

The Metatarsi of the Fulgoroidea (Homoptera: Auchenorrhyncha)

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ABSTRACT

The segmentations and apical teeth of the metatarsi in the first to fifth instar nymphs and adults of the Coleorrhyncha and Auchenorrhyncha are examined phylogenetically. The ground plan for the metatarsi of Auchenorrhyncha has two segments. The segmentations and apical teeth of the metatarsi appear to be accelerated during their ontogenetic development. By a thorough comparison of morphological data of the metatarsi, a cladogram for the Fulgoroidea is reconstructed as (Coleorrhyncha ((Cicadoidea, Cercopoidea, Membracoidea) (Tettigometridae (Ricaniidae-group (Tropiduchidae-group (Fulgoridae-group, Cixiidae-group)))))). On the basis of metatarsal characters analyzed, the Fulgoroidea has the most advanced character state in the Auchenorrhyncha and the Cixiidae-group has the most advanced character state in the Fulgoroidea.

Key words: Auchenorrhyncha, Fulgoroidea, metatarsi, phylogeny.

Introduction

The phylogenetic relationships of the Fulgoroidea, based mainly on adult characters, have been published by Muir (1923, 1930), Bourgoïn (1985), Asche (1987) and Emeljanov (1990). But the relationships among subgroups of the Fulgoroidea are still unclear.

Studying the nymphs of Fulgoroidea has revealed that the segmentations and apical teeth of the metatarsi may contain more phylogenetic information. In the present work, this single, new, potential character was chosen for ontogenetical study. The Coleorrhyncha, Cicadoidea, Cercopoidea, and Membracoidea were selected as outgroups. The authors hope that the data thus obtained can make significant contributions to future discussions on the phylogeny of the Fulgoro-

idea.

Morphological observations

1. Coleorrhyncha

1. *Hemiodoeus veitchi* Hacker (Fig.1)

First instar nymph: Metatarsi 2-segmented, first metatarsus without apical tooth (Helmsing and China, 1937)

2. *Oiophysa distincta* Woodward (Fig.2)

Fifth instar nymph and adult: Metatarsi 2-segmented, first metatarsus without apical tooth.

Other species examined

1. *Pantinia darwini* China (fifth instar nymph and adult).

2. *Peloridium hammoniorum* Breddin (fifth instar nymph and adult).

3. *Oiophysa pendergrasti* Woodward (fifth instar nymph and adult).

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4. *Xenophysella pegasusensis* Evans (fifth instar nymph and adult).

The inferred whole features

First to fifth instar nymphs and adult: Metatarsi 2-segmented, first metatarsus without apical tooth.

II. Cicadoidea

1. *Cryptotympana atrata* Fabricius (Fig.3)

First instar nymph: Metatarsi 2-segmented, first metatarsus without apical tooth.

2. Cicadoidea sp. (Fig.4)

Fifth instar nymph: Metatarsi 2-segmented, first metatarsus without apical tooth.

3. *Mogannia hebes* Walker (Fig.5)

Adult: Metatarsi 3-segmented, first 2 metatarsi without apical teeth.

The inferred whole features

First to fifth instar nymphs: Metatarsi 2-segmented, first metatarsus without apical tooth.

Adult: Metatarsi 3-segmented, first 2 metatarsi without apical teeth.

III. Cercopoidea

1. *Cosmoscatar rubroscutellata* Matsumura (Fig.6)

Second to fifth instar nymphs: Metatarsi 2-segmented, first metatarsus without apical tooth.

Adult: Metatarsi 3-segmented, first 2 metatarsi with 12-13 apical teeth, respectively.

Other species examined

1. *Poophilus costalis* Walker (second instar nymph to adult).

The inferred whole features

First instar nymph: Segmentations of metatarsi inferred from Coleorrhyncha should be 2. Apical tooth of first metatarsus inferred from second instar nymph should be none.

Second to fifth instar nymphs: Metatarsi 2-segmented, first metatarsus without apical tooth.

Adult: Metatarsi 3-segmented, first metatarsus with 8-12 apical teeth, second metatarsus with 13-19 apical teeth.

IV. Membracoidea

1. *Aetalion flavascens* Yuan (Fig.7)

Fifth instar nymph: Metatarsi 2-segmented, first metatarsus without apical tooth.

Adult: Metatarsi 3-segmented, first metatarsus with 1 apical tooth, second metatarsus without apical tooth.

2. *Erythroneura subrufa* (Motschulsky) (Fig.8)

First to fifth instar nymphs: Metatarsi 2-segmented, first metatarsus without apical tooth.

Adult: Metatarsi 3-segmented, first two metatarsi with 2 apical teeth, second metatarsus without apical tooth.

Other species examined

1. *Nirvara orientalis* Matsumura (fourth instar nymph to adult).

2. *Tricentrus* sp. (First instar nymph to adult).

The whole features

First to third instar nymphs: Metatarsi 2-segmented, first metatarsus without apical tooth.

Fourth instar nymph: Metatarsi 2-segmented, first metatarsus with 0-3 apical teeth.

Fifth instar nymph: Metatarsi 2-segmented, first metatarsus with 0-3 apical teeth, potential second metatarsus¹ with 0-3 apical teeth (present in *Nirvara orientalis*)

Adult: Metatarsi 3-segmented, first metatarsus with 1-3 apical teeth, second metatarsus with 0-3 apical teeth.

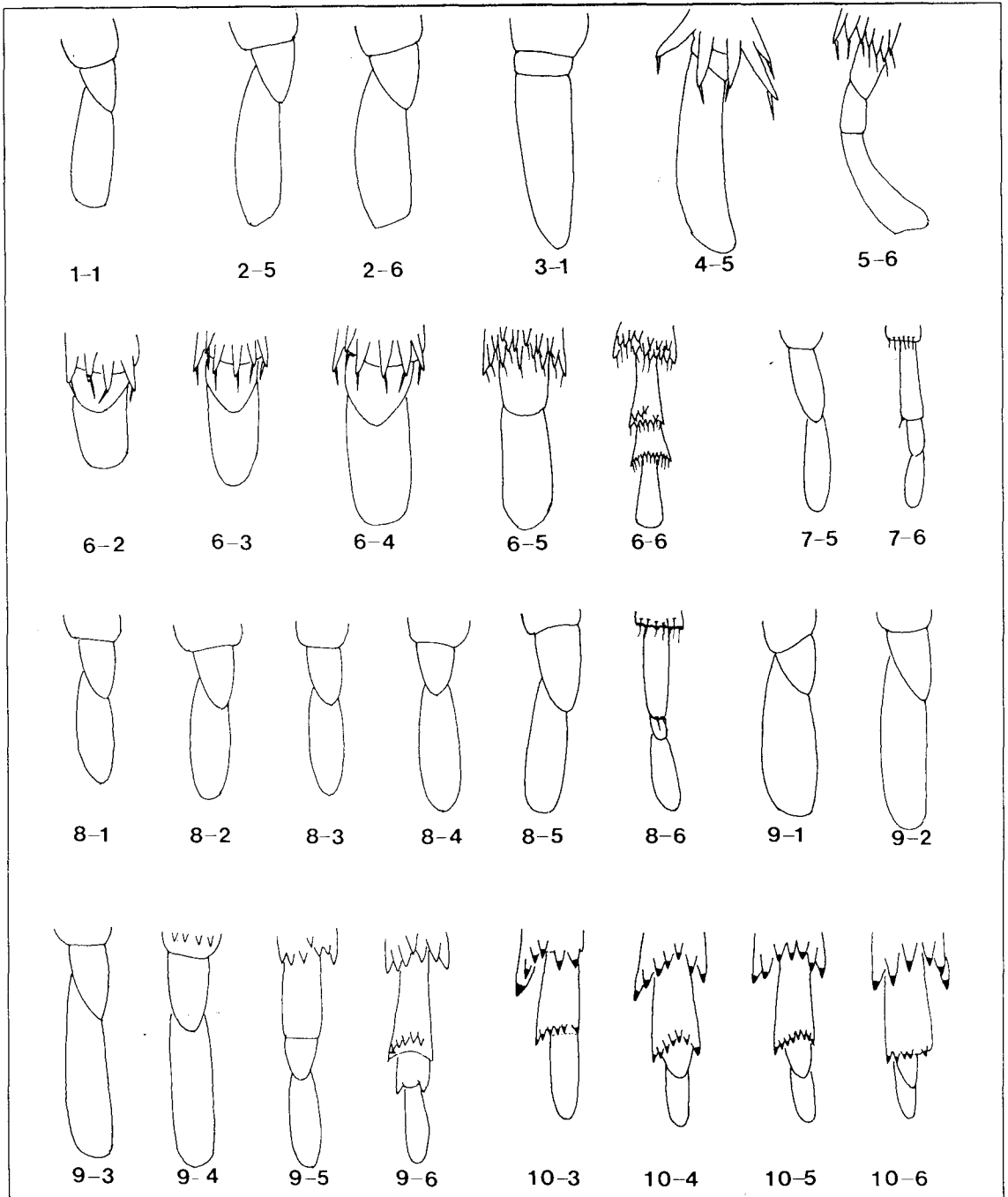
V. Fulgoroidea

(I) Tettigometridae

1. *Euphyonarthex phyllostoma* Schmidt (Fig.9)

First to fourth instar nymphs: Metatarsi 2-segmented, first metatarsus without apical tooth.

¹ When metatarsi 2-segmented and teeth appear near the middle of the true second metatarsus, the basal portion before the teeth is called the potential second metatarsus.



Figs. 1-10. Metatarsi of the Coleorrhyncha and Auchenorrhyncha. 1(1), *Hemiodoecus veitchi* Hacker; 2(5-6), *Oiophysa distincta* Woodward; 3(1), *Cryptotympana atrata* Fabricius; 4(5), Cicadoidea sp.; 5(6), *Mogannia hebes* Walker; 6(2-6), *Cosmoscatar rubroscutellata* Matsumura; 7(5-6), *Aetalion flavascens* Yuan; 8(1-6), *Erythroneura subrufa* (Motschulsky); 9(1-6), *Euphyonarthex phyllostoma* Schmidt; 10(3-6), *Ricania fumosa* (Walker). (numbers 1-5 in parentheses indicate nymphal stages with 6 indicating an adult).

Fifth instar nymph: Metatarsi 3-segmented, first metatarsus without apical tooth, second metatarsus conical at apex, without apical tooth.

Adult: Metatarsi 3-segmented, first metatarsus with 7 apical teeth, second metatarsus conical at apex, with 2 apical teeth on each side.

Other species examined:

1. *Hilda patruelis* Stal (third to fifth instar nymph).

(II) Ricaniidae-group

The Ricaniidae, Lophopidae, Eurybrachidae, Hypochthonellidae and Gengidae² comprise the Ricaniidae-group.

1. *Ricania fumosa* (Walker) (Fig.10)

Third instar nymph: Metatarsi 2-segmented, first metatarsus with about 6 apical teeth.

Fourth to fifth instar nymphs: Metatarsi 3-segmented, first metatarsus with 7-8 apical teeth, second metatarsus conical at apex, without apical tooth.

Adult: Metatarsi 3-segmented, first metatarsus with 5 apical teeth, second metatarsus conical at apex, without apical tooth.

Other species examined:

1. *Scalyopopa australia* (Walker) (Ricaniidae) (fourth instar nymph to adult).

2. *Lophops carinata* (Kirby) (Lophopidae) (fourth instar nymph to adult).

3. *Hypochthonella caeca* China and Fennah (Hypochthonellidae) (fifth instar nymph to adult).

4. Eurybrachidae sp. (Eurybrachidae) (fifth instar nymph).

The inferred whole features

First to second instar nymphs: Segmentations of metatarsi inferred from Coleorrhyncha should be 2.

Third instar nymph: Metatarsi 2-segmented, first metatarsus with about 6 apical teeth, second metatarsus conical at apex, without apical tooth.

Fourth and fifth instar nymphs: Metatarsi 3-segmented, first metatarsus

with 3-8 apical teeth, second metatarsus conical at apex, without apical tooth.

Adult: Metatarsi 3-segmented, first metatarsus with 3-12 apical teeth, second metatarsus conical at apex, without apical tooth.

(III) Tropicuchidae-group

The Tropicuchidae, Flatidae, Nogodiniidae, Issidae and Acanaloniidae comprise the Tropicuchidae-group.

1. *Kallitaxila sinica* (Walker) (Tropicuchidae) (Fig.11)

First to fourth instar nymphs: Metatarsi 2-segmented, first metatarsus with 4-5 apical teeth.

Fifth instar nymph: Metatarsi 3-segmented, first metatarsus with 5 apical teeth, second metatarsus conical at apex, with 2 apical teeth on each side.

Adult: Metatarsi 3-segmented, first metatarsus with about 5 apical teeth, second metatarsus conical at apex, with 2 apical teeth on each side.

2. *Neommatissus basifuscus* Kato (Tropicuchidae) (Fig.12)

Second instar nymph: Metatarsi 2-segmented, first metatarsus with about 5 apical teeth.

Third instar nymph: Metatarsi 2-segmented, first metatarsus with about 6 apical teeth, potential second metatarsus with a tooth on each side.

Fourth and fifth instar nymphs and adult: Metatarsi 3-segmented, first metatarsus with 7-8 apical teeth, second metatarsus conical at apex, with 2-3 apical teeth.

Other species examined or referred to

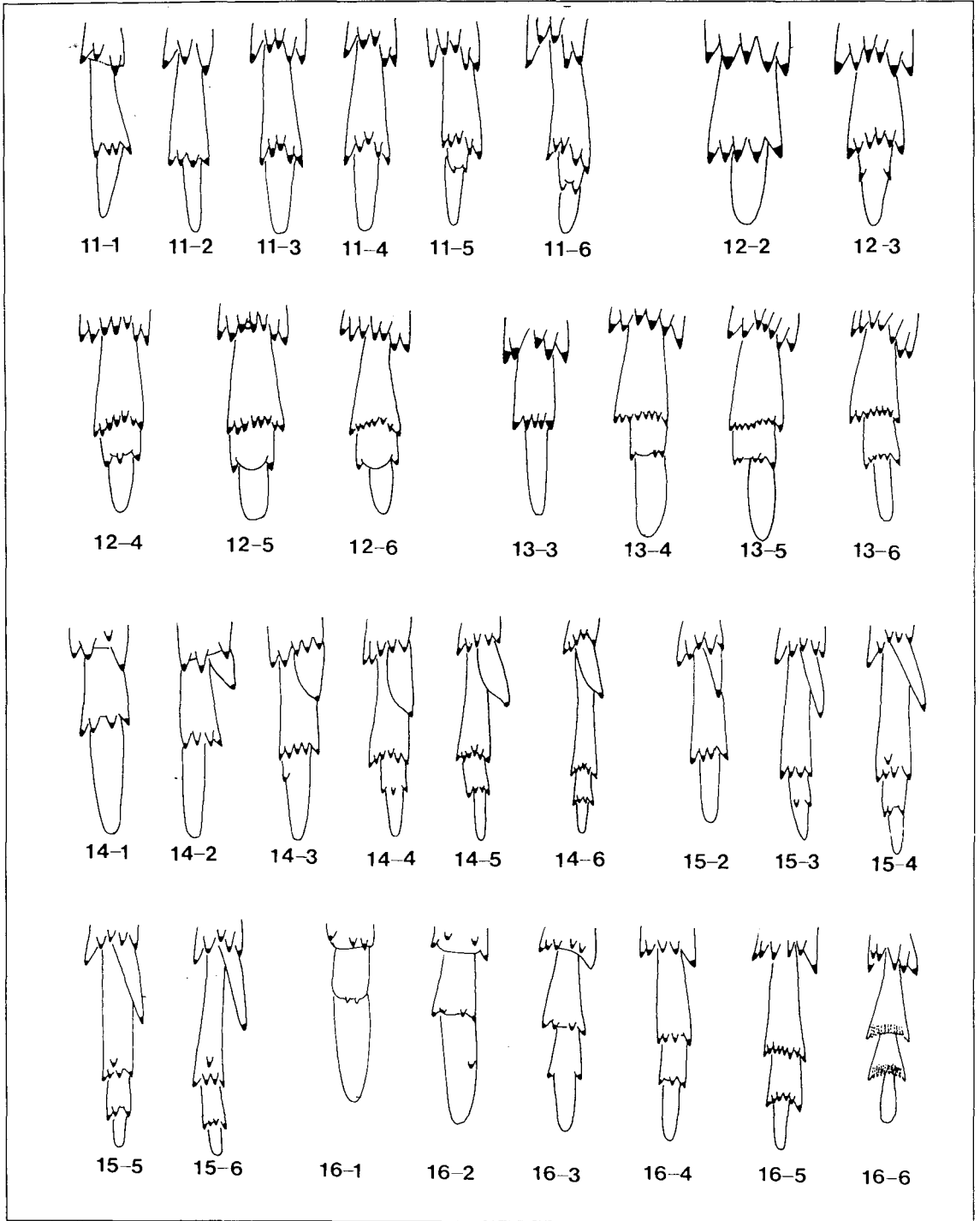
1. *Ossoides lineatus* Bierman (Tropicuchidae) (fourth instar nymph to adult).

2. *Pelitropis rotulata* Van Duzee (Tropicuchidae) (third instar nymph to adult) (Wilson and Wheeler, 1984).

3. *Phylliana serva* Walker (Flatidae) (first instar nymph to adult).

4. *Anormenis septentrionalis* (Spinola) (Flatidae) (first to fifth instar nymphs).

² Gengid specimens were not available, but they should be in the Ricaniidae-group.



Figs. 11-16. Metatarsi of the Fulgoroidea. 11(1-6), *Kallitaxila sinica* (Walker); 12(2-6), *Neommatissus basifuscus* Kato; 13(3-6), *Lycorma meliae* Kato; 14(1-6), *Bambusiphaga taiwanensis* (Muir); 15(2-6), *Ugyops tripunctatus* (Kato); 16(1-6), *Pentastiridius pachycephs* (Matsumura). (numbers 1-5 in parentheses indicate nymphal stages with 6 indicating an adult).

(Wilson and McPherson, 1981b).

5. *Metcalfa pruinosa* (Say) (Flatidae) (first to fifth instar nymphs) (Wilson and McPherson, 1981b).

6. *Ormenaria rufifascia* (Walker) (Flatidae) (first to fifth instar nymphs) (Wilson and Tsai, 1984).

7. *Ormenoides venusta* (Melichar) (Flatidae) (first to fifth instar nymphs) (Wilson and McPherson, 1981b).

8. *Mindura subfasciata kotoshonis* Matsumura (Nogodinidae) (second instar nymph to adult).

9. *Parasarima pallizona* (Matsumura) (Issidae) (second instar nymph to adult).

10. *Mushy quadrivittata* Kato (Issidae) (fourth and fifth instar nymphs).

11. *Bruchomorpha oculata* Newman (Issidae) (first to fifth instar nymphs) (Wilson and McPherson, 1981c).

12. *Eusarima astuta* Yang (Issidae) (third to fifth instar nymphs).

13. *Gergithoides carinatifrons* Schmacher (Issidae) (second, third and fifth instar nymphs and adult).

14. *Gergithus formosanus* Metcalf (Issidae) (Third to fifth instar nymphs).

15. *Tonga westwoodi* Signoret (Issidae) (Third to fifth instar nymphs).

16. *Acanalonia bivittata* (Say) (Acanaloniidae) (first to fifth instar nymphs) (Wilson and McPherson, 1981a).

17. *Acanalonia conica* (Say) (Acanaloniidae) (First to fifth instar nymphs) (Wilson and McPherson, 1981a).

The whole features

First to second instar nymphs: Metatarsi 2-segmented, first metatarsus with 4-5 apical teeth.

Third instar nymph: Metatarsi 2-segmented, first metatarsus with 2-7 apical teeth. Some species of Tropicodidae with potential second metatarsus with 1-2 apical teeth on each side.

Fourth instar nymph: Metatarsi 3-segmented (except some species of Tropicodidae still 2-segmented; if 2-segmented, potential second metatarsus with an apical tooth on each side). First metatarsus

with 2-10 apical teeth, second metatarsus conical at apex, with 2-3 apical teeth on each side.

Fifth instar nymph and adult: Metatarsi 3-segmented, first metatarsus with 2-8 apical teeth, second metatarsus conical at apex, with 2-3 apical teeth on each side.

(IV) Fulgoridae-group

The Fulgoridae and Dictyopharidae comprise the Fulgoridae-group.

1. *Lycorma meliae* Kato (Fulgoridae) (Fig.13)

Third instar nymph: Metatarsi 2-segmented, first metatarsus with about 5 apical teeth.

Fourth instar nymph: Metatarsi 3-segmented, first metatarsus with about 4 apical teeth, second metatarsus conical at apex, with 2-3 apical teeth on each side.

Fifth instar nymph and adult: Metatarsi 3-segmented, first metatarsus with 8-9 apical teeth, second metatarsus truncate at apex, with 6 apical teeth in a row.

2. Dictyopharidae sp.

Second instar nymph: Metatarsi 2-segmented, first metatarsus with about 6 apical teeth.

Third instar nymph: Metatarsi 2-segmented, first metatarsus with about 7 apical teeth. Potential second metatarsus with 3 apical teeth laterally.

Fourth and fifth instar nymphs: Metatarsi 3-segmented, first metatarsus with 9-13 apical teeth, second truncate at apex, with 5-8 apical teeth in a row.

The other species referred to

1. *Itzalana submaculata* Schmidt (Fulgoridae) (Third to fifth instar nymphs) (Wilson and O'Brien, 1986).

2. *Nersia florens* Stal (Dictyopharidae) (First, second and fifth instar nymphs) (Wilson and McPherson, 1981c).

The whole features

First and second instar nymphs: Metatarsi 2-segmented, first metatarsus with 5-6 apical teeth.

Third instar nymph: Metatarsi 2-segmented, first metatarsus with 5-7 apical

teeth. Some species of Dictyopharidae with 3 apical teeth laterally at potential second metatarsus.

Fourth instar nymph: Metatarsi 3-segmented, first metatarsus with 4-9 apical teeth, second metatarsus conical or truncate at apex, with 2-5 apical teeth on each side or in a row.

Fifth instar nymph and adult: Metatarsi 3-segmented, first metatarsus with 6-13 apical teeth, second metatarsus truncate at apex, with 2-8 apical teeth in a row.

(V) Cixiidae-group

The Delphacidae, Meenoplidae, Kinnaridae³, Cixiidae, Achilidae Achilixiidae⁴ and Derbidae comprise the Cixiidae-group.

1. *Bambusiphaga taiwanensis* (Muir) (Delphacidae) (Fig.14)

First and second instar nymphs: Metatarsi 2-segmented, first metatarsus with about 4 apical teeth.

Third instar nymph: Metatarsi 2-segmented, first metatarsus with about 5 apical teeth, potential second metatarsus with a single apical tooth laterally.

Fourth instar nymph: Metatarsi 2-segmented, first metatarsus with about 6 apical teeth, potential second metatarsus with 2 apical teeth on each side.

Fifth instar nymph and adult: Metatarsi 3-segmented, first metatarsus with about 6 apical teeth, second metatarsus truncate at apex, with about 4 apical teeth in a row.

2. *Ugyops tripunctatus* (Kato) (Delphacidae) (Fig.15)

Second instar nymph: Metatarsi 2-segmented, first metatarsus with 4 apical teeth.

Third instar nymph: Metatarsi 2-segmented, first metatarsus with about 5 apical teeth, potential second metatarsus with 2 apical teeth on each side.

Fourth instar nymph: Metatarsi 3-seg-

mented, first metatarsus with about 3 apical teeth, second metatarsus truncate at apex, with about 3 apical teeth in a row.

Fifth instar nymph and adult: Metatarsi 3-segmented, first metatarsus with 5 apical teeth, second metatarsus truncate at apex, with 3-4 apical teeth in a row.

3. *Pentastiridius pachycephs* (Matsumura) (Cixiidae) (Fig.16)

First instar nymph: Metatarsi 2-segmented, first metatarsus with 2 apical teeth.

Second to third instar nymphs: Metatarsi 2-segmented, first metatarsus with about 4 apical teeth, potential second metatarsus with 1-2 apical teeth laterally.

Fourth, fifth instar nymphs and adult: Metatarsi 3-segmented, first metatarsus with 8-12 apical teeth, second metatarsus truncate at apex, with 6-11 apical teeth in a row.

The other species examined or referred to

1. *Delphacodes bellicosa* Muir and Giffard (Delphacidae) (first to fifth instar nymphs) (Wilson, 1985).

2. *Harmalia commelinae* Yang (Delphacidae) (first to fifth instar nymphs).

3. *Megamelus davisii* Van Duzee (Delphacidae) (first to fifth instar nymphs) (Wilson and McPherson, 1981d).

4. *Nilaparvata lugens* (Stal) (Delphacidae) (first, third instar nymphs to adult).

5. *Saccharosydne procerus* (Matsumura) (Delphacidae) (first instar nymph to adult).

6. *Stenocranus lautus* Van Duzee (Delphacidae) (first instar nymph to adult) (Calvert and Wilson, 1986).

(Species 1-6 with 2-segmented metatarsi of fourth instar nymph).

7. *Pentagramma longistylata* Penner (Delphacidae) (third to fifth instar nymphs) (Wilson and Wheeler, 1986).

^{3,4} Kinnarid and achilixiid specimens were not available, but they should be in the Cixiidae-group.

8. *Purohita taiwanensis* Muir (Delphacidae) (first instar nymph to adult).

(Species 7 and 8 with 3-segmented metatarsi of fourth instar nymph).

9. *Nisia carolinensis* Fennah (Meenoplidae) (first instar nymph to adult)

10. *Nisia serrata* Tsaur (Meenoplidae) (First instar nymph to adult).

11. Achilidae sp. (second to fifth instar nymphs).

12. *Neoproutista pseudoalbicosta* (Muir) (Derbidae) (third to fifth instar nymphs).

13. *Vekunta novensilis* Yeh and Yang (Derbidae) (third to fifth instar nymphs).

14. *Zoraida insolita* Yang (Derbidae) (second to fifth instar nymphs).

15. *Zoraida kotoshoensis* Matsumura (Derbidae) (first instar nymph to adult).

The whole features

First instar nymph: Metatarsi 2-segmented, first metatarsus with 2-4 apical teeth.

Second and third instar nymphs: Metatarsi 2-segmented, first metatarsus with 4-5 apical teeth. Potential second metatarsus with 1-2 apical teeth except some species of Delphacidae without apical teeth.

Fourth instar nymph: Metatarsi 3-segmented, except some species of 2-segmented Delphacidae. First metatarsus with 6-7 apical teeth, second metatarsus truncate at apex, with 4-5 apical teeth in a row.

Fifth instar nymph and adult: Metatarsi 3-segmented, first metatarsi with 5-12 apical teeth, second metatarsus truncate at apex, with 4-11 apical teeth in a row.

Discussion

Data on the segmentations of metatarsi in the Coleorrhyncha and Auchenorrhyncha are summarized in Table 1. Data of the apical teeth of the second and potential second metatarsus is summarized in Table 2.

Table 1. Segmentations of metatarsi in the Coleorrhyncha and Auchenorrhyncha

Taxa	Instar nymph					Adult
	1	2	3	4	5	
Coleorrhyncha	2	2	2	2	2	2
Cicadoidea	2	2	2	2	2	3
Cercopidea	2	2	2	2	2	3
Membracoidea	2	2	2	2	2	3
Tettigometridae	2	2	2	2	3	3
Ricaniidae	2	2	2	3	3	3
Lophopidae	?	?	?	3	3	3
Eurybrachidae	?	?	?	?	3	3
Hypochthonellidae	?	?	?	?	3	3
Tropiduchidae	2	2	2	2/3	3	3
Flatidae	2	2	2	3	3	3
Nogodinidae	2	2	2	3	3	3
Issidae	2	2	2	3	3	3
Acanaloniidae	2	2	2	3	3	3
Fulgoridae	2	2	2	3	3	3
Dictyopharidae	2	2	3	3	3	3
Delphacidae	2	2	2	2/3	3	3
Meenoplidae	2	2	2	3	3	3
Cixiidae	2	2	2	3	3	3
Achilidae	2	2	2	3	3	3
Derbidae	2	2	2	3	3	3

2: 2-segmented 3: 3-segmented

Table 2. Apical teeth of the second and potential second metatarsus in the Fulgoroidea

Taxa	Instar nymph					Adult
	1	2	3	4	5	
Tettigometridae	X	X	X	X	X	0
Ricaniidae	X	X	X	X	X	X
Lophopidae	X	X	X	X	X	X
Eurybrachidae	X	X	X	X	X	X
Hypochthonellidae	X	X	X	X	X	X
Tropiduchidae	X	X	X/0	X/0	0	0
Flatidae	X	X	X	0	0	0
Nogodinidae	X	X	X	0	0	0
Issidae	X	X	X	0	0	0
Acanaloniidae	X	X	X	0	0	0
Fulgoridae	X	X	X	0	0	0
Dictyopharidae	X	X	0	0	0	0
Delphacidae	X	X	X/0	0	0	0
Meenoplidae	X	0	0	0	0	0
Cixiidae	X	0	0	0	0	0
Achilidae	?	0	0	0	0	0
Derbidae	X	0	0	0	0	0

O: present X: absent

The 2-segmented metatarsi (Table 1.) are more general, while 3-segmented metatarsi are less general. According to Bear's Biological Law (Nelson, 1978), the 3-segmented metatarsi are regarded as advanced. However, Evans (1963) inferred that Protohomoptera had 3-segmented metatarsi, and the 3-segmented metatarsi were regarded as primitive.

Data on segmentations are recognized as a category of acceleration⁵. In the Cicadoidea, Cercopoidea and Membracoidea, the 3-segmented metatarsi are found in adults, but 3-segmented metatarsi appear earlier in the ontogeny of the Tettigometridae, i.e., in the fifth instar nymph, and even earlier in the Fulgoroidea (except the Tettigometridae), i.e., in the fourth instar nymph.

The ground plan of the second metatarsus of the Fulgoroidea should be a conical apex, with no apical tooth, and this is the character state in the fifth instar nymph of the Tettigometridae and the fourth instar nymph of the Ricaniidae-group. The second metatarsus of Tettigometrid adults having two apical teeth on each side is thus considered as a causal or a phylogenetically late modification. This does not agree with Fennah (1952), who suggested that "if it be assumed that the family (=Tettigometridae) is a natural member, possibly nearest to Tropicuchidae.....then it may be claimed that Tettigometridae could have evolved in this group."

The evolutionary hypothesis is as follows.

In the Tettigometridae, the second metatarsus of the fifth instar nymph has a conical apex, and no apical teeth (ground plan). Developing two apical teeth on each side in the adult is secondary.

In the Ricaniidae-group, the second metatarsus is the same as in the ground

plan, but it shows up earlier in the fourth instar nymph, and is maintained in the fifth instar nymph and adult.

In the Tropicuchidae-group, the second metatarsus has a terminal addition of 2-3 apical teeth earlier in the fourth instar nymph, except in the fifth instar nymph for some species of Tropicuchidae, which are maintained in the fifth instar nymph and adult.

In the Fulgoridae-group, the second metatarsus of the fourth instar nymph of Fulgoridae is the same as the fourth instar nymph of the Tropicuchidae, but there are additional number of terminal teeth which show a later modified arrangement in a row. The second metatarsus of the Dictyopharidae develops three apical teeth laterally earlier in the third instar nymph (in the potential second metatarsus condition) and the conical apex stage is eliminated to make room for an additional number of terminal teeth which show a later modified arrangement in a row.

In the Cixiidae-group, the Delphacidae develops 1-3 apical teeth on one or both sides in the third instar nymph. The Cixiidae-group, except the Delphacidae, develops an apical tooth (teeth) earliest in the second instar nymph, and the second metatarsus at the conical apex stage is eliminated to make room for an additional number of terminal teeth which show a later modified arrangement in a row.

Cladistic analysis

On the basis of these results, the characters are coded and defined in Table 3 and give data matrix in Table 4.

Character 1, bearing by the largest number of taxa, is selected as the basal branch (Fig.17). Here the Coleorrhyncha

⁵ Acceleration is defined by Gould (1977) as "a speeding up of development in ontogeny (relative to any criterion of standardization), so that a feature appears earlier in the ontogeny of a descendant than it did in a ancestor."

Table 3. Characters, codes-and states definitions

1. Segmentations of metatarsi in the adult: (0) 2-segmented; (1) 3-segmented.
2. Segmentations of metatarsi in the fifth instar nymph: (0) 2-segmented; (1) 3-segmented.
3. Segmentations of metatarsi in the fourth instar nymph: (0) 2-segmented ; (1) 2-segmented to 3-segmented or 3-segmented.
4. Apical teeth of the second metatarsus in the fourth instar nymph: (0) without 3-segmented second metatarsus; if with, then without apical teeth; (1) with apical teeth.
5. Apical shape of second metatarsus in the adult: (0) without 3-segmented second metatarsus; if with, then apex conical; (1) apex truncate.
6. Apical tooth (teeth) of the potential second metatarsus in the second or third instar nymph: (0) without apical tooth; or if with, then centrally located; (1) with apical teeth if only one, then located laterally; if 2-3, then located on each side.

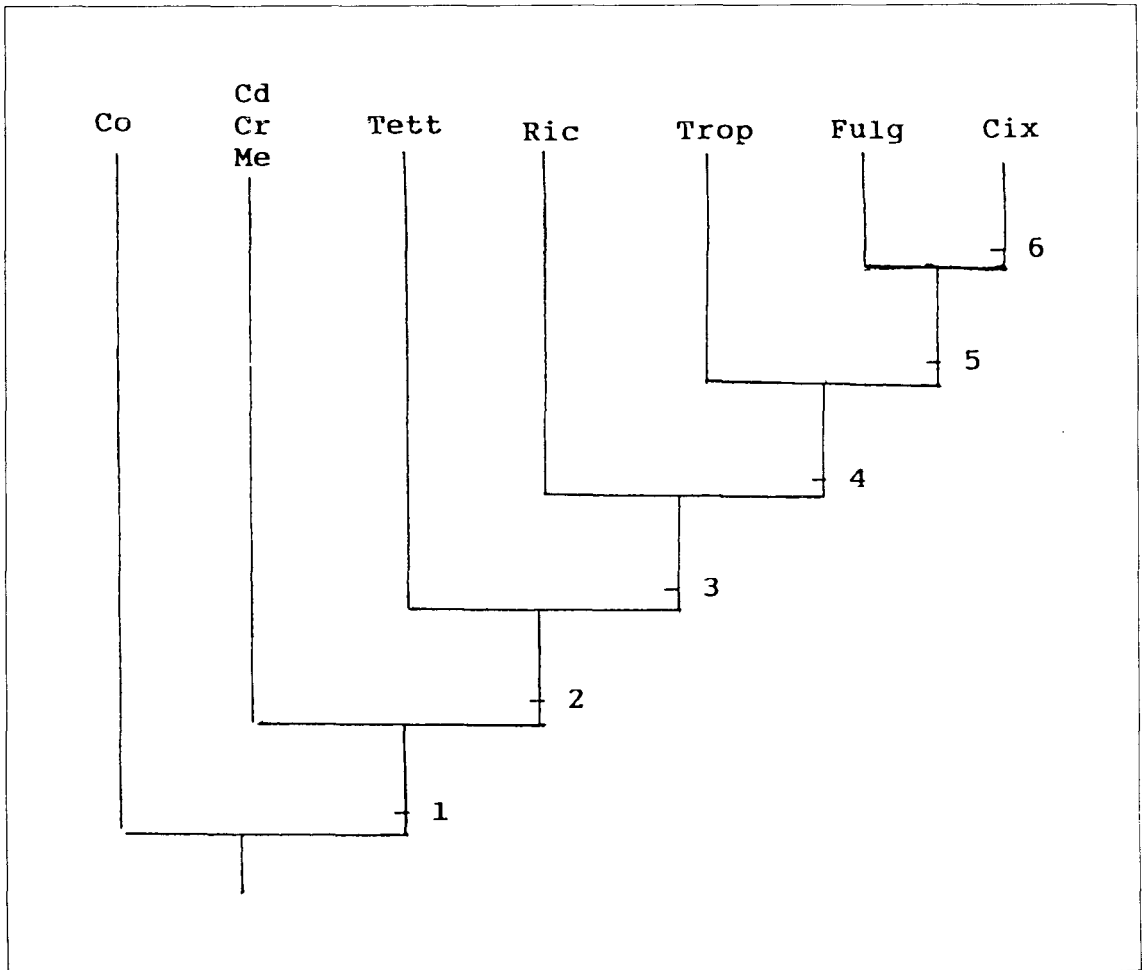


Fig. 17. Cladogram of the Fulgoroidea; Co: Coleorrhyncha; Cd: Cicadoidea; Cr: Cercopoidea; Me: Membracoidea; Tett: Tettigometridae; Ric: Ricaniidae-group; Trop: Tropiduchidae-group; Fulg: Fulgoridae-group; Cix: Cixiidae-group.

Table 4. Data matrix

Character	Taxa						
	Co.	Cd.	Tett.	Ric.	Trop.	Fulg.	Cix
		Cr. Me.					
1	0	1	1	1	1	1	1
2	0	0	1	1	1	1	1
3	0	0	0	1	1	1	1
4	0	0	0	0	1	1	1
5	0	0	0	0	0	1	1
6	0	0	0	0	0	0	1
Co: Coleorrhyncha		Me: Membracoidea		Trop: Tropiciduchidae-group			
Cd: Cicadoidea		Tett: Tettigometridae		Fulg: Fulgoridae-group			
Cr: Cercopoidea		Ric: Ricaniidae-group		Cix: Cixiidae-group			

is excluded from the holophyletic taxon Auchenorrhyncha. Character 2, bearing the second largest number of taxa, is selected as the second branch. Here the Cicadoidea, Cercopoidea and Membracoidea are excluded from the holophyletic taxon Fulgoroidea. Character 3, bearing the third largest number of taxa, is selected as the third branch. Here the Tettigometridae is excluded from the holophyletic taxon Ricaniidae-group to Cixiidae-group. Character 4, bearing fourth largest number of taxa, is selected as the fourth branch. Here the Ricaniidae-group is excluded from the holophyletic taxon Tropiciduchidae-group to Cixiidae-group. Character 5, bearing the fifth largest number of taxa, is selected as the fifth branch. Here the Tropiciduchidae-group is excluded from the holophyletic taxon Fulgoridae-group to Cixiidae-group. For character 6, the autoapomorphy of the Cixiidae-group is added as the last branch. Here the Fulgoridae-group is excluded from the holophyletic taxon Cixiidae-group. The cladogram was thus reconstructed. The characters are used in reverse order instead of in ontogenetic sequence because they are accelerated.

Acknowledgments

This research was financially sup-

ported by the National Science Council under the project NSC84-2321-B005-062.

Thanks are also extended to Dr. Lois B. O'Brien, Florida A & M University and Dr. Lariviere M. C. New Zealand, Arthropod Collection, for loaning the Coleorrhyncha specimens, whose data were essential for this research.

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Received for publication August 10, 1995;

Revised manuscript accepted October 7, 1995.