Cratomyia macrorrhyncha, a Lower Cretaceous brachyceran fossil from the Santana Formation, Brazil, representing a new species, genus and family of the Stratiomyomorpha (Diptera)

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A new fossil Brachycera (Diptera), *Cratomyia macrorrhyncha* gen. n. & sp. n. is described from the Santana Formation, Lower Cretaceous, situated on the Araripe Basin (Northeastern Brazil). Its remarkable features are the large body size, very long proboscis, antenna with multi-articled flagellum, robust thorax and abdomen, and wing characters like the abbreviated costal vein, distally forked veins R_{4+5} and M_{1+2}, strongly arched M_1, and closed cells m_3 and cup. The new genus and species does not reasonably fit in any of the existing families and a new family, Cratomyiidae is proposed. The systematic position of the family is discussed. Reasons are given for not including it in the following higher taxa of Brachycera: Xylophagomorpha, Tabanomorpha, Vermileonomorpha, Asilomorpha, and Eremoneura. The Cratomyiidae are included in Stratiomyomorpha as the sister-group of Xylomyidae + Stratiomyidae, above the origin of Pantophthalmidae.

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Introduction

Systematists attempt not only to describe existing diversity, but also to understand its historical origin. In a phylogenetic context, this means recovering the phylogenetic relationships among known taxa. Systematic knowledge gradually increases as a result of better understanding of the known species, and by discovery and description of new species, living as well as fossil. The fossil record in particular may bring many-sided evidence about the otherwise hidden temporal dimension of evolution. See Grimaldi & Cumming (1999) for a summary of the potential virtues of fossils.

Our knowledge about Cretaceous brachyceran Diptera is relatively scanty, though important data from different sources have recently been made available through the works of Grimaldi (1990) and Grimaldi & Cumming (1999). The present paper adds a new piece of information by dealing with a new, very distinctive and well-preserved brachyceran fossil from the Lower Cretaceous. It comes from the Santana Formation situated in the Araripe Basin, NE Brazil, a deposit of Lower Cretaceous age with abundant fossils. Hitherto, twelve species of fossil Diptera have been described therefrom, four of them belonging to the Brachycera, viz. three Asilidae and one doubtful Therevidae (see Grimaldi 1990).

We describe below a new fossil genus and species of Brachycera, *Cratomyia macrorrhyncha* gen. n. & sp. n. based on two rather well preserved specimens collected at the Fazenda Tatajuba, near Santana do Cariri (see Martins-Neto 1996). The species cannot be included in any of the described recent or extinct families of Diptera. We consequently propose a new family for it. Also, we address the systematic position of the new taxon within the Brachycera.

The Araripe Basin and Santana Formation

The Araripe Basin ranges over the limits of three Brazilian States: Piaui, Pernambuco and Ceará. It

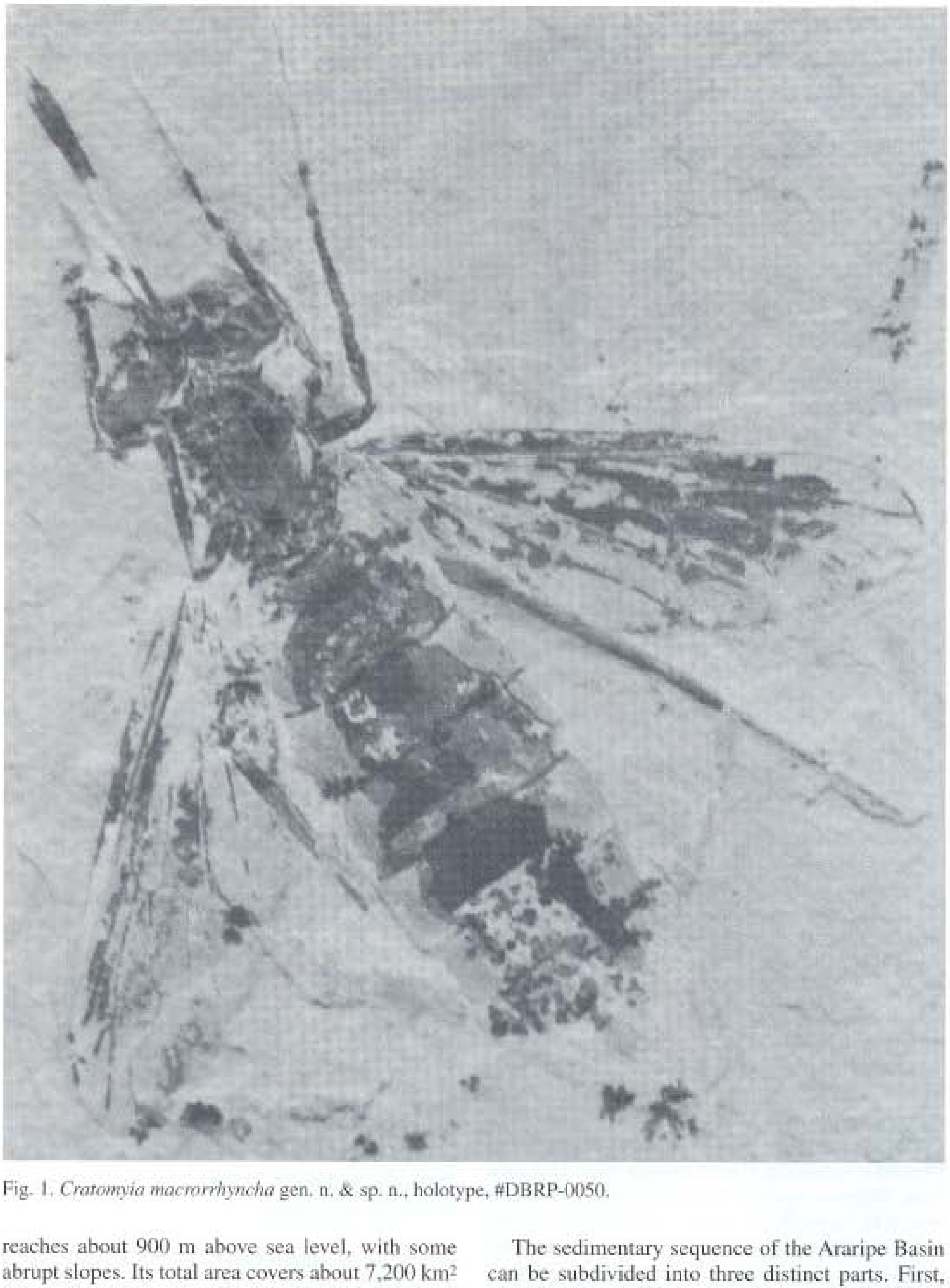

Fig. 1. *Cratomyia macrorrhyncha* gen. n. & sp. n., holotype, #DBRP-0050.

reaches about 900 m above sea level, with some abrupt slopes. Its total area covers about 7,200 km² of subrectangular shape, elongated on the east-west axis and some 180 km long and 40 km wide.

The sedimentary sequence of the Araripe Basin can be subdivided into three distinct parts. First, there is a 'pre-rift' sequence made up by the Cariri Formation. Second, there is a 'rift' sequence repre-

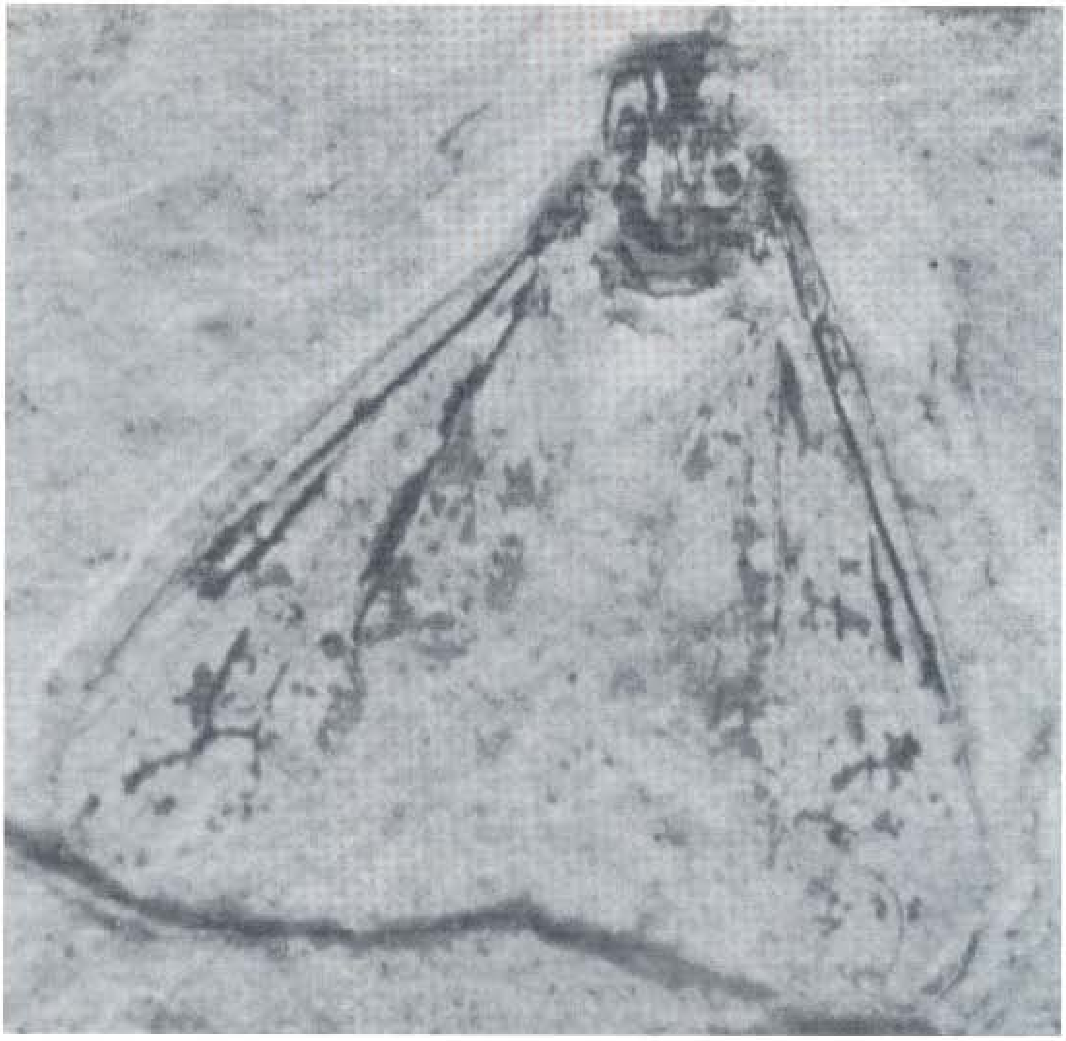

Fig. 2. *Cratomyia macrorrhyncha* gen. n. & sp. n., paratype, #DBRP-0051.

sented by the Brejo Santo, Missão Velha and Rio Batateiras Formations. Finally, there is a 'post-rift' sequence made up by the Santana and Exu Formations.

The material studied here comes from the lamellate calcareous level, the upper part of the Crato Member, which is the Santana Formation's lowest component. The fine sediments at this level are of continental lake origin and material conservation indicates a slow transport. The Araripe paleo-lake was formed after the separation of South America and Africa by continental drift. The age of this formation is lies between the Upper Aptian and the Lower Albian of the Lower Cretaceous. It is characterized by an abundant fossil record along its height of 200 m. Fossil diversity is very high, including both vertebrates, invertebrates and plants. The known invertebrates groups include Bivalvia and Gastropoda (Mollusca), Echinoidea (Echinodermata), Crustacea, Arachnida, and Insecta (Arthropoda). Major diversity occurs in the insects. Hundreds of thousands of fossil specimens have been collected so far, representing Ephemeroptera, Odonata, Dermaptera, Isoptera, Homoptera, Hymenoptera, Neuroptera, Raphidioptera, and Diptera. Twelve specimens of Diptera from the Santana

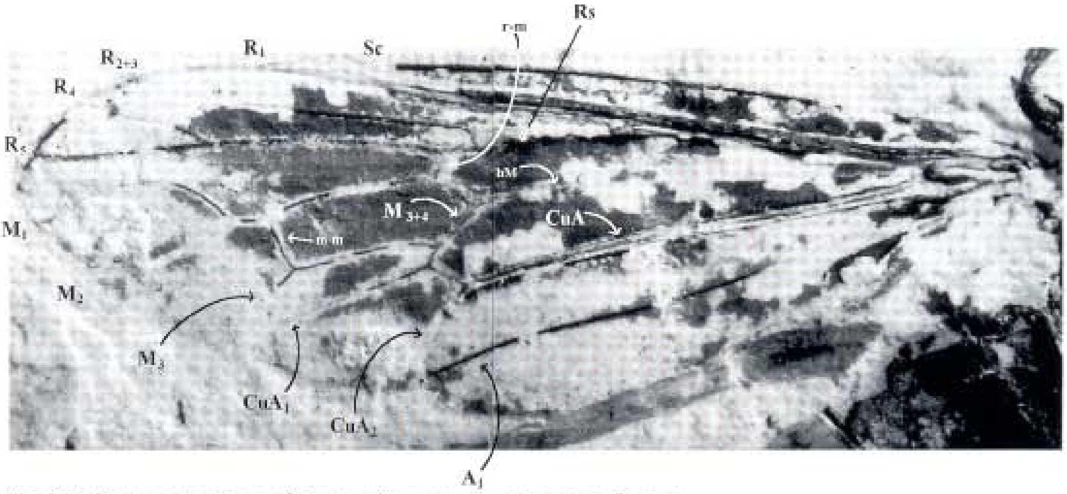

Fig. 3. Left wing of holotype of *Cratomyia macrorrhyncha* gen. n. & sp. n.

formation have been referred to the Tipulidae, Chironomoidea, Bibionidae, Mycetophilidae, Sciaroidea, Tabanidae, Asilidae, and doubtfully to the Therevidae (for details, see Grimaldi 1990, Martins-Neto 1994).

Family **CRATOMYIIDAE fam. n.**

Genus ***Cratomyia* gen. n.**

***Cratomyia macrorrhyncha* sp. n.**

(Figs 1-8)

Material examined. – Holotype, MZUSP; paratype, FFCLRP/USP, #DBRP-0051.

Description. – Head. Present only in the holotype (Fig. 1), which is preserved with the head rotated 180°. The head is large, flattened posteriorly, with large eyes (Fig. 6). No signs of conspicuous ocular setae can be observed. Proboscis well developed, at least three times longer than the head, with an apical enlargement (Figs 6, 7c). Maxillary palpus possibly 2-segmented, long, almost one-fourth the length of the proboscis (Figs 6, 7c). Antenna long (only distal part visible), rather slender, with a clearly multi-articulated flagellum (Figs 7c, d).

Thorax. Large, robust, about twice as long as wide (Figs 1, 2). Scutellum differentiated. Mediotergite well-developed. No visible sign of insertion

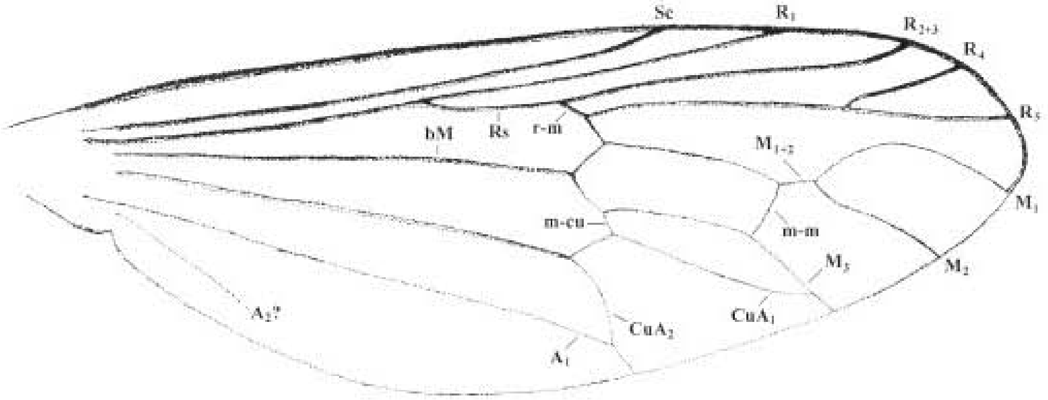

Fig. 4. Wing venation of *Cratomyia macrorrhyncha* gen. n. & sp. n. reconstructed on basis of right and left wings of the holotype and paratype.

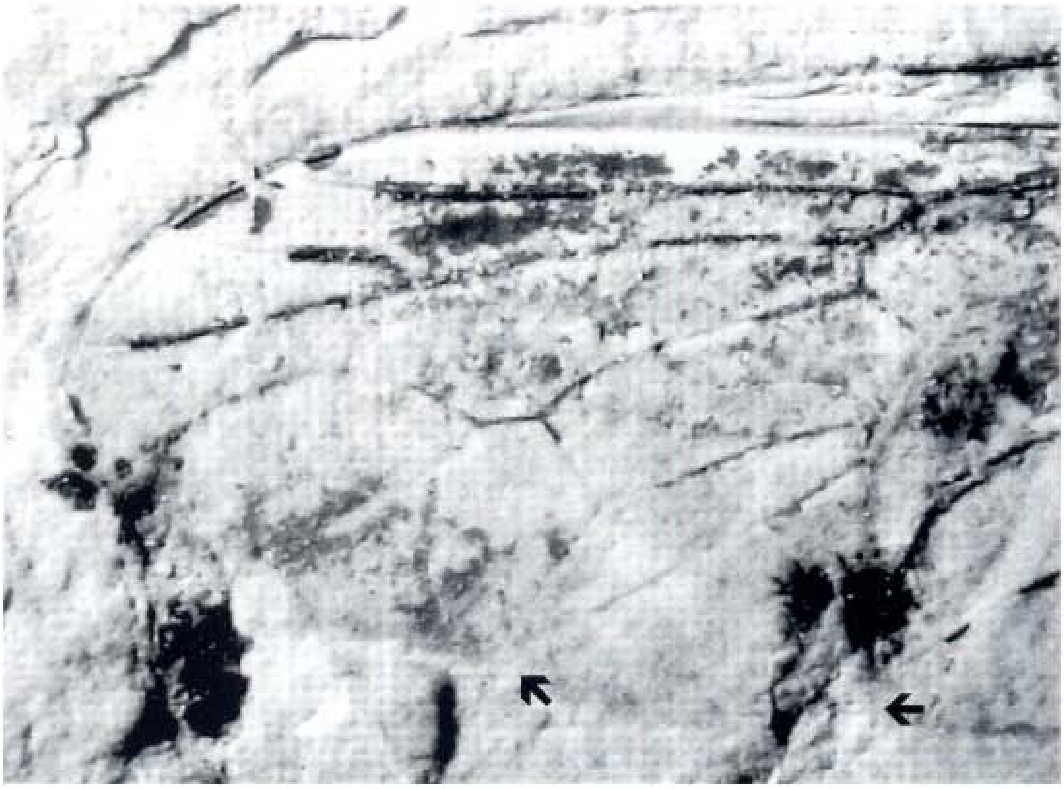

Fig. 5. Apex of left wing of the holotype of *Cratomyia macrorrhyncha* gen. n. & sp. n. Arrows indicate fusion of M_3 to CuA_1 and CuA_2 to A_1.

of large setae or spines. Legs well developed, femora appearing relatively short, tibiae longer and more delicate (Fig. 1). Tibiae with very well preserved dense setae, spurs not visible (Figs 7a, b).

Wing. Large, with dark brown pigmentation (Figs 3-5). Vein C apparently ending between M_1 and M_2. Sc complete, long, ending close to R_1. R_{2+3} well developed, unforked, reaching the wing margin closer to R_4 than to R_1. R_4 forking from R_{4+5} rather apically, nearly straight from origin to margin. R_5 reaching the wing margin before the wing apex. Origin of Rs in basal half of the wing, R_{2+3} originating closer to r-m than to base of Rs. Cross-vein r-m at the basal fourth of the discal cell. M_{1+2} with a distinct petiole, M_1 strongly arched forward. Cross-vein m-m fused, M_3 connected to CuA_1 before the wing margin. Cross-vein bm-cu produced just below r-m, fusing right to CuA_1. Medial and cubital forks rather apical, beyond the middle of the wing. A_1 well developed, connected to CuA_2 apically, before the wing margin, closing cell cup. CuP clear.

Abdomen (only present in the holotype, Fig. 1). Large, robust, slightly wider than thorax, about twice as long as wide. Seven well-developed tergites entirely covered in short setae (Fig. 8), first tergite about half as long as each of the following five tergites, hind margin of terminal seventh tergite obtusely rounded.

Measurements. Entire body (with proboscis) 24.0 mm; proboscis 7.0 mm; head (without proboscis) 1.5 mm long, 5.0 mm wide; thorax 4.5 mm long, 3.0 mm wide; abdomen 11.0 mm long, 5.5 mm wide; wing 12.0-13.5 mm long, 3.5-4.0 mm wide.

Comments on the basal phylogeny of Brachycera and the position of *Cratomyia*

In recent years, important advances have been

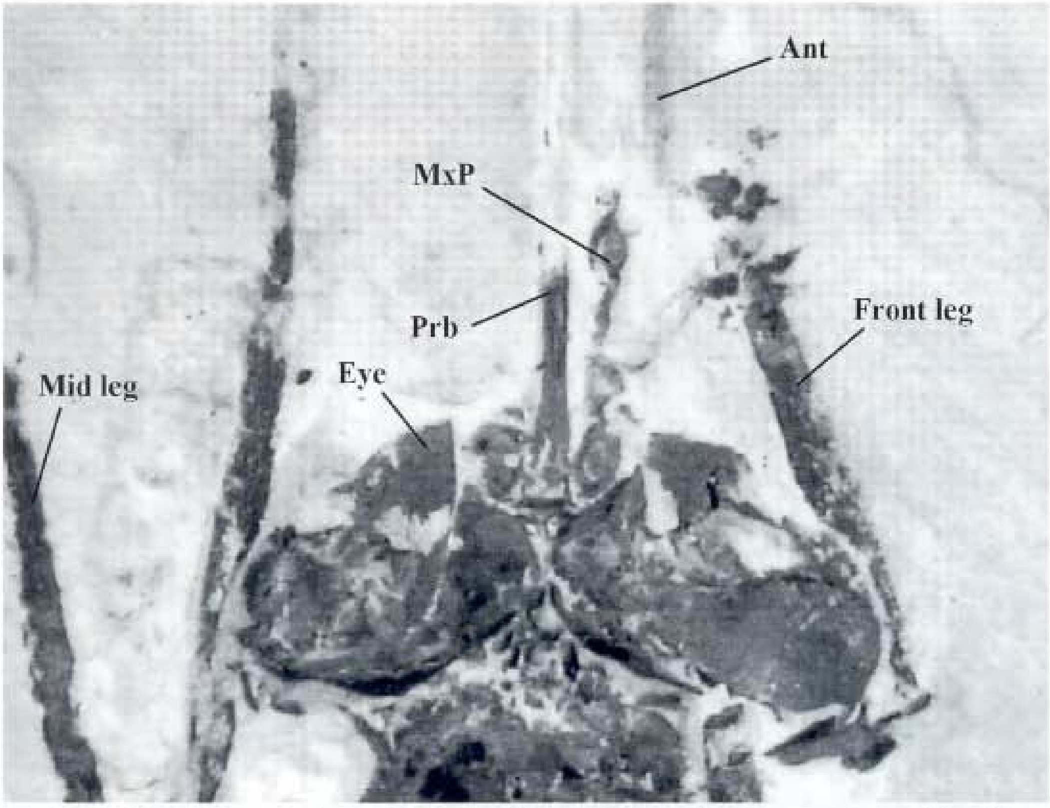

Fig. 6. Parts of head and anterior legs of the holotype of *Cratomyia macrorrhyncha* gen. n. & sp. n. Abbreviations: Ant = antenna, Prb = proboscis, MxP = maxillary palp.

made to the understanding of the basal phylogeny of the Brachycera, but there is still considerable conflict between different proposed schemes. The first phylogeny proposed for the group is that of Hennig (1954), slightly updated in Hennig (1973), and it stood for a long time as the only attempt to understand the basal relationships of the group.

More recently, Woodley (1989) presented a new hypothesis for the higher level relationships of the Brachycera. Important additional comments on brachyceran phylogeny were later published by Griffiths (1994) and Sinclair et al. (1994b) based on Woodley's (1989) paper. Woodley (1989) gave infraorder rank to four major monophyletic taxa in the Brachycera, viz. the Xylophagomorpha, Stratiomyomorpha, Tabanomorpha and Muscomorpha and presented five synapomorphies for the entire group, three of which relate to adult morphology (reduction of antennal flagellomeres to eight, maxillary palpus two-segmented and veins CuA_2 and A_1 with apices approximate, forming a nearly closed cell cup).

Griffiths (1994) divided the Brachycera into five subgroups: Stratiomyomorpha (including Pantophthalmidae), Vermileonomorpha (including Vermileonidae and the extinct Eremochaetoidea of the Mesozoic), Tabanomorpha (including Xylophagomorpha and Nemestrinoidea sensu Woodley, but excluding Vermileonidae and Pantophthalmidae), Pleroneura (= Asiloidea sensu Woodley) and Eremoneura. Griffiths suggested that the Stratiomyomorpha could be the sister-group of all other Brachycera, based on his interpretation of the distal hook of the larval mouthparts.

Sinclair et al. (1994) kept the Vermileonidae in the Tabanomorpha and, considering that the apex of the aedeagus to be completely encircled by and fused to the parameral sheath, suggest a close rela-

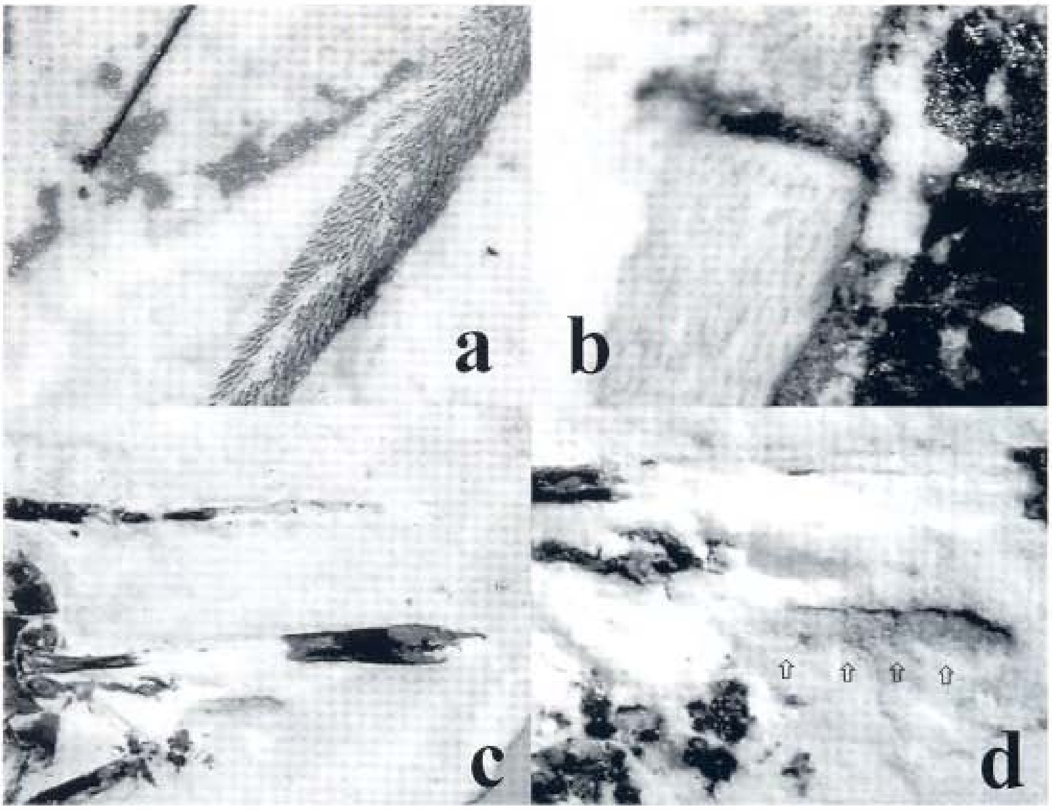

Fig. 7. *Cratomyia macrorrhyncha* gen. n. & sp. n., holotype: (a) detail of left posterior tibia; (b) detail of abdomen. (c) detail of head appendages showing long proboscis; (d) detail of antennal flagellum; divisions between flagellomeres indicated by arrows.

tionship between Stratiomyomorpha and Muscomorpha, just one level above the first division of the Brachycera. We have rejected here this position for the Stratiomyomorpha.

The observation in the fossil species described here of an antenna with at least seven articles, an apparently two-segmented maxillary palpus with long and robust articles, and veins CuA_2 and A_1 close together, strongly suggests that *Cratomyia macrorrhyncha* belongs in the Brachycera. Nevertheless, its precise position within the suborder is a difficult question. The presence of a long proboscis with large and robust maxillary palpi could suggest its inclusion in the Tabanidae or in the Vermileonidae. This seems untenable, however, for different reasons. Most Tabanidae and nearly all Tabanomorpha, as discussed below, have vein R_5 reaching the wing margin beyond the wing apex. Also, they have an open cell cup, different from the closed cup cell of *Cratomyia*. The wing of *Cratomyia* also differs from that of the Vermileonidae, since in this latter family the anal lobe is very reduced, R_4 ends near the wing apex, and R_5 clearly ends beyond the wing apex, much more distally than in *Cratomyia*. Finally, there are no known robust vermileonid species.

The wing of *Cratomyia* rather resembles that of Xylomyidae, except that in the fossil M_1 and M_2 are petiolate basally beyond the discal cell, an autapomorphy of *C. macrorhyncha*. This feature is known to occur in some recent and fossil Trichoceridae and in some Tipulidae (see Alexander 1981, Alexander & Byers 1981, Shcherbakov et al. 1995), but it is quite rare in the Brachycera – as an example found in the dasypogonine asilid *Dasycyrton tener* (see Artigas 1970: 207, fig. 76). Another point is that the Xylomyidae have a short and stout proboscis, very different from that of *Cra-*

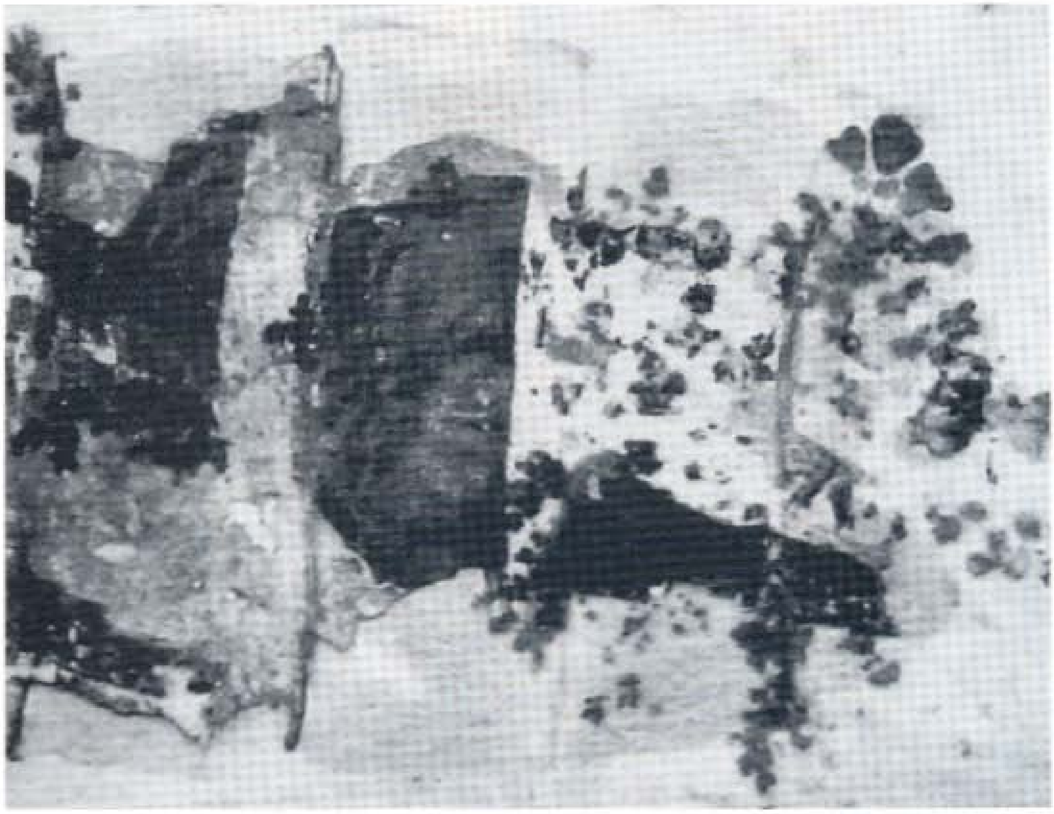

Fig. 8. *Cratomyia macrorrhyncha* gen. n. & sp. n., holotype, posterior abdominal tergites.

tomyia. These two features, however, are autapomorphies of *Cratomyia* and as such provide no information on its systematic position.

Another remarkable feature of *Cratomyia* is the presence of a long, 7- or 8-articled antenna. According to Woodley (1989), a ground-plan condition of the Brachycera is an antenna consisting of eight flagellomeres plus scape and pedicel. The co-existence of genera with multi-segmented and reduced antennal flagellomeres in many different families of Brachycera can only be explained in terms of multiple origins and/or reversals of these character states. Thus, the structure of the flagellomere is not a strong indicator of relationships for *Cratomyia*, though it helps to exclude it from some of the higher brachyceran lineages.

Character optimization for *Cratomyia*

To deal more closely with the problem of the position of *Cratomyia*, it is necessary to make an assumption about the brachyceran higher level phylogeny to properly guide the character discussion. In the cladogram (Fig. 9) it is attempted to gather phylogenetic information for all basal families and lineages of the Brachycera based on the papers by Hennig (1973), Woodley (1989), Sinclair et al. (1994) and Griffiths (1994). Our intention is merely to make an optimization study (see Maddison et al. 1984) of characters verifiable in *Cratomyia*, not to solve the relationships of the basal Brachycera lineages. Accordingly, character support is not indicated for all branches in the cladogram. We have also excluded the Nemestrinoidea from the cladogram since they do not seem relevant to the discussion of the position of *Cratomyia*. There has been considerable dispute over the position of the Nemestrinoidea but we agree with Woodley (1989) that the Nemestrinoidea are a good candidate as the sister-group of the Asilomorpha + Eremoneura.

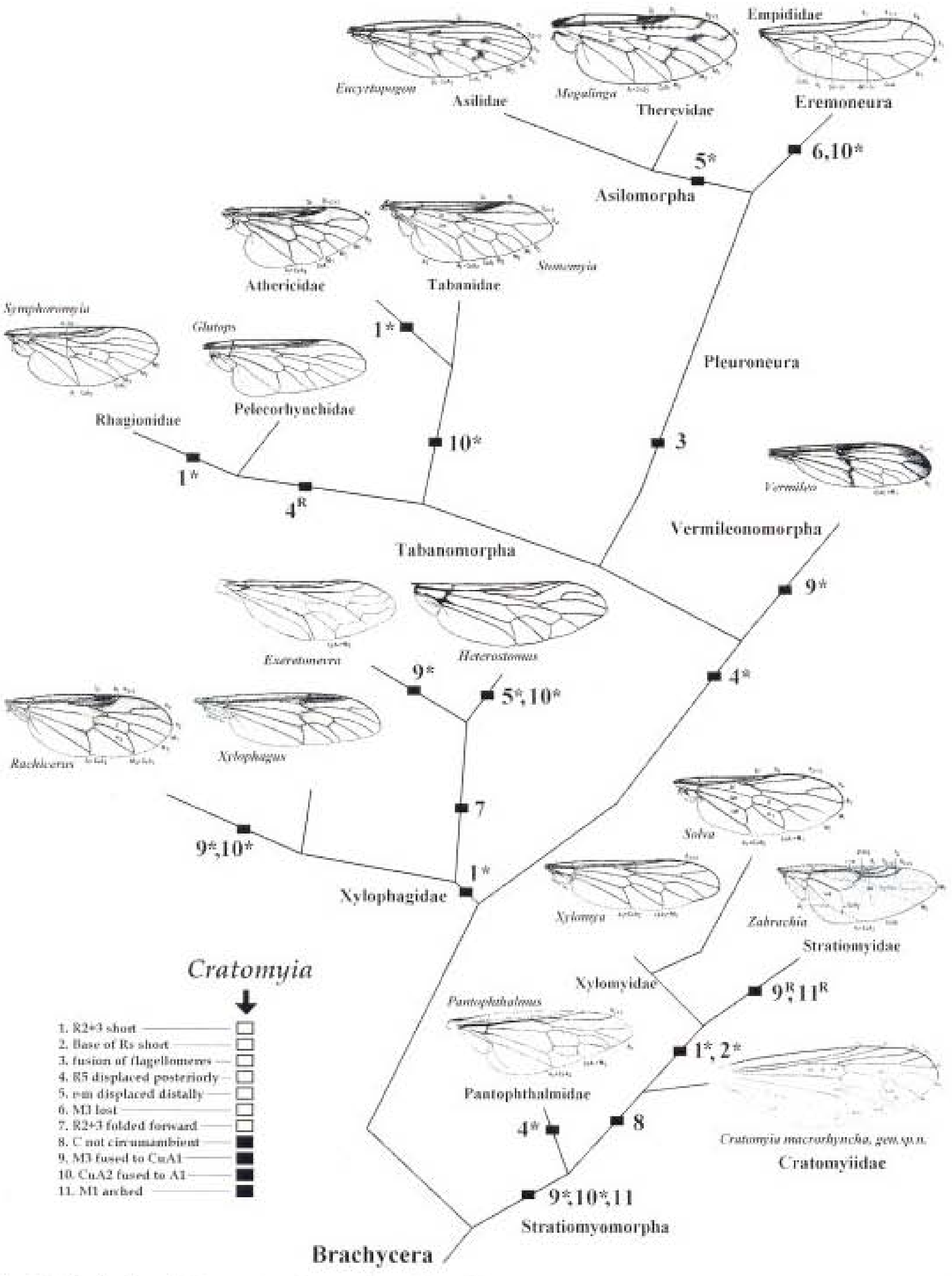

Fig. 9. Optimization of characters and assumed position of *Cratomyia macrorrhyncha* gen. n. & sp. n. on a phylogeny of the Brachycera derived from Hennig (1973), Woodley (1989), Sinclair et al. (1994), and Griffiths (1994). An overall plesiomorphic type of wing venation is included for each terminal taxon. Characters gained independently are marked with an asterisk (*), those representing reversals with an R.

The cladogram (Fig. 9) presents the optimization of some character states observed in *Cratomyia*. Evidently, most of them show independent, homoplastic occurrences in different groups of Brachycera. Hence, it is necessary to gather positive and negative evidence to respectively include or exclude the new taxon from the different clades. Plesiomorphic features of *Cratomyia* help to exclude it from a number of clades, while apomorphic features give some clues for its inclusion in other clades. Each character appearing in Fig. 9 is presented below, followed by a short discussion. Other observable head features, such as the number of segments in the maxillary palpi and the length of the proboscis, show pronounced variation below the family-group level, so they are not useful at this level of study. Character numbers followed by an asterisk (*) indicate homoplastic origin of the character within the cladogram.

1. Vein R_{2+3} long, ending near at the apex of the wing far apart from R_1 / short, ending close to R_1

A long R_{2+3} is also seen, among other Brachycera, in the Pantophthalmidae, Vermileonidae and part of the Tabanomorpha. Even though some therevids and many Eremoneura have a short R_{2+3}, these are independent developments and the long R_{2+3} belongs also to the ground plan of these groups. The apomorphic condition most probably originated independently at the base of the Athericidae, the Xylophagidae and the Xylomyidae + Stratiomyidae. *Cratomyia* exhibits the plesiomorphic condition and so can be excluded from clades with a short R_{2+3}.

2. Basal sector of Rs long / short.

The length of the basal sector of Rs varies considerably within different families and in some cases the variation is nearly continuous. Most families have this feature in the plesiomorphic condition, as is also found in *Cratomyia*. Xylomyidae and Stratiomyidae, however, have the basal sector of Rs consistently shorter than the condition found in Pantophthalmidae. This feature excludes *Cratomyia* from the recent Xylomyidae or Stratiomyidae.

3. Distal flagellomeres separated / fused.

There is considerable variation in the number of flagellomeres in the basal families of Brachycera, but a fusion of flagellomeres may be considered autapomorphic for the Pleuroneura. Independent reductions of flagellomere below the family level has taken place, for example, in the Vermileonidae, Rhagionidae and Stratiomyidae. Little or no fusion of the flagellomeres has taken place in *Cratomyia* and excludes it from many groups.

4. Vein R_5 reaching wing margin just before apex of the wing / well behind apex of the wing.

The displacement of R_5 to a position behind the wing apex seems to be a synapomorphy for the Vermileonomorpha, Tabanomorpha and Pleuroneura, with an independent gain in the Pantophthalmidae. A reversal to the plesiomorphic condition has appararently taken place in the Rhagionidae + Pelecorhynchidae. The plesiomorphic state of R_5 in *Cratomyia* is clearly plesiomorphic and rather incompatible with, for example, the hypothesis that it fits into the Tabanidae.

5. Crossvein r-m at the basal fourth of the discal cell / placed more distally.

A distal displacement of r-m is found in *Heterostomus* and in the Asilidae + Therevidae lineage. It is plesiomorphic in *Cratomyia*.

6. Vein M_3 present / absent.

At the level focused in this study, a reduction of M_3 appears to be an autapomorphy of the Eremoneura. Independent reductions of M_3 have in Brachycera occurred repeatedly below the family level and are not focused on here. Stratiomyidae, as an example, show the plesiomorphic condition in the ground plan, while the genus illustrating the family in Fig. 9 shows the apomorphic condition. *Cratomyia* is plesiomorphic for this character.

7. Vein R_{2+3} straight / R_{2+3} with a forward arch midway to the apex.

The characteristic forward arch of R_{2+3} appears synapomorphic for *Heterostomus* and *Exeretonevra* among the Xylophagidae. *Cratomyia* is plesiomorphic for this feature.

8. Vein C circumambient / falling short of posterior margin of wing.

The incomplete vein C is a probable synapomorphy for *Cratomyia* and the Xylomyidae + Stratiomyidae. The plesiomorphic condition is seen in Pantophthalmidae among the Stratiomyomorpha and in the most other families of lower Brachycera.

9. Vein M_3 reaching wing margin / fused to CuA_1 distally.

The distal fusion of M_3 and CuA_1 has occurred many times in the evolution of the Brachycera. It is seen in Pantophthalmidae, Xylomyidae, some Xylophagidae, Vermileonidae, and in occasional genera of larger families such as Asilidae and Therevidae. Those genera of Stratiomyidae with a preserved M_3 have this vein free from CuA_1, but this condition may be due to a secondary reversal, so the fused condition is here considered as an autapomorphy for the Stratiomyomorpha. The fused M_3 and CuA_1 once again points to an inclusion of *Cratomyia* in the Stratiomyomorpha and contraindicates, for example, an association with the Tabanidae.

10. Vein CuA_2 reaching wing margin / fused to A_1 distally.

The distal fusion of CuA_2 and A_1 has also occurred many times within the evoloution of the Brachycera. It is apparently been indepedently attained in Eremoneura, in Tabanidae + Athericidae, twice within Xylophagidae (*Heterostomus* and *Rachicerus*), and in Stratiomyomorpha. The apomorphic condition in *Cratomyia* supports its inclusion in the Stratiomyoimorpha.

11. Vein M_1 almost straight / strongly arched.

Vein M_1 is only slightly arched in most families of Brachycera. Pantophthalmidae and Xylomyidae, however, have M_1 strongly arched. In Stratiomyidae all the veins originating from the discal cell are considerably modified. It is plausible, therefore, that the straight M_1 in this family is due to a secondary modification. Even though the medial fork is petiolate distal to the discal cell in *Cratomyia*, the M_1 arch is very prominent and adds support to the inclusion of *Cratomyia* in the Stratiomyomorpha.

Final comments

The plesiomorphic condition of characters 1-7 in *Cratomyia* is sufficient to exclude it from most recent lineages of Brachycera, but especially from families with higher position in the system with which it shares some similarities, as is the case of the Tabanidae. Still, a couple of apomorphies that *Cratomyia* shares with other groups of lower Brachycera give some clues to its phylogenetic position. Especially the distal fusion of CuA_2 with A_1, the arched M_1, the distal fusion of M_3 with CuA_1, and the abbreviated vein C are all features supporting the inclusion of *Cratomyia* in the Stratiomyomorpha. Alternative options, given the data presently available, are less likely in our opinion.

Within the infraorder Stratiomyomorpha, *Cratomyia* is definitely not a member of the Pantophthalmidae or Stratiomyidae, as it shows none of the autapomorphies known for these families. There exists some similarities with the Xylomyidae, especially *Xylomya*, but these are mainly based on plesiomorphies. The abbreviated vein C (character 5) is an apomorphic state that *Cratomyia* shares with Xylomyidae and Stratiomyidae and suggests that *Cratomyia* is the sister-group of Xylomyidae + Stratiomyidae. Woodley (1989) listed the costal reduction, among other characters, as a possible autapomorphy for Stratiomyomorpha. Pantophthalmidae have a circumambient vein C and the family was not included in the Stratiomyomorpha by Woodley (1989). Subsequently, as proposed by Griffiths (1994) and followed by Grimaldi & Cumming (1999), has been incuded as the most basal lineage of the Stratiomyomorpha. We have studied three species of Pantophthalmidae (two *Pantophthalmus* and one *Opetiops*) which all showed a complete costal vein along the wing margin. The costal reduction, hence, is shared only by *Cratomyia* and the Xylomyidae and Stratiomyidae among recent Stratiomyomorpha. The extended proboscis of *Cratomyia* is certainly derived and strikingly different from the short proboscis found in Xylomyidae and in the groundplan of Stratiomyidae. The very short basal sector of Rs (character 2) is a possible synapomorphy for Xylomyidae and Stratiomyidae and reinforces that *Cratomyia* is the sister-group and thus demands a family-status of its own. Autapomorphies for Cratomyiidae fam. n. are the petiolate vein M_{1+2}, the long proboscis, and the darkly patterned wing membrane.

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