Entomological Review, Vol. 85, No. 2, 2005, pp. 131–136. Translated from Zoologicheskii Zhurnal, Vol. 84, No. 2, 2005, pp. 190–194.

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

A. A. Legalov

Siberian Zoological Museum, Institute of Animal Taxonomy and Ecology, Siberian Division, Russian Academy of Sciences, Novosibirsk, 630091, Russia

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)].

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: Clitostylini, 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 Clitostylini 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 Clitostylini 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 Clitostylini.

The tribe Hoplapoderini is distributed as widely, as Clitostylini, 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.

REFERENCES

1. A. B. Egorov, “Family Attelabidae, or Leaf-rolling Weevils,” in *A Key to Insects of the Russian Far East* (Vladivostok, 1996), Vol. 3, No. 3, pp. 199–215 [in Russian].

2. G. Kuschel, “A Phylogenetic Classification of Curculionoidea to Families and Subfamilies,” Mem. Entomol. Soc. Washington **14**, 5–33 (1995).
3. A. A. Legalov, “The Taxonomy, Classification, and Phylogeny of Leaf-rolling Weevils (Coleoptera: Rhynchitidae, Attelabidae) of the World Fauna,” CD-ROM (Novosibirsk, 2003).
4. A. A. Legalov, “A New Classification of Ecological Groups of Leaf-rolling Weevils (Coleoptera: Rhynchitidae, Attelabidae),” Eurasian Entomol. J. **3** (1), 43–45 (2004).
5. J. J. Morrone, “The Impact of Cladistics on Weevil Classification, with a New Scheme of Families and Subfamilies (Coleoptera: Curculionoidea),” Trends in Entomol. **1**, 129–136 (1997).
6. A. G. Ponomarenko and A. G. Kireitshuk, “A Taxonomic List of Fossil Beetles of the Suborder Scarabaeina (Part 2),” http:/www.zin.ru.
7. A. Riedel, “Taxonomy, Phylogeny, and Zoogeography of the Weevil Genus *Euops* (Insecta: Coleoptera: Curculionoidea) in the Papuan Region,” Ph D Thesis (Munich, 2002).
8. M. E. Ter-Minassian, *Fauna of the USSR. Coleoptera*, Vol. 27, No. 2: *Leaf-Rollers (Attelabidae)* (Moscow: Nauka, 1950) [in Russian].
9. R. T. Thompson, “Observations on the Morphology and Classification of Weevils (Coleoptera, Curculionoidea) with a Key to Major Groups,” J. Nat. Hist. **26**, 835–891 (1992).
10. E. Voss, “Die Unterfamilie Camarotinae, ihre Beziehungen zur Familie Attelabidae sowie ein Versuch die phylogenetischen Zusammenhange innerhalb der letzteren zur Darstellung zu bringen (Coleoptera, Curculionidae),” Entomol. Abhandl. **32** (11), 222–244 (1965).