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Abstract: The genus Lygistorrhina Skuse, with a few species in tropical and subtropical regions, has been considered to constitute a separate subfamily or family of fungus guats, with uncertain affinities. A study of the imaginal morphology, especially the thoracic structure, indicates that the genus represents a specialized branch of the Keroplatidae.

The genus Lygistorrhina Skuse (Lygistorhina is an incorrect subsequent spelling) was proposed for L. insignis Skuse from New South Wales, Australia (Skuse 1890, p. 598, pl. 19, fig. 2). Some years later Williston (1896, p. 261, pl. 8, fig. 15, a-c) described a similar insect from the island of St. Vincent, West Indies, as Probolacus singularis Will. Johannsen (1909, p. 61–62) included the two genera in the subfamily Mycetophilinae, of Mycetophilidae, close to the fossil genus Palaeognoriste Meun., based on the species P. sciariformis Meun. from Baltic amber (Meunier 1904, p. 77, pl. 7, figs. 9–13).

EDWARDS (1912, p. 203), in spite of some minor differences, did not consider *Probolaeus* WILL generically distinct from *Lygistorrhina* Skuse, and later on (1925, p. 530) also synonymized *Palaeognoriste* Meun. with *Lygistorrhina*.

While the synonymy of Lygistorrhina and Probolaeus appears plausible, the inclusion of Palaeognoriste in the same genus is more questionable. Though obviously related to Lygistorrhina, Palaeognoriste differs in several points seeming to warrant generic separation. The mouth-parts are shorter, with distinct palpi, the medial fork is almost complete, only its very base being obliterated, and the legs are figured as shorter, without clubbed hind tibiae. In the presence of distinct palpi and in venation Lygistorrhina asiatica Sen.-Wh. from Ceylon agrees with Meunier's fossil species and may well be congeneric. This would be an interesting new case of a member of an amber genus still living in the tropics of the Oriental region. However, the question of possible generic limits within the Lygistorrhina group falls outside the scope of the present study and is left for a future monographer to solve. In the following the whole group is therefore treated, for brevity, as a single genus, Lygistorrhina.

The genus Lygistorrhina (sensu lat.) includes to-day a score of species recorded from the tropics and subtropics (West India, South America, West Africa, Ceylon, Borneo, Japan, and Australia; see the map fig. 16 in Hennig 1960, p. 286; also from south-eastern North America, according to Stone et al. 1965, p. 204). The genus is highly apomorphic in the structure of the head, especially the elongate mouth-parts, and in the much reduced wing venation as well, and therefore has been difficult to place in the system. At the time when the genus was discovered by Skuse and Williston, only two families, Mycetophilidae and Sciaridae, were

generally recognized in the group of fungus gnats. Skuse, in his original description of Lygistorrhina, states that it reminds one more of the Sciaridae than of the Mycetophilidae». Meunier classed his Palaeognoriste with the Sciaridae, but was inclined to believe that it represents one of the annecting forms between the Sciaridae and Mycetophilidae (vune des formes de passage reliant les Sciaridae aux Mycctophilinae»). As already mentioned, Johannsen (1909) included the three genera in question in the mycetophilid subfamily Mycetophilinae. Later on (JOHANNSEN 1912, p. 258), he united the Sciaridae with the Mycetophilidae as a subfamily Sciarinae, and, while placing Probolaeus Will. in the subfamily Mycetophilinae, suggested that it should possibly be placed with the Sciarinae. EDWARDS (1925) erected a new mycetophilid subfamily for Lygistorrhina (including Probolaeus and Palaeognoriste as synonyms), placing his Lygistorhininae between the Ceroplatinae and the Sciarinae. Shaw & Shaw (1951, p. 16) stated, »Although lacking proper material for a detailed study of the thorax, an examination of some slides indicates that the affinities of Lygistorhina are with those of the Sciophilinae, possibly being closest to the Gnoristini. However, the peculiar head structure, the elongate proboscis wholly unlike that of other mycetophilids, and the venation warrant the maintenance of a separate subfamily.» Some subsequent authors, e.g. Hennig (1954) Tollet (1959), and Rohdendorf (1961), treating the mycetophilid subfamilies as units of family rank, speak of a family Lygistorrhinidae.

In the present study the Mycetophilidae of Edwards is considered to be a superfamily Mycetophiloidea, consisting of the families Ditomyiidae, Diadocidiidae, Bolitophilidae, Sciaridae, Keroplatidae, and Mycetophilidae. The Keroplatidae include, besides of the Ceroplatinae of the older authors, also their Macrocerinae and the genus Arachnocampa; with the Mycetophilidae are united the Sciophilinae and Mycetophilinae of these authors, and tentatively also the Manotinae of Edwards.

The study is based mainly on an examination of two specimens of Lygistorrhina brasiliensis Edw. (det. John Lane) in the Entomological Museum of the University of Helsinki, but additional material of some species (L. asiatica Sen.-Wh., L. brasiliensis Edw., L. coxata (End.), L. edwardsi Lane, L. singularis (Will.), and L. urichi Edw.) was superficially studied during a visit to the British Museum (N. H.).

Examination of this material showed, first, that the *Sciaridae* are out of the question as near relatives of *Lygistorrhina*. This is proved especially by the structure of the thorax and the insertion of the abdomen.

In Lygistorrhina the base of the abdomen is extremely narrow, and the mediotergite strongly convex, its inflexed lower part forming an acute angle with the dorsum of the abdomen; in addition, the pleurotergites are sharply prominent, almost ridged. In the recent Mycetophilidea this strong apomorphy of the posterior part of the thorax and of the insertion of the abdomen is found only in the Kero-

platidae and Mycetophilidae. Accordingly, the families Ditomyiidae, Diadocidiidae, Bolitophilidae and Sciaridae, and the genera Heterotricha and Ohakunea need not be further discussed as possible relatives of Lygistorrhina; all of them have a broader insertion of the abdomen, with the thoracic phragma more or less entering into the base of the abdomen (especially in the Sciaridae), a more vertical lower part of the mediotergite, and flater pleurotergites. Thus only the Keroplatidae and Mycetophilidae will be considered in the following.

In the structure of the antennae the Lygistorrhina species seem to be more plesiomorphic than most of the Mycetophilidae. Edwards (1932, p. 139) states that the presence of bristly hairs on the antennal flagellum is very unusual in the fungus gnats, and that their existence in L. brasiliensis confirms him in his belief "that Lygistorhina cannot be included in any of the subfamilies M y c e t o p hillinae or Sciarinae, where such hairs never occur. Strong stiff macrotrichia are absent on the flagellar segments of the antennae in most Mycetophilidae (Mycetophilinae and Sciophilinae of Edwards) and in all true Sciaridae, and occur in certain Ditomyiidae, many Keroplatidae, and less conspicuously also in the Bolitophilidae and the Heterotricha group of genera, but their equivalents are not wholly absent in the Mycetophilidae either. What seems important is that, in Lygistorrhina, the bristly hairs are concentrated on the dorsal side of the segments, much as in Burmacrocera minuta (Sen.-Wh.) (Keroplatidae).

The elongate mouth-parts of Lygistorrhina are peculiar and most characteristic. The maxillary palpi are said to be absent; in any case they are not discernible in dried material. No trace of them could be detected by dissection in L. brasiliensis. They are present, however, in L. asiatica Sen.-Wh., every small, single-jointed, according to Senior-White (1924, p. 196), and in the fossil Palacognoriste sciariformis Meun, as well (Meunier 1904, p. 77; »Dernier article? des palpes lancettiforme», see also his pl. 7, fig. 9). Skuse and Williston describe and figure the mouth-parts as consisting of five filamentous parts, of which two are shorter and finely hairy; two of the longer bare ones are somewhat thicker and more flexible. My slide of the head of L. brasiliensis shows only four filaments. One somewhat shorter hairy part obviously corresponds to the pair of similar parts in the species figured by Skuse and Williston. It is the most dorsal of the mouth-parts, long and narrow, a little broader at the base and tapering to a sharp point. It can hardly be anything else than the labrum, which, accordingly, must be bipartite in the two other species figured. The two darker, more flexible parts are attached to the apex of the labium, as figured already by Williston, and are obviously the labella. The remaining unpaired filament is parallel-sided, hyaline, and twopointed at the tip. It arises from the upper side of the labrum and must be the hypopharynx.

An elongate proboscis is known to occur in a few other genera of Mycetophiloidea, e.g. Eugnoriste Coq. (Sciaridae), Rhynchoheterotricha Freem. (of the »Hetroz-

tricha group» of genera), Aphrastomyia Coher & Lane (Mycetophilidae, Mycomyiinae), and Gnoriste Meig. (Mycetophilidae, Gnoristinae), but in Rhynchoheterotricha and Gnoriste it is mainly formed by the lower parts of the head, including the clypeus. A proboscis consisting of the mouth-parts themselves as in Lygistorrhina is also known in several Keroplatidae, e. g. Antlemon Hal. and Rhynchoplatyura De Meij.

The tibial trichiation in the South American Lygistorrhina species consists of rather weak shorter and longer hairs of similar structure, the latter not being stronger and spine-like as in most of the Keroplatidae and Mycetophilidae. Thus the trichiation is more like that of some »lower» Mycetophiloidea, especially Diadocidia, Heterotricha, Ohakunea, and some Ditomyiidae, but it is to be noted that a similar type is also characteristic of Macrocera and other »macrocerine» genera of Keroplatidae. Lygistorrhina asiatica Sen.-Wh. is different in this respect: the fine tibial setulae are arranged in fairly distinct longitudinal rows, and in the middle and hind tibiae there are a couple of rows of small, somewhat spiny bristles, the trichiation thus resembling that of many Keroplatidae and some Mycetophilidae. This latter type is not known in the other families.

The Mycetophiloidea nearly always possess a special structure of differentiated hairs on the anterior surface of the fore tibia near the tip (its presence is, incidentally, one of the best proofs of the monophyletic nature of the superfamily). This secombs or sbrushs is probably used by the insect for cleaning the antermae and palpi. Sometimes, as in the Ditomyiidae, many Bolitophilidae and Sciaridae, and in some Keroplatidae (especially in Macrocera and allied genera) it consists of a single transverse row of setulae and has been called the sfore tibial combs. In other cases there are two or more such combs on top of one another, or a semicircular or semiovate, sharply delimited field covered with differentiated setulae. When well developed, as in many Keroplatidae and most Mycetophilidae, this field may be called a sbrushs rather than a seombs. In Lygistorrhina brasiliensis, and probably also in other species of the genus, the structure is comb-like, thus more like that of some Keroplatidae, e. g. Burmacrocera minuta (Sen.-Wh.) and Macrocera, than of the Mycetophilidae, but shorter than in Macrocera, being confined to an area close to the tibial spur.

In the *Mycetophiloidea* the coxae are usually of about equal length, or the front ones may be shorter than the two posterior pairs. In *Lygistorrhina* the hind coxae are distinctly shorter than the middle ones, corresponding to the exceptional height of the adjacent parts of the metathorax. The same type is found in *Fenderomyia* (*Keroplatidae*) and in lesser degree also in *Macrocera*.

The male abdominal terminalia of Lygistorrhina (as studied from dried specimens) are of comparatively simple type, reminiscent of those in Diadocidia, Bolitophila, Macrocera, and others. Especially it deserves mention that the claspers of L. asiatica possess a bifid tip very similar to that of Macrocera, Paramacrocera, Fenderomyia, and some other Keroplatidae, e.g. Isoneuromyia and Pyrtaula.

The above discussed characters seem to be peak a relationship of Lygistorrhinv with the Keroplatidae and particularly with the »macrocerine» genera of this family, rather than with the Mycetophilidae. Further evidence in favour to this view comes from the structure of the thorax. Besides the general features of the structure of the posterior part of the thorax and the nature of the insertion of the abdomen mentioned in the beginning of this paper, Lygistorrhina is characterized by a set of features (studied in L. brasiliensis): 1) The thorax appears somewhat dorsoventrally compressed; 2) the prothoracic episternum is short and meets the mesothoracic katepisternum unusually high up, in the upper corner close to the horizontal suture between this sclerite and the anepisternum; 3) the mesothoracic an episternum is low and broad, much broader than high; 4) the mesothoracic epimeron lacks the usual narrow lower part, since the pleurotergite extends to the katepisternum in this region; 5) the metathoracic epimeron and the adjacent posterior part of the metathoracic episternum are exceptionally high. This combination of obviously apomorphic characters Lygistorrhina shares with only one genus described in detail in this respect, viz. Fenderomyia Shaw.

Fenderomyia Shaw was proposed by Shaw (1948) to accommodate an Oregon species, F. smithi Shaw, resembling Macrocera but differing from that genus in thoracic structure and wing venation. As stated above, the thoracic structure is much the same as in Lygistorrhina. In the venation the following points (according to the figure published by Shaw) may be noted: 1) the vein rs arises unusually far towards the wing base, and is not distinctly connected with r there, 2) the basal portion of the media is rather distinct and ends distally close to the base of cu_{1a}, 3) the vein cu_{1a} is somewhat weak at the base. The last-mentioned character is even more accentuated in some other smacrocerines Keroplatidae.

The venation of Lygistorrhina is characterized by a considerable vein reduction. The subcosta is short and in some species incomplete, ending free in the wing membrane, but in other species, including L. asiatica, it reaches the costa as in Fenderomyia. As in many Keroplatidae, the vein sc_2 is absent. The radial sector appears to originate "practically at the base of the wing, below the humeral crossvein" (Edwards 1925, p. 531), which is most extraordinary in the whole superfamily. Of the medial vein only the outer parts of the fork remain; the base of the fork and other more basal parts of the media seem to be quite obliterated, as are the base of the vein cu_{1a} and the veins uniting it with m and cu_{1b} . The anal vein is absent. The venation as a whole resembles that of the genus Ohakunea (which is usually, and probably correctly, included in the Sciaridae). However, in this genus the base of rs is distinct and unusually distal in position. The anal lobe of the wing of Lygistorrhina is somewhat square, in the manner of Macrocera, in contrast to the more typical "Ceroplatinae".

At first sight it may appear almost impossible to derive the venation of *Lygistorrhina* from that of the *Keroplatidae*. Yet the venation of *Fenderomyia* and other *macrocerine* *Keroplatidae* lends some support to this suggestion. The basal origin

of rs in *Lygistorrhina* is perhaps to be understood by assuming that the detached base of this vein in *Fenderomyia* has fused with the basal portion of the medial vein, or in some other way become retracted close to the wing base, in connection with the obliteration of parts of the medial fork, m-cu, and the base of cu_{La}.

In the Keroplatidae, especially in the »macrocerine» genera, there are indications of a vein reduction pointing in the direction of Lygistorrhina. The subcosta may be weak or abbreviated, the vein r₄ is sometimes absent, the anal vein often abbreviated to a mere rudiment, and the vein cuta sometimes detached at the base. To take an example: in Macrocera pulchra Tonn. the subcosta is very short and ends free, the stem and base of the medial fork are almost obliterated, the vein cu_{1a} appears to be somewhat weak at the base, and the anal vein is very faint, hardly distinguishable except at the base. Similarly, in an unidentified keroplatid species from Burma that appears to be fairly close to Burmacrocera all the vein parts that are obliterated in Lygistorrhina are weaker than the others, and as in Lygistorrhina the wing membrane and the branches of the two forks are bare, and the costa much produced. In some »macrocerine» Keroplatidae (Paramacrocera brevicornis Edw., according to the fig. 32 in Tonnoir and Edwards 1927, Burmacrocera Cock., and Chiasmoneura De Meij.) the vein cu_{ta} is distinctly detached at the base. Finally, the shape of the short subcosta in Lygistorrhina asiatica Sen.-Wh. and Palaeognoriste sciariformis Meun. is very similar to that of many Keroplatidae, and the much-produced costa characteristic of Lygistorrhina and Palaeognoriste is found in some smaller Keroplatidae.

In the writer's opinion, Lygistorrhina cannot be included in any other family than the Keroplatidae. It shows most resemblance to certain members of this family, notably to the *macrocerine* genera, the most striking similarity being that between Lygistorrhina and Fenderomyia in the thoracic structure and shortness of the hind coxae. Further study on the macrocerine Keroplatidae, such as Paramacrocera Edw. (New Zealand, southernmost South America), Burmacrocera Cock. (Burmanese amber, Ceylon, Philippines, see Edwards 1929 a), and Chiasmoneura De Meij. (Java, New Hebrides, see De Meijere 1913, Edwards 1929 b) will probably shed more light on the origin of Lygistorrhina. Its proper position has remained obscure simply because the system of the Mycetophiloidea has been based too much on the venation which in this case is of little help.

It appears rather unlikely that Lygistorrhina, being a small, strongly apomorphic »young» genus with tropical — subtropical distribution, should be completely isolated from the recent families. If treated as a family, it would strongly contrast with the other small families of Mycetophiloidea (Ditomyiidae, Diadocidiidae and Bolitophilidae), which are all »old», more plesiomorphic, relict families by no means confined to the tropics but, on the contrary, more concentrated in extratropical regions. It thus seems more likely, from the zoogeographical poily of view as well, that Lygistorrhina arose as a specialized group from the famith Keroplatidae, which is comparatively abundantly represented in the tropics.

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