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A New Genus of Hover Wasps from Southeast Asia (Hymenoptera: Vespidae; Stenogastrinae)

JAMES M. CARPENTER[1] AND CHRISTOPHER K. STARR[2]

ABSTRACT

Chalogaster spatulata, **new genus and species,** is described from Viet Nam and northern Thailand. The genus belongs to the subfamily Stenogastrinae, a group of social wasps endemic to the Oriental Region. Cladistic analysis indicates that *Chalogaster* is the sister-group of the genus *Metischnogaster* van der Vecht. A revised key to the genera of Stenogastrinae is presented.

INTRODUCTION

The hover wasps, so called for their remarkable hovering flight (Carpenter, 1988), form the subfamily Stenogastrinae of the family Vespidae. These wasps are endemic to the Oriental Region, ranging from India to New Guinea. The group is taxonomically not well understood: 45 species in six genera are formally recognized (Carpenter and Kojima, 1997), but numerous undescribed species were provided with manuscript names by the late J. van der Vecht. Van der Vecht was revising the entire subfamily before his death, and described five genera (van der Vecht, 1969, 1972, 1977), but published only four generic revisions (van der Vecht, 1972, 1975, 1977). One of Van der Vecht's genera has since been synonymized (Carpenter, 1988), and although a few species descriptions have been published by other workers (Reyes, 1988; Turillazzi, 1988; Turillazzi and Carfì, 1996), the largest genera (viz., *Eustenogaster*, *Liostenogaster*, *Parischogaster*) lack published revision, but work is in progress on *Liostenogaster*, by Turillazzi, and *Parischnogaster,* by CKS.

The species of Stenogastrinae that have

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been studied are social wasps, but are primitively social, and present some notable differences in their biology from other social wasps (reviewed by Turillazzi, 1991). Cladistic analysis of the relationships among subfamilies of the Vespidae supported a sister-group relationship between Stenogastrinae and the other social wasps, Polistinae and Vespinae (Carpenter, 1981), a conclusion that was upheld in consideration of basal vespid fossils (Carpenter and Rasnitsyn, 1990) and more detailed consideration of behavior (Carpenter, 1988). That conclusion has recently been challenged by Schmitz and Moritz (1998), who published a molecular data set and analysis that supported closer relationship of their eumenine sample to the polistines + vespines than the stenogastrines, but remarkably showed Vespidae as paraphyletic in terms of Apidae. This latter result is certainly not credible: Vespidae and Apidae are in different superfamilies, and a large body of evidence indicates that they are well separated (see Brothers and Carpenter, 1993). The morphological evidence supporting a sister group relationship between Stenogastrinae and Polistinae + Vespinae is not strong, as pointed out by Carpenter (1988), but the evidence that Vespidae are monophyletic is substantial (Carpenter, 1981; Brothers and Carpenter, 1993), as is the behavioral evidence grouping stenogastrines with other social wasps (Carpenter, 1988). Lacking two of the six extant subfamilies of Vespidae, Schmitz and Moritz's conclusion differs from Carpenter (1981) only in the placement of the root (see Nixon and Carpenter, 1993, for basic concepts), and their placement is clearly spurious, presumably an artifact of low taxonomic sampling, as is all too common in current molecular analyses. Combination of Schmitz and Moritz's molecular data with morphological characters from Carpenter (1981, 1987, 1988, 1991) and Brothers and Carpenter (1993) supports vespid monophyly, and combination with the behavioral characters from Carpenter (1988) and others supports closer relationship of Stenogastrinae to Polistinae + Vespinae than Eumeninae. We will not present details of that exercise here; instead JMC is pursuing a more comprehensive analysis of molecular data within Vespidae, which will re-examine subfamily relationships with a better taxon sample.

In 1997, the Center for Biodiversity and Conservation at the American Museum of Natural History initiated a collaborative project with the Institute of Ecology and Biological Resources, Ha Noi, Viet Nam. The project aims to develop scientific knowledge and expertise to protect biotically rich and endangered habitats in Viet Nam. As part of this effort, biotic inventories are being conducted in several areas, and in April, 1998, JMC participated in surveys of sites in the northern Truong Son Mountain Range. One of these sites is a mountain pass known as Cha Lo, in the Minh Hoa District of Quang Binh Province. The pass is close to the Lao frontier, and the road through it was part of the old Ho Chi Minh Trail. In 1998, the road was being improved, and JMC spent four days in a preliminary survey of the forest systems near the pass. A riparian area near the road, at the Cha Lo Frontier Post, was undergoing rapid degradation due to the construction. The vegetation along the streams was disturbed, secondary growth, but further away from the road old secondary and some primary forest was intact. It consisted of evergreen seasonal broadleaf hill forest, dominated by *Lithocarpus* and *Mangletia*. Along one of the streams of the watershed, collecting with an aerial net produced two species of hover wasps, patrolling along the stream. One of these species presents some remarkable features, justifying recognition of a new genus. This species was hitherto undescribed, but more than a decade ago CKS recognized it as new based on two specimens from northern Thailand. In this paper, we describe this new genus, and analyze its phylogenetic relationships to the other hover wasps.

The new genus is clearly distinguished from other stenogastrines, as the following key will show. A cladistic analysis is presented after the description, to address the placement of this genus within Stenogastrinae.

KEY TO GENERA OF THE SUBFAMILY STENOGASTRINAE

1. Occipital carina evanescing before reaching the hypostomal carina . . . . *Liostenogaster* van der Vecht
Occipital carina reaching and fused with the hypostomal carina 2

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2\. Metasomal segment II not petiolate basally 3
Metasomal segment II petiolate basally: extending approximately parallel-sided for at least 1.5 times its basal width 5

3\. Scutum with notauli strongly impressed, outstanding on smooth integument; male antennae spatulate apically; maxillary palpi with the length of segment 2 approximately equal to that of segment 3 . . . . *Chalogaster* new genus
Scutum with notauli present at most as traces, obscured by punctation; male antennae not spatulate apically; maxillary palpi with the length of segment 2 greater than the combined length of segments 3–6 4

4\. Propodeum with raised lamella above propodeal orifice; scutellum without longitudinal median carina; male antennae with apical flagellomere truncate and flattened, often dilated; male hindwings without pigmented area . . . . *Stenogaster* Guérin
Propodeum without raised lamella above propodeal orifice; scutellum strongly carinate; male antennae with apical flagellomere conical; male hindwings with pigmented area posterobasally . . . . *Eustenogaster* van der Vecht

5\. Propodeal valvulae large, rounded; male mandibles with proximal teeth quite blunt . . . . *Anischnogaster* van der Vecht
Propodeal valvulae reduced, completely attenuate at least posteriorly; male mandibles with proximal teeth sharp 6

6\. Hindwings with posterior fringe of hairs greatly elongated, more so in males; vertex with median longitudinal groove; scutum with notauli strongly impressed, outstanding on smooth integument; males with bidentate mandibles, antennae with flagellomeres flattened, pleural area sunken and densely pubescent, and foretibiae with spatulate setae . . . . *Metischnogaster* van der Vecht
Hindwings with posterior fringe of hairs very short; vertex without median longitudinal groove; scutum with notauli if strongly impressed then partly obscured by punctation; males with tridentate mandibles, without flattened flagellomeres, sunken pleural area, and spatulate setae on foretibiae . . . . *Parischnogaster* von Schulthess

Chalogaster, new genus

Figures 1–7

TYPE SPECIES: *Chalogaster spatulata*, **new species**.

DESCRIPTION: Occipital carina fused with hypostomal carina (fig. 1); vertex without median longitudinal groove; eyes exceptionally large, about 85% as long as entire head and occupying almost all of side view of head, only very narrowly separated from clypeus; maxillary palpi with the length of segment 2 approximately equal to that of segment 3; labial palpi with first segment subequal in length to combined lengths of segments 2–4; scutum with notauli strongly impressed (fig. 4), cuticle shining; propodeum smooth, with valvulae reduced posteriorly, without raised lamella above orifice; hindwings with posterior fringe of hairs very short; metasomal segment II not petiolate basally (fig. 5), spiracles not visible in dorsal view (fig. 5). Female with scutellum carinate medially. Male with terminal antennal flagellomere spatulate (figs. 2–3), flagellomeres not flattened (fig. 2); clypeus rounded apically; mandibles bidentate, teeth sharp; without sunken metapleura; foretibiae lacking spatulate setae; foretarsomeres not ventrally produced into spines; apical midtarsomeres symmetrical, flattened and expanded (fig. 6), distitarsi rounded (fig. 6); hindwings without pigmented area posterobasally; metasomal Sternum VII flattened; parameral spines not dilated (fig. 7A), with median inner processes (fig. 7B), bent in towards each other near the base, then arching out apart; cuspis + lamina volsellaris broad medially (fig. 1C), aedeagus apically strongly compressed (fig. 7D), apex dilated in lateral view (fig. 7E), with pair of small projections located laterobasally (fig. 7D–E), none subapically.

DISTRIBUTION: Viet Nam and Thailand.

ETYMOLOGY: The name combines the root used in all other genera in the subfamily Stenogastrinae with the type locality.

Chalogaster spatulata, new species

DIAGNOSIS: Among the characters given for the genus, the spatulate antennae, dilated midtarsi and the lobate parameral spines of the male will at once distinguish this species from other Stenogastrinae. Among characters listed below, the elongate third submarginal cell and single midtibial spur may also distinguish this species.

DESCRIPTION: *Male.* Forewing length 8.5–9.2 mm. Head, including clypeus, moderately

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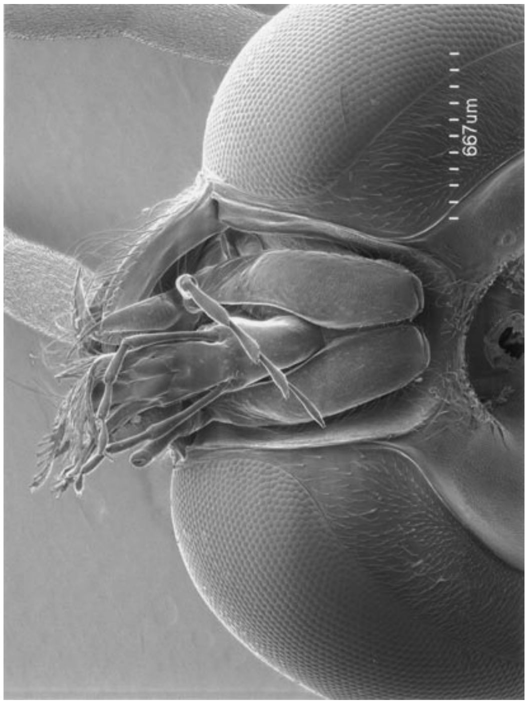

Fig. 1. *Chalogaster spatulata*, n. sp., male paratype. Head in ventral view.

Fig. 2. *Chalogaster spatulata*, n. sp., male paratype. Head and antennae in lateral view.

wider than long; clypeus with apex convex, roundly angled; frontoclypeal suture distinct, strong; antennal sockets far apart and separated from clypeus by long supraclypeal area; antennae with scape and pedicel roundly flattened; ocelli large, ratio of width to distance from eye about 0.7 for anterior ocellus and 1.4 for either posterior ocellus; pronotum lacking dorsal carina and pretegular carinae; parapsidal and admedian lines deeply impressed; scutellum lacking median carina; length of metanotum along midline about equal to that of scutellum; forewings with RS straight along posterior border of marginal cell, second submarginal cell rectangular, third submarginal cell elongate, nearly attaining wing apex. One of the paratypes has an adventitious marginal cell in the left wing. Hindwings with two closed cells; forefemora in dorsal view curving anteriorly; midtibiae with single spur; metasomal segment I about 1.5× the length of the mesosoma, apical bulb of segment I about three times as broad as main part of petiole, scarcely narrowed behind. The genitalia are illustrated in figure 7. Cuticle smooth and shining, appearing duller and more granulate on metasoma, clypeus with shallow, dense punctures, coarser on frons, forming weak striae, ventral angle of pronotum, notauli, dorsal groove of mesepisterna, median groove of propodeum crenulate, pronotum with striae anteriorly above, weak striae dorsally on metapleura and propodeum, dense striae anterodorsally on mesepisterna. Vestiture pale short hairs on clypeus, frons and mandible, denser on genae, longer more scattered hairs on vertex, dorsum of thorax, propodeum, and legs, denser on coxae and femora; mid- and hindtibiae and tarsi with numerous very long, fine, erect hairs; very dense, short hairs on mesepisterna dorsally and posteriorly, metapleura and propodeum anteriorly; metasoma with scattered short hairs on terga and a few longer hairs on sterna. Coloration black; yellow are clypeus except for apex and a variably developed mark above the apex, solid or U- to W-shaped, broad stripes below antennal sockets, hind margin of pronotum entirely or posteriorly, and occasional spots or stripes at an-

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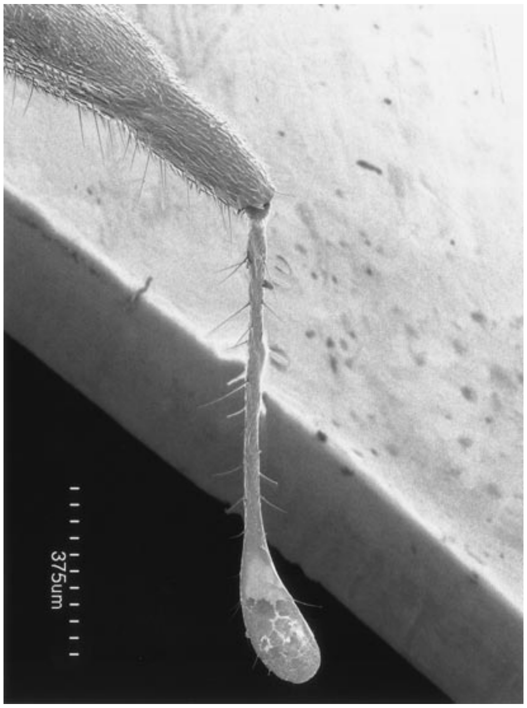

Fig. 3. *Chalogaster spatulata*, n. sp., male paratype. Terminal antennal flagellomere.

Fig. 4. *Chalogaster spatulata*, n. sp., male paratype. Scutum in oblique dorsal view.

terior margin and in ventral angle, short lines anteriorly along the notauli, tegulae variably, spots or most of scutellum, most of metanotum, large mesepisternal spot dorsally, occasionally small ventral spots, variably spots anterodorsal to propodeal spiracle and above orifice, variably developed hindcoxal spots, all femora at least apically, and mid- and hindfemora sometimes mostly, midtibiae and stripes to much of fore- and hindtibiae, midtarsi largely to at least basistarsi, sometimes foretarsi largely; pale whitish are the spatulate processes of the antennae apically, propleura, metasomal Tergum II basally or spots, Terga IV–VII each with a broad white basal band, conspicuous when the segments are even a little extended; brownish are the base of Tergum II–III, the sides of Terga II–VII, Sterna II–VII variably.

Female. Forewing length 9.2–9.4 mm. Clypeus with apex convex, sharply pointed; antennae moderately clavate, with tenth article less than twice as wide as fourth; mandibles tridentate; scutellum with carina weak but clear, developed only anteriorly; mesometapleural and thoracic-propodeal sutures subparallel; metasomal Tergum VI without spine. Cuticle generally as in male, but metasoma more shining, not appearing dull and granulate. Vestiture differs from the male in hairs generally longer and more abundant, but lacking dense pilosity on sides of thorax. Coloration differs from the male in the clypeus with only yellow stripes laterally, scutellum with small lateral spots, broad separated spots on metanotum, variable spots dorsally on propleura, broad ventrolateral stripes on mesepisterna, metapleura with dorsal spots, broad spots above propodeal orifice, legs with only stripes on coxae, tips of femora, foretibiae with stripes to mostly, foretarsi variably, metasoma with only small lateral stripes on Tergum I, base of Tergum II, basal spots on Tergum III; only Sternum II basally pale.

Nest, Larva: Unknown.

Type Material: Holotype male from **Viet Nam**: Quang Binh Prov., Cha Lo, 17°42′N 105°46′E, 14–17 April 1998, 298 m (James M. Carpenter), in the Institute of Ecology

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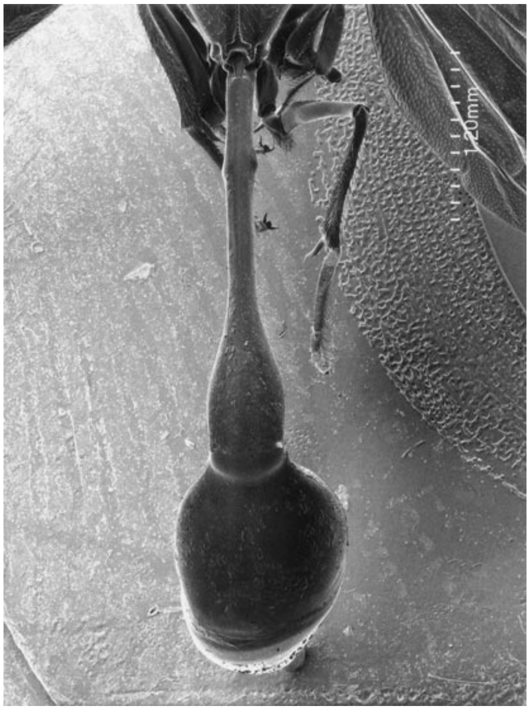

Fig. 5. *Chalogaster spatulata*, n. sp., male paratype. Metasomal segments I and II in dorsal view.

Fig. 6. *Chalogaster spatulata*, n. sp., male paratype. Midtarsus.

and Biological Resources (IEBR), Ha Noi; on long-term loan to the American Museum of Natural History (AMNH). Paratype female and four paratype males with the same data in the IEBR; paratype female and four paratype males with the same data in the AMNH. Two more paratype males are from **Thailand**: Chieng Mai Prov., Doi Suthep, 1100 m, 2 October 1981, Zool. Museum Copenhagen leg. (Zoologisk Museum, Copenhagen); and **Thailand**: Loei Prov., Phu Luang, Wildlife Sanctuary, 8–14. October 1984, Karsholt, Lomholdt and Nielsen leg. (National Museum of Natural History, Washington, DC).

Known Distribution: Cha Lo, in the Truong Son Mountains of central Viet Nam (type locality), and northern Thailand (fig. 8). These three localities are not close to each other, so that *Chalogaster spatulata* may well be widespread in Indochina. There is no evident reason not to expect it in Laos and Cambodia, or even Yunnan.

Etymology: The specific name refers to the remarkable terminal antennal article of the male.

Remarks: Although the spatulate antennal flagellomere is a remarkable apomorphy, and unique in Stenogastrinae, even more striking spatulate modifications are found in the nomiine bee *Spatunomia* (Pauly, 1990: figs. 331–332).

CLADISTIC ANALYSIS

The phylogenetic relationships among the genera of Stenogastrinae proposed by Carpenter (1988) are shown in figure 9. That study considered 24 characters of adult morphology, two of larvae and 14 of behavior. The cladogram of figure 9 resulted from analysis of 10 morphological characters that varied among the genera. Those ten characters are scored for *Chalogaster* in table 1. In addition, three other characters are included in table 1. These were characters discussed by Carpenter (1988) but were considered autapomorphies, thus uninformative on relationships among genera. The discovery of

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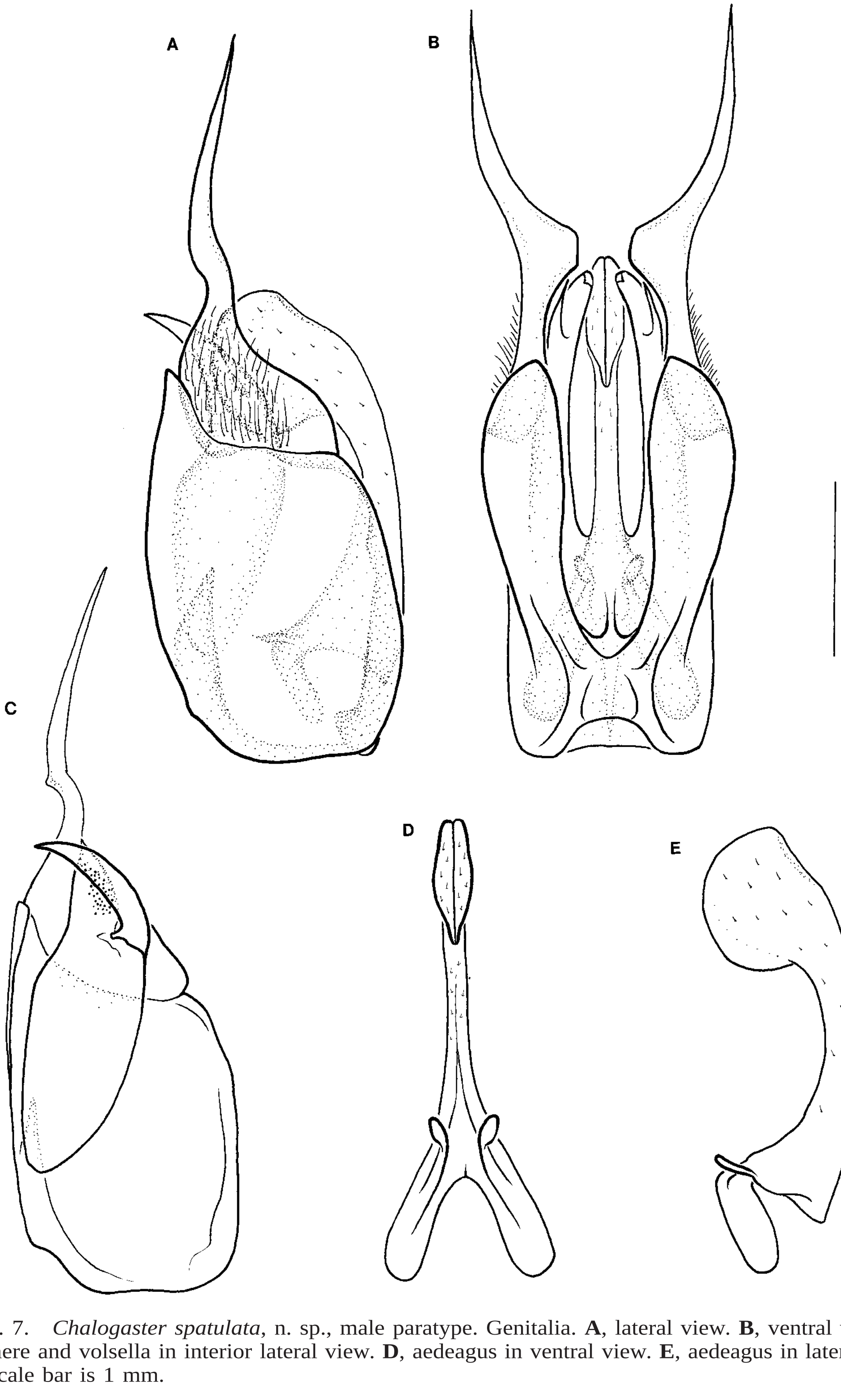

Fig. 7. *Chalogaster spatulata*, n. sp., male paratype. Genitalia. **A**, lateral view. **B**, ventral view. **C**, paramere and volsella in interior lateral view. **D**, aedeagus in ventral view. **E**, aedeagus in lateral view. The scale bar is 1 mm.

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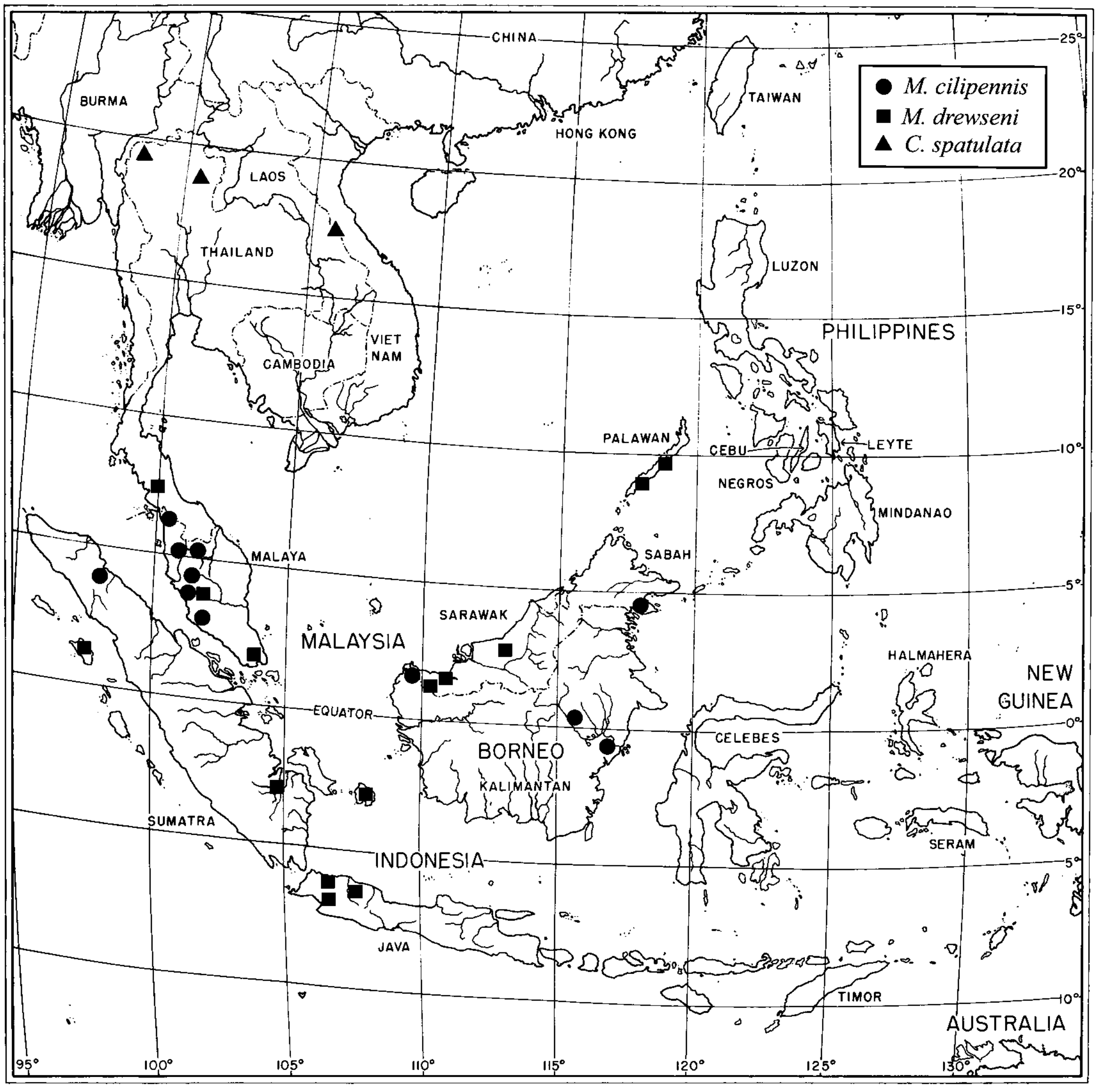

Fig. 8. Known distribution of *Chalogaster* and species of its sister-genus *Metischnogaster*.

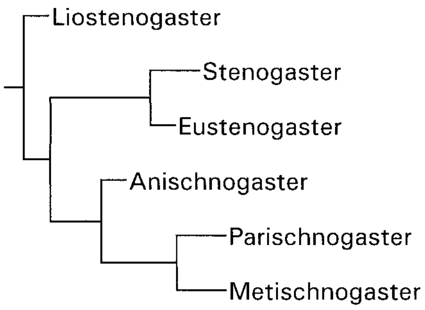

Fig. 9. Cladogram for genera of Stenogastrinae after Carpenter (1988).

Chalogaster changes that interpretation. The outgroup is the subfamily Eumeninae, relatively basal to the Stenogastrinae in the cladogram of Carpenter (1981).

Analysis of the data in table 1 with the exact routine of the program Nona (Goloboff, 1998a) results in two cladograms (figs. 10–11). The length is 27 steps, the consistency index is 0.81, and the retention index is 0.66. These same cladograms result from implied weighting using the program Piwe (Goloboff, 1998b; default concavity).

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TABLE 1

Data on Genera of Stenogastrinae

An asterisk denotes a polymorphism showing all applicable states; a dollar sign denotes a subset polymorphism. Multistate characters are treated as nonadditive. The subset polymorphisms are as follows: Eumeninae—character #5 [states 0 2]; *Liostenogaster*—3 [0 1], 9 [1 2]; *Parischogaster*—9 [0 1].

Eumeninae	0330$*00**000
Liostenogaster	00$00000$0000
Parischnogaster	10000001$1110
Metischnogaster	1010110201011
Anischnogaster	1000000011000
Stenogaster	1221200000000
Eustenogaster	1121001020000
Chalogaster	1110311120211

Character list

1. Occipital carina: not reaching hypostomal carina (0); fused to hypostomal carina (1).
2. Male clypeus: pointed apically (0); rounded (1); depressed (2); emarginate (3).
3. Male mandibular teeth: three (0); two (1); one (2); four or five (3).
4. Maxillary palpi: palpomeres 2 and 3 equal in length (0); 2 3× longer than 3 (1).
5. Male antennae: conical (0); flattened (1); apically broad, truncate (2); spatulate (3).
6. Notauli: weak (0); strong (1).
7. Scutellum: ecarinate (0); carinate in female (1).
8. Propodeal valvulae: round (0); posteriorly attenuate (1); narrow throughout (2).
9. Propodeal sculpture: striate (0); punctate (1); smooth (2).
10. Metasomal segment II: not petiolate (0); petiolate (1).
11. Parameral spines: spinose (0); broadly flattened (1); elbowed (2).
12. Aedeagus: normal (0); dilated (1).
13. Aedeagal processes: absent (0); present laterobasally (1).

The consensus tree for the two cladograms resulting from the analysis is given in figure 12. The length for the consensus is 28 steps, just one more step than either cladogram. The clade concordance index (Nixon and Carpenter, 1996) is zero, indicating complete disagreement between the characters supporting the differing resolutions of figures 10–11. Those characters are #10, metasomal segment II petiolate or not, and #9, propodeal sculpture. In the cladogram of figure 10, a petiolate metasomal segment II is interpreted as a synapomorphy for the clade composed of *Anischogaster* + (*Parischnogaster* + (*Metischnogaster* + *Chalogaster*)) - but with a subsequent reversal in *Chalogaster*. In the cladogram of figure 11, the propodeal sculpture is interpreted as transforming from punctate to striate in the clade composed of (*Stenogaster* + *Eustenogaster*) + (*Parischnogaster* + (*Metischnogaster* + *Chalogaster*))—but then changing to smooth separately in *Eustenogaster* and *Chalogaster*, and moreover reversing to punctate within *Parischnogaster*, which is polymorphic for this character (as for that matter are *Liostenogaster* and the outgroup Eumeninae). Both of the characters are homoplastic, but in particular we regard the propodeal sculpture as unreliable, because of the ambiguity due to polymorphism. If the polymorphisms in table 1 are replaced with ambiguity codes, as is necessary for analysis with programs such as Hennig86 (Farris, 1988), only the cladogram of figure 10 results. But although the character supporting this cladogram was perfectly consistent in the earlier analysis by Carpenter (1988), that is not the case now: the placement of *Chalogaster* as sister-group to *Metischnogaster* is supported by several characters, and thus the petiole of segment II is homoplastic. In this light, the variation in length of the petiole within *Parischnogaster* may indicate that it is not a reliable character. We therefore regard the consensus tree of figure 12 as a better representation of phylogenetic relationships among stenogastrine genera given present knowledge, with the placement of *Anischnogaster* unresolved.

In any case, the analysis indicates that *Metischnogaster* and *Chalogaster* are sister-groups. This is supported by the bidentate male mandibles (#3), the strongly impressed notauli (#6), and the laterobasal processes of the aedeagus (#13), none of which show homoplasy. In addition, the posteriorly attenuate valvulae (#8) is shared by *Parischnogaster*, *Chalogaster*, and *Metischnogaster* (further reduced in this genus), as is the apically dilated aedeagus (#12). These three genera form a clade. The flash-bands of the metasomal terga are an additional character uniting these three genera: males of all studied species have Terga IV–VII with broad, basal white or pale yellow bands, which can be exposed or hidden as the segments are more or less telescoped together and which func-

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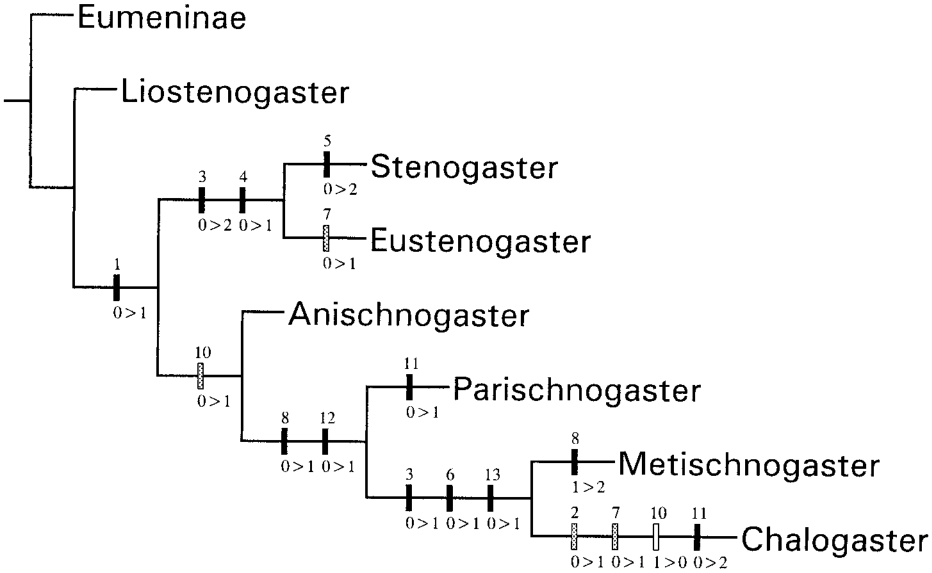

Fig. 10. Cladogram resulting from analysis of data in table 1. Characters have been optimized with the program Clados (Nixon 1999), plotting only unambiguous changes. Character numbers are above the hashmarks; state changes are shown below, with the respective primitive and derived conditions separated by ">". Filled hashmarks indicate a unique derivation, grayscale denotes convergent derivations, while open hashmarks are reversals.

tion in sexual display (reviewed in Turillazzi, 1991). The phylogenetic relationships of *Chalogaster* thus appear clear.

At the same time, *Chalogaster* is distinct from its sister-group *Metischnogaster* by a number of apomorphies: the male clypeus rounded apically (#2, as scored in table 1 convergent in *Eustenogaster*, but of a differ-

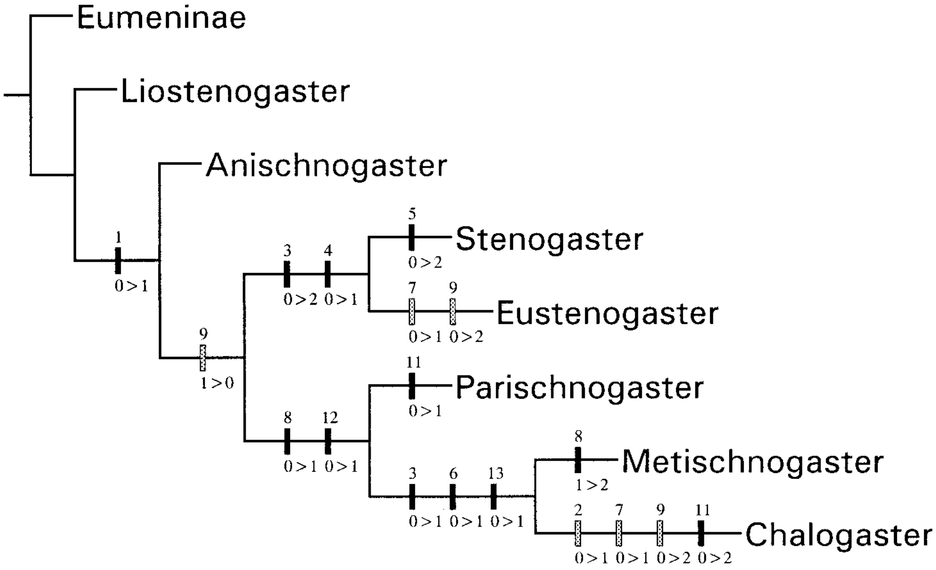

Fig. 11. Cladogram resulting from analysis of data in table 1. Plotting conventions as in fig. 10.

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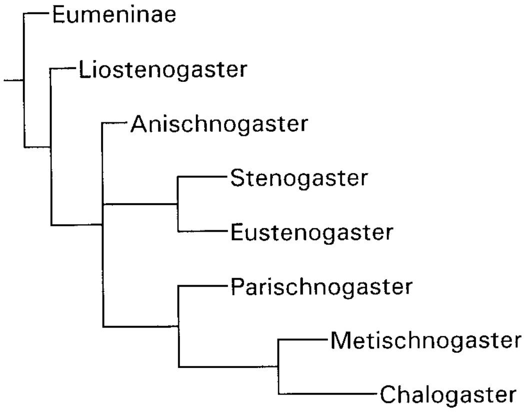

Fig. 12. Consensus tree for cladograms of figs. 10–11.

ent form in that genus), the scutellum clearly carinate in females (#6, as scored in table 1 convergent in *Eustenogaster*, but in that genus the males have the scutellum carinate as well, and weak traces of a carina are present in other stenogastrine genera), propodeal sculpture smooth (#9; it is striate in *Metischnogaster*), the parameral spines with a median process (#11; it is spiniform in *Metischnogaster*). Among the characters scored in Table 1, *Metischnogaster* is distinguished from *Chalogaster* by the apomorphy of the propodeal valvulae further reduced (#8), but also has a large number of other derived features, discussed by Carpenter (1988), viz., vertex with median longitudinal groove; spiracles of metasomal Segment II are visible in dorsal view; male with antennae having flagellomeres flattened, pleural areas sunken and densely pubescent, foretibiae with spatulate setae, hindwings with posterior fringe of hairs greatly elongated, and the aedeagus with a pair of small subapical projections. Given this distribution of features, recognition of a new genus for *Chalogaster* seems amply justified, thereby allowing the generic classification to convey information on the distribution of a number of remarkable characters, which is the point of classification (Farris, 1979).

All recorded localities of *Chalogaster spatulata* and the two species of its sister-genus *Metischnogaster* are shown in figure 8. Extensive collecting by CKS in various parts of the Philippines proper (i.e., the Philippines except Palawan and smaller associated islands on the continental shelf) persuades us these genera are in fact absent from that area. It is less certain that they are absent from Sulawesi or the Lesser Sunda Islands, but each has been subjected to a moderate amount of collecting. The present distributional information is consistent with the hypothesis that the speciation separating *Chalogaster* and *Metischnogaster* occurred as a single vicariance event around the Isthmus of Kra.

The recognition of a new genus underscores the point made earlier that the hover wasps are not well understood. The threat to the biota brought about by rapid deforestation and population growth in nations such as Viet Nam and Thailand underscores the need for a committed effort to protect and manage natural heritage, or the elements of that biota, such as the fascinating hover wasps, will never be understood.

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