The systematics and phylogeny of the Stylonurina
(Arthropoda: Chelicerata: Eurypterida)

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The first well-resolved phylogeny of stylonurine eurypterids (30 taxa, 58 characters) is presented, prompting a taxonomic
revision at the familial and superfamilial levels. The monophyletic suborder Stylonurina consists of four superfamilies:
Rhenopteroidea, Stylonuroidea, Kokomopteroidea and Hibbertopteroidea. The enigmatic hibbertopterids – large sweep-
feeding forms from the Carboniferous to end-Permian – are therefore demonstrated to be an in-group Stylonurina clade,
within Eurypterida, in contrast to some earlier hypotheses. Furthermore, the genus Drepanopterus is shown to be polyphyletic:
‘Drepanopterus’ bembycoides is transferred to Moselopteridae fam. nov. along with Moselopterus and Vinetopterus at the
base of the Eurypterina, defined by their possession of a pediform appendage VI bearing a modified podomere 7a. Evolution
towards a sweep-feeding mode of life occurred independently in stylonuroids and hibbertopteroids, involving either multiple
rows of fixed spines on the prosomal appendages (in stylonuroids) or paired movable flattened spines (‘blades’) on the
prosomal appendages alongside a posteriorly cleft metastoma and coxal laden (in hibbertopteroids). The Stylonurina have a
relatively poor fossil record (RCI 15%), when compared to more derived Eurypterina clades (e.g. Adelophthalmoidea RCI
66%; Pterygotoidea RCI 53%), but is relatively more complete than basal Eurypterina clades (RCI -21%). The fit between
phylogeny and stratigraphical occurrences of stylonurid taxa is good (SCI 0.65 and GER 0.77, with only 0.3% of 1000
randomisation tests yielding greater congruence; GER* 0.995), and generic-level collector curves of the Stylonurina and
Eurypterina show no major discrepancies in their sampling histories. These differences could be explained by geographic
collection bias, taxa having different habitat preferences (and hence fossilisation potential), and ontogenetic factors: these
results support previous suggestions that stylonurine eurypterids are oversplit.

Key words: Palaeozoic; eurypterid; relative completeness; sweep-feeding; Moselopteridae

Introduction

Eurypterids were an extinct group of predatory aquatic
chelicerates found in a progression of marine to freshwater
environments throughout most of the Palaeozoic. Almost
three quarters of known eurypterid species (Eurypterina) were active nektonic predators, using their posterior
(sixth) pair of prosomal appendages as swimming paddles
(Tettie 2007). Stylonurine eurypterids (Stylonurina) were
a comparatively rare group which retained their poste-
rior prosomal appendages for walking. Despite this, the
Stylonurina have the longer temporal range: the oldest
recorded eurypterid, from the Late Ordovician (Størmer
1951), is a stylonurin as is the youngest from the Late
Permian (Ponomarenko 1985). Stylonurina remain rare
throughout the Ordovician and Silurian, although the radi-
ation of the hibbertopterids (large sweep-feeding forms) in
the Late Devonian and Carboniferous represents the last
major genus-level radiation within the Eurypterida (Tettie
2007).

The phylogeny of the monophyletic Eurypterina is now
reasonably well-resolved (Tettie & Cuggy 2007; Braddy
et al. 2008; Tettie & Poschmann 2008), yet the rela-
relationships between the Stylonurina remain poorly under-
stood: previous analyses were too limited in taxonomic
scope, or resolution, to determine whether Stylonu-
rina was monophyletic with respect to Eurypterina.
Confounding this issue, the large hibbertopterids have
even been suggested to represent a separate order to
Eurypterina (Størmer & Waterston 1968; Tollerton 1989),
and no previous phylogenetic analysis has confirmed
their status. Stylonurine taxonomy has remained prob-
lematic since Tollerton’s (1989) phenetic approach, and
a robust and comprehensive phylogeny permits a modern
systematic revision. Following Tettie & Cuggy (2007)
and Tettie & Poschmann (2008) the completeness of the
stenurine fossil record is tested using the Relative
Completeness Index (RCI) developed by Benton
& Storrs (1994) and compared to other eurypterid
clades.

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Materials and methods

The phylogenetic analysis was performed using PAUP* 4.0b10 PPC (Swofford 2003) and analysed with MacClade 4.08 (Maddison & Maddison 2005), with all characters unordered and of equal weight. Trees were searched for with the branch-and-bound algorithm using furthest addition sequence. Jacknifing was performed using simple addition sequence and tree bisection-reconnection (TBR) branch swapping, with 1000 repetitions and 20% character deletion. The taxa were coded from stylonurine descriptions in the published literature and from personal observations (see Appendix). Representatives of genera were selected based on data completeness rather than type status, with multiple species of Drepanopterus included to test the possible polyphyletic nature of this genus. Weinbergina opitzi was selected as outgroup as it represents the most plesiomorphic known xiphosuran (Anderson & Selden 1997), outgroup to Eurypterida (Selden & Dunlop 1998). Although Limulus is often used as the outgroup for chelicerate analyses, it is actually highly apomorphic and so Weinbergina is preferred as a suitable outgroup. Hughmilleria socialis Sarle, 1903, Eurypterus remipes DeKay, 1825 and Onychopterella augusti Braddy et al., 1995 were included to represent the Euryptera and test the monophyly of Stylonurina. A number of genera were excluded from the analysis: Stylonuroides Kjellesvig-Waering, 1966, due to it being poorly known and lacking any useful synapomorphies, along with Campylocephalus Eichwald, 1860, Hastimima White, 1908, Dunsopterus Waterston, 1968 and Vernonopterus Waterston, 1968. While these four genera are clearly hibbertopterids most are based on incomplete specimens that add no information to the analysis and may be synonyms of either Hibbertopterus or Cyrtoctenus (see Systematic Palaeontology). Eurypterid terminology follows Tollerton (1989), Selden (1981), and Lamsdell et al. (2009) for the hibbertopterids.

The Relative Completeness Index (RCI), a metric of the relative completeness of the fossil record to the phylogenetic topology (Benton & Storrs 1994), was calculated and compared to calculations for phylogenetic fit with stratigraphical occurrence using Stratigraphic Consistency Index (SCI: Huelsenbeck 1994) and Gap Excess Ratio (GER: Wills 1999). The RCI estimates the relative completeness of the fossil record by calculating the sum of cladistically-implied gaps relative to observed stratigraphic range. RCI values are unbounded, and therefore difficult to interpret straightforwardly. They also confute completeness with the stratigraphic congruence of a particular cladogram. In general, however, negative values (no theoretical minimum) indicate that there are more gaps than known stratigraphic ranges, while positive values (up to a maximum of 100%) imply more known ranges than gaps. Values of 100% are not possible except in the trivial case where all taxa originate at the same time. In order to test directly the congruence between the order of first occurrences in the fossil record and inferred phylogenetic relationships the SCI and GER were calculated. Both of these can range from 0 (worse fit) to 1 (best fit), although the SCI can only achieve these extremes for fully pectinate trees, unless several taxa originate at the same horizon. Randomisation tests were performed and GER* (Wills et al. 2008) calculated to test the statistical significance of these results. Collector curve analysis was performed using data from Tetlie (2004), updated to include the latest discoveries, and plotted based on year of discovery rather than year of naming. Family-level assignment of taxa follows Tetlie (2004) for the Eurypterina, while the assignment of Stylonurina follows our revised taxonomy (see Systematic Palaeontology). This dataset comprises 291 species, 66 genera and 19 families.

Results

Phylogeny

Analysing all characters unordered and with equal weight yielded a single most parsimonious tree (MPT) with a Tree Length (TL) of 94, ensemble Consistency Index (CI) of 0.628, Retention Index (RI) of 0.760, and Rescaled Consistency Index (RC) of 0.477 (Fig. 1). The support values given above the nodes were retrieved through a Jackknife analysis of the dataset using 20% character deletion with 1000 repetitions, while the numbers beneath the nodes in bold italics are Bremer support values (Bremer 1994) calculated manually using PAUP*. Attempted bootstrap analysis proved problematic, with the search time for each repetition increasing astronomically after the first few.

There have been few published studies of stylonurine phylogeny. Waterston (1979, fig. 13) presented a genus-level cladogram based largely on appendage spinosity and carapace shape. Constraining the tree presented herein to that of Waterston, the resulting tree length of 119 steps is 25 steps longer. Only two phylogenetic analyses have included a large sample of Stylonurina. Firstly, an analysis by Plotnick (1983), simplified to the level of families and figured by Beall & Labandeira (1990, fig. 2), retrieved most of the familial groups recovered in this analysis but has a tree length of 97, 3 steps longer. Secondly, a limited number of Stylonurina featured in Tetlie’s (2007, fig. 1) species-level eurypterid phylogeny. Despite retrieving a similar clade topology to that here familial interrelationships were poorly resolved, and constraining the current data to Tetlie’s topology results in a tree length of 105, 11 steps longer than herein. This new tree is therefore shorter, and better-resolved, than either previous phylogenetic hypothesis.

Moselopterid clade

The results of the phylogenetic analysis confirm that the genus Drepanopterus consists only of the type species, D. pentlandicus, and D. abonensis. Of the other species currently included within this genus, only ‘D’. bembycoides
The systematics and phylogeny of the Stylonurina

Figure 1. The single tree retrieved from analysis of the matrix (see Appendix). Support values above the nodes were retrieved through Jackknife analysis (20% character deletion, 1,000 repetitions), while those beneath the nodes are Bremer support values.

is sufficiently described to warrant inclusion within the analysis, and it is here shown to be a primitive member of the Eurypterina, united by the possession of podomere 7a on appendage VI, and as such will need elevating to its own genus pending a full redescription. In order to ascertain that the moselopterid clade is a natural one, *Vinetopterus* and *Drepanopterus* bembycoides were coded for Tetlie & Cuggy’s (2007) basal Eurypterina matrix (Table 1). A

| Table 1. The basal Eurypterina ‘Drepanopterus’ bembycoides and Vinetopterus struwei, coded for inclusion in the matrix presented by Tetlie & Cuggy (2007) which lists characters and their states. |
|---|---|---|---|---|---|---|---|
| Char  | 5  | 0  | 1  | 1  | 2  | 2  | 3  |
| Character  | 00-?? | ?!100 | 00??0 | 00110 | 10000 | 0200? | ?230? | 00 |
| ‘Drepanopterus’ bembycoides  | 00-00 | ?!100 | 00??0 | 00111 | 00000 | 120?? | ?1200 | 00 |
| Vinetopterus struwei  |
Figure 2. Majority-rule consensus of the 10 MPTs retrieved from running the data matrix presented by Tetlie & Cuggy (2007) with the addition of *Vinetopterus struiei* and 'Drepanopterus' *bembycoides* (see Table 1 for coding). The topology is identical to that in the original analysis, with the addition of *Vinetopterus* and 'Drepanopterus' forming a clade with *Moselopterus*. Support values above the nodes were retrieved through Jackknife analysis (20% character deletion, 1000 repetitions), while those beneath the nodes are majority rule support when less than 100%.

Majority rule consensus of the resulting 10 MPTs (TL = 110, CI = 0.609, RI = 0.753, RC = 0.459) produces an identical topology to the original analysis with the addition of *Vinetopterus* and 'Drepanopterus' *bembycoides* forming a clade with *Moselopterus* as sister-group to all other Eurypterina (Fig. 2). This will render the family Drepanopteridae (Kjellesvig-Waering, 1966) as previously defined redundant, although the diagnosis of the family by Poschmann & Tetlie (2004) is applied to a new family here, under the name Moselopteridae fam. nov., as a basal clade of Eurypterina.

**Systematic palaeontology**

Order *Eurypterida* Burmeister, 1843

(= Gigantostraca Haeckel, 1866; Cyrtoctenida Størmer & Waterston, 1968)

Suborder *Stylonurina* Deiner, 1924

(= Woodwardopterina Kjellesvig-Waering, 1959

(nom. trans. Kjellesvig-Waering, 1979);

Hibbertopterina Störmer, 1974)
**Diagnosis.** Eurypterids with transverse sutures on the ventral plates and lacking a modified podomere 7a on appendage VI.


( = Brachyopterelloidea Tollerton, 1989)

**Diagnosis.** Stylonurina with posterior margin of metastoma rounded.

Family **Rhenopteridae** Størmer, 1951

( = Brachyopterellidae Tollerton, 1989; Alkenopteridae Poschmann & Tetlie, 2004)


**Diagnosis.** Rhenopteroidea with single fixed spines on prosomal appendage III and a short telson. Appendages II—IV with short, fixed spines; V—VI non-spiniferous.

**Occurrence.** Middle Ordovician to Middle Devonian.

Subfamily **Rhenopterinae** Størmer, 1951 (nom. trans.)


**Diagnosis.** Rhenopteridae with non-spiniferous appendage IV and caudal postabdomen.

**Occurrence.** Early Devonian to Middle Devonian.

Superfamily **Stylonuroidea** Diener, 1924

**Diagnosis.** Stylonurina with flattened or truncated posterior metastoma margin.

Family **Stylonuridae** Diener, 1924

( = Laurieipteridae Kjellesvig-Waering, 1966; Pageidae Kjellesvig-Waering, 1966)


**Diagnosis.** Stylonuroidea with undifferentiated opisthosoma; appendages II—IV spiniferous *Ctenopterus*-type; V—VI non-spiniferous *Pagea*-type.

**Occurrence.** Early Silurian to Early Devonian.

**Remarks.** Despite originally describing an epistoma in *Pagea*, Waterston (1979) later revised this opinion, stating instead that the ‘sutures’ were cracks in the carapace. Although lacking the ventral structures and anterior appendages, *Stylonurus* shares several characters with the other members of this group including the shape of the carapace, positioning of the eyes and trilobation of the opisthosoma, and is therefore assigned to the family.

Subfamily **Laurieipterinae** Kjellesvig-Waering, 1966 (nom. trans.)


**Diagnosis.** Stylonuridae with broad metastoma and epistoma with rostral field.

**Occurrence.** Early Silurian.

Family **Parastylonuridae** Waterston, 1979


**Diagnosis.** Stylonuroidea with posterior second order opisthosomal differentiation; appendages II—IV spiniferous *Hughmilleria*-type; V—VI non-spiniferous *Parastylonurus*-type or *Pagea*-type.

**Occurrence.** Silurian.

**Remarks.** The family as defined here is paraphyletic, but is retained for the present until more complete material of *Stylonurus* and *Stylonurella* is described.


**Diagnosis.** Stylonurina with spiniferous appendage V and posterior notch on metastoma.

Family **Kokomopteridae** Kjellesvig-Waering, 1966


**Diagnosis.** Kokomopteroidea with opisthosoma undifferentiated with marginal rim; appendages II—V spiniferous *Lamontopterus*-type; VI non-spiniferous *Kokomopterus*-type.

**Occurrence.** Silurian.

Family **Hardieopteridae** Tollerton, 1989

Diagnosis. Kokomopteroidea with lateral pleurae on metasoma and pretelson; large lunate scales on posterior carapace margin; telson clavate. Opisthosoma shows both a second and fourth order differentiation into a mesosoma and metasoma. Appendages II-IV unknown; V spiniferous *Hardieopterus*-type; VI non-spiniferous *Hardieopterus*-type.

Occurrence. Early Silurian to Late Devonian.


Diagnosis. Stylonurina with posterior cleft on metastoma, round lenses overlying the lateral eyes and the anterior prosomal appendages modified for sweep-feeding.

Family *Drepanopteridae* Kjellesvig-Waering, 1966

Included genus. *Drepanopterus* Laurie, 1892.

Diagnosis. Small to medium Hibbertopteroidea with prosoma horseshoe-shaped and with broad marginal rim; non-spiniferous appendage IV; cuticular ornament pustular.

Occurrence. Lower Silurian to Upper Devonian

Family *Hibbertopteridae* Kjellesvig-Waering, 1959 (= *Cyrtoctenidae* Waterston et al., 1985)


Diagnosis. Large Hibbertopteroidea with broad prosoma; telson hastate with paired ventral keels; cuticular ornament of scales or mucrones; spiniferous appendage IV; tongue-shaped scales on posterior opisthosomal tergite margins; posterolateral lobes on prosoma.

Occurrence. Lower Silurian to Upper Devonian

Family *Hibbertopteridae* Kjellesvig-Waering, 1966

Remarks. *Cyrtocenus*, *Dunsopterus* and *Vernonopterus* may be synonyms, based on similarities in the podomeres (*Dunsopterus/Cyrtocenus*) and opisthosomal ridges (*Vernonopterus/Cyrtocenus*). Jeram & Selden (1994) also suggested that *Cyrtocenus* and *Hibbertopterus* may be different ontogenetic stages of each other, whereby rachis are developed in the later moult stages. This would explain why the smaller *Hibbertopterus* specimens are more complete than the fragmentary *Cyrtocenus* specimens; the majority of *Hibbertopterus* specimens would be exuviae, whereas the larger *Cyrtocenus* specimens would represent mortalities, susceptible to scavenging. The largest *Hibbertopterus* specimen is an isolated carapace, and therefore does not preclude the possibility that *Hibbertopterus* developed rachis.

Family *Mycteropidae* Cope, 1886


Diagnosis. Large Hibbertopteroidea with prosoma parabolic; telson hastate with paired ventral keels; cuticular ornament of scales or mucrones; nonspiniferous appendage IV; elongation of first and second opisthosomal tergites.

Occurrence. Carboniferous.

Remarks. *Mycterops*, *Woodwardopterus* and *Megaraechine* possibly represent different ontogenetic stages of each other, based on specimen sizes and patterns in mucronation (Selden et al. 2005), and therefore may be synonyms. If *Mycterops (?) whitei* does have a caudal postabdomen (Schram 1984) then it is not a *Mycterops*.

Suborder *Stylonurina incertae sedis*


Remarks. The shape of the carapace, position and morphology of the lateral eyes and shape of coxa VI indicate that the affinities of *Stylonuroides* lie within the Rhenopteridae; however, further specimens showing the metastoma and genital operculum are needed before this assignment can be confirmed.

Suborder *Eurypterina* Burmeister, 1843


Remarks. The shape of the carapace, position and morphology of the lateral eyes and shape of coxa VI indicate that the affinities of *Stylonuroides* lie within the Rhenopteridae; however, further specimens showing the metastoma and genital operculum are needed before this assignment can be confirmed.

Superfamily * Moselopteroidea* sup. fam. nov.


Diagnosis. Large Hibbertopteroidea with broad prosoma; telson hastate with paired ventral keels; cuticular ornament of scales or mucrones; spiniferous appendage IV; elongation of first and second opisthosomal tergites.

Occurrence. Late Devonian to Late Permian.

Remarks. *Cyrtocenus*, *Dunsopterus* and *Vernonopterus* may be synonyms, based on similarities in the podomeres (*Dunsopterus/Cyrtocenus*) and opisthosomal ridges (*Vernonopterus/Cyrtocenus*). Jeram & Selden (1994) also suggested that *Cyrtocenus* and *Hibbertopterus* may be different ontogenetic stages of each other, whereby rachis are developed in the later moult stages. This would explain why the smaller *Hibbertopterus* specimens are more complete than the fragmentary *Cyrtocenus* specimens; the majority of *Hibbertopterus* specimens would be exuviae, whereas the larger *Cyrtocenus* specimens would represent mortalities, susceptible to scavenging. The largest *Hibbertopterus* specimen is an isolated carapace, and therefore does not preclude the possibility that *Hibbertopterus* developed rachis.

Family *Mycteropidae* Cope, 1886


Diagnosis. Large Hibbertopteroidea with prosoma parabolic; telson hastate with paired ventral keels; cuticular ornament of scales or mucrones; nonspiniferous appendage IV; elongation of first and second opisthosomal tergites.

Occurrence. Carboniferous.

Remarks. *Mycterops*, *Woodwardopterus* and *Megaraechine* possibly represent different ontogenetic stages of each other, based on specimen sizes and patterns in mucronation (Selden et al. 2005), and therefore may be synonyms. If *Mycterops (?) whitei* does have a caudal postabdomen (Schram 1984) then it is not a *Mycterops*.

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Remarks. The shape of the carapace, position and morphology of the lateral eyes and shape of coxa VI indicate that the affinities of *Stylonuroides* lie within the Rhenopteridae; however, further specimens showing the metastoma and genital operculum are needed before this assignment can be confirmed.

Suborder *Eurypterina* Burmeister, 1843


Remarks. The shape of the carapace, position and morphology of the lateral eyes and shape of coxa VI indicate that the affinities of *Stylonuroides* lie within the Rhenopteridae; however, further specimens showing the metastoma and genital operculum are needed before this assignment can be confirmed.

Superfamily * Moselopteroidea* sup. fam. nov.


Diagnosis. Large Hibbertopteroidea with broad prosoma; telson hastate with paired ventral keels; cuticular ornament of scales or mucrones; spiniferous appendage IV; elongation of first and second opisthosomal tergites.

Occurrence. Late Devonian to Late Permian.

Remarks. *Cyrtocenus*, *Dunsopterus* and *Vernonopterus* may be synonyms, based on similarities in the podomeres (*Dunsopterus/Cyrtocenus*) and opisthosomal ridges (*Vernonopterus/Cyrtocenus*). Jeram & Selden (1994) also suggested that *Cyrtocenus* and *Hibbertopterus* may be different ontogenetic stages of each other, whereby rachis are developed in the later moult stages. This would explain why the smaller *Hibbertopterus* specimens are more complete than the fragmentary *Cyrtocenus* specimens; the majority of *Hibbertopterus* specimens would be exuviae, whereas the larger *Cyrtocenus* specimens would represent mortalities, susceptible to scavenging. The largest *Hibbertopterus* specimen is an isolated carapace, and therefore does not preclude the possibility that *Hibbertopterus* developed rachis.


**Diagnosis.** Legs II—IV spiniferous, *Hughmilleria*-type; legs V—VI non-spiniferous, at least VI of *Drepanopterus*-type. Metastoma ovate, notched anteriorly (emended after Poschmann & Tetlie 2004).

**Occurrence.** Early Silurian to Early Devonian.

**Remarks.** *Moselopterus* purportedly has a podomere 7a on appendage V, although the evidence for this is not convincing. Neither *Vinetopterus* nor ‘D’. *bembycoides* show any evidence of a V-7a; if it is confirmed in *Moselopterus* it would indicate that *Vinetopterus* and ‘D’. *bembycoides* belong within a separate family.

**Discussion**

Results of the phylogenetic analysis show that the Stylonurina comprises four clades: Rheopteroidea, Stylonuroidea, Kokomopteroidea and Hibbertopteroidea (Fig. 1). The most primitive clade, Rheopteroidea, accommodates a number of previously enigmatic eurypterids, including *Brachyopterus*, *Brachyopterella*, *Kiæropterus*, *Alkenopterus* and *Rhenopterus*, united by a rounded posterior margin to the metastoma and prosomal appendage III bearing single fixed spines. *Brachyopterus* is the oldest known eurypterid (Størmer 1951), and is fittingly the sister taxon to all other rheopterids. The problematic genera *Stylonurus* and *Stylonurella* were resolved within the clade of Stylonuroidea, due to an undifferentiated opisthosoma and quadrate carapace, although this clade also has the least well-supported internal topology, with Jackknife support values in the high fifties. This is due, in part, to the incomplete nature of the single specimen of *Stylonurus powriei*, which lacks anterior prosomal appendages or any details of ventral structures. The problem is compounded by the lack of a preserved metastoma or pretelson and telson in *Stylonurella spinipes* and lack of dorsal structures in *Pagea sturrockii*.

The Hibbertopteroidea are resolved as sister group to Kokomopteroidea, united by a median ridge on the carapace between the lateral eyes and a distal thickening to the podomers of the prosomal appendages (Lamsdell et al. 2009). The Kokomopteroidea are united by a spiniferous prosomal appendage V and posterior notch on the metastoma and form two clades: the Kokomopteridae consisting of *Kokomopterus* and *Lamontopterus* and the Hardieopteridae consisting of *Hardieopterus*, *Tarsopterella* and *Hallipterus*. *Drepanopterus* resolves as the sister taxon to all other Hibbertopteroidea, befitting its Silurian origins, and shares characters with the Kokomopteroidea (clavate metastoma) and the other Hibbertopteroidea (posteriorly cleft metastoma, blades on the anterior prosomal appendages). The remaining hibbertopteroids are divided into the Hibbertopteridae (represented by *Hibbertopterus* and *Cyttoctenus*, which have blades on appendage IV and a broad carapace) and the Mycteropidae (consisting of *Woodwardopterus*, *Megarachne* and *Mycteropus*, which have a parabolic carapace, nonspiniferous appendage IV, and an elongated first tergite). The Hibbertopteridae and Mycteropidae are united by the possession of a hastate telson with paired ventral keels and a cuticular ornament consisting of scales or mucrones. The results of our analysis clearly place the hibbertopterids within Stylonurina following Lamsdell et al. (2009), contrary to the previous placement of hibbertopteroids as a separate order, outside Eurypterida (Tollerton 1989).

**Quality of the stylonurine fossil record**

The quality and congruence of the eurypterid fossil record was tested using three metrics (RCI, SCI, GER) derived from the phylogenetic topology with plotted range data (Fig. 3). Benton & Hitchin (1996) considered any RCI below +50% to be poor, and so the RCI of 15% retrieved from the stylonurine phylogeny suggests they have a poor fossil record (i.e. there are only 1.2 times more observed ranges than ghost ranges, worse than 92% of the trees analysed by Benton & Hitchin). The SCI of 0.65 and GER of 0.77 show a generally good congruence compared to the average SCI (0.55) and GER (0.56) of 1,000 trees compiled by Benton (2001), and only 0.3% of 1000 range permutations had a greater congruence than the observed results. GER*, calculated from the same randomisation tests, is 0.995. The topology of most clades fits well with the stratigraphic record, the main exception being the Stylonuroidea, within which the most derived genera (*Ctenopterus* and *Laurieipterus*) first appear at the same time as the most primitive (*Parastylonurus* and *Stylonurella*).

When comparing the RCI of 15% at genus level for Stylonurina with those of other eurypterid groups, there is a clear difference between that of -21% for basal Eurypterina (extrapolated from -41% calculated using species-level range data; Tetlie & Cuggy 2007), 66% for Adelophthalmoidea (from 34% calculated using species-level range data; Tetlie & Poschmann 2008) and 53% for Pterygotoidea (calculated from the phylogenetic tree of Braddy et al. 2008). The derived Euryptera clades have a more complete fossil record than the Stylonurina, while that of the primitive clade is less complete. When comparing collector curves for Stylonurina and Euryptera, however, it is clear that the two suborders have similar relative completeness in terms of known taxa, at species, genus, and family level (Fig. 4). Possible causes for the differences in RCI vary. It
is not thought that there is any major difference between the cuticle preservation of the two eurypterid clades, however different habitat preferences could influence their fossilisation potential (Tetlie & Poschmann 2008). There also appears to be some correlation with age: both Stylonurina and Adelophthalmoidea extend into the younger strata of the Devonian and Carboniferous, while Pterygotoidea are primarily known from their heavily sclerotised chelicerae which have a greater chance of preservation than the thin unmineralised cuticle that forms their bodies and that of other eurypterids. We note that in the hibbertopteroids, several genera may represent different ontogenetic stages (Jeram & Selden 1994; Selden et al. 2005). Assuming synonymy of these taxa, the RCI is 28%, closer to those of the derived Eurypterina and the results of the collector curves. Further work is needed to determine the ontogenetic variation in such taxa, but these results support previous suggestions that Stylonurina are oversplit. Neither result suggests that the generic record of Eurypterida is anywhere near complete: only the Adelophthalmoidea have an RCI significantly over 50%, and the generic collector curve shows no indication of reaching an asymptote. Part of the problem is that eurypterids are mainly known from North America and Europe. Collector curve analysis of trilobites (Tarver et al. 2007) has shown that these areas have a more highly sampled fossil record, largely as a result of more intense worker effort.

**Sweep-feeding niche convergence**

Stylonurina independently evolved sweep-feeding strategies in two of their four major clades, Stylonuroidea and Hibbertopteroidea. In both cases, however, these involve modifications of the spines on their anterior prosomal appendages for raking through the substrate. Primitive Stylonurina (Rhenopteroidea) and the families Parastylonuridae (Parastylonurus and Stylonurella) and Kokomopteridae (Kokomopterus and Lamontopterus) retained primitive Hughmilleria-type prosomal appendages II—IV, unsuited to sweep-feeding, and probably adopted a scavenging lifestyle (Waterston 1979). The Hardieopteridae, while displaying some sweep-feeding characters including a broadening of the metastoma and the spines of the anterior prosomal appendages, may even have been benthic bottom-dwellers living partially buried in the substrate (Waterston...
The systematics and phylogeny of the Stylonurina

Figure 4. Collector curves of the Eurypterida, showing both the Eurypterina (black) and Stylonurina (grey). Of the three taxonomic ranks presented, only the family-level curve has reached an asymptote. Vertical bars show the taxonomic or descriptive papers published since 1900. Publication data retrieved from WebCT.

1979). The Stylonuridae had fixed spines on appendages II—IV which they could have used as dragnets to rake through the sediment, indiscriminately entangling anything within their sweeping arc, whereas the Hibbertopteroidea would have been more selective feeders. The modified blades on their anterior prosomal appendages possessed sensory setae, the tactile function of which could have allowed them to preferentially select prey items from the substrate in a way the Stylonuridae could not.

Hibbertopteroids show some of the most extreme adaptions to sweep-feeding, possessing blades on prosomal appendages II—III (and IV in the Hibbertopteroidea), distinct from the flattened spines in Hallipterus, being laterally expanded with a blunt, rounded termination and possessing sensory setae. The basal hibbertopteroid Drepanopterus has a mix of characters found in all hibbertopteroids (i.e. the cleft metastoma, blades on anterior appendages, calcareous lens overlying the lateral eyes) and some specific to mycteropids: appendage IV was not used in food capture and the coxae are large, as in Megarachne. Furthermore, appendage III retains some Hughmilleria-type conical spines suggesting that it also took larger invertebrate prey (Lamsdell et al. 2009). In mycteropids only appendages II and III were used in prey capture, whereas hibbertopteroids also involved appendage IV, whilst still retaining its use as a walking leg. The coxae in Hibbertopterus are reduced, however part of the food masticatory process was assumed by the laden (plates overlying the coxae). Cyrtoctenus displays an extraordinary degree of adaptation to sweep-feeding, with its blades modified into comb-like rachis that could entrap smaller prey or organic food particles. Moveable accessory spines then pushed the prey off the rachis towards the gnathobases and metastoma (Waterston et al. 1985). The coxae in Cyrtoctenus are still rather large, and so it is likely that it would also take larger invertebrates when the opportunity arose.

The metastoma (post-oral ventral feeding plate) in these sweep-feeding taxa also displays adaptations associated with a sweep-feeding mode of life: in stylonuroids it becomes rather broad, whilst in kokomopteroids it bears a posterior notch, and in hibbertopteroids, including Drepanopterus, it is cleft posteriorly, becoming broader in more derived taxa like Hibbertopterus. This suggests that a broad metastoma was a derived adaptation to a sweep-feeding life habit, and that the posterior cleft found in hibbertopteroids was a further development, in some way beneficial to this mode of life. Uncompressed specimens show the metastoma to be concave in shape (Waterston 1957), forming a chamber around the oral opening, although it is unlikely that the metastoma and the prosomal appendages interacted to scrape food off the blades, in that the appendages could not flex underneath the carapace to the necessary degree (Waterston et al. 1985) and the appendages in Hibbertopterus were too short to reach the posterior of the metastoma.
Acknowledgements

Thanks go to Paul Shepherd (BGS Keyworth) for access to stylonurine material, Mark Bell for comments on the phylogenetic method and Markus Poschmann for discussions on eurypterid relationships. Matthew Wills (University of Bath) and an anonymous referee are thanked for the invaluable suggestions that greatly improved earlier stages of the manuscript. JCL acknowledges the Palaeontological Association for a Sylvester-Bradley Award into stylonurine phylogeny and the Palaeontographical Society for a research grant into early eurypterid relationships.

References

Appendix: character list and matrix

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<th>Character</th>
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27. Prosomal appendage V [0 = spiniferous; 1 = non-spiniferous].
28. Spines on prosomal appendage V reduced [0 = absent; 1 = present].
29. Prosomal appendage VI [0 = walking leg; 1 = swimming leg].
30. Appendage VI length [0 = reaching postabdomen; 1 = reaching pretelson].
31. Shape of proximal podomere of appendage VI [0 = narrow (L/W ≥ 2.0); 1 = expanded (L/W < 2.0)].
32. Distal podomere margin of VI-6 modified [0 = absent; 1 = present]. Only the swimming forms have a podomere 6 with this distal modification to allow movement of the paddle.
33. ‘Ear’ on coxa VI [0 = absent; 1 = present]. Expansion of anterior coxa margin seen within the Eurypterina (Størmer 1974).
34. Podomere 7a on sixth prosomal appendage [0 = absent; 1 = present].
35. Width of VI-7a [0 = narrow (less than 50% of width of VI-7); 1 = wide (more than 50%)].
36. Shape of VI-7a [0 = oval; 1 = triangular].
37. Longitudinal grooves on podomeres [0 = absent; 1 = present].
38. Podomere cuticle [0 = rounded; 1 = ridged].
39. Podomere thickness [0 = undifferentiated; 1 = thickening distally]. Possibly represents an adaptation to supporting a large body along with longitudinal grooves on podomeres.
40. Metastomal cleft [0 = absent; 1 = present].
41. Notch on anterior margin of metastoma [0 = absent; 1 = present].
42. Shape of posterior margin of metastoma [0 = rounded; 1 = flattened or recurved].
43. Paired tubercles on opisthosomal tergites 2–5 [0 = absent; 1 = present]. Only found in Drepanopterus, however is included in this analysis as it further differentiates between the two valid species and D. (?) bembycoides.
44. Width of opisthosoma relative to the carapace [0 = wider or of equal width; 1 = narrower].
45. Marginal rim on opisthosoma [0 = absent; 1 = present].
46. Differentiation of first opisthosomal segment [0 = none; 1 = positive third order].
47. Second tergite developed into round macrotergite [0 = absent; 1 = present].
48. Caudal postabdomen [0 = absent; 1 = present].
49. Lateral pleurae [0 = absent; 1 = present].
50. Pretelson elongated [0 = absent; 1 = present]. A pretelson is considered elongated if the length of the pretelson is equal to or more than one and a half the length of segment 11. Possibly a sexual dimorph.
51. Pretelson postlaterally expanded [0 = absent; 1 = present].
52. Dorsal pretelson lobes [0 = absent; 1 = present].
53. Telson size [0 = equal to or longer than postabdomen; 1 = shorter than postabdomen].
54. Telson elongate (greater than 33% of total body length) [0 = absent; 1 = present].
55. Dorsal median keel on telson [0 = absent; 1 = present].
56. Paired, broad rounded ventral keels on telson [0 = absent; 1 = present].
57. Carapace ornament of large lunate scales surrounding and pointing away from the central area and eyes [0 = absent; 1 = present].
58. Row of large, tongue-shaped scales on posterior margin of opisthosomal segments [0 = absent; 1 = present].
### Appendix 1

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The systematics and phylogeny of the Stylonurina