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ISSN 0968-0454

Bulletin of The Natural History Museum

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Entomology Series



VOLUME 68 NUMBER 2 25 NOVEMBER 1999

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The Entomology Series is produced under the editorship of the
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World List abbreviation: *Bull. nat. Hist. Mus. Lond.* (Ent.)

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ISSN 0968-0454

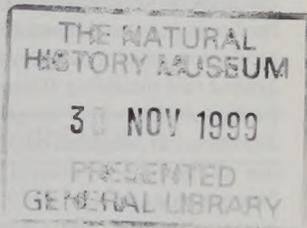
The Natural History Museum
Cromwell Road
London SW7 5BD

Entomology Series
Vol. 68, No. 2, pp. 93-193

Issued 25 November 1999

Typeset by Ann Buchan (Typesetters), Middlesex
Printed in Great Britain by Henry Ling Ltd, at the Dorset Press, Dorchester, Dorset

A revision of the African and Malagasy species of the genus *Leptomastix* (Hymenoptera, Encyrtidae), parasitoids of mealybugs (Homoptera: Pseudococcidae)



JEAN-MARC ANGA

International Cocoa Organisation, 22 Berners Street, London W1P 3DB, England.

JOHN S. NOYES

The Natural History Museum, London SW7 5BD, England.

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SYNOPSIS. The 11 species of *Leptomastix* known from Africa and Madagascar are revised. Three are described as new (*herreni*, *africana*, *jonesi*), three synonymies are proposed (*lyciae* with *nigrocincta*, *phenacocci* with *nigrocoxalis*, *superba* with *dactylopii*), and a lectotype is designated for *algorica* Trjapitzin. A dichotomous key to all species is provided and each species is further characterised by a taxonomic diagnosis or description, and notes are provided on distribution, hosts and use in biocontrol.

XX(320627.1)

INTRODUCTION

In recent years, increasing consideration has been given to alternative methods to the use of chemicals for pest control resulting from growing public concern

about the effect of the indiscriminate use of pesticides on the environment. This is especially so in Africa where the continued use of pesticides may be unrealistic for reasons other than environmental risk alone, eg. poor financial resources or the remoteness of some of

the areas involved. In recent years, the use of natural enemies to control pests has proven to be a valuable alternative to pesticides. This form of control is relatively cheap, self sustaining and is not harmful to the environment. Furthermore, many biocontrol agents can disperse very rapidly over large areas thus greatly facilitating control in remote places. The recent spectacular successes of two encyrtid parasitoids introduced against two mealybug (Homoptera: Pseudococcidae) pests in Africa, *Phenacoccus manihoti* and *Rastrococcus invadens*, has done much to promote the use of biological control on the continent (see Neuenschwander, 1989, 1990; Herren & Neuenschwander, 1991; Agricola et al, 1989). However, these successes have also highlighted the need for reliable taxonomic work to facilitate the identification of pests and their parasitoids in order to provide early control. For instance, Rosen and DeBach (1979) pointed out that their taxonomic revision of *Aphytis* (Hymenoptera: Aphelinidae) resulted in some 35 new species being made available for biological control projects against armored scale pests (Homoptera: Diaspididae). On the other hand, misidentifications of pest or natural enemies can have potentially disastrous consequences. The control of *Phenacoccus manihoti* in Africa was delayed for several years because the pest mealybug was initially wrongly identified as having originated in Central America and northern South America whereas the species was actually of central South American origin (Herren & Neuenschwander, 1991; Noyes & Hayat, 1994).

Worldwide, several mealybug pests have been the subject of biocontrol projects utilising species of the encyrtid genus *Leptomastix*. This genus includes about 35 described species, all of which are almost certainly parasitoids of mealybugs and therefore have the potential to be used as biocontrol agents against these pests. To date, three species of *Leptomastix* have been associated with biocontrol projects (see below), especially in Africa and in greenhouses in Europe and North America. However, in Africa the species are poorly known, most being difficult to identify with any degree of certainty. The only available key to species is that of Compere (1938) which relies heavily on colour to discriminate between them. The present study is therefore an attempt to provide a reliable means of identifying the African species of *Leptomastix* by means of a dichotomous key to new and known species, together with diagnostic notes, illustrations and information on their distribution and hosts. The work is based on material collected from all over the African continent including north Africa and also Madagascar.

DEPOSITORIES

BMNH	The Natural History Museum, London, United Kingdom
IEEM	Instituto di Entomología Español, Madrid, Spain
IITA	International Institute of Tropical Agriculture, Cotonou, Benin
INMP	Università Degli Studi Di Napoli Federico II, Italy
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NMP	Natural History Museum, Prague, Czech Republic
PPRI	Plant Protection Research Institute, Pretoria, South Africa
UCR	University of California, Riverside, California, USA
USNM	United States National Museum, Washington D.C., USA
ZAMU	Zoological Museum of the Aligarh Muslim University, India.

ACKNOWLEDGEMENTS We are grateful to the following for the loan of material: E. Guerrieri (INMP), J. Macek (NMP), J-L. Nieves Aldrey (IEEM), G.L. Prinsloo (PPRI), M.E. Schauff (USNM), S. Triapitsyn (UCR) and C. Villemant (MNHN). Thanks are expressed also to the Biological Control Center for Africa of the International Institute of Tropical Agriculture, Cotonu, Peoples' Republic of Benin, for financial support and to the Government of Côte d'Ivoire for study leave for the first author from the Ministry of Agriculture and Animal Resources. We also thank the Trustees of The Natural History Museum for providing facilities.

TERMS AND MEASUREMENTS

<i>Clava</i>	Terminal segments of antenna, composed of one to three segments. Segments are separated by partial or complete sutures and are not as clearly separated as funicle segments.
<i>EL</i>	Maximum length of eye (see eye).
<i>EW</i>	Maximum width of eye (see eye).
<i>Eye</i>	The measurements of length (EL) and breadth (EW) are the maximum and minimum diameters respectively. The points from which the measurements are taken should be equidistant from the objective of the microscope (i.e. both in focus simultaneously). Occasionally, when stated, the length of an eye is measured in facial view from a slide mounted specimen.
<i>F1, F2, etc.</i>	First funicle segment, second funicle segment, etc.
<i>Flagellum</i>	All segments constituting the funicle and clava (sometimes termed flagellomeres).
<i>Funicle</i>	This is part of the antenna between the pedicel

	and clava. There are no anelli present in <i>Leptomastix</i> .
<i>FV</i>	Relative width of the frontovertex. The measurement is taken either in frontal view or from above and is the measurement across the narrowest part of the frontovertex which is normally near the anterior ocellus.
<i>FWL</i>	Length of forewing excluding the marginal fringe and measured from the extreme base of the costal cell to the apex of the wing.
<i>FWW</i>	Maximum width of the forewing excluding the marginal fringe and normally measured along an imaginary line at right angles to the anterior margin of the wing to the anal angle opposite.
<i>GL</i>	Relative length of gonostylus.
<i>Gono-stylus</i>	Third valvula, or ovipositor sheath, as seen in slide-mounted material (Fig. 7).
<i>HW</i>	Head width measured in facial view.
<i>Hypopygium</i>	Apical, externally visible sternite of abdomen.
<i>Linea calva</i>	An oblique hairless line extending from the stigmal vein to posterior margin of the forewing.
<i>Marginal vein</i>	Measured from the distal margin of the subhyaline break at the apex of the submarginal vein to the distal margin of the stigmal vein where it joins the marginal and postmarginal veins. Occasionally the subhyaline break is obliterated but its position can be determined by the position of a single placoid sensillum on the dorsal surface of the submarginal vein a little before it joins the marginal vein. The position of the hyaline break is immediately distad of this sensillum.
<i>MS</i>	Malar space or the minimum distance between eye and mouth margin. The measurement is taken as for the eye (above). Occasionally, when stated, the malar space is measured in facial view from a slide mounted specimen.
<i>MT</i>	Length of middle tibia for comparison with length of the ovipositor or last tergite.
<i>MV</i>	Relative length of marginal vein.
<i>OCL</i>	The minimum distance between the posterior ocelli and occipital margin.
<i>OL</i>	Relative length of ovipositor.
<i>OOL</i>	Minimum distance between the eye margin and the nearest posterior ocellus.
<i>Post-marginal vein</i>	Measured from the distal side of the stigmal vein where it joins the marginal vein to the apex of the postmarginal vein (Fig. 6). Its apex is occasionally indicated by a single erect seta, although in anagyrines this is frequently difficult to see or absent.
<i>PMV</i>	Relative length of postmarginal vein.
<i>POL</i>	Minimum distance between the posterior ocelli.
<i>Scale-like structures</i>	Structures on apical segments of antennae of males which are usually scale-like in appearance (see Figs 60–68). These are almost certainly not sensilla but ‘release and spread structures’ associated with mating (see Isodoro <i>et al.</i> , 1996).
<i>SL</i>	Relative length of the scape. This excludes the

radicle and is most accurately measured along the internal surface of the scape.

<i>Stigmal vein</i>	Measured from its proximal margin, where it joins the marginal vein, to its apex (Fig. 6).
<i>SV</i>	Relative length of stigmal vein.
<i>SW</i>	Maximum width of scape. This is best measured on a card-mounted specimen.

LEPTOMASTIX FÖRSTER

Leptomastix Förster, 1856: 34, 37. Type-species *Leptomastix histrio* Mayr by subsequent monotypy.
Sterrhocoma Förster, 1856: 33, 36. Type-species *Sterrhocoma histrio* Förster by monotypy. Synonymy with *Leptomastix* by Graham, 1969a: 216–217.

Stenoterys Thomson, 1876: 115, 128. Type-species *Stenoterys orbitalis* Thomson, by monotypy. Synonymy with *Leptomastix* by Mercet, 1921: 119.

Leptomastix belongs to the encyrtid subfamily Tetracneminae, tribe Anagyrini (see Noyes & Hayat, 1994 for diagnostic characters of these taxa) and can be separated from all other genera of Encyrtidae using the following combination of character states (characters separating *Leptomastix* from other anagyrine genera in italics).

DIAGNOSIS. Body moderately robust and stout, yellow, orange, dark brown or completely black; mandibles bidentate; maxillary palpi 4-segmented; labial palpi 3-segmented; *frontovertex between top of antennal scrobes and anterior ocellus with fairly regular, hexagonally reticulate sculpture of mesh size, about equal to that of an eye facet*; eyes not reaching occipital margin, normally separated by at least the diameter of an ocellus; eyes inconspicuously hairy, the hairs sparse and shorter than diameter of a facet; funicle 6-segmented; mesoscutum without notauli; sculpture on mesoscutum and scutellum finely reticulate but not hexagonally reticulate; *linea calva interrupted, but not closed*; filum spinosum absent; *forewing normally with postmarginal vein at least as long as stigmal, rarely shorter*; hindwings about 4–6× as long as broad; Female: scape subcylindrical, at least 4× as long as broad; all funicle segments clearly longer than broad, F6 shortest; clava 3-segmented; costal cell narrow with only a single complete line of setae ventrally; forewings varying, about 2.5–4× as long as broad; gaster with hypopygium reaching apex and paratergites present; ovipositor not longer than mid tibia and never exerted. Male: all funicle segments much longer than broad and clothed in long setae, normally at least about 3× as long as diameter of segments; *F6 without scale-like structures ventrally* (but see *digitariae*, Fig. 65);

clava solid and with a line scale-like structures ventrally in basal half (see Figs 61–68); forewings normally about 2.5–3× as long as broad; *phallobase* with a pair of apical digits, each with two or three hooks (Figs 69, 70).

IDENTIFICATION OF SPECIES. Identification keys to species of *Leptomastix* include those of Compere, 1938 (Afrotropical); Trjapitzin, 1978 (western Palearctic); Trjapitzin, 1989 (Palearctic) and Noyes & Hayat, 1994 (Oriental).

DISTRIBUTION. *Leptomastix* includes about 35 described species and is almost exclusively Old World in distribution. The only possible exception is *Leptomastix dactylopii*, first described from Brazil and introduced throughout the New World and elsewhere. However it is very likely that this species is of Afrotropical origin (see Noyes & Hayat, 1994). The known species are fairly evenly distributed between the Palearctic (12), Africa and Madagascar (11) and the Oriental region (16) with only three species known from Australia and New Zealand (one introduced), with some overlap between these regions.

BIOLOGY. Several workers have investigated the biology of *Leptomastix* species. Their records suggest that they are primary, solitary endoparasitoids of mealybugs (Moursi, 1948; Zinna, 1959). Bess (1939) and Lloyd (1958) recorded *Leptomastix dactylopii* ovipositing in several mealybug species while Bess (1939) and Su & Li (1993) found that, of the hosts tested, it would only develop successfully in *Planococcus citri*. However, numerous other mealybug species have been recorded as hosts of *dactylopii* (see Noyes & Hayat, 1994). Lloyd (1964) showed that host preference cannot be changed by rearing the parasitoid for several generations on an 'unnatural' host species. Van Baaren and Nenon (1994) reported some parameters relating to host discrimination and potential superparasitism in *Leptomastix* species, arguing that females can distinguish between unparasitised and parasitised hosts and generally avoid the latter more often, whatever the time elapsed since the first oviposition. Discrimination seems to be based on several markers which interact either simultaneously or successively. Kirkpatrick (1953) and Jong & Alphen (1989) reported that a female of *Leptomastix dactylopii* can lay up to ten eggs per day and that oviposition can take place into third instar or adult mealybugs. Fecundity is greatest at about 30°C (Tingle & Copland, 1989) and the egg is coated with minute spherulae which contain a protein which probably prevents encapsulation of the egg by the host (Barbier & Rambault, 1985; Barbier *et al.*, 1988). Zinna (1959) and Moursi (1948) respectively reported four larval instars for *Leptomastix dactylopii* and six for *nigrocoxalis* (= *phenacocci*). According to them, the number of

segments varies from 11 to 13, the last four not clearly segmented in the earlier instars. Lloyd (in Zinna, 1959) reported that at 27°C, development in *Leptomastix dactylopii* is complete in a little over two weeks, development of the male generally being completed a day or two before the females. In *Leptomastix nigrocoxalis* (= *phenacocci*) the rate of development is linked to the age of the host into which oviposition has occurred. In 10-day-old hosts at 27°C, development takes 30 days, whilst in 20-day-old hosts, development is complete in 20 days (Moursi, 1948). Su & Li (1993) reported that the sex ratio of progeny of *Leptomastix dactylopii* was female biased, with males generally developing in smaller hosts. Adults of *Leptomastix nigrocoxalis* (= *phenacocci*) can live up to 70 to 80 days, females generally living longer than males (Moursi, 1948). In adults of *Leptomastix dactylopii*, longevity is slightly greater at 26°C. Battaglia and Tranfaglia (1994) reported that isolated adults of *Leptomastix dactylopii* lived longer than those in other conditions. Survival was strongly affected by diet; longevity without food was nearly three days while the highest values of longevity were recorded for adults fed with honey solution and pure honey.

USE IN BIOCONTROL. The use of the three species of *Leptomastix* which have been associated with biocontrol projects is summarised in Table 1.

Key to African species of *Leptomastix* (females and males)

- 1 Females: clava 3-segmented; flagellum with short appressed hairs 2
- Males: clava entire; flagellum with whorls of long setae, each longer than diameter of segments 12

FEMALES

- 2 Head completely yellow, without even dark areas on temples behind eyes; forewings at least about 3.5× as long as broad *tsukumiensis* Tachikawa (p. 98)
- Head with at least temples behind eyes brown, sometimes completely blackish; forewings at most about 3× as long as broad 3
- 3 Forewing with postmarginal vein not more than one-third longer than stigmal vein (Figs 11, 18) 4
- Forewing with postmarginal vein at least about 1.5× as long as stigmal vein (Figs 25, 29, 35, 43, 53, 59) 6
- 4 Linea calva interrupted by at least 5 lines of setae (Fig. 10); tegulae with base white and apex brown *digitariae* Risbec (p. 100)
- Linea calva interrupted by at most 3 lines of setae (Fig. 17); tegulae with base orange and apex greyish brown or completely brown 5

Table 1. A summary of the worldwide use of *Leptomastix* species in biocontrol projects.

Parasitoid	Target pest	Country/Region	Year	Result	Reference	
<i>dactylopii</i>	<i>Planococcus citri</i>	Australia (Qd)	1980	SCI	Smith <i>et al.</i> (1988)	
		Belgium	1989	SCG	Ronse (1990)	
		Bermuda	1952	NC	Cock (1985)	
		USA (California)	1934	P	Compere (1939b), Bartlett (1978)	
		Canada	1939–1945	SCG	Baird (1938, 1939, 1940a, 1941, 1942, 1943, 1944, 1946, 1947), McLeod (1962), Turnbull & Chant (1961)	
		Chile	1930–1958	SC	Duran (1944), Gonzalez & Rojas (1966), Graf Marin & Peña (1940)	
		Costa Rica	1968	E	Molina (1977), Noyes & Hayat (1994)	
		Cyprus	1966–1977	SC	Cock (1985), Greathead (1976), Krambias & Kotziosis (1980)	
		UK	1982–1987	SCG	Copland (1983), Copland & Varley (1987), Tingle & Copland (1988a,b, 1989)	
		Georgia	1961	E	Kobakhidze (1965)	
		Greece	?	P	Jourdheuil (1986)	
		India	1983–1985	SC	Manjunath (1985b), Krishnamoorthy & Singh (1987), Ramesh (1987), Prakasan (1987)	
		Israel	1984, 1987	SCG	Argov & Rössler (1988), Rubin (1985)	
		Israel	1941	NE	Rivnay (1960)	
		Italy	1956–1980	SCI	Greathead (1976), Luppino (1979), Viggiani (1975a,c), Barbagallo <i>et al.</i> (1983), Longo & Benfatto (1982)	
		Morocco	?	P	Jourdheuil (1986)	
		Netherlands	1984	PG	Hennekam <i>et al.</i> (1987); Kole & Hennekam (1990)	
		Pakistan	1985–1985	P	CIBC (1985, 1986, 1987)	
		Portugal	?	P	Jourdheuil (1986)	
		South Africa	1935	NR	Greathead (1971)	
		Spain	1948, 1977	NE	Carrero (1980a,b), Greathead (1976), Gomez Clemente (1951)	
		Sweden	1989–1990	?	Noyes & Hayat (1994)	
		Turkmenia	1968	SC	Niyazov (1969b)	
		USA (California)	1934	P	Bartlett (1978)	
		USA (Florida)	1934	SC	Watson & Thomson (1940a,b)	
		USA (Texas)	1970–1983	SCG	Meyerdirk <i>et al.</i> (1978), Summy <i>et al.</i> (1986)	
		Uzbekistan	1959–1960	E	Rozanova & Loseva (1963)	
		Yugoslavia (former)	?	P	Jourdheuil (1986)	
		<i>Planococcoides njalensis</i>	Ghana	1949–1955	NE	Greathead (1971)
		<i>Planococcus kenyae</i>	Kenya	1937, 1938	NR	Greathead (1971)
		<i>Pseudococcus comstocki</i>	USA (California)	1973–1975	R	*Meyerdirk & Newell (1979)
		<i>Pseudococcus calceolariae</i>	Chile	1931	SC	Marco (1959), Rojas (1967)
<i>abyssinica</i>	<i>Planococcus citri</i>	USA (California)	1931	NR	Compere (1931)	
<i>nigrocoxalis</i>	<i>Maconellicoccus hirsutus</i>		Egypt	1934	P Kamal (1951)	
	<i>Nipaecoccus viridis</i>	Jordan	1986	?	Meyerdirk <i>et al.</i> (1988)	

* Parasitoid misidentified as *Leptomastix flava* (see below under *L. dactylopii*)

? – no subsequent information; E – established but no further information available; NC – established but no significant control achieved; NE – not established; NR – not released; P – partial control achieved; PG – partial control in greenhouses only; R – released but no further information available; SC – successful control achieved; SCG – successful control in greenhouses only; SCI – successful control by inundative releases only.

- 5 Scape less than 7× as long as broad (Fig. 15); mesoscutum clothed in fairly conspicuous translucent, silvery setae; forewing with marginal vein about as long as postmarginal (Fig. 18) *herreni* Anga & Noyes **sp. n.** (p. 101)
- Scape at least 9× as long as broad; mesoscutum clothed in brown setae; forewing with marginal vein about 2× as long as postmarginal vein ... *algerica* Trjapitzin (p. 102)
- 6 Antenna with F1 at least 4× as long as pedicel (Fig. 22) *africana* Anga & Noyes **sp. n.** (p. 103)
- Antenna with F1 not more than 3× as long as pedicel (Figs 26, 32, 33, 39, 49, 50, 56) 7
- 7 Bases of mandibles blackish, occasionally mouth margin also blackish; forewings completely hyaline, without any longitudinal fuscous streaks (Fig. 27, 34) 8
- Bases of mandibles yellow or orange, mouth margin never blackish; forewings frequently with two longitudinal fuscous streaks (Figs 41, 51) 9
- 8 Distance of posterior ocelli from eye margin (OOL) less than 1.4× distance from occipital margin (OCL); ocellar area of frontovertex orange, axillae orange *nigrocoxalis* Compere (p. 00)
- Distance of posterior ocelli from eye margin more than 1.4× distance from occipital margin; ocellar area of frontovertex and axillae dark brown *nigra* Compere (p. 103)
- 9 Mid coxae completely yellow *dactylopii* Howard (p. 106)
- Mid coxae at least partly brown 10
- 10 Linea calva interrupted by at least 4 lines of setae; mid coxae generally orange and only brown laterally *jonesi* Noyes **sp. n.** (p. 108)
- Linea calva interrupted by not more than 4 lines of setae (Figs 52, 58); mid coxae completely brown or almost so 11
- 11 Hind and fore coxae concolorous, yellow *nigrocincta* Risbec (p. 109)
- Hind coxae brown contrasting with yellow fore coxae *abyssinica* Compere (p. 110)
- structures (Fig. 61); head and thorax usually largely orange *herreni* (p. 101)
- Clava with 5–7 short, straight, scale-like structures (Fig. 62); head and thorax dark brown *algerica* (p. 102)
- 15 Hind coxae brown 16
- Hind coxae yellow 17
- 16 Fore coxae brown *africana* (p. 103)
- Fore coxae yellow *abyssinica* (p. 110)
- 17 Temples and occiput yellow *tsukumiensis* (p. 98)
- Temples and occiput largely blackish 18
- 18 Scale-like structures arranged in line at base of clava very slender and elongate and difficult to distinguish from setae (Fig. 64) *jonesi* (p. 108)
- Scale-like structures arranged in line at base of clava flattened and short and relatively easy to distinguish from setae (Figs 63, 66, 67) 19
- 19 Longest setae on F1 at least 4× as long as diameter of segment measured in middle (Fig. 63); mesosternum dark brown, almost black, mid coxae yellow; forewing with linea calva interrupted by not more than two setae (Fig. 45) *dactylopii* (p. 106)
- Longest setae on F1 less than 4× as long as diameter of segments measured in middle (Figs 66, 67); mesosternum orange, or pale brown, mid coxae sometimes brown; forewing with linea calva normally interrupted by at least three setae, frequently by three or more lines of setae (Figs 31, 38, 55) 20
- 20 Forewing with linea calva interrupted by at most only three or four setae (Fig. 55); mandibles and mouth margin never darkened *nigrocincta* (p. 109)
- Forewing with linea calva interrupted by at least five setae (Figs 31, 38); bases of mandibles and mouth margin sometimes blackish 21
- 21 Frontovertex and axillae almost completely orange *nigrocoxalis* (p. 103)
- Frontovertex and axillae dark brown *nigra* (p. 105)

MALES

- 12 Forewings with postmarginal vein not longer than stigmal vein; head mostly dark brown (Figs 14, 20, 21) 13
- Either forewings with postmarginal vein clearly longer than stigmal vein (Figs 31, 38, 46, 55, 60) or head orange without any brown areas 15
- 13 Tegulae white with brown apex; F6 with scale-like structures (Fig. 65) *digitariae* (p. 100)
- Tegulae with base orange or completely dark brown; only clava with scale-like structures (Figs 61, 62) (sometimes apparently absent) 14
- 14 Clava with 5–7 longish, slender, recurved scale-like

REVISION OF SPECIES

Leptomastix tsukumiensis Tachikawa

(Figs 1–7, 68)

Leptomastix tsukumiensis Tachikawa, 1963a:66–68. Holotype, ♀ Japan, ELKU, not examined.

Leptomastix singularis Shafee, 1971:50–51. Holotype ♀, India, ZAMU, not examined). Synonymized with *tsukumiensis* by Noyes & Hayat (1994).

[*Leptomastix longipennis* Mercet; Otanes, 1935:503–504. Misidentification.]

DIAGNOSIS. Female (length 1.42–2.41); body

slender; including gaster generally dusky yellow to orange; head dusky yellow; mesopleuron orange, concolorous with mid coxa and mesosternum; forewing hyaline (Fig. 3) or with variable fuscous markings adjacent to anterior and posterior margins distad of venation (Figs 4, 5), sometimes also adjacent to linea calva (Fig. 5); posterior ocelli equidistant from eye and occipital margins or hardly closer to eyes; antenna (Figs 1, 2) with F1 generally at least about 2.5× as long as pedicel; forewing comparatively long and narrow, from slightly more than 3× as long as broad to about 4× (Figs 3–5); postmarginal vein varying from about as long as stigmal vein to about 1.3× as long and varying from slightly longer than marginal to a little shorter (Figs 6, 7); linea calva interrupted by 4 or 5 lines of setae (Figs 3–5); gaster as long as thorax. Male (length 0.90–1.80 mm): generally similar to female; funicular segments clothed in relatively short setae (Fig. 68), each generally not longer than twice as long as diameter of segments, although this can be variable (see below); a line of about 10 scale-like structures present on the basal half of clava; forewing completely hyaline, about 3.0× as long as broad; marginal vein slightly longer than postmarginal which is subequal to stigmal vein in length; aedeagus about one-third as long as midtibia; phallobase with elongate digiti, each with two elongate apical spines.

VARIATION. Slightly more extensive than in extralimital material (see Noyes & Hayat, 1994) in that in the female the forewing may vary from completely hyaline to almost uniformly dusky or with a distinct fuscous pattern (see Figs 3–5), the posterior ocelli may be conspicuously closer to the eye than occipital margin, the funicle segments vary from relatively slender (Fig. 1) to distinctly flattened (Fig. 2) with F1 varying from only 4× to nearly 7× as long as broad and the forewing may be only slightly more than 3× as long as broad. The males show some considerable variation in the density and length of setae on the funicle, some specimens having the setae relatively dense and short (about 2× as long as diameter of segments, see Fig. 68) whilst in others they may be relatively sparse and long (about 4× as long as diameter of segments, similar to Fig. 63).

HOSTS. *Leptomastix tsukumiensis* has been recorded from an unknown mealybug on *Citrus* sp. by Shafee (1971) and from *Ferrisia virgata* by Otanés (1935). This species is also recorded for the first time in Africa, from undetermined hosts.

DISTRIBUTION. Gambia, Ivory-Coast, Benin, Nigeria, Cameroon, Somalia, Kenya, Zambia, Zimbabwe, South Africa, Madagascar, India, Laos, Philippines, China and Japan.

MATERIAL EXAMINED.

Non-type material. **Gambia**, ♂2, Bakau, i.1978 (Huggert); 1♂, Fajara, i.1978 (Huggert); **Ivory Coast**, 1♂, Lamto, 6°13'N 5°02'W, 16.v.1985 (Rasplus); 8♀, 13♂, Lamto, 6°13'N 5°02'W, xi.1988 (Noyes); 1♀, Bouake, xi.1981 (Cochereau); **R.P. Benin**, 1♂, 25Km N Ohicon, 4.xii.1988 (Noyes); **Nigeria**, 11♀, 20♂, Kaduna St., 20 Km N Kaduna, 8.xi.1987 (Noyes, Neuenschwander); 1♂, 81Km NW Jos, 1.xi.1987 (Neuenschwander); 6♀, 6♂, Plateau St., 20 Km NW Jos, 12.xi.1987 (Noyes, Neuenschwander); 1♀, 6♂, Bauchi St., 74 Km W. Bauchi, 14.xi.1987 (Noyes, Neuenschwander); 1♀, Sokoto St., 54 Km E. Sokoto, 8.xi.1987 (Noyes, Neuenschwander); **Cameroon**, 1♀, Sanyere, 18.xii.81 (Compton); **Somalia**, 1♀, Lr. Shabelli Valley, Mogadiscio, v.1977 (Bin); **Uganda**, 1♂, Serere, 22.vii.1934, BM 1935–459 (Ford); **Kenya**, 1♀, Nairobi, Kusen, vi.1982 (Dewhurst); **Zambia**, 1♀, 15Km E Lusaka, 11–19.ii.1980 (Beaver); **Zimbabwe**, 14♀, 2♂, Harare, Chishawasha, i.81–xii.84 (Watsham); **South Africa**, 3♀, Cape Province, Swellendam, 17.xii.31–18.i.32 (Turner), 16♀, 9♂, Cape Province, Ceres, various dates iii.1921–iv.1925 (Turner); 1♀, Cape Province, Matjesfontein, 7–13.xi.1928 (Turner); 1♀, Cape Province, summit of Du Toits Kloof, 4.v.1972 (BMNH Southern African Expedition); 1♀, Natal, Kloof, 1500ft (=572m), ix.1926 (Turner), 1♀, Natal, Cape Vidal, 28°10'S 32°32'E, 13.i.1981 (Prinsloo); 3♀, Tvl, D'Nyala Nat. Res. Ellisras District, 23°45'S 27°49'E, 23–26.ii.1987 (Prinsloo); 1♀, Natal, Vernon Crookes Nat Res., Umzinto, 30°17'S 30°37'E, 443m, 25–26.iii.1985 (Prinsloo); 1♀, C.P., Andries Vosloo Kudu Res. nr. Grahamstown, 33°07'S 26°38'E, 30.xi.1983 (Prinsloo, Grobbelaar); 2♀, Tvl, Blyderivierspoortdaam Nat. Res., 24°32'S 30°47'E, 25–26.x.1984 (Prinsloo); 1♀, C.P., Grahamstown, 33°19'S 26°32'E, 13.i.1983 (Prinsloo, Grobbelaar); 1♀, Tvl, Hans Merensky nat. Res., 23°40'S 30°39'E, 27–30.i.1981 (Prinsloo); 1♀, Tvl, Mogol Nat. Res., Ellisras District, 23°58'S 27°45'E., 21.i.1983 (Prinsloo); 1♂, Tvl, Pretoria, T3754, iii.1971 (Annecke); 1♀, Tvl, Letsitele, xi.1978 (Prinsloo); also material from **India, Laos, China and Philippines** as detailed in Noyes & Hayat (1994). Material in BMNH, PPRI.

COMMENTS. In Africa, *Leptomastix tsukumiensis* can be recognized by its relatively narrow forewing which is usually infusate along its anterior margin distad of the venation. It is most similar to *Leptomastix dactylopii* and can be separated on the coloration of the temple and mesosternum and relative lengths of the forewings. In *tsukumiensis* the temples and mesosternum are yellow and the forewings are 3.3–4.1× as long as broad whilst in *dactylopii* the temple and mesosternum are dark brown and the forewings are 2.6–3.0× as long as broad.

The considerable variation in both sexes as outlined above initially led us to believe that at least two species were present. After careful examination of all the material at hand we have been unable to recognise any discrete groups. Intermediate forms for all combinations of the variable character states are present in both African and Oriental material and therefore we are assigning all material listed above to *tskumiensis*.

Leptomastix digitariae Risbec

(Figs 8–14, 65, 69)

Leptomastix digitariae Risbec, 1959:23–6. Lectotype ♀, designated by Noyes & Prinsloo (1998), Madagascar, examined, MNHN.

DIAGNOSIS. Female (length 1.70–1.85 mm): body, including gaster, dark-brown to black; head and dorsum of thorax clothed in white setae; tegulae yellow basally; legs brown, except mid tibia which is yellow; posterior ocelli closer to eye margin than occipital margin; antenna (Fig. 8) with F1 about 2× as long as pedicel, segments subequal in length; forewing (Fig. 9) hyaline and about 2.6× as long as broad; linea calva interrupted by five lines of setae; postmarginal vein slightly shorter than either marginal or stigmal veins (Fig. 11); gaster as long as thorax; ovipositor slightly exserted. Male (length 1.34–1.42 mm): generally similar to female but antenna (Fig. 65) with setae on funicle longer, up to 3.5× as long as diameter of F1; scale-like structures on F6 and clava.

FEMALE (PARALECTOTYPE). Body, including gaster, dark-brown to black; head and thoracic dorsum clothed in white setae; mandibles brown; antennae dark-brown; coxae dark brown; legs generally dark brown except for distal apex of mid femur and entire mid tibia which are yellow; mid tarsi testaceous; subalar sclerites pale-yellow; tegulae whitish basally, dark brown apically.

Head with inner eye margins diverging ventrad; frontovertex with regular, polygonally reticulate sculpture of fine mesh size which is on average a little smaller than an eye facet; piliferous punctures small, but distinct; posterior ocelli closer to eye margin than occipital margin; antennae (Fig. 8) as long as body; scape 5× as long as broad; pedicel 2× as long as broad; funicle segments subequal in length, at least 2× as long as broad; F1 1.6× as long as pedicel; clava 1.7× as long as F1 and twice as long as F6. Relative measurements: HW 85, HL 75, FV 35, POL 15.5, OCL 8, OOL 6, EL 52, EW 37, MS 23, SL 43, SW 12.

Thorax with mesoscutum regularly clothed in white setae; mesoscutum and scutellum with similar sculpture to frontovertex; wings hyaline; forewing (Fig. 9) about 2.6× as long as broad; linea calva interrupted by 5 lines of setae (Fig. 10); postmarginal vein (Fig. 11) about 0.75× as long as either marginal or stigmal veins; hindwing hyaline, 4.6× as long as broad.

Gaster as long as thorax, with ovipositor (Fig. 12) slightly exserted, the exserted part slightly shorter than the mid tibial spur.

MALE (PARALECTOTYPE). Similar to female, differing slightly as follows. Posterior ocelli equidistant from eye and occipital margins; linea calva interrupted by 3 lines of setae; antennae (Fig. 65) clothed with long setae, each about 4× as long as diameter of segments; F6 ventrally with 5 scale-like structures and clava with two. Aedeagus and phallobase as in Fig. 69.

VARIATION. Little in material available.

HOSTS. *Leptomastix digitariae* was reared originally from mealybugs on leaves of *Digitaria humberti*. (Poaceae) (Risbec, 1959).

DISTRIBUTION. Madagascar.

MATERIAL EXAMINED.

Type material. Lectotype ♀ originally mounted in slide labelled '*Leptomastix digitariae* Risbec 1079' '*Leptomastix nigrocoxalis* Compere 1079' '1079 1 ex, *Leptomastix nigrocoxalis* Compere 13 *Leptomastix*', remounted on card 21.vii.1988 by JSN and labelled 'LT ♀' on ventral side of card. Paralectotypes: 8 ♀, 6 ♂, same data as lectotype and remounted on cards. According to Risbec (1958:26) the type material was reared in Madagascar from mealybugs on the leaves of *Digitaria humberti* by Renaud Paulian. Lectotype and paralectotypes in MNHN, 1 ♀, 2 ♂ paralectotypes in BMNH.

Non type material. **Madagascar**, 1 ♀, Tananarive, Tsimbazaza Gdns, 27.v.1983 (Noyes, Day). Material in BMNH.

COMMENTS. *Leptomastix digitariae*, although superficially similar to several species of *Leptomastix* may be incorrectly placed in the genus and is retained in *Leptomastix* pending further work on the phylogenetic relationships of the taxa currently included in the tribe Anagyrini. A preliminary phylogenetic analysis of the taxa of this tribe undertaken by the first author was inconclusive with regards to the recognition of two separate lineages identified previously (see Noyes & Hayat, 1994). These lineages were defined on the sculpture of the frontovertex and the distribution of the scale-like structures on the antenna of the male. The lineage including *Leptomastix* includes species which have regular polygonal sculpture on the frontovertex and males with scale-like structures on the clava only. The second lineage, which includes *Anagyrus*, is defined by irregular, fine sculpture on the frontovertex and presence of scale-like structures on F6 of the male antenna. In *L. digitariae* the sculpture is somewhat intermediate, and scale-like structures are present on F6.

Leptomastix digitariae is superficially similar to *Leptomastix herreni*, both sharing the same general

coloration of the body (dark-brown to black), white setae on the head and relatively short postmarginal vein of the forewing. Apart from the sculpture of frontovertex and distribution of scale-like structures on the antenna of the male as stated above, they can be separated by the relative position of the posterior ocelli, the colour of the tegulae and in the females by the number of lines of setae interrupting the linea calva. In *digitariae* the posterior ocelli are closer to the eye than the occipital margin and the tegulae are basally yellow and the linea calva of the female is interrupted by five lines of setae (Fig. 10) whilst in *herreni* the posterior ocelli are closer to the occipital margin than the eye, the tegulae are completely brown and the linea calva of the female is interrupted by only three lines of setae (Fig. 17). There is also some similarity between *digitariae* and *algorica* (see comments under *algorica*).

Leptomastix herreni Anga & Noyes sp. n.

(Figs 15–20, 61)

DIAGNOSIS. Female (length 0.50–1.70 mm): colour varying from almost completely orange to almost completely dark brown (see below); at least mid and hind coxae orange-brown to dark brown; wings hyaline; inner eye margin diverging ventrad; minimum width of frontovertex 0.8–1.2× eye length; posterior ocelli closer to occipital margin than eye margin; F1 about as long as pedicel to twice as long; forewing about 2.5× as long as broad (Fig. 16); postmarginal vein only about as long as either marginal or stigmal or even slightly shorter (Fig. 18); linea calva interrupted by 2 or 3 lines of setae (Fig. 17); gaster as long as thorax. Male (length 0.50–1.35 mm): generally similar to female in coloration, but each torulus always connected to mouth margin by a yellowish streak even in the darkest specimens; antennae (Fig. 61) clothed with long setae, the longest about 3× as long as diameter of F1, F1 twice as long as pedicel, basal half of clava with about 8–10 very fine, recurved scale-like structures ventrally; forewings about 2.3× as long as broad; postmarginal vein very nearly as long as stigmal (Fig. 21).

FEMALE (HOLOTYPE). Length 1.48 mm. Head dark-brown, with inner eye margins yellow; temples dark-brown, occiput dark orange-brown, dark brown adjacent to temples; clypeal area pale orange, with white setae; mandibles dark-brown; radicle dark-brown; scape brown dorsally and dusky-orange ventrally; flagellum unicolorous brown; dorsum of thorax dusky-orange, dark brown on dorsal part of pronotum, anterior margin of mesoscutum, axillae, anterior median part of scutellum and metanotum; mesopleuron orange; prosternum anteriorly and mesosternum brown; mid coxa orange-brown; fore coxa

brown anteriorly; subalar sclerites below base of forewing dusky-yellow; propodeum dark brown with spiracular area orange; gaster dark-brown.

Head with inner eye margin diverging ventrad; width of frontovertex 0.85× eye length; posterior ocelli closer to occipital margin than eye margin; antennae (Fig. 15) 0.9× as long as body; scape 5× as long as broad; F1 about as long as pedicel; clava 1.5× as long as F1 and 2.1× as long as F6; pedicel 1.9× as long as broad. Relative measurements (holotype): HW 101, HH 92, FV 50, POL 19.5, OCL 5, OOL 11, EL 58, EW 37, MS 28, SL 52, SW 10.

Thorax and gaster: mesoscutum and scutellum with finely reticulate sculpture; wings hyaline; forewing (Fig. 16) about 2.6× as long as broad; linea calva interrupted by two or three lines of setae (Fig. 17); postmarginal vein about 0.7× as long as either marginal or stigmal veins (Fig. 18); hindwing 4.2× as long as broad; gaster as long as thorax, with ovipositor hidden. Relative measurements: FWL 230, FWW 90; HWL 153, HWW 36.

Gaster as long as thorax, with ovipositor (Fig. 19) hidden. Relative measurements (paratype): OL 35, MT 51.

MALE. See diagnosis. Relative measurements: HW 45, FV 27, POL 10, OOL 7, OCL 2.5, EL 23, EW 16, MS 14, SL 20, SW 5; FWL 103, FWW, 45.

VARIATION. The most noticeable variation is that of colour, in both sexes from almost completely orange with only the mandibles, interantennal prominence, occiput, pronotum, tegulae and gaster brown to completely brown, including all coxae and femora, but not the tibiae and tarsi which are always more or less orange. Morphological variation is mostly related to size. The smallest females have a slightly wider frontovertex, antennae about as long as the body, and the postmarginal vein slightly longer than either the marginal or stigmal veins. Some larger females may have the scape only about 4× as long as broad and F1 about 2× as long as the pedicel. Smaller males tend to have relatively shorter setae on the funicle and fewer scale-like structures on the clava.

HOSTS. *Leptomastix herreni* recorded below from *Octococcus* sp. on Compositae and 'mesem', from *Octococcus pentziae* on *Pentzia globosa*, *Octococcus* sp. nr *pentziae* on *Athenasia trifurcata*, *Octococcus* sp. on *Oedera imbricata*, and unidentified mealybugs on *Rehmania ericoides*, *Chrysocoma ?coma-aurea*, and *?Athenasia* sp.

DISTRIBUTION. South Africa.

MATERIAL EXAMINED.

Type-material: Holotype ♀, **South Africa**, C.P., Klipheuwel, ex *Octococcus* sp. on Compositae, T2783, x.1968 (*Insley*). Paratypes: **South Africa**, 9 ♀, 5 ♂,

C.P., x.1968, ex mealybug on *Rehmania ericoides*, T2779, x. 1968 (*Insley*); 2 ♀, 2 ♂, C.P., Klipheuwel, ex *Octococcus* sp. on Compositae, T2783, x.1968 (*Insley*) 3 ♀, 2 ♂, same data as holotype; 3 ♀, 2 ♂, C.P., Tulbagh district, ex mealybug on *Rehmania ericoides*, T2833, x.1968 (*Gillioomee*); 6 ♀, 5 ♂, C.P., Caledon, x.1969, ex *Octococcus* sp.n. on *Oedera imbricata*, T3219, x.1969 (*Insley*); 3 ♀, 1 ♂, C.P., Villiersdorp District, ex mealybug on *Chrysocoma ?coma-aurea*, T3217, x.1969 (*Insley*); 1 ♀, 1 ♂, C.P., Paarl, x.1971, H.P. Insley, ex mealybug on Cape Macchia, T3971, x.1971 (*Insley*); 1 ♀, 4 ♂, C.P., Worcester, ix.1972, ex mealybug on unknown plant, T4525, ix.1972 (*Neser*); 3 ♀, C.P., Windmeul nr Paarl, ex *Octococcus* sp. nr. *pentziae* on *Athenasia trifurcata*, T4922, 3.x.1974 (*Prinsloo*) 2 ♀, 1 ♂, C.P., Ceres, 9.x.1974, on *Rehmania genistaefolia*, T4927, 9.x.1974 (*Prinsloo*); 9 ♀, 6 ♂, C.P., Tulbagh, ex ?*Octococcus* sp. on ?*Athenasia* sp., T5469, vi, 1978 (*Neser*); 5 ♀, 9 ♂, OFS, Edenville, OFS, ex *Octococcus pentziae* on *Pentzia globosa*, T3503, i.1970 (*Insley*); 2 ♀, 3 ♂, C.P., Oudtshoorn, ex *Octococcus* sp. on 'Mesem', T6915, iii.1979 (*Laubscher*). Holotype in PPRI, paratypes in PPRI and BMNH.

COMMENTS. *Leptomastix herreni* is most similar to *nigra*, both species having the same variable colour from largely orange to more or less completely dark brown or blackish and the ocelli closer to the occipital margin than to the eyes. They differ in the number of lines of setae interrupting the linea calva and the relative length of the postmarginal vein of the forewing. In *herreni* there are at most three lines of setae interrupting the linea calva (Fig. 17) and the postmarginal vein is about as long as the stigmal (Fig. 18) whereas in *nigra* there are generally at least four lines of setae interrupting the linea calva (Fig. 34) and the postmarginal vein is at least about 1.5× as long as the stigmal (Fig. 35). The males can be separated as in the females by the relative length of the postmarginal vein (compare Figs 20, 38) and number of lines of setae interrupting the linea calva and also by the number and structure of the scale-like structures on the clava. In *herreni* there are about 8–10 very fine, almost seta-like, recurved structures (Fig. 61) whilst in *nigra* there are only about 6 relatively broad, distinctly flattened structures (Figs 66, 67). The species is also very similar to *Leptomastix nigrocoxalis* and *Leptomastix digitariae* (see under *nigrocoxalis* and *digitariae* for comments). Paler forms of *herreni* might be mistaken for *flava* but the females differ in having the forewings completely hyaline, the mandibular bases almost black, and only two or three lines of setae interrupting the linea calva whereas in *flava* the forewings are frequently distinctly infusate, the mandibles are orange and there are four or five lines of setae interrupting the linea calva. The males on the other hand can be

separated by the elongate, recurved scale-like structures on the clava whilst those in *flava* are very short and broad.

The species is named in honour of Dr Hans Herren for his contribution to biological control in Africa.

Leptomastix algerica Trjapitzin

(Fig. 21, 62)

Leptomastix algerica Trjapitzin 1989:126.

LECTOTYPE ♂ (here designated), Algeria, NMP, examined.

DIAGNOSIS. Female (length 1.40–1.50 mm): body moderately robust; generally dark brown, including coxae, femora and gaster; mouth margin yellowish; tibiae and tarsi pale orange; wings hyaline; F1 about 2× as long as pedicel; posterior ocelli slightly closer to occipital margin than eyes; forewing 2.5× as long as broad; postmarginal vein variable, from slightly shorter than stigmal to about one-third longer; stigmal vein about as long as marginal vein; linea calva interrupted by 2 to 4 lines of setae; gaster as long as thorax. Male (length 0.90 mm): similar to female; antennae clothed with long setae, longest about 3.3× as long as diameter of F1; base of clava with 5 or so scale-like structures ventrally; forewing venation as in Fig. 21.

VARIATION. Little in material examined, but see comments.

HOSTS. Unknown, but see comments.

DISTRIBUTION. Greece, Cyprus, Algeria

MATERIAL EXAMINED.

Type material. LECTOTYPE ♀, here designated: **Algeria**, 1 ♀, Aures: Ain Zaatout, 1.–4.vi.1971 (*Hoffer, Horak* [Expedition 'SCARABAEUS']) 'Holotypus *Leptomastix algerica* Hoffer ♀'. Paralectotypes: **Algeria**, 1 ♀, Biskra, 7.–8.vi.1971 (*Hoffer, Horak* [Expedition 'SCARABAEUS']); 1 ♂, Auresi, Ainzaatout, 1.–4.vi.1971 (*Hoffer, Horak* [Expedition 'SCARABAEUS']). Lectotype in NMP, paralectotypes in BMNH.

Non-type material. **Greece**, 1 ♀, Kos, 4Km W Kos Town, 20.viii.1994 (*Noyes*); **Cyprus**, 1 ♀, 13Km SW Kyrenia, Karaman, 22–23.viii.1993 (*Noyes*). Material in BMNH, both specimens part of longer series of probably the same species.

COMMENTS. The name *algerica* was made available in a review of the Palaearctic Encyrtidae by Trjapitzin (1989) and accredited to Hoffer. However, in that publication there is no indication that Hoffer was responsible for meeting the criteria for making the name available and therefore in compliance with Article 50 of the International Code of Zoological Nomenclature (1985) the name is here attributed to

Trjapitzin. No reference was made to the primary type by Trjapitzin and therefore a lectotype is selected above.

We are of the opinion that *algorica* may be a dark form of *epona* Walker since we are unable to find any consistent morphological characters to separate the two. We have examined a long series (BMNH) of specimens reared in Israel from *Pseudococcus cryptus* which have been identified as *algorica*. Females of this series vary from entirely dark brown as in the type material of *algorica* to the scutellum being almost entirely orange. The males are inseparable from darker forms of *epona* from western Europe. For the present we are not including this material in the present study because this 'Israeli' form is currently the subject of experimental studies to ascertain its status.

Leptomastix africana Anga & Noyes *sp. n.*

(Figs 22–25)

DIAGNOSIS. Female (length 1.30–1.60 mm): body including gaster dark-brown to black; all coxae dark brown; F1 nearly 4× as long as pedicel (Fig. 22); posterior ocelli closer to occipital margin than eye margin; wings hyaline; forewing (Fig. 23) about 2.7× as long as broad; postmarginal vein about twice as long as stigmal vein which is subequal to marginal (Fig. 25); lineal calva interrupted by two lines of setae (Fig. 24); gaster as long as thorax. Male (1.10–1.40 mm): generally similar to female but antennae clothed with long setae, the longest about 5× as long as diameter of F1; basal half of clava with 9 or so scale-like structures ventrally.

FEMALE (HOLOTYPE). Length 1.48 mm. Body including gaster dark-brown to black; lower face with conspicuous silvery setae; antennae dark-brown; mesoscutum with contrasting silvery setae; scutellum similar to mesoscutum but setae not as conspicuous; wings hyaline; all coxae brown; femora brown but for apex of mid femora which is yellow; fore and hind tibiae and tarsi brown; mid tibia and tarsi pale orange; propodeum laterally with silvery setae.

Head with inner eye margins diverging ventrad; minimum frontovertex width slightly less than eye length; posterior ocelli closer to occipital margin than eye; antennae (Fig. 22) 1.3× as long as body, scape 5× as long as broad, pedicel 1.25× as long as broad, F1 nearly 4× as long as pedicel, clava 1.2× as long as F1 and 2× as long as F6. Relative measurements (holotype): HW 43, HH 40, FV 22, POL 15, OCL 5, OOL 8, EL 22, EW 7, MS 12, SL 25, SW 5.

Thorax with finely reticulate sculpture on mesoscutum and scutellum; forewing (Fig. 23) about 2.7× as long as broad, with postmarginal vein twice as long as either marginal or stigmal veins (Fig. 25); lineal calva interrupted by two lines of setae (Fig. 24); hindwing hyaline, about 4.4× as long as broad.

Gaster as long as broad, with ovipositor hidden. Relative lengths (paratype): OL 29, MT 65.

MALE. Generally similar to female but inner eye margin subparallel, minimum frontovertex width about equal to eye length, forewing about 2.6× as long as broad, lineal calva interrupted by a single line of setae, antennae clothed with long setae, the longest about 5× as long as diameter of F1; basal half of clava with 9 or so scale-like structures ventrally.

VARIATION. Very little except in body colour and size: smaller specimens tend to be brownish and larger ones dark-brown to black.

HOSTS. *Leptomastix africana* has been reared from a mealybug, probably *Octococcus* sp., on *Elytropappus rhinocerotis* (see below).

DISTRIBUTION. South Africa.

MATERIAL EXAMINED.

Type material. Holotype ♀: **South Africa**, C.P., Stellenbosch, Idas Valley, ex ?*Octococcus* sp. on *Elytropappus rhinocerotis*, T5976, ii.1979 (Neser). Paratypes: **South Africa**, 3♀, 1♂, same data as holotype; 2♂, C.P., Paarl, ex ?*Octococcus* on *Elytropappus rhinocerotis*, T2737, ex 14.x.1968 (Insley); 7♀, 3♂, Cape Province, Ceres, iii.1925 (Turner). Holotype in PPRI, paratypes in PPRI, BMNH and IITA.

COMMENTS. *Leptomastix africana* is most similar to *abyssinica* and *nigrocincta* (see comments under those species).

Leptomastix nigrocoxalis Compere

(Figs 26–31)

Leptomastix nigrocoxalis Compere, 1928:219–220.

Holotype ♀, South Africa, USNM, not examined.

Leptomastix phenacocci Compere, 1938:325. Holotype ♀, Egypt (ex. Java), BMNH, examined. **syn. n.**

[*Leptomastix flavus* Mercet; Risbec 1951:103. Misidentification (part).]

Leptomastix brevis Hayat, Alam & Agarwal, 1975:14–16. Holotype ♀, India, BMNH, examined. Synonymized with *Leptomastix nigrocoxalis* by Noyes & Hayat (1994).

Leptomastix aligarhensis Khan & Shafee, 1975:194. Holotype ♀, India, ZAMU, not examined. Synonymized with *Leptomastix nigrocoxalis* by Noyes & Hayat (1994).

Leptomastix longiscapus Khan & Agarwal, 1976:378–380. Lectotype ♀ (designated Noyes & Hayat, 1994), India, ZAMU. Synonymized with *Leptomastix nigrocoxalis* by Noyes & Hayat (1994).

DIAGNOSIS. Female (length 0.90–2.10 mm): body

including gaster orange to dusky orange; head with a dark brown area adjacent to each eye which extends across occiput towards foramen; mandibles always with bases dark brown, almost black; mesoscutum completely orange or with a brown wedge-shaped mark medially; mesosternum always brown and mid coxa always dark-brown; wings hyaline; position of ocelli relative to eye and occipital margin variable, generally about equidistant from eye and occipital margin, but sometimes clearly a little closer to occipital margin; antenna (Fig. 26) with F1 about 1.3–2.0× length of pedicel; forewing (Fig. 27) about 2.7× as long as broad; postmarginal vein about 1.5× as long as stigmal or slightly longer (Fig. 29); linea calva interrupted by 4 or 5 lines of setae (Fig. 28); gaster as long as thorax. Male (length 1.06–1.50 mm): generally similar to female, but head and thorax predominantly yellow; head with a dark-brown area on occiput adjacent to each eye, extending towards foramen; mandibles varying from orange to dark brown; dorsum of thorax orange or with anterior part of mesoscutum marked with dark brown; metanotum and sides of propodeum yellow; side and sternum of thorax mostly dusky-yellow; mid coxae occasionally hardly darkened; legs pale orange except mid and hind tibia which is brown dorsally; tarsi of fore and hind legs brownish, those of midlegs dusky-yellow except towards apex; funicle clothed in setae about 3× as long as diameter of segments; antenna with 5 or 6 scale-like structures on base of clava; forewing about 2.5–2.8× as long as broad; linea calva interrupted by about four lines of setae; aedeagus a little more than one-third as long as mid tibia, each digitus with a pair of moderate apical teeth.

VARIATION. The colour of the dorsum of the thorax of both sexes varies as outlined above. In general the frontovertex is not more than half head width with posterior ocelli about equidistant from eye and occipital margin, OOL:OCL never greater than 1.4.

HOSTS. *Leptomastix nigrocoxalis* has been recorded as a parasitoid of *Nipaeococcus graminis* on *Hyparrhenia hirta* (Prinsloo, 1981); ?*Nipaeococcus graminis* on wild grass (Compere, 1928); *Pseudococcus* sp. on *Melia azedarach*, 'coccid' on hibiscus (Risbec, 1959); *Planococcus citri* on *Citrus medica* (Agarwal, 1965) and on coffee (Prakasan and Kumar, 1985); and *Rastrococcus capparidae* (Avasthi and Shafee, 1983); *Maconellicoccus* (= *Phenacoccus*) *hirsutus* (Compere, 1939c) and *Nipaeococcus viridis* (Moursi, 1948; as *Pseudococcus filamentosus* Cockerell, misidentification). It has also been recorded by Hayat *et al.* (1975) from *Coccidohystrix* (= *Centrocooccus*) sp. on *Achyranthes aspera* and *Pupalia lappacea*; *Coccidohystrix* (= *Centrocooccus*) *insolita* on *Achyranthes aspera* and *Wittania somnifera*; *Nipaeococcus* sp. on citrus, *Acacia*, *Peritropha*

bicalyculata and *Morus alba*; *Nipaeococcus viridis* on *Ziziphus*, *Acacia* and *Tephrosia purpurea*, a 'coccid' on *Tamarindus indica*, *Leucas cephalotus*, *Hemigraphes* and *Acacia*, and from the margarodid *Icerya aegyptica*. Additionally recorded from *Rastrococcus iceryoides* on *Ziziphus* and from *Pseudococcus* sp. on tamarind (Noyes & Hayat, 1994). The record of this species as a parasitoid of *Nimboa basipunctata* (Neuroptera, Coniopterygidae) by Sharma *et al.* (1985) is unlikely and requires confirmation as does the record from *Saissetia nigra* (CIBC, 1970).

DISTRIBUTION. Egypt, Sudan, Zimbabwe, Namibia, South Africa, India and Indonesia.

MATERIAL EXAMINED.

Type material. Holotype ♀ of *Leptomastix phenacocci*: 'Egypt sent by Priesner' 'ex *Pseudococcus hirsutus*'; according to Priesner in Compere (1939c) this was from material originally obtained in **Indonesia** (Java) (BMNH); paratypes of *Leptomastix phenacocci*: 6 ♀, 5 ♂, same data as holotype (BMNH, UCR). Holotype ♀ of *Leptomastix brevis*, **India**, Kerala, Kalamasseri, ex *Icerya aegyptica* (Douglas), 12.iii.1967 (Hayat) (BMNH). Lectotype ♀ of *Leptomastix longiscapus*: **India**, Uttar Pradesh, Garhwal, ex coccid on citrus, 5.ix.1975 (Khan) (ZAMU); Paralectotypes of *Leptomastix longiscapus*: **India**, 9 ♀, 4 ♂, same data as holotype (ZAMU).

Non-type material. **Sudan**, 1 ♀, Wad Medani, from mealybugs on *Tamarindus indica*, 17.v.1939 (Cowland); 1 ♀, Wad Medani, ex mealybug on *Citrus medica*, ii.1938 (Ruttledge); **Egypt**, 5 ♀ Giza, 7.ix.1929, ? hibiscus mealybug breeding room, (Kamal); **Senegal**, 12 ♀, 6 ♂, Louga, ex cochenille sur *Euphorbia*, 1945 (Risbec) (misidentified as *Leptomastix flava* by Risbec); 1 ♀, Bambey, sur Sourour (misidentified as *Leptomastix flava* by Risbec); **South Africa**, 3 ♀, 5 ♂, Tvl, Dendron, ex, mealybug on grass, T6067, i.1980 (Prinsloo); 1 ♀, Tvl, Soutpan, Pretoria Dist., 25°24'S 28°06'E, 11–12.i.1984 (Grobbeelaar); 11 ♀, 1 ♂, Tvl, Levubu Tvl, ex mealybug on grass, T6924, i.1987 (Prinsloo); 1 ♀, Tvl, Entabeni For. Res., 33°00'S 30°16'E, 7–1.i.1987 (Prinsloo); 1 ♀, Tvl, Weltevreden Farm nr Karino, ii.1990 (Prinsloo); **India**, material as listed in Noyes & Hayat (1994). Material in BMNH, PPRI.

COMMENTS. Although there are slight differences in the coloration of the head and mesoscutum of type and other material identified as *phenacocci* and *nigrocoxalis* (see Noyes & Hayat, 1994) we are unable to find any significant morphological characters by which to separate the two and therefore we treating the two names as synonymous.

Leptomastix nigrocoxalis is very close to *nigra*, the species possibly being synonymous (see comments

under *nigra*). It is also very similar to *nigrocincta* (see comments under *nigrocincta*). At a glance, females of *nigrocoxalis* may be mistaken for those of *herreni* but can be separated readily on the relative length of the postmarginal vein. In *nigrocoxalis* the postmarginal vein is at least nearly twice as long as the stigmal (Fig. 29) whereas in *herreni* it is only about as long as the stigmal vein (Fig. 18). *Leptomastix nigrocoxalis* might be confused with *epona* and *histrion*, both of which are Palaearctic species and yet to be recorded in Africa. Females of *nigrocoxalis* can be distinguished from both of these species by the blackish mandibular bases, postmarginal vein at least about twice as long as the stigmal, brown mid coxae and hyaline forewings. In both *epona* and *histrion* the mandibular bases are always orange or orange-brown, the postmarginal vein is at most only about 1.5x as long as the stigmal, the mid coxae are orange, except in uniformly dark brown specimens, and the forewings almost always have two faint longitudinal fuscous streaks (similar to *dactylopii*). The males are very similar to those of *dactylopii*, *nigrocincta*, and *nigra*, but can be separated with difficulty using the characters given in the key. It is possible that these characters are unreliable.

Leptomastix nigra Compere

(Figs 32–38, 66–67)

Leptomastix nigrum Compere 1938:324–5.
Holotype ♀, South Africa, examined, BMNH.

DIAGNOSIS. Female (length 0.50–2.10 mm): head and thorax varying from orange with frontovertex and axillae dark brown, to almost completely dark brown, blackish; paler specimens always with a dark-brown area adjacent to each eye, extending across occiput, towards foramen, mandibles always with bases dark brown, almost black; mesosternum always brown and mid coxa always dark-brown; wings hyaline; gaster mostly dark brown, occasionally mixed with orange basally; posterior ocelli clearly closer to occipital margin than to eye; antenna (Figs 32, 33) with F1 about as long as pedicel to about twice as long; forewing (Fig. 34) about 2.7x as long as broad; postmarginal vein about 1.5x as long as stigmal or slightly longer (Fig. 35); lineal calva interrupted by about 4 or 5 lines of setae, 3 lines in the smallest specimens; gaster as long as thorax; ovipositor as in Fig. 36. Male (length 0.50–1.50 mm): generally similar to female, but head and thorax always largely yellow; head with a dark-brown area on occiput adjacent to each eye which extends towards the foramen; median area of frontovertex brown; mandibles varying from orange to dark brown; mesoscutum orange laterally and brown to dark-brown medially; axillae dark-brown; scutellum orange to dark brown; metanotum and sides of

propodeum yellow; side and sternum of thorax mostly dusky-yellow; mid coxae occasionally hardly darkened; legs pale orange except mid and hind tibia which are brown dorsally; tarsi of fore and hind legs brownish, those of midlegs dusky-yellow except towards apex; funicle (Fig. 66, 67) clothed in setae about 3x as long as diameter of segments; five or six scale-like structures on base of clava; forewing (Fig. 37) about 2.5–2.8x as long as broad; lineal calva interrupted by about four lines of setae (Fig. 38); aedeagus a little more than one-third as long as mid tibia, each digitus with a pair of moderate apical teeth.

VARIATION. As mentioned in the diagnosis for the females there is a notable amount of variation in the coloration of the body, some specimens being largely yellow or pale orange, but almost without exception with the axillae dark brown whilst in others the head and thorax is more or less completely dark brown. We have also noted variation in the relative lengths of the antennal segments with the smallest specimens having F1 only about as long as the pedicel (Fig. 33) whilst in larger specimens it may be about twice as long (Fig. 32). On the other hand, apart from a slight variation in the relative lengths of the funicle segments (Figs 66, 67), males appear to vary little. Some males have the brown areas of the dorsum of the thorax more extensive than others with sometimes the whole of the scutellum almost completely dark brown.

HOSTS. *Leptomastix nigra* was recorded as a parasitoid of *Pseudococcus* sp. on oleander by Compere (1938). The host is very probably *Paracoccus burnerae*, as this mealybug on *Nerium oleander* has been recorded as the host for *Leptomastix nigra* by Prinsloo (1981). In addition, the species is recorded below from *Octococcus africanus* on *Stoebe cinerea*; *Octococcus* ?*minor* on *Athenasia trifurcata*; *Octococcus pentziae* on *Metalasia muricata* and *Pentzia globosa*; *Octococcus* on *Elytropappus*; ?*Octococcus* on *Stoebe* and *Elytropappus gnaphaloides*; *Paracoccus burnerae* on ?*Diospyros lycioides*; *Spilococcus* on *Metalasia muricata* and an unidentified mealybug on *Gazania*. Also recorded below in association with *Parasaissetia nigra* (Homoptera: Coccidae) on *Loranthus elegans*, *Saissetia somereni* (Coccidae) on grapefruit, and *Ceroplastes sp.* (Coccidae) on *Metalasia muricata*, but these are unlikely to be the true hosts.

DISTRIBUTION. Zimbabwe, Namibia, South Africa.

MATERIAL EXAMINED.

Type material. Holotype ♀ of *Leptomastix nigra*, **South Africa**, Tvl, Johannesburg, May 1937 (Compere) (BMNH). Paratypes: **South Africa**, 1 ♀, 2 ♂, Tvl, Johannesburg, ex mealybug, iv.1937 (Compere). Other material. **Zimbabwe**, 5 ♀, Salisbury, near Harare and Chishawasha, various dates iii.1979–vii.1982

(*Watsham*); **Namibia**, 1 ♀, Helmeringhausen, with *Parasaissetia nigra* on *Loranthus elegans*, T6925, v.1973 (*Prinsloo*); 2 ♀, 2♂, Otavi, ex mealybug on unidentified plant, T6928, 17.v.1973 (*Prinsloo*); 4 ♀, Karibib, ex mealybug, T6931, 16.ii.1978 (*Kok*); 6 ♀, 1♂, Otavi, ex mealybug, T6930, 24.ii.1978 (*Kok*); **South Africa**, 6 ♀ and 9♂, OFS, Edenville, OFS, ex *Octococcus pentziae* on *Pentzia globosa*, T2503, i.1970 (*Insley*); 17 ♀, C.P., Jeffreys Bay, ex mealybug in axils of *Gazania rigens*, T6916, 3.i.1980 (*Neser*); 19♂, C.P., Jeffreys Bay, ex mealybug in axils of *Gazania*, T6917, 3.i.1980 (*Neser*); 2 ♀, 7♂, Tvl, S. of Pongola, 27°23'S 30°38'E, ex *Saissetia somereni* on grapefruit, T6932, vii.1979 (*Kambourov*); 1 ♀, C.P., Witzenberg Vall., 3, 000ft, 19.i.1921 (*Turner*); 1 ♀, 1♂, C.P., Paarl District, ex ?*Octococcus* on *Stoebe*, T2736, x.1968 (*Insley*); 2 ♀, 2♂, C.P., Du Toits Kloof Pass, ex ?*Octococcus* sp. on *Elytropappus gnaphaloides*, T2795, x.1968 (*Insley*); 4 ♀, 1♂, Du Toits Kloof Pass, ex mealybug on *Metalasia muricata*, T2832, x.1968 (*Insley*); 2 ♀, 2♂, C.P., Villiersdoorp, ex mealybug on *Stoebe* sp., T3205, x.1969 (*Insley*); 8 ♀, 9♂, C.P., Swellendam, T3226, ex *Spilococcus* sp. on *Metalasia muricata*, x.1969 (*Insley*); 3 ♀, C.P., Stellenbosch, ex *Octococcus* ?*minor* on *Athenasia trifurcata*, T3231, x.1969 (*Insley*); 8 ♀, 15♂, C.P., Jeffreys Bay C.P., ex *Octococcus* sp. on *Metalasia muricata*, T3378, iii.1970 (*Insley*); 3 ♀, C.P., Garcia Pass, ex *Octococcus* sp., T3414, iii.1970 (*Insley*); 1 ♀, 4♂, C.P., Stellenbosch, on *Stoebe plumosa*, T5383, v.1978 (*Neser*); 4 ♀, 3♂, C.P., Kleimond, ex *Octococcus africanus* on *Stoebe cinerea*, T5475, viii.1978, (*Neser*); 2 ♀, 4♂, C.P., Floraberg, ex prob. *Octococcus* sp. on *Metalasia* sp., T5793, vi.1978 (*Neser*); 7 ♀, 1♂, C.P., Franschhoek Pass, ex *Octococcus pentziae* on *Metalasia muricata*, T5883, xii.1978 (*Neser*); 2 ♀, 15♂, C.P., D.F. Malan Airport C.P., ex *Octococcus* prb. *pentziae* on *Metalasia muricata*, T6114, iv.1979 (*Neser*); 3♂, C.P., D.F. Malan Airport, with *Ceroplastes* sp. on *Metalasia muricata*, 10.iv.1979 (*Neser*); 4 ♀, 1♂, C.P. Goudini, ex. prob *Octococcus* sp., on *Stoebe* sp., T6914 (*Neser*); 5 ♀, 1♂, C.P., Goudini, ex prob. *Octococcus* sp. on *Elytropappus rhinocerotis*, T6920, 25.ix.1979 (*Neser*); 5♂, CP, Algeria, Cadarberg, ex prob. *Octococcus* sp. on *Elytropappus* sp. cf. *gnaphaloides*, T6921 16.vii.1979 (*Neser*); 4 ♀, 1♂, C.P., Sir Lowry's Pass rd. nr. Somerset, ex *Octococcus* sp. on *Athenasia* sp., T6922, 29.viii.1979 (*Neser*); 6♂, Tvl, Irene, ex *Paracoccus burnerae* on ?*Diospyros lycioides*, T6927, 16.iii.1969 (*Insley*); 14 ♀, 15♂, C.P., Capetown, D.F. Malan Airport, ex *Octococcus* prb. *pentziae* on *Metalasia muricata*, T6230, vii.1980 (*Neser*); 2 ♀, 1♂, C.P., Gamtoos Sta., with *Ceroplastes* sp. on *Metalasia muricata*, T6933, 22.xi.1983 (*Grobbelaar*). Material in BMNH, PPRI.

COMMENTS. *Leptomastix nigra* is extremely close to *nigrocoxalis* and may represent different forms of that species. In general, the two can be separated by the relative width of the frontovertex and position of the ocelli in the females, with some degree of overlap between unusually small specimens of *nigrocoxalis* from India and specimens identified here as *nigra*. In *nigra* the frontovertex is almost always half as wide as the head or wider and OOL:OCL is at least 1.4, whilst in *nigrocoxalis* the frontovertex is less than half the head width except in the smallest specimens and OOL:OCL is less than 1.4. Other differences, such as coloration, may be unreliable, but in *nigra* the axillae and frontovertex are nearly always dark brown and in *nigrocoxalis* at most only the occipital margin is marked with brown and the axillae are always orange. The males can be separated only by the coloration of the frontovertex and axillae (see key), but this is probably unreliable.

Darker females of *Leptomastix nigra* are similar to *Leptomastix abyssinica*, both species having a general dark brown coloration and forewing about 2.7× as long as broad. They can be separated by the colour of the clypeal area and prosternum, and the number of lines interrupting the linea calva. In *nigra* the clypeal area and prosternum are dark brown and there are four or five lines of setae interrupting the linea calva (Fig. 34), whereas in *abyssinica* the clypeal area and prosternum are yellow and there are only two lines of setae interrupting the linea calva (Fig. 58). Paler females of *nigra*, those which are generally orange but have dark axillae, can be mistaken for *flava*, a species known from Mediterranean Europe and the Middle East. However, in *flava* the forewing has the postmarginal vein about as long as the stigmal vein and the mandibles are orange, whereas in *nigra* the postmarginal vein is at least 1.5× as long as the stigmal vein and the mandibles are dark brown. *Leptomastix nigra* can also be very similar to *herreni*, both species exhibiting the same range of colour variation (see comments under *herreni*)

Leptomastix dactylopii Howard

(Figs 39–46, 63, 70)

Leptomastix dactylopii Howard, 1885:23–24.

Lectotype ♀ (designated Noyes & Hayat, 1994), USA, USNM examined.

Leptomastix superba Silvestri, 1915:348. Holotype ♀, Eritrea, INMP examined. **Syn.n.**

Leptomastix longipennis Mercet, 1927:497–498. Lectotype ♀ (designated Noyes, 1981), Eritrea, IEEM, examined. Synonymized with *Leptomastix dactylopii* by Noyes & Hayat (1994).

Leptomastix bifasciatus Compere, 1938:323–325. Holotype ♀, Tanzania, examined. Synonymized by Noyes & Hayat (1994).

Paraleptomastix dactylopii (Howard); Mani, 1939:70–71.

Leptomastix tambourissae Risbec, 1952:16–19. Lectotype ♀ (designated Noyes & Hayat, 1994), Madagascar, MNHN, examined. Synonymized by Noyes & Hayat (1994).

[*Leptomastix flavus* Mercet; Risbec, 1951:103; Meyerdirk & Newell, 1979:72. Misidentification.]

DIAGNOSIS. Female (length 1.10–2.30 mm): body including gaster yellow to orange, moderately robust and stout; head with dark-brown area adjacent to each eye, extending across occiput towards foramen; mesopleuron yellow, concolorous with mid coxa; mesosternum dark-brown; wings more or less hyaline (Fig. 40), sometimes with two distinct fuscous longitudinal streaks (Fig. 41); position of posterior ocelli relative to eyes and occiput variable; F1 about 2× length of pedicel; forewing fairly wide, about 3× as long as broad (Figs 40, 41); postmarginal vein at least 1.5× as long as stigmal (Fig. 43); linea calva interrupted by at most two lines of setae (Fig. 42); gaster as long as thorax; ovipositor about 12× as long as gonostyli. Male (length 0.90–1.54 mm): generally similar to female, but posterior margin and dorsal part of pronotum and anterior margin of mesoscutum brownish; antenna (Fig. 63) clothed with long setae, each at least 4× as long as diameter of F1; basal two-thirds of clava with 9 or so scale-like structures present ventrally; aedeagus about half as long as midtibia; phallobase (Fig. 70) with elongate digiti, each with a pair of apical hooks.

HOSTS. *Leptomastix dactylopii* has been reared from many species of mealybugs. Ashmead (1900) and later Viereck (1916) first recorded *Planococcus citri* (as *Dactylopius destructor*) as its host whilst Mercet (1927) noted that the species (as *L. longipennis*) was a parasitoid of *Ferrisia virgata* and Compere (1938) recorded it from *Pseudococcus longispinus* as *Leptomastix bifasciatus*. *Leptomastix dactylopii* has also been recorded from *Birendracoccus saccharifolii* on sugarcane by Mani (1939), but this is a possible misidentification of *Leptomastix tsukumiensis*. Kerrich (1953) noted it as a parasitoid of *Planococcus vovae* (as *Pseudococcus inamabilis*) while Annecke & Insley (1971) recorded it from *Planococcus aemulor* on *Combretum splendens*. *Leptomastix dactylopii* has also been recorded from stem galls on *Tambourissa* sp. by Risbec (1952), from *Pseudococcus* sp. on guava by Compere (1938), *Pseudococcus bukbenis*, *Planococcus citri*, *Ferrisia virgata*, *Phenacoccus madeirensis*, *Pseudococcus longispinus* (= *adonidum*) and *Pseudococcus concavocerarii* by Donald (1956), *Planococcus kenya* on coffee (Noyes & Hayat, 1994), *Pseudococcus occiduus* on *Psidium guajava* by Annecke & Insley (1971), *Planococcoides njalensis* by Strickland (1951), *Planococcoides lamabokensis*

by Prinsloo (1983a), *Planococcus kraunhiae* in Japan by Tachikawa (1963a) and *Dysmicoccus brevipes* in Hawaii by Bartlett (1978). The parasitoid has been laboratory reared from the last host in Ghana by Anonymous (1953). Tachikawa (1963b) recorded *Leptomastix dactylopii* from *Phenacoccus gossypii* but this was based on a record of specimens reared from a mixed population of *Phenacoccus gossypii* and '*Pseudococcus kraunhiae*', the latter being a misidentification of *Planococcus citri* and therefore the most likely host. *Leptomastix dactylopii* has been reared from several mealybug species in the laboratory: *Phenacoccus gossypii*, *Phenacoccus solani*, *Pseudococcus calceolariae*, *Pseudococcus longispinus* and *Pseudococcus maritimus* by Bess (1939), *Pseudococcus comstocki* by Clancy (1944) and *Planococcus lilacinus* by Krishnamoorthy (1988). Manichote & Middlekauff (1967) noted that *Leptomastix dactylopii* would not attack *Spilococcus leucopogi* (= *cactearum*) in the laboratory. Recorded below from *Delotococcus* (= *Allococcus*) *quaesitus* on *Acacia* and *Planococcus ficus* on *Ficus carica* and an unidentified species of *Planococcus* on *Erythrina lysistemon*.

DISTRIBUTION. Senegal, Gambia, Sierra Leone, Ivory-Coast, Togo, Benin, Nigeria, Cameroon, Gabon, Uganda, Zimbabwe, Zambia, Kenya, Seychelles, South Africa, Mauritius, Canada (introduced), USA (introduced), Hawaii (introduced), Caribbean, Costa Rica, Chile, Brazil, Mediterranean Europe (introduced), Pakistan (introduced), India (introduced), Taiwan (introduced) and Australia (introduced).

MATERIAL EXAMINED.

Type material. *Leptomastix dactylopii*: lectotype ♀ on card point labelled '1170o Pars on *Dactylopius destructor* Oct.4.[18]84' 'Type 2649 U.S.N.M. (USNM)'. Paralectotypes 1♂, on single point, labelled '1170o, Oct.4.1884' 'Type No 2649 U.S.N.M.'; 1♀, same data but 14.10[18]84 (USNM). *Leptomastix superba*: holotype ♀ fragmented on a slide, labelled '*Leptomastix superbus* Silv. F Nefasit' (INMP). *Leptomastix longipennis*: lectotype ♀ on card labelled 'ex *Pseudococcus virgata*' 'Somalia Italiana' '*Leptomastix longipennis* Mercet' '*Leptomastix longipennis* Mercet Lectotype det. J.S. Noyes, 1979' (IEM). *Leptomastix bifasciata*: holotype ♀, **South Africa**, Uitenhage, ex *Pseudococcus longispinus* on oleander, 12.i.1937 (Compere) (BMNH). Paratypes: **Tanzania** (as Tanaganyika), 3♀, Bukoba, ex *Pseudococcus* on guava, 20.vii.1935 (Ritchie) (BMNH). *Leptomastix tambourissae*: lectotype ♀, labelled 'Elevage du 1.4.50 Eclos 20.6.50 No G20P galles de tege des *Tambourissa* sp. d'Ambatoloana (R.P.)' 'Encyrtidae *Leptomastix tambourissae* Risbec T' (MNHN). Paralectotypes: 3♀, 1♂ (not four as stated by Risbec, 1952) remounted from same slide

onto card rectangles as lectotype (MNHN, BMNH).

Non-type material. No data, 1 ♀ (misidentified as *L. flava* by Risbec); **Senegal**, 1 ♀, 3 ♀, Bambey, ex coccid, (*Risbec*); 2 ♀, Bambey, ex *Pseudococcus* on *Prosopis*, 12.x.1945 (*Risbec*) (misidentified as *L. flava* by Risbec); **Gambia**, 1 ♂, Bakan, i.78 (*Huggert*); 2 ♂, Fajara, i.78 (*Huggert*); **Sierra Leone**, 1 ♂, Njala, ex mealybug on *Cassia javanica*; **Ivory Coast**, 7 ♀, 1 ♂, Lamto, 6°13'N 5°02'W, MT/YPT, xi.1988 (*Noyes*); 2 ♂, Korhogo, 18–21.iii.1984 (M. Matthews); 1 ♀, 3 ♂, Gagnoa, 2–5.iii.1984 (*Matthews*); 1 ♀, 3 ♂, Bouaffle; **R.P. Benin**, 5 ♀, 7 ♂, 15Km N. Cotonou, Abomey-Calavi, MT, xii.1988 (*Noyes*); **Togo**: 2 ♀, Kpalime, xii.1988 (*Noyes*); **Nigeria**, 3 ♀, 1 ♂, Kaduna St. 20km N., 8.xi.1987, (*Noyes, Neuenschwander*); 5 ♀, 5 ♂, Ibadan, IITA compound, MT/YPT, xi.1987 (*J.S.Noyes*); 6 ♂, Zaria, 8.xi.1987 (*J.S. Noyes*); **Cameroun**, 2 ♀, 2 ♂, S.W. Cameroun, Musone, Lake Mboandong, 11.xii.1981 (*Compton*); 2 ♀, 3 ♂, Victoria Bot. Gdns, 6.xii.1981, (*Compton*); 1 ♀, Nyassosso, Mt Koupe, 8.i.1982 (*Compton*); **Gabon**, 2 ♀, 2 ♂, Foret de la Mondah, 15–25km N.Libreville, 25.xi–3.xii.87 (*Noyes*); **Uganda**, 1 ♀, Bujumbura, iv.1939 (*Taylor*); 3 ♀, 4 ♂, ex *Pseudococcus kenyae* on *C. arabica*, 12.iv.1938 (*Melville*); **Zimbabwe**, 6 ♀, 3 ♂, Salisbury, i.1979 (*Watsham*); 6 ♀, 2 ♂, Harare, Chishawasha, xii.1982 (*Watsham*); **Zambia**, 9 ♀, 13 ♂, 15km E.Lusaka, 27.xi–29.xii.1979 and 11–19.ii.1980 (*Beaver*); **Kenya**, 1 ♀, Nairobi, ii.1982, Brit. Mus. 1982–347; 3 ♂, Gazi, viii.1982 (*Barnett*); **South Africa**, 18 ♀, 29 ♂, Cape Province, 10–22.xii.1930, Brit. Mus. (*Turner*); 1 ♀, Mossel Bay, April.1921, 1921–210, (*Turner*); 3 ♀, Blyderivierspoortdam Nat. Reserve, 29°32'5, 30°47'E, 25–26.x.1984, (*Prinsloo*); 1 ♀, Cape Province, Grahamstown, i.1979 (*Prinsloo*); 1 ♀, 1 ♂ Letaba, ex suction trap on citrus, T2504, xi.1966 (*Catling*); 4 ♀, 1 ♂ Cape Province, Ashton, ex mealybug on *Ficus carica*, T5306, iii.1978 (*Neser, Kok & Urban*); 1 ♀, Okahandja, 2–18.iii.1928; 1 ♀, Transvaal, Roodeplaat, nr Pretoria, ex *Allococcus quaesitus* on *Acacia* sp., T4292, iii.1992, (*Insley*); 1 ♂, Mogol Nature Reserve, Ellisras Dist. 23°58'S 27°45'E, 27–29.ii.1984 (*Prinsloo*); 1 ♂, Entabeni Forest Res. Soutlanberg, 25°00'S 30°16'E, 3–7.xi.1980 (*Prinsloo*); 1 ♂, C.P., Jeffreys Bay, with unidentified coccoidea on *Euclea* sp., T6918, 13.i.1980 (*Neser*); 1 ♂, Natal, Umzinto, ex *Planococcus* sp. on *Erythrina lysistemon*, T4135 i.1972 (*Insley*); 2 ♀, C.P., De Dooms, ex *Planococcus ficus* on *Ficus carica*, T6919; **Mauritius**, 2 ♂, Rose Hill, 29.ix.32 (*Mamet*). Material in BMNH, PPRI, MNHN.

Voucher material. **Israel**, 1 ♀, California, Riverside, lab culture, ex *Planococcus citri*, 30.viii.1974, R74–81–1, shipped, reared and released in California, Porterville by Meyerdirk as *Leptomastix flavus*; 1 ♀, 1 ♂, Negev, lab reared, California, Porterville, ex comstock mealybug, Warkentin, R76–42, 17.v.1976,

shipped and released in California, Porterville, by Meyerdirk as *Leptomastix flavus*; 1 ♂, Sde Boker, lab culture, California, Porterville, ex *Planococcus vitis* on grape, R–75–34–2B, 30.iv.1975, shipped, reared and released in California, Porterville by Meyerdirk as *Leptomastix flavus*. Material in UCR and part of a longer series of voucher material of the species released in California from Israel and referred to by Meyerdirk & Newell (1979) as *Leptomastix flava*.

COMMENTS. The holotype of *Leptomastix superba* is mounted on a slide and in very poor condition, but it is clearly the same as *Leptomastix dactylopii* and therefore we have no hesitation in treating the two names as synonymous.

Females of *Leptomastix dactylopii* are similar in general appearance to *Leptomastix tsukumiensis*, both species having similar habitus and generally yellow coloration of body and mid coxae (see comments under *tsukumiensis*). The males are very similar to those of *nigrocoxalis*, *nigrocincta*, and *nigra* and can be difficult to separate. Males of these four species can be separated using the characters given in the key, although it is likely that these characters are not totally reliable.

Leptomastix jonesi Noyes sp. n.

(Figs 47–48, 64)

DIAGNOSIS. Female (length 1.58–2.24 mm): body mostly yellow, but with temples part of occiput, mesosternum, mid coxae externally and occasionally mesopleuron brown; gaster orange brown; posterior ocelli about equidistant from eye and occipital margins; antenna with F1 about 3× as long as pedicel; forewing about 3× as long as broad, with a longitudinal fuscous streak along anterior wing margin from apex of venation and another parallel streak in disc (similar to Fig. 47); postmarginal vein about 2× as long as stigmal and slightly longer than marginal; linea calva interrupted by 4 or 5 lines of setae. Male (length 1.77–1.83 mm): generally similar to female, antenna (Fig. 64) clothed with long setae, each at least 3× as long as diameter of F1; basal two-thirds of clava with 9 or 10 slender, elongate and straight scale-like structures ventrally; forewings (Fig. 47) with two fuscous longitudinal streaks as in female; postmarginal vein about 1.5× as long as stigmal (Fig. 48); aedeagus less than one-third as long as midtibia; phallobase with elongate digiti, each with three apical hooks.

FEMALE (HOLOTYPE). Length 2.21 mm. Head orange with a small brown spot on interantennal prominence dorsally, temples and occiput laterally dark brown; radicle dark brown; scape brown with ventral margin yellow; pedicel brown; flagellum dark brown; dorsum of thorax mostly orange with neck of pronotum and extreme anterior part of mesoscutum

brown; mesosternum and metanotum dark brown, remainder of thorax orange; legs orange except for mid coxae which are dark brown laterally; gaster orange-brown dorsally, orange laterally and ventrally.

Head with inner eye margins subparallel, diverging slightly ventrally; posterior ocelli about equidistant from eye and occipital margins; scape about 5.5× as long as broad; F1 3× as long as pedicel; clava very slightly shorter than F1 and 1.6× as long as F6; pedicel about 2× as long as broad. Relative measurements: HW 50.5; HH 44; FV 21; SL 33.5; SW 6.

Mesoscutum and scutellum with coriaceous sculpture; forewings 3× as long as broad, with postmarginal vein very nearly 2× as long as stigmal and a little longer than marginal; linea calva interrupted by 4 or 5 lines of setae; hindwing 4.5× as long as broad.

Gaster slightly longer than thorax, with ovipositor hidden. Relative measurements: OL 38.5, GL 5.5 [MT 84].

MALE. See diagnosis. Relative measurements (specimen 1): HW 93, FV 48, POL 17, OOL 10.5, OCL 7, EL 53, EW 35, MS 23, SL 52, SW 11.5; (specimen 2): FWL 148, FWW, 54.5, AL 22, MT 80.

VARIATION. Very little, but the female excluded from the type series has the mesopleuron brown instead of orange.

HOSTS. Unknown.

DISTRIBUTION. South Africa.

MATERIAL EXAMINED.

Type material. Holotype ♀ (slide-mounted), **South Africa**, Cape Province, Mossel Bay, xii.1921 (*Turner*). Paratypes: 1♂, same data as holotype; 1♀, Cape Province, Mossel Bay, 18–30.xi.1921 (*Turner*); 1♂, Cape Province, Mossel Bay, vi–vii.1930 (*Turner*); 3♀, Cape Province, Somerset East, 1–26.i.1931 (*Turner*). Holotype in BMNH, paratypes in BMNH and PPRI.

Non type material. **South Africa**, 1♀, Pondoland, Port St John, ix.1923 (*Turner*)

COMMENTS. *Leptomastix jonesi* is superficially very similar to *dactylopii* and females of the two species can be difficult to separate with certainty. In *jonesi* the mid coxae are partially brown, the linea calva is interrupted by at least 4 lines of setae, the ovipositor is less than half as long as the mid tibia and only about 7× as long as the gonostyli whereas in *dactylopii* the mid coxae are completely orange or yellow, the linea calva is generally interrupted by only 2 lines of setae, the ovipositor is at least about 10× as long as the gonostyli and more than half as long as the mid tibia. The males of *jonesi* are fairly easy to separate from those of *dactylopii* and other species of the genus by the scale-like structures at the base of the clava being very elongate, slender and straight (Fig. 64). In the

only other species where these structures are slender (*herreni*) they are relatively short and apically strongly curved (Fig. 61).

The species is named in honour of Mr Peter Jones for his contribution to children's education.

Leptomastix nigrocincta Risbec

(Figs 49–55)

Leptomastix nigrocincta Risbec, 1959:27. Lectotype ♀, designated by Noyes & Prinsloo (1988), Madagascar, MNHN, examined.

Leptomastix lyciae Noyes & Hayat, 1994:275–278. Holotype ♀, India, BMNH, examined. **Syn.n.**

DIAGNOSIS. Female (length 0.91–2.20 mm): body including base and venter of gaster yellow to orange, dorsum of gaster at least partially dark brown; head always with a dark-brown area on temple adjacent to each eye extending a short way onto occiput towards foramen; base of mandibles yellow; mesopleuron generally orange, rarely dark brown (see below); prosternum and mesosternum adjacent to coxae usually with a distinct brown tinge; mid coxae always dark-brown or black; propodeum dark-brown above coxae; wings hyaline or with a pair of longitudinal fuscous streaks (Fig. 51); position of posterior ocelli variable (see below), but usually ocelli about equidistant from eye and occipital margin; antenna (Figs 49, 50) with F1 about 1.7 to 2.3× as long as pedicel; forewing (Fig. 51) about 3× as long as broad; postmarginal vein slightly longer than marginal and at least nearly twice as long as stigmal (Fig. 53); linea calva interrupted by two or three lines of setae, rarely by four (Fig. 52); gaster as long as thorax; ovipositor about 6.5× as long as gonostyli. Male (length 0.80–1.59 mm): similar to female but darker, although mid coxae not or hardly dusky; funicle clothed in long setae, longest about 4× as long as diameter of F1; a line of six or so scale-like structures ventrally on base of clava; forewing (Fig. 54) about 2.5× as long as broad; postmarginal vein distinctly longer than marginal which is subequal in length to stigmal (Fig. 55); aedeagus about one-third length of mid tibia.

VARIATION. Very little variation has been noted in material from India, China and the African mainland, but specimens from Madagascar exhibit a striking degree of variation in coloration and some minor morphological characters. In Malagasy females the area between the toruli and eyes is sometimes marked with black as is the median area of the pronotum; the mesoscutum may have a wedge-shaped dark brown area; the tegulae vary from almost completely orange to completely dark brown or black; the axillae may be dark brown laterally; the mesopleuron is sometimes almost entirely black. In the Malagasy material the

frontovertex varies from slightly less than two-fifths head width to nearly half with a corresponding variation in the relative position of the posterior ocelli. In some specimens the posterior ocelli are distinctly nearer the occipital margin whilst in others they are distinctly nearer the eyes with the angle formed varying from about 50° to only slightly less than 90°. In the Malagasy material the relative width of the funicle segments varies with some specimens having slender antennae with F6 about 2.5× as long as broad and others having slightly broader segments with F6 slightly less than 1.5× as long as broad (compare Figs 49, 50); the postmarginal vein varies from about 2.0–2.5× as long as the postmarginal vein. Males from Madagascar exhibit a similar, but less marked range of variation.

HOSTS. *Leptomastix nigrocincta* was recorded as a parasitoid of mealybugs on *Hibiscus* sp. by Risbec (1959). Recorded in India from *Coccidohystrix insolita* and *Phenacoccus* sp. (probably misidentification of *C. insolita*) on aubergine, *Solanum melongena* L. (Noyes & Hayat, 1994).

DISTRIBUTION. Togo, Zambia, Madagascar, India, China.

MATERIAL EXAMINED.

Type material. Lectotype ♀ of *nigrocincta*: 'Elevage du 5.12.50 No 810 Eclose du 20.12.50 Parasites des cochenilles sur le feuille d'Hibiscus sp. de Tsimbazaza (R.P.) Inst. Scient. Madagascar' 'Leptomastix nigrocincta', remounted on a card rectangle and labelled 'LT ♀' on ventral side of card (MNHN). Paralectotypes: 6 ♀, 3 ♀, remounted on card rectangles, same data as lectotype. Lectotype of *nigrocincta* in MNHN, paralectotype in MNHN and BMNH. Holotype ♀ of *lyciae*: **India**, Delhi, IARI area, x.1979 (*Boucek*). Paratypes: 53 ♀, 13 ♂ from **India** and **China** as detailed in Noyes & Hayat (1994). Holotype of *lyciae* in BMNH, paratypes in BMNH, USNM, CNC, AMU, PPRI, QM.

Non-type material. **Togo**, 10 ♀, 10km NW Kpalime, xii.1988 (*Noyes*); **Zambia**, 1 ♀, Lusaka, 6–12.xi.1979 (*Beaver*); **Madagascar**, 1 ♂, Tananarive, Angavokely for sta., 28km E. Angavokely, 24.iv.1983 (*Noyes*) 2 ♀, 2 ♂, Perinet, 27.iv.–3.v. 1983 (*Noyes, Day*); 51 ♀, 70 ♂, Tulear, Berenty 12km, NW Amboasary, 5–15.v.1983 (*Noyes, Day*); 3 ♀, 11 ♂, Tulear, Bereboka 60km, N.E. Morondova, 18–23.v.1983 (*Noyes, Day*); 1 ♀, 20km S. Mandrivazo, 24.v.1983 (*Noyes, Day*). Material in BMNH, PPRI.

COMMENTS. As we are unable to find any consistent differences to discriminate between the type series of *lyciae* and the long series of *nigrocincta* from Madagascar, we are here treating the two species as synonymous.

Females of *Leptomastix nigrocincta* can be very

similar to *nigrocoxalis* and might be mistaken for that species. In general, both species have similar coloration with the body generally yellowish with the mid coxae partially dark brown. The two species can be separated by the coloration of the base of the mandibles and number of lines of setae interrupting the linea calva. In *nigrocincta* the mandibles are entirely yellowish and the linea calva is interrupted by at most three lines of setae (very rarely four), whilst in *nigrocoxalis* the bases of the mandibles are dark brown and the linea calva is interrupted by four or more lines of setae. In general, males are very similar to those of *nigrocoxalis*, *nigrocincta*, and *nigra* and can be difficult to separate. They can be separated using the characters given in the key, although it is likely that these characters are not totally reliable. Females of *Leptomastix nigrocincta* can also be similar to those of *Leptomastix africana*, both species having the posterior ocelli closer to eyes than occiput, F1 at least 2× as long as pedicel; mesopleuron brown, postmarginal vein distinctly longer than stigmal, and only two lines of setae interrupting the linea calva. They differ in general coloration, and relative length of postmarginal vein. In *nigrocincta* the body is largely pale orange and the postmarginal vein is about 2.6× as long as the marginal vein and about 3× as long as the stigmal vein, whereas in *africana* the body is entirely dark brown and the postmarginal vein is twice as long as either the marginal or stigmal veins. At a glance, females of some colour forms of *nigrocincta* might be confused with those of *herreni*, but the two species can be separated easily on the relative length of the postmarginal vein. In *nigrocincta* the postmarginal vein is at least nearly twice as long as the stigmal (Fig. 53) whilst in *herreni* it is about as long as the stigmal (Fig. 18). *Leptomastix nigrocincta* might also be mistaken for *histrion* or *epona*, both of which are Palaearctic and currently unknown in the Afrotropical region. Females of *nigrocincta* differ from those of the two other named species in always having the postmarginal vein at least nearly twice as long as the stigmal, the mid coxae dark brown and the linea calva generally interrupted by not more than three lines of setae, whereas in *histrion* and *epona* the postmarginal vein is only about 1.5× as long as the stigmal and the mid coxae are yellow, except in the darkest specimens where the linea calva is interrupted by at least five lines of setae.

Leptomastix abyssinica Compere

(Figs 56–60)

Leptomastix abyssinica Compere, 1931:267–9.

Holotype ♀, Eritrea, not examined, USNM.

DIAGNOSIS. Female (length 1.60–2.40 mm); body including gaster generally brown to dark-brown; head

with inner eye margins, genal area and area below toruli yellow; antennae dark brown with ventral margin of scape yellow or translucent; prosternum and fore coxae yellow; mid and hind coxae orange-brown; wings hyaline; posterior ocelli about equidistant from eye and occipital margins; antenna (Fig. 56) with F1 about 2.5× length of pedicel; forewing (Fig. 57) about 2.9× as long as broad, with postmarginal vein about 1.75× as long as stigmal (Fig. 59); linea calva interrupted by 2 lines of setae (Fig. 58); gaster as long as thorax; ovipositor about 10× as long as gonostyli. Male (length 1.30–1.70 mm): generally similar to female but for antennae and genitalia; yellow coloration of head more extensive than in female; antennae with about 10 scale-like structures ventrally on base of clava; forewing (Fig. 60) about 2.5× as long as broad; linea calva interrupted by only a single setae; aedeagus about one-third as long as mid tibia, each digitus with two long apical teeth.

HOSTS. *Leptomastix abyssinica* has been recorded from *Planococcus citri* on *Olea chrysophylla* (Compere, 1931, 1938).

DISTRIBUTION. Eritrea.

MATERIAL EXAMINED.

Type material. Paratypes: **Eritrea**, 11 ♀, 3 ♂, Nefasit, ex *Pseudococcus citri* on *Olea chrysophylla*, iii.1930 and iv.1930 (Compere); 1 ♀, Nefasit, ex *Pseudococcus citri* on *Olea chrysophylla*, iv.1930 (Compere); 3 ♀, 2 ♂, Nefasit, ex *Pseudococcus* No 4630 on *Olea chrysophylla*, 15.iv.1930 (Compere); 1 ♂, Nefasit, ex *Pseudococcus* No 4630 on *Olea chrysophylla*, 16.iv.1930 (Compere); 1 ♀, Nefasit, on window, out of mealybug, 31.iii.1930 (Compere). Material in BMNH and UCR.

Non type material. **Eritrea**, 5 ♂, Nefasit, ex *Pseudococcus* No 4630 on *Olea chrysophylla*, 11.iv.1930 (Compere); 4 ♂, Nefasit, ex *Pseudococcus* No 4630 on *Olea chrysophylla*, 10.iv.1930 (Compere); 1 ♀, Ezdaclesan, ex *Croton macrostachys*, 1.v.1930 (Compere); 5 ♀, 1 ♂, Nefasit, ex *Pseudococcus citri* (Compere). Material in UCR.

COMMENTS. *Leptomastix abyssinica* is close to *Leptomastix africana*, females of both species having similar dark-brown general coloration, the forewing about 2.7–2.9× as long as broad and two lines of setae interrupting the linea calva. They differ by the colour of the scape, lower face, prosternum and forelegs, position of posterior ocelli in relation to occipital margin and relative length of the clava. In *abyssinica* the scape is yellow ventrally, the lower face, prosternum and fore coxae are yellow, the posterior ocelli are equidistant from the eye and occipital margins and the clava is longer than F1 (Fig. 56), whereas in *africana* the scape is entirely brown, the prosternum and coxae are dark brown, the posterior ocelli are nearer the

occipital margin and the clava is shorter than F1 (Fig. 22). Males of the two species can be separated by colour as in the female. *Leptomastix abyssinica* might also be mistaken for *Leptomastix nigra* (see comments under *nigra*).

HOSTS OF AFRICAN SPECIES OF *LEPTOMASTIX*

* extralimital record

? doubtful record

! laboratory rearing

HEMIPTERA

Coccidae

Parasaissetia nigra (Nietner) (= *Saissetia nigra*) – ?**nigrocoxalis*

Saissetia nigra, see *Parasaissetia nigra*

Dactylopiidae

Dactylopius destructor, see *Planococcus citri* (Pseudococcidae)

Margarodidae

Icerya aegyptiaca (Douglas) – **nigrocoxalis*

Pseudococcidae

Allococcus quaesitus, see *Delottococcus quaesitus*

Birendracoccus saccharifolii (Green) (= *Phenacoccus saccharifolii*) – ?**dactylopii*

Coccidohystrix – **nigrocoxalis*

Coccidohystrix insolita (Green) – **nigrocincta*, **nigrocoxalis*

Delottococcus quaesitus (Brain) (= *Allococcus quaesitus*) – *dactylopii*

Dysmicoccus brevipes (Cockerell) – **dactylopii*

Ferrisia virgata (Cockerell) – *dactylopii*, **tsukumiensis*

Maconellicoccus hirsutus (Green) – *nigrocoxalis*

Nipaeoccus – **nigrocoxalis*

Nipaeoccus graminis (Maskell) – *nigrocoxalis*

Nipaeoccus viridis (Newstead) – *nigrocoxalis*

Octococcus – *herreni*, *africana*, *nigra*

Octococcus africanus (Brain) – *nigra*

Octococcus minor De Lotto – *nigra*

Octococcus pentziae Hall – *herreni*, *nigra*

Paracoccus burnerae (Brain) – *nigra*

Phenacoccus – **nigrocincta*

Phenacoccus gossypii Townsend & Cockerell – !?**dactylopii*

Phenacoccus madeirensis Green – *dactylopii*

Phenacoccus saccharifolii, see *Birendracoccus saccharifolii*

Phenacoccus solani Ferris – !*dactylopii*

Planococcoides njalensis (Laing) – *dactylopii*

Planococcoides lamabokensis Balachowsky & Ferrero – *dactylopii*
Planococcus – *dactylopii*
Planococcus aemulor De Lotto – *dactylopii*
Planococcus aetri (Risso) (= *Dactylopius destructor*) –
abyssinica, *dactylopii*, **nigrocoxalis*
Planococcus ficus (Signoret) – *dactylopii*
Planococcus kenya (Le Pelley) – *dactylopii*
Planococcus kraunhia (Kuwana) – **dactylopii*
Planococcus lilacinus (Cockerell) – *dactylopii*
Planococcus vovae (Nasonov) – **dactylopii*
Pseudococcus – *dactylopii*, *nigra*, *nigrocoxalis*
Pseudococcus adonidum, see *Pseudococcus*
longispinus
Pseudococcus bukbenensis Laing – *dactylopii*
Pseudococcus calceolariae (Maskell) – !*dactylopii*
Pseudococcus comstocki (Kuwana) – !*dactylopii*
Pseudococcus concavocerarii James – *dactylopii*
Pseudococcus inamabilis, see *Planococcus vovae*
Pseudococcus longispinus (Targioni Tozzetti) (= *Pseudococcus adonidum*) – *dactylopii*
Pseudococcus occidius De Lotto – *dactylopii*
Rastrococcus cappariae Avasthi & Shafee –
 **nigrocoxalis*
Rastrococcus iceryoides (Green) – **nigrocoxalis*
Spilococcus – *nigra*

NEUROPTERA

Nimboa basipunctata Withycombe – ?**nigrocoxalis*

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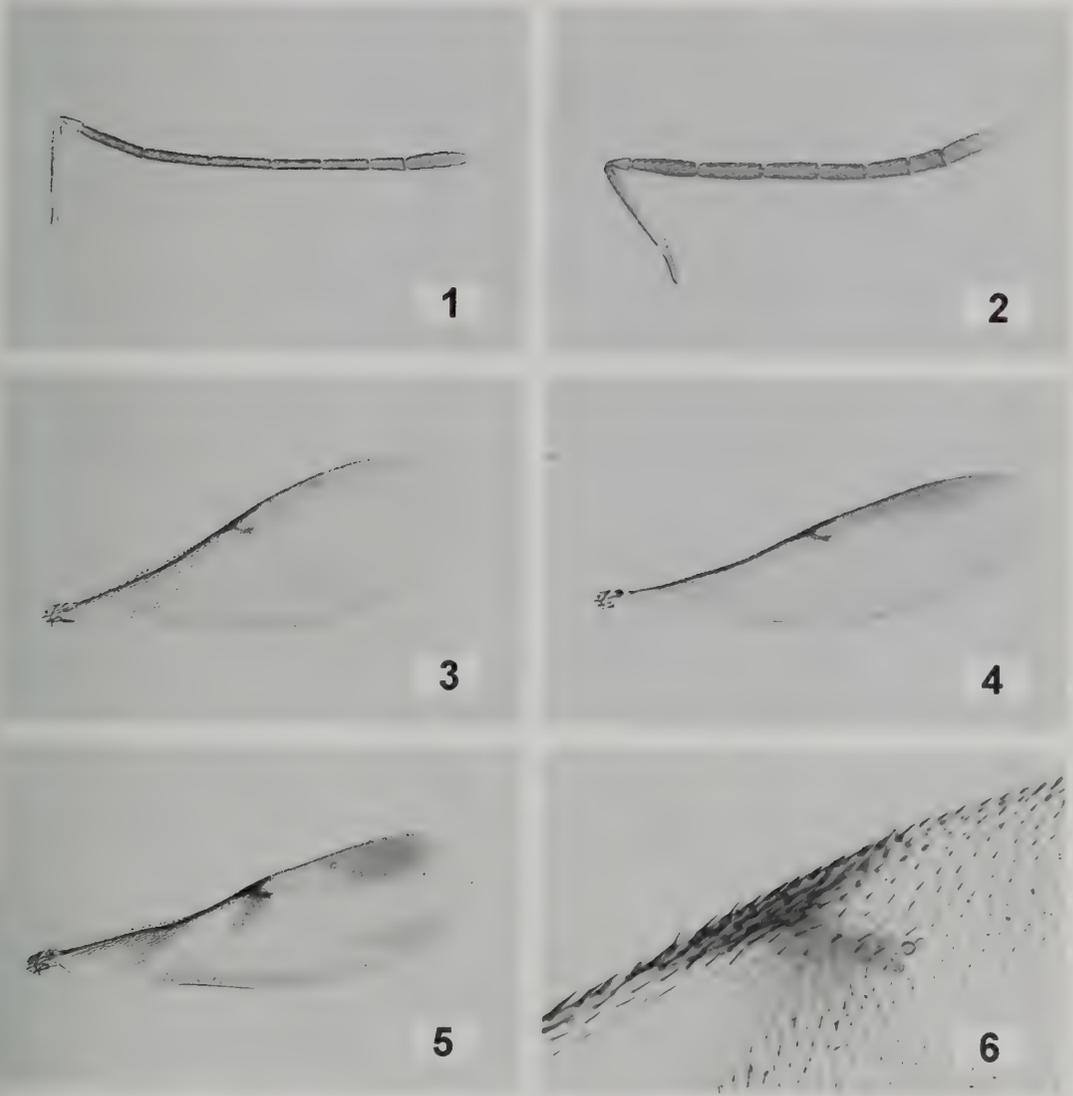
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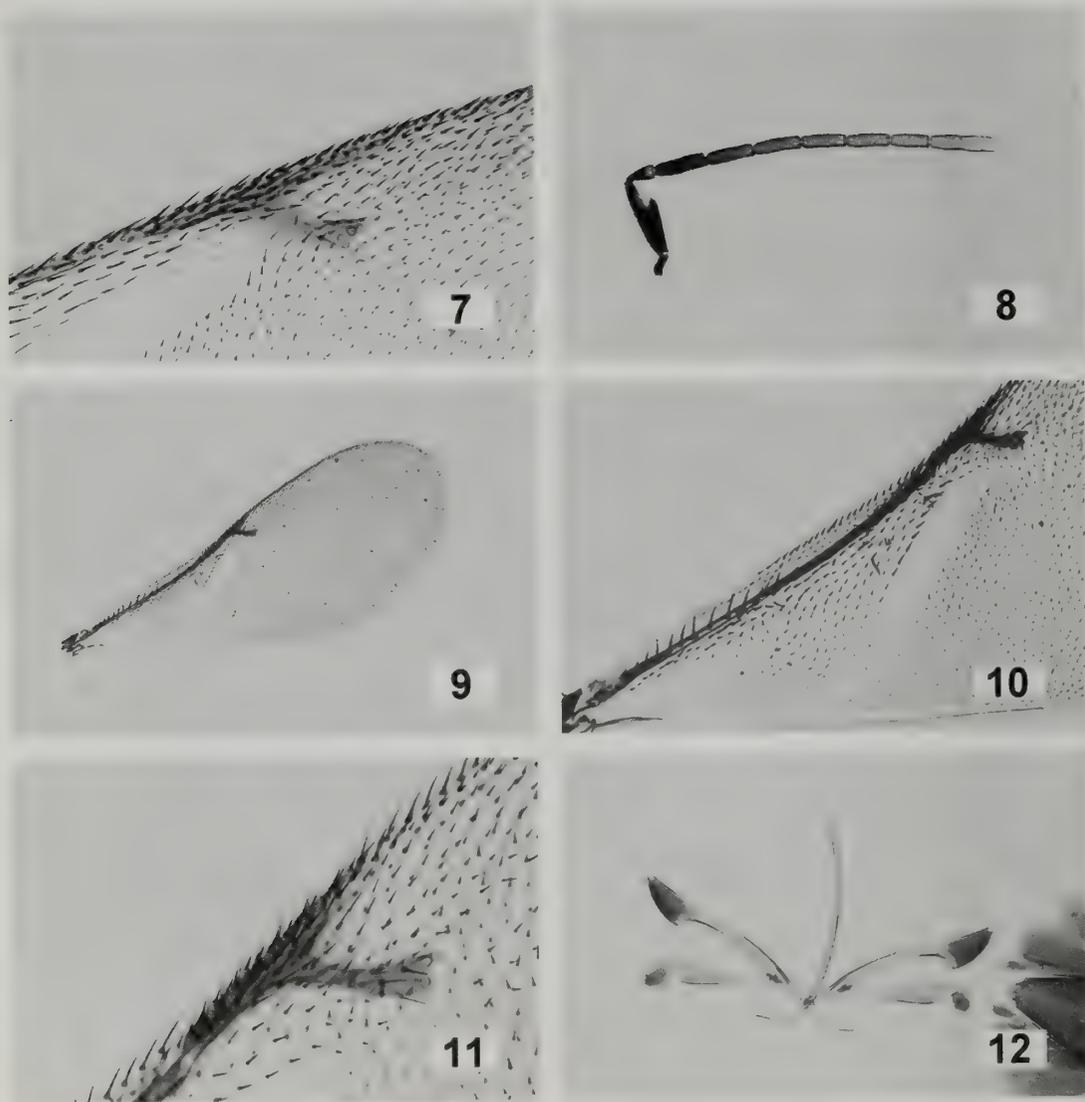
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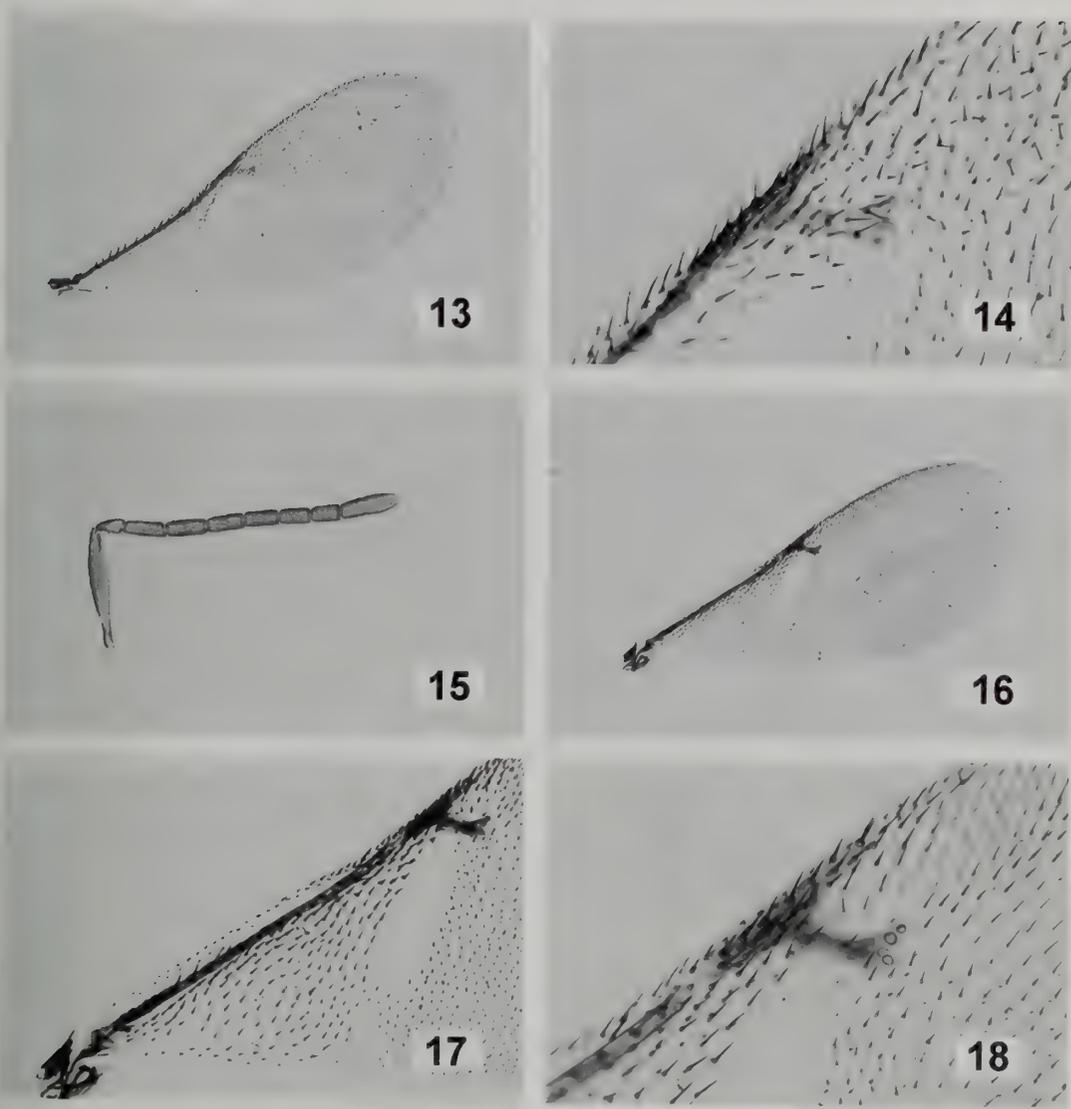
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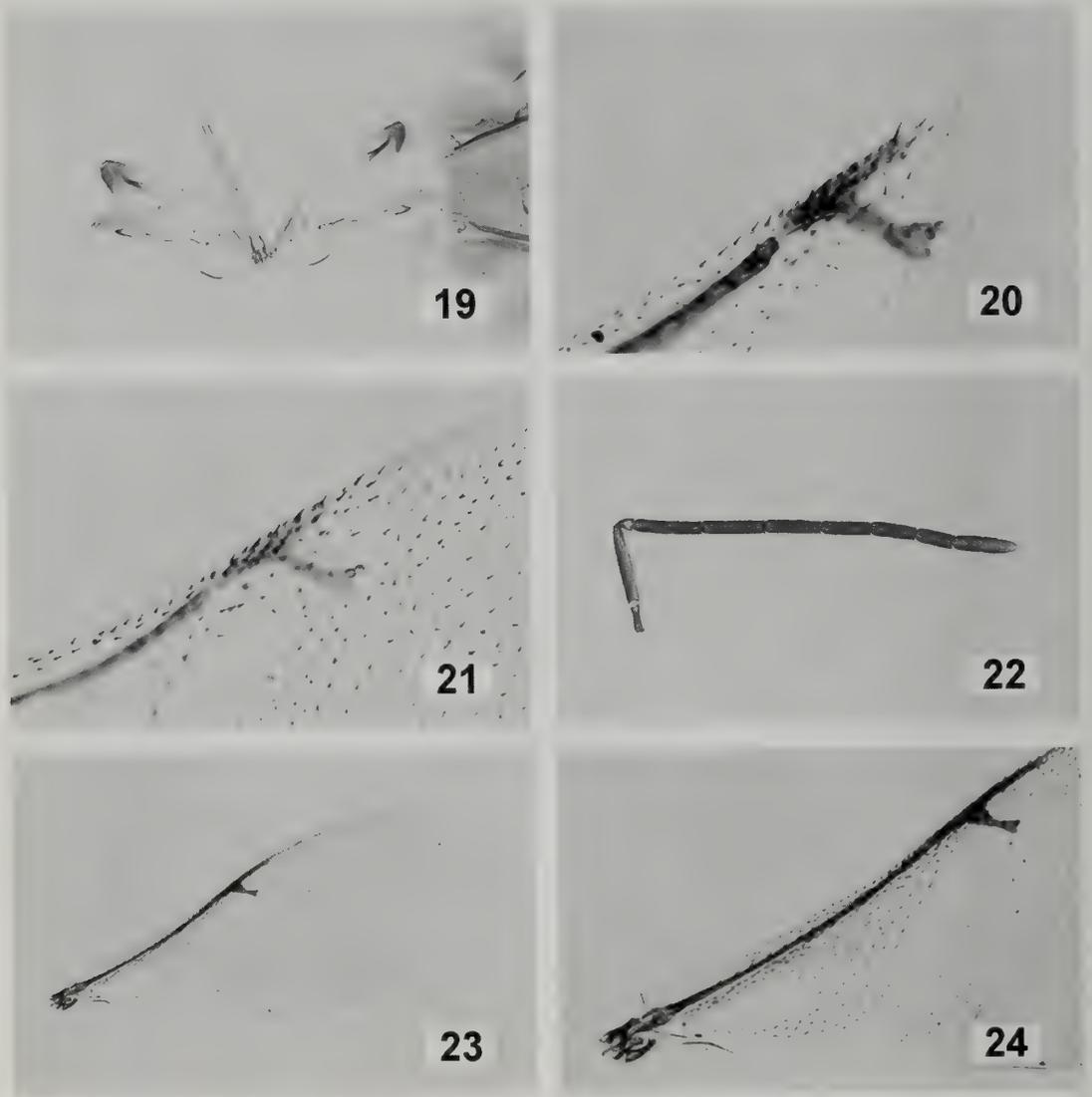
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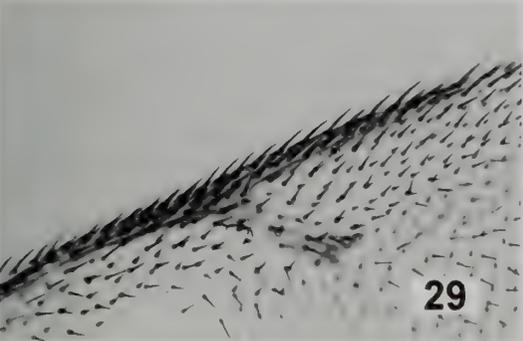
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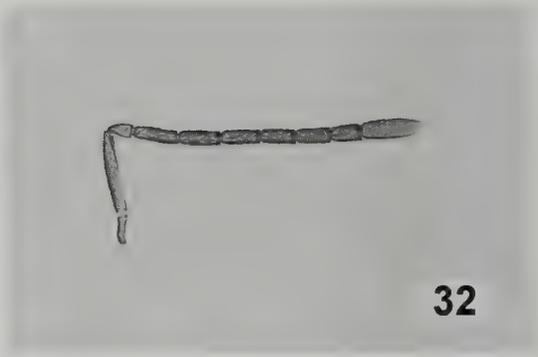


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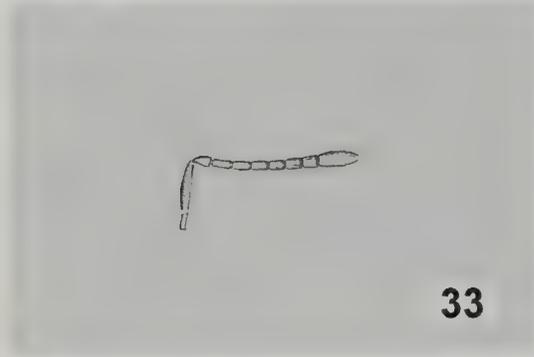
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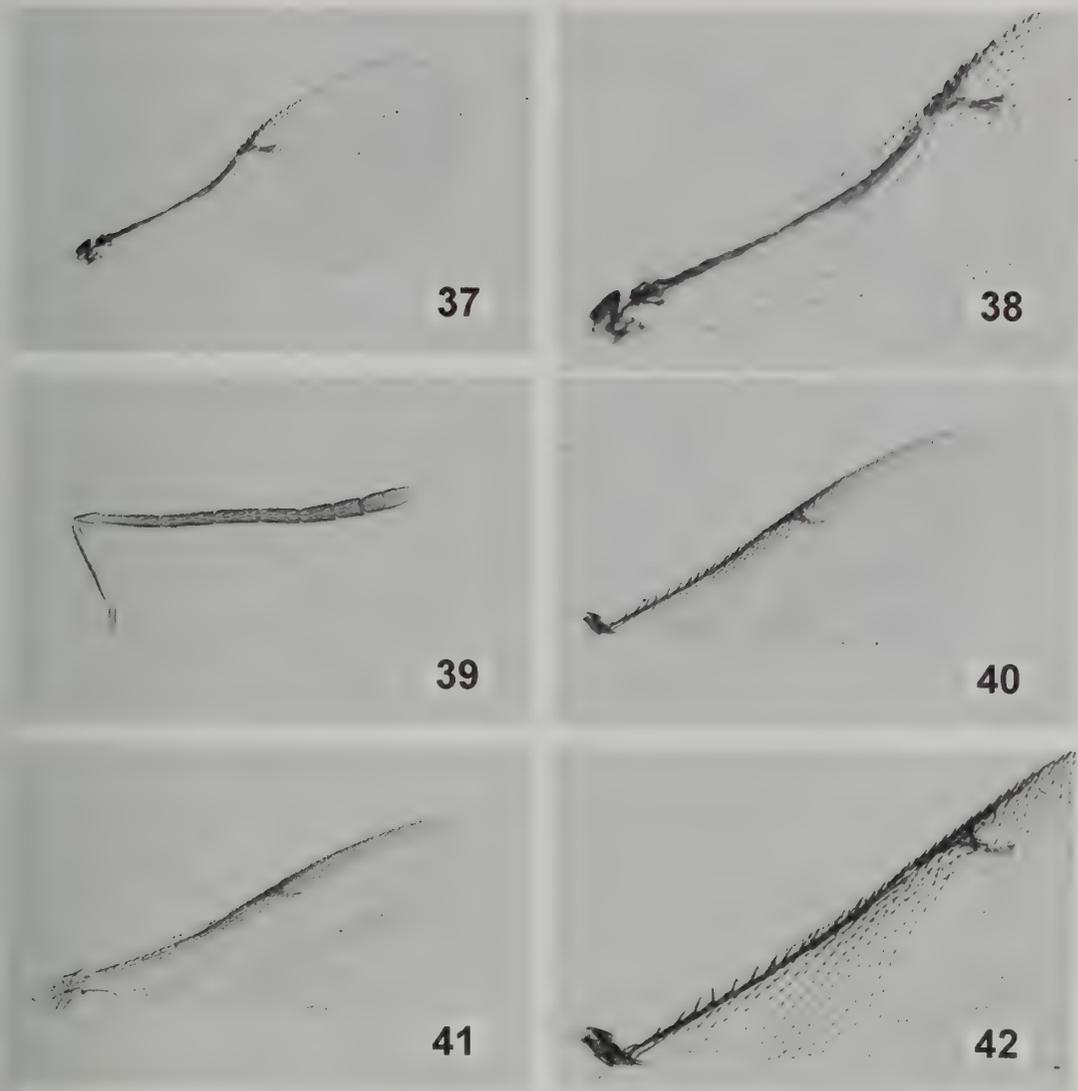


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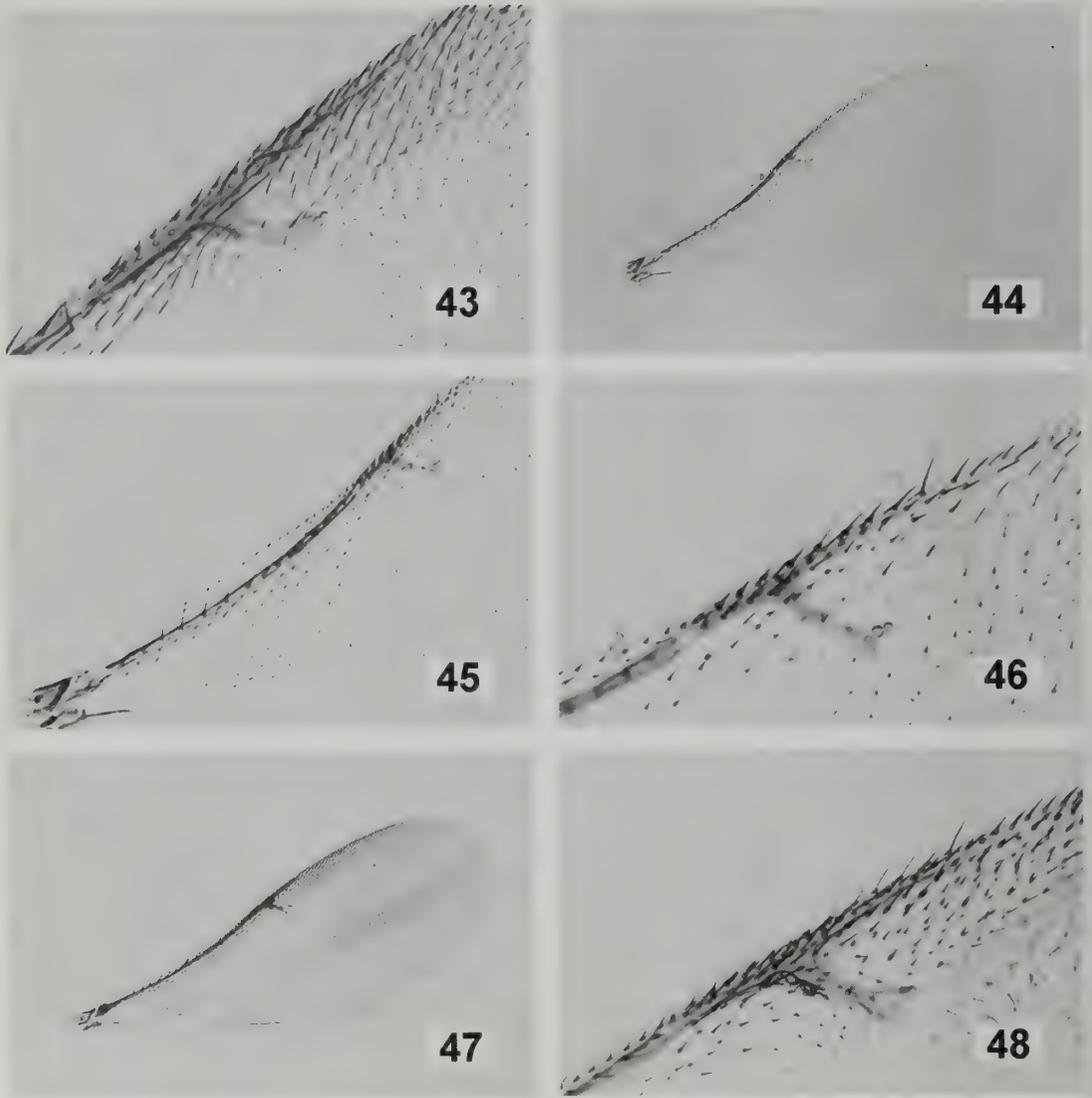


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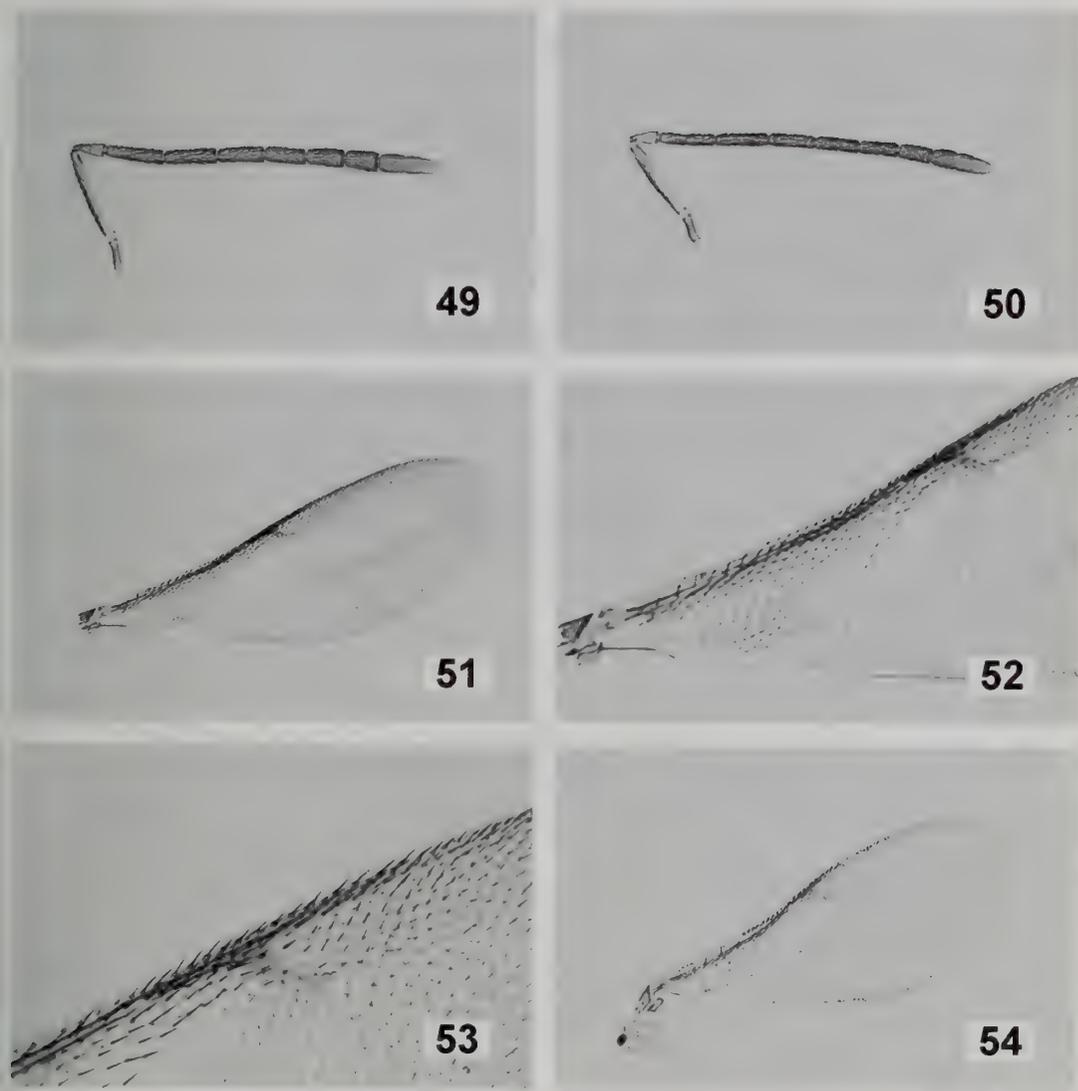
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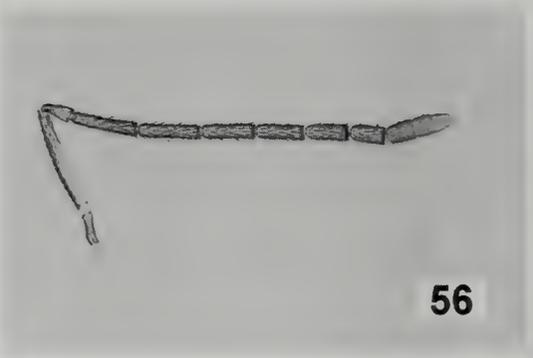
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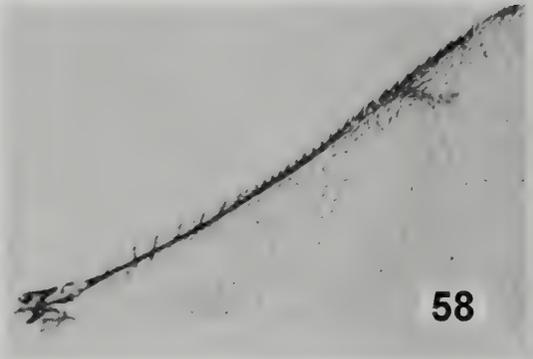
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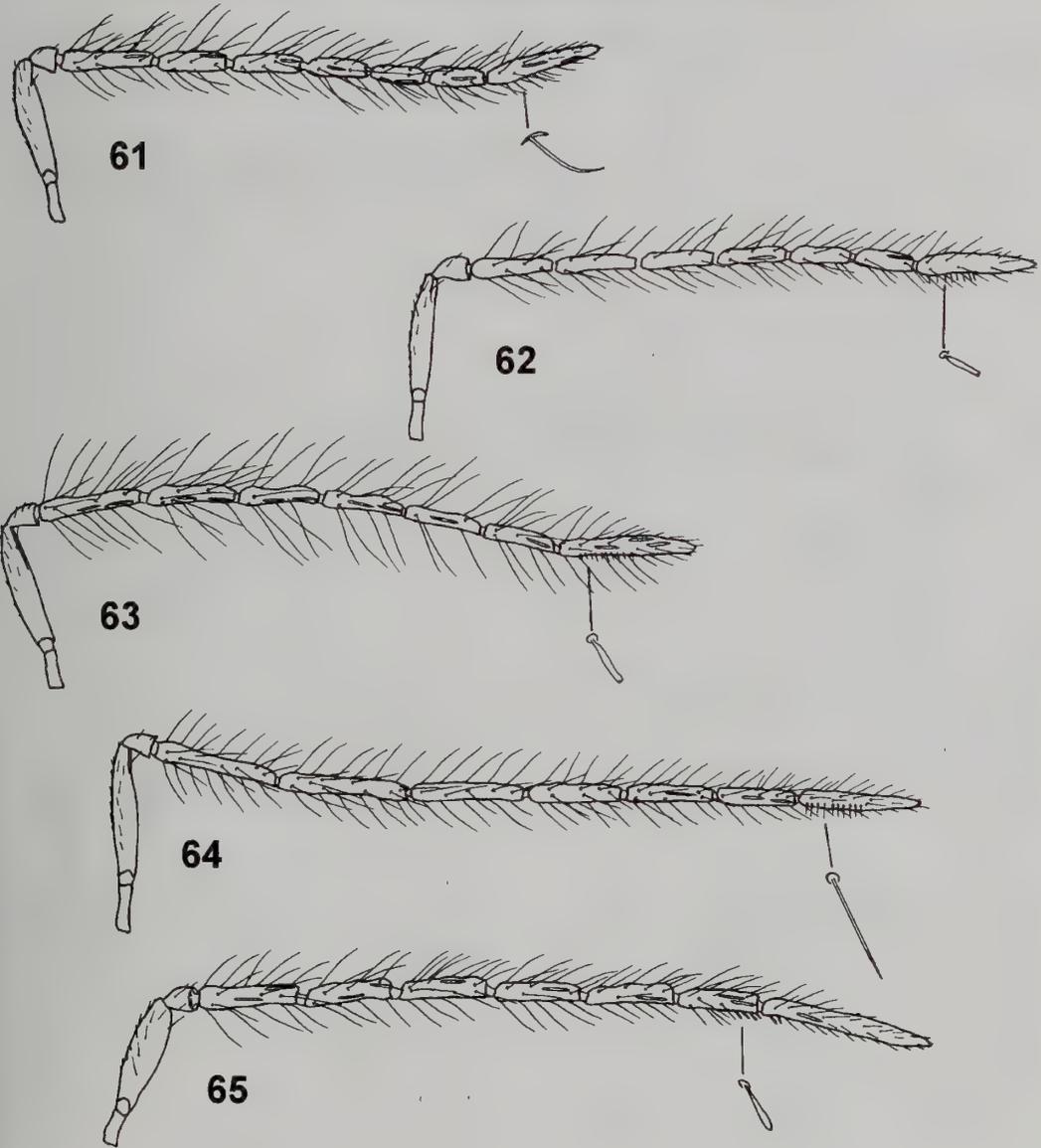


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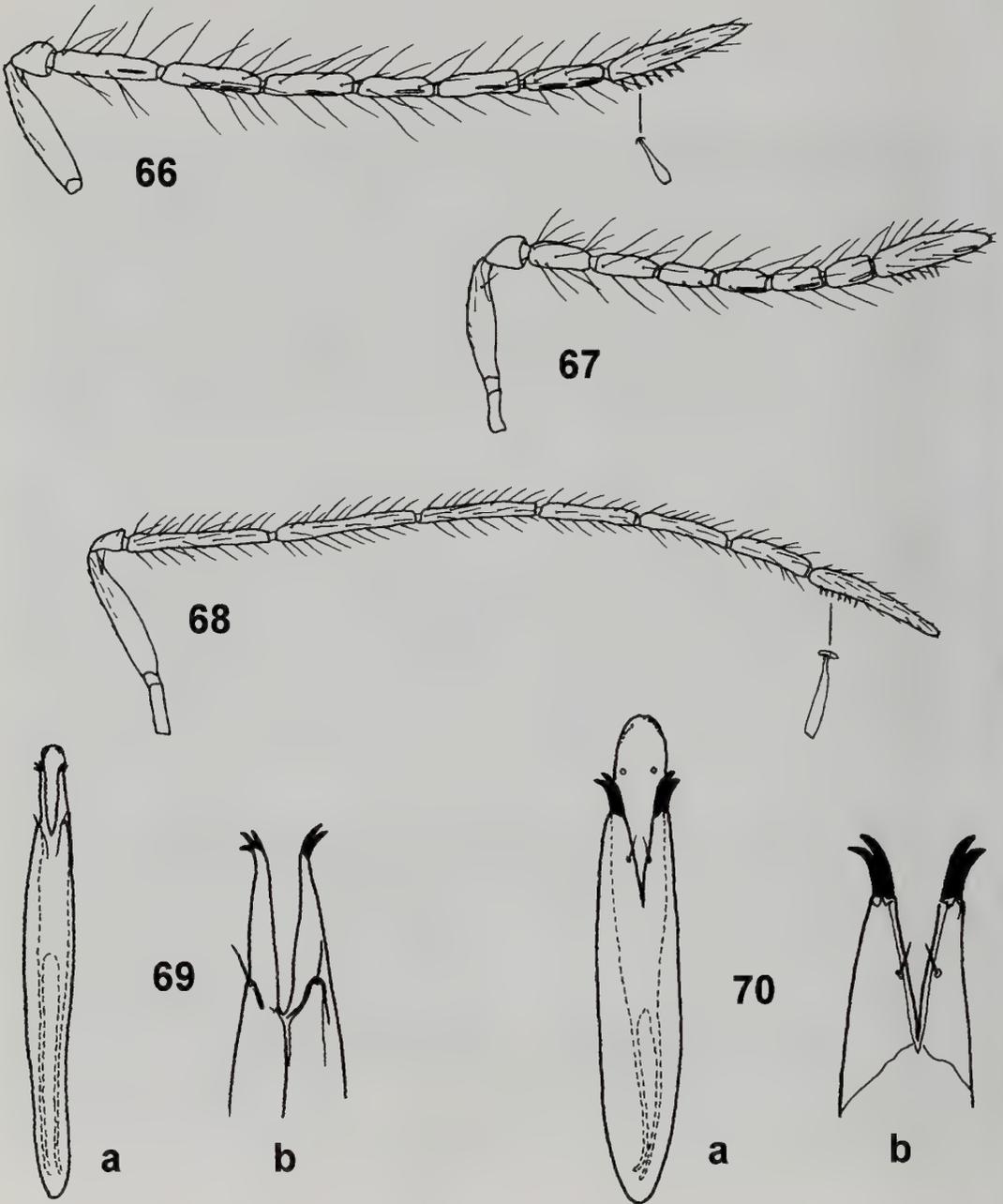


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A revision of the north-west European species of the *formosus* species group of *Spilomicrus* (Hymenoptera, Diapriidae)

DAVID G. NOTTON

Reading Museum Service, The Museum of Reading, Blagrove Street, Reading, RG1 1QH, United Kingdom.

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Synopsis. A revision of north-west European species of the *formosus* species group of *Spilomicrus* is given including an outline of the characters of the group, a key to all species and descriptions of all species. *S. crassiclavis* is removed from synonymy with *S. integer*. *S. pelion* is placed in synonymy with *S. crassiclavis*. Lectotype designations are made for *S. crassiclavis* and *S. formosus*. *S. sanbornei* is recorded as new to the Palaearctic and *S. crassiclavis* and *S. formosus* as new to the east Palaearctic.

INTRODUCTION

The *formosus* group of *Spilomicrus* is a small species group of inconspicuous diapriid parasitoid wasps with seven described species from the Palaearctic and Nearctic regions. The group may be distinguished from other *Spilomicrus* by the unusual form of the clypeus, which protrudes in front of the mandibles as a triangular or rounded projection and by associated modifications of the face (Figs 2–3, 5–6). Some members of this group have an unusual way of life as pseudohyperparasitoids of cicadellid bugs via the puparia of pipunculid flies. The *formosus* group is also significant because, although only a small group, it includes two species, *S. formosus* and *S. sanbornei*, with Holarctic distributions. It is becoming clear that such distributions are not uncommon among Diapriinae; examples are known within other species

groups of *Spilomicrus*, e.g. *S. antennatus* (Jurine) and *S. stigmatalis* Westwood (Masner, 1991) as well as species belonging to a number of other diapriine genera.

The aim of this paper is to revise the *formosus* species group of *Spilomicrus* occurring in north-west Europe. A revision was needed because of the confusion over species resulting from the mixed and partly lost type series of *S. crassiclavis* and from later misidentifications. Type material of all species was examined and type restrictions made where necessary. Nomenclatural changes were made as follows: lectotype designations were made for *S. formosus* and *S. crassiclavis*; *S. crassiclavis* was removed from synonymy with *S. integer*; *S. pelion* was placed in synonymy with *S. crassiclavis*. Currently three species are recognised in the region and, since previous keys are now inadequate, a new partial key to *Spilomicrus* is presented here. *S. crassiclavis* is recorded as new to Czechia, Denmark, Finland, Japan,

Norway and Sweden and *S. formosus* as new to Belgium, Ireland, Japan and Norway. *S. sanbornei* is recorded as new to Britain and the Palaearctic.

Morphological terminology largely follows Masner (1991). Wing vein terminology follows the convention of Mason (1986).

DEPOSITORIES

BMNH	The Natural History Museum, London, United Kingdom (formerly the British Museum, Natural History)
CNC	Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada
DN	D. G. Notton collection, Reading, United Kingdom
NMS	National Museums of Scotland, Edinburgh, United Kingdom
RAS	Russian Academy of Sciences, Palaeontological Institute, Arthropod Laboratory, Moscow, Russia
SEL	Department of Applied Zoology, University of Helsinki, Helsinki, Finland
ZI	Universitets Zoologiska Institutionen, Lund, Sweden
ZM	Zoological Museum, University of Copenhagen, Copenhagen, Denmark

ACKNOWLEDGEMENTS. Thanks are due to the above institutions and the following people: Ferdinando Bin; Peter Buhl; Roy Danielsson; the staff of the Entomology Library of the Natural History Museum, London; Jeremy Field; Mike Fitton; Gary Gibson; the Hamiltons of Abbots Moss; Peter Holmes; Karen Hull; Viktor Kolyada; Martti Koponen; Nina Laurence; Suzanne Lewis; Andrew Polaszek; Mark Shaw; Lars Vilhelmsen; Claire Villemant and especially to Lubomir Masner.

SPILOMICRUS WESTWOOD

Spilomicrus Westwood, 1832: 129. Type species: *Spilomicrus stigmatalis* Westwood by monotypy. Extensive generic synonymy may be found in Masner (1991) and Johnson (1992).

DIAGNOSIS (north-west European species only). Antenna 13-segmented in both sexes; for the female, apical antennal segment subequal to the preapical; for the male the fourth antennal segment usually modified; lateral surface of pronotum without a row of foveae; scutellum with two anterior pits, sometimes faint in some females of *S. antennatus*; macropterous to apterous; winged forms with costal cell wide, 2–3 times width of submarginal vein and

marginal vein short, not more than twice length of stigmal vein; anterior margin of metasomal sytergite (2+3) entire, and without keels, ridges or grooves, fitting loosely over apex of petiole and more or less hiding it; female with apex of gaster blunt to moderately conical.

DISTRIBUTION. *Spilomicrus* is a worldwide genus with many species: Johnson includes 144 described species in his World catalogue and there are many more undescribed. The number of species in north-west Europe is unclear: Nixon (1980) recorded 14 in Britain and Kozlov (1978) 22 in Europe, however there is no recent authoritative treatment covering north-west Europe. Of the four species groups recognised by Masner (1991) only the *stigmatalis* group and the *formosus* group have been found in north-west Europe, where they are both widely distributed.

BIOLOGY. *Spilomicrus* species have been recorded mostly as solitary endoparasitoids of the puparia of Diptera, including the host families Tephritidae, Tachinidae and possibly Bibionidae (Hoffmeister, 1989); Syrphidae, Pipunculidae, Muscidae, Sciomyzidae (Masner, 1991); Phoridae (Disney, 1994). A small number of species have been reared from the pupae (not larvae) of Staphylinidae (Coleoptera) (Nixon, 1980; Masner, 1991; Notton, 1996). Hoffmeister (1989) gives an account of the laboratory culture of *Spilomicrus hemipterus* Marshall on a species of *Drosophila* (Diptera, Drosophilidae) including descriptions of larval morphology. *Spilomicrus* species occur mainly in forest habitats although some may be common in grassland or wetland.

COMMENTS. North-west European *Spilomicrus* may be recognised using the generic key of Nixon (1980). The taxonomy of *Spilomicrus* on a world scale is poorly understood as are the interrelationships of its major species groups. Within north-west Europe many types need to be located and reinterpreted and a number of disparate regional studies need to be reconciled (see refs. in Masner, 1991 and Johnson, 1992). The species groups recognised by Masner (1991) are admittedly only provisional but are practical working groups: in particular the *formosus* group is easily recognisable in north-west Europe from the form of the clypeus (see key below).

formosus species group: Masner

(Figs 2–20)

formosus species group of *Spilomicrus*: Masner, 1991: 111.

DESCRIPTION. Habitus robust. Head in dorsal view transverse, 1.1–1.4× as wide as long; surface of head with scattered, long, semidecumbent hairs; occipital

flange narrow but distinct, not foveolate medially; head in frontal view subcircular, slightly transverse; space between anterior margins of toruli without a carina; face just below toruli smooth, without punctures; clypeal margin medially with a ventrally directed, triangular or rounded projection, either side of this projection the clypeal margin is strongly impressed forming two deep concavities; tentorial pits absent; malar sulcus complete, strongly curved. Antenna: scape smooth and shining at least in part, if sculptured then no more than weakly coriaceous; female antenna with 5- to 8-segmented club; male antenna with segment 3 equal to or a little shorter than segment 4, segment 4 cylindrical to weakly expanded apically with a weak to moderately deep emargination and carina or flange in basal 0.3–0.7. Mandibles stout, with upper tooth short, about 0.5–0.6 of length of the lower. Mesosoma: pronotum without epomia, strongly concave between the projecting pronotal shoulder and spiracle, anteriorly with long, scattered grey hairs which do not form a distinct cushion, posteriorly with a narrow strip of short, fine hairs extending downwards from the spiracle; acetabular carina complete, extending from the lower corner of the pronotum to the mid-line of the mesosternum; transscutal sulcus weakly curved; anterior scutellar pits large, deep, rounded, 0.35–0.4 of length of scutellum, separated by a narrow medial carina, which broadens out posteriorly into the scutellar disc; lateral scutellar pits broad, deep, broadened posteriorly; 7–12 distinct, posterior, scutellar pits; medial propodeal keel low posteriorly, its highest point anteriorly well below level of mesoscutum. Fore wing with subcostal, marginal and stigmal veins tubular; costal, basal, cubital and radial sector veins nebulous; costal cell broad, at widest point at least 2.5× as wide as subcostal vein; marginal vein short, thick, about 1.7–3.0× as long as wide when its length is measured from the start of its basal expansion to the fork of the postmarginal and stigmal veins, and its width measured at the mid-point of this length; stigmal vein short to very short; radial area indicated by distal abscissa of radial sector and anterior wing margin long, extending 0.45–0.60 of distance between marginal vein and wing tip. Legs unremarkable; tarsal segments slender; basitarsi longer than telotarsi. Metasoma with dorsally visible part of petiole relatively short, 1.2–2.2× as long as wide, a little flared anteriorly, sparsely hairy at base; tergites 4–7 with scattered micropunctures and scattered hairs; sternites 3–6 (♀) or 3–7 (♂) with deep, fine micropunctures. Ovipositor sheaths and apical sternite without pegs or dense pilosity. Colour: body mainly black; fore wing weakly tinged brown, without maculae.

DISTRIBUTION. The *formosus* group is widely distributed throughout the Nearctic, Palaearctic, Oriental and Australian regions (Masner, 1991) although only

seven species are described so far from the Palaearctic and Nearctic. Currently three species are recognised from north-west Europe. A number of species are widespread: *S. formosus* is known to be Holarctic (Masner, 1991) and *S. sanbornei* was found to be so in the current study.

BIOLOGY. The only published host record for the *formosus* group (Masner, 1991) is for *S. formosus* itself: much reared material of this species was also seen during this study and supported Masner's observation that it attacks the puparia of *Pipunculus* species (Diptera, Pipunculidae) in Europe. It is therefore a pseudohyperparasitoid of cicadellid bugs (the primary hosts of *Pipunculus* species – Coe, 1966). Curiously *Spilomicrus formosus* and *S. crassiclavis* show a number of morphological similarities with some diapriines of the genus *Basalys* including *B. fumipennis*, *B. tuberculatus* and *B. erythropus* which also attack pipunculid puparia (Lundbeck, 1922; this study). These similarities include: a compact, robust habitus, transverse head and a short mesosoma with domed mesoscutum. It is speculated that this apparent convergence has resulted from independent adaptation to development inside the short ovoid puparia of pipunculids.

COMMENTS. The *formosus* group was recognised by Masner (1991) who defined the group by the possession of the following putative apomorphies: presence of malar sulci; a pointed clypeus; mandibles with the lower tooth stronger than the upper. On the basis of species included by Masner, the group is difficult to define because of a number of exceptions to the above characters: malar sulci do not occur throughout the *formosus* group and occur in some other *Spilomicrus* and other Spilomicrini such as *Idiotypa*; when viewed from in front, the clypeus is not pointed in all *formosus* group species, although clearly pointed in *S. formosus*, it is rounded in a number of species including *S. sanbornei*; lastly, while the mandibles do have the lower tooth stronger in the *formosus* group, this can occur in other *Spilomicrus*. Thus none of the three characters given by Masner uniquely defines the *formosus* group, however, from material seen during this study and from Masner's descriptions, this group may still be defined by a character of the clypeus, that is, in all species the clypeus protrudes well over the mandibles as a pointed or rounded projection. In addition to the malar sulcus and mandible characters noted by Masner, other supporting characters which occur frequently though not universally in this species group include: absence or reduction of tentorial pits; absence of the epistomal suture; moderately to strongly impressed clypeal margin either side of the medial projection; weakly marked dorsal margin of the clypeus so that in lateral view the surface of the face forms an even curve.

Key to north-west European species of the formosus species group of *Spilomicrus*

- 1 Clypeus not protruding over mandibles (Fig. 1); clypeal margin not strongly impressed submedially; malar sulcus usually absent; tentorial pits usually present *Spilomicrus stigmatalis* group
- Clypeus protruding over mandibles as a pointed or rounded projection (Figs 2, 3, 5, 6); clypeal margin strongly impressed submedially; malar sulcus present and strong; tentorial pits absent (*Spilomicrus formosus* group) 2
- 2 Antennal flagellum apically clubbed (Figs 7, 10, 13); post-petiole with 6 sternites (females) 3
- Antennal flagellum not clubbed (Figs 9, 12, 15); post-petiole with 7 sternites (males) 5
- 3 Antennal club 5- to sub-6-segmented (Fig. 13); in frontal view, apex of medial projection of clypeus rounded, blunt (Fig. 5); mesosoma depressed, no more than 0.8x as high as wide, mesoscutum weakly convex (Fig. 16); medial propodeal keel low, hardly raised in front (Fig. 16); body length 1.9–2.5 mm *sanbornei*
- Antennal club 7- to 8-segmented (Figs 7, 10); in frontal view, apex of medial projection of clypeus triangular, pointed (Figs 2–3); mesosoma less depressed, at least 0.9x as high as wide, mesoscutum strongly convex (Fig. 18); medial propodeal keel raised in front to form a right-angled to acute projection (Fig. 18); body length 2.2–3.1 mm 4
- 4 Antennal club 7-segmented, with segments 8–12 strongly transverse (Fig. 7); notauli convergent anteriorly, extending over no more than basal 0.25 of mesoscutum (Fig. 19); eye height 1.4–1.5x as long as malar space (Fig. 2) *crassiclavis*
- Antennal club 8-segmented, with segments 8–12 quadrate to slightly elongate (Fig. 10); notauli divergent anteriorly, extending over at least basal 0.35 of mesoscutum (Fig. 20); eye height 1.7–2.2x as long as malar space (Fig. 3) *formosus*
- 5 In frontal view, apex of medial projection of clypeus rounded, blunt (cf. ♀ – Fig. 5); antennomere 4 with a moderately deep, curved emargination over basal 0.45–0.5 (Fig. 14); mesosoma depressed, no more than 0.8x as high as wide (cf. ♀ – Fig. 16); medial propodeal keel low, hardly raised in front (cf. ♀ – Fig. 16); body length 2.0–2.3 mm *sanbornei*
- In frontal view, apex of medial projection of clypeus triangular, pointed (cf. ♀ ♀ – Figs 2–3); antennomere 4 with at most a shallow emargination, over basal 0.3–0.7 (Figs 8, 11); mesosoma less depressed, at least 0.9x as high as wide (Fig. 17); medial propodeal keel raised in front to form a right-angled to acute projection (Fig. 17); body length 2.1–3.7 mm 6
- 6 Mesopleuron with a sternaulus, delimited dorsally by a sharp carina (Fig. 17); apical antennomere no longer than

- preapical (Fig. 9); notauli absent or vestigial, extending over no more than posterior 0.2 of mesoscutum (cf. ♀ – Fig. 19); eye height 1.0x as long as malar space; surface of eye with sparse hairs *crassiclavis*
- Mesopleuron without such a sternaulus or carina (cf. ♀ – Fig. 18); apical antennomere at least 1.5x as long as preapical (Fig. 10); notauli extending over at least posterior 0.35 of mesoscutum (cf. ♀ – Fig. 20); eye height 2.3x as long as malar space; surface of eye without hairs *formosus*

***Spilomicrus crassiclavis* Kieffer**

(Figs 2, 7–9, 17, 22)

Spilomicrus crassiclavis Kieffer, 1911: 788, 797. LECTOTYPE ♀, Great Britain: Mugdock (BMNH), here designated [examined]. **Stat. rev.** Lectotype labels: Mugdock, 11–7 [under mount]; Cameron coll., 1910–302; Mugdock; Determined by Dr. Kieffer.; *Spilomicrus crassiclavis* K.; *Spilomicrus formosus* Janss., G. Nixon det., 1972; B. M. TYPE HYM. 9.645a. Lectotype glued onto a card, with the right fore wing disarticulated, apical segment of left antenna lost and right hind telotarsus disarticulated.

[*Spilomicrus formosus* Jansson: Nixon, 1980: 16, Figs 30, 31. Misidentification in part (♀).]

Spilomicrus pelion Nixon, 1980: 17. Holotype♂, Great Britain: Surrey (BMNH) [examined]. **Syn. n.** Holotype labels: Holotype [red BMNH type label]; Surrey, Horsley, 14.vi.1930, G. Nixon; *Spilomicrus pelion* Nixon, Type♂, 197; B. M. TYPE HYM. 9.811. Holotype entire, mounted on a card point.

DESCRIPTION. ♀. Head (Fig. 2) in dorsal view 1.25–1.32x as wide as long; temples weakly to moderately contracted just behind eyes; dorsal part of occipital flange barely widened medially; post-genal pilosity sparse, not forming a defined cushion; head, in lateral view suboval, 1.13–1.17x as high as long; frons behind toruli weakly convex, almost flat; eye sparsely hairy; eye height 1.4–1.5x as long as malar space; in frontal view, apex of medial projection of clypeus triangular, pointed when seen from in front; lateral margins of clypeus undefined; malar sulcus a finely impressed line becoming a little deeper towards mandible. Antenna (Fig. 7): scape entirely smooth or at most weakly coriaceous at base; segment 3 about 2.5x as long as wide; segments 7–13 expanded to form a long-fusiform 7-segmented club; segments 8–12 strongly transverse; apical segment 1.49–1.74x as long as the preapical and slightly narrower than it; apical segment without a ventral pit. Mesosoma 1.29–1.37x as long as wide; anteriorly mesoscutum usually without a pair of short, submedial, parallel lines, rarely these are weakly indicated; notauli short but sharply incised, deep, weakly sinuate, narrowed anteriorly,

extending over posterior 0.18–0.24 of mesoscutum with no trace in front of this, convergent anteriorly (Fig. 19); humeral sulcus running 0.5–0.7 of the way from the transscutal suture to the posterior corner of pronotum; mesoscutum without other impressions; transscutal suture deeply incised; anterior scutellar pits subround, medial carina separating pits narrow; floor of anterior pits usually with one or two fine carinae running from front to back, rarely entirely smooth; lateral scutellar pits broad, deep, broadened posteriorly; posterior margin of scutellum with a row of 7–9, small, deep pits; dorsellum differentiated into dorsal and posterior faces, with three keels, which form three blunt projections dorsally; mesosoma slightly compressed laterally, 1.11–1.16 \times as high as wide; pronotum evenly concave between spiracle and pronotal shoulder; mesoscutum strongly convex; acetabular carina evenly curved across mesosternum and close behind fore coxae; sulcus just behind acetabular carina foveolate, with scattered pilosity; sternaulus absent; two to four deep foveolae just above the mid coxa and a weak flange immediately above the mid coxa; medial propodeal keel anteriorly forming a right-angled to acute, dorsally directed triangular projection. Fore wing with basal vein strongly pigmented and well defined; marginal vein 1.8–2.6 \times as long as wide; stigmal vein short, about as long as width of marginal vein; distal abscissa of radial sector moderately pigmented. Metasoma: dorsally visible part of petiole short, 1.3–1.5 \times as long as wide, longitudinal rugose, superimposed with weak coriaceous sculpture; in dorsal view, gaster short oval with apex obtusely pointed; metasomal syntergite (2+3) strongly convex, without micropunctures posteriorly; in lateral view metasomal tergites 7–8 almost perpendicular to long axis of gaster; metasomal sternite 2 without micropunctures, with two submedial tracts of hairs arising from fine punctures. Colour: mandibles dark brown to black; palps orange-yellow; radicle and basal 0.6–0.7 of scape black; apex of scape and antennal segments 2–6 orange-yellow, the more apical of these brownish; segments 7–13 black; tegulae orange-yellow; basal vein brown and marginal vein brown to dark brown; legs including coxae orange-yellow except for telotarsi and basal 0.6–0.7 of femora which are more or less darkened. Body length: 2.2–2.9 mm, fore wing length 2.00–2.46 mm.

♂. Differing from female as follows: Head in dorsal view 1.13–1.17 \times as wide as long; temples weakly contracted just behind eyes; head, in lateral view 1.08–1.22 \times as high as long; eye height 1.0 \times as long as malar space. Antenna (Fig. 9): scape mostly smooth, coriaceous as base; segments 3–13 cylindrical; third segment 2.1–2.5 \times as long as wide; segment 4 (Fig. 8) cylindrical, very slightly expanded apically, 2.6–2.8 \times as long as wide, about 1.2 \times as long as segment 3, weakly emarginate and with a low carina extending

over basal 0.7; preapical segment 1.6–1.7 \times as long as wide; apical segment no longer than and a little narrower than preapical. Mesosoma (Fig. 17) in dorsal view 1.46–1.52 \times as long as wide; notauli absent or represented by weak traces or at most represented by two small pits just in front of transscutal suture, extending over no more than posterior 0.2 of mesoscutum; humeral sulcus broad, running all the way from the transscutal suture to the posterior corner of the pronotum; mesoscutum sometimes with very shallow parapsidal impressions; posterior margin of scutellum with a row of 8–10 indistinct pits, which tend to coalesce; dorsellum less clearly differentiated into dorsal and posterior faces and with lateral keels indistinct; mesosoma depressed, 0.91–0.92 \times as high as wide; acetabular carina bowed posteriorly, almost reaching mid coxae; sternaulus present, defined dorsally by a strong carina which extends right across mesopleuron; mesopleuron with 3–4 rugae just above mid coxa. Fore wing with basal vein moderately pigmented; marginal vein 1.8–3.0 \times as long as wide; distal abscissa of radial sector weakly pigmented, almost spectral. Metasoma: dorsally visible part of petiole 1.3–2.2 \times as long as wide; in dorsal view, gaster oval, with apex rounded; in lateral view metasomal tergites 7–8 at about 45° to long axis of gaster; metasomal sternite 2 with medial area of micropunctures in apical half; metasomal syntergite (2+3) moderately convex with a small area of micropunctures posteriorly. Colour: mandibles dark brown to black; palps brown; antenna brown except for scape which has the basal 0.5–0.7 dark brown and apex orange to brown; tegulae brown; legs variable, orange to dark brown with coxae, base of tibiae and telotarsi darkened. Body length 2.1–3.7 mm; fore wing length 2.03–3.11 mm.

MATERIAL EXAMINED. **Czechia:** ♀, Bohemia, Šumava, Hurka v Pošum, 20.vii.1954 (*Hoffer*); ♂, Moravia, Javorina, 800–900 m, 10.viii.1991, climax eufagion for. (*Masner*) (CNC). **Denmark:** ♀, north-east Zealand, Færgelunden, 55°51'N 12°02'E, 21.vi.1988 (*Buhl*) (DN); ♂, north-east Zealand, Boserup Skov, 55°40'N 12°01'E, 12.vi.1988 (*Buhl*) (DN); ♂, 28.vi.1878 (*Schlick*) (ZM). **Finland:** ♀, Pohjois-Karjala, Tohmajärvi, 6908:660, 17.vii.1982 (*Koponen*) (SEL). **Great Britain:** ♀, Stirling, Mugdock, 11.vii.[pre-1910] (*Cameron*) (BMNH) (lectotype); ♀, W. Ross, Rassel National Nature Reserve, NG845432, 1–15.vi.1992, Malaise trap (*Brown*) (NMS); ♀, West Glamorgan, Crymlyn Bog, SS6995, 14.vi.1989 (*Holmes*) (DN); 3 ♀, Cheshire, Abbots Moss, SJ596680, 1–19.vi.1990, Malaise trap/swept (*Notton*) (DN); ♀, Cambridgeshire, Chippenham Fen, TL650693, 6.vii.1983, Malaise trap, carr/reed bed (*Field*) (DN); 2 ♀, Norfolk, Catfield, TG374204, 21.vi–5.vii.1988, water trap (DN); ♂, Surrey, Horsley,

14.vi.1930 (*Nixon*) (BMNH) (holotype); ♂, Kent, Eynsford, 7.vi.1930 (*Nixon*) (BMNH) (paratype). **Japan:** ♀, Iwate Prefecture, Mount Hayachie, 400 m, 19–26.vii.1989 (*Makihara & Sharkey*) (CNC). **Norway:** ♂, Røyken, Kinnertangen, EIS 28 BØ, vii.1993, Malaise trap (*Hansen*) (DN). **Sweden:** ♀, Närke, Örebro, 12.vii.1957 (*Jansson*) (ZI); ♀, Rørvik, Lammhult, 15.vii.1986 (*Buhl*) (ZM); ♀, Uppsala, Ericksburg, 14–17.vii.1986, pan trap (*Ronquist*) (CNC).

DISTRIBUTION. Widespread in north-west Europe including: Czechia, Denmark, Finland, Great Britain, Japan, Norway and Sweden (Fig. 22). Previously recorded from Britain (Kieffer, 1911; Nixon, 1980 as *Spilomicrus pelion*; Notton, 1996 as *S. near formosus*) and Algeria (Kieffer, 1911; cited in Jansson 1942). No evidence was found to support the occurrence of *S. crassiclavis* in Africa, the identity of the syntype material Kieffer recorded from Algeria is uncertain now that the type series has been found to be mixed.

BIOLOGY. Host unknown. Flight period June–July. Recorded mainly from woodland, fen habitats and other wetland.

COMMENTS. As well as the male syntype from Bishopton (Masner, 1965) a female syntype of *Spilomicrus crassiclavis* was discovered (BMNH) but the Algerian syntypic material collected by du Buysson is lost. Horn & Kahle (1937) note that the du Buysson collection is at the Muséum National d'Histoire Naturelle, Paris but this material could not be found there (Claire Villemant, pers. com.). Since the two syntypes located are considered to belong to different species the female was chosen as a lectotype. The previous synonymy established by Nixon (1980) of *S. crassiclavis* is not supported by this designation and so *S. crassiclavis* is removed from synonymy with *S. integer*. Also *S. pelion* is here synonymised with *S. crassiclavis*. Character states associating the sexes include the following: shorter antennal segments, shorter notauli, less bulging temples and generally smaller size than for *S. formosus*. A re-examination of the material seen by Nixon (1980) showed that the female he referred to as *S. formosus* was in fact *S. crassiclavis*. Teodorescu (1970; 1986) figured the male genitalia, however, owing to the taxonomic problems outlined above, the identity of this material is doubtful.

Spilomicrus formosus Jansson

(Figs 3–4, 10–12, 18, 20–21)

Spilomicrus formosus Jansson, 1942: 215. **LECTOTYPE** ♀, Sweden: Örebro, Oset (ZI), here designated [examined]. Lectotype labels: Ör. Oset, 10–8 39 A. J.; Typus [red label]; *Spilomicrus*

formosus Janss., ♀; Zool. Mus. Lund Sweden, Diapriidae Type No. 1411:1–7; ZML 1997.026. Lectotype entire, clean and glued onto a card with its wings raised.

DESCRIPTION. ♀. Head (Fig. 3) in dorsal view 1.36–1.42× as wide as long; temples weakly expanded to parallel just behind eyes; dorsal part of occipital flange widened medially; post-genal pilosity sparse, not forming a defined cushion; head, in lateral view suboval, 1.04–1.20× as high as long; frons behind toruli weakly convex, almost flat; eye sparsely hairy; eye height 1.7–2.2× as long as malar space; apex of medial projection of clypeus triangular, pointed when seen from in front; lateral margins of clypeus undefined; malar sulcus a finely impressed line, becoming a little deeper towards mandible. Antenna (Fig. 10) slender; scape entirely smooth or at most weakly coriaceous at extreme base of dorsum; segment 3 about 3.5× as long as wide; segments 7–13 expanded to form a long, cylindrical, 8-segmented club; segments 8–12 quadrate to slightly elongate; apical segment 1.7–1.8× as long as the preapical and as wide or very slightly narrower than it; apical segment without a ventral pit. Mesosoma (Fig. 18) short, 1.25–1.26× as long as wide; anteriorly mesoscutum usually without a pair of short, submedial, parallel lines, rarely these are weakly indicated; notauli sharply incised, deep, weakly sinuate, narrowed anteriorly, extending over posterior 0.35–0.45 of mesoscutum with no trace in front of this, divergent anteriorly (Fig. 20); humeral sulcus running all the way from the transscutal suture to posterior corner of pronotum; mesoscutum without other impressions; transscutal suture deeply incised; anterior scutellar pits subround, medial carina separating pits narrow; floor of anterior pits smooth; lateral scutellar pits broad, deep, broadened posteriorly; posterior margin of scutellum with a row of 7–9 small, deep pits; dorsellum differentiated into dorsal and posterior faces, with three keels which project dorsally as three, sharp points; mesosoma slightly depressed, 0.90–0.93× as high as wide; pronotum evenly and shallowly concave between spiracle and pronotal shoulder; mesoscutum strongly convex; acetabular carina evenly curved across mesosternum and close behind fore coxae; sulcus just behind acetabular carina foveolate with scattered pilosity; sternaulus absent; four to five deep foveolae just above mid coxa and a broad flange immediately above mid coxa; medial propodeal keel anteriorly forming a right-angled to acute, dorsally directed, triangular projection. Fore wing with basal vein strongly pigmented and well defined; marginal vein 2.0–2.3× as long as wide; stigmal vein short, about as long as width of marginal vein; distal abscissa of radial sector moderately pigmented. Metasoma: dorsally visible part of petiole short, 1.2–1.4× as long as wide, longitudinally rugose superimposed with weak

coriaceous sculpture; in dorsal view, gaster short oval, with apex obtusely pointed; metasomal syntergite (2+3) strongly convex, without micropunctures posteriorly; in lateral view metasomal tergites 7–8 almost perpendicular to long axis of gaster; metasomal sternite 2 without micropunctures, with two submedial tracts of hairs arising from large punctures. Colour: mandibles dark brown to black; palps orange-yellow; antennal segments 1–5 orange-yellow except for the radicle which is black and basal 0.2 of scape which is occasionally black as well; segment 6 brown and segments 7–13 usually black; rarely the sixth orange-yellow and seventh dark brown; tegulae transparent, orange-yellow; fore wing with basal vein brown and marginal vein brown to dark brown; legs including coxae orange-yellow. Body length 2.2–3.1 mm; fore wing length 2.70–2.86 mm.

♂. Differing from female as follows: head (Fig. 4) in dorsal view 1.35–1.39× as wide as long; head, in lateral view, 1.11–1.20× as high as long; eye height 2.3× malar space; eye without hairs. Antenna (Fig. 12): segments 3–13 cylindrical; third segment 3.5–3.7× as long as wide; fourth segment 3.4–3.6× as long as wide and as long as segment 3; segment 4 cylindrical, with at most a weak basal emargination and a low, weak carina in basal 0.3–0.4 (Fig. 11); preapical segment 2.0–2.1× as long as wide; apical segment 1.5–1.6× as long as wide as the preapical and a little narrower than it. Mesosoma in dorsal view 1.31–1.35× as long as wide; notauli extending over posterior 0.3–0.4 of mesoscutum; posterior margin of scutellum with a row of 9–12 small deep pits; dorsellum with keels usually projecting dorsally as sharp points but sometimes rounded; mesosoma slightly depressed to slightly compressed, 0.98–1.15× as high as wide. Fore wing: marginal vein 1.7–2.2× as long as wide. Metasoma: dorsally visible part of petiole 1.3–1.5× as long as wide; gaster short oval, its apex rounded; in lateral view metasomal tergites 7–8 at about 45° to long axis of gaster. Colour: mandibles black to dark brown; palps orange-yellow to brown; antennal colour variable, in lightest individuals, scape orange yellow with basal third black, pedicel orange-yellow and flagellum brown, in darkest individuals, scape all black, pedicel dark brown and flagellum black; tegulae transparent orange-yellow; legs with ground colour varying from orange-yellow to brown; telotarsi and basal 0.5–0.65 of femora blackened and coxae and trochanters brown. Body length 2.8–3.4 mm; fore wing length 2.71–3.20 mm.

MATERIAL EXAMINED. **Belgium:** ♂, Mont Rigi, stat. se. Hautes Fagnes, 18–24.viii.1983, Université Liège (CNC). **Czechia:** ♀, Moravia, Lednice, env., 7–9.viii.1991, yellow pan trap, riparian forest (*Masner*); ♂, Bohemia C., Řevnice (*Masner*) (CNC). **Denmark:** 2 ♀, ♂, north Zealand, iv.1891, each

mounted with a pipunculid puparium (*Schlick*) (ZM); ♂, v.1889; 4 ♀, 2 ♂, iv.1890, each mounted with a pipunculid puparium (*Schlick*) (ZM); ♀, Zealand, Ruderhegen, v.1910, ex. *Pipunculus* sp., mounted with a pipunculid puparium (*Kryger*) (CNC). **Finland:** ♀, Uusimaa, Espoo, 6669:373, 27.viii.1982 (*Koponen*) (SEL); ♀, Kemin Lappi, Kittilä, 7469:409, 17.viii.1983 (*Koponen*) (DN); ♂, Etelä-Savo, Mäntyharju, 6795:508, 1.viii.1981 (*Koponen*) (SEL); ♂, Etelä-Pohjanmaa, Töysä, 6948:336, 23.vii.1987 (*Koponen*) (SEL); ♂, Helsinki, 28.vi–11.vii.1989, Malaise trap (*Goulet*) (CNC). **Germany:** 3 ♂, Bayern, Oberstdorf, 12–29.viii.1936 (*Nixon*) (BMNH). **Great Britain:** 2 ♂, Elgin, Aviemore, 26.vii & 5.viii.1946 (*Harwood*) (BMNH); ♀, 2 ♂, W. Ross, Rassa National Nature Reserve, NG845432, x.1991, Malaise trap (*Brown*) (DN); 2 ♀, Cambridgeshire, Chippenham Fen, TL6469, 17–24.vi.1985, Malaise trap (*Field*) (DN); ♂, Chippenham Fen, TL650693, 6–20.vii.1985, Malaise trap (*Field*) (DN); ♂, Pembrokeshire, Brynberian Moor, SN106346, 20.vii.1987, pitfall trap, *Juncus* sp., soligenous flush (*Holmes*) (DN); ♂, Wiltshire, Savernake Forest, SU21366708, 26.vii–16.viii.1990, Malaise trap (DN); ♂, Oxfordshire, Weston Fen, SP526194, 22.vii–20.viii.1987, Malaise trap (DN); ♂, Surrey, Oxshott, 9.viii.1930 (*Nixon*) (BMNH). **Ireland:** ♂, Co. Wexford, Benroe, Killybegs district, 18.viii.1933 (*Stelfox*) (BMNH). **Japan:** 2 ♂, Hokkaido, Tomuraushi area, 500 m, 13.viii.1996 (*Masner*) (CNC). **Norway:** 2 ♀, ♂, Bærum, Kjaglidalen, EIS 28 AK, 27.vii–11.viii.1990, Malaise trap (*Falck*) (DN); ♂, Rollag, Vårviken, EIS 35 BV, viii.1992, Malaise trap (*Sagvolden*) (DN). **Russia:** ♀, Moscow, Bitsa Park, 18.viii.1993 (*Kolyada*) (RAS); ♂, Moscow, 13.vii.1993 (*Kolyada*) (RAS). **Slovakia:** ♂, {illegible}, Nizké Tatry, Kysla, 10.viii.1989 (*Macek*) (CNC). **Sweden:** ♂, Blekinge, Rödeby Gagnekulla, 56°16'N 15°34'E, 8.ix.1956 (*Sundholm*) (ZI); ♀, 2 ♂, Dalarna, Ål, 10 km south east of Leksand, 60°42'N, 15°02'E, 4.viii.1968 (*Sundholm*) (ZI); 3 ♂, Dalarna, Järna, 60°33'N, 14°15'E, 3.viii.1968 (*Sundholm*) (ZI); 2 ♀, Hälsingland, Loos, pre-1942 (*Sjöberg*) (ZI) (paralectotype); 5 ♂, Jämtland, Fors, 63°01'N, 16°37'E, 7.viii.1964 (*Sundholm*) (ZI); ♂, Lulelappmark, Jokkmokk Messaure, 66°43'N, 20°20'E, 7.viii.1966 (*Sundholm*) (ZI); ♀, Närke, Örebro, Oset, 59°17'N, 15°10'E, 10.viii.1939 (*Jansson*) (ZI) (lectotype); ♂, Närke, Örebro, Oset, 59°17'N, 15°10'E, 17.viii.1944 (*Jansson*) (ZI); ♀, Närke, Örebro, Ö. Mark, 59°15'N, 15°12'E, 20.viii.1944 (*Jansson*) (ZI); ♂, Närke, Örebro, 22.viii.1937 (*Jansson*) (ZI) (paralectotype); ♀, Närke, Örebro, 20.viii.1939 (*Jansson*) (ZI) (paralectotype); ♀, Närke, Örebro, 16.viii.1941 (*Jansson*) (ZI) (paralectotype); 2 ♀, 11 ♂, Närke, Örebro, 28.vii.1941–20.vii.1960 (*Jansson*) (ZI); ♂, Närke,

15.viii.1955 (*Sundholm*) (ZI); ♂, Norrbotten, Edefors, 66°05'N, 20°54'E, 31.vii.1958 (*Sundholm*) (ZI); ♂, Norrbotten, Nedertorneå, 65°50'N, 24°07'E, 24.vii.1966 (*Sundholm*) (ZI); ♀, Nu., 15.viii.1955 (*Jansson*) (ZI); ♂, Öland, Gårdby, 56°37'N, 16°05'E, 7.viii.1967 (*Sundholm*) (ZI); ♂, Östergötland, Skedevi, 58°08'N, 15°42'E, 2.viii.1970 (*Sundholm*) (ZI); ♂, Skåne, Skaralid, 16.vii.1937 (*Jansson*) (ZI) (paralectotype); 3♂, Skåne, Yngsjö, 55°57'N, 14°11'E, 23.vii.1964 (*Sundholm*) (ZI); ♂, Småland, Halltorp Värnanäs, 56°30'N, 16°07'E, 8.viii.1967 (*Sundholm*) (ZI); ♂, Småland, 20.ii.1943 (*Jansson*) (ZI); 5♂, Södermanland, Dalarö, Malmen, viii.1976 (BMNH); ♂, Södermanland, Länna, 10 km south of Strängnäs, 59°18'N, 16°54'E, 9.viii.1958 (*Sundholm*) (ZI); ♂, 24.vii.1940 (ZI); ♀, 25.vii.1943 (ZI); ♂, 1.viii.1944 (*Jansson*) (ZI). **Canada:** ♀, ♂, British Columbia, Hollyburn, 24.viii.1930 (*Whittaker*) (BMNH). **U.S.A.:** ♂, Washington, Okanagan C., N. Waconde, 25.vii.1985 (*Tinnamore*) (BMNH); ♀, Virginia, Shenandoah N. P., Big Meadow, 1,300 m, vii–viii.1987, Malaise trap, natural meadow (*BRC Hym. Team*) (BMNH).

DISTRIBUTION. Widespread in north-west Europe, extending well inside the Arctic circle (Fig. 21) including: Belgium, Czechia, Denmark, Finland, Germany, Great Britain, Ireland, Norway, Russia, Slovakia and Sweden, also occurring in Japan, Canada and the U.S.A. Previously recorded from Czechia (Masner, 1991), Denmark (Masner, 1991), Finland (Hellén, 1963; Masner, 1991), Germany (Nixon, 1980), Great Britain (Nixon, 1980 – males only), Russia (Hellén, 1963), Slovakia (Masner, 1991) and Sweden (Masner, 1991).

BIOLOGY. Eleven Danish specimens of *S. formosus* were seen each mounted with the puparium of a pipunculid (Diptera). Of these Kryger's specimen was identified as *Pipunculus* sp., supporting Masner's (1991) observation that this genus is attacked in Europe. The developmental stage of host attacked is unknown, although by analogy with other *Spilomicrus*, it is likely that oviposition is into the young host puparium. This would necessarily be after the pipunculid has emerged from its own cicadellid (Homoptera) host, and is therefore likely to be a case of pseudohyperparasitism *sensu* Shaw & Askew (1976). There are no host records yet from the Nearctic. In Europe both sexes are found most often from July to August, with a few females also in June, the dates of reared Danish material, April to May, may not be representative as they are much earlier and these wasps may have been reared indoors in warmer conditions than would be natural. In Europe *S. formosus* is recorded from a range of habitats including fen and other wetland, forest and grassland. This is very similar to its behaviour in north America where the flight period

is from July to October and it frequents mainly forest habitats (Masner, 1991).

COMMENTS. Nixon (1980) misinterpreted the female of *S. formosus* although he correctly identified the male. The single female he mentioned belongs to *S. crassiclavis* q. v. One male *S. formosus* from Örebro, dated 28.vii.1941 (ZI), is erroneously labelled 'typus'; its date is not among those given in the original description and so it was not considered a syntype. Hellén's (1963) material of this species is thought to be at the Museum of Helsinki University but is apparently lost.

Spilomicrus sanbornei Masner 1991

(Figs 5–6, 13–16, 23)

Spilomicrus sanbornei Masner 1991: 145. Holotype ♀, Canada: Ontario, Thunder Bay (CNC) [not examined].

DESCRIPTION. ♀. Head (Figs 5–6) in dorsal view 1.12–1.17× as long as wide; dorsal part of occipital flange of even width; post-genal pilosity, forming only a small cushion; temples parallel just behind eyes; head in lateral view very rounded, subcircular 1.00–1.05× as high as long; frons convex; vertex evenly rounded; eye sparsely hairy, small, its height 1.6–1.8× as long as malar space; apex of medial projection of clypeus rounded when seen from in front; malar sulcus, narrow near eye and distinctly widened towards mandible, where it has the form of a step rather than a groove, so that the anterior gena is depressed relative to the posterior gena; lateral margin of clypeus defined by a deep groove. Antenna (Fig. 13) robust: scape smooth dorsally, weakly coriaceous ventrally; segment 3 about 1.7× as long as wide; segment 8 slightly expanded and segments 9–13 strongly expanded to form a short-fusiform 5- to sub-6-segmented club; segments 8–12 weakly to strongly transverse; apical segment 1.0–1.1× as long as the preapical and only 0.85× as wide as it; apical segment with a large, shallow, ventral pit. Mesosoma (Fig. 16) in dorsal view 1.45–1.54× as long as wide; notauli deeply impressed over posterior 0.30–0.45 of mesoscutum, indicated as a shallow trace for a short distance in front of this; anteriorly mesoscutum with a pair of short, submedial, parallel lines usually distinct but sometimes weak or absent; mesoscutum with a slight impression in front of each hind corner of the mesoscutum; humeral sulcus fine, running all the way from the transscutal suture to the posterior corner of the pronotum; transscutal suture moderately incised becoming weaker laterally; anterior scutellar pits deep, oblique oval, the medial carina separating the two pits usually narrow but sometimes a little wider; floor of anterior pits with fine carinae running from front to back; lateral scutellar pits usually deep and slightly

broadened posteriorly but shallower in specimens with a more depressed mesosoma; posterior margin of scutellum with a row of 9–12 small pits; dorsellum rounded, not differentiated into dorsal and posterior faces, its keels weakly developed, the lateral keels vestigial, the medial keel rounded, only weakly projecting dorsally; mesosoma strongly depressed, 0.73–0.77× as high as wide; pronotum with a shallow but distinct fovea between spiracle and pronotal shoulder; mesoscutum only weakly convex, flattened dorsally; sulcus just behind acetabular carina not foveolate, almost glabrous; sternaulus absent; area above middle coxa with only a few rugae; medial propodeal keel low, hardly raised in front. Fore wing with basal vein moderately pigmented; marginal vein 2.1× as long as wide; stigmal vein very short, about half as long as width of marginal vein; distal abscissa of radial sector barely pigmented, almost spectral. Metasoma with dorsally visible part of petiole short, 1.4× as long as wide with 3–6 strong, almost parallel, longitudinal keels; in dorsal view gaster elongate oval, its apex pointed, approximately right-angled; metasomal syntergite (2+3) weakly convex, with area of micropunctures postero-medially; in lateral view, metasomal tergites 7 to 8 at about 45° to long axis of gaster; metasomal sternite 2 without micropunctures, with sparse, scattered hairs arising from fine punctures. Colour: antennal segments 1–8, palps and legs including coxae orange yellow, telotarsi more or less darkened; antennal club shading from brown to dark brown or black; mandibles and tegulae brown. Body length: 1.9–2.5 mm; fore wing length 1.51–1.80 mm.

♂. Differing from female as follows: head in dorsal view 1.18–1.25× as long as wide; temples parallel to very slightly receding just behind eyes; head in lateral view 1.03–1.07 as high as long; eye height 2.1 as long as malar space. Antenna (Fig. 15) with flagellar segments cylindrical; flagellum slightly narrowed apically and basally; third segment 2.2–2.5× as long as wide; fourth segment 2.2–2.4× as long as wide and about 1.1× as long as segment 3; emargination of segment 4 moderately deep, curved, with a low carina over basal 0.45–0.5, ending in a small tooth (Fig. 14); preapical segment 1.6–1.7× as long as wide; apical segment 1.3–1.4× as long as preapical and barely narrower than it; apical segment without a ventral pit. Mesosoma in dorsal view 1.34–1.43× as long as wide; notauli deeply impressed over posterior 0.25–0.45 of mesoscutum; mesosoma strongly depressed, 0.76–0.79× as long as high; marginal vein 1.8–2.2× as long as wide. Metasoma with dorsally visible part of petiole short, 1.2–1.4× as long as wide; in dorsal view gaster with apex rounded. Colour: antennal scape varying from orange-yellow to brown, pedicel orange-yellow; flagellum orange-yellow to yellow brown, usually darkened apically; palps yellow; legs, including coxae, orange-yellow with coxae, femoral clubs, tibial clubs

and telotarsi more or less darkened. Body length: 2.0–2.3 mm; fore wing length 1.84–1.96 mm.

MATERIAL EXAMINED. **Great Britain:** ♂, Cheshire, Abbots Moss, SJ596680, 1–19.6.1990, Malaise trap (*Notton*) (NMS); ♀, ♂, Cheshire, Abbots Moss, SJ596680, 19.6–10.7.1990, Malaise trap (*Notton*) (DN). **Canada:** ♀, Ontario, Guelph, 8–24.vi.1981, pan trap (*Barber*) (CNC) (paratype); ♂, Ontario, Rondeau Prov. Pk, 9–26.vi.1980, interception trap (*Goulet*) (CNC) (paratype); ♂, Quebec, Gatineau Pk, 28.vi–5.vii.1983, beaver pond, interception trap (*Denis*) (CNC) (paratype); ♀, Quebec, Old Chelsea, 5–15.vi.1987, NCC woodpile, pan trap (*Masner*) (CNC) (paratype); ♂, Québec, Old Chelsea, 5–15.vi.1987, pan trap in dead wood pile (*Masner*) (BMNH) (paratype).

DISTRIBUTION. Newly recorded from Britain and the Palaearctic (Fig. 23). Previously recorded from the Nearctic including Canada and the United States (*Masner*, 1991).

BIOLOGY. Host unknown. In both North America and Britain the flight period is June to July and forest habitats are frequented.

COMMENTS. *Spilomicrus sanbornei* is superficially similar in appearance to *S. abnormis* but easily distinguished from it by the presence of a malar sulcus, lack of pubescence at the base of metasomal syntergite (2+3). British material of *S. sanbornei* does not encompass the full range of variation shown by Nearctic material in the length of the notauli, sculpture of the floor of the basal scutellar pits and body length. This is probably because few British specimens were examined. British material also has the anterior parallel lines of the mesoscutum either absent or less well developed than in Nearctic specimens and the mesosoma very slightly more depressed. This is not considered significant because such variation in these features of the mesosoma is common in diapriines, particularly in groups where wing reduction is frequent.

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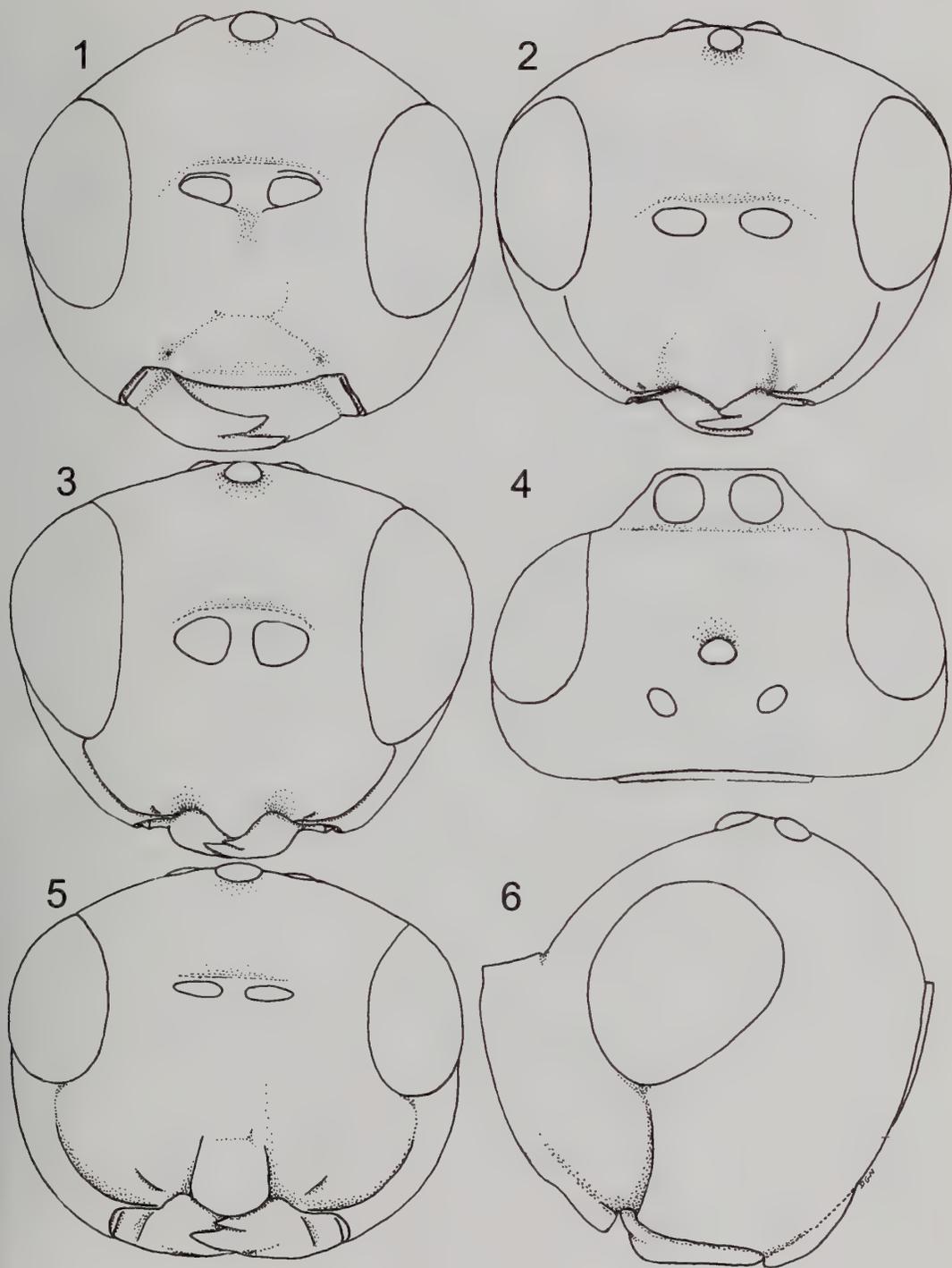
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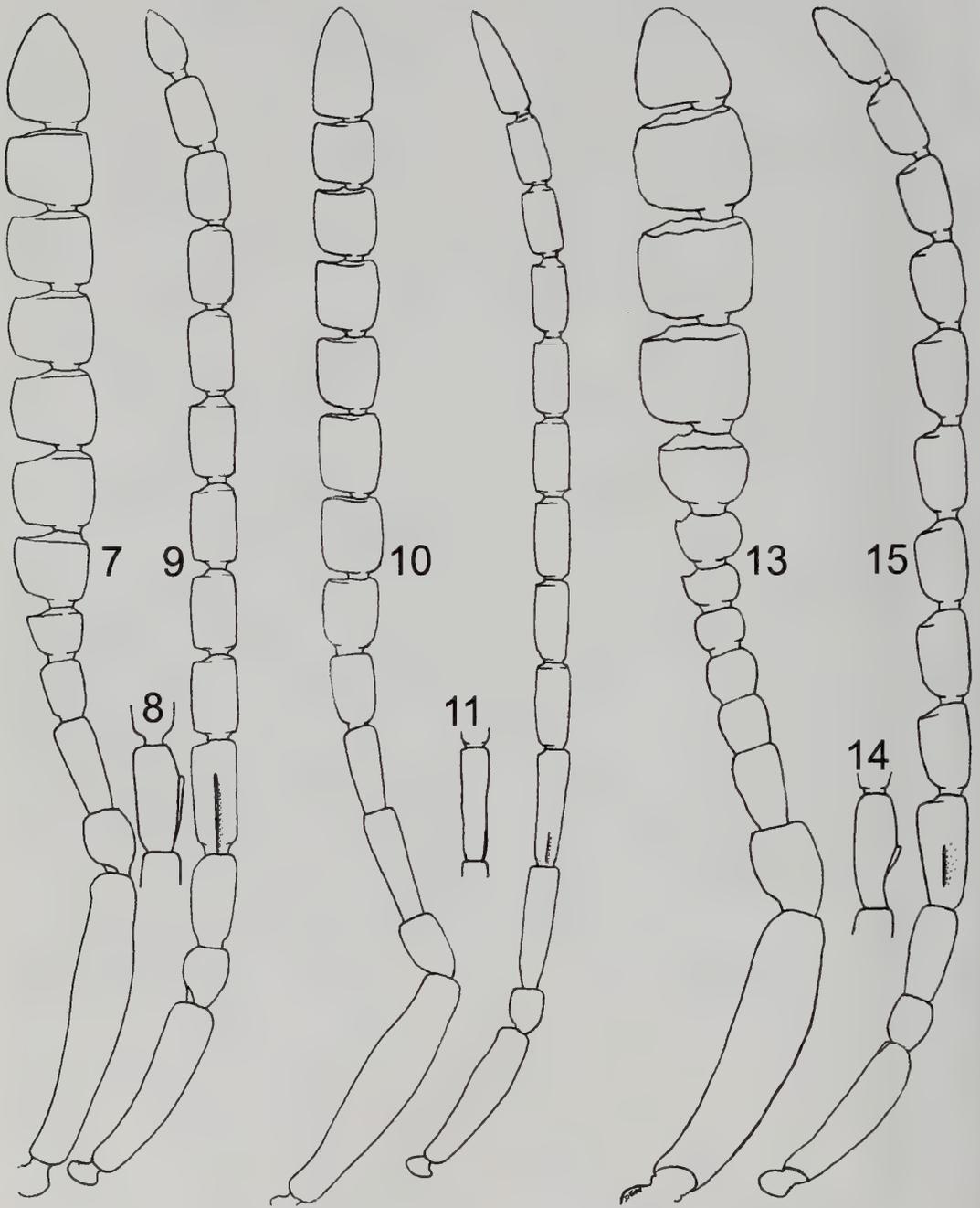
Synonyms and misidentifications are in *italics*; principle references are in **bold**.

- | | | |
|------------------------------------|---|-------------------------------------|
| antennatus 129, 130 | formosus species group 129, 130 , 131, 132 | Pipunculus 131, 136 |
| Basalys 131 | fumipennis 131 | Sanbornei 129, 131, 132, 132 |
| Bibionidae 130 | hemipterus 130 | Sciomyzidae 130 |
| crassiclavus 129, 132 | Idiotypa 131 | Spilomicrini 131 |
| Diapriidae 129 | integer 129 | Spilomicrus 129, 130 |
| Diapriinae 129 | Juncus 135 | Staphylinidae 130 |
| Drosophila 130 | Muscidae 130 | stigmatalis 129, 130 |
| Drosophilidae 130 | <i>pelion</i> 129, 132 | stigmatalis species group 130 |
| erythropus 131 | Phoridae 130 | Syrphidae 130 |
| formosus 129, 131, 132, 134 | Pipunculidae 130 | Tachinidae 130 |
| <i>formosus</i> 132 | | Tephritidae 130 |
| | | tuberculatus 131 |



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Fig. 1. *Spilomicrus stigmaticalis* – head, anterior, ♂. Fig. 2. *S. crassiclavis* – head, anterior, ♀. Figs 3–4. *S. formosus* – 3, head, anterior, ♀; 4, head, dorsal, ♂. Figs 5–6. *S. sanbornei* – 5, head, anterior, paratype ♀; 6, head, lateral, paratype ♀.

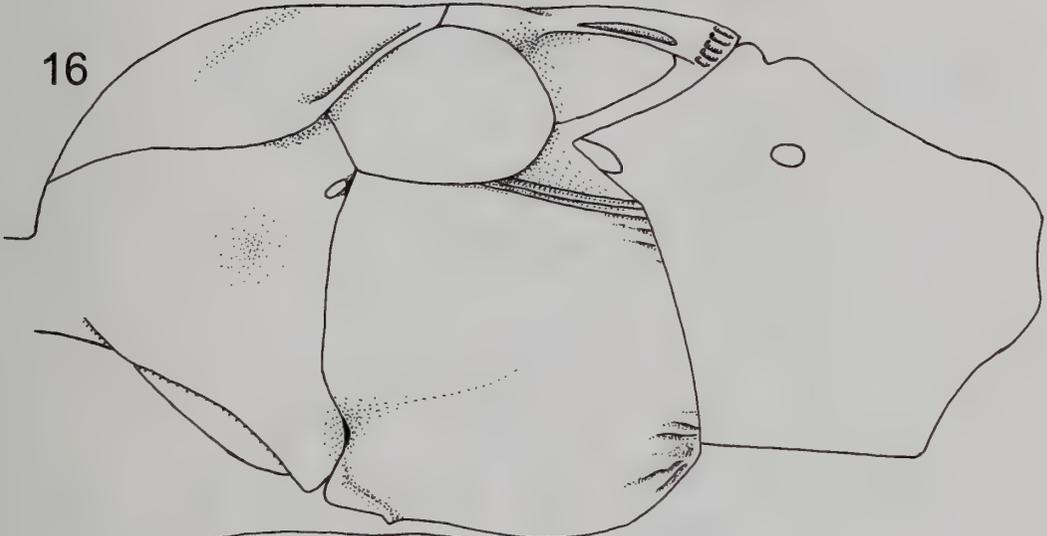


Figs 7-9. *Spilomicrus crassiclavis* - 7, left antenna, posterior, ♀; 8, left antenna, fourth segment, posterior, ♂; 9, left antenna, posterior ♂.

Figs 10-12. *S. formosus* - 10, left antenna, posterior ♀; 11, left antenna, fourth segment, posterior, ♂; 12, left antenna, posterior, ♂.

Figs 13-15. *S. sanbornei* - 13, left antenna, posterior, paratype ♀; 14, left antenna, fourth segment, posterior, paratype ♂; 15, left antenna, posterior, paratype ♂.

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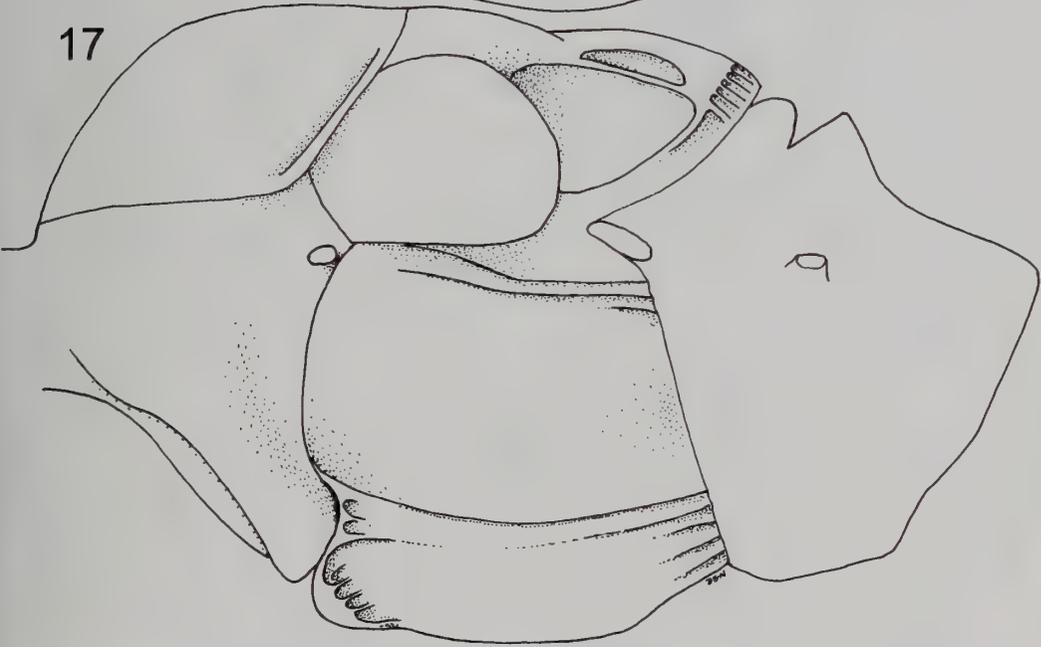
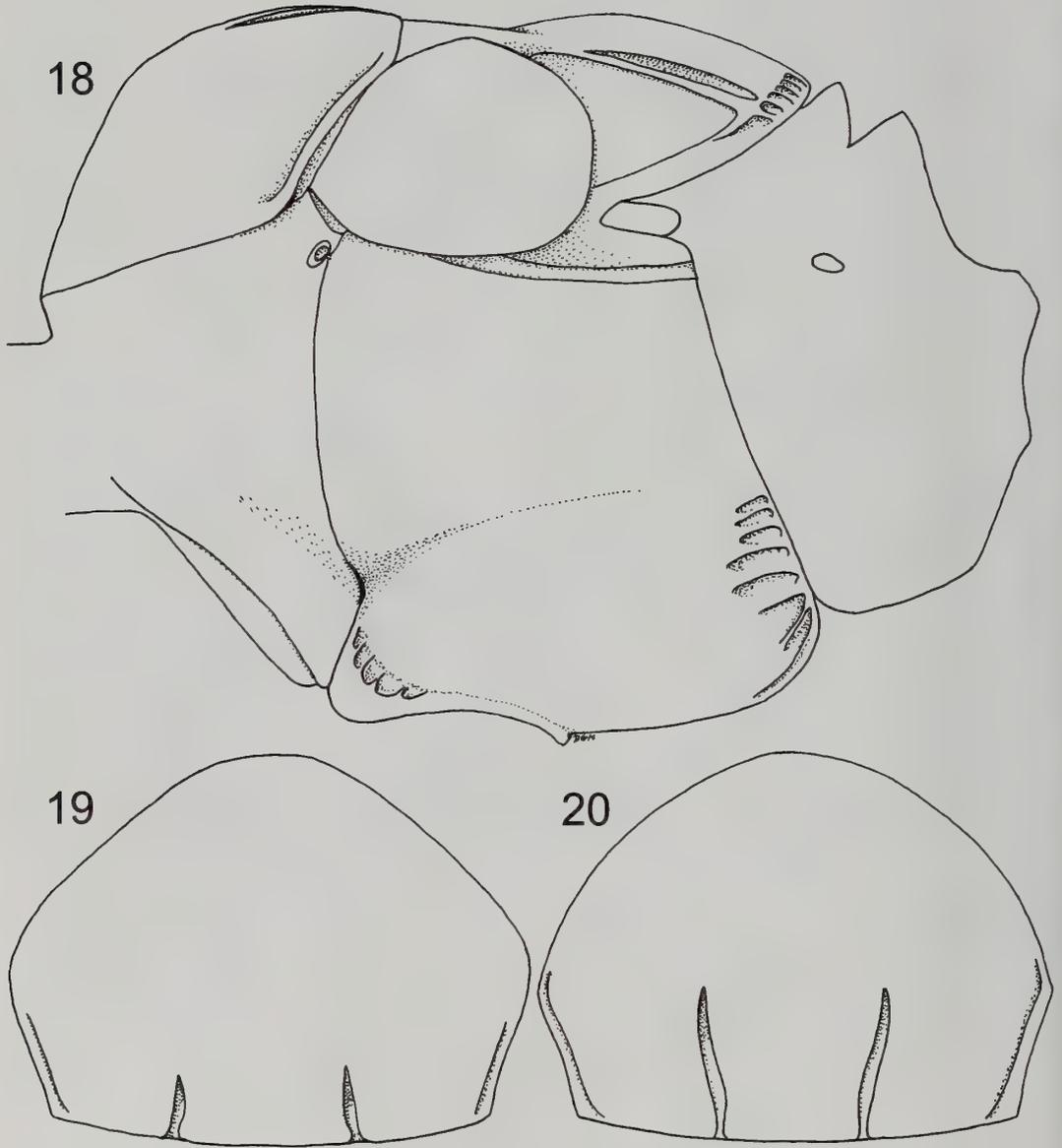


Fig. 16. *Spilomicrus sanbornei* – mesosoma, lateral, paratype ♀. **Fig. 17.** *S. crassiclavis* – mesosoma, lateral, ♂.



Figs 18 & 20. *Spilomicrus formosus* – 18, mesosoma, lateral, ♀; 20, mesoscutum, dorsal, ♀. **Fig. 19.** *S. crassiclavus* – mesoscutum, dorsal, ♀.



Fig. 21. *Spilomicrus formosus* – North-west European distribution.

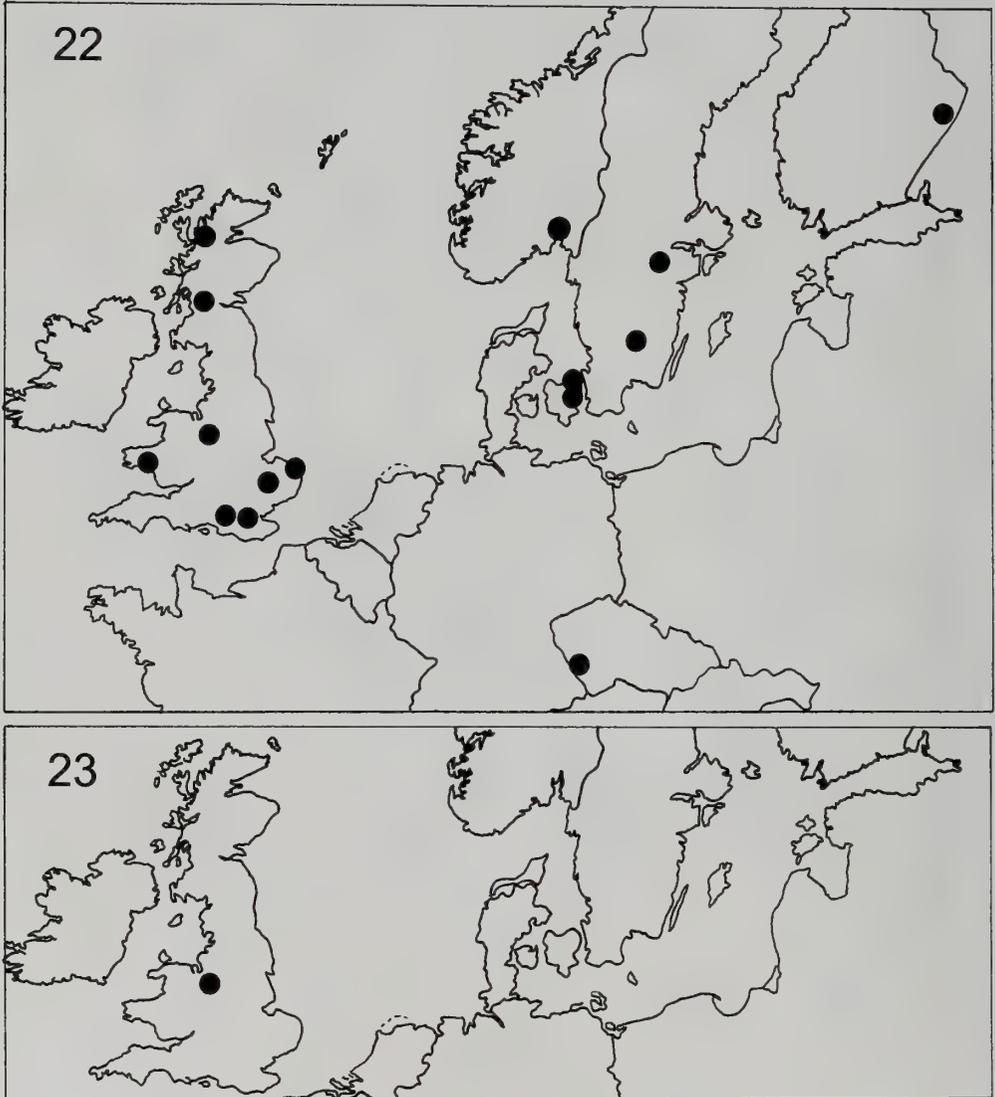


Fig. 22. *Spilomicrus crassiclavis* – distribution. Fig. 23. *S. sanbornei* – North-west European distribution.

A review of the soldierless African termite genus *Amicotermes* Sands 1972 (Isoptera, Termitidae, Apicotermitinae)

W.A. SANDS

Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK.

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SYNOPSIS. The termite genus *Amicotermes* is a member of the soldierless Apicotermitinae (Isoptera, Termitidae), recognised as important constituents of the soil fauna in tropical Africa. Before the current work was begun, 60 species belonging to 16 genera had been recorded, among them the single species from the southern Congo for which the genus was named. New intensive ecological transect sampling in Cameroon and Congo (Brazzaville) by members of the Termite Research Group at The Natural History Museum has greatly increased the observed species diversity of the soil. Eleven new species of *Amicotermes* are keyed and fully described here from a database compiled in DELTA format in PANKEY, which also allows the matrix to be converted to HENNIG86 input or similarity coefficients for phenetic analysis. Phenetic and cladistic analyses of the relationships between the species are provided. All species are illustrated with line drawings and photographic plates.

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INTRODUCTION

It has been noted before that the soldierless Apicotermittinae (Isoptera, Termitidae) are very important constituents of the soil fauna in tropical Africa, being soil or root feeders, or, some of them, active at the soil/wood/litter interface. Soil sampling has shown them to be both abundant and diverse in forest and savanna ecosystems, accounting for a significant part of the live biomass of soil organisms and responsible for a major proportion of soil movement and aeration, contributing also to water penetration (Sands, 1965, Eggleton *et al.*, 1996). Before the current study began, a total of 60 species of soldierless termites belonging to 16 genera had been recorded from the African continent by Sands (1972). A few more genera and species were known from the worker castes alone, but were not described at that time because their characters were not considered to provide as reliable identification as those of the imagos. Since then, further studies of the distinguishing features of the worker castes (Sands, 1992, 1995, 1998) have shown that they can be identified as readily as the imagos, in many cases more easily, and that it is no longer logical to abstain from describing species of soldierless termites recognisable on the basis of their workers alone.

Among the genera previously known, *Amicotermes* was represented by a single species from the southern Congo. The new species described here were, with two exceptions, all collected from rain forest, or degraded derivatives of it, by the members of the termite group at The Natural History Museum, either as part of the NERC-funded TIGER project team in different selected habitats in Cameroon in the Mbamayo forest reserve, or, using a similar transect sampling technique, in the Republic of Congo (Brazzaville) at Mayombe. The purpose of the former project was to examine the effects of different levels of forest degeneration and regeneration, resulting from cultivation and selective logging, on the biodiversity of the soil fauna and its relationship to the carbon cycle (Eggleton *et al.*, 1996).

When the first collections from the Mbalmayo area of Cameroon came to be sorted out, it quickly became evident that the diversity and abundance of termite species in the soil, especially the soil-feeders, of which about half were soldierless Apicotermittinae, was far greater than had been anticipated for this project or had been recorded previously from any ecological sampling, even in rain forests elsewhere. Abundances up to 10,488 m⁻² and live weight biomass up to 123 gm⁻² were recorded. In a significant proportion of the genera examined, new species were found, and indeed, genera new to science were also present. All of these will have to be described and properly enumerated in due course, but the work presented here covers, as a

first instalment, the 11 new species recognised in *Amicotermes*, bringing the total of recorded species for the genus up to 12. This genus was chosen to be examined first because, in an otherwise very difficult group, it has an enteric valve armed with spines and spicules which offer useful taxonomic characters that define species relatively well. Some other genera that remain to be worked out lack this feature and will take much longer to resolve. In the published account of the ecological sampling (Eggleton *et al.* 1996) morpho-species that were thought to be new were designated numerically, there being three such in the genus *Amicotermes*. Further, more careful examination of the material has doubled this number for the Cameroon, and four more were found in the Congo. The last new species was recognised in material acquired earlier from the Upper Guinean Forest in the Ivory Coast. Because of the unevenness of the sampling and knowledge of the ecology of the group in the rest of the Afrotropical zoogeographical region, it is evident that if the entire continent were to be covered in the same detail, the number of species and genera would be multiplied several times over. However, a diligent search through the unidentified accessions from all parts of tropical Africa at The Natural History Museum, including many samples from soil pits collected in the course of earlier ecological studies in Guinean savannah in Nigeria (Sands, 1965a), have failed to produce any further records of *Amicotermes*. It is therefore probably safe to conclude that it is confined to rain forest and this study amounts to a new revision of a single soldierless genus.

METHODS

In order to speed up the recording of taxonomic data and facilitate its processing by computer, the character set was coded and stored in PANKEY (Pankhurst 1986) DELTA [DEscriptive Language for TAXonomy] (Dallwitz & Paine, 1986, Partridge *et al.*, 1986) format. In this state, it may be converted by several sets of programmes into natural language descriptions, dichotomous printed keys, analysed by cladistic or phenetic procedures, or converted into 'expert systems', that is, interactive computerised polyclaves. Other recently published works (Pankhurst, 1991, Sands, 1992, 1998) go into the details of how this is done. The key and descriptions that follow were produced in this way, as were the comparisons between related species. In order to incorporate the new species into the existing genus, the data from Sands (1972) were coded and added by means of the dedicated editor, DEDIT, to the DELTA file, a copy of which is included as an appendix to illustrate the format, because in the author's view, too few taxonomists are

either aware of its value as a tool, or of its relative simplicity in use once the requirements are understood. The full data matrix itself with ranges, means and standard deviations of measurements has been converted to the key and descriptions and is therefore not repeated here, but it can be supplied on request to those interested as a copy of the entire DELTA file on receipt of a single 3.5 inch high density diskette.

COMMENTS ON CHARACTERS USED

Some of the characters used require further explanation. Apart from *A. dibogi*, the genus is remarkably homogeneous in its external features, and a great deal of emphasis is therefore placed on the enteric valve armature and on morphometrics. However, it was thought desirable in constructing a key to give summary descriptions of the salient externally observable characters as well as measurements, to supplement the usually distinctive valve structures, because the latter require quite a difficult dissection and slide mount. An annotated character list is given below, followed by a condensed version of the data matrix as used in the HENNIG86 analysis, since it includes *Acholotermes*, the sister genus of *Amicotermes*, as an outgroup.

Character descriptions, with states

Some of the characters require quite difficult dissections to display them properly. Full descriptions of the techniques involved are published elsewhere (Sands 1998), but summary accounts are given below where appropriate.

Characters 1–5: The system of coding colour of body parts as an ordered multi-state character has been used since 1965. Only the first five grades (Sands 1965) are required here for the relatively lightly sclerotised worker caste, being re-numbered for each character.

1. Head capsule colour: 1. yellow-white 2. pale yellow 3. yellow 4. pale yellow-brown.
2. Antennal flagellum colour of darkest part 1. yellow-white 2. pale yellow 3. yellow 4. pale yellow-brown.
3. Pronotum colour 1. yellow-white 2. pale yellow 3. yellow.
4. Legs colour 1. yellow-white 2. pale yellow 3. yellow.
5. Abdominal tergites colour 1. hyaline 2. yellow-white 3. pale yellow.

Characters 6–10: Head capsule shape is evaluated in facial view. Pilosity is best viewed from below and in front against a lit background; sparse is intended to

mean when the setae are spaced further apart than the length of the longest; two lengths of setae are usually evident, the shorter, general pilosity being randomly distributed while the longer, emergent setae are commonly paired on each side of the mid-line. The term 'fontanelle' is used for convenience although workers do not have a true fontanelle, which is the opening of the frontal gland in soldiers and imagos; some species have a pale spot in this position. The degree of inflation of the postclypeus is estimated partly by its dimensions, but also in profile by the regularity of convexity of its outline.

6. Head capsule shape 1. circular 2. short oval near circular 3. oval.
7. Head capsule setae 1. sparse 2. numerous but not dense.
8. Head capsule emergent, longest setae 1. randomly scattered 2. regularly and symmetrically arranged.
9. Fontanelle: 1. present as pale spot or small depression 2. absent.
10. Postclypeus contour: 1. clearly inflated 2. strongly inflated, bulging, length more than half width at ginglymi.

Characters 11 & 12: The presence of prominent setae arranged in a line or group on the front surface of the fore coxa may be difficult to detect because in this genus they are not particularly 'spine-like'. If viewed in profile against a lit background they can usually be detected as more robust than normal. Fore tibial apical spurs always number three in this genus with the third, outer spur subject to size variation.

11. Fore coxae 1. without prominent larger setae on anterior surface 2. with one to three prominent larger setae on anterior surface 3. with four or more prominent larger setae arranged in line or group on anterior surface.
12. Fore tibial apical spurs numbering three 1. third well developed, at least half the size of the others 2. third much smaller than the other two.

Characters 13–17: Mandible characters including measurements require the cutting edges to be secured transverse, i.e. at right angles, to the optic axis of the lens system containing the graticule. This is particularly important in assessing the visibility and alignment of the left fourth marginal tooth. In order to see these characters clearly, a simple dissection by slitting the adductor apodemes is needed, allowing the mandibles to swing open on their articulations. It is undesirable to detach them from the specimen, since their tetrahedral shape makes them impossible to mount on a slide or secure in a dish in the required position. The dissection is best done with the specimen secured on its back with the finest grade of

stainless steel headless entomological points. The point of a fine scalpel or needle is inserted into the mouth of the specimen, to push aside the labium and hypopharynx. The adductor apodemes are usually visible at the base of the mandibles and can be cut with a single stroke of a fine blade in each direction. A gentle push will then swing the mandibles outwards in turn, and the labrum can be deflected between their separated bases to secure them in position; if necessary the labrum can be pushed out again to allow the mandibles to return to a natural position. The designations of the marginal teeth of the left mandible need further explanation. The first is that immediately proximal to the apical tooth, but the second is incorporated into the cutting edge behind it, forming its curved inner end; the third marginal is separated from the first-plus-second by a distinct notch, while the fourth appears out of alignment with the other marginals, being visible in the gap between the third marginal and the molar prominence; its proximal end, which forms the point of the tooth, is sometimes hidden behind the molar prominence. There are only two marginal teeth on the right mandible in this genus.

13. Left mandible, first marginal tooth 1. with anterior edge distinctly longer than posterior 2. approximately equilateral.
 14. Left third marginal tooth with anterior edge 1. shorter than that of first 2. equal in length to that of first 3. longer than that of first.
 15. Left fourth marginal tooth in front view 1. with proximal end clear of molar prominence 2. just reaches side of molar prominence 3. with proximal end hidden behind molar prominence.
 16. Anterior margin of right first marginal tooth 1. longer than that of second 2. equal in length to that of second 3. shorter than that of second.
 17. Right first marginal tooth with exposed posterior edge 1. equal to that of second marginal 2. longer than that of second marginal.
- Characters 18–22:** The configuration of the parts of the alimentary canal as seen through the unopened body wall has been used and illustrated extensively (Sands, 1972, 1995, 1998) in identifying worker castes. The most important features in *Amicotermes* are the position of the enteric valve seating and the length and width of the first section of the proctodeum (P1). The lines of the heart dorsally and the nerve cord ventrally, although sometimes hard to see, are used to mark the positions of features.
18. Junction of mesenteron and proctodeum 1. starting to left of nerve cord in ventral view 2. starting beneath nerve cord in ventral view 3. starting to right of nerve cord in ventral view.
 19. Proctodeal first segment 1. shorter, length up to eight times proximal width 2. very long, over eight times proximal width.
 20. Proctodeal first segment beyond junction with mesenteron 1. tubular or conical throughout its length 2. dilated to about twice its basal width throughout length.
 21. Lateral displacement of enteric valve in unopened abdomen 1. to left of heart in dorsal view 2. to right of heart in dorsal or to left of nerve cord in ventral view.
 22. Enteric valve 'seating' third lobe 1. smaller than outer pair 2. approximately equal in size to outer pair.

Characters 23–45: The enteric valve is variably sclerotised and armed within its lumen with scales, spines or spicules. In order to display these a dissection is required. Having opened the abdomen by pulling away a section of the body wall with forceps, it is possible simply to pull on the first section of the proctodeum near its distal end to extract the enteric valve from the third (the valve being the second). The valve then needs to be slit longitudinally by inserting into the lumen a micro-scalpel, cleaned, separated where possible from the muscle coats that surround it, and mounted on a microscope slide. The choice of mounting medium is dictated by the fragility of the wisp of tissue that makes up the enteric valve. This prevents the usual dehydration procedures required by most permanent mounts, and necessitates the use of a direct, relaxant temporary medium such as a variant of 'Swan's Berlese'.

Within the enteric valve there are six longitudinal ridges (the 'bourrelets' of Grasse and Noirod (1954)) which carry the main sclerotisations, spines and spicules. The system of numbering the ridges adopted here is that of Sands (1972), in which the single ridge nearest to the front of the specimen, or innermost to the coiling of the gut, is designated 'position number one'; the pair on each side of it are numbered 'position two', the pair beyond them 'position three' and the distal singleton, 'position four'. This is because these positions describe the most common independent dimensions of variation of symmetry, sclerotisation and armature. Because they vary independently, they have to be described separately for each character and its states. This has resulted in a set of characters that appear repetitive for taxa with hexaradially symmetrical valves; however, to do otherwise would mean losing a large proportion of the information content of this important structure. The characters referring to the positions of the largest spines as proximal, mesal or distal, are not intended to imply that there are no spines on the rest of the ridges, merely that where present, they are smaller than the most elongate and conspicuous spines. The ridges also carry subsidiary

armature of scales, spines or spicules. Between and beyond the ridges the wall of the valve may also bear scales, sometimes armed with small spicules.

23. Enteric valve ridges, shape 1. more or less tapering ellipsoid to base of apical spines 2. distinctly 'waisted' at base of apical spines, then wider.
24. Enteric valve ridge in position one 1. sclerotised at distal end, pale brown or yellow-brown 2. weakly sclerotised distally, pale yellow or yellow 3. unsclerotised or colourless throughout.
- 25, 26, 27, as 24 but referring respectively to positions two, three and four.
28. Main armature of enteric valve ridge in position one 1. without large apical spines (retained to allow for the outgroup, but does not apply to *Amicotermes*) 2. with large backwardly directed erect conical spines 3. with very elongated tapered spines.
- 29, 30, 31 as 28 but referring respectively to positions two, three and four.
32. Largest apical spines on ridge one 1. numbering 1-9 2. numbering 10-14 3. numbering 15-20 4. numbering over 20.
- 33, 34, 35 as 32 but referring respectively to positions two, three and four.
36. Longest spines of main armature 1. straight and evenly tapered 2. curved but still evenly tapered.
37. Longest apical spines 1. longer than least width of ridges in position three at base of spines 2. shorter than or equal to least width of ridges in position three.
38. Subsidiary armature on one or more of enteric valve ridges mainly 1. reticulate 2. with backwardly directed scales 3. with backwardly directed scales fringed with small spines or spicules 4. with small single backwardly directed spines on scales 5. with prominent spines different from or smaller than main armature.
39. Subsidiary armature of enteric valve ridges 1. with scales or reticulations well defined, distinct 2. with scales or reticulations indistinct, outlines vague or incomplete.
40. Subsidiary armature of one or more of enteric valve ridges 1. prominent, covering entire ridge surface 2. scattered, somewhat sparse 3. very sparse, few scales fringed with spines or spicules.
41. Subsidiary armature on one or more enteric valve ridges 1. more or less uniform throughout length of ridge 2. graduated, spines or spicules becoming longer towards distal end of ridge.
42. Symmetry of enteric valve armature 1. more or less hexa-radial apart from slight differences in ridge size 2. more or less tri-radial, alternate ridges reduced 3. bilateral due to marked differences in spine and ridge size.
43. Membranous wall of enteric valve between and beyond ridges 1. smooth 2. scaly.

44. Membranous wall of enteric valve between and beyond ridges 1. armed with minute spines or spicules 2. armed with short spines or spicules.
45. Spines or spicules on membranous wall 1. very sparse, scattered 2. numerous but not dense, scattered, fringing scales proximally 3. dense distally, fringing scales proximally.

Characters 46-60: Some of the listed ratios may appear unusual in the comparisons they make; they result from selecting measurements that carried large contrasting weighting coefficients in principal component and canonical variates analyses. Such procedures are now so much the routine that no extended treatment is given here. The rationale for the use of complex ratios rather than the actual discriminant functions is explained in Sands (1972) which also lists the set of measurements used as standard in the soldierless termites (and see also Fig. 1). The measurements are given here to three places of decimals because they were recorded automatically from an electronic filar micrometer and processed simultaneously; it seemed less artificial to give them as recorded rather than to round them to fewer places arbitrarily. In practice it has been found that at this level with this equipment measurements are repeatable within about 3%. The measurements used are mostly self explanatory being the maximum distance between identifiable fixed points. Those that need further explanation are the following: Postclypeus width, taken between the inner curves of the ginglymi of the mandibles, which are always recognisable as strongly sclerotised articulations at the corners of the postclypeus; Left mandible, La, distance between the points of the apical and first marginal teeth; L1, distance between the points of the first marginal tooth and the third marginal, because the second is often reduced or obsolete; Lm, distance between the point of the third marginal and the intersection of the fourth, subsidiary marginal (some authors call this the 'molar tooth' but its function is marginal) with the molar prominence, whether this is a notch or the point where the fourth marginal passes behind the prominence; Right mandible, Ra, as left; R1, distance between the points of the first and second marginal teeth; Rm, distance between point of second marginal and the intersection of its hind margin with the molar plate; the front edge of this tooth is also measured, in order to provide a 'second marginal index' to indicate its degree of reduction. It is important when taking measurements to ensure that the specimen is held exactly transverse to the optic axis of the lens tube of the eyepiece containing the graticule.

46. Head capsule width (range, mean, SD) mm.
47. Postclypeus width (range, mean, SD) mm.
48. Postclypeus length (range, mean, SD) mm.
49. Left mandible index (range, mean).

50. Right mandible index (range, mean).
51. Right second marginal index (range, mean).
52. Right first to second marginal index (range, mean).
53. Pronotum width (range, mean, SD) mm.
54. Pronotum length (range, mean, SD) mm.
55. Hind tibia length (range, mean, SD) mm.
56. Fore tibia length (range, mean, SD) mm.
57. Fore tibia thickness (range, mean, SD) mm.
58. Fore tibial index (length over width) (range, mean).
59. Left mandible, complex ratio La divided by L1.Lm (range, mean).
60. Right mandible, complex ratio Ra divided by R1.Rm (range, mean).

Condensed data matrix with outgroup

The condensed data matrix, outgroup included, is shown in Table 1. The programmes used to process descriptions and keys were DESCRIP3 and KCONP with KCONI, the interactive key construction programme and KPRINT from the PANKEY set (Pankhurst, 1986, 1991). An MS-DOS binary file of the data to run with PANKEY ONLIN7 that will provide an interactive but un-illustrated polyclave is available, for use in conjunction with the illustrations in this paper, from the author on request and provision of one MS-DOS-formatted 3.5" or 5.25" HD diskette. The programme itself must be obtained from EXETER SOFTWARE, 100 North Country Road, Setauket, New York 11733, USA. The advantage of a polyclave is that it can be entered with any character found easiest by the user and any path can be followed through the data matrix, as opposed to the fixed path set by a dichotomous key.

The Cameroon material examined was all collected by members of the TIGER team, some in the period July to December, 1992 and some later, up to 1997. They were variously Drs D. Bignell, P. Eggleton, D. Jones, J. Lawton and T. Wood, and Luc Dibog (Eggleton *et al.*, 1996). The Congo material was collected later, in the course of a single expedition by Dr Eggleton and Mr. Davies. It is not practicable to distinguish the contributions of individual participants in the lists of material examined.

AMICOTERMES Sands 1972

(Amicus, L., 'friend (ly), kind')

Type-species: *Amicotermes galenus* Sands 1972

Imago. See Sands 1972. None known apart from Type-species.

Worker. Small to medium-sized, head capsule width 0.565 to 0.800 mm; head capsule setae usually sparse; postclypeus strongly inflated, bulging, length more than half its width at the ginglymi, width 0.3–0.434, length 0.154–0.25 mm. Fore tibia moderately to strongly

swollen, index (length/width) 2.954 to 4.759. Apical teeth of mandibles longer than first marginals, left mandible index 0.697 to 1.205, right mandible index 0.879 to 1.374; left fourth marginal tooth with proximal point clear or hidden behind molar prominence, complex ratio La divided by L1.Lm 17.556 to 37.866; point of first marginal tooth of right mandible behind line from apical to second marginal, front edge of first marginal shorter than or subequal to that of second, its exposed posterior edge longer than that of the second marginal, right first to second marginal index 1.35 to 2.094; second marginal prominent, second marginal index 0.788 to 1.262, complex ratio Ra divided by R1.Rm 20.164 to 34.01. Crop large with hemispherical 'bursters' on front dorsum, gizzard bell-shaped, not tapered to enter mesenteron. Mesenteric junction with proctodeum nearly transverse, slightly angled, in ventral view of unopened abdomen beneath or to right of malpighian knot, beneath or slightly to left or right of nerve cord. Enteric valve seating three-lobed, the third, inner, smaller than or equal to the outer two, connected to third section of proctodeum ('pouch') by very long neck, left lateral or dorsal in position in unopened abdomen. Main armature of enteric valve ridges consists of tapered apical spines, protruding through valve exit into third section of proctodeum, subsidiary armature varies from prominent spines different from or smaller than main armature to scales fringed with minute spicules or bearing single small spines; membranous wall of enteric valve between and beyond ridges usually scaly, with spicules.

Amicotermes is a genus easily recognised in the worker caste by the several features of the abdominal anatomy visible from the exterior and especially by the very characteristic internal armature of the enteric valve, which also supplies many important specific characters. The workers are small to medium-sized among soldierless Apicotermitinae, and although fairly common, are not the most numerous members of this group to be found in ecological soil samples.

Autothysis (the suicidal rupture of the body wall by the contraction of abdominal muscles, accompanied by the discharge of defensive fluids or gut contents) as a defence mechanism against small predators such as ants is common in the soldierless Apicotermitinae (Sands, 1972, 1982) and its development may be responsible for the loss of the soldier caste. In this genus, extreme autothysis is characterised by a pair of hemi-spherical 'bursters', apparently inflated from the front of the crop by pressure from the contracting abdominal wall muscles, which cause the dorsal body wall to rupture in front of the first abdominal tergite, so that few specimens in any series are not so damaged and most of these have distorted abdomens. Only in one species, *A. tithasus* Sands, 1972 of the sister-group *Acholotermes* has a similar bell-shaped proventriculus been observed and here the rupture of

Table 1 Condensed data matrix, outgroup (in parentheses) included. Continuous variables (measurements) are coded as means allocated to key states, while variable multi-states are coded as medians. Missing or inapplicable data is shown as a query.

	characters 1–60						
(<i>Acholotermes</i>)	2322121122	1111132211	2213333111	1??????211	112125??34	??????6??	
<i>autothysis</i>	2311122122	2111122211	2121111333	3213212512	2221321222	3412211322	
<i>camerunensis</i>	1111121222	2121222222	2112222222	2323212521	2121242223	3422333312	
<i>congoensis</i>	1211121212	3212132211	222222333	3212122512	2221242234	3322221422	
<i>cristatus</i>	2211121212	3222232211	2211111222	2111112212	1122343333	33?3331422	
<i>dibogi</i>	2312121122	2121232122	1213333333	3222212511	2121132323	3322331512	
<i>galenus</i>	3311211122	3211122211	212222333	3112111512	2321264456	3434321524	
<i>gasteruptus</i>	1311121122	2111132211	2121111333	3313121522	2221221222	331?111322	
<i>ivorensis</i>	222221112	1221122211	221222333	3111111323	22111??33	3423221312	
<i>mayombei</i>	1111121222	3112232211	2121111333	3113122512	2322332234	4311221412	
<i>multispinus</i>	1111121222	3122232211	212222333	3314121522	22222?2223	32?1111322	
<i>mbalmayoensis</i>	1311122222	1121332211	211222333	3212212422	1121364334	344344?422	
<i>spiculatus</i>	2211131222	3122132211	2113212222	2113112521	2322243323	3423432412	

the body wall in autothysis appears to be mediated more by pressure from the crop against the underside of the slightly inflated colon which crosses it at this point. The proctodeal first segment beyond the junction with the mesenteron is usually tubular throughout its length. The mandibles are generally similar to those of *Acholotermes*.

In *Acholotermes* the main armature of the hexa-radially symmetrical enteric valve ridges is never more than a few minute spicules fringing scales, but the membranous wall between and beyond the ridges is scaly and spiculate like that of *Amicotermes*. The other genera having enteric valve armature apparently related to that of *Amicotermes* are *Apagotermes* and *Ateuchotermes*. The former is smaller and the latter larger, both having different mandibles from *Amicotermes* and both having specialised features of their valve armature, which, however, do not include a spiculate and scaly or carunculate inter-ridge membrane (Sands 1972, 1998).

Key to the species of *AMICOTERMES*

Sands 1972

The disadvantages of dichotomous keys resulting from forcing on the user a single path chosen by the author through the data matrix are well-known. In the key which follows, some couplets appear longer than usual, especially when nearing an identification. This is necessitated by the extreme difficulty of identifying worker castes on the basis of variable characters and some that require delicate dissections. The solution

offered is a combination of more easily observed features that are currently diagnostic and may provide a simple identification but might break down because the variation is imperfectly known, and more difficult but possibly more reliable characters. This is an attempt at compromise between the fallible simplicity of a normal dichotomous key and the greater flexibility of a polyclave.

- 1 Head capsule width 0.763 to 0.800 mm, postclypeus width 0.413 to 0.434 mm 2
- Head capsule width 0.565 to 0.717 mm, postclypeus width 0.300 to 0.395 mm 3
- 2 Hind tibia length 0.725 mm, fore tibia length 0.563 mm, fore tibia thickness 0.13 mm, fore tibial index (length over width) 4.327, left mandible index 1.092, right mandible, complex ratio Ra divided by R1.Rm, 31.28. Fore coxae with four or more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, but third vestigial or much smaller than the other two. Left mandible, first marginal tooth with anterior edge distinctly longer than posterior, left fourth marginal tooth in front view with proximal end clear of molar prominence; anterior margin of right first marginal tooth equal in length to that of second. Enteric valve ridges, distinctly 'waisted' at base of apical spines, then wider, longest apical spines on ridge one numbering 1–9, those of ridges in position three longer than least width at base of spines, subsidiary armature on one or more of enteric valve ridges mainly with prominent spines different from or smaller than main armature, graduated, spines or spicules becoming longer towards distal end of ridge, scales or reticulations well defined, distinct, symmetry of enteric valve armature bilateral due

- to marked differences in spine and ridge size, spines or spicules on membranous wall numerous but not dense, scattered, fringing scales proximally
- *galenus* (page 159, Figs 76–82, 177, 178)
- Hind tibia length 0.779 to 0.82 mm, fore tibia length 0.614 to 0.677 mm, fore tibia thickness 0.159 to 0.173 mm, fore tibial index (length over width) 3.602 to 4.077, left mandible index 0.896 to 0.978, right mandible, complex ratio Ra divided by R1.Rm, 20.164 to 26.881. Fore coxae without prominent larger setae on anterior surface, fore tibial apical spurs numbering three, third well developed, at least half the size of the others. Left mandible, first marginal tooth approximately equilateral, left fourth marginal tooth in front view just reaches side of molar prominence, or with proximal end hidden behind molar prominence; anterior margin of right first marginal tooth shorter than that of second, enteric valve ridges, more or less tapering ellipsoid to base of apical spines, longest apical spines on ridge one numbering 10–14, those of ridges in position three shorter than or equal to least width, subsidiary armature on one or more of enteric valve ridges mainly with small single backwardly directed spines on scales, more or less uniform throughout length of ridge, scales or reticulations indistinct, outlines vague or incomplete, symmetry of enteric valve armature more or less hexa-radial apart from slight differences in ridge size, spines or spicules on membranous wall dense distally, fringing scales proximally
- ... *mbalmayoensis* (page 163, Figs 125–137, 183, 184)
- 3 Symmetry of enteric valve armature more or less hexa-radial apart from slight differences in ridge size 4
- Symmetry of enteric valve armature more or less tri-radial, alternate ridges reduced, or bilateral due to marked differences in spine and ridge size 6
- 4 Lateral displacement of enteric valve in unopened abdomen to left of heart in dorsal view, first section of proctodeum very long. Main armature of enteric valve ridges with very elongated tapered spines, ridges unsclerotised or colourless, spines or spicules on membranous wall very sparse, scattered
- *dibogi* (page 158, Figs 62–75, 176)
- Lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view. Main armature of enteric valve ridges with large backwardly directed erect conical spines, ridges sclerotised at distal ends, pale yellow to pale brown or yellow-brown, spines or spicules on membranous wall numerous or dense distally, fringing scales proximally
- 5
- 5 Fore coxae with four or more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, but third much smaller than the other two. Left mandible, third marginal tooth with anterior edge equal in length to that of first. Proctodeal first segment shorter, up to eight times proximal width, enteric valve ‘seating’ third lobe approximately equal in size to outer pair. Enteric valve ridges sclerotised at distal end, pale brown or yellow-brown, largest spines on ridges numbering up to 12; subsidiary armature on one or more ridges mainly with backwardly directed, well defined distinct scales, some fringed with small, scattered, sparse spines or spicules, more or less uniformly distributed throughout length of ridge; membranous wall of enteric valve between and beyond ridges armed with short spines or spicules, dense distally, fringing scales proximally
- *cristatus* (page 157, Figs 47–61, 173, 174)
- Fore coxae without prominent larger setae on anterior surface, or with one to three at most, fore tibial apical spurs numbering three, third well developed, at least half the size of the others. Left mandible, third marginal tooth with anterior edge shorter than that of first. Proctodeal first segment longer, over eight times proximal width, enteric valve ‘seating’ third lobe smaller than outer pair. Enteric valve ridges weakly sclerotised distally, pale yellow or yellow, largest spines on ridges numbering 12–25; subsidiary armature on one or more ridges mainly with prominent spines different from or smaller than main armature, borne on indistinct scales or reticulations, covering entire ridge surface, graduated, spines or spicules becoming longer towards distal ends of ridges; membranous wall of enteric valve between and beyond ridges armed with minute spines or spicules, numerous but not dense, scattered, fringing scales proximally
- *camerunensis* (page 154, Figs 16–28, 175)
- 6 Hind tibia length 0.784 to 0.794 mm, fore tibia length 0.620 to 0.625 mm Enteric valve main armature of all ridges with large backwardly directed erect conical spines, but ridge in position one unsclerotised or colourless throughout, ridge two weakly and ridges three and four fully sclerotised yellow-brown; subsidiary armature of enteric valve ridges prominent, covering entire ridge surface *spiculatus* (page 165, Figs 151–161, 186)
- Hind tibia length 0.565 to 0.736 mm, fore tibia length 0.489 to 0.574 mm Enteric valve main armature of all ridges with very elongated tapered spines, uniformly sclerotised, yellow-brown or weakly sclerotised distally, pale yellow or yellow; subsidiary armature of enteric valve ridges scattered, somewhat or very sparse, few scales fringed with spines or spicules
- 7
- 7 Longest apical spines of enteric valve armature shorter than or equal to least width of ridges in position three, subsidiary armature of enteric valve ridges with scales or reticulations well defined, distinct
- 8
- Longest apical spines of enteric valve armature longer than least width of ridges in position three at base of spines, subsidiary armature of enteric valve ridges with scales or reticulations indistinct, outlines vague or incomplete
- 10
- 8 Left fourth marginal tooth in front view just reaches side of molar prominence. Symmetry of enteric valve armature bilateral due to marked differences in spine and ridge size, membranous wall of enteric valve between and beyond ridges armed with short spicules
- *mayombei* (page 162, Figs 111–124, 181, 182)
- Left fourth marginal tooth in front view with proximal end clear of molar prominence. Symmetry of enteric

DESCRIPTIONS OF SPECIES

Amicotermes autothysius sp. n.

(Figs 1–15, 169, 170)

Head capsule pale yellow or yellow, antennal flagellum colour of darkest part yellow or pale yellow-brown, pronotum and legs yellow-white, abdominal tergites hyaline.

Head capsule short oval near circular, setae numerous but not dense, emergent, longest setae randomly scattered. Fontanelle absent. Fore coxae without prominent larger setae or with up to four or sometimes more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, third well developed, at least half the size of the others.

Left mandible, first marginal tooth with anterior edge distinctly longer than posterior or approximately equilateral, third marginal tooth with anterior edge shorter than or equal in length to that of first, fourth marginal tooth in front view with proximal end clear of molar prominence. Right mandible, anterior edge of first marginal tooth equal in length to or shorter than that of second.

Junction of mesenteron and proctodeum starting beneath or to right of nerve cord in ventral view, proctodeal first segment shorter, up to eight times proximal width tubular throughout its length, lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view, enteric valve ‘seating’ third lobe smaller than outer pair.

Enteric valve ridges, distinctly ‘waisted’ at base of apical spines, then wider, all ridges sclerotised at distal end, pale brown or yellow-brown, main armature with very elongated tapered spines, the largest on ridges one and four numbering 1–14, those on ridges two, 1–9, and on ridges three, 10–20, symmetry of enteric valve armature more or less tri-radial, alternate ridges reduced; longest spines of main armature straight or curved but still evenly tapered, shorter than or equal to least width of ridges in position three; subsidiary armature on one or more of enteric valve ridges mainly with scattered, somewhat sparse prominent spines different from or smaller than main armature, graduated, spines or spicules becoming longer towards distal end of ridge, scales or reticulations well defined, distinct; membranous wall of enteric valve between and beyond ridges scaly, armed with minute spicules, dense distally, fringing scales proximally.

Measurements and diagnostic ratios [24 individuals from 9 series]:

Head capsule width 0.565 to 0.717 mm (mean 0.633 SD 0.039).

valve armature more or less tri-radial, alternate ridges reduced, membranous wall of enteric valve between and beyond ridges armed with minute spicules 9

9 Head capsule with emergent, longest setae regularly and symmetrically arranged. Fore tibial apical spurs numbering three, but third vestigial or much smaller than the other two. Enteric valve ‘seating’, third lobe approximately equal in size to outer pair; enteric valve ridges weakly sclerotised distally, pale yellow or yellow; spines or spicules on membranous wall of valve between ridges numerous but not dense, scattered, fringing scales proximally *congoensis* (page 156, figs 29–46, 171, 172)

– Head capsule with emergent, longest setae randomly scattered. Fore tibial apical spurs numbering three, third well developed, at least half the size of the others. Enteric valve ‘seating’, third lobe smaller than outer pair, enteric valve ridges sclerotised at distal ends, pale brown or yellow-brown, spines or spicules on membranous wall dense distally, fringing scales proximally *autothysius* (page 153, figs 1–15, 169, 170)

10 Anterior margin of first marginal tooth of right mandible equal in length to that of second. Enteric valve ‘seating’ third lobe approximately equal in size to outer pair; largest apical spines of enteric valve armature on ridges one and three numbering 1–9; subsidiary armature on enteric valve ridges very sparse, with a few backwardly directed scales fringed with small spines or spicules, or with small single backwardly directed spines on scales; membranous wall of enteric valve between and beyond ridges smooth, with very sparse, scattered spines or spicules *ivoensis* (page 161, figs 99–110, 180)

– Anterior margin of right first marginal tooth shorter than that of second. Enteric valve ‘seating’ third lobe smaller than outer pair; largest apical spines of enteric valve armature on ridge one numbering 10–20, those on ridges three numbering 10 to over 20; subsidiary armature on one or more of enteric valve ridges with scattered, somewhat sparse prominent spines different from or smaller than main armature; membranous wall of enteric valve between and beyond ridges scaly, with numerous but not dense scattered spicules, fringing scales proximally 11

11 Head capsule with emergent, longest setae regularly and symmetrically arranged. Left mandible, third marginal tooth with anterior edge equal in length to that of first. Enteric valve ridges weakly sclerotised distally, pale yellow or yellow, positions one and three with 20 or more apical spines; membranous wall of enteric valve between and beyond ridges armed with short spicules *multispinus* (page 164, figs 138–150, 185)

– Head capsule with emergent, longest setae randomly scattered. Left mandible, third marginal tooth with anterior edge shorter than that of first. Enteric valve ridges sclerotised at distal end, pale brown or yellow-brown, positions one and three with 10–20 apical spines; membranous wall of enteric valve between and beyond ridges armed with minute spicules *gasteruptus* (page 160, figs 83–98, 179)

Postclypeus width 0.300 to 0.395 mm (mean 0.332 SD 0.026).

Postclypeus length 0.154 to 0.233 mm (mean 0.185 SD 0.021).

Left mandible index 0.697 to 1.144 (mean 0.843).

Right mandible index 0.879 to 1.278 (mean 1.040).

Right second marginal index 0.817 to 1.166 (mean 0.982).

Right first to second marginal index 1.432 to 2.095 (mean 1.734).

Pronotum width 0.375 to 0.495 mm (mean 0.424 SD 0.027).

Pronotum length 0.169 to 0.293 mm (mean 0.209 SD 0.024).

Hind tibia length 0.565 to 0.706 mm (mean 0.649 SD 0.032).

Fore tibia length 0.489 to 0.556 mm (mean 0.517 SD 0.018).

Fore tibia thickness 0.131 to 0.144 mm (mean 0.138 SD 0.004).

Fore tibial index (length over width) 3.441 to 3.984 (mean 3.741).

Left mandible, complex ratio La divided by L1.Lm 17.556 to 29.807 (mean 23.846).

Right mandible, complex ratio Ra divided by R1.Rm 20.717 to 34.01 (mean 25.475).

COMPARISONS. The Cameroonian species most closely related to *A. autothysius* is *A. gasteruptions*, from which it is only distinguished by the shorter apical spines of the enteric valve main armature and the more distinct outlines of the scales of the subsidiary armature. Its symmetry in *A. autothysius* also tends towards the bilateral rather than being clearly tri-radial. This pair of species forms a terminal group in all the trees apart from the Saitou and Nei (1987) Neighbour-Joining tree. *A. camerunensis* has the fourth marginal tooth of the left mandible just reaching the side of the molar prominence, a proportionately longer fore tibia, and a hexa-radial enteric valve armature with large straight conical spines. In *A. congoensis* the third fore tibial apical spur is reduced, being one third or less the length of the others, and the third lobe of the enteric valve seating is roughly equal in size to the outer pair; the largest apical spines of the enteric valve armature are generally longer and the ridges more clearly triradial. *A. cristatus* is generally larger and also shares the features that separate *A. camerunensis*. *A. dibogi* differs in the proportions of the mandibular teeth, but most notably in the greater length and inflation of the first proctodeal segment, hence also the dorsal position of the enteric valve seating; the valve armature is quite different from any other member of the genus being armed with very fine long apical spines and highly spiculate fringed scales. *A. galenus* is, again, larger and the enteric valve armature differs in the length and straightness of the

apical spines. *A. ivorensis* has fewer head setae and lacks prominent fore coxal setae, while its enteric valve has fewer but longer apical spines and a much less developed subsidiary armature. In *A. mayombei* the fourth marginal tooth of the left mandible just reaches the side of the molar prominence; the spiculate fringes of the inter-ridge membrane of the enteric valve are denser and longer than in *A. autothysius* and the symmetry of the valve is more bilateral. *A. mbalmayoensis* is considerably larger and its enteric valve is hexa-radially symmetrical with differently shaped ridges on which the subsidiary armature consists of single small spines on indistinct scales, more or less uniform over the entire ridge surface. In *A. multispinus* the left fourth marginal tooth just reaches the side of the molar prominence; the enteric valve ridges carry longer and more numerous apical spines, while the scales of the subsidiary armature are very indistinct in outline. Finally, *A. spiculatus* has longer and slightly more slender legs, and the enteric valve is bilaterally symmetrical, ridges three and four being differentially sclerotised and three, much larger while ridge one is colourless and two intermediate; the entire ridge surfaces are spiny with the subtending scales very weakly marked.

MATERIAL EXAMINED. [total 13 series]

Holotype, worker and Paratypes from Type series (field collection number, H₂P-2), **Cameroon:** Mbalmayo Forest Reserve, Ekombitie July 1996 (Eggleton *et al.*); other Paratype material, Eboufiek, July–Aug. 1992, Ekombitie, Ebogo, Nov. 1995, Ebogo, Ekombitie, 5 series, Feb. 1996, Ebogo, Mar. 1996, Ekombitie, Ebogo, 3 series, July 1996, (Eggleton *et al.*) (all in BMNH).

Amicotermes camerunensis sp. n.

(Figs 16–28, 175)

Head capsule yellow-white or pale yellow, antennal flagellum, colour of darkest part, pronotum and legs yellow-white, abdominal tergites hyaline.

Head capsule circular or short oval near circular, setae sparse, emergent, longest setae regularly and symmetrically arranged. Fontanelle absent. Fore coxae without or with one to three prominent larger setae on anterior surface, fore tibial apical spurs numbering three, third well developed, at least half the size of the others.

Left mandible, first marginal tooth approximately equilateral, third marginal tooth with anterior edge shorter than that of first, fourth marginal tooth in front view just reaches side of molar prominence. Right mandible, anterior edge of first marginal tooth equal in length to or shorter than that of second.

Junction of mesenteron and proctodeum starting to left of or beneath nerve cord in ventral view, proctodeal

first segment longer, over eight times proximal width, tubular throughout its length or dilated to about twice its basal width, lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view; enteric valve 'seating' third lobe smaller than outer pair.

Enteric valve ridges, more or less tapering ellipsoid to base of apical spines, weakly sclerotised distally, pale yellow or yellow, main armature of all valve ridges with large backwardly directed erect conical spines, the largest numbering 10–20, the longest straight and evenly tapered, shorter than or equal to least width of ridges in position three, symmetry of enteric valve armature more or less hexa-radial apart from slight differences in ridge size; subsidiary armature on one or more of enteric valve ridges mainly with prominent spines different from or smaller than main armature covering entire ridge surface, graduated, spines or spicules becoming longer towards distal end of ridge, scales or reticulations indistinct, their outlines vague or incomplete; membranous wall of enteric valve between and beyond ridges scaly, armed with numerous but not dense minute spines or spicules, scattered, fringing scales proximally.

Measurements and diagnostic ratios [15 individuals from 5 series]:

Head capsule width 0.652 to 0.711 mm (mean 0.687 SD 0.016).

Postclypeus width 0.340 to 0.370 mm (mean 0.360 SD 0.009).

Postclypeus length 0.172 to 0.215 mm (mean 0.199 SD 0.012).

Left mandible index 0.731 to 0.902 (mean 0.839).

Right mandible index 0.992 to 1.187 (mean 1.093).

Right second marginal index 0.806 to 1.175 (mean 0.973).

Right first to second marginal index 1.643 to 2.088 (mean 1.820).

Pronotum width 0.411 to 0.468 mm (mean 0.447 SD 0.017).

Pronotum length 0.192 to 0.251 mm (mean 0.218 SD 0.019).

Hind tibia length 0.696 to 0.794 mm (mean 0.74 SD 0.026).

Fore tibia length 0.589 to 0.632 mm (mean 0.607 SD 0.014).

Fore tibia thickness 0.147 to 0.205 mm (mean 0.168 SD 0.013).

Fore tibial index (length over width) 2.954 to 4.121 (mean 3.624).

Left mandible, complex ratio La divided by L1.Lm 18.546 to 23.477 (mean 21.018).

Right mandible, complex ratio Ra divided by R1.Rm 22.193 to 29.197 (mean 25.539).

COMPARISONS. *A. camerunensis* has already been compared with *A. autothysius* under that species. *A. congoensis* differs in having shorter legs; the anterior edge of the left third marginal tooth is equal to that of the first and the fourth marginal has its proximal end clear of the side of the molar prominence; the third lobe of the enteric valve seating is approximately equal to the other two, while the spines of the main armature are curved on a tri-radial valve. In *A. cristatus* the third fore tibial apical spur is smaller and the front edge of the third marginal tooth of the left mandible is equal in length to that of the first; the apical spines of the main enteric valve armature are fewer and the subsidiary armature is much less developed. *A. dibogi* is characterised externally by the very long, dilated P1 which pushes the enteric valve seating with its three equal lobes into a dorsal position to the left of the heart line; the main armature of the enteric valve is quite different, with its slender apical spines and the subsidiary armature with well defined scales fringed with spicules. *A. galenus* is larger and has the front edge of the left first marginal tooth longer than the hind edge, with the fourth marginal clear of the molar prominence; the mandibular indices are higher; the apical spines of the main enteric valve armature are fewer, more slender and longer on a bilaterally symmetrical valve. *A. gasteruptus* is smaller, with shorter hind tibiae; its enteric valve ridges are 'waisted' apically with elongated tapered curved spines, fewer in number on ridges two and four of a tri-radially symmetrical valve. While about the same size, *A. ivorensis* has shorter legs and the left fourth marginal tooth clear of the molar prominence; the third lobe of the enteric valve seating is approximately equal to the other two and the main armature has fewer, longer apical spines on a tri-radial valve with reduced subsidiary armature. In *A. mayombei* the front edge of the left first marginal tooth is longer than its hind edge and equal to that of the third, while the front edge of the right first marginal is shorter than that of the second; the enteric valve ridges are, again, 'waisted' and one, two and four bear fewer spines on a bilaterally symmetrical valve. *A. mbalmayoensis* is larger and the subsidiary armature of its enteric valve ridges consists of small single spines on scales, more or less uniform throughout the length of each ridge. *A. multispinus* is smaller, with shorter legs; the front edges of the left first and third marginals are subequal and that of the right first marginal is shorter than that of the second; the enteric valve ridges are again, 'waisted' and the longest apical spines on ridges three are longer than the least width of these ridges, the symmetry of the valve being tri-radial. Finally, in *A. spiculatus* the front edges of the left first and third marginals are subequal, the proximal end of the fourth marginal is clear of the molar prominence and the front edge of the right first marginal is shorter than that of the second; the enteric

valve armature, while superficially similar, is distinctive in being bilaterally symmetrical owing to differential sclerotisation of the ridges.

MATERIAL EXAMINED. [total, 6 series]

Holotype worker and Paratypes from Type series (field collection no. Soil#1), **Cameroon:** Mbalmayo Forest Reserve, Eboufek July–Aug. 1992 (Eggleton *et al.*); other Paratype material, Ebogo, 2 series, July–Aug. 1992, Ebogo, Feb. 1996, Ekombitie, Ebogo July 1996 (Eggleton *et al.*) (all in BMNH).

Amicotermes congoensis sp. n.

(Figs 29–46, 171, 172)

Head capsule yellow-white or pale yellow, antennal flagellum, colour of darkest part, pale yellow or yellow, pronotum and legs yellow-white, abdominal tergites hyaline.

Head capsule short oval near circular, setae sparse or numerous but not dense, emergent, longest setae regularly and symmetrically arranged. Fontanelle present as pale spot or small depression or absent. Fore coxae with four or more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, but third vestigial or much smaller than the other two.

Left mandible, first marginal tooth with anterior edge distinctly longer than posterior or approximately equilateral, third marginal tooth with anterior edge equal in length to that of first, fourth marginal tooth in front view with proximal end clear of molar prominence. Right mandible, anterior edge of first marginal tooth shorter than that of second.

Junction of mesenteron and proctodeum starting to left of or beneath nerve cord in ventral view, proctodeal first segment shorter, up to eight times proximal width, tubular throughout its length, lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view, enteric valve 'seating' third lobe approximately equal in size to outer pair.

Enteric valve ridges, more or less tapering ellipsoid to base of apical spines or distinctly 'waisted' at base of apical spines, then wider, weakly sclerotised distally, pale yellow or yellow, main armature with very elongated tapered spines, the largest on ridges one and three numbering 10–14, those on ridges two and four numbering up to 10, longest spines curved but still evenly tapered, shorter than or equal to least width of ridges in position three, symmetry of enteric valve armature more or less tri-radial, alternate ridges reduced; subsidiary armature on one or more of enteric valve ridges with scattered, somewhat sparse, prominent spines different from or smaller than main armature, graduated, spines becoming longer towards distal end of ridge, scales or reticulations well defined,

distinct; membranous wall of enteric valve between and beyond ridges scaly armed with minute numerous but not dense spicules, scattered, fringing scales proximally.

Measurements and diagnostic ratios [15 individuals from 4 series]

Head capsule width 0.659 to 0.705 mm (mean 0.684 SD 0.014).

Postclypeus width 0.340 to 0.380 mm (mean 0.365 SD 0.013).

Postclypeus length 0.177 to 0.215 mm (mean 0.197 SD 0.011).

Left mandible index 0.808 to 1.205 (mean 0.940).

Right mandible index 0.971 to 1.374 (mean 1.168).

Right second marginal index 0.885 to 1.174 (mean 1.019).

Right first to second marginal index 1.350 to 1.921 (mean 1.695).

Pronotum width 0.410 to 0.472 mm (mean 0.450 SD 0.019).

Pronotum length 0.184 to 0.236 mm (mean 0.213 SD 0.017).

Hind tibia length 0.670 to 0.710 mm (mean 0.692 SD 0.013).

Fore tibia length 0.535 to 0.574 mm (mean 0.553 SD 0.011).

Fore tibia thickness 0.136 to 0.150 mm (mean 0.142 SD 0.004).

Fore tibial index (length over width) 3.598 to 4.185 (mean 3.889).

Left mandible, complex ratio La divided by L1.Lm 17.791 to 37.866 (mean 25.316).

Right mandible, complex ratio Ra divided by R1.Rm 21.345 to 32.805 (mean 25.805).

COMPARISONS. *A. congoensis* has already been compared with the preceding two species; It forms a terminal pair with *A. multispinus* in most of the phenetic trees, but joins with *A. autothysius*, *A. gasteruptus* and *A. mayombe* at node 16 in the strict consensus tree; the comparisons with the two latter species are given below. *A. cristatus* is larger with longer fore legs and the left fourth marginal tooth just reaching the side of the molar prominence; the spines of the main armature of the enteric valve ridges are large, straight and conical on a more or less hexa-radially symmetrical valve. *A. dibogi* has the front edge of the left third marginal tooth shorter than that of the first, and the fourth just reaching the side of the molar prominence; the main distinguishing feature is again the long dilated P1 with the enteric valve seating dorsal, to the left of the heart; the hexa-radial enteric valve armature with its fine straight spines and spiculate scales is unique in the genus. *A. ivorensis* lacks prominent setae on the fore coxa, the front edge of the left third

marginal tooth is shorter than that of the first, and of the right first marginal, equal to that of the second; the longest apical spines of the main enteric valve armature are longer than the least width of ridges three but all armature, main and subsidiary, is notably sparse. *A. galenus* is larger, the front edge of the left third marginal is shorter than that of the first and that of the right first marginal equal to the second; the longest apical spines of the main enteric valve armature are straight, longer than the least width of ridges three and fewer on the bilaterally symmetrical valve. *A. gasteruptus* is slightly smaller, the front edge of the left third marginal tooth is shorter than the first and the third lobe of the enteric valve seating is smaller than the other two; the longest apical spines of the main enteric valve armature are longer than the least width of ridges three and the scales of the subsidiary armature are indistinct. *A. mayombei* has the third fore tibial apical spur well developed, the fourth marginal tooth of the left mandible just reaching the side of the molar prominence, and the third lobe of the enteric valve seating smaller than the outer pair; the enteric valve armature is bilaterally symmetrical. *A. mbalmayoensis* is considerably larger; it lacks prominent setae on the fore coxae and the third apical spur of the fore tibia is well developed; the proximal end of the fourth marginal tooth of the left mandible reaches the side of the molar prominence or is hidden behind it; the third lobe of the enteric valve seating is smaller than the outer pair and the longest apical spines of the main enteric valve armature are straight on a hexa-radially symmetrical valve. *A. multispinus* is slightly smaller and has the third fore tibial spur well developed; the left fourth marginal reaches the side of the molar prominence; the longest apical spines of the enteric valve armature are longer than the least width of ridges three and more numerous on one and three. Finally, *A. spiculatus* is about the same size but has markedly longer legs, the fore tibiae with well developed third spurs; the apical spines of the main armature of the enteric valve are straight and conical and the symmetry is bilateral largely because of markedly different degrees of sclerotisation of the ridges.

MATERIAL EXAMINED. [total 5 series]

Holotype worker and Paratypes from Type series (field collection no. T.13), **Congo (Brazzaville):** Mayombe, Feb. 1997; other Paratype material, Feb. 1997, 4 series (Eggleton and Davies) (all in BMNH).

Amicotermes cristatus sp. n.

(Figs 47–61, 173, 174)

Head capsule pale yellow, antennal flagellum, colour of darkest part, pale yellow or yellow, pronotum and legs yellow-white, abdominal tergites hyaline.

Head capsule short oval near circular or oval, setae

sparse, emergent, longest setae regularly and symmetrically arranged. Fontanelle present as pale spot or small depression or absent. Fore coxae with four or more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, but third vestigial or much smaller than the other two.

Left mandible, first marginal tooth approximately equilateral, third marginal tooth with anterior edge equal in length to that of first, fourth marginal tooth in front view just reaches side of molar prominence. Right mandible, anterior margin of first marginal tooth shorter than that of second.

Junction of mesenteron and proctodeum starting beneath nerve cord in ventral view, proctodeal first segment shorter, up to eight times proximal width tubular throughout its length, lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view, enteric valve 'seating' third lobe approximately equal in size to outer pair.

Enteric valve ridges, more or less tapering ellipsoid to base of apical spines, sclerotised at distal ends, pale brown or yellow-brown, main armature of all ridges with large backwardly directed erect conical spines, those on ridges one, three and four numbering up to 14, those on ridges two, less than 10, straight and evenly tapered, shorter than or equal to least width of ridges in position three, symmetry of enteric valve armature more or less hexa-radial apart from slight differences in ridge size; subsidiary armature of enteric valve ridges with scattered, sparse spines or spicules on scales, scales or reticulations well defined, distinct, more or less uniform throughout length of ridge; membranous wall of enteric valve between and beyond ridges scaly, armed with short spicules, dense distally, fringing scales proximally.

Measurements and diagnostic ratios [8 individuals from 3 series]:

Head capsule width 0.673 to 0.717 mm (mean 0.690 SD 0.015).

Postclypeus width 0.360 to 0.395 mm (mean 0.379 SD 0.013).

Postclypeus length 0.187 to 0.228 mm (mean 0.204 SD 0.015).

Left mandible index 0.871 to 0.965 (mean 0.915).

Right mandible index 0.968 to 1.265 (mean 1.099).

Right second marginal index 0.861 to 1.113 (mean 0.963).

Right first to second marginal index 1.523 to 1.816 (mean 1.701).

Pronotum width 0.448 to 0.512 mm (mean 0.479 SD 0.021).

Pronotum length 0.221 to 0.265 mm (mean 0.241 SD 0.016).

Hind tibia length 0.727 to 0.765 mm (mean 0.742 SD 0.015).

Fore tibia length 0.575 to 0.608 mm (mean 0.589 SD 0.011).

Fore tibia thickness 0.144 to 0.148 mm (mean 0.146 SD 0.002).

Fore tibial index (length over width) 3.974 to 4.165 (mean 4.049).

Left mandible, complex ratio La divided by L1.Lm 21.913 to 26.987 (mean 24.192).

Right mandible, complex ratio Ra divided by R1.Rm 21.978 to 27.22 (mean 24.533).

COMPARISONS. *A. cristatus* is one of the more distinctive species with its 'crest' of large conical spines on the enteric valve ridges and has already been compared with the three that precede it. The next species, *A. dibogi*, is distinctive in the longer, dilated P1 that pushes the enteric valve seating around to the dorsal side of the unopened abdomen; the fine apical spines of the enteric valve main armature and the highly spiculate fringed scales of the subsidiary armature are also different from any other species. *A. galenus* is larger with higher mandibular indices and has the front edge of the left first marginal tooth longer than the hind edge, the third marginal shorter than the first, while the fourth marginal is clear of the molar prominence; the front edge of the right first marginal is equal to that of the second; the ridges of the enteric valve armature are 'waisted' at the base of the apical spines, which are elongated, straight and longer than the least width of ridges three, the symmetry of the valve being bilateral. *A. gasteruptus* is considerably smaller and has the third lobe of the enteric valve armature smaller than the outer pair; the valve ridges are 'waisted' at the base of the apical spines which are elongated, curved, and longer than the least width of ridges three, the symmetry of the valve being tri-radial. *A. ivorensis* is smaller, lacks prominent setae on the fore coxae, has the left third marginal tooth shorter than the first and the fourth marginal clear of the molar prominence; the front edge of the right first marginal tooth is equal to that of the second; the apical spines of the main armature of the enteric valve ridges are straight but elongated and tapered, longer than the least width of ridges three, on a tri-radially symmetrical valve with subsidiary armature and that between the ridges very sparse. *A. mayombei* has well developed third fore tibial spurs, the third lobe of the enteric valve seating smaller than the outer pair and the left third marginal tooth shorter than the first; the ridges of the enteric valve armature are 'waisted' at the base of the apical spines, which are elongated and more numerous on ridges three on a bilaterally symmetrical valve. *A. mbalmayoensis* is considerably larger without prominent setae on the fore coxae and with well developed third fore tibial spurs; the third lobe of the enteric valve

seating is smaller than the outer pair; the apical spines of the main armature of the enteric valve ridges are straight but elongated and tapered, while the subsidiary armature consists mainly of small single spines on scales. *A. multispinus* is smaller, with well developed third fore tibial spurs and the third lobe of the enteric valve seating is smaller than the outer pair; the valve ridges are 'waisted' at the base of the apical spines which are elongated, curved, more numerous and longer than the least width of ridges three, the symmetry of the valve being tri-radial. Lastly, *A. spiculatus* also has well developed third fore tibial spurs, while the left fourth marginal tooth is clear of the molar prominence; the enteric valve armature is distinctive in being bilateral owing to differential sclerotisation of the ridges, one being colourless and three fully sclerotised.

MATERIAL EXAMINED. [total 3 series]

Holotype worker and Paratypes from Type series (field collection no. T₂.11), **Congo (Brazzaville):** Mayombe, Feb. 1997; other Paratype material, Feb. 1997, 2 series (*Eggleton* and *Davies*) (all in BMNH).

Amicotermes dibogi sp. n.

(Figs 62–75, 176)

Head capsule pale yellow or yellow, antennal flagellum, colour of darkest part, yellow or pale yellow-brown, pronotum yellow-white or pale yellow, legs pale yellow, abdominal tergites hyaline.

Head capsule circular to oval, setae sparse, emergent, longest setae more or less regularly and symmetrically arranged. Fontanelle absent. Fore coxae usually with four or more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, third well developed or much smaller than the other two.

Left mandible, first marginal tooth approximately equilateral, third marginal tooth with anterior edge shorter than that of first, fourth marginal tooth in front view just reaches side of molar prominence. Right mandible, anterior margin of right first marginal tooth shorter than that of second.

Junction of mesenteron and proctodeum starting to left of nerve cord in ventral view, proctodeal first segment very long, over eight times proximal width, dilated to about twice its basal width throughout length, lateral displacement of enteric valve in unopened abdomen to left of heart in dorsal view; enteric valve 'seating' third lobe approximately equal in size to outer pair.

Enteric valve ridges, more or less tapering ellipsoid to base of apical spines, unsclerotised or colourless throughout with very elongated tapered spines, the largest numbering up to 14, straight and evenly tapered, shorter than or equal to least width of ridges in position

three, symmetry of enteric valve armature more or less hexa-radial apart from slight differences in ridge size; subsidiary armature on one or more of enteric valve ridges with prominent spines smaller than main armature, covering entire ridge surface, graduated, spines or spicules becoming longer towards distal end of ridge, scales or reticulations well defined, distinct; membranous wall of enteric valve between and beyond ridges scaly, armed with very sparse, scattered minute spines or spicules.

Measurements and diagnostic ratios [12 individuals from 3 series]:

Head capsule width 0.656 to 0.701 mm (mean 0.676 SD 0.014).

Postclypeus width 0.324 to 0.362 mm (mean 0.347 SD 0.011).

Postclypeus length 0.192 to 0.227 mm (mean 0.206 SD 0.012).

Left mandible index 0.801 to 0.902 (mean 0.852).

Right mandible index 0.973 to 1.295 (mean 1.101).

Right second marginal index 0.788 to 1.262 (mean 0.994).

Right first to second marginal index 1.458 to 1.783 (mean 1.632).

Pronotum width 0.440 to 0.489 mm (mean 0.470 SD 0.015).

Pronotum length 0.192 to 0.227 mm (mean 0.206 SD 0.012).

Hind tibia length 0.659 to 0.730 mm (mean 0.703 SD 0.018).

Fore tibia length 0.576 to 0.618 mm (mean 0.594 SD 0.013).

Fore tibia thickness 0.127 to 0.148 mm (mean 0.139 SD 0.006).

Fore tibial index (length over width) 3.952 to 4.759 (mean 4.272).

Left mandible, complex ratio La divided by L1.Lm 18.009 to 23.312 (mean 20.937).

Right mandible, complex ratio Ra divided by R1.Rm 20.653 to 30.758 (mean 23.927).

COMPARISONS. *A. dibogi* has already been compared individually with the species that precede it; however, it is so distinctive with its long, dilated P1 that pushes the enteric valve seating into a left dorsal position and the finely spiny and spiculate enteric valve armature, that it does not need detailed comparisons with the remaining species under its own heading. Although distinct from the other species of the genus in the characters specified, it is not so widely different as to require separation in another genus.

MATERIAL EXAMINED. [total 7 series]

Holotype worker and Paratypes from Type series (field collection no. H₂C-1), **Cameroon:** Mbalmayo Forest Reserve, Ekombitie, Aug. 1997 (*Eggleton et al.*); other

Paratype material, Ekombitie, Aug. 1995, Nov. 1995, July 1996, Aug. 1997, Ebogo, Feb. 1996 (*Eggleton et al.*) (all in BMNH). This species is named in honour of Dr. Luc Dibog, a member of the TIGER team, who was first to recognise that it was a distinct species on the strength of its enteric valve armature and long first proctodeal segment.

Amicotermes galenus Sands, 1972 [Type species]

(Figs 76–82, 177, 178)

Head capsule yellow, antennal flagellum, colour of darkest part, pronotum and legs, yellow-white or pale yellow, abdominal tergites yellow-white.

Head capsule circular, setae sparse, emergent, longest setae randomly scattered. Fontanelle absent. Fore coxae with four or more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, but third vestigial or much smaller than the other two.

Left mandible, first marginal tooth with anterior edge distinctly longer than posterior, third marginal tooth with anterior edge shorter than that of first, fourth marginal tooth in front view with proximal end clear of molar prominence. Right mandible, anterior margin of first marginal tooth equal in length to that of second.

Junction of mesenteron and proctodeum starting beneath nerve cord in ventral view, proctodeal first segment shorter, up to eight times proximal width, tubular throughout its length, lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view, enteric valve 'seating' third lobe smaller than or approximately equal in size to outer pair.

Enteric valve ridges, distinctly 'waisted' at base of apical spines, then wider, weakly sclerotised distally, pale yellow or yellow, main armature with very elongated tapered spines, the largest on ridges one and two numbering 1–9, those on ridges three numbering 10–14, and on ridge four, up to 14, straight and evenly tapered, longer than least width of ridges in position three at base of spines, symmetry of enteric valve armature bilateral due to marked differences in spine and ridge size; subsidiary armature on ridges with scattered, somewhat sparse prominent spines different from or smaller than main armature, graduated, spines or spicules becoming longer towards distal end of ridge, scales or reticulations well defined; membranous wall of enteric valve between and beyond ridges scaly, armed with minute spicules, numerous but not dense, scattered, fringing scales proximally.

Measurements and diagnostic ratios [1 individual]:

Head capsule width 0.763 mm.

Postclypeus width 0.425 mm.
 Postclypeus length 0.25 mm.
 Left mandible index 1.092.
 Right mandible index 1.329.
 Right second marginal index 0.957.
 Right first to second marginal index 1.793.
 Pronotum width 0.485 mm.
 Pronotum length 0.269 mm.
 Hind tibia length 0.725 mm.
 Fore tibia length 0.563 mm.
 Fore tibia thickness 0.13 mm.
 Fore tibial index (length over width) 4.327.
 Left mandible, complex ratio La divided by L1.Lm
 26.495.
 Right mandible, complex ratio Ra divided by R1.Rm
 31.280.

COMPARISONS. *A. galenus* has already been compared with the preceding species. *A. gasteruptus* is smaller with lower mandible indices and has the front edge of the right first marginal tooth equal in length to that of the second; the largest apical spines of the main enteric valve armature are curved on a tri-radially symmetrical valve. *A. ivorensis* is again smaller with lower mandible indices and has the left first marginal tooth roughly equilateral; it lacks prominent fore coxal setae; the largest apical spines of the enteric valve main armature are less numerous on a tri-radially symmetrical valve with very sparse subsidiary armature. *A. mayombi* is also smaller, with lower mandible indices and has the front edge of the left third marginal tooth equal to that of the first, while the fourth marginal reaches the side of the molar prominence; the largest apical spines of the main enteric valve armature are curved and shorter than or equal to the least width of ridges three. *A. mbalmayoensis* is larger, lacks prominent fore coxal setae and has well developed fore tibial apical spurs; the left first marginal tooth is roughly equilateral while the fourth marginal reaches the side of the molar prominence; the largest apical spines of the main enteric valve armature are shorter than or equal to the least width of ridges three and the subsidiary armature consists of small single spines on scales, the valve symmetry being hexa-radial. *A. multispinus* is smaller with lower mandible indices and has the left first marginal tooth roughly equilateral while the fourth marginal reaches the side of the molar prominence; the front edge of the right first marginal tooth is shorter than that of the second; the largest apical spines of the main enteric valve armature are curved on a tri-radially symmetrical valve and much more numerous on ridges one and three. *A. spiculatus* is smaller, with lower main mandible indices and has the left first marginal tooth roughly equilateral while the front edge of the left third marginal tooth is equal to that of the first; it has well developed fore tibial apical spurs; the largest apical spines of the main

enteric valve armature are conical and shorter than the least width of ridges three, while the differential sclerotisation of the valve ridges is characteristic.

MATERIAL EXAMINED.

Democratic Republic of Congo: Katanga, Keyburg near Elizabethville, 1948 single Paratype from Type series, in the Natural History Museum, London (*Emerson*). (Holotype imago and other Paratypes in American Museum of Natural History, examined and designated at the time of the first description).

Amicotermes gasteruptus sp. n.

(Figs 83–98, 179)

Head capsule yellow-white or pale yellow, antennal flagellum, colour of darkest part, yellow or pale yellow-brown, pronotum and legs yellow-white, abdominal tergites hyaline.

Head capsule short oval near circular or oval, setae sparse, the emergent, longest setae randomly scattered. Fontanelle present as pale spot or absent. Fore coxae without prominent larger setae or with four or more prominent larger setae arranged in line or group on anterior surface; fore tibial apical spurs numbering three, third well developed, at least half the size of the others or much smaller than the other two.

Left mandible, first marginal tooth with anterior edge distinctly longer than posterior or approximately equilateral, third marginal tooth with anterior edge shorter than that of first, fourth marginal tooth in front view with proximal end clear of or just reaches side of molar prominence. Right mandible, anterior edge of first marginal tooth shorter.

Junction of mesenteron and proctodeum starting to left of or beneath nerve cord in ventral view, proctodeal first segment shorter, up to eight times proximal width, tubular throughout its length; lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view; enteric valve 'seating' third lobe smaller than outer pair.

Enteric valve ridges, distinctly 'waisted' at base of apical spines, then wider, sclerotised at distal ends, pale brown or yellow-brown; main armature with very elongated tapered spines, the largest apical spines on ridges one and three numbering 10–20, those on ridges two and four numbering 1–9; longest spines curved but still evenly tapered, longer than least width of ridges in position three at base of spines, symmetry of enteric valve armature more or less tri-radial, alternate ridges reduced; subsidiary armature on one or more of enteric valve ridges with scattered, somewhat sparse prominent spines different from or smaller than main armature, on scales or reticulations with indistinct vague or incomplete outlines, the spines being graduated, becoming longer towards distal end of ridge; membranous wall of enteric valve between and beyond

ridges scaly, armed with numerous but not dense, scattered, minute spines or spicules fringing scales proximally.

Measurements and diagnostic ratios [11 individuals from 5 series]:

Head capsule width 0.598 to 0.635 mm (mean 0.620 SD .011).

Postclypeus width 0.301 to 0.339 mm (mean 0.322 SD 0.013).

Postclypeus length 0.166 to 0.205 mm (mean 0.184 SD 0.013).

Left mandible index 0.751 to 0.935 (mean 0.818).

Right mandible index 0.895 to 1.228 (mean 1.015).

Right second marginal index 0.796 to 1.097 (mean 0.987).

Right first to second marginal index 1.561 to 1.838 (mean 1.705).

Pronotum width 0.390 to 0.424 mm (mean 0.408 SD 0.01).

Pronotum length 0.168 to 0.246 mm (mean 0.200 SD 0.020).

Hind tibia length 0.597 to 0.6436 mm (mean 0.622 SD 0.014).

Fore tibia length 0.495 to 0.535 mm (mean 0.518 SD 0.011).

Fore tibia thickness 0.131 to 0.154 mm (mean 0.139 SD 0.006).

Fore tibial index (length over width) 3.393 to 3.876 (mean 3.726).

Left mandible, complex ratio L_a divided by $L_1.L_m$ 20.184 to 28.664 (mean 23.214).

Right mandible, complex ratio R_a divided by $R_1.R_m$ 20.67 to 30.394 (mean 24.89).

COMPARISONS. *A. gasteruptus* has already been compared with the preceding species. It forms a terminal pair with *A. autothysius* in all of the trees apart from the Saitou and Nei tree and is close to it in the ordination. *A. ivorensis* is a little larger and has the front edge of the right first marginal tooth equal to that of the second; the apical spines of the enteric valve main armature are fewer in number on ridges one and three, while the subsidiary armature is very sparse. *A. mayombeii* appears closely related, but the front edge of the left third marginal is roughly equal to that of the first; the longest apical spines of the enteric valve main armature are shorter than or equal to the least width of ridges three and on ridge one number less than ten, the valve symmetry being bilateral. *A. mbalmayoensis* is much larger and the longest spines of the main enteric valve armature are shorter than or equal to the least width of ridges three, while the subsidiary armature consists of small single spines on scales, the symmetry being hexa-radial. *A. multispinus* is very slightly larger and has more numerous apical spines on ridges one and three of the enteric valve main armature.

A. spiculatus is much larger with proportionately longer legs; its enteric valve ridges are ellipsoid, not 'waisted' and bear straight apical spines, while the symmetry of the valve is bilateral owing to differential sclerotisation of the ridges.

MATERIAL EXAMINED. [total 9 series]

Holotype worker and Paratypes from Type series (field collection no. 38P-1) **Cameroon:** Mbalmayo Forest Reserve, Ebogo, Feb. 1996 (*Eggleton et al.*); other Paratype material, Eboufek, 5 series, Bilik, July–Aug. 1992, Ekombitie, Nov. 1995, Ebogo, Mar. 1996 (*Eggleton et al.*) (all in BMNH).

Amicotermes ivorensis sp. n.

(Figs 99–110, 180)

Head capsule, antennal flagellum, colour of darkest part, pronotum and legs, pale yellow, abdominal tergites yellow-white.

Head capsule circular or short oval near circular, setae sparse, emergent, longest setae randomly scattered. Fontanelle present as pale spot or small depression. Fore coxae without prominent larger setae on anterior surface, fore tibial apical spurs numbering three, but third vestigial or much smaller than the other two.

Left mandible, first marginal tooth approximately equilateral, third marginal tooth with anterior edge shorter than that of first, fourth marginal tooth in front view with proximal end clear of molar prominence. Right mandible, anterior edge of first marginal tooth equal in length to that of second.

Junction of mesenteron and proctodeum starting beneath nerve cord in ventral view, proctodeal first segment shorter, up to eight times proximal width, tubular throughout its length, lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view, enteric valve 'seating' third lobe approximately equal in size to outer pair.

Enteric valve ridges, more or less tapering ellipsoid to base of apical spines or distinctly 'waisted' at their base, then wider, all ridges weakly sclerotised distally, pale yellow or yellow, main armature with very elongated tapered spines, the largest on each ridge numbering 1–9, straight or curved but still evenly tapered, longer than least width of ridges in position three at base of spines, symmetry of enteric valve armature more or less tri-radial, alternate ridges reduced; subsidiary armature on one or more of enteric valve ridges with backwardly directed indistinct scales, outlines vague or incomplete, fringed with very sparse small spines or spicules or small single backwardly directed spines, the latter graduated, becoming longer towards distal end of ridge; membranous wall of enteric

valve between and beyond ridges smooth, armed with very sparse scattered minute spicules.

Measurements and diagnostic ratios [3 individuals from 1 series]:

Head capsule width 0.657 to 0.713 mm (mean 0.684 SD 0.028).

Postclypeus width 0.359 to 0.381 mm (mean 0.368 SD 0.011).

Postclypeus length 0.205 to 0.241 mm (mean 0.227 SD 0.019).

Left mandible index 0.824 to 0.953 (mean 0.889).

Right mandible index 0.947 to 1.149 (mean 1.061).

Right second marginal index 0.839 to 1.136 (mean 0.969).

Right first to second marginal index 1.743 to 1.998 (mean 1.829).

Pronotum width 0.429 to 0.468 mm (mean 0.445 SD 0.020).

Pronotum length 0.206 to 0.293 mm (mean 0.252 SD 0.044).

Hind tibia length 0.665 to 0.692 mm (mean 0.680 SD 0.014).

Fore tibia length 0.525 to 0.549 mm (mean 0.540 SD 0.014).

Fore tibia thickness 0.135 to 0.148 mm (mean 0.142 SD 0.007).

Fore tibial index (length over width) 3.696 to 3.890 (mean 3.818).

Left mandible, complex ratio La divided by L1.Lm 21.554 to 24.308 (mean 22.474).

Right mandible, complex ratio Ra divided by R1.Rm 23.91 to 27.495 (mean 25.224).

COMPARISONS. *A. ivorensis* has already been compared with the preceding species. It stands somewhat isolated in the ordination, but is closest to *A. galenus* and *A. mbalmayoensis* in the consensus tree while variously attached in the other, phenetic trees. *A. mayombe* has prominent fore coxal setae, the left third marginal tooth with its front edge equal in length to that of the first and the fourth marginal just reaching the side of the molar prominence, while the front edge of the right first marginal is shorter than that of the second; the longest apical spines of the enteric valve main armature are curved and shorter than or equal to the least width of ridges three, the valve being bilaterally symmetrical. *A. mbalmayoensis* is considerably larger with much longer legs, while the proximal end of the left fourth marginal tooth just reaches or is hidden behind the molar prominence and the front edge of the right first marginal is shorter than that of the second; the longest apical spines of the enteric valve main armature are more numerous and shorter than the least width of ridges three, the valve being hexa-radially symmetrical. *A. multispinus*

has prominent fore coxal setae, the left third marginal tooth with its front edge equal in length to that of the first and the fourth marginal just reaching the side of the molar prominence, while the front edge of the right first marginal is shorter than that of the second; the ridges of the main enteric valve armature have more numerous apical spines. Finally, *A. spiculatus* has much longer legs with prominent fore coxal setae and the left third marginal tooth with its front edge equal in length to that of the first, while the front edge of the right first marginal is shorter than that of the second; the largest apical spines of the main enteric valve armature are conical, shorter than the least width of ridges three, and more numerous on a bilaterally symmetrical valve with differential sclerotisation of the ridges.

MATERIAL EXAMINED. [one series]

Holotype worker and Paratypes from Type series, **Ivory Coast:** near Ndouci in forest, 1969 (*Josens*) (all in BMNH).

Amicotermes mayombe sp. n.

(Figs 111–124, 181, 182)

Head capsule, antennal flagellum, pronotum and legs yellow-white, abdominal tergites hyaline.

Head capsule short oval near circular or oval, setae sparse, emergent, longest setae regularly and symmetrically arranged. Fontanelle absent. Fore coxae with four or more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, third well developed, at least half the size of the others.

Left mandible, first marginal tooth with anterior edge distinctly longer than posterior, third marginal tooth with anterior edge equal in length to that of first, fourth marginal tooth in front view just reaches side of molar prominence. Right mandible, anterior margin of first marginal tooth shorter than that of second.

Junction of mesenteron and proctodeum starting to left of or beneath nerve cord in ventral view proctodeal first segment shorter, up to eight times proximal width, tubular throughout its length, lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view, enteric valve 'seating' third lobe smaller than outer pair.

Enteric valve ridges, distinctly 'waisted' at base of apical spines, then wider, sclerotised at distal end, pale brown or yellow-brown with very elongated tapered spines, the largest on ridges one, two and four numbering up to 10, those on ridges three 10–20, longest spines curved but still evenly tapered, shorter than or equal to least width of ridges in position three, symmetry of enteric valve armature bilateral due to marked differences in spine and ridge size; subsidiary armature on one or more of enteric valve ridges with

scattered, somewhat sparse prominent spines different from or smaller than main armature, graduated, spines becoming longer towards distal end of ridge, scales or reticulations well defined, distinct; membranous wall of enteric valve between and beyond ridges scaly armed with short spicules, dense distally, fringing scales proximally.

Measurements and diagnostic ratios [14 individuals from 6 series]:

Head capsule width 0.614 to 0.713 mm (mean 0.651 SD 0.028).

Postclypeus width 0.322 to 0.373 mm (mean 0.344 SD 0.014).

Postclypeus length 0.162 to 0.214 mm (mean 0.185 SD 0.014).

Left mandible index 0.772 to 0.984 (mean 0.888).

Right mandible index 0.921 to 1.307 (mean 1.138).

Right second marginal index 0.936 to 1.169 (mean 1.047).

Right first to second marginal index 1.461 to 1.932 (mean 1.638).

Pronotum width 0.382 to 0.448 mm (mean 0.408 SD 0.018).

Pronotum length 0.175 to 0.22 mm (mean 0.191 SD 0.012).

Hind tibia length 0.637 to 0.736 mm (mean 0.683 SD 0.027).

Fore tibia length 0.499 to 0.571 mm (mean 0.542 SD 0.019).

Fore tibia thickness 0.133 to 0.145 mm (mean 0.139 SD 0.005).

Fore tibial index (length over width) 3.759 to 4.028 (mean 3.912).

Left mandible, complex ratio La divided by L1.Lm 18.707 to 26.77 (mean 22.184).

Right mandible, complex ratio Ra divided by R1.Rm 21.009 to 29.644 (mean 25.813).

COMPARISONS. *A. mayombei* has already been compared with the preceding species. In most of the phenetic trees it joins *A. autothysius* and *A. gasteruptus* at a slightly lower phenon level and in the strict consensus tree it links with them at node 14. *A. mbalmayoensis* is considerably larger and lacks prominent fore coxal setae while the left first marginal tooth is approximately equilateral; The enteric valve ridges are tapering ellipsoid bearing straight spines and the valve is hexa-radially symmetrical. *A. multispinus* is a little smaller and has the left first marginal tooth approximately equilateral; the longest apical spines of the main enteric valve armature are more numerous on ridges one and three and longer than the least width of three, while the symmetry of the valve is tri-radial. In *A. spiculatus* the legs are distinctly longer, the left first marginal tooth is

equilateral and the fourth marginal is clear of the molar prominence; the enteric valve ridges are tapering ellipsoid, not 'waisted' and differentially sclerotised, ridge one being colourless while ridges three and four are pale brown, two being intermediate; the largest apical spines are straight and conical.

MATERIAL EXAMINED. [total 5 series]

Holotype worker and Paratypes from Type series (field collection no. T1.10) **Congo (Brazzaville):** Mayombe, Feb. 1997 (*Eggleton and Davies*); other Paratype material, Feb. 1997, 4 series (*Eggleton and Davies*) (all in BMNH).

Amicotermes mbalmayoensis sp. n.

(Figs 125–137, 183, 184)

Head capsule yellow-white or pale yellow, antennal flagellum, colour of darkest part, yellow or pale yellow-brown, pronotum and legs yellow-white, abdominal tergites hyaline.

Head capsule short oval near circular, setae numerous but not dense, emergent, longest setae regularly and symmetrically arranged. Fontanelle absent. Fore coxae without prominent larger setae on anterior surface, fore tibial apical spurs numbering three, third well developed, at least half the size of the others.

Left mandible, first marginal tooth approximately equilateral, third marginal tooth with anterior edge shorter than or equal in length to that of first, fourth marginal tooth in front view just reaches side of or with proximal end hidden behind molar prominence. Right mandible, anterior edge of first marginal tooth shorter than that of second.

Junction of mesenteron and proctodeum starting beneath nerve cord in ventral view, proctodeal first segment shorter, up to eight times proximal width tubular throughout its length, lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view, enteric valve 'seating' third lobe smaller than outer pair.

Enteric valve ridges, more or less tapering ellipsoid to base of apical spines, weakly sclerotised distally, pale yellow or yellow, main armature with very elongated tapered spines, the largest on each ridge numbering 10–14, straight and evenly tapered, shorter than or equal to least width of ridges in position three; subsidiary armature on one or more of enteric valve ridges with scattered, somewhat sparse small single backwardly directed spines on scales, more or less uniform throughout length of ridge, scales or reticulations indistinct, outlines vague or incomplete; symmetry of enteric valve armature more or less hexa-radial apart from slight differences in ridge size; membranous wall of enteric valve between and beyond ridges scaly, armed with minute spicules, dense distally, fringing scales proximally.

Measurements and diagnostic ratios [9 individuals from 3 series]:

- Head capsule width 0.765 to 0.800 mm (mean 0.781 SD 0.013).
 Postclypeus width 0.413 to 0.434 mm (mean 0.424 SD 0.008).
 Postclypeus length 0.199 to 0.239 mm (mean 0.215 SD 0.012).
 Left mandible index 0.896 to 0.978 (mean 0.944).
 Right mandible index 1.065 to 1.366 (mean 1.174).
 Right second marginal index 0.88 to 1.245 (mean 1.013).
 Right first to second marginal index 1.606 to 1.987 (mean 1.811).
 Pronotum width 0.523 to 0.582 mm (mean 0.545 SD 0.019).
 Pronotum length 0.230 to 0.267 mm (mean 0.252 SD 0.013).
 Hind tibia length 0.779 to 0.82 mm (mean 0.796 SD 0.014).
 Fore tibia length 0.614 to 0.677 mm (mean 0.651 SD 0.019).
 Fore tibia thickness 0.159 to 0.173 mm (mean 0.166 SD 0.005).
 Fore tibial index (length over width) 3.602 to 4.078 (mean 3.916).
 Left mandible, complex ratio La divided by L1.Lm 22.319 to 27.038 (mean 23.941).
 Right mandible, complex ratio Ra divided by R1.Rm 20.164 to 26.881 (mean 24.080).

COMPARISONS. *A. mbalmayoensis* has already been compared with the preceding species. *A. multispinus* is much smaller and has prominent fore coxal setae; the front edge of the left third marginal tooth is equal in length to that of the first and the right mandible first to second marginal index is lower; the enteric valve ridges are 'waisted' at the base of the apical spines which are curved, longer than the least width of ridges three and more numerous on ridges one and three, the valve being tri-radial. *A. spiculatus* is smaller with a lower left mandible index; the apical spines of the enteric valve main armature are conical and more numerous on ridges three which are differentially sclerotised along with four, while one is unsclerotised and two intermediate, the valve being bilaterally symmetrical.

MATERIAL EXAMINED. [total, 3 series]

Holotype worker and Paratypes from Type series (field collection no. H₃P.2) **Cameroon:** Mbalmayo Forest Reserve, Ekombitie, Nov. 1996 (*Eggleton et al.*); other *Paratypes*, Ekombitie, Nov. 1995, Ebogo, Mar. 1996 (*Eggleton et al.*) (all in BMNH).

Amicotermes multispinus sp. n.

(Figs 138–150, 185)

Head capsule, antennal flagellum, colour of darkest part, pronotum and legs, yellow-white, abdominal tergites hyaline.

Head capsule short oval near circular, setae sparse, emergent, longest setae regularly and symmetrically arranged. Fontanelle absent. Fore coxae with four or more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, third well developed, at least half the size of the others.

Left mandible, first marginal tooth approximately equilateral, third marginal tooth with anterior edge equal in length to that of first, fourth marginal tooth in front view just reaches side of molar prominence. Right mandible, anterior edge of first marginal tooth shorter than that of second.

Junction of mesenteron and proctodeum starting beneath nerve cord in ventral view, proctodeal first segment shorter, up to eight times proximal width, tubular, throughout its length, lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view, enteric valve 'seating' third lobe smaller than outer pair.

Enteric valve ridges, distinctly 'waisted' at base of apical spines, then wider, weakly sclerotised distally, pale yellow or yellow, main armature with very elongated tapered spines, the largest on ridge one numbering 15–20, those on ridges two and four numbering 1–9, those on ridges three numbering 15 to over 20, the longest, curved but still evenly tapered, longer than least width of ridges in position three at base of spines, symmetry of enteric valve armature more or less tri-radial, alternate ridges reduced; subsidiary armature on one or more of enteric valve ridges with scattered, somewhat sparse prominent spines different from or smaller than main armature, graduated, spines becoming longer towards distal end of ridge, scales or reticulations indistinct, outlines vague or incomplete; membranous wall of enteric valve between and beyond ridges scaly, armed with numerous but not dense, scattered, short spicules fringing scales proximally.

Measurements and diagnostic ratios [3 individuals from 1 series]:

- Head capsule width 0.642 to 0.647 mm (mean 0.645).
 Postclypeus width 0.334 to 0.356 mm (mean 0.342).
 Postclypeus length 0.183 to 0.191 mm (mean 0.186).
 Left mandible index 0.802 to 0.903 (mean 0.852).
 Right mandible index 1.049 to 1.163 (mean 1.100).
 Right second marginal index 0.924 to 1.021 (mean 0.974).
 Right first to second marginal index 1.569 to 1.594 (mean 1.581).

Pronotum width 0.412 to 0.436 mm (mean 0.427).
 Pronotum length 0.183 to 0.191 mm (mean 0.186).
 Hind tibia length 0.624 to 0.629 mm (mean 0.626).
 Fore tibia length 0.525 to 0.531 mm (mean 0.528).
 Fore tibia thickness 0.134 to 0.141 mm (mean 0.138).
 Fore tibial index (length over width) 3.732 to 3.974
 (mean 3.834).

Left mandible, complex ratio La divided by L1.Lm
 23.999 to 27.622 (mean 25.824).

Right mandible, complex ratio Ra divided by R1.Rm
 23.347 to 26.271 (mean 24.767).

COMPARISONS. *A. multispinus* has already been compared with all of the preceding species, only *A. spiculatus* remaining. The latter is slightly larger and has the left fourth marginal tooth clear of the molar prominence; the enteric valve ridges are tapering ellipsoid, not 'waisted', and differentially sclerotised with fewer, straight conical spines on ridges one and three, the valve being bilaterally symmetrical.

MATERIAL EXAMINED. [one series]

Holotype worker and Paratypes from Type series (field collection no. T1.20) **Congo (Brazzaville)**: Mayombe, Feb. 1997 (Eggleton and Davies) (all in BMNH).

Amicotermes spiculatus sp. n.

(Figs 151–161, 186)

Head capsule pale yellow, antennal flagellum, colour of darkest part pale yellow or yellow, pronotum and legs yellow-white, abdominal tergites hyaline.

Head capsule oval, setae sparse, emergent, longest setae regularly and symmetrically arranged. Fontanelle absent. Fore coxae with three or more prominent larger setae arranged in line or group on anterior surface, fore tibial apical spurs numbering three, third well developed, at least half the size of the others. Left mandible, first marginal tooth approximately equilateral, third marginal tooth with anterior edge equal in length to that of first, fourth marginal tooth in front view with proximal end clear of molar prominence. Right mandible, anterior edge of first marginal tooth shorter than that of second.

Junction of mesenteron and proctodeum starting beneath nerve cord in ventral view, proctodeal first segment shorter, up to eight times proximal width, tubular throughout its length, lateral displacement of enteric valve in unopened abdomen to right of heart in dorsal or to left of nerve cord in ventral view, enteric valve 'seating' third lobe smaller than outer pair.

Enteric valve ridges, more or less tapering ellipsoid to base of apical spines, enteric valve ridge in position one unsclerotised or colourless throughout, positions two and four weakly sclerotised distally, pale yellow or yellow, position three sclerotised at distal end, pale brown or yellow-brown main armature of all ridges with large backwardly directed erect conical spines,

those on ridges one and two numbering up to 14, on ridges three, 15–20 and on ridge four, 1–9, the longest being straight and evenly tapered, shorter than or equal to least width of ridges in position three, symmetry of enteric valve armature bilateral due to marked differences in spine and ridge size; subsidiary armature on one or more of enteric valve ridges with prominent spines different from or smaller than main armature, covering entire ridge surface, graduated, spines or spicules becoming longer towards distal end of ridge, scales or reticulations indistinct, outlines vague or incomplete; membranous wall of enteric valve between and beyond ridges scaly, armed with short scattered spicules, numerous but not dense, fringing scales proximally.

Measurements and diagnostic ratios [only two specimens available]:

Head capsule width 0.696 to 0.706 mm.

Postclypeus width 0.370 to 0.379 mm.

Postclypeus length 0.203 to 0.206 mm.

Left mandible index 0.855 to 0.88.

Right mandible index 1.069 to 1.149.

Right second marginal index 1.016 to 1.029.

Right first to second marginal index 1.788 to 1.813.

Pronotum width 0.438 to 0.460 mm.

Pronotum length 0.233 to 0.239 mm.

Hind tibia length 0.784 to 0.794 mm.

Fore tibia length 0.620 to 0.625 mm.

Fore tibia thickness 0.15 to 0.152 mm.

Fore tibial index (length over width) 4.119 to 4.135.

Left mandible, complex ratio La divided by L1.Lm
 20.586 to 23.569.

Right mandible, complex ratio Ra divided by R1.Rm
 24.213 to 25.340.

COMPARISONS. All the necessary comparisons of *A. spiculatus* have been made under the preceding species.

MATERIAL EXAMINED. [one series]

Holotype worker and one Paratype (field collection no. CHR 35–40) **Cameroon**: Ebolowa, Akok, June 1997, (Eggleton *et al.*) (all in BMNH).

PHENETIC AND PHYLOGENETIC ANALYSIS

The purpose in undertaking these analyses was to examine the apparent relationships between the twelve species of the genus now recognised and their geographical distribution. Phenetics, that is the study of relationships based on overall similarity between taxa, has largely gone out of use in favour of cladistics because the methods take no account of homoplasy.

However, in a small, relatively homogeneous set of species such as this, where convergence was thought unlikely to be a major feature, they offered an alternative way of looking at the character matrix. In practice, it can be seen from the relatively low values of the consistency and retention indices of the Hennig strict consensus tree, and the character states marked on it that there was more homoplasy than might have been expected. The precise topography of the individual trees depends on differences in the algorithms that define them, and there is no clear 'best' tree, although some taxonomists would claim this role for the Hennig tree. Where a cluster of species is robust through several methods including the cladistic format, it seems likely that the underlying relationships are more clearly illustrated.

The DELTA file of *Amicotermes* was converted by means of the PANKEY programmes SC3 and DELPAUP1 respectively into a matrix of similarity coefficients for input to NTSYS (Rohlf, 1993) phenetics and Principal Coordinates analyses and a coded character matrix for HENNIG86 (Farris 1988) phylogenetic analysis. *Acholotermes* was included as an outgroup, being the most closely related other genus. The first analyses were based on the original DELTA file, but because that included ranges of variation in the character codings, many of the characters were represented by queries in the HENNIG matrix. Since measurements had proved important in distinguishing some of the species, it was undesirable they should be inactive in the study of relationships. In order to avoid this, the variable characters were recoded to their median (in multi-states) or mean values (in continuous variables). In the latter case, the DELTA file included the facility to allocate measurements or ratios to KEY STATES, equal sub-divisions of the total range of each variable. It was observed that for these, closely similar members of the same genus the variances were roughly equal and it was not thought necessary to standardise the data. In practice this amounted to a crude form of gap coding for the morphometrics. Most of the characters then became fully active, but the effects of this procedure turned out to be comparatively slight in terms of the branching of trees and the positions of terminal taxa. The results of both phylogenetic and phenetic analysis are shown in Figs 162–168.

The strict consensus tree derived from the most parsimonious two Hennig trees (Fig. 162) has essentially the same topology as one of them. The states of those characters with retention indices greater than 50 are marked on the tree at each node; in addition, the tree also indicates the autapomorphies of individual taxa on their stems. It places *A. dibogi* separated from the rest of the genus and close to the outgroup, *Acholotermes*, with a considerable range of autapomorphies. The character states shown at node

24 are the plesiomorphic states of the characters concerned on this particular tree. Succeeding single branches from low on the tree are occupied by *A. camerunensis*, *A. spiculatus* and *A. cristatus*, which show progressive development and localisation of straight spiny armature of the enteric valve. The rest of the species appeared to divide into two groups, one of three (*A. mbalmayoensis*, *A. ivorensis* and *A. galenus*) and one of five (*A. multispinus*, *A. congoensis*, *A. mayombei*, *A. gasteruptus* and *A. autothysius*), the two last named forming a terminal pair, with *A. congoensis* and *A. multispinus* joining the group at slightly lower levels. The lower nodes of the tree are determined largely by features of the main armature of the enteric valve, while above node 19, measurement characters predominate. However, the shape of the enteric valve ridges ('waisted', 23a) and the type of spines in the main armature (elongated, curved taper, 36a) are important synapomorphies at node 18 that define the group of five species mentioned above; they also suggest a trend towards certain other genera such as *Ateuchotermes* and perhaps *Apagotermes*.

The Principal Coordinates plot (Fig. 163) shows the positions of the taxa in relation to the first three eigenvectors of the similarity matrix transformed by double centering. *A. dibogi* is again widely separated on vectors one and two from the other species and placed near to the outgroup. *A. camerunensis*, *A. spiculatus* and *A. cristatus* are separated on vectors two and three while most of the separation of *A. mbalmayoensis*, *A. ivorensis* and *A. galenus* is accounted for by vector three. *A. congoensis* is also separated mainly on V3 while the remaining two pairs are relatively close together on all three vectors. The minimum spanning tree is superimposed on the ordination in order to show up any local distortions. It links the outgroup to *A. dibogi* which in turn is linked to *A. autothysius*, *A. gasteruptus* and *A. mayombei* in series. It then branches to *A. cristatus*, *A. spiculatus* and *A. camerunensis* in turn and to *A. multispinus* and *A. congoensis*, with further branches to *A. mbalmayoensis* and *A. galenus*, which is finally linked to *A. ivorensis*.

The various SAHN phenetic clustering methods, (Single (Fig. 164), Flexible (Fig. 165) and Complete (Fig. 166) Linkage methods and Unweighted pair-group method of averages (Fig. 167)) based on the matrix of similarity coefficients give comparable results, allowing for a small amount of branch-swapping, in terms of the terminal groups of taxa, to the HENNIG86 (Farris, 1988) tree. *A. dibogi* is always separate and near to *Acholotermes*, the successive additions at lower levels are largely similar, and the two terminal groups also retain their cohesion to a certain extent. The Single-linkage tree, with its tendency to form long chain clusters, has the *A. autothysius*–*A. gasteruptus*–*A. congoensis*–*A. may-*

ombei-*A. multispinus* group but adds in *A. galenus* at about the 0.57 phenon level. The other group has broken up with *A. ivorensis* and *A. mbalmayoensis* separated; *A. spiculatus* and *A. cristatus* unite at the 0.53 phenon level. Both Flexible and Complete linkage methods keep *A. autothysius*-*A. gasteruptus*-*A. mayombe* together at about 0.55 phenon level and also *A. congoensis*-*A. multispinus*-*A. galenus* at 0.50 phenons. *A. spiculatus* and *A. cristatus* similarly combine, but Flexible linkage adds *A. camerunensis* at about 0.35 phenons and Complete linkage adds *A. ivorensis*. The UPGMA tree keeps *A. autothysius*-*A. gasteruptus*-*A. mayombe* together at about 0.58 phenon level and also *A. congoensis*-*A. multispinus*-*A. galenus* at 0.55 phenons; *A. spiculatus* and *A. cristatus* combine at 0.53, and *A. camerunensis* at 0.42. A strict consensus tree of the Complete and Flexible linkage methods only leaves the *A. mayombe*-*A. gasteruptus*-*A. autothysius* group recognisable, the rest being reduced to a comb and nothing remains if Single linkage is added in, while that of the UPGMA and Neighbour-joining trees apparently also leaves no grouping in common.

The only exception to the above arrangement occurs in the Saitou and Nei (1987) Neighbour-joining tree (Fig. 168), which uses an algorithm based on the principle of parsimony to produce from the dissimilarity matrix a 'phylogenetic' tree. Here the species closest to the outgroup is *A. gasteruptus*, while *A. dibogi* forms a terminal pair high up the tree with *A. cristatus*. Considering how far apart these two appear in the ordination of the first three vectors, it might be concluded that they come to be 'neighbours' as a result of closeness on other, lower level vectors that cannot be plotted; however, this is not borne out by their positions at almost the extreme ends on the minimum spanning tree, which agrees with both the cladistic and the other phenetic classifications in placing *A. dibogi* next to the outgroup. None of the terminal groups recognised in the other methods remains.

The results of the HENNIG, SAHN and ordination analyses all share aspects with an intuitive view of the probable relationships of most of the species. Perhaps the most interesting feature that is found in all of the trees apart from the Saitou and Nei tree is the distribution of taxa from each of the two regions sampled among the terminal groups. Each fauna appears to include representatives of the different trends within the genus, and it would be interesting to see whether this were to be maintained through further sampling on a wider geographical basis. A surprise is the apparently close relationship of *A. dibogi* to the outgroup which must be a reflection of its relatively unspecialised, hexa-radially symmetrical, finely spiny and spiculate enteric valve armature. Other, apparently derived features of the gut, such as the elongated and dilated P1, which pushes the enteric valve seating

into a dorsal position, only account for three 'characters' out of the total set of 60 and they appear as autapomorphies on the tree. The Saitou and Nei is the only tree to place *A. dibogi* in a derived position distant from *Acholotermes*.

ACKNOWLEDGEMENTS I am grateful to Dr Paul Eggleton for reading and commenting on the manuscript of this paper, and to my colleagues in the Termite Group at The Natural History Museum for helpful discussions and testing the key to species. Thanks are also due to the Trustees of The Natural History Museum for permission to examine specimens in the collection.

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APPENDIX

The entire DELTA file is shown below, except that the character states recorded for the species are omitted, since they have been converted to keys and descriptions. The symbols for character types are OM, ordered multistate and RN, real numbers, the default being unordered multistate. The format is rigid in that certain lines must end in a slash, and every line begins with a single space. the numbers of characters, states and items stated at the beginning must correspond exactly to those included in the file

*HEADING THE AFRICAN SOLDIERLESS TERMITE
GENUS AMICOTERMES/

*SPECIAL STORAGE

*KEY OPTIONS OLDKEY PARTIAL /

*NUMBER OF CHARACTERS 60

*MAXIMUM NUMBER OF STATES 6

*MAXIMUM NUMBER OF ITEMS 13

*CHARACTER TYPES

1, OM 2, OM 3, OM 4, OM 5, OM 6, OM 11, OM 14, OM 16, OM 18, OM 24, OM 25, OM 26, OM 27, OM 28, OM 29, OM 30, OM 31, OM 32, OM 33, OM 34, OM 35, OM 38, OM 40, OM 42, OM 45, OM 46, RN 47, RN 48, RN 49, RN 50, RN 51, RN 52, RN 53, RN 54, RN 55, RN 56, RN 57, RN 58, RN 59, RN 60, RN

*NUMBERS OF STATES

1, 4 2, 4 3, 3 4, 3 5, 3 6, 3 11, 3 14, 3 15, 3 16, 3 18, 3 24, 3 25, 3 26, 3 27, 3 28, 3 29, 3 30, 3 31, 3 32, 4 33, 4 34, 4 35, 4 38, 5 40, 3 42, 3 45, 3

*KEY STATES

46, 0.565-0.604/0.605-0.644/0.645-0.683/0.684-0.722/
0.723-0.761/0.762-0.800

47, 0.300-0.333/0.334-0.367/0.368-0.401/0.402-0.434

48, 0.154-0.178/0.179-0.202/0.203-0.227/0.228-0.250

49, 0.697-0.781/0.782-0.866/0.867-0.951/0.952-1.036/
1.037-1.121/1.121-1.205

50, 0.879-0.962/0.963-1.044/1.045-1.127/1.128-1.209/
1.21-1.291/1.292-1.374

51, 0.788-0.867/0.868-0.946/0.947-1.025/1.026-1.104/
1.105-1.183/1.184-1.262

52, 1.350-1.474/1.475-1.598/1.599-1.722/1.723-1.846/
1.847-1.971/1.971-2.094

53, 0.375-0.426/0.427-0.478/0.479-0.53/0.531-0.582

54, 0.168-0.199/0.2-0.231/0.232-0.262/0.263-0.293

55, 0.565-0.629/0.63-0.693/0.694-0.756/0.757-0.820

56, 0.489-0.536/0.537-0.583/0.584-0.63/0.631-0.677

57, 0.127-0.147/0.148-0.166/0.167-0.185/0.186-0.205

58, 2.953-3.255/3.256-3.556/3.557-3.857/3.858-4.157/
4.158-4.458/4.459-4.759

59, 17.556-22.634/22.635-27.712/27.713-32.789/32.79-
37.867

60, 20.164-23.626/23.627-27.087/27.088-30.549/30.55-
34.010

*CHARACTER DESCRIPTIONS

#1. head capsule <colour>/

1. yellow-white/

2. pale yellow/

3. yellow/

4. pale yellow-brown/

#2. antennal flagellum <colour of darkest part>/

1. yellow-white/

2. pale yellow/

3. yellow/

4. pale yellow-brown/

#3. pronotum <colour>/

1. yellow-white/

2. pale yellow/

3. yellow/

#4. legs <colour>/

1. yellow-white/

2. pale yellow/

3. yellow/

#5. abdominal tergites <colour>/

1. hyaline/

2. yellow-white/

3. pale yellow/

#6. head capsule <shape>/

1. circular/

2. short oval near circular/

3. oval/

#7. head capsule setae/

1. sparse/

2. numerous but not dense/

#8. head capsule emergent, longest setae/

1. randomly scattered/

2. regularly and symmetrically arranged/

#9. fontanelle/

1. present as pale spot or small depression/

2. absent/

#10. postclypeus <contour>/

1. clearly inflated/

2. strongly inflated, bulging, length more than half width at ginglymi/

#11. fore coxae/

1. without prominent larger setae on anterior surface/

2. with one to three prominent larger setae on anterior surface/

3. with four or more prominent larger setae arranged in line or group on anterior surface/

#12. fore tibial apical spurs/

1. numbering three, third well developed, at least half the size of the others/

2. numbering three, but third much smaller than the other two/

#13. left mandible, first marginal tooth/

1. with anterior edge distinctly longer than posterior/

2. approximately equilateral/

#14. left third marginal tooth with anterior edge/

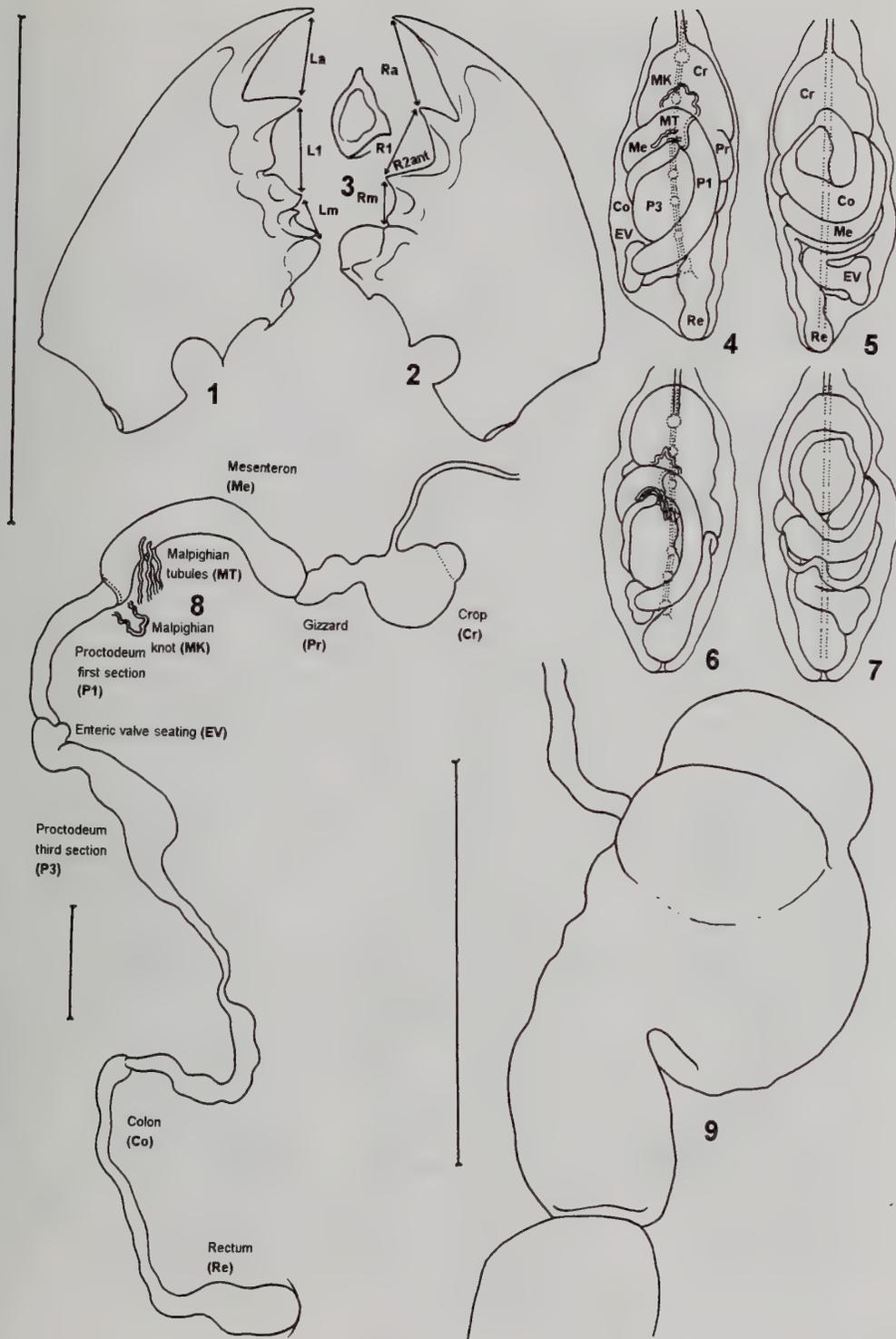
1. shorter than that of first/

2. equal in length to that of first/

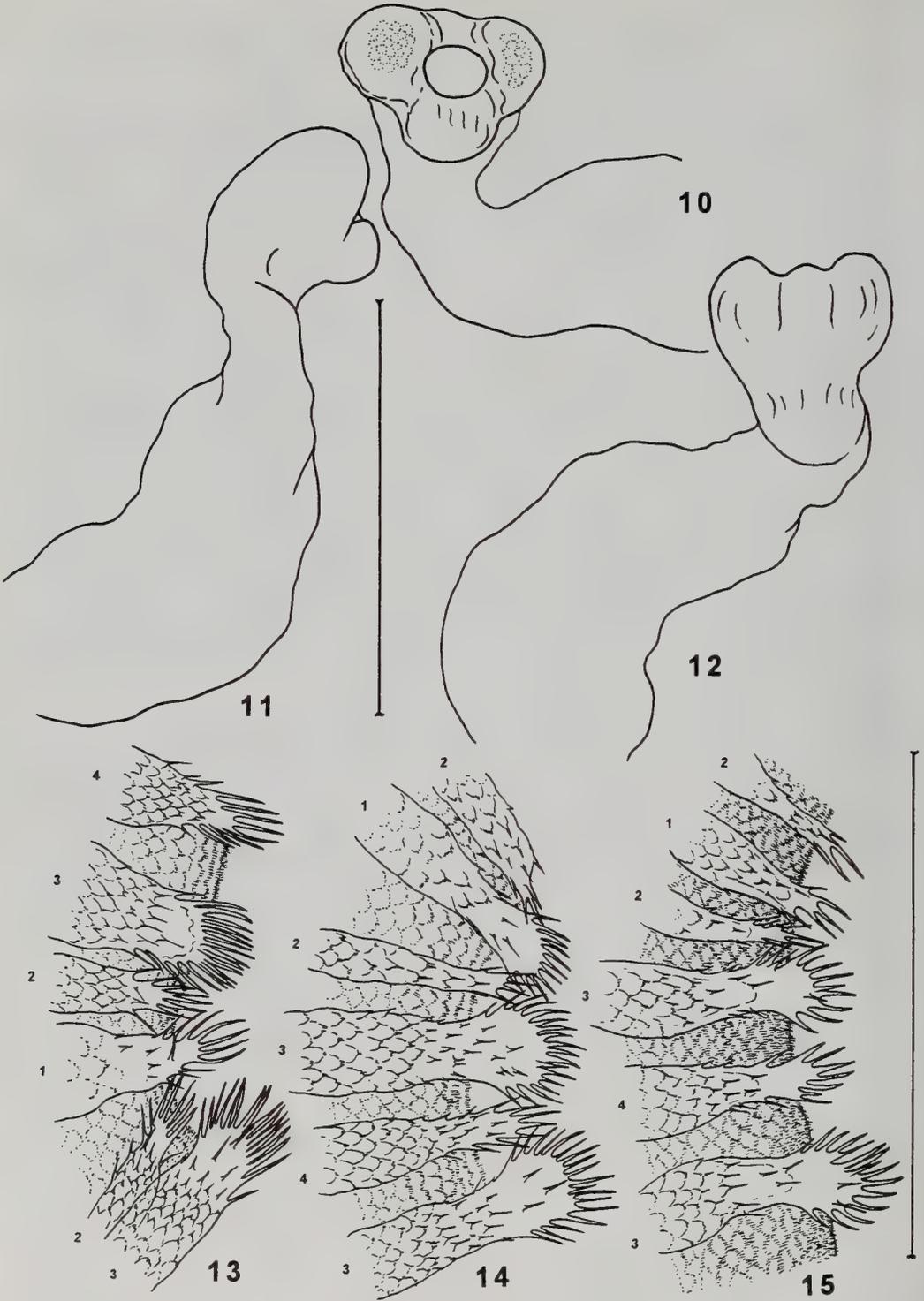
3. longer than that of first/

- #15. left fourth marginal tooth in front view/
 1. with proximal end clear of molar prominence/
 2. just reaches side of molar prominence/
 3. with proximal end hidden behind molar prominence/
- #16. anterior margin of right first marginal tooth/
 1. longer than that of second/
 2. equal in length to that of second/
 3. shorter than that of second/
- #17. right first marginal tooth with exposed posterior edge/
 1. equal to that of second marginal/
 2. longer than that of second marginal/
- #18. junction of mesenteron and proctodeum/
 1. starting to left of nerve cord in ventral view/
 2. starting beneath nerve cord in ventral view/
 3. starting to right of nerve cord in ventral view/
- #19. proctodeal first segment <length>/
 1. shorter, up to eight times proximal width/
 2. very long, over eight times proximal width/
- #20. proctodeal first segment beyond junction with mesenteron <condition>/
 1. tubular or conical throughout its length/
 2. dilated to about twice its basal width throughout length/
- #21. lateral displacement of enteric valve in unopened abdomen/
 1. to left of heart in dorsal view/
 2. to right of heart in dorsal or to left of nerve cord in ventral view/
- #22. enteric valve 'seating' third lobe <size>/
 1. smaller than outer pair/
 2. approximately equal in size to outer pair/
- #23. enteric valve ridges, <shape>/
 1. more or less tapering ellipsoid to base of apical spines/
 2. distinctly 'waisted' at base of apical spines, then wider/
- #24. enteric valve ridge in position one/
 1. sclerotised at distal end, pale brown or yellow-brown/
 2. weakly sclerotised distally, pale yellow or yellow/
 3. unsclerotised or colourless throughout/
- #25. enteric valve ridges in position two/
 1. sclerotised at distal end, pale brown or yellow-brown/
 2. weakly sclerotised distally, pale yellow or yellow/
 3. unsclerotised or colourless/
- #26. enteric valve ridges in position three/
 1. sclerotised at distal end, pale brown or yellow-brown/
 2. weakly sclerotised distally, pale yellow or yellow/
 3. unsclerotised or colourless/
- #27. enteric valve ridge in position four/
 1. sclerotised at distal end, pale brown or yellow-brown/
 2. weakly sclerotised distally, pale yellow or yellow/
 3. unsclerotised or colourless/
- #28. main armature of enteric valve ridge in position one/
 1. without large apical spines/
 2. with large backwardly directed erect conical spines/
 3. with very elongated tapered spines/
- #29. main armature of enteric valve ridges in position two/
 1. without large apical spines/
 2. with large backwardly directed erect conical spines/
 3. with very elongated tapered spines/
- #30. main armature of enteric valve ridges in position three/
 1. without large apical spines/
 2. with large backwardly directed erect conical spines/
 3. with very elongated tapered spines/
- #31. main armature of enteric valve ridge in position four/
 1. without large apical spines/
 2. with large backwardly directed erect conical spines/
 3. with very elongated tapered spines/
- #32. largest apical spines on ridge one <of main armature, number>/
 1. numbering 1-9/
 2. numbering 10-14/
 3. numbering 15-20/
 4. numbering over 20/
- #33. largest spines on ridges two <of main armature, number>/
 1. numbering 1-9/
 2. numbering 10-14/
 3. numbering 15-20/
 4. numbering over 20/
- #34. largest spines on ridges three <of main armature, number>/
 1. numbering 1-9/
 2. numbering 10-14/
 3. numbering 15-20/
 4. numbering over 20/
- #35. largest spines on ridge four <of main armature, number>/
 1. numbering 1-9/
 2. numbering 10-14/
 3. numbering 15-20/
 4. numbering over 20/
- #36. longest spines of main armature <type>/
 1. straight and evenly tapered/
 2. curved but still evenly tapered/
- #37. longest apical spines <length>/
 1. longer than least width of ridges in position three at base of spines/
 2. shorter than or equal to least width of ridges in position three/
- #38. subsidiary armature on one or more of enteric valve ridges mainly/
 1. reticulate/
 2. with backwardly directed scales/
 3. with backwardly directed scales fringed with small spines or spicules/

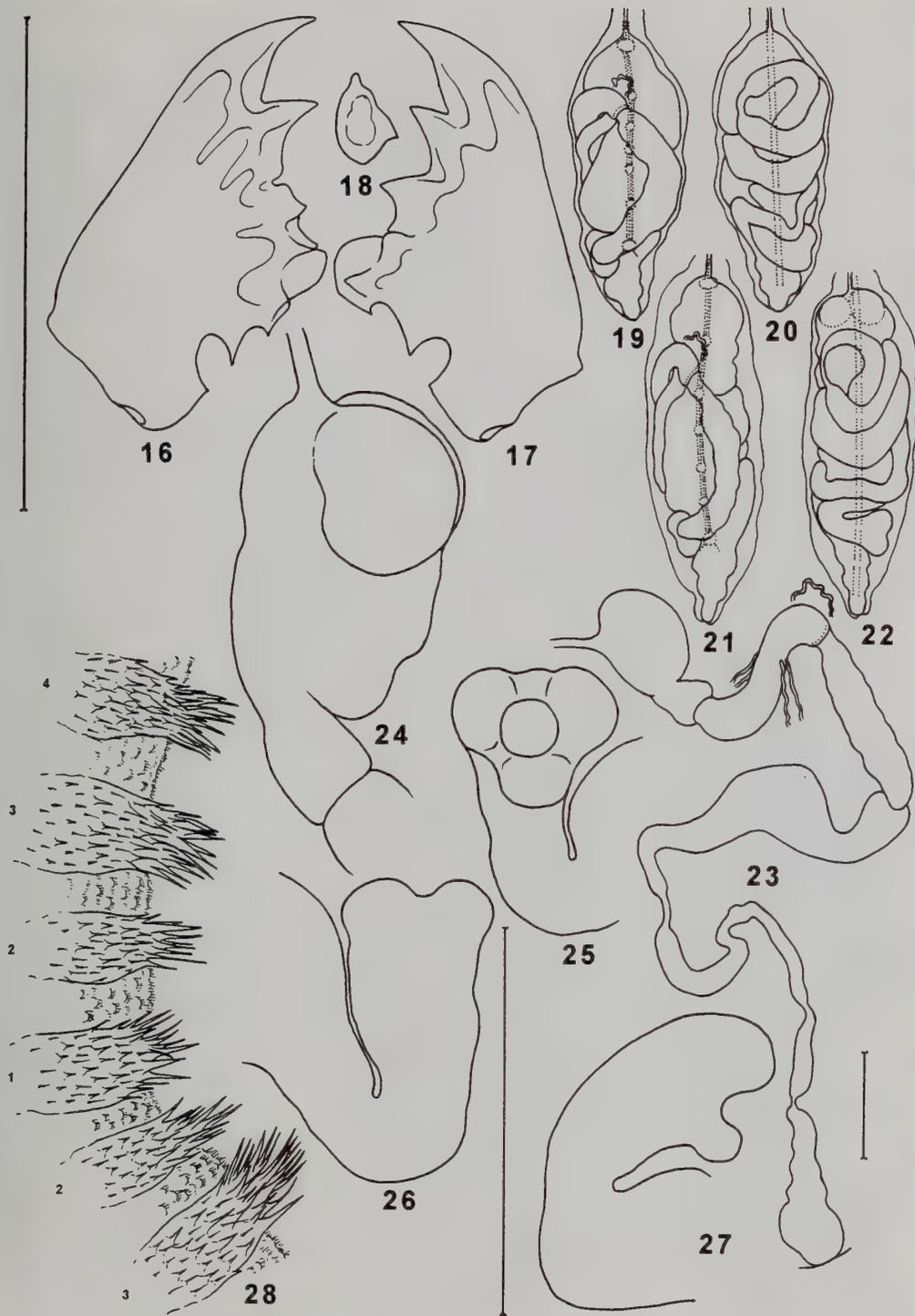
4. with small single backwardly directed spines on scales/
5. with prominent spines different from or smaller than main armature/
- #39. subsidiary armature of enteric valve ridges/
1. with scales or reticulations well defined, distinct/
2. with scales or reticulations indistinct, outlines vague or incomplete/
- #40. subsidiary armature of one or more of enteric valve ridges/
1. prominent, covering entire ridge surface/
2. scattered, somewhat sparse/
3. very sparse, few scales fringed with spines or spicules/
- #41. subsidiary armature on one or more enteric valve ridges/
1. more or less uniform throughout length of ridge/
2. graduated, spines or spicules becoming longer towards distal end of ridge/
- #42. symmetry of enteric valve armature/
1. more or less hexa-radial apart from slight differences in ridge size/
2. more or less tri-radial, alternate ridges reduced/
3. bilateral due to marked differences in spine and ridge size/
- #43. membranous wall of enteric valve between and beyond ridges/
1. smooth/
2. scaly/
- #44. membranous wall of enteric valve between and beyond ridges/
1. armed with minute spines or spicules/
2. armed with short spines or spicules/
- #45. spines or spicules on membranous wall/
1. very sparse, scattered/
2. numerous but not dense, scattered, fringing scales proximally/
3. dense distally, fringing scales proximally/
- #46. head capsule width <range, mean, SD>/ mm/
#47. postclypeus width <range, mean, SD>/ mm/
#48. postclypeus length <range, mean, SD>/ mm/
#49. left mandible index <range, mean>/
- #50. right mandible index <range, mean>/
#51. right second marginal index <range, mean>/
#52. right first to second marginal index <range, mean>/
#53. pronotum width <range, mean, SD>/ mm/
#54. pronotum length <range, mean, SD>/ mm/
#55. hind tibia length <range, mean, SD>/ mm/
#56. fore tibia length <range, mean, SD>/ mm/
#57. fore tibia thickness <range, mean, SD>/ mm/
#58. fore tibial index (length over width) <range, mean>/
#59. left mandible, complex ratio La divided by L1.Lm <range, mean>/
#60. right mandible, complex ratio Ra divided by R1.Rm <range, mean>/
- *ITEM DESCRIPTIONS
- #1.Acholotermes <outgroup>/
#2.Amicotermes autothysius sp. n./
#3.Amicotermes camerunensis sp. n./
#4.Amicotermes congoensis sp. n./
#5.Amicotermes cristatus sp. n./
#6.Amicotermes dibogi sp. n./
#7.Amicotermes galenus Sands 1972/
#8.Amicotermes gasteruptus sp. n./
#9.Amicotermes ivorensis sp. n./
#10.Amicotermes mayombe sp. n./
#11.Amicotermes mbalmayoensis sp. n./
#12.Amicotermes multispinus sp. n./
#13.Amicotermes spiculatus sp. n./



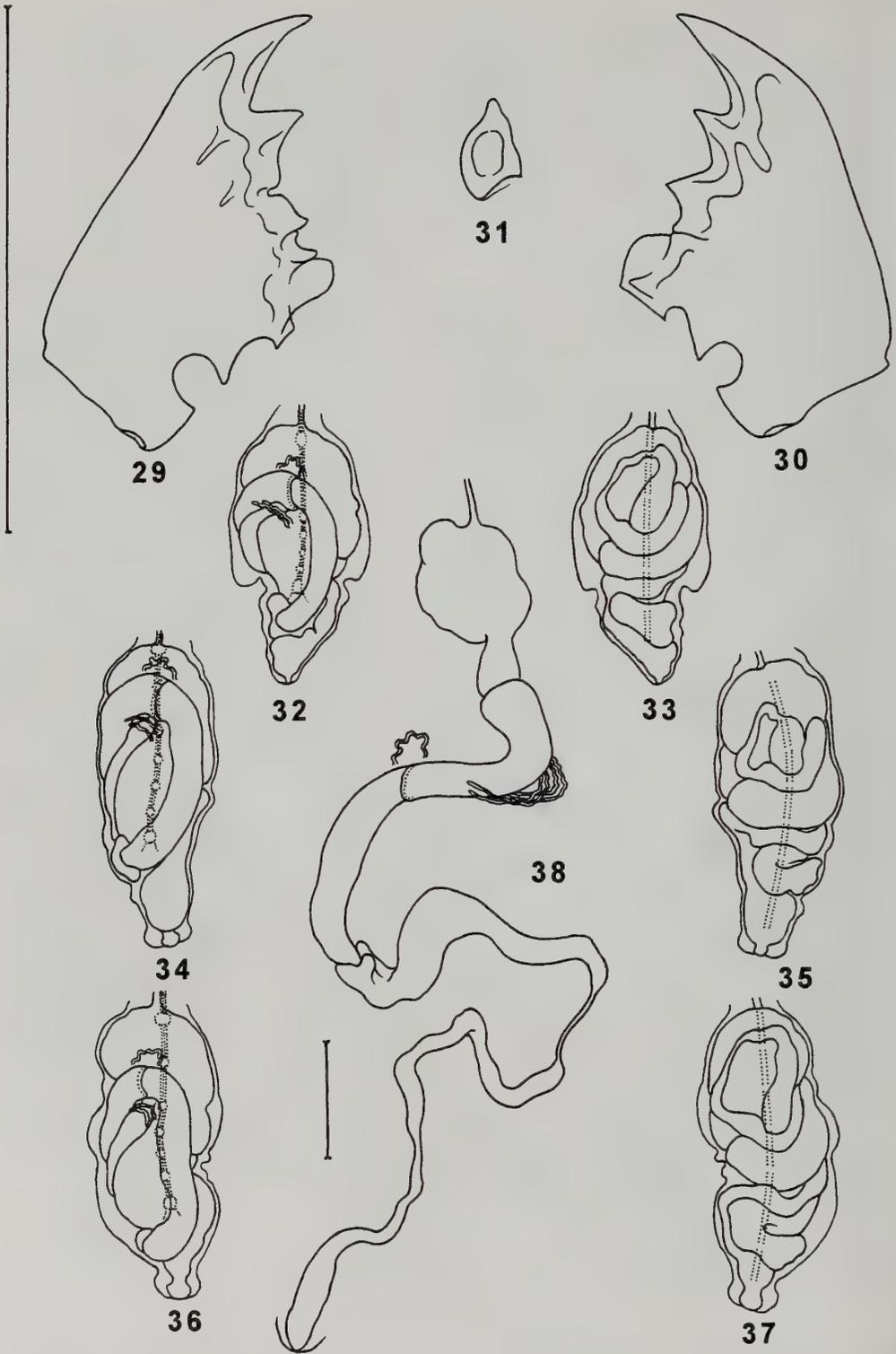
Figs 1-9. *Amicotermes autothysius*. 1-3, mandibles with surface view of right molar plate; 4, 6, ventral and 5, 7, dorsal views of abdomen to show gut coiling *in situ*; 8, gut dissected and uncoiled; 9, crop with 'burstlers' and proventriculus [bar, 0.5 mm: top left, mandibles; 1 mm: bottom left, abdomens and uncoiled gut; bottom middle, crop and proventriculus]. Abbreviations in Figs 1 and 2 indicate standard measurements (see text).



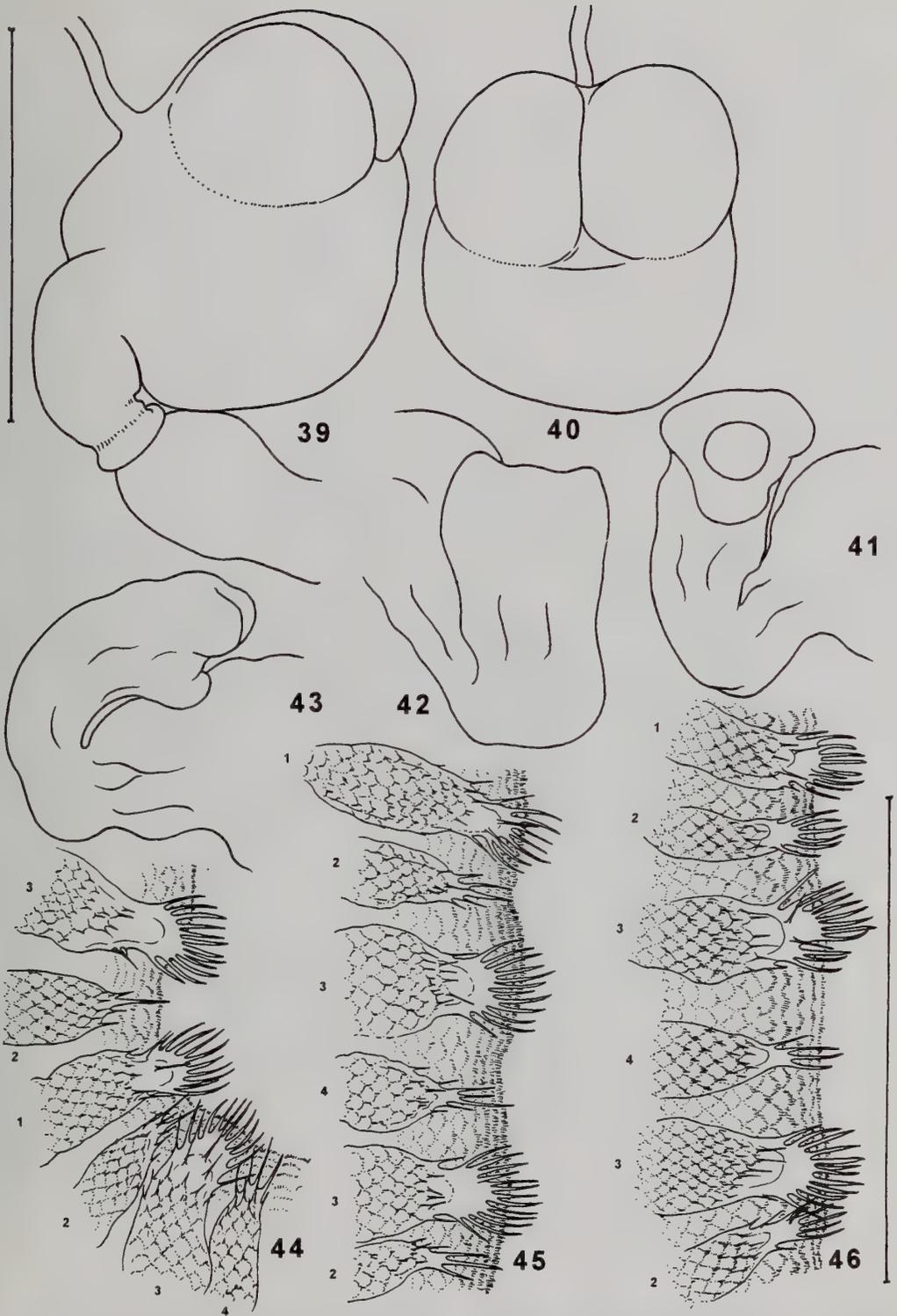
Figs 10–15. *Amicotermes autothysius*. 10–12, enteric valve seating and part of P3; 13–15, enteric valve armature opened out to show detail and variation, ridge positions numbered [bar, 1 mm: middle, valve seating; 0.5 mm: bottom right valve armature].



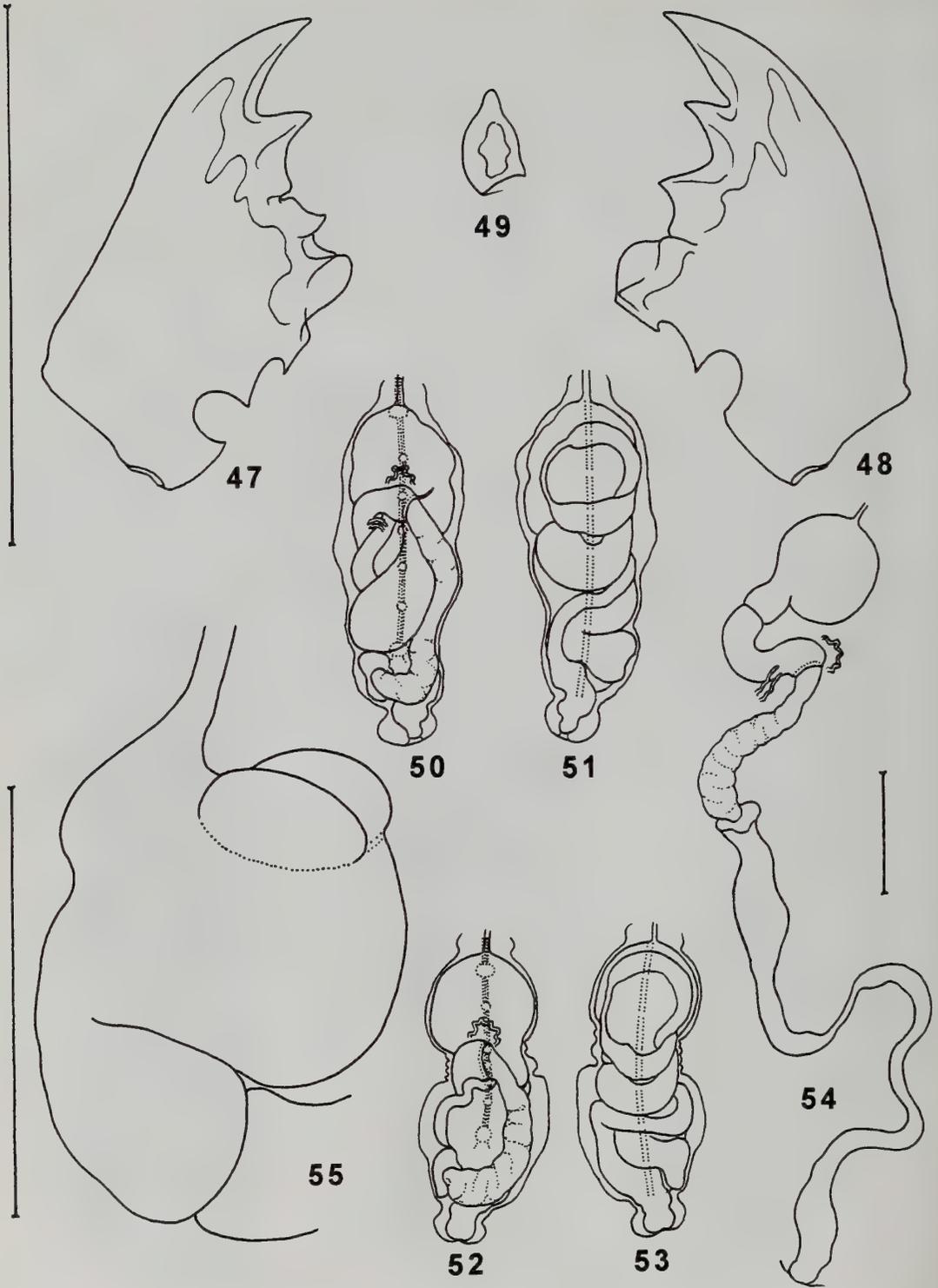
Figs 16–28. *Amicotermes camerunensis*. 16–18, mandibles with surface view of right molar plate; 19, 21, ventral and 22, 24, dorsal views of abdomen to show gut coiling *in situ*; 23, gut dissected and uncoiled; 24, crop with 'burst' and proventriculus; 25–27, enteric valve seating and part of P3; 28, enteric valve armature opened out to show detail, ridge positions numbered [bar, 0.5 mm: top left, mandibles and enteric valve armature; 1 mm: bottom right, abdomens and uncoiled gut; bottom middle, valve seating and crop].



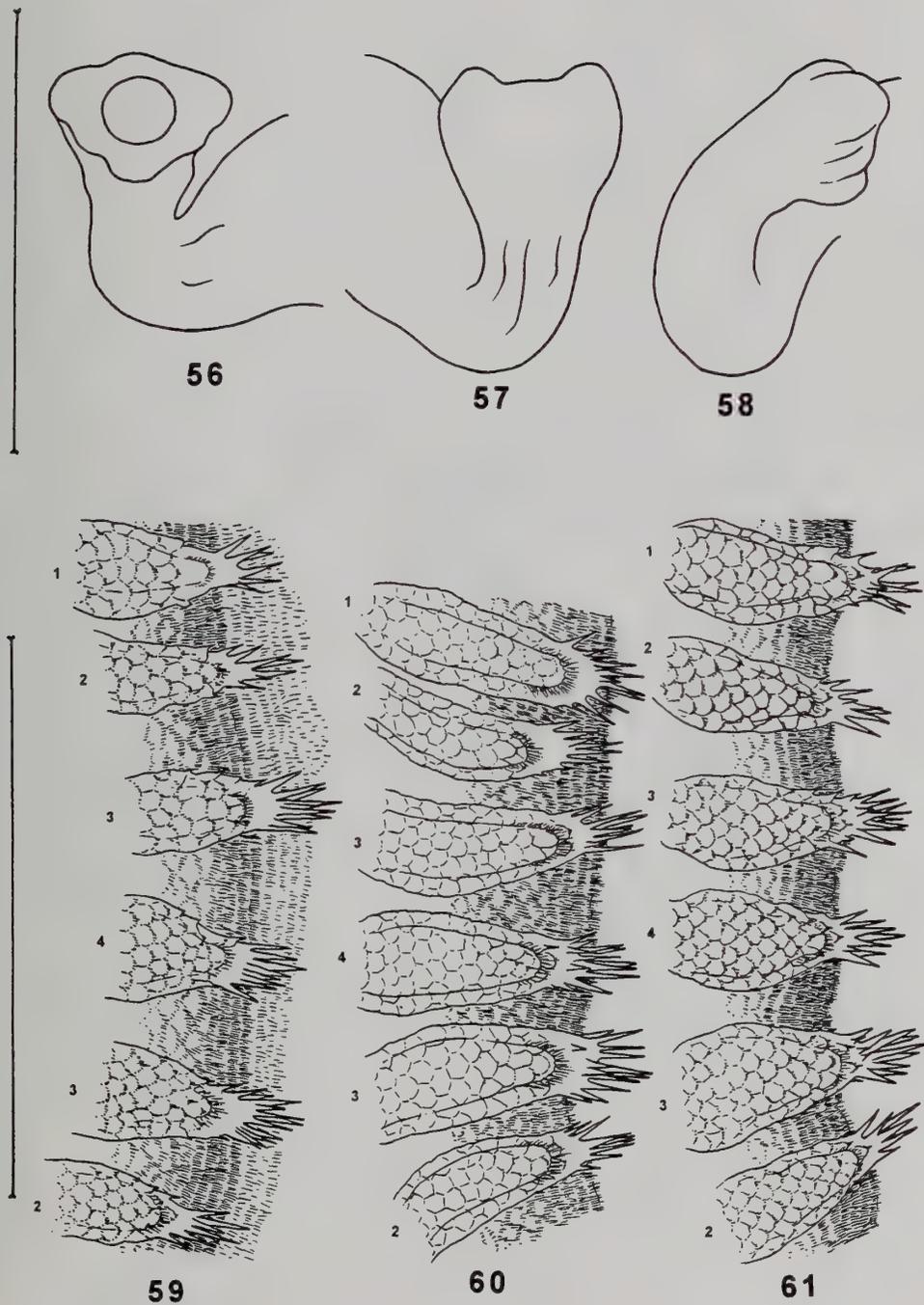
Figs 29–38. *Amicotermes congoensis*. 29–31, mandibles with surface view of right molar plate; 32, 34, 36, ventral and 33, 35, 37, dorsal views of abdomen to show gut coiling *in situ*; 38, gut dissected and uncoiled [bar, 0.5 mm: top left, mandibles; 1 mm: bottom middle, abdomens and uncoiled gut].



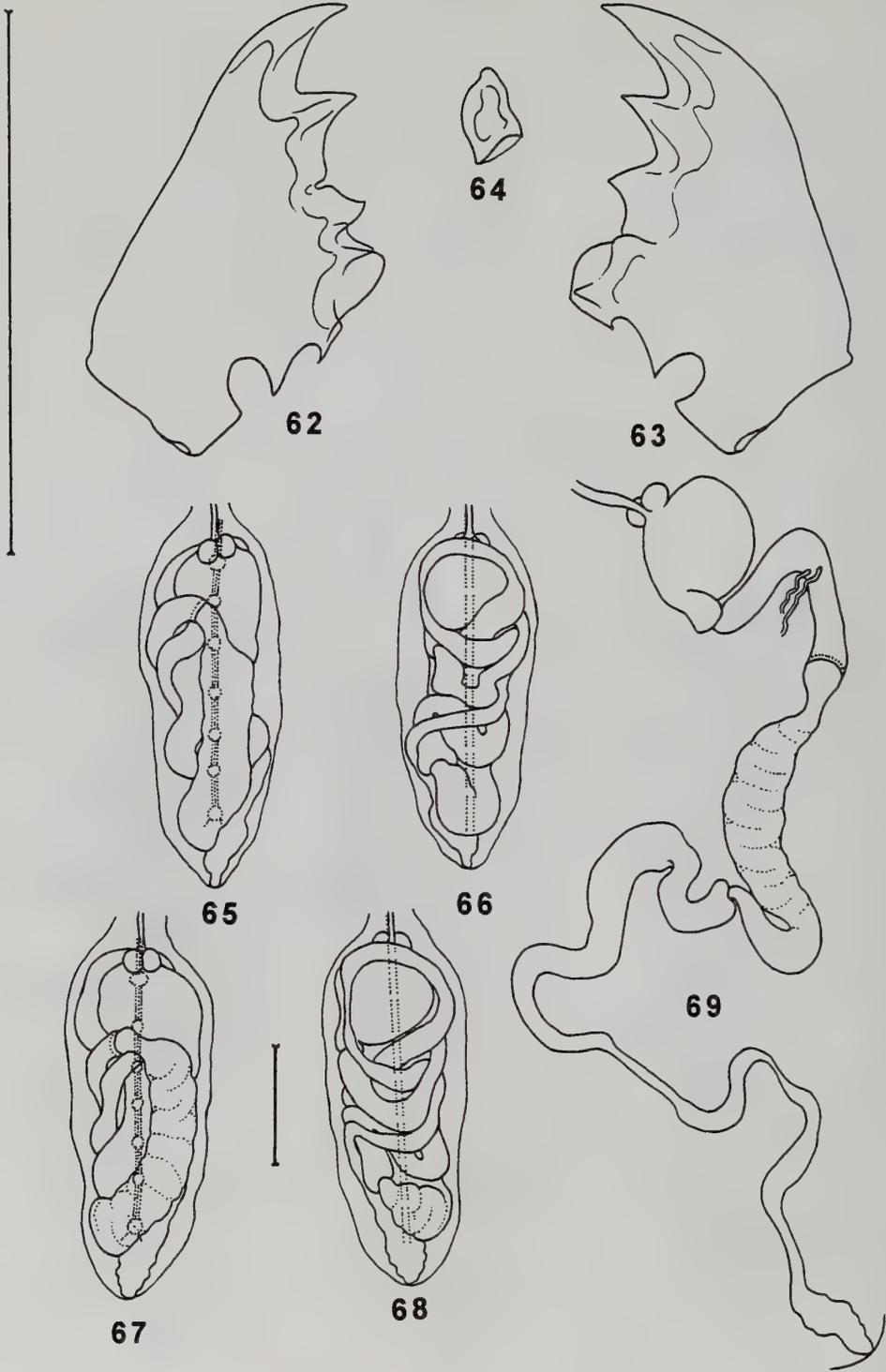
Figs 39–46. *Amicotermes congoensis*. 39–40, crop with ‘burst’ and proventriculus; 41–43, enteric valve seating and part of P3; 44–46, enteric valve armature opened out to show detail and variation, ridge positions numbered [bar, 1 mm: top left, crop and valve seating; 0.5 mm: bottom right valve armature].



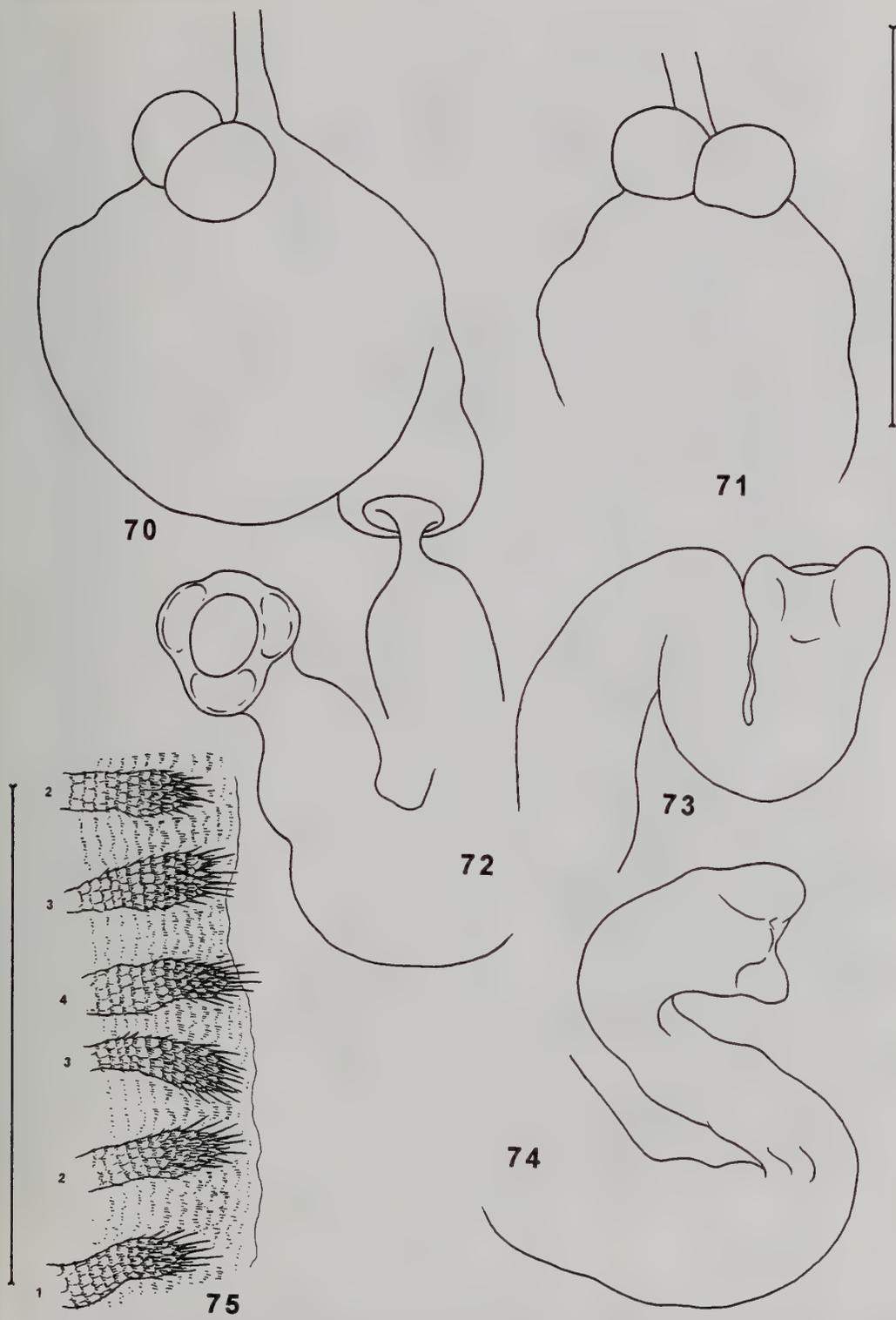
Figs 47–55. *Amicotermes cristatus*. 47–49, mandibles with surface view of right molar plate; 50, 52, ventral and 51, 53, dorsal views of abdomen to show gut coiling *in situ*; 54, gut dissected and uncoiled; 55, crop with 'burstlers' and proventriculus [bar, 0.5 mm: top left, mandibles; 1 mm: bottom right, abdomens and uncoiled gut; bottom left, crop and proventriculus].



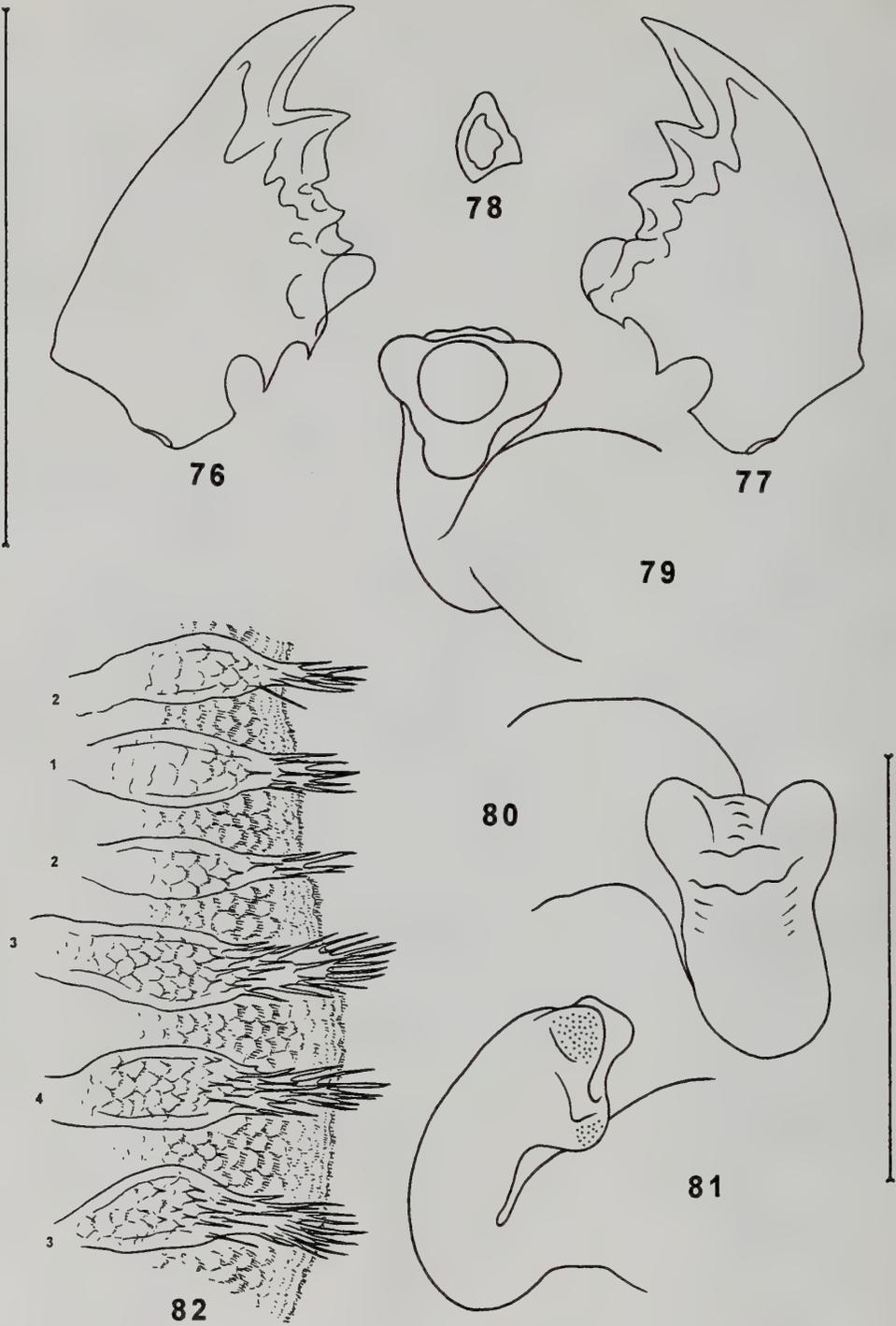
Figs 56-61. *Amicotermes cristatus*. 56-58, enteric valve seating and part of P3; 59-61, enteric valve armature opened out to show detail and variation, ridge positions numbered [bar, 1 mm: top left, valve seating; 0.5 mm: bottom left valve armature].



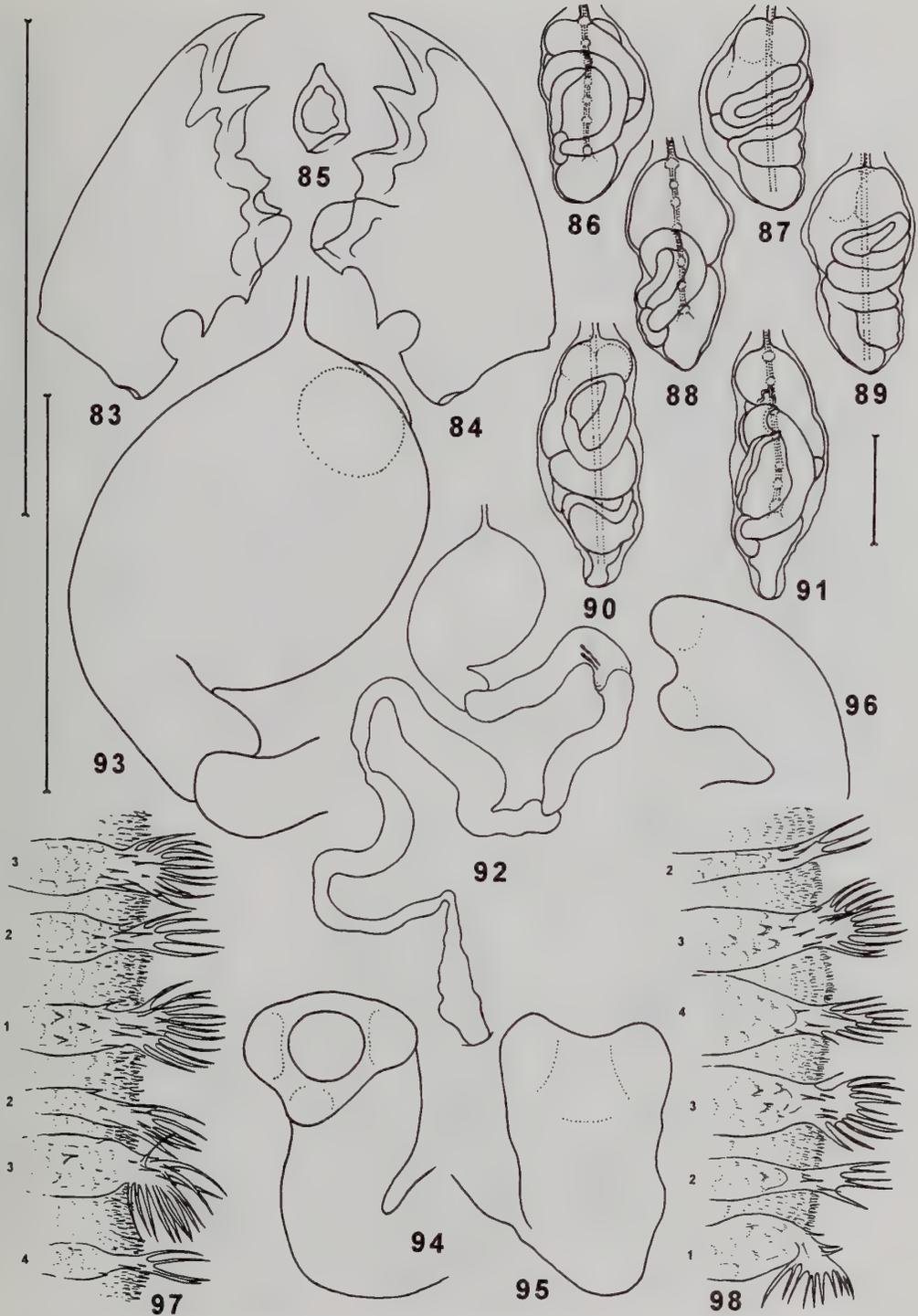
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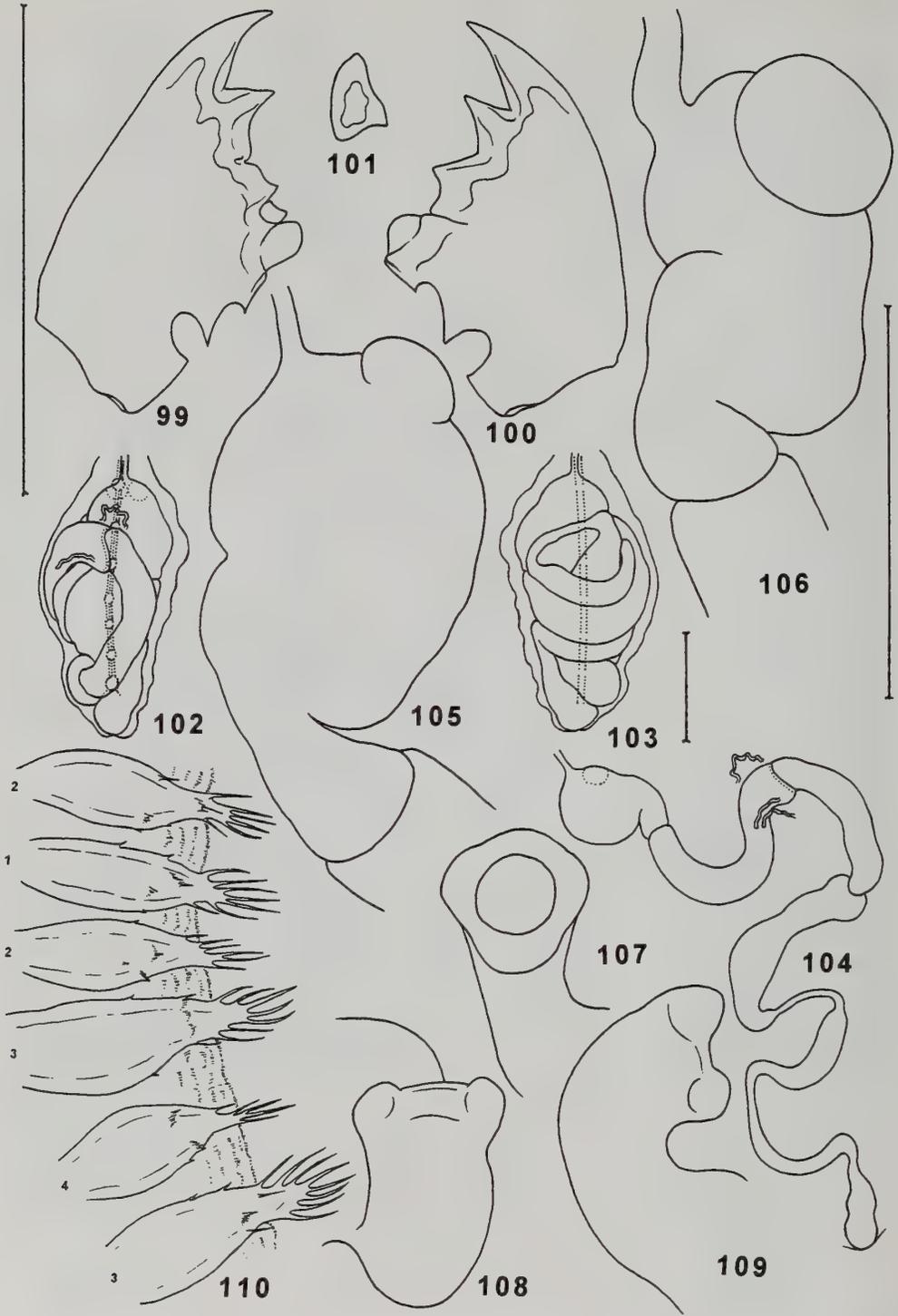
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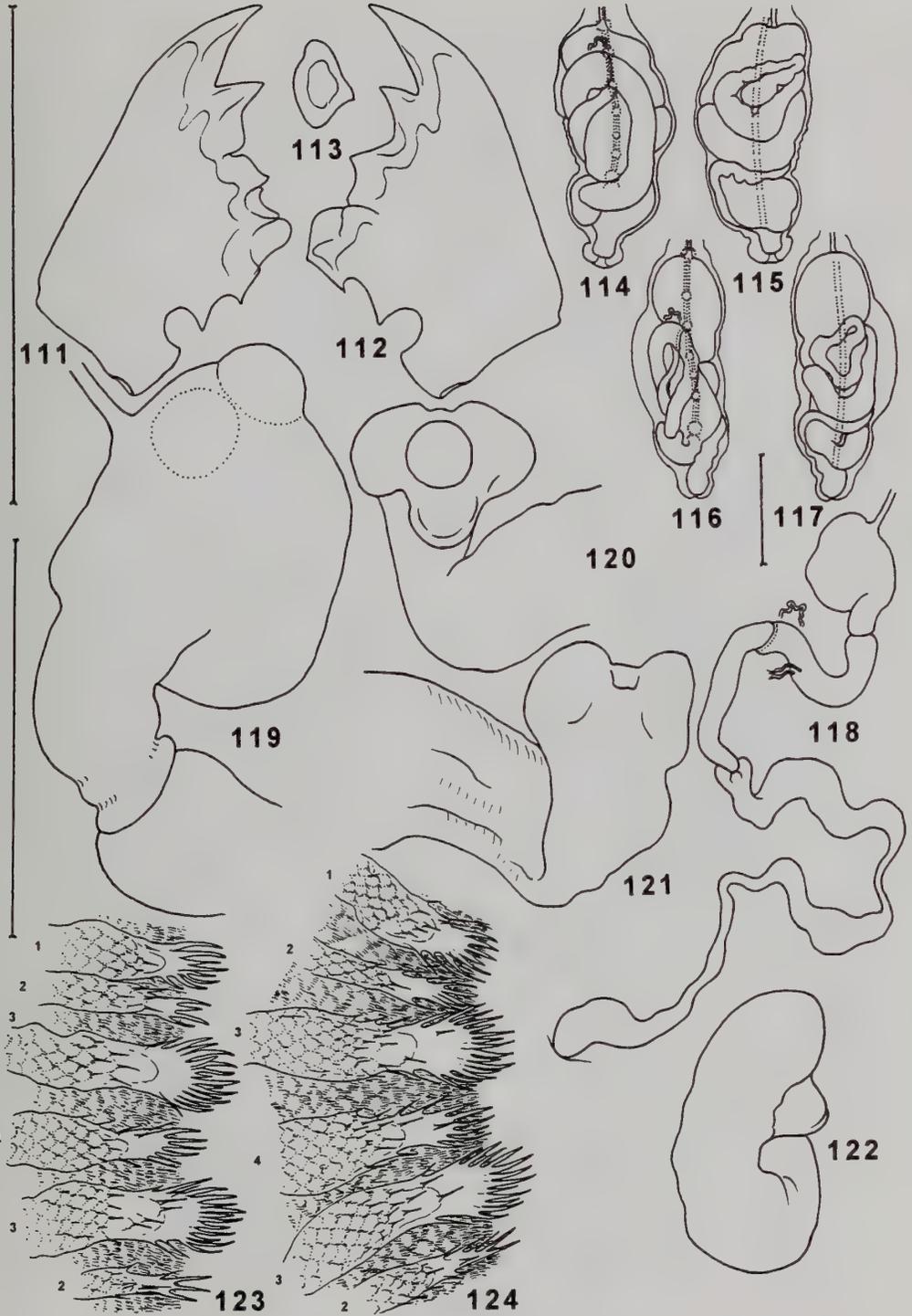
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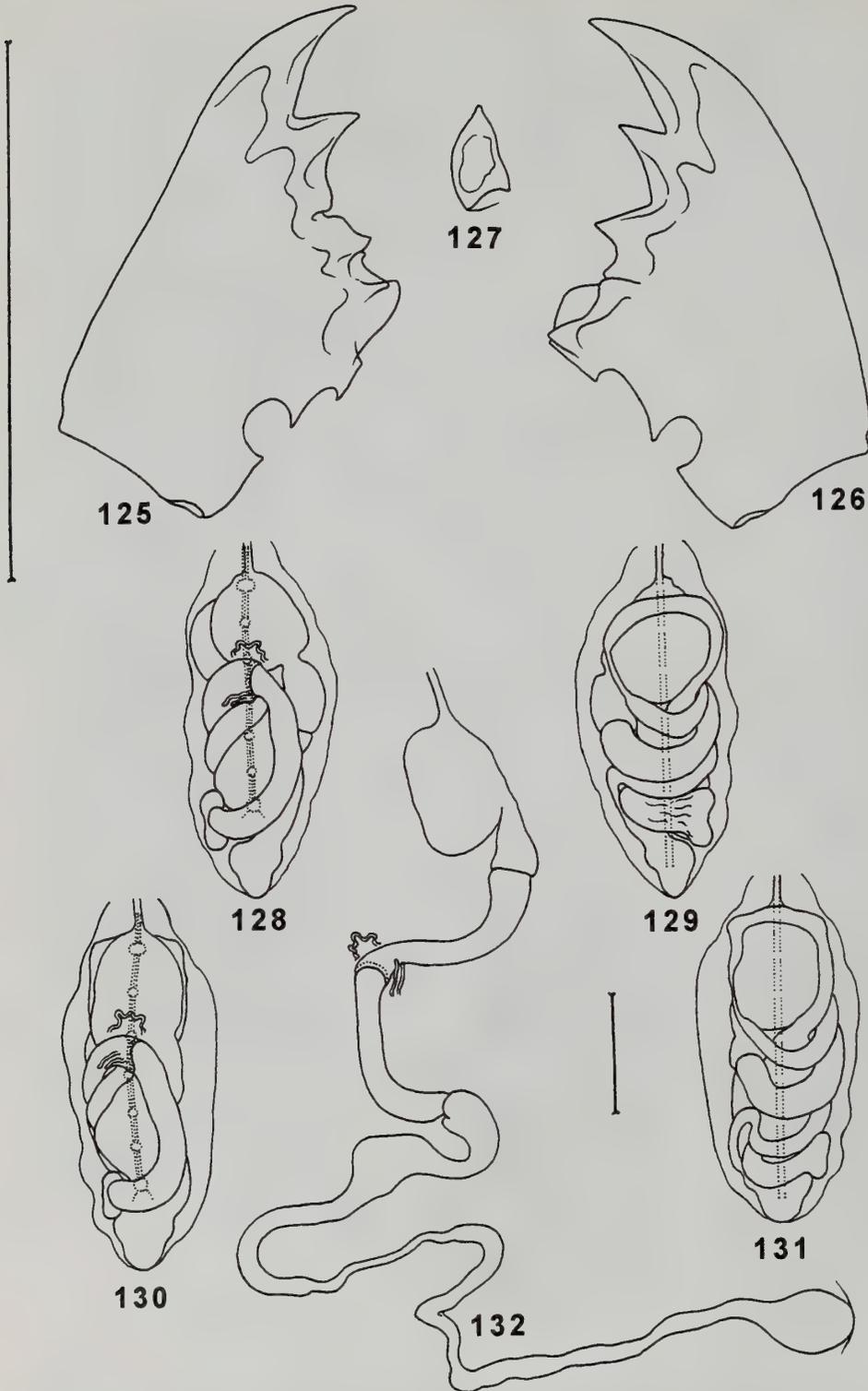
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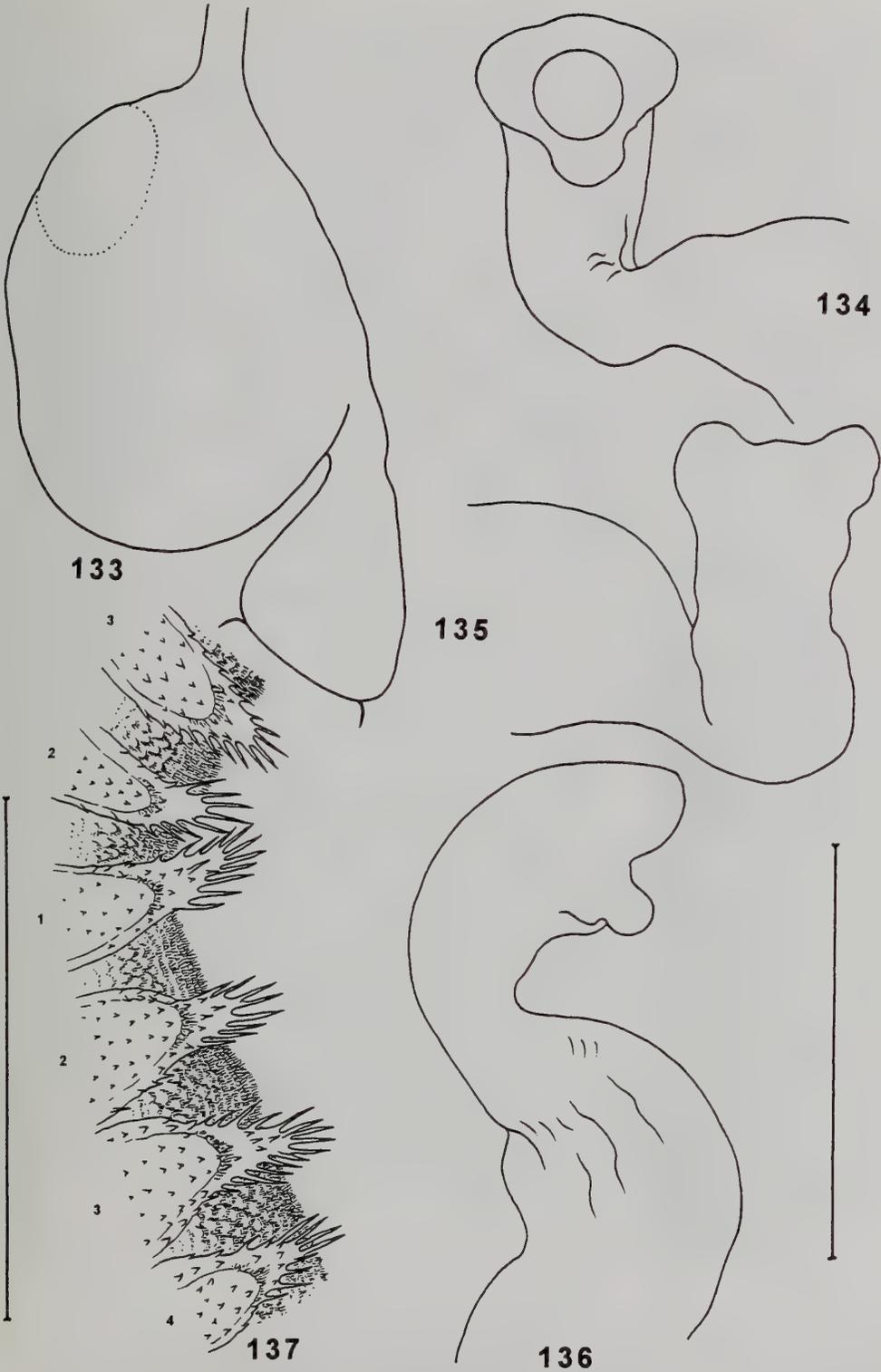
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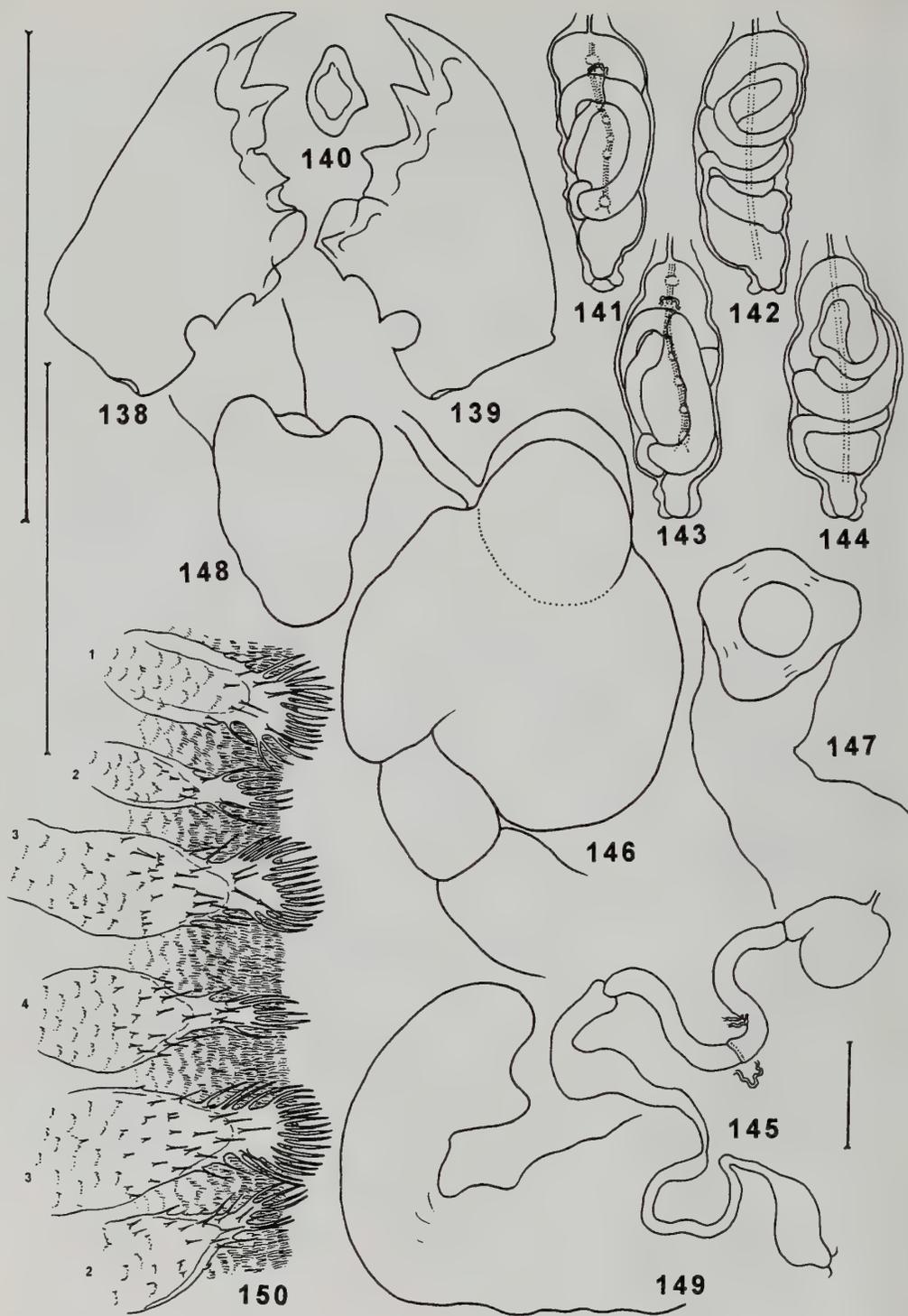
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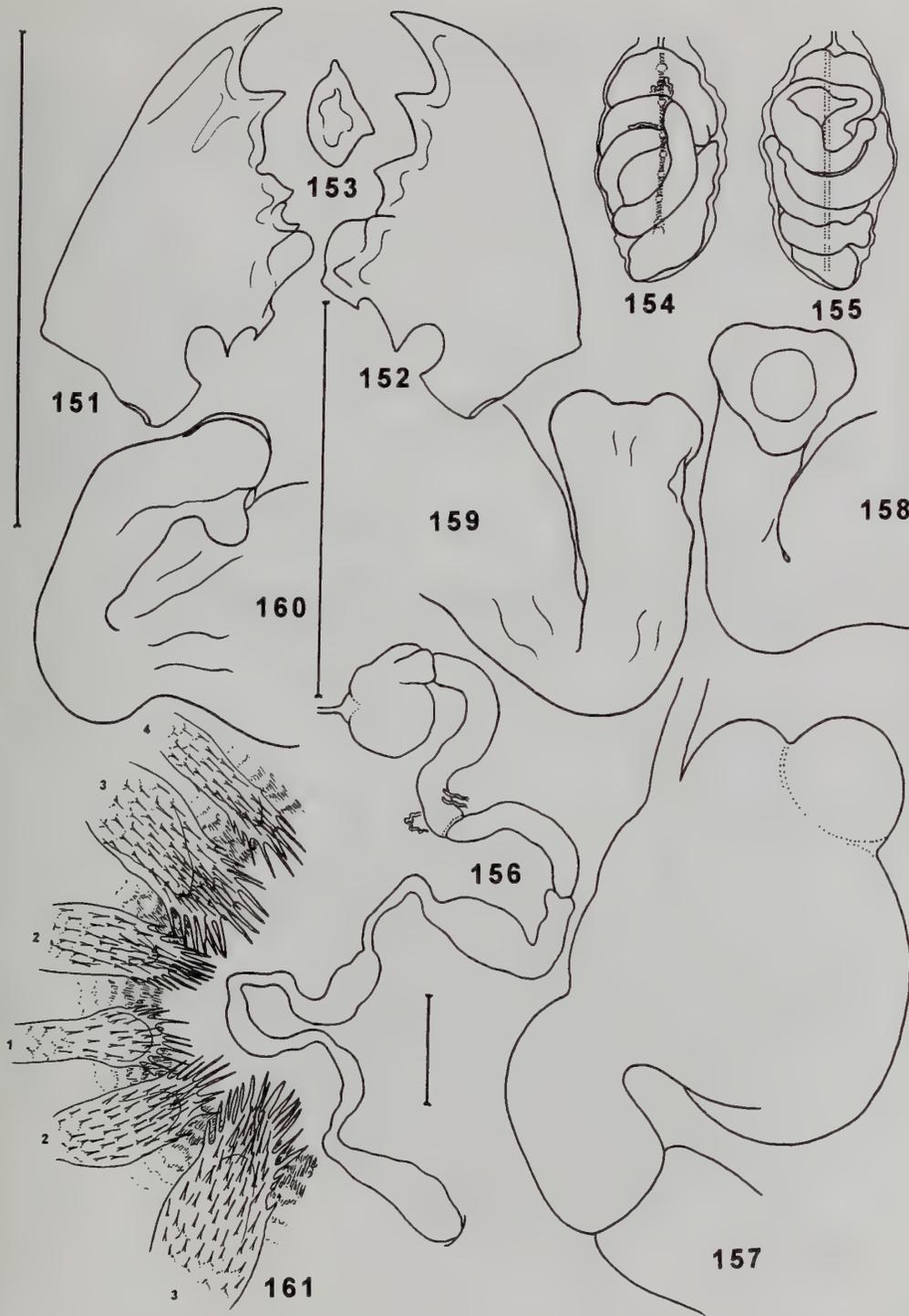
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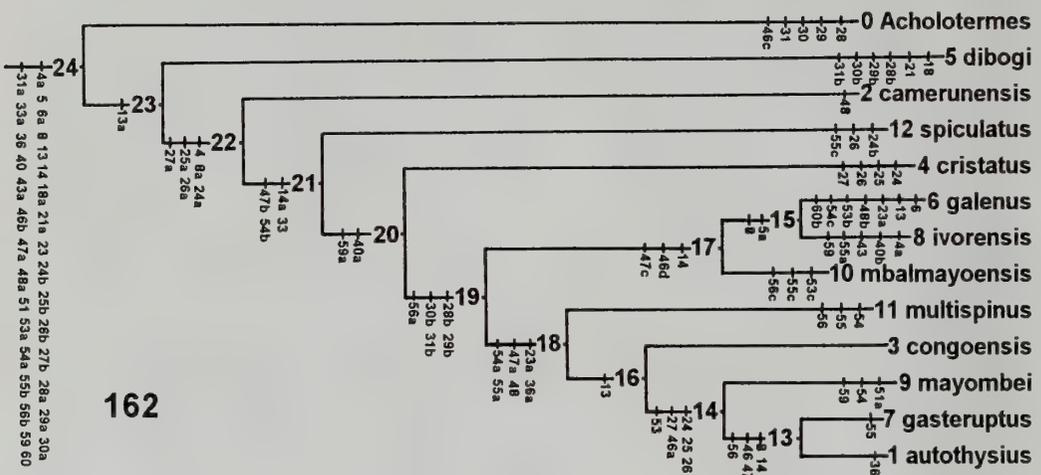


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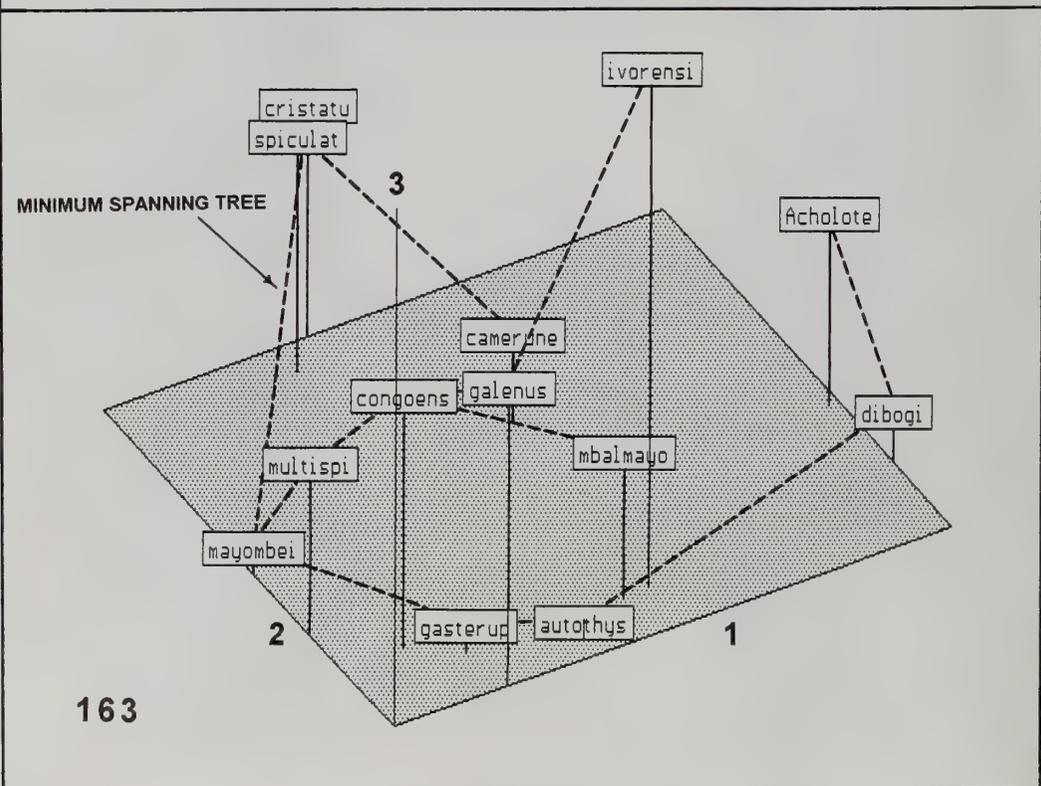


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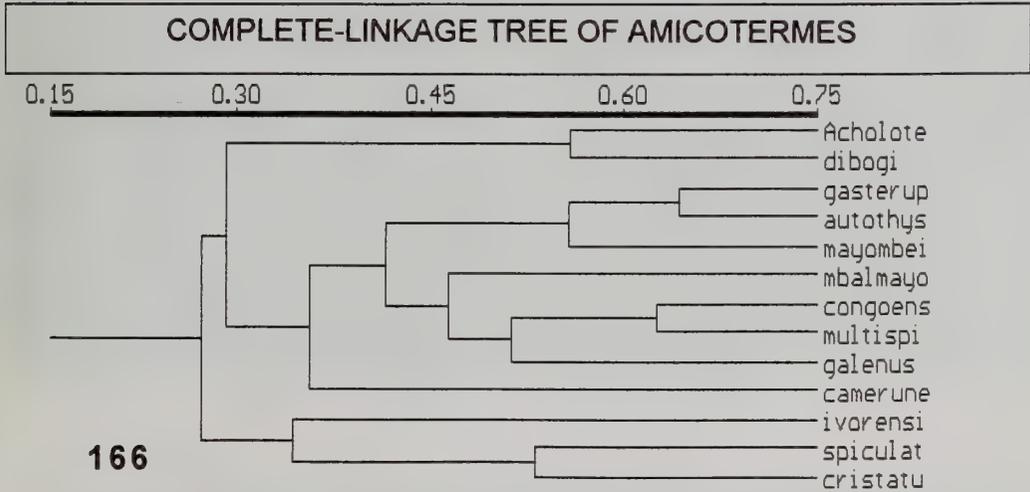
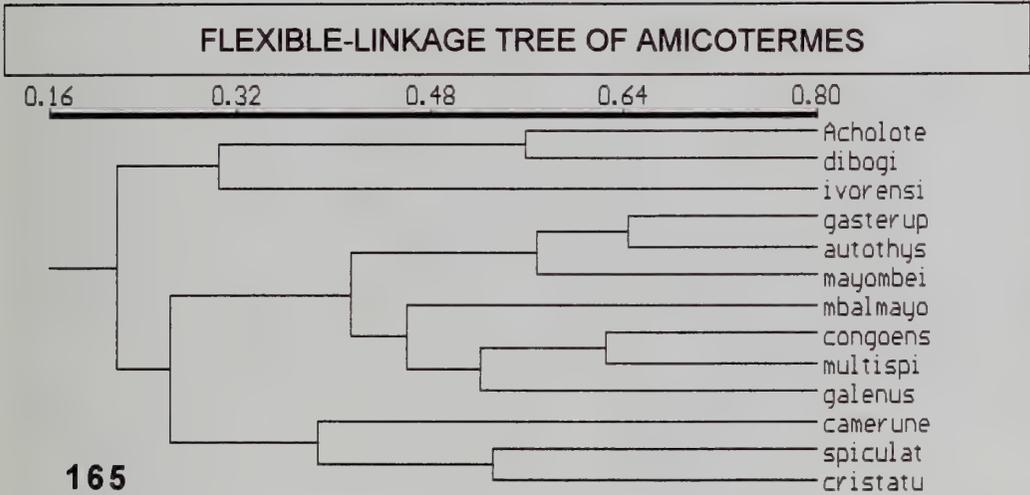
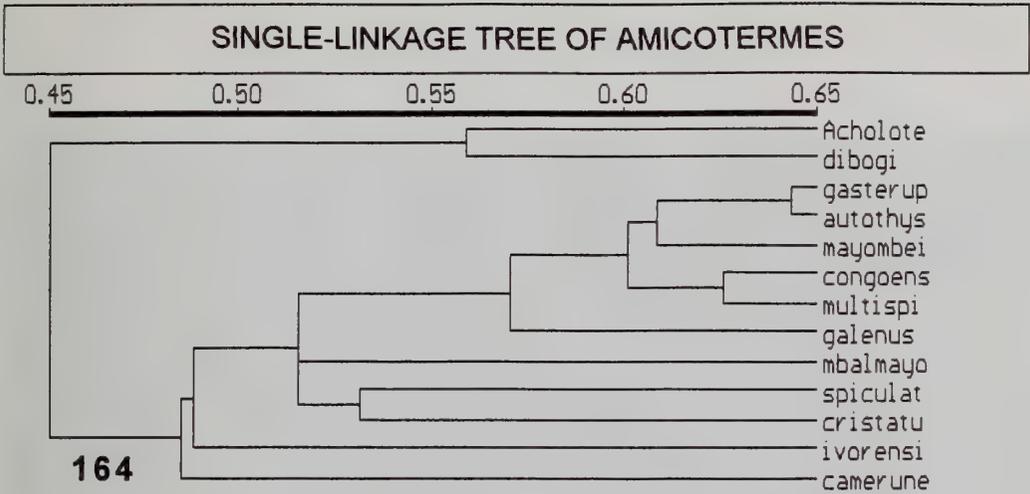
**STRICT CONSENSUS TREE OF AMICOTERMES Length 217 CI 47 RI 44
from mhennig*;bb*; two trees**



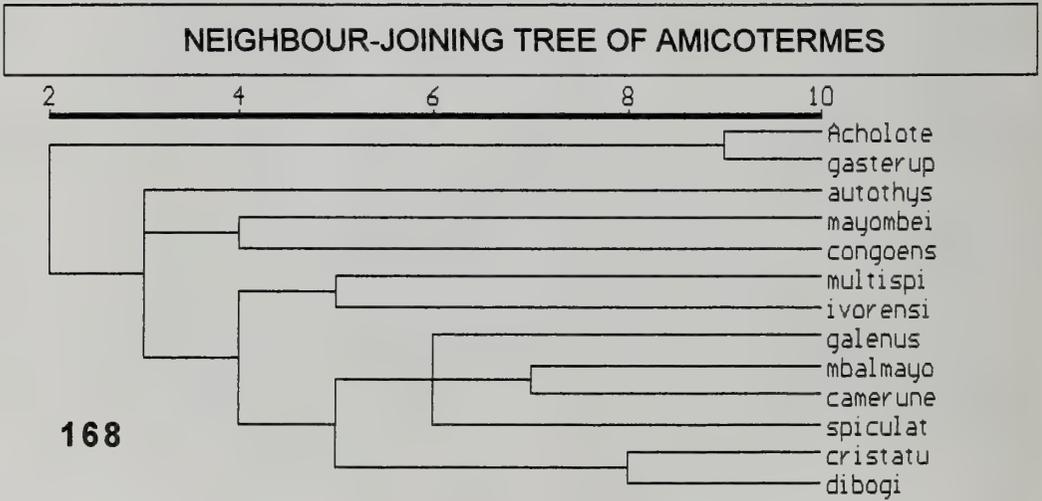
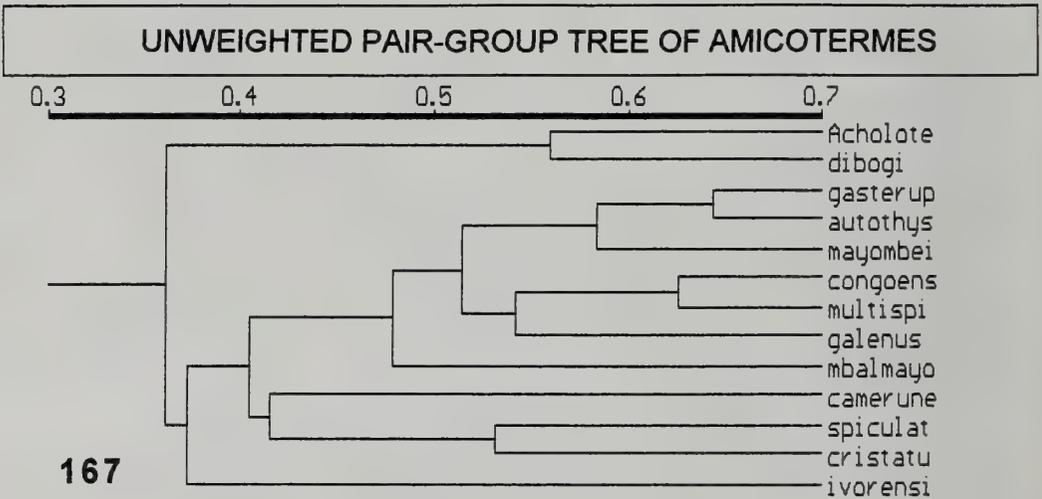
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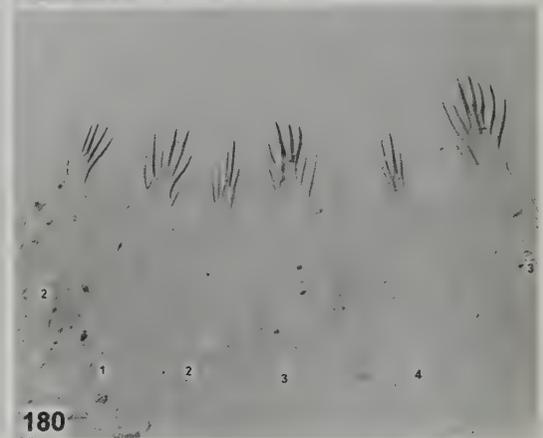
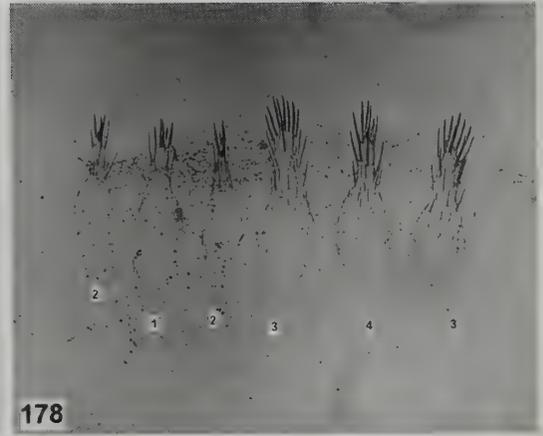
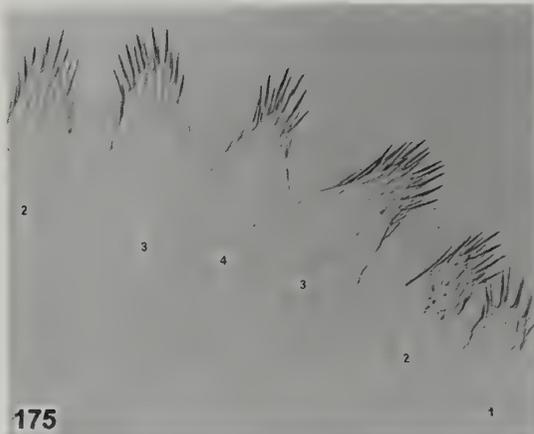
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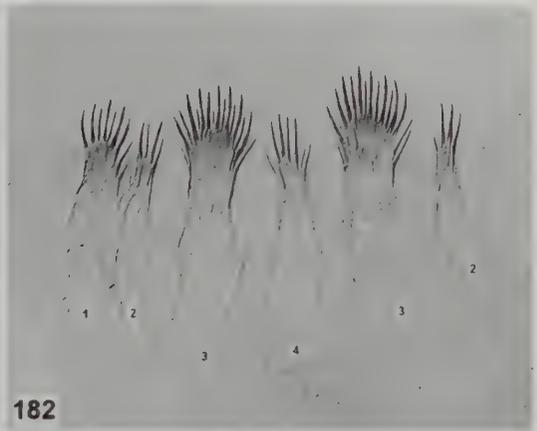
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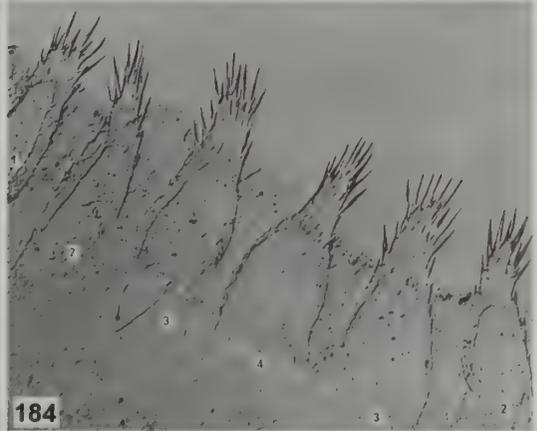
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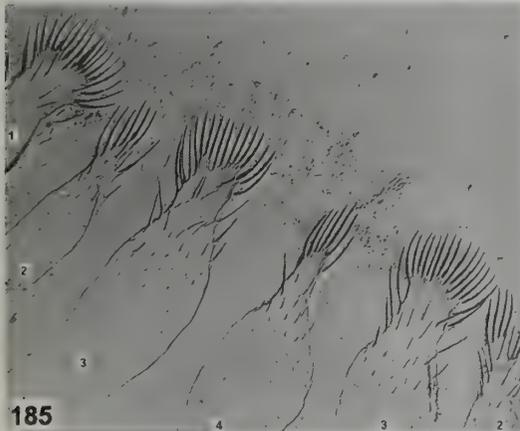
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