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Systematic notes on the Cerambycidae (Insecta: Coleoptera) described from Burmese amber

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Introduction

The description of a new fossil taxon presupposes the global knowledge of the examined group and of the existence of possible sibling, mimicking or simply superficially similar taxa. The older the fossils are, the greater the possibility of misidentification. Moreover, the knowledge of the assumed phylogeny and of the evolution centres of the extant taxa allows understanding the real taxonomy of new fossil entities, giving consistency and support to the descriptions.

Because of its unusual morphological characters, the recent description of *Apophisandra ammytae* Molino-Olmedo, 2017 (new genus, species and tribe) was disconcerting to most specialists in cerambycids. This taxon evidently belongs to another family.

This paper also revises the status of *Qitianniu zhihaoi* Lin & Bai, 2017 (whose systematic position inside Cerambycoidea remained inconclusive in the original description) and clarifies the systematic position of all assumed cerambycids in Burmese amber.

Material and methods

Burmite originates from mines located in Myanmar, Kachin State, Myitkyina District, Hukawng Valley. Based on radiometric data, Burmese amber is currently dated back to the earliest Cenomanian, mid-Cretaceous, with an age of 98.79 ± 0.62 Ma (Shi *et al.*, 2012).

The characters and pictures provided in the original descriptions (Lin & Bai, 2017; Molino-Olmedo, 2017) are sufficient to discriminate the systematic position of the assumed cerambycids with the help of several general and specific works on the systematics of this group (Lamarck, 1817; Thomson, 1860; Mulsant, 1862; Lacordaire, 1869; Gahan, 1906; Lameere, 1912; Saalas, 1936; Müller, 1949–1953; Linsley, 1962; Villiers, 1968; Švácha *et al.*, 1997; Vitali, 2006; Sýkorová, 2008; Nearns, 2013; Švácha & Lawrence, 2014; Bouyer, 2015).

Systematic palaeontology

Order Coleoptera Linnaeus, 1758
Superfamily Cerambycoidea Latreille, 1802
Family Cerambycidae Latreille, 1802
Subfamily Prioninae Latreille, 1802
Tribe Meroscelisini Thomson, 1861 stat. nov.

Genus *Qitianniu* Lin & Bai, 2017
***Qitianniu zhihaoi* Lin & Bai, 2017**

According to its authors, *Qitianniu zhihaoi* is characterised by minute body size (4.6 mm), body slightly flattened dorsoventrally, tarsi cryptopentamerous, eyes very large and coarsely facetted, last segment of palpi not tapered apically, pronotum with complete lateral margin and antennae longer than body (Lin & Bai, 2017).

Instead of using these diagnostic characters, the authors, without explanation, inserted them into the data matrix proposed by Napp (1994) in order "to clarify the phylogenetic position" of this taxon. Although they noted and accordingly corrected some significant errors of this matrix concerning missing groups (Dorcasominae, Chrysomelidae) or keyed characters (*Saphanus, Atimia, Philus*), they overlooked the fact that the conclusions were still inconsistent even after the corrections. In fact, the resulting phylogenetic tree appears incoherent since "the four genera of Spondylidinae [are] very widely separated and the eight subfamilies of Cerambycidae are not in a monophyletic clade". This contradicts the generally accepted taxonomy of these subfamilies, which is supported by recent phylogenetic analyses (Sýkorová, 2008). Consequently, the authors admitted that "the trees did not provide strong evidence to differentiate the cerambycoid complex or elucidate the position of *Qitianniu* clearly".

Afterwards, they briefly examined all known subfamilies without being able to classify the new taxon. But, this analysis also revealed uncertainty and several misconceptions of the peculiar characters of each subfamily. For example, the reason that *Qitianniu* does not belong to Lamiinae is not "its

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prognathous head" but its truncate palps (Lacordaire, 1869). Actually, the definition of "prognathous head" is erroneous as well since the provided photos show that the mandibles are obliquely directed and the frons is vertical; thus, the head can not be defined as truly "prognathous". In addition, this condition can be also observed in several Lamiinae, as e.g. in the genus *Sternotomis* Percheron, 1836, or in most Tmesisternini.

The authors had evidence of the presence of a complete lateral margin of the pronotum, which properly excluded some subfamilies, but they did not draw the logical conclusion due to misconceptions concerning the phylogeny of the Prioninae.

The claims that a "prionine ancestor was probably a larger beetle" and that "the small forms (some Neotropical Anacolini) are strongly derived" are considered as wrong for nearly a century (Saalas, 1936; Müller, 1949–1953; Vitali, 2006; Švácha & Lawrence, 2014).

On the contrary, primordial Prioninae were in all likelihood small forms, similar to other basal cerambycoid tribes (Cyrtonopini, Disteniini, Dynamostini, Heteropalpini, Distenini, Vesperini, Philini), which include relatively small taxa. For a long time, close relationships were noticed among primitive Prioninae and Philini (Gahan, 1906; Linsley, 1962) and among Anacolini / Meroscelisini and Philini, Cyrtonopini and Xystrocerini (Lameere, 1912). Thus, Anacolini are actually among the most basal tribes of Prioninae and small representatives of Meroscelisini are even more archaic. In this last tribe, members of the genus *Anoeme* Gahan, 1890 can be only 8.5 mm long (Villiers, 1968; Bouyer, 2015).

The complete lateral margin of the pronotum is the well-known peculiar character of the Prioninae since the origins of the classification of the cerambycids (Lamarck, 1817; Thomson, 1860; Mulsant, 1862; Lacordaire, 1869).

Moreover, *Qitianniu* shows other evident diagnostic characters. The simple pronotum and the shape of the head suggest some tribes of the transition Prioninae-Cerambycinae, i.e. Meroscelisini and Xystrocerini, but the margined pronotum points unequivocally to the former tribe.

The authors also described a slightly groove at the apex of the protibiae that might make think to some Cerambycinae Xystrocerini (*Auxesis* Thomson, 1858). Nonetheless, the real existence of this character is rather doubtful. In the discussion, the protibiae are defined as "sinuate", a completely different character. No detailed photo supports it, but, on the contrary, the published photos seem to suggest a misinterpreted air bubble. However, the fact that tibial grooves are present in several unrelated Cerambycoidea (Disteniidae, Cerambycinae, Lamiinae) implies that this character evolved many times in the Cerambycoidea without having a particular phylogenetic importance.

Accordingly, *Qitianniu* looks similar to *Anoeme*, especially to *A. murphyi* Bouyer, 2015, with which it shares most characters, while its short elytra are reminiscent of other congeners. The pronotum looks still similar to more primitive lepturoid Cerambycidae, e.g. *Caraphia* Gahan, 1906, but this is perfectly coherent with the phylogenetic position of this taxon.

Anoeme is currently widespread in the whole Tropical Africa (Bouyer, 2015) with an endemic species in India (Gahan, 1906). This split distribution and its systematic position inside Cerambycidae support the primitiveness of this taxon, whose origin should be dated before the separation of India from Africa (Early Cretaceous). The assumed existence of *Anoeme* already in the Cretaceous is harmonious with the classification of *Qitianniu* inside Meroscelisini, even suggesting a larger distribution of this tribe during this period.

Superfamily Cucujoidea Latreille, 1802
Family ?Parandrexidae Kirejtshuk, 1994
Tribe Apophisandrini Molino-Olmedo, 2017

Genus *Apophisandra* Molino-Olmedo, 2017
Apophisandra ammytae Molino-Olmedo, 2017

According to its author, *Apophisandra ammytae* is characterised by minute body size (4.9 mm), flattened body, pentamerous tarsi and falciform mandibles without teeth or dorsal ridges (Molino-Olmedo, 2017). The beadlike antennae are inserted close to the mandibular condyles, without antennal tubercles and they surpass the elytral base.

Some characters were not considered as belonging to Parandrini, implying the definition of the new tribe Apophisandrini: scape elongated and tubular; antennomeres II–III equal in length and width; eyes projected and horizontally enlarged, pronotum with rounded basal angles. The author supported the assignment of this taxon to Parandrinae (sic!) claiming that this group—having pentamerous tarsi and short antennae—is considered as the oldest among cerambycids. He mentioned McKenna & Farrell (2009), who hypothesised its existence in the Cretaceous.

Nonetheless, *Apophisandra ammytae* appears as a very odd cerambycid. First, the mandibles are exceptionally narrow, too projected and, especially, having their base too far from the antennal supports, which are even described as absent. In all Cerambycidae and in the Oxypeltidae, the base of the mouthparts is as wide as the frons. The mandibles of some Disteniidae and Vesperidae might resemble those of *Apophisandra*, but these families are completely unrelated to this fossil. In contrast, these characters can be consistently observed in many Cucujoidea, such as Cucujidae, Laemophloeidae, Passandridae and Parandrexidae.

Secondly, the antennae are unusually longer than in typical Parandrini but they do not show, however, any cerambycoid aspect. They are "moniliform", another bizarre character for cerambycids, which show threadlike, toothed or eventually comb-like antennae. In addition, the usual differentiated pedicel is absent, while the last three antennomeres are not progressively smaller or thinner but flattened and enlarged, even suggesting the presence of an apical club.

Thirdly, the abnormally projected eyes do not correspond to any known cerambycid but are reminiscent of those of some Cucujoidea, such as Cucujidae *sensu lato* and Smicripidae.

Finally, from a phylogenetic point of view, *Apophisandra* is doubtfully placeable. As many authors have indicated (Saalas, 1936; Müller, 1949–1953; Vitali, 2006; Švácha & Lawrence, 2014) and some genetic analyses (Nearns, 2013) have confirmed, Parandrini are not a primitive tribe but modified Prioninae, whereas the most primitive Cerambycoidea are lepturoid families close to the Chysomeloidea (Švácha *et al*., 1997). Though living during the Cretaceous, this taxon shows specialised characters unknown in any other known cerambycids (beadlike, nearly club-shaped antennae, falciform mandibles, projected eyes and rounded basal angles of the pronotum) but no primitive characters present in other taxa.

The minute size and the pentamerous tarsi confirm the suspicion that *Apophisandra* has nothing to do with Parandrini or other Cerambycoidea. Thus, it is about a cerambycid-like Cucujoidea, such as *Laemophloeus*, *Uleiota* and other ones, which also show an analogous pronotum.

In reality, all characters of *Apophisandra ammytae* fit the superfamily Cucujiodea. The absence of furrows on the pronotal disc seems to exclude Laemophloeidae, while the lateral ridge boarding the pronotum resembles some Passandridae. The characters separating true Cucujidae from Silvanidae are still unclear (Thomas, 2002) and some of them, i.e. tarsal proportions and genitalia, are neither mentioned nor visible in the description of *Apophisandra*. However, no extant taxon shows similar large mandibles.

Apophisandra ammytae might belong to the Mesozoic family Parandrexidae Kirejtshuk, 1994, already confused with cerambycids in the past (Rohdendorf, 1962), which is characterised by flattened body, transverse flattened procoxae with exposed trochantin, large elongated prognathous head, long palpi and a movable articulation between pronotum and head (Kirejtshuk, 1994). Many species show analogous mandibles but also antennae as long as body; nonetheless, a species with shorter antennae was described from the Lower Cretaceous of Spain (Soriano *et al*., 2006).

Though I am unable to perform further analyses, the tribe Apophisandrini and *Apophisandra ammytae* should be removed from Cerambycidae and transferred into the superfamily Cucujiodea, tentatively near the family Parandrexidae.

Conclusion

After this systematic review, mid-Cretaceous Burmese amber now contains only one species of Cerambycidae, i.e. *Qitianniu zhihaoi* Lin & Bai, 2017, belonging to Prioninae, tribe Meroscelisini. The oldest fossil belonging to the Prioninae is *Cretoprionus liutiaogouensis* Wang *et al*., 2014 from the Lower Cretaceous of China (Wang *et al*., 2014). Although this fossil shows rather clear diagnostic characters, the authors remained somewhat uncertain about its tribal position.

Considering that this taxon already shows some specialised characters, i.e. saw-toothed antennae, toothed pronotum, lobed tarsi, the origin of Prioninae should be dated to even more ancient times.

In fact, the earliest known longhorn beetle is not *Cretoprionus liutiaogouensis*, as Wang *et al*. (2014) claimed, but *Cerambycinus dubius* Germar, 1839 from Late Jurassic of Solnhofen (Germany). Giebel (1856) described this species again as *Mesosa germari*, underlining its close resemblance to this extant genus. Though the attribution to *Mesosa* seems almost uncertain, the fossil shows unequivocal long antennae supporting its belonging to the Cerambycoidea.

In conclusion, it seems evident that the origin of Cerambycoidea should be dated back at least to the Jurassic, or, as supposed on the basis of the chorology of some extant tribes as Macrotomini, maybe even to the Triassic (Vitali, 2008), before the splitting of Laurasia-Gondwana.

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