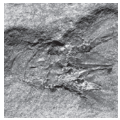# Closing a major gap in mantis shrimp evolution – first fossils of Stomatopoda from the Triassic

Christopher P.A. Smith, Paul Aubier, Sylvain Charbonnier, Thomas Laville, Nicolas Olivier, Gilles Escarguel, James F. Jenks, Kevin G. Bylund, Emmanuel Fara & Arnaud Brayard

Mantis shrimps (Stomatopoda) are marine benthic predators well known for their raptorial claws that have, through time, evolved into unique structures with exceptional stunning, piercing or even dismembering functions. Known since the Carboniferous, Stomatopoda fossils have started providing insights into the rise of these predators, however, major gaps in the fossil record remain. In particular, neither Permian, nor Triassic specimens have ever been uncovered. Such a long hiatus strongly hinders our understanding of their evolutionary history, especially regarding the transition between Palaeozoic and Mesozoic forms. We here report two mantis shrimp specimens from the Early Triassic Paris Biota of Idaho, USA, formally described as *Triassosculda ahyongi* gen. et sp. nov., partially closing an over 100 myr gap in the fossil record. Despite being incomplete, these specimens present distinct and well-preserved diagnostic characters on the posterior trunk and the tail fan. The telson shows a triangular shape closely resembling that of Palaeozoic mantis shrimps. The broadness of both the pleon and anterior rim of the telson, however, differs from that of most Palaeozoic forms, which have an overall narrow telson, and is more similar to that of modern representatives of Stomatopoda. Additionally, the uropodal exopods of *Triassosculda ahyongi* gen. et sp. nov. presents a considerable number of movable spines that are common among Jurassic and more recent taxa, but that have never been reported among Palaeozoic Stomatopoda. These features further support and above all, allow temporal refinement of previously suggested evolutionary scenarios. In the latter, and as for other major clades of crustaceans, Stomatopoda are assumed to have evolved from a shrimp-like morphology with a narrow triangular telson to a more lobster-like one with a broad and rather square-shaped telson. *Triassosculda ahyongi* gen. et sp. nov. indicates this transition was underway by the Early Triassic. • Key words: Hoplocarida, *Triassosculda ahyongi* gen. et sp. nov., phylogeny, early Spathian, Paris Biota, USA.

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Mantis shrimps (Stomatopoda, Latreille 1817) are marine crustaceans of the Class Malacostraca Latreille, 1802. These predators include over 520 extant species, of which the majority are tropical (Ahyong *et al.* 2014, Schram & Koenemann 2021). Stomatopoda are particularly well known for their unique massive raptorial claws, some of which can strike so fast that they create cavitation bubbles that induce secondary impacts after explosion (Patek & Caldwell 2005). They also possess an exceptional monocular stereoscopic vision, with eyes comprised of up to twelve different colour receptors (Kleinlogel & Marshall 2006, Chiou *et al.* 2008).

The Stomatopoda fossil record, on the other hand, is still scarce (Schram 2010). The oldest known representatives of Stomatopoda are dated from the early Tournaisian (Early Mississippian, early Carboniferous) with *Archaeocaris graffhami* Brooks, 1962 (uncovered in the Upper Pilot Shale of the Bactrian Mountain, Nevada,

USA) and *Archaeocaris vermiformis* Meek, 1872 (found in the Waverly Group near Danville, Kentucky, USA). Throughout the Carboniferous of North America and Europe, twelve other Stomatopoda species are recognised among which some feeding apparatus specialization is already observable (Schram 2007, Haug *et al.* 2010). However, following the Carboniferous, the next earliest species known is *Ostenosculda teruzzii* Braig, Haug, Ahyong, Garassino, Schädel & Haug, 2022 dated only from the Sinemurian (Early Jurassic), leaving an over 100 myr gap in the Stomatopoda fossil record (Braig *et al.* 2023). Additionally, the next earliest species of Stomatopoda are only known from the Tithonian (Late Jurassic), another 50 myr later (Haug & Haug 2021).

Among these Jurassic species, some preserved an overall body morphology similar to that of their Carboniferous relatives (Haug & Haug 2021), but others appear to resemble modern mantis shrimps (Haug *et al.* 2010). The fossil record of Stomatopoda is relatively more complete after the Jurassic and documents a rather gradual evolution towards modern forms (Haug *et al.* 2010, 2013). Nonetheless, the Permian–Triassic hiatus strongly hinders our understanding of their early evolutionary history, especially regarding the transition from Palaeozoic forms to Mesozoic ones.

Here we report two incomplete specimens of mantis shrimps from the Early Triassic. They were found within the Paris Biota, which is one of the oldest-known complex marine ecosystem following the Permian/Triassic mass extinction (Brayard *et al.* 2017, Smith *et al.* 2021). After comparing the morphology of the new fossils with that of Palaeozoic and Mesozoic relatives, and introducing them within a phylogenetic analysis of all pre-Cenozoic species, we discuss the phylogenetic and macroevolutionary implications of this discovery.

## Material and methods

*Material.* – The two specimens come from the early Spathian (Early Triassic) Paris Biota (Brayard *et al.* 2017). This biota was uncovered from multiple sites in the western USA basin (Smith *et al.* 2021). The specimens described here come from Paris Canyon, Idaho, USA (Fig. 1). They were collected from exposures of the Thaynes Group (*sensu* Lucas *et al.* 2007) that is mainly characterized by alternating limestones and shales corresponding to outer platform deposits. Biostratigraphy in the region is well-constrained by Smithian and Spathian ammonoid assemblages (Smith 1932, Guex *et al.* 2010, Jenks *et al.* 2013, Brayard *et al.* 2019). The specimens were uncovered alongside a rich and diverse marine fauna that includes, among others, sponges (Botting *et al.* 2019), brachiopods, bivalves, cephalopods (Doguzhaeva *et al.* 2018, Brayard *et al.* 2019), echinoderms (Saucède *et al.* 2019, Thuy *et al.* 2019), vertebrates (Romano *et al.* 2019), thylacocephalans (Charbonnier *et al.* 2019, Laville *et al.* 2021) and decapods (Smith *et al.* 2022). During the Early Triassic, the western USA basin was located at a near-equatorial position, east of the Panthalassa Ocean and west of the Pangea (Fig.1B).

*Documentation methods.* – The specimens were examined under natural light and UV illumination (wavelength of 365 nm). Photographs under natural light were recorded using a Nikon D750 camera coupled to a AF-S VR Micro-Nikkor 105mm f/2.8G IF-E (Nikon) lens. Photographs under UV illumination were recorded using an ORCA Flash 4.0 v2 LT+ (Hamamatsu) camera coupled to a UV-VIS-IR 60 mm 1:4 APO Macro – Multispectral High Performance (Jenoptik) lens. The brightness and contrast of each image was optimised to highlight some anatomical parts using ImageJ 1.52s and the auto "Brightness/Contrast…" tool.

*Repositories and institutional abbreviations.* – The specimens are reposited in the public collections of the Université de Bourgogne, Géologie Dijon, France (UBGD).

*Phylogenetic framework.* – A phylogenetic analysis was conducted with all known Palaeozoic Stomatopoda taxa in addition to *Triassosculda ahyongi* gen. et sp. nov. and most Mesozoic Stomatopoda. Unfortunately, the Early Jurassic specimens of *Ostenosculda teruzzii* Braig, Haug, Ahyong, Garassino, Schädel & Haug, 2022 exhibit too few characters to be integrated in the analysis. Among Cretaceous taxa, *Paleosquilla brevicoxa* Schram, 1968 and *Squilla cretacea* Schlüter, 1868 are both known only from one very incomplete specimen and therefore, are not included in the analysis either. *Spinosculda ehrlichi* Haug, Haug & Waloszek, 2009 and *Gigantosculda ehrlichfeckei* Haug, Wiethase & Haug, 2015 were not included as they are larval forms. *Squilla mantis* (Linnaeus, 1758) was included in the analysis in order to have a modern representative of Stomatopoda. *Kallidecthes richardsoni* Schram, 1969 is used as an outgroup as it is a well-documented representative of Aeschronectida Schram, 1969, the supposed sister group of Stomatopoda (Schram 1969, Jenner *et al.* 1998, Haug *et al.* 2010). The matrix used here is based on that used by Haug *et al.* (2010) to which modifications were made. Anatomical features with multiple dependent states that were coded as multiple binary characters were coded as multistate characters in order to avoid the overweighting of the phylogenetic signal of such structures induced by the redundancy of information in the dataset (Pimentcl & Riggins 1987, Hauser & Presch 1991). Redundant characters [*e.g.* character 15 – first raptorial limb sub-equal (0) or dif-
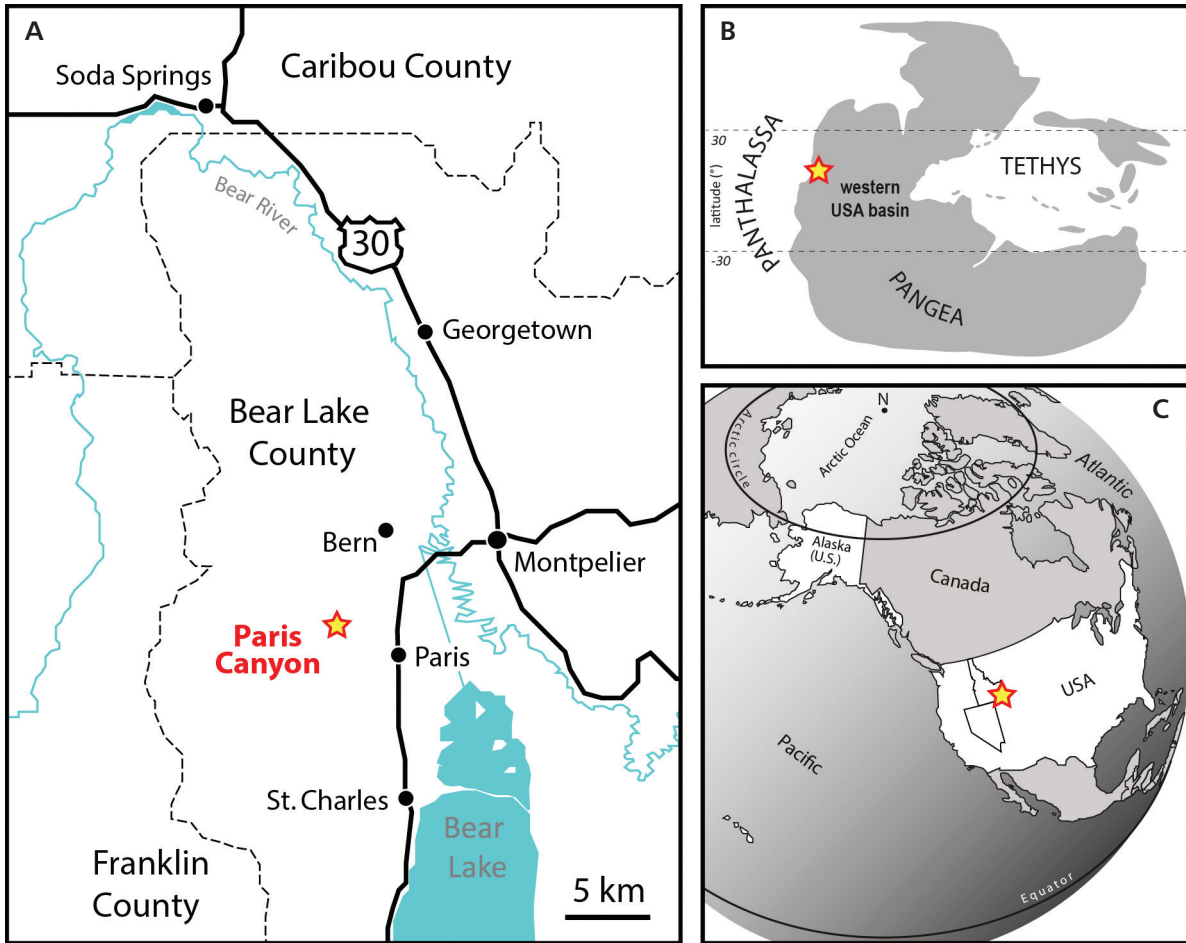
**Figure 1.** Location of the site of Paris Canyon (star) from which the studied specimens were collected. • A – simplified map of southeastern Idaho. • B – Early Triassic paleogeographic map. • C – present-day map. Maps modified from Smith *et al.* (2021).

ferentiated (1) compared to second; character 34 – first raptorial limb differentiated compared to the fourth: (0) for "no", and (1) for "yes"] were also removed for the same reason. The characters used by Ahyong & Harling (2000) in a phylogenetic framework focusing on modern representatives of Unipeltata Latreille, 1825, and observable on fossil material, were also included (characters 23 to 29). A final character on the thickness of the raptorial appendage (Mxp2) propodus (character 30) was added, as it is easily observable and relatively variable among all studied species. When reasonable, *i.e.* presence of clear 'intermediate' states showing a linear series of transformations, multistate characters were ordinated as this coding method has been shown to increase resolution when using parsimony (Slowinski & Guyer 1993, Rineau *et al.* 2015). All characters were equally weighted. The final matrix (Supplementary File 1) includes 25 species and 30 characters (Tab. 1, Fig. 2), 10 of which are ordered.

The analysis was performed using parsimony with PAUP 4.0a165 (Swofford & Sullivan 2003). The max length rule was chosen for the collapse of the branches

(branches are collapsed when the maximum length equals 0). The "accelerated transformation" (ACCTRAN) optimization was preferred over the "delayed transformation" (DELTRAN) as it maximises the number of secondary homologies in the final tree (Farris 1983, De Pinna 1991). Tree search was performed using the branch-and-bound algorithm and a bootstrap analysis (1000 replicates) was run to measure node robustness.

**Systematic palaeontology**
by Christopher P.A. Smith, Sylvain Charbonnier, Emmanuel Fara & Arnaud Brayard

Eucrustacea Walossek, 1999
Class Malacostraca Latreille, 1802
Subclass Hoplocarida Calman, 1904
Order Stomatopoda Latreille, 1817
Unipeltata *sensu lato*, following Haug *et al.* (2010) (non-Linnaean rank)
Suborder Unipeltata Latreille, 1825

**Table 1.** List of characters used for the phylogeny. The numbers in brackets correspond to the character number used in Haug *et al.* (2010). The numbers in brackets preceded by a "*" correspond to the character number used in Ahyong & Harling (2000). When the states of character are ordinated, a brief justification of why they are ordinated is provided in brackets.

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**1** – [1,2,3] Carapace covering:
(0) Thorax segment 8  (1) Thorax segment 7  (2) Thorax segment 6  (3) Thorax segment 5
(4) No thorax segment
[*ordinated as it appears reasonable to assume that the carapace gradually covered less thoracic segments*]
**2** – [4] Carapace rounded in lateral view:
(0) Yes  (1) No
**3** – [5] Carapace laterally enveloping the whole thorax:
(0) Yes  (1) No
**4** – [6] Carapace subdivided into three fields, one median, two lateral ones:
(0) No  (1) Yes
**5** – [7] Thorax subdivided into functional units, *i.e.*, thoracic segments differentiated:
(0) No  (1) Yes
**6** – [8] Raptorial appendage (Mxp 2) ischium (most proximal segment):
(0) Reduced  (1) Rather elongated (longer than carps)
**7**– [10,11] Raptorial appendage (Mxp 2) merus (second most proximal segment) with saddle:
(0) Absent  (1) Present but incipient  (2) Present and well developed
[*ordinated as it is logical the structure gradually developed*]
**8** – [12] Carpus (third most distal segment) of maxilipeds:
(0) Long  (1) Short
**9** – [13] Jackknife articulation on maxilliped:
(0) Absent  (1) Present
[14] *removed because a lot to biased by taphonomy (Jackknife joint between limb portion 4 ("merus") and 3 (carpus) (0) or portion 3 (carpus) and 2 (propodus) (1)).*
**10** – [15,16,17] Raptorial appendage (Mxp 2) length:
(0) Sub–equal to other maxilipeds (Mxp 3–5) (1) A bit longer than other maxilipeds (Mxp 3–5)
(2) Three times or more longer than other maxilipeds (Mxp 3–5)
[*ordinated as it appears reasonable to assume that the structure gradually became longer*]
**11** – [18,19; *used Unipeltata character*] Raptorial appendage propodus (second most distal segment):
(0) Smooth or sparsely pectinate  (1) Spinous  (2) Evenly pectinate for full length
(3) Proximally pectinate  (4) Fully pectinate proximally, becoming sparse distally
**12** – [20,21] Uropodal exopod composed of:
(0) One element blade–like  (1) One element lobated  (2) Two elements
[*ordinated as it appears reasonable to assume that the structure gradually became more complex*]
**13** – [22] Uropodal exopod outer margin:
(0) Smooth  (1) Serrated/teeth  (2) With distinct spines, *i.e.*, articulated spines
[*ordinated as it appears reasonable to assume that the structure gradually became more complex*]
**14** – [23] Uropodal endopod:
(0) Simple  (1) Reduced
**15** – [24] Uropod with dorsal basipodal spine:
(0) Absent  (1) Present
**16** – [25,26] Uropod with ventral basipodal spine:
(0) Absent  (1) Present but incipient  (2) Present and well developed
[*ordinated as it appears reasonable to assume that the structure gradually developed*]
**17** – [27] Telson with median carina:
(0) No  (1) Yes
**18** – [28] Telson with submedian carina:
(0) No  (1) Yes
**19** – [29,30,31] Telson with median terminal end, *i.e.*, triangular shaped telson:
(0) Yes  (1) Yes, and terminated by a spike  (2) No
[*ordinated as it is the order in which it appears in the fossil record through time*]
**20** – [32] Telson lateral margins:
(0) Smooth  (1) With movable spines only distally  (2) With lateral serrations/fixed spines
(3) With lateral movable spines
[*ordinated as it appears reasoned to assume that the structures gradually became more complex*]
**21** – [33] Telson length to width:
(0) Elongated (more than 1.5)  (1) Stouter
**22** – [1*] Carapace gastric groove:
(0) Absent  (1) Present
**23** – [6*] Carapace lateral carina:
(0) Absent  (1) Posteriorly only  (2) Present all along
[*ordinated as it appears reasoned to assume that the structures gradually became more complex*]
**24** – [13*] Pleonal submedian carinae:
(0) Absent  (1) Present
**25** – [14*] Pleonal intermediate and lateral carinae:
(0) Absent  (1) Present
**26** – [15*] Pleonal marginal carinae:
(0) Absent  (1) Present
**27** – [17*] p6 with posterolateral spine:
(0) Present  (1) Absent
**28** – [18*] p6 dorsal surface:
(0) Lacking upright spines  (1) With upright spines
**29** – [21*] Telson dorsal surface:
(0) Unadorned or carinate only  (1) Tuberculate or spinous  (2) Sculptured, irregular
**30** – Raptorial appendage (Mxp2) propodus (second most distal segment):
(0) Slender  (1) Enlarged  (2) Inflated (oval shape)
[*ordinated as it appears reasonable to assume that the structure gradually became more complex*]
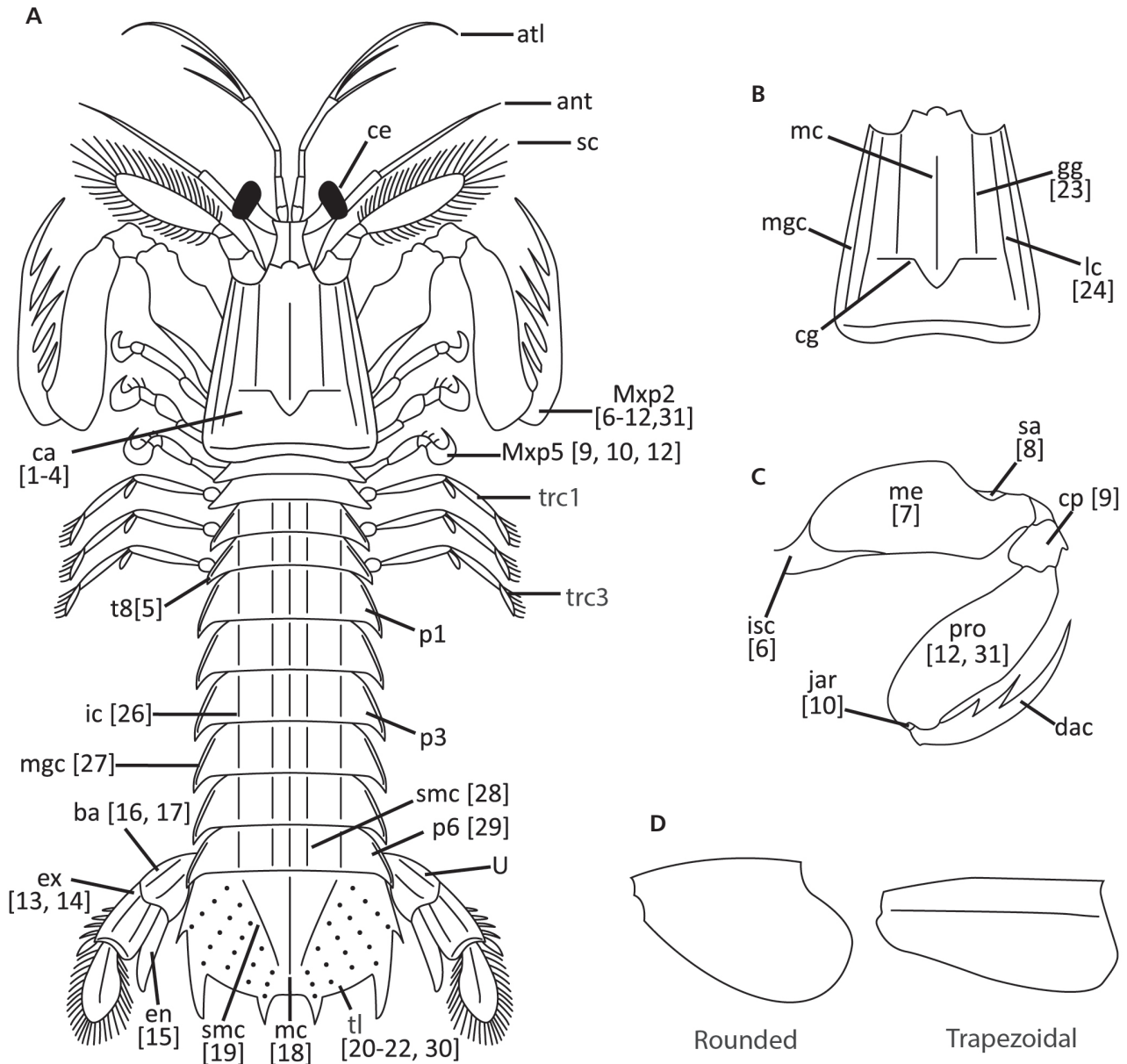
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**Figure 2.** Morphology of Stomatopoda. A – general morphology; B – carapace (dorsal view); C – maxilliped 2, *i.e.* raptorial appendage; D – carapace general shape in lateral view. Numbers in brackets correspond to characters for the phylogenetic analysis. Abbreviations: ant – antenna; atl – antennula; ba – uropodal basipod; ca – carapace; ce – compound eyes; cg – cervical groove; cp – carpus; dac – dactylus; en – uropodal endopod; ex – uropodal exopod; gg – gastric groove; ic – intermediate carina; isc – ischium; jar – jackknife articulation; lc – lateral carina; mc – median carina; me – merus; mgc – marginal carina; Mxp – maxilliped; p – pleonal segment; pro – propodus; sa – saddle (merus); sc – scaphocerite; smc – submedian carina; trc – thoracopod; t – thoracic segment 8; tl – telson; U – uropod.

**Genus *Triassosculda* gen. nov.**

*Type species.* – *Triassosculda ahyongi*.

*Etymology.* – "*Triasso-*" in reference to the age of the fossil; "*-sculda*" in reference to a common name of Mesozoic representatives of Stomatopoda.

*Diagnosis.* – As for the type species by monotypy.

***Triassosculda ahyongi* sp. nov.**
Figure 3

 2017  *Litogaster* sp. – Brayard *et al.*, supplementary material, p. 31, fig. s18.

*Types.* – The holotype is UBGD 30550 and the paratype is UBGD 294010.

*Type horizon and locality.* – Early Spathian, Early Triassic; Paris Canyon, southeastern Idaho, USA.

*Etymology.* – The specific epithet honors Shane Ahyong who has greatly contributed to the current understanding of the macroevolutionary history of Stomatopoda.

*Diagnosis.* – Mostly referring to tail fan. Mantis shrimp with rather broad (about as long as anterior margin width) but triangular telson. Telson with distinct median ridge and two serrations midway on its lateral margin. Uropods prominent. Exopods with 17 movable spines along lateral and distal edge.

*Description.* – Holotype UBGD 30550 (Fig. 3A–C): Incomplete eumalacostracan preserved in ventral view. Posterior region preserved, including the posterior three pleonal segments (pleonal segments 4–6), the telson, and the uropods (appendages of pleonal segment 6). Pleonal segments represented by their ventral sclerites (sternites).

Pleon: Sternites sub-similar, simple, basically rectangular, about three times wider than long. Surface smooth with perhaps a median carina but no apparent spines, pits, or otherwise. Possibly with a single lateral protrusion on each side (spine?), yet it is difficult to evaluate due to the state of preservation.

Telson: Telson incomplete. Anteriorly as broad as pleonal segments, posteriorly tapering, and roughly triangular in dorsal view. About as long as broad at anterior rim. Lateral margins with two serrations midway on each side. Distinct submedian ridge-like keel of triangular outline, about one third of width anteriorly, and median top-keel slender. Posterior extremity not fully preserved. Presence of a circular depression medio-anteriorly most likely representing the anal opening.

Pleonal appendages: Uropods prominent, with basipod and two rami, endopod and exopod. Basipod slightly longer (proximo-distal axis) than wide (median-lateral axis), and gently widening distally. No clear indication of a basipod spine. Basipod with two distinct slightly concave insertion areas for the rami. Endopod insertion occupying about 40% and exopod insertion occupying about 60% of the distal rim of the basipod. Endopod and Exopod traversed longitudinally in their centre by a distinct carina. Endopod paddle-shaped, about three times as long as wide and distally slightly widening with a distal rim rounded. No evidence of setae or spines. Exopod larger and a little longer than endopod. Lateral and distal edge with 17 movable spines. Along the lateral edge the spines increase in size towards the distal end. The spines along the distal end are smaller.

Paratype UBGD 294010 (Fig. 3D–F): Incomplete eumalacostracan with the larger part of the trunk region preserved in dorso-lateral orientation. Eleven major units, recognisable mostly by tergites, with some remains of appendages arising from the segments. The last unit most likely represents remains of the telson. Possible uropod remains directly linked ventrally to penultimate segment. Thoracic appendages also present anteriorly, although poorly preserved.

Thorax: Four segments anterior to the six pleonal segments, interpreted as thoracic segments 5–8. These segments are also recognisable by their tergites. Tergites progressively narrower towards the anterior with the most anterior one that is only about 50% the width of pleonal segment 1, yet all more or less of the same length.

Thoracic appendages: Poorly preserved. Nonetheless, the base of three pairs of appendages is discernible, perhaps maxillipeds 3 to 5. Proximal units of appendages slender. Additionally, two distinct wider units, inflated proximally, most likely propodus of second maxilliped.

Pleon: Six segments anterior to telson interpreted as pleonal segments 1–6, recognisable mostly by their tergites. Tergites sub-similar, more than three times wider than long. Surface smooth with no apparent spines, pits, or otherwise. Short simple structures protruding from under the tergites on the ventral side, most likely representing remains of the pleopods.

Internal structures: Exhibits remains of the digestive track throughout the pleon and thorax. The intestine extends parallel to the median line, slightly dorsally on the left flank.

*Remarks.* — The two specimens are rather incomplete. Yet, both provide sufficient evidence to confidently identify them as mantis shrimps. UBGD 30550 has prominent uropods (Fig. 3A–C) with especially large exopods presenting pronounced lateral movable spines typical of Mesozoic and younger Stomatopoda (*e.g.* Haug *et al.* 2010, Yaraghi *et al.* 2019). The tail fan in UBGD 294010 is poorly preserved. This specimen is ascribed to Stomatopoda mainly based on the number and morphology of its trunk segments. Indeed, six pleonal and four thoracic segments are identified, with only a slight differentiation in length between the pleonal and the thoracic segments that are progressively narrower towards the anterior, excluding an interpretation as representative of the Decapoda Latreille, 1802 and Isopoda Latreille, 1817, and comforting that of Stomatopoda. Although the two specimens mostly present different anatomical parts, the few that overlap (the posterior part of the pleon and the telson, although poorly preserved in UBGD 294010) show no characters that could be used to differentiate them. Therefore, we consider the two specimens as conspecific.
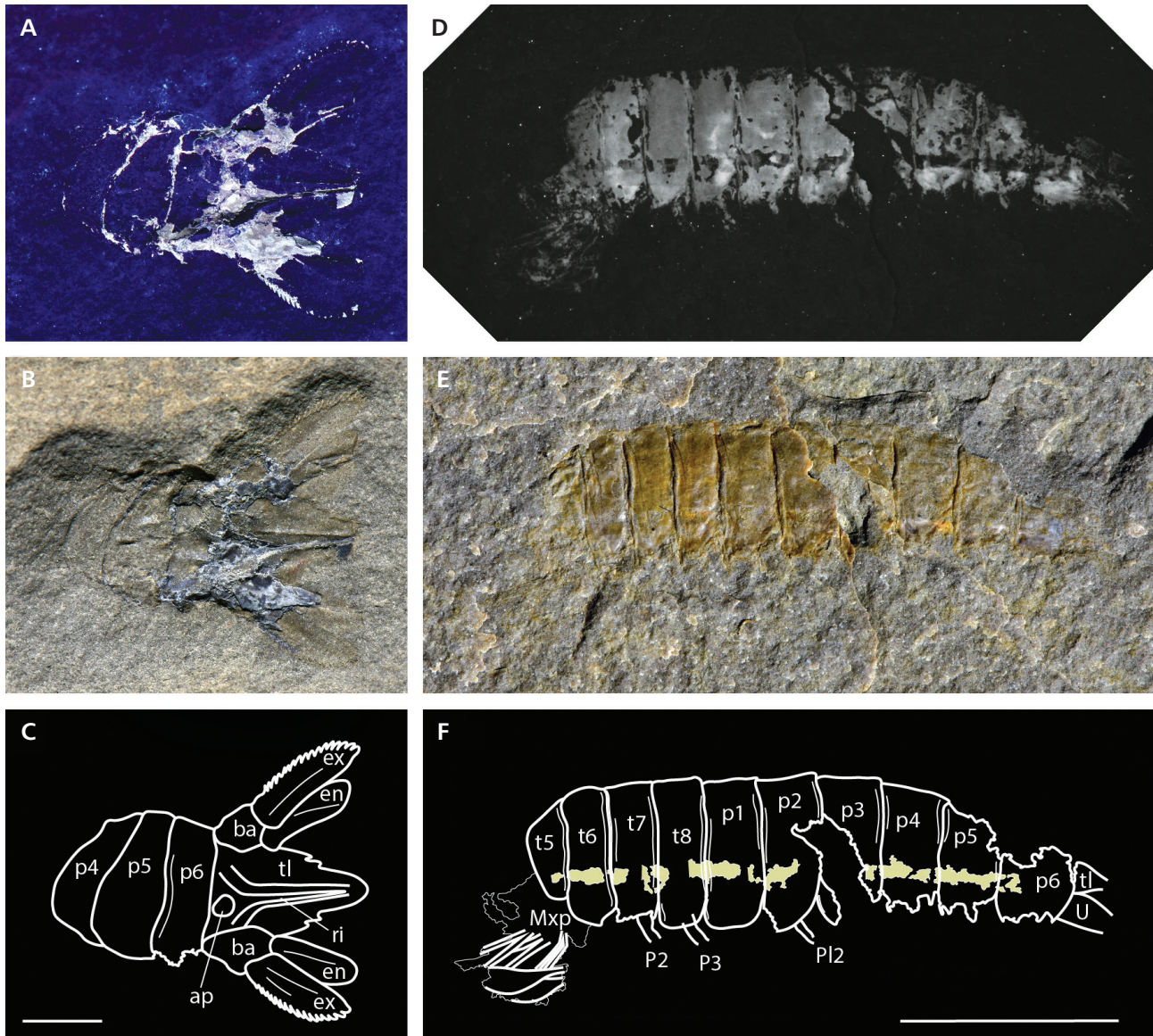
**Figure 3.** *Triassosculda ahyongi* gen. et sp. nov. A–C – ventral view of holotype UBGD 30550; D–F – dorso-lateral view of paratype UBGD 294010. Under UV illumination (A, D); under natural illumination (B, E); line drawings (C, F). Abbreviations: ap – anal plate; ba – uropodal basipod; en – uropodal endopod; ex – uropodal exopod; Mxp – maxilliped; P – pereiopod; p – pleonal segments; Pl – pleopod; ri – ridge-like keel; tl – telson; t – thoracic segments; U – uropod. Scale bar = 1 cm.

This new taxon is ascribed to Unipeltata Latreille, 1825 on the basis of its seemingly hypertrophied 2nd maxillipeds that appear a lot bigger than the others (which is typical of this taxon; *e.g.* Schram & Koenemann 2021), attesting of somewhat of a specialisation. It is easily distinguishable from other younger Unipeltata, and in particular from Unipeltata *sensu stricto*, due to its triangular telson with two serrations midway through its lateral margin (the telson is square-shaped in Unipeltata *sensu stricto*; Haug & Haug 2021). It also differs from Palaeozoic species by the broad anterior rim of its telson, and in having many (17) movable spines all along its uropodal exopod lateral margin.

## Discussion

### Morphological character differentiations

The known Carboniferous Stomatopoda fossil record currently comprises fourteen species of seven different genera and five families among the two suborders Palaeo-stomatopodea Brooks, 1962 and Archaeostomatopodea Schram, 1969 (Tab. 2). A first attempt to resolve the phylogenetic relationships between these Carboniferous species was carried out by Jenner *et al.* (1998) based on eleven species (eight Carboniferous Stomatopoda and three Mesozoic or younger Stomatopoda), and led to the

**Table 2.** List of all valid pre-Cenozoic Hoplocarida known to date and their stratigraphic range per period and stage. "*" indicates non-monophyletic taxa.

Order Aeschronectida Schram, 1969
    Family Aenigmacarididae Schram & Horner, 1978
        Genus *Aenigmacaris* Schram & Horner, 1978
            *A. cornigerum* Schram & Horner, 1978
                middle Carboniferous – Late Mississippian/Early Pennsylvanian – Serpukhovian/Bashkirian
            *A. minima* Schram & Schram, 1979
                late Carboniferous – Late Pennsylvanian – Gzhelian
        Genus *Joanellia* Schram, 1979
            *J. lundi* Schram & Schram, 1979
                middle Carboniferous – Late Mississippian – Serpukhovian
            *J. elegans* (Peach, 1883)
                early Carboniferous – Early Mississippian – Tournaisian
    Family Aratidecthidae Schram, 1979
        Genus *Aratidecthes* Schram, 1979
            *A. johnsoni* Schram, 1969
                late Carboniferous – Early & Middle Pennsylvanian – Bashkirian & Moscovian
    Family Kallidecthidae Schram, 1969
        Genus *Crangopsis* Salter, 1863
            *C. eskdalensis* (Peach, 1882)
                early Carboniferous – Early Mississippian – Tournaisian
            *C. socialis* (Salter, 1861)
                early Carboniferous – Early Mississippian – Tournaisian
            *C.* cf. *socialis* (Salter, 1861)
                middle Carboniferous – Late Mississippian – Serpukhovian
            *Crangopsis* sp. Schram & Horner, 1978
                middle Carboniferous – Late Mississippian/Early Pennsylvanian – Serpukhovian/Bashkirian
        Genus *Kallidechtes* Schram, 1979
            *K. eagari* Schram, 1979
                late Carboniferous – Early & Middle Pennsylvanian – Bashkirian & Moscovian
            *K. richardsoni* Schram, 1969
                Late Carboniferous – Middle Pennsylvanian – Moscovian

Order Stomatopoda Latreille, 1817
Suborder Archaeostomatopodea* Schram, 1969
    Family Daidalidae* Schram, 2007
        Genus *Daidal** Schram, 2007
            *D. acanthocercus* (Jenner, Hof & Schram, 1998)
                middle Carboniferous – Late Mississippian
            *D. pattoni* (Peach, 1908)
                middle Carboniferous – Late Mississippian
            *D. schoellmanni* Schram, 2007
                late Carboniferous – Early Pennsylvanian
    Family Gorgonophontidae* Schram, 2007
        Genus *Chabardella* Racheboeuf, Schram & Vidal, 2009
            *C. spinosa* Racheboeuf, Schram & Vidal, 2009
                late Carboniferous – Late Pennsylvanian
        Genus *Gorgonophontes** Schram, 1984
            *G. fraiponti* (Van Straelen, 1923)
                late Carboniferous – Early Pennsylvanian
            *G. peleron* Schram, 1984
                late Carboniferous – Late Pennsylvanian
    Family Tyrannophontidae* Schram, 1969
        Genus *Tyrannophontes* Schram, 1969
            *T. gigantion* Schram, 2007
                late Carboniferous – Middle Pennsylvanian
            *T. theridion* Schram, 1969
                late Carboniferous – Middle Pennsylvanian
Suborder Palaeostomatopodea* Brooks, 1962

Family Archeocarididae Schram, 2008
    Genus *Archaeocaris* Meek, 1872
        *A. graffhami* Brooks, 1962
            late Carboniferous – Early & Middle Pennsylvanian
        *A. vermiformis* Meek, 1872
        late Carboniferous – Early Pennsylvanian
Family Perimecturidae* Peach, 1908
    Genus *Bairdops** Schram, 1979
        *B. beargulchensis* Schram & Horner, 1978
            middle Carboniferous – Late Mississippian
        *B. elegans* (Peach, 1908)
            early Carboniferous – Early Mississippian
    Genus *Perimecturus* Peach, 1908
        *P. parki* (Peach, 1882)
            early Carboniferous – Early Mississippian
        *P. rapax* Schram & Horner, 1978
            middle Carboniferous – Late Mississippian
Suborder Unipeltata Latreille, 1825
Family Lysiosquillidae Giesbrecht, 1910
    Genus *Lysiosquilla* Dana, 1852
        *L. nkporoensis* Förster, 1982
            Late Cretaceous – Early Maastrichtian
Family Pseudosculdidae* Dames, 1886
    Genus *Archaeosculda* Ahyong, Garassino & Giron, 2007
        *A. phoenicia* Ahyong, Garassino & Giron, 2007
            Late Cretaceous – Cenomanian
    Genus *Pseudosculda* Dames, 1886
        *P. laevis* (Schlüter, 1872)
            middle Cretaceous – Cenomanian
Family Sculdidae* Dames, 1886
    Genus *Nodosculda* Franţescu, 2012
        *N. fisherorum* Franţescu, 2012
    Genus *Sculda* Münster, 1840
        *S. pennata* Münster, 1840
            Late Jurassic – Tithonian
        *S. spinosa* Kunth, 1870
            Late Jurassic – Tithonian
        *S. syriaca* Dames, 1886
            Late Cretaceous – Cenomanian
    Genus *Spinosculda* Haug, Haug & Waloszek, 2009
        *S. ehrlichi* Haug, Haug & Waloszek, 2009
            Late Jurassic – Tithonian
Family Squillidae* Latreille, 1802
        Early Cretaceous – Albian
    Genus *Squilla* Fabricius, 1787
        *S. cretacea* Schlüter, 1868
            Late Cretaceous – late Senonian
    Genus *Ursquilla* Hof, 1998
        *U. yehoachi* (Remy & Avnimelech, 1955)
            Late Cretaceous – Campanian
Family *Incertae sedis*
    Genus *Gigantosculda* Haug, Wiethase & Haug, 2015
        *G. ehrlichfeckei* Haug, Wiethase & Haug, 2015
            late Jurassic – Tithonian
    Genus *Ostenosculda* Braig, Haug, Ahyong, Garassino, Schädel & Haug, 2022
        *O. teruzzii* Braig, Haug, Ahyong, Garassino, Schädel & Haug, 2022
            Early Jurassic – Sinemurian
    Genus    *Paleosquilla* Schram, 1968
        *P. brevicoxa* Schram, 1968
            Late Cretaceous – Cenomanian
    Genus *Triassosculda* gen. nov.
        *Tr. ahyongi* gen. et sp. nov.
            Early Triassic – Olenekian (early Spathian)
    Genus *Tyrannosculda* Haug & Haug, 2021
        *T. laurae* Haug & Haug, 2021
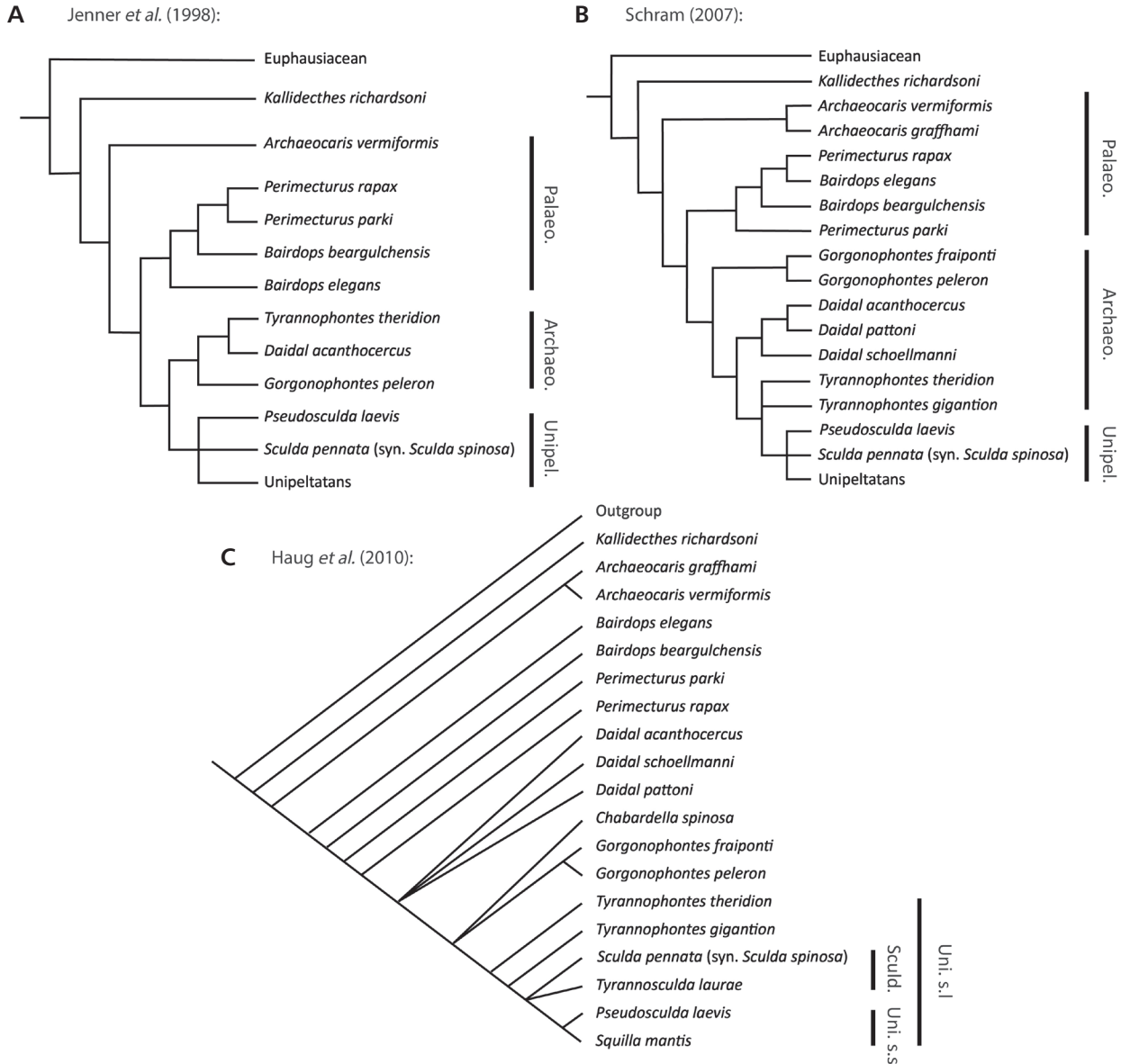            Late Jurassic – Tithonian

**Figure 4.** Previously proposed phylogenetic hypotheses. • A – phylogenetic hypothesis proposed by Jenner *et al.* (1998). • B – phylogenetic hypothesis proposed by Schram (2007). • C – phylogenetic hypothesis proposed by Haug *et al.* (2010). Abbreviations: Palaeo. – Palaeostomatopodea Brooks, 1962; Archaeo. – Archaeostomatopodea Schram, 1969; Unipel. – Unipeltata Latreille, 1825; Scld. – Sculdidae Dames, 1886; Uni. s.l – Unipeltata *sensu lato;* Uni. s.s. – Unipeltata *sensu stricto.*

highlighting of the paraphyly of Palaeostomatopodea (Fig. 4A). In the continuity of Jenner *et al.* (1998), and following the description of a new Carboniferous Stomatopoda and the examination of additional material, Schram (2007) confirmed this paraphyly and also showed the paraphyletic nature of Archaeostomatopodea (Fig. 4B). Schram (2007) raised other potential phylogenetic issues, such as the paraphyletic nature of the two genera *Perimecturus* Peach, 1908 and *Bairdops* Schram, 1979. Later, Haug *et al.* (2010) slightly amended and reconducted Schram's (2007) phylogenetic analysis after gaining new insights on the raptorial appendages of some

representatives of Unipeltata Latreille, 1825 (all post-Palaeozoic Stomatopoda), confirming Jenner *et al.* (1998) and Schram's (2007) previous phylogenetic hypothesis (Fig. 4C). Additionally, following their work, Haug *et al.* (2010) erected the non-Linnaean taxa Unipeltata *sensu lato* and Unipeltata *sensu stricto.*

The only common monophyletic clade retrieved in all above-mentioned studies (Fig. 4) is Unipeltata *sensu stricto* (Pseudosculdidae Dames, 1886 and all post Meso-zoic Stomatopoda) + Sculdidae Dames, 1886, that present two synapomorphies: a shield subdivided into three fields (one median and two lateral), and a large, more or less
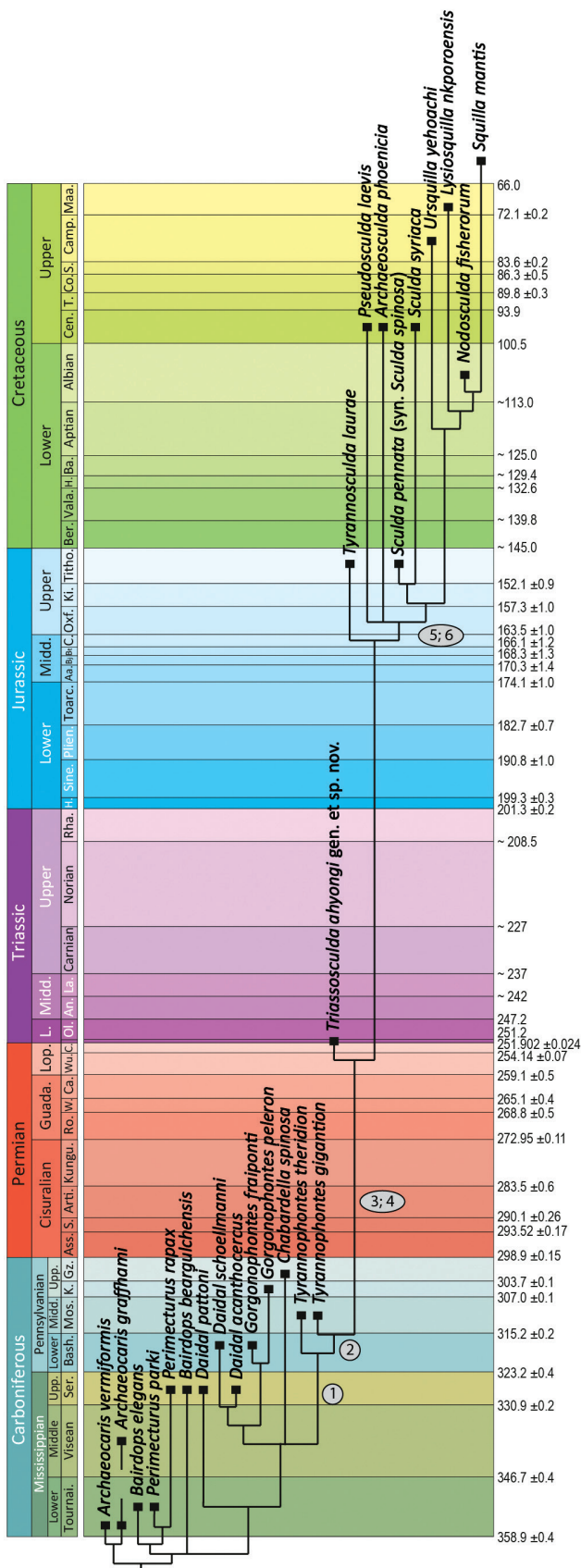
square-shaped telson. However, in these previous studies, the clade Unipeltata *sensu stricto* is only represented by no more than two taxa that are over 150 myr younger than the palaeostomatopods and archaeostomatopods.

The phylogenetic relationships among modern Unipeltata Latreille, 1825 has also been studied, both with and without fossil representatives, and based on morphological characters (*e.g.* Ahyong 1997, Ahyong & Harling 2000) as well as molecular data (*e.g.* Van Der Wal *et al.* 2017, Koga & Rouse 2021). However, when these studies take into consideration Carboniferous taxa, they are only used as outgroups. Therefore, the nature and the timing of the differentiation between Sculdidae, Unipeltata *sensu stricto* and older relatives (palaeostomatopods and archaeo-stomatopods) remains unclear. *Triassosculda ahyongi* gen. et sp. nov. provides new insights on this matter. It is dated from the Early Triassic, therefore about 50 myr younger than the Carboniferous taxa, but also almost 100 myr older than the most ancient known Sculdidae, and 150 myr older than the most ancient known Unipeltata *sensu stricto*. The phylogenetic position of *Tr. ahyongi* gen. et sp. nov. is consistent with its geological age, as it appears to be derived from the Palaeozoic archaeo-stomatopods, and more basal to Sculdidae and Unipeltata *sensu stricto* (Fig. 5).

The region presenting the most characters in the new fossils is the tail fan that is the most diagnostic element within Stomatopoda. The telson of *Tr. ahyongi* gen. et sp. nov. is of triangular shape with a marked median keel (Fig. 6D), similarly to that of Carboniferous Stomatopoda (Fig. 6A–C). However, it is wider at the anterior rim than the telson of Carboniferous species that had a rather narrow telson. This broad pleon and anterior rim is somewhat reminiscent of Jurassic species such as those of the Sculdidae Dames 1886 (Fig. 6F) and more modern Stomatopoda that have a large telson, although more or less square shaped. This suggests that the transition from a triangular shaped telson to a square shape telson was underway during the Early Triassic. Indeed, *Tr. ahyongi*

**Figure 5.** Stratigraphic occurrences of all known Palaeozoic and Mesozoic Stomatopoda, coupled to their phylogenetic relationships derived from the majority-rule (50%) consensus tree (retained from 566 trees, Supplementary File 3). Chronostratigraphic chart based on March 2020 updated version of Cohen *et al.* (2013). The length of the branches is not informative. Strict consensus tree available in Supplementary File 4. Detailed changes of character states available in Supplementary File 5. Main characters discussed here: 1 – Character 20, appearance of lateral structures on the lateral margins of the telson; 2 – Characters 6 & 30, raptorial appendage with reduced ischium and inflated propodus; 3 – Character 21, telson changes from elongated to stout; 4 – Character 13, appearance of distinct spines, *i.e.* articulated spines on uropodal exopod outer margins; 5 – Character 2, carapace shape from rounded to trapezoidal; 6 – Characters 27 & 28, presence of spines on the pleonal segments.
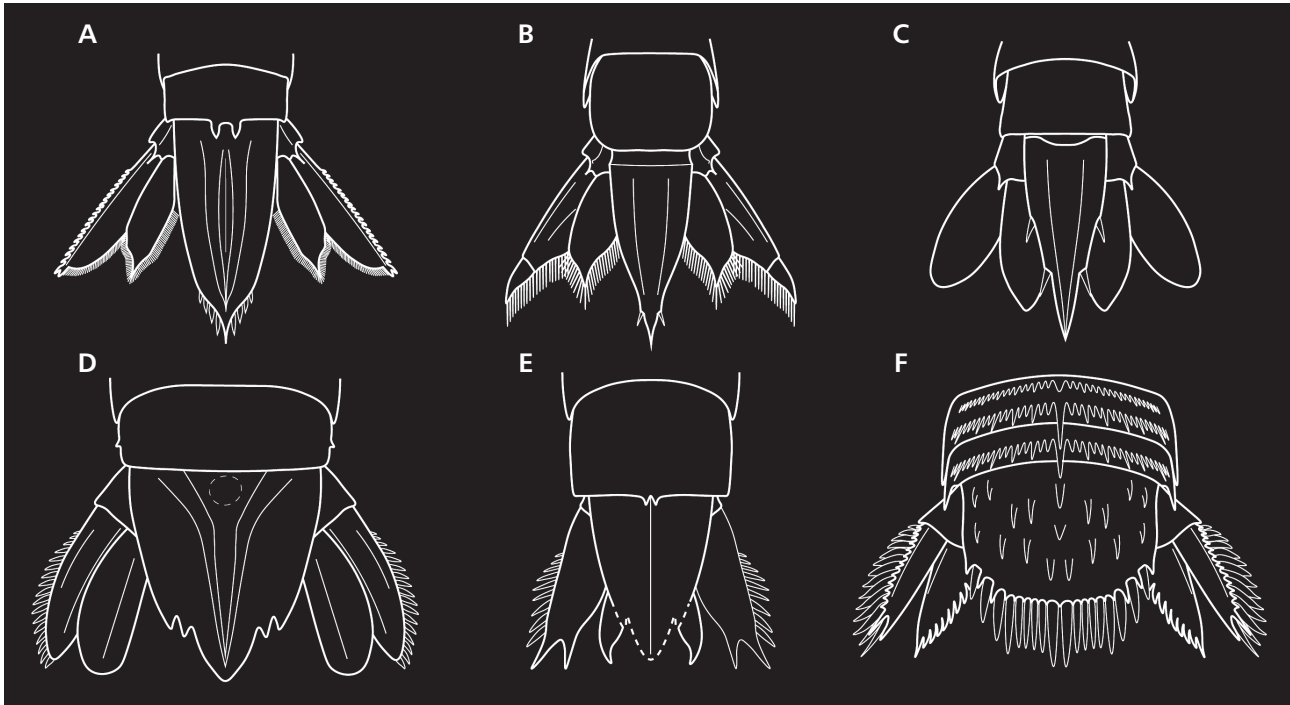
**Figure 6.** Comparison of the tail fan of *Triassosculda ahyongi* gen. et sp. nov. with other Stomatopoda fossil species. • A – *Daidal schoellmanni*. • B – *Gorgonophontes fraiponti*. • C – *Tyrannophontes theridion*. • D – *Triassosculda ahyongi* gen. et sp. nov. • E – *Tyrannosculda laurae*. • F – *Sculda* sp. Figures A–C, F are based on Haug *et al.* (2010); E is based on Haug & Haug (2021).

gen. et sp. nov. indicates that by the Triassic, at least some species of Stomatopoda had an enlarged telson, and perhaps it is only between the Early Triassic and the Jurassic that the shape of the telson went from triangular, *i.e.* shrimp-like, to square, *i.e.* lobster-like.

The lateral margin of the telson of *Tr. ahyongi* gen. et sp. nov. presents two clear serrations midway antero-posteriorly. Such structures are common in post-Jurassic Stomatopoda (Fig. 6E, F) and are also occasionally accompanied with articulated spines. On the other hand, only some Carboniferous Stomatopoda (Fig. 6A, B) present distal posterior articulated spines. Only *Tyrannophontes theridion* Schram, 1969 exhibits two lateral articulated spines (Fig. 6C), which is all the more interesting as this taxon appears to be the second closest older relative to *Tr. ahyongi* gen. et sp. nov. + *Tyrannosculda laurae* Haug & Haug, 2021 + Sculdidae Dames, 1886 + Unipeltata *sensu stricto*, after *Tyrannophontes gigantion* Schram, 2007 whose telson is unknown. Based on the present phylogenetic analysis, it appears that the presence of lateral structures on the telson is a synapomorphy for Unipeltata *sensu lato*, *i.e.* the clade formed by *Tyrannophontes* Schram, 1969 + *Tyrannosculda laurae* Haug & Haug, 2021 + Sculdidae + Unipeltata *sensu stricto* (Haug *et al.* 2010), and now also *Tr. ahyongi* gen. et sp. nov.

The thoracic appendages are poorly preserved in UBGD 294010. Nonetheless, it appears that *Tr. ahyongi* gen. et sp. nov. possessed rather robust raptorial appendages, at least three times longer than the other thoracic appendages, with a long merus and an inflated propodus. These features are synapomorphies of the clade formed by *Tyrannophontes gigantion* Schram, 2007 and more recent Stomatopoda, perhaps testifying of an evolution in their predatory behaviour.

The uropodal exopod of *Tr. ahyongi* gen. et sp. nov. exhibits movable spines on its lateral and posterior margin. This feature is characteristic of post-Palaeozoic Stomatopoda. Although one distant (both temporally and phylogenetically) Carboniferous species, *Bairdops beargulchensis* Schram & Horner 1978, also exhibits uropodal exopods with movable spines, this feature appears to be a synapomorphy for the clade formed by *Tr. ahyongi* gen. et sp. nov. and the other post-Palaeozoic Stomatopoda. Additionally, these spines have been suggested to serve as a mean of defence against predators (Caldwell & Dingle 1975, Yaraghi *et al.* 2019). Their appearance, as soon as the Early Triassic, may therefore testify of an increase of predation pressures on mantis shrimps prior to the Early Triassic, *i.e.* during the Permian.

## Phylogenetic observations (Figures 5, 7)

Among the specimens included in our phylogenetic analysis, some are poorly preserved and lack many characters, therefore incertitude remains (bootstrap results
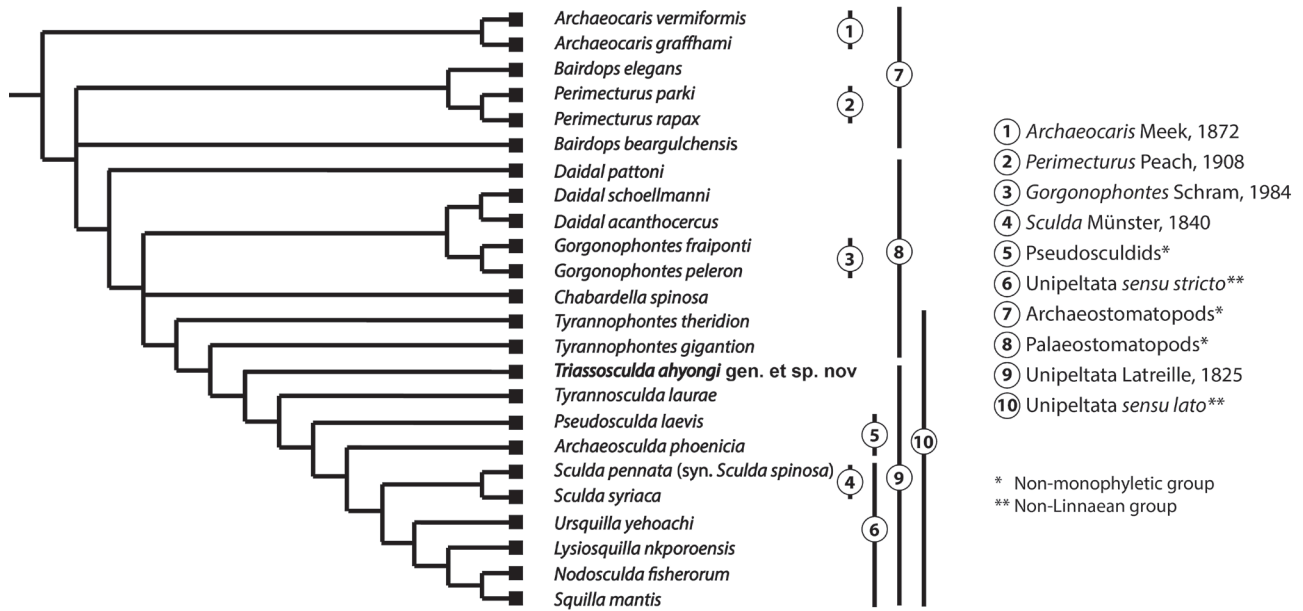
**Figure 7.** Simplified amended representation of the different groups discussed here, overlaid on the phylogenetic relationships derived from the majority-rule (50%) consensus tree (retained from 566 trees, Supplementary File 3). The length of the branches is not informative.

available in Supplementary File 2). Nonetheless, as it stands with the available material, the phylogenetic analysis supports once more the paraphyly of archaeostomatopods and palaeostomatopods. Additionally, it corroborates the monophyly of Unipeltata *sensu lato* (*Tyrannophontes* Schram, 1969 + all post-Palaeozoic Stomatopoda).

Among Palaeozoic taxa, the genera *Archaeocaris* Meek, 1872 and *Gorgonophontes* Schram, 1984 appear monophyletic, as in previous studies (Schram 2007, Haug *et al.* 2010). The genus *Perimecturus* Peach, 1908 was initially described as monophyletic by Jenner *et al.* (1998). However, in Schram (2007) and Haug *et al.* (2010) studies, it appeared to be non-monophyletic. In our phylogenetic reconstruction, the monophyly of *Perimecturus* is supported. On the other hand, the monophyly of *Daidal* Schram, 2007 remains ambiguous as *Daidal pattoni* (Peach, 1908) appears less derived than the clade composed by *Daidal acanthocercus* (Jenner, Hof & Schram, 1998) and *Daidal schoellmanni* Schram, 2007 that forms the sister group of *Gorgonophontes* Schram, 1984. Additionally, the clade *Daidal acanthocercus* (Jenner, Hof & Schram, 1998) + *Daidal schoellmanni* Schram, 2007 + *Gorgonophontes* Schram, 1984 appear in polytomy with *Daidal pattoni* (Peach, 1908), *Chabardella spinosa* Racheboeuf, Schram & Vidal, 2009, and Unipeltata *sensu lato*. Such pattern may result from the lack of knowledge regarding the thoracic appendages of *Daidal pattoni* that should hopefully be improved in the future with the discovery and study of new specimens.

Among Unipeltata *sensu lato*, there is no evidence for the monophyly of *Tyrannophontes* Schram, 1969. However, the poor knowledge about *Tyrannophontes gigantion* Schram, 2007 strongly hinders any interpretation. The monophyly of Pseudosculdidae Dames, 1886 that is comprised of *Archaeosculda phoenicia* Ahyong, Garassino & Gironi, 2007 and *Pseudosculda laevis* (Schlüter, 1872) is also equivocal, here again, perhaps due to the limited knowledge of *A. phoenicia*. The genus *Sculda* Münster, 1840 of the family Sculdidae Dames 1886 however, appears clearly monophyletic, and more derived than pseudosculdids, unlike in Haug *et al.* (2010). The main morphological changes from pseudosculdids to more derived relatives are the shape of the carapace that evolves from rounded to trapezoidal, and the development of pleonal ornament, including in particular posterolateral spines on the pleonal segments. We therefore suggest repositioning Sculdidae within Unipeltata *sensu stricto*, and removing the pseudosculdids of it in order to preserve its monophyletic nature. Additionally, to avoid any future confusion we propose a taxonomical definition for Unipeltata *sensu stricto* (that is a *non* Linnaean rank, yet commonly used) that is the presence of a trapezoidal carapace and pleonal segment spines.

Finally, the last monophyletic clade is that formed by Squillidae Latreille, 1802, *Lysiosquilla nkporoensis* Förster, 1982 and *Nodosculda fisherorum* Franțescu, 2012. The two representatives of Squillidae are *Ursquilla yehoachi* (Remy & Avnimelech, 1955) and *Squilla mantis* (Linnaeus, 1758), yet it is *N. fisherorum* that appears as

the sister taxon of *S. mantis*. Additionally, *N. fisherorum* who is the only representative of its genus, appears more derived than *L. nkoporensis* which is itself more derived than *U. yehoachi*. The three later taxa are poorly known, which may explain their current phylogenetic position. Nonetheless, as it is, the monophyly of Squillidae remains unresolved, illustrating well the need of more material.

## From shrimp-like to lobster-like

Haug & Haug (2021) discussed a stepwise transition from a shrimp-type morphology to a lobster-type morphology within other Eumalacostraca lineages, both morphs being distinguished among others by: (i) the cross section of the body and the pleon that is laterally flattened in the shrimp morphotype whereas it is dorsoventrally flattened in the lobster morphotype, (ii) the pleon of the shrimp morphotype is curled whereas that of the lobster morphotype has the ability to fully flatten, (iii) the telson is relatively narrow and triangular in the shrimp morphotype whereas it is more square shape in the lobster morphotype, and (iv) all thoracopods present exopods in the shrimp morphotype but not in the lobster morphotype. By drawing the parallel within other Eumalacostraca lineages, Haug & Haug (2021) suggested a similar transition from shrimp-like to lobster-like morphology for Stomatopoda. However, due to the lack of Late Palaeozoic and Early Mesozoic fossils, and therefore the lack of potential transitional character states, they could not reconstruct this morphological transition, leaving this scenario hypothetical.

*Triassosculda ahyongi* gen. et sp. nov. appears to be rather shrimp-like and laterally flattened, but it is also stretched out straight in UBGD 294010 (Fig. 3D–F), indicating a lobster-like sprawled-type stance. Regarding the telson, it is triangular but very enlarged (about as long as anterior margin width), which seems to correspond to an intermediate state between typical shrimp-type and lobster-type telson morphologies. Given the temporal and phylogenetic position of *Tr. ahyongi* gen. et sp. nov., particularly with its intermediate telson morphology between shrimp-like and lobster-like, this species is consistent with Haug & Haug's (2021) hypothesis of a transition from a shrimp-type to a lobster-type morphology within Stomatopoda. Besides, some characters observed in *Tr. ahyongi* gen. et sp. nov. and shared with more modern Stomatopoda, such as the robust raptorial appendages that are a great predation adaptation (*e.g.* Ahyong & Jarman 2009, Van Der Wal *et al.* 2017) and the presence of multiple spines on the tail fan that are key defensive structures (Caldwell & Dingle 1975, Yaraghi *et al.* 2019), suggest that this morphological transition may be concomitant with a change of prey and/or predator behaviour.

## Conclusion

Although known since the early Carboniferous, the evolutionary history of Stomatopoda is poorly understood, especially regarding the transition between the Palaeozoic and the Mesozoic forms. This is mainly due to the heretofore complete lack of known Permian and Triassic Stomatopoda fossils and the poor preservation of the only known Early Jurassic Stomatopoda. The newly described Early Triassic *Triassosculda ahyongi* gen. et sp. nov. provides new insights on this matter as it fills in an over 100 myr hiatus. It presents features comparable to those of both the Paleozoic and the Jurassic–Cretaceous, as well as characters showing somewhat intermediate states. Among the intermediate features, it presents transitional states of characters between the Carboniferous and the oldest Mesozoic Stomatopoda, mainly on the tail fan. Notably, the telson shows a broad triangular shape, whereas it is narrow among Carboniferous representatives, and square among younger Mesozoic species. The overall morphology of this new species is also in agreement with previous hypotheses of a transition from a shrimp-type morphology to a lobster-type morphology within Stomatopoda and suggests that this transition was underway by the Early Triassic. The phylogeny conducted with all known Carboniferous and Mesozoic Stomatopoda species corroborates the transitional nature of *Tr. ahyongi* gen. et sp. nov. and allowed us to clarify some phylogenetic relationships among pre-Cenozoic species. In particular, the monophyly of the genus *Perimecturus* is documented, and the content of Unipeltata *sensu lato* is clarified. However, many Stomatopoda taxa appear non-monophyletic. Others, such as Sculdidae, appear of doubtful phylogenetic nature due to the current limited material. This illustrates the need of a future thorough revision of Stomatopoda as well as the strong potential of future discoveries. Overall, *Triassosculda ahyongi* gen. et sp. nov. fills in a 100 myr gap in the fossil record, yet a 50 myr gap prior, and a 50 myr gap following the Early Triassic remain. Therefore, many questions on the evolutionary history of mantis shrimps are still open.

## Acknowledgements

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## Electronic supplementary material

**Supplementary File 1.** Matrix used for phylogenetic reconstruction presented here.

**Supplementary File 2.** Majority-rule (50%) consensus tree retained from 566 trees of length 90. In total, 25 taxa and 30 characters were used, 20 of which are parsimony-informative, and 10 are ordered. *Kallidecthes richardsoni* is used as outgroup. Values at the nodes correspond to: In the square – node number; Left – Consensus values; Right – Bootstrap values.

**Supplementary File 3.** All 566 optimal trees found by the parsimony analysis and retained for computing the Majority-rule (50%) consensus.

**Supplementary File 4.** Strict consensus tree.

**Supplementary File 5.** List of characters' state changes associated to the Majority-rule (50%) consensus tree.