

## AN EFFACED HORSESHOE CRAB (ARTHROPODA: CHELICERATA: XIPHOSURA) FROM THE UPPER CARBONIFEROUS OF THE CARNIC ALPS (FRIULI, NE ITALY)

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*Abstract.* A carapace of a new horseshoe crab (Arthropoda: Chelicerata: Xiphosura) is described from the Upper Carboniferous (Kasimovian) Meledis Formation of the Carnic Alps, Friuli, Italy. It is named as *Stilpnocephalus pontebbanus* n. gen. & n. sp., and belongs to the family Belinuridae Zittel in Zittel & Eastman, 1913. The large (>8 cm width) carapace is strongly effaced and appears to lack eyes. The new specimen is the first fossil horseshoe crab to be described from Italy and the largest known belinurid.

### INTRODUCTION

Horseshoe crabs (Chelicerata: Xiphosura) have a long and distinguished fossil record, being considered by many palaeontologists as archetypal living fossils or stabilomorphs (Fisher 1984; Kin & Błażejowski 2014). They were at their most diverse in the Upper Carboniferous when numerous non-marine forms, represented at that time by the suborder Belinurina Zittel in Zittel & Eastman, 1913, were present (Lamsdell 2013, 2016). The fossil described here consists of a relatively large carapace with greatly effaced features. In the latter respect it most closely resembles other belinurines from the Upper Carboniferous such as *Alanops* Racheboeuf et al., 2002, *Liomesaspis* Raymond, 1944, and *Pringlia* Raymond, 1944, but lacks characters which would place it in any of these genera. Hence, a new genus and species, *Stilpnocephalus pontebbanus* n. gen. & n. sp., is established.

The Meledis Formation, in which the fossil was found, consists of arenitic and pelitic facies and rarer dolomitic algal limestones, which cor-

respond to fluvio-deltaic and shallow-water marine environments (Venturini 1990). As well as typical marine fossils, e.g. fusulinids (Krainer & Davydov 1998), brachiopods, and trilobites (Venturini 2006), non-marine and terrestrial fossils occur in the formation, including plant material (Ronchi et al. 2012), eurypterids (Lamsdell et al. 2013), and thelyphonid arachnids (whip-scorpions: Selden et al. 2016). Moreover, horseshoe-crab trackways have been described from two sites in the Meledis Formation (Conti et al. 1991). Indeed, due to the exceptional abundance, diversity, and preservation of trace fossils from localities in the area, a Pramollo Ichnolagerstätte has been established (Baucon & Neto de Carvalho 2008). The extremely smooth carapace of the xiphosuran, possibly lacking eyes, suggests that this animal was probably a burrower. The new fossil is the largest known belinurid, and the first body fossil of a horseshoe crab to be described from Italy.

### GEOLOGICAL SETTING

The single specimen was found in a loose block in the gravel bank of the Rio degli Uccelli (Vogelbach), north-east of the village of Pontebba

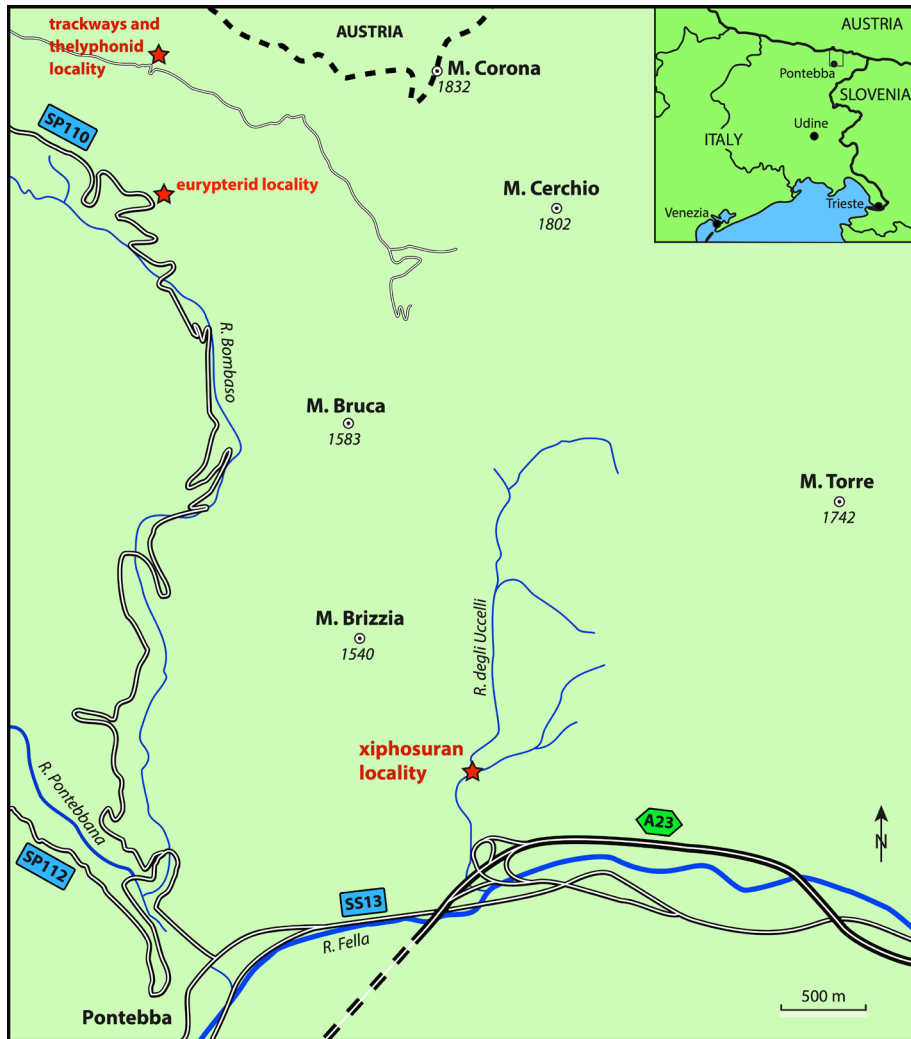


Fig. 1 - Position of the fossil xiphosuran locality (star) on the bank of the Rio degli Uccelli (Vogelbach), north-east of the village of Pontebba. The location of the find of the eurypterid *Adeloptalmus piussii* Lamsdell et al., 2013 in the Meledis Formation near the SP110 road from Pontebba to Passo Pramollo is also indicated, and the landslide locality Frana Vecchia where the trackways and the thelyphonid *Parageralinura marsiglioi* Selden et al., 2016 were found. Inset: location map of the area near Pontebba in the north of Friuli. Spot heights are in metres.

(Fig. 1). It is preserved in a small slab of thin sandstone that, on the basis of lithological features (e.g. grain size, colour, schistosity) and taking into account the geological setting of the area, is presumed to belong to the Meledis Formation (upper Moskovian–lower Kasimovian) (Venturini pers. com.), the oldest among the five formations of the Pramollo Group (upper Moskovian–Gzhelian, Upper Carboniferous) (Venturini 1990, 2002).

The Pramollo Group is characterized by transgressive–regressive cycles mostly related to glacio-eustatic control and subordinate tectonic control (Vai & Venturini 1997). The result is a 1000 m thick sequence of conglomerates, pelites, and arenites (sublitharenites and subarkoses: Fontana & Venturini 1983), referable to fluvio-deltaic and marine shallow-water environments, which intercalates with scattered algal carbonates.

In the lower part of the Meledis Formation, there are some carbonate levels and abundant bioturbated siltstones with frequent ichnofossils and

marine fossils. They are arranged in a transgressive sequence mostly driven by transtensive tectonics responsible for scattered slumps. However, the deposits of the upper part of the Meledis Formation reflect local transpressive tectonics which was responsible for a fluvio-deltaic environment, testified by channelized quartz-rich fluvial conglomerates and shoreface arenites (Venturini 1991) that abruptly cut the lower shallow marine to offshore sequence. The lithology of the matrix of the specimen suggests that it could have come from the upper sequence of the Meledis Formation.

#### MATERIAL AND METHODS

The body fossil (Figs 2–3) consists of a relatively complete carapace preserved in dorsal view. It is held in the Museo Archeologico e Naturalistico, via G. Pascoli 25, 33017 Tarcento, Udine, Italy, under the inventory number MPT18062301. The specimen is a highly three-dimensional fossil, with a very smooth and lustrous surface. The shiny surface resembles the slickensides of the pseudofossil *Gnilelmites*, which is commonly found around fossils in Coal Measures

strata. The only ornament on the carapace is a pair of widely spaced grooves running from the posterior border diverging forwards to near the anterior border. On the left side, the groove contains some sedimentary matrix. Elsewhere on the carapace, subcircular marks possibly represent epizoan attachment scars.

Trace fossils from the Meledis Formation held in the Museo Friulano di Storia Naturale, Udine, are illustrated here in Fig. 4. They originate from the locality informally known as Frana Vecchia (Old Landslide), on the southern side of Mt Auernig, on the mountain road leading to Casera For and Casera Cerchio from Passo Pramollo, approximately one kilometre from Casera Auernig, north of the village of Pontebba (Fig. 1), which is where the thelyphonid *Parageralinura marsiglioi* Selden et al., 2016 was found.

The fossils were photographed using a Canon EOS 5D MkII camera, with a 50 mm macro lens and polarizing filter attached, mounted on a copy stand, under low-angle illumination. To enhance depth of field, several photographs were taken of the specimen at different focus distances and then stacked using the Focus Merge function in Affinity Photo 1.6.7 (www.affinity.serif.com). The drawing and measurements were made from the photograph using Graphic 3.1 (www.graphic.com). All manipulation was done on an Apple MacBook Pro computer.

## SYSTEMATIC PALAEOLOGY

### Order Xiphosurida Latreille, 1802

**Remarks.** The new fossil is interpreted as a horseshoe crab on the basis of the resemblance of the specimen to a xiphosuran carapace, with a fairly straight posterior margin, gently curved anterior and lateral margins with a slight rim and, though greatly effaced, distinct, slightly diverging grooves.

Interpretation of the pair of widely spaced grooves running from the posterior border diverging forwards to near the anterior border is problematic. On xiphosuran carapaces, there is normally a pair of grooves delimiting the cardiac lobe, lateral to which lie a pair of ophthalmic ridges bearing the eyes (see fig. 3 in Størmer 1955 of modern *Limulus polyphemus* Linnaeus, 1758). However, these cardiac grooves are never widely divergent; they usually converge and meet in front of the cardiac lobe. The grooves in the new specimen are very wide apart, so they could correspond to the ophthalmic ridges. Interestingly, some of the specimens belonging to the Belinuridae, the family to which our new fossil is referred, show grooves rather than ridges in this position. For example, the paratype of *Liomesaspis laevis* Raymond, 1944 (MCZ 109534) figured by Anderson (1997: fig. 1b,c) appears to show grooves rather than ridges running from the posterior border, past the eye, to the anterior border, and not converging but subparallel. Specimens of *Pringlia fritschi* Remy & Remy, 1951 (see

their pl.1) show a groove alongside a ridge. In some cases, e.g. *Paleolimulus longispinus* Schram, 1979 (see his fig. 1), the ophthalmic ridge and groove are more akin to a small cuesta or terrace. It may be that, in some cases, taphonomy preserves the groove better than the adjacent ridge or, indeed, there may be a true ophthalmic furrow rather than a ridge in life. What would resolve the dilemma in our specimen would be to find eyes along the ophthalmic line, but none can be seen. So, we suggest that the diverging lines across the carapace do represent ophthalmic furrows rather than cardiac ones, and that eyes may be absent.

The absence of eyes is unusual in xiphosurids, although several middle Palaeozoic Xiphosura and their allies are eyeless, e.g. *Offacolus* Orr et al., 2000 and *Dibasterium* Briggs et al., 2012 from the Silurian Herefordshire Lagerstätte, *Vennustulus* Moore et al., 2005 from the Silurian Waukesha Lagerstätte, and *Weinbergina* Richter & Richter, 1929, from the Devonian Hunsrückschiefer (see Dunlop & Lamsdell 2017). Nevertheless, the ancestors and close relatives of the new genus possessed eyes, so we presume that any blindness would be secondary. Commonly, the loss of eyes in animals is related to adaptation to a dark environment, e.g. caves, deep water, or in substrate.

### Suborder Belinurina Zittel in Zittel & Eastman, 1913

**Included family:** Belinuridae Zittel in Zittel & Eastman, 1913.

**Remarks.** The fossil is placed in this suborder on the basis of its similarity to other genera of the Belinuridae, and not to members of the coeval limuline families Rolfeidae Selden & Siveter, 1987 or Paleolimulidae Raymond, 1944. The monotypic *Rolfeia* Waterston, 1985 bears strong ophthalmic ridges, and members of the Paleolimulidae bear not only strong ophthalmic ridges but also additional ornament on the carapace; in contrast, the new fossil is distinctly effaced.

### Family Belinuridae Zittel in Zittel & Eastman, 1913

**Included genera:** *Alanops* Racheboeuf et al., 2002; *Anacontium* Raymond, 1944; *Bellinurus* Pictet, 1846; *Euproops* Meek, 1867; *Liomesaspis* Raymond, 1944; *Pringlia* Raymond, 1944; *Prolimulus* Frič, 1899; *Stilpnocephalus* n. gen.

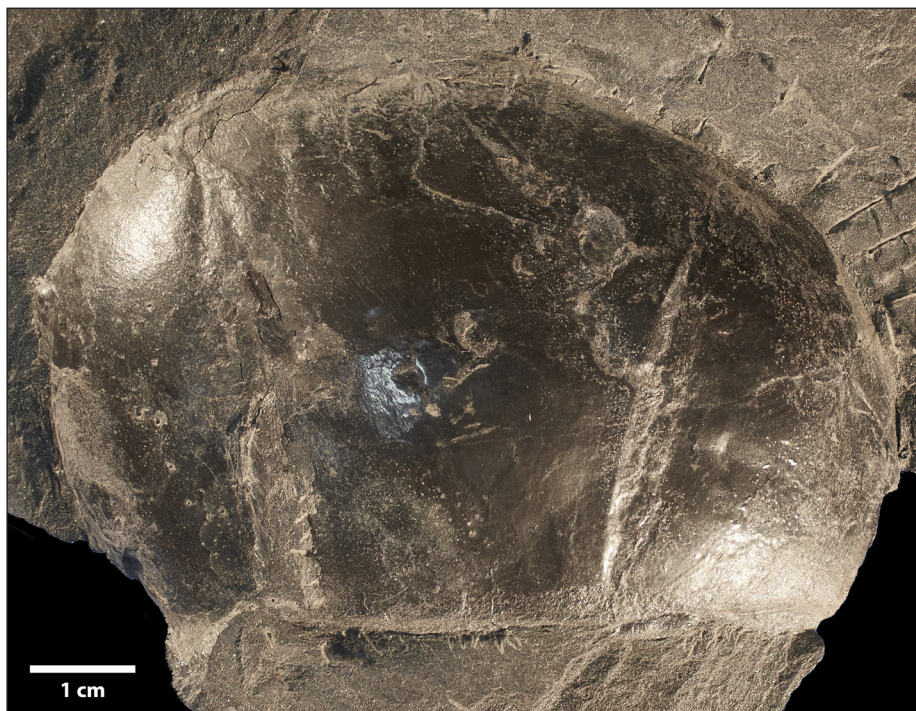


Fig. 2 - *Stilpnocephalus pontebbanus* n. gen. & n. sp. from the Upper Carboniferous (Kasimovian) Meledis Formation, Friuli, specimen MPT18062301, photograph of holotype and only known specimen, dorsal view.

### Genus *Stilpnocephalus* n. gen.

**Etymology:** The genus name comes from the Greek *στιλπνός*, glossy, and *κεφάλι*, head, in reference to the smooth and glossy nature of the carapace in the fossil.

**Diagnosis:** Belinurid with large, highly vaulted, strongly effaced carapace, lacking ophthalmic ridges and genal and ophthalmic spines. Eyes, if present, lacking relief.

**Remarks.** The new genus most closely resembles *Alanops* in being highly effaced. The other genera in the family Belinuridae all bear some sort of cardiac lobe, ridges, or genal spines.

### *Stilpnocephalus pontebbanus* n. sp.

Figs 2, 3

**Material:** Holotype (part only) and only known specimen, MPT18062301 in the Museo Archeologico e Naturalistico, via G. Pascoli 25, 33017 Tarcento, Udine, Italy.

**Horizon and locality:** Meledis Formation, Auernig Group of Upper Carboniferous Kasimovian age (~304–307 Ma); from Rio degli Uccelli (Vogelbach), north-east of the village of Pontebba, Friuli, Italy.

**Etymology:** The trivial name relates to the village of Pontebba, near the type locality.

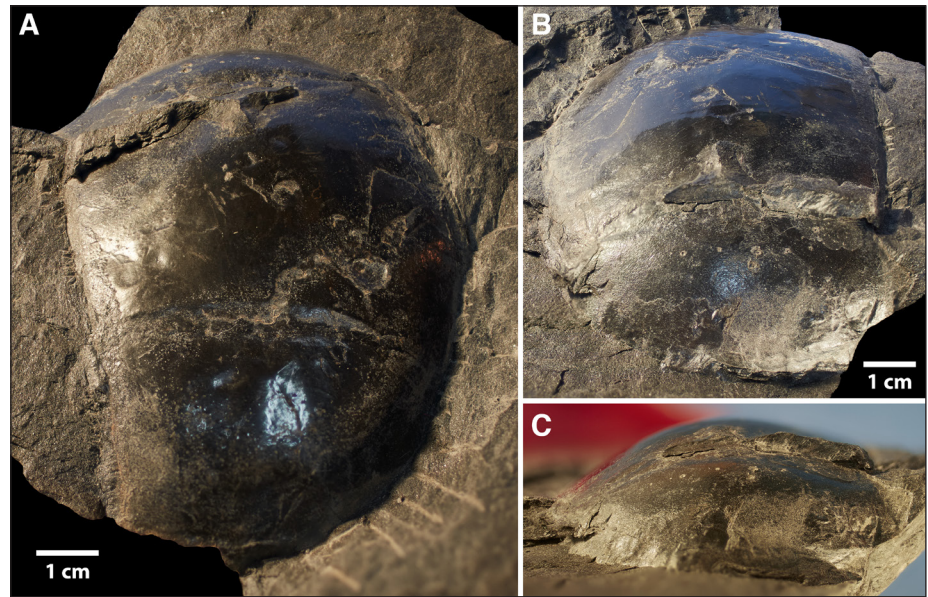
**Description.** Carapace highly domed, 1.5× wider than long, width 8.32 cm, length 5.50 cm, height 3.00 cm; effaced, with widely spaced grooves, 3.25 cm apart at posterior margin, diverging gently from posterior margin to ~5.00 cm apart near anterior margin. Eyes lacking relief or absent. Anterior

and lateral edges of carapace a continuous, gentle curve, increasing in curvature towards posterior; posterior margin narrower than width of carapace. Anterior border very slightly procurved medially. Posterior margin straight between posterior ends of grooves, lateral parts slightly sinuous. Thin rim along anterior and lateral carapace margins. No genal or ophthalmic spines.

**Discussion.** Lamsdell (2016) reanalysed the belinurine genera *Alanops*, *Anacantium*, *Belinurus*, *Euproops*, *Liomesaspis*, *Pringlia*, and *Prolimulus*, in a wider-ranging study of the Xiphosura, and came to the conclusion that the genera *Belinurus* and *Euproops* were both paraphyletic, with *Belinurus* grading into *Euproops* which, in turn, grades into a clade comprising *Liomesaspis*, *Pringlia*, and *Alanops*. Anderson (1997) had previously suggested that the suborder Belinurina was over-split at the generic level. However, further work will be necessary to sort out this unsatisfactory taxonomy. To add to this state of affairs, we can include our new genus *Stilpnocephalus*.

*Stilpnocephalus* differs from *Alanops* in that, whilst both genera show effacement, *Alanops* presents a narrow cardiac lobe and lacks ophthalmic structures (see pl. 1 in Racheboeuf et al. 2002), while the cardiac lobe is effaced in *Stilpnocephalus*, which genus presents ophthalmic furrows. *Pringlia* also shows an effaced carapace, but in this genus

Fig. 3 - *Stilpnocephalus pontebbanus* n. gen. & n. sp. from the Upper Carboniferous (Kasimovian) Meledis Formation, Friuli, specimen MPT18062301. A) Photograph of specimen in oblique right view. B) Photograph of specimen in oblique left view. C) Photograph of specimen in left lateral view, showing its three-dimensional nature.



there are genal spines (see text-fig. 1 in Racheboeuf et al. 2002). *Liomesaspis* closely resembles *Pringlia* in the form of its carapace; indeed, the two genera were synonymized by Anderson (1997), but this was later rejected by Racheboeuf et al. (2002). Moreover, *Stilpnocephalus* is much larger than any other belinurid.

Table 1 lists all of the currently accepted members of the family Belinuridae, together with their authors, localities, and the recorded widths of the carapace of the largest specimens. It can be seen that, first, *Stilpnocephalus pontebbanus* is the only belinurid known from Italy. Indeed, according to the list in Dunlop et al. (2018), it is the first body fossil of a horseshoe crab to be described from the country. Moreover, *Stilpnocephalus*, with a carapace width of 8.32 cm, is clearly the largest belinurid known. Fig. 5 plots the measurements from Table 1 in a simple graph to illustrate how much larger *Stilpnocephalus* is than the other known belinurids. The next largest is a specimen of *Euproops rotundatus* Prestwich, 1840, described by Lomax et al. (2014) from Yorkshire, England, with a carapace width (including genal spines) of 5.69 cm; this is closely followed by a *Euproops* sp. described by Schram (1979) from Bear Gulch, USA, with a carapace width of 5.66 cm. Members of the suborder Limulina Richter & Richter, 1929 attain much larger proportions; in the Palaeozoic, *Xaniopyramis linseyi* Siveter & Selden, 1987, from the Namurian of Durham, England, has a carapace width of about 15.6 cm (including genal spines). Modern *Limulus*

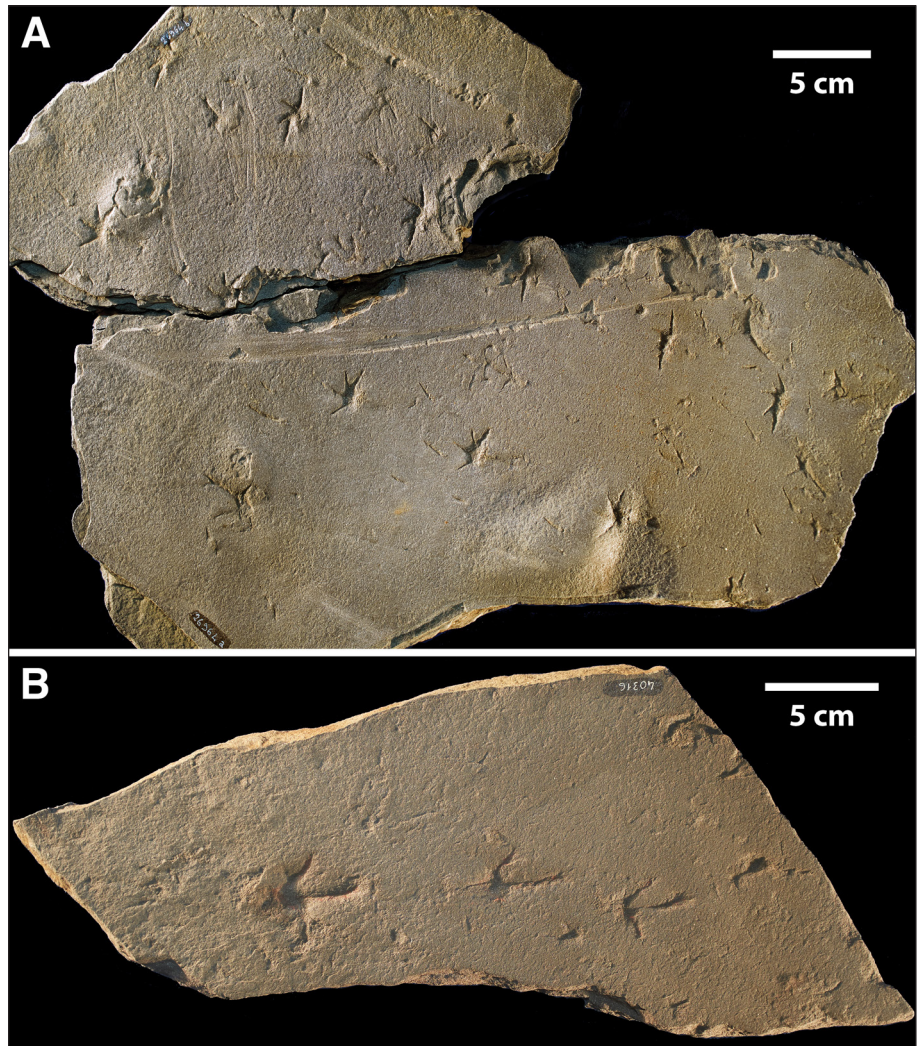
females in Delaware Bay, USA, reach up to about 35.0 cm in carapace width (Shuster 1957), but the large sizes of horseshoe crabs seen today only begin to be achieved in the Mesozoic. A review by Moreau et al. (2014) showed that, whilst the general sizes of body fossils of xiphosurans increased from the Palaeozoic to the present day, extrapolation from the widths of horseshoe crab trackways show that there was at least one episode, in the Late Jurassic, of gigantism among fossil limulines, with carapace widths reaching 39.3 cm.

Conti et al. (1991) described limuloid trackways from two localities in the upper part of the Meledis Formation (Fig. 4). This part of the formation is considered to represent a fluvio-deltaic environment (Venturini 1991), which is the type of paleoenvironment in the Upper Carboniferous that commonly preserves horseshoe crab trace fossils (e.g. Hardy 1970; Higgs 1970; Chisholm 1983; Buatois et al. 1998; Buhler & Grey 2016). The widths of the trackways described by Conti et al. (1991) range from 8–9 cm on one slab (Fig. 5A), and 11–13 cm on another. According to Malz (1964), the size of the trackway maker can be deduced from the external width of the trackway. For modern *Limulus polyphemus*, the width of the carapace is 1.5× wider than the external width of its trackway (Malz 1964); these ratios are similar for other modern limulids (Sekiguchi 1988; Moreau et al. 2014). On this basis, the producers of the Meledis Formation trackways would have had carapaces in the order of 12–19.5 cm width. Since the carapace width of *Stilpnocephalus*

Taxon	Authorship	Age	Locality (Reference)	Max. carapace width (cm)
<i>Alanops magnifica</i>	Racheboeuf <i>et al.</i> , 2002	U. Carb.	Montceau les Mines, France	0.90
<i>Anacontium brevis</i>	Raymond, 1944	Permian	Wellington Formation, Oklahoma, USA	1.00
<i>Anacontium carpenteri</i>	Raymond, 1944	Permian	Wellington Formation, Oklahoma, USA	1.20
<i>Bellinurus arcuatus</i>	Baily, 1863	U. Carb.	County Laois, Ireland	1.70
<i>Bellinurus baldwini</i>	Woodward, 1907	U. Carb.	Sparth Bottoms, UK	1.50
<i>Bellinurus bellulus</i>	Pictet, 1846	U. Carb.	South Wales, UK (Dix & Pringle 1930)	0.78
<i>Bellinurus carwayensis</i>	Dix & Pringle, 1929	U. Carb.	South Wales, UK	1.55
<i>Bellinurus cf. truemani</i>	Dix & Pringle, 1930	U. Carb.	South Wales, UK (Dix & Pringle 1930)	0.75
<i>Bellinurus concinnus</i>	Dix & Pringle, 1929	U. Carb.	South Wales, UK	1.80
<i>Bellinurus grandaevus</i>	Jones & Woodward, 1899	U. Carb.	Nova Scotia, Canada	0.70
<i>Bellinurus iswariensis</i>	(Chernyshev, 1928)	U. Carb.	Donetz Basin, Russia (Shpinev 2018)	1.40
<i>Bellinurus kiltorkensis</i>	Baily, 1869	U. Carb.	Kiltorcan, Ireland	1.70
<i>Bellinurus koenigianus</i>	Woodward, 1872	U. Carb.	Dudley, UK	2.54
<i>Bellinurus lacoei</i>	Packard, 1885	U. Carb.	Mazon Creek, USA	2.50
<i>Bellinurus longicaudatus</i>	Woodward, 1907	U. Carb.	Sparth Bottoms, UK	2.30
<i>Bellinurus lunatus</i>	(Martin, 1809)	U. Carb.	Sparth Bottoms, UK (Baldwin 1906)	2.10
<i>Bellinurus lunatus</i>	(Martin, 1809)	U. Carb.	Silesia, Poland (Filipiak & Krawczyński 1996)	4.80
<i>Bellinurus metschetensis</i>	(Chernyshev, 1928)	U. Carb.	Donetz Basin, Russia (Shpinev 2018)	-
<i>Bellinurus morgani</i>	Dix & Pringle, 1930	U. Carb.	South Wales, UK	1.10
<i>Bellinurus pustulosus</i>	Dix & Pringle, 1929	U. Carb.	South Wales, UK	3.00
<i>Bellinurus reginae</i>	Baily, 1863	U. Carb.	County Laois, Ireland	1.30
<i>Bellinurus stepanovi</i>	(Chernyshev, 1928)	U. Carb.	Donetz Basin, Russia (Shpinev 2018)	0.88
<i>Bellinurus trechmanni</i>	Woodward, 1918	U. Carb.	Durham, UK	0.90
<i>Bellinurus trilobitoides</i>	(Buckland, 1837)	U. Carb.	Coalbrookdale, UK	2.40
<i>Bellinurus truemani</i>	Dix & Pringle, 1929	U. Carb.	South Wales, UK	0.60
<i>Euproops anthrax</i>	(Prestwich, 1840)	U. Carb.	Sparth Bottoms, UK	2.50
<i>Euproops bifidus</i>	Siegfried, 1972	U. Carb.	Westphalia, Germany	4.40
<i>Euproops cambrensis</i>	Dix & Pringle, 1929	U. Carb.	South Wales, UK	4.10
<i>Euproops danae</i>	(Meek & Worthen, 1865)	U. Carb.	Pennsylvania, USA ( <i>Euproops darrahi</i> Raymond, 1944)	1.30
<i>Euproops danae</i>	(Meek & Worthen, 1865)	U. Carb.	Mazon Creek ( <i>Euproops laevicula</i> Raymond, 1944)	1.80
<i>Euproops danae</i>	(Meek & Worthen, 1865)	U. Carb.	South Wales, UK ( <i>Euproops graigolae</i> Dix & Pringle, 1929)	2.00
<i>Euproops danae</i>	(Meek & Worthen, 1865)	U. Carb.	Donetz Basin, Russia (Chernyshev, 1928, from Shpinev 2018)	2.10
<i>Euproops danae</i>	(Meek & Worthen, 1865)	U. Carb.	Pennsylvania, USA ( <i>Euproops longispina</i> Packard, 1885)	2.40
<i>Euproops danae</i>	(Meek & Worthen, 1865)	U. Carb.	South Wales, UK ( <i>Euproops gventi</i> Dix & Pringle, 1929)	2.75
<i>Euproops danae</i>	(Meek & Worthen, 1865)	U. Carb.	Mazon Creek, USA ( <i>Euproops amiae</i> Woodward, 1918)	2.90
<i>Euproops danae</i>	(Meek & Worthen, 1865)	U. Carb.	Pennsylvania, USA ( <i>Euproops packardi</i> Willard & Jones, 1935)	3.00
<i>Euproops danae</i>	(Meek & Worthen, 1865)	U. Carb.	Donetz Basin, Russia (Shpinev 2018)	3.28
<i>Euproops danae</i>	(Meek & Worthen, 1865)	U. Carb.	South Wales, UK ( <i>Euproops ishwyni</i> Dix & Pringle, 1929)	3.40
<i>Euproops danae</i>	(Meek & Worthen, 1865)	U. Carb.	Mazon Creek, USA ( <i>Euproops thompsoni</i> Raymond, 1944)	3.80
<i>Euproops danae</i>	(Meek & Worthen, 1865)	U. Carb.	South Wales, UK ( <i>Euproops meeki</i> Dix & Pringle, 1929)	3.80
<i>Euproops danae</i>	(Meek & Worthen, 1865)	U. Carb.	Mazon Creek ( <i>Euproops laticephalus</i> Raymond, 1944)	4.00
<i>Euproops danae</i>	(Meek & Worthen, 1865)	U. Carb.	South Wales, UK ( <i>Euproops cambrensis</i> Dix & Pringle, 1929)	4.10
<i>Euproops danae</i>	(Meek & Worthen, 1865)	U. Carb.	Mazon Creek, USA	5.30
<i>Euproops danae</i>	(Meek & Worthen, 1865)	U. Carb.	Somerset, UK ( <i>Euproops kilmersdonensis</i> Ambrose & Romano, 1972)	5.30
<i>Euproops longispina</i>	Packard, 1885	U. Carb.	Mazon Creek, USA	3.70
<i>Euproops mariae</i>	Crônier & Courville, 2005	U. Carb.	Massif Central, France	2.50
<i>Euproops nitida</i>	Dix & Pringle, 1929	U. Carb.	South Wales, UK	2.85
<i>Euproops orientalis</i>	Kobayashi, 1933	Permian	Korea	1.64
<i>Euproops rotundatus</i>	Prestwich, 1840	U. Carb.	Silesia, Poland (Filipiak & Krawczyński 1996)	3.80
<i>Euproops rotundatus</i>	Prestwich, 1840	U. Carb.	Yorkshire, UK (Lomax <i>et al.</i> 2014)	5.69
<i>Euproops sp.</i>		L. Carb.	Bear Gulch, USA (Schram 1979)	3.63
<i>Euproops sp.</i>		U. Carb.	Osnabrück, Germany (Brauckmann, 1982)	-
<i>Liomesaspis laevis</i>	Raymond, 1944	U. Carb.	Mazon Creek, USA	1.50
<i>Liomesaspis laevis</i>	Raymond, 1944	U. Carb.	Mazon Creek ( <i>Pringlia bispinosa</i> Raymond, 1944)	1.55
<i>Liomesaspis laevis</i>	Raymond, 1944	U. Carb.	Germany ( <i>Pringlia fritschi</i> Remy & Remy, 1959)	1.65
<i>Liomesaspis laevis</i>	Raymond, 1944	U. Carb.	Germany ( <i>Palatinaspis beimbaueri</i> Malz & Poschmann, 1993)	1.70
<i>Liomesaspis laevis</i>	Raymond, 1944	U. Carb.	( <i>Pringlia demaisterei</i> Vandenbergh, 1961)	1.80
<i>Liomesaspis leonardensis</i>	(Tasch, 1961)	Permian	Kansas, USA	0.75
<i>Pringlia birtwelli</i>	(Woodward, 1872)	U. Carb.	Padiham, Lancashire, UK	1.50
<i>Pringlia birtwelli</i>	(Woodward, 1872)	U. Carb.	Coseley, Staffordshire, UK	1.50
<i>Prolimulus woodwardi</i>	Frič, 1899	U. Carb.	Nýřany, Czech Republic	2.20
<i>Stilpnocephalus pontebbanus</i>	this paper	U. Carb.	Carnic Alps, Italy	8.32

Tab. 1 - All currently recognized belinurid taxa (as listed in Dunlop *et al.* 2018) with their taxon authorities, ages, localities, and measured maximum width of the carapace (including genal spines where present). Measurements are those given in the reference or taken from published illustrations; - denotes carapace unknown. Note that the list of measurements is not completely comprehensive, but gives an idea of the range of published sizes.

Fig. 4 - *Kouphichnium* sp. xiphosurid trails from the Upper Carboniferous (Kasimovian) Meledis Formation, Friuli. A) Specimen MFSN26964a,b, same specimen as shown in Conti et al. (1991: fig. 5). B) Specimen MFSN40316.



is 8.32 cm, the trackways are somewhat larger than those which might have been produced by this animal, but possibly within the range of sizes that larger specimens of *Stilpnocephalus* might have produced.

Whilst only the carapace of *Stilpnocephalus* is known, we can speculate upon its likely mode of life. Effacement in trilobites is commonly associated with a burrowing habit, (e.g. Westrop 1983) because efficient passage through sediment would be hindered by bumps, ridges, and spines. Examples of effaced trilobites include asaphids and illaenine corynexochids and, like *Stilpnocephalus*, some are highly effaced and blind, e.g. *Thomastus* Öpik, 1953 from the Silurian of Australia (Sandford & Holloway 1998). However, the habitat of these trilobites was considered to be deep marine; similarly, Fortey & Owens (1987) described blind trilobites inhabiting dark marine waters in the Arenig of South Wales. However, the supposed palaeoenvironment of

the upper part of the Meledis Formation, where the fossil likely originated and where the limuloid trackways were also found, is considered to have been fluvio-deltaic. Thus, *Stilpnocephalus* may have

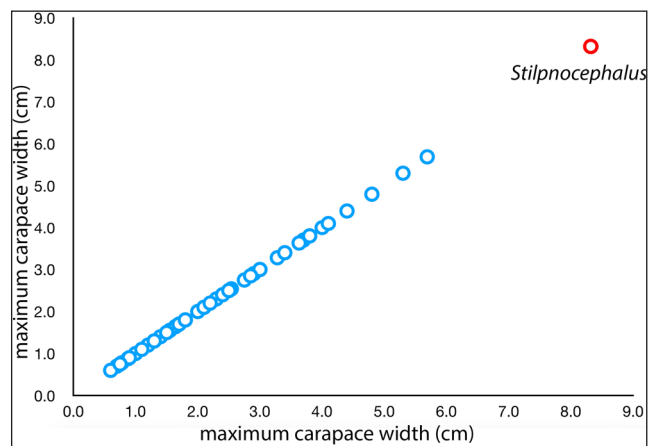


Fig. 5 - Graph to show the size of *Stilpnocephalus* (carapace width in cm) relative to other known belinurids. Data from Table 1.

been a burrower in a non-marine, fluvio-deltaic environment.

Belinurines range from the Early Carboniferous to the Early Permian, and are most abundant in the coal measure sequences of North America and Europe (Lamsdell 2016). So, the age of *Stilpnocephalus* is in the acme of abundance and diversity of the suborder. Geographically, the nearest relatives are found some considerable distance away, in the coal measures of France (Montceau les Mines), Germany, Czech Republic (Nýřany) and Poland (Silesia). Nevertheless, the supposed palaeoenvironments in which all of these animals lived are similar. The discovery of *Stilpnocephalus* in the Carnic Alps extends the geographic range of the belinurines in Europe southwards. The most important features of the new genus, however, are its large size and its effaced, possibly blind, morphology, by which *Stilpnocephalus* stands out among its contemporary relatives.

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