Arthropoda Selecta 28(4): 549–555

Euproops danae (Belinuridae) cluster confirms deep origin of gregarious behaviour in xiphosurids

Скопление *Euproops danae* (Belinuridae) подтверждает давнее происхождение грегарного поведения у мечехвостов

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KEY WORDS: *Euproops danae*, clustering, gregarious behaviour, Carboniferous, evolutionary stasis.

КЛЮЧЕВЫЕ СЛОВА: *Euproops danae*, скопление, грегарное поведение, каменноугольный период, эволюционный стазис.

ABSTRACT. Xiphosurids are archetypal marine arthropods that have received considerable research interest from both biologists and palaeontologists. Mating clusters of extant horseshoe crabs have informed research on clustering in other fossil arthropods, such as trilobites. Furthermore, the evolutionary stasis exhibited by horseshoe crabs suggests that fossil xiphosurids may also have mated in clusters. However, no body fossil evidence has been presented to support this idea. Here, we document a cluster of seven *Euproops danae* (Meek et Worthen, 1865) specimens preserved on the same bedding plane of Pennsylvanian-aged Farrington Group siltstone. These specimens record potential reproductive strategies of belinurids that are comparable to extant counterparts. This gregarious behaviour may have decreased the impact of predation and/or contributed to genetic diversity. The cluster ultimately highlights a further example of xiphosurid evolutionary stasis.

How to cite this article: Bicknell R.D.C., Pates S., Botton M.L. 2019. *Euproops danae* (Belinuridae) cluster confirms deep origin of gregarious behaviour in xiphosurids // Arthropoda Selecta. Vol.28. No.4. P.549–555. doi: 10.15298/arthsel. 28.4.07

РЕЗЮМЕ. Мечехвосты Xiphosurida — архетипические морские членистоногие, представляющие значительный интерес для исследований биологов и палеонтологов. Наличие скоплений при спаривании у рецентных мечехвостов привело к исследованию аналогичных группировок у ископаемых членистоногих, таких как трилобиты. Более того, вследствие эволюционного стазиса, проявляемого мечехвостами, можно предположить, что ископаемые Xiphosurida также спариваются в скоплениях. Тем не менее, до сих пор это предположение не было подтверждено ископаемыми находками. Здесь задокументировано скопление семи *Euproops danae* (Meek et Worthen, 1865), сохранившихся на той же поверхности напластования алевролита группы Фаррингтон пенсильванского возраста. Эти экземпляры проявляют потенциальную репродуктивную стратегию Belinuridae, которая сравнима с таковой рецентных форм. Грегарное поведение может уменьшить вероятность нападения хищников и/или быть связанным с генетическим разнообразием, и представляет собой еще один пример эволюционного стазиса Xiphosurida.

Introduction

True horseshoe crabs (Chelicerata: Xiphosurida) are arguably the most iconic group of extant marine chelicerates [Shuster Jr., 1982; Bicknell *et al.*, 2018a; Bicknell, Pates, 2019a]. The domed, crescent-shaped prosoma, rounded to trapezoidal opisthosoma, and elongate telson give the extant taxa an archaic appearance [Rudkin *et al.*, 2008; Rudkin, Young, 2009; Bicknell *et al.*, 2018b; Bicknell, Pates, 2019b]. This morphology, coupled with a stunning fossil record and exhibition of apparent evolutionary stasis, has driven palaeontological interest in xiphosurids [Babcock *et al.*, 2000; Anderson, Shuster Jr., 2003; Kin, Błażejowski, 2014; Bicknell *et al.*, 2019a, d]. Due to their phylogenetic position, extant horseshoe crabs are often used as modern analogues to explore facets of extinct arthropod groups. In particular, the annual spawning events of the American horseshoe crab, *Limulus polyphemus* (Linnaeus, 1758), are compared to clusters of fossil arthropods such as trilobites [Shuster Jr., 1982; Hughes, Cooper, 1999; Paterson *et al.*, 2008; Brockmann *et al.*, 2000; Gutiérrez-Marco *et al.*, 2009; Shuster Jr., Sekiguchi, 2009; Bicknell *et al.*, 2019c] and eurypterids [Braddy, 2001; Vrazo, Braddy, 2011]. Similarities between clusters of articulated trilobites and the patterns of horseshoe crab spawning have been used to suggest that, in exceptional circumstances, trilobites exhibited gregarious behaviour [Hughes, Cooper, 1999; Karim, Westrop, 2002; Paterson *et al.*, 2008; Gutiérrez-Marco *et al.*, 2009; Brett, 2015; Bicknell et al., 2019c]. However, no record of fossil horseshoe crab clusters are known. One might therefore ask: has horseshoe crab spawning arisen recently in their evolutionary history, or does it have a deeper origin in their fossil record that has simply not been reported. The only records of multiple fossil horseshoe crab specimens preserved on a same bedding plane are Ambrose & Romano [1972] and unfigured discussions in Fisher [1979]. Here, we reconsider the Ambrose & Romano [1972] slab that preserves specimens of the belinurid *Euproops danae* (Meek et Worthen, 1865) and, in doing so, discuss the first record of a fossil horseshoe crab cluster.

Methods and Materials

A slab of silty mudstone from the Farrington Group, collected from within a coal spoil heap in Sommerset, England, was considered. It has limited geological context, but is considered Westphalian D in age [Ambrose, Romano, 1972]. The authors of the original description assigned the seven specimens on the slab to *Euproops kilmersdonensis* Ambrose et Romano, 1972. This taxon was later synonymised with *E. danae* [Anderson, 1994]. The slab, housed in the Natural History Museum (NHMUK PI In 61012–61018), was photographed with a Canon EOS 5DS R under normal light. Carapace length (excluding telson) and prosoma-opisthosoma joint width measurements were taken for 5 specimens using ImageJ to explore possible patterns in specimen size (Addition 1). Two specimens (NHMUK PI In 61014 and NHMUK PI In 61018) are not preserved completely enough for these measurements.

Results

Five of the seven *Euproops danae* specimens (NHMUK PI In 61012, 61013, 61015, 61016, 61017) are preserved as complete prosoma and opisthosoma (Fig. 1). The telson is completely preserved in NHMUK PI In 61012 (Fig. 2A) and NHMUK PI In 61016 (Fig. 3A), partly preserved in NHMUK PI In 61015 (Fig. 2D), and absent in NHMUK PI In 61013 (Fig. 2B) and NHMUK PI In 61017 (Fig. 3B). Specimens NHMUK PI In 61014 (Fig. 2C) and NHMUK PI In 61018 (Fig. 3C) are partly preserved. NHMUK PI In 61014 (Fig. 2C) lacks the posterior right prosoma and the left opisthosomal side. NHMUK PI In 61018 (Fig. 3C) preserved the prosoma but lacks the left opisthosomal side. As Ambrose & Romano [1972] noted, the specimens lack an obvious orientation, although at least five specimens (NHMUK PI In 61013, 61015, 61016, 61017, 61018; Figs 1A, B, 2B, D, 3A–C) are aligned with the slab's shorter axis. Carapace length measurements ranged between 24.8–27.5 mm and prosoma-opisthosoma joint width measurement ranged between 20.0–27.9 mm. These points plot into two distinct groups (Fig. 4).

Discussion

Preservation of multiple horseshoe crab specimens on the same bedding plane is definitely unusual and allowed Ambrose & Romano [1972] to explore intraspecific variation. Here, the significance of the cluster itself is considered. Fisher [1979] suggested that the preservation of multiple specimens on the same slab recorded the imprisonment of *Euproops danae* within tree trunks, where the trunks functioned as pitfall traps. However, one would expect specimens to be preserved in different bedding planes, unless all individuals fell in at exactly the same time; an outcome that seems unparsimonious. As NHMUK PI In 61012–61018 are preserved on the same bedding plane, and as separate specimens, we suggest that the cluster records gregarious behaviour, such as mating or moulting, that was potentially preserved by a storm event and rapidly buried [Speyer, Brett, 1985; Karim, Westrop, 2002; Paterson *et al.*, 2008; Brett *et al.*, 2012; Brett, 2015]. The articulated nature of NHMUK PI In 61012–61018 precludes a moulting event [Vrazo, Braddy, 2011], but likely the lack of preferential specimen orientation, and similarity to clusters of extant xiphosurids suggests that the slab records a mating aggregation (*sensu* Gutiérrez-Marco *et al.*, 2009). It is also interesting to note that the brackish palaeoenvironment that preserved this cluster is comparable to the environment the smallest extant taxon — *Carcinoscorpius rotundicauda* [Latreille, 1802] — spawns: "brackish estuaries and rivers in muddy sand and mangrove swamps" [Brockmann, Smith, 2009: 200; Fairuz-Fozi *et al.*, 2018].

The mating system in extant horseshoe crabs has been reviewed at length (see Brockmann, 1990, 2003; Brockmann *et al.*, 2000, 2015; Brockmann, Smith, 2009; references therein), and several common patterns have emerged. Spawning behaviour in all extant species is often synchronized to the lunar cycle, with the largest number of animals typically nesting on the full and new moon high tides. Modified prosomal appendages (claspers) on the male are used to attach to the opisthosoma of the female. After amplexus, the male places his gonopores close to the female's eggs to facilitate fertilization as she deposits the eggs into the substrate. Two pairs of claspers are found in the Asian horseshoe crabs [*Carcinoscorpius rotundicauda*, *Tachypleus gigas* (Müller, 1785) and *T. tridentatus* (Leach, 1819)], whereas *Limulus polyphemus* only has one pair of claspers. Botton *et al.* [1996] theorised that the double claspers in *T. tridentatus* are an adaptation to

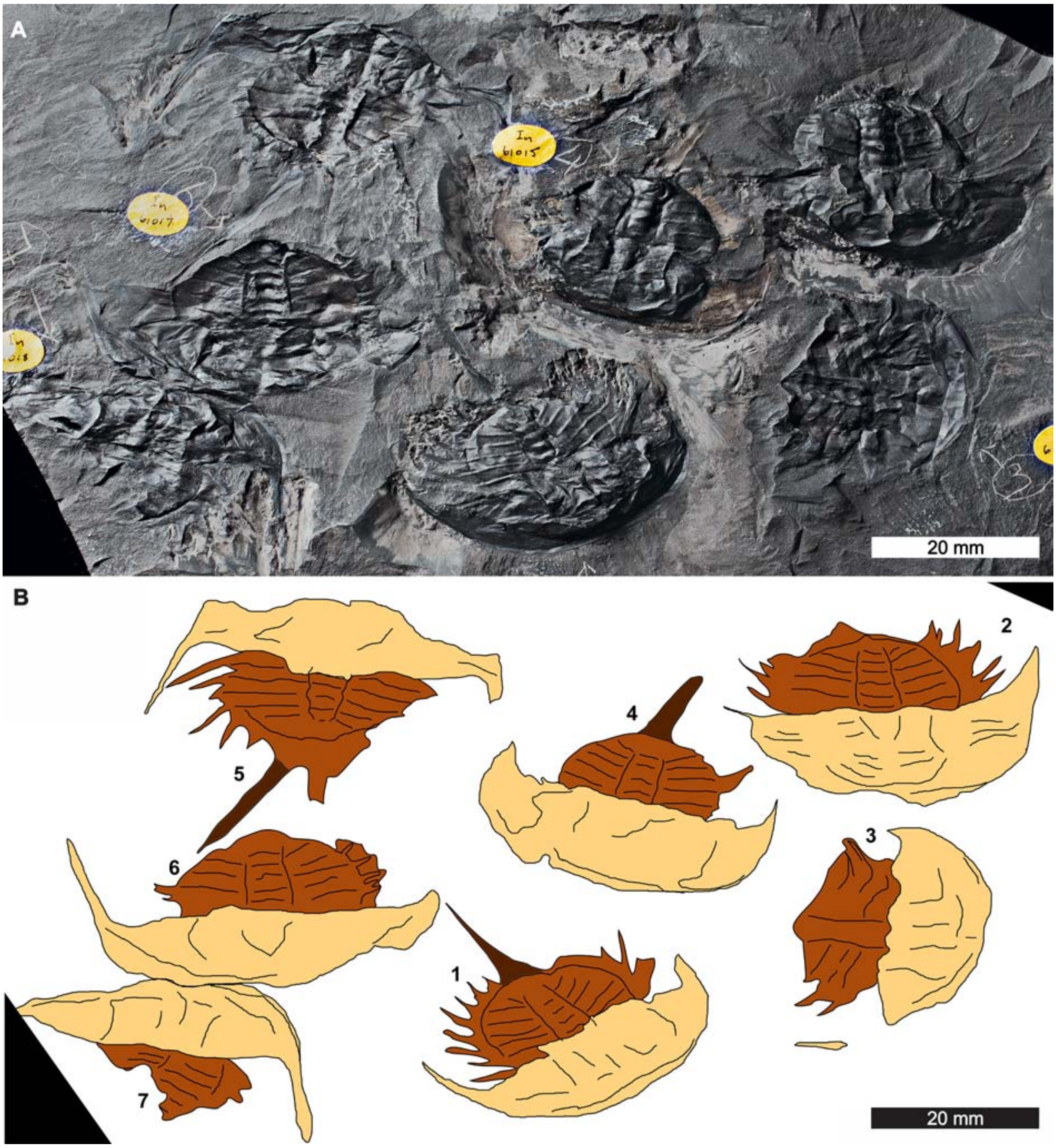

Fig. 1. Complete slab showing the seven specimens (NHMUK PI In 61012–61018). A — photograph of complete slab; B — line drawings of all specimens. 1 — NHMUK PI In 61012; 2 — NHMUK PI In 61013; 3 — NHMUK PI In 61014; 4 — NHMUK PI In 61015; 5 — NHMUK PI In 61016; 6 — NHMUK PI In 61017; 7 — NHMUK PI In 61018. Image credit: (A) Lucie Goodayle and the Natural History Museum, London.

Рис. 1. Целый кусрк породы с семью экземплярами (NHMUK PI In 61012–61018). A — фото целого куска породы; B — прорисовки всех экземпляров. 1 — NHMUK PI In 61012; 2 — NHMUK PI In 61013; 3 — NHMUK PI In 61014; 4 — NHMUK PI In 61015; 5 — NHMUK PI In 61016; 6 — NHMUK PI In 61017; 7 — NHMUK PI In 61018. Любезно предоставлено Lucie Goodayle и Музеем естественной истории (Лондон) (A).

prolonged amplexus. Conversely, *L. polyphemus* satellite males are often found in association with amplexed pairs [Brockmann, Smith, 2009; Brockmann *et al.*, 2015] but this phenomenon is seldom observed in the Asian species [Botton *et al.*, 1996; Brockmann, Smith, 2009].

Reproduction in extant horseshoe crabs is a dangerous event as predation by gulls and the possibility of being stranded can result in mortality [Botton, Loveland, 1989]. The threat from predators can be decreased through mass spawning and clustering and *Euproops danae* would have benefited from this defence strategy

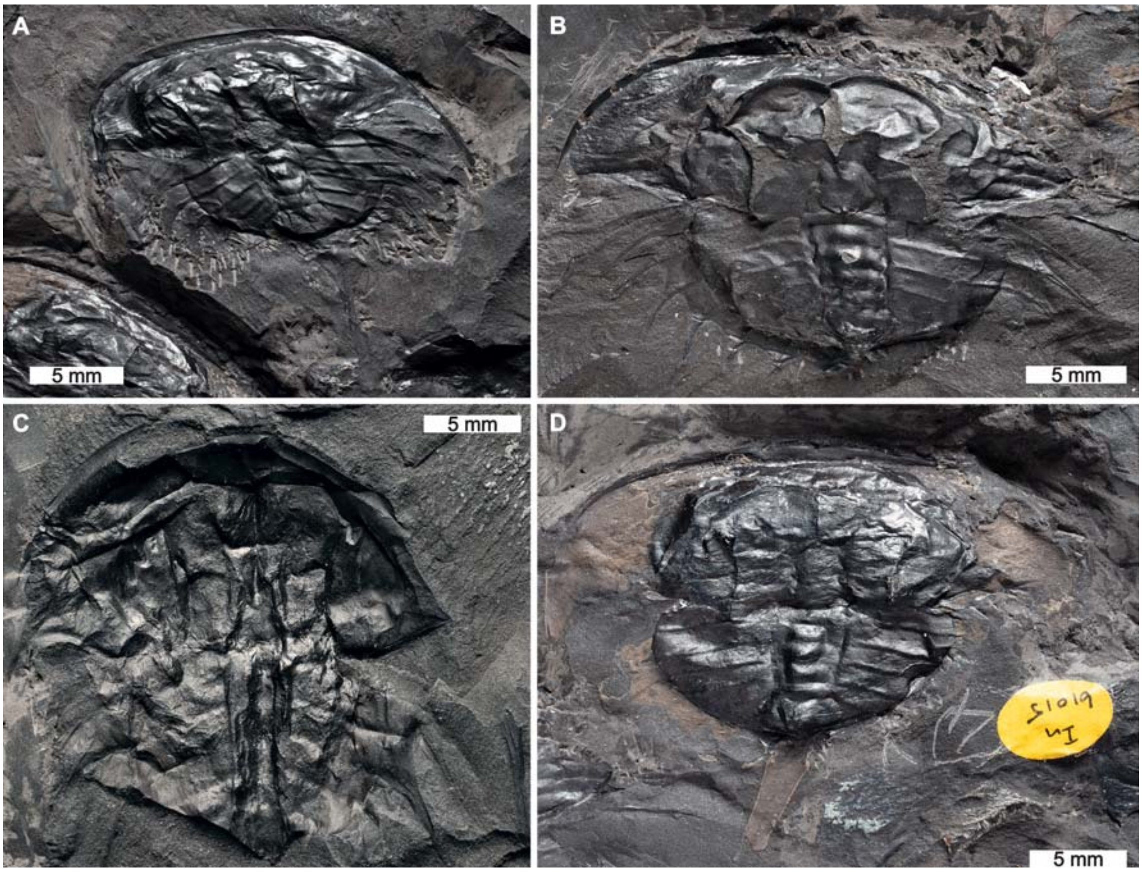

Fig. 2. *Euproops danae* specimens NHMUK PI In 61012–61015. A — NHMUK PI In 61012; B — NHMUK PI In 61013; C — NHMUK PI In 61014; D — NHMUK PI In 61015. Image credit: (A–D) Lucie Goodayle and the Natural History Museum, London.

Рис. 2. Экземпляры *Euproops danae* NHMUK PI In 61012–61015. A — NHMUK PI In 61012; B — NHMUK PI In 61013; C — NHMUK PI In 61014; D — NHMUK PI In 61015. Любезно предоставлено Lucie Goodayle и Музеем естественной истории (Лондон) (A–D).

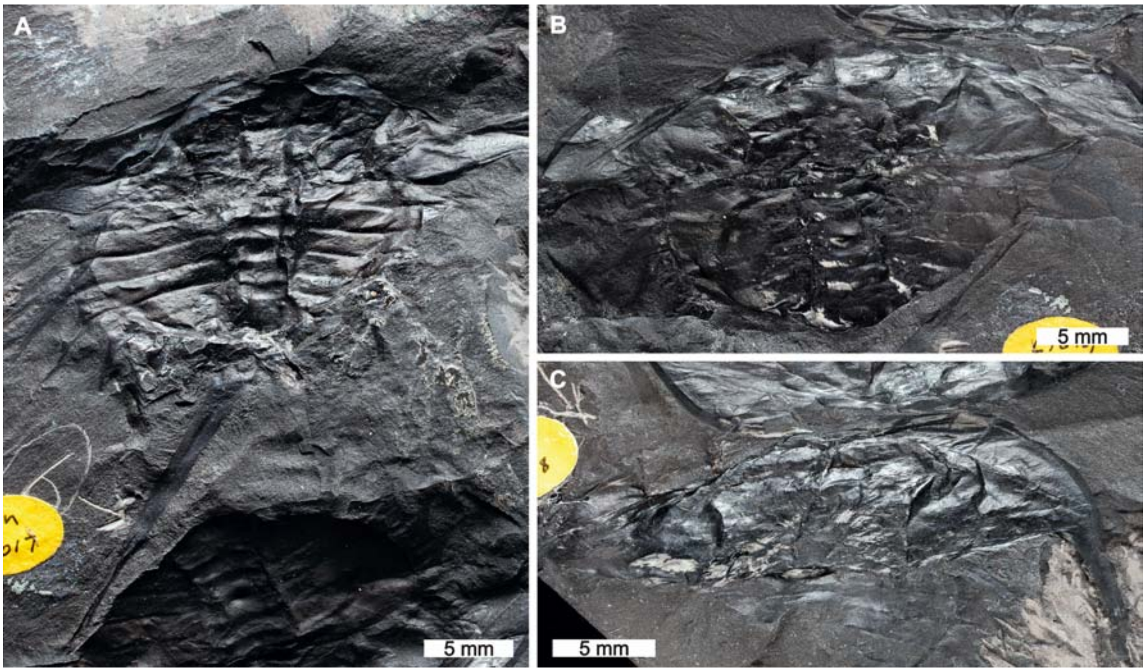

Fig. 3. *Euproops danae* specimens NHMUK PI In 61016–61018. A — NHMUK PI In 61016; B — NHMUK PI In 61017; C — NHMUK PI In 61018. Image credit: (A–C) Lucie Goodayle and the Natural History Museum, London.

Рис. 3. Экземпляры *Euproops danae* NHMUK PI In 61016–61018. A — NHMUK PI In 61016; B — NHMUK PI In 61017; C — NHMUK PI In 61018. Любезно предоставлено Lucie Goodayle и Музеем естественной истории (Лондон) (A–C).

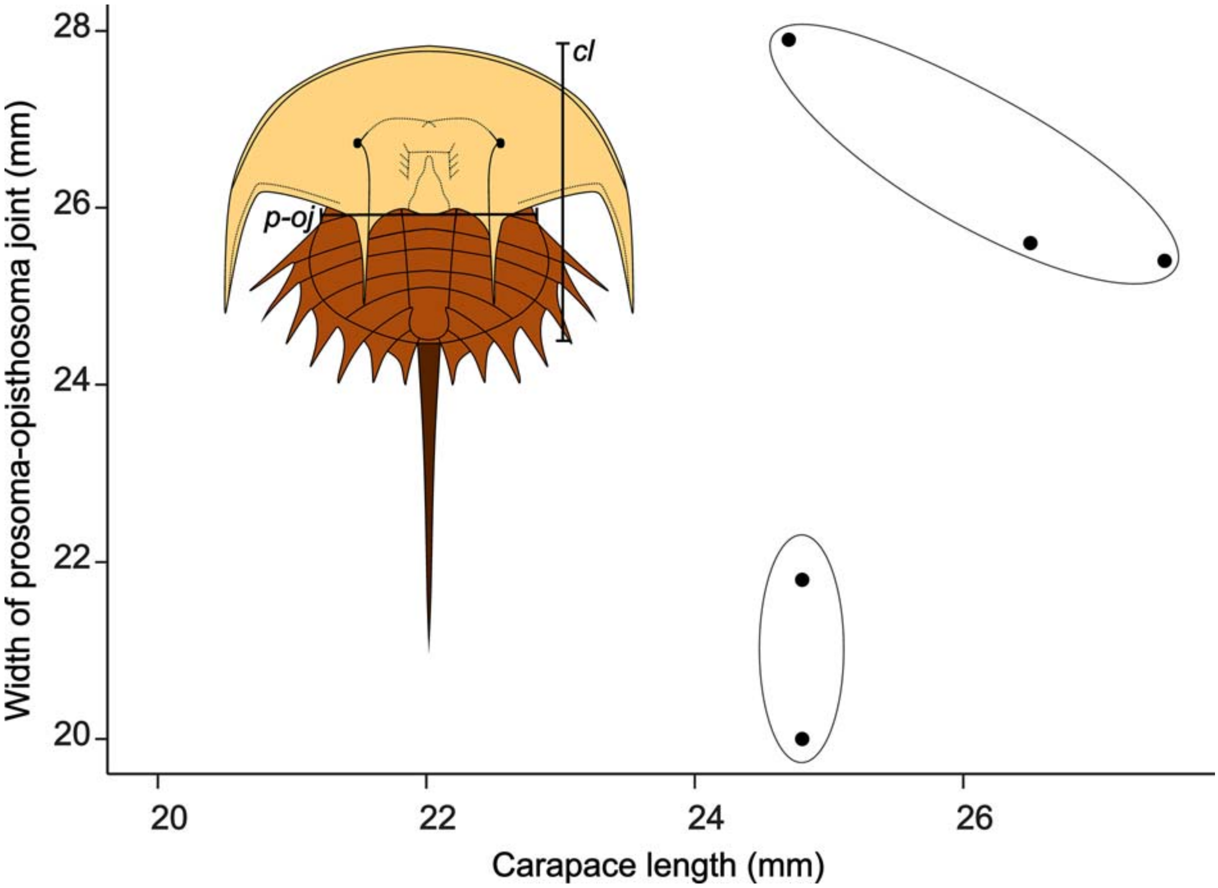

Fig. 4. Scatter plot of the five measured specimens and a reconstruction of *Euproops danae*. The two clusters are putative evidence for sexual dimorphism. Abbreviations: *p-oj* — prosoma-opisthosoma join; *cl* — carapace length (excluding telson).

Рис. 4. График промеров (диаграмма рассеивания) пяти экземпляров и реконструкция *Euproops danae*. Два кластера возможно свидетельствуют о половом диморфизме. Сокращения: *p-oj* — сочленение просомы и опистосомы; *cl* — длина карапакса (без тельсона).

giving similar safety in numbers (see discussion on predation in Fisher, 1977; Bicknell *et al.*, 2018b). The record of gregarious behaviour in body specimens here adds support to previously documented trace fossil evidence of mass spawning (see Mujal *et al.*, 2018). An alternative hypothesis for the evolution of clustering relates to the possible benefits of multiple paternity: sperm contributed by several males, as seen in typical clusters of *Limulus polyphemus*, a strategy which enhances genetic diversity [Brockmann *et al.*, 2000].

The studied slab, and associated reproductive behaviour, is a further example of evolutionary stasis exhibited by horseshoe crabs [Fisher, 1984; Kin, Błażejowski, 2014; Bicknell *et al.*, 2018a, b]. While the morphological similarity of extant horseshoe crab to ancestral xiphosurids is well-established (e.g., Fisher, 1984; Anderson, Shuster Jr., 2003; Rudkin *et al.*, 2008; Rudkin, Young, 2009; Bicknell *et al.*, 2018b, 2019a; Bicknell, Pates, 2019a), it also now seems quite likely that intertidal spawning and amplexus behaviour are also ancient. Diedrich [2011] interpreted the *Kouphichnium* Nopsca, 1923 ichnogenus found in the Middle Triassic from Bernburg, Germany as records of adult horseshoe crabs in an intertidal area during mating activity; of particular interest is a set of tracks that appears to record an amplexed pair. Related to this is the recently documented *Yunnanolimulus luopingensis* Zhang, Hu, Zhou, Lü et Bai, 2009 specimens from the Middle Triassic in Yunnan Province, China [Hu *et al.*, 2017] that record well-preserved paired claspers with similar morphology to those seen in extant *Carcinoscorpius rotundicauda*. They suggest that the more highly modified and more bulbous claspers in *Tachypleus* and *Limulus* are more recently evolved.

As sexual dimorphism has been noted in fossil horseshoe crab taxa [Bicknell *et al.*, 2019a], it is worth considering the topic in the context of the studied slab. The two loosely defined groups in bivariate space (Fig. 4) suggest a possible combination of male and female specimens; a possibility that has been suggested for *Euproops danae* from the Pennsylvanian-aged Mazon Creek fauna (Illinois, USA) [Haug, Rötzer, 2018]. However, we are cautious in assigning much meaning to these groups as only five specimens were assessed, the taphonomic alteration will have introduced error into the data (see the excellent discussion in Tashman, *et* *al*., 2019), and definite sexual dimorphic features such as modified anterior walking legs are unknown to the studied specimens [Shuster Jr., 1982; Bicknell *et al.*, 2018a, 2019a]. Further specimens from the Farrington Group, ideally showing appendage data, may therefore support the notion of two genders and further highlight sexual dimorphism within fossil horseshoe crabs. One final consideration is given to a comment in Shpinev [2017] who suggested that the co-occurrence of *Euproops* with *Bellinurus* Pictet, 1846 records the morphological, potentially sexually dimorphic, extremes of the same organism. Further studies of the Russian deposits outlined in Shpinev [2017], and indeed Belinuridae in general, are needed to determine if the two genera do represent sexual dimorphism in fossil xiphosurids.

Acknowledgements

This research was supported by funding from an Australian Postgraduate Award (to R.D.C.B.), a Charles Schuchert and Carl O. Dunbar Grants-in-Aid award (to R.D.C.B.), a James R. Welch Scholarship (to R.D.C.B.), a University of New England ostdoctoral Fellowship (to R.D.C.B.), a Betty Mayne Scientific Research Fund (to R.D.C.B.), and an Alexander Agassiz Postdoctoral Fellowship (to S.P). We thank Lucie Goodayle and the Natural History Museum, London for images of the studied specimens, and Claire Mellish for access to material. Finally we thank Serge V. Naugolnykh for his helpful review.

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Responsible editor K.G. Mikhailov

Addition 1. Dataset of measurements used in Fig. 4.
Дополнение 1. Промеры, использованные в рис. 4.

Specimen number	length of body (mm)	Width of prosomal-opisthosomal joint (mm)
NHMUK PI In 61012	24.8	20
NHMUK PI In 61013	27.5	25.4
NHMUK PI In 61015	24.8	21.8
NHMUK PI In 61016	26.5	25.6
NHMUK PI In 61017	24.7	27.9