

Pterygotid eurypterid palaeoecology: praedichnia and palaeocommunities

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Pterygotid eurypterids (Chelicerata) were all regarded as active apex nektonic predators, particularly in the Silurian. The chelicerae and lateral eyes of *Acutiramus cummingsi* were then interpreted as being inconsistent with a predatory lifestyle. *Jaekelopterus*, *Pterygotus* and *Erettopterus* were interpreted as having more acute vision than *Acutiramus*, but their chelicerae implied they had different ecologies, with not all taxa as top predators. The chelicerae of *Acutiramus* are here interpreted as being much more robust than was previously assumed, and their eyes as adapted to hunting at depth, at night or in murky water, so neither precludes a predatory lifestyle. Previous models of the mode of life of pterygotid eurypterids are assessed, based on a review of their trace fossils, functional morphology and a new analysis of their biotic associations. All pterygotid taxa are here interpreted as slow swimming vagrant and ambush predators, using their chelicerae to rapidly capture prey, and their more robust coxal gnathobases and metastoma to process it. *Slimonia*, and *Acutiramus* with more gracile cutting chelicerae, tend to associate with, and likely specialised on, lightly-armoured phyllocarid crustaceans. *Erettopterus* and *Pterygotus*, with more robust chelicerae, tend to associate with more heavily armoured thelodonts and osteostracans, respectively. *Jaekelopterus* tend to associate with osteichthyans, placoderms and pteraspids. Praedichnia (predation traces) on the pteraspids *Lechriaspis* and *Larnovaspis*, eurypterids *Eurypterus* and *Acutiramus* and trilobite *Spinisscutellum*, and their coprolites, provide further evidence for such predatory interactions. The cheliceral morphology, visual acuity, associations and fossil record all support the hypothesis that *Acutiramus* is actually more basal to *Jaekelopterus* and *Pterygotus*, the largest ever arthropods, with *Jaekelopterus* now estimated at 2.59 m long. • Key words: Arthropoda, Chelicerata, Eurypterida, Chelicerata, Palaeozoic, predation, gigantism.

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Eurypterids are a group of *ca.* 250 species of Palaeozoic aquatic chelicerate arthropods known from the Middle Ordovician (Darriwilian, 467 Ma; Lamsdell *et al.* 2015) to the late Permian (Changhsingian, 253 Ma; Poschmann & Rozefelds 2021). The Superfamily Pterygotioidea is the most diverse (*ca.* 50 species in 10 genera) and cosmopolitan clade, comprising hughmilleriids (Tetlie *et al.* 2007), slimonids and the giant pterygotids. It is unclear whether this diversity is due to their presumed increased dispersal ability (Tetlie 2007), shift in prey capture to using their chelicerae (Lamsdell 2022) or taxonomic oversplitting (Ciuca & Tetlie 2007, Braddy 2022).

Eurypterids have chelate (pincer-like) anterior prosomal appendages (chelicerae), composed of a fixed and free (movable) ramus. Most Eurypterina (generally paddled forms, with a podomere 7a on appendage VI; Tetlie & Cuggy 2007) and Stylonurina (forms with walking-legs) possess small chelicerae but pterygotoids have large, anteriorly orientated chelicerae. Pterygotid chelicerae are particularly large and equipped with den-

titles of various sizes. *Jaekelopterus*, *Pterygotus* and *Erettopterus* have a curved terminal denticle on their free ramus, *Erettopterus* with less differentiated denticles (Fig. 1). *Acutiramus* has an acute terminal denticle on both rami and a large obliquely orientated denticle with a serrate posterior margin on its fixed ramus. Many pterygotid species are known only from their chelicerae because they were more robust than their thinner body cuticle, so preserved more frequently. Pterygotid taxa also vary in their body (Fig. 2), metastoma, genitalia and telson shape (Tollerton 1989; most taxa paddle-shaped but *Erettopterus* bilobed).

Pterygotid body fossils reliably range for *ca.* 37 million years from the early Silurian (late Llandovery, 428 Ma; Tetlie 2007) to the Middle Devonian (391 Ma; Lamsdell 2017, Plotnick 2022), only 17% of the entire duration of the Order Eurypterida, with their acme during the late Silurian. Putative Ordovician (Tremadoc) pterygotids from Morocco are based on an anomalocaridid (Braddy 2022). A late Devonian putative chelicera (Olive *et al.* 2019,

fig. 10) is tiny (preserved length 7 mm), its denticles too short and broad to be a pterygotid; it is possibly an arthropod (Plotnick 2022), vertebrate tooth plate or large conodont (Braddy 2022). *Pterygotus bolivianus*, the next youngest putative pterygotid (preserved length 24 mm) is similar and probably the chondrichthyan *Pucapambella* (Plotnick 2022). A putative new genus (McCoy *et al.* 2015), based on an assumed angular distal denticle on the fixed ramus (Wang & Gai 2014) is actually not preserved, so is a *Pterygotus* (Braddy 2022; *P. wanggaili* Ma *et al.*, 2022).

Pterygotid species are probably taxonomically oversplit due to taphonomic or ontogenetic variation. Potential synonyms particularly may co-occur at the same locality (Braddy 2022). The following locality numbers refer to Plotnick (1999): *Erettopterus brodiei* and *E. spatulatus* (locality 60, Downton Castle Sandstone, Herefordshire); *E. spatulatus* and *E. gigas* (locality 61, Temeside Shale, Herefordshire); *E. carinatus* (dorsal) and *E. serricaudatus* (ventral) (locality 65, Hogkint Group of Visby, Gotland); *Pterygotus minor* (juvenile) and *P. anglicus* (locality 54, Dundee Formation, Strathmore, Scotland; Braddy 2000); *P. juvenis* (juvenile) and *Acutiramus macrophthalmus* (locality 30, Fiddlers Green Member of the Bertie Waterlime, New York; Poschmann & Tetlie 2006). Some *non* co-occurring species are also considered synonyms (e.g. *P. atlanticus* is a synonym of *P. anglicus*; Miller 2007). Ontogenetic trends in pterygotids may indicate further potential synonyms. Juvenile *E. bilobus* have curved terminal denticles, whereas in adults they are more angular (Ciarca & Tetlie 2007). Positive allometry occurs in the lateral eyes, telson and terminal denticle of the free ramus of *J. rhenaniae* (Braddy *et al.* 2008b). *Jaekelopterus howelli* also shows positive allometry in its denticles, although the extremely long stillette (i_2') denticle (Lamsdell & Selden 2013, fig. 24b) was interpreted as a piece of cuticle or plant overlying the base of the free ramus (*Ibid.*, fig. 17a) by Braddy (2022). *Jaekelopterus* and *Pterygotus* are particularly similar and potentially synonymous (Braddy *et al.* 2008b, Lamsdell & Legg 2010, Lamsdell & Selden 2013, see below).

Most pterygotids were up to 72 cm long (Plotnick & Baumiller 1988, Chlupáč 1994) but some grew up to 2.5 m long (Braddy *et al.* 2008a, Briggs & Roach 2020), the largest ever arthropod (but see Evolutionary Implications for a revised size estimate). The Howick Bay *Arthropleura* (Davies *et al.* 2022), in comparison, has an estimated average body length of 2.3 m. If 12 to 14 tergites are 76 cm long, a complete individual with 32 tergites would have been just over 2 m long (excluding the head), *i.e.* the L/W body ratio decreased during growth. It is also more likely that an aquatic arthropod would be larger than a terrestrial one, due to biomechanical limitations. With their giant size, streamlined body, large chelicerae and lateral eyes,

and powerful gnathobases, pterygotid eurypterids were all interpreted as fierce active visual predators (Woodward 1872, Romer 1933), occupying high trophic levels, as primary aquatic carnivores (Selden 1984). However, the predatory abilities of some pterygotid taxa have been questioned, with their morphology regarded “as consistent with a scavenging or even a browsing mode of life, as a predatory one” (Plotnick & Baumiller 1988, p. 14).

The enlarged chelicerae of pterygotids were adapted to rapidly capture prey, as evident by their low mechanical advantage (Selden 1984). They also would have moved prey into the mouth. The terminal denticles are more pointed, for puncturing and gripping prey. Backwardly directed denticles on the rami would have effectively snared, grasped and sliced slippery or struggling prey. The oblique denticle on the fixed ramus of *Acutiramus*, with a serrate posterior margin (Fig. 1) may have speared prey when the rami were held open or could have sawn up prey by repeated movements (Romer 1933, Chlupáč 1994, Bicknell *et al.* 2022b). Pterygotid chelicerae are remarkably similar to those of a solifuge (camel or sun spiders), an arachnid that uses its chelicerae to capture and kill prey (Van der Meijden *et al.* 2012). They are also similar to some cutter crustacean claws, particularly the harpoon-like appendages of mantis shrimps (Selden 1984). Cutter chela are long and slender with many denticles, like *Acutiramus*, and evolved for faster closing speeds. Crusher claws are more robust, with larger denticles to break harder shelled prey (Yamada & Boulding 1998), more like *Jaekelopterus* and *Pterygotus*. The green crab *Carcinus maenas* has both kinds of pincers. The blue crab *Callinectes sapidus* has a cutter pincer with an average closing force of 24.6 N and a crusher with a force of 42.8 N (Govind & Blundon 1985). Pterygotids, however, do not show both kinds of chelicerae in the same individual.

The gracile chelicerae of *Acutiramus cummingsi* were suggested by Laub *et al.* (2010) to merely trap, grasp and slice soft-bodied and relatively weak prey. Biomechanical analysis, based on the cuticle strength of *Limulus*, suggested that structural failure would occur on the oblique denticle and thinnest part of the free ramus. The failure force estimated for a mid-sized free ramus (8.9 N) and (largest) denticle (8.3 N) suggests that they would snap if used upon hard prey. The apparent lack of an elbow joint, it was argued, also limited their movement, such that they could only grasp prey on the sea floor, rather than capture active prey, suggesting that they were not actually predators (Laub *et al.* 2010).

Finite element analysis (FEA) of the chelicerae of *A. bohemicus* indicates that stress was concentrated in the proximal free ramus and denticles, also suggesting it targeted softer prey (Bicknell *et al.* 2022b). FEA indicates *Erettopterus bilobus* and *P. anglicus* had a more generalised diet that probably included armoured

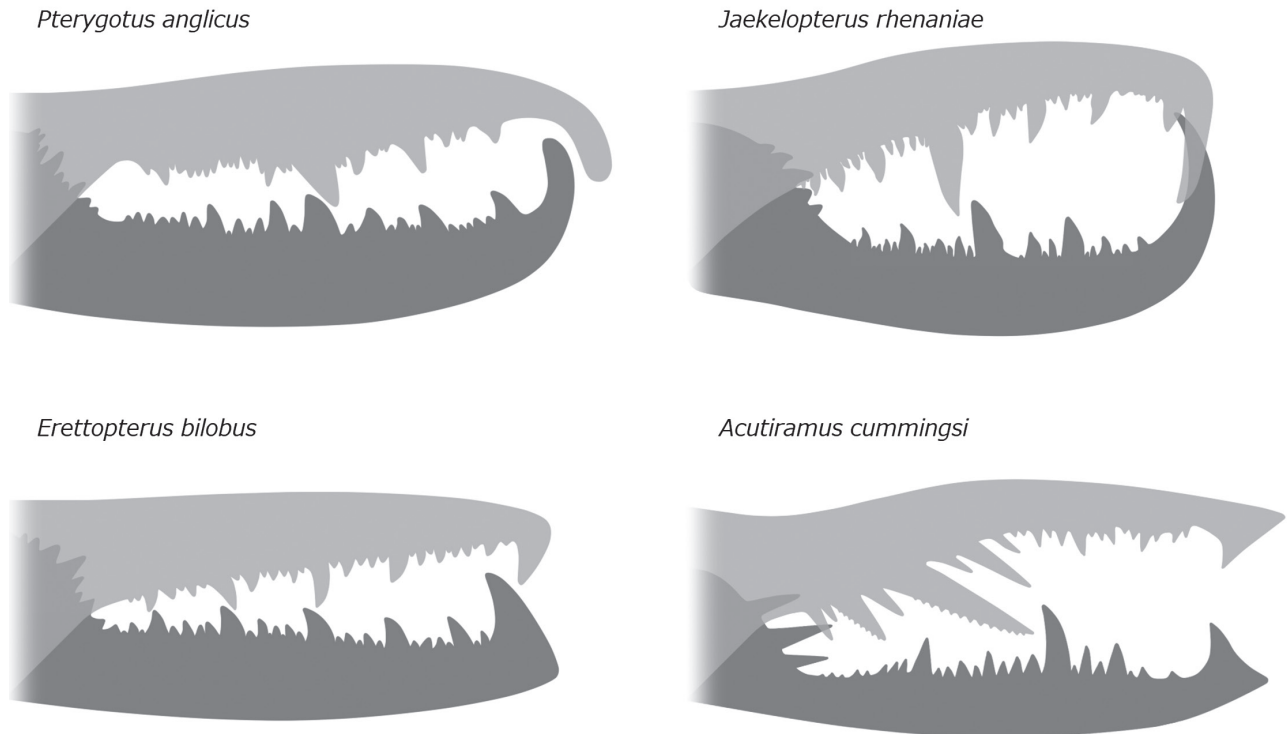


Figure 1. Pterygotid eurypterid chelicerae morphology. *Pterygotus* and *Jaekelopterus* have more robust chelicerae with smaller denticles, adapted for catching harder prey like armoured fishes while *Acutiramus* has more delicate chelicerae with longer denticles, adapted for more lightly armoured prey like phyllocarids. Image credit: Jun (Junnn11/CC BY-SA 4.0).

fishes. *Jaekelopterus rhenaniae* has lower stress across its chelicerae, suggesting that it fed on larger and harder prey, including heavily armoured fishes, such as placoderms.

The eurypterid mouth is situated on the ventral midline between the prosomal appendage coxae, which were capable of adduction and abduction to masticate food. The mouth is surrounded by coxal gnathobases, spinose or saw-like projections on the mesial margin of the coxae of appendages II–VI. In *Eurypterus*, one of the anatomically best known eurypterids, appendages IV–VI were used for walking and appendages I–III gathered food (Selden 1981), each equipped with different types of teeth on their gnathobases (Haug 2020); anterior gnathobases are less robust. These structurally weaker gnathobasic spines were likely used to shred soft prey (Selden 1981, Bicknell *et al.* 2022a). The gnathobases of appendage VI crushed harder food items; stronger anterior teeth reached under the metastoma and were elongated to achieve a larger bite force (Haug 2020), effectively functioning as antagonistic jaws. On each gnathobase some teeth were larger and movable (Selden 1981). Follicles at the base of the teeth were sensory setae. The epicoxa is a small setose sac with a mesial bristled surface, forming a movable endite on the gnathobase of appendages II–V (Selden 1981). The metastoma (a post-oral ventral plate) may result from the

fused epicoxa of appendage VI (Tetlie & Braddy 2004, Plotnick & Bicknell 2022).

In pterygotids, once a prey was captured it was pulled into the oral aperture. Small prey or dismembered parts of larger prey were masticated by the gnathobases (Kjellesvig-Waering 1964). The coxal gnathobases were more powerfully developed in pterygotids (Clarke & Ruedemann 1912, Miller 2007, Poschmann *et al.* 2017, Haug 2020) than in *Eurypterus*, indicating that they were able to feed on larger prey, including those with solid exoskeletons or tough dermal armour (Størmer 1944). The very powerfully developed coxae of appendage VI would have had a major role in killing, cracking and crushing hard-shelled prey, which were masticated further by the more anterior gnathobases of limbs II–V. The metastoma probably functioned to retain food in the oral cavity, similar in function to the chilaria of xiphosurans, by closing the oral region posteriorly (Selden 1981) and acting as a guide rail for the coxae of appendages V and VI (Haug 2020). The metastoma of *Eurypterus* also probably had a sensory function, as indicated by follicles on its ventral surface, which held setae in life (Selden 1981). Many eurypterids had a notch at the anterior of their metastoma (Tollerton 1989, fig. 5) with teeth similar to those of the posterior gnathobases, indicating that they contributed to the mastication of prey. The size and morphology of

the metastoma varies among eurypterids (Tollerton 1989, fig. 5), reflecting their predatory capabilities, functional requirements and feeding mechanisms. Pterygotids (and carcinosomatids) had a broader metastoma than the other eurypterids, indicating that they could deal with larger prey. *Eurypterus*, and likely all other eurypterids, also had an endostoma situated slightly supero-anteriorly to the metastoma (Selden 1981, Plotnick & Bicknell 2022) that functioned to push food forward across the mouth.

All pterygotoids had large, anteriorly placed eyes, with overlapping visual fields, as expected in a predator. Anderson *et al.* (2014) compared the visual acuity of the lateral eyes of *A. cummingsi* with *Eurypterus* and other arthropods; its large lenses are undifferentiated, it lacks an area of increased visual acuity and its interommatidial angle (IOA) is outside the range of modern arthropod predators, suggesting that it hunted thin-shelled or soft-bodied prey, perhaps at night (Anderson *et al.* 2014). McCoy *et al.* (2015) analysed the average number of eye lenses (ommatidia), the angle between them (IOA) and the Eye Parameter (EP; the diameter of a single ommatidium (D) multiplied by the IOA; Poschmann *et al.* 2016) of *Jaekelopterus* (>2979 lenses, IOA 0.87°, EP 1.41) and *Pterygotus* (4303 lenses, IOA 0.77°, EP 4.36), which had a better visual acuity (lower IOA and more lenses) than *Acutiramus* (1407 lenses, IOA 2.01°, EP 11.96). *Slimonia* (4075 lenses, IOA 1.52°, EP 5.55) and *Erettopterus* (4079 lenses, IOA 1.23°, EP 4.98) had higher IOA values, so were not regarded as specialised or active predators (McCoy *et al.* 2015).

McCoy *et al.* (2015) recognised three pterygotid groups: 1) Large *Jaekelopterus* and *Pterygotus* species with high visual acuity (low IOA with many lenses, correlating with living active high-level predators), enlarged and robust chelicerae with prominent, differentiated denticles and a curved free ramus correlating with a strong grasping and puncturing ability; 2) Mid-sized *Slimonia* (small chelicerae with no denticles) and *Erettopterus* (enlarged chelicerae with less differentiated denticles) species, with high visual acuity with many lenses (higher IOA values than *Jaekelopterus* and *Pterygotus*), but not regarded as highly specialised or active predators; 3) Large *Acutiramus* species with enlarged gracile chelicerae with differentiated denticles, but with a relatively low visual acuity (high IOA with fewer lenses), indicating a distinct ecology that involved less active predation.

Eurypterid eyes are more like those of xiphosurans (*i.e.* apposition type, constrained within cones; Poschmann *et al.* 2016) with cuticular lens cylinders and an eccentric cell in their sensory apparatus (Schoenemann *et al.* 2019). Edge enhancement (lateral inhibition), organised by the eccentric cell is useful in aquatic scattered light-conditions, while the single-lens system of arachnids is a terrestrial adaptation (Schoenemann *et al.* 2019).

Dunlop *et al.* (2002) noted the frequent co-occurrence of eurypterids and fishes; one-third of all Silurian and Early Devonian eurypterid localities (Plotnick 1999) are associated with fishes. Analysing this data further may reveal more interesting patterns. Trace fossils represent the remains of an organism's life activities, and provide important, but often overlooked, evidence for the ecology of extinct animals. They include trackways, fossil faeces (coprolites) and bite marks (praedichnia) (Bertling *et al.* 2006). Evidence for the predatory abilities of pterygotids comes from such trace fossils, so is reviewed here, alongside a more detailed analysis of their faunal associations.

Methods

Ecological occurrence data (locality numbers listed below) was compiled from Plotnick's (1999) published database, additional literature on associations at those localities (*i.e.* locality 15, Miller 2007; locality 26, Flower & Wayland-Smith 1952; locality c, Sudkamp & Burrow 2007) and the Paleobiology Database (PBDB). Taxonomic revisions follow Cieurca & Tetlie (2007) and Tetlie & Briggs (2009): *Pterygotus monroensis* and *P. impacatus* are assigned to *E. osiliensis*; *Pterygotus impacatus* to *Erettopterus*; *Pterygotus ventricosus* and *P. sarlei* to *Ciurcopterus*. *Pterygotus siemiradzki* (locality 79) is interpreted as a fish scale (Dunlop & Tetlie 2006), so is excluded. Stratigraphic and geological details of each locality can be found in Plotnick (1999), so are not repeated here. Subsequently published localities (*e.g.* Burrow *et al.* 2001, Naugolnykh & Shpinev 2018, Bicknell *et al.* 2020, Plotnick 2022) do not always specify associations, so are excluded. *Jaekelopterus* is limited in terms of data provided in Plotnick (1999), therefore is compiled from the primary literature and the PBDB, and given additional locality letter codes (a–d): (a) Beartooth Butte and Cottonwood Canyon (*J. howelli*; Bryant 1932, 1933, 1934, 1935; Ruedemann 1934, 1935; Lamsdell & Legg 2010; Lamsdell & Selden 2013); (b) Alken, Overath and Waxweiler (*J. rhenaniae*; Störmer 1973; Poschmann 2008); (c) Hunsrück (*J. rhenaniae*; Poschmann *et al.* 2017); (d) Willwerath (*J. rhenaniae*; Anderson *et al.* 1998). Associations are divided into nine categories, two arthropod (trilobite and phyllocarid) and seven vertebrate (thelodont, osteostracan, pteraspid – *i.e.* Pteraspidomorphi, anaspid, osteichthyan – *i.e.* Osteichthyes, *e.g.* dipnoans), placoderm and chondrichthyan (*i.e.* Chondrichthyes, *e.g.* sharks), based on assignments in Elliott *et al.* (2021). These nine categories were chosen based on previous interpretations of typical pterygotid associations and ichnological evidence (see below).

An association is considered one in which taxa occur in the same assemblage (*i.e.* same stratigraphic unit at

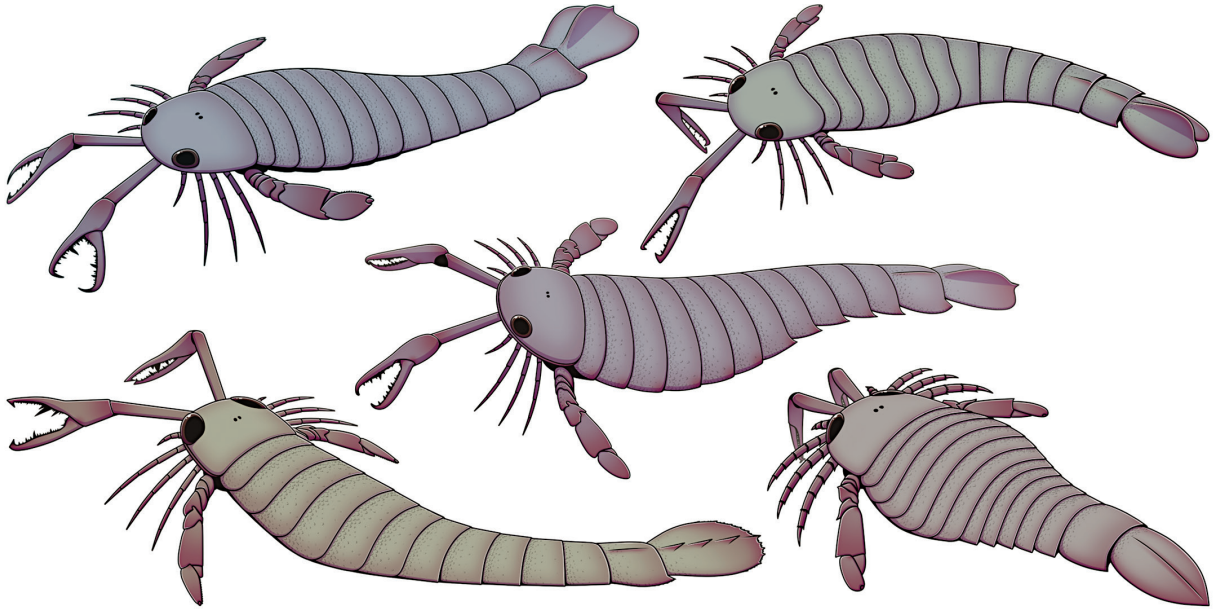


Figure 2. Pterygotid eurypterid reconstructions (not to scale): top left *Jaekelopterus rhenaniae*, top right *Erettopterus bilobus*, center *Pterygotus anglicus*, bottom left *Acutiramus macrophthalmus*, bottom right *Ciurcopterus ventricosus*. Image credit: Jun (Junnn11/CC BY-SA 4.0).

the same locality), not necessarily on exactly the same bedding plane, information that is rarely recorded. Of course, this means that some elements of the fauna may have been transported. Associations in the same unit at nearby localities, e.g. *Nerepisacanthus* in the Bertie Waterlime at Ridgemount Quarry in Ontario (Burrow & Rudkin 2014) do not form part of this data. Some localities (17 (with fishes) 29 and 73 (both with trilobites and phyllocarids), 74 (with trilobites), 82 and 83) list only indeterminate pterygotid fragments, so are also excluded.

Faunal association data was also compared with evidence from a critical review of the literature on the functional morphology of the chelicerae, lateral eyes and swimming biomechanics, in order to develop a coherent scenario of the likely predatory relationships and predatory techniques employed by the different genera of pterygotid eurypterids.

Results

Trilobites occur at localities 6, 10, 11, 12, 15, 16, 29, 46, 49, 56, 73, 80, 81 and 88. Phyllocarids occur at localities 26, 27, 29, 33, 42, 46, 48, 49, 50, 51, 53, 56, 60, 71, 80, 81 and 87. *Slimonia* occur at localities 48, 49, 50, 60, 81 and 85 in association with: Thelodonts *Loganellia* (49, 50, 60) and *Thelodus* (60); anaspids *Jamoytius* (49) and *Birkenia* (50); pteraspid *Cyathaspis* (60); trilobites (49, 81) and phyllocarids (48, 49, 50, 60 and 81). *Salteropterus* occur at localities 56 and 61 in association with: Thelodonts

Loganellia (61) and *Thelodus* (61); osteostracan *Hemicyclaspis* (61); trilobites (56) and phyllocarids (56). *Ciurcopterus* occur at localities 24 (no fishes) and 26 in association with: Pteraspids *Vernonaspis* (26) and *Archegonaspis* (26) and phyllocarids (26).

Acutiramus occur at localities 28, 30, 32, 33, 37, 42, 80, 81 and 91 in association with: Pteraspids *Vernonaspis* (28) and *Steinaspis* (91); acanthodians *Onchus* (80); trilobites (80, 81) and phyllocarids (32, 33, 42, 80 and 81). *Erettopterus* occur at localities 1, 2, 3, 4, 9, 18, 22, 23, 25, 26, 28, 32, 49, 50, 56, 57, 58, 60, 61, 63, 65, 66, 71, 72 and 80 in association with: Pteraspids *Vernonaspis* (1, 23, 28), *Americaspis* (23), *Cyathaspis* (60), *Traquairaspis* (72), *Corvaspis* (72), *Poraspis* (72), *Homalaspidella* (72), *Dinaspidella* (72), *Anglaspis* (72), *Ctenaspis* (72) and *Protopteraspis* (72); thelodonts *Loganellia* (50, 57, 60, 61, 71), *Thelodus* (57, 60, 61) and unspecified thelodonts (63, 66); acanthodians *Onchus* (80) and unspecified acanthodians (63); anaspids *Jamoytius* (49), *Birkenia* (50), *Pterygolepis* (71) and unspecified anaspids (63); osteostracans *Thyestes* (63), *Hemicyclaspis* (63), *Ateleaspis* (71) and unspecified osteostracans (66); trilobites (49, 56, 80, 81) and phyllocarids (26, 32, 49, 50, 56, 60, 71 and 80).

Pterygotus occur at localities 11, 15, 32, 34, 35, 41, 43, 50, 53, 54, 55, 56, 57, 60, 63, 68, 76 and 80 in association with: Pteraspids *Allocryptaspis* (41), *Zachinaspis* (41), *Traquairaspis* (53), *Cyathaspis* (60); thelodonts *Loganellia* (50, 57, 60), *Turinia* (54), *Thelodus* (57, 60) and unspecified thelodonts (63, 68); acanthodians *Climatius*

(15, 54), *Ischnacanthus* (54), *Mesacanthus* (15, 54), *Cheiracanthus* (15), *Gyracanthus* (15), *Onchus* (41, 80) and unspecified acanthodians (63); anaspids *Birkenia* (50) and unspecified anaspids (63); osteostracans *Yvonaspis* (15), *Hemicyclaspis* (53, 63), *Cephalaspis* (54), *Thyestes* (63) and unspecified osteostracans (68); placoderms *Phlyctaenius* (15) and *Aethaspis* (41); Chondrichthyes *Doliodus* (15), *Protodus* (15) and *Ctenacanthus* (15); trilobites (80) and phyllocarids (32, 43, 50, 53, 56, 60 and 80). *Jaekelopterus* occur at locality 9 (no fishes), a, b, c and d in association with: Pteraspids *Allocryptaspis* (a), *Cardipeltis* (a), *Cosmaspis* (a), *Lampraspis* (a), *Protaspis* (a), *Drepanaspis* (b), *Rhinopteraspis* (b) and unspecified pteraspids (d); acanthodians *Bulbocanthus* (a), *Machaeracanthus*, *Onchus* (a) and unspecified acanthodians (d); osteostracan *Cephalaspis* (a) and unspecified osteostracan (d); placoderms *Anarthraspis* (a), *Bryantolepis* (a), *Aethaspis* (a), *Simblaspis* (c), *Stuertaspis* (c), *Paraplesiobatis* (c), *Lunaspis* (c) and *Tiaraspis* (d); osteichthyan (dipnoans) *Uranolophus* (a), *Porolepsis* (b), *Dipnorhynchus* (c) and an unspecified crossopterygian (d); trilobites (c); phyllocarids (a).

Trilobites are associated with 15% of all eurypterid localities. At 9% of localities, trilobites are associated with pterygotids. Phyllocarids are associated with 18% of all eurypterid localities. At 13% of localities, phyllocarids are associated with pterygotids. Fishes are associated with 31% of all eurypterid localities. More detailed results of the associations of pterygotoids are shown in Table 1. In summary, *Slimonia* and *Acutiramus* tend to associate with phyllocarids more than fishes. *Erettopterus* and *Pterygotus* tend to associate with fishes, mainly thelodonts and osteostracans respectively, and *Jaekelopterus* tend to associate with osteichthyans, placoderms, pteraspids and acanthodians. Trilobites generally comprise minor associations at pterygotid localities.

Discussion

The analysis of associations herein suggests that there was some degree of prey specialisation amongst pterygotids, supporting previous studies based on their biomechanics. A general criticism of palaeoecology is that faunal associations do not prove that animals were in a close ecological relationship with each other. There is always the possibility that these eurypterids simply shared their environment with their associations and had relatively little interaction. In other words, eurypterids could have lived alongside armoured fishes but preferred softer prey. However, this evidence supports the evidence from trace fossils and their biomechanics suggesting that such patterns infer an ecological interaction. A eurypterid – phyllocarid association was noted by Kluessendorf (1994),

Table 1. Results of the analysis of biotic association of pterygotoid eurypterids. Percentage of localities that show association between taxa. Shaded cells indicate the most common association.

Eurypterid	<i>Slimonia</i>	<i>Salteropterus</i>	<i>Ciurcopterus</i>	<i>Acutiramus</i>	<i>Erettopterus</i>	<i>Pterygotus</i>	<i>Jaekelopterus</i>
Phyllocarids	83%	50%	50%	56%	32%	38%	20%
Trilobites	33%	50%		22%	16%	6%	20%
Fishes	50%	50%	50%	33%	52%	56%	80%
Thelodont	50%	50%			28%	22%	
Osteostracan		50%				27%	40%
Pteraspid	17%		50%	22%	18%	17%	60%
Anaspid	33%				16%	11%	
Osteichthyan					12%		80%
Acanthodian				11%	8%	17%	60%
Placoderm						11%	60%
Chondrichthyan						6%	

based on a cluster analysis of Silurian North American Lagerstätten surrounding the Michigan Basin. The results herein suggest that *Slimonia* and *Acutiramus* were associated with phyllocarids more than trilobites or fishes, which were mainly lightly-armoured forms such as pteraspids (with head shields). Bicknell *et al.* (2022b, p. 13) noted that “*Acutiramus* does not occur with a diverse fish fauna”; the results herein indicate that they only associate with pteraspids and acanthodians. *Erettopterus* mainly associate with lightly-armoured thelodonts (with scales instead of large plates or armour). *Pterygotus* associate with fishes more than phyllocarids or trilobites, generally heavily armoured osteostracans (with head shields). *Jaekelopterus* is the only pterygotid to associate with osteichthyans and (with *Pterygotus*) the heavily armoured placoderms.

The ecology and size of pterygotid prey also had implications for pterygotid predation. IOA values of pterygotid eyes change during ontogeny (McCoy *et al.* 2015); vision became less acute in adult *A. cummingsi* and more acute in *J. rhenaniae* (McCoy *et al.* 2015). Prey probably varied throughout ontogeny, with juveniles preferring smaller and less armoured prey. Juveniles occupied a broader ecological niche, ensuring less competition within a species. A juvenile *Jaekelopterus* could not tackle a large osteichthyan or placoderm. Prey preference also varied between taxa throughout their lives. Pterygotid taxa had more similar visual acuity as juveniles but this became more differentiated during growth.

Pterygotids (and carcinosomatids) are generally regarded as the most marine eurypterids, in the C/P bio-

facies (Braddy 2001). Most pterygotids are associated with Benthic Assemblage (B.A.) 1–3, but *Pterygotus* and *Jaekelopterus* extend into B.A. 0, representing non-marine settings (Plotnick 1999, tab. 1). The Benthic Assemblage scheme (Boucot 1975), based mainly on brachiopod assemblages, assesses palaeobathymetry (higher numbers indicating deeper water). Some *Pterygotus anglicus* were interpreted as living entirely in fresh water, since a wide size range of individuals are found in the Early Devonian lacustrine fish beds of Scotland (Trewin & Davidson 1996) and Emsian fluvial or alluvial-lacustrine sequences of New Brunswick (Miller 1996, 2007). Eurypterids generally are found in a wide range of palaeoenvironments, including deep marine, marginal marine, reef, hypersaline, brackish and freshwater settings (Braddy 2001, Vrazo & Braddy 2011). Because *P. anglicus* is found in both marine and freshwater, it may have been euryhaline (Braddy 2001), and able to seasonally migrate from coastal areas up rivers, following potential prey.

Ichthyology

Trace fossils attributed to pterygotid eurypterids are very rare. A fossil trackway attributed to a pterygotid (Sharpe 1932), from the Middle Ordovician of New York State, was reinterpreted as being produced by a stylonurid eurypterid (Braddy & Gass 2023). Pterygotids likely used an in-phase octopodous (appendages III–VI) lobster-like ‘tripling’ gait (Selden 1984), buoyed by the water, but could not have achieved stable locomotion as their opisthosoma was too long (Braddy & Gass 2023).

Praedichnia

Evidence for predator-prey interactions are rare in the fossil record. Two examples of pterygotid predation traces (praedichnia) on armoured vertebrates have been reported. A single, healed (*i.e.* non-fatal) puncture to the left posterolateral dorsal head shield of the pteraspid *Larnovaspis kneri*, from the Emsian of Gorodok, Podoli, Ukraine, is attributed to the terminal denticle of a chelicera of a pterygotid (Lebedev *et al.* 2009). Three holes puncture the dorsal head shield of the cyathaspid (pteraspid) *Lechriaspis patula*, from the Emsian Water Canyon Formation of northern Utah (Elliott & Petriello 2011). This attack was presumably fatal as there is no evidence of repair. The size and spacing of these holes exactly match the denticles of *J. howelli*.

Two reliable reports of pterygotid praedichnia on arthropods also exist. Injuries to *Eurypterus* and *Acutiramus*, from the Bertie Waterlime (McKenzie & Nypaver 2016) comprising torn and punctured remains, including

healed wounds from unsuccessful attacks. Puncture patterns correlate with the denticles of *Acutiramus macrophthalmus*. Malformed trilobites (*Spinisscutellum umbelliferum*), from the Early Devonian of Czechia were probably the result of failed predation attempts, grabbed and torn during the soft-shelled moult phase (Bicknell *et al.* 2021). *Acutiramus perneri*, from the Lochkov Formation, was the likely producer of these injuries. These healed injuries do not mean that pterygotids were ineffective predators, rather successful predation tends to leave no trace, because prey were eaten (McKenzie & Nypaver 2016), so the fossil record of praedichnia is inherently biased.

Healed injuries in the trilobite *Dalmanitina socialis* from the Upper Ordovician Letná Formation of Czechia (Fatka *et al.* 2021), comprising repaired eyes and malformed librigena, were attributed to a large arthropod interpreted as a pterygotid (Van Roy *in* Fatka *et al.* 2021). However, this arthropod is represented by several undiagnostic body segments that lack the scaly ornament of a pterygotid, and are too early (Ordovician) to be a pterygotid.

A cluster of 18 *Arctinurus boltoni* trilobites from the Silurian Rochester Shale of Orleans County, New York (Bicknell *et al.* 2019) shows 44% of specimens with W, U and V-shaped injuries, mostly (87.5%) on the right side, primarily the pygidium, but none on the cephalon. Various mollusc and arthropod predators, including eurypterids, may have caused these injuries. The trilobites either adopted a lateral defense or the predators attacked from behind or the side. Trilobites may also have gathered in a group to provide protection from predators, making it harder for one individual to be picked off.

Digestion

Evidence for the digestive system of eurypterids comes from a comparative approach and occasional well-preserved fossils (Selden 1984). In xiphosurans most of the prosoma is taken up by organs associated with food gathering, feeding and digestion. *Limulus* passes food down the oesophagus and into the gizzard for further internal grinding (Selden 1984). Indigestible particles are regurgitated through the oesophagus whereas digestible particles are passed posteriorly through a valve into the stomach. Two pairs of lateral diverticula forming glandular caeca secrete digestive enzymes into the stomach through two pairs of ducts. The intestine of *Limulus* extends posteriorly into the opisthosoma and waste is expelled via a short sclerotised rectum and out the anus, located ventrally just in front of the telson. Eurypterids probably had a similar digestive system (Selden 1984). Their prosoma probably contained some organs associated with

digestion (gut diverticula), but digestion also took place in their much larger opisthosoma.

Coprolites

Coprolites (fossil faeces) associated with the mixopterid *Lanarkopterus dolichoschelus*, from the Silurian of the Hagshaw Hills in Scotland, contain disarticulated bony fragments of an agnathan (Selden 1984, Schmidt *et al.* 2022). Other coprolites attributed to eurypterids contain thelodont (*Loganellia*) scales (Rolfe 1973, Selden 1984). Coprolites of *Megalograptus ohioensis*, from the Ordovician of Ohio contain trilobites and other *M. ohioensis*, indicating cannibalism (Caster & Kjellesvig-Waering 1964). The coprolites of related predatory eurypterid taxa therefore suggest that pterygotids fed on trilobites, agnathans and even their own kind, supporting the evidence from praedichnia. A putative pterygotid coprolite from the Silurian (Přídolí) of New South Wales in Australia, contain abundant, partially articulated, fragments of the trilobite *Denckmannites rutherfordi* (Bicknell *et al.* 2023).

Predatory strategies

The mode of life of pterygotids can be interpreted by a consideration of their functional morphology and comparisons with extant taxa. A lurking model (Selden 1984) considers pterygotids as ambush predators, hiding on or in the substrate, relying on their eyes to detect prey and their chelicerae to rapidly capture it, as depicted in the Walking with Monsters TV series. This model is comparable to dragonfly larvae, the praying mantis and mantis shrimps (Selden 1984). The stomatopod *Harpisquilla harpax* hunts from a burrow as a lie-in-wait predator or it can actively stalk fish (Dingle & Caldwell 1978). However, comparisons with pterygotids are tentative, given differences in their size and ecology. Pterygotids were large, especially as adults, making it difficult for them to hide. Their gills needed to be ventilated (Selden 1984) so prolonged burial in the substrate was unlikely. Alternatively, pterygotids may have hunted at night (Anderson *et al.* 2014) or are here interpreted as lurking in deep, dark or murky estuarine water, with prey encountered essentially by chance. In well-lit waters it is unlikely that they used this strategy. Osteostracans may have been captured with the lurking model.

A nektonic model (Clarke & Ruedemann 1912, Trewin & Davidson 1996) regards pterygotids as primarily nektonic predators able to swim down prey in open water. Poschmann *et al.* (2016) regarded *J. rhenaniae* as an agile swimmer that likely chased active prey. However, it is

unlikely that pterygotids were very fast or manoeuvrable swimmers, especially as adults, given their large size (Braddy & Gass 2023). The pterygotid telson is flat, with a raised median keel, that was initially interpreted as an adaptation for propulsion (Størmer 1934), with the paddles acting as balancing organs (Kjellesvig-Waering 1964). Plotnick & Baumiller (1988) then interpreted the telson as acting more like a rudder, with propulsion primarily achieved by appendage VI (paddles); pterygotids were interpreted as agile swimmers capable of quick turns and even hovering.

Analysis of eurypterid swimming (Knight 1997), predicting their behaviour from models in flume tank experiments to determine the body resistance and a computer model to determine paddle thrust (varying stroke angle and angle of attack), agreed with observed portunid crab swimming techniques. A 22 cm long *Eurypterus* would swim using a lift-based stroke, with the paddle swept forwards and down on the forestroke and backwards and up on the backstroke at an angle of about 45 degrees, as in sea lions, at a speed of 3–4 m/sec, as in turtles. Swimming was not to hunt fast prey but instead to find and feed on worms and small arthropods. Smaller species (and juveniles) had higher drag coefficients than larger animals, so swam relatively faster (although actual speeds were lower) but juveniles were likely more agile than adults and used more drag-based (rowing) techniques.

Computer modelling of pterygotid swimming techniques (Knight 1997) indicates that they were actually rather poor swimmers due to their large size. Drag and lift coefficients of pterygotid paddles are higher than those of *Eurypterus* (Plotnick 1985), due to their greater area, and they were good lift-producing hydrofoils. The paddles would need to beat at 3 Hz to provide sufficient thrust, even at low speeds, but scaling of portunid crab paddles indicates that they could only beat at 0.4 Hz. Pterygotids were too big for their paddles to provide sufficient thrust. Objection to carangiform swimming (Plotnick & Baumiller 1988) highlighted whales, sharks and ichthyosaurs, with a narrow caudal peduncle and a broad tail fin, which maximise speed. Although the telson was an optimal shape to function as a rudder, this does not preclude it from propulsion; it probably did both (Braddy & Gass 2023). This swimming technique has recently been tested experimentally with an 80 cm long modular (*i.e.* long chelicerae, paddle and telson morphology) robotic swimming eurypterid called ‘Robopterus’ (Toshiyasu Kondo, pers. comm.). Pterygotid telsons were also unlikely to be used as a weapon (Lamsdell *et al.* 2018). Juveniles would have been more agile, not so biomechanically constrained. If pterygotid prey were relatively slow swimming (*e.g.* pteraspids and osteostracans with armour; Morrissey *et al.* 2004, 2006) speed may not have been the primary concern. A predator need

only be slightly faster than its prey. The chelicerae were adapted as the rapid capture structures, not the swimming ability. If some pterygotids hunted in low light levels, speed and agility would also have been less of a concern. Acanthodians may have been captured with the nektonic model (e.g. in low-light conditions).

A mud grubbing model (King *et al.* 2017), based largely on assessments of *Acutiramus* chelicerae by Laub *et al.* (2010) and raking marks, from the Emsian of New Brunswick, suggests that pterygotids used their chelicerae to rake around in the mud. These raking traces, referred to *Monomorphichnus*, consist of sub-parallel straight to sigmoidal hyporelief ridges (elliptical in shape, 15–42 mm long and 13–22 mm wide, spaced 2 mm apart), the central scratches deeper than the outer ones. King *et al.* (2017) attributed them to *Pterygotus anglicus*, known from the same formation, as it was the only known arthropod large enough (65 to 170 cm; Miller 2007) to have produced them. The denticles on the chelicerae were suggested to have raked or sieved the sediment like some modern crabs (Bauchau & Passelecq-Gerin 1988). A raking-and-sieving feeding method was also proposed for some fossil decapods (Tshudy & Sorhannus 2000) but their chelae were able to open much wider, up to 180°. Pterygotids would not have been able to open their chelicerae wide enough to create such scratch marks, and their low mechanical advantage indicates that they were rapid-capture structures (Selden 1984). It is more likely that these *Monomorphichnus* traces were produced by a stylonurid eurypterid, crustacean or euthycarcinoid (Braddy & Gass 2023).

A newly proposed vagrant model regards pterygotids as essentially nekto-benthonic animals, swimming just above the substrate, feeling for prey with their appendages, which were then caught by their chelicerae. This model is supported by the more palpal nature of limb II (Selden 1986). Infaunal and epifaunal worms and arthropods may have been captured with the vagrant model. Pterygotids may have fed on worms if other prey were not available, but this does not preclude them from primarily being a predator of arthropods and/or vertebrates.

Functional morphology

An unresolved question concerning pterygotid chelicerae concerns their functional morphology. Whilst many specimens of *E. bilobus*, for example, show their long chelicerae preserved in a reversed position in front of the moulted exoskeleton, we still do not know exactly how they attached to the prosoma and sprung out to catch prey. They presumably had sufficient basal articulation to extend forward and retract back to move food into the mouth and sufficient musculature and tendons to extend rapidly.

The articulation at the base of the fixed ramus could presumably rotate 90° enabling the chelicerae to close both vertically and horizontally, to catch and manipulate prey. The denticles may have been strengthened with Mn, Fe or Zn metal ions for durability, as in scorpions (Schofield 2001). The reversed orientation of preserved chelicerae, in front of exuvia, can be explained as the animal pulled out its freshly moulted chelicerae and the shed chelicerae flipped forward as the animal emerged anteriorly. Crustaceans bury their appendages in the substrate to provide sufficient resistance to help pull out the freshly moulted cuticle. Perhaps eurypterids used a similar behaviour.

The chelicerae (Laub *et al.* 2010) and lateral eyes (Anderson *et al.* 2014) of *Acutiramus cummingsi* have been interpreted as being inconsistent with a predatory lifestyle. Here, *Acutiramus* is interpreted as a predator specialised on lightly armoured prey (e.g. phyllocarids). The cuticle thickness (1 mm) used by Laub *et al.* (2010) in their equations was just an assumption. The free ramus was actually composed of solid cuticle. The muscle cavity in a chelicera was located in the proximal part of the fixed ramus, as in *Limulus* (Bicknell *et al.* 2018, fig. 2e, f). Pterygotid chelicerae were much more robust than Laub *et al.* (2010) assumed, which explains why they are preserved more frequently than the rest of the animal. A table lamp-like action of the chelicerae was also considered unlikely by Laub *et al.* (2010), as pterygotids apparently lack an elbow joint. “The supposed first joint had to be divided into at least two joints” (Kjellesvig-Waering 1964, p. 335). However, the articulation at the base of the fixed ramus was effectively the elbow joint. The chelicerae were probably held open, ready to strike, then moved in a rotational movement. The chelicerae did not push forwards, rather swept in from the sides or from underneath. Even though the chelicerae of *Acutiramus* were more gracile than the other pterygotid taxa, they were primarily used to just capture prey. Killing and dismemberment would also have taken place in the oral cavity by the much more powerful saw-like gnathobases and metastoma, which were better suited to kill and cut up prey. These structures have generally been overlooked in previous studies that interpret *Acutiramus* as an ineffective predator.

Modern analogs for eurypterid vision should ideally be based on aquatic arthropods. The only modern, aquatic, high-level, arthropod predator used by Anderson *et al.* (2014) and McCoy *et al.* (2015), was the mantis shrimp *Squilla* (IOA 0.2–1.5°; Wehner 1981), a carnivorous crustacean with stalked compound eyes. Anderson *et al.* (2014) and McCoy *et al.* (2015) defined a predator based on an IOA of 0.9° or less. However, some insects with a low IOA include non-predators such as bees (*Apis* 0.8°) and butterflies (*Papilio* 0.9°), to locate mates or prey

in fast aerial manoeuvres (Land 1997). This shows the problem of using IOA to arbitrarily identify an arthropod as a predator; interpreting *Slimonia* and *Erettopteris* as not being a specialised or active predator, based on IOA (McCoy *et al.* 2015) is therefore questionable. Although the vision of some pterygotid taxa was apparently worse than other taxa, this does not preclude them from being a predator. They probably did not require exceptional visual acuity to locate prey that was relatively large and relatively close or probably just reacted to prey movement or used other senses (*e.g.* chemosensory or tactile perception) to locate prey, especially in dark conditions.

Evolutionary implications

The chelicerae of hughmilleriids, slimonids, pterygotids (and carinosomatids) are anteriorly facing and larger than those of other eurypterids, indicating that they were capable of dealing with larger prey. The *Hughmilleria*-type of (spiniferous) appendage (Tollerton 1989) was more primitive than that of the pterygotids (Lamsdell *et al.* 2015, Lamsdell 2022), capable of both locomotion and prey capture, so the lack of spines on limbs II–V in pterygotids reflects a shift away from their role in prey capture to walking, with the chelicerae specialised for prey capture (Selden 1984). The chelicerae of *Slimonia*, the sister taxon to Pterygotidae, were short and robust (Lamsdell 2022), but not as powerfully developed as in the pterygotids.

Hypotheses of the phylogenetic relationships of pterygotoids have varied (*e.g.* Plotnick & Baumiller 1988, fig. 2; Dunlop *et al.* 2002, fig. 6) but more recently settled on (excluding *Grossopterus*, a waeringopterid and *Truncatiramus*, an *Erettopteris*) the topology: *Slimonia* (*Salteropterus* (*Ciurcopteris* (*Erettopteris* (*Pterygotus* (*Jaekelopterus* + *Acutiramus*)))) (*e.g.* Braddy *et al.* 2008a, fig. 2; McCoy *et al.* 2015, fig. 1a; Lamsdell *et al.* 2015, fig. 21). The position of *Acutiramus* is somewhat surprising, given the obvious similarities between *Jaekelopterus* and *Pterygotus* (Figs 1, 2); they are probably even cogenetic (*cf.* Waterston 1964). Given *Acutiramus* has gracile chelicerae with a large obliquely-orientated denticle on its fixed ramus, unlike the more robust chelicerae of *Jaekelopterus* and *Pterygotus* (Fig. 1), this prompts a reevaluation of the characters used in previous analyses (*e.g.* Braddy *et al.* 2008a, characters 3 and 15; McCoy *et al.* 2015, characters 6, 8, 17, 18, 22, 28 and 31); Character 3/6 (large denticle on the fixed ramus) is incorrectly coded for *Jaekelopterus*, and 8 (based on similar trends in *E. bilobus*; Ciurca & Tetlie 2007), 17, 18 (both metastoma), 28 and 31 (both telson) likely ontogenetic. Variation in the visual acuity (itself based on morphology) and associations, based

on the analysis presented herein, support the hypothesis that *Acutiramus* is actually more basal to *Jaekelopterus* and *Pterygotus*. The stratigraphic ranges and ecology (extending into freshwater) of these taxa also supports this revised phylogenetic hypothesis; *Acutiramus* is older than both *Jaekelopterus* and *Pterygotus*, which ranges almost exactly overlap (*e.g.* Braddy *et al.* 2008a, fig. 2). This also has implications for the maximum size that *Jaekelopterus* (and therefore all Arthropoda) could attain; if the giant chelicerae described by Braddy *et al.* (2008a) were scaled by *Pterygotus* (its closest relative, if not even the same genus) alone, it would have been 2.59 m long.

Changes in pterygotid ecology were interpreted in a phylogenetic context by McCoy *et al.* (2015). Evolving from a slimonid ancestor, *Erettopteris* was interpreted by McCoy *et al.* (2015) as a generalist, evolving larger chelicerae, but not a giant body size or an advanced visual system. In this model the ancestor of *Pterygotus*, *Jaekelopterus* and *Acutiramus* evolved giant body size, specialised chelicerae and an advanced visual system as a high-level active predator but these adaptations, except large body size, were apparently lost in *Acutiramus* (McCoy *et al.* 2015) with its inferred weak chelicerae and eyes, as a specialised ambush predator or scavenger. Herein, pterygotid evolution is interpreted much more simply. All taxa are regarded as predators, each specialised on certain types of prey. If *Acutiramus* was more basal to *Jaekelopterus* and *Pterygotus*, no reversals are needed and the overall trend in pterygotid evolution is towards increased predatory abilities.

Romer (1933) proposed that eurypterids influenced early vertebrate (jawless fish) evolution and were ultimately outcompeted by jawed vertebrates. An increase in size in pterygotids throughout the mid-Palaeozoic may represent an arms race between eurypterids and armoured fishes (Lamsdell & Braddy 2010, Bicknell *et al.* 2022b). Such competitive replacement is sometimes dismissed as playing only a minor role in taxon survivorship. Previous assessments of *Acutiramus* chelicerae limitations (Laub *et al.* 2010) were suggested to have effectively falsified Romer's (1933) hypotheses but the pterygotid praedichnia reviewed herein provide strong evidence that pterygotids had some influence on some early vertebrates. The analysis of pterygotid associations herein also supports the interpretation that they were much more capable predators than some workers have assumed and were able to prey on early vertebrates. Competition with cephalopods as either prey and/or predators on eurypterids, or as competitors could also be considered (Klug *et al.* 2015).

Indeed, some megalograptids, mixopterids and carinosomatids, with long spinose raptorial appendages forming a catching basket (Schmidt *et al.* 2022), are also associated with fishes and should to be included in an analysis to test Romer's (1933) hypothesis. The methods

presented here could be extended to the entire Eurypterina, and the timing of predatory adaptations in eurypterids correlated with defensive adaptations in fishes. The sweep-feeding Stytonurina (Hughes & Lamsdell 2021, Braddy *et al.* 2023) are much less likely to have had any influence on early vertebrate evolution.

Summary

In conclusion, pterygotid eurypterids are most consistent with having been slow swimming vagrant and ambush predators, each genus probably specialised on certain types of prey; previous analyses of the chelicerae (Laub *et al.* 2010) and lateral eyes (Anderson *et al.* 2014) of *Acutiramus cummingsi* were based on assumptions and do not preclude a predatory lifestyle. Trace fossils (praedichnia and coprolites) provide strong evidence that pteraspids, other eurypterids and trilobites, were amongst the prey of pterygotids, as were phyllocarid crustaceans and other early fishes, based on an analysis of their faunal associations. *Acutiramus* is interpreted as being more basal to *Jaekelopterus* and *Pterygotus* and Romer's (1933) hypothesis that eurypterids influenced early vertebrate evolution could be tested by extending this analysis, in a phylogenetic context, to the entire Eurypterina.

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