Ceracyclini, tribe nov. of Passalidae Aulacocyclinae for Cylindrocaulus Fairmaire and †Ceracyclus, gen. nov., with two new species from the Cenomanian Burmese amber (Coleoptera, Scarabaeoidea)

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Abstract

The Ceracyclini tribe nov., in the Passalidae Leach, Aulacocyclinae Kaup, is described to accommodate the genus Cylindrocaulus Fairmaire (Continental Asia, Japan) and two sympatric fossil species of the Cretaceous amber from the Hukawng Valley, Myanmar, for which the genus †Ceracyclus g. nov. is created. These species described here are closely related one to each other, but can be easily separated, especially by sizes: C. lotus sp. nov. (9-9.5 mm) and C. jirouxi sp. nov. (4 mm). Homologies of some morphological characters are highly informative and show that Cylindrocaulus and †Ceracyclus g. nov. could be sister groups. The discovery of true Passalidae from the same amber deposit than the possibly sister family †Passalopalpidae Boucher & Bai, suggests new perspectives and hypotheses on the common distributional past, diversity and biology of both taxa.
Résumé

La tribu nouvelle des Ceracyclini est créée dans les Passalidae Leach, Aulacocyclinae Kaup, pour le genre *Cylindrocaulus* Fairmaire (Asie continentale, Japon) et pour deux espèces fossiles sympatriques, regroupées dans †*Ceracyclus* g. nov., de l’ambre Crétacé de Birmanie, vallée de Hukawng. Ces deux espèces décrites ici sont très voisines, mais peuvent être séparées en premier lieu par les dimensions : *C. lotus* n. sp. (9-9,5 mm) et *C. jirouxi* n. sp. (4 mm). Les homologies de plusieurs caractères morphologiques sont très informatives et montrent que *Cylindrocaulus* et †*Ceracyclus* g. nov. seraient groupes frères. La découverte de vrais Passalidae dans le même dépôt d’ambre que le possible groupe frère †Passalopalpidae Boucher & Bai, suggère de nouvelles perspectives et hypothèses sur la distribution passée, la diversité et la biologie des deux taxons.

Keywords

Amber fossil, Cretaceous, Myanmar, Passalidae, Passalopalpidae.

Introduction

Since the discovery of the family †Passalopalpidae Boucher & Bai, with one species, *Passalopalpus cheni* Boucher, Bai & Zhang 2016, we follow a study of taxa from the amber mine in northern Myanmar (earliest Cenomanian, near 100 Ma). A number of additional samples of the passalopalpid species were examined, but we found also some true Passalidae Leach. However, the first picture of a passalid from Burmese amber was given by Xia et al. (2015: 108 top left), on a specimen identified « Passalidae sp. ». This specimen is a †*Ceracyclus lotus*, g. nov., sp. nov., here described. With respect to a second species found, †*C. jirouxi* sp. nov., it seems that it has never been seen before. Otherwise, two other specimens, also identified Passalidae sp. by Xia et al. in their book (2015: 107 top, 108 bottom right), are in fact *P. cheni*, as stated Boucher et al. (2016).

The two new fossils *Ceracyclus* represent the first passalids known from the Cretaceous period. Other confirmed fossils in the family are much more recent, from Continental China and North America (see Boucher 2006, Chap. I). The species of *Ceracyclus* g. nov. belong to the subfamily Aulacocyclinae Kaup and are closely allied to the genus *Cylindrocaulus* Fairmaire 1880, from Continental Asia and Japan. Since the morpho-anatomic and phylogenetic studies by Boucher (2006), interesting issues on Aulacocyclinae modified some previous results within the tree of the subfamily (Hosoya & Araya 2008, Hosoya 2008 *ms*). The discovery of the two fossils of
the Burmese amber is an opportunity for confirming the complementary hypothesis of these authors. Consequently, both species belong to a typically passaloid supra-generic group, sensu Boucher et al. (2016), precisely the Aulacocyclinae, but not to the Aulacocylini Kaup nor the Ceracupini Boucher. The tribe Ceracyclini tribe nov., is thus created to include Ceracyclus g. nov. and Cylindrocaulus. Major characters give strong assumption that both genera are sister groups, or from the same cline. This monophyletic tribe appears to be sister group of the remaining clade of Aulacocyclinae. The phylogeny, distribution, biogeography and paleobiogeography of Aulacocyclinae, sensu novo, is revealed as more coherent among the late Laurasia and the present Eastern Asia.

The systematic interpretation of the fossils Ceracyclus g. nov. indicates that first passalids were probably not only Gondwanian. They were diversified in Laurasia. However, we don’t know if the vicariance of the Aulacocyclinae and Passalinae occurred on each of the super-continents, as previously supposed. On the other hand, we know that Passalidae were present at -100 Ma, whereas an estimated age for the family, or for the first passaloids taxa, was moved back from basal Cretaceous (-130 Ma; Krell 2000) to upper Jurassic (-145/150 Ma; Boucher 2006, Chap. I; Krell 2006).

Thanks to Ceracyclus, it is confirmed that Cylindrocaulus is an old group, as presumed Gravely (1914), followed by Boucher & Reyes-Castillo (1996). Finally, Cylindrocaulus stayed distributed, up to day, near from where it is native. Moreover, there is no doubt that Ceracyclus and the passalopalpid Passalopalpus Boucher & Bai, 2016 were sympatric in some forests of Laurasia, in any case at the present point of the amber mine, northern Myanmar.

**Materials and methods**

Specimens come from amber deposits, the « burmite » inclusions of Hukawng Valley, Kachin State, Myanmar (26°21’33.41”N - 96°43’11.88”E). The age is ca. 99 Ma, earliest Cenomanian, following U-Pb dating of zircons from the volcaniclastic matrix of the amber (Shi et al. 2012). Other useful details on the geology, age and biological diversity of the deposit can be seen in Zherikhin & Ross (2000), Grimaldi et al. (2002), Cruickshank & Ko (2003), Ross et al. (2010), Xia et al. (2015).

The condition of the amber, the used optical systems and methods followed for observations and photographies are quite similar to the ones exposed in Boucher et al. (2016), who examined the Passalopalpidae of same origin. Scanning and performed scanning of two specimens were made at the Institute of Zoology, Chinese Academy of Sciences, Beijing.
Observations of samples are made on the whole body and appendages. Among external sclerites only mandibles were partially observed with respect to their basal part, as in no specimen the appendages were opened. It was also not possible to examine complete hindwings and to determine sexes. Otherwise, most of characters are remarkably accessible on these fossils, after adapted preparation of the nugget of amber and the use of powerful cold light source.

The followed morphological terminology is that of Boucher (2006) and Boucher et al. (2016). Other current terminology is found in Gravely (1914, 1918). The total length of specimens is taken from the anterior border of evaginated labrum to the apex of elytra.

Results
Systematic paleontology
Order Coleoptera Linnaeus
Scarabaeoidea Latreille, Passalidae Leach, Aulacocyclinae Kaup

Ceracyclini Boucher & Bai tribe nov.

_Type genus._ – †_Ceracyclus_ g. nov.

It is noticed here that no described diagnostic character of passalopalpid (Boucher et al. 2016) was found in the two species of _Ceracyclus_ g. nov. and in the four species of _Cylindrocaulus_.

Key characters among Aulacocyclinae Aulacocyclini and Ceracupini. – Habitus and body shape dorsoventral less convex, especially the disk of elytra (Figs. 3-4). Head (Fig. 6) without central tubercle. Mediofrontal area, as a whole concave and forming a large depression. Inner tubercles totally regressed or not visible. One vertically developed horn on each external side of the laterofrontal area. Clypeus more or less exposed, but clearly visible in dorsal view of the insect; reaching or not, from above, the anterior angles of the head. Anterior angles of the head highly developed, pointed upward forward, forming the limits of the latero-anterior margin of the clypeus. Epicranial suture poorly marked, on the external side and at the basis of the anterior angles of the head. Supra-orbital ridges regressed totally or with a small median tubercle.

Mandibles simple, less convex; dorsal teeth poorly developed to obsolete (Fig. 6). Lacinia with 2-3 spines before the apex, the distal spine stronger (Fig. 13; see also Boucher & Reyes-Castillo 1996, Figs 6-7).

Ventral face of protibiae with inner row of spines, more or less developed (Figs. 8-10). Prosternal projection as high as the procoxae (Fig. 5). Boucher (2006) considered erroneously this very informative character as identical in the genus _Cylindrocaulus_ and remaining Aulacocyclinae. The prosternal exposure in Cecacyclini is in fact most similar, maybe homologous, with the second subfamily, Passalinae Kaup.
Figs. 1-2. †Ceracyclus g. nov., photos of habitus in amber, holotypes. 1, *C. lotus* sp. nov. (elaborate nugget). 2, *C. jirouxi* sp. nov. (untreated nugget). Scale: 1 mm.

Figs. 3-5. †Ceracyclus lotus* sp. nov. 3-4, habitus of head, pronotum and elytra, dorsal and lateral. Pubescence of labrum not shown. – 5, thorax and abdomen, ventral. Pubescence of prothorax not shown; empty coxal cavities in grey (SB del.). Scale: 1 mm.
Fig. 6. †*Ceracyclus lotus* sp. nov. Details of head and anterior part of pronotum, dorsal and lateral. Pubescence of labrum not shown (SB *del.*). Scale: 1 mm.

Figs. 7-14. Ceracyclini tribe nov.: 10, *Cylindrocaulus bucerus* Fairmaire; 7-9, 11-14, †*Ceracyclus lotus* sp. nov. – 7-10, protibia. 7, dorsal; 8, ventral; 9-10, ventral ¾ internal. Homologous infra-internal rows of spines shown with arrows. — 11, mesotibia, ventral. — 12, metatibia, ventral. — 13, maxilla (ventral maxillary palp in natural position). – 14, mentum, ventral. Scales: 7-12, 1 mm; 13-14, 0.5 mm.
†Ceracyclus Boucher & Bai g. nov.

Type species. – Ceracyclus lotus Boucher, Bai & Montreuil sp. nov.

Key characters compared to Cylindrocaulus. – Small to very small size (<10 mm; vs 14-23 mm). Color uniform dorsoventral, dark brown (vs black).

Head (Fig. 6) with a developed horn on each external side of the latero-frontal area, directed a little backward the eyes (vs forward the eyes; see Boucher 2006, Figs. 23-24). Clypeus much less exposed, narrower but longer, not reaching the anterior angles of the head; integument with fine setigerous punctures (vs smooth and glabrous). Epicranial suture shorter. Supra-orbital ridges with a small median tubercle (vs regressed totally), elsewhere regressed throughout. Postfrontal area widely covered with punctures and on each side with a marked groove between the horn and the postorbital area. Postorbital pits absent (vs large and marked). Antennal clubs more rounded and without smooth integument below each article. Eyes somewhat globulous. Mandibles thin, almost flat (pars incisive), with the dorsal teeth obsolete. Mentum flat, without lateral pits (Fig. 14). Mandibles less convex; dorsal teeth poorly developed to obsolete (Fig. 6).

Pronotum with anterior border almost straight or poorly concave, with complete marginal groove, like in Aulacocylini (vs with pronounced median convexity, more or less bifid at the apex) (Fig. 6; see also Boucher & Reyes-Castillo 1996, Figs 1-2). Sides widely wrinkled, without clear pits. Metasternum with disk delimited by a semicircular ridge reaching the lateroposterior angles; lateral pits absent (Fig. 5).

Ventral face of protibiae with a latero-internal row of developed spines (vs widely regressed; Figs. 8-10). Meso- and metatibiae with strong median spines.

Sternite IV with a tuft of setae on the disk (Fig. 5).

Etymology. – Reference to the genera Ceracupes Kaup and Aulacocyclus Kaup: cera (horn, two in lateral position on the head in the Ceracyclini); cyclus (like circle, reference to the convex body shape).

Ceracyclus lotus Boucher, Bai & Montreuil sp. nov.

Type material. – 6 ex. from 5 pieces of amber from Hukawng Valley (see above). Holotype and three Paratypes from SB (HT deposited in MNHN); two Paratypes, n° NIGP165094, NIGP165095 from BW (deposited in the Institute of Geology Palaeontology, Chinese Academy of Sciences, Nanjing; contact with MB or BW).

Description. – Macropterous. Habitus subparallel, convex, slightly depressed on the disk of elytra, glabrous dorsally (Figs. 1, 3-5). Color of body and legs dark brown dorsoventral.
Dimensions small for a passaloid species. Total length: 9-9.5 mm; greatest width: 3.5 mm over pronotum or elytra.

Head (Figs. 1, 3-4, 6). Frontal border (clypeus) exposed dorsally on its half, straight, thick and large, with long and spaced setae and fine punctures; sides prominent; external angles (anterior angles of the head) pointed upward forward, acute. Labrum large, rectangular; anterior border almost straight, with setae throughout. Medio- and laterofrontal areas large, concave and deep, glabrous, more or less smooth and without any convex cuticular structure (ridge or tubercle). Postmediofrontal area more concave than previously, forming a narrow and smooth cavity. Epicranial sutures short. Lateropostfrontal areas with a pair of developed horns, pointed upward, with apex like bifid. Postfrontal groove absent. Postfrontal area glabrous, with extended regular punctures throughout. Supraocular ridges absent, except a small rounded tubercle in the middle, between the anterior angles of the head and the lateral horns. Eyes almost globulous, exceeding the width of the head. Ocular canthus rather long, subparallel; apex obtuse shorter than the eye. Postocular pits absent. Antennae with 10 articles, rather short; scape short and curved; scape and articles II-VII smooth, with some setae; club with 3 rather long articles, thick, slightly rounded. Mandibles large but thin; dorsal face hairless and smooth except at the base, with some setae and fine punctures; dorsal teeth simple, like regressed and contiguous with the pars incisive; apex with two teeth poorly developed; other mandibular structures not accessible on our samples. Labial palps with 3 developed articles, straight, smooth and with rare setae. Maxillae (Fig. 13) with long maxillary palps of 4 articles; galea folded and simple; lacinia with three spines, the distal stronger, more the apical spine. Mentum (Fig. 14) trapezoid, flat, setigerous, the winged sides without pits; integument almost granulous. Hypostomal processes small, poorly visible.

Pronotum (Figs. 1, 3-5) slightly elongated. Anterior border almost straight to slightly concave; anterior angles rounded; marginal groove narrow, but complete throughout; posterior border slightly but regularly rounded; median groove marked, narrow, reaching both anterior and posterior borders of the pronotum. Sides like straight, wrinkled; lateral pits almost obsolete. Ventral face setigerous.

Mesosternum (Fig. 5) covered with fine punctures and minute setae, without lateral scares.

Metasternum (Fig. 5) with latero-anterior and latero-posterior areas covered by short setae and spaced punctuations; elsewhere smooth. Disk flat, delimited by a peculiar semicircular ridge from the procoxae to the posterior angles of the metasternum.

Elytra (Figs. 1, 3-4) subparallel, glabrous, with 10 striae and fine punctuations throughout, a little larger on sides; apex rounded, with a transversal convexity covering the distal part of discal striae I-V, up to the junction of elytra. Hindwings of macropterous type, hyaline (median and proximal parts not seen on our samples).
Legs rather short and strong, setigerous, the setae spaced and long. Superior spolons long, slightly curved inward, the apex acute; inferior spolons short, almost straight, sharp. Protibiae (Figs. 7-9) above slightly enlarged, setae rather short and numerous; ventral ridges, on each side with a row of 3-5 strong spines. Meso- and metatibias (Figs. 11-12) with 2-3 strong to very strong spines, more the apical fork which is powerful and curved downward. Profemurs large and short, with long setae on the inframargin (Fig. 5); mesofemurs narrow and elongated, subparallel, almost glabrous; metafemurs slightly widened, with a few inframarginal setae. Tarsomeres with 5 articles of normal conformation like other Passalidae.

Abdomen (Fig. 5) smooth, without scares and other marks, glabrous except the sternite III with a tuft of spaced and setigerous punctures in the middle; sII totally invaginated (Fig. 15); sIII-VII complete; sVII without distinct groove at the apex.

_Etymology._ – The lotus, _Nelumbo nucifera_, is one of the flowers embodying most symbols, among which the knowledge.

_Polymorphism._ – Only noticeable with regard to the development of the cephalic horns, themselves dependent on the body size of the specimen, as observed in most of passalids.

_Ceracyclus jirouxi_ Boucher, Bai & Montreuil sp. nov.

_Type material._ – Two specimens from 2 pieces of amber from Hukawng Valley (see above). _Holotype_ and _paratype_ from SB (HT deposited in MNHN).

_Diagnosis._ – A species very close to _C. lotus_, but which is easily distinguished from it by its size, almost twice as small: total length 4 mm and greatest width 1 mm over elytra (Fig. 2). Some other characters are also well distinct: dorsal crests of mandibles clearly convex at the base; cephalic horns shorter, arranged obliquely with regard to the axis of the body; anterior angles of the head much less developed.

This remarkable species is the smallest registered among passaloids. It is friendly dedicated to E. Jiroux.

_Conclusion_

The distribution of _Cylindrocaulus_ is restricted to Continental Asia and Japan (Fig. 16): _C. patalis_ (Lewis, 1883) in Kyushu and Shikoku; _C. bucerus_ Fairmaire 1880, in the region of Moupin (Baoxing, Sichuan, China) (completed by Fairmaire 1887); _C. davidi_ Boucher & Reyes-Castillo, 1996 from Wa Shan, Sichuan, China, completed by Kon _et al._ (1997, 1999), from Daliang Shan, Sichuan, and from Min Shan, Gansu; _C. mishmi_ Kon, Araya & Johki, 2015, from
NE India, Arunachal Pradesh, Lower Dibang Valley. It is a typical Laurasian distribution. These species live for a good part in temperate forests of Coniferous at high elevation, up to 2000 m. The *Ceracyclus* were living at low elevation in subtropical to tropical wet forests, much before the existence of the first mountains produced since the Himalayan accretion. *Cylindrocaulus* may be considered as a survivor of this period, but adapted to very distinct conditions than during the earliest Cenomanian.

Among the morphological characters observed in *Cylindrocaulus* and *Ceracyclus*, two are very informative. The pair of cephalic horns and the row of infra-internal spines on the protibiae, are so original among Passalidae that their homology makes no doubt. In *Cylindrocaulus*, the cephalic horns are acute, except *C. mishmi*. In this species, like in the two species of *Ceracyclus*, the apex of the horns is concave, like bifid, with very similar conformation. Regarding the protibiae, the existence of a row of spines - although regressed - on the infra-internal ridge, is observed in the four species of *Cylindrocaulus*, whereas this character does not exist in any other Passalidae. However, it is strongly marked in the Passalopalpidae *Passalopalpus*.

In their contributions to the phylogeny of the Aulacocyclinae, Hosoya & Araya (2008), on morphological data, then Hosoya (2008 ms), on molecular data, suggested that the tribe Ceracupini does not form a monophyletic group. The renewed examination of Ceracupini, of *Cylindrocaulus*, and the discovery of *Ceracyclus*, allows to support this last hypothesis. The Aulacocyclinae, which are a large monophyletic group, would include on one hand the Aulacocyclini and Ceracupini, on the other hand their sister group Ceracyclini. New analyses should confirm these phylogenetic hypotheses and some paleobiogeographic scenarios.

Besides, we found easily various similarities between the two sympatric fossil groups, *Ceracyclus* and the passalopalpid *Passalopalpus*, especially with respect to the adaptation of general morphology, fly ability, food and microhabitat, and behaviour. The *Ceracyclus* species being macropterous, it is the most likely that they could fly, like *Passalopalpus*. Also like *Passalopalpus*, some detritus found in the amber with *Ceracyclus* come from ligneous plants. There is little doubt that both groups were associated with similar decayed wood or like wood. Moreover, the small to very small size of the species indicate that they could live in small hosts. At least, like passalopalpids it would be possible to find various *Ceracyclus* samples in the same nugget of resin, which allows thinking that they were gregarious.

These amazing passaloids will bring certainly other unknown elements which lived in the fauna of the Burmese Cretaceous.
Fig. 15. †Ceracyclus lotus sp. nov. Abdomen (ventral, right side) based on Micro-CT data (MB) showing lacking of sternite II and complete III as first exposed sternite. Scale : 0.5 mm.

Fig. 16. Distribution map in Continental Asia and Japan of Passalidae Ceracyclini tribe nov. (Cylindrocaulus Fairmaire, †Ceracyclus g. nov.) and †Passalopalpidae Passalopalpus cheni Boucher, Bai & Zhang.
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