

# Historical Biology

An International Journal of Paleobiology

ISSN: (Print) (Online) Journal homepage: <https://www.tandfonline.com/loi/ghbi20>

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To cite this article: María B. Lara , John R. Foster , James I. Kirkland & Thomas F. Howells (2020): First fossil true water bugs (Heteroptera, Nepomorpha) from Upper Jurassic strata of North America (Morrison Formation, southeastern Utah), *Historical Biology*

To link to this article: <https://doi.org/10.1080/08912963.2020.1755283>



Published online: 18 May 2020.



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ARTICLE



# First fossil true water bugs (Heteroptera, Nepomorpha) from Upper Jurassic strata of North America (Morrison Formation, southeastern Utah)

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## ABSTRACT

The first fossil hemipteran from the Late Jurassic of North America, *Morrisonnepsa jurassica* n. gen. et n. sp., is reported and described from the Morrison Formation, Jurassic Salad Bar locality, San Juan County, Utah, USA. The new specimen is characterised and illustrated, showing morphological characters similar to nepomorphs such as forewing well-developed and folded flat on the abdomen, oval abdomen shape, and the presence of a short pair of appendages. The taxonomic allocation close to members of the Nepomorpha is discussed. *Morrisonnepsa jurassica* n. gen. et n. sp. was collected with abundant plants, spinicaudatan carapaces, and a small amphibian from a finely laminated shale that overlies a coarser plant debris bed, supporting the presence of a possible oxbow lake or pond, environments developed within the greater ecosystem of the Morrison Formation during the Late Jurassic. In this context, we analyse the taphonomic and palaeoecological implications of the presence of aquatic insects. Besides providing morphological information on Jurassic nepomorphs, the new fossil helps illustrate how the aquatic insect assemblage was integrated during the Jurassic in North America.

## ARTICLE HISTORY

Received 24 March 2020  
Accepted 9 April 2020

## KEYWORDS

Heteroptera; Nepomorpha;  
Late Jurassic; Morrison  
Formation; North America  
(Utah)

## Introduction

The Suborder Heteroptera (Latreille 1810), ‘sucking bugs or true bugs’, a group of about 40,000 species of insects in the Order Hemiptera, has a long fossil record dating back to the Permian?–Middle Triassic (Shcherbakov 2010; Criscione and Grimaldi 2017; Derka et al. 2019). The heteropterans that live in aquatic and semi-aquatic ecosystems (~4800 species) belong to three monophyletic infraorders: Gerromorpha (Popov 1971), Nepomorpha (Popov 1968), and Leptopodomorpha (Popov 1971). They are a significant component of the world’s aquatic insect biota, occurring on all continents except Antarctica (Polhemus and Polhemus 2008; Derka et al. 2019).

The Infraorder Nepomorpha (Popov 1968) (Clade Euheteroptera Stys 1985) includes the only truly aquatic heteropterans, having their greatest diversity in tropical zones and classified in the Nepidae (Latreille 1802) ‘water scorpions’ (~268 species); Belostomatidae (Leach 1815) ‘water bugs’ (~169 species); Corixidae (Leach 1815) ‘water boatmen’ (~662 species); Notonectidae (Leach 1815) ‘backswimmers’ (~422 species); Naucoridae (Fallén 1814) ‘creeping water bug’ (~398 species); Ochteridae (Kirkaldy 1906) ‘velvety shore bugs’ (~75 species); Gelastocoridae (Kirkaldy 1897) ‘toad bugs’ (~116 species); and Pleidae (Fieber 1851) ‘pygmy backswimmers’ (~44 species); among other small families with more limited distributions (Polhemus and Polhemus 2008; Panizzi and Grazia 2015; Szewo 2018; Ye et al. 2019; Zhen et al. 2020). The majority of nepomorphs species are predatory, although some can be phytophagous (Corixidae). They are confined to the aquatic environment (lotic and lentic) throughout their entire life cycle, leaving the water only in occasional dispersal flights (Schuh and Slater 1995; Ye et al. 2019).

The nepomorphs have the best fossil record of all Heteroptera, the oldest member being *Arlecoris louisi* (Shcherbakov 2010), from the earliest Middle Triassic (early Anisian) of the northern Vosges

Mountains of France (Guillot 2005; Grimaldi and Engel 2005; Criscione and Grimaldi 2017). Most fossil insects recorded in the Jurassic belonged to extinct families or to stem groups of recent families (Grimaldi and Engel 2005). The lotic and lentic entomological assemblages were dominated by diverse and widespread aquatic heteropteran bugs (e.g. corixids, belostomatids, gerrids) or adepagan beetles (e.g. coptoclauids, girinids), or both (Buatois et al. 2016).

Jurassic deposits are abundant in Eurasia, but very few Jurassic insect localities have been discovered in North America and Gondwanaland, because insects are extremely rare even in formations widely known as productive for other types of fossils (Sinitshenkova 2002, 2003; Schlüter and Kohring 2008). In North America, fossil insects have been found in Middle Jurassic lagoonal, marginal marine ecosystems of the Callovian Sundance Formation in northern Wyoming and southern Montana (Kilibarda and Loope 1997; Santiago-Blay et al. 2001) and the Todilto Formation of northern New Mexico (Kirkland et al. 1995). The insect records in the Sundance Formation (Grimaldi and Engel 2005) include hemipterans (nepomorphs) and beetles (Dytiscidae, *Holcoptera*-suggestive of a polyphagan lineage), with nepomorphs nymphs preserved in the Todilto Formation (Polhemus 2000). However, although in lesser numbers, Jurassic insects have also been collected from the: Lower Jurassic of Mount Toby Formation, Massachusetts (beetle larvae) (Hitchcock 1858) and Newark Supergroup (beetles, blattids, abundant larvae, and various undetermined fragments (Giebel 1856; Zeuner 1962; Huber et al. 2003); Middle Jurassic of the Toldito Formation, New Mexico (nepomorphs nymphs) (Polhemus 2000); and Upper Jurassic of the Morrison Formation (orthopteran) (Smith et al. 2011).

Here, we present the description and illustration of the first hemipteran collected from the Upper Jurassic strata of North America and only second insect body fossil from the Morrison

Formation. Trace fossils suggest a variety of insects were present in the Morrison Formation, but so far, only isolated caddisfly cases can be attributed to a specific group of aquatic insects, the Trichoptera (Hasiotis et al. 1998; Hasiotis 2004). Based on morphological characters preserved, we placed the new specimen as a true aquatic heteropteran proposing a new taxon and providing a discussion about its taxonomic allocation in the Infraorder Nepomorpha. Finally, we offer taphonomical and palaeoenvironmental information regarding its habitat in the Morrison Formation, increasing our understanding of freshwater aquatic insects and their ecosystems during Jurassic times.

## Geological setting

The Late Jurassic-age Morrison Formation is well known for dinosaurs such as *Stegosaurus*, *Brachiosaurus*, and *Allosaurus*. The formation crops out in eight states of the western USA, from northern Arizona to Montana and from Utah to South Dakota and far western Oklahoma (Dodson et al. 1980; Foster 2003). The Morrison Formation also preserves several lacustrine settings with relatively abundant plants, spinicaudatans, ostracods, gastropods, bivalves, and fish, most of which have been only preliminarily studied (Ash and Tidwell 1998; Evanoff et al. 1998; Lucas and Kirkland 1998; Kirkland 1998; Schudack 1998; Good 2004; Gorman et al. 2008; Buatois et al. 2016). Despite its extensive outcrops, to date, the only reported insect body fossil is an orthopteran wing of *Parapleurites morrisonensis* (Locustopsidae) described from the Temple Canyon site (Colorado) by Smith et al. (2011).

In southeastern Utah, the Morrison Formation is divided into several members and the stratigraphically highest is the Brushy Basin Member (Gregory 1938; Turner and Peterson 2004; Kirkland et al. in press). The Brushy Basin consists of red, green, and grey, often smectitic mudstones, with some laterally restricted channel sandstones that are fine-grained to gravelly. The majority of large dinosaur fossil occurrences in the Morrison are in the Brushy Basin Member (Turner and Peterson 1999), including such sites as the Carnegie Quarry at Dinosaur National Monument, Utah (Carpenter 2013), and the Dry Mesa Quarry in western Colorado (Miller et al. 1991). The Brushy Basin Member also preserves several plant localities in lacustrine, pond, or marsh settings. In San Juan County in southeastern Utah, the member includes two sites that have particularly well-preserved plants: the Montezuma Creek locality (Ash and Tidwell 1998) and the Jurassic Salad Bar locality, just found in late 2016 by J. Kirkland near Gregory's (1938) original type section for the Brushy Basin Member (Kirkland et al. in press).

In the area of the Jurassic Salad Bar locality, the Morrison Formation dips gently to the east-northeast on the east side of the Comb Ridge monocline, a structure exposing Late Triassic- to Early Cretaceous-age stratigraphic units flanking the east side of the Cedar Mesa uplift.

The Jurassic Salad Bar locality, where the fossil described in this paper was collected, is in the medial Brushy Basin Member of the Morrison Formation (Figure 1), approximately 50 metres below the uncomformable contact with the overlying Burro Canyon Formation (Lower Cretaceous) (Kirkland et al. in press). The matrix consists of a finely laminated, light tan to grey, silty shale that is lightly indurated and thus soft and fissile when excavated. The shale is overlain by a highly smectitic mudstone, when naturally weathered, expresses the typical 'popcorn' surface texture of many Brushy Basin mudstones in outcrop. The shale matrix is nearly an organic-rich laminite (Renaut and Gierlowski-Kordesch 2010) that yields a diverse palynoflora (Baghai-Riding et al. 2018). The productive layer is approximately 35 cm thick, with most

material concentrated in an approximately 10 cm thick middle interval. Stratigraphically below this productive layer is several metres of grey sandy mudstone interbedded with muddy sandstone and thin bentonite layers that fine upward from a 1–2 metre-thick, plant- and bone-supported, plant debris bed atypical of the Brushy Basin Member (Parrish et al. 2004; Kirkland 2006). The underlying plant debris bed is similar to those in the Lower Cretaceous Wessex Formation of England, which are famous for the abundance and diversity of the flora and fauna they preserve (Martill 2001; Sweetman and Insole 2010). The palaeoenvironment represented by the productive shale layer appears to represent the final stage of an infilling oxbow lake or pond.

The fossil insect FHPR 17299 was found among abundant plant macrofossils in the 35-cm-thick productive bed. The plant material includes the ginkgophytes *Czekanowskia* and *Ginkgoites*, the conifer *Brachyphyllum*, and the fern *Coniopteris* (Ash et al. in prep.). The plant material in the productive layer is of plant taphofacies LM and LW of Parrish et al. (2004), and overall the plant macrofossil record at the site is similar to that of the Montezuma Creek locality in the medial Brushy Basin Member 60–65 kilometres to the southwest, excepting the apparent lack of fossil fish (Ash and Tidwell 1998; Kirkland 1998). Plant fossils are on thin bedding planes within the laminated mudstone and often preserve cuticle. The insect fossil is preserved as a thin, brown organic film somewhat similar to the colour and preservational appearance of the plant material but of course lacking the dark cuticle often preserved on at least most of the plant specimens. Spinicaudatans carapaces and bones of a small amphibian, probably a salamander, were also found at the site in the same shale layer as the plants and insect.

## Material and methods

This study is based on an impression of a single part and counterpart specimen from the Jurassic Salad Bar locality (Sa1212p), west of the town of Blanding in San Juan County, southeastern Utah, USA (Figure 1).

The specimen was studied with a Fisher Scientific Allied binocular microscope and photographed with a Canon 5D Mark IV digital SLR. Measurements were made using digital calipers. Line drawings were prepared over the photographs using CorelDraw 16 image-editing software. For morphological terminology, we follow that of Popov's (1971) and Betts' (1986). Fossil material reported herein is housed at the Utah Field House of Natural History State Park Museum, Vernal, Utah (USA), under the acronym FHPR.

## Systematic palaeontology

*Order:* HEMIPTERA Linnaeus (1758)

*Suborder:* HETEROPTERA Latreille (1810)

*Infraorder:* NEPOMORPHA Popov (1968)

*Family:* Incertae Sedis

*Genus:* *Morrisonnepe* Lara, Foster, Kirkland, and Howells, n. gen.

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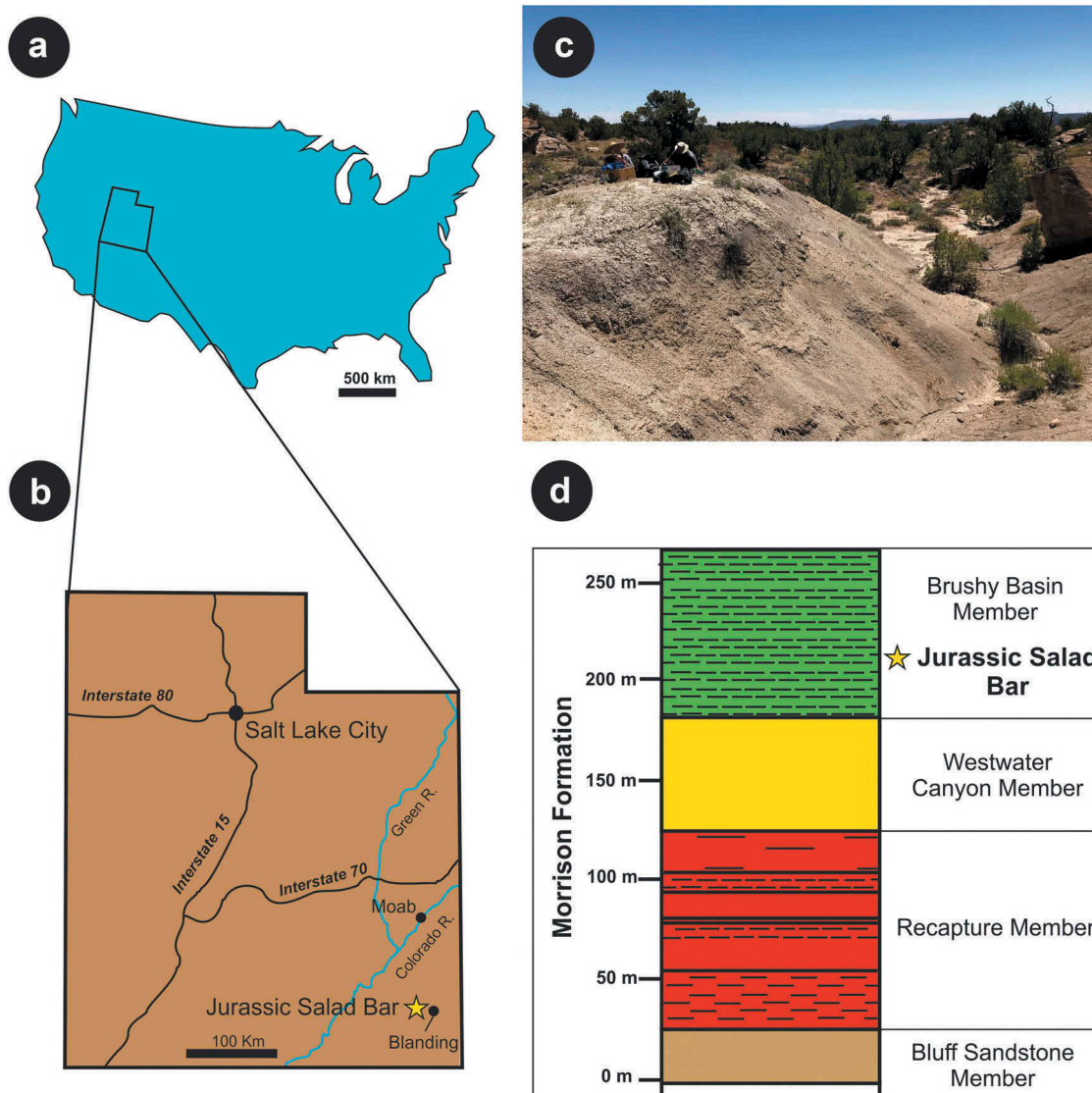
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## Type species

*Morrisonnepe jurassica* Lara, Foster, Kirkland, and Howells, n. sp.; by monotypy.

## Diagnosis

Giant adult insects with elongate body, presumably organised into three segments, head, thorax and abdomen. Pair of short and



**Figure 1.** Location and stratigraphy of the Jurassic Salad Bar locality, San Juan County, Utah. **(A)** Location of Utah within the USA. **(B)** Map of Utah with location of Jurassic Salad Bar locality (yellow star) in Utah. **(C)** Jurassic Salad Bar locality at top of a small hill; B. Engh and M. Wedel at left working the main plant layer (which also produced the insect FHPR 17299). **(D)** Stratigraphic section of the Morrison Formation from the northwest side of Black Mesa, east of Comb Ridge, several kilometres south of the Jurassic Salad Bar locality, showing formation members and the stratigraphic position of the site within the Brushy Basin Member indicated by a yellow star (data based on Kirkland et al. [in press](#)).

tubular structures close to the scutellum visible. Hemelytra: forewing partly coriaceous (corium plus clavus) and partly membranous. Corium with venation preserved: R (radial) and M (medial) fused in an anterior sector (stem R + M), and CuA (anterior cubital) parallel to the claval furrow and it anastomoses distally into diverse irregular cells between CuA and M and between CuA and the claval furrow. Costal margin curved. Membrane of hemelytra well-developed, with its greatest width more than that of clavus; most of its cells irregular with polygonal and pentagonal shape, of various lengths. Clavus sclerotised, wide and large with anal veins visible. Abdomen with five broad, robust and rectangular segments. Finally, close to first abdominal segment and to clavus, two undetermined structures preserved with similar to rectangular and conic shape, respectively.

#### Derivation of name

The generic name derives from the Morrison Formation, and *-nepa*, a standard suffix used for the superfamily Nepoidea.

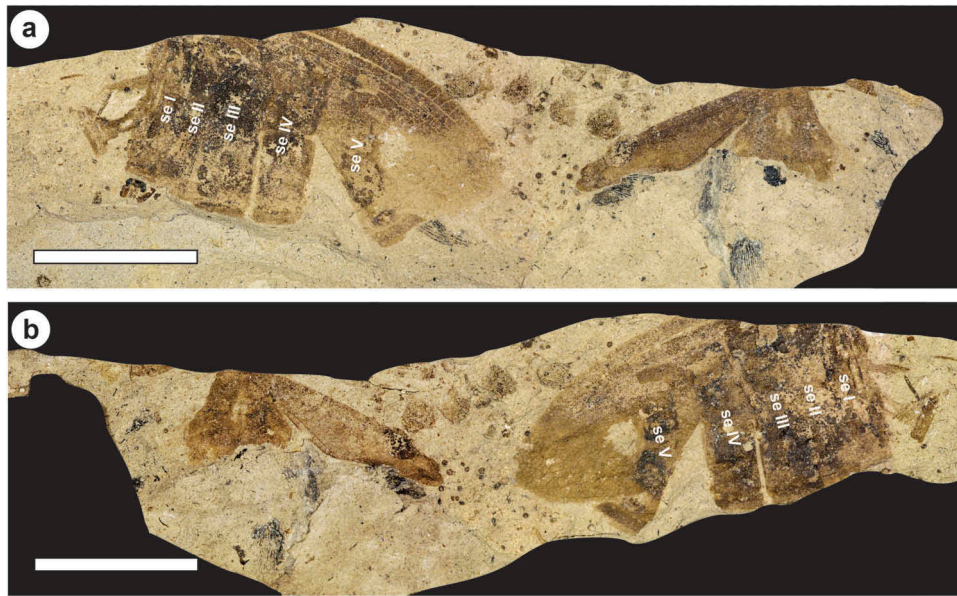
#### Occurrence

Upper Brushy Basin Member of the Morrison Formation, Jurassic Salad Bar locality (Utah Geological Survey site # Sa1212p), San Juan County, Utah, USA ([Figure 1](#)); Late Jurassic, age is ~151 Ma (based on a U-Pb date of  $\sim 150.7 \pm 0.3$  Ma from near the top of section ~40 metres stratigraphically higher and several kilometres to the south along the same outcrop belt, Kirkland et al. [in press](#)).

#### Remarks

*Morrisonnepa* n. gen. is placed under Hemiptera (Linnaeus 1758) and Heteroptera (Latreille 1810) by the presence of forewing with the proximal part strongly coriaceous (corium plus clavus) and the distal one membranous (called hemelytra) (Carpenter 1992). This new genus belongs to the Infraorder Nepomorpha (Popov 1968) based on several characters: forewing well-developed and folding flat on the abdomen; abdomen with oval shape typical of aquatic hemipterans and the presence of a pair short appendages similar to respiratory processes observed in true water bugs (Popov 1971; Schuh and Slater 1995).





**Figure 2.** *Morrisonnepsa jurassica* n. gen. and n. sp., from the Morrison Formation (Upper Jurassic), San Juan County, Utah, USA, holotype, FHPR 17299, incomplete specimen in dorsal view. (A–B) Photograph of part and counterpart, respectively. se I–V, abdominal segments I–V. Scale bar = 10 mm.

*Species:* *Morrisonnepsa jurassica* Lara, Foster, Kirkland, and Howells, n. sp. (Figure 2–3, Figure 4(A)) LSID Zoobank: urn:lsid:zoobank.org:act:F637F6AE-2036-43C5-94CF-31147D533825

#### Derivation of name

The specific name *jurassica* refers to Jurassic Period from which the species is derived.

#### Type material

Holotype (FHPR 17299) curated into the collections at Utah Field House of Natural History State Park Museum, Vernal, Utah, USA; partial insect body fossil including thoracic and abdominal segments, forewing, clavus, and possible head.

#### Occurrence

As for genus, Brushy Basin Member of the Morrison Formation, Jurassic Salad Bar locality, San Juan County, Utah, USA; Late Jurassic.

#### Diagnosis

See generic diagnosis above.

#### Description

Incomplete specimen in dorsal view (Figures 2–3), missing the legs and hindwing. Surface of the specimen dark to pale brown. Body elongate and apparently flattened. Thorax incomplete, represented by scutellum-mesonotum triangular (Figure 3(B scut.), Figure 4(A scut.)) and metathorax partly visible (Figure 3(B metatx.), Figure 4(A metatx.)). On the left lateral side, close to the scutellum, a pair of short and tubular structures visible, about 1.6 mm of length (Figure 2, Figure 3(A undet. I), Figure 4(A undet. I)). Additionally, on the left side and close to the 1<sup>st</sup> abdominal segment, a small undetermined structure observable (Figure 3(A undet. II), Figure 4(A undet. II)). The abdomen size indicates clearly that the specimen was macropterous and probably was taphonomically flattened, which explains its relatively large width. Right forewing (hemelytra) long, ca. 18.66 mm long and 10.5 mm wide, base not preserved (Figure 2, Figure 3(C–D hem)), with corium-membrane boundary distinct (Figure 4(A lim. c-m)) and probably

reaching end of abdomen. Costal margin curved. Corium ca. 10.31 mm long and 3.41 mm wide with numerous veins preserved: radial (R), medial (M) and anterior cubital (CuA) (Figure 4(A)). Stem M, in its proximal sector, completely fused with R in a thick vein R + M, and in the distal sector, M apparently fused with CuA. Stem CuA parallel to the claval furrow and it anastomoses distally into diverse irregular cells between CuA and M and between CuA and the claval furrow (Figure 4(A)). Membrane of hemelytra well-developed (about 4.61 mm long and 6.01 mm wide), relatively large and with various polygonal and pentagonal vein cells which are better observed on the counterpart (Figure 2(B), Figure 3(D), Figure 4(A)). Hindwing not visible, probably not preserved. Clavus sclerotised, 13.81 mm long and 3.78 mm wide, with a pronounced depression and evident anal veins (Figure 3(E–F), Figure 4(A)). Abdomen robust and broad, ca. 16.13 mm long and 12.48 mm wide, with five visible rectangular segments (the first four segments nearly the same length) (Figure 2 (se I–V)). Dorsal surface of abdominal segments partly hidden under the hemelytra (Figure 2). The first four abdominal segments joined to each other (Figure 2 (se I–IV)): se I (ca. length 1.68 mm/width 8.19 mm), se II (ca. length 1.48 mm/width 7.33 mm), se III (ca. length 2.87 mm/width 8.45 mm), se IV (ca. length 2.87 mm/width 8.45 mm); and an abdominal segment displaced (Figure 2 (se V)) (ca. length 2.98 mm/width 8.7 mm). Close to clavus, a small conic undetermined structure preserved, ca. 4.15 mm long and 5.71 mm wide ([Figure 3(E–F) undet. III]).

#### Measurements

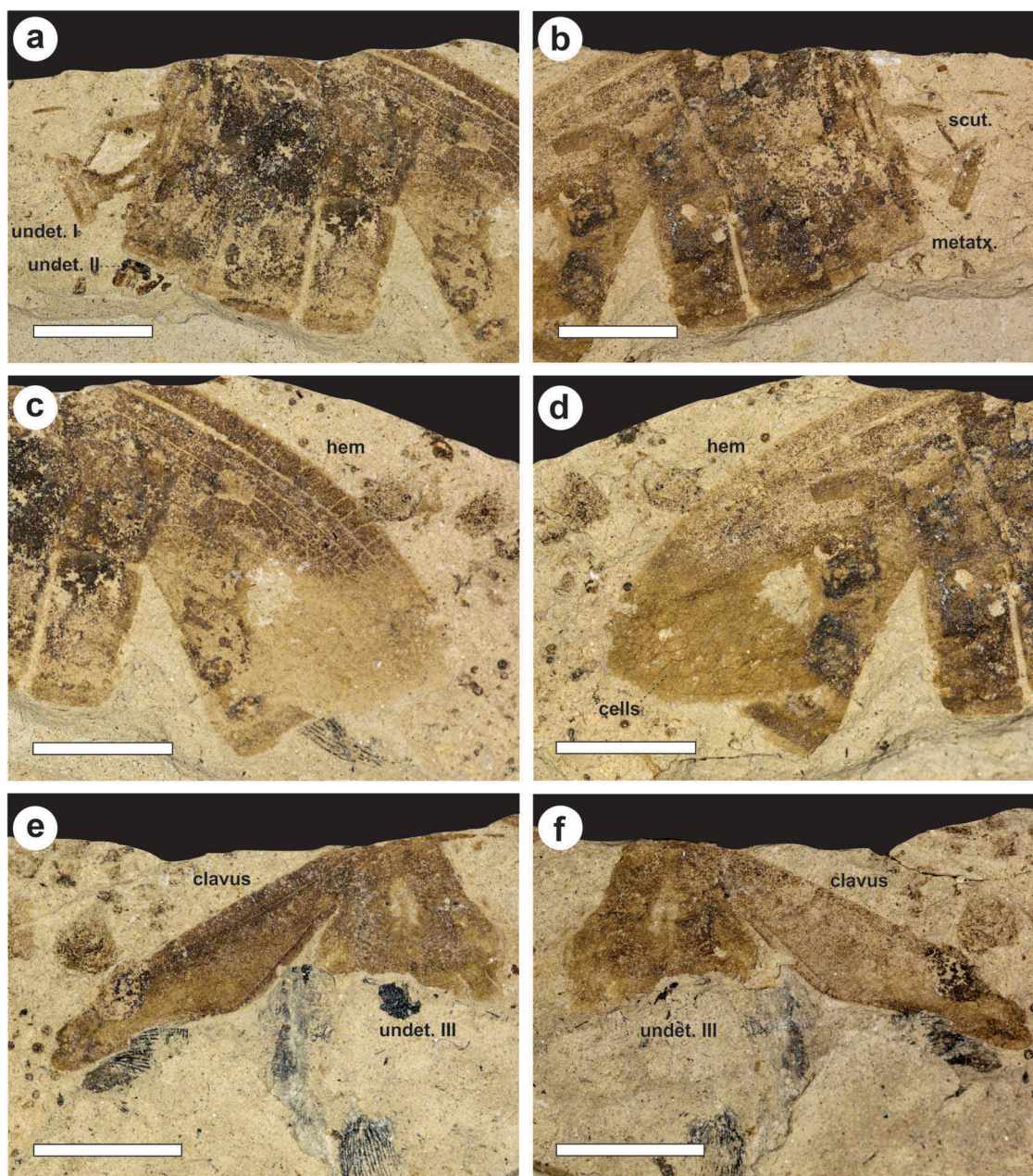
Total body length 25.37 mm (from preserved scutellum to the forewing tip); total length of hemelytra 18.66 mm, maximum width of hemelytra 10.5 mm; clavus length 13.81 mm, width 3.78 mm; abdomen length 16.13 mm, width 12.48 mm.

#### Discussion

##### Taxonomic position of *Morrisonnepsa jurassica* n. gen. n. sp. (Figures 4–5)

The poor preservation of *Morrisonnepsa jurassica* n. gen. n. sp. makes its interpretation and taxonomic allocation at family level



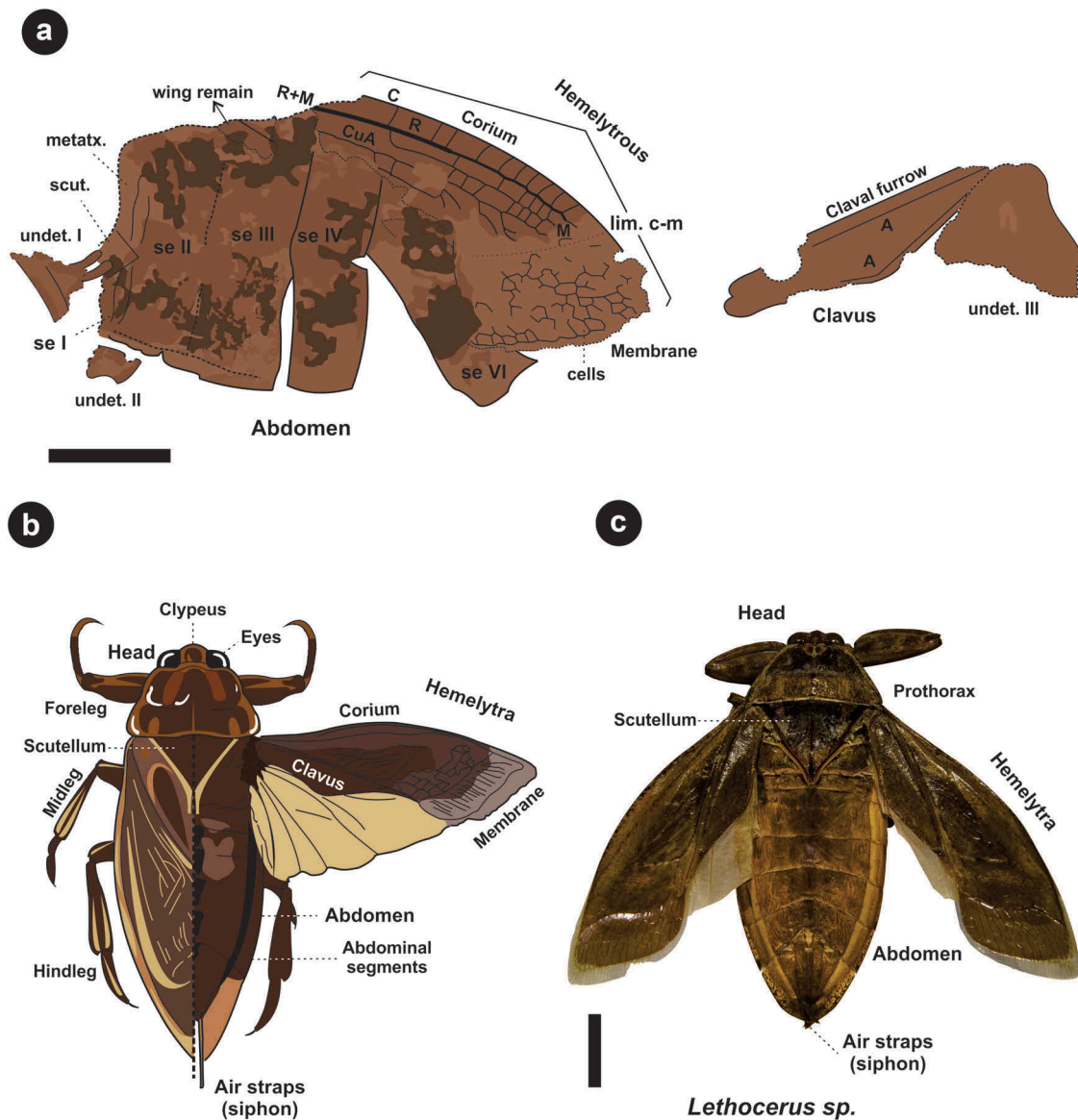


**Figure 3.** *Morrisonnepe jurassica* n. gen. and n. sp., from the Morrison Formation (Upper Jurassic), San Juan County, Utah, USA, holotype, FHPR 17299, incomplete specimen in dorsal view. (A–F) Photograph of holotype showing, in detail, the morphologic characters: (A–B) thorax and abdomen; (C–D) hemelytra. (E–F) clavus and undetermined structure associated. hem, hemelytra; metatx., metathorax; scut., scutellum; undet. I–III, undetermined structures I–III. Scale bar = 5 mm.

difficult. However, within Infraorder Nepomorpha (Popov 1968) a possible affinity with Superfamily Nepoidea (Latreille 1802) and Family Belostomatidae Leach (1815) (Triassic to Recent) (Figure 4 (B–C)) could be suggested by the presence of: (i) well-developed hemelytra; (ii) distinctive venation pattern (stem M, in its proximal sector, is completely fused with R in a thick vein R + M, and in the distal sector, M apparently is fused with CuA); (iii) membrane of the forewing with numerous irregular vein cells; (iv) total body length, *M. jurassica* n. sp. has a preserved length of about 25.37 mm, falling within the range of modern belostomatids (9–130 mm) and nepids (15–45 mm) (Schuh and Slater 1995; Panizzi and Grazia 2015); (v) body (abdomen) apparently robust and flattened (in nepids, the body has a highly elongated shape); (vi) colour pattern preserved in *M. jurassica* n. sp. possibly resembles the light or dark brown colour observed in belostomatids; and (vii)

a pair of short and tubular undetermined processes, close to the scutellum, which could be analogous to the caudal short appendages of belostomatids used as an adaptation to the aquatic mode of life (Figure 2, Figure 3(A undet. I), Figure 4(A undet. I, B–C)) (different from nepids where the caudal breathing siphon is long). The five abdominal segments preserved in *Morrisonnepe jurassica* n. gen. n. sp. are probably related to pregenital segments II, III, IV, V, VI in true water bugs (Figure 4). Popov (1971) reported that the abdomen in heteropterans consists of 11 segments, the first being a reduced tergite. A tiny undetermined structure, close to abdominal segment I (se I), is probably related to a portion of the belostomatids' thorax (Figure 3(A undet. II), Figure 4(A undet. II)). Moreover, we can observe a small and wide conic structure, closely associated to the clavus which could possibly be related to the belostomatids head (Figure 3(E–F undet. III), Figure 4(A undet.





**Figure 4.** (A) Interpretive drawing of *Morrisonnepsa jurassica* n. gen. and n. sp., holotype, FHPR 17299, showing the morphological characters preserved. (B) Diagram of morphological features of belostomatids. (C) Photo of an extant belostomatid, *Lethocerus* sp. Mayr, 1853, FHPR 17329. C, costal margin; CuA, anterior cubital; lim. c-m, corium-membrane boundary; M, medial; metatx., metathorax; se I–V, abdominal segments I–V; undet. I–III, undetermined structures I–III; R, radial; scut., scutellum. Scale bar = 5 mm (A), 10 mm (C).

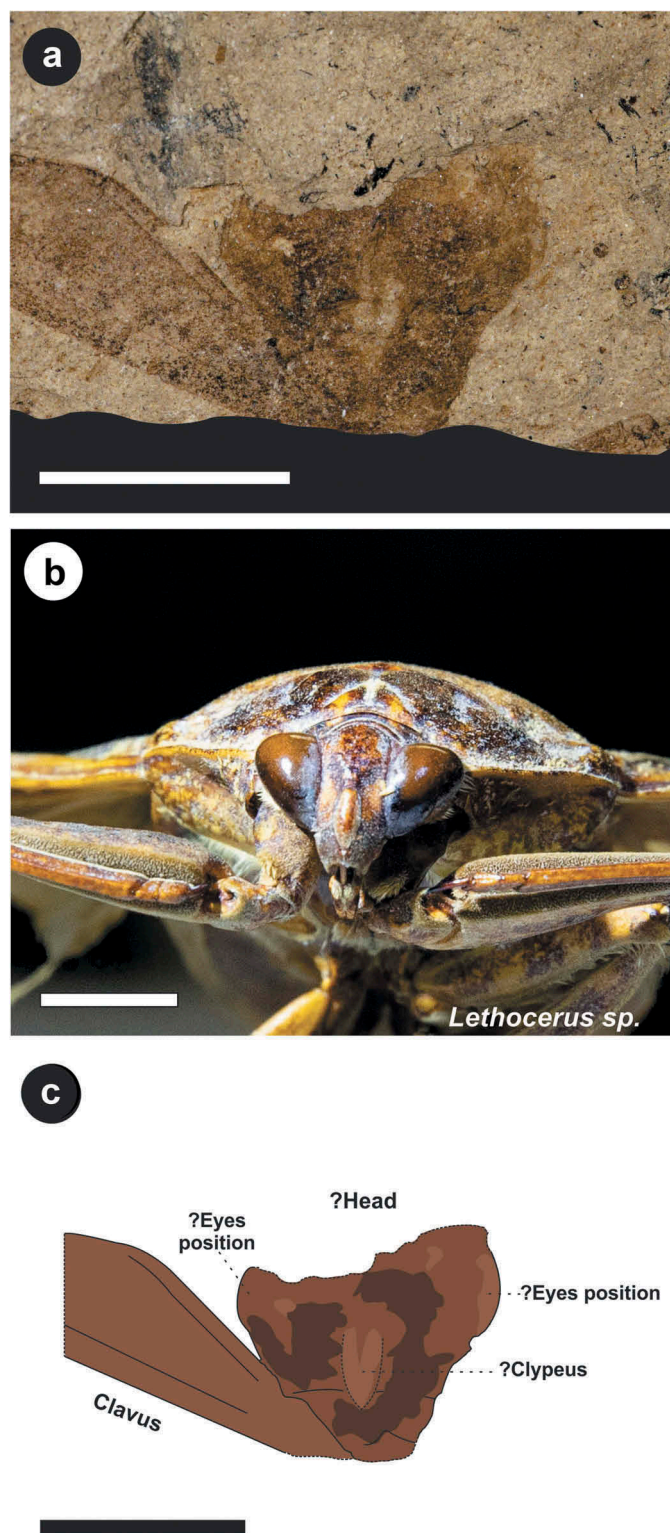
III), Figure 5)). Some parts in this structure could indicate the position of globose eyes and clypeus (Figure 5(C)). These morphological similarities observed in *Morrisonnepsa jurassica* n. gen. n. sp. could support an attribution to the Belostomatidae rather than to any other fossil or extant nepomorphan family. However, we prefer to maintain this new fossil specimen within Nepomorpha as Family *Incertae sedis* due to a lack, or poor preservation, of crucial characters (e.g. head well-preserved, forelegs) and until more and better-preserved specimens are collected from the Morrison Formation in Utah or elsewhere.

Additionally, the combination of characters observed in *Morrisonnepsa jurassica* n. gen. n. sp., such as a distinctive hemelytron shape; venation pattern (stem M, proximally fused with vein R, and distally with vein CuA); membrane relatively large and with various polygonal and pentagonal vein cells; long claval furrow; and big and robust abdomen allows us to distinguish this new specimen from previously known species of fossil belostomatids and other Nepomorpha. Moreover, *Morrisonnepsa jurassica* n. gen. n. sp.

particularly differs from other fossil belostomatids described from the USA: *Triassonepa solensis* (Upper Triassic, Cow Branch Formation) (Criscioni and Grimaldi 2017) and *Aenictobelostoma primitivum* (Middle Jurassic, Todilto Formation) (Polhemus 2000) in body size and robust abdomen (in *T. solensis* the total length is 10.6–14.1 mm and in *A. primitivum* [adult] about 15 mm, the two species being smaller than *M. jurassica*), hemelytra large and membrane wide and with numerous polygonal and pentagonal cells of variable length.

#### Taphonomic and palaeoenvironmental inferences

*Morrisonnepsa jurassica* n. gen. n. sp. has been found in a soft light tan to grey mudstone that is very finely laminated at the Jurassic Salad Bar locality. These finely laminated lithologies, when bearing abundant organics, are suggestive of more open-water settings and meromictic conditions, such as those found in a large lacustrine setting (Renaut and Gierlowski-Kordesch 2010). Therefore, the Jurassic



**Figure 5.** (A) Detail of undetermined structure III preserved close to clavus. (B) Photo of an extant belostomatid, *Lethocerus* sp., FHPR 17329. (C) Interpretive drawing showing the morphological characters preserved. Scale bar = 5 mm.

Salad Bar locality represents an oxbow lake or perhaps less likely a small pond or marsh setting; all environments developed within the greater ecosystem of the extensive Morrison Formation during the Late Jurassic. Extant nepomorphs are associated with mainly lentic environments, such as small pools and lakes, and lotic environments, ranging from small streams to large rivers (e.g. lateral slack waters,

and/or among protected aquatic weeds) (Thorp and Rogers 2011; Barbosa and Rodrigues 2015). *Morrisonnepa jurassica* n. gen. n. sp. supports the presence of a shallow, lacustrine palaeoenvironment where, like modern nepomorphs, they probably lived associated with other arthropods (spinicaudatans) surrounded by abundant vegetation (ginkgophytes, conifers and ferns) at the Jurassic Salad Bar locality (Ash et al. in prep). On the other hand, the presence of a single specimen of *Morrisonnepa jurassica* n. gen. n. sp. at this locality might be related to the insect being an occasional visitor or temporary inhabitant in the freshwater body (Sinitshenkova 2002) and/or the bugs were probably attacked by predators there (absence of body remains). However, we do not rule out a potential collection or taphonomic bias as the site is newly discovered and further collection is essential.

The extant nepomorphs, in general, are strictly predaceous (e.g. feed on crustaceans, dipteran larvae, and other insects, small fishes and tadpoles), although corixids feed on algae and decaying vegetal matter (Panizzi and Grazia 2015). The large and robust abdomen in *Morrisonnepa jurassica* n. gen. n. sp. is suggestive of a predatory habit. Extant belostomids have been observed feeding on animals many times larger than themselves such as fishes and salamanders (Barbosa and Rodrigues 2015; Ohba 2018).

The main air supply of adult aquatic bugs is atmospheric, with secondary replenishment of air stores from oxygen dissolved in the water (Barbosa and Rodrigues 2015). For obtaining oxygen, some submerged species of true aquatic bugs travel to the surface and expose a breathing tube through the surface film (e.g. belostomatids, nepids) (Thorp and Rogers 2011; Barbosa and Rodrigues 2015). *Morrisonnepa jurassica* n. gen. n. sp. has a pair of appendages that probably also served as modification for respiration under freshwater (Figure 2, Figure 3(A undet. I), Figure 4(A undet. I)).

The state of preservation of *Morrisonnepa jurassica* n. gen. n. sp. demonstrates a combination of incomplete material with articulated parts (forewing attached to abdomen, abdominal segments) (Figure 2) and isolated but closely associated parts (clavus, undetermined structures) (Figure 3(A, E–F undet. I–III)). The disarticulation and disintegration of the insect probably occurred in the freshwater body, probably shortly after death while the body floated on the water surface. Possible attack by predators (biological activity), random or selective, resulted in articulated and disarticulated parts, with limited transport, before its deposition (autochthonous) (Martínez-Delclòs et al. 2004). Also, physical agents promote fragmentation and rapid decay in sedimentary deposits, and, therefore, this pathway should not be ruled out. Rasnitsyn and Quicke (2002) mentioned that the compact abdomen of hemipterans and beetles is often completely preserved and in taxa that possess a well-defined clavus of the forewings (as hemipterans), the wing breaks easily along the claval furrow, producing the incomplete preservation of the forewing and clavus. This would explain the state of preservation of the abdomen, hemelytra and clavus observed in *Morrisonnepa jurassica* n. gen. n. sp.

Finally, in the new genus and species described herein, we observe a monochromatic colouration of varying tones of brown. Most nepomorph species show a uniform brown colour, varying from yellow to black (Barbosa and Rodrigues 2015). Rasnitsyn and Quicke (2002) and Vinther et al. (2008) mentioned that the monochromatic pattern could be reflecting original variations in cuticle thickness and/or pigment concentrations (eumelanin), respectively (Mcnamara 2013). However, a taphonomic alteration should not be ruled out for the tonal pattern observed in *Morrisonnepa jurassica* n. gen. n. sp. Future chemical analyses of this, as well as new material, could help elucidate the true pigmentation of the fossil insects.



## Conclusion

The newly described of *Morrisonnepa jurassica* n. gen. n. sp. represents the first fossil insect at the Jurassic Salad Bar locality, San Juan County (Utah, USA), and the second insect body fossil reported and described from the Morrison Formation (Upper Jurassic).

The new genus and species is placed under the Order Hemiptera, Infraorder Nepomorpha by the presence of a well-developed forewing (hemelytra); abdomen with oval shape typical of aquatic hemipterans; and the presence of a pair short appendages similar to respiratory processes observed in true water bugs. The morphological similarities observed in *Morrisonnepa jurassica* n. gen. n. sp. such as forewing with distinctive venation pattern and membrane with numerous irregular vein cells, total body length, body (abdomen) robust and flattened, colour pattern, and a pair of short and tubular undetermined processes, could be support for an attribution to the Belostomatidae. However, we prefer to maintain this new fossil specimen within Nepomorpha as Family *Incertae sedis* due to marginal preservation of the type specimen and until more and better-preserved specimens are collected from the Morrison Formation in Utah or elsewhere.

*Morrisonnepa jurassica* n. gen. n. sp. adds new morphological information about Jurassic nepomorphs, allowing a better understanding about how the aquatic entomological assemblages were integrated during the Late Jurassic in this part of the Laurasian continent. Moreover, this new fossil insect locality (this report; Kirkland et al. *in press*; Ash et al. *in prep.*) and that of Temple Canyon in Colorado (Gorman et al. 2008; Smith et al. 2011), indicates that the Morrison Formation in general still remains relatively unexplored in a palaeontological context, and most probably, the small lacustrine deposits in the unit hold promise for additional data on these rare elements of the fauna.

## Acknowledgments

Fieldwork conducted under Bureau of Land Management (BLM) paleontological resources use permit UT18-003E to the Utah Field House, with special thanks to Greg McDonald and the Monticello Field Office. Initial assistance in the field with the UGS included Don DeBlieux and Scott Madsen under BLM permit UT07-003S-SW. Thanks also to Christy Bills and the Natural History Museum of Utah for donation of the specimen of *Lethocerus* to the Utah Field House. Technical reviews by Don DeBlieux, Grant Willis, and Stephenie Carney are appreciated. The authors also thanks to Dr Jacek Szwedo (University of Gdańsk, Poland) for comments on the specimen. We sincerely thank Dr Gareth Dyker (Editor) and two anonymous reviewers, for their useful comments on the first version of this paper.

## Disclosure statement

No potential conflict of interest was reported by the authors.

## Funding

This work was supported by the Bureau of Land Management with match by Utah Geological Survey (J.I.Kirkland) and Museum of Moab, Utah (J.R.Foster), and Utah Field House, Utah (J.R.Foster, T.F.Howells).

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