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The first aquatic insect fossil from the Cenomanian Konservat-Lagerstätte of Haqel (Lebanon) fills a gap in the fossil record of giant water bugs (Heteroptera: Belostomatidae)

MATHIEU BODERAU[1,2], ANDRÉ NEL[1,*], SIBELLE MAKSOUD[2,3], PIERRE ABI-SAAD[4] & DANY AZAR[2,3,*]
[1]*Institut de Systématique, Évolution, Biodiversité (UMR 7205) Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, F-75005 Paris, France*
mathieuboderau@gmail.com; https://orcid.org/0000-0001-7088-9560
anel@mnhn.fr; https://orcid.org/0000-0002-4241-7651
[2]*State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China*
sibelle.maksoud@ul.edu.lb; https://orcid.org/0000-0001-7437-7490
danyazar@ul.edu.lb; https://orcid.org/0000-0002-4485-197X
[3]*Lebanese University, Faculty of Sciences II, Department of Natural Sciences, Fanar, P.O. Box 26110217, Fanar-Matn, Lebanon*
[4]*Memory of Time, Byblos old sook, Byblos, Lebanon*
pierre@memoryoftime.com; https://orcid.org/0009-0009-6718-0054
**Corresponding authors*

Abstract

Libanobelostoma calineae **gen. et sp. nov.**, the first mid-Cretaceous giant water bug, is characterized, illustrated and described from the fossil fish Konservat-Lagerstätte of Haqel, Lebanon. This new discovery is important for both the fossil record of the Belostomatidae and for increasing our understanding of the paleoenvironment of Haqel. The new genus displays a combination of synapomorphies and symplesiomorphies for Belostomatidae, along with putative autapomorphies justifying its taxonomic treatment. Together with *Libanoaeshna mikhaeli* Azar *et al.*, 2024 they represent the first insect discoveries in the fossil fish Konservat-Lagerstätte of Haqel, making it an additional palaeoentomological site to the numerous other sites in Lebanon.

Key words: Aquatic bug, Nepomorpha, fossil record, mid-Cretaceous, taxonomy, Lebanon

Introduction

Belostomatidae Leach, 1815, commonly known as "giant water bugs", are well-known aquatic insects from temperate and tropical regions of the world (Lauck & Menke, 1961). Extant Belostomatidae are classified into two subfamilies: Belostomatinae Leach, 1815 and Lethocerinae Lauck and Menke, 1961 (Ribeiro *et al*., 2018). Eleven extant belostomatid genera and approximately 150 species are hitherto described, known mostly from the New World (Polhemus, 1995; Perez-Goodwyn, 2006; Estévez & Ribeiro, 2011; Moreira *et al*., 2011; Ribeiro *et al*., 2018; Schuh & Weirauch, 2020). Belostomatids are predators that use their raptorial fore legs to capture prey. They inject salivary secretions and venom, and then extract the liquefied tissues of their prey (Cullen, 1969; Walker *et al*., 2018). These predatory adaptations allow Belostomatidae to attack a wide variety of prey, including fishes (Schuh & Slater, 1995), turtles (Ohba, 2011), water snakes (Wilson, 1958), and even woodpeckers (Hungerford, 1919). Giant water bugs are also notable for displaying paternal care by maintaining oxygen and humidity conditions of the egg masses and providing protection against predators (Ichikawa, 1988; Ohba *et al*., 2006; Matthews & Matthews, 2010; Ohba, 2018). Two types of brooding behaviours have been reported: (i) in *Lethocerus* with emergent brooding, the male supplies water to the eggs that the female deposited on emergent vegetation, and (ii) in *Belostoma* Latreille, 1807 with back brooding, the eggs are deposited on the backs of the males (Ohba, 2018).

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The infraorder Nepomorpha has one of the most ancient and abundant fossil records among the Heteroptera (Grimaldi & Engel, 2005). Fossil Belostomatidae currently encompasses 21 genera and 23 species (Table 1), ranging from the Late Triassic to the Late Pleistocene (Montandon, 1913; Criscione & Grimaldi, 2017). The Late Triassic origin of giant water bugs is congruent with recent phylogenetics estimates (Johnson *et al*., 2018; Ye *et al*., 2020).

TABLE 1. Fossil record of Belostomatidae.

Taxon	**Age**	**Formation (Locality)**	**References**
Triassonepa solensis	Late Triassic	Triassic Cow Branch Formation (USA)	Criscione & Grimaldi, 2017
Odrowazicoris polonicus	Early Jurassic	Zagaje (Poland)	Popov, 1996
Tarsabedus menkei	Early Jurassic	Lias (Dorset, England)	Popov *et al.* 1994
Lethonectes naucoroides	Early Jurassic	Lias (Dorset, England)	Popov *et al.* 1994
Aenictobelostoma primitivum	Late Jurassic	Todilto (New Mexico, USA)	Polhemus, 2000
Morrisonnepa jurassica	Late Jurassic	Morrison Formation (Utah, USA)	Lara *et al.* 2021
Mesobelostomum deperditum	Late Jurassic	Solnhofen (Germany)	Germar, 1839; Lakshminarayana, 1984
Mesonepa primordialis	Late Jurassic	Solnhofen (Germany)	Germar, 1839; Lakshminarayana, 1984
Stygeonepa foersteri	Late Jurassic	Solnhofen (Germany)	Popov, 1971
Nettelstedtia breitkreutzi	Late Jurassic	Bed 103 Schwarze Quarry (Nettelstedt, Germany)	Popov, *et al.,* 2000
Araripebelostomum martinsnetoi	Early Cretaceous	Crato Formation (Brazil)	Nel & Paicheler, 1992
Neponymphes godoii	Early Cretaceous	Crato Formation (Brazil)	Zamboni, 2001
Paranoika placida = Lethocerus placidus	Early Cretaceous	Crato Formation (Brazil)	Zamboni *et al*., 2002; Moura-Júnior *et al*., 2021
Lethocerus vetus	Early Cretaceous	Crato Formation (Brazil)	Nel & Waller, 2006
Lethopterus multinervosus	Early Cretaceous	Crato Formation (Brazil)	Popov, 1989
Sinobelostoma liui	Early Cretaceous	Huachi-Huanhe (Gansu Province, China)	Chou & Hong, 1989
Iberonepa romareli	Early Cretaceous	La Huérguina (Las Hoyas, Spain)	Martínez-Delclòs *et al.* 1995
***Libanobelostoma calineae* gen. et sp. nov.**	**Late Cretaceous**	**Haqel (Lebanon)**	**This paper**
Belostomatidae sp.	Paleocene	Paskapoo (Alberta, Canada)	Mitchell & Wighton, 1979
Belostomatidae sp.	Eocene	Fur (Denmark)	Larsson, 1975
Belostomatidae sp.	Eocene	Fur (Denmark)	Rust & Ansorge, 1996
Lethocerus sulcifemoralis	Oligocene	Bechlejovicer Diatomite (Czech Republic)	Říha and Kukalová, 1967
Belostomatidae sp.	Oligocene	Enspel (Germany)	Wedmann, 2000
Propoissonia beskonakensis	Oligocene–Miocene	Turkey	Nel & Paicheler, 1992
Lethocerus turgaicus	Miocene	Abrosimovka (Siberia, Russia	Popov, 1971
Manocerus stagnans	Miocene	Shanwang (Shandong Province, China)	Zhang, 1989
Diplonychus microcephalum = Sphaerodema microcephalum	Miocene	Shanwang (Shandong Province, China)	Zhang & Zhang, 1994
Belostomatidae sp. = *Belostomum speciosum*	Miocene	Öhningen (Germany)	Heer, 1847
Lethocerus americanus	Late Pleistocene	Rancho La Brea Asphalt (California, USA)	Leidy, 1847; Miller, 1983
Belostoma bakeri	Late Pleistocene	McKittrick Asphalt (California, USA)	Montandon, 1913; Miller, 1983

Herein, we report the first occurrence of Belostomatidae in the Cenomanian Konservat-Lagerstätte of Haqel, Lebanon, corresponding to a marine palaeoenvironment and co-eval to the fossil fish Konservat-Lagerstätte of Hjoula and En-Nammoura (also in Lebanon) in which fossil insects were described (Nel *et al.*, 2004; Vršanský & Makhoul, 2013; Azar *et al.*, 2019; Azar & Nel, 2022, 2023, 2024; Maksoud & Azar, 2021; Maksoud *et al.*, 2022). Moreover, this occurrence is the first (mid-) Late Cretaceous record of the Belostomatidae. Together with *Libanoaeshna mikhaeli* Azar *et al.*, 2024, they constitute the first insects to be found in the fossil fish Konservat-Lagerstätte of Haqel, making it an additional palaeoentomological site to the numerous other sites in Lebanon (Maksoud *et al.*, 2022).

Material and methods

The new fossil originated from the marly limestones of Haqel (Fig. 1), famous for containing more than 70 genera of fossil fishes. These deposits are from the lower upper Cenomanian and are located within a region of thick basin sediments. This area preserved local nerineids, rudists, and orbitolinids, suggesting a warm and shallow sea environment (Krings & Mayr, 2004). Haqel limestones are hard, fine-grained, well-bedded and laminated, and rich in fossils (Hückel, 1970, 1974) with some levels rich in flint nodules (Fuchs *et al.*, 2009).

Since the original attribution of the outcrop to the Cretaceous (Botta, 1833), several ages were proposed. The attribution of Cenomanian age for the Haqel limestones was proposed by Patterson (1967) based on the fish fauna and Hückel (1970) based on benthic foraminifera. Dubertret (1959, 1966), and Saint-Marc (1974) estimated a lower Cenomanian age for the sequences at Haqel, based on biostratigraphic studies. A late Cenomanian age was proposed by Hemleben (1977) based on a study of planktonic Foraminifera, and is currently the most accepted age estimation (Wippich & Lehmann, 2004; Fuchs *et al.*, 2009).

The photographs were taken with an AxioCam MRc 5 camera attached on a Zeiss Discovery V16 stereomicroscope. Photographs of the fossils were digitally stacked using Helicon Focus 8 software and processed with Adobe Photoshop CC 2019. Drawings were made with a camera lucida attached to Zeiss Discovery V12 and digitally vectorized with Pixelmator Pro 3.3.6 Mosaic software.

Morphological terminology mainly follows Hebsgaard *et al.* (2004) and Ribeiro *et al.* (2018). We follow the recent classification for Belostomatidae provided by Ribeiro *et al.* (2018).

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Systematic palaeontology

Suborder Heteroptera Latreille, 1810

Infraorder Nepomorpha Popov, 1968

Superfamily Nepoidea Latreille, 1802

Family Belostomatidae Leach, 1815

Libanobelostoma gen. nov.

Figs 2–3
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Type species. *Libanobelostoma calineae* **sp. nov.** (by monotypy and present designation).

Diagnosis. *Libanobelostoma* is distinguished from all other belostomatid genera by the following unique combination of characters: total body length of 28.5 mm; first rostrum segment much longer than the second segment; pronotum as wide as mesonotum; protarsus three-segmented; membranous area occupying at most one-third of wing.

Etymology. The genus name is composed of 'Libano-' from the Latin *Libanus*, referring to the country from which the specimen originated and '-belostoma', referring to the type genus in Belostomatidae. Gender feminine.

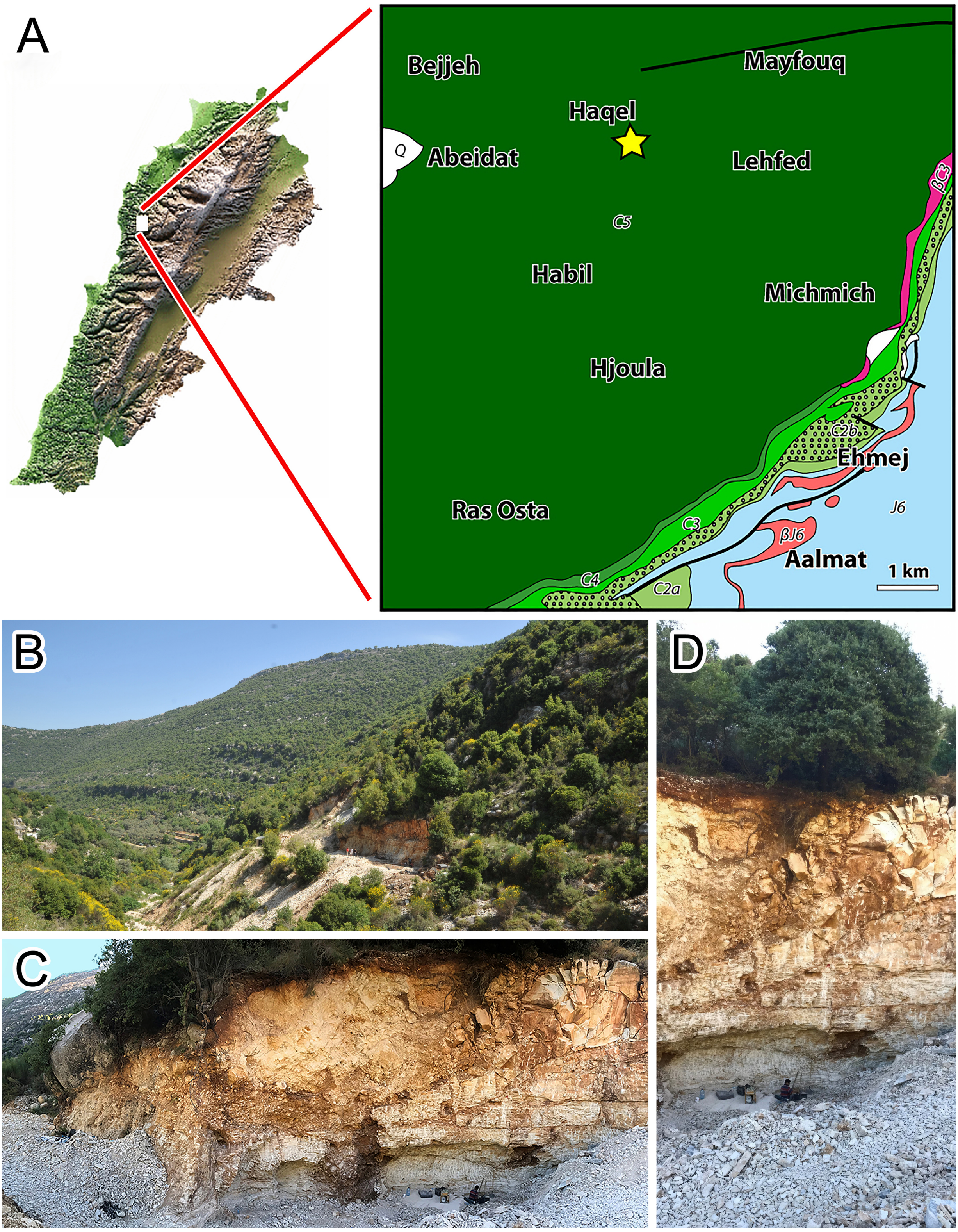

FIGURE 1. Mid-Cretaceous fossil site Konservat-Lagerstätte of Haqel, Lebanon. **A**, Geological map of outcrop (modified from Dubertret, 1945; Dubertret & Wetzel, 1945). J6 = uppermost Jurassic; C2a = lower Barremian 'Grès du Liban' sandstone; C2b = Barremian clay and oolitic deposition of upper part of 'Grès du Liban' and oolitic deposition of lower part of Jezzinian; C3 = micritic part of Jezzinian (uppermost Barremian-lowermost Aptian); C4 = Albian; C5 = Cenomanian; Q = Quaternary scree; βJ6 = Kimmeridgian volcanic deposition; βC3 = Jezzinian volcanic deposition. Thick lines represent faults. **B**, General view of outcrop. **C**–**D**, Details of stratigraphic layers of outcrop.

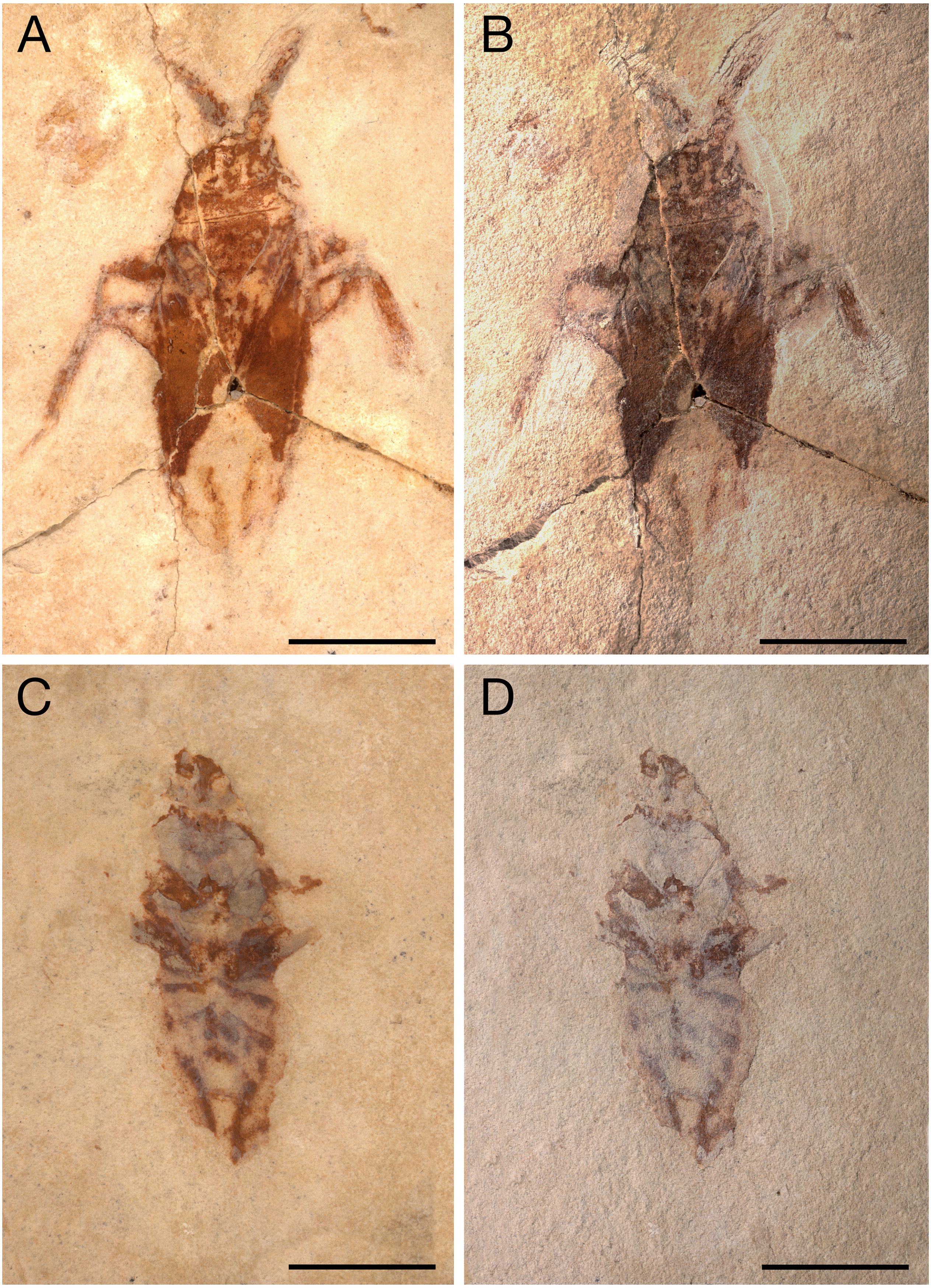

FIGURE 2. *Libanobelostoma calineae* **gen et sp. nov.**, holotype I-26247/2A (part) and B (counterpart), general habitus. **A–B**, Dorsum under natural light (A) and under alcohol (B). **C–D**, Venter under natural light (C) and under alcohol (D). Scale bars = 1 cm.

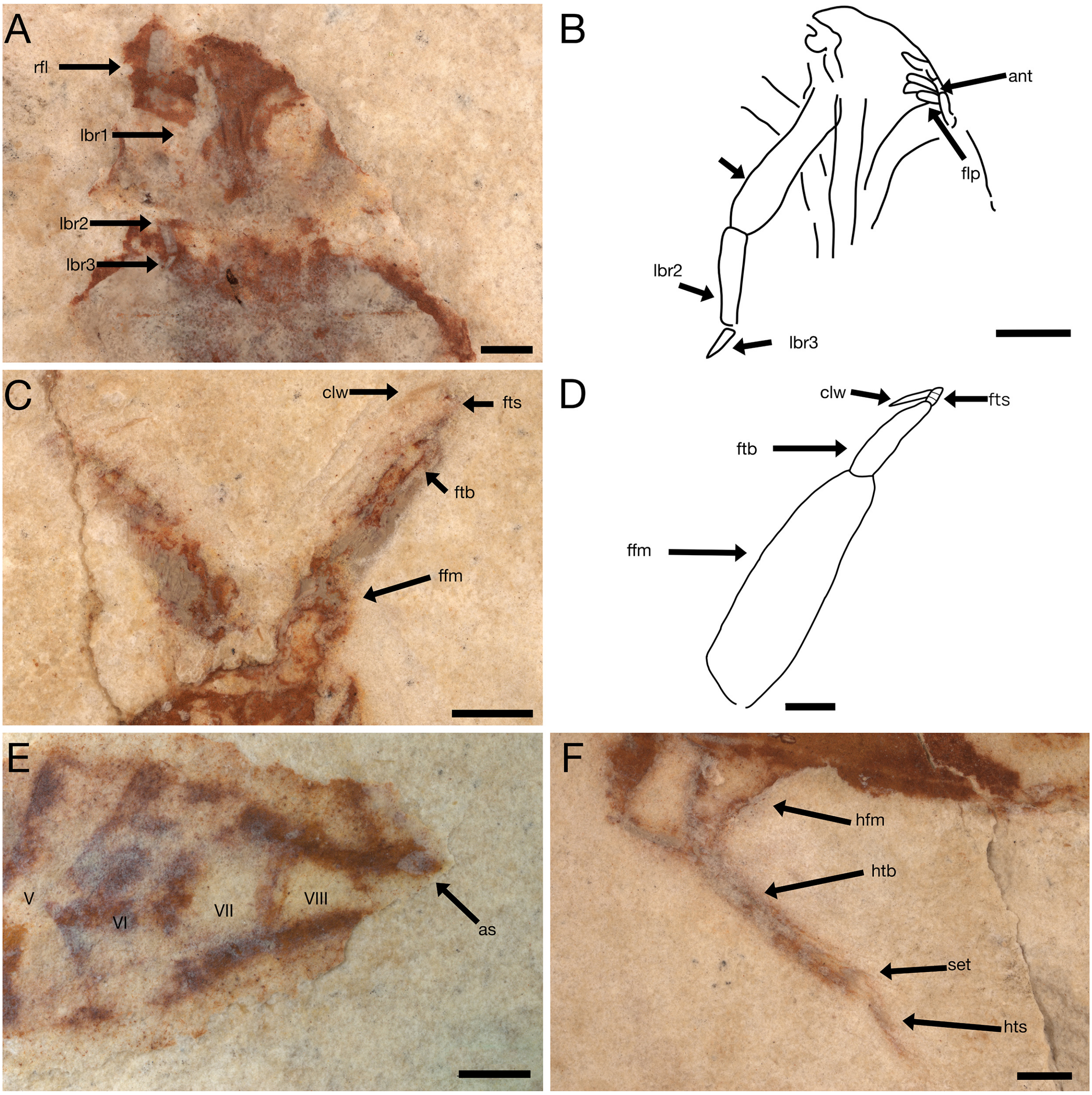

FIGURE 3. *Libanobelostoma calineae* **gen et sp. nov.**, holotype I-26247/2A (part) and B (counterpart). **A**, Ventral view of head. **B**, Reconstruction of rostrum. **C**, Dorsal view of head and prothoracic legs. **D**, Reconstruction of right raptorial fore leg. **E**, Abdominal sternum. **F**, Hind leg in dorsal view. *Abbreviations*: ant = antennae; as = air straps (siphon); clw = claw; ffm = forefemur; flp = finger-like projections; ftb = foretibia; fts = foretarsus; hfm = hind femur; htb = hind tibia; hts = hind tarsus; lbr1 = first labial segment; lbr2 = second labial segment; lbr3 = third labial segment; rfl = right foreleg; set = setae. IV–VII: abdominal sterna IV–VII. Scale bars: **A**–**D** = 1 mm; **E**–**F** = 2 mm.

Libanobelostoma calineae sp. nov.

Figs 2–3
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Type material. Holotype I-26247/2A and B (part and counterpart of entire body), housed at the Natural History Museum of the Lebanese University.

Diagnosis. As for the genus (*vide supra*).

Etymology. The specific epithet honours Caline Abi Saad, wife of PAB, who found the new fossil.

Locality and horizon. Lower Late Cenomanian, Haqel, Caza Byblos, Governorate Jbeil-Kesserouan, Central Lebanon.

Description. Body rounded and flattened (Fig. 2A–B), 28.5 mm length; 10.6 mm, greatest width across abdomen; coloration pattern poorly preserved.

Head short, *ca.* 1.6 mm long, 4.3 mm wide; one triangular eye preserved (Fig. 1A); anteclypeus rounded, *ca.* 8 mm long; clypeus triangular, two times shorter than anteclypeus; rostrum preserved ventrally (Fig. 1C–D; Fig. 2A–B), with three segments visible, lengths of rostrum segments one to three: 1.8 mm, 1.3 mm, and 0.3 mm. One antenna poorly preserved ventrally, three antennomeres with finger-like projections preserved for first two.

Thorax 10.2 mm long. Pronotum with slightly convex lateral margins; pronotum and mesonotum subequal in length (0.21 mm). Scutellum triangular and longer than pronotum + mesonotum. Hemelytra incompletely preserved, with clavus and corium distinguishable, 15.8 mm long, no visible cells or veins, membranous area corresponding to at most one-third of wing. Forelegs raptorial-shaped with elongate and stout femur (4.55 mm), foretibia about twice shorter than forefemur and subequal in width with foretarsi, three tarsomeres; one preserved simple long claw (Fig. 2C–D). Middle legs poorly preserved with only middle femur visible, slightly enlarged, and one middle tibia. Hind legs long (*ca.* 12 mm), metacoxa conical, firmly united with metapleuron, femur slightly enlarged at base and narrower at apex, tibia apparently flattened, bearing few poorly preserved setae (Fig. 2F), hind tarsus short, with segmentation difficult to state. Abdomen robust and broad, 14.1 mm long, only abdominal segments V–-VIII distinguishable (Fig. 2E), air siphon incomplete, short, probably *ca.* 3.8 mm long.

Discussion

Hebsgaard *et al.* (2004) proposed the following synapomorphies for the clade Nepoidea (= Nepidae + Belostomatidae), shared with *Libanobelostoma calineae* **gen. et sp. nov.**: base of second labial segment reduced, without median, longitudinal groove for the reception of stylets; forewings with thorny fields and apex of abdomen with paired respiratory processes (siphon). Furthermore, Mahner (1993) proposed a set of apomorphies for the Nepoidea, of which the new fossil presents 'abdominal sternites divided into parasternites and median sternites', visible as a longitudinal darkened band on the ventral part of abdomen. This character plus the general body shape and presence of elongate raptorial forelegs support an attribution to clade Nepoidea. The Belostomatidae and Nepidae further have a 3–4 segmented labium and foretarsus without a fringe of setae (Schuh & Weirauch, 2020). These characters are observed in the new fossil with a three-segmented rostrum and the foretarsus apparently lacking setae.

The monophyly of Nepidae is supported by the following synapomorphies: abdomen with three pairs of static sense organs (unknown in the new fossil); respiratory siphon non-retractile, long and filiform (Hebsgaard *et al.*, 2004). Thus, the new fossil has the plesiomorphic characters 'respiratory siphon at most present as short, retractile air straps'.

Hebsgaard *et al.* (2004) defined the following synapomorphies for the clade Belostomatidae: metacoxae conical, firmly united with metapleuron (short and free in Nepidae), and hind tibiae flattened, with swimming hairs (simple and narrow in Nepidae). In *Libanobelostoma calineae* **gen. et sp. nov.**, the metacoxae resemble those of the extant Belostomatidae (see Mahner, 1993: fig. 8D), and the hind tibiae have swimming hairs, even if they are not very flattened. Moreover, the classification within Belostomatidae has been revised in Ribeiro *et al.* (2018) providing a comprehensive phylogenetic framework. The crown group Belostomatidae is currently divided into two extant subfamilies: Belostomatinae and Lethocerinae; the extinct subfamily Stygeonepinae (represented by *Iberonepa* Martínez-Delclòs, Popov & Nel, 1995 and *Stygeonepa* Popov, 1971) belongs to the stem group. *Libanobelostoma calineae* **gen. et sp. nov.** recovers three synapomorphies of the total group Belostomatidae*:* eyes somewhat projected laterally with angled borders, tarsi three-segmented, and the siphon retracted into the abdomen. Additionally, the new fossil presents the only synapomorphy proposed by Ribeiro *et al.* (2018) for the crown group Belostomatidae with the metacoxae conical and firmly united with the metapleuron.

Jattiot *et al.* (2012) described *Cratonepa enigmatica*, an enigmatic Nepoidea from the Cretaceous of the Crato Formation in Brazil, which has a respiratory siphon at most present as short, retractile air straps, but exhibits nepid-type hind coxae. *Libanobelostoma calineae* **gen. et sp. nov.** differs from *Cratonepa* in the shape of the hind coxae, as mentioned above, and in having long setae on the hind tibia.

Within the total group Belostomatidae, the affinities of this new fossil with Stygeonepinae can be eliminated, because the fossil lacks the apomorphic 'paddle-like' hind legs of this clade (Martínez-Delclòs *et al*., 1995).

The only external morphological synapomorphy provided by Hebsgaard *et al*. (2004) to support the Lethocerinae is the presence of one large and one small claw on the foretarsi; however, this condition is absent in the new fossil, which has only one large claw. Additionally, the presence of a distally closed frontogenal suture is proposed as a synapomorphy of Lethocerinae (Ribeiro *et al*., 2018), but is impossible to verify in the new fossil.

The clade Belostomatinae is supported by several characters and among them, the presence of foretarsi bearing both claws vestigial (Ribeiro *et al*., 2018). However, the new fossil presents the plesiomorphic condition for this character, with a simple claw. Moreover, following Estévez & Ribeiro (2011), the fossil fails to fall in Lethocerinae or Belostomatinae, sharing with the latter abdominal sternites apparently not subdivided by a suture, but having a unique condition with the first segment of rostrum being the longest and much longer than the second. Therefore, we discount affinities with any extant or extinct Belostomatinae and Lethocerinae, leaving this fossil placed in Belostomatidae.

Mesozoic belostomatid genera include: *Mesobelostomum* Haase, 1890, *Aenictobelostoma* Polhemus, 2000, *Lethopterus* Popov, 1989, *Triassonepa* Criscione & Grimaldi, 2017, and *Araripebelostomum* Nel & Paicheler, 1992. *Mesobelostomum* is a poorly known taxon; however, the new fossil's body is twice shorter in length, and in *Mesobelostomum deperditum* (Germar, 1939) the hind tibiae are not basally enlarged (Nel & Paicheler, 1992). *Libanobelostoma* **gen. nov.** can be distinguished from *Triassonepa* by the pronotum as wide as the mesonotum, abdomen wider; protarsus not elongated, and apparently three-segmented (Criscione & Grimaldi, 2017). It can also be distinguished from *Aenictobelostoma* by its longer and less rounded body (Polhemus, 2000), even if *Aenictobelostoma* lacks key features for giant water bugs (*e.g.*, rostrum or hind legs). The genus *Lethopterus* is known only by a poorly preserved forewing; however, the new fossil can be distinguished from *Lethopterus* by its wing length almost half shorter, the membranous area occupying at most one-third of the wing (Popov, 1989). Finally, the new genus differs from *Araripebelostomum* in body shape and forewing membrane; *Araripebelostomum* has a greatly rounded body and a net of cells in membrane.

The new specimen presents both synapomorphies and symplesiomorphies for Belostomatidae, leading us to not attribute it to any extinct or extant subfamily within Belostomatidae. Additionally, all the differences with other Mesozoic genera in Belostomatidae justify the definition of *Libanobelostoma* **gen. nov.**

The discovery of insects in Haqel Konservat-Lagerstätte (Azar *et al*., 2024) is very important for understanding the palaeoenvironnement of the area during the Cenomanian. Haqel is traditionally considered a marine basin on its sedimentation pattern, turbidites, and fossil assemblages. However, the presence of dragonflies and giant water bugs may indicate that Haqel was likely very close to an insular system with freshwater source, explaining the presence of such insects and several odonatan groups, some endemic to date. This situation could be somewhat similar to that of the Kimmeridgian lithographic limestone of Bavaria, *viz.* small atoll islands with a rather rich terrestrial fauna and flora surrounded by warm, shallow marine water without oxygen at the bottom in which the limestone was deposited with the organisms. This suggestion is also reinforced by the presence of families considered to be extinct after the Jurassic Period, leading to consider such environments as refugee areas.

Conclusion

We describe the first aquatic insect fossil *Libanobelostoma calineae* **gen. et sp. nov.**, from Haqel Cenomanian Konservat-Lagerstätte, Lebanon. This new taxon displays both synapomorphies and symplesiomorphies for Belostomatidae, justifying to unassigned it within Belostomatidae. This new occurrence fills a gap in the fossil record of Belostomatidae, lacking occurrences between the early Upper Cretaceous and Paleocene. This discovery justifies intensive fieldwork to enhance our knowledge of the late Cretaceous insect fossil record.

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