view c) female fore tibia and first two tarsal segments, antiaxial view d) same as c), but axial view.

Sycoecus taylori **sp. nov.**

(fig. 6.1 f)

Etymology: Named after the collector.

Type material. Holotype ♀ (slide mounted): Uganda, 1939, leg. T.H.C. Taylor, T850. Paratypes, 4 ♀: same data as holotype.

FEMALE. Faded, due to alcohol storage, probably metallic black. Total length with head in orthognathous position excluding ovipositor 2.0 mm.

Head (fig. 6.1 f) elongate, parallel sided (l = 0.63, w = 0.49, h = 0.19), wedge shaped in lateral view, not as dorso-ventrally compressed as previous species, convex dorsally, flat ventrally. Eye oval (l = 0.24, w = 0.15, h = 0.08), 0.38X as long as head. Cheek l = 0.25 slightly longer than eye. Malar sulcas present for definitely the first half possibly the whole of the cheek length (difficult to determine due to poor preservation). Lateral ocelli visible in dorsal view, excavations on vertex very shallow, medial ocellus situated in posterior end of scrobe. Medial prominence on vertex with strong occipital carina, open as in *S. oculabulbus* but not as broad. POL = 0.12, OOL = 0.06. Toruli touching, situated below the eyes; TE 0.78X as long as scrobe length (TE = 0.25, SL = 0.32). Epistomal margin ca. a quarter of the head width, medial indentation deeper than paraclypeal margins. Mandible with two teeth on ventral edge closer to apex, proximal ventral edge plain ridge (much as in *S. oculabulbus*, fig. 6.2 a). Antennal flagellum (l = 0.60) subequal to head length. Scape 8X longer than wide (l = 0.24), 4X longer than pedicel. MPS present, as 2-3 alternating rows on funicle and first club segments, as a single row on remaining club segments. First funicle segment subequal in length to rest.

Thorax. Pronotum square (l = 0.30, w = 0.32), trapezoid.

Propodeum l = 0.20, w = 0.36. Mesoscutum l = 0.26, w = 0.43. Scutellum, including axillae l = 0.29, w = 0.36. Fore femur 3.8X longer than wide (l = 0.46), 1.6X longer than fore coxa (C = 0.29, TR = 0.09, TI = 0.16, TA = 0.24). Tibial plate (l = 0.18) subequal to fore tibia, with few coarse teeth. Fore tibia with eight-nine larger inner teeth and six smaller outer teeth (much as in *S. oculabulbus*, fig. 6.2 c). Fore wing (l = 1.67, w = 0.59), pilose. Postmarginal vein subequal to stigmal (SM = 0.50, M = 0.26, PM = 0.16, S = 0.17). Marginal vein 8.6X longer than wide.

Gaster. Hypopygial setae present. Eighth urotergite spiracle l = 0.024. Ovipositor 4.3X as long as valve (valve l = 0.24).

Comments. Most closely related to *S. oculabulbus*.

Sycoecus medleri sp. nov.

(figs. 6.1 b & d)

Etymology: Named after the collector.

Type material: Holotype ♀ (slide mounted): Nigeria, S.E. State, Obudu cattle range, 12 April 1973, leg. J.T. Medler, ex *F. "winkleri"*. 6 ♀ paratypes: same data as holotype.

FEMALE. Metallic black/brown, scape and pedicel testaceous. Total length with head in orthognathous position excluding ovipositor 2.8 mm.

Head (fig. 6.1 b) elongate (l = 0.74, w = 0.47, h = 0.19), wedge shaped in lateral view, dorso-ventrally compressed, convex dorsally, flat ventrally. Eye elongate (l = 0.24, w = 0.13, h = 0.064), 0.32X as long as the head. Cheek 1.5X longer than eye. Malar sulcas present for full length of cheek, but indistinct towards oral fossa. Lateral ocelli half visible in dorsal view, situated in lateral vertex excavations. Strong medial prominence on vertex. Occipital carina extends as a U around the foramen magnum, not as tight as *S. bergi*, excavation around foramen magnum also broader. POL = 0.12, OOL = 0.09. Toruli touching, situated below the eyes; TE 0.77X as long as scrobe length (TE = 0.30, SL = 0.39). Epistomal margin 0.28X as wide as head, medial concavity deeper than paraclypeal margins. Hypostoma very reduced, covered by stipes. Mandible with two widely spaced teeth on the ventral edge (fig. 6.1 d). Antennal flagellum (l = 0.67) shorter than head length. Scape 6.9X longer than wide (l = 0.28), 3.5X as long as pedicel. MPS present as 2-3 alternating rows on the funicle and first club segments, as a single row on last two club segments. MPS reduced on the ventral surface of funicle segments. First funicle segment three-quarters as long as the second and third segments, subequal in length to the fourth segment.

Thorax. Pronotum elongate (l = 0.45, w = 0.32). Propodeum l = 0.27, w = 0.44. Mesoscutum l = 0.30, w = 0.37. Scutellum, including axillae l = 0.35, w = 0.47. Fore femur 4X longer than wide (l = 0.60), 1.8X longer than fore coxa (C = 0.33, TR = 0.11, TI = 0.21, TA = 0.23). Tibial plate same length as fore tibia, with many fine teeth. Two rows of fore tibial teeth, inner with ca. 8 teeth, outer with 8-10 teeth (much as in *S. bergi*). Fore wing (l = 2.06, W = 0.79), very pilose, maximum fringe length 0.06, anal and medial setal tracts present. Postmarginal and stigmal subequal in length (SM = 0.69, M = 0.27, PM = 0.20, S = 0.21). Marginal vein 9X longer than wide. Hind wing (l = 1.40) 4X longer than wide.

Gaster. Hypopygial setae absent. Eighth urotergite spiracle l = 0.025. Ovipositor 5.5X as long as valve (valve l = 0.28).

Comments. *F. winkleri* Mildbr. & Burret has been synonymised with *F. tesselata* Warb. However, the wasp fauna including the pollinator (see Wiebes, 1989a) collected by J.T. Medler from *F.* "*winkleri*" is distinct from the fauna of *F. tesselata*, although closely related. *S. medleri* can be separated from *S. bergi* by the number of ventral mandibular teeth.

Sycoecus bergi sp. nov.

(figs. 6.3 c-g)

Etymology: Named after Prof. C.C. Berg, botanical taxonomist and co-collector of this sample.

Type material: Holotype ♀, allotype ♂ (slide mounted): Liberia, Cavally River, S.E. of Taï, 27 November 1982, leg. C.C. Berg & J.T. Wiebes, no. 1473, RMNH 4697, 4706, 4709, ex *F. tesselata* Warb. (det. Berg). Paratypes, pair in copula, series ♀, ♂: same data as holotype.

FEMALE. Faded due to alcohol storage, probably metallic black, anterior half of head, antennae, mid and hind legs testaceous. Total length with head in orthognathous position excluding ovipositor 2.5 mm.

Head (fig. 6.3 c) elongate, narrows anteriorly in dorsal view (l = 0.67, w = 0.45), height = 0.18, wedge shaped in lateral view, convex dorsally and concave ventrally, such that it curves downwards anteriorly. Eye elongate (l = 0.24, w = 0.13, h = 0.07), 0.36X as long as the head. Cheek 1.34X longer than eye. Malar sulcas (foveal l = 0.12) present for full cheek length, indistinct towards oral fossa, slightly curved dorsad. Lateral ocelli half visible in dorsal view, situated in lateral vertex excavations. Vertex is overall generally flattened such that it meets the face anteriorly and the gena posteriorly at almost 90 degrees, making the posterior end of the head almost box-like. Carina U-shaped around the foramen magnum, produced as a tooth where it crosses the corner of the vertex and gena, fades out laterally of the foramen magnum. POL = 0.10, OOL = 0.07. Toruli touching, situated below the eyes; TE three-quarters of scrobe length (TE = 0.26, SL = 0.35). Epistomal margin subsquare, ca. a quarter of head width, medial concavity ca. a third of epistomal width and extends deeper than paraclypeal margins. Hypostoma very reduced, covered by stipes. Mandible with three widely and equally spaced teeth on the ventral edge (fig. 6.3 e). Antennae much as in *S. crinitus* (fig. 28), flagellum (l = 0.72) longer than head length. Scape 9X longer than wide (l = 0.27). Pedicel a quarter of scape length. MPS present, as 2 or 3 alternating rows dorsally (reduced on ventral surface of funicle segments) on funicle and first club segments, as a single row on last two club segments. First funicle segment three-quarters as long as second and third, subequal in length to the fourth segment.

Thorax. Pronotum elongate (l = 0.38, w = 0.30). Propodeum l = 0.22, w = 0.36. Mesoscutum l = 0.26, w = 0.47. Scutellum, including axillae l = 0.33, w = 0.35. Fore femur 3.3X longer than wide (l = 0.54), 1.7X longer than fore coxa (C = 0.31, TR = 0.11, TI = 0.20, TA = 0.27). Tibial plate (l = 0.22) subequal in length to fore tibia, with fewer, coarser teeth than *S. medleri*. Two rows of fore tibial teeth, inner with ca. eight-nine teeth, outer with ten teeth (fig. 6.3 f). Fore wing (l = 1.65, w = 0.63) very pilose, maximum fringe length = 0.05, anal and medial setal tracts present. Postmarginal vein subequal in length to stigmal (SM = 0.58, M = 0.23, PM = 0.17, S = 0.18). Marginal vein 7X longer than wide. Hind wing 4.3X longer than wide, l = 1.2.

Gaster. Few setae present on hypopygium. Eighth urotergite spiracle l = 0.03. Ovipositor 4.3X as long as valve (l = 0.39).

MALE. Testaceous, mandibles, eyes and vertex darker. Total length with head in orthognathous position excluding ovipositor 2.17 mm.

Head (fig. 6.3 d) approximately square (l = 0.46, w = 0.45), height normal (h = 0.20). Eye oval (l = 0.21, w = 0.13, h = 0.074), 0.46X as long as the head. Cheek length 0.76X eye length. Malar sulcas present for first half of cheek. Lateral ocelli visible in dorsal view, situated in shallow excavation. POL =

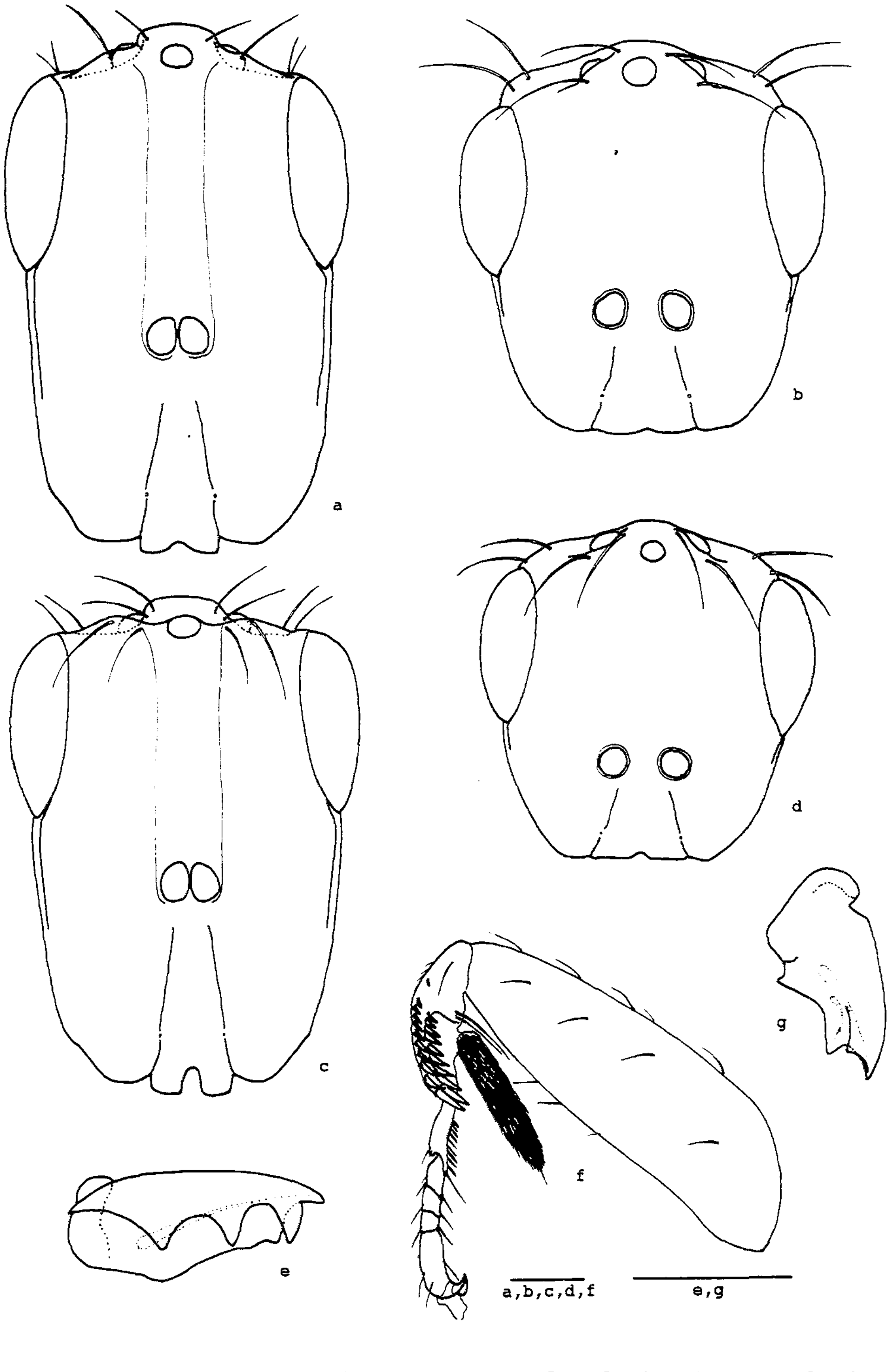


Fig. 6.3 a-b: *Sycoecus lamtoensis* sp. nov. a) female head, dorsal view b) male head, dorsal view; c-g: *Sycoecus bergi* sp. nov. c) female head, dorsal view d) male head, dorsal view e) female mandible, ventral aspect f) female fore femur, tibia and tarsus, antiaxial aspect g) male mandible, ventral aspect. Scale bars = 0.1 mm.

0.08, OOL = 0.09. Toruli separated by almost three-quarters of torulus width, situated below the eyes. TE 0.37X as long as scrobe length (TE = 0.11, SL = 0.30). Clypeal margin 0.29X head width. Mandible (fig. 6.3 g). Epistomal margin slightly convex, with medial indentation. Antennal flagella length 3.9X as long as pedicel (l = 0.35). Scape broad, ca. 4.2X longer than wide (l = 0.22). Pedicel 0.41X scape length. MPS present as a single row of ca. 3, 5, 6, 7, (7, 7, 6) on the funicle and club segments.

Thorax. Parapsidal sulci curved anteriorly. Propodeal plical furrows complete. Fore femur 3X as long as wide (l = 0.45). Fore tarsus ca. half of tibial length (C = 0.29, TR = 0.12, TI = 0.30, TA = 0.17). Fore wing 2.6X longer than wide, l = 1.67, very pilose. Postmarginal vein longer than stigmal (SM = 0.55, M = 0.28, S = 0.17, PM = 0.20). Marginal vein 8.5X longer than wide. Hind wing 4.7X longer than wide, l = 1.28.

Eighth urotergite spiracle small and round. Aedeagus large (l = 0.76). Four teeth on aedeagus claspers.

Comments. Most closely related to *S. nyassossoensis* and *S. thaumastocnema*, differs from both by possessing a shorter tibial plate.

Sycoecus ivoryensis sp. nov.

Etymology: Named after the Ivory Coast where the sample was collected.

Type material. Holotype ♀ (slide mounted): Ivory Coast, Lamto, 4-8 December 1982, leg. C.C. Berg & J.T. Wiebes, no. 1455, RMNH 4743, ex *F. scott-elliotii* Mildbr. & Burr. (det. Berg). Paratypes, 3 ♀ (slide mounted), remains of 4 ♀ (card mounted): same data as holotype.

FEMALE. Metallic black/brown, antennae, mid and hind legs testaceous. Total length with head in orthognathous position excluding ovipositor 2.4 mm.

Head much as in *S. nyassossoensis* (fig. 6.6 g) elongate (l = 0.72, w = 0.45, h = 0.15), wedge shaped in lateral view, dorso-ventrally compressed, convex dorsally, flat ventrally. Eye elongate (l = 0.25, w = 0.12, h = 0.08), 0.31X as long as the head. Cheek 1.63X longer than eye. Malar sulcas present for full length of cheek. Lateral ocelli half visible in dorsal view, situated in lateral vertex excavations. Occipital carina and foramen magnum situation much as in *S. bergi*. POL = 0.12, OOL = 0.07. Toruli touching, situated below the eyes; TE 0.85X as long as scrobe length (TE = 0.32, SL = 0.37). Epistomal margin ca. a quarter of the head width, medial concavity shallower than junction with paraclypeal margin. Hypostoma reduced, covered by stipes. Mandible with two teeth on proximal ventral edge, distally the edge is a plain sharp ridge. Antennal flagellum (l = 0.68) shorter than head length. Scape 9.7X longer than wide (l = 0.29), 4.2X longer than pedicel. MPS present, as 2-4 alternating rows on funicle and first club segments, as a single row on last two club segments. MPS reduced on ventral surface of funicle segments. First funicle segment two-thirds the length of second.

Thorax. Pronotum elongate (l = 0.41, w = 0.32), trapezoid. Propodeum l = 0.21, w = 0,38. Mesoscutum l = 0.27, w = 0.41. Scutellum, including axillae (l = 0.32, w = 0.35). Fore femur 3.8X longer than wide (l = 0.58), 1.8X longer than fore coxa (C = 0.32, TR = 0.10, TI = 0.17, TA = 0.26). Tibial plate (l = 0.31) 1.8X longer than fore tibia, with many fine teeth. Two rows of fore tibial teeth, inner with 7 larger teeth, outer with 14-15 smaller teeth. Fore wing (l = 1.63, w = 0.63), very pilose, maximum fringe length 0.05. Postmarginal vein same length as stigmal (SM = 0.56, M = 0.24, PM = 0.16, S = 0.15). Marginal vein 8X longer than wide. Hind wing 4.8X longer than wide, l = 1.2.

Gaster. Hypopygial setae present. Eighth urotergite spiracle l

= 0.032. Ovipositor 4.1X as long as valve (valve 1 = 0.38).

Comments. In terms of the mandible and the tibial plate *S. ivoryensis* is most similar to *S. lamtoensis* from which it can be separated by the CL:EL ratio. The head shape is very similar to *S. nyassossoensis*, from which it can be separated by the number of ventral mandibular teeth, and also to that of *S. crinitus* and *S. wiebesi* with a shallow epistomal margin indentation as in the former, but smaller eye as in the latter. However, the tibial plate of *S. ivoryensis* is shorter than both that of *S. crinitus* and *S. wiebesi*.

Sycoecus lamtoensis sp. nov.

(figs. 6.3 a-b, 6.4 a-b)

Etymology: Named after the type locality.

Type material. Holotype ♀, allotype ♂ (slide mounted): Ivory Coast, Lamto, 4-8 December 1982, leg. C.C. Berg & J.T. Wiebes, no. 1489, RMNH 4738, ex *F. sagittifolia* Berg (det. Berg). Paratypes, 3 ♀, 3 ♂ (slide mounted), series ♀, ♂: same data as holotype.

FEMALE. Faded due to alcohol storage, metallic black/brown, antennae, mid and hind legs, excluding hind coxae, testaceous. Total length with head in orthognathous position excluding ovipositor 2.9 mm.

Head (fig. 6.3 a, 6.4 a) elongate (l = 0.72, w = 0.47, h = 0.17), wedge shaped in lateral view, dorso-ventrally compressed, convex dorsally, slightly concave anterio-ventrally. Eye elongate (l = 0.27, w = 0.13, h = 0.08), 0.37X as long as head. Cheek 1.2X longer than eye length. Malar sulcas present for full cheek length, indistinct towards oral fossa. Lateral ocelli half visible in dorsal view, situated in lateral vertex excavations. Occipital carina and foramen magnum situation much as in *S. bergi*. POL = 0.11, OOL = 0.08. Toruli touching, situated below the eyes; TE 0.6X as long as scrobe length (TE = 0.27, SL = 0.45). Epistomal margin (w = 0.11) ca. a fifth of head width, medial indentation shallower than paraclypeal margins. Hypostoma reduced, covered by the stipes. Mandible with two teeth on ventral edge closer to apex, proximal edge plain ridge (6.4 a). Antennal flagellum (l = 0.78) longer than head length. Scape narrow, 6.7X longer than wide (l = 0.30), 4X longer than pedicel. MPS present as 2-4 alternating rows on the dorsal and lateral surfaces of the funicle and complete surfaces of first two club segments, as a single row on the last club segment. First funicle segment three-quarters the length of the second.

Thorax. Pronotum elongate (l = 0.43, w = 0.36), trapezoid. Propodeum l = 0.26, w = 0.44. Mesoscutum l = 0.28, w = 0.47. Scutellum, including axillae l = 0.37, w = 0.40. Fore femur 3.4X as long as wide (l = 0.64), 1.8X longer than fore coxa (C = 0.35, TR = 0.13, TI = 0.22, TA = 0.30). Tibial plate (l = 0.29) 1.3X longer than fore tibia, with fewer, coarser teeth than *S. ivoryensis*. Two rows of fore tibial teeth, inner with 9-10 larger teeth, outer with 11-13 smaller teeth, gap between the sixth and seventh tooth (fig. 6.4 b). Fore wing (l = 1.88, w = 0.71), pilose, maximum fringe length, 0.06. Postmarginal vein subequal to stigmal (SM = 0.65, M = 0.26, PM = 0.18, S = 0.20). Marginal vein 7X longer than wide. Hind wing 4.6X longer than wide, l = 1.39.

Gaster. Hypopygial setae present. Eighth urotergite spiracle normal, l = 0.04. Ovipositor 4.2X as long as valve (valve l = 0.41).

MALE. Testaceous, mandibles and eyes darker. Total length with head in orthognathous position excluding ovipositor 2.25 mm.

Head (fig. 6.3 b) elongate (l = 0.53, w = 0.49, h = 0.19). Eye oval (l = 0.23, w = 0.13), protrudes laterally (h = 0.08), 0.43X as long as head. Cheek length 0.77X eye length. Malar sulcas present for half of cheek length. Lateral ocelli visible in dorsal view, situated in very shallow excavation. POL = 0.11, OOL = 0.10. Toruli separated by four-fifths of torulus width, TE 0.41X as long as scrobe length (TE = 0.14, SL = 0.34). Width of clypeal margin (w = 0.13) ca. a quarter of the head width. Epistomal margin slightly convex, with medial indentation. Mandible much as in *S. crinitus* (fig. 6.5 c). Antenna much as in *S. crinitus* (fig. 6.5 e), flagellum (l = 0.42) 4.2X as long as pedicel. The two anelli are sometimes fused together and appear as one. Scape broad, 4.2X longer than wide (l = 0.26). Pedicel 0.39X scape length. MPS present as a single row of 7, 7, 8, 8, (7, 8 & 5) sensilla on the flagella segments respectively. On each of the first and third funicle segments a single MPS is offset basally.

Thorax. Parapsidal sulci curved anteriorly. Propodeal plical furrows reduced. Fore femur 2.9X as long as wide (l = 0.54). Fore tarsus half of tibial length (C = 0.35, TR = 0.13, TI = 0.37, TA = 0.19). Fore wing 2.5X longer than wide l = 1.9. Postmarginal vein subequal to stigmal (SM = 0.63, M = 0.31, S = 0.20, PM = 0.22). Marginal vein 7.8X longer than wide. Hind wing 4.5X longer than wide, l = 1.4.

Gaster. Eighth urotergite spiracle small and round. Aedeagus large (l = 0.83). Four teeth on aedeagus claspers.

Sycoecus crinitus sp. nov.

(figs. 6.5 a-g, 6.6 c, 6.4 c-d)

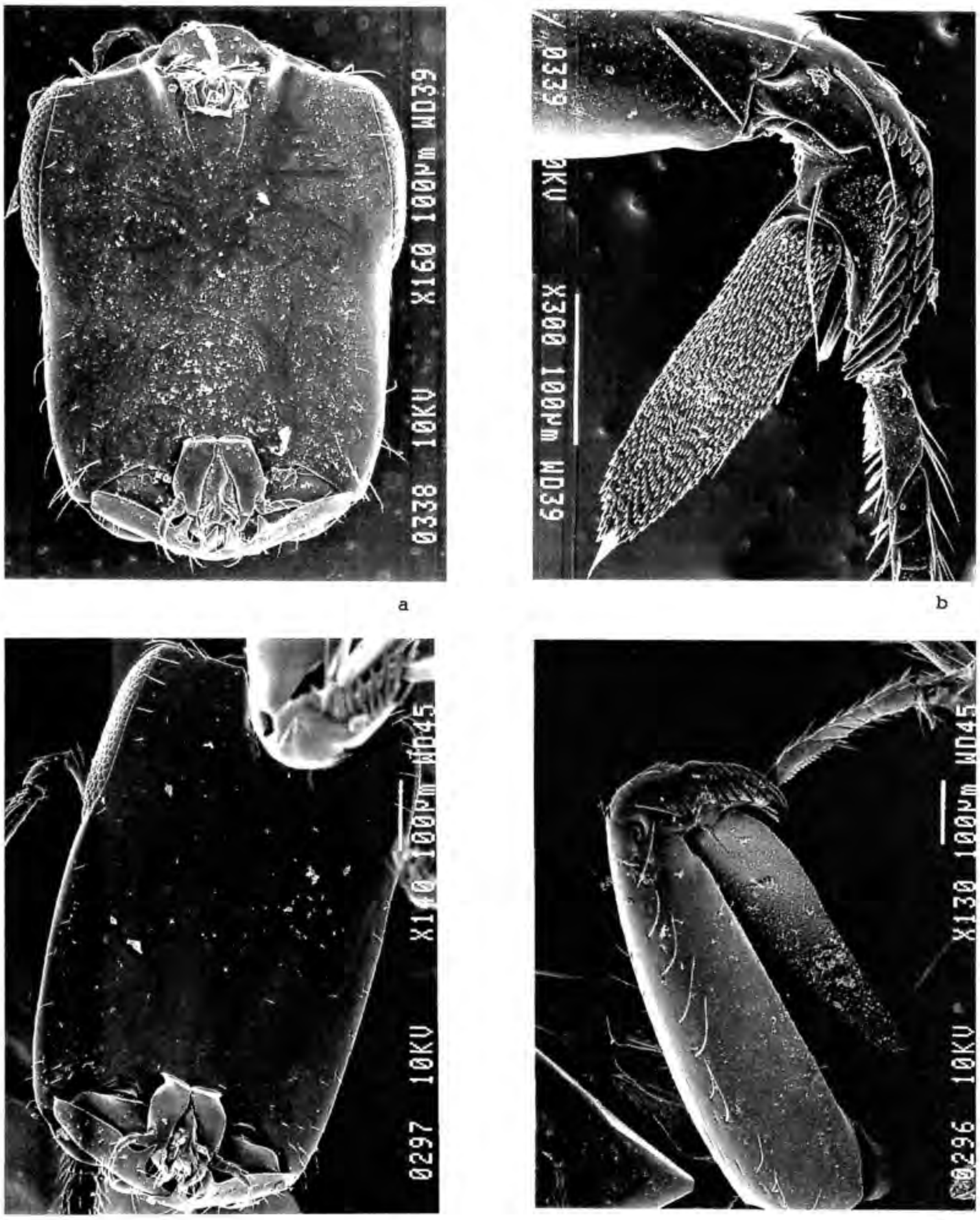
Etymology: Crinitus (latin) = hairy, referring to the dense setae present on the eighth urotergite.

Type material: Holotype ♀, allotype ♂ (slide mounted): Ivory Coast, Taï forest, 28 February 1980, leg. D. Lachaise & G. Couturier, F25, RMNH 4100 & 4104, ex *F. lyrata* Warb. Paratypes, 3 ♀, 3 ♂ (slide mounted), series ♀, ♂: same data as holotype.

FEMALE. Faded due to alcohol storage, metallic black/brown, anterior third of head, antennae, mid and hind legs, excluding coxae testaceous. Total length with head in orthognathous position excluding ovipositor 3.1 mm.

Head (figs. 6.4 c, 6.5 a) elongate (l = 0.87, w = 0.47, h = 0.16), very compressed dorso-ventrally, wedge shaped in lateral view, convex dorsally, concave ventrally, such that head curves down anteriorly. Eye elongate (l = 0.29, w = 0.12, h = 0.07), 0.32X as long as the head. Cheek 1.6X longer than eye. Malar sulcas present for first third of cheek length as fovea. Lateral ocelli not visible in dorsal view, situated in deep excavations on the vertex. Occipital carina and foramen magnum excavation much as in *S. bergi*. POL = 0.12. OOL = 0.09. Toruli touching, situated below the eyes, TE 0.88X as long as scrobe length (TE = 0.39, SL = 0.44). Epistomal margin ca. a quarter of the head width, medial indentation shallower than paraclypeal margins. Hypostoma reduced, covered largely by the stipes. Mandible with two ventral teeth (figs. 6.4 c, 6.5 e). Antenna (fig. 6.5 c), flagellum equal to head length. Scape 8.7X longer than wide (l = 0.33). Pedicel a quarter of scape length. MPS present as two alternating rows on first funicle and first club segments, 3 alternating rows on remaining funicle segments and as a single row on the last two club segments. MPS reduced on the ventral surface of the funicle segments. First funicle segment three-quarters the length of second and third, subequal in length to the fourth segment.

Thorax (fig. 6.5 b). Pronotum elongate (l = 0.57, w = 0.39), trapezoid. Propodeum (l = 0.27, w = 0.48). Mesoscutum l = 0.31, w = 0.51. Scutellum, including axillae broad (l = 0.37, w = 0.43). Fore femur (fig. 6.4 d) 4X as long as wide (l = 0.82), twice as long as fore coxa (C = 0.42, TR = 0.16, TI = 0.21, TA = 0.36). Tibial plate 2.6X as long as fore tibia, with many, fine teeth. Two rows of fore tibial teeth, inner with 7 large teeth, outer with 17-18 smaller teeth (fig. 6.4 d). Fore wing (l = 2.05



a b

c d

Fig. 6.4 a-b: *Sycoecus lamtoensis* sp. nov. a) female head, ventral view b) female fore tibia and first two tarsal segments, antiaxial view; c-d: *Sycoecus crinitus* sp. nov. c) female head, ventral view d) female fore femur, tibia and tarsus, antiaxial view.

w = 0.75), pilose, maximum fringe length, 0.05. Postmarginal vein longer than stigmal (SM = 0.70, M = 0.29, PM = 0.22, S = 0.19). Marginal vein 9X longer than wide. Hind wing 4.5X longer than wide, l = 1.53.

Gaster. Hypopygial setae extensive. Eighth urotergite spiracle normal, l = 0.05. Ovipositor 3.8X as long as valve (valve l = 0.55).

MALE. Testaceous, mandibles and eyes darker. Total length with head in orthognathous position excluding ovipositor 2.5 mm.

Head (figs. 6.5 f & g) elongate (l = 0.60, w = 0.50), height normal (h = 0.23). Eye oval (l = 0.28, w = 0.14), protrudes laterally (h = 0.074), 0.47X as long as the head. Cheek length 0.68X eye length. Malar sulcas present for first third of cheek. Lateral ocelli visible in dorsal view, situated in shallow excavation. POL = 0.12, OOL = 0.09. Toruli separated by just less than a third of torulus width. TE 0.38X as long as scrobe length (TE = 0.15, SL = 0.40). Width of clypeal 0.28X the head width. Mandible (fig. 6.5 d). Epistomal margin slightly convex, with medial indentation. Antenna (fig. 6.6 c), flagellum 4.6X as long as pedicel, l = 0.10. Scape 5.2X longer than wide (l = 0.31). Pedicel 0.32X scape length. MPS present as a single row of 6, 7, 7, 8, (8, 8, & 5) sensilla on the funicle and club segments respectively.

Thorax. Parapsidal sulci straight. Propodeal plical furrows complete. Fore femur 3.4X as long as wide (l = 0.64). Fore tarsus half of tibial length (C = 0.38, TR = 0.16, TI = 0.40, TA = 0.20). Three spines on adaxial dorsal margin of hind tibia. Fore wing 2.7X longer than wide, l = 2.1. Postmarginal vein subequal to stigmal (SM = 0.72, M = 0.36, S = 0.19, PM = 0.20). Marginal vein 7.7X longer than wide. Hind wing 4.4X longer than wide, l = 1.57.

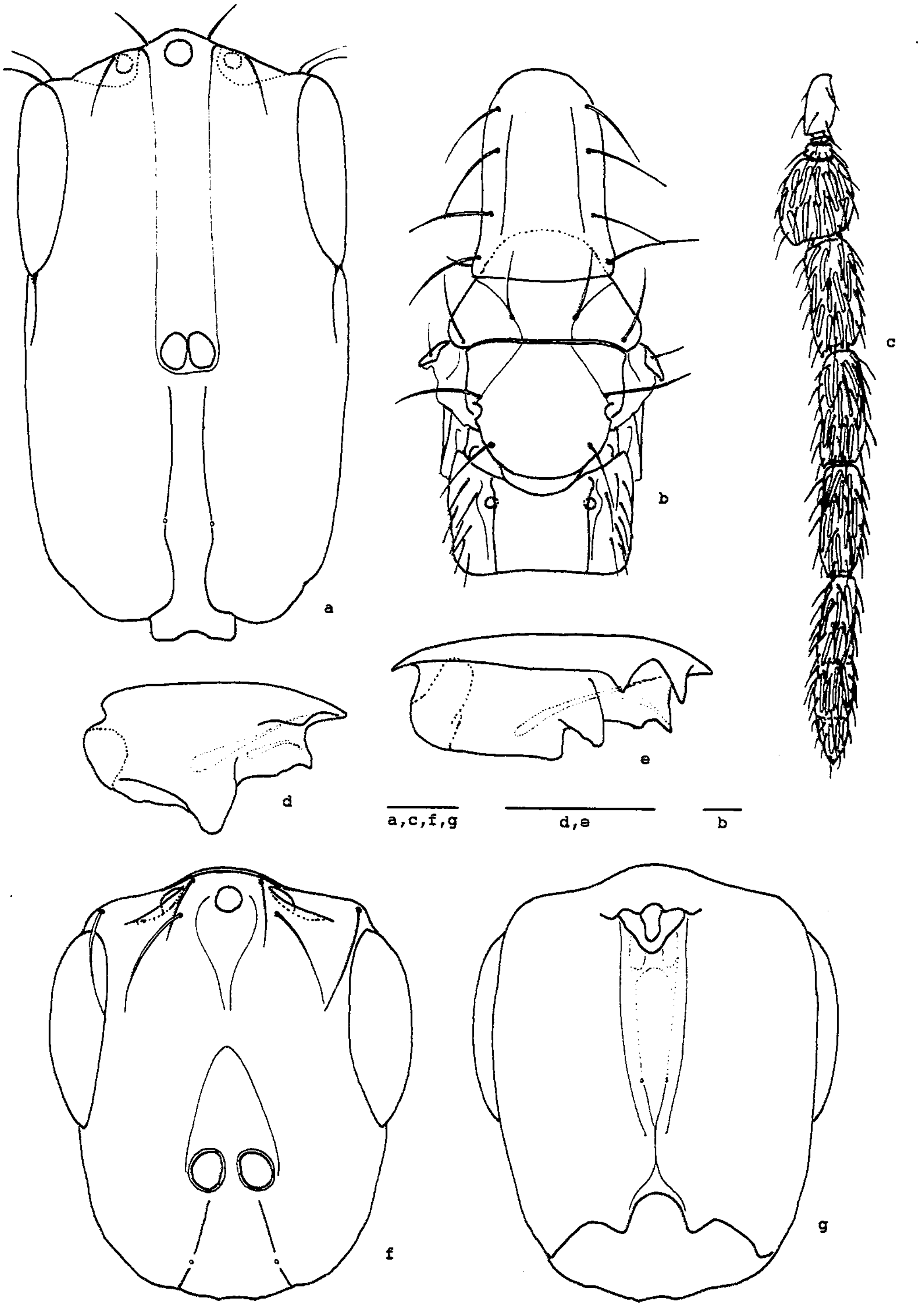


Fig. 6.5 a-g: *Sycoecus crinitus* sp. nov. a) female head, dorsal view b) female thorax, dorsal view c) female antenna, dorsal view d) male mandible, ventral view e) female mandible, ventral view f) male head, dorsal view g) male head, ventral view. Scale bars = 0.1 mm.

Gaster. Eighth urotergite spiracle small and round. Aedeagus large (l = 0.92). Five teeth on aedeagus claspers.

Comments. Most closely related to *S. wiebesi*. Head proportions are very similar to *S. nyassossoensis*, but differs in the number of mandibular ventral teeth.

Sycoecus wiebesi sp. nov.

(figs. 6.6 a,b,d,f & 6.7 a-c)

Etymology: Named after Prof. J.T. Wiebes.

Type material. Holotype ♀, allotype ♂ (slide mounted): Ivory Coast, Taï Forest, 18-21 November 1982, leg. C.C.Berg & J.T.Wiebes, no. 1462, RMNH 4713, ex *F. cyathistipuloides* Wild. (det. Berg). Paratypes, 2 ♀, 1 ♂ (slide mounted), series ♀, 1 ♂: same data as holotype; 1 ♀: Gabon, Makokou, 10 February 1978, leg. G. Michaloud, F. no. 1005, RMNH 4926, ex *F. subsagittifolia* Berg.

FEMALE. Faded, metallic black/brown, antennae, mid and hind legs excluding coxae testaceous. Total length with head in orthognathous position excluding ovipositor 2.5 mm.

Head (fig. 6.6 a & 6.7 a) elongate (l = 0.73, w = 0.42, h = 0.14), very dorso-ventrally compressed, wedge shaped in lateral view, slightly convex dorsally, flat ventrally. Eye elongate (l = 0.20, w = 0.12, h = 0.06), 0.27X as long as the head. Cheek twice eye length. Malar sulcas present for full length of cheek, curves up onto dorsal face anteriorly where it is very faint and indistinct (foveal l = 0.11). Lateral ocelli not visible, situated in lateral excavations on vertex. Slight medial prominence on vertex, medial ocellus situated very close to edge. Occipital carina only present dorsally to foramen magnum. POL = 0.10. OOL = 0.08. Toruli touching, situated below the eyes; TE 0.92X as long as scrobe length (TE = 0.34, SL = 0.37). Epistomal margin ca. a quarter of the head width, medial concavity shallower than paraclypeal margins. Hypostoma reduced, covered largely by the stipes. Mandible with two ventral teeth, situated closer to apex, proximally straight ventral edge (fig. 6.7 a). Labial and maxillary palp segments (fig. 6.6 f). Antennae much as in *S. crinitus* (fig. 6.5 c), flagellum (l = 0.74) equal to head length. Scape 10X longer than wide (l = 0.28). Pedicel a quarter of scape length. MPS present, as 2 - 4 alternating rows dorsally (reduced on ventral surface of funicle segments) on funicle and first club segments, as a single row on last two club segments. First funicle segment half the length of second.

Thorax. Pronotum elongate (l = 0.46, w = 0.32), trapezoid. Propleural excavations (fig. 6.7 c). Propodeum l = 0.22, w = 0.37. Mesoscutum l = 0.24, w = 0.41. Scutellum, including axillae l = 0.32, w = 0.34. Fore femur 4.3X longer than wide (l = 0.63), twice as long as fore coxa (C = 0.32, TR = 0.11, TI = 0.17, TA = 0.23). Fore tibial plate (l = 0.40) 2.4X longer than fore tibia, with many, fine teeth (fig 6.7b). Inner row of fore tibial teeth with seven teeth, outer with 14-15 teeth (fig. 6.7 b). Fore wing (l = 1.70, w = 0.66) with sparse setation, maximum fringe length 0.05, anal setal tract present. Postmarginal equal in length to stigmal (SM = 0.60, M = 0.22, PM = 0.17, S = 0.17). Marginal vein 7.5X longer than wide (fig. 6.6 d). Hind wing 4.6X longer than wide, l = 1.23.

Gaster. Hypopygial setae present. Eighth urotergite spiracle l = 0.034, with setae present around the edge. Ovipositor 4.6X longer than valve (valve l = 0.35).

MALE. Testaceous, mandibles and eyes darker. Total length with head in orthognathous position excluding ovipositor 2 mm.

Head (fig. 6.6 b) elongate (l = 0.46, w = 0.41), height normal (h = 0.18). Eye oval (l = 0.21, w = 0.12), protrudes laterally (h = 0.06), 0.48X as long as the head. Cheek length 0.71X eye length. Malar sulcas present for first quarter of cheek. Lateral ocelli visible in dorsal view, situated in axial end of shallow excavation. POL = 0.09, OOL = 0.08. Toruli separated by ca. half of torulus width, situated below the eyes. TE 0.33X as long as scrobe length (TE = 0.10, SL = 0.30). Width of clypeal margin 0.29X head width. Mandible much as in *S. crinitus* (fig. 6.5 d). Epistomal margin straight. Antennae much as in *S. crinitus* (fig. 6.6 c), flagellum 4.4X as long as pedicel (l = 0.085). Scape 5.4X longer than wide (l = 0.23). Pedicel 0.37X scape length. MPS present as a single row of 3, 4, 4, 7, (6, 6, & 4) sensilla on the funicle and club segments.

Thorax. Parapsidal sulci straight. Propodeal plical furrows complete. Fore femur 3.7X longer than wide (l = 0.48). Fore tibia 1.7X tarsal length (C = 0.30, TR = 0.10, TI = 0.29, TA = 0.17). Three spines on adaxial dorsal margin of hind tibia. Fore wing 2.6X longer than wide, l = 1.7. Postmarginal vein same length as stigmal (SM = 0.55, M = 0.25, S = 0.17, PM = 0.17). Marginal vein 6.3X longer than wide. Hind wing 4.6X longer than wide, l = 1.23.

Gaster. Eighth urotergite spiracle small and round. Aedeagus large (l = 0.70). Four teeth on aedeagus claspers.

Comments. I can not separate the single female specimen from *F. subsagittifolia* with any degree of confidence from the present sample. The minor differences in eye length to head length and cheek length ratios may simply be the result of size differences, the specimen from *F. subsagittifolia* is much larger than the specimens from *F. cyathistipuloides*. I can not find any other distinguishing morphological characters. For the moment I conclude that they are the same species. *S. wiebesi* is very closely related to *S. crinitus*, and can be separated by the eye length: cheek length ratio.

Sycoecus thaumastocnema Waterston

Type material: *Sycoecus thaumastocnema* Waterston 1914: 253-256 (figs. 3{a-b}, 4{a-c}). Holotype ♀: Uganda, Bugalla Island, Sesse, Lake Victoria. [Examined paratype, The Natural History Museum, London, det. Z. Boucek 1979, with the following data: Uganda, Kawanda, November 1942, leg T.H.C. Taylor, T852].

Additional material. Series ♀, ♂: Uganda, Mpanga Forest, 6 September 1968, leg D.S. Hill, tree 54, ex *F. c. cyathistipula* Warb.

The female is here redescribed and the male described for the first time, from material collected by D.S. Hill in Uganda.

FEMALE. Material collected by D.S. Hill is faded due to alcohol storage, but the paratype is metallic black, with antennae, mid and hind legs (excluding the coxae) testaceous. Total length with head in orthognathous position excluding ovipositor 2.5 mm.

Head (l = 0.69, w = 0.43, h = 0.17), wedge shaped in lateral view, dorso-ventrally compressed, convex dorsally, flat ventrally. Eye elongate (l = 0.26, w = 0.12), 0.38X as long as head. Cheek 1.1X longer than eye. Malar sulcas present for full length of cheek as sinusoidal curve, indistinct towards oral fossa, length of fovea at eye ca. 0.16. Lateral ocelli half visible in dorsal view, situated inside lateral vertex excavations. Occipital carina on medial prominence extends in a U-shape around the foramen magnum, which is situated in a medial excavation in the 90 degrees junction of the vertex with the posterior gena. Carina produced as a tooth where it passes over the junction and fades out laterally of the foramen magnum on the ventral side of the head. POL = 0.10, OOL = 0.07. Toruli touching, situated below the eyes, TE 0.72X as long as scrobe length (SL = 0.36). Epistomal margin convex with medial concave indentation extending as deep as paraclypeal margins, ca. a quarter of the head width (w = 0.12). Hypostoma reduced, covered largely by the stipes. Mandible with three equally spaced ventral teeth. Flagellum (l = 0.70) subequal to head length. Scape 8.4X longer than wide (l = 0.27). Pedicel ca. a quarter of scape length (l = 0.07). MPS present, as 2 to 3 alternating rows dorsally (reduced on ventral surface of funicle segments) on funicle and first club segments, as a single row on last two club segments. First funicle segment three-quarters the length of the second and third, subequal in length to the fourth segment.

Thorax. Pronotum elongate (l = 0.43, w = 0.30), trapezoid. Propodeum l = 0.24, w = 0.38. Mesoscutum l = 0.25, w = 0.43. Scutellum, including axillae subsquare (l = 0.32, w = 0.35). Fore femur 3.4X as long as wide (l = 0.61), 1.9X longer than fore coxa. C = 0.33, TR = 0.12, TI = 0.20, TA = 0.28. Tibial plate (l = 0.32) 1.6X as long as fore tibia, with many, fine teeth. Inner row of tibial teeth on adaxial face consists of eight teeth, outer of thirteen teeth. Fore wing 2.5X longer than wide (l = 1.92), very pilose, maximum fringe length = 0.05, anal and medial vein remnants present. Postmarginal vein subequal in length to stigmal (SM = 0.61, M = 0.30, PM = 0.19, S = 0.20). Marginal vein 9.4X longer than wide. Hind wing 4.6X longer than wide, l = 1.43.

Gaster. Few setae present on hypopygium. Eighth urotergite spiracle l = 0.03. Ovipositor (l = 1.46) 4.6X as long as ovipositor valve.

MALE. Testaceous - faded. Total length with head in orthognathous position excluding ovipositor 2.17 mm.

Head much as in *S. bergi* (fig. 6.3 d), elongate (l = 0.48, w = 0.45), height normal (h = 0.18). Eye elongate (l = 0.22, w = 0.12), protrudes laterally (h = 0.07), 0.46X as long as the head. Cheek length 0.68X eye length. Malar sulcas present for first half of cheek. Lateral ocelli visible in dorsal view, situated in shallow excavation, also shallow excavation anterior to medial ocellus. POL = 0.10, OOL = 0.08. Toruli separated by three-quarters of torulus width, situated below the eyes. TE 0.37X as long as scrobe length (TE = 0.11, SL = 0.30). Width of clypeal margin ca. a quarter of the head width (w = 0.11). Epistomal margin slightly convex, with medial indentation. Antennal flagellum 4X as long as pedicel (l = 0.09). Scape 4.8X longer than wide (l = 0.24). Pedicel 0.38X as long as scape. MPS present as a single row of ca. 3, 4, 6, 6, (7, 5 & 4) sensilla on the funicle and club segments respectively.

Thorax. Parapsidal furrows curved anteriorly. Propodeal plical furrows complete. Fore femur 3.1X longer than wide, l = 0.46. Fore tibia 1.67X longer than tarsus (C = 0.30, TR = 0.12, TI = 0.30, TA = 0.18). Fore wing 2.55X longer than wide, l = 1.86. Postmarginal vein longer than stigmal (SM = 0.55, M = 0.32, S = 0.19, PM = 0.23). Marginal vein thick 10.7X longer than wide. Hind wing 4.5X longer than wide, l = 1.34.

Eighth urotergite spiracle small and round. Aedeagus large (l = 0.75). Four teeth on aedeagus claspers.

Comments. Most closely related to *S. bergi* and *S. nyassossoensis*, and can be separated from the former by the length of the tibial plate and from the latter by the depth of the epistomal margin indentation.

Sycoecus nyassossoensis sp. nov.

(fig. 6.6 e & g)

Etymology: Named after the type locality.

Type material. Holotype ♀, allotype ♂, (slide mounted): Cameroun, North West Province, Nyassosso, 7 January 1982, leg. R.G.E. Baker & S.G. Compton, C1014, ex *Ficus* sp. no. 19 (from fallen figs in montane forest). Paratypes, 3 ♀: same data as holotype.

FEMALE. Metallic black, antennae, mid legs (excluding coxae), hind legs (excluding coxae), and femora testaceous. Total length with head in orthognathous position, excluding ovipositor 2.1mm.

Head (fig. 6.6 g), elongate, narrows anteriorly in dorsal view (l = 0.69, w = 0.49, h = 0.14), wedge shaped and very compressed in lateral view, slightly convex dorsally, flat ventrally. Eye elongate (l = 0.21, w = 0.1, h = 0.05), 0.30X as long as the head. Cheek 1.76X longer than the eye. Malar sulcus present for ca. two-fifths of cheek length. Lateral ocelli hidden from dorsal view, in deep lateral vertex excavations. Occipital carina on medial prominence extends in a U-shape around the foramen magnum, much as in *S. thaumastocnema*. POL = 0.11, OOL = 0.08. Toruli touching, situated below the eyes, TE 0.83X as long as the scrobe (TE = 0.30, SL = 0.36). Epistomal margin convex, subsquare, 0.22X as wide as head, medial concavity shallower than paraclypeal margins. Hypostoma reduced, covered largely by the stipes. Mandible with three equally spaced ventral teeth (fig. 6.6 e). Antennal flagellum (l = 0.6) shorter than head length. Scape 8.7X longer than wide (l = 0.26). Pedicel 0.31X as long as scape. MPS present, as two alternating rows on the funicle and first club segment and a single row on the last two club segments. First funicle segment three-quarters the length of second and third, subequal to fourth.

Thorax. Pronotum elongate (l = 0.45, w = 0.32). Propodeum l = 0.20, w = 0.39. Mesoscutum l = 0.27, w = 0.36. Scutellum, including axillae l = 0.33, w = 0.42. Fore femur 3.5X longer than wide (l = 0.59), 1.8X longer than fore coxa (C = 0.32, TR = 0.11, TI = 0.19, TA = 0.25). Tibial plate 2.1X longer than tibia, with many, fine teeth. Inner row of fore tibial teeth with seven large teeth, outer with 11-13 smaller teeth. Fore wing 2.5X longer than wide (l = 1.67), pilose, maximum fringe length 0.07, anal and medial setal tracts present. Postmarginal vein subequal to marginal (SM = 0.55, M = 0.24, PM = 0.17, S = 0.16). Marginal vein 8X longer than wide. Hindwing 4.3X longer than wide (l = 1.28).

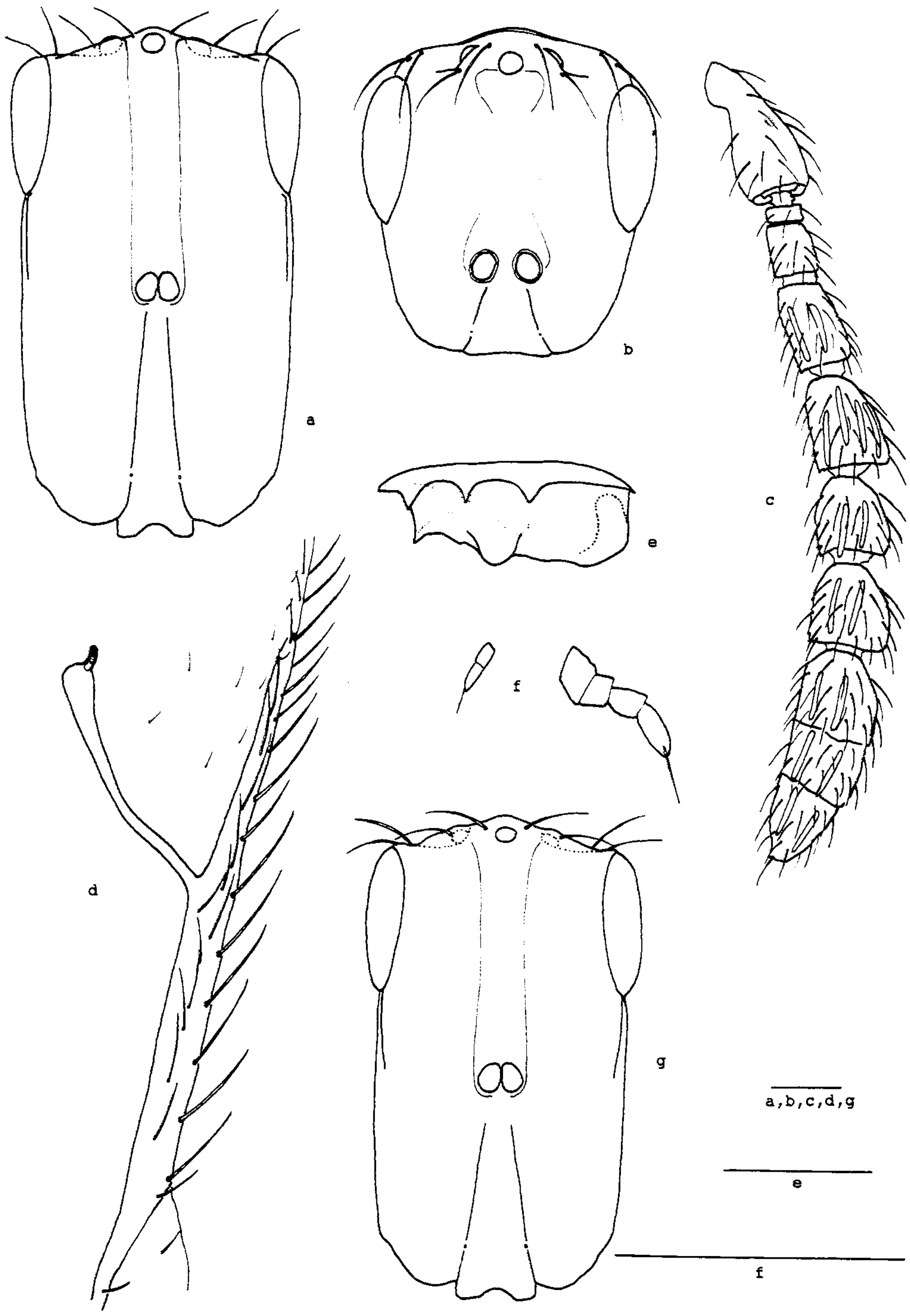


Fig. 6.6 a,b,d,f: *Sycoecus wiebesi* sp. nov. a) female head, dorsal view b) male head, dorsal view d) female forewing venation: marginal, postmarginal and stigmal veins f) female labial and maxillary palps; c: *Sycoecus crinitus* sp. nov. c) male antenna, axial view; e & g: *Sycoecus nyassossoensis* sp. nov. e) female mandible, ventral view f) female head, dorsal view. Scale bars = 0.1 mm.

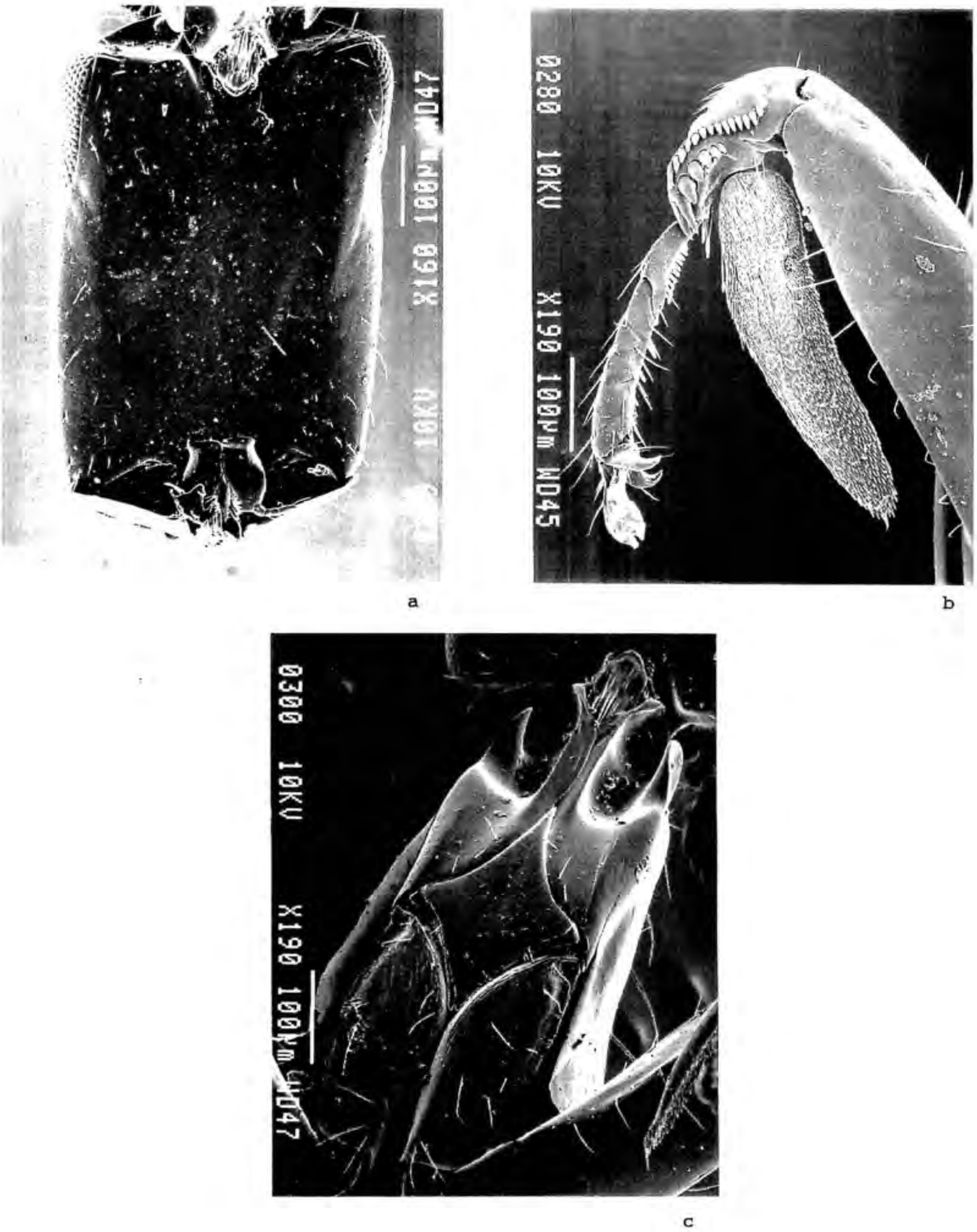


Fig. 6.7 a-c: *Sycoecus wiebesi* sp. nov. a) female head, ventral view b) female fore tibia and tarsus, antiaxial view c) female fore coxae, prosternum and propleura, showing excavations of the propleura.

Gaster. Eighth urotergite spiracle l = 0.032. Ovipositor 4.5X longer than valve (valve l = 0.28).

MALE. Testaceous, gaster, eyes and vertex darker. total length with head in orthognathous position, excluding ovipositor 2.0mm.

Head elongate (l = 0.51, w = 0.44, h = 0.2). Eye elongate (l = 0.21, w = 0.12), protrudes laterally (h = 0.06), 0.41X as long as the head. Cheek length 0.83X as long as eye. Malar sulcus present for first two-fifths of cheek. Lateral ocelli visible in dorsal view, situated in shallow excavation on vertex, also shallow excavation in front of medial ocellus and around and posterior to the toruli. POL = 0.10, OOL = 0.09. Toruli separated by three-quarters of torulus width, TE 0.38X as long as the scrobe length, TE = 0.12, SL = 0.32. Width of clypeal margin 0.34X head width. Antennal flagellum 3.3X pedicel length. Scape 4.3X longer than wide (l = 0.26), 2.6X longer than pedicel. MPS present as a single row of ca. 3, 4, 5, 4, (6, 6, 5) sensilla on the funicle and club segments.

Thorax. Parapsidal sulci curved anteriorly. Propodeal plica furrows complete. Fore femur 2.8X longer than wide, l = 0.47. Fore tibia 1.68X longer than tarsus (C = 0.32, TR = 0.12, TI = 0.32, TA = 0.19). Fore wing 2.6X longer than wide, l = 1.85. Postmarginal vein longer than stigmal (SM = 0.61, M = 0.30, S = 0.17, PM = 0.21). Marginal vein 10X longer than wide. Hindwing 4.7X longer than wide, l = 1.35.

Gaster. Eighth urotergite spiracle small and round. Aedeagus large (l = 0.62). Four teeth on aedeagus claspers.

Comments. Most similar to *S. thaumastocnema*.

7

SYSTEMATICS OF *SERES*

INTRODUCTION

Seres Waterston as originally delimited is paraphyletic, because *S. levi* Waterston is in fact a species of *Philocaenus* Grandi. The species are all associated with *Ficus* species belonging to the subsection *Caulocarpae*, section *Galoglychia*, which are pollinated by agaonines of the genus *Courtella* Kieffer. However, these are not the only sycoecine species to be associated with this subsection, which is also host to some *Philocaenus* and *Crossogaster* species. Five species are currently placed in *Seres*, two of which also have distinct subspecies. Four of these species are described here for the first time. One synonymy is established.

GENERIC DEFINITION

Seres Waterston

Seres Waterston 1919, 275-276.
Type species: *Seres armipes* Waterston 1919, by original designation.

FEMALE. Head elongate, dorso-ventrally flattened, smooth, polished; clypeus narrow, epistomal margin produced; toruli in close apposition or touching; malar sulcus either absent or present for the first quarter to third of the cheek length. Compound eyes situated posteriorly on face, the temple may still be present laterally above the eyes. Temple and frons may meet the vertex at ninety degrees, such that the vertex is flat with broad, shallow excavations laterally or else a medial prominence is present and the vertex is more rounded. Lateral ocelli situated on axial lip of excavations. Occipital carina is situated medially on the vertex, ventral to the scrobe invagination and lateral ocelli, extending laterally to the outside of the lateral ocelli. Strong setae present on vertex/temple junction. Ventral tentorial pits in very close apposition situated approximately half way between the oral fossa and the foramen magnum. Hypostoma may be present or absent, mouthparts sunken such that the stipes are flush with the ventral surface of the head, cardo absent. Two labial palp segments, basal segment half to subequal the length of the distal segment. Three maxillary palp segments. Mandible with two apical teeth, inner shorter and smaller, with either a single ventral tooth extending proximally as a ridge or two or three large evenly spaced ventral teeth, two glands. Dorsal tentorial pits situated on clypeal sutures close to epistomal margins. Antennae either eleven segmented, formula 1124(3), or twelve segmented, formula 1134(3), anelli in close apposition, second larger than first. Multi-porous plate sensilla (MPS) numerous, placoid, thin and elongate, present in a single row in close apposition to one another, reduced ventrally on funicle segments.

Thorax dorso-ventrally flattened, smooth, polished; pronotum elongate, laterally depressed, concave; mesonotum suboval, parapsidal sulci complete, curved; propodeal spiracles medially situated with sulci well defined posterior to spiracles, more shallow anterior to the spiracles. General form of legs typical for sycoecines, fore femur stout, elongate, subcylindrical. Fore tibial spur elongate, articulated half way up tibia, no ventral tooth next to spur insertion. Wings almost glabrous, microsetae indistinct, very short insignificant fringe on forewing, longer fringe on hindwing.

Gaster, tergites with five to seven evenly spaced incisions on the posterior edge, otherwise edge smooth. Medial three incisions on first tergite in close approximation, with the lateral two incisions closing posteriorly with the medial incision. Eighth urotergite spiracle normal, ventro-laterally situated, may have a slightly expanded peritreme.

MALE. Head either subquadrate and slightly longer than wide, or distinctly narrower anteriorly than across the eyes and slightly broader than long; broadly excavated posterio-ventrally; clypeus subtriangular in area, epistomal margin broader than in female, slightly concave, may be medially slightly convex. Toruli separated, situated just below or in line with the base of the eyes, closer to the epistomal margin than to the vertex. Antennal formula either 1124(3) with the second anellus 3X the length of the first and subequal in length to the funicle segments or 1134(3). MPS thin, placoid, number per segment very reduced. Dorsal tentorial pits situated on lateral clypeal sutures, closer to margin than to toruli. Malar sulcus either absent or if present then only for posterior half of cheek. Medial prominence present on vertex, with weak occipital carina along edge, dorsal to foramen magnum. Head as viewed posteriorly is broadly concave ventrally. Ventral tentorial pits slightly to well separated, situated ca. half way between the foramen magnum and the oral fossa. Three maxillary palp segments, two labial palp segments, ratios much as in the females. Mandible either with a larger outer apical tooth and a shorter inner subapical tooth which may be uni- or bicuspid, or as before but with a ventral apical tooth extending as a ridge to the base of the mandible; two glands, subapical gland smaller.

Thorax. Pronotum torpedo shaped, with a carina present on the anterio-dorsal margin; mesonotum broad, semicircular, parapsidal sulci complete, evenly curved or straight. Propodeal sulci present, spiracles medially situated. Either two strong subequal dorso-apical teeth on fore tibia, or a single strong tooth with 1-3 strong setae; spur elongate, articulated ca. a quarter of the way up the fore tibia, no ventral tooth next to spur insertion. Wings pilose, axial third bare, rest covered in microsetae, anal and medial setal tracts present on forewing. Thick marginal vein.

Gaster. Posterior edges of tergites straight, with short setae along the edge. Aedeagus small.

Comments. *Seres* can be immediately identified by the medially situated propodeal spiracles with a plica posteriorad, although the latter may be indistinct.

KEY TO THE SPECIES OF *SERES*:

FEMALES

1. Fore tibial armature consists of a plate of many teeth fused to the dorso-axial face of the tibia (fig. 7.2 f); mandible with a single ventral ridge (fig. 7.2 d), ex *F. bubu* .... *S. wardi*
- Fore tibial armature consists of a dorso-apical comb of teeth that may have an additional two combs above it; mandible with two or three ventral teeth (figs. 7.1 f & 7.4 c, e) 2

2. Epistomal margin with a medial tooth (fig. 7.1 a); 3 anelli, 4 funicle segments (figs. 7.1 c); proximal maxillary palp segment shorter than the medial segment (figs. 7.1 e), ex *F. artocarpoides* .... *S. longicalcar*
- Epistomal margin subquadrate (figs. 7.4 a, b, f & g); 2 anelli, 4 funicle segments (fig. 7.4 h); proximal maxillary palp segment longer than the medial segment (fig. 7.4 d) 3

3. Epistomal margin protrudes anteriorly no further than the paraclypeal margins (fig. 7.4 b), ex *F. ovata* (Zambia), *F. p. polita*, *F. s. sansibarica* .... *S. solweziensis*
- Epistomal margin protrudes anteriorly further than the paraclypeal margins (figs. 7.4 a, f & g) 4

4. Head more than twice as long as wide and more than 4.5X wider than the epistomal margin (fig. 7.4 f), ex *F. ovata*

(West Africa) .... *S. a. armipes*

- Head less than twice as long as wide and less than 4.1X wider than the epistomal margin (figs. 7.4 a & g) 5

5. Gaster 2X longer than ovipositor valves, ex *F. s. macrosperma* (West Africa) .... *S. longivena bidens*

- Gaster more than 2.5X longer than the ovipositor valves 6

6. Gaster 2.6X longer than ovipositor valves; three ventral mandibular teeth (fig. 7.4 e), ex *F. s. macrosperma* (Zambia) .... *S. l. longivena*

- Gaster more than 3X longer than ovipositor valves; two ventral mandibular teeth (fig. 7.4 c), ex *F. ovata* (East Africa) .... *S. a. breviceps*

MALES*

1. Head metallic green, rest of body testaceous; head narrows anteriorly (fig 7.3 a), ex *F. bubu* .... *S. wardi*

- Head and rest of body testaceous; head parallel sided, as broad anteriorly as posteriorly (fig. 7.3 g) 2

2. Subapical mandibular tooth bicuspid (fig. 7.3 h), ex *F. ovata* .... *S. a. armipes*

- Subapical mandibular tooth unicuspid (fig. 7.3 f) 3

3. Marginal vein elongate, 6X longer than wide, ex *F. sansibarica* .... *S. longivena*

- Marginal vein shorter, less than 5.4X longer than wide, ex *F. ovata, F. p. polita, F. s. sansibarica* .... *S. a. breviceps* and *S. solweziensis*

* The male of *S. longicalcar* is unknown.

SPECIES DESCRIPTIONS

Seres longicalcar sp. nov.

(figs. 7.1 a-f)

Etymology: calcar (latin) = spur, referring to the elongate fore tibial spur.

Type material: Holotype ♀ (slide mounted): Gabon, Makokou, 21 August 1978, leg. G. Michaloud, no. 1012, RMNH 3724, ex *F. artocarpoides* Warb.; paratype, 1 ♀: same data as holotype, but RMNH 3722.

FEMALE. Faded, head metallic black, thorax, gaster, antennae, mandibles, coxae and femora dark brown, tibia and tarsi testaceous. Total length with head in orthognathous position excluding ovipositor 2.9 mm.

Head (figs. 7.1 a & b) elongate, parallel sided (l = 0.90, w = 0.55, h = 0.24). Eye oval (l = 0.36, w = 0.14, h = 0.07), 0.4X as long as head. Cheek length (l = 0.38) subequal to eye length. Malar sulcas present for first third of cheek. Very pronounced broad, medial prominence on vertex, dorsally upon which the ocelli are situated; strong carina present on posterior edge, fading out to the sides of the lateral ocelli. POL = 0.18, OOL = 0.07. Toruli situated below the eyes, touching. TE 0.75X as long as scrobe length (TE = 0.37, SL = 0.46). Clypeus narrow and elongate in area. ca. a quarter of the head width. Ventral tentorial pits in very close apposition, slightly closer to the foramen magnum than to the oral fossa (fig. 7.1 b). Mandible (fig. 7.1 f) with two apical teeth, inner shorter and two ventral teeth, proximal smaller - half the size of the distal tooth; two glands. Two labial segments, segments subequal. Three maxillary segments, basal segment shorter than distal two which are subequal (fig. 7.1 e). Antenna (fig. 7.1 c), flagella length = 0.57. Scape 7.5X longer than wide (l = 0.29). Pedicel relatively short, 0.35X scape length. MPS placoid, offset alternately from

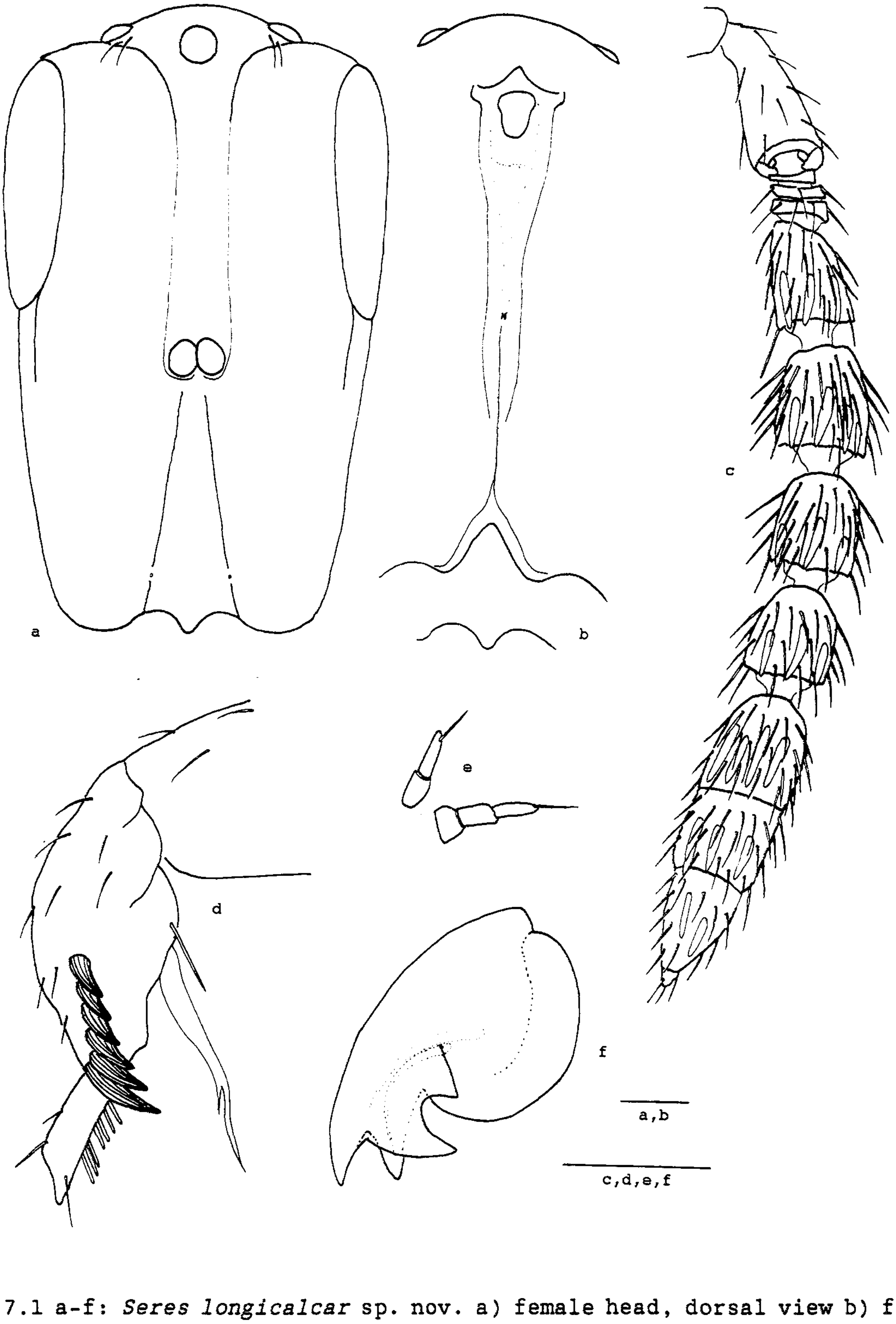


Fig. 7.1 a-f: *Seres longicalcar* sp. nov. a) female head, dorsal view b) female head, ventral view c) female antenna, antiaxial view d) female fore tibia and first tarsal segment e) female labial and maxillary palps f) female mandible, ventral view. Scale bars = 0.1 mm.

each other on dorsal surface, shorter and in even line ventrally; numerous strong sensilla, ventrally more prominent.

Thorax. Pronotum (l = 0.44, w = 0.49). Propodeum l = 0.24, w = 0.47, shallow, indistinct plical furrows present posteriorly to the medially situated spiracles. Mesoscutum l = 0.41, w = 0.55.

Scutellum, including axillae (l = 0.43, w = 0.44). Fore femur 4X as long as wide (l = 0.59). Fore tibial armature consists of a comb of six or seven teeth (fig. 7.1 d), bifurcate spur elongate. Fore leg coxa ca. four-fifths of femur length (C = 0.46, TR = 0.16, TI = 0.20, TA = 0.29). Fore wing 2.5X longer than wide, l = 2.07, sparse, maximum fringe length = 0.04. Postmarginal vein longer than stigmal (SM = 0.69, M = 0.33, PM = 0.27, S = 0.18). Marginal vein 11X longer than wide. Hind wing 3.9X longer than wide, l = 1.52.

Gaster. Posterior edge of tergites smooth with five incisions. Eighth urotergite spiracle with very small peritreme (l = 0.07). Ovipositor 3.7X as long as valve (valve l = 0.40).

Seres wardi **sp. nov.**

(figs. 7.2 a-f & 7.3 a-e)

Etymology: Named in memory of Dr. Mark Ward who tragically lost his life at an early age.

Type material: Holotype ♀ (slide mounted): South Africa, Natal, Eastern shore of Lake Sibaya, 30 July 1989, leg. M. Ward, C73, ex *F. bubu* Warb. Paratypes, 5 ♀ (3 slide mounted, 2 card mounted): same data as holotype.

FEMALE. Metallic green/black, antennae, tibia and tarsi testaceous. Total length with head in orthognathous position excluding ovipositor 2.4 mm.

Head (figs. 7.2 a & b) elongate, parallel sided (l = 0.78, w = 0.6, h = 0.14), thin wedge in lateral view, very compressed dorso-ventrally. Eye very elongate (l = 0.32, w = 0.11, h = 0.07), 0.4X as long as head. Cheek length 0.85X eye length. Malar sulcas indistinctly present for first quarter of cheek length. Lateral ocelli half visible in dorsal view, situated in the axial lip of shallow lateral excavations on the vertex. Vertex with medial prominence ventral to ocelli. Occipital carina runs along posterior edge of the prominence, bordering and dorsal to the foramen magnum invagination into the vertex. POL = 0.17, OOL = 0.11. Toruli situated below the eyes, touching. TE 0.85X as long as scrobe length (TE = 0.33, SL = 0.39). Clypeus narrow and elongate in area. Epistomal margin subquadrate, with shallow concavity in anterior edge, ca. a quarter of the head width. Ventral tentorial pits in close apposition, situated ca. half way between the foramen magnum and the oral fossa (fig. 7.2 b). Mandible (fig. 7.2 d) with two apical teeth, one ventral tooth from which a sharp edge leads to the base of the mandible, two glands. Two labial palp segments, subequal in length. Three maxillary palp segments, ca. in ratio 1:2:4 (fig. 7.2 e). Antenna (fig. 7.2 c), funicle segments subequal in size; club tapering to apex. Antennal flagellum (l = 0.45). Scape 9.4X longer than wide (l = 0.28). Pedicel relatively short, 0.32X scape length. MPS placoid, offset from one another, reduced on the ventral antennal surface. First funicle segment dorso-ventrally flattened, rest progressively becoming more cylindrical towards apex.

Thorax. Pronotum broad (l = 0.38, w = 0.52), torpedo shaped. Propodeum l = 0.19, w = 0.53, spiracles medially situated. Mesoscutum l = 0.37, w = 0.61. Scutellum, including axillae (l = 0.42, w = 0.48). Fore femur 3.5X as long as wide (l = 0.60). Fore tibial armature consists of a plate of many teeth, two-thirds of which is fused with the dorso-adaxial length of the tibia (fig. 7.2 f). At the apex of the plate a single much larger tooth is present. Tibial plate same length as tibia. Fore leg

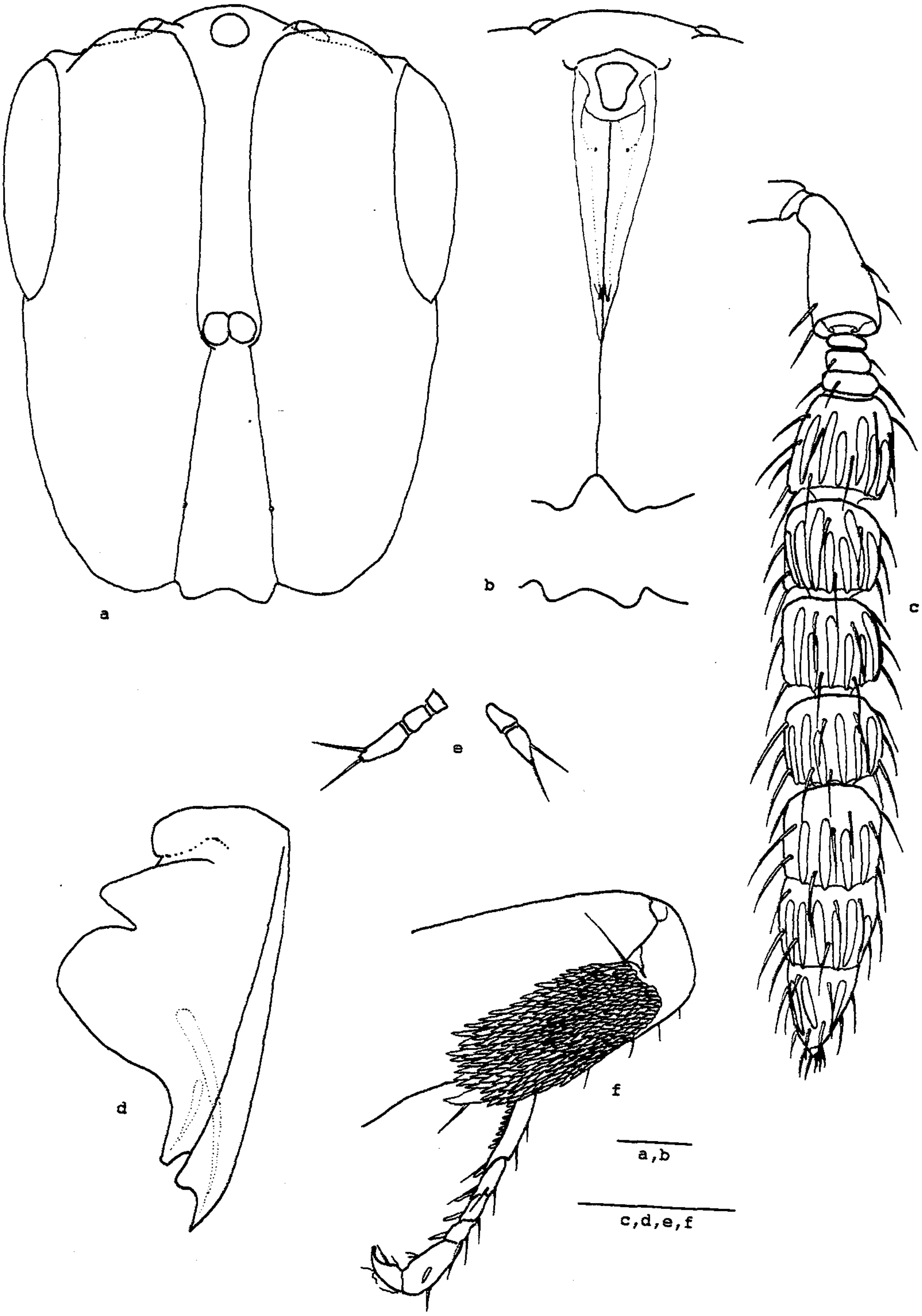


Fig. 7.2 a-f: *Seres wardi* sp. nov. a) female head, dorsal view b) female head, ventral view c) female antenna, antiaxial view d) female mandible, ventral view e) female labial and maxillary palps f) female fore tibia and tarsus, antiaxial view. Scale bars = 0.1 mm.

coxa 0.58X femur length (C = 0.35, TR = 0.14, TI = 0.27, TA = 0.31). Fore wing 2.4X longer than wide, l = 1.82, glabrous, maximum fringe length = 0.02, very fine. Postmarginal vein longer than stigmal (SM = 0.61, M = 0.26, PM = 0.22, S = 0.16). Marginal vein 8.7X longer than wide. Hind wing 3.7X longer than wide, l = 1.36.

Gaster. Posterior edge of tergites smooth with five evenly spaced incisions. Eighth urotergite spiracle with a large and ovoid peritreme (l = 0.096). Ovipositor 3.6X as long as valve (valve l = 0.38).

MALE. Head metallic green, rest of body testaceous. Total length with head in orthognathous position 2.34 mm.

Head (figs. 7.3 a & b) slightly broader than long, narrowing anteriorly (l = 0.59, w = 0.62, h = 0.24). Eye elongate, 2.1X longer than wide (l = 0.32), protrudes laterally (h = 0.1), 0.54X as long as the head. Cheek length 0.44X eye length. Malar sulcus present for posterior half of cheek length. POL = 0.18, OOL = 0.09. Toruli situated in line with the base of the eyes, separated by ca. a fifth of a torulus width. TE 2.3X longer than the scrobe length (TE = 0.16, SL = 0.37). Epistomal margin slightly convex with a shallow medial concavity, 0.14X as wide as the head. The paraclypeal margins extend further anteriorly than the epistomal margin. Ventral tentorial pits well separated (fig. 7.3 b). Mandible female-like, with a larger outer apical tooth, a unicuspid subapical tooth and a ventral apical tooth extending as a ridge towards the base of the mandible (fig. 7.3 e). Two labial palp segments, basal shortest. Three maxillary palp segments, distal 3X longer than the basal, 1.5X longer than the medial. Antenna (fig. 7.3 c), flagella length 3.1X as long as the pedicel. Scape 5.7X longer than wide (l = 0.34). Pedicel 0.35X scape length. Three anelli, four funicle segments with numerous thin MPS present on all the funicle and club segments.

Thorax. Parapsidal furrows complete, straight. Fore femur 3.4X longer than wide (l = 0.57). Fore tibial armature with a single strong tooth accompanied by 1-3 strong setae (fig. 7.3 d). Fore tibia 1.46X longer than the fore tarsal length (C = 0.35, TR = 0.15, TI = 0.41, TA = 0.28). Fore wing 2.5X longer than wide (l = 1.9), very pilose. Postmarginal vein longer than stigmal (SM = 0.60, M = 0.33, S = 0.17, PM = 0.22). Marginal vein thick, only 7.8X longer than wide. Hind wing 3.9X longer than wide (l = 1.45).

Gaster. Eighth urotergite spiracular peritremata slightly expanded. Aedeagus small (l = 0.40). Five teeth on aedeagus claspers.

Seres armipes Waterston

(figs. 7.3 g-i, 7.4 d & 7.5 d)

Seres a. armipes Waterston 1919, 276-277, Holotype ♀, Ghana. Waterston 1920, 135, fig. 3. Grandi 1952, 34-38, redescription of female, Senegal. [Examined paratype, The Natural History Museum, London, with following data: Gold Coast, Accra, leg. Dr. J.W.S. Macfie).
Seres longicephalus Risbec 1951, 381-383, fig. 171, holotype ♀, Senegal, **syn. n.** [Examined 5 ♀ types, Museum National d'Histoire Naturelle, Paris].

Additional material: Series ♀ and ♂: Ivory Coast, Lamto, 11-12 November 1982, leg. C.C. Berg & J.T. Wiebes, no 1440, RMNH 4773, ex *F. ovata* Vahl (det. Berg).

FEMALE. Head (fig. 7.4 d). Antenna (fig. 7.5 d).

MALE. Testaceous, eyes darker. Total length with head in orthognathous position 2.51 mm.

Head (fig. 7.3 g) elongate, parallel sided (l = 0.60, w = 0.54), height normal (h = 0.33). Eye elongate (l = 0.25, w = 0.14), protrudes laterally (h = 0.08), 0.43X as long as the head. Cheek length ca. half of eye length. POL = 0.12, OOL = 0.16. TE 0.29X as long as scrobe length (TE = 0.11, SL = 0.38). Width of clypeal margin ca. two fifths of head width. Mandible (fig. 7.3 h) with inner tooth bicuspid. Antenna (fig. 7.3 i), flagellum (l = 0.30) 2.5X as long as pedicel. Scape 4.3X longer than wide (l = 0.26). Pedicel very elongate, 0.46X scape length. Placoid MPS present on all four funicle segments and the three club segments.

Thorax. Fore femur 2.9X longer than wide (l = 0.53). Fore tarsus half of tibial length (C = 0.40, TR = 0.13, TI = 0.37, TA = 0.19). Fore wing 2.65X longer than wide, l = 1.72. Postmarginal vein shorter than stigmal (SM = 0.60, M = 0.25, S = 0.13, PM = 0.11). Marginal vein 5X longer than wide. Hind wing 4.1X longer than wide, l = 1.24.

Eighth urotergite spiracle small and round. Aedeagus small (l = 0.47). Five or six teeth on aedeagus claspers.

Comments. The eye length of the types of *S. longicephalus* [*S. longicephala* as originally named by Risbec (1951); corrected to *S. longicephalus* by Wiebes (1970)] is in fact a third of the head length, as in *S. a. armipes* and not a seventh of the head length as described and figured by Risbec (1951). After examination of the type slide which has five females mounted on it, (one without a head and two with squashed heads), I conclude that *S. longicephalus* is a junior synonym of *S. a. armipes*.

Seres armipes breviceps Wiebes
(figs. 7.4 c, e & 7.5 c)

S. a. breviceps Wiebes 1961, 233, holotype ♀, Uganda.

Additional material: Allotype ♂ (slide mounted): Uganda, Entebbe Botanical Gardens, 14 October 1967, leg. D.S. Hill, tree 13, RMNH 1350, ex *F. brachypoda* Hutch. (= *F. ovata* Vahl); Series ♀ and ♂

paratypes: same data; 8 ♀, 1 ♂: Uganda, Kampala, 1968, leg. W.A. Rykes - Jongbloed, RMNH 1361, ex *F. ovata* Vahl.

FEMALE. Head (fig. 7.4 e), mandible (fig. 7.4 c) and fore tibial armature and tarsus (fig. 7.5 c).

MALE. Testaceous, mandibles darker. Total length with head in orthognathous position 2.67 mm.

Head much as in *S. a. armipes* (fig. 7.3 g), elongate, parallel sided (l = 0.60, w = 0.56), height normal (h = 0.31). Eye elongate (l = 0.26, w = 0.15), protrudes laterally (h = 0.08), 0.43X as long as head. Cheek length 0.54X eye length. POL = 0.11, OOL = 0.15. TE 0.37X as long as scrobe length (TE = 0.13, SL = 0.35). Width of clypeal margin ca. two fifths of head width. Ventral tentorial pits slightly separated. Mandible as in *S. l. longivena* (fig. 7.3 f). Antenna much as in *S. a. armipes* (fig. 7.3 g), flagellar length (l = 0.36) 3X as long as pedicel. Scape 5.4X longer than wide (l = 0.29). Pedicel elongate, 0.41X scape length. Placoid MPS present on all four funicle segments and the three club segments.

Thorax. Femur 3.3X as long as wide (l = 0.56). Tibia 1.5X tarsal length (C = 0.41, TR = 0.14, TI = 0.39, TA = 0.26). Two spines on adaxial dorsal margin of hind tibia. Fore wing 2.7X longer than wide, l = 2.05. Postmarginal vein longer than stigmal (SM = 0.65, M = 0.29, S = 0.16, PM = 0.18). Marginal vein 4.8X longer than wide. Hind wing l = 1.35, w = 0.30.

Eighth urotergite spiracle small and round. Aedeagus small (l = 0.64). Five teeth on aedeagus claspers.

Seres solweziensis **sp. nov.**

(figs. 7.4 b & 7.5 a)

Etymology: Named after the type locality.

Type material: Holotype ♀ and allotype ♂ (slide mounted): Zambia, NW Province, Chingda, Solwezi 156 km, 25 February 1982, leg. C.C. Berg and M.G. Bingham, no. 1418, RMNH 4591, ex *F. ovata* Vahl; series ♀ and ♂ paratypes: same data; 2 ♀: Zimbabwe, Mashonaland, Bindura, R. Pare's farm, 27 September 1987, leg. A.J. Gardiner, C51, ex *F. s. sansibarica* Warb.; 2 ♂: South Africa, Transvaal, Kruger National Park, Olifants Camp, 23 January 1987, leg. S.G. Compton & V.K. Rashbrook, C14, ex *F. s. sansibarica* Warb.; series ♀ and ♂: Zambia, 15 km north of Lusaka, 19 July 1990, leg. S.G. Compton, C308, ex *F. s. sansibarica* Warb.; series ♀ and ♂: Senegal, Keniya, 21 March 1980, leg. J. Etienne, SR 151, RMNH 4112, ex *F. p. polita*? Vahl [host record inferred from associated agaonine = *Courtella bekiliensis bispinosa* (Wiebes)]; 2 ♀, 1 ♂: Ivory Coast, Lamto, 5 02'W 6 13'N, 22 June 1989, leg. J-Y. Rasplus, ex *F. p. polita* Vahl.

FEMALE. Uniform. Total length with head in orthognathous position excluding ovipositor 2.4 mm.

Head (fig. 7.4 b & 7.5 a) elongate, parallel sided (l = 0.74, w = 0.44, h = 0.20). Eye elongate (l = 0.28, w = 0.15, h = 0.06), 0.41X as long as head. Cheek length 1.05X eye length. POL = 0.10, OOL = 0.12. TE subequal to scrobe length (TE = 0.35, SL = 0.34). Epistomal margin protrudes less than the paraclypeal margins, width a quarter of the head width. Mandible with two ventral teeth (fig. 7.5 a). Antenna as in *S. l. longivena* (fig. 7.4 h), flagellum (l = 0.52) shorter than head length. Scape narrow, 6.1x longer than wide (l = 0.23). Pedicel relatively short, 0.35X scape length. Funicle segments in shape of arrow in dorsal view such that the second segment is the widest tapering to club tip, dorso-ventrally flattened. Many placoid MPS in close apposition and in a single row on each flagella segment.

Thorax. Pronotum square (l = 0.39, w = 0.38), trapezoid. Propodeum l = 0.20, w = 0.40. Mesoscutum l = 0.33, w = 0.45.

Scutellum, including axillae l = 0.34, w = 0.36. Femur 3.7X as long as wide (l = 0.55). Tibial armature consists of three combs of 8, 8 & 2 teeth. Fore leg coxa 0.71X femur length (C = 0.39, TR = 0.10, TI = 0.19, TA = 0.26). Fore wing 2.5X longer than wide, l = 1.74, maximum fringe length = 0.035. Postmarginal vein shorter than stigmal (SM = 0.65, M = 0.20, PM = 0.10, S = 0.13). Marginal vein 6.7X longer than wide. Hind wing 3.5X longer than wide, l = 1.24.

Gaster. Eighth urotergite spiracle normal, l = 0.05. Ovipositor 3.3X as long as valve (valve l = 0.44).

MALE
Indistinguishable from the *S. armipes breviceps* male.

Comments. There is some variation present between samples. The specimens ex *F. ovata* have shorter heads (the length to width ratio in the range 1.61 to 1.67), and the gaster is 3.2X longer than the ovipositor valves. Those ex *F. p. polita* have more elongate heads (the length to width ratio ranging from 1.80 to 1.91), and the gaster is only 2.7X longer than the valves. Those ex *F. s. sansibarica* have head shapes intermediate between the two previous samples with length to width ratios ranging from 1.68 to 1.77, and gasters 2.4 to 2.8X longer than the valves.

This species as here defined may thus prove to be three distinct taxa at species or subspecies level, but based on the few samples available (only a single collection from *F. ovata* and two from *F. p. polita* and *F. s. sansibarica*) I do not believe that a separation is warranted at this stage. Once the host records have been clarified and adequate samples have been collected, the delimitation of the species can be revised. The females of *S. solweziensis* can immediately be distinguished by the flat epistomal margin which protrudes no further than the paraclypeal margins (additionally, in slide mounted specimens a distinct ventral, second epistomal margin is distinguishable, fig 7.4 b).

***Seres longivena* sp. nov.**

(figs. 7.3 f, 7.4 a, d, e, h & 7.5 b)

Etymology: Longus (latin) = long, vena (latin) = vein, referring to the longer marginal vein in the forewing of the males.

Type material: Holotype ♀ and allotype ♂ (slide mounted): Zambia, North West Province, Kabombo, 23 February 1988, leg. R.J. Nefdt, C125, ex *F. sansibarica* Warb. *?macrosperma* (Mildbr. & Burr.); series ♀ and ♂ paratypes: same data except: 15 February 1988, C142.

FEMALE. Uniform. Total length with head in orthognathous position excluding ovipositor 2.7 mm.

Head (figs. 7.4 a & 7.5 b) elongate, parallel sided (l = 0.89, w = 0.48, h = 0.23). Eye elongate (l = 0.32, w = 0.14, h = 0.06), 0.35X as long as the head. Cheek length 1.4X eye length. POL = 0.11, OOL = 0.13. TE 1.1X as long as scrobe length (TE = 0.42, SL = 0.39). Epistomal margin protrudes further than angular paraclypeal margins, ca. a quarter of the head width. Mandible with three ventral teeth, third tooth much shorter than first two (fig. 7.4 e & 7.5 b). Labial and maxillary palps (fig. 7.4 d). Antenna (fig. 7.4 h), flagellum (l = 0.51), shorter than head length. Scape 5.8X longer than wide (l = 0.23), 2.3X longer than pedicel. Funicle segments in shape of arrow in dorsal view such that the second segment is the widest tapering to club tip, dorso-ventrally flattened. Many placoid MPS in close apposition, present as a single row on each of the flagella segments.

Thorax. Pronotum elongate (l = 0.49, w = 0.41), trapezoid. Parapsidal furrows evenly curved. Propodeum l = 0.21, w = 0.44. Mesoscutum l = 0.38, w = 0.49. Scutellum, including axillae broad (l = 0.37, w = 0.41). Fore tibia with a row of nine teeth on the antiaxial anterior margin and two rows consisting of seven and one to four teeth respectively, situated dorsal of the first row.

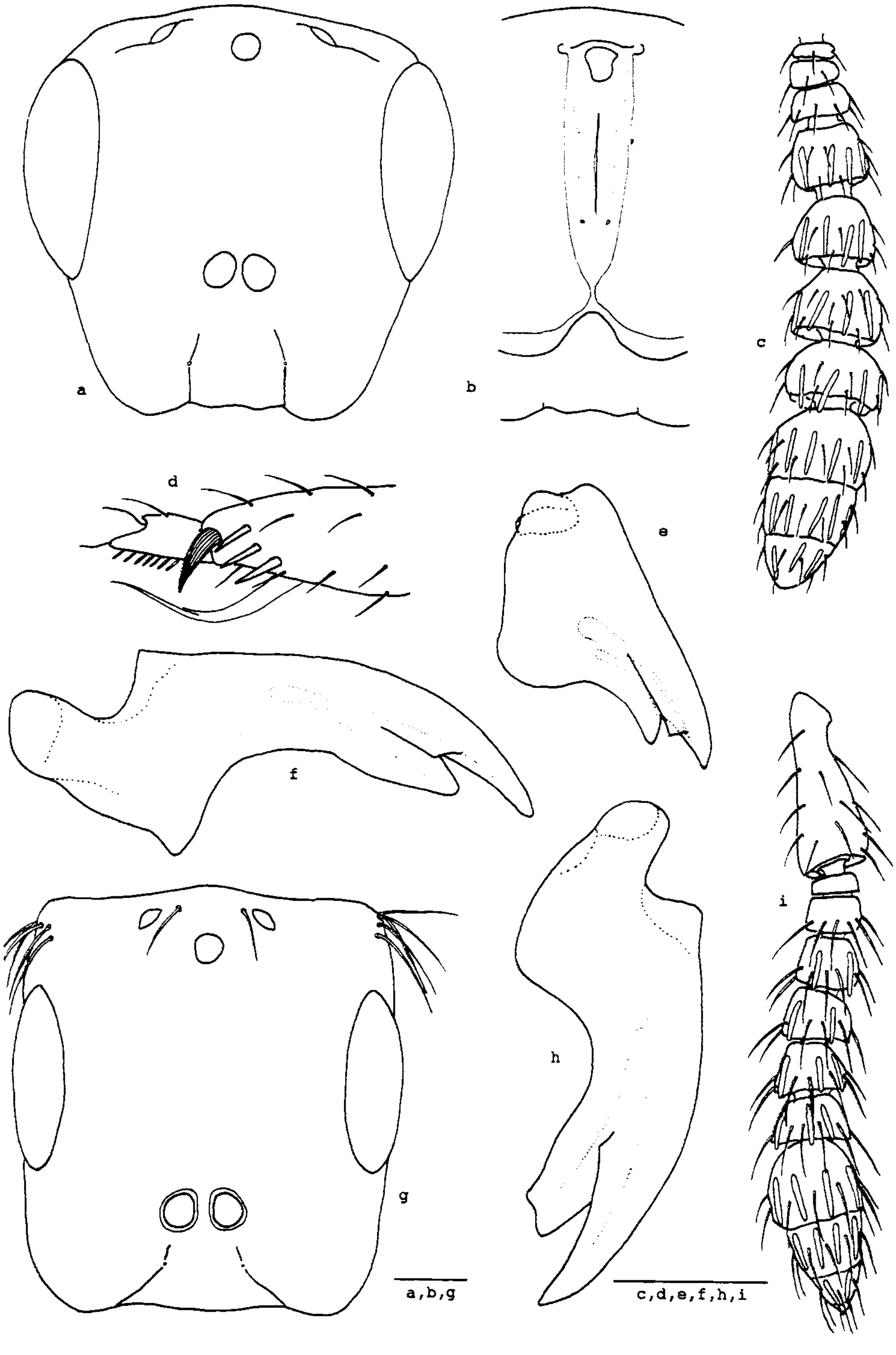


Fig. 7.3 a-e: *Seres wardi* sp. nov. a) male head, dorsal view b) male head, ventral view c) male antenna, dorsal view d) male fore tibia (in part) and first tarsal segment e) male mandible, ventral view; f: *S. l. longivena* sp. nov. f) male mandible, ventral view; g-i: *S. a. armipes* Waterston g) male head, dorsal view h) male mandible, ventral view i) male antenna, antiaxial view. Scale bars = 0.1 mm.

Fore femur 3.9X as long as wide (l = 0.64). Fore leg coxa 0.58X femur length (C = 0.37, TR = 0.14, TI = 0.20, TA = 0.26). Fore wing 2.6X longer than wide, l = 1.90, maximum fringe length = 0.03. Postmarginal vein subequal to stigmal (SM = 0.67, M = 0.24, PM = 0.13, S = 0.14). Marginal vein 7.5X longer than wide. Hind wing 3.8X longer than wide, l = 1.38.

Gaster. Eighth urotergite spiracle, l = 0.04. Ovipositor 2.9X as long as the ovipositor valves (valve l = 0.65). Valves 0.38X gaster length.

MALE. Testaceous. Total length with head in orthognathous position 2.5 mm.

Head much as in *S. a. armipes* (fig. 7.3 g) elongate, parallel sided (l = 0.66, w = 0.63), height normal (h = 0.31). Eye very elongate (l = 0.30, w = 0.15), protrudes laterally (h = 0.10), 0.46X as long as the head. Cheek length 0.47X eye length. POL = 0.12, OOL = 0.17. TE 0.36X as long as scrobe length (TE = 0.14, SL = 0.39). Width of clypeal margin approximately half the width of the head. Mandible as in *S. l. longivena* (fig. 7.3 f). Antenna much as in *S. a. armipes* (fig. 7.3 i), flagellum (l = 0.40) 3.3X as long as pedicel. Scape 4.7X longer than wide (l = 0.33), 2.8X longer than pedicel. Placoid MPS present on all four funicle segments and the three club segments.

Thorax. Fore femur 3X as long as wide (l = 0.60). Fore tibia 1.33X longer than the fore tarsus (C = 0.46, TR = 0.16, TI = 0.40, TA = 0.30). Fore wing 2.5X longer than wide, l = 2.14. Postmarginal vein same length as stigmal (SM = 0.76, M = 0.35, S = 0.15, PM = 0.15). Marginal vein 7X longer than wide. Hind wing 4.5X longer than wide, l = 1.63.

Gaster. Eighth urotergite spiracle small and round. Aedeagus small (l = 0.54). Five teeth on aedeagus claspers.

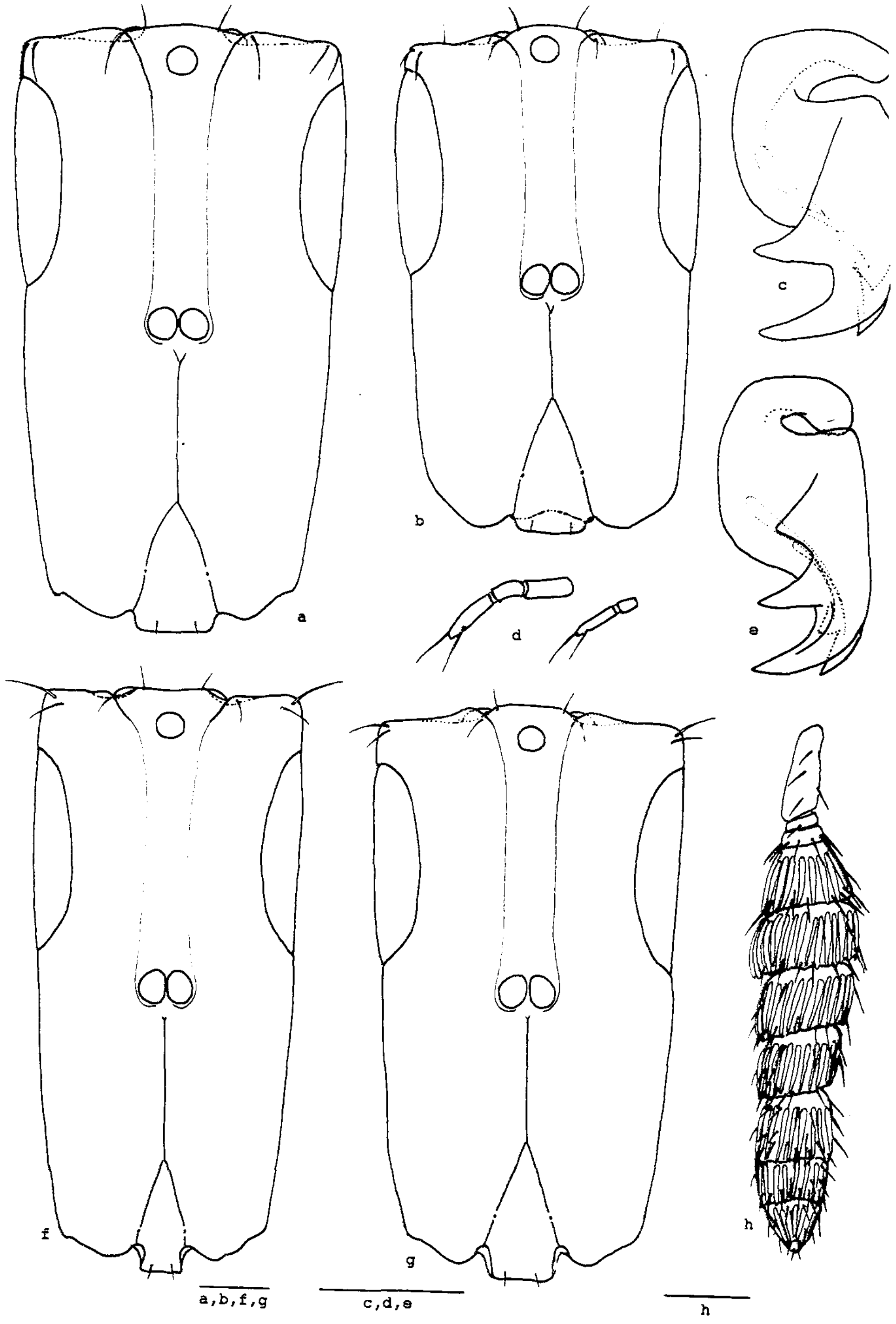


Fig. 7.4 a, d, e & h: *Seres longivena* sp. nov. a) female head, dorsal view d) female labial and maxillary palps e) female mandible, ventral view h) female antenna, dorsal view; b: *Seres solweziensis* sp. nov. b) female head, dorsal view; c & g: *Seres armipes breviceps* Wiebes c) female mandible, ventral view g) female head, dorsal view; f: *Seres armipes* Waterston f) female head, dorsal view. Scale bars = 0.1 mm.

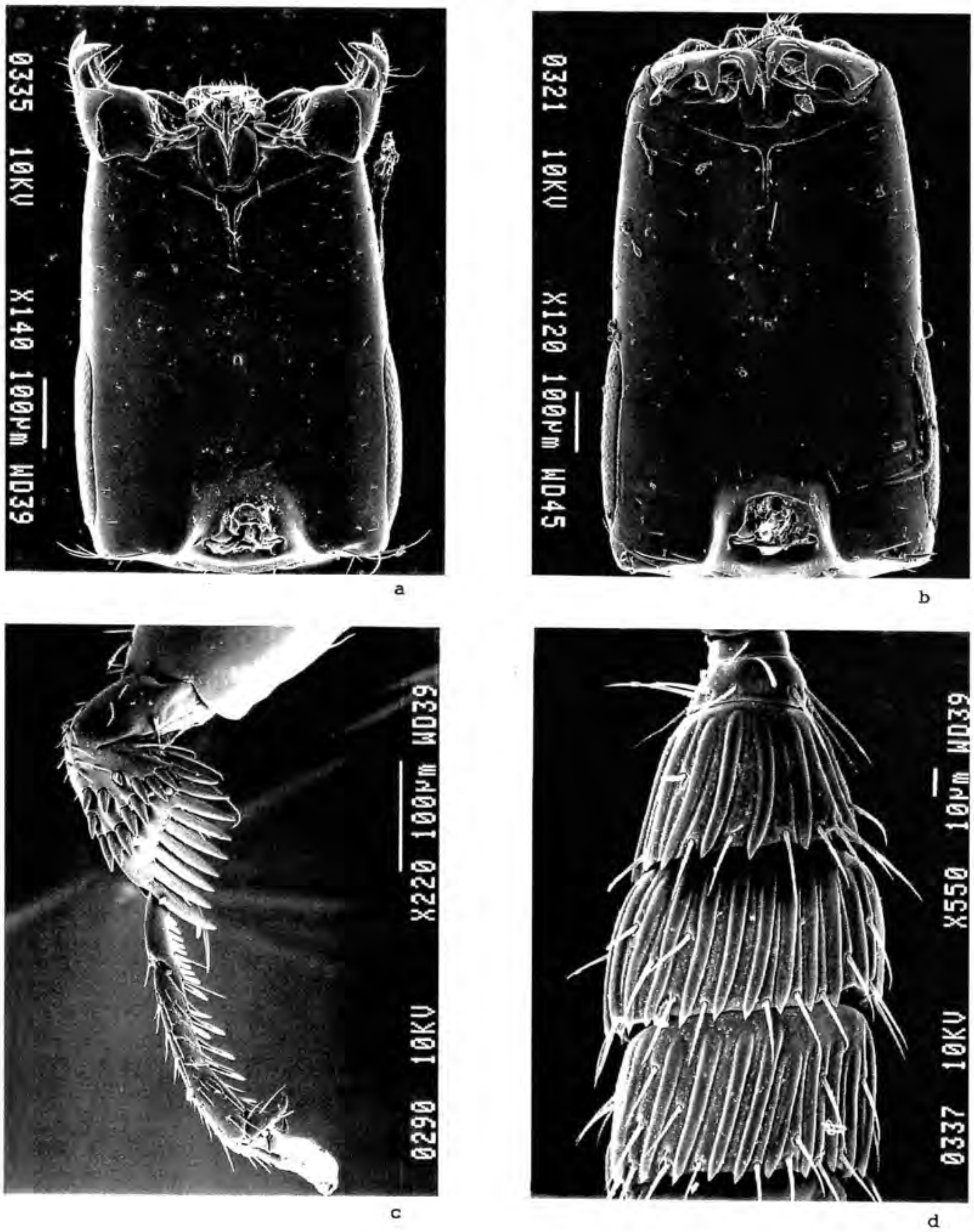


Fig. 7.5 a: *Seres solweziensis* sp. nov. a) female head, ventral view b: *S. longivena* sp. nov. b) female head, ventral view c: *Seres armipes breviceps* Wiebes c) female fore tibia and tarsus, antiaxial view d: *Seres armipes* Waterston d: female antenna - anelli and first three funicle segments, dorsal view.

Comments. This species is immediately distinguishable from *S. solweziensis*, which also occurs in Zambia, by the anteriorly projecting epistomal margin. *S. l. longivena* is very similar to *S. a. breviceps* from which it can be separated by the possession of three ventral mandibular teeth as opposed to two, longer ovipositor valves and a more elongate head. The two species may also be geographically separated.

Seres longivena bidens subsp. nov.

Etymology: Bidens (latin) = having two teeth, referring to the female ventral mandibular dentition.

Type material: Holotype ♀ and allotype ♂ (slide mounted): Ivory Coast, Taï, 17 February 1980, leg. D. Lachaise & G. Couturier, F.47, RMNH 4065 & 4070, ex *F. sansibarica* Warb. *macrosperma* (Mildbr. & Burret); series ♀ and ♂ paratypes: same data; 1 ♀: Ivory Coast, Taï, leg. D. Lachaise & G. Couturier, 23 February 1980, RMNH 4086, ex *F. sansibarica* Warb. *macrosperma* (Mildbr. & Burr.), (found dead in young syconium).

FEMALE. Head slightly more elongate than nominate subspecies (l = 0.90, w = 0.47). Mandible with only two ventral teeth, as in *S. a. breviceps* (fig. 7.4 c). Ovipositor valves much longer than the nominate subspecies, half the length of the gaster.

MALE. Indistinguishable from the nominate subspecies.

Comments. This subspecies is distinguishable from *S. a. armipes*, which also occurs in Ivory Coast, by its less elongate head.

DISCUSSION

The species and subspecies in the *S. a. armipes* species complex, which includes *S. solweziensis* and *S. longivena*, are morphologically very similar and the current delimitation may prove to be incorrect. As a result of this similarity, host *Ficus* associations and geographic distribution (Table 7.1) where also considered in the delimitation of these species and subspecies.

Geographic variability has made species delimitation very difficult in this group. Head shape and ovipositor valve length appear to vary geographically within a species. This is likely to be a result of geographic variation in host fig size, since fig size affects both ostiole size and style length of the florets. As a result of this variation these two characters have not been used in the delimitation of the species. Instead two characters that are probably less likely to be influenced by fig size have been used. These are the extent of the protrusion of the epistomal margin and the presence/absence of a second ventral epistomal margin. In the current species delimitation these are geographically conservative.

TABLE 7.1. Host relationships and known distribution of the species and subspecies in the *Seres armipes* species group.

***Seres* species**	**Host**	**Locality**
S. a. armipes	*F. ovata*	Ghana, Senegal, Ivory Coast
S. a. breviceps	*F. ovata*	Uganda
S. solweziensis	*F. ovata*	Zambia
	F. p. polita	Senegal
	F. s. sansibarica	Zimbabwe, South Africa, Zambia
S. l. longivena	*F. s. ?macrosperma*	Zambia
S. l. bidens	*F. s. macrosperma*	Ivory Coast

Based on host associations, *S. solweziensis* from Zambia could be argued to be a subspecies of *S. armipes*. However, *S. solweziensis* also occurs in Senegal in west Africa in sympatry with *S. a. armipes* where these two species are morphologically distinct. The same is true for *S. longivena*, the Zambian population of which could be argued to be a subspecies of *S. armipes*. However, *S. longivena* is distinct from *S. armipes* in west Africa.

Many more collections of these species and records of their host relationships are required before any confidence can be placed in these species delimitations.

8

SYSTEMATICS OF *CROSSOGASTER*

INTRODUCTION

Crossogaster Mayr is one of the more derived sycoecine genera along with *Philocaenus* Grandi. Thirteen *Crossogaster* species are recognised, of which eleven are described here for the first time. They are associated with the *Ficus* subsections *Platyphyllae*, *Chlamydodorae* and *Caulocarpae* of section *Galoglychia*. One of the species, *C. oculagrandis* sp. nov., possesses character states associated with nocturnal flight, viz. large eyes and testaceous colouring, as do the species in the pollinator genus *Alfonsiella* Waterston.

GENERIC DEFINITION

Crossogaster Mayr

Crossogaster Mayr 1885: 189-192. Type species: *Crossogaster triformis* Mayr 1885, by original designation.

FEMALE. Head square to very elongate, may be dorso-ventrally compressed; smooth, without sculpture, except for the presence of multiple plicae on the vertex in species where the vertex is not excavated; clypeus reasonably broad to narrow, never dramatically produced; toruli touching, either situated in line with, or below the bases of the eyes; malar sulcus either present for varying degrees of cheek length or absent. Compound eyes situated posteriorly on face. Vertex either smooth, slightly concave, or flat and excavated laterally. Ventral tentorial pits distinctly separated, usually widely spaced but may be in close apposition; usually closer to the oral fossa than the foramen magnum. Hypostoma reduced or absent. Posterior portion of stipes usually overlaps hypostoma. Two maxillary palp segments, basal segment usually very short, one labial palp segment. Mandible with two apical teeth and a longitudinal ventral row of teeth, sometimes with a second or a second and third row anterior to this row; two glands. Dorsal tentorial pits situated on clypeal suture closer to the epistomal margin than to the toruli. Antenna eleven segmented, formula either 1115(3) or 1124(3), or twelve segmented, formula 1125(3). Multiporous plate sensilla (MPS), are either placoid and fused to the segments, or are elongate and free.

Thorax usually not compressed, smooth; pronotum square or elongate; mesonotum subtriangular to distinctly broader than long, semicircular, parapsidal sulci complete, straight to distinctly curved; propodeal spiracles anteriorly situated. Fore femur stout, elongate to subtriangular; tibial armature usually bidentate, may be tridentate. Ventral tooth next to spur insertion on fore tibia usually present, may be absent. Axial third of forewing glabrous, rest may be glabrous or pilose; fringe present. Postmarginal vein from distinctly longer to shorter than stigmal vein.

Gaster may have five to seven evenly spaced incisions on the posterior edge of the tergites, with the rest of the edge smooth, or the tergal edge may be crenulated with three medial, evenly spaced incisions. Eighth urotergite spiracle with an expanded peritreme of variable size.

MALE. Head square, cheeks short, paraclypeal margin distinctly protruding. Clypeus subtriangular in area, epistomal margin convex. Toruli separated, situated well below the base of the compound eyes, a quarter of the head length from the epistomal margin. Antenna eleven or twelve segmented, MPS very reduced in number. Dorsal tentorial pits situated on the clypeal sutures very close to the epistomal margin. Malar sulcus present or absent. Vertex convex, smooth; occipital carina reduced or absent. Ventral tentorial pits distinctly separated, close together to widely spaced. Two maxillary palp segments, basal shortest; one labial palp segment. Mandible with two apical teeth, inner tooth from just, to much longer than outer; two glands.

Thorax. Much as in the females; parapsidal sulci may be indistinct posteriorly. Fore tibia and femur normal. Wings more pilose than in females.

Gaster, posterior margin of tergites uniformally straight; aedeagus very small. Eighth urotergite spiracular usually normal, but may be slightly expanded.

Comments. *Crossogaster* can be recognised by the following autapomorphies: both sexes with one labial palp segment and two maxillary palp segments; the female eighth urotergite spiracular peritremata distinctly expanded; the male inner apical mandibular tooth is subequal (but still longer) to much longer than the outer tooth.

KEY TO THE SPECIES OF *CROSSOGASTER*:

FEMALES

1. First funicle segment twice the length of any of the rest, multiporous plate sensilla (MPS) short and stumpy (fig. 8.2 a); first tarsal segments of the mid and hind legs expanded and enlarged, ex *F. s. sansibarica* .... *C. inusitata*
 - First funicle segment subequal or shorter than the rest, MPS either placoid or free and elongate; first tarsal segments of the mid and hind legs not enlarged 2

2. Antenna twelve segmented with two anelli and five funicle segments (figs. 8.1 c & 8.3 e); head very elongate, more than 1.5X longer than wide 3
 - Antennae eleven segmented with either one anellus and five funicle segments (fig. 8.7 c) or two anelli and four

funicle segments (fig. 8.11 b); head less elongate, less than 1.3X longer than wide 4

3. Epistomal margin with a small medial convexity (fig. 8.1 a); cheek 1.48X longer than the eye, ex *F. artocarpoides* .... *C. michaloudi*
- Epistomal margin smooth (fig 8.3 a); cheek twice as long as the eye, ex *F. sansibarica macrosperma* .... *C. lachaisei*

4. Antennal MPS placoid, fused for at least three-quarters of their length to the segment (fig. 8.12 d); one or two anelli 5
- Antennal MPS elongate, free for at least half their length (figs. 8.6 h & 8.8 d,f); one anellus 11

5. Clypeal margin convex, sometimes with a medial concavity (figs. 8.11 d & 8.12 a,i) 6
- Clypeal margin flat, with a weak medial concavity (fig. 8.11 a,e,h) 9

6. Head elongate, at least 1.20X longer than wide, cheek at least 1.2X longer than the eye length; lateral ocelli completely visible in dorsal view (fig. 8.12 a,i) 7
- Head square; cheek length equal to eye length; lateral ocelli half hidden in dorsal view (fig. 8.11 d) 8

7. Head elongate, 1.20X longer than wide; cheek 1.2X eye length; epistomal margin medially straight (fig. 8.12 a), ex *F. trichopoda* (southern Africa) ..... *C. r. robertsoni*
- Head 1.26X longer than wide; cheek 1.26X eye length; epistomial margin medially acute (fig. 8.12 i), ex *F. trichopoda* (west Africa) .... *C. robertsoni rasplusi*

8. Two anelli, four funicle segments, as in (fig. 8.11 b) ex *Ficus* sp. .... *C. vansomereni*
- One anellus, five funicle segments, first funicle segment

reduced with only a single MPS present, as in (fig. 8.11 f) ex *F. vasta* .... *C. triformis*

9. Two anelli, four funicle segments (fig. 8.11 b), ex *Ficus* sp. .... *C. hilli*
- One anellus, five funicle segments, first funicle segment reduced with only a single MPS present (fig. 8.11 f) .. 10

10. Head ca. square, l:w = 1.06; cheek same length as eye (fig. 8.11 e), ex *Ficus* sp. .... *C. rashbrooki*
- Head elongate, l:w = 1.24; cheek 1.45X eye length, (fig. 8.11 h), ex *F. ovata* .... *C. ovata*

11. Head elongate, more than 1.2X longer than wide; malar sulcus present 12
- Head approximately square; malar sulcus absent 13

12. Clypeal margin medially pointed (fig 8.9 a); mandible with three rows of teeth (fig. 8.9 d), ex *Ficus* sp. .... *C. praeacuta*
- Clypeal margin slightly convex, set into paraclypeal margins (fig. 8.10 a); single row of 14 long teeth on mandible (fig. 8.10 b), ex *Ficus* sp. .... *C. rastellus*

13. Thorax and gaster testaceous 14
- Thorax and gaster metallic black or brown 15

14. Eye enlarged, 5.2X as long as cheek (fig. 8.8 a) .... *C. oculagrandis*
- Eye normal, 1.6X longer than cheek (fig. 8.7 a), ex *F. n. natalensis* .... *C. lurida*

15. Clypeal margin bilobed, with shallow medial concavity (fig. 8.6 a); eighth urotergite spiracular peritremata extremely expanded, horizontal diameter 0.61X the length of the ovipositor valves (fig. 8.6 f), ex *F. glumosa* .. *C. stigma*

- Clypeal margin slightly convex (fig. 8.6 e & 8.8 e); eighth urotergite spiracular peritremata less expanded, horizontal diameter 0.4X or less than the length of the ovipositor valves 16

16. Cheek length usually half of eye length, if longer than this then the vertex is concave; epistomal margin broader, width 0.31X or more than head width (fig 8.8 e); horizontal diameter of the eighth urotergite spiracular peritremata 0.28X the length of the ovipositor valves, ex *F. thonningii* & *F. stuhlmannii* .... *C. odorans*

- Cheek length 0.7X eye length, vertex always straight; epistomal margin narrower, width 0.27X head width (fig. 8.6 e); horizontal diameter of the eighth urotergite spiracular peritremata 0.4X the length of the ovipositor valves, ex *F. glumosa* .... *C. quadrata*

MALES*

1. Head metallic brown/black (possibly metallic green in fresh specimens), rest of body and antenna testaceous; mandibular apical teeth subequal, inner tooth just longer than outer, antennae with twelve segments, ex *F. artocarpoides* .... *C. michaloudi*

- Head and body testaceous, but may be dark brown on the vertex, scutellum and mesoscutum; inner mandibular tooth distinctly longer than outer, antennae with only eleven segments 2

2. Two types of multiporous plate sensilla (MPS) present, one short and stumpy, other narrow and free; first tarsal segments on the mid and hind legs expanded and enlarged, ex *F. sansibarica* .... *C. inusitata*

- Single MPS type - placoid; first tarsal segments on the mid and hind legs not enlarged 3

3. Epistomal margin medially convex (e.g. figs. 8.9 e & 8.10

c) 4

- Epistomal margin medially flat or concave (e.g. figs. 8.7 f, 8.8 h) 6

4. Cheek length less than 0.5X eye length, ex *F.* "*thonningii*" .... *C. hilli*

- Cheek length more than 0.6X eye length 5

5. Lobes of paraclypeal margins project further anteriorly than the epistomal margin (fig. 8.10 c); MPS only present on the last two club segments, ex *F.* "*natalensis*" .... *C. rastellus*

- Lobes of paraclypeal margins project anteriorly only as far as the epistomal margin (fig. 8.9 e); MPS present on all three club segments, ex *Ficus* sp. K .... *C. praeacuta*

6. Cheek length 0.4X or less than eye length; head quadrate or transverse 7

- Cheek length 0.57X or more than eye length; head slightly longer than wide 10

7. Epistomal margin flat but with slight medial indentation; MPS present on all three club segments, ex *F. n. natalensis* .... *C. lurida*

- Epistomal margin medially flat; MPS either only present on the last two club segments or present on all the club segments and one or two funicle segments 8

8. MPS only present on the last two club segments, ex *F. thonningii* .... *C. odorans*

- MPS present on all the club segments and either the last funicle segment or the last two funicle segments 9

9. Toruli separated by a fifth of the torulus width, axillae and parapsides dark brown; MPS present on the last funicle segment and all the club segments, ex *F. glumosa* .. *C. stigma*

- Toruli separated by a third of the torulus width, thorax uniformly testaceous; MPS present on the last two funicle segments and all the club segments, ex *F. glumosa* .... *C. quadrata*

10. Large species, total length with head in orthognathous position = 1.84 mm; MPS only present on the last funicle segment and all the club segments, ex *F. ovata* .. *C. ovata*
- Smaller species, total length with head in orthognathous position = 1.4 mm; MPS present on the last three funicle segments and all the club segments, ex *F. trichopoda* .... *C. robertsoni*

* The males of *C. lachaisei*, *C. vansomereni*, *C. rashbrooki* and *C. oculagrandis* are unknown.

The type male of *C. triformis* was not available for examination and since it was not sufficiently described by Mayr (1885) nor by Grandi (1928b) in his redescription to include it in the key, it has been omitted.

SPECIES DESCRIPTIONS

***Crossogaster michaloudi* sp. nov.**

(figs. 8.1 a-f; 8.2 c-e; 8.3 d)

Etymology: Named after G. Michaloud the collector of the holotype.

Type material: Holotype ♀ and allotype ♂ (slide mounted): Gabon, Makokou, 21 August 1978, leg. G. Michaloud, no. 1012, RMNH 3722 & 3724, ex *F. artocarpoides* Warb. [associated pollinator = *Courtella penicula* (Wiebes); series ♀ and ♂ paratypes: same data as holotype; series ♀, ♂: Uganda, Mpanga Forest, on Masata Road, 4 May 1969, leg. D.S. Hill, no. 58, ex *Ficus* sp. U. [= *F. artocarpoides* Warb., associated pollinator = *Courtella penicula* (Wiebes)]; series ♀, ♂:Gabon, Makokou/Mpassa, 28 November 1979, leg. G. Michaloud, no 147, RMNH 4893, ex *Ficus* probably *artocarpoides* Warb. (det. Berg) [associated pollinator = *Courtella hladikae* (Wiebes) and 1 ♀ *Courtella camerunensis* (Wiebes), a straggler? as suggested by Wiebes in Michaloud *et* *al.*, (1985)]; 17 ♀: Ivory Coast, Taï Forest, 27 February 1980, leg. D. Lachaise & G. Couturier, no. F 56, RMNH 4088, ex *Ficus* probably *artocarpoides* (det. Berg) [associated pollinator = *Courtella hladikae* (Wiebes)].

FEMALE. Uniform. Total length with head in orthognathous position excluding ovipositor 3.0 mm.

Head (fig. 8.1 a-b) elongate, parallel sided (l = 0.95, w = 0.63, h = 0.25). Eye oval (l = 0.28, w = 0.21, h = 0.10), 0.31X as long as the head. Cheek length 1.5X eye length. Malar sulcas present for full cheek length, sinusoidal, anterior third manifested as a wider fovea. Lateral ocelli half visible in dorsal view, situated in axial lip of lateral vertex excavations. POL = 0.21, OOL = 0.07. TE 1.18X as long as scrobe length (TE = 0.46, SL = 0.39). Clypeus equilateral in area, clypeal sutures meet before toruli. Epistomal margin concave with small medial convexity, width ca. a quarter of the head width. Ventral tentorial pits only slightly separated (fig 8.1 b). One labial palp segment and two maxillary palp segments (fig. 8.1 e). Mandible with two apical teeth, first ventral tooth short and stout, remaining fourteen ventral teeth long and slender; two glands (fig. 8.1 d). Hypostoma absent. Antenna (fig. 8.1 c) twelve segmented, formula 1125(3), flagellum l = 0.57. Scape 6.45X longer than wide (l = 0.29). Pedicel elongate 0.38X scape length. MPS placoid, numerous, close together.

Thorax. Pronotum (l = 0.45, w = 0.50), torpedo shaped. Parapsidal furrows complete, evenly curved. Propodeum l = 0.25, w = 0.55, plical furrows absent, spiracles anteriorly situated. Mesoscutum l = 0.41, w = 0.59. Scutellum, including axillae (l = 0.45, w = 0.47). Fore femur 3.9X as long as wide (l = 0.57). Fore tibial armature bidentate (fig. 8.1 f). No ventral tooth next to spur insertion. Fore leg coxa 0.70X femur length (C = 0.40, TR = 0.13, TI = 0.20, TA = 0.30). Fore wing 2.5X longer than wide, l = 2.21, sparse, maximum fringe length = 0.03. Postmarginal vein longer

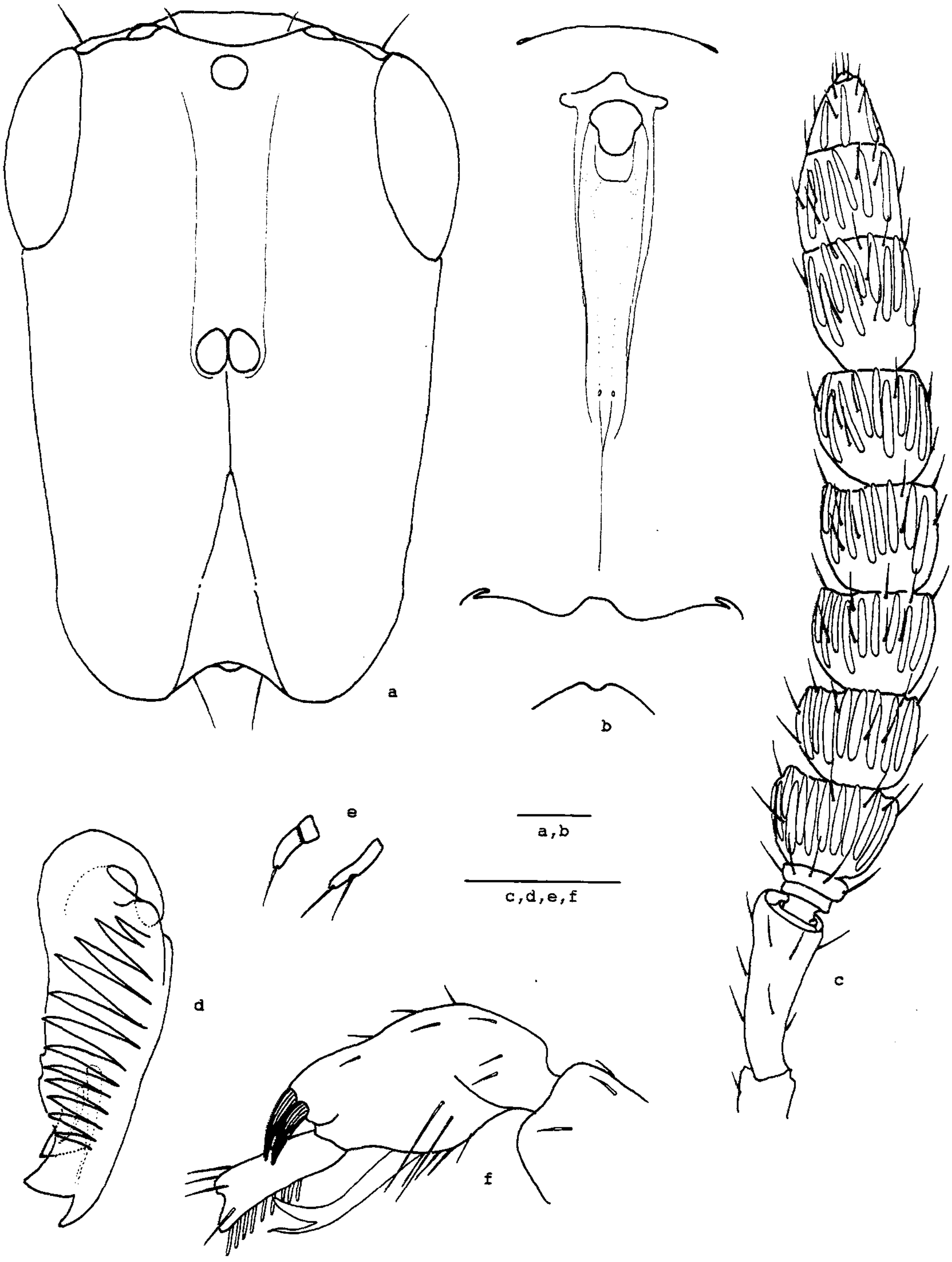


Fig. 8.1 a-f: *Crossogaster michaloudi* sp. nov. a) female head, dorsal view b) female head, ventral view c) female antenna, dorsal view d) female mandible, ventral view e) labial and maxillary palps f) fore tibia and first fore tarsal segment, antiaxial view. Scale bars = 0.1 mm.

than stigmal (SM = 0.76, M = 0.33, PM = 0.24, S = 0.17). Marginal vein 11X longer than wide. Hind wing 3.7X longer than wide, l = 1.61.

Gaster tergite smooth with five evenly spaced incisions. Eighth urotergite peritremata large and ovoid (l = 0.14), with a few large setae around the edges. Ovipositor 4.3X as long as valve (valve l = 0.36).

MALE. Testaceous, mesoscutum, scutellum and axillae darker, head metallic dark brown. Total length with head in orthognathous position, excluding ovipositor valves = 3.1 mm.

Head (fig. 8.2 c-d) slightly broader than long (l = 0.64, w = 0.67, h = 0.30). Eye elongate (l = 0.29, w = 0.19, h = 0.11), 0.45X as long as head. Cheek length 0.59X eye length. Malar sulcus present for first two-thirds of cheek but very faint. Lateral ocelli visible in dorsal view, thin occipital carina. POL = 0.16. OOL = 0.08. Toruli situated below the eyes, separated by four-fifths of torulus width. TE 0.34X as long as scrobe length. TE = 0.13. SL = 0.38. Clypeus trapezoid in area. Epistomal margin very convex, width of margin 0.43X head width; paraclypeal margins project slightly more than the epistomal margin. Ventral tentorial pits closer together than other *Crossogaster* species (fig. 8.2 d). Inner tooth of mandible only slightly longer than the outer, subequal in size, inner margin smooth, outer apical tooth with a small ventral tooth at the base of the tooth, two glands (fig. 8.3 d). One labial palp segment; two maxillary palp segments, distal only slightly longer. Antennae (fig 8.2 e) twelve segmented, formula 1125(3). Flagellum (l = 0.51), 4.25X longer than pedicel. Scape broad 4X longer than wide (l = 0.28). Pedicel 0.43X scape length. MPS are placoid, present on the last four funicle segments and the club segments.

Thorax. Parapsidal furrows complete. Fore femur 3.3X longer than wide (l = 0.63). Fore tibial armature bidentate, no ventral tooth

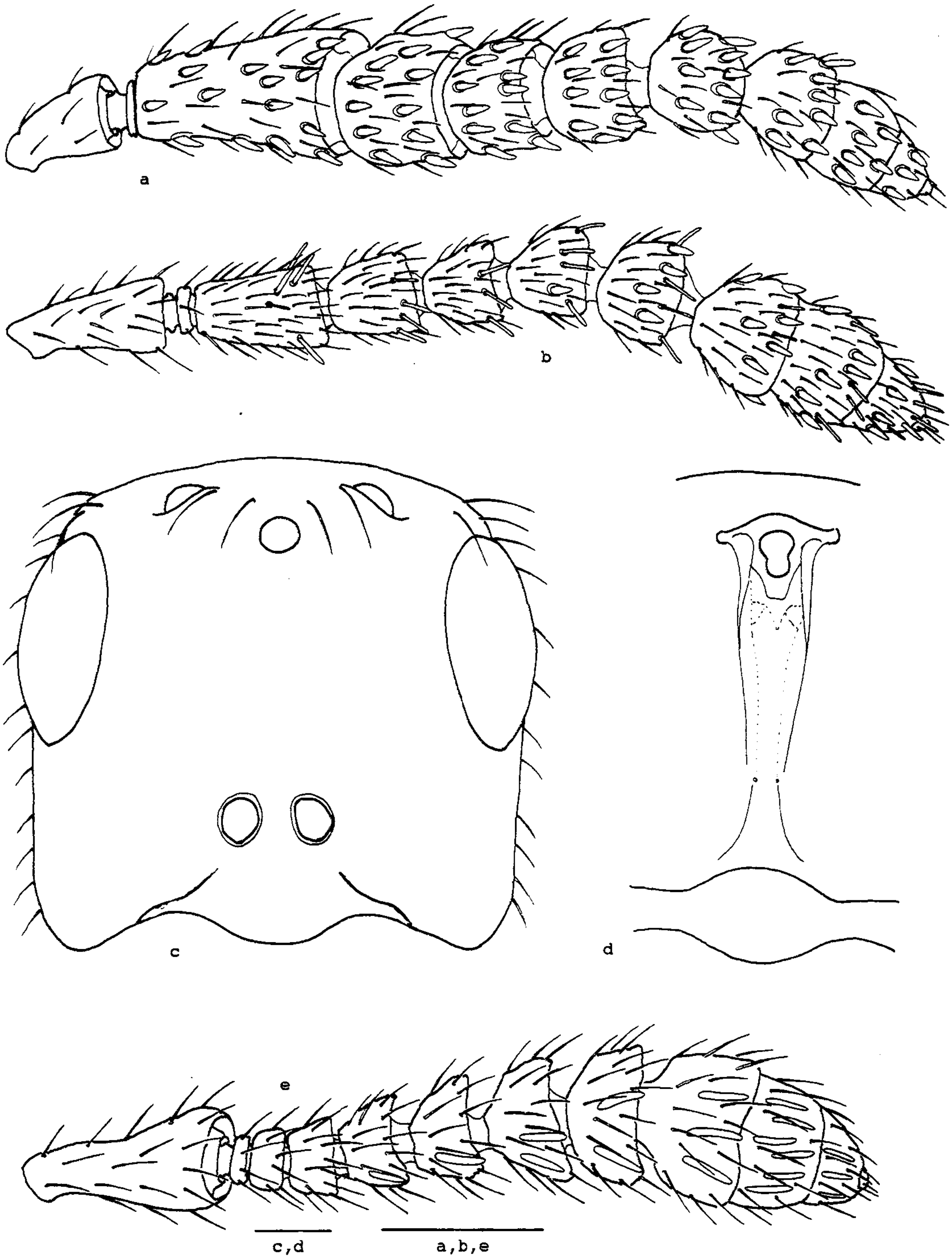


Fig. 8.2 a-b: *Crossogaster inusitata* sp. nov. a) female antenna, antiaxial view b) male antenna, antiaxial view; c-e: *Crossogaster michaloudi* sp. nov. c) male head, dorsal view d) male head, ventral view e) male antenna, dorsal view. Scale bars = 0.1 mm.

next to the spur on the fore tibia. Fore tibia 1.5X longer than fore tarsus (C = 0.43, TR = 0.16, TI = 0.39, TA = 0.26). Fore wing 2.3X longer than wide (l = 2.3), very pilose, anal setal tract present. Postmarginal vein longer than stigmal (SM = 0.80, M = 0.40, S = 0.19, PM = 0.26). Marginal vein thin, 13.3X longer than wide. Hind wing 4X longer than wide, l = 1.73.

Gaster. Eighth urotergite spiracle with a very slightly expanded peritreme. Aedeagus small (l = 0.48). Four teeth on aedeagus claspers.

Crossogaster lachaisei **sp. nov.**

(figs. 8.3 a-e)

Etymology: Named after D. Lachaise, one of the collectors of the holotype.

Type material: Holotype ♀ (slide mounted): Ivory Coast, Taï, leg. D. Lachaise & G. Couturier, 23 February 1980, RMNH 4086, ex *F. sansibarica* Warb. *macrosperma* (Mildbr. & Burr.) Berg. (Found dead in young syconium).

FEMALE. Faded due to storage in alcohol - uniform brown, front third of head and tarsi testaceous. Total length with head in orthognathous position excluding ovipositor 2.6 mm.

Head (figs. 8.3 a-b) elongate, parallel sided (l = 0.93, w = 0.53, h = 0.26), compressed dorso-ventrally, wedge shaped, convex dorsally, concave ventrally, such that anterior part of head curves downwards. Eye oval (l = 0.25, w = 0.18, h = 0.07), 0.27X head length. Cheek length twice eye length. Malar sulcas present for full cheek length, for first three fifths of length straight, then curves up and down to oral fossa. Lateral ocelli half visible in dorsal view situated in deep lateral vertex excavations on dorsal axial lip; prominent carina, V-shaped in posterior view. POL = 0.13, OOL = 0.087. Toruli situated below

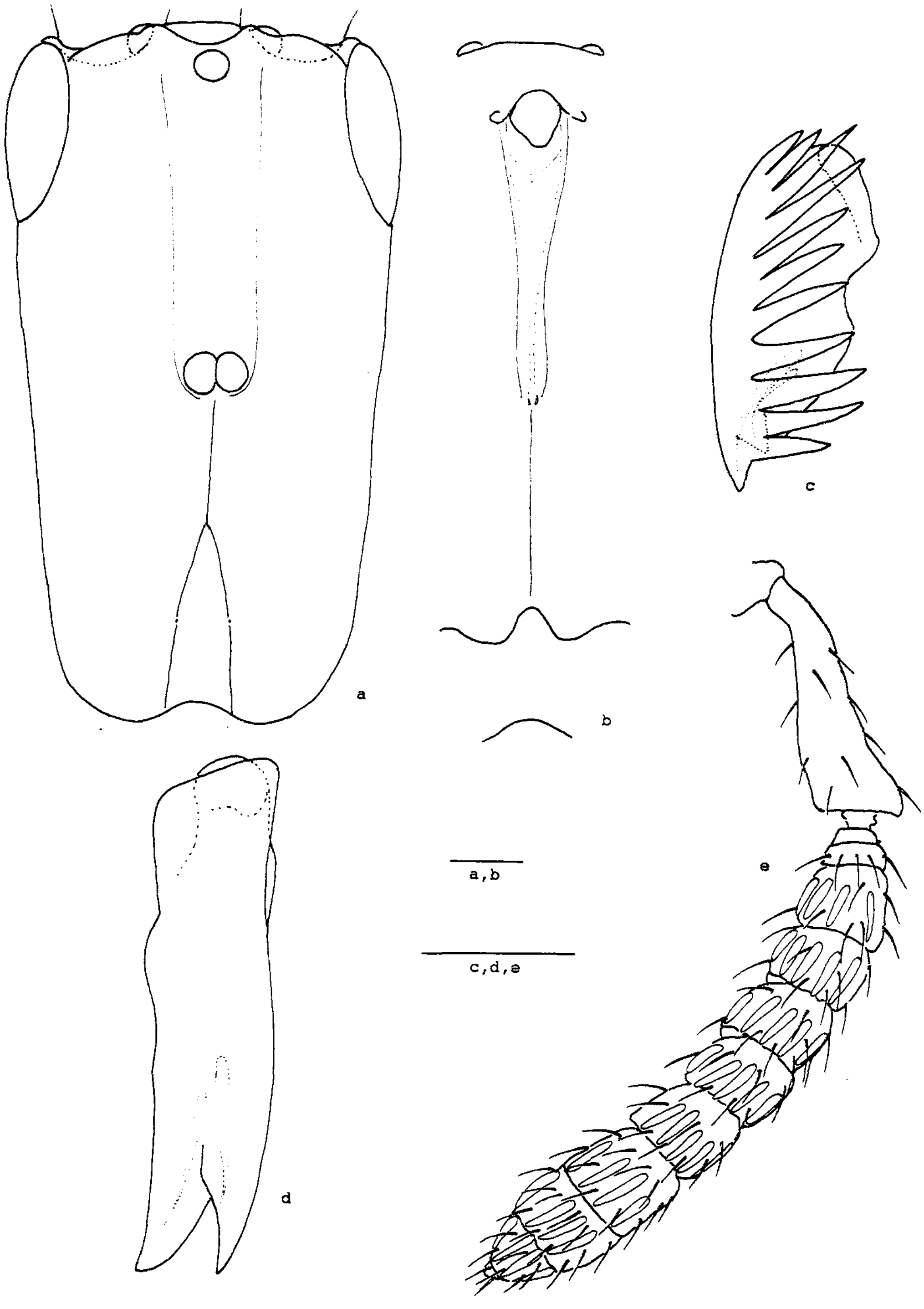


Fig. 8.3 a-c, e: *Crossogaster lachaisei* sp. nov. a) female head, dorsal view b) female head, ventral view c) female mandible, ventral view e) female antenna, antiaxial view; d: *Crossogaster michaloudi* d) male mandible, ventral view. Scale bars = 0.1 mm.

the eyes, touching. TE as long as scrobe length, SL = 0.42, which is deep, subsquare in X-section. Clypeus narrow and elongate in area, sutures meet before toruli. Epistomal margin concave, smooth, width of margin 0.15X head width. Ventral tentorial pits in close apposition (fig 8.3 b). Mandible with two apical teeth and a longitudinal row of eleven long ventral teeth; two glands (fig. 8.3 c). Hypostoma absent. Antenna (fig. 8.3 e) twelve segmented, formula 1125(3). Flagellum (l = 0.38). Scape narrow, 7.3X longer than wide (l = 0.29). Pedicel very elongate, 0.57X scape length. MPS placoid, more numerous on dorsal surface, reduced in number on the ventral surface.

Thorax. Pronotum elongate (l = 0.44, w = 0.40). Parapsidal furrows complete, almost straight. Propodeum wider than long (l = 0.23, w = 0.42), slight depression anteriorly and laterally to the large anteriorly situated spiracle. Mesoscutum (l = 0.35, w = 0.51). Scutellum, including axillae (l = 0.37, w = 0.41). Fore femur 3.6X as long as wide (l = 0.54). Fore tibial armature much as in *C. michaloudi* (except one of the fore tibiae in the holotype has three teeth), teeth subequal and strong. Fore leg coxa ca. two thirds of femur length (C = 0.36, TR = 0.14, TI = 0.17, TA = 0.31). Fore wing 2.6X longer than wide, l = 1.84, setae very sparse, maximum fringe length = 0.03. Postmarginal vein longer than stigmal (SM = 0.62,M = 0.32, PM = 0.16, S = 0.15). Marginal vein thin, 13X longer than wide. Hind wing 4.8X longer than wide, l = 1.4.

Gaster. Posterior edge of tergites smooth with five evenly spaced incisions. Eighth urotergite spiracular peritremata expanded (l = 0.07). Ovipositor 4X as long as valve (valve l = 0.46).

Comments. The fact that this single female was not reared but found as a foundress in *F. s. macrosperma*, along with a single foundress female of *S. l. longivena* may indicate that this is not the correct host for *S. lachaisei*.

***Crossogaster inusitata* sp. nov.**

(figs. 8.2 a-b; 8.4 a-f; 8.5 a)

Etymology: Inusitatus (latin) = unusual, strange, uncommon, referring to the expanded first tarsal segments and unusual antennal sensilla.

Type material. Holotype ♀, allotype ♂: Zambia, North West Province, Kabombo, 23 February 1988, leg. R.J. Nefdt, C125, ex *F. sansibarica* Warb. *?macrosperma* (Mildbr. & Burr.) Berg; series ♀, ♂ paratypes: same data as holotype; series ♀, ♂: same data, 15 February 1988, C142.

FEMALE. Metallic black, legs and antennae lighter brown. Total length with head in orthognathous position excluding ovipositor 2.8 mm.

Head (figs. 8.4 a & 8.5 a) elongate, parallel sided (l = 0.89, w = 0.57, h = 0.26), wedge shaped in lateral view, convex dorsally, concave ventrally, such that anteriorly the head curves slightly downwards. Eye oval (l = 0.27, w = 0.17, h = 0.06), 0.30X as long as the head. Cheek length 1.75X as long as eye. Malar sulcas absent. Vertex ninety degrees to dorsal and ventral surfaces of the head, with broad lateral excavations, lateral ocelli situated on the inside axial lip of the excavations. Two smaller excavations between the medial ocellus and each lateral ocellus. Occipital carina medially situated, straight, fades out ventral to the lateral ocelli. Ventrally the foramen magnum invagination is broadly subsquare. POL = 0.17, OOL = 0.10. Toruli situated below the eyes, touching. TE 0.93X as long as scrobe length (TE = 0.39, SL = 0.42). Epistomal margin very shallowly concave, second ventral margin bilobed with medial concavity equivalent in size to the lobes, margin ca. a sixth of head width. Mandible (fig. 8.4 e) with two apical teeth, inner squatter, nine ventral teeth, distally the teeth are long, becoming progressively shorter proximally; two glands. One labial segment. Two maxillary segments, distal segment largest.

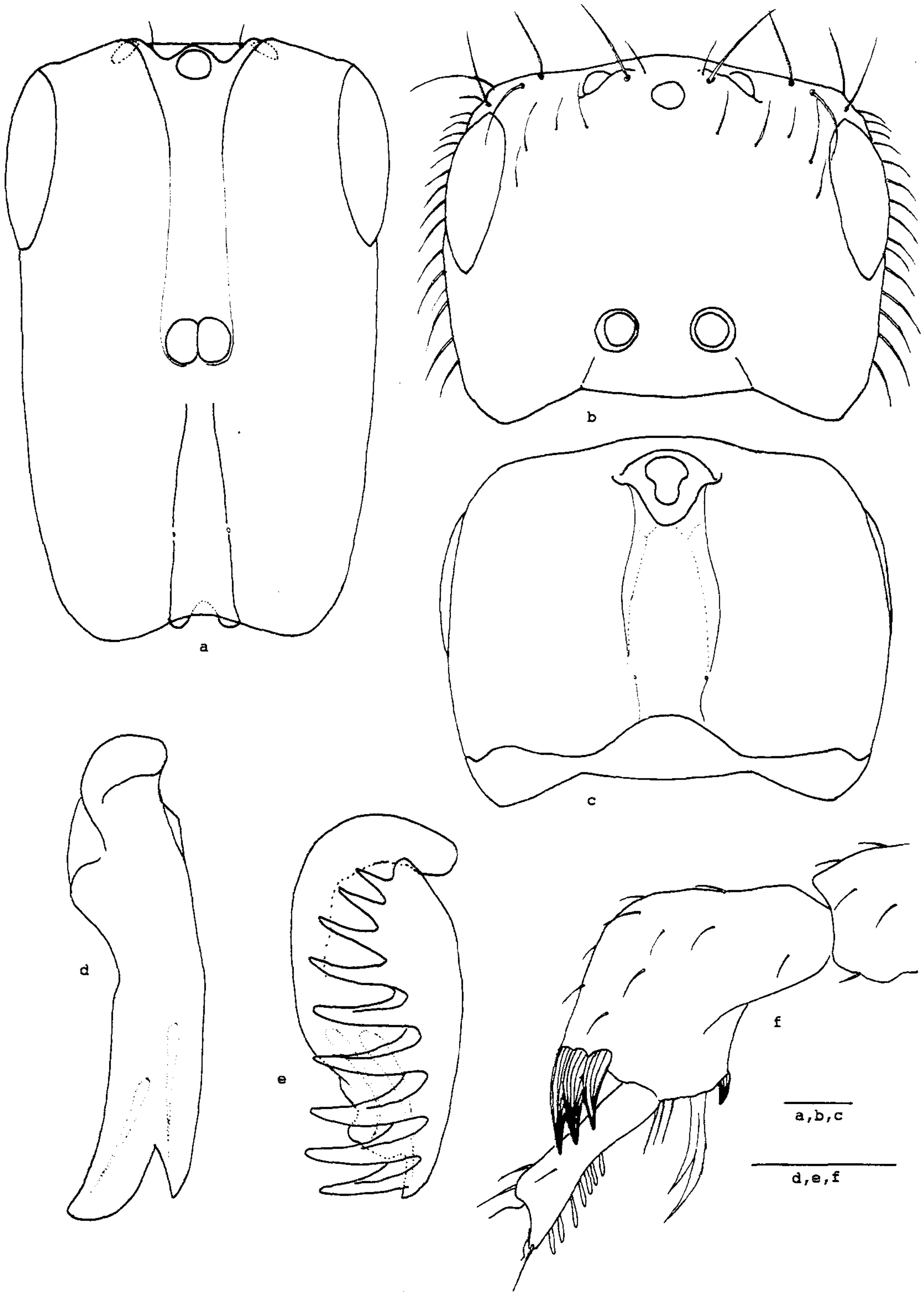


Fig. 8.4 a-f: *Crossogaster inusitata* sp. nov. a) female head, dorsal view b) male head, dorsal view c) male head, ventral view d) male mandible, dorsal view e) female mandible, ventral view f) fore tibia and first fore tarsal segment, antiaxial view. Scale bars = 0.1 mm.

Hypostoma distinct, not overlapped by the mouthparts. Antennae (fig. 8.2 a) eleven segmented, formula 1115(3); flagellum (l = 0.55). Scape 6.8X longer than wide (l = 0.27). Pedicel relatively short, 0.30X scape length. Anellus plate-like; first funicular segment twice as long as remaining segments, widening distally; second segment widest, rest tapering off to apex; segments slightly dorso-ventrally compressed. MPS numerous, very short, stumpy, free apically (fig. 8.2 a).

Thorax. Pronotum (l = 0.48, w = 0.43), trapezoid, concave laterally. Parapsidal furrows complete, evenly curved. Propodeum l = 0.23, w = 0.48, spiracles anteriorly situated. Mesoscutum l = 0.40, w = 0.53. Scutellum, including axillae (l = 0.38, w = 0.44). Fore femur 3.5X as long as wide (l = 0.60). Fore tibial armature tridentate, teeth equal (fig. 8.4 f). Fore leg coxa ca. two-thirds of femur length (C = 0.38, TR = 0.15, TI = 0.15, TA = 0.26). Fore wing 2.8X longer than wide, l = 2.15, very sparse, maximum fringe length = 0.03. Postmarginal vein same length as stigmal (SM = 0.75, M = 0.29, PM = 0.19, S = 0.19). Marginal vein 9.8X longer than wide. Hind wing 3.9X longer than wide, l = 1.54.

Gaster. First two tergal edges with slight crenulations, otherwise posterior edge of tergites smooth with 5-7 evenly spaced incisions. Eighth urotergite spiracular peritremata expanded (l = 0.06). Ovipositor 4.4X as long as valve (valve l = 0.35).

MALE. Testaceous, eyes, vertex, posterior two thirds of gaster darker. Total length with head in orthognathous position excluding ovipositor 2.25 mm.

Head (figs. 8.4 b-c) broad (l = 0.54, w = 0.64), height normal (h = 0.30). Eye elongate (l = 0.24, w = 0.14, h = 0.08), 0.44X as long as head. Cheek length 0.63X eye length. Malar sulcas absent. Lateral ocelli visible in dorsal view, thin occipital carina. POL = 0.16, OOL = 0.12. Toruli situated below the eyes, widely separated by almost twice torulus width. TE = 0.06, SL = 0.36. Clypeus trapezoid in area. Epistomal margin slightly convex with very small medial concavity, but set back into paraclypeal margins, width of margin ca. two fifths of head width; paraclypeal margins convex, angular. Ventral tentorial pits very widely separated (fig. 8.4 c). Mandible (fig. 8.4 d) with inner tooth larger, two glands. One labial segment. Two maxillary segments, segments subequal. Antenna (fig. 8.2 b) eleven segmented, formula 1115(3). Flagellum (l = 0.47). Scape broad, 4x longer than wide (l = 0.31). Pedicel relatively short, 0.32X scape length. Female type MPS are present on the distal two funicle and club segments, in addition more elongate, narrower and freer MPS are also present on all the funicle and club segments (fig. 8.2 b).

Thorax. Parapsidal furrows incomplete. Fore femur 2.6X as long as wide (l = 0.55). Fore tibial armature bidentate, no ventral tooth next to fore tibial spur. Fore tarsus ca. two thirds of fore tibial length (C = 0.42, TR = 0.18, TI = 0.36, TA = 0.23). Fore wing 2.5X longer than wide, l = 2.15, pilose, anal setal tract present. Postmarginal vein shorter than stigmal (SM = 0.70, M = 0.35, S = 0.18, PM = 0.10). Marginal vein thin, 17.5X longer than wide. Hind wing 4.2X longer than wide, l = 1.55.

Gaster. Eighth urotergite spiracle small and round. Aedeagus small (l = 0.58). Four teeth on aedeagus claspers.

The remaining *Crossogaster* species can be separated into two species groups, delimited by MPS type. One has elongate MPS (*C. odorans* group) and the other placoid MPS (*C. triformis* group).

Crossogaster odorans species-group.

This species-group is characterised by the presence of elongate MPS on the five antennal funicle segments.

Crossogaster odorans Wiebes
(fig. 8.8 e & f)

Crossogaster odorans Wiebes 1981, in Boucek *et al.* (1981): 170-173, figs. 16-24, 29-36, pl. 1 figs. 2 & 4, holotype ♀, allotype ♂, Zimbabwe, Harare. (Examined paratypes, Rijksmuseum van Natuurlijke Historie, Leiden).

Additional material: Series ♀ & ♂: Zambia, Lusaka, Cathedral, 25 January 1988, leg. R.J.F. Nefdt, C61, ex *F. thonningii* Bl.; Zimbabwe, Mazoe, nr. club, 29 January 1987, leg. A.J. Gardiner, C64, ex *F. thonningii* Bl.; South Africa, Eastern Transvaal, Hazyview, 5 September 1989, leg. S. van Noort & A.B. Ware, C172, ex *F. thonningii* Bl.; Zimbabwe, Mashonaland, Mazoe Citrus Estates, 6 March 1990, leg. I. Waters, C286, ex *F. thonningii* Bl.; Zambia, Locinvar Game Park, 14 July 1990, leg. S.G. Compton, C320, ex *F. thonningii* Bl.; Malawi, Zomba Town University Campus, 6 April 1991, leg. S.G. Compton, C337, ex *F. thonningii* Bl.; 5 females: Malawi, Mt. Mulanje Forestry Station, 7 July 1990, leg. S.G. Compton, C322, ex *F. thonningii* Bl.; Uganda, Kigesi District, Kisoro, 10 June 1968, tree no. 52, leg. D.S. Hill, ex *Ficus* sp. S.; Kenya, nr. Nairobi, Kaun, 6000 ft. alt., August 1967, leg. C. van Someron, ex *Ficus* sp. (C.v.S. no. 1); Uganda, Entebbe, 23 April 1968, leg. D.S. Hill, ex *F. "dekdekena"* (tree no. 31); South Africa, Natal, Hluhluwe Game Reserve, 2832AA, 9 December 1986, leg. S.G. Compton & A.J. Gardiner, C38, ex *F. stuhlmannii* Warb.; Zambia, Lusaka, Cathedral, 25 January 1988, leg. R.J.F. Nefdt, C62, ex *F. stuhlmannii* Warb.; South Africa, Transvaal, Pongola, 6 September 1989, leg. S. van Noort & A.B. Ware, C148, ex *F. stuhlmannii* Warb.; South Africa, E. Transvaal, Pullen Farm, 30 km N of Nelspruit, 1 June 1989, leg. P. Hawks, C72, ex *F. stuhlmannii* Warb.; South Africa, Transvaal, Magaboeskloof, De Hoek State Forest, 1 September 1989, leg. S. van Noort & A.B. Ware, C144, ex *F. craterostoma* Mildbr. & Burr.

Comments. There is a certain amount of geographical variation in the southern African populations. The specimens from both *F. stuhlmannii* and *F. thonningii* in Zambia, and *F. thonningii* in Zimbabwe and Zomba (Malawi) have longer ovipositor valves, smaller spiracular peritremata and a longer eye relative to the width than do the specimens from *F. thonningii*, *F. stuhlmannii* and *F. craterostoma* in South Africa. However the specimens from Mt. Mulanje (Malawi) are the same as the South African specimens.

The specimens in the east African collections from *Ficus* sp. S and *Ficus* sp. C.v.S. no.1 have a longer cheek, a narrower epistomal margin, fewer mandibular ventral teeth and a larger spiracular peritreme, much as in *C. quadrata* sp. nov. from *F. glumosa*, but the vertex is concave and the epistomal margin projects distinctly further than the paraclypeal margins. The associated pollinator in the east African collections keys out to *E. stuckenbergi* (Grandi), using the key in Wiebes (1989b) (the antennal scape is distinctly expanded dorsad). In the sample from *Ficus* sp. C.v.S. no. 1, *P. barbarus* Grandi is also present, but in the sample from *Ficus* sp. S. *C. vansomereni*, which belongs to the second *Crossogaster* species group, and does not occur in the *F. thonningii* collections from elsewhere in Africa, is also present. Until further samples are obtained and host relationships clarified, I include these two east African samples here. An indication that this is possibly the incorrect decision is provided by another east African sample from *F. "dekdekena"* in which the *Crossogaster* specimens have the same cheek length and epistomal margin as the southern African specimens, but have fewer ventral mandibular teeth (9 to 11). However, in this sample the associate pollinator is *Alfonsiella fimbriata* Waterston, whose hosts are *F. natalensis* Hochst. *leprieurii* (Miq.) Berg and *F. kamerunensis* Mildbr. & Burret (Wiebes & Compton, 1990). This may mean that the variation in the first two east African samples is not geographically related, and that they represent a distinct species. Many further collections need to be made before any decisions can be made in this regard.

The pollinator from *F. craterostoma* in South Africa is an undescribed species of *Alfonsiella* and not *A. michaloudi* Wiebes, the species associated with *F. craterostoma* in West Africa. This suggests that the South African *F. craterostoma* may be biologically distinct, which is also supported by the associated sycoecines. In South Africa *C. odorans* and *Philocaenus quatuordentatus* sp. nov. breed in *F. craterostoma* while in west Africa *P. insolitus* sp. nov. and *P. liodontus* (Wiebes) are associated with this host species.

Crossogaster stigma **sp. nov.**

(fig. 8.6 a-d, f, h)

Etymology: Stigma (latin) = spiracle, referring to the extremely expanded eighth urotergite spiracular peritremata.

Type material: Holotype ♀, allotype ♂ (slide mounted): South Africa, Natal, Ubombo, 2732CA, 9 December 1986, leg. S.G. Compton, C33, ex *F. glumosa* Delile; series ♀ and ♂ paratypes: same data; Zambia, Kafue Town, leg. M.G. Bingham, 16 September 1980, 2503, RMNH 4418, ex *F. glumosa* Delile; South Africa, Natal, Hluhluwe Game Reserve, 2832AA, 5 December 1986, leg. S.G. Compton & A.J. Gardiner, C48, ex *F. glumosa* Delile; South Africa, Transvaal, Strydom Tunnels, 1 January 1988, leg. P. Raal, C58, ex *F. glumosa* Delile; Zimbabwe, Mazoe Citrus Estates Ranch, 1 March 1987, leg. A.J. Gardiner, C66, ex *F. glumosa* Delile; South Africa, Natal, Zululand, N. of Jozini, 8 December 1988, leg. S.G. Compton, C103, ex *F. glumosa* Delile; South Africa, Natal, Zululand, S. of Jozini, 8 December 1988, leg. S.G. Compton & V.K. Rashbrook, C104, ex *F. glumosa* Delile; South Africa, Transvaal, Pongola, 6 September 1989, leg. S. van Noort & A.B. Ware, C170, ex *F. glumosa* Delile; South Africa, Natal, Jozini, 21 January 1990, leg. S. van Noort & A.B. Ware, C236, ex *F. glumosa* Delile; same data, C237; South Africa, Natal, Jozini, 21 January 1990, leg. S. van Noort & A.B. Ware, C241, ex *F. glumosa* Delile; South Africa, Natal, Ingwavuma, 23 January 1990, leg. S. van Noort & A.B. Ware, C243, ex *F. glumosa* Delile; same data, C246; same data, C247; Zimbabwe, Mashonaland Central, Mazoe Cattle Ranch, 5 March 1990, leg. I. Waters, C285, ex *F. glumosa* Delile.

FEMALE. Head and thorax metallic black, gaster and antennae matt dark brown, legs yellowish brown with mid and hind proximal segments darker. Total length with head in orthognathous position, excluding ovipositor = 1.3 mm.

Head (figs. 8.6 a & b) approximately square (l = 0.35, w = 0.35, h = 0.14). Eye oval (l = 0.17, w = 0.11), protrudes laterally (h = 0.05), 0.45X as long as the head. Cheek length 0.79X eye length. Malar sulcas absent. Lateral ocelli visible in dorsal view, medial ocellus situated in posterior end of scrobe, occipital carina present as a straight thin fold, below the

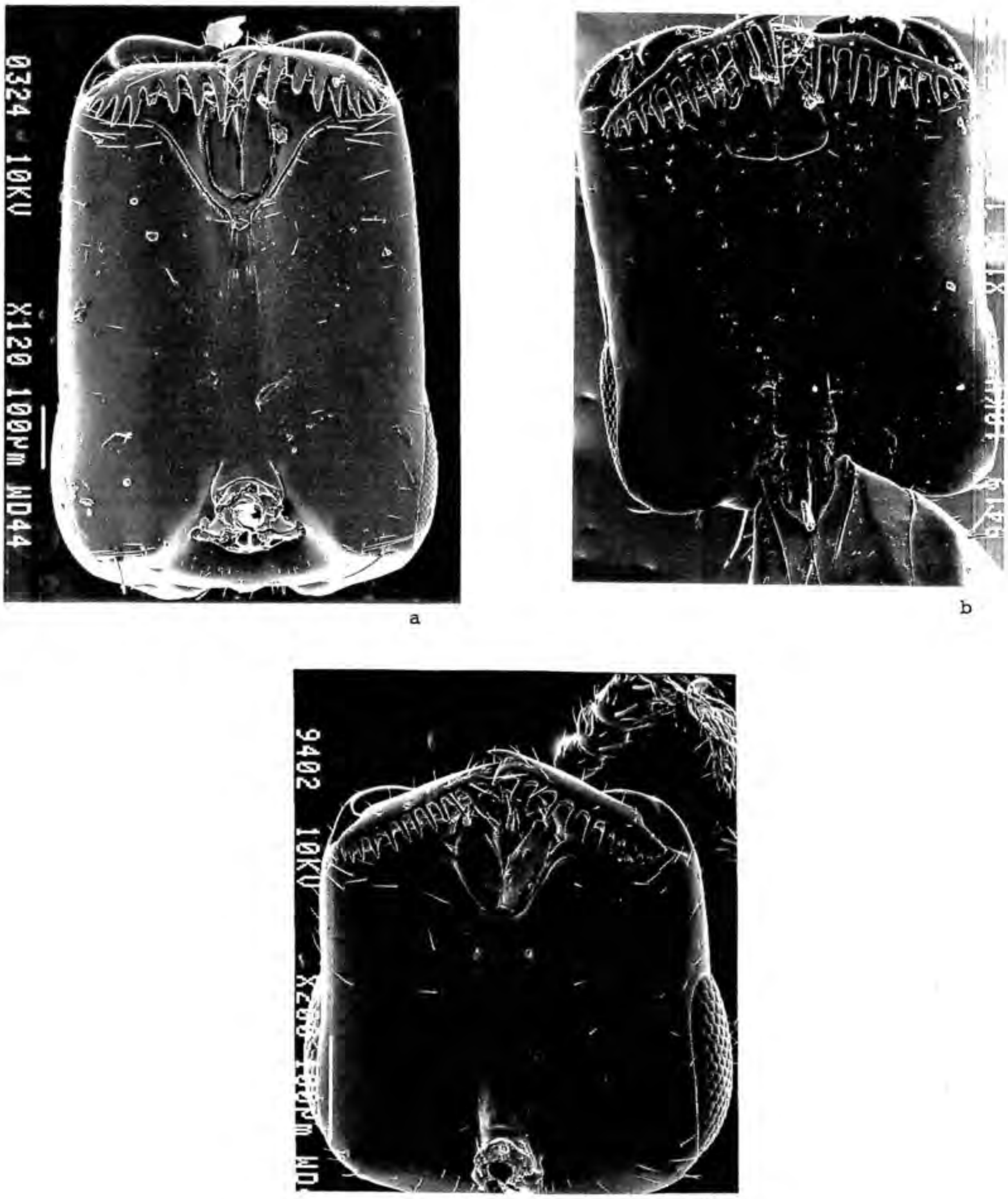


Fig. 8.5 a: *Crossogaster inusitata* sp. nov. a) female head, ventral view; b: *Crossogaster rastellus* sp. nov. b) female head, ventral view; c: *Crossogaster lurida* sp. nov. c) female head, ventral view.

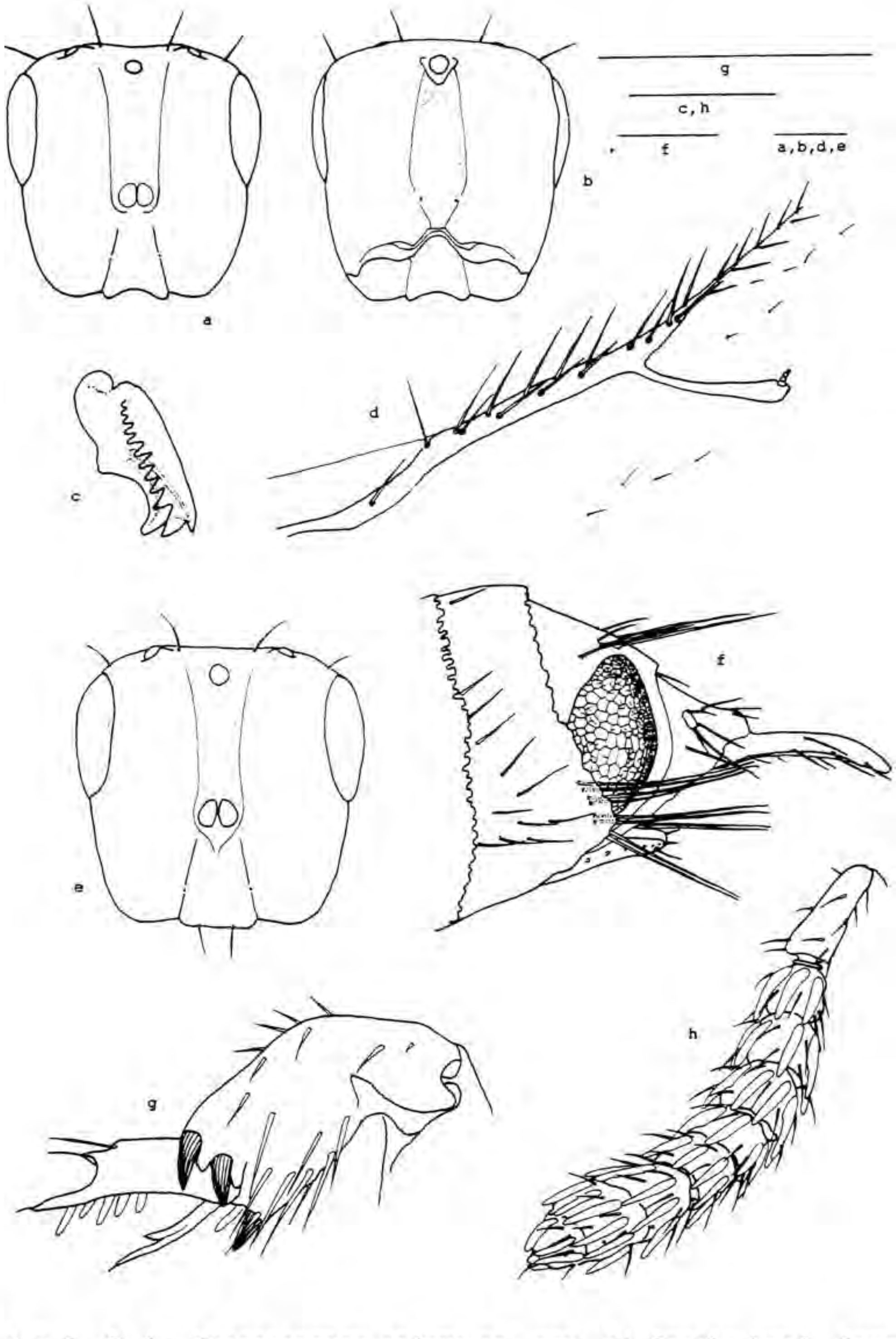


Fig. 8.6 a-d, f, h: *Crossogaster stigma* sp. nov. a) female head, dorsal view b) female head, ventral view c) female mandible, ventral view d) female fore wing marginal, stigmal and postmarginal venation f) female seventh, eighth and ninth tergites, ovipositor valves and hypopygium h) female antenna, antiaxial view; e & g: *Crossogaster quadrata* sp. nov. e) female head, dorsal view g) female fore tibia and first tarsal segment. Scale bars = 0.1 mm.

lateral ocelli. POL = 0.15, OOL = 0.05. Toruli situated below the eyes, with top of toruli touching imaginary line joining the base of eyes, touching; TE 0.64X as long as scrobe length (TE = 0.12, SL = 0.19). Epistomal margin bilobed at lateral extremes, with shallow concavity in between, ca. a quarter of the head width. Ventral tentorial pit widely separated (fig. 8.6 b). Mandible with two apical teeth and a longitudinal row of twelve ventral teeth, teeth relatively short, two glands (fig. 8.6 c). One labial segment. Two maxillary segments, basal segment very reduced. Antenna (fig. 8.6 h) eleven segmented, formula 1115(3), funicle segments subequal in size. Scape 5.4X longer than wide (l = 0.146). Pedicel elongate, 0.41X scape length. MPS are elongate, but are much shorter than in *C. odorans*, ca. the same length as the funicle segments (fig. 8.6 h).

Thorax. Pronotum broad (l = 0.21, w = 0.28), torpedo shaped. Parapsidal furrows complete, evenly curved. Propodeum wider than long (l = 0.11, w = 0.25). Mesoscutum broad (l = 0.18, w = 0.31). Scutellum, including axillae broad (l = 0.19, w = 0.24). Fore femur 2.9X as long as wide (l = 0.23). Fore tibial armature bidentate. Fore leg coxa ca. three quarters of femur length (C = 0.17, TR = 0.07, TI = 0.09, TA = 0.15). Seven hind tibial spines on the dorsal margin. Fore wing 2.4X longer than wide, l = 1.05, pilose, long fringe. Postmarginal vein shorter than stigmal (SM = 0.36, M = 0.15, PM = 0.07, S = 0.10). Marginal vein 15X longer than wide. Hind wing 4.2X longer than wide, l = 0.78.

Gaster, posterior edge of tergites very crenulated, with three medial incisions. Eighth urotergite spiracular peritremata extremely large and ovoid (l = 0.14), with extensive long setae around the edge, which are subequal in length to the length of the ovipositor valves (fig. 8.6 f). Ovipositor 3.5X as long as the ovipositor valve (valve l = 0.23).

MALE. Testaceous, axillae, parapsides, vertex and gaster dark brown. Total length with head in orthognathous position excluding ovipositor 1.25 mm.

Head approximately square (l = 0.33, w = 0.34, h = 0.17). Eye oval (l = 0.15, w = 0.10, h = 0.05), 0.46X as long as the head. Cheek length 0.4X as long as eye. Malar sulcas absent. Lateral ocelli visible in dorsal view, thin occipital carina present. POL = 0.14. OOL = 0.06. Toruli situated below the eyes, with the top of toruli in line with base of eyes, only just separated by ca. a fifth of torulus width; TE 0.35X as long as scrobe length (TE = 0.07, SL = 0.20). Epistomal margin slightly convex, with flat medial section, width of margin ca. two fifths of head width. Ventral tentorial pits widely spaced. Mandible much as in *C. quadrata* (fig. 8.8 g); two glands. One labial segment. Two maxillary segments, basal ca. half the length of distal. Antenna eleven segmented, formula 1115(3). Antennal flagellum length 2.7X as long as pedicel. Scape narrow, 5.8X longer than wide (l = 0.15). Pedicel very elongate, 0.06X scape length. MPS are elongate, but basal half is fused to flagella segments, only one on each of the last two funicle segments and first club segment, five on the last two club segments.

Thorax. Parapsidal furrows complete, but indistinct posteriorly. Fore femur 3.6X longer than wide, l = 0.29. Fore tibial armature bidentate. Fore tarsus ca. same length as fore tibia (C = 0.22, TR = 0.08, TI = 0.16, TA = 0.17). Fore wing 2.6X longer than wide, l = 1.05, pilose. Postmarginal vein shorter than stigmal (SM = 0.37, M = 0.18, S = 0.10, PM = 0.04). Marginal vein 18X longer than wide. Hind wing 4.6X longer than wide, l = 0.82.

Eighth urotergite spiracle normal. Aedeagus small (l = 0.25). Three teeth on aedeagus claspers.

Crossogaster quadrata **sp. nov.**

(figs. 8.6 e & g; 8.8 g-h)

Etymology: quadratus (latin) = square, referring to the square epistomal margin.

Type material: Holotype ♀, allotype ♂ (slide mounted): South Africa, Natal, Hluhluwe Game Reserve, 2832AA, 5 December 1986, leg. S.G. Compton & A.J. Gardiner, C48, ex *F. glumosa* Delile; series ♀ and ♂ paratypes: same data; series ♀ and ♂: South Africa, Transvaal, Strydom Tunnels, 2430DB, 1 January 1988, leg. P. Raal, C58, ex *F. glumosa* Delile; South Africa, Natal, Zululand, South of Jozini, 8 December 1988, leg. S.G. Compton & V.K. Rashbrook, C104, ex *F. glumosa* Delile; South Africa, Natal, Pongola, 6 September 1989, leg. S. van Noort & A.B. Ware, C170, ex *F. glumosa* Delile; South Africa, Natal, Ingwavuma, 23 January 1990, leg. S. van Noort & A.B. Ware, C247, ex *F. glumosa* Delile.

FEMALE. Metallic black, antennae and legs testaceous. Total length with head in orthognathous position, excluding ovipositor valves = 1.5 mm.

Head (fig. 8.6 e) approximately square (l = 0.39, w = 0.41, h = 0.17). Eye oval (l = 0.18, w = 0.12, h = 0.05), 0.45X as long as head. Cheek length 0.70X eye length. Lateral ocelli visible in dorsal view, occipital carina runs lengthwise along vertex. POL = 0.17, OOL = 0.06. Toruli situated below the eyes, top of toruli on the same plane as line joining base of compound eyes. TE 0.69X as long as scrobe length (TE = 0.14, SL = 0.20). Toruli touching. Clypeus narrow and elongate in area. Epistomal margin subsquare, protruding with straight leading edge, ca. a quarter of the head width. Ventral tentorial pits widely separated. Mandible with two apical teeth and a longitudinal row of eleven to thirteen short ventral teeth, two glands. Antennae much as in *C. stigma* (fig. 8.6 g), formula 1115(3); funicle segments subequal in size. Flagellum (l = 0.31). Scape 5.2X longer than wide (l = 0.16). Pedicel elongate, 0.41X scape length. MPS elongate (less so than *C. odorans* much as in *C. stigma*), free, about eight on each funicle and club segment.

Thorax. Pronotum broad (l = 0.23, w = 0.32), torpedo shaped. Parapsidal furrows complete, evenly curved. Propodeum wider than long (l = 0.12, w = 0.30). Mesoscutum broad (l = 0.21, w = 0.34).

Scutellum, including axillae (l = 0.20, w = 0.29). Fore femur 3.1X as long as wide (l = 0.28). Fore tibial armature bidentate. Fore leg coxa 0.71X femur length (C = 0.19, TR = 0.07, TI = 0.11, TA = 0.15). Eight hind tibial spines on the dorsal margin. Fore wing 2.4X longer than wide, l = 1.15, with sparse setae, fringe short. Postmarginal vein ca. half the length of the stigmal, (SM = 0.40, M = 0.18, PM = 0.05, S = 0.11). Marginal vein 9.2X as long as broad. Hind wing 4.4X longer than wide, l = 0.88.

Gaster, posterior edge of tergites crenulated, with three large medial incisions. Eighth urotergite spiracular peritreme large and ovoid (l = 0.08), with extensive long setae around the edge. Ovipositor 4.1X as long as ovipositor valves (valve l = 0.20).

MALE. Testaceous, gaster dark brown. Total length with head in orthognathous position excluding ovipositor 1.5 mm.

Head (fig. 8.8 h) approximately square (l = 0.40, w = 0.41, h = 0.21). Eye oval (l = 0.17, w = 0.12, h = 0.053), 0.43X as long as head. Cheek length 0.41X as long as eye. Malar sulcas absent. Lateral ocelli visible in dorsal view. POL 0.36X as wide as head (POL = 0.15, OOL = 0.09). Toruli situated below the eyes, top margin on the line joining the base of the compound eyes, separated by ca. a third of torulus width; TE 0.28X as long as scrobe length (TE = 0.07, SL = 0.25). Epistomal margin slightly convex, with straight medial section, width of margin 0.44X head width. Ventral tentorial pits widely spaced. Mandible (fig. 8.8 g) with ca. seven serrations on the inner margin; two glands. One labial segment. Two maxillary segments, basal segment very reduced. Antenna eleven segmented, formula 1115(3). Antennal flagellum length 3.2X as long as pedicel. Scape narrow, 6.3X longer than wide (l = 0.19). Pedicel very elongate, 0.47X scape length (p.l = 0.09). MPS fused for half their length to the flagella segments, only one present on the last funicle segment, two on the first and five each on the remaining two club segments.

Thorax. Parapsidal furrows incomplete, fades out posteriorly. Fore femur 3.2X as long as wide (l = 0.35). Fore tibial armature bidentate. Fore tarsus ca. four-fifths of fore tibial length (C = 0.27, TR = 0.10, TI = 0.22, TA = 0.18). Fore wing 2.6X longer than wide, l = 1.27, pilose. Postmarginal vein shorter than stigmal (SM = 0.45, M = 0.21, S = 0.10, PM = 0.05). Marginal vein 21X longer than wide. Hind wing 5.3X longer than wide, l = 1.00.

Eighth urotergite spiracle normal, without expanded peritreme. Aedeagus small (l = 0.27). Three teeth on aedeagus claspers.

Comments. *C. quadrata* is closely related to *C. odorans*, but has a longer cheek and a narrower, subquadrate epistomal margin, which projects further anteriorly, than the southern African specimens of *C. odorans*; the cheek length and epistomal margin are the same as the specimens of *C. odorans* from east Africa, however these *C. odorans* specimens have a curved, concave vertex and a more pronounced epistomal margin, that projects beyond the paraclypeal margins. The antennal MPS of *C. quadrata* are also less elongate than the MPS of *C. odorans*, with a greater proportion of the sensilla still fused to the funicular segment.

Crossogaster lurida **sp. nov.**

(figs. 8.5 c & 8.7 a-j)

Etymology: Luridus (latin) = pale yellow, with reference to the unusual body colouration.

Type material. Holotype ♀ (slide mounted): South Africa, Natal, Kosi Bay, 21 November 1989, leg. M. Ward, C215, ex *F. natalensis* Hochst. Paratypes: 3 ♀ (slide mounted), series ♀, one ♂: same data as holotype. Allotype ♂ (slide mounted): South Africa, Natal, Kwangwanase, 27 January 1990, leg. S. van Noort & A.B. Ware, C262, ex *F. natalensis natalensis* Hochst.; series ♀, one ♂: same data as allotype.

FEMALE. Testaceous, except for the posterior half of the head, ovipositor valves and sometimes the posterior third of the gaster, which are all dark brown. Total length with head in orthognathous position, excluding ovipositor valves = 1.5 mm.

Head (figs. 8.5 c & 8.7 a & b) approximately square (l = 0.44, w = 0.43, h = 0.17). Eye oval (l = 0.18, w = 0.11), protrudes laterally (h = 0.06), 0.43X as long as head. Cheek length 0.64X eye length. Malar sulcas absent. Lateral ocelli visible in dorsal view, carina present as a straight, thin fold below the ocelli. POL = 0.17. OOL = 0.06. Toruli situated on imaginary line joining anterior margin of the eyes, touching. TE 0.79X as long as scrobe length (TE = 0.17, SL = 0.22). Clypeus trapezoid in area. Epistomal margin convex, slightly angular laterally, ca. a third of head width. Ventral tentorial pits widely spaced (figs. 8.5 c & 8.7 b). Mandible with two apical teeth and a longitudinal row of twelve to thirteen ventral teeth, two glands (figs. 8.5 c & 8.7 h). One labial segment. Two maxillary segments, basal segment reduced, short (fig. 8.7 e). Antenna (fig. 8.7 c) eleven segmented, formula 1115(3), funicle segments subequal in size. Scape 5.3X longer than wide (l = 0.18). Pedicel elongate, 0.39X scape length. MPS are elongate, subequal in length to the funicle segments, but usually originate half way up the segment, much as in *C. odorans*.

Thorax. Pronotum broad (l = 0.27, w = 0.38), torpedo shaped. Parapsidal furrows complete, evenly curved. Propodeum wider than long (l = 0.14, w = 0.34). Mesoscutum broad (l = 0.24, w = 0.41). Scutellum, including axillae (l = 0.24, w = 0.33). Fore femur 3.3X as long as wide (l = 0.32). Fore tibial armature bidentate (fig. 8.7 d). Fore leg coxa ca. three quarters of femur length (C = 0.24, TR = 0.10, TI = 0.12, TA = 0.18). Nine hind tibial spines on dorsal margin. Fore wing 2.4X longer than wide, l = 1.36, pilose, fringe long. Postmarginal vein shorter than stigmal (SM = 0.49, M = 0.21, PM = 0.06, S = 0.13). Marginal vein 12X longer than wide. Hind wing 4.6X longer than wide, l = 1.02.

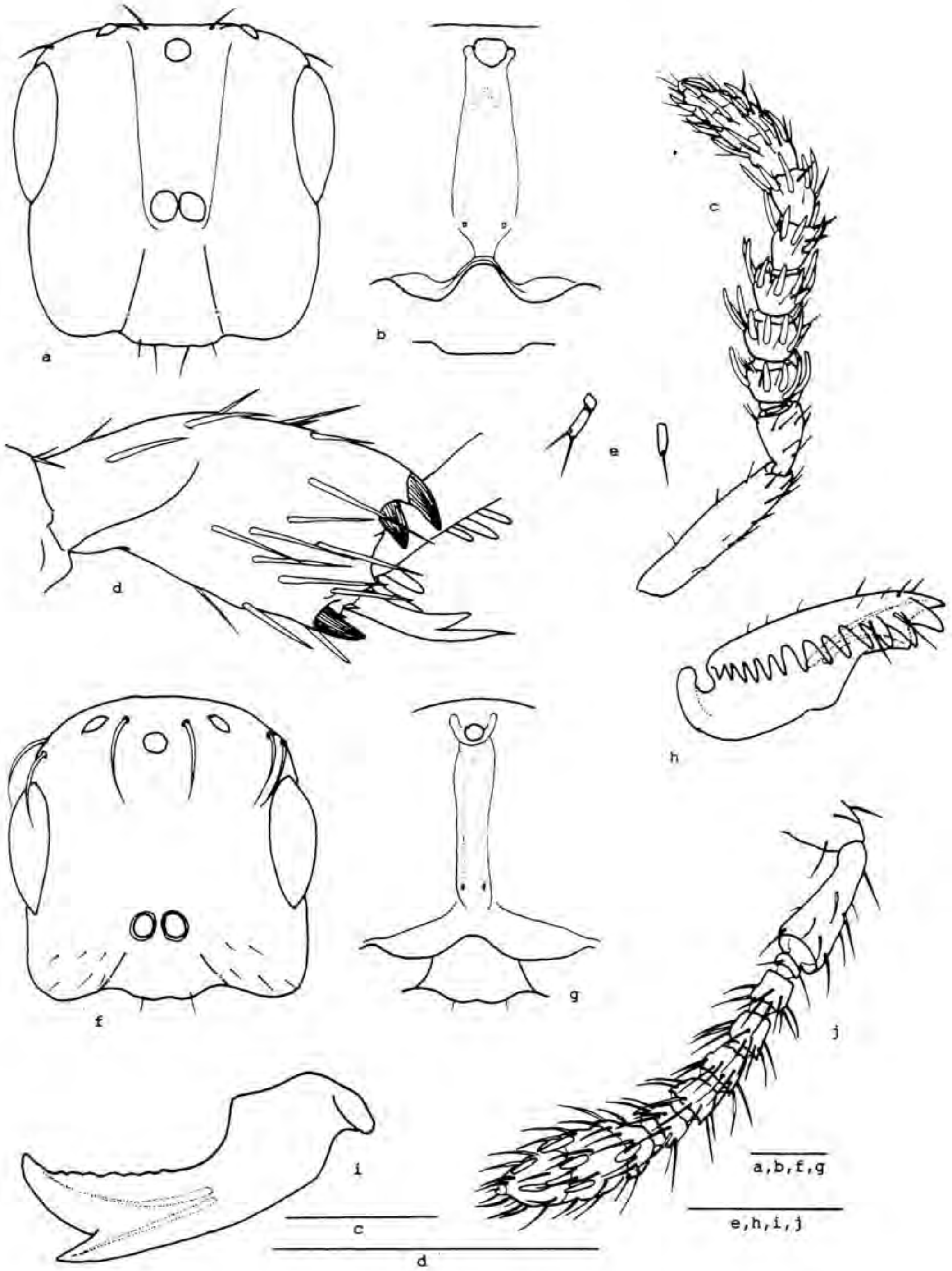


Fig. 8.7 a-j: *Crossogaster lurida* sp. nov. a) female head, dorsal view b) female head, ventral view c) female antenna, antiaxial view d) female fore tibia e)female labial and maxillary palps f) male head, dorsal view g) male head, ventral view h) female mandible, ventral view i) male mandible, dorsal view j) male antenna, antiaxial view. Scale bars = 0.1 mm.

Gaster, posterior edge of tergites very crenulated, with three medial incisions. Eighth urotergite spiracular peritremata large and ovoid (l = 0.08), with extensive long setae around the edge. Ovipositor 5.6X as long as valve (valve l = 0.20).

MALE. Testaceous, mandibles and eyes darker. Total length with head in orthognathous position excluding ovipositor 1.5 mm.

Head (figs. 8.7 f & g) approximately square (l = 0.40, w = 0.40, h = 0.22). Eye oval (l = 0.17, w = 0.12, h = 0.064) 0.42X as long as head. Cheek length 0.37X eye length. Malar sulcas absent. Lateral ocelli visible in dorsal view. POL = 0.14. OOL = 0.09. Toruli situated below the eyes, separated by a quarter of torulus width. TE 0.30X as long as scrobe length (TE = 0.08, SL = 0.26). Clypeus trapezoid in area. Epistomal margin convex, with shallow medial concavity, 0.37X head width. Ventral tentorial pits widely spaced (fig. 8.7 g). Mandible with inner tooth larger, with 8 - 10 serrations on the inner margin, two glands (fig. 8.7 i). One labial segment. Two maxillary segments. Antenna (fig. 8.7 j) eleven segmented, formula 1115(3). Antennal flagellum 3.1X as long as pedicel. Scape 4.8X longer than wide (l = 0.19). Pedicel elongate, 0.44X scape length. MPS only present on the club segments.

Thorax. Parapsidal furrows indistinct posteriorly. Fore femur 3.6X as long as wide (l = 0.36). Fore tibial armature bidentate. Fore tarsus 0.87X fore tibial length (C = 0.27, TR = 0.10, TI = 0.23, TA = 0.20). Fore wing 2.7X longer than wide, l = 1.3, very pilose. Postmarginal vein shorter than stigmal (SM = 0.45, M = 0.21, S = 0.11, PM = 0.06). Marginal vein thin, 21X longer than wide. Hind wing 5.3X longer than wide, l = 0.95.

Eighth urotergite spiracle normal. Aedeagus small (l = 0.24). Three teeth on aedeagus claspers.

***Crossogaster oculagrandis* sp. nov.**

(figs. 8.8 a-d)

Etymology: Oculus (latin) = eye, grandis (latin) = great, referring to the extremely large compound eyes.

Type material: Holotype ♀ (slide mounted): Cameroun, SW Province, Mt. Koupe', nr. Nyassosso, 4° 50'N 9° 40'E, ca. 1000m alt., 6 January 1982, net sweep (montane forest), leg. S.G. Compton.

FEMALE. Only head and parts of thorax metallic black, eyes and ocelli reddish brown; gaster legs and antennae testaceous, flagellum darker; scutellum, axillae and gaster brown - mesoscutum and mesopleuron darker. Total length with head in orthognathous position excluding ovipositor 1.2 mm.

Head (figs. 8.8 a & b) approximately square (l = 0.33, w = 0.33), height normal (h = 0.17). Eye oval (l = 0.26, w = 0.16), protrudes laterally (h = 0.09), 0.78X as long as the head. Cheek length 0.17X eye length. Malar sulcas absent. Lateral ocelli visible in dorsal view, carina indistinct, no excavations. POL = 0.13. OOL = 0.017. Toruli situated between the eyes, touching. TE 0.77X as long as scrobe length (TE = 0.13, SL = 0.18). Clypeus narrow and elongate in area. Epistomal margin very slightly convex, with medial area flat, ca. a third of head width. Two widely spaced ventral tentorial pits situated a quarter of the way from the oral fossa to the foramen magnum (fig. 8.8 b). Mandible with two apical teeth and a longitudinal row of nine ventral teeth, teeth relatively long near the apex becoming progressively shorter basally, two glands (fig. 8.8 c). One labial palp segment. Maxillary palp absent, but probably consists of two segments. Antenna (fig. 8.8 d) eleven segmented, formula 1115(3), funicle segments subequal in size. Scape broad, 3.3X longer than wide (l = 0.14). Pedicel very elongate, 0.5X scape length. Most of the MPS are very elongate, 3 - 3.5X longer than the funicle segments, shorter on last two club segments. A few

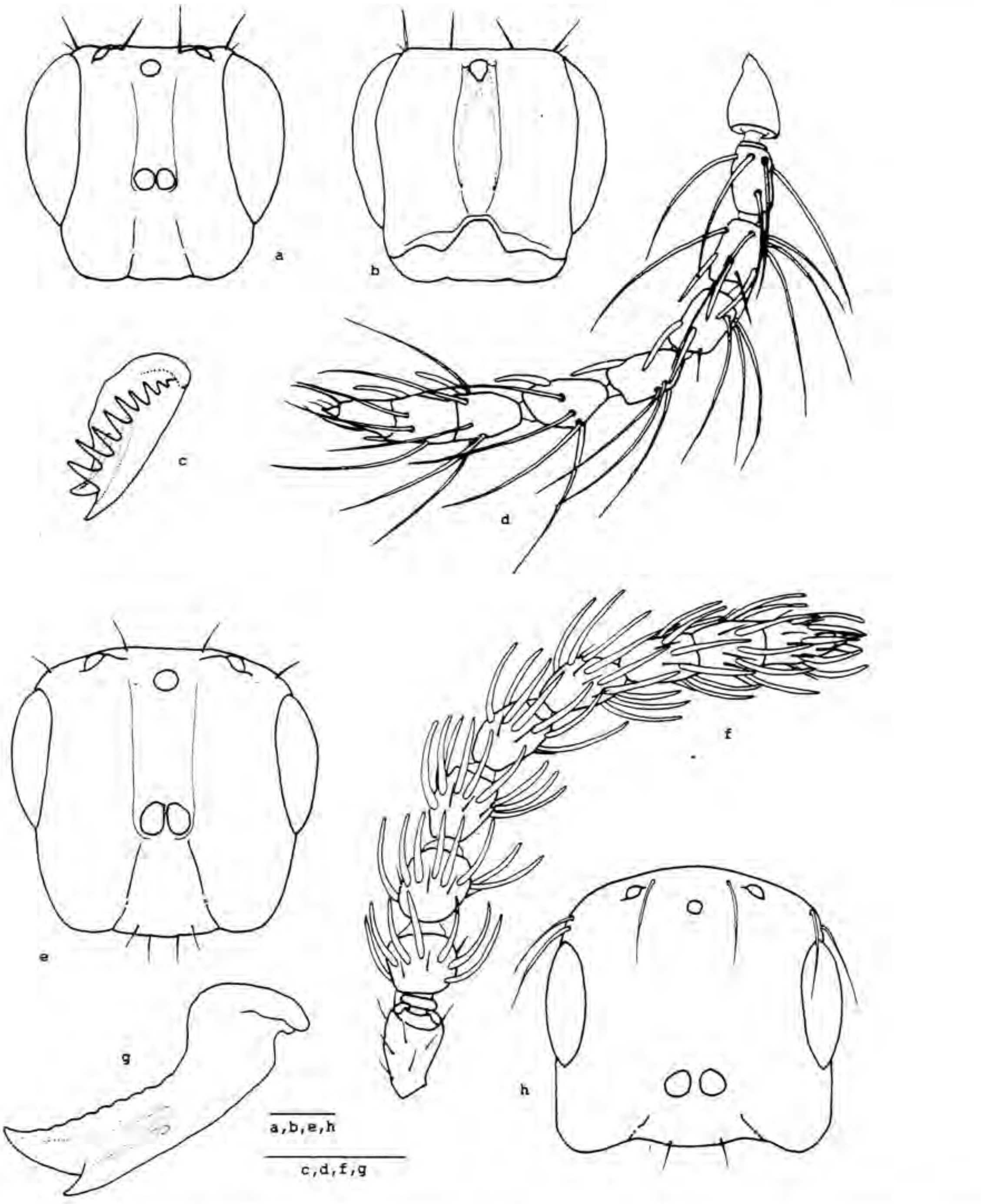


Fig. 8.8 a-d: *Crossogaster oculagrandis* sp. nov. a) female head, dorsal view b) female head, ventral view c) female mandible, ventral view d) female antenna, antiaxial view; e & f: *Crossogaster odorans* Wiebes, ex *F. stuhlmannii* Warb. e) female head, dorsal view f) female antenna, antiaxial view; g & h: *Crossogaster quadrata* sp. nov. g) male mandible, dorsal view h) male head, dorsal view. Scale bars = 0.1 mm.

MPS on each segment are shorter and squatter (fig. 8.8 d).

Thorax. Pronotum broad (l = 0.2, w = 0.28), torpedo shaped. Parapsidal furrows complete, evenly curved. Propodeum wider than long (l = 0.14, w = 0.28). Mesoscutum broad (l = 0.17, w = 0.31). Scutellum, including axillae (l = 0.19, w = 0.27). Fore femur 3.5X as long as wide (l = 0.24). Fore tibial armature bidentate. Fore leg coxa ca. four fifths of femur length (C = 0.2, TR = 0.08, TI = 0.1, TA = 0.15). Five hind tibial spines on dorsal margin. Fore wing 2.4X as long as broad (l = 1.3), very pilose, fringe long. Postmarginal vein shorter than stigmal (SM = 0.48, M = 0.18, PM = 0.07, S = 0.13). Marginal vein 8.8X longer than wide. Hind wing 4.8X as long as broad (l = 0.93).

Gaster, posterior edge of tergites crenulated with three medial incisions. Eighth urotergite spiracular peritremata very large and ovoid (l = 0.08), with a few long setae present around the edge. Ovipositor 4.4X longer than the valves (valve l = 0.14).

Crossogaster praeacuta sp. nov.

(figs. 8.9 a-h)

Etymology: Praeacutus (latin) = pointed, referring to the pointed epistomal margin.

Type material: Holotype ♀ and allotype ♂ (slide mounted): Uganda, Jinja, Roundabout nr. Crested Crane Hotel, 23 April 1968, tree no. 41, leg. D.S. Hill, ex *Ficus* sp. K.; 3 ♀ and 2 ♂ paratypes (slide mounted), series ♀ and ♂ paratypes: same data; series ♀ and ♂: Uganda, Jinja, Crested Crane Hotel, 9 April 1968, tree no. 33, leg. D.S. Hill, ex *Ficus* sp. K.; series ♀ and ♂: same data, 23 April 1968.

FEMALE. Faded due to storage in alcohol (uniform brown), probably metallic black. Total length with head in orthognathous position, excluding ovipositor valves = 1.6 mm.

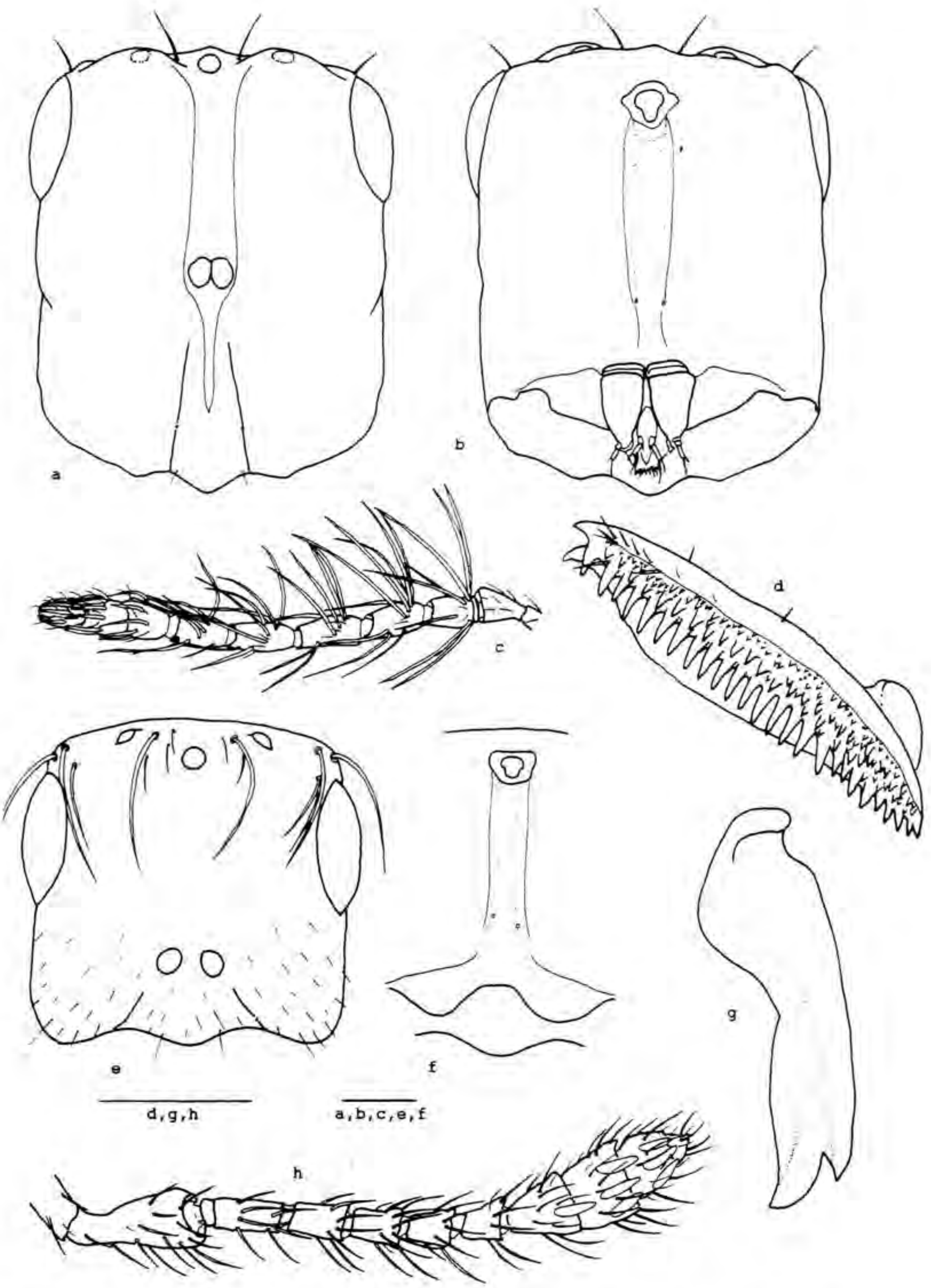


Fig. 8.9 a-h: *Crossogaster praeacuta* sp. nov. a) female head, dorsal view b) female head, ventral view c) female antenna, antiaxial view d) female mandible, ventral view e) male head, dorsal view f) male head, ventral view g) male mandible, dorsal view h) male antenna, antiaxial view. Scale bars = 0.1 mm.

Head (figs. 8.9 a & b) elongate, parallel sided (l = 0.60, w = 0.49, h = 0.22). Eye (l = 0.17, w = 0.18), fairly flush with sides of head (h = 0.05), 0.28X as long as the head; situated very posteriorly, in proximation with vertex. Cheek length 1.6X eye length. Malar sulcas present for first half of cheek closest to eye, curves up to dorsal surface of the head. Lateral ocelli not visible in dorsal view, situated in lateral excavations on vertex, occipital carina weak, almost straight, below ocelli. Ventrally on vertex there is a broad excavation in which the foramen magnum is situated. POL = 0.16. OOL = 0.08. Toruli situated well below the eyes, touching; TE 0.94X as long as scrobe length (TE ≐ 0.28, SL = 0.30). Scrobe continues anterior to toruli, tapering to a point. Clypeus narrow and elongate in area, subrectangular. Epistomal margin projecting, angular, coming to a medial point. Ventral tentorial pits widely separated, situated a quarter of the distance from the oral fossa to the foramen magnum (fig. 8.9 b). Mandible with two apical teeth and a longitudinal row of twenty-four teeth on the ventral edge, anterior to which there are two to three indistinct rows of progressively smaller teeth; two glands (fig. 8.9 d). One labial segment. Two maxillary segments, basal segment very reduced and short. Antenna (fig. 8.9 c) eleven segmented, formula 1115(3), first funicle segment smallest, rest subequal in size. Scape narrow, 6.3X longer than wide (l = 0.20). Pedicel relatively short, 0.29X scape length. MPS are very elongate, ranging from twice the length of the funicle segments to subequal the length, progressively shortening from the first funicle segment to the last club segment (fig. 8.9 c).

Thorax. Pronotum broad (l = 0.27, w = 0.38). Parapsidal furrows complete, evenly curved. Propodeum wider than long (l = 0.15, w = 0.35). Mesoscutum broad (l = 0.23, w = 0.41). Scutellum, including axillae (l = 0.24, w = 0.35). Fore femur 3.2X as long as wide (l = 0.35). Fore tibial armature bidentate, with a projection of the tibial chitin between the teeth and also a projection ventral to the second tooth. Fore leg coxa ca. two thirds of femur length (C = 0.24, TR = 0.06, TI = 0.10, TA = 0.20). Six hind tibial spines on the dorsal margin. Fore wing 2.3X longer than wide, l = 1.28, glabrous, fringe short. Postmarginal vein shorter than stigmal (SM = 0.44, M = 0.21, PM = 0.07, S = 0.11). Marginal vein 10.5X longer than wide. Hind wing 4X longer than wide, l = 0.99.

Gaster, posterior edge of tergites very crenulated. Eighth urotergite spiracular peritremata large and ovoid (l = 0.05), with a few setae present around the edge. Ovipositor 5.2X as long as ovipositor valve (valve l = 0.18).

MALE. Testaceous. Total length with head in orthognathous position excluding ovipositor 1.5 mm.

Head (fig. 8.9 e & f) approximately square (l = 0.44, w = 0.45, h = 0.22). Eye elongate (l = 0.18, w = 0.10, h = 0.05), 0.41X as long as head. Cheek length 0.61X eye length. Malar sulcas absent. Lateral ocelli visible in dorsal view, thin occipital carina present. POL = 0.16. OOL = 0.09. Toruli situated below the eyes, separated by two-thirds of torulus width; TE 0.31X as long as scrobe length (TE = 0.09, SL = 0.29). Clypeus trapezoid in area. Epistomal margin convex with medial projection, width of margin two fifths of head width. Ventral tentorial pits widely spaced (fig. 8.9 f). Mandible with inner tooth larger, inner margin smooth but swollen; two glands, outer smaller (fig. 8.9 g). One labial segment. Two maxillary segments, basal segment short. Antenna (fig. 8.9 h) eleven segmented, formula 1115(3), first funicle segment longest. Flagellar length 3.7X as long as pedicel. Scape 5.3X longer than wide (l = 0.21). Pedicel elongate, 0.43X scape length. MPS only present on the three club segments, two on the first and six on each of the last two (fig. 8.9 h).

Thorax. Parapsidal furrows complete. Fore femur 3.9X as long as wide (l = 0.39). Fore tibial armature bidentate. Fore tarsus subequal to fore tibia (C = 0.29, TR = 0.10, TI = 0.23, TA = 0.21). Fore wing 2.6X longer than wide, l = 1.37, pilose. Postmarginal vein shorter than stigmal (SM = 0.47, M = 0.23, S = 0.11, PM = 0.04). Marginal vein 13.5X longer than wide. Hind wing 4.8X longer than wide, l = 1.0.

Eighth urotergite spiracle normal. Aedeagus small (l = 0.29). Three teeth on aedeagus claspers.

Crossogaster rastellus **sp. nov.**

(figs. 8.5 b & 8.10 a-f)

Etymology: Rastellus (latin) = rake, referring to the rake like mandible.

Type material: Holotype ♀ and allotype ♂ (slide mounted): Uganda, Katalemwa, 18 November 1967, tree no. 9, leg. D.S. Hill, ex *F.* "*natalensis*"; 3 ♀ and 3 ♂ paratypes slide mounted, series ♀ and ♂ paratypes: same data.

FEMALE. Faded due to storage in alcohol for 22 years, head and thorax dark brown, probably metallic in fresh specimens, gaster, legs and antennae lighter brown. Total length with head in orthognathous position, excluding ovipositor = 1.57 mm.

Head (figs. 8.5 b & 8.10 a) elongate, parallel sided (l = 0.55, w = 0.43), dorsoventrally compressed (h = 0.15). Eye oval (l = 0.18, w = 0.11), fairly flush with the sides of the head (h = 0.05), 0.32X as long as the head. Cheek length 1.5X eye length. Malar sulcas present (curves up to meet face plane about two thirds down cheek). Lateral ocelli hidden in dorsal view, situated in axial lip of lateral vertex excavations. POL = 0.13, OOL = 0.06. Toruli situated well below the eyes, touching. TE 0.70X as long as scrobe length (TE = 0.21, SL = 0.29). Clypeus narrow and elongate in area. Epistomal margin slightly convex, round, set back into paraclypeal margins, laterally overlapping paraclypeal area, ca. a fifth of head width; paraclypeal margin

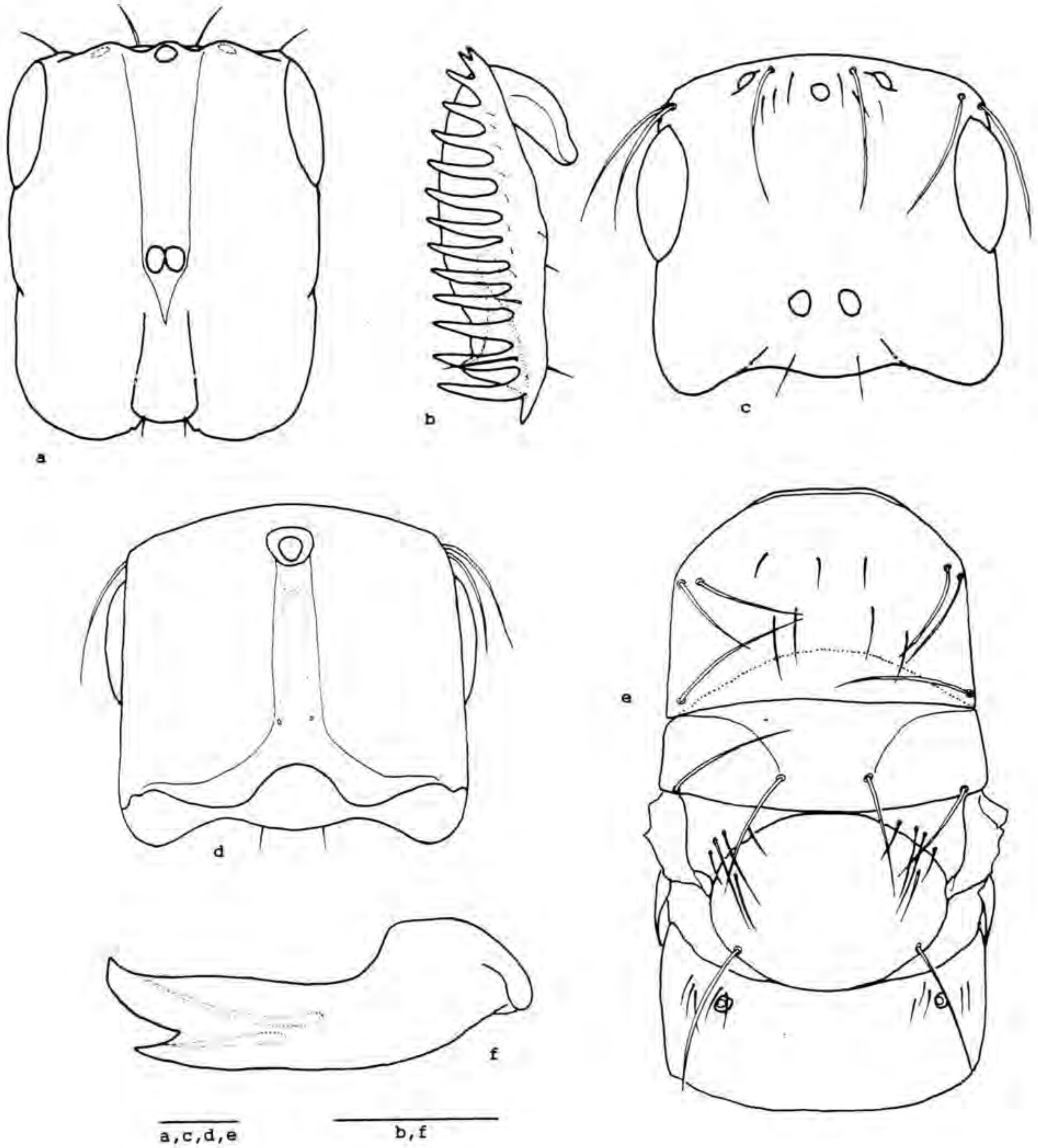


Fig. 8.10 a-f: *Crossogaster rastellus* sp. nov. a) female head, dorsal view b) female mandible, ventral view c) male head, dorsal view d) male head, ventral view e) female thorax, dorsal view f) male mandible, dorsal view. Scale bars = 0.1 mm.

has a step close to the epistomal margin (fig. 8.10 a). Ventral tentorial pits widely separated (fig 8.5 b). Mandible with two apical teeth and a longitudinal row of fourteen long teeth on the ventral anterior edge; two glands, inner gland small (figs. 8.5 b & 8.10 b). One labial segment. Two maxillary segments, basal segment reduced. Antenna much as in *C. praeacuta* (fig. 8.9 c), eleven segmented, formula 1115(3); first funicle segment shortest, rest subequal in size. Scape narrow, 7X longer than wide (l = 0.22). Pedicel relatively short, 0.27X scape length. MPS are very elongate, twice the length of the funicle segments, but on the club they are subequal to the segment length.

Thorax (fig. 8.10 e). Pronotum broad (l = 0.26, w = 0.33). Parapsidal furrows complete, evenly curved. Propodeum (l = 0.15, w = 0.33). Mesoscutum broad (l = 0.24, w = 0.37). Scutellum, including axillae (l = 0.22, w = 0.31). Tibial armature bidentate. Fore femur 3.1X as long as wide (l = 0.35). Fore leg coxa ca. two-thirds of femur length (C = 0.24, TR = 0.09, TI = 0.10, TA = 0.24). Ca. six hind tibial spines. Fore wing 2.5X longer than wide, l = 1.37, sparsely setous, fringe short. Postmarginal vein shorter than stigmal (SM = 0.46, M = 0.22, PM = 0.06, S = 0.11). Marginal vein 9.6X longer than wide.

Gaster, posterior edge of tergites very crenulated, with three larger medial incisions. Eighth urotergite spiracular peritremata large and ovoid (l = 0.07), with a few long setae present around the edge. Ovipositor 5X as long as ovipositor valves (valve l = 0.20).

MALE. Testaceous, gaster and eyes darker. Total length with head in orthognathous position excluding ovipositor 1.29 mm.

Head (fig. 8.10 c & d) broad (l = 0.43, w = 0.46, h = 0.21). Eye elongate (l = 0.17, w = 0.10), protrudes laterally (h = 0.06), 0.4X as long as head. Cheek length 0.65X eye length. Malar sulcas present for first quarter of cheek. Lateral ocelli visible in dorsal view. POL = 0.14. OOL = 0.10. Toruli situated below the eyes, separated by width of torulus. TE = 0.07. SL = 0.28. Clypeus trapezoid in area. Epistomal margin slightly convex, with straight medial section, width of margin ca. two fifths of head width. Ventral tentorial pits widely spaced. Mandible with inner tooth larger, inner margin smooth and swollen, two glands (fig. 8.10 f). One labial segment. Two maxillary segments. Antenna eleven segmented, formula 1115(3). Flagellar length 3X as long as pedicel. Scape 5X longer than wide (l = 0.20). Pedicel very elongate, half of scape length. MPS only present on last two club segments.

Thorax. Parapsidal furrows incomplete. Fore femur 3.5X as long as wide (l = 0.40). Fore tibial armature bidentate. Fore tarsus ca. four-fifths of fore tibial length (C = 0.29, TR = 0.10, TI = 0.24, TA = 0.20). Fore wing 2.6X longer than wide, l = 1.49, very pilose. Postmarginal vein shorter than stigmal (SM = 0.47, M = 0.28, S = 0.12, PM = 0.06). Marginal vein thin, 14X longer than wide. Hind wing 4.8X longer than wide, l = 1.06.

Eighth urotergite spiracle normal. Aedeagus small (l = 0.34). Three teeth on aedeagus claspers.

Crossogaster triformis species-group.

This species-group is characterised by the presence of placoid MPS on the antennal funicle segments. There may be either two anelli and four funicle segments, or a single anellus and five funicle segments. However, in the latter case the first funicle segment is reduced and intermediate between an anellus and a funicle segment, with only a single MPS present.

Crossogaster triformis Mayr

Crossogaster triformis Mayr 1885, 189 - 192, figs. 20-22, holotype ♀, allotype winged ♂ (the apterous ♂ is *Alfonsiella*, Wiebes 1975, pg. 226), Socotra, ex *F. salicifolia* Vahl, corrected to *F. vasta* Forsk. (Wiebes 1977b, pg. 210); redescribed by Grandi 1928b, 203-206, figs. xlii-xliii. [Examined ♀ holotype (card mounted), Naturhistorisches Museum, Vienna, Austria (the winged ♂ allotype was not seen)].

Comments. There is some question as to whether the third tooth of the female fore tibial armature is in fact a tooth and not just an extension of the tibial chitin as occurs in a number of other *Crossogaster* species. However, as it is impossible to tell from the card mounted specimen the answer will have to wait until further material is obtained.

This is the most primitive species in this species group, having five funicle segments with the normal complement of MPS. The remaining species either have five funicle segments, but with the first segment reduced with only a single MPS present on it, or four funicle segments and two anelli.

Crossogaster rashbrooki sp. nov.

(figs. 8.11 e & f)

Etymology: Named after the collector V. K. Rashbrook.

Type material: Holotype ♀ (slide mounted): Tanzania, Arusha, 10 August 1988, leg. V.K. Rashbrook, ex *Ficus* sp. (nr. *sansibarica* ?, figs on trunk).

FEMALE. Head, thorax, gaster and hind coxa metallic black, legs testaceous, antennae and mandibles brown. Total length with head in orthognathous position excluding ovipositor 1.89 mm.

Head (fig. 8.11 e) approximately square (l = 0.55, w = 0.52, h = 0.21). Eye oval (l = 0.20, w = 0.13, h = 0.06), 0.36X as long as the head. Cheek length equal to eye length. Malar sulcas absent. Lateral ocelli visible in dorsal view, occipital carina strong, lateral excavations present on vertex. POL = 0.21. OOL

= 0.10. Toruli situated below the eyes, touching. TE 0.63X as long as scrobe length (TE = 0.18, SL = 0.28). Clypeus trapezoid in area. Epistomal margin very slightly convex with shallow medial concavity, width a quarter of head width. Ventral tentorial pits widely spaced. Mandible, much as in *C. ovata* (fig. 8.11 g), with two apical teeth and a longitudinal row of sixteen ventral teeth, two glands. One labial segment. Two maxillary segments, basal segment reduced, short. Antenna (fig. 8.11 f) eleven segmented, formula 1115(3), first funicle segment smallest, rest subequal in size. Scape 7.7X longer than wide (l = 0.23). Pedicel elongate, 0.44X scape length. MPS are placoid, much as in *Philocaenus* Grandi. Only a single MPS present on the first funicle segment which is reduced in size (fig. 8.11 f).

Thorax. Pronotum broad (l = 0.33, w = 0.43), torpedo shaped. Parapsidal furrows complete, evenly curved. Propodeum wider than long (l = 0.19, w = 0.40). Mesoscutum broad (l = 0.28, w= 0.38). Scutellum, including axillae (l = 0.30, w = 0.50). Fore femur 3X as long as wide (l = 0.38). Fore tibial armature bidentate, may be an extension of the tibial chitin ventral to the second tooth. Fore leg coxa 0.71X femur length (C = 0.27, TR = 0.11, TI = 0.12, TA = 0.24). Seven hind tibial spines on the dorsal margin. Fore wing 2.5X longer than wide, l = 1.5, pilose, fringe long. Postmarginal vein shorter than stigmal (SM = 0.55, M = 0.23, PM = 0.08, S = 0.13). Marginal vein 11.7X longer than wide. Hind wing 4X longer than wide, l = 1.2.

Gaster, posterior edge of tergites very crenulated, with three medial deeper incisions. Eighth urotergite spiracular peritremata large and ovoid (l = 0.10), with a few long setae present around the edge. Ovipositor 5.5X as long as valve (valve = 0.18).

Crossogaster ovata sp. nov.

(figs. 8.11 g & h)

Etymology: referring to the host, *F. ovata*.

Type material: Holotype ♀, allotype ♂ (slide mounted): Uganda, Entebbe Botanical Gardens, 14 October 1967, tree no. 13, leg. D.S. Hill, ex *F. brachypoda* Hutch. (= *F. ovata* Vahl); 3 ♀ and 3 ♂ paratypes slide mounted, series ♀ and ♂: same data.

FEMALE. Faded, due to alcohol storage, brown, legs and antennae testaceous. Total length with head in orthognathous position, excluding ovipositor valves = 1.9 mm.

Head (fig. 8.11 h) elongate, parallel sided (l = 0.62, w = 0.50), dorso-ventrally compressed (h = 0.19). Eye oval (l = 0.20, w = 0.13), protrudes laterally (h = 0.07), 0.33X as long as the head. Cheek length 1.4X eye length. Malar sulcas absent. Lateral ocelli not visible, extensive lateral excavations on vertex behind eyes, thin straight carina present below ocelli. POL = 0.19. OOL = 0.09. Toruli situated below the eyes, touching. TE 0.69X as long as scrobe length (TE = 0.22, SL = 0.32). Clypeus narrow and elongate in area. Epistomal margin straight with very shallow medial concavity, 0.23X the head width. Ventral tentorial pits widely spaced. Mandible with two apical teeth and a longitudinal row of fourteen to fifteen ventral long teeth; two glands (fig. 8.11 g). One labial segment. Two maxillary segments, basal segment reduced, short. Antenna eleven segmented, formula 1115(3); first funicle segment shortest, rest subequal in size. Scape narrow, 7.8X longer than wide (l = 0.23). Pedicel very elongate, 0.54X scape length. MPS are placoid, only one present on the first funicle segment, which is intermediate between a normal funicle segment and an anellus, as in *C. rashbrooki* (fig. 8.11 f).

Thorax. Pronotum broad (l = 0.35, w = 0.42). Parapsidal furrows complete, evenly curved. Propodeum (l = 0.18, w = 0.40). Mesoscutum broad (l = 0.29, w = 0.46). Scutellum, including axillae (l = 0.27, w = 0.38). Fore femur 3.9X as long as wide (l = 0.43). Fore tibial armature tridentate, teeth long. Fore leg coxa ca. two thirds of femur length (C = 0.29, TR = 0.10, TI = 0.11, TA = 0.24). Seven hind tibial spines on dorsal margin. Fore wing 2.4X longer than wide, l = 1.54, sparsely setous, short fringe. Postmarginal vein shorter than stigmal (SM = 0.57, M = 0.22, PM = 0.07, S = 0.14). Marginal vein 11X longer than wide. Hind wing 4.4X longer than wide, l = 1.17.

Gaster, posterior edge of tergites very crenulated, with three large medial incisions. Eighth urotergite spiracular peritremata large and ovoid (l = 0.10), with a few long setae present around the edge. Ovipositor 5.5X as long as ovipositor valve (valve l = 0.18).

MALE. Dark testaceous, eyes darker. Total length with head in orthognathous position excluding ovipositor 1.84 mm.

Head elongate, parallel sided (l = 0.51, w = 0.49, h = 0.26). Eye elongate (l = 0.20, w = 0.13, h = 0.06), 0.39X as long as head. Cheek length 0.6X eye length. Malar sulcas absent. Lateral ocelli visible in dorsal view. POL = 0.16. OOL = 0.12. Toruli situated below the eyes, separated by two-fifths of torulus width. TE 0.33X as long as scrobe length. TE = 0.09. SL = 0.33. Clypeus trapezoid in area. Epistomal margin slightly convex, with straight medial section, ca. two fifths of head width. Ventral tentorial pits widely spaced. Mandible with inner tooth larger, no serrations, two glands. One labial segment. Two maxillary segments. Antenna eleven segmented, formula 1115(3). Antennal flagellum twice as long as pedicel. Scape broad, 5.8X longer than wide (l = 0.23). Pedicel very elongate, 0.61X scape length. MPS present on the last funicle and all three club segments, only a single sensillum present on the funicle and first club segment, the last two club segments with a number of sensilla.

Thorax. Parapsidal furrows incomplete. Fore femur 3.6X as long as wide (l = 0.47). Fore tibial armature bidentate, ventral tooth extremely elongate. C = 0.35, TR = 0.12, TI = 0.29, TA = 0.25. Fore wing 3X longer than wide, l = 1.70, very pilose. Postmarginal vein shorter than stigmal (SM = 0.60, M = 0.29, S

= 0.13, PM = 0.07). Marginal vein thin 14.5X longer than wide. Hind wing 4.3X longer than wide, l = 1.2.

Eighth urotergite spiracle normal. Aedeagus small (l = 0.35). Three teeth on aedeagus claspers.

***Crossogaster vansomereni* sp. nov.**

(fig. 8.11 d)

Etymology: Named after C. van Someren.

Type material: Holotype ♀ (slide mounted): Uganda, Kigesi District, Kisoro, 10 June 1968, tree no. 52, leg. D.S. Hill, ex *Ficus* sp. S. Paratype ♀: Kenya, Nairobi, Mayfair Hotel, 5400 ft., 10 February 1968, leg. C. van Someren, ex *Ficus* sp. (C.v.S. no. 17).

FEMALE. Faded due to storage in alcohol; head and thorax dark brown, probably metallic in fresh specimens; gaster, legs and antennae lighter brown. Total length with head in orthognathous position excluding ovipositor 1.35 mm.

Head (fig. 8.11 d) approximately square (l = 0.40, w = 0.39, h = 0.14). Eye oval (l = 0.15, w = 0.10, h = 0.05), 0.38X as long as head. Cheek length equal to eye length. Malar sulcas absent. Lateral ocelli half visible in dorsal view, shallow excavation laterally on vertex, occipital carina thin fold dorsal to ventral invagination of vertex in which the foramen magnum is situated. POL = 0.15. OOL = 0.073. Toruli situated below the eyes, touching. TE 0.69X as long as scrobe length (TE = 0.14, SL = 0.20). Clypeus trapezoid in area. Epistomal margin very slightly convex with very shallow broad medial concavity, width 0.23X head width. Ventral tentorial pits widely spaced. Mandible much as in *C. hilli* (fig. 8.11 c), with two apical teeth and a longitudinal row of thirteen ventral long teeth, two glands. Two labial segments. Two maxillary segments, basal segment reduced, short. Antenna much as in *C. hilli* (fig. 8.11 b), eleven segmented, formula 1124(3), funicle segments subequal in size. Scape 7.6X longer than wide (l = 0.16). Pedicel elongate, 0.44X scape length. MPS are placoid, much as in *Philocaenus* Grandi.

Thorax. Pronotum l = 0.20, torpedo shaped. Parapsidal furrows complete, evenly curved. Propodeum l = 0.14. Mesoscutum l = 0.17. Scutellum, including axillae l = 0.20. Fore femur 3.1X as long as wide (l = 0.29). Fore tibial armature bidentate. Fore leg coxa ca. two thirds of femur length (C = 0.20, TR = 0.07, TI = 0.10, TA = 0.15). Fore wing l = 1.15, pilose, fringe long. Postmarginal vein shorter than stigmal (SM = 0.43, M = 0.15, PM = 0.05, S = 0.08). Marginal vein 8.3X longer than wide.

Gaster, posterior edge of tergites very crenulated, with three medial incisions. Eighth urotergite spiracular peritremata large and ovoid (l = 0.07), with a few long setae present around the edge. Ovipositor 4.4X as long as valve (valve = 0.18).

Crossogaster hilli **sp. nov.**

(figs. 8.11 a-c)

Etymology: Named after the collector Dennis Hill.

Type material: Holotype ♀, allotype ♂ (slide mounted): Uganda, Makerere University Campus, Cluny Castle, 10 October 1967, tree no. 6, leg. D.S. Hill, ex *F.* "*thonningii*"; 3 ♀ and 3 ♂ paratypes slide mounted, series ♀ and ♂: same data; series ♀ and ♂: Uganda, Kabanyolo, 20 August 1968, tree no. 56, leg. D.S. Hill, ex *F.* "*thonningii*"; 1 ♀: Uganda, Kampala, 1 September 1968, tree no. 9, leg. D.S. Hill, ex *F.* "*natalensis*"; 2 ♀: Uganda, Katalemwa, 18 November 1967, tree no. 9, leg. D.S. Hill, ex *F.* "*natalensis*"; series ♀: Uganda, Katalemwa, 30 July 1968, tree no. 20, leg. D.S. Hill, ex *F.* "*natalensis*"; series ♀ and ♂: Uganda, Makerere University Campus, Mvule Lane, 30 October 1967, tree no. 7, leg. D.S. Hill, ex *Ficus* sp. B.

FEMALE. Faded due to storage in alcohol for 23 years, uniform brown. Total length with head in orthognathous position, excluding ovipositor valves, = 1.2 mm.

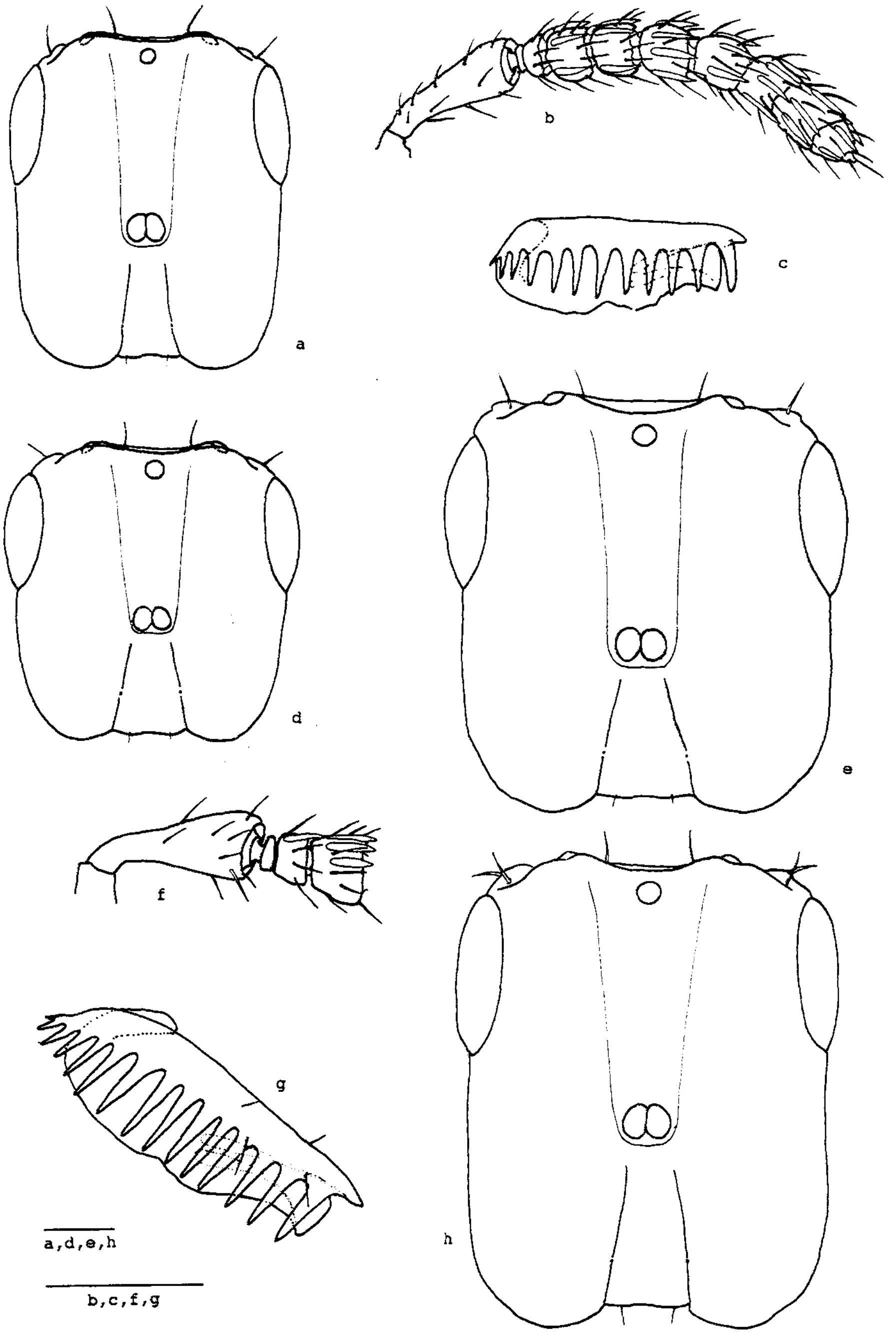


Fig. 8.11 a-c: *Crossogaster hilli* sp. nov. a) female head, dorsal view b) female antenna, axial view c) female mandible, ventral view; d: *Crossogaster vansomereni* sp. nov. d) female head, dorsal view; e & f: *Crossogaster rashbrooki* sp. nov. e) female head, dorsal view f) female antennal pedicel, anellus and first two funicular segments, axial view; g & h: *Crossogaster ovata* sp. nov. g) female mandible, ventral view h) female head, dorsal view. Scale bar = 0.1 mm.

Head (fig. 8.11 a) elongate, parallel sided (l = 0.45, w = 0.37), dorso-ventrally compressed (h = 0.13). Eye oval (l = 0.15, w = 0.09), fairly flush with sides of head (h = 0.05), 0.35X as long as the head. Cheek length 1.21X eye length. Malar sulcas absent. Lateral ocelli half visible in dorsal view,, situated in the axial lip of the lateral vertex excavations. Occipital carina present as a straight, thin fold below the ocelli. POL = 0.14. OOL = 0.07. Toruli situated well below the eyes, touching. TE 0.65X as long as scrobe length (TE = 0.16. SL = 0.24). Clypeus narrow and elongate in area. Epistomal margin almost straight with a very shallow medial concavity, ca. a quarter of the head width. Ventral tentorial pits widely separated. Mandible with two apical teeth and a longitudinal row of 12-13 long, ventral teeth; two glands (fig. 8.11 c). One labial segment. Two maxillary segments, basal reduced. Antenna (fig. 8.11 b) eleven segmented, formula 1124(3); funicle segments subequal in size. Scape narrow, 7.4X longer than wide (l = 0.18). Pedicel very elongate, 0.52X scape length. MPS are placoid, as in *Philocaenus*.

Thorax. Pronotum broad (l = 0.23, w = 0.28). Parapsidal furrows complete, evenly curved. Propodeum wider than long (l = 0.13, w = 0.29). Mesoscutum broad (l = 0.2, w = 0.33). Scutellum, including axillae (l = 0.19, w = 0.28). Fore femur 3.5X as long as wide (l = 0.3). Fore tibial armature bidentate, third tooth is an extension of the tibial chitin (fig. X). Fore leg coxa ca. three quarters of femur length (C = 0.22, TR = 0.08, TI = 0.07, TA = 0.18). Six - eight hind tibial spines on dorsal margin. Fore wing 2.3X longer than wide, l = 1.19, pilose, fringe long. Postmarginal vein shorter than stigmal (SM = 0.40, M = 0.19, PM = 0.07, S = 0.10). Marginal vein 11X longer than wide.

Gaster, posterior edge of tergites very crenulated, with three large medial incisions. Eighth urotergite spiracular peritremata large and ovoid (l = 0.06), with a few long setae present around the edge. Ovipositor 4.6X as long as ovipositor valve (valve l = 0.19).

MALE. Testaceous. Total length with head in orthognathous position, excluding ovipositor = 1.17 mm.

Head approximately square (l = 0.31, w = 0.32, h = 0.16). Eye elongate (l = 0.13, w = 0.075), protrudes laterally (h = 0.04), 0.4X as long as head. Cheek length 0.49X eye length. Malar sulcas absent. Lateral ocelli visible in dorsal view. POL = 0.10. OOL = 0.08. Toruli situated below the eyes, separated by a third of the torulus width. TE = 0.05. SL = 0.21. Clypeus trapezoid in area. Epistomal margin slightly convex, with straight medial section, width of margin ca. a third of head width. Ventral tentorial pits widely spaced. Mandible with inner tooth larger, with five weak serrations on inner margin, two glands. One labial segment. Two maxillary segments, basal segment reduced. Antenna eleven segmented, formula 1115(3). Antennal flagellum 2.4X as long as pedicel. Scape 5X longer than wide (l = 0.15). Pedicel very elongate, 0.53X scape length. MPS only present on the last two club segments.

Thorax. Parapsidal furrows complete. Fore femur 3.6X as long as wide (l = 0.29). Foretibial armature bidentate, ventral tooth elongate, situated above the spur. Fore tarsus 0.88X fore tibial length (C = 0.21, TR = 0.08, TI = 0.17, TA = 0.15). Fore wing 3.1X longer than wide, l = 1.05, pilose. Postmarginal vein shorter than stigmal (SM = 0.35, M = 0.19, S = 0.08, PM = 0.06). Marginal vein thin 12X longer than wide. Hind wing 3.7X longer than wide, l = 0.59.

Eighth urotergite spiracle normal. Aedeagus small (l = 0.23). Three teeth on aedeagus claspers.

***Crossogaster robertsoni* sp. nov.**

(figs. 8.12 a-h)

Etymology: Named after H.G. Robertson, one of the collectors of the holotype.

Type material: Holotype ♀ and allotype ♂ (slide mounted): South Africa, Natal, Mselini, 12 December 1986, leg. S.G. Compton & H.G. Robertson, C46, ex *F. trichopoda* Baker. Paratypes: 5 ♀ and 3 ♂ (slide mounted), series ♀ and ♂: same data as holotype; series ♀: South Africa, Natal, Kosi Bay, 2 December 1988, leg. S.G. Compton, C96, ex *F. trichopoda* Baker; series ♀: S. Africa, Natal, Mapelane, 11 December 1988, leg. S.G. Compton, C97, ex *F. trichopoda* Baker; South Africa, Natal, Kwazibi, North of Manzengwenya Plantation, 26 54'S 32 19'E, 15 November 1989, leg. M. Ward, C201, ex *F. trichopoda* Baker; South Africa, Natal, Sodwana, 25 January 1990, leg. S. van Noort & A.B. Ware, C251, ex *F. trichopoda* Baker; South Africa, Natal, Mselini, 26 January 1990, leg. S. van Noort & A.B. Ware, C257, ex *F. trichopoda* Baker; South Africa, Natal, Kosi Bay, 26 January 1990, leg. S. van Noort & A.B. Ware, C259, ex *F. trichopoda* Baker; South Africa, Natal, Dukuduku, 30 January 1990, leg. S. van Noort & A.B. Ware, C271, ex *F. trichopoda* Baker.

FEMALE. Metallic black, gaster dark brown, tibia, tarsi and antennae testaceous. Total length with head in orthognathous position, excluding ovipositor valves = 1.6 mm.

Head (figs. 8.12 a & b) elongate, parallel sided (l = 0.52, w = 0.44), dorsoventrally compressed (h = 0.15). Eye oval (l = 0.19, w = 0.12), fairly flush with sides of head (h = 0.05), 0.36X as long as the head. Cheek length 1.2X eye length. Malar sulcas absent. Lateral ocelli visible in dorsal view, no excavations, occipital carina present as a thin fold ventral to the lateral ocelli. POL = 0.17. OOL = 0.07. Toruli situated well below the eyes, touching. TE 0.75X as long as scrobe length (TE = 0.20, SL = 0.26). Clypeus narrow and elongate in area. Epistomal margin slightly convex and angular, set back into paraclypeal margins, ca. a fifth of head width. Ventral tentorial pits widely spaced (fig. 8.12 b). Mandible (fig. 8.12 c) with two apical teeth and a longitudinal row of twelve ventral teeth, which are not as long as in *C. hilli*; two glands. One labial segment. Two maxillary segments, basal segment reduced, short. Antenna (fig. 8.12 d) eleven segmented, formula 1124(3); funicle segments subequal in size. Scape narrow, 5.8X longer than wide (l = 0.19). Pedicel very elongate, 0.56X scape length. MPS are placoid, antennae much as in *Philocaenus*.

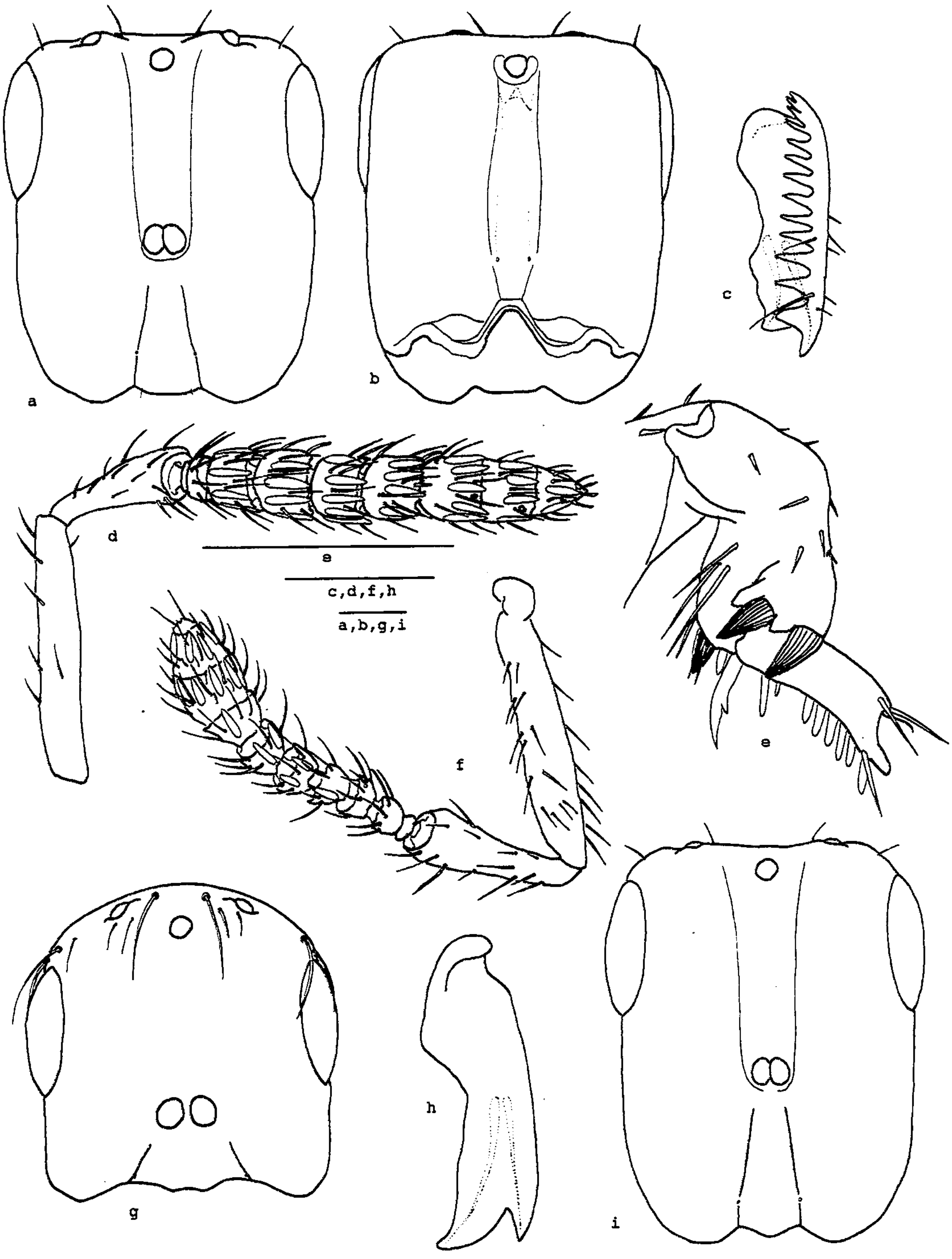


Fig. 8.12 a-h: *Crossogaster r. robertsoni* sp. nov. a) female head, dorsal view b) female head, ventral view c) female mandible, ventral view d) female antenna, antiaxial view e) female fore tibia and first tarsal segment, antiaxial view f) male antenna, antiaxial view g) male head, dorsal view h) male mandible, dorsal view; i: *Crossogaster robertsoni rasplusi* subsp. nov. i) female head, dorsal view. Scale bars = 0.1 mm.

Thorax. Pronotum broad (l = 0.29, w = 0.35). Parapsidal furrows complete, evenly curved. Propodeum wider than long (l = 0.13, w = 0.33). Mesoscutum broad (l = 0.23, w = 0.37). Scutellum, including axillae (l = 0.22, w = 0.31). Fore femur 2.8X as long as wide (l = 0.34). Fore tibial armature bidentate, third tooth is an extension of the tibial chitin and not a proper tooth (fig. 8.12 e). Fore leg coxa ca. two thirds of femur length (C = 0.23, TR = 0.09, TI = 0.10, TA = 0.21). Six hind tibial spines on dorsal margin. Fore wing 2.3X longer than wide, l = 1.13, sparsely setous, short fringe. Postmarginal vein shorter than stigmal (SM = 0.42, M = 0.19, PM = 0.06, S = 0.11). Marginal vein 11X longer than wide. Hind wing 4.8X longer than wide, l = 0.92.

Gaster, posterior edge of tergites very crenulated, with three deeper medial incisions. Eighth urotergite spiracular peritremata large and ovoid (l = 0.06), with a few long setae present around the edge. Ovipositor 4.6X as long as valve (valve l = 0.21).

MALE. Testaceous. Total length with head in orthognathous position excluding ovipositor 1.4 mm.

Head (fig. 8.12 g) approximately square (l = 0.43, w = 0.43, h = 0.21). Eye oval (l = 0.18, w = 0.12, h = 0.051), 0.41X as long as head. Cheek length 0.57X eye length. Malar sulcas absent. Lateral ocelli visible in dorsal view. POL = 0.14. OOL = 0.10. Toruli situated below the eyes, separated by a third of the torulus width, TE 0.35X as long as scrobe length. TE = 0.09. SL = 0.26. Clypeus trapezoid in area. Epistomal margin slightly convex, with straight medial section, width 0.36X head width. Ventral tentorial pits widely spaced. Mandible with inner tooth larger, no significant serrations present on inner margin; two glands (fig. 8.12 h). One labial palp segment. Two maxillary palp segments. Antenna (fig. 8.12 f) eleven segmented, formula 1115(3). Antennal flagellum 1.9X longer than pedicel. Scape 5.5X longer than wide (l = 0.19). Pedicel very elongate, 0.6X scape length. MPS present on the last three funicle segments (1, 2, 2) respectively, starting basally and on the three club segments (2, 9, 6) respectively.

Thorax. Parapsidal furrows complete. Fore femur 3.6X as long as wide (l = 0.36, w = 0.10). Fore tibial armature bidentate, ventral tooth next to the spur insertion elongate. Fore tibia 1.1X fore tarsal length (C = 0.28, TR = 0.10, TI = 0.22, TA = 0.20). Fore wing 2.9X longer than wide, l = 1.23, very pilose. Postmarginal vein shorter than stigmal (SM = 0.44, M = 0.20, S = 0.12, PM = 0.03). Marginal vein thin, 11X longer than wide. Hind wing 5.1X longer than wide, l = 0.92.

Eighth urotergite spiracle normal. Aedeagus small (l = 0.26). Four teeth on aedeagus claspers.

Crossogaster robertsoni rasplusi **subsp. nov.**

(fig. 8.12 i)

Etymology: Named after the collector J.Y. Rasplus.

Type material: Holotype ♀ (card mounted): Ivory Coast, Lamto, 5° 02'W 6° 13'N, 26 June 1989, leg. J.Y. Rasplus, ex *F. trichopoda* Baker; 1 ♀: same data, but 5 July 1989; 1 ♂: same data, but 30 June 1989.

FEMALE. The head is more elongate and dorsoventrally compressed than in the nominate subspecies, with an epistomal margin that comes medially to a point (fig. 8.12 i).

Comments. This population may warrant specific status, or the two populations may only be the extremes of a geographical cline. Until further samples are obtained in order to determine whether there is a gradual change in morphology from South Africa to the Ivory Coast or not, I believe that the population is best delimited as a subspecies.

9

SYSTEMATICS OF *PHILOCAENUS*

INTRODUCTION

Philocaenus Grandi as here defined incorporates *Phagoblastus* Grandi, which is recognised as a junior synonym. These two genera were based on differences in female morphology, which with the acquisition of material of new species has proven to be only the extremes of a continuum of variation. Male morphology also strongly supports the synonymising of these genera. No males were available when Grandi described these genera, but if they had been it seems unlikely that he would have separated them, because they are hardly separable, let alone indicative of generic level differences. This genus thus encompasses a broad range of female morphological variation, whereas the males are morphologically conservative. This is typical of sycoecines, as female variation is a result of adaptations that have evolved to facilitate entrance through the fig ostiole, whereas the males have not been subjected to this selective pressure.

Philocaenus consists of a number of distinct species-groups, usually only recognisable in the female sex. An exception is the *P. silvestrii* group which is defined by male characters. This latter species group is also the most distinct and may warrant generic status. However, I have refrained from separating it as there are no female autapomorphies defining the group, and the cladogram suggests that it would be better placed within *Philocaenus*.

Philocaenus now contains 22 species, with 17 of those being described here for the first time. The species are associated with the *Ficus* subsections *Galoglychia*, *Platyphyllae* and *Chlamydodorae* of section *Galoglychia*.

GENERIC DEFINITION

Philocaenus Grandi

Philocaenus Grandi 1952, 38-40
Type species: *P. barbatus* Grandi, by original designation. Holotype ♀, Senegal.

Phagoblastus Grandi 1955, 100-102, **syn. n.**
Type species: *Phagoblastus barbarus* Grandi 1955. Holotype ♀, Grahamstown, South Africa.

FEMALE. Head as broad as long, or distinctly longer than wide, slightly to extremely dorso-ventrally compressed; smooth, without sculpture; clypeus narrow to broad, shape very variable. Compound eyes large. Malar sulcus ranging from present for the full cheek length to completely absent. Vertex with pronounced occipital carina situated dorsal to a broad invagination of the ventral margin of the vertex, the vertex may have shallow lateral excavations; strong setae are present on the vertex. Toruli either situated between the eyes or on an imaginary line joining the anterior margins of the eyes. Antennae with two anelli, four funicle segments and three club segments. Multiporous plate sensilla (MPS) placoid. Ventral tentorial pits usually in close apposition, often difficult to distinguish as paired under the light microscope, situated posteriorly in a short medial depression, ca. third of distance from oral fossa; sometimes distinctly separated without a medial groove present. Tentorial beams diverge dorsally such that the dorsal tentorial pits are widely spaced, situated on the clypeal sutures. Hypostoma usually present, but may be absent. One or two labial palp segments, segments subequal; three maxillary palp segments, proximal segment either subequal to longer than the distal two segments combined, or subequal to the distal segment and two-three times as long as the medial. Mandible very variable, with two apical teeth and ranging from a single ventral tooth to a ventral plate of many teeth.

Thorax. Pronotum broad to elongate, with a weak carina present on the dorso-anterior margin; mesonotum subtriangular, parapsidal sulci complete, evenly curved; propodeal spiracles anteriorly situated, may be surrounded by a shallow excavation. Very stout fore femur, subtriangular or cylindrical and elongate; tibial armature either a comb of teeth on dorso-apical adaxial tibial margin or plate of teeth fused along the length of the adaxial face of tibia. Ventral tooth next to the spur insertion may be present or absent. Axial third of forewing glabrous, rest covered in microsetae, fringe present, anal and medial setal tracts present. Postmarginal vein shorter than stigmal, marginal vein thick.

Gaster. Posterior tergal edges crenulated (frayed) with three dorsal medial incisions. Eighth urotergite spiracle normal, may have a slightly expanded peritreme. Ovipositor valves from 0.28X to half the length of the gaster.

MALE. Head broader than long to square; epistomal margin broader than in the females. Toruli slightly separated, situated on or below an imaginary line joining the base of the eyes. Antennal formula 1124(3), second anellus larger than the first. MPS may be very reduced. Flagellum short ca. the same length to 1.5X as long as the pedicel. Dorsal tentorial pits situated about half way between the toruli and the epistomal margin on the clypeal sutures. Malar sulcus present for full length of the cheek, but not well defined. Very strong setae present on the vertex. Ventral tentorial pits separated, situated closer to the oral fossa than to the foramen magnum. One or two labial palp segments, three maxillary palp segments. Mandibular apical teeth subequal, outer tooth slightly longer, two glands.

Thorax. Pronotum broad with many strong setae; mesonotum subtriangular, parapsidal sulci may be incomplete posteriorly, evenly curved, strong setae present. Propodeal spiracles anteriorly situated. Fore tibia may have two dorso-apical teeth or they may be absent, ventral tooth next to the bifurcate spur absent or present. Wings pilose, axial third bare, anal and medial setal tracts present, fringe present. Relatively thick marginal vein.

Gaster, posterior edge of tergites uniformally straight, with a row of strong setae along the edge. Aedeagus large.

Comments. *Philocaenus* females may be recognised by the combined possession of two anelli and four funicle segments, crenulated posterior edges to the gastral tergites and the ventral tentorial pits in very close apposition. Some species of *Crossogaster* also have two anelli and four funicle segments with a crenulated posterior margin to the tergites, but then the tentorial pits are widely spaced and the eighth urotergite peritremata are expanded. *Philocaenus* males have the outer mandibular tooth longer than the inner, without any ventral teeth present.

KEY TO THE SPECIES OF *PHILOCAENUS*:

FEMALES

1. Mandible with more than one ventral tooth, head may be square or elongate 2
 - Mandible with a single large ventral tooth, head always elongate (e.g. fig. 9.9 d) 19

2. Mandible with two to four ventral teeth apically situated (e.g. fig. 9.12 c) 10
 - Mandible with a row of at least 9 teeth on ventral edge, or a ventral plate of teeth (e.g. fig. 9.3 c) 3

3. Four well spaced teeth anterior to a ventral row of 13-20 teeth (fig. 9.4 e) 4
 - Mandible otherwise 5

4. Epistomal margin distinctly bilobed, projecting further than paraclypeal margins (fig. 9.4 d); mandible with 18-20 ventral teeth (fig. 9.4 e); tibial armature a comb of 7-8 teeth, with 1-2 teeth dorsal to the comb, ex *Ficus* sp. K. .... *P. jinjaensis*

- Slight lateral projections on epistomal margin, the margin not projecting further than the paraclypeal margins (fig. 9.4 a); mandible with 13-15 ventral teeth; tibial armature a comb of 5-6 teeth, with a single tooth dorsal to the comb (fig. 9.4 c), ex *F.* "*natalensis*" .... *P. geminus*

5. Mandible with at least two rows of ventral teeth, if only two rows are present then the anterior row is uneven (fig. 9.5 g), often many rows forming a plate of teeth (e.g. fig. 9.6 c & d) 6

- Mandible with a single row of ventral teeth (e.g. fig. 9.3 c). A second row of teeth may be present, but it is then inconspicuous and in a straight line (fig. 9.1 c) 14

6. Head square; epistomal margin weakly produced (fig. 9.5 h); two rows of ventral teeth on the mandible (fig. 9.5 g), ex *F. craterostoma* .... *P. insolitus*

- Head elongate, more than 1.25X longer than wide; epistomal margin strongly produced; more than two rows of ventral teeth on the mandible 7

7. Toruli situated completely between the eyes (fig. 9.5 a & d); ventral tentorial pits situated in the posterior end of a medial groove (fig. 9.6 b & c) 8

- Toruli situated on an imaginary line joining the anterior margins of the eyes (fig. 9.7 a & d); no medial groove present on the underside of the head (fig. 9.6 d) 9

8. Head 1.34X longer than wide, medial concavity of the epistomal margin as deep as broad (fig. 9.5 a); three to four uneven rows of ventral teeth on the mandible,

posterior row with ca. 26 teeth (fig. 9.6 b), ex *F. natalensis natalensis* .... *P. medius*

- Head 1.55X longer than wide, medial concavity of the epistomal margin deeper than broad (fig. 9.5 d); more than three rows of ventral mandibular teeth (plate of teeth), posterior row with ca. 44 teeth (fig. 9.6 c), ex *F. "natalensis"*, *F. "thonningii"* and *F. "dekeknena"* .... *P. ugandensis*

9. Eye length 1.5X cheek length; epistomal margin with a broad v-shaped medial indentation (fig. 9.7 a); hypostoma present (fig. 9.6 d), ex *F. trichopoda* .... *P. hippopotomus*

- Eye length 2X cheek length; epistomal margin with a narrow v-shaped medial indentation, flanked by a step on each side (fig. 9.7 d); hypostoma absent (fig. 9.7 e), ex *F. platyphylla* .... *P. barbatus*

10. Four ventral teeth on mandible (fig. 9.12 c), ex *F. craterostoma* .... *P. quatuordentatus*

- Two or three ventral teeth on mandible (figs. 9.10 c & 9.13 c) 11

11. Ovipositor valves more than half as long as the gaster, ex *F. bussei* .... *P. zambesiacus*

- Valves a third or less than a third of gaster length ... 12

12. Two ventral teeth on mandible (fig. 9.10 c), ex *F. glumosa* .... *P. warei*

- Three ventral teeth on mandible (figs. 9.11 b & 9.13 c) ... .13

13. Four teeth on the dorso-apical margin of the fore tibia (fig. 9.13 d), ex *F. abutilifolia* .... *P. rotundus*

- Three teeth on dorso-apical fore tibial margin (e.g. 9.10 d), ex *F. burtt-davyi*, *F. thonningii*, *F. l. lingua*, *F. stuhlmannii*, *F. craterostoma* and *F. natalensis leprieurii*

.... *P. liodontus*

14\. Malar sulcus absent 15
- Malar sulcus distinct for complete cheek length 17

15\. Head square (fig 9.3 k), ex *F. thonningii* ..... *P. barbarus*
- Head elongate, at least 1.3X longer than wide (Figs. 9.3 a & h) 16

16\. Eye 1.5X longer than cheek; epistomal margin with shallow medial concavity (fig. 9.3 h), ex *F. reflexa* ... *P. bouceki*
- Eye length equal to cheek length; epistomal margin convex (fig. 9.3 a), ex *F. antandronarum bernardii* .... *P. comorensis*

17\. Comb of six teeth present on dorso-apical margin of tibia; epistomal margin with a deep medial incision (fig. 9.3 f), ex *F. lutea* .... *P. silvestrii*
- Plate of teeth present for most of dorso-antiaxial length of tibia (figs. 9.1 e & 9.2 d & e); epistomal margin with only a shallow medial concavity (figs. 9.1 a & 9.2 a) .. 18

18\. Tibial plate subequal in length to first tarsal segment (fig. 9.2 d & e); antennal funicle segments longer than wide (fig. 9.2 c), ex *F. saussureana* .... *P. cavus*
- Tibial plate 2.5X as long as first tarsal segment (fig. 9.1 e); antennal funicle segments broader than long, ex *F. chlamydocarpa* .... *P. comptoni*

19\. Fore tibial armature on dorso-apical margin bidentate (fig. 9.9 f); eye length twice or more than twice as long as cheek 20
- Fore tibial armature on dorso-apical margin tridentate; eye length less than 1.6X as long as cheek 21

20. Head 1.6X longer than wide, eye length 2.4X longer than cheek; epistomal margin broadly and shallowly concave (fig. 9.9 a), ex *F. t. tremula* .... *P. clairae*
  - Head 1.4X longer than wide, eye length twice as long as cheek; epistomal margin concavity less broad and more medially situated (fig. 9.9 h), ex *F. ottonifolia lucanda* .... *P. levis*

21. Epistomal margin concavity deeper than paraclypeal margins, laterally projecting, width 0.4X head width (fig. 9.8 a); head 1.5X longer than wide; eye length 1.37X longer than cheek, ex *F. ottonifolia ulugarensis* .... *P. bifurcus*
  - Epistomal margin concavity shallower than paraclypeal margins, laterally less projecting, width 0.26X head width (fig. 9.8 e); head 1.25X longer than wide; eye length 1.56X longer than cheek, ex *Ficus* sp. .... *P. bakeri*

MALES

1. Mandibular apical teeth subequal, outer tooth less than twice the length of the inner (measured along the opposing inner edges); antennal flagellum shorter than scape length 2
  - Outer mandibular apical tooth more than twice the length of the inner; antennal flagellum longer than scape length 4

2. Toruli situated in line with the base of the eyes; deep medial incision in the epistomal margin; inner mandibular tooth truncate (fig. 9.3 i), ex *F. lutea* .... *P. silvestrii*
  - Toruli completely below the base of the eyes; epistomial margin with only a shallow medial concavity (fig. 9.1 f & 9.2 f); inner mandibular tooth pointed (figs. 9.1 g & 9.2 h) 3

3. Head ca. square, L:W = 1.02; vertex rounded (fig. 9.2 f), ex *F. saussureana* .... *P. cavus*

- Head broad, L:W = 0.90; vertex subquadrate (fig. 9.1 f) ex *F. chlamydocarpa* .... *P. comptoni*

4. Epistomal margin smoothly concave (e.g. figs. 9.3 e, 9.10 e & 9.12 d) 5
- Epistomal margin straighter with a medial convexity, which may be indistinct (e.g. figs. 9.5 b, 9.5 e, 9.7 b, 9.9 b & 9.13 e) 8

5. Vertex rounded (fig. 9.10 e), mesoscutum, scutellum and vertex dark brown, ex *F. glumosa* .... *P. warei*
- Vertex straight (fig. 9.3 e), head and body testaceous 6

6. Head elongate, 1.5X longer than wide (fig. 9.3 e), ex *F. antandronarum bernardii* .... *P. comorensis*
- Head ca. square, L:W = 0.97-1.1 7

7. Head slightly longer than wide L:W = 1.1; small species, total length, with head in orthognathous position = 1.2 mm, ex *F. reflexa* .... *P. bouceki*
- Head broad, L:W = 0.97 (fig. 9.12 d); larger species, total length, with head in orthognathous position = 1.84 mm, ex *F. bussei* .... *P. zambesiacus*

8. Epistomal margin in line with or projecting further anteriorly than the paraclypeal margins; toruli in line with the base of the eyes (figs. 9.5 e, 9.7 b & g) 9
- Epistomal margin is laterally of the medial convexity deeper than the paraclypeal margins, toruli situated completely between the eyes, even if only just (e.g. fig. 9.5 b) 11

9. Head slightly elongate, L:W = 1.1; vertex straight (fig 9.5 e), ex *Ficus* sp. .... *P. ugandensis*
- Head square, L:W = 1.0; vertex round 10

10. Head testaceous, ex *F. trichopoda* .... *P. hippopotomus*
- Posterior two-thirds of head dark brown, almost black, ex *F. platyphylla* .... *P. barbatus*

11. Anterior edge of the toruli situated above the base of the eyes by at least the length of a torulus, ex *F. n. leprierii*, *F. craterostoma*, *F. burtt-davyi*, *F. thonningii*, *F. stuhlmannii* and *F. abutilifolia* .... *P. liodontus* and *P. rotundus*
- Anterior edge of the toruli situated only just above the base of the eyes by less than the length of a torulus .. 12

12. Toruli very slightly separated (fig. 9.9 b), ex *F. t. tremula* .... *P. clairae*
- Toruli touching along inner edges 13

13. Epistomal margin slightly concave, ex *F. thonningii* .... *P. barbarus*
- Epistomal margin almost straight with a slight medial convexity 14

14. Cheek length 0.42X the eye length, ex *Ficus* sp. .... *P. jinjaensis*
- Cheek length 0.3X the eye length (fig. 9.5 c), ex *F. n. natalensis* .... *P. medius*

SPECIES DESCRIPTIONS

Philocaenus silvestrii species-group.

This species group can be defined in both sexes by the presence of strong setae on the head and body and a complete malar sulcus. Additionally, the males have subequal mandibular teeth, an antennal flagellum that is shorter than the scape and a head that narrows anteriorly as in *Sycoecus* males.

Philocaenus silvestrii (Grandi) **comb. n.**

(figs. 9.3 f, g, i & j)

Crossogaster silvestrii Grandi 1916, 253-264, holotype ♀, allotype ♂, Senegal. [examined ♀ types, Istituto di Entomologia "Guido Grandi", Bologna, (in a poor state of preservation)].

Crossogaster atratus Masi 1917, 125-126, holotype ♀, Seychelles, **syn. n.**

Additional material: series ♀, 1 ♂: Kenya, 4 miles from Embu, 3 March 1968, C.v.S. no. 28, leg. C. von Someren, ex *Ficus* sp.; series ♀: Kenya, Forthall, 19 March 1969, C.v.S. no. 29, leg. C. von Someren, ex *Ficus* sp.; 4 ♀: Kenya, Nairobi, 12 October 1971, leg. J. Galil, RMNH 1901, ex *F. vogelii* (Miq.) Miq. (= *F. lutea* Vahl); 15 ♀, 16 ♂: Madagascar, 1000 m, Arabalavao, 11 km S. on R.N. 7, 14 August 1972, leg. Cremers & Delobal, RMNH 2123, ex *F. baroni* Baker (= *F. lutea* Vahl) (Blommers no. 17); 25 ♀: Aldabra Island, Bassin Cabri, 10 March 1974, RMNH 2469, leg. J.T. Wiebes, ex *F. nautarum* Baker (= *F. lutea* Vahl); 3 ♀: Aldabra Island, Takamaka Grove, 10 February 1974, RMNH 2477, leg. J.T. Wiebes, ex *F. nautarum* Baker (= *F. lutea* Vahl); series ♀, ♂: Ghana, Kumasi, U.S.T. Campus, January 1981, leg. Newton & Hayford, RMNH 4350, ex *F. vogelii* (Miq.) Miq. (= *F. lutea* Vahl); 23 ♀, series ♂: Seychelles, Cousin Island, July 1981, no. 357 & 361, leg. G.M. Bathe, RMNH 4637, ex *F. nautarum* Baker (= *F. lutea* Vahl); 15 ♀, 3 ♂: Ivory Coast, Taï Forest, 20-22 November 1982, leg. C.C. Berg & J.T. Wiebes, RMNH 4802, ex *F. lutea* Vahl (det. Berg); series ♀, ♂: South Africa, Natal, Umhlanga Rocks, 3 December 1986, C29, leg. S.G. Compton & A.J. Gardiner, ex *F. lutea* Vahl; series ♀, ♂: South Africa, Natal, Hibberdene, 13 December 1986, C30, leg. S.G. Compton, ex *F. lutea* Vahl; 4 ♀, 2 ♂: South Africa, Natal, Mtunzini, 12 December 1988, C99, leg. S.G. Compton, ex *F. lutea* Vahl; series ♀, 3 ♂: South Africa, Natal, Mselini, 26 January 1990, C255, leg. S. van Noort & A.B. Ware, ex *F. lutea* Vahl; 2 ♀: South Africa, Eastern Cape, Grahamstown, 1 January 1991, leg. S.G. Compton, C342, ex *F. lutea* Vahl; series ♀, ♂: Comore Islands, Grand Comore, Maoeni Forest, 24 July 1990, leg. S.G. Compton, C2002, ex *F. lutea* Vahl.

Comments. In the description of *Crossogaster silvestrii* Grandi (1916), Grandi incorrectly described *C. silvestrii* as having a single labial palp segment and two maxillary palp segments, whereas there are actually two and three segments respectively. Masi (1917) correctly attributed *Crossogaster atratus* with two labial palp segments and three maxillary palp segments in his description of this species. However, he was only describing a different geographic population of *Philocaenus silvestrii* (Grandi), and hence *Crossogaster atratus* is a junior synonym of *P. silvestrii*.

The following redescription is made from material collected at Umhlanga Rocks, Natal, South Africa, C29.

FEMALE. Metallic black, antennae and mandibles dark brown, legs testaceous. Total length with head in orthognathous position, excluding ovipositor = 1.8 mm.

Head (fig. 9.3 f) approximately square (l = 0.53, w = 0.55), height compressed (h = 0.18). Eye elongate (l = 0.25, w = 0.14, h = 0.07), 0.47X as long as the head. Cheek length 0.64X as long as eye. Malar sulcas present for full cheek length. POL = 0.20, OOL = 0.10. Toruli touching, situated between the eyes. TE 0.69X as long as scrobe length (SL = 0.28). Clypeus trapezoid in area. Epistomal margin protruding with a medial indentation that is quadrate at the base, margin width 0.28X as wide as head. Ventral tentorial pits very close together, situated a third of the way between the oral fossa and foramen magnum. Mandible with two apical teeth and a longitudinal row of nine relatively short teeth on the ventral anterior edge, two glands (fig. 9.3 g). Two labial palp segments, distal segment longest. Three maxillary palp segments, proximal segment longest (fig. 9.3 j). Antennae: second anellus larger than first, funicle segments subequal in size; flagellum (l = 0.73). Scape narrow, 6.7X longer than wide (l = 0.24). Pedicel relatively short, 0.37X as long as the scape.

Thorax. Pronotum broad (l = 0.30, w = 0.48). Propodeum wider than long (l = 0.17, w = 0.42). Mesoscutum broad (l = 0.27, w = 0.51). Scutellum, including axillae broad (l = 0.29, w = 0.41). Fore femur 2.9X as long as wide (l = 0.35). Fore tibial armature consists of a comb of five teeth on the dorso-apical margin;

ventral tooth next to the spur insertion present. Fore leg coxa ca. three-quarters of femur length (C = 0.27, TR = 0.11, F = 0.54, TI = 0.15, TA = 0.20). Eleven to thirteen hind tibial spines. Fore wing 2.3X longer than wide, l = 1.42, pilose, fringe short. Postmarginal vein shorter than stigmal (SM = 0.51, M = 0.20, PM = 0.09, S = 0.14). Marginal vein 6.8X as long as broad. Hind wing 3.6X longer than wide, l = 1.11

Gaster, posterior edge of tergites very crenulated, with three medial incisions. Eighth urotergite spiracle normal. Ovipositor 3.7X as long as valve (valve length = 0.30).

MALE. Testaceous. Total length with head in orthognathous position excluding ovipositor 1.67 mm.

Head broad (l = 0.45, w = 0.51), height normal (h = 0.22). Eye oval (l = 0.22, w = 0.14, h = 0.073), 0.49X as long as the head. Cheek length 0.36X as long as eye. Malar sulcas present for full length of cheek. Lateral ocelli visible in dorsal view. POL = 0.15, OOL = 0.11. Toruli situated on imaginary line joining anterior margin of the eyes, slightly separated. TE 0.36X as long as scrobe length (TE = 0.10, SL = 0.28). Clypeus trapezoid in area. Epistomal margin very slightly convex, with medial indentation, width of margin three-tenths of head width. Ventral tentorial pits slightly separated. Mandible with apical teeth subequal, two glands (fig. 9.3 i). Two labial palp segments, segments subequal. Three maxillary palp segments, segments subequal. Antennae: second anellus larger than first. Flagella length 1.46X as long as pedicel. Scape broad, 3.6X longer than wide (l = 0.25). Pedicel very elongate, half of scape length.

Thorax. Parapsidal furrows incomplete, indistinct posteriorly. Fore femur 3.1X as long as wide (l = 0.46). Fore tibial armature bidentate. Fore tibia 1.74X longer than tarsus (C = 0.38, TR = 0.14, TI = 0.33, TA = 0.19). Fore wing 2.46X longer than wide, l = 1.6, very pilose. Postmarginal vein shorter than stigmal (SM

= 0.54, M = 0.24, S = 0.16, PM = 0.10). Marginal vein very thick 6X longer than wide. Hind wing 4.4X longer than wide, l = 1.2.

Gaster. Eighth urotergite spiracle normal. Aedeagus large (l = 0.46). Five teeth on aedeagus claspers.

***Philocaenus comptoni* sp. nov.**

(figs. 9.1 a-h)

Etymology: Named after Dr. S. G. Compton.

Type material. Holotype ♀, allotype ♂, (slide mounted): Cameroun, South West Province, Bambili, 21 December 1981, leg. S.G. Compton & R.G.E. Baker, no. 6, C1010, ex *F. chlamydocarpa* Mildbr. & Burr. Paratypes, 1 ♀, 1 ♂, (card mounted): same data as holotype; 1 ♂: Cameroun, South West Province, Mt. Koupe, Nyassosso, 7 January 1982, leg. S.G. Compton & R.G.E. Baker, no. 17, C1012, ex *F. chlamydocarpa* Mildbr. & Burr.

FEMALE. Uniform dark brown, including fore femora and antennae, rest of legs testaceous. Total length, with head in orthognathous position, excluding ovipositor valves = 1.8 mm.

Head (fig. 9.1 a & b) elongate, narrowing anteriorly (l = 0.50, w = 0.43), height compressed (h = 0.17). Eye elongate (l = 0.23, w = 0.11, h = 0.07), 0.45X as long as head. Cheek length 0.63X as long as eye. Malar sulcas present for full cheek length. Lateral ocelli visible in dorsal view, medial ocellus situated in posterior end of scrobe. Pronounced carina on vertex, with excavation ventral to it, in which the foramen magnum is situated. POL = 0.15. OOL = 0.07. Toruli in close apposition, situated below the eyes. TE 0.49X as long as scrobe length (TE = 0.15, SL = 0.30). Clypeus equilateral in area. Epistomal margin very slightly convex with shallow medial concavity, ca. a third of head width across compound eyes. Two ventral tentorial pits in close apposition (fig. 9.1 b). Mandible (fig. 9.1 c) with two apical teeth (each with a gland) and a longitudinal ventral ridge of 32 very small fine teeth (first tooth twice the size of the rest), with a second row of twenty smaller teeth anterior to the first. Two labial palp segments, the basal segment very short; three maxillary palp segments. Antenna (fig 9.1 d). Antennal funicle segments subequal in size, flagella length = 0.24. Scape narrow, 5.7X longer than wide (l = 0.22). Pedicel very elongate, half of scape length. MPS placoid, present on all three club, and all four funicle segments.

Thorax. Pronotum square (l = 0.33, w = 0.33). Propodeum (l = 0.19, w = 0.38). Mesoscutum (l = 0.26, w = 0.43). Scutellum, including axilla (l = 0.30, w = 0.35). Fore femur 3X as long as wide (l = 0.48). Fore tibial armature consists of a plate of fine teeth fused to tibia for ca. two thirds of dorsal length (fig. 9.1 e), bifurcate spur present, no ventral tooth. Fore leg coxa 0.56X femur length (C = 0.27, TR = 0.10, TI = 0.29, TA = 0.21). Hind tibial spines not distinguishable from rest of setae. Fore wing 2.4X as long as broad (l = 1.5), pilose, fringe long. Postmarginal vein shorter than stigmal (SM = 0.54, M = 0.23, PM = 0.06, S = 0.12). Marginal vein 10X as long as broad. Hind wing 4.4X as long as broad (l = 1.17, w = 0.27).

Gaster, posterior edge of tergites very crenulated, with three medial incisions. Eighth urotergite spiracle normal (l = 0.02). Ovipositor 4.3X longer than the valves (valve length = 0.3).

MALE. Testaceous; mandibles, eyes, flagella, mesoscutum, scutellum, axilla and gaster darker; very setous. Total length with head in orthognathous position excluding ovipositor 1.75 mm.

Head (fig. 9.1 f) broad (l = 0.44, w = 0.49), height normal (h = 0.25). Eye oval (l = 0.20, w = 0.13, h = 0.07), 0.46X as long as the head. Cheek length 0.55X as long as eye. Malar sulcas present for full cheek length, but indistinct. Lateral ocelli visible in dorsal view. POL = 0.16, OOL = 0.11. Toruli situated below the eyes, slightly separated. TE = 0.07. SL = 0.29. Clypeus trapezoid in area. Epistomal margin slightly convex, with medial

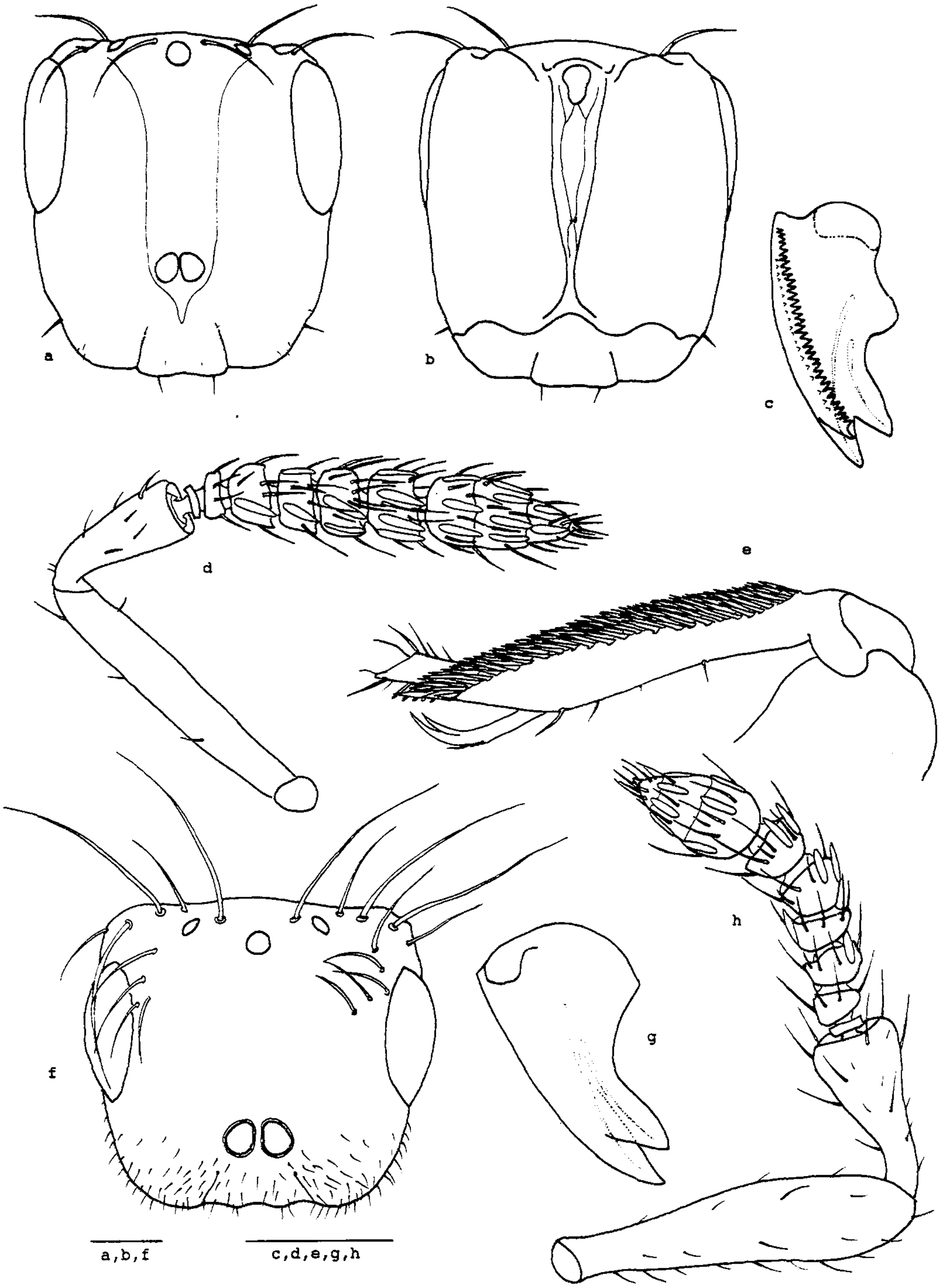


Fig. 9.1 a-h: *Philocaenus comptoni* sp. nov. a) female head, dorsal view b) female head, ventral view c) female mandible, ventral view d) female antenna, axial view e) female fore tibia and first tarsal segment, antiaxial view f) male head, dorsal view g) male mandible, dorsal view h) male antenna, axial view. Scale bars = 0.1 mm.

indentation, 0.29X as wide as head. Ventral tentorial pits slightly separated. Mandible (fig. 9.1 g) with apical teeth subequal; two glands. Two labial palp segments, basal segment very short. Three maxillary palp segments, segments subequal. Antenna (fig. 9.1 h). Antennal flagellum 2.1X as long as pedicel. Scape 5X longer than wide (l = 0.25). Pedicel very elongate, 0.48X scape length. MPS present on all four funicle and three club segments.

Thorax. Parapsidal furrows complete. Fore femur 2.6X as long as wide (l = 0.49). Fore tibia almost twice as long as tarsal length (C = 0.35, TR = 0.14, TI = 0.35, TA = 0.18). Fore wing 2.73X longer than wide, l = 1.75, very pilose. Postmarginal vein shorter than stigmal (SM = 0.56, M = 0.29, S = 0.15, PM = 0.06). Marginal vein thick, 8.5X longer than wide. Hind wing 4.6X longer than wide, l = 1.24.

Gaster. Eighth urotergite spiracle normal. Aedeagus large (l = 0.59). Five teeth on aedeagus claspers.

Philocaenus cavus sp. nov.

(figs. 9.2 a-i)

Etymology: Cavus (latin) = hollow, concave, referring to the excavation on the ventral surface of the head.

Type material. Holotype ♀, allotype ♂ (slide mounted): Ivory Coast, Taï, Guiglio, 29 November 1982, leg. C.C. Berg & J.T. Wiebes, RMNH 4815, ex *F. saussureana* D.C. (det. Berg). Paratype, 1 ♂: same data as holotype.

FEMALE. Faded - head, thorax and gaster dark brown, antennae, mandibles and legs testaceous. Total length with head in orthognathous position excluding ovipositor 1.59 mm.

Head (fig. 9.2 a & b) elongate, wedge shaped (l = 0.52, w = 0.42), height compressed (h = 0.15). Eye elongate (l = 0.21, w

= 0.10), 0.4X as long as head. Cheek length 0.76X eye length. Malar sulcas present for full length of cheek. Lateral ocelli visible in dorsal view, medial ocellus situated in posterior end of scrobe, strong carina present between lateral ocelli, vertex flat behind eyes, with a ventral invagination below carina in which the foramen magnum is situated. POL = 0.14, OOL = 0.068. Toruli in close apposition, situated below the eyes. TE 0.68X scrobe length (TE = 0.19, SL = 0.28), scrobe deep, V - shaped. Clypeus equilateral in area. Epistomal margin very slightly convex with shallow medial concavity, 0.24X head width across compound eyes. Two ventral tentorial pits in close apposition, situated a third of distance between oral fossa and foramen magnum (fig 9.2 b). Ventral anterior two thirds of head with broad shallow excavation. Mandible (fig. 9.2 g) with two apical teeth, each with a gland, and a longitudinal ventral ridge of one large (closest to apex) and 23 very small fine teeth. Two labial palp segments, basal segment very short; three maxillary palp segments, basal segment longest. Antenna (fig. 9.2 c), first funicle segment shortest, rest subequal in size (segments tubular - almost as high as wide); flagella length = 0.36. Scape narrow, 6.8X longer than wide (l = 0.24). Pedicel relatively short, a third of scape length. MPS placoid, present on three club and four funicle segments.

Thorax. Pronotum broad (l = 0.27, w = 0.31). Propodeum l = 0.16, w = 0.36; slight depression around spiracle. Mesoscutum l = 0.21, w = 0.42. Scutellum, including axillae l = 0.25, w = 0.33. Fore femur 3.4X as long as wide (l = 0.44). Fore tibial armature consists of a plate of many teeth, that originates half way down the tibia and is fused to the distal half of the dorso-antiaxial tibial facet (fig. 9.2 d & e); bifurcate spur present, no ventral tooth. Tibial plate same length as tibia. Fore leg coxa 0.57X femur length (C = 0.25, TR = 0.10, TI = 0.14, TA = 0.25). Hind tibial spines not distinguishable from setae. Fore wing l = ca.

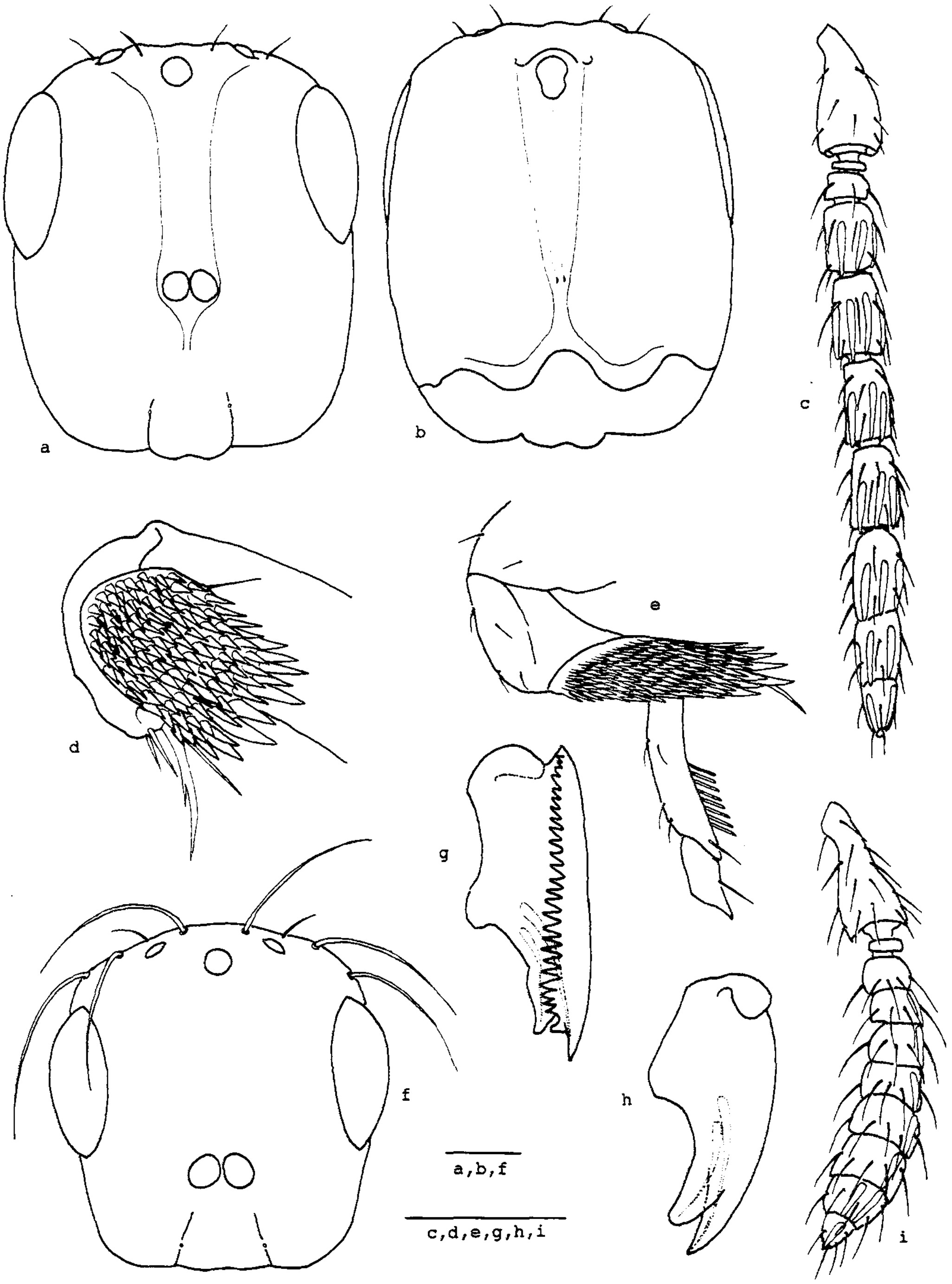


Fig. 9.2 a-i: *Philocaenus cavus* sp. nov. a) female head, dorsal view b) female head, ventral view c) female antenna, axial view d) female fore tibia, anterior view with tarsus missing e) female fore tibia and first two tarsal segments, antiaxial view f) male head, dorsal view g) female mandible, ventral view h) male mandible, dorsal view i) male antenna, antiaxial view. Scale bars = 0.1 mm.

1.4, w = ca. 0.50 (damaged), pilose, fringe long. Postmarginal vein shorter than stigmal (SM = 0.45, M = 0.22, PM = 0.07, S = 0.11). Hind wing 5.6X longer than wide, l = 1.00.

Gaster, posterior edge of tergites crenulated (less so than *S. comptoni*) with three medial incisions. Hypopygial setae extensive (row of setae down each ridge). Eighth urotergite spiracle medium (l = 0.043). Ovipositor 2.9X as long as valve (valve l = 0.45).

MALE. Testaceous, mandibles and eyes darker. Total length with head in orthognathous position excluding ovipositor 1.5mm.

Head (fig. 9.2 f) approximately square (l = 0.44, w = 0.43), height normal (h = 0.28). Eye oval (l = 0.19, w = 0.12, h = 0.07), 0.43X as long as head. Cheek length 0.55X eye length (l = 0.10). Malar sulcas present for full cheek length, but not well defined. Lateral ocelli visible in dorsal view. POL = 0.12, OOL = 0.09. Toruli situated below the eyes, slightly separated. TE 0.37X as long as scrobe length (TE = 0.10, SL = 0.27). Clypeus trapezoid in area. Epistomal margin slightly convex, with medial indentation, 0.26X as wide as head. Ventral tentorial pits slightly separated. Mandible (fig. 9.2 h) with apical teeth subequal, two glands. Two labial palp segments, basal segment short. Three maxillary palp segments, medial segment indistinct. Antenna (fig. 9.2 i). Antennal flagellum twice as long as pedicel. Scape 4.6X longer than wide (l = 0.23). Pedicel elongate, 0.44X scape length. MPS present on all the funicle and club segments.

Thorax. Parapsidal furrows complete. Fore femur 3.5X longer than wide (l = 0.45). Fore tibial armature bidentate. Fore tibia 1.88X longer than tarsal length (C = 0.32, TR = 0.12, TI = 0.32, TA = 0.17). Fore wing 2.7X longer than wide, l = 1.62, very pilose. Postmarginal vein shorter than stigmal (SM = 0.52, M = 0.27, S = 0.13, PM = 0.10). Marginal vein thick 9X longer than wide. Hind wing 5.2X longer than wide, l = 1.2.

Gaster. Eighth urotergite spiracle normal. Aedeagus large (l = 0.64). Six teeth on aedeagus claspers.

***Philocaenus barbatus* species-group.**

This species-group is characterised by the following combination of characters: the mandible with a ventral row of teeth that with the evolution of subsequent rows has in the extreme form developed into a plate of many teeth, the absence of a complete malar sulcus, and the male mandibular outer tooth being distinctly longer than the inner tooth.

Philocaenus barbarus (Grandi) **comb. n.**

(figs. 9.3 k & 9.6 a)

Phagoblastus barbarus Grandi 1955, 102-106, figs. viii-ix, holotype ♀, Grahamstown, South Africa. Female redescribed, male described by Wiebes 1981, in Boucek *et al.* (1981), 174-175, figs. 25-28, 37-40.

Additional material. Series ♀: South Africa, Transvaal, Abel Erasmus Pass, N. of Lydenburg, 2430BC, 22 October 1987, leg. S.G. Compton & P. Raal, C2, ex *F. thonningii* Bl.; series ♀ and ♂: South Africa, Transvaal, Louis Trichardt Hotel, 2329BB, 26 January 1987, leg. S.G. Compton & V.K. Rashbrook, C16, ex *F. thonningii* Bl.; 1 ♀: South Africa, Eastern Cape, Addo Elephant National Park, 28 December 1985, leg. S.G. Compton, ex *F. thonningii* Bl.; series ♀ and ♂: South Africa, Natal, West of Ubombo, 2732CA, 9 December 1986, leg. S.G. Compton, C43, ex *F. thonningii* Bl.; 2 ♀: South Africa, Natal, Hluhluwe Game Reserve Rest Camp, 5 December 1986, leg. S.G. Compton, C44, ex *F. thonningii* Bl.; 1 ♀ & 2 ♂: Zimbabwe, Mazoe, 29 January 1987, leg. A.J. Gardiner, C64, ex *F. thonningii* Bl.; series ♀, one ♂: Zambia, Lusaka, Cathedral, 25 January 1988, leg. R.J.F. Nefdt, C61, ex *F. thonningii* Bl.; series ♀: Transkei, Port St. Johns, 15 January 1989, leg. A. Pretorius, C113, ex *F. thonningii* Bl.; series ♀ & ♂: South Africa, Eastern Cape, Grahamstown, 24 February 1989, leg. S. van Noort, C117, ex *F. thonningii* Bl.; series ♀, ♂: South Africa, Transvaal, Strijdom Tunnel, 4 September 1989, leg. S. van Noort & A.B. Ware, ex *F. thonningii* Bl.; series ♀, ♂: South Africa, Natal, False Bay Park Camp, 6 September 1989, leg. S. van Noort & A.B. Ware, C156, ex *F. thonningii* Bl.; series ♀, ♂: South Africa, Natal, Umtamvuna Nature Reserve, 8 September 1989, leg. S. van Noort & A.B. Ware, C157, ex *F. thonningii* Bl.; series ♀, ♂: South Africa, Transvaal, Pongola, 27° 17'S 31° 20'E, 6 September 1989, leg. S. van Noort & A.B. Ware, C171, ex *F. thonningii* Bl.; series ♀, ♂: South Africa, Transvaal, Pretoria, 31 August 1989, leg. S. van Noort & A.B. Ware, C173, ex *F. thonningii* Bl.; series ♀, 3 ♂: South Africa, Eastern Cape, Grahamstown Botanical Gardens, 28 November 1989, leg. A.B. Ware, C205, ex *F. thonningii* Bl.; series ♀, 3 ♂: Transkei, Port St. Johns, 2nd Beach, 28 November 1989, leg. S. van Noort, C206, ex *F. thonningii* Bl.; series ♀, ♂: South Africa, Grahamstown, Rhodes Avenue, 30 January 1985, leg. S.G. Compton, C207, ex *F. thonningii* Bl.; 4 ♀: South Africa, Natal, Umtamvuna, 20 January 1990, leg. S. van Noort & A.B. Ware, C227, ex *F. thonningii* Bl.; series ♀: South Africa, Natal, Port Edward, Broadmoor Farm House, 20 January 1990, leg. S. van Noort & A.B. Ware, C228, ex *F. thonningii* Bl.; series ♀, ♂: South Africa, Natal, Ramsgate, 21 January 1990, leg. S. van Noort & A.B. Ware, C234, ex *F. thonningii* Bl.; series ♀, ♂: same data, C235; series ♀, ♂: South Africa, Natal, Ubombo, 27 January 1990, leg. S. van Noort & A.B. Ware, C265, ex *F. thonningii* Bl.; series ♀, ♂: same data, C266; series ♀, ♂: South Africa, Natal, St. Lucia Estuary, 28 January 1990, leg. S. van Noort & A.B. Ware, C269, ex *F. thonningii* Bl.; series ♀, ♂: South Africa, Natal, Umhlanga Rocks, Oyster Box Hotel, 30 January 1990, leg. S. van Noort & A.B. Ware, C273, ex *F. thonningii* Bl.;series ♀, ♂: same data, C274; series ♀, ♂: Zimbabwe, Central Mashonaland, Mazoe Citrus Estates, 6 March 1990, leg. I. Waters, C286, ex *F. thonningii* Bl.; series ♀, ♂: South Africa, Eastern Cape, Bathurst, 5 May 1990, leg. A.B. Ware, C288, ex *F. thonningii* Bl.; series ♀, ♂: same data, C289; series ♀, ♂: same data, C290; series ♀, ♂: South Africa, Transvaal, Pretoria, National Botanic Gardens, 23 August 1990, leg. S. van Noort, C296, ex *F. thonningii* Bl.; series ♀, ♂: same data, C297; 4 ♀: Zambia, Locinvar Game Park, 14 July 1990, leg. S.G. Compton, C320, ex *F. thonningii* Bl.; 4 ♀, 3 ♂: Malawi, Zomba Plateau, 6 July 1990, leg. S.G. Compton, C321, ex *F. thonningii* Bl.; series ♀, ♂: Malawi, Zomba Town University Campus, 6 April 1991, leg. S.G. Compton, C337, ex *F. thonningii* Bl.; series ♀, ♂: South Africa, Eastern Cape, Grahamstown Botanic Gardens, 7 June 1991, leg. S.G. Compton, C343, ex *F. thonningii* Bl.; series ♀: Malawi, Mt. Mulanje Forestry Station, 7 July 1990, leg. S.G. Compton, C322, ex *F. thonningii* Bl.; 12 ♀: South Africa, Durban, Reservoir Hills, 30 May 1988, leg. H. Baijnath, RMNH 4969, ex *F. thonningii* Bl. (B-phase figs); 15 ♀: South Africa, Durban, Reservoir Hills, 29 June 1988, leg. H. Baijnath, RMNH 4967, ex *F. n. natalensis* Hochst. (B-phase figs); 5 ♀: South Africa, Natal, Hluhluwe Game Reserve, 2832AA, 9 December 1986, leg. S.G. Compton & A.J. Gardiner, C38, ex *F. stuhlmannii* Warb.; series ♀, 3 ♂: South Africa, Natal, Mbaswana, 9 December 1986, leg. S.G. Compton, C39, ex *F. stuhlmannii* Warb.; series ♀, 2 ♂: Kenya, nr. Nairobi, Kaun, 6000 ft. August 1967, leg. C. van Someren, ex *Ficus* sp. (C.v.S. no. 1); series ♀, 1 ♂: Kenya, nr. Nairobi, Kaun, 6000 ft., 15 September 1967, leg. C. van Someren, ex *Ficus* sp. (Fig. 10).

Comments. A certain amount of geographical variation is present in this species with respect to the number of ventral mandibular teeth, number of fore tibial teeth, and projection of the epistomal margin. South African specimens have 6 to 7 tibial teeth, and 15 to 20 ventral mandibular teeth. Moving further north both decrease in number with Malawian and Zimbabwean specimens having 4 to 5 tibial teeth and 13 to 15 ventral mandibular teeth. Specimens in Kenya have 4-5 tibial teeth and only 9-10 mandibular teeth. Specimens from the Ivory Coast in West Africa have the reduced number of tibial teeth (four), but 15-16 mandibular teeth. The epistomal margin projects slightly more in the South African and Kenyan specimens.

Philocaenus bouceki (Wiebes) comb. n.

(fig. 9.3 h)

Phagoblastus bouceki Wiebes 1981, 554-555, holotype ♀, allotype ♂, Reunion. Examined paratypes (Rijksmuseum van Natuurlijke Historie, Leiden).

Philocaenus comorensis sp. nov.

(fig. 9.3 a-e)

Etymology: Named after the type locality.

Type material: Holotype ♀, allotype ♂ (slide mounted): Comores, Grand Comore, leg. S.G. Compton, ex *F. antandronarum* (Perrier) Berg *bernardii* Berg. Paratypes, one ♂ (slide mounted), 3 ♀, 3 ♂ (card mounted), series ♂?: same data as holotype.

FEMALE. Head, dorsal thorax except propodeum and gaster metallic dark brown, ventral thorax, propodeum and legs testaceous, antennae and mandibles dark brown. Total length with head in orthognathous position, excluding ovipositor 1.09 mm.

Head (figs. 9.3 a & b) elongate, (l = 0.46, w = 0.30), height compressed (h = 0.13). Eye elongate (l = 0.16, w = 0.08), fairly flush with the sides of the head (h = 0.04), 0.35X as long as the head. Cheek length 0.75X eye length. Occipital carina present ventral to and between the outer margins of the lateral ocelli, shallow concavity above carina and between the lateral ocelli. POL = 0.11. OOL = 0.12. TE 1.2X as long as scrobe length (TE = 0.23, SL = 0.19). Clypeus narrow and elongate in area. Epistomal margin protrudes, subsquare, slightly convex on anterior edge, width 0.28X head width. Ventral tentorial pits in close apposition (fig. 9.3 b). Mandible with two apical teeth and a longitudinal row of ten to twelve ventral teeth, two glands (fig. 9.3 c). Two labial palp segments. Three maxillary palp segments, proximal segment longest, distal two very short. Antennal funicle segments subequal in size, flagella 1 = 0.26. Scape narrow, 6.1X longer than wide (l = 0.14). Pedicel very elongate, half of scape length.

Thorax. Pronotum square (l = 0.21, w = 0.25). Propodeum wider than long (l = 0.11, w = 0.26). Mesoscutum broad (l = 0.14, w = 0.28). Scutellum, including axillae broad (l = 0.20, w = 0.24). Fore femur 3.7X as long as wide (l = 0.27). Fore tibial armature tridentate. Fore leg coxa 0.70X femur length (C = 0.19, TR = 0.07, TI = 0.08, TA = 0.12). Four to five hind tibial spines on the dorsal margin. Fore wing 2.3X longer than wide, l = 0.98, pilose, fringe long. Postmarginal vein shorter than stigmal (SM = 0.32, M = 0.14, PM = 0.05, S = 0.10). Marginal vein thick 5.8X longer than wide. Hind wing 6.1X longer than wide, l = 0.73.

Gaster, posterior edge of tergites very crenulated, with three medial incisions. Eighth urotergite spiracle normal (l = 0.018). Ovipositor 3.7X longer than valve (valve = 0.19).

MALE. Testaceous, eyes, club, mandibles and posterior half of gaster darker. Total length with head in orthognathous position excluding ovipositor 1.25 mm.

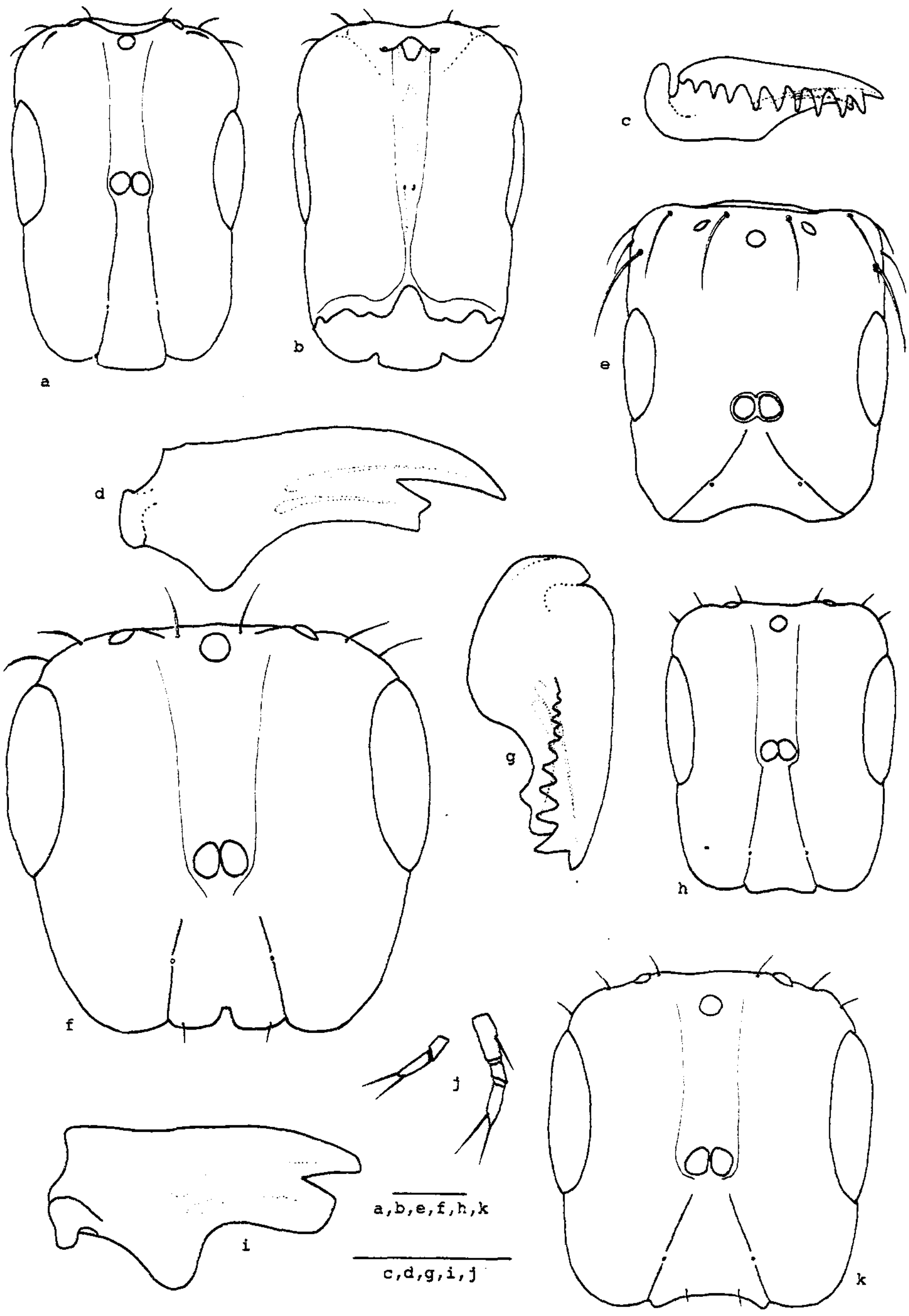


Fig. 9.3 a-e: *Philocaenus comorensis* sp. nov. a) female head, dorsal view b) female head, ventral view c) female mandible, ventral view d) male mandible, ventral view e) male head, dorsal view; f, g, i & j: *Philocaenus silvestrii* (Grandi) f) female head, dorsal view g) female mandible, ventral view i) male mandible, dorsal view j) female labial and maxillary palp segments; h: *Philocaenus bouceki* (Wiebes) h) female head, dorsal view; k: *Philocaenus barbarus* (Grandi) k) female head, dorsal view. Scale bars = 0.1 mm.

Head (fig. 9.3 e) elongate, parallel sided (l = 0.40, w = 0.33), height normal (h = 0.18). Eye elongate (l = 0.15, w = 0.09, h = 0.04), 0.38X as long as head. Cheek length 0.53X eye length (l = 0.08). POL = 0.11. OOL = 0.12. Toruli situated just above the line joining the base of the eyes. TE half scrobe length (TE = 0.11, SL = 0.22). Clypeus equilateral in area. Epistomal margin flat laterally, concave medially, width of margin 0.46X head width. Ventral tentorial pits in close apposition. Outer mandibular tooth longer than the bicuspidate inner tooth (fig. 9.3 d). Two labial palp segments, basal segment shorter, division indistinctly defined. Three maxillary palp segments, proximal segment longest, large and swollen distally, distal two segments subequal, combined length subequal the proximal segment length. Antennal flagellar length twice as long as pedicel. Scape broad, 3.7X longer than wide (l = 0.13). Pedicel very elongate, 0.69X scape length. MPS present on all the funicle (one on each of the first three) and all the club segments.

Thorax. Parapsidal furrows complete. Fore femur 3.3X as long as wide (l = 0.30). Fore tibial armature bidentate. Fore tarsus subequal in length to tibia (C = 0.25, TR = 0.09, TI = 0.18, TA = 0.19). Fore wing 2.7X longer than wide, l = 1.10, pilose, anal and medial setal tracts present. Postmarginal vein same length as stigmal (SM = 0.35, M = 0.16, S = 0.10, PM = 0.10). Marginal vein thick 5.3X longer than wide. Hind wing 4.7X longer than wide, l = 0.80.

Gaster. Eighth urotergite spiracle normal. Aedeagus small (l = 0.26). Four teeth on aedeagus claspers.

Philocaenus geminus sp. nov.

(figs. 9.4 a-c)

Etymology: Geminus (latin) = twin, referring to the extreme similarity with the sister species *P. jinjaensis*.

Type material: Holotype ♀ (slide mounted): Uganda, Kampala, 1 September 1968, tree no. 9, leg. D.S. Hill, ex *F.* "*natalensis*"; series ♀ paratypes: same data as holotype; series ♀: Uganda, Katalemwa, 30 July 1968, tree no. 20, leg. D.S. Hill, ex *F.* "*natalensis*".

FEMALE. Faded due to alcohol storage, dark brown, legs testaceous. Total length with head in orthognathous position, excluding the ovipositor valves = 1.34 mm.

Head (figs. 9.4 a & b) elongate, parallel sided (l = 0.52, w = 0.42), dorso-ventrally compressed (h = 0.17). Eye elongate (l = 0.24, w = 0.11), fairly flush with sides of head (h = 0.05), 0.46X as long as the head. Cheek length 0.55X eye length. POL = 0.14. OOL = 0.10. Occipital carina runs in a straight line, ventral to and between the outer margins of the lateral ocelli. Shallow excavation dorsal to the carina, below the medial ocellus and between the lateral ocelli. TE equal to scrobe length (TE = 0.24). Clypeus narrow and elongate in area. Epistomal margin protrudes slightly, with shallow medial concavity, 0.29X head width. Ventral tentorial pits in very close apposition, situated in posterior end of a short medial groove (fig. 9.4 b). Mandible with two apical teeth, a second tooth subapical to the inner apical tooth, thirteen to seventeen ventral teeth and four widely spaced teeth anterior to this row, two glands (much as in *P. jinjaensis* fig. 9.4 e). Two labial palp segments, segments subequal. Three maxillary palp segments, proximal segment largest. Antennal funicle segments subequal in size. Scape narrow, 7.7X longer than wide (l = 0.18). Pedicel very elongate, 0.51X scape length.

Thorax. Pronotum broad (l = 0.28, w = 0.35). Propodeum l = 0.14, w = 0.32. Mesoscutum l = 0.20, w = 0.38. Scutellum, including axillae broad (l = 0.23, w = 0.31). Femur 3.1X as long as wide (l = 0.35). Tibial armature consists of a comb of five to six teeth, with a single tooth dorsal to this comb (fig. 9.4 c). Fore leg coxa ca. two thirds of femur length (C = 0.24, TR = 0.10, TI

= 0.09, TA = 0.16). Five hind tibial spines. Fore wing 2.6X longer than wide, l = 1.2, sparsely setous, maximum fringe length = 0.025. Postmarginal vein shorter than stigmal (SM = 0.44, M = 0.15, PM = 0.08, S = 0.10). Marginal vein 7.5X longer than wide. Hind wing 4.3X longer than wide, l = 0.94.

Gaster, posterior edge of tergites very crenulated, with three medial incisions. Eighth urotergite spiracle normal (l = 0.02). Ovipositor 5.1X as long as valve (valve l = 0.16).

Philocaenus jinjaensis **sp. nov.**

(fig. 9.4 d-h)

Etymology: Named after the type locality.

Type material: Holotype ♀ and allotype ♂ (slide mounted): Uganda, Jinja, roundabout nr. Crested Crane Hotel, 23 April 1968, tree no. 41, leg. D.S. Hill, ex *Ficus* sp. K.; series ♀, ♂ paratypes: same data as holotype.

FEMALE. Faded due to alcohol storage, head and thorax metallic black; gaster, antennae and legs lighter brown. Total length with the head in orthognathous position, excluding the ovipositor = 2.4 mm.

Head (fig. 9.4 d) elongate, parallel sided (l = 0.61, w = 0.50), height compressed (h = 0.17). Eye elongate (l = 0.26, w = 0.12), fairly flush with the sides of the head (h = 0.06), 0.44X as long as head. Cheek length 0.53X eye length. Occipital carina runs in a straight line, ventral to and between the outer margins of the lateral ocelli. Vertex excavated between the lateral ocelli, above the occipital carina and below the median ocellus. POL = 0.15. OOL = 0.11. TE 1.18X as long as scrobe length (TE = 0.30, SL = 0.25). Clypeus narrow and elongate in area. Epistomal margin bilobed with shallow medial concavity, 0.29X head width. Ventral tentorial pits in close apposition. Mandible with two apical teeth, second tooth subapical to inner apical tooth, longitudinal

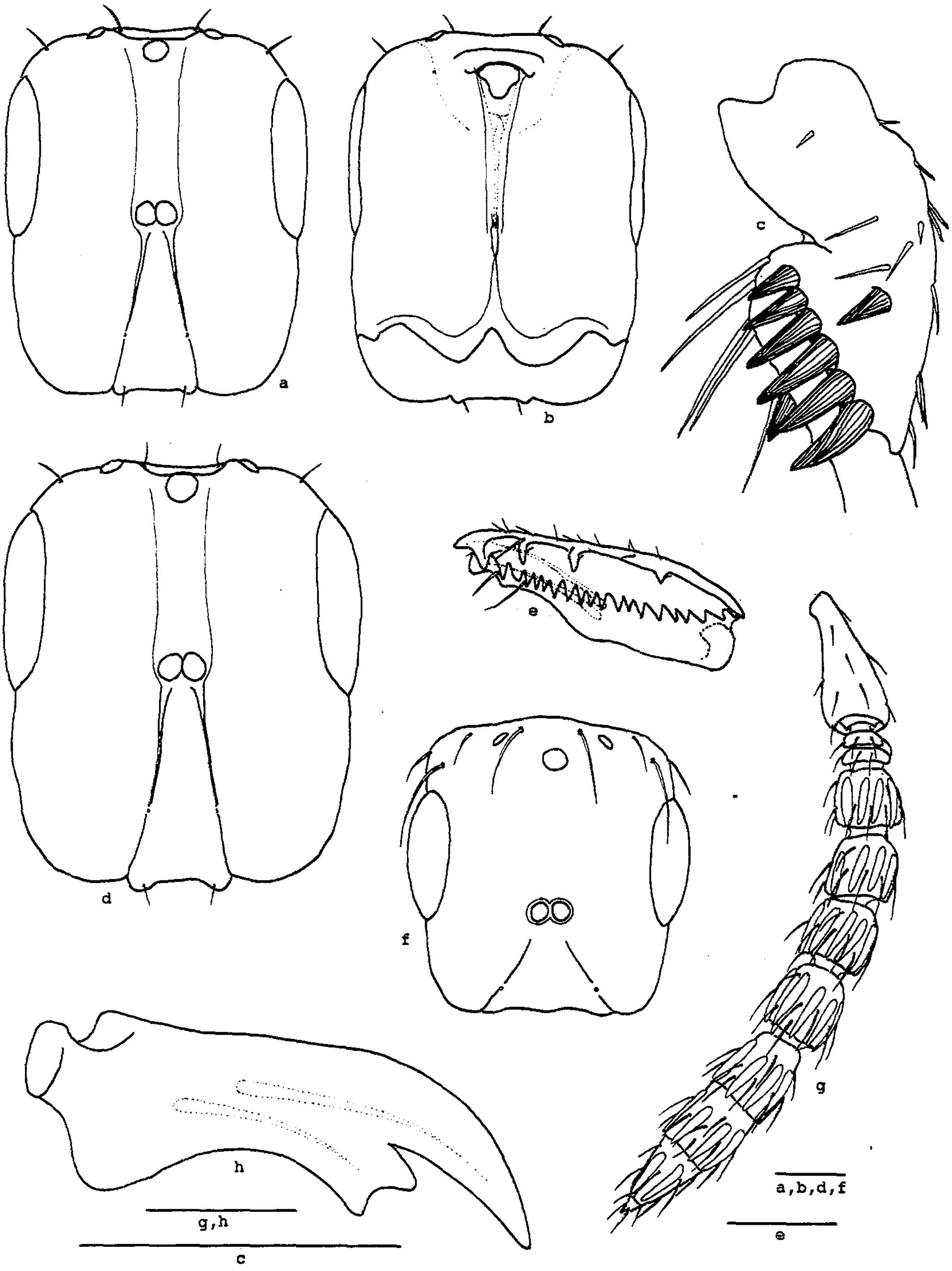


Fig. 9.4 a-c: *Philocaenus geminus* sp. nov. a) female head, dorsal view b) female head, ventral view c) female fore tibia, antiaxial view; d-h: *Philocaenus jinjaensis* sp. nov. d) female head, ventral view e) female mandible, ventral view f) male head, ventral view g) female antenna, axial view h) male mandible, dorsal view. Scale bars = 0.1 mm.

row of nineteen to twenty ventral teeth, anterior to this row are four widely spaced teeth, two glands (fig. 9.4 e). Two labial palp segments, proximal segment largest. Three maxillary palp segments, proximal segment largest. Antenna (fig. 9.4 g), funicle segments subequal in size, flagellar length = 0.38. Scape narrow, 6.5X longer than wide (l = 0.21). Pedicel elongate, 0.44X scape length (l = 0.09).

Thorax. Pronotum broad (l = 0.34, w = 0.41). Propodeum wider than long (l = 0.15, w = 0.37). Mesoscutum l = 0.21, w = 0.44. Scutellum, including axillae broad (l = 0.26, w = 0.37). Fore femur 2.7X as long as wide (l = 0.39). Fore tibial armature consists of a comb of seven to eight teeth, with one or two teeth dorsal to this. Fore leg coxa ca. half of femur length (C = 0.20, TR = 0.11, TI = 0.10, TA = 0.17). Five hind tibial spines on dorsal margin. Fore wing 2.2X as long as broad (l = 1.25), sparsely setous, fringe short. Postmarginal vein just longer than stigmal (SM = 0.50, M = 0.17, PM = 0.12, S = 0.10). Marginal vein 7.2X longer than wide. Hind wing 4X as long as broad (l = 0.99).

Gaster, posterior edge of tergites crenulated, with three medial incisions. Eighth urotergite spiracle normal (l = 0.032). Ovipositor 4.7X as long as valve (valve l = 0.21).

MALE. Testaceous, eyes, mandibles, vertex, mesoscutum, scutum, axillae and gaster darker. Total length with head in orthognathous position excluding ovipositor 1.59 mm.

Head (fig. 9.4 f) elongate, parallel sided (l = 0.42, w = 0.40), height normal (h = 0.21). Eye elongate (l = 0.19, w = 0.10, h = 0.05), 0.45X as long as the head. Cheek length 0.42X eye length. POL = 0.12. OOL = 0.10. Toruli situated on imaginary line joining anterior margin of the eyes, touching. TE 0.59X as long as scrobe length (TE = 0.13, SL = 0.22). Clypeus equilateral in area. Epistomal margin biconcave with the medial tooth projecting as far as the lateral lobes, width of margin two-fifths of head row of nineteen to twenty ventral teeth, anterior to this row are four widely spaced teeth, two glands (fig. 9.4 e). Two labial palp segments, proximal segment largest. Three maxillary palp segments, proximal segment largest. Antenna (fig. 9.4 g), funicle segments subequal in size, flagellar length = 0.38. Scape narrow, 6.5X longer than wide (l = 0.21). Pedicel elongate, 0.44X scape length (l = 0.09).

Thorax. Pronotum broad (l = 0.34, w = 0.41). Propodeum wider than long (l = 0.15, w = 0.37). Mesoscutum l = 0.21, w = 0.44. Scutellum, including axillae broad (l = 0.26, w = 0.37). Fore femur 2.7X as long as wide (l = 0.39). Fore tibial armature consists of a comb of seven to eight teeth, with one or two teeth dorsal to this. Fore leg coxa ca. half of femur length (C = 0.20, TR = 0.11, TI = 0.10, TA = 0.17). Five hind tibial spines on dorsal margin. Fore wing 2.2X as long as broad (l = 1.25), sparsely setous, fringe short. Postmarginal vein just longer than stigmal (SM = 0.50, M = 0.17, PM = 0.12, S = 0.10). Marginal vein 7.2X longer than wide. Hind wing 4X as long as broad (l = 0.99).

Gaster, posterior edge of tergites crenulated, with three medial incisions. Eighth urotergite spiracle normal (l = 0.032). Ovipositor 4.7X as long as valve (valve l = 0.21).

MALE. Testaceous, eyes, mandibles, vertex, mesoscutum, scutum, axillae and gaster darker. Total length with head in orthognathous position excluding ovipositor 1.59 mm.

Head (fig. 9.4 f) elongate, parallel sided (l = 0.42, w = 0.40), height normal (h = 0.21). Eye elongate (l = 0.19, w = 0.10, h = 0.05), 0.45X as long as the head. Cheek length 0.42X eye length. POL = 0.12. OOL = 0.10. Toruli situated on imaginary line joining anterior margin of the eyes, touching. TE 0.59X as long as scrobe length (TE = 0.13, SL = 0.22). Clypeus equilateral in area. Epistomal margin biconcave with the medial tooth projecting as far as the lateral lobes, width of margin two-fifths of head width. Ventral tentorial pits in close apposition. Two labial palp segments, segments subequal in length. Three maxillary palp segments, proximal segment longest. Mandible with outer tooth longer than the inner bicuspidate tooth (fig. 9.4 h). Antennal flagella length 3X as long as pedicel. Scape narrow, 6.3X longer than wide (l = 0.19). Pedicel very elongate, 0.47X scape length. MPS present on all the funicle and club segments.

Thorax. Parapsidal furrows complete. Fore femur 3.6X longer than wide (l = 0.36). Fore tibial armature bidentate. Fore tarsus ca. four-fifths of tibial length (C = 0.25, TR = 0.10, TI = 0.23, TA = 0.19). Fore wing 2.5X longer than wide, l = 1.22, very pilose, anal and medial setal tracts present. Postmarginal vein same length as stigmal (SM = 0.73, M = 0.16, S = 0.10, PM = 0.10). Marginal vein thick, 8X longer than wide. Hind wing 4.5X longer than wide, l = 0.89.

Gaster. Eighth urotergite spiracle normal. Aedeagus small (l = 0.30). Four teeth on aedeagus claspers.

Comments. The last two species are morphologically very similar. However, they can at once be distinguished by the epistomal margin and differences in the number of teeth on the mandible and on the fore tibia. It seems unlikely that these differences could be the result of geographical variation, because the two populations are probably sympatric, given the relatively close proximity of the localities (Jinja and Kampala are only 70 km apart). I therefore regard the two taxa as distinct sister species, that may have diverged relatively recently.

Philocaenus insolitus **sp. nov.**

(figs. 9.5 g-i)

Etymology: Insolitus (latin) = unusual, referring to the unusual epistomal margin and mandibular teeth configuration for *Philocaenus*.

Type material: Holotype ♀ (slide mounted): Gabon, Makokou, April 1979, leg. G. Michaloud, RMNH 3815, ex *F. craterostoma* Mildbr. & Burr. Paratypes, 3 ♀ (slide mounted), series ♀: same data as holotype.

FEMALE. Metallic black/brown, legs lighter, tarsi testaceous. Total length with head in orthognathous position, excluding the ovipositor valves = 1.09 mm.

Head (figs. 9.5 h & i) approximately square (l = 0.37, w = 0.37), height normal (h = 0.15). Eye elongate (l = 0.18, w = 0.10, h = 0.05), 0.48X as long as the head. Cheek length 0.48X eye length (l = 0.09). POL = 0.13. OOL = 0.08. TE (l = 0.17) as long as scrobe length (l = 0.17). Clypeus narrow and elongate in area. Epistomal margin protruding, with a small medial concave indentation, 0.28X the head width across the compound eyes. Ventral tentorial pits in close apposition. Mandible (fig. 9.5 g) with two apical teeth and a longitudinal row of sixteen to eighteen unequal ventral teeth, with an uneven row of smaller teeth situated anteriorly to the first row, two glands. Two labial palp segments, distal segment largest. Three maxillary palp segments, proximal segment largest. Antenna much as in *P. jinjaensis* (fig. 9.4 g). Antennal funicle segments subequal in size. Scape narrow, 7.2X longer than wide (l = 0.15). Pedicel elongate, 0.4X scape length.

Thorax. Pronotum broad (l = 0.22, w = 0.31), torpedo shaped. Propodeum wider than long (l = 0.10, w = 0.28). Mesoscutum broad (l = 0.16, w = 0.33). Scutellum, including axillae broad (l = 0.19, w = 0.28). Fore femur 2.6X longer than wide (l = 0.24). Fore tibial armature tridentate, teeth long, subequal in length. Fore leg coxa ca. two thirds of femur length (C = 0.16, TR = 0.06, TI = 0.10, TA = 0.14). Seven spines on the dorsal margin of the hind tibia. Fore wing 2.2X longer than wide, l = 0.95, pilose, fringe short. Postmarginal vein equal in length to stigmal (SM = 0.36, M = 0.11, PM = 0.07, S = 0.07). Marginal vein

7.5X longer than wide. Hind wing 4.5X longer than wide, l = 0.75.

Gaster tergite very crenulated, with three medial evenly spaced incisions. Eighth urotergite spiracle normal (l = 0.01). Ovipositor 3.7X as long as valve (valve l = 0.20).

Philocaenus medius **sp. nov.**

(figs. 9.5 a-c, f & j; 9.6 b; 9.11 d)

Etymology: Medius (latin) = intermediate, referring to the intermediate morphology that made apparent the linkage between *Philocaenus* and *Phagoblastus*.

Type material: Holotype ♀, allotype ♂ (slide mounted): South Africa, Kosi Bay, 21 November 1989, leg. M. Ward, C215, ex *F. natalensis natalensis* Hochst. Paratypes, 3 ♀, 3 ♂ (slide mounted), 1 ♀, 1 ♂ (card mounted): same data as holotype; series ♀, ♂: Malawi, last town before Mt. Mulanje, 6 July 1990, leg. S.G. Compton, C307, ex *F. natalensis natalensis* Hochst.; series ♀, ♂: Malawi, Mt. Mulanje Forestry Station, 7 July 1990, leg. S.G. Compton, C322, ex *F. thonningii* Bl.; 8 ♀, 1 ♂: Malawi, Mt. Mulanje, 18 April 1991, leg. S.G. Compton, C335, ex *F. natalensis natalensis* Hochst.

Comments. The associated pollinator in the *F. n. natalensis* collections is *Alfonsiella longiscapa* Joseph. The associated pollinator in the *F. thonningii* collection is *Alfonsiella brongersmai* Wiebes.

FEMALE. Metallic green/black, antennae and mandibles brown, legs testaceous. Total length with head in orthognathous position excluding ovipositor 1.42 mm.

Head (figs. 9.5 a & 9.6 b) elongate, parallel sided (l = 0.55, w = 0.41, h = 0.16). Eye elongate (l = 0.23, w = 0.10, h = 0.06), 0.43X as long as head. Cheek length 0.38X eye length. POL = 0.15. OOL = 0.10. Toruli situated between the eyes. TE 1.13X as long as scrobe length (TE = 0.26, SL = 0.23). Clypeus narrow and elongate in area. Epistomal margin strongly projecting, bilobed,

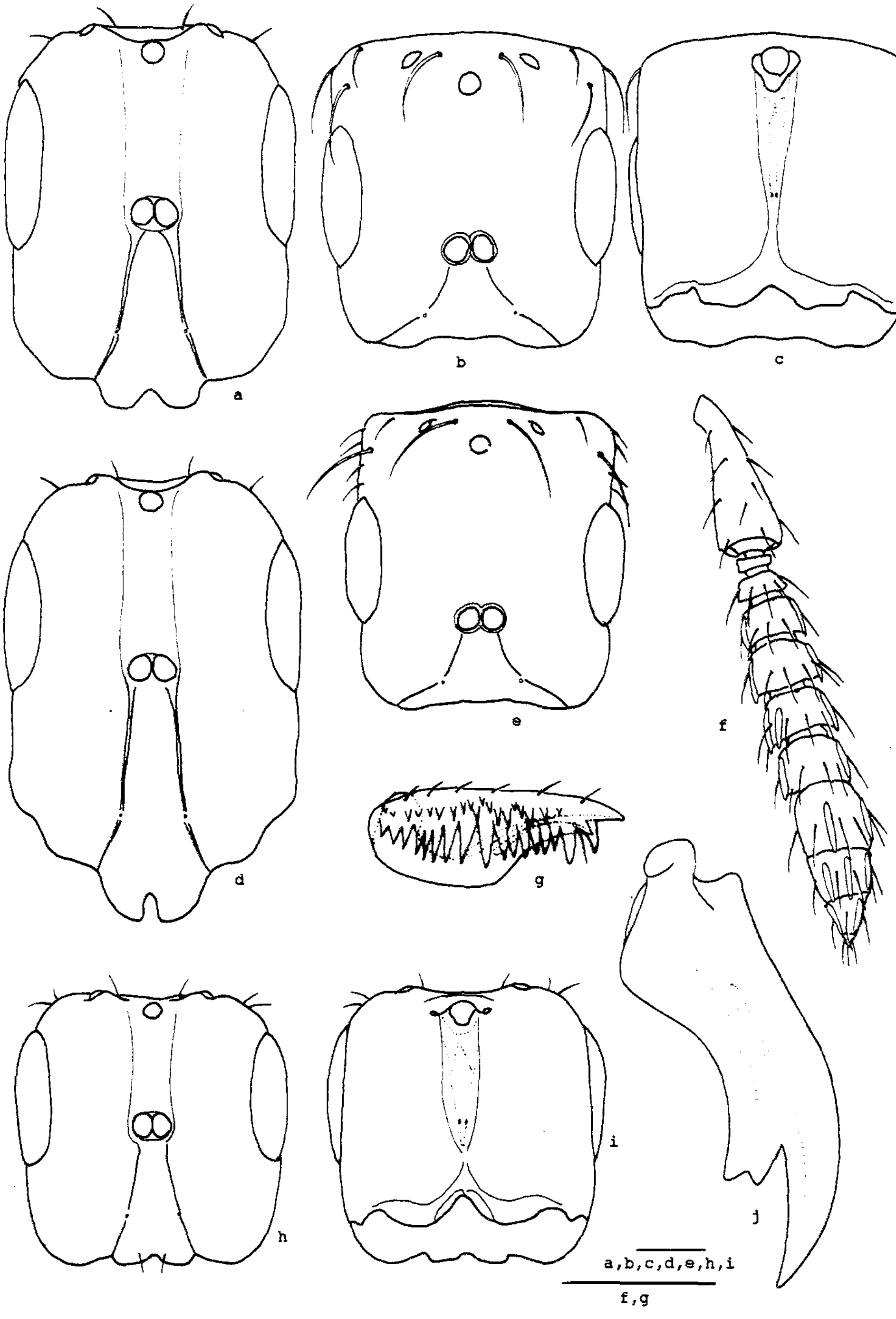


Fig. 9.5 a-c, f, j: *P. medius* sp. nov. a) female head, dorsal view b) male head, dorsal view c) male head, ventral view f) male antenna, antiaxial view j) male mandible, dorsal view; d,e: *Philocaenus ugandensis* sp. nov. d) female head, dorsal view e) male head, dorsal view; g-i: *Philocaenus insolitus* sp. nov. g) female mandible, ventral view h) female head, dorsal view i) female head, ventral view. Scale bars = 0.1 mm.

with smooth medial concavity, width of margin 0.37X head width. Ventral tentorial pits in close apposition, situated in posterior end of a short medial groove (fig. 9.6 b). Mandible with two apical teeth, a longitudinal row of ca. 26 ventral teeth, anterior to this row are ca. three or four uneven rows of progressively smaller teeth (fig. 9.6 b), two glands. Two labial palp segments, segments subequal. Three maxillary palp segments, proximal segment longest and widest. Antenna much as in *P. jinjaensis* (fig. 9.4 g), funicle segments subequal in size, flagella l = 0.29. Scape narrow, 6X longer than wide (l = 0.18). Pedicel very elongate, 0.51X scape length.

Thorax. Pronotum broad (l = 0.28, w = 0.34). Propodeum l = 0.14, w = 0.33. Mesoscutum l = 0.21, w = 0.39. Scutellum, including axillae broad (l = 0.22, w = 0.30). Propleura and prosternum (fig. 9.11 d). Fore femur 3.1X as long as wide (l = 0.35). Fore tibial armature consists of a comb of four teeth on the dorso-apical adaxial margin. Fore leg coxa 0.69X femur length (C = 0.24, TR = 0.10, TI = 0.11, TA = 0.18). Six hind tibial spines on the dorsal margin. Fore wing 2.2X longer than wide, l = 1.13, sparsely setous. Postmarginal vein shorter than stigmal (SM = 0.44, M = 0.13, PM = 0.08, S = 0.10). Marginal vein 6.4X longer than wide. Hind wing 4.2X longer than wide, l = 0.90.

Gaster, posterior edge of tergites very crenulated, with three medial incisions. Eighth urotergite spiracle normal (l = 0.017). Ovipositor 3.8X as long as valve (valve l = 0.25).

MALE. Testaceous, mandibles, eyes and posterior half of gaster darker. Total length with head in orthognathous position excluding ovipositor 1.45 mm.

Head (figs. 9.5 b & c) elongate, parallel sided (l = 0.44, w = 0.41), height normal (h = 0.25). Eye elongate (l = 0.20, w = 0.12, h = 0.06), 0.46X as long as the head. Cheek length 0.3X eye length. POL = 0.13. OOL = 0.12. Toruli situated just above the base of the eyes, touching. TE 0.43X as long as scrobe length (TE = 0.10, SL = 0.24). Clypeus equilateral in area. Epistomal margin slightly bilobed laterally, with a slight, broad, medial convexity. Ventral tentorial pits in close apposition (fig. 9.5 c). Two labial palp segments, segments subequal. Three maxillary palp segments, proximal segment longest. Mandible (fig. 9.5 j). Antenna (fig. 9.5 f), flagellar length 2.5X as long as pedicel. Scape 5X longer than wide (l = 0.20). Pedicel very elongate, 0.55X scape length.

Thorax. Parapsidal furrows complete. Fore femur 3.4X as long as wide (l = 0.37). Fore tibial armature bidentate. Fore tarsus 0.88X tibial length (C = 0.30, TR = 0.11, TI = 0.24, TA = 0.21). Fore wing 2.4X longer than wide, l = 1.20, very pilose. Postmarginal vein same length as stigmal (SM = 0.44, M = 0.18, S = 0.10, PM = 0.10). Marginal vein thick, 6X longer than wide. Hind wing 4.8X longer than wide, l = 0.95.

Gaster. Eighth urotergite spiracle normal. Aedeagus small (l = 0.27). Four teeth on aedeagus claspers.

Philocaenus ugandensis sp. nov.

(figs. 9.5 d & e; 9.6 c)

Etymology: Named after the country of origin.

Type material: Holotype ♀, allotype ♂ (slide mounted): Uganda, Katalemwa, 6 August 1968, leg. D.S. Hill, tree no. 20, ex *Ficus "natalensis"*. Paratypes, series ♀, ♂: same data as holotype; series ♀: same data, but 12 August 1968; series ♀, ♂: Uganda, Kampala, 1 September 1968, tree no. 9, leg. D.S. Hill, ex *F. "natalensis"*; series ♀: Uganda, Katalemwa, 30 July 1968, tree no. 20, leg. D.S. Hill, ex *F. "natalensis"*; series ♀, ♂: Uganda, Makerere University Campus, Cluny Castle, 10 October 1967, tree no. 6, leg. D.S. Hill, ex *F. "thonningii"*; series ♀, ♂: Uganda, Kabanyolo, 20 August 1968, tree no. 56, leg. D.S. Hill, ex *F. "thonningii"*; series ♀, ♂: Uganda, Makerere University Campus, Mvule Lane, 30 October 1967, tree no. 7, leg. D.S. Hill, ex *Ficus* sp. B.; series ♀, ♂: Uganda, Katalemwa Estate no. 3, 15 September 1968, tree no. 24, leg. D.S. Hill, ex *Ficus* sp. F.; series ♀, ♂: Uganda, Gayaza Rd., Kampala, 1 mile East of Katalemwa, 18 July

1968, tree no. 55, leg. D.S. Hill, ex *Ficus* sp. T.; series ♀: Uganda, Entebbe, 23 April 1968, tree no. 31, leg. D.S. Hill, ex *F.* "*dekdeknena*"; 5 ♀: Uganda, 1939, leg. T.H.C. Taylor, T675; 37 ♀: Kenya, Nairobi, Mayfair Hotel, 5400 ft., 10 February 1968, leg. C. van Someren, CvS no. 17; series ♀, ♂: Kenya, Nairobi, Nursery school, Forest road, 30 March 1965, leg. C. van Someren, CvS no. 25.

FEMALE. Faded due to storage in alcohol, dark brown, probably metallic green/black in fresh specimens, legs testaceous. Total length with head in orthognathous position excluding ovipositor 1.6 mm.

Head (fig. 9.5 d & 9.6 c) elongate, parallel sided (l = 0.64, w = 0.41), dorso-ventrally compressed (h = 0.12). Eye elongate (l = 0.22, w = 0.09, h = 0.04), 0.34X as long as the head. Cheek length 0.47X eye length. Occipital carina present ventral to the ocelli, shallow excavation between the lateral ocelli, the carina and the medial ocellus. Deep subquadrate ventral invagination of the vertex in which the foramen magnum is situated. POL = 0.15. OOL = 0.12. TE 1.32X as long as scrobe length (TE = 0.33, SL = 0.25). Malar sulcus present for anterior half of cheek. Clypeus narrow and elongate in area. Epistomal margin strongly projecting, convex, with a narrow medial indentation that is twice as deep as wide, width of margin 0.36X head width. Ventral tentorial pits in close apposition (fig. 9.6 c). Mandible with two apical teeth, a single larger tooth at the apex of a ventral plate of many fine teeth, the posterior row containing ca. 44 teeth, extending posteriorly just past the meeting point of the cheek with the oral fossa, two glands (fig. 9.6 c). Two labial palp segments, proximal segment largest. Three maxillary palp segments, proximal segment longest. Antenna much as in *P. jinjaensis* (fig. 9.4 g), funicle segments subequal in size, flagella l = 0.33. Scape 9.1X longer than wide (l = 0.27). Pedicel elongate, 0.37X scape length (l = 0.10).

Thorax. Pronotum square (l = 0.32, w= 0.34). Propodeum l = 0.13, w = 0.31. Mesoscutum l = 0.19, w = 0.36. Scutellum, including axillae broad (l = 0.22, w = 0.30). Fore femur 3X as long as wide (l = 0.36). Fore tibial armature consists of a comb of five or six teeth on the dorso-apical antiaxial margin. Fore leg coxa 0.69X femur length (C = 0.25, TR = 0.09, TI = 0.11, TA = 0.17). Six hind tibial spines on the dorsal margin. Fore wing 2.1X longer than wide, l = 1.16, sparsely setous. Postmarginal vein subequal to stigmal (SM = 0.46, M = 0.15, PM = 0.09, S = 0.10). Marginal vein 6.8X longer than wide. Hind wing 4.2X longer than wide, l = 0.93.

Gaster, posterior edge of tergites very crenulated, with three medial incisions. Eighth urotergite spiracle normal (l = 0.018). Ovipositor 4X as long as valve (valve l = 0.23).

MALE. Testaceous, eyes, mandibles and posterior half of gaster darker. Total length with head in orthognathous position excluding ovipositor 1.42 mm.

Head (fig. 9.5 e) elongate, parallel sided (l = 0.43, w = 0.39), height normal (h = 0.23). Eye elongate (l = 0.18, w = 0.10, h = 0.05), 0.42X as long as head. Cheek length 0.33X eye length. Malar sulcas absent. POL = 0.11. OOL = 0.12. Toruli situated on imaginary line joining anterior margin of the eyes, touching. TE 0.4X as long as scrobe length (TE = 0.10, SL = 0.25). Clypeus equilateral in area. Epistomal margin almost flat with slight lateral lobes, width of margin 0.54X head width. Ventral tentorial pits in close apposition. Two labial palp segments, segments subequal. Three maxillary palp segments, proximal segment longest. Mandible much as in *P. medius* (fig. 9.5 j). Antenna much as in *P. medius* (fig. 9.5 f), flagella length 2.4X as long as pedicel. Scape 4.8X longer than wide (l = 0.19). Pedicel very elongate, 0.58X scape length. MPS present on all four funicle segments and all the club segments.

Thorax. Parapsidal furrows complete. Fore femur 3.3X as long as wide (l = 0.36). Fore tibial armature bidentate. Fore tarsus

0.9X tibial length (C = 0.27, TR = 0.11, TI = 0.23, TA = 0.21). Fore wing 2.5X longer than wide, l = 1.25, very pilose. Postmarginal vein subequal in length to stigmal (SM = 0.42, M = 0.21, S = 0.09, PM = 0.10). Marginal vein thick, 9.1X longer than wide. Hind wing 4.8X longer than wide, l = 0.92.

Gaster. Eighth urotergite spiracle normal. Aedeagus small (l = 0.25). Four teeth on aedeagus claspers.

Philocaenus barbatus Grandi
(figs. 9.7 d, e, g & h)

Philocaenus barbatus Grandi 1952, 40-45, figs. vi-ix. Holotype ♀, Senegal. [Examined ♀ types, Istituto di Entomologia "Guido Grandi", Bologna].

Additional material. Allotype ♂: Senegal, Manpalago, SR47, 27 September 1979, leg. J. Etienne, RMNH 4123, ex *Ficus* sp. (accompanying agaonine near but not = to *E. articulata* Joseph); 2 ♀: same data as allotype; 2 ♀, 2 ♂: Ivory Coast, Lamto, 5° 02'W 6° 13'N 14 June 1989, leg. J.Y. Rasplus, ex *F. platyphylla* Delile.

The female is here redescribed and the male described for the first time from material collected in Senegal by J. Etienne.

FEMALE. Metallic green/black, antennae and mandibles brown, legs testaceous. Total length with head in orthognathous position, excluding ovipositor 1.5 mm.

Head (fig. 9.7 d & e) elongate, parallel sided (l = 0.55, w = 0.43), dorso-ventrally compressed (h = 0.15). Eye elongate (l = 0.22, w = 0.11, h = 0.06), 0.39X as long as head. Cheek length half of eye length. Malar sulcas present for ca. three-quarters of the cheek length, foveal-like at oral fossa fading towards eye. Occipital carina present ventral to ocelli. POL = 0.16. OOL = 0.09. Toruli situated on imaginary line joining anterior margin

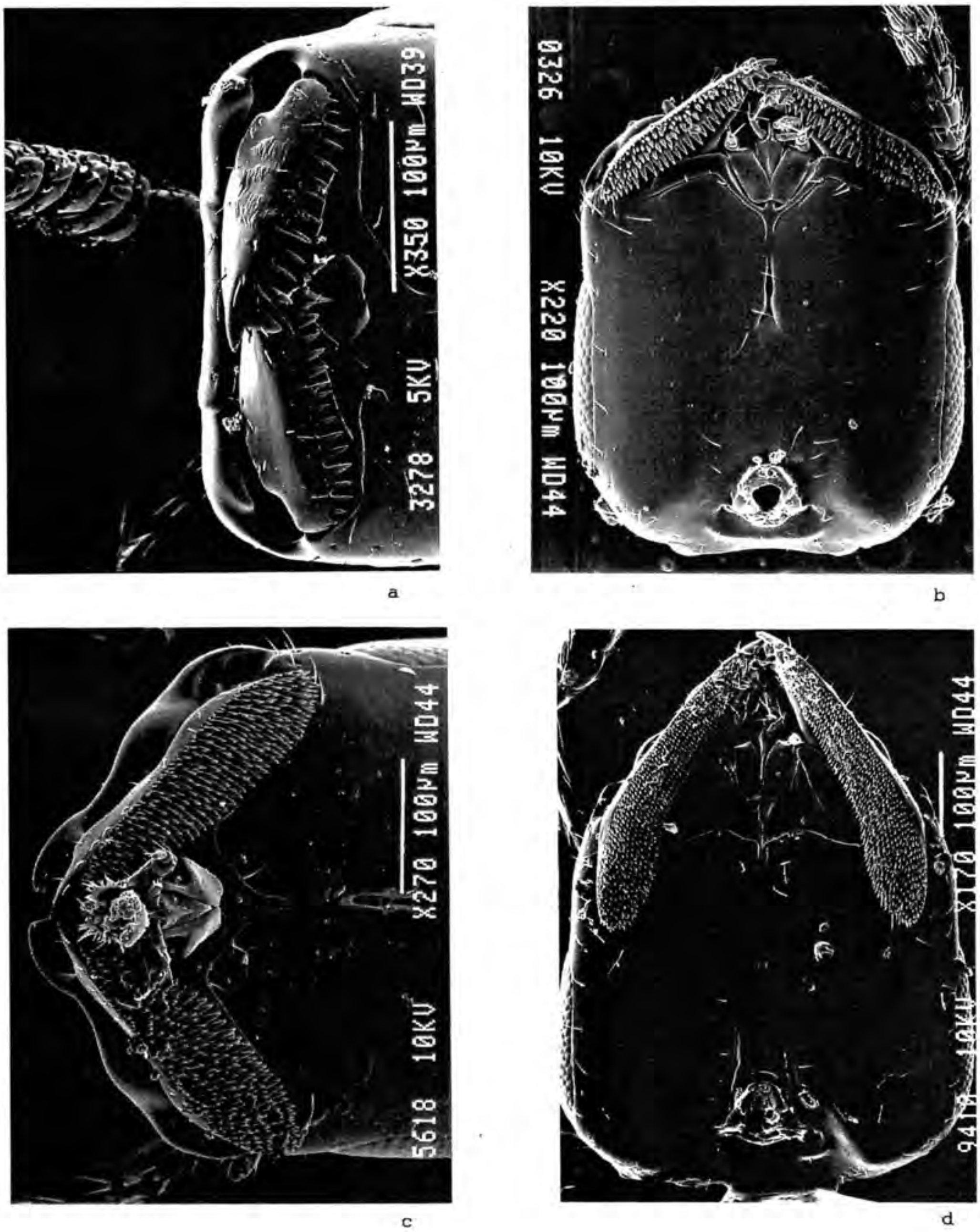


Fig. 9.6 a: *Philocaenus barbarus* (Grandi) a) female mandibles and anterior portion of head, ventral view; b: *Philocaenus medius* sp. nov. b) female head and mandibles, ventral view; c: *Philocaenus ugandensis* sp. nov. c) female mandibles and anterior half of head, ventral view; d: *Philocaenus hippopotomus* sp. nov. d) female head and mandibles, ventral view.

of the eyes. TE subequal to scrobe length (TE = 0.26, SL = 0.25). Clypeus narrow and elongate in area, clypeal sutures present as deep foveas at the toruli, narrowing to dorsal tentorial pits, thereafter to epistomal margin present as normal sutures. Epistomal margin strongly protruding, broadly bilobed, with a medial narrow triangular indentation flanked by a step on each side (fig. 9.7 d), margin width ca. a third of head width. Ventral tentorial pits separated, situated closer to the foramen magnum than to the oral fossa (fig. 9.7 e). Mandible (much as in *P. hippopotomus* fig. 9.6 d) with two apical teeth and a ventral plate of many teeth, that extends posteriorly below the head for more than half the head length, two glands. Two labial palp segments, segments subequal. Three maxillary palp segments, distal segment longest. Antenna (much as in *P. jinjaensis*, fig. 9.4 g), funicle segments subequal in size, flagella l = 0.32. Scape narrow, 7.4X longer than wide (l = 0.19). Pedicel very elongate, 0.48X scape length.

Thorax. Pronotum broad (l = 0.24, w = 0.33). Propodeum l = 0.12, w = 0.34. Mesoscutum l = 0.22, w = 0.39. Scutellum, including axillae broad (l = 0.22, w = 0.31). Fore femur 3.2X as long as wide (l = 0.30). Fore tibial armature bidentate. Fore leg coxa ca. three-quarters of femur length (C = 0.22, TR = 0.08, TI = 0.12, TA = 0.19). Six hind tibial spines. Fore wing 2.3X longer than wide, l = 1.10, sparsely setous. Postmarginal vein subequal to stigmal (SM = 0.42, M = 0.15, PM = 0.09, S = 0.10). Marginal vein 6.4X longer than wide. Hind wing 3.9X longer than wide, l = 0.86.

Gaster, posterior edge of tergites very crenulated, with three medial incisions. Eighth urotergite spiracle slightly larger than normal (l = 0.035). Ovipositor 3.8X as long as valve (valve l = 0.26).

MALE. Testaceous, posterior two thirds of head very dark brown almost black, eyes, mesoscutum, scutellum and axillae and posterior half of gaster darker brown. Total length with head in orthognathous position excluding ovipositor 1.39 mm.

Head (figs. 9.7 g & h) approximately square (l = 0.41, w = 0.41), height normal (h = 0.20). Eye oval (l = 0.18, w = 0.12, h = 0.06), 0.44X as long as the head. Cheek length 0.39X eye length (l = 0.07). Malar sulcas absent. POL = 0.12. OOL = 0.10. Toruli situated on imaginary line joining anterior margin of the eyes, separated by ca. a quarter of torulus width. TE 0.52X as long as scrobe length (TE = 0.12, SL = 0.23). Clypeus equilateral in area. Epistomal margin protruding, bilobed laterally, with medial convexity, width of margin approximately half the head width. Ventral tentorial pits separated (fig. 9.7 h). Two labial palp segments, distal segment longest. Three maxillary palp segments, proximal segment subequal in length to distal, twice the length of the middle segment. Mandible much as in *P. hippopotomus* (fig. 9.7 i). Antenna (much as in *P. medius*, fig 9.5 f), flagella length 2.5X as long as pedicel. Scape broad, 4.3X longer than wide (l = 0.17). Pedicel very elongate, 0.59X scape length.

Thorax. Parapsidal furrows complete. Fore femur 3.6X as long as wide (l = 0.32). Fore tibial armature bidentate. Fore tarsus subequal in length to tibia (C = 0.24,TR = 0.09, TI = 0.18, TA = 0.20). Fore wing 2.8X longer than wide, l = 1.14, sparsely setous. Postmarginal vein subequal to stigmal (SM = 0.42, M = 0.16, S = 0.10, PM = 0.09). Marginal vein thick, 5.3X longer than wide. Hind wing 4.4X longer than wide, l = 0.83.

Gaster. Eighth urotergite spiracle normal. Four teeth on aedeagus claspers.

Philocaenus hippopotomus sp. nov.

(figs. 9.6 d; 9.7 a-c, f & i)

Etymology: Named after a junior synonym, *F. hippopotomi*, of the host fig tree.

Type material: Holotype ♀, allotype ♂ (slide mounted): South Africa, Natal, Kosi Bay, 2 December 1988, leg. S.G. Compton, C96, ex *F. trichopoda* Baker. Paratypes, 5 ♀, 5 ♂ (slide mounted) series ♀, ♂: same data as holotype; 6 ♀, 1 ♂: Madagascar, Tsimbazaza, Botanical Gardens, 26 May 1980, leg. D. Lachaise, RMNH 4279, ex *Ficus* probably *trichopoda* Baker.; 35 ♀, 3 ♂: Zambia, Luapula, Manunga, Lake Mweru, leg. M.G. Bingham, 9 October 1980, 2505 I, RMNH 4434, ex *F.trichopoda* Baker; 19 ♀, 1 ♂: Malawi, Malosa, 12 miles NNE Zomba, Chilema Lay training centre, 31 October 1982, leg. H. Meredith, RMNH 4901, ex *F. trichopoda* Baker; 1 ♀: South Africa, Natal, Mapalane, 2832AD, 4 December 1986, leg. S.G. Compton, C45, ex *F. trichopoda* Baker; series ♀, ♂: South Africa, Natal, Mselini, 12 December 1986, leg. S.G. Compton & H.G. Robertson C46, ex *F. trichopoda* Baker; 6 ♀, 4 ♂: South Africa, Natal, Umlalazi Rest Camp, 2831DD, 13 December 1986, leg. A.J. Gardiner, C47, ex *F. trichopoda* Baker; 1 ♀, 1 ♂: South Africa, Natal, Kosi Bay, N.W. Nhlange, 15 October 1989, C198, leg. M. Ward, ex *F. trichopoda* Baker; 1 ♂: South Africa, Natal, Kwazibi, North of Manzengwenya Plantation, 26° 54'S 32° 19'E, 15 November 1989, leg. M. Ward, C201, ex *F. trichopoda* Baker; series ♀, ♂: South Africa, Natal, Sodwana, 25 January 1990, leg. S. van Noort & A.B. Ware, C251, ex *F. trichopoda* Baker; series ♀, ♂: South Africa, Natal, Sodwana, 25 January 1990, leg. S. van Noort & A.B. Ware, C252, ex *F. trichopoda* Baker; series ♀, ♂: South Africa, Natal, Sodwana, 25 January 1990, leg. S. van Noort & A.B. Ware, C253, ex *F. trichopoda* Baker; series ♀, ♂: South Africa, Natal, Mselini, 26 January 1990, leg. S. van Noort & A.B. Ware, C257, ex *F. trichopoda* Baker; series ♀, ♂: South Africa, Natal, Kosi Bay, 26 January 1990, leg. S. van Noort & A.B. Ware, C259, ex *F. trichopoda* Baker; series???? South Africa, Natal, Dukuduku, 30 January 1990, leg. S. van Noort & A.B. Ware, C271, ex *F. trichopoda* Baker.

FEMALE. Metallic green/black, antennae and mandibles brown, legs testaceous. Total length with head in orthognathous position excluding ovipositor 1.55 mm.

Head (figs. 9.6 d & 9.7 a) elongate, parallel sided (l = 0.59, w = 0.44), dorso-ventrally compressed (h = 0.15). Eye elongate (l = 0.21, w = 0.10, h = 0.05), 0.35X as long as the head. Cheek length 0.66X eye length. Malar sulcas present for anterior half of cheek. Occipital carina present below the lateral ocelli. POL = 0.15. OOL = 0.12. Toruli situated on imaginary line joining anterior margin of the eyes. TE 1.08X as long as scrobe length (TE = 0.29, SL = 0.26). Clypeus narrow and elongate in area. Epistomal margin strongly projecting, bilobed, with broad,

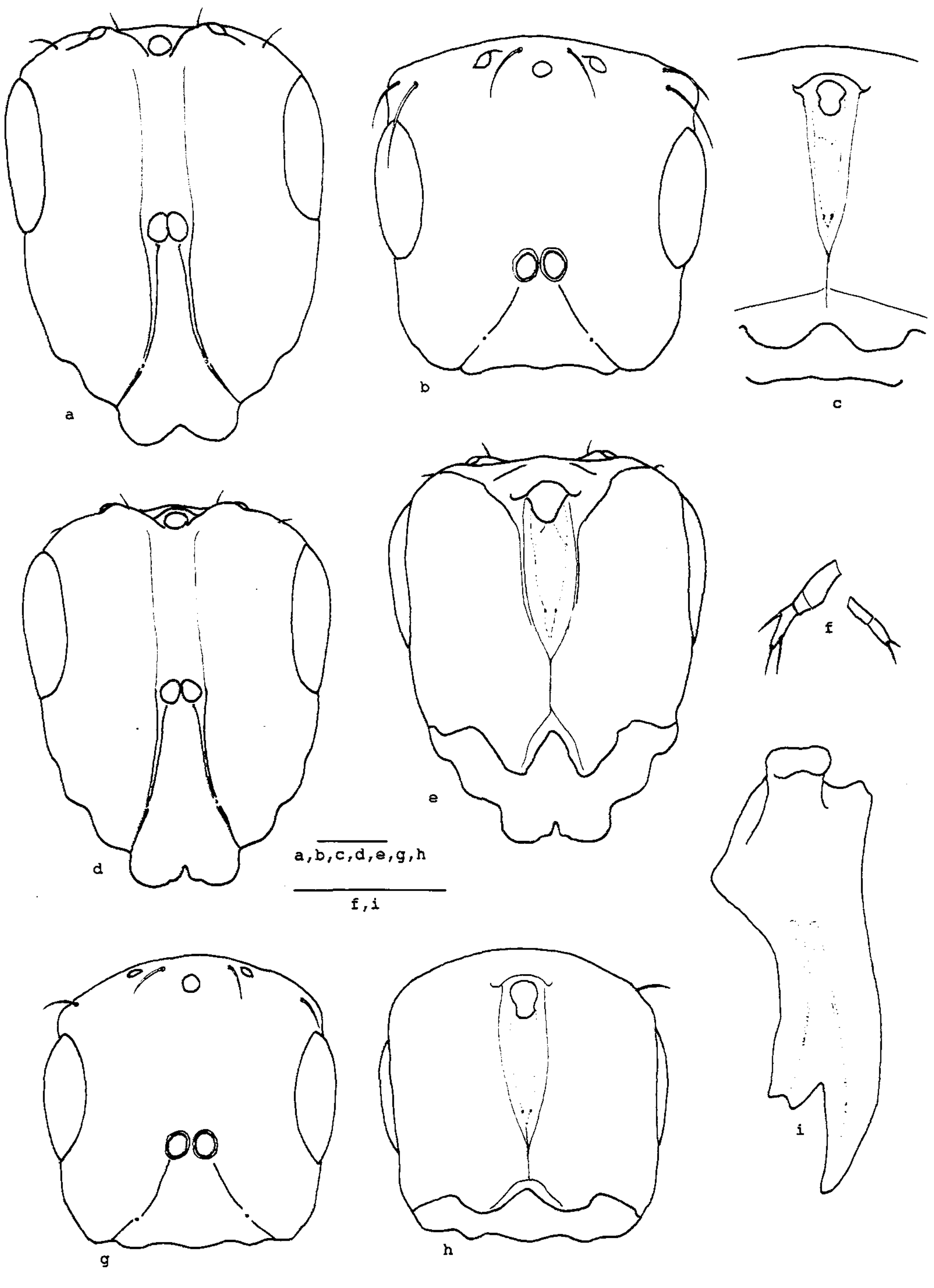


Fig. 9.7 a-c, f & i: *Philocaenus hippopotomus* sp. nov. a) female head, dorsal view b) male head, dorsal view c) male head, ventral view f) male labial and maxillary palps i) male mandible, dorsal view; d, e, g & h: *Philocaenus barbatus* Grandi d) female head, dorsal view e) female head, ventral view g) male head, dorsal view h) male head, ventral view. Scale bars = 0.1 mm.

medial, V-shaped indentation (fig. 9.7 a), width of margin 0.38X head width. Ventral tentorial pits separated (fig. 9.6 d). Mandible with two apical teeth and a single larger tooth at the apex of the ventral plate of many fine elongate teeth in close apposition, two glands (fig. 9.6 d). Hypostoma extensive, expanded posteriorly (fig. 9.6 d). Two labial palp segments, segments subequal. Three maxillary palp segments, distal segment longest and subequal to proximal segment, which is three times wider. Both are 3X longer than the medial segment, which is indistinct as it is partially fused to the first segment. Antenna (much as in *P. jinjaensis*, fig. 9.4 g), funicle segments subequal in size, flagella l = 0.31. Scape 8.1X longer than wide (l = 0.19). Pedicel very elongate, 0.46X scape length.

Thorax. Pronotum broad (l = 0.25, w = 0.33). Propodeum l = 0.14, w = 0.32. Mesoscutum l = 0.22, w = 0.38. Scutellum, including axillae broad (l = 0.21, w = 0.30). Fore femur 2.8X as long as wide (l = 0.31). Fore tibial armature bidentate. Fore leg coxa 0.64X femur length (C = 0.20, TR = 0.09, TI = 0.10, TA = 0.17). Fore wing 2.2X longer than wide, l = 1.11, sparsely setous. Postmarginal vein shorter than stigmal (SM = 0.42, M = 0.15, PM = 0.08, S = 0.10). Marginal vein 5.5X longer than wide. Hind wing 4.3X longer than wide, l = 0.90.

Gaster, posterior edge of tergites very crenulated, with three medial incisions. Eighth urotergite spiracle normal (l = 0.02). Ovipositor 3.65X as long as valve (valve l = 0.27).

MALE. Testaceous, mesoscutum, scutellum, axillae and the gaster brown. Total length with head in orthognathous position excluding ovipositor 1.4 mm.

Head (figs. 9.7 b & c) square (l = 0.46, w = 0.46), height normal (h = 0.21). Eye oval (l = 0.19, w = 0.11, h = 0.06), 0.42X as long as head. Cheek length 0.52X eye length. Malar sulcas absent. POL = 0.13. OOL = 0.13. Toruli situated on imaginary line joining anterior margin of the eyes, separated by ca. a quarter of the torulus width. TE 0.42X as long as scrobe length (TE = 0.12, SL = 0.29). Clypeus equilateral in area. Epistomal margin projecting, bilobed laterally, with a medial convexity. Ventral tentorial pits slightly separated (fig. 9.7 c). Two labial palp segments, subequal in length (fig. 9.7 f). Three maxillary palp segments, proximal segment widest, subequal in length to the distal, both 3X longer than the medial segment (fig. 9.7 f). Mandible (fig. 9.7 i). Antenna (much as in *P. medius*, fig. 9.5 f), flagellar 2.5X as long as pedicel. Scape 5X longer than wide (l = 0.20). Pedicel very elongate, 0.6X scape length.

Thorax. Parapsidal furrows complete. Fore femur 3.5X as long as wide (l = 0.38). Fore tibial armature bidentate. Fore tarsus equal to the tibial length (C = 0.28, TR = 0.10, TI = 0.22, TA = 0.22). Fore wing 2.5X longer than wide, l = 1.28, very pilose. Postmarginal vein shorter than stigmal (SM = 0.45, M = 0.20, S = 0.12, PM = 0.08). Marginal vein very thick, 5.4X longer than wide. Hind wing 4.6X longer than wide, l = 0.97.

Gaster. Eighth urotergite spiracle normal. Aedeagus small (l = 0.27). Four teeth on aedeagus claspers.

Philocaenus levis species-group.

This species-group is characterised by the presence of only a single large ventral tooth on the female mandible, numerous MPS on the female antennae that are in close apposition, suboval head shape and a broadly bifurcate epistomal margin.

Philocaenus bakeri sp. nov.

(figs. 9.8 d-f)

Etymology: Named after R.G.E. Baker, the collector of the holotype.

Type material: Holotype ♀ (slide mounted): Cameroun, S.W.

Province, Bomana, 22 January 1982, leg. R.G.E. Baker, no. 21, C1008, ex *F. sansibarica* Warb *?macrosperma* (Mildbr. & Burr.) Berg; 2 ♀ paratypes (card mounted): same data as holotype.

FEMALE. Metallic black, tibia and tarsi testaceous. Total length with head in orthognathous position, excluding ovipositor 2.5 mm.

Head (figs. 9.8 e & f) elongate, parallel sided (l = 0.83, w = 0.67), dorso-ventrally compressed (h = 0.21). Eye very elongate (l = 0.39, w = 0.13, h = 0.09), 0.46X as long as the head. Cheek length 0.64X eye length. Occipital carina in a straight line below the ocelli, curved ventrally at lateral ends, parallels the ventral invagination of the vertex; slight excavation lateral of the lateral ocelli. POL = 0.20. OOL = 0.13. TE 1.12X as long as scrobe length (TE = 0.40, SL = 0.36). Clypeus equilateral in area. Epistomal margin projects, laterally angular, with a broad, shallow medial concavity. Ventral tentorial pits in close apposition (fig. 9.8 f). Mandible (fig. 9.8 d) with two apical teeth, and a single large ventral tooth, two glands. Two labial palp segments, segments subequal. Three maxillary palp segments, proximal segment longest. Antenna (much as in *P. bifurcus*, fig. 9.8 c), funicle segments subequal in size, flagella length = 0.49. Scape narrow, 7.3X longer than wide (l = 0.29). Pedicel relatively short, 0.35X scape length. MPS numerous, eighteen to twenty per segment, often offset from one another.

Thorax. Pronotum l = 0.38, w = 0.47. Propodeum l = 0.23, w = 0.48. Mesoscutum l = 0.36, w = 0.56. Scutellum, including axillae l = 0.40, w = 0.45. Fore femur 3.1X longer than wide (l = 0.50). Fore tibia much as in *P. clairae* (fig. 9.9 f), except the armature on the dorso-apical margin is tridentate. Fore leg coxa ca. three quarters of femur length (C = 0.37, TR = 0.14, TI = 0.20, TA = 0.25). Fore wing 2.5X longer than wide, l = 1.84, pilose, fringe short. Postmarginal vein shorter than stigmal (SM = 0.69, M = 0.28, PM = 0.12, S = 0.15). Marginal vein 9.3X longer than wide. Hind wing 4.1X longer than wide, l = 1.38.

Gaster, posterior edge of tergites very crenulated, with three medial incisions. Eighth urotergite spiracle normal. Ovipositor 3.6X longer than the ovipositor valves (valve 1 = 0.55).

Philocaenus bifurcus sp. nov.

(figs. 9.8 a-c)

Etymology: Bifurcus (latin) = forked, referring to the epistomal margin shape.

Type material: Holotype ♀ (slide mounted): Kenya, Kilifi distr., leg. L. Lap., no. 210, RMNH 4889, ex *F. ottonifolia* (Miq.) Miq. *ulugurensis* (Mildbr. & Burr.) Berg. (det. Berg, from herbarium material) [associated pollinator = *Courtella camerunensis* (Wiebes)].

FEMALE. Head metallic green, rest metallic green/black, gaster browner, antennae, legs and mandibles testaceous. Total length with head in orthognathous position excluding ovipositor 2 mm.

Head (fig. 9.8 a) elongate, parallel sided (l = 0.76, w = 0.51), dorso-ventrally compressed (h = 0.18). Eye very elongate (l = 0.33, w = 0.11, h = 0.062), 0.44X as long as head. Cheek length 0.73X eye length (l = 0.24). Thin occipital carina present. POL = 0.17. OOL = 0.12. TE 1.23X as long as scrobe length (TE = 0.39, SL = 0.32). Clypeus long and narrow in area, broadening near the epistomal margin. Epistomal margin projects with angular bilobed margins and a medial concavity that extends deeper than the paraclypeal margins, width of margin ca. two-fifths of head width (fig. 9.8 a). Ventral tentorial pits very close together in slight depression, situated a third of the distance from the foramen magnum to the oral fossa. Mandible with two apical teeth and a single large ventral tooth, situated near the apex, rest of ventral edge a smooth ridge, two glands (fig. 9.8 b). Two labial palp segments, segments subequal in length. Three maxillary palp segments, proximal segment longest. Antenna (fig. 9.8 c), funicle segments subequal in size, dorso-ventrally

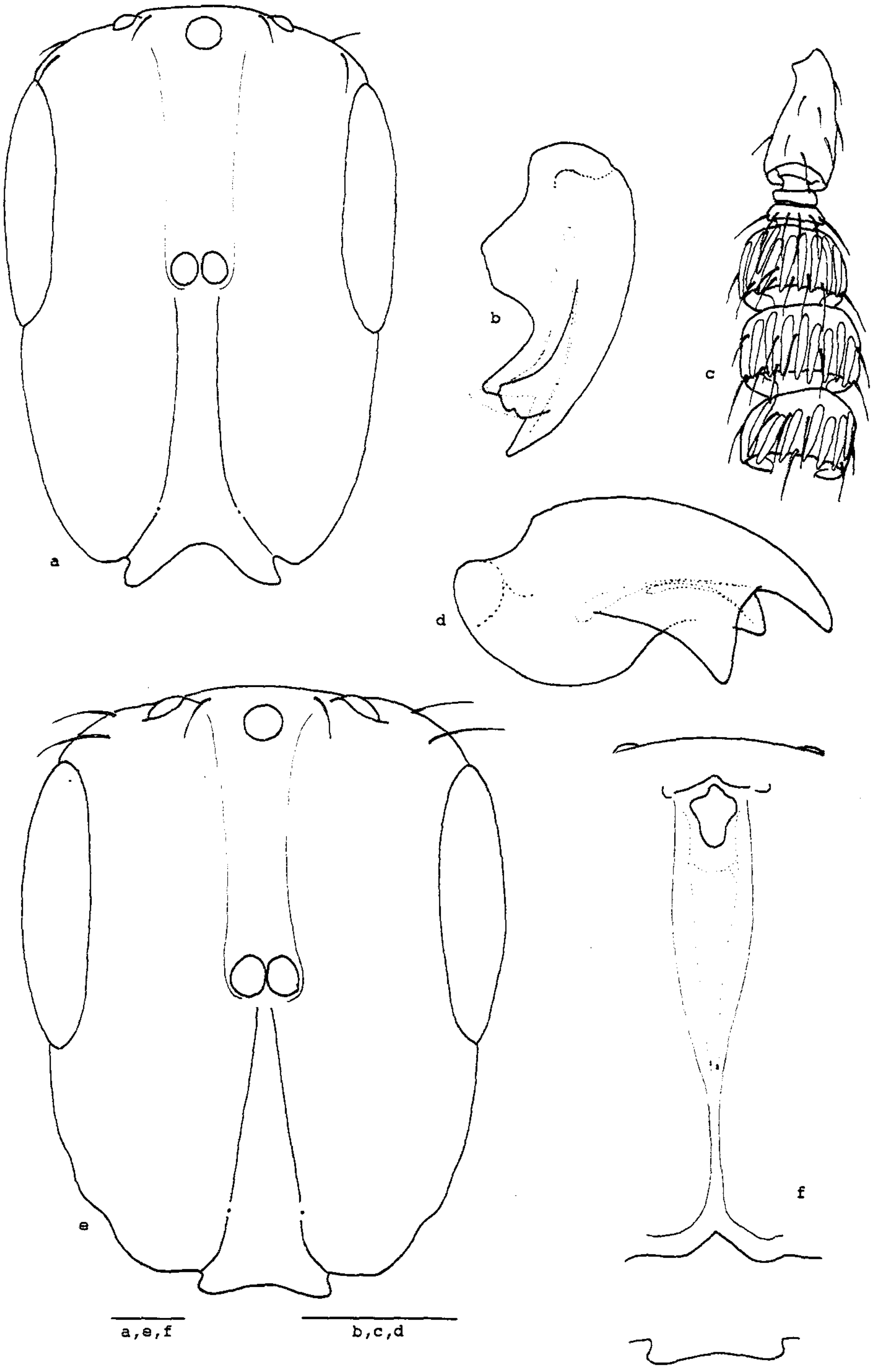


Fig. 9.8 a-c: *Philocaenus bifurcus* sp. nov. a) female head, dorsal view b) female mandible, ventral view, c) female antenna -pedicel, anelli and the first three funicle segments, antiaxial view; d-f: *Philocaenus bakeri* sp. nov. d) female mandible, ventral view e) female head, dorsal view f) female head, ventral view. Scale bars = 0.1 mm.

compressed, flagella l = 0.41. Scape narrow, 7X longer than wide (l = 0.21). Pedicel elongate, 0.43X scape length. MPS numerous, ca. fourteen per segment, more numerous dorsally.

Thorax. Pronotum broad (l =0.32, w = 0.38). Propodeum wider than long (l = 0.16, w = 0.39). Mesoscutum broad (l = 0.29, w = 0.45). Scutellum, including axillae broad (l = 0.29, w = 0.36). Fore femur 3.3X as long as wide (l = 0.40). Fore tibia much as in *P. clairae* (fig. 9.9 f), except the armature on the dorso-apical margin is tridentate. Fore leg coxa 0.70X femur length (C = 0.28, TR = 0.10, TI = 0.15, TA = 0.20). Six spines on the dorsal margin of the hind tibia. Fore wing 2.3X longer than wide, l = 1.38, sparsely setous, fringe short. Postmarginal vein same length as stigmal (SM = 0.55, M = 0.18, PM = 0.10, S = 0.10). Marginal vein 9X longer than wide. Hind wing 4.7X longer than wide, l = 1.09.

Gaster, posterior edge of tergites crenulated with three medial incisions. Eighth urotergite spiracle normal (l = 0.037). Ovipositor 3.8X as long as valve (valve l = 0.32).

Philocaenus levis (Waterston) **comb. n.**

(fig. 9.9 h)

Seres levis Waterston 1920, 135-136, fig. 3(d-f), ♀ holotype, Uganda. [Examined paratype, The Natural History Museum, London].

Philocaenus clairae **sp. nov.**

(figs. 9.9 a-g & 9.11 a)

Etymology: Named after my wife, Claire.

Type material: Holotype ♀, allotype ♂ (slide mounted): South Africa, Natal, Sihangwane, 27° 03'S 32° 25'E, 3 March 1989, leg. M. Ward, C127, ex *F. t. tremula* Warb. Paratypes, series ♀, ♂: same data as holotype; series ♀, ♂: South Africa, Natal, False Bay Park, Mpophomeni Trail, 28 January 1990, leg. S. van Noort & C. Zachiarides, C268, ex *F. t. tremula* Warb.

FEMALE. Metallic green/black, antennae, mandibles and legs testaceous. Total length with head in orthognathous position excluding ovipositor 1.75 mm.

Head (figs. 9.9 a & 9.11 a) elongate, parallel sided (l = 0.66, w = 0.41), dorso-ventrally compressed,' h = 0.18. Eye very elongate (l = 0.33, w = 0.13, h = 0.06) 0.5X as long as the head. Cheek length 0.42X eye length. Occipital carina present ventral to the lateral ocelli, curved, parallels the ventral invagination of the vertex in which the foramen magnum is situated, fades out at outer margin of lateral ocelli. POL = 0.16. OOL = 0.09. TE same length as scrobe length (TE = 0.30). Clypeus equilateral in area. Epistomal margin protrudes, angular laterally, with broad medial concavity, two-fifths of head width. Ventral tentorial pits in close apposition (fig. 9.11 a). Mandible (fig. 9.9 d) with two apical teeth and a single large ventral tooth apically situated, two glands. Two labial palp segments, segments subequal in length (fig. 9.9 e). Three maxillary palp segments, proximal segment longest (fig. 9.9 e). Antenna (fig. 9.9 g), funicle segments subequal in size, flagella length = 0.34, dorso-ventrally compressed. Scape narrow, 6X longer than wide (l = 0.18). Pedicel very elongate, half of scape length. MPS more numerous per segment (fig. 9.9 g) than is normal for *Philocaenus*.

Thorax. Pronotum broad (l = 0.28, w = 0.35). Propodeum l = 0.16, w = 0.36. Mesoscutum l = 0.28, w = 0.41. Scutellum, including axillae broad (l = 0.27, w = 0.35). Fore femur 2.9X as long as wide (l = 0.35). Fore tibial armature bidentate (fig. 9.9 f). Fore leg coxa four-fifths of femur length (C = 0.28, TR = 0.09, TI = 0.15, TA = 0.19). Fore wing 2.2X longer than wide, l = 1.28, sparsely setous, fringe very short, absent on the anal lobe. Postmarginal vein subequal in length to stigmal (SM = 0.48, M = 0.18, PM = 0.10, S = 0.11). Marginal vein thick, 4.5X longer than wide. Hind wing 4X longer than wide, l = 0.95.

Gaster, posterior edge of the tergites very crenulated, with

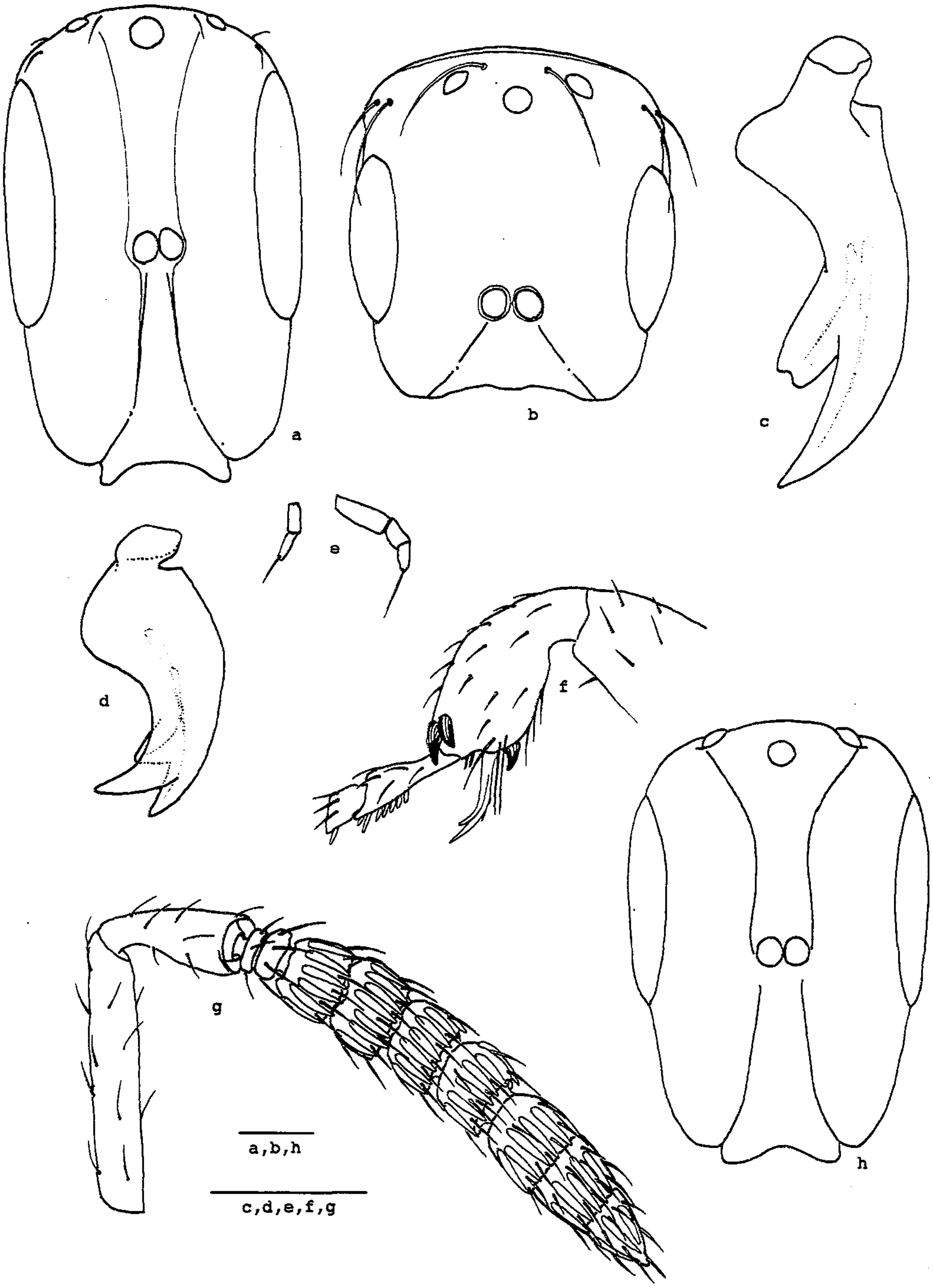


Fig. 9.9 a-g: *P. clairae* sp. nov. a) female head, dorsal view b) male head, dorsal view c) male mandible, dorsal view d) female mandible, ventral view e) female labial and maxillary palps f) female fore tibia and first two tarsal segments, antiaxial view g) female antenna, antiaxial view; h: *Philocaenus levis* (Waterston) h) female head, dorsal view (redrawn from Waterston, 1920). Scale bars = 0.1 mm.

three medial incisions. Eighth urotergite spiracle normal (l = 0.02). Ovipositor 3.7X as long as valve (valve l = 0.30).

MALE. Testaceous, eyes, ocelli and mandibles darker. Total length with head in orthognathous position excluding ovipositor 1.67 mm.

Head (fig. 9.9 b) elongate, parallel sided (l = 0.47, w = 0.43), height normal (h = 0.21). Eye very elongate (l = 0.22, w = 0.10), protrudes laterally (h = 0.06), 0.47X as long as the head. Cheek length 0.23X eye length. POL = 0.13. OOL = 0.12. TE 0.30X as long as scrobe length (TE = 0.09, SL = 0.28). Toruli very slightly separated. Clypeus equilateral in area. Epistomal margin generally concave with a medial convexity, width of margin ca. two-fifths of head width. Ventral tentorial pits in close apposition. Mandible elongate and narrow (fig. 9.9 c). Two labial palp segments, segments subequal in length. Three maxillary palp segments, proximal segment longest. Antenna (much as in *P. rotundus* fig. 9.13 h), flagellar length 2.4X as long as pedicel. Scape broad, 3.8X longer than wide (l = 0.19). Pedicel very elongate, 0.58X scape length. MPS present on all four funicle and the three club segments.

Thorax. Parapsidal furrows complete. Fore femur 3.2X as long as wide (l = 0.42). Fore tibial armature bidentate. Fore tarsus ca. four-fifths of tibia length (C = 0.28, TR = 0.12, TI = 0.27, TA = 0.22). Fore wing 2.5X longer than wide, l = 1.34, very pilose. Postmarginal vein same length as stigmal (SM = 0.46, M = 0.23, S = 0.11, PM = 0.11). Marginal vein thick 7.7X longer than wide. Hind wing 4.8X longer than wide, l = 1.05.

Gaster. Eighth urotergite spiracle normal. Aedeagus large (l = 0.40). Four or five teeth on aedeagus claspers.

Philocaenus liodontus species-group.

This species-group is characterised by female mandibles that are male-like, in that they are narrow and elongate and articulated such that they protrude forwards and downwards. The female epistomal margin is broadly concave, often with an indistinct medial convexity.

Philocaenus warei **sp. nov.**

(figs. 9.10 a-i; 9.11 c)

Etymology: Named after A.B. Ware.

Type material: Holotype ♀, allotype ♂ (slide mounted): South Africa, Natal, Ubombo, 2732CA, 9 December 1986, leg. S.G. Compton, C33, ex *F. glumosa* Delile. Paratypes, 5 ♀, 5 ♂ (slide mounted), series ♀, ♂: same data as holotype; 7 ♀, 4 ♂: Zambia, Kafue Town, leg. M.G. Bingham, 16 September 1980, no. 2503, RMNH 4417, ex *F. glumosa* Delile; 1 ♀: South Africa, Natal, Mkuzi Game Reserve, 2732CA, 7 December 1986, leg. S.G. Compton, C32, ex *F. glumosa* Delile; series ♀, 3 ♂: South Africa, Natal, Hluhluwe Game Reserve, 2832AA, 5 December 1986, leg. S.G. Compton & A.J. Gardiner, C48, ex *F. glumosa* Delile; series ♀, 4 ♂: South Africa, Transvaal, Strydom Tunnels, 1 January 1988, leg. P. Raal, C58, ex *F. glumosa* Delile; series ♀, 5 ♂: Zimbabwe, Mazoe Citrus Estates Ranch, 1 March 1987, leg. A.J. Gardiner, C66, ex *F. glumosa* Delile; series ♀, 7 ♂: Malawi, Cape Maclear, Lake Malawi, 17 January 1989, leg. P. Lloyd, C91, ex *F. glumosa* Delile; series ♀, ♂: South Africa, Natal, Zululand, South of Jozini, 8 December 1988, leg. S.G. Compton & V.K. Rashbrook, C104, ex *F. glumosa* Delile; series ♀, ♂: South Africa, Natal, Pongola, 6 September 1989, leg. S. van Noort & A.B. Ware, C170, ex *F. glumosa* Delile; 6 ♀, 3 ♂: South Africa, Natal, Jozini, 21 January 1990, leg S. van Noort & A.B. Ware, C236, ex *F. glumosa* Delile; series ♀, ♂: same data, C237; 5 ♀, 2 ♂: South Africa, Natal, Jozini, 21 January 1990, leg. S. van Noort & A.B. Ware, C241, ex *F. glumosa* Delile; series ♀, 5 ♂: South Africa, Natal, Ingwavuma, 23 January 1990, leg. S. van Noort & A.B. Ware, C243, ex *F. glumosa* Delile; series ♀, 4 ♂: same data, C246; series ♀, ♂: same data, C247; series ♀, 2 ♂: South Africa, Ubombo, 27 January 1990, leg. S. van Noort & A.B. Ware, C264, ex *F. glumosa* Delile; series ♀: Zimbabwe, Mashonaland Central, Mazoe Cattle Ranch, 5 March 1990, leg. I. Waters, C285, ex *F. glumosa* Delile.

FEMALE. Metallic black, legs, antennae and mandibles light brown. Total length with head in orthognathous position, excluding ovipositor = 1.4 mm.

Head (figs. 9.10 a & b) approximately square (l = 0.41, w = 0.40, h = 0.16). Eye elongate (l = 0.21, w = 0.11, h = 0.05), 0.52X as long as the head. Cheek length 0.37X eye length. Malar sulcas absent. POL = 0.14. OOL = 0.11. Toruli situated between the eyes. TE 0.90X as long as scrobe length (TE = 0.17, SL = 0.19). Clypeus equilateral in area. Epistomal margin broadly bilobed with a deep, smooth medial concavity, margin width ca. half the head width. Ventral tentorial pits in close apposition (fig. 9.10 b). Labial and maxillary palps (fig. 9.10 b). Mandible with two apical teeth and two ventral teeth apically situated, two glands (fig. 9.10 c). Antenna (fig. 9.10 g), funicle segments subequal in size, flagella l = 0.29. Scape narrow, 7.1X longer than wide (l = 0.17). Pedicel very elongate, 0.45X scape length. MPS are spaced widely apart.

Thorax. Pronotum broad (l = 0.21, w = 0.32). Propodeum wider than long (L = 0.10, w = 0.31). Mesoscutum l = 0.19, w = 0.36. Scutellum, including axillae broad (l = 0.18, w = 0.29). Fore femur 3X as long as wide (l = 0.28). Fore tibial armature tridentate (fig. 9.10 d). Fore leg coxa ca. three-quarters of femur length (C = 0.21, TR = 0.07, TI = 0.12, TA = 0.17). Five hind tibial spines on the dorsal margin. Fore wing 2.3X as long as broad (l = 1.01, w = 0.44), sparsely setous. Postmarginal vein subequal in length to stigmal (SM = 0.38, M = 0.12, PM = 0.08, S = 0.10). Marginal vein 5X as long as wide. Hind wing 4.2X as long as wide (l = 0.80).

Gaster (fig. 9.11 c), posterior edge of tergites very crenulated, with three medial incisions. Eighth urotergite spiracle normal (l = 0.02). Ovipositor 3.3X as long as valve (valve l = 0.28).

MALE. Variable - testaceous, flagella, eyes, vertex, gaster and sometimes the mesoscutum, scutellum and axillae dark brown. Total length with head in orthognathous position excluding ovipositor 1.25 mm.

Head (fig. 9.10 e & f) elongate, parallel sided (l = 0.37, w =

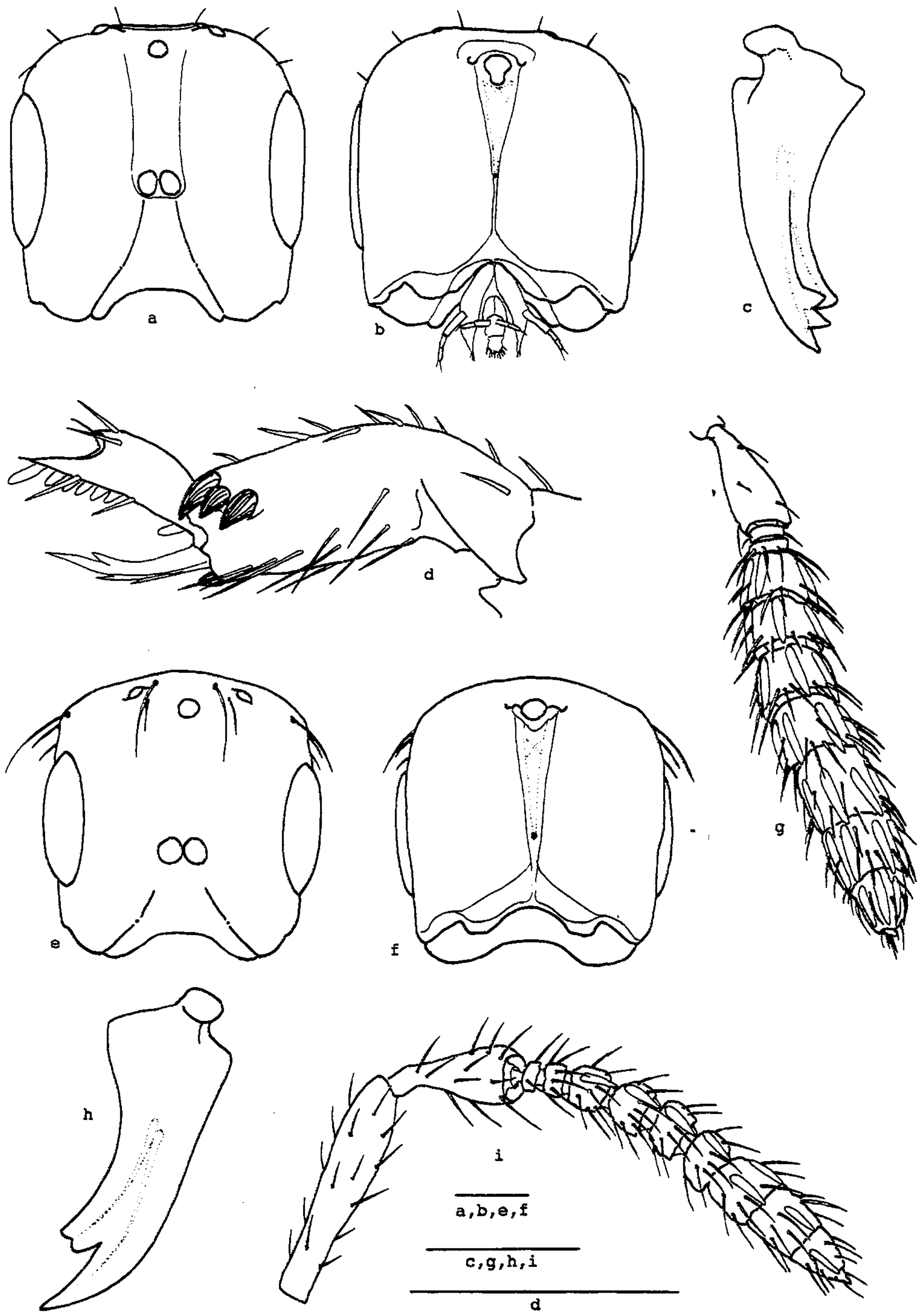


Fig. 9.10 a-i: *Philocaenus warei* sp. nov. a) female head, dorsal view b) female head, ventral view c) female mandible, ventral view d) female fore tibia and first tarsal segment, antiaxial view e) male head, dorsal view f) male head, ventral view g) female antenna, antiaxial view h) male mandible, dorsal view i) male antenna, antiaxial view. Scale bars = 0.1 mm.

0.35), height normal (h = 0.21). Eye elongate (l = 0.17, w = 0.10, h = 0.05), 0.46X as long as the head. Cheek length 0.34X eye length. Malar sulcas absent. POL = 0.11. OOL = 0.10. Toruli situated between the eyes, touching. TE 0.47X as long as scrobe length (TE = 0.09, SL = 0.19). Clypeus, equilateral in area. Epistomal margin broadly bilobed with a medial smooth concavity. Ventral tentorial pits in close apposition (fig. 9.10 f). Labial and maxillary palp segments as in the female. Mandible (fig. 9.10 h). Antenna (fig. 9.10 i), flagella length 3.3X as long as pedicel. Scape 5.3X longer than wide (l = 0.16). Pedicel very elongate, half of scape length.

Thorax. Parapsidal furrows complete. Fore femur 3.2X longer than wide (l = 0.29). Fore tibial armature bidentate. Fore tarsus 1.1X tibial length (C = 0.24, TR = 0.09, TI = 0.18, TA = 0.20). Fore wing 2.4X longer than wide, l = 0.97, pilose. Postmarginal vein longer than stigmal (SM = 0.35, M = 0.14, S = 0.08, PM = 0.09). Marginal vein very thick, 4.7X longer than wide. Hind wing 5.1X longer than wide, l = 0.76.

Gaster. Eighth urotergite spiracle normal. Aedeagus small (l = 0.24). Five teeth on aedeagus claspers.

Philocaenus liodontus (Wiebes) **comb. n.**

(fig. 9.11 b)

Phagoblastus liodontus Wiebes 1979: 397-400, figs 20-37, holotype ♀, allotype ♂, Gabon.

Additional material: 2 ♀: Gabon, Makokou, 1 April 1975, leg. G. Michaloud, no. 84, RMNH 3759, ex *F. natalensis* Hochst. *leprieurii* (Miq.) Berg; 11 ♀, 1 ♂: Gabon, Makokou, 24 January 1978, leg. G. Michaloud, no 100 Bis, RMNH 3769, ex *F. natalensis* Hochst. *leprieurii* (Miq.) Berg; 2 ♀, 1 ♂: Gabon, Makokou, 15 February 1978, leg. G. Michaloud, no. 100 Bobine no. 2/7242, 120 m, RMNH 3760, ex *F. natalensis* Hochst. *leprieurii* (Miq.) Berg; 3 ♀: Gabon, Makokou, 15 February 1978, leg. G. Michaloud, no. 100 Bobine no. 3/7242, RMNH 3763, ex *F. natalensis* Hochst. *leprieurii* (Miq.) Berg; 5 ♀, 10 ♂: Gabon, Makokou, February 1978, RMNH 3823,

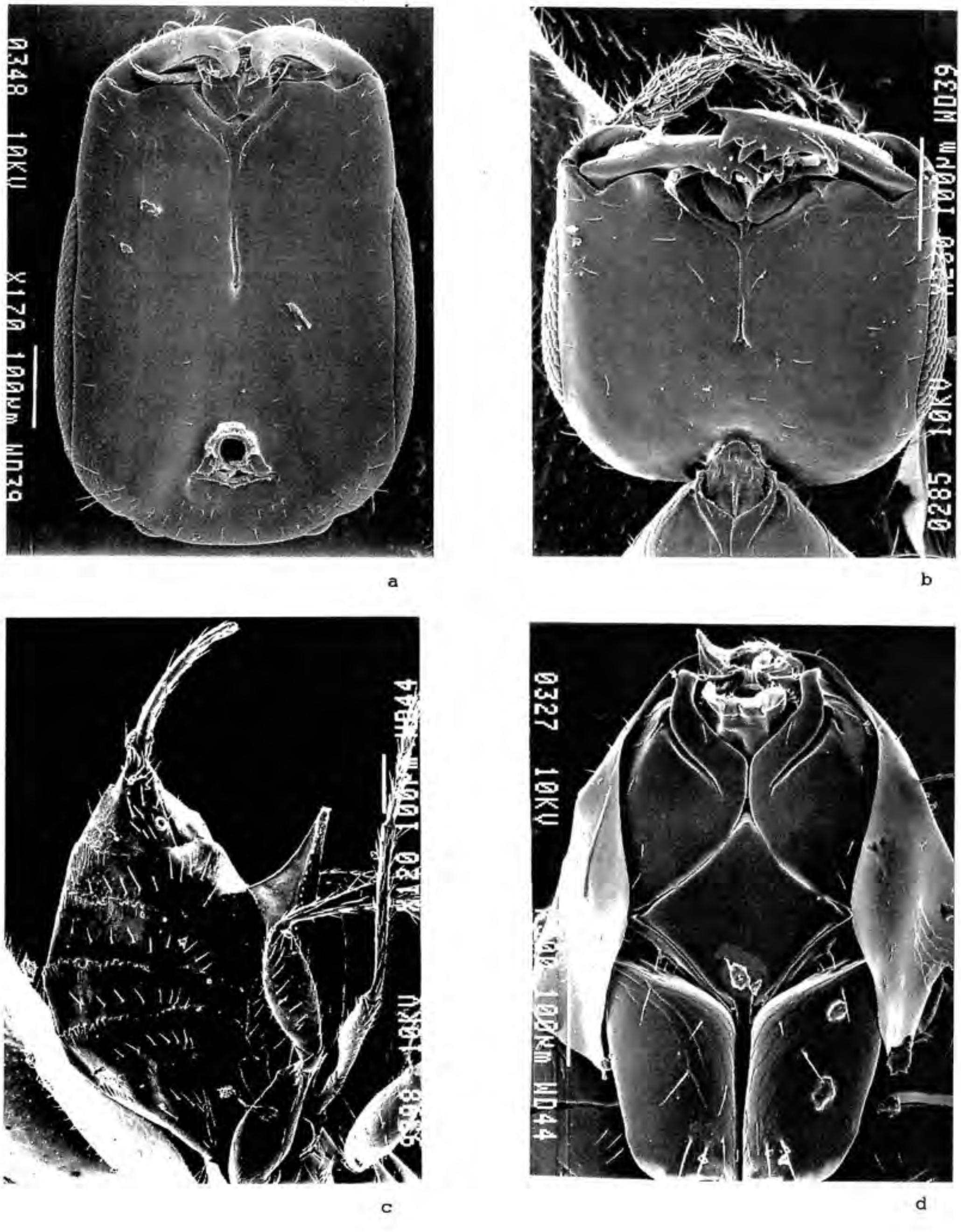


Fig. 9.11 a) *Philocaenus clairae* sp. nov., female head, ventral view b) *Philocaenus liodontus* (Wiebes), ex *F. craterostoma* Mildbr. & Burr., RMNH 3815, female head, ventral view c) *Philocaenus warei* sp. nov., female gaster, lateral view d) *Philocaenus medius* sp. nov., female propleura, prosternum and fore coxae, ventral view.

ex *F. natalensis* Hochst. *leprieurii* (Miq.) Berg; 8 ♀: Gabon, Makokou, April 1979, leg. G. Michaloud, RMNH 3815, ex *F. craterostoma* Mildbr. & Burret.; 30 ♀: Gabon, Makokou, 17 July 1977, leg. G. Michaloud, no. 24, RMNH 3734, ex *F. craterostoma* Mildbr. & Burret.; 25 ♀: Gabon, Makokou, 27 March - 1 April 1977, leg. G. Michaloud, no. Pl. 1, RMNH 3798, ex *F. lingua lingua* Wild. & Dur.; 10 ♀: Gabon, Makokou, 29 March - 1 April 1977, leg. G. Michaloud, no. Pl. 1, RMNH 3800, ex *F. lingua lingua* Wild. & Dur.; 20 ♀: same data, RMNH 3807; series ♀: South Africa, Natal, Hluhluwe Game Reserve, 2832AA, 9 December 1986, leg. S.G. Compton & A.J. Gardiner, C38, ex *F. stuhlmannii* Warb.; series ♀: Zambia, Lusaka, Cathedral, 25 January 1988, leg. R.J.F. Nefdt, C62, ex *F. stuhlmannii* Warb.; series ♀: South Africa, Natal, Tshongwe, 23 January 1990, leg. S. van Noort & A.B. Ware, C249, ex *F. stuhlmannii* Warb.; series ♀: South Africa, Natal, Mselini, 26 January 1990, leg. S. van Noort & A.B. Ware, C256, ex *F. stuhlmannii* Warb.; series ♀: Uganda, Entebbe, 23 April 1968, leg. D.S. Hill, tree no. 31, ex *Ficus "dekdeknena"*; 7 ♀ : Malawi, Mt. Mulanje Forestry Station, 7 July 1990, leg. S.G. Compton, C322, ex *F. thonningii* Bl.; 12 ♀, 22 ♂: South Africa, Durban, 1982, leg. H. Baijnath, RMNH 4663, ex *F. burtt-davyi* Hutch.; series ♀, ♂: South Africa, Transkei Wild Coast, Mkambati Nature Reserve, 8 April 1988, leg. S. Vincent & S.G. Compton, C55, ex *F. burtt-davyi* Hutch.; 5 ♀: South Africa, Durban, Treasure Beach, 19 June 1988, leg. H. Baijnath, RMNH 4965, ex *F. burtt-davyi* Hutch. (B-phase figs); series ♀, ♂: South Africa, Eastern Cape, Alexandria Forest, 17 September 1989, leg. S.G. Compton, C92, ex *F. burtt-davyi* Hutch.; series ♀, ♂: same data, C94; series ♀, ♂: same data, C135; series ♀, ♂: same data, C137; series ♀, ♂: same data, C138; series ♀, ♂: South Africa, Eastern Cape, Alexandria Forest, 14 May 1989, leg. S. van Noort, C139, ex *F. burtt-davyi* Hutch.; series ♀, ♂: same data, C140; 1 ♀: same locality, leg. S. van Noort & A.B. Ware, 21 May 1989, C141, ex *F. burtt-davyi* Hutch.; 1 ♀: South Africa, Natal, Manzengwenya, Foredunes opposite Island Rock, 25 November 1989, leg. M. Ward, C219, ex *F. burtt-davyi* Hutch.; series ♀, ♂: South Africa, Eastern Cape, Grahamstown, Botanical Gardens, 15 April 1990, leg. N. Deacon, C293, ex *F. burtt-davyi* Hutch.

Comments. As defined here *P. liodontus* is associated with at least six different *Ficus* species, but I cannot separate the specimens from the different tree species with any degree of confidence. The species is variable, but not necessarily in relation to its host trees. Thus, within the population from a single host species (e.g. *F. burtt-davyi* and *F. craterostoma*) there is geographical variation, or even variation between samples. For example, the specimens from *F. burtt-davyi* in Grahamstown (where *F. thonningii* is not a host tree) have a thick marginal vein separating this population from the rest of the *F. burtt-davyi* samples. However, specimens from *F. burtt-davyi* in Durban have a thinner marginal vein which is no thicker than the specimens from *F. thonningii* (in Malawi) or *F. stuhlmannii* (in Natal). The females from *F. craterostoma* (Gabon, RMNH 3815) have more elongate heads, L:W = 1.11, than those from *F. n. leprieurii* (Gabon), L:W = 1.00. But the specimens from *F. craterostoma* (Gabon, RMNH 3734) have an even broader head, L:W = 0.92. Given this variation, and that some of the host species only have one or two collections made from them it would be premature to describe any new species within what is likely to be a species complex.

***Philocaenus quatuordentatus* sp. nov.**

(figs. 9.12 b & c)

Etymology: Quatuor (latin) = four, dentatus (latin) = toothed, referring to the four ventral mandibular teeth.

Type material: Holotype ♀ (slide mounted): South Africa, Transvaal, Sibasa, Pipithi Waterfalls, 2230CD, 20 January 1987, leg. S.G. Compton & V.K. Rashbrook, C12, ex *F. craterostoma?* Mildbr. & Burret. Paratypes, 1 ♀ (slide mounted), 3 ♀ (card mounted): same data as holotype; 2 ♀: South Africa, Magoebaskloof, De Hoek State Forest, 1 September 1989, leg. S. van Noort & A.B. Ware, C144, ex *F. craterostoma?* Mildbr. & Burret.

FEMALE. Metallic black, flagellum dark brown, scape, mandibles and legs testaceous. Total length with head in orthognathous position, excluding ovipositor = 1.6 mm.

Head (fig. 9.12 b) approximately square (l = 0.45, w = 0.47, h = 0.20). Eye elongate (l = 0.23, w = 0.12, h = 0.06), 0.52X as long as head. Cheek length 0.47X eye length. Malar sulcas absent. POL = 0.15. OOL = 0.12. TE 0.83X as long as scrobe length (TE = 0.19, SL = 0.22). Clypeus equilateral in area. Epistomal margin laterally bilobed, concave with a medial convexity or tooth, approximately half the head width. Ventral tentorial pits in close apposition. Mandible with two apical teeth and four ventral teeth (fig. 9.12 c), two glands. Antenna as in *P. warei* (fig. 9.10 g), funicle segments subequal in size, flagella l = 0.33. Scape narrow, 5.8X longer than wide (l = 0.17). Pedicel elongate, 0.45X scape length.

Thorax. Pronotum broad (l = 0.25, w = 0.36). Propodeum l = 0.16, w = 0.33. Mesoscutum l = 0.2, w = 0.41. Scutellum, including axillae broad (l = 0.21, w = 0.34). Fore femur 3.3X as long as wide (l = 0.33). Fore tibial armature consists of a comb of four teeth on the dorso-apical margin as in *P. rotundus* (fig. 9.13 d). Fore leg coxa ca. three-quarters of femur length (C = 0.25, TR = 0.08, TI = 0.14, TA = 0.18). Six hind tibial spines on the dorsal margin. Fore wing 2.2X longer than wide, l = 1.18, pilose. Postmarginal vein subequal in length to stigmal (SM = 0.43, M = 0.16, PM = 0.09, S = 0.11). Marginal vein 7X longer than wide. Hind wing 4X longer than wide, l = 0.9.

Gaster, posterior edge of tergites very crenulated, with three medial incisions. Eighth urotergite spiracle normal (l = 0.02). Ovipositor 3.9X as long as valve (valve l = 0.24).

MALE. The few male specimens were in too poor a state of preservation for adequate description.

Philocaenus zambesiacus **sp. nov.**

(figs. 9.12 a, d-f)

Etymology: Named after a junior synonym, *F. zambesiaca*, of the host fig tree.

Type material: Holotype ♀, allotype ♂ (slide mounted): Malawi, North of Mangochi, 4 June 1990, leg. S.G. Compton, C1009, ex *F. bussei* Mildbr. & Burret. Paratypes, 1 ♀, 1 ♂ (slide mounted), 3 ♀, 2 ♂ (card mounted): same data as holotype.

FEMALE. Metallic greenish-black, antennae, hind coxae and femora dark brown, pedicel, scape and rest of legs testaceous. Total length with head in orthognathous position, excluding ovipositor valves = 2 mm.

Head (fig. 9.12 a) approximately square (l = 0.52, w = 0.57, h = 0.22). Eye very elongate (l = 0.28, w = 0.068, h = 0.13), 0.54X as long as the head. Cheek length 0.39X eye length. Malar sulcas absent. POL = 0.19. OOL = 0.13. TE 0.91X as long as scrobe length (TE = 0.22, SL = 0.24). Clypeus equilateral in area. Epistomal margin projecting, laterally bilobed with a broad shallow medial concavity and a slight medial convexity, width of margin 0.42X head width. Ventral tentorial pits. Mandible with two apical teeth and three ventral teeth, much as in *P. rotundus* (fig. 9.13 c). Two labial palp segments, segments subequal. Three maxillary palp segments, proximal segment longest. Antenna as in *P. warei* (fig. 9.10 g), funicle segments subequal in size, flagella l = 0.43. Scape narrow, 6X longer than wide (l = 0.24). Pedicel elongate, 0.42X scape length.

Thorax. Pronotum broad (l = 0.30, w = 0.50). Propodeum wider than long (l = 0.16, w = 0.45). Mesoscutum broad (l = 0.27, w = 0.53). Scutellum, including axillae broad (l = 0.30, w = 0.44). Fore tibial armature consists of a comb of four teeth on the dorso-apical margin, as in *P. rotundus* (fig. 9.13 d). Fore femur 3.1X longer than wide (l = 0.40). Fore leg coxa three-quarters of femur length (C = 0.30, TR = 0.10, TI = 0.18, TA = 0.24). Fore wing 2.4X longer than wide, l = 1.49, glabrous, fringe very short and weak. Postmarginal vein shorter than stigmal (SM = 0.55, M = 0.16, PM = 0.09, S = 0.11). Marginal vein 5.7X longer than wide. Hind wing 3.9X longer than wide, l = 1.1.

Gaster, posterior edge of tergites very crenulated, with three medial incisions. Eighth urotergite spiracle normal (l = 0.022). Ovipositor 2.7X as long as valve (valve = 0.62).

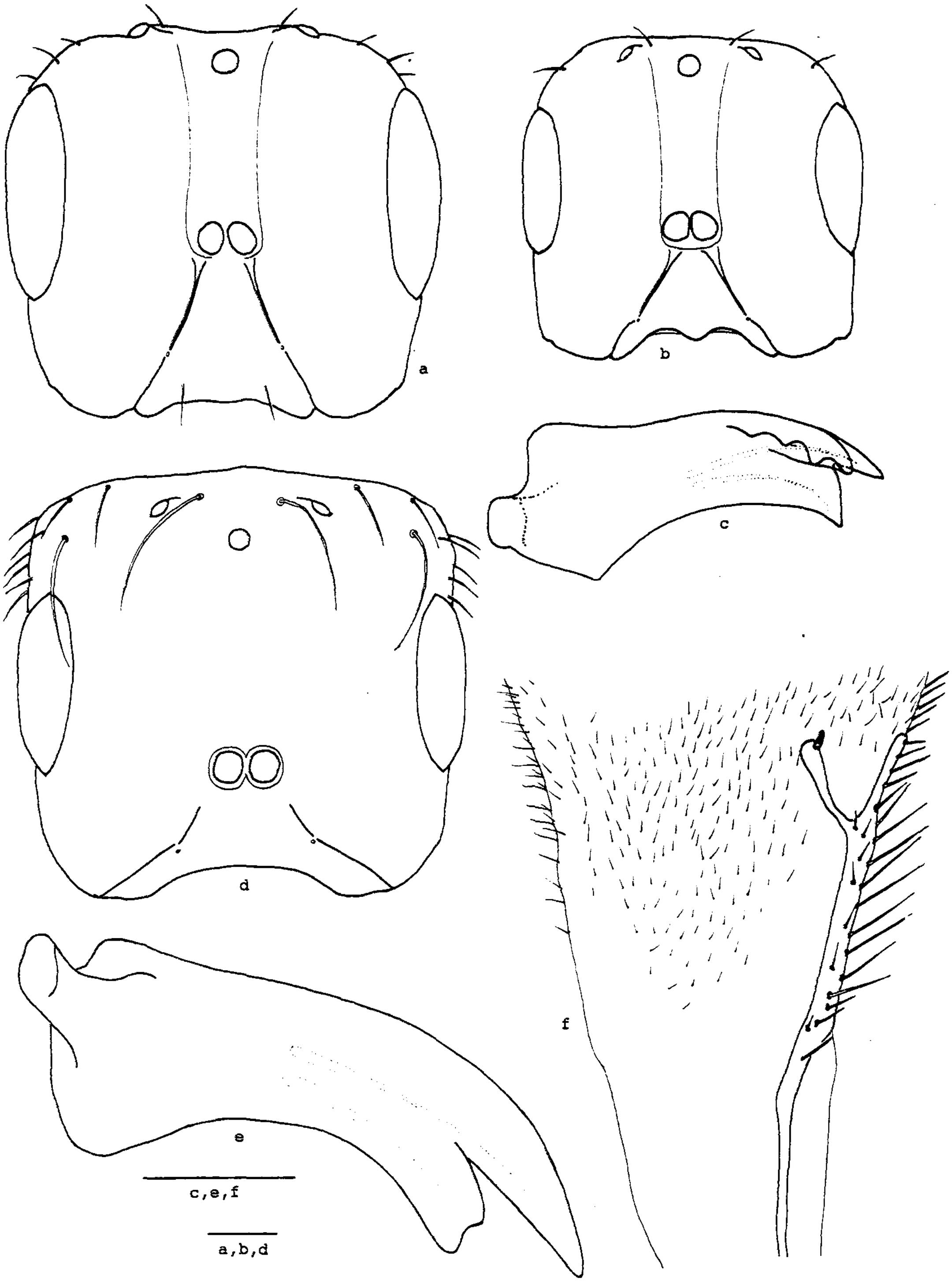


Fig. 9.12 a, d-f: *Philocaenus zambesiacus* sp. nov. a) female head, dorsal view d) male head, dorsal view e) male mandible, dorsal view f) male fore wing venation; b & c: *Philocaenus quatuordentatus* sp. nov. b) female head, dorsal view c) female mandible, ventral view. Scale bars = 0.1 mm.

MALE. Testaceous, axillae and eyes darker. Total length with head in orthognathous position excluding ovipositor 1.84 mm.

Head (fig. 9.12 d) broad (l = 0.57, w = 0.59, h = 0.32). Eye elongate (l = 0.23, w = 0.13, h = 0.063), 0.4X as long as head. Cheek length 0.44X eye length. Malar sulcas absent. POL = 0.18. OOL = 0.17. Toruli situated on imaginary line joining anterior margin of the eyes, touching. TE 0.34X as long as scrobe length (TE = 0.11, SL = 0.32). Clypeus equilateral in area. Epistomal margin laterally straight, with a broad and shallow medial concavity; width of margin 0.58X head width. Ventral tentorial pits in close apposition. Mandible (fig. 9.12 e). Labial and maxillary palp segments as in the female. Antenna as in *P. warei* (fig. 9.10 i), flagella length 2.2X as long as pedicel. Scape broad, 4.3X longer than wide (l = 0.30). Pedicel very elongate, 0.5X scape length.

Thorax. Parapsidal furrows incomplete. Fore femur 2.9X longer than wide, l = 0.47. Fore tibial armature bidentate. Fore tarsus subequal to tibial length (C = 0.38, TR = 0.13, TI = 0.31, TA = 0.29). Fore wing (fig. 9.12 f) 2.7X longer than wide, l = 1.59, pilose. Postmarginal vein subequal in length to stigmal (SM = 0.55, M = 0.26, S = 0.12, PM = 0.13). Marginal vein thick, 8.7X longer than wide. Hind wing 4.6X longer than wide, l = 1.25.

Gaster. Eighth urotergite spiracle normal. Aedeagus small (l = 0.35). Four teeth on aedeagus claspers.

Philocaenus rotundus **sp. nov.**

(figs. 9.13 a-h)

Etymology: Rotundus (latin) = round, referring to the roundness of the paraclypeal area.

Type material: Holotype ♀, allotype ♂ (slide mounted): South Africa, Natal, Road to Mkuzi Game Reserve, 15 December 1988, leg. S.G. Compton, C95, ex *F. abutilifolia* (Miq.) Miq. Paratypes, 5

♀, 5 ♂ (slide mounted), series ♀, ♂: same data as holotype; series ♀, 1 ♂: South Africa, Transvaal, Abel Erasmus Pass, R36, N. of Lydenburg, 2430BC, 22 October 1987, leg. S.G. Compton & P.R., C5, ex *F. abutilifolia* (Miq.) Miq.; 5 ♀, series ♂: South Africa, Transvaal, Giyani-Klein Letaba Road, Gazankulu, 2330BC, 18 October 1987, leg. S.G. Compton, C7, ex *F. abutilifolia* (Miq.) Miq.; series ♀, ♂: South Africa, Natal, Mkuzi Game Reserve, 2732CA, 7 December 1986, leg. S.G. Compton, C36, ex *F. abutilifolia* (Miq.) Miq.; 6 ♀, 3 ♂: Malawi, Island off Monkey Bay, 20 June 1988, leg. M.F., C70, ex *F. abutilifolia* (Miq.) Miq.; series ♀, ♂: Zimbabwe, Kariba Border Post, 20 December 1988, leg. P. Lloyd, C121, ex *F. abutilifolia* (Miq.) Miq.; series ♀, ♂: Botswana, Tuli Block, above river bed, leg. P. Lloyd, C123, ex *F. abutilifolia* (Miq.) Miq.; series ♀, 2 ♂: Zimbabwe, Kariba Border Post, 20 December 1988, leg. P. Lloyd, C124, ex *F. abutilifolia* (Miq.) Miq.; series ♀, 1 ♂: South Africa, Pretoria, National Botanical Gardens, 31 August 1989, leg. S. van Noort & A.B. Ware, C163, ex *F. abutilifolia* (Miq.) Miq.; series ♀, 4 ♂: South Africa, Pretoria, National Botanical Gardens, 19 October 1989, leg. S. van Noort, C197, ex *F. abutilifolia* (Miq.) Miq.; 7 ♀, 1 ♂: South Africa, Transvaal, Hoedspruit, nr. Middlesex Farm, 18 November 1989, leg. M. Ward, C218, ex *F. abutilifolia* (Miq.) Miq.; 2 ♀: South Africa, Jozini, 21 January 1990, leg. S. van Noort and A.B. Ware, C238, ex *F. abutilifolia* (Miq.) Miq.; series ♀, ♂: same data, C239; series ♀, ♂: same data, C240; 1 ♀, 1 ♂: South Africa, Natal, Ingwavuma, 23 January 1990, leg. S. van Noort & A.B. Ware, C245, ex *F. abutilifolia* (Miq.) Miq.; series ♀, ♂: South Africa, Natal, Ubombo, 27 January 1990, leg. S. van Noort & A.B. Ware, C263, ex *F. abutilifolia* (Miq.) Miq.

FEMALE. Head, thorax, hind and mid coxa and gaster metallic greenish-black; forelegs testaceous; antennae, mandibles and mid and hind legs darker brown.

Head (fig. 9.13 a & b) approximately square (l = 0.18, w = 0.58), height compressed (h = 0.18). Eye very elongate (l = 0.32, w = 0.12, h = 0.07), 0.58X as long as the head. Cheek length 0.3X eye length. Malar sulcus absent. POL = 0.20. OOL = 0.13. TE 0.86X as long as scrobe length (TE = 0.24, SL = 0.28). Clypeus equilateral in area. Epistomal margin broadly bilobed with a slight medial convexity, width of margin ca. two-fifths of head width. Ventral tentorial pits in close apposition (fig. 9.13 b). Mandible with two apical teeth and three ventral teeth, two glands (fig. 9.13 c). Two labial palp segments, proximal segment longest. Three maxillary palp segments, proximal segment twice as long as distal two combined. Antenna much as in *P. warei* (fig. 9.10g), funicle segments subequal in size, flagella l = 0.38. Scape narrow, 7.9X longer than wide (l = 0.24). Pedicel elongate, 0.42X scape length.

Thorax. Pronotum broad (l = 0.34, w = 0.49). Propodeum wider than long (l = 0.17, w = 0.45). Mesoscutum broad (l = 0.28, w = 0.53). Scutellum, including axillae broad (l = 0.30, w = 0.43). Fore femur 2.8X as long as wide (l = 0.40). Fore tibial armature consists of a comb of four teeth on the dorso-apical margin (fig. 9.13 d). Fore leg coxa ca. three quarters of femur length (C = 0.29, TR = 0.12, TI = 0.17, TA = 0.22). Eight hind tibial spines on the dorsal margin. Fore wing 2.3X as long as broad (l = 1.42), sparsely setous, fringe short. Postmarginal vein same length as stigmal (SM = 0.52, M = 0.21, PM = 0.12, S = 0.12). Marginal vein 7.3X as long as wide. Hind wing 3.8X as long as broad (l = 1.13).

Gaster, posterior edge of tergites very crenulated, with three medial incisions. Eighth urotergite spiracle normal (l = 0.023). Ovipositor 3.7X as long as valve (valve l = 0.33).

MALE. Testaceous, with eyes, mandibles, parapsides, scutellum and axillae dark brown. Total length with head in orthognathous position excluding ovipositor 1.67 mm.

Head (fig. 9.13 e & f) approximately square (l = 0.50, w = 0.48), height normal (h = 0.23). Eye elongate (l = 0.25, w = 0.13, h = 0.06), 0.5X as long as the head. Cheek length 0.28X eye length. Malar sulcas absent. POL = 0.15. OOL = 0.12. Toruli situated between the eyes, touching. TE 0.52X as long as scrobe length (TE = 0.14, SL = 0.27). Clypeus equilateral in area. Epistomal margin flat laterally, shallow medial concavity with a slight medial convexity. Ventral tentorial pits in close apposition (fig. 9.13 f). Mandibular subapical tooth wide (fig. 9.13 g). Labial and maxillary palp segments as in the female. Antenna (fig. 9.13 h), flagella 2.6X longer than the pedicel. Scape narrow, 6.4X longer

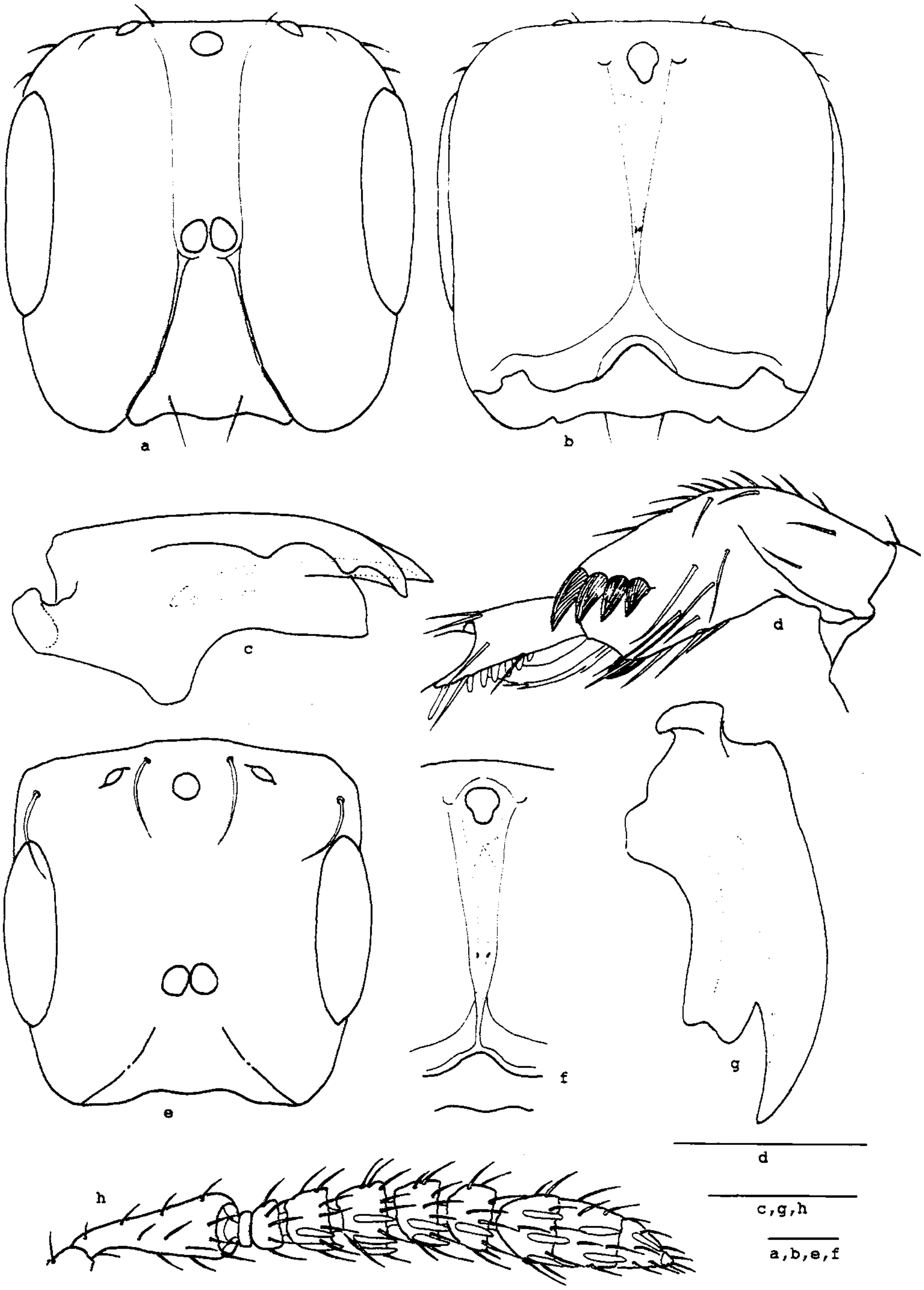


Fig. 9.13 a-h: *Philocaenus rotundus* sp. nov. a) female head, dorsal view b) female head, ventral view c) female mandible, ventral view, d) female fore tibia and first tarsal segment, antiaxial view e) male head, dorsal view f) male head, ventral view g) male mandible, dorsal view h) male antenna axial view. Scale bars = 0.1 mm.

than wide (l = 0.22). Pedicel very elongate, 0.49X scape length.

Thorax. Parapsidal furrows incomplete. Fore femur 3X as long as wide (l = 0.40). Fore tibial armature bidentate. Fore tarsus subequal in length to tibia (C = 0.32, TR = 0.12, TI = 0.25, TA = 0.23). Fore wing 2.6X longer than wide, l = 1.42, very pilose. Postmarginal vein subequal in length to stigmal (SM = 0.52, M = 0.21, S = 0.12, PM = 0.11). Marginal vein thick, 7X longer than wide. Hind wing 4.9X longer than wide, l = 1.08.

Gaster. Eighth urotergite spiracle normal. Aedeagus large (l = 0.34). Five teeth on aedeagus claspers.

10

PARALLELISM AND CONVERGENCE IN THE SYCOECINAE AND AGAONINAE

INTRODUCTION

Homoplasies are regarded by most cladists as simply incongruent characters that are in conflict with the most parsimonious solutions to phylogenetic questions (Farris, 1983). Some cladists even go so far as to advocate that these homoplasies should be identified before the analysis and reweighted or excluded (Hecht & Edwards, 1976; Gosliner & Ghiselin, 1984; Gosliner, 1985). In contrast the successive weighting option (Farris, 1988) as utilised in the phylogenetic analysis of the Sycoecinae (Chapter 4) assigns low weights to homoplasious characters only after these have been identified by an initial phylogenetic analysis. Other cladists regard certain parallelisms to be the result of an inherited capacity within a monophyletic group to develop similar structures even though not all members of the group possess the structure, and then utilise these parallelisms to define the group, terming them underlying synapomorphies (Saether, 1979; 1983; 1986; Sluys, 1989).

Parallelism, convergence and reversal are the three kinds of homoplasy recognised by systematists (Futuyma, 1986). Parallelism has been reported in taxa as diverse as marine triclads (Maricola) (Sluys, 1989), opisthobranch gastropods (Gosliner & Ghiselin, 1984), Chironomidae (Saether, 1979a), drosophilid flies (Lachaise & McEvey, 1990) and proteid salamanders (Hecht & Edwards, 1976). Parallelism and convergence are recognised here as distinct phenomena, although authors such as Eldredge & Cracraft (1980) regard the concepts as synonymous. It is therefore necessary to make the distinction clear. The definition utilised by Sluys (1989) is adhered to in this thesis and is as follows: convergence is due to analogous similarity, whereas parallelism is due to homologous similarity. Hecht & Edwards (1976) and Saether (1983) advocated similar distinctions between the two concepts. Convergence is thus the evolution of superficially similar characters that perform the same function, but whose origins and development are different, whereas parallelism results from the independent evolution of the same character state in two different, but related lineages. Reversal is the reversion of a character to a previous ancestral state from a derived state. Reversals can result in parallelisms, although it is unlikely that convergence would be the result of a reversal, due to the morphological complexity that is often characteristic of convergent characters.

Convergence does not rely on a cladogram for identification. Careful observation of the characters will usually reveal differences between what superficially appear to be homologous characters. Parallelism on the other hand is more difficult to ascertain. Since, by definition, two independent derivations of a character state are homologous, and thus morphologically identical, they will not be identifiable by observation. Parallelisms can therefore only be recognised once a parsimonious phylogeny has identified homoplasious characters (Wheeler & Blackwell, 1984; Sluys, 1989). If the homoplasy cannot be resolved by reassessment of the character's polarity, or morphological reinterpretation, which may reveal convergence, then it is reasonable to assume that the homoplasy is due to parallelism or reversal. Examination of character state transitions on the cladogram will identify reversals, which may also be parallelism. The conclusion of parallelism can be further substantiated if an environmental condition can be identified that provides selection pressures which act on both of the lineages that have evolved characters in parallel (Wheeler & Blackwell, 1984).

The fig ostiole clearly provides a strong selection pressure on fig wasps, as it has resulted in the evolution of some remarkable morphological adaptations to facilitate their entry into the figs. These include the elongation of the head and the development of rows or plates of backward pointing teeth on the mandible and/or the fore tibia (Ramirez, 1976). Both the Sycoecinae and the Agaoninae enter the figs to oviposit and are thus subjected to the same selection pressures. Similar adaptations have evolved more than once, in a number of different lineages, resulting in examples of both parallelism and convergence within and between these two subfamilies.

This chapter identifies parallelism indicated by the phylogenetic analysis of the Sycoecinae and highlights several instances of convergent evolution.

MATERIALS AND METHODS

The heads of females of eighteen agaonine and twenty-seven sycoecine species were measured using an ocular micrometer. Measurements of nine additional species were obtained from the literature. The wasps were associated with twenty-five African *Ficus* species of subgenus *Urostigma*, section *Galoglychia*. Each of the agaonine species had one to three associated sycoecine species. Head length was measured as the maximum length and head width as the greatest width, which was across the compound eyes. Where possible, measurements of the wasps associated with a particular tree species were made from specimens obtained from the same crop. This reduced the possible effects of inter-crop or geographical variation in wasp size. Two to ten specimens (depending on availability) of each species were measured and the mean values calculated. The degree of correlation between the head shape of the sycoecines and agaonines was determined using regression analysis.

Measurements of fig size were obtained from the literature (Berg, 1986; Berg & Hijman, 1989; Berg *et al.*, 1984; Berg *et al.*, 1985). The maximum diameters recorded by Berg for fresh and dry figs were used as separate indices of fig size. The relationships between agaonine head shape and each of the indices of fig size and between sycoecine head shape and each of the indices of fig size were examined using regression analysis. Fresh fig measurements were not available for *F. antandronarum bernardii* Berg, *F. reflexa* Thunb., *F. tesselata* Warb., and *F. sagittifolia* Berg. Dry fig measurements were not available for *F. lyrata* Warb. These species and their associated fig wasps were consequently not included in the appropriate analyses.

Parallelisms were identified by the phylogenetic analysis carried out on the Sycoecinae (Chapter 4). Superficially similar characters were identified as being the result of convergent evolution through morphological examination using light microscopy and scanning electron microscopy.

RESULTS

Within the Sycoecinae, various character states have evolved independently on a number of occasions. Based on the cladogram of the Sycoecinae (Chapter 4) the following six parallelisms can be identified: 1) the reversal to a square head shape has occurred independently in the ancestor of *Diaziella*, within *Crossogaster* and in the ancestor of *Philocaenus*; 2) derived species of *Crossogaster* and *Philocaenus* have independently evolved antennae with 2 anelli, 4 funicle segments and the same multiporous plate sensilla size, number and positioning; 3) the development of a ventral plate of teeth on the mandibles has evolved in both *Crossogaster* as well as *Philocaenus* (figs. 10.1 a & b); 4) testaceous body colouring in the females (presumably associated with nocturnal flight) has arisen independently in *Diaziella* and *Crossogaster*; 5) a crenulated posterior edge to the tergites has evolved in *Crossogaster* and *Philocaenus*; 6) an homologous plate of fine teeth, fused for much of its length to the fore tibia, has evolved independently in *Seres* and

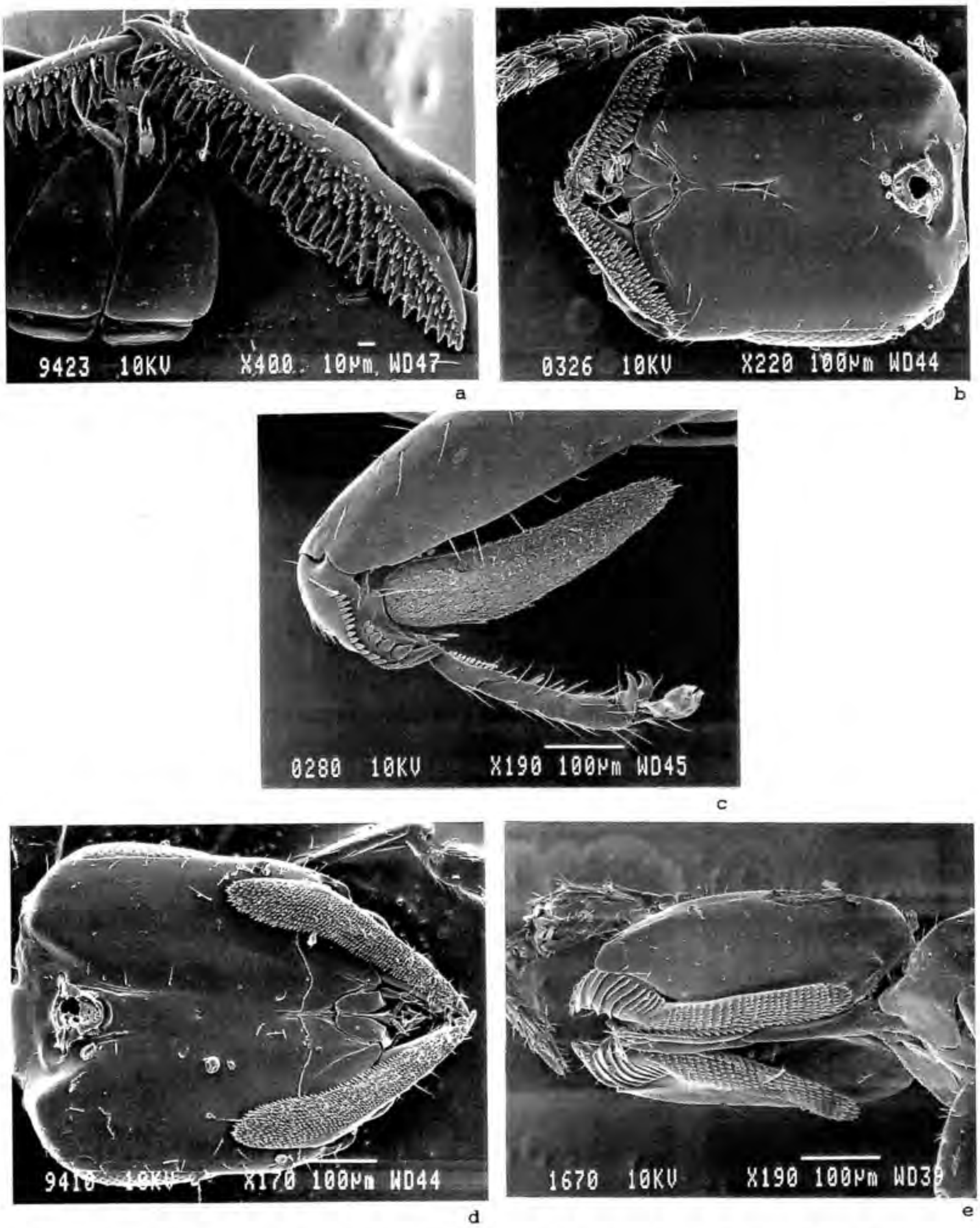


Fig. 10.1. Convergence and parallelism in the Sycoecinae (a-d) and the Agaoninae (e). a) Crossogaster praeacuta sp. nov., female mandible, ventral aspect, showing parallelism of mandibular structure with that of b) *Philocaenus medius* sp. nov., female head, ventral view; c) *Sycoecus wiebesi* sp. nov., female fore tibia and tarsus, showing the convergent development of an expanded fore tibial spur in *Sycoecus*; d) *Philocaenus hippopotomus* sp. nov., female head, ventral view, showing convergence of mandibular morphology with that of the Agaoninae, for example - e) *Elisabethiella* sp., female head, ventral view.

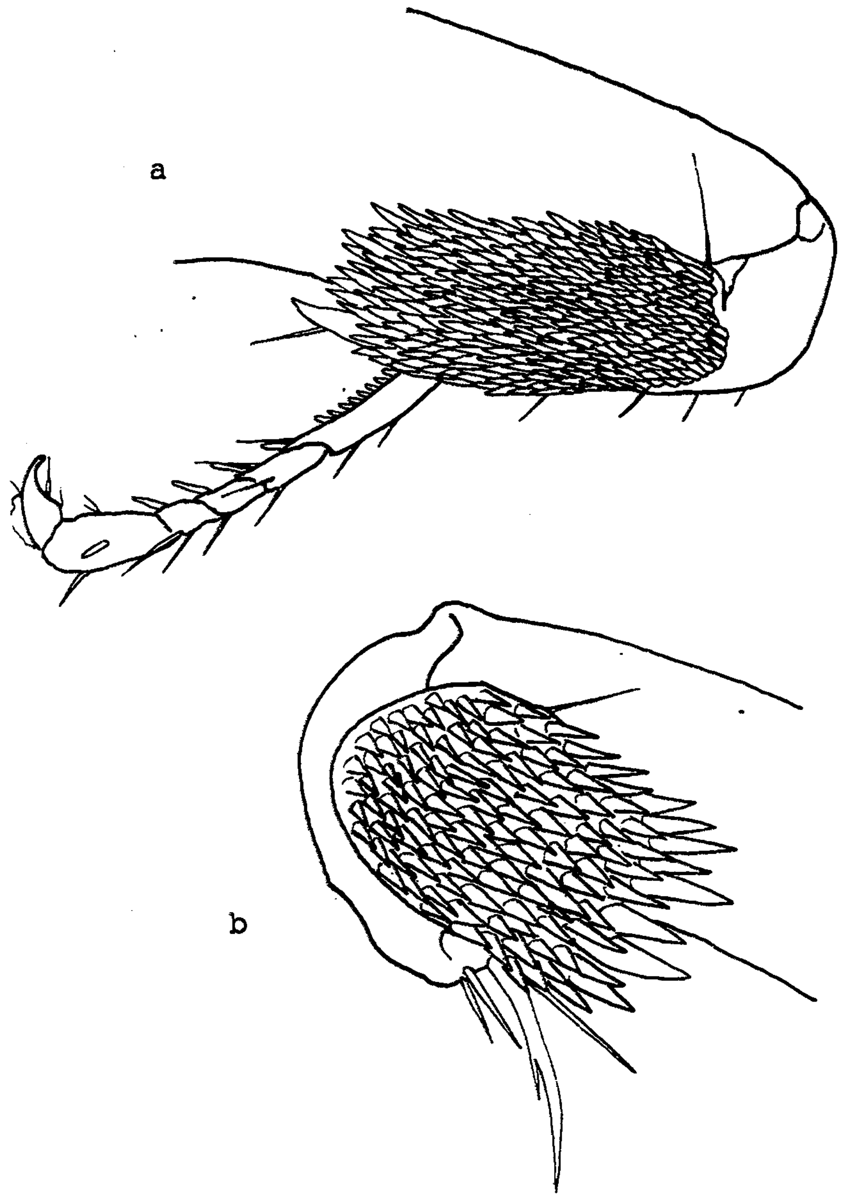


Fig. 10.2. Parallelism a) *Seres wardi* sp. nov., fore tibia and tarsus, antiaxial view, showing the parallel development of the plate of teeth with that of b) *Philocaenus cavus* sp. nov., fore tibia, with the tarsus missing, anterior view.

TABLE 10.1. Species of fig wasps studied and their host relationships. Head shape = average head length to head width ratio. * denotes ratio obtained from the literature. Ranges indicate the extreme head shapes recorded. These were not available when values were obtained from the literature.

HOST *FICUS* AGAONINE SPECIES	**AVERAGE HEAD WIDTH (mm)/HEAD SHAPE/RANGE**	**ASSOCIATED SYCOECINE**	**AVERAGE HEAD WIDTH (mm)/HEAD SHAPE/RANGE**	**SAMPLE LOCALITY**
SUBSECTION GALOGLYCHIA				
Allotriozoon		***Philocaenus***		
1. *F. chlamydocarpa* Mildbr. & Burret		***P.*** *comptoni* sp. nov.	0.426/1.14/1.12-1.15	Bambili, Cameroon
A. *nigeriense* Wiebes	0.488/1.33/1.26-1.40			
2. *F. lutea* Vahl	0.505/1.06/1.04-1.09	***P.*** *silvestrii* (Grandi)	0.570/0.95/0.93-0.97	Umhlanga Rocks, South Africa
A. *heterandromorphum* Grandi				
SUBSECTION PLATYPHYLLAE				
Elisabethiella, Alfonsiella		***Philocaenus, Crossogaster***		
3. *F. bussei* Mildbr. & Burret ***Elisabethiella*** sp.	0.564/0.84/0.78-0.88	***P.*** *zambesiacus* sp. nov.	0.600/0.90/0.88-0.92	Salima-Monkey Bay Road, Malawi
4. *F. glumosa* Delile		***C.*** *quadrata* sp. nov.	0.409/0.97/0.95-0.99	Hluhluwe, South Africa
E. *glumosae* Wiebes	0.342/0.96/0.94-0.98	***C.*** *stigma* sp. nov.	0.365/1.03/1.01-1.05	
		P. *warei* sp. nov.	0.414/1.03/1.02-1.04	

5. *F. stuhlmannii* Warb		**C.** *odorans* Wiebes	0.426/0.96/0.94-0.99	Hluhluwe, South Africa
A. *binghami* Wiebes	0.384/1.08/1.08-1.09	**P.** *liodontus* sp. nov.	0.442/1.07/1.05-1.09	
		P. *barbarus* Grandi	0.472/0.99/0.97-1.03	
6. *F. abutilifolia* (Miq.) Miq.		**P.** *rotundus* sp. nov.	0.545/1.00/0.99-1.04	Mkuzi, South Africa
E. *comptoni* Wiebes	0.503/0.95/0.92-0.97			
7. *F. trichopoda* Baker		**C.** *r. robertsoni* sp. nov.	0.455/1.16/1.14-1.19	Kosi Bay, South Africa
E. *bergi breviceps* Wiebes	0.447/1.08/1.01-1.10	**P.** *hippopotamus* sp. nov.	0.433/1.34/1.32-1.36	
SUBSECTION CHLAMYDODORAE				
Elisabethiella*, *Alfonsiella		***Philocaenus*, *Crossogaster***		
8. *F. craterostoma* Mildbr. & Burr.		**P.** *insolitus* sp. nov.	0.348/1.00/0.99-1.02	Makokou, Gabon
A. *michaloudi* Wiebes	0.370/0.96*	**P.** *liodontus* (Wiebes)	0.338/1.11/1.08-1.13	
9. *F. n. natalensis* Hochst.		**P.** *medius* sp. nov.	0.426/1.33/1.31-1.34	Kosi Bay, South Africa
A. *longiscapa* Joseph	0.369/1.22/1.21-1.26	**C.** *lurida* sp. nov.	0.414/1.01/1.00-1.03	
10. *F. n. leprieurii* (Miq.) Berg		**P.** *liodontus* (Wiebes)	0.400/1.00*	Makokou, Gabon
A. *fimbriata* Waterston	0.330/0.97*			
11. *F. burtt-davyi* Hutch.		**P.** *liodontus* (Wiebes)	0.353/1.02/0.99-1.04	Grahamstown, South Africa
E. *baijnathi* Wiebes	0.355/0.80/0.76-0.83			
12. *F. antandronarum bernardii* Berg		**P.** *comorensis* sp. nov.	0.31/1.50/1.36-1.56	Grande Comore, Comores
Elisabethiella sp.	0.321/1.24/1.15-1.27			

13. *F. reflexa* Thunb.		**P.** *bouceki* (Wiebes)	0.429/1.30*	La Reunion
E. *reflexa* Wiebes	0.312/1.21*			
14. *F. thonningii* Bl.		**C.** *odorans* Wiebes	0.356/1.00*	Grahamstown, South Africa
E. *stuckenbergi* Grandi	0.397/0.99/0.95-1.00	**P.** *barbarus* (Grandi)	0.399/1.03/1.00-1.07	
SUBSECTION CYATHISTUPULAE				
Agaon		***Sycoecus***		
15. *F. tesselata* Warb.		**S.** *bergi* sp. nov.	0.440/1.51/1.44-1.61	Cavally River, Liberia
A. *taiense* Wiebes	0.520/1.50*			
16. *F. c. cyathistipula* Warb.		**S.** *thaumastocnema* Waterston	0.430/1.65/1.62-1.67	Mpanga Forest, Uganda
A. *fasciatum* Waterston	0.510/1.51/1.46-1.56			
17. *F. c. pringsheimiana* (Braun & Schum.)		**S.** *oculabulbus* sp. nov.	0.534/1.43/1.43-1.44	Bambili, Cameroun
A. *kiellandi* Wiebes	0.515/1.25*			
18. *F. lyrata* Warb.		**S.** *crinitus* sp. nov.	0.480/1.81/1.82-1.85	Taï, Ivory Coast
A. *spatulatum* Wiebes	0.520/1.69*			
19. *F. sagittifolia* Berg		**S.** *lamtoensis* sp. nov.	0.468/1.56/1.55-1.58	Lamto, Ivory Coast
A. *c. cicatriferens* Wiebes	0.570/1.40*			
SUBSECTION CAULOCARPAE				
Courtella		***Philocaenus, Crossogaster, Seres***		
20. *F. ottoniifolia lucanda* (Ficalho) Berg		**P.** *levi* (Waterston)	0.451/1.43*	Uganda
C. *scobinifera* (Waterston)	-/1.23*			

21. *F. t. tremula* Warb. ***C.*** *wardi* Compton	 0.470/1.20/1.17-1.24	***P.*** *clairae* sp. nov.	0.386/1.61/1.59-1.63	Sihangwane, South Africa
22. *F. artocarpoides* Warb. ***C.*** *penicula* (Wiebes)	 0.586/1.61/1.59-1.64	***C.*** *michaloudi* Wiebes	0.572/1.56/1.51-1.60	Mpanga Forest, Uganda
23. *F. s. macrosperma* (Mildbr. & Burret) Berg ***C.*** *armata* (Wiebes)	 0.600/1.66/1.63-1.68	***S.*** *l. longivena* sp. nov. ***C.*** *inusitatus* sp. nov.	0.498/1.85/1.84-1.87 0.572/1.59/1.57-1.61	Kabompo, Zambia
24. *F. bubu* Warb. ***C.*** *michaloudi* (Wiebes)	 0.603/1.47/1.41-1.51	***S.*** *wardi* sp. nov.	0.584/1.34/1.33-1.35	Lake Sibaya, South Africa
25. *F. ovata* Vahl ***C.*** *hamifera modesta* (Wiebes)	 0.592/1.59/1.54-1.62	***S.*** *armipes breviceps* Wiebes	0.462/1.83/1.80-1.86	Entebbe, Uganda

SUBSECTION UNKNOWN

Elisabethiella

26. *Ficus* sp. K ***E.*** *hilli* Wiebes	 0.440/1.23/1.19-1.26	***C.*** *rastellus* sp. nov. ***P.*** *jinjaensis* sp. nov.	0.517/1.24/1.21-1.26 0.479/1.25/1.24-1.26	Jinja, Uganda

Philocaenus (fig. 10.2).

Similar mandibular and tibial armature has evolved convergently several times. A plate of fine teeth has evolved as an appendage to the tibia in the *Sycoecus* species (fig. 10.1 c), which is analogous to the plate of fine teeth which is present on the fore tibia of *Seres wardi* sp. nov., *Philocaenus comptoni* sp. nov. and *Philocaenus cavus* sp. nov. (fig. 10.2). The *Sycoecus* structure has developed from the tibial spur whereas in the other cases the structure is fused to the tibia, probably having evolved from the condition of a comb of teeth, which is present on the dorsoapical margin of the tibia in many *Philocaenus* species. The plate of ventral teeth on the mandible which has evolved independently in *Crossogaster* and *Philocaenus* (fig. 10.1 d), is analogous to the mandibular plate in the Agaoninae (fig. 10.1 e), as is the tibial plate in *Sycoecus* and *Philocaenus*, which serve the same function during ostiolar entry.

All these structures aid the wasp in ostiolar penetration, primarily by preventing the wasp slipping backwards when it squeezes its way through the tight ostiole (Ramirez, 1974; Janzen, 1979). The mandibles, through their opening and closing, are used to actively pull the wasp through the ostiole.

The head measurements of the wasps are shown in Table 10.1. Sycoecine head shape (length:width) was strongly correlated with that of their associated agaonine (fig. 10.3; correlation coefficient = 0.89; $P < 0.001$). Parallel variation in head shape was evident both within and between genera (figs. 10.4-10.7).

The sycoecine species fell into two main groups in terms of head shape relative to that of their associated agaonines. Those associated with smaller figs, such as most *Crossogaster* species and *Philocaenus* species, had a square or moderately elongate head shape, corresponding with their associated agaonine genera *Alfonsiella*, *Allotriozoon* and *Elisabethiella*, but their heads

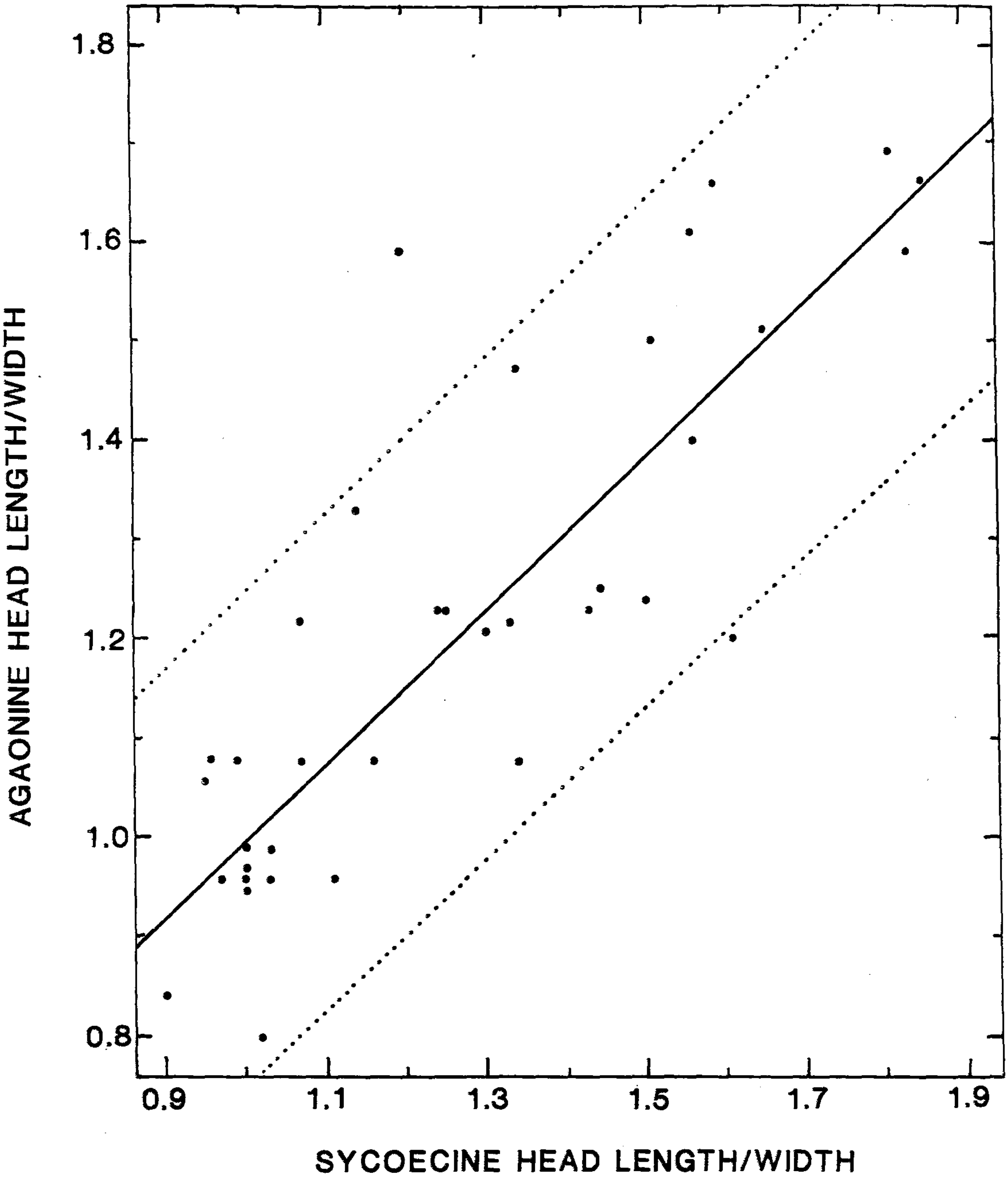


Fig. 10.3. The relationship between the head shapes of female sycoecine and agaonine fig wasp pairs from the same *Ficus* host species. The line of best fit is y = 0.06 + 1.00x. Dotted lines indicate the 95% confidence limits.

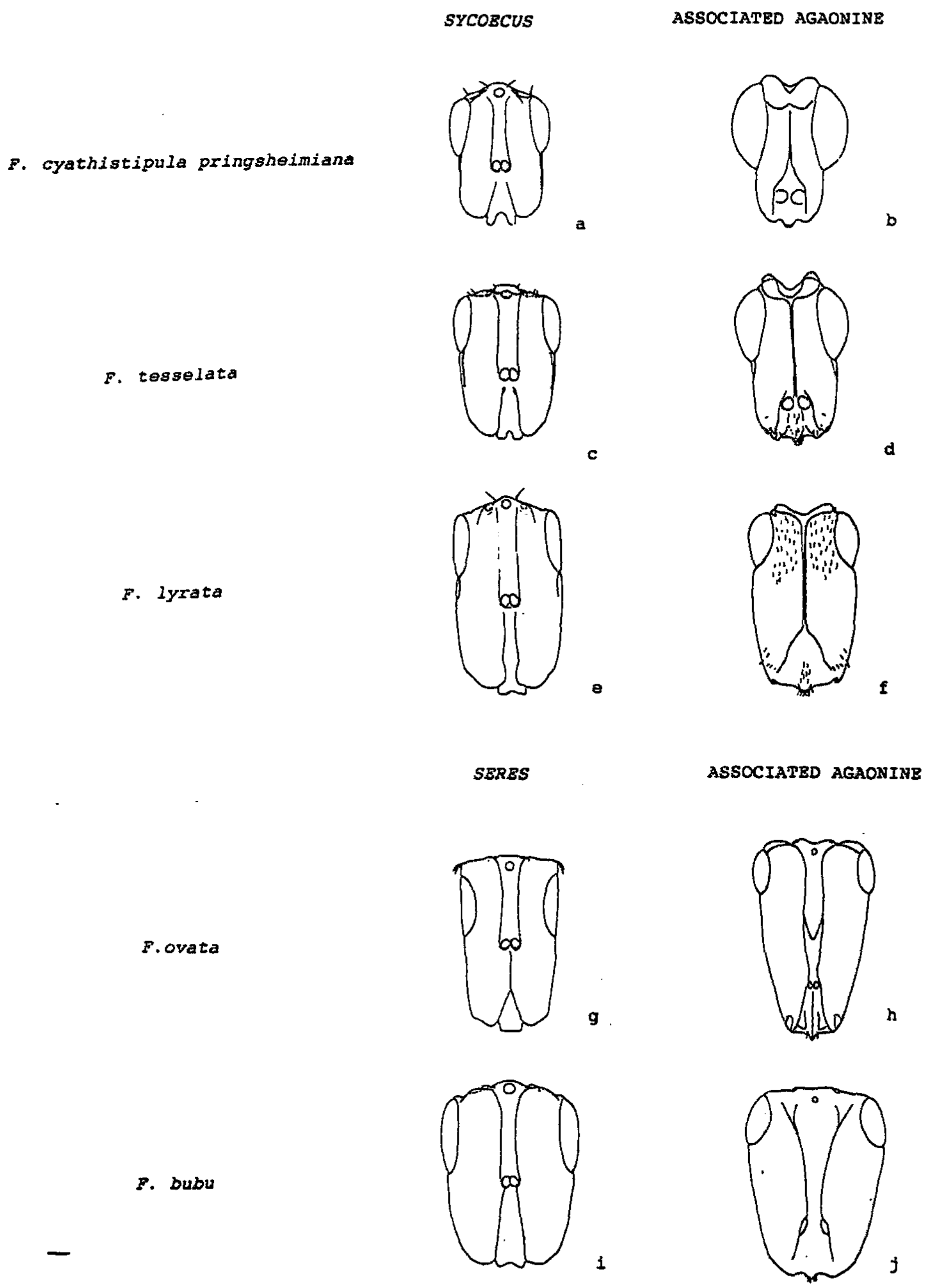


Fig. 10.4. Representatives of *Sycoecus* and their associated Agaoninae (a-f), and *Seres* and their associated Agaoninae (g-j), depicting head shape similarity of the wasps from the same host *Ficus* species. a) *Sycoecus oculabulbus* sp. nov. b) *Agaon kiellandi* Wiebes c) *Sycoecus bergi* sp. nov. d) *Agaon taïensis* Wiebes e) *Sycoecus crinitus* sp. nov. f) *Agaon spatulatum* Wiebes g) *Seres a. breviceps* Wiebes h) *Courtella hamifera modesta* (Wiebes) i) *Seres wardi* sp. nov. j) *Courtella michaloudi* (Wiebes). Scale bar = 0.1mm. Agaoninae redrawn from Wiebes (1961; 1968; 1974a; 1979a; 1989a).

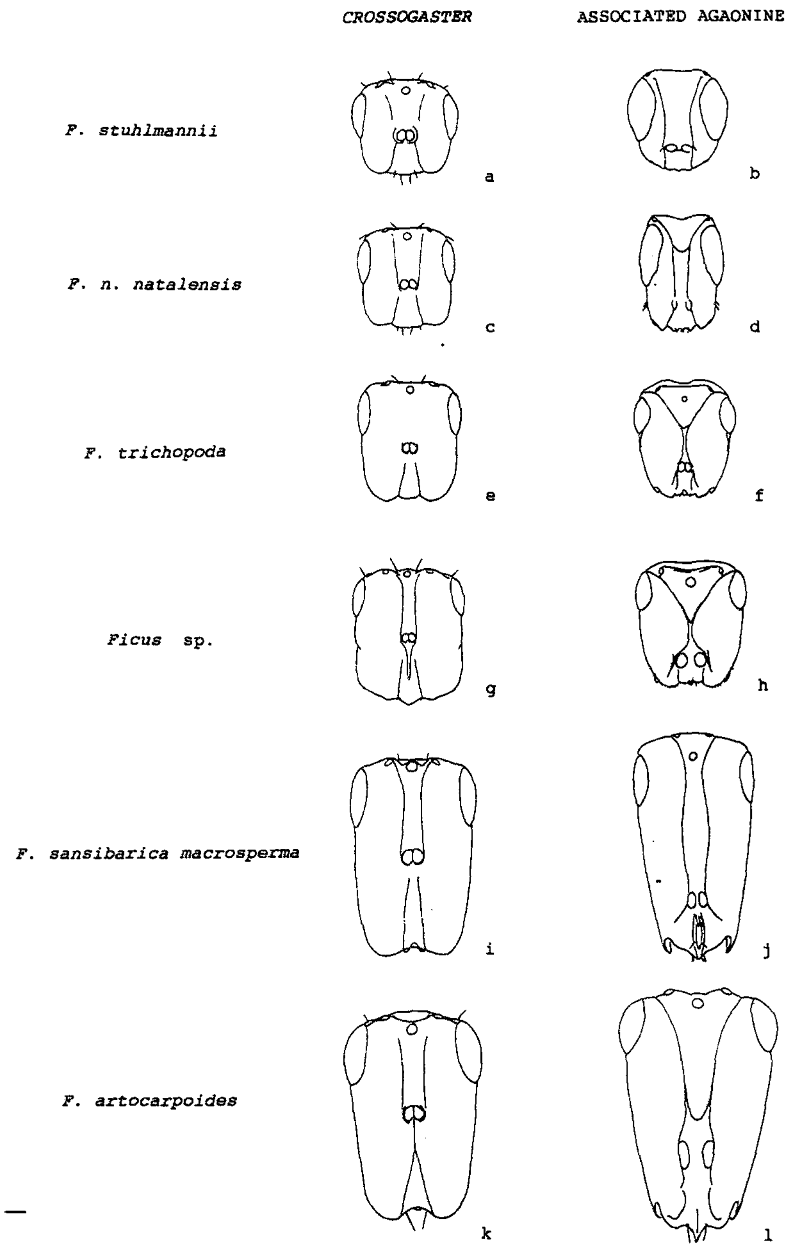


Fig. 10.5. Representatives of *Crossogaster* and their associated Agaoninae, depicting head shape similarity between the wasps from the same host *Ficus* species. a) *Crossogaster odorans* Wiebes b) *Alfonsiella binghami* Wiebes c) *Crossogaster lurida* sp. nov. d) *Alfonsiella longiscapa* Joseph e) *Crossogaster r. robertsoni* sp. nov. f) *Elisabethiella bergi breviceps* Wiebes g) *Crossogaster praeacuta* sp. nov. h) *Elisabethiella hilli* Wiebes i) *Crossogaster inusitata* sp. nov. j) *Courtella armata* (Wiebes) k) *Courtella michaloudi* (Wiebes) l) *Courtella penicula* (Wiebes). Scale bar = 0.1mm. Agaoninae redrawn from Wiebes (1972; 1974a; 1988; 1989b).

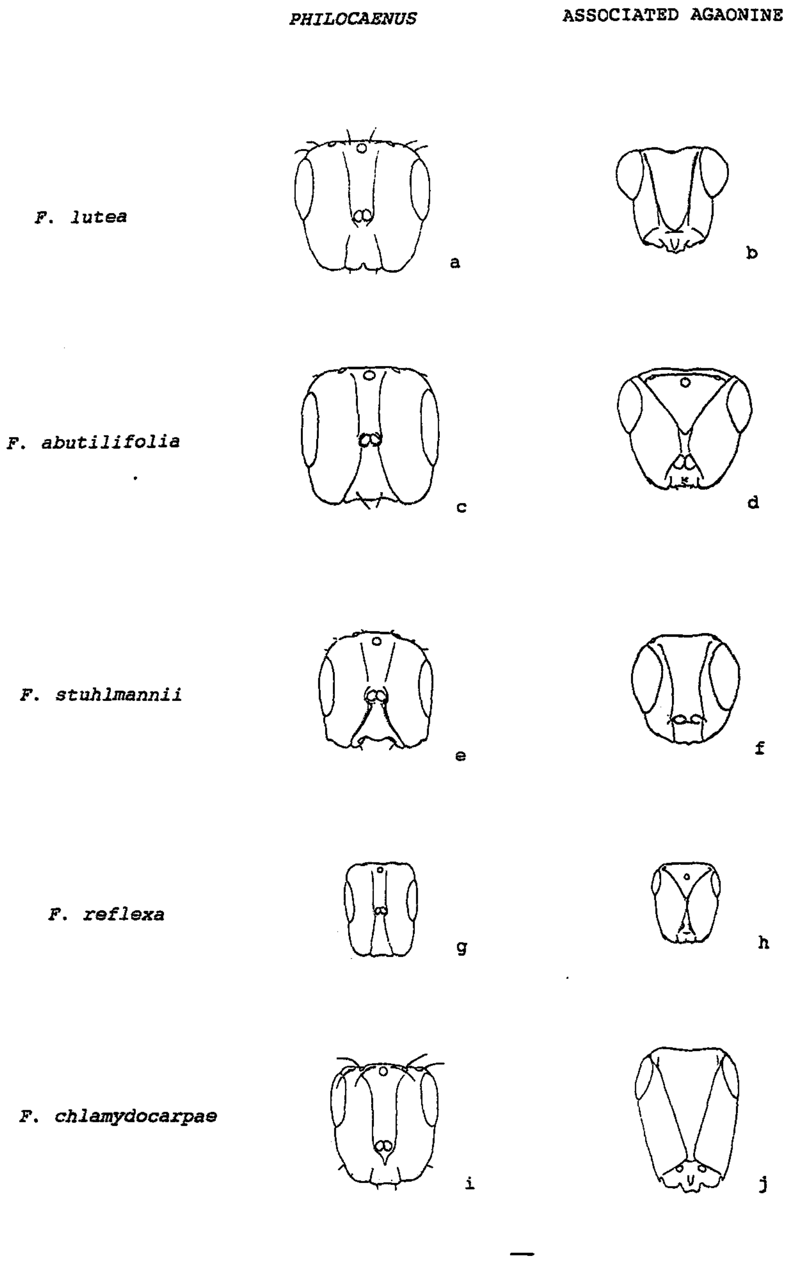


Fig. 10.6. Representatives of *Philocaenus* and their associated Agaonine, depicting similarity in head shape between wasps from the same host *Ficus* species. a) *Philocaenus silvestrii* (Grandi) b) *Allotriozoon heterandromorphum* Grandi c) *Philocaenus rotundus* sp. nov. d) *Elisabethiella comptoni* Wiebes e) *Philocaenus liodontus* (Wiebes) f) *Alfonsiella binghami* Wiebes g) *Philocaenus bouceki* (Wiebes) h) *Elisabethiella reflexa* Wiebes i) *Philocaenus comptoni* sp. nov. j) *Allotriozoon nigeriense* Wiebes. Scale bar = 0.1mm. Agaoninae redrawn from Wiebes (1974a; 1975; 1988; 1989a).

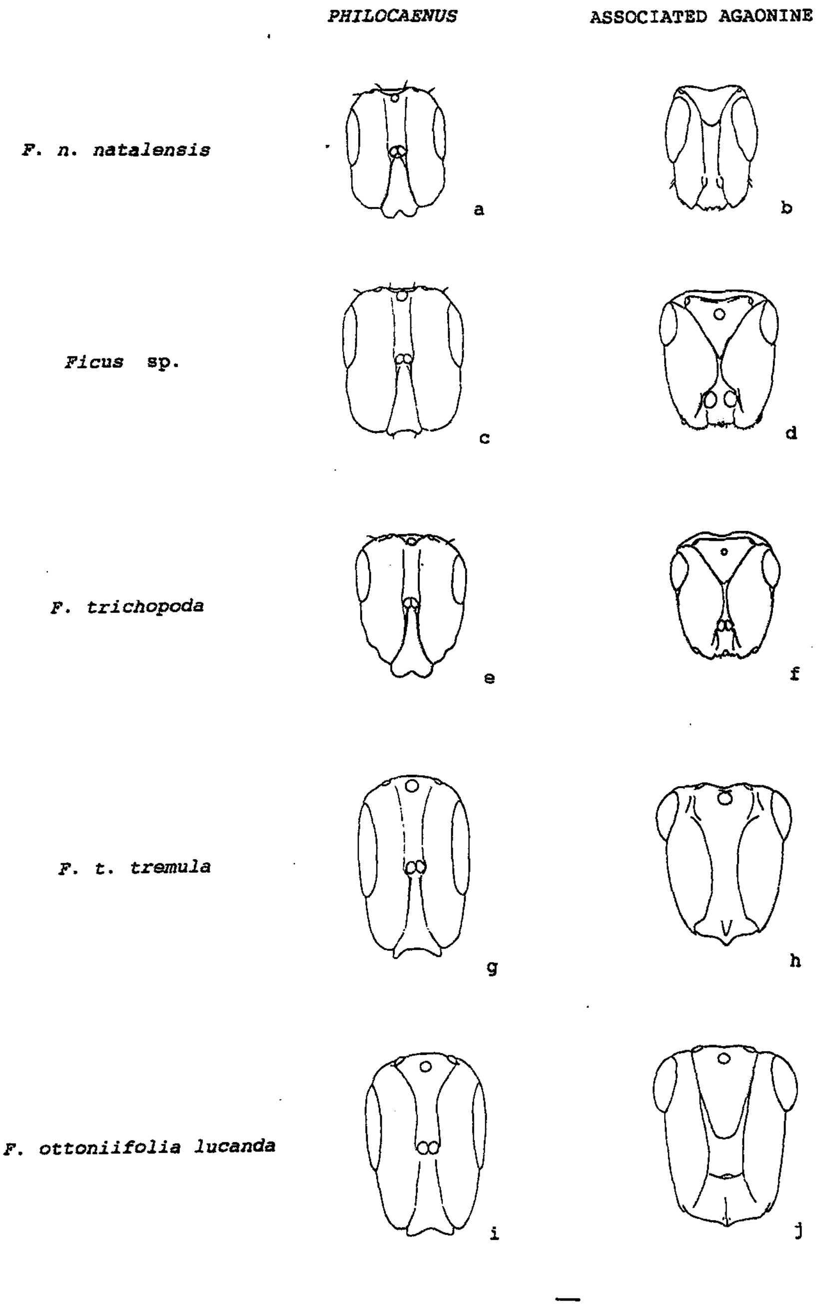


Fig. 10.7. *Philocaenus* continued. a) *Philocaenus medius* sp. nov. b) *Alfonsiella longiscapa* Joseph c) *Philocaenus jinjaensis* sp. nov. d) *Elisabethiella hilli* Wiebes e) *Philocaenus hippopotomus* sp. nov. f) *Elisabethiella bergi breviceps* Wiebes g) *Philocaenus clairae* sp. nov. h) *Courtella wardi* Compton i) *Philocaenus levis* Waterston j) *Courtella scobinifera* (Waterston). Scale bar = 0.1mm. (i) and (j) redrawn from Waterston (1920). Rest of Agaoninae redrawn from Wiebes (1972; 1989a) and Wiebes & Compton (1990).

were usually both longer and broader than those of their respective agaonines. Those sycoecines, such as all *Sycoecus* species, *Seres* species and some *Crossogaster* and *Philocaenus* species, associated with larger figs, had elongate heads like those of their corresponding agaonines *Agaon* and *Courtella*, but with their heads normally both shorter and narrower.

The head shapes of both the agaonine and sycoecine wasps were also correlated with both estimates of fig size. For agaonine head shape and dry fig diameter, $r = 0.76$, $P < 0.001$, and for fresh fig diameter, $r = 0.80$, $P < 0.001$. For sycoecine head shape and dry fig diameter, $r = 0.60$, $P < 0.001$, and for fresh fig diameter, $r = 0.83$, $P < 0.001$. The correlation between the head shape of agaonines and sycoecines sharing the same figs is therefore likely to be the result of head shape in both groups being related to factors associated with the size of the figs they inhabit.

DISCUSSION

Ramirez (1974) associated agaonine head shape with the form of the fig ostioles they have to enter. He concluded that square heads were associated with an ostiolar entrance where the bracts are arranged in a helicoidal fashion, and elongate heads with a tubular ostiolar entrance where the bracts are all pointing downwards. The situation seems to be more complex than suggested by Ramirez, however, because section *Galoglychia* as a whole is characterised by a tubular ostiolar entrance with downward pointing bracts (Berg, 1986; Verkerke, 1989), yet this section has fig wasps with both square and elongate heads. The similarity in the head shapes of agaonines and sycoecines from the same host fig nonetheless agrees with the view that some aspect of fig structure, very likely ostiole morphology, exerts a strong selection pressure on head shape. Male fig wasps do not need to crawl through the fig ostiole, and do not show any equivalent variation in head shape. A high percentage of the variation in head shape appears to be related to fig size. Generally the agaonine and sycoecine fig wasps with elongate heads are associated with the subsections *Cyathistipulae* and *Caulocarpae* of section *Galoglychia*, whose representatives usually have larger figs than those of the other subsections. However, individual *Ficus* species belonging to other subsections that have larger figs, such as *F. chlamydocarpa* Mildbr. & Burret, also have associated wasps with elongated heads. It is reasonable to assume that fig size will affect the length of the ostiolar entrance, as larger figs have thicker fig walls. Within the fig wasps associated with section *Galoglychia* an elongate head therefore appears to be an adaptation to a long ostiolar entrance, rather than to a specific type of bract arrangement.

Since the plesiomorphic sister groups of the sycoecinae have square heads and the primitive sycoecines have elongate heads (Chapter 4), an elongate head probably evolved in the ancestor of the sycoecines. The reappearance of a square head in the sycoecinae would therefore be a reversal, possibly due to selection pressures provided by fig size. This suggests that large figs may have been the ancestral condition within section *Galoglychia*, with smaller figs having evolved more recently. Some support for this is provided by Corner (1967) who, in his treatise on *Ficus* in the Solomon Islands, regards pachycaul fig trees ("short tree of massive primary construction"), with large figs as ancestral. Leptocaul trees ("slender construction, which builds most loftily"), which have small figs are considered to be derived. Although the fig tree species in section *Galoglychia* are all leptocaul trees, the general evolutionary trend from large to small figs as suggested by Corner (1967) probably still holds true.

Further support arises from the distribution patterns of African fig trees. *Ficus* species diversity is centred in tropical forests (Corner, 1967) and in Africa, drier habitat *Ficus* species have probably evolved in response to the new conditions created by the drying of the continent and the shrinkage of the rainforests (Berg, 1990a). Those groups of fig trees that are centred in rainforest are thus likely to be primitive. The subsections *Caulocarpae* and *Cyathistipulae* are largely confined to the tropical forest habitat (Berg, 1986; 1990a; 1990b) and these have large figs. An elongate head may then have appeared early in the evolution of the Sycoecinae as an adaptation to the long ostiolar entrance of a large ancestral fig. Subsequently, in section *Galoglychia* fig size has decreased, forcing the wasps to adapt their heads to a shorter ostiole entrance. This may then have resulted in the reversal to a square or broad head shape.

The advantage of having an elongate head when entering large figs is unknown. Similarly it is not clear why having a long head would be disadvantageous for wasps associated with smaller figs. One possibility is that there is some general disadvantage to having an elongate head, but this disadvantage is outweighed by being able to more efficiently negotiate a long ostiole entrance. As soon as this advantage is removed and the ostiole entrance is able to be negotiated with a square head, then a long head will be selected against.

The cladogram of the agaonine genera produced by Wiebes (1982a) suggests that a square head is also derived in this subfamily and since the agaonines and sycoecines are distinct monophyletic units and thus distinct lineages (Wiebes, 1982a; Boucek, 1988), the reversals to a square head shape in both subfamilies have been independent evolutionary occurrences. The phenomenon can therefore be regarded as an example of parallelism between the subfamilies. Similarly within the Sycoecinae the reversal to a square head shape has occurred independently in *Diaziella*, *Crossogaster* and *Philocaenus* and the same appears to be true in various agaonine genera. Fig size, or features correlated with it, have therefore provided a selection pressure resulting in the parallel evolution of square or broad heads both within the subfamilies and between them. At the level of individual species, ostiolar morphology has resulted in the parallel evolution of a specific head shape in the agaonines and the sycoecines associated with the same fig tree species. These differences in head shape, related to different *Ficus* species, could be due to the tightness and shape of the bilabiate entrance or the density of the packing of the ostiolar bracts, in addition to the ostiole length.

The females of at least three *Philocaenus* species are able to leave figs after laying some of their eggs and are therefore able to oviposit in a number of different figs (Michaloud, 1982; pers. obs.). In contrast, no agaonines are known to exit after oviposition (Ramirez, 1974). The wider heads of *Philocaenus* females, relative to those of their associated agaonines, may therefore be an adaptation to widen the ostiole, and thus lessen the chance of damage to the body of the wasp (Michaloud, 1982). Preservation of the wings is important if the wasp is going to leave the fig again. In contrast, *Seres* and *Sycoecus* have narrower heads than their corresponding agaonines, which suggests a major difference in their biology. Possibly they are like the agaonines in that they are unable to exit after oviposition and must lay all their eggs in one fig. As they occur in large figs, numerous oviposition sites are available to them, although they consistently have shorter ovipositors than their associated agaonines (Nefdt & Compton, pers. comm.).

Besides highlighting the strong selection pressures exerted by the ostioles, the correlation between agaonine and sycoecine head shape can be used to predict the head proportions of any one member of an agaonine/sycoecine association where the other is known. For example, no sycoecines have yet been collected from *Ficus ilicina* (Sonder) Miq., which is pollinated by *Elisabethiella enriquesi* (Grandi). Some confidence can be placed in the prediction that if any sycoecines are ever reared from *F. ilicina*, they will be *Philocaenus* or *Crossogaster* species, with a head approximately 1.1 times as wide as long.

CONCLUSIONS

Parallel evolution of head shape has probably occurred at the subfamily level between the Agaoninae and Sycoecinae as well as on several occasions within the subfamilies. Sycoecine head shape also correlates very well with the head shape of their associated agaonine, both of which are correlated with fig size. Head shape in both the Sycoecinae and Agaoninae appears adapted to facilitate entry through the fig ostiole, with those species with elongate heads generally being associated with larger figs. A plate of teeth has convergently evolved on the mandibles of both the agaonines and the sycoecines, and two different but functionally equivalent structures to those on the mandibles have evolved on the fore tibia in two sycoecine genera.

11

SYCOECINE EVOLUTION

INTRODUCTION

An hypothesis of the evolutionary sequence within the Sycoecinae is provided by the phylogenetic analysis (Chapters 3 and 4) of the group. A logical extension of this analysis is to determine the extent to which sycoecine evolution has been influenced by the evolution of their host *Ficus* species, and consequently the extent to which sycoecine evolution has paralleled the evolution of their hosts and that of the pollinating agaonine wasps. All three components may have coevolved *sensu lato* with one another, since there appears to be a reasonable degree of host specificity between the agaonine species and their host *Ficus* species (Wiebes & Compton, 1990) and the sycoecine species and their host *Ficus* species (Table 11.1). Taxa exhibiting such one-to-one host specific relationships are the most likely to be coevolved (Thompson, 1982; 1989; Zwolfer & Herbst, 1988), although host specificity is not proof of coevolution, even in the broad sense (Brooks, 1988). Furthermore, only the Agaoninae and the fig trees are likely to have coevolved *sensu stricto* (Thompson, 1982; 1989), as the Sycoecinae do not meet the requirements of reciprocal evolution with their hosts that the strict definition of coevolution demands (Thompson, 1989). This is because they do not control the gene flow of the hosts, whereas the agaonine pollinators do, and therefore the sycoecines will have no direct effect on host speciation. Nonetheless, if they damaged the plants sufficiently then antagonistic herbivore/host coevolution is possible, if unlikely. Similarly, competition for oviposition sites between agaonines and sycoecines, leading to coevolution between them, cannot be entirely ruled out.

Farrell and Mitter (1990) demonstrated nearly complete congruence between the phylogenies of *Phyllobrotica* leaf beetles and their lamialean host plants, leading them to hypothesise a coevolutionary interaction. Similarly, an indication that the Sycoecinae, Agaoninae and their host *Ficus* species may have coevolved *sensu lato* would be provided if the phylogenies of all three groups were congruent (Mitter & Brooks, 1983). Coevolution is not the only interaction to result in congruent phylogenies (Futuyma, 1984), although in the case of host-parasite interactions, congruence of the two phylogenies is automatically assumed to indicate cospeciation between the hosts and their parasites (Brooks, 1979; 1988; Gardner, 1991). Congruence can also arise from subsequent colonisation after host cladogenesis, particularly if colonisation ability is determined by host characteristics that are in concordance with the host phylogeny. This is termed sequential/radiating speciation (Jermy, 1976; Mitter *et al.*, 1991). Miller (1987) concluded that the host plant relationships in the Papilionidae were the result of sequential evolution, resulting from the repeated colonisation of plants belonging to a relatively small number of families. The species in the lycaenid genus *Euphilotes* were also considered to have evolved sequentially on their host plants of the genus *Eriogonum* (Shields & Reveal, 1988). In the case of the *Phyllobrotica* leaf beetle - Lamiales relationship, the distribution of the insects and age of the plant fossils date both clades in the mid-Tertiary, disfavouring an hypothesis of sequential evolution (Farrell & Mitter, 1990). In contrast, Futuyma and McCafferty (1990) in their study on *Ophraella* species (Chrysomelidae) that feed on several genera of Asteraceae found no evidence for parallel diversification, only a suggestion of colonisation of successively more chemically distinctive hosts, which possibly indicated sequential evolution. Furthermore, allozyme distances among the *Ophraella* species indicated a more recent diversification than that of their hosts, supporting a non-coevolutionary hypothesis.

From an alternative perspective, an hypothesis of coevolution cannot be rejected even if phylogenies are found not to be parallel, as colonisation and extinction events within an intense coevolutionary interaction may still result in incongruent phylogenies (Wiebes, 1984; Gould, 1988; Mitter *et al.*, 1991).

If two interacting lineages are established to have coevolved *sensu stricto*, then the degree of congruence or fit between the two phylogenies can be assessed in order to determine the extent to which colonisation and host switching have occurred. A number of procedures are available to assess the degree of fit between the phylogenies, such as the use of consensus trees and parsimony techniques (Brooks, 1979; 1988; Brooks & Mitter, 1984), correlation of genetic distance matrices (Hafner & Nadler, 1990), or comparing molecular clocks using component analysis (Page, 1991).

The interaction between the Agaoninae and their host *Ficus* species is a particularly appropriate system to examine for parallel phylogenetic congruence (once their phylogenies have been determined), since such a high proportion of the agaonines have been described. The pollinators are known for 70% of the African *Ficus* species listed by Berg (1990a) (Wiebes & Compton, 1990). A similarly high proportion of the sycoecines have also been collected, as estimated below.

ESTIMATION OF THE NUMBER OF EXTANT AFRICAN SYCOECINE SPECIES

Unusually for any group of insects, a reasonably accurate estimate can be made of the total number of species belonging to the subfamily Sycoecinae in Africa. This is possible by extrapolating from the available data on sycoecine species richness per host *Ficus* species.

Ficus species that had been adequately sampled, but had not produced any sycoecines, were included in the count of the total number of *Ficus* species in the sampled population. These were *F. tettensis* Hutch. (collections made from 7 different trees in

Botswana and South Africa, Transvaal), *F. bizanae* Hutch. & Burtt Davy (collections made from 5 different trees in Natal, South Africa) and *F. ilicina* (Sonder) Miq. (collections made from 10 different trees in Cape Province, South Africa and Namibia). These were assumed to have no sycoecines associated with them.

Berg (1990) lists 72 *Ficus* species in section *Galoglychia*. No sycoecines have yet been obtained from subsection *Crassicostae*, nor from any trees pollinated by *Nigeriella* species, but this is assumed to be due to lack of collections, rather than unsuitability, and consequently all 72 species were considered to be potential hosts for sycoecines. In addition, where the subspecies of a particular *Ficus* species have both distinct pollinators and different sycoecines, they appear to constitute distinct resources for the insects and thus were treated separately. As a result 75 potential host taxa were recognised. This is likely to be an underestimate, given that wasps have not been collected from various distinct subspecies recognised by Berg.

A simple estimate can be obtained from the relative frequencies of trees sampled to sycoecines collected. 41 *Ficus* taxa have been sampled, from which 49 associated sycoecines have been recorded, giving an average of 1.2 sycoecines per *Ficus* species. Extrapolation to 75 *Ficus* taxa predicts the probable existence of 90 sycoecine species in Africa. 53 African sycoecine species are currently known, which means that 59% of the estimated number of sycoecine species in Africa have been described, and around 37 species remain to be collected.

CURRENT PHYLOGENETIC KNOWLEDGE OF *FICUS* AND THE AGAONINAE

The current classification of *Ficus* (Berg, 1989; 1990b), while hierarchical and thus specifying which groups of species are morphologically similar, does not claim to be phylogenetically based (Berg, pers. comm.). Section *Galoglychia*, which is restricted to the African floristic region and comprises 72 species, was split by Berg (1986) into the six subsections *Galoglychia*, *Platyphyllae*, *Chlamydodorae*, *Crassicostae*, *Cyathistipulae* and *Caulocarpae* (Table 11.1), based on overall morphological and ecological similarities between the species. Ramirez (1980) did produce a cladogram for the genus *Ficus*, but he did not resolve relationships below section level. Furthermore, this phylogeny was based primarily on his phylogenetic analysis of agaonine fig wasps (Ramirez, 1978) and therefore is not a true indication of *Ficus* phylogeny, unless the *a priori* assumption is made that the two have coevolved. The phylogeny of *Ficus* species within section *Galoglychia* thus remains to be determined. It may be resolved in the next few years using molecular techniques (F. Kjellberg, pers. comm.).

A similar lack of resolution exists in the phylogenetic cladograms of the Agaoninae (*sensu* Boucek 1988) put forward by Ramirez (1978) and Wiebes (1982a), where relationships below the generic level were not resolved. Resolution is also not entirely complete at the generic level, as these analyses were carried out before *Courtella* Kieffer was separated from *Agaon* Dalman. The close affinity of these nonetheless suggests that they are sister groups. Ramirez (1978) based his phylogeny of the Agaoninae primarily on the mechanisms used by the female wasps to carry pollen, and concluded that *Alfonsiella* and *Elisabethiella* were the most plesiomorphic agaonine genera associated with section *Galoglychia*, with *Agaon* and *Paragaon* the most derived (Fig. 11.1 a). Wiebes (1982a) included an additional twenty characters in his phylogenetic analysis of the Agaoninae, resulting in a rather different conclusion to that of Ramirez, in that *Elisabethiella*, *Nigeriella* and *Agaon* are considered to be the more derived genera (Fig. 11.1 b).

The resolution of the Agaoninae is thus not sufficient for any phylogenetic comparison of the Sycoecinae to be made with the Agaoninae at the species level, although a comparison can be made at the generic level (Fig. 11.1). The lack of a *Ficus* phylogeny similarly prevents a definitive comparison of sycoecine phylogeny with that of their host trees. Nevertheless, hypotheses of sycoecine evolution in relation to that of their host fig trees and the associated agaonines can be produced based on the current classifications of the latter two groups.

HOST RELATIONSHIPS

Agaonine host specificity

The pollinating agaonine wasps are usually host specific, with a single species of pollinator wasp for each *Ficus* species (Wiebes, 1964b; Wiebes, 1986b, Wiebes & Compton, 1990; Table 11.1). This hypothesis of host specificity was first put forward by Wiebes (1963) and was based on his revision of the Indo-Australian species of *Ceratosolen* and a world survey of the host records of the Agaonidae. However, there are at least 12 records of the same pollinator being associated with more than a single host species in Africa (Wiebes & Compton, 1990; Compton *et al.*, in press) indicating potential breakdowns in host specificity. Similarly, from the host fig tree's point of view, there are exceptions to the one-to-one relationship, although the pollinators are still host specific. At present a number of well documented examples are available. *Ficus sycomorus* L. has two associated agaonines, the legitimate pollinator, *Ceratosolen arabicus* Mayr and a "cuckoo", *Ceratosolen galili* Wiebes, that plays no role in pollination (Galil & Eisikowitch, 1968; 1969; Compton *et al.*, 1991). These two agaonines are also associated with *F. mucoso* Ficalho, exhibiting the same relationship with this host as they do with *F. sycomorus* (Wiebes, 1989c). Michaloud *et al.* (1985) reported on two species of pollinators, *Courtella camerunensis* (Wiebes) and *Courtella gabonensis* Wiebes, inhabiting *F. ottoniifolia* (Miq.) Miq. in Gabon, but with different frequencies in different habitats. Similarly, *F. sur* Forssk. has two associated species of *Ceratosolen*, *C. capensis* Grandi and *C. flabellatus* Grandi, that can occur together on the same tree in

TABLE 11.1. The host fig trees and agaonine pollinating fig wasps associated with the sycoecine species and subspecies. Classification of *Ficus* after Corner (1965) and the subdivision of Section *Galoglychia* after Berg (1986). Agaoninae associations after Wiebes (1982b; 1991), Wiebes & Compton (1990) and Compton, pers. comm.

FICUS, **SUBSECTION**	**AGAONINAE**	**SYCOECINAE**
Section *Conosycea* ***Dictyoneuron***		
1. *F. glaberrima* Bl. var. *bracteata* Corner	*Waterstoniella williamsi* Wiebes	*Diaziella falcata* Wiebes
Section *Galoglychia* ***Galoglychia***		
2. *F. saussureana* D.C.	*Allotriozoon prodigiosum* Grandi	*Philocaenus cavus* sp. nov.
3. *F. chlamydocarpa* Mildbr. & Burr.	*Allotriozoon nigeriense* Wiebes	*Philocaenus comptoni* sp. nov.
4. *F. lutea* Vahl	*Allotriozoon heterandromorphum* Grandi	*Philocaenus silvestrii* (Grandi)
Platyphyllae		
5. *F. platyphylla* Delile	*Elisabethiella* near *pectinata*	*Philocaenus barbatus* Grandi
6. *F. bussei* Mildbr. & Burr.	*Elisabethiella* sp.	*Philocaenus zambesiacus* sp.nov.
7. *F. vasta* Forssk	*Elisabethiella socotrensis* Mayr	*Crossogaster triformis* Mayr
8. *F. glumosa* Delile	*Elisabethiella glumosae* Wiebes	*Crossogaster quadrata* sp. nov. *Crossogaster stigma* sp. nov. *Philocaenus warei* sp. nov.
9. *F. stuhlmannii* Warb	*Alfonsiella binghami* Wiebes	*Philocaenus liodontus* Wiebes *Philocaenus barbarus* Grandi *Crossogaster odorans* Wiebes

10. *F. abutilifolia* (Miq.) Miq.	*Elisabethiella comptoni* Wiebes	*Philocaenus rotundus* sp. nov.
11. *F. trichopoda* Baker	*Elisabethiella b. bergi* Wiebes	*Crossogaster robertsoni rasplusi* sp. nov. *Philocaenus hippopotomus* sp. nov.
	Elisabethiella b. breviceps Wiebes	*Crossogaster r. robertsoni* sp. nov. *Philocaenus hippopotomus* sp. nov.
Chlamydodorae		
12. *F. craterostoma* Mildbr. & Burret	*Alfonsiella michaloudi* Wiebes	*Philocaenus liodontus* Wiebes *Philocaenus insolitus* sp. nov.
	Alfonsiella sp.	*Philocaenus quatuordentatus* sp. nov. *Crossogaster odorans* Wiebes
13. *F. l. lingua* Wild. & Dur.	*Alfonsiella michaloudi* Wiebes	*Philocaenus liodontus* Wiebes
14. *F. n. natalensis*	*Alfonsiella longiscapa* Joseph	*Philocaenus medius* sp. nov. *Crossogaster lurida* sp. nov.
	Elisabethiella socotrensis Mayr	*Philocaenus barbarus* Grandi
15. *F.n. leprieurii* (Miq.) Berg	*Alfonsiella fimbriata* Waterston	*Philocaenus liodontus* Wiebes
16. *F. burtt-davyi* Hutch.	*Elisabethiella baijnathi* Wiebes	*Philocaenus liodontus* Wiebes
17. *F. antandronarum bernardii* (Perrier) Berg	*Elisabethiella* sp.	*Philocaenus comorensis* sp. nov.
18. *F. reflexa* Thunb.	*Elisabethiella reflexa* Wiebes	*Philocaenus bouceki* Wiebes
19. *F. thonningii* Bl.	*Elisabethiella stuckenbergi* Grandi	*Philocaenus barbarus* Grandi *Crossogaster odorans* Wiebes

	Alfonsiella brongersmai Wiebes	*Philocaenus barbarus* grandi *Crossogaster odorans* Wiebes *Philocaenus liodontus* Wiebes *Philocaenus medius* sp. nov.
	Alfonsiella longiscapa Joseph	-
20. *F. kamerunensis* Mildbr. & Burret	*Alfonsiella fimbriata* Waterston	*Philocaenus liodontus* Wiebes
Cyathistipulae		
21. *F. tesselata* Warb.	*Agaon taïense* Wiebes	*Sycoecus bergi* sp. nov.
22. *F. c. cyathistipula*	*Agaon fasciatum* Waterston	*Sycoecus thaumastocnema* Waterston
23. *F. c. pringsheimiana* (Braun & Schum.)	*Agaon kiellandi* Wiebes	*Sycoecus oculabulbus* sp. nov.
24. *F. cyathistipuloides* De Wild	*Agaon obtusum* Wiebes	*Sycoecus wiebesi* sp. nov.
25. *F. scott-elliotii* Mildbr. & Burr.	*Agaon* spec.	*Sycoecus ivoryensis* sp. nov.
26. *F. lyrata* Warb.	*Agaon spatulatum* Wiebes	*Sycoecus crinitus* sp. nov.
27. *F. sagittifolia* Berg	*Agaon c. cicatriferens* Wiebes	*Sycoecus lamtoensis* sp. nov.
28. *F. subsagittifolia* Berg	*Agaon c. multum* Wiebes	*Sycoecus wiebesi* sp. nov.
Caulocarpae		
29. *F. o. lucanda* (Ficalho) Berg	*Courtella scobinifera* (Waterston)	*Philocaenus levis* (Waterston)
30. *F. o. ulugarensis* (Mildbr. & Burr.)	*Courtella camerunensis* (Wiebes)	*Philocaenus bifurcus* sp. nov.
31. *F. t. tremula* Warb.	*Courtella wardi* Compton	*Philocaenus clairae* sp. nov.

32. *F. artocarpoides* Warb.	*Courtella penicula* (Wiebes)	*Seres longicalcar* sp. nov. *Crossogaster michaloudi* sp. nov.
	Courtella hladikae (Wiebes)	*Crossogaster michaloudi* sp. nov. *Seres solweziensis* sp. nov.
33. *F. p. polita* Vahl	*Courtella b. bispinosa* (Wiebes)	-
	Courtella b. bekiliensis (Risbec)	*Seres solweziensis* sp. nov.
34. *F. s. sansibarica* Warb.	*Courtella armata* (Wiebes)	*Seres l. longivena* sp. nov.
35. *F. s. macrosperma* (Mildbr. & Burr.)	*Courtella armata* (Wiebes)	*Seres l. bidens* sp. nov. *Crossogaster lachaisei* sp. nov.
36. *F. bubu* Warb.	*Courtella michaloudi* (Wiebes)	*Seres wardi* sp. nov.
37. *F. ovata* Vahl	*Courtella h. hamifera* Kieffer *Courtella h. modesta* (Wiebes)	*Seres a. armipes* Waterston *Seres a. breviceps* Wiebes *Seres solweziensis* sp. nov. *Crossogaster ovata* sp. nov.
Section *Malvanthera*		
36. *F. xylosycia* Diels	*Pleistodontes rieki* Wiebes	*Robertsia mandibularis* Boucek *Robertsia xylosyciae* Boucek

areas where their ranges overlap (Wiebes, 1989c). *F. thonningii* Bl. has also been associated with three pollinators, *Elisabethiella stuckenbergi* Grandi, *Alfonsiella brongersmai* Wiebes and *Alfonsiella longiscapa* Joseph, although they have not been collected together from the same tree, except for *A. brongersmai* where a single female was present together with 50 females of *E. stuckenbergi*. This record could have been the result of a 'mistake' by *A. brongersmai*. The examples of pollinators colonising two or more host tree species must also be treated with caution, due to possible misidentifications of hosts (Compton *et al.*, in press).

Sycoecine host specificity.

Most sycoecines appear to be host tree specific (Table. 11.1), although more oligophagous species are present than in the Agaoninae. This is perhaps to be expected, considering the difference in mutual interdependence of the two groups with their host fig trees. Since there is no control of host gene flow by the sycoecines, host specificity in this subfamily is probably the result of their intricate biological relationship with the host figs. The sycoecines may utilise the same host tree-specific volatiles that attract the pollinating fig wasps to receptive figs, as they arrive at the figs around the same time as do the pollinators (pers. obs). Such volatile dependence may have initially been selected for because of the synchrony of volatile release with the opening of the ostiole, which is the only time when the figs can be colonised. In contrast, externally ovipositing fig wasps do not necessarily arrive at fig trees during the stage when volatiles are released (Compton & Dallas, pers. comm.). Since the nature of the agaonine-fig tree interaction results in selection for host specific volatiles, it follows that volatile specificity will potentially influence sycoecine specificity. Ostiolar morphology also provides a selection pressure favouring host specificity, as ability to negotiate the entrance appears to be linked to head shape (Chapter 10). This physical barrier does not always prevent alien wasp species from entering figs, however. For example, *Philocaenus barbarus* (Grandi) from *F. thonningii* Bl., along with two alien pollinators and one other alien non-pollinator, managed to enter figs of *F. lutea* Vahl growing in Grahamstown, with *P. barbarus* and *Elisabethiella stuckenbergi* successfully reproducing (Compton, 1990; Ware & Compton, in press b).

Since both the sycoecines and the agaonines are generally host specific, it follows that a one-to-one association also exists between the sycoecines and the agaonines, with each sycoecine usually only being associated with a single pollinator species, although the reverse does not hold true.

Exceptions to the one-to-one relationship of the Sycoecinae with their host fig trees

Five sycoecine species are associated with more than a single host species (Table 11.2). However, some of these sycoecine species belong to taxonomically difficult groups from a morphological point of view and thus may prove to be composites of cryptic species that are in fact host specific. These do not correspond with the equivalent cases in the Agaoninae where a pollinator is associated with more than a single host, although within the group of *Ficus* species that are associated with *Philocaenus liodontus* (Wiebes) there are two pairs out of the six *Ficus* species that share the same pollinator (Table 11.2).

The fig species in the subsections *Galoglychia* and *Cyathistipulae* always have only a single associated sycoecine species in the respective genera, *Philocaenus* and *Sycoecus*. However, in the subsections *Platyphyllae*, *Chlamydodorae* and *Caulocarpae*, there are nine cases where host *Ficus* species have more than a single sycoecine species associated with them, although some of these are still host tree-specific (Table 11.3). This is usually as a result of a *Philocaenus* and a *Crossogaster* species occurring together, although in subsection *Caulocarpae*, *Crossogaster* occurs together with *Seres*. Sometimes two or more species from the same genus are also associated with a single host species (Table. 11.3).

Reasons for exceptions to the one-to-one relationship of fig wasps and their host fig trees

Incongruencies in the one-to-one host specific relationship between fig wasps and their hosts may be explained by the presence of undetected biological species or alternatively through colonisation events by the wasps, or division of the wasps into sister species still sharing the same host tree. Thus the apparent association of the same wasp species with two or more different *Ficus* species may be due to morphologically indistinguishable wasp species (cryptic species) being associated with distinct *Ficus* species (Wiebes, 1987; Compton *et al.*, in press), or may be a result of colonisation of additional hosts by a single wasp species. Incongruencies may similarly arise from morphologically indistinguishable *Ficus* species. This results in more than one host tree-specific wasp being associated with what appears to be a single host species. Again, this may alternatively be a genuine reflection of a relationship that has resulted from the colonisation of a *Ficus* species by one or more wasp species from other hosts. A third possibility is that the pollinator may speciate in allopatry without the host *Ficus* population diverging and if subsequent sympatry of the two populations occurs, the result may be two sister species associated with a single *Ficus* species. This can potentially be identified using the cladogram in chapter 4. A possible example is the two species of *Crossogaster*, *C. stigma* sp. nov. and *C. quadrata* sp. nov., associated with *F. glumosa* Delile that are identified as sister species by the cladogram.

An example of a possible cryptic species complex in the Sycoecinae is provided by *Crossogaster odorans* Wiebes which is associated with *F. thonningii* only in the Transvaal and Zimbabwe, but not further south. In contrast it is associated with *F. stuhlmannii* Warb. both in the Transvaal and in Natal, where *F. thonningii* also occurs but is not colonised. This geographical disparity with regard to the hosts suggests that *Crossogaster odorans* may be two species, one associated with *F. thonningii* and one with *F. stuhlmannii*. Similarly, *Philocaenus liodontus* is associated with *F. thonningii* only in Malawi, but is also associated with *F. burtt-davyi* Hutch. in South Africa where this

TABLE 11.2. Sycoecine species associated with more than a single *Ficus* species.

SYCOECINE SPECIES	**HOST *FICUS* SPECIES**	**ASSOCIATED AGAONINE**
Sycoecus wiebesi	*F. cyathistipuloides*	*Agaon obtusum*
	F. subsagittifolia	*Agaon cicatriferens multum*
Seres zolweziensis	*F. p. polita*	*Courtella b. bispinosa*
	F. ovata	*Courtella hamifera*
	F. s. sansibarica	*Courtella armata*
Crossogaster odorans	*F. thonningii*	*Elisabethiella stuckenbergi* and *Alfonsiella brongersmai*
	F. stuhlmannii	*Alfonsiella binghami*
	F. craterostoma	*Alfonsiella* sp.
Philocaenus barbarus	*F. thonningii*	*Elisabethiella stuckenbergi* and *Alfonsiella brongersmai*
	F. n. natalensis	*Elisabethiella socotrensis*
	F. stuhlmannii	*Alfonsiella binghami*
Philocaenus liodontus	*F. natalensis leprieurii*	*Alfonsiella fimbriata*
	F. craterostoma	*Alfonsiella michaloudi*
	F. l. lingua	*Alfonsiella michaloudi*
	F. burtt-davyi	*Elisabethiella baijnathi*
	F. thonningii	*Alfonsiella brongersmai*
	F. kamerunensis	*Alfonsiella fimbriata*

TABLE 11.3. *Ficus* species with more than a single associated sycoecine species.

FICUS **SPECIES**	**SYCOECINE SPECIES**
F. glumosa	*Philocaenus warei* *Crossogaster quadrata* *Crossogaster stigma*
F. stuhlmannii	*Philocaenus liodontus* *Philocaenus barbarus* *Crossogaster odorans*
F. trichopoda	*Philocaenus hippopotomus* *Crossogaster robertsoni*
F. craterostoma	*Philocaenus liodontus* *Philocaenus insolitus* *Philocaenus quatuordentatus* *Crossogaster odorans*
F. n. natalensis	*Philocaenus medius* *Crossogaster lurida* *Philocaenus barbarus*
F. thonningii	*Philocaenus barbarus* *Philocaenus liodontus* *Philocaenus medius* *Crossogaster odorans*
F. artocarpoides	*Seres longicalcar* *Crossogaster michaloudi*
F. sansibarica	*Seres solweziensis* *Seres longivena* *Crossogaster lachaisei*
F. ovata	*Seres armipes* *Seres solweziensis* *Crossogaster ovata*

tree is sympatric with *F. thonningii*. This again suggests that the population of *P. liodontus* associated with *F. burtt-davyi* is a cryptic species.

The fig wasp associations with *Ficus* species in the *F. thonningii* complex, suggest that there may be a number of cryptic tree species involved (Table 11.4). Apparent non host specificity of the sycoecines clouds the issue, however. The discrepancies may also be the result of misidentifications of the host trees or of the fig wasps that are involved. Ramcharun *et al.* (1990) reported on hybridisation between *F. thonningii* and *F. n. natalensis* Hochst. in Natal, both of which they found to be pollinated by *Elisabethiella stuckenbergi*. Pollinators intermediate between *Elisabethiella stuckenbergi* and *Elisabethiella socotrensis* (Mayr) have also been identified from *F. thonningii* and *F. n. natalensis* in Natal (Wiebes, pers. comm.). This suggests that the status of these two pollinators and their two hosts is questionable. In contrast, the *F. n. natalensis* population in Natal that is pollinated by *Alfonsiella longiscapa* appears to be a good species, which is also supported by the associated sycoecines (Table 11.4). Similarly the associated fig wasps of *F. craterostoma* Mildbr. & Burret suggest that the population in South Africa is specifically distinct from the population in west Africa.

To resolve whether incongruencies such as these are genuinely the result of cryptic species that have not been separated taxonomically or whether they are the result of colonisation events, methods other than classical morphological ones may need to be applied. Enzyme electrophoresis has been used successfully by Dawah (1987, 1988 and 1989) to separate closely related species complexes in the Eurytomidae, Eulophidae and the Pteromalidae and would thus more than likely be applicable to difficult groups in the Agaonidae. Molecular differences in protein or DNA structure (E.A. Herre, pers. comm.) for both the fig trees and the wasps, and cuticular hydrocarbons (Hadley *et al.*, 1981) may be two other possible taxonomic tools useful in separating cryptic species. A combination of ecological and

TABLE 11.4. Associated agaonines and sycoecines of some of the *Ficus* species in the *F. thonningii* complex.

HOST *FICUS*	**ASSOCIATED POLLINATOR**	**ASSOCIATED SYCOECINE**	**LOCALITY**
F. thonningii	*Elisabethiella stuckenbergi*	*Philocaenus barbarus* *Crossogaster odorans*	South Africa; Zimbabwe; Zambia
F. thonningii	*Alfonsiella brongersmai*	*Philocaenus barbarus* *Crossogaster odorans* *Philocaenus liodontus* *Philocaenus medius*	Malawi
F. n. natalensis	*Elisabethiella socotrensis*	*Philocaenus barbarus*	Natal, South Africa.
F. n. natalensis	*Alfonsiella longiscapa*	*Philocaenus medius* *Crossogaster lurida*	Natal, South Africa.
F. n. leprieurii	*Alfonsiella fimbriata*	*Philocaenus liodontus* *Philocaenus insolitus*	Gabon, west Africa
F. craterostoma	*Alfonsiella* sp.	*Philocaenus quatuordentatus* *Crossogaster odorans*	Transvaal, S. Africa.
F. craterostoma	*Alfonsiella michaloudi*	*Philocaenus liodontus* *Philocaenus insolitus*	Gabon, west Africa

genetic evidence as utilised by Dodson & George (1986) to separate two cryptic species of *Aciurina* (Diptera) may be an alternative approach, although this requires biological evidence from field observations, which are sorely lacking for most fig wasps.

EVIDENCE OF CONGRUENCE IN THE RELATIONS OF THE SYCOECINAE, AGAONINAE AND THEIR HOST *FICUS* SPECIES

There is a degree of congruence between the classifications of the Agaoninae and the host *Ficus* species, with related *Ficus* species having related wasp species (Wiebes, 1963; 1979b; 1984; 1986b). This is particularly evident at the *Ficus* section level, with each section usually being associated with a single agaonine genus (Wiebes, 1984; 1986b). Section *Galoglychia* is nonetheless an exception (as is section *Conosycea*), as its members play host to seven agaonine genera (Wiebes, 1984; 1986b; Berg, 1989; Wiebes & Compton, 1990; Table 11.5). At a higher taxonomic level there is no agreement between the agaonine classification and the four recognised subgenera of *Ficus*, nor the *Ficus* classification with the division of the Agaoninae into the two tribes Agaonini and Blastophagini (Wiebes, 1984). The tribal division of the Agaoninae is based on geographical distribution rather than phylogenetic relationships (Wiebes, 1982a; 1984). Thus, although the Blastophagini is defined by a synapomorphy, the Agaonini has no supporting synapomorphies, meaning that this tribe may be paraphyletic (Wiebes, 1984). The genera associated with the sections *Galoglychia*, *Malvanthera*, and *Pharmocosycea* belong to the Agaonini, whilst those associated with the remaining sections belong to the Blastophagini (Wiebes, 1982a). The sections *Galoglychia* and *Malvanthera* may be closely related, but section *Pharmocosycea* is in the same subgenus as section *Oreosycea*, whose associated pollinator genus *Dolichoris* belongs to the Blastophagini (Berg, 1989). This lead Berg (1989) to suggest that the subdivision of the agaoninae may be related to ostiolar morphology, as this is similar in the three host sections of the Agaonini. For the *Ficus* classification to parallel the tribal division of the Agaoninae the subgenus *Pharmacosycea* would have to be split, which may be feasible if the two constituent sections are only linked by plesiomorphies.

There is no congruence at the generic level between the phylogeny of the Sycoecinae and either of the two very different phylogenies of the Agaoninae produced respectively by Ramirez (1978) and Wiebes (1982a) (fig. 11.1). There is however a certain amount of conformity at the generic level between these two subfamilies in terms of relationships with the *Ficus* subsections (Tables 11.1, 11.5 & 11.6). Three of the subsections of *Galoglychia* have unique clades of both agaonines and sycoecines associated with them (Table 11.5), suggesting that in some instances the sycoecines may have diversified and speciated along with the agaonines and their host fig trees.

Within section *Galoglychia*, three of the subsections (*Galoglychia*, *Cyathistipulae* and *Caulocarpae*) are associated with a single unique pollinator genus, whereas the remaining three subsections (*Platyphyllae*, *Chlamydodorae* and *Crassicostae*) each have two or three associated agaonine genera, none of which (except the monobasic *Paragaon* Joseph) are unique to a subsection (Berg, 1989; Wiebes & Compton, 1990; Table 11.1 & 11.5). The sycoecines follow this pattern with two genera (*Philocaenus* and *Crossogaster*) being associated with each of the subsections *Platyphyllae* and *Chlamydodorae* (no sycoecines have been collected from the subsection *Crassicostae*), but there is no congruence between the sycoecine genera and the agaonine genera inhabiting these two subsections. Both *Philocaenus* and *Crossogaster* are each associated with both *Elisabethiella* and *Alfonsiella*. This is exemplified when their associated agaonines are plotted onto the cladogram of the *Crossogaster* and *Philocaenus* species (fig. 11.2). At the species group level there is again no congruence. However, in the case of the subsections associated with unique agaonine genera the sycoecine genera are less tightly associated with the fig subsections than the agaonine genera (Tables 11.1 & 11.5). The most notable discrepancy occurs in subsection *Caulocarpae* where all the pollinating fig wasps belong to the single genus *Courtella* which is exclusively associated with this subsection. In contrast, there are three sycoecine genera (*Seres*, *Philocaenus* and *Crossogaster*) associated with subsection

TABLE 11.5. Associations of the fig trees from Section *Galoglychia* with fig wasps of the subfamilies Agaoninae and Sycoecinae. The subdivision of Section *Galoglychia* is after Berg (1986), agaonine associations after Wiebes & Compton (1990).

***FICUS*, SUBSECTION**	**AGAONINAE**	**SYCOECINAE**
Galoglychia	*Allotriozoon*	*Philocaenus*
Platyphyllae	*Elisabethiella* *Alfonsiella* *Nigeriella*	*Philocaenus* *Crossogaster*
Chlamydodorae	*Elisabethiella* *Alfonsiella*	*Philocaenus* *Crossogaster*
Crassicostae	*Elisabethiella* *Nigeriella* *Paragaon*	None known
Cyathistipulae	*Agaon*	*Sycoecus*
Caulocarpae	*Courtella*	*Seres* *Philocaenus* *Crossogaster*

TABLE 11.6. Associations of the agaonine and the sycoecine genera.

AGAONINE GENERA	**SYCOECINE GENERA**
Allotriozoon	*Philocaenus*
Elisabethiella	*Philocaenus* *Crossogaster*
Alfonsiella	*Philocaenus* *Crossogaster*
Nigeriella	None known
Paragaon	None known
Agaon	*Sycoecus*
Courtella	*Seres* *Philocaenus* *Crossogaster*

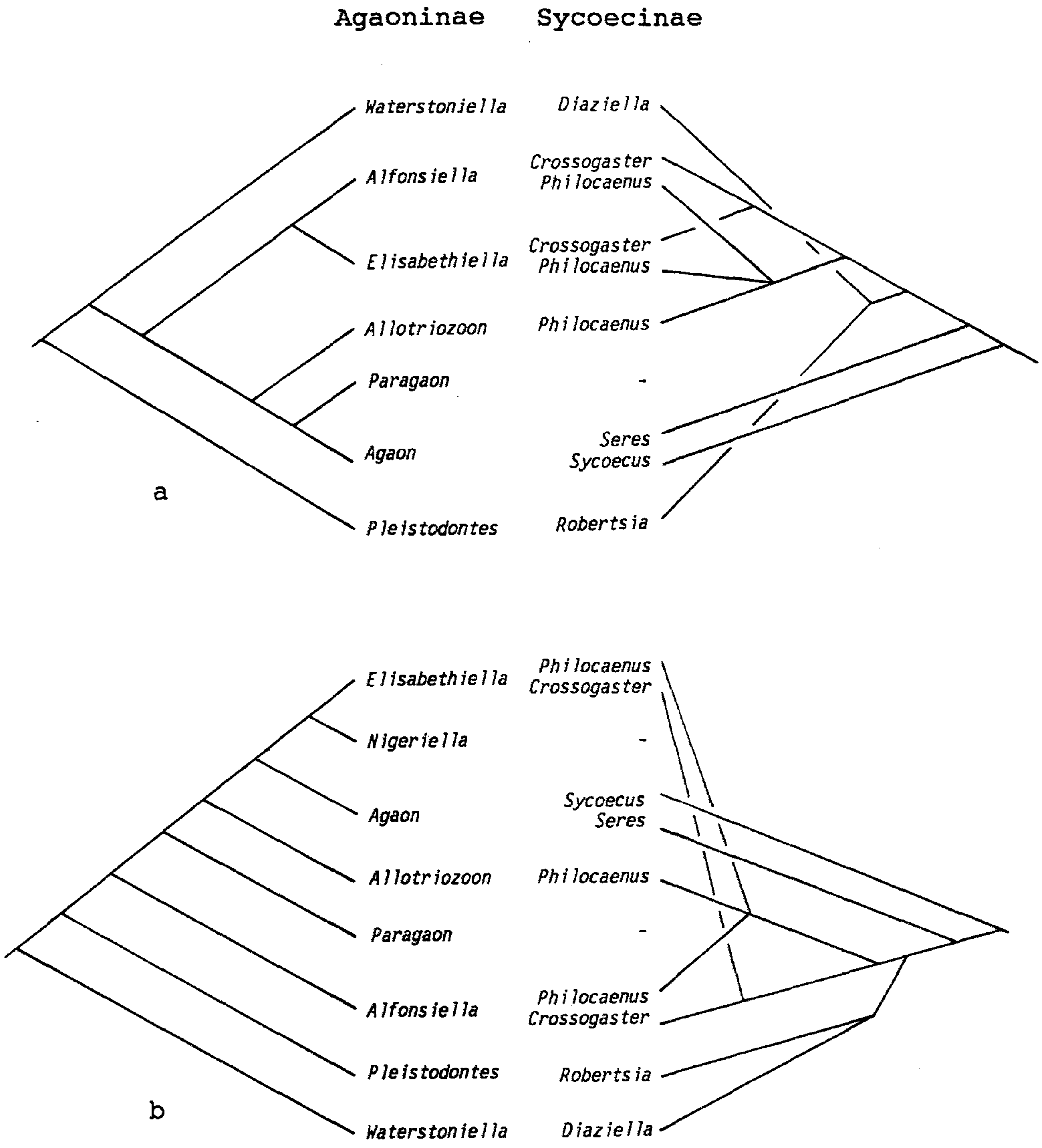


Fig. 11.1. Comparison of the phylogeny of the sycoecine genera with two independently derived phylogenies of their associated agaonine genera. a) the agaonine phylogeny of Ramirez (1978) b) with the agaonine phylogeny of Wiebes (1982a). Both agaonine cladograms are simplified from the original cladograms of the world agaonine genera produced by Ramirez (1978) and Wiebes (1982a). Consequently the *Waterstoniella* lineage in both cladograms includes further bifurcations than depicted. However, these do not alter the relationship between *Waterstoniella* and the other depicted genera. *Agaon* in both cladograms includes the sister genera of *Agaon* and *Courtella*, as currently recognised (Wiebes & Compton, 1990).

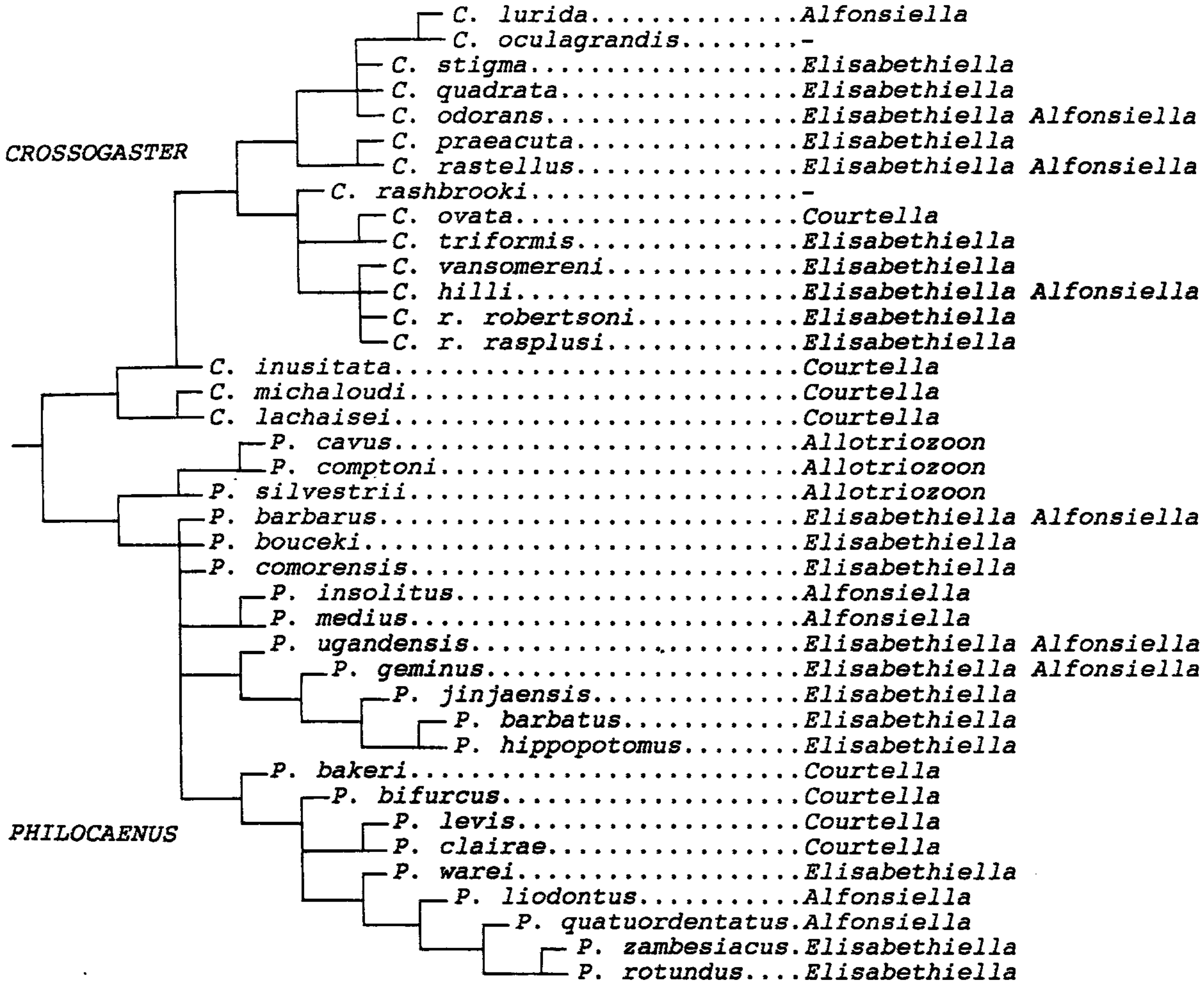


Fig. 11.2. The cladogram of the *Crossogaster* and *Philocaenus* species, showing incongruence with their associated agaonine genera.

Caulocarpae, with only *Seres* being restricted to it. This may be a result of extinctions of *Seres* species in many of the hosts, during or after speciation of the host *Ficus* species and subsequent colonisation by sycoecine species from other genera. Nonetheless, the association of *Seres* and *Courtella* with the subsection *Caulocarpae* seems to be one of cospeciation *sensu lato*.

The *Philocaenus silvestrii* species group found in association with subsection *Galoglychia* is suggested by the sycoecine cladogram (Chapter 4) to be an early divergence from the ancestral stock of *Philocaenus*. This fits in with the distinction of the pollinators associated with this subsection, namely the genus *Allotriozoon*. The relationship of *Sycoecus* and *Agaon* with the subsection *Cyathistipulae* also appears to indicate a strong possibility of cospeciation *sensu lato*, although within this subsection there is also limited evidence of host switching in both the agaonines and the sycoecines or at least incongruencies with the host *Ficus* species.

Two alternative explanations can be forwarded for the diversification of the African Sycoecinae in section *Galoglychia*. Both explanations assume that *Caulocarpae* and *Cyathistipulae* are primitive subsections within section *Galoglychia*, an assumption expanded upon in the discussion of chapter 10. The sycoecines may then have originated in one of these two subsections, or with their common ancestor. This hypothesis is supported by the cladogram, as the two genera (*Seres* and *Sycoecus*) that are restricted to these subsections, are primitive clades. The ancestors of *Crossogaster* and *Philocaenus* may then have evolved in parallel with the diversification of the subsections *Galoglychia*, *Platyphyllae*, *Chlamydodorae* and *Crassicostae*. Alternatively, these subsections may have diversified without the sycoecines. A colonisation event (or possibly even a number of distinct repeated colonisation events) by the ancestor/s of *Philocaenus* and *Crossogaster* and subsequent sequential radiation of the species would then produce the pattern observed today.

The presence of *Crossogaster* and *Philocaenus* in the subsections *Caulocarpae* and *Cyathistipulae* may have independent explanations. The association of the three most primitive *Crossogaster* species with subsection *Caulocarpae* suggests that this genus was delimited before the more derived species evolved with, or colonised, the subsections *Platyphyllae* and *Chlamydodorae*. An alternative explanation is that *Crossogaster* only diverged from the primitive sycoecine stock during cospeciation *sensu lato* with *Platyphyllae* and *Chlamydodorae* and a primitive *Crossogaster* species colonised subsection *Caulocarpae*. An example of a more recent possible colonisation of subsection *Caulocarpae* is exhibited by *Crossogaster ovata* sp. nov. which belongs to the *C. triformis* Mayr species group that is normally associated with subsections *Platyphyllae* and *Chlamydodorae*. *C. ovata* appears to have colonised *F. ovata* and now coexists with *Seres armipes breviceps* Wiebes, a sycoecine that has an evolutionary history more closely aligned with that of its host. *Philocaenus* appears to have followed the same evolutionary route as in the latter explanation for *Crossogaster*. The presence of *Philocaenus* in subsection *Caulocarpae* must be considered to represent a colonisation of this subsection, since the species of *Philocaenus* associated with subsection *Caulocarpae* are not primitive species. It is nevertheless always possible that there are primitive *Philocaenus* species associated with *Caulocarpae* that have not yet been discovered.

THE EXTRA-AFRICAN GENERA

The pan-tropical distribution and antiquity of the Moraceae suggests that this family is of Gondwana origin. The family is considered old enough to have been dispersed directly between Africa and South America (Raven & Axelrood, 1974; Poinar & Herre, 1991), and therefore between Africa and Australia, via Antartica. The genus *Ficus* on the other hand has been argued to be both of

Gondwana origin (Croizat, 1968) and of Laurasian origin (Corner, 1985). However, there appears to be agreement that the present day *Ficus* with its closed inflorescence arose in the mid Cretaceous Period, about a 100 million years ago (Galil, 1977; Murray, 1985; Boucek, 1988). Furthermore Poiner & Herre (1991) consider it to be probable that the relationship between fig wasps and *Ficus* was already established by this date, as fossil fig wasps are present in Oligocene Florissant shales of Colorado and in Domininincan amber (dated from the lower Miocene to the upper Eocene), approximately coinciding with the earliest fossil record for *Ficus* (in the mid Eocene). The mid Cretaceous was approximately the age when the component fragments of Gondwana started separating (De Wit, 1990) and the current geographical distribution of the *Ficus* sections supports the diversification of the genus at this stage.

The phylogenetic relationships of the Sycoecinae suggest that Africa is the centre of origin of this subfamily. As noted in chapter 4, the two extra-African genera appear to have diverged from within the African genera, although this conclusion must be treated with caution, because the resolution of the relationships between the clades that define the sycoecine genera is not strongly supported. The relationships between the genera could very easily be changed by the addition of one or two characters. The geographical distribution of the Sycoecinae may either be the result of dispersal subsequent to the breakup of Gondwanaland, or as a result of this breakup. The divergence of *Robertsia*, after that of *Sycoecus* and *Seres* suggests that the ancestor of *Robertsia* colonised section *Malvanthera* from section *Galoglychia*, rather than the alternative scenario where a common ancestor of the Sycoecinae diverged with the diversification of these two *Ficus* sections. The colonisation of section *Malvanthera* by sycoecines may have occurred before Australia became separated from Africa. However, section *Galoglychia* and *Malvanthera* are probably closely related (Berg, 1989) and from the classification of *Ficus* they could be sister groups, which by definition are of equal age (Hennig, 1966), supporting the common ancestor hypothesis, rather than the colonisation hypothesis.

Both Ramirez (1978) and Wiebes (1982a) place *Pleistodontes*, the pollinators of section *Malvanthera* as primitive to the agaonine genera that are associated with section *Galoglychia*. The pollinating wasps therefore suggest that section *Malvanthera* may be the more primitive of the two sections, as also indicated by Ramirez (1980) in his phylogeny of *Ficus*, although this is to be expected as this phylogeny is based on his phylogeny of the Agaoninae (Ramirez, 1978). From this reasoning the African genera would be expected to have arisen from *Robertsia*. Despite the position of *Robertsia* in the cladogram, it is still possible that this genus could turn out to be primitive, which seems to be a more realistic hypothesis from a biogeographical point of view.

In the cladogram *Diaziella* is the sister group of *Robertsia* yet is associated with section *Conosycea* of subgenus *Urostigma*. Ramirez (1978) places the agaonine genera associated with this section as a more derived clade than the genera associated with the sections *Galoglychia* and *Malvanthera* (fig. 11.1) and hence in his corresponding phylogeny of *Ficus* (Ramirez, 1980), section *Conosycea* is considered as more derived than *Malvanthera* and *Galoglychia*. Wiebes (1982a) maintained the basal split of the Agaoninae into two tribes, and hence the pollinators associated with section *Conosycea* are considered as distantly related to those associated with sections *Galoglychia* and *Malvanthera*. As the Blastophagini, to which *Waterstoniella* belongs, is well defined phylogenetically, this seems likely to be correct. This suggests that the ancestor of *Diaziella* colonised section *Conosycea* from section *Malvanthera*, presumably subsequent to the joining of Australasia with south-east Asia. The alternative biogeographical/ phylogenetic hypothesis for the host relationships of *Diaziella* would involve the ancestors of the genus spreading from Africa to south-east Asia via India. However, there are no *Diaziella* species in India and if this was the route then *Diaziella* would not be expected to be the sister group of *Robertsia*, unless *Robertsia* also followed this route.

Clearly there is much uncertainty surrounding the biogeography of the Sycoecinae and without complete confidence in the phylogenetic relationships of the genera, the course of phylogenetic events must remain speculative.

CONCLUSIONS

From a comparison of the respective classifications, elements of the Sycoecinae may have cospeciated *sensu lato* with their host *Ficus* species and the associated agaonine species. At the same time they also appear to be more flexible than the Agaoninae in their ability to colonise new hosts, as they exhibit more discrepancies in their associations with the host *Ficus* species than do the Agaoninae. This suggests a more complicated pattern of host switching and colonisation events within the Sycoecinae than in the Agaoninae, which may be more constrained by the obligate mutualism they have with the host *Ficus*. However, without the availability of phylogenies of the other groups, no firm conclusions can be reached about the evolutionary interactions of the Agaoninae, the Sycoecinae and their host *Ficus* species.

The current taxonomic revision and phylogenetic analysis is far from exhaustive, but it does provide a base from which to build a picture of the evolution of the Sycoecinae, which can be refined as further species and characters are discovered. Current species delimitations are based purely on morphology and thus some of the species as presently defined may prove to be species complexes. In some instances host relationships indicate that this may be the case and these will need to be tested using alternative taxonomic methods, particularly molecular techniques. Molecular differences in cuticular hydrocarbons identified using gas chromatography analysis (Hadley *et al.*, 1981) may be one.

Techniques have been developed, whereby the hydrocarbons of a single insect, as small as a fig wasp, can be analysed using gas chromatography (Brill & Bertsch, 1985; Morgan, 1990). Other approaches may be electrophoretic analysis of enzyme systems (Dawah, 1987; 1988; 1989), molecular differences in protein or DNA structure (E.A. Herre, pers. comm.), or by additional morphological investigation of internal characters such as spermatozoal morphology (S.G. Compton & T. Barnard, pers. comm.). Spermatozoal ultrastructure has successfully been used to determine the evolutionary relationships between seventeen species of South African patellid limpets (Jamieson *et al.*, 1991). With the acquisition of additional material it will also eventually be feasible to perform morphometric analyses as well.

The phylogenetic relationships outlined in chapter 4 represent an hypothesis based on the information available. This hypothesis will be put to the test by the input of new information from new species and new characters. The nature of the biological interaction of the Sycoecinae with their host figs, results in selection pressures provided by fig morphology, that act on a number of different sycoecine lineages concurrently. This results in the evolution of homoplasies, which can cloud phylogenetic relationships. It would therefore not be surprising if new information altered the current perception of the phylogenetic relationships.

The Chalcidoidea are a taxonomically difficult superfamily, and as a result resolution of the phylogeny of the superfamily has been hampered. This is exemplified by Rasnitysin (1988) who in his treatment of the phylogeny of the Hymenoptera excluded the families within the Chalcidoidea due to lack of data. Nonetheless, inroads into phylogenetic relationships of families in the Chalcidoidea have been made by Schauff (1984) who determined the phylogeny of the holarctic Mymaridae, Darling (1988) in his phylogenetic revision of the perilampid genus *Krombeinus*, Woolley (1988) with the phylogeny of the

Signiphoridae and Gibson (1989) who provided a phylogenetic analysis of the Eupelmidae. The phylogenetic analysis of the Sycoecinae is a beginning to the phylogenetic determination of the Agaonidae. The obvious next agaonid subfamily to examine from a phylogenetic perspective is the Agaoninae, and hopefully a botanist will meanwhile resolve the phylogeny of *Ficus*. The availability of these phylogenies, supported by data from molecular biologists, should enable the complex evolutionary relationships of fig wasps and fig trees to be elucidated.

12

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