

A redescription of the Late Carboniferous eurypterids *Adelophthalmus granosus* von Meyer, 1853 and *A. zadrαι* Přibyl, 1952

O. Erik Tetlie^{*,1,2} & Jason A. Dunlop^{** ,3}

¹ Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, UK

² Current address: Department of Geology & Geophysics, Yale University, P.O. Box 208109, New Haven, CT 06520-8109, USA

³ Museum für Naturkunde der Humboldt-Universität zu Berlin, Institut für Systematische Zoologie, Invalidenstraße 43, D-10115 Berlin, Germany

Received 15 November 2004, accepted 23 March 2005

Published online 02. 11. 2005

With 3 figures and 1 table

Key words: Carboniferous, Germany, Czech Republic, systematics.

Abstract

The earliest named, and type species, of the Middle Devonian–Middle Permian eurypterid genus *Adelophthalmus*, the monotypic, Late Carboniferous *A. granosus* von Meyer, 1853, is redescribed as a first step towards resolving the number of species and phylogenetic relationships within the adelophthalmid clade. A second Late Carboniferous monotypic species, *A. zadrαι* Přibyl, 1952, is also redescribed, since the part of the holotype was discovered in the Berlin collection under an erroneous manuscript name. The two species are different, but can only be separated using characters whose validity and stability must be tested against a wider spectrum of taxa. A list of described adelophthalmids is presented together with an overview of the synonyms previously suggested, with discussions of the validity of at least some of the species currently synonymised.

Schlüsselwörter: Karbon, Deutschland, Tschechien, Systematik.

Zusammenfassung

Der historisch früheste Nachweis von der vom Devon bis zum Perm überlieferten Eurypteriden-Gattung *Adelophthalmus*, die monotypische Typus-Art *A. granosus* von Meyer, 1853, wird revidiert. Es ist dies ein erster Schritt, um die Anzahl der Arten und die phylogenetischen Verhältnisse innerhalb des Adelophthalmiden-Clades zu klären. Eine zweite monotypische Art, *A. zadrαι* Přibyl, 1952, wird ebenfalls neu beschrieben, nachdem ein Teil des Holotypus in der Berliner Sammlung unter einem fehlerhaften Manuskript-Namen wieder aufgefunden wurde. Beide Arten lassen sich derzeit nur durch Merkmale unterscheiden, deren Gültigkeit erst noch vor dem Hintergrund eines weiteren Spektrum von Taxa überprüft werden muss. Die bisher beschriebenen Adelophthalmiden, einschließlich bisherige vorgeschlagenen Synonyme, werden aufgelistet; die Gültigkeit wenigstens einiger dieser Synonyme wird diskutiert.

© 2005 WILEY-VCH Verlag GmbH & Co. KGaA, Weinheim

Introduction

Eurypterids are a diverse group of Palaeozoic chelicerates known from the Middle Ordovician to the Late Permian, occurring most frequently

in Silurian – Early Devonian strata from Europe and North America. After the Devonian, eurypterids as a group become rarer and appear to have migrated, or been driven, from their earlier marginal marine environments into more brack-

* Corresponding author: e-mail: erik.tetlie@yale.edu

** E-mail: jason.dunlop@museum.hu-berlin.de

ish and freshwater ones (Přibyl 1952), the Carboniferous Coal Measures being a typical example. Although also known from Devonian rocks (Table 1), adelophthalmids constitute most of the post-Devonian eurypterids, both in terms of the number of described species and the number of specimens, and are one of only three eurypterid clades to survive into the Carboniferous; the others being the gigantic, bizarre-looking hibbertopterids (*Hibbertopterus*, *Cyrtoctenus*, *Campylocephalus*, *Hastimima*, *Dunsotterus*, *Vernonopterus* and now *Megarachne*; see Selden et al. 2005) and the enigmatic woodwardopterids (*Woodwardopterus* and *Mycterops*).

Adelophthalmids (Fig. 1) are small, streamlined, swimming eurypterids with prominent scaly ornamentation. They have previously been referred to six genera: *Adelophthalmus* von Meyer, 1853, *Lepidoderma* Reuss, 1855, *Anthraconectes* Meek & Worthen, 1868, *Polyzosterites* Goldenberg, 1873, *Glyptoscorpius* Peach, 1882 and *Unionopterus* Chernyshev, 1948. The last is poorly known, but appears to be distinct, while the other five genera have, at one time or another, been considered synonyms (see Systematics). It is clear that the oldest name, *Adelophthalmus*, has priority. In this respect, *Adelophthalmus granosus* von Meyer, 1853 is very important as the oldest available name for any adelophthalmid species and a potential senior synonym of some of the less convincing taxa; at least some of which have been assigned to *A. imhofi* (Reuss, 1855) (Table 1). *A. granosus* is redescribed here from the holotype in the Museum für Naturkunde (MfN) Berlin as a first step towards resolving the complex systematics of the *Adelophthalmus* species assemblage. During this work we also discovered the mislabelled part of the holotype of the Czech species, *A. zadrai* Přibyl, 1952 in Berlin. We take the opportunity to redescribe this fossil here too, and discuss its affinities in comparison to *A. granosus*.

Material

The holotype, and only known specimen, of *Adelophthalmus granosus* is held in the arthropod palaeontology collections of the MfN under the repository number MB.A. 890. The counterpart was not described by Jordan & von Meyer (1854) and is presumably lost. The *A. granosus* specimen is preserved in a grey siltstone and, according to the original description, was found between layers of coal of Westphalian C (= Moscovian) age. It retains much of its original convexity. Several patches on the carapace and mesosomal segments of the fossil are pyritised. A further specimen, MB.A. 889, preserved flattened in a lignified coal, is labelled with what appears to be an unpublished manuscript name. It was not

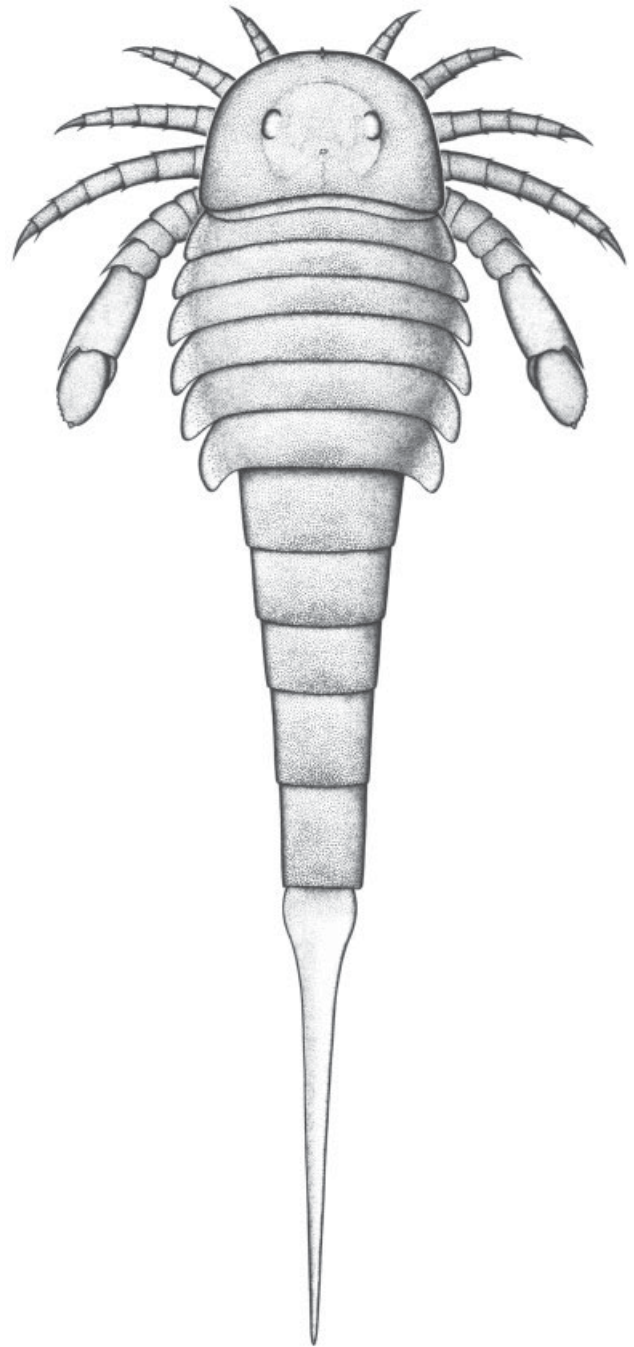


Fig. 1. Morphology of a generalised adelophthalmid eurypterid, but with proportions and ornament derived from *Adelophthalmus granosus* von Meyer, 1853 to form a plausible reconstruction of this species. Note the following diagnostic features for the genus: (a) the triangular, hinged 'double lock' anteriorly on carapace, (b) the circular, raised area containing the lateral eyes and ocelli, (c) the coarse, granular ornament, (d) the short and laterally tapering first opisthosomal segment and (e) the elongate telson. Adapted mainly from Van Oyen (1956). Total length of animal in life c. 15 cm.

labelled as a type, but comparison with published descriptions revealed that it is actually the part of the holotype of *Adelophthalmus zadrai* Přibyl, 1952 (see Systematics) of Westphalian A (= Bashkirian) age.

Both specimens were whitened with ammonium chloride and photographed with a Nikon 4500 Coolpix camera,

(Figs 2A–B). Both were drawn with the help of a *camera lucida* (Figs 3A–B). General eurypterid terminology follows Tollerton (1989), but specific terminology for adelophthalmids is introduced, mainly following, and translated from, Van Oyen (1956).

Systematic palaeontology

Order **Eurypterida** Burmeister, 1843
Family **Adelophthalmidae** Tollerton, 1989

Type genus *Adelophthalmus* von Meyer, 1853

Remarks: Tollerton (1989) raised this family for *Parahughmilleria*, *Bassipterus*, *Adelophthalmus* and *Unionopterus*, based on the presence of *Adelophthalmus*-type spiniferous (II–V) and swimming appendages (VI) respectively.

Genus ***Adelophthalmus*** von Meyer, 1853

Type species: *Adelophthalmus granosus* von Meyer, 1853.

Additional species: See Table 1.

Emended diagnosis: Medium-sized, streamlined eurypterids; carapace parabolic with narrow marginal rim and small, hinged triangular ‘locking’ mechanism anteriorly; intermarginal eyes reniform; ocelli between or slightly behind lateral eyes; prosomal appendages II–V *Adelophthalmus*-type; VI swimming leg of *Adelophthalmus*-type; metastoma oval; first opisthosomal segment of reduced length and tapering in length laterally; midsection (and usually anterior and posterior) second order opisthosomal differentiation; genital operculum with spatulae; telson long and styliform; dense ornament of minute scales (emended from Størmer 1973).

Remarks: Most authors have considered Jordan & von Meyer (1854) as the correct authors of *Adelophthalmus*. The title page of the relevant issue of *Palaeontographica* bears the publication date 1856, but the contents page clearly lists the “erste Lieferung” containing their paper as January 1854. Here they named their fossil (p. 8) “*Adelophthalmus (Eurypterus) granosus* Jord.”, leading some authors (e.g. Clarke & Ruedemann 1912; Brauckmann 1991; Brauckmann et al. 2003) to accept Jordan (1854) alone as the correct author and date. However, the name was

Table 1

Chronological list showing the described species thought to belong to *Adelophthalmus* by Kjellesvig-Waering (1948), Van Oyen (1956), Plotnick (1983), Poschmann (in press) and this study, and the epoch(s) when found. Westphalian refers here to Bashkirian or Moscovian (not specified). The *Rhenopterus* records included in this list appear to be Devonian age adelophthalmids. This will be addressed in detail in forthcoming papers and they are included here for completeness.

Species	Author(s)	Status according to Van Oyen (1956)	Age (ICS stage where known)
<i>Adelophthalmus granosus</i>	von Meyer, 1853	Valid	Moscovian
<i>Lepidoderma imhofi</i>	Reuss, 1855	Valid	Gzhelian or Asselian
<i>Anthraconectes mazonensis</i>	Meek & Worthen, 1868	= <i>A. imhofi</i>	Moscovian
<i>Eurypterus mansfieldi</i>	C. E. Hall, 1877	= <i>A. imhofi</i>	Westphalian
<i>Eurypterus pennsylvanicus</i>	C. E. Hall, 1877	Valid	Westphalian
<i>Glyptoscorpium perornatus</i>	Peach, 1882	Not considered	Viséan
<i>Eurypterus stylus</i>	J. Hall, 1884	Subspecies of <i>A. imhofi</i>	Westphalian
<i>Eurypterus approximatus</i>	J. Hall & Clarke, 1888	Valid	Famennian?
<i>Eurypterus wilsoni</i>	Woodward, 1888	= <i>A. imhofi</i>	Moscovian?
<i>Glyptoscorpium kidstoni</i>	Peach, 1888	= <i>A. imhofi</i>	Moscovian?
<i>Eurypterus douvillei</i>	De Lima, 1890	Valid	Asselian?
<i>Eurypterus moyseyi</i>	Woodward, 1907	= <i>A. imhofi</i>	Bashkirian
<i>Eurypterus derbiensis</i>	Woodward, 1907	Valid	Bashkirian
<i>Anthraconectes nebraskensis</i>	Barbour, 1914	Valid	Sakmarian?
<i>Eurypterus dumonti</i>	Stainier, 1915	= <i>A. derbiensis</i>	Westphalian
<i>Anthraconectes chinensis</i>	Grabau, 1920	Valid	Asselian?
<i>Eurypterus brasidorensis</i>	Bell, 1922	= <i>A. imhofi</i>	Moscovian
<i>Anthraconectes sellardsi</i>	Dunbar, 1924	= <i>A. imhofi</i>	Artinskian?
<i>Anthraconectes cambieri</i>	Pruvost, 1930	= <i>A. imhofi stylus</i>	Bashkirian
<i>Adelophthalmus carbonarius</i>	Chernyshev, 1933	= <i>A. imhofi</i>	‘Middle’ Carboniferous
<i>Eurypterus raniceps</i>	Waterlot, 1934	Not considered	Moscovian
<i>Eurypterus “de Houthaalen”</i>	Stainier, 1935	= <i>A. imhofi</i>	Bashkirian
<i>Eurypterus “d’Havre”</i>	Stainier, 1935	= <i>A. imhofi</i>	Moscovian
<i>Anthraconectes corneti</i>	Pruvost, 1939	= <i>A. imhofi</i>	Bashkirian
<i>Lepidoderma pruvosti</i>	Kjellesvig-Waering, 1948	= <i>A. imhofi</i>	Westphalian
<i>Unionopterus anastasiae</i>	Chernyshev, 1948	Not considered	Early Carboniferous
<i>Adelophthalmus zadrai</i>	Přibyl, 1952	Subspecies of <i>A. imhofi</i>	Bashkirian
<i>Adelophthalmus ‘d’Espagne’</i>	Van Oyen, 1956	Valid	Bashkirian
<i>Rhenopterus sievertsi</i>	Størmer, 1969	post 1956	Emsian
<i>Lepidoderma asturica</i>	Melendez, 1971	post 1956	Westphalian
<i>Eurypterus (?) trapezoides</i>	Størmer, 1974	post 1956	Emsian
<i>Adelophthalmus luceroensis</i>	Kues & Kietzke, 1981	post 1956	Gzhelian or Asselian
<i>Eurypterus</i> sp.	Mamay & Bateman, 1991	post 1956	Artinskian
<i>Rhenopterus</i> ? sp.	Manning & Dunlop, 1995	post 1956	Early Carboniferous
<i>Rhenopterus waterstoni</i>	Tetlie et al., 2004	post 1956	Frasnian

first introduced by von Meyer (1853, p. 161), who wrote “Die ubrigen Kruster der Saarbrücken Steinkohlen-Formation bestehen in 3 neuen Genera, einem fast vollständigen blinden *Eurypterus*, *Adelophthalmus* (*Eurypterus*) [*sic*] *granosus* genannt ...”. While there is clearly a case for regarding this as a *nomen nudum*, the reference to blindness could be treated as a diagnostic character, especially since absence of eyes is directly reflected in the choice of genus name: *Adelophthalmus*. This admittedly brief and unsatisfactory description would nevertheless qualify as an indication under ICZN rules (C. Brauckmann, pers. comm., 2005). A similar situation exists for the giant fossil millipede *Arthropleura* von Meyer, 1853. It was also mentioned in the same paper – again with a vague differential diagnosis – leading Kraus & Brauckmann (2003) to accept von Meyer, 1853 as the correct author and date. Likewise, we treat *Adelophthalmus* (*Eurypterus*) *granosus* von Meyer, 1853 as the oldest available name, but accept that this is a borderline situation.

The priority of *Adelophthalmus* over its later synonyms was reviewed by, among others, Přibyl (1952). In summary, the main problem stems from the fact that *Adelophthalmus granosus* lacks eyes – probably a preservational artefact, but nevertheless the basis for the genus name (see above) – while the similar-looking Czech species described shortly afterwards, *Lepidoderma imhofi* Reuss, 1855 has them. Reuss conceded that the two genera were probably synonyms, but ignored the rules of priority and adopted his younger name as the correct form on the grounds that it was based on better-preserved material. *Anthraconectes* was introduced as a subgenus by Meek & Worthen (1868) for a Carboniferous species from Mazon Creek (USA). Guthörl (1934) suggested that it was so similar to *Adelophthalmus* that if the latter had eyes it would almost certainly be considered the senior synonym. *Polyzosterites* was coined by Goldenberg (1873) for Jordan & von Meyer’s fossil in the belief that it was a modern-looking cockroach. This questionable interpretation was accepted uncritically by Kjellesvig-Waering (1948) in his review of the Mazon Creek eurypterids and led him to accept Reuss’s *Lepidoderma* as the correct generic name. Finally, *Glyptoscorpium* was introduced by Peach (1882) for Scottish Carboniferous material. The status of at least some of its species as members of *Lepidoderma* (= *Adelophthalmus*) was discussed by Kjellesvig-Waering (1948, pp. 7–8). Størmer & Waterston (1968, p. 65) considered the type spe-

cies, *Glyptoscorpium perornatus*, to belong to *Adelophthalmus*, while assigning its other species to *Cyrtoctenus*, *Vernonopterus*, *Dunsopterus* (all hibbertopterids) and *Adelophthalmus*.

The poorly known Carboniferous genus *Unionopterus* has rarely been mentioned in the literature. It has not been proposed as a synonym of *Adelophthalmus*, but merits brief consideration here. *Unionopterus anastasiae* Chernyshev, 1948, only known from a single specimen from Kazakhstan, has been neglected due to the poorly known original description (in Russian), the general lack of interest in Carboniferous eurypterids and uncertainty over the whereabouts of the holotype. The very wide marginal rim of the carapace and very small eyes well in front of the ocelli in *U. anastasiae* illustrated by Chernyshev (1948) is not consistent with the morphology of *Adelophthalmus*. We suspect *Unionopterus* is a valid taxon, but one that nevertheless merits redescription. Moreover, there are similarities between the morphology of *U. anastasiae* and *A. dumonti* (Stainier, 1915), and it is likely that the latter – clearly juvenile – specimen should be assigned to *Unionopterus*.

Despite Přibyl’s convincing resolution of the *Adelophthalmus* priority problem, Størmer (1955) in the *Treatise on Invertebrate Paleontology* incorrectly interpreted the publication date as 1856, and consequently treated it as a junior synonym of the 1855 name *Lepidoderma*. In his extensive treatment (see below), Van Oyen (1956) followed Přibyl and regarded *Adelophthalmus* as correct; an opinion now accepted by Kjellesvig-Waering (1958, 1959). However, Wills (1964) noted that scorpions with similar dorsal anatomies can be quite different ventrally and thus preferred to retain *Anthraconectes* for those Carboniferous eurypterids where the ventral morphology was known; the nomenclature thus depending on the preservational state. Other authors (e.g. Owens & Bassett 1976; Brauckmann 1991; Brauckmann et al. 2003) have returned to *Adelophthalmus*. The number of ‘adelophthalmid’ genera and species has yet to be resolved. Provisionally, we follow Přibyl and Van Oyen and assign all species, except *U. anastasiae* and *U. dumonti*, to *Adelophthalmus* pending wider revisions of type material.

***Adelophthalmus granosus* von Meyer, 1853**

Figs 1, 2A, 3A

1853 *Adelophthalmus* (*Eurypterus*) [*sic*] *granosus* von Meyer: 161.

- 1854 *Adelophthalmus (Eurypterus) granosus*. – Jordan: 8–12, pl. 2, figs 1–2.
 1873 *Polyzosterites granosus*. – Goldenberg: 18, pl. 1, fig. 17.
 1882 *Adelophthalmus granosus*. – v. Ammon: 530.
 1884 *Eurypterus granosus*. – Kliver: 17.
 1912 *Eurypterus (Adelophthalmus) granosus*. – Clarke & Ruedemann: 111.

Transfers only summarised here, see e.g. Guthörl (1934) for a more complete synonymy list.

Holotype (and only specimen): MB.A. 890 – specimen preserving posterior part of carapace and opisthosomal segments 1 to 9, with good preservation of ornament. Collected by Dr. med. H. Jordan, 1851.

Type locality: Railroad cutting at Jägersfreude, three-quarters of a mile from Saarbrücken, Saarland, Germany.

Type horizon: Middle part of the “Saarbrücken’schen Kohlengebirges”. Late Carboniferous: Moscovian (= Westphalian C).

Diagnosis: Broad *Adelophthalmus* with large rounded epimera on mesosoma, and lacking epimera on metasoma; posterior half of epimera with ornament of curved lines laterally; tergites with three distinct zones of ornamentation; anterior fifth of segments with no (or extremely fine) ornament; median fifth with fine ornament (less than 0.1 mm) and posterior three-fifths with larger (0.2 mm) mainly angular scales.

Description: Carapace incomplete anteriorly, 13 mm preserved length and 28.5 mm width. Lateral angle ca 100°. No marginal rim observed. The posterior carapace margin is recurved, and the preserved part of the carapace is covered by small (0.2 mm wide) angular scales. No lateral eyes, ocelli or prosomal appendages preserved.

First opisthosomal segment of reduced length with no preserved ornament. Left posterolateral margin rounded, on right side concealed by carapace. Second segment also with left rounded posterolateral margin. Right margin appears to have large, more or less rounded epimeron. Second segment with ornament on the posterior half medially. Segments three and four essentially similar to two, but slightly longer; segments five and six similar to three and four, but with three distinct zones of ornament. Anterior 1 mm without any ornament followed by 1 mm with very fine ornament (pustules < 0.1 mm). Posterior 2.5–3 mm is covered with small angular scales of same size as on carapace. First segment of the

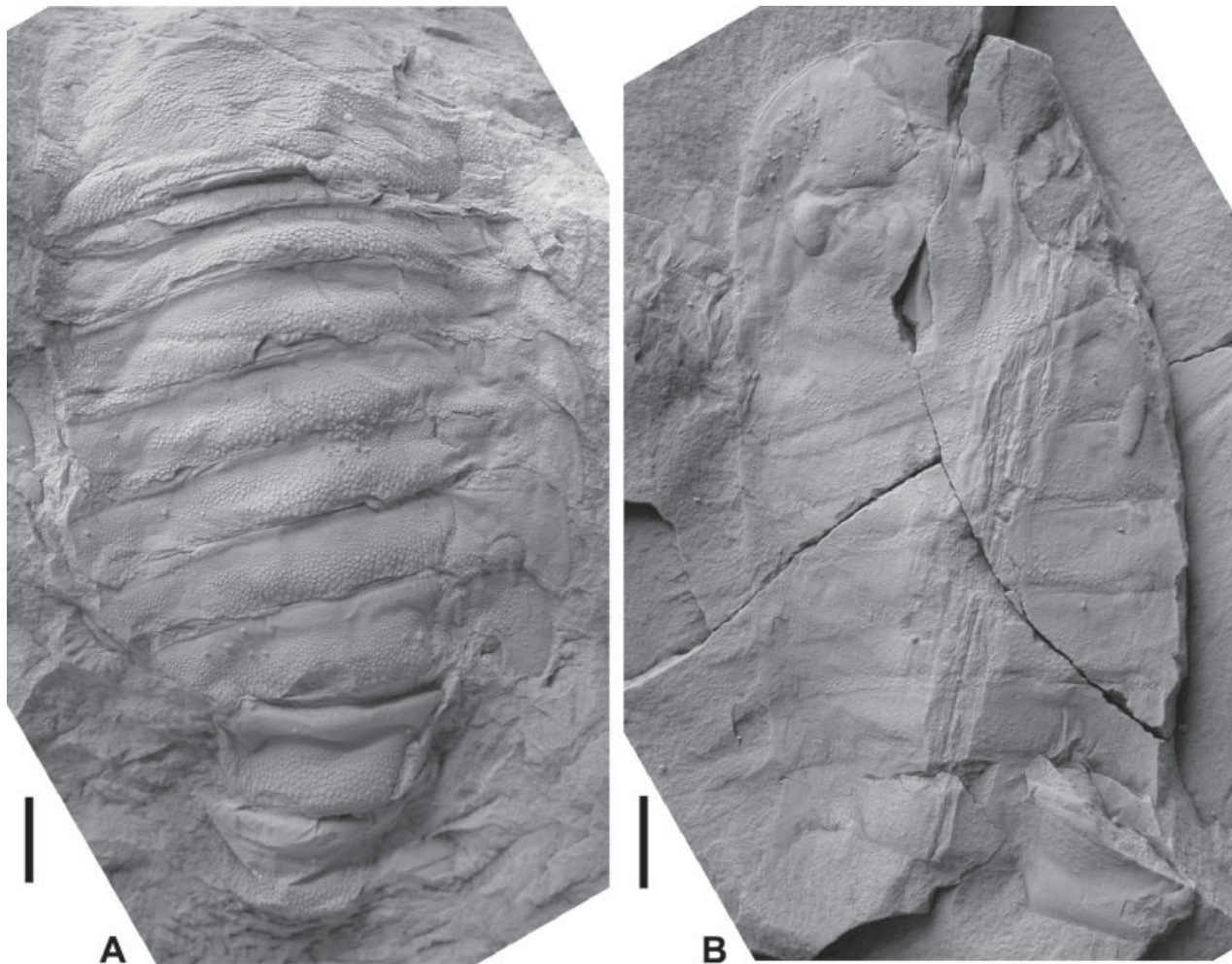


Fig. 2. **A** – Photograph of the part of the holotype and only known specimen of *Adelophthalmus granosus* von Meyer, 1853 (MB.A. 890); **B** – Photograph of the part of the holotype and only known specimen of *Adelophthalmus zadrai* Přibyl, 1952 (MB.A. 889). Scale bars are 5 mm.

metasoma with large epimeron on right side, and similar pattern of ornament as preceding segments. Epimera on segments six and seven with lateral ornament of curved lines perpendicular to lateral margins. Moderate first order differentiation between seventh and eighth segments. Eighth segment tapers and has similar pattern of ornament divided into three distinct zones, each zone a little longer than on preceding segments, but as the segment is longer, the proportions are the same. Ninth segment slightly narrower than eighth, but has same ornament. Eighth and ninth segments lack preserved epimerae.

Length and width measurements (in mm) of carapace and preserved segments (* = incomplete): ca -13.0*, 28.5; 1-2.0, 25.0; 2-3.0, 28.1; 3-4.5, 28.0; 4-4.5, 28.3; 5-4.5, 28.9; 6-4.5, 27.4; 7-6.5, 23.0*; 8-7.5, 12.0*; 9-8.0*, 11.0*.

Remarks: In their drawing, Jordan & von Meyer (1854) illustrated two poorly preserved additional segments (ten and eleven) of the post-abdomen of *A. granosus*. These could not be seen here, and were not figured by Guthörl (1934) or Přibyl (1952). An additional difference between the description provided here and the figure of Jordan & von Meyer is the smaller and less complete segment nine indicated in their illustration. The left side of the mesosoma has probably broken away. The break on the right side (Fig. 3A) is probably due to deformation and not the boundary between the dorsal tergites and ventral Blattfüße. An alternative, but less likely, interpretation is that this break represents the ventral Blattfüße displaced to the right and exposing the large lateral epimera, which are not on the tergites, but on the sternites, as illustrated for *A. nebraskensis* (Barbour, 1914).

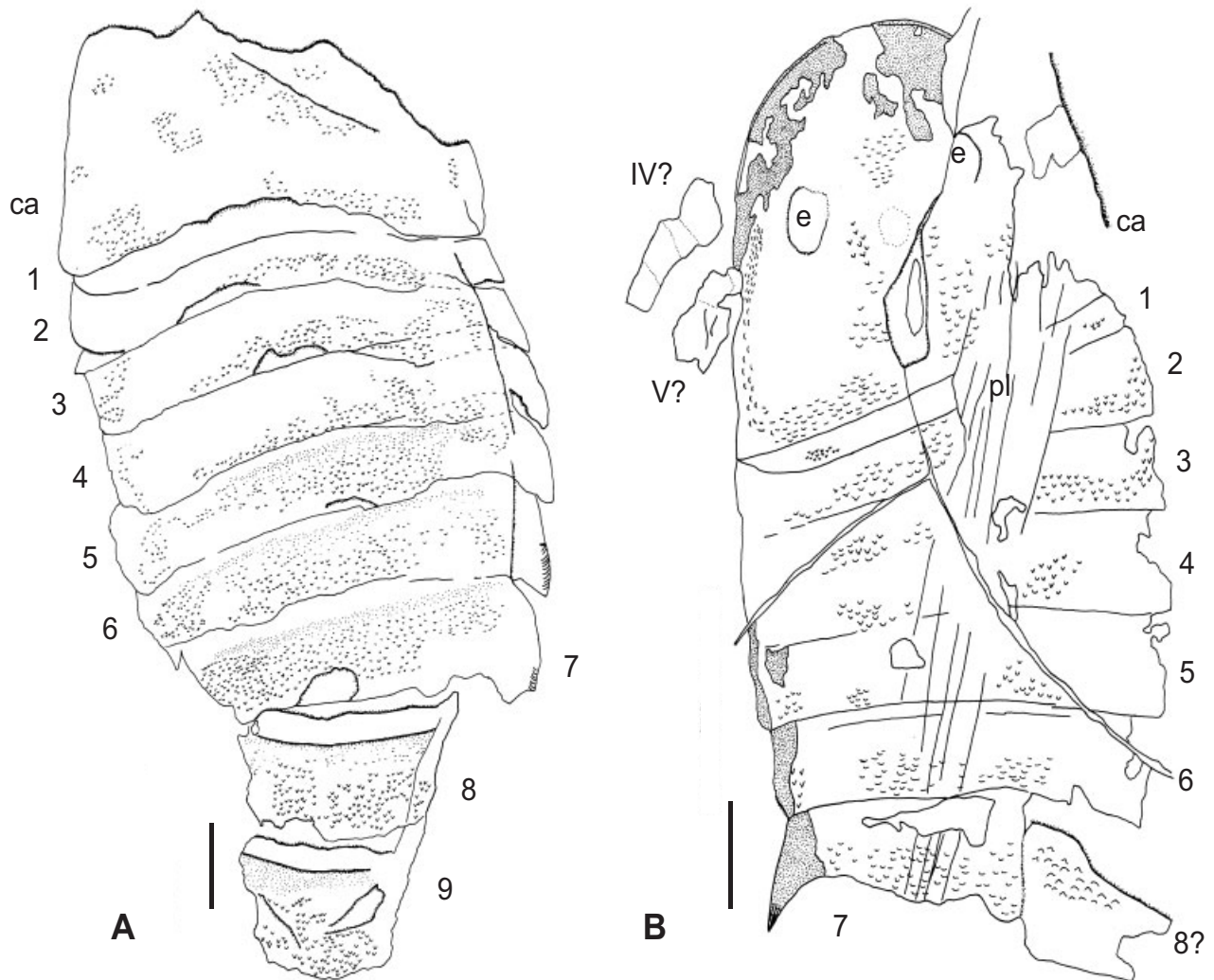


Fig. 3. **A** – *Camera lucida* drawing of the part of the holotype and only known specimen of *Adelophthalmus granosus* von Meyer, 1853 (MB.A. 890); **B** – *Camera lucida* drawing of the part of the holotype and only known specimen of *Adelophthalmus zadrai* Přibyl, 1952 (MB.A. 889). Abbreviations used: **ca** – carapace, **e** – eye, **pl** – plant, **IV–V** – prosomal appendages 4 and 5, **1–9** – opisthosomal segments 1–9. Dark shading on B shows where cuticle is still present. Scale bars are 5 mm.

However, the majority of other adelophthalmids have the tergites developed into epimera and this is our preferred interpretation of *A. granosus*.

Although the specimen lacks appendages and eyes, there can be little doubt that it must be considered diagnostic material, and *A. granosus* considered valid. No other species has ever been considered a junior synonym of *A. granosus*; a view provisionally supported here pending revisions of other type material.

Adelophthalmus zadrαι Přibyl, 1952

Figs 2B, 3B

1932 *Eurypterus* sp., Šusta: 138.

1933 *Eurypterus* (*Anthraconectes*) *Zadrαι* Pruvost: 150 (nomen nudum).

1952 *Adelophthalmus zadrαι* Přibyl: 72–74, pl. 1, figs. 3–4.

1957 *Adelophthalmus zadrαι*. – Schwarzbach: 112.

Holotype (part): MB.A. 889 – specimen preserving carapace (with eyes and ocellar mound), two fragmentary prosomal appendages and opisthosomal segments 1 to 7 (and partly a detached 8), with relatively good preservation of ornament. Counterpart could not be traced. Collected by Dr Palisa, 1930/31.

Type locality: Horní Suchá, Klement Gottwald pit (formerly František Mine), Moravo-Silesia, Czech Republic.

Type horizon: Seam D (= 31st Karviná seam), Karviná beds, Suchá zone. Upper Carboniferous, Bashkirian (= Lower Westphalian A).

Emended diagnosis: Slender *Adelophthalmus* with angular epimera on opisthosomal segment 7, apparently having angular epimera on mesosoma; ornament of large (0.3 mm), rounded and angular scales on posterior half of each mesosomal segment and on parts of carapace; eyes relatively close to carapace margin (emended from Přibyl 1952).

Description: Carapace incomplete on right side, 17.3 mm long and 20.5 mm preserved width. Lateral angle 105°. Very narrow marginal rim (0.2 mm wide) present in front of eyes. Posterior carapace margin straight; carapace covered by larger (0.3 mm wide) scales; angular behind the ocellar mound, and more lunate closer to anterior, lateral and posterior margins. Partial outlines of both eyes seen, but poorly preserved. Ocellar mound preserved between posterior parts of eyes, but no ocelli can be seen. Two fragmentary prosomal appendages preserved on left side; their position suggests they represent appendages IV and V, and appear relatively robust, with no preserved spines.

First opisthosomal segment of reduced length with preserved ornament of small angular scales (0.1 mm); narrowing laterally, almost to the degree where carapace apparently articulates with second segment on left lateral margin. Second to sixth segments all approximately same length and preserved width (see below), with 0.3 mm

wide angular and lunate scales on posterior half. No epimera preserved in mesosoma, but left side of segment six suggest angular epimera similar to those on segment seven were present. First segment of metasoma with large, angular epimeron on left side, and similar pattern of ornament as preceding segments. Possible part of seventh or eighth segment preserved to right of seventh segment. This piece inverted, because scales point anteriorly. Nothing preserved of the more posterior segments (the missing counterpart is more complete; see Přibyl 1952, pl. 1, fig. 4).

Length and width measurements (in mm) of carapace and preserved segments (* = incomplete): ca –17.3, 20.5*; 1–1.5, 20.5*; 2–2.5, 22.1*; 3–3.0, 22.2*; 4–3.5, 22.2*; 5–4.5, 21.2; 6–4.5, 19.3*; 7–5.2*, 12.0*.

Remarks: According to Přibyl (1952), this fossil was collected by Dr. Palisa in 1930 or 1931. After being noted as *Eurypterus* sp. by Šusta (1932), Palisa is reported to have sent the specimen to the French Carboniferous worker Pierre Pruvost. He mentioned it in print (Pruvost 1933) under the name “*Eurypterus* (*Anthraconectes*) *Zadrαι*”, but did not formally describe or figure the fossil here, rendering his name a *nomen nudum* (Přibyl 1952, p. 64, 74). It also seems that someone – bearing in mind the label, probably Pruvost – toyed with an alternative species name based on the collector, Palisa, and the Berlin specimen is labelled with what we now know to be a manuscript name of this form. We do not know how the fossil came to be deposited in Berlin, but for some reason it was not labelled with the correct name “*zadrαι*”, or even noted as a type! Přibyl (1952) formally described the fossil as *Adelophthalmus zadrαι* – thus adopting Pruvost’s species name – but was evasive about the repository of the type material. Přibyl did include (retouched) photographs of both a part and counterpart. From these we can be certain that the Berlin specimen is the figured part (Přibyl 1952, pl. 1, fig. 3) of *A. zadrαι*, since it matches both the overall outline and has a distinctive series of cracks running across the specimen and a plant fragment diagonally overlying the carapace and mesosoma (Figs 2B, 3B). The counterpart (Přibyl 1952, pl. 1, fig. 4) could not be found in Berlin and efforts to trace it in other museums, such as the National Museum Prague, were unsuccessful.

However, the collection information on the Berlin label is slightly confusing and does not match that published by Přibyl. It reads:

“D-Plöz, Franz-Schacht, Suchau, Oberschlesien, Upper Carboniferous. Specimen collected by Patteisky”. Přibyl (1952) gave a slightly different account, i.e. Palisa as the collector, which is the one adopted in the systematics above. Přibyl (1952, p. 74) mentions K. Patteisky as an authority on the coal seams of Silesia.

Discussion

Phylogenetic position: *Adelophthalmus* can be fairly convincingly placed as the sister group (or perhaps even an in-group) of the Silurian – Devonian genus *Parahughmilleria* Kjellesvig-Waering, 1961. Their close relationship is supported by the almost identical carapace shape, paddle shape, eye shape, eye position and walking legs in which some podomeres have a crenulate distal margin, and occasional isolated spines. More explicit putative synapomorphies are the presence of epimera on segment 7 (= midsection second order differentiation; Tollerton 1989) and genital spatulae, although both epimera and spatulae are much larger in *Adelophthalmus*. Autapomorphies for *Adelophthalmus*, (absent in *Parahughmilleria*) appear to include (1) epimera on the pre- and post-abdomen and (2) a triangular, hinged ‘locking’ mechanism anteriorly on the carapace; although the presence of these has not been demonstrated in all species of *Adelophthalmus*. The ornamentation is much coarser in *Adelophthalmus* than in *Parahughmilleria* and the former lacks the ornament of lines parallel to the segment margins found in the latter (see e.g. Størmer 1973). The telson is generally longer in *Adelophthalmus* than in *Parahughmilleria*, but the consistency of this character is equivocal. A final difference between the two genera is in the morphology of the anterior-most opisthosomal segment. This is tapering in length towards the lateral margin in the two species of *Adelophthalmus* described here, and this is not known from any *Parahughmilleria*. The precise phylogenetic position of the poorly known genus *Unionopterus* remains equivocal.

Species diversity: Around thirty named species of adelophthalmids have been described (Table 1), mainly by authors who were not eurypterid specialists. Most eurypterid workers concentrated their efforts on the more numerous and diverse pre-Carboniferous forms. In addition, there are a number of unnamed occurrences. Questions have been raised about the

often trivial differences between proposed adelophthalmid species; differences which may be preservational artefacts resulting in an artificially high species count. Twenty-six of the species were described before 1948, when the first overview paper on the group was published, and diagnoses and comparisons with previous species were usually lacking in these older works.

Van Oyen (1956) suggested synonymising the number of species in *Adelophthalmus* (and its synonyms) down to eleven (Table 1), mainly based on ratios of the carapace. Kjellesvig-Waering (1963, p. 98) defended variety, criticising Van Oyen for not taking into account the morphology of parts other than the carapace (see also comments in Wills 1964) and ignoring taphonomic effects. This is not an attempt to settle this discussion, but Kjellesvig-Waering (1963) had at least one point: it improbable that *A. mansfieldi* with its extremely large post-abdominal epimera is a synonym of *A. imhofi* in which the epimera are much smaller; although Poschmann (in press) has demonstrated the unreliability of absence of postabdominal epimera as they are often broken off during collecting. Tollerton (1989) suggested that the differences in appendage spinosity within *Adelophthalmus* might justify an additional genus, but that this had to be based on further evidence. We offer both the full species list (except previously accepted synonyms, see below) and Van Oyen’s prospective synonymies (Table 1) as a starting point for further revision. The next major question must be to resolve the relationship between *A. granosus* and the second oldest available name, *A. imhofi*; the latter having been proposed as the senior synonym of numerous adelophthalmid taxa.

A. granosus and *A. zadrai*: There are several differences between the two species redescribed in this paper. The lack of finer ornament anteriorly on the segments of *A. zadrai* is probably preservational rather than taxon-specific. However, there are other differences like the presence of epimera on the mesosoma of *A. granosus* and the apparent lack of these in *A. zadrai*, and the epimera on opisthosomal segment 7 are more angular in *A. zadrai* and more rounded in *A. granosus*. It is also obvious that *A. zadrai* has a coarser ornament of lunate scales than *A. granosus*, with more angular scales on the posterior part of the segments, despite the fact that the specimen of *A. zadrai* is smaller than that of *A. granosus*. The body shape is also marginally different. *A. granosus* is proportionally wider than *A. zadrai*, even though *A. granosus* retains

some original relief, while *A. zadrai* has been flattened, suggesting an even bigger difference when the animals were alive. We are confident that these are separate species, but the consistency of these differences has to be evaluated against other taxa when they are formally redescribed.

Previously suggested synonyms and identities: A few described taxa have previously been accepted as synonyms, and *E. oklahomensis* Decker, 1938 is excluded from Table 1. Branson (1959) with support from Decker (who described *A. oklahomensis*) synonymised *A. oklahomensis* with *A. sellardsi* (Dunbar, 1924), from similar stratigraphical horizons in the two neighbouring states of Oklahoma and Kansas respectively.

Other suggested synonyms include *E. stylus* Hall, 1884 and *E. derbiensis* Woodward, 1907. These two are retained in the table, as there are still disagreements over their identity. *E. stylus* Hall, 1884 was synonymised with *A. mansfieldi* by Kjellesvig-Waering (1948; 1963). The species are from the same locality, and Kjellesvig-Waering suggested the differences were preservational. Van Oyen, on the other hand, suggested *A. stylus* was a valid subspecies of *A. imhofi*. Kjellesvig-Waering (1948) also synonymised *E. derbiensis* Woodward, 1907 with *E. moyseyi* Woodward, 1907, but again, Van Oyen did not agree and considered *A. derbiensis* valid and *A. moyseyi* a synonym of *A. imhofi*.

Eurypterus (?) *dewalquei* Fraipont, 1889 was considered by Kjellesvig-Waering (1948) to belong to the adelophthalmids, but we suggest it is probably a *Cyrtoctenus* (an identity also discussed, but ultimately rejected, by Kjellesvig-Waering), based on its large size and the similarity of the ornament and large, articulating spines to those described in hibbertopterids by Waterston et al. (1985). In addition, the species *E. potens* Hall, 1884, was transferred to the genus *Hibbertopterus* by Kjellesvig-Waering (1963; 1966), although Van Oyen considered it a synonym of *Adelophthalmus imhofi*. We feel the size and shape is more consistent with a hibbertopterid than an adelophthalmid. *E. lohesti* Dewalquei (date unknown, but mentioned and figured in Fraipont, 1889) was questionably referred to *Adelophthalmus* by Plotnick (1983), but the morphology of the only known carapace is very wide, the eyes very large and the carapace appears to have a median ridge; none of which is consistent with *Adelophthalmus*. These three dubious taxa are excluded from Table 1.

Acknowledgements

We thank Christian Neumann (MfN, Berlin) for access to the fossils and preparing the photographs. Simon J. Braddy, Rachel A. Moore and Simon R. Harris (University of Bristol) are thanked for helpful discussions and suggestions for improving the manuscript. Roy E. Plotnick, Victor P. Tollerton Jr., Markus Poschmann and Samuel J. Czurca Jr. are thanked for helping confirm the nature of the manuscript name associated with *A. zadrai*. Vojtech Turek (National Museum, Prague) is thanked for trying to trace the counterpart of *A. zadrai*. Carsten Brauckmann and Paul Selden provided valuable comments – CB particularly with respect to nomenclature – in their reviews of this paper. The *camera lucida* drawings were made by OET during a visit to Berlin funded by the UK Palaeontological Association's Sylvester Bradley Award. OET also acknowledges financial support from the Norges Forskningsråd, grant 145565/432, and the University of Bristol.

References

- Ammon, L. von 1882. Ein Beitrag zur Kenntniss der fossilen Asseln. – Jahresbericht der math.-phys. Klasse Akademie der Wissenschaft, München **4**: 507–551.
- Barbour, E. H. 1914. Carboniferous eurypterids of Nebraska. – American Journal of Science, Fourth Series **38**: 507–510.
- Bell, W. A. 1922. A new genus of Characeae and new Merostomata from the Coal Measures of Nova Scotia. – Transactions of the Royal Society of Canada **4**: 159–167.
- Branson, C. C. 1959. Permian sea scorpions from Oklahoma. – Oklahoma Geology Notes **19** (5): 111–112.
- Brauckmann, C. 1991. Ein neuer Eurypteriden-Fund aus dem Ober-Karbon des Ruhrgebietes. – Jahresbericht des naturwissenschaftlichen Vereins Wuppertal **44**: 155–161.
- Brauckmann, C., Schöllmann, L. & Sippel, W. 2003. Die fossilen Insekten, Spinnentiere und Eurypteriden von Hagen-Vorhalle. – Geologie und Paläontologie in Westfalen **59**: 1–89.
- Burmeister, H. 1843. Die Organisation der Trilobiten, aus ihren lebenden Verwandten entwickelt; nebst einer systematischen Übersicht aller zeither beschriebenen Arten. 148 pp. G. Reimer, Berlin.
- Chernyshev, B. I. 1933. Arthropoda s Urala i drugikh S.S.S.R. [Arthropods from the Urals and other regions of the U.S.S.R.]. – Sbornik Tsentral'nogo Nauchno – Issledovatel'skogo Geolograzvedochnogo Instituta, Paleontologiya i Stratigrafiya **1**: 15–24.
- 1948. New representative of Merostomata from the Lower Carboniferous. – Kievski Gos. Universitet Im T. G. Shevchenko Geoloisheskii Sbornik **2**: 119–130.
- Clarke, J. M. & Ruedemann, R. 1912. The Eurypterida of New York. – New York State Museum Memoir **14**: 1–439.
- De Lima, W. 1890. Note sur un Nouvel *Eurypterus* du Rothliegendes de Bussaco. – Communicações da Comissão dos Trabalhos Geológicos da Portugal **2**: 153–157.
- Decker, C. E. 1938. A Permian eurypterid from Oklahoma. – Journal of Paleontology **12**: 396–397.
- Dunbar, C. O. 1924. Kansas Permian insects, Part 1. The geologic occurrence and the environment of the insects. – American Journal of Science **207**: 171–209.
- Fraipont, J. 1889. Euryptérides nouveaux du Dévonien Supérieur de Belgique (Psammites du Condroz). – Annales de la Société Géologique de Belgique **17**: 53–62.
- Goldenberg, F. 1873. Fauna Saraepontana Fossilis. Die fossilen Thiere aus der Steinkohlenformation von Saarbrücken. Erstes Heft. 26 pp., Chr. Möllinger Verlag, Saarbrücken.
- Grabau, A. W. 1920. A new species of *Eurypterus* from the Permian of China. – Bulletin of the Geological Survey of China **2**: 61–68.
- Guthörl, P. 1934. Die Arthropoden aus dem Karbon und Perm des Saar-Nahe-Pfalz-Gebietes. – Abhandlungen

- der Preußischen Geologischen Landesanstalt, N. F., **164**: 1–219.
- Hall, C. E. 1877. Contributions to paleontology from the museum of the second geological survey (Pennsylvania). – Proceedings of the American Philosophical Society **16**: 621.
- Hall, J. 1884. Note on the Eurypteridæ of the Devonian and Carboniferous Formations of Pennsylvania. – Geological Survey of Pennsylvania, Report of Progress **2**: 23–39.
- Hall, J. & Clarke, J. M. 1888. Paleontology of New York. 236 pp., New York.
- Jordan, H. & Meyer, H. von 1854. Ueber die Crustaceen der Steinkohlenformation von Saarbrücken. – Palaeontographica **4** (1): 1–15.
- Kjellesvig-Waering, E. N. 1948. The Mazon Creek eurypterid: a revision of the genus *Lepidoderma*. – Scientific Papers of the Illinois State University **3** (4): 1–48.
- 1958. The genera species and subspecies of the Family Eurypteridae, Burmeister 1854. – Journal of Paleontology **32**: 1107–1148.
- 1959. A taxonomic review of some late Paleozoic Eurypterida. – Journal of Paleontology **33**: 251–256.
- 1961. The Silurian Eurypterida of the Welsh Borderlands. – Journal of Paleontology **35**: 789–835.
- 1963. Pennsylvanian Invertebrates of the Mazon Creek area, Illinois, Eurypterida. – Fieldiana, Geology **12**: 85–106.
- 1966. A revision of the families and genera of the Stylonuracea (Eurypterida). – Fieldiana, Geology **14** (9): 169–197.
- Kliver, M. 1884. Über *Arthropura armata* Jordan. – Palaeontographica **31**: 11–18.
- Kraus, O. & Brauckmann, C. 2003. Fossil giants and surviving dwarfs. Arthropleurida and Pselaphognatha (Atelocerata, Diplopoda): characters, phylogenetic relationships and construction. – Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF) **40**: 5–50.
- Kues, B. S. & Kietzke, K. K. 1981. A large assemblage of a new eurypterid from the Red Tanks Member, Madera Formation (Late Pennsylvanian–Early Permian) of New Mexico. – Journal of Paleontology **55**: 709–729.
- Mamay, S. H. & Bateman, R. M. 1991. *Archaeocalamites lazarii*, sp. nov.: the range of Archaeocalamitaceae extended from the lowermost Pennsylvanian to the mid-lower Permian. – American Journal of Botany **78**: 489–496.
- Manning, P. L. & Dunlop, J. A. 1995. The respiratory organs of eurypterids. – Palaeontology **38**: 287–297.
- Meek, F. B. & Worthen, A. H. 1868. Paleontology of Illinois. – Illinois Geological Survey Report **3**: 544.
- Melendez, B. 1971. Un novel Eurypteride du Westphalien des Asturies (NW Espagne). In: Krefeld, Ed. – Septieme Congres de Stratigraphie et de Geologie du Carbonifere **3**: 415–417.
- Meyer, H. von 1853. Mitteilung an Prof. Bronn. – Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrographik **1853**: 161–165.
- Owens, R. M. & Bassett, M. G. 1976. A Westphalian eurypterid from South Wales. – Palaeontology **19**: 185–190.
- Peach, B. N. 1882. Further researches among Crustacea and Arachnida. – Transactions of the Royal Society of Edinburgh **30**: 511–529.
- 1888. On a new eurypterid from the Upper Coal-measures of Radstock, Somersetshire. – Proceedings of the Royal Physical Society Edinburgh **9**: 438–445.
- Plotnick, R. E. 1983. Patterns in the evolution of the eurypterids. Ph.D. thesis, Department of the Geophysical Sciences, The University of Chicago, Chicago, 411 pp.
- Poschmann, M. In press. On the Emsian (Lower Devonian) arthropods of the Rhenish Slate mountains: 5. The eurypterid *Adelophthalmus sievertsi* from Willwerath, Germany. – Palaeontology.
- Příbyl, A. 1952. On the Genus *Adelophthalmus* Jordan & Meyer, 1854 (Eurypterida) and its representatives in the Upper Carboniferous of Czechoslovakia. – Bulletin International de l'Académie tchéque des Sciences **53**: 63–79.
- Pruvost, P. 1930. La faune continentale du terrain houiller de la Belgique. – Mémoires du Musée Royal d'Histoire Naturelle de Belgique **44**: 206–217.
- 1933. Un ancêtre des Libellules dans le Terrain houiller de Tchécoslovaquie. – Annales de la Société Géologique du Nord **58**: 149–155.
- 1939. *Eurypterus (Antraconectes) corneti* du Westphalien A du couchant de Mons. – Annales de la Société Scientifique de Bruxelles **59**: 56–59.
- Reuss, A. E. 1855. Palaeontologische Miscellen. III. Über eine neue Krusterspecies aus der Böhmisches Steinkohlenformation. – Denkschriften der königlich-kaiserlichen Akademie der Wissenschaften in Wien **10**: 81–83.
- Schwarzbach, M. 1957. Zum Vorkommen von Eurypteriden im oberschlesischen Karbon. – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte **1957** (3): 112–114.
- Selden, P. A., Corronca, J. A. & Hünicken, M. A. 2005. The true identity of the supposed giant fossil spider *Megarachne*. – Biological letters **42**: 1–5.
- Stainier, X. 1915. On a new Eurypterid from the Belgian Coal Measures. – Quarterly Journal of the Geological Society **284**: 639–647.
- 1935. Matériaux pour la faune du houiller de Belgique. – Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie **45**: 15–19.
- Størmer, L. 1955. Merostomata. In R. C. Moore, Ed. Treatise on Invertebrate Paleontology, Part P, Arthropoda 2, pp. 4–41. – Geological Society of America and University of Kansas Press, Lawrence, Kansas.
- 1969. Eurypterids from the Lower Devonian of Willwerath, Eifel. – Senckenbergiana lethaea **50** (1): 21–35.
- 1973. Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 3: Eurypterida, Hughmilleriidae. – Senckenbergiana lethaea **54**: 119–205.
- 1974. Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 4: Eurypterida, Drepanopteridae, and other groups. – Senckenbergiana lethaea **54**: 359–451.
- Størmer, L. & Waterston, C. D. 1968. *Cyrtoctenus* gen. nov., a large late Palaeozoic arthropod with pectinate appendages. – Transactions of the Royal Society of Edinburgh: Earth Sciences **68** (4): 63–104.
- Šusta, V. 1932. Přeběžná zpráva o nálezu šupin a zubů sladkovodních ryb a jiné kontinentální fauny z vrstev karvinských. – Sborník Přírodověd. Spol., r. VII.: 135–143.
- Tetlie, O. E., Braddy, S. J., Butler, P. D. & Briggs, D. E. G. 2004. A new eurypterid (Chelicerata: Eurypterida) from the Upper Devonian Gogo Formation of Western Australia, with a review of the Rhenopteridae. – Palaeontology **47**: 801–809.
- Tollerton Jr., V. P. 1989. Morphology, taxonomy, and classification of the Order Eurypterida Burmeister, 1843. – Journal of Paleontology **63**: 642–657.
- Van Oyen, F. H. 1956. Contribution a la connaissance du genre *Adelophthalmus* Jordan et Meyer 1854. – Meddelingen van de Geologische Stichting, series C, **3**: 4–98.
- Waterlot, G. 1934. Étude de la Faune continentale du Terrain houiller Sarro-Lorrain. II. Faune Fossile. – Études des Gites Minéraux de la France. Lille.
- Waterston, C. D., Oelofsen, B. W. & Oosthuizen, R. D. F. 1985. *Cyrtoctenus wittebergensis* sp. nov. (Chelicerata: Eurypterida), a large sweep-feeder from the Carboniferous of South Africa. – Transactions of the Royal Society of Edinburgh: Earth Sciences **76**: 339–358.
- Wills, L. J. 1964. The ventral anatomy of the Upper Carboniferous eurypterid *Antraconectes* Meek and Worthen. – Palaeontology **7**: 474–507.
- Woodward, H. 1888. Note on *Eurypterus* from the Carboniferous. – Geological Magazine, Decade III **5**: 419–421.
- 1907. Two New Species of *Eurypterus* from the Coal-Measures of Ilkeston, Derbyshire. – Geological Magazine **4**: 277–282.