
Systematics of the sycoecine fig wasps (Agaonidae, Chalcidoidea, Hymenoptera), III (*Crossogaster*)

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Communicated by Prof. J.T. Wiebes at the meeting of January 25, 1993**ABSTRACT**

Crossogaster Mayr, an African genus of sycoecine fig wasps, is revised. Members of this genus are associated with *Ficus* species (Moraceae) of the subsections *Platyphyllae*, *Chlamydorae*, and *Caulocarpae* of section *Galoglychia*. Unlike *Seres* Waterston and *Sycoecus* Waterston these species are therefore associated with a number of agaonine genera, namely *Elisabethiella* Grandi, *Alfonsiella* Waterston, and *Courtella* Kieffer. Fourteen new species are described: *Crossogaster michaloudi* (Gabon, Ivory Coast, Uganda, ex *F. artocarpoides* Warb.); *C. lachaisei* (Ivory Coast, ex *Ficus sansibarica macrosperma* (Mildbr. & Burr.) Berg); *C. inusitata* (Zambia, ex *F. sansibarica (?) macrosperma* (Mildbr. & Burr.) Berg); *C. quadrata* (South Africa, ex *F. glumosa* Delile); *C. stigma* (South Africa, Zimbabwe, Zambia, ex *F. glumosa* Delile); *C. oculagrandis* (Cameroun, swept); *C. lurida* (South Africa, ex *F. natalensis natalensis* Hochst.); *C. rastellus* (Uganda, ex *F. 'natalensis'*); *C. praeacuta* (Uganda, ex *Ficus* spec. K); *C. rashbrooki* (Tanzania, ex *Ficus* spec.); *C. ovata* (Uganda, ex *F. ovata* Vahl); *C. vansomereni* (Uganda, Kenya, ex *Ficus* spec.); *C. hilli* (Uganda, ex *F. 'natalensis'*); *C. robertsoni* (South Africa, Ivory Coast, ex *F. trichopoda* Baker). A key is provided to separate the species in both sexes.

INTRODUCTION

Crossogaster Mayr contains some of the more derived sycoecine species (van Noort & Compton, in prep.). Sixteen *Crossogaster* species are recognised, of which fourteen are described here for the first time. The genus can be split into two monophyletic species-groups, leaving three species that retained plesiomorphic character states.

The host associations of *Crossogaster* species are less tight than those of *Seres* Waterston and *Sycoecus* Waterston, which are each associated with a single *Ficus*

(Moraceae) subsection. The derived *Crossogaster* species are usually associated with the *Ficus* subsections *Platyphyllae* and *Chlamydodora* of section *Galoglychia*. However, a single derived species, *C. ovata* spec. nov., is associated with subsection *Caulocarpae* of section *Galoglychia*, which is also host to the three primitive *Crossogaster* species. This subsection usually plays host to the species of *Seres*.

C. oculagrandis spec. nov., appears to be nocturnal, as it possesses character states associated with nocturnal flight, viz. large eyes and testaceous colouring, similar to the species of the pollinator (agaonine) genus *Alfonsiella* Waterston.

Morphological terminology, definitions and abbreviations are as defined in van Noort (1993). All measurements are in millimetres. The following acronyms are used for institutions and collections housing *Crossogaster* specimens:

NHML – The Natural History Museum, London

NHMV – Naturhistorisches Museum, Vienna

RMNH – Rijksmuseum van Natuurlijke Historie, Leiden

SAMC – South African Museum, Cape Town

SANC – National Collection of Insects, Pretoria

SGCC – Collection of Dr. S.G. Compton, Leeds

Crossogaster Mayr

Crossogaster Mayr 1885: 189–192. Type species: *Crossogaster triformis* Mayr 1885, by monotypy.

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

Thorax usually not compressed, smooth; pronotum square or elongate; mesonotum subtriangular to distinctly broader than long and semicircular; parapsidal sulci complete, straight to distinctly curved; propodeal spiracles anteriorly situated. Fore femur stout, elongate to subtriangular; tibial armature usually bidentate, may be tridentate. Ventral tooth next to spur insertion on fore tibia

usually present, but may be absent. Axial third of forewing glabrous, rest may be glabrous or pilose; fringe present. Postmarginal vein from distinctly longer to shorter than stigmal vein.

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

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

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

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

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

KEY TO THE SPECIES OF *CROSSOGASTER*

FEMALES

1. First funicle segment twice the length of any of the rest, multiporous plate sensilla (MPS) short and stumpy (fig. 8); first tarsal segments of the mid and hind legs expanded and enlarged, ex *F. sansibarica (?) macrosperma* *C. inusitata* ⓧ
- First funicle segment subequal or shorter than the rest, MPS either placoid or free and elongate; first tarsal segments of the mid and hind legs not enlarged 2
2. Antennae twelve segmented with two anelli and five funicle segments (figs. 3 & 16); head very elongate, more than 1.5X longer than wide 3
- Antennae eleven segmented with either one anellus and five funicle segments (fig. 37) or two anelli and four funicle segments (fig. 69); head less elongate, less than 1.3X longer than wide 4
3. Epistomal margin with a small medial convexity (fig. 1); cheek 1.48X longer than the eye, ex *F. artocarpoides* *C. michaloudi* ⓧ
- Epistomal margin smooth (fig. 13); cheek twice as long as the eye, ex *F. sansibarica macrosperma* *C. lachaisei* ⓧ
4. Funicular MPS placoid, fused for at least three-quarters of their length to the segment (figs. 69 & 79); one or two anelli 5
- Funicular MPS elongate, free for at least half their length (figs. 32, 37, 49 & 51); one anellus .. 10

5. Clypeal margin convex, sometimes with a weak medial concavity (figs. 71, 76 & 84) 6
 - Clypeal margin flat, with a weak medial concavity (figs. 68, 72 & 75) 8
6. Head elongate, at least 1.20X longer than wide, cheek at least 1.2X longer than the eye length; lateral ocelli completely visible in dorsal view (fig. 76 & 84), ex *F. trichopoda* *C. robertsoni*
 - Head square; cheek length equal to eye length; lateral ocelli half hidden in dorsal view (fig. 71) .. 7
7. Two anelli, four funicle segments (as in fig. 69), ex *Ficus* spec. *C. vansomereni*
 - One anellus, five funicle segments, first funicle segment reduced with only a single MPS present (as in fig. 73), ex *F. vasta* *C. triformis*
8. Two anelli, four funicle segments (fig. 69), ex *Ficus* spec. *C. hilli*
 - One anellus, five funicle segments, first funicle segment reduced with only a single MPS present (fig. 73) 9
9. Head ca. square, l:w = 1.06; cheek length equal to eye length (fig. 72), ex *Ficus* spec. ... *C. rashbrooki*
 - Head elongate, l:w = 1.24; cheek length 1.45X eye length, (fig. 75), ex *F. ovata* *C. ovata*
10. Head elongate, more than 1.20X longer than wide; malar sulcus present 11
 - Head approximately square; malar sulcus absent 12
11. Clypeal margin medially pointed (fig. 54); mandible with uneven rows of smaller teeth anterior to the ventral row of main teeth (fig. 57), ex *Ficus* spec. *C. praeacuta*
 - Clypeal margin slightly convex, set into paraclypeal margins (fig. 62); mandible with a single ventral row of 14 long teeth (fig. 63), ex *Ficus* spec. *C. rastellus*
12. Thorax and gaster testaceous 13
 - Thorax and gaster metallic black or brown 14
13. Eye enlarged, 5.2X as long as cheek (fig. 46) *C. oculagrandis*
 - Eye normal, 1.6X longer than cheek (fig. 35), ex *F. n. natalensis* *C. lurida*
14. Clypeal margin bilobed, with shallow medial concavity (fig. 27); eighth urotergite spiracular peritremata extremely expanded, horizontal diameter 0.61X the length of the ovipositor valves (fig. 31), ex *F. glumosa* *C. stigma*
 - Clypeal margin slightly convex (figs. 33 & 50); eighth urotergite spiracular peritremata less expanded, horizontal diameter 0.4X or less than the length of the ovipositor valves 15
15. Cheek length usually half of eye length, if longer than this then the vertex is concave; epistomal margin broad, width 0.31X or more than head width (fig. 50); horizontal diameter of the eighth urotergite spiracular peritremata 0.28X the length of the ovipositor valves, ex *F. thonningii* & *F. stuhlmannii* *C. odorans*
 - Cheek length 0.70X eye length, vertex always straight; epistomal margin narrower, width 0.27X head width (fig. 33); horizontal diameter of the eighth urotergite spiracular peritremata 0.40X the length of the ovipositor valves, ex *F. glumosa* *C. quadrata*

MALES*

1. Head metallic brown/black (possibly metallic green in fresh specimens), rest of body and antennae testaceous; mandibular apical teeth subequal, inner tooth just longer than outer (fig. 7); antennae with twelve segments (fig. 12), ex *F. artocarpoides* *C. michaloudi*
 - Head and body testaceous, but may be dark brown on the vertex, scutellum and mesoscutum; inner mandibular tooth distinctly longer than outer (figs. 21 & 44); antennae with only eleven segments (fig. 9) 2
2. Two types of multiporous plate sensilla (MPS) present, one short and stumpy, other narrow and free (fig. 9); first tarsal segments on the mid and hind legs expanded and enlarged, ex *F. sansibarica* (?) *macrosperma* *C. inusitata*
 - Single MPS type – placoid (fig. 45); first tarsal segments on the mid and hind legs not enlarged .. 3
3. Epistomal margin medially convex (e.g. figs. 58 & 65) 4
 - Epistomal margin medially flat or with a medial concavity (figs. 42 & 53) 6
4. Cheek length less than 0.5X eye length, ex *F. 'thonningii'* *C. hilli*
 - Cheek length more than 0.6X eye length 5

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

5. Lobes of paraclypeal margins project further anteriorly than the epistomal margin (fig. 65); MPS only present on the last two club segments, ex *F. natalensis* *C. rastellus*
 - Lobes of paraclypeal margins project anteriorly only as far as the epistomal margin (fig. 58); MPS present on all three club segments, ex *Ficus* spec. K *C. praeacuta*
6. Cheek length 0.4X or less than eye length; head quadrate or transverse 7
 - Cheek length 0.57X or more than eye length; head slightly longer than wide 10
7. Epistomal margin with a slight medial concavity (fig. 42); MPS present on all three club segments, ex *F. n. natalensis* *C. lurida*
 - Epistomal margin medially flat (fig. 53); MPS either only present on the last two club segments or present on all the club segments and one or two funicle segments 8
8. MPS only present on the last two club segments, ex *F. thonningii* *C. odorans*
 - MPS present on all the club segments and either the last funicle segment or the last two funicle segments 9
9. Toruli separated by a fifth of the torulus width, axillae and parapsides dark brown; MPS present on the last funicle segment and all the club segments, ex *F. glumosa* *C. stigma*
 - Toruli separated by a third of the torulus width, thorax uniformly testaceous; MPS present on the last two funicle segments and all the club segments, ex *F. glumosa* *C. quadrata*
10. Large species, total length with head in orthognathous position = 1.84 mm; MPS only present on the last funicle segment and all the club segments, ex *F. ovata* *C. ovata*
 - Smaller species, total length with head in orthognathous position = 1.40 mm; MPS present on the last three funicle segments and all the club segments, ex *F. trichopoda* *C. robertsoni*

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

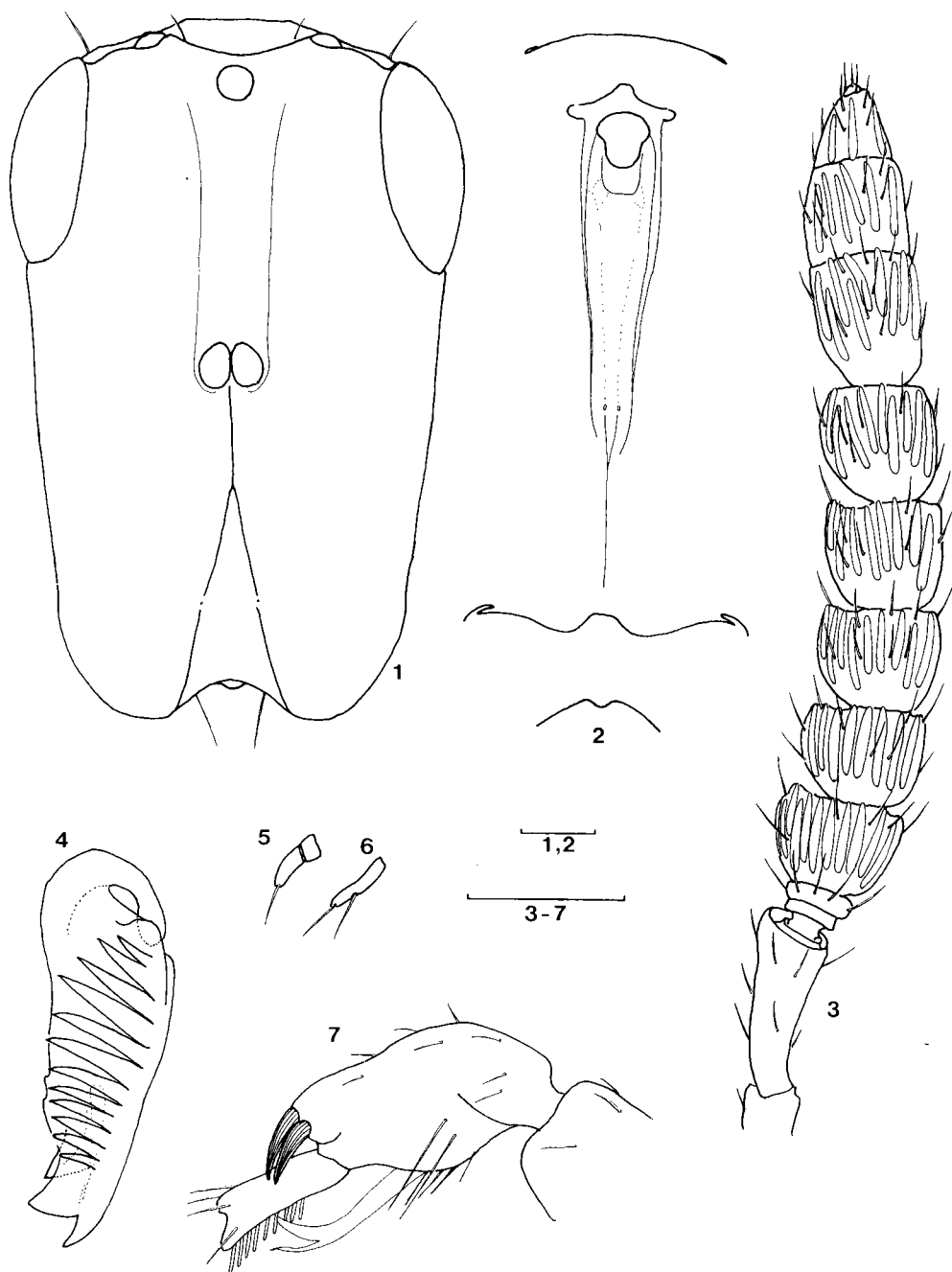
***Crossogaster michaloudi* spec. nov.**
 (figs. 1–6, 10–12 & 17)

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

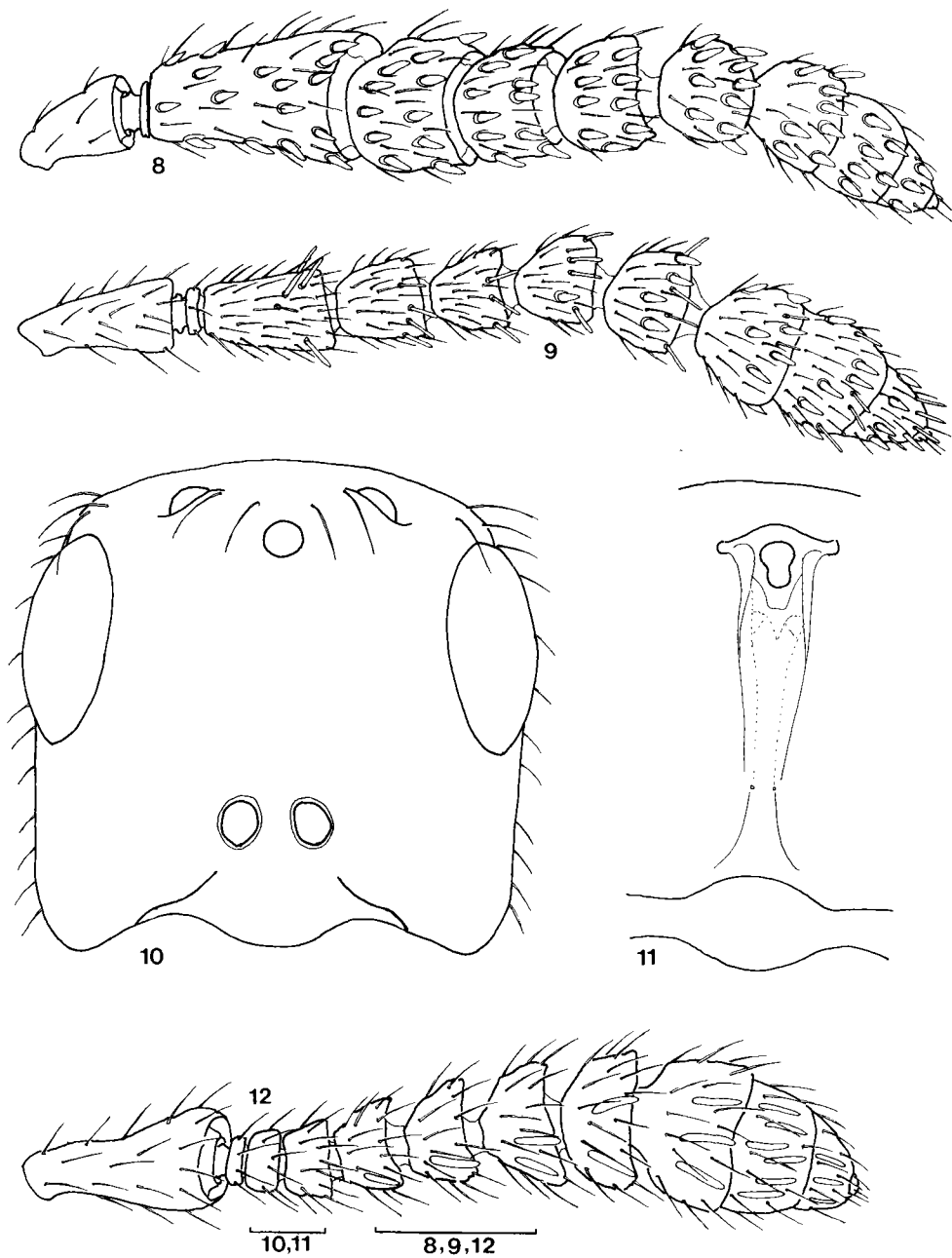
Type material. Holotype ♀ and allotype ♂ (slide mounted): Gabon, Makokou, 21 August 1978, leg. G. Michaloud, no. 1012, RMNH 3722 & 3724, ex *F. artocarpoides* Warb. [associated pollinator = *Courtella penicula* (Wiebes)]. Paratypes, series ♀♀ and ♂♂: same data as holotype; series ♀♀, ♂♂: Uganda, Mpanga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

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

Head (fig. 1 & 2) elongate, parallel sided ($l = 0.95$, $w = 0.63$, $h = 0.25$). Eye oval ($l = 0.28$, $w = 0.21$, $h = 0.10$), 0.31X as long as the head. Cheek length 1.5X eye length. Malar sulcus present for full cheek length, sinusoidal, anterior third manifested as a wider fovea. Lateral ocelli half visible in dorsal view, situated in axial lip of lateral vertex excavations. POL = 0.21, OOL = 0.07. TE 1.18X as long



Figs. 1-7. *Crossogaster michaloudi* spec. nov., female: 1, head, dorsal view; 2, head, ventral view; 3, antenna, dorsal view; 4, mandible, ventral view; 5, maxillary palp; 6, labial palp; 7, fore tibia and first fore tarsal segment, antiaxial view. Scale bars = 0.1 mm.



Figs. 8–9. *Crossogaster inusitata* spec. nov.: 8, female antenna, anti-axial view; 9, male antenna, anti-axial view. Figs. 10–12. *Crossogaster michaloudi* spec. nov., male: 10, head, dorsal view; 11, head, ventral view; 12, antenna, dorsal view. Scale bars = 0.1 mm.

as scrobe length ($TE = 0.46$, $SL = 0.39$). Clypeus equilateral in area, clypeal sutures meet before toruli. Epistomal margin concave with small medial convexity, width ca. a quarter of the head width. Ventral tentorial pits only slightly separated (fig. 2). One labial palp segment (fig. 6) and two maxillary palp segments (fig. 5). Mandible with two apical teeth, first ventral tooth short and stout, remaining fourteen ventral teeth long and slender, two glands (fig. 4). Hypostoma absent. Antennae (fig. 3) twelve segmented, formula 1125(3). Flagellum 5.2X longer than pedicel length. Scape 6.45X longer than wide ($l = 0.29$). Pedicel elongate, 0.38X scape length. MPS placoid, numerous, close together.

Thorax. Pronotum ($l = 0.45$, $w = 0.50$), torpedo shaped. Parapsidal furrows complete, evenly curved. Propodeum $l = 0.25$, $w = 0.55$, plical furrows absent, spiracles anteriorly situated. Mesoscutum, $l = 0.41$, $w = 0.59$. Scutellum (including axillae), $l = 0.45$, $w = 0.47$. Fore femur 3.9X as long as wide ($l = 0.57$). Fore tibial armature bidentate (fig. 7). No ventral tooth next to spur insertion. Fore leg coxa 0.70X femur length ($C = 0.40$, $TR = 0.13$, $TI = 0.20$, $TA = 0.30$). Fore wing 2.5X longer than wide, $l = 2.21$, sparse, maximum fringe length = 0.03. Postmarginal longer than stigmal ($SM = 0.76$, $M = 0.33$, $PM = 0.24$, $S = 0.17$). Marginal vein 11X longer than wide. Hind wing 3.7X longer than wide, $l = 1.61$.

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

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

Head (figs. 10 & 11) slightly broader than long ($l = 0.64$, $w = 0.67$, $h = 0.30$). Eye elongate ($l = 0.29$, $w = 0.19$, $h = 0.11$), 0.45X as long as head. Cheek length 0.59X eye length. Malar sulcus present for first two-thirds of cheek but very faint. Lateral ocelli visible in dorsal view, thin occipital carina. $POL = 0.16$. $OOL = 0.08$. Toruli situated below the eyes, separated by four-fifths of torulus width. $TE = 0.34X$ as long as scrobe length. $TE = 0.13$. $SL = 0.38$. Clypeus trapezoid in area. Epistomal margin very convex, width of margin 0.43X head width; paraclypeal margins project slightly more than the epistomal margin. Ventral tentorial pits closer together than other *Crossogaster* species (fig. 11). Inner tooth of mandible only slightly longer than the outer, subequal in size, inner margin smooth, outer apical tooth with a small ventral tooth at the base of the tooth, two glands (fig. 17). One labial palp segment; two maxillary palp segments, distal only slightly longer. Antennae (fig. 12) twelve segmented, formula 1125(3). Flagellum ($l = 0.51$) 4.25X longer than pedicel. Scape broad 4X longer than wide ($l = 0.28$). Pedicel 0.43X scape length. MPS are placoid, present on the last four funicle segments and the club segments.

Thorax. Parapsidal furrows complete. Fore femur 3.3X longer than wide ($l = 0.63$). Fore tibial armature bidentate, no ventral tooth next to the spur on the fore tibia. Fore tibia 1.5X longer than fore tarsus ($C = 0.43$, $TR = 0.16$, $TI = 0.39$, $TA = 0.26$). Fore wing 2.3X longer than wide ($l = 2.3$), very pilose, anal setal tract present. Postmarginal vein longer than stigmal ($SM = 0.80$, $M = 0.40$, $S = 0.19$,

PM = 0.26). Marginal vein thin, 13.3X longer than wide. Hind wing 4X longer than wide, $l = 1.73$.

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

Crossogaster lachaisei spec. nov.
(figs. 13–16)

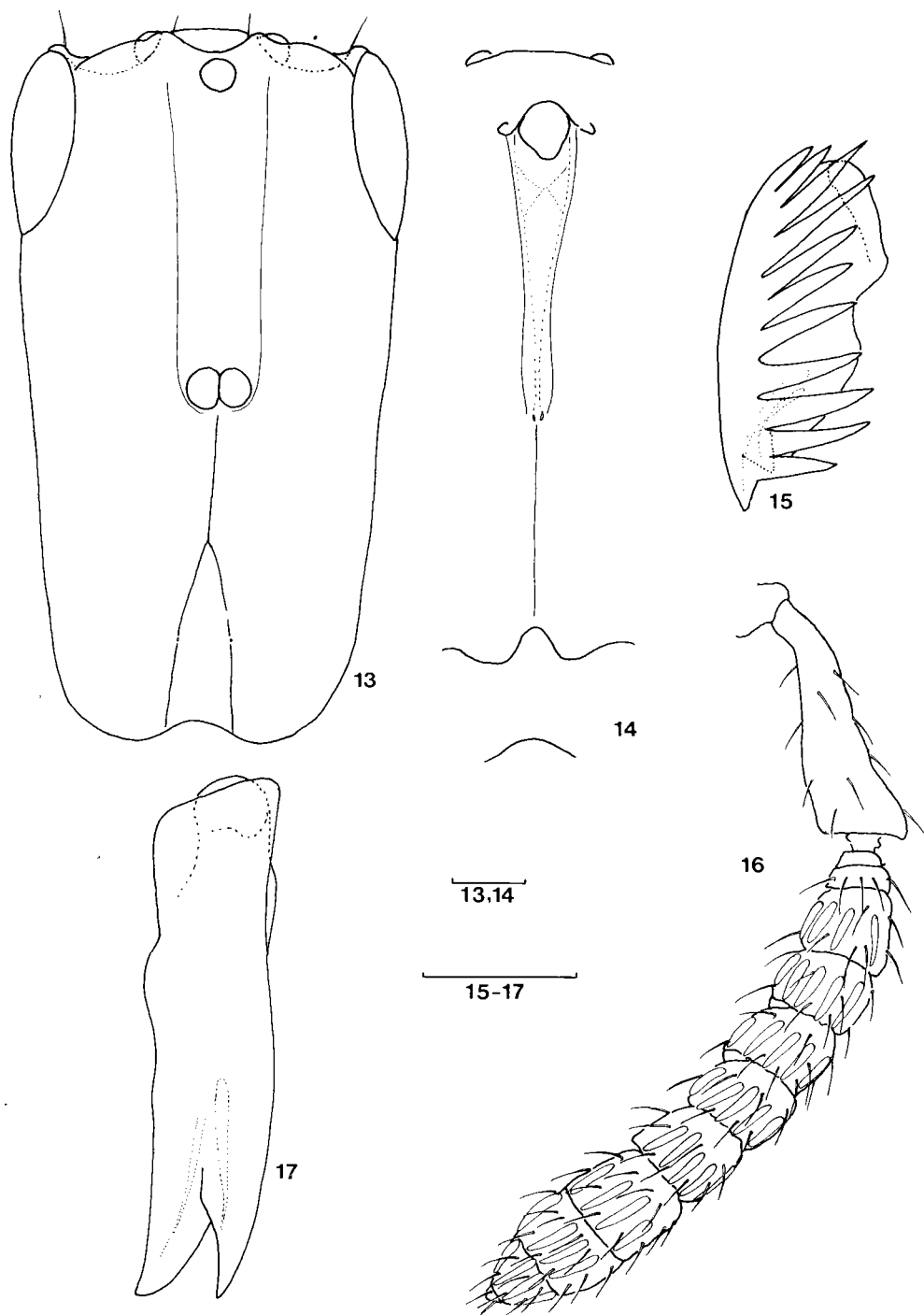
Etymology. Named after D. Lachaise, co-collector of the holotype.

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

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

Head (figs. 13 & 14) elongate, parallel sided ($l = 0.93$, $w = 0.53$, $h = 0.26$), compressed dorsoventrally, wedge shaped, convex dorsally, concave ventrally, such that anterior part of head curves downwards. Eye oval ($l = 0.25$, $w = 0.18$, $h = 0.07$), 0.27X head length. Cheek length twice eye length. Malar sulcus present for full cheek length, for first three-fifths of length straight, then curves up and down to oral fossa. Lateral ocelli half visible in dorsal view situated in deep lateral vertex excavations on dorsal axial lip; prominent carina, V-shaped in posterior view. POL = 0.13, OOL = 0.087. Toruli situated below the eyes, touching. TE as long as scrobe length, SL = 0.42, which is deep, subsquare in X-section. Clypeus narrow and elongate in area, sutures meet before toruli. Epistomal margin concave, smooth, width of margin 0.15X head width. Ventral tentorial pits in close apposition (fig. 14). Mandible with two apical teeth and a longitudinal row of eleven long ventral teeth; two glands (fig. 15). Hypostoma absent. Antennae (fig. 16) twelve segmented, formula 1125(3). Flagellum 2.3X longer than pedicel length. Scape narrow, 7.3X longer than wide ($l = 0.29$). Pedicel very elongate, 0.57X scape length. MPS placoid, more numerous on dorsal surface, reduced in number on the ventral surface.

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



Figs. 13–16. *Crossogaster lachaisei* spec. nov., female: 13, head, dorsal view; 14, head, ventral view; 15, mandible, ventral view; 16, antenna, antiaxial view. Fig. 17. *Crossogaster michaloudi* spec. nov.: male mandible, ventral view. Scale bars = 0.1 mm.