Two new Silurian species of *Eurypterus* (Chelicerata: Eurypterida) from Norway and Canada and the phylogeny of the genus

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SYNOPSIS A new species of *Eurypterus* from the Wenlock of Ringerike, Norway is described as *E. hankeni* sp. nov., based on fine pustular ornament on the carapace and opisthosoma, an enlarged distal podomere of the swimming leg and long angular epimera on the pretelson. *Eurypterus* species are reviewed: the oldest species, *E. minor* Laurie, 1898 from the Llandovery of the Pentland Hills in Scotland is redescribed and diagnosed as having eyes with large palpebral lobes, posterior second order opisthosomal differentiation, a coarse pustular ornament on both carapace and tergites and lacking the rows of raised scales found in other representatives of the genus. Material described previously and left in open nomenclature from the Late Ludlow of Somerset Island, Canada, is here named *E. leopoldi* sp. nov. It is relatively similar to *E. pittsfordensis*, but differs in the rhombiovate outline of the metastoma. An overview of morphological features carrying phylogenetic information in *Eurypterus* is provided. A phylogenetic analysis indicates that the earlier-used genus, *Baltoeurypterus* Størmer, 1973, is not monophyletic and even use of the name for its type species only (and its sister taxon) will render *Eurypterus* paraphyletic, unless assigning most terminals to new genera. This is not considered appropriate and the genus name *Eurypterus* is here proposed for use for all species, including the three previously assigned to *Baltoeurypterus*.

KEY WORDS *Baltoeurypterus*, metastoma ontogeny, Ringerike, Somerset island

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INTRODUCTION

Eurypterida is a monophyletic order of aquatic, Palaeozoic predatory chelicerates, attracting interest as possibly the largest ever arthropods (Chlupác 1994), as well as their phylogenetic position as sister-group to Arachnida (Weygoldt & Paulus 1979; Shultz 1990). The first eurypterid to be described was *Eurypterus remipes* from the Upper Silurian Bertie Formation of New York State, USA, although it was originally described by Mitchill (1818) as a catfish. *Eurypterus* was later the first erected eurypterid genus when DeKay (1825) recognised *E. remipes* as an arthropod. *Eurypterus tetragonophthalmus* Fischer, 1839 is the best known eurypterid, following the brilliant work of Holm (1898), where dissolution of limestone from the Rootsikula Formation of Estonia completely freed exquisitely preserved cuticle. Subsequent work on his material has added much more knowledge to the palaeobiology of this animal (Wills 1965; Selden 1981; Braddy & Dunlop 1997; Dunlop & Braddy 1997).

The genus *Eurypterus* existed for a short period (10–14 million years), but specimens of *Eurypterus* are still the most common eurypterid fossils in university, museum and private collections, as it tends to dominate faunas in which it occurs (Plotnick 1999). The best-known *Eurypterus*-bearing horizons are the Fiddlers Green and Williamsville Members of the Bertie Formation, New York State, USA and Ontario, Canada, the Rootsikula Formation, Estonia and the Kitaigorod, Ustje, Malinovetski and Rashkov Formations, Ukraine; at most of these localities they are commonly found complete.

Most eurypterid species, with the exception of most pterygotids and stylonurids, have at one time been assigned to the genus, but gradually genera were split from *Eurypterus* as taxonomical schemes developed. *Erieopterus* was separated from *Eurypterus* by Kjellesvig-Waering (1958) for species with more centrally placed eyes, pustulate ornament, no suture on the ventral marginal plate, fixed appendage spines and podomere 9 of the swimming leg developed into a long, narrow spine. Although *Erieopterus* is relatively similar to *Eurypterus*, their precise phylogenetic interrelationship has not yet been determined. *Baltoeurypterus* was separated from *Eurypterus* by Størmer (1973) for species with a distal paddle (i.e. podomere 8 the same size as, or larger than, podomere 7), although this distinction is not considered significant herein and such forms are re-assigned to *Eurypterus*, an action supported by, for instance, Andrews *et al.* (1974: 82).

Two species of *Eurypterus* have earlier been described from Norway; *E. tetragonophthalmus* was described from Sundvollen, Ringerike by Størmer (1938) and *E. henningsmoeni* (Tetlie 2002) was described from Gjettum, Bærum. In addition, the genus *Erieopterus* was reported by Størmer (1933) from Sundvollen, Ringerike.

A new eurypterid fauna was discovered by the author in May 2001 at Sønsterud farm, Ringerike, Norway. The site has since been sampled with help from staff and students at the Geologisk Museum, Universitetet i Oslo. The material consists of a new species of *Eurypterus*, here described as *E. hankeni* sp. nov. and a possible new species of *Pterygotus*, closely resembling, but older than, *P. anglicus*, *P. atlanticus* and *P. carmani*, which will be described later in a broader treatment of pterygotids.

The search resulting in the discovery of this locality was initiated after discussion with Dr N. M. Hanken (Universitetet i Tromsø) who, during fieldwork at Ringerike in the 1970s, discovered numerous eurypterid fragments, including a carapace questionably assigned to *E. hankeni* sp. nov. Hanken's locality could not be relocated as his specimens were discovered on a large exposed bedding plane, something not possible from this new locality. In addition, the lithologies of the two localities are very different (see geological setting, below).

This contribution also redescribes *E. minor* Laurie, 1898 from the Pentland Hills of Scotland and names a new species, *E. leopoldi* sp. nov., from arctic Canada based on

material described by Jones & Kjellesvig-Waering (1985). It also discusses the validity of other species of *Eurypterus* and morphological features carrying phylogenetic information are analysed. The first phylogeny of the *Eurypterus* clade is presented.

MATERIALS AND METHODS

All material of *E. hankeni* sp. nov. has been deposited in the Geologisk Museum, Universitetet i Oslo. The best material was brought to the University of Bristol where a description was prepared. Material from *E. minor* Laurie, 1898 and '*E.' cyclophthalmus* Laurie, 1892 were borrowed from the National Museums of Scotland and material from *E. remipes* was collected from the quarry of A. Langheinrich in New York for comparative purposes. Material from *E. dekayi*, *E. lacustris* and *E. tetragonophthalmus* from the author's and Simon Harris' collections were also used for comparison.

Camera lucida drawings were prepared with the material immersed in a 70% alcohol solution using a WILD stereoscope with a drawing tube attachment and photographs were taken with specimens illuminated by plane-polarised light. Morphological terminology follows Tollerton (1989) and taxonomy follows Novojilov (1962). Prosomal appendages are numbered I–VI, individual podomeres in prosomal appendages are P2–P9 (where P1 is termed the coxa, which are numbered CII–CVI) and opisthosomal segments are numbered 1–12. Short denotation of specific podomeres of individual appendages is used, combining appendage number (Roman numerals) and podomere number, e.g. VI-P8 denotes the eighth podomere of appendage VI, the swimming leg. In addition, the term 'genal facet' (Tollerton, 2003 pers. comm.) is introduced. The posterior margin of an *Eurypterus* carapace (and some other genera) have a recurved median part making up around 75% of the carapace width, while on each side there is a margin that is neither re- or procurved. A genal facet is one of these two 'flat' margins, each making up around one-eighth of the carapace width.

Specimens with PMO numbers are stored in the Geologisk Museum, Universitetet i Oslo, Norway. Other institutional abbreviations are: NMS, National Museums of Scotland, Edinburgh; GSC, Geological Survey of Canada, Ottawa; NYSM, New York State Museum, Albany; YPM, Yale Peabody Museum, New Haven; BMS, Buffalo Museum of Science, Buffalo; NMNH, National Museum of Natural History, Washington, DC; AMNH, American Museum of Natural History, New York.

GEOLOGICAL SETTING

The material from *E. hankeni* sp. nov. comes from the Sjørvoll Member of the Steinsfjorden Formation. This formation is around 260 m thick in the Ringerike district (Worsley *et al.* 1983) and is composed of greenish grey shales, marls, red dolomitic shales, dolomites and limestones (Olaussen 1978). The Sjørvoll Member comprises the most basal 200 m of the formation. At the locality, the formation is structurally very complex following the Caledonian orogeny and stratigraphical interpretations are difficult. However, the 100 cm thick eurypterid bed lies several tens of metres above a massive dolomitic limestone with ripple laminations, sug-

gesting it belongs somewhere in the interval between 150 and 180 m above the base of the formation (Fig. 1A). The fossiliferous section is a dark calcareous siltstone that breaks up into small fragments when collected. Collecting is difficult as the beds are orientated almost vertically and the most easily accessible exposure is 4 m up in the cliff face. Samples taken from above and below the eurypterid-bearing horizon contained very few and indeterminable conodonts, but contained large numbers and a great variety of thelodonts (H. A. Nakrem, pers. comm., 2003), which may help constrain the age in future work. Worsley *et al.* (1983) suggested that the entire Steinsfjorden Formation is of Wenlock age, a view adopted here following the failure to retrieve identifiable conodonts.

Fragmentary eurypterids occur throughout the entire 100 cm, but two horizons with very abundant and more complete specimens were identified. The lower of these occur 35 cm above the base of the bed and the higher 60 cm above the base. Additional fauna found in the bed include: a pterygotid eurypterid (*Pterygotus* sp.), inarticulate brachiopods (*Lingula* sp.), ostracods (*Leperditia* sp.: D. Siveter, pers. comm., 2002), rare cephalopods (orthocone nautiloids), rare bivalves (probably a *Colpomya* sp. or a *Modiolopsis* sp.: J. Cope, pers. comm., 2004) and rare gastropods (*Straparollus* sp.: J. O. Ebbestad, pers. comm., 2004). This is a very similar faunal composition to many other localities producing *Eurypterus* (see Plotnick 1999). Of the 21 localities and locality assemblages producing *Eurypterus*, 15 produce pterygotid eurypterids, 13 produce ostracods (almost exclusively *Leperditia* sp.), 11 produce inarticulate brachiopods, 9 produce articulate brachiopods, 9 produce gastropods, 9 produce cephalopods, 7 produce bivalves, 7 produce graptolites and 6 produce vertebrates. Recorded occurrences of other fossil groups are minor.

The specimen collected by Hanken occurs in a thick-bedded, competent 'waterlime' (=high magnesium calcareous mudstone) similar to, but slightly darker than those in which *E. remipes* and *E. lacustris* are found in New York State and Ontario. No information about additional fauna is known, as the bed of Hanken has not been relocated, although it should be in the same general area as the locality described here.

SYSTEMATIC PALAEONTOLOGY

Phylum **CHELICERATA** Heymons, 1901

Order **EURYPTERIDA** Burmeister, 1843

Suborder **EURYPTERINA** Burmeister, 1843

Superfamily **EURYPTEROIDEA** Burmeister, 1843

Family **EURYPTERIDAE** Burmeister, 1843

Genus ***EURYPTERUS*** DeKay, 1825

Eurypterus hankeni sp. nov. (Figs 2–3)

TYPES. Holotype: PMO 169.425, specimen showing prosoma from ventral side, with appendages II-IV and showing pustuled ornament on carapace (Figs 2A, 2B). Paratypes: PMO 169.290, 372, 410, 426, 427, 434, 441, 453, 470, 479, 206.622–629.
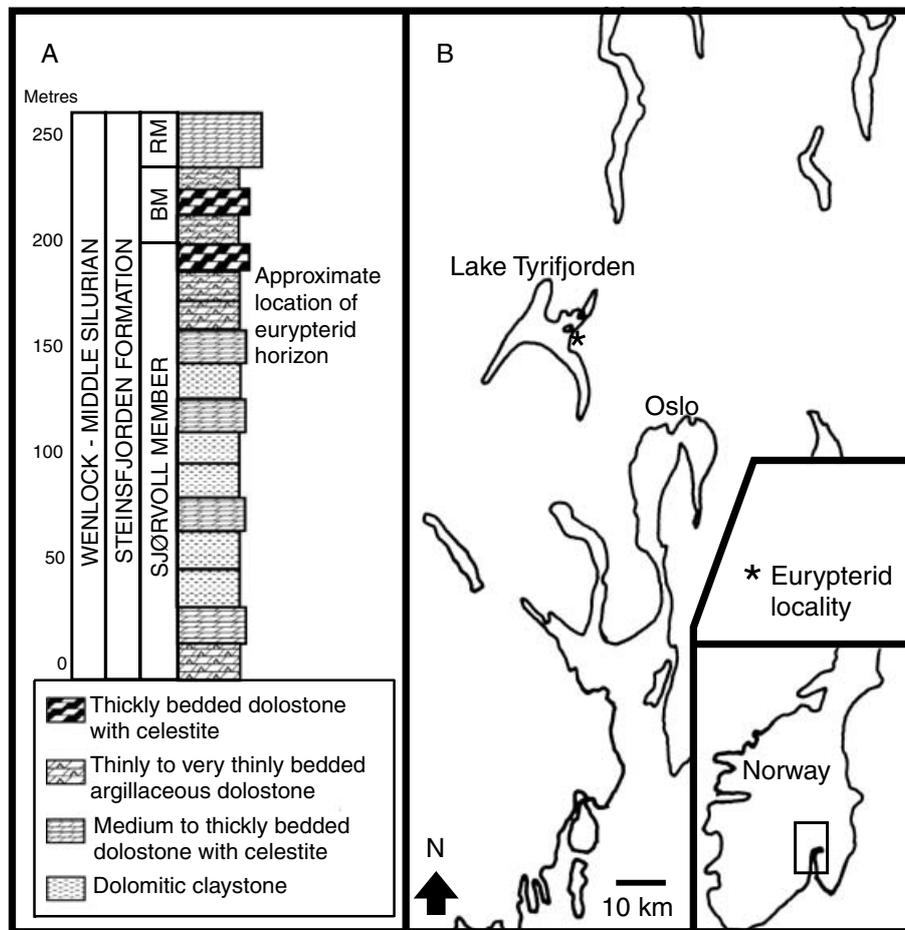
Figure 1 **A**, Simplified stratigraphical section through the Steinsfjorden Formation at Ringerike (modified from Worsley *et al.* 1983), indicating where in the section the eurypterid bed is possibly situated. BM, Brattstad Member; RM, Ranberget Member. **B**, Map showing where the eurypterid locality (indicated by an asterisk) is situated in relation to Oslo and Lake Tyrifjorden.

DIAGNOSIS. *Eurypterus* with a carapace with ornament of pustules and six raised principal scales on posterior carapace margin; two spines on each podomere of appendages II–IV; VI-P9 pentagonal and large (20–22% of length of VI–P8); oval metastoma with length/width (L/W) ratio of 1.46; postabdomen with small epimera; pretelson with long pointed epimera and sparse striations; telson with striate ornament close to base.

OCCURRENCE. Sjørvoll Member, Steinsfjorden Formation, Sønsterud farm, Ringerike, Norway.

ETYMOLOGY. The species is named after Dr Nils Martin Hanken (Universitetet i Tromsø), to whom I am extremely grateful for sharing information about his eurypterid discoveries in the 1970s. Although this locality is not the one he discovered, this new assemblage would not have been discovered without his encouragement.

REMARKS. Most specimens are small, suggesting animals from 10–15 cm long, but the largest carapace found so far suggests that this species reached between 20 and 25 cm in length.

DESCRIPTION. The carapace is highly variable, due to distortion (evident by wrinkles and lack of symmetry) and onto-genetic changes, but appears to follow the same ontogenetic trends observed by Andrews *et al.* (1974) for *E. remipes* and *E. tetragonophthalmus*. The carapaces of juveniles are longer and narrower than those in more mature specimens, which are trapezoid in shape. The eyes and palpebral lobes are reniform (e.g. in PMO 169.290: Figs 2E & 2F) and placed in the normal position for the genus. The ocelli are placed on an ocellar node between the anterior parts of the eyes. The marginal rim is widest on the anterior margin and becomes narrower posteriorly (Figs 2E & 2F). The same specimen also shows the ornament of fine pustules, like those seen in the holotype, and the pustules clearly covered most of, or possibly the entire, carapace.

Chelicerae not known, but appendages II–V are best known from the holotype (PMO 169.425: Figs 2A & 2B). Appendage II is poorly preserved, but the distal spine and two or three other podomeres are preserved. One of these podomeres has a distal spine. The four penultimate podomeres of appendage III are well-preserved (distal spine is missing) and, as in *E. remipes* and *E. tetragonophthalmus*, the posterior spines are longer than the anterior ones on a single podomere. No enlarged, sexually dimorphic spine, as seen in *E. tetragonophthalmus*, is observed on this specimen of unknown gender. Appendage IV has the five penultimate podomeres present, but spines are only preserved on the penultimate
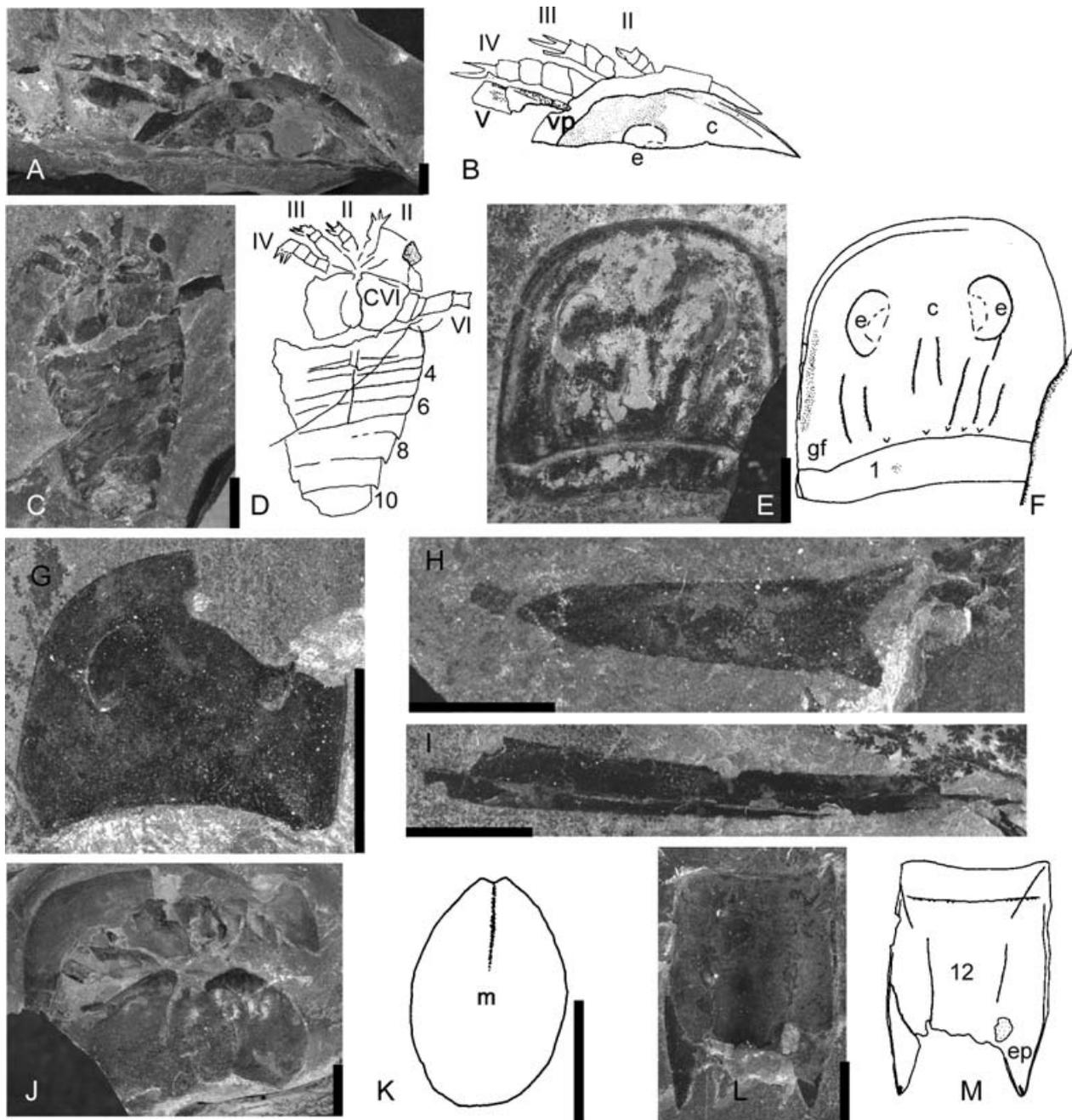
Figure 2 *Eurypterus hankeni* sp. nov. **A**, Photograph and **B**, *camera lucida* drawing of the holotype PMO 169.425. **C**, Photograph and **D** *camera lucida* drawing of PMO 206.622. **E**, Photograph and **F**, *camera lucida* drawing of PMO 169.290. **G**, Photograph of PMO 169.470. **H**, Photograph of PMO 206.623. **I**, Photograph of PMO 169.479. **J**, Photograph of PMO 206.625. **K**, *Camera lucida* drawing of metastoma figured in **J**. **L**, Photograph and **M**, *Camera lucida* drawing of of PMO 206.629. Scale bars = 5 mm. Abbreviations: c, carapace; e, eye; ep, epimeron; gf, genal facet; m, metastoma; vp, ventral marginal plate.

podomere and, also here, the posterior spine is longer than the anterior one. Appendage V on the holotype is fragmentary and has no preserved spines, but an ornament of scales is present.

Most of the coxae can also be seen on PMO 206.625 (Fig. 2J) and the gnathobases, coxal shapes and coxal ornamentation are all typical for the genus. An isolated coxa V (PMO 206.626: Figs 3G & 3H) has a circular coxal gland preserved, similar to the one known in *E. tetragonophthalmus* (Holm 1898; Selden 1981). The distal five podomeres

of the swimming leg are well known. PMO 206.627 (Figs 3C & 3D) shows podomeres VI-P6 and VI-P7 and the quite flexible joint between these two podomeres (Selden 1981). VI-P7 and VI-P7a are both unassuming and similar to those of *E. tetragonophthalmus*. VI-P8 is about the same size as P7 (PMO 169.441: Figs 3E & 3F), but is slightly different from those found in other species. The anterior margin is serrated; the serrations becoming deeper towards the notch where VI–P9 is inserted (Figs 3E, 3F, 3I & 3J). Podomere VI–P9 is large and more or less pentagonal in outline (Figs 3I & 3J),
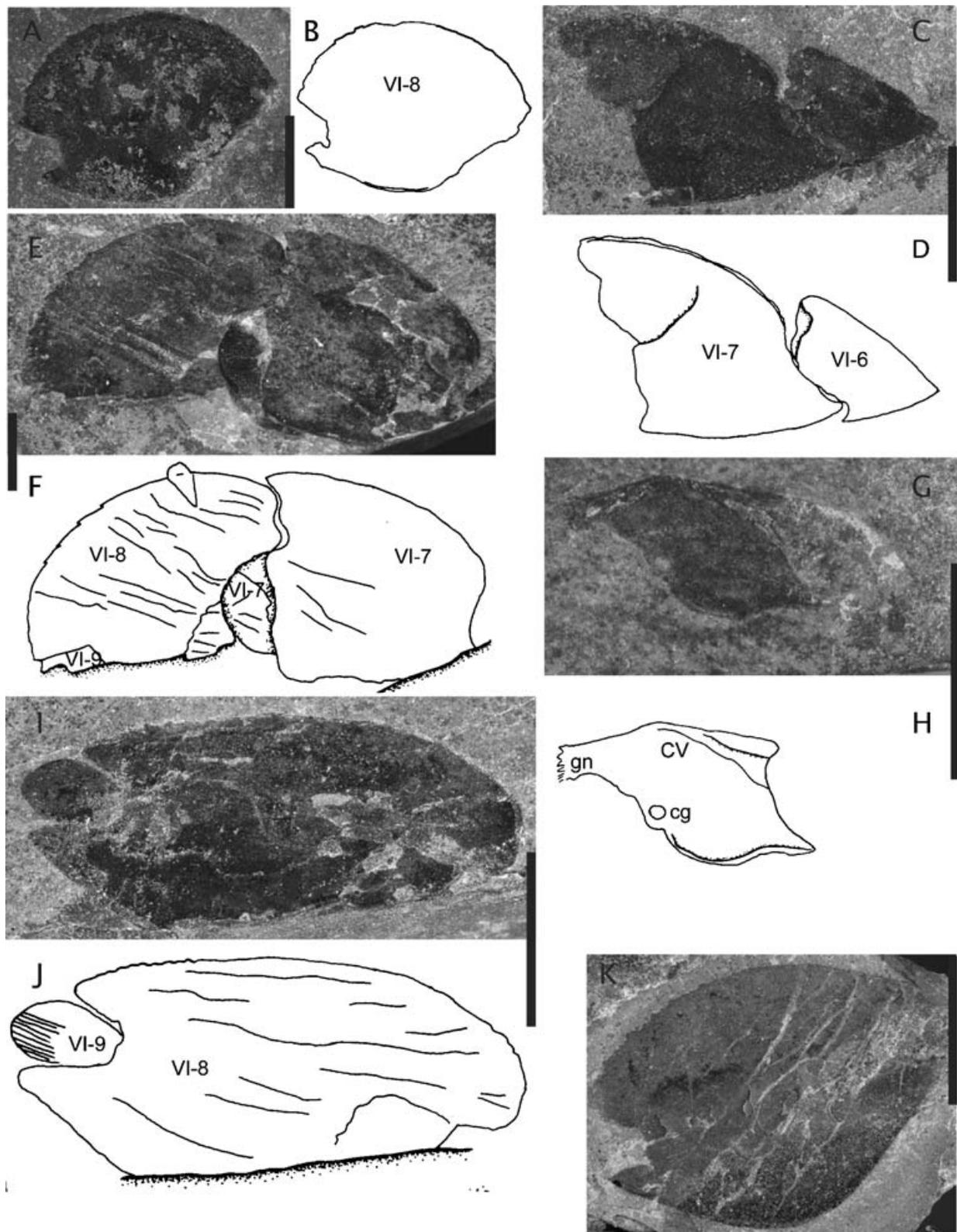
Figure 3 *Eurypterus hankeni* sp. nov. **A,** Photograph and **B,** *camera lucida* drawing of PMO 206.624. **C,** Photograph and **D,** *camera lucida* drawing of PMO 206.627. **E,** Photograph and **F,** *camera lucida* drawing of PMO 169.441. **G,** Photograph and **H,** *camera lucida* drawing of PMO 206.626. **I,** Photograph and **J,** *camera lucida* drawing of PMO 206.628. **K,** Photograph of PMO 169.372. Scale bars = 5 mm. Abbreviations: cg, coxal gland, gn, gnathobase; CV, fifth coxa.

but with a somewhat rounded juncture between the two outer margins. There are no marginal serrations on the podomere, but it is striated parallel to its longest axis (Fig. 3J).

The ventral marginal plate is evident in the holotype (PMO 169.425: Fig. 2B) and has an even inner margin and a median suture. The metastoma is only known from PMO 169.426 (Figs 2J & 2K) and 427 (part and counterpart). It has an oval shape, with a L/W ratio of 1.46, i.e. slightly longer than the standard (Tollerton 1989: fig. 5.2). Symmetrical impressions close to the lateral sides are possibly muscle attachment sites.

The opisthosoma is partially preserved in many specimens; some show that the pustulate ornament found on the carapace can also be found on the anterior half of each segment, while an ornament of raised principal scales dominates the posterior half of each segment. The number of these scales on each segment is difficult to establish with certainty since preservation is variable between different specimens, but it appears to be similar to the distribution in *E. tetragonophthalmus* (see Holm 1898). Ventrally, the segments have a much more pronounced ornament of smaller, broad lunules of both angular and curved types, as in most other representatives of the genus. The pretelson has long, angular epimera (24% the length of the entire pretelson), with no marginal ornament, but the angular lines on the tip of the epimera are similar in morphology, but reduced in extent and numbers, to those found in *E. pittsfordensis*.

With only two incomplete specimens, the telson is relatively poorly known. PMO 206.623 (Fig. 2H) is attached to the pretelson and shows the anterior part, which indicates the telson is lanceolate, not styliform. PMO 169.479 (Fig. 2I) represents a more distal part of the telson. There is no marginal ornament on the distal part of the telson, but there are indications of a zone of around 5 mm anteriorly that could have had some ornament of angular striations, but nothing like the type or extent found in some later taxa.

REMARKS. The new species differs from all other species in the large size of podomere VI-P9 and the coarser serrations on VI-P8. For other differences, compare diagnoses and character states with the other species.

Eurypterus leopoldi sp. nov

1985 *Baltoeurypterus* sp. A; Jones & Kjellesvig-Waering: 411–413, 416, figs 3–5.
1985 *Eurypterus* sp. A; Jones & Kjellesvig-Waering: 411–412, 416, fig. 6.
1999 *Baltoeurypterus* sp.; Plotnick: 120.
1999 *Eurypterus* sp.; Plotnick: 120.

TYPES. Lectotype: GSC 48520 – telson with angular striation (figured by Jones & Kjellesvig-Waering 1985). Paralectotypes: GSC 48505; 507–514; 518–9; 521; 524; 73064 (all 14 figured by Jones & Kjellesvig-Waering 1985).

DIAGNOSIS. *Eurypterus* with reduced anterior tergite, rhombiovate metasoma with L/W ratio of 1.67 which has anterior dentition; pretelson with serrated fringe medially and large, semi-angular epimera, marginally ornamented by angular striations; telson styliform, ornamented marginally with sparse large angular striations and numerous smaller angular striations between the large ones.

OCCURRENCE. Cape Clarence Member, Leopold Formation, Port Leopold, Somerset Island, Canada.

ETYMOLOGY. After Port Leopold and the Leopold Formation where the specimens were found.

REMARKS. Jones & Kjellesvig-Waering (1985) assigned their 15 specimens to two different genera; 12 specimens to *Baltoeurypterus* and three specimens to *Eurypterus*. All specimens came from units D13 and D15, but *Eurypterus* was only registered from D13. The carapace assigned to *Eurypterus* is narrower than the ones assigned to *Baltoeurypterus*, but this is because it belongs to a juvenile (see Andrews *et al*. 1974 for more information about ontogeny of *Eurypterus* carapaces), not because it belonged to a different species or genus. The two paddles assigned to *Eurypterus* and the one assigned to *Baltoeurypterus* are very similar. That they belong to one species is evident from the size of the notch to accommodate podomere 9. These have a similar large size in the specimens assigned to *Baltoeurypterus* and *Eurypterus* and, as discussed below, this notch would be small if the species was related to *E. remipes* or *E. lacustris* and larger if *Baltoeurypterus*. There is some variation in the shapes of VI-P8, possibly due to ontogeny (Andrews *et al*. 1974) or distortion, but this is within the same range of variation seen in *E. hankeni* sp. nov. and other species in the genus. The figures in Jones & Kjellesvig-Waering (1985) are good and the species is not refigured here. It is curious that Kjellesvig-Waering, himself having redescribed *E. pittsfordensis* 21 years before his death in 1979, failed to recognise the many synapomorphies (i.e. reduced anterior tergite, dentition in metastoma, pretelson fringe, semi-angular epimera on pretelson, telson shape and ornament of telson and pretelson) between *E. leopoldi* sp. nov. and *E. pittsfordensis* and, instead, assigned this species to *Baltoeurypterus*, then including only *E. serratus* (Kjellesvig-Waering 1979) and *E. tetragonophthalmus* (with which it only shares characters in the metastoma, such as general shape and dentition). The new species is very similar to *E. pittsfordensis*, but can be separated on the wider and differently shaped metastoma and the different morphology of the marginal ornament of the telson. The metastoma figured for these two species are of the same size and are therefore not ontogenetic varieties, but the difference in telson ornament could be preservational.

Eurypterus minor Laurie, 1898 (Fig. 4)

1898 *Eurypterus minor*; Laurie, 587, pl. V. figs 27–29.

TYPES. NMS 1897.32.120 (holotype); NMS 1897.32.110 and 1897.32.166 (paratypes).

ADDITIONAL MATERIAL. NMS G.1897.32.152, 1897.32.867 and possibly 1897.32.129.

DIAGNOSIS. Small *Eurypterus* with eyes with large palpebral lobes, posterior second order opisthosomal differentiation, ornament of coarse pustules on carapace and abdomen and apparently lacking the ornament of scales found in most other species of *Eurypterus*.

OCCURRENCE. Eurypterid bed, Reservoir Formation, Pentland Hills, Scotland.

REMARKS. This is now the earliest known (Late Llandovery) species of *Eurypterus* after the transfer of *E. cyclophthalmus*
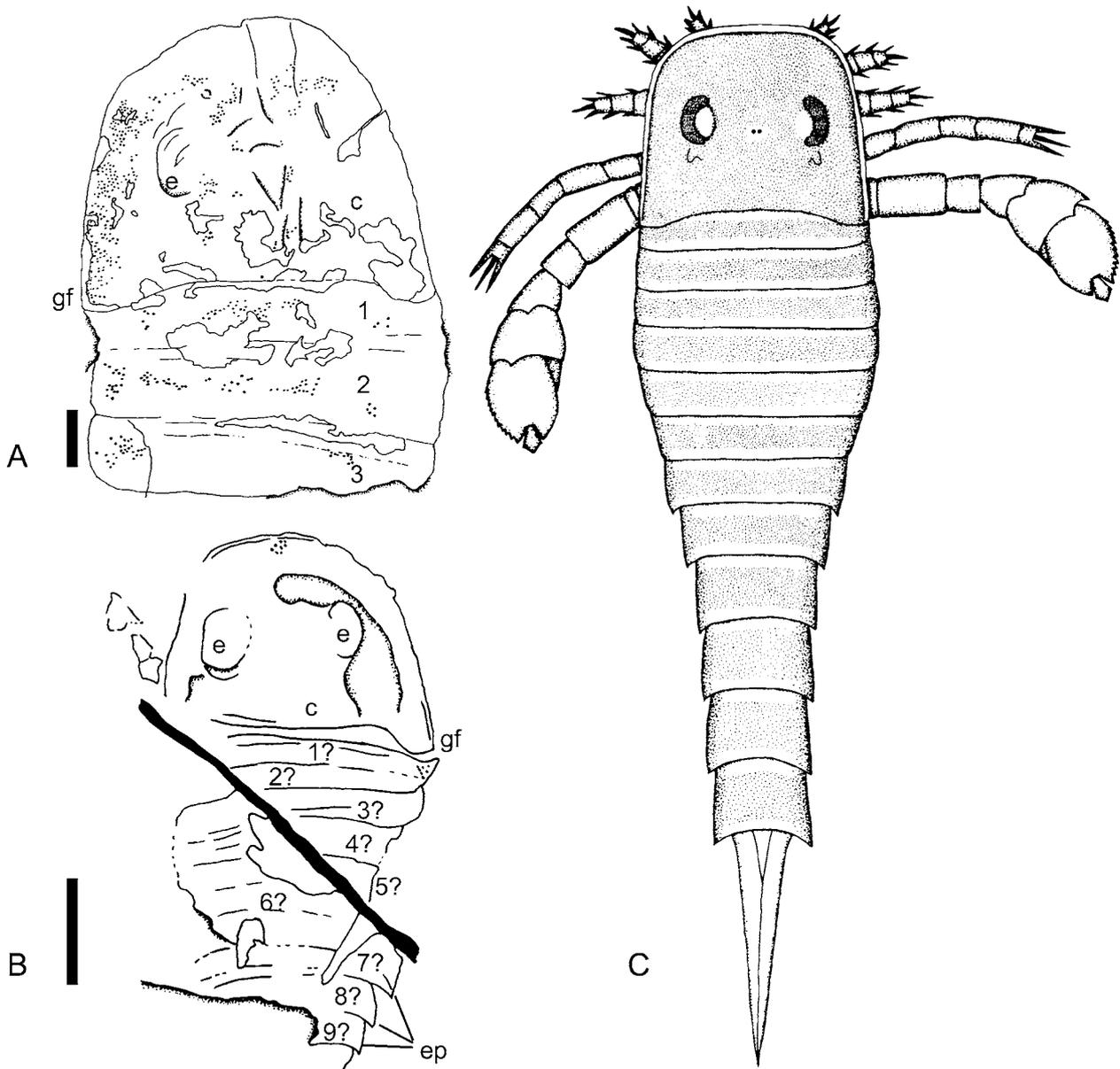
Figure 4 *Eurypterus minor* Laurie, 1898. **A,** *Camera lucida* drawing of NMS G.1897.32.867. **B,** *Camera lucida* drawing of NMS G. 1897.32.152. **C,** Dorsal reconstruction of *E. minor* based on the three specimens described by Laurie (1898) and the two specimens described here. Appendages are based on related species. Scale bars = 5 mm. Abbreviations: c, carapace; e, eye; ep, epimeron; gf, genal facet.

Laurie, 1892 (from the same locality) to *Kiaeropterus* (Tetlie, *et al.*, in press). *Eurypterus minor* is only known from five (or possibly six) small specimens. The carapace is slightly less tapering anteriorly than in other species (which typically have a trapezoid carapace) and is slightly more elongated, but this is also seen in smaller individuals of other *Eurypterus* species. Eyes are poorly preserved in the two specimens described here, but the specimens described by Laurie (1898: figs 27–29) have crescentric eyes surrounding a large palpebral lobe (Fig. 4C); Laurie confused this with 'oval eyes'. However, this shape of eye is more similar to the one found in *Dolichopterus* than in *Eurypterus*. The genal facets are typical, but not diagnostic, for *Eurypterus* (but are not found in *Dolichopterus* or other dolichopterids); their presence

help assign this species to *Eurypterus*, rather than for instance *Drepanopterus pentlandicus* Laurie, 1892, a highly pustulate stylonurid eurypterid from the same locality that lacks genal facets. The measurements of the segments show that the anterior segment is slightly shorter than the following segment. The posterior second order opisthosomal differentiation, the presence of epimera, is more distinct in this species than in any other representative of the genus (Fig. 4B). The large size of the pustules also sets it apart from all other representatives of the genus. Equally important as the presence of pustules is the absence of ornamentation consisting of pairs of raised scales posteriorly on the carapace and on each opisthosomal segment dorsally, present in most other species of *Eurypterus*. The smallest specimen is too poorly preserved,

but the largest specimen preserves the smaller pustules and should preserve scaly ornament if it were present. There is probably sufficient morphological evidence to erect a new genus for *E. minor*, but since it is relatively safe to assume that *E. minor* is ancestral to all other species in *Eurypterus*, it is deemed unnecessary to do so at the moment. This is also because the ventral morphology of *E. minor* is unknown and the interrelationship with the genus *Erieopterus* is presently unknown. A dorsal, tentative reconstruction of the species is given in Fig. 4C.

DESCRIPTION OF NMS G.1897.32.867 (Fig. 4A) Carapace 20.0 mm long, 25.8 mm wide, L/W ratio 0.78, lateral angle approximately 95°, on the border between the subquadrate and trapezoid carapace shapes (Tollerton 1989). Left eye preserved, but outline poorly defined. No marginal rim preserved. Carapace longer on postero-lateral genal area than along midline and developed into genal facets. The three most anterior opisthosomal segments are present. Their lateral margins are poorly preserved, but the segments are all wider than the carapace. The first segment is 4.5 mm long, the second 6.3 mm and the third 5.4 mm. The specimen is pustuled on both the carapace and the opisthosomal segments. On the carapace, the ornament is most dense along the lateral margins and on the segments, on the median two-thirds of the segment lengths.

DESCRIPTION OF NMS G. 1897.32.152 (Fig. 4B) This specimen is very small and very poorly preserved, but is important as it is one of the most complete *E. minor* known. The carapace is 9.5 mm long, 13.5 mm wide, L/W ratio of 0.70 and lateral angle approximately 95°, giving the same carapace shape as the previous specimen. Both eyes are preserved, the right one being crescentric or reniform. A narrow marginal rim is present anteriorly and on the right postero-lateral margin. The right genal facet is clearly seen, and is slightly more elongate than that seen in the larger specimen. Fragments of a left prosomal appendage are present, but too poorly preserved to warrant description. Nine or ten incomplete opisthosomal segments are preserved. Outlines of ventral elements seen through the tergites obscures interpretation. However, it is clear that there is a posterior second order opisthosomal differentiation present as evident by the epimera on the right side of the specimen. Pustular ornament is evident on the anterior of the carapace and on the right side of the most anterior segment.

Other species of *Eurypterus*

Eurypterus cephalaspis Salter, 1856

DIAGNOSIS. None provided.

REMARKS. The descriptions provided so far (Salter 1856,1859; Woodward 1866–1878 (fig. 53, pl. 28, figs 10–12), Kjellesvig-Waering (1951: pl. 3, fig. 1, 1958, 1961) are all inadequate and the species is in need of redescription. Plotnick (pers. comm., 2005) has suggested that only three carapaces, including the holotype, of *E. cephalaspis* can be assigned to *Eurypterus*, while the remainder of the specimens assigned to the species by Kjellesvig-Waering (1961) probably belong to a hughmilleriid, a view supported here.

Eurypterus dekayi Hall, 1859

DIAGNOSIS. *Eurypterus* with no raised scales on the posterior margin of carapace or three most anterior segments; four raised scales on remaining segments of mesosoma; four to six spines per podomere on prosomal appendages III and IV; metasoma with L/W ratio of around 1.80; pretelson with large, rounded epimera; telson without marginal ornament.

REMARKS. Species is very similar to *E. laculatus* Kjellesvig-Waering, 1958.

Eurypterus flintstonensis Swartz, 1923

DIAGNOSIS. None provided.

REMARKS. Only the carapace is known and Kjellesvig-Waering (1958) suggested future work might show it to be a synonym of either *E. remipes* or *E. lacustris*.

Eurypterus henningsmoeni (Tetlie, 2002)

DIAGNOSIS. *Eurypterus* with a broad paddle (L/W ratio 1.8); broad metastoma (L/W ratio 1.36); postabdomen with small epimera; pretelson with large, rounded epimera; pretelson and telson with marginal ornament of imbricate scales (emended from Tetlie 2002).

REMARKS. Very similar and closely related to *E. tetragonophthalmus*.

Eurypterus laculatus Kjellesvig-Waering, 1958

DIAGNOSIS. *Eurypterus* with a depression surrounding the visual area of the eyes, small ocelli and ocellar mound; no ornament of pustules or raised scales present on carapace or first segment.

REMARKS. Preservation in the holotype is so good (ocelli preserved), that one would expect ornament to be preserved if present. It is likely that the depression surrounding the eyes is preservational. The species is interpreted as closely related to *E. dekayi*.

Eurypterus lacustris Harlan, 1834

DIAGNOSIS. As for *E. remipes*, but with the eyes in a slightly more posterior position and metastoma L/W ratios from 1.80 to 2.03, averaging 1.92.

REMARKS. The status of this species has for some time been disputed. It is impossible to separate from *E. remipes* without using multivariate statistics and, even then, some studies have not been able to separate them (e.g. Cuggy 1994). A detailed, analysis by Tollerton (1993: 75) was able to separate the carapaces on eight measurements, but only one, relating to eye position, had a significant gap between the two species. The average L/W ratio of the metastoma in *E. lacustris* appears to be sligly higher than that of *E. remipes*.

Eurypterus (?) *loi* Chang, 1957

DIAGNOSIS. None provided.

REMARKS. This and the two other species erected by Chang (1957) have to be restudied to determine their taxonomic

position. It would be highly unusual to have three species of *Eurypterus* amongst four specimens from one locality. No attempt to create diagnoses for these three species has been made.

Eurypterus ornatus Leutze, 1958

DIAGNOSIS. *Eurypterus* with ornament of pustules covering the carapace and (at least) first opisthosomal segment; ornament of raised scales apparently lacking.

REMARKS. The ornament suggests *E. ornatus* might be related to *E. dekayi* and *E. laculatus*.

Eurypterus remipes DeKay, 1825

DIAGNOSIS. *Eurypterus* with ornament of four raised scales on the posterior margin of carapace; two spines per podomere on prosomal appendages II–IV, no scimitar lobe on male appendage III; VI-P8 considerably smaller than VI-P7; metastoma with L/W ratios from 1.76–2.00, averaging 1.87; postabdomen with small epimera; pretelson with small, semi-angular epimera, marginally ornamented by imbricate scales; telson with serrated marginal ornament along almost entire length.

REMARKS. Can be separated from *E. lacustris* by the position of the eyes (Tollerton 1993). See remarks under *E. lacustris*.

Eurypterus pittsfordensis Sarle, 1903

DIAGNOSIS. *Eurypterus* with ornament of three raised scales on the posterior margin of carapace; two spines per podomere on prosomal appendages II–IV; VI-P7 and VI-P8 of approximately same size; metasoma rhomboid with L/W ratio of 1.79–1.83 with deep, angular anterior notch; postabdomen with serrated fringe medially on segments and small angular epimera laterally; pretelson with large, semi-angular epimera, marginally ornamented by angular striations; telson styliform, ornamented marginally with sparse angular striations.

REMARKS. The three scales on the posterior of the carapace are arranged symmetrically, i.e. there is not one scale missing from a 'normal' arrangement of four scales. Shows similarities with *E. leopoldi* sp. nov., but can be differentiated on metastomal shape.

Eurypterus quebecensis Kjellesvig-Waering, 1958

DIAGNOSIS. *Eurypterus* with ornament of six raised scales on the posterior margin of carapace, but lacking pustulate ornament.

REMARKS. The presence of six raised scales and lack of pustuled ornament suggest this species is close to *E. hankeni* sp. nov. in the phylogeny.

Eurypterus serratus (Jones & Woodward, 1888)

DIAGNOSIS. *Eurypterus* with a metastoma L/W ratio of 1.68; telson styliform, ornamented marginally with dense angular striations.

REMARKS. Can be separated from *E. pittsfordensis and E. leopoldi* by the denser marginal ornament of striations on the telson. The metastoma is more similar to that of *E. leopoldi* sp. nov. than *E. pittsfordensis*.

Eurypterus (?) styliformis Chang, 1957

DIAGNOSIS. None provided.

REMARKS. See remarks under *E.* (?) *loi* Chang, 1957.

Eurypterus tetragonophthalmus Fischer, 1839

DIAGNOSIS. *Eurypterus* with ornament of four raised scales on the posterior margin of carapace; two spines per podomere on prosomal appendages II–IV, one cuticular growth on III-P6 developed into scimitar lobe on male; VI-P8 considerably larger than VI-P7; metasoma with L/W ratio from 1.62–1.74; postabdomen with small epimera; pretelson with large, rounded epimera, marginally ornamented by imbricate scales; telson with marginal ornament of imbricate scales proximally and serrations distally.

REMARKS. The diagnosis is based on *E. tetragonophthalmus* from Ösel, Estonia (Holm 1898) as it is better known than the original material of *E. tetragonophthalmus* from Zwilewcy, Smoltriz, Podolia, Ukraine. The material from Romania, Moldova and Ukraine is from a number of horizons and should be restudied to confirm the presence of only one species from the area and the similarity to the material from Ösel.

Eurypterus (?) yangi Chang, 1957

DIAGNOSIS. None provided.

REMARKS. See remarks under *E.* (?) *loi* Chang, 1957.

Species previously assigned to *Eurypterus*

Most non-pterygotid and non-stylonurid eurypterids have at one point been assigned to *Eurypterus*. It is beyond the scope of this work to list the identities of all species assigned to this genus in the past, but below is a discussion of some species recently assigned to *Eurypterus*.

Eurypterus (?) *decipiens* Ruedemann, 1942 and *E.* (?) *pristinus* Clarke & Ruedemann, 1912 are considered lithic clasts following Tollerton & Landing (1994) and Tollerton (2004). *Eurypterus cyclophthalmus* Laurie, 1892 is a stylonurid eurypterid, belonging to the genus *Kiaeropterus* (Tetlie, *et al.*, in press). *Eurypterus* (?) *trapezoides* Størmer, 1974 has a small triangular anterior process bent under the carapace, an autapomorphic character for the genus *Adelophthalmus*, as suggested by Kjellesvig-Waering (*in* Størmer 1974: 411) and discussed and rejected on stratigraphical concerns by Størmer (1974: 411). Poschmann (2006) considers *E.* (?) *trapezoides* a junior synonym of *A. sievertsi* (Størmer, 1969). *Eurypterus indicus* Dubey, 1985 and *E. vermai* Dubey, 1985 are both considered slickensides on fault planes with vague resemblance to the outline of eurypterids, besides being from an 870 Ma old sedimentary sequence (P. Kathal, pers. comm., 2003). *Eurypterus swartzi* Kjellesvig-Waering, 1958 has been interpreted (V. P. Tollerton, pers. comm., 2004) as the swimming leg of *Waeringopterus cumberlandicus* (Swartz, 1923).

When visiting museum collections (NYSM and AMNH), the author has encountered two unpublished genera '*Alloeurypterus*' (e.g. NYSM 40751) and '*Acanthoeurypterus*' (e.g. NYSM 40836). Both were apparently manuscript names of Kjellesvig-Waering that were never published, but are here interpreted as belonging to *Eurypterus*. However, with the suite of characters identified in this paper, these specimens should be restudied and their identities and phylogenetic positions determined.

PHYLOGENY

The swimming eurypterids, or Eurypterina, are clearly monophyletic (Plotnick 1983; Tetlie 2004) based on the presence of swimming legs that always have a podomere 7a. Invariably, these analyses have also found *Eurypterus* to be close to the base of the Eurypterina clade. They have also always resolved the dolichopterids close to *Eurypterus* although their interelationship has varied. Tetlie (2004) found the dolichopterids to belong to the same clade as *Eurypterus*, but the dolichopterids also have much in common with the walking eurypterids, or Stylonurina. The morphologically best known of the dolichopterids is the genus *Dolichopterus*, which is therefore used here as an outgroup for this analysis.

The genus *Erieopterus* might also belong to the 'ingroup' of the taxa analysed here, but is excluded because it might just as well belong close to *Onychopterella* or *Buffalopterus*. Clearly, more synapomorphies must be identified to resolve relationships between these genera further, but unlike *Eurypterus*, these three genera are poorly known.

Phylogeny versus ontogeny in *Eurypterus*

Before discussing the phylogeny of *Eurypterus*, it is necessary to examine the known literature on ontogeny of the genus to prevent ontogenetic noise from entering the analysis. Andrews *et al*. (1974) did the first serious attempt to study the ontogeny of eurypterids and covered *E. remipes* and *E. tetragonophthalmus*. They discovered that carapaces changed shape from parabolic to trapezoid during growth, while the eyes became smaller and the axes of the eyes rotated from almost parallel in juveniles to more converging anteriorly in adults. They also discovered that the L/W ratio of the opisthosoma increased during ontogeny and this was mainly due to relative lengthening of the preabdomen compared to the carapace and postabdomen. This might be a result of respiratory or reproductive requirements of adults, as the organs with these functions are housed in the preabdomen. Andrews *et al*. (1974) also noted that the swimming leg became narrower during ontogeny, but this was based on *E. remipes* and analysis of *E. tetragonophthalmus* would possibly have given an opposite result. Plotnick (1983: 71) noted that telsons of *E. remipes* became relatively shorter and broader during ontogeny. Little has been previously done on ontogenetic changes in the pretelson, but Holm (1898) and Tetlie (2002) demonstrated that the epimera on the pretelson in *E. tetragonophthalmus* and *E. henningsmoeni* were small and angular in juveniles, becoming larger and more rounded in adults. In other taxa, the angular epimera just seem to become larger and in *E. remipes* and *E. lacustris* they remain relatively small. It is obvious that characters that are dependent on ontogeny, like carapace shape and eye position, should not be used in a phylogeny. One character where the

Table 1   Dimensions of different museum specimens belonging to *Eurypterus remipes* and *E. lacustris*, illustrating the effect of ontogeny on the metastoma.

Species	Number	Length (mm)	Width (mm)	L/W ratio
E. remipes	NYSM 10010	9.5	5.4	1.76
E. remipes	NYSM 13141	3.6	1.8	2.00
E. remipes	NMNH 23692	19.8	10.6	1.87
E. remipes	AMNH 35214	13.1	7.4	1.77
E. remipes	YPM 33470	7.5	4.1	1.89
E. remipes	YPM 33477	14.4	8.2	1.76
E. remipes	YPM 33480	14.4	7.4	1.95
E. remipes	YPM 33519	9.3	4.8	1.94
E. remipes average				1.87
E. lacustris	BMS E913	24.1	13.4	1.80
E. lacustris	BMS E875	24.8	13.1	1.89
E. lacustris	BMS E6558	25.6	13.5	1.90
E. lacustris	BMS E874	19.4	9.6	2.02
E. lacustris	BMS E880	20.6	10.2	2.02
E. lacustris	BMS E18608	15.6	8.2	1.90
E. lacustris	NYSM 9953	26.2	12.9	2.03
E. lacustris	YPM 33532	23.6	12.2	1.93
E. lacustris	YPM 33560	22.3	12.4	1.80
E. lacustris average				1.92

ontogenetic influence is believed to have been understood, the development of the epimera on the pretelson, has here been coded.

Ontogeny of the metastoma

The metastoma is a ventral plate that probably aided eurypterids in containing food items within the coxal cavity while they were being masticated. The effects of ontogeny on this plate has previously escaped our attention. The length and width of the metastoma of eight specimens of *E. remipes* and nine of *E. lacustris* were obtained from Plotnick (1983: table 50) or from specimens in the YPM collections (Table 1). Analysis of these specimens suggests there is some variation within a single species (Table 1), but the metastoma retains its proportions throughout ontogeny (Fig. 5). A linear regression line fitted to the series of *E. remipes* show an extremely good fit with a R^2 value of 0.989 and with the regression line given by $y = 0.54x - 0.22$ (Fig. 5A). *Eurypterus lacustris* has a lower R^2 value of 0.915, mainly because of higher variability in L/W ratio among larger specimens with a regression line given by $y = 0.53x - 3.00$ (Fig. 5B). Since the relationships between length and width are slightly higher than 0.5 (0.54 and 0.53) and the L/W ratios average 1.87 and 1.92, the products of these values are 1.01 (*E. remipes*) and 1.02 (*E. lacustris*). These values demonstrate that the length is increasing by about twice that of the width, so the overall metastoma shape is kept more or less unchanged. The shape of the metastoma is, therefore, constant within these two species of *Eurypterus*, but its value as a character is still ambiguous.

Phylogenetic characters

The species within *Eurypterus* are very similar and there are few informative characters compared to the number of recognised species, making a phylogenetic analysis of the
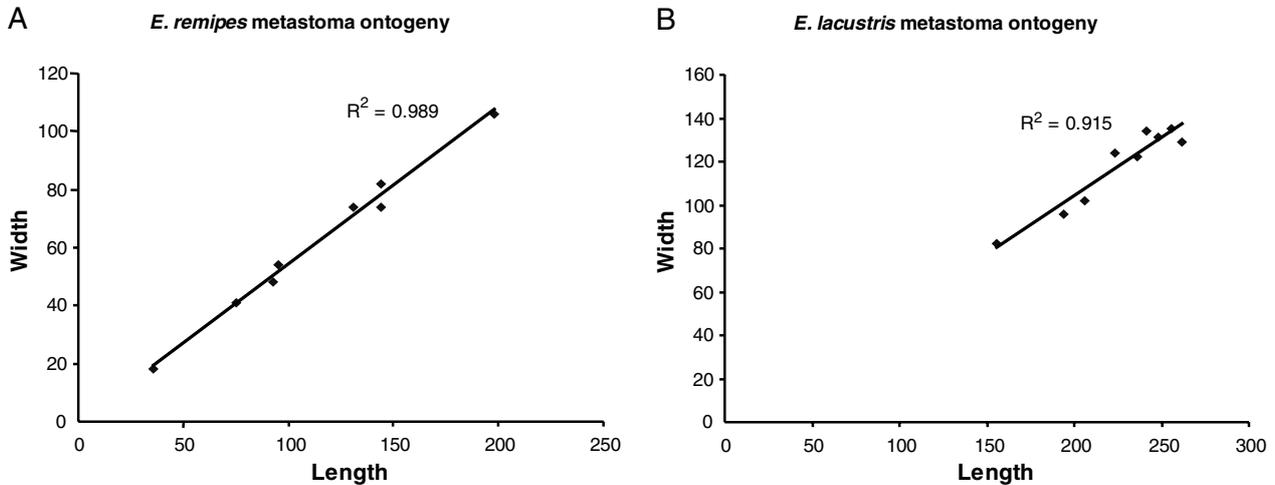
A

E. remipes metastoma ontogeny

B

E. lacustris metastoma ontogeny

Figure 5 **A,** Scatter plot of length versus width for the metastoma of *Eurypterus remipes*. **B,** Scatter plot of length versus width for the metastoma of *E. lacustris*. See the text for discussion.

Table 2 Character state matrix for phylogenetic analysis of the genus *Eurypterus*.

Species	05	10	15	20
Dolichopterus macrocheirus	00000	00000	00000	00000 0
Eurypterus dekayi	12001	11012	101?1	00000 0
Eurypterus hankeni	12111	10?01	10101	000?0 ?
Eurypterus henningsmoeni	??1?1	1??02	10110	10001 ?
Eurypterus laculatus	??001	1????	?0???	?0??? ?
Eurypterus lacustris	00121	10023	20220	10000 1
Eurypterus leopoldi	?0??1	1???2	11?01	01110 0
Eurypterus minor	12000	1????	?00??	000?? ?
Eurypterus ornatus	12001	1????	?????	????? ?
Eurypterus pittsfordensis	00131	10012	11101	01110 0
Eurypterus quebecensis	00111	1????	?????	????? ?
Eurypterus remipes	00121	10023	20220	10000 1
Eurypterus serratus	?????	?????	1???1	??110 0
Eurypterus tetragonophthalmus	11121	10102	10110	10001 1

clade difficult. The following list of characters and character states refer to the data matrix (Table 2).

1. *Carapace ornament of pustules* (0 = absent; 1 = present). A pustulate ornament of the carapace is present in *E. tetragonophthalmus*, *E. dekayi*, *E. ornatus*, *E. hankeni* sp. nov. and *E. minor*, while absent (or not known) in other taxa. From stratigraphical evidence (*E. minor* and *E. hankeni* sp. nov. are among the oldest species in the clade), the pustulate ornament is probably plesiomorphic within the genus, although not present in the selected outgroup. *Eurypterus minor*, the oldest species, has coarse ornament while the two others have finer ornament, suggesting a gradual decrease in pustular ornamentation.

2. *Coverage of pustules* (0 = absent; 1 = partial; 2 = complete). Ordered. The pustules are more-or-less completely covering the carapace in *E. dekayi*, *E. ornatus*, *E. hankeni* and *E. minor* while *E. tetragonophthalmus* has pustules only along the carapace margin.

3. *Carapace ornament of principal scales* (0 = absent; 1 = present). *Eurypterus hankeni*, *E. tetragonophthalmus*, *E.* *henningsmoeni*, *E. lacustris*, *E. quebecensis*, *E. remipes* and *E. pittsfordensis* have principal scales, while these are not present in *E. minor*, *E. ornatus*, *E. laculatus* and *E. dekayi*.

4. *Number of principal scales on carapace* (0 = no scales; 1 = six scales; 2 = four scales; 3 = three scales). Ordered. Principal scales are enlarged raised scales dorsally at the base of the carapace and opisthosomal segments. *Eurypterus minor* lack these principal scales, while *E. dekayi*, *E. ornatus* and *E. laculatus* lack these on the carapace (and probably also on segments 1–3). The others have principal scales in varying numbers on the carapace; six in *E. quebecensis* and *E. hankeni*, four in *E. remipes*, *E. lacustris*, *E. tetragonophthalmus* and three in *E. pittsfordensis*.

5. *Eye shape* (0 = crescentric with large palpebral lobe; 1 = reniform with small palpebral lobe). *Dolichopterus* and *E. minor* have crescentric eyes with large palpebral lobes, the rest have reniform eyes with small palpebral lobes.

6. *Genal facets* (0 = absent; 1 = present). Genal facets are absent in *Dolichopterus* and present in all species of *Eurypterus*.

7. *Number of spines per podomere of prosomal appendages II–IV* (0 = two spines; 1 = four to six spines). This character is easy to polarise, as only *E. dekayi* has 4–6 spines on each podomere of appendages II–IV, compared to two spines in all other taxa where appendages are known in sufficient detail, including *Dolichopterus*, the outgroup. The condition is unknown in *E. laculatus* and *E. ornatus*.

8. *Sexual dimorphism of prosomal appendage III* (0 = absent; 1 = present). Only in *E. tetragonophthalmus* are specimens with a type B genital appendage known to have a scimitar lobe, a recurved cuticular outgrowth on III-P6 (Braddy & Dunlop 1997). This structure is not present in *E. remipes* or *E. lacustris*, both known from thousands of specimens. Furthermore, no structure like this is known from *E. dekayi* or *E. pittsfordensis*.

9. *Morphology of VI-P7 and VI-P8* (0 = P8 > P7; 1 = P8 ≈ P7; 2 = P8 < P7). Ordered. Størmer (1973)

erected the genus *Baltoeurypterus* based on the different ratio of elements in the paddle. *Baltoeurypterus* had a distal paddle where P8 was larger than P7 or 'length of segment 7: width of segment 8 more than 2', while *Eurypterus* had a proximal paddle where 'the ratio is less than 2' (Størmer 1973: 128–129). Størmer wrote: 'the swimming leg . . . has considerable taxonomic value', but why this continuous character deserves higher status than other characters (for instance the number of spines on prosomal appendages III and IV) was never discussed. The taxa with a distal paddle (0) are *E. hankeni* sp. nov., *E. tetragonophthalmus* and *E. henningsmoeni*. *Eurypterus remipes* and *E. lacustris* have a proximal paddle (2). The paddles of *E. dekayi* and *E. pittsfordensis* have ratios close to 2, i.e. the two podomeres are approximately the same size.

10. *Morphology of VI-P9 (as ratio of VI-P8)* (0 = very large (100% of P8 length); 1 = large (20–22% of P8 length); 2 = medium (10–14% of P8 length); 3 = small (6–7% of P8 length)). Ordered. P9 is large (20–22% of P8 length) and pentagonal in *E. hankeni* sp. nov., but is medium (13–14% of P8 length) in *E. dekayi* (already noted by Hall 1859), *E. pittsfordensis* (11–13% of P8 length) and in *E. tetragonophthalmus* and *E. henningsmoeni* (10–12% of P8 length in both). It is small (6–7% of P8 length) in *E. remipes* and *E. lacustris*.

11. *Metastoma shape* (0 = lyrate; 1 = oval; 2 = elliptical). The metastoma shape is evidently somewhat variable within the genus, but is lyrate in *Dolichopterus*, oval (also including rhombiovate, which is similar to oval) in *E. tetragonophthalmus*, *E. henningsmoeni*, *E. dekayi*, *E. pittsfordensis*, *E. hankeni* sp. nov., *E. leopoldi* sp. nov. and *E. serratus* and is elliptical (very narrow – L/W ratio 1.76–2.03) in *E. remipes* and *E. lacustris*.

12. *Anterior tergite* (0 = fully developed; 1 = reduced). The anterior tergite is fully developed in all taxa where known except *E. pittsfordensis* and *E. leopoldi* sp. nov. where it is very short and just fills the area between the genal facets. In these two taxa, the genal facets of the carapace therefore articulates towards the second tergite, not the first. For illustrations of this character, see Sarle (1903: 17, fig. 1) and Jones & Kjellesvig-Waering (1985: figs 3.1, 3.2 and 3.4).

13. *Epimera on metasoma* (0 = large, angular; 1 = small, angular; 2 = very small or absent). Ordered. Large angular epimera on the metasoma is present in *Dolichopterus* and *E. minor*, while small epimera are present in *E. hankeni* sp. nov., *E. henningsmoeni*, *E. pittsfordensis*, *E. tetragonophthalmus* and *E. dekayi*. They are very small to not present in *E. remipes* and *E. lacustris*.

14. *Epimera on pretelson* (0 = long or medium, angular; 1 = long, rounded; 2 = short, angular). The epimera on the pretelson are long and angular in *Dolichopterus* and *E. hankeni* sp. nov., medium long and angular in *E. pittsfordensis*, *E. leopoldi* sp. nov., long and rounded in *E. tetragonophthalmus*, *E. henningsmoeni* and short and angular in *E. remipes* and *E. lacustris*. The status of this character in *E. dekayi* is confusing, as the holotype has angular epimera while a second specimen of similar size figured by Clarke & Ruedemann (1912: 19, fig. 2) has long rounded epimera. Care must be taken when using this character, as the epimera in some taxa increase in length and become rounder during ontogeny.

15. *Angular striated ornament of pretelson* (0 = absent; 1 = present). *Eurypterus hankeni* sp. nov., *E. dekayi*, *E. pittsfordensis*, *E. serratus* and *E. leopoldi* sp. nov. have ornament of angular striations.

16. *Imbricate scale ornament of pretelson* (0 = absent; 1 = present). *Eurypterus tetragonophthalmus*, *E. henningsmoeni*, *E. remipes* and *E. lacustris* have ornament of imbricate scales on the pretelson, while these are not present in other taxa.

17. *Serrated fringe medially on postabdominal segments* (0 = absent; 1 = present). The serrated fringe medially on each segment of the postabdomen is present in *E. pittsfordensis* and *E. leopoldi* sp. nov. For an illustration of this fringe see Sarle (1903: pls 19, 20 & 22).

18. *Telson shape* (0 = lanceolate; 1 = styliform). The telson shape is styliform (Tollerton 1989: fig. 15-2) in *E. pittsfordensis*, *E. serratus* and *E. leopoldi* sp. nov. and more lanceolate (Tollerton 1989: fig. 15-1) in *E. dekayi*, *E. hankeni* sp. nov., *E. minor*, *E. remipes*, *E. lacustris*, *E. tetragonophthalmus* and *E. henningsmoeni*.

19. *Striated ornament of telson* (0 = absent; 1 = present). Striated marginal ornament has been observed on the telson of *E. pittsfordensis*, *E. serratus*, *E. leopoldi* sp. nov. and possibly on *E. hankeni* sp. nov.

20. *Imbricate scale ornament of telson* (0 = absent; 1 = present). *Eurypterus henningsmoeni* and *E. tetragonophthalmus* has an ornament of imbricate scales anteriorly on the telson.

21. *Serrate ornament of telson* (0 = absent; 1 = present). *Eurypterus tetragonophthalmus*, *E. remipes* and *E. lacustris* have serrate ornament along most of the telson length.

Additional characters that might be utilised in future works are: (1) The morphology or relative size of VI-P7a. This character shows a similar trend (and is possibly linked) to the character describing relative sizes of VI-P7 and VI-P8. Taxa with small VI-P7 (*E. tetragonophthalmus*, *E. henningsmoeni*) have small VI-P7a, while those with a large 7 have a large 7a (*E. remipes*, *E. lacustris*). (2) The ornament of principal scales on the opisthosoma. Although the ornamentation of the segments also certainly carries phylogenetic information, the numbers of scales are poorly known and only the number of scales on the carapace is here utilised. (3) The presence or absence of minute 'teeth' on the anterior notch of the metastoma. *Eurypterus pittsfordensis* (Kjellesvig-Waering 1958), *E. leopoldi* sp. nov. (Jones & Kjellesvig-Waering 1985) and *E. tetragonophthalmus* (Holm 1898) have these 'teeth' present, which has not been seen in the other species of *Eurypterus*, but this is probably a question of preservation.

Phylogeny of *Eurypterus*

The data matrix in Table 2 was analysed using PAUP* 4.0b10 (Swofford 2002). Five of the characters (2, 4, 9, 10 and 13) were ordered. This gave 138 most parsimonious trees differing in the relative positions of *E. serratus*, *E. hankeni*, *E. dekayi*, *E. ornatus* and *E. laculatus*. The strict consensus tree of these 138 is shown in Fig. 6A. After removing uninformative characters, the tree length was 36, the consistency index was 0.75 and the retention index was 0.82. Bootstrap support values, based on 1000 replicates, are indicated
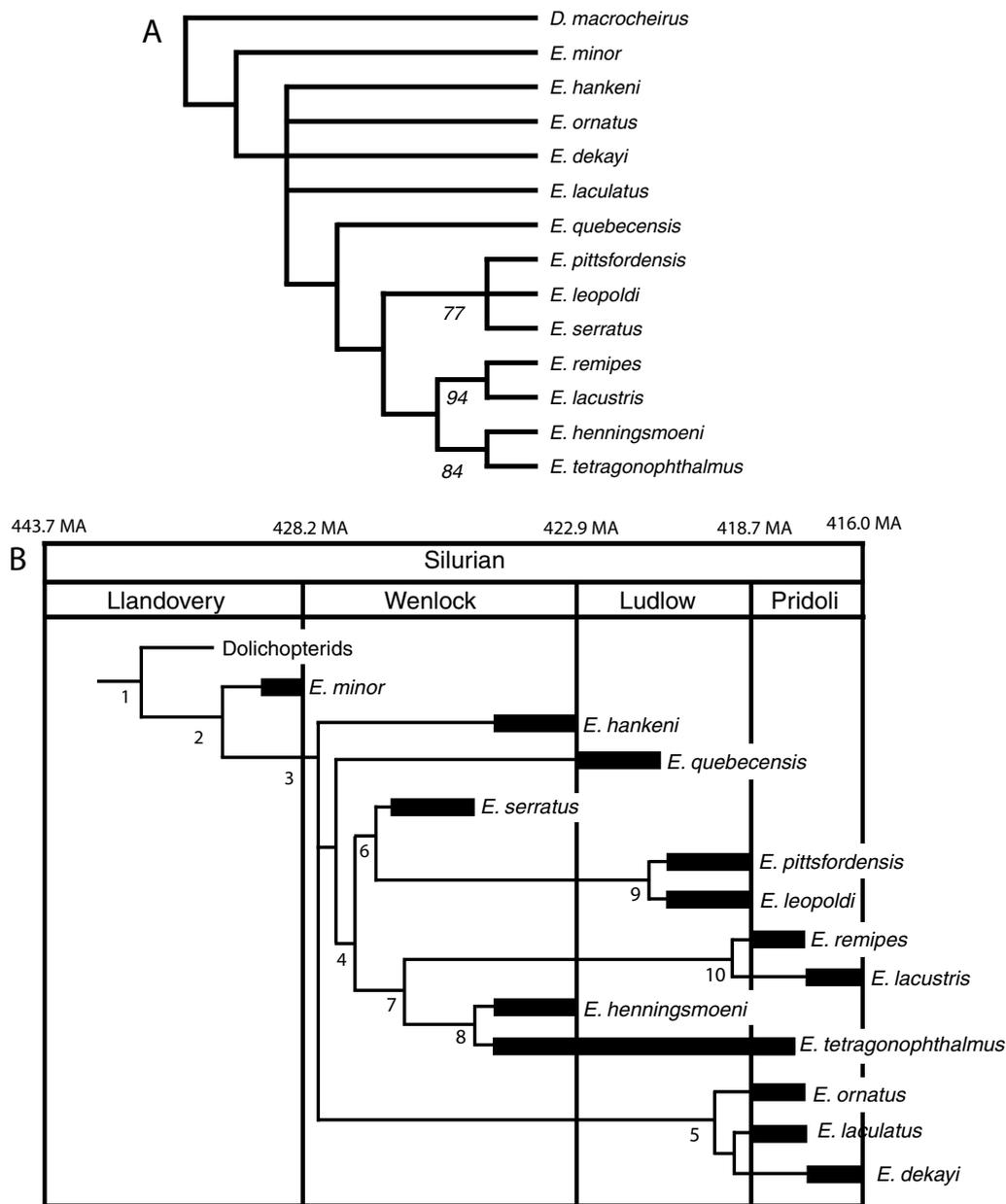
Figure 6 **A,** Strict consensus tree of the 138 most parsimonious trees from the analysis of the data in Table 2, with bootstrap support indicated beneath nodes (see the text for details). Tree length = 36 steps; Consistency Index = 0.75; Retention Index = 0.82; *D.*, *Dolichopterus*; *E.*, *Eurypterus*. **B,** Interpreted evolutionary relationships between the different species of *Eurypterus* superimposed on a Silurian timescale.

under the nodes. A phylogeny (Fig. 6B) of the species belonging to *Eurypterus* was constructed based on calibrating the cladogram in Fig. 6A against the known fossil record. The character transformations indicated at the numbered nodes in Fig. 6B are given in Table 3.

As seen in Fig. 6A, the most basal taxon in *Eurypterus* is undoubtedly *E. minor* which has a coarse ornament of pustules, no ornament of raised principal scales, crescentric eyes with large palpebral lobes and large epimera on the postabdomen, the latter two characters shared with the outgroup, *Dolichopterus. Eurypterus hankeni* sp. nov. retains pustules, but has six raised principal scales on the carapace and a large, pentagonal VI-P9, something possibly also present in *E. minor*.

Eurypterus flintstonensis probably belongs somewhere on the *remipes* clade, but this has not been illustrated since its position on the clade is not known. *Eurypterus* (?) *cephalaspis*, *E.* (?) *loi*, *E.* (?) *styliformis* and *E.* (?) *yangi* are all too poorly described to include in Fig. 6B. The clades with the longest ghost ranges are the *remipes* clade and the *dekayi* clade, both with ghost ranges from the Upper Wenlock to the Lower Pridoli.

The *dekayi* group
This does not resolve as a clade in the analysis, but since *E. laculatus* and *E. ornatus* are coded exactly as *E. dekayi* for their known character states, it is highly likely that they form a clade. It is supported by an ornament of fine pustules

Table 3   Character changes on the numbered nodes of Fig. 6B.

Node	Character changes
1	Eyes crescentric around large palpebral lobe; 2 spines per podomere in appendages II–IV; appendage V non-spiniferous *Eurypterus* type; long angular epimera on pretelson; telson lanceolate and unornamented
2	Genal facets developed; ornament of coarse pustules
3	Eyes reniform and palpebral lobe reduced; ornament of fine pustules and six raised principal scales on carapace; VI-P8 approximately same size as VI-P7; VI-P9 pentagonal and much smaller than VI-P8
4	Less than six principal scales on carapace; VI-P9 small and triangular
5	4–6 spines per podomere in appendages III–IV; carapace and segments 1–3 have lost ornament of raised scales (the first of these might be present only in *Eurypterus dekayi*)
6	Telson styliform; telson with marginal ornament of dense angular striations
7	Four principal scales on carapace; telson with serrate marginal ornament
8	Pretelson with long rounded epimera; VI-P7 < VI-P8
9	Reduced anterior tergite (or possibly at 5), fringe of serrations medially on postabdominal segments; pretelson with marginal ornament of striations; telson with ornament of many small striations and a few larger ones
10	P7 > P8 in the swimming leg; metastoma narrow; pretelson with small, angular epimera

covering most of the carapace and three anterior segments, while lacking raised scales on the carapace and these segments and, possibly, by having 4–6 spines per podomere in appendages III–IV. An additional, possible synapomorphy is the short and broad carapace in these taxa, but as this character is highly dependent on ontogeny, it needs to be examined in more detail.

Eurypterus quebecensis apparently has six principal scales on the carapace, while lacking pustulate ornament and, therefore, resolves as a sister group to the main clade in the genus containing the *pittsfordensis*, the *tetragonophthalmus* and *remipes* clades.

The *pittsfordensis* clade

This contains *E. pittsfordensis*, *E. leopoldi* sp. nov. and *E. serratus*. It is recognised by having three principal scales on the carapace, a reduced anterior tergite, a serrated fringe medially on the postabdominal segments, long, angular epimera on the pretelson with marginal ornament of angular striations and a styliform telson with marginal ornament of angular striations. This clade is a sister clade to the *tetragonophthalmus* and *remipes* clades. *Eurypterus serratus* is positioned basally on Fig. 6B mainly because of its age, but it also has a more densely serrated telson than the other two taxa.

The *tetragonophthalmus* and *remipes* clades

A clade of *E. remipes*, *E. lacustris*, *E. henningsmoeni* and *E. tetragonophthalmus* is supported by having four principal scales on the carapace, a pretelson with marginal ornament of imbricate scales (however, these are only seen in very large individuals of *E. remipes* and *E. lacustris*) and a telson

that is serrated posteriorly. A clade of *E. henningsmoeni* and *E. tetragonophthalmus* is supported by having a distal paddle (VI-P8 is bigger than VI-P7) rounded epimera on the pretelson and a telson with an ornament of imbricate scales anteriorly on the telson. The clade comprising *E. remipes* and *E. lacustris* is supported by having a proximal paddle (VI-P7 is bigger than VI-P8) and by small angular epimera on the pretelson, a character that is probably due to paedomorphism, as all the species in *Eurypterus* have small angular epimera on the pretelson in juveniles, but these tend to develop into larger angular or rounded epimera in more mature animals. *E. flintstonensis* might also belong to the *remipes* clade.

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