

Hallipterus excelsior, a Stylonurid (Chelicerata: Eurypterida) from the Late Devonian Catskill Delta Complex, and Its Phylogenetic Position in the Hardieopteridae

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ABSTRACT

The priority of the names *Stylonurus excelsior* and *S. lacoanus* from the Late Devonian of the eastern United States has been disputed since they were first recognized as synonyms. The genus *Hallipterus* was later erected for the two known specimens, and they were again separated into distinct species, based on six listed differences, seemingly resolving the priority dispute. However, four of the differences are not present or can be interpreted as ontogenetically or taphonomically induced, and the remaining two are putatively interpreted as sexually dimorphic based on comparisons with *Tarsopterella*, a closely related taxon. The two species are therefore synonymized again and the species epithet *excelsior* is considered to have priority. Advocates of both names also provided different reconstructions, mainly based on other stylonurids. *Hallipterus* is placed in the Hardieopteridae based on putative synapomorphies with *Hardieopterus* and particularly *Tarsopterella*, the latter also clearly a hardieopterid, and the phylogenetic position of the Hardieopteridae is discussed. Although only the original two specimens of *H. excelsior* are known today, as a century ago, a new reconstruction is provided, supported by phylogenetic evidence, to replace the two earlier versions.

KEYWORDS

Carapace, Catskill delta, chelicerates, eurypterid, ICZN, North America, synonymy.

Introduction

Eurypterids, commonly referred to as sea scorpions, are chelicerate arthropods that lived in marginal marine environments during the middle Paleozoic Era, and which later in the Paleozoic inhabited mainly lacustrine, fluvial and estuarine environments. Eurypterida was the most diverse chelicerate order before the Permian mass extinction, according to the current fossil record. However, several of the species represented in this diversity are based on undiagnostic material, and revising material to evaluate the true diversity of Eurypterida is a continuous effort.

Eurypterids include some of the largest and most impressive arthropods ever to inhabit the planet. Largest of all were the Silurian and Early Devonian pterygotid eurypterids, which occasionally reached lengths of more than 2 m; the largest fragments suggest total lengths (including chelicerae) of more than 3 m (Braddy et al. 2008).

Some of the stylonurids (forms without swimming legs) were also very large, especially those of Devonian to Permian age, when they chiefly occur in deposits of fluvial and lacustrine origin. The largest of these were the hibbertopterids; one carapace of *Hibbertopterus scouleri* (Hibbert, 1836) from the Carboniferous of Scotland is 65 cm wide (Jeram and Selden 1993). These eurypterids were very wide compared to their length, and an animal with a 65-cm-wide carapace was probably less than 2 m long. The hibbertopterids were extremely deep-bodied compared to other eurypterids, and although their body mass has not been estimated, they would certainly rival any other arthropod in weight. The Late Devonian genus *Hallipterus* Kjellesvig-Waering, 1963, which might be related to the hibbertopterids, was slightly smaller. Only two specimens can be assigned to *Hallipterus*, and these two suggest animals approaching at least 1 m in length; earlier estimates of 1.5 m

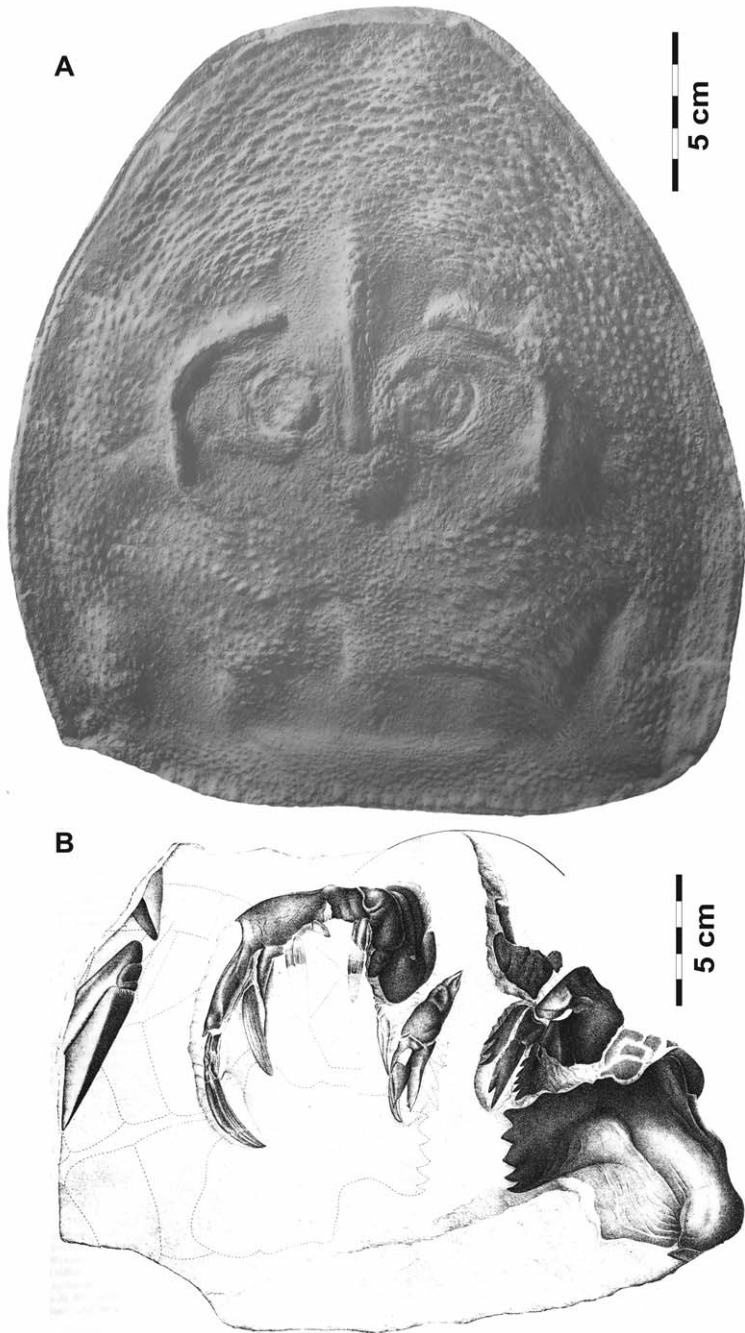


FIGURE 1. *Hallipterus excelsior*. A. Photograph of the illustration provided by Clarke and Ruedemann (1912, pl. 48). B. Interpretive drawing of the ventral appendages of the Claypole specimen (modified from Hall and Clarke 1888, pl. 26A).

(Beecher 1900; Clarke and Ruedemann 1912) are probably too high.

The two fossils referred to *Hallipterus* were found and described almost simultaneously around 1883 (Claypole 1883; Hall 1884a), a coincidence that later caused much confusion about the priority of the names. The two names were recognized at an early stage as synonyms (Hall and Clarke 1888). Advocates of both available names, *Stylonurus lacoanus* (Claypole, 1883) and *S. excelsior* Hall, 1884a, supported priority. Hall and Clarke (1888), Clarke and Ruedemann (1912) and Ruedemann (1939) supported the priority of *S. excelsior*, while Beecher (1900) supported *S. lacoanus*. Each group provided its own reconstruction (Beecher 1900; Clarke and Ruedemann 1912), as if to further justify their claims for priority. Kjellesvig-Waering (1963) erected the genus *Hallipterus* and interpreted both species as valid, based on six differences between the two specimens, thereby seemingly resolving the priority dispute.

The present study suggests that four of the differences noted by Kjellesvig-Waering (1963) can be explained as effects of taphonomy or ontogeny. The other two differences are interpreted as examples of sexual dimorphism, since they are also noted in the closely related *Tarsopterella scotica* (Woodward, 1865), and it is here suggested that *H. excelsior* and *H. lacoanus* are indeed synonyms, as claimed before 1963. Drawing on the International Code of Zoological Nomenclature (ICZN 1999), the name *Hallipterus excelsior* is retained, based on the action of the first reviser of the taxon. The morphology of the carapace suggests a close phylogenetic relationship to the Early Devonian *T. scotica* and the Early Silurian form *Hardieopterus macrophthalmus* (Laurie, 1892), both from Scotland. I provide a phylogenetic model of the Hardieopteridae and, on the basis of these relationships, new reconstructions of *Hardieopterus macrophthalmus* and *Hallipterus excelsior* to accommodate these observations.

Historical Research

The history of the two names *lacoanus* and *excelsior*, introduced almost simultaneously for two specimens of *Hallipterus* from a similar horizon and nearly the same area, is full of contradictory

statements about publication dates. The timeline unfolded something like this, mainly based on the account of Beecher (1900) and dates in the published works: In 1882 James Hall received from Dr. Cook, State Geologist of New Jersey, a plaster cast of a complete carapace of a large stylonurid (Figure 1A) from the Catskill Group of New York State, USA. D. S. Martin, who examined the cast sent to Hall at the New York State Museum in Albany, New York, made the first reference to the specimen before the New York Academy of Sciences, in an abstract dated 16 October 1882. The specimen was neither figured nor described, but Martin introduced the name *Stylomurus* [sic] *excelsior* without any reference to Hall; the name is clearly a *nomen nudum*. The next mention was probably of the second specimen (but the order of events is equivocal; see below), a larger, less complete and more poorly preserved carapace also from the Catskill Group, but from Pennsylvania, USA. Claypole (1883) presented this to the American Philosophical Society on 21 September 1883. He erected the name *Dolichocephala lacoana*, and this paper was printed on 2 November 1883. Hall (1884a) published his full description of the more complete carapace (see Figure 1A) in the 36th Annual Report of the New York State Museum under the name *Stylonurus excelsior*. An inscription in front of this report reads: "Transmitted to the legislature January 12, 1883," suggesting that the report was finished and sent to the printer long before Claypole gave his paper. The New York State Museum report was apparently printed in 1884, but a copy in the Geology Library at Yale University includes a handwritten note beside the 1884 date that says "some copies seem to be dated 1883." Hall (1885) repeated some aspects of his original description of the carapace, but was still not aware of the specimen described by Claypole.

Hall and Clarke (1888) were the first to consider the two species synonymous. They developed the ventral side of the Claypole specimen, exposing parts of the prosomal appendages (see Figure 1B), and figured both specimens as *S. excelsior*. The generic name *Dolichocephala* used by Claypole (1883) had already been introduced by Macquart (1823) for a dipteran (Insecta), but the two eurypterid specimens were united under the name *Stylonurus excelsior* by Hall and Clarke

(1888) before this was discovered. Beecher (1900) disputed the priority of *S. excelsior*, noting that Claypole's paper predated the 1884 report with Hall's description. Later, Ruedemann (1939) refuted Beecher's claim and stated that, while Claypole's paper was printed on 2 November 1883, Hall's paper had to be published before the end of the fiscal year, which at the time was 30 September 1883, according to New York State Senate laws.

Priority of Name

Hall, Clarke and Ruedemann, in their subsequent mentions of the species (e.g., Hall and Clarke 1888; Clarke and Ruedemann 1912; Ruedemann 1939) use the name *Stylonurus excelsior* Hall and refer to the abstract of Martin (1882). However, since Martin did not mention Hall and provided only a misspelled name with no description, illustration or diagnosis, Martin's name should be considered a *nomen nudum* (see above). The confusion as to whether Claypole or Hall first published the description makes it more or less impossible to determine which name has priority by publication date. Beecher (1900) was convinced that Claypole's name was published first, and that Hall's paper appeared a few months later than Claypole's, supported by the 1884 date in the report in which Hall's description appeared. Ruedemann (1939) claimed that Hall's paper was published before Claypole's, based on the printing requirements of the New York State legislature. Claypole's description was published at the end of 1883. While Hall's paper came out either at the end of 1883 or the start of 1884, clearly Hall's description was prepared a year before its publication.

Hall and Claypole must have worked more or less simultaneously on their descriptions without knowledge of the other's work, but precedence cannot be determined objectively in this case, although most of the evidence suggests that Claypole's name was published first. Whatever the true timing of events, the result was that Hall's name *Stylonurus excelsior* was used from 1885 until 1963, when Kjellesvig-Waering interpreted both species as valid.

The International Code of Zoological Nomenclature (ICZN 1999), article 24.2.1, states: "When the precedence between names or

nomenclatural acts cannot be objectively determined, the precedence is fixed by the action of the first author citing in a published work those names or acts and selecting from them; this author is termed the 'First Reviser'." In this particular case, the first revisers are Hall and Clarke (1888) as the first to realize the synonymy of the two specimens and, according to the Code, their nomenclatural act gives precedence to *S. excelsior* over *S. lacoanus*.

Materials and Methods

The specimens of the gigantic Late Devonian stylonurid are at the Rutgers University Geological Museum (RUGM 232), New Brunswick, New Jersey, USA (the Hall specimen "S. excelsior") and at the United States National Museum (USNM 25673), Washington, D.C. (the Claypole specimen "S. lacoanus"). However, there are excellent reproductions in many museums. The casts and model examined here are at the Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA (YPM 33545 [Hall specimen] and YPM 33546 [Claypole specimen]). The photographs were made using a Sony Cyber-shot® DSC-H5 digital camera. Most morphological terminology follows Tollerton (1989) and terminology for the synapomorphies of the Hardieopteridae is adopted from Tetlie (2004).

Geological Setting

It is not known precisely from which stratigraphic horizons the two specimens originated (Plotnick 1983). The incomplete specimen from Meshoppen, Pennsylvania, seems to be from the Catskill Formation of Fammenian age, while the complete carapace from Andes, New York, is from lower in the sequence. At lower elevations at Andes, the lower Walton Formation of the Sonyea Group is exposed, while the upper Walton Formation of the West Falls Group is exposed at higher elevations; however, the entire Walton Formation is apparently Frasnian (R. Plotnick, pers. comm. 2007). The sections are both within the Catskill Magnafacies, which is a Middle to Late Devonian sequence of shale, limestone, siltstone and sandstone preserved within the Allegheny syncline. This mainly clas-

tic wedge represents a progradational sequence that accumulated in a foreland basin on the western slopes of the eroding mountains produced by the Acadian orogeny, which has been dated at 380 to 410 Ma (Isachsen et al. 1991). The sequence is thickest towards the west, reaching more than 2300 m in thickness close to the New York–Pennsylvania border, and thins eastwards. The nonmarine sequences have generally been interpreted as fluvial in origin (Johnson and Friedman 1969) and detailed work by Gordon and Bridge (1987) allowed reconstruction of much of this fluvial system. The common carbonate is indicative of lacustrine settings (Dunagan and Driese 1999) or brackish settings along the paleoshoreline (Knox and Gordon 1999). Both known specimens occur in olive sandstone, probably laid down in a river channel. It was this river system that *Hallipterus excelsior* inhabited; many other late Paleozoic stylonurid eurypterids are also encountered in freshwater deposits. *Tarsopterella scotica* and the other stylonurids from the Early Devonian of the Midland Valley of Scotland were also found in sediments representing a fluvial system (e.g., Braddy 2000, fig. 4). Earlier in the Paleozoic, many stylonurid eurypterids, such as the Silurian *Hardieopterus macrophthalmus*, were apparently fully marine (Anderson et al. 2007).

Phylogenetic Position

Originally *H. excelsior* was considered to be in the genus *Stylonurus*, to which most species of stylonurid eurypterids then belonged. Hall and Clarke (1888) and Beecher (1900) did not indicate to which other species of *Stylonurus* *H. excelsior* was closely related, although the three species that aided Beecher's reconstruction must have been considered close (see Reconstructions of *Hallipterus excelsior*, below). Clarke and Ruedemann (1912) were the first to consider relationships within the genus, when they erected the subgenus *S. (Ctenopterus)* for some species, including *S. (C.) excelsior*, *S. (C.) cestrotus* (Clarke, 1907) and *S. (C.) elegans* (Laurie, 1899). The genus *Laurieipterus* was erected for *S. (C.) elegans* by Kjellesvig-Waering (1966), who had already suggested (Kjellesvig-Waering 1963) that *Hallipterus* was more closely related to *Tarsopterella* than to *Ctenopterus* and *Laurieipterus*, a

suggestion endorsed here. Tollerton (1989) placed *Hallipterus* in the Laurieipteridae, and *Hardieopterus* in his new family Hardieopteridae, but did not place *Tarsopterella* because of the virtually unknown prosomal appendages. Tetlie (2004) identified several synapomorphies uniting *Tarsopterella* and *Hardieopterus*, but did not identify *Hallipterus* as a hardieopterid. *Hallipterus* is considered here to belong to the Hardieopteridae for the following reasons: (1) it shares with both *Hardieopterus* and *Tarsopterella* the coarse ornamentation of semilunate scales following the carapace margin; (2) this ornamentation is indented anteriorly along the mid-line on the carapace in all three taxa; (3) there is a similar row of raised pustules along the posterior margin of the carapace in all three taxa; (4) the ocellar ridge (the ridge along the mid-line of the carapace) present in *Hallipterus* is also found in *Tarsopterella* and *Hardieopterus* (not reconstructed by Waterston [1979], but described in the text); (5) the orbital ridges (the crescentic ridges anterior and lateral to the eyes) present in *Hallipterus* are also found in *Tarsopterella*, although very poorly developed and more anteromedially positioned than in *Hallipterus*; (6) the eye shape, size and position are more or less identical in *Hallipterus* and *Tarsopterella*; and (7) a raised, circular “pre-ridge area” is present anterior to the ocellar ridge in both *Tarsopterella* and *Hallipterus*.

The following characters were defined as synapomorphies for Hardieopteridae (Tetlie 2004) since the family is defined to include only *Hardieopterus* and *Tarsopterella*: (1) lateral pleural epimera on postabdomen; (2) pretelson with dorsal lateral lobes; and (3) xiphous telson (see Tollerton 1989). Clearly, there are similarities between the cuticular ornaments on the posterior half of the tergites in these two taxa, but the value of this as a synapomorphy is presently equivocal. The Silurian taxa *Kokomopterus longicaudatus* Clarke & Ruedemann, 1912 and *Lamontopterus knoxae* Waterston, 1979 are also basal (or a sister group) to the Hardieopteridae, but lack most of the synapomorphies uniting the Hardieopteridae, such as the lateral pleurae and several of the carapace features listed above (Tetlie 2004). However, shared characters include the telson shape, the demarcated lateral “rim” of the opisthosoma, and the spiniferous fifth prosomal

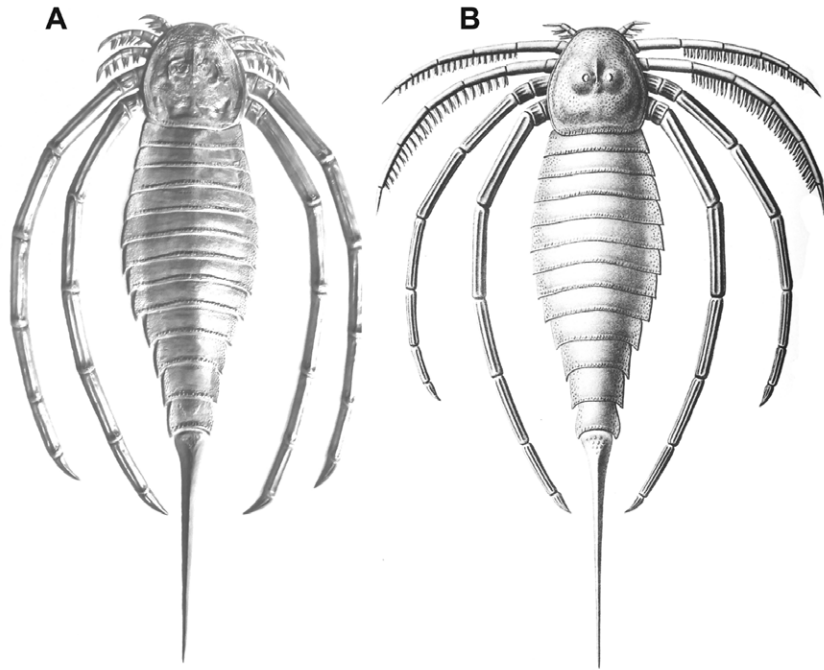


FIGURE 2. *Hallipterus excelsior*. **A.** Model by Beecher (1900), YPM 220638. **B.** As reconstructed by Clarke and Ruedemann (1912, pl. 47).

appendage. It is not presently known whether the Upper Paleozoic forms in the Woodwardopteridae and Hibbertopteridae originated within this clade that, at least basally, is characterized by a spiniferous appendage V. There are similarities between the metastomata, with a posterior indentation found in *Kokomopterus* (see Kjellesvig-Waering 1966 and Størmer 1974) and *Hardieopterus* (see Waterston 1979), and the posteriorly cleft metastoma present in *Hibbertopterus* (see Waterston 1957), but this is poor evidence on which to postulate a phylogenetic relationship. *Stylonurus* likewise shares some characters, like a lateral “rim” of the opisthosoma, an ocellar ridge, and eye shape and position, but lacks many of the other characters.

Reconstructions of *Hallipterus excelsior*

Beecher (1900) first reconstructed *H. excelsior* as an animal of 147 cm total length, scaled on the sizes of the isolated carapaces (YPM 220638, Figure 2A). He used comparisons with the two British species *Stylonurus powriei* Page, 1856 and *Stylonurella spinipes* (Page, 1859) and the Amer-

ican species *Stylonurella* (?) *beecheri* (Hall, 1884b). Clarke and Ruedemann (1912) responded to Beecher’s attack on the priority of Hall’s name by providing their own reconstruction of *H. excelsior* (Clarke and Ruedemann 1912, pl. 47), which is similar to that of Beecher (1900), differing mainly in the reconstruction of the prosomal appendages III–V (see Figure 2B). Clarke and Ruedemann (1912) reconstructed appendages III–V mainly after the morphology observed in *Ctenopterus cestrotus*, giving the third and fourth appendage a comb-like appearance and illustrating the fifth appendage as shorter than reconstructed by Beecher (1900). Clarke and Ruedemann (1912:292) stated that “*S. excelsior* is, according to the form and character of the carapace, manifestly more nearly related to the species [*Ctenopterus cestrotus*] than to any other...” Clarke and Ruedemann’s reconstruction also indicated an animal around 150 cm in length. Both reconstructions were based on taxa that were interpreted as closely related (almost all stylonurids were at this time assigned to the genus *Stylonurus*), but are now known to be phylogenetically distant from *H. excelsior*. A new reconstruction is presented here (Figure 3), suggesting that earlier

reconstructions have overestimated the known size range of *Hallipterus*. To fit a *Hallipterus* carapace to an opisthosoma similar to that of *Tarsopterella*, a length slightly in excess of 100 cm is more realistic, given the material known today. From the phylogenetic considerations discussed here, the new reconstruction is based mainly on other hardieopterids. The prosomal appendages in the new reconstruction (see Figure 3) are a mixture of features from *Hallipterus* and *Hardieopterus*. The general aspects of the opisthosoma and telson have been reconstructed after *Tarsopterella scotica*. This new reconstruction is almost certainly not accurate in all respects, but it is here considered a more reasonable reconstruction than those of either of Beecher (1900) or Clarke and Ruedemann (1912). The reconstructions of the latter authors have commonly been used, especially in textbooks (see synonymy list and cited references), and an updated reconstruction is justified on that basis.

Results

Although the two specimens were considered to belong to a single species after 1888, Kjellesvig-Waering (1963) suggested six differences between the two carapaces and concluded that they represented distinct species. The six differences that Kjellesvig-Waering (1963) used to distinguish *H. lacoanus* from *H. excelsior* were: (1) the presence of a sharp ridge anterior to the ocellar ridge; (2) ocellar mound further posterior to the eyes; (3) ocellar mound and ocellar ridge proportionally wider; (4) smaller eyes; (5) orbital ridges further away from eyes; and (6) much coarser ornamentation.

However, Kjellesvig-Waering (1963) ignored three possible explanations for these differences: ontogeny, taphonomy and sexual dimorphism. The incomplete carapace (*H. lacoanus*) described by Claypole (1883) is around 10% larger than the complete carapace (*H. excelsior*) described by Hall (1884a). The incomplete carapace is wrinkled and folded, and in a much less favorable state of preservation than the complete carapace. The anterior ridge (difference 1) seems longer and higher in the incomplete carapace, as described by Kjellesvig-Waering (1963), but this is interpreted here as a result of distortion, perhaps combined with an underestimation by

Kjellesvig-Waering (1963) of the ridge length on the complete carapace. The ridge is approximately 95 mm long on the complete carapace and 110 mm on the other carapace; that is, the difference in ridge length is approximately proportional to the differences in carapace size. The ridge in the incomplete carapace is more elevated than on the other specimen. However, this ridge is not straight as it originally would have been; this supports the interpretation that the ridge elevation was introduced by wrinkling prior to fossilization. The ocellar mound (difference 2) does not lie farther posterior to the eyes in the incomplete carapace: the posterior margin of the ocellar mound is around 6 mm posterior of the posterior margin of the eyes in both specimens.

The ocellar mounds do indeed differ in size (difference 3). When comparing them in the two specimens (see Clarke and Ruedemann 1912, text-fig. 66 [incomplete carapace], pl. 48 [com-

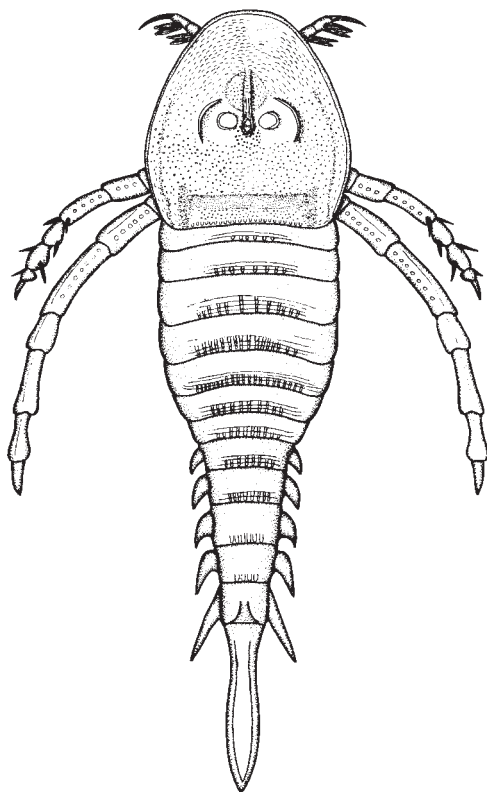


FIGURE 3. Idealized reconstruction of *Hallipterus excelsior*. Opisthosoma and telson predominantly based on *Tarsopterella scotica*, and appendages based on *Hardieopterus macrophthalmus* and evidence from the Claypole specimen of *H. excelsior*.

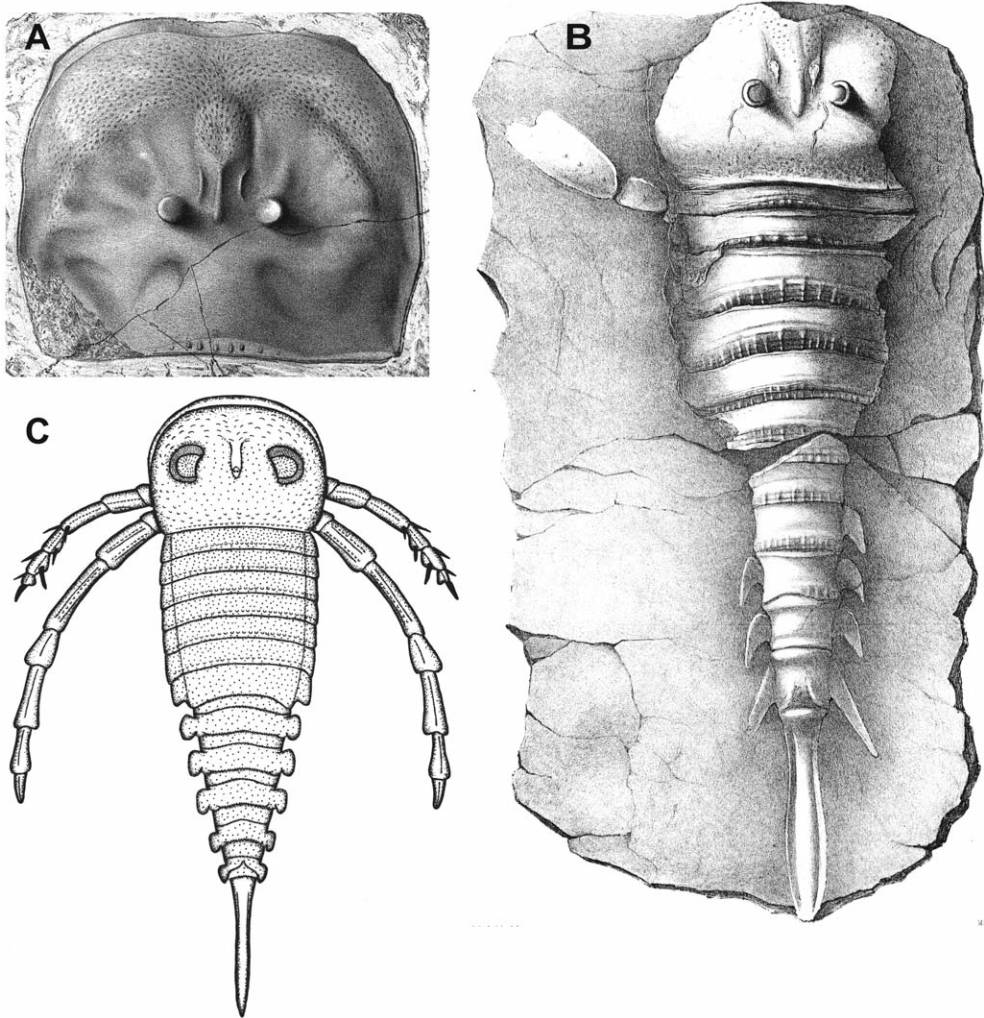


FIGURE 4. *Tarsopterella scotica* and *Hardieopterus macrophthalmus*. A. Isolated carapace of *T. scotica* (from Woodward 1866–1878). B. Almost complete specimen of *T. scotica* (from Woodward 1866–1878). C. Reconstruction of *H. macrophthalmus* (redrawn and modified from Waterston 1979). Not to scale.

plete carapace]), it is easy to see a difference in preservation. The ocellar mound area is the only part of the incomplete carapace that is preserved in better detail than in the complete carapace. The ocellar ridge is oval in both cases and extends laterally almost to the eyes. Inside the oval, a flat terrace surrounds the ocellar mound, which is situated slightly behind the center of the ocellar ridge. Both the ocellar mound (10 mm wide) and the terrace surrounding it (14 mm wide) are more pronounced in the incomplete carapace than in the complete one, for which the corresponding values are 5 mm and 10 mm, respectively. This difference would possibly justify

separating the specimens into different species of *Hallipterus*, but the two known specimens of *Tarsopterella scotica* also show a similar variation in the width of the ocellar ridge, the isolated carapace having a narrower ridge than that found in the more complete specimen (Figure 4A, B). Nothing is known about sexual dimorphism in these eurypterids, although the carapaces known from *Hardieopterus macrophthalmus* (see Waterston 1979) suggest a similar type of sexual dimorphism in carapace length-to-width ratio as seen in *Rhenopterus diensti* Størmer, 1936 (see Tetlie et al. 2004) and *Parastylonurus ornatus* (Laurie, 1892) (see Waterston 1979). Based on

the two individuals of *H. excelsior* and two *T. scotica*, it seems a more parsimonious view to consider both as examples of sexual dimorphism rather than as two species of each genus.

The eyes in the incomplete carapace are not smaller (difference 4) than those in the complete carapace: they are about 22 mm long in both. It is possible that Kjellesvig-Waering misinterpreted the eye size of the incomplete carapace because of the difference in preservation between the two carapaces. Because the incomplete carapace is larger, the eyes might be proportionally smaller in the larger specimen; it is well known that smaller eurypterids have proportionally larger eyes than larger exemplars of the same species (e.g., Andrews et al. 1974; Brower and Veinus 1974). The orbital ridges are farther away from the eyes in the incomplete carapace (difference 5), especially anterior (16 and 12 mm, respectively) and lateral (30 and 21 mm, respectively) to the eyes. It is impossible to compare this observation with the two specimens of *T. scotica* since this taxon has very underdeveloped orbital ridges, only present anteromedially to the eyes. There is no evidence of a difference in the size of the ornament (difference 6). The ornamentation is generally poorly preserved in the incomplete specimen, but is comparable to that in the complete specimen, at least within the 10% size disparity in the two specimens. Both specimens have very large semicircular scales anterior to the eyes and smaller, but still quite large, pustulate ornament on the rest of the carapace. The largest pustules are around 3 mm in diameter and the largest scales around 7 mm in width on both specimens. Again, this is comparable to *T. scotica*, in which there is no evidence for substantial differences in ornament between the two specimens.

Discussion

Several clear synapomorphies between *H. excelsior* and the two hardieopterids, *Hardieopterus macrophthalmus* and *Tarsopterella scotica*, indicate that *H. excelsior* should also be considered a hardieopterid. These synapomorphies are the carapace ornament and its unique patterns, especially anteriorly, but also posteriorly on the carapace, the ocellar ridge, the orbital ridges, eye shape, size and position, and a raised, circular “pre-ridge area.” The orbital ridges, eyes and

“pre-ridge area” are different or lacking in *Hardieopterus* compared to *Hallipterus-Tarsopterella*, indicating the phylogenetic topology (*Hardieopterus* (*Tarsopterella* + *Hallipterus*)) that is also concordant with their stratigraphic occurrence. In the new reconstruction of *H. excelsior*, most emphasis has therefore been made in reconstructing unknown morphology from *Tarsopterella*, but appendages are mainly from *Hardieopterus* (see Figure 4C), since they are practically unknown in *Tarsopterella*.

Among the differences claimed by Kjellesvig-Waering (1963) that separate *H. excelsior* from *H. lacoanus*, points 2, 4 and 6 above are not valid. Point 1 is valid, but is here explained partly as a taphonomic artifact and partly by size differences between specimens. Two of the differences (points 3 and 5) are undeniably present: the wider ocellar mound and corresponding ocellar ridge and the different position of the orbital ridges. The difference in ocellar ridge morphology is also seen in the two known carapaces of the close relative *Tarsopterella scotica* (see Figure 4A, B), while *T. scotica* only has rudimentary orbital ridges that cannot be compared to those in *H. excelsior*. It is tempting to interpret the differences in ocellar ridge morphology as a result of sexual dimorphism, because the same dimorphism is seen in these closely related taxa. This suggests that the difference in orbital ridge morphology might also be favorably interpreted as sexual dimorphism, although the differences are relatively minor and could also be individual differences. With such limited material, it is not advisable to treat the two specimens as separate species, because by following the same line of evidence we would also need to split *T. scotica* into two species on the basis of the same character(s).

Systematic Paleontology

ORDER Eurypterida Burmeister, 1843

SUBORDER Styronurina Diener, 1924

SUPERFAMILY uncertain

FAMILY Hardieopteridae Tollerton, 1989

Remarks. The family was created by Tollerton (1989) only to include the type genus, the Lower Silurian *Hardieopterus*. Tollerton (1989) included *Hallipterus* in the Lauriepteridae Kjellesvig-Waering, 1966 and *Tarsopterella* as *incertae sedis*. Tetlie (2004) pointed out clear synapomorphies between *Hardieopterus* and *Tarsopterella*, namely the lateral pleura, or

epimera of the postabdominal segments originating on the lateral edge rather than on the posterolateral corner, as in other eurypterids. In addition, both genera have a pretelson with dorsal lobes (Tetlie 2004); i.e., raised lateral areas separated by a depression along the mid-line (see Figure 4B, C). There are strong similarities between many carapace characters in the two Devonian genera *Tarsopterella* and *Hallipterus* (as outlined above). All these three genera are therefore included here in the Family Hardieopteridae.

Some other eurypterid genera that could also be related to the Hardieopteridae are in the Family Kokomopteridae (i.e., *Kokomopterus* Kjellesvig-Waering, 1966 and *Lamontopterus* Waterston, 1979). Tetlie (2004) suggested that this family was sister taxon to the Hardieopteridae. The systematic relationship of some other taxa with a ocellar ridge, like *Stylonurus powriei* and *Stylonurus* sp. (Plotnick and Elliott 1995), with respect to the Hardieopteridae, is currently hard to resolve because they lack many of the other synapomorphies uniting the clade. A relationship between the Hardieopteridae and the late Paleozoic hibbertopterids and woodwardopterids cannot be ruled out, but the evidence for this is presently equivocal.

GENUS *Hallipterus* Kjellesvig-Waering, 1963

Type and only species. *Stylonurus excelsior* Hall, 1884a by original designation.

Discussion. Based on this revision, only the species *H. excelsior* can be assigned to the genus *Hallipterus*.

Diagnosis. Large hardieopterid with triangular carapace; ovoid eyes in a central position; prominent orbital ridges surrounding eyes; median eyes on prominent, elongate ocellar ridge between eyes; pedipalp with flattened, foliate spines; carapace with ornament of large pustuled sculpture and large lunate sculpture largely parallel to carapace margin.

Hallipterus excelsior (Hall, 1884a)

Figures 1, 2 and 3

- Stylonurus* [sic] *excelsior*; Martin 1882:8 [*nomen nudum*].
Dolichocephala lacoana Claypole; Claypole 1883:238-239, fig. e, pl. 1.
Stylonurus excelsior Hall; Hall 1884a:77, pl. 5; Hall 1885:421; Hall and Clarke 1888:158, 160, 221-222, pl. 26, 26A; Lesley 1889:1139-1142, 2 figs; Miller 1889:568; Laurie 1893:519; Laurie 1899:582; Clarke 1913:784, fig. 1510; Woodward 1913:297; Ruedemann 1916:134; Grabau 1921:433, fig. 1137; Kjellesvig-Waering 1934:386; Størmer 1934:23; Ehlers 1935:291; Twenhofel and Schrock 1935:468, fig. 172c; Ruedemann 1939, card 8; Waterlot 1953:537, fig. 24.
Stylonurus lacoanus Claypole; Beecher 1900:145-149, pl. 1; Grabau and Shimer 1910:414, fig. 1715.
Stylonurus (*Ctenopterus*) *excelsior* Hall; Clarke and Ruedemann 1912:292-295, figs. 65-66, pl. 47-48; O'Connell 1916:48; Ruedemann 1921:88; Versluys 1923:315, fig. 14; Diener 1924:23; Størmer 1934:34; Størmer 1944:50, fig. 10(4).
Stylonurus excelsior [sic]; Størmer 1935:7, fig. 3d.

Ctenopterus excelsior (Hall); Størmer 1936:33; Augusta and Přibyl 1951:3-4; Lamont 1955:209; Waterston 1962:141, 143.

Ctenopterus (?) *lacoana* (Claypole); Størmer 1955:38, fig. 27(4b); Kjellesvig-Waering 1961:81.

Hallipterus excelsior (Hall); Kjellesvig-Waering 1963:491-493; Kjellesvig-Waering 1966:192; Størmer 1969:26; Waterston 1979:294; Plotnick 1983:388; Copeland and Bolton 1985:16, fig. 8A; Tetlie 2004:115, 230.

Hallipterus lacoanus (Claypole); Kjellesvig-Waering 1963:491-493; Kjellesvig-Waering 1966:192; Briggs and Rolfe 1983:385; Plotnick 1983:388; Tetlie 2004:115.

Hallipterus locanus [sic] (Claypole); Størmer 1969:26.

Discussion. The reconstructions of this species are popular in geology textbooks and overviews of eurypterid groups. However, as discussed here, these reconstructions are erroneous; a lesson to be learned from this is that reconstructions should really not be based on very fragmentary material. An updated reconstruction is attempted here to replace two clearly erroneous precursors.

Types. RUGM 232 (carapace in dorsal view and its counterpart) must now be considered the holotype of *H. excelsior*, while the former holotype of *H. lacoanus*, USMN 25673 (a more poorly preserved and incomplete carapace showing chelicera and appendage II on the ventral side) must now be considered a hypotype.

Diagnosis. As for the genus.

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