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ZOOLOGY

Phylogenetic Reconstruction of Weevil Superfamily Curculionoidea (Coleoptera) Using the SYNAP Method

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Abstract—Phylogenetic relationships within the superfamily Curculionoidea were reconstructed. Autapomorphies of the superfamily Curculionoidea include more or less pronounced snout, clubbed antennae, and partially sclerotized or completely membranous male tergite 9. Weevil families can be divided into three groups. The first group includes the most primitive family Nemonychidae. The second group includes nine families (Anthribidae, Belidae, Oxycorynidae, Eccoptarthridae, Allocorynidae, Rhynchitidae, Attelabidae, Ithyceridae, and Brentidae). The third ("higher") group includes six families (Brachyceridae, Cryptolaryngidae, Dryophthoridae, Curculionidae, Scolytidae, and Platypodidae).

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The problem of phylogenetic relationships between families of the superfamily Curculionoidea and of their number remains the key problems in weevil research. Phylogenetic reconstruction of Curculionoidea is complicated, on the one hand, by the ancient origin of this family known from the late Jurassic period (Ponomarenko and Kireichuk, 2003) and, on the other hand, by a huge number of the constituent taxa (about 60000 species and over 6000 genera). Triassic Obrieniidae have been recently excluded from the considered superfamily (Legalov, 2002).

Many attempts were made to develop a natural system of the superfamily. Nearly all authors recognize the families Nemonychidae, Anthribidae, Curculionidae, and recently described Eccoptarthridae (Arnoldi, 1977; Thompson, 1992; Kuschel, 1995). Most systems also include the families Belidae, Oxycorynidae, Attelabidae, Ithyceridae, Apionidae, and Brentidae. However, the volume of the families Belidae, Oxycorynidae, Attelabidae, Apionidae, Brentidae, and particularly Curculionidae is ambiguous. Some authors recognize Allocorynidae, Rhynchitidae, Brachyceridae, Dryophthoridae, Scolytidae, Platypodidae, Cimberididae, Urodontidae, Aglycyderidae, Raymondionymidae, Cryptolaryngidae, Antliarhinidae, Eurhynchidae, Pterocolidae, Erirhinidae, Nanophyidae, and Barididae as independent families.

Two trends can be traced in the development of the weevil system: phenetic and phylogenetic. The similarity-based phenetic systems relying on both symplesiomorphies and synapomorphies have a higher number of families in the Curculionoidea superfamily, which is quite significant in recent publications (Thompson, 1992; Zimmermann, 1993a, 1993b, 1994; Zherikhin and Gratshev, 1995; Alonso-Zarazaga and Lyal, 1999). The relationship-based phylogenetic systems (Rasnitsyn, 2002) relying on synapomorphies starting from Crowson's works usually have a low number of families (Crowson, 1955, 1981, 1984, 1985, 1986; Kuschel, 1995; Morrone, 1997; Marvaldi et al., 2002).

MATERIALS AND METHODS

The cladistic method was used in this work (Pavlinov, 1989, 1990; Rasnitsyn, 2002). Cladogram generation using the Hennig86 and Phylip software was rejected since an explanation of calculations underlying diagram plotting was required. PAUP 2.4.1 and SYNAP 420 yielded similar results, particularly, for weighed characters. However, SYNAP not only marked the branches with phylogenetic events and allowed tracing of the calculation progress but also generated two additional parameters (the advancement index and the index of phylogenetic relationship), which substantiated the use of this software for the phylogenetic reconstruction (Baikov, 1999). The following abbreviations are used in this work: advancement index (AI), sum of advanced characters; and index of phylogenetic relationship (IPR), AI minus unique advanced characters. In the case of equal IPRs, polytomy (merging of equivalent nodes), emergence of a new unique character, and minimum reversions were preferred. No matrix optimization was carried out. The reversion value was taken as –1. Character states: 0, plesiomorphic; 1, apomorphic. Step-by-step protocols of phylogenetic reconstruction were published elsewhere (Legalov, 2003). Sixteen weevil families with marked apomorphic characters were considered. These families included extinct forms. The previous analysis of the relationships (Legalov, 2003) suggested the inclusion of Cimberididae into Nemonychidae; Urodontidae into Anthribidae; Aglycyderidae into Oxycorynidae; Pterocolidae into Rhynchitidae; Apionidae, Nanophyidae, Antliarhinidae, and Eurhynchidae into Brentidae; and Raymondionymidae, Erirhinidae, and Baridae into Curculionidae.

Representatives of 5 genera of the family Nemonychidae, 26 genera of the family Anthribidae, 7 genera of the family Belidae, 3 genera of the family Oxycorynidae, 1 genus of the families Eccoptarthridae, Ithyceridae, Brachyceridae, and Platypodidae each, 132 genera of the family Rhynchitidae, 116 genera of the family Attelabidae, 83 genera of the family Brentidae, 2 genera of the family Cryptolaryngidae, 10 genera of the family Dryophthoridae, 403 genera of the family Curculionidae, and 31 genera of the family Scolytidae have been analyzed.

Phylogenetic relationships between 16 families of the superfamily Curculionoidea were revealed using 111 arbitrarily arranged characters (Table): 1. The imago can live and feed inside a host plant: (0) false, (1) true; 2. Ant-shaped body: (0) false, (1) true; 3. Body is covered with scales: (0) false, (1) true; 4. Body has a metallic lustre: (0) false, (1) true; 5. Aedeagal apodeme: (0) present, (1) absent; 6. Sexual dimorphism of the snout: (0) inexplicit; (1) more or less explicit or secondarily lost; 7. Snout: (0) inexplicit, (1) more or less explicit; 8. Yellow prominent hairs on the snout underside: (0) absent, (1) present; 9. Gular suture: (0) paired or reduced, (1) unpaired; 10. Laterodorsal edge of the snout: (0) blunt, (1) pointed; 11. Detached labrum: (0) true, (1) false; 12. Mandibles: (0) with simple top, (1) with more than two teeth in the incisor area; 13. Mandibles with molas: (0) true, (1) false; 14. Outer edge of the mandibles: (0) not dentate, (1) dentate; 15. Mandibles are thick relative to the base: (0) true, (1) false; 16. Male mandibles: (0) symmetrical, (1) left one is larger; 17. Labial palps have: (0) three segments, (1) one or two segments; 18. Maxillary palps have: (0) four segments, (1) two or three segments; 19. Eyes: (0) advanced,(1) reduced; 20. Eyes: (0) not lustrous, (1) completely lustrous with cornea-like coaching; 21. Eyes: (0) convex, (1) flat or almost flat; 22. Eyes: (0) have no notch on the front edge, (1) demonstrate a tendency to notch formation on the front edge or are completely detached; 23. Eyes: (0) have normal structure, (1) are flat and commonly almost fused on the snout downside; 24. Antennal grooves: (0) absent, (1) developed on the snout sides; 25. Head: (0) with inexplicit neck, (1) with explicit neck; 26. Head behind the eyes: (0) has no constriction, (1) commonly has a deep constriction; 27. Antennal grooves: (0) on the snout side, (1) on the snout top; 28. The main sclerite on the endophallus: (0) not whiplike, (1) whiplike; 29. Antennae: (0) not geniculate, (1) geniculate; 30. Antennae: (0) have normal structure, (1) are wide and flat; 31. The 1st and 2nd segments of the antennae: (0) symmetrical, (1) asymmetrical and notably bent; 32. Funiculus: (0) has at least seven segments, (1) has six or less segments; 33. Antennae: (0) with no explicit club, (1) with explicit club; 34. The 1st segment of the club: (0) is not elongated, (1) is very elongated; 35. Prothorax: (0) has no wide subbasal ring, (1) has a wide subbasal ring; 36. Precoxal part of the prothorax: (0) is long and clearly longer than the postcoxal one, (1) is short; 37. Tegmen: (0) not oxycorynoid, (1) oxycorynoid; 38. Prothorax: (0) has no snout groove, (1) has a snout groove; 39. Ovipositor: (0) weakly sclerotized with parallel sides, (1) strongly sclerotized with arched sides; 40. Prothorax: (0) with no prominent lateral edge, (1) with a lateral edge; 41. Pronotum: (0) with no transverse or lateral carina, (1) with transverse and lateral carina; 42. Penis: (0) weakly sclerotized, (1) strongly sclerotized; 43. Prothorax sides: (0) with no femur groove, (1) with a femur groove; 44. Prothoracic suture between the episternite and epimerite: (0) prominent, (1) obsolete; 45. Fore coxae: (0) highly protruding, (1) mildly protruding and semicircular; 46. Fore coxae: (0) joint, (1) separated by the intercoxal process; 47. Spermatheca: (0) weakly sclerotized, (1) strongly sclerotized; 48. Club: (0) loose, (1) compact; 49. Back edge of metepisternite before coxae (0) at most slightly bent, (1) strongly bent; 50. Postnotal constriction: (0) absent, (1) attelaboid type; 51. Mesothorax: (0) hidden by prothorax and elytra, (1) visible; 52. Scutellum: (0) open, (1) hidden; 53. Scutellum: (0) not protruding over elytra, (1) protruding; 54. Club: (0) has three segments, (1) has one or two segments; 55. Elytra: (0) smooth, (1) prickly and tuberous; 56. Elytra: (0) not connate, (1) connate; 57. Elytra: (0) irregularly pointed, the points form no striae, (1) striated; 58. Elytra: (0) with no rows of prominent scales, (1) with rows of prominent scales; 59. Sheath top: (0) forms no long process, (1) forms a long process; 60. Larval clypeolabral suture: (0) prominent, (1) erased; 61. Elytra: (0) have no “barrow”, (1) have a “barrow”; 62. Scutellar striole: (0) present, (1) absent on striate elyta; 63. Elytra: (0) with no sharp lateral carina, (1) with a sharp lateral carina; 64. Larval frontal suture: (0) reaches mandibles, (1) does not reach mandibles; 65. Snout: (0) prominent, (1) secondarily thickened; 66. Male abdomen: (0) without deepening framed by teeth, (1) with deepening framed by teeth; 67. Ventrites 1–5: (0) are detached, (1) at least some are connate or tightly coupled; 68. Suture between ventrites 1 and 2: (0) continuous, (1) partially smoothed; 69. Ventrites 1 and 2: (0) are level with ventrite 3 in a side view, (1) protrude over ventrite 3 in a side view; 70. Gular suture: (0) paired, (1) reduced; 71. Ventrite 1: (0) not rimmed at coxal cavity, (1) ventrite rimmed at coxal cavity; 72. Female ventrite 5: (0) with no hair cushion, (1) with a hair cushion; 73. Male sternite 8: (0) with a prominent apodeme, (1) with no prominent apodeme; 74. Gular suture: (0) paired, (1) fused in the top region; 75. Male tergite 9: (0) completely sclerotized, (1) partially sclerotized or completely membranous; 76. Male tergite 9: (0) present, (1) absent; 77. Preular suture: (0) present, (1) absent; 78. Male sternite 8: (0) hidden

Matrix table for families of superfamily Curculionoidea

Taxa	Characters*																												
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Chrysomelidae	0	0	0	B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	B	0	B	0	0
Nemonychidae	0	0	0	0	0	0	1	0	0	0	0	B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	B	0	0
Anthribidae	0	0	0	0	0	0	1	0	0	B	0	1	0	0	0	0	0	0	0	0	1	B	0	0	0	0	B	B	0	0
Belidae	0	0	0	B	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	B
Oxycorynidae	0	0	B	0	0	1	1	B	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	B	0	0	0	0
Eccoptarthridae	0	0	0	0	0	1	1	0	1	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Allocirynidae	0	0	0	0	0	1	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhynchitidae	0	0	0	B	0	1	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Attelabidae	0	0	0	B	0	1	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	B	0	0	B	0	0
Ithyceridae	0	0	0	0	0	1	1	0	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Brentidae	B	B	B	B	0	1	1	0	1	0	1	1	1	0	0	B	1	1	0	B	B	B	0	B	0	B	0	B	B	B
Brachyceridae	0	0	0	0	0	1	1	0	1	0	1	1	1	0	0	0	0	1	0	0	1	0	0	1	0	0	B	0	0	0
Cryptolaryngidae	0	0	1	0	0	1	0	0	1	0	1	1	1	0	0	0	0	1	0	0	1	0	0	1	0	0	1	B	1	0
Dryophthoridae	B	0	B	0	0	1	1	0	1	0	1	1	1	0	0	0	0	1	0	0	1	B	1	1	0	0	0	0	B	0
Curculionidae	B	B	1	B	0	1	1	0	1	0	1	1	1	0	0	0	0	1	B	0	1	0	0	1	0	0	B	B	1	0
Scolytidae	1	0	B	0	0	1	0	0	1	0	1	1	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	1	0
Platypodidae	1	0	0	0	1	1	0	0	1	0	1	1	1	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0

Taxa	Characters*																												
	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Chrysomelidae	0	0	0	0	0	B	0	0	B	B	0	0	0	0	0	B	0	M	0	0	0	0	0	M	B	B	B	0	0	0
Nemonychidae	0	0	1	0	0	0	0	0	B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	B	0	0	1
Anthribidae	B	B	1	B	0	0	0	0	B	B	B	0	0	0	B	1	B	B	0	0	0	0	0	0	B	0	1	0	0	0
Belidae	0	0	1	0	0	B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	B	0	B	0	0	0	0	0
Oxycorynidae	0	0	1	0	0	B	B	0	0	0	0	0	0	0	1	B	0	0	0	0	0	0	0	B	0	0	0	B	0	0
Eccoptarthridae	0	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	1	0	0	0
Allocirynidae	0	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	1	0	0	0
Rhynchitidae	0	0	1	B	0	1	0	0	0	B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Attelabidae	0	0	1	B	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	B	0	1	0	0	0
Ithyceridae	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0
Brentidae	0	B	1	B	B	B	0	0	0	0	0	0	B	B	B	B	B	1	B	0	0	B	B	0	B	0	1	0	B	0
Brachyceridae	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	B	1	1	0	0	0
Cryptolaryngidae	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0
Dryophthoridae	0	1	1	0	0	0	0	0	0	0	0	0	0	0	B	B	B	1	0	0	0	0	0	1	0	0	1	0	0	0
Curculionidae	0	B	1	0	0	B	0	B	0	B	0	B	0	0	B	1	1	1	0	0	0	B	B	0	B	B	1	0	0	0
Scolytidae	0	B	1	0	0	1	0	0	0	B	0	1	0	0	B	1	0	1	0	0	0	0	0	B	0	0	1	0	0	0
Platypodidae	0	1	1	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	0	1	0	0	1	0	0	1	0	0	0

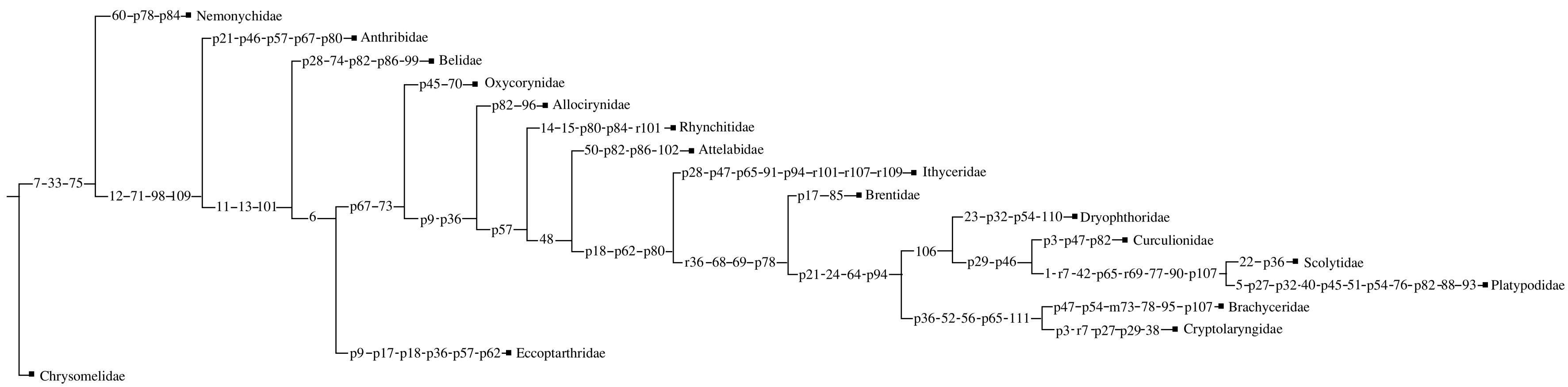
Table. (Contd.)

Taxa	Characters*																													
	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
Chrysomelidae	0	0	B	0	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	B	0	B	M	0	0	0	0	0	0	0
Nemonychidae	0	0	0	0	0	0	0	0	0	0	B	B	0	0	1	0	0	1	0	B	0	0	0	1	0	0	0	0	0	0
Anthribidae	0	0	0	0	M	B	1	0	0	B	1	0	B	M	1	0	0	B	0	1	0	0	0	M	0	0	0	0	0	0
Belidae	0	M	0	0	0	0	0	0	0	M	1	0	0	1	1	0	0	B	0	0	0	1	B	M	0	1	0	0	0	0
Oxycorynidae	0	0	B	0	B	0	1	0	0	1	1	0	1	M	1	0	0	0	B	0	0	0	0	M	0	0	0	0	0	0
Eccoptarthridae	0	1	0	0	0	0	0	0	0	M	1	0	0	M	1	0	0	0	0	0	0	0	0	M	0	0	0	0	0	0
Allocirynidae	0	M	0	0	0	0	1	0	0	M	1	0	1	M	1	0	0	0	0	0	0	1	0	M	0	0	0	0	0	0
Rhynchitidae	0	0	0	0	B	0	1	0	0	M	1	0	1	M	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
Attelabidae	0	B	0	0	B	B	1	0	0	M	1	0	1	M	1	0	0	0	0	B	0	1	0	M	0	1	0	0	0	0
Ithyceridae	0	1	0	0	1	0	1	0	0	M	1	0	1	M	1	0	0	U	0	1	0	0	0	M	0	0	0	0	0	0
Brentidae	0	1	0	0	B	0	1	1	1	M	1	0	1	M	1	0	0	1	B	1	B	B	B	M	1	0	B	0	0	0
Brachyceridae	0	1	0	1	1	0	1	1	1	M	1	0	M	M	1	0	0	B	0	1	0	B	0	M	0	0	0	0	B	0
Cryptolaryngidae	0	1	0	1	1	0	1	1	1	M	1	0	1	M	1	0	0	1	0	1	0	0	0	M	0	0	0	0	0	0
Dryophthoridae	0	1	0	1	0	0	1	1	1	M	1	0	1	M	1	0	0	1	0	1	0	0	0	M	0	0	0	0	0	0
Curculionidae	0	1	0	1	B	B	1	1	1	M	1	0	1	M	1	0	0	1	0	1	0	1	0	M	0	B	B	0	0	0
Scolytidae	B	1	0	1	1	0	1	1	0	M	1	0	1	M	1	0	1	1	0	1	0	0	0	M	0	0	0	0	0	1
Platypodidae	B	1	0	1	1	0	1	1	0	M	1	0	1	M	1	1	1	1	0	1	0	1	0	M	0	0	0	1	0	1

Taxa	Characters*																				
	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111
Chrysomelidae	M	0	0	0	0	0	0	0	0	0	0	0	0	B	0	B	B	0	B	0	0
Nemonychidae	M	B	0	0	0	0	0	B	0	0	0	0	B	B	0	0	0	0	B	0	0
Anthribidae	M	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Belidae	0	0	0	0	0	0	0	1	1	0	1	B	0	0	0	0	0	0	1	0	0
Oxycorynidae	M	0	0	B	0	B	0	1	0	0	1	B	0	0	0	0	0	0	1	0	0
Eccoptarthridae	M	0	0	B	0	0	0	1	B	0	1	0	0	0	0	0	0	0	1	0	0
Allocirynidae	M	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0
Rhynchitidae	M	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Attelabidae	M	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0
Ithyceridae	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Brentidae	M	0	B	B	B	0	B	1	B	0	1	B	0	0	0	0	B	B	1	0	0
Brachyceridae	M	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1
Cryptolaryngidae	M	0	0	1	B	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1
Dryophthoridae	M	0	0	1	B	0	0	1	0	0	1	B	0	0	0	1	0	0	1	1	0
Curculionidae	M	0	0	1	B	0	0	1	0	0	1	B	0	B	B	1	B	0	1	0	0
Scolytidae	M	0	0	1	B	0	0	1	0	0	1	0	0	0	0	1	1	0	1	0	0
Platypodidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0

Note: 0, plesiomorphic state; 1, apomorphic state; B, polymorphism; M, missing character; U, unspecified.
* For details, see Materials and Methods.

under sternite 7, (1) visible; 79. The top of female tergite 8: (0) not dentate, (1) dentate; 80. Female tergite 9: (0) sclerotized with a continuous top, (1) only laterally sclerotized or completely membranous; 81. Trochanters: (0) short, (1) long and almost cylindrical; 82. Femurs: (0) without teeth, (1) with teeth; 83. Club: (0) prominent, (1) secondarily lost; 84. Male tergite 9: (0) partially sclerotized, (1) completely membranous; 85.



Cladogram of families of the superfamily Curculionoidea; numbers indicate character nos.; p, parallelisms; r, reversions.

Brentoid pygidium: (0) false, (1) true; 86. Tibia: (0) without teeth on the inner edge, (1) with teeth on the inner edge; 87. Penile shafts look detached: (0) false, (1) true; 88. Tibiae: (0) with notches, (1) with no notches; 89. Ovipositor styli are large, short, sclerotized, and dentate: (0) false, (1) true; 90. Female tergite 8 detached from the bottom: (0) false, (1) true; 91. Gular suture: (0) paired and fused in the top region, (1) wide and coarse; 92. Larval lower jaw: (0) has no diagonal masticatory ridge, (1) has a diagonal masticatory ridge; 93. Tarsi: (0) are almost longer than tibiae, (1) are much longer than tibiae; 94. Larval labrum: (0) has four bristle pairs, (1) has three bristle pairs; 95. Third tarsal segment is bilobate: (0) false, (1) true; 96. Second tarsal segment is bilobate; 97. Claw segment is longer than the 2nd and 3rd segments together: (0) false, (1) true; 98. Larval legs: (0) with claws, (1) with no claws; 99. First tarsal segment in both sexes is wide and long: (0) false, (1) true; 100. First tarsal segment is longer than the following segments: (0) false, (1) true; 102. Claws: (0) detached, (1) connate; 103. Top of penis protrudes as a dens: (0) false, (1) true; 104. Endophallic armature: (0) inside and outside of penis, (1) inside penis; 105. Upper part of penis is separated from the lower one by a membrane: (0) true, (1) false; 106. Tegmen in most representatives: (0) developed, (1) reduced; 107. Tegmen top: (0) weakly or not divided, (1) deeply divided; 108. Male sternite 9 has a medial sclerite: (0) false, (1) true; 109. Tegmen plate: (0) divided, (1) joint; 110. Lower part of penis has a lateral line or groove: (0) false, (1) true; 111. Brachyceroid male sternite 8: (0) false, (1) true. Character nos. 5, 14, 15, 18, 20, 47, 60, 64, 73, 75–78, 80, 84, 92, 94, 98, 105, and 110 were proposed elsewhere (Kuschel, 1995; Wood, 1986).

RESULTS AND DISCUSSION

Nemonychidae (figure) proved to be the most primitive family (AI = 6). It emerged in the upper Jurassic and features erased larval clypeolabral suture, apparent sternite 8, and completely membranous sternite 9 in males. All other families differ from Nemonychidae by mandibles with more than two teeth in the incisor area, ventrite 1 framed near the acetabulae, joint tegmen plate, and clawless larval legs.

The family Anthribidae split off next from the main trunk (AI = 12); it features apomorphic state of characters 21, 46, 57, 67, and 80. An important synplesiomorphy, detached labrum, brings the families Nemonychidae and Anthribidae together (IPR = 3).

The remaining 14 families (AI from 15 to 44) share not detached labrum, mandibles without molas, and simple claws.

The family Belidae (AI = 15) can be considered as the most primitive of them. It emerged in the upper Jurassic and has the following apomorphies: whiplike main sclerite on the endophallus, indented femur, tibia with indented inner edge, and wide and long first tarsal segment. Character 6 is plesiomorphic. Notice paired gular suture in Belidae similar to Nemonychidae and Anthribidae.

In the upper Jurassic, the family Eccoptarthridae (AI = 17) formed a separate branch. It featured six apomorphies: single gular suture, 1- or 2-segment labial palps, 2- or 3-segment maxillary palps, a clearly shorter precoxal than postcoxal part of the prothorax, elytra with striae and scutellar striole absent. Characters 67 and 73 are plesiomorphic.

The family Oxycorynidae (AI = 15) has apomorphic state of characters 45 and 70 (mildly protruding and semicircular fore coxae and reduced gular suture).

The following 11 families share single gular suture and short precoxal part of the prothorax as well as high mean AI of 26.4.

The family Allocorynidae (AI = 17) features indented femurs and bilobate second tarsal segment but, in contrast to other 10 families, have not synapomorphic character 57.

Four apomorphies (dentate outer edge of the mandibles, thin mandibles relative to the base, laterally sclerotized or completely membranous female tergite 9, and completely membranous male tergite 9), and one reversion (indented claws) allowed us to recognize the family Rhynchitidae (AI = 19), which emerged in the late Jurassic period. This family is close to the families Allocorynidae (IPR = 13) and Eccoptarthridae (IPR = 12).

The more advanced family Attelabidae (AI = 21), reliably identified in the Paleocene (similar to other remaining families of the main trunk), features a compact club (apomorphic character). It has apomorphic state of characters 50, 82, 86, and 102 (attelaboid postnotal constriction, femurs without teeth, tibia without teeth on the inner edge, and connate claws). It has the highest IPR (16) with the families Allocorynidae and Rhynchitidae.

The family Ithyceridae (AI = 24), represented by a single species in the recent fauna, is of considerable interest. It features apomorphic state of characters 28, 47, 65, 91, 94, and 107; reversion of characters 101 and 109, and plesiomorphic state of characters 68, 69, and 78.

The last seven families have 2- or 3-segment maxillary palps, reduced scutellar striole, and latterly sclerotized or completely membranous female tergite 9.

The family Brentidae (AI = 24) split off next from the trunk in the lower Cretaceous. It features 1- or 2-segment labial palps and brentoid pygidium.

The top of the tree is formed by the families Brachyceridae, Cryptolaryngidae, Dryophthoridae, Curculionidae, Scolytidae, and Platypodidae, apparently, emerged in the middle Cretaceous. They share flat or almost flat eyes, antennal grooves on the snout sides, larval frontal suture not reaching the mandibles, and larval labrum with three bristle pairs. Their mean AI equals 34.8. These families form two sister groups. The first group includes the families Brachyceridae

(AI = 33) and Cryptolaryngidae (AI = 34); while the second one includes Dryophthoridae (AI = 31), Curculionidae (AI = 32), Scolytidae (AI = 35), and Platypodidae (AI = 44).

The first group has apomorphic state of characters 36, 52, 56, 65, and 111 characters and plesiomorphic state of character 106.

The second group features a notably reduced tegmen (in most species). The families Dryophthoridae and Curculionidae are the most separate in it, while Scolytidae and Platypodidae are the closest (IPR = 31).

Thus, the analysis of the superfamily Curculionoidea allows us to divide its families into three groups corresponding to three evolutionary levels. The first group includes the most primitive family Nemonychidae (AI = 6). The second group is composed of nine families (Anthribidae, Belidae, Oxycorynidae, Eccoptarthridae, Allocorynidae, Rhynchitidae, Attelabidae, Ithyceridae, and Brentidae) with IP from 12 to 24 (the mean IP = 18.2) with mandibles carrying more than two teeth in the incisor area, ventrite 1 framed near the acetabulae, joint tegmen plate, and clawless larval legs. The third (higher) group includes six families (Brachyceridae, Cryptolaryngidae, Dryophthoridae, Curculionidae, Scolytidae, and Platypodidae) with the main IP of 34.8 (from 31 to 44). These families share flat or almost flat eyes, antennal grooves on the snout sides, larval frontal suture not reaching the mandibles, and larval labrum with three bristle pairs. The autapomorphies of the Curculionoidea superfamily include more or less pronounced snout, antennae with a prominent club, and partially sclerotized or completely membranous male tergite 9.

Comparison of this system with the available current phylogenetic systems (Kuschel, 1995; Morrone, 1997; Marvaldi et al., 2002) demonstrates a match in the recognition of independent families Nemonychidae, Anthribidae, Belidae, Attelabidae, Brentidae, and Curculionidae as well as in the order of their splitting off from the main trunk. At the same time, the volume of the families Belidae, Attelabidae, Brentidae, and Curculionidae is smaller. Together with Morrone (1997) and Marvaldi et al. (2002), we recognize the separate family Eccoptarthridae but we consider it a more primitive group similar to the families Belidae and Oxycorynidae, which agrees with the views of Kuschel (1995) who included it into Belidae. This system is most similar to the system of Morrone (1997), which also considers Ithyceridae, Brachyceridae, and Platypodidaethe as independent families. The main distinction of this system is the recognition of Oxycorynidae, Allocorynidae, Rhynchitidae, Cryptolaryngidae, Dryophthoridae, and Scolytidae as separate families as well as the justification of sequential branching of weevil families from the main trunk.

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