

## Catotrichinae Subfam. N.: a Re-examination of Higher Classification in Gall Midges (Diptera: Cecidomyiidae)

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**Abstract.** *Catotricha* is a species-poor, relict group of ancient gall midges (Cecidomyiidae), formerly classified in the subfamily Lestremiinae. It is here excluded from the Lestremiinae and given subfamily rank of its own. The Catotrichinae subfam. n. are sister group of the remainder of the Cecidomyiidae, Lestremiinae s. str. + (Porricondylinae + Cecidomyiinae). The Lestremiinae in this new, strict sense are shown to be monophyletic, justified by a peculiarity of their antennae. Details of the antennae, palpi and thorax in *Catotricha* are discussed phylogenetically and with consideration of homologous structures in other Mycetophiliformia. *Catotricha fraterna* sp. n. from Australia is described. *Catotricha nipponensis* (Alexander, 1924) from Japan is redescribed; *Catotricha antennata* Alexander, 1959 is considered a junior synonym of *nipponensis*.

**Key words:** Mycetophiliformia, Cecidomyiidae, Catotrichinae, new subfamily, Lestremiinae, *Catotricha*, new species.

### Introduction

For more than 30 years, almost all major works on Cecidomyiidae accepted its classification into three subfamilies: Lestremiinae, Porricondylinae and Cecidomyiinae. While species within the latter two subfamilies together were for long recognized to be monophyletic, the Lestremiinae were explicitly considered paraphyletic by Gagné (1989). More recently Jaschhof (1998a) pointed out that the Lestremiinae should be reclassified when natural grouping alone was the aim of a classification. A reclassification of the Cecidomyiidae into nine subfamilies has been proposed by Tastas-Duque (Doctoral Thesis, Stockholm University, 2000) but has not been formally published to meet the requirements of the International Code of Zoological Nomenclature and therefore does not merit comment here.

*Catotricha* is a small genus of large-sized, lestremiine gall midges, poorly known and sparsely represented in collections. It includes five species from cooler parts of the Northern Hemisphere and, as shown here, one species from the Southern Hemisphere. These are *C. americana* (Felt, 1908), *C. subobsoleta* (Alexander, 1924), *C. nipponensis* (Alexander, 1924) = *C. antennata* Alexander, 1959 syn. n., *C. marinae* Mamaev, 1985, *C. subterranea* Mamaev, 1985, and *C. fraterna*

sp. n. described in this paper. As for their distribution, *americana* and *subobsoleta* are western-North American (New Hampshire and Washington, Oregon, California, respectively), *nipponensis* is Japanese, *marinae* is West Siberian, *subterranea* is Far East Russian, and *fraterna* is Australian. Of these six species together, not more than 33 adult specimens are known from collections, with 21 belonging alone to *fraterna*.

The *Catotricha* species described early by Felt in 1908 (*americana*) and Alexander in 1924 (*subobsoleta* and *nipponensis*) were classified in the genus *Catocha* within the Lestremiinae. For these species, Edwards (1938) founded a new genus, *Catotricha* (type species: *americana*), simultaneously proposing a new lestremiine tribe, Catotrichini. This classification was followed by subsequent authors (Pritchard, 1947; Kleesattel, 1979; Mamaev, 1985). A *Catotricha* species described by Alexander in 1959 (*antennata*) is here shown to be identical with *nipponensis* that he had published on in 1924. Adults of two more species (*marinae* and *subterranea*; Mamaev, 1985), described on the basis of females, were reared from larvae, but details of their larval morphology or biology remained unpublished. Jaschhof (1998a), in a revision of the Lestremiinae, treated in depth four of the known *Catotricha* species and listed two more which he was unable to examine in more detail because specimens

were not available for microscopic study. The two last, *nipponensis* and *antennata*, are those which are shown here to be identical. Previous authors agreed that *Catotricha* species were the most primitive cecidomyiids, a view derived from adult morphology. Several distinct characters served to justify its generic status (cf. Edwards, 1938), but those characters were used irrespective of whether they were apomorphic or plesiomorphic until Jaschhof (1998a) interpreted the slightly binodal antennal flagellomeres as a shared, derived feature in *Catotricha* species. *Catotricha* has never been classified with any family other than Cecidomyiidae, nor was another classification ever seriously taken into consideration.

The biology of *Catotricha* still remains obscure. None of the sites from which specimens were collected have been described in more detail. As for *subobsoleta*, *nipponensis* (incl. *antennata*) and *fraterna*, some specimens originate from mountains. At least for one species, *nipponensis*, there are indications that its adults were flying during comparatively low temperatures.

At first, the motive for this paper was to describe the first Southern Hemisphere *Catotricha* and to redescribe one of its most poorly known congeners, *nipponensis*, from Japan. While studying adult morphology of these two species, it became apparent that some characters in *Catotricha* and Lestremiinae needed further evaluation. Thus the description of *Catotricha* is reworked and supplemented by re-examining specimens of four of its species (excl. *marinae* and *subterranea*). Further, a re-interpretation of characters in antennae resulted in the Lestremiinae becoming understandable as a monophyletic group when *Catotricha* was excluded. With the phylogenetic significance of *Catotricha* in mind, several of its adult morphological structures were compared with those in other Mycetophiliformia. By doing this, terminological disagreement among various authors became apparent and thus the homology of those structures is discussed in more detail.

Morphological terminology follows usage in Jaschhof (1998a, b) or is explained elsewhere in this paper. Mycetophiliformia is used here in the sense of Hennig (1954, as Fungivoriformia), i.e. a lineage comprising Mycetophilidae s.l., Sciaridae and Cecidomyiidae. Sciaroidea sensu Matile (1990), as used in this paper, includes Ditomyiidae, Diadocidiidae, Bolitophilidae, Keroplatidae, Lygistorrhinidae, Mycetophilidae (with these six families of fungus gnats forming the Mycetophilidae s.l.), and Sciaridae.

## Key to *Catotricha* species

- 1 Male ..... 2
- Female ..... 5
- 2 Genitalia with the tegmen having two processes directed distad, gonostyli bilobed ..... 3
- Genitalia with the tegmen lacking processes directed distad, gonostyli one-lobed  
..... *C. fraterna* sp. n.
- 3 Gonostyli with the outer lobe at least as long as gonocoxites ..... 4
- Gonostyli with the outer lobe clearly shorter than gonocoxites ..... *C. subobsoleta* (Alex.)
- 4 Gonostyli with the inner lobe having an apical tooth, outer lobe three times as long as inner lobe  
..... *C. americana* (Felt)
- Gonostyli with the inner lobe lacking a tooth, outer lobe twice as long as inner lobe  
..... *C. nipponensis* (Alex.)
- 5 Antennal flagellomeres with long necks having a subterminal swelling with sensory hairs  
..... *C. fraterna* sp. n.
- Antennal flagellomeres without distinct necks  
..... 6
- 6 Spermathecae sclerotized, globular  
..... *C. subobsoleta* (Alex.)
- Spermathecae membranous, ovoid or pear-shaped  
..... 7
- 7 Spermathecae ovoid; ocelli 3  
..... *C. marinae* Mam.
- Spermathecae pear-shaped; ocelli 2  
..... *C. subterranea* Mam.

## *Catotricha nipponensis* (Alexander, 1924)

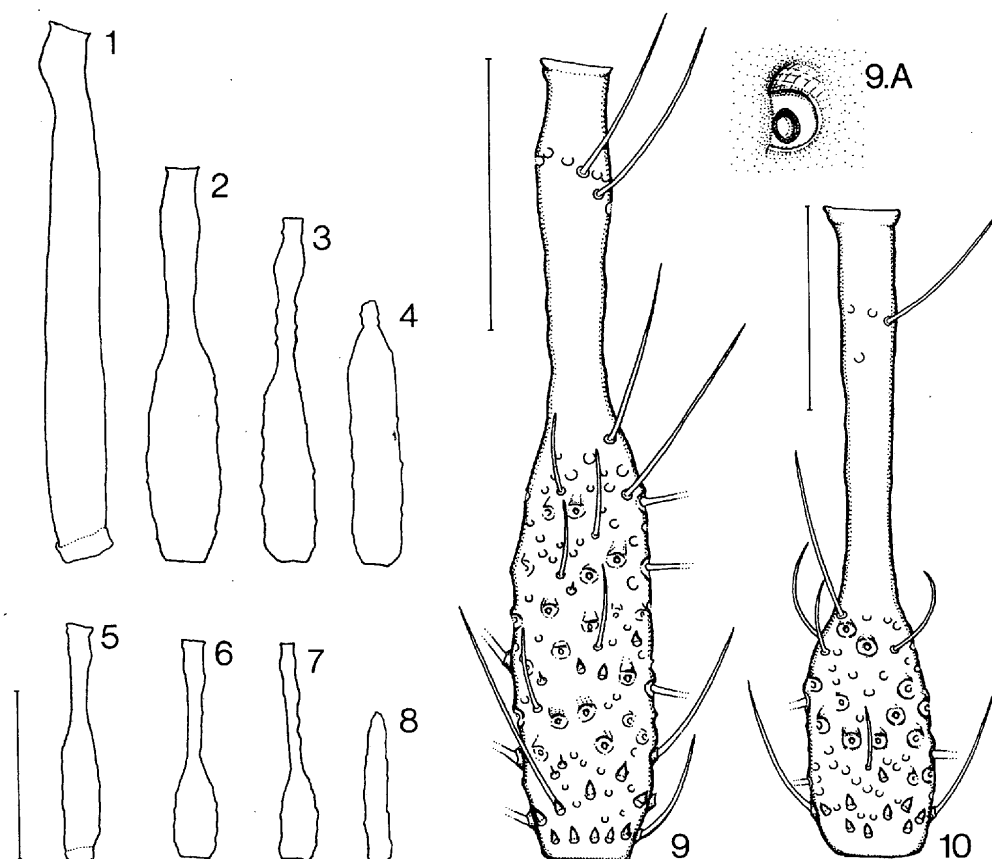
(Figs. 1-4, 9, 11-12)

= *Catotricha antennata* Alexander, 1959 syn. n.

### Redescription

**Male.** Body length: 6.0-7.0 mm. Wing length: 8 mm (holotype of *nipponensis*), 10 mm (holotype of *antennata*), 8 and 9.5 mm, respectively (specimens from Hyogo Pref.).

**Head:** Postfrons non-setose in two of the specimens but seems setose in another. Eye bridge 4-6 facets long laterally, incomplete at vertex with a space of 3 facets diameter between both eye portions. Antennae with scape larger than pedicel. Flagellomeres very long and slender, necked except last one (Figs. 1-4). Neck of flagellomere 4 (Figs. 2 and 9) shorter than node, with a subterminal group of sensory hairs inserted on a slight swelling; node elongate, barrel-



Figs. 1-10. Antennal flagellomeres, male, lateral view. — 1-4 and 9, *Catotricha nipponensis* (Alex.); 5-8 and 10, *Catotricha fraterna* sp. n.; 1 and 5, flagellomere 1; 2, 6, 9 and 10, flagellomere 4 (Fig. 9A: hooded pore, enlarged); 3 and 7, flagellomere 11; 4 and 8, flagellomere 14. 1-4 and 9, specimens from Hyogo Pref.; 5-8 and 10, paratype from Black Mountain. Length of scale bar for 1-8 0.5 mm, for 9: 0.2 mm, for 10: 0.1 mm; Fig. 9A without scale.

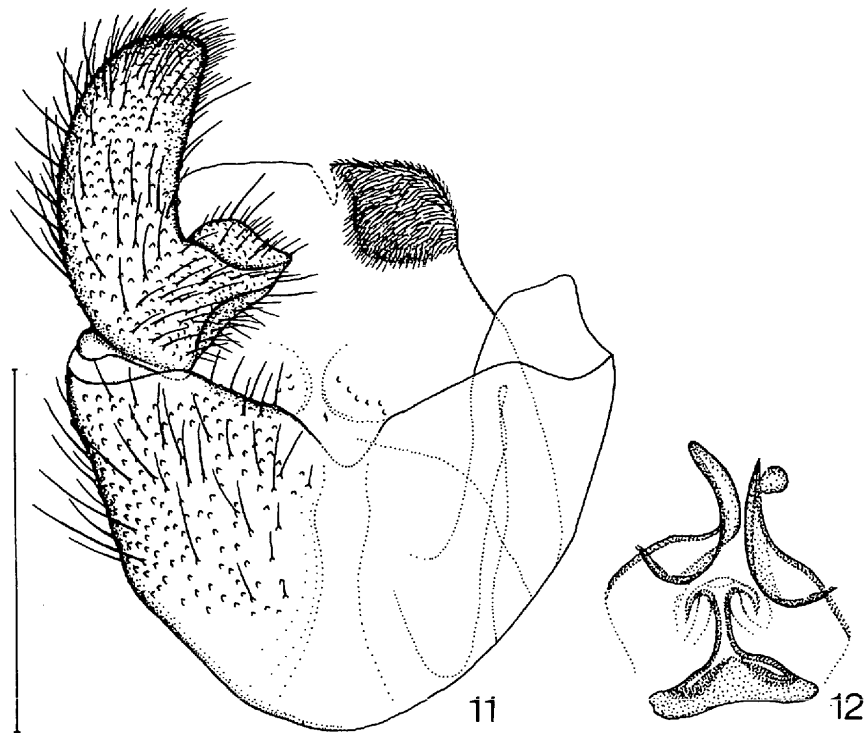
shaped, with setae and sensory hairs irregularly arranged and mixed, setae strong but short and inserted in basal half of node, sensory hairs variable in length with the strongest almost as long as the individual flagellomere and with large, hooded basal pores, additionally with a few, minute sensory spines. Palpi 5-segmented, with the first segment short and non-setose but distinct, terminal segment longest, segments 2-4 with short, strong sensory hairs ventrally, segments 2-5 setose.

**Thorax:** Pronotum non-setose. Claws with 4 teeth equal in size. Wings as usual in *Catotricha*, with true anal lobe, without break in C, Sc reaching wing margin, sc-r faint but present, r-m=2-3 1/2 rs, M-fork shorter than  $M_{1+2}$ -stem and slightly diverging distally, CuA slightly sinuous distally, A reaching wing margin, all veins with macrotrichia dorsally and ventrally on Sc distally, R1 distally, rs,  $R_5$ ,  $M_{3+4}$  distally, CuA distally, and A. Pattern of sensory pores:  $R_1$  7-9, rs 3,  $R_5$  9-12.

**Abdomen:** Pattern of tergal plaques uncertain, but

plaques present from tergite 1 on and arranged in two groups within an individual tergite (for example in holotype, tergite 2 with 3+6 plaques, tergite 3 with 3+5, tergite 4 with 3+5), presence of pleural or ventral plaques uncertain.

**Terminalia:** Gonocoxites (Fig. 11) very densely covered with short setae except membranous medial and most proximal portions, their distal margin slightly emarginated ventrally, along longitudinal midline weakly membranous, gonocoxal apodemes long and wide. Gonostyli (Fig. 11) bilobed, inner lobe smaller and little flattened, with extremely dense, short setation, outer lobe long and rounded apically, setation increasingly denser and shorter distad. Tegmen (Fig. 12) membranous, its three-dimensional structure hard to study but with its parameral apodemes curved ventrad and with 2 long apical processes directed ventrad in unmounted specimens (cf. discussion). Genital rod (Fig. 12) stout, weakly sclerotized, with extensive basal pedestal and membranous ducts running into a membranous head at both sides. Tergite 9



Figs. 11–12. *Catotricha nipponensis* (Alex.), male. — 11, genitalia, ventral view; 12, tegmen and genital rod, ventral view. 11: holotype of *antennata*; 12: specimen from Hyogo Pref. Length of scale bar: 0.5 mm.

long, covering more than half of hypopygium, nearly trapezoid with long proximolateral processes (resulting in halfmoon-shaped proximal margin), with straight distal margin or the latter slightly emarginated, covered with long setae outside, inside with 2 distolateral, almost rectangular lobes with extremely dense cover of hairs mixed with a few short setae. Tergite 10 (Fig. 11) situated at proximal margin of tergite 9 which it is obviously linked with, short and small, bilobed, with a few short setae. Sternite 10 absent.

*Female.* Unknown.

## Discussion

*Catotricha nipponensis* was formerly known from a single specimen, described by Alexander (1924) and redescribed and figured by Edwards (1938). One wing, prepared on a microscopic slide by Edwards in 1938, is all that remains of the holotype. Since the original description by Alexander lacks many details, *nipponensis* was best described by the drawings of wing, antennae and genitalia made by Edwards (1938: 103, Figs. 4c–g) who was certainly the last to study the complete specimen. With respect to those drawings, in particular of the genitalia, there is no doubt

that *nipponensis* is identical with *Catotricha antennata* Alexander, 1959. Consequently, the latter name is here considered a junior synonym. Of *antennata*, only the pinned holotype specimen was previously known until two more pinned males were recently found in the insect collections of the Faculty of Agriculture of the Hokkaido University, in Sapporo. All three specimens were slide-mounted by me for microscopic study and used for the redescription given above. When describing *antennata*, Alexander (1959) compared it with *nipponensis*, emphasizing differences between both species in size, antennal flagellomeres, and details of coloration and venation. I cannot evaluate possible differences in coloration, but those in size and venation are so small that they are considered a matter of individual variability. Further, there is no reason to doubt that *nipponensis* lacks the “very long and outspreading flagellar verticils” (Alexander, l.c.) described for *antennata*. As indicated by Edwards’ drawings, antennae of the *nipponensis* specimen had simply lost most of their setation.

As for the tegmen in unmounted specimens of *nipponensis* (incl. *antennata*), its apical processes were directed strongly ventrad and extended beyond the surface level of the gonocoxites. This was adequately described by Edwards (1938: 104, “lobes turned downwards”) for the type of *C. nipponensis*. When

slide-mounted, they were distorted or easily broken by the pressure of the cover glass.

The general structure of male genitalia in *nipponensis* corresponds with that in other northern hemisphere *Catotricha* and, in the details, it is similar to *C. americana*. Differences between *nipponensis* and *americana* (in parenthesis) are as follows: inner lobe of gonostyli without tooth-like structure (with tooth-like structure apically), outer lobe of gonostyli shorter in *nipponensis*, tergite 9 slightly trapezoid with long proximolateral processes and inside with almost rectangular distolateral lobes densely covered by hairs (tergite 9 clearly trapezoid without proximolateral processes and with distolateral lobes smaller-sized, rounded and situated rather outside than inside). Other differences concern wing venation.

#### Distribution

Palaeartic (Manchurian). Japan: Honshu (Gifu Pref., Osaka Pref., Hyogo Pref.).

#### Biology

Details are unknown. Specimens of *nipponensis* were collected at three sites in mountainous elevations (up to 1800 m a.s.l.) in October and November. This suggests that adults are active under temperatures which are usually too low for most lestreminiine species, i.e. below 10°C. I searched for Lestremiinae at Mt. Ontake, one of the known collecting sites, in mid-August/early September without finding *Catotricha*.

#### Material studied

1 male (wing), Japan, Honshu, Settsu-no-kuni [= historical locality name, identical with present southern part of Hyogo plus northern part of Osaka Prefectures], Mt. Minomo [incorrect for Minoo, Osaka Pref.], 15 November 1923, leg. C. Teranishi [holotype, in United States National Museum of Natural History, Washington, on slide]; 1 male, Japan, Honshu, Shinano-Hida [= historical locality names, identical with present Nagano and Gifu Prefectures], Mt. Ontake, Akigami [in Gifu Pref.], 1800 m, 4 October 1957, leg. T. Mishima [holotype, in United States National Museum of Natural History, Washington, no. 10636, prepared on three slides]; 2 males, Japan, Honshu, Tajima-koku [= historical locality name for the northern part of present Hyogo Pref.], 20 November 1934, leg. Okada [in Hokkaido University, Faculty of Agriculture, Sapporo, specimens prepared on three slides each].

### *Catotricha fraterna* sp. n.

(Figs. 5–8, 10, 13–20, 22)

#### Description

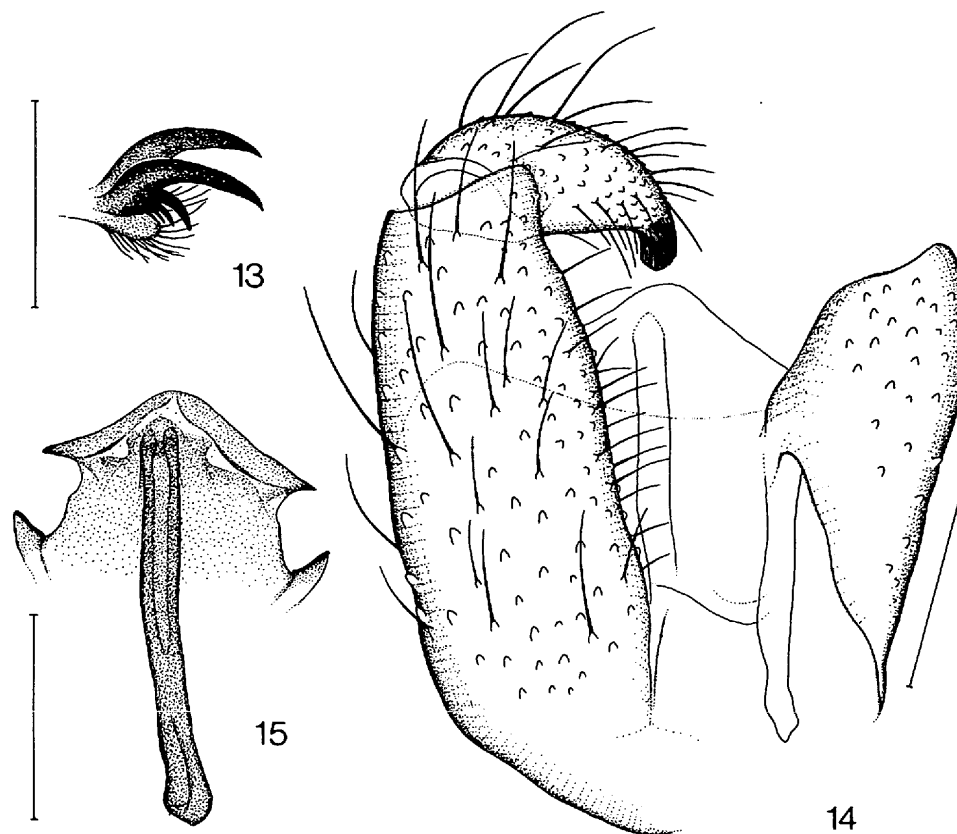
**Male.** Body length: 3.5–4.0 mm. Wing length: 3.5–5 mm.

**Head:** Postfrons non-setose. Eye bridge complete, 5–6 facets long laterally and 2–3 facets long at vertex. Antennae with scape larger than pedicel. Flagellomeres slender, necked except last one (Figs. 5–8 and 10). Neck of flagellomere 4 (Fig. 10) longer than node, with a subterminal group of setae inserted on a slight swelling sometimes; node elongate, barrel-shaped, with setae and sensory hairs irregularly arranged and mixed, setae strong and inserted on basal third of node, sensory hairs variable in length with the strongest longer than the individual flagellomere and having large, hooded basal pores, additionally with a few, minute sensory spines. Palpus 5-segmented, with the first segment short but distinct and having 2 strong setae, terminal segment longest, segments 2–4 with short, strong sensory hairs ventrally, segments 2–5 setose.

**Thorax:** Pronotum non-setose. Katepisternum with a few short setae laterally. Anepisternum occasionally with 1 or 2 short setae. Claws (Fig. 13) with 3–4 teeth outside, each progressively stronger towards apex with the most distal one reaching 1/3 of claw length. Wings (Fig. 16) as usual in *Catotricha*, with anal area slightly convex, with indistinct break in C between R<sub>5</sub> and M<sub>1</sub>, Sc joining C, sc-r very faint, lacking or indicated by just a short appendix of sc, r-m = 2–3 rs, M-fork longer than M<sub>1+2</sub>-stem and slightly diverging distally, CuA straight or slightly sinuous distally, A not reaching wing margin, with macrotrichia on all veins dorsally except r-m and with macrotrichia ventrally on R<sub>1</sub> in distal half and on R<sub>5</sub>. Pattern of sensory pores: R<sub>1</sub> 5–6, rs 0–1, R<sub>5</sub> 4–6.

**Abdomen:** Pattern of tergal plaques (Fig. 17): 3–4/3–4/3–5/3–4/4–5/3–4/1/0, pleural plaques present, presence of ventral plaques uncertain.

**Terminalia:** Gonocoxites (Fig. 14) long, fused just in proximal fourth by a membranous link, ventrally covered with setae of various length except the most proximal portion, with long gonocoxal apodemes. Gonostyli (Fig. 14) densely covered with setae, in distal half tapering to tip, with very dense apical brush of stiff, spine-like hairs forming a tooth-like structure. Tegmen (Fig. 15) rather membranous, its three-dimensional structure hard to study but with the parameral apodemes curved strongly ventrad and with its distal margin cap-like and running into 2 lateral



Figs. 13–15. *Catotricha fraterna* sp. n., male. — 13, claws and empodium (0.05 mm); 14, terminalia, ventral view (left side) and dorsal view (right side) (0.1 mm); 15, tegmen and genital rod (0.1 mm). 13: paratype from Black Mountain; 14–15: holotype. In parenthesis: length of scale bar.

points. Genital rod (Fig. 15) strong, sclerotized, without modifications except a membranous cap variable in shape. Tergite 9 long (i.e., covering proximal half of hypopygium), rectangular to trapezoid, with straight distal margin, covered with long setae. Tergite 10 small, bilobed with the individual lobe almost globular, setose and pubescent, obviously not linked with tergite 9. Sternite 10 ovoid, bilobed, pubescent.

**Female.** Body length: 3.8–6.2 mm. Wing length: 4.5–5 mm.

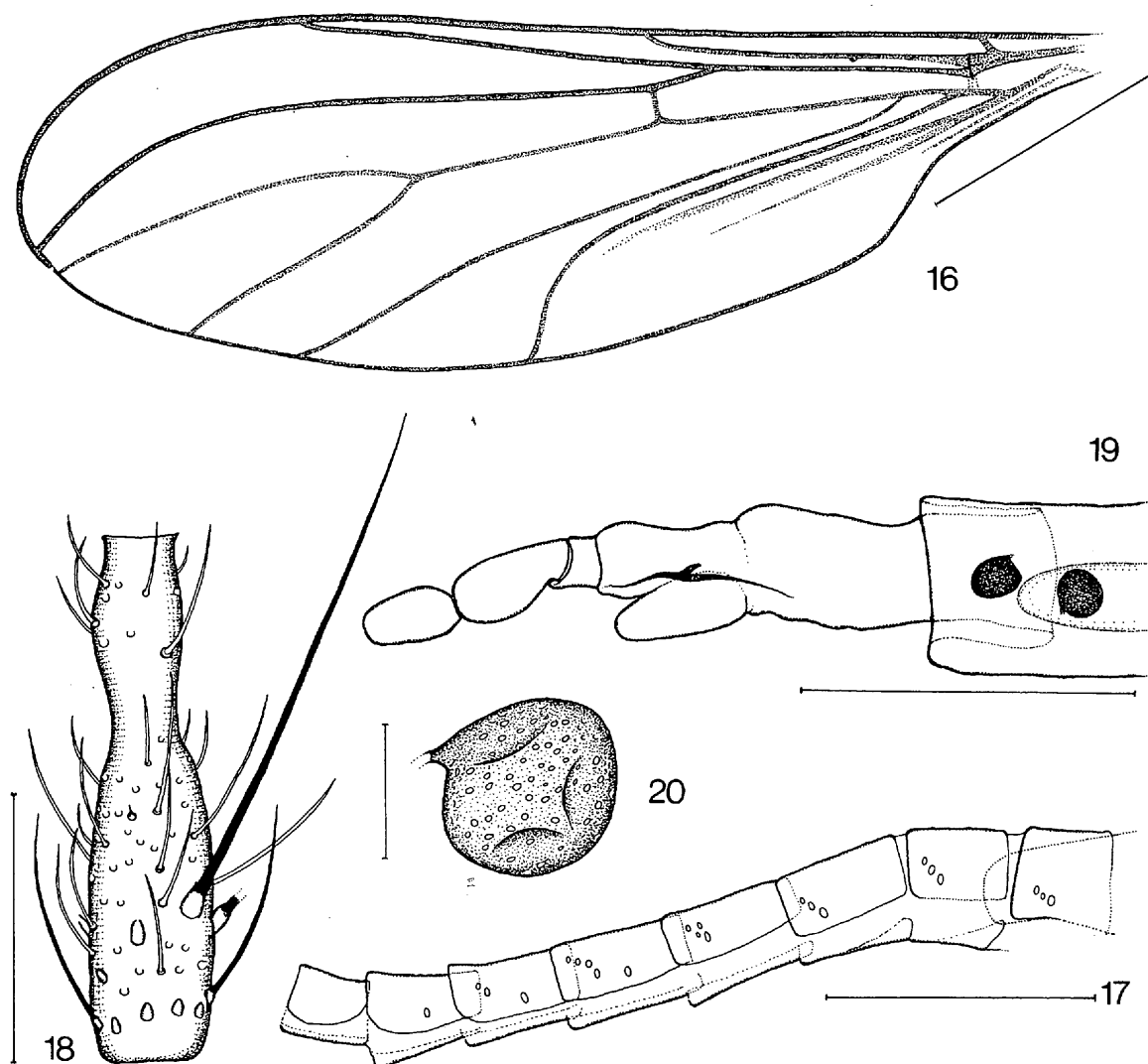
**Head:** Antennae with 14 flagellomeres. Flagellomeres slender, necked except last one. Neck of flagellomere 4 (Fig. 18) with subapical swelling with sensory hairs; node cylindrical, with strong setae in basal third and a few very strong and long setae at midlength, with scattered sensory hairs of various length and a very few sensory spines elsewhere.

**Thorax:** Setae on katapisternum and anepisternum (cf. male) sometimes lacking, at least in two of the specimens available. Legs: T5 in all legs with sole of short, spine-like setae.

**Terminalia** (Fig. 19): Proximal segments of cerci longer than the distal ones. Spermathecae (Figs. 19,

20) 2, strongly sclerotized and entirely covered with pores, about globular (collapsed in specimens available). Eggs elongate.

**Types.** Holotype: male, Australian Capital Territory, Black Mountain, Malaise site 1, 12–15 May 1980, leg. D. H. Colless. Paratypes: 5 males, same data as holotype; 1 male, 1 female, same locality, but 16–18 May 1980; 1 male, same locality, but 28–29 May 1980; 1 female, same locality, but Malaise site 2, 21 April 1980; 3 males, same locality, but Malaise site 2, 9–11 May 1980; 1 male, New South Wales, 15 miles southwest of Thredbo Village, 23 March 1966, leg. N. Dobrotworsky; 1 male, Victoria, Swan Reach, 27 June 1964, leg. N. Dobrotworsky; 1 male, Victoria, Toorongo Falls, 13 April 1965, leg. N. Dobrotworsky; 2 males, Victoria, Maroondah, 16 April 1964, leg. N. Dobrotworsky; 1 male, same locality, but 18 April 1967; 1 female, same locality, but 31 August 1966; 1 female, Victoria, Mt. Baw Baw, 3800 feet, 3 March 1965, leg. N. Dobrotworsky [all on microscope slides, in CSIRO Division of Entomology, Canberra].



Figs. 16–20. *Catotricha fraterna* sp. n. — 16, wing in male (1 mm); 17, abdominal segments 1–8 with tergal plaques in male, lateral view (1 mm); 18, flagellomere 4 in female, lateral view (0.2 mm); 19, postabdomen with spermathecae in female, lateral view (0.5 mm); 20, spermatheca, collapsed (0.1 mm). 16–20: paratypes from Black Mountain. In parenthesis: length of scale bar.

## Discussion

*Catotricha fraterna*, with its typical *Catotricha*-like antennae, fits the diagnosis of the genus as given in Jaschhof (1998a: 54). Morphological differences between *fraterna* and northern hemisphere *Catotricha* are the presence of a complete eye bridge, of setae on some of its thoracic pleural sclerites, and of a break, even if faint, in the costa beyond the juncture with  $R_5$ . Females of *fraterna* have the necks of flagellomeres with a subterminal swelling with sensory hairs, a feature that corresponds with that in its males but differs from *Catotricha* females known from the Holarctic. As for the male genitalia, the structures in *fraterna* are simpler compared with those in northern hemisphere congeners and differ in almost all details. For example,

in *fraterna* the gonostyli are one-lobed (bilobed in holarctic species), the tegmen lacks apical processes (present), the genital rod forms a simple, elongate rod (stout and variously modified), the tergite 9 lacks distolateral lobes (present), and sternite 9 is present (obviously lacking). Wing characters in *fraterna* tend to reduction as found in some holarctic species as well: sc-r is rudimentary, A is short and does not reach wing margin, ventral setation of wing veins is widely reduced, and a true anal lobe is lacking.

### Distribution

Australian. Canberra (Australian Capital Territory), New South Wales, Victoria.

**Biology**

Details of biology and collecting sites are unknown. Adults were collected in southeast Australia in March–June and August.

**Etymology**

The name *fraterna* (in Latin fraternus=fraternal, or closely allied) refers to the relationship of the new species to its northern congeners.

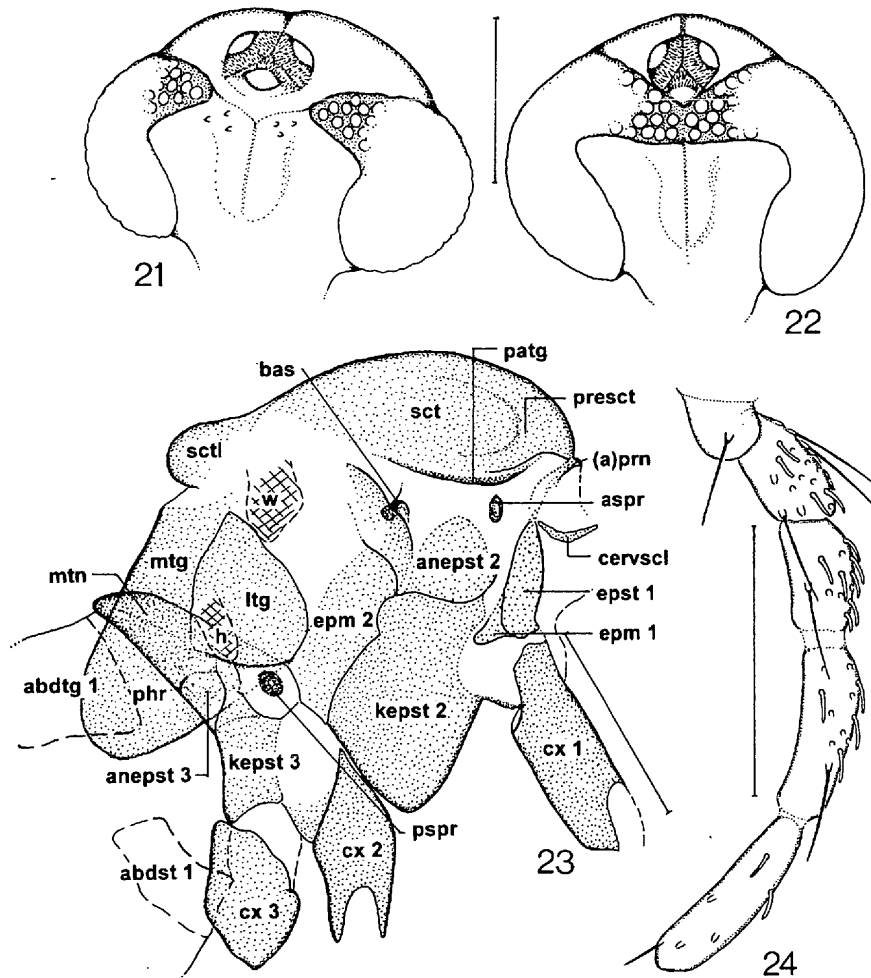
**Redescription of the genus *Catotricha***

**Diagnosis:** Within the family Cecidomyiidae, *Catotricha* is unique in having the antennal flagellomeres with long necks that are partially covered with sensory

hairs. Additionally, the vestiture on the flagellomeral nodes is irregularly arranged, i.e. without forming whorls of setae or sensory hairs. Wing venation is distinct for the presence of sc-r and the  $M_{3+4}$  (=CuA<sub>1</sub> according to other authors) joining M. All these characters are plesiomorphic. No characters of *Catotricha* species may be considered synapomorphic.

**Body length:** 4–7 mm in males, 4–8 mm in females.

**Head:** Postfrons bilobed, slightly prominent, non-setose or exceptionally setose. Postcranium setose, without postocellar and postocular bristles. With 3 ocelli just behind eye bridge (if eye bridge is complete then ocellar triangle is touching eye bridge), equal in size and closely joined together to form a triangle (Figs. 21 and 22), in one species with 2 ocelli (C.



Figs. 21–24. Morphology in *Catotricha* spp. — 21, head in frontal view with ocelli and incomplete eye bridge (*C. subobsoleta*, female) (0.25 mm); 22, dito, eye bridge complete (*C. fraterna*, paratype female) (0.25 mm); 23, thorax, lateral view (*C. subobsoleta*, female) (0.5 mm); 24, palpus (*C. americana*, holotype male) (0.2 mm). Abbreviations in Fig. 23: *abdst*, abdominal sternite; *abdtg*, abdominal tergite; (*a*)*prn*, (ante)pronotum; *anepst*, anepisternum; *aspr*, anterior spiracle; *bas*, basalare; *cervscl*, cervical sclerite; *cx*, coxa; *epm*, epimeron; *epst*, episternum; *h*, halter base; *kepst*, katepisternum; *ltg*, laterotergite; *mtg*, mediotergite; *mtn*, metanotum; *patg*, paratergite; *phr*, phragma; *presct*, prescutum; *pspr*, posterior spiracle; *sct*, scutum; *sctl*, scutellum; *w*, wing base.



*subterranea*). Eye bridge closed at vertex or incomplete with a space of up to 8 facets diameter in between both eye portions (Figs. 21 and 22). Interfacetal setulae lacking or, if present, extremely scarce. Antennae in males long, with scape little larger than pedicel or both equal in size, both setose ventrally. With 14 flagellomeres (Figs. 1–10) elongate and slender, progressively slenderer towards apex, all flagellomeres necked except terminal one, neck longer or shorter than node, neck of flagellomeres 2–13 with subterminal swelling with sensory hairs (swelling may be indistinct sometimes), in distal flagellomeres between node and subterminal swelling with warts, scars and sometimes single sensory hairs, flagellomeres with microtrichia few in number and situated only most basally (on flagellomere 1, microtrichia covering up to one half of node). Node of flagellomere 4 (Figs. 9 and 10) with strong setae, sensory hairs of various length and a few sensory spines, with some of the sensory hairs very strong and long (i.e., about as long as the single flagellomere) and with large basal pores having slightly prominent hoods (thus called hooded pores, cf. Fig. 9A), with the setae and sensory hairs irregularly arranged and mixed, with the setae situated mainly in proximal half of node. Antennae of females with 14 (exceptionally 13) flagellomeres, flagellomeres with very short necks, or necks longer and with subterminal swelling having sensory hairs as in males (Fig. 18), vestiture as in males but shorter in all and without hooded basal pores. Palpi (Fig. 24) 5-segmented, with the first segment short but distinct and setose in at least some of the species, at least segments 2–4 with scattered, short sensory hairs, segments 2–5 always setose.

*Thorax* (Fig. 23): In lateral view, about as long as high, twice as high as the length of forecoxae. Cervical sclerites in one pair, slender. Pronotum weakly sclerotized except its (antepnotal?) lobes which are setose or not. Pleuron 1 distinct, with large episternum and small epimeron. Sternum 1 in lateral view hidden behind coxae. Scutum slightly convex, setose along (dorsocentral) parapsidal sutures and laterally. Scutellum separated from scutum by slight depression, setose. Paratergite distinct. Postnotum with large mediotergite and undivided laterotergites. Episternum 2 with small, weakly sclerotized anepisternum and large, nearly triangular katepisternum, both bare or with a few setae in one species. Basalare distinct, its surface apparently invaginated resulting in a sclerotized depression. Epimeron 2 large, weakly sclerotized. Pleural pit indistinct. Episternum 3 large, with the smaller anepisternum separated from the katepister-

num by a clear suture. Epimeron 3 lacking. Metanotum forming a sclerotized bow extending from the basis of one halter to the other and extending beyond the level of dorsal margins of mediotergite plus postphragma. Postphragma large and produced into abdominal cavity, its dorsal margin forming a straight line with that of mediotergite. Hind thorax with a broad junction with abdomen, i.e. extending from dorsal apex of metanotum to ventral apex of episternum 3.

*Legs*: Slender and much longer than body, coxae rather short compared with height of thorax and—compared with more distal segments—sparsely covered with long setae, more distal segments evenly and densely covered with setae of various length but setae short in all, without scales or peculiar setae or spines, tibiae without a trace of spurs or tibial organs. Females with T5 having a sole of short, spine-like setae at least in fore- and midlegs. Claws (Fig. 13) small but strong, very slightly curved, with a row of strong teeth. Empodia (Fig. 13) widely reduced, forming a short hair brush. Halteres club-shaped, with long and slender stem, covered with short setae.

*Wings* (Fig. 16): About as long as body or longer, membrane densely covered with mixed, scattered microtrichia and macrotrichia, anal area with slightly convex margin or forming a true lobe. Venation strong with the  $M_{1+2}$  including fork paler, with C broken before point of contact with  $M_1$ , or not broken but weaker from that point on, with h distinct, Sc comparatively long and evanescent distally or joining C, sc-r present or not,  $R_1$  very long (i.e., its point of contact with C lies beyond the level of midlength of  $R_5$ ),  $R_5$  joining C close to or beyond wing apex, rs longer than r-m,  $M_{1+2}$ -stem little longer or shorter than  $M_{1+2}$ -fork, fork slightly diverging distally or not,  $M_{3+4}$  (=CuA<sub>1</sub> according to other authors) joins M beyond level of h, almost straight throughout its length, never joining CuA (=CuA<sub>2</sub> according to others) to form a fork, CuA strongly curved proximad and sometimes sinuous distally, CuP distinct, A (=A<sub>1</sub>) long and sometimes reaching wing margin. Veins with macrotrichia dorsally and, at least on  $R_5$ , ventrally. Pattern of sensory pores not stable infraspecifically, with 3–9 pores on  $R_1$ , 0–3 pores on rs, and 3–12 pores on  $R_5$ , additional pores on Sc proximally and on R.

*Abdomen*: All non-hypopygial tergites and sternites evenly covered with rather short setae. Pattern of tergal plaques (Fig. 17) not stable infraspecifically, tergal plaques present in tergites 1–7 and within a individual segment tending to form two groups, the

one group (with fewer and larger plaques) at mid-length of tergite, the other group (with more and smaller plaques) near anterior margin of tergite, generally with 1–8 plaques in an individual tergite. Presence of pleural and ventral plaques widely uncertain.

**Terminalia:** In males in two different types. In holarctic species (cf. Figs. 11 and 12) with: gonocoxites widely connected ventrally and with wide membranous portion along longitudinal midline; gonostyli bilobed; tegmen with 2 sclerotized processes apically; short, stout genital rod; tergite 9 with distolateral lobes; and sternite 9 obviously lacking. The Australian species represents another, more simplified type. See the description and discussion of *C. fraterna* above. Male genitalia always with strong gonocoxal apodemes, with tegmen mostly membranous and with its three-dimensional structure complicated and thus hard to study, with tergite 10 small and joined with tergite 9 or not. Terminalia in females (Fig. 19) of generalized type, all outer parts evenly setose without peculiar modification, cerci ovoid in lateral view with the proximal cerci up to two times as long as the distal ones, sternite 8 extending to level of tergite 10, sternite 9 forming an inner, sclerotized fork. Spermathecae 2 (Figs. 19 and 20), globular, pear-shaped or ovoid, sclerotized or membranous, their surface covered with pores or not.

### Discussion of antennae, palpi and thorax in *Catotricha*, compared with other Mycetophiliformia

The generic redescription given here should allow comparison of *Catotricha* with representatives of Lestremiinae as well as of non-lestremiine, or non-ccidomyiid Mycetophiliformia. *Catotricha* material currently available for study is generally poor in condition because it consists of balsam mounted specimens previously pinned for decades. Fresh material is needed to study more thoroughly and with more confidence all parts of the body. For example, there exists only one *Catotricha* specimen which is in good enough condition to study thoracic sclerites in extensive detail.

As for the antennae in *Catotricha*, it is worth noting the peculiar shape of their flagellomeres as well as the completely irregular arrangement of their setae and hair-like sensilla. The latter is clearly an ancestral character state as found in most non-ccidomyiid Mycetophiliformia. With respect to the Lestremiinae, an irregularly arranged vestiture of the *Catotricha*-type is found only in the antennae of *Amedia flori-*

*dana*, an extraordinary species regressive in its morphology and rather uncertain in its current classification. All other Lestremiinae have the flagellomeres with at least parts of their vestiture arranged in whorls. Further, in male Lestremiinae (excluding *Catotricha*) the strongest and longest hair-like sensilla (incorrectly considered setae in Jaschhof, 1998a) are arranged in crenulate whorls (cf. Gagné, 1981: 265, Figs. 38, 39, 41, 45, 47, 48; Jaschhof, 1998a: 31, Fig. 10a). The term "crenulate" was derived from the peculiar pattern which appears when the basal pores of sensory hairs are connected with each other. Crenulate whorls occur exclusively in flagellomeres of the Lestremiinae. Typically, they are concentrated on the ventral sides of the nodes with at least one whorl extending around the complete circumference. They are reduced secondarily and independently in several species or species groups (for example, in *Anarete*, *Anodontoceras*, *Micromya*, *Peromyia*, *Pseudoperomyia*, and *Skuhraviana*). When reduced, this is usually correlated with other modifications in the flagellomeres, for example, a reduction in their number. Additionally, nodes which lack crenulate whorls are subglobular rather than barrel-shaped, and necks arise from the center of the nodes rather than from their dorsal margins. As for the flagellomeres in *Catotricha*, their strongest sensory hairs are inserted in large pores having a small hood above (Fig. 9A) and thus are called hooded pores here. They are found in male and female flagellomeres of many other Cecidomyiidae too, in which they are even more prominent and sometimes arranged in regular whorls (cf. Gagné, 1981: Figs. 16, 53–60), but they never occur in Lestremiinae other than *Catotricha*. Hooded pores, in their external structure, correspond widely with the individual pores of crenulate whorls and I consider both homologous.

The flagellomeres in *Catotricha* are remarkable for their necks having a subterminal, swollen portion with sensory hairs. Subterminally swollen necks are present in the flagellomeres of almost all Lestremiinae and some other Cecidomyiidae but in those the necks are completely bare. The evolution towards bare-necked flagellomeres in cecidomyiids has obviously passed through a state which is still retained in recent *Catotricha* species, i.e. flagellomeres having the necks partially covered with sensory hairs. Consequently, the latter situation must be considered plesiomorphic, not apomorphic as in Jaschhof (1998a).

With respect to other Mycetophiliformia, antennal flagellomeres with distinct necks and nodes having their vestiture partially arranged in whorls are deve-

loped also in some groups of Sciaridae (cf., for example, Hippa *et al.*, 1998). In those species all other characters are clearly sciarid-like. Without doubt, flagellomeres with long necks and distinct whorls have evolved independently in Sciaridae and Cecidomyiidae. Within Mycetophilidae s.l., necked flagellomeres are most exceptional (cf. Kallweit, 1998).

The palpi in *Catotricha* are here described as five-segmented. In Cecidomyiidae, palpi are usually considered four-segmented maximally, but sometimes the first segment is preceded by a small presegment (cf., for example, Panelius (1965) in Porricondyliinae). In Lestremiinae, such a presegment is present as well, at least, in some larger-sized species (for example, in *Lestremia* sp., or *Catocha* sp.), but I could not find it in ordinary slide-preparations of smaller species. Consequently, the difference in numbering maximally four or five segments in Cecidomyiidae results from whether the presegment is counted or not. For taxonomic purposes in Cecidomyiidae, the presegment is usually ignored because it is hardly or not apparent, membranous and non-setose. In some *Catotricha* species, however, it is more conspicuous because it appears harder and has one or two strong setae. I consider the first setose segment in *Catotricha* homologous to the non-setose presegment in (other) Lestremiinae because it is always the following segment that is the first to show specialized sensilla. These sensilla are short, hair-like and transparent and may be present in the distal palpal segments as well. They are most numerous and dense in that palpal segment which is the first to have sensilla at all, and only in that segment are sensillae sometimes concentrated in depressions. As for the Porricondyliinae+Cecidomyiinae, the palpi usually lack specialized sensilla (Spungis, in litt.; Gagné, in litt.), but within a few, slide-mounted porricondyline specimens I have at hand one was found that has hair-like sensilla on all palpal segments (except the presegment).

In Sciaridae, the maximal number in palpal segments was described as three, with a weak presegment usually present (but ignored by taxonomists) and with the first distinct segment having sensilla (Steffan, 1966, 1981; Menzel & Mohrig, 1997). Considering that five palpal segments are the maximum possible and the presegment is a true segment, the fifth is apparently reduced throughout the family. Further, the second segment would be the one with sensilla, a situation which corresponds with that in the Lestremiinae including *Catotricha*.

In Mycetophilidae s.l., the situation is more diverse and confused in that segments may be reduced as well

as fused imperceptibly (cf. Söli, 1997 in Mycetophilidae s. str.). Nevertheless, five palpal segments represent the generalized pattern also in fungus gnats. But it is noteworthy that it is the third segment that is presumed to have specialized sensilla (Vockeroth, 1981; Söli, l.c.). Such a condition would differ from that in Lestremiinae and Sciaridae if the assumptions are correct that the five palpal segments in various Mycetophiliformia are homologous throughout and their sensorial areas are so too.

So far, the origin of the body considered above the first palpal segment was not questioned. Matile (1990) in Keroplatidae, however, called it the palpifer (even though he did not preclude its possible identity as the first palpal segment). Since not a single species within the Mycetophiliformia seems to have six palpal bodies in total (i.e., a palpifer plus five palpal segments corresponding to the ground pattern in Nematocera), the above question might appear purely theoretical. But, also theoretically, one has to take into account that in Mycetophilidae s.l. five-bodied palpi may consist of the palpifer plus four palpal segments, with the fifth segment being reduced as in Sciaridae. Then it would be the second palpal segment that has sensilla, corresponding to the situation presumed in Keroplatidae (Matile, l.c.) and found in *Catotricha*, Lestremiinae and Sciaridae.

The thorax in *Catotricha* (Fig. 23) is structured as in other Cecidomyiidae, but one should keep in mind that thoracic sclerites are hard to study in many Cecidomyiidae because of their small size. Nevertheless, the thoracic structure in *Catotricha* may be considered the generalized pattern of the cecidomyiid thorax. Outside the Cecidomyiidae, it widely corresponds with that in Sciaridae (cf. Steffan, 1966: Fig. 9) except for certain small sclerites. The pronotum in *Catotricha* is much less developed compared with that in Sciaridae. The epimeron 2 in *Catotricha* is reduced insofar as its posterior portion (posterior mesepimeron in Steffan, l.c.) is lacking. The meron 2 is absent in *Catotricha* and epimeron 3 is also absent. The episternum 3 in *Catotricha* has its katepisternum fairly distinct from its anepisternum, if the latter was adequately homologized here. In contrast to many Mycetophilidae s.l., the laterotergites in *Catotricha* (and Lestremiinae) are bare and not prominent. A striking feature of the cecidomyiid thorax, corresponding with that in sciarids, is the well developed sclerite extending into the abdominal cavity. In Sciaridae, it was previously considered the metanotum (cf. Steffan, l.c.; Menzel & Mohrig, 1997), but that is certainly incorrect. Instead, it should represent the

mesothoracic postphragma which belongs to the endoskeleton (cf. Colless & McAlpine, 1991). The postphragma, or simply phragma, forms a very close structural unit together with the mediotergite (of postnotum), with the suture separating both sclerites being faint. In both Cecidomyiidae and Sciaridae, the phragma (almost?) completely closes the posterior thoracic cavity. In Mycetophilidae s.l., it is usually shorter and does not extend into the abdomen, but Diadocidiidae are exceptional in having it better developed. The metanotum in *Catotricha* and Cecidomyiidae (as well as in Sciaridae) is a bow-like sclerite which extends approximately from the base of one halter to the other (cf. Colless & McAlpine, l.c.). In *Catotricha*, it is most intensively contoured along its posterior margin and extends dorsally beyond the level of phragma plus mediotergite, covering the faint suture in between them. In Diadocidiidae, of which I studied a few slide-mounted specimens, it looks very similar (cf. also Fig. 14A in Söli, 1997) while it is much smaller in other Mycetophilidae s.l. (cf. also Matile, 1990 in Keroplatidae; Söli, l.c. in Mycetophilidae s. str.). To generalize, both phragma and metanotum are better developed in groups in which the thorax and abdomen are broadly jointed. That applies to Cecidomyiidae, Sciaridae and Diadocidiidae. In mycetophilids with a short phragma and inconspicuous metanotum, the abdomen, where it meets thorax, is constricted resulting in a slightly "wasp-like" appearance. A short, unproduced postphragma was considered a synapomorphy of the Mycetophilidae s.l. (under exclusion of the Diadocidiidae) by Blaschke-Berthold (1994).

### Conclusions: the Catotrichinae as a new subfamily within the Cecidomyiidae

External adult morphology gives no indications that *Catotricha* was not properly classified with the Cecidomyiidae. *Catotricha* lacks tibial spurs, as pointed out by other authors, and it has the antennal flagellum of the moniliform type with the individual flagellomeres having proximal nodes and distal necks. Both characters are clearly synapomorphies of the Cecidomyiidae (cf. Fig. 25).

If *Catotricha* is excluded from the Lestremiinae, the remainder are distinct in having crenulate whorls of sensory hairs on the male antennal flagellomeres. These crenulate whorls are here considered a synapomorphic character supporting the monophyly of the Lestremiinae s. str. (cf. Fig. 25). The Catotri-

chini, excluded from the Lestremiinae s.l., should be given subfamily rank of its own within the Cecidomyiidae. The Catotrichinae subfam. n. comprise a single genus, *Catotricha*, and the diagnosis for the subfamily is identical with that for the genus and tribe Catotrichini.

The idea of *Catotricha* as the sister group of all other Cecidomyiidae is not new and makes sense. As stated earlier, *Catotricha* species are undoubtedly the most primitive cecidomyiids currently known. However, the two distinct types of male genitalia in *Catotricha*, besides other characters, suggest that the clade had its separate evolution over a long period of time. What is known about its present distribution supports a view that *Catotricha* is a relict group of cecidomyiids, probably once more widespread and rich in species. One may speculate whether *Catotricha* species have survived in an ecological niche left unoccupied by the bulk of other free-developing gall midges. The peculiar activity period of their adults seems to support such an idea and finds a parallel with the primitive, species-poor Catochini within the Lestremiinae (cf. Pritchard, 1947; Jaschhof, 1998a). I have no doubt about the monophyly of *Catotricha* even if not justified by shared, derived characters in its adult morphology.

A monophyletic group, Lestremiinae + (Porricondylinae + Cecidomyiinae), may be justified by two synapomorphies: by having the flagellomeres with bare

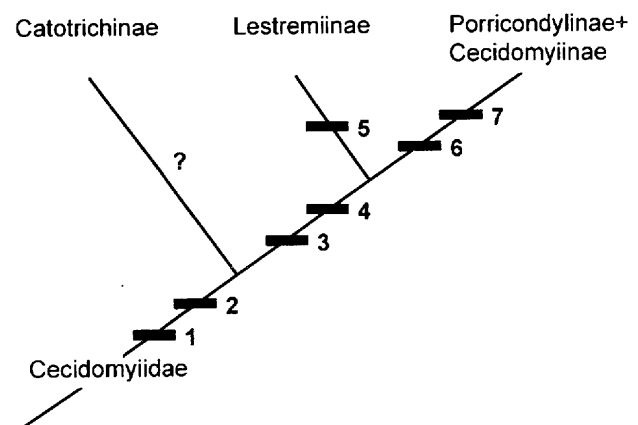


Fig. 25. Interrelationships between large groups of Cecidomyiidae, partially resulting from this study. Strong bars numbered 1-7: synapomorphies (1 = lack of tibial spurs, 2 = antennal flagellomeres with distinct necks and nodes, 3 = flagellomeres with bare necks, 4 = flagellomeral vestiture partially arranged in whorls, 5 = male flagellomeres with crenulate whorls, 6 = lack of ocelli, 7 = first tarsomeres shortened).

necks, and by having their nodal vestiture arranged partially in whorls (cf. Fig. 25). Formerly, the latter character was usually used to support the monophyly of the Cecidomyiidae as a whole. The idea of the Lestremiinae as the sister group of Porricondylinae + Cecidomyiinae (P+C) is not new. Kleesattel (1979), who was the latest to support that idea, argued this point with a derived character shared by all cecidomyiids, i.e. the lack of tibial spurs. The argument here employed to hypothesize the monophyly of the Lestremiinae may appear weak for workers less familiar with the flies discussed. But one should keep in mind that in groups like Lestremiinae, morphologically uniform and consequently poor in characters, each single, true argument may be of great significance for phylogenetic considerations. Further, there is no evidence against a sister group relationship between the Lestremiinae s. str. and a monophylum P+C. No group within the Lestremiinae can be hypothesized to be more closely related to P+C than to the remainder of Lestremiinae. The idea that *Catocha* (within the Lestremiinae) might be the sister group of *Diallactes* (within the Porricondylinae) (cf. Mamaev, 1975: 138 ff.; Jaschhof, 1998a: 16) is based on characters that are certainly plesiomorphic or homoplastic and occur abundantly in Lestremiinae as well as in Porricondylinae.

Palpi, antennae and thorax are shown once more here to be of great potential value for higher level phylogenetic considerations within recent Mycetophiliformia. The same certainly applies to other body parts or structures too, as for example, the abdomen, including genitalia, and sensilla. Perhaps disproportionately much attention was previously paid to wing venation alone. Current comparative studies of adult morphology throughout the Mycetophiliformia are much impeded by terminological disagreements, sometimes occurring even within one and the same family. Detailed, trustworthy morphological studies completely covering certain families, like those on Keroplatidae by Matile (1990) or on Mycetophilidae by Söli (1997), are still too scarce.

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