Zootaxa 1302: 43–59 (2006)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

1302

Phylogeny of the subfamily Mycetophilinae (Diptera: Mycetophilidae)

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Abstract

A phylogenetic analysis of the Mycetophilinae is presented and discussed. The analysis is based on morphological characters for 27 genera. Fourteen equally parsimonious trees were found. The monophyly of the Mycetophilinae and the two tribes, Exechiini and Mycetophilini, is well supported. Within the Exechiini, good support for the sister-group relationship of *Exechia* and *Exechiopsis* was found, as was support for the inclusion of *Cordyla* in the tribe. The analysis provides good resolution within the Mycetophilini, with *Trichonta* as the sister group of the remaining taxa.

Key words: Mycetophilidae, Mycetophilinae, Exechiini, Mycetophilini, phylogeny, morphology

Introduction

The Mycetophilidae are a large family of medium-sized gnats. Their biology is still insufficiently known; most described larvae, however, seem to feed on mycelium, either sporophores or hyphae penetrating rotting organic material. Members of the family are known throughout the world, except Antarctica. Based on present knowledge, the family is represented by more genera in cool and temperate areas than in the tropics.

The classification and systematics of the family Mycetophilidae have varied much through time. The subfamily Mycetophilinae was first introduced by Edwards (1925). Although several genera have later been included, they all comply with his original description of the subfamily. Edwards (1925) recognized two tribes, Mycetophilini and Exechiini, based on the following sets of characters: “Anepisternal and pteropleural bristles absent; hind coxa with a fairly strong bristle at base; empodia absent or

Accepted by P. Adler: 1 Aug 2006; published: 24 Aug. 2006

rudimentary; hind tibial comb usually indefinite or absent; tibial bristles short (Tribe Exechini)" and "Anepisternal bristles present, hind coxa usually without basal bristle; empodia and hind tibial comb nearly always distinct (Tribe Mycetophilini)".

Edwards' (1925) classification was left unaltered until Tuomikoski's (1966) revision of Exechiini. *Cordyla* Meigen was then transferred from Mycetophilini to Exechiini, and six new genera and ten new subgenera were erected and one genus was reestablished (*Brevicornu* Marshall, formerly included in *Allodia* Winnertz). This interpretation has been generally accepted, and is also adopted in the present study. Tuomikoski (1966) implied that several of his subgenera should be raised to the generic level, and this was partially done by Matile (1987) and Søli *et al*. (2000), whereby *Allodiopsis* Tuomikoski was split into four genera. Tuomikoski (1966) questioned the polarity of several commonly used characters and implicitly suggested some phylogenetic relationships between the genera commonly included in the Mycetophilinae. He considered Exechiini to be a monophyletic group, with a close relationship between *Cordyla* and *Brachypeza* Winnertz, and between *Allodiopsis* and *Notolopha* Tuomikoski. He also assumed the Mycetophilini to be paraphyletic and that three tribes in addition to the Exechiini could be recognized in the Mycetophilinae: one containing *Pseudoalysiina* Tonnoir; another containing *Pleurogymnus* Freeman, *Phronia* Winnertz, *Zygophronia* Edwards, *Trichonta* Winnertz, and *Dynatosoma* Winnertz; and a third containing, among others, *Mycetophila* Meigen, *Zygomyia* Winnertz, *Sceptonia* Winnertz, and *Epicypta* Winnertz.

Little is known about the phylogeny of the Mycetophilidae in general, and of Mycetophilinae in particular. A previous study (Søli 1997), aimed at genera commonly ascribed to the subfamily Sciophilinae, included 39 genera of Mycetophilidae, of which 3 belonged to the Mycetophilinae, viz. *Exechiopsis* Tuomikoski, *Mycetophila*, and *Phronia*. In general, the study gave little support for the monophyly of most commonly recognized tribes and subfamilies. Notwithstanding, the three genera of Mycetophilinae appeared in a common clade in all the most parsimonious trees. The objectives of the present study are to test the monophyly of the Mycetophilinae and the two tribes, Mycetophilini and Exechiini, and to resolve the internal generic relationships within the two tribes.

Material and methods

Altogether 27 genera are included in this study (Table 5), and to allow comparison with previous studies, genera from the Palaearctic fauna were selected. In the phylogenetic analysis, each genus is represented by a single species (males only), although more species were examined. The material is kept at the Natural History Museum in Oslo. The terminology follows that of Søli (1997) and McAlpine (1981). Slides were produced as described by Søli (1997).

Phylogenetic analysis. Only morphological characters were selected for the analysis, dealing with structures of the head, thoracic sclerites, wings, and legs. Genitalic characters

were omitted, pending better understanding and homology of these features. The characters in the analysis were scored as binary (54) or multistate (11); no characters were polymorphic within any of the genera (Table 1).

The matrix was constructed using MacClade (Maddison & Maddison 1992) and includes 65 morphological characters (Table 2). Missing data were coded as "?". Paup 4.0.b10 (Swofford 2003) was used for the phylogenetic analysis and the trees were viewed in Treeview (Page 1996). Bootstrap (Felsenstein 1985) was conducted with 1000 replicates of 100 heuristic searches each. Bremer support (Bremer 1988) was calculated with 20 heuristic searches on each clade.

TABLE 1. List of characters used in the phylogenetic analysis of the subfamily Mycetophilinae.

1. **Head** (0) with strong frontal bristles in a line between the eyes (Fig. 4b); (1) with bristles on the sides only. (Fig. 4a)
2. **Eyes** (0) concave; (1) not concave
3. **Compound eye, each ommatidium** (0) surrounded by 0-3 setulae; (1) surrounded by more than 3 setulae
4. **Number of ocelli** (0) three; (1) two
5. **Occipital furrow** (0) lacking; (1) present
6. **Frontal furrow** (0) long, reaching frontal tubercle (Fig. 4b); (1) long, but not reaching frontal tubercle (Fig. 4a); (2) very short, confined to the back of the head; (3) absent
7. **Frontal tubercle** (0) broad; (1) narrow
8. **Small plate above antennal socket** (0) absent; (1) present - *Phronia* type (Fig. 4a); (2) present - *Mycetophila* type (Fig. 4b)
9. **Font, setae on lower part** (0) absent; (1) present
10. **Face** (0) undivided; (1) divided by a transverse furrow
11. **Palpus with** (0) five palpomeres; (1) four palpomeres
12. **Sensory pit** (0) situated basally (or starts basally); (1) not so
13. **Sensory pit** (0) longer than 0.5 of palpal segment; (1) shorter
14. **Second palpal segment** (0) with setae; (1) without setae
15. **Premental apodeme** (1) with one process; (0) with two processes
16. **Antennal ratio (= flagellomere 2/flagellomere 1)** (0) larger than 2/3; (1) smaller than 2/3
17. **Costa** (0) not distinctly produced beyond the tip of R5; (1) distinctly produced beyond the tip of R5
18. **Humeral** (1) without setae; (0) with setae
19. **Apex of Sc** (0) distinct; (1) diminishing
20. **Distal median plate, ventral setae** (0) absent; (1) present
21. **Distal median plate, dorsal setae** (0) absent; (1) present
22. **Basicosta** (0) without large bristles; (1) with large bristles
23. **Crossvein ta** (0) with setae; (1) without setae
24. **M stem** (0) weak; (1) distinct

25. **M1** (0) with setae; (1) with row of trichia; (2) without setae and trichia
26. **M2** (0) with setae; (1) with row of trichia; (2) without setae and trichia
27. **CuA stem** (0) with setae; (1) without setae and trichia; (2) with small row of trichia
28. **CuA1** (0) present; (1) absent
29. **CuA1** (0) with setae; (1) with row of trichia; (2) without setae and trichia
30. **CuA2** (0) with setae; (1) with row of trichia; (2) without setae and trichia
31. **Wing membrane, setae** (0) absent; (1) present
32. **Wing membrane, trichia** (0) irregularly dispersed, not forming distinct rows; (1) forming distinct rows
33. **Basisternum 1** (0) without setae; (1) with setae
34. **Proepimeron** (0) without setae; (1) with setae
35. **Anepimeron** (0) without setae; (1) with setae
36. **Anepimeron, ventral part** (0) ends before the ventral side; (1) reaches the ventral side (Figs 10–11)
37. **Preepisternum 2, line on anterodorsal part** (0) absent (1) present
38. **Preepisternum 2**, v**entral part** (0) not round and covering base of coxa; (1) round and covering base of coxa
39. **Anepisternum, shape** (0) taller than wide; (1) wider than tall
40. **Anepisternum** (0) without setae; (1) with setae and bristles; (2) with setae only
41. **Posterior basalare** (0) without setae; (1) with setae
42. **Metepisternum** (0) without setae; (1) with setae; (2) with some small setae on the anterodorsal part
43. **Metepimeron** (0) without setae; (1) with setae
44. **Metanotum** (0) with setae behind halter; (1) without setae behind halter
45. **Mediotergite** (0) without setae; (1) with setae
46. **Prescutum and notum** (0) not produced beyond upper rim of anepisternum; (1) well produced beyond upper rim of anepisternum
47. **Notum** (0) with large setae; (1) with small setae
48. **Notum** (0) with setae in rows; (1) with setae irregularly dispersed
49. **Empodium** (0) present; (1) rudimentary
50. **Mid femur, apical bristles** (0) absent; (1) present
51. **Fore leg** (0) with tibia shorter than femur; (1) with tibia longer than femur
52. **Fore tibia, trichia** (0) irregularly dispersed; (1) in distinct rows
53. **Mid tibia** (0) with large setae; (1) without large setae
54. **Mid tibia, trichia** (0) irregularly dispersed; (1) in distinct rows
55. **Hind coax, bristles at basis** (0) one or two; (1) absent; (2) several
56. **Hind femur, apical bristles** (0) absent; (1) present
57. **Hind femur** (0) not arched (width/length < 0,2); (1) arched (width/length > 0,2)
58. **Hind tibia, length of setae** (0) two times width of tibia; (1) less than two times width of tibia
59. **Hind tibia, apical brush** (0) not produced across tibia; (1) produced across tibia
60. **Hind leg, trichia** (0) irregularly dispersed; (1) in distinct rows

61. **Hind tibia, dorsal surface** (0) normal; (1) with a triangular depression
62. **Hind spur and basitarsus** (0) spur less than half the length of basitarsus; (1) longer/ equal to
63. **Foldline on abdominal sternites** (0) absent; (1) with 2 fold liens; (2) 3 foldlines
64. **Basalt bristles on Tergite 9** (0) absent; (1) present
65. **Terminal bristles on cerci** (0) absent; (1) present

TABLE 2. Character matrix used in the phylogenetic analysis of the subfamily Mycetophilinae.

Character no.:		1	11111	11112	22222	22223	33333
	12345	67890	12345	67890	12345	67890	12345
Macrobrachius	01001	10111	10101	01011	10000	00000	11001
Zygomyia	01011	10200	00101	00111	11000	001??	11001
Trichonta	?0001	00101	00101	00011	10100	01000	11001
Sceptonia	01001	00200	00101	00011	11000	211??	11001
Platurocypta	01001	00200	00101	01011	10010	01000	11001
Phronia	10001	10111	10101	00011	10000	00000	11001
Mycetophila	01011	00201	00101	00011	10000	01000	11001
Epicypta	10011	00201	01101	00011	10010	01000	11001
Dynatosoma	10011	00011	10111	00001	10011	10011	11001
Exechiopsis	00010	21000	11011	10010	01101	12011	01110
Exechia	00010	21000	11011	10110	01001	12011	11010
Cordyla	00010	01000	10011	00100	01112	21022	01000
Brevicornu	00010	21000	11101	00000	01102	21022	11100
Anatella	00010	21000	10011	01000	01100	02000	01000
Allodiopsis	00000	21000	10011	00000	01100	02000	11100
Allodia	00000	21000	11011	00100	01101	12011	01100
Rymosia	10010	21000	11101	10010	01101	12011	01000
Tarnania	11010	21000	11011	10001	01002	21022	01000
Pseudorymosia	10010	21000	11111	10001	01100	01000	11110
Pseudobrachypeza	10010	21000	11101	10000	01001	11011	01110
Notolopha	10010	21000	11101	00000	01110	01000	11110
Pseudexechia	10010	21000	11111	10110	01102	21022	01000
Brachypeza	10000	21000	11111	10011	01000	01000	11110
Boletina	10101	00000	00000	00100	00100	01000	00000
Leia	00100	00000	00000	00100	01000	00000	00000
Docosia	00000	30000	00000	01010	00000	00000	00000
Dziedzickia	10101	20000	01100	01100	00100	00000	00100

continued.

Character no.:	33334	44444	44445	55555	55556	66666
	67890	12345	67890	12345	67890	12345
Macrobrachius	00101	11011	00000	01111	01101	01100
Zygomyia	00101	02011	10101	01011	11001	01101
Trichonta	01101	12010	00000	01011	00101	011?0
Sceptonia	01111	01010	10101	01011	11101	01101
Platurocypta	10111	12011	01101	01010	11001	01100
Phronia	01101	12010	00000	01111	01101	01101
Mycetophila	01101	12011	10001	01010	11001	01101
Epicypta	10111	02010	01101	01011	11001	01101
Dynatosoma	10011	12010	11101	01010	11001	01100
Exechiopsis	01000	01010	00010	11110	00111	10110
Exechia	01000	01010	00010	11110	00111	10110
Cordyla	10101	01010	11110	01111	01111	01100
Brevicornu	01000	01010	00010	11110	00111	01110
Anatella	01000	01010	00010	11110	00111	01110
Allodiopsis	01000	01010	00010	11110	00011	01110
Allodia	01000	01010	00010	11110	00111	01110
Rymosia	10002	01011	00110	11110	00111	01110
Tarnania	11002	01110	00010	01110	00111	01110
Pseudorymosia	11002	11011	00010	01110	00111	00110
Pseudobrachypeza	11002	01110	01110	11110	00011	01110
Notolopha	11000	01110	00010	11110	00011	01110
Pseudexechia	01000	01110	01110	11110	00111	01100
Brachypeza	00002	01010	11110	01110	01011	01100
Boletina	11110	00000	00001	10000	10000	00200
Leia	10100	10010	00001	00002	10010	01000
Docosia	00100	00000	00010	00002	00100	000??
Dziedzickia	11100	01000	00011	10000	10100	00200

Phylogeny

The parsimony analysis yielded 14 equally parsimonious trees of 239 steps, with an ensemble consistency index (CI) of 0.322 and an ensemble retention index (RI) of 0.663. The strict consensus tree shows strong support for the monophyly of the subfamily and the two tribes (Fig. 1). The results reveal good resolution within the Mycetophilini, with only

one trichotomy: *Dynatosoma* is found in a sister-group relationship with either *Epicypta* or *Platurocypta* Enderlein, while the latter two never form a sister-group relationship. In the Exechiini, there is much larger variation, and the strict consensus tree (Fig. 1) shows little resolution. The majority rule tree (Fig. 2) shows four monophyletic clades within the Exechiini in a polytomy that also includes *Allodia*; this large clade includes all taxa except *Anatella* Winnertz and *Cordyla*. Within this large clade, *Allodia* is often found in a sister-group relationship with the *Exechia*/*Exechiopsis* clade, and *Allodiopsis* usually forms a sister group with these and all remaining taxa (Fig. 2).

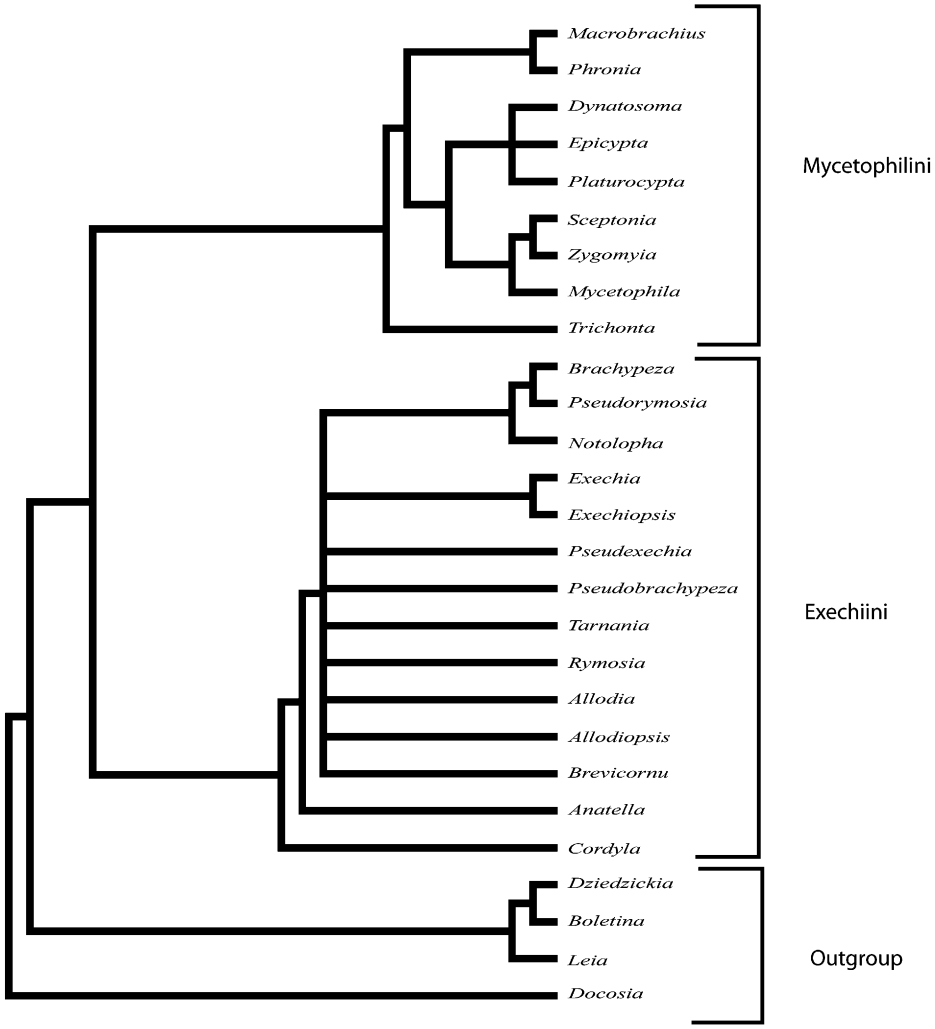


FIGURE 1. Strict consensus tree of 14 most parsimonious trees of 239 steps, with CI=0.322 and RI=0.663, for the subfamily Mycetophilinae.

The relatively higher proportion of characters per taxon within the Mycetophilini, might explain the higher resolution found within this clade. However, the results are also in accordance with the much better generic diagnoses found within the Mycetophilini.

A consecutive search with successive character weighting, using ri (Farris 1969), was performed, and the reweighting was repeated until the weights had stabilized (four times). This procedure yielded one tree, identical to one of the original 14 most parsimonious trees, and is the preferred tree (Fig. 3). All unambiguous character changes are listed in Table 3, while consistency and retention indices are given in Table 4.

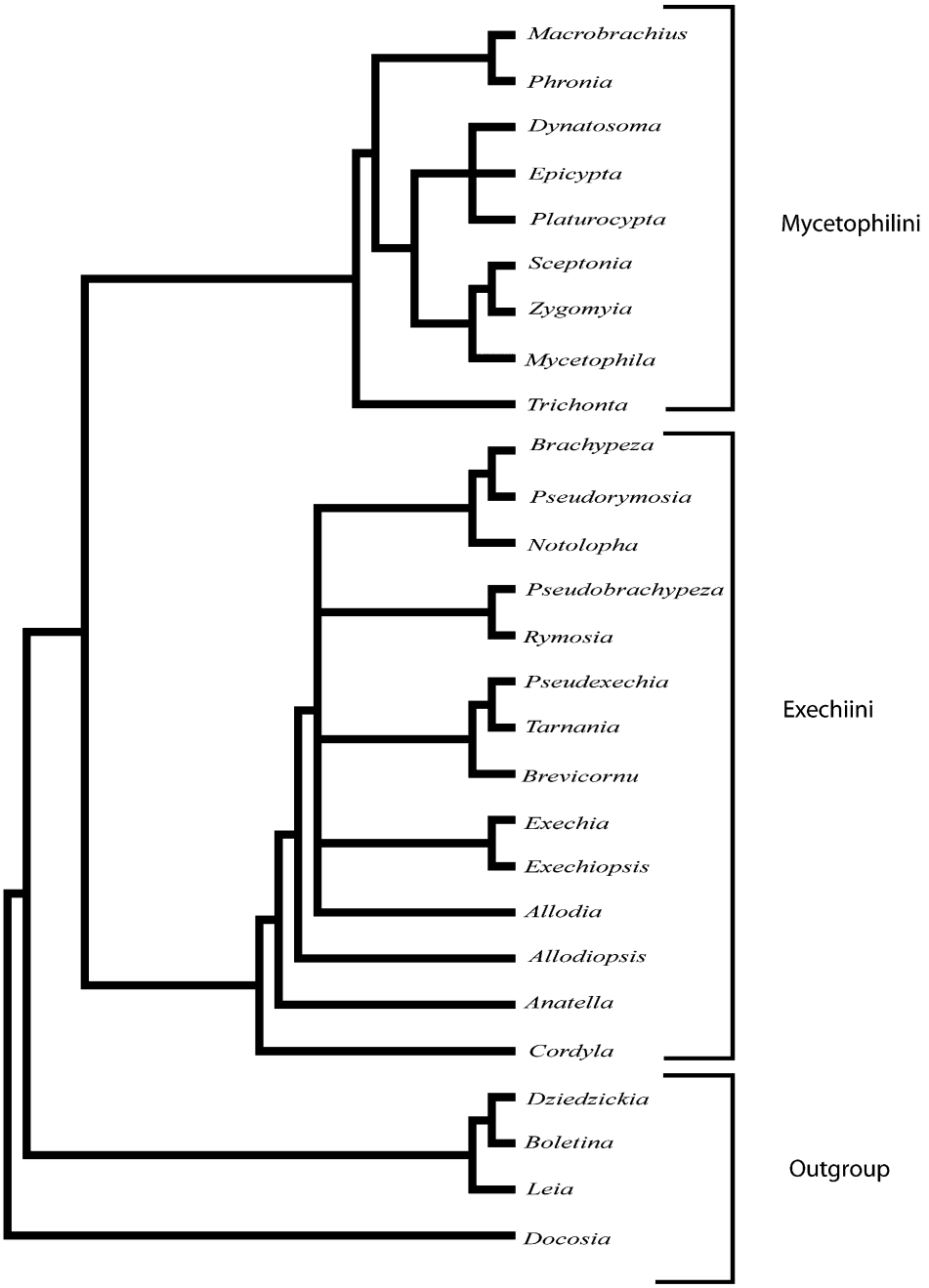


FIGURE 2. The 50% majority rule tree for the subfamily Mycetophilinae.

TABLE 3. All unambiguous character changes in the preferred tree for the subfamily Mycetophilinae (Fig. 3).

Branch no	Character	States	**Branch no**	Character	States	**Branch no**	Character	States	**Branch no**	Character	States
2			7			14			22		
	15	0→1		24	0→1		12	0→1		13	1→0
	27	0→1		36	0→1		13	0→1	23		
	32	0→1		39	0→1	15				19	0→1
	52	0→1		47	0→1		34	0→1		34	0→1
	54	0→1	8			16				61	0→1
	55	2→1		55	1→0		16	0→1		62	1→0
	60	0→1	9				20	0→1	24		
	63	0→1		2	0→1		40	0→2		3	0→1
3				46	0→1		51	0→1		18	0→1
	5	0→1	10			17				36	0→1
	8	0→1		10	1→0		25	0→2		50	0→1
	10	0→1		22	0→1		26	0→2		56	0→1
	13	0→1		28	0→1		29	0→2	25		
	20	0→1		41	1→0		30	0→2		1	0→1
	21	0→1	11			18				5	0→1
	31	0→1		4	0→1		16	0→1		51	0→1
	35	0→1		7	0→1		31	1→0		55	2→0
	41	0→1		11	0→1	19				63	0→2
4				14	0→1		33	1→0			
	57	0→1		22	0→1		43	0→1			
5				53	0→1	20					
	6	0→1		59	0→1		25	2→1			
	9	0→1	12				26	2→1			
	11	0→1		6	0→2		29	2→1			
	27	1→0		38	1→0		30	2→1			
	53	0→1		51	0→1	21					
6				55	1→0		14	1→0			
	4	0→1		64	0→1		36	0→1			
	8	1→2	13				40	0→2			
	50	0→1		31	0→1		48	0→1			
	56	0→1		33	0→1						
	58	1→0									

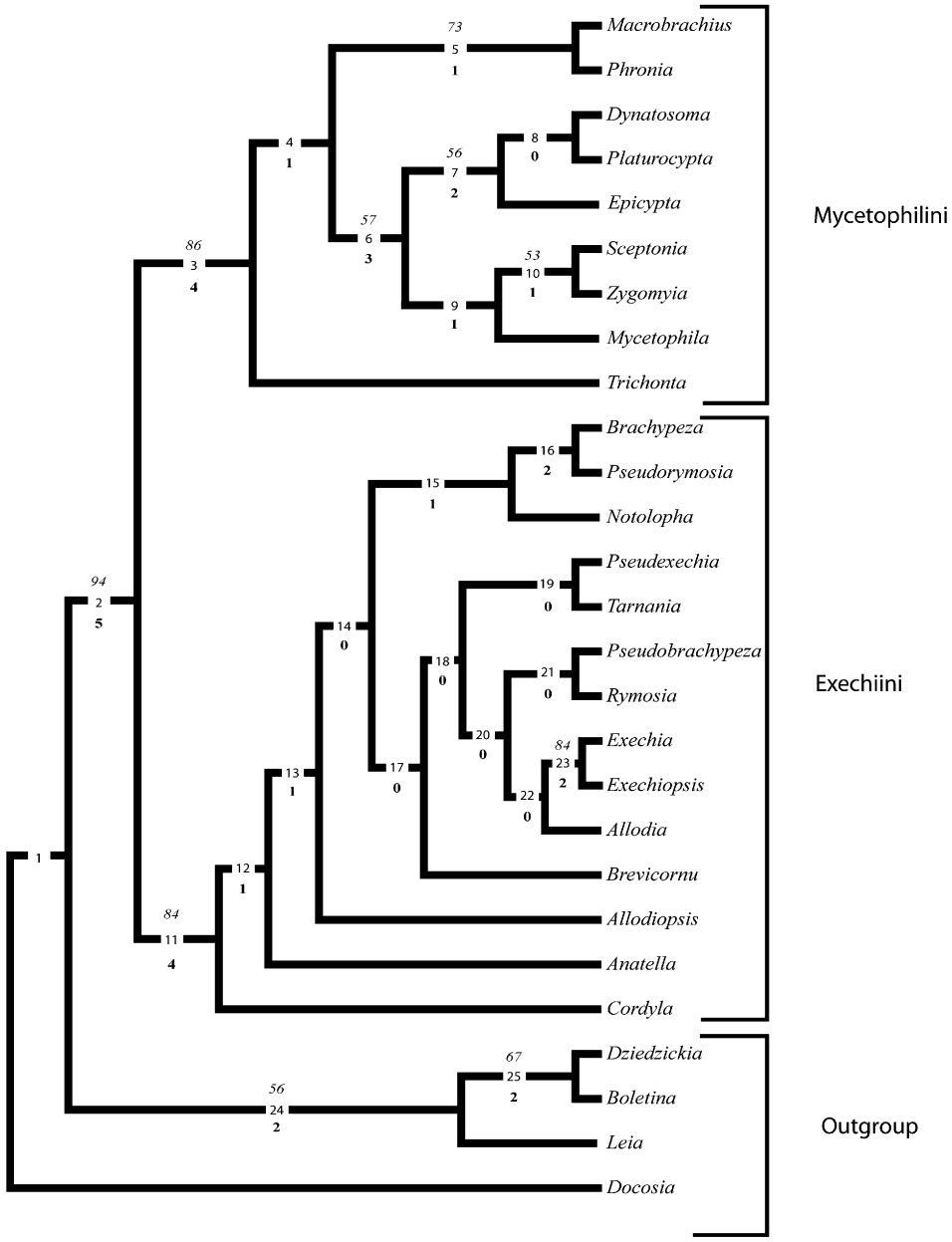


FIGURE 3. The preferred tree for the subfamily Mycetophilinae; 239 steps, CI=0.322, and RI=0.663. Branch numbers in regular type, Bootstrap values (> 50%) in *italics*, Bremer support in **bold**.

Systematics

The choice of outgroups is always a matter of discussion, with regard to both their number and relatedness to the ingroup in question. Moreover, the choice of outgroups might

influence the polarity of the characters. The basis for the present study was the phylogeny presented by Søli (1997). The outgroup taxa were selected without reference to the commonly recognized tribes. Four taxa were selected, two of them belonging to the same clade as the Mycetophilinae (*Leia* Meigen and *Docosia* Winnertz) and the other two more distantly related.

TABLE 4. Consistency (ci) and retention (ri) indices for each of the 65 characters in the preferred tree for the subfamily Mycetophilinae (Fig. 3).

No.	1	2	3	4	5	6	7	8
ci	0.143	0.250	1.000	0.143	0.500	0.600	1.000	0.667
ri	0.455	0.400	1.000	0.455	0.900	0.800	1.000	0.833
No.	9	10	11	12	13	14	15	16
ci	0.500	0.333	0.333	0.333	0.200	0.200	1.000	0.333
ri	0.500	0.600	0.778	0.833	0.556	0.600	1.000	0.714
No.	17	18	19	20	21	22	23	24
ci	0.200	0.167	0.143	0.333	1.000	0.333	0.143	0.333
ri	0.000	0.286	0.500	0.818	1.000	0.778	0.500	0.500
No.	25	26	27	28	29	30	31	32
ci	0.500	0.400	0.222	1.000	0.500	0.500	0.250	1.000
ri	0.750	0.667	0.364	1.000	0.750	0.750	0.727	1.000
No.	33	34	35	36	37	38	39	40
ci	0.200	0.333	1.000	0.143	0.125	0.500	0.333	0.400
ri	0.500	0.600	1.000	0.455	0.222	0.917	0.500	0.769
No.	41	42	43	44	45	46	47	48
ci	0.200	0.400	0.333	0.500	0.167	0.250	0.200	0.167
ri	0.429	0.625	0.333	0.500	0.000	0.400	0.333	0.444
No.	49	50	51	52	53	54	55	56
ci	0.333	0.500	0.250	1.000	0.500	1.000	0.400	0.500
ri	0.800	0.875	0.727	1.000	0.900	1.000	0.571	0.875
No.	57	58	59	60	61	62	63	64
ci	0.333	0.125	0.500	1.000	1.000	0.250	1.000	0.333
ri	0.778	0.300	0.909	1.000	1.000	0.400	1.000	0.800
No.	65							
ci	0.333							
ri	0.500							

TABLE 5. Taxa included in the phylogenetic study of the subfamily Mycetophilinae.

Tribe Mycetophilini	Tribe Exechiini	Outgroups
Dynatosoma norwegiense Zaitzev & Okland, 1994	*Allodia truncata* Edwards, 1921	*Boletina cincticornis* (Walker, 1848)
Epicypta n. sp.	*Allodiopsis domestica* (Meigen, 1830)	*Docosia gilvipes* (Walker, 1856)
Mycetophila fungivorum (De Geer, 1776)	*Anatella aquila* Zaitzev, 1985	*Dziedzickia marginata* (Dziedzicki, 1885)
Phronia forcipata Winnertz, 1863	*Brevicornu griseicolle* (Staeger, 1940)	*Leia subfasciata* (Meigen, 1818)
Platurocypta testata (Edwards, 1925)	*Cordyla fusca* Meigen, 1804	
Sceptonia fumipes Edwards, 1925	*Exechia exigua* Lundström, 1909	
Trichonta submaculata (Stæger, 1840)	*Exechiopsis crucigera* (Lundström, 1909)	
Zygomyia notata (Stannius, 1831)	*Notolopha cristata* (Staeger, 1840)	
Macrobrachius kowarzii Dziedzicki, 1889	*Pseuodbrachypeza helvetica* (Walker, 1856)	
	Pseudorymosia fovea (Dziedzicki, 1910)	
	Tarnania tarnanii (Dizieldzicki 1910)	
	Brachypeza radiata Jenkinson, 1908	
	Rymosia placida Winnertz, 1863,	

The subfamily

The subfamily Mycetophilinae (Branch 2) is supported by eight unambiguous character changes (Table 3), of which six show no reversals within the family and are not present in the outgroup. The clade has a Bremer support of 5 and bootstrap value of 94, and is the best supported branch in the entire tree. Except for the characters previously used to delimit the subfamily, additional characters include one upper rod on the premental apodeme (Character 15) and two foldlines on the abdomen (Character 63). Of these, a single, upper rod on the premental apodeme is, however, present in several genera outside the subfamily, including *Eumanota* Edwards and *Megophthalmidia* Dziedzicki, which appear close to the Mycetophilinae in the analysis of Søli (1997). The same holds true for the two abdominal foldlines, which are found in many genera related to the Sciophilini. Thus, none of these characters can be used independently in delimiting the Mycetophilinae.

The tribes

The tribe Mycetophilini (Branch 3) is supported by nine unambiguous character changes, of which three are unique for the subfamily: presence of an occipital furrow, either complete or on the back of the head (as in *Zygomyia* and *Sceptonia*) (Character 5); dorsal setae on the distal median plate (Character 21); and setae on the anepimeron (Character 35). The tribe has a Bremer support of 4 and a bootstrap value of 86.

The presence of an occipital furrow (Character 5) is here interpreted as a synapomorphy for the Mycetophilini, although according to Søli (1997: fig 2), several

other genera in the Mycetophilidae possess this character, i.e., *Grzegorzekia* Edwards, *Manota* Williston, *Coelosia* Winnertz, *Boletina* Staeger, and *Dziedzickia* Johannsen, making the polarization of the character uncertain; one can not exclude the possibility that the absence of an occipital furrow is a synapomorphy for the Exechiini, which would be in accordance with the interpretation by Tuomikoski (1966).

Within the subfamily, dorsal setae on the distal median plate (dmp) is a unique feature for the Mycetophilini. A setose dmp was also found in 13 genera studied by Søli (1997, Character 64, state 1), but the study did not make a distinction between dorsal and ventral setae. Such setae were present in some genera normally ascribed to the Sciophilini, but not in any genera placed close to the Mycetophilinae in the preferred tree. Both dorsal and ventral setae are found throughout the Mycetophilini, but in the Exechiini such setae are usually absent, except in *Rymosia* Winnertz, *Tarnania* Tuomikoski, and *Brachypeza*, which have ventral setae (Character 20).

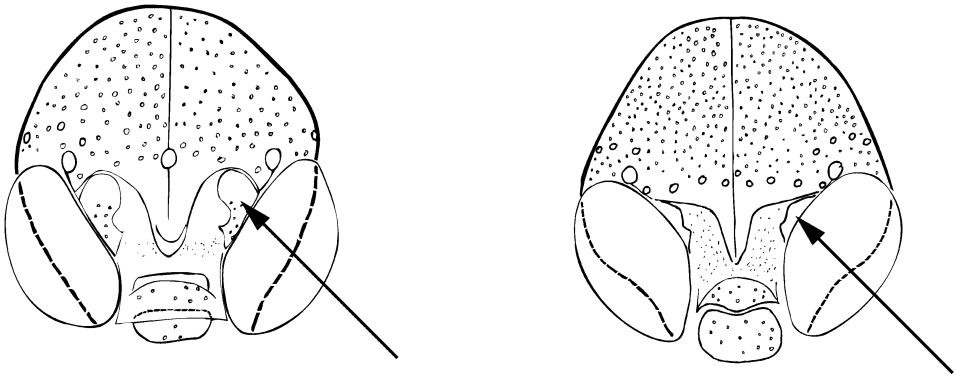
According to Edwards (1925), the Exechiini all have a bare anepimeron ("pteropleurite"). In the present study, the apomorphic state is interpreted to be setose, and it seems to be a good synapomorphy for the Mycetophilini. Bristles are also present in all Mycetophilini, except in *Dynatosoma*, *Phronia*, *Trichonta*, and *Macrobrachius* Dziedzicki.

The presence of setae and bristles on the anepisternum (Character 40), mentioned by Tuomikoski (1966), is found not only in the Mycetophilini, but also in *Cordyla*. Interpreted as an accelerated transformation (gain at Branch 2 and reversal at Branch 12), this would be compatible with the position of *Cordyla* above Branch 11.

The tribe Exechiini (Branch 11) is supported by seven unambiguous changes. Of these, a narrow frontal tubercle (Character 7) and a short apical brush (Character 59) are unique to the tribe, while a short frontal furrow (Character 6) and the presence of basal bristles on tergite 9 (Character 64) show reversal in *Cordyla* only. The rudimentary empodium (Character 29 state 1) also might be a synapomorphy for the Exechiini, although the character could not be unambiguously polarized.

Genera and clades within *Mycetophilini*

The three genera *Phronia*, *Macrobrachius*, and *Trichonta* share a common, seemingly unique feature, a characteristic pair of small sclerites in the frons (Character 8) (Fig. 4a). This might be a good synapomorphy for these genera, thus justifying a "*Phronia* group". Also, the lack of bristles on the anepimeron (Character 40, state 2), shared with *Dynatosoma*, supports this suggestion. These genera also share some features with the Exechiini (Characters 50, 56, 58). These finding are in accordance with Edwards (1925), who stated that *Phronia*, *Macrobrachius*, and *Trichonta* must belong to the same group. Gagné's (1975) assumption that the similarities between *Phronia* and *Macrobrachius* are due to convergence is thus not supported.



a. *Phronia* b. *Mycetophila*

FIGURE 4. Head of **a.** *Phronia*, **b.** *Mycetophila.*

The *Mycetophila* group (Branch 6; *Epicypta, Dynatosoma, Mycetophila, Platurocypta, Sceptonia*, and *Zygomyia*) constitutes an assemblage of robust and stout genera within the Mycetophilini. The group has a Bremer support of 3 and a bootstrap value of 57. There is much variation within the group, but good support for the grouping of these six genera in a common clade is found in the following set of characters: presence of a *Mycetophila*-type of plate in the frons (Character 8) (Fig 4b), notum produced well beyond the upper rim of the anepisternum (Character 46), large setae on the mid and hind tibia (Characters 53 and 58), and two ocelli (Character 4). All these characters, however, show reversals within the group.

Dynatosoma is the only genus within the tribe to take a variable position in the most parsimonious trees, either in a sister-group relationship with *Epicypta* or *Platurocypta*. The latter two genera, however, never form a sister-group relationship.

The sister-group relationship between *Zygomyia* and *Sceptonia* (Branch 10) is supported by an interesting feature: the lack of CuA1 (Character 28). This is a unique feature within the subfamily, and together with the presence of setae on the posterior basalare (shared with *Epicypta*) and the occipital furrow produced only on the back of the head, it gives good support for this grouping. A possible sister group of these two genera is found in the Samoan genus *Zygophronia* Edwards, which also has CuA1 reduced (Edwards 1928).

Genera and clades within *Exechiini*

Anatella and *Cordyla* take an isolated position in relation to the remaining genera in the Exechiini (Branch 13) due to the absence of setae on the basisternum (Character 33) and

on the wing membrane (Character 31), both characters showing reversals within the clade. *Cordyla* was originally placed in the Mycetophilini by Edwards (1925) due to the presence of bristles on the anepisternum; Tuomikoski (1966), however, transferred it to its present position in the Exechiini. It is a highly divergent genus and shows affinity to both tribes; the revealed position is thus not unexpected. The present analysis, however, gives good support for the inclusion of *Cordyla* in the Exechiini.

Two clades within the Exechiini, above Branch number 15 and 23, are present in the strict consensus tree. The sister-group relationship between *Exechia* Winnertz and *Exechiopsis* (Branch 23) is supported by four unambiguous character changes (Tab. 4). Of these, the dorsal surface of the tibiae with a triangular depression (Character 61) is the only unique character for this clade (illustrated by Vockeroth (1981: figs 78-80)), the remaining characters are all homoplastic. The weakly supported group (*Notolopha* (*Brachypeza*, *Pseudorymosia* Tuomikoski)) (Branch 15) is unambiguously supported by the presence of setae on the proepimeron, a character that shows much homoplasy in the analysis. The clade consisting of *Brachypeza* and *Pseudorymosia* is supported by 4 unambiguous character changes, all of them present elsewhere in the tree.

Conclusion

The present analysis confirms that the genera commonly ascribed to the subfamily Mycetophilinae constitute a monophyletic grouping, as do the two tribes, Mycetophilini and Exechiini. Given the Mycetophilinae as a subfamily, the present study supports the tradition of dividing the genera into two tribes. The genera included in each tribe seem also to be correct.

These findings are in striking contrast with the phylogenetic assumptions presented by Tuomikoski (1966). Apparently, some consensus can be found only within the Mycetophilinae: one clade consisting of *Mycetophila* and its allies and one clade of *Phronia* and its allies. The suggested paraphyly of the Mycetophilini is clearly rejected.

In general, the reduction and formation of setae on different thoracic sclerites appear common, and several characters based on these features show much variation across the studied genera, especially within the Exechiini, e.g., setae on the proepimeron (Character 34), posterior basalare (Character 41), basisternum (Character 33), and mediotergite (Character 45). Thus, grouping based on the presence or absence of setae on the thoracic sclerites may lead to erroneous conclusions. A seemingly good character such as the number of ocelli (Character 4) appears to be of little or no use in classification within the Mycetophilini.

In future studies, larval and pupal characters should be included, as these stages, in particular the pupa, are likely to reveal several phylogenetically important characters. So far, the larvae have only been studied for a small number of genera. The only larger studies of larval morphology are those by Madwar (1937) and Plachter (1979). In his detailed

study of the Keroplatidae, Matile (1997) demonstrated that a thorough study of larvae can help in resolving the systematic position of several enigmatic genera. There are good indications that such characters exist within the Mycetophilidae. For example, Edwards (1925) mentioned that the larvae of one group (most likely the Mycetophilini) have black ambrucal setae, while the larvae of the other group (most likely the Exechiini) do not (see also Johannsen 1909). Madwar (1937) mentioned that the locomotory pads are well developed in the Mycetophilini and poorly developed in most Exechiini. This structure may be the same as that referred to by Johannsen (1909) and Edwards (1925).

Moreover, it would be desirable to include more species from each genus and representatives of all subgenera and species groups in future phylogenetic studies of the subfamily and the family. In such studies, molecular data may be of great importance. Future studies should also be extended to include species from other zoogeographical regions, as they may add valuable information to our assumptions about character transformations.

Acknowledgments

We thank Lars Ove Hansen and Trond Andersen for commenting on an earlier draft of the manuscript. The work was partly funded by the Strategic University Program ”National Centre for Biosystematics” (Grant no. 146515/420), co-funded by the Research Council of Norway and the NHM, University of Oslo.

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