

Kiaeropterus (Eurypterida; Stylonurina) recognized from the Silurian of the Pentland Hills

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Synopsis

Eurypterus cyclophthalmus Laurie, 1892 from the Llandoverly of the Pentland Hills, Scotland, is redescribed and assigned to the stylonurid eurypterid genus *Kiaeropterus* Waterston, 1979, previously only known from *Kiaeropterus ruedemanni* (Størmer, 1934) from the Wenlock of Norway. Another species previously assigned to *Kiaeropterus*, *K. otisius* Clarke 1907, is reassigned to the previously monotypic genus *Clarkeipterus* Kjellesvig-Waering 1966. The genus *Kiaeropterus* shares a previously unrecognized synapomorphy with the genus *Brachyopterus* Størmer 1951, namely a large bulbous 'ocellar area'. In *Kiaeropterus* this area is cardioid whereas it is triangular in *Brachyopterus*. The two genera also share a number of less significant characters such as large anteriorly converging crescentic eyes, a lack of cuticular ornament and podomeres of the prosomal appendages with pronounced ridges, supporting a phylogenetic relationship between *Kiaeropterus* and *Brachyopterus*.



Introduction

The eurypterid *Eurypterus cyclophthalmus* was described by Laurie (1892) based on a single specimen from the Lower Silurian (Llandoverly) Eurypterid Bed of the Pentland Hills near Edinburgh, Scotland. The Gutterford Burn Eurypterid Bed was discovered in 1880 by Mr John Henderson, Curator of the Phrenological Museum, Edinburgh, and this specimen was acquired as part of a larger collection, through purchase by the Edinburgh Museum of Science and Art (the forerunner of the National Museums of Scotland, Edinburgh) in 1885. At the time of initial description, knowledge regarding eurypterid taxonomy was in its infancy, and as a result almost all eurypterids were assigned to the genus *Eurypterus* DeKay 1825. In this case, an assignment to *Eurypterus* was not unreasonable, due to the limited preservation of appendages in the specimen, morphological characteristics which have found major use in taxonomic classification of the group. The relevance of this specimen came to our attention when one of us (O.E.T.) prepared a phylogeny of the *Eurypterus*-clade, and specimens of the two species assigned to *Eurypterus* (*E. minor* and *E. cyclophthalmus*) from the Pentland Hills were restudied. *E. minor* has all the characteristics of a *Eurypterus*, whilst *E. cyclophthalmus* does not. The large eyes of *E. cyclophthalmus* had been noted since the original description, but the fact that crescentic eyes are more commonly found in stylonurid eurypterids (i.e. forms with appendage VI developed into walking legs) than in swimming forms, had not.

This study places *E. cyclophthalmus* with the stylonurids. However, at the outset, it was debated whether *E. cyclophthalmus* belonged in the stylonurid genus *Alkenopterus*, based on the description of two species of *Alkenopterus* from the Siegenian and Emsian of western Germany by Poschmann & Tetlie (2004), but detailed study of the lesser known stylonurids revealed more similarities to *Kiaeropterus ruedemanni* (Størmer 1934a) than *Alkenopterus*. A lack of consideration of the morphology accurately described by Laurie (1892) and the poorly known morphology of *K. ruedemanni* probably explains why the species has remained within the genus *Eurypterus* for so long (i.e. Kjellesvig-Waering 1958).

The phylogeny of stylonurid eurypterids has proved more difficult to resolve than that of nektonic eurypterids (*Eurypterina sensu* Novojilov 1962), and any new information relating to stylonurids is therefore of importance. This reassignment moves the first appearance of the genus *Kiaeropterus* approximately 5 million years back from the Late Wenlock (425 Ma) to the Late Llandoverly (430 Ma), a time when most eurypterid families first appear (Tollerton 2004). The specimen also adds to our meagre knowledge of the overall morphology of *Kiaeropterus*.

Material and methods

The only known specimen of *K. cyclophthalmus* consists of the counterpart to that figured by Laurie (1892) and is housed in the Type and Figured collections of the

National Museums of Scotland (NMS), Edinburgh, registered as NMS G.1885.26.72P. The more complete part described and figured by Laurie (1892, pl. III, fig. 15) could not be located, so we must make do with the less complete counterpart and Laurie's figure of the part. It was explicitly stated by Laurie (1892, p. 151) that he 'was given an opportunity of examining Mr Henderson's collection, which was acquired by the Museum some years since', suggesting that the missing part was originally in the NMS collection.

Consultation of the original collection register in the NMS does not detail the exact composition of the collections Henderson sold to the museum. A later typed copy of the register for this period does list NMS G.1885.26.72P amongst a suite of '521 Carboniferous and Silurian fossils' purchased from John Henderson. However, other eurypterid fossils registered under NMS G.1885.26.72A – NMS G.1885.26.72R received a letter suffix for both the part and counterpart where present. NMS G.1885.26.72P has only a single register entry, and as such the single counterpart specimen appears to be the only fossil registered under this number. Furthermore, a card index of the Type and Figured invertebrates prepared by the former Keeper, Dr C. D. Waterston, details 'Counterpart of the Holotype, reverse of the type figured by M. Laurie ...' to accompany this registration number. This leads us to believe that the fossil part originally illustrated by Laurie (1892) may well have accompanied the original acquisition, but subsequent to Laurie's examination of the material and prior to the compilation of the typed register, the specimen had gone missing. R. E. Plotnick has informed us (pers. comm. 2005) that the figured specimen was already missing in 1975, when he came to Edinburgh to study the eurypterid collections.

In any case, the counterpart is figured here for the first time. All mention of 'left' and 'right' refers to left or right on the counterpart, directions that would be the opposite in life position, and on the missing part. Morphological terminology follows Tollerton (1989) and the term 'ocellar area' is introduced for the large, raised area between the eyes, and taxonomy follows Novojilov (1962). The following abbreviations are used in the *camera lucida* drawings: c, carapace; e, eye; o, ocelli; oa, heart-shaped 'ocellar area'; p, palpebral lobe; pvp, posterior ventral plate; V, VI, appendages V and VI; 1–6, anterior six opisthosomal segments. In addition to NMS, the abbreviations NYSM and PMO refer to the New York State Museum, Albany and Paleontologisk Museum, Oslo, respectively.

Geological setting

The Silurian rocks exposed in the North Esk Inlier of the Pentland Hills, south of Edinburgh, are rich in invertebrate fossil remains. The sediments represent a marine regression, commencing with sediments laid down in relatively deep water (Reservoir Formation), through to a quiet water lagoon (Wether Law Linn Formation) and ending up in the desert-fluvialite

red-beds (Henshaw Formation) as outlined by Clarkson *et al.* (2001); Clarkson & Taylor (2002).

Eurypterid remains have been reported from a number of different localities within the North Esk Inlier, but these consist predominantly of isolated fragments bearing eurypterid cuticle sculpture of little diagnostic value. However, the highest concentration occurs within the Eurypterid Bed, a distinct lithology exposed on the east bank of the Gutterford Burn. Here a rich faunal assemblage of eurypterids, synziphosurines and scorpions are mixed with sheets of *Dictyocaris*, crinoid ossicles, monograptids, brachiopods and stick bryozoans. Anderson & Moore (2004) gave a preliminary description of the Eurypterid Bed following an NMS excavation of the site in July 2003. The eurypterid fossils here were recognized as consisting of black carbonaceous compressions in a light green, clay-rich siltstone. This is of interest because the preservational state of *Kiaeropterus cyclophthalmus* (Laurie 1892) differs markedly, indicating that it *did not* originate from the Eurypterid Bed. The cuticle of NMS G.1885.26.72P is preserved as a light pink-red compression in a well-indurated, blue-grey, micaceous siltstone. The original label accompanying the specimen does indicate that the general locality was the Gutterford Burn, but we must face the possibility that additional horizons bearing eurypterids may exist within the enclosing Reservoir Formation. Indeed, the holotype of *Lamontopterus knoxae* (Lamont 1955) was collected from Green Cleugh, a separate locality probably lying stratigraphically below the horizon of the Eurypterid Bed. During July 2004 one of us (L.I.A.) discovered similarly 'red-dened' cuticles at a new locality downstream from the Eurypterid Bed, closer to where the Gutterford Burn enters into the North Esk Reservoir.

Systematic palaeontology

- Phylum CHELICERATA Heymons 1901
- Order EURYPTERIDA Burmeister 1843
- Suborder STYLONURINA Diener 1924
- Superfamily STYLONUROIDEA Diener 1924
- Family DOLICHOPTERIDAE Kjellesvig-Waering & Størmer 1952
- Clarkeipterus* Kjellesvig-Waering 1966

Diagnosis Small eurypterids with spatulate carapace; posterior margin procurved and with marginal rim; greatest width of carapace at midsection; eyes crescentic, converging anteriorly and placed in front of midsection; palpebral lobes very large and circular; ocelli midway between eyes; no ornamentation (emended from Kjellesvig-Waering 1966).

Clarkeipterus otisius (Clarke 1907)

- 1907 *Pterygotus ? otisius* nov.; Clarke 308, pl. 6, fig. 7.
- 1907 *Eurypterus ? myops* nov.; Clarke pl. 6, fig. 6.
- 1912 *Dolichopterus otisius* Clarke; Clarke and Ruedemann 88, 270–272, pl. 46, figs. 1–8.
- 1934b *Dolichopterus otisius* Clarke; Størmer 285.

- 1951 *Dolichopterus otisius* (Clarke); Størmer 415.
 1961 *D. otisius*; Leutze 52.
 1966 *Stylonurella otisius* (Clarke 1907); Kjellesvig-Waering 180.
 1979 *Kiaeropterus otisius* (Clarke); Waterston 291.
 1983 *Kiaeropterus otisius*; Plotnick 388.
 1999 *Kiaeropterus otisius*; Plotnick 114.

Holotype NYSM 9925 – carapace with fragmentary appendages in dorsal view.

Type locality Otisville, New York State, USA.

Type horizon Shawangunk Formation.

Diagnosis *Clarkeipterus* with variable morphology; eyes on anterior third (further forward than in *C. testudineus*); posterior margin of carapace less concave than in *C. testudineus* (Clarke & Ruedemann 1912).

Remarks A vagabond species that has been assigned to six different genera in the ten known publications where mentioned. It now returns to the Dolichopteridae where Clarke & Ruedemann (1912) assigned it. The synapomorphies the species shares with *C. testudineus* are a triangular anterior carapace margin and a posterior marginal carapace rim. The latter character is a promising synapomorphy for *Dolichopterus* Hall 1859 and *Clarkeipterus*, while apparently lacking in *Ruedemanniapterus* Kjellesvig-Waering 1966 and *Strobilopterus* Ruedemann 1935. V. P. Tollerton (pers. comm. 2004) pointed out several differences in morphology between *C. testudineus* and *C. otisius*, a view with which we agree, but as there is no other available genus to accommodate *C. otisius*, we prefer not to erect a new genus, while we recognize that the assignment to *Clarkeipterus* might be temporary.

The genus *Syntomopterus*, Kjellesvig-Waering 1961 is possibly a junior synonym of *Strobilopterus* Ruedemann 1935 (O.E.T. pers. obs. on additional material of *Strobilopterus princetonii* (Ruedemann 1934) in the Field Museum of Natural History, Chicago and the Peabody Museum, Yale University).

Family Stylonuridae Diener 1924

Kiaeropterus Waterston 1979

Diagnosis Small eurypterids with subquadrate carapace with broad marginal rim; crescentic eyes large (c. one-third of carapace length) on anterior half of carapace; cardioid raised ocellar area between eyes; appendages V and VI non-spiniferous and simple; individual podomeres with pronounced ridges; mesosoma not wider than carapace; metasoma narrow (emended from Waterston 1979).

Kiaeropterus cyclophthalmus (Laurie 1892)
(Figs 1–3)

- 1892 *Eurypterus cyclophthalmus* n. sp.; Laurie 158–159, 161, pl. III, fig. 15.
 1899 *Eurypterus cyclophthalmus*; Peach and Horne, 594.
 1916 *Eurypterus cyclophthalmus*; O’Connell 39.
 1924 *Eurypterus cyclophthalmus*; Diener 16.
 1934 *Eurypterus cyclophthalmus*; King 563.

1955 *E. (?) cyclophthalmus* Laurie; Lamont 200.

1958 *Eurypterus cyclophthalmus* Laurie; Kjellesvig-Waering 1108, 1123.

1979 *Eurypterus cyclophthalmus* Laurie; Waterston 316.

1983 *E. cyclophthalmus*; Plotnick 60, 387.

1994 *E. cyclophthalmus*; Cuggy 731.

1999 *Eurypterus cephalaspis*; Plotnick 120.

Holotype and only known specimen NMS G.1885.26.72P – almost complete specimen in dorsal view, lacking most of the prosomal appendages and telson.

Type locality Gutterford Burn, Pentland Hills, Midlothian, Scotland.

Type horizon Eurypterid Bed (*sensu lato?*), Gutterford Burn Flagstones, Reservoir Formation.

Diagnosis *Kiaeropterus* with wide carapace (L/W ratio of 0.69), large circular palpebral lobes and large ocelli not set on an ocellar node.

Remarks The type species *K. ruedemanni* (Størmer 1934a) is known from two specimens, PMO H1733 and H1711. Two other specimens (PMO H1661 and H1678) were listed by Størmer (1934a, p. 100) as possibly belonging to the species, but these two specimens could not be found in the type or systematic collections at PMO (Tetlie 2000). However, two types of unidentified type A genital opercula were figured by Størmer (1934a). The largest of these (two specimens) can with relative confidence be assigned to *Brachyopterella pentagonalis* (Størmer 1934a), while the smaller type (one specimen; PMO H1735) most probably belongs to *K. ruedemanni*, based on its small size, although it could also belong to a small specimen of *Stylonuroides dolichopteroides* (Størmer 1934a).

Description of the fossil

The carapace of the counterpart is incomplete with the right side less complete than the left. The carapace is 11.6 mm long and has a preserved width of 11.5 mm and a lateral angle of 95°. L/W ratio of the restored carapace would be around 0.69. If complete, it would have a subquadrate outline, but with a more rounded anterior margin than figured for this standard shape (Tollerton 1989, fig. 2.4). The carapace has a relatively wide (0.5 mm) marginal rim that narrows slightly posteriorly. The left eye is very large, having a maximum length of 3.9 mm, approximately one-third of the carapace length. The shape of the well-preserved left eye is broadly crescentic, but is slightly wider anteriorly than posteriorly, and is situated on a large, almost circular palpebral lobe. Both the outer and the inner margins of the left eye are almost perfect semi-circles. Only the anterior part of the right eye and its palpebral lobe are preserved. The ocelli lie between the central part of the eyes, and have a diameter of 0.5 mm (4% of carapace length). No small, round ocellar mound is preserved, but the ocelli are preserved in a large, heart-shaped depression, which on the part would have been raised, the ‘ocellar area’. This

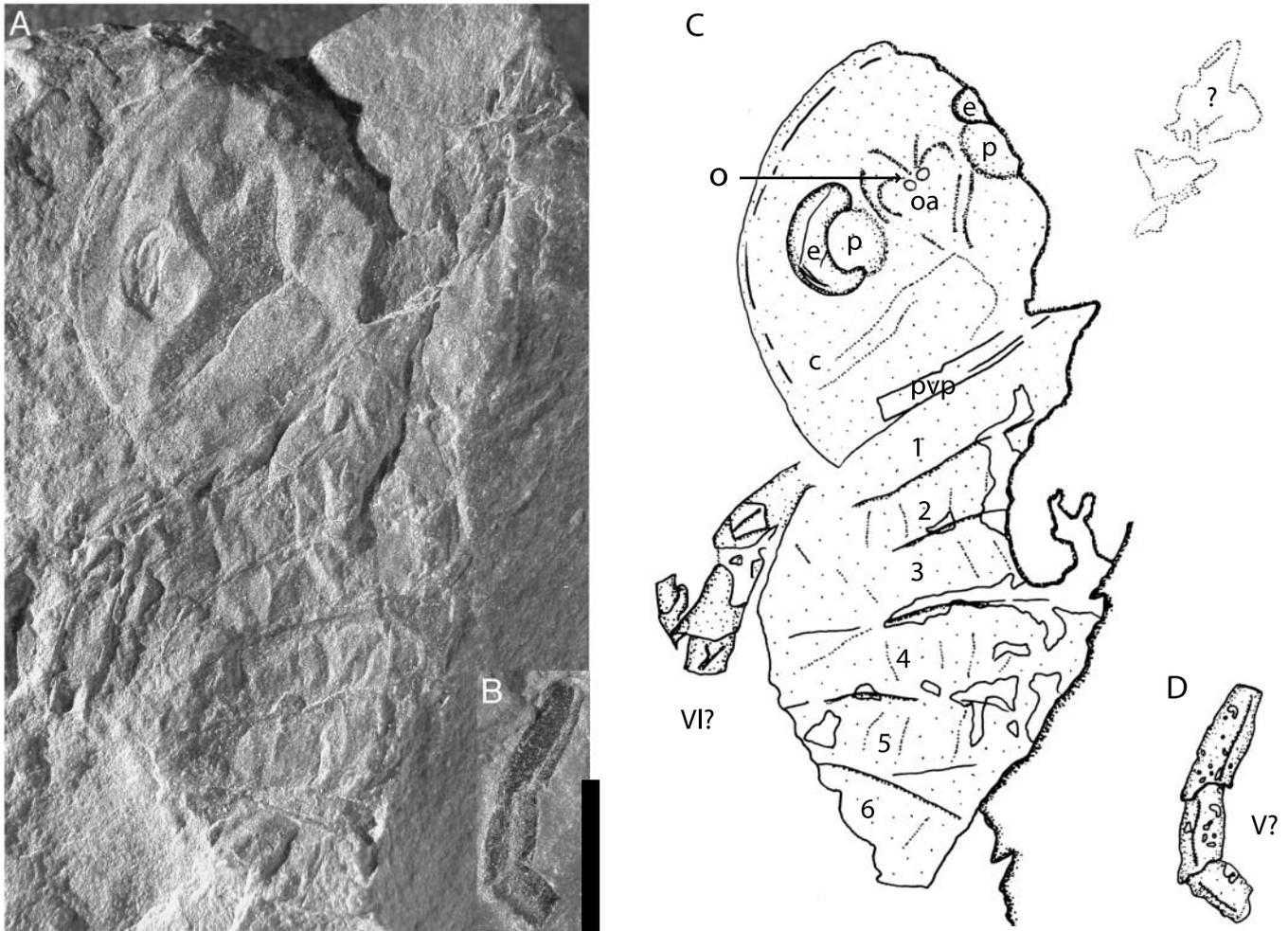


FIG. 1. *Kiaeropterus cyclophthalmus* (Laurie 1892). (A) Photograph of specimen NMS G.1885.26.72P; (B) photograph of isolated appendage on same specimen; (C) interpretative drawing of specimen figured in A; (D) interpretative drawing of specimen figured in B. Scale bar=5 mm.

structure is composed of two heart-shaped outlines, one inside the other: the outer one is 5 mm long and 4 mm wide; the inner one is 4 mm long and 3 mm wide (Fig. 1C, oa). A posteriorly positioned plate 0.7 mm long and 7.0 mm wide (incompletely preserved) seen through the carapace is interpreted as the posterior ventral plate (pvp).

Three fragmentary prosomal appendages are preserved: two are associated with the carapace and one is 20 mm left of the carapace. The isolated appendage is the best preserved with three podomeres, each having a depression along the length of the podomeres (ridge on the part). Distally, each podomere is slightly expanded anteriorly and laterally. This is most likely to represent podomeres of the middle part of appendage V. Two incomplete and poorly preserved podomeres of appendage IV or V are preserved on the left. Appendage VI is preserved on the left side, three podomeres (probably 4–6) are partially preserved. Podomeres 4 and 5 are both slightly expanded anteriorly and laterally and there are also traces of a similar ridge to that found on the isolated appendage. On the right side, poorly preserved cuticle could represent an appendage, but its position (compare with Fig. 2) suggests that it is a part of the carapace on the right side.

The six anteriormost opisthosomal segments are preserved. Preservation is incomplete on both lateral margins, but all opisthosomal segments have approximately the same lengths (2.2, 2.2, 2.6, 3.1, 3.1 and 3.2 mm respectively (anterior to posterior)). All segments except the first have longitudinal depressions. No ornamentation is preserved on the specimen.

Information from the missing part

We believe that Laurie's original description and figure (Laurie 1892, pl. III, fig. 15) are relatively accurate based on our examination of the counterpart. His figure of the missing part indicates the heart-shaped prominence described above on the counterpart. It also shows that the carapace on the part is more complete than on the counterpart, and it appears to be slightly distorted (i.e. the carapace is not bilaterally symmetrical). The length measurements of the six opisthosomal segments preserved on both part and counterpart show that none of Laurie's measurements are more than 0.4 mm divergent from ours, and the average divergence is around 0.2 mm. We therefore put considerable faith in Laurie's interpretation and measurements of the post-abdomen, the most important feature not preserved on

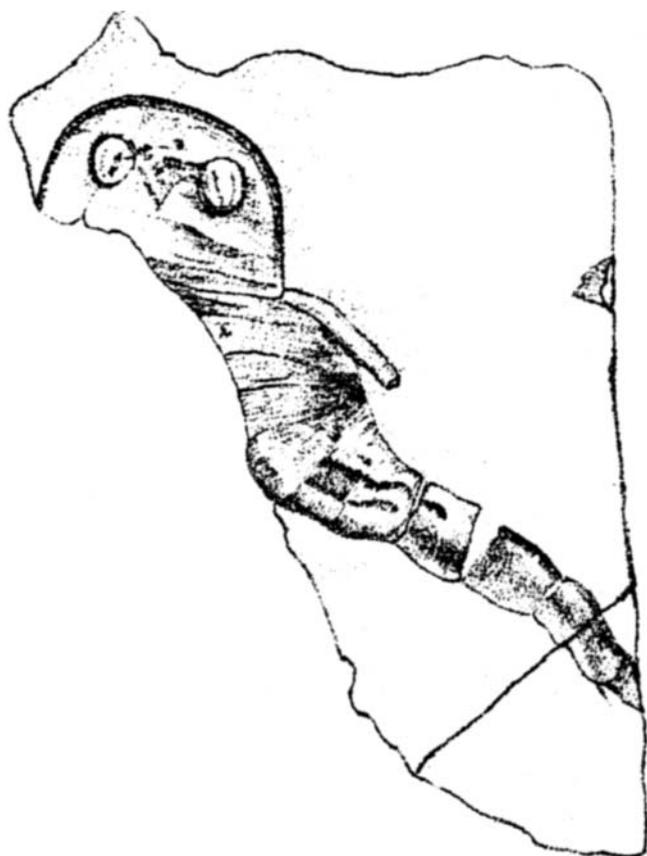


FIG. 2. *Kiaeropterus* Waterston 1979. Original drawing of the missing part of *K. cyclophthalmus* figured by Laurie (1892, pl. III, fig. 15).

the counterpart. The measurements (in mm) as provided by Laurie follow this format: segment 7, length/width 4/6; segment 8, 4.9/6; segment 9, 5/5; segments 10–12, 9 mm long combined; segment 10, 4 mm wide. The measurements and Figure 2 show that the postabdomen in *K. cyclophthalmus* is very slender, but probably not to the same extent as in *Alkenopterus* (see Poschmann & Tetlie 2004). Laurie (1892, p. 158) noted about the opisthosoma: 'The body increases in width to about the 3rd segment, and then decreases rapidly to the 7th, which is conical in form, and more gradually from the 7th to the end of the tail'. The telson is not preserved on the part.

Discussion

There are numerous similarities between *K. cyclophthalmus* and *K. ruedemanni*, including carapace shape, eye shape and size, the broad marginal rim that narrows slightly posteriorly, appendages with simple podomeres with distinct longitudinal ridges. The carapace shape is almost the same as for *K. ruedemanni* (Størmer 1934a). *K. cyclophthalmus* has a L/W ratio of 0.69, while that of *K. ruedemanni* is 0.90. This difference is mainly due to different degree of flattening. *K. cyclophthalmus* is flattened and displays creases in the cuticle, while *K. ruedemanni*, preserved in sandstone, retains its relief. The relatively broad marginal rim in *K. cyclophthalmus* is slightly narrower than in the Norwegian species (but

otherwise slightly narrowing posteriorly as in *K. ruedemanni*). The bluntly angular genal region is also similar to *K. ruedemanni*. The eyes have the same shape and position as in *K. ruedemanni* but are relatively shorter and wider, similar to the differences in carapace dimensions, which might all be due to preservational differences as discussed above. The large ocelli combined with the large eyes suggest that this could be a juvenile, as the eyes and ocelli are relatively larger in juvenile eurypterids than in adults (Andrews *et al.* 1974). However, the only known specimen of *K. cyclophthalmus* would be around 50 mm long if complete; the same as *K. ruedemanni* (also reconstructed to approximately 50 mm long). The genital operculum herein questionably assigned to *K. ruedemanni* (Størmer 1934a, pl. 12, fig. 4) suggests a mature animal, and also belongs to an animal in the same size category as all the other specimens of *Kiaeropterus*. It is therefore possible that *Kiaeropterus* had relatively large eyes and specimens of both species represent adults.

The prosomal appendages are similar to those of *K. ruedemanni* having robust podomeres with ridges running along the podomere length. However, they are anterolaterally expanded, something not apparent in *K. ruedemanni*. The ridges present on the opisthosoma are clearly preservational in origin, and not morphological features of the species as they are not entirely parallel within a single segment and vary too much in direction between the different segments (Fig. 1C). Similar compressional ridges were also identified in the German species of *Alkenopterus* (Poschmann & Tetlie 2004) and it is likely that both *Alkenopterus* and *Kiaeropterus* had very thin cuticles, prone to wrinkling during compaction of the entombing sediments. *K. cyclophthalmus* lacks all signs of cuticular sculpture, a rather rare feature among eurypterids, only known from *Alkenopterus*, *Brachyopterus*, *Dolichopterus*, *Nanahughmilleria* and *Waeringopterus*, and of these, only *Alkenopterus* and *Brachyopterus* are stylonurids. Størmer (1934a, p. 101) suggested that *K. ruedemanni* was sculptured, but was not able to determine cuticle sculpture type. Re-examination of the two original specimens of *K. ruedemanni* did not find any traces of cuticle sculpture. The posterior ventral plate, also seen in *Megalograptus* (Caster & Kjellesvig-Waering 1964), *Hughmilleria* (Sarle 1903) and *Buffalopterus* (Kjellesvig-Waering & Heubusch 1962) is rarely observed in eurypterids. Two alternative, but less likely, interpretations are as a reduced first tergite or a concealed microtergite (see Dunlop & Webster 1999), the first rejected since stylonurids generally do not have a reduced anterior opisthosomal segment and the second because a microtergite would be expected to be much more reduced.

The raised, heart-shaped area on which the ocelli are situated is not known from any other stylonurid genus, although a differently shaped raised area between the eyes can be found in other taxa. Species known to have an ocellar structure resembling that of *K. cyclophthalmus* are: *Stylonurus* sp. Plotnick & Elliott 1995, *Brachyopterus stubblefieldi* Størmer 1951 and *K. ruedemanni*

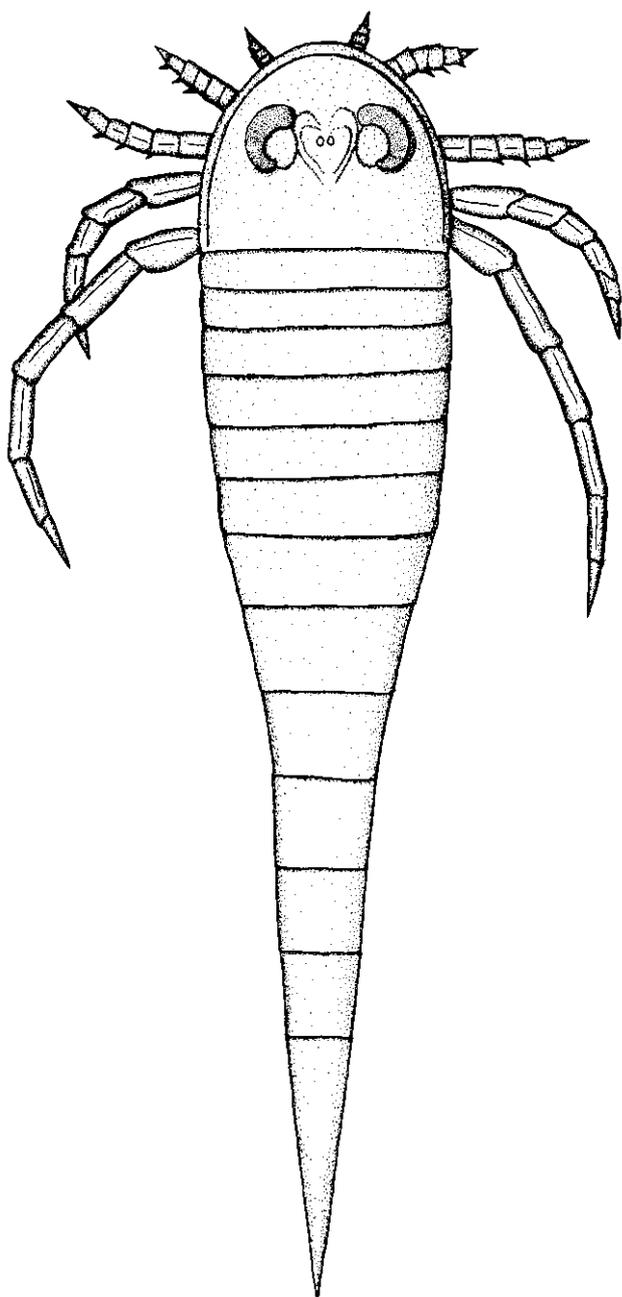


FIG. 3. Reconstruction of *Kiaeropterus cyclophthalmus* (Laurie 1892) based on the counterpart and the drawing of the part by Laurie (1892). The prosomal appendages and telson are reconstructed from the presumed relative *Brachyopterus stubblefieldi*.

(Størmer 1934a). The well-developed system of prosomal ridges exhibited by *Stylonurus* sp. Plotnick & Elliott 1995 also included a median ridge (Kjellesvig-Waering 1966; Plotnick 1983), suggesting this structure is not homologous to the heart-shaped ocellar area in *K. cyclophthalmus*. *Stylonurus* sp. is also ornamented and has a nearly square carapace. The ocellar area in *Brachyopterus* resembles the one described here, but is less visible posteriorly and is triangular rather than cardioid. In *K. ruedemanni*, the structure is more or less identical to that of *K. cyclophthalmus*: even two cardioid ridges, one inside the other, are present as in *K. cyclophthalmus*.

From the above-mentioned evidence, we assign the Scottish species to *Kiaeropterus*. A dorsal reconstruction of *K. cyclophthalmus* (Laurie 1892) is provided in Figure 3.

Phylogenetic position of *Kiaeropterus*

The higher phylogenetic position of *Kiaeropterus* remains uncertain. Waterston (1979) assigned it to the Stylonuridae, and as a sister-taxon to (((*Pagea* + *Stylonurus*) *Stylonurella*) *Stylonuroides*) + ((*Brachyopterus* + *Brachyopterebella*) (*Laurieipterus* + *Ctenopterus* + *Hallipterus* + *Mazonipterus*)). The genus *Mazonipterus* was later interpreted as plant remains (Plotnick 1997).

The nature of the ocellar area is here considered a synapomorphy between *Kiaeropterus* and the oldest well-known eurypterid, *Brachyopterus stubblefieldi*. Other, less important characters supporting a phylogenetic relationship between these two genera are large eyes that converge anteriorly, no cuticular ornament, and simple rectangular appendage podomeres with pronounced ridges. Unfortunately, the telson is not known in *Kiaeropterus*, but it is likely to have been similar to *B. stubblefieldi*, i.e. long and lanceolate, the presumed plesiomorphic telson within Eurypterida. The appendages appear primitive in both genera; only non-spiniferous appendages are known in *Kiaeropterus* while in *Brachyopterus*, a few short spines are present on appendages III–V. Appendage II (the pedipalps) of *B. stubblefieldi* has specialized (sexually dimorphic?) spines, interpreted by Størmer (1951) as ‘claspers’. No structure of this nature is known from *Kiaeropterus*, because the pedipalps have not been observed.

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