

Phylogeny of the Ammobatini and Revision of the Afrotropical Genera (Hymenoptera: Apidae: Nomadinae)

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Abstract.—The phylogeny of the genera of Ammobatini was studied using cladistic methods and the classification is consequently revised. The tribe forms a monophyletic group that comprises five monophyletic genera: *Pasites* Jurine, *Sphecodopsis* Bischoff, *Ammobates* Latreille, *Melanempis* Saussure and *Oreopasites* Cockerell, and one monotypic genus *Spinopasites* Warncke. They all occur in the Afrotropical Region except *Oreopasites*, and the Afrotropical species are revised. *Pasites* (*Morgania* Smith, *Omachthes* Gerstaecker and *Pasitomachthes* Bischoff, **new synonymy**) includes 17 Afrotropical species, *Sphecodopsis* (*Pseudopasites* Bischoff and *Pseudodichroa* Bischoff, **new synonymy**) 10 species, and *Ammobates* and *Melanempis* are each known from a single Afrotropical species. Ten **new species** are described (all attributed to Eardley alone): *Pasites nilssoni*, *P. paulyi*, *P. humectus*, *P. gnomus*, *P. namibiensis*, *P. somalicus*, *Sphecodopsis vespericena*, *S. longipygidium*, *S. namaquensis* and *Ammobates auster*. Thirty-four species names are **newly synonymized**: *Pasites nigerrimus* Friese and *Pasitomachthes argentatus* Baker = *Pasites barkeri* (Cockerell); *Morgania chubbi* Cockerell, *M. nigrigula* Bischoff and *M. peratra* Cockerell = *Pasites friesei* Friese; *Omachthes nigripes* Friese, *Morgania fortis* Cockerell, *M. subfortis* Cockerell, *M. stordyi* Cockerell, *M. voiensis* Cockerell and *M. altior* Cockerell = *Pasites carnifex* (Gerstaecker); *M. nigrithorax* Strand = *P. dichrous* Smith; *Omachthes alboguttatus* Friese, *Morgania natalensis* Cockerell and *M. ogilviei* Cockerell = *Pasites jenseni* (Friese); *Morgania histrio transvaalensis* Bischoff, *M. alivalensis* Cockerell and *M. rufitarsis* Cockerell = *Pasites histrio* (Gerstaecker); *Morgania marshalli* Cockerell = *Pasites jonesi* (Cockerell); *Omachthes abessinicus* Friese, *Morgania fulviventris* Bischoff, *M. rhodesiana* Bischoff, *M. apicalis* Bischoff, *M. turneri* Cockerell, *M. politula* Cockerell, *M. indecisa* Cockerell, *M. nudicauda* Cockerell, *M. bechuanica* Cockerell and *M. breviceps* Cockerell = *Pasites appletoni* (Cockerell); *Morgania rufula* Cockerell = *Sphecodopsis minutissima* (Cockerell); *Pasites pygmaeus* Friese, *Sphecodopsis rufescens* Bischoff, *S. algoensis* Bischoff and *Morgania perpunctata* Cockerell = *Sphecodopsis aculeata* (Friese); *Morgania leonis* Cockerell = *Sphecodopsis semirufa* (Cockerell). Keys to the genera and Afrotropical species are provided.

The purpose of this study is to provide a comprehensive revision of the systematics of the Afrotropical Ammobatini (Apidae: Nomadinae). To attain this objective, three main aspects were investigated. The first was to establish whether the Ammobatini is a monophyletic taxon and, in so doing, establish its validity. The second was to review the generic classification of the Ammobatini and gain an understanding of the relationships among the genera. The third was to acquire a sound knowl-

edge of the identity of the Afrotropical species and the relationships between species.

The Ammobatini are cleptoparasitic bees, also known as cuckoo-bees. They lay their eggs in the nests of pollen-collecting bees that provision each larval cell with sufficient food for the larva to develop to maturity. Like other Nomadinae, the ammobatines lay each egg in a hole in the wall of the host's larval cell. When the egg hatches the tiny mobile first-instar larva,

which has elongate sharp-pointed mandibles, kills the host larva or egg and then consumes the food provided for the host. An outstanding account of cleptoparasitism is given by Alexander (1990).

Pollinating bees are one of the most important groups of beneficial insects. It is therefore important to study the systematics and biology of their cleptoparasites because they affect the population dynamics of pollen-collecting bees. Bees of the ammobatine genus *Sphecodopsis* Bischoff, for example, are known to parasitise species of *Scapter* Lepeletier & Serville (Rozen & Michener 1968). Both of these genera are endemic to southern Africa. *Scapter* species pollinate indigenous plants and are potentially important in the pollination of agricultural crops. The genus is prevalent in the semi-arid regions of southern Africa where insect-pollinated indigenous plants form an important component of the ground cover and pasture.

Cleptoparasitism among bees is a derived trait and it has evolved independently several times within the bees (Alexander 1990). The features that are unique to cleptoparasitic bees, such as the loss of the scopa, are derived, although they may resemble the primitive state for the bees as a whole. Other features that separate cleptoparasitic bees from pollen-collecting bees are the thickened integument and the more robust sting (Alexander 1990). There are many other convergent traits in the cleptoparasitic bees which, as indicated by Alexander (1990), complicate attempts to trace their phylogeny.

In spite of the difficulties involved in the study of the phylogeny of cleptoparasitic bees, the Nomadinae, the largest and most diverse lineage of cleptoparasitic bees (about 1200 described species), has been well studied by Rozen (1966, 1974, 1977, 1991), Rozen *et al.* (1978), Roig-Alsina (1987, 1991), Alexander (1990) and Roig-Alsina & Michener (1993). Roig-Alsina (1991), Rozen (1991) and Roig-Alsina

& Michener (1993) defined the Nomadinae to include only those genera that comprise a monophyletic group, namely the Ammobatini, Ammobatoidini (including *Holcopasites* Ashmead), Biastini, Caenoproso-pidini, Epeolini, Neolarrini, Townsendiellini, Hexepeolini, Nomadini and Brachynomadini. Other groups that were previously included in the Nomadinae (now Anthophorinae) are: Isepeolini, Protepeolini, Osirini (including Epeoloidini and *Parepeolus* Ducke, Roig-Alsina 1989) and *Coelioxoides*, now in the Tetrapediini (Alexander 1990, Roig-Alsina & Michener 1993).

The Nomadinae has its greatest diversity in the Nearctic and Neotropical Regions, is fairly well represented in the Afrotropical and Palaearctic Regions and is poorly known from the Oriental and Australian Regions. In the Afrotropical Region, it comprises four tribes: Nomadini, Epeolini, Ammobatoidini and Ammobatini. The Nomadini, Epeolini and Ammobatoidini are represented there only by their nominate genera. The Nomadini and the Epeolini were revised by Eardley & Schwarz (1991) and Eardley (1991), respectively. The Ammobatoidini is known from the Afrotropical Region from a single female specimen described as *Ammobatoides braunsi* Bischoff. The Ammobatini is the largest and most diverse tribe of Afrotropical nomadine bees.

The Ammobatini occur mainly in the Nearctic, Palaearctic and Afrotropical Regions. Although they have not been recorded from the Oriental Region, several Palaearctic species are known from areas that border the Oriental Region and these species possibly extend into that Region. They do not occur in the Neotropical and Australian Regions. The Nearctic (Rozen 1992) and Palaearctic (Warncke 1983) faunas have been well studied and the Afrotropical fauna is revised here.

Most of the previous work on the systematics of the Afrotropical Ammobatini consists of descriptions of new species and

distribution records. The original descriptions are generally vague, without illustrations and inadequate for the recognition of the species. Bischoff (1923) provided a comprehensive revision of the Afrotropical Ammobatini, but his work has several shortcomings (e.g., he did not study much of the type material) and it has become outdated. The present study is the first treatment of these bees that has included an examination of nearly all the type material and a study of male and female terminalia.

Authorship of the new species described in this paper is attributed to CDE only.

HISTORICAL REVIEW OF THE AMMOBATINI

The history of the classification of this group of closely related bees may be outlined as follows. An early attempt to arrange them into a system of higher classification was by Dalla Torre (1896). He placed all bees in the family Apidae and placed the genera that are currently considered to belong to the Ammobatini, namely *Ammobates* Latreille, *Pasites* Jurine and *Omachthes* Gerstaecker, together with several other genera, in the subfamily Coelioxynae. Ashmead (1899) divided the Apidae into several families and transferred the Coelioxynae to the family Stelidae, which included most of the parasitic bees.

Michener (1944) provided the first comprehensive study in which bees were assigned to tribes. He placed *Oreopasites* Cockerell, *Ammobates*, *Morgania* Smith, *Omachthes* and *Pasites* in the tribe Ammobatini (Apidae: Anthophorinae). Michener (1944) also suggested that *Caesarea* Friese, *Melanempis* Saussure, *Parammobatodes* Friese, *Pasitomachthes* Bischoff, *Pseudodichroa* Bischoff and *Sphecodopsis* Bischoff might belong in the Ammobatini.

Popov (1951) divided Michener's (1944) Ammobatini into two distinct tribes, the Ammobatini and the Pasitini, placed in

the subfamily Anthophorinae of the family Anthophoridae. Popov's Ammobatini contained the genera *Ammobates* (for which he described two new subgenera, *Xerammbates* Popov and *Euphileremus* Popov), *Caesarea*, *Parammobatodes* Popov and *Oreopasites*. His Pasitini consisted of *Pasites*, *Morgania*, *Omachthes*, *Pseudopasites*, *Sphecodopsis*, *Pasitomachthes* and *Pseudodichroa*. He made no mention of *Melanempis*. Suster (1958), in contrast, placed the Nomadini, Ammobatini and Pasitini in the Andrenidae.

Baker (1971), in his discussion on *Pasitomachthes*, supported Popov's (1951) classification. Rozen & McGinley (1974) found evidence in their study on the systematics and phylogeny of the larvae of these bees that *Oreopasites* and *Pasites* are closely related, with *Ammobates* somewhat divergent and *Sphecodopsis* farthest away.

Warncke (1983), in a revision of the Palearctic fauna, took a completely different approach and placed almost the entire Palearctic and Afrotropical faunas of ammobatine bees (*sensu* Michener) into the genus *Pasites*, which he subdivided into six subgenera: *Parammobatodes*, *Spinopasites* Warncke, *Micropasites* Warncke, *Euphileremus*, *Ammobates* and *Pasites*. He considered *Morgania*, *Omachthes*, *Pasitomachthes*, *Pseudopasites* and *Sphecodopsis* to be junior synonyms of *Pasites* (*sensu stricto*). Warncke (1983) did not give a detailed explanation for his actions and made no mention of *Oreopasites* and *Melanempis*, except that in changing the name *Phileremus ater* Saussure (= *Melanempis atra*) to *Pasites madagascarensis* he indicated that he considered *Melanempis* to be a synonym of *Pasites*.

Subsequent to Warncke's (1983) study, the tribal classification of the Nomadinae, based on adult morphology, was studied by Roig-Alsina (1987, 1991) and Alexander (1990), neither of whom adopted Warncke's (1983) classification. Roig-Alsina (1987), in his discussion on the phylogenetic relationship between the Caeno-

prosopidini, Biastini and Ammobatini, defined the Ammobatini in the 'sense of Michener (1944)'. Alexander (1990), in his table on the distribution and host records of the Nomadinae, stated that he did not use Warncke's (1983) classification because he had not studied the group in sufficient detail. Rozen (1992) discussed the tribal characters in detail without recognising either tribes.

Roig-Alsina (1987, 1991) and Alexander (1990) demonstrated that the Caenoprosopidini is the sister group of the Ammobatini. In the Ammobatini the sixth metasomal sternum (S6) of the female is bifurcate or secondarily simple posteriorly, and in the Caenoprosopidini this structure is bilaterally separated. The inference, by the above mentioned authors, that the bifurcate female S6 in the Ammobatini gave rise to the bilaterally separated condition in the Caenoprosopidini implies that the Caenoprosopidini is a monophyletic group. The monophyly of the Ammobatini, however, was not demonstrated by either Roig-Alsina (1987, 1991) or Alexander (1990).

In his studies on the phylogeny of the Nomadinae, Roig-Alsina (1987) demonstrated the sister taxon of the (Ammobatini + Caenoprosopidini) clade to be the Biastini. Alexander (1990), however, indicated that the Neolarrini was possibly the sister group of this clade. Subsequently Roig-Alsina (1991), using different characters, came to the same conclusion as Alexander (1990). The absence of a pygidial plate, as mentioned by Roig-Alsina (1987) is not a synapomorphy of the ((Ammobatini + Caenoprosopidini) + Biastini), as several species of *Pasites* have well developed pygidial plates. Recently, Roig-Alsina & Michener (1993) considered them to belong in the Apidae. The current familial placement of these bees, a topic that is beyond the scope of the study, has been accepted.

MATERIALS AND METHODS

In an attempt to demonstrate the monophyly of and elucidate the generic classification of the Afrotropical Ammobatini, all the known Afrotropical species (represented by over 800 specimens) and all available extra-African representatives of the tribe (183 specimens from the Palearctic and Nearctic Regions) were studied. All the available type material of the Afrotropical species was examined during the course of the study. The type material of eight species was not studied because it could not be obtained: *Pasitomachthes argentatus* Baker was identified from the detailed description and comparison with type material of other species; *Omachthes capensis* Friese, *Pseudodichroa fumipennis* Bischoff and *Phileremus (Melanempis) ater* Saussure were reliably identified from authoritatively determined material; *Pasites atratulus* Friese, *Omachthes gabonensis* Vachal, *Morgania rotundiceps* Bischoff and *Morgania tropica* Cockerell remain *incertae sedis*. The study of extra-African taxa was based mostly on previously determined material. Information on the labels of type specimens is recorded verbatim from the labels. For other material, the locality, date, collector and floral record are given in that sequence. The **distribution** records of material that was not studied are given under 'Other published distribution records'. **Vegetation types** are from White (1983). The **acronyms** for the museums from which material was borrowed are listed in the acknowledgements section. Where geographic coordinates are given, they are in degrees and minutes (separated by a period), not decimal degrees. Where reference is made to 'the Code', this means the International Code of Zoological Nomenclature, 3rd Edition (International Commission on Zoological Nomenclature 1985).

Morphology.—The terminology mainly follows that of Michener (1944). Sexual dimorphism in adult Ammobatini is slight

and, apart from *Sphcodopsis*, *Oreopasites*, *Melanempis* and *Spinopasites* in which males have eleven flagellar segments, is largely confined to the posterior region of the metasoma. A single detailed description for both sexes of each species has therefore been given, with the diagnostic sex-limited characters of each sex explicitly described. The abbreviations **T** and **S** are used for the metasomal terga and sterna, respectively (e.g. T1 and S1 refer to the first metasomal tergum and sternum, respectively). **Vestiture** generally refers to the relatively fine hairs and where setae are specifically mentioned these are thicker hairs. The sixth metasomal tergum of the female of some species has a brush posteriorly (located below the pygidial plate when this structure is present). This brush has been referred to as the **subpygidial brush** (Fig. 6); when it has thick hairs dorsally and fine vestiture ventrally it has been referred to as differentiated. In certain taxa the posteromedian region of the **fifth metasomal sternum** of the female, when viewed from behind, forms a distinct furrow. Rozen's (1968a) terminology has been used for this structure which he referred to as being 'gutter-like'. In the illustrations of the **male terminalia** the anterior end is at the bottom and the posterior end at the top.

Cladistics: Adults of each included species were thoroughly examined and each character for which distinct states occurred in different species was included in the matrix. Polarization of characters was based strictly on out-group comparison and the putative sister group was taken as the out group. In the analysis attempting to demonstrate the monophyly of the Ammobatini as a whole, the sister group of the Ammobatini, the Caenoprosopidini, was included in the in group. The Neolarrini (represented by *Neolarra vigilans* (Cockerell)), which is the sister group of (Ammobatini + Caenoprosopidini) (Roig-Alsina 1991), was then taken as the out group. For one character (50) the state in

the Neolarrini was entirely different from that in the (Ammobatini + Caenoprosopidini), and the sister group of the (Neolarrini + (Ammobatini + Caenoprosopidini)), the Townsendiellini (Roig-Alsina 1991) (represented by *Townsendiella californica* Michener) was used to polarize that character (the relationships between the Ammobatini + Caenoprosopidini and the Neolarrini, Townsendiellini and Ammobatoidini were questioned by Alexander (pers. comm.) following additional research, however). Where a possible evolutionary progression could be determined between different states of a character within the in group, successive derived states (0 = primitive; 1, 2 & 3 = successive derived states), with nonadditive binary coding, was used.

The different states of each character were incorporated in data matrices. A question mark (?) was used where the state in a species could not be studied, such as sex-limited characters for species in which the appropriate sex is unknown or was not available for study. In order to root the cladogram, a hypothetical ancestor with all characters coded as 0 was added. The first matrix (Table 1) gives all the relevant information on each species. In the formation of the second data matrix (Table 2) some species were grouped into species groups (reasons given below), each of which is represented by the ground plan of that group (derived as explained below). The third matrix (Table 4) includes only ground plans of the genera and was derived from the second matrix.

Cladograms were generated using Hennig86, version 1.5 (Farris 1988). The first, second and fourth cladograms (Figs. 1, 2 & 4) originate from the analysis of the information in Tables 1, 2 & 4, respectively, without using character weighting (commands *m**; *bb**). The third cladogram (Fig. 3) resulted from the use of successive approximations character weighting (repeated application of *m**; *bb**; *xs w*) in the analysis of the information in Table 2.

Table 1. Data matrix of character states for species (characters and coding of states according to Appendix 2).

Taxon	Characters					
Ancestor	0000000000	0000000000	0000000000	0000000000	0000000000	00000000
<i>Sph. capicola</i>	2001111101	0110010001	0012110100	1000010001	1001001101	10000000
<i>Sph. vespericena</i> & <i>Sph. longipygidium</i>	20011111?1	0110010001	0012110110	1000010001	1001001101	1????????
<i>Sph. villosa</i>	2001111101	0110010001	0012110100	1?0001????	????????????	?0000000
<i>Sph. namaquensis</i>	20011111?1	0110010001	0012110100	1000010001	1001001101	1????????
<i>Sph. minutissima</i>	20011111001	0110010001	0012111100	1000010001	1001001101	10000000
<i>Sph. aculeata</i>	2001111101	0110010001	0012110100	1000010001	0001001101	10000000
<i>Sph. semirufa</i>	2001111101	0110010001	0012110100	1000010001	0001001201	10000010
<i>Sph. capensis</i> & <i>Sph. fumipennis</i>	20011111?1	0110010001	0012110100	1000010001	0001002301	2????????
<i>P. barkeri</i>	1001100011	0110010101	0021001010	1010010000	0110010001	10000000
<i>P. friesei</i>	1001100011	0110010101	0021001010	1110110100	0110010001	10010000
<i>P. nilssoni</i>	1001100011	0110010101	0021001010	1?1011????	????????????	?0010000
<i>P. paulyi</i>	1001100011	0110010101	0021001000	1110110100	0210010001	10010000
<i>P. braunsi</i>	10011000?1	0110010101	0021001010	1110110100	0210010001	1????????
<i>P. humectus</i>	1001100011	0110010101	0021001000	1110110110	0110010001	10010000
<i>P. bicolor</i>	1001100011	0110010101	0021001010	1010110110	0110010001	10010000
<i>P. tegularis</i>	1001100011	0110010101	0021001010	1010110100	0110010001	10010000
<i>P. gnomus</i>	1001100011	0111010001	0021001000	1110010000	0110010001	12010100
<i>P. carnifex</i>	1001100011	0110010101	0022110110	1110010000	0210010001	10000000
<i>P. dichrous</i>	1001100011	0110010101	0022110110	1110010000	0210010001	10010010
<i>P. jenseni</i> & <i>P. histrio</i>	0011100011	0110010101	0011001010	1110010000	0210020001	10000000
<i>P. namibiensis</i> & <i>P. jonesi</i>	0111100012	0110012101	0011001010	1110010000	0210020001	10000000
<i>P. rufipes</i>	20011111?1	0110010101	0022110010	0111001000	0210020001	1????????
<i>P. appletoni</i>	1001100011	0110010101	0021001010	1110010100	0210020001	10000000
<i>P. somalicus</i>	10011000?1	0110010101	0021001010	1110010100	0210020001	1????????
<i>P. maculatus</i>	1011100011	0101010101	0021001010	1111010000	0210020001	10000000
<i>Spi. spinotus</i>	10011000?1	0100010111	0021001000	1100000001	0001001201	2????????
<i>M. atra</i>	2101111102	1001011111	0022110010	0000011010	0001001301	10010000
<i>O. vanduzeei</i>	1001100002	1000011011	0020010000	1100010001	0001001201	11000000
<i>O. linsleyi</i>	1001100002	1000021011	0020010000	1100010001	0001001201	11000000
<i>A. verhoeffi</i>	1001100002	1000010111	0021000000	0010010001	0000101211	11000010
<i>A. rostratus</i>	0111100002	1000010111	0020001000	0110000001	0000101211	11000010
<i>A. robustus</i>	0111100002	100??10111	0020001000	01????????	????????????	????????
<i>A. teheranicus</i> & <i>A. baueri</i>	01111000?2	1000010111	0020001000	0110000001	0000101211	1????????
<i>A. hipponensis</i>	0111100002	1000011111	0020001000	0?1000????	????????????	?1000010
<i>A. mavromoustakisi</i>	0111100002	1000010111	0020001000	1110000001	0001101211	10000010
<i>A. handlirschi</i>	0111100002	100??11111	0020001000	111000????	????????????	?1000010
<i>A. depressus</i>	01111000?2	1000010111	0020001000	0100000001	1000101211	11000020
<i>A. punctatus</i>	1011100002	1000010111	0020001000	0110010101	0000101211	11000000
<i>A. ancylae</i>	1111100002	100??10111	0020001000	1110010001	0000101201	11000020
<i>A. solitarius</i>	10111000?2	1000010111	0020001000	1110010001	0000101201	1????????
<i>A. vinctus</i>	10111000?2	1000011111	0020001000	1110010001	0000101211	11000010
<i>A. auster</i> , <i>A. similis</i> , <i>A. niveatus</i> & <i>A. syriacus</i>	1011100002	1000010111	0020001000	1110010001	0000101201	11000010
<i>A. rufiventris</i>	1011100002	1000011111	0020001000	1110010001	0000101201	11000010
<i>A. iranicus</i>	1011100002	1000011111	0020001000	1110010001	0000101201	11000020
<i>A. dubius</i>	1011100002	1000010111	0020001000	1110010001	0000101201	11000020
<i>A. assimilis</i>	1011100002	1000010111	0020001000	111001????	????????????	?1000020
<i>A. opacus</i>	10111000?2	100??11111	0020001000	1110010001	0000101201	1????????
<i>A. armeniacus</i>	1011100002	100??10111	0020001000	1110010001	0000101201	11000020
<i>A. sanguineus</i>	1011100002	1000010111	0020001000	1111010001	0000101201	11000020
<i>A. biastoides</i>	0001100002	1000010111	0020001000	1111010001	0000101201	11000010

Table 1. Continued.

Taxon	Characters						
<i>A. persicus</i>	1011100002	1000010111	0020001000	1010010001	0000101211	11000010	
<i>A. minutus</i>	1001100012	1000011111	0020001000	1110010001	0000101201	11001020	
<i>A. orientanus</i>	1001100012	0100010001	0020001000	1110010001	0000101201	11001020	
<i>A. aegyptiacus</i>	10011000?2	010?010001	0020001000	11????10001	00?????????1	1?????????	
<i>A. muticus</i>	1011100002	1000010111	0022011000	1100011001	0000101201	11000010	
<i>A. oraniensis</i>	10111000?2	1000010111	0022011000	1100011001	0000101201	1?????????	
<i>A. latitarsis</i>	1011100002	1000010111	0022011000	1100011001	0000101201	110???????	
<i>A. oxianus</i>	1001100000	000??10101	1020001000	1110010001	0000101201	11000020	
<i>A. lebedevi</i>	10011000?1	1000?10111	1020001000	1110010001	0000101201	1?????????	
<i>C. crabronina</i>	2010011001	0000101110	1110001101	0010010001	1000000002	10101001	

Character weighting was applied to give an indication of which cladogram derived without weighting might be preferred. (For the fourth analysis, using the data in Table 4, only one most parsimonious tree was obtained (Fig. 4), making successive approximations character weighting unnecessary.) Plotting of characters on the cladograms was done using Clados, version 1.2 (Nixon 1992) the accelerated transformation option, a criterion of Farris (1970) in which reversals are maximised and parallelisms minimized. On theoretical grounds this approach was preferred by Pinna (1991). Characters for which states are unknown in some taxa were 'squeezed' (Nixon 1992) to avoid the indication of apparent synapomorphies based only on sharing of missing states. Each homoplastic state was considered individually to determine whether the homoplasy could be more appropriately explained by a parallelism rather than by a reversal, but no such state was found.

During the characterization of the species and species groups only adult morphological characters were taken into account, as insufficient larval material was available. Some larvae were investigated by Eardley (1994), but no synapomorphies were found. In spite of the excellent work on ammobatine larvae by Rozen (1954, 1966), Rozen & McGinley (1974) and Rozen & Roig-Alsina (1991), Rozen & McGinley (1974) clearly stated that insuffi-

cient data were available on ammobatine larvae for a phylogenetic analysis of the tribe, and little additional information has subsequently accrued.

The reason for not including zoogeographical information is that it is not genetic but historical, and therefore should not be included in the analysis of the genealogy. It was, however, used to evaluate the results of the study.

The initial analysis (all species considered separately) resulted in over 1200 equally parsimonious cladograms, and the strict consensus tree had several polytomies, some of which contained numerous branches (Fig. 1). The polytomies made it difficult to analyze the result. The optimisation and placement of characters on consensus trees is often problematic because of the conflicts in the underlying data; the character distributions shown (in Figs. 2 & 3) should thus be treated appropriately.

A study of the species data matrix (Table 1) indicated that missing data, such as the sex-limited characters for species only known from one sex, contributed significantly to the poor resolution of the cladogram. This problem was overcome to a large extent by grouping morphologically similar species into species groups. Appendix 1 is a list of the species that were studied and their groupings. Species were generally grouped on the basis of overall similarity of the characters coded in Ap-

Table 2. Data matrix of character states for species groups (characters and coding of states according to Appendix 2).

Taxon	Character					
Ancestor	0000000000	0000000000	0000000000	0000000000	0000000000	00000000
<i>Sph. capicola</i> group	2001111101	0110010001	0012110100	1000010001	1001001101	10000000
<i>Sph. minutissima</i>	20011111001	0110010001	0012111100	1000010001	1001001101	10000000
<i>Sph. aculeata</i>	2001111101	0110010001	0012110100	1000010001	0001001101	10000000
<i>Sph. semirufa</i>	2001111101	0110010001	0012110100	1000010001	0001001201	10000010
<i>Sph. capensis</i> group	20011111?1	0110010001	0012110100	1000010001	0001002301	2????????
<i>P. barkeri</i>	1001100011	0110010101	0021001010	1010010000	0110010001	10000000
<i>P. friesei</i> group	1001100011	0110010101	0021001000	1110110100	0110010001	10010000
<i>P. gnomus</i>	1001100011	0111010001	0021001000	1110010000	0110010001	12010100
<i>P. carnifex</i> group	1001100011	0110010101	0022110110	1110010000	0210010001	10010000
<i>P. jenseni</i> group	0011100011	0110010101	0011001010	1110010000	0210020001	10000000
<i>P. rufipes</i>	20011111?1	0110010101	0022110010	0111001000	0210020001	1????????
<i>P. appletoni</i> group	1001100011	0110010101	0021001010	1110010100	0210020001	10000000
<i>P. maculatus</i>	1011100011	0101010101	0021001010	1111010000	0210020001	10000000
<i>Spi. spinotus</i>	10011000?1	0100010111	0021001000	1100000001	0001001201	2????????
<i>M. atra</i>	2101111102	1001011111	0022110010	0000011010	0001001301	10010000
<i>O. vanduzeei</i> group	1001100002	1000011011	0020010000	1100010001	0001001201	11000000
<i>A. verhoeffi</i>	1001100002	1000010111	0021000000	0010010001	0000101211	11000010
<i>A. rostratus</i> group	0111100002	1000010111	0020001000	1110000001	0000101211	11000010
<i>A. punctatus</i> group	1011100002	1000010111	0020001000	1110010001	0000101201	11000010
<i>A. biastoides</i>	0001100002	1000010111	0020001000	1111010001	0000101201	11000010
<i>A. persicus</i>	1011100002	1000010111	0020001000	1010010001	0000101211	11000010
<i>A. minutus</i>	1001100012	1000011111	0020001000	1110010001	0000101201	11001020
<i>A. orientanus</i> group	1001100012	0100010001	0020001000	1110010001	0000101201	11001020
<i>A. muticus</i> group	1011100002	1000010111	0022011000	1100011001	0000101201	11000010
<i>A. oxianus</i> group	1001100001	1000?10111	1020001000	1110010001	0000101201	11000020
<i>C. crabronina</i>	2010011001	0000101110	1110001101	0010010001	1000000002	10101001

pendix 2. Where different states of a character were found in a single putative group each character was considered in the light of the degree of homoplasy found in an analysis of the entire data matrix (Table 1), and each group was delimited to ensure that only characters which are also homoplastic elsewhere are those which have different states in the group. For *Oreopasites*, whose species were not studied in detail, the two species groups represent the two subgenera (Rozen 1992). As much of the missing data was among the sex-limited characters of species of which only one sex was available, the assumption was made that species that closely resembled one another in one sex would be similar in the opposite sex. Because the grouping was done primarily to overcome the problem of missing data, it was done conservatively to minimise the

possibility of grouping species for which the states of the opposite sex were different. Known intra-group differences represent highly homoplastic states that appeared to have little significance in grouping species in this tribe.

The grouping of species required the development of a ground plan of character states for each species group. This was done by first developing a ground plan comprising the most primitive state of each character that occurs in that species group. The resultant data matrix was analyzed (command used: m*) and the tree length recorded. Then, for each character for which more than one state occurs within the species group the matrix was systematically altered, taking one character at a time, by replacing the primitive state with the derived state (for characters represented by more than two states in a

Table 3. Weight assigned to each character during analysis of data in Table 2 after successive approximations character weighting (maximum weight = 10).

Weight	Character
Weight 10:	4, 5, 15, 16, 20, 21, 22, 30, 35, 39, 42, 43, 45, 47, 49, 50, 53, 56, 58.
Weight 5:	10, 46, 48, 52, 57.
Weight 4:	9, 25, 29, 44.
Weight 3:	23.
Weight 2:	6, 7, 8, 11, 13, 26, 28, 33, 40, 41, 54, 55, 57.
Weight 1:	1, 12, 18, 19, 24, 32.
Weight 0:	2, 3, 14, 17, 27, 31, 34, 36, 37, 38, 51.

single species group, the matrix was altered in a stepwise manner from the most primitive to the most derived state). After each alteration the resultant matrix was re-analyzed and the tree length compared with that of the former analyses. The data set that gave the shortest tree was chosen. Where the different states provided cladograms of equal length, each state was studied for evidence suggesting which state was primitive for the group. In the absence of such evidence the more primitive state was chosen. This procedure was repeated for each species group.

For *Ammobates*, in the oxianus group the more derived state for characters 10, 11 & 19 gave the shortest tree (i.e., state 1). In both the rostratus and punctatus groups the more derived state for character 31 (i.e., state 1) and in the rostratus group for character 52 (i.e., state 2) gave a shorter tree and was therefore preferred. In the punctatus group character 57 is represented by three different states (i.e., states 0, 1 & 2), of which state 1 gave the shortest tree.

The same approach was adopted in the development of ground plans for the genera (Table 4), which resulted in the more derived state (i.e., state 1) being preferred for two characters in *Ammobates*. For character 1 states 0 and 1 gave trees of similar length. State 1 was preferred because it is apparently more primitive for the group, being reversed in *A. rostratus*. In *Ammobates* state 1 is more common and this state also occurs in *Spinopasites* and *Oreopasites*, whereas state 2 occurs in (*Melanempis* + *Sphecodopsis*) (Fig. 2). For character 31 the derived state (i.e., state 1) gave the shortest tree.

PHYLOGENY OF THE AMMOBATINI

As indicated above, an analysis including all species separately was not successful because of missing data. The analysis of ground-plan adult character states (Appendix 2) of the species groups (Table 2), however, resulted in 48 most parsimonious cladograms, each with a length of 154 steps. The study of each of these 48 trees, and the strict consensus tree (Fig. 2) indicated a con-

Table 4. Data matrix of character states for genera (characters and coding of states according to Appendix 2).

Taxon	Characters						
Ancestor	000000000	000000000	000000000	000000000	000000000	000000000	000000000
<i>Sphecodopsis</i>	200111101	011001001	0012110100	100001001	0001001101	10000000	
<i>Pasites</i>	0001100011	0100010101	0011000000	0010000000	0110010001	10000000	
<i>Spinopasites</i>	10011000?1	0100010111	0021001000	1100000001	0001001201	1???????	
<i>Melanempis</i>	2101111102	1001011111	0022110010	0000011010	0001001301	10010000	
<i>Oreopasites</i>	1001100002	1000011011	0020010000	1100010001	0001001201	11000000	
<i>Ammobates</i>	1001100002	0000010111	0020000000	1100000001	0000101201	11000000	
<i>Caenoprosopis</i>	2010011001	0000101110	1110001101	0010010001	1000000002	10101001	

sistent pattern of seven major clades. The basal branch consistently represented the Caenoprosopidini, which was included in an attempt to demonstrate the monophyly of the Ammobatini, while the other six major clades more or less represented the ammobatine genera as defined by Michener (1944). The consistency in the composition of these six clades led to their being considered here to constitute genera (*Pasites*, *Spinopasites*, *Oreopasites*, *Ammobates*, *Sphecodopsis* and *Melanempis*, Fig. 1). Most of the trees differed only in the relative positions of the species groups within each clade.

Analysis of the data using successive approximations character weighting resulted in 12 most parsimonious trees, each with a raw length of 156 steps. The differences in the lengths of the trees produced with and without character weighting apparently resulted from the different configurations of the species groups within each genus and not from differences in the configuration of the genera. The final weight assigned to each character in the weighted analysis is recorded in Table 3.

The only difference in the relationships between the genera in the 48 most parsimonious unweighted cladograms was the relative position of *Oreopasites*. In some of the cladograms it formed the sister group of *Ammobates*, with (*Sphecodopsis* + *Melanempis*) as the sister group of (*Ammobates* + *Oreopasites*) (Fig. 3), while in the other cladograms it formed the sister group of (*Sphecodopsis* + *Melanempis*), with *Ammobates* as the sister group of (*Oreopasites* + (*Sphecodopsis* + *Melanempis*)). This resulted in a polytomy for *Oreopasites*, *Ammobates* and (*Sphecodopsis* + *Melanempis*) in the consensus tree (Fig. 2). The position of *Oreopasites* in the consensus tree, produced using successive approximations character weighting (Fig. 3), was the same as that which occurred most frequently among the trees produced without character weighting and was accepted as the most probable phylogeny. Evidence supporting this choice is the reduction in the male py-

gidial plate (state 52.1), which associates *Ammobates* and *Oreopasites* and was given a weight of 5 in the analysis using successive approximations character weighting (Table 3). The mandibles posterolaterally directed in repose (18.0) and the undifferentiated vestiture on the ventrolateral region of the mesepisternum (27.0), which group *Oreopasites* with (*Melanempis* + *Sphecodopsis*), have weights of 1 and 0 respectively (Table 3). The grouping of *Oreopasites* with *Ammobates* can also be more easily explained when considering the biogeography of these bees, the former genus is Neotropical and the latter mainly Palaearctic, where as the other ammobatine genera are primarily Afrotropical.

The analysis of generic ground plans (Table 4), without character weighting, gave a single most parsimonious tree (Fig. 4). The configuration of the tree differs from that produced by the former analyses (Figs. 1-3) only in the placement of *Spinopasites*. The difference is significant because it makes *Oreopasites* the sister group of *Ammobates*, whereas in the analysis of species and species groups *Oreopasites*, *Ammobates* and (*Melanempis* + *Sphecodopsis*) (Figs. 2 & 3) are more closely related to one another than to *Spinopasites*. The reason for the change is that in the generic ground plans of *Spinopasites*, *Oreopasites* and *Ammobates* the hind tibia has thick setae (32.1) and the posteromedian region of the female S5 has a distinct protuberance (48.2). In *Sphecodopsis* and *Melanempis* the hind tibia has fine vestiture (32.0). *Sphecodopsis* has a small posteromedian protuberance on the female S5 (48.1) and *Melanempis* has a large, gutter-like protuberance (48.3), making the derivation of the posteromedian protuberance on the female S5 dichotomous. Because of the absence of information on the male of *Spinopasites* it is possible that discovery of the male may alter the interpretation of the relationship between *Spinopasites* and its congeners.

Discussion of the generic relationships is based mainly on the cladogram of the

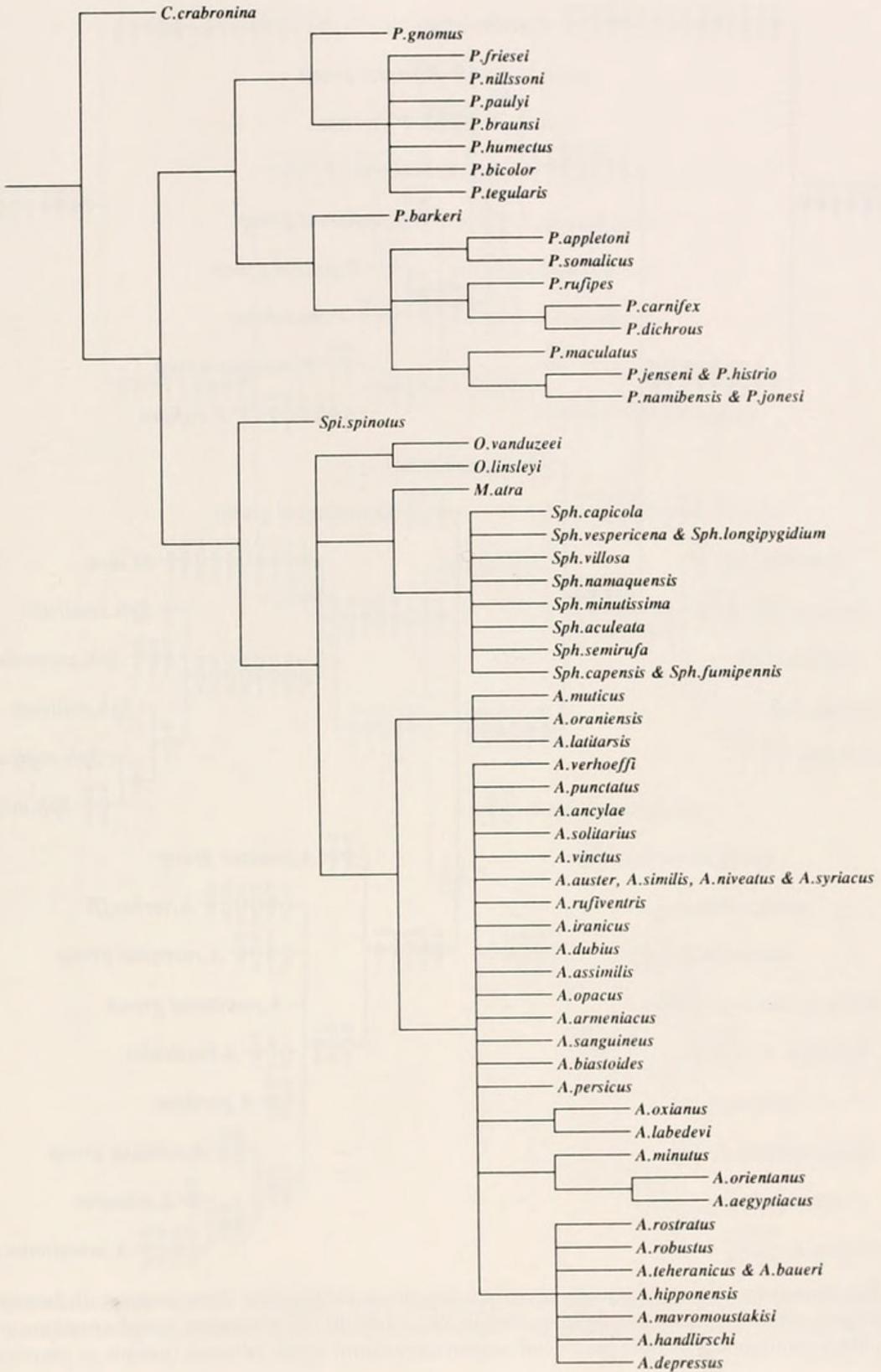


Fig. 1. Strict consensus tree of over 1200 equally most parsimonious cladograms from analysis of data in Table 1 (species), without character weighting (length 190, consistency index (CI) 38, retention index (RI) 83).

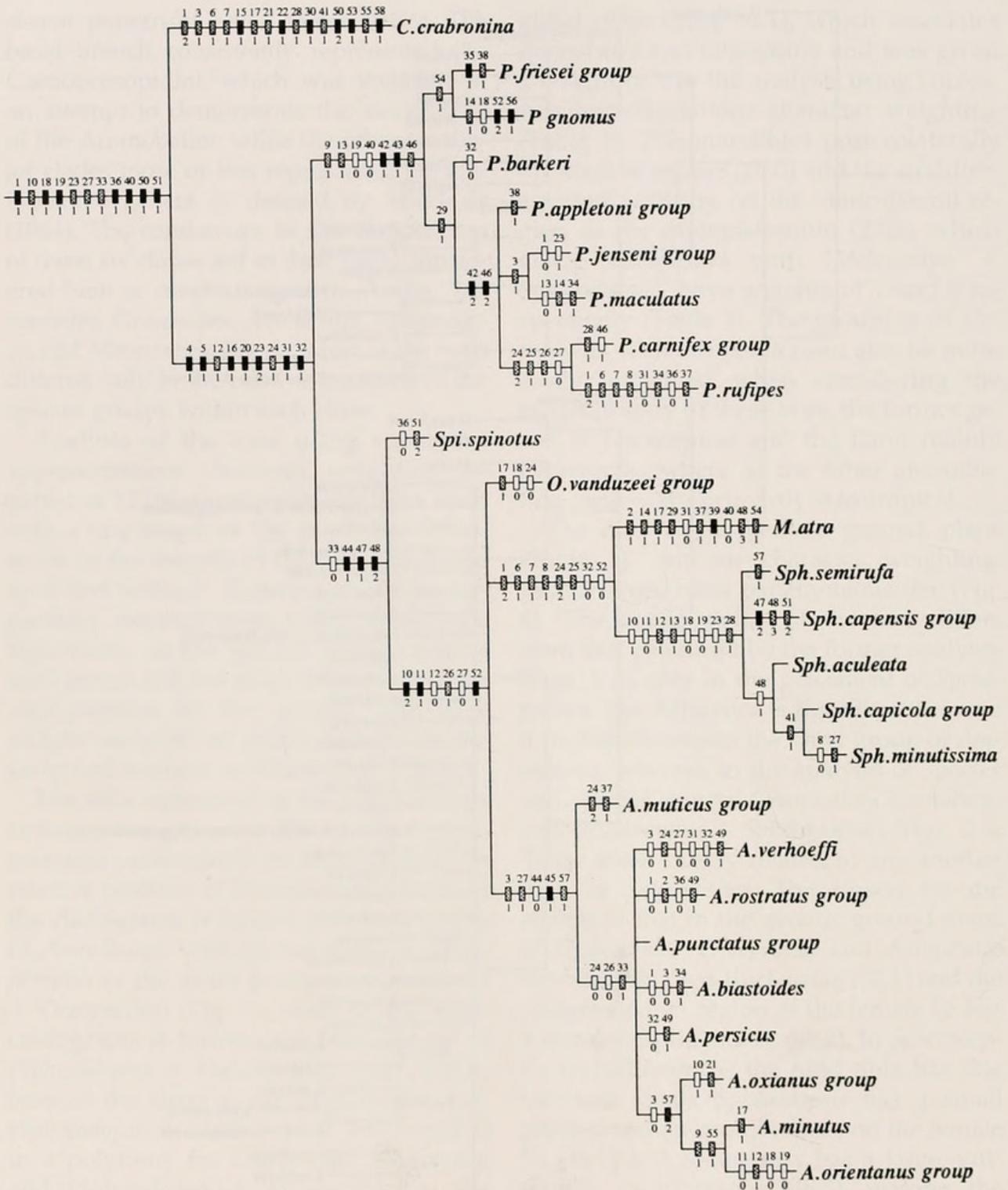


Fig. 2. Strict consensus tree of 48 equally most parsimonious cladograms from analysis of data in Table 2 (species groups), without character weighting (length 156, CI 45, RI 73). Character transformation symbolised as follows: black=unique derivation; grey=convergent derivation; open=reversal (unique or convergent).

species groups derived without weighting of characters (Fig. 2). Emphasis has not been placed on the generic analysis because the formation of generic ground plans for the more diverse genera, such as

Ammobates, resulted in the loss of information. The loss of information in the formation of ground plans for species groups was minimal.

The Caenoprosopidini is the sister

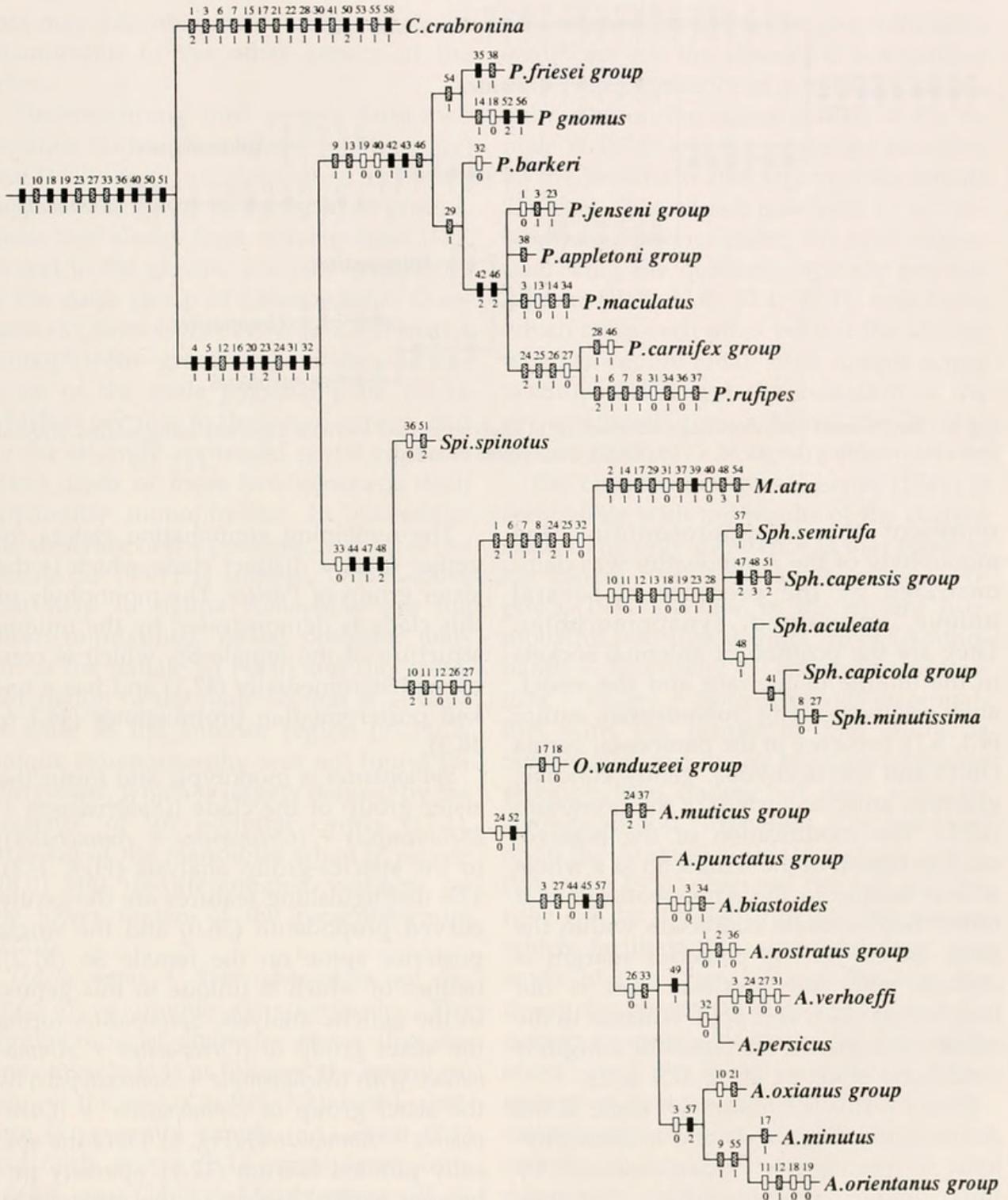


Fig. 3. Strict consensus tree of 12 equally most parsimonious cladograms from analysis of data in Table 2 (species groups), using successive approximations character weighting (raw length 158, CI 72, RI 88). For symbols see Fig. 2.

group of the Ammobatini, as was demonstrated by Roig-Alsina (1987, 1991) who adequately discussed the relationship between these two tribes. Roig-Alsina (1987, 1991) clearly demonstrated the Caenopro-

sopidini to be monophyletic by the presence of several unique synapomorphies, but was unable to demonstrate the monophyly of the Ammobatini in this way. By including *C. crabronina* in this study, to

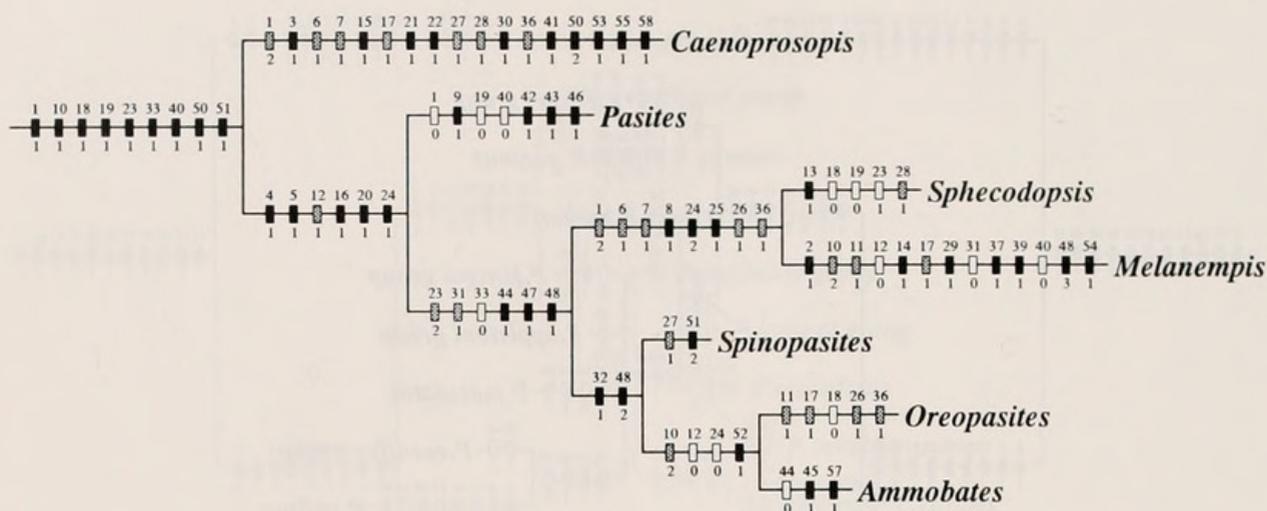


Fig. 4. Single most parsimonious cladogram from analysis of data in Table 3 (genera using adults), without character weighting (length 88, CI 69, RI 52). For symbols see Fig. 2.

represent the Caenoprosopidini, the monophyly of the Ammobatini was demonstrated by the presence of several unique, unreversed, synapomorphies. They are the position of antennal sockets in the middle of the face and the associated relatively long subantennal suture (4.1, 5.1), presence of the paraocular carina (16.1) and the declivous, gently concave, glabrous anterior surface of the pronotum (20.1). The modification of the posteromedian region of the female S5 as a whole is also unique to the Ammobatini, but it forms two separate characters within the tribe. In *Pasites* the posterior margin is clothed with fine vestiture and is not lengthened (44.1, 46.1 & 2), whereas in the other Ammobatini the posterior margin is naked and elongate (44.0, 47.1 & 2).

Pasites forms the first major clade of the Ammobatini (Figs. 1-4) and is monophyletic. Its monophyly is demonstrated by three unique synapomorphies, the presence of a subpygidial brush in the female (state 42.1), the fine vestiture and structure of the posteromedian region of the female S5 (43.1, 46.1). Supporting character states are: 10-segmented male antennal flagellum (9.1); spatulate labrum (13.1); position of the mandibles when in repose in both sexes (19.0) and presence of a pygidial plate in the female T6 (40.0).

The remaining ammobatine genera together form a distinct clade which is the sister group of *Pasites*. The monophyly of this clade is demonstrated by the unique structure of the female S5, which is concave posteromedially (47.1) and has a naked posteromedian protuberance (44.1 & 48.2).

Spinopasites is monotypic and forms the sister group of the clade ((*Sphecodopsis* + *Melanempis*) + (*Oreopasites* + *Ammobates*)) in the species-group analysis (Figs. 1-3). The distinguishing features are the gently curved propodeum (36.0) and the single posterior spine on the female S6 (51.2), neither of which is unique to this genus. In the generic analysis, *Spinopasites* forms the sister group of (*Oreopasites* + *Ammobates*), with (*Melanempis* + *Sphecodopsis*) as the sister group of (*Spinopasites* + (*Oreopasites* + *Ammobates*)) (Fig. 4). Here the apically pointed labrum (12.1), sparsely pubescent ventral region of the mesepisternum (27.1) and the single posterior spine on the female S6 (51.2) are the distinguishing characters. The reason for the different distinguishing characters in the two trees is the changes made in the development of ground plans for the genera and possible ambiguities resulting from the use of consensus trees for the species-group analyses. The discovery of the male of this ge-

nus may unambiguously demonstrate its relationship to the other genera in the tribe.

The remaining four genera form two separate clades, (*Ammobates* + *Oreopasites*) and (*Melanempis* + *Sphecodopsis*). In the accepted cladogram of the species groups, these two clades form sister groups (Fig. 3) and in the generic analysis *Spinopasites* is the sister group of (*Ammobates* + *Oreopasites*). (*Ammobates* + *Oreopasites*) forms a monophyletic group defined by the absence of the male pygidial plate (52.1), which is peculiar to these two genera, and by the strongly appressed scutal vestiture (24.0). Each of these two genera is itself apparently monophyletic. In *Ammobates* the structure of the posterior margin of the female S5 (45.1) is unique. Other states that help to define *Ammobates* are the short, unmodified, naked posterior margin of the female S5 (44.0) and the posterior region of the male S8 that is at least as wide as the anterior region (57.1). A unique synapomorphy was not found for *Oreopasites*, which is largely defined by the presence of an occipital carina (17.1), crossing of the mandibles when in repose (18.0) and undifferentiated vestiture on the lower region of the mesepisternum (27.0).

(*Melanempis* + *Sphecodopsis*) is not defined by a unique synapomorphy. The combination of character states that defines this clade is as follows: the lateral region of the vertex is flat (1.2); facial vestiture is generally simple (6.1), erect (7.1) and fairly sparse (8.1); scutal vestiture is mostly erect (24.2) and fairly sparse (25.1); vestiture on the ventrolateral region of the mesepisternum is not obviously different from that on the upper region (27.0); setation on the hind tibia is more or less uniform (32.0) and the male pygidial plate is well developed (52.0). *Melanempis* is clearly monophyletic, defined primarily by the truncate female T6 which is naked and surrounded by a small carina (39.1). Of the

other states that define this genus the most significant are the absence of a maxillary palp (14.1), presence of a mediolongitudinal carina on the dorsal surface of the female T6 (37.1) and the gutter-like structure on the posteromedian region of the female S5 (48.3). *Sphecodopsis* is defined by a combination of several states, the most important being the quadrate, apically pointed labrum (10.0, 11.0, 12.1, 13.1), mandibles which cross each other behind the labrum when in repose (18.0, 19.0), simple scutal vestiture (23.1) and the extension of the pre-epistomal groove below the scrobal groove (28.1).

The classification of Michener (1944) is compatible with the results of the current study. The only difference is that some of his genera have been synonymized. Popov's (1951) division of the current Ammobatini into two distinct tribes (Ammobatini = *Ammobates* + *Oreopasites* and Pasitini = *Pasites* + *Sphecodopsis*) is incompatible with the results of this study as *Sphecodopsis* and *Pasites* belong to separate monophyletic clades, but does associate *Ammobates* and *Oreopasites*. The inclusion of all the Ammobatini into a single genus (Warncke 1983) obscured the fact that the tribe can be divided into definite groups which facilitate the understanding and study of these bees. The differences between the genera, as delimited above, appear to be more consistent with the differences used to define genera in other groups of bees, and a subgeneric classification could even be gainfully applied to certain of the ammobatine genera, expressly *Pasites* and *Ammobates*.

Five of the ammobatine genera are confined to the Old World: *Sphecodopsis* (southern Africa; 9 species) and *Melanempis* (Madagascar, four species, R.W. Brooks pers. comm.) are Afrotropical; *Pasites* is predominantly Afrotropical (23 species) but has 1 species in the Palaearctic Region; *Spinopasites* is Palaearctic (Tunisia, 1 species), and *Ammobates* is predominantly Pa-

laearctic (Mediterranean, eastern Europe and Iran, 47 species being revised by M. Schwarz (pers. comm.)) but has 1 species in southern Africa. *Oreopasites* is the only New World genus and its 11 species occur in the southwest of the Nearctic Region (Rozen 1992).

The sister group of the Ammobatini, the Caenoprosopidini (Roig-Alsina 1987, 1991), is Neotropical and its species occur mainly in the Patagonian Subregion of South America (Roig-Alsina 1987; Kuschel 1969). This suggests that the common ancestor of the (Caenoprosopidini + Ammobatini) occurred in that part of Gondwanaland which today forms southern Africa and the southern part of South America. It also suggests that the Ammobatini evolved subsequent to the separation of South America from southern Africa, about 120 million years ago (Smith *et al.* 1981). The common ancestor of the (Caenoprosopidini + Ammobatini) must, however, have occurred before that time. Therefore, it may be assumed that the Ammobatini originated in the Old World, and most probably in the Afrotropical Region because *Pasites*, which forms the basal clade of the Ammobatini, is primarily Afrotropical (the Palaearctic *P. maculatus* Jurine is one of the most derived species in the genus). The Ammobatini are assumed to have spread from the Afrotropical into the Palaearctic Region. *Ammobates* and *Oreopasites* are evidently sister groups, and the colonization of the Nearctic probably took place from the Palaearctic Region.

Our knowledge of the paleovegetation in Africa is inadequate to facilitate a detailed hypothesis on the vegetation types that the ancestors of the extant ammobatine genera inhabited. Soon after the breakup of Gondwanaland the vegetation in Africa was vastly different from that of today (Axelrod & Raven 1978) and it consisted largely of rain forest and woodland.

Although most of the extant Ammobatini live in the semi-deserts of southern Africa and the Mediterranean Region, *Pasites* inhabits a variety of different vegetation types, and occurs in rain forest, woodland and desert. This supports the conclusion that *Pasites* is the oldest ammobatine genus and suggests that the habitation of arid areas is derived for the tribe. The occurrence of *Ammobates auster* spec. nov. in the arid areas of southern Africa suggests that *Ammobates* was previously more widely distributed in Africa.

REVISION OF AFROTROPICAL AMMOBATINI HANDLIRSCH

The tribe Ammobatini was first proposed by Handlirsch (1925). Ammobatine bees are small to medium sized (2.3–12.5 mm long). They are mostly black to reddish with short, densely plumose, appressed vestiture and the metasoma is strongly convex dorsally. Most species of *Sphecodopsis*, however, have long, weakly plumose, semi-erect vestiture and the metasoma is flattish. The principal diagnostic features of the Ammobatini are: paraocular carina well developed on lower half of face; male with a tuft of hairs on lower lateral part of labrum, except *Melanempis*; pronotal collar carinate laterally; female T5 lacks a pseudopygidial area, S5 concave posteromedially when viewed from behind; apex of concavity of female S5 extended into a protuberance that may be gutter-like in all genera except *Pasites*; female S6 reduced and largely internal, visible externally as one or two sclerotized spines, not longitudinally separated, without coarse setae.

Many of the species are dealt with in groups (Appendix 1). The purpose of the species groups is to facilitate the description and discussion of closely related species, and should also facilitate the recognition of the species.

KEY TO THE GENERA OF AMMOBATINI
(Males and Females)

1. Distal ends of mandibles crossing diagonally in repose 2
- Distal ends of mandibles entirely overlapping in repose 3
2. Labrum short (about quadrate) and pointed apicomediaally, mandibles closing behind labrum (Afrotropical) *Sphcodopsis* Bischoff
- Labrum long (about 1.4× as long as wide) and truncate distally, mandibles traversing labrum so that distal end of labrum is visible posterior to closed mandibles (Nearctic) ..
..... *Oreopasites* Cockerell
3. Female; metasoma with six exposed terga 4
- Male; metasoma with seven exposed terga 7
4. S5 with posteromedian region naked (often entire posterior margin naked) and with a small protuberance or a weak to well developed gutter posteromedially 5
- Always with entire posterior margin of S5 clothed with fine vestiture, and devoid of any modifications as described above *Pasites* Jurine
5. S6 forming a single spine posteriorly (North Africa) *Spinopasites* Warncke
- S6 bifurcate posteriorly 6
6. T6 with posterior end naked and circumscribed by a carina (Madagascan)
..... *Melanempis* Saussure
- T6 with posterior end setose, without a peripheral carina (southern African and Palaearctic)
..... *Ammobates* Latreille
7. Antenna 13-segmented; posterior end of T7 convex (except *Melanempis* which has 12 antennal segments and posterior end of T7 concave) 8
- Antenna 12-segmented, and T7 convex posteriorly *Pasites* Jurine
8. T7 spatulate, devoid of a pygidial plate and concave posteriorly (Madagascan)
..... *Melanempis* Saussure
- T7 usually with a pygidial plate, never concave posteriorly (southern African and Palaearctic) *Ammobates* Latreille

GENUS PASITES JURINE

Pasites Jurine 1807:224. Type species: *Pasites maculatus* Jurine 1807 (original designation).

Pasites (*Pasites*) Jurine; Warncke 1983:261–347.

Morgania Smith 1854:253; Cockerell 1933c:106; Warncke 1982:104–105 [synonymised]. Type species: *Pasites dichrous* Smith 1854 (monobasic).

Morgania (*Morgania*) Smith; Bischoff 1923:586.

Omachthes Gerstaecker 1869:154. Type species: *Omachthes carnifex* Gerstaecker 1869 (designated by Sandhouse 1943). Warncke 1983:291 [synonymized].

Homachthes Gerstaecker; Dalla Torre 1896:499 [unjustified emendation for *Omachthes*].

Morgania (*Omachthes*) Gerstaecker; Bischoff 1923:586.

Omachtes [sic.] Gerstaecker; Friese 1909:436–438 [lapsus].

Pasitomachthes Bischoff 1923:596; Warncke 1983:

291 [synonymised]. Type species: *Pasites nigerrimus* Friese 1922 (original designation).

Pasitomachtes [sic.] Bischoff; Sandhouse 1943:586 [lapsus].

The name *Pasites* is masculine according to the Code, Article 30(b), which specifies this for names with the suffix *-ites*. (Although Jurine gave no derivation for the name, it was probably derived from *pas* (Greek, all) and the suffix *-ites* (Greek, like), since he listed the ways in which the genus was similar to four other genera.) Jurine (1807) gave the specific epithet of the type species (*'maculata'*) a feminine ending, however, indicating that he considered the name to be feminine. According to the Code this must be considered an error, which was apparently first corrected by Gerstaecker (1869).

Smith (1854), at the end of his original

description of *P. dichrous* (as '*dichroa*'), stated that 'It is very probable that the present species may be separated from *Pasites* by a monographer of these parasitic genera, in which case we would propose the name of *Morgania*'. According to the Code, Article 11(d)(i), this made the name *Morgania* Smith, 1854 available. Subsequently, Gerstaecker (1869) described the genus *Omachthes* for *P. carnifex*, a species that closely resembles *P. dichrous* in all respects. Thereafter the names *Pasites*, *Morgania* and *Omachthes* were commonly applied, in an inconsistent manner, to this group of bees.

Bischoff (1923) provided the first monographic study of the Afrotropical cuckoo bees, and clearly stated that *Pasites* does not occur in the Afrotropical Region. He placed the Afrotropical species that had previously been placed in *Pasites* into *Morgania* (which he divided into two subgenera, namely *Morgania sensu stricto* and *Omachthes*) except for two species that were previously assigned to *Pasites* for which he described the genus *Pasitomachthes*. The two species are *P. nigerrimus* (= *P. barkeri* (Cockerell)) and *P. bicolor* Friese. The only information that Bischoff (1923) provided on his interpretation of *Pasites*, *Morgania*, *Omachthes* and *Pasitomachthes* was in a key to the ammobatine genera. The characters referred to in the key were either poorly described, which does not allow for an accurate interpretation of his ideas, or unreliable (Cockerell 1933c). Bischoff (1923) did not state whether he had studied the type species of *Morgania* and *Omachthes*, *P. dichrous* and *O. carnifex* respectively, which are clearly more closely related to one another than to any of the other species that he placed in either *Morgania sensu stricto* or *Omachthes*. The characters that Bischoff (1923) used to identify *Pasites* are, furthermore, clearly evident in some of the Afrotropical species. It is, therefore, inexplicable as to why he stated that *Pasites* does not occur in Africa. It is also not clear why he described the genus

Pasitomachthes for two species that apparently conform with his interpretation of *Morgania*. The current study, during which the type species of *Pasites*, *Morgania*, *Omachthes* and *Pasitomachthes* were studied, demonstrated that these four taxa are synonymous.

Pasites is primarily Afrotropical. *P. maculatus* Jurine, which is Palearctic, is the only species in the genus that does not occur in the Afrotropical Region. There are 15 subsaharan species, namely: *P. barkeri* Cockerell, *P. friesei* Cockerell, *P. paulyi* spec. nov., *P. braunsi* Bischoff, *P. humectus* spec. nov., *P. gnomus* spec. nov., *P. carnifex* (Gerstaecker), *P. dichrous* (Smith), *P. jenseni* (Friese), *P. namibiensis* spec. nov., *P. histrio* (Gerstaecker), *P. jonesi* (Cockerell), *P. rufipes* (Friese), *P. appletoni* (Cockerell) and *P. somalicus* spec. nov. Three species are endemic to Madagascar: *P. nilssoni* spec. nov., *P. tegularis* Friese and *P. bicolor*.

The species of *Pasites* are very small to large (3.9–12.5 mm long) and their colour varies from completely black to almost entirely reddish-orange. The diagnostic features of the genus are as follows: vertex, frontal view, distinctly convex (Figs. 5, 42), except that of *P. rufipes* in which vertex is flat laterally, raised between lateral ocelli (cf. Fig. 63); face with short brown to white or whitish vestiture, that on lower half of face densely plumose and that on upper half relatively sparse and mostly simple (Figs. 5, 42), except *P. rufipes* in which entire face is sparsely clothed with long, black, weakly plumose vestiture (cf. Fig. 63) and *P. maculatus* in which only area around antennal socket has plumose vestiture; antenna 12-segmented in both sexes; labrum variable in length and shape, ranging from little shorter to distinctly longer than its maximum width and from pointed apicomediaally to more or less truncate distally (Fig. 14); mandibles behind labrum in repose; scutellum gently and evenly curved mediolongitudinally, gently swollen paramediaally; last exposed metasomal tergum (T6 female, T7

male) either with or without pygidial plate; female S5 with strong conical (posterior apices of S5 diverging, Fig. 6) or elliptical concavity (posterior apices of S5 converging, Fig. 46), without posteromedian protuberance, border of concavity clothed with fine vestiture; female S6 bifurcate posteriorly.

The diagnostic characters of the species are diverse, ranging from their general colour, sculpture and vestiture to the structure of the maxillary palp, pygidium and S5 of the female, and the male ter-

minalia, as described below. Males are difficult to identify, but can usually be associated with conspecific females taken from the same area, by their colour and sculpture. This, together with the fact that the males of three species are unknown, has made it difficult to produce a reliable key to the males.

The genus has been divided into eight species groups, four of which are monotypic (Appendix 1). A diagnosis of *P. maculatus* has been included in order to bring this single extra-Afrotropical species into context with the remainder of the group.

KEY TO SPECIES OF *PASITES*
(Males and Females)

1. Palaearctic; upper paraocular area distinctly swollen, resulting in it being strongly incurved above antennal sockets and dorsomedially *P. maculatus* (Jurine)
 - Afrotropical; upper paraocular area flat to slightly swollen, resulting in it being gently curved above antennal sockets and dorsomedially 2
2. Occurring in subsaharan Africa 3
 - Madagascan (ater group, part) 22
3. Head, viewed perpendicular to lower region of clypeus, with upper margin of vertex between eye and lateral ocellus straight (cf. Fig. 63); facial vestiture weakly plumose and black; metasoma black; pygidial plate absent (male unknown) *P. rufipes* (Friese)
 - Vertex convex (Figs. 5, 42); facial vestiture densely plumose near antennal sockets and usually whitish, if brown or black then metasoma orange; metasoma black, reddish black or orange; female with well developed pygidial plate 4
4. Very small, 2.3–2.5 mm long; pygidial plate absent in both sexes, female with subpygidium well developed posteriorly, about half as long as its maximum width and densely clothed with fine brownish-yellow vestiture (Fig. 29); male S8 with two well developed anterior lobes (Fig. 31); gonocoxite of genitalia broadly rounded posteriorly (Fig. 32) ...
 - *P. gnomus* Eardley
 - Small to large, 3.7–12.5 mm long; pygidial plate always present, but sometimes reduced; female with subpygidial brush short, distinctly less than half as long as its maximum width (Figs. 6, 15, 19, 20, 24, 28); male terminalia otherwise 5
5. Metasoma orange and largely naked, with a little orange vestiture; vestiture on head and mesosoma brown to white (large, 7.0–12.5 mm long) (carnifex group) 6
 - Metasoma with integument usually black or blackish, sometimes reddish to orange, always with white plumose vestiture; vestiture on head and mesosoma always pallid (small to large, 3.7–8.8 mm long) (Males are difficult to identify and for some species are unknown, females are usually required for a positive identification.) 7
6. First flagellomere 1.2× as long as second flagellomere; female subpygidial brush expanded dorsally (Fig. 38); male S8 parallel-sided posteriorly and weakly concave posteromedially (Fig. 39) *P. dichrous* Smith
 - First flagellomere 2.5× as long as second flagellomere; female subpygidial brush not expanded dorsally (Fig. 34); male S8 tapering posteriorly and with posterior end distinctly emarginate (Fig. 36) *P. carnifex* (Gerstaecker)
7. Female with posteromedian concavity on S5 conical [posterior apices diverging] (Figs. 6,

- 15, 19, 20, 24, 28); male integument usually completely black to blackish, legs always black; pygidial plate of male tapering posteriorly when viewed from above 8
- Female with posteromedian concavity on S5 elliptical [posterior apices converging] (Figs. 43, 47, 50, 51, 53, 57, 58); male integument black to orangish; pygidial plate with posterior end more or less parallel-sided in dorsal view, except for *P. appletoni* in which legs and metasoma orangish 12
8. Female with pygidial plate well developed laterally and posteriorly (Fig. 6); vestiture on posterior margin of T2-T4 directed laterally *P. barkeri* (Cockerell)
- Female pygidial plate either well developed laterally and notched posteriorly or entire plate strongly reduced (Figs. 15, 19); vestiture on posterior margin of T2-T4 directed posteriorly (ater group, part) 9
9. Female with entire pygidial plate strongly reduced laterally, only posterior margin clearly visible (Fig. 20); male S7 tapering evenly towards posterior end which is distinctly emarginate (Fig. 21) *P. humectus* Eardley
- Female pygidial plate well developed laterally, notched posteriorly (Figs. 15, 19); male S7 otherwise 10
10. Maxillary palp five-segmented *P. paulyi* Eardley
- Maxillary palp two or three-segmented 11
11. Maxillary palp two-segmented *P. friesei* Eardley
- Maxillary palp three-segmented (male unknown) *P. braunsi* (Bischoff)
12. Metasoma with six exposed terga and five exposed sterna, excluding highly modified S6; terminal tergum (T6) with a well developed subpygidial brush; terminal sternum (S5) strongly concave posteromedially (female) 13
- Metasoma with seven exposed terga and six exposed sterna; terminal tergum without a subpygidial brush; terminal sternum entire (male) 18
13. Pygidial plate distinct laterally, either notched or absent posteriorly (Figs. 53, 57) (*appletoni* group, part) 14
- Pygidial plate never notched posteriorly, sometimes reduced laterally (Figs. 43, 47, 50) (*jenseni* group, part) 15
14. Pygidial plate fully developed, except for a small notch posteromedially (Fig. 53) *P. appletoni* (Cockerell)
- Pygidial plate only visible laterally, without a distinct posterior margin (Fig. 57) *P. somalicus* Eardley
15. Propodeum with mediolongitudinal region punctate and clothed with fine vestiture . . . 16
- Propodeum with mediolongitudinal region glabrous and naked 17
16. Pygidial plate well developed both laterally and distally (Fig. 43); labrum tuberculate apicomediaally *P. jenseni* (Friese)
- Pygidial plate reduced laterally so that it exists only as a distinct carina on posterior end of T6 (Fig. 50); labrum with a transverse carina apically *P. jonesi* (Cockerell)
17. Labrum relatively long, 1.2–1.3× as long as its maximum width . . . *P. namibiensis* Eardley
- Labrum quadrate *P. histrio* (Gerstaecker)
18. Head and mesosoma mostly black, with mandible, labrum, antenna, pronotal lobe, tegula and legs orangish, and metasoma orange; scutum fairly densely covered with small, well separated punctures; propodeum with a broad, naked, glabrous mediolongitudinal band; S8 strongly expanded laterally and weakly emarginate posteriorly (Fig. 55) (*appletoni* group, part) *P. appletoni* (Cockerell)
- Generally with head, mesosoma and metasoma mostly black; if with orange coloration similar to that described above, then with large widely spaced scutal punctures and mediolongitudinal region of propodeum either hisute or with glabrous area greatly expanded dorsally; S8 either moderately expanded laterally and pointed posteriorly or weakly expanded laterally and truncate posteriorly (Figs. 45, 49) (*jenseni* group, part) 19
19. Propodeum with mediolongitudinal region punctate and clothed with fine vestiture . . . 20
- Propodeum with mediolongitudinal region glabrous and naked 21

20. Labrum tuberculate apicomediaally *P. jenseni* (Friese)
 – Labrum with a transverse carina apically *P. jonesi* (Cockerell)
21. Labrum relatively long, 1.2–1.3× as long as its maximum width *P. namibiensis* Eardley
 – Labrum quadrate *P. histrio* (Gerstaecker)
22. Integument of head and mesosoma mostly reddish; S7 acutely pointed posteriorly and carinate posteroventrally (Fig. 11) *P. nilssoni* Eardley
 – Integument of head and mesosoma black; S7 parallel-sided posterolaterally with posterior end emarginate (Fig. 25), without a posteroventral carina (males of the following two species are indistinguishable) 23
23. Female pygidial plate absent (Fig. 24) *P. bicolor* Friese
 – Female pygidial plate well developed laterally and notched posteriorly (Fig. 28)
 *P. tegularis* Friese

BARKERI SPECIES GROUP

This species group is monotypic.

Pasites barkeri (Cockerell), **comb. nov.**
 (Figs. 5–10)

Morgania barkeri Cockerell 1919:189–190.

Pasites nigerrimus Friese 1922:39; Cockerell 1932: 115 [part].

Pasitomachthes nigerrimus (Friese); Bischoff 1923: 596–598.

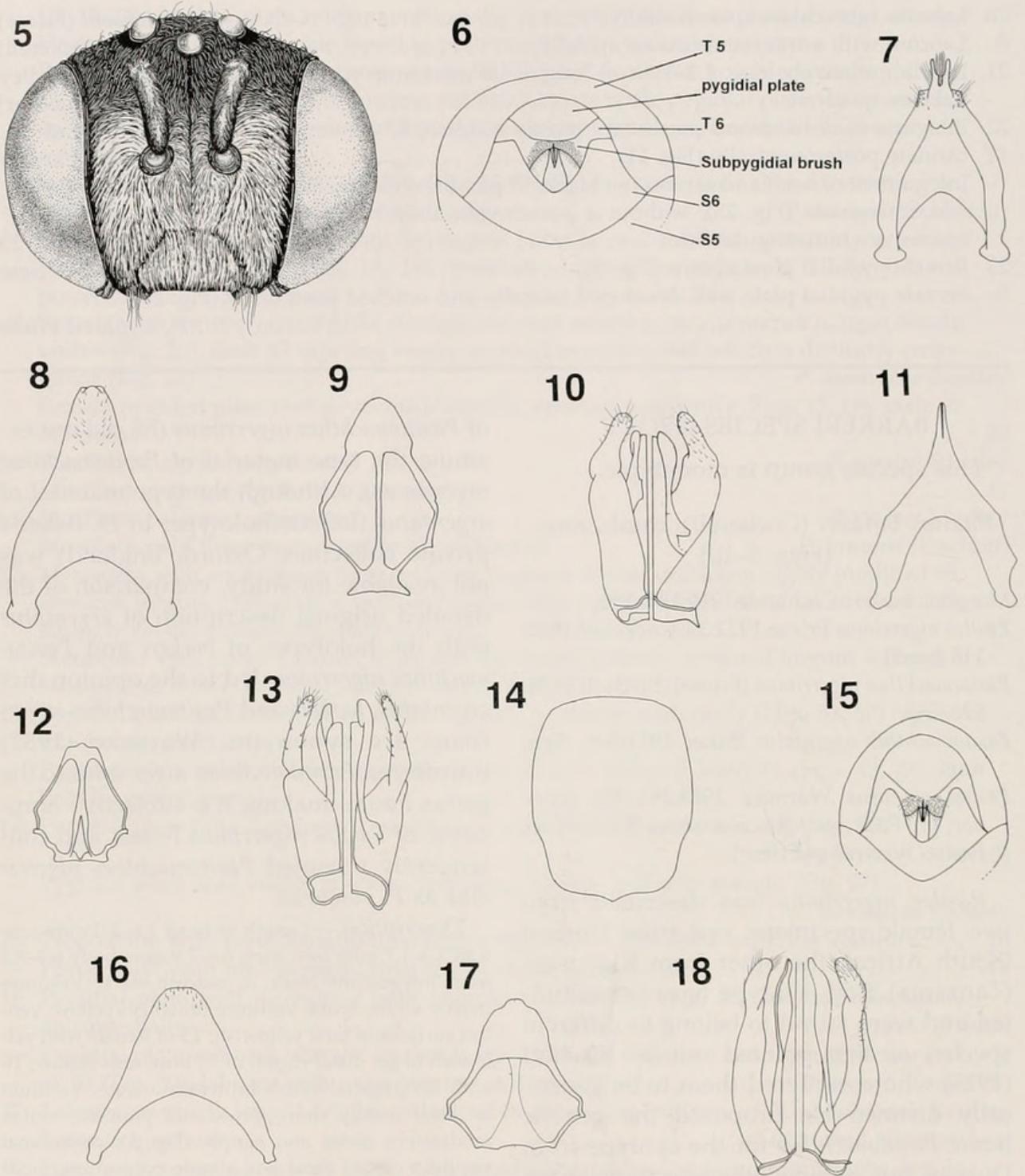
Pasitomachthes argentatus Baker 1971:3–8. **Syn. nov.**

Pasites obscurus Warncke 1983:291–292 [*nom. nov. pro Pasitomachthes nigerrimus* Bischoff *nec Pasites nigerrimus* Friese].

Pasites nigerrimus was described from two female specimens, one from Durban (South Africa), the other from Kigonsera (Tanzania). Both syntype have been studied and were found to belong to different species, as first pointed out by Bischoff (1923) who considered them to be generically distinct. He proposed the generic name *Pasitomachthes* for the syntype from Durban but retained the specific epithet, calling his new species *Pasitomachthes nigerrimus*. The types of *barkeri* and *Pasitomachthes nigerrimus* closely resemble one another and are clearly conspecific, which suggests that Friese (1922) was not aware that the species had been described by Cockerell (1919) (*Pasites nigerrimus* Friese is a junior synonym of *friesei*, q.v.). Baker (1971) described *argentatus* in detail, and compared it with the original description

of *Pasitomachthes nigerrimus* (he did not examine the type material of *Pasitomachthes nigerrimus*). Although the type material of *argentatus* (female holotype, in D. Baker's private collection, Oxford, England) was not available for study, comparison of the detailed original description of *argentatus* with the holotypes of *barkeri* and *Pasitomachthes nigerrimus* led to the opinion that *argentatus*, *barkeri* and *Pasitomachthes nigerrimus* are synonyms. Warncke (1983) transferred *Pasitomachthes nigerrimus* to the genus *Pasites* making it a subjective homonym of *Pasites nigerrimus* Friese, and consequently renamed *Pasitomachthes nigerrimus* as *P. obscurus*.

Description.—Length of head 1.6–2.0 mm; scutum 1.3–1.7 mm; fore wing 6.4–7.9 mm; body 6.3–8.8 mm. Integument black to reddish-black. Vestiture mostly white, scutal vestiture brownish-yellow; ventral surfaces of tarsi yellowish; T5 of female with yellowish tinge, distal region of S5 brownish-yellow; T6 with subpygidial brush brownish-orange. Vestiture on head mostly short, dense and plumose, vertex moderately dense and simple (Fig. 5); mesosomal vestiture dense, short and simple on scutum, moderately sparse on ventrolateral region of mesepisternum, very sparse on trochanters and femora, very dense on ventral surfaces of tarsi; T1 with anterior surface and posterolateral regions with dense plumose vestiture, vestiture on remainder of T1 sparse; T2–T4 with anterior regions sparsely, distal regions with moderately dense fringes of laterally directed vestiture; female T5, male T5–T6 with vestiture of distal fringes directed posteriorly; female T6 with subpygidial brush (Fig. 6); metasomal venter moderately sparsely to densely pubescent, with velvety vestiture surrounding distal concavity of S6. Labrum quadrate,



Figs. 5-18. *Pasites* spp. 5-10. *P. barkeri*. 5. Head, front view, ♀; 6. Terminalia, posterior view, ♀; 7. S6, ♀; 8. S7, ♂; 9. S8, ♂; 10. Genital capsule, left half dorsal, right half ventral, ♂ (♂ terminalia: anterior below, posterior above). 11-13. *P. nilssoni*, ♂. 11. S7; 12. S8; 13. Genital capsule. 14-18. *P. friesei*. 14. Labrum, ♀; 15. Terminalia, posterior view, ♀; 16. S7, ♂; S8, ♂; 18. Genital capsule, ♂.

apex carinate with carina strongly tuberculate medially, rounded apicolaterally; maxillary palp five-segmented, about twice as long as pedicel of antenna; scutum densely punctate, punctures small and separate; scutellum strongly convex, but only slightly swollen paramedially; mesopleuron generally mod-

erately densely punctate, punctures fairly large and separate; propodeum largely punctate, narrowly glabrous medioposteriorly; pygidial plate broad and well developed in both sexes; female with subpygidial brush short and devoid of ventral tuft (Fig. 6); female S5 with deep, conical concavity (Fig. 6), S6

narrowly bifid (Fig. 7); male S7, S8 and genital capsule as in Figs. 8–10.

Distribution.—Tropical and subtropical regions of Africa, mostly in forest and woodlands; known from Zaïre, Uganda, Burundi, Tanzania, Zimbabwe and east coast of South Africa.

Discussion.—This is the only species that is black or blackish with short simple vestiture on the scutum, laterally directed vestiture on T2–T4 and a well developed pygidial plate in the female.

It resembles certain of its congeners, the friesei species group, *P. gnomus* and the carnifex species group, in that the lateral margins of the posteromedian concavity of the female S5 diverge (Figs. 6, 15, 29, 34). The structure of the male gonocoxite (Fig. 10) resembles that of *P. paulyi* and *P. nilssoni* (Fig. 13), both of which belong to the friesei group, more closely than to any other species in the genus. In the cladistic analysis (Fig. 2) it is demonstrated as the sister species to the clade that comprises the appletoni, carnifex and jenseni groups, *P. rufipes* and *P. maculatus*.

Cockerell (1933c) recorded the host of this species as possibly being *Nomia garua* Strand (Halictidae: Nomiinae).

Type material examined.—*Morgania barkeri*, holotype ♀: 'Durban, Natal, 9.iii.1918, C.N. Barker; *Morgania barkeri* Ckll. Type; TYPE' (DMSA). *Pasitomachthes nigerrimus*, holotype ♀ & *Pasites nigerrimus*, paralectotype ♀: 'Durban 10.3.1, Hayar 1219 [on reverse side of label]; *Pasitomachthes nigerrimus* Bisch. Typ. ♀; War Cotytype des *Omachthes nigerrimus* Fr., Coll. Friese; Typus; Zool Mus Berlin' (ZMHB).

Additional material examined.—17♀ 11♂: **ZAIRE:** 'SL Edourd, Bitshumbi (925m), Parc Nat. Albert', 22.iv.1936, L. Lippens (1♂ MRAC). **ZIMBABWE:** Victoria Falls, 20.i.1927 (1♀ 5♂ SAMC, 1♂ SANC). **SOUTH AFRICA:** Kosi Bay, 26.58S 32.48E, 10–11.ii.1990, C.D. Eardley (1♂ SANC); Mfongosi, iv & xii.1916 & iii.1917, W.E. Jones (9♀ SAMC, 1♀ SANC); Charters Creek, St Lucia, 28.12S 32.25E, 14–16.i.1981, R. Oberprieler (1♀ SANC); Durban, Bluff, 26.ii.1921, C.N. Barker (1♂ DMSA); Burman Bush, 8–18.iii.1963, H. Empey (2♀ 2♂ SANC); Montclair, Durban, 25.iii.1945 (1♀ DMSA, 1♀ SAMC); Port St. John, 19.iii.1969, L.C. Starke (1♀ SANC).

Other published distribution records.—**TANZANIA:** Kigonsera (Friese 1922); **ZAIRE:** Dilolo

& 50 km S. Bukavu (Cockerell 1932); **LIBERIA:** Monrovia, **GHANA:** Aburi, **UGANDA:** Kampala, **TANZANIA:** Uvira (Cockerell 1933c); **CAMEROON & GHANA** (Medler 1980); and **ZIMBABWE:** Bulawayo (Baker 1971).

FRIESEI SPECIES GROUP

This species group comprises the following seven species: *P. nilssoni*, *P. friesei*, *P. paulyi*, *P. braunsi*, *P. humectus*, *P. bicolor* and *P. tegularis*. In most of these species the head and mesosoma are black and the metasoma ranges from black to reddish. In *P. nilssoni* the head, mesosoma and metasoma are reddish. The most useful diagnostic characters of the group are the conical posteromedian concavity of the female S5 in combination with the female subpygidial brush which is undifferentiated and either longer than wide or quadrate (Figs. 15, 19, 20, 24, 28). The female of *P. nilssoni* is unknown. The females are generally more distinctive and can be separated more easily than the males.

Pasites nilssoni Eardley, spec. nov. (Figs. 11–13)

This species is named for the collector, Prof. L.A. Nilsson, of Uppsala University, Sweden, who recognized it as being new.

Description.—Male (female unknown). Lengths: head 1.4 mm; scutum 1.1 mm; fore wing 4.8 mm; body 5.3 mm. Integument of head mostly orange with upper region of face and posterior region of gena partly black; mesosoma orange with mediolongitudinal region of scutum, anterior and ventral areas of pleuron, venter and propodeum black to orangish-black; legs more or less with ventral surface of femora, most of tibia and entire tarsi black or blackish; metasoma mostly orangish-black anteriorly, blackish-orange posteriorly. Vestiture mostly white to whitish, scutum with pale yellow tinge, ventral surfaces of tarsi pale yellow, S6 yellowish. Vestiture generally ranges from strongly to weakly plumose, fairly dense; upper region of face, vertex, most of scutum and scutellum, lower region of mesopleuron, trochanters and femora mostly with simple vestiture; propodeum with lateral surface and mediolongitudinal region of posterior surface naked; T1 mostly pubescent, distal margin naked; T2–T6 mostly with fine vestiture anteriorly and dense pubescent cross-bands posteriorly; T7 with sparse simple vestiture on pygidial plate; metasomal venter largely densely pubescent, S6 with

simple vestiture. Structure similar to *P. barkeri* except as follows: labrum without distinct carina or tubercle; maxillary palp little longer than pedicel of antenna (1.4:1); scutellum strongly convex with distinct mediolongitudinal cleft; propodeum with naked areas laterally, glabrous posteriorly; pygidial plate weakly pointed posteriorly; posterior end of S7 pointed and distinctly keeled ventrally (Fig. 11); S8 and genital capsule as in Figs. 12–13.

Distribution.—Morondava, forested west coast of Madagascar.

Discussion.—Within the group, this species can be easily recognized by the unique orangish integument of the male head and mesosoma. A more precise determination of the relationship between this and the other species in the group must await the discovery of the female.

Type material.—Holotype ♂: 'MADAGASCAR: OUEST: Toliary Morondava, Florêt de Kirindy, 25.xi.1989, PL. REPR. ECOL. PRO.' (NCUS).

Pasites friesei Cockerell
(Figs. 14–18)

Pasites ater Friese 1909b:148 [*nec Pasites ater* Spinola 1806].

Morgania (Omachthes) ater [*sic.*] (Friese); Bischoff 1923:588.

Pasites friesei Cockerell 1910:217. [*nom. nov. pro P. ater* Friese *nec* Spinola].

Morgania friesei (Cockerell); Cockerell 1933c: 109–110.

Pasites nigerrimus Friese 1922:39; Cockerell 1932: 115 [part]. **Syn. nov.**

Morgania (Omachthes) nigerrimus [*sic.*] (Friese); Bischoff 1923:596.

Morgania nigerrimus [*sic.*] (Friese); Cockerell 1933c:108.

Morgania chubbi Cockerell 1919:189–190. **Syn. nov.**

Morgania (Omachthes) nigritula Bischoff, 1923: 588. **Syn. nov.**

Omachthes nigritulus (Bischoff); Anonymous 1958:32.

Morgania peratra Cockerell 1933c:109–110. **Syn. nov.**

Although *P. ater* Friese is a junior objective homonym of *P. ater* Spinola (1806), the latter was synonymized with the Palearctic species *Biastes brevicornis* (Panzer 1798) by Dalla Torre (1896). *Biastes brevicornis* is the senior synonym of *Pasites uni-*

color Jurine, one of the two species originally placed in *Pasites* by Jurine (1807).

The type material of *Pasites nigerrimus* has been studied and comprises two distinct species, as originally noticed by Bischoff (1923) who described the Durban syntype as *Pasitomachthes nigerrimus*. The syntype from Kigonsera is designated here as the lectotype of *Pasites nigerrimus*; it is clearly conspecific with the holotype of *P. ater*.

Cockerell (1919) described *chubbi* from a single female from Durban. He did not give a comparison between this species and any of its congeners. Bischoff (1923) separated *ater* and *nigritula* primarily on the structure of the distal fringe on the female T5, and he did not refer to *chubbi*. As *nigritula* closely resembles *chubbi*, it appears that Bischoff (1923) was not aware of Cockerell's (1919) paper. During the course of this study much material of this species, from numerous localities, was studied and the species was found to be widely distributed and the extent of the vestiture variable. The study, which included the examination of the type material, revealed that *friesei*, *chubbi* and *nigritula* are synonyms.

The male of this species was first described by Cockerell (1933c) as *M. peratra*. The association of the sexes, by the study of specimens of both sexes taken together resulted in the synonymy of *friesei* and *peratra*.

Morgania nigritula was described from two females, from Sunday's River and Plat River (eastern Cape, South Africa). The Sunday's River specimen is the only syntype that was traced, and it is here designated as the lectotype.

Description.—Length of head 1.3–2.0 mm; scutum 0.8–1.8 mm; fore wing 4.4–6.9 mm; body 4.5–7.1 mm. Integument black, except tegula, legs and metasoma sometimes reddish. Vestiture mostly white, ventral surfaces of tarsi, female T5, S5 and male T6, S6 with pale yellow tinge; female subpygidial brush brownish-orange. Head mostly densely pubescent, upper region of face and vertex with sparse vestiture (*cf.* Fig. 5); mesosoma with pronotal collar, most of

pronotal lobe, lateral regions of mesopleuron (excluding lower hypopimeral area) and posterolateral regions of mesopodeum densely pubescent; remainder of mesosomal vestiture sparse; vestiture on legs dense, except trochanters and femora sparse to very sparse, ventral surfaces of tarsi very dense; T1 anterior surface and posterolateral region with dense plumose vestiture, remainder with sparse, simple vestiture; T2 and sometimes T3 posterolaterally with dense, directed, vestiture posterolaterally, anterior regions of each tergum with sparse, simple vestiture; female T3/T4-T5, male T3/T4-T6 with moderately dense distal fringes of laterally directed hairs (vestiture sparse and simple anteriorly); female T6 with sparse vestiture and with weakly developed subpygidial brush (Fig. 15); female S2-S4 with vestiture fairly sparse anteriorly, dense posteriorly, S5 with moderately dense vestiture, distal margin velutinous; male metasomal venter moderately densely pubescent. Labrum little longer than wide, weakly tuberculate apicomediaally (Fig. 14); maxillary palp two-segmented, less than one-half as long as pedicel (except three-fourths as long as pedicel in one specimen); scutum 1.1× as long as narrowest width, punctures moderately large, often confluent; scutellum strongly convex but only slightly swollen paramediaally; propodeum distinctly glabrous mediolongitudinally; mesopleuron mostly densely punctate, hypopimeral and ventral regions sparsely punctate; female T6 without distinct pygidial plate, but with weak carina posterolaterally (Fig. 15), pygidial brush short, devoid of ventral tuft, shallowly concave ventrally (Fig. 15); male with well developed, broadly rounded pygidial plate; female S5 with deep conical concavity (Fig. 15), S6 narrowly bifurcate (*cf.* Fig. 7); male S7, S8 and genital capsule as in Figs. 16-18.

Distribution.—Widespread through greater part of subsaharan Africa, occurring in a variety of different biomes from semi-desert to rain forest.

Discussion.—*Pasites friesei* differs from the other species in the group by the two-segmented maxillary palp, female pygidial plate which is well developed laterally and notched posteriorly and subpygidial brush which is completely brownish-orange. In *P. friesei* the male S7 tapers gradually towards the gently rounded posterior end.

Floral records.—Asteraceae: *Ageratum* sp., *Aspilia africana* (Pers.) C.D. Adams, *Aspilia helianthoides* Benth. & Hook. f. Gsn., *Emilia coccinea* Sweet and *Mikania natalensis* DC.; Verbenaceae: *Stachytarpheta angustifolia* Vahl; Rubiaceae: *Spermacoce verticil-*

lata L.; Hypericaceae: *Harungana madagascariensis* Lam. ex Pair.

Type material examined.—*Pasites ater*, holotype ♀: 'Kilimandjaro; 6 Sept.; Typus; *Pasites ater* ♀ Fr. 1908 Friese det.' (NHRS). *Pasites nigerrimus*, lectotype ♀: 'D.O. Africa, Kigonsera, 1903; *Pasites nigerrimus* Fr. ♀ 1904 Friese det.; Type; *Omachthes nigerrimus* ♂ (Fr.) Typ.; Coll. Friese; Zool. Mus. Berlin' (ZMHB). *Morgania chubbi*, holotype ♀: 'Natal, Bellair, E.C. Chubb, 13 Jan. 1919; *Morgania chubbi* Ckll. Type; TYPE' (DMSA). *Morgania nigrifula*, lectotype ♀: 'Sunday's River, Dr Brauns, Cape Colony, 27.xii.1897; *O. nigrifula* Bisch. Typ. ♀.; *Omachthes nigrifula* TYPE Bischoff; *Omachthes nigrifula* ♀ Type No. 564' (TMSA). *Morgania peratra*, holotype ♂: 'NATAL, Weenen, iii.iv.1924, H.P. Thomasset; *Morgania peratra* Ckll TYPE; Pres. by Imp. Inst. Ent. B.M. 1933-582; B.M. TYPE HYM. 17B 81' (NHML).

Additional material examined.—53♀ 47♂: **SENEGAL:** Ziguinchor, viii.1979, A. Pauly (1♂ PCGB). **BURKINA FASO:** Sources du Kou, 13.x.1079, A. Pauly (3♀ PCGB); River Lahissa S., 5.x.1979, A. Pauly, on *Aspilia helianthoides* (1♀ PCGB). **LIBERIA:** Bakratown, x.1926 (1♀ MCZC, 1♀ MRAC). **IVORY COAST:** Grand-Béréby, 18.xii.1979, A. Pauly (1♂ PCGB); Tabou, 21.xii.1979, A. Pauly (1♀ PCGB). **TOGO:** Sokodé, xii.1982, A. Pauly (1♀ PCGB). **CAMEROON:** Wum, maquis d'altitude, 6.24N 10.03E, 20.viii.1987, A. Pauly, on *Emilia coccinea* (2♀ PCGB), on *Aspilia africana* (1♀ 2♂ PCGB) on *Ageratum* sp. (1♂ PCGB); Kriegschiffsha, 15.iii.1892, Dr Brauns (1♂ TMSA). **CENTRAL AFRICAN REPUBLIC:** Kembe, 4.29N 21.53E, 13.viii.1985, Dollfuss (1♀ SCAA). **EQUATORIAL GUINEA:** Bioko, Sa. Jsabel, 25.iii.1900, L. Conradt S. (1♀ TMSA). **GABON:** Og. Lolo., Paris, 1.19S 12.30E, 29.i.1986, A. Pauly (1♀ 3♂ PCGB); Og. Lolo., Pana, 700m, 29.i.1986, A. Pauly, on *Mikania cordata* (1♂ PCGB); Og. Iv., Sassamongo, 2.v.1986, A. Pauly (2♂ PCGB, 2♂ SANC), on *Stachytarpheta angustifolia* (1♂ PCGB, 1♂ SANC); Botouala, 2.v.1986, A. Pauly, on *Stachytarpheta angustifolia* (1♂ PCGB); Cap, Santa Clara, 29.ix.1985, A. Pauly (2♀ 1♂ PCGB, 1♀ SANC); Sindara, riv. Ngounié, 29.xii.1985, A. Pauly, on *Spermacoce verticillata* (1♀ PCGB); Kango, 22.ix.1985, A. Pauly, on *Harungana madagascariensis* (1♀ PCGB); Ayem W., 25.xii.1985, A. Pauly, on *Aspilia africana* (1♂ PCGB); Forêt des Abeilles, 00.22S 11.52E, 1.ii.1986, A. Pauly, on *Harungana madagascariensis* (1♂ PCGB); W. NT., Bilé-Mélen, 21.iii.1987, A. Pauly (1♂ PCGB). **BURUNDI:** Bururi, 900m, Nyamurembe, 7.iii.1953, P. Basilewsky (1♂ PCGB). **ZAIRE:** Tshuapa, Bokuma, i-iii.1954, R.P. Lootens, 3♀ MRAC; Equateur, Bokuma, ii & vii.1952, R.P. Lootens (1♀ 1♂ MRAC); Ubangi, Nouvelle Anvers, 9.xii.1952, P. Basilewsky (1♀ PCGB); Kivu, Uvira, 25-26.xii.1952, P. Basilewsky (1♀ 1♂ MRAC); Kivu, Mulungu, 5.iv.1937, H.J. Brédo (1♀ MRAC); Kivu, Bukavu, 26.vii.1931, J. Ogilvie (1♂ MRAC); Terr. de Kasongo,

riv. Lumami, i.1960, P.L.G. Benoit (1♂ MRAC); Kisangani [= Stanleyville] 9.iv.1928, A. Collart (1♂ MRAC); Kisangani, 16.iv.1932, J. Vrydagh (2♂ MRAC); Kunzulu, ix.1917, R. Mayné (1♂ MRAC); Boma, vii.1920, H. Schouteden (1♀ MRAC); Kisantu, 1932, R.P. Vanderyst (1♀ MRAC). **KENYA:** Karen, Nairobi, 20.v.1967, C.D. Michener (1♀ SEMK). **RWANDA:** Gitarama, 1850m., terr. Nyanza, i.1953, P. Basilewsky (1♀ MRAC). **ZIMBABWE:** Victoria Falls, 4.i.1920 (1♀ TMSA); Bulawayo, 15.ii.1926, R.H.R. Stevenson (1♀ TMSA). **BOTSWANA:** Xugana, 19.03S 23.02E, 22–26.xi.1979, B. Lamoral (1♂ BCSA). **NAMIBIA:** 24 km S.E. Outjo, 23.ii.1977, J.G. & B.L. Rozen (1♂ AMNH); Gobabis, 21.xii.1974, H. Empey (1♂ SANC). **SOUTH AFRICA:** Entabeni Forest Reserve, 33.00S 30.16E, 7–11.i.1987, C.D. Eardley (1♀ SANC); Mogoto Nature Reserve, Zebediela, 24.15S 29.13E, 22–25.x.1979, C.D. Eardley (1♀ SANC); Nylsvley Nature Reserve, 24.39S 28.42E, 10–11.xii.1979, C.G. Moolman (1♀ SANC); Lydenburg district, 1896, P.A. Krantz (1♀ SANC); O.T.K. Reserve, near Loskop Dam, 25.27S 29.24E, 9–11.xii.1985, C.D. Eardley (1♀ 2♂ SANC); Weltevreden, 25.34S 31.10E, 24.i.1990, G.L. Prinsloo (1♂ SANC); Mogol Nature Reserve, Ellisras district, 23.58S 27.45E, 25–26.i.1982 & 27–29.ii.1984, C.D. Eardley (2♀ SANC); D'Nyala Nature Reserve, 23.45S 27.49E, 8–12.xii.1989, C.D. Eardley (1♀ 1♂ SANC); Hope, near Ellisras, 17.xi.1962, H. Empey (1♂ SANC); Ben Alberts Nature Reserve, near Thabazimbi, 24.37S 27.23E, 24–28.xi.1980, C.D. Eardley (1♂ SANC); Schoongeleen, between Bulgeriver & Matlabas, 24.12S 27.45E, 14.i.1991, V.M. Uys (1♂ SANC); Rustenburg, 6.xii.1969, L.C. Starke (1♂ SANC); Botanical Gardens, Pretoria, 25.45S 28.17E, 6.iv.1989, C.D. Eardley (1♀ SANC); Johannesburg, i.1908, G. Kobrow (1♂ TMSA); Strubens Valley, 31.xii.1965, H. Empey (1♀ SANC); Potchefstroom, T. Ayrs (1♀ SAMC); Mfongosi, iii.1916, W.E. Jones (1♂ SAMC); Umlaas Road, 19 km S.E. Pietermaritzburg, 23.i.1967, C.D. Michener, D.J. Brothers (1♀ SEMK); Nagle Dam, 27 km E. Pietermaritzburg, 5.i.1967, C.D. Michener, D.J. Brothers (1♀ SEMK); Weenen, iii.1924, H.P. Thomasset (1♂ SANC); Tongaat Beach, 10–11.iv.1971, F.L. Farquharson (1♂ DMSA); Umgeni River, near Table Mountain, 4.ii.1940, L. Bevis (1♀ AMGS); Amanzimtoti, 10.iv.1952, C. Jacot-Guillarmod (2♀ AMGS); Drakensberg Botanic Gardens, near Harris-mith, 28.17S 29.09E, 27.xii.1986, C.D. Eardley (1♂ SANC); Cookhouse, 14.i.1965, H. Empey (1♂ SANC); Hilton, Grahamstown, 3–16.xi.1977, F.W. Gess (3♀ 1♂ AMGS); Boesmans River, near Grahamstown, iii.1954 (1♂ SAMC); Hunts Drift, Fish River, 11.xii.1960, C. Jacot-Guillarmod (1♀ AMGS).

Other published distribution record.—**UGANDA:** Kampala (Cockerell 1933c).

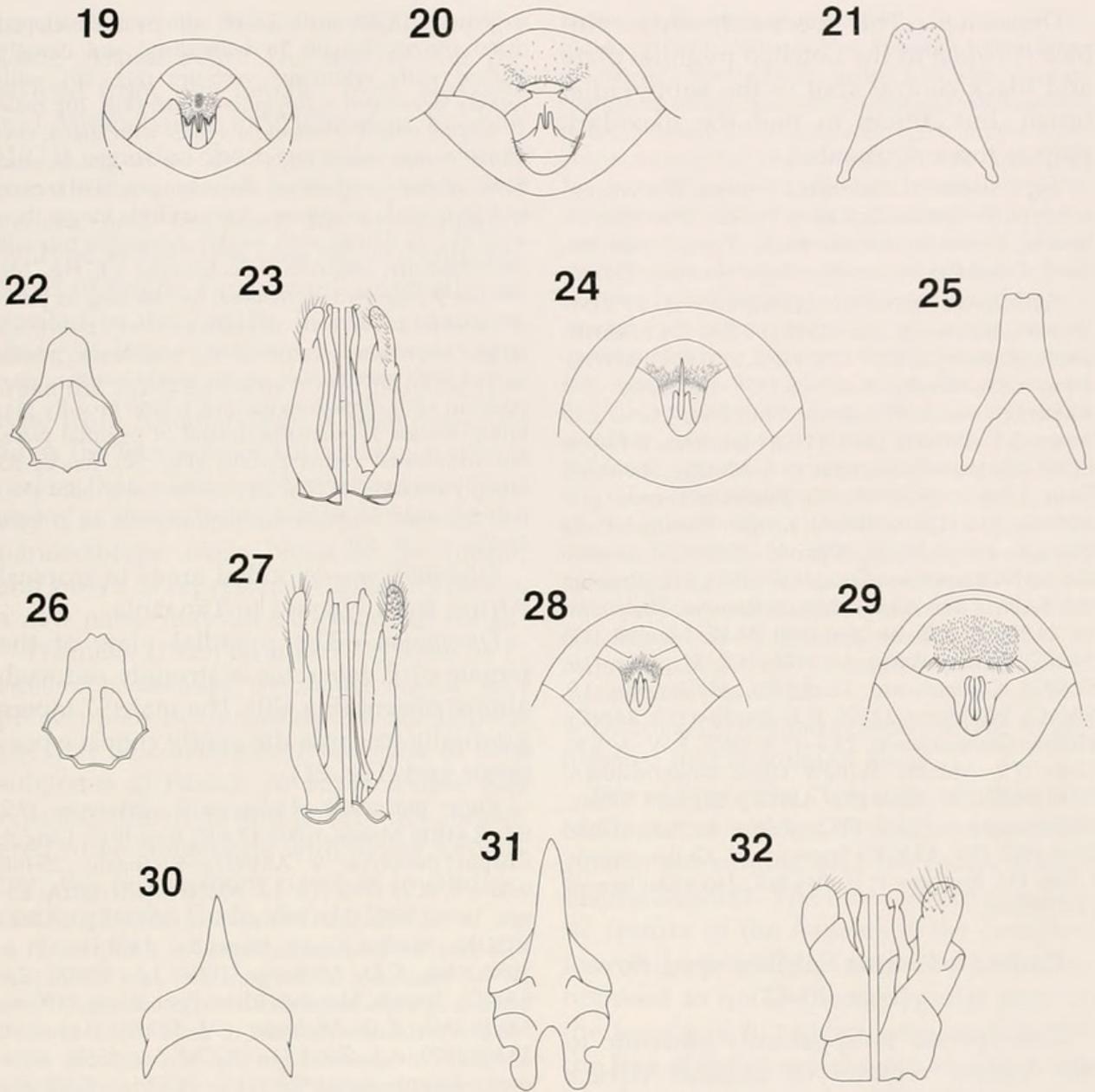
Pasites paulyi Eardley, *spec. nov.*
(Fig. 19)

This species is named for the collector, Dr A. Pauly (PCGB).

Description.—Similar to *P. friesei*. Length of head 1.5–1.6 mm; scutum 1.1–1.3 mm; fore wing 4.5–5.5 mm; body 5.0–6.4 mm. Integument black, except tegula, legs and metasoma sometimes reddish. Vestiture mostly white, ventral surfaces of tarsi, female T5, S5 and male T6, S6 with pale yellow tinge; female T6 with subpygidial brush black medially, circumscribed by brownish-orange (Fig. 19, dense central region black, relatively sparse peripheral area brownish-orange). Head mostly densely pubescent, upper region of face and vertex with sparse vestiture (*cf.* Fig. 5); mesosoma with pronotal collar, most of pronotal lobe, lateral regions of mesopleuron (excluding lower hypoepimeral area) and posterolateral regions of propodeum densely pubescent; remainder of mesosomal vestiture sparse; vestiture on legs dense, except trochanters and femora sparse to very sparse, ventral surfaces of tarsi very dense; T1 anterior surface and posterolateral region with dense plumose vestiture, remainder of T1 sparse, simple vestiture; T2 and sometimes T3 with dense, posterolaterally directed, vestiture posterolaterally, anterior regions of each tergum with sparse, simple vestiture; female T3/T4–T5, male T3/T4–T6 with moderately dense distal fringes of posteriorly directed hairs (vestiture sparse and simple anteriorly); female T6 with sparse vestiture, weakly developed subpygidial brush (Fig. 19); female S2–S4 with vestiture fairly sparse anteriorly and dense posteriorly, S5 with moderately dense vestiture, distal margin velutinous; male metasomal venter moderately densely pubescent. Labrum little longer than wide, labrum with small tubercle apicomediaally; maxillary palp five-segmented, subequal in length to pedicel; scutum consistently 1.1× as long as its narrowest width, punctures moderately large, often confluent; scutellum evenly convex, without pronounced paramedian swelling; propodeum distinctly glabrous mediolongitudinally; mesopleuron mostly densely punctate, hypoepimeral and ventral regions sparsely punctate; female pygidial plate with posterolateral carina more strongly developed than in *P. friesei* (Fig. 19), subpygidial brush quadrate (Fig. 19), S5 deeply emarginate posteromedially (Fig. 19), S6 narrowly bifid; male with well developed, broadly rounded pygidial plate (*cf.* Fig. 7); male S7 and genital capsule as in *P. barkeri* (*cf.* Figs. 8 & 10); male S8 similar to that of *P. friesei*, except little more truncate distally (*cf.* Fig. 17).

Distribution.—Woodlands of northern Cameroon.

Discussion.—In this species the maxillary palp is five-segmented, female pygidial plate notched posteriorly and subpygidial brush brownish-orange with a black centre. The male S7 has the lateral margins gently concave and posterior end more or less gently rounded (*cf.* Fig. 8).



Figs. 19–32. *Pasites* spp. 19. *P. paulyi*, terminalia, posterior view, ♀; 20–23. *P. humectus*. 20. Terminalia, posterior view, ♀; 21. S7, ♂; 22. S8, ♂; 23. Genital capsule, ♂. 24–27. *P. bicolor*. 24. Terminalia, posterior view, ♀; 25. S7, ♂; 26. S8, ♂; 27. Genital capsule, ♂. 28. *P. tegularis*, terminalia, posterior view, ♀. 29–32. *P. gnomus*. 29. Terminalia, posterior view, ♀; 30. S7, ♂; 31. S8, ♂; 32. Genital capsule, ♂.

Type material.—Holotype ♂, paratypes 3♀: CAMEROON: Parc Nat. Waza, 11.21N 14.35E, 5.viii.1987, A. Pauly (holotype ♂ 1♀ PCGB, 1♀ SANC); Maga, 10.50N 14.59E, 3.viii.1987, A. Pauly, Fl. No. 374 (1♀ PCGB).

***Pasites braunsi* (Bischoff), comb. nov.**

Morgania (*Omachthes*) *braunsi* Bischoff 1923:587.
Omachthes braunsi (Bischoff); Anonymous 1958: 31.

Description.—Female (male unknown). Length

of head 1.4–1.9 mm; scutum 1.2–1.6 mm; fore wing 4.7–5.8 mm; body 5.0–6.5 mm. Similar to *P. friesei* except as follows: subpygidial brush black medially, circumscribed by brownish-orange; labrum pointed, very weakly tuberculate apicomediaally; maxillary palp three-segmented, subequal in length to antennal pedicel; pygidial plate with posterolateral carina more strongly developed; subpygidial brush quadrate.

Distribution.—Ranges from bushveld, in Zimbabwe, Namibia and parts of South Africa, to montane grassland in Lesotho.

Discussion.—This species closely resembles *P. paulyi* in the notched pygidial plate and black central spot in the subpygidial brush, but differs in that the maxillary palp is three-segmented.

Type material examined.—*Omachthes braunsi*, holotype ♀: 'Bothaville, Oranje Fr. Sta., 13.xi.1898, Dr Brauns; *Omachthes braunsi* Bisch. Typ.; Typus Bischoff; *Omachthes braunsi* Biss. Type No. 566' (TMSA).

Additional material examined.—31 ♀: **ZIMBABWE:** Bulawayo, 21.xii.1919 (1 ♀ SANC). **NAMIBIA:** Regenstein 32, 2217 CA, 12.xii.1973 (2 ♀ SMWH). 5 km S. Okahandja, 30.iii-1.iv.1979, J.G. Rozen (3 ♀ AMNH); 3 km S. Windhoek, 11.iii.1976, J.G. & B.L. Rozen (1 ♀ AMNH). **LESOTHO:** Mamathes, ii.1946 & i.1961, C. Jacot-Guillarmod (3 ♀ AMGS); Hensley's Dam Leribe, 29.ii.1948, C. Jacot-Guillarmod (1 ♀ AMGS). **SOUTH AFRICA:** Kruger National Park, Skukuza, 24.59S 31.55E, 292m, 19.i.1984, C.D. Eardley (2 ♀ SANC); same locality, 14-17.i.1985, G.L. Prinsloo (3 ♀ SANC); Ben Alberts Nature Reserve, Thabazimbi, 24.37S 27.32E, 24-28.xi.1980, M.W. Mansell (1 ♀ SANC); Johannesburg, 4.ii.1978, H.R. Hepburn (1 ♀ SEMC); Queenstown, 16.xii.1979, H. Empey (1 ♀ SANC); Whittlesea, i.1979, C.D. Eardley (1 ♀ SANC); Hilton, Grahamstown, 28.ii-17.iii.1978, F.W. & S.K. Gess (7 ♀ AMGS); Willow Glen, Grahamstown, 24.xi.1982, D.W. Gess (1 ♀ AMGS); Belmont Valley, Grahamstown, 24.xi.1982, F.W. & S.K. Gess, 24.xi.1982 (2 ♀ AMGS); Strowan, W. Grahamstown, i.1980, D.J. Brothers, P. Hulley & C. Jacot-Guillarmod (1 ♀ BCSA).

Pasites humectus Eardley, *spec. nov.*
(Figs. 20-23)

This species is apparently endemic to the humid regions of tropical Africa, hence the name *humectus*.

Description.—length of head 1.1-1.5 mm; scutum 0.8-1.2 mm; fore wing 4.0-5.6 mm; body 3.7-4.5 mm. Integument of head and mesosoma black, except labrum, mandible, antennal flagellum, tegula, pronotal lobe and legs (coxae excluded) which are mostly reddish-black; metasoma black to reddish-black. Vestiture mostly white, ventral surfaces of tarsi pale yellowish, terminal segment of metasoma brownish-orange. Head mostly moderately densely pubescent, lower half very densely pubescent (*cf.* Fig. 5); mesosoma with scutum and ventrolateral region of mesepisternum sparsely pubescent, remainder of mesosoma very densely pubescent; legs densely pubescent, except trochanters and femora sparsely pubescent; metasoma naked to very sparsely pubescent, except T1 with anterior (subvertical) surface mostly densely plumose, with dense posterolateral tuft; T2-T3 with broadly medially interrupted distal fringes;

female T4-T5, male T4-T6 with well developed distal fringes; female T6 with distal end densely clothed with velutinous vestiture (Fig. 20), with weakly developed subpygidial brush (Fig. 20); male T7 largely naked; metasomal venter with sparse vestiture, except distal ends of S2-S4, in female, and S2-S5, in male, with dense distal fringes; S5 in female and S6 in male velutinous. Labrum little longer than wide (1.1:1), flattish with weakly developed tubercle apicomediaally, angulate apicolaterally (*cf.* Fig. 14); maxillary palp two-segmented, half as long as pedicel; scutum moderately densely punctate, punctures large, sometimes convergent; scutellum gently curved with paramedian region gently swollen; propodeum with mediolongitudinal region broadly glabrous; female T6 virtually devoid of pygidial plate, but with small carina distally (Fig. 20); female S5 broadly emarginate (Fig. 20), S6 narrowly bifid posteriorly; male S7, S8 and genital capsule as in Figs. 21-23.

Distribution.—Wooded areas in tropical Africa, from Nigeria to Tanzania.

Discussion.—The pygidial plate of the female of *P. humectus* is strongly reduced, almost absent (Fig. 20). The male S7 tapers gradually towards the gently concave posterior end (Fig. 21).

Type material.—Holotype ♀, paratypes 17 ♀ 8 ♂: **ZAIRE:** Malela, 6.00S 12.40E, 8.vii.1915, Lang & Chapin (holotype ♀ AMNH); Kisangani, 25.10E 0.30N, ii & iv.1915 (1 ♀ 1 ♂ AMNH). **NIGERIA:** Lagos, 18.viii.1966, C.D. Michener (2 ♂ SEMK). **CAMEROON:** Bambui, near Bamenda, 1400 m, 9 & 20.vii.1966, C.D. Michener (12 ♀ 1 ♂ SEMK, 2 ♀ SANC); Tingoh, Menchin River, near Wum, 7100 m, 14.viii.1966, C.D. Michener (1 ♂ SEMK); Lolodorf, 10.viii.1920, A.I. Good (1 ♂ ICCM Acc 6552); same data except 6.vii.1926 (1 ♀ ICCM). **GABON:** 4.xii.1909, A.I. Good (1 ♂ SANC Acc 4189); same data except 23.xi.1909 (1 ♀ SANC). **TANZANIA:** Morogoro, 19.x.1956, W.E. Kerr (1 ♂ SEMK).

Pasites bicolor Friese
(Figs. 24-27)

Pasites bicolor Friese 1900:262.

Pasitomachthes bicolor (Friese); Bischoff 1923: 597-598.

Pasites bicoloratus Warncke 1983:291 [*nom. nov.* pro *P. bicolor* Friese *nec* (Lepelletier)].

Friese (1900) attributed the authorship of this species to 'de Saussure *in litt.*', but the article was clearly written by Friese, as it is in his distinct style and part of a larger paper by him. The name should therefore

be attributed to Friese, according to the Code, Article 50(a). The species was described from two females from Nossi-Bé and Antananarivo in Madagascar. Bischoff (1923) regarded the type series to contain two different species, belonging to distinct genera, and described the Antananarivo syntype as *Pasitomachthes bicolor*. Both syntypes of *Pasites bicolor* were originally deposited in the ZMHB, but the curator of that collection, Dr F. Koch, was unable to trace the syntype from Nossi-Bé. The syntype from Antananarivo is here designated as the lectotype of *Pasites bicolor*, which makes that name an objective senior synonym of *Pasitomachthes bicolor*. Should the paralectotype from Nossi-Bé be found, and prove to represent a different species, a new name may then be required for it.

Warncke (1983) renamed *P. bicolor* as *P. bicoloratus* because the name *bicolor* was preoccupied by *Ammobates bicolor* Lepeletier and he considered *Ammobates* to be a subgenus of *Pasites*. As *bicolor* Friese was rejected after 1960 and is here not considered to be congeneric with *bicolor* Lepeletier, the replacement name is invalid according to the Code, Article 59(d).

Description.—Length of head 1.5–1.9 mm; scutum 1.3–1.7 mm; fore wing 5.9–7.3 mm; body 5.9–7.6 mm. Integument of head, mesosoma and legs entirely black to mostly black or blackish with labrum, mandible, pronotal lobe and tegula orange to orangish, legs blackish-orange to orange; metasoma completely orange to reddish-black (latter with mottled appearance). Vestiture mostly white, anteromedian region of scutum with slight yellow tinge, ventral surfaces of tarsi pale yellow, T6 and S5 mostly pale yellowish, subpygidial brush reddish. Vestiture on lower region of face and gena plumose, upper region of face and vertex simple (cf. Fig. 5); mesosoma mostly pubescent, dorsum and ventral region of mesopleuron with simple to weakly plumose vestiture; vestiture on coxae plumose, remainder of legs simple; propodeum densely pubescent, except propodeal triangle which is naked; T1 with anterior surface sparse, plumose, remainder of vestiture fine and simple, except posterolateral region which ranges from naked to sparsely clothed with simple to weakly plumose vestiture (never densely plumose); distal margin of T1 naked and glabrous; T2 with sparse fine vestiture, except posterolaterally where it is dense; female T3 and male T3–T4 similar to T2, except vestiture on posteromedial

region ranges from sparse and simple to dense and plumose (where latter occurs, vestiture forms dense cross-band); female T4–T5, male T5–T6 with vestiture sparse and simple anteriorly, dense and plumose posteriorly; female T6 with sparse, erect, simple hairs, except subpygidial brush which is fairly dense (Fig. 24), male T7 sparsely pubescent; metasomal venter fairly sparsely clothed with fine, simple vestiture, except distal margin of female S5 with fine dense vestiture. Labrum quadrate, apex strongly tuberculate, rounded apicolaterally; maxillary palp three-segmented, half as long as pedicel of antenna; scutum densely punctate, punctures small, distinctly separate; tegula weakly convex, giving the impression that it is proportionately larger than in its congeners; scutellum strongly convex with deep mediolongitudinal cleft, appearing strongly swollen paramedially; propodeal triangle glabrous, weakly striated in places; mesopleuron fairly densely punctate, punctures separate; female T6 devoid of pygidial plate (Fig. 24), male pygidial plate well developed, broadly rounded distally; female subpygidial brush weakly defined (Fig. 24); female S5 distinctly concave (Fig. 24); S6 narrowly bifid (cf. Fig. 7); male S7, S8 and genital capsule as in Figs. 25–27.

Distribution.—Madagascar, forest to deforested and cultivated areas.

Discussion.—The females of the two Madagascan species, *P. bicolor* and *P. tegularis*, are similar, and the males are indistinguishable. The most salient diagnostic feature of the females is the complete loss of the pygidial plate in the former, as opposed to the reduced pygidial plate in the female of *P. tegularis*. Associated with the loss of the pygidial plate, the T6 is distinctly more rounded in *P. bicolor*; the remnants of the pygidial plate in *P. tegularis* form two dorsolateral carinae which give the T6 more angulate appearance. The males of *P. bicolor* and *P. tegularis* can be separated from the other species in the group by the S7 which is more or less parallel-sided posterolaterally and emarginate posteriorly (Fig. 25).

Type material examined.—Lectotype ♀: 'Madagasc, Annanarivo [label almost illegible]; *Pasites bicolor* Sau. ♀. Madacascar; Typus; *Pasitomachthes bicolor* Bisch. Typ. ♀; Zool. Mus. Berlin' (ZMHB).

Additional material examined.—8♀ 4♂: MADAGASCAR: N.E., Fampanambo, iv.1959, J. Vardon (2♀ MRAC); Centre Province: Antananarivo, Angavokely, 17.ii.1992, 18.56S 47.45E, PL. REPR. ECOL.

PROI. (5♀ 3♂ NCUS); Centre Province, Angavokely, 17.iii.1988, L.A. Nilsson (1♀ 1♂ NCUS).

Pasites tegularis Friese
(Fig. 28)

Pasites tegularis Friese 1922:38–39.

Morgania (Omachthes) tegularis (Friese); Bischoff 1923:589.

This species is most closely related to *P. bicolor*, which Bischoff (1923) placed in *Pasitomachthes*.

Description.—Length of head 1.3–1.6 mm; scutum 1.0–1.4 mm; fore wing 4.2–6.1 mm; body 5.2–6.9 mm. Integument of head and mesosoma mostly black or blackish with labrum, mandible, pronotal lobe and tegula orange to orangish; legs blackish-orange to orange; metasoma completely orange to reddish-black (latter with mottled appearance). Vestiture similar to *P. bicolor* in colour except as follows: scutum mostly pale yellow, sometimes white; pygidial brush brownish; propodeum densely pubescent, except mediolongitudinal region which is naked; T1 with posterolateral region densely pubescent; female T6 with sparse, erect, simple vestiture, except with dense subpygidial brush. Structure similar to *P. bicolor* except as follows: maxillary palp three-fourths as long as pedicel of antenna; mediolongitudinal region of propodeum glabrous (dorsolateral region of propodeal triangle pubescent, glabrous area not confined to propodeal triangle mediolongitudinally), without any striations; female pygidial plate reduced to weakly developed dorsolateral carina on T6 (Fig. 28).

Distribution.—Madagascar, forest to deforested and cultivated.

Discussion.—The pygidial plate of *P. tegularis* is weakly developed laterally and absent posteriorly. It is the only known Madagascan species in which a pygidial plate occurs in the female. The male is indistinguishable from that of *P. bicolor*.

Type material examined.—Holotype ♀: 'Nossi-Bé, *Pasites bicolor* ♀ var.; *Pasites tegularis* ♀ Fr. 1904 Friese det.; Type; *Omachthes tegularis* (Fr.) ♂ Typ.; Coll. Friese, Zool. Mus. Berlin' (ZMHB).

Additional material examined.—12♀ 7♂: MADAGASCAR: N.E., Fampanambo, J. Vadon, iv.1959 (3♀ 5♂ MRAC), vi.1960 (1♀ MRAC), xii.1962 (1♀ MRAC), 1962 (1♀ MRAC); Tamatave Province, 6 km N. Tamatave, 15.i.1985, J.W. Wenzel (2♀ SEMK); Tulear Province, 45 km S. Mahabo, 20.42S 44.38E, 24–26.xi.1986, J.W. Wenzel (2♀ SEMK); Tananarive Province, 17 km W. Ambatolampy, 19.24S 47.25E, 1650m, 30.i.1985, J.W. Wenzel (1♂ SEMK); Rogez, vii.1937, A. Seyrig (1♂ MRAC); Est. Neaux Nottes, S. St. Marie,

6.xii.1983, L.A. Nilsson, L. Jonsson (1♀ NCUS); Est. Soanierana Ivongo S, 27.x.1987, L.A. Nilsson (1♀ NCUS).

GNOMUS SPECIES GROUP

This species group is monotypic.

Pasites gnomus Eardley, **spec. nov.**
(Figs. 29–32)

The specific epithet of the name of this tiny species is New Latin and refers to its small size.

Description.—Length of head 0.7–0.8 mm; scutum 0.4–0.5 mm; fore wing 2.0–2.2 mm; body 2.3–2.5 mm. Integument generally black to blackish-orange, with mandible, antenna, distal ends of tibiae, tarsi, basal region of T1 and metasomal venter orange to orangish (female more extensively orange coloured than male). Vestiture mostly white; ventral surfaces of tarsi and female T6 and S5 pale yellow. Scutal vestiture largely simple; trochanters and femora sparsely pubescent; metasoma with anterior and posterolateral regions of T1 densely pubescent; T2 with broadly interrupted distal fringe, female T3–T4, male T3–T5 with continuous distal fringes; female T6 densely pubescent posteriorly (Fig. 29), with short and long vestiture (distal end of male metasoma damaged and cannot be accurately described); S1–S4 sparsely pubescent, female S5 with sparse vestiture which comprises mixture of short and long hairs. Labrum quadrate, generally flat, distinctly pointed apically; maxillary palp absent; scutum moderately densely punctate, punctures small, shallow and separate; scutellum gently and evenly convex, devoid of any exaggerated swelling paramedially; propodeum devoid of mediolongitudinal glabrous area; punctation on propodeum and mesopleuron similar to scutum; pygidial plate absent in both sexes; female T6 flattened posteromedially, this area densely clothed with short, fine vestiture, that on subpygidial area very short, subpygidial brush weakly developed (Fig. 29); female S5 conically emarginate, S6 narrowly bifid (Fig. 29); male S7–S8 acutely pointed posteriorly, S8 with two anterior lobes (Figs. 30–31); male genital capsule as in Fig. 32.

Distribution.—Niger, near Tahoua, which is grassland wooded with *Acacia* and deciduous shrubs.

Discussion.—*Pasites gnomus* is distinct from its congeners. It can be easily recognised by its small size, absence of a pygidial plate in both sexes, truncate and finely pubescent posteromedian region of the female T6, acute apices of the male S7 & S8 and two anterior lobes of the male S8

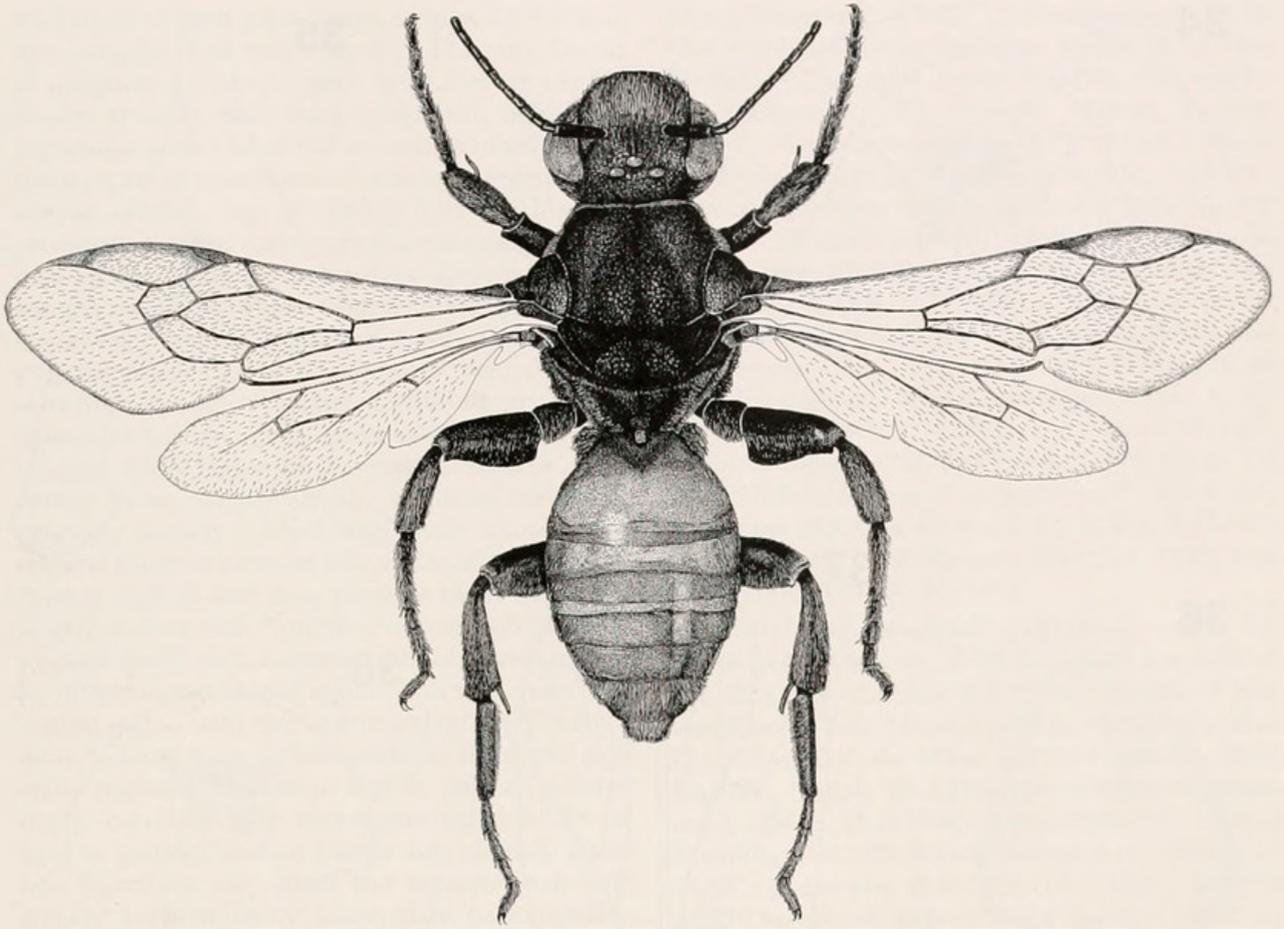


Fig. 33. *Pasites carnifex*, habitus, dorsal view (dark shading represents black integument and lightly shaded areas are orange), ♀.

(Figs. 29–31). In the cladistic analysis it is grouped with *P. friesei* by the loss of the anteromedian lobe on the male S8 (Fig. 31).

Type material.—Holotype ♀, paratype ♂: NIGER: 20km S. Tahoua, 14.45N 5.20E, 13.viii.1987, A. Pauly (PCGB).

CARNIFEX SPECIES GROUP

Two species have been placed in the carnifex species group: *P. carnifex* and *P. dichrous*. These two species are large (7.0–12.5 mm) with the head and mesosoma black and metasoma orange. The distal fasciae of T2–T4 are sparse, with posteriorly directed vestiture. The female pygidial plate and subpygidial brush are well developed, and the S5 is conically emarginate posteromedially. Males resemble females in colour, but do not have any other obvious unique features.

Pasites carnifex (Gerstaecker), **comb. nov.**

(Figs. 33–37)

Omachthes carnifex Gerstaecker 1869:155.

Omachthes nigripes Friese 1915:276, 296, 298.

Syn. nov.

Morgania nigripes (Friese); Cockerell 1919:190.

Morgania (*Omachthes*) *nigripes* (Friese); Bischoff 1923:591.

Morgania fortis Cockerell 1921:207–208. **Syn. nov.**

Pasites magnificus Brauns 1926:207–208.

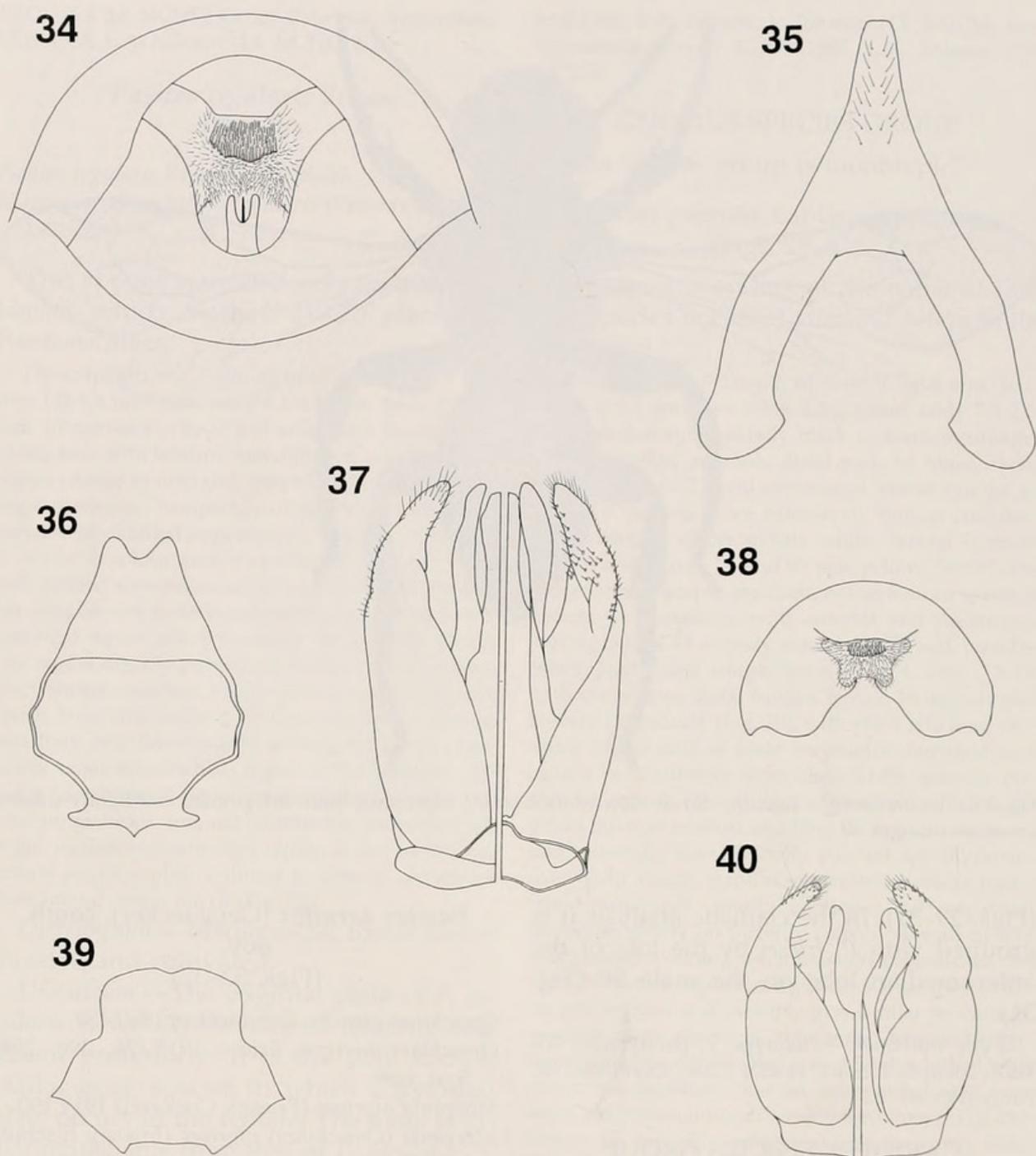
Morgania magnificus [sic.] (Brauns); Cockerell 1933b:130 [lapsus].

Morgania subfortis Cockerell 1933c:107. **Syn. nov.**

Morgania (*Omachthes*) *stordyi* Cockerell 1933a:377. **Syn. nov.**

Morgania (*Omachthes*) *voiensis* Cockerell 1937a:155. **Syn. nov.**

Morgania (*Omachthes*) *altior* Cockerell 1937a:155. **Syn. nov.**



Figs. 34–40. *Pasites* spp. 34–37. *P. carnifex*. 34. Terminalia, posterior view, ♀; 35. S7, ♂; 36. S8, ♂; 37. Genital capsule, ♂. 38–40. *P. dichrous*. 38. Terminalia, posterior view, ♀; 39. S8, ♂; 40. Genital capsule, ♂.

Small differences in size, colour and wing venation of this striking species led to the description of several synonyms. *Pasites magnificus* was synonymized with *fortis* by Cockerell (1933b), and *nigripes*, *fortis*, *subfortis*, *stordyi*, *voiensis* and *altior* are here synonymized with *carnifex*. The synonymy of these six species follows the study of the type material of each species,

which was found to be within the range of variation established for this species during the study. *Omachthes nigripes* was described from a male and female from Eritrea, neither of which could be obtained for study, and a female from Usambara, Tanzania, which was studied and is here designated as the lectotype.

Description.—Habitus, dorsal aspect, as in Fig.

33. Length of head 2.4–2.7 mm; scutum 2.3–2.5 mm; fore wing 8.6–10.0 mm; body 11.1–12.5 mm. Colour of integument, dorsal aspect, as in Fig. 33 (darkly shaded areas illustrate black integument, light shading orange areas); head and mesosoma mostly black, distal region of mandible and sometimes antenna and labrum reddish, legs completely black to blackish proximally, orange distally; metasoma orange to reddish-orange. Vestiture on head brown to white; mesosoma mostly brownish, ventral surface of hind tarsus always orange; metasoma mostly orange, subpygidial brush mostly black, except ventral region sometimes orange or orangish. Middle and lower regions of face and gena, entire labrum densely pubescent; upper region of face and vertex with moderately dense, largely simple, vestiture; mesosoma generally densely clothed with short vestiture, peripheral fringe of pronotal lobe, coxae, tibiae and tarsi densely clothed with long plumose hairs; metasoma largely clothed with short, fine, simple vestiture; subpygidial brush well developed, not expanded dorsally, differentiated, dorsal region with thick hairs and ventral region with fine vestiture (Fig. 34); S5 velutinous. Labrum more or less quadrate, distal end generally rounded, sometimes slightly pointed picomedially; maxillary palp four-segmented, 1.4–1.7× as long as pedicel; scutum mostly very densely punctate, punctures very small and separate; scutellum weakly to moderately tuberculate paramedially; punctation on pleural and ventral regions of mesosoma and entire propodeum moderately dense to very dense; pygidial plate well developed in both sexes (female pygidial plate, as in Fig. 34); female S6 broadly bifurcate; male S7 and S8 as in Figs. 35–36; genital capsule (Fig. 37) more elongate than *P. dichrous*.

Distribution.—Apparently occurring throughout East and South-East Africa, and from a single locality in West Africa, mostly in forest and woodland.

Discussion.—In *P. carnifex* the subpygidial brush is gently concave ventrally (Fig. 34), not distinctly bilobed as in *P. dichrous* (Fig. 38). The males of these two species differ in the shape of the S8, in *P. carnifex* it tapers towards the distinctly concave posterior end, whereas in *P. dichrous* the posterior region is parallel-sided and the posterior end more or less entire (notched medially) (cf. Figs. 36, 39).

Type material examined.—*Omachthes carnifex*, holotype ♀: 'Capland, Drège S., 639; Type, *carnifex* Gerst. *dichrous* Klug i.l., *Omachthes carnifex* Gerst. 1907 Friese det.; *Omachthes dichrous* Spin.; Zool. Mus. Berlin' (ZMHB). *Omachthes nigripes*, lectotype ♀: 'D.O.-

Africa, Usambara, 6.1903; *Omachthes nigripes* ♀ Fr. 1914 Friese det., Type; *Omachthes nigripes* Fr. i.l. Type Bischoff ♀; Zool. Mus. Berlin' (ZMHB). *Morgania fortis*, holotype ♀: 'F.J. Kroeger, Moboki, Lydenb. Transv.; *Morgania fortis* Ckll. TYPE' (SAMC). *Pasites magnificus*, holotype ♀: 'Sawmills S.R., 22.3.1919, Rhodesia Museum; *Pasites magnificus* ♀ Type No. 571' (TMSA). *Morgania subfortis*, holotype ♀: 'Musée du Congo, Ituri: Blukwa, 3/4.xii.1928, A. Collart; *Morgania subfortis* Ckll. TYPE' (MRAC). *Morgania stordyi*, holotype ♂: 'Brit E. Africa, R.J. Stordy, 1912-329; *Morgania stordyi* Ckll. TYPE; B.M. TYPE HYM. 17B 80' (NHML). *Morgania voiensis*, holotype ♂: 'Brit E. Af., Voi., 1 800 ft. Mch. 21-23, 1911, S.A. Neave, 1911-177; *Morgania voiensis* Ckll. TYPE; B.M. TYPE HYM. 17B 77' (NHML). *Morgania altior*, holotype ♂: 'Brit E. Afr., S.E. Slopes of Kenya, 6 000 to 7 000 ft., Feb. 3-12, 1911, S.A. Neave, 1911-177; *Morgania altior* Ckll. TYPE; B.M. TYPE HYM. 17B 78' (NHML).

Additional material examined.—10♀ 2♂: **BURKINA FASO**: riv. Volta Rouge, 15 Km Kokholo, 22.x.1979, A. Pauly (1♀ PCGB). **ZAIRE**: 'P.N.A. vers Rweru (Volc. Mikeno) 2400 m., (Bambous), 26 au 27.vii.1934, G.F. de Witte: 501' (1♀ MRAC). **ZIMBABWE**: Umtali, 26.ii.1942 (1♀ SAMC); Chimanimani, 1050 m, 25.iv.1985, J. Gusenleitner (1♀ SCAA); Sawmills, 24.ii.1925, R.H.R. Stevenson (1♀ TMSA, 1♀ SANC); Bulawayo, 16.iii.1919 (1♀ SAMC). **SOUTH AFRICA**: Umhlali, 14.iv.1946, R.F. Smith (1♀ AMGS); Waterval Boven, 18.ii.1969, L.C. Starke (2♀ SANC); Magoebaskloof, 23.58S 30.00E, 5.ii.1986, J.S. Donaldson (1♂ SANC); Schoemanville, 26.xii.1959, H. Empey (1♂ SANC).

Other published distribution records.—**ERITREA** (Friese 1909b); **UGANDA**: Semliki Plain (Cockerell 1933a); **KENYA**: Laikipia Escarpment; **TANZANIA**: Sanje (Cockerell 1933c); **UGANDA**: Busongora; **MALAWI**: Mulanje & Blantyre (Cockerell 1937b).

Pasites dichrous Smith (Figs. 37–40)

- Pasites dichroa* [sic.] Smith 1854:253 [*lapsus*].
Homachthes dichrous (Smith); Dalla Torre 1896: 499.
Morgania dichroa (Smith); Cockerell 1904:207.
Omachthes dichroa [sic.] (Smith); Friese 1909a:437 [*lapsus*].
Homachthes gerstaeckeri Schulz 1906:267 [*nom. nov. pro P. dichrous* Smith nec '*Ammobates dichrous*' Spinola, *nomen nudum*].
Morgania gerstaeckeri (Schulz); Cockerell 1910: 217.
Morgania (*Morgania*) *gerstaeckeri* (Schulz); Bischoff 1923:592.

Morgania nigrithorax Strand 1912:310–311. **Syn. nov.**

Morgania (Morgania) nigrithorax Strand; Bischoff 1923:593.

When Smith (1854) described this species he suggested that it was probably generically distinct, and recommended the generic name *Morgania* for the taxon. Spinola (1843) mentioned the existence of a specimen in 'Mus, Berol' (= ZMHB) that had been labelled *Ammobates dichrous*. According to the Code, Article 12(a), this name has no standing in zoological nomenclature, however, because the species was not described. Schulz (1906) established that Spinola's (1843) '*Ammobates dichrous*' and Smith's (1854) *Pasites dichrous* were congeneric, but not synonymous. He disregarded the fact that '*Ammobates dichrous*' had never been described and unjustifiably renamed Smith's (1854) species, which he considered to be a junior homonym, as *gerstaeckeri*.

Strand (1912), in the original description of *M. nigrithorax*, indicated that the type series comprised three females. In reality the type series consists of two females and a male (Bischoff 1923), of which one female and the male were studied. The female that was studied is here designated as the lectotype.

Description.—Length of head 1.8–2.0 mm; scutum 1.5–1.6 mm; fore wing 7.1–8.0 mm; body 7.0–8.6 mm. Similar to *P. carnifex* except as follows: legs with femora, tibiae and tarsi orange; vestiture on head and mesosoma mostly white, scutum yellowish-brown; subpygidial brush of female mostly brownish-orange, black dorsomedially, well developed, differentiated, expanded dorsally, bilobed ventrally (Fig. 38); flagellar segment I around 0.34× as long as scape, 1.2× as long as flagellar segments II; labrum distinctly pointed apicomediaally; maxillary palp 1.0–1.2× as long as pedicel; scutum moderately densely punctate, with small, well separated punctures; scutellum strongly tuberculate paramediaally; punctuation of area above scrobal sulcus moderately dense; female S6 narrowly bifid posteriorly; male S8 and genital capsule as in Figs. 39–40 (male S7 missing from specimen studied).

Distribution.—Central Zaïre, Equatorial Guinea and northern Angola, dominant vegetation evergreen forest.

Discussion.—The female of *P. dichrous* can be separated from *P. carnifex* by the dorsal expansion and two ventral lobes of the subpygidial brush (Fig. 38). The posterior region of the male S8 is parallel sided and the posterior end gently curved with a median notch (Fig. 39).

Type material examined.—*Pasites dichrous*, holotype ♂: 'dichroa Type SM.; *Morgania dichroa* TYPE Smith; B.M. TYPE HYM. 17B 79' (NHML). *Morgania nigrithorax*, lectotype ♀: 'Sp. Guinea, Uelleburg, 6–8.1908, G. Tessmann S.G.; *Morgania nigrithorax* Strand det. ♀ m.; Type; Zool. Mus. Berlin' (ZMHB); paralectotype ♂: 'Span. Guinea, Uelleburg, G. Tessmann S.G.; *Morgania nigrithorax* Strand det. ♀ m.; Type; *Morgania nigrithorax* Strd. ♂ Bischoff, Lectotype' (ZMHB).

Additional material examined.—2♀: ZAIRE: Kisangani (= Stanleyville), 0.30N 25.10E, 13.iv.1915, Lang & Chapin (1♀ AMNH). ANGOLA: Dundo (Distr. Lunda), ii–iv.1958 (1♀ BLCU).

Other published distribution records.—ZAIRE: Kasai, Dungu & Lac Kivu (Cockerell 1933c).

JENSENI SPECIES GROUP

This species group comprises four species, *P. jenseni*, *P. namibiensis*, *P. histrio* and *P. jonesi*. These four species all have the head, mesosoma and legs mostly black; the metasoma ranges from black to orange. The vestiture on the lower half of the face is pallid, densely plumose and appressed. The most useful diagnostic features of the females of the group are the elliptical posteromedian concavity on S5, in combination with the pygidial plate, which is at least visible posteriorly (posterior margin entire), and the differentiated subpygidial brush. Males can only be identified as belonging to the group by their association with females.

Pasites jenseni (Fries), **comb. nov.** (Figs. 41–46)

Omachthes graenicheri var. *jenseni* Fries 1915: 298.

Morgania graenicheri jenseni (Fries); Cockerell 1919:190.

Morgania (Omachthes) jenseni (Fries); Bischoff 1923:587.

Epeolus jenseni (Fries); Fries 1941:101.

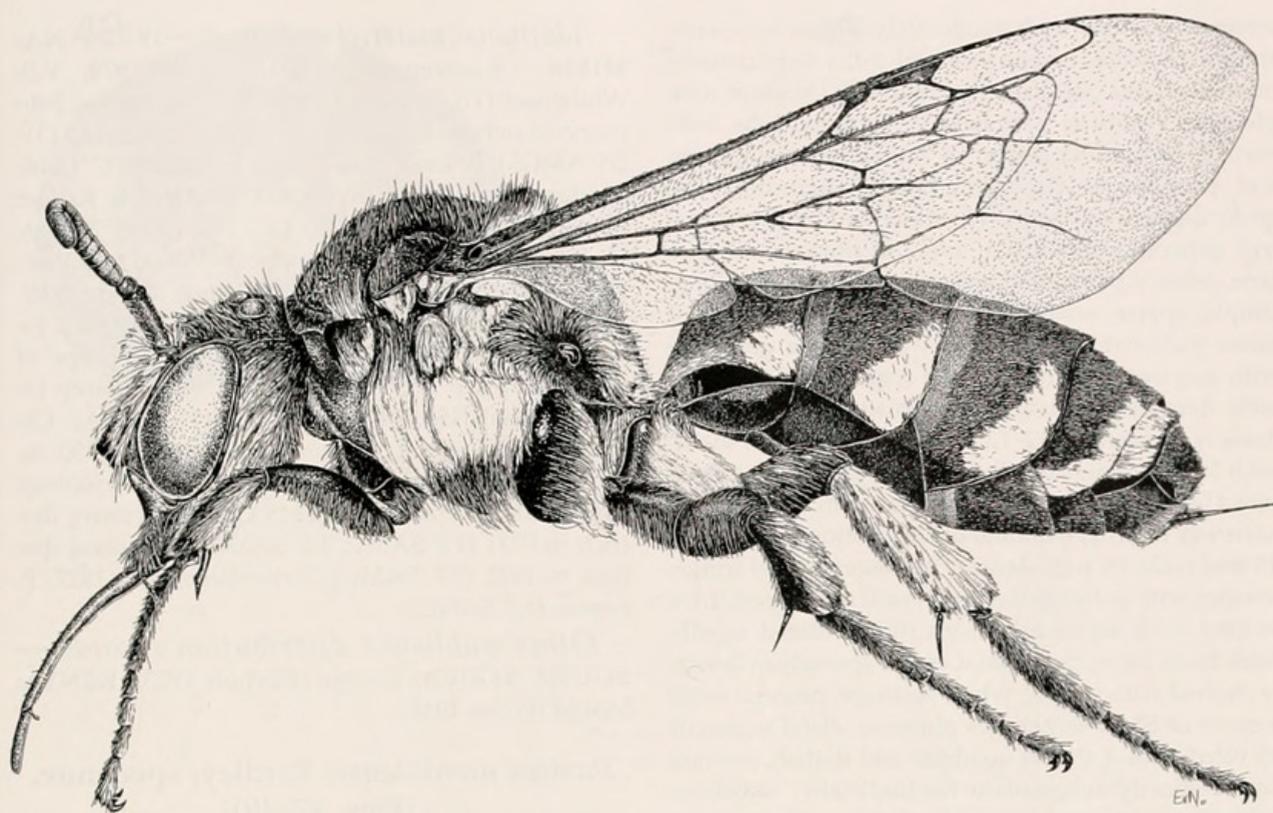


Fig. 41. *Pasites jenseni*, habitus, lateral view (integument black and vestiture largely white), ♀.

Omachthes jenseni Friese; Anonymous 1958:32.

Omachthes (Ammobates) graenicheri Brauns; Friese 1915:298, *nomen nudum*.

Morgania graenicheri (Brauns); Cockerell 1919:190.

Morgania graenicheri Bischoff 1923:587–588. **Syn. nov.**

Omachthes graenicheri Brauns; Friese 1922:38.

Pasites graenicheri (Brauns); Anonymous 1958:31.

Omachthes alboguttatus Friese 1922:38. **Syn. nov.**

Morgania (Omachthes) alboguttatus [sic.] (Friese); Bischoff 1923:588 [*lapsus*].

Morgania alboguttata (Friese); Cockerell 1933b:130.

Morgania natalensis Cockerell 1933b:129–130. **Syn. nov.**

Morgania (Omachthes) ogilviei Cockerell 1935:560–561. **Syn. nov.**

Friese (1915) described *jenseni* as a 'variety' of *graenicheri*, which he attributed to Brauns *in litt.* But neither Brauns nor anybody else had described *graenicheri* at that time, so *jenseni* is the oldest available name for this species, according to the

Code, Articles 12 & 23. Bischoff (1923) provided a brief description of *graenicheri* in a key and also attributed it to Brauns 'i.l.', the name was thus made available from that date.

Intraspecific variation in the colour, vestiture and punctuation of the species led Friese (1922) and Cockerell (1933b, 1935) to describe three morphological variants as distinct species. Following the study of both the type and other material, *alboguttata*, *natalensis* and *ogilviei* were found to fall within the range of variation of *jenseni* and are here synonymized with it.

Description.—Habitus, lateral aspect, as in Fig. 41. Length of head 2.1–3.0 mm; scutum 1.8–2.7 mm; fore wing 7.3–9.8 mm; body 7.8–12.5 mm. Integument, including tegula, mostly black, reddish-black in places. Vestiture white, except mandible, ventral surfaces of tarsi and distal region of S5 pale yellow, subpygidial brush completely black to mostly black with lateral and ventral regions orangish. Middle and lower regions of face, labrum and gena very densely pubescent, upper region of face and vertex moderately densely clothed with simple vestiture (Fig. 42); me-

mesosomal dorsum with moderately dense to sparse, simple vestiture, except pronotal collar very densely pubescent and posterolateral regions of scutum with plumose vestiture; periphery of pronotal lobe, subvertical (posterior) region of scutellum, metanotum and propodeum (including mediolongitudinal region) densely clothed with short to long vestiture; legs generally with coxae, most of tibiae and entire tarsi densely pubescent, remainder of legs with long, simple, sparse vestiture or naked; dorsal surface of tibiae also with reddish scales; metasoma generally with anterior and anterolateral regions of T1 moderately densely pubescent, posterolateral regions very densely pubescent; T2-T3 in females, T2-T4 in males with lateral regions of distal margins densely pubescent (T4 in female and T5 in male with distal fringe narrowly interrupted medially or continuous); female T5 and male T6 with densely pubescent distal fringe; females with subpygidial brush well developed, 1.1× as long as its maximum width, differentiated, mostly thick black hairs; metasomal venter sparsely to densely clothed with simple, white vestiture, posterolateral regions of S3-S4 sometimes plumose, distal region of S5 velutinous. Labrum quadrate and flattish, pointed and distinctly tuberculate mediolaterally; maxillary palp five-segmented, generally 2–3× as long as antennal pedicel; scutum moderately densely punctate with large, deep punctures that occasionally merge; scutellum with weakly developed paramedian tubercle; pygidial plate well developed in both sexes; terminal tergum truncate in female (Fig. 43), broad and rounded posteriorly in male; female S5 with elliptical concavity (Fig 43); male S7, S8 and genital capsule as in Figs. 44–46.

Distribution.—South Africa, Lesotho and central region of northern Namibia. Vegetation ranges from bushveld to montane grassland.

Discussion.—In this species the labrum is quadrate, propodeum completely clothed with fine vestiture and female pygidial plate fully developed.

Type material examined.—*Omachthes jenseni*, holotype ♀: 'Transvaal, Zeerust, 1897, Jensen; *Omachthes graenicheri* v *jenseni* ♀ Fr. 1914 Friese det.; type; *O. jenseni* Fr. ♀; Coll. Friese; Zool. Mus. Berlin' (ZMHB). *Omachthes alboguttatus*, holotype ♂: '[locality label illegible]; *Omachthes alboguttatus* ♂ Fr. 1914 Friese det.; type; Coll. Friese; Zool. Mus. Berlin' (ZMHB.) *Morgania natalensis*, holotype ♂: 'Natal: National Park, 3–15.iii.1932, A. Mackie, T.D.A. Cockerell Exp. to Africa 1931; Pres. by Imp. Inst. Ent. B.M. 1932-291; *Morgania natalensis* Ckll TYPE; B.M. TYPE HYM. 17B 98' (NHML). *Morgania ogilviei*, holotype ♂: 'AFRICA: Belmont, J. Ogilviei, 23.ii.1934, B.M. 1934-157; *Morgania ogilviei* TYPE; B.M. TYPE HYM. 17B 91' (NHML).

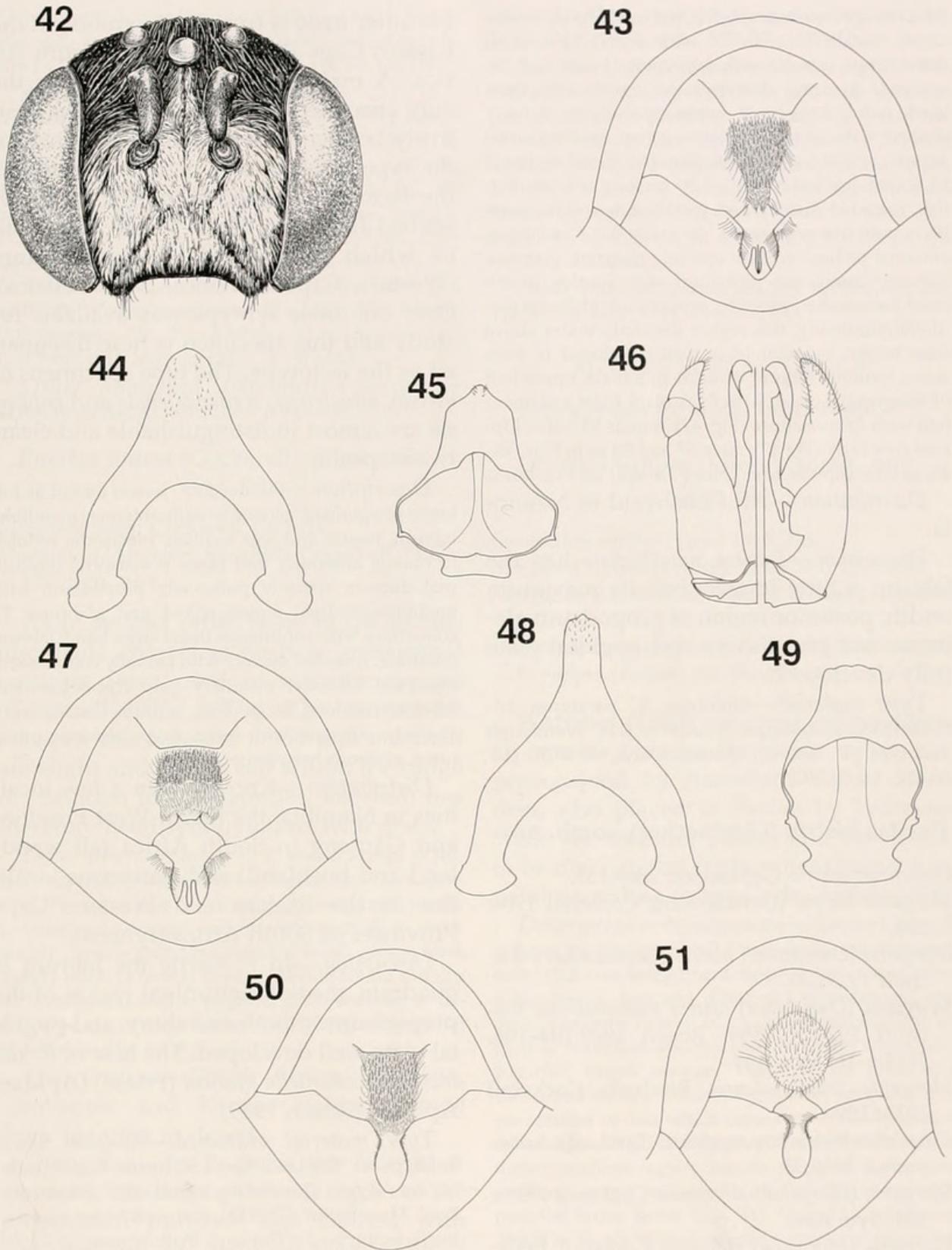
Additional material examined.—18♀ 7♂: **NAMIBIA:** Okozongominja, 2017CA, 6.iii.1979, V.B. Whitehead (1♂ SAMC). **LESOTHO:** Mamathes, February–March in 1949–1954, C. Jacot-Guillarmod (3♀ 2♂ AMGS); Bokong Post Office, 26.xii.1946, C. Jacot-Guillarmod (1♂ AMGS). **SOUTH AFRICA:** Kruger National Park, Letaba, 2331 DC, 16.xii.1965, A.,L. & H. Braack (1♀ SKNP); Woodbush Village, xii.1918, C.J. Swierstra (1♀ TMSA); Wolkberg, 21 km S.W. Tzaneen, 11.iii.1976, R.H. Watmough (1♀ SANC); Johannesburg, iv.1906, G. Kobrow (1♀ ZMHB ['type' of *graenicheri*], 4♀ 1♂ TMSA, 1♀ SANC); Delarey [= Delareyville], 15.i.1917, H. Brauns (1♀ TMSA); Cathedral Peak Hotel, 45 km S. Winterton, 1450 m, 16.ii.1967, C.D. Michener (2♀ SEMK); Modderfontein, 18.iv.1920, H. Brauns (1♀ TMSA); Murraysburg district, iii.1931 (1♀ SAMC, 1♂ SANC); Richmond district, iii.1931 (1♀ SAMC); Stellenbosch, 5.iv.1927, F. Beyers (1♂ SANC).

Other published distribution records.—**SOUTH AFRICA:** George (Bischoff 1923); **KENYA:** Morijo (Friese 1941).

***Pasites namibiensis* Eardley, spec. nov.**
(Figs. 47–49)

This new species is known to occur only in Namibia, and it takes its name from that country.

Description.—Similar to *P. jenseni* (habitus, lateral aspect, cf. Fig. 41). Length of head 2.2–2.8 mm; scutum 1.8–2.6 mm; fore wing 7.5–8.9 mm; body 8.0–12.0 mm. Integument mostly black, orange maculation limited to ventral region of clypeus, labrum, basal region of antenna, and middle and hind femora; metasomal venter usually orange or orangish. Vestiture white, except mandible, ventral surfaces of tarsi and distal region of S5 pale yellow, subpygidial brush completely black to mostly black with lateral and ventral regions orangish. Middle and lower regions of face, labrum and gena very densely pubescent, upper region of face and vertex moderately densely clothed with simple vestiture (cf. Fig. 42); mesosomal dorsum with sparse, simple vestiture, except pronotal collar very densely pubescent and posterolateral regions of scutum with plumose vestiture; periphery of pronotal lobe, subvertical (posterior) region of scutellum and metanotum densely clothed with short to long vestiture; mediolongitudinal region of propodeum naked; legs generally with coxae, most of tibiae and entire tarsi densely pubescent, remainder of legs with long, simple, sparse vestiture or naked; dorsal surface of tibiae also with reddish scales; metasoma generally with anterior and anterolateral regions of T1 moderately densely pubescent, posterolateral regions very densely pubescent; T2-T3 in females, T2-T4 in males with lateral regions of distal margins densely pubescent (T4 in female and T5 in male with



Figs. 42-51. *Pasites* spp. 42-46. *P. jenseni*. 42. Head, front view, ♀; 43. Terminalia, posterior view, ♀; 44. S7, ♂; 45. S8, ♂; 46. Genital capsule, ♂. 47-49. *P. namibiensis*. 47. Terminalia, posterior view, ♀; 48. S7, ♂; 49. S8, ♂. 50. *P. jonesi*, terminalia, posterior view, ♀. 51. *P. rufipes*, terminalia, posterior view, ♀.

distal fringe narrowly interrupted medially or continuous); female T5, male T6 with densely pubescent distal fringe; females with subpygidial brush well developed, quadrate, differentiated, mostly with thick black hairs; metasomal venter sparsely to densely clothed with simple, white vestiture, posterolateral regions of S3-S4 sometimes plumose, distal region of S5 velutinous. Labrum 1.2–1.3× as long as wide, flat-tish, rounded distally and weakly tuberculate; maxillary palp five-segmented, generally 2–3× as long as antennal pedicel; scutum sparsely punctate, glabrous between punctures; scutellum with weakly developed paramedian tubercle; propodeum glabrous mediolongitudinally, this region distinctly wider above than below; pygidial plate well developed in both sexes; terminal tergum truncate in female, upper half of subpygidial brush with thick black hairs and lower half with fine vestiture (Fig. 47); female S5 with elliptical concavity (Fig. 47); male S7 and S8 as in Figs. 48–49, genital capsule resembles *P. jenseni* (cf. Fig. 46).

Distribution.—Arid bushveld in Namibia.

Discussion.—*Pasites namibiensis* has the labrum a little longer than its maximum width, posterior region of propodeum glabrous and impunctate and pygidial plate fully developed.

Type material.—Holotype ♀, paratypes 2♂: NAMIBIA: Spitzkoppe, 8.vii.1976, R.H. Watmough (holotype ♀ SANC); Kaoko Otavi, iii.1926 (1♂ SAMC, 1♂ SANC).

***Pasites histrio* (Gerstaecker), comb. nov.**

Omachthes histrio Gerstaecker 1869:155.

Morgania histrio (Gerstaecker); Cockerell 1904: 208.

Morgania (Omachthes) histrio (Gerstaecker); Bischoff 1923:589.

Morgania (Omachthes) histrio transvaalensis Bischoff 1923:587–589; Rozen 1969:104–106, 1974:6–16. **Syn. nov.**

Morgania transvaalensis Bischoff; Cockerell 1933c:109.

Omachthes histrio transvaalensis (Bischoff); Anonymous 1958:33.

Morgania (Morgania) alivalensis Cockerell 1933a: 380. **Syn. nov.**

Morgania (Morgania) rufitarsis Cockerell 1937a: 155–157. **Syn. nov.**

Bischoff (1923) described *transvaalensis* from a female and two male specimens. The female and one male are from Delarville, in the North-West Province, and

the other male is from Willowmore, in the Eastern Cape Province, both in South Africa. A male from Willowmore was the only specimen examined that could positively be identified as constituting part of the type series and is here designated as the lectotype. *Morgania rufitarsis* was described from two males and a female, all of which were taken at Swellendam (Western Cape Province, South Africa). Only one male syntype was available for study and this specimen is here designated as the lectotype. The type specimens of *histrio*, *alivalensis*, *transvaalensis* and *rufitarsis* are almost indistinguishable and clearly conspecific.

Description.—Similar to *P. jenseni* except as follows: integument generally with antenna, mandible, labrum, tegula and legs reddish, metasoma reddish to orange anteriorly and black posteriorly; mesosomal dorsum sparsely pubescent, propodeum with mediolongitudinal region naked and glabrous; T3 sometimes with continuous distal cross-band; labrum quadrate, rounded distally with laterally compressed, subapical tubercle; maxillary palp five-segmented, 2.5–3.3× as long as pedicel; scutum usually very sparsely punctate with large, deep, separate punctures, glabrous between punctures.

Distribution.—Known from a few localities in Namibia, the North-West Province and Gauteng in South Africa (all woodland and bushland) and numerous localities in the Eastern and Western Cape Provinces of South Africa (fynbos).

Discussion.—In *P. histrio* the labrum is quadrate, mediolongitudinal region of the propodeum smooth and shiny, and pygidial plate well developed. The host of *P. histrio* is *Tetraloniella minuta* (Friese) (Apidae: Apinae) (Rozen 1969).

Type material examined.—*Morgania histrio*, holotype ♀: Capland, Krebs S.; *histrio* Gerst*, caffer N. ant.; Type; *Omachthes histrio* 1907 Friese det.; Zool. Mus. Berlin' (ZMHB). *Morgania histrio transvaalensis*, lectotype ♂: Capland, Willowmore, 18.2.1904, Dr. Brauns; *O. histrio transvaalensis* Bisch. Typ.; Typus; Bischoff ♂; *Omachthes histrio transvaalensis* Bischoff HOLOTYPE No: 1190' (TMSA). *Morgania alivalensis*, holotype ♀: Aliwal North, Cape Province, Dec. 1922, S. Africa, R.E. Turner; Brit. Mus., 1923-45; *Morgania alivalensis* Ckll. TYPE; B.M. TYPE HYM 17B 93' (NHML). *Morgania rufitarsis*, lectotype ♂:

ˆCape Province, Swellendam 17-xii.31–18.i.32, S. Africa, R.E. Turner; Brit. Mus., 1932-56; *Morgania rufitarsis* Ckll. TYPE; B.M. TYPE HYM 17B 89' (NHML).

Additional material examined.—22♀ 10♂: **NAMIBIA:** Kaoko Otavi, iii.1926 (1♀ SANC); Gobabis, 21.xii.1974, H. Empey (1♀ 1♂ SANC). **SOUTH AFRICA:** Delarey [= Delareyville], 15.i.1917, H. Brauns (1♀ SANC); Roodeplaas, 20–25.ii.1916, Dr Breyer (1♂ TMSA); Resolution, Albany district, 23.iii.1928, A. Walton (2♂ TMSA); Strowan, Grahamstown, xi–xii.1966, C. Jacot-Guillarmod (3♀ 3♂ AMGS); Grahamstown, 7.xii.1966, C.D. Michener (2♀ AMNH); W. Grahamstown, 27.xi.1966, J.G. Rozen, D.J. Brothers (7♀ 2♂ AMNH); Grahamstown, 6–7.xii.1966, C.D. Michener (7♀ 1♂ SEMK).

Other published distribution record.—**SOUTH AFRICA:** near Ceres (Cockerell 1933c).

Pasites jonesi (Cockerell), **comb. nov.**
(Fig. 50)

Morgania jonesi Cockerell 1921:207.

Morgania (Morgania) marshalli Cockerell 1937a: 157. **Syn. nov.**

As in several other cases in the genus, unreliable characters such as metasomal vestiture were used to separate species (Cockerell 1921, 1937a). The differences between the types of *jonesi* and *marshalli* are slight and clearly fall within the range of variation for this species; *marshalli* has therefore been synonymized with *jonesi*.

Description.—Similar to *P. jenseni* except as follows: certain specimens (from Karoo and Namaqualand, Western Cape Province) with metasoma mostly to completely orange; scutum very sparsely to moderately densely punctate; pygidial brush ranges from mostly black to mostly orange; labrum round distally with subapical carina; pygidial plate reduced to carina near top of pygidial brush (Fig. 50), subpygidial brush as in Fig. 50.

Distribution.—South Africa, Namibia, Zimbabwe and Kenya. Habitats range from savanna to desert.

Discussion.—In *P. jonesi* the labrum is quadrate, mediolongitudinal region of the propodeum punctate and clothed with fine vestiture and pygidial plate reduced laterally, so that only the posterior end is visible.

Type material examined.—*Morgania jonesi*, holotype ♀: ˆMfongosi, Zululand, W.E. Edwards, 1914; *Morgania jonesi* Ckll. TYPE' (SAMC). *Morgania marshalli*, holotype ♀: ˆMazoe, Mashonal'd, Dec. 05,

G.A.K. Marshall, 1908-212; *Morgania marshalli* Ckll. TYPE; B.M. TYPE HYM. 17B 90' (NHML).

Additional material examined.—7♀ 1♂: **KENYA:** Karen, Nairobi, 3 & 20.v.1967, C.D. Michener (2♀ SEMK). **NAMIBIA:** 40 km N. Omaruru, 19.ii.1977, J.G. & B.L. Rozen (1♀ AMNH). **SOUTH AFRICA:** Kruger National Park, Shipandani Picket, 2331CB, A., L. & H. Braack (2♀ SANC); Dikbome, Koup, Laingsburg div., iv–v.1950, H. Zinn (2♀ SAMC); Vogelfontein, P. Albert div., iii–iv.1929, A.J. Hesse (1♂ SAMC).

Other published distribution record.—**KENYA:** Masai Reserve (Cockerell 1933c).

RUFIPES SPECIES GROUP

This species group is monotypic.

Pasites rufipes (Fries), **comb. nov.**
(Fig. 51)

Omachthes rufipes Fries 1915:298.

Morgania rufipes (Fries); Cockerell 1919:190.

Morgania (Omachthes) rufipes (Fries); Bischoff 1923:591–592.

Pasites capensis Warncke 1983:292 [*nom. nov. pro P. rufipes* (Fries) *nec* (Saunders)].

Warncke (1983) renamed *rufipes* Fries as *capensis* because the name *rufipes* was preoccupied by *Ammobates rufipes* Saunders, also placed in *Pasites* by Warncke. Since we consider *Pasites* and *Ammobates* to be distinct, this replacement name is invalid according to the Code, Article 59(d).

Description.—Female (male unknown). Length of head 2.6 mm; scutum 2.1 mm; fore wing damaged; body 10.2 mm. Integument mostly black, scape, mandible, tegula, legs and distal end of metasoma reddish. Vestiture mostly black, mediolongitudinal region of scutellum and metanotum partly white, subpygidial brush orange. Vestiture on head and mesosoma mostly moderately sparse, long and simple (similar to that which occurs in certain species of *Sphécodopsis*, Figs. 62–63); propodeum, including mediolongitudinal region, largely plumose; metasomal vestiture sparse and simple (*cf.* Fig. 62), except subpygidial brush dense (Fig. 51); S6 pallid, velutinous distally. Vertex flattish laterally, strongly raised between lateral ocelli (*cf.* Fig. 63); labrum about 1.3× as long as wide, flattish and gently rounded distally; maxillary palp five-segmented, 4.1× as long as pedicel; scutum quadrate, fairly densely punctate, punctures large, often confluent; scutellum weakly tuberculate paramedially; punctation on mesopleuron similar to scutum; pygidial plate absent (Fig. 51); S5 with

well developed, elliptical, concavity posteromedially (Fig. 51); S6 widely bifurcate.

Distribution.—Known from two widely separated localities in South Africa, namely Zeerust (woodland) in the North-West Province, and Bowesdorp, near Kamieskroon (shrubland) in Namaqualand. Both these localities are fairly arid, but Zeerust has summer rainfall and Namaqualand has a Mediterranean climate.

Discussion.—*Pasites rufipes* can be easily recognized by the long, black, erect, weakly plumose vestiture on the head and mesosoma in combination with the vertex which is more or less flat laterally (cf. Fig. 63), absence of a pygidial plate and elliptical concavity on the posteromedian region of the female S5 (Fig. 51). The structure of the vertex and vestiture on the head and mesosoma of *P. rufipes* resembles that of certain species of *Sphecodopsis*, but the elliptical concavity of the female S5 concurs with that of *Pasites*, and the structure of the pygidium is unique. The male of *P. rufipes* is unknown.

Type material examined.—*Omachthes rufipes*, holotype ♀: Transvaal, Zeerust, 1897, Jensen; *Omachthes rufipes* ♀ Fr. 1914 Friese det.; Type; *Morgania rufipes* Fr. i.l.Bisch. Type ♀; Zool. Mus. Berlin (ZMHB).

Additional material examined.—1♀: SOUTH AFRICA: Bowesdorp, ix.1941 (1♀ SAMC).

APPLETONI SPECIES GROUP

Pasites appletoni and *P. somalicus* comprises this species group. The head and mesosoma of these two species are black, as in most of their congeners, but the legs and metasoma are usually orange. The female S5 is elliptically concave posteromedially and the pygidial plate is either notched or absent posteriorly. The most conspicuous salient feature of the male of *P. appletoni* is the simple, erect, yellowish vestiture on the scutum in combination with the legs that are usually orange. The male of *P. somalicus* is unknown.

In the scutal vestiture and colour of the integument, especially the orangish legs, these two species resemble the Palaearctic

species *P. maculatus* in which the pygidial plate is absent in the female and reduced in the male.

Pasites appletoni (Cockerell), **comb. nov.** (Figs. 52–56)

Morgania appletoni Cockerell 1910:216–217.

Omachthes abessinicus Friese 1915:297–298. **Syn. nov.**

Morgania abessinica (Friese); Cockerell 1919:190.
Morgania (Omachthes) abessinicus [sic.] (Friese);
Bischoff 1923:589–590 [lapsus].

Morgania (Omachthes) fulviventris Bischoff 1923:590. **Syn. nov.**

Morgania fulviventris Bischoff; Cockerell 1937a:154.

Omachthes fulviventris (Bischoff); Anonymous 1958:31.

Morgania (Omachthes) rhodesianus [sic.] Bischoff 1923:590 [lapsus]. **Syn. nov.**

Omachthes rhodesianus (Bischoff); Anonymous 1958:33.

Morgania (Omachthes) apicalis Bischoff 1923:591. **Syn. nov.**

Morgania apicalis Bischoff; Cockerell 1933a:379.

Omachthes apicalis (Bischoff); Anonymous 1958:30.

Morgania (Omachthes) turneri Cockerell 1933a:378–379. **Syn. nov.**

Morgania (Pseudopasites) politula Cockerell 1933a:382, 384 [incorrectly given masculine gender on p. 382]. **Syn. nov.**

Morgania (Omachthes) indecisa Cockerell 1936:31. **Syn. nov.**

Morgania (Omachthes) nudicauda Cockerell 1937a:153. **Syn. nov.**

Morgania (Omachthes) bechuanica Cockerell 1937a:153–154. **Syn. nov.**

Morgania (Omachthes) breviceps Cockerell 1937a:154. **Syn. nov.**

This species is widely distributed in subsaharan Africa. Throughout its range it varies greatly in size and moderately in colour. The density of the vestiture varies gradually and cannot be used to separate species. However, specimens from the Karoo and Namaqualand tend to have less pilosity, especially on the metasoma, than material from localities to the north of this region. The large amount of variation that is displayed, together with the species'

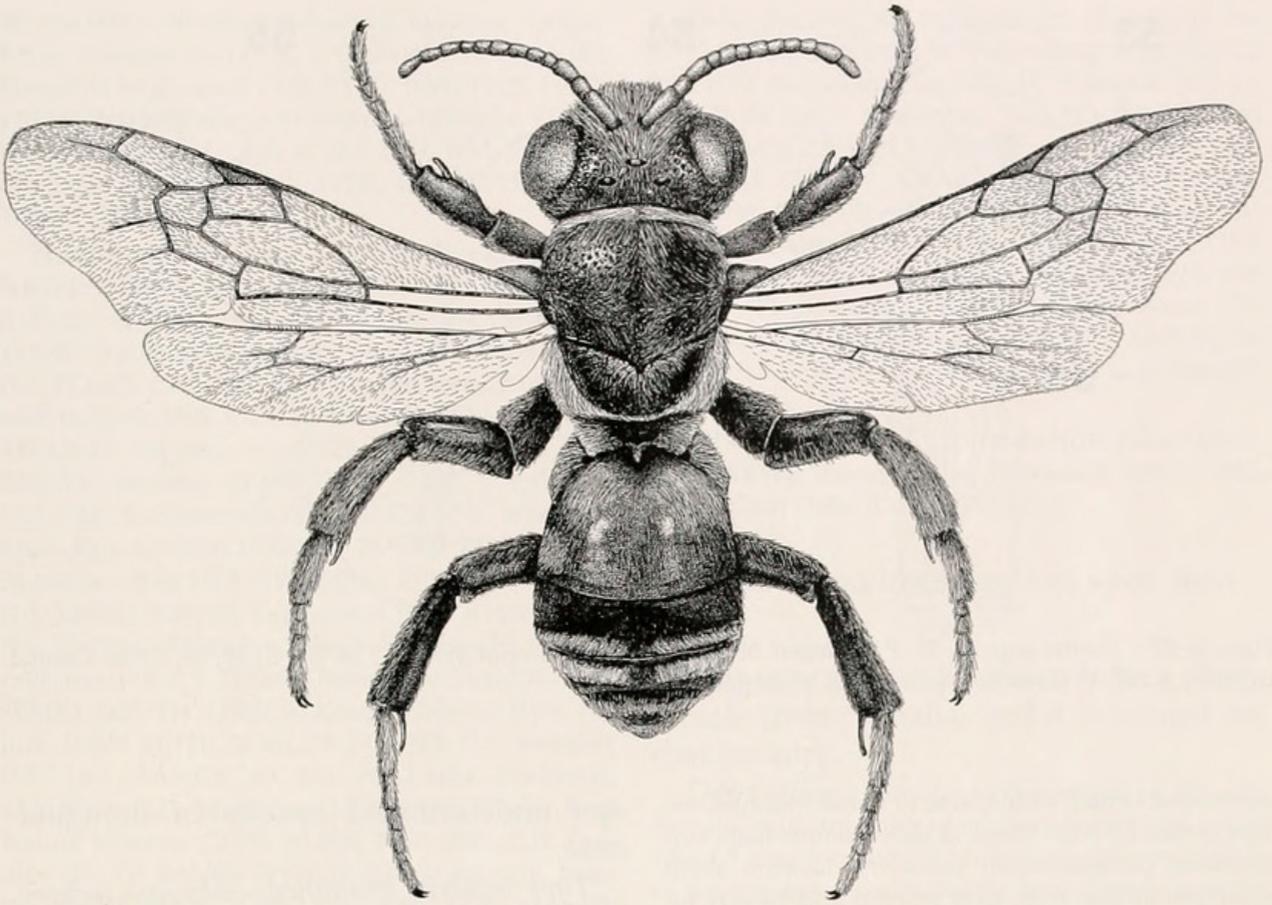
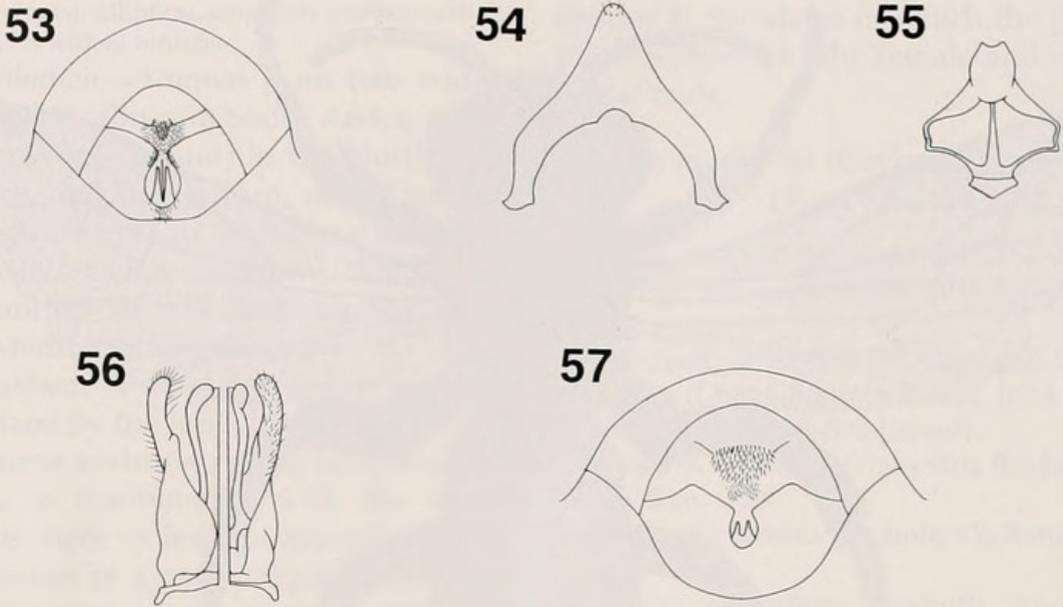


Fig. 52. *Pasites appletoni*, habitus, dorsal view (dark shading represents black or blackish integument and lightly shaded areas are orange), ♀.

wide distribution, has led to the description of a large number of synonyms. This was revealed through study of all the relevant type material.

Description.—Habitus, dorsal aspect, as in Fig. 52. Length of head 1.0–1.7 mm; scutum 0.8–1.3 mm; fore wing 3.3–5.8 mm; body 3.9–7.2 mm. Colour of integument of head mostly black, ventral margin of clypeus sometimes orange, antenna often partly to mostly orange or orangish, labrum and mandible usually mostly orangish (distal end of mandible blackish, labrum often with mediobasal, lateral and mediobasal regions black); mesosoma ranges from almost completely black to completely orange, most commonly with scutum, scutellum, propodeum and upper region of mesopleuron black or reddish-black, lower region of mesopleuron and mesosomal venter orange; pronotal lobe usually partly orange; tegula translucent orange; legs mostly orange, coxae sometimes black or blackish, femora, tibiae and tarsi occasionally black; metasoma generally reddish to orange, sometimes with blackish tinge and/or black distally. Vestiture on head white, except mandible white to yellowish; mesosoma mostly white, scutum yellowish except lateral region which is white, dorsal

surface of scutellum concolorous with scutum; legs largely white, ventral surfaces of tarsi yellowish, outer surfaces of tibiae with few reddish scales; mesosomal vestiture mostly white, subpygidial brush usually black medially, circumscribed with orange; mesosomal venter orange to white vestiture, except female S5 with orange fringe surrounding posteromedian concavity. Vestiture on head usually mostly moderately dense and plumose, that on upper region of face and vertex sparse and simple, occasionally lower region partly clothed with simple hairs; mandible with few simple hairs; pronotal collar and lobe densely pubescent; scutum with short, simple moderately dense, vestiture, except lateral region which is densely pubescent; scutellum with dorsum largely similar to scutum, posterior (subvertical) surface plumose; propodeum naked mediolongitudinally; legs with femora largely naked; metasoma with T1 naked to sparsely pubescent anteriorly (subvertical surface), with dense posterolateral spots; female T2–T5, males T2–T6 with sparse to dense pubescence on posterior margins which may be interrupted medially; female T6 with well developed, subpygidial brush; differentiation of subpygidial brush unique in that thick hairs occur in centre and fine vestiture around edge (Fig. 53); male T7 sparsely clothed with pale vestiture;



Figs. 53–57. *Pasites* spp. 53–56. *P. appletoni*. 53. Terminalia, posterior view, ♀; 54. S7, ♂; 55. S8, ♂; 56. Genital capsule, ♂. 57. *P. somalicus*, terminalia, posterior view, ♀.

metasomal venter with sparse to dense vestiture, except female S5 with fringe of short, simple hairs surrounding posteromedian concavity. Labrum about quadrate, flattish with apex pointed and weakly tuberculate; maxillary palp four-segmented, 1.5–2.2× as long as antennal pedicel; scutum fairly densely covered with small well separated punctures; scutellum gently and evenly convex to unevenly convex with paramedian regions weakly swollen; propodeum with broad glabrous area mediolongitudinally; mesopleuron mostly densely punctate, ventrolateral and ventral regions sparsely punctate; pygidial plate well developed, broadly rounded in both sexes, female with distinct notch mediodistally (Fig. 53); female S5 with elliptical concavity (Fig. 53); male S7, S8 and genital capsule as in Figs. 54–56.

Distribution.—Niger and Cameroon, in the north-west, Somalia, in the north-east, and from much of southern Africa. Habitat ranges from rain forest to desert.

Discussion.—*Pasites appletoni* can be identified by the female terminalia. The pygidial plate is notched posteromedially, the subpygidial brush is mostly orangish with a black centre and S5 with an elliptically concave posteromedially (Fig. 53). The male can be identified by the shape of the S7 and S8 (Figs. 54–55), and in orange coloured specimens, by the colour of the legs and metasoma.

Floral records.—Pedaliaceae: *Sesamum*

sp.; undetermined species of Boraginaceae.

Type material examined.—*Morgania appletoni*, holotype ♀: 'Bohotle, Somaliland, 1903, Verty. Major A.F. Appleton, 1907–89; *Morgania appletoni* Ckll. TYPE; B.M. TYPE HYM. 17B 84.' (NHML). *Omachthes abessinicus*, holotype ♀: 'NO.-Afrika, Eritrea, 08; *Omachthes abessinicus* Fr. ♀ 1914 Friese det.; Type; Zool. Mus. Berlin' (ZMHB). *Morgania fulviventris*, holotype ♂: 'Capland, Willowmore, 1.12.1904, Dr Brauns; *Omachthes fulviventris* Bisch. ♂ Typ.; *Omachthes fulviventris* Biss. ♂ Type No. 569' (TMSA). *Morgania rhodesiana*, holotype ♂: 'Bulawayo, S. Rhodesia, 14.12.1919, Rhodesia Museum; *Omachthes rhodesianus* Bisch. ♂ Typ.; *Omachthes rhodesianus* Biss. ♂ Type No. 572' (TMSA). *Morgania apicalis*, holotype ♂: 'Capland, Willowmore, März 10 1919, Dr Brauns; *Omachthes apicalis* Bisch. Typ.; *Omachthes apicalis* Biss. ♂ Type No. 568' (TMSA). *Morgania turneri*, holotype ♀: 'S.W.Africa, R.E. Turner, Brit. Mus., 1928-61; Okahandja, 1–12.i.1928; *Morgania turneri* Ckll. TYPE; B.M. TYPE HYM. 17B 83' (NHML). *Morgania politula*, holotype ♂: 'Cape Province, Little Karoo, 38 m. E. of Ceres, 17–25.xi.1924, S.Africa, R.E. Turner, Brit. Mus. 1924-518; *Morgania politula* Ckll. TYPE; B.M. TYPE HYM. 17B 97' (NHML). *Morgania indecisa*, holotype ♀: 'S.W.Africa, Cape of Good Hope, Nelspoort, 5.xii.1933, J. Ogilvie, T.D.A. Cockerell, Exp. to Africa 1931, Pres. by Imp. Inst. Ent. B.M. 1932-291; *Morgania indecisa* Ckll. TYPE; B.M. TYPE HYM. 17B 92' (NHML). *Morgania nudicauda*, holotype ♀: 'AFRICA, Belmont, J. Ogilvie, 23.ii.1934, B.M. 1934-157; *Morgania nudicauda*; B.M. TYPE HYM. 17B

88' (NHML). *Morgania bechuanica*, holotype ♀: 'AFRICA, Palapye, 5.iii.1934, J. Ogilvie, B.M. 1934-172; *Morgania bechuanica* Ckll. TYPE; B.M. TYPE HYM. 17B 86' (NHML). *Morgania breviceps*, holotype ♀: 'AFRICA, Upington, J. Ogilvie, 21.ii.1934, B.M. 1934-157; *Morgania breviceps* Ckll. TYPE; B.M. TYPE HYM. 17B 87' (NHML).

Additional material examined.—210♀ 55♂: **NIGER**: 20 km S. Tahoua, 14.45N 05.20E, 13.viii.1987, A. Pauly, on Boraginaceae (1♀ 1♂ PCGB); Tsernaoua, 13.53N 05.20E, 13.viii.1987, A. Pauly, On *Sesamum* sp. (1♂ PCGB). **CAMEROON**: Bambui, near Bamenda, 1400 m, 5.viii.1966, C.D. Michener (1♀ SEMK). **BOTSWANA**: Serowe, 17.x.1923, R. Stevenson (1♀ TMSA); Serowe, iii.1986 (3♀ SANC); Palapye, 18.x.1923, R. Stevenson (1♀ SANC); V.-L. Kal. Exp. Kuke Pan, 21-30.iii.1930 (1♀ TMSA). **ZIMBABWE**: Sawmills, 28.xii.1919 (2♀ TMSA); Hillside, 17.ii.1923 (1♂ TMSA); Sanyati Valley, ix-x.1925, R. Stevenson (1♀ TMSA); Bulawayo, December-March, various collectors (9♀ 7♂ TMSA); Bulawayo, 23.xi.1924 (2♀ SEMK). **SOUTH AFRICA**: Kruger National Park, Pafuri, 22.26S 31.12E, 264m, 20-24.i.1985, G.L. Prinsloo (53♀ 8♂ SANC); 40 km N. Louis Trichardt, 24.iii.1967, C.D. Michener (2♀ SEMK); Happy Rest Nature Reserve, 22.59S 29.46E, 10.iii.1990, C.D. Eardley (2♀ 2♂ SANC); D'Nyala Nature Reserve, Ellisras district, 23.45S 27.49E, 19.xii.1987, M.W. Mansell, G.L. Prinsloo, C.D. Eardley (3♀ SANC); Mogol Nature Reserve, Ellisras district, 23.58S 27.45E, 27-29.ii.1984, C.D. Eardley (1♀ 1♂ SANC); Ben Alberts Nature Reserve, Thabazimbi, 24.37S 27.23E, 24-28.xi.1980, M.W. Mansell, C.D. Eardley (2♀ SANC); Ellisras, 7.x.1961, 3.i.1971 & 19.ii.1972, H. Empey (1♀ 1♂ SANC); Soutpan, Pretoria district, 25.24S 28.06E, 29.i.1987, C.D. Eardley (1♀ SANC); Scottburgh, 14.ii.1926, R.H.R. Stevenson (1♀ SAMC); Olifantshoek, 24.iii.1990, W. Pulawski (1♀ 2♂ CASC); Carlisle Bridge, 14.i.1965, H. Empey (1♀ SANC); Graaff-Reinet, 3.i.1978, H. Empey (1♂ SANC); Willowmore, i-ii.1911 & ii.1912, H. Brauns (1♀ 1♂ TMSA, 1♀ 2♂ SANC). **NAMIBIA**: Rundu, 10.iii.1990, W. Pulawski (1♀ CASC); Otavi, iii.1926 (1♀ SAMC); Namakunde, ii.1922 (1♀ SAMC); 61 km W. Omaruru, 22.iii.1979, J.G. Rozen (2♀ AMNH); 11-46 km W. Usakos, 14.iii.1979, J.G. & B.L. Rozen (8♀ AMNH); 17-19 km E. Usakos, 18.iii.1976, J.G. & B.L. Rozen (2♀ AMNH); 50km S.W. Usakos, 21.ii.1990, W. Pulawski (1♀ CASC); 11 km N. Karibib, 27.ii.1990, W. Pulawski (1♀ CSAC); 62 km E. Karibib, 20.ii.1990, W. Pulawski (2♀ CSAC); 43 km E. Karibib, 20.ii.1990, W. Pulawski (1♀ CSAC); Otjituo, i.1920, W. Tucker (1♀ SAMC); 70 km N. Okahandja, 16.iii.1990, W. Pulawski (2♀ 2♂ CASC); 5 km S. Okahandja, 13-17.iii.1979, J.G. & B.L. Rozen (6♀ AMNH); 5 km S. Okahandja, 30.iii.-1.iv.1979, J.G. Rozen (53♀ AMNH); 27 km S. Okahandja, 18.ii.1990, W. Pulawski (3♀ CASC); 3 km N.E.

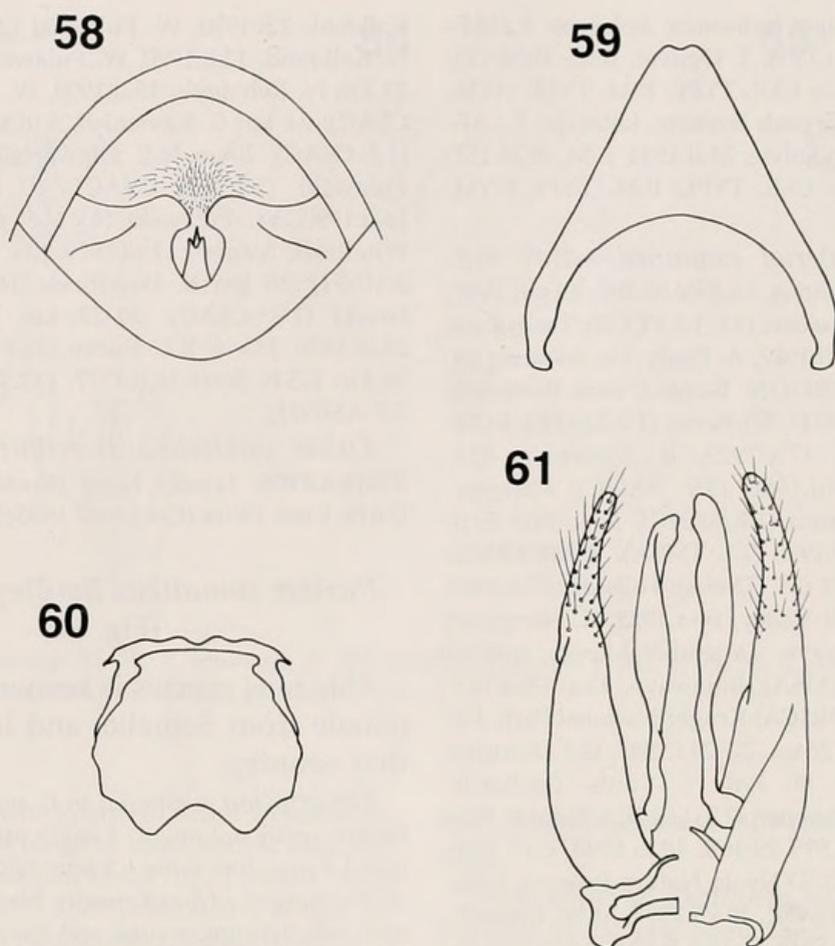
Kalkfeld, 2.ii.1990, W. Pulawski (2♀ CASC); 15 km N. Kalkrand, 13.ii.1990, W. Pulawski (2♀ 1♂ CSAC); 23 km N. Rehoboth, 15.ii.1990, W. Pulawski (1♀ 1♂ CSAC); 24 km S. Kamanjab, 5.iii.1990, W. Pulawski (1♂ CSAC); 20km N.E. Otjiwarongo, 13.iii.1990, W. Pulawski (3♀ 2♂ CSAC); 40 km W. Witvlei, 16.ii.1990, W. Pulawski (4♀ 1♂ CSAC); 8 km W. Windhoek Airport, 11.iii.1979, J.G. & B.L. Rozen (1♂ AMNH); 36 km E. Windhoek, 16.ii.1990, W.J. Pulawski (1♀ CSAC); 20-22 km E.S.E. Seeis, 13-29.iii.1976, J.G. & B.L. Rozen (16♀ 12♂ AMNH); 9-36 km E.S.E. Seeis 16.ii.1977, J.G. & B.L. Rozen (5♀ 3♂ AMNH).

Other published distribution records.—**ZIMBABWE**: Lonely Mine (Cockerell 1933a); **SUDAN**: Cash Delta (Cockerell 1933c).

Pasites somalicus Eardley, spec. nov. (Fig. 57)

This new species is known from a single female from Somalia, and it is named for that country.

Description.—Similar to *P. appletoni* (cf. Fig. 52). Female (male unknown). Length of head 1.9 mm; scutum 1.7 mm; fore wing 6.5 mm; body 9.4 mm. Colour of integument of head mostly black, antenna partly orangish, labrum orange and mandible orange, except distal end which is blackish; mesosoma black; legs orange, except middle and hind coxae which are black; metasoma orange. Vestiture on head white, except mandible white to yellowish; mesosoma mostly white, scutum yellowish except lateral region which is white, dorsal surface of scutellum concolorous with scutum; legs largely white, ventral surfaces of tarsi yellowish, outer surfaces of tibiae with few reddish scales; metasomal vestiture mostly white, subpygidial brush black dorsally, orange ventrally (Fig. 57); metasomal venter with orange to white vestiture, except S5 with an orange fringe surrounding posteromedian concavity. Vestiture on head dense and plumose, that on upper region of face and vertex sparse and simple; mandible with few simple hairs; pronotal collar and lobe densely pubescent; scutum with short, simple moderately dense, vestiture, except lateral region which is densely pubescent; scutellum with dorsum largely similar to scutum, posterior (subvertical) surface plumose; propodeum naked mediolongitudinally; legs with femora largely naked; metasoma with T1 naked to sparsely pubescent anteriorly (subvertical surface), with dense posterolateral spots; T2 with dense white pubescence posterolaterally; female T3-T5 with dense white subapical fringes; T6 with well developed subpygidial brush, which has thick hairs above and fine vestiture below (Fig. 57); metasomal venter with sparse to dense vestiture, except S5 with fringe of short, simple hairs surrounding pos-



Figs. 58–61. *Pasites maculatus*. 58. Terminalia, posterior view, ♀; 59. S7, ♂; 60. S8, ♂; 61. Genital capsule, ♂.

teromedian concavity. Labrum about quadrate, flat-tish with apex pointed and weakly tuberculate; maxillary palp four-segmented, subequal in length to antennal pedicel; scutum fairly densely covered with small well separated punctures; scutellum with paramedian region distinctly swollen; propodeum narrowly naked mediolongitudinally; mesopleuron mostly densely punctate, ventrolateral regions sparsely punctate; pygidial plate only visible posterolaterally (Fig. 57); S5 with elliptical concavity (Fig. 57).

Distribution.—Somalia, *Acacia-Commiphora* woodland.

Discussion.—*Pasites somalicus* closely resembles *P. appletoni*. They can be separated by the structure of the female pygidium. In *P. somalicus* the pygidial plate is visible as two lateral carinae only and the subpygidial brush is black dorsally and orangish ventrally.

Type material.—Holotype ♀: **SOMALIA**: locality illegible, 25.11.53, Desert Locust Survey (AMGS).

MACULATUS SPECIES GROUP

This species group is monotypic.

Pasites maculatus (Jurine) (Figs. 58–61)

Pasites maculata Jurine 1807: 224.

Diagnosis.—Length of head 1.7–2.3 mm; scutum 1.2–1.5 mm; forewing 4.8–5.8 mm; body 5.8–7.3 mm. Colour of integument of head ranges from mostly black, ventral margin of clypeus, labrum and mandible orange, to completely orange; mesosoma ranges from almost completely black, except pronotal lobe and tegula orange, to completely orange, except mediolongitudinal region of propodeum black; legs mostly orange, coxae, trochanters and proximal region of femora sometimes black; metasoma generally reddish to orange, sometimes with blackish tinge and/or black distally. Vestiture mostly white to whitish, ventral surfaces of tarsi yellowish, outer surfaces of tibiae with few reddish scales, subpygidial brush of female mostly infuscated, black dorsomedially, metasomal partly orange. Vestiture on head mostly

sparse and simple, moderately dense and plumose around antennal socket; pronotal collar densely pubescent; scutum and scutellum mostly with short, simple, sparse vestiture; propodeum naked mediolongitudinally; femora with sparse vestiture; T1 with sparse vestiture; T2 with sparse to dense vestiture; female T3-T5, male T3-T6 with bands of dense pubescence on posterior region which are interrupted medially and mediolaterally; female T6 with well developed, subpygidial brush (Fig. 58); male T7 largely naked; metasomal venter with sparse vestiture, except female S5 with fringe of short, simple hairs surrounding posteromedian concavity. Labrum 1.3× as long as its maximum width, flattish with apex pointed; without maxillary palp; scutum fairly densely covered with large well separated punctures; scutellum unevenly convex with paramedian regions distinctly swollen; propodeum with mediolongitudinal area broad and glabrous; mesopleuron mostly densely punctate, ventrolateral and ventral regions sparsely punctate; pygidial plate absent in female (Fig. 58), reduced in male; female S5 with elliptical concavity (Fig. 58); male S7, S8 and genital capsule as in Figs. 59-61.

Distribution.—North-west Africa and Spain to Japan (Rozen 1986).

Discussion.—The synonymy of this species is given by Warncke (1983) and aspects of the biology are discussed by Rozen (1986) where he shows that *P. maculatus* parasitizes *Pseudapis* (Halictidae: Nomiinae).

Although *P. maculatus* resembles the *apletoni* species group in colour, it is most closely related to the *jenseni* species group. The female can be identified by the absence of the pygidial plate and the subpygidial brush which is mostly black and dorsoventrally differentiated (Fig. 58). In the male the elongate labrum, reduced pygidial plate and quadrate S8 (Fig. 60), in combination, are diagnostic.

Material examined.—4♀ 4♂: SPAIN: Sierra Nevada (1300 m), 18-24.vii.1980, K.M. Guichard (1♀ NHML). SOUTH TUNISIA: Mareth, 30.vii.1978, K.M. Guichard, G.R. & A.C. Else (1♀ NHML). GREECE: Rhodes Ixia, 15-29.viii.1984, M.C. Day (1♂ NHML). ISRAEL: Lubban (500 m), 20.v.1975, K.M. Guichard (1♂ NHML). CYPRUS: Akrotiri, 16.vii.1944, G.A. Mavromoustakis (1♂ NHML); Li-massol, 12.vi.1929, G.A. Mavromoustakis (1♀ NHML). AUSTRIA: N.E. Marchfeld, Oberweiden, (Sandberge), 21.vii.1952, F. Koller (1♀ 1♂ SCAA).

SPECIES OF UNCERTAIN IDENTITY

The following four species, *Pasites atratulus* Friese, *Omachthes gabonensis* Vachal, *Morgania rotundiceps* Bischoff and *Morgania tropica* Cockerell, could not be identified from the literature alone and the type material could not be located. Although *Omachthes* and *Morgania* have been synonymized with *Pasites*, it could not be established whether the last three species really belong in *Pasites*.

Pasites atratulus Friese

Pasites atratulus Friese 1922:36 (syntypes 3♂).
Morgania (Omachthes) atratulus [sic.] (Friese); Bischoff 1923:588 [lapsus].
Morgania atratulus [sic.] (Friese); Medler 1980:483.

The type material of this species comprised three males. One was placed in the ZMHB and two in the Zoologische Institut und Zoologische Museum, Universität von Hamburg, Hamburg, Germany. The first-mentioned type is not in the ZMHB, and the other two were destroyed during World War II.

Omachthes gabonensis Vachal

Omachthes gabonensis Vachal 1903:382-383 (holotype ♀).
Morgania gabonensis (Vachal); Cockerell 1919:190.
Morgania (Omachthes) gabonensis (Vachal); Bischoff 1923:587-588.
Omachthes gabonensis (Vachal); Medler 1980:483.

The holotype of this species was apparently originally deposited in Vachal's collection, now housed in the MNHN. However, it could neither be found here nor in any of the other major European museums.

Morgania rotundiceps Bischoff

Morgania (Omachthes) rotundiceps Bischoff 1923:588 (syntypes 2♂).

The species was described from two males, both of which were taken in Tanzania. Although Bischoff said he deposit-

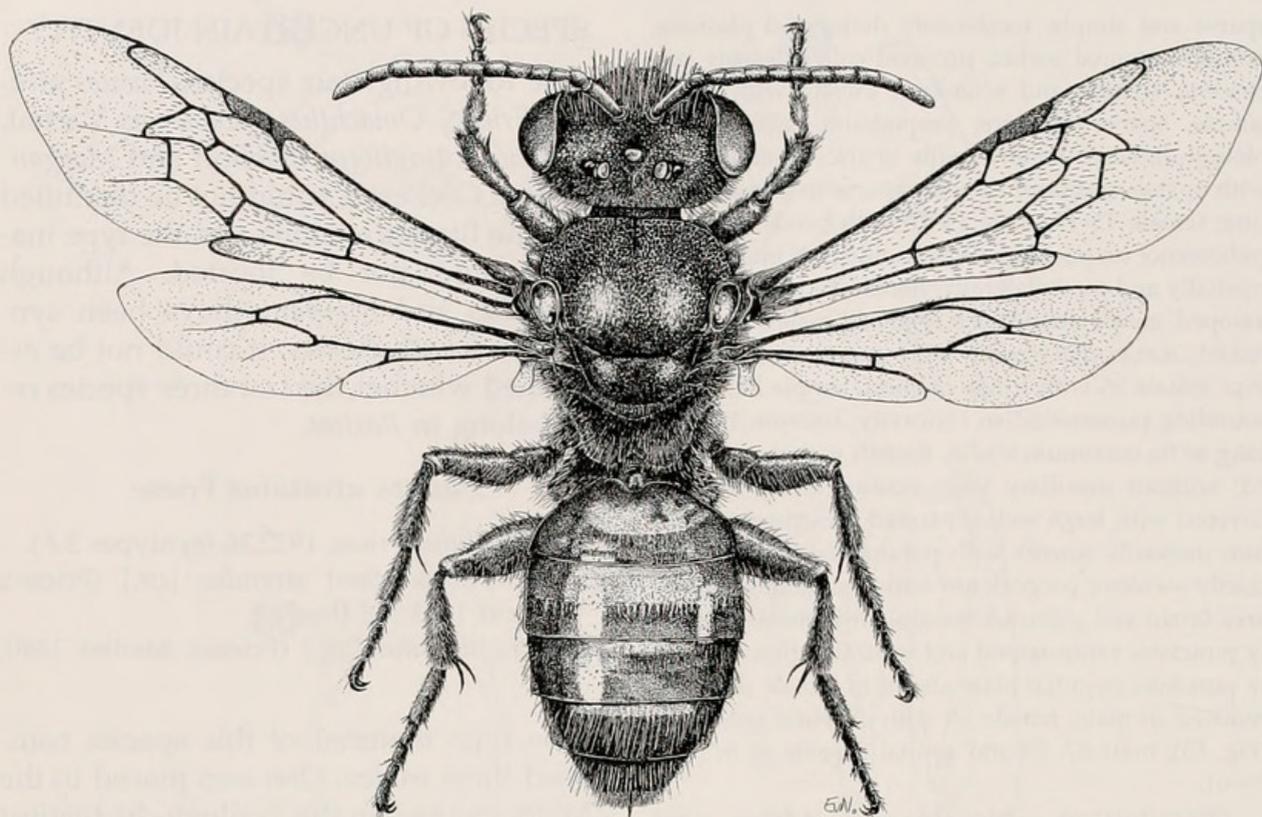


Fig. 62. *Sphecodopsis capicola*, habitus, dorsal view (dark shading represents black or blackish integument and lightly shaded areas are reddish), ♀.

ed the type material in the ZMHB, it could not be found there.

Morgania tropica Cockerell

Morgania tropica Cockerell 1933c:106–107 (holotype ♀, MRAC).

The type material of this species is housed in the MRAC. The material was on loan during the course of this study and the museum was unable to retrieve it.

GENUS *SPHECODOPSIS* BISCHOFF

Sphecodopsis Bischoff 1923:593. Type species: *Omachthes capicola* Strand 1911 (original designation).

Sphecodopsis (*Sphecodopsis*) Bischoff 1923:593.

Sphecodopsis (*Pseudopasites*) Bischoff 1923:593.

Type species: *Pasites pygmaeus* Friese 1922 (subsequent designation, Sandhouse 1943).

Syn. nov.

Pseudodichroa Bischoff 1923:586, 595; Rozen 1968a:1–10. Type species: *Omachthes capensis* Friese (subsequent designation, Sandhouse 1943). **Syn. nov.**

The following ten species comprise the genus *Sphecodopsis*: *S. capicola* (Strand), *S. vespericena* spec. nov., *S. villosa* Friese, *S. longipygidium* spec. nov., *S. namaquensis* spec. nov., *S. minutissima* (Cockerell), *S. aculeata* (Friese), *S. semirufa* (Cockerell), *S. capensis* (Friese) and *S. fumipennis* (Bischoff). Of these, *S. vespericena*, *S. longipygidium*, *S. namaquensis*, *S. capensis* and *S. fumipennis* are only known from female specimens, and *S. villosa* is only known from the male. The diagnostic characters of many of the species are sex-limited, and in the absence of suitable material of these species it is impossible to associate the sexes. This led to the unassociated and undescribed males of two species, of which material was available, being omitted from the study. As the males of most of the described species are unknown or cannot be identified, a key for the identification of the males has not been provided. The male terminalia have the most reliable diagnostic features of this sex and have

been illustrated for the species of which males are known. These illustrations, in combination with the descriptions, should enable the recognition of those males.

The genus is endemic to southern Africa. Five species (*S. vespericena*, *S. longipygidium*, *S. namaquensis*, *S. capensis* and *S. fumipennis*) are known only from Namaqualand and the south-western region of the Western Cape, an additional three species (*S. capicola*, *S. aculeata* and *S. semirufa*) occur in Namaqualand and the Karoo. The distribution of one of these, namely *S. aculeata*, extends eastward to Grahamstown. The other two species (*S. villosa* and *S. minutissima*) apparently occur throughout the greater part of southern Africa.

Bischoff (1923) divided *Sphecodopsis* into two subgenera. The nominotypical subgenus comprised *S. capicola* and *S. villosa*, while the subgenus *Pseudopasites* comprised *S. minutissima* and *S. aculeata*. *Sphecodopsis capensis* and *S. fumipennis* were placed in the genus *Pseudodichroa* by Bischoff (1923). Cockerell (1919 & 1933c) consistently placed the species here recognised as belonging to *Sphecodopsis* in the genus *Morgania*, and (Cockerell 1933a) considered *Sphecodopsis* and *Pseudopasites* to be subgenera of *Morgania*. In the cladistic analysis of these species, *Pasites* (= *Morgania*) and *Sphecodopsis* form distinct clades and are here considered to be distinct genera. The analysis did not reveal any characteristics that supported the subdivision of *Sphecodopsis* into subgenera, nor the placement of *S. capensis* and *S. fumipennis* in a separate genus. The only features that separate *Pseudodichroa* from *Sphecodopsis sensu stricto* are its gutter-like female S5 and the S6 which forms a single posterior spine (in the latter the female S5 has a small protuberance (Figs. 65, 80, 82, 93) and a posteriorly bifid S6 (Fig. 66)). Material of males that apparently belong to either *S. capensis* or *S. fumipennis* was studied and found to be virtually indistinguishable from *Sphecodopsis*. The two sub-

genera and *Pseudodichroa* have therefore been synonymized.

Sphecodopsis species are smallish (4.0–9.0 mm long), wasp-like bees in which the head and mesosoma are black, the metasoma is generally reddish and/or orangish anteriorly, black posteriorly; occasionally the entire metasoma is black. The genus is characterized as follows: vertex, frontal view, flat laterally, area between lateral ocelli distinctly raised (Fig. 63); antenna 12-segmented in female, 13-segmented in male; labrum more or less quadrate, pointed and weakly tuberculate apicomediaally; mandibles behind labrum in repose; facial vestiture generally black (Fig. 63), white in *S. aculeata* and *S. minutissima*, long and weakly pubescence, except in *S. minutissima* which has short, dense facial pubescence; scutellum gently and evenly curved; last exposed metasomal tergum (T6 female, T7 male) without pygidial plate, but with dorsum broad and with dorsolateral region strongly incurved posteriorly, especially in male where dorsum resembles a pygidial plate; female S5 either shallowly or strongly concave distally, when viewed from behind, with weakly to strongly developed protuberance posteromedially, when viewed from below (Figs. 65, 78, 80, 82, 93); female S6 with distal end either simple or bifid posteriorly (Figs. 66, 79, 81, 83, 94).

In the discussion that follows some of the species have been placed in two species groups, on the basis of their morphology, while three species have been regarded as comprising three monotypic groups. These species groups are not clearly defined units suitable for description as distinct taxa. They have been used simply to facilitate discussion on the similarities between species. The *capicola* group comprises *S. capicola*, *S. vespericena*, *S. villosa*, *S. longipygidium* and *S. namaquensis*. The *capensis* group comprises *S. capensis* and *S. fumipennis*. The three species that have not been grouped are *S. minutissima*, *S. aculeata* and *S. semirufa*.

KEY TO SPECIES OF *SPHECODOPSIS*
(Females)

1. Metasoma with S6 simple posteriorly (capensis group) 2
- S6 bifid posteriorly 3
2. Posterior margin of first submarginal cell in fore wing distinctly longer than in second submarginal cell; posterior margin of S5 with area clothed with pallid vestiture distinctly pointed anteromedially (illustrated in Rozen, 1968a) *S. fumipennis* (Bischoff)
- Posterior margin of first and second submarginal cells in fore wing subequal in length; posterior margin of S5 with area clothed with pallid vestiture rounded anteromedially (illustrated in Rozen, 1968a) *S. capensis* (Friese)
3. Side of T5 notched (Fig. 75) (capicola group, part) *S. longipygidium* Eardley
- Side of T5 gently curved (Fig. 64) 4
4. Facial vestiture white 5
- Facial vestiture completely to mostly black 6
5. Vestiture on lower region of face plumose, virtually obscuring facial integument; upper region of face with integument clearly visible through short, simple vestiture; T5 with well developed distal fringe medially; T6 with lateral region of distal fringe long, hairs curved outwards *S. minutissima* (Cockerell)
- Integument of entire face visible as a result of all facial vestiture being weakly plumose; T5-T6 devoid of clearly discernable distal fringes *S. aculeata* (Friese)
6. Median region of T5 with a well developed distal fringe of straight, posteriorly projecting setae (capicola group, part) 7
- T5 either naked and impunctate posteriorly or with a sparse subapical fringe 8
7. Distal fringe on T5 black to brownish; legs largely orange *S. vespericena* Eardley
- Distal fringe on T5 white; legs black to blackish *S. capicola* (Strand)
8. T5 naked and impunctate posteriorly; vestiture on anterior region long and black *S. semirufa* (Cockerell)
- T5 densely punctate posteriorly and completely clothed with short white vestiture (capicola group, part) *S. namaquensis* Eardley

CAPICOLA SPECIES GROUP

This species group is made up of the following five species: *S. capicola*, *S. vespericena*, *S. villosa*, *S. longipygidium* and *S. namaquensis*. The vestiture on the head and mesosoma is black, and consists mostly of fairly long, weakly plumose hairs, and the female T5 has a distinct apical or subapical fringe.

Sphecodopsis capicola (Strand)
(Figs. 63–71)

Omachthes capicola Strand 1911:224–225.

Morgania capicola (Strand); Cockerell 1919:190, 1933c:109.

Sphecodopsis (Sphecodopsis) capicola (Strand); Bischoff 1923:593–595.

Description.—Habitus, dorsal aspect, as in Fig.

62. Length of head 1.4–2.0 mm; scutum 1.0–1.7 mm; fore wing 4.3–7.0 mm; body 4.8–7.7 mm. Integument of head black, except distal end of mandible orange; mesosoma black, except tegula, pronotal lobe, most of femora, tibiae and tarsi usually orangish; metasoma mostly orange, distal segments black. Vestiture on head black; mesosoma black, except short pubescence (described below) on scutum, scutellum and surrounding pronotal lobe white; legs generally white, femora black, dorsal surfaces of tibiae and basitarsi with black setae intermixed with white vestiture, ventral surfaces of tarsi blackish-orange; metasomal vestiture pallid in areas where integument is orange, black in regions where integument is black, except posterior region of female T5 with white vestiture (median region with well developed white distal fringe), T6 black to brownish-orange, S5 with brownish-orange tinge, especially posterolaterally; male T6 white distally, T7 completely white. Face densely clothed with long, weakly plumose vestiture (Fig. 63), lower region of gena with short and long pubescence intermixed; mesosoma with mixture of long, weakly plumose vestiture and short pubescence; legs, except

femora, generally clothed with very short, simple to weakly plumose, vestiture, femoral vestiture sparse, long and simple to weakly plumose, dorsal surfaces of tibiae and basitarsi with black setae intermixed with vestiture; metasomal vestiture very short and simple, except median region of T5 with well developed white distal fringe. Scutum with fine, dense punctation; propodeum largely punctate, propodeal triangle finely sculptured; female T5 straight posteriorly, except for weakly developed notch posteromedially (Fig. 64), pygidium short and devoid of subpygidial brush; male T7 rounded posteriorly, strongly incurved ventrolaterally (Fig. 67); female S5 broadly protuberant posteromedially, with small prominence on each side of protuberance (Fig. 65); female S6 widely bifurcate posteriorly (Fig. 66); male S7, S8 and genital capsule as in Figs. 68–71.

Distribution.—Karoo and Namaqualand, in the Western and Eastern Cape Provinces.

Discussion.—The female of this species can be identified by the black to blackish legs in combination with the posterior fringe of white setae on T5. The male can be identified by the gonocoxite of the genitalia being truncate posteriorly (Figs. 70–71). Its closest relative is *S. vespericena*, to which it is remarkably similar. In these two species the posteromedian protuberance of the female S5 is broad with very small posterolateral prominences (Fig. 65).

Floral Record.—Rosaceae.—*Grielum humifusum* Thunb.

Type material examined.—Holotype ♂: 'Capland berg, 1774, Morgania capicola ♂ Strand det.; Type; Zool. Mus. Berlin' (ZMHB).

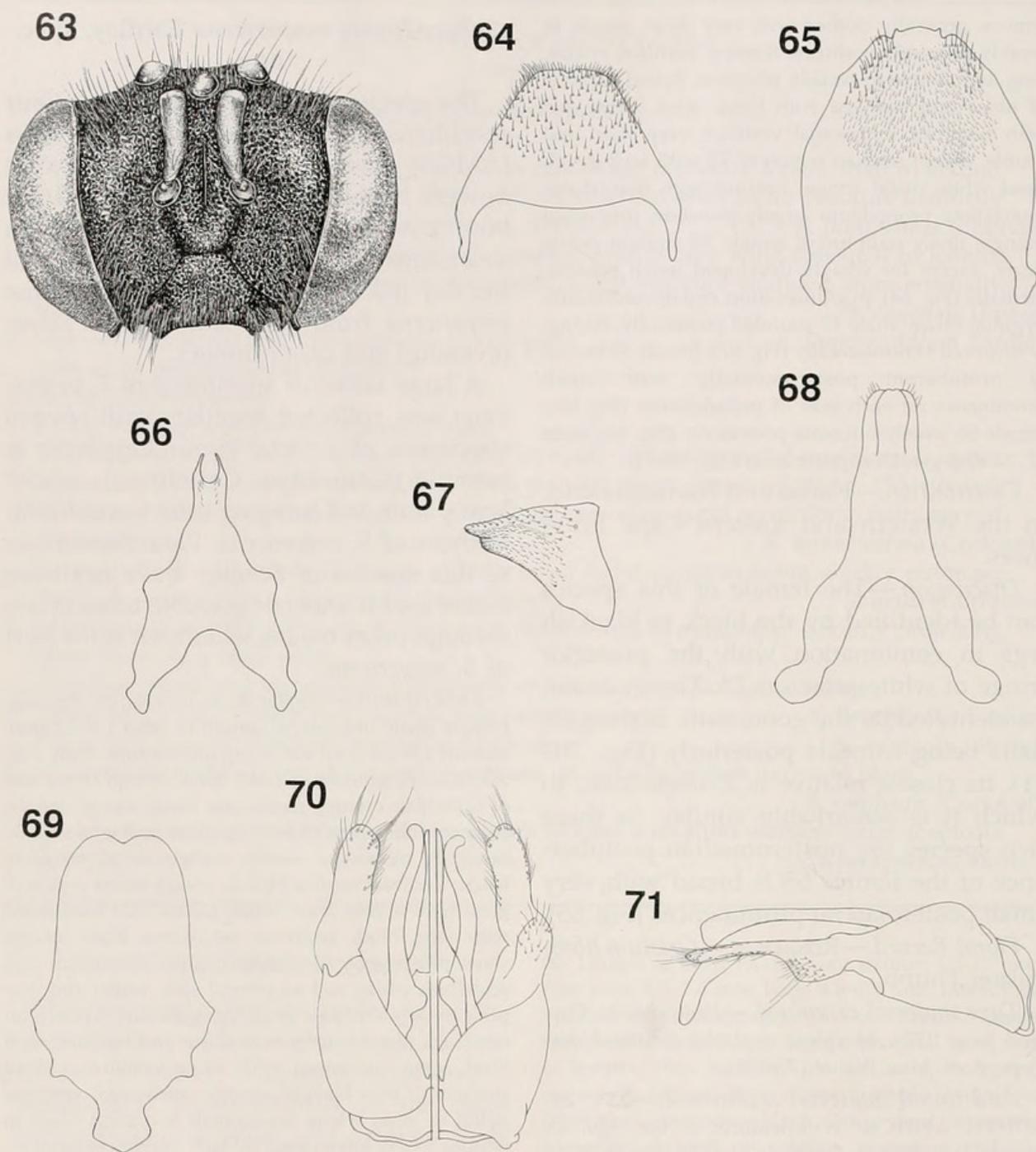
Additional material examined.—22♀ 2♂: SOUTH AFRICA: Willowmore, 15.viii.1920, Dr Brauns (1♀ TMSA); Ceres district, 15–30.x.1934, M. Versfeld (1♀ SAMC); 8 km W. Graafwater, 3218BA, 27.ix.1978, V.B. Whitehead (3♀ TMSA, 1♀ SANC); 20 km N. Clanwilliam, 9.ix.1982, V.B. Whitehead, on *Grielum humifusum* (1♀ SANC); Sandberg Station, 32.18BC, 11.viii.1988, V.B. Whitehead (1♀ SAMC); Biedouw Valley, Clanwilliam district, 32.08S 19.14E, 5–7.ix.1987, C.D. Eardley (1♀ 1♂ SANC); 20 km N. Klawer, 9.ix.1983, V.B. Whitehead (2♀ SAMC); 5 km S. Niewoudville, 3119AC, 2.viii.1984, 25.viii.1988, V.B. Whitehead (4♀ SAMC, 1♀ SANC); Vanrhynsdorp, 12.viii.1927, Dr. Brauns (1♀ TMSA, 1♀ 1♂ SANC); Hester Malan Nature Reserve, Springbok, 17.ix.1983, V.B. Whitehead (1♀ SAMC); Springbok, 7.ix.1966, C.D. Michener (3♀ SEMK).

Sphecodopsis vespericena Eardley, *spec. nov.*

The species was only known from four specimens before Drs F.W. & S.K. Gess (AMGS) discovered that the bees visit flowers in the late afternoon (after 16:00 hours). At that time they were collected in abundance. Their habit of feeding late in the day led to the derivation of the name *vespericena* from the Latin words *vesper* (evening) and *cena* (dinner).

A large series of specimens of *S. vespericena* was collected together with several specimens of *Scrapter bicolor* Lepelletier & Serville (Colletidae: Colletinae), whose host plants and foraging time were similar to those of *S. vespericena*. Parasitised nests of this species of *Scrapter* have not been found and it was not possible to ascertain through other means whether it is the host of *S. vespericena*.

Description.—Similar to *S. capicola* (cf. Fig. 62). Female (male unknown). Length of head 1.9–2.2 mm; scutum 1.6–1.8 mm; fore wing 6.4–7.4 mm; body 7.3–9.0 mm. Integument of head black, except distal end of mandible orange; mesosoma black, except tegula, pronotal lobe, most of femora, tibiae and tarsi usually orangish; metasoma mostly orange, distal segments black. Vestiture on head black, except lower region of gena with a little short white pubescence intermixed with long black vestiture; mesosoma black, except short pubescence (described below) on scutum and scutellum white, and on pleural area, venter and propodeum white to pale grey; legs generally white, femora black, dorsal surfaces of tibiae and basitarsi with black setae intermixed with white vestiture, ventral surfaces of tarsi blackish-orange; metasomal vestiture pallid in areas where integument is orange, black in regions where integument is black, except posterior region of T5–T6 black to brownish-orange (T5 with well developed blackish distal fringe medially). Face densely clothed with long, weakly plumose vestiture (Fig. 63), lower region of gena with short and long pubescence intermixed; mesosoma with mixture of long, weakly plumose vestiture and short pubescence; legs, except femora, generally clothed with very short, simple to weakly plumose, vestiture; femoral vestiture sparse, long, simple to weakly plumose; dorsal surfaces of tibiae and basitarsi with black setae intermixed with vestiture; metasomal vestiture very short, simple, except median region of T5 with well developed black distal fringe. Scutum with fine, dense punctation; propodeum largely punctate, propodeal triangle finely sculptured; T5 straight posteriorly, except for weakly



Figs. 63–71. *Sphecodopsis capicola*. 63. Head, front view, ♀; 64. T5, dorsal view, ♀; 65. S5, ventral view, ♀; 66. S6, ventral view, ♀; 67. T7, lateral view, ♂; 68. S7, ♂; 69. S8, ♂; 70. Genital capsule, dorsal left & ventral right, ♂. 71. Genital capsule, lateral view, ♂.

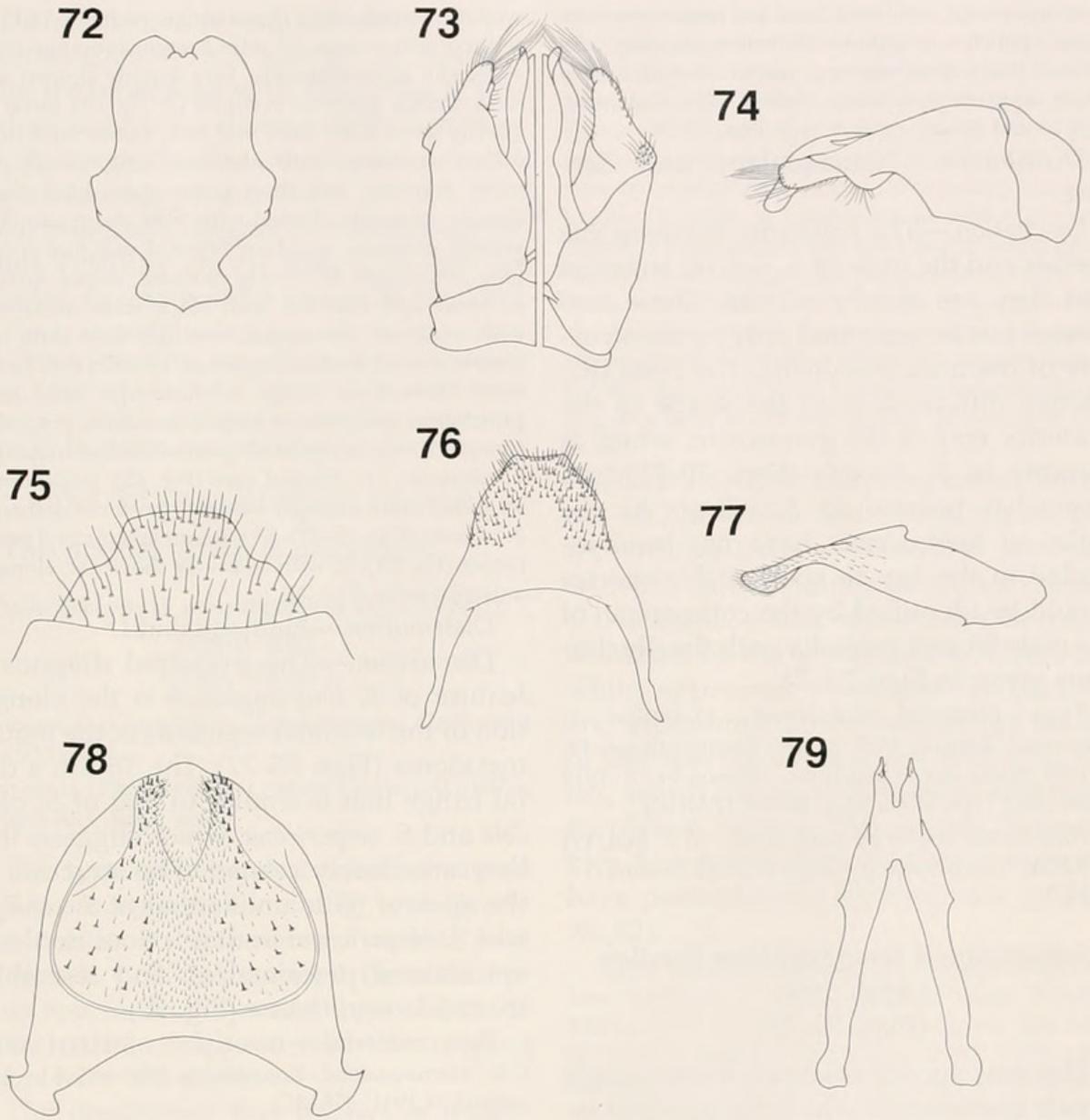
developed notch posteromedially (cf. Fig. 64), pygidium short, devoid of subpygidial brush; S5 broadly protuberant posteromedially, with small prominence on each side of protuberance (cf. Fig. 65); S6 widely bifurcate posteriorly (cf. Fig. 66).

Distribution.—Southern region of Namaqualand.

Discussion.—In *S. vespericena* the legs are largely orange and the distal fringe of the

female T5 is black to brownish. Otherwise this species is remarkably similar to *S. capicola*.

Floral records.—Rosaceae: *Grielum humifusum*; Asteraceae: *Senecio* probably *arenarius* Thunb. and *Helichrysum* sp.; Mesembryanthemaceae: *Herrea* sp.; Scrophulariaceae: *Hemimeris montana* L.f.



Figs. 72–79. *Sphecodopsis* spp. 72–74. *S. villosa*, ♂. 72. S8; 73. Genital capsule, dorsal left & ventral right. 74. Genital capsule, lateral view. 75–79. *S. longipygidium*, ♀. 75. T5, dorsal view; 76. T6, dorsal view; 77. T6, lateral view; 78. S5, ventral view; 79. S6, ventral view.

Type material.—Holotype ♀, paratypes 67 ♀: SOUTH AFRICA: 11 km W. Clanwilliam, 32.10S 18.47E, 1.x.1990, C. Eardley (holotype ♀ 24 ♀ SANC, 2 ♀ MRAC, 3 ♀ AMNH, 2 ♀ NHML, 2 ♀ TMSA, 2 ♀ SAMC, 3 ♀ SEMK, 2 ♀ MNHN, 2 ♀ DMSA, 2 ♀ ZMHB, 3 ♀ SCAA, 2 ♀ CASC); same locality, 2–8.x.1990, F.W. & S.K. Gess, on *Grielum humifusum* (1 ♀), *Senecio* prob. *arenarius* (1 ♀), *Herrea* sp. (5 ♀), *Helichrysum* sp. (1 ♀) (14 ♀ AMGS); Holfontein, 20 km S. Clanwilliam, 24.viii.1983, V.B. Whitehead, on *Hemimeris racemosa* (1 ♀ SAMC); Ramskop Camp, Clanwilliam, 3218BB, 30.viii.1984, V.B. Whitehead, M. Macpherson (1 ♀ SAMC); Saldanha Bay, ix.1960 (1 ♀

SAMC); Malmesbury Road, 20.x.1923, W.C. Eales (1 ♀ SAMC).

***Sphecodopsis villosa* (Friese)**
(Figs. 72–74)

Pasites villosus Friese 1909a:438–439.
Omachthes villosus (Friese); Friese 1915:297.
Morgania villosa (Friese); Cockerell 1919:190.
Sphecodopsis (*Sphecodopsis*) *villosa* (Friese); Bischoff 1923:593–594.

Description.—Male (female unknown). Similar to

S. capicola except as follows: head and mesosoma more densely punctate (punctuation difficult to quantify, refer Bischoff 1923); distal region of metasoma with area in which integument is black, clothed with black vestiture; S8 and genital capsule as in Figs. 72-74.

Distribution.—Namaqualand and Zeerust.

Discussion.—The similarity between this species and the male of *S. capicola* suggests that they are closely related. These two species can be separated only by the structure of the male terminalia. The most distinctive difference is in the shape of the posterior end of the gonocoxite, which is truncate in *S. capicola* (Figs. 70-71) and somewhat pointed in *S. villosa*. As the males of *Sphécodopsis* have not been included in the key to species, this species should be identified by the comparison of the male S8 and genitalia with the illustrations given in Figs. 72-74.

Type material examined.—Holotype ♂: Transvaal, Zeerust, 1897, Jensen; *Psites villosus* Fr. ♂ 1908 Friese det.; *Omachthes villosus* Fr. ♂ 1914 Friese det.; Type; Zool. Mus. Berlin' (ZMHB).

Additional material examined.—1♂: SOUTH AFRICA: Vanrhynsdorp, 12.viii.1927, H. Brauns (1♂ SANC).

Sphécodopsis longipygidium Eardley,
spec. nov.
(Figs. 75-79)

This new species is known from a single female specimen in which the pygidial region of S5 is elongate. It is from this unique feature that the name *longipygidium* was derived.

Description.—Female (male unknown). Similar to *S. capicola* (cf. Fig. 62). Length of head 2.3 mm; scutum 1.8 mm (fore wing damaged in holotype); body 8.1 mm. Integument of head black, except distal end of mandible orange; mesosoma black, except tegula, pronotal lobe, most of femora, tibiae and tarsi usually orangish; metasoma mostly orange, distal segments black. Vestiture on head black; mesosoma black with short white pubescence apparently confined to scutum (scutal pubescence damaged in holotype); legs generally white, femora black, dorsal surfaces of tibiae and basitarsi with black setae intermixed with white vestiture, ventral surfaces of tarsi blackish-orange; metasomal vestiture pallid in areas where integument is orange, black in regions where integument is blackish, posterior region of T5 with

well developed, black distal fringe medially, T6 black to brownish-orange, S5 with brownish-orange tinge, especially posterolaterally. Face densely clothed with long, weakly plumose vestiture (cf. Fig. 63), lower region of gena with short and long pubescence intermixed; mesosoma with mixture of long, weakly plumose vestiture and short pubescence; legs, except femora, generally clothed with very short, simple to weakly plumose, vestiture; femoral vestiture sparse, long and simple to weakly plumose, dorsal surfaces of tibiae and basitarsi with black setae intermixed with vestiture; metasomal vestiture very short and simple, except median region of T5 with well developed black distal fringe. Scutum with fine, dense punctuation; propodeum largely punctate, propodeal triangle finely sculptured; posteromedian region of T5 elongate, i.e., fringed area (Fig. 75); pygidium of T6 much more strongly elongate posteriorly than in *S. capicola* (Figs. 76-77); S5 without apicolateral prominence (Fig. 78); S6 with relatively short disc, elongate anterolaterally (Fig. 79).

Distribution.—Namaqualand.

Discussion.—The principal diagnostic feature of *S. longipygidium* is the elongation of the terminal segments of the female metasoma (Figs. 75-77). The T5 has a distal fringe that is similar to that of *S. capicola* and *S. vespericena*, which suggests that they are closely related. The structure of the apex of S5 is unlike that of *S. capicola* and *S. vespericena*, in that it does not have apicolateral prominences, and resembles that of *S. minutissima* (Fig. 82).

Type material.—Holotype ♀: SOUTH AFRICA: Namaqualand, Knersvlakte, Niewerust [= Nuwerus], ix.1941' (SAMC).

Sphécodopsis namaquensis Eardley, spec.
nov.
(Figs. 80-81)

This new species takes its name from the region it inhabits, Namaqualand.

Description.—Female (male unknown). Length of head 1.5-1.7 mm; scutum 1.3-1.5 mm; fore wing 5.1-5.5 mm; body 5.6-7.9 mm. Similar to *S. capicola* except as follows: pronotal lobe black; femora largely black, distal ends orangish; posterior margin of T2 slightly blackish, that of T3 black; mesopleuron with little or no white pubescence; metasomal vestiture mostly white, few black hairs occur on proximal regions of T3-T5, on S2-S5 and on pygidium; distal fringe on T5 subapical, weakly developed; S5 narrow posteriorly, with well developed apicolateral prominence (Fig. 80); S6 with disc long and slender, very narrowly bifid posteriorly (Fig. 81).

Distribution.—Namaqualand.

Discussion.—This species is distinct from the other species in this group in that it does not have a distinct distal fringe on T5. It resembles the other species in the posterolateral prominences on S5. The most important diagnostic features are the white vestiture on the female S5 and the slender, narrowly bifid female S6 (Fig. 81).

Type material.—Holotype ♀, paratypes 2♀: SOUTH AFRICA: Biedouw Valley, Clanwilliam district, 32.08S 19.14E, 5–7.ix.1987, C.D. Eardley (holotype ♀ SANC); Kleinberg, near Langebaanweg, 3218CC, 26.ix.1978, V.B. Whitehead (2♀ SAMC).

MINUTISSIMA SPECIES GROUP

This species group is monotypic.

Sphecodopsis minutissima (Cockerell),
comb. nov.
(Figs. 82–87)

Morgania (*Omachthes*) *minutissima* Cockerell 1933a:379.

Morgania (*Pseudopasites*) *rufula* Cockerell 1933a: 382–383. **Syn. nov.**

The type specimens of *minutissima* and *rufula* are remarkably similar and clearly conspecific. It is, therefore, unclear why Cockerell (1933a) described them as distinct species in different subgenera in the same article without even comparing them with one another.

The description that follows is incomplete because the metasoma is missing, except the terminal terga, sterna and genitalia, in the only known male specimen.

Description.—Length of head 1.1–1.3 mm; scutum 0.9–1.1 mm; fore wing 3.2–4.3 mm; body 4.6–5.8 mm. Integument of head and mesosoma black to reddish-black, antenna, mandible, pronotal lobe, tegula, most of femora, tibiae and tarsi orangish; labrum orange to black; metasoma orange. Vestiture white, except ventral surfaces of tibiae and tarsi pale orangish, female T6 and S5 pale orangish, fringe on distal end of pygidium blackish. Lower region of face and gena very densely pubescent; upper region of face and gena, and vertex sparsely pubescent, vestiture short and simple; mesosomal vestiture sparse, except pronotal collar, anterior region of scutum, lateral regions of scutellum and metanotum, posterolateral region of propodeum and most of dorsal region of mesopleuron densely pubescent; legs generally with vestiture

on coxae, tibiae and tarsi dense, trochanters and femora sparse; female with vestiture on T1–T3 sparse (T2–T3 with little white pubescence posterolaterally), T4 sparse with weakly developed distal fringe, T5 sparse with distal fringe well developed medially, T6 generally sparsely pubescent (distal fringe short, sometimes blackish medially). Structurally similar to *S. capicola* except as follows: lateral region of vertex sloping upwards towards raised lateral ocelli, giving vertex convex appearance; propodeum broadly glabrous mediolongitudinally; female S5 resembles that of *S. longipygidium* in that it does not have an apicolateral protuberance (Fig. 82); female S6 very narrowly bifid, disc fairly wide, keeled mediolongitudinally (Fig. 83); male S7, S8 and genital capsule as in Figs. 84–87.

Distribution.—Widely separated localities in Zimbabwe and South Africa. Biotypes range from woodland to semi-desert, with either summer or winter rainfall.

Discussion.—This species can be easily identified by the gently convex vertex and white, appressed, pubescence on the head and mesosoma. These features are unique to this species, being more similar to *Pasites*, which makes it difficult to determine its closest relative. The female S5 resembles *S. longipygidium* in that it does not have posterolateral prominences (*cf.* Figs. 78, 82).

Type material examined.—*Morgania minutissima*, holotype ♀: 'Aliwal North, Cape Province, 450ft., 1–13.i.1923, S. Africa, R.E. Turner, Brit. Mus., 1923-70; *Morgania minutissima* Ckll TYPE; B.M. TYPE HYM. 17B 72' (NHML). *Morgania rufula*, holotype ♀: 'Cape Province, Little Karoo, 38 km E. of Ceres, 17–25.xi.1924, S. Africa, R.E. Turner, Brit. Mus., 1924-518; *Morgania rufula* Ckll TYPE; B.M. TYPE HYM. 17B 96' (NHML).

Additional material examined.—4♀ 1♂: ZIMBABWE: Victoria Falls, 3.i.1920 (1♀ SAMC). SOUTH AFRICA: Farm Arkoep, 6 km N. Kamieskroon, 30.19S 17.56E, 1–2.x.1990, C. Eardley (1♀ SANC); Clanwilliam Dam, 32.11S 18.53E, 3–7.x.1988, F.W. & S.K. Gess (1♀ AMGS); Vanrhynsdorp, 20.x.1968, J.G. Rozen, E. Martinez (1♀ 1♂ AMNH).

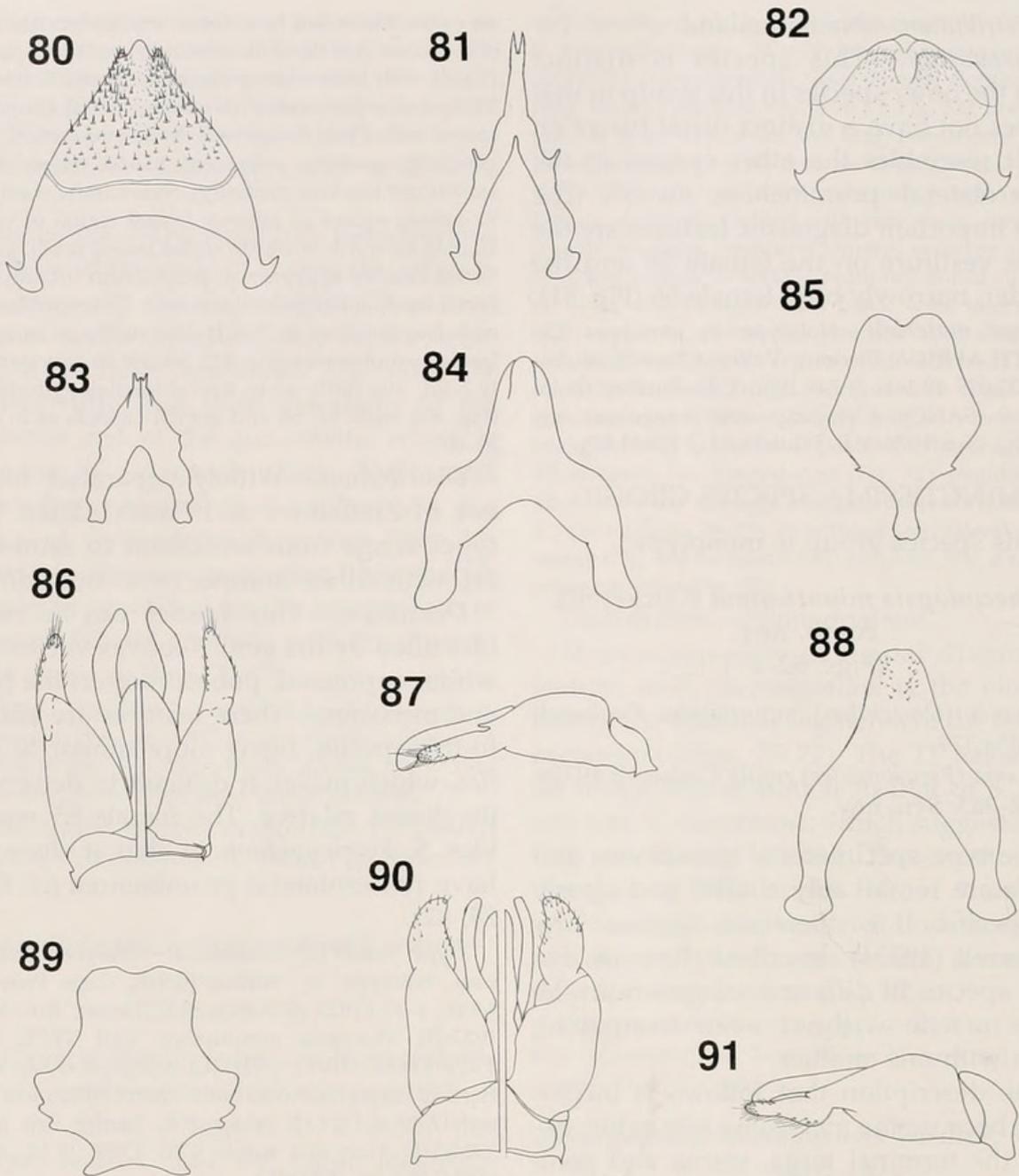
ACULEATA SPECIES GROUP

This species group is monotypic.

Sphecodopsis aculeata (Friese)
(Figs. 88–91)

Pasites aculeatus Friese 1922:37.

Sphecodopsis (*Pseudopasites*) *aculeata* (Friese); Bischoff 1923:595.



Figs. 80-91. *Sphecodopsis* spp. 80-81. *S. namaquensis*, ♀. 80. S5, ventral view; 81. S6, ventral view. 82-87. *S. minutissima*. 82. S5, ventral view, ♀; 83. S6, ventral view, ♀; 84. S7, ♂; 85. S8, ♂; 86. Genital capsule, dorsal left & ventral right, ♂. 87. Genital capsule, lateral view, ♂. 88-91. *S. aculeata*, ♂. 88. S7; 89. S8; 90. Genital capsule, dorsal left & ventral right. 91. Genital capsule, lateral view.

Morgania aculeata (Friese); Cockerell 1933a:383.

Pasites pygmaeus Friese 1922:37. **Syn. nov.**

Sphecodopsis (*Pseudopasites*) *pygmaeus* [sic.] (Friese); Bischoff 1923:595 [*lapsus*].

Morgania pygmaea (Friese); Cockerell 1933a:384.

Sphecodopsis (*Pseudopasites*) *rufescens* Bischoff 1923:593-594. **Syn. nov.**

Sphecodopsis (*Pseudopasites*) *algoensis* Bischoff 1923:595. **Syn. nov.**

Morgania algoensis (Bischoff); Cockerell 1933a:384.

Pseudopasites algoensis (Bischoff); Anonymous 1958:30.

Morgania (*Pseudopasites*) *perpunctata* Cockerell 1933a:382-384 [specific epithet erroneously recorded as masculine on p. 382]. **Syn. nov.**

Bischoff (1923) and Cockerell (1933a)

recognized five distinct species for what is here considered to be a single taxon, mainly based on differences in the colour of the vestiture and the metasoma. An exception is the female paralectotype of *algoensis* (which could not be found) that Bischoff (1923) separated from *aculeata*, *pygmaea* and *rufescens* by its relatively long vestiture on the upper region of the head and scutum. (Confirmation as to whether that specimen was correctly described awaits its discovery.) A comparative study of the colour differences that Bischoff (1923) and Cockerell (1933a) used to separate species indicated that these differences could not be used to define distinct species.

Morgania pygmaea and *M. algoensis* were each described from a pair of specimens of opposite sexes. The type series of *pygmaea* was collected in Cape Town and that of *algoensis* at Algoa Bay. In each case the female could not be located. The male syntypes are therefore designated as the lectotypes of these two species.

Description.—Length of head 1.2–1.5 mm; scutum 0.9–1.2 mm; fore wing 4.0–5.0 mm; body 4.4–6.3 mm. Integument of head and mesosoma black to blackish, except distal end of mandible orange; posterolateral region of tegula translucent; metasoma completely black to orange anteriorly, black posteriorly. Pubescence white, except ventral surfaces of tarsi pale yellow. Head and mesosoma generally moderately densely pubescent, except femora sparsely pubescent; tibiae and tarsi densely pubescent; metasoma with sparse vestiture, except pygidium in which it is dense. Structurally similar to *S. capicola* except as follows: scutum moderately densely punctate, punctures large, mostly separate; propodeal triangle weakly sculptured to glabrous; female S5 similar to that of *S. namaquensis*, except without black setation (cf. Fig. 80); S6 narrowly bifid (cf. Fig. 81); male S7, S8 and genital capsule as in Figs. 88–91.

Distribution.—Southern region of South Africa. Vegetation types fynbos and karoo.

Discussion.—*Sphecodopsis aculeata* closely resembles other species in the capicola species group. This species can be recognized by the pallid, simple vestiture on the head and mesosoma, absence of distal fringe on the female T5 and expansion of

the anterior lobe of the male S8 (Fig. 89). The pallid, simple vestiture and the structure of the male S8 are unique, within the genus, to this species. The absence of a distal fringe on the female T5 suggests an affinity with both *S. namaquensis* and *S. semirufa*. The structure of the female S5 and S6 of *S. aculeata*, however, resembles that of *S. namaquensis*.

Type material examined.—*Pasites aculeatus*, holotype ♀: 'Cape Town, L.C. Peringuey, 1911; *Pasites aculeatus* Fr. ♀ 1904 Friese det.; Type, *Pseudopasites*; Zool. Mus. Berlin' (ZMHB). *Pasites pygmaeus*, lectotype ♂: 'Capland; *Pasites pygmaeus* Fr. ♂ 1904 Friese det.; Coll Friese, *Pseudopasites*, Type; Zool. Mus. Berlin' (ZMHB). *Sphecodopsis rufescens* holotype ♀: 'T. us Afr. *Pseudopasites rufescens*, Type; Zool. Mus. Berlin' (ZMHB). *Sphecodopsis algoensis*, lectotype ♂: 'Algoa bay, Capland, Dr Brauns, 20.8.96; *Pseudopasites algoensis* Bisch. ♂ Typ.; *Pseudopasites algoensis* Type ♂ Bischoff; *Pseudopasites algoensis* Biss. ♂ Type No. 567' (TMSA). *Morgania perpunctata*, holotype ♂: 'Rapenburg, Cape Flats, 1–14.x.1920, S. Africa, R.E. Turner, 1920–424; *Morgania perpunctata*, B.M. TYPE HYM. 17B 95' (NHML).

Additional material examined.—26♀ 21♂: SOUTH AFRICA: 19 km N.W. Grahamstown, 16.xi.1970, H.V. Daly (1♀ SEMK); Grahamstown, Hilton, 12.x.1977 & 26.ix.1983, F.W. & S.K. Gess (3♀ AMGS); same locality, 9.x.1972, 29.ix.1977 & 12.x.1977, F.W. Gess (4♀ AMGS); Boknes, 33.43S 26.35E, 5.iv.1984, S.K. Gess (1♀ AMGS); Willowmore, 11.x.1904, H. Brauns (1♀ TMSA); Cango River, Oudtshoorn district, x.1937 (1♀ SAMC); Seven Weeks Poort, Ladismith district, 10.ix.1948, C.J. Jacot-Guillarmod (2♀ AMGS); Pearly Beach, Bredasdorp, ix.1959 (1♀ SAMC); Cape Town, vii & ix.1913 & 1915 (1♀ 16♂ SAMC, 2♂ SANC); Hout Bay, 15.ix.1966, C.D. Michener (3♀ 1♂ SEMK); Kommetjie, 15–25.x.1972, J.G. Rozen, R. McGinley, C. Thompson (2♀ AMNH); Kommetjie, 15.x.1966, C.D. & B.J. Michener (4♀ SEMK); Stellenbosch, 1919, Lightfoot (1♀ AMNH); Pakhuis Pass, ix.1961 (1♂ SANC); Kamieskroonberg, near Kamieskroon, 30.32S 18.08E, 3.x.1990, C.D. Eardley (1♀ 1♂ SANC).

SEMIRUFA SPECIES GROUP

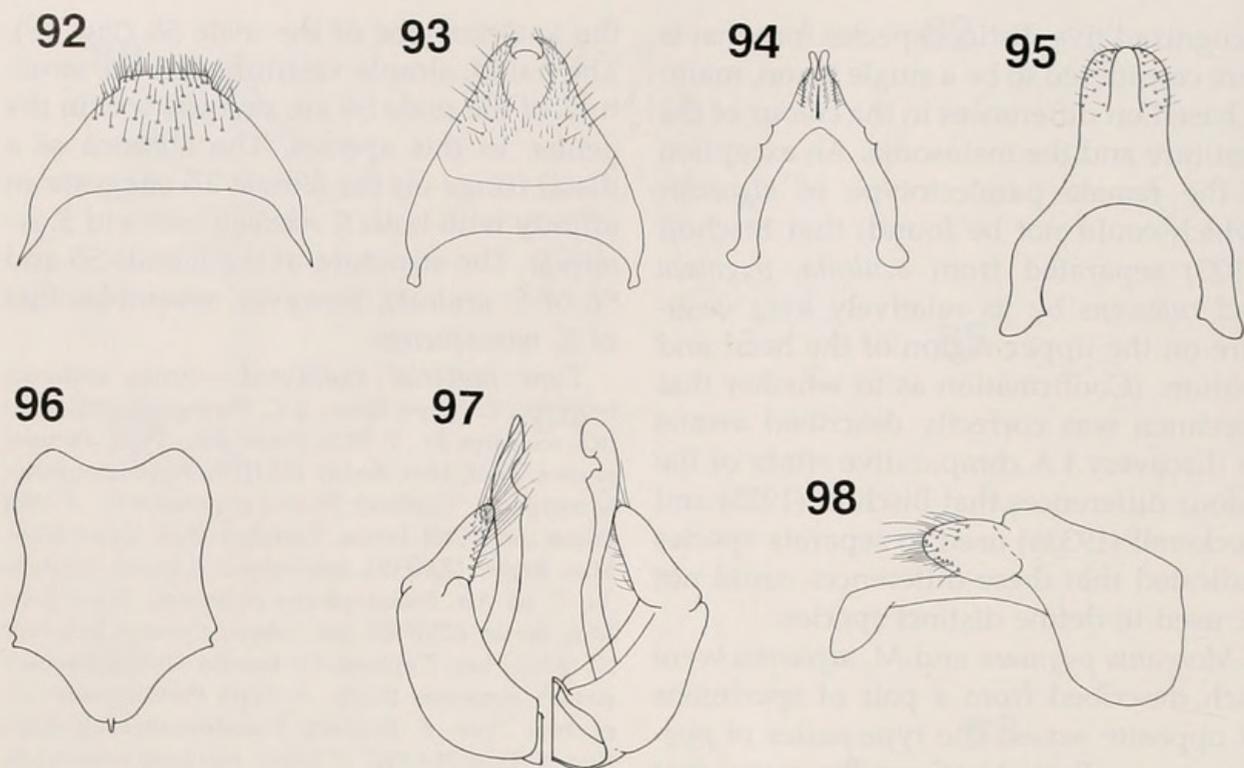
This species group is monotypic.

Sphecodopsis semirufa (Cockerell), **comb. nov.**

(Figs. 92–98)

Morgania semirufa Cockerell 1933a:380–381.

Morgania (Sphecodopsis) leonis Cockerell 1933a: 382, 384. **Syn. nov.**



Figs. 92-98. *Sphecodopsis semirufa*. 92. T6, dorsal view, ♀; 93. S5, ventral view, ♀; 94. S6, ventral view, ♀; 95. S7, ♂; 96. S8, ♂; 97. Genital capsule, dorsal left & ventral right, ♂. 98. Genital capsule, lateral view, ♂.

The type specimens of *leonis* are considerably smaller than those of *semirufa*, otherwise they are almost indistinguishable.

Description.—Length of head 1.1–1.7 mm; scutum 0.8–1.3 mm; fore wing 3.6–5.8 mm; body 3.9–6.1 mm. Integument of head and mesosoma mostly black, distal half of mandible, antenna and pronotal lobe sometimes orange to reddish-black; tegula always orange, legs black to reddish-black, often with femur orangish; metasoma orange anteriorly, black posteriorly. Vestiture on head black; mesosoma with short, white and long, black vestiture intermixed; vestiture on coxae and trochanters largely white, femora generally black (posterodistal region of hind femur white), tibiae and tarsi pallid with few black setae on dorsal surfaces (those on middle and hind legs thick and spinose); female metasoma generally with vestiture on orange areas short and pallid, black regions long and black, except T6 and S5 mostly with mixture of black and white vestiture, posterior region pale brownish; male metasomal vestiture mostly black. Vestiture on head long and moderately dense, hairs simple to weakly plumose; mesosoma with short white pubescence intermixed with long, black, weakly plumose hairs; femora generally sparsely pubescent, dense posterodistally on hind femur; black setae on dorsal surfaces of middle and hind tibiae and tarsi thick and spinose; female metasoma generally with vestiture on areas in which integument is orange short, on areas with integument black long; metasoma

of male with vestiture mostly long. Scutum fairly sparsely punctate, punctures small, shallow and mostly separate; propodeal triangle glabrous, mediolongitudinal region below triangle punctate; female T6 as in Fig. 92, S5 with posteromedian protuberance small, posterolateral prominence large and incurved, forming a distinct concavity posteromedially (Fig. 93); female S6 very narrowly bifid, mediolongitudinally carinate on ventral surface (Fig. 94); male S7, S8 and genital capsule as in Figs. 95–98, genitalia with gonocoxite shorter than penis valve.

Distribution.—Southern and western regions of South Africa. Vegetation types fynbos and karoo.

Discussion.—*Sphecodopsis semirufa* can be easily identified by the sparsely pubescent, glabrous face; posteromedian concavity and enlarged apicolateral prominences of the female S5 (Fig. 93), absence of a distinct anterior lobe on the male S8 (Fig. 96) and bowed gonocoxite of the male genitalia (Fig. 97). These features are all unique within the genus. The mosaic of characters that occur in *S. semirufa* makes it difficult to determine its closest relative.

Type material examined.—*Morgania semirufa*,

holotype ♀: 'Worcester, Cape Province, Sept. 1928, S. Africa, R.E. Turner, Brit. Mus. 1928-457; *Morgania semirufa* Ckll TYPE; B.M. TYPE HYM. 17B 94' (NHML). *Morgania leonis*, holotype ♂: 'S. Africa, R.E. Turner, 1920-342, Lion's Head, Cape Town, Aug. 1920; *Morgania leonis* Ckll., TYPE; B.M. TYPE HYM. 17B 85' (NHML).

Additional material examined.—7♀: SOUTH AFRICA: Grahamstown, Hilton, 12.iv.1968, C. Jacot-Guillarmod (1♀ AMGS); Willowmore, 19.v.1903 & 5.ix.1903, H. Brauns (1♀ TMSA, 1♀ SANC); Lammerskraal, Prince Albert District, ix.1947 (1♀ SAMC, 1♀ SANC); Kamieskroon, ix.1930 (1♀ SAMC); Lambert's Bay, 32.04S 18.20E, 4.x.1974, R.H. Watmough (1♀ SANC).

CAPENSIS SPECIES GROUP

This species group comprises *S. capensis* and *S. fumipennis*. These two species are unique in the structure of the female terminalia. The posteromedian region of S5 is gutter-like and the posterior end of S6 forms a single spine.

Sphecodopsis capensis (Friese), **comb. nov.**

Omachthes capensis Friese 1915:296-297 (holotype ♀, ZMHB).

Morgania capensis (Friese); Cockerell 1919:190.

Pseudodichroa capensis (Friese); Bischoff 1923: 595-596; Rozen 1968a:1-9, 1968b:3-13.

The holotype of this species was not examined during the course of the study because material that was reliably identified by Dr J.G. Rozen (AMNH), who examined the holotype (Rozen 1968a), was studied together with Rozen's (1968a) outstanding redescription.

The host of this species is *Scapter longula* (Friese) (Colletidae: Colletinae) (Rozen 1968b).

Material examined.—26♀: SOUTH AFRICA: Rapenburg, 1-14.x.1920, R.E. Turner (4♀ SAMC); Kommetjie, 29.x-9.xi.1966, C.D. Michener & J.G. Rozen (7♀ AMNH); Kommetjie, 14.x.1972, J.G. Rozen, R. McGinley & C. Thompson (10♀ AMNH); 25 km E. Velddrif, 23.x.1972, J.G. Rozen, R. McGinley & C. Thompson (5♀ AMNH.)

Sphecodopsis fumipennis (Bischoff), **comb. nov.**

Pseudodichroa fumipennis Bischoff 1923:596; Rozen 1968a:1-9, 1968b:3-13, 1974:6-8 (syntypes 2♀, ZMHB).

Bischoff (1923) described this species from two female specimens, one from Cape Town, and the other with 'Java' on the label. Bischoff (1923) regarded the accuracy of the locality label of the second specimen as questionable, and Rozen (1968a), who examined the specimen (the Cape Town syntype has been lost), shared Bischoff's (1923) sentiments. During the course of the current study, material of this species which was identified by Dr J.G. Rozen was studied and compared with his (Rozen 1968a) excellent redescription. This species is endemic to southwestern region of South Africa. It was adequately dealt with by Rozen (1968a) and requires no further comment.

The host of *S. fumipennis* is *Scapter crassula* Cockerell (Colletidae, Colletinae) (Rozen 1968b).

Material examined.—10♀: SOUTH AFRICA: Kommetjie, 29.x-9.xi.1966, C.D. Michener & J.G. Rozen (4♀ AMNH); Kommetjie, 14.x.1972, J.G. Rozen, R. McGinley & C. Thompson (2♀ AMNH); Between Nieuwoudtville & top Vanrhyns Pass 29-30.ix.1990, F.W. & S.K. Gess (3♀ AMGS); Nieuwoudtville flower reserve, 31.19 AC, V.B. Whitehead & M. Macpherson, 28.viii.1984 (1♀ SAMC.)

SPECIES OF UNCERTAIN IDENTITY

Sphecodopsis argyrura (Cockerell), **comb. nov.**

Morgania argyrura Cockerell 1933c:108-109 (holotype ♀, NHML).

All that remains of the holotype is the thorax and part of the legs, which allow only for it to be recognised as belonging to *Sphecodopsis*. Cockerell (1933c) described it in the genus *Morgania*, but mentioned that it belonged to 'the genus or subgenus *Sphecodopsis*'.

GENUS AMMOBATES LATREILLE

Ammobates Latreille 1809:169. Type species *Ammobates rufiventris* Latreille 1809 (subsequent designation by Latreille 1810:439, Sandhouse 1943).

Phileremus Latreille 1809:169. Type species *Epeolus punctatus* Fabricius 1804 (subsequent des-

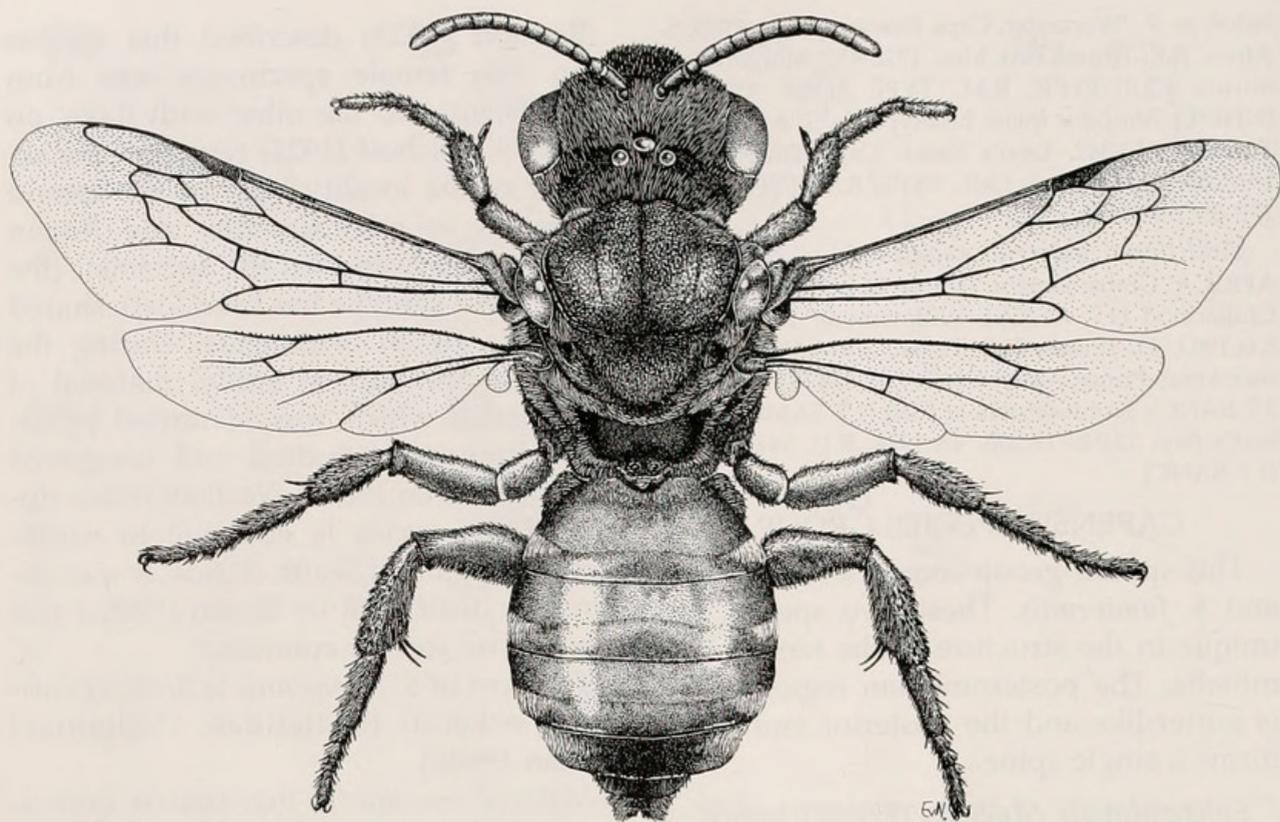


Fig. 99. *Ammobates auster*, habitus, dorsal view (dark shading represents black or blackish integument and lightly shaded areas are reddish), ♀.

ignation by Latreille 1810:439, Sandhouse 1943).

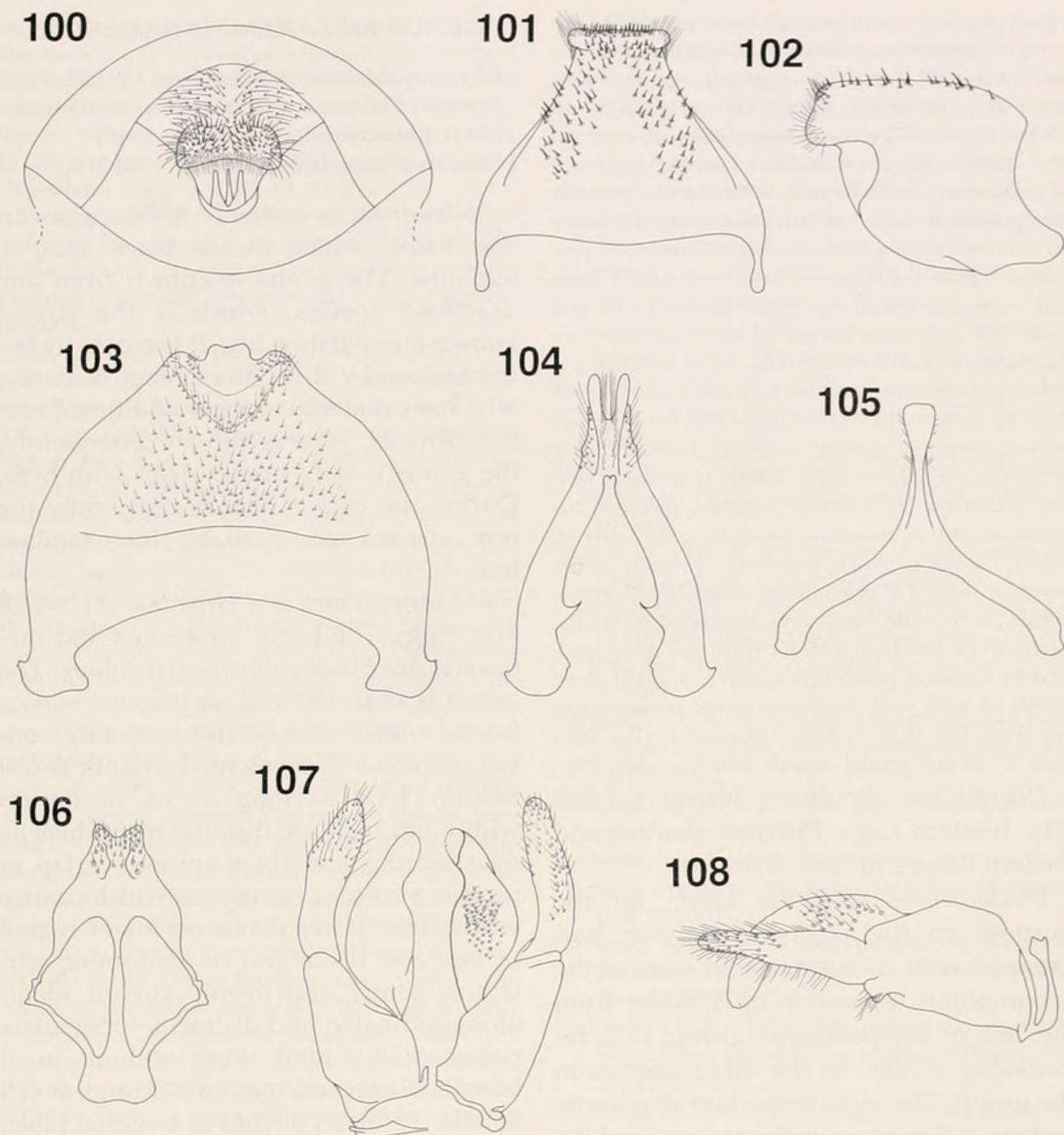
Ammobatoides Schenck 1869:349, not Radoszkowski 1868. Type species *Ammobates bicolor* Lepeletier 1825 (= *Epeolus punctatus* Fabricius) (monobasic, Sandhouse 1943).

Ammobates (*Caesarea*) Friese 1911d:142. Type species *Ammobates depressa* Friese 1911 (subsequent designation by Sandhouse 1943, Brooks pers. comm. 1997).

A single species of *Ammobates*, namely *A. auster* spec. nov., was recently discovered in southern Africa. *Ammobates* is otherwise known from the Palaearctic Region (Popov 1951), where it is particularly diverse in the Mediterranean basin. Because only one species is known from the Afrotropical Region the subgeneric classification is beyond the scope of this article. As *A. auster* is known only from five specimens, it is difficult to speculate on the distribution of *Ammobates* in the Afrotropical Region. However, several other genera of bees, including *Meliturgula* Friese and *Mel-*

itturga Latreille (both Andrenidae) and *Ochreriades* (Megachilidae), occur in southern Africa and the Eremic Region and not in the intermediate area. It is, therefore, possible that *Ammobates* does not occur in the area between southern Africa and the Mediterranean Basin.

Ammobates auster is a medium sized (7.3–9.0 mm long) bee. The head and mesosoma are mostly black and the metasoma is at least partly orangish (posterior region sometimes black). The generic diagnostic features are: vertex, in front view, gently convex; antenna 12-segmented in female, 13-segmented in male; labrum distinctly longer than its maximum width, truncate distally; mandibles lie over labrum, their apices overlap in repose; facial vestiture white and mostly sparse, dense pubescence occurs in vicinity of antennal sockets, and appressed; scutellum essentially gently and evenly curved; female T6 without pygidial plate, male T7 with pygidial plate; female with pygidial region



Figs. 100–108. *Ammobates auster*. 100. Terminalia, posterior view, ♀; 101. T6, dorsal view, ♀; 102. T6, lateral view, ♀; 103. S5, ventral view, ♀; 104. S6, ventral view, ♀; 105. S7, ♂; 106. S8, ♂; 107. Genital capsule, dorsal left & ventral right, ♂; 108. Genital capsule, lateral view, ♂.

densely setose (Figs. 101–102); female S5 shallowly concave posteriorly, with fairly well developed gutter posteromedially (Figs. 100, 103); female S6 bifid posteriorly (Fig. 104).

***Ammobates auster* Eardley, spec. nov.**
(Figs. 100–108)

This new species takes its name from the Latin word *auster*, which means south.

It is the only species of the genus known from the southern hemisphere.

Description.—Habitus, dorsal aspect, as in Fig. 99. Length of head 2.0–2.7 mm; scutum 1.5–2.2 mm; fore wing 6.1–8.6 mm; body 7.3–9.0 mm. Integument of head and mesosoma mostly black, appendages generally reddish to orange; metasoma either mostly reddish to orange or orangish anteriorly, black posteriorly. Vestiture generally white, posterior surface of hind tibia and ventral surfaces of all basitarsi with dense yellow to orange setation; female T6 orangish,

female pygidium with blackish tinge; female S5 with orangish velutinous vestiture subapically, male S6 pale yellowish. Vestiture generally sparse, often dense and pubescence around antennal sockets, on lateral region of pronotal collar, edge of pronotal lobe, anterior margin of scutum, posterior region of scutellum, entire metanotum, anterodorsal region of mesepisternum, adjacent to epimeral suture, entire area above scrobal sulcus, dorsolateral region of propodeum, posterior regions of middle and hind tibiae and on posterolateral regions of female T1-T5 and male T1-T6; posterior surface of hind tibia and ventral surfaces of all basitarsi with dense setation; pygidial area with coarse, dense setation. Labrum about $1.6\times$ as long as its maximum width, strongly incurved laterally, truncate distally; maxillary palp two-segmented, subequal in length to antennal pedicel; scutum fairly sparsely punctate, glabrous between punctures; scutellum generally gently curved, slightly concave medioposteriorly; virtually entire posterior surface of propodeum naked and glabrous; female T6 truncate posteriorly, expanded posterolaterally (Figs. 100–102); male T7 with well developed, broadly rounded, posteriorly concave, pygidial plate; female S5 with well developed gutter posteromedially (Figs. 100, 103), S6 forked posteriorly (Fig. 104); male S7, S8 and genital capsule as in Figs. 105–108.

Distribution.—Southern Namibia (desert), Western Cape Province (karoo) and Eastern Cape Province (fynbos).

Discussion.—*Ammobates auster*, for the purpose of the cladistic analysis, was grouped with *A. punctatus*. In spite of the geographical separation of *A. auster* from the rest of the punctatus group, it is remarkably similar to the other species in the group. The most important diagnostic feature of the group is the structure of the female pygidium, and within the group the female of *A. auster* can be identified by the shape of this structure. The pygidium of *A. auster* is truncate and expanded laterally (Figs. 100–102). The male can be identified by the structure of the S8 which narrows posteriorly (Fig. 106).

Type material.—Holotype ♀, paratypes 3♀ 1♂: **NAMIBIA:** 40 km S. Kolmanskop, 23.x.1974, R.H. Watmough (holotype ♀ SANC). **SOUTH AFRICA:** Strowan, 27.xi.1968, F.W. Gess (2♀ AMGS); 29 km E. Touwsrivier towards Hondewater, xii.1962 (1♀ SAMC); 77 km E. Barrydale, 13.xi.1966, C.D. Michener (1♂ SEMK).

GENUS MELANEMPIS SAUSSURE

Phileremus (Melanempis) Saussure 1891:84. Type species *Phileremus (Melanempis) ater* Saussure 1891 (monobasic) (Sandhouse 1943).

Melanempis Saussure; Michener 1944:276.

Melanempis is endemic to Madagascar. The name, which means black spot, is feminine. The genus is known from one described species, which is the largest known ammobatine bee. It is currently being revised by R.W. Brooks and A. Pauly, who have material of three additional species (Brooks, pers. comm.). Consequently, the genus is only briefly dealt with here. During the course of this study only the type species was available for examination.

Melanempis atra is a large bee (11.2–15.8 mm long). The head, mesosoma and metasoma are blackish-brown in colour. The genus is characterized as follows: vertex, frontal view, weakly and unevenly convex; antenna 12-segmented in both sexes; labrum $1.4\times$ as long as its maximum width and truncate distally; mandibles lie over labrum and their apices overlap in repose; vestiture mostly brownish-orange and sparse, fairly dense on lower region of face and distal end of metasoma; scutellum gently and evenly curved mediolongitudinally, and distinctly tuberculate paramedially; hind wing without jugal lobe; last exposed metasomal tergum (T6 female, T7 male) devoid of pygidial plate; female T6 distinctly truncate, pygidial region naked and circumscribed by small carina; male T7 abruptly curved under laterally and posterolaterally, forming pseudopygidial plate; female S5 with well developed gutter posteromedially; female S6 bifid posteriorly.

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APPENDIX 1

Species studied and their groupings. Following each species name are: genera to which species were assigned before this study, for genera synonymized here; number of specimens studied; whether the holotype or lectotype was studied, indicated by a 'T'; and general distribution. The zoogeographic region in which each species occurs is indicated as follows: P = Palaearctic, A = Afrotropical, Na = Nearctic and Nt = Neotropical.

Pasites**barkeri group**

P. barkeri (Cockerell) [19♀ 11♂; T; A: tropical & subtropical Africa]

ater group

P. friesei Cockerell [57♀ 49♂; T; A: widespread in Africa]

P. nilssoni spec. nov. [1♂; T; A: Madagascar]

P. paulyi spec. nov. [3♀ 1♂; T; A: Cameroon]

P. braunsi (Bischoff) [32♀; A: Southern Africa]

P. humectus spec. nov. [18♀ 8♂; T; A: equatorial Africa]

- P. bicolor* Friese [*Pasitomachthes*; 9♀ 4♂; T; A: Madagascar]
- P. tegularis* Friese [13♀ 7♂; T; A: Madagascar]
- gnomus group
- P. gnomus* spec. nov. [1♀ 1♂; T; A: Niger]
- carnifex group
- P. carnifex* (Gerstaecker) [15♀ 5♂; T; A: East & southern Africa]
- P. dichrous* Smith [4♀ 2♂; T; A: equatorial West Africa]
- jenseni group
- P. jenseni* (Friese) [19♀ 10♂; T; A: southern Africa]
- P. namibiensis* spec. nov. [1♀ 2♂; T; A: southern Africa]
- P. histrio* (Gerstaecker) [24♀ 12♂; T; A: southern Africa]
- P. jonesi* (Cockerell) [9♀ 1♂; T; A: East & southern Africa]
- rufipes group
- P. rufipes* (Friese) [2♀; T; A: southern Africa]
- appletoni group
- P. appletoni* (Cockerell) [217♀ 59♂; T; A: wide-spread in Africa]
- P. somalicus* spec. nov. [1♀; T; A: Somalia]
- maculatus group
- P. maculatus* Jurine [5♀ 4♂; P: Morocco to Japan]

Sphecodopsis

- capicola group
- S. capicola* (Strand) [22♀ 3♂; T; A: southern Africa]
- S. vespericena* spec. nov. [68♀; T; A: southern Africa]
- S. villosa* (Friese) [2♂; T; A: southern Africa]
- S. longipygidium* spec. nov. [1♀; T; A: southern Africa]
- S. namaquensis* spec. nov. [3♀; T; A: southern Africa]
- minutissima group
- S. minutissima* (Cockerell) [6♀ 1♂; T; A: southern Africa]
- aculeata group
- S. aculeata* (Friese) [28♀ 24♂; T; A: southern Africa]
- semirufa group
- S. semirufa* (Cockerell) [8♀ 1♂; T; A: southern Africa]
- capensis group
- S. capensis* (Friese) [*Pseudodichroa*; 29♀; A: southern Africa]
- S. fumipennis* (Bischoff) [*Pseudodichroa*; 11♀; A: southern Africa]

Melanempis

- M. atra* (Saussure) [2♀ 1♂; A: Madagascar]

Spinopasites

- S. spinotus* (Warncke) [1♀; P: Tunisia]

Ammobates

- orientanus group
- A. orientanus* (Warncke) [1♀ 1♂; P: Mediterranean]
- A. aegyptiacus* (Warncke) [1♂; P: Mediterranean]
- minutus group
- A. minutus* (Mocsary) [4♀ 5♂; P: East Europe]
- muticus group
- A. muticus* Spinola [45♀ 28♂; P: North Africa]
- A. oraniensis* (Lepelletier) [5♀ 6♂; P: South-east Europe]
- A. latitarsis* Friese [2♀ 2♂; P: East Mediterranean]
- biastoides group
- A. biastoides* Friese [2♀ 1♂; P: Mediterranean]
- unctatus group
- A. punctatus* (Fabricius) [5♀ 4♂; P: Mediterranean]
- A. ancylae* (Warncke) [1♀ 1♂; P: Mediterranean]
- A. solitarius* Nurse [1♀ 1♂; P: Pakistan]
- A. vinctus* Gerstaecker [6♀ 6♂; P: Mediterranean]
- A. auster* spec. nov. [4♀ 1♂; A: southern Africa]
- A. similis* Mocsary [1♀ 1♂; P: Mediterranean]
- A. rufiventris* Latreille [3♀ 2♂; P: Algeria]
- A. iranicus* (Warncke) [1♀ 1♂; P: Iran to Turkey]
- A. dubius* Benoist [1♀ 1♂; P: Egypt & Sudan]
- A. niveatus* (Spinola) [1♀ 2♂; P: Mediterranean]
- A. assimilis* (Warncke) [1♂; P: Tunisia]
- A. syriacus* Friese [1♀; P: Mediterranean]
- A. opacus* Popov [1♀; P: Bulgaria]
- A. armeniacus* Morawitz [1♀ 1♂; P: Turkey]
- A. sanguineus* Friese [1♀ 1♂; P: Turkey & Greece]
- rostratus group
- A. rostratus* Friese [3♀ 3♂; P: Mediterranean]
- A. robustus* Friese [1♀ 1♂; P: Turkey]
- A. teheranicus* Mavromoustakis [1♂; P: Iran]
- A. hipponensis* Pérez [2♂; P: Algeria]
- A. baueri* (Warncke) [1♀; P: Mediterranean]
- A. mavromoustakisi* Popov [2♀ 2♂; P: Mediterranean]
- A. handlirschi* Friese [1♂; P: Algeria]
- A. depressus* Friese [1♀; P: Turkey]
- verhoeffi group
- A. verhoeffi* Mavromoustakis [1♀ 1♂; P: North Africa]
- persicus group
- A. persicus* Mavromoustakis [1♀ 1♂; P: Iran]
- oxianus group
- A. oxianus* Popov [1♀ 1♂; P: Turkey]
- A. lebedevi* Popov [1♀; P: Turkey]

Oreopasites

vanduzeei group

- O. vanduzeei* Cockerell [1♀ 1♂; Na: western U.S.A.]
- O. linsleyi* Rozen [1♀ 1♂; Na: western U.S.A.]

Caenoprosopis

- C. crabronina* Holmberg [1♀ 1♂; Nt: Argentina, Paraguay & south-eastern Brazil]

APPENDIX 2

Adult morphological characters used in the cladistic analysis and their states. The states assigned to taxa are recorded in Tables 1, 2, & 4. Characters are treated as additive. Polarity was determined with reference to Neolarrini as the out group, except for character 50.

1. Vertex contour, when viewed perpendicular to lower region of inner eye margins: strongly convex laterally, lateral ocelli distinctly below vertex (Fig. 42) (0); gently convex, lateral ocellus slightly protuberant above vertex or a little below vertex (Fig. 5) (1); straight, lateral ocellus mostly protuberant above lateral region of vertex (Fig. 63) (2).
2. Vertex length: relatively short, less than twice diameter of lateral ocellus (0); elongate, at least twice as long as diameter of lateral ocellus (1).
3. Vertex profile: curved gently downwards to occiput (0); extending more or less straight behind lateral ocellus, curved abruptly downwards posteriorly (1).
4. Position of antennal socket: on lower half of face, much closer to ventral edge of clypeus than to lateral ocellus (0); near middle of face, usually closer to lateral ocellus than to ventral edge of clypeus (Fig. 5) (1).
5. Length of subantennal suture: much shorter than clypeus (0); subequal in length to clypeus (Fig. 5) (1).
6. Facial vestiture, hair structure: densely plumose, at least in area surrounding antennal sockets (0); simple to weakly plumose (1).
7. Facial vestiture, hair posture: appressed (0); erect (1).
8. Facial vestiture, hair density: dense, at least on lower region of face (Fig. 5) (0); sparse over entire face (Fig. 63) (1).
9. Segmentation of male antennal flagellum: 11-segmented (0); 10-segmented (1).
10. Length of labrum: distinctly shorter than its maximum width (0); quadrate (1); clearly longer than wide, about 1.2–1.9 times as long as its basal width (2).
11. Shape of labrum, apical truncation: apex gently rounded (or pointed) (0); truncate, distal end straight to weakly concave medially (1).
12. Shape of labrum, apex pointed: apex gently rounded (or truncate) (0); pointed apicomediaally (1).
13. Shape of apex of labrum: unmodified (0); spatulate (1).
14. Maxillary palp: present (0); absent (1). The number of segments in the maxillary palp is highly variable in several species groups, and sometimes within a single species. However, what appeared to be of significance is that some species have lost the maxillary palp.
15. Length of segments of labial palp: segment 2 about twice as long as segment 3 (0); segment 2 at least four times as long as segment 3 (1).
16. Paraocular carina: absent (0); present (1).
17. Occipital carina: absent (0); present and short (1); long, extending down posterior edge of gena (2).
18. Angle of mandibles, in repose: directed posterolaterally so that they clearly cross one another, and their apices do not overlap (illustrated by Rozen 1968a) (0); directed mesad so that their distal ends overlap in repose (1).
19. Position of mandibles, when in repose, in relation to labrum: mandibles close behind labrum (0); close over or in front of distal edge of labrum (1).
20. Pronotum: curved distinctly upwards postero-medially, but not declivous (0); declivous with vertical surface usually gently concave and glabrous (1).
21. Lateral region of pronotal collar: rounded (0); carinate (1).
22. Lateral edge of axilla: curved gently downward to wing base (0); carinate (1).
23. Scutal vestiture, hair structure: densely plumose (0); with weakly plumose and densely plumose vestiture intermixed (1); simple (2).
24. Scutal vestiture, hair posture: strongly appressed (0); weakly appressed (1); mostly erect (2).
25. Scutal vestiture, hair density: dense (0); sparse (1).
26. Mesepisternal vestiture, hair structure: densely plumose (0); mostly weakly plumose (1).
27. Ventrolateral region of mesepisternum: vestiture similar to remainder of sclerite (0); sparsely pubescent to naked, in strong contrast to densely pubescent upper region of mesepisternum (1).
28. Pre-episternal groove: extending from near wing base to scrobal groove (0); extending below scrobal groove (1).
29. Mediolongitudinal region of scutellum: unmodified or weakly raised (0); strongly swollen (1).
30. Dorsolateral edge of scutellum: rounded (0); carinate (1).
31. Shape of median region of metanotum: swollen or tuberculate (0); flat (1).
32. Setae on hind tibia of female: all setae fine, not thickened and spine-like (0); fine setae mixed with greatly thickened, spine-like, setae (1).
33. Anterior region of S1: flat to gently curved (0); strongly swollen (1).
34. Posterior region of S1: more or less in same plane as S2 (0); strongly declivous (1).
35. Mediolongitudinal region of S1: gently rounded (0); carinate anteriorly (1).
36. Mediolongitudinal region of propodeum: gently and evenly curved (0); declivous (1).
37. Dorsal surface of female T6: flat to gently convex (0); carinate mediolongitudinally (1).
38. Posterior end of female pygidial plate: fully de-

- veloped (Fig. 6) or absent (0); reduced, including posteromedian notch (1).
39. Female T6 truncate, following loss of pygidial plate: Pygidial plate present, fully developed or reduced (or absent with distal end of T6 spatulate) (0); absent, posterior end of T6 truncate and setose (1); absent, posterior end of T6 truncate and naked, circumscribed by a small carina (2).
 40. Female T6 spatulate, following loss of pygidial plate: pygidial plate present, either fully developed or reduced (or absent with distal end of T6 truncate) (0); pygidial plate absent, posterior end of T6 spatulate (1).
 41. Posterior fringe on female T6: absent (0); present (1).
 42. Female subpygidial brush: absent (0); present, but not differentiated (Fig. 6) (1); well developed and differentiated dorsoventrally (Figs. 34, 38, 43, 47, 50, 51, 53, 57) (2).
 43. Posterior margin of female S5: posteromedian region naked (0); clothed with fine vestiture (1).
 44. Posteromedian elongation of naked posterior margin of female S5: naked posterior margin short and of uniform length (or elongate and more or less of uniform length throughout its width) (0); elongate posteromedially only, due to the apparent recession of the vestiture, more or less pointed anteromedially (1).
 45. Posterior elongation of naked posterior margin of female S5: naked posterior margin short and of uniform length (or elongate posteromedially) (0); naked posterior margin widely elongate due to an apparent elongation of naked posterior margin, of uniform length (1).
 46. Posteromedian concavity of female S5 in species in which the posterior margin is clothed with fine vestiture, when viewed from behind: broadly and moderately concave (or variable with posterior margin naked) (0); with a well developed, conical concavity (Figs. 6, 15, 19, 20, 28, 29, 34) (1); concavity well developed and elliptical (Figs. 43, 47, 50, 51, 53, 57) (2) (see character 47).
 47. Posteromedian concavity of female S5 in species in which the posterior margin is naked, when viewed from behind: broadly and moderately concave (or strongly concave with posterior margin clothed with fine vestiture) (0); with a well developed, conical concavity (1); concavity well developed and more or less elliptical (2). The structure of the posterior margin of the female S5 differs between those bees in which this structure is naked and those in which it is clothed with fine vestiture. Apparently the posteromedian concavity evolved independently in these two groups of bees in response to similar requirements associated with the laying of the eggs in the cell wall of the host's nest.
 48. Posteromedian protuberance of female S5: posterior edge entire or concave and without a posteromedian protuberance (0); with a very small posteromedian protuberance (Figs. 65, 78, 82) (1); protuberance distinct (Fig. 80) (2); protuberance gutter-like (illustrated by Rozen 1968a) (3).
 49. Carina on female S5: absent (0); present (1).
 50. Structure of female S6: external (0); mostly internal, not longitudinally separated (Fig. 7) (1); mostly internal and longitudinally separated (illustrated by Roig-Alsina 1987) (2). Polarity determined with Townsendiellini as the out group.
 51. Posterior edge or apex of female S6: entire (0); forming two sclerotized spines (Fig. 7) (1); forming a single sclerotized spine (2).
 52. Reduction of male pygidial plate: pygidial plate present, sometimes reduced and confined to distal end of tergum (0); absent (1).
 53. Structure of male pygidial plate: pygidial plate simple, reduced or absent (0); well developed and bilobed (illustrated by Roig-Alsina 1987) (1).
 54. Loss of anteromedian lobe of male S8: anteromedian lobe short (Fig. 9) (or long) (0); lobe absent (Fig. 12) (1).
 55. Elongation of anteromedian lobe of male S8: anteromedian lobe short (or absent) (Fig. 9) (0); elongate (1).
 56. Anterolateral lobes of male S8: very small and unmodified or absent (Figs. 9, 12, 69) (0); well developed (Fig. 31) (1).
 57. Relative width of posterior region of male S8: narrower than anterior region (Fig. 9) (0); with anterior and posterior regions of more or less equal width (Fig. 96) (1); posterior region wider than anterior region (illustrated by Warncke 1983) (2).
 58. Expansion of anterolateral region of male S8: weakly expanded (Fig. 9) (0); strongly expanded (illustrated by Roig-Alsina 1987) (1).



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