

The first Silurian chasmataspid, *Loganamaraspis dunlopi* gen. et sp. nov. (Chelicerata: Chasmataspidida) from Lesmahagow, Scotland, and its implications for eurypterid phylogeny

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ABSTRACT: A new chasmataspid (Chelicerata: Chasmataspidida) is described from the Early Silurian (Late Llandovery–Early Wenlock) of Lesmahagow, Scotland, as *Loganamaraspis dunlopi* gen. et sp. nov. It is distinguished from related forms by the low tapering ratio of the postabdomen, pediform sixth prosomal appendage and a heart-shaped metastoma. Additionally, a genital operculum with a genital appendage is preserved. The recognisable morphology of *L. dunlopi* gen. et sp. nov. bridges some of the gap between the Ordovician Chasmataspididae and the Devonian Diploaspidae. Traces of the gut are reported for the first time from a chasmataspid. Chasmataspids are regarded as sister group to the eurypterids: an anterior opercular plate anterior to the genital appendage in *L. dunlopi* gen. et sp. nov. is regarded as homologous to the anterior opercular plate of the three-segmented genital operculae of *Dolichopterus* and *Stylonurina*. This is considered a plesiomorphic character within Eurypterida, whilst the two-segmented genital operculum (with deltoid plates) of Eurypterina is considered apomorphic.

KEY WORDS: Arthropod, Diploaspidae, Eurypterida, genital operculum, metastoma.



Chasmataspids are a small and poorly known group of chelicerates that are distinguished from eurypterids by the segmentation pattern of their opisthosoma. They have a preabdomen of four and a postabdomen of nine segments, while eurypterids usually (i.e. excluding megalograptids) have a preabdomen of eight and a postabdomen of five segments. Prior to 1999, only three species of chasmataspids were known: *Chasmataspis laurencii* Caster & Brooks, 1956 from the Middle Ordovician (?Late Llandeilo) of Tennessee, USA; and *Diploaspis casteri* Størmer, 1972 and *Heteroaspis novojilovi* Størmer, 1972 from the Early Devonian (Emsian) of Alken, Germany. The number of described chasmataspids has more than doubled in recent years (Table 1), based mainly on specimens previously considered to be juvenile eurypterids. Chasmataspids are thus more common than previously thought and more discoveries may await in museum collections of ‘juvenile eurypterids’.

A restudy of *C. laurencii* Caster & Brooks, 1956 by Dunlop *et al.* (2004) has increased our understanding of early members of the group. A restudy of the original Alken material and some new specimens suggests that *Heteroaspis novojilovi* Størmer, 1972 is a preservational and/or ontogenetic junior synonym of *Diploaspis casteri* Størmer, 1972 (Dunlop *et al.* 2001). In addition, more material still awaits description or redescription: among these are Late Cambrian chasmataspid resting traces from Texas (Wahlman & Caster 1978; Dunlop *et al.* 2004), a new species of *Diploaspis* from the Early Devonian of Hombach, Germany (M. Poschmann, pers. comm.; Dunlop *et al.* 2001), and a specimen from the Early Devonian of Siberia, described by Novojilov (1959) as *Eurypterus stoermeri* Novojilov, 1959, that probably represents a chasmataspid (Table 1) based on its opisthosomal differentiation.

Morphologically, chasmataspids resemble both xiphosurans and eurypterids, but were originally referred to an order of Xiphosura: Chasmataspida (=Chasmataspidida) (Caster & Brooks, 1956). Bergström (1968) considered *C. laurencii* to be a synziphosurine and questioned the ordinal status of chasmataspids. Størmer (1972) supported the view of Caster & Brooks and regarded *C. laurencii* and his two new genera as belonging to the order Chasmataspidida within Xiphosura. Anderson & Selden (1997) excluded chasmataspids from Xiphosura, but left their status open. Dunlop & Selden (1997) raised Chasmataspida (=Chasmataspidida) to a separate taxon within Chelicerata on the basis of their differentiation of the opisthosoma into a four-segmented preabdomen (buckler) and a nine-segmented postabdomen, which is unique for this taxon. The first opisthosomal tergite of chasmataspids is reduced and can only be observed in *Octoberaspis ushakovi* Dunlop, 2002 and *C. laurencii* (Dunlop *et al.* 2004), confirming a total of 13 opisthosomal segments. Thirteen opisthosomal segments is a character also shared with eurypterids and scorpions (Dunlop & Webster 1997). *Octoberaspis ushakovi* possesses both a genital appendage and a metastoma, features previously thought to be autapomorphies for eurypterids only. This further provides strong evidence for a sister group relationship between Chasmataspidida and Eurypterida (see section 4).

When studying the eurypterid collections at the National Museums of Scotland (NMS), Chambers Street, Edinburgh, Scotland, the present authors and Dr Lyall I. Anderson (Invertebrate Curator at NMS) discovered a small specimen (NMS G. 1957.1.649) labelled as a ‘young eurypterid’. They report here on this specimen, the first Silurian chasmataspid. Like *O. ushakovi*, it possesses fragmentary prosomal appendages, a genital appendage and a metastoma.

Table 1 Summary of chasmataspid occurrences in approximate stratigraphical order, including 'postabdominal tapering ratios' (i.e. the width of opisthosomal segment 5 divided by the width of segment 13) and inferred palaeoenvironment

Taxon	Age	Stratigraphy and locality	Palaeoenvironment	(W5/W13)	References
' <i>Chasmataspis</i> -like resting trace'	Upper Cambrian	Riley Formation, Texas, USA	Shoreline or lacustrine	?	Wahlman & Caster 1978; Dunlop <i>et al.</i> 2004
<i>Chasmataspis laurencii</i>	Middle Ordovician (Late Llandeilo)	?Five Oaks Formation, Douglas Dam, Tennessee, USA	Carbonate platform margin	1.5	Caster & Brooks 1956; Dunlop <i>et al.</i> 2004
<i>Loganamaraspis dunlopi</i>	Late Llandovery or Early Wenlock	Patrick Burn Formation, Lesmahagow, Scotland	Non-marine or marginal marine	c. 2.5	This paper
<i>Forfarella mitchelli</i>	Early Devonian	Dundee Formation, Angus Region, Midland Valley, Scotland	?Lacustrine	c. 5	Dunlop <i>et al.</i> 1999
<i>Octoberaspis ushakovi</i>	Early Lochkovian	Severnaya Zemlya Formation, October Revolution Island, Russia	?Lagoonal	c. 3.5	Dunlop 2002
<i>Diploaspis</i> n. sp.	Emsian (?)	?Hombach, Germany	Shallow deltaic	?	Poschmann (pers. comm.)
<i>Diploaspis casteri</i>	Early Emsian	Nellenköpfchen Formation, Alken an der Mosel, Germany	?Shallow deltaic	4.1	Stormer 1972; Dunlop <i>et al.</i> 2001
' <i>Eurypterus</i> ' <i>stoermeri</i>	Emsian (?)	Zubova Suite Formation, Imaigda River, Norilsk, Russia	?Marginal marine	c. 3.4	Novojilov 1959; Plotnick 1999
<i>Achanarraspis reedi</i>	Late Eifelian	Achanarras Limestone Formation, Caithness, Scotland	Lacustrine	3.4	Anderson <i>et al.</i> 2000

1. Material and methods

The specimen, NMS G. 1957.1.649, was examined and drawn in a 70% alcohol solution using a binocular microscope with a drawing tube attachment. The photographs were taken under polarised light. Since no morphological standards have been proposed for chasmataspids, the terminology follows that of Tollerton (1989) for eurypterids. However, Tollerton (1989) did not propose any terminology for the segmentation of the genital operculum, and therefore, the present authors follow the nomenclature of Waterston (1979, fig. 4a); the segments anterior, lateral and posterior to the base of the genital appendage are the anterior, median and posterior opercular plates, respectively. All three plates are present only in chasmataspids, dolichopterid and stylonurid eurypterids. Euryptera (*sensu* Novojilov 1962; appendage VI expanded into a paddle) have lost the anterior opercular plates. A structure dorsal to the metastoma, previously not reported from any chasmataspid or eurypterid, is termed the 'metastomal plate.'

1.1. Locality and geological setting

The specimen described here was collected by Robert Dunlop of Dunfermline, Scotland, and presented to the NMS by the Carnegie Dunfermline Trust in 1957. The specimen comes from the Patrick Burn Formation (lower part of Priesthill Group), from Dunside, Logan Water, Lesmahagow, Scotland. The formation is at least 850 m thick, and composed of grey and olive mudstones laminated with silty mudstones with laminae of dark grey carbonaceous siltstones (Paterson *et al.* 1998). The formation is regarded as late Llandovery (Paterson *et al.* 1998) or possibly early Wenlock (Plotnick 1999) in age. The precise bed that yielded the specimen is unknown, but based upon lithologic similarity, we suspect it is from the famous *Jamoytius* horizon, interpreted as non-marine or marginal marine (BA1) by Plotnick (1999), or the middle of a

constricted marine basin occasionally flushed by turbiditic flows by Paterson *et al.* (1998).

Although no other fossils are associated on the same slab, the lithology is the same as that yielding the eurypterids *Slimonia acuminata* Salter, 1855, *Erettopterus bilobus* Salter, 1855, *Nanahughmilleria lanceolata* Salter, 1855, ?*Hardieopterus lanarkensis* Waterston, 1979, the synziphosurids *Cyamocephalus loganensis* Currie, 1927 and an undescribed specimen of *Pseudoniscus* (Eldredge 1974), the phyllocarid *Ceratiocaris papilio*, the fish *Jamoytius kerwoodi* White, 1946, *Logania scotica* Traquair, 1899, and the ?thylacocephalan *Ainiktozoon loganense* Scourfield, 1937.

1.2. Preservation and taphonomy

NMS G. 1957.1.649 is preserved as black material and is partially flattened in a siltstone matrix. This preservation is typical for specimens (see above) from the Patrick Burn Formation. NMS G. 1957.1.649 b (Figs 1b, 2b) shows the ventral side of the animal, while NMS G. 1957.1.649 a (Figs 1a, 2a) shows superimposed dorsal (e.g. tergites), ventral (e.g. appendages) and internal features (i.e. traces of the gut, a feature never previously reported from any chasmataspid). The preservation of the appendages, metastoma and genital appendage is very faint.

Towards the posterior of the postabdomen, dark oval areas can be observed on the anterior parts of the segments, symmetrical around the midline. They are not close to the ventral segment margins on NMS G. 1957.1.649 b, but when superimposed with NMS G. 1957.1.649 a, it is clear that they are close to the dorsal anterior segment boundaries. The specimen has been obliquely flattened, and the oval areas represent impressions of the anterior and posterior openings of the flattened, ring-like postabdominal segments. The two posteriormost segments are preserved only as patches of cuticle, offering only indistinct segment boundaries.

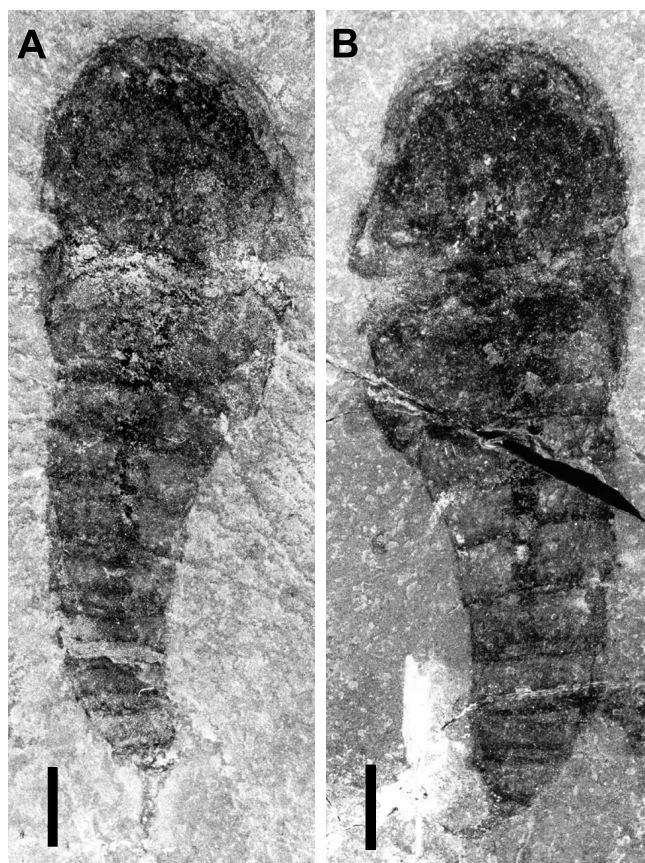


Figure 1 *Loganamaraspis dunlopi* gen. et sp. nov.: (A) NMS G. 1957.1.649 a, showing mainly the dorsal surface of the holotype; and (B) NMS G. 1957.1.649 b, showing the ventral surface. Scale bars = 5 mm.

1.3. Abbreviations

The following abbreviations are used in the text and figures: (aop) anterior opercular plate; (ca) carapace; (do) doublure; (ga) genital appendage; (met) metastoma; (mp) 'metastomal plate'; (mt) microtergite; (op) operculum; (sp) spine; (tel) telson; and (ubl) unfused Blattfüsse. Prosomal appendages are labelled I–VI, coxae of prosomal appendages cIV–cVI, and opisthosomal segments 1–13.

2. Systematic palaeontology

Chelicerata Heymons, 1901
Chasmataspidida Caster & Brooks, 1956
Family Diploaspididae Størmer, 1972

Emended diagnosis. Small chasmataspid with semicircular, subrectangular or subquadrate carapace, preabdomen with curved segments, a tapering postabdomen and a short telson; no division of preabdominal segments into median and lateral plates (emended from Dunlop *et al.* 2001).

Remarks. The presence of a pediform sixth appendage in *L. dunlopi* gen. et sp. nov. might justify the erection of a new family, since all other members of Diploaspididae, where prosomal appendage VI is known, have an expanded swimming leg. Since the appendages in this specimen are so poorly preserved, the present authors choose not to erect a new family.

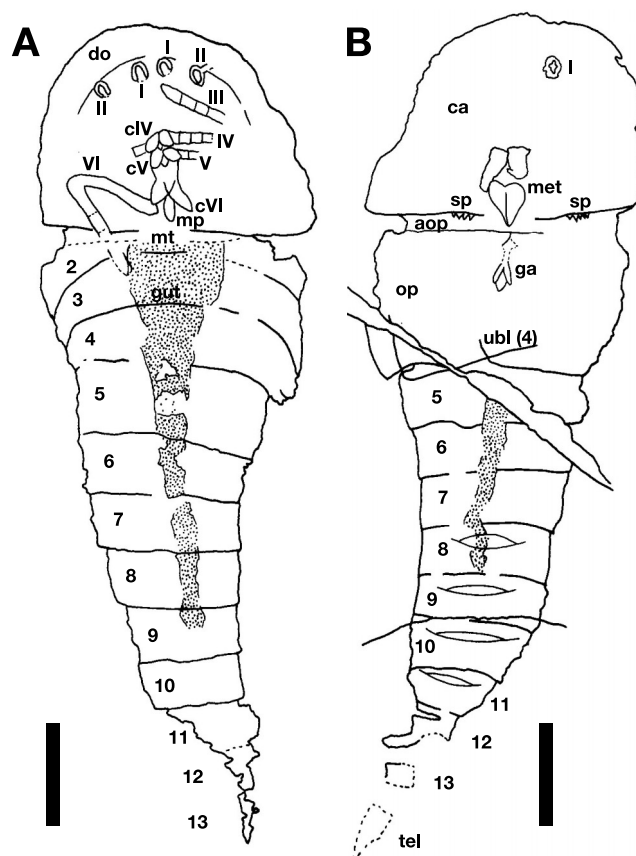


Figure 2 *Loganamaraspis dunlopi* gen. et sp. nov. Camera lucida drawings of the two specimens illustrated in Fig. 1. (A) NMS G. 1957.1.649 a; (B) NMS G. 1957.1.649 b. Scale bars = 5 mm.

Loganamaraspis gen. nov.

Diagnosis. Large diploaspid with posterolaterally expanded prosoma lacking genal spines; prosomal appendage VI, a pediform walking leg; metastoma cardioid (heart-shaped). Postabdominal segments long with a tapering ratio (W5/W13) of c. 2.5.

Remarks. The tapering ratio (W5/W13) is low (c. 2.5) compared to other known Devonian diploaspid genera (3.4–c. 5.0; Table 1).

Type species. *Loganamaraspis dunlopi* gen. et sp. nov., by monotypy.

Etymology. The generic name is based on *Logan*, after Logan Water, where the specimen was discovered; *amare*, Latin for love, after the heart-shaped metastoma; and *aspis*, Greek for shield.

Loganamaraspis dunlopi gen. et sp. nov. (Figs 1–3)

Diagnosis. As for the genus.

Etymology. The species is named in joint honour of the discoverer of this specimen, Robert Dunlop of Dunfermline and Dr Jason A. Dunlop (Museum für Naturkunde, Berlin, Germany) for his valuable contributions to our rapidly expanding knowledge of chasmataspid.

Holotype. NMS G. 1957.1.649 a+b from the Patrick Burn Formation of the Priesthill Group, Dunside, Logan Water, Lesmahagow, Ayrshire, Scotland.

Additional material. None.

Description. Entire specimen approximately 35 mm long and devoid of any ornamentation. Prosoma subquadrate, posterolaterally expanded with no preserved genal spines.

Prosomal length 8.5 mm, width 11.4 mm, giving a L/W ratio of 0.75. Lateral angles are 90° on the right side and 100° on the left because of taphonomic distortion. Prosomal doublure (Fig. 2a, do) has even width anteriorly and laterally, but no sutures are evident. Posterior ventral margin of prosoma bears 0.25 mm long serrations on either side of the metastoma. Eyes and other dorsal structures are not preserved.

Two pairs of ring-like structures positioned anteriorly are interpreted as the cross-section of appendages I (chelicerae) and II, comparable in width to that of the posterior appendages, indicating that the chelicerae were very robust. Posterior to these appendages is a more slender appendage III (Fig. 2a, III), preserved length 3 mm, width 0.5 mm. It is possible to identify individual podomeres in this appendage; all are rectangular, 0.6–0.7 mm long, 0.5 mm wide. Both coxae of appendage IV are clearly present (Fig. 2a, cIV), but lack gnathobases; each coxa is 0.7 mm long and 0.5 mm wide. Proximal portions of both appendage IV preserved; individual podomeres slightly shorter (0.5 mm long) than those on appendage III. Two similar-sized coxae of appendage V are present (Fig. 2a, cV), lacking gnathobases; each coxa 0.7 mm long and 0.5 mm wide. On the left side, podomeres of a slender appendage V are preserved (Fig. 2a, V); individual podomeres are approximately the same size as appendage IV. The larger coxae (1.5 mm long, 0.8 mm wide) of both appendage VI (Fig. 2a, cVI) are preserved although no gnathobases are evident. From posterior right coxa, a long (total preserved length 8.5 mm) and slender appendage VI (constant width 0.6 mm) projects towards the prosomal rim, and bends posteriorly onto the opisthosoma. Individual podomeres cannot be distinguished, although they must have been longer than those of the anterior appendages since the appendage itself is longer than the anterior appendages.

Posteriormost on the prosoma, partially extending into the opisthosoma, a cardioid (heart-shaped) metastoma is evident (Fig. 2b, met) with a median suture. An oval plate overlies the metastoma posterior to coxae VI (Fig. 2a, mp).

Ventrally, the anterior opercular plate is evident anterior to the genital appendage (see sections 3 and 4). The genital appendage is 2.5 mm long (extending half-way down the preabdomen) and composed of two segments. The proximal segment of the genital appendage is split into two lobes, separated by an angle of approximately 35° (Fig. 2b, ga). Between these two lobes is the distal segment, widest at the point where the lobes of the proximal segment end and taper distally. The number of opercular plates is unclear since no sutures are evident on the operculum posterior to the base of the genital appendage. The presumed fourth segment appears to have been unfused at the midline since the left and right plates overlap in the posterior median portion of the preabdomen (Fig. 2b, ubl).

Dorsally, the three posterior segments of the preabdomen can be identified on NMS G. 1957.1.649 a, and although not complete laterally, have approximately the same width as the posterior portion of the prosoma. The posterior margin of these segments is strongly convex.

The first postabdominal segment is very long and is slightly disarticulated from the preabdomen (see the left side of Fig. 2b), but is easily distinguished from the preabdomen since it is narrower with an almost straight posterior segment margin. The succeeding postabdominal segments taper slightly. The postabdominal segments are approximately the same length except for the last two, which are shorter. The opisthosomal segments have the following preserved lengths and widths in millimetres (*denotes incomplete lateral preservation): (1) 1.5/?; (2) 0.5/11.0*; (3) 2.2/10.2*; (4) 2.4/9.5*; (5) 3.1/7.9; (6) 2.4/6.7; (7) 2.3/6.4; (8) 2.4/5.5; (9) 2.2/4.6*; and

(10) 1.9/4.3. The posterior structure (Fig. 2b, tel) is interpreted as a short telson.

A dark area, interpreted as the midgut and intestine, can be followed medially along the specimen from the posterior edge of the prosoma to the middle of the ninth segment (Fig. 2a, gut). The gut trace increases in width along the opisthosoma to a maximum width (4.1 mm) under the second and third segments, and decreases in width towards the posterior part of the abdomen.

3. Discussion

3.1. Prosoma and prosomal appendages

The appendages of *L. dunlopi* gen. et sp. nov. are very poorly preserved. The form of the distal parts (i.e. chelate as in xiphosurids and apparently *C. laurencii*, or non-chelate as in eurypterids and *D. casteri*) is unknown. Appendage VI is long and slender with a constant width and obviously used primarily for walking rather than swimming, as in the Devonian diploaspids and Eurypterina (*sensu* Novojilov 1962). This suggests that the swimming appendage in diploaspids and Eurypterina evolved independently (Fig. 4), an interpretation also supported by the different morphology of the swimming appendage in the two groups. The diploaspids appear to lack a small distal podomere (9) in appendage VI. More importantly, the small triangular podomere (7a in eurypterids) that occurs between the two largest podomeres of the swimming leg is situated posterolateral in eurypterids (e.g. Størmer 1955, figs 17 & 21–25), but anterolateral in diploaspids (Dunlop *et al.* 2001, fig. 8b; Dunlop 2002, fig. 9a).

The metastoma is cardioid (Tollerton 1989, fig. 5), but with a pointed posterior termination similar to that of *O. ushakovi* Dunlop, 2002. The suture along the midline suggests that the metastoma formed by the fusion of two structures, similar to the metastoma in many eurypterids, for example *Baltoeurypterus tetragonophthalmus* (Holm 1898, pl. 3, figs 19 & 21). The metastoma has previously been interpreted as homologous to the xiphosurid chilaria (Størmer 1934, 1970) and the fused coxae of the same (seventh) appendage of *Weinbergina opitzi* (Stürmer & Bergström 1981) or to the fused epicoxae of appendage VI (Brady 1996). The oval plate observed between and posterior to coxae VI (Fig. 2a, mp) was probably connected to the dorsal side of the metastoma.

3.2. Genital appendages and sexual dimorphism

The genital appendage of *L. dunlopi* gen. et sp. nov. is composed of two segments. The proximal segment is divided into two lobes distally, and the smaller distal segment is a median lobe between these two distal lobes of the proximal segment. This is the same morphology as that in *O. ushakovi* (Dunlop 2002), although the lateral lobes are larger in *L. dunlopi* gen. et sp. nov. Dunlop (2002) hesitated to assign the metastoma and genital appendages in his material to chasmataspid, and suggested that they may represent eurypterids since the specimens showing these features had poorly preserved opisthosomal differentiation. However, the similarities between the present material and *O. ushakovi* remove any doubt that the structures described were truly features of chasmataspid, hence *O. ushakovi*.

Sexual dimorphism is poorly known in chasmataspid, although Dunlop (2002) reported two types of genital appendage in *O. ushakovi*. There are close similarities between the genital appendage of *L. dunlopi* gen. et sp. nov. and the two-segmented type A appendages (Størmer 1934) of *O. ushakovi* and *Dolichopecterus jewetti* Caster & Kjellesvig-Waering (1952) (Fig. 4), suggesting that the holotype of

Table 2 Homology of opisthosomal segments for chasmataspids and eurypterids: ? unknown; (Mt) microtergite; (Con) concealed; (Ank) ankylosed; (B) Blattfüsse; and (T) tergite

Taxon	Opisthosomal segment									
	Aspect	1	2	3	4	5	6	7	8–13	Telson
<i>Chasmataspis laurencii</i> (Caster & Brooks)	Dorsal	Mt	Buckler			Ank	Ank	Ank	Ank	Long styliform
	Ventral	?	Ventral buckler							
<i>Loganamaraspis dunlopi</i>	Dorsal	Mt	Buckler			Ank	Ank	Ank	Ank	Short styliform
	Ventral	Aop	Operculum		B					
<i>Dolichopterus jewetti</i>	Dorsal	Con?	T	T	T	T	T	T	Ank	Long styliform
	Ventral	Aop	Operculum		B	B	B	B		
<i>Baltoeurypterus tetragonophthalmus</i>	Dorsal	Con	T	T	T	T	T	T	Ank	Long styliform
	Ventral	Lost	Operculum		B	B	B	B		

L. dunlopi gen. et sp. nov. could be a female (see also Braddy & Dunlop 1997). The proximal segment is divided into two lobes in *L. dunlopi* gen. et sp. nov. and *O. ushakovi*, but these lobes are fused along a midline in *D. jewetti*. The type B appendage assigned to *O. ushakovi* was short and ovate, as in most eurypterids, but is very poorly preserved.

3.3. Opisthosoma and gut

Devonian chasmataspids and *L. dunlopi* gen. et sp. nov. (i.e. diploaspids) can be separated from eurypterids and the Ordovician *C. laurencii* by the broadly convex tergite boundaries on the preabdomen. The present authors cannot demonstrate that the preabdominal segments are fused into one unit in *L. dunlopi* gen. et sp. nov., although this seems to be the case in morphologically better understood chasmataspids (e.g. *C. laurencii* and *D. casteri*), and is probably the explanation for the vague segment boundaries in the preabdomen of *L. dunlopi* gen. et sp. nov. Assuming the holotype of *L. dunlopi* gen. et sp. nov. has an untelescoped abdomen (cf. *O. ushakovi*), it is 35 mm long, and is only rivalled in size by *C. laurencii* among other chasmataspids.

Based on the observed morphology of *L. dunlopi* gen. et sp. nov. alone, the preabdomen apparently consists of a microtergite and three fused segments dorsally, and an anterior opercular plate, one fused posterior opercular plate and one pair of non-fused Blattfüsse (opisthosomal segment four) ventrally. However, based on a Late Cambrian chasmataspid resting trace (Wahlman & Caster 1978) and reinterpretation of the ventral morphology of *C. laurencii* (*sensu* Dunlop *et al.* 2004), the ventral morphology of *L. dunlopi* gen. et sp. nov. might have consisted of two Blattfüsse-like segments (2 and 3) of the operculum which are not preserved (or not present as the operculum is in its place). The fourth is apparent and overlapping (Fig. 2b, ubl). Dunlop *et al.* (2004) discussed the possibility that the 'ventral plate' (cf. Caster & Brooks 1956) or 'median plate' (cf. Størmer 1972) was a sclerotised layer above a series of gill-bearing opercula. This seems to have been the case for *O. ushakovi*. One problem with this interpretation in *C. laurencii* is that Caster & Brooks (1956, p. 165) listed the number of specimens examined: pieces of 50 dorsal bucklers and 49 'ventral bucklers' were found, and it may be expected that examples of the operculae, ventral to this plate, should also occur if they were sclerotised. An alternative explanation

could be that they were lost during transportation or decay. Babcock *et al.* (2000) reported that the book gills become detached during the first week of transport in *Limulus polyphemus*, much earlier than the prosomal appendages (which become detached after 10–18 days). However, if these operculae were very lightly sclerotised, they may never have been preserved. It is also possible that the Upper Cambrian animal producing the traces in Texas and the Ordovician *C. laurencii* had not developed sclerotised ventral operculae, but *L. dunlopi* gen. et sp. nov., the Devonian chasmataspids and the eurypterids had developed them, and the genital appendage was developed in response to the sclerotisation of the ventral side. An attempt to homologise the ventral and dorsal segments of chasmataspids and eurypterids is given in Table 2.

The dark area along the midline is interpreted as the outline of the midgut and intestine, rather than the midgut glands reported from the Burgess Shale arthropod *Leanochoilia superlata* by Butterfield (2002). This is supported by the regular outline of the area, lack of internal structure and visible extent of the area all the way to the ninth segment. A gut trace has never been reported previously from chasmataspids, but examples are known from several eurypterid genera (e.g. Ruedemann 1921; Kjellesvig-Waering 1958, 1963; Heubusch 1962; Waterston 1979). The widening of the dark patch in the second and third segments corresponds to the gut that lay protected under the preabdomen, and this widened area may represent the midgut. If so, this might suggest that chasmataspids only had two pairs of serially repeated midgut glands (assuming one pair of glands per somite, as in *L. superlata*), a number shared with xiphosurans (Fahrenbach 1999). Scorpions have five pairs of midgut glands (Farley 1999) and the number in spiders is variable (Foelix 1996), while the number in eurypterids is still not known.

4. Implications for chasmataspid and eurypterid phylogeny

4.1. Chelicerate phylogeny

Chelicerate phylogeny is problematic. The most comprehensive study including fossil taxa was by Dunlop & Selden (1997). They identified two clades of chelicerates: the first

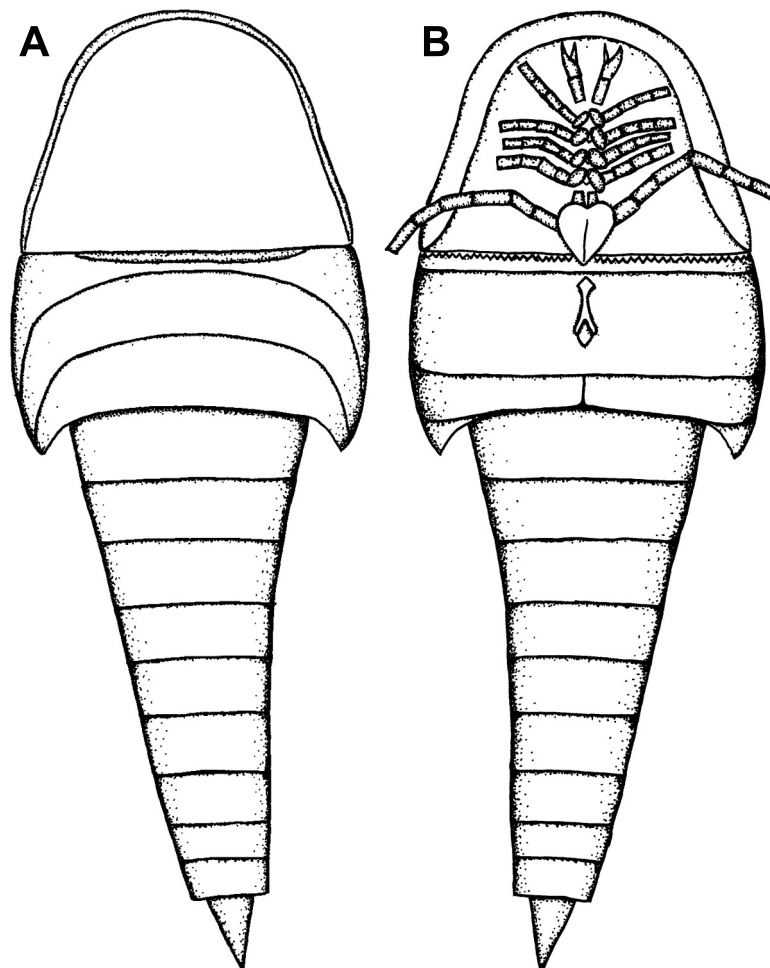


Figure 3 Morphological reconstruction of (A) the dorsal side of *Loganamaraspis dunlopi* gen. et sp. nov. and (B) the ventral side, illustrating the prosomal appendages, metastoma and genital operculum. The morphology of the prosomal appendages and telson is reconstructed according to Fig. 2, but distal parts of the appendages are not reconstructed since it is uncertain whether they are chelate. The postero-ventral serrated margin of the prosoma is reconstructed extending to the lateral margins. The anterior three segments on the postabdomen are not reconstructed with Blattfüsse since no evidence for this is provided by the specimen, although Blattfüsse on these segments are present in eurypterids.

composed of synziphosurines and xiphosurids (for a more comprehensive analysis of this clade, see Anderson & Selden 1997); and the second clade composed of chasmataspids, eurypterids, scorpions and non-scorpion arachnids, although concerns persist that Arachnida is paraphyletic (Dunlop & Webster 1999; Dunlop & Braddy 2001). This new chasmataspid casts no further light upon this question, but the presence of a metastoma and a genital appendage support a sister group relationship between eurypterids and chasmataspids.

4.2. Chasmataspid phylogeny

Concern that chasmataspids might be polyphyletic exists (Bergström 1979, 1980; R. E. Plotnick, pers. comm), in which case the Ordovician *Chasmataspis* would be separated from the Devonian forms based on its chelate appendages and a more complex, tripartite preabdomen. The present study of *L. dunlopi* reveals it to be morphologically intermediate in postabdominal tapering ratio and appendage morphology between the Ordovician and Devonian chasmataspids, although it is referred to the same family as the latter. However, the presence of a metastoma and a genital appendage in *O. ushakovi*, *L. dunlopi* gen. et sp. nov. and eurypterids combined with the apparent lack of these structures in *C.*

laurencii, renders support for a paraphyletic Chasmataspida more likely (Fig. 4).

4.3. The anterior opercular plate and implications for eurypterid phylogeny

The anterior opercular plate in front of the genital appendage of *L. dunlopi* gen. et sp. nov. (Figs 2b, aop, & 3b) is unusual compared to eurypterids, but far from unique. The importance of this character has not been noted previously. Caster & Kjellesvig-Waering (1952) described *Dolichopterus jewetti* and *D. stoermeri* on the basis of two, type A operculae with a segment anterior to the deltoid plates (Fig. 4). An anterior third segment has also been noted several times in stylonurid eurypterids: *Parastylonurus ornatus* (Waterston 1979, fig. 4A, B), *Stylonurella spinipes* (see Kjellesvig-Waering in Waterston 1979, fig. 12D), *Rhenopterus diensti* (Størmer 1936, fig. 9), possibly *Moselopterus ancylotelson* and *M. elongatus* (Størmer 1974, figs 25 & 29), and finally, an operculum sp. II (Størmer 1934) that can be referred to *Brachyoptereella pentagonalis* (Størmer, 1934) because of the character presented here, its size and provenance (OET pers. obs.). As mentioned earlier, this anterior segment probably represents the ventral expression of the dorsal microtergite or the appendages of this segment. The latter interpretation is problematic with respect to the origin of

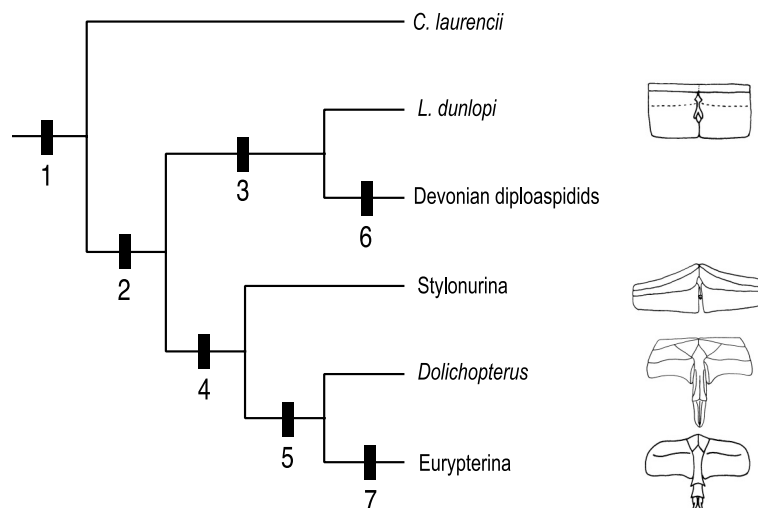


Figure 4 Chasmataspid phylogeny showing inferred position of *Loganamaraspis dunlopi* gen. et sp. nov. relative to other chasmataspids and the major groups of eurypterids based on the characters discussed herein. The figured genital operculae belong to *L. dunlopi* gen. et sp. nov., *Stylonurella spinipes*, *Dolichopterus jewetti* and *Baltoeurypterus tetragonophthalmus*. Character transformations occurring at the numbered nodes: (1) opisthosoma of 13 segments, 'ventral plate', chelate prosomal appendages; (2) non-chelate appendages, metastoma, operculum with genital appendage; (3) broadly curved preabdominal segments; (4) preabdomen of eight segments, microtergite concealed dorsally, 'ventral plate' lost; (5) deltoid plates on genital operculum, prosomal appendage VI expanded swimming leg with podomere 7a posteriorly; (6) prosomal appendage VI expanded swimming leg with podomere '7a' anteriorly; and (7) anterior opercular plate lost, prosomal appendage VI broad swimming leg with reduced podomere nine.

the metastoma; the anterior opercular plates in *D. jewetti* and *L. dunlopi* gen. et sp. nov. are here considered homologous, and both also have a metastoma. Therefore, whether the seventh pair of appendages in *Weinbergina opitzi* is homologous to the metastoma or the anterior opercular plate remains speculative. The anterior opercular plate is reduced in the suborder Eurypterina (*sensu* Novojilov 1962). Caster & Kjellesvig-Waering (1952, p. 26) suggested that a three-segmented operculum was the plesiomorphic state for eurypterids and this new evidence from *L. dunlopi* gen. et sp. nov. supports their view. Although a three-segmented operculum cannot be seen in *L. dunlopi* gen. et sp. nov., the homology of the anterior opercular segments of *L. dunlop* gen. et sp. nov., *Dolichopterus* and stylonurid eurypterids has wide implications for eurypterid phylogeny. It suggests that stylonurids are plesiomorphic with respect to this character, and *Dolichopterus* has a position intermediate between Stylonurina and Eurypterina. However, no stylonurids have deltoid plates which are present in *Dolichopterus* and the suborder Eurypterina (*sensu* Novojilov 1962). The phylogeny of the major clades of chasmataspids and eurypterids can be tentatively mapped from the morphology of appendage VI and the development of the genital operculum (Fig. 4).

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