

Redefinition of the Clusiinae and Clusiodinae, description of the new subfamily Sobarocephalinae, revision of the genus *Chaetoclusia* and a description of *Procerosoma* gen. n. (Diptera: Clusiidae)

OWEN LONSDALE and STEPHEN A. MARSHALL

Insect Systematics Laboratory, Department of Environmental Biology, University of Guelph, Guelph, ON, N1G 2W1, Canada;
e-mails: olonsdal@uoguelph.ca; samarsha@uoguelph.ca

Key words. Clusiidae, Clusiodinae, Clusiinae, Sobarocephalinae, *Chaetoclusia*, *Trichoclusia*, *Chaetocclusiella*, *Procerosoma*, *Sobarocephaloides*, *Sobarocephala*, revision

Abstract. The higher classification of the Clusiidae is reviewed, and the family is divided into the subfamilies Clusiodinae, Clusiinae and the new subfamily Sobarocephalinae, all of which are (re)defined. The newly defined Clusiinae includes the genera *Phylloclusia* Hendel, 1917, *Tetrameringia* McAlpine, 1960, *Amuroclusia* Mamaev, 1987, *Clusia* Haliday, 1838, *Paraclusia* Czerny, 1903, *Alloclusia* Hendel, 1917 and *Apiochaeta* Czerny, 1903. The Sobarocephalinae includes the genera *Sobarocephala* Czerny, 1903, *Procerosoma* gen. n., and *Chaetoclusia* Coquillett, 1904. The new genus *Procerosoma* is described for two species, *Procerosoma alini* (Shatalkin) comb. n. from Brazil and *P. prominens* sp. n. from Mexico. *Sobarocephaloides* Soós, 1962 is treated as a junior synonym of *Sobarocephala*, and *Chaetoclusia* is redefined to include the monotypic genera *Chaetocclusiella* Soós, 1962, syn. n. and *Trichoclusia* Soós, 1962, syn. n. Six new species of *Chaetoclusia* are described (*C. centrofasciata* sp. n., *C. amplipenis* sp. n., *C. transversa* sp. n., *C. inbionella* sp. n., *C. flava* sp. n., and *C. furva* sp. n.). *Chaetoclusia bakeri peruana* Hennig, 1938 is included as a junior synonym of *C. bakeri* Coquillett, 1904. The phylogeny of *Chaetoclusia* is discussed and a key is provided for its 13 species.

INTRODUCTION

Frey (1960) divided the Clusiidae into two subfamilies, Clusiinae (with one or more inclinate fronto-orbital bristles) and Clusiodinae (all fronto-orbitals reclinate). Later authors narrowed the Clusiinae to include only those genera with the anterior fronto-orbital bristle inclinate (Sasakawa, 1977; Pitkin & Evenhuis, 1989; Figs 7, 11–13). Male and female genitalic characters, however, as well as previously unrecognized external morphological characters, suggest alternative subfamilial divisions of the Clusiidae. We here redefine the existing subfamilies, erect the new subfamily Sobarocephalinae, and revise *Chaetoclusia* Coquillett, 1904 and *Procerosoma* gen. n., which are the sobarocephaline genera other than *Sobarocephala* Czerny, 1903.

Most previous treatments of the New World tropical Clusiidae have focused on the immense sobarocephaline genus *Sobarocephala*, a frequently encountered genus of well over 200 Neotropical species. *Chaetoclusia*, in contrast, has received very little attention, because of the apparent rarity of species other than *C. bakeri* Coquillett. Six of the thirteen species of *Chaetoclusia* are described as new below, but the group's biology or immature stages remain unknown. *Procerosoma* is the least frequently encountered New World genus of Clusiidae, with its two species known from only three specimens collected in Mexico and Brazil.

MATERIALS AND METHODS

Approximately 180 specimens were examined from the following institutions: University of Guelph Insect Collection (DEBU); British Museum of Natural History, London (BMNH);

Canadian National Collection, Ottawa (CNCI); Carnegie Museum of Natural History, Pittsburgh (CMNH); Entomological Museum of Utah State, Logan (EMUS); Biological Collection, University of Bielefeld (FBUB); Instituto Nacional de Biodiversidad, Santo Domingo de Heredia (INBC); Staatliches Museum für Tierkunde, Dresden (SMTD); United States National Museum, Washington, D.C. (USNM); Zoological Museum, University of Moscow (ZMUM).

Most specimens were pinned, either air-dried or prepared in a critical-point drier. FBUB specimens were stored in alcohol. Male and female genitalia were prepared by macerating abdomens in hot potassium hydroxide (10% solution) for 12–13 min, followed by washing in glacial acetic acid and deionized water. Terminology follows that in Caloren & Marshall (1998), with the exception of the pregonite and postgonite, which are illustrated in Figs 4 and 5. The M_{1+2} ratio is defined as the length of the ultimate section of vein M divided by the length of the penultimate section.

Representatives of all clusiid genera were examined (excluding the fossil genus *Electroclusiodes* Hennig, 1965), as were representatives of all recognized sobarocephaline species (defined below) and a range of exemplars from possible out-group families, including all families in the superfamily Opmomyzoidea (in sense of McAlpine, 1989) except Xenasteiidae (cf. Papp, 1998). A phylogenetic hypothesis for the species of *Chaetoclusia* (Fig. 58) was generated through analysis of a morphological character matrix (Table 2) using PAUP version 4.0b10 [Phylogenetic Analysis Using Parsimony (Swofford, 2003)], using a simple heuristic search with all characters unweighted. To polarize characters, the lineage made up of *Sobarocephala* and *Procerosoma* was treated as the sister group to *Chaetoclusia*; this allowed for the construction of a hypothetical ancestor characterized by plesiomorphic states. Trees were drawn with the aid of Winclada (Nixon, 2002).

RESULTS

Redefinition of the subfamily Clusioidinae

Most members of the Clusioidinae (all genera excluding the basal genus *Allometopon* Kertész, 1906) form a strongly supported clade defined by an antenna that arises at or below the midpoint of the head, a blunt and obtuse angulate extension on the outer surface of the pedicel, a reduced or absent extension on the inner surface of the pedicel, a scutellum that is flat and longitudinally wrinkled dorsally, an extremely reduced phallapodeme, an enlarged ejaculatory apodeme, fusion of the components of the phallus, loss of the epiphallus, loss of the postgonite, loss of the lateral lobe of the distiphallus, articulation of the hypandrial complex to the epandrium and annulus (and less so to the subepandrial sclerite), and fusion of the pregonite (which is lengthened and enlarged) to the hypandrium. Outside of this group, the pregonite is well defined and separate from the hypandrium (Fig. 5), with membranous or stronger sclerotized connections seen in only a few derived lineages. This group includes the genera *Clusiodes* Coquillett, 1904, *Craspedochaeta* Czerny, 1903, *Hendelia* Czerny, 1903, *Heteromeria* Czerny, 1903, *Prohendelia* Frey, 1960, *Tranomeria* Sasaki, 1966 and *Xenoclusia* Frey, 1960.

The entire subfamily, comprised of the above genera plus *Allometopon*, is less well supported. Synapomorphies of the entire subfamily include longitudinally segmented (not spherical and undifferentiated) spermathecae, loss of the ventrolateral lobes of the hypandrium, entirely reclinate fronto-orbital bristles and loss of the presutural intra-alar bristle. The latter two characters are of equivocal polarity. Presutural intra-alars have also been lost in *Chaetoclusia richardfreyi* (Soós, 1962), *Sobarocephala* (regained in several species) and most *Apiochaeta* Czerny, 1903, and they also reappear in several species of *Craspedochaeta*. This character is also subject to frequent homoplasy in related families, as these bristles are often reduced in the Anthomyzidae, and are lost in the Acartophthalmidae and most Asteioinea sensu McAlpine (1989). The Acartophthalmidae was treated as the sister group to the Clusiidae by McAlpine (1989), but this family is probably more closely related to the Carnidae, Chloropidae and Milichiidae (Griffiths, 1972; Brake, 2000). The fossil genus *Electroclusiodes* also lacks presutural intra-alar bristles (Hennig, 1965), providing some evidence for inclusion of this genus in the Clusioidinae. The placement of *Electroclusiodes* in the Clusioidinae is further supported by its possession of entirely reclinate fronto-orbital bristles, although this is another homoplastic character providing relatively weak additional support for the subfamily.

Redefinition of the subfamily Clusiinae

Inclinate anterior fronto-orbital bristles have previously been used to define the Clusiinae, but similar bristles appear independently in the clusioidine lineage containing *Heteromeria* and *Tranomeria*. As discussed above, a large suite of synapomorphies support the placement of *Heteromeria* and *Tranomeria* in the Clusioidinae,

indicating that this character has evolved at least twice in the family. Furthermore, although entirely reclinate fronto-orbitals were treated as the ancestral state for the Opomyzoidea by McAlpine (1989), inclinate anterior bristles appear frequently throughout the superfamily, being entirely absent only in the Opomyzoinea (Opomyzidae + Anthomyzidae) (McAlpine, 1989). Inclinate anterior fronto-orbitals are most notably present in the Agromyzidae and Odiinidae, which are possibly the closest relatives of the Clusiidae, suggesting that these bristles are in the groundplan of the family.

Given the above uncertainties regarding the polarity and homology of the character previously used to define the Clusiinae (inclinate anterior fronto-orbital bristles), it is not surprising to find that the subfamily as previously defined does not withstand scrutiny, and we were unable to find any other reliable synapomorphies that would support its monophyly. Within the Clusiinae, however, we have found two well-supported clades that we here treat as the Clusiinae in a narrowed sense and the new subfamily Sobarocephalinae. The relationships between the subfamilies of Clusiidae are currently unresolved.

The redefined Clusiinae includes *Clusia* Haliday, 1838, *Paraclusia* Czerny, 1903, *Apiochaeta*, *Alloclusia* Hendel, 1917, *Phylloclusia* Hendel, 1917, *Tetrameringia* McAlpine, 1960, *Amuroclusia* Mamaev, 1987, and at least two undescribed genera. The Clusiinae in this revised sense is supported by six synapomorphies: the M_{1+2} ratio of the wing is less than 2.7 (reversed in several species); the fore femur has several outstanding bristles on the postero-dorsal surface; the pleuron has a subnotal stripe (obscured or lost in several genera); the surstylus has developed an internal spur (lost in several species, possibly absent in the ancestor of *Phylloclusia* and *Tetrameringia*); the distiphallus is elongate and bent or jointed medially; the vertex has a posteromedial truncate notch behind the ocelli (also found in *Allometopon*).

Sobarocephalinae subfam. n.

The new subfamily Sobarocephalinae includes the genera *Sobarocephala*, *Chaetoclusia* and *Procerosoma*, the latter two of which we revise below. *Sobarocephaloides* Soós, 1964 is synonymized with *Sobarocephala*, and the monotypic *Chaetoclesiella* Soós, 1962 and *Trichoclusia* Soós, 1962 are synonymized with *Chaetoclusia* (see below). This subfamily is defined by male genital characters: loss of the sixth spiracle (otherwise left lateral on the annulus), a ventral lobe of the hypandrium that is usually at least as long as the hypandrial arm (secondarily reduced in several species of *Chaetoclusia* and *Sobarocephala*), and a relatively large surstylus (usually more than 0.67 times the length of the epandrium, but smaller in *Procerosoma alini* (Shatalkin, 1991) and several species of *Sobarocephala*). Large surstyli are also found in *Alloclusia*, *Allometopon*, and certain clades within several clusioidine genera.

Procerosoma and *Sobarocephala* share a number of synapomorphies, including an open cell bm (confluent with cell dm), a small pregonite, and (possibly) a loss of the presutural intra-alar bristle. *Procerosoma*, however,

lacks the basal shield on the distiphallus and the thumb-like process on the lateral lobe of the distiphallus, both of which characterize *Sobarocephala*. Although *Procerosoma* and *Sobarocephala* are sister groups, *Procerosoma* is here given generic status for practical reasons. It would have been extremely difficult to provide a definition for *Sobarocephala* including *Procerosoma* because there are no apparent synapomorphies of both genera that have been retained in every species of *Sobarocephala*. Furthermore, *Procerosoma* lacks dorsal preapical tibial bristles, similar to *Heteromeringia* and most genera of Clusiinae, and *Procerosoma* is easily recognized in that the head is relatively wide with the mouthparts situated more ventrally and posteriorly, most dimensions of the body are elongate with respect to those of *Sobarocephala*, and the scutellum and metatergites have become distinctly convex, slightly shortened, and angled dorsally.

Status of the genus *Sobarocephaloides*

Sobarocephaloides discolor Soós, 1964 (the type species of *Sobarocephaloides* by monotypy; Holotype label data: Costa Rica. La Suiza, 26.x [year not given], P. Schild (1♂, USNM)) belongs to the *Sobarocephala plumata* clade of the *S. flaviseta* species group (which will be revised in an upcoming paper) on the basis of a frons that is strongly narrowed posteriorly, minute ocellar bristles, a slight protuberance on the face below and between the antennal bases, a distinct brown spot on the first flagellomere and a densely plumose arista. The first character is a synapomorphy of the *S. flaviseta* species group, and the latter four are synapomorphies of the *S. plumata* clade. *Sobarocephaloides* is therefore synonymized with *Sobarocephala*.

Soós (1964) erected the genus *Sobarocephaloides* for *Sobarocephala discolor* based on a reduction of the post-vertical, fronto-orbital and anterior dorsocentral bristles. It is now apparent that a reduction of the bristles on the head and thorax is characteristic of most species in the *S. plumata* clade, of which *S. discolor* is an extreme example. A second species, *Sobarocephaloides alini* Shatalkin, 1991, was described as a *Sobarocephaloides* on the basis of a similar reduction of the bristles on the head and thorax (Shatalkin, 1991), but it is only remotely related to *S. discolor*. *Sobarocephaloides alini* is discussed below as the type species for the new genus *Procerosoma*.

Key to the clusiid subfamilies and sobarocephaline genera

- 1 Anterior fronto-orbital bristle reclinate. Mid and hind tibiae with dorsal preapical bristles; tibial bristles absent in Oriental genus *Allometopon*. Clusiodinae (excl. *Heteromeringia* and *Tranomeringia*)
- Anterior fronto-orbital bristle inclinate. Hind tibia never with dorsal preapical bristle; mid tibia various. 2

- 2 Triangular projection on outer margin of pedicel obtuse and blunt; inner projection absent. Scutellum flat and longitudinally wrinkled dorsally. One pair of hair-like lateral scutellar bristles. Mid tibia without dorsal preapical tibial bristle. Middle fronto-orbital bristle well developed and head without wide truncate notch. M_{1+2} ratio variable, but rarely less than 3.0–4.0. Epandrium small and usually much narrower than tergite 5. Distiphallus extremely long, coiled, dark and with one pair of well sclerotized lateral ribs. Clusiodinae (*Heteromeringia* and *Tranomeringia*)
- Triangular projection on outer margin of pedicel acute and projecting; inner projection usually distinct. Scutellum smooth and distinctly (if slightly) convex. Usually two pairs of lateral scutellar bristles, but if only one pair present, then well developed and subequal in size to notopleural bristles. Mid tibia usually with dorsal preapical bristle (if absent then middle fronto-orbital bristle reduced in length and cell bm open (*Procerosoma*), or posterodorsal margin of head with wide truncate notch, fore femur with bristles on posterodorsal surface and M_{1+2} ratio less than 2.7 (some Clusiinae)). Epandrium well developed and usually comparable in width to tip of abdomen. Distiphallus relatively short and straight, or long and bent medially. 3
- 3 M_{1+2} ratio of wing usually less than 2.7. Fore femur with bristles on posterodorsal surface. Frons usually covered with minute black (sometimes yellow) setulae. Strong subnotal stripe usually present on pleuron. Posterior margin of frons with shallow truncate notch behind ocelli. Segment 7 of female conical and well sclerotized; usually more thin, elongate and heavily sclerotized than preceding segments. Surstylus usually with basal process on inner face. Distiphallus elongate and either bent or broken medially. Clusiinae
- M_{1+2} ratio of wing greater than 3.0 (often less in species of *Sobarocephala* with elaborately patterned wings). Fore femur setulose on posterodorsal surface. Frons shiny or covered with pale, inconspicuous setulae. Pleuron almost always without subnotal stripe. Posterior margin of frons flat to gradually concave. Segment 7 of female cylindrical and inconspicuous. Surstylus rarely with basal process. Distiphallus entire and relatively straight. . . . Sobarocephalinae
- 4 Vein R_1 setulose dorsally. Gena usually shiny. Presutural intra alar bristle almost always present. Anterior lateral scutellar bristle minute to absent (larger in *Chaetoclusia richardfreyi*, but still significantly smaller than posterior bristle). Cell bm closed. Neotropics. *Chaetoclusia* Coquillett
- Vein R_1 bare dorsally. Gena usually pilose or silvery tomentose. Presutural intra alar bristle almost always absent. Lateral scutellar bristles variable. Cell bm usually open. 5
- 5 Mid tibia with dorsal preapical bristle. Ocellar and/or post-vertical bristles present (usually small). Mid fronto-orbital rarely reduced. Scutellum horizontal. Basiphallus bare. Distiphallus with basal shield. Lateral lobe of distiphallus variably reduced and occasionally fused to base of distiphallus; often with subbasal “thumb”. Common in New World. Worldwide (except Europe). *Sobarocephala* Czerny
- Mid tibia without dorsal preapical bristle. Ocellar and post-vertical bristles absent. Mid fronto-orbital reduced. Scutellum slightly angled dorsally. Basiphallus setose laterally. Distiphallus exposed basally. Lateral lobe of distiphallus without “thumb”; small and fused to base of distiphallus. Uncommon. Neotropics. *Procerosoma* gen. n.

Procerosoma gen. n.

Type species: *Sobarocephaloides alini* Shatalkin, 1991: 928–930.



Fig. 1. *Procerosoma alini* (Shatalkin, 1991), female habitus with male head inset.

Diagnosis

Cell bm narrowly open, confluent with cell dm (Fig. 1). Vein R₁ bare. Scutum bivittate. Face with one pair of lateral stripes. Two pairs of postsutural dorsocentral bristles (anterior bristle 0.6 times length of posterior bristle). Presutural dorsocentral and presutural intra-alar bristles absent. Acrostichal, ocellar, and postvertical bristles absent. Mid fronto-orbital bristle 0.8 times length of remaining fronto-orbitals or extremely reduced and setula-like (Fig. 6). Preapical tibial bristles absent.

Etymology. The generic name is Latin for “slender-bodied”; gender female.

Generic description

Adult. General. Length 4.0–5.3 mm. Body elongate, with thorax, abdomen and legs long and slender; colour yellow with brown pattern (scutum bivittate and face with one pair of lateral stripes) (Figs 1, 7 and 8). Angular extensions on pedicel producing 90° angle, with apex broadly rounded. Arista black with base white; sparsely or densely plumose. Gena and parafacial shiny to micro-setulose or silvery tomentose. Frons shiny with sides parallel. Halter white to light yellow. Wing length 3.0 times width. Subcostal break distinct. R₁ bare. Cell bm narrowly open. M₁₊₂ ratio 1 : 3 or 1 : 4.6. Wing hyaline with faint distal (and sometimes medial) clouding.

Chaetotaxy. Bristles yellow. Anterior and mid fronto-orbital bristles close to each other on anterior margin of frons, with hind bristle on posteromedial margin; mid fronto-orbital bristle 0.8 times length of remaining fronto-orbitals or extremely reduced and setulae-like (Figs 1, 6 and 7). Acrostichal, ocellar, and postvertical bristles absent. Pedicel with one outstanding dorsal bristle. Two postsutural dorsocentral bristles with anterior bristle 0.6–0.8 times length of posterior bristle, sometimes with

small bristle in front of anterior dorsocentral. Presutural dorsocentral and presutural intra-alar bristles absent. Scutellum wide, short and angled dorsally, with one pair of strong cruciate apical bristles and 0–2 pairs of weak lateral bristles. One strong anepisternal and katepisternal bristle; proepisternal bristle small. Preapical tibial bristles absent. Male mid femur with at least six stout ctenidial bristles basally. One postpronotal and two notopleural bristles; two postsutural intra-alar bristles; intra post-alar bristle absent.

Male abdomen. Males only known for *Procerosoma alini*. Tergites 1 and 2 fused; sternite 1 reduced to thin, weakly sclerotized strip; tergites 3–6 and sternites 2–5 complete. Spiracles in membrane below tergites 1–5 and ventrally between sternites 6 and 8. Abdomen encircled by an annulus comprised of sternites 6–8 (Fig. 3); sternite 8 setose, and dorsal (with right lateral extension); sternite 7 on left side between sternites 6 and 8 and heavily sclerotized anteriorly; sternite 6 fused to sternite 7 laterally, membranously attached to sternite 8 ventrally, and heavily sclerotized anteriorly. Epandrium dome-shaped; length 0.75 times height; width and height subequal. Surstylus small and rounded, with width slightly less than half that of epandrium; bristles on distal half of inner face stout and pointed. Cerci projecting and evenly rounded apically; bristles short and of equal length. Hypandrium with one pair of arms articulating with subepandrial sclerite, which in turn articulates with epandrium; hypandrium with one pair of parallel ventrolateral lobes (“ventral lobe of hypandrium”) that lie on either side of phallapodeme, becoming arched medially and strongly tapered distally; ventral lobe of hypandrium with two central bristles (strong and closely spaced) and one small distal bristle; hypandrial arm shorter than lobe and projecting from long axis of phallapodeme at 45° (Fig. 5). Phallapodeme long

and thin, articulating with basiphallus and thin anterior-transverse portion of hypandrium to form lever; articulation with hypandrium facilitated by suspended ventral plate ("aedeagal guide" of Soós, 1987) confluent with anterior margin of phallapodeme and entirely separate from hypandrium. Pregonite with three small bristles on expanded apex. Postgonite small and lobate; two (of four) bristles on right postgonite and one (of four) bristles on left postgonite long, wide, and darkly pigmented. Basiphallus well developed, "C" shaped and setose laterally. Epiphallus well developed and fin-like. Distiphallus triangular, 0.4 times length of phallapodeme, with one pair of short, hyaline basal lobes. Ejaculatory apodeme half length of phallapodeme.

Female abdomen. Tergites 1 and 2 fused; sternite 1 reduced to thin, weakly sclerotized strip; tergites 3 to 6 and sternites 2 to 6 complete. Abdomen past segment 6 narrowed into long, thin tube; segments separated by long membranous area nearly equaling segment length. Sternite 8 bifid on distal fourth and divided lengthwise by median desclerotized line. Length of cercus approximately 0.67 times that of sternite 8. Spiracles in membrane below tergites on segments 1 to 7. Spermathecae (two) weakly sclerotized, spherical, smooth-surfaced and almost 0.33 times length of sternite 8 (Fig. 9). Spermathecal ducts thin, weakly sclerotized and eight times length of spermatheca. Ventral receptacle weakly sclerotized, sac-like and recurved ventrally. Ventral receptacle and reproductive ducts opening close together into anterior end of genital chamber.

Egg. (Fig. 10) (Based on examination of single known female of *P. prominens* with two eggs in abdomen): Width 0.3 times length, length 0.7 mm. Tapered at ends with micropyle distinct. Surface minutely tuberculate and longitudinally wrinkled.

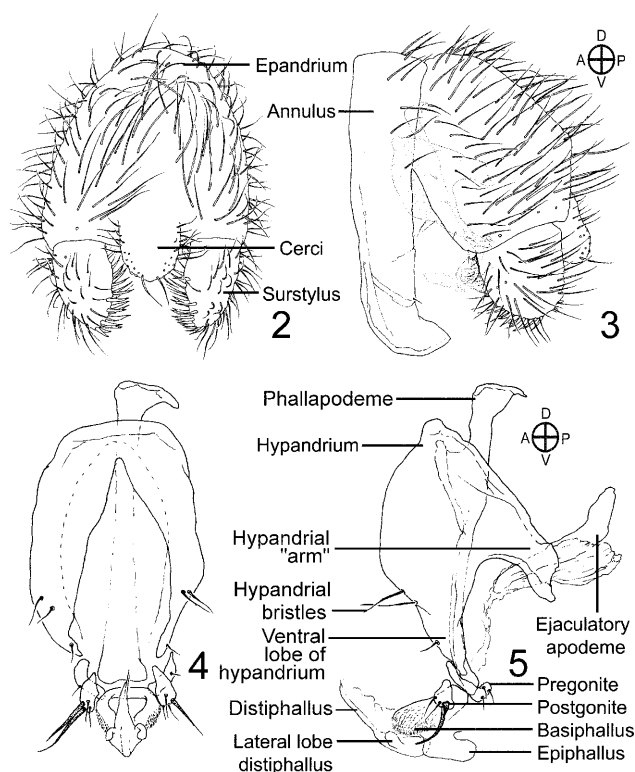
***Procerosoma alini* (Shatalkin, 1991) comb. n.**

(Figs 1–5)

Sobarocephaloides alini Shatalkin, 1991: 928–930.

Redescription (Fig. 1)

Male. Body length 4.0 (female) – 5.3 mm (male). Arista sparsely short-plumose. Small bristle in front of anterior dorsocentral. Mid fronto-orbital bristle 0.8 times length of remaining bristles. One pair of lateral scutellar bristles. Scutum yellow with one pair of stripes extending presuturally along dorsocentral line, thinned medially behind suture on outer face. Scutellum yellow. Metatergites yellow with one pair of faded stripes lateral to scutellum and one faded stripe below. Pleuron yellow. Legs yellow with fore tibia brown (darkest basally) and fore tarsi brown. Head predominantly yellow; sides of face with wide brown stripes; ocellar tubercle brown; bulbous distal portion of genal process white. Head strongly swollen and 1.2 times width of scutum; gena with prominent process (swollen distally); face not produced. Abdomen black with epandrium and surstylus dark yellow to orange. Wing yellowish/dusky with distal fifth lightly clouded. M_{1+2} ratio 3.0.



Figs 2–5: *Procerosoma alini* (Shatalkin, 1991) male, genitalia. 2 – terminalia, posterior; 3 – terminalia, left lateral (shaded hypandrium inserted; D = dorsal, V = ventral, A = anterior, P = posterior); 4 – hypandrial complex, anterior; 5 – hypandrial complex, left lateral.

Female. As described for male except as follows: head and notum subequal in width; genal process absent; tergites 1–4 black; tergite 5 with wide central stripe (narrowing anteriorly); remainder of abdomen yellow; wide truncate notch present behind ocelli; frons and face bulging; lateral scutellar bristle absent.

Male terminalia (Figs 2–5). See generic description.

Female terminalia not dissected.

Distribution. Brazil (São Paulo).

Holotype. Brazil. São Paulo, 29.xi.1971, B. Alin (1♂, ZMUM).

Paratype. Same collection as holotype (1♀, ZMUM).

Comments. Shatalkin (1991) described *Procerosoma alini* as a *Sobarocephaloides* (now a synonym of *Sobarocephala*) on the basis of a single pair of dorsocentral bristles. We have, however, found two pairs of dorsocentral bristles in the paratype female and a second pair of sockets in the holotype male where the anterior dorsocentrals had broken off.

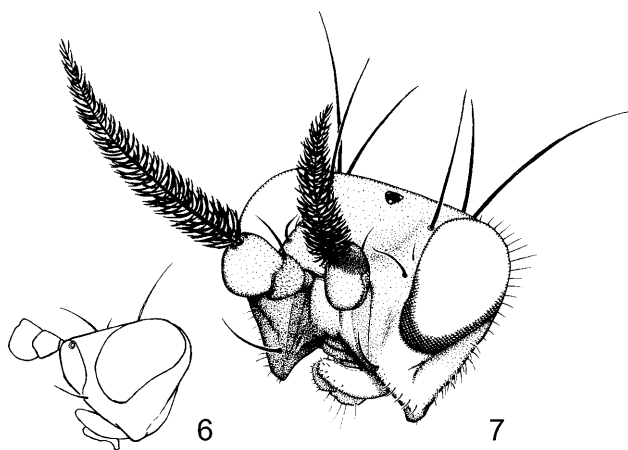
See comments for *Procerosoma prominens*.

***Procerosoma prominens* sp. n.**

(Figs 6–10)

Description (Figs 6–8)

Female. Body length approximately 5.3 mm. Arista densely plumose. No small bristle in front of anterior dorsocentral. Mid fronto-orbital bristle minute; hind fronto-



Figs 6, 7: *Procerosoma prominens* sp. n., head. 6 – outline drawing, left lateral (arista and bristles removed, excluding vibrissa and fronto-orbital bristles); 7 – habitus.

orbital bristles broken off (reconstructed in illustrations based on diameter of sockets). Two pairs of weak lateral scutellar bristles. Scutum yellow with one pair of stripes extending presuturally along dorsocentral line, with stripes thinned medially behind suture on outer face; posterior margin of notopleuron with brown line reaching longitudinal dorsocentral stripe. Scutellum yellow with lateral margin brown. Metatergites yellow with katatergite and anatergite below scutellum brown (faded medially). Pleuron yellow with thin line extending from postpronotum along anterior suture of anepisternum to lateral diagonal suture of katepisternum. Legs yellow except as follows: fore tarsi brown excluding basal 2/3 of first tarsomere; mid and hind tarsi brown distally on all tarsomeres. Head predominantly yellow; sides of face with one pair of wide dark yellow stripes; gena white and silvery-tomentose; stripe on outer-dorsal surface of first flagellomere; back of head with one pair of large lateral spots; ocellar tubercle brown. Gena relatively high with posterior angle distinctly produced. Vertex projecting and face strongly carinate. Head as wide as scutum. Abdomen yellow except as follows: posterior-lateral corners of tergite 1 brown; tergites 2–6 with large spot along posterior margin (wide apical emargination on tergites 2 and 3); tergite 7 with light brown, transverse, lateral stripe. Wing narrowly infuscated around dm-cu and darkly clouded apically. M_{1+2} ratio 4.6.

Male unknown.

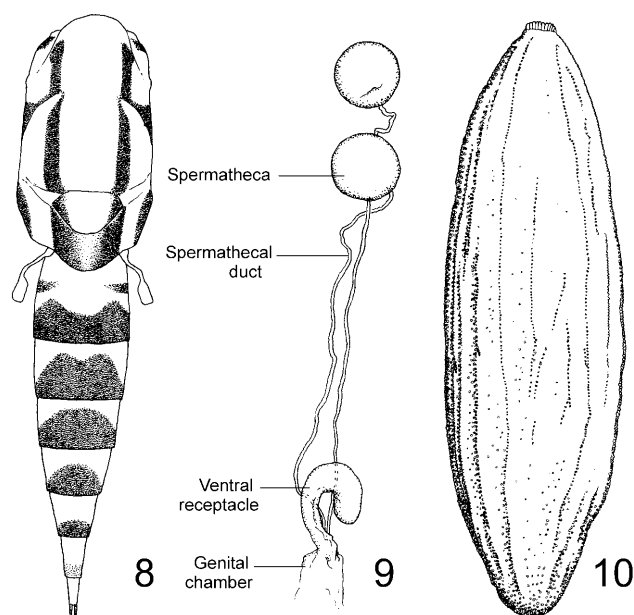
Female genitalia (Fig. 9). See generic description.

Etymology. The specific name refers to the characteristic structure of the face (L. “to stand out”, “to extend”).

Distribution. Mexico.

Holotype. Mexico. Chiapas, 8 mi SE San Cristobal, 17.v.1969, B.V. Peterson (1 ♀, CNCI).

Comments. *Procerosoma prominens* is most easily separated from *P. alini* as follows: the arista is densely plumose, the first flagellomere has a dorsolateral stripe, the mid fronto-orbital bristle is minute, there are two pairs of lateral scutellar bristles, the gena is silvery-tomentose and a brown vertical stripe is present anteriorly on the



Figs 8–10: *Procerosoma prominens* sp. n., female. 8 – dorsal (excluding head); 9 – internal genitalia, right lateral; 10 – egg.

pleuron. Furthermore, the face of this species is strongly carinate dorsally and deeply recessed ventrally, and the gena is high and acutely projecting on the posterior angle.

Two eggs (Fig. 10) were found in the abdomen of the holotype and are described above in the generic description.

Chaetoclusia Coquillett, 1904

Chaetoclusia Coquillett, 1904: 93. Malloch, 1918: 5. Melander & Argo, 1924: 7. Type species: *Chaetoclusia bakeri* Coquillett, 1904 (by monotypy).

Chaetoclesiella Soós, 1962: 138. Type species: *Chaetoclesiella richardfreyi* Soós, 1962 (by monotypy). Syn. n.

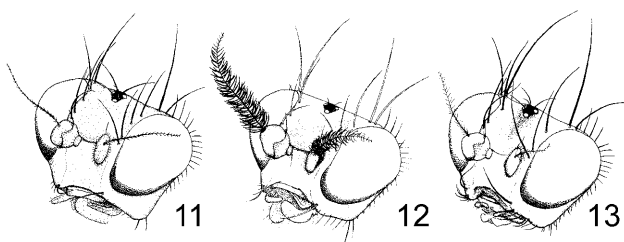
Trichoclusia Soós, 1962: 135. Type species: *Trichoclusia sabroskyi* Soós, 1962 (by monotypy). Syn. n.

Diagnosis

Cell bm closed. Vein R_1 setulose dorsally. Gena usually shiny. Anterior lateral scutellar bristle minute to absent. Two postsutural dorsocentral bristles, sometimes with one weak to well-developed bristle directly in front of anterior dorsocentral. Presutural dorsocentral and presutural intralar bristles absent. Sternites 6 and 7 of annulus atrophied into thin but well-sclerotized ventral band. Mid tibia with preapical dorsal bristle.

Generic description

Adult. General. Length 3.0–5.4 mm. Body slender, colour yellow with brown to black pattern. Angular extension on outer face of pedicel acute and longer than wide; inner face with angular projection acute to 90° and broadly rounded at apex. Arista black with base white; usually sparsely long or short-plumose (sometimes densely long-plumose). Gena and parafacial shiny to microsetulose or silvery tomentose. Frons shiny with sides parallel to slightly divergent anteriorly. Halter white to light yellow. Wing length 2.5–3.0 times width. Sub-

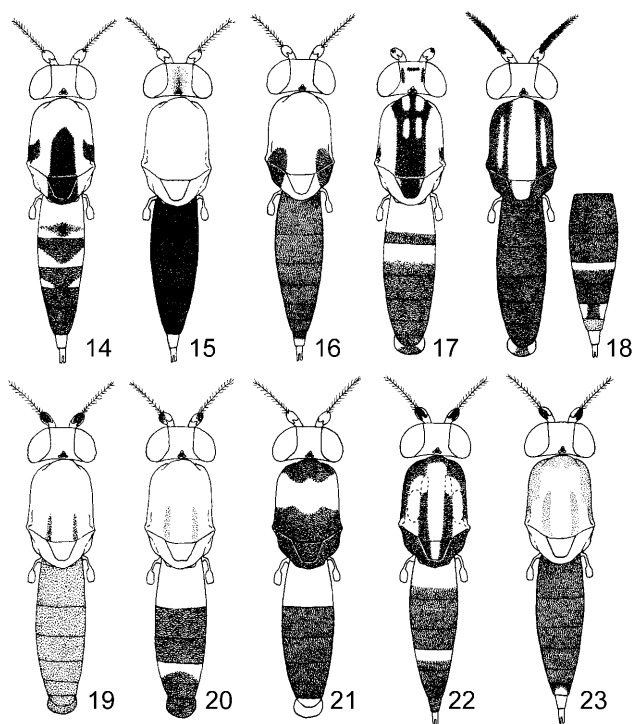


Figs 11–13: heads. 11 – *Chaetoclusia richardfreyi* (Soós, 1962); 12 – *C. bakeri* Coquillett, 1904; 13 – *C. sabroskyi* (Soós, 1962).

costal break distinct. Vein R_1 setulose dorsally. Cell bm closed. M_{1+2} ratio 1 : 3 to 1 : 6. Wing hyaline to cloudy, often infuscated on distal third and sometimes infuscated around cross veins. Abdomen brown to black with basal segments and terminalia often yellow.

Chaetotaxy. Bristles yellow to black. Anterior and mid fronto-orbital bristles close to each other on anterior margin of frons with hind bristle on posteromedial margin; sometimes with additional reclinate bristle between mid and hind bristles; bristles subequal in length. Ocellar and postvertical bristles divergent and strong to minute or (occasionally) absent. Pedicel with one outstanding dorsal bristle. Prescutellar acrostichal bristle usually absent. Two postsutural dorsocentral bristles with anterior bristle usually 0.6–0.8 times length of posterior bristle, sometimes with small bristle in front of anterior dorsocentral. Prescutellar acrostichal bristles usually absent. One postpronotal and two notopleural bristles; two intra-alar bristles; one minute intra post-alar bristle. One strong anepisternal and katapisternal bristle; proepisternal bristle small. Scutellum with one pair of long cruciate apical bristles and one pair of short lateral bristles (sometimes with one pair of additional minute bristles anteriorly). Mid tibia with dorsal preapical bristle; fore and mid femora of male with posteroventral row of ctenidial bristles.

Male abdomen. Tergites 1 and 2 fused; sternite 1 reduced to thin, weakly sclerotized band; tergites 3 to 6 and sternites 2 to 5 complete. Spiracles in membrane below tergites 1–5 and ventrally between tergites 6 and 8. Abdomen encircled by annulus comprised of sternites 6–8; sternite 8 setose and dorsal (with right lateral extension); sternites 6 and 7 forming narrow, heavily sclerotized ventral band with membranous attachment between sternites 6 and 8. Epandrium dome-shaped. Surstylus at least 0.75 times height of epandrium and usually rounded apically; tubercles on inner face along apex and at least distal half of posterior margin. Cerci setulose, rounded, lobate, and slightly projecting. Hypandrium with one pair of arms articulating with subepandrial sclerite, which in turn articulates with epandrium; hypandrium with one pair of parallel ventrolateral lobes (“ventral lobe of hypandrium”) that lie on either side of phallapodeme; medial two bristles on ventral lobe often close and long and third bristle distal and small to absent. Phallapodeme long and thin, articulating with basiphallus and thin anterior-transverse portion of hypandrium to form lever;

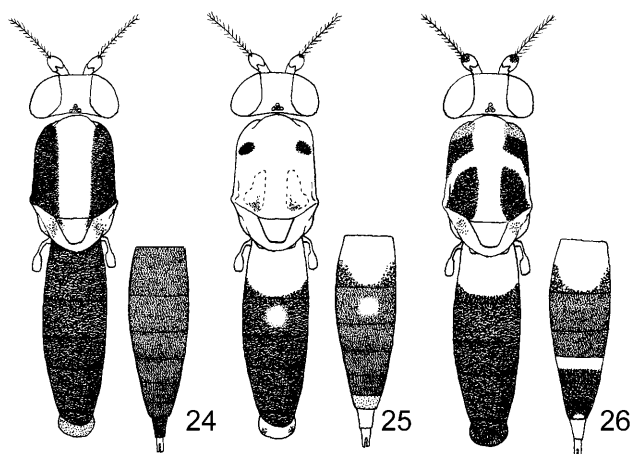


Figs 14–23: dorsal colouration. 14 – *Chaetoclusia richardfreyi* (Soós, 1962), female; 15 – *C. sabroskyi* (Soós, 1962), female; 16 – *C. nigromaculata* Melander & Argo, 1924, female; 17 – *C. centrofasciata* sp. n., male; 18 – *C. bakeri* Coquillett, 1904, male (left) and female abdomen (right); 19 – *C. amplipenis* sp. n., male; 20 – *C. longifilata* sp. n., male; 21 – *C. transversa* sp. n., male; 22 – *C. inbionella* sp. n., female; 23 – *C. quadrivittata* Melander & Argo, 1924, female.

articulation with hypandrium facilitated by suspended ventral plate on phallapodeme. Pregonite usually large, setulose, and round or clavate (small and rectangular with two setulae in one species). Postgonite usually round and small with several distal setae. Basiphallus “C” shaped, smooth and often curved medially. Epiphallus absent or small; fin-like and occasionally lengthened. Distiphallus never longer than phallapodeme. Ejaculatory apodeme 0.33 times length of phallapodeme; width approximately 0.2 times length.

Female abdomen. Tergites 1 and 2 fused; sternite 1 reduced to thin, weakly sclerotized strip; tergites 3 to 6 and sternites 2 to 6 complete. Abdomen past segment 6 narrowed into long, thin tube; segments separated by long membranous area sometimes equaling segment length. Sternite 8 bifid on distal fourth and divided lengthwise by weakly sclerotized line. Length of cercus approximately 0.67–0.75 times that of sternite 8. Spiracles in membrane below tergites on segments 1 to 7. Spermathecae (two) weakly sclerotized, spherical, smooth-surfaced and almost half as long as sternite 8 (Figs 27–29). Spermathecal ducts thin and poorly sclerotized (wide and distally segmented in one species (Fig. 28). Ventral receptacle poorly sclerotized, sac-like and often recurved distally.

Chaetoclusia, as defined above, includes the five species previously described as *Chaetoclusia*, six new spe-



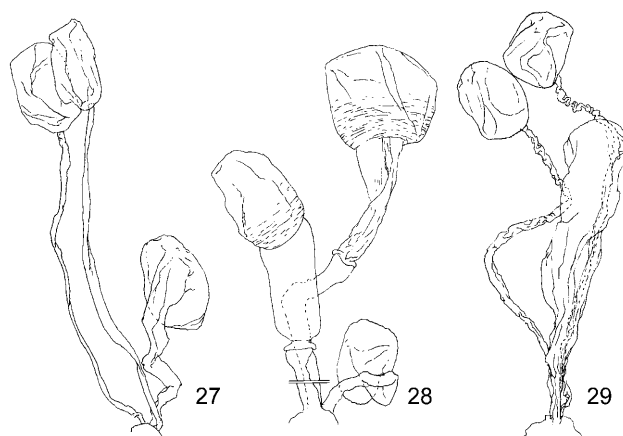
Figs 24–26: Dorsal colouration. 24 – *Chaetoclusia xanthops* (Williston, 1896), male (left) and female abdomen (right); 25 – *C. flava* sp. n., male (left) and female abdomen (right); 26 – *C. furva* sp. n., male (left) and female abdomen (right).

cies and two species formerly placed in the monotypic genera *Chaetoclesiella* and *Trichoclusia*. Melander & Argo (1924) listed the absence of the postvertical bristles in their definition of *Chaetoclusia*, but they apparently overlooked the presence of these bristles in *C. nigromaculata* Melander & Argo, 1924 and *C. xanthops* (Williston, 1896). We here redefine *Chaetoclusia* on the basis of setulae on vein R_1 (character 3), the reduction or absence of the anterior lateral scutellar bristle (character 2; independently evolved in some *Procerosoma* and *Sobarocephala*) and the reduction of sternites 6 and 7 of the annulus ventrally into a thin, but well-sclerotized ventral band (character 12). Black bristles (character 1) are also a synapomorphy of *Chaetoclusia*, but this state has been retained in only the four most ancestral species (*C. richardfreyi*, *C. sabroskyi* (Soós, 1962), *C. nigromaculata*, and *C. quadrivittata* Melander & Argo, 1924).

Of the synapomorphies listed above (characters 1, 2, 3 and 12), the presence of setulae along vein R_1 is the most easily observed and does not appear to have become reversed in any species. The presence of these setulae also appear to be a unique synapomorphy within the Clusiidae, although *Craspedochaeta novaeguineae* Soós, 1962 (Bismarck Islands, New Guinea) has two or three setulae on R_1 near its junction with the costa. The reduction of the annulus and the anterior lateral scutellar bristle are good diagnostic characters, but these states occur independently in a number of *Sobarocephala*, occasionally in tandem.

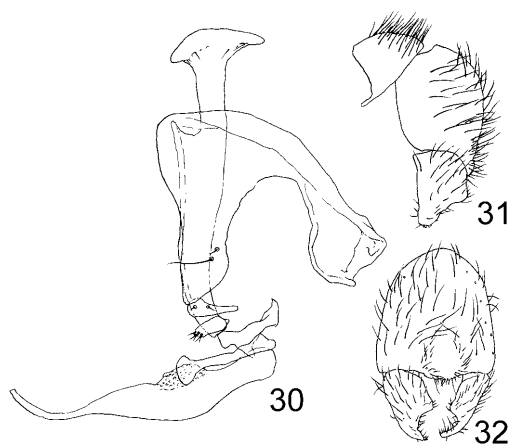
Key to the species of *Chaetoclusia*

- 1 Four fronto-orbital bristles (Fig. 11). Acrostichal bristle strong. Anterior lateral scutellar bristle relatively well developed, but still much smaller than anterior bristle. Presutural intra-alar bristle absent. Brazil. *C. richardfreyi* (Soós)
- Three fronto-orbital bristles (Figs 12, 13). Acrostichal bristle absent. Anterior lateral scutellar bristle minute to absent. Presutural intra-alar bristle present. 2



Figs 27–29: Female internal genitalia. 27 – *Chaetoclusia bakeri* Coquillett, 1904; 28 – *C. furva* sp. n. (double line refers to elongate median section removed from figure); 29 – *C. richardfreyi* (Soós, 1962).

- 2 Postvertical bristle minute to absent (Fig. 12). Arista sometimes densely plumose with hairs dark and flattened. Mainland Central and South America including Trinidad. 3
- Postvertical bristle well-developed (Fig. 13). Arista sparsely plumose with hairs thin. West Indies. 9
- 3 Anepisternum brown, at least in part. 4
- Pleuron entirely light yellow. 5
- 4 Arista densely plumose with hairs dark and flattened (Fig. 12). Ocellar bristle minute. First flagellomere with infuscation at base of arista. Fore legs entirely yellow. Scutum with two pairs of longitudinal stripes joined anteriorly and posteriorly (Fig. 18). Mexico to Brazil and Peru; Trinidad. *C. bakeri* Coquillett
- Arista sparsely plumose with hairs thin. Ocellar bristle well-developed. First flagellomere white. Fore tibia and tarsi light brown to brown. Scutum brown with wide transverse yellow stripe (Fig. 21). Costa Rica, Panama, Peru. *C. transversa* sp. n.
- 5 Notum with central brown stripe and supra-alar spot (Fig. 17). Frons with several brown spots. Scutellum with wide central brown stripe. Male terminalia short, never reaching past midpoint of abdomen (Fig. 43). Ecuador. *C. centrofasciata* sp. n.
- Notum bivittate; sometimes with additional markings. Frons yellow. Scutellum yellow, at least medially. Male terminalia elongate, extending almost to sternite 2 (males of *C. quadrivittata* unknown) (Figs 34, 37, 40). 6
- 6 Metatergites brown, at least laterally. First flagellomere dark brown on dorsal half. Scutellum brown with thin yellow stripe medially (Fig. 22). Costa Rica. *C. inbionella* sp. n.
- Metatergites yellow. First flagellomere with infuscation at base of arista or with dorsal stripe. Scutellum yellow. 7
- 7 Gena silvery tomentose. One lateral scutellar bristle. Wing clouded apically and along distal half of vein R_{2+3} . Mexico. *C. amplipenis* sp. n.
- Gena shiny. One strong and one weak lateral scutellar bristle. Wing clouded along anterior margin of wing, excluding base. 8
- 8 Bristles yellow. Scutum yellow presuturally (Fig. 20). Back of head yellow to white. Tergites 1 and 2 yellow. Panama. *C. longifilata* Melander & Argo



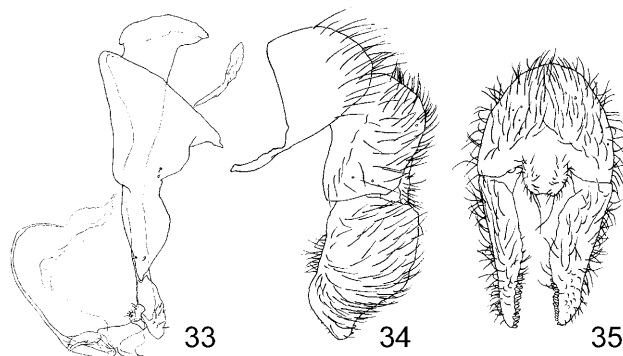
Figs 30–32: *Chaetoclusia transversa* sp. n., male genitalia. 30 – hypandrial complex, left lateral; 31 – terminalia, left lateral; 32 – terminalia, posterior.

- Bristles black. Scutum with brown pattern presuturally (Fig. 23). Back of head with brown markings. Tergites 1 and 2 brown. Costa Rica. *C. quadrivittata* Melander & Argo
- 9 Ocellar bristle absent. Pleuron white. Inner surface of surstylus with “spur” (Figs 53, 54). Distiphallus recurved and extending ventrally (Fig. 52). 10
- Ocellar bristle present. Pleuron yellow. Inner surface of surstylus flat. Distiphallus simple and straight. 12
- 10 Scutum brown with central yellow stripe (Fig. 24). Abdominal tergite 1 brown. Epandrium orange. Spermatheca lightly pigmented. St. Vincent. *C. xanthops* (Williston)
- Scutum yellow with notopleuron and one pair of wide basal stripes brown. Tergite 1 yellow. Epandrium brown or yellow with brown spots. Spermatheca unpigmented. 11
- 11 Length 3.0–3.5 mm. Spot on notopleuron separated from lateral margin (Fig. 25). Fore tarsi yellow. First flagellomere, scutellum, and metatergites yellow to white. Epandrium yellow with brown spots. Spermathecal duct thin and unsegmented (Fig. 27). British Virgin Islands, Grand Cayman, U.S. Virgin Islands. *C. flava* sp. n.
- Length 4.9–5.1 mm. Spot on notopleuron reaching lateral margin (Fig. 26). Fore tarsi light brown to brown. First flagellomere, scutellum, and metatergites sometimes with brown spots. Epandrium brown. Spermathecal duct at least 1/3 width of spermatheca and segmented distally (Fig. 28). Barbados, Dominica, Dominican Republic, Puerto Rico. *C. furva* sp. n.
- 12 Pleuron entirely yellow. Presutural intra-alar bristle strong with two strong bristles directly in front of it. Anterior genal bristle vibrissa-like (Fig. 13). Bristle in front of anterior dorsocentral bristle strong. Scutum yellow (Fig. 15). Cuba. *C. sabroskyi* (Soós)
- Anepisternum with large brown quadrate spot. Presutural intra-alar bristle weak; only setulae or setulae-like bristles in front of it. Genal bristles weak (as in Figs 11 and 12). Bristle in front of anterior dorsocentral bristle weak. Scutum with one pair of large spots in posterior corners (Fig. 16). Haiti. *C. nigromaculata* Melander & Argo

SPECIES DESCRIPTIONS FOLLOW PHYLOGENETIC ORDER (FIG. 55)

Chaetoclusia richardfreyi (Soós, 1962) comb. n.

(Figs 11, 14, 29, Map 1)



Figs 33–35: *Chaetoclusia amplipenis* sp. n., male genitalia. 33 – hypandrial complex, left lateral (ejaculatory apodeme depicted); 34 – terminalia, left lateral; 35 – terminalia, posterior.

Chaetoclesiella richardfreyi Soós, 1962: 138–140.

Redescription (Figs 11 and 14)

Female. Body length 5.3 mm. Bristles black. One small bristle in front of anterior dorsocentral. Ocellar bristle present. Arista sparsely plumose. Presutural intra-alar bristle absent (present in other *Chaetoclusia*). Prescutellar acrostichal bristle strong (absent in other *Chaetoclusia*). Anterior lateral scutellar bristle small but well developed. Additional reclinate bristle behind mid and hind fronto-orbital bristles (absent in other *Chaetoclusia*). Scutum yellow with central postsutural stripe (tapered anteriorly) and one pair of supra-alar spots. Scutellum brown. Metatergites brown below scutellum. Pleuron yellow. Coxae white. Legs yellow with tibiae and fore tarsi brown. Head largely yellow; spot present behind head below ocellar tubercle; ocellar tubercle brown. Abdomen yellow in part; tergite 2 with central brown transverse stripe; tergites 3–7 brown with posterior corners of tergites 3 and 4 yellow. Wing slightly dusky on distal third and around R₂₊₃ on distal half.

Male unknown.

Female terminalia (Fig. 29). Spermatheca unpigmented and lightly sclerotized. Spermathecal duct 5 times length of spermatheca and also lightly sclerotized. Ventral receptacle approximately 0.8 times length of spermathecal duct and not recurved ventrally; gradually constricted to base.

Distribution. Brazil (Map 1).

Holotype. Brazil. Teresopolis, Rio de Janeiro, iv.1938 (1 ♀, USNM).

Additional material examined. Brazil. Para: Rio Xingu camp (52°22'W, 3°39'S), ca. 60 km S Altamira, 2–8.x.1986, P. Spangler and O. Flint, jungle stream trail, Malaise trap, day and night coll. (1 ♀, USNM).

Comments. This distinctive species is known from two females collected from widely separated localities in Brazil. *Chaetoclusia richardfreyi* is relatively large and robust, characterized by strong acrostichal, ocellar, lateral scutellar, and postvertical bristles, as well as an additional reclinate bristle inserted between the mid and hind fronto-orbitals (Fig. 11). Furthermore, the presutural intra-alar bristle is absent (at least weakly developed in all other

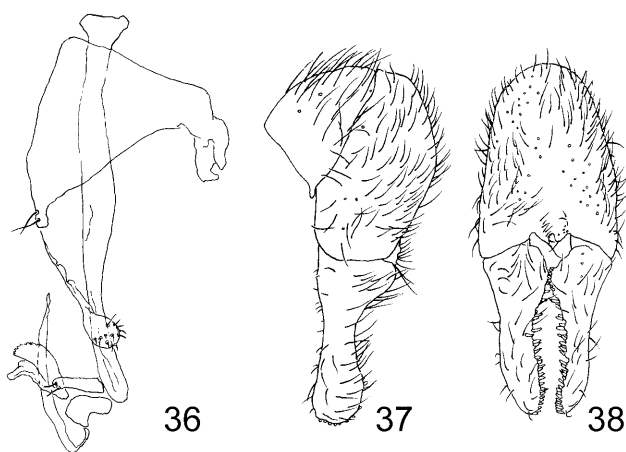


Fig. 36–38: *Chaetoclusia longifilata* Melander & Argo, 1924, male genitalia. 36 – hypandrial complex, left lateral; 37 – terminalia, left lateral; 38 – terminalia, posterior.

species of *Chaetoclusia*) and the ventral receptacle is not small and recurved, but elongate, straight and only gradually constricted towards the base (Fig. 29).

***Chaetoclusia sabroskyi* (Soós, 1962) comb. n.**

(Figs 13, 15, Map 1)

Trichoclusia sabroskyi Soós, 1962: 135–138.

Redescription (Figs 13 and 15)

Male. Body length 5.3 mm. Bristles black. One strong bristle in front of anterior dorsocentral. Acrostichal bristle absent. Anterior lateral scutellar bristle small but well developed. Arista sparsely plumose. Postvertical and ocellar bristles well developed. Anterior genal bristle strong and vibrissa-like; remaining genal bristles small and thin. Two short, but strong bristles in front of presutural intra-alar bristle. Thorax yellow. Coxae and legs yellow with hind tibia brown. Head yellow with ocellar tubercle brown and frons brownish-orange centrally. Abdomen dark brown. Wing with band from CuA₁ to R₂₊₃, curving distally to meet costa; band extending along wing tip to R₄₊₅ posteriorly.

Male terminalia not dissected.

Female. Externally as described for male except stripe on frons wider and abdominal segment 8 and terminalia yellow.

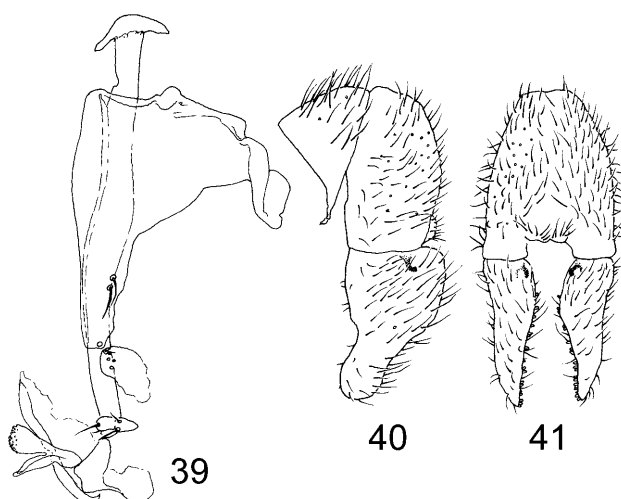
Female terminalia not dissected.

Distribution. Cuba (Map 1).

Holotype. Cuba. Las Animas, Sierra Rangel, 1500', 28.iv.1933, S.C. Brunner and A.R. Otero (1 ♂, USNM).

Paratype. Cuba. Las Animas, S Range, Pinar del Rio, 1500', 3–5.ix.1934, S.C. Brunner and A.R. Otero (1 ♀, USNM).

Comments. *Chaetoclusia sabroskyi*, like *C. richard-freyi*, is relatively large and robust with well-developed bristles, but it is further characterized by a yellow thorax (Fig. 15), one pair of short, strong bristles in front of the presutural intra-alar bristle and a strong anterior genal bristle (Fig. 13).



Figs 39–41: *Chaetoclusia inbionella* sp. n., male genitalia. 39 – internal genitalia, left lateral; 40 – terminalia, left lateral (internal process shaded); 41 – terminalia, posterior.

***Chaetoclusia nigromaculata* Melander & Argo, 1924**

(Fig. 16, Map 1)

Chaetoclusia nigromaculata Melander & Argo, 1924: 9.

Redescription (Fig. 16)

Female. Body length 4.0 mm. Bristles black. Two dorsocentral bristles. Acrostichal bristle absent. Presutural intra-alar bristle strong. Postvertical and ocellar bristles present. Anterior lateral scutellar bristle absent. Arista sparsely plumose. Scutum yellow with one pair of large posterolateral spots. Scutellum yellow. Metatergites brown with wide yellow stripe below scutellum. Pleuron yellow with large quadrate spot in anepisternum. Legs yellow with tibiae and fore tarsi light brown. Abdomen brown with posterior half of tergite 8 and terminalia yellow. Head yellow with ocellar tubercle brown. Wing clouded on distal third along R₂₊₃.

Male unknown.

Female terminalia not dissected.

Distribution. Haiti (Map 1).

Holotype. Haiti. "Manti" (1 ♀, USNM).

Comments. *Chaetoclusia nigromaculata* can be readily separated from congeners by its distinct notal pattern (Fig. 16).

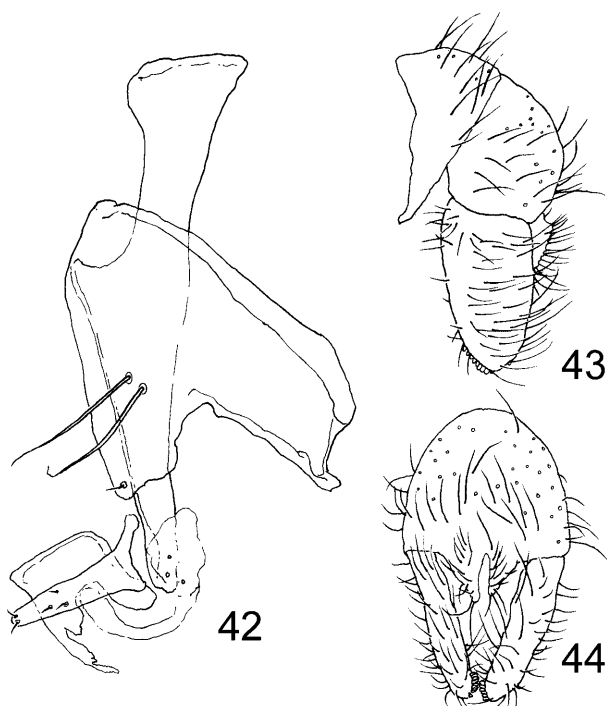
***Chaetoclusia quadrivittata* Melander & Argo, 1924**

(Fig. 23, Map 2)

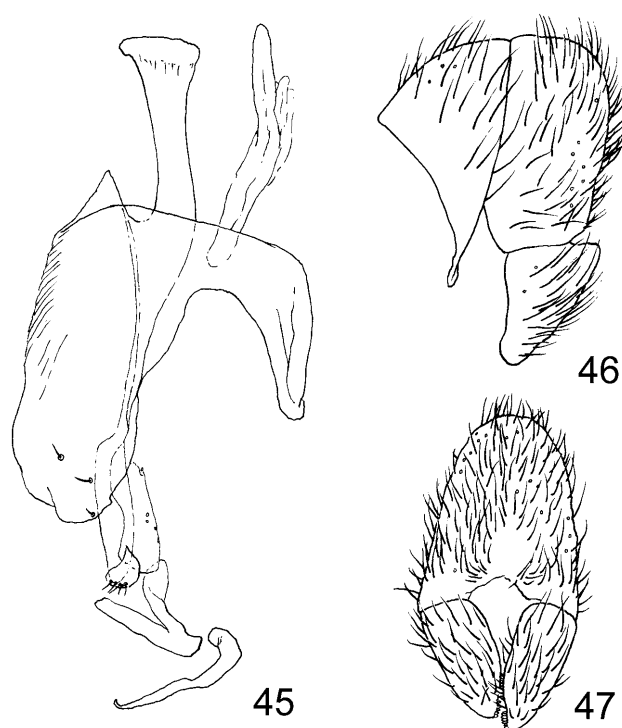
Chaetoclusia quadrivittata Melander & Argo, 1924: 9.

Redescription (Fig. 23)

Female. Body length 4.1–4.6 mm. Bristles black. Two dorsocentral bristles (subequal in length) plus one small bristle in front of anterior dorsocentral. Acrostichal bristle absent. Presutural intra-alar bristle strong. Arista sparsely short-plumose. Postvertical bristle absent. Ocellar bristle relatively long. Anterior lateral scutellar bristle minute. Scutum yellow with one pair of light brown postsutural stripes and with anterior and lateral margins of scutum



Figs 42–44: *Chaetoclusia centrofasciata* sp. n., male genitalia. 42 – hypandrial complex, left lateral; 43 – terminalia, left lateral; 44 – terminalia, posterior.



Figs 45–47: *Chaetoclusia bakeri* Coquillett, 1904, male genitalia. 45 – hypandrial complex, left lateral (ejaculatory apodeme depicted); 46 – terminalia, left lateral; 47 – terminalia, posterior.

and postpronotum light brown; lateral brown margin thinnest behind suture. Scutellum and metatergites yellow. Pleuron and legs yellow. Head predominantly yellow; first flagellomere with brown dorsolateral stripe; back of head brown above foramen; ocellar tubercle brown. Abdomen brown on tergites 1–6 and brown on anterior and lateral margins of tergite 7; remainder of abdomen yellow. Wing pattern as described for *C. longifilata*.

Male unknown.

Distribution. Costa Rica (Map 2).

Holotype. Costa Rica. La Suiza, vii.1922, P. Schild (1 ♀, USNM).

Paratypes. Costa Rica. “Costa Rica” (1 ♀, USNM), La Suiza, iv.1922, P. Schild (1 ♀, USNM).

Comments. We have not seen the holotype, but its description agrees entirely with the paratypes examined.

***Chaetoclusia transversa* sp. n.**

(Figs 21, 30–32, Map 2)

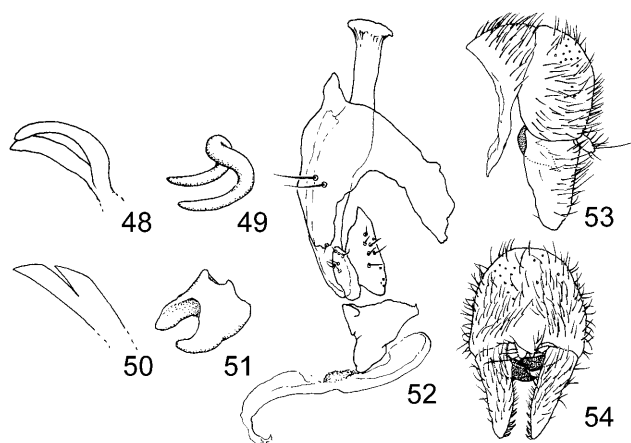
Description (Fig. 21)

Male. Body length 3.3–4.8 mm. Cephalic bristles light brown with remaining bristles dark brown. Acrostichal bristles absent. Anterior dorsocentral bristle 0.75 times length of posterior bristle, or if small additional bristle present anteriorly, that bristle half length of anterior dorsocentral, which is half length of posterior dorsocentral. Presutural intra-alar bristle weak. Arista sparsely plumose. Postvertical bristle minute. Ocellar bristle small and thin. Anterior lateral scutellar bristle absent. Scutum brown with wide transverse yellow stripe at level of suture; postpronotum sometimes yellow. Scutellum and

metatergites brown. Pleuron mostly yellow, with posterior half of anepisternum brown. Legs yellow with tip of hind femur, fore and hind tibiae, and fore tarsi brown. Head yellow with first flagellomere white, ocellar tubercle brown, and back of head with one pair of stripes and one spot below ocellar tubercle. Abdomen yellow with tergites 3–6 brown. Wing clouded lightly along apex and in first radial cell. One male and one female paratype from Peru with brown spot reduced on anterior margin of scutum and with large yellow spot on apex of scutellum; additional male paratype from Peru with brown anterior spot nearly absent and posterior brown stripe widely emarginate anteriorly. One male from Costa Rica (INBC) differing as follows: stripes behind head attached dorsally and extending around base of reclinate orbital and hind fronto-orbital bristles; transverse yellow stripe thin; tergites 2–6 dark brown.

Female. Externally as described for male.

Male terminalia (Figs 30–32). Length of epandrium 0.6 times height; width 0.9 times height. Surstylus curved inwards in cross-section; truncate with anteroventral corner projecting; tubercles on inner anteroventral face. Cerci slightly elevated; bristles short and subequal in length. Hypandrial arm curved medially, narrow basally, and bulbous distally; one short and one minute bristle distally on ventral lobe of hypandrium. Basiphallus small and thin. Epiphallus as long as basiphallus, well sclerotized basally and curved distally. Pregonite elongate-globose with two minute basal bristles. Postgonite well developed. Distiphallus 0.75 times length of ejaculatory apodeme; medially with one pair of bulbous, spinulose



Figs 48–54: *Chaetoclusia xanthops* (Williston, 1896) and *C. flava* sp. n., male genitalia. Figs 48, 49: *C. xanthops*. 48 – ventro-lateral detail of distiphallus tip; 49 – dorso-lateral detail of basiphallus tip. Figs 50–54: *C. flava*. 50 – ventro-lateral detail of distiphallus tip; 51 – dorso-lateral detail of basiphallus tip; 52 – internal genitalia, left lateral; 53 – terminalia, left lateral (internal spur shaded); 54 – terminalia, posterior.

lateral swellings; lateral lobe widest distally and nearly half length of distiphallus.

Female terminalia not dissected.

Etymology. The specific name refers to the transverse yellow stripe on the scutum.

Distribution. Costa Rica, Panama, Peru (Map 2).

Holotype. Peru: Madre de Dios, Manu, Diamante, 400 m, 12°25'S, 70°57'W, R. Alto, Madre de Dios, 7.ix.1988, A. Freidberg (1♂, USNM).

Paratypes. Costa Rica. Pedregoso, D.L. Rounds (1♀, USNM), Puntarenas: Alrededor del Río Corcovado, 30 m, 25.v.1995, A.M. Maroto (1♀, INBC), Cartago: Turrialba, P.N. Barbilla Sendero pos las Quebradas, 300 m, 16.x.2000, Red de Golpe, E. Rojas (1♂, INBC). Panama. C.Z., 19.i.1929, C.H. Curran (1♀, USNM), Close's, Cano Saddle, C.Z. 3.v.1923, R.C. Shannon (1♂, USNM). Peru. Madre de Dios, 26.–30.x.1962, L. Pena, 400 m (1♀, 1♂, CNCI), 10.–20.ix.1962 (1♂, CNCI), 26.–30.x.1962 (1♀, CNCI), Avispas, Madre de Dios, 10.–20.ix.1962, 400 m, L.E. Pena (4♂, CNCI).

Comments. The yellow transverse stripe on the scutum of *Chaetoclusia transversa* is unique within *Chaetoclusia* and a good diagnostic character (Fig. 21). The male terminalia is distinct in that the apex of the surstylus is truncate and strongly curved in cross-section and the pregonite is reduced in size with only two bristles (a similar pregonite is found in *Procerosoma* and most *Sobarocephala*) (Figs 30–32).

Chaetoclusia amplipenis sp. n.

(Figs 19, 33–35, Map 2)

Description (Fig. 19)

Male. Body length 4.1 mm. Bristles light brown to yellow. One small bristle in front of anterior dorsocentral. Ocellar bristles present. Acrostichal bristle absent. Arista sparsely plumose. Presutural intra-alar bristle weak. Postvertical bristle minute. Anterior lateral scutellar bristle absent. Scutum yellow with one pair of thin, short, brown

posterior stripes. Scutellum and metatergites yellow. Pleuron and legs light yellow. Head predominantly yellow with face, gena, parafacial, and first flagellomere white; first flagellomere with brown dorsal stripe; ocellar tubercle brown; back of head with one pair of brown stripes; gena silvery tomentose. Abdomen piceous; surstylus yellow; epandrium sometimes yellow with brown basal spot. Wing clouded along distal half of R_{2+3} and along apex.

Female unknown.

Male terminalia (Figs 33–35). Terminalia elongate, with apex of surstylus nearly reaching sternite 2 in repose. Epandrium as wide as high and length 0.6 times height. Surstylus 1.2 times height of epandrium, posteriorly lobate and tapered distally. Cerci projecting, rounded, as wide as long and with one longer pair of bristles medially. Hypandrial complex relatively elongate. Phallapodeme well developed with distal head relatively bulbous. Hypandrial arm highly reduced; ventral lobe of hypandrium sinuate on anterior and posterior faces and with one pair of minute bristles medially and distally. Pregonite ovate with numerous setulae on distal half. Postgonite elongate, nearly perpendicular to long axis of complex with minute bristles along length. Distiphallus 0.6 times length of phallapodeme and curved distally; lateral lobes short, pointed and joined to distiphallus by membranous enclosure.

Etymology. The specific name refers to the size of the male terminalia.

Distribution. Southern Mexico (Map 2).

Holotype. Mexico. Chiapas: El Trifundo (49 km S Jaltenango), 13.–15.v.1985, 1300–2000 m, W.N. Mathis (1♂, USNM).

Paratype. Mexico. Morelos, Cuernavaca, vi.1945, N.L.H. Krauss (1♂, USNM).

Comments. *Chaetoclusia amplipenis*, *C. longefilata* and *C. inbionella* are monophyletic on the basis of characters of the male genitalia: the terminalia are elongate, almost reaching sternite 2, and the arms of the hypandrium are strongly reduced. These species also have a dark dorsal stripe on the first flagellomere, but this can be found in *C. quadrivittata* as well. *Chaetoclusia amplipenis* can be separated from the above species by a largely piceous abdomen, one lateral scutellar bristle and no additional process on the lateral lobe of the distiphallus. It is also the only species, aside from the widespread *C. bakeri*, to be found in Mexico.

Chaetoclusia longefilata Melander & Argo, 1924

(Figs 20, 36–38, Map 2)

Chaetoclusia longefilata Melander & Argo, 1924: 8–9.

Redescription (Fig. 20)

Male. Body length 3.4 mm. Bristles yellow. Two dorsocentral bristles. Presutural intra-alar bristle strong. Arista sparsely plumose. Ocellar bristle present. Postvertical bristle absent. Anterior lateral scutellar bristle minute. Scutum yellow with one pair of short, thin, light brown stripes posteriorly. Scutellum and metatergites yellow. Pleuron and legs light yellow. Head yellow with

TABLE 1. Character list for Sobarocephalinae (plesiomorphic state listed first).

External characters:	
1 . Bristle colour	black brown to yellow
2 . Anterior lateral scutellar bristle	well developed small to absent
3 . Vein R ₁	bare setulose
4 . Postvertical bristle	well developed minute to absent
5 . Ocellar bristle	well developed to weak absent
6 . Prescutellar acrostichal bristle	well developed absent
7 . Pleura	yellow to light yellow, sometimes with variable markings predominantly white
8 . Clypeus	yellow orange to brown, in at least some specimens
Male characters	
9 . Terminalia	short, not reaching midpoint of abdomen elongate, with apex of surstylus nearly reaching sternite 2 in repose.
10 . Inner face of surstylus	without elaboration, or with weak internal evagination with strong basal spur
11 . Annulus	well developed sternites 6 and 7 reduced to thin ventroanterior band
12 . Arm of hypandrium	well developed atrophied
13 . Pregonite	separated from hypandrium fused to hypandrium
14 . Basiphallus	planar medially bent
15 . Distiphallus	simple with one pair of minutely spinulose, latero-median swellings
16 . Distiphallus	not extending ventrally past basiphallus extending well past basiphallus and curled basally
17 . Lateral lobe of distiphallus	present absent
18 . Lateral lobe of distiphallus	absent or undivided bifid

large brown dorsal spot on first flagellomere; ocellar tubercle brown. Abdomen yellow except as follows: tergites 3, 4, 6, annulus, and epandrium brown; tergite 5 with posterior margin brown centrally. Wing infuscated in first and second radial cells (excluding base) and very lightly clouded in third radial cell and along apex.

Female unknown.

Male terminalia (Figs 36–38). Terminalia elongate, with apex of surstylus nearly reaching sternite 2 in repose. Width of epandrium 0.7 times height; length 0.6 times height. Surstylus height 0.9 times height of epandrium; widest basally, thin medially and rounded distally; tubercles on inner face along ventral margin (excluding base). Cerci small and emarginate. Hypandrial arm small and projecting at 90° from long axis of phallapodeme; ventral lobe of hypandrium triangular (small truncate projection apically with two small bristles). Phallapodeme well developed. Basiphallus small. Epiphallus absent. Pregonite elongate, clavate and densely setose distally.

Postgonite subrectangular with two distal bristles. Distiphallus 0.4 times length of phallapodeme; lateral lobe bifid with inner branch rounded and serrate.

Distribution. Costa Rica, Panama (Map 2).

Holotype. Panama. Alhajuela, A. Busck, 12.iii.1912 (1♂, USNM).

Additional material examined. Costa Rica. Limon. 7 mi N Guacimo, 22.ii–3.iii.1988, F.D. Parker (1♂, EMUS).

Comments. While it appears as though *Chaetoclusia longefilata* and *C. inbionella* have a “thumb” on the lateral lobe of the distiphallus (Figs 36, 39), it is more likely that the lateral lobe has become split medially. A “thumb” on the lateral lobe of the distiphallus is considered to be a synapomorphy restricted to the species of *Sobarocephala*.

***Chaetoclusia inbionella* sp. n.**

(Figs 22, 39–41, Map 2)

TABLE 2. Character matrix for the species of *Chaetoclusia* (characters listed in Table 1).

	1 11111111																
	1234567890	12345678															
ancestor	0000000000	00000000															
<i>C. richardfreyi</i>	11100000??	????????															
<i>C. sabroskyi</i>	111001000?	????????															
<i>C. flava</i>	0110111001	10111110															
<i>C. xanthops</i>	01101?1001	10111110															
<i>C. furva</i>	0110111001	10111110															
<i>C. nigromaculata</i>	11100100??	????????															
<i>C. bakeri</i>	0111110100	10000010															
<i>C. longifilata</i>	0111010010	11000001															
<i>C. quadrivittata</i>	11110100??	????????															
<i>C. transversa</i>	0111010000	10001000															
<i>C. amplipenis</i>	0111010010	11000000															
<i>C. centrofasciata</i>	0111010000	10000010															
<i>C. inbionella</i>	0111010110	11000001															

Description (Fig. 22)

Male. Body length 3.4–4.1 mm. Bristles light brown. One small bristle in front of anterior dorsocentral. Acrostichal bristle absent. Arista sparsely pubescent. Presutural intra-alar bristle weak. Ocellar bristle present. Postvertical bristle absent. Anterior lateral scutellar bristle minute. Scutum yellow with anterior margin, postpronotum, and lateral margins to wing base light brown to brown; one pair of darker postsutural dorsocentral stripes present. Scutellum brown with thin median yellow stripe. Metatergites light brown lateral to scutellum or just on katatergite. Pleuron light yellow with anepisternum yellow. Legs yellow. Head mostly yellow; dorsal half of first flagellomere dark brown; face, gena, parafacial and occiput white; back of head with one pair of stripes (not extending to lateral margin); ocellar tubercle brown. Abdomen brown from tergite 3 to annulus; tergite 5 with anterior half yellow; epandrium with large brown basal spot; remainder of abdomen yellow. Wing clouded extensively along anterodistal margin, darkest towards costa.

Female. Externally as described for male except as follows: more darkly pigmented; sometimes hind tibia brown on basal 3/5; clypeus orange to brown; abdomen brown excluding anterior half of tergite 5 and terminalia; one female with anterior margin of scutum yellow and posterior corners brown, and with postsutural stripes reaching anterior margin of scutum.

Male terminalia (Figs 39–41). Terminalia elongate, with apex of surstylus nearly reaching sternite 2 in repose. Width of epandrium 0.7 times height and length nearly half height. Cerci small and lobate with numerous small bristles. Surstylus nearly triangular in outline with apex rounded, distal half tapered and posterior margin broadly rounded; inner face with minute basal process; tubercles along distal 3/4 of posterior margin. Hypandrial arm short and projecting at 90° from long axis; ventral lobe of hypandrium with two small bristles and one empty socket distally (only holotype dissected). Pregonite

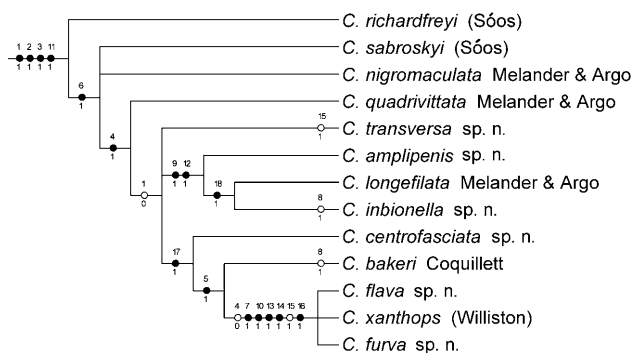


Fig. 55. Phylogenetic hypothesis for species of *Chaetoclusia* selected from one of the 3 equally parsimonious trees calculated from the morphological character matrix in Table 2 (9 external and 10 male genitalic characters, described in Table 1). Characters were polarized using *Sobaroccephala* and *Procerosoma* as an outgroup and a hypothetical ancestor was included in the analysis to root the cladogram (removed from the above phylogeny). Cladistic analysis was performed using PAUP [Phylogenetic Analysis Using Parsimony (Swofford, 2003)], with a simple heuristic search, and all characters unweighted. Length of tree 22 steps with a CI of 0.82 and a RI of 0.89. Solid circles indicate unique characters, and open circles are homoplasies or character reversals.

ovate and irregular in outline with several minute basal setulae. Postgonite as described for *C. amplipenis*. Epiphallus as large as basiphallus (viewed laterally). Distiphallus and lateral lobe as described for *C. longifilata*.

Female terminalia not dissected.

Etymology. The specific name refers to the collection from which the type series was borrowed.

Distribution. Costa Rica (Map 2).

Holotype. Costa Rica. Guanacaste: Est. Cacao, 1000–1400 m, SW side Volcan Cacao, xi.–xii.1989, R. Blanco and C. Chavez (1♂, INBC).

Paratype. Costa Rica. Alajuela: Upala, Dos Rios, Estacion San Gerrardo, 600 m, 10.ix.–10.x.2000, Malaise, D. Briceno (1♀, INBC). Puntarenas: Est. Altamira, 1 km S del Cerro Biolley, 1450 m, i.–ii.1995, J.F. Quesada and M. Segura, Malaise trap (1♀, INBC), Est. Agujos, Send. Leyba, 300–350 m, 29.viii–12.ix.1998, M. Lobo, tp. Malaise, seca (1♀, INBC), Guanacaste: Est. Cacao, 1000–1400 m, SW side Volcan Cacao, xi.–xii.1989, R. Blanco and C. Chavez (1♂, INBC).

Comments. *Chaetoclusia inbionella* is sometimes patterned much like *C. bakeri* (Figs 18, 22), but differs in having a sparsely pubescent arista, well developed ocellar bristles, an entirely light yellow pleuron and an entirely brown first abdominal tergite.

Chaetoclusia centrofasciata sp. n.

(Figs 17, 42–44, Map 2)

Description (Fig. 17)

Male. Body length 4.8 mm. Bristles brown. Two dorsocentral bristles. Acrostichal bristle absent. Arista missing. Anterior lateral scutellar bristle minute. Postvertical bristle minute. Ocellar and presutural intra-alar bristles missing in specimen, but sockets well developed. Scutum yellow with supra-alar spot and central stripe brown; stripe with two pairs of yellow presutural internal spots.

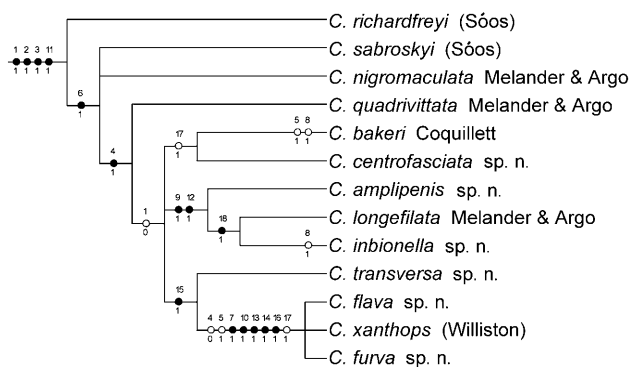


Fig. 56. Phylogenetic hypothesis for the species of *Chaetoclusia* if those species with lateral spinulose swelling on the distiphallus (character 15) are presumed monophyletic. Length of tree 23 steps (one step longer than the most parsimonious hypotheses). Solid circles indicate unique characters, and open circles are homoplasies or character reversals.

Scutellum brown with lateral corners yellow. Metatergites yellow. Pleuron light yellow. Legs yellow with hind tibia brown. Head largely yellow; frons with one median transverse and one lateral pair of stripes; first flagellomere with infuscation at base of arista; face with brownish-orange tint; lower margin of gena with shiny orange strip; face pilose; back of head with one pair of light brown stripes; upper half of gena silvery tomentose. Abdomen yellow except as follows: posterior half of tergites 2 and 3

brown; tergite 4 to annulus brown; epandrium with large brown basal spot. Wing dark along anterodistal margin from costa to vein M_1 (excluding basal half of spot along costal margin); additional spot present along distal half of CuA_1 .

Female unknown.

Male terminalia (Figs 42–44). Epandrium as wide as high and length 0.8 times height. Height of surstylus 1.2 times that of epandrium; tubercles along inner-distal margin. Cerci projecting, deeply emarginate and pointed distally; bristles subequal in length. Hypandrial arm longer than ventral lobe of hypandrium and truncated distally; ventral lobe of hypandrium with one minute distal and two long medial bristles. Phallapodeme and basiphallus well developed. Pregonite membranous with three central bristles. Postgonite elongate and thin with two distal and three medial bristles. Epiphallus level with anterior face of basiphallus, well sclerotized, and with distal and posterior margins irregular. Distiphallus absent (see comments).

Etymology. The specific name refers to the characteristic brown longitudinal stripe on the scutum.

Distribution. Ecuador (Map 2).

Holotype. Ecuador. Napo: Tena, ii.1983, M.J. Sharkey (1♂, DEBU).

Comments. The spots on the frons and the complete median stripe on the scutum are unique within *Chaetoclusia*, and can be used as reliable diagnostic features to



Map 1. Distribution of the species of *Chaetoclusia* with well-developed postvertical bristles: *C. richardfreyi* (Soós, 1962) (circle with dot), *C. sabroskyi* (Soós, 1962) (diamond), *C. nigromaculata* Melander & Argo, 1924 (star), *C. flava* sp. n. (dot), *C. furva* sp. n. (circle), *C. xanthops* (Williston, 1896) (square).



Map 2. Distributions of *Chaetoclusia* species that lack strong postvertical bristles (excluding *C. bakeri* Coquillett, 1904): *C. centrofasciata* sp. n. (circle with dot), *C. quadrivittata* sp. n. (dot), *C. transversa* sp. n. (square), *C. longefilata* Melander & Argo, 1924 (circle), *C. amplipenis* sp. n. (empty diamond), *C. inbionella* sp. n. (x).

identify this species (Fig. 17). *Chaetoclusia centrofasciata* also appears to be unique in that it has lost the distiphallus (Fig. 42), although this should be verified with the examination of more males. Elongation and elaboration of the postgonite possibly serves as a functional adaptation associated with this loss.

Chaetoclusia bakeri Coquillett, 1904

(Figs 12, 18, 27, 45–47, Map 3)

Chaetoclusia bakeri Coquillett, 1904: 94. Melander & Argo, 1924: 8.

Chaetoclusia bakeri peruana Hennig, 1938: 92–94. Syn. n.

Redescription (Figs 12 and 18)

Male. Body length 3.6–5.4 mm. Bristles yellow. One small bristle in front of anterior dorsocentral. Acrostichal bristle absent. Arista densely plumose with hairs black and flattened. Anterior lateral scutellar bristle minute. Postvertical and ocellar bristles minute. Presutural intralar bristle weak. Scutum yellow with two pairs of thin lateral stripes (outer stripe continuous with lateral margin), each pair joined anteriorly and posteriorly; sometimes enclosed yellow stripe faded medially, particularly around transverse suture; sometimes brown pattern faded around area of notopleuron and postpronotum (particularly in those specimens collected in Venezuela and Central America); specimen from Mexico with inner pair of stripes broken medially. Scutellum yellow with one pair of lateral brown stripes. Metatergites brown, sometimes yellow below scutellum. Pleuron light yellow with anepisternum, anepimeron, and proepisternum brown; anepisternum centrally with yellow longitudinal stripe, sometimes bordered ventrally by brown longitudinal stripe (variably faded). Legs light yellow with hind tibia brown on (at least) basal half, excluding extreme base. Head mostly yellow; first flagellomere white with brown

infuscation around base of arista; clypeus and lower half of face sometimes brown; ocellar tubercle brown. Abdomen brown with surstylus and lateral third of epandrium yellow; tergite 1 sometimes yellow. Wing clouded on distal third and lightly infuscated around cross veins.

Female. Externally as described for male except as follows: face and clypeus always yellow; proepisternum sometimes yellow; tergite 1 rarely yellow; anterior half of tergite 4 yellow; tergite 6 sometimes yellow laterally; tergite 7 light brown; tergite 8 and terminalia yellow.

Male terminalia (Figs 45–47). Length of epandrium 0.6 times height; width 0.7 times height. Height of surstylus 0.6 times that of epandrium with anterior surface straight and posterior surface tapering distally; inner-posterior margin tuberculate (excluding basal third); apex of surstylus sometimes thin and tapered. Cerci rounded, emarginate and setose with one pair of slightly longer bristles medially (sometimes small or folded backwards, appearing absent, as in figure). Ventral lobe of hypandrium with transverse wrinkles along anterior margin; hypandrial arm perpendicular to long axis of ventral lobe of hypandrium basally and parallel distally; three minute bristles present distally. Phallapodeme well developed with anterior face fused to hypandrium (separate in all other *Chaetoclusia*). Pregonite large, minutely setose and somewhat fused to hypandrium basally. Postgonite small. Basiphallus and epiphallus well developed. Distiphallus not much longer than basiphallus; wide basally and strongly tapered distally (appearing “spade”-shaped).

Female terminalia (Fig. 27) Spermatheca pale and weakly sclerotized. Spermathecal duct thin, poorly sclerotized and four times length of spermatheca.

Distribution. Brazil, Costa Rica, Ecuador, Mexico, Nicaragua, Panama, Peru, Trinidad, Venezuela (Map 3).

Holotype. Costa Rica. La Suiza de Turrialba, P. Schild (1♀, USNM).

Holotype (*C. bakeri peruana*). Peru. Meshagua, Urubambafluss, 4.x.1903, Schnuse (coll.) (1♀, SMTD).

Additional material examined. [Illegible; brown handwritten label] (1♂, USNM). “Chapada, May” (1♀, USNM). Bolivia. La Paz: Mapiri (5 km W, 15°17.8'S, 68°15.6'W, 750 m), 16.iii.2001, A. Freidberg (1♂, USNM). Brazil. Para, Tucuruí, Pura quequara, 13.viii.1980, ep. Nunes de Mello (1♀, INPA), Nova Teutonia, 27°11'S, 52°23'W, 300–500 m, ii.1965, F. Plaumann (1♂, CNCI), Rondonia, 62 km SE Ariquemes, 180 m, 17.–24.iii.1989, W.J. Hanson (2♀, EMUS). Costa Rica. Pedregoso, D.L. Rounds (1♀, 1♂, USNM), Alajuela: 20 km S Upala, F.D. Parker, 1.–15.vii.1991 (2♀, EMUS), 11.xii.1990 (1♀, EMUS), 27.xi.1990 (1♀, EMUS), 21.ii.1991 (1♀, EMUS), 16.–25.ix.1990 (1♀, EMUS), 28.x.1990 (1♀, EMUS), 16.x.1990 (1♀, EMUS), 21.vi.1991 (1♀, EMUS), 3.vi.1991 (1♀, EMUS), 21.–30.iv.1991 (1♀, EMUS), 10.–21.v.1991 (1♀, EMUS), 15.–18.vii.1990 (2♀, EMUS), Guanacaste: 14 km S Canas, F.D. Parker, 16.–19.ix.1990 (1♂, EMUS), 1.–5.viii.1992 (1♀, EMUS), 26.–30.vii.1990 (1♀, EMUS), 14.–16.x.1989 (1♀, EMUS), 24.–31.viii.1990 (2♀, 1♂, EMUS), 20.–30.x.1989 (4♀, EMUS), 10.–15.x.1990 (1♂, EMUS), 5.–10.ix.1990 (1♀, EMUS), 1.–15.ix.1990 (2♀, EMUS), 26.–30.ix.1989 (1♀, EMUS), 3 km SE Naranjo, F.D. Parker, 1.–10.viii.1992 (2♀, EMUS), 5.–9.vii.1993 (1♂, EMUS), 21.vii.1993 (1♀, EMUS), 21.–28.xii.1992 (1♀, EMUS), 22.–25.i.1993 (1♂, EMUS), 19.v.1993 (1♀, EMUS), 10.–23.vii.1993 (1♀, EMUS), Heredia:

Est. Biol. La Selva, 50–150 m, 10°26'N, 84°01'W, vii.1992 (1♂, INBC), Puntarenas: P.N. Manu el Antonio, 80 m, Quepos, viii.1991, G. Varela (1♀, INBC), Est. Sirena, 0–100 m, P.N. Corcovado, 21.iii–21.iv.1992, Z. Fuentes (1♂, INBC), Est. Carara, Res. Biol. Carara, 200 m, iv.1990, Malaise (2♀, INBC), 6 km S San Vito, 19–21.iv.1967, 8°42'N, 83°00'W, D.F. Veirs (1♀, EMUS), Rincon de la Osa, 26.vii.1966, D. Veirs (1♂, EMUS). Ecuador. Pichilingue, iii.1958, M.R. Wheeler (2♂, USNM). Mexico. Chiapas: El Trifundo (49 km S Jaltenango), 13.–15.v.1985, 1300–2000 m, W.N. Mathis (1♀, USNM). Panama. Zona del Canal, Barro Colorado Island, 10.vii.1980, R. Silberglied/A. Aiello, Barbour House (1♀, USNM), Barro Colorado Island, C.Z. vii.1967, light trap, W.W. Wirth (1♀, USNM), Gamboa, C.Z., Pipeline Rd., vii.1967, Malaise trap, W.W. Wirth (1♀, USNM), Pt. Gulick, Qtrs. 40, at light, vi.1980, H.J. Harlan (1♀, USNM), Barro Colorado Nat. Monm., 20.ii–13.iii.1985, D.A. Grimaldi (1♀, 1♂, USNM), C.Z. Ft. Kobbe, 18.xi.1958, W.J. Hanson (1♀, EMUS). Peru. Madre de Dios: Manu, Rio Manu, 250 m, Pakitza, 12°07'S, 70°58'W, 9.–23.ix.1988, A. Freidberg (6♂, 3♀, USNM), Madre de Dios: Manu, Rio Manu, Cocha Salvador, 240 m, 14.ix.1988, A. Freidberg (2♂, USNM), Madre de Dios: Manu, Rio Manu, Pakitza (5 km E), Aguaja, 19.ix.1988, A. Freidberg (1♂, USNM), Madre de Dios: Manu, Erika (nr Salvacion), 550 m, 5.–6.ix.1988, A. Freidberg (1♂, USNM), Depto Loreto, 1.5 km N Teniente Lopez, 18.vii.1993, 230–405 m, FIT, R. Leschen (1♀, USNM), Monzon Valley, Tingo Maria, E.I. Schlinger & E.S. Ross, 21.xi.1954 (1♀, CASC), 26.x.1954 (1♀, CASC). Venezuela. San Vicente, Zula, i.1970, J. Maldonado C (1♀, USNM), Aragua, Rancho Grande Biol. Stn., H. Pittier N. Pk., 1250 m, 8.iii.1995, trail, S.A. Marshall (1♀, DEBU), Provincia Falcon, Sierra de San Luis, 25 km SSE Coro, forest in front of Cueva ('Cave') Acuritz, Leaf litter on ground, along calcareous rocks and footpath, swept, aspirated, 11°10.42'N, 69°37.75'W, 2650', 23.iii.1998, M. v.Tschirnhaus (1♀, FBUB).

Comments. *Chaetoclusia bakeri* is characterized by a densely plumose arista and a reduction of the postvertical and ocellar bristles (Fig. 12). *Chaetoclusia bakeri* is also the most widespread and common species of *Chaetoclusia* on the continental mainland, with records not extending further from the coast than Trinidad or Barro Colorado Island.

The slight difference in thoracic colouration between the type specimen of the nominate subspecies (Coquillett, 1904) and the type specimen of the subspecies *Chaetoclusia bakeri peruana* Hennig, 1938 was exaggerated by the more extensive pigmentation on the anepisternum of Hennig's specimen, which revealed the unpigmented median longitudinal stripe on the sclerite. This median portion of the anepisternum is always unpigmented, but was not apparent on the specimen examined by Coquillett since the background of this sclerite was also yellow. The extensive new material available to us has shown that the thoracic pigmentation of *C. bakeri* is quite varied, with different phenotypes often occurring in the same localities. There is a similar amount of variation in wing pigmentation, which ranges from light to dark. *Chaetoclusia bakeri peruana* is therefore included here as a junior synonym of *C. bakeri*.

Chaetoclusia flava sp. n.

(Figs 26, 50–54, Map 1)



Map 3. Distribution of *Chaetoclusia bakeri* Coquillett, 1904.

Description (Fig. 26)

Male. Body length 3.0–3.5 mm. Bristles yellow. One small bristle in front of anterior dorsocentral. Arista sparsely plumose. Ocellar bristle minute. Anterior lateral scutellar bristle minute or absent. Thorax yellow except as follows: notopleuron with dark central spot; one posterior pair of wide stripes on scutum (sometimes atrophied); proepisternum, katepisternum and meron white. Head predominantly yellow with ocellar tubercle light brown, first flagellomere light yellow to white, and face, gena and parafacial white. Legs yellow with coxae, basal half of femora and tarsi white. Abdomen yellow except as follows: tergite 2 brown posteriorly; tergite 3 to annulus brown with central yellow spot sometimes present on tergite 3; one pair of spots present laterally on epandrium.

Female. Externally as described for male except tergite 7 light brown and tergite 8 and terminalia yellow.

Male terminalia (Figs 50–54). Epandrium as wide as high; length 0.67 times height. Surstylus 0.67 times height of epandrium and elongate triangular (broadly rounded apically); distal third of inner-posterior margin with stout, pointed tubercles; inner-basal face with short pointed spur. Cerci triangular with apical emargination; setose with one pair of longer central bristles. Hypandrium with ventral lobe and arm subequal in length; arm narrow medially and ventral lobe of hypandrium with one minute distal and two short medial bristles. Pregonite large and ovate with numerous central setulae. Postgonite and epiphallus well developed. Basiphallus saddle-shaped with slight dorsal arch. Base of distiphallus produced ventrally with ventral section 0.67 times length of dorsal section (from intersection with basiphallus); ventral section strongly curved; one pair of lateral spinulose swellings present medially; distally bifid and truncate; lateral lobe absent.

Female terminalia. As described for *C. bakeri* except spermathecal duct 2.5 times length of spermatheca.

Etymology. The specific name refers to the yellow colouration of this species relative to a similar species, *C. furva*.

Distribution. British Virgin Islands, Grand Cayman, U.S. Virgin Islands (Map 1).

Holotype. U.S. Virgin Islands. St. John, Reef Bay trail, 1200', Grimaldi and Stark, moist stream bed, 5.iii.1992 (1B USNM).

Paratypes. British Virgin Islands. Guana Isl., 0–300 m, 9.–11.iii.1992, Grimaldi and Stark (2♂, USNM). Grand Cayman. Georgetown, 15.–30.iii.1965, J.R. McLintock (2♂, CNCI). U.S. Virgin Islands. St. John, Reef Bay trail, 1200', Grimaldi and Stark, moist stream bed, 5.iii.1992 (6♂, 4♀, USNM; 1♀, 1♂, DEBU), St. Thomas, Crown Mtn., 1500', 3.iii.1992, Grimaldi and Stark, sweeping forest floor (1♂, USNM).

Comments. See comments for *Chaetoclusia furva*.

Chaetoclusia xanthops (Williston, 1896)

(Figs 24, 48, 49, Map 1)

Heteroneura xanthops Williston, 1896: 386 (in part); Czerny, 1903: 100.

Chaetoclusia xanthops Melander & Argo, 1924: 9–10.

Redescription (Fig. 24)

Male. Body length 3.4 mm. Bristles light brown. Two dorsocentral bristles. Arista sparsely plumose. Ocellar bristle minute. Anterior lateral scutellar bristle minute. Scutum brown with central stripe and anterior margin of postpronotum yellow. Scutellum yellow with lateral corners brown. Metatergites yellow with one pair of brown stripes lateral to scutellum. Pleuron and legs white. Head yellow with ocellar tubercle light brown and with first flagellomere, face, gena and parafacial white. Abdomen brown with epandrium orange and surstylus and cerci white. Wing dusky on distal half in first and second radial cells.

Female. Externally as described for male except abdomen entirely brown excluding yellow terminalia. Holotype with tergite 1 yellow.

Male terminalia (Figs 48, 49). As described for *Chaetoclusia flava* except as follows: distiphallus deeply emarginate with tips rounded (not square); basiphallus more linear than saddle-shaped.

Female terminalia. As described for *C. flava* except spermatheca lightly pigmented.

Distribution. St. Vincent (Map 1).

Holotype. St. Vincent. W.I. Leeward side, H.H. Smith (1♀, BMNH) [head missing].

Additional material examined. St. Vincent. W.I., vii.–viii.1957, W.B. Heed (1♀, USNM), Mangaroo, 28.iii.1989, A. Freidberg (1♂, USNM), Majorica, 1500', vii.–viii.1972, A.D. Harrison (1♀, CNCI), Malaise trap (1♀, CNCI).

Comments. *Chaetoclusia xanthops* is the only known species of Sobarocephalinae with pigmented spermathecae.

Chaetoclusia furva sp. n.

(Figs 25, 28, Map 1)

Description (Fig. 25)

Male. Body length 4.9–5.1 mm. Bristles light brown to dark brown. One small bristle in front of anterior dorso-central. Acrostichal bristle absent. Presutural intra-alar bristle weak. Ocellar bristle minute. Anterior lateral scutellar bristle minute or absent. Arista sparsely plumose. Scutum yellow with notopleuron and one pair of wide

postsutural stripes brown; sometimes scutum light brown laterally in front of notopleuron. Scutellum yellow, sometimes with one pair of lateral postsutural stripes. Metatergites yellow, sometimes with one pair of faded stripes lateral to scutellum. Pleuron and legs light yellow to white with fore tarsi light brown to brown, sometimes with fore tibia or all tibiae brown. Head yellow with ocellar tubercle light brown and head white below antenna, sometimes with first flagellomere narrowly infuscated around base of arista. Abdomen brown with tergite 1 and surstylus yellow, sometimes tergite 2 only brown posteriorly and laterally. Wing dusky on distal ¼ (darkest around R_{2+3}).

Female. Externally as described for male except as follows: colour often darker; sometimes anterior half of tergite 5 yellow; tergite 8 and terminalia yellow.

Male terminalia. As described for *C. flava*.

Female terminalia (Fig. 28). Spermatheca poorly sclerotized and with minute transverse wrinkles on basal third. Spermathecal duct up to half as wide as spermatheca and divided into two sections: basal section no more than 0.3 times width of spermatheca and approximately three times length of spermatheca; distal section wide, membranous and 1.2 times longer than spermatheca. Ventral receptacle approximately 1.5 times length of spermatheca; wide distally, sac-like and recurved ventrally.

Etymology. The specific name refers to the dark colouration of this species (L. “dark”) relative to a similar species, *C. flava*.

Distribution. Barbados, Dominica, Dominican Republic, Puerto Rico (Map 1).

Holotype. Dominica. Pont Casse, 22.xi.1964, P.J. Spangler (1♂, USNM).

Paratypes. Barbados. W.I. Syndicate, 6.iii.1964, H. Robinson (1♀, USNM). Dominica. W.I., Clarke Hall, Est. 15.iv.1966, R.J. Gagne (1♀, USNM). Dominican Republic. San Rafael, 18 km W Barahona, roadside ditch, 28.i.1989, S.A. Marshall (1♀, DEBU), Pedernales, 23.5 km N Cabo Rojo, 18–06 N, 71–38 W, 540 m, 13.–19.vii.1990, L. Masner, J. Rawlins, C. Young, deciduous forest, intercept trap (1♀, CMNH), Pedernales, 26 km N Cabo Rojo, 18–06 N, 71–38 W, 730 m, 13.–25.vii.1990, L. Masner, J. Rawlins, C. Young, wet deciduous forest, intercept trap (1♀, CMNH), Hato Mayor, Parque Los Haitises, 3 km W Cueva de Arena, 19–04 N, 69–29 W, 20 m, 7.–9.vii.1992, R. Davidson, J. Rawlins, S. Thompson, C. Young, mesic lowland forest (2♂, CMNH). Puerto Rico. Mayaguez, M. Wasserman, x.1957 (1♂, USNM).

Comments. *Chaetoclusia furva* is similar in appearance to *C. flava*, but it is distinguished by the derived female genitalia (Fig. 28) and differences in cephalic and notal colouration (see key) (Figs 25, 26). These two species appear to be most closely related to *C. xanthops*, which is also Caribbean in distribution, on the basis of chaetotaxy, colouration, and numerous derived characters of the male genitalia (see Discussion).

PHYLOGENETIC DISCUSSION

Cladistic analysis of the character matrix in Table 2 using PAUP produced three equally parsimonious trees (22 steps in length, CI = 0.82, RI = 0.89), one of which

(Fig. 55) was identical to the strict consensus tree. Synapomorphies of *Chaetoclusia* include a reduction or absence of the anterior lateral scutellar bristles (character 2), setulae along most of vein R₁ (character 3), a reduction of sternites 6 and 7 of the annulus (character 11) and black bristles (character 1; reversed in most species). Excluding *C. richardfreyi*, *Chaetoclusia* is further characterized by the absence of prescutellar acrostichal bristles (character 6), three fronto-orbital bristles and weak to well-developed presutural intra-alar bristles.

The Caribbean species *Chaetoclusia xanthops*, *C. flava*, and *C. furva* comprise a well-supported clade related to the Central American and Ecuadorian species. These three species all have the ocellar bristles minute to absent (shared with *C. bakeri*), a weak presutural intra-alar bristle (also found in several other species of *Chaetoclusia*), a pleuron that is white to yellowish-white, a basal spur on the inner face of the surstylus, a pregonite that is lobate dorsally and somewhat fused to the hypandrium, a curved basiphallus and a distiphallus that is strongly recurved and produced ventrally (characters 5, 6, 7, 10, 13, 14 and 16, respectively). The consensus tree suggests that these Caribbean species plus *C. bakeri* (Central and South America) form a monophyletic group based on a reduction of the ocellar bristles (character 5), and together form the sister-group to *C. centrofasciata* (Ecuador) (Fig. 55), with which they share a loss of the lateral lobes of the distiphallus (character 17). This, however, is poor support for the clade because both of these characters reappear regularly throughout the Clusiidae, particularly within the Sobarocephalinae. We prefer a slightly less parsimonious arrangement in which *C. xanthops*, *C. flava*, and *C. furva* form a monophyletic group with the widespread Central and South American species *C. transversa* based on the presence of minutely spinulose, mediolateral swellings on the distiphallus (character 15), a novel character within the Clusiidae. The latter phylogeny (Fig. 56) is 1 step longer (24 steps) than the most parsimonious trees. *Chaetoclusia longefilata* appears to be most closely related to *C. amplipenis* and *C. inbionella*, as the males share extremely elongate terminalia (character 9) and a minute hypandrial arm (character 12).

DISTRIBUTION

Most species of *Chaetoclusia* appear to have narrow ranges within confined regions of Central America and the Caribbean (maps 1 and 2). Aside from *C. transversa*, which extends from Costa Rica and Panama to Peru, *C. bakeri* is the only species of *Chaetoclusia* to exhibit an extensive neotropical range (map 3).

The phylogenies outlined above (Figs 55, 56) suggest either a Caribbean or South American origin for *Chaetoclusia*, because all Central American taxa belong to a single clade for which Caribbean species form the first two outgroups. Furthermore, it appears as though once *Chaetoclusia* reached Central America from the Caribbean, the genus experienced a successful localized radiation with one lineage extending into Ecuador (*C.*

centrofasciata), and one lineage subsequently returning to the Caribbean (*C. xanthops*, *C. flava* and *C. furva*).

ACKNOWLEDGEMENTS. We would like to thank a number of people for their aid in the preparation of this paper. M. Buck helped with suggestions on earlier versions of this paper, and we are particularly grateful for the hospitality received from D.M. Wood, J.R. Vockeroth, J. O'Hara and J. Cumming at the Canadian National Collection (CNCI). The loan of material from the following institutions and curators is also gratefully acknowledged, for without them, this paper would not have been possible: N. Wyatt (BMNH), C. Young (CMNH), W. Hanson (EMUS), M. von Tschirnhaus (FBUB), M. Zumbado (INBC), U. Kallweit (SMTD), D. Furth and A. Norrbom (USNM) and A. Shatalkin (ZMUM). This study was supported by an NSERC discovery grant to S. Marshall and an OGS grant to O. Lonsdale.

REFERENCES

- BRAKE I. 2000: Phylogenetic systematics of the Milichiidae. *Entomol. Scand. (Suppl.)* **57**: 1–120.
- CALOREN D.C. & MARSHALL S.A. 1998. A revision of the New World species of Clusiodes Coquillett (Diptera: Clusiidae). *Stud. Dipterol.* **5**: 261–321.
- COQUILLETT D.W. 1904: New Diptera from Central America. *Proc. Entomol. Soc. Wash.* **6**: 90–98.
- CZERNY P.L. 1903: Revision der Heteroneuriden. *Wiener Entomol. Ztg* **22**(3): 61–108.
- FREY R. 1960: Studien über indoaustralische Clusiiden (Dipt.) nebst Katalog der Clusiiden. *Comment. Biol.* **22**(2): 1–31.
- GRIFFITHS G.C.D. 1972: *The Phylogenetic Classification of Diptera Cyclorrhapha with Reference to the Structure of the Male Postabdomen*. W. Junk, The Hague, 340 pp.
- HENNIG W. 1938: Beiträge zur Kenntnis der Clusiiden und ihres Kopulationsapparates (Dipt. Acalypt.). *Encycl. Entomol.* **9** (B II): 121–138.
- HENNIG W. 1965: Die Acalypterae des baltischen Bernsteins und ihre Bedeutung für die Erforschung der phylogenetischen Entwicklung dieser Dipteren-Gruppe. *Stuttg. Beitr. Naturk.* **145**: 1–215.
- MALLOCH J.R. 1918: A revision of the dipterous family Clusiodidae (Heteroneuridae). *Proc. Entomol. Soc. Wash.* **20**(1): 2–8.
- MCALPINE J.F. 1989: Phylogeny and classification of the Muscomorpha. In McAlpine J.F. (ed.): *Manual of the Nearctic Diptera, Vol. 3*. Monograph No. 32. Research Branch, Agriculture Canada, Ottawa, pp. 1397–1518.
- MELANDER A.L. & ARGO N.G. 1924: Revision of the two-winged flies of the family Clusiidae. *Proc. U. S. Nat. Hist. Mus.* **64**: 1–54.
- NIXON K.C. 2002: *Winclada, Version 0.9.99.70*. Published by the author.
- PAPP L. 1998: Family Xenasteiidae Papp L. & Darvas B. (eds): *Contributions to a Manual of Palaearctic Diptera. Vol. 3: Higher Brachycera*. Science Herald, Budapest, pp. 305–308.
- PITKIN B.R. & EVENHUIS N.L. 1989: Family Clusiidae. In Evenhuis N.L. (ed.): *Catalog of the Diptera of the Australasian and Oceanian Regions*. Bishop Museum Press and E.J. Brill, Honolulu, pp. 534–536.
- SASAKAWA M. 1977: Family Clusiidae. In Delfinado M.D. & Hardy D.E. (eds): *A Catalog of the Diptera of the Oriental Region*. University Press of Hawaii, Honolulu, pp. 234–239.
- SHATALKIN A.I. 1991: Sobarocephaloides alini sp. n. (Diptera: Clusiidae) – A new species of clusiid flies from Brasil with peculiar cheek processes in male. *Rev. Entomol.* **70**: 928–930.

- Soós A. 1962: New genera and species of Clusiidae (Diptera: Acalyptrata). *Ann. Hist. Nat. Mus. Natn. Hung.* **54**: 135–149.
- Soós A. 1964: Sobarocephaloides discolor gen. n., sp. n., eine neue Clusiidae aus Costa-Rica, nebst einer Bestimmungstabelle der Gattungen der Familie Clusiidae (Diptera: Acalyptrata). *Reichenbachia* **4**(1): 1–8.
- Soós A. 1987: Clusiidae. In McAlpine J.F. (ed.): *Manual of Nearctic Diptera. Vol. 2.* Monograph 28, Research branch, Agriculture Canada, Ottawa, pp. 853–857.
- Swofford D.L. 2003: *Phylogenetic Analysis Using Parsimony*, v. 4.0; Program and documentation. Illinois Natural History Survey, Urbana.
- Williston S.W. 1896: The Diptera of St. Vincent: Heteroneuridae. *Trans. Entomol. Soc. Lond.* (pt. III): 386–389.

Received January 31, 2005; revised and accepted August 1, 2005