

# Generic taxonomy of the Exechiini (Dipt., Mycetophilidae).

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## Abstract.

The tribe *Exechiini* is a sharply delimited and no doubt monophyletic branch of the *Mycetophilinae*. Contrary to the opinion of EDWARDS, it also includes *Cordyla* MEIG.

The current generic system of the *Exechiini*, dating back to WINNERTZ (1863), is to some extent artificial and cannot meet the demands of a natural and if possible phylogenetic taxonomy. Only *Anatella* WINN. and *Cordyla* MEIG. appear to be homogeneous and monophyletic.

*Rymosia* WINN. is a paraphyletic grouping and is divided into four genera: *Rymosia* WINN. s. str. and the new genera *Tarnania*, *Pseudorymosia*, and *Allodiopsis*, the latter with four subgenera.

*Exechia* WINN. is a polyphyletic grouping consisting of three genera: *Exechia* WINN. s. str., *Pseudexechia* n. gen., and *Exechiopsis* n. gen., the latter consisting of two subgenera.

*Allodia* WINN. is divided into two genera, viz. *Allodia* WINN. s. str. and *Brevicornu* MARSH., each with two subgenera.

*Brachypeza* WINN., sensu EDW., is considered to consist of two genera: *Brachypeza* WINN. (with two subgenera) and *Pseudobrachypeza* n. gen.

There is some indication that the proposed segregates of the traditional genera show affinities crossing the customary generic boundaries. Thus *Brevicornu*, with certain apomorphic characters in common with *Cordyla*, appears to have phylogenetic connexions with that genus rather than with *Allodia* s. str. Similarly, *Pseudexechia* may in reality be more closely allied to *Allodiopsis* and *Allodia* than to *Exechia* s. str. *Allodiopsis*, in turn, is more nearly related to *Allodia* s. str. than to *Rymosia* s. str.

## 1. Delimitation and characterization of the tribe Exechiini.

The subfamily *Mycetophilinae*, as delimited by EDWARDS (1925), is a nicely homogeneous and no doubt monophyletic grouping. EDWARDS divided it into two tribes, as follows:

Anepisternal and pteropleural bristles absent; hind coxa with a fairly strong bristle at base; empodia absent or rudimentary; hind tibial comb usually indefinite or absent; tibial bristles short (Tribe *Exechini*)

Anepisternal bristles present; hind coxa usually without basal bristle; empodia and hind tibial comb nearly always distinct (Tribe *Mycetophilini*)

According to EDWARDS, the tribe *Exechiini* comprises the genera *Anatella*, *Rhymosia*, *Exechia*, *Allodia*, and *Brachypeza*; in the tribe *Mycetophilini* he included the genera *Cordyla*, *Trichonta*, *Phronia*, *Dynatosoma*, *Mycetophila*, *Epicrypta*, *Platurocypta*, *Delopsis*, *Zygomyia*, and *Platyprosthogyne*.

Subsequent writers, on the whole, have accepted this division without further comment. However, FREEMAN (1951, p. 88), when describing a new *Mycetophilini* genus from southern South America, suggested that a revision of the tribal limit might be necessary: «*Pleurogymnus*, gen. n., is interesting because its characters are such as to cast some doubt upon the validity of the two tribes. It is possible that a future reclassification of the subfamily will abolish the tribes and show that some genera such as *Trichonta* require redefining.» Furthermore, he says (op. c., p. 93): «It is, therefore, probable that the two tribes require a redefinition on characters other than those used by EDWARDS (1925).»

The words «usually» and «nearly always» in the above cited key of EDWARDS indicate that the distinguishing characters are not absolutely correlated. In doubtful cases, the author appears to have regarded the absence or presence of anepisternal bristles as decisive. In fact, this is one of the best diagnostic characters, but not absolutely reliable. In many of the *Exechiini* the mesanepisternum is completely devoid of any kind of macrotrichia, whereas in others at least a part of it is covered with small setulae. In *Cordyla* some of these macrotrichia are true bristles, not smaller than in the typical *Mycetophilini*; in consequence the genus was placed by EDWARDS in the latter tribe, though in other respects it is rather close to some *Exechiini*, such as *Brachypeza*. On the other hand, *Pleurogymnus* FREEM. and *Pseudoalysiina* TONN. do not belong to the *Exechiini* in spite of their bare mesanepisternum.

Neither is the presence of a single strong dark basal bristle on the hind coxae an absolute criterion, though it is a useful additional character of the *Exechiini*. The basal bristle is weak or absent in some *Anatella* species; many other *Exechiini*, especially of the compound genera *Rhymosia* and *Brachypeza*, have two basal bristles (the upper one mostly shorter), and in *Cordyla* the basal bristle is sometimes replaced by a cluster of a few shorter bristles. A similar, though less conspicuous, patch of tiny bristles also occurs in the *Mycetophilini* (at least in *Mycetophila fungorum*); in *Trichonta* and *Dynatosoma* the presence of a basal bristle (though usually rather weak and pale in colour) is a common feature.

Nevertheless, the *Exechiini* are a natural group and can be sharply delimited by other characters. Two of them were not used by EDWARDS, viz. the absence

of a long sagittal line on the head and the shape of the mesothoracic katepisternum. These two features are especially useful, because they seem to be absolutely correlated with each other and with the reduction of the empodium.

FREEMAN (op. cit.) pointed out that the furrowing of the head along the sagittal suture in *Pleurogymnus*, in correlation with other characters, places this genus close to some species of *Trichonta* (*Mycetophilini*) rather than to the *Exechiini*, where, in view of the absence of mesanepisternal bristles, it would seem to belong. I have checked this head character for a large number of *Mycetophilinae*, and found no exception to the rule that the *Mycetophilini* have a distinct median line extending from the middle ocellus to the highest point of the head, while the *Exechiini* at most show a short stump of this furrow above the insertion of the antennae at the site of the rudimentary median ocellus. As the presence of a long sagittal line on the head is the rule in other *Mycetophilidae* (*Sciophilinae*, of EDWARDS), its absence in the *Exechiini* is to be considered an apomorphic character.

In the *Exechiini*, the lower part of the mesothoracic katepisternum is rounded and somewhat dilated in a characteristic way to cover the base of the middle coxa (see figs. 34 – 37 in SHAW & SHAW 1951). In the *Mycetophilini* the lower margin of the katepisternum usually has a distinct anterior angle (figs. 38 – 41 in SHAW & SHAW) and hardly overlaps the base of the middle coxa; a similar shape of the katepisternum is typical of all other fungus gnats except for the *Exechiini* which, accordingly, are apomorphic in this respect as well. In one group of *Mycetophilini* showing a pronounced dorsiventral depression of the whole thorax, the katepisternum is also different, but in another way than in the *Exechiini*: it is very low and horizontal (figs. 42 – 43 in SHAW & SHAW) without a distinct anterior angle. The rounded dilation of the lower border of the katepisternum in the *Exechiini* is probably connected with the peculiar position of the middle legs in repose. EDWARDS (1921 b, p. 23) has studied the resting postitions of the *Mycetophilinae* and found that the *Exechiini* (*Exechia*, *Rymosia*, *Allodia*, *Brachypeza* and *Cordyla*) «all raise their middle legs high above the body, the tarsi being curved towards each other so that they almost meet». No member of the *Mycetophilini* is known to have this capacity.

The larval and pupal characters are too insufficiently known to be used in the delimitation of the *Exechiini*. According to MADWAR (1937), the larvae of the two tribes of the *Mycetophilinae* may readily be told apart by examining the locomotory pads, which are well developed in the *Mycetophilini* and poorly developed in the *Exechiini*, though there are exceptions to this rule.

Considering the diagnostic characters and their variation, the *Exechiini* may be distinguished from other *Mycetophilinae* (i.e., the *Mycetophilini*, of EDWARDS) as follows:

*Exechiini*

Sagittal furrow of the head only indicated by a short stump above the insertion of the antennae at the site of the middle ocellus

Mesanepesternum bare, or with small short macrotrichia, with true bristles only in *Cordyla* and *Neoallodia*

Lower part of the mesothoracic katepisternum with an evenly rounded dilation overlapping the base of the middle coxa; middle legs raised above the body in resting position

Hind coxa usually with a single strong dark basal bristle, sometimes accompanied by a shorter one, or with a small cluster of shorter basal bristles (*Cordyla* spp.), rarely basally bare (*Anatella* spp.)

Tip of hind tibia on the posterior surface usually with a dense field of decumbent setulae; the end bristles below it not forming a pronounced comb

Empodium rudimentary

Other *Mycetophilinae*

Sagittal furrow of the head long, extending above the site of the middle ocellus close to the highest point of the head

Anepisternum with bristly macrotrichia, except in *Pleurogymnus* and *Pseudalysiina*

Lower border of katepisternum with distinct anterior angle, not distinctly covering the base of the middle coxa, or else katepisternum low and horizontal and the thorax dorsiventrally flattened; middle legs not raised in repose

Base of hind coxa without a long and dark basal bristle; if a strong one is present (*Trichonia* spp., *Dynatosoma* spp.), it is usually pale in colour

Tip of hind tibia on the posterior surface without such a dense field of setulae; the end bristles in a more definite comb-like row

Empodium small but well developed

The revised delimitation of the *Exechiini* conforms with that of EDWARDS with the one exception that *Cordyla* belongs to the *Exechiini* and not to the *Mycetophilini*. Of the later described genera *Neoallodia* EDW., as suggested by EDWARDS, comes near *Cordyla*, and thus belongs to the *Exechiini*.

The *Exechiini* are characterized by some features which, when compared with the situation in the other *Mycetophilidae*, must be considered apomorphic, thus offering proof of the monophyletic nature of the tribe. Such are at least the reduction of the empodium and of the sagittal furrow of the head, and the shape of the lower part of the katepisternum in connexion with the resting position of the middle legs. This delimitation of the *Exechiini* leaves the *Mycetophilini* characterized mainly by the corresponding plesiomorphies and accordingly not easy to establish as monophyletic. In fact, the tribe *Mycetophilini* may be a paraphyletic grouping, the *Exechiini* representing only one specialized branch of it. There is rather strong evidence that one group of genera of *Mycetophilini*, viz. *Mycetophila* and its allies (*Zygomyia*, *Sceptonia*, *Epicypta*, etc.) with their strong tibial bristles and bristly mesepimeron, constitute a monophyletic group, and that the peculiar Tasmanian genus *Pseudalysiina* TONN., with tibial setulae and wing microtrichia not arranged in lines, perhaps represents a «sister group» of all the other known *Mycetophilinae* (including *Exechiini*), whereas the

*Asp. fuscus* Freeman

remaining genera (*Pleurogymnus*, *Phronia*, *Zygophronia*, *Trichonta* and *Dynatosoma*) appear in a certain way to be more related to each other. Thus, in addition to the *Exechiini*, three tribes might be recognized. However, these questions fall outside the scope of the present study, and for the present there appears to be no need of nor sufficient evidence for a further division of the *Mycetophilini*.

## 2. The genera of *Exechiini*.

### Introduction.

While the delimitation of the *Exechiini* as a natural and monophyletic group thus presents no serious difficulties, its current division into genera is far from satisfactory, and the problems involved not easy to solve.

The present-day generic division of the tribe dates back to WINNERTZ (1863), whose genera have been accepted practically unaltered by the more modern writers, including DZIEDZICKI, JOHANNSEN, LUNDSTRÖM, EDWARDS, and LANDROCK. The only exceptions are that *Brachycampta* WINN. is considered to be a synonym of *Allodia* WINN., and that one new exotic genus *Neoallodia* EDW. has been added.

WINNERTZ based the genera nowadays included in the *Exechiini* mainly on the venation, which is rather monotonous in the whole subfamily, with only comparatively small deviations from the general rule, such as the length of the cubital fork,  $cu_2$ , and the anal vein. Other characters have only occasionally been utilized.

It is apparent that genera based on single trivial venational features showing poor correlation, if any, with other characters often do not represent natural, still less monophyletic, units. A closer study indicates that this is actually true of some of the genera of *Exechiini*. *Exechia* WINN. is probably a partially polyphyletic grouping held together by a single convergent feature, the shortness of the cubital fork. *Rymosia* WINN., in turn, appears to be paraphyletic, being based on venational characters that are plesiomorphic compared with the situation in *Exechia* and *Allodia*. *Allodia* WINN., again, seems to be paraphyletic insofar as a portion of it perhaps stands closer to one part of *Rymosia*, whilst another part seems to exhibit a closer relationship to *Brachypeza* and *Cordyla* than to the former. *Brachypeza* WINN. is not quite homogeneous either, since one part of it is different enough to make a close relationship doubtful. Thus of the old Winnertzian genera, only *Anatella* and *Cordyla* seem to be properly delimited monophyletic genera.

In the present author's opinion, the current generic system of the *Exechiini*, however convenient for practical pigeon-holing, cannot meet the demands of a natural taxonomy such as is required, for example, for zoogeographical purposes

(see HENNIG 1960). The question is how to master the situation in the present imperfect state of our knowledge.

According to our present knowledge, the *Exechiini* appear to be mainly of Holarctic distribution and perhaps also origin, and comparatively poorly represented in the tropics and in the Southern Hemisphere, or at least without any greatly deviating or really original types there. It is felt, therefore, that the situation as regards the generic taxonomy of the tribe can be judged in its essential points from a regionally limited material from the main area of the group. The safest step forward seems to be a sharper delimitation and characterization of the smaller units within *Exechia*, *Rymosia*, *Allodia* and *Brachypeza* as they are seen in the better known European material, a work which was already initiated by the earlier authors, especially EDWARDS. However, those subdivisions only too often show affinities crossing the customary generic boundaries. This suggests that while more conservative workers may prefer to treat the smaller groups at most as subgenera of the traditional Winnertzian genera, the future aim should perhaps be to group them in a new, more natural way into larger genera irrespective of the customary generic limits. It is not intended to embark on the latter task in the present study. The smaller units are treated as genera in the hope that such a method of dealing with them will at least have the advantage of directing attention to the neglected characters and affinities. In some cases the subgeneric status is employed if the genus in question appears reasonably monophyletic, or simply as a provisional solution in an especially imperfectly clarified case. Of course, a study like the present, being based on but a limited number of the species described, cannot claim to be a final or authoritative contribution to these questions. However, it appears by no means too early to take the more than hundred year old system of the Winnertzian genera under review, and it always facilitates discussion if we provide names for the natural groups which, at least in part, are already familiar to specialists.

A representative collection from Finland, put together in 1962–1965 mainly by Dr. WALTER HACKMAN and the present author, served as the main material for the study. To this was added the other collections in the Entomological Museum of the University of Helsinki, and a fairly comprehensive material from northern Burma, collected by Dr. RENÉ MALAISE in 1934. During a visit to the British Museum (N. H.) some additional extra-European material was superficially studied.

As to the lists of species included in the genera and subgenera, no completeness was aimed at beyond the Finnish fauna, the study being a preparatory one for an account of the Finnish Mycetophilidae. New combinations are proposed only for species actually studied or more rarely for those which, on grounds of adequate published descriptions and figures, are easy to place.

## Short artificial key to the genera of Exechiini.

- 1 (4) Mesepimeron with a sharply delimited black dot near front margin. Antennae short. Mesanepisternum finely hairy to bristly. Stem of the medial fork at least twice as long as r-m ..... 2
- 2 (3) Antennae with 2 + 14 segments. Antepenultimate segment of palpi not conspicuously enlarged ..... *Neomallosia* EDW.
- 3 (2) Number of flagellar segments diminished, especially in female. Antepenultimate palpal segment greatly swollen, especially in male ..... *Cordyla* MEIG. (192)
- 4 (1) Mesepimeron without such a black dot. Mesanepisternum without strong bristles ..... 5
- 5 (6) Costa distinctly produced beyond the tip of  $r_s$  ..... *Anatella* WINN.
- 6 (5) Costa stopping at the tip of  $r_s$  ..... 7
- 7 (12) Base of cubital fork beyond that of the medial; all fork veins usually bare ..... 8
- 8 (9) Scutum without discal bristles. Clypeus ovate. Stem of the medial fork subequal in length to r-m. Pale markings on abdomen, when present, broadest along the hind margins of tergites. Male cerci with a small median lobe <sup>as Edwards, 1964</sup> ..... *Pseudexechia* m. (192)
- 9 (8) Discal bristles usually well developed. Clypeus shorter, more rounded or cordate. Male cerci otherwise ..... 10
- 10 (11) Subcosta ending free; r-m more than twice as long as the medial stem;  $r_s$  and  $m_1$  divergent in apical half. Two to four propleural bristles. Pale markings of abdomen, when present, usually situated mainly towards bases of tergites .. *Exechia* WINN. s.str. (176)
- 11 (10) Subcosta more or less distinctly ending in r; r-m at most twice as long as the stem of the medial fork, rarely longer;  $r_s$  and  $m_1$  not apically divergent. One strong propleural bristle, a second shorter one sometimes present. Pale markings on abdomen broadest along hind margins of tergites ..... *Exechiopsis* m. (172)
- 12 (7) Base of the cubital fork usually well in front of, rarely under, that of the medial fork ..... 13
- 13 (22) Medial fork and mostly also cubital fork with macrotrichia, at least towards tip .. 14
- 14 (17) Subcosta ending free ..... 15
- 15 (16)  $cu_2$  very long and distinct. Discal bristles reduced or absent .. *Pseudobrachypeza* m. 3 D
- 16 (15)  $cu_2$  shorter. Discal bristles well developed, though closely decumbent ..... *Brevicornu* MARSH. (subg. *Stigmatomeria* m.) 3
- 17 (14) Subcosta ending in r ..... 18
- 18 (19) Body stout. Antennae short; flagellar segments closely sessile. Thorax dorsiventrally flattened; discal bristles reduced or absent. Legs strong; tibiae somewhat clavate, the front ones shorter than the femora. Male terminalia small .. *Brachypeza* WINN. 3
- 19 (18) Not so ..... 20
- 20 (21) Pale markings on the abdomen situated towards the bases of the tergites. Legs long and slender ..... *Pseudorymosia* m.
- 21 (20) Hind margins of abdominal tergites pale. Legs not particularly slender *Allodiopsis* m.
- 22 (13) Fork veins bare ..... 23
- 23 (24) Subcosta ending free. Pale markings on abdomen, if present, situated mainly towards bases of the tergites. Male inner stylar lobe tapering to a long and slender tip. Female cerci one-segmented ..... *Rymosia* WINN. s.str.
- 24 (23) Subcosta ending in r. Male terminalia otherwise constructed. Female cerci two-segmented ..... 25
- 25 (26) Anal vein distinct; r-m, and the portion of m before r-m with macrotrichia. Hind tibiae with the posterior bristles in approximately three rows .... *Tarnania* m.
- 26 (25) Anal vein reduced; r-m, and the portion of m before it, bare. Hind tibiae with the posterior bristles arranged in one row or absent ..... 27

- 27 (28) Discal bristles decumbent, more or less evenly dispersed over the scutum; three or more propleural bristles. Hind tibiae with posterior bristles towards the tip. Male 9th tergite without very long bristles. Basal segment of female cerci apically slender ..... *Brevicornu* MARSH.
- 28 (27) Discal bristles arranged in two dorsocentral stripes (sometimes also a median stripe present), or absent; two propleurals. No posterior bristles on the hind tibiae. Male 9th tergite with one or two pairs of long bristles. Basal segment of female cerci short, conical ..... *Allodia* WINN. s. str.

### *Anatella* Winn.

*Anatella* WINNERTZ 1863, p. 854. Type-species: *Anatella gibba* WINNERTZ 1863, p. 855; by designation of JOHANNSEN 1909, p. 101.

Discussion: *Anatella* is the only genus of *Exechiini* having the costa distinctly produced beyond the tip of  $r_5$  (this character is also known in one species of *Neoallodia* EDW.). In *Anatella*, this may represent the plesiomorphic condition, and as such the character would be of dubious value for the delimitation of the genus. Moreover, *Anatella* exhibits an unusually wide variation in characters which are often considered of generic value in the fungus gnat system: the medial and cubital fork veins in some species bear macrotrichia, in others not; the two middle tibial spurs may be subequal in length, or one of them reduced to absent; the base of the cubital fork is mostly situated beyond that of the medial fork, but not in all species included in the genus; as for the basal bristles, one or two may be present on the hind coxa, or all absent. Yet in other respects the species (some 15 of which were studied for the present work) are very similar, giving the impression of a natural and monophyletic group. Even the main diagnostic character of the genus, the produced costa, may in this case in reality be apomorphic, i.e. resulting from a fusion of the tips of  $c$  and  $r_5$ , as it most probably is in *Platurocypta* (*Mycetophilini*) and apparently also in *Neoallodia*.

Some natural species groups in *Anatella* may be discerned, but they appear to be indistinctly separated. Thus, for the present, there seems to be no need nor possibility to divide the genus. The relationships of *Anatella* are obscure, beyond the fact that it undoubtedly belongs to the *Exechiini*. The genus appears to be essentially Holarctic, being known from North America, Europe, and Asia (several species studied from northern Burma).

### *Rymosia* Winn. as a compound genus.

The genus *Rymosia* WINN. in reality represents the residue that is left of the tribe when the other genera, each marked by their own special, mostly apomorphic characters, are removed. Accordingly, *Rymosia* becomes characterized by the corresponding plesiomorphies, viz. longer cubital fork than in *Exechia*,



and a better developed anal vein than in *Allodia*, *Brachypeza* and *Cordyla*, and, as might be expected, is a paraphyletic and heterogeneous grouping.

WINNERTZ (1863) divided his *Rymosia* into two sections according to the course of the subcosta. The species with the subcosta ending free (an apomorphic condition!) constitute a natural and monophyletic genus, here called *Rymosia* (s. str.). Among the remaining species *R. fenestralis* and its allies stand rather distinctly apart, and are treated below as a separate genus, *Tarnania*. *R. optiva* is likewise distinct in several respects and is made the type species of a separate genus, *Pseudorymosia*. The other species with the subcosta ending in r are more difficult to deal with. The species studied fall into four distinct groups, which may ultimately deserve recognition as genera. For the time being, however, they are tentatively treated as subgenera of a new genus *Allodiopsis*, because the present material is too restricted and the descriptions of additional species too insufficient to allow conclusions as to their final position. Some poorly known species (among the European ones *Rymosia exclusa*, *R. frenata*, and *R. venosa*) cannot for the present be finally placed in the proposed system, and it is to be expected that a thorough revision of a more comprehensive material will make clearer the interrelationships of the groups now included in *Allodiopsis*.

Key to the genera and subgenera segregated from the compound genus  
*Rymosia* WINN.

- 1 ( 2) Subcosta ending free; the portion of m situated before r-m, the medial fork, and the cubital fork, bare. Clypeus rather short, broadly truncate. One or two strong propleural bristles; scutellum mostly with two stronger marginal bristles. Pale markings of abdomen situated mainly or entirely towards bases of tergites. Male terminalia ventrally closed, without conspicuous crotch and sternal process; cerci simple; styli with an inner lobe tapering to a slender tip which ends in a couple of short spines. Female cerci one-segmented ..... *Rymosia* WINN. s. str.
- 2 ( 1) Subcosta ending in r; some wing veins other than costal and radial bearing macrotrichia. Abdominal tergites with the pale markings broadest along the hind margins (except in *Pseudorymosia*). Male terminalia usually with a well developed sternal process; the inner styler lobe broad and blunt. Female cerci two-segmented .... 3
- 3 ( 4) Medial fork and cubital fork bare, but r-m, and the portion of m situated before r-m, with short macrotrichia; r-m almost longitudinal, in line with the base of  $r_s$ . Clypeus broader than high. Mesanepisternum with short hairs; one or two propleural bristles; scutellum with two stronger marginal bristles. Hind tibia with several curved posterior bristles arranged irregularly in about three rows. Male terminalia with a deep ventral crotch and long sternal process ..... *Tarnania* m.
- 4 ( 3) Medial and cubital forks with at least some dorsal macrotrichia towards the tip; r-m and the portion of m before it bare. Hind tibia with the usual single row of posterior bristles towards the tip ..... 5
- 5 ( 6) Pale markings of the abdomen situated towards the bases of the tergites. Clypeus very short, transverse, distinctly broader than high. Antennae and legs slender; front basitarsus about 1.5 times as long as front tibia; hind tibial spurs distinctly less than half as long as basitarsus. Male 9th tergite with two pairs of bristles of moderate length; cerci double. Female 8th sternite with short, broad lobes without stronger marginal bristles ..... *Pseudorymosia* m.

- 6 ( 5) Pale markings of abdomen broadest along the hind margins of the tergites. Clypeus ovate, usually distinctly higher than broad. Legs not particularly slender; hind tibial spurs about half, or more than half, as long as basitarsus. Female 8th sternite tipped with some stronger bristles ..... *Allodiopsis* m. 7
- 7 ( 8) Scutum without discal bristles, covered with pale setulae for the most part. Two propleural bristles and two stronger scutellars. Hind coxa with two basal bristles, the upper one shorter. Male 9th tergite with a pair of very long blunt-tipped bristles; cerci simple. Female 7th tergite short ..... subg. *Gymnagonia* m.
- 8 ( 7) Discal bristles of scutum more or less developed, at least in posterior part. Three to four propleural bristles, four scutellars. Bristles of male 9th tergite otherwise. Female 7th tergite distinctly longer than the corresponding sternite ..... 9
- 9 (10) Scutum covered with dark setulae; discal bristles well developed. Mesanepisternum setulose. Hind coxae with two basal bristles as in *Gymnagonia* .... subg. *Myrosia* m.
- 10 ( 9) Scutum covered with pale setulae. Anepisternum quite bare. Hind coxae with a single dark basal bristle, the other hairs in the same row minute and pale ..... 11
- 11 (12) Flagellar segments of the antennae short, barely as long as broad, and provided with short stiff macrotrichia. Discal bristles of scutum well developed. Male 9th tergite without long bristles ..... subg. *Notolopha* m.
- 12 (11) Flagellar segments of antennae longer, at least in the male, and without conspicuous macrotrichia. Discal bristles usually reduced. Male terminalia large; 9th tergite with two pairs of long bristles, the outer one shorter ..... subg. *Allodiopsis* m.

*Rymosia* WINN., emend. (s. str.)

*Rymosia* WINNERTZ 1863, p. 810, partim (section A). Type-species: *Mycetophila discoidea* MEIGEN 1818, p. 268 = *Rymosia fasciata* (MEIG.); by designation of JOHANNSEN 1909, p. 102. *Rhymosia* auctt. (incorrect emendation).

Characters: Antennal flagellum without conspicuous macrotrichia. Clypeus short, broadly truncate. Antepenultimate palpal segment with a sharply delimited rounded sensory pit. Scutum with well developed discal (dorsocentral) bristles, or these reduced, or absent; one or two propleural bristles; scutellum mostly with two strong marginal bristles; mesanepisternum bare or with a few minute setulae. Subcosta short and ending free; r-m often distinctly longer than the medial pedicel;  $r_5$  divergent from  $m_1$ , or apically subparallel with it; cubital fork typically long, narrow in basal half, then abruptly wider, the base of the fork before the base of the medial pedicel; anal vein long and distinct. Medial fork, cubital fork, r-m, and m before r-m, without macrotrichia. Hind coxae with one or two basal bristles (if two, the upper one smaller); front tarsi of male in some species with segments 3 and 4 spinose beneath. Pale markings of abdomen situated mainly or exclusively towards bases of tergites. Male terminalia with 9th tergite and cerci simple; underside of the terminalia much closed without conspicuous crotch or sternal process; inner stylar lobe tapering to a slender tip, which ends in a couple of short spiny bristles. Lobes of the 8th sternite in the female tipped with some few bristles; cerci one-segmented.

Species: European species belonging here are *Rymosia acta* DZIEDZ., *R. armata* LACKSCH., *R. beaucournui* MAT., *R. bifida* EDW., *R. britteni* EDW., *R. connexa* WINN., *R. cottii* TOLL., *R. cretensis* LUNDSTR., *R. fasciata* (MEIG.), *R. fraudatrix* DZIEDZ., *R. gracilipes* DZIEDZ., *R. guttata* LUNDSTR., *R. lundstroemi* DZIEDZ., *R. placida* WINN., *R. setigera* WINN. (? syn. *R. appendiculata* LACKSCH.), *R. spiniforceps* MAT., *R. spinipes* WINN., *R. truncata* WINN. (syn. *R. signatipes* v.d. WULP), *R. virens* DZIEDZ., and *R. winnertzii* BARENDR. In addition, the genus includes *R. scopulosa* BECK. (Canary Islands), *R. maderensis* STORÅ (Madeira, Azores), of the North American species apparently at least *R. filipes* LOEW, *R. imitator* JOH., *R. inflata* JOH., *R. lacki* EDW., *R. serripes* JOH., and *R. triangularis* SHAW, and of the South American ones probably at least *R. ariosai* LANE, *R. damascenoi* LANE, and *R. pilosa* EDW.

The genus has a wide distribution in the Northern Hemisphere and extends from the Arctic at least to Peru and Brazil, Central Africa, India and northern Burma, but is not known from southernmost South America or from New Zealand.

Discussion: *Rymosia* s. str. is a well marked, homogeneous and obviously monophyletic genus, as is demonstrated by the set of apomorphies: free-ending subcosta, bare fork veins, colour distribution on abdomen, one-segmented female cerci, and the structure of the male terminalia. The three first-named characters *Rymosia* shares with *Exechia* s. str., and a close relationship with this genus is therefore possible, though not very probable; at any rate neither of them can be derived from the other.

#### *Pseudorymosia* gen. n.

Type-species: *Rymosia optiva* DZIEDZICKI 1910, p. 98, figs. 103 – 104.

Characters: Antennae long and slender; flagellar segments much longer than broad. Clypeus very low, distinctly broader than high. Scutum strongly arched, dull, covered with a rather sparse, shaggy (not closely decumbent), dark pile, without discal bristles, except just before scutellum; marginal sclerite above the anterior stigma very narrow. Prothoracic episternum with 1 – 2 (– 3?) bristles; two scutellars. Pleura high; anepisternum with some short setulae. Subcosta ending in  $r_1$ ;  $r_5$  towards tip somewhat curved downwards, parallel to or slightly convergent with  $m_1$ ;  $r-m$  somewhat longer than the medial pedicel; base of the cubital fork approximately under that of the medial pedicel or even under the base of the medial fork. Branches of both forks with dorsal macrotrichia towards apex and not becoming very weak before attaining the wing margin; some membrane macrotrichia present on the anal lobe, as in *Exechiopsis* subg. *Exechiopsis* or *Trichonta*. Legs long and slender; hind coxae often with a couple of smaller bristles around the usual strong basal one, or with a few longer bristles between the basal and apical ones; tarsi long; front basitarsus about half as long again as front tibia; hind basitarsus more than twice as long as the hind tibial spurs; male front tarsi simple. Abdomen long and slender; the pale markings situated

towards the bases of the tergites. Male terminalia rather large, much closed beneath, without conspicuous crotch or sternal process; 9th tergite with two pairs of longer, finely pointed bristles; cerci double. Female 7th tergite short, about as long as the sternite; 8th sternite short, its lobes rounded, finely hairy, without strong marginal bristles; cerci short, two-segmented.

Species: *Pseudorymosia optiva* (DZIEDZ.) comb. n. (see above). *Rymosia fovea* DZIEDZ. is also probably a *Pseudorymosia*; it is said to have three propleural bristles, whereas *P. optiva* has one or two. Outside Europe the genus occurs at least in Burma.

Discussion: The type species differs from the other «*Rymosia*» species with bristly fork veins in its more slender appearance, which is more reminiscent of an *Exechiopsis*, and in the coloration of the abdomen, which is exactly as in some species of *Rymosia* s. str. From the latter genus *Pseudorymosia* differs mainly in being more plesiomorphic in several respects (course of sc, trichiation of the fork veins and hind coxae, structure of male and female terminalia).

#### *Tarnania* gen. n.

Type-species: *Rymosia tarnanii* DZIEDZICKI 1910, p. 99, figs. 107, 108.

Characters: Head broad; clypeus short, cordate. Antennae rather short; flagellar segments without conspicuous macrotrichia. Palpi long, distinctly setulose; the antepenultimate segment not shortened, with a long sensory groove. Scutum rather highly arched, dull, not silvery at sides, covered with small dark setulae; the discal (dorsocentral) bristles well developed. One or two propleural bristles; two stronger scutellars. Mesothoracic anepisternum with short hairs, rather high, rounded, hexagonal ovate. The fork veins bare, but r-m, and the portion of m before r-m with numerous ventral macrotrichia. Subcosta ending in r; r-m almost longitudinal, appearing as a direct inward continuation of the base of  $r_5$ , not much longer than the pedicel of the medial fork, and without a distinct weaker break;  $r_5$  in basal part diverging from, then subparallel with,  $m_1$ ; branches of the medial fork not distinctly weaker at tip; cubital fork long, as in *Rymosia*;  $cu_2$  long and strong; anal vein long and distinct. Hind coxae with two basal bristles (the upper one smaller); hind tibiae with several curved posterior bristles placed irregularly in more than one row; male front tarsi simple. The pale markings on the abdomen broadest along the hind margins of the tergites. Male abdominal terminalia with a deep ventral crotch and a long sternal process; the inner lobe of the styli broad and blunt, finely striate dorsally. Female 7th tergite a little longer than the corresponding sternite; 8th sternite long, tipped with some stronger bristles; cerci two-segmented, with the basal segment almost parallel-sided in profile, and the end segment elongate ovate.

Species: *Tarnania dziedickii* (EDW.) comb. n. (*Rhymosia dziedickii* EDWARDS 1941a, p. 78, fig. 8, h, i), *T. fenestralis* (MEIG.) comb. n. (*Mycetophila fenestralis* MEIGEN 1818, p. 265; *Rymosia fenestralis* WINNERTZ 1863, p. 822), *T. nemoralis* (EDW.) comb. n. (*Rhymosia nemoralis* EDWARDS 1941a, p. 78, fig. 8, j, k), *T. tarnanii* (DZIEDZ.) comb. n. (*Rymosia tarnanii* DZIEDZICKI 1910, p. 99, figs. 107, 108).

The genus is not known outside Europe.

Discussion: *Tarnania* is well marked as a monophyletic genus by the apomorphies of the wing vein trichiation, arrangement of the posterior bristles on the hind tibiae, and details of the male terminalia. In other respects it is one of the most plesiomorphic genera of the tribe.

### *Allo diopsis* gen. n.

Type-species: *Rhymosia rustica* EDWARDS 1941a, p. 75, figs. 7, a-c.

Characters: Clypeus rather long, higher than broad. Palpi weakly setulose, the antepenultimate segment short. Thorax not dorsiventrally depressed; two to four propleural bristles; two or four scutellars. Subcosta ending in r; r-m oblique, bare, subequal in length to the medial pedicel, or somewhat longer; branches of both forks strong, but becoming faint apically; base of the cubital fork situated before to beyond the base of the medial pedicel, and before the base of the medial fork; anal vein rather long but not particularly strong. Humeral crossvein, r, r<sub>1</sub>, r<sub>5</sub>, and tips of the fork veins with macrotrichia; the portion of m before r-m bare. Hind tibiae towards tip with some short posterior bristles placed in one row; hind tibial spurs about half as long as the basitarsus, or longer; male front tarsi simple. Pale markings on the abdomen broadest along the hind margins of the tergites. Male terminalia with a distinct sternal process and a large dorsally striate inner stylar lobe. Female 7th tergite longer than the corresponding sternite, the lobes of the 8th sternite tipped with distinct bristles; cerci two-segmented.

Discussion: The genus is a provisional one (see p. 167), and probably paraphyletic. The better known species may tentatively be divided into four more natural subgenera.

### Subgenus *Gymnogonia*, subg. n.

Type-species: *Rhymosia sintenisi* LACKSCHEWITZ 1937, p. 30, fig. 13.

Characters: As stated below for the subgenus *Allo diopsis* s. str. but differing as follows. Clypeus elongate ovate, distinctly longer than broad, arched in side view. Discal bristles absent, or rudimentary ones present on the posterior part of the scutum; 2 (-3) propleurals; 2 scutellars. Hind coxa with two basal bristles, the uppermost smaller. Male terminalia large; 9th tergite with a single pair of

very long blunt-tipped bristles; ventral crotch shallow; sternal process short, dark, with capitate tip; dorsal stylomere with the apex truncate and densely serrate with dark peg-like spinulae, and with an inner basal projection; ventral stylomere weakly sclerotized. Female 7th tergite short, not distinctly longer than the corresponding sternite; basal segment of the cerci not conspicuously lengthened.

Species: Of the European «*Rymosia*» species the following belong to *Gymnogonia*: *Allo-diopsis ducta* (DZIEDZ.) comb. n. (*Rymosia ducta* DZIEDZICKI 1910, p. 99, figs. 105 – 106), *Allodiopsis dulcia* (DZIEDZ.) comb. n. (*Rymosia dulcia* DZIEDZICKI 1910, p. 100, figs. 117 – 118), *Allodiopsis excogitata* (DZIEDZ.) comb. n. (*Rymosia excogitata* DZIEDZICKI 1910, p. 98, figs. 98 – 99; *Rymosia simulatrix* LACKSHEWITZ 1937, p. 31, fig. 14; perhaps not specifically distinct from *R. gracilis* WINN.), *Allodiopsis gracilis* (WINN.) comb. n. (*Rymosia gracilis* WINNERTZ 1863, p. 820), *Allodiopsis macrura* (WINN.) comb. n. (*Rymosia macrura* WINNERTZ 1863, p. 818; imperfectly known), *Allodiopsis praeformida* (DZIEDZ.) comb. n. (*Rymosia praeformida* DZIEDZICKI 1910, p. 100, figs. 112 – 113), *Allodiopsis rufilatera* (EDW.) comb. n. (*Rymosia rufilatera* EDWARDS 1941a, p. 76, figs. 8, a-c), and *Allodiopsis sintenisi* (LACKSCH.) comb. n. (*Rymosia sintenisi* LACKSHEWITZ 1937, p. 30, fig. 13). In addition to these, *Rymosia exclusa* DZIEDZ. and *R. venosa* DZIEDZ. may also belong to *Gymnogonia*. The North American *Rymosia akeleyi* JOH. and perhaps also *R. diffissa* JOH. belong here, as do some few apparently undescribed European and Asiatic species in the present material. *Rymosia cinerea* FREEM. from southernmost South America has macrotrichia towards the tips of the fork veins and should also perhaps be placed in *Gymnogonia* on account of the thoracic chaetotaxy, coloration of the abdomen, and structure of the male terminalia.

Discussion: The subgenus *Gymnogonia* shows remarkable similarities with *Allodia*. It agrees with the subgenus *Allodia* s. str. of that genus in the long clypeus, lack of discal bristles, and colour pattern on the abdomen, and with the subgenus *Brachycampta* in having a single pair of very long bristles on the male 9th tergite. From both subgenera of *Allodia* it differs in the generally larger body size, more distinct anal vein, setulose tips of the fork veins, and presence of posterior bristles on the hind tibiae (these latter seem, however, to be lacking in *Allodiopsis ducta*).

Subgenus *Allodiopsis* s. str., subg. n.

Type-species: that of the genus, see above.

Characters: Flagellar segments of antennae without conspicuous stiff macrotrichia. Head, including clypeus, scutum, scutellum, and part of front coxae, clothed with decumbent pale setulae; scutum somewhat silvery grey along the sides when viewed from above. Discal bristles usually short or absent from the anterior part of the scutum. Mesanepisternum quite bare; three to four propleural bristles; four scutellars.  $R_5$  nearly straight, distinctly diverging from  $m_1$ ; r-m without distinct weaker point; anal vein not very strong. Hind coxae with a single dark basal bristle; the other hairs of the same row minute and pale, except

towards tip of coxae. Male abdominal terminalia large and of distinctive structure, different from that of the other subgenera in many details, including the two pairs of longer bristles on the 9th tergite, distinctly double cerci, shape of the sternal process, and the styli with a strongly sclerotized, narrow and sigmoid ventral lobe. Female 7th tergite long and sheathing; basal segment of the cerci long, with a slender apical part.

Species: *Allodiopsis domestica* (MEIG.) comb. n. (*Mycetophila domestica* MEIGEN 1830, p. 303; *Rymosia domestica* WINNERTZ 1863, p. 824), *Allodiopsis rustica* (EDW.) comb. n. (*Rhymosia rustica* EDWARDS 1941a, p. 75, figs. 7, a-c), *Allodiopsis pseudodomestica* (LACKSCH.) comb. n. (*Rhymosia pseudodomestica* LACKSCHEWITZ 1937, p. 29, fig. 12). The subgenus also occurs in North America, since *Rhymosia captiosa* JOH. (considered to be synonymous with *A. domestica* by SHAW and FISCHER 1952, p. 203) clearly belongs to it, in Japan (OKADA 1939, p. 318), and in Burma.

Discussion: The species are very like each other, differing chiefly in details of the male terminalia, and the subgenus is therefore no doubt monophyletic.

#### Subgenus *Notolopha* subg. n.

Type-species: *Mycetophila cristata* STAEGER 1840, p. 254; *Rymosia cristata* (STAEG.) WINNERTZ 1863, p. 819.

Characters: Antennae short; the flagellar segments barely as long as broad and provided with short stiff macrotrichia. Clypeus shorter than in *Gymnogonia*. Head and scutum covered with pale setulae; dorsocentral discal bristles well developed, in the type-species rather unusual, short and very strong, many of them broadly truncate; three to four propleural bristles; four scutellars; mesanepisternum elongate hexagonal, bare. Hind coxae with a single strong and dark basal bristle. Male terminalia not as large as in *Allodiopsis* s. str. and *Gymnogonia*, and of different structure; no long bristles on the 9th tergite; cerci double. Female 7th tergite and cerci shorter than in *Allodiopsis* s. str.

Species: *Allodiopsis cristata* (STAEG.) comb. n. (*Mycetophila cristata* STAEG.), and a closely allied species with normal finely pointed discal bristles, from Northern Europe. The subgenus seems to be known exclusively from Europe, but probably also occurs elsewhere, at least in Northern Asia.

Discussion: *Notolopha* comes nearest to *Allodiopsis* s. str., but the antennae and male terminalia are distinctive.

#### Subgenus *Myrosia* subg. n.

Type-species: *Mycetophila maculosa* MEIGEN 1818, p. 268; *Rymosia maculosa* (MEIG.) WINNERTZ 1863, p. 821.

This is the only species referred to the subgenus *Myrosia*. It differs from the representatives of the three other subgenera in having the setulae of the scutum, head and clypeus dark instead of pale, and also in the setulose anepisternum, and differently shaped male terminalia. The hind coxae bear two basal bristles, as in the subg. *Gymnogonia*.

#### Exechia Winn. as a compound genus.

In the current generic system of the *Exechiini*, *Exechia* WINN. is distinguished from the other genera (except for certain *Anatella* and *Cordyla* species) by the shortness of the cubital fork, which has its base situated distinctly beyond that of the medial fork. Apart from this character and the lack of the special ones of *Anatella*, *Cordyla*, *Allodia* and *Brachypeza*, the genus is not easy to characterize. The *Exechia* species are rather slender insects with moderately long antennae, palpi and legs, non-produced costa, and normal, not unusually distinct  $cu_2$ . The media and cubitus are usually bare, but in one South American group the medial fork bears macrotrichia. The anal vein is often rather long and distinct, but one group occurring in the tropics of the Old World, Australia and New Zealand is said to lack this vein. The main diagnostic character, the shortness of the cubital fork, is clearly an apomorphic one. Its value in generic distinction is diminished, however, by the fact that it represents a common trend in the fungus gnats. The cubital fork has evidently become short several (perhaps as many as ten) times independently along different evolutionary lines in the *Sciophilini*, *Gnoristini*, *Exechiini* and *Mycetophilini*, even leading in parallel lines to complete abolition of the fork in the *Sciophilini* (*Parvicellula*, *Acnemia*, etc.), *Exechiini* (*Boraceomyia* LANE) and *Mycetophilini* (*Zygophronia*, *Zygomyia*, *Sceptonia*). In the *Exechiini*, apart from *Exechia*, a shortened cubital fork is known in most *Anatella* and some *Cordyla* species. Accordingly, the possible synapomorphy of this character in *Exechia* has to be checked against other apomorphic features correlated with it. I have failed to find such proof; no conclusive evidence could be adduced in favour of the view that all the species customarily included in *Exechia* really belong together and form a monophyletic group. On the contrary, these species fall into three distinct groups, apparently having no close connexion with each other but rather exhibiting affinity relations in different directions outside *Exechia*. Thus, for the present, the possibility cannot be excluded that in *Exechia* the shortness of the cubital fork is to some extent a convergent rather than a true synapomorphic character, in which case the genus, in its traditional delimitation, cannot be maintained in a more natural and phylogenetic system.

WINNERTZ (1863) himself divided his *Exechia* into two sections, which were characterized in detail by EDWARDS (1925) as follows:



*Rs* almost or quite straight; fork of *Cu* short, *Cu*<sub>2</sub> quite straight; *r-m* very long, more than twice as long as the stem of the median fork; *Sc* ending free; pale markings of abdomen when present nearly always situated towards the bases of the segments; two or three propleural bristles, placed side by side; ninth abdominal sternite of male small (Group I)

*Rs* usually distinctly curved downwards at the tip; fork of *Cu* often rather long, *Cu*<sub>2</sub> more or less curved; *r-m* not more than twice as long as the stem of the median fork; *Sc* more or less distinctly ending in *R*; hind margins of abdominal tergites pale; one long propleural bristle, with sometimes a second shorter one above or below it; ninth abdominal sternite of male often quite large, occupying the underside of the hypopygium (Group II)

As so often in such divisions into two parts, one group, in the present case the first, is based mainly on apomorphic characters and fulfils the requirements of a phylogenetically natural grouping, whereas the other does not or doubtfully does so. EDWARDS's Group I (Group II b of WINNERTZ) is called below *Exechia* (s. str.). The second group (Group II of EDWARDS) comprises two natural sections, here called *Exechiopsis* and *Pseudexechia*. It remains to be seen whether this division into three genera will hold good as regards exotic material; some preliminary studies in this direction indicate that to some extent it will, but that probably some subgenera are needed to express the whole variation of the old *Exechia*.

Key to the genera and subgenera segregated from the compound genus

*Exechia* WINN.

- 1 ( 2) Subcosta ending free; *r*<sub>1</sub> little if any longer than *r*; *r*<sub>5</sub> almost straight, mostly divergent from *m*<sub>1</sub>; *r-m* more than twice as long as the stem of the medial fork. Scutum with pale decumbent setulae and usually with discal bristles; 2-4 propleural bristles placed side by side. Tip of hind tibia normal. Pale markings of abdomen, when present, usually situated towards the bases of the tergites. Female cerci mostly two-segmented ..... *Exechia* WINN.
- 2 ( 1) Subcosta more or less distinctly ending in *r*; *r-m* at most twice as long as the stem of the medial fork, rarely longer. One strong propleural bristle, often accompanied by a second shorter one. Abdominal tergites pale apically. Female cerci often one-segmented ..... 3
- 3 ( 4) Scutum without discal bristles. Clypeus ovate, higher than broad. Tip of hind tibia normal. Male 9th tergite rather high, not divided into two distant halves; cerci bipartite with shorter median lobe; 9th sternite basally fused with the gonocoxopodites and ending in a short free bud-like sternal process ..... *Pseudexechia* m.
- 4 ( 3) Discal bristles of scutum well developed. Clypeus short, broader than high. Male 9th tergite divided into two somewhat pointed halves, each tipped with one or two longer bristles; cerci otherwise ..... *Exechiopsis* m. 5
- 5 ( 6) Hind tibial tip distinctly oblique on the posterior side. Wings long; *r*<sub>5</sub> more or less distinctly curved downwards at tip and convergent with *m*<sub>1</sub> apically. Male 9th sternite with a conspicuous setulose basal part separated from the bases of the gonocoxopodites by grooves or sutures. Female cerci one-segmented ..... subg. *Exechiopsis* s. str.
- 6 ( 5) Tip of hind tibia not conspicuously oblique. *R*<sub>5</sub> subparallel with *m*<sub>1</sub> towards the tip of the wing. Male 9th sternite otherwise constructed. Female cerci, as far as is known, two-segmented ..... subg. *Xenexechia* m.

*Exechia* WINN., emend.

*Exechia* WINNERTZ 1863, p. 879, partim (section II b), EDWARDS 1924, partim (Group I)  
Type-species: *Tipula fungorum* DE GEER sensu WINNERTZ 1863, p. 886 (as *Exechia fungorum* (DEG.)) = *Exechia fusca* (MEIG.); by designation of JOHANNSEN 1909, p. 106.

*Parexechia* BECHER 1886, p. 62. Type-species: *Parexechia concolor* BECHER 1886, p. 63 = *Exechia frigida* (BOHEM.), teste EDWARDS (1923, p. 237); by monotypy.

? *Brachydicrania* SKUSE 1888, p. 1215, pl. 32, fig. 16. Type-species not designated.

WINNERTZ (l. c.) cites *Mycetophila fusca* MEIG. as a synonym for his *Exechia fungorum* (DEG.), and DZIEDZICKI (1915, figs. 266 – 267) has shown by figures drawn from a specimen of WINNERTZ that his *E. fungorum* is the species nowadays known as *Exechia fusca* (MEIG.). See also STONE et al. 1965, p. 206. The possible synonymy of *Brachydicrania* SKUSE has not been checked.

Characters: Antennae of medium length; the flagellar segments usually somewhat longer than thick, and without conspicuous stiff macrotrichia. Clypeus short. The antepenultimate segment of the palpi short, with an ovate sensory pit. Scutum and scutellum covered with pale, decumbent, on the whole backwardly directed setulae; the acrostichal and dorsocentral rows of discal bristles well developed, separated from the lateral bristles by rather narrow areas, or more seldom the discal bristles reduced to absent; scutellum with two strong marginal bristles; anterior part of pronotum and the prothoracic episternum each with two to four stronger bristles; pleura somewhat lower than in *Exechiopsis*; mesothoracic anepisternum usually bare, in some larger species with some minute setulae. Wing membrane with the microtrichia arranged in definite lines; no macrotrichia on the membrane except in some species on the anal angle between 2a and the wing margin; humeral cross-vein bare or with a few ventral macrotrichia; median fork and cubital fork bare. Subcosta very short, ending free;  $r_1$  not much longer than  $r$ ;  $r_5$  almost straight and widely divergent from  $m_1$ , or slightly curved downwards towards the tip and there subparallel with  $m_1$ ;  $r-m$  oblique, long, bare or at the distal end with some macrotrichia, with an indistinct weaker spot, at least twice as long as the stem of the medial fork, usually much longer; cubital fork short, its base distinctly beyond that of the medial fork;  $cu_{1b}$  straight;  $cu_2$  moderately long; 1a variable from distinct and rather long to very weak or practically absent. Legs moderately slender; front basitarsi a little shorter than front tibiae, or usually longer, but seldom by more than a quarter of its length; hind basitarsus about twice as long as the longer hind tibial spur; hind coxae with a single strong basal bristle; hind tibiae with the usual row of posterior bristles towards tip. Abdomen with the pale markings, if present, usually situated mainly towards the bases of the tergites. Male 9th tergite divided into two separate, somewhat pointed halves, each tipped with one or two longer bristles; cerci simple; 9th sternite variously developed, but mostly inconspicuous, its basal hairy part being narrow and more or less fused with the gonocoxopodites; styli without a large blunt, dorsally striate inner lobe. Female cerci usually two-segmented.

Species: *Exechia* s. str. includes the following European species: *bicincta* (STAEG.), *cincta* WINN., *confinis* WINN., *contaminata* WINN., *cornuta* LUNDSTR., *dizona* EDW., *dorsalis* (STAEG.), *exigua* LUNDSTR., *festiva* WINN., *frigida* (HOLMGR.), *fusca* (MEIG.), *lucidula* (ZETT.), *lundstroemi* LANDR., *maculipennis* (STANN.), *nana* (STAEG.), *nigra* EDW., *nigrofusca* LUNDSTR., *nigroscutellata* LANDR., *nitidicollis* LUNDSTR., *pallida* (STANN.), *parva* LUNDSTR., *papyracea* STACK., *pseudocincta* STROBL., *pseudofestiva* LACKSCH., *separata* LUNDSTR., *sororcula* LACKSCH., *spinigera* WINN., *spinosa* BUK., *spinuligera* LUNDSTR., *unifasciata* LACKSCH., and *unimaculata* (ZETT.). Of the North American *Exechia* species, at least the following obviously belong here; many of them are close to, if not identical with, the European ones mentioned in parentheses: *absoluta* JOH. (*separata*), *absurda* JOH. (*cincta*), *attrita* JOH., *auxiliaria* JOH. (*unifasciata*), *bella* JOH. (*cornuta*), *bellula* JOH. (*exigua*), *capillata* JOH., *captiva* JOH. (*dorsalis*), *casta* JOH. (*frigida*), *cinnamata* JOH., *nativa* JOH. (*pseudocincta*), *nugatoria* JOH. (*nigroscutellata*), *obediens* JOH. (*dizona*), *palmata* JOH., *pollex* SHAW, *repanda* JOH. (*parva*), *quadrata* JOH. (*pallida*), *satjata* JOH. A number of species probably belonging to *Exechia* s. str. are on record from the Oriental Region, Africa, Australia and New Zealand, but none of the *Exechia* species described from South America by FREEMAN and LANE can be referred to the genus with certainty.

Discussion: Some natural species groups can be discerned within *Exechia* s. str. Among the European species *E. pallida* deviates most strikingly from the others in the colouring of the abdomen, and in having the posterior row of spiny bristles on the front tibiae modified to a dense comb-like structure of pale blunt peg-like spinulae; this structure is repeated on the anterior side of the middle tibiae. Several other (non-European) species agree with *E. pallida* in the latter character, indicating the possibility of discerning a natural subgenus.

### *Exechiopsis* gen. n.

Type-species: *Exechia subulata* WINNERTZ 1863, p. 881, as figured by DZIEDZICKI 1915, figs. 258 – 259.

Characters: Antennae usually slender; the flagellar segments distinctly longer than broad, at least the basal ones mostly with some distinct fine and straight macrotrichia. Clypeus short. The antepenultimate segment of the palpi with a longitudinal sensory groove. Scutum highly arched, dull, covered by a rather shaggy pile of short dark setulae; the dorsocentral discal bristles well developed; scutellum mostly with two strong marginal bristles. Pleura high; prothoracic epimeron with one or two stronger bristles; mesothoracic anepisternum high and bare. Subcosta ending in  $r$ ;  $r_1$  longer than  $r$ ;  $r_5$  more or less curved downwards at tip, not divergent from  $m_1$ ;  $r-m$  oblique, with a weaker spot in the apical part, practically bare, at most twice as long as the pedicel of the medial fork, rarely longer; medial fork and cubital fork usually without macrotrichia; the base of the cubital fork extending beyond that of the medial fork, often but slightly;  $cu_{1b}$  not quite straight;  $1a$  more or less distinct. Legs slender; fore basitarsus longer than the tibia; hind basitarsus more than twice as long as the hind tibial spurs; hind coxa with a strong basal bristle, and often some quite conspicuous

smaller bristles in the same row; hind tibiae with the usual row of posterior bristles. Abdomen slender; the pale markings mostly present in some segments, occupying the hind margins of the tergites. Male 9th tergite distinctly divided into two parts, each ending in one or two longer bristles; a distinct sternal process usually present; male cerci simple.

Discussion: *Exechiopsis* differs from *Exechia* in several points, and is on the whole more plesiomorphic. The difference between them in the present material is sharp enough to justify generic separation and even to make a close relationship doubtful. It is possible but not clearly established that the shortness of the cubital fork in the two genera is convergent. *Pseudexechia* is superficially more similar to *Exechiopsis*, but the features they have in common are all plesiomorphic except for the shortness of the cubital fork.

*Exechia goianensis* LANE (1947, p. 356) and some other South American species described by LANE (1947, 1951, 1956) under *Exechia* may prove to belong to *Exechiopsis*, in which case the name *Boraceomyia* LANE (1948, p. 231) will be the valid name for this genus. The type-species of *Boraceomyia*, *B. edwardsi* LANE, was considered by the author (LANE 1956, p. 147) to be a synonym of *Exechia goianensis*.

The present material of *Exechiopsis* may be divided into two subgenera *Exechiopsis* s. str. and *Xenexechia*.

#### Subgenus *Exechiopsis* s. str., subg. n.

Type-species: that of the genus, see above.

Characters: Mostly larger, slender species. Wings long;  $r_1$  in most cases much (up to 60 %) longer than  $r$ ;  $r_5$  distinctly curved down towards tip and there convergent with the apical part of  $m_1$  (which is slightly upcurved);  $r-m$  about twice as long as the stem of the median fork. Basal hind margin of the wing (behind 2a) with some few macrotrichia on the membrane. Apex of hind tibia with a dorsal split; the posterior end margin of the tibia distinctly oblique. Male 9th sternite with a conspicuous setulose basal part which may be quite broad and occupy a considerable part of the underside of the terminalia, or is narrower, but nearly always quite distinctly separated from the bases of the gonocoxopodites (basistyli) by grooves or sutures. The male 9th tergite usually divided into two distant, somewhat pointed halves, each ending in a longer bristle; cerci simple. Female cerci one-segmented.

Species: *Exechiopsis clypeata* (LUNDSTR.) comb. n. (*Exechia clypeata* LUNDSTRÖM 1911, p. 405, pl. 13, figs. 3–4), *Exechiopsis distendens* (LACKSCH.) comb. n. (*Exechia distendens* LACKSCHWITZ 1937, p. 28, fig. 11), *Exechiopsis fimbriata* (LUNDSTR.) comb. n. (*Exechia fimbriata* LUNDSTRÖM 1909, p. 47, figs. 98–99), *Exechiopsis forcipata* (LACKSCH.) comb. n. (*Exechia forcipata* LACKSCHWITZ 1937, p. 27, fig. 10), *Exechiopsis furcata* (LUNDSTR.) comb. n. (*Exechia furcata* LUNDSTRÖM 1911, p. 406, pl. 13, figs 5–7), *Exechiopsis hammi*

(EDW.) comb. n. (*Exechia hammi* EDWARDS 1925, p. 598, figs. 57–59), *Exechiopsis indecisa* (WALK.) comb. n. (*Mycetophila indecisa* WALKER 1856, p. 22), *Exechiopsis ingrca* (STACKELB.) comb. n. (*Exechia ingrca* STACKELBERG 1948, p. 102, figs. 13–15), *Exechiopsis intersecta* (MEIG.) comb. n. (*Mycetophila intersecta* MEIGEN 1818, p. 271), *Exechiopsis januarii* (LUNDSTR.) comb. n. (*Exechia januarii* LUNDSTRÖM 1913a, p. 104, figs. 1–2), *Exechiopsis jenkinsoni* (EDW.) comb. n. (*Exechia jenkinsoni* EDWARDS 1925, p. 600, fig. 62), *Exechiopsis lackschewitziana* (STACKELB.) comb. n. (*Exechia lackschewitziana* STACKELBERG 1948, p. 97, figs. 11–12; *Rhymosia leruthi* TOLLET 1955, p. 464, figs. 13–14, new synonymy), *Exechiopsis landrocki* (LUNDSTR.) comb. n. (*Exechia landrocki* LUNDSTRÖM 1912, p. 36, figs. 36–37), *Exechiopsis ligulata* (LUNDSTR.) comb. n. (*Exechia ligulata* LUNDSTRÖM 1913b, p. 312, figs. 13–14), *Exechiopsis magnicauda* (LUNDSTR.) comb. n. (*Exechia magnicauda* LUNDSTRÖM 1911, p. 404, pl. 13, figs. 1–2), *Exechiopsis pseudopulchella* (LUNDSTR.) comb. n. (*Exechia pseudopulchella* LUNDSTRÖM 1912, p. 31; *Exechia pulchella* LUNDSTRÖM 1909, p. 45, figs. 83–84), *Exechiopsis pulchella* (WINN.) comb. n. (*Exechia pulchella* WINNERTZ 1863, p. 883; ?*Exechia forciposa* TOLL.), *Exechiopsis subulata* (WINN.) comb. n. (*Exechia subulata* WINNERTZ 1863, p. 881), *Exechiopsis trisetata* (TOLL.) comb. n. (*Exechia trisetata* TOLLET 1955, p. 460, figs. 7–9), and *Exechiopsis unguiculata* (LUNDSTR.) comb. n. (*Exechia unguiculata* LUNDSTRÖM 1911, p. 408, pl. 13, figs. 13–14), all from Europe. *Exechiopsis* s. str. obviously also includes *Exechia coremura* EDW. and *E. wizzavonensis* EDW. from Corsica, and the North American species *E. aviculata* SHAW., *E. nugax* JOH., and *E. umbratica* JOH. (the last is doubtfully distinct from *Exechiopsis subulata*), possibly also *E. nexa* JOH. Finally, there are some apparently undescribed species in the present material from Finland and Burma.

According to our present knowledge the subgenus is thus mainly Holarctic in distribution.

Discussion: This subgenus appears to be quite natural, except that the inclusion of *Exechia pulchella* WINN. and probably also of the related *E. jenkinsoni* EDW. is uncertain because of the different shape of the male 9th sternite, the indistinctly separated basal part of the male 9th sternite, and the absence of macrotrichia on the anal angle of the wing. However, since the hind tibial end is typical of *Exechiopsis* s. str., the species are tentatively placed here.

#### Subgenus *Xenexechia* subg. n.

Type-species: *Exechia perspicua* JOHANNSEN 1912, p. 67, figs. 31, 159.

Characters: Differs from the subgenus *Exechiopsis* s. str. in the usually smaller body size, shorter and less curved  $r_5$ , absence or poor development of the dorsal split on the tip of the hind tibia, and less conspicuous basal part of the 9th sternite in the male. The females are poorly known, but *E. pollicata* EDW. has two-segmented cerci.

Species: *Exechiopsis crucigera* (LUNDSTR.) comb. n. (*Exechia crucigera* LUNDSTRÖM 1909, p. 48, figs. 100–101), *Exechiopsis leptura* (MEIG.) comb. n., sensu DZIEDZICKI 1915, figs. 260–261 (*Mycetophila leptura* MEIGEN 1830, p. 301), *Exechiopsis perspicua* (JOH.) comb. n. (*Exechia perspicua* JOHANNSEN 1912, p. 67, figs. 31, 159), *Exechiopsis pollicata* (EDW.) comb. n. (*Exechia pollicata* EDWARDS 1925, p. 599, figs. 60–61), and a couple of undescribed species in the present material.

Discussion: The *Exechia* species described by FREEMAN (1952, 1953) from southernmost South America (*E. bifida*, *E. brevifurcata*, *E. extensa*, *E. funerea*, *E. furcilla*, *E. setigera*, and *E. truncata*) appear to be rather close to *Xenexechia*, but they have a better developed dorsal split to the hind tibial tip (though not as extreme as in the subgenus *Exechiopsis* s. str.), and the branches of the medial fork (at least the anterior one) bear some macrotrichia. For clarification of the position of these species more information is needed about other South American species described under *Exechia*; in any case they do not belong to *Exechia* s. str.

*Pseudexechia* gen. n.

Type-species: *Exechia trisignata* EDWARDS 1913, p. 370, figs. 73–75.

Description: Flagellar segments of antennae longer than broad, with only a few inconspicuous macrotrichia. Clypeus ovate, higher than broad, arched in lateral view; face very short, narrowly band-like. Scutum without discal bristles, its sides often with a silvery sheen when viewed from above. One or two propleural bristles; two scutellars; mesanepisternum bare. Subcosta short, curved against  $r$ ; but not actually connected with it;  $r_1$  not much longer than  $r$ ;  $r_5$  nearly straight, usually rather distinctly divergent from  $m_1$ ;  $r-m$  subequal in length to the medial stem, or slightly shorter; cubital fork short, as in *Exechia* s. str., with the base beyond (rarely under) that of the medial fork; only  $r$ ,  $r_1$  and  $r_5$  with macrotrichia. Front basitarsus somewhat longer than front tibia; hind coxa with a single basal bristle; hind tibia with a row of posterior bristles towards tip; tip of hind tibia not conspicuously oblique on the posterior side. The pale markings on the abdomen broadest along the hind margin of the tergites. Male terminalia rather large; 9th tergite high, not distinctly divided into two halves or prolonged in two lateral lobes, and without conspicuous longer bristles; 9th sternite basally narrow and completely fused with the basistyli; its tip forming a short bud-like sternal process; cerci double, with a shorter inner lobe; styli with a blunt and often dorsally striate inner process. Female cerci one-segmented.

Species: *Pseudexechia parallela* (EDW.) comb. n. (*Exechia parallela* EDWARDS 1925, p. 596), *Pseudexechia trisignata* (EDW.) comb. n. (*Exechia trisignata* EDWARDS 1913, p. 370, figs. 73–75), *Pseudexechia trivittata* (STAEG.) comb. n. (*Mycetophila trivittata* STAEGER 1840, p. 261, *Exechia trivittata* WINNERTZ 1863, p. 884). Here apparently also belong *Exechia canalicula* JOH. (perhaps not distinct from *P. trisignata*), *E. hamulata* LACKSCH. (close to *P. parallela*?), and *Phronia silhouettensis* END. (type seen). In the present material there are several undescribed species from Europe and Asia.

Discussion: *Pseudexechia* is a rather well marked genus showing no closer relationship to *Exechia* s. str. and probably not even to *Exechiopsis*, but rather to *Allodiopsis* and *Allodia*.

*Allodia* Winn. as a compound genus.

In the systems of JOHANNSEN and EDWARDS, *Allodia* WINN. is distinguished from *Exechia* by the longer cubital fork, from *Rymosia* by the less developed anal vein, from *Brachypeza* by the normal, less distinct  $cu_1$ , and from *Cordyla* by the undiminished number of antennal segments, simple palpi, and lack of mesanepisternal bristles. Of these diagnostic characters only one, viz. the reduction of the anal vein, is apomorphic, and even this is a very slight and trivial difference which *Allodia* shares with *Brachypeza*, *Cordyla*, and some *Exechia*. The situation does not become any better if other features common to all or most species of *Allodia* are considered: compared with the other genera the characters are either plesiomorphic, as are the bare anepisternum, the course of the subcosta (usually ending in r), the length of the medial stem (not particularly long or short), the two-segmented female cerci, etc., or, if the character is apomorphic, as is the lack of macrotrichia on the fork veins, it is even less useful as a diagnostic difference than the reduction of the anal vein. Accordingly, the status of *Allodia* as a monophyletic genus is open to considerable doubt.

WINNERTZ (1863) separated his genera *Allodia* and *Brachycampta* by the somewhat longer cubital fork and shorter anal vein in the latter. JOHANNSEN (1909) did not consider them generically distinct, and subsequent authors could only agree with him. Indeed the type-species of *Allodia* and *Brachycampta*, as designated by JOHANNSEN and COQUILLET, respectively, are sufficiently closely related to be kept within one genus. Nevertheless, this *Allodia*, in the current amplified sense, is not very homogeneous. EDWARDS (1925) pointed out that the genus, apart from the rather isolated *A. crassicornis*, is composed of three natural groups, viz. the *lugens* group, the *alternans* group, and the rest. The first two groups are more closely allied and appear only subgenerically distinct; in the present paper they are united to constitute the genus *Allodia* as subgenera *Allodia* s. str. and *Brachycampta*, respectively. The remaining species represent a distinct genus, here called *Brevicornu*, which also includes *A. crassicornis* as a separate subgenus *Stigmatomeria*.

The recognition of *Brevicornu* as a genus separate from *Allodia* calls for some arguments. The chief reason is that, as stated above, *Allodia* in the current broad sense cannot be proved to be a monophyletic grouping, nor can the possibility of convergence be ruled out altogether. The affinities of *Allodia* and *Brevicornu* seem to lie in different directions, *Allodia* showing resemblances to a group of species customarily placed in *Rymosia* (*Allodiopsis* of the present study, see p. 172), while *Brevicornu* has some apomorphic features in common with *Brachypeza* and *Cordyla*. If this correctly reflects the phylogenetic relationships, *Allodia* in the current sense would be not a monophyletic, but at most a paraphyletic, grouping. Since, furthermore, the dividing line between *Allodia* and *Brevicornu* is quite sharp, it is deemed safer to separate them generically, since keeping them united would involve an unverified hypothesis.

Key to the genera and subgenera segregated from *Allodia* Winn. s. lat.

- 1 ( 4) Hind tibiae without posterior bristles. Two propleural bristles directed downwards. Antennal flagellum simple. Clypeus rather long, ovate. Discal bristles of scutum arranged in stripes or absent. Male 9th tergite with one or two pairs of long bristles. Basal segment of female cerci short ..... *Allodia* WINN. 2
- 2 ( 3) Discal bristles minute or absent, at least on the anterior half of the scutum. Base of the cubital fork usually beyond or under the base of the medial pedicel. Pale colour of abdomen, when present, broader towards the hind margin of the tergites. Male 9th tergite usually with two pairs of longer bristles .... subg. *Allodia* s. str.
- 3 ( 2) Distinct discal bristles extending to the front of the scutum. Base of cubital fork usually before or under the base of the medial pedicel. Pale markings of abdomen, when present, more extended towards the base of the tergites. A single very long bristle on each side of the 9th tergite in the male ..... subg. *Brachycampia* WINN.
- 4 ( 1) Hind tibia with small bristles on the posterior side, at least near the tip. Three or more propleural bristles projecting downwards. Female antennal flagellum often more or less swollen at base. Clypeus short, rounded. Discal bristles more evenly dispersed over the scutum. Male 9th tergite without conspicuous long bristles. Basal segment of female cerci usually longer, with a slender apical part .. *Brevicornu* MARSH. 5
- 5 ( 6) Subcosta ending free. Branches of the medial fork with dorsal macrotrichia towards tip. Mesanepisternum with distinct setulae. Four strong scutellar bristles ..... subg. *Stigmatomeria* m.
- 6 ( 5) Subcosta ending in r. Medial fork and anepisternum bare. Two scutellars, or if four, the outer pair distinctly shorter ..... subg. *Brevicornu* s. str.

*Allodia* WINN.

*Allodia* WINNERTZ 1863, p. 826, partim. Type-species: *Mycetophila ornatcollis* MEIGEN 1818, p. 269, sensu WINNERTZ 1863, p. 830 = *Allodia lugens* (WIED.), sensu EDWARDS 1921a, p. 122, fig. 3; by designation of JOHANNSEN 1909, p. 104.

*Allodia* WINN. originally comprised the species *A. obscura* WINN., *A. crassicornis* (STANN.), *A. punctipes* (STAEG.), *A. ornatcollis* (MEIG.), and *A. barbipes* WINN. The first three species belong to *Brevicornu*, subg. *Stigmatomeria*, and the last is probably the same as *Pseudo-brachypeza helvetica* (WALK.) (see p. 189). According to the wording of JOHANNSEN's designation, the type-species of *Allodia* is *A. lugens*, Wiedemann (= *ornatcollis*, Meigen); at that time *lugens* and *ornatcollis* were not separated as distinct species. WINNERTZ describes an *Allodia ornatcollis* (MEIG.), citing *lugens* as a synonym. His description of the male terminalia clearly refers to *Allodia lugens* sensu EDW., which is also confirmed by the figures drawn by DZIEDZICKI (1915, figs. 118–119) from an original Winnertzian specimen.

Characters: Antennae normal, not thickened or shortened; flagellar segments with tiny straight macrotrichia. Clypeus ovate, higher than broad. Discal bristles of scutum in two (dorsocentral) stripes, sometimes also a median stripe present, or else all discal bristles reduced to absent, at least on the anterior half of the scutum; scutellum with two strong marginal bristles. Prothoracic parts rather narrow; pleurae rather high; the angle between the pronotum and scutum around the anterior spiracle rather wide; mesanepisternum rounded hexagonal ovate, bare; two propleural bristles projecting downward. Subcosta very short, ending



in  $r$ ;  $r_1$  not much longer than  $r$ ;  $r_5$  nearly straight, apically divergent from  $m_1$ ;  $r-m$  bare, oblique, mostly slightly longer than the medial pedicel; base of the cubital fork before, under, or beyond the base of the medial pedicel, and before or under the base of the medial fork; anal vein very weak and short to absent. Fork veins without macrotrichia. Legs normal; hind coxa with a single basal bristle; male front tarsi simple; hind tibiae without posterior bristles. First abdominal sternite with or without a pair of longer marginal bristles. Male terminalia of medium or large size; 9th tergite with one or two pairs of longer bristles; cerci double. Female cerci two-segmented (one exception); basal segment rather short, obliquely conical in side view.

Discussion: *Allodia* in the present sense appears to be a natural and probably monophyletic grouping. This is indicated by the shape of the clypeus, reminiscent of that of *Allodiopsis* and *Pseudexechia*, the absence of the posterior bristles on the hind tibiae, a feature seemingly all but unique in the whole tribe (otherwise known only for one species of *Allodiopsis*, subg. *Gymnogonia*), and the type of the male and especially female terminalia. The relationships of *Allodia* seem closest to *Allodiopsis*, especially with its subgenera *Gymnogonia* and *Allodiopsis*, which exhibit the same shape of clypeus, a weaker anal vein than is usual in the «*Rymosia*», and a pair or two of longer bristles on the male 9th tergite, and in addition the reduction of discal bristles correlated with the silvery whitish sides of the scutum as in the subgenus *Allodia* s. str. of *Allodia*. *Allodiopsis* differs primarily in its larger body size, and perhaps in correlation with this in the presence of some posterior bristles on the hind tibiae and of macrotrichia towards the apex of the medial and cubital fork veins. *Pseudexechia*, too, appears to be more closely allied to *Allodia* than to *Exechia* proper. It is not impossible that *Allodiopsis*, *Allodia*, and perhaps also *Pseudexechia* will ultimately be included as subgenera in an enlarged genus *Allodia*, but for the present there do not seem to be sufficient reasons for such a rearrangement.

Within *Allodia* two subgenera may be discerned, viz. *Allodia* s. str. and *Brachycampta*. They were clearly distinguished as groups, but not named by EDWARDS (1925).

#### Subgenus *Allodia* s. str., subg. n.

Type-species: that of the genus, see above.

Characters: Distinguished from subg. *Brachycampta* by the apomorphic features of the reduction of the discal bristles and on average longer clypeus, and by the probably plesiomorphic distribution of the yellow colour on the abdomen. The male terminalia also offer points of difference in having two pairs of longer bristles on the 9th tergite, and a longer and differently shaped sternal process. The legs may be a trifle more slender; the hind tibiae have numerous

setulae between the external bristles. The cubital fork is on the whole shorter than in *Brachycampta* (a more apomorphic condition), the base of this fork being in exceptional cases situated clearly beyond that of the medial fork («exechioid» type of venation). The stem of the medial fork is often slightly shorter than r-m. The fine pale setulae of the scutum are rather closely decumbent throughout, and the sides of the scutum silvery white when seen from a certain angle, especially in front, there contrasting rather sharply with the dull dark median parts.

Species: *Allodia anglofennica* EDW., *A. lugens* (WIED.), *A. lundstroemi* EDW., *A. ornatocollis* (MEIG.), *A. truncata* EDW., and apparently some additional European and Asiatic species.

As far as our present knowledge goes, the range of the subgenus seems to be mainly Holarctic.

#### Subgenus *Brachycampta* WINN., emend., subg. n.

*Brachycampta* WINNERTZ 1863, p. 833, genus, partim. Status n. Type-species: *Mycetophila alternans* ZETTERSTEDT 1838, p. 866, sensu WINNERTZ 1863, p. 834 (as *Allodia alternans* (ZETT.)) = *Allodia grata* (MEIG.), sensu EDWARDS 1925, p. 607 (*A. nigricollis* EDW. nec ZETT., EDWARDS 1921b, p. 124, fig. 10); by designation of COQUILLET 1910, p. 515.

Of the eight species originally included in *Brachycampta* all except the first (*alternans*) belong to *Brevicornu* subg. *Brevicornu*. The description of WINNERTZ indicates that his *alternans* is the *Allodia grata* (MEIG.), sensu EDWARDS, which is confirmed by the figures by DZIEDZICKI (1915, figs. 129–130), drawn from a specimen from the collection of WINNERTZ. Therefore, this latter species should perhaps be considered the type of *Brachycampta*, rather than *Allodia alternans* (ZETT.), sensu EDWARDS.

Characters: See p. 181 and the key p. 182. The clypeus is somewhat shorter than in *Allodia* s. str., though longer than in *Brevicornu*. The hind legs usually show no setulae or very few between the bristles in the external row (except between the two uppermost ones). The position of the base of the cubital fork varies considerably; only seldom, however, is it situated beyond the base of the medial stem. The medial stem tends to be a little longer than r-m. The male terminalia exhibit a wider variation than in the European representatives of *Allodia* s. str.; a single pair of very long bristles on the 9th tergite is characteristic.

Species: *Allodia alternans* (ZETT.), *A. barbata* (LUNDSTR.), *A. czernyi* (LANDR.), *A. foliifera* (STROBL), *A. grata* (MEIG.), *A. neglecta* EDW., *A. pistillata* (LUNDSTR.), *A. silvatica* (LANDR.), *A. triangularis* (STROBL), etc.

This subgenus likewise seems largely confined to the northern extratropical regions.

#### *Brevicornu* MARSH.

*Brevicornu* MARSHALL 1896, p. 306. Type-species: *Brevicornu flavum* MARSHALL 1896, p. 307, present designation.

Characters: Antennae varying in length; flagellar segments longer or shorter than broad, without conspicuous macrotrichia, the basal ones in the female tending to be thickened. Head broader than in *Allodia*; clypeus shorter, rounded,

not higher than broad. Thorax usually lower than in *Allodia*; scutum less highly arched, pleurae lower, prothoracic parts broader and more fused; angle between scutum and pronotum narrower, more or less wedge-shaped; mesanepisternum rather low, broadly rhomboidal. Scutum with decumbent bristles not arranged in distinct stripes, often almost evenly distributed over the disc; three to five propleural bristles; two or four (or even six?) scutellar bristles. Wings as in *Allodia*, but cubital fork often longer, with its base distinctly before the base of the medial pedicel. Hind tibiae with the usual row of short posterior bristles towards the tip. The yellow colour of the abdomen in the female most extended along the hind and especially side margins of the tergites, in the male usually present in tergites 2 to 4 and more extended than in the female, often leaving only a dorsal median patch dark. Male 9th tergite not distinctly divided into two halves and without very long bristles. Female cerci with the basal segment slenderer than in *Allodia*.

Discussion: JOHANNSEN (1909, p. 99) tentatively ranked *Brevicornu* MARSH. as a synonym of *Cordyla* MEIG., but TONNOIR and EDWARDS (1927, p. 834 – 835) placed the two species described by MARSHALL in *Allodia*. The present author studied specimens of *Brevicornu flavum* and found no reason to distinguish the species generically from the European *Allodia* species here included in *Brevicornu* and listed below.

The two subgenera, *Brevicornu* s.str. and *Stigmatomeria*, are perhaps better considered as distinct genera, but as they agree in some features which are probably to be interpreted as synapomorphic differences from *Allodia*, *Allodiopsis* and *Pseudexechia*, they are kept united within one genus. Such characters are 1) the tendency of the female antennal flagellum to be thickened at the base, 2) the broader and more fused prothoracic parts with three or more propleural bristles, and 3) the on the whole more dorsiventrally compressed thorax, showing a narrower angle between the scutum and pronotum, a shorter mesanepisternum etc. Also the coloration pattern of the abdomen is similar in the two subgenera, and different from that in the above-mentioned genera. The trichiation of the scutal disc is also characteristic, with the longer bristles more evenly dispersed and not arranged in distinct longitudinal stripes.

As thickened antennae, a more uniform trichiation of the scutal disc, a similar type of pleura, and in addition the reduction of the anal vein, also characterize *Neoallodia* and *Cordyla*, it appears possible that these genera, with *Brevicornu*, constitute a monophyletic group. The greater length of the medial pedicel in comparison with r-m in several *Brevicornu* species, and the reduction of the tip of  $m_2$  in *B. serenum* may indicate relationship with *Neoallodia* and *Cordyla*.

#### Subgenus *Stigmatomeria* subg. n.

Type-species: *Mycetophila crassicornis* STANNIUS 1831, p. 22.

Characters: Base of antennal flagellum usually incrassated in the female. Scutum densely covered with pale setulae; dorsocentral stripes of discal bristles

indicated on the posterior part of the scutum, in front more confluent with the lateral stripes because of interstitial bristles; four (to six?) strong scutellars. Upper part of mesanepisternum with a few short setulae. Subcosta ending free, very short, almost rudimentary; tips of fork veins with dorsal macrotrichia; anal vein faint but discernible. Hind coxae with two posterior basal bristles; hind and often also middle coxae with a vertical black dash at tip on outer side. Male cerci apparently two-segmented. Basal segment of female cerci rather short, not prolonged to a narrow tip.

Species: *Brevicornu crassicorne* (STANN.) comb. n. (*Mycetophila crassicornis* STANNIUS 1831, p. 22), Europe, and related, perhaps not specifically distinct, types in Europe (*Allodia obscura* WINN.) and North America.

#### Subgenus *Brevicornu* s. str., subg. n.

Type-species: that of the genus, see above.

Characters: The dorsocentral stripes of the discal bristles not clearly separated from other similar scutal bristles, often the whole scutum covered with uniformly dispersed shorter and longer setae; two scutellars, or if four, the outer pair usually shorter than the inner; mesanepisternum bare. Subcosta short, ending in r; fork veins bare. Hind coxae (always?) with a single basal bristle; tips of coxae not dotted. Male cerci simple. Basal segment of female cerci more or less distinctly prolonged to a narrow apical part.

Species: Of the European species, the following belong to *Brevicornu* s. str.: *Brevicornu auriculatum* (EDW.) comb. n. (*Allodia auriculata* EDWARDS 1925, p. 610, figs. 90–92), *Brevicornu boreale* (LUNDSTR.) comb. n. (*Brachycampta borealis* LUNDSTRÖM 1914, p. 17, figs. 14–15), *Brevicornu fasciculatum* (LACKSCH.) comb. n. (*Allodia fasciculata* LACKSCHEWITZ 1937, p. 36, fig. 17), *Brevicornu fissicauda* (LUNDSTR.) comb. n. (*Brachycampta fissicauda* LUNDSTRÖM 1911, p. 398, pl. 12, figs. 3–4), *Brevicornu foliatum* (EDW.) comb. n. (*Allodia foliata* EDWARDS 1925, p. 609, figs. 83–85), *Brevicornu fuscipenne* (STAEG.) comb. n. (*Mycetophila fuscipennis* STAEGER 1840, p. 259), *Brevicornu griseicollis* (STAEG.) comb. n. (*Mycetophila griseicollis* STAEGER 1840, p. 258), *Brevicornu griseolum* (ZETT.) comb. n. (*Mycetophila griseola* ZETTERSTEDT 1852, p. 4225), *Brevicornu karpathicum* (LANDR.) comb. n. (*Allodia karpathica* LANDROCK 1928, p. 240, figs. 7–9; perhaps not specifically distinct from *B. griseolum*), *Brevicornu kingi* (EDW.) comb. n. (*Allodia kingi* EDWARDS 1925, p. 611, figs. 96–98), *Brevicornu luteum* (LANDR.) comb. n. (*Allodia lutea* LANDROCK 1925, p. 37, figs. 1, 2), *Brevicornu nigrofuscum* (LUNDSTR.) comb. n. (*Brachycampta nigrofusca* LUNDSTRÖM 1909, p. 27, figs. 40–41), *Brevicornu proximum* (STAEG.) comb. n. (*Mycetophila proxima* STAEGER 1840, p. 258), *Brevicornu radiatum* (LUNDSTR.) comb. n. (*Brachycampta radiata* LUNDSTRÖM 1911, p. 401, pl. 15, figs. 9–10), *Brevicornu ruficorne* (MEIG.) comb. n. (*Mycetophila ruficornis* MEIGEN 1838, p. 45), *Brevicornu serenum* (WINN.) comb. n. (*Brachycampta serena* WINNERTZ 1863, p. 839), *Brevicornu sericoma* (MEIG.) comb. n. (*Mycetophila sericoma* MEIGEN 1830, p. 302), *Brevicornu spathulatum* (LUNDSTR.) comb. n. (*Brachycampta spathulata* LUNDSTRÖM 1911, p. 399, pl. 12, figs. 5–6), and *Brevicornu verralli* (EDW.) comb. n. (*Allodia*

*verralli* EDWARDS 1925, p. 610, figs. 86 – 88, 220). *Brevicornu* s. str. also apparently includes, apart from the type-species (*B. flavum* MARSH.), all the other species recorded under *Allodia* from New Zealand, further *Allodia similis* FREEM. and some other South American species, and several «*Allodia*» species (*beata* JOH., *callida* JOH., *delita* JOH., *elata* JOH., etc.) described from North America.

#### Brachypeza Winn. as a compound genus.

*Brachypeza* WINN. is customarily distinguished from other related genera by the long cubital fork, long and distinct  $cu_2$ , and short or weak anal vein. WINNERTZ, in his original description of the genus, also laid stress on the course of the subcosta (ending in r), the shortness of the antennae, and the stoutness of the legs. The inclusion of *Mycetophila helvetica* WALK. (by EDWARDS 1913, p. 365, as *Brachypeza spuria* EDW.) rendered these additional characters untenable as general diagnostic features of the genus.

All species included in *Brachypeza* have a short, cordate clypeus; on the scutum discal bristles are absent or greatly reduced; the fork veins of the media and usually also the cubitus are setose on the dorsal side at least towards the apex; the hind coxa possesses a strong basal bristle and always at least one additional shorter one. In the female the 7th tergite and sternite are of equal length, the cerci two-segmented, with the basal segment somewhat conical and the apical segment elongate ovate. In certain species the anal vein is fairly distinct and long, not unlike that of some species included in *Rymosia*.

In contrast to the Winnertzian genera *Exechia*, *Allodia* and *Rymosia*, *Brachypeza* is a small genus with only a few known species. For the European fauna six or seven species are enumerated, and there are some additional North American and East Asiatic representatives of the genus which do not appear to alter the picture presented by the European ones. One might suppose that such a small genus would be homogeneous enough, but it comprises three distinct groups of species considered here to deserve recognition as separate genera or subgenera. *B. helvetica* (WALK.) with its allies differs sufficiently to justify generic separation, and to accommodate them the genus *Pseudobrachypeza* is proposed. Around the type-species, *B. bisignata* WINN., most of the species constituting the subgenus *Brachypeza* s. str. of *Brachypeza* WINN. group themselves. Finally, *B. obscura* WINN. and a related Asiatic species are remarkable in seeming to approach *Cordyla* in some respects; they are separated as a subgenus *Paracordyla*, of *Brachypeza*.

In the following key *Neoallodia* EDW. and *Cordyla* MEIG. are also considered.

#### Key to the genera and subgenera segregated from the compound genus *Brachypeza* WINN. and to *Neoallodia* EDW. and *Cordyla* MEIG.

- 1 ( 4) Scutum with short setulae and scattered longer bristles irregularly mixed up (the latter not arranged in distinct stripes). Mesepimeron with a sharply delimited black dot on the anterior border opposite to the katapisternum. Fork veins bare; pedicel of the medial fork much longer than r-m ..... 2

- 2 ( 3) Antepenultimate segment of palpi not conspicuously enlarged. Antennae with 2 + 14 segments ..... *Neallodia* EDW.
- 3 ( 2) Antepenultimate palpal segment distinctly swollen. Antennae (always?) with less than 14 flagellar segments. Mesanepisternum with some stronger bristles close to its posterior border ..... *Cordyla* MEIG.
- 4 ( 1) Scutum without discal bristles, or more rarely with short ones in two dorsocentral stripes not reaching the front. Mesepimeron without such a black dot. Fork veins with macrotrichia, at least towards tip;  $cu_2$  long and distinct ..... 5
- 5 ( 6) Subcosta ending free; r-m nearly horizontal, almost in line with the base of  $r_5$ . All parts of body rather slender; flagellar segments of antennae all longer than broad; front tibia not shorter than femur; hind tibial spurs hardly more than half as long as basitarsus. Male terminalia of medium size ..... *Pseudobrachypeza* m.
- 6 ( 5) Subcosta ending in r; r-m oblique. Body more or less stout; antennae short with the most flagellar segments not longer than broad; front tibia shorter than femur; the longer hind tibial spur well exceeding half the length of the basitarsus. Male terminalia very small ..... *Brachypeza* WINN. 7
- 7 ( 8) Scutum rather broadly ovate. Some strong black bristles along outer margin of front coxa. Pedicel of medial fork shorter than or subequal to r-m; base of cubital fork usually well before base of medial stem;  $1a$  stronger or very weak, but always traceable and reaching close to the base of the cubital fork .. subg. *Brachypeza* WINN.
- 8 ( 7) Scutum narrower, somewhat compressed laterally. No strong black bristles along outer border of front coxae, except at tip. Medial pedicel as long to about twice as long as r-m; base of cubital fork usually under base of medial pedicel;  $1a$  absent ..... subg. *Paracordyla* m.

*Pseudobrachypeza* gen. n.

Type-species: *Brachypeza spuria* EDWARDS 1913, p. 365, figs. 71, 72 (*Boletina helvetica* WALKER 1856, p. 416, teste EDWARDS 1925, p. 612).

The figures given by DZIEDZICKI (1910, figs. 7 – 10) for his «*Rymosia affinis*» indicate the possibility that there may be two species of *Pseudobrachypeza* in Europe, and that the synonymy of *spuria* EDW. and *helvetica* WALK. may thus prove questionable. This is the reason why *spuria*, which is better described and of which better type material exists, has been chosen as the type-species.

Characters: Antennae and palpi rather slender, of the ordinary Exechiinae type; flagellar segments of antennae slightly longer than broad. Scutum rather dull (not silky), covered with dark setulae; dorsocentral bristles absent, or else greatly reduced and visible only in the posterior part; 3 – 6 propleural bristles; 4 scutellars. The angle between the pronotum and scutum around the anterior spiracle rather wide; the marginal sclerite of the scutum above the spiracle narrow; mesanepisternum rounded hexagonal and provided with small dark setulae in its upper front part. Subcosta straight, ending free;  $r_5$  somewhat curved apically, divergent from the direction of  $r_1$ , and subparallel with the apical part of  $m_1$ ; r-m without distinct weaker part in the middle, rather long, somewhat longer than the medial stem, and almost longitudinal in position, appearing as a direct

continuation of  $r_5$  inwards; base of the cubital fork approximately under the base of the medial stem;  $cu_2$  very long and distinct; anal vein varying in distinctness, sometimes very weak, but may reach the base of the cubital fork. Fork veins, at least  $m_1$ , with densely placed tiny macrotrichia on the dorsal surface. Legs rather slender, in structure and chaetotaxy of the ordinary Exechiinae type, somewhat as in *Rymosia*; coxae and femora not particularly stout; front coxae with some dark bristles along their outer margin; hind coxae with two stronger basal bristles; tibiae not clavate, the front ones not shorter than the corresponding femora, with the apical »brush» area on the anterior side slightly higher than broad; hind tibial spurs hardly longer than half the basitarsus; in the male the second and subsequent segments of the front tarsi bristly or spinulose beneath. Abdomen slender; in the intermediate tergites, if variegated in dark and pale, the pale markings broadest at the posterior margin. Male terminalia of medium size, somewhat elongate, deeply cleft ventrally, with a distinct sternal process; styli with small external stylomeres and a stripe-like, not striate, inner lobe; 9th tergite divided into two halves, each tipped with a stronger bristle; cerci simple. Female 8th sternite rather short; cerci 2-segmented.

Species: *Pseudobrachypeza helvetica* (WALK.) comb. n. (*Boletina helvetica* WALKER 1856, p. 416, *Brachypeza helvetica* (WALK.) EDW.,? *Allodia barbipes* WINN., *Rymosia affinis* DZIEDZ. nec WINN., *Brachypeza spuria* EDW.) from Europe, and two additional, apparently undescribed species from Burma.

Discussion: Though similar in the reduction of the discal bristles, the number of the propleural, scutellar and hind coxal bristles, the structure of the male front tarsi, and the conspicuousness of  $cu_2$ , *Pseudobrachypeza* is separated from *Brachypeza* and especially from its subgenus *Paracordyla* by a distinct gap in several respects. It combines the plesiomorphic, more slender appearance of an ordinary Exechiinae type with a couple of apomorphies in venation (free-ending sc, horizontal r-m), whereas the *Brachypeza* species are of stouter build with strong legs and signs of a dorsiventral compression of the pleurae. The male terminalia are also of different type. It thus seems that *Pseudobrachypeza* represents an, on the whole, more plesiomorphic »sister group» of *Brachypeza* and is better kept generically separate from that genus. As the synonymy indicates, the only better known species was variously placed in the past, by WINNERTZ probably in *Allodia*, by DZIEDZICKI in *Rymosia*, and by EDWARDS in *Brachypeza*. If *Allodia barbipes* WINN. really is the same as *helvetica* and *spuria*, then WINNERTZ placed the species outside his *Brachypeza*, and the erection of a separate genus for it would only reinstate *Brachypeza* in the original Winnertzian sense.

### *Brachypeza* WINN.

*Brachypeza* WINNERTZ 1863, p. 806. Type-species: *Brachypeza bisignata* WINNERTZ 1863, p. 807; by designation of JOHANSEN 1909, p. 101.

Characters: All parts of the body stouter than in *Pseudobrachypeza*. Antennae short; the flagellar segments sessile, most of them not longer but often distinctly shorter than broad. Palpi short, 2nd and 3rd segments dilated. Scutum without discal bristles, appearing smooth and glossy owing to a silky coating of closely decumbent pale setulae; more rarely the pale setulosity somewhat shaggy, and short discal bristles present in two stripes in the posterior part of the scutum. Prothoracic parts broad, much fused; 3–7 propleural bristles; 4–6 stronger scutellars; angle between pronotum and scutum narrow; marginal sclerite of scutum above the anterior spiracle broader than in *Pseudobrachypeza*; mesanepisternum rather low, subquadrate or rounded, in the upper half densely clad with closely decumbent pale setulae. Subcosta curving downwards and ending in  $r$ ;  $r_5$  almost straight, subparallel to  $r_1$  and divergent from  $m_1$ ;  $r-m$  oblique with a weaker part in or beyond the middle;  $cu_2$  very long and distinct; anal vein weak to absent. Fork veins becoming very weak or fading away before attaining the wing margin;  $m_1$  with numerous macrotrichia, other fork veins bristly at tip only. Legs strong and stout; coxae much thickened; base of hind coxa with at least one bristle in addition to the usual strong one; tibiae thicker than in *Pseudobrachypeza*, somewhat clavate, the front ones shorter than the corresponding femora; the longer hind tibial spur about three-quarters or four-fifths of the length of the basitarsus. Male terminalia small.

Discussion: Two subgenera, *Brachypeza* s. str. and *Paracordyla*, can be recognized. The structure of the antennae, thorax and legs, and the small male terminalia suggest some kind of closer relationship with *Cordyla*, an impression which is accentuated in the subgenus *Paracordyla*. The mesanepisternum bears distinct setulae, of which some in the upper hind part may have been changed into true bristles in *Cordyla*, and the condition with more than one basal bristle on the hind coxa is similar to that in *Cordyla*.

Subgenus *Brachypeza* WINN. s. str., subg. n.

Type-species: that of the genus, see above.

Characters: Medium or larger species, yellowish with dark markings. Scutum rather broadly ovate, evenly arched, without discal bristles or with short ones in two stripes not reaching the front part; the marginal sclerite above the anterior spiracle not covering the upper margin of the mesanepisternum, which is subquadrate. Wings mostly with dark markings; medial stem not longer but usually shorter than  $r-m$ ; base of the cubital fork well before to under the base of the medial stem; anal vein weak but rather long; fork veins becoming very weak before reaching the wing margin. Front coxae with black bristles along the outer margin; front tibiae with a number of posterior bristles and with the apical «brush» area higher than broad; in the male second and third segments of front



tarsi often modified, spinose and bristly beneath. Male terminalia with double cerci. Lobes of female 8th sternite sheathing and tipped with several long setae; cerci short, two-segmented.

Species (not revised): *Brachypeza armata* WINN. (Europe), *B. bisignata* WINN. (Europe), *B. brevitibia* (VAN DUZEE) (North America), *B. dentica* (GUTHRIE) (North America), *B. divergens* JOH. (North America), *B. flavipennis* OKADA (Japan), *B. hilaris* WINN. (Europe; perhaps not specifically distinct from *B. bisignata*), ? *B. macrochaeta* BUK. (Europe), *B. radiata* JENK. (Europe), and two apparently undescribed Burman species in the present material.

Discussion: *Brachypeza armata* (and *B. dentica*?) differs in having unicoloured wings, short but distinct discal bristles, more shaggy setulosity of the scutum, and a somewhat shorter and more open cubital fork, but has the male terminalia of the same type as the others and is hardly subgenerically distinct.

#### Subgenus *Paracordyla* subg. n.

Type-species: *Brachypeza obscura* WINNERTZ 1863, p. 80.

Characters: Smaller, dark species reminiscent of a larger *Cordyla*. Antennae very short; the flagellar segments distinctly broader than long and closely sessile. Scutum highly arched, somewhat depressed laterally, narrower than in *Brachypeza* s. str., without discal bristles save a prescutellar pair. The weakly chitinized area around the anterior thoracic spiracle very narrow; the marginal sclerite above the spiracle very broad, partly overlapping the upper margin of the mesanepisternum, which is rounded. Wings unicolourous; medial stem as long to about twice as long as r-m; base of the cubital fork approximately under the base of the medial stem;  $m_1$  apically weak but complete, the other fork veins fading away before reaching the wing margin; anal vein quite rudimentary or absent. Front coxae without dark bristles along their outer margin except close to tip; front tibiae with only some few posterior bristles towards tip, and with the »brush» area on the anterior side at the tip slightly broader than high; male front tarsi simple. Male terminalia very small, superficially similar to those in *Cordyla*; cerci broad, simple. (Females not seen.)

Species: *Brachypeza obscura* WINN. (Europe), and an apparently undescribed species from Burma.

Discussion: This subgenus, when better known, may prove to deserve recognition as a separate genus. The similarity with *Cordyla* is striking enough, but may be a result of convergence. The presence of irregularly dispersed discal bristles in *Cordyla* excludes a direct derivation from *Paracordyla*.

#### *Neoallodia* Edw.

*Neoallodia* EDWARDS 1932, p. 146. Type-species: *Neoallodia flavida* EDWARDS l. c.; by monotypy.

The two South American species, *flavida* EDW. and *brevicornis* (END.), placed in *Neoallodia* by EDWARDS, differ considerably from each other, *N. flavida* having the costa distinctly produced beyond the tip of  $r_5$ , and *N. brevicornis* possessing several fairly strong anepisternal bristles in the manner of *Cordyla*. The antennae are short, the flagellar segments in *N. flavida* being twice as broad as long. Both species also have the peculiar black dot on the pleurae in common with *Cordyla*. According to EDWARDS (1941 b, p. 311), »they are evidently not nearly related to *Allodia*, but are much more like *Cordyla*, from which genus they differ chiefly in that the second palpal segment is not at all swollen.»

LANE (1958, p. 154) did not consider *Neoallodia flavida* EDW. specifically distinct from *Allodia brevicornis* END., and placed them in *Cordyla* (which may be correct) under the invalid name combination *C. brevicornis* (END.), preoccupied by *C. brevicornis* STAEG.).

#### *Cordyla* Meig.

*Cordyla* MEIGEN 1803, p. 263. Type-species: *Cordyla fusca* MEIGEN 1804, p. 93, pl. 5, figs. 6–8; by subsequent monotypy.

*Cordyla* is a well marked monophyletic genus, characterized by a number of apomorphies, of which the following are the most distinctive: 1) short antennae with a diminished number of flagellar segments, especially in the female, 2) greatly swollen antepenultimate segment of palpi, especially in the male, 3) presence of true bristles on mesanepisternum, 4) presence of a sharply marked black spot on the anterior part of the mesepimeron, 5) long pedicel of medial fork, typically also short cubital fork and  $m_2$  which is abbreviated and does not reach the wing margin, 6) distinctive male and female terminalia. The trend in the dorsoventral depression of the thorax, which is initiated in *Brevicornu* and *Brachypeza*, culminates in *Cordyla*: the angle between the anterior pronotum and the scutum is very narrow, almost linear, barely allowing room for the compressed anterior spiracle. The situation is accentuated by the very broad marginal sclerite (paratergite) of the scutum above the spiracle. The mesanepisternum is low and somewhat quadrate, and the prothoracic parts broad and much fused, with rather numerous propleural bristles. The distribution of the bristles on the scutum is similar to that in *Brevicornu* and *Neoallodia*.

The exact position of *Cordyla* in the system of the *Exechiini* is not easy to decide. What is established is that the genus does not belong to the *Mycetophilini* as suggested by EDWARDS, and that its closest relative is *Neoallodia*. It is impossible at present to state whether the group comprising *Neoallodia* and *Cordyla* took its origin near *Brachypeza* or from *Brevicornu*, or whether some third alternative is more probable. *Brevicornu*, *Neoallodia* and *Cordyla* resemble each other and differ from *Brachypeza* in the bristly disc of the scutum and in having the fork veins bare. All the four genera concerned exhibit some degree of thickening or shortening of the antennae and a similar trend in the development of the thorax.

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