

Reconstruction of the Phylogeny of the Rhynchitids and Leaf-rolling Weevils (Coleoptera, Rhynchitidae, Attelabidae) Using the Synap Method: Communication 1

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Abstract—The phylogenetic relationships in the families Rhynchitidae and Attelabidae have been reconstructed. The main synapomorphies have been revealed. The morphologically advanced groups have been distinguished in the families studied. The family Attelabidae forms two large branches. The most advanced is the supertribe Rhynchititae, the representatives of which could adapt not only to development in various parts of a plant, but also to rolling leaf packages. This supertribe consists of eight well-defined tribes forming three groups: (1) Auletini and Minurini; (2) Cesauletini, Eugnamptini and Isotheini; (3) Pterocolini, Rhynchitini and Byctiscini.

The families Rhynchitidae and Attelabidae (leaf-rolling weevils) belong to the most surprising beetles on our planet. Some of them have developed the ability to make leaf packages in which their larvae feed; others put eggs into fruits or vegetative parts of plants in which the larval development proceeds. The both families mostly inhabit forests and are associated with arboreal vegetation; those species that occur in open landscapes develop on herbs. These weevils are widely distributed over the planet, the most of species occur in the subtropical and tropical zones.

These families are poorly investigated despite their wide distribution and a comparatively simple collecting both adults and larvae. The classification used until the present time was elaborated in the first half of the XX century by E. Voss. Unfortunately, when creating it, he used formal characters, therefore the classification is artificial: many closely allied species are placed in different genera, and close genera, in different tribes. Therefore Voss's (1965) concept of the phylogeny of the Rhynchitidae and Attelabidae was largely erroneous. The problem of revealing the phylogenetic relationships in these groups remained unsolved.

In last decades, the cladistic analysis has been widely used in the systematics and phylogeny of insects (Pavlinov, 1989, 1990; Rasnitsyn, 2002). Two authors (Sawada, 1993; Riedel, 2002) have undertaken attempts of the cladistic analysis of the Rhynchitidae and Attelabidae. Sawada (1993) proposed a phyloge-

netic hypothesis for species of the Rhynchitidae from Japan. He has managed to show that the tribes Eugnamptini and Isotheini, and also Rhynchitini and Byctiscini are sister-groups and form two lineages, both widely separated from the tribe Auletini. Sawada has made a number of mistakes. For example, *Temnocerus japonicus* (Morimoto) (tribe Rhynchitini) was united with species of the tribe Auletini; *Teretriorhynchites amabilis* (Roelofs) and *Involvulus pilosus* (Roelofs) (subtribe Rhynchitina) were grouped together with species of the subtribes Lasiorhynchitina, Temnocerina, and Perrhynchitina. The situation appeared worse with the final phylogenetic tree (Sawada, 1993) constructed on the basis of the method of minimisation of the number of characters (Sawada, 1988). This scheme reflected the traditional Voss's classification where Isotheini are considered the most advanced tribe, and Eugnamptini are placed close to Rhynchitini. The erroneousness of the Sawada's hypothesis may result primarily from including a small number of taxa in the analysis.

Riedel (2002) has carried out a cladistic analysis of species of the tribe Euopsini of the New Guinea fauna (PAUP program). He has investigated representatives of various species-groups now promoted to genera (Legalov, 2003a). It should be noted that other Euopsini from the Oriental, Afrotropical, and Australian biogeographical regions have not been included in the analysis. The genera *Epirhynchites* (family Rhynchitidae), *Attelabus*, *Lamprolabus*, *Euscelophilus* (subfam-

ily Attelabinae) and *Apoderus* (subfamily Apoderinae) have been taken as outgroups. Riedel has studied the most advanced representatives of the family Attelabidae, which was inevitably reflected in the result. In the cladogram, only close species were united. Relationships between groups of species have remained unrevealed. Surprising is Riedel's conclusion: admitting that he had failed to reconstruct the phylogeny of the New Guinea fauna of Euopsini; he writes, however, that Apoderinae do not deserve the subfamily rank and should be considered a tribe. This judgment, based on the study of a single species, is obviously incorrect.

My attempt to revise separate groups of species (Legalov, 2001) has faced the problem of a poor supraspecific classification, which made impossible revealing the relationships between the taxa. Therefore a decision was taken to start not stem-up but top-down. The supraspecific classification of the Rhynchitidae and Attelabidae of the world fauna (Legalov, 2003a) has been reconsidered, and their phylogenetic relationships were reconstructed. Some preliminary results of this research on the phylogeny of these groups have been published (Legalov, 2003).

I investigated the material from state museums and private collections. The type or authenticated material of most of the supraspecific taxa of Rhynchitidae and Attelabidae was examined, totaling more than 20000 specimens of more than 700 species (36%), representing 82% of supraspecific taxa of Rhynchitidae, and 86%, of Attelabidae..

The choice of a program for the construction of cladograms was important. I compared the results obtained with use of the programs Hennig 86, Phylip, PAUP 2.4.1., and SYNAP 420. The first two do not provide an explanation of calculations and therefore have been rejected. PAUP and SYNAP provided similar results especially if characters were weighed. Yet SYNAP 420 not only marks branches by phylogenetic events and allows checking up calculations, but also provides two additional parameters (index of advance and index of phylogenetic relationship). For this reason, the reconstruction of the phylogeny was carried out with the SYNAP 420 program (Baikov, 1999). The following abbreviations are adopted in the paper. 1. Index of advance (IP) is a sum of advanced characters 2. Index of phylogenetic relationship (IPHR) is IP minus unique advanced characters. For identical IPHR, a preference was given to the polytomy (a coalescence of identical nodes), an appearance of a uni-

que new character, and the minimum of reversions. When weighing characters, those most important were assigned the values of 2 or 3 points (see table). The matrix was not optimized, the value of a reversion was identified as -1; 0 is a plesiomorphic, and 1, an apomorphic state of the character. The results of the phylogeny reconstruction have been presented in a preceding publication (Legalov, 2003a).

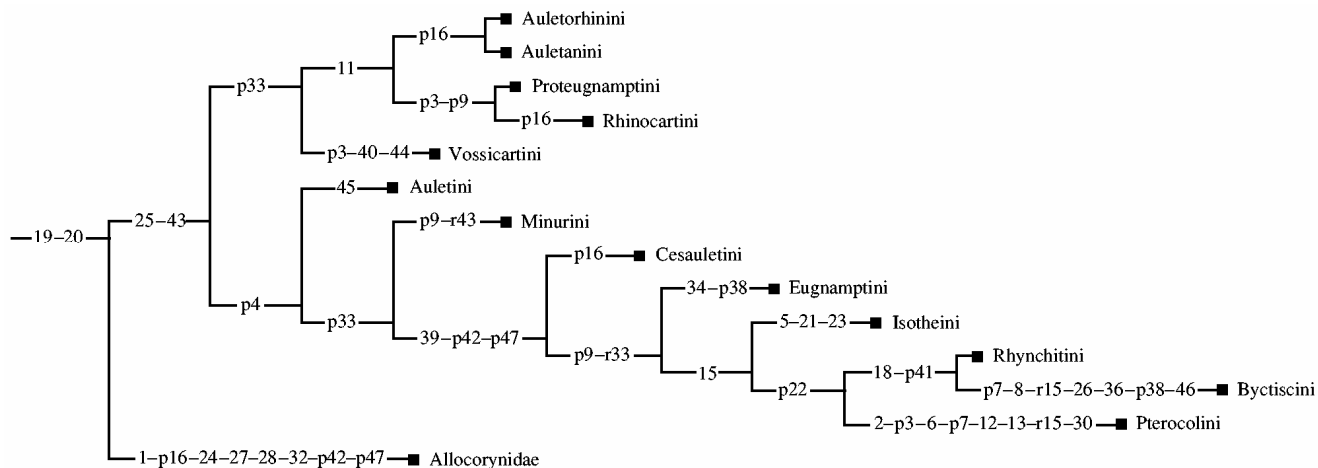
The Characteristic of Rhynchitidae and Principles of Cladograms Construction

Rhynchitidae are ancient beetles known from the late Jurassic (Oxford epoch) (Legalov, 2003a). It might be assumed that originally they developed in reproductive organs of gymnosperms (similarly to Nemonychidae), but subsequently adapted to development on angiosperms. Rhynchitidae have formed five ecological groups (three groups including species which do not roll leaves and two groups which are classified as "leaf-rollers") (Legalov, 2003a) which have obtained a considerable species-richness (1087 known species).

The family Rhynchitidae is represented in the recent fauna by 1087 species from 250 supraspecific taxa (2 supertribes, 13 tribes, 18 subtribes, 141 genera and 76 subgenera). 33 species are known as fossil records (Legalov, 2003a).

For revealing the phylogenetic relationships between tribes in the family Rhynchitidae a cladogram was constructed (figure), for which 47 morphological characters were used (table).

1. Body with setae (0), without setae (1). 2. Metallic sheen present (0), absent (1). 3. Rostrum long (0), short (1). 4. Tooth on exterior side of mandible absent (0), present (3). 5. Labial palps of female 3-segmented (0), 1- or 2-segmented (1). 6. Pro- and mesocoxa approximate (0), widely separated (1). 7. Frons wide (0), narrow (1). 8. Eyes convex (0), almost flat (1). 9. Antennae attached subbasally (0), submedially or subapically (1). 10. Antennal club symmetrical (0), asymmetrical (1). 11. Club short (0), usually long (1). 12. Keel on sides of pronotum absent (0), present (1). 13. Elytra almost rectangular (0), rounded (1). 14. Sculpture of elytra smooth (0), coarse (1). 15. Prescutellar striae present in the majority of genera (0), absent or present only in primitive genera (1). 16. Striae on elytra present (0), absent (1). 17. Wings developed (0), reduced (1). 18. Spines directed forwards on prothorax of males absent (0), present (1). 19. 1st–5th ventrites free



Cladogram of tribes of the family Rhynchitidae

(0), 1st and 2nd ventrites fused (1). 20. Sternite VIII of males with distinctly pigmented apodema (0), without distinct apodema (1). 21. Spiculum gastrale directed dextro-anteriorly (0), sinistro-anteriorly (1). 22. Spiculum ventrale of auletoid type (0), of rhynchitoid type (2). 23. Propygidium concealed by elytra (0), exposed (1). 24. Tergite IX of males desclerotized to a well-pigmented narrow band arching over sternite IX (0), completely membranous (1). 25. Tergite IX of females sclerotized, entire at apex (0), only laterally sclerotized (1). 26. Metepisternum reaching metacoxa (0), not reaching metacoxa (1). 27. Femora weakly widened (0), strongly widened (1). 28. Teeth on femora absent (0), present (1). 29. Protuberances on femora absent (0), present (1). 30. Teeth on tibiae absent (0), present (1). 31. Mucro at apex of tibiae absent (0), present (1). 32. Claws toothed (0), simple (1). 33. Styli of ovipositor normally developed (0), strongly reduced (2). 34. Apex of aedeagus entire (0), excised (1). 35. Armament of endophallus developed (0), reduced (1). 36. Armament of endophallus of auletoid type (0), of byctiscoid type (1). 37. Hairy spots on elytra absent (0), present (1). 38. Armament of endophallus symmetrical (0), asymmetrical (1). 39. Procoxa of males without fovea and bunch of setae (0), at least with bunch of setae (1). 40. Rostrum not or weakly flattened (0), strongly flattened (1). 41. Procoxa of males without fovea but with a bunch of setae (0), with fovea and bunch of setae (3). 42. Elytra jointly round ed apically (0), separately rounded (1). 43. Only 1st and 2nd ventrites fused (0), 1st-3rd ventrites fused (1). 44. Antennal club distinct (0), indistinct (1). 45. Apex of elytra in males without hairy spots (0), with hairy spots (1). 46. Head not conical (0), conical (1). 47. Pygidium concealed by elytra (0), exposed (1).

Phylogeny of the Family Rhynchitidae

According to the resulting phylogram, the tribes of the family Rhynchitidae can be united in the two supertribes Rhinocartitae and Rhynchititae (figure).

Supertribe Rhinocartitae

The supertribe Rhinocartitae is an ancestral group of the family Rhynchitidae. Rhinocartitae are known from the late Cretaceous; the supertribe probably arose in the Jurassic, not later than the supertribe Rhynchititae, but its fossil remains probably are misidentified as members of the family Nemomychidae because of the externally edentate mandibles. Rhinocartitae is a small tropical group consisting of 5 most primitive tribes (Vossicartini, Rhinocartini, Proteugnampini, Auletanini, and Auletorhinini) with an average IP of 8.8. They are united by symplesiomorphic characters (edentate externally mandibles and primitive structure of spiculum gastrale of the auletoid type). The vestigial styli of the ovipositor, usually non-striate elytra, and elongated segments of the antennal club in both sexes are apomorphic characters of this supertribe. The tribes of Rhinocartitae are rather clearly separated from each other.

The South African tribe Vossicartini (IP = 9) is most widely separated from other Rhinocartitae and is very primitive. It is characterized by apomorphic features: short, strongly flattened rostrum and indistinct club of antennae. Vossicartini are the only tribe of the Rhinocartitae with striate elytra, which is a plesiomorphic character. Of other tribes of the Rhinocartitae, Vossicartini is rather close only to the more advanced tribe Rhinocartini (IPHR = 7).

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	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4											
Allocorynidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	M	1	0	0	1	1	0	M	0	1	0	0	1	1	0	0	0	1	0	0	0	M	0	0	M	0	M	1	M	0	0	0	1										
Rhinocartini	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	M	0	1	0	0	0	0									
Proteugnamptini	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	M	0	1	0	0	0	0							
Vossicartini	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	M	0	1	1	0	0	0						
Auletorhinini	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	M	0	1	0	0	0	0						
Auletanini	0	B	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	M	0	1	0	0	0	0						
Auletini	B	0	0	1	0	0	0	0	B	0	0	0	0	0	0	B	B	0	1	1	0	B	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	B	B	0	B	0	B	0	B	0	0	0	0	1	0	1	0	0				
Minurini	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
Cesauletini	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	
Eugnamptini	0	B	B	1	0	0	B	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Isotheini	0	B	B	1	1	0	B	0	1	0	0	0	0	0	1	0	0	0	1	1	1	B	1	0	1	0	B	B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	B	0	1	0	0	1	1	0	0	0	0	1				
Pterocolini	0	1	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Rhynchitini	0	B	B	1	0	0	B	1	B	B	0	0	B	1	0	0	1	1	1	0	1	0	0	1	0	B	B	B	B	0	0	0	B	0	B	B	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Byctiscini	B	B	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Symbols: 0, plesiomorphic state of the character; 1, apomorphic state of the character; M, absence of the character; B, polymorphism of the character.

The tribes Auletanini (IP = 8), Auletorhinini (IP = 8), Proteugnamptini (IP = 9), and Rhinocartini (IP = 10) form a separate lineage. The major synapomorphic characters are the long club of the antennae in both sexes and usually completely confused striae of the elytra. In the latter character, these tribes are similar to Auletini and Cesauletini of the Rhynchitidae.

The tribes Rhinocartini and Proteugnamptini, and also Auletanini and Auletorhinini are united in pairs, forming sister groups, and have IPHR equal to 8 and 9, respectively. The first group consisting of Rhinocartini and Proteugnamptini from Africa and Madagascar is characterized by two apomorphic characters (short, unflattened rostrum and submedially attached antennae). The second, Oriental group (tribes Auletanini and Auletorhinini), differs in always irregularly punctate elytra.

The Afro-Madagascan tribes (Vossicartini, Rhinocartini and Proteugnamptini) have weak relationships (IPHR from 1 to 3) with representatives of the supertribe Rhynchititae and apparently are terminal branches. The tribes Auletanini and Auletorhinini, be contrast, are very similar to primitive Rhynchitidae and therefore are of great interest for revealing the relationships of Rhynchitidae. The similarity of these two

tribes to the Rhynchititae is basically due to simple-siomorphies. The IPHR relationship of the two tribes Auletanini and Auletorhinini with the tribe Minurini is two and with Cesauletini, six. No phylogenetic relationship with other tribes of the Rhynchititae have been revealed. It is noteworthy that representatives of Auletanini and Auletorhinini are rather similar to species of the tribe Auletini. They differ from primitive forms of this supertribe in plesiomorphic mandibles and an apomorphic club of the antennae. The aedeagus and armament of the endophallus in Auletanini and Auletorhinini are plesiomorphic and practically indistinguishable from those in the majority of species of the tribe Auletini. The presence of rather numerous apotypical forms in the tribe Auletini, in addition to plesiotypical forms, obscures the relationships of the latter with the tribes Auletanini and Auletorhinini.

Supertribe Rhynchititae

Rhynchititae is the largest supertribe among Rhynchitidae. The average IP of tribes included in the supertribe is 14.9. The basic autapomorphy of this supertribe is the presence of a tooth on the external edge of the mandible. The most ancient Rhynchitidae from the late Jura and the early Cretaceous belong to Rhynchititae.

Auletini (IP = 8) is the first tribe that branches off from the main stem of the supertribe Rhynchititae. It is characterized by the following plesiomorphic characters: elytra jointly rounded at apex; spiculum gastrale of auletoid type; and armament of endophallus primitive. Of important apomorphic characters, possessed by the most primitive representatives of the tribe, the hairy spots at the apices of the elytra and bunches of setae on the procoxa of males are to be mentioned. The primitiveness of the tribe Auletini is manifested, in addition to the morphology, first, by the association of some species with gymnosperms, and, second, the development of larvae (group 1a) in reproductive organs of the host, previously nibbled by the female (Legalov, 2004). I would like to note that this method of preparation of the fodder substrate for larvae is ancestral for the supertribe Rhynchititae. It is present not only in representatives of all tribes of Rhynchitidae and Attelabidae, but also in some Curculionidae. Nearly worldwide distribution of the tribe Auletini (Nearctic, Palaearctic, Oriental, Afrotropical, and Australian regions) also presumes its ancient origin.

The South American tribe Minurini, close to Auletini, is peculiar in possessing a unique in the Rhynchitidae plesiomorphic character: 3rd ventrite not fused with 2nd one. All other genera of the Rhynchitidae have the 1st–3rd ventrites fused. Plesiomorphies of this group are well-developed elytral striae, jointly rounded apices of the elytra, and the absence of bunches of setae on the male procoxa. Two important apomorphic states of characters are found in the tribe Minurini: submedially attached antennae and strongly reduced styli of ovipositor.

The rest tribes of the Rhynchititae differ from primitive Auletini and Minurini in the following apomorphic characters: procoxae of males with bunch of setae and in some taxa with a fovea; the elytra are separately rounded at the apices and usually do not conceal the pygidium. These tribes are characterized by a higher average IP (17).

The North American tribe Cesauletini includes species very similar to those of the tribe Auletini but is clearly distinct. Its similarity to the tribe Auletini is manifested by completely reduced elytral striae and the structure of the spiculum gastrale. Probably, from this tribe the Eugnamptini could have arisen; the IPHR between Cesauletini and Eugnamptini is high, equaling nine.

The tribes Eugnamptini, Isotheini, Pterocolini, Rhynchitini and Byctiscini are separated in a special complex based on the submedial or subapical attachment of the antennae (apomorphy), normally developed styli of the ovipositor (reversion), and ability of imago to make leaf-rolls. The tribe Eugnamptini is the most primitive of these tribes; it has the spiculum gastrale of the auletoid type similarly to the plesiomorphous tribes Rhinocartitae, Auletini, Minurini, and Cesauletini, but is characterized by an apomorphic asymmetrical armament of the endophallus and usually an excised apically aedeagus. Species of this tribe develop within the leaf lamina (subgroup 1b3).

The tribe Isotheini is represented by species, most of which form leaf packages, and was considered by the majority of the systematists (Voss, 1938; Ter-Minassian, 1950; Sawada, 1993; Egorov, 1996; Alonso-Zarazaga, Lyal, 1999) the most advanced tribe of the family Rhynchitidae. Yet I have found that not only it is not the most advanced tribe, with the IP equalling only 8, but represents a special lineage (together with Eugnamptini) in the Rhynchitidae, which was the first to begin rolling funnel-shaped leaf packages (subgroup 2b). The tribe Isotheini is characterized by the following important apomorphic characters: 1- or 2-segmented labial palps, sinistro-anteriorly directed spiculum gastrale, and usually exposed propygidium. These characters, as also shortening of the rostrum and appearance of the neck constriction, have appeared in the course of accomplishing the techniques of the leaf rolling.

The rhynchitoid type of the spiculum ventrale is typical of the tribe Pterocolini and also closely related to it Rhynchitini and Byctiscini. The tribe Pterocolini has a very high IP of 20. Thompson (1992) and Hamilton (1998) promote it to a subfamily, which is probably incorrect because species of the tribe Pterocolini retain structural characteristics which make them undistinguishable from the supertribe Rhynchititae. The main apomorphic characters of the tribe Pterocolini are the widely separated pro- and metacoxae, structure of the tibiae, and superficial similarity to some Attelabinae (especially to the genus *Hybolabus*). Of other characters distinctive of this group, the metallic sheen, short rostrum, narrowed frons, carinate sides of the pronotum, and the rounded elytra may be mentioned. These structures of the tribe Pterocolini can be considered as an adaptation formed by an ancestral group similar to the subtribe Temnocerina (tribe Rhynchitini)

in the course of transition to commensalism in the leaf packages made by the American Attelabinae (tribes Pilolabini and Hybolabini).

The closely allied (IPHR = 16) tribes Rhynchitini and Byctiscini may be conventionally considered the most advanced ones in the Rhynchitidae. They are sister groups and are distinguished from other tribes by the procoxae of males having a fovea and a bunch of setae (synapomorphy). In these tribes males sometimes have anteriorly-directed spines on sides of the prothorax.

Tribe Rhynchitini (IP = 18) is species-richest within the family and has a very complicated taxonomic structure. The genera are characterized by various apomorphies. The species of this tribe develop in both the vegetative (groups 1b, 1c and 2b) and reproductive parts of plants (group 1a). Development in the vegetative parts of plants probably was initial in this tribe, and transition to flowers and fruits is the result of a reversion.

The tribe Byctiscini is a young, compact group mainly distributed in the Oriental Region. Its major apomorphic characters are the narrowed frons, metepisternum not reaching the metacoxa, byctiscoid type of the endophallus armament, and conical head. In the tribe Byctiscini, the transition from development inside fruits (group 1a1) to rolling leaves into packages (group 2a) is observed. This tribe includes the primitive Svetlanaebyctiscina (IP = 11) characterized by the larval development in fruit and also the more advanced Byctiscina (IP = 14) and Listrobyctiscina (IP = 16).

Calculations have revealed that there were 56 phylogenetic events in the evolution of leaf-rolling weevils, of which 29 were unique, 23 were parallelisms, and 4, reversions.

The family Rhynchitidae forms two large branches. The most apotypical is the supertribe Rhynchititae. Its genera have adapted to development in various parts of plants and to rolling tubes. This supertribe consists of 8 distinctive tribes, which form three groups according to their IP: (1) Auletini and Minurini; (2) Cesauletini, Eugnamptini, and Isotheini; (3) Pterocolini, Rhynchitini, and Byctiscini.

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