Mem. Inst. Oswaldo Cruz, Rio de Janeiro, Vol. *84,* Supl. IV, 365-371 1989

THE TAXONOMIC POSITION OF THE CTENOSTYLIDAE (= LOCHMOSTYLIINAE; DIPTERA: SCHIZOPHORA)

DAVID K. MCALPINE

Australian Museum, Box A285, Sydney South 2000, Australia

It is shown that Ctenostylidae Bigot (1882) is a valid senior synonym of Lochmostylidae Hendel (1935). The morphology of the Ctenostylidae is considered and compared with the Pyrgotidae. It is concluded that the Ctenostylidae are not closely related to the Pyrgotidae, but form an isolated taxon of obscure relationships. Notes on a specimen of Ctenostylum *sp. and a revised key to genera of Ctenostylidae are given.*

Key words: Ctenostylidae – Pyrgotidae – Lochmostyliinae – phylogenetic relationships

The group of acalyptrate flies recently known as Pyrgotidae-Lochmostyliinae is noted for its rarity in collections and for some very unusual features for acalyptrate flies, including vestigial mouthparts, lack of ocelli, viviparity, and very complex branching of the arista in females.

I became interested in this group when Prof. Hugo de Souza Lopes sent me a specimen of *Lochmostylia* on exchange. Further study has indicated that Prof. Lopes (1935) was correct in attributing family status to this group under the name Ctenostylidae.

The genus *Ctenostylum* was first described by Macquart (1851) with the only included species *C. rufum* Macquart from the banks of the Amazon in the collection of J. M. F. Bigot. Bigot (1882) reported further on the type specimen and proposed the tribe Ctenostylidae which he placed next to the Conopidae or Myopidae. The family name Ctenostylidae was further used by Brues et al. (1932) and Lopes (1935).

Hendel (1934) described *Lochmostylia borgmeieri* from Costa Rica as a new genus and species of Pyrgotidae, but later (Hendel, 1935) set up the family Lochmostylidae (sic) for it. Lopes (1935) described a species of the same genus from Brazil, but, being then unaware of Hendel's work, set up for it the genus *Travassomyia* in the family Ctenostylidae. He compared the genus with *Tauroscypson* which Curran (1934) had established in the Pyrgotidae for a species from British Guiana (Guyana). Keiser (1951) reviewed what he termed the subfamily Lochmostyliinae of the Pyrgotidae including the genera *Lochmostylia (= Travassomyia), Tauroscypson,* and the newly described *Ramuliseta* from Lesser Sunda Islands (Indonesia). *Ramuliseta* was subsequently recorded from East Africa (Keiser, 1952) and Brazil (Hennig, 1952), but Aczél (1956) separated the Brazilian *R. plaumanni* Henning in a new genus *Furciseta,* leaving only the Old World species in *Ramuliseta.*

The position of the above-mentioned genera has been a source of diverse opinions but the recent tendency has been to place them in the subfamily Lochmostyliinae of the Pyrgotidae (superfamily Tephritoidea).

Family group names based on *Ctenostylum* have been rejected (e. g. by Steyskal, 1967) because no authentic material of that genus has been available, and some features mentioned by Macquart have not seemed reconcilable with the characters of Lochmostyliinae. In fact the arrangement of the ocelli as given by Macquart (1851) for *Ctenostylum,* a pair in front and an odd one behind, does not agree with any known dipteran. I have been satisfied for some time that Macquart's description and figure of *Ctenostylum rufum,* though inaccurate in detail, could only refer to the male of some otherwise unknown lochmostyliine. Recent discovery of a male of *Ctenostylum* confirms this viewpoint.

My study of the abdominal morphology of several species of this group led to the conviction that they are not closely related to the

Pyrgotidae, nor can they be referred to any other recognized family of Diptera.

In the succeeding treatment I use the family name Ctenostylidae to cover the genera *Ctenostylum* Macquart, *Tauroscypson* Curran, *Lochmostylia* Hendel, *Ramuliseta* Keiser, and *Furciseta* Aczél.

MORPHOLOGY AND COMPARISON WITH PYRGOTIDAE

Chaetotaxy – The chaetotaxy of the Ctenostylidae is characterised by a degree of reduction but otherwise shows little that is remarkable. It might be considered derivable by reduction from that of a generalised pyrgotid (or from patterns existing in numerous other fly families), except that in *Furciseta* the fronto-orbital series of bristles is more developed than in the Pyrgotidae.

Ocelli – Absence of ocelli has often been considered diagnostic or at least generally characteristic for the Pyrgotidae, particularly by workers on the fauna of Europe and North America. In the southern hemisphere there are many pyrgotid species with the ocelli perfectly developed or in various stages of reduction, and these (including some with perfect ocelli) are of quite diverse relationships within the family. It is clear, then, that ocelli are present in the pyrgotid groundplan and that reduction has taken place in several lineages. Outside the Pyrgotidae very few fully winged acalyptrates lack ocelli, but some individuals of the African platystomatid genus *Bromophila* are without them, as are some conopids. All known ctenostylids (including *Ctenostylum*) lack ocelli, but unless the group can be shown to have a particular phylogenetic affinity to a group of pyrgotids without ocelli, this feature is at best ambiguous evidence of relationship to Pyrgotidae. No such particular affinity seems to have been proposed and I have not found evidence for any.

Head structure – Sexual dimorphism of the head in Ctenostylidae may affect eye size, facial structure, and antennal structure. In *Furciseta* the eyes are very much larger in the male than in the female, the anterior eye facets are enlarged, and the postfrons is narrowed to accommodate the eyes. The male of *Ctenostylum* is similar in these respects to that of *Furciseta*, and, though the female is unknown, similar sexual dimorphism is to be expected. The face of female ctenostylids generally has a median sclerotized zone more or less differentiated from lateral zones which are transparent and, though apparently membranous, do not collapse in dried material. In females of *Lochmostylia* and *Tauroscypson* the transparent lateral zones are very large, whereas in males they are narrower and less strongly differentiated. I have seen no modification of the face comparable to this in any pyrgotid. Among pyrgotids available to me, only *Prodalmannia* has the head noticeably sexually dimorphic, the postfrons of the male being much narrowed. *Prodalmannia* does not otherwise show special resemblance to ctenostylids, and its male lacks the enlarged anterior eye facets seen in male ctenostylids with narrowed postfrons. Examples of narrow-fronted males occur widely but infrequently among the acalyptrate families, and the condition is liable to repetition by convergence.

The Ctenostylidae are characterized by the vestigial condition of the proboscis. The maxillary palpus is distinct in some forms, but is generally very small. This probably indicates that adult ctenostylids do not ingest any form of food.

The arista – In females of Ctenostylidae (female of *Ctenostylum* unknown) the arista is very complex. It always has complex more or less dendritic branching and never has a single main axis with one or more longitudinal series of hair-like branches as, for instance, in *Drosophila*. The known males always have a simpler type with a main axis which may be almost bare *(Lochmostylia)*, or short-haired *(Tauroscypson* and *Furciseta)*. *Ctenostylum* has the most complex arista known for a male ctenostylid (Fig. 6). It has a main axis with a number of dorsal pectinate branches, which are themselves branched. In a specimen of *Ramuliseta* there is "no arista, not even a vestige or insertion point" (G. A. Holloway personal communication, based on specimen from Bwamba Pass, Uganda, (Natural History Museum, London)). If this condition can be confirmed from other material, it would constitute a very remarkable sexual dimorphism. In none of the available ctenostylids can I discern any basal segmentation of the arista, but I have not examined cleared material under a compound microscope.

Pyrgotids have a simple arista, generally with only very short hairing or pubescence, and usually consisting of 3 visible segments (antennal segments 4-6), with segment 4 very short, but sometimes having it almost as long as segment 5 (some *Cardiacera* spp.).

The prosternum – The ctenostylid prosternum is very broadly trapezoid (at least twice as broad as long) and very convex. The form of the prosternum is variable in the Pyrgotidae but I have found no approach to the ctenostylid condition in any pyrgotid. Usually the prosternum of pyrgotids is longer than broad and none of the types I have seen is markedly inflated.

The wing – The wing of ctenostylids shows several of the characteristic features of pyrgotids. Vein 1 is setulose above, vein 7 is visible well beyond the alula, and the membrane has a pattern of pigmentation. Most pyrgotids have the anal cell (cell CuP) produced into a short acute lobe posterodistally, but this lobe is absent in ctenostylids. Patterned wings are frequent in several other families of Schizophora, but particularly in the tephritoid families Otitidae, Platystomatidae, and Tephritidae.

In male ctenostylids vein 4 is incomplete basally leaving the second basal cell open anteriorly (Fig. 8). In females this vein is complete or nearly so (Hennig, 1952, Figs. 8, 9). I am not aware of similar sexual dimorphism in any other dipterous family.

Ctenostylids share with most acalyptrate flies the absence of a squama or lower calypter attached to the thorax on the posterior side of the wing base. However, in some pyrgotids the squama is developed into a distinct but short lobe, and in many taxa of the related family Platystomatidae it is greatly developed.

Abdominal sternite 1 – Probably the two major alliances in the Pyrgotidae are to be distinguished from the condition of abdominal sternite 1. In the genera *Teretrura* Bigot, *Maenomenus* Bezzi, *Prodalmannia* Bezzi, *Frontalia* Malloch, and perhaps other genera, sternite 1 is well developed, fully sclerotized, and separate from sternite 2. These genera are here considered to constitute the subfamily Tereturinae in a revised sense. In the vast majority of pyrgotid genera and species (here regarded as the subfamily Pyrgotinae, including Toxurinae) sternites 1 and 2 are fused into one large sclerite (see Colless et al., 1970, Fig. 34.28F). In the Ctenostylidae, sternite 1 is free from sternite 2 and is reduced to an X- or V-shaped sclerite (Figs. 1, 2). In this feature they fit neither of the pyrgotid subfamilies.

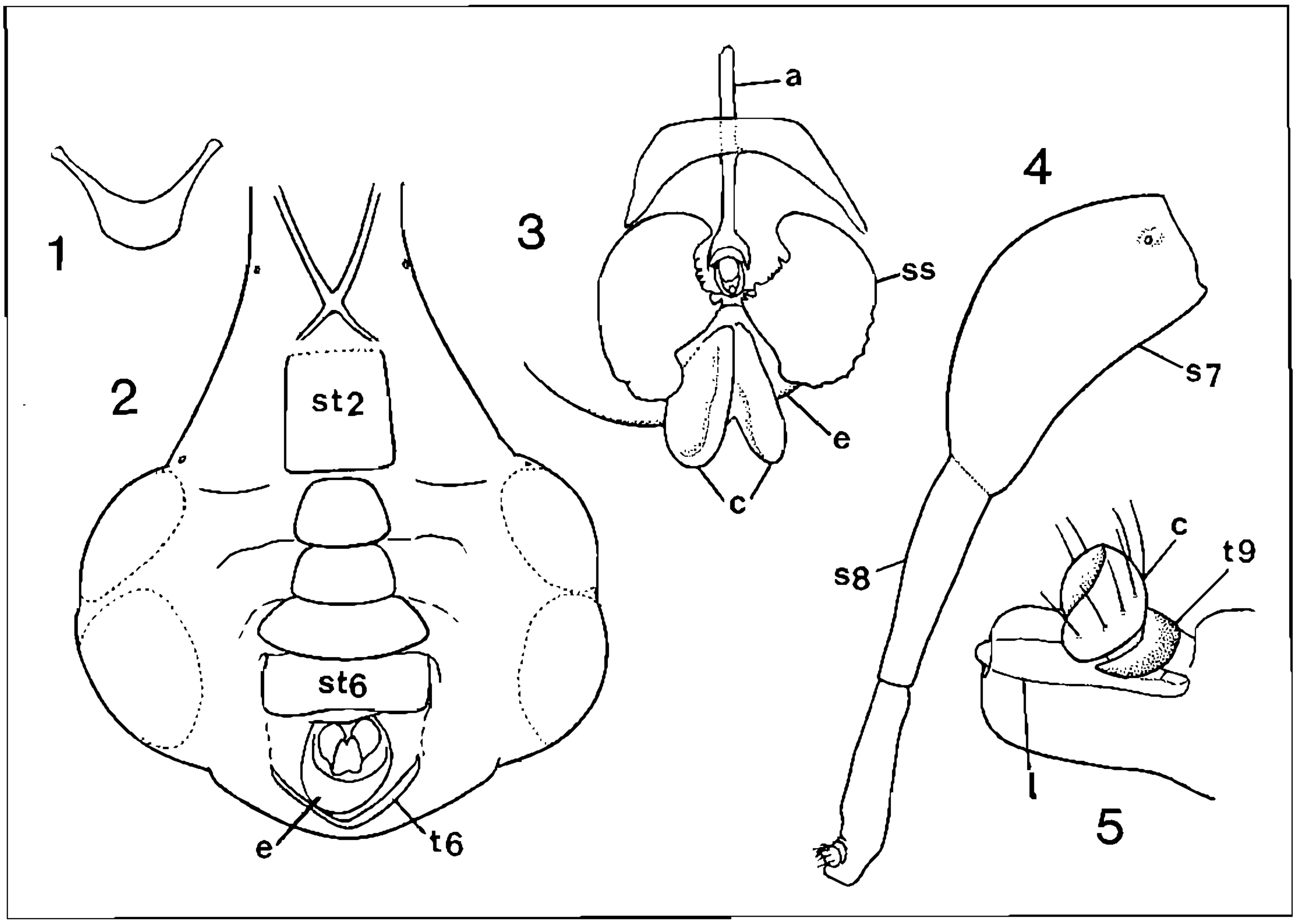
Female postabdomen – The abdomen of female ctenostylids (Figs. 4, 5) resembles that of pyrgotids in having segment 7 enlarged, with tergite and sternite fused to form a more or less posteriorly tapered tube, into which the terminal structures can be withdrawn. In all pyrgotid genera I have examined, the terminal abdominal structures are fused to form a well sclerotised, lance-like aculeus, at the end of a long, soft, eversible, tubular structure formed largely from segment 8. Though situated at the end of an eversible tube, the terminal structure in ctenostylids is, where known, quite different. There are 2 sclerotized parts, a more proximal dorsal sclerite which appears to represent tergite 9, and a distal sclerite, also open ventrally, which is short, convex, setulose, and quite blunt, and appears to represent the fused cerci surmounting the proctiger.

The presence of first-instar larvae in the oviduct of both *Lochmostylia* (Lopes, 1935) and *Tauroscypson* (my Fig. 5) is of great interest and indicates that viviparity (including oviviparity) may be an attribute of the Ctenostylidae in general. Viviparity, though common among calyptrate Diptera, seems to be very infrequent among acalyptrates. The heleomyzid *Dichromya sanguiniceps* (Wiedemann) is another viviparous acalyptrate (Hennig, 1971).

Male postabdomen – I have examined postabdominal structures in the male of *Lochmostylia* (Figs. 2, 3) and a less perfect example of *Tauroscypson*.

The protandrium is symmetrical, with segment 6 represented by well developed, quadrate tergite and sternite, and there are no sclerites representing segments 7 and 8 (Fig. 2). Typical pyrgotids, on the other hand, have no distinct tergite 6, sternites 6 and 7, when present, are asymmetrically placed on the left side, and sternite 8 is a large, convex dorsal sclerite (Crampton, 1942, Fig. 121).

The ctenostylid epandrium supports a pair of short, broad surstyli, articulating loosely with its lateral margins, but has no other marginal lobes. The epandrium of typical



Abdominal structures of Ctenostylidae. Fig. 1: *Furciseta plaumanni* (Hennig), abdominal sternite 1. Fig. 2: *Lochmostylia borgmeieri* Hendel, ventral view of ♂ abdomen. Fig. 3: ventral view of ♂ genital segment of same. Fig. 4: *Tauroscypson* sp., ♀ postabdomen. Fig. 5: apex of ♀ abdomen of same. c, cerci. e, epandrium. l, young larva. s7-s8, segment 7 to segment 8. st2-st6, sternite 2 to sternite 6. t5-t9, tergite 5 to tergite 9, a, aedeagal apodeme, ss, surstylus.

pyrgotids is produced on each side into a large, rigid lobe (the outer surstylus of McAlpine, 1973), which ensheaths the articulated, but not very mobile, inner surstylus.

In the Ctenostylidae the aedeagus is extremely short and almost papilliform, in contrast to the very elongate, coiled or looped aedeagus of typical Pyrgotidae. However, *Commoniella* is undoubtedly a true pyrgotid (subfamily Pyrgotinae), but has a very short aedeagus.

DISCUSSION OF RELATIONSHIPS

Ctenostylids have often been taken for somewhat modified pyrgotids because they possess certain characters of that family, viz.: absence of ocelli; a series of setulae on vein 1; an enlarged subcylindrical female abdominal segment 7 with totally fused tergite and sternite, into which the more posterior segments can be telescoped; general body form and proportions resembling those of typical pyrgotids, together with marked pigmentation pattern of the wings. Certain peculiarities of ctenostylids might be interpreted as autapomorphies, which would not disprove their derivation from a more plesiomosphic pyrgotid ancestor. These peculiar features would include the vestigial mouth-parts, the sexually dimorphic antennae and wing venation, the facial structure, the shape of the prosternum and abdominal sternite 1, the reduction of the aedeagus, and viviparity. The postabdominal structures in both sexes of the Ctenostylidae cannot, however, be explained in these terms.

The female terminal structures which I interpret as a separate tergite 9 and the fused cerci do not appear derivable from the single terminal structure (aculeus) of the Pyrgotidae. Furthermore the compound aculeus has not been acquired within the evolutionary development of the Pyrgotidae, but apparently was present before the Pyrgotidae and other families of Tephritoidea became differentiated. The female terminal structures of Ctenostylidae therefore tend not only to remove the ctenostylids from the Pyrgotidae, but also to throw serious doubt on their position in the superfamily Tephritoidea.

The males of Pyrgotidae and other families of higher Tephritoidea or Tephritoidea s. str. (as defined by Steyskal, 1961; McAlpine, 1973) have a very characteristic arrangement of the protandrial sclerites, which apparently became stabilised in an early ancestral form. I consider it most improbable that the ctenostylid protandrium could be derived from that of typical tephritoids, among which the Pyrgotidae undoubtedly belong (McAlpine, 1973). This development would entail the addition of a complete, symmetrical segment 6 with both tergite and sternite, from a form with the sclerites of segment 6 reduced to the vestigial, lateral sternite attached to sternite 7 + 8. I have interpreted approximate symmetry of segment 6 as a secondary derivation from asymmetrical types in the Heleomyzidae and Neurochaetidae (McAlpine, 1985; 1988), but this interpretation does not involve an evolutionary saltation from such a highly advanced and stabilised type as the transition from typical tephritoid to ctenostylid.

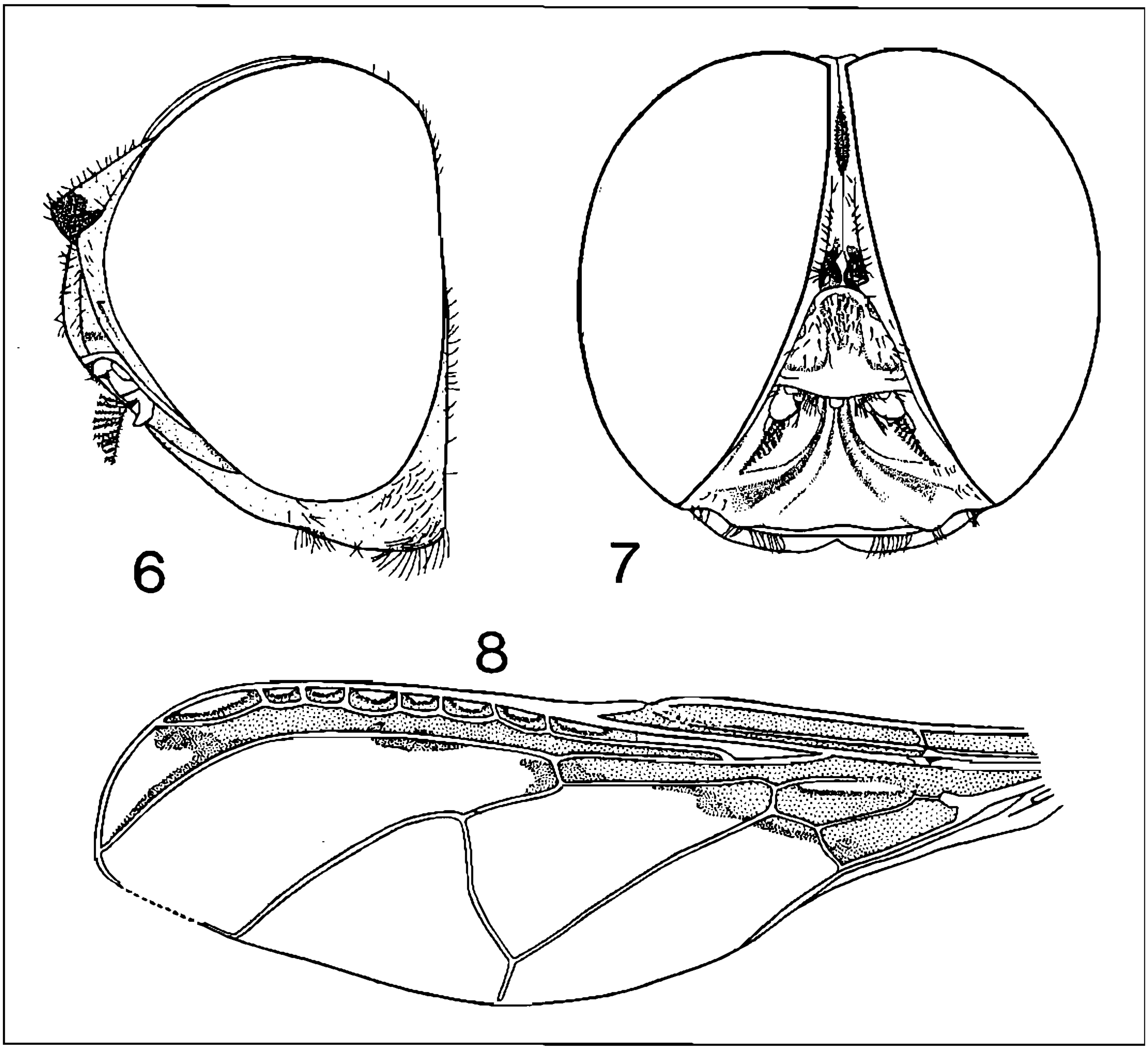
If the Ctenostylidae do not belong in the superfamily Tephritoidea s. str., an alternative solution to the question of their relationships becomes a desideratum. The presence of a long visible vein 7 (2A or A2) in most ctenostylids is a plesiomorphic character for the Schizophora, and appears to indicate that they are not closely related to taxa included in those superfamilies which uniformly lack any manifestation of vein 7 beyond the alula. Using the classification of Colless et al. (1970, modified by Colless et al., 1975, and now updated in nomenclature), vein 7 extends beyond the alula in numerous representatives of the superfamilies Sciomyzoidea, Heleomyzoidea, Tephritoidea, Chloropoidea (Milichioidea), and Muscoidea (Calyptrata), but appears to be uniformly absent beyond the alula in the Diopsoidea (Tanypezoidea), Nerioidea (Micropezoidea), Asteioidea, Opomyzoidea, and Agromyzoidea. Excluding the second group of superfamilies from further consideration, I am unable to find any evidence, in the form of distinctive shared apomorphies, for close relationship to the Sciomyzoidea and Heleomyzoidea, and the distinctive features of the Chloropoidea and Muscoidea are quite absent in the Ctenostylidae.

Despite the fundamental differences from the Tephritoidea, the resemblances of Ctenostylidae to this superfamily are the only possible indications of affinities which have yet come to light. These resemblances may not, however, be significant if they are points of convergence with certain more advanced taxa of the superfamily.

I summarise my conclusions on ctenostylid relationships as follows: (1) The Ctenostylidae are not closely related to the Pyrgotidae. (2) There is no available evidence for relationship of Ctenostylidae to any schizophoran superfamily other than the Tephritoidea. (3) Indications of relationship to the Tephritoidea are at best ambiguous. (4) For reference purposes the Ctenostylidae may be listed under the Tephritoidea, until they can be shown either to have a particular relationship to another schizophoran taxon, or to be so isolated phylogenetically as to need their own superfamily.

KEY TO GENERA OF CTENOSTYLIDAE

1. Marginal cell with 2 or more crossveins connecting costa to vein 1; frontal lunule deep, haired 2
   Marginal cell without crossveins; frontal lunule reduced to a transversely narrow; bare strip 3
2. Palpus present; wing with alula and anal lobe moderately developed; ♂: postfrons not narrowed; arista simple. . . . *Tauroscypson*
   Palpus absent; wing basally narrowed, without alula and anal lobe; ♂: postfrons much narrowed; arista pectinate. . . . . *Ctenostylum*
3. Face with broad flat central plate; palpus absent; veins 3 and 4 distally convergent; size larger, wing over 6 mm long. . . . . *Lochmostylia*
   Face with weakly elevated median carina; palpus present; veins 3 and 4 not distinctly convergent; size smaller, wing under 6 mm long .4
4. Incurved anterior fronto-orbital bristles present, at least in ♀; arista of ♀ with 2 ciliate branches; arista of ♂ unbranched; vein 6 not reaching wing margin; Neotropical Region . . . . *Furciseta*
   Anterior fronto-orbital bristles absent; arista of ♀ with numerous ciliate branches; arista of ♂ absent (? consistently); vein 6 reaching wing margin or almost so; Old World tropics . . . . *Ramuliseta*



Ctenostylum sp., male from la Suiza, Costa Rica. Fig. 6: head, lateral view. Fig. 7: head, anterior view. Fig. 8: wing.

Ctenostylum sp.
(Figs 6-8)

The available specimen is apparently the only representative of the genus known, apart from the lost type of *Ctenostylum rufum* Macquart. It is impossible to decide if it is an example of *C. rufum*, because (1) Macquart's description is not very detailed and his illustrations are always inaccurate, (2) the new specimen is from Costa Rica, whereas the type was from the banks of the Amazon, (3) without series of specimens of *Ctenostylum* one cannot descriminate between individual variation and specific characters.

DESCRIPTIVE NOTE. MALE – General coloration brownish; thorax paler ventrally; legs fulvous. *Head* nearly as bulky as thorax; postfrons very narrow, particularly towards vertex, with deeply incised median line and blackish bifid prominence anteriorly; ocelli absent; frontal lunule large, subtriangular, subshining finely setulose; antennal sockets separated by a node-like carina; face with pair of grooves, which converge near antennal sockets; eye very large, with facets on ventral third smaller than those on rest of eye. *Antenna* very short; segment 1 broad, somwhat bilobed; segment 2 attenuated basally, with small basal dorsal fascicle of setulae; segment 3 with deep depression in which arista is inserted; arista pectinate, with about 10 dorsal branches, some of which are forked; both main rachis and branches with numerous hairs. Proboscis and palpus apparently absent. *Thorax* without strong bristles; mesoscutum with numerous short decumbent setulae, and erect supra-alar tuft of dense dark setulae; notopleural region bare; scutellum with numerous setulae dorsally, and a tuft of dense, dark setulae on each side of centre; humeral callus, posterior part of mesopleuron, and part of pteropleuron and sternopleuron setulose. Legs elongate; tibiae basally attenuated, without apical spurs; fore tarsus more slender than, hind tarsus stouter than mid tarsus. *Wing* much narrowed basally, without alula; with anterior yellowish brown to darker brown zone as illustrated; costa extending to vein 4; vein 1 with sparse, weak setulae; marginal cell with 7 crossveins. Abdomen clavate, much as in *Lochmostylia.*

Material examined. COSTA RICA: La Suiza, no date, 1 ♂, P. Schild (National Museum of Natural History, Washington).

ACKNOWLEDGEMENTS

To the following for assistance or sending material: P. Arnaud Jr., D. H. Colless, W. D. Duckworth, G. A. Holloway, R. de Keyzer, H. de S. Lopes, A. L. Norrbom.

REFERENCES

ACZÉL, M., 1956. Revisión parcial de las Pyrgotidae neotropicales y antarcticas, con sinopsis de los géneros y especies (Diptera, Acalyptrate). *Rev. Brasil. ent., 4:* 161-184, 5: 1-70, 6: 1-38.

BIGOT, J. M. F., 1882. Diptères nouveaux ou peu connus. 19e partie. *Ann. Soc. Ent. France, 1882:* 5-22.

BRUES, C. T. & MELANDER, A. L., 1932. Classification of insects. *Bull. Mus. comp. Zool., 73:* 1-672.

COLLESS, D. H. & MCALPINE, D. K., 1975. Diptera. p. 656-740. In *The insects of Australia.* Melbourne University Press, Melbourne.

COLLESS, D. H. & MCALPINE, D. K., 1970. Diptera. p. 91-96. *The insects of Australia.* Supplement 1974. Melbourne University Press, Melbourne.

CRAMPTON, G. C., 1942. The external morphology of the Diptera. *Bull. Conn. geol. nat. Hist. Surv., 64:* 10-165.

CURRAN, C. H., 1934. The Diptera of Kartabo, Bartica District, British Guiana, with descriptions of new species from other British Guiana Localities. *Bull. Amer. Mus. nat. Hist., 66:* 287-532.

HENDEL, F., 1934. ÜBERSICHT über die Gattungen der Pyrgotiden nebst Beschreibung neuer Gattungen und Arten. *Encycl. ent. (B, II), 7:* 111-156.

HENDEL, F., 1935. *Bemerkungen zu "The families and genera of North-American Diptera",* by C. H. Curran, New York, 1934. *Konowia, 14:* 51-57.

HENNIG, W., 1952. Bemerkenswerte neu Acalyptraten in der Sammlung des Deutschen Entomologischen Institutes (Diptera: Acalyptrata). *Beitr. Ent., 2:* 604-618.

KEISER, F., 1951. Die Unterfamilie der Lochmostyliinae (Dipt., Pyrgotidae). *Mitt. Schweiz. ent. Ges., 24:* 113-124.

KEISER, F., 1952. *Ramuliseta lindneri* n. sp. eine Lochmostyliine aus Ostafrika (Dipt. Pyrgotidae). *Bonn. zool. Beitr., 3:* 325-327.

LOPES, H. de S., 1935. Um novo gênero de Diptera Acalyptratae e considerações sobre a família Ctenostylidae. *Arch. Inst. Biol. Veget., 2:* 247-253.

MACQUART, P. J. M., 1851. Diptères exotiques nouveaux ou peu connus. Suite du 4e supplement. *Mem. Soc. Nat. Sci. Agric. Arts Lille, 1850:* 134-294, pls 15-28.

MCALPINE, D. K., 1973. The Australian Platystomatidae (Diptera, Schizophora) with a revision of five genera. *Mem. Aust. Mus., 15:* 1-256.

MCALPINE, D. K., 1985. The Australian genera of Heleomyzidae (Diptera: Schizophora) and a reclassification of the family into tribes. *Rec. Aust. Mus., 36:* 203-251.

MCALPINE, D. K., 1988. Studies in upside-down flies (Diptera: Neurochaetidae). Part II. Biology, adaptations, and specific mating mechanisms. *Proc. Linn. Soc. N. S. W., 110:* 59-82.

STEYSKAL, G. C., 1961. The genera of Platystomatidae and Otitidae known to occur in America north of Mexico (Diptera, Acalyptratae). *Ann. Ent. Soc. Amer., 54:* 401-410.

STEYSKAL, G. C., 1967. 56. Family Pyrgotidae. p. 1-8. In *A catalogue of the Diptera of the Americas south of the United States.* Secretaria da Agricultura, São Paulo.