

Reconstruction of the Phylogeny of the Rhynchitids and Leaf-rolling Weevils (Coleoptera, Rhynchitidae, Attelabidae) Using the Synap Method: Communication 2

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Received January 13, 2004

Abstract—The phylogenetic relationships between the tribes of the family Attelabidae were reconstructed. Independence of the subfamily Apoderinae is confirmed. Serial branching of tribes from the main stem is the most important feature of the cladogram. It demonstrates isolation of tribes from each other and the consecutive purchase of apomorphies.

While the origin of some groups of Rhynchitidae and relations between them are rather clear,¹ the situation is quite different in the family Attelabidae.

At present, an erroneous opinion exists that leaf-rolling weevils originated from highly specialized tribes of the family Rhynchitidae as a result of passing to more advanced methods of leaf-rolling (Ter-Minassian, 1950; Kuschel 1995; Egorov, 1996).

This opinion is first of all based on the similar structure of the abdomen in Rhynchitidae and Attelabidae, and also on their ability to make leaf rolls for larval development. However, some morphological features (the structure of mandibles, legs, and the pronotum; the presence of scutellar groove in the elytrum; and also the structure of the genitalia) made us doubt the generally accepted hypothesis. The absence of any transitional forms between the families Rhynchitidae and Attelabidae and also of any related taxa played an important role in appearance of these doubts. My study of representatives of all the families of the superfamily Curculionidae and comparison of the family Attelabidae with these families demonstrated the strong isolation of the family Attelabidae and its close similarity with the family Belidae.

The tribe Pilolabini is the most primitive tribe in the family Attelabidae (Voss, 1965). Comparison of its

representatives with the family Belidae showed that it was a group similar to Belidae rather than to Rhynchitidae that was the original group of the family Attelabidae. The following features bring together the family Belidae and the tribe Pilolabini; similar structure of mandibles lacking tooth on outer margin; presence of small teeth on femur; presence of tibiae, serrate along inner margin; and similarity in structure of armament of endophallus. It should be noted that the appearance and hairs on elytra in the genus *Pilolabus* and South American genera of the family Belidae (*Callirhynchus* and *Dicordylis*) are very similar. At the same time, the proper Belidae cannot be direct ancestors of Attelabidae because of significant differences, such as the presence of the double gular suture (main difference), and also the presence of denticles on the claws, a more plesiomorphic structure of the female genitalia, more or less pointed apices of the elytra, and a different structure of the antennae.

Characteristics of Leaf-Rolling Weevils and Principles of Cladogram Construction

The recent fauna of leaf-rolling weevils comprises 968 species of 255 superspecies taxa (2 subfamilies, 2 supertribes, 11 tribes, 31 subtribes, 126 genera, and 83 subgenera). In spite of such richness of forms, only 6 fossil species of leaf-rolling weevils of the subfamily Attelabinae are known. The most ancient finding (Ponomarenko and Kireitshuk, 2003) belongs to the Pliocene (Tanet century, USA). Unfortunately, it is still

¹ See Communication 1 (Zool. Zh. **83** (12), 1427–1432 (2004) [Entomol. Rev. **84** (7), 764–770 (2004)].

impossible to determine the tribe to which that taxon belongs.

The family Attelabidae includes two subfamilies: Attelabinae and Apoderinae. These closely related subfamilies also possess significant differences. It could be assumed that the family Apoderinae originated from the tribe Euscelophilini, because they are united by such a sinapomorphy, as temples narrowing toward the pronotum. On the other hand, as already mentioned by Voss (1965), the African tribe Lagenoderini, closely related to Euscelophilini, is a probable ancestor form. The highest IPHR between Apoderinae and the tribe Euscelophilini (11) and lower IPHR (9) between Apoderinae and Lagenoderini confirm the first assumption.

In recent works on the taxonomy and phylogeny of weevils (Thompson, 1992; Kuschel, 1995; Morrone, 1997; Riedel, 2002), it has been assumed that Apoderinae should be treated not as an independent subfamily, but only as a tribe of the subfamily Attelabinae. I think that it is erroneous, because Apoderinae is a large group, possessing many apomorphies and distinctly isolated morphologically. The apomorphies mentioned include the presence of the neck and

2-segmented labial palps; the absence of the scutellar groove; partly sclerotized female abdominal tergite IX; nearly or entirely reduced ventral spicules; the presence of hairs on the apical margin of the metepisterna and on the entire surface of the mesepisterna; nearly glabrous elytra; the presence of a single large and frequently elongate sclerite in the asymmetric armament of the endophallus; pronotal band of the clitostyloid type; and ring-shaped single-chambered spiracles in larvae. The separation of the families mentioned is also demonstrated by the fact that the tribes Clitostyliini, Hoplapoderini, Trachelophorini, and Apoderini from the family Apoderinae are characterized by a high IP (from 22 to 25), whereas all the other tribes of the family Attelabidae (subfamily Attelabinae), by IP varying only from 6 to 13. Representatives of these subfamilies also differ in the mode of leaf-rolling (Legalov, 2003, 2004): species of Attelabinae make simpler rolls with a double (subgroup 2Ic1), and species of Apoderinae, more advanced rolls with a single cut (subgroup 2Ic2).

For revealing the phylogenetic relationships between tribes in the family Attelabidae (figure), the following 40 characters were used (table).

Data matrix for the family Rhynchitidae

Taxon	Character																																								
	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	4				
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	
Rhynchitidae	0	B	0	B	B	0	B	0	1	M	B	B	B	B	B	0	0	0	1	M	0	0	0	0	0	B	0	B	B	0	B	1	0	M	M	0	M	B	0		
Pilolabini	0	B	0	0	0	0	0	0	0	0	1	1	1	0	B	0	0	B	0	1	0	1	0	0	0	0	0	0	B	0	B	0	0	M	M	M	0	0	0	0	
Euopsini	1	B	0	1	1	0	0	0	0	B	0	1	1	0	B	1	0	1	0	B	1	1	1	0	B	0	0	0	B	B	1	0	1	0	M	M	M	M	B	0	
Euscelini	B	B	0	B	B	0	0	0	0	1	0	1	1	0	B	0	0	B	0	0	1	1	1	0	0	1	B	0	B	B	0	B	1	0	M	M	M	M	0	0	
Hybolabini	0	B	0	B	1	0	0	0	0	B	0	B	1	0	B	0	0	0	0	B	1	1	1	0	0	1	B	0	1	B	0	B	1	1	0	M	M	M	0	0	
Attelabini	0	B	0	0	B	0	0	0	0	0	1	1	0	1	0	0	0	0	0	B	1	1	1	0	0	1	B	0	0	B	0	1	1	1	1	M	M	M	0	0	
Lagenoderini	0	0	0	0	0	1	0	0	0	0	1	1	1	0	1	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0	0	1	1	1	M	M	M	0	0	0	
Euscelophilini	0	B	0	0	B	0	0	0	0	B	B	1	1	0	B	0	0	B	0	B	1	1	1	0	0	1	1	0	0	B	0	B	1	1	1	M	M	0	0	0	
Clitostyliini	0	B	0	0	0	1	1	B	1	M	1	1	1	1	B	0	0	0	1	0	1	1	1	1	0	1	1	1	0	1	M	1	1	1	1	1	0	B	1	0	1
Hoplapoderini	B	0	1	0	0	1	1	0	1	M	1	1	1	1	B	0	0	0	1	1	1	1	1	1	0	1	1	1	0	1	M	1	1	1	1	1	0	B	1	0	1
Trachelophorini	0	0	0	0	0	1	1	B	1	M	1	1	1	1	B	0	0	0	1	1	1	1	1	1	0	1	1	1	0	1	M	1	1	1	1	1	0	0	1	0	1
Apoderini	0	B	0	0	0	1	1	B	1	M	1	1	1	1	B	0	B	0	1	1	1	1	1	1	B	1	1	1	0	1	M	1	1	1	1	1	1	1	M	1	1

1. Lower apodema of aedeagus usual (0), triangular (1). 2. Metallic sheen present (0), absent (1). 3. Maximum head height before base (0), in most representatives, at base (1). 4. Frons wide (0), narrow (1). 5. Eyes convex (0), weakly convex (1). 6. Temples not narrowing toward neck (0), narrowing (even if in

highest forms) (1). 7. Neck absent (0), present (1). 8. Neck short (0), long (1). 9. Labial palps 3-segmented (or 1-segmented) (0), 2-segmented (1). 10. Precoxal part of prothorax long in male, short in female (0), short in both sexes. 11. Pronotal band indistinct (0), distinct (1). 12. Postnotal band indistinct (0),

distinct (1). 13. Striae on elytra present (0), absent (1). 14. Prescutellar striole present (0), absent (1). 15. Sculpture of elytra smooth (0), coarse (1). 16. Tufts of hairs on female abdomen absent (0), present. 17. Tufts of pale hairs in ventral part of male metathorax absent (0), present. 18. Rows of hairs on male abdomen absent (0), present (1). 19. Tergite IX of female sclerotized, entire at apex (0), partly sclerotized (1). 20. Teeth on femora present (even if in most primitive representatives) (0), absent (1). 21. In female tibia, only mucro and uncus found in different sides (0), on one side (1). 22. Tibia without teeth along inner margin (0), with teeth (1). 23. Claws free (0), fused (1). 24. Ventral spicule more or less developed (0), reduced or absent (1). 25. Macrochaetae on tegmen apex short (0), long (1). 26. In most species, mentum with 3 teeth (0), in most species, with 1 or 2 teeth. 27. Armament of endophallus symmetric (0), asymmetric (1). 28. Mesepisternae entirely and metepisterna along apical margin, without hairs (0), with hairs (1). 29. Ovipositor in all species with styli (0), without styli (1). 30. Elytra with dense hairs, occasionally forming pattern (0), nearly glabrous (1). 31. Labial palps 3-segmented (0), 1-segmented (1). 32. Scutellum quadrangular (0), triangular or pentagonal (1). 33. Transfer apparatus undifferentiated (0), differentiated (1). 34. Armament more or less symmetric, even if primitive species (0), distinctly asymmetric (1). 35. Asymmetric armament usually including two large sclerites (0), one large, frequently elongate sclerite (1). 36. Pronotal band of clitostyloid type (0), of centro-corynoid type (1). 37. Lobes of 1st ventrite absent in majority of species (0), present in majority of species (1). 38. Pronotal band of pilolaboid type (0), of clitostyloid type (1). 39. Sides of pronotum rounded (0), nearly straight (1). 40. Larval spiracles two-chambered (0), circular, single-chambered (1).

Phylogeny of the Family Attelabidae

It has already been mentioned that the tribe Pilolabini is the most primitive group (IP = 6) of leaf-rolling weevils (see figure). It possesses a series of plesiomorphic characters, including the presence of the mucro on the ventral, and of the uncus, on the dorsal apical margin of the tibia. All the other tribes of the family Attelabidae, both mucro and uncus are situated on the ventral apical margin of the tibia. This character allows dividing of the subfamily Attelabinae into 2 supertribes Pilolabitae and Attelabitae.

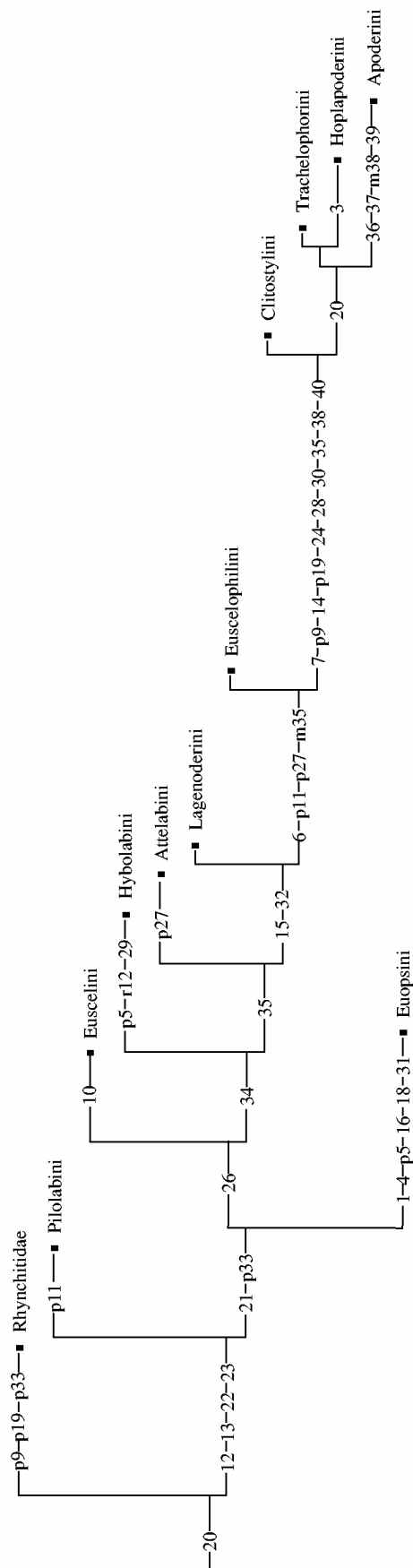
Euopsini, the most primitive tribe in the supertribe Attelabitae, was the next to branch off the main stem.

According to Voss (1965), Euopsini is considered to be the second ancient tribe after Pilolabini, which agrees with my opinion. This tribe possesses an important plesiomorphic character, the presence of 3 teeth on the mentum, whereas all the other tribes usually possess 1 or 2 teeth. At the same time, in the course of evolution, species of the tribe Euopsini acquired a significant number of apomorphies: the presence of a triangular lower apodema of the aedeagus and a narrow frons; weakly convex eyes; the presence of tufts of hairs on the female abdomen and of rows of hairs on the male one; and also single-segmented labial palps. These characters raise the IP of the tribe mentioned up to 12. By this index, the tribe Euopsini surpasses the tribes Euscelini, Hypolabini, Attelabini, and Lagenoderini, being inferior only to Euscelophilini (IP = 13).

The American tribe Euscelini originated from Euopsini. Relations between these tribes are expressed even in a similar appearance of some representatives of Euscelini and Australian and New Guinean species of the tribe Euopsini. The most pronounced similarity is observed between the tribe Euopsini and representatives of the subtribe Archeuopsina and especially the New Guinean genus *Riedelinius*; representative of this genus possess the femoral teeth; tooth-shaped, elongate humerus; and weakly connivent or non-connivent eyes. Such an apomorphic character as a short precoxal part of the prothorax, typical of males and females, strongly distinguishes Euscelini among all the other Attelabidae.

The next branch is formed by a strongly diverse American tribe Hybolabini. By the IP index (8), it occupies the next place after Euscelini (9). The main apomorphies of the group include weakly convex eyes (character developed in tribe Euopsini in a parallel way), a pronounced postnatal band, and the absence of styli of the ovipositor in all the species. Similarly to Euscelini, the tribe Hybolabini is represented only in America, being, however, distributed wider, from Canada in the north to Chile in the south.

Then, the tribe Attelabini branches off the stem (IP = 10). It is impossible to treat Hybolabini as ancestors of Attelabini, because this group possesses well-developed styli of the ovipositor; these groups are mainly brought together by a series of parallelisms. Most probably, this tribe originated from some extinct group related to Euscelini. Three fossil species of the genera *Oedeuops* and *Eneuops* of the subtribe Paramecolabina were described from Miocene (China).



Cladogram of tribes of the family Attelabidae.

An asymmetric armament of the endophallus is the most important apomorphy of this group. The high degree of similarity between Attelabini and Lagenoderini and Euscelophilini (in both cases, IPHR = 9), gives us all reason to assume their close relationship. The tribe Attelabini is spread in the Palaearctic and Indo-Malayan regions.

The Afro-Madagascan tribe Lagenoderini can be treated as one of the most advanced tribes of the subfamily Attelabini. This is a small, but very heterogeneous group with a high variability of characters; e.g., primitive and advanced representatives of the tribe possess 3 and 1 teeth on the mentum, respectively. This tribe is most similar to the tribe Euscelophilini (IPHR = 10).

The tribe Euscelophilini, the most advanced tribe in the subfamily Attelabinae (IP= 13), occupies a special position in the classification of Attelabidae. Its similarity to Apoderinae is of especial interest. The following apomorphies unite Euscelophilini with this family: temples narrowing toward neck (at least in advanced forms); pronotal band distinct; and armament of endophallus asymmetric.

The ancestor group of Apoderinae is yet unknown and, as it has been already mentioned, it could be the tribe Euscelophilini. In spite of the young age of Apoderinae, where no fossil forms are known, I managed to reveal phylogenetic relations of the family Apoderinae mainly by mathematical treatment of the data. This family is divided into 4 tribes: Clitostyliini, Hoplapoderini, Trachelophorini, and Apoderini, possessing IP 22, 23, 24, and 25, respectively.

Voss (1965) considers African representatives of Hoplapoderini to be the most primitive and, probably, ancestor group in Apoderinae. Contrary to this author, I assume that the widely distributed tribe Clitostyliini plays this role. This tribe possesses such an important plesiomorphic character, as the presence of teeth on the femur (even if only in primitive species), relating Clitostyliini to the subfamily Attelabinae. Based on the morphological characters of this tribe, it could be assumed that the other tribes of the subfamily Apoderinae, namely, sister Hoplapoderini (+ Trachelophorini) and Apoderini, originated from primitive Clitostyliini.

The tribe Hoplapoderini is distributed as widely, as Clitostyliini, confirming the earlier origin of both tribes in comparison with Trachelophorini and Apoderini. The head highest at base is the most important apomorphy of this tribe.

The endemic tribe Trachelophorini originated from the subtribe Paratomapoderina in Madagascar. Previously it was believed that representatives of this tribe are spread not only in Madagascar, but also in Asia. However, the detailed morphological study allowed explaining similarity between the Madagascar and Asiatic genera by parallelisms. The structure of the pronotal band (strongly distinct in both sexes) is an apomorphy of the tribe Trachelophorini.

Apoderini is the most diverse tribe possessing the highest IP. This tribe is characterized by several apomorphies: presence of pronotal band of centrocorynoid type; presence of blades on first ventrite of majority of species; and nearly straight sides of pronotum. It is mainly spread in the eastern Palaearctic and Indo-Malayan region. Two species penetrate into the western Palaearctic Region.

On the basis of the analysis conducted, it is possible to assume that Attelabidae is a rather young family probably originating from Belidae-shaped forms in the Paleogene as a result of changes in the mode of life, namely, passing on to leaf-rolling. It is subdivided into two clearly separated subfamilies Attelabinae and Apoderinae; the latter family is characterized by the largest number of apomorphies.

My calculations demonstrated that 45 phylogenetic events had occurred in the history of leaf-rolling weevils, including 32 unique events, 12 parallelisms, and 1 reversion. The phylogenetic relationships between the tribes of the family Attelabidae were reconstructed on the basis of a morphological analysis. A serial branching of tribes off the main stem is the most important character of the dendrogram obtained; this character of branching demonstrates the isolated character of tribes and consecutive appearance of apomorphies.

ACKNOWLEDGMENTS

This work was supported by the grant of the Lavrentiev Competition of youth projects of the Siberian Branch of the Russian Academy of Sciences, the prize of the European Academy for young scientists of Russia for 2003, and the grant of the Russian Science Support Foundation for 2004.

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