

The most ancient bark beetle known: a new tribe, genus and species from Lebanese amber (Coleoptera, Curculionidae, Scolytinae)

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Abstract. *Cylindrobrotus pectinatus* **gen. et sp.n.**, a new scolytine species from Cretaceous Lebanese amber, is described. A new tribe, *Cylindrobrotini* **trib.n.**, is proposed for this unique species, which demonstrates an unusual combination of some archaic and many advanced characters. This finding suggests that the Scolytinae became a distinct lineage of Curculionoidea from the Lower Cretaceous. Fossil records are reviewed, and some remarks on the origin and taxonomic position of bark and ambrosia beetles are made. Some comments on the various phylogenetic interpretations of the last 30 years are given, particularly in respect of their correspondence with the fossil record. The early appearance of Scolytinae in the fossil record before other Curculionidae (which appeared in the Upper Cretaceous) can be used as evidence against the hypothesis of bark beetles as offspring of weevils. The question of the taxonomic rank of bark beetles (separate subfamily or family) and their placement among other groups of the superfamily remains unsolved.

Introduction

Amber is a 'gold mine' for palaeontologists because it contains a variety of biological inclusions in pristine, three-dimensional condition. The oldest amber with a high number of biological inclusions is from Lebanon (Azar, 1997). Although more than 375 outcrops have been discovered following recent geological field searches made by one of the co-authors (D. Azar) during the last decade, curiously, only 15 outcrops have yielded biological inclusions. Lebanese amber ranges from the Late Jurassic to Albian in age. The fossiliferous outcrops are all approximately of the same age and are mainly late Barremian to lowermost Aptian (Azar *et al.*, 2003a). Precise dating of the Lebanese material was possible following the discovery of strati-

graphical marker fossil pollen trapped in the amber (J. Dejax, personal communication).

The source of Lower Cretaceous amber from Jordan and Lebanon has been identified as trees of the genus *Agathis* (Coniferales: Araucariaceae) (Bandel & Haddadin, 1979; Poinar & Milki, 2001). Poinar & Milki (2001) described *Agathis levantensis* from Jordan as the amber-producing plant of Middle East amber. No remains of such a plant have been found in the Hammana outcrop (from where *Cylindrobrotus pectinatus* **gen. et sp.n.** originated), but another resin-producing plant may be present.

Coleoptera from Lebanese amber were recorded first by Crowson (1981), who found Micromalthidae, Scydmaenidae, Elateridae, Dermestidae as well as 'a very remarkable Scarabaeoid type', 'Clavicorn type possibly of *Pharaxonothini*' and 'two small *Heteromera*' (Crowson, 1981: 668). A few coleopteran groups from Lebanese amber are mentioned briefly in later publications (e.g. Grimaldi & Engel, 2005), but the specimens need detailed examination. Kuschel & Poinar (1993) described *Libanorhinus succinus* (Nemonychidae), and Lefebvre *et al.* (2005), *Libanoeuasthetus pentatarsus*

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(Staphylinidae). Currently, F.-T. Krell and colleagues are describing a new family of Scarabaeoidea from Lebanese amber. The present publication is the fourth dealing with Lebanese amber Coleoptera.

The 'fauna' of coleopterous inclusions obtained from Lebanese amber consists of about 60 specimens of varying condition, all of which have comparable ages and biotic and ecological circumstances. The information from the inclusions in the Lebanese amber corroborates the palynological data, and shows that the palaeoenvironment of the amber deposit corresponds to a tropical dense, humid and hot forest with an intense, complex fluvial system, not far from the sea. A characteristic feature of the coleopteran inclusions is their body size, which in most cases is between 1.0 and 2.0 mm. Only very few specimens are somewhat larger.

Many coleopteran specimens belong to the Elateroidea (mostly Elateridae, Throscidae, Eucnemidae), but Micro-malthidae, Carabidae, Scydmaenidae, Ptiliidae, Scirtidae, Clambidae, Cerophytidae, Chelonariidae, Ptilodactylidae, Lymexylidae, Dermestidae, Melyridae, Kateretidae, Monotomidae, Silvanidae, Latridiidae, Aderidae, Melandryidae, Anthicidae, Nemonychidae and even some new families are represented (Kirejtshuk & Azar, in press). Even if family attribution seems evident, many examined forms differ from Recent groups, although they can sometimes be regarded as isolated genera inside well-defined subfamilies. However, some inclusions show such unusual combinations of characters that their family attribution is not clear, notably in the superfamily Cucujoidea. Furthermore, attributable forms may be so outstanding that it is not advisable to place them in any extant tribe. Here we describe a new palaeoendemic tribe (*Cylindrobrotini trib.n.*) within the curculionid subfamily Scolytinae. We follow Crowson (1955), Kuschel (1995) and Marvaldi *et al.* (2002), among others, in accepting the Scolytinae as a subfamily of the family Curculionidae, rather than as the separate family of Wood (1986), Wood & Bright (1992) and Morimoto & Kojima (2003). We consider the subfamily to consist of two lineages [corresponding to the subfamilies Scolytinae and Hylesininae in the interpretation of Wood (1986)], and all tribes retain ranks as proposed by Wood.

The material under consideration was prepared following the method described by Azar *et al.* (2003b).

Family Curculionidae

Subfamily Scolytinae

Cylindrobrotini trib.n.

Type genus. *Cylindrobrotus gen.n.*

Composition. The new tribe is proposed for the only genus consisting of one species.

Description. Body subcylindrical and with smooth integument; with only few long and very fine suberect hairs. Surface with shallow punctures, arranged in slightly irregular rows on elytra (apparently no fewer than 10 rows on each elytron), replaced on head by weak granulation. Pronotum diffusely, shallowly and sparsely punctured.

Head subtrapezoid, short, with entire, moderately coarsely faceted eyes, with occipital dorsal process angular at apex (lateral thickened arms of this process extending posteriorly); mentum ['prementum' of Morimoto & Kojima (2003) or 'submentum' of Stickney (1923)] flat; gular sutures conjoined from base for two-thirds of length and divergent anteriorly. Mandibles very stout and widely triangular, right mandible with simple apex and two subapical teeth along inner edge; left mandible with bidentate apex, somewhat declined ventrally, with one subapical tooth. Antennal funicle 5-segmented, scape rather long, longer than funicle; club asymmetrical, obliquely truncate, subtriangular to oval and somewhat dorsoventrally compressed. Prothorax subcylindrical (barrel-shaped, without concavity externally from procoxae), without lateral carina, rounded at sides; dorsum (pronotum) about 5× as long as underside (prosternum). Scutellum flat, rather large, flush with elytral surface. Elytra simple at base (without transverse crenulation or costa) subcylindrical, jointly rounded at apex; declivity convex, unmodified.

Procoxal cavities contiguous, somewhat transverse and narrowing externally. Procoxae spherical, apparently with narrow exposed trochantin (because of reduced and translucent outer prohypomera), contiguous prosternal process absent. Mesocoxae narrowly separated. Metacoxae contiguous with somewhat exposed trochantin (because of reduction of fine outer sclerites or translucent parts of mesothoracic sclerites looking through amber like absent). Abdomen apparently with four ventrites (ventrite 1 seems to include fused ventrites 1 and 2 corresponding to abdominal sternites 1–3 and 4). Tibiae with four socketed denticles along lateral edge, but without tubercles on posterior face. Tarsi 5-segmented, all tarsomeres simple, tarsomere 4 smallest.

Diagnosis. All features summarized by Wood (1986) as distinctive for bark beetles seem to be in accord with the fossil specimen. This new species should be regarded as a member of the Scolytinae (sensu Crowson, 1955; Kuschel, 1995) owing to the following combination of characters: (i) two gular sutures [continuing by 'subgenal sutures' to cervical sclerites (postgula): Lyal, 1995] clearly visible; (ii) anterior part of head ('rostrum') not extended; (iii) mandibles clearly characteristic of Scolytinae but not of other groups of Curculionidae (i.e. socket not deep) (this is a derived character within the Curculionoidea, but could be plesiomorphic for Phytophaga), and with the cutting edge mesal and not apical; (iv) pro- and mesotibiae possess several distinct socketed teeth – a characteristic feature of many Scolytinae but lacking in almost all other Curculionidae (found in a few Conoderinae and some Cossoninae); (v) Antennae clearly geniculate with long scape and obliquely truncate club – a feature rare or absent in Scolytinae

except in tribes Dryocoetini and Xyleborini; and (vi) habitus of Scolytine type. The large mentum ('prementum' or 'submentum'), apparently exposed protrochantins, open mesocoxal cavities and broadly contiguous metacoxal cavities put this new species in a rather isolated position not only among bark beetles, but among weevils in general.

The simple base of the elytra (characteristic of the Scolytine lineage *sensu stricto*), 5-segmented antennal funicle, contiguous procoxae, and narrow tibiae with socketed denticles might suggest placement near Dryocoetini. However, important differences between the two tribes are discussed further below, and characters of Dryocoetini and the proposed new tribe are compared in Table 1.

Comparison. The traditional tribal discrimination in Scolytinae depends in part on the form of the metaternal sutures and the elytral locking mechanism (Wood, 1986). Although these features are not accessible for observation in the fossil specimen examined, we consider the combination of characters that the specimen possesses sufficient to justify erection of a new tribe *Cylindrobrotini*. Superficially in dorsal view the fossil beetle resembles species of *Hylastes* Erichson, 1836 (Hylesinine lineage), with its rather barrel-shaped pronotum and elongate elytra with a strongly convex declivity, lacking any strong sculpture – but it is excluded from that tribe by, *inter alia*, the characters of the antenna and tibiae (Hylastini have a 7-segmented funicle and conical club, and the protibia is much broader and has many lateral teeth). However, the lack of any crenulations or a costa at the elytral base is expected for the members of the Scolytine lineage rather than of the Hylesinine lineage. In many representatives of the Scolytine lineage, the pronotum is strongly declivous anteriorly, and the anterior slope is armed with asperities, but there are many exceptions, so the slight slope of the pronotum and the apparent absence of asperities in *Cylindrobrotus gen.n.* do not exclude it.

The form of the antennae with the 5-segmented funicle and obliquely truncate antennal club excludes it from the

Scolytini, Cryphalini, Corthylini, Xyloctonini, Crypturgini, Cactopinini, Carphodicticini, Scolytoplatypini, Ctenophorini, Micracini and Xyloterini. The form of the tibiae, not widely expanded, lacking an apical groove for the reception of the tarsus and with only four socketed teeth on the lateral margin, excludes it from most of these tribes and from the Xyleborini. The mentum ('prementum' or 'submentum') appears to be flat and not depressed as it is in Xyleborini (partly reminiscent of that in some Anthribidae and some Platypodinae). The species seems to be more closely related to the Ipini and Dryocoetini, which have similar protibiae, contiguous procoxae and, in some genera of Dryocoetini, similar antennae. *Cylindrobrotus gen.n.* differs from the Ipini in the form of the pronotum, which is not strongly declivous anteriorly and lacks asperities. A few Ipini lack a sulcate or excavate elytral declivity with marginal spines, but have quite a different antenna. Furthermore, all known Dryocoetini have emarginate (occasionally sinuate) eyes, although in Cryphalini, for example, in some genera we find both entire and emarginate eyes (Wood, 1986). The epicranium of the new species, forming a triangular process with the apex oriented posteriorly and with a longitudinal dark suture, is not unique to *Cylindrobrotus*, but resembles that of the recent species, *Dryocoetes autographus* (Ratzeburg, 1837) (Dryocoetini). The recent species *Dryocoetes hectographus* Reitter, 1913 (Dryocoetini) and *Xyleborinus saxesenii* (Ratzeburg, 1837) [Xyleborini, derived from Dryocoetini (Normark *et al.*, 1999; Jordal *et al.*, 2000)] have a mesosternum with thickened inner sclerotization somewhat similar in shape to that of *Cylindrobrotus gen.n.* In the tribe Ipini [*Ips typographus* (Linnaeus, 1758), *Ips sexdentatus* (Börner, 1776), *Orthotomicus laricis* (Fabricius, 1796), *Orthotomicus proximus* (Eichhoff, 1867)], the shape of this plate is rather different, with divergent triangular wedges at the edge of each mesocoxa (absent in Dryocoetini and Xyleborini). *Cylindrobrotus gen.n.* has a general appearance similar to some Dryocoetini, and the Dryocoetini and *Cylindrobrotini trib.n.* share some taxonomically important character states

Table 1. Comparison of *Cylindrobrotini trib.n.* and Dryocoetini.

Character	Dryocoetini	<i>Cylindrobrotini trib.n.</i>
Eye	Distinctly emarginate to divided	Entire
Antennal funicle	(2)-4-5-(6) segmented	5-segmented
Antennal club	Obliquely truncate to strongly flattened	Obliquely truncate and somewhat dorsoventrally compressed
Mentum	Small unlobed	Large with projecting anterior lobes
Pronotum	Arched from base or not; if anteriorly declivous then declivity usually involving more than anterior half	Not declivous anteriorly
Pronotum	Armed or not; if armed then asperities small, usually abundant	Unarmed
Prohypomera	Normally concave at least posteriorly	Convex
Procoxae	Contiguous to narrowly separated	Contiguous
Protibia	Lateral margin usually with 4 to several socketed teeth	4 socketed teeth
Metacoxae	Widely separated	Broadly contiguous
Elytral declivity	Usually convex, sometimes shallowly sulcate or flattened, sometimes with small granules	Convex, unarmed
Vestiture	Hair-like, without scales or deeply divided setae	Hair-like

(Table 1). However, because of fundamental differences of *Cylindrobrotini* from all other known scolytine tribes, they are probably not close relatives.

Several features of the new fossil species, especially of the mouthparts, including the rather large mentum ('prementum' or 'submentum') with large projecting anterolateral lobes, and the widely contiguous metacoxae are unique in the Curculionoidea. Broadly contiguous metacoxae have not been recorded in any weevil (if contiguous, only at the anterior tip). The exposed protrochantin is recorded among weevils only in Attelabidae, Rhynchitinae, a few Belinae and Nemonychidae, but never in the 'higher' families (Caridae, Brentidae and Curculionidae) and never previously in Scolytinae (R. Oberprieler, personal communication). The prothorax of many bark beetles has a very thin cuticle extending externally from the procoxae and covering the trochantins. This thin covering could be reduced and lost easily during the evolution of this lineage. Open mesocoxal cavities occur in weevils only in Nemonychinae (*Nemonyx* Redtenbacher, 1845), some Belidae (Belinae) and most Attelabidae: Rhynchitinae, but never in Caridae, Brentidae and Curculionidae (with the sole exception of the larviform male of *Ozopemon* Hagedorn, 1910 (Dryocoetini) (R. Oberprieler, personal communication)). However, this condition of mesocoxal cavities could be a consequence of reduction of outer sclerites. The shape of the pronotum, with its wholly convex sides, is rare within the Scolytinae. Based on these and other characters summarized in Table 1, we consider the specimen sufficiently different for a new tribe to be erected.

In making this comparison we studied all extant tribes of Scolytinae, including the recently described tribe Amphiscolytini (Mandelstam & Beaver, 2003) and nearly three-quarters (143/215) of modern genera considered valid by Wood (1986). Moreover, the new fossil species has no resemblance to any extinct species described from either Baltic or Dominican amber. All Baltic amber species can be assigned readily to Recent tribes and even to extant genera (Schedl, 1947; Wood, 1986). The somewhat younger but more species-rich Dominican amber includes several palaeoendemic genera named by Bright & Poinar (1994): *Protosinus*, *Paleosinus*, *Dryomites*, *Micracites* and *Corthylites*, all of which were assigned to extant tribes and do not resemble the fossil species considered here. Other fossil Scolytidae (some *Scolytus* Geoffroy, 1762 from the Miocene; *Xylechinus* Chapuis, 1869; *Hylesinus* Fabricius, 1801 (including *Adipoccephalus* Wickham, 1916) from the Miocene and Oligocene) partly described or reviewed recently by Petrov & Zherikhin (2000, 2004) clearly are species from extant genera.

One fossil considered to be a bark beetle, *Cryphalites rugosissimus* Cockerell, 1917 from Burmese amber, was known previously from the Lower Cretaceous. Subsequently this fossil was listed as belonging to Colydiidae (Ross & York, 2000); however, this position of this fossil is tentative and we therefore follow Cockerell (1917) in considering it as a possible Scolytinae. Moreover, the assignment of Cockerell's species to the tribe Cryphalini is rather

doubtful, because all extant members of this tribe have the head concealed under the pronotum, but the head evidently is visible from above in *Cryphalites*. According to the description and Cockerell's original drawing, the legs of the fossil *Cryphalites* resemble those of some scolytines, but do not serve to identify the tribe clearly. Many tibial spines can be found both in Cryphalini and in *Xyleborus dolosus* Blandford, 1896 and close relatives (Xyleborini). Both Dryocoetini and *Cylindrobrotus* **gen.n.** have more widely placed tibial spines compared with *Cryphalites rugosissimus*. Importantly, *Cylindrobrotus*, like many modern Dryocoetini, but unlike *Cryphalites*, possesses only four and not seven protibial spines. The tibiae in *Cryphalites* are broad and strongly flattened, whereas in *Cylindrobrotus* the tibiae are of normal width, i.e. rather narrow. The tarsi in *Cryphalites* are simple as in *Cylindrobrotus*, but the shape of the tarsomeres is different, and the long flattened tarsal hairs that are a feature of *Cryphalites* are absent in *Cylindrobrotus*. The rough sculpture of the pronotum and elytra in *Cryphalites rugosissimus* is not seen in *Cylindrobrotus*, which has the pronotum and elytral declivity completely unarmed. Antennae of both taxa cannot be compared, as they are absent in *Cryphalites*. The combination of features suggests a clear separation and lack of close relationship between *Cryphalites* and *Cylindrobrotus*, thus demonstrating some differentiation of Scolytinae in the Cretaceous. Very recently, one more species, clearly belonging to Scolytinae and even assigned to an extant genus, *Microborus inertus*, was described from Cretaceous Burmese amber (Cognato & Grimaldi, 2009). Although antennomere 1 (scape) is not visible in this fossil, and the antennae were only suspected to be geniculate, the authors put the fossil specimen into subtribe Ctenophorina (Coleoptera: Curculionidae: Scolytinae) based on the habitus. Differences between *Microborus inertus* and *Cylindrobrotus* are essentially the same as those between the extant tribes Ctenophorini and most Dryocoetini. The most important features are: (i) an obliquely truncate club in *Cylindrobrotus* compared with a strongly flattened club in *Microborus*; and (ii) the rounded sides of the pronotum in *Cylindrobrotus* compared with acutely marginate sides for most of the pronotal length in *Microborus*.

Only two segments of the labial palpi of *Cylindrobrotus* are visible in the amber piece examined, but they look like those in other bark beetles. Scolytines, and almost all Curculionoidea, are known to have 3-segmented labial palpi (although some Platypodinae have 2-segmented palpi). The basal palpomeres in this fossil species may be concealed or perhaps fused to the ligula. The curiously projecting mandibles could be the result of agonistic movements of the beetle before its death in resin. It is difficult to assign the fossil examined to either sex. The horseshoe-shaped sclerite visible through the translucent integument of the body is very similar to the anal sclerite of males in many Cucujiformian groups (frequently homologized with tergite VIII). However, in Scolytinae this tergite is not retracted in males and represents the pygidium. Furthermore, the similar sclerite with a comparatively heavy sclerotization is retracted in females and forms part of the genital capsule.

Cylindrobrotus **gen.n.**

Type species. Cylindrobrotus pectinatus **sp.n.**

Notes. This new genus is represented by the only species, and therefore the description of it overlaps with the description of the species ('descriptio generica specifica').

Etymology. The name of this new genus is formed from the Greek 'Cylindros' (cylinder) and 'Brotos' (deceased). The gender is masculine.

Cylindrobrotus pectinatus **gen. et sp.n.** (Figs 1–3)

Specimen examined. Holotype: '956', temporarily deposited in the Laboratoire d'Entomologie, Muséum National d'Histoire Naturelle, Paris, France, awaiting the creation of a national natural history museum in Lebanon. The beetle with a rather clear integument is included in a small elongate piece amber together with many small pieces of organic matter of various kinds; the right antenna, except scape, both pro- and metatarsi and left metatibia, are missing; head and anterior legs are detached.

Type locality and horizon. Early Cretaceous, Hammana/Mdeyrij, Caza Baabda, Mouhafazit Jabal Loubnan (Mont Lebanon district), Lebanon.

Description of holotype. Length 2.0, width 0.7, height 0.7 mm. Elongate, rather convex both dorsally and ventrally, subcylindrical; dark chestnut brown with somewhat lighter appendages and partly visible inner sclerites owing to translucent integument; mostly shining; dorsum with only a few long and very fine suberect hairs on anterior part of head, and throughout pronotum and elytra; underside with slightly denser hairs very similar to those on dorsum, and also some much shorter, subrecumbent, fine hairs located on anterior part of head and sclerites of head. Elytra with sparse interstitial hairs originating from granules and slightly longer than the width of the interstriae; hairs not becoming denser and longer towards the apex; no tuft of hairs at the elytral apex.

Head without clear punctures, but with smoothed outlines of very coarse circular microreticulation looking like granulation, which could replace punctation. Pronotum with shallow punctures about as large as eye facets in diameter, interspaces smooth, about twice as broad as puncture diameter. Elytra with shallow and not quite regular punctures about 3× as large as those on pronotum (somewhat smaller at base and becoming larger apically), arranged in slightly irregular rows (apparently no fewer than 10 rows on each elytron), interspaces between punctures one-quarter to one-third of puncture diameter, distance between them within rows slighter narrower than that between rows (in some cases up to a puncture diameter), rows of punctures slightly depressed and integument between them smoothed. Prosternum at sides with punctation and

sculpture as on dorsal surface of segment, but punctation in middle becoming obsolete and sculpture rather alutaceous. Mesosternum with very shallow and not quite regular punctures intermediate in size between those on pronotum and on elytra, interspaces between them one-third to two-thirds of puncture diameter, smoothly alutaceous to smoothly microreticulate. Metasternum without clear punctation and rather smooth. Abdominal ventrites apparently without clear punctures and somewhat alutaceous.

Head subtrapezoid, about as long as wide at base, rather convex dorsally and ventrally, its anterior edge widely subtransverse and seemingly steeply sloping, and bearing a dense row of short hairs, without trace of antennal grooves; moderately coarsely faceted eyes dorsally rather narrow and elongate, but quite wide on underside with diameter (width) about two-fifths as great as distance between eyes; antennal insertions located on underside in front of eyes; vertical foramen dorsally with flat process ending in angular apex extending somewhat above foramen (process has inner sclerotized ridge along middle and lateral arms disposed externally); gular sutures conjoined from base for two-thirds of length, and divergent anteriorly. Mentum ('prementum' or 'submentum') truncate at base, widened anteriorly before widely rounded anterior angles, its anterior edge rather deeply excised, base of excision transverse. Maxillae with wide and moderately short exposed apex of one lobe and two short and thick terminal palpomeres; its ultimate palpomere about twice as long as wide, slightly narrowing to transverse apex. Ligula with somewhat extended lateral parts and medially closely spaced labial palpi with two visible palpomeres: penultimate palpomere strongly transverse, asymmetric and strongly enlarged externally, about twice as wide anteriorly as long; ultimate palpomere somewhat transverse, subsymmetrical, about one-half as long as penultimate palpomere and subtruncate at apex.

Mandibles very stout and widely triangular, with row of very short and slightly visible microtrichia, rather exposed before anterior edge of frons; right mandible with simple apex and two subapical teeth along inner edge; left mandible with bidentate apex somewhat declined ventrally and with one subapical tooth. Antennae apparently 9-segmented and rather short and about as long as width of anterior edge of frons; funicle 5-segmented; scape rather narrow and somewhat longer than remaining antennomeres combined; antennomere 2 (first segment of funicle) about as long as wide at apex, strongly enlarged apically from narrow base; antennomere 3 subtriangular, widened apically, about one-half as long as antennomere 2 and about as long as antennomeres 4–6 combined; antennomeres 4–6 strongly transverse and gradually widened from apex of antennomere 3; club strongly asymmetrical, obliquely truncate and partly dorsoventrally compressed, two apical antennomeres strongly reduced and apparently partly retracted into antennomere 7, which is largest in club.

Prothorax strongly built and without intercoxal process, its underside nearly 5× shorter than dorsum; pronotum somewhat longer than wide, about 1.5× as long as epicranium,

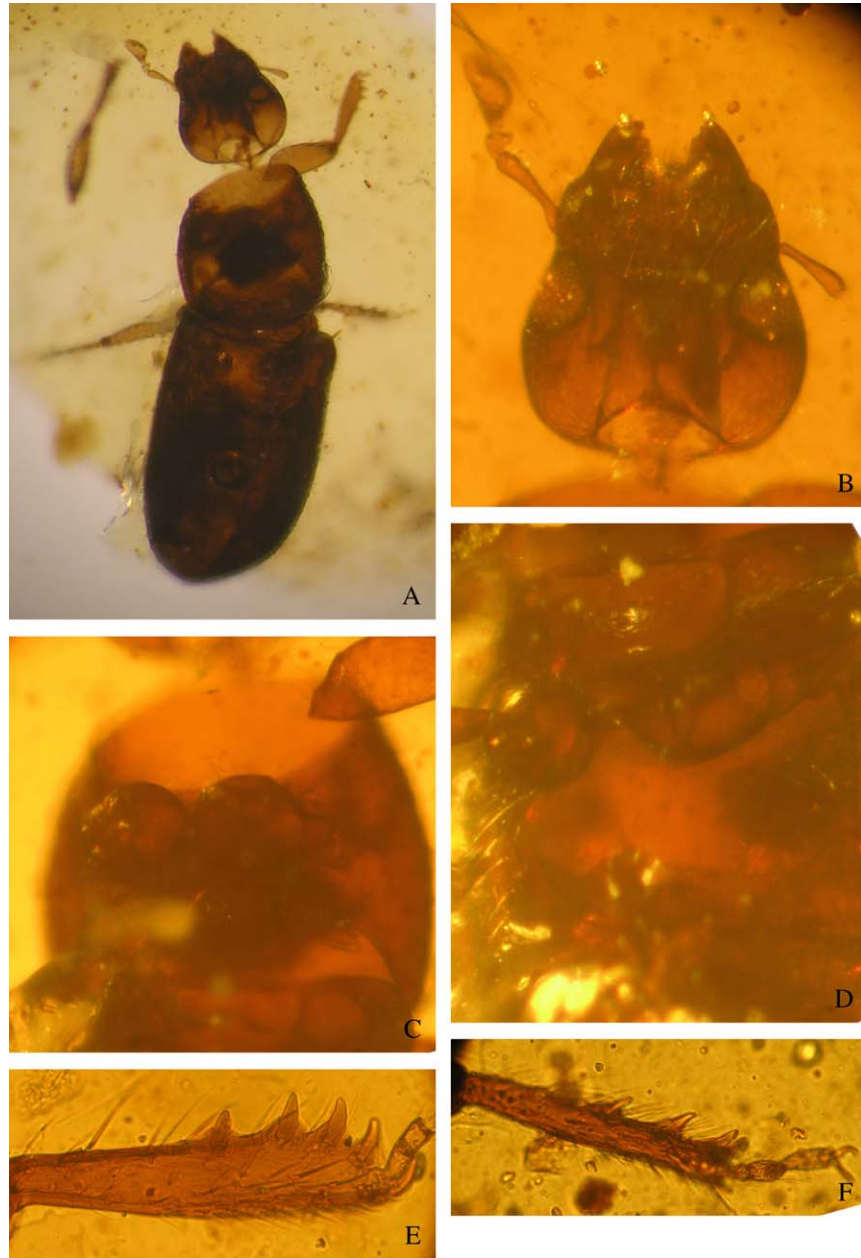


Fig. 1. *Cylindrobrotus pectinatus* gen. et sp.n. (A) Body, dorsal view, length 2.0 mm; (B) head, ventral view, length 0.45 mm; (C) prosternum, ventral view, length 4.2 mm; (D) pterothorax, ventral view, length 0.54 mm; (E) protibia, dorsal view, length 0.28 mm; and (F) mesotibia and tarsus, dorsal view, length 0.27 mm.

rather vaulted at disk and steeply sloping laterally, with strongly convex anterior and slightly convex posterior edges, without raised margins and without apical constriction; sides without carina and gently arcuate; prosternum about two-fifths as long as epicranium, most of its length occupied by coxae and only narrow strips separating these from anterior and posterior margins. Procoxal cavities contiguous, somewhat transverse and narrowing externally. Anterior legs with exposed trochantin (because of reduced

and translucent outer prohypomera) and strongly projecting globular coxa. Scutellum rather large, flat, subtriangular (probably fused with prescutum). Elytra strongly convex, about 1.7× as long as wide, nearly 1.8× as long as pronotum, with slightly raised shoulders, arcuately narrowing to subacute and gently sloping apices, adsutural lines expressed along total length of suture and subparallel, rather steeply sloping at sides and somewhat curved ventrally, without traceable epipleura; elytral base simple

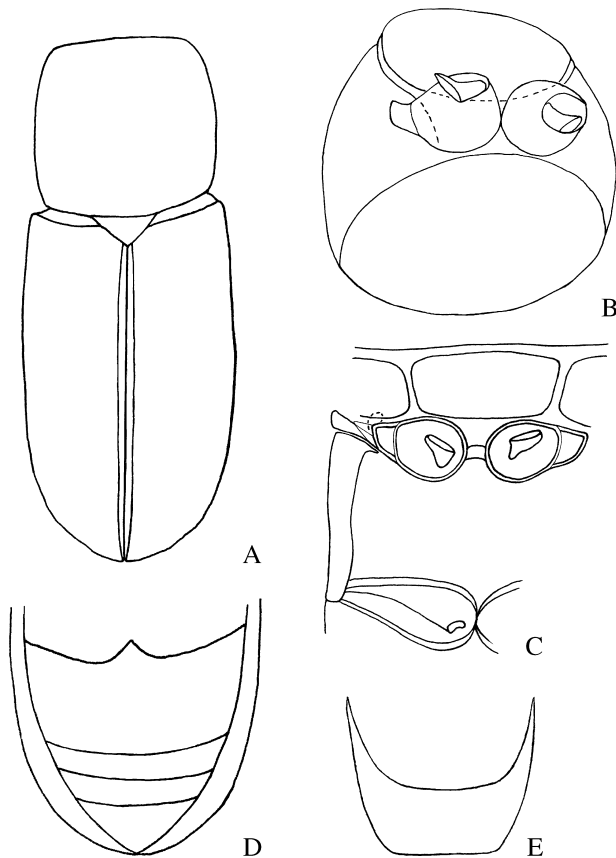


Fig. 2. *Cyllindrobrotus pectinatus* gen. et sp.n. (A) Pronotum, scutellum and elytra, dorsal view, length 2.0 mm; (B) prosternum, ventral view, length 0.46 mm; (C) meso- and metasterna, ventral view, length 0.54 mm; (D) abdomen, ventral view, length 0.52 mm; (E) inner sclerite at abdominal apex, dorsal view, length 0.1 mm.

(neither crenulated nor elevated); declivity rather steep, convex, only slightly flattened, occupying only posterior one-quarter of elytra; elytral apices conjointly arcuately narrowing, and suture at the declivity neither elevated nor emarginated. Mesosternum slightly longer than prosternum in middle, not excavate in relation to pro- and metasternal planes and without distinct sutures, although mesepimeron partly separated and reaching outer edge of mesocoxal cavity; subquadrangular sternal sclerite clearly visible (formed by thickening, probably homologous to mesepisternal sutures). Mesocoxae transverse and slightly oblique, somewhat shorter than procoxae, with probably partly exposed trochantin and lateral part of coxa apparently showing through integument, separated by about width of antennal club or half length of mesocoxa. Metasternum rather vaulted, about twice as long as mesosternum; its anterior edge between coxae somewhat convex, without both submesocoxal lines and paracoxal sutures (lines). Metepisternum somewhat widened anteriorly and with projecting inner anterior angle almost reaching outer edge of mesocoxal cavity and with distal end meeting with outer edge of metacoxal cavity. Metacoxae transverse and contiguous,

not oblique, about as long as procoxae. Submetasternal lines not expressed.

Abdomen with four ventrites [because of fusion of first two ventrites (corresponding to abdominal sternites 1–3 and 4) or tsuture between first and second ventrites invisible owing to transparency of the fossil]; ventrite 1 markedly longer than ventrites 2–4 combined; hypopygidium slightly longer than each of ventrites 2 and 3. Sclerite of genital capsule not exposed externally, but visible through external integument, horseshoe-shaped.

Legs well developed, rather narrow and very long. All trochanters rather short, clearly of ‘normal type’ (sensu Crowson, 1955) and with wide apex. All tibiae strongly dorsoventrally compressed and with some rather long setae mostly along outer edge. Protibia widened to rounded apex, in distal half with four socketed denticles, subequal in size and with coarse setae nearly $2.5\times$ as long as denticle, the denticles somewhat thicker and shorter than terminal spur and separated from each other by different distances, with denser and shorter setae mostly along inner edge and at apex, in addition to long ones along outer edge; proximal part of protibia without teeth. Mesotibia with four denticles without clear socket in distal half, most proximal in mid-tibia, two most distal ones close together at apex; with denser and shorter setae mostly along inner edge and at apex in addition to long setae along outer edge. Metatibia very similar to mesotibia, but slightly more dilated. Femora as usual, with gently convex anterior and posterior edges, $1.5\text{--}2.0\times$ as wide as tibiae. Tarsi with five simple segments. Mesotarsomeres one and three subcylindrical and subequal in length, each about twice as long as subcylindrical mesotarsomere 2 and nearly $3\times$ as long as subcylindrical mesotarsomere 4; mesotarsomere 5 longest, thickened apically and about $1.5\times$ as long as antennomeres 1 (scape); claws somewhat dentate at base.

Etymology. The epithet of this new species refers to its dentate tibia (from Latin ‘pecten’ – comb).

Discussion

Wood (1986) lists the states of some characters that he considers ‘primitive’ or ‘specialized’. The authors have compared these with the characters of *Cyllindrobrotus* gen.n. as far as is possible (Table 2).

Comments

An elongate or subtriangular scape is a plesiomorphic character state within the Curculionidae sensu lato, although apomorphic for the Curculionoidea in general (e.g. Morimoto, 1962, etc.). A flattened or obliquely truncate antennal club occurs in several groups, including some Cossoninae. The prohypomera are quite variable across the Curculionoidea, and seem to be related to their form of locomotion across or within the substrate.

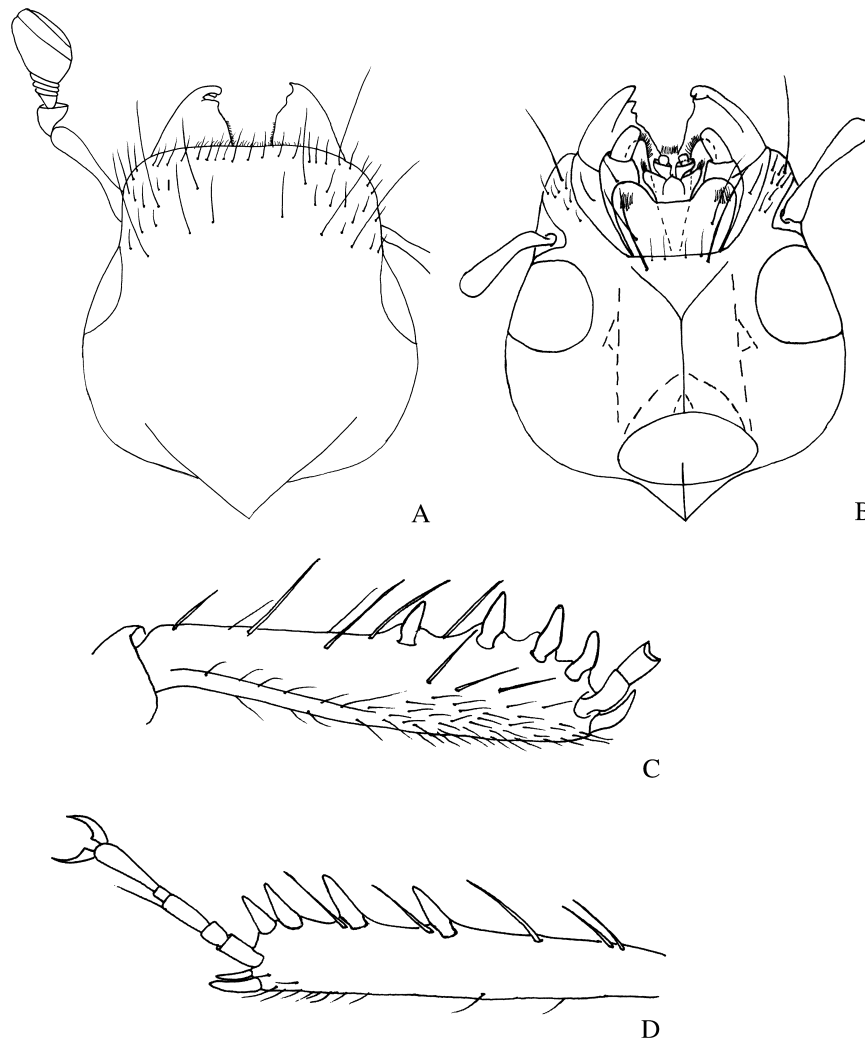


Fig. 3. *Cylindrobrotus pectinatus* gen. et sp.n. (A) head, dorsal view, length 0.45 mm; (B) idem, ventral view, length 0.45 mm; (C) protibia, dorsal view, length 0.28 mm; (D) mesotibia and tarsus, dorsal view, length 0.27 mm.

If Wood's (1986) interpretation of the polarization of these characters is accepted, considerable evolution must have occurred within the Scolytinae before the appearance in the early Lower Cretaceous of this fossil. Wood (1986) placed the origin of the subfamily in the Upper or Middle Jurassic from 'Eobelid-like' ancestors with a short rostrum, and notes that scolytine galleries have been found in Middle and Late Cretaceous 'conifer' bark. (Amber with Scolytinae is known only from the Cenozoic and originated apparently from resin of Pinaceae, whereas the Cretaceous amber with the Scolytine derives from trees of the Araucariaceae.) The superfamily Curculionoidea could have appeared during the Upper Triassic (Kirejtshuk, 1992; Ponomarenko *et al.*, 2008), if the family Obrieniidae is present there. However, Gratshev & Zherikhin (2003) had doubts about the attribution of the latter family to the superfamily Curculionoidea and even the suborder Polyphaga, and Kuschel (2003) also excluded Obrieniidae from the Curculionoidea. Archaic

groups of this superfamily have been recorded mostly from the Upper Jurassic (Arnoldi, 1977; Zherikhin & Gratshev, 1993; Gratshev & Zherikhin, 2003, etc.); however, the archaic members of Curculionidae (except Scolytinae) appear in the fossil record only in the late Lower Cretaceous (Zherikhin, 1993).

Compared with the trapping in exuded resin from modern Pinaceae, there are usually markedly fewer bark beetles in amber (fossil resin) of all origins, even in the Cenozoic. Perhaps the significance of this group has been increasing during the Recent epoch. Nevertheless, many species of Scolytinae have been described from Upper Eocene Baltic and Lower Miocene Dominican amber (Schedl, 1947; Bright & Poinar, 1994). However, only two representatives of this group are recorded from Lower Cretaceous Burmese amber (Cockerell, 1917; Cognato & Grimaldi, 2009), Lower Oligocene Colti amber (Protescu, 1937) and Upper Oligocene Bitterfelder amber (Barthel & Hetzer, 1882). Moreover,

Table 2. Primitive and specialized characters in *Cylindrobrotus* gen.n. (according to the interpretation of Wood, 1986).

'Primitive'	'Specialized'	<i>Cylindrobrotus</i> gen.n.
Head more or less truncate on its posterior face	Dorsomedian area prolonged caudad	Specialized
Frons convex in both sexes	Male or female frons variously impressed	Not known
Eye oval, entire, finely faceted	Eye elongate, emarginate or divided, coarsely faceted	Primitive
Antennal scape short relative to 'pedicel'	Scape elongate or subtriangular	Specialized
Antennal funicle 7-segmented	Funicular segments reduced in number	Specialized
Antennal club conical with three transverse sutures	Club flattened or obliquely truncate with or without sutures	Specialized
Procoxae widely separated	Procoxae contiguous	Specialized
Prohypomera concave with lateral edges acutely costate	Prohypomera convex with lateral edge unmarked	Specialized
Pronotum longitudinally straight in dorsal profile, unarmed	Pronotum strongly arched and armed by crenulations or asperities	Primitive
Basal margins of elytra costate	Basal margins either procurved and crenulate, or transversely straight and longitudinally rounded	Specialized
Male eighth tergum visible and pubescent	Male eighth tergum hidden	Not known
Tibiae with spines	Tibiae with socketed teeth	Specialized

galleries attributed to Scolytinae have been recorded from Lower Cretaceous sites (Brongniart, 1877; Jarzembowski, 1990; Zherikhin & Gratshev, 1995; Grimaldi & Engel, 2005), the Upper Oligocene Novograd Bobrzansky deposit (Karpinski, 1962), the Lower-Middle Miocene Shanwang deposit (Guo, 1991), and also from the Quaternary period (e.g. Claus, 1958; Scudder, 1890). Walker (1938) described some engravings in petrified Triassic wood from Arizona as ichnotaxa of Scolytinae, but later researchers raised serious doubts about this attribution (Wood, 1982), and even about the more reasonable supposition that these holes in tree trunks were made by Archostemata, and not by Polyphaga at all (e.g. Crowson, 1975). The Lower Cretaceous bark beetle described by Cognato & Grimaldi (2009) is very different from *Cylindrobrotus* gen.n. (see above), suggesting that the Cretaceous fauna of the subfamily was already quite diverse at this period, although the representation of the group is markedly weaker than in the Cenozoic.

The tribe *Cylindrobrotini* trib.n. is characterized by some unique, and also by some initial (plesiomorphic) but mostly rather advanced (apomorphic), characters (see above). *Cryphalites rugosissimus* Cockerell, 1917 from Burmese amber may also belong to the Scolytine, but not to the Hylesinine lineage. Importantly, *Microborus inertus* recently described from Burmese amber (Cognato & Grimaldi, 2009) also clearly belongs to the Scolytine lineage. Thus, the time of origin of this group could be lowered to the Upper Jurassic or at least to the Rubicon between the Jurassic and Cretaceous. However, only in the Cenozoic did the bark and ambrosia beetles reach a considerable representation in forest assemblages and become a relatively common component in amber and lacustrine sites.

Scolytinae have been described also from Cenozoic outcrops. They are known from the Lower Oligocene Florissant shales, but, like many other beetles, are badly preserved, lacking the antennae important to clarify their taxonomic

position. However, most of these can be assigned to modern tribes, and many were assigned in original descriptions even to modern genera. *Adipocephalus hydropicus* Wickham, 1916 from the Florissant beds, for example, was recently transferred to the genus *Hylesinus* Fabricius, 1801 (Petrov & Zherikhin, 2004). One more species referred to the same genus (*Hylesinus extractus* Scudder, 1893) was mentioned for Florissant by Wickham (1911). *Pityophthoridea diluvialis* Wickham, 1916 may represent a genus either from Cryphalini or from Corthylini. One species, *Phloeotribus zimmermani* Wickham, 1916, was assigned on the basis of elytral microsculpture to an extant genus; however, its placement in the Hylesinine and not the Scolytine lineage seems to be correct. Heer's (1856) figure and description of *Hylesinus facilis* from the Lower Oligocene Aix are insufficient to place the species in a genus; however, it also probably belongs to the Hylesinine lineage. The bark and ambrosia beetles of Baltic and Dominican amber are extremely diverse. Whereas in Baltic amber representatives of Hylasini, Tomicini, Polygraphini, Phloeosinini (all of the Hylesinine lineage) were most rich in species (Schedl, 1947), Dominican amber demonstrated many species of the most specialized genera of the extant tribes Corthylini (*Pityophthorus*, *Gnathotrichus*, *Microcorthylus*, *Corthylites*) and Cryphalini (*Hypothenemus*) (Bright & Poinar, 1994) in addition to many Hylesinine beetles. According to recent studies, *Taphramites gnathotrichus* Schedl, 1947 (Dryocoetini) is the most abundant species in Baltic amber (as represented in the private collection of Dr. A. D. Krylov, Kaliningrad). Importantly, the tribe Dryocoetini, which perhaps has some relation to the newly described *Cylindrobrotus*, is represented in all fossil resources rich in Scolytinae, including Dominican amber (*Dryomites*) and Baltic amber (*Taphrorynchus*, *Taphramites*) and in fact may be very old.

Many different interpretations have been published on the phylogenetic relationships of the subfamily Scolytinae during

the last 30 years, but further study is still needed. One extreme regards this group, together with the subfamily Platypodinae, as originating at the base of the lineage that gave rise to the Brentidae, Attelabidae and Curculionidae as separate families (e.g. Morimoto, 1962; Wood, 1982). Zherikhin & Egorov (1990) concluded that Scolytinae and Platypodinae could be distantly related to the rest of the Curculionidae (with some doubts), but were unlikely to have a common ancestry with the subfamily Cossoninae. A very similar position is maintained by Lyal (1995), who considered that Scolytinae and Platypodinae cannot be derived from Curculionidae, because Curculionidae *sensu stricto* lack 'pregular sutures'.

A more common placement of Scolytinae and Platypodinae was proposed by Erichson (1842), and later by Crowson (1955), as more or less derivative taxa within the family Curculionidae, and these groups have fairly frequently been placed far from the base of diversification (e.g. May, 1993; Kuschel, 1995; Marvaldi *et al.*, 2002). Other researchers consider Scolytinae as a subfamily of Curculionidae, regarding Platypodidae as a separate family because of an earlier separation from a common ancestor (e.g. Thomson, 1992; Lyal & King, 1996; Alonso-Zarazaga & Lyal, 1999).

We do not discuss the relationship of the Platypodines to the Scolytines and other curculionids here. The early appearance of Scolytinae in the fossil record before other Curculionidae (see above) may be used as evidence for or against the previous interpretations. Of course, the inhabitants of tree trunks are much more likely to be found in fossil resin, but Curculionidae *sensu stricto* (without Scolytinae) have not been found in any other types of deposit. The presence of the Lower Cretaceous Scolytinae in Burmese and Lebanese amber supports an early origin of this group rather than other interpretations. The fossil evidence thus suggests that the Scolytinae evolved as a definite and recognizable group at the beginning of the basal diversification of the Curculionoidea or at least the Curculionidae. This tends to support those authors (e.g. Wood, 1982, 1986; Morimoto & Kojima, 2003) who suggest that the Scolytidae should be considered as a separate family from the Curculionidae. Because the first true weevils seem to have been quite good flyers and had considerable chances of appearing as fossils, negative evidence (the absence of other Curculionid fossils earlier than in the upper layers of the Lower Cretaceous, and the presence of much evidence of the existence of bark beetles at the same time) is also quite substantial, but cannot be considered as a conclusive proof. In our opinion, all relevant evidence should be taken into account. Further studies are clearly necessary, but we note that whether the Scolytinae are considered to be a family or subfamily remains a subjective matter open to discussion, but not to proof.

Acknowledgements

The authors thank the reviewers, particularly C.H.C. Lyal, A.I. Cognato and R. Oberprieler, and also the editors, P. Cranston and F.-T. Krell, for their constructive criticisms and recommendations. The authors also greatly appreciate the assistance

in various ways of M.V.L. Barclay and R.T. Thompson in the Natural History Museum, London. B.A. Korotyaev and N.N. Yunakov from the Zoological Institute of the Russian Academy of Sciences gave valuable advice and provided the authors with many references and reprints on the systematics of Curculionoidea. E. Anton (Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum in Jena) readily discussed the position of the specimen here described. The senior author and D.A. have a pleasant duty to express their thanks to the administration of the Museum National d'Histoire Naturelle, which permitted them to work in the museum for three months in 2006. This study was supported by the Programme of the Presidium of the Russian Academy of Sciences 'Origin and Evolution of Biosphere' and by grants from the Russian Foundation of Basic Research (070400540a and 07-04-92105-GFEN_a).

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Accepted 15 May 2008