A reappraisal of *Eurypterus dumonti* STAINIER, 1917 and its position within the Adelophthalmidae TOLLERTON, 1989

by O. Erik TETLIE & Peter VAN ROY

Abstract

The Carboniferous eurypterid *Eurypterus dumonti* STAINIER, 1917 from Mechelen-aan-de-Maas (Maasmechelen), Belgium is redescribed and assigned to the genus *Adelophthalmus*. It is diagnosed as having a raised triangle of unknown function, dorsally on opisthosomal segment 7 and a carapace articulating laterally against the second opisthosomal segment. Earlier assignments of this species to the genus *Unionopterus*, based on the carapace shape figured in the original description (STAINIER 1917), are incorrect and the existence of a Carboniferous eurypterid with the characteristics described for *Unionopterus* must be questioned. The appendages in *A. dumonti* are completely exposed and provide an unrivalled insight into the number of appendage podomeres in the genus; this species is interpreted to have a podomere count consistent with most other eurypterids. Small pustules previously thought to be cuticle sculpture are here interpreted as diagenetic "dumb-bells" (see BRIGGS & WILBY 1996) following microbial activity on the carcase prior to fossilisation. These "dumb-bells" are the oldest non-marine record of this diagenetic feature. A number of other features are also interpreted differently from the original description. Possible lineages within the *Adelophthalmus* clade are identified, *A. dumonti* is probably closely related to *A. imhofi* (Czech Republic) and *A. moyseyi* (United Kingdom).

Key words: Eurypterida, appendages, '*dumb-bells*', Belgium, Coal Measures.

Résumé

L'euryptéride carbonifère de Mechelen-sur-Meuse (Maasmechelen), Belgique, originalement décrit comme *Eurypterus dumonti* STAINIER, 1917 fait ici le sujet d'une nouvelle description, résultant de son transfert au genre *Adelophthalmus*. Cet euryptéride est caractérisé par la possession d'un triangle surélévé sur le segment opisthosomal 7, et par une carapace articulant latéralement contre le deuxième segment opisthosomal. L'attribution de cette espèce au genre *Unionopterus*, basée sur la forme de la carapace comme figurée dans la description originale (STAINIER 1917) s'est révélée incorrecte. L'existence d'un euryptéride carbonifère avec des caractéristiques comme celles décrites pour *Unionopterus*, est assez douteuse. Les appendices d'*Adelophthalmus dumonti* sont exceptionellement bien exposées et permettent d'obtenir une idée précise du nombre de podomères appendiculaires de ce genre. Le nombre de podomères de *A. dumonti* est interprété comme comparable à celui d'autres euryptérides. Des petites pustules originalement considérées comme ornementales sont réinter-

prétées ici comme des "*dumb-bells*" (cfr. BRIGGS & WILBY 1996), résultant d'action bactérielle avant la fossilisation. Ces structures indiquent que le fossile n'est pas une exuvie. L'interprétation d'un nombre d'autres caractéristiques diffère aussi de celle de la description originale. Des lignes de descendance possible du clade *Adelophthalmus* sont identifiées, et la proximité d'*A. dumonti* à *A. imhofi* (République Tchèque) et à *A. moyseyi* (Royaume-Uni) est suggérée.

Mots-clefs: Eurypterida, appendices, '*dumb-bells*', Belgique, terrain houiller.

Introduction

Eurypterids are a diverse group of Palaeozoic, aquatic chelicerates ranging from the Upper Ordovician (TOLLERTON 2004) to the Upper Permian (PLOTNICK 1983). They occur most frequently in the Silurian and Lower Devonian of Europe and North America. Post-Devonian eurypterids are rare and had migrated from their earlier marginal marine environments into brackish and freshwater settings (PLOTNICK 1983; TETLIE 2004) – the Carboniferous Coal Measures of Europe, North America and China being classic examples. Although known from the Devonian (TETLIE *et al.* 2004; TETLIE & DUNLOP 2005; POSCHMANN 2005), adelophthalmids constitute most of the post-Devonian eurypterids, both in terms of the number of species and individuals. They represent one of only two eurypterid clades to survive into the Carboniferous; the other, and more diverse clade, includes the gigantic sweep-feeding hibbertopterids (*Hibbertopterus, Cyrtoctenus, Campylocephalus, Hastimima, Dunsopterus* and *Vernonopterus*) and the peculiar woodwardopterids (the Devonian *Borchgrevinkium* and the Carboniferous *Woodwardopterus, Mycterops* and *Megarachne*), this latter group being allied to the hibbertopterids (SELDEN *et al.* 2005).

Adelophthalmids are small, streamlined, nektonic eurypterids with prominent cuticle sculpture, which have previously been referred to six genera. As discussed by TETLIE & DUNLOP (2005) only *Adelophthalmus* VON MEYER, 1853 and *Unionopterus* CHERNYSHEV, 1948 appear to be valid, and the four other proposed genera are synonyms of *Adelophthalmus*. While the morphology of *Adelophthalmus* is relatively well-known (KJELLESVIG-

WAERING 1948, 1963; VAN OYEN 1956; WILLS 1964; KUES & KIETZKE 1981; POSCHMANN in press), our knowledge of *Unionopterus* is extremely poor; this genus contains only one species and is known only from a single specimen from Kazakhstan, described by CHERNYSHEV (1948) as *U. anastasiae*. The original description was in Russian and contained rather poor illustrations. Based solely upon these figures of CHERNYSHEV (1948), the genus has variously been interpreted as allied to *Adelophthalmus* (CASTER & KJELLESVIG-WAERING 1964; TOLLERTON 1989), *incertae sedis* (NOVOJILOV 1962; STØRMER 1974; PLOTNICK 1983), or was ignored altogether (STØRMER 1955). TETLIE (2004) and TETLIE & DUNLOP (2005) realised that the specimen described by STAINIER (1917) as *Eurypterus dumonti* and later assigned to *Adelophthalmus* by VAN OYEN (1956), appeared different from other species of *Adelophthalmus*. They listed some similarities, especially in terms of carapace shape and the width of the marginal rim, to the specimen described by CHERNYSHEV (1948) and suggested that the Belgian species might also belong to *Unionopterus*. As demonstrated below, this conclusion was incorrect; the anterior of the carapace of the Belgian fossil is incompletely preserved, and its shape is not trapezoid as figured by STAINIER (1917), but parabolic, with a narrow marginal rim, as in other species of *Adelophthalmus*.

Except for *A. dumonti*, several other eurypterids are recorded from Belgium. The oldest Belgian eurypterids are *Cyrtoctenus dewalquei* (FRAIPONT, 1889) and *Adelophthalmus* (?) *lohesti* (DEWALQUE in FRAIPONT, 1889) from the middle to late Famennian (late Devonian) of the Condroz Group at Pont de Bonne Modave. The single specimen of *E. lohesti* was first interpreted as possibly belonging to *Adelophthalmus* by KJELLESVIG-WAERING (1958, p. 1141). However, STØRMER & WATERSTON (1968, p. 83) interpreted it as a possible stylonurid, a view supported here. Most of the other fragmentary fossils figured by FRAIPONT (1889) were reinterpreted by STØRMER & WATERSTON (1968) as belonging to *Cyrtoctenus*. The probably related woodwardopterid *Mycterops matthieui* PRUVOST, 1924, is known from the Mons Mbr. of the Charleroi Fm., Charleroi, Bashkirian. Apart from *A. dumonti*, the Belgian Carboniferous has also yielded three other unequivocal adelophthalmids. *A. moyseyi* (WOODWARD, 1907) was recorded from the Mons Mbr. of the Charleroi Fm., in the Coal Measures of Bernissart, Bashkirian by PRUVOST (1930). Also from the same unit comes *A. corneti* (PRUVOST, 1939), collected from a drill core at Rieu-du-Cur, Quaregnon. Finally, *A. cambieri* (PRUVOST, 1930) is known from the As Mbr. of the Charleroi Fm. Charbonnages Reunis coal mine, Charleroi, Bashkirian. All named occurrences of eurypterids in Belgium are from the Upper Devonian or Carboniferous; the country has one of the most diverse Upper Palaeozoic eurypterid faunas known.

Late Carboniferous geology of the Campine Basin

The Belgian Carboniferous is classically divided into a fully marine, carbonate-dominated "Dinantian", overlain by a predominantly continental, siliciclastic coal-bearing "Silesian". The internationally agreed chronostratigraphic standard scale for the late Carboniferous has not found wide acceptance in Belgium, and the traditional divisions of the "Silesian" into Namurian A, B and C, and Westphalian A, B, C and D are still widely used (Fig. 1).

Whereas the southern Wallonian Basin outcrops at the surface, the coal deposits of the northern Campine Basin are entirely covered by post-Carboniferous deposits. The Campine Basin can be further subdivided into the western Antwerp Campine, only containing Serpukhovian (Namurian A-C) and Bashkirian (Westphalian A-B) deposits poor in coal, and the eastern Limburg Campine, preserving coal-rich Moscovian (Westphalian C-D) deposits. In the Campine Basin, the transition from the fully-marine carbonate-dominated "Dinantian" to the continental "Silesian" is represented by the Souvré Fm., dating to the Viséan-Serpukhovian boundary. It is overlain by the Belgian Coal Measures Group, containing all Carboniferous siliciclastic coal-bearing sediments. This group evidences a regression, with a transition from a marine pro-delta environment near the base, through lower/upper delta plain, to lower/upper alluvial plain near the top (LANGENAEKER & DUSAR 1992; DREESEN et al. 1995). In their recent review of the late Carboniferous stratigraphy of Belgium, DELMER et al. (2001) subdivided the Belgian Coal Measures Group into six formations (Fig. 2).

Because Belgian Carboniferous eurypterid discoveries are limited to the Châtelet and Charleroi formations, only these two units are discussed. The sediments of the Châtelet Fm. are composed of non-marine shales, sandstones, thin coal seams and rootlet beds. Two pervasive marine horizons divide the Châtelet Fm. into two members: the Sarnsbank marine band at the base of the Châtelet Fm. forms the base of the Ransart Mbr., while the Finefrau Nebenbank band defines the base of the overlying Floriffoux Mbr. The Châtelet Fm. attains a thickness of 500 m in the Campine area. The succeeding Charleroi Fm. contains several thick coal seams, and consists of a very characteristic rhythmic succession of coal-mudstone-sandstone sedimentary sequences. Faint marine bands subdivide the Charleroi Fm. into three members: the basal Mons Mbr., the As Mbr. and the Eikenberg Mbr. The Charleroi Fm. reaches a thickness of over 1000 m in the northeastern Campine basin.

Stratigraphical assignment and age of the specimen

The eurypterid fossil was recovered from a depth of 435 m, from the core of boring no. 32, carried out in the southern Campine coalfield near Mechelen-aan-de-Maas, which nowadays is a borough of Maasmechelen (Fig. 1).
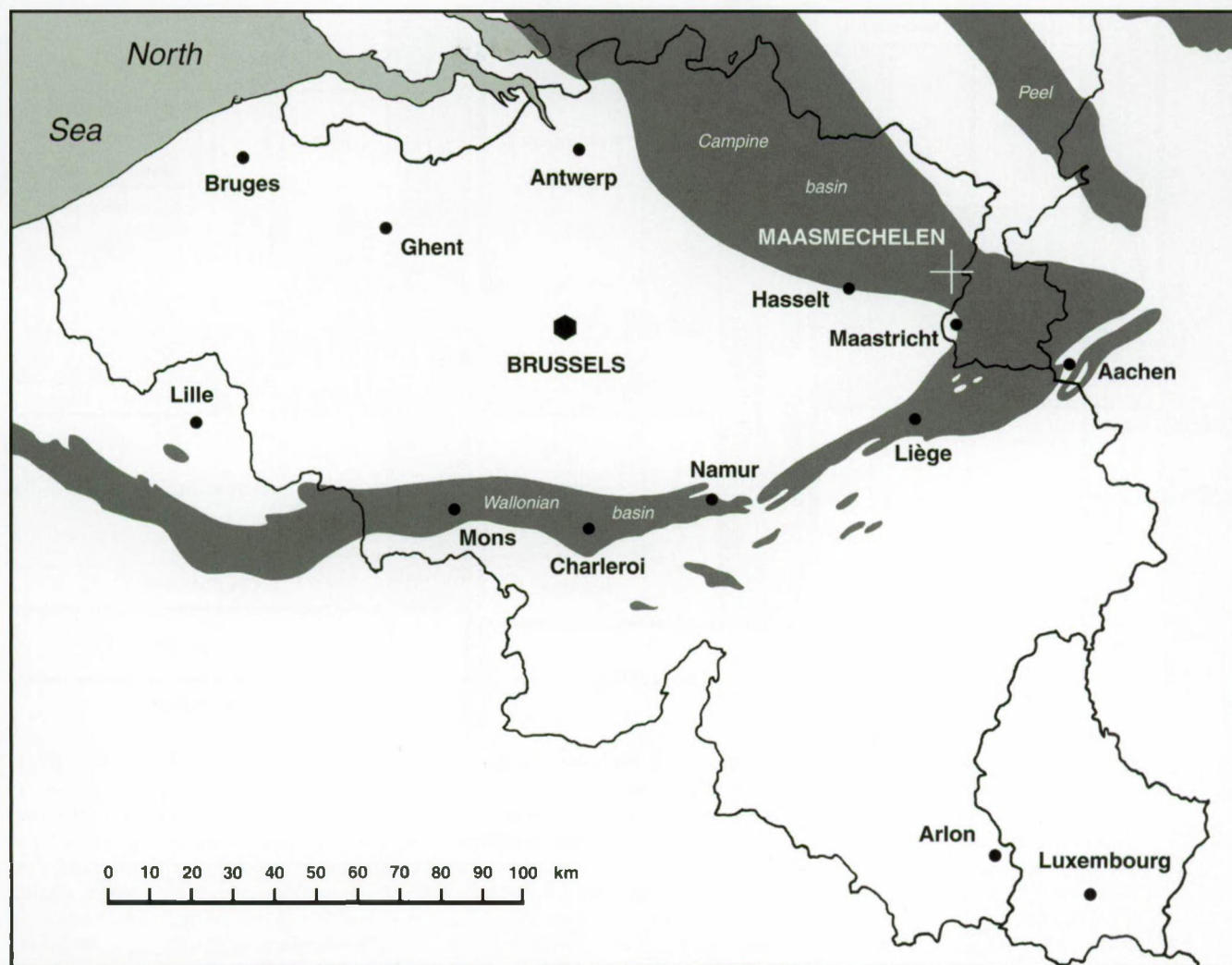
Fig. 1 — Map of Belgium showing the geographic extent of the Belgian Coal Measures Group. The position of Maasmechelen, of which Mechelen-aan-de-Maas nowadays is part, is indicated by the cross-hairs. Adapted from RENIER 1930 and PAPROTH *et al.* 1983.

In his original description, STAINIER (1917) stated that the fossil was found in a grey, fine-grained sandstone containing scattered plant fragments, above a thin seam of coal, about midway through the "great barren measure" ("grande stampe stérile") and approximately 570 m above the "Millstone Grit" ("poudingue"). The "great barren measure" was the upper subdivision of the Lower Westphalian A "assise de Châtelet" (STAINIER 1911). The "Millstone Grit" was considered by STAINIER (1911, 1917) to be a single, widespread grit-level forming the boundary between the Namurian and Westphalian stages. RENIER (1930), however, showed there was no such thing as a single, continuous "Millstone Grit" reference stratum, and subdivided the "assise de Châtelet" into the lower "zone d'Oupeye" and the upper "zone de Beyne". The eurypterid described herein was discovered in the "zone de Beyne", as recognised by PRUVOST (1930). PAPROTH *et al.* (1983) formally established the "zone d'Oupeye" as the Ransart Mbr., and the "zone the Beyne" as the Floriffoux Mbr.. In the latest

review of Belgian Carboniferous stratigraphy, DELMER *et al.* (2001), recognizing the "assise de Châtelet", erected the Châtelet Fm. to contain the Ransart and Floriffoux members. Accordingly, the eurypterid comes from approximately the middle of the Floriffoux Mbr. of the Châtelet Fm. in the Belgian Coal Measures Group, and is of early Late Bashkirian age (Fig. 2).

Material and methods

STAINIER (1917) gave no repository details for the specimen he described. The single specimen of *A. dumonti* (STAINIER, 1917) is now held at the Royal Belgian Institute of Natural Sciences in Brussels, Belgium registered under number RBINS a7706. It consists of part and counterpart; the part being relatively complete, lacking some appendages, pretelson and telson, while the counterpart is less complete, consisting of only the carapace, partial appendages and six anterior segments. The counterpart has been repaired after breakage during original splitting of the

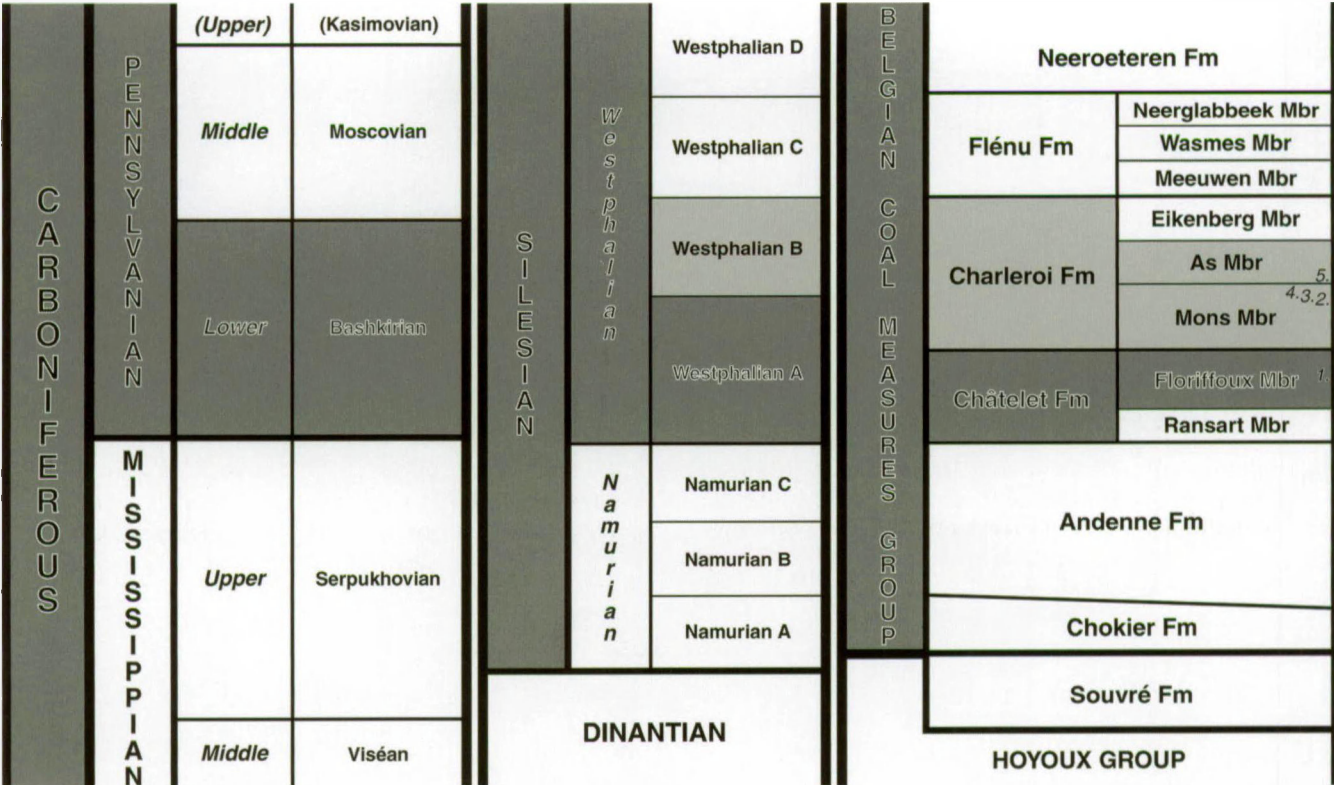| CARBONIFEROUS			SILESIAN / DINANTIAN		BELGIAN COAL MEASURES GROUP / HOYOUX GROUP	
PENNSYLVANIAN	(Upper)	(Kasimovian)	Westphalian	Westphalian D	Neeroeteren Fm	
	Middle	Moscovian		Westphalian C	Flénu Fm	Neerglabbeek Mbr
						Wasmes Mbr
						Meeuwen Mbr
	Lower	Bashkirian		Westphalian B	Charleroi Fm	Eikenberg Mbr
						As Mbr 5.
						4.3.2. Mons Mbr
				Westphalian A	Châtelet Fm	Floriffoux Mbr 1.
						Ransart Mbr
MISSISSIPPIAN	Upper	Serpukhovian	Namurian	Namurian C	Andenne Fm	
				Namurian B		
				Namurian A	Chokier Fm	
	Middle	Viséan	DINANTIAN		Souvré Fm	
					HOYOUX GROUP	

Fig. 2 — Stratigraphy of the late Carboniferous Belgian Coal Measures Group in the Campine Basin. Ages and units relevant to *A. dumonti* are indicated in dark grey. Units containing other eurypterids, and that do not overlap with the occurrence of *A. dumonti* are in light grey. Left column shows the internationally agreed chronostratigraphical division of the late Carboniferous. Late Pennsylvanian deposits are not represented in Belgium. Therefore, the Kasimovian is put in brackets, and the Gzhelian is omitted. Middle column shows the traditional late Carboniferous time-scale as still often used in Belgium. The Stephanian is omitted because no deposits of this age are known in Belgium. Right column shows the lithostratigraphic division of the late Carboniferous in the Campine Basin. Italic numbers on the right hand side of the column denote the approximate stratigraphical distribution of Belgian Carboniferous eurypterids: *1. A. dumonti*; *2. A. corneti*; *3. A. moyseyi*; *4. M. mathieui*; *5. A. cambieri*. Lithostratigraphic division adapted from DELMER *et al.* 2001.

core sample. The original orientation of the core sample is not indicated, so the way-up of the eurypterid is not known. The bedding planes intersect the core at an angle of around 70°, suggesting the beds originally had a dip of around 20° if the core was drilled vertically. Photographs were taken using a Nikon D100 digital SLR camera. The part was photographed initially under alcohol and subsequently with a coating of ammonium chloride, while the counterpart was photographed dry (the old glue was too brittle and fragile for alcohol) and coated with ammonium chloride. *Camera lucida* drawings were made using a Wild stereoscope with a drawing tube attachment. Morphological terminology follows TOLLERTON (1989) and higher systematics follows TETLIE (2004). The following abbreviations are used in the text and figures: c = carapace, ch = chelicerae, cx = coxa, db = dumb-bells, e = eye, gl = genal lobe, o = ocelli, pl = plant fragment, s = spine, t = raised triangle; prosomal appendages are numbered with Roman numerals I-VI, individual podomeres in prosomal appendages 1-9 (1 is the coxa) and opisthosomal segments 1-11 (pretelson and telson not preserved). In the text, short denotation of individual podomeres of appendages is made by combining appendage numbers with podomere numbers, e.g. III-7. All reference to left and right in the text refer to the more complete part unless otherwise stated.

Systematic palaeontology

Order **Eurypterida** BURMEISTER, 1843
Superfamily **Adelophthalmoidea** superfam. nov.
Diagnosis: Small swimming eurypterids with very generalised appearance; carapace parabolic (possible exception *Unionopterus*) with intramarginal eyes; swimming leg of *Adelophthalmus* type; genital spatulae possibly present in all taxa; midsection second order differentiation present; telson lanceolate.
Remarks: TETLIE (2004) informally raised this superfamily based on his cladogram, and encompassing the same genera as suggested here. TETLIE (2004) suggested that this superfamily could be divided into the basal Nanahughmilleridae (*Nanahughmilleria* KJELLESVIG-WAERING, 1961 and possibly *Pittsfordipterus* KJELLESVIG-WAERING & LEUTZE, 1966) with appendages II-V of *Hughmilleria* type, and the more derived Adelophthalmidae (*Parahughmilleria* KJELLESVIG-WAERING, 1961 and *Adelophthalmus*) with reduced spinosity of the appendages. The enigmatic *Unionopterus* might represent the only post-Silurian occurrence of the Nanahughmilleridae if the

appendage spinosity indicated by CHERNYSHEV (1948) was correct.

Family **Adelophthalmidae** TOLLERTON, 1989
Remarks: TOLLERTON (1989) raised this family for *Parahughmilleria*, *Bassipterus* KJELLESVIG-WAERING & LEUTZE, 1966, *Adelophthalmus* and *Unionopterus*, based on having *Adelophthalmus* types of spiniferous (II-V) and swimming (VI) appendages respectively. TETLIE (2004) interpreted *Bassipterus virginicus* KJELLESVIG-WAERING & LEUTZE, 1966, the only known species of *Bassipterus*, as a junior synonym of *Parahughmilleria bellistriata* (KJELLESVIG-WAERING, 1950). As mentioned above, *Unionopterus* was described as having appendages II-V of *Hughmilleria* type although its stratigraphical position would be more consistent with an identity within the Adelophthalmidae. TOLLERTON (1989) claimed that species within *Adelophthalmus* with completely non-spiniferous appendages would constitute a new genus of a new family within the Slimonioidea. A new genus might be warranted, but to erect a new family, and transferring it into the Slimonioidea based on a character loss, which clearly has happened independently in the two clades in question (TETLIE 2004), cannot be defended from a phylogenetic point of view.

Genus *Adelophthalmus* VON MEYER, 1853
Diagnosis: Medium sized streamlined eurypterid; carapace parabolic with narrow marginal rim and small, hinged triangular "locking" mechanism anteriorly; intramarginal reniform eyes; ocelli between or slightly behind 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 cuticular sculpture of minute scales (emended from TETLIE & DUNLOP 2005).

Adelophthalmus dumonti (STAINIER, 1917)
Figs. 3-5

Eurypterus sp.; SCHMITZ & STAINIER 1910, pp. 293, 296.
v*Eurypterus dumonti*; STAINIER 1917, p. 646, pl. 53, figs. 1-4.
Eurypterus Dumonti STAINIER; PRUVOST 1930, p. 191.
Eurypterus dumonti STAINER [sic]; MOORE 1936, p. 371.
Eurypterus? dumonti STAINIER; KJELLESVIG-WAERING 1948, p. 6.
Adelophthalmus dumonti STAINIER; VAN OYEN 1956, p. 49.
Adelophthalmus derbiensis WOODWARD; VAN OYEN 1956, p. 61.
Adelophthalmus dumonti; PLOTNICK 1983, p. 385.
Unionopterus dumonti; TETLIE 2004, pp. 183, 250, 283.
Unionopterus dumonti; TETLIE & DUNLOP 2005, p. 6.

Diagnosis: Small *Adelophthalmus* with thickened bands distally on podomeres of walking legs; genal lobes on carapace which articulate laterally with second tergite, and correspondingly laterally reduced first tergite; anterior and midsection, but lacking posterior second order

opisthosomal differentiation; raised triangle on opisthosomal segment 7.
Type locality: Mechelen-aan-de-Maas (= Maasmechelen), Limburg, Belgium.
Type horizon: Above a thin coal seam, approximately in the middle of the Floriffoux Mbr. of the Châtelet Fm., in the Belgian Coal Measures Group.
Remarks: The suspicion that this species should be assigned to the poorly known *Unionopterus* (TETLIE & DUNLOP 2005) was mainly based on the carapace shape and the broad marginal carapace rim figured by STAINIER (1917). As demonstrated herein, the indicated shape was influenced by an incomplete anterior margin and was not the true carapace shape, while the marginal rim is narrow as in other species of *Adelophthalmus*. Also note that we do not acknowledge the synonymy of *A. dumonti* with *A. derbiensis* WOODWARD, 1907 as suggested by VAN OYEN (1956). *A. derbiensis* itself was synonymized with *A. moyseyi* by KJELLESVIG-WAERING (1948), something we support, but we also note that *A. moyseyi* and *A. dumonti* are very similar (see below).

Description

Almost complete specimen with preserved length 32.5 mm, maximum opisthosomal width 11.5 mm. Preserved part of carapace 7.5 mm long, 9.7 mm wide at posterior margin. Anterior and left carapace margins are incomplete (Figs 3A, 4A). Lateral angle 95°, carapace L/W ratio restored to approximately 0.79, giving a parabolic shape (TOLLERTON 1989). Carapace with very narrow (0.1 – 0.2 mm wide) marginal rim on lateral margins. Right eye well-preserved and reniform, 1.2 mm long. The ocelli are positioned between the eyes on the counterpart (Fig. 4B). On the right postero-lateral carapace corner of the part (Fig. 4A), a large rounded genal lobe projects posteriorly. A curious cardioid (heart-shaped) depression (Fig. 4A) is positioned between the eyes and the anterior carapace margin; interpreted as representing very unusual preservation of the chelicerae (see below). Four partial podomeres of left appendage II may possibly be observed. Poorly preserved remains of appendage II extend past the carapace margin on the right and this appendage evidently did not extend far beyond the margin. No podomere details can be seen on this appendage. Appendage III is preserved on both sides. On the right, podomeres III-4 to III-7 (for podomere abbreviations, see Fig. 4C) are probably preserved, although podomere boundaries are not seen (Fig. 4B). On the left, some of the carapace has been broken away (Figs 3A, 4A), exposing more of the proximal podomeres, and eight podomeres (coxa to III-8) can be seen (Fig. 4C). Appendage IV is best preserved on the left where coxa to IV-8 can be seen; on the right only a fragment is present. Appendage V is only preserved on the left, and seven podomeres (V-2 to V-8) are preserved. V-7 has the proximal end of a very large spine preserved. The podomeres do not have crenulated distal margins, but a thickened distal margin is
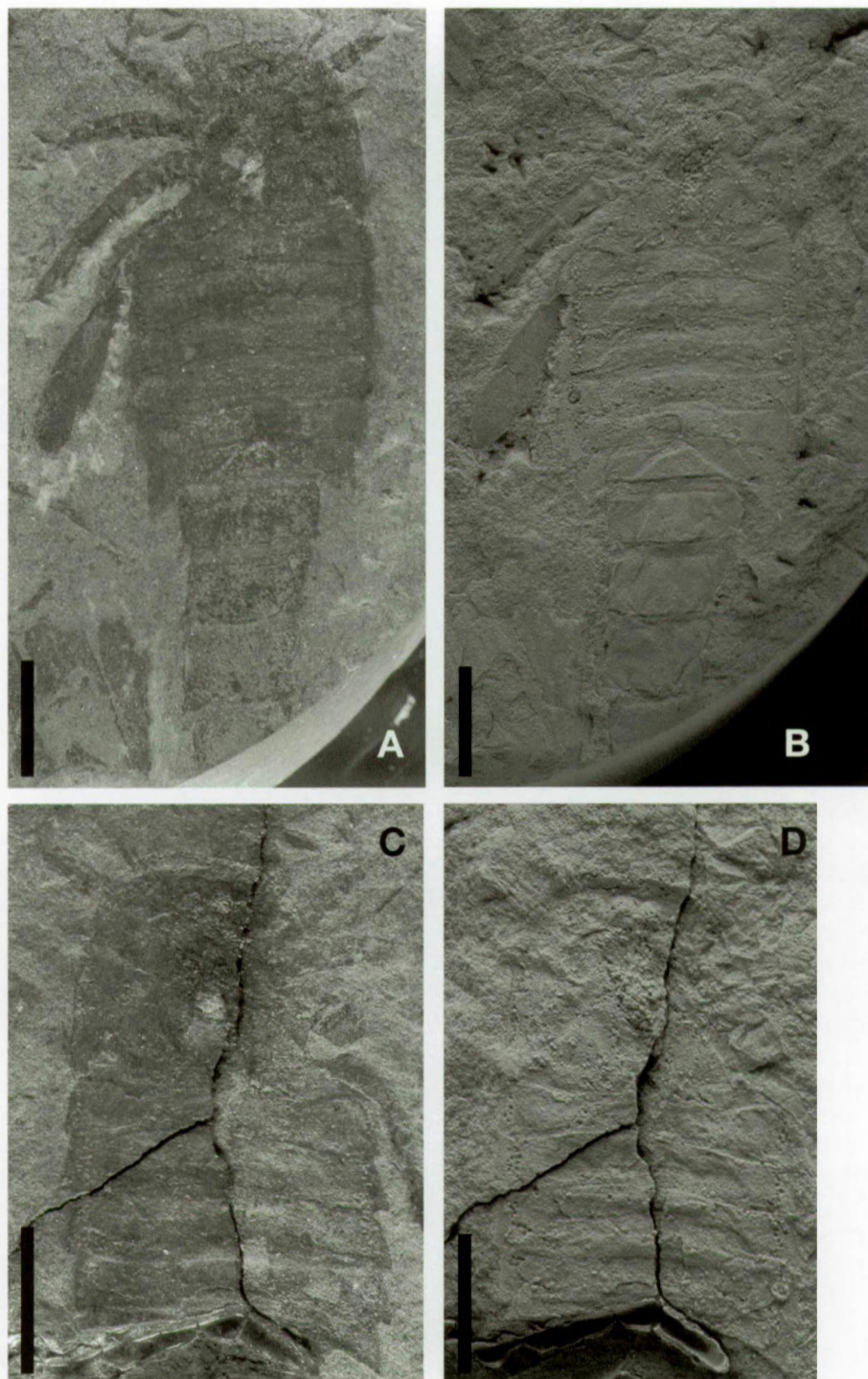
Fig. 3 — *Adelophthalmus dumonti* (STAINIER, 1917). A) Photograph of RBINS a7706 (part) submersed in alcohol; B) Photograph of RBINS a7706 (part) coated with ammonium chloride; C) Photograph of RBINS a7706 (counterpart) taken under normal conditions; D) Photograph of RBINS a7706 (counterpart) coated with ammonium chloride. Scale bars are 5.0 mm.

observed on several podomeres on appendages IV and V. The podomere lengths (parallel to longest axis of appendage) and widths (perpendicular to longest axis of appendage) in mm of appendages III-V on the left side are: III-2 0.5/1.2*; III-3 0.8/1.4*; III-4 0.8/1.3*; III-50.9/1.1*; III-6 0.7/1.0*; III-7 0.7/0.6*; III-8 0.9*/0.4*; IV-2 0.6/1.5; IV-3 1.1/1.3; IV-4 1.0/1.3; IV-5 1.0/1.2; IV-6 0.9/1.0; IV-7 0.9/0.8/ IV-8 0.3*/0.4; V-2 0.6*/1.4*; V-3 1.0/1.5; V-4 1.4/1.5; V-5 1.8/1.3; V-6 2.0/1.0; V-7 2.1/0.8 V-8 0.9*/ 0.5 (* denotes measurement of incomplete podomeres).

Posterior to the eyes, on the carapace and extending onto the anterior opisthosomal segment, two depressions mimic the outline of the posterior parts of coxae VI. Appendage VI also has podomeres 7, 7a and 8 preserved on the left side, and a minute notch in VI-8 suggest the position of VI-9. Proximally, the podomeres between the
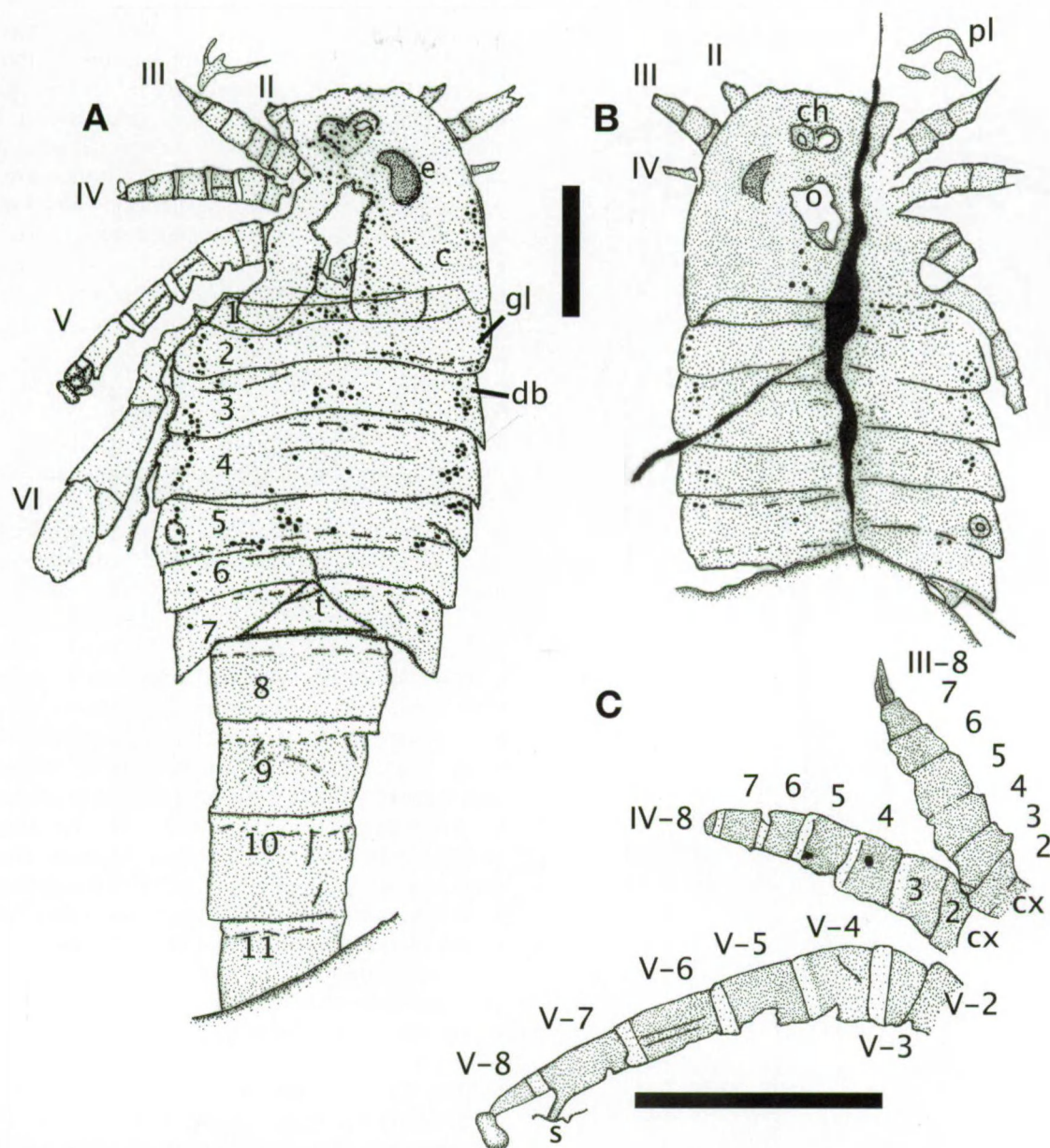
Fig. 4 — *Adelophthalmus dumonti* (STAINIER, 1917). A) *Camera lucida* drawing of RBINS a7706 (part); B) *Camera lucida* drawing of RBINS a7706 (counterpart); C) details of the appendages exposed on the left side of the part. Scale bars are 5.0 mm.

coxa and VI-7 are present, but partly covered by tergites and their outlines cannot be identified. The posterior margin of the metastoma is interpreted as relatively straight or truncated.

The anterior opisthosomal segment is strongly reduced in length compared to the more posterior ones, and is surrounded by genal lobes, almost giving the appearance of being incorporated into the carapace. The postero-lateral corner (genal lobe) of the carapace surrounds the entire anterior segment, so the carapace articulates with the second opisthosomal segment laterally. The second segment lacks lateral epimera just like the anterior segment. The following segments become wider until the opisthosoma reaches its maximum width on the fourth segment. Gradually, these segments develop longer epimera until those of the seventh segment. On the seventh

segment, a median raised area forms a triangle with its apex pointing towards the carapace. There is a moderate first order opisthosomal differentiation (TOLLERTON 1989). The four anterior-most segments (8-11) represent the incomplete postabdomen. As in most eurypterids, these segments are narrower, but longer than the segments in the preabdomen. The segments in the postabdomen have no epimera preserved. The preserved segment lengths (along the midline) and widths in mm are: 1) 0.6/9.3*; 2) 1.3/11.0*; 3) 1.8/10.9*; 4) 3.0/11.5; 5) 1.7/11.2; 6) 1.4/10.4; 7) 1.9/9.5; 8) 3.9/6.6; 9) 3.4/5.4; 10) 3.7/5.2; 11) 3.2*/4.2 (* denotes measurement of an incomplete segment). The pretelson and the telson are not preserved as they were outside of the area covered by the core, but comparison with other species of *Adelophthalmus* (e.g. *A. imhofi* REUSS, 1855) suggest that this species probably
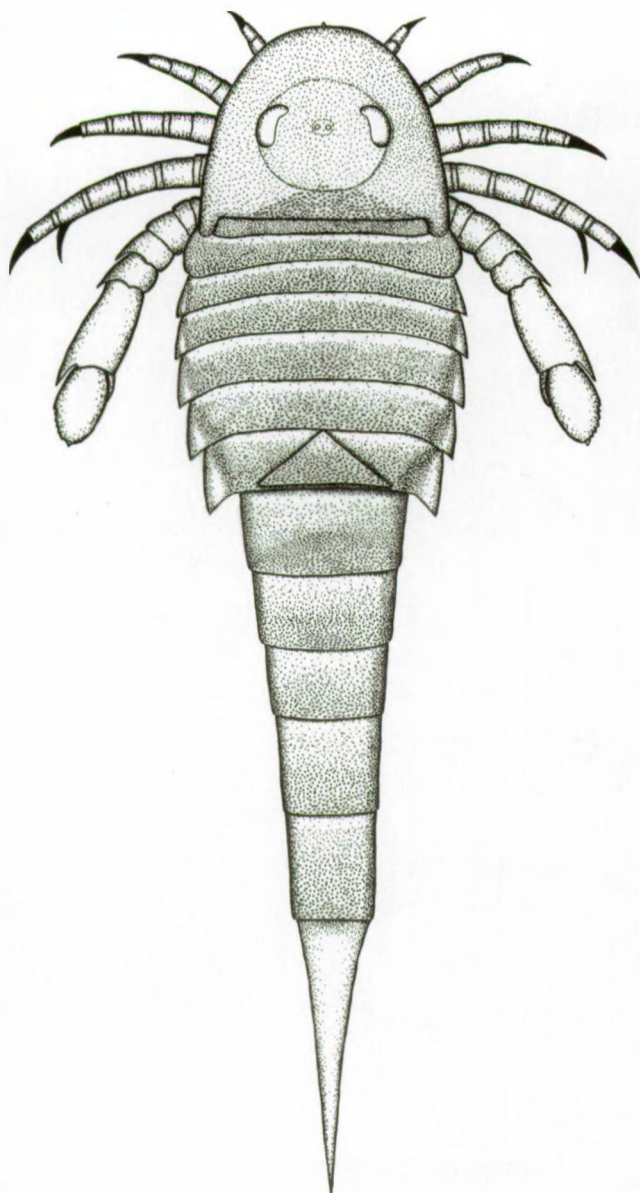
Fig. 5 — Dorsal reconstruction of *Adelophthalmus dumonti*
(STAINIER, 1917) based on RBINS a7706 and a pre-
telson and telson based on the presumably closely
related *Adelophthalmus imhofi*.

also had a relatively long, lanceolate telson and we have
reconstructed it as such (Fig. 5).

Taphonomy

A number of post-mortem changes have affected this
eurypterid, which misled STAINIER in his original descrip-
tion. The identification of these is a stark reminder that
taphonomical processes were not understood by most
earlier authors and older publications are therefore occa-
sionally inaccurate in the information they portray. Illus-
trations are sometimes idealised, to the extent that, rather
than being a reliable depiction of the specimen, they
reflect the author's personal views on what the fossil

should actually look like. It is therefore imprudent to
place too much emphasis on illustrations without re-ex-
amining the fossil. As previously mentioned, STAINIER's
(1917) description is defective on many counts. First, the
anterior carapace margin was interpreted as complete by
STAINIER (1917). This is certainly not the case, and the
jagged anterior and left-hand margins suggest that the
animal might have been scavenged prior to fossilisation.
From the partially complete right-hand margin, it is clear
that the carapace was more or less parabolic, as in other
species of *Adelophthalmus*, not trapezoid as suggested by
STAINIER (1917).

Second, as the carcase decomposed, small (0.1 –
0.2 mm) crystal bundles, or "dumb-bells" (BRIGGS &
WILBY 1996) were formed along the lateral margins,
the oral cavity and anterior parts of the digestive system.
'Dumb-bells' are very early diagenetic features, starting
to form three days after death in shrimp carcases (BRIGGS
& KEAR 1994). They are originally composed of arago-
nite, but aragonite is less stable than calcite and all
'dumb-bells' found in fossils have been recrystallised to
calcite (BRIGGS & KEAR 1994). We have not analysed the
composition of the suspected 'dumb-bells' in this fossil.
They are commonly found in association with phospha-
tization, but nothing resembling phosphatized muscle
tissue was identified in the Belgian eurypterid. These
'dumb-bells' (Figure 6) were identified as ornamentation
by STAINIER (1917). No 'dumb-bells' are seen on the
postabdomen, which had thicker, annulate segments, a
condition not favourable for aragonite precipitation as pH
would become too low following decomposition of the
locally more abundant organic material (BRIGGS & WILBY
1996). 'Dumb-bells' are most commonly developed in
restricted marine conditions, but have also been found
previously in specimens from a non-marine (lacustrine)
setting at Las Hoyas, Spain (BRIGGS & WILBY 1996). The
Belgian Carboniferous occurrence is the oldest example
of 'dumb-bells' from a non-marine locality. The speci-
men has ornamentation, seen on the counterpart consist-
ing of fine scales as typical for the genus. This was not
mentioned by STAINIER (1917) who largely ignored the
relevance of the counterpart, stating that: "the counter-
part of the fossil is fractured and incomplete, and there-
fore of little use for palæontological purposes" (STAINIER
1917, p. 639).

Fig. 6 — Dumb bells on right side, third and fourth segments of
Adelophthalmus dumonti (STAINIER, 1917) holotype,
RBINS a 7706.

When the dorsal cuticle of the eurypterid became malleable, the outline of the underlying coxae VI and metastoma became visible through the carapace (Fig. 4A), as interpreted correctly by STAINIER (1917), although figured too symmetrically by him. When the drill core was split, another anomaly was created. The ventral chelicerae followed the dorsal-most incomplete counterpart, creating a large cardioid depression in the part. STAINIER (1917) acknowledged that this was possibly "accidental", but failed to realise its true nature. The size of the depression suggests the chelicerae, like the other appendages, were relatively robust, something also seen in other species of *Adelophthalmus* (see WILLS 1964).

Discussion

The main differences between the initial description of STAINIER (1917) and our work are: 1) the carapace shape; 2) the marginal rim of the carapace; 3) the ocelli that can be observed on the counterpart; 4) the spine on appendage V; 5) the nature of the circular nodes, and finally 6) the typical scaly sculpture that can be found localised on the counterpart. Additional minor differences include the accuracy of the prosomal appendages including the coxae of appendage VI, the accuracy of the junction between the carapace, segments 1 and 2, the broken outline of the segments of the left side of the part, and the lack of epimera on the postabdomen.

The partial destruction of the left side of the carapace was a fortuitous accident. There has long been uncertainty about the number of appendage podomeres (here given in this form: number of podomeres in appendage I-II-III-IV-V-VI respectively) in *Adelophthalmus*. WILLS (1964, p. 486) suggested that *Adelophthalmus* had ?-6?-7-8?-9-9, although he stated "it is not possible to be certain about the exact number of joints in each". Among eurypterids, this potential podomere count could only be matched in *Stylonurella* (?-?-7?-8-9-9?) (PLOTNICK 1983). This specimen, with well exposed *in situ* appendages, suggests there are 8, not 7 podomeres in appendage III and this implies for *Adelophthalmus* the same podomere count (i.e. 3-7-8-8-9-9) as most other eurypterids, although there are still uncertainties about the very small appendage II in the genus. The spine on V-P7 suggests *A. dumonti* had a very similar appendage to the one described by SCOTT (1971) for *A. mansfieldi*, also figured as the *Adelophthalmus* type of spiniferous appendage by TOLLERTON (1989).

The only puzzling morphology described by STAINIER (1917) that cannot be assigned to taphonomical processes is the raised triangular area on the most posterior preabdominal segment. This is a very regular structure although its anterior symmetry has been slightly distorted by a depression continuing onto the segment anterior to the triangle. Whether this triangle had a hydrodynamic or another function is not readily obvious. It could alternatively have been some kind of 'boss' for articulation of the pre- and postabdomen (L. Anderson pers. comm. 2005).

The posterior margin of the metastoma seen through the carapace might represent a rare metastoma shape in *Adelophthalmus*, as most species have an oval metastoma with a rounded posterior margin. However, since the posterior margin in the specimen of *A. dumonti* is very poorly exposed, the possibility cannot be excluded that this aberrant shape in fact is a taphonomical artefact.

Lineages of *Adelophthalmus*

Although this work does not attempt to resolve the phylogeny of the adelophthalmids – for that our knowledge is still too limited – some lineages can be identified since they are defined by unique synapomorphies. One potential strong synapomorphy of certain species is the presence of a raised triangle on segment 7. This structure is previously known from *A. imhofi* (REUSS, 1855) as pointed out by STAINIER (1917) and *A. moyseyi* as noted by MOORE (1936, p. 371) in addition to *A. dumonti*. The latter two are of Bashkirian age, while *A. imhofi* is Gzhelian (Late Carboniferous) or Asselian (Early Permian). The triangle is not present in *A. luceroensis*, *A. sellardsi*, *A. granosus* and *A. sievertsi* and probably not present in *A. mansfieldi* and *A. mazonensis*.

The differentiation of the anterior tergite might also be of phylogenetic importance in adelophthalmids. The simplest type of differentiation of this segment is simply to have reduced segment length. This is found in *A. wilsoni* (see MOORE 1936). A second type is the gradual reduction in segment length laterally found in *A. sievertsi* (see POSCHMANN in press), possibly *A. imhofi* (see REUSS 1855 or KJELLESVIG-WAERING 1948) and *A. luceroensis* (KUES & KIETZKE 1981). A third type is the one found in *A. dumonti* and possibly *A. moyseyi* (see indication of this in MOORE 1936, fig. 63 both left and right sides), where the anterior segment is obscured laterally by the expanded posterolateral corners of the carapace that articulate with the second segment laterally. The importance of this character is still uncertain, especially since the three species with a triangle on segment 7 appear to fall into two groups. A second possible lineage is defined by having epimera on the postabdomen; these are *A. mansfieldi*, *A. wilsoni* and *A. mazonensis*. The latter two of these are Moscovian in age while *A. mansfieldi* is Westphalian. However, most adelophthalmids cannot be assigned to any major lineage.

Is *Unionopterus* valid, and if so, is it an adelophthalmid?

One could agree unquestionably with CASTER & KJELLESVIG-WAERING (1964) and TOLLERTON (1989) and interpret *Unionopterus anastasiae* as an adelophthalmid. However, based only on the illustrations provided by CHERNYSHEV (1948), there is scant evidence to suggest that this genus belongs to the adelophthalmids other than the fact that *Adelophthalmus* and *Unionopterus* are the only known swimming eurypterids to survive into the

Carboniferous, and their swimming legs are of a similar morphology. Before the specimen of *A. dumonti* was restudied, an assignment to *Unionopterus* seemed likely based on similarities between the illustrations of STAINIER (1917) and CHERNYSHEV (1948). However, can more unique synapomorphies for this proposed relationship be found even when *A. dumonti* is not a *Unionopterus*?

Adelophthalmus can be fairly convincingly interpreted as being closely related to the Silurian – Devonian genera *Nanahughmilleria* KJELLESVIG-WAERING 1961, *Parahughmilleria* KJELLESVIG-WAERING, 1961 and the monotypic *Pittsfordipterus* KJELLESVIG-WAERING & LEUTZE 1966. *Pittsfordipterus* is indistinguishable from *Nanahughmilleria* except for the morphology of its genital appendage, and is treated as a nanahughmillerid for the remainder of this discussion. Their almost identical carapace, paddle, eye shapes and eye position support the relationship between *Adelophthalmus*, *Nanahughmilleria* and *Parahughmilleria* in the new superfamily Adelophthalmoidea. More explicit putative synapomorphies for these genera are the presence of epimera on segment 7 (= midsection second order differentiation; TOLLERTON 1989) and genital spatulae, although the spatulae are very large in *Adelophthalmus*, medium-sized in *Parahughmilleria* and very small in *Nanahughmilleria* (STØRMER 1973; TETLIE 2000). The walking legs in *Nanahughmilleria* probably had paired spines on each podomere (STØRMER 1934; TETLIE 2000), a condition seen for instance in *Hughmilleria* (SARLE 1903), while *Parahughmilleria* and *Adelophthalmus* have appendage podomeres with occasional isolated spines and crenulated distal podomere margins. Autapomorphies for *Adelophthalmus* (absent in *Nanahughmilleria* and *Parahughmilleria*) include: (1) epimera on the pre- and postabdomen, 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 cuticular sculpture is much coarser in *Adelophthalmus* than in *Nanahughmilleria* and *Parahughmilleria* and the former lacks the ornament of lines parallel to the segment margins found in the latter two (see e.g. STØRMER 1973). The telson is generally longer in *Adelophthalmus* than in *Nanahughmilleria* and *Parahughmilleria*, but the consistency of this character is equivocal. A final difference between *Adelophthalmus* versus *Nanahughmilleria* and

Parahughmilleria is in the morphology of the anterior opisthosomal segment. This tapers in length towards the lateral margins in at least some species of *Adelophthalmus* (TETLIE & DUNLOP 2005; see also *A. dumonti*), a condition not known in any *Nanahughmilleria* or *Parahughmilleria*. Thus, the Silurian *Nanahughmilleria* and *Pittsfordipterus*, with paired spines on the appendages and none or small genital spatulae, were basal to the predominantly Devonian *Parahughmilleria*, with reduced appendage spinosity and enlarged spatulae. This trend is further continued in the Devonian to Permian *Adelophthalmus*, which have also developed a triangular carapace "locking" mechanism, a reduced anterior tergite, epimera on the pre- and (occasionally) postabdomen and a longer telson.

So where does this leave us in respect to the phylogenetic position of *Unionopterus*? The trapezoid carapace shape is different to all other taxa in the lineage, which retain a parabolic shape. *Unionopterus* does share some similarities to *Adelophthalmus*, such as epimera on the preabdomen, and it is therefore possible that *Unionopterus* is a sister-taxon to, or in-group of, *Adelophthalmus*. Alternatively, the presence of paired spines on the appendages suggests that *Unionopterus* is the only known post-Silurian survivor of *Nanahughmilleria-Pittsfordipterus* affinity.

A third alternative is that CHERNYSHEV (1948), like STAINIER (1917), misinterpreted the carapace shape and appendage spinosity, and that he too was describing a specimen belonging to the genus *Adelophthalmus*. But since the whereabouts of the holotype and only specimen of *U. anastasiae* are presently not known, this question may never be answered.

Acknowledgments

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O. Erik TETLIE
Department of Geology and Geophysics, Yale University
PO Box 208109, New Haven, CT 06520-8109, U.S.A.
Email: erik.tetlie@yale.edu

Peter VAN ROY
Department of Geology & Soil Science, Ghent University
Krijgslaan 281 / S8, B-9000 Ghent, Belgium
Email: peter.vanroy@ugent.be