

Modelling of phylogeny of the Rhynchitid-beetles (Coleoptera: Rhynchitidae)

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Legalov A. A. 2005. Modelling of phylogeny of the Rhynchitid-beetles (Coleoptera: Rhynchitidae). *Proceedings on Taxonomy and Faunistics of Beetles (Coleoptera) dedicated to the 100th birthday of the Latvian entomologist Mihails Stiprais (1905 - 1990)*, pp. 37 - 45.

Modelling of phylogenetic relationships in family Rhynchitidae was undertaken using the SYNAP programme to allocate the supraspecific taxonen. This method revealed basic autapomorphies and synapomorphies. The most advanced is supertribe Rhynchititae whose representatives are adapted not only to development in various parts of their hosts, but also turning to leaves into barrel. This supertribe will consist of nine well detached tribes. These tribes form three groups: Auletini, Brentorrhinoidini and Minurini; Cesauletini, Eugnamptini and Isotheini; Pterocolini, Rhynchitini and Byctiscini.

Key words: Coleoptera, Curculionoidea, Rhynchitidae, phylogeny

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Introduction

Family Rhynchitidae (Rhynchitid-beetles) form a widespread monophyletic group including about 1100 species (Legalov, 2003). These beetles are characterised by their specific parental care of their offspring (Prell, 1924; Ter-Minassian, 1950; Zuppa, Osella, Biondi, 1994; Legalov, 2004a). Some produce leaf rolls for their larvae; others damage fruits or vegetative parts of plants in which their larvae develop (Legalov,

2004a). The Rhynchitid-beetles are characteristically inhabit forest biomes, reach their greatest diversity in tropical and subtropical forests, and play an essential role in ecosystems as customers of foliage. These weevils are widely distributed throughout most parts of the world, except for New Zealand and the Hawaiian Islands. The greatest number of species is found in the Oriental and Neotropical biogeographic regions.

In the last decade, cladistic analysis has been widely applied to the determination of the sys-

tematics and phylogeny of insect groups (Pavlinov, 1989, 1990; Rasnitsyn, 2002). One authors (Sawada, 1993) have undertaken attempts of carrying out cladistic analysis of the Rhynchitid-beetles weevils. Sawada (1993) has proposed the phylogenetic hypothesis for species of the Rhynchitidae from Japan.

The work described here is the first attempt at modelling of the phylogeny of Rhynchitidae of the world fauna. Some initial results of research of the author on the phylogeny of these groups have been published earlier (Legalov, 2003). The phylogenetic analysis of family Rhynchitidae without the fossil groups has been lead Legalov (2004b).

Materials and methods

As part of the review of the family Rhynchitidae I investigated material from state museums and private collections in Russia. Typical or authenticated material mainly from the supraspecific taxa Rhynchitidae was investigated. More than 20000 specimens encompassing more than to 400 species were examined.

Construction of the phylogeny was carried out with program SYNAP 500 (Baikov, 1999). As part of the program the following values were accepted: 1. Index of progress (IP) - sum of the advanced characters; 2. Index of phylogenetic relationships (IPHR) - IP minus unique advanced characters. For identical IPHR, preference was given to a coalescence of identical units and originating of unique new character, with a minimum of reversions. Weighing characters were applied with the most important characters assigned values of 2 or 3 points. The matrix was not optimised. Value of a reversion was assigned a value equal to 1, 0 - plesiomorphic state of the character, 1 - apomorphic state of the character, M - absence of the character, U - unknown character and B - polymorphism of the characters.

Results and Discussion

Modelling of phylogeny of the family Rhynchitidae Gistel, 1848

Rhynchitidae are ancient beetles known from the late Jura (Oxford century) (Legalov, 2003). It is possible to assume that originally they developed and survived in generative organs of Gymnospermaes, but adapted to feed on Angiospermaes. Rhynchitidae have formed five ecological groups (three groups which do not turn leaves and two groups which are classified as "leaf-rolling") (Legalov, 2003).

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

For revealing phylogenetic relationships between tribes in the family Rhynchitidae a cladogram was constructed (fig. 1). To create the cladogram, 50 characters were used (Table 1):

1. Body with setae (0); - body without setae (1);
2. Metallic lustre present (0); - metallic lustre absent (1);
3. Length of the rostrum: rostrum long (0); - rostrum short (1);
4. Tooth on exterior side of mandible absent (0); - tooth on exterior side of mandible present (3);
5. Labial palp of female 3-segments (0); - labial palp of female 1- or 3-segments (1);
6. Pro- and metacoxa close together (0); - pro- and metacoxa widely separated (1);
7. Width of the forehead: forehead wide (0); - forehead narrow (1);

8. Eyes convex (0); - eyes almost flat (1);
9. Antennae attached subbasal of the rostrum (0); - antennae attached submedial or subapical of the rostrum (1);
10. Form of antennal clava: clava symmetric (0); - clava asymmetric (1);
11. Length of clava: clava short (0); - clava usually long (1);
12. Keel on sides of the pronotum absent (0); - keel on sides of the pronotum present (1);
13. Form of the elytra: elytra almost rectangular (0); - elytra round shape (1);
14. Sculpture of the elytra smooth (0); - sculpture of the elytra rough (1);
15. Scutellar striole present at the majority genera (0); - scutellar striole absent or present only at primitive genera (1);
16. Striae of the elytra available (0); - striae of the elytra absent (1);
17. Wings advanced (0); - wings reduced (1);
18. Teeth on the prothorax of males absent (0); - teeth on the prothorax of males present (1);
19. 1-5 ventrites free (0); - 1 and 2 ventrites fused (1);
20. Sternite 8 of males with distinctly pigmented apodeme (0); - sternite 8 of males lacking distinct apodeme (1);
21. Spiculum gastrale directed dextro-anteriorly (0); - spiculum gastrale directed sinistro-anteriorly (1);
22. Type of the ventral spicula: auletoid type (0); - rhynchitoid type (2);
23. Propygidium ulterior by the elytra (0); - propygidium not ulterior by the elytra (1);
24. Tergite 9 of males desclerotized to well-pigmented narrow band arching over sternite 9 (0); - tergite 9 of males completely membranous (1);
25. Tergite 9 of females sclerotized, entire at apex (0); - tergite 9 of females only laterally sclerotized (1);
26. Metepisternum reach metacoxa (0); - metepisternum do not reach metacoxa (1);
27. Width of the femora: femora weakly widened (0); - femora strongly widened (1);
28. Teeth on the femora absent (0); - teeth on the femora available (1);
29. Protuberances on the femora absent (0); - protuberances on the femora available (1);
30. Teeth on the tibiae absent (0); - teeth on the tibiae available (1);
31. Mucro at apex of the tibiae absent (0); - mucro at apex of the tibiae present (1);
32. Claws with teeth (0); - claws simple (1);
33. Styles of the ovipositor normally advanced (0); - styles of the ovipositor strongly reduced (2);
34. Form of apex of the aedeagus: apex not divided (0); - apex divided (1);
35. Armament of the endophallus advanced (0); - armament of the endophallus reduced (1);
36. Armament of the endophallus auletoid type (0); - armament of the endophallus byctiscoid type (1);
37. Maculae from setae on the elytra absent (0); - maculae from setae on the elytra available (1);

38. Armament of the endophallus symmetric (0); - armament of the endophallus asymmetric (1);
39. Procoxa of males without depression and bunch of setae (0); - procoxa of males with depression and bunch of setae, or even with bunch of setae (1);
40. Rostrum not flattened or weakly flattened (0); - rostrum strongly flattened (1);
41. Procoxa of males without depression but with a cluster of setae (0); - with depression and cluster of setae (3);
42. Apex of the elytra rounded and fused (0); - apex of the elytra separated (1);
43. Only first and second ventrites fused (0); - first, second and third ventrites fused (1);
44. Antennal clava well expressed (0); - clava feebly marked (1);
45. Apex of the elytra of males without maculae from setae (0); - apex with maculae from setae (1);
46. Head not conical (0); - head conical (1);
47. Pygidium latent by the elytra (0); - pygidium not latent by the elytra (1).
48. Imago do not turning of tubes from leaf (0); - imago (even at some species) turning of tubes (1);
49. Maxillary palp long (0); - maxillary palp short (1);
50. First segment of the tarsi normal structure (0); - first segment of the tarsi lengthened and strongly widening (1).

The tribes of the family Rhynchitidae can be broadly divided into two supertribes Rhinocartitae and Rhynchititae (fig. 1).

The supertribe Rhinocartitae is known from the late Cretaceous period. It is the original group for the family Rhynchitidae. This supertribe probably arose in the Jura period, with fossil specimens found in association with the family Nemonychidae. Rhinocartitae include the most primitive tribes with an average IP of 8.3. Rhinocartitae is represented by a small tropical group consisting of six tribes (Paleocartini, Sanyrevilleini, Auletorhinini, Vossicartini, Rhinocartini and Proteugnampini) with simple sinapomorphic characters (tooth on exterior side of mandible absent and primitive structure of spiculum gastrale auletoid type). Reduced styles of the ovipositor, elytra without striae and lengthened segments of the antennal clava characterise apomorphic characters this supertribe. Two branches are recognised from the six tribes. The first branch consists of three primitive tribes (Paleocartini, Sanyrevilleini and Auletorhinini) a characterised by a reduced striae of the elytra (sinapomorphy) and an average IP of 7.3. The fossil tribe Paleocartini (IP = 7) is characterised by an apomorphic arrangement of antennae. Oriental tribes Sanyrevilleini (IP = 7) and Auletorhinini (IP = 8) form sisterly group (IPHR = 7) and differ in the eighth sternite of males lacking distinct apodeme.

The second branch is formed by tribes Vossicartini, Rhinocartini and Proteugnampini and characterised by a short rostrum. Their average IP equal 9.3. The Southern African tribe Vossicartini (IP = 9) is most detached from other tribes of the supertribe and is very primitive. It is characterised by apomorphic characters: short, strongly flattened rostrum and feebly marked clava of antennae. Of all tribes in the Rhinocartitae, only Vossicartini possess striae on elytra which are well expressed (plesiomorphy). Tribes Proteugnampini (IP = 9) and Rhinocartini (IP = 10) form a special group (IPHR = 9). The major apomorphic characters uniting these tribes is the short, not flattened rostrum, submedial attached antennae and usually long clava of antennae of both sexes.

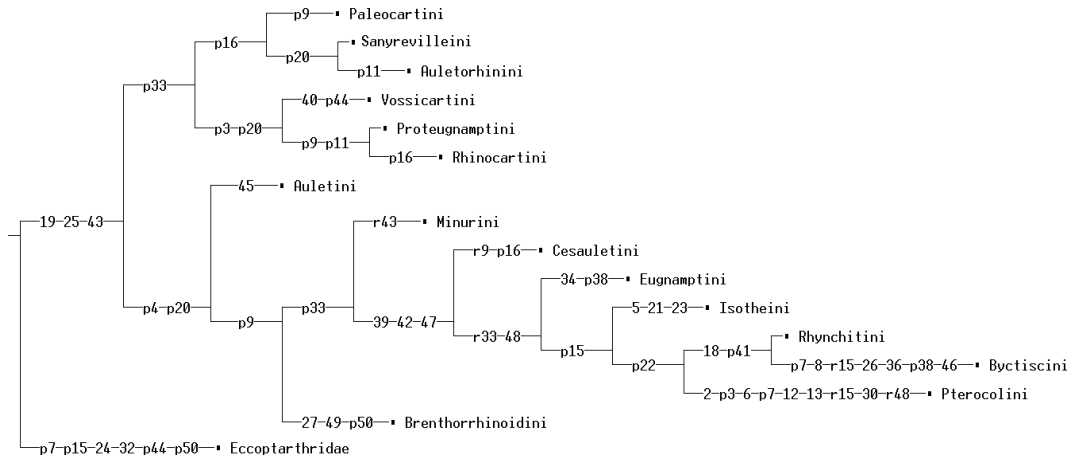


Fig. 1. Phylogenetic trees of family Rhynchitidae.

Table 1. Data matrix for family Rhynchitidae

Taxonen	Characters																																											
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Paleocartini	0000000010000001001?00001000000?10000000M010000000																																											
Vossicartini	00100000000000000001100001000000010000001M011000000																																											
Auletanini	0B00000000B00001001100001000000010000000M010000000																																											
Auletorhinini	0000000000100001001100001000000010000000M010000000																																											
Rhinocartini	0010000010100001001100001000000010000000M010000000																																											
Proteugnampini	0010000010100000001100001000000010000000M010000000																																											
Brenthorrhinoidini	0?010000100000?000110?001010000?????0?0M010000011																																											
Auletini	B0010000B000000BB0110B001000000BB0B0B0B00010100000																																											
Minurini	00010000100000000011000010000000100000000000000000																																											
Cesauletini	00010000000000010011000010000000100000100110001000																																											
Eugnampini	0BB100B0100000000011000010000000010001100110001100																																											
Isotheini	0BB110B01000001000111B1010BB00000000B0100110001100																																											
Pterocolini	01110110100110000011010010000100000000100110001000																																											
Rhynchitini	0BB100BB1BB00B100111010010BBBBB000B0BB101110001100																																											
Byctiscini	BB010011100000000111010011000000000101101110011100																																											

Symbol: 0 - plesiomorphic state of the character, 1 - apomorphic state of the character, M - absence of the character, ? - unknown character and B - polymorphism of the characters

Afro-Madagascar tribes (Vossicartini, Rhinocartini and Proteugnampini) have weak relationships (IPHR from 1 to 3) with representatives of the supertribe Rhynchitidae. Tribes

Sanyrevilleini and Auletorhinini are very similar to primitive Rhynchitidae. The similarity of these two tribes with Rhynchitidae is basically due to simple sinapomorphies. The IPHR relationship

for the two tribes Sanyrevilleini and Auletorhinini to the tribe Minurini is two and for Cesautetini six. Phylogenetic relationships with other tribes within the supertribe Rhynchititae do not occur.

The second supertribe Rhynchititae within the family Rhynchitidae will consist of nine tribes. The average IP of tribes included in the supertribe is 14.9. The basic autapomorphy of this supertribe is the presence of a tooth at external edge of the mandible, while in some genera of the advanced tribes Isotheini and Rhynchitini there is a reduction in the size of the tooth. The most ancient Rhynchitidae from the late Jura and the early Cretaceous (tribe Brenthorrhinoidini) belongs to the Rhynchititae.

The tribe Auletini (IP = 8) is the first branches off from the main trunk (fig. 1) in supertribe Rhynchititae. It is characterised by plesiomorphic characters: apex of the elytra rounded in common, spiculum gastrale auletoid type, primitive armament of the endophallus and apomorphic characters: maculae from setae on the elytra available and bunches of setae on procoxa of males. Primitive species from the tribe Auletini are distinguished by a close association with Gymnospermaes whereby development of larvae in generative organs of the host is essential for survival. The widespread distribution of the tribe Auletini throughout (Nearctic, Palaearctic, Oriental, Ephiopian and Australian regions) also indicates its primitive origins.

Other tribes of this supertribe are characterised by submedial or subapical attached antennae.

The fossil tribe Brenthorrhinoidini (IP = 11) shows strong divergence from the other tribes. It is characterised by three apomorphies (sometimes strongly widened femora, unusually short maxillary palps, and also the lengthened and strongly widening first segment of the tarsi). This tribe is closest to tribe Minurini (IPHR = 8).

Tribe Minurini (IP = 9) is close to tribes Auletini and Brenthorrhinoidini. It has a unique plesiomorphic character with the first and sec-

ond ventrites fused. At all other genera within the Rhynchitidae have the first, second and third ventrites fused. Plesiomorphies of this group are advanced elytral striae, common rounded apex of the elytra, absence of bunches of setae on procoxa of males. In the tribe Minurini two important apomorphic states of characters are found: submedial attached antennae and strongly reduced styles of the ovipositor.

Other tribes of the supertribe Rhynchititae differ from primitive Auletini, Brenthorrhinoidini and Minurini by the following apomorphic characters: procoxa of males with bunch of setae, with sometimes depressed, separately rounded elytra and pygidium not latent by the elytra. They are characterised by a higher average IP of 17.7.

The North American tribe Cesautetini (IP = 13) is habitually very similar to tribe Auletini (Legalov, 2003). Its similarity to tribe Auletini by the completely reduced elytral striae and structure of the spiculum gastrale. From the given tribe there arise the tribe Eugnamptini. IPHR between Cesautetini and Eugnamptini is nine.

Tribes Eugnamptini, Isotheini, Pterocolini, Rhynchitini and Byctiscini are allocated in a special complex (fig. 1). They differ in the submedial or subapical attachment of the antennae (apomorphy), normally advanced styles of ovipositor (reversion) and ability imago to turning of tubes from leaves.

Tribe Eugnamptini (IP = 14) has are auletoid type of structure of the specula gastrale as plesiotypic tribes Rhinocartitae, Auletini, Minurini and Cesautetini is most primitive from these tribes. Tribe Eugnamptini is characterised by apomorphic asymmetric armament of the endophallus and usually divided apex. Some genera of this tribe are known to form tubes from leaves.

Tribe Isotheini (IP = 16) is represented by species which are mainly found to form tubes by leaf rolling. This tribe is considered by the majority scientists (Voss, 1938, 1965; Ter-Minassian, 1950,

Sawada, 1993; Egorov, 1996; Alonso-Zarazaga, Lyal, 1999) to represent the most advanced tribe of the family Rhynchitidae. It is a special direction (together with Eugnamptini) in the evolution of the Rhynchitidae to begin to turning of funnelled tubes. Tribe Isotheini (fig. 1) is characterised by the apomorphic characters of 1- or 2-segmented labial palps, spiculum gastrale directed sinistro-anteriorly, propygidium usually not latent by elytra, short rostrum and presence of neckal groove. These characters are a development to aiding of the turning of tubes.

Tribes Pterocolini, Rhynchitini and Byctiscini are characterised by possessing of a rhynchitoid type of spiculum ventrale. Tribe Pterocolini has a very high IP of 20 with Thompson (1992) and Hamilton (1998) allocate to an independent subfamily. Species of the tribe Pterocolini possess structured characteristics which comm of be separated from the supertribe Rhynchititae. On the basis of results of the phylogenetic analysis I consider Pterocolini as a tribe. Apomorphic characters of tribe Pterocolini include: pro- and metacoxa widely shared, structure of tibiae and habitually similarity to the some Attelabinae (especially with the genus *Hybolabus*), and also presence of metallic lustre, short rostrum, narrowed forehead, carina on sides of the pronotum, and the round form the elytra. Such structures of tribe Pterocolini can be considered as arising from adaptation at transition to commensal way of life in tubes, ar represented by the American Attelabinae (tribes Pilolabini and Hybolabini).

The most advanced tribes Rhynchitidae are within the (IRHR = 16) the tribes Rhynchitini and Byctiscini with an IRHR of 16. They form sister group and distinguished from other tribes to the procoxa of males having a depression and clump of setae (sinapomorphy). In these tribes males sometimes have teeth directed forward on sides of the prothorax.

Tribe Rhynchitini (IP = 18) contains the most species within the family with very complex taxonomically structures. The genera are characterised by various apomorphic characters. Spe-

cies of this tribe develop in both the vegetative and generative bodies of plants (Legalov, 2003).

Tribe Byctiscini is the young, compact group distributed mainly in Oriental biogeographic regions. To the major apomorphic characters is the narrowed forehead, metepisternum not reaching the metacoxa, first ventrite with blades, armament of the endophallus byctiscoid type and conical head. In the tribe Byctiscini, transition from development inside fruits to turning leaves in package is observed. This tribe includes primitive Svetlanaebyctiscina (IP = 11) characterised by development of larvae in fruit to advanced Byctiscina (IP = 14) and Listrobyctiscina (IP = 16).

The family of the Rhynchitidae forms two large branches. Most apotipically is supertribe Rhynchititae. Its genera have adapted to development in various parts of plant and to turning tubes. This supertribe will consist of nine distinctive tribes. On the basis of IP, these tribes form three groups: 1. Auletini, Brenthorrhinoidini and Minurini; 2. Cesauletini, Eugnamptini and Isotheini; 3. Pterocolini, Rhynchitini and Byctiscini.

The system of the family Rhynchitidae developed on the basis of the phylogenetic analysis is as follows:

- supertribe Rhinocartitae Voss, 1931
- tribe Paleocartini Legalov, 2003
- tribe Vossicartini Legalov, 2003
- tribe Proteugnamptini Legalov, 2003
- tribe Rhinocartini Voss, 1931
- tribe Sanyrevilleini Legalov, 2003
- tribe Auletorhinini Voss, 1935
- supertribe Rhynchititae Gistel, 1848
- tribe Brenthorrhinoidini Legalov, 2003
- tribe Auletini Desbrochers des Loges, 1908
- tribe Minurini Legalov, 2003
- tribe Cesauletini Legalov, 2003
- tribe Eugnamptini Voss, 1930
- tribe Isotheini Scudder, 1893
- tribe Pterocolini Lacordaire, 1866
- tribe Rhynchitini Gistel, 1848

tribe Byctiscini Voss, 1923

Acknowledgments

The author is sincerely grateful to Dr. Mark McNeill (Lincoln), for their kind help with a revision of the manuscript.

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Received: 06.10.2005.

Accepted: 01.12.2005.

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