



# A new Ordovician eurypterid (Arthropoda: Chelicerata) from southeast Turkey: Evidence for a cryptic Ordovician record of Eurypterida

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## ARTICLE INFO

### Article history:

Received 27 January 2012

Received in revised form 20 April 2012

Accepted 20 April 2012

Available online 2 May 2012

Handling Editor: J.G. Meert

### Keywords:

Katian

Eurypterina

*Paraeurypterus*

Ghost ranges

Phylogeny

## ABSTRACT

A new species of eurypterid, *Paraeurypterus anatoliensis* gen. et sp. nov., is described from the Upper Ordovician (Katian) Şort Tepe Formation of southeast Turkey. The single specimen, preserving the carapace, mesosoma and fragments of appendages, appears morphologically intermediate between the eurypteroid families Dolichopteridae and Eurypteridae. *P. anatoliensis* retains the plesiomorphic conditions of crescentic eyes with enlarged palpebral lobes and a quadrate carapace with ornamentation consisting of small pustules but also displaying the derived characteristics of genal facets and a row of large acicular scales across the posterior of each tergite. Phylogenetic analysis incorporating each of the major eurypterine clades and all Eurypterina having a three-segmented genital operculum (the triploperculate condition) resolves eurypteroids to be an unnatural group, with Dolichopteridae and Eurypteridae forming part of a grade leading to diploperculate Eurypterina. *P. anatoliensis* is intermediate between the two eurypteroid families, as is '*Eurypterus*' *minor* from the Pentland Hills of Scotland, which is shown to be a distinct genus and assigned to *Pentlandopterus* gen. nov. Using the phylogenetic topology to infer ghost ranges for each of the major eurypterid clades reveals that the majority of eurypterid superfamilies must have originated by the Katian, indicating a largely unsampled record of Ordovician eurypterids. The occurrence of poor dispersers such as *Paraeurypterus* in the Ordovician of Gondwana is puzzling, and it has been suggested that they dispersed to the continent during periods of sea level lowstand in the Sandbian and Hirnantian, however this does not explain the lack of Ordovician species in North America and Europe, given the well-sampled nature of these continents, and an alternative is proposed whereby eurypterids originated in Gondwana and radiated out to Laurentia and Baltica in the late Ordovician and early Silurian, thus explaining their sudden appearance in the European and North American rock record.

Published by Elsevier B.V. on behalf of International Association for Gondwana Research.

## 1. Introduction

Eurypterids are a monophyletic group of Palaeozoic aquatic chelicerates with a distribution largely limited to the palaeocontinents of Avalonia, Armorica, Baltica, Iberia and Laurentia. Of the 246 currently valid eurypterid species only 22 have been reported from outside these palaeocontinents; however, of these, only 13 can be confidently assigned to a eurypterid clade (Table 1). While it has been suggested that the lack of eurypterids other than from Europe and North America is a collecting and research bias (Plotnick, 1999), and a number of further unnamed or fragmentary eurypterids have been reported from outside of these continents (Braddy et al., 1995, 2002; Braddy and Almond, 1999; Tetlie et al., 2004), it is the currently

held view that the observed distributions represent a true signal, with eurypterids originating in Laurentia and being limited to dispersal along coastlines, with only the pterygotoids being able to cross open oceans (Tetlie, 2007a). Any new record of eurypterids from outside North America and Europe is, therefore, of extreme interest, especially if they can be assigned to a group lacking the dispersal capabilities of the pterygotoids, and have a pre-Carboniferous age.

The majority of eurypterid occurrences outside North America and Europe consist of presumably poor dispersers (hibbertopteroids) which occurred during the Carboniferous and Permian, after Gondwana has come into close proximity to Laurentia as a prelude to the amalgamation of Pangaea, or taxa with higher dispersal potential such as pterygotoids or carinosomatids. *Adelophthalmus* Jordan in Jordan and von Meyer, 1854, another widespread genus, is also known from Gondwanan localities from the Devonian onwards and it is likely that it was able to cross the already narrowing gulf

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**Table 1**

Chronological list of undoubted eurypterids from palaeocontinents other than Baltica, Laurentia, Avalonia, Iberia and Armorica. *Stylonurus* (?) *menneri* and *Borchgrevinkium taimyrensis* from the early Devonian of Siberia (Novojilov, 1959) and *Melbournopterus crossotus* from the Silurian of Australia (Caster and Kjellesvig-Waering, 1953) are not eurypterids and so have not been included. *Eurypterus loi*, *Eurypterus styliformis* and *Eurypterus yangi* from the Silurian of China (Chang, 1957) are probably based on undiagnostic material and have been excluded pending reevaluation of the original material, as have *Nanahughmilleria schiraensis* and *Parahughmilleria matarakensis* from the Devonian of Siberia (Pirozhnikov, 1957), *Adelophthalmus carbonarius* (Chernyshev, 1933) from the Carboniferous of Ukraine, and *Pterygotus* (?) *australis* from the Silurian of Australia (McCoy, 1899). Note however that reports of unnamed or undescribed eurypterids (Braddy et al., 1995, 2002; Braddy and Almond, 1999; Tetlie et al., 2004) are not listed here.

Eurypterids by period	Author	Age	Region
Ordovician			
<i>Onychopterella augusti</i>	Braddy et al., 1995	Hirnantian	South Africa
Silurian			
<i>Hughmilleria wangi</i>	Tetlie et al., 2007a	Llandovery	China
<i>Rhinocarcinosoma dosonensis</i>	Braddy et al., 2002	Ludlow–Pridoli	Vietnam
<i>Slimonia boliviana</i>	Kjellesvig-Waering, 1973	Ludlow/Pridoli	Bolivia
Devonian			
<i>Acutiramus</i> cf. <i>bohemicus</i>	Burrow et al., 2002	Pridoli	Australia
<i>Adelophthalmus waterstoni</i>	Tetlie et al., 2004	Frasnian	Australia
<i>Pterygotus bolivianus</i>	Kjellesvig-Waering, 1964a	Emsian/Eifelian	Bolivia
Carboniferous			
<i>Adelophthalmus irinae</i>	Shpinev, 2006	Tournaisian	Siberia
<i>Cyrtoctenus wittebergensis</i>	Waterston et al., 1985	Tournaisian	South Africa
<i>Megarachne servinei</i>	Hünicken, 1980	Gzhelian–Asselian	Argentina
<i>Unionopterus anastasiae</i>	Chernyshev, 1948	Tournaisian–Visean	Kazakhstan
Permian			
<i>Adelophthalmus chinensis</i>	Grabau, 1920	Asselian	China
<i>Campylocephalus oculatus</i>	Kutorga, 1838	Guadalupian?	Russia
<i>Hastimima whitei</i>	White, 1908	Sakmarian	Brazil

between Gondwana and Laurentia. One occurrence, however, appears to defy explanation: *Onychopterella augusti* Braddy et al., 1995, from the Soom Shale of South Africa, which has been dated as latest Hirnantian to earliest Rhuddanian (Vandenbroucke et al., 2009). *O. augusti* does not appear to be a good disperser, as its posterior pair of appendages are not overly expanded into a swimming paddle, and its relatively basal phylogenetic position combined with its early occurrence (before the major period of eurypterid radiation during the early Silurian) makes its appearance in Gondwana somewhat problematic.

Here, we report a second Gondwanan Ordovician eurypterid, *Paraerypterus anatoliensis* gen. et sp. nov., a single specimen from the Şort Tepe Formation (middle Katian) near Çukurca, southeast Turkey. The new species is placed in a phylogenetic context as intermediate between the families Dolichopteridae and Eurypteridae and forms part of a basal grade of Eurypterina leading to a clade defined by having only two fused plates in the genital operculum. The phylogeny allows for ghost ranges to be estimated for each of the main eurypterid clades which indicate the existence of a diverse record of Ordovician eurypterids and the potential for discovery of further early Palaeozoic eurypterids in Gondwana.

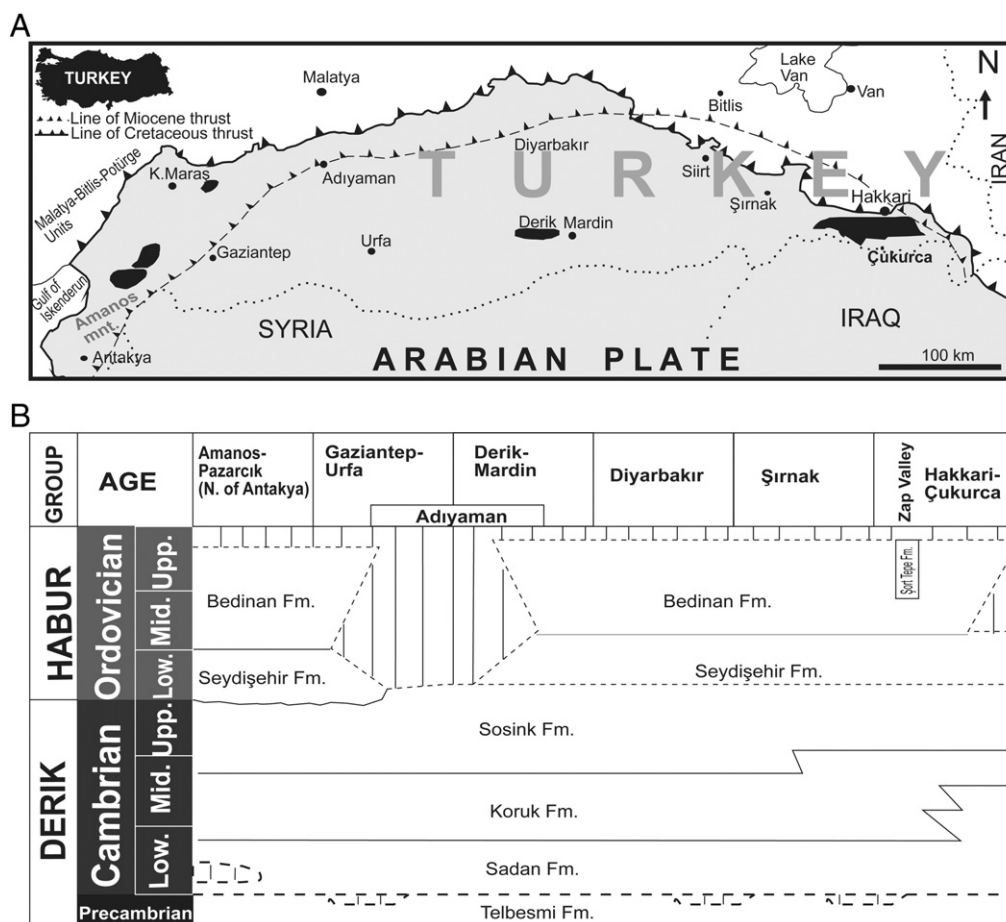
## 2. Geological setting

The Border Folds of southeast Turkey represent the northern part of the Arabian Plate dominated by the East Anatolian Fault where it contacts the Anatolian Plate (Fig. 1A), and consists largely of Mesozoic and Cenozoic surface crops with subsurface Palaeozoic formations cropping out in places (e.g. at the Derik, Mardin, Şort Tepe, and Zap areas) that represent an almost complete Cambrian–Ordovician succession (Fig. 1B). The eurypterid specimen was discovered during a geological survey of the most southeastern regions of Anatolia, near the border with Iraq. Here, the early Palaeozoic strata encompass the Derik and the Habur groups which extend from the Amanos–Pazarcık area in the west to Hakkari–Çukurca in the east (Cater and Tunbridge, 1992; Bozdoğan and Ertuğ, 1997) and palaeogeographically belong to the northern margin of the Arabian Plate of Gondwana throughout the Palaeozoic.

Lower Palaeozoic strata were first recognised in southeastern Turkey about 30 km southwest of Hakkari by Altınlı (1963) who reported

unnamed, thick, Cambrian limestones overlain by approximately 1000 m of the Giri Formation, comprising Silurian (actually Cambrian and Ordovician) quartzites with subsidiary limestones and siltstones. Some of the latter contained *Cruziana* trace fossils and have been compared to analogous strata in northern Iraq (Dean and Monod, 1990; Dean, 2006). Between Hakkari and Çukurca the River Zap cuts a deep valley to expose two inliers of Cambrian and Ordovician sediments, mostly clastics, that form part of the Arabian Platform (Ghienne et al., 2010). Dean et al. (1981) recognised that the Giri Formation was equivalent to the shales and sandstones of the Seydişehir Formation, described from the western Taurus Mountains but widespread in the eastern Taurus, southeastern Turkey, and neighbouring parts of Iraq, and of Upper Cambrian and Lower Ordovician age. The strata disconformably overlying the formation, mainly comprising shales and siltstones, were named the Şort Tepe Formation and considered to be of Ashgillian age (Upper Ordovician, late Katian–Hirnantian). In the Zap Valley, the thick Seydişehir Formation is unconformably overlain by a Lower and Upper Palaeozoic succession that comprises the Upper Ordovician Şort Tepe Formation, the Upper Devonian Yığınlı Formation and the Lower Carboniferous Köprülü Formation (Fig. 2A) (Higgs et al., 2002). It is in the Şort Tepe beds of this succession, on the northeast side of the Zap Valley 7.5 km northwest of Çukurca (Fig. 2B), that the eurypterid specimen was discovered. The depositional environment of the Şort Tepe Formation is considered to be that of an outer shelf environment representing the culmination of a period of marine transgression throughout the Seydişehir Formation which it unconformably overlies (Ghienne et al., 2010).

In the Hakkari–Çukurca area the Şort Tepe Formation is known for its well-preserved trilobite faunas, with Dean and Zhou (1988) reporting the genera *Lonchodomas* Angelin, 1854, *Dindymene* Hawle and Corda, 1847, *Prionocheilus* Rouault, 1847, *Calymenesun* Kobayashi, 1951 and *Birmanites* Sheng, 1934, along with fragments of diplograptid graptolites and the brachiopod *Aegiromena* Havlíček, 1961, all located in the grey shale beds within the formation, the same lithology from which the eurypterid was discovered. These macrofossils were used, through comparison with similar faunas elsewhere, to infer a pre-Hirnantian Ashgill age for the formation. Palynological investigations on Ordovician deposits from Turkey are fairly rare and deal principally with the less mature organic-walled microfossils recorded in the Border Folds area where rich and well preserved Upper Ordovician acritarchs, sporomorphs, and



**Fig. 1.** A, map showing the region surrounding the border between the Arabian and Anatolian plates. Early Palaeozoic outcrops are shown in black. The Zap Valley is located between Hakkari and Çukurca; B, diagram showing the lateral extent of the early Palaeozoic formations between Antakya and Hakkari on the Arabian plate. After Bozdoğan and Ertuğ, 1997.

chitinozoans have been reported from the Habur Group (Steevens et al., 1996). More recently, Paris et al. (2007a, 2007b) have determined chitinozoan assemblages in the upper parts of the Şort Tepe Formation dated to the late Caradoc (middle Katian), thus making the new eurypterid older than *Orcanopterus manitoulinensis* Stott et al., 2005 and *Megalograptus ohioensis* Caster and Kjellesvig-Waering in Størmer, 1955 (both from the late Katian of Laurentia) and *Onychopterella augusti* (from the Hirnantian of Gondwana), but younger than the stylonurine *Brachyopterus stubblefieldi* Størmer, 1951 (from the Sandbian of Avalonia).

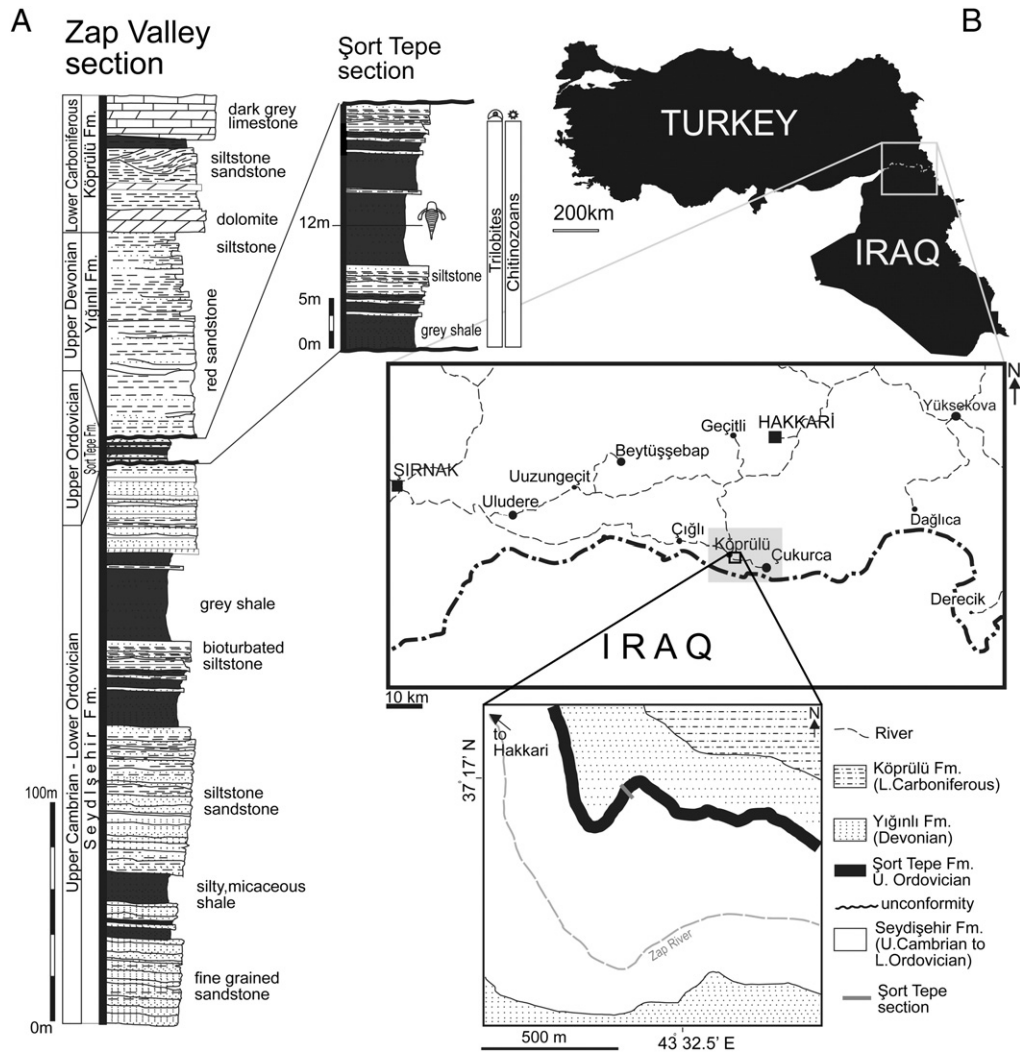
### 3. Materials and methods

The specimen was recovered from the Upper Ordovician Şort Tepe Formation of southeast Turkey and is deposited in the Natural History Museum of Maden Tetkik ve Arama Genel Müdürlüğü, Ankara (MTANHMSETR). Material of *Eurypterus minor* (Laurie, 1899), studied for comparison, is held at the National Museums of Scotland (NMS), Edinburgh, UK. Eurypterid terminology largely follows Tollerton (1989) for morphology of the carapace, metastoma, lateral eyes, prosomal appendages, genital appendage, opisthosomal differentiation, telson, and patterns of ornamentation; however, the terminology for the ventral plate morphologies follows the revised types of Tetlie et al. (2008). Selden (1981) is followed for prosomal structures and cuticular sculpture and the labelling of the appendages. Terminology for the segmentation of the genital operculum follows Waterston (1979). The specimen was studied using a Leica M205C stereomicroscope and photographs were taken on a Canon EOS 5D

Mk II digital camera with a Canon macro MP-E 65 mm 1:2.8 lens with a polarizing filter and a polarized light source with the specimen submerged in alcohol. Image processing was carried out using Adobe Photoshop CS4, and interpretive drawings were prepared for publication using Adobe Illustrator CS4, on a MacBook Pro running OS X.

The specimen consists of parts of the prosoma and mesosoma preserved in a pale grey siltstone with red-brown coloured cuticle preserved in places (Fig. 3), such as on the carapace dorsal surface anterior to the left lateral eye, where it shows a concentric, pustular ornament. Part of the carapace posterior is broken away, revealing the prosoma–opisthosoma junction and the usually hidden, poorly sclerotized, true first tergite. Anteriorly on the right side, the carapace is broken away to reveal the ventral plate (doublure). The median suture of the doublure is not visible, but there is clearly no epistomal plate or transverse suture. Lateral eyes are preserved, but median ocelli seen only as pale, circular impressions, and the right one is mostly obscured by a crack. Anterior to the right lateral eye, and posterior to the left lateral eye, are what appear to be worm burrows or grazing traces.

To the right of the carapace, the remains of four appendages can be seen. The most anterior (appendage III) consists of a single podomere that is angled underneath the following appendage and thus lost from view. Appendage IV consists of a single visible podomere and a spine from the preceding podomere that is hidden under the carapace. No details are available of appendage V apart from its existence: it appears from beneath the carapace but is then covered by the overlying, forward-thrust appendage VI.



**Fig. 2.** A, generalized columnar section of the Upper Cambrian–Lower Carboniferous rock units of the Zap Valley section (after Ghienne et al., 2010) with the location of the eurypterid shown within the Şort Tepe Formation; B, location and geological maps of the Zap Valley and Şort Tepe section.

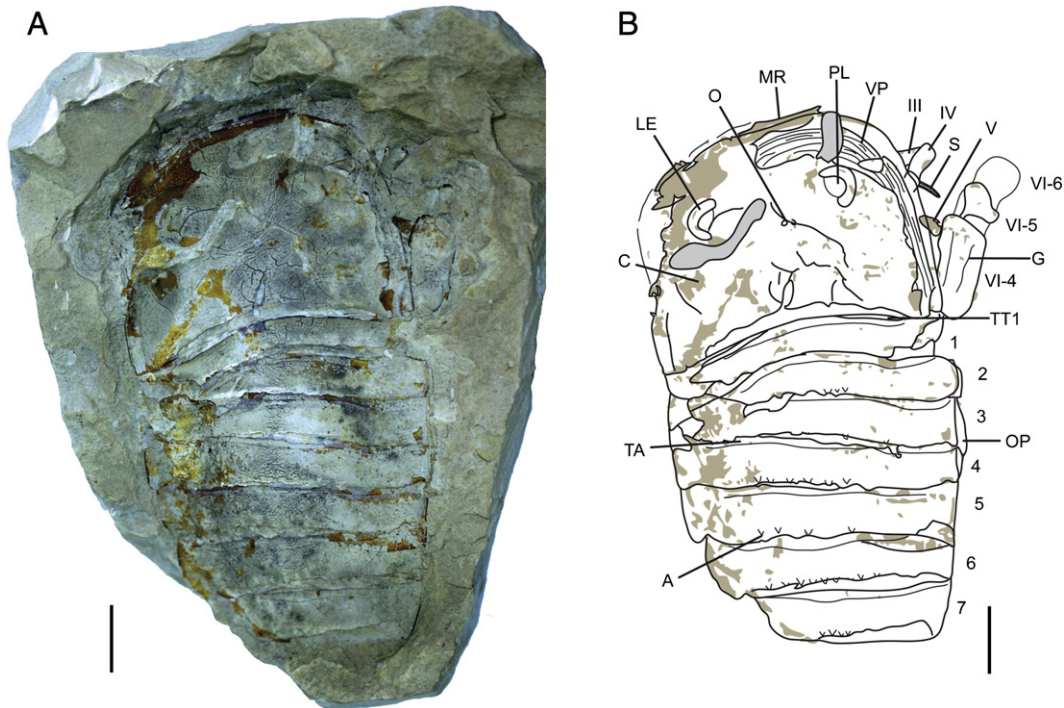
In the mesosoma, seven fully expressed tergites and the first, usually hidden, true tergite are preserved which, though poorly preserved, can be seen on both lateral margins. On the right side of the specimen, the opercular plates can be seen projecting from beneath the tergites. The exact number of large, acicular scales on each tergite is difficult to ascertain due to damage around the posterior margins; however, it is clear that each tergite bore three sets of large scales for a total of six to nine scales on each segment.

For the phylogenetic analysis, a matrix of 81 characters and 45 taxa was compiled, which can be found in the Appendix along with character descriptions. The synziphosurine *Weinbergina opitzi* Richter and Richter, 1929 was specified as the outgroup following Lamsdell et al. (2010a, 2010b) as it supposedly represents the most plesiomorphic known xiphosuran (Anderson and Selden, 1997) which are sister group to Eurypterida (Selden and Dunlop, 1998); however, given the unclear nature of synziphosurine intra-relationships (see Lamsdell, 2011) the chasmataspidids *Chasmataspis laurencii* Caster and Brooks, 1956, *Loganamaraspis dunlopi* Tetlie and Braddy, 2004, *Diploaspis casteri* Størmer, 1972 and *Octoberaspis ushakovi* Dunlop, 2002 are included due to the shared synapomorphies of a metastoma and genital appendage. These, however, were left as ingroup taxa to test whether chasmataspidids fall outside Eurypterida or are a clade within Eurypterina, as suggested by Shultz (2007). In order to test the placement of the Turkish specimen among the basal

Eurypterina, all the taxa from the analysis of Tetlie and Cuggy (2007) were included, along with taxa from the analysis of Lamsdell (2011). In order to test the ramifications of the ghost ranges for each of the major Eurypterina clades, representatives from each of the more derived groups were also included, each represented by multiple exemplars which more accurately represent the character states and transitions of the group than a single exemplar, such as a single species or a composite taxon (see Brusatte, 2010). *Mixopteris kiaeri* Størmer, 1934a and *Carcinosoma newlini* (Claypole, 1890a) were included to represent the mixopteroids, *Adelophthalmus sievertsi* (Størmer, 1969) and *Nanahughmilleria norvegica* (Kiær, 1911) for the adelophthalmoids, and *Hughmilleria socialis* Sarle, 1903 and *Pterygotus anglicus* Agassiz, 1844 for the pterygotoids. Two other problematic Ordovician taxa were also included: *Megalograptus ohioensis* and *Orcanopterus manitoulinensis*. *O. manitoulinensis* was considered by Tetlie (2007a) and Tetlie and Poschmann (2008) to be part of an unnamed clade consisting of *Orcanopterus* Stott et al., 2005, *Waeringopterus* Leutze, 1961 and *Grossopterus* Størmer, 1934b which forms the sister-group to adelophthalmoids and pterygotoids, while *M. ohioensis* has traditionally been considered a member of the Mixopteroida (Caster and Kjellesvig-Waering, 1964), although Tetlie (2007a) considered it to be a basal taxon positioned between *Onychopterella* Størmer, 1951 and Eurypteroida.

The analysis was performed using TNT (Goloboff et al., 2008; made available with the sponsorship of the Willi Hennig Society)





**Fig. 3.** *Paraeurypterus anatoliensis* gen. et sp. nov. MTANHMSETR 10-IZ-01-1. A, Photograph of holotype and only known specimen; B, Interpretive drawing of holotype. Shaded areas represent preservation of original cuticle. Label abbreviations: A, acicular scales; C, carapace; G, grooves; LE, lateral eye; MR, marginal rim; O, ocelli; OP, opercular plate; PL, palpebral lobe; S, spine; TA, tergite articulation; TT1, true tergite 1; VP, ventral plate; 1–7, tergites; III–VI, prosomal appendages; VI-4–VI-6, podomeres of prosomal appendage VI. Scale bars equal 10 mm.

employing random addition sequences followed by branch swapping (the *mult* command in TNT) with 100,000 repetitions with all characters unordered and of equal weight. Jackknife (Farris et al., 1996) and Bremer support (Bremer, 1994) values were calculated in TNT and the Consistency, Retention and Rescaled Consistency Indices were calculated in Mesquite 2.73 (Maddison and Maddison, 2010). Nonparametric bootstrapping is often difficult with morphological data due to the limited size of the dataset (Zander, 2003) and so was not performed for this analysis. Jackknifing was performed using simple addition sequence and tree bisection-reconnection (TBR) branch swapping, with 100,000 repetitions and 25% character deletion. The matrix and character listing can be found in the electronic appendix has been deposited in the online MorphoBank database (O'Leary and Kaufman, 2007) under the project code p568 and can be accessed from <http://morphobank.org/permalink/?P568>.

#### 4. Systematic palaeontology

Phylum Arthropoda Latreille, 1829  
 Subphylum Chelicerata Heymons, 1901  
 Superclass Sclerophorata Kamenz et al., 2011  
 Order Eurypterida Burmeister, 1843

##### Diagnosis

Chelicerates with the opercula of somites VIII and IX fused into a genital opercular plate.

##### Remarks

After the identification of a metastoma and genital appendage in two species of chasmataspidid (Dunlop, 2002; Tetlie and Braddy, 2004), Lamsdell (2011) determined the sole eurypterid autapomorphy to be the possession of the fused opercula of somites VIII and IX forming the genital operculum. The fact that the median and posterior opercular

plates were functionally fused had also been recognised by Laurie (1893), Holm (1898) and Wills (1965) but appears to have been missed by subsequent authors.

Suborder Eurypterina Burmeister, 1843

Grade 'Eurypteroidea'

##### Remarks

Tetlie and Cuggy (2007) retrieved Eurypteroidea as a natural group; however, the analysis herein resolves the group as paraphyletic with a monophyletic Dolichopteridae sister-group to Eurypteridae and the remaining Eurypterina (Mixopteridae, Adelophthalmoidea and Pterygotoidea). This result was somewhat foreshadowed by Tetlie and Cuggy (2007), who remarked that the Eurypteridae were, in most respects, more derived morphologically than the Dolichopteridae and appears to confirm the results from a less inclusive analysis performed by Lamsdell (2011). Paraphyly invalidates Eurypteroidea as a superfamily; however, the term is currently retained as an identification for the grade of basal Eurypterina that it encompassed. In due course, this may be expanded to also encompass both the Moselopteridae and Onychopterellidae; but these are, for the moment, retained in their own superfamilies.

Genus *Paraeurypterus* gen. nov.

##### Type species

*Paraeurypterus anatoliensis* gen. et sp. nov.

##### Etymology

From the Greek παρὰ (similar) and *Eurypterus* due to its close similarities to the genus *Eurypterus* DeKay, 1825.

##### Diagnosis

'Eurypteroid' with quadrate carapace possessing genal facets; small, crescentic lateral eyes with large palpebral lobe; carapace ornamentation consists of small pustules, opisthosomal ornamentation consists of scales with a series of large acicular scales across the posterior region of the tergites.

*Paraeurypterus anatoliensis* gen. et sp. nov. (Figs. 3–4)

**Holotype**

MTANHMSETR 10-İZ-01-1.

**Etymology**

Named after the Anatolian Peninsula where the specimen was found.

**Locality and age**

The only known specimen is derived from the Upper Ordovician (middle Katian) Şort Tepe Formation, southeast Turkey.

**Diagnosis**

As for genus.

**Description**

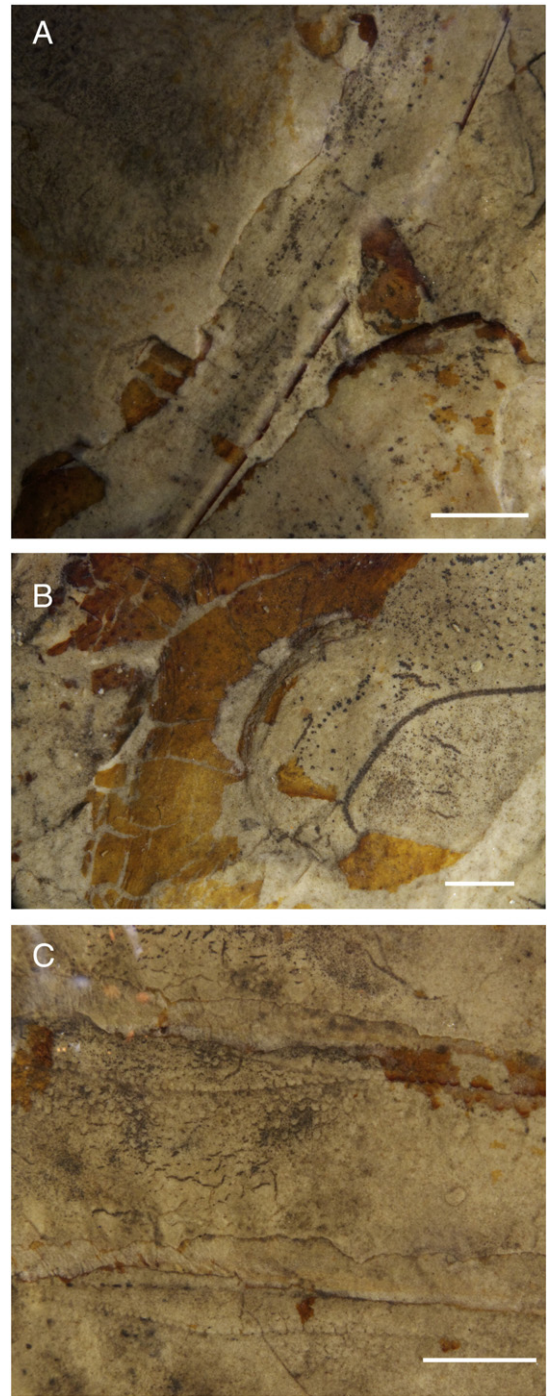
Preserved body length 84 mm; maximum width (at third tergite) 46 mm. Carapace maximum width 45 mm (at posterior), 32 mm long. Carapace anterior margin relatively straight, very slightly procurved medially; length:width ratio 0.70; genal angle 85°, therefore carapace subquadrate (Tollerton, 1989); posterior margin recurved, angling anteriorly for 2 mm. No epistomal plate or transverse suture (therefore *Eurypterus*- or *Erieopterus*-type); plates ornamented with series of striate terrace lines (Fig. 4A), as seen in *Eurypterus tetragonophthalmus* Fischer, 1839 (Selden, 1981), *Stoermeropterus conicus* (Laurie, 1892) (Lamsdell, 2011), *Parahughmilleria hefteri* Størmer, 1973 and *Erieopterus* sp. (Poschmann and Tetlie, 2006). Lateral eyes centrilateral at most antero-lateral limit of quadrant (Tollerton, 1989); crescentic, associated with small palpebral lobe giving appearance of circular outline (Fig. 4B); the defunct ovocrescentic of Tollerton, 1989; 6 mm long, 3 mm wide (5 mm including palpebral lobe). Median ocelli central between posteriormost limit of lateral eyes; 1 mm × 1 mm diameter. Carapace marginal rim narrow, extends across entire width of anterior and lateral margins, narrowing very slightly towards posterior, 1.5 mm at widest.

Only small part of one podomere of appendage III preserved. Single preserved podomere of appendage IV 5.5 mm long, 3 mm wide, unornamented; spine from preceding podomere 3.48 mm long, 1.22 mm wide at base, ornamented with series of longitudinal striations; appendage of *Hughmilleria*-type. Only small part of one podomere of appendage V preserved. Visible portions of appendage VI consists of long, slightly curved podomere ornamented with slight scale projections or distally angled serrations on dorsal and ventral (probably podomere 4); longitudinal, parallel grooves run down length of podomere; 15 mm long, 7.5 mm wide; podomere 5 is 7 mm long, flaring distally from 6 mm to 7 mm wide.

True first tergite 1 mm long. Opercular plates project from beneath tergites. First fully expressed tergite (from hereon just 'first tergite') shorter than following tergites; broadest point of body at third tergite (Table 2). Dorsal ornamentation consisting of continuous row of semilunate scales 1–1.5 mm from each tergite anterior border (Fig. 4C). Scale ridges indicate degree of overlap with preceding tergite; portion of tergite before ridge forms smooth articulating facet. Posterior to scale ridge are three discontinuous rows of semilunate scales before ornamentation becomes sparse, still consisting of isolated semilunate scales. Row of acicular scales interspersed with much larger acicular scales across posterior region of each tergite. Large scales, absent from first tergite, increase in size from second to seventh tergite. Each tergite with three sets of large scales (total 6–9 scales), number of scales possibly increasing with size of tergite.

**Remarks**

In general appearance, *Paraerypterus anatoliensis* looks very much like a species of *Eurypterus*, drawing initial comparison with *Eurypterus tetragonophthalmus*. A number of features, however, show it to be distinct from that genus: the quadratic carapace, which is trapezoidal in all *Eurypterus* species, the crescentic lateral eyes with an enlarged palpebral lobe (a plesiomorphic state which is lost in the *Eurypteridae* and the remaining derived *Eurypterina*), and the carapace ornamentation consisting of small pustules. Pustules



**Fig. 4.** *Paraerypterus anatoliensis* gen. et sp. nov. MTANHMSETR 10-İZ-01-1. A, Magnification of exposed ventral plate, showing fine striate 'terrace line' ornament; B, Magnification of crescentic lateral eye with enlarged palpebral lobe; C, Magnification of tergite ornament, showing the row of flattened scales at the posterior of the articulating facet and the large acicular scales towards the rear of the tergite. Scale bars equal 2 mm.

are known from the carapace of a number of *Eurypterus* species, including *E. dekayi* Hall, 1859 and *E. tetragonophthalmus*; however, in all of these, the pustules are limited to the margins of the carapace and anterior to the lateral eyes, and not covering the carapace, as appears to be the case in *P. anatoliensis*. The scale ornamentation of the opisthosoma in *P. anatoliensis* also appears different to that of *Eurypterus*, possessing more large acicular scales than in any known *Eurypterus* species, although the number of scales can vary between



**Table 2**

Proportions (length/width) of the holotype specimen MTANHMSETR 10-IZ-01 of *Paraeurypterus anatoliensis*.

1	2	3	4	5	6	7
5/44	7/34 <sup>a</sup>	7/46	8/45	8/42	8/40	8/31 <sup>a</sup>

<sup>a</sup> Preserved dimensions.

them. While the species resembles *Eurypterus*, it possesses a number of plesiomorphic characteristics that have already been lost in *Erieopterus* Kjellesvig-Waering, 1958, the sister-taxon of *Eurypterus*, and this is considered justification for its erection as a new genus, a conclusion borne out by the phylogenetic analysis presented herein.

*Pentlandopterus* gen. nov.

Type species

*Eurypterus minor* (Laurie, 1899)

Etymology

Named after the Pentland Hills, Scotland, from which the only known species is described.

Diagnosis

'Eurypteroid' with a quadrate carapace possessing genal facets; cuticular ornamentation consisting of closely spaced pustules; lateral eyes crescentic with large palpebral lobe.

*Pentlandopterus minor* (Laurie, 1899)

1899 *Eurypterus minor* Laurie, pp. 587–588, plate V Figs. 27–29.

1899 *Eurypterus minor* Peach and Horne, pp. 594.

1912 *Eurypterus minor* Clarke and Ruedemann, pp. 132.

1916 *Eurypterus minor* O'Connell, pp. 40.

1955 *Eurypterus minor* Lamont, pp. 200.

1958 *Eurypterus minor* Kjellesvig-Waering, pp. 1123–1124.

1999 *Eurypterus minor* Plotnick, pp. 120.

2006 *Eurypterus minor* Tetlie, pp. 403–405, Fig. 4.

2007a 'Eurypterus' minor Tetlie, pp. 560.

Holotype

NMS G.1897.32.120

Additional material

NMS G.1897.32.166 (paratype), G.1897.32.129, G.1897.32.152, G.1897.32.867.

Remarks

The species was given a modern redescription by Tetlie (2006), who considered it to be a *Eurypterus*. Tetlie and Cuggy (2007), however, showed it to be phylogenetically distinct from *Eurypterus* but did not change the taxonomy due to uncertainty as to the exact position of the species. Our analysis confirms that *Pentlandopterus minor* is not a *Eurypterus* and it is here assigned to its own genus. While it shares many characteristics with *Paraeurypterus anatoliensis*, the difference in opisthosomal ornamentation clearly places *P. anatoliensis* phylogenetically closer to the Eurypteridae and the two species are therefore assigned to different genera.

Tetlie (2006) listed NMS G.1897.32.110 as a second paratype, but this specimen number is actually associated with a specimen of *Drepanopterus pentlandicus* Laurie, 1892. The accession number of the *Pentlandopterus* second paratype is at present unknown.

Infraorder Diploperculata nov.

Included groups

Mixopteroidea, Adelophthalmoidea, Pterygopteroidea and the 'waeringopterid' clade.

Etymology

From the Greek διπλῶν (double) and operculum.

Diagnosis

Eurypterina with a genital operculum consisting of two fused segments.

Remarks

Diploperculata represents the clade of 'derived Eurypterina' as denoted by Tetlie and Cuggy (2007); those eurypterine groups to which 'Eurypteroidea' is sister-taxon, incorporating Mixopteroidea, the unnamed 'waeringopterid' clade, Adelophthalmoidea and Pterygopteroidea. Two characters potentially define the clade: the first, having a fused genital operculum composed of two segment (the diploperculata condition), gives the clade its name and is used to define the limits of the infraorder. The form of the genital operculum is thought to be an important character, as the possession of a fused genital operculum may be the only eurypterid synapomorphy (Lamsdell, 2011), with the Stylonurina and the basal Eurypterina (Moselopteridae, Onychopterellidae, Dolichopteridae, and Eurypteridae) sharing the plesiomorphic triploperculata (three segmented) condition (Tetlie and Braddy, 2004; Lamsdell, 2011). The other potential characteristic of the clade is having a podomere VI-4 of equal length to podomere VI-3 and VI-5, however *Megalograptus* (which is clearly diploperculata) has a VI-4 longer than VI-3 and VI-5 while the dolichopterid *Strobilopterus* Ruedemann, 1934 also has all three podomeres of equal length and so the character is not included in the diagnosis of the clade.

## 5. Comparison with other eurypterids

*Paraeurypterus* is clearly differentiated from the supposedly more primitive suborder Stylonurina, based on the lack of a transverse suture on the prosomal ventral plates and having prosomal appendage VI expanded into a swimming paddle. Although the distal podomeres of the paddle (including those that undergo the characteristic broadening) are not preserved, the fourth, fifth and sixth podomeres are. In eurypterids with a pediform prosomal appendage, the fifth podomere is longer than the fourth, whereas those with a paddle have a fourth podomere that is longer or equal in length to the fifth. *Paraeurypterus* has a VI-4 that is longer than VI-5, and therefore has a swimming paddle. Furthermore, the fact that VI-4 is longer than VI-5 precludes it from comparison with the mixopterooid, adelophthalmoid and pterygopterooid clades, which all have a VI-4 equal in length to VI-5. *Paraeurypterus* is therefore most comparable to *Megalograptus* Miller, 1874, Eurypteridae and Dolichopteridae (which with the exception of *Strobilopterus* all have VI-4 longer than VI-5).

*Paraeurypterus*, along with *Pentlandopterus*, shares several characteristics with dolichopterids, including a dorsal carapace ornamentation consisting of granular pustules, and crescentic lateral eyes associated with enlarged palpebral lobes; however, these are plesiomorphic conditions, also observed in onychopterellids, moselopterids and Stylonurina. Both *Paraeurypterus* and *Pentlandopterus* lack the synapomorphies of either dolichopterid clade, namely a short appendage VI that barely projects from beneath the carapace or an articulating angle between VI-3 and VI-4 of less than 180°. Both genera are separated from *Eurypterus*, however, in lacking a scale ornament on the carapace and having a quadratic rather than trapezoid carapace. *Eurypterus* has also lost the plesiomorphic lateral eye condition, instead having an expanded visual surface with reduced palpebral lobe. One character that separates *Paraeurypterus* from *Pentlandopterus*, but suggests a closer affinity to *Eurypterus* and *Megalograptus*, is its possession of a row of large acicular scales across the posterior margin of each tergite. It is predominantly similarities in opisthosomal ornamentation, along with the morphology of appendage V, that have led to comparison between *Eurypterus* and *Megalograptus* and so encountering a similar morphology in a new taxon may help indicate whether the similarities between the two

are synapomorphies, due to convergence or a result of retained plesiomorphic conditions.

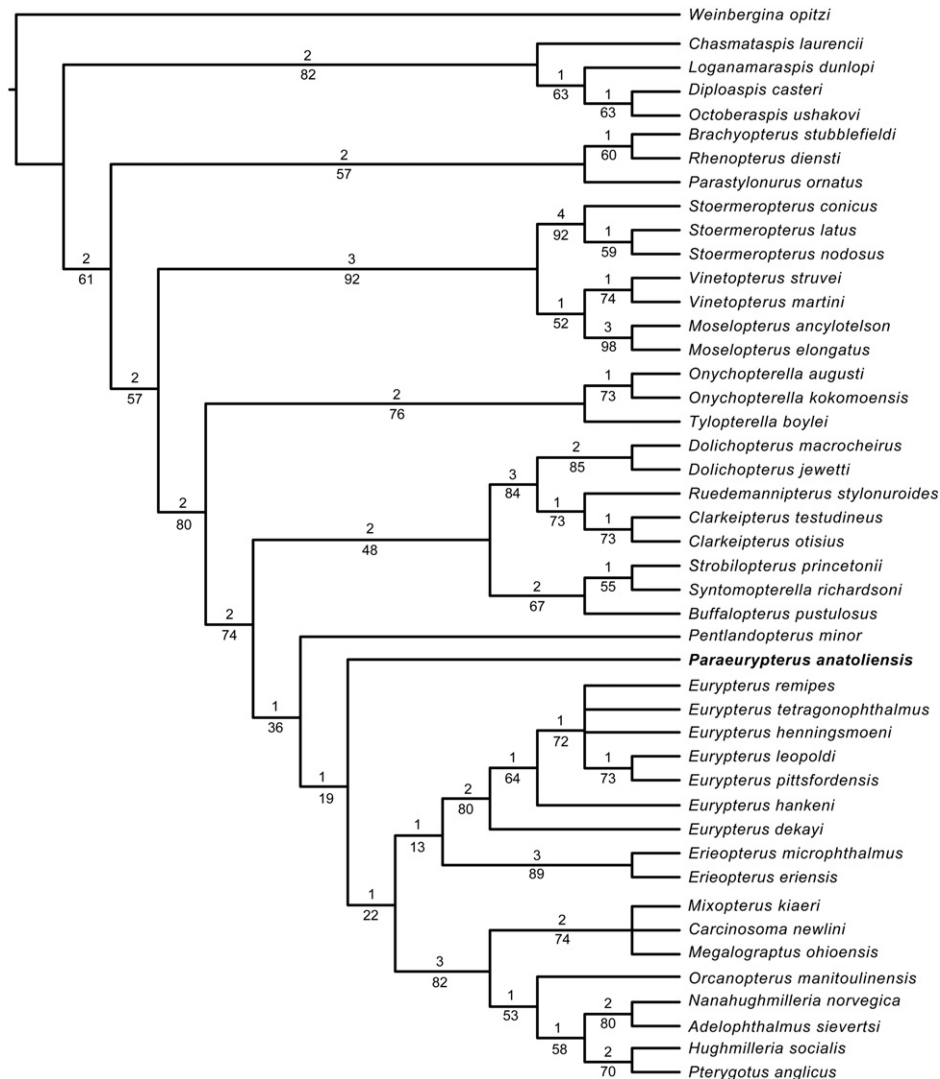
Several species of *Eurypterus* (*E. tetragonophthalmus*, *E. dekayi*, *E. ornatus* Leutze, 1958 and *E. hankenii* Tetlie, 2006) have a pustular carapace ornament; however, in all four species the pustules are smaller than in *Paraerypteris* and *Pentlandopterus*, and in *E. tetragonophthalmus* the pustules are only found around the carapace margin. Most species of *Eurypteris* also have a row of principal scales across the posterior of the carapace which is absent in *Pentlandopterus*, *Paraerypteris* and *Megalograptus*; however, these are absent in *E. dekayi*, *E. ornatus* and *E. laculatus* Kjellesvig-Waering, 1958. The opisthosomal ornament of *Paraerypteris* is very similar to that of *E. tetragonophthalmus* (Wills, 1965 pl. 2 Fig. 4) with a row of tightly packed semi-lunate scales across the anterior margin, delineating the articulating facet, followed by three discontinuous rows of loosely spaced scales, and a posterior row of larger acicular scales. This type of ornamentation is also seen in *Megalograptus*; however, *Megalograptus* and *Eurypteris* differ from *Paraerypteris* in having each acicular scale preceded by a longitudinal row of smaller scales. It seems clear that the similarities in ornamentation between the three taxa are not due to convergence, and the age of *Paraerypteris* and *Megalograptus*, combined with

the fact that *Megalograptus* shares several synapomorphies with mixopteroids that are absent from *Eurypteris*, indicates that the rows of acicular scales likely represent a plesiomorphic characteristic for the more derived Eurypterina. This is supported by some other eurypterine species, such as the adelophthalmoid *Adelophthalmus sievertsi*, also having similar rows of scales across the posterior margins of the tergites.

## 6. Phylogenetic analysis of basal Eurypterina

Analysing the matrix as detailed above yielded two most parsimonious trees with a tree length of 229, an ensemble Consistency Index of 0.498, Retention Index of 0.782, and Rescaled Consistency Index of 0.389, the strict consensus of which is presented here (Fig. 5). The two most parsimonious trees differ solely in the internal topology of the mixopteroid clade, with one tree having *Carcinosoma* Claypole, 1890b as sister taxon to *Megalograptus* and *Mixopterus* Ruedemann, 1921a and the other with *Megalograptus* sister to *Mixopterus* and *Carcinosoma*. The polytomy of *Eurypteris* species is present in both trees.

Eurypterids are resolved as a monophyletic clade with Chasmataspidida forming their monophyletic sister-group. Chasmataspidid



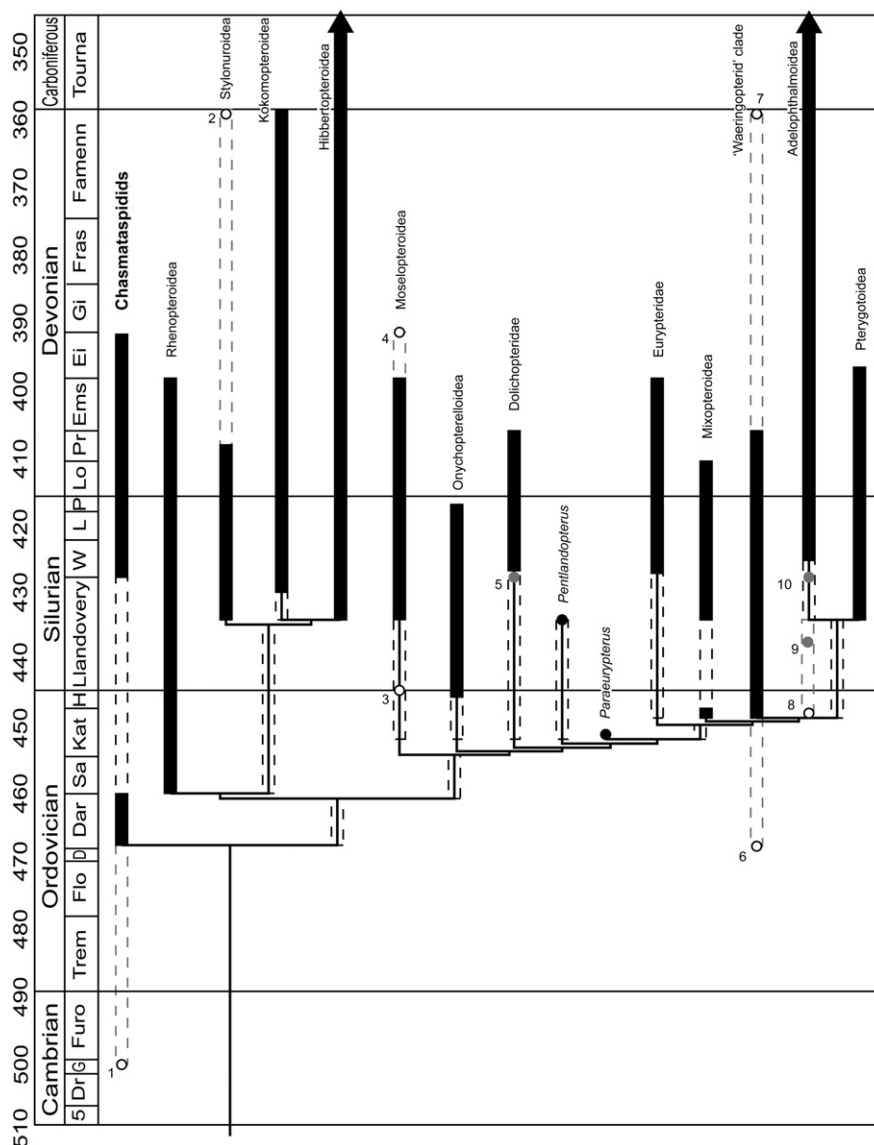
**Fig. 5.** Strict consensus of phylogenetic analysis consisting of 81 characters coded for 45 taxa, resulting in two most parsimonious trees of 229 steps each. The numbers above the branches are Bremer support values while those beneath each branch are jackknife support values after 100,000 repetitions with 25% deletion. *Paraerypteris anatoliensis* is highlighted in bold.



monophyly is, in itself, a noteworthy result as they have previously been suggested not to represent a natural group (Tetlie and Braddy, 2004). However, in order to test this fully, all the chasmataspid species should ideally be included in the analysis with synziphosurines and xiphosurids as in-group taxa to test whether *Chasmataspis* Caster and Brooks, 1956 has closer affinities to xiphosurans. Eurypterida is split into two broad clades: Stylonurina and Eurypterina. Although only a few Stylonurina were included in the analysis, their monophyly was also retrieved in more comprehensive studies of their relationships by Lamsdell et al. (2010a, 2010b). This is the first time that representatives of every major eurypterine clade have been included in a published analysis, and it is interesting to compare the topology with the composite tree presented by Tetlie (2007a). Tetlie's composite tree was compiled using the internal topologies of clades retrieved by Tetlie and Cuggy (2007), Tetlie and Poschmann (2008), and Braddy et al. (2008), with the relationships between the major clades inferred

based on Tetlie's unpublished PhD thesis. The topology retrieved in this analysis broadly correlates with that presented by Tetlie (2007a), with Mixopteroida as sister-group to a large clade consisting of Pterygtoidea, Adelophthalmoidea and the waeringopterid clade, within which waeringopterids are sister-group to Adelophthalmoidea and Pterygtoidea. The analysis differs, however, in the treatment of the basal Eurypterina, including the eurypteroids.

The data for the phylogeny of the basal Eurypterina in Tetlie's (2007a) tree predominantly comes from the analysis of Tetlie and Cuggy (2007) which united Dolichopteridae and Eurypteridae as a monophyletic clade, sister-group to the newly named Diploperculata, with *Moselopter* Størmer, 1974 and *Onychopterella* forming a paraphyletic stem-lineage. The genus *Onychopterella* was resolved as paraphyletic and '*Eurypterus*' minor was shown to be phylogenetically separate from *Eurypterus sensu stricto*. *Megalograptus* was excluded from the analysis, however, and in the strict consensus of the eight



**Fig. 6.** Composite tree showing the relationships of the major eurypterid clades derived from this analysis and that of Lamsdell et al. (2010a, 2010b) with the inferred chasmataspid sister-group. Solid black bars indicate known ranges, while the black dashed bars show ghost ranges. Grey dashed bars are potential range extensions suggested by fossils in need of further study. The circles indicate single species occurrences; where these are solid grey the taxonomic assignment is certain but the dating is uncertain, while hollow black circles are species that have a confirmed date but are of uncertain taxonomic assignment. Solid black are of definite age and taxonomic assignment. These single species are as follows: 1, Chasmataspid-like trace fossil (Dunlop et al., 2004); 2, *Stylonurella* (?) *becheri* (Hall, 1884), which is probably a *Ctenopterus* Clarke and Ruedemann, 1912; 3, *Onychopterella* (?) *pumilus* (Savage, 1916), which is probably a *Stoermeropterus* Lamsdell, 2011; 4, *Moselopter* *lancmani* (Delle, 1937); 5, *Dolichopterus* *gotlandicus* Kjellesvig-Waering, 1979; 6, Undescribed 'waeringopterid' from the St. Peter Formation (Liu et al., 2006); 7, *Grossopterus* *inexpectans* (Ruedemann, 1921b); 8, 'Hughmilleriid' bearing resemblance to *Eysyslopterus* Tetlie and Poschmann, 2008 from the Manitoba formations (Young et al., 2007 Fig. 4f); 9, *Parahughmilleria* *maria* (Clarke, 1907); 10, *Nanahughmilleria* *clarkei* Kjellesvig-Waering, 1964b.

most parsimonious trees, the dolichopterid clade broke down into a number of smaller clades that formed a polytomy with Eurypteridae. Lamsdell et al. (2010a) later added *Vinetopterus* Poschmann and Tetlie, 2004 and '*Drepanopterus*' *bembycoides* Laurie, 1899 to the matrix, resulting in them forming a clade with *Moselopterus* to which they assigned the name Moselopteridae.

Tetlie's (2007a) tree differs in placing *Megalograptus* above *Onychopterella* in the eurypterine stem-lineage and '*Eurypterus*' *minor* well within the dolichopterid clade. The position of *Megalograptus* is based on a single character, the lack of a modified distal margin of the sixth podomere of the swimming leg, but has never been recovered in a phylogenetic analysis. Lamsdell (2011) conducted a more restricted analysis of the basal Eurypterina and retrieved a topology that differed in three ways: *Onychopterella* monophyletic; *Megalograptus* forming a clade with *Mixopterus* rather than the more basal taxa; and eurypteroids paraphyletic, with Eurypteridae phylogenetically closer to Diploperculata than Dolichopteridae. The current analysis supports these results, even with a more inclusive sampling of the dolichopterid and eurypterid clades. Dolichopteridae is shown to be monophyletic and composed of two clades: one comprising *Buffalopterus* Kjellesvig-Waering and Heubusch, 1962, *Strobilopterus* and *Syntomopterella* Tetlie, 2007b, the other *Dolichopterus* Hall, 1859, *Ruedemannipterus* Kjellesvig-Waering, 1966 and *Clarkeipterus* Kjellesvig-Waering, 1966. *Clarkeipterus* has been suggested to be a dolichopterid before (Tetlie et al., 2007b) however this is the first time the genus has been given phylogenetic treatment. '*Eurypterus*' *minor* is again distinct from *Eurypterus sensu stricto* but neither is it a dolichopterid, instead resolving as a transitional form between the two clades and elevated to the new genus *Pentlandopterus*. *Paraerypterus anatoliensis* is also a transitional form, appearing morphologically closer to Eurypteridae but still separated from the clade due to its possession of crescentic lateral eyes with enlarged palpebral lobes and the lack of scales on the carapace. Neither of these two species are assigned to any taxon higher than the level of genus; instead, they are considered members of a grade incorporating the basal members of the Eurypterina of which the Dolichopteridae and Eurypteridae represent radiations of offshoots from the main lineage.

## 7. Implications for the Ordovician record of eurypterids

Since Tollerton (2004) recognized that the majority of Ordovician eurypterids from New York State (accounting for approximately 75% of Ordovician eurypterid diversity at the time) were either pseudofossils or, in one case, a phyllocarid carapace, Ordovician eurypterids have been considered rare, with the majority of family-level clades originating in the early Silurian. The recent discovery of as yet undescribed eurypterids from the late Ordovician Manitoba biotas (Young et al., 2007) and the Middle Ordovician St Peter Formation in Iowa (Liu et al., 2006) suggests, however, that Ordovician eurypterids are not as rare as has been assumed, and the discovery of *Paraerypterus* serves to strengthen this possibility. Furthermore, by combining the deeper-level relationships of eurypterine clades retrieved here with those of Stylonurina recovered by Lamsdell et al. (2010a, 2010b), it is possible to estimate ghost ranges of the superfamily-level clades, each of which represent a major species diversification within Euryptera. Ghost ranges are simply the inferred ranges of clades in time based on sister-group comparison where the sister taxa do not have the same observed temporal point of origination (see Wills, 1999 Fig. 1) given a cladogenetic mode of speciation. Furthermore, if the range of the sister taxon to the initial pair temporally predates this ghost range, then a ghost range for their ancestor is inferred. Ghost range inference can drastically affect estimations of speciation rates (Pachut and Anstey, 2007), lineage survival across mass extinctions (Davis et al., 2010), and the nature of lineage diversification (Davis et al., 2011) and so can have a major impact on our understanding

of the evolution of a group and responses to global climatic and tectonic changes. One key condition for inferring ghost ranges is that the sister taxa compared are both monophyletic, something of particular concern at taxonomic levels higher than species. Monophyly of the eurypterid superfamilies is generally well supported; exceptions are the eurypteroids, dealt with herein, and uncertainty over the position of *Megalograptus*. For the purposes of ghost range inference, *Megalograptus* has been considered to be a mixopteroid, probably in a basal position; however, one of the strongest characters uniting *Megalograptus* with the mixopteroids, the enlarged spines on appendage III, show some differences in structure that may suggest that they are convergent. Further study of *Megalograptus* is needed; however, even if it is eventually shown to be distinct from Mixopteroidea and has closer affinities to Eurypteridae this will have little effect on the ghost ranges inferred under the present topology.

After inferring the relationships of the major eurypterid clades, and comparing their temporal ranges (Fig. 6), it is apparent that the majority have extensive ghost ranges. The majority of these stem from the triploperculate Eurypterina such as moselopterids and dolichopterids. The ages of *Paraerypterus*, *Megalograptus* and *Orcanopterus* suggest that major cladogenesis of eurypterine groups occurred before the Silurian period, during the Katian at the latest. The longest ghost ranges, however, are jointly those of Dolichopteridae and the inferred stylonurine ancestor of the stylonuroid/kokomopteroid/hibbertopteroid clade, each extending for approximately 25 million years, while the ghost range for Eurypteridae extends some 22 million years. If, indeed, chasmataspidids are monophyletic and sister group to Euryptera, then the entire order has a ghost range of 7 million years given the estimated age of *Chasmataspis* (Dunlop et al., 2004). However, if the Cambrian resting trace is indeed assignable to a *Chasmataspis*-like creature, as suggested by Dunlop et al. (2004), then this ghost range would be extended by a further 33 million years. Alternatively, the trace maker could represent a form ancestral to both chasmataspidids and eurypterids; potential support for this stems from the possible identification of a metastoma-like plate on one of the traces, the apparent lack of a genital appendage, and most clearly the possession of six unfused opercula. Where opercula have been identified in chasmataspidids they have only been recognized on the three buckler segments (Dunlop, 2002; Tetlie and Braddy, 2004), while having six unfused opercula is the plesiomorphic condition found in xiphosurids. Another potential ghost range extension would be required if some of the eurypterids from the St Peter Formation are related to *Orcanopterus*, as suggested by Liu et al. (2006), resulting in a further inferred gap of 20 million years for all of the triploperculate Eurypterina. Even without this further extension, it is clear that the majority of eurypterid clades must have existed prior to the late Ordovician extinction pulses during the Hirnantian (Brenchley et al., 2001) and were, therefore, either largely unaffected by the mass extinction events or were able to rapidly diversify in their aftermath.

Despite the recognition that eurypterids were able to persist through the end-Ordovician mass extinction, with few long-term detrimental effects, it is still unclear where the clade originated geographically, and to what degree their range included Gondwana prior to its collision with Laurussia during the late Devonian and Carboniferous. Tetlie (2007a) considered eurypterids to have originated in Laurentia, with Gondwanan occurrences being the result of isolated transoceanic dispersal, something generally limited to pterygotoids and some mixopteroids. Lamsdell (2011) proposed a method by which the population of *Onychopterella augusti* – which was not likely to have been a strong swimmer – could have become established in what is now South Africa by traversing the sea floor during periods of sea level lowstand during the Sandbian or Hirnantian (Saltzman and Young, 2005). *Paraerypterus*, phylogenetically bracketed by dolichopterids and Eurypteridae, was also unlikely to have been a good swimmer and may have crossed to Gondwana during the Sandbian lowstand. It is also

possible that the opposite occurred: periods of lowstand allowed Gondwanan eurypterids to cross into Laurentia and then undergo an explosive radiation. Currently, the earliest known eurypterid is a stylonurine from the Sandbian of Avalonia, which was at the time located southwards of Laurentia, and this may, in fact, represent an early stylonurine colonist from Gondwana. This would explain the dearth of Ordovician eurypterids in the well-sampled regions of Europe and North America, and would also go some way to explaining why so many of the earliest encountered species are relatively advanced swimming forms – these would have had a greater dispersal ability than the basal walking forms and so could conceivably appear first in the Laurentian and Baltic fossil record if the group did indeed have its origin in Gondwana. In this scenario, it should still be no surprise that eurypterids are rare in Gondwanan provinces; being a single large continent Gondwana had comparatively less of the shallow marine environments that eurypterids tend to favour, meaning that populations would likely have been smaller and had a more restricted range. Colonizing the shallow seas and island coastlines of Laurentia and Baltica would have led to a period of explosive radiation, resulting in the relatively sudden appearance of multiple clades in the European and North American fossil record. The fact that the only eurypterids known from the Silurian and Devonian of Gondwana are able swimmers suggests the possibility that the Late Ordovician mass extinction did, indeed, impact the eurypterids, causing them to go extinct on Gondwana while the Laurentian species were relatively unaffected, with subsequent Gondwanan records representing re-colonization by good dispersers.

The concept that there is an unsampled, early record of chelicerates in Gondwana has been mooted previously by Anderson (1996) who suggested that the sudden appearance of weinberginid synziphosurines during the early Devonian, which retain an extreme number of plesiomorphic morphological features, was due to their radiation from a Gondwanan refuge. The discovery of synziphosurines and xiphosurids (which together probably are not a monophylum – see Lamsdell, 2011) from the Tremadocian and Floian Lower and Upper Fezouata Formations of Morocco (Van Roy et al., 2010) shows that these groups certainly had a Gondwanan presence early in their evolution and their dispersal may have followed a pattern similar to that proposed here for eurypterids. Eurypterids and xiphosurans often co-occur throughout the Palaeozoic and eurypterids were probably also present in the Fezouata Formations (Van Roy, pers. comm.); if this is the case it would further strengthen the possibility that the group had a Gondwanan origin.

## 8. Conclusions

*Paraeurypterus anatoliensis* gen. et sp. nov., described from a single specimen, is the tenth eurypterid species known from Ordovician strata and is only the second of that age from Gondwana. Morphologically it appears intermediate between the eurypteroid families Dolichopteridae and Eurypteridae, possessing the plesiomorphic conditions of crescentic eyes with enlarged palpebral lobes and a quadrate carapace with ornamentation consisting of small pustules but also displaying the derived characteristics of genal facets and a row of large acicular scales across the posterior of each tergite. These two last characters are therefore plesiomorphic for both *Eurypterus* and *Megalograptus*, an important recognition as they have previously been used to suggest a sister-group relationship between the two taxa. The eurypterine nature of *Paraeurypterus* is further supported by prosomal appendage VI having a fourth podomere that is longer than the fifth and appears to expand distally into a swimming paddle, while a megalograptid affinity can be ruled out because appendage IV is unspecialized, with only a single pair of spines on each podomere. The new species most closely resembles *Pentlandopterus minor*, differing only in size and the possession of the acicular opisthosomal scales.

Phylogenetic analysis incorporating representatives of each of the major eurypterine clades and all triploperculate Eurypterina

retrieves a topology similar to that of Tetlie (2007a), with a few differences: *Onychopterella* is retrieved as a monophyletic genus and *Megalograptus* is considered to be part of the mixopteroid clade rather than resolving among the more basal Eurypterina while eurypteroids are shown not to be a natural group but that Dolichopteridae and Eurypteridae are part of a grade leading to diploperculate Eurypterina with *Pentlandopterus* and *Paraeurypterus* being intermediate taxa between the two families. Combining this revised topology of eurypterine relationships with that of Stylonurina retrieved by Lamsdell et al. (2010a, 2010b) permits calculation of ghost ranges for each of the major clades of Eurypterida and reveals that the majority of eurypterid superfamilies must have originated by the Katian. The occurrence of *Onychopterella* and *Paraeurypterus* in the Ordovician of Gondwana is puzzling as neither genus was likely to have had a spectacular dispersal ability, however it is possible that they colonized the continent during periods of sea level lowstand in the Sandbian and Hirnantian. One problem with this interpretation is the implication of a large undocumented record of Ordovician eurypterids in the well-sampled regions of North America and Europe. An alternative scenario is proposed whereby eurypterids originated in Gondwana and radiated out to Laurentia and Baltica in the late Ordovician and early Silurian, explaining their sudden appearance in the European and North American rock record and shifting the Ordovician record to the historically understudied Gondwanan continents. It is likely that further study of Gondwanan Ordovician Fossil-Lagerstätten such as the Fezouata formations will reveal more eurypterid species.

## Acknowledgments

We thank Sam Cui (New York), Peter Van Roy (Ghent University) and Erik Tetlie (Norway) for discussion on the specimen and its possible affinities, Alicia Rosales (University of Kansas) for looking at the potential burrows, and Curtis Congreve (University of Kansas) for general discussion. Wes Gapp (University of Kansas) assisted with the search for some of the more obscure trilobite literature. Úna Farrell (University of Kansas) provided invaluable assistance with interpretation of Turkish antique laws and advice on accessioning the specimen. Peter Van Roy provided valuable suggestions and comments during review that greatly improved the manuscript.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.gr.2012.04.006>.

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