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Revision of "*Bellinurus*" *carteri* (Chelicerata: Xiphosura) from the Late Devonian of Pennsylvania, USA

Révision de ¨Belinurusc̈arteri *(Chelicerata: Xiohosura) du Dévonien supérieur de Pennsylvanie, États-Unis*

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ABSTRACT

Horseshoe crabs are an iconic group of marine chelicerates that have an impressive fossil record extending back to at least the Lower Ordovician. Despite their long fossil record and associated palaeontological interest, a range of fossil horseshoe crab taxa erected in the 19th and 20th centuries have remained understudied. Recent phylogenetic hypotheses have led to improvements in the understanding of xiphosuran origins and evolutionary history; however, the resolution among the basal-most Devonian-aged members remains poor. Here, the type specimen of "*Bellinurus*" *carteri* Eller, 1940 from the Late Devonian of Pennsylvania is reconsidered. Based on a revised morphological description and comparison, we conclude that the species is not referable to the genus *Bellinurus* and erected a new genus: *Pickettia* gen. nov. A phylogenetic analysis resolves *Pickettia carteri* within a polytomy containing taxa previously considered to comprise the group Kasibelinuridae, but which is currently a paraphyletic assemblage. We discuss *P. carteri* within the context of other stem xiphosurids and conclude that the diversity of this assemblage has been overstated. The redescription of *P. carteri* highlights the need for more inclusive studies to resolve the evolutionary relationships of stem xiphosurids.

Mots-clés :
Dévonien supérieur
Pichettia
Formation Cattaraugus
Pennsylvanie
Famennien
Ordre des Xiphosurida

RÉSUMÉ

Les crabes fer à cheval sont un groupe icône des chélicérates marins, qui ont un impressionnant registre fossile remontant au moins jusqu'à l'Ordovicien inférieur. En dépit de ce vaste registre fossile et de l'intérêt paléontologique qui est attaché, une gamme de taxons fossiles de crabes fer à cheval, érigés au XIX^{e} et XX^{e} siècles, est restée sous-étudiée. Des hypothèses phylogénétiques récentes ont conduit à des progrès dans la compréhension des origines des Xiphosura et de l'histoire de leur évolution ; cependant, la résolution parmi les membres d'âge Dévonien basal demeure pauvre. Dans cet article, le spécimen type « *Bellinurus* » *carteri* Eller, 1940 du Dévonien terminal de Pennsylvanie est reconsidéré. Sur la base d'une description morphologique révisée et de comparaison, les auteurs concluent que l'espèce ne peut être rapportée à *Bellinurus* et ont créé un nouveau genre : *Pickettia*

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gen. nov. Une analyse phylogénétique résout *Pickettia* au sein d'une polytomie incluant les taxons primitivement considérés comme comportant le groupe des Kasibelinuridae, mais qui est actuellement un assemblage paraphylétique. Les auteurs discutent *P. carteri* dans le contexte d'autres branches de xiphosuridés et concluent que la diversité de cet assemblage a été exagérée. La redescription de *P. carteri* souligne le besoin d'études plus poussées pour résoudre les relations évolutives des différentes branches de xiphosuridés.

1. Introduction

Horseshoe crabs are archetypal marine chelicerates with an array of unique biological features and an extensive fossil record. This combination has inspired substantial biological interest in the group (Bicknell et al., 2018a; Lamsdell, 2016; Owen, 1872; Sokoloff, 1978; Shultz, 2001; Shuster Jr., 1982) that has been matched by extensive palaeontological scrutiny (Anderson and Selden, 1997; Bicknell et al., 2019a; Błażejowski, 2015; Dunlop and Selden, 1998; Eldredge, 1974; Haug and Rötzer, 2018; Lamsdell, 2013, 2016; Raymond, 1944; Rudkin and Young, 2009; Størmer, 1934, 1955; Woodward, 1867). Palaeontological research specifically reflects both their extensive fossil record (ranging from the Lower Ordovician to today; Van Roy et al. (2010, 2015)) and apparent evolutionary conservatism since the Jurassic (Błażejowski, 2015; Kin and Błażejowski, 2014; Fisher, 1984), despite experiencing evolutionary radiations during the Carboniferous and Triassic (Moore et al., 2007; Bicknell et al., 2019c). Fossil horseshoe crabs have been examined somewhat sporadically over the past 180 years. This research effort has resulted in many underexplored species. Such taxa may be suitable for taxonomic revision in the light of new specimens, more recent descriptions, and phylogenetic hypotheses. This will undoubtedly help uncover a more complete evolutionary history of horseshoe crabs. To this end, we redescribe "*Bellinurus*" *carteri* Eller, 1940, a taxon from the Late Devonian of Pennsylvania that has not been formally re-examined since its original description. Morphological comparisons of "*Bellinurus*" *carteri* with similar horseshoe crabs and a new phylogenetic analysis are performed in an attempt to resolve its taxonomic position. Our reassessment confirms theses presented in Pickett (1993) and Lamsdell et al. (2013): the taxon is not a belinurid. We therefore move the taxon into the stem lineage leading to Xiphosurida and erect the new genus *Pickettia* gen. nov.

2. Institutional abbreviations

AM F: Australian Museum, Sydney, NSW, Australia; BMSC: Buffalo Society of Natural Sciences, Buffalo, New York State, USA; CM: Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; YPM IP: Yale Peabody Museum, Diversion of Invertebrate Paleontology New Haven, Connecticut, USA; USNM PAL: United States National Museum, Washington, DC, USA.

3. Material and methods

"*Bellinurus*" *carteri* (note that, although Pickett (1993) emended the feminine suffix to "*B*". *carterae*, the species spelling of *carteri* must be retained as "Article 32.5.1. (ICZN, 1999) states that incorrect latinization must not be corrected, and the original spellings be maintained" (Krell et al., 2017, p. 8)) was originally described by Eller (1940) from one specimen (BMSC E 9644) from the Hanley Quarry, an outcrop of the lower Cattaraugus Formation (Late Devonian, Fammenian), Pennsylvania, USA (Tesmer, 1975). BMSC E 9644 is preserved as a slightly domed internal mould without cuticle on a slab of dark-reddish sandstone and lacks a counterpart. BMSC E 9644 was photographed with a Canon EOS 5D Mark IV under normal and low angle light. Measurements were obtained from photographs using ImageJ.

3.1. Systematic framework

We follow the systematic taxonomy of Pickett (1993) and Lamsdell (2013, 2016) and anatomical terms presented in Siveter and Selden (1987), Dunlop and Lamsdell (2017), and Bicknell et al. (2018a).

3.2. Phylogenetic analysis

To evaluate the phylogenetic position of *Pickettia carteri* gen. nov., we coded it as an additional taxon into the recently published matrix of Lamsdell (2016) which contains a broad sampling of fossil and extant euchelicerates (Supplementary Information 1). The analysis was performed under equally weighted parsimony in TNT 1.5 (Goloboff and Catalano, 2016). Implied weighting was also used with the concavity constant set to the default value ($k = 3$) and a higher value that weights homoplasy less strongly ($k = 12$), following the results of simulation studies (Goloboff et al., 2018). The implied weighting trees were almost identical those of the equally weighted analysis, and thus we use the results of this analysis herein (see Results). We performed five replications of a "New Technology" tree search strategy using random sectorial searches, 1000 iterations of the parsimony ratchet, 50 cycles of drifting and 5 rounds of tree fusing, holding a maximum of 10 trees per replication. All multistate characters were considered unordered as in the original analysis.

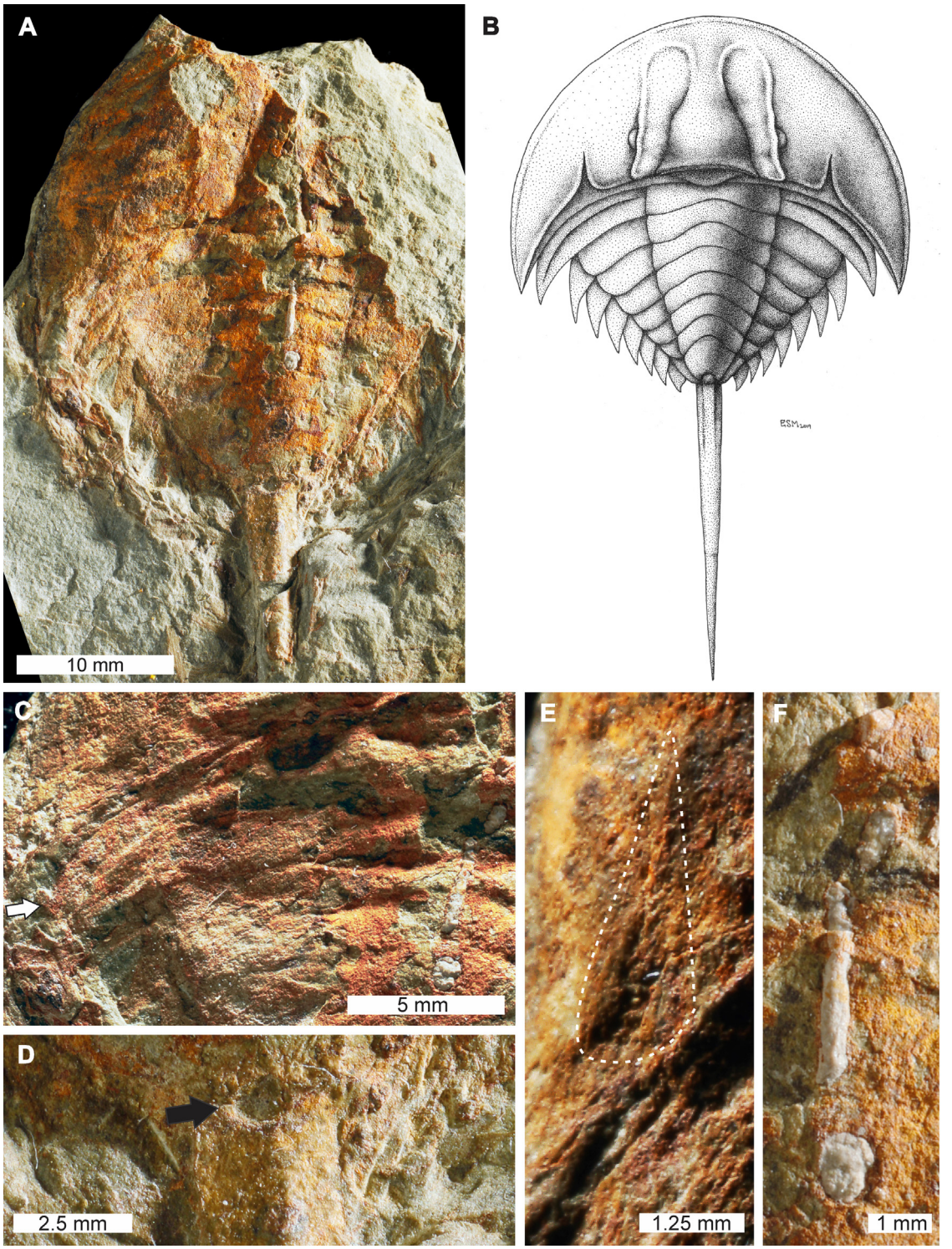

Fig. 1. *Pickettia carteri* holotype (BMSC E 9644). (A) Complete specimen. (B) Reconstruction of taxon showing proposed "M"-shaped ophthalmic ridge. (C) Close up of left opisthosoma. Most anterior opisthosomal tergite is overdeveloped into a free lobe (white arrow). (D) Close up of an indentation on the opisthosoma-telson joint (black arrow). (E) Close up of subtriangular triradiate node leading into cheek ridge (area in dotted white). (F) Close up of cololite along the opisthosomal axis. Image credit: (A, C–F) K.C. Pratt; (B) reconstruction by Elissa Johnson.

Fig. 1. *Pickettia carteri* holotype (BMSC E 9644). (A) Spécimen complet. (B) Reconstitution du taxon montrant l'arête ophtalmique en forme de « M ». (C) Occlusion de l'opisthosoma. Le tergite opisthosomal le plus antérieur est surdéveloppé dans un lobe libre (flèche blanche). (D) Occlusion d'une indentation sur l'articulation telson-opisthosoma (flèche noire). (E) Occlusion d'un nœud subtriangulaire triradié, conduisant à l'arête de la joue (zone entourée d'une ponctuation blanche). (F) Occlusion de cololite le long de l'axe opisthosomique. Crédit photo : (A, C–F) K.C. Pratt ; (B) reconstitution par Elissa Johnson.

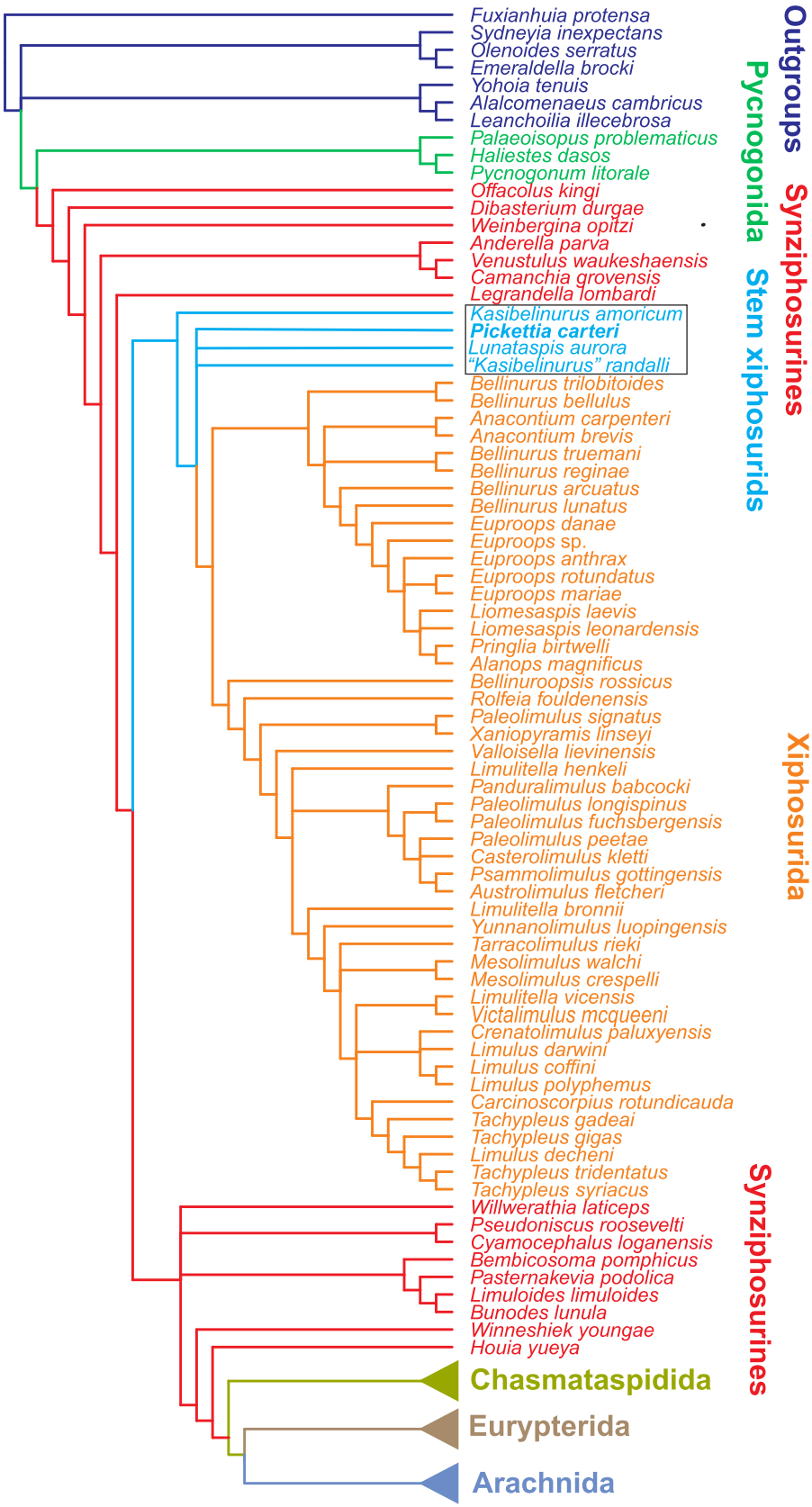

Fig. 2. Results of the phylogenetic analysis. Strict consensus of the 18 trees resulting from analysing the data matrix in Supplementary Information 1.

4. Systematic palaeontology

Subphylum Chelicerata Heymons, 1901.
Class Xiphosura Latreille, 1802.
Pickettia gen. nov. (Fig. 1).
Pickettia gen. nov. (Fig. 1).
1940 *Belinurus carteri* Eller, p. 134, Fig. 1.
1982 *Belinurus carteri* Eller; Fisher, 1982, p. 177, Fig. 1.
1984 *Belinurus carteri* Eller; Fisher, p. 199, Fig. 2.
1987 *Bellinurus carteri* Eller; Siveter and Selden, p. 384, Fig. 1F.
1993 "*Bellinurus carterae*" Eller; Pickett, p. 282.
1994 *Bellinurus carteri* Eller; Schultka, 1994, p. 347.
1997 *Bellinurus carterae* Eller; Anderson and Selden, p. 22.
2013 "*Bellinurus*" *carterae* Eller; Lamsdell et al., p. 368.
2016 *"Bellinurus" carterae* Eller; Lerner et al., p. 208.

Etymology. The generic name *Pickettia* is used in honour of John Pickett and for his contributions to invertebrate palaeontology, specifically with focus on horseshoe crabs, across his career.

Type and only species. *Belinurus carteri*.

Emended diagnosis. Distinguished from other stem xiphosurids by an anterior-most opisthosomal tergite overdeveloped into a free lobe, and opisthosomal tergites that terminate in pleural spines.

Holotype specimen. BMSC E 9644.

Locality, horizon and age. Hanley Quarry, lower Cattaraugus Formation, northwestern Pennsylvania, Late Devonian (Fammenian).

Preservation. BMSC E 9644 is preserved as an internal mould on yellow-red sandstone. The slightly vaulted nature of the exoskeleton suggests the taxon was vaulted in life. No counterpart reported.

Description of holotype. BMSC E 9644 is an articulated prosoma, opisthosoma, and partial telson (Fig. 1). A small degree of three-dimensional relief is present. Specimen is 39.8 mm long, including partial telson. Prosoma is semi-circular and only partly preserved; most of the left side and posterior section of right side are preserved. Distance between the posterior margin of left prosomal side and prosomal midline is 17.8 mm. Prosomal rim is preserved and has a maximum width of 0.57 mm. No prosomal doublure is visible. Left ophthalmic ridge is slightly preserved and not parallel to cardiac lobe (Fig. 1A). Ophthalmic ridge is straight and 7.47 mm long. No lateral compound eyes can be confidently identified. Cardiac lobe is convex, cone-shaped, and both sides of the posterior section are preserved (Fig. 1A). Cardiac lobe is 8.36 mm wide posteriorly, tapering to ~4.5 mm anteriorly, although the anterior-most section is not preserved. Lobe is bordered by two interophthalmic ridges. Left interophthalmic ridge is 9.79 mm long and right interophthalmic ridge is 5.5 mm long. No obvious cardiac ridge is preserved. Ocelli are not observed. A subtriangular triradiate node appears to be present on the left side of the posterior boarder of the prosomal shield. The node is located 8.7 mm to the left of the prosomal midline and 5.02 mm from the left lateral prosomal border. Node leads into what appears to be a 2.8 mm long cheek ridge (Fig. 1E). Left genal spine extends 9.6 mm posterolaterally from the prosomal-opisthosomal hinge to anteroposterior midpoint of the opisthosoma. Lateral extent between preserved genal spine tip and opisthosoma is 6.4 mm. Angle between genal spine and opisthosoma is 57.8°. Genal spine is curved to maintain a horseshoe shape (Fig. 1A–C). Inner margin of genal spines is curved anteriorly. No prosomal appendages are preserved.

Preservation of the opisthosoma is better than that of the prosoma. Opisthosoma is trapezoidal, 17.2 mm long and 21.8 mm wide (where both sides are preserved), tapering to 6.3 mm posteriorly. Opisthosoma is segmented with the expression of tergites VIII–XV. Most anterior tergite (VIII) is a prominent free lobe (tergal expression of somite VIII) and extends laterally out to the genal spine tip (Fig. 1C). Only the left side of the free lobe is preserved. The most distal point of the left VIII tergite is 14.61 mm from the opisthosomal midline. The subsequent tergites are smaller: XV is 30% width of VIII. Tergites VIII–XIV are 1.8 mm long, and XV is 3.03 mm long, suggesting that it is a pretelson section (Fig. 1A). Opisthosomal axis is lobe-shaped: 17 mm long, 9.9 mm wide anteriorly, tapering to 4.76 mm posteriorly. No apodemes are noted. Left pleural lobe is flat, lacks relief and is segmented. Excluding overdeveloped VIII tergite, the left plural lobe is 6.7 mm wide anteriorly, tapering to 0.88 mm posteriorly. Marginal rim is poorly defined but when noted is ~0.5 mm wide. Right pleural lobe is incompletely preserved. Tergites VIII to IX are partly preserved. Tergites X–XV are completely preserved. Right side of the right lobe is flat, lacks relief and is segmented. Lobe is 5.01 mm wide anteriorly (where complete), tapering to 0.69 mm posteriorly. The right marginal rim is slightly better preserved than the left side and is up to 0.5 mm wide. Tergites IX–XIV terminate with triangular pleural spines. On the left opisthosoma side, pleural spines are triangular and the length of posterior spine side decreases from 3.84 mm (tergite IX) to 2.19 mm (tergite XIV). The distance between spine tips to left opisthosomal border decreases from 3.6 mm (tergite IX) to 2.6 mm (tergite XIV). On the right opisthosomal side, only tergites X and XI have spines preserved. Length of posterior spine side is 3.8 mm for both spines. Distance of distal spine tips to right opisthosomal border is 3.5 mm. A cololite (fossilised gut contents) is preserved along the opisthosomal axis, spanning tergites VIII–XI and is 6.5 mm long (Fig. 1F). The telson is lanceolate

Stem xiphosurids, following the definition in Lamsdell (2016), are located in blue and a black box. *Pickettia carteri* is shown in bold. The topology of Chasmataspidida, Eurypterida and Arachnida clades were *collapsed as they are unchanged from Selden et al. (2015)* and were not the focus our study.
Fig. 2. Résultats de l'analyse phylogénétique. Strict consensus des trois arbres résultant de l'analyse de la matrice des données (matériel supplémentaire 1). La branche des xiphosuridés, selon la définition de Lamsdell (2016), est figurée en bleu et est localisée dans une boîte noire. *Picketta carteri* figure en gras. La topologie des clades de Chamataspidida, Eurypterida et Arachnida est inchangée selon Selden et al. (2015) ; ces clades sont mis ensemble et ne sont pas l'objet de cette étude.

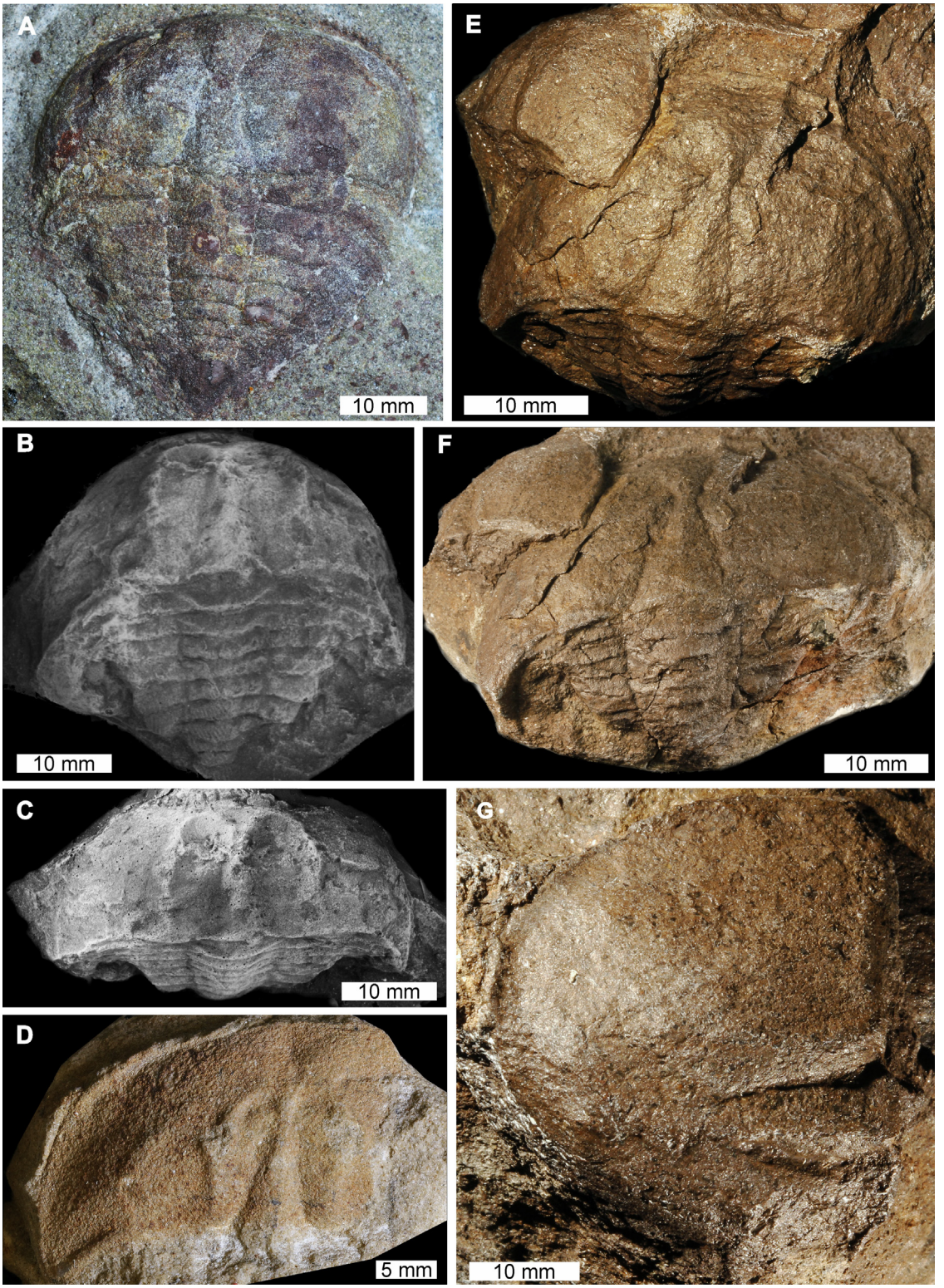

Fig. 3. Further examples of Devonian-aged stem xiphosurids. (A) *Kasibelinurus amicorum* from the Late Devonian (Famennian)-aged Mandagery Sandstone, Australia (holotype, AM F68969). (B–C) "*Bellinurus*" *alleganyensis* from the Late Devonian (Famennian)-aged Chadakoin Formation, New York, USA (cast of holotype, CM 11065); a taxon that is synonymised here with "*K.*" *randalli.* (B) Cast in dorsal view showing "M"-shaped ophthalmic ridge. (C) Cast in anterior view. Specimen is ammonium chloride coated. (D) "*Kasibelinurus*" *randalli* from the Late Devonian (Famennian)-aged Venango Formation, Pennsylvania, USA (holotype, YPM IP 09010). (E–G) "*Kasibelinurus*" *randalli* from the Late Devonian (Famennian)-aged Chadakoin Formation, Pennsylvania, USA (USNM PAL

and articulated with the posterior opisthosoma margin. A sub-circular hole is present at the opisthosoma-telson joint is noted (Fig. 1D). Telson is incomplete; the preserved portion is 11.5 mm long. No axial ridge is present noted along telson. Anterior section of telson is 3.39 mm wide tapering to 1.28 mm. Posterior tip of telson has a slight transverse ridge.

Remarks. The triradiate node and the cheek ridge were not mentioned in Eller (1940). These features are known for Paleolimulidae (Siveter and Selden, 1987), but in this case may reflect taphonomic distortion of the specimen; more specimens are needed to determine if this is indeed a real feature. The hypertrophic free lobe is interpreted as the first opisthosomal tergite. The movable spines described by Eller (1940) are reinterpreted here as pleural spines. The pretelson is substantially more pronounced than Eller (1940) suggested. We also propose that the ophthalmic ridges would have probably converged into an "M"-shaped double arch (Fig. 1B), as is observed in other stem xiphosurids from the Late Devonian of the USA (Babcock et al., 1995).

5. Results

The phylogenetic analysis resulted in 18 most parsimonious trees of length 738 (CI: 0.472; RI: 0.879). The topology of the strict consensus tree is similar to that presented in Lamsdell (2016) and Selden et al. (2015); see Fig. 2) in hypothesising a monophyletic Xiphosurida, with synziphosurines represented as polyphyletic grade (*sensu* Lamsdell, 2013) forming the basal members of the sister taxon of, Xiphosurida + stem xiphosurids. *Pickettia carteri* resolves within a polytomy containing "*Kasibelinurus*" *randalli* (Beecher, 1902) and *Lunataspis aurora* Rudkin et al., 2008 and immediately crownward of *K. amicorum* Pickett, 1993). All four species form successive outgroups to Xiphosurida. The implied weighting analysis resulted in a single most parsimonious tree under both concavity constants and differed only in "*K.*" *randalli* and *P. carteri* forming a polytomy with *L. aurora* + Xiphosurida ($k = 3$), and the complete resolution of the polytomy of "*K*". *randalli*, *L. aurora* and *P. carteri* as successive outgroups of Xiphosurida ($k = 12$).

6. Discussion

Pickett (1993) suggested that *Pickettia carteri* belonged in Kasibelinuridae. Here, we consider *P. carteri* a stem xiphosurid as Kasibelinuridae is a paraphyletic group: a notion supported by Lamsdell (2016). As stem horseshoe crabs, these taxa have features observed in Paleolimulidae and Belinuridae. *Pickettia carteri* has possible evidence of a triradiate node and cheek ridge diagnostic of Paleolimulidae (Lamsdell, 2016; Siveter and Selden, 1987). Furthermore, *P. carteri* lacks movable spines, a derived character observed in Limulina and unknown from Belinurina. Finally, the pronounced pretelson section in *P. carteri* is a feature known from at least *Paleolimulus woodae* Lerner et al., 2016 and *Bellinuroopsis rossicus* Chernyshev, 1933. In light of the character combination presented here, there is no justification for placing this taxon within Belinuridae. The taxon does not belong in the stem genus *Kasibelinurus* as *P. carteri* has a hypertrophic free lobe and genal spines extending posteriorly to the third opisthosomal tergite (X): both features not known from *Kasibelinurus* (*sensu* Pickett, 1993).

Stem xiphosurids are an apparently rare grade of horseshoe crabs and their early divergence and basal phylogenetic position have presented issues regarding a clear understanding of their place within Xiphosurida. Furthermore, few studies have considered which taxa might belong in this grade (Babcock et al., 1995; Lamsdell et al., 2013; Pickett, 1993). A consideration of select Devonian taxa therefore seems appropriate and four Devonian-aged taxa in Dunlop et al. (2019) are considered (Fig. 3): "*Bellinurus*" *alleganyensis* (Eller, 1938b) from the Late Devonian (Famennian)-aged Chadakoin Formation, New York, USA (Babcock et al., 1995); *Kasibelinurus amicorum* from the Late Devonian (Famennian)-aged Mandagery Sandstone, Australia; "*K*." *randalli* from the Late Devonian (Famennian)-aged Venango and Chadakoin formations, Pennsylvania, USA (Babcock et al., 1995); and *Pickettia carteri*. Comparisons between these four taxa suggest that "*K.*" *randalli* is the same taxon as "*B.*" *alleganyensis* (Fig. 3B–G) as the two taxa have very comparable prosomal and opisthosomal morphologies. Furthermore, both taxa are found in the Chadakoin Formation. Building on Babcock et al. (1995), "*B.*" *alleganyensis* is considered a junior synonym of "*K.*" *randalli*. Additionally, "*K.*" *randalli* should be moved out of the genus *Kasibelinurus*. This change is suggested as the holotype of *Kasibelinurus*, *K. amicorum*, lacks the double arched, "M"-shaped, ophthalmic ridge described in "*K*". *randalli* (compare Fig. 3A with Fig. 3B–D) (Lamsdell et al., 2013; Selden and Siveter, 1987). Together, these data suggest that stem xiphosurid diversity has been overstated and thorough taxonomic revision is needed to uncover the true diversity of stem horseshoe crabs.

484524). Specimen displays a complete individual and an isolated prosoma. (E) Complete specimen, showing entire prosoma with "M"-shaped ophthalmic ridge. (F) Complete specimen, showing enrolled nature and opisthosoma. (G) Isolated potential prosoma. Image credit: (A) Patrick Smith; (B–G) Russell Bicknell.

Fig. 3. Autres exemples de xiphosuridés d'âge Dévonien. (A) *Kasibelinurus amicorum* en provenance du grès du Dévonien final (Famennien) de Mandagery, Australie (holotype AM F68969). (B–C) « *Bellinurus* » *alleganyensis*, en provenance de la formation Chadakoin d'âge Dévonien final (Famennien), New York, États-Unis (moulage d'holotype, CM 11065), taxon qui est ici synonyme de « *K* » *randalli*. (B) Moulage en vue dorsale montrant l'arête ophtalmique en forme de « M ». (C) Moulage en vue antérieure. Le spécimen est recouvert de chlorure d'ammonium. (D) « *Kasibelinurus* » *randalli* en provenance de la formation Venango d'âge Dévonien final (Famennien), Pennsylvanie, États-Unis (holotype YPM IP 09010). (E–G) « *Kasibelinurus* » *randalli* de la Formation Chadacoin, d'âge Dévonien final, Pennsylvanie, États-Unis (USNM PAL 484524). Le spécimen montre une prosoma complète individuelle et isolée. Spécimen complet (E) montrant une prosoma entière avec l'arête ophtalmique en forme de « M ». (F) Spécimen complet montrant une nature et une opisthosoma enroulées. (G) Prosoma potentielle isolée. Illustrations (A) Patrick Smith ; (B–G) Russell Bicknell.

Although the life mode and the diet of basal horseshoe crabs have been considered briefly in Lamsdell et al. (2013), we will explore this topic in more detail here. *Pickettia carteri* was likely a marine organism (see paleoenvironmental discussion of the Cattaraugus Formation in Tesmer, 1967) and therefore similar to other pre-Carboniferous horseshoe crabs (Lamsdell et al., 2013; Moore et al., 2007). The marine trace fossil *Selenichnites* sp. (Romano and Whyte, 1987) has been described from localities close to the Hanley Quarry (Eller, 1938a, 1940; Williams, 1885). *Selenichnites* represents "partial burial of the anterior (exoskeletal) region (of a horseshoe crab) while working the sediment with its appendages, presumably for concealment or in the search for food" (Whyte and Romano, 2013, p. 205). Babcock et al. (1995) suggested that "*Kasibelinurus*" *randalli* may have produced the Devonian-aged *Selenichnites* trace fossils, and by extension we suggest that *P. carteri* may have made similar traces. Devonian horseshoe crabs were therefore potentially capable of burrowing and, by extension, finding and consuming prey in a similar fashion to extant horseshoe crabs (Bicknell et al., 2018a). Although appendage data is not known for *P. carteri*, it likely had an appendage set similar to extant and fossil taxa (Bicknell et al., 2018a, 2019b; Haug et al., 2012; Lamsdell and McKenzie, 2015; Racheboeuf et al., 2002; Shultz, 2001). *Pickettia carteri* likely used gnathobases on prosomal appendages II–VI to masticate the abundant shelly and possible soft prey (Caster, 1930) with feeding mechanisms similar to extant horseshoe crabs (Bicknell et al., 2018b, 2018c; Botton, 1984; Razak and Kassim, 2018). Further exploration of this topic would require determination of the contents of the preserved cololite using non-destructive three-dimensional imaging techniques such as computed tomographic scanning. Similar cololites have been documented in specimens of *Tachypleus syriacus* (Woodward, 1879) (Bicknell et al., 2019b), and identification of gut contents of a range of basal xiphosurans would allow significant insights into the evolution of predator – prey interactions within basal horseshoe crabs (Bicknell and Paterson, 2018). However, this is beyond the scope of the current study.

Stem xiphosurids have been placed into the group Kasibelinuridae (*sensu* Lamsdell, 2016). Due to this paraphyletic status, we have refrained from referring our new taxon to the group. It is possible that the group is invalid and, if so, should no longer be used; further phylogenetic studies are needed to determine if this is the case. A particularly acute problem for coding xiphosurans into phylogenetic matrices is the lack of representative taxa that preserve characters pertaining to the appendages. So far, these data are limited primarily to *Alanops magnificus* Racheboeuf et al., 2002, *Euproops danae* (Meek and Worthen, 1865), *Tachypleus syriacus* (*Yunnanolimulus luopingensis* Zhang et al., 2009 (Bicknell et al., 2019b; Haug and Rötzer, 2018; Haug et al., 2012; Hu et al., 2017; Lamsdell and McKenzie, 2015). The discovery of more xiphosurans and xiphosurids with complete appendages would therefore contribute a plethora of new morphological data that can aid in refining phylogenetic hypotheses. Other sources of data aside from discrete characters, such as continuous and morphometric data, also offer potential avenues for resolving xiphosuran interrelationships. Continuous characters have implementations under both parsimony and Bayesian criteria (Goloboff et al., 2006; Höhna et al., 2016) and both two- and three-dimensional morphometric data can be analysed as such in TNT 1.5 (Goloboff and Catalano, 2016). Morphometric data in particular have another use: they can be used to explore morphological evolutionary patterns of the group to uncover the tempo and mode of horseshoe crab evolution (Bicknell et al., 2019c). Finally, the involvement of genomic data to produce a total evidence phylogeny, building on the work of Ballesteros and Sharma (2019), will undoubtedly prove central to uncovering the timing and patterns of major diversification events in Xiphosura, and other chelicerate groups (Giribet and Edgecombe, 2019).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at: https://doi.org/10.1016/j.crpv.2019.08.002.

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