PHYLOGENY AND PALAEOECOLOGY OF THE ADELOPHTHALMOIDEA (ARTHROPODA; CHELICERATA; EURYPTERIDA)

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SYNOPSIS A phylogenetic analysis of the monophyletic superfamily Adelophthalmoidea suggests that there is a basal, hitherto unrecognised genus, Eysyslopterus gen. nov., in the clade, on the basis of carapace shape, anterior ornament and eye position. The two comparatively poorly known genera Pittsfordipterus and Bassipterus form a relatively basal clade and are united by their shared possession of elongated eyes and a type A genital appendage consisting of two articles forming a complex distal termination. The genera Parahughmilleria and Nanahughmilleria are represented in the analysis by only one well-known species each and the monophyly of these two genera remains untested. The geologically long-lasting Adelophthalmus is monophyletic and supported by a number of synapomorphies. The clade probably had a marine origin. Most known representatives are brackish (estuarine–deltaic) or freshwater (laminated lacustrine–fluvial) inhabitants, but with a marine influence commonly encountered within the sequences. The fossil record of the clade is relatively poor with a Relative Completeness Index value of between 31 and 34%. However, the fit between phylogeny and stratigraphical occurrences of the taxa analysed is very good (Stratigraphic Consistency Index = 0.73; Gap Excess Ratio = 0.96–0.97). The sister group of Adelophthalmus, the genus Parahughmilleria, is reported for the first time from the Silurian of Lesmahagow, Scotland and these specimens are questionably referred to P. cf. hefteri, previously known only from the Siegenian and Emsian of western Germany and Luxembourg.

KEY WORDS Adelophthalmus, Carboniferous, chelicerate, hughmilleriid, Parahughmilleria, Palaeozoic

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INTRODUCTION

Eurypterida is a monophyletic order of predatory aquatic chelicerates that ranged from the early Late Ordovician (Størmer 1951) to the Late Permian (Ponomarenko 1985). However, eurypterids are most common and diverse in the Silurian and Lower Devonian and by the Carboniferous there are only two clades of eurypterids still surviving, both found mainly in fresh or brackish waters. These are the clade consisting of the stylonurids (walking forms) known as hibbertopterids and woodwardopterids (Selden et al. 2005) and the streamlined swimming forms in the Adelophthalmidae Tollerton, 1989. The adelophthalmids represent the most common eurypterids in the Late Palaeozoic, both in terms of species and specimen numbers. Taxonomically they are the second most diverse of all eurypterid clades, after the Pterygotidae, their putative sister group (Tetlie 2004). Tollerton’s (1989) classification was not phylogenetic and the taxa here interpreted as belonging to the adelophthalmoid clade were assigned to two different families by Tollerton (1989). Tetlie (2004), in an unpublished phylogeny, identified the Adelophthalmoida Tollerton, 1989 as monophyletic, but with the addition of Nanahughmilleria Kjellesvig-Waering, 1961. However, Tetlie (2004) only included three terminals (less than half of the genera in the clade) in his phylogeny and also failed to resolve any relationships within the clade. Recently, a number of contributions have advanced our knowledge of some of these taxa (Tetlie & Dunlop 2005; Poschmann 2006; Shpinev 2006; Tetlie & Van Roy 2006) and a more detailed, species-level phylogeny of this clade is thus timely. However, from the results presented here, it is obvious that more work is still needed, especially in the provision of detailed descriptions of some species of Nanahughmilleria, Parahughmilleria Kjellesvig-Waering, 1961 and Adelophthalmus Jordan, in Jordan & von Meyer, 1854, and in the identification of new phylogenetic characters, especially those that might resolve the relationships between the Carboniferous and Permian representatives of the genus Adelophthalmus.

With this contribution, we aim to better understand the phylogenetic relationships within the Adelophthalmoida, to investigate the quality of their fossil record and how their palaeoecological preference changed through the Palaeozoic. We also describe the earliest occurrence, a Lower Silurian representative, of the genus Parahughmilleria, the sister group of the important Devonian to Permian genus Adelophthalmus. From the results of the phylogeny, a new basal genus, Eysysopterus, is erected for the species formerly known as Nanahughmilleria patteni (Størmer, 1934c) from the island of Saaremaa, Estonia (Ludlow).

MATERIAL AND METHODS

The material described herein is deposited at the American Museum of Natural History, New York (AMNH), the British Geological Survey, Keyworth (BGS GSM), the Hunterian Museum, Glasgow University (GLAHM), the Senckenberg Museum, Frankfurt (SMF) and Landesammlung für Naturkunde, Rheinland-Pfalz, Mainz (PWL). The Parahughmilleria material has been compared to material in M.P.’s reference collection and the new genus Orcanopterus material in the Royal Ontario Museum, Toronto. Camera lucida drawings were prepared using a Wild stereoscope and photographs were taken partly using normal light and partly using plane polarised light. The morphological terms used are mainly adopted from Tollerton (1989). In addition, the individual podomeres in prosomal appendages have been labelled following the terminology used by Tetlie & Van Roy (2006). Length of a prosomal appendage and its podomeres are measured sagittally (longest direction) and width is measured coronally (shortest direction), while all other measurements follow the regular protocols, i.e. length is coronal and width sagittal.

Phylogenetic analysis

Characters were coded from adelophthalmoid descriptions in the published literature and from personal observations (see Appendix). Species have been coded rather than genera to provide some possibility of identifying paraphyletic or polyphyletic genera (for a complete list of species included and excluded, see Fig. 1). In addition to these taxa, a few more have previously been assigned to the clade, but are here excluded from this analysis for a number of reasons. Adelophthalmus stylus (Hall, 1884) was considered a synonym of A. mansfieldi (Hall, 1877) by Kjellesvig-Waering (1948), A. oklahomensis (Decker, 1938) was considered a synonym of A. sellardsi (Dunbar, 1924) by Branson (1959), N. schiraensis (Pirozhnikov, 1957) might be a synonym of P. mataraensis (Pirozhnikov, 1957) and P. salteri Kjellesvig-Waering, 1961 is probably a synonym of N. pygmaea (Salter, 1859) although none of these three latter pairs (all from one locality) have yet been demonstrated. Adelophthalmus perornatus (Peach, 1882) is very large and the ornament suggests a hibbertopterid (Tetlie & Dunlop 2005). Nanahughmilleria conica (Laurie, 1892) probably represents a stylonurid eurypterid (O.E.T., pers. obs., 2003) and N. (?) lanceolata (Salter, 1856) might belong to this clade. The absence of eyes on all the known specimens precludes a conclusion on its phylogenetic position, but the morphology of the known prosomal and genital appendages are incompatible with this clade and N. (?) lanceolata is probably closer to the Eurypteroidea (see Tetlie & Cuggy 2007).

The phylogenetic analysis was performed with PAUP* 4.0b10 PPC (Swofford 2002). All characters have equal weight and were treated as unordered. To polarise the characters, the Late Ordovician Orcanopterus mantoulinensis Stott et al., 2005 was selected as the outgroup. Orcanopterus mantoulinensis was interpreted as the most basal taxon (Tetlie 2004) in a clade that also comprised Waeringopterus Leutze, 1961 and Grossopterus Stormer, 1934a, the sister-clade to (Adelophthalmoida + Pterygotoida) and is well-known except for its type A genital appendage. The excluded species that are also thought to belong to the clade, but which are
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Results and discussion

Phylogenetic results

Analysing all characters with equal weight and unordered, after removing the uninformative characters, yielded five most parsimonious trees (MPTs) with a Tree Length = 29, Consistency Index (CI) = 0.86, Retention Index (RI) = 0.92 and Rescaled Consistency Index (RC) = 0.79. The strict and majority rule consensus trees of these MPTs are shown in Figs 2A and 2B, respectively. Unequivocal character transformations are indicated on Fig. 2A. The support values given under the nodes (Fig. 2B) were retrieved through a Jackknife analysis of the dataset using 10% character deletion with 1000 repetitions, while the values in bold italics over the nodes are values from a bootstrap analysis based on 1000 repetitions. The trees (Fig. 2) demonstrate that all the genera under consideration, with the exception of Nanahughmilleria, are, or have the potential to be, monophyletic. In Nanahughmilleria, the species N. (?) patteni is clearly different from the other species previously placed in the genus and we choose to erect here a new genus for this basal form presently too incompletely known to contribute to the analysis, are listed in Fig. 1.

Figure 1  A, Strict consensus tree superimposed onto a stratigraphical column indicating the stratigraphical ranges of the taxa analysed. B, Taxa interpreted as belonging to the clade, but too incompletely known to be included in the analysis, also with stratigraphical ranges indicated. If the synonymies suggested by Van Oyen (1956) are accepted (marked with asterisks), this would lengthen the range (grey) of Adelophthalmus imhofi.
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Nanahughmilleria also represent a separate genus, having eyes in a more anterior position than other species of Nanahughmilleria and Parahughmilleria. This question is not pursued further here, because of the lack of reliable characters. The remaining species previously assigned to Nanahughmilleria and Parahughmilleria appear to be more typical for these two genera, but until more of the species are better known, it will be difficult to demonstrate whether these two genera are monophyletic or not. A clade comprising Bassipterus Kjellesvig-Waering & Leutze, 1966 and Pittsfordipterus Kjellesvig-Waering & Leutze, 1966 is also positioned relatively basally as sister group to (Nanahughmilleria norvegica (Parahughmilleria hefteri + Adelophthalmus)) and is supported by two synapomorphies, the possession of relatively long and narrow eyes and a complex termination of the genital zipfel. Nanahughmilleria norvegica (Kier, 1911) is situated more basally than P. hefteri Størmer, 1973, on the basis of the spinosity of appendage V. Nanahughmilleria norvegica apparently has small paired spines on each podomere of appendage V while P. hefteri has enlarged spines on at least one podomere, apparently a synapomorphy of Parahughmilleria and Adelophthalmus. Other synapomorphies of this latter clade include the presence of epimera on the postabdomen and the large spatulae associated with the genital operculum. The monophyly of Adelophthalmus is supported in our analysis by a number of synapomorphies: an anterior triangle of unknown function on the carapace, a centrally raised circular area on the carapace, apparent lack of terrace lines anteriorly on the carapace (but these might be present in A. nebraskensis (Barbour, 1914) unless the illustrated lines are products of compression), eyes closer to the ocelli than to the carapace margin, oval metastoma, rounded postero-lateral angles on the anterior opisthosomal segment, epimera on the preabdomen, long telson and lack of striate cuticular sculpture anteriorly on the preabdominal segments. Adelophthalmus sievertsi (Størmer, 1969) is basal to the other species in the genus. This position is in line with its much earlier occurrence in the fossil record than the other Adelophthalmus species and is supported mainly by the relatively wide swimming leg, a sympleisiomorphy shared with N. norvegica and P. hefteri. The remaining species in Adelophthalmus have a more narrow swimming leg, a synapomorphy of this group. However, there is a lack of resolution in the remaining taxa in Adelophthalmus in our analysis, suggesting more work is needed in terms of redescribing older taxa (and possibly recognising synonyms) and identifying more phylogenetically informative characters for the genus.

Figure 3 shows the relationships between the genera in the three most derived clades of Eurypterina as elucidated by Tetlie (2004) and this analysis. The interpreted basal members of each clade are very similar. For instance, the carapace shape in Figs 3A (Herefordopterus Tetlie, 2006), 3D (Eysyslopterus) and 3H (Orcanopterus Stott et al., 2005) are almost identical and they are most easily separated on eye position. In the most basal clade consisting of Orcanopterus, Waeringopterus and Grossopterus, the eyes are nearly marginal, but are separated from the margin by the marginal rim. Furthermore, they also possess a strongly curved inner eye margin. In Waeringopterus, the eyes appear marginal (Fig. 3I), but the extremely bulbous eyes actually have a continuous marginal rim running beneath them. The Adelophthalmidea have more centrally positioned eyes with less curved inner margins. It is also clear from Fig. 3 that the eyes have migrated towards the centre of the carapace in the more derived taxa in this clade, especially seen in Adelophthalmus (Fig. 3G). In the Pterygoidea, the oval eyes

Figure 2 A. Strict consensus of the five most parsimonious trees recovered in the phylogenetic analysis, with unequivocal character transformations indicated. B. Majority rule consensus tree of the same analysis, with support values indicated, based on a bootstrap analysis (1000 replicates) in bold italics above nodes and a jackknife analysis with 10% deletion (1000 replicates) in roman type below nodes.
are marginal in all known taxa, culminating in the large eyes found in the pterygotids *sensu stricto* (Fig. 3C). Although eye position and shape certainly reflect the inhabited environments and life habits of different eurypterids (e.g. Størmer 1934b; Waterston 1979), they also clearly preserve phylogenetic information.

It is, therefore, with considerable reservations that the new genus (Fig. 3D) is assigned to the Adelophthalmoidea and *Orcanopterus* to the Waeringopteroidea. The new genus might possibly be a sister group to (Adelophthalmoidea + Pterygotoidea), but until more information about the genus is available, this will not be known for certain.

**Palaeoecology of the clade**

The adelophthalmoids have usually been considered denizens of coal swamps and fluvial systems (Kjellesvig-Waering 1948; Plotnick 1983; Tetlie 2004), both being freshwater environments, but how accurate is this picture? A critical review of the palaeoecology of the clade was conducted. The data (see “Supplementary data” available on Cambridge Journals Online: http://www.journals.cup.org/abstract_S1477201907002416) are arranged approximately in stratigraphical order. There is much more of a marine influence in many of the sections yielding *Adelophthalmus* than has previously been acknowledged.

The data, mostly compiled from recent literature, show that adelophthalmoids as a whole, throughout the history of the clade, inhabited environments situated near the coastal realm, predominantly those with reduced salinities, such as lagoons, estuaries or deltas. A marine influence is commonly found within the sections that comprise the eurypterid-bearing horizons, but in many of these cases (when known) marine index fossils are not found in close association with the eurypterids. In some cases, where adelophthalmoids are particularly rare, they might have suffered transportation and been deposited allochthonously (e.g. the Late Devonian *A. waterstoni* (Tetlie et al., 2004)). The earliest adelophthalmoids, exemplified by *Parahughmilleria* cf. *hefteri*, are often preserved within deposits that have been interpreted as ‘non-marine’, brackish–estuarine with possible tidal influences, although some basal forms are known from fully marine deposits. This habitat preference apparently did not change significantly over time, except in the genus *Adelophthalmus*. With the advent of *Adelophthalmus*, there seems to be an ecological shift in favour of freshwater-dominated habitats (Fig. 4) as indicated in some Early Devonian German localities, where *P. hefteri* and *A. sievertsi* are found.
associated. There, Parahughmilleria-dominated eurypterid associations occur in sections that show a more obvious marine influence than those bearing Adelophthalmus-dominated ones (Poschmann & Tetlie 2006). Those localities clearly illustrate a gradational series between marginal marine and freshwater habitats where palaeosalinity can only be determined relatively (cf. Anderson et al. 1999). The strongest preference for freshwater habitats among Adelophthalmus might be deduced from the supplementary information to have occurred during Bashkirian and Moscovian times, when they are usually encountered within coal-bearing strata and associated with terrestrial organisms and ‘freshwater bi-valves’. These horizons were usually interpreted as reflecting freshwater conditions, but nevertheless a marine influence is commonly, but not always, encountered within the respective sequences. Although speculative, the conquest of predominantly freshwater habitats might be related to the apparent radiation in the genus Adelophthalmus in the Bashkirian/Moskovian (Fig. 1). However, Adelophthalmus seems to be mainly confined to paralic or lowland basins, in depositional environments that had a close connection to the marginal marine realm. For example, the youngest occurrence of Adelophthalmus in the German Saar-Nahe basin (i.e. A. granosus Jordan, in Jordan & von Meyer, 1854) dates from the Moscovian when this basin was still connected to, or was even part of, a vast subsiding western area (Schäfer 1986) and drainage was to the Palaeoethys Ocean some 1500 km to the south.

In Late Pennsylvanian and Early Permian times, due to uplift in the south, drainage was northwards to the Panthalassa Ocean, resulting in a greater distance from the ocean (some 2400 km: T. Schindler, pers. comm., 2006). In these younger strata, Adelophthalmus is lacking, whereas other faunal components interpreted by some authors as indicating a connection to the marginal marine realm persisted into the latest Pennsylvanian/earliest Permian ‘Rotliegend’ strata of the Saar-Nahe basin, e.g. euproopid xiphosurans (e.g. Poschmann & Scindller 2004). The exact palaeogeographical position of such intramontane basins in relation to a marine palaeoshoreline, and to what extent the encountered taphocoenoses reflect a marine connection, is still a matter of debate (for a recent discussion, see Schultz & Soler-Gijon 2004). However, Adelophthalmus is either rare or lacking in so-called intramontane basins and was apparently confined mostly to depositional settings that show some indication of a connection to the marginal marine realm. Some of the later adelophthalmoid occurrences (Late Moscovian and younger) may imply a kind of reversal in ecological preferences in favour of environments that again show a stronger marine influence. Some of the respective Lagerstätten were interpreted as representing tidally influenced estuarine environments (Feldman et al. 1993). As a result, Adelophthalmoida can be viewed as a euryhaline clade of eurypterids that inhabited stressful habitats with regard to palaeosalinity (and possibly to other factors, such as oxygen) throughout their fossil history. Their conquest of the limnic realm, at least in terms of distance from a supposed palaeoshoreline, was evidently not as successful as it was in e.g. euproopid xiphosurans, which in turn are commonly encountered within freshwater lake sediments of Permo–Carboniferous intramontane basins devoid of eurypterids. However, although our understanding of eurypterid palaeoecology has been improved since earlier attempts (e.g. O’Connell 1916), it is still in its infancy and only detailed examinations, i.e. bed-by-bed excavations of eurypterid-bearing sequences, may further improve our knowledge (cf. Maples & Schultz 1988).

Quality of the adelophthalmoid fossil record

The Relative Completeness Index (RCI: Benton & Storrs 1994) was used to estimate the relative completeness of the fossil record by calculating the ratios of stratigraphical representation compared to gaps. Values of RCI range from negative values, where the sum of the gaps exceeds the represented stratigraphical range, to 100%, where there are no gaps in the stratigraphical record (Benton & Storrs 1994). Benton & Hitchin (1996) consider any RCI < 50% to be poor for higher-level category group phylogenetic analyses. For a discussion of high-level versus low-level category group analyses, see Benton & Storrs (1994) and Tetlie & Cuggy (2007). The RCI value of Tetlie & Cuggy (2007) for the basal Euryper- terina was based on a slightly larger selection of taxa than this analysis. There is not thought to be any substantial difference in cuticular preservation potential between the different eurypterid clades, but diverging habitat preferences would undoubtedly influence the fossilisation potential. The RCI for the basal Euryperterina analysed by Tetlie & Cuggy (2007) was −41%, while RCI values of between 31 and 34% were obtained for the different adelophthalmoid trees. The higher values shown by adelophthalmoids compared to the basal swimming forms are puzzling, especially considering the sparse occurrence of members of the adelophthalmoid clade in the mid-Devonian to Early Carboniferous fossil record.

The adelophthalmoid phylogeny fits very well to the stratigraphical occurrences of the taxa in the fossil record, having Gap Excess Ratios (GER: Wills 1999) of 0.96–0.97 and a Stratigraphic Consistency Index (SCI: Hulsensbech 1994) of 0.73. However, three gaps in the fossil record of the Adelophthalmoida can be observed in Fig. 1A and all three of them are also, to some degree, present in Fig. 1B. The clade must have come into existence in the Llandover at the latest, as shown both by the existence of P. maria (Clarke, 1907) and N. (?) prominens, and the presence of basal representatives of the sister-clade, the Pterygotoidea, in the Llandover. However, the fossil record of the clade is very poor in the Early Silurian and these taxa have disputed ages (Plotnick 1999).

There is a second notable gap in the fossil record between the Middle Devonian and the Late Carboniferous (Fig. 1A). Four species are known from this interval (A. approximatus (Hall & Clarke, 1888), Unionopterus anastas-iae Chernyshev, 1948, A. waterstoni and A. irinai Shpivey, 2006). The holotypes of the two earliest described species may be lost and the two more recently described are poorly known, so they do not currently add any information about the phylogeny of the clade. Even taking into account the poorly known taxa, there is a lack of representatives of the clade in the mid-Devonian and the mid-Carboniferous. Only four species known from an 80 million year interval suggests that the adelophthalmoids were rare, adelophthalmoid-bearing outcrops of this age are rare or, just as likely, the preservation potential was limited during the interval (Fig. 1B). From the Late Carboniferous to the Early Permian, diversity or preservation potential must have increased, since in addition to the six species in the cladogram (Fig. 1A), an additional 15 species are known from that time (Fig. 1B). The last known
representative of Adelphilthmus is A. sellardsi from the Early Permian (Artinskian) of Kansas and Oklahoma and this third gap extends from the late Early Permian to the end of the Permian. However, the quality of the Late Palaeozoic fossil record of the clade precludes a conclusion to be drawn about the precise timing of the extinction of Adelophilthmus.

**SYSTEMATIC PALAEOLOGY**

Order **EUPHYTHERIDA** Burmeister, 1843

Suborder **EUPHYTHERINA** Burmeister, 1843

Superfamily **ADELOPHTHALMOIDEA** Tollerton, 1989

**REMARKS.** Superfamilies are regulated by the International Code for Zoological Nomenclature (ICZN) codes and they are derived from family-group names. Tollerton (1989) erected the Adelophilthmidae, albeit with a different taxonomic content than that recognised by Tetlie & Van Roy (2006), who were the first to recognise this as a superfamily. Tollerton (1989) is, therefore, the correct author of this superfamily.

Genus **PARAHUGHMILLERIA** Kjellesvig-Waering, 1961

**Parahughmilleria** cf. hefteri Størmer, 1973

**DESCRIPTION.** The first specimen (BGS GSM 103940: Figs 5A, 6A) is 34.8 mm long. The carapace is 7.0 mm long (L) and 10.7 mm wide (W), giving a L/W ratio of 0.65. The carapace has reniform eyes and the lack of symmetry of the eyes in this specimen shows that it has been slightly distorted. No ocellar mound or ocelli are preserved. A narrow marginal rim borders the carapace. Four partial prosomal appendages are preserved. On the right side only a very poorly preserved appendage (possibly V) is present. On the left side, IV, V and VI are preserved in better detail. On IV, only the distal spine can be identified of the individual podomeres. It is 0.5 mm long and 0.15 mm wide proximally. V is better preserved and the six distal podomeres are identified. The distal tapering spine (V-9) is 0.25 mm wide proximally and 0.5 mm long. The rectangular V-8 is 1.0 mm long and 0.5 mm wide. The triangular V-5 is 0.5 mm long and 0.8 mm wide. The more or less quadratic V-4 is 0.4 mm long and 0.5 mm wide, while V-6 is 0.7 mm long and 0.8 mm wide. V-2 and V-3 are both 0.5 mm long and 0.8 mm wide. The ring-like V-2 and V-3 have a ridge running the length of the podomeres. V-6, V-5 and V-4 are more poorly preserved and all appear to have been around 0.8 mm wide and approximately 0.5–0.7 mm long. No spines can be seen on appendages IV or V. Appendage VI is a swimming leg showing parts of VI-4 to VI-8 posterior to the carapace. Through the carapace it is possible to see coxae of both swimming legs. However, only the left one is well-preserved enough to merit description. The basal part of the coxa has an almost quadrate shape, but with an anterolateral flange. Towards the gnathobase, the neck is strongly curved anteriorly but posteriorly hidden. Even the coxal ornament can be seen and consists of lines more or less parallel to the anterior and posterior margins. VI-4 and VI-5 are poorly preserved but were around 1.2–1.5 mm long and 2 mm wide. VI-6 has a well-preserved antero-lateral portion developed into a short (1 mm) projection. The preserved part of VI-6 is 1.5 mm long and 1.0 mm wide. VI-7 is completely preserved and has a maximum length of 2.9 mm and a maximum width of 2.6 mm, giving a L/W ratio of 1.12. The triangular VI-7a is 1.3 mm long and 1.7 mm wide. The oval VI-8 is 3.5 mm long and 2.2 mm wide. VI-9 is not preserved.

The metastoma can be observed through the carapace and unless some of the observed lines partially represent the outline of the coxae, it is 3.5 mm long and 2.65 mm wide, giving a L/W ratio of 1.32. The shoulders are rounded, surrounding an angular notch with an angle of cordation of 100 degrees. The lateral sides are convex with the position of greatest width being central. The posterior margin is also rounded with a lateral angle of around 60 degrees. This represents an oval metastoma *sensu* Tollerton (1989).

The first opisthosomal segment is reduced. The left lateral margins of the three anterior segments are not preserved. The first five segments are easily identified, while segments six and seven are to a large degree overlapping; on the left side mainly segment six is seen, while mainly segment seven is observed on the right side. A rather short (0.7 mm) epimeron can be seen on the seventh segment on the right side. Likewise, the eighth and ninth segments are overlapping, but here more symmetrical so that the ninth segment is almost concealed under segment eight. There is a slight first order differentiation (Tollerton 1989) of the opisthosoma between the seventh and eighth segment. Segments 10–12 decrease in width towards the posterior and have small epimeras (*ca. 0.5 mm long*) on the posterolateral corners of the segments. The opisthosoma is mainly without discernible ornamentation; the notable exception being parallel lines on the anterior half of the two first segments. Opisthosomal segment lengths/widths in mm (*indicate incomplete lateral preservation*): 1 = 1.0/10.9; 2 = 1.9/10.8; 3 = 1.8/10.8; 4 = 1.6/10.7; 5 = 1.6/10.5; 6 = 1.5 (median)/9.6; 7 = 1.6 (median)/8.4; *8 = 2.1/7.6; 9 = 1.9/7.1; 10 = 2.8/6.3; 11 = 1.8/5.2; 12 = 1.7/4.0. The telson is lanceolate (*sensu* Tollerton 1989), 2.6 mm wide at the anterior base and 6.7 mm long.

The second specimen (BGS GSM 103941: Figs 5B, 6B) is a carapace, which is 6.9 mm long and has a preserved width of 9.6 mm (reconstructed width 10.0 mm), giving a reconstructed L/W ratio of 0.69. The left eye is best preserved and is 1.65 mm long and 0.85 mm wide. Again, the lack of symmetry in the specimen shows it to have been slightly distorted. A narrow (0.15–0.2 mm) marginal rim borders the carapace. Fragmentary remains of coxa VI are preserved on the left side and the ornament on the ventral side of the coxa consists of small scales. Posteriorly, a gently curving line might be the right posterior margin of the metastoma, suggesting the same shape as in BGS GSM 103940.

The third specimen (GLAHM A2568a: Figs 5C, 6C) is a more or less complete juvenile and, although preservation is good, its interpretation is hampered by a slight dislocation of ventral structures which can be seen through much of the dorsal surface. The total length of this specimen is 24 mm. The carapace is anteriorly incomplete, 3.4 mm long and 6.2 mm wide. On the left side of the carapace, a complete series of prosomal appendages from II to V is preserved. Details are sparse on the anterior four appendages and no spines can be seen, but individual, rectangular podomeres are distinguishable on appendages II to IV. The appendages gradually increase in length posteriorly. V is poorly preserved. VI has a subquadrate coxa, with lines parallel to the neck of the coxa. The coxa is 2.0 mm wide and 2.1 mm long. Laterally, the ring-like VI-2 and VI-3 are both 0.5 mm long and 1.0 mm wide. The more or less quadratic VI-4 is 0.4 mm long and 0.5 mm wide. The triangular VI-5 is 0.5 mm long and 0.5 mm wide, while VI-6 is 0.7 mm long and 0.8 mm wide.
Interestingly, the complete VI-7 is 1.9 mm wide and 1.7 mm long with a L/W ratio of 0.89, which is much lower than in BGS GSM 103940. VI-7a is 0.8 mm long and 1.2 mm wide, while VI-8 is 2.4 mm long and 1.7 mm wide. The anterior margin of VI-8 has a coarse serration, often seen in the genus. VI-9 is not preserved. Traces of the posterior part of the metastoma seem to be similar to those of the other two specimens. The mesosomal ventral plates have been separated from the dorsal plates and their left margins are 0.6 mm to the left of the margins of the dorsal plates.

The mesosoma has the same width as the carapace. A short (0.3 mm) epimeron is seen on the right side of the seventh segment. There is again a slight first order differentiation (Tollerton 1989) of the opisthosoma between the seventh and eighth segment. Segments 9 and 11 have small epimera (ca. 0.2 mm long) on the postero-lateral corners of the segments. The opisthosoma is mainly without discernible ornamentation, except parallel lines on the anterior half of the three first segments. Opisthosomal segment lengths/widths in mm (* indicate incomplete lateral preservation): 1 = 0.4/7.2;
2 = 0.9/7.7; 3 = 1.1/7.2; 4 = 1.3/7.0; 5 = 1.8/6.6; 6 = 1.7/6.6; 7 = 1.3/5.1; 8 = 1.3/4.6; 9 = 1.7/4.1; 10 = 1.6/3.2; 11 = 1.8/2.2; 12 = 1.9/1.9. The telson is lanceolate, 0.8 mm wide at the anterior base and 3.0 mm long, but is incomplete both proximally and distally.

REMARKS. *Parahughmilleria hefteri* was previously known only from a number of Early Devonian localities in western Germany and Luxembourg. We report here three specimens from the Silurian Kip Burn Formation, Lesmahagow, Lanarkshire, Scotland that are morphologically very similar to *P. hefteri*. These are BGS GSM 103940 (a more or less complete individual in dorsal aspect, but with ventral structures of the prosoma visible through the carapace), BGS GSM 103941 (a smaller but more well-preserved carapace) and GLAHM A2568a (a more or less complete juvenile).

One possible difference between the Early–Middle Silurian Lesmahagow material described here and the Early Devonian *P. hefteri* from Germany lies in the shape of the metastoma. The L/W ratio in the Scottish forms appears to be 1.32, having a rounded posterior margin. In comparison (see Table 1), the German forms have L/W ratios ranging from 1.70–1.81 (*P. hefteri*) and 1.83–1.95 (*P. major* Størmer, 1973) (cf. Størmer 1973). In addition, these species have a sharply truncated posterior margin of the metastoma. The metastoma in *P. salteri* has a L/W ratio of 1.93, with a deep angular notch and angular shoulders in addition to a truncated posterior margin. The metastomata of *P. bellistriata*...
O. E. Tetlie and M. Poschmann

Table 1: Comparative measurements of Parahughmilleria specimens (in mm)

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Locality</th>
<th>Total length</th>
<th>Carapace L/W ratio</th>
<th>Opisthosoma length</th>
<th>Telson L/W ratio</th>
<th>Opisthosoma/telson length</th>
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<tr>
<td>SMF VIII 112</td>
<td>Aiken</td>
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<td>?</td>
<td>?</td>
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<td>?</td>
<td>?</td>
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<td>2.4</td>
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<tr>
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<td>Aiken</td>
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<td>?</td>
<td>?</td>
<td>2.4/0.95</td>
<td>2.53</td>
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<td>MP Coll</td>
<td>Aiken</td>
<td>14</td>
<td>2.2/3.8 (0.58)</td>
<td>8.9</td>
<td>3.0/1.2</td>
<td>2.5</td>
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<tr>
<td>445-D</td>
<td>Aiken</td>
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<td>4.8</td>
<td>13.7</td>
<td>ca.4.0/1.75</td>
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<tr>
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<td>?</td>
<td>?</td>
<td>5.7/1.9</td>
<td>3.0</td>
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<td>Hombach</td>
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<td>18</td>
<td>5.9/1.9</td>
<td>3.10</td>
<td>3.05</td>
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<tr>
<td>631-DaA</td>
<td>Hombach</td>
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<td>5.0/8.0 (0.63)</td>
<td>19.5</td>
<td>7.0/1.9</td>
<td>3.68</td>
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<td>Aiken</td>
<td>?</td>
<td>?</td>
<td>?</td>
<td>&gt;11.7/4.4</td>
<td>&gt;2.66</td>
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<td>Holotype P. hefteri, SMF VIII 55</td>
<td>Aiken</td>
<td>55</td>
<td>10.0/13.75 (0.73)</td>
<td>32</td>
<td>13.0/3.0</td>
<td>4.3</td>
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<tr>
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<td>Aiken</td>
<td>?</td>
<td>?</td>
<td>15.7/4.9</td>
<td>3.20</td>
<td>?</td>
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<tr>
<td>854-D, P. major?</td>
<td>Aiken</td>
<td>62.3</td>
<td>15.3</td>
<td>31.0</td>
<td>16.0/4.8</td>
<td>3.33</td>
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<tr>
<td>BGS GSM 103940</td>
<td>Lesmahagow</td>
<td>34.8</td>
<td>7.0/10.7 (0.65)</td>
<td>21.6</td>
<td>6.7/2.7</td>
<td>2.48</td>
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</table>

SMF specimens measured from Størmer (1973); specimens from Hombach are Pragian (to possibly earliest Emsian), the others are Early Emsian in age except the one from Lesmahagow. L, length; W, width.

(Kjellesvig-Waering, 1950), P. maria and P. maturakensis are not known.

Another possible character that might separate the Lesmahagow specimens from the German ones is in the relatively broad telson of the Scottish material. The only specimen with a completely preserved telson has a telson L/W ratio of 2.6. However, telson shape changes significantly during ontogeny in the genus; larger individuals having longer and more slender telsons. As reported for P. hefteri by Størmer (1973), the telsons of juveniles had a L/W ratio of 1.6, while larger individuals could have a L/W ratio of up to 3.4. The larger P. major, occurring in the same beds, had L/W ratios from 3.6–4.3. This trend of having longer telsons in adults is in contrast to that reported by Plotnick (1983: 71) for Eurypterus remipes DeKay, 1825. It is obvious that one needs to compare telson L/W ratios in similarly sized animals. A German P. hefteri of similar size as the Scottish specimen was figured by Størmer (1973: fig. 49), and has a L/W ratio of 3.0. A specimen of P. salteri, figured by Kjellesvig-Waering (1961: fig. 10) that is slightly larger than the Scottish telson.

The great variation in dimensions of VI-7 suggest that this character might be strongly influenced by ontogeny. With only this limited material at hand it is impossible to distinguish the paddles of the Scottish specimens from the paddles of similar-sized German P. hefteri.

Although we have tentatively identified subtle differences between the Parahughmilleria from Lesmahagow and P. hefteri, we feel the preservation of the metastoma that is observed through the carapace and the ontogenetically influenced telson shape are not sufficient to erect a new species, and we prefer to tentatively assign the three specimens described here to P. cf. hefteri.

Genus EYSYSLOPTERUS nov.

Type (and only) species. Hughmilleria patteni Størmer, 1934c.

Diagnosis. Carapace with slightly pointed anterior margin and bordered by narrow marginal rim; reniform eyes closer to lateral margin than to ocelli; ocelli on posterior half of carapace; anterior half of carapace with cuticular sculpture of deep transverse furrows.

Occurrence. The Rootskila Formation (Wenlock: Ho- merian) of the island of Saaremaa, west coast of Estonia.

Etymology. Eysis, after Eysysla – the Viking name for the island of Saaremaa – and opterus, the traditional suffix for eurypterid genera, derived from ‘wing’.

Remarks. The results of the phylogenetic analysis necessitate erection of this new genus (Fig. 2). However, apart from the recovery of a polyphyletic Nanahughmilleria, the taxonomy presently followed for the Adelophthalmoidea is consistent with the results recovered in this phylogenetic analysis.

Eysyslopterus patteni (Størmer, 1934c) (Fig. 7) v°9134c. Hughmilleria patteni n. sp.; Størmer: 245–246, 248–249, text-fig. 1, pl. 1 (figs 1–2).

1950 Hughmilleria patteni Størmer; Kjellesvig-Waering: 228.

1957 Hughmilleria patteni Størmer; Pirozhnikov: 207.

1961 Hughmilleria (Nanahughmilleria) patteni Størmer; Kjellesvig-Waering: 796.

1973 Parahughmilleria patteni (Størmer); Størmer: 176. 1999 Nanahughmilleria patteni (Størmer); Plotnick: 123.

Holotype (and only known specimen). AMNH 32720 – an isolated carapace.

Diagnosis. As for the genus.

Remarks. The taxa at the base of the three most derived clades of Eurypterina, the swimming eurypterids, Pterygotoidea, Adelophthalmoidea and an unnamed clade comprising Orcanopterus, Waeringopterus and Glossopterus, are very similar in many respects and the phylogenetic position of incompletely known taxa is therefore problematic. For the three clades discussed here, the only character
took the photographs. V. P. Tollerton (New York State Museum) provided data on A. mansfieldi. O.E.T. was funded by Norges Forskningsråd (the Norwegian Research Council) grant 166647/V30. This manuscript benefited from the comments on an earlier draft by Dr S. J. Braddy (University of Bristol) and V. P. Tollerton (New York State Museum), editorial comments from Dr A. B. Smith (Natural History Museum, London) and the reviews of S. J. Braddy and an anonymous reviewer.

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that seems to be useful in assigning basal taxa to clades is the eye position. Perhaps the most useful synapomorphy for the Pterygotidea is the marginally positioned eyes in adults, not found in any other eurypterids. The eyes in Orcanopterus, Waeringopterus and Grossopterus are all submarginal and this is likely to be the plesiomorphic condition for this part of the Eurypterina tree. The evolution of eye position in Adelophthalmoidea has taken a different route compared to the other two clades. The eyes in *Eysyslopterus patteni* are far from being marginal or submarginal and the taxon therefore probably belongs to the Adelophthalmoidea, in agreement with the assignment of all authors previously mentioning this species. However, the eyes are closer to the margin than in any other taxon belonging to the clade and, therefore, provide a valuable glimpse into the origin of the more centrally positioned eyes in later members of the Adelophthalmoidea. The eyes are placed most centrally in the genus *Adelophthalmus* where they are closer to the ocelli than to the carapace margin (Fig. 3). The carapace of *Eysyslopterus patteni* is illustrated in Fig. 7A and the cuticular sculpture of the anterior carapace margin in Fig. 7B. Comparison with the figure published by Størmer (1934c) shows that more than half of the cuticle has been lost from the carapace between 1934 and 2007.

**REFERENCES**


**APPENDIX: CHARACTER LIST AND DATA MATRIX**

1. Triangular ‘doublure lock’ anteriorly on carapace: 0: absent; 1: present.


3. Terrace lines on anterior carapace margin: 0: present; 1: absent.

4. Eye length: 0: short (shorter than a quarter of carapace length); 1: long (longer than a quarter of carapace length).
5. Semi-marginal eyes: 0 = present; 1 = absent.

6. Eye closer to margin than to ocelli: 0 = present; 1 = absent.

7. Vaulted central portion of carapace: 0 = absent; 1 = present.

8. Isolated large spine on V-7: 0 = absent; 1 = present.

9. Walking leg podomeres distally serrated: 0 = absent; 1 = present.

10. Raised ridge distally on podomeres: 0 = absent; 1 = present.

11. Length of paddle (VI-7–9)/width of paddle: 0 = > 3.2; 1 = < 2.76.

12. Length of VI-7 (including 7a)/width of VI-7: 0 = > 2.15; 1 = < 2.04.

13. Size of VI-9: 0 = large; 1 = small.

14. Metastoma shape: 0 = petaloid A; 1 = elongate vase-shaped; 2 = paraelliptical; 3 = oval; 4 = vase-shaped.

15. Metastoma posterior margin: 0 = truncated; 1 = rounded.

16. Laterally reduced anterior opisthosomal segment: 0 = absent; 1 = present.

17. Rounded postlateral angles anterior segment: 0 = absent; 1 = present.

18. Epimera on opisthosomal segments 2–6: 0 = absent; 1 = present.

19. Epimera on opisthosomal segment 7: 0 = absent; 1 = present.

20. Raised median triangle on segment 7: 0 = absent; 1 = present.

21. Epimera on opisthosomal segments 8–12: 0 = absent; 1 = present.

22. Size of epimera on 8–12: 0 = small; 1 = large.

23. Spatula on genital operculum: 0 = absent; 1 = present.

24. Size of genital spatula: 0 = small; 1 = large.

25. Genital zipfel A: 0 = long, slender; 1 = short, bulky.

26. Genital zipfel A termination: 0 = complex, tri-/tetrafurcate; 1 = simple, unicate/bilobed.

27. Genital zipfel A segments: 0 = 2; 1 = 3.

28. Telson shape: 0 = xiphus; 1 = lanceolate; 2 = styliform (see Tollerton 1989, fig. 15). Orcanopterus has a xiphus telsion, a telsion that expands in width posteriorly, while a lanceolate (evenly tapering) telsion is plesiomorphic within the Adelophthalmoidea and a styliform (rapidly tapering anteriorly to a narrow, gently tapering spike) telsion is a synapomorphy of Adelophthalmus.

29. Telson length: 0 = short (less than half of the length of the opisthosoma); 1 = long (more than half of the length of the opisthosoma).

30. Cuticular sculpture of transverse striae on anterior half of mesosomal segments: 0 = present; 1 = absent.

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