



Short communication

Cretocrenis burmanicus, the first Mesozoic amber inclusion of a water scavenger beetle (Coleoptera: Hydrophilidae)



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ABSTRACT

Cretocrenis burmanicus, gen. et sp. nov. is described from Burmese amber and represents the oldest known amber inclusion of the family Hydrophilidae (Coleoptera: Polyphaga). The new genus resembles the small-bodied modern genera of the tribe Anacaenini and the subfamily Acidocerinae, and the morphology of the venter and male genitalia suggest that it belongs to the *Horelophus*+*Crenitis* clade of the tribe Anacaenini. The fossil is described in detail, illustrated, and compared with extant hydrophilid genera.

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1. Introduction

The water scavenger beetles (Hydrophilidae) are the largest group of the polyphagan superfamily Hydrophiloidea, comprising ca. 2900 extant and ca. 150 extinct species (Short and Fikáček, 2011, 2013; Fikáček, unpubl. data). Hydrophilidae are frequently encountered as fossils in Cenozoic deposits (e.g., Scudder, 1890, 1900; Fikáček et al., 2010a,b; Fikáček and Schmied, 2013). Their presence and world-wide distribution in the Mesozoic was recognized only recently by Fikáček et al. (2014) based on compressed fossils from the Upper Jurassic deposits of central Europe and Australia, as well as the Lower Cretaceous deposits of China, eastern

Russia and Australia. Amber inclusions of Hydrophilidae are rare, and only a few specimens are known from Baltic and Dominican ambers to date (Fikáček and Engel, 2011). Fossil-calibrated dated phylogenies revealed that modern hydrophilid tribes and genera originated and radiated during the Mesozoic (Bloom et al., 2014, Toussaint et al., 2017; but see an alternative hypothesis by McKenna et al. (2015)), and the scarcity of the well-preserved fossils from this era thus limits our understanding of the early evolution of the family.

In this study, we describe the first Mesozoic species of the family Hydrophilidae, based on two specimens preserved in Upper Cretaceous Burmese amber. Both fossils are well preserved, including details of ventral morphology and genitalia, and provide a unique opportunity to examine a 99 Ma species in detail usually reserved for studies of extant specimens. The species is described and illustrated; its comparison with modern hydrophilids justifies its placement in a new extinct genus.

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2. Material and methods

The new species is known from two specimens of adult beetles preserved in relatively transparent pieces of Burmese amber. The amber has been prepared, including trimmed with a hand-held saw and polished with sandpapers of different grain sizes and with polishing powder. The specimen was examined with the Olympus BX41 compound microscope, using both transmitted and reflected light. Multilayer photographs were taken using the Canon EOS 1100D camera and combined by HeliconFocus software, drawings were done using the drawing tube attached to the same microscope. Photomicrographs with green background are taken using green fluorescence as light source attached to a Zeiss Axio Imager 2 compound microscope. The specimens are deposited in the Nanjing Institute of Geology and Palaeontology (NIGP) and Oregon State Arthropod Collection (OSAC).

Comparison with modern hydrophilids is based on specimens deposited in the National Museum in Prague (Anacaenini, Acidocerinae), Naturhistorisches Museum in Vienna (*Agraphydrus* Régimbart, all extant species accumulated for the prepared revision of the genus by A. Komarek), Kitakyushu Museum of Natural History and Human History (*Crenitis* Bedel incl. *Acrenitis* Matsui & Nakane and part of *Agraphydrus*) and the University of Kansas in Lawrence (Acidocerinae). Classification follows Short and Fikáček (2013) and Seidel et al. (2016), morphological terminology follows Komarek (2004).

Full resolution photographs of the fossil, including additional ones not presented in this paper (photomicrographs taken using green fluorescence) are deposited online on <https://www.flickr.com/photos/142655814@N07/collections/72157680207975025/>. The nomenclatural acts established herein are registered under LSID urn:lsid:zoobank.org:pub:A26B7ABA-95B9-435C-AF01-66615D01C5C6.

3. Systematic paleontology

Order: Coleoptera
Suborder: Polyphaga
Superfamily: Hydrophiloidea
Family: Hydrophilidae
Subfamily: Chaetarthriinae
Tribe: Anacaenini

Genus: *Cretocrenis* gen. nov.
Type species: *Cretocrenis burmanicus* sp. nov.

Diagnosis. Clypeus not excised anteriorly; galea with setae arranged in rows; maxillary palpus relatively long, palpomere 3 not excised basally; labial palpomere 2 with few setae; gula wide; antenna with nine antennomeres, antennal club loosely segmented; prosternum moderately long in front of procoxae, without median carina, with transverse groove anteriorly; mesoventrite divided from mesanepisterna by distinct anapleural sutures, triangularly narrowing anteriorly; elytron with series of larger punctures; sutural stria present; abdominal ventrite 1 without median carina; abdominal ventrite 5 without apical emargination or group of stout setae; all tarsi with long swimming hairs on dorsal face; ventral thoracic surface and ventral surface of femora except extreme apices with dense pubescence; aedeagus with simply shaped parameres and median lobe, phallobase at least moderately long.

Etymology. The genus name consists of the prefix *Creto*-referring to its Cretaceous age, and the root *-crenis* referring to its resemblance to the modern genus *Crenitulus* Winters. Gender masculine. The genus is registered under LSID urn:lsid:zoobank.org:act:0DFD E4B5-C64B-4011-ACC0-9081CCAF70B6.

Differential diagnosis. The morphology of *Cretocrenis* corresponds to two modern hydrophilid clades: tribe Anacaenini (subfamily Chaetarthriinae) and subfamily Acidocerinae. It can be easily diagnosed from remaining hydrophilid groups by the following characters: (1) basal metatarsomere short, mesoventrite separated from mesanepisterna by anapleural sutures, [excludes the subfamily Sphaeridiinae]; (2) labial palpomere 2 with few long setae only [excludes subfamilies Cylominae and Sphaeridiinae]; (3) tarsi with swimming hairs, tibiae without swimming hairs, antennae with 9 antennomeres [excludes tribes Amphiopini and Berosini]; (4) mesoventrite flat, with weak transverse ridge [excludes tribes Hydrophilini and Hydrobiusini]; (5) first abdominal ventrite without transverse row of long hairs [excludes Chaetarthriini]; (6) tarsal formula 5-5-5, maxillary palpomere 3 not excised basally [excludes Enochrinae]; and (7) prosternum without median longitudinal carina, galea with setae arranged in series [excludes Laccobiini] (Komarek and Beutel, 2007; Short and Fikáček, 2013).

Within Anacaenini, the anteriorly narrowing mesoventrite of *Cretocrenis* corresponds to modern genera *Crenitulus*, *Crenitis* (including *Acrenitis*), *Horelophus* Orchymont and *Phelea* Hansen (while remaining anacaenine genera have anteriorly wide mesoventrite) (Komarek, 2005; Fikáček et al., 2012; Fikáček and Watts, 2015; Jia et al., 2016). Of the genera with similar mesoventral morphology, *Phelea* and *Acrenitis* may be excluded by the antennae with 8 antennomeres, and all genera except *Crenitulus* have tarsi without swimming hairs. *Crenitulus* corresponds to *Cretocrenis* in tarsal swimming hairs, minute body size (1.4–2.5 mm) and mesoventrite with low transverse ridge in some species (Komarek, 2005). *Cretocrenis* however differs from *Crenitulus* by presence of elytral series of punctures (absent or with subserially arranged punctures in *Crenitulus*), tarsomeres with strong spines at distal apex (absent in *Crenitulus*), and long and rather slender maxillary palpi (shorter and with subapically swollen palpomere 2 in *Crenitulus*).

Within Acidocerinae, *Cretocrenis* differs from most genera except of some *Quadriops* Hansen, *Tobochares* Short & García, *Horelophopsis* Hansen, *Radicitus* Short & García, a few *Agraphydrus* and a few *Helochares* Mulsant in the posterior margin of abdominal ventrite 5 entire, without emargination and/or group of stouter setae (emarginated, or at least with series of stouter setae in remaining genera) (Hansen, 1999; Satô and Yoshitomi, 2004; Short and García, 2007, 2014; Minoshima et al., 2015; Minoshima, 2016). Mesoventrite narrowing anteriorly distinguishes *Cretocrenis* from most acidocerine genera except *Quadriops*, *Tobochares*, some *Agraphydrus* and some *Helochares*. The sutural stria on the elytron is only present in *Chasmogenus* and *Dieroxenus*, which both differ from *Cretocrenis* by an anteriorly wide mesoventrite and apically emarginated last abdominal ventrite. *Quadriops* and *Tobochares* both differ in metafemora without dense pubescence, *Quadriops* also in narrow gula, *Tobochares* in antennae with 8 antennomeres. In general habitus, *Cretocrenis* is closest to *Agraphydrus* based on small body size, relatively short maxillary palpi (longer than width of the head in most Acidocerinae) and ventral morphology. It differs from *Agraphydrus* by straight or weakly convex anterior margin of clypeus (weakly to deeply concave in *Agraphydrus*), tarsi with stout spines ventrally, entire abdominal ventrite 5 (rare in *Agraphydrus*), absence of stouter setae on posterior margin of abdominal ventrite 5 (present in all *Agraphydrus* including those without apical excision) and presence of sutural stria.

See Discussion for detailed justification of the phylogenetic position of the genus.

***Cretocrenis burmanicus* sp. nov.**

Type material. Holotype, NIGP165247, male (Figs. 1A–C, 2A–G); lowermost Cenomanian (ca. 99 Ma; see details in Shi et al., 2012),

from an amber mine located near Noije Bum Village, Tanaing Town, Hukawng Valley (26°21'33.41"N, 96°43'11.88"E), northern Myanmar; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Additional material examined. 1 female, OSAC_0002900118 (Figs. 1D–E, 3A–D); preserved in a piece of Burmese amber with the following labels: “Purchased (\$20) February 2017 from Yanling Ying (Global Burmite Amber)” and “Northern Myanmar, probably Hukawng valley, most of his specimens are from the Noije Bum amber mines or nearby, Kachin state; a few from around Nam Sakhaw in Sagaing Division (NW of Haungpa). 2016”; deposited in Oregon State Arthropod Collection, Corvallis, Oregon, USA.

Etymology. The specific name derives from the country where the type specimen has been collected. The species is registered under LSID urn:lsid:zoobank.org:act:815EF66E-6800-42D6-B644-E30259820EDF.

Description of the holotype. Body widely elongate oval, body length 1.7 mm, body width ca. 0.9 mm. Coloration uniformly reddish brown (partly possibly as an artifact of the preservation in amber).

Head. Clypeus large, anteriorly straight or slightly convex. Frontoclypeal suture clearly apparent laterally. Eyes large, slightly

protruding laterally. Labrum well sclerotized, declined and hence partly covered by clypeus in dorsal view, anteriorly excised. Maxilla with triangular basistipes; galea bearing curved setae arranged in regular rows; maxillary palpus slightly shorter than maximal width of head, all palpomeres bending inside, second and fourth palpomeres subequal in length, third palpomere slightly shorter; ultimate palpomere asymmetrical. Mentum ca. twice as wide as long, subquadrate with slightly convex anterior margin; labial palps slender and rather long, apical palpomere ca. twice as long as penultimate palpomere; penultimate palpomere with few long setae, apical palpomere with one long distal seta. Antenna slightly shorter than width of head, bearing nine antennomeres; scapus moderately long, cylindrical, bending basally; pedicel short, conical; antennomeres 3 ca. twice as long as palpomeres 4 and 5 each; antennomere 6 small but distinctly cup-like; antennal club consisting of 3 very loosely segmented pubescent antennomeres. Posterior tentorial pits moderately separated, gular sutures slightly converging anteriorly.

Prothorax. Pronotum transverse, widening posteriorly, with rounded posterior and anterior corners; lateral margin with a narrow bead; dorsal punctation fine and sparse laterally, anterolaterally with distinct hair-bearing trichobothria. Prosternum

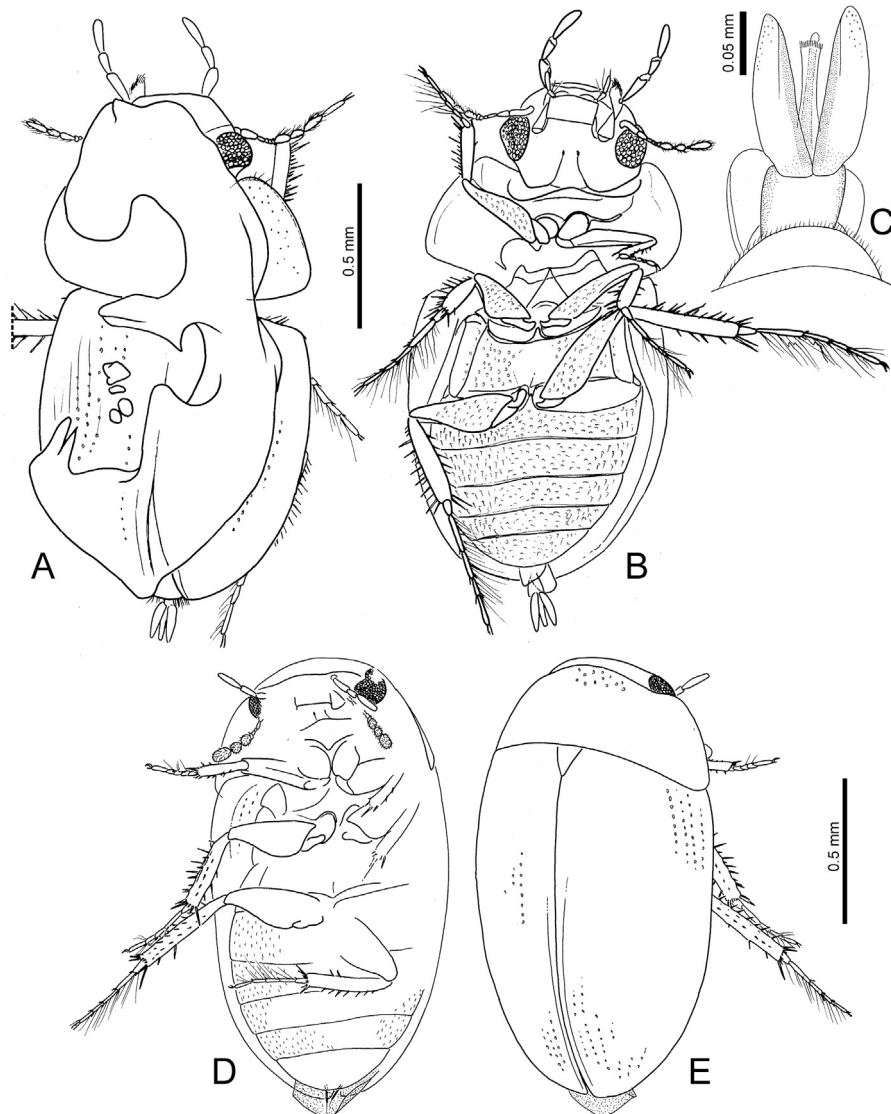


Fig. 1. *Cretocrenis burmanicus* gen. and sp. nov. A–C. Holotype (NIGP165247), male (A. dorsal view; B. ventral view; C. detail of the aedeagus). D–E. Additional specimen (OSAC_0002900118), female (D. ventral view; E. dorsal view). The scale bar refers to Figs A–B and D–E.

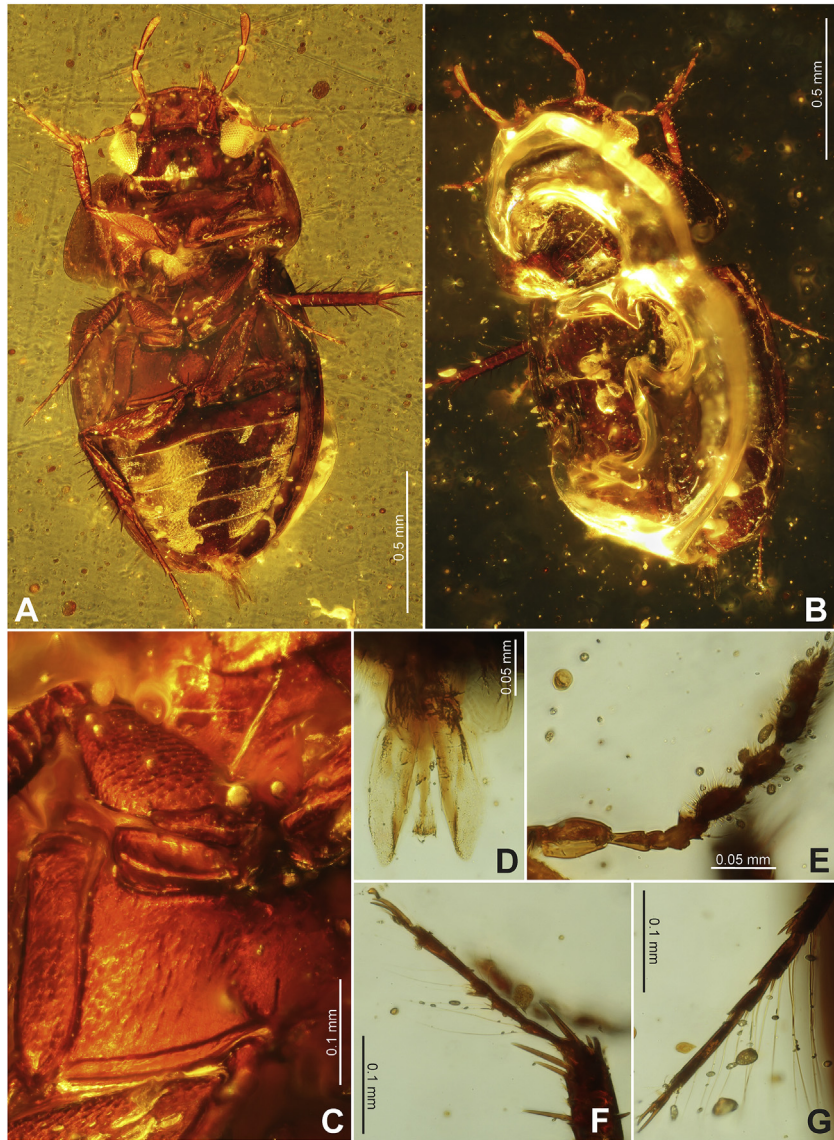


Fig. 2. *Cretochenis burmanicus* gen. and sp. nov., holotype (NIGP165247). A. Ventral view; B. Dorsal view; C. Detail of the meso- and metaventrите; D. Male genitalia; E. Antenna (only extreme apex of scapus shown); F. Protarsus; G. Metatarsus.

rather wide in front of procoxae, without median carina, with a weak transverse groove; prosternal process short. Procoxal cavities open posteriorly, with a long narrowly open fissure laterally. Hypomeron without antennal groove and without any other special structures.

Mesothorax. Mesoventrite triangular anteriorly, with anapleural sutures converging to anterior margin, widening into narrow lateral projections posteriorly; posteromedian portion of mesoventrite with a weak transverse elevation. Mesanepisterna meeting each other on anterior margin of mesothorax, bearing a distinct wide “collar” anteriorly. Elytron with distinct sutural stria developed posteriorly, elytral disc with several series of punctures; lateral margin of each elytron with a minute strong spine basally; epipleuron rather wide anteriorly, narrowing at level of metacoxae, vanishing more posteriorly.

Metathorax. Metaventrите ca. as long as mesoventrite, without elevated median portion, bearing sparse but coarse punctation; metaventral process short and narrow, only very narrowly dividing mesocoxal cavities. Metanepisternum narrow, ca. 4× as long as

wide, slightly widening anteriorly, anterior portion subdivided by oblique ridge.

Legs. Procoxae globular, meso- and metacoxae distinctly transverse. Trochanters subtriangular, with distal portion facing only posterior part of femora; mesotrochanters sinuate on posterior margins. Femora flat, narrowing distally, with distinct tibial grooves, ventral surface bearing dense coarse punctation except on distalmost portion. Tibiae cylindrical, ca. as long as femora, outer and inner faces bearing series of long spines; longest spines of all tibiae longer than width of tibia; distal spurs not apparently longer than tibial spines. Tarsi long, with 5 tarsomeres each; tarsomeres of all legs with unordered series of long swimming hairs, tarsomeres 1–4 each with few strong spines distally; protarsomeres 1–4 subequal in length, protarsomere 5 longest; meso- and metatarsomere 1 short, conical, meso- and metatarsomere 2 very long and slender; meso- and metatarsomeres 3 and 5 shorter, subequal in length, meso- and metatarsomere 4 shortest. Tarsal claws long, slender, arcuate; protarsal claws equally shaped, meso- and metatarsal claws slightly asymmetrical and different in length.

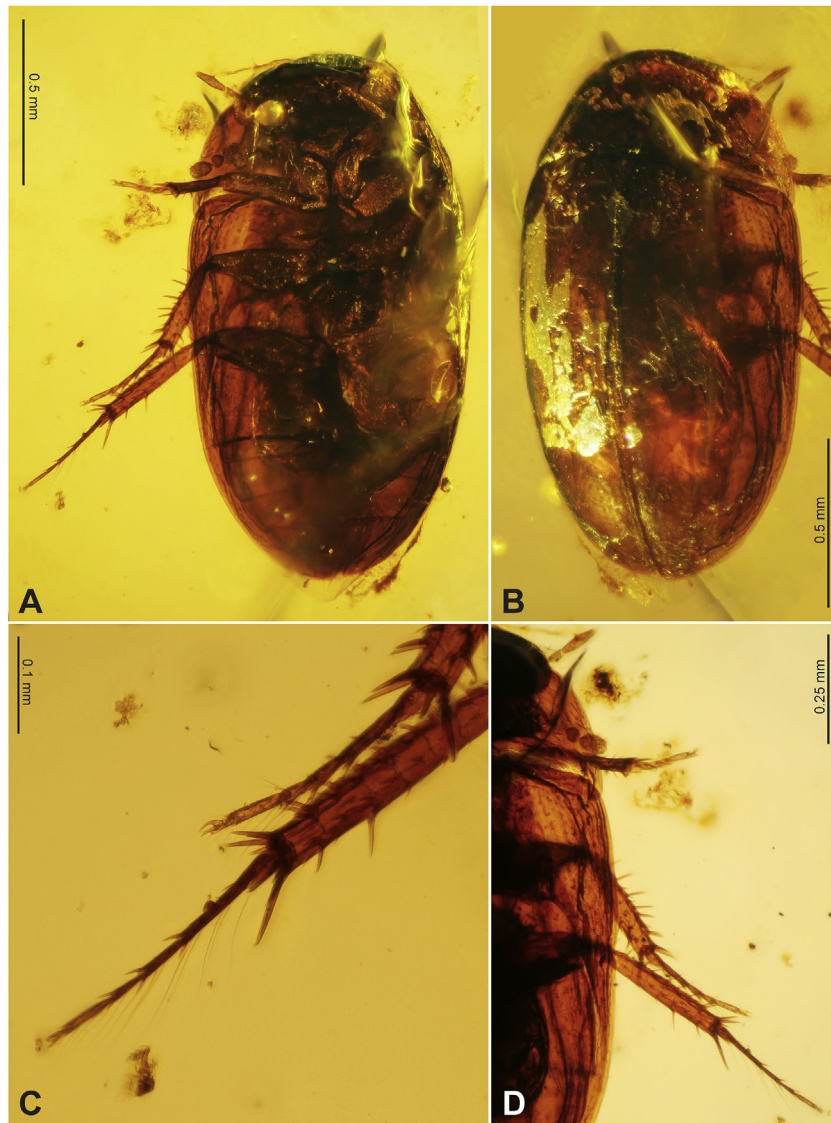


Fig. 3. *Cretocrenis burmanicus* gen. & sp. nov., additional specimen (OSAC_0002900118). A. Ventral view; B. Dorsal view; C. Detail of meso- and metatarsus and metatibia in ventral view. D. Detail of legs and head appendages in transmitting light, dorsal view.

Abdomen with 5 ventrites subequal in length, all ventrites without median carina. Posterior margin of ventrite 5 entire, without emargination or group of stout setae.

Male genitalia. Median lobe narrow, with a peg-like sclerotized part and slightly wider membranous part with apical gonopore; apex of median lobe not reaching parameral apices. Paramere narrowly rounded apically, arcuate on outer margin, widest in basal third. Phallobase at least half as long as parameres, likely even longer.

Morphology of the additional specimen. Body narrowly oval, body length 1.6 mm. The specimen corresponds with the holotype in the following characters (Figs. 1D–E, 3A–D): Antenna with 9 antennomeres, antennal club loosely segmented; prosternum rather wide anterior of procoxae; mesoventrite gradually narrowing towards anterior margin, anapleural sutures arcuate; abdomen with 5 ventrites; posterior margin of ventrite 5 entire posteriorly, without stout setae posteromesally; ventral surface of abdominal ventrites with uniform moderately dense pubescence; elytra with well-developed sutural stria and with series of subserially arranged punctures on the disc; meso- and metatrochanters bisinuate on

posterior margin; tibiae (especially mesotibia) with long protruding spines; tarsal formula 5-5-5; all tarsomeres with long swimming hairs on dorsal surface; ventral face of each meso- and metatarsomere with a pair of strong spines.

A few characters cannot be compared with the holotype or differ from the holotype: Eyes weakly emarginated anteriorly by a lateral ridge of clypeus (Figs. 1D, 3A; not visible in holotype); maxillary palpomere 4 spindle-like (Fig. 3A, D; asymmetrical in the holotype); antennal club with antennomeres 7–8 ca. as long as wide (Figs. 1D, 3A,D; elongate in the holotype); metatarsal claws equally shaped (slightly unequal in shape in the holotype); styli of ovipositor long and thin (not seen in the holotype due to the opposite sex).

Identity of the additional specimen. The additional specimen corresponds with the holotype of most external characters preserved, including the tarsal morphology with strong ventral spines and long swimming hairs (unique for *Cretocrenis*), tibiae with long spines, shape of the mesoventrite, absence of apical abdominal emargination and loosely segmented antennal club. It differs from the

holotype if few details: the shape of the terminal maxillary palpomere (spindle-like versus asymmetrical), slightly smaller and much narrower body, wider antennomeres of the antennal club, and equally shaped metatarsal claws. Some of these differences may be caused by the fact that both specimens are of the opposite sex (the shape of tarsal claws often slightly differs between male and female in many clades of the Hydrophilidae) or may be caused by the combination of the observation of the body part from a different direction and the optical conditions and taphonomy of the amber: antennomeres of the antennal club are seen in lateral view in the holotype, but in dorsal/ventral view in the additional specimen; terminal maxillary palpomere may be seen in lateral view in the additional specimen, and in dorsal/ventral view in the holotype; and the body may seem relatively narrower due to the slightly oblique position of the additional specimen in the amber its 'curled up' prothorax and head (compared to expanded and slightly disarticulated prothorax and head in the holotype). However, we are not able to exclude that some of these differences are real. For that reason we are assigning the additional specimen to *C. burmanicus*, but we treat it as an additional specimen without any type status.

4. Discussion

Cretocrenis gen. nov. is definitely a member of the family Hydrophilidae, as indicated e.g. by antennae with 3-segmented pubescent club, long maxillary palpi, large clypeus nearly reaching anterior margin of eyes, the presence of dense ventral pubescence and long thin styli of the ovipositor (present in the additional specimen only); additional characters preserved in the fossil moreover correspond to those found in modern clades of the family Hydrophilidae.

Cretocrenis is in most characters similar to the tiny-sized genera of modern Anacaenini (*Crenitulus*, *Crenitis* subg. *Acrenitis*) and Acidocerinae (*Agraphydrus*, *Horelophopsis*, *Tobochares*) (see under Differential diagnosis of the genus for details). Anacaenini and Acidocerinae are not closely related phylogenetically (Short and Fikáček, 2013) and their external similarity may be partly due to body miniaturization. The best diagnostic characters separating these two groups are the morphology of male sternite 9 and male genitalia (Minoshima et al., 2013) and characters of the head (details of excision of eyes and clypeus, detailed morphology of labrum). These characters are not visible in *Cretocrenis*, except of the aedeagus, in which all parts but the basal part of the phallobase are seen. By the aedeagal morphology, *Cretocrenis* is very similar to *Crenitulus* by acuminate parameres and median lobe with narrow median sclerite and slightly wider membranous part with subapical gonopore. It does not agree with the genital morphology known for the acidocerine genera *Horelophopsis* (Hansen, 1997; Satô and Yoshitomi, 2004) and most species of *Agraphydrus* (Minoshima et al., 2015; Minoshima, 2016; Komarek, in prep.) which usually have wide and short parameres and/or median lobe without narrow median sclerite. Many species-groups of *Agraphydrus* as well as *Tobochares* and the majority of the genera of Acidocerinae are moreover characterized by a very short phallobase, even though some exceptions exist in the subfamily (e.g., *Dieroxenus*, *Horelophopsis* and few *Agraphydrus*: Spangler, 1979; Hansen, 1997; Satô and Yoshitomi, 2004; Minoshima, 2016). The genital morphology of *Cretocrenis* hence corresponds more to its placement in Anacaenini than in Acidocerinae.

The assignment to the Anacaenini is further supported by the fact that the combination of the characters seen in *Cretocrenis* (entire abdominal ventrite 5, mesoventrite narrowing anteriorly, presence of sutural stria, simple male genitalia with long phallobase) is usual and frequent in this tribe, and moreover characteristic for the genera of the *Horelophus*+*Crenitis* clade (sensu Fikáček

and Vondráček, 2014; see below). The combination of characters may be also close to the plesiomorphic conditions for the whole tribe Anacaenini. The same combination of characters does not occur together in any known modern genus of the Acidocerinae, and at least some characters (e.g., entire abdominal ventrite 5) seem to be rare reversals from the plesiomorphic character states (i.e., emarginated abdominal apex with row of stout setae in this case). All genera of the *Horelophus*+*Crenitis* clade of the Anacaenini are moreover characterized by the median lobe of the aedeagus having a more less narrow median sclerite, similar to that present in *Cretocrenis*; such a sclerite is rare in Acidocerinae.

The *Horelophus*+*Crenitis* clade of the Anacaenini, to which *Cretocrenis* very likely belongs, includes four modern genera: *Crenitis* distributed world-wide (Hebauer, 1994; Bilton, 2013; Jia et al., 2016), monotypic *Horelophus* endemic to New Zealand (Fikáček et al., 2012), *Crenitulus* widely distributed in the Neotropical and southern part of Nearctic Regions and reaching to Australia (Fikáček and Vondráček, 2014), and likely also *Phelea* endemic to Tasmania (Fikáček and Watts, 2015). The relationships between these genera are unclear, and especially the monophyly of *Crenitis* has to be tested. It includes the tiny-sized species classified in the subgenus *Acrenitis* (confined to the Oriental and eastern Palaearctic regions: Hebauer, 1994; Ji and Komarek, 2003), morphologically slightly aberrant South African species (Bilton, 2013), and very likely may include also species today classified in *Horelophus* (judging from a high similarity of that genus to some Japanese species of *Acrenitis*, e.g., *Crenitis* (A.) *neglecta*) and *Phelea*. The species of *Crenitis* (s.str.), *Horelophus* and *Phelea* are characterized by an aedeagus with a large phallobase and huge manubrium, which does not seem to be the case of *Cretocrenis* (though the phallobase is not completely visible in the fossil). The aedeagus of the subgenus *Acrenitis* and the genus *Crenitulus* is more simply shaped (Ji and Komarek, 2003; Komarek, 2005), and closely resembles that of *Cretocrenis*. *Acrenitis* differs from *Cretocrenis* by antennae with eight antennomeres, metafemora without dense pubescence, and tarsi without swimming hairs. *Crenitulus* differs from *Cretocrenis* by elytra without serial punctures or with only subserially arranged ones, tarsomeres without strong spines at distal apex, and shorter maxillary palpi with subapically swollen palpomere 2. Dated phylogenies by Bloom et al. (2014) revealed the Late Jurassic origin of the *Horelophus*+*Crenitis* clade of the Anacaenini (ca. 160 Ma) and the Early Cretaceous origin of the genera within the clade (between ca. 145 and 105 Ma). The presence of *Cretocrenis* in the Cenomanian corresponds well with these age estimates. Denser taxon sampling would be, however, necessary for proper understanding the relationships of the genera of this clade including the position of *Cretocrenis*.

5. Conclusions

Based on the detailed comparison with modern hydrophilid beetles, the Burmese fossil examined in this study does not match any modern genus, and is therefore assigned to a new extinct genus *Cretocrenis*. The new genus most likely belongs to the *Horelophus* clade of the tribe Anacaenini based on characters preserved, even though in many aspects it also resembles some representatives of the subfamily Acidocerinae. Its precise phylogenetic position should be corroborated once the phylogenetic relationships within both mentioned clades are better understood.

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References

- Bilton, D.T., 2013. *Crenitis bicolor* sp.n. from Kamiesberg of South Africa (Coleoptera: Hydrophilidae). *Zootaxa* 3626 (4), 589–592.
- Bloom, D.D., Fikáček, M., Short, A.E.Z., 2014. Clade age and diversification rate variation explain disparity in species richness among water scavenger beetle (Hydrophilidae) lineages. *PLoS One* 9 (6), e98430, 1–9.
- Fikáček, M., Engel, M.S., 2011. An aquatic water scavenger beetle in Early Miocene amber from the Dominican Republic (Coleoptera: Hydrophilidae). *Annales Zoologici (Warszawa)* 61 (4), 621–628.
- Fikáček, M., Schmied, H., 2013. Insect fauna of the Late Miocene locality of Öhningen (Germany) less diverse than reported: an example of the hydrophilid beetles (Coleoptera). *Journal of Paleontology* 87 (3), 427–443.
- Fikáček, M., Vondráček, D., 2014. A review of *Pseudorygmodus* (Coleoptera: Hydrophilidae) with notes on the classification of the Anacaenini and on distribution of genera endemic to southern South America. *Acta Entomologica Musei Nationalis Pragae* 54 (2), 479–514.
- Fikáček, M., Watts, C.H.S., 2015. Notes on the Australian Anacaenini (Coleoptera: Hydrophilidae): description of male of *Phelea breviceps* Hansen and unravelling the identity of *Crenitis neogalica* Gentili. *Zootaxa* 3980 (3), 427–434.
- Fikáček, M., Schmied, H., Prokop, J., 2010a. Fossil hydrophilid beetles (Coleoptera: Hydrophilidae) of the late Oligocene Rott Formation (Germany). *Acta Geologica Sinica (English Edition)* 84 (4), 732–750.
- Fikáček, M., Wedmann, S., Schmied, H., 2010b. Diversification of the greater hydrophilines clade of giant water scavenger beetles dated back to the Middle Eocene (Coleoptera: Hydrophilidae: Hydrophilina). *Invertebrate Systematics* 24, 9–22.
- Fikáček, M., Leschen, R.A.B., Newton, A.F., Gunter, N., 2012. *Horelophus walkeri* rediscovered: adult morphology and notes on biology (Coleoptera: Hydrophilidae). *Acta Entomologica Musei Nationalis Pragae* 52 (1), 129–146.
- Fikáček, M., Prokin, A., Yan, E., Yue, Y., Wang, B., Dong, R., Beattie, R., 2014. Modern hydrophilid clades present and widespread in the Late Jurassic and Early Cretaceous (Coleoptera: Hydrophiloidea: Hydrophilidae). *Zoological Journal of the Linnean Society* 170, 710–734.
- Hansen, M., 1997. A new subfamily for a remarkable new genus and species of Hydrophilidae from New Guinea (Coleoptera: Hydrophilidae). *Annales Zoologici (Warszawa)* 47 (1/2), 107–110.
- Hansen, M., 1999. Fifteen new genera of Hydrophilidae (Coleoptera), with remarks on the generic classification of the family. *Entomologica Scandinavica* 30, 121–172.
- Hebauer, F., 1994. The *Crenitis* of the Old World (Coleoptera, Hydrophidae). *Acta Coleopterologica* 10 (2), 3–40.
- Ji, L., Komarek, A., 2003. HYDROPHILIDAE: II. The Chinese species of *Crenitis* Bedel, with description of two new species (Hydrophilidae). In: Jäch, M.A., Ji, L. (Eds.), *Water Beetles of China*, volume III, pp. 397–409.
- Jia, F., Tang, Y., Minoshima, Y.N., 2016. Description of three new species of *Crenitis* Bedel from China, with additional faunistic records for the genus (Coleoptera: Hydrophilidae: Chaetarhriinae). *Zootaxa* 4208 (6), 561–576.
- Komarek, A., 2004. Taxonomic revision of *Anacaena* Thomson, 1859. I. Afrotropical species (Coleoptera: Hydrophilidae). *Koleopterologische Rundschau* 74, 303–349.
- Komarek, A., 2005. Taxonomic revision of *Anacaena* Thomson, 1859. II. Neotropical species (Coleoptera: Hydrophilidae). *Koleopterologische Rundschau* 75, 253–301.
- Komarek, A., Beutel, R.G., 2007. Phylogenetic analysis of Anacaenini (Coleoptera: Hydrophilidae: Hydrophilinae) based on morphological characters of adults. *Systematic Entomology* 32, 205–226.
- McKenna, D.D., Wild, A.L., Kanda, K., Bellamy, C.L., Beutel, R.G., Caterino, M.S., Farnum, C.W., Hawks, D.C., Ivie, M.A., Jameson, M.L., Leschen, R.A.B., Marvaldi, A.E., McHugh, J.V., Newton, A.F., Robertson, J.A., Thayer, M.K., Whiting, M.F., Lawrence, J.F., Ślipiński, A., Maddison, D.R., Farrell, B.D., 2015. The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology* 40, 835–880.
- Minoshima, Y.N., 2016. Taxonomic review of *Agraphhydrus* from Japan (Coleoptera: Hydrophilidae: Acidocerinae). *Entomological Science* 19 (4), 351–366.
- Minoshima, Y., Hayashi, M., Kobayashi, N., Yoshitomi, H., 2013. Larval morphology and phylogenetic position of *Horelophopsis hanseni* Satō et Yoshitomi (Coleoptera, Hydrophilidae, Horelophopsinae). *Systematic Entomology* 38, 708–722.
- Minoshima, Y.N., Komarek, A., Ōhara, M., 2015. A revision of *Megagraphhydrus* Hansen (Coleoptera, Hydrophilidae): synonymization with *Agraphhydrus* Régimbart and description of seven new species. *Zootaxa* 3930 (1), 1–63.
- Satō, M., Yoshitomi, H., 2004. Discovery of a second representative of the genus *Horelophopsis* (Coleoptera, Hydrophilidae) from the Ryukyu archipelago, Japan. *Elytra* 32, 41–49.
- Scudder, S.H., 1890. The fossil insects of North America with notes on some European species. Volume 2. The Tertiary insects of North America. Report of the United States Geological Survey of the Territories 13, 1–734.
- Scudder, S.H., 1900. Adepagous and clavicorn Coleoptera from the Tertiary deposits at Florissant, Colorado with descriptions of a few of other forms and a systematic list of the non-rhynchophorous Tertiary Coleoptera of North America. In: *Monographs of the United States Geological Survey*, 40, pp. 3–148.
- Seidel, M., Arriaga-Varela, E., Fikáček, M., 2016. Establishment of *Cylominae* Zaitzev, 1908 as valid name for the subfamily *Rygmodinae* Orchymont, 1916 with updated list of genera (Coleoptera: Hydrophilidae). *Acta Entomologica Musei Nationalis Pragae* 56 (1), 159–165.
- Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Wang, M., Lei, W., Li, Q., Li, X., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research* 37, 155–163.
- Short, A.E.Z., Fikáček, M., 2011. World catalogue of the Hydrophiloidea (Coleoptera): additions and corrections II (2006–2010). *Acta Entomologica Musei Nationalis Pragae* 51 (1), 83–122.
- Short, A.E.Z., Fikáček, M., 2013. Molecular phylogeny, evolution and classification of the Hydrophilidae (Coleoptera). *Systematic Entomology* 38, 723–752.
- Short, A.E.Z., García, M.M., 2007. *Tobochares sulcatus*, a new genus and species of water scavenger beetle from Amazonas State, Venezuela (Coleoptera: Hydrophilidae: Hydrophilini). *Aquatic Insects* 29 (1), 1–7.
- Short, A.E.Z., García, M.M., 2014. A new genus of egg-carrying water scavenger beetle from the Guiana Shield (Coleoptera: Hydrophilidae: Acidocerinae). *Zootaxa* 3835 (2), 251–262.
- Spangler, P.J., 1979. A new genus of madicolous beetles from Ecuador (Coleoptera: Hydrophilidae: Hydrobiinae). *Proceedings of the Biological Society in Washington* 92 (4), 753–761.
- Toussaint, E.F.A., Seidel, M., Arriaga-Varela, E., Hájek, J., Král, D., Sekerka, L., Short, A.E.Z., Fikáček, M., 2017. The peril of dating beetles. *Systematic Entomology* 42 (1), 1–10.