Cretaceous Research 34 (2012) 344–347

Contents lists available at SciVerse ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

An enigmatic Nepoidea from the Lower Cretaceous of Brazil (Hemiptera: Heteroptera)

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ARTICLE INFO

Article history:
Received 20 September 2011
Accepted in revised form 28 November 2011
Available online 7 December 2011

Keywords:
Nepomorpha
Nepidae
Belostomatidae
Evolution
Mesozoic

ABSTRACT

Cratonepa enigmatica gen. and sp. nov., an enigmatic new nepoid bug, is described from the Lower Cretaceous Crato formation in Brazil. Although its general habitus is strikingly similar to that of the Cenozoic and recent Nepidae, it has several plesiomorphic characters, the most obvious being the siphon retractiled into the abdomen, which supports a basal position as a sister group of either all Nepidae or even Nepoidea. The morphology of its legs suggests that it was a walking predator living in mud or in aquatic vegetation, as for extant Nepidae, although the absence of a long siphon suggests a very different way of breathing.

1. Introduction

Even though Nepomorpha have the best fossil record of all Heteroptera (Popov, 1971; Carpenter, 1992; Rasnitsyn and Quicke, 2002; Grimaldi and Engel, 2005), the fossils of the family Nepidae are very rare, with fewer than ten specimens in five species known from the Cenozoic (see annotated list in Nel and Paicheler, 1992, to which it is necessary to add a record from the Chinese Miocene by Zhang et al., 1994). Since *Mesonepa* from the Upper Jurassic of Solnhofen belongs in the Belostomatidae (Carpenter, 1992), the only Mesozoic fossil that has been attributed previously to the Nepidae is *Laccotrephes incertus* Popov, 1971, also from the Upper Jurassic of Germany. This fossil lacks an abdominal siphon and its legs, except for the forefemora. Even if the general body shape is similar to that of modern Nepidae, nothing supports its attribution to this family, as Nel and Paicheler (1992) have previously indicated. In contrast, the fossil record of the Belostomatidae, sister group of Nepidae, is better documented from the Jurassic to the Miocene (Nel and Paicheler, 1992; Polhemus, 2000; Popov et al., 2000; Prokop and Nel, 2000), even including a very specialized Mesozoic subfamily Stygeonepinae with paddle-like swimming legs that is of rather enigmatic position (Martínez-Delclòs et al., 1995). As sister groups, Nepidae and Belostomatidae must of course have the same age of origin. Therefore the lack of Mesozoic Nepidae has been very surprising. The discovery of a small series of nepid-like bugs in the Lower Cretaceous of the Crato Formation partly fills this gap. This formation is one of the most important for Cretaceous insects and has already yielded many tens of thousands of excellently preserved specimens, with about 375 species representing most insect orders (Martill et al., 2007).

2. Material

The material discussed in this paper is stored in the following institutions: Muséum national d'Histoire naturelle Paris (MNHN); Staatliches Museum für Naturkunde Stuttgart (SMNS); private collection, Burkhard Pohl/Wyoming Dinosaur Center (WDC).

3. Systematic palaeontology

Order Hemiptera
Superfamily Nepoidea
Family Nepidae or Belostomatidae

Genus *Cratonepa* gen. nov.

Type species. *Cratonepa enigmatica* sp. nov.

Derivation of name. After the Crato Formation and the Recent genus *Nepa*. Gender feminine.

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doi:10.1016/j.cretres.2011.11.020

Diagnosis. Forefemora with a sulcus but no proximal protuberance; foretibia curved; hind tibiae narrow without swimming hairs, foretarsi two-segmented; mid and hind tarsi three-segmented; abdominal sternites divided into parasternites and median sternites; siphon not visible, retractile in abdomen; abdomen and pronotum broad.

Cratonepa enigmatica sp. nov.
Figs. 1–4

Derivation of name. After the rather enigmatic position of this fossil among the Nepoidea.

Material. Holotype SMNS 66380; paratype MNHN.F.A45784 (Borschukewitz leg.); further material: specimen WDC 107-399 (part and counterpart), and a specimen without a number in private coll. Schwickert, Sulzbachtal, Germany.

Type locality and horizon. Chapada do Araripe, northeastern Brazil; Upper Aptian, Nova Olinda Member of the Crato Formation (Martill et al., 2007).

Diagnosis. Male apterous; female with well-developed wings; female interocular space narrower than in male.

Description of holotype (SMNS 66380; Fig. 1). The fossil is visible in dorsal view but ventral structures of abdomen partly visible. It is thought to be a female adult specimen owing to the presence of wings and absence of a genital capsule, but this structure could well be invisible in dorsal view. Body about 2.4 times as long as wide, 21.5 mm long, 8.9 mm wide (= abdomen width). Eyes twice as large as in MNHN.F.A45784, globular, ca. 1.0 mm in diameter, interocular space only ca. 0.6 mm long, narrower than in MNHN.F.A45784; base of rostrum visible, projected in front, rostrum apparently short, ca. 0.9 mm long; clypeus and maxillary plates not visible. "Neck" between head and pronotum clearly visible; pronotum transverse, median length 2.3 mm, humeral width 5.7 mm, of same shape as in MNHN.F.A45784; anterior margin slightly concave, posterior margin of pronotum apparently straight. Scutellum as long as broad, 2.9 mm long, 2.8 mm wide. Hemelytra 13.5 mm long, ca. 5.4 mm wide, with corium strongly sclerotized, 12.0 mm long, membrane 3.8 mm long, apparently divided into large cells. Metathoracic wing well developed and clearly functional, preserved part 9.5 mm long, with strong veins. Front femora 8.3 m long, 1.0 mm wide, slightly longer than middle femora; without preserved proximal protuberance or sulcus; front tibiae almost as long as femora, tarsi not visible, hidden under femora. Middle and hind legs: femora and tibiae not flattened, narrow, parallel-sided; mid femora 5.8 mm long, 0.6 mm wide, tibia 4.0 mm long,

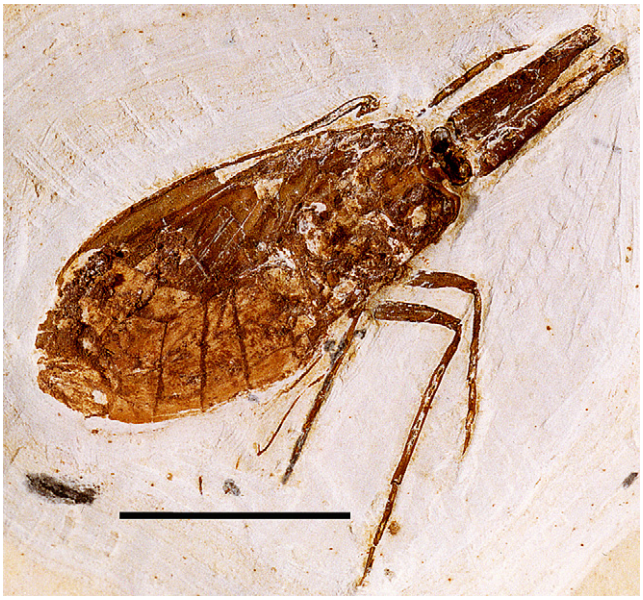

Fig. 1. *Cratonepa enigmatica* gen. and sp. nov., holotype SMNS 66380, photograph of habitus, dorsal view. Scale bar represents 10 mm.

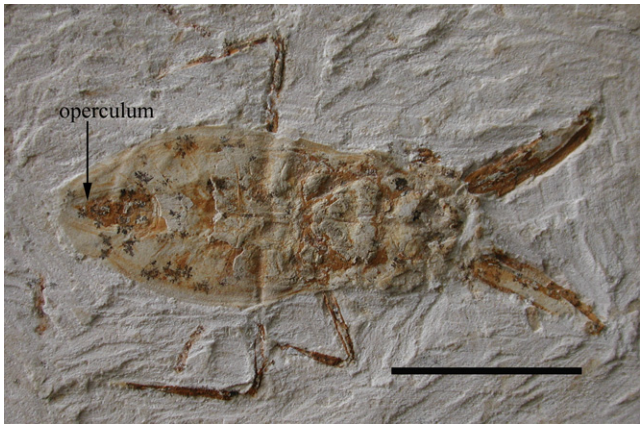

Fig. 2. *Cratonepa enigmatica* gen. and sp. nov., paratype MNHN.F.A45784, photograph of habitus, ventral view. Scale bar represents 10 mm.

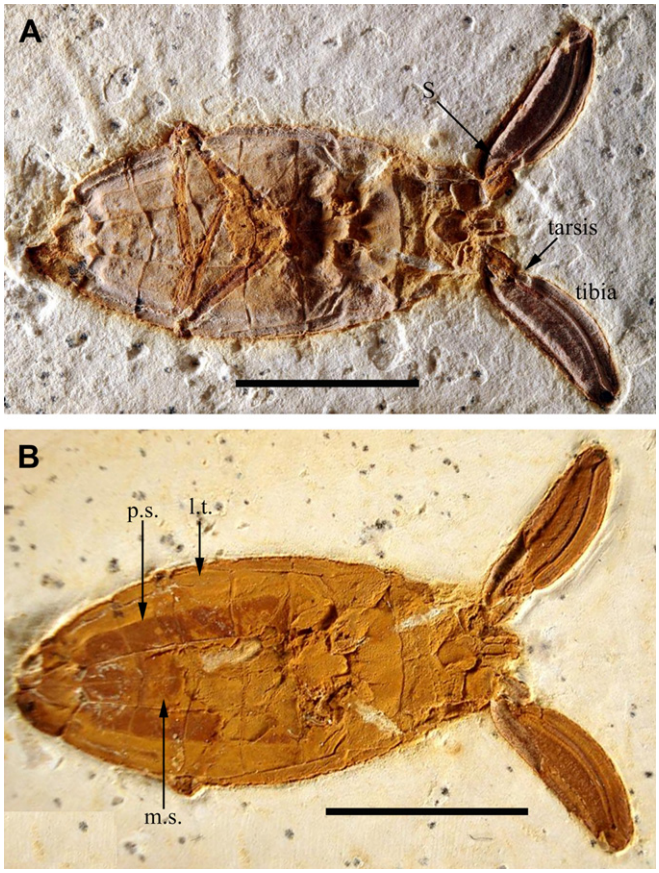

Fig. 3. *Cratonepa enigmatica* gen. and sp. nov., specimen WDC 107-399 (part and counterpart), photograph of habitus ventral views. A, 107; B, 399; l.t., ventral laterotergite; p.s., parasternite; m.s., median sternite; S, sulcus of profemora. Scale bars represent 10 mm.

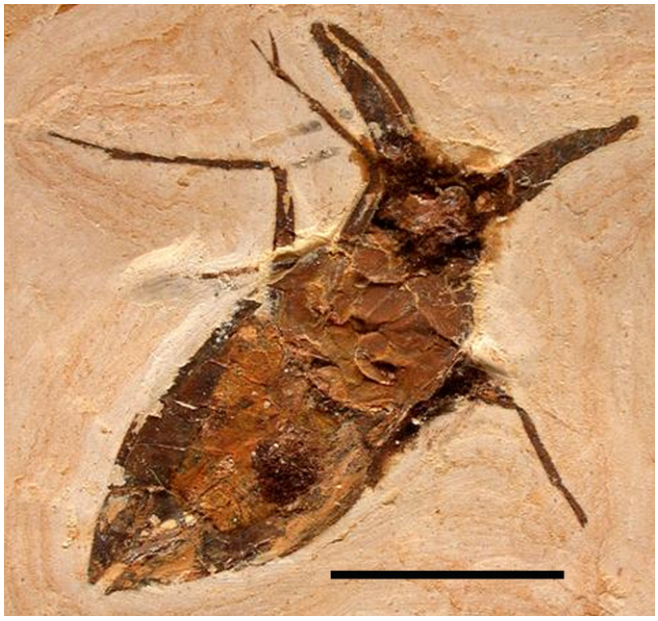

Fig. 4. *Cratonepa enigmatica* gen. and sp. nov, specimen without number, private coll. Schwickert; photograph of habitus, ventral view. Scale bar represents 10 mm.

0.3 mm wide; hind femora 8.1 mm long, 0.7 mm wide, tibia 7.7 mm long, 0.3 mm wide; middle and hind tarsi well preserved, clearly three-segmented, with first segment 1.2 mm long, second 0.9 mm long, third 0.6 mm long in mid leg, while in hind leg, first segment is 1.7 mm long, second 1.3 mm long, and third 1.3 mm long. Abdomen flattened, 12.5 mm long, 8.9 mm wide; second abdominal sternite not visible, hidden by wings; ventral subdivision of abdominal segments III–VI into ventral laterotergites, parasternites and median sternites partly visible on segments V and VI, respectively 1.1 mm, 1.7 mm, and 1.5 mm wide; abdominal spiracles not visible; median length of sternite VI 2.4 mm, sternite V 1.8 mm, sternite IV 1.5 mm, sternite III 2.4 mm; operculum not preserved; respiratory siphon not visible, probably retracted inside the abdomen; no genital capsule visible inside the abdomen.

Description of paratype (MNHN.F.A45784; Fig. 2). The fossil is visible in ventral view. It is thought to be a male adult specimen, owing to the presence of a typical genital capsule. Body about 2.5 times as long as wide, 23.4 mm long, 9.2 mm wide (= abdomen width). Head ca. 1.7 mm long and 2.5 mm wide, but poorly preserved, only the eyes being partly visible, globular, ca. 0.4 mm in diameter, interocular space nearly twice width of an eye. Pronotum transverse, median length 4.2 mm, humeral width 4.3 mm; subdivision of pronotum into an anterior and a posterior lobes very weakly indicated by a slight median constriction, lateral margins more or less parallel in middle, anteriorly not expanded; anterior margin poorly visible, but may be weakly concave; posterior margin of pronotum weakly concave. Prosternum only partly visible, fossilised impressed on pronotum with a median longitudinal groove. Scutellum slightly broader than long, basally elevated, and with a narrow median groove. Hemelytra and hind wings not visible, probably absent. Front femora 7.6 m long, 1.2 mm wide, slightly longer than middle femora; without any visible proximal protuberance or sulcus; front tibiae almost as long as femora, tarsi not preserved. Middle and hind legs: femora and tibiae not flattened, narrow, parallel-sided; mid femora 6.0 mm long, 0.4 mm wide, tibia 5.0 mm long, 0.4 mm wide; hind femora 7.6 mm long, 0.6 mm wide, tibia circa 7.6 mm long, 0.5 mm wide; tarsi not preserved. Abdomen flattened, 12.0 mm long, 9.2 mm wide; second abdominal sternite rounded, extending beyond projections of metasternum; ventral subdivision of abdominal segments III–VI into ventral laterotergites, parasternites and median sternites clearly visible, respectively 1.3 mm, 1.4 mm, and 1.8 mm wide; abdominal spiracles not very distinct but placed along lateral margins of abdomen; median length of sternite VI 1.8 mm, sternite V 1.4 mm, sternite IV 1.6 mm, and sternite III 2.0 mm; male operculum triangular, 2.6 mm long, 2.2 mm wide, and reaching end of connexivum; respiratory siphon not visible, probably retracted inside the abdomen; a long, broad male genital capsule visible inside the abdomen.

Description of specimen 107-399 (coll. Burkhard Pohl/WDC; Fig. 3). A nearly complete specimen visible from below; body 2.2 times as long as wide, 26.2 mm long, 11.6 mm wide; head only partly visible with mouthparts short but strong. Prosternum 4.2 mm long, 7.2 mm wide, with a general shape corresponding to that of MNHN.F.A45784. Distance between insertions of median legs 1.3 mm, between insertions of hind legs 0.3 mm. Front femora better preserved than on other specimens, 9.2 m long, 1.6 mm wide, without preserved proximal protuberance but with a distinct sulcus; front tibiae curved, almost as long as femora; foretarsus apparently two-segmented, with a basal tarsomere distinctly larger and longer than second one and with large claws, middle legs missing; hind femora and tibiae not flattened, narrow, parallel-sided; hind femora 7.8 mm long, 0.7 mm wide, tibia 7.6 mm long, 0.3 mm wide; hind tarsi three-segmented. Second abdominal sternite rounded, extending beyond projections of metasternum. Abdomen flattened, ventral subdivision of abdominal segments III–VI into ventral laterotergites, parasternites and median sternites clearly visible, respectively ca. 1.6 mm, 1.6 mm, and 2.0 mm wide; abdominal spiracles not very distinct but placed along lateral margins of abdomen; median length of sternite VI 3.0 mm, sternite V 2.7 mm, sternite IV 2.7 mm, sternite III 3.0 mm; operculum triangular, 2.9 mm long, 2.9 mm wide, and reaching end of connexivum; respiratory siphon not visible, probably retracted inside abdomen.

Description of specimen without number (coll. Schwickert; Fig. 4). A nearly complete specimen visible from below, with all legs preserved; body 2.4 times as long as wide, 24.0 mm long, 9.9 mm wide; head only partly visible. Prosternum deformed and useless. Distance between insertions of median legs 0.9 mm, between insertions of hind legs 0.2 mm. Front femora 6.8 m long, 1.5 mm wide, without preserved proximal protuberance but with a distinct sulcus; front tibiae curved, almost as long as femora; foretarsus apparently two-segmented, with basal tarsomere distinctly larger and longer than second one and with large claws. Middle and hind legs: femora and tibiae not flattened, narrow, parallel-sided; mid femora ca. 5.7 mm long, 0.6 mm wide, tibia 5.8 mm long, 0.4 mm wide; hind femora 7.9 mm long, 0.7 mm wide, tibia 7.1 mm long, 0.4 mm wide; hind tarsi three-segmented. Second abdominal sternite rounded, extending beyond projections of metasternum. Abdomen flattened, ventral subdivision of abdominal segments III–VI into ventral laterotergites, parasternites and median sternites clearly visible, abdominal spiracles not clearly visible; operculum triangular, broken at apex but ending just before apex of connexivum; respiratory siphon not visible, probably retracted inside abdomen.

4. Discussion

Several structures of these four fossils cannot be compared because three are fossilised in ventral view while one is in dorsal view. Nevertheless these fossils are similar in size, body shape (especially the pronotum and abdomen) and leg structure. Both

have a hidden siphon, retracted inside the abdomen. MNHN.F.A45784 is apparently apterous whereas SMNS 66380 has well-developed wings. It is not possible to determine whether the other two have wings. Such differences can be explained by sexual dimorphism. The presence of a genital capsule in MNHN.F.A45784 supports the hypothesis that it is a male, while its apparent absence (not visible) in SMNS 66380 suggests that it is a female. The interoccular space is narrower in SMNS 66380 than in MNHN.F.A45784, which confirms this hypothesis (Lansbury, 1974). Therefore we consider that they belong to different sexes of the same species.

Hebsgaard et al. (2004) proposed the following synapomorphies for the clade Nepoidea (= Nepidae + Belostomatidae): apex of abdomen with paired respiratory processes (siphon); forewings with thorny fields; and base of labial segment 2 reduced, without median, longitudinal groove for the reception of stylets. All of these characters are unavailable in our fossils. Mahner (1993) proposed a set of apomorphies for this clade and of these *Cratonepa* has the following: "abdominal sternites divided into parasternites and median sternites". This character plus the general body shape and presence of elongate grasping forelegs support an attribution to this clade.

Hebsgaard et al. (2004) proposed the following synapomorphies for the clade Belostomatidae: metacoxae conical, firmly united with metapleuron, while they are short and free in Nepidae and in our fossils (at least in specimen WDC 107-399); and hind tibiae flattened, with swimming hairs, while they are simple in Nepidae. The apomorphic state for this last character is convergently present in recent Belostomatidae, Corixidae, and Notonectidae. The Mesozoic belostomatid Stygeonepinae have very different hind tibiae, greatly flattened into paddles (Martínez-Delclòs et al., 1995). It remains that *Cratonepa* and the Nepidae have the plesiomorphic character.

Hebsgaard et al. (2004) also proposed the following synapomorphies for the clade Nepidae: abdomen with three pairs of static sense organs (unknown in *Cratonepa*); respiratory siphon non-retractile, long and filiform. *Cratonepa* has thus the plesiomorphic character "respiratory siphon at most present as short, retractile air straps"; all tarsi one-segmented. *Cratonepa* has thus the plesiomorphic state "tarsi two- or three-segmented". Only the Nepidae have one tarsal segment in all legs. Recent Belostomatidae have three-segmented mid and hind tarsi (two-segmented in the Jurassic *Mesobelostomum* Haase, 1890; see Nel and Paicheler, 1992), one- to three-segmented foretarsi (Schuh and Slater, 1995) and eggs with 2–26 respiratory horns (unknown in *Cratonepa*).

In consequence, *Cratonepa* remains a bug of enigmatic position within the Nepoidea. Its general habitus is that of a Nepidae, but with several plesiomorphic characters that imply that it could be in a very basal position in Nepidae, as sister group of all other representatives of the family, or even represent the sister group of all the Belostomatidae + Nepidae, either fossil or Recent. It is noteworthy that all known fossil and Recent Belostomatidae have flattened hind tibiae, which is a derived character state compared to the plesiomorphic walking legs in Nepidae and *Cratonepa*.

The non-flattened hind tibiae of *Cratonepa* suggest that it had a way of locomotion similar to that of the recent Nepidae, walking on the bottom of a pond or on emergent vegetation, while the Belostomatidae are better able to swim. Nevertheless, the biology of this predatory aquatic predator was probably different from those of Cenozoic and Recent Nepidae in the absence of an elongate siphon that stopped it breathing under water deeper than its length. The scarcity of the Nepidae before the Early Cretaceous and the presence of this nepid-like bug in the Crato Formation could be related to changes in freshwater ecosystems during the Aptian–Cenomanian and the diversification of aquatic angiosperms: Belostomatidae and the Stygeonepinae are swimming insects while Nepidae walk in the mud on the bottom of small ponds and/or hunt among aquatic plants. The Crato lagoon was brackish and all Crato freshwater insects and plants are allochthonous. Nevertheless their high diversity shows that somewhere near this lagoon there was a freshwater habitat with aquatic bugs and diverse aquatic angiosperm vegetation (see Fanton et al., 2006; Martill et al., 2007). This environment could have favoured the diversification of Nepidae or nepid-like bugs that were hunting in this newly developed biota. Perhaps at the same time the highly specialized Jurassic–Early Cretaceous Stygeonepinae became extinct, because they are no longer recorded in the aquatic biotas of the Upper Cretaceous. This point needs confirmation because there are only few localities for aquatic fossil insects from this time.

Acknowledgement

We thank Paul Tinerella, University of Minnesota, for his kind help in the study of these fossils.

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