THE OLDEST HORSESHOE CRAB: A NEW XIPHOSURID FROM LATE ORDOVICIAN KONSERVAT-LAGERSTÄTTEN DEPOSITS, MANITOBA, CANADA

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Abstract: A remarkable new fossil horseshoe crab, *Lunataspis aurora* gen. et sp. nov., from recently discovered Upper Ordovician (*c.* 445 Ma) shallow marine Konservat-Lagerstätten deposits in Manitoba (Canada), is characterized by fusion of opisthosomal tergites into two sclerites. A broad mesosoma of six or seven fused segments, followed by a narrow metasoma of three reduced segments, represents an advanced transitional condition in the development of the xiphosurid thoracetron. *Lunataspis* further possesses a large crescentic prosomal shield bearing lateral compound eyes on weak ophthalmic ridges that flank a low cardiac lobe, and a keeled lanceolate telson. *Lunataspis* is much older than the proposed 'synziphosurine' stem lineage of Carbon-iferous and post-Palaeozoic Xiphosurida, yet is strikingly similar to crown group limuline horseshoe crabs, indicating that major features of the distinctive and highly conserved xiphosurid Bauplan evolved considerably earlier in the Palaeozoic than was previously suspected. In addition to establishing a new temporal benchmark for assessing hypotheses of early chelicerate relationships, the discovery of horseshoe crabs in a Late Ordovician marginal marine setting marks the earliest definitive record of this persistent ecological association.

Key words: horseshoe crab, Xiphosurida, Late Ordovician, Konservat-Lagerstätten, Manitoba.

LIVING horseshoe crabs, typified by the intensively studied *Limulus polyphemus* (Linnaeus) (Tanacredi 2001; Walls *et al.* 2002), are aquatic, non-biomineralizing chelicerate arthropods (order Xiphosura, suborder Limulina) whose familiar and unmistakable morphology has become inextricably linked with the concept of evolutionary stasis. Widely regarded as the exemplars of bradytelic evolution, they are the quintessential 'living fossils' of biology textbooks, palaeontological treatises, and popular natural history accounts (Fisher 1984; Selden and Siveter 1987; Avise *et al.* 1994; Xia 2000). Fossil xiphosurids have a sparse record, restricted almost exclusively to a handful of marginal marine, brackish, and possibly freshwater Konservat-Lagerstätten; this record reveals little apparent change in the limuline body plan over the last 150–200 myr (Anderson and Shuster 2003; Shuster and Anderson 2003). The highly conservative xiphosurid Bauplan consists of a large crescentic prosomal shield bearing lateral compound eyes, opisthosomal tergites fused into a thoracetron, and a styliform telson. Efforts to trace its origin have so far focused on a disparate group of rare Middle–Late Palaeozoic fossil arthropods once classified with subordinal status (Eldredge 1974), but subsequently grouped informally as 'synziphosurines'. These were considered by Anderson and Selden (1997) to comprise a paraphyletic stem lineage to Xiphosurida within the class Xiphosura. In contrast to the fully fused opisthosoma (thoracetron) that characterizes nearly all Xiphosurida, synziphosurines featured a mesosoma of 9–11 freely articulated tergites; in a few forms the posterior three tergites were differentiated to form a narrow, subcylindrical metasomal pseudotagma. The most recently generated cladistic analyses and evolutionary trees (Anderson and Selden 1997; Dunlop and Selden 1998) tentatively depicted the earliest thoracetron-bearing xiphosurids in a sister-group relationship with *Kasibelinurus*, a Late Devonian synziphosurine bearing nine unfused segments in the opisthosoma (Pickett 1993). Neither *Kasibelinurus* nor any other known synziphosurine, however, closely resembles post-Devonian xiphosurids in a number of critical features, and the same studies have also suggested that Xiphosurida and *Kasibelinurus* might instead share a common ancestor of undetermined earlier age. The upper range of the synziphosurines has now been extended into the Carboniferous with the

description of *Anderella parva* (Moore *et al.* 2007), which clearly co-occurs with xiphosurids in the Bear Gulch Limestone of Montana. Following recent rejection of the poorly preserved Early Ordovician *Lemoneites* both as a basal xiphosuran and an arthropod fossil (Moore and Braddy 2005), the oldest accepted synziphosurines are *Venustulus waukeshaensis* from Early Silurian (Late Llandovery) deposits in Wisconsin (Moore *et al.* 2005*a*) and *Bembicosoma pomphicus* from rocks of approximately equivalent age in Scotland (Anderson and Moore 2004). Putative xiphosuran fossils reported from still older strata have been dismissed as too incomplete for adequate identification (*Eolimulus* in Selden and Dunlop 1998), or reassigned to other chelicerate or 'arachnomorph' groups (e.g. *Paleomerus* in Tetlie and Moore 2004).

Here we report the discovery of a new genus and species of remarkable fossil horseshoe crab, *Lunataspis aurora*, in Late Ordovician Konservat-Lagerstätten deposits preserving a variety of soft-bodied organisms (Young *et al.* 2007), from Manitoba, Canada (Tex-fig. 1). In most discernible characters, *Lunataspis* appears to be much closer to certain Late Palaeozoic Paleolimulidae (Xiphosurida) than to any described synziphosurine, and is in fact more limuline in external morphology than many of the bizarre and clearly specialized Carboniferous xiphosurids, such as the Euproopidae (Anderson and Selden 1997; Racheboeuf *et al.* 2002). The presence of a presumed horseshoe crab of such modern appearance in Late Ordovician shallow subtidal to intertidal depositional settings has broader potential for constraining other critical stages in euchelicerate phylogeny, and adds substance to evolutionary and ecological arguments linking long-term morphological stability with the persistence of specific environments through geological time (Anderson and Schuster 2003).

SYSTEMATIC PALAEONTOLOGY

Phylum CHELICERATA Heymons, 1901
Class XIPHOSURA Latreille, 1802
Order XIPHOSURIDA Latreille, 1802

Genus LUNATASPIS gen. nov.

Derivation of name. Latin, *luna*, moon, crescent moon, hence lunate, and Greek, *aspis*, shield, in allusion to the large crescentic prosomal shield.

Type species. *Lunataspis aurora* gen. et sp. nov.

Diagnosis. Xiphosurid horseshoe crab with opisthosomal thoracetron-like unit composed of broad (trans.) subpentagonal mesosomal sclerite of six or seven tergites, and short, narrow, parallel-sided metasomal unit of three tergites. Proportionally large, lunate prosomal shield bearing lateral compound eyes on weak ophthalmic ridges flanking low cardiac lobe. Posterior margin of prosomal shield bowed forward in shallow U- to blunt V-shaped embayment between broad-based genal spines. Telson lanceolate, depressed triangular in cross-section, about as long as combined sagittal lengths of mesosoma and metasoma; maximum width (at articulation with metasoma) about one-quarter length.
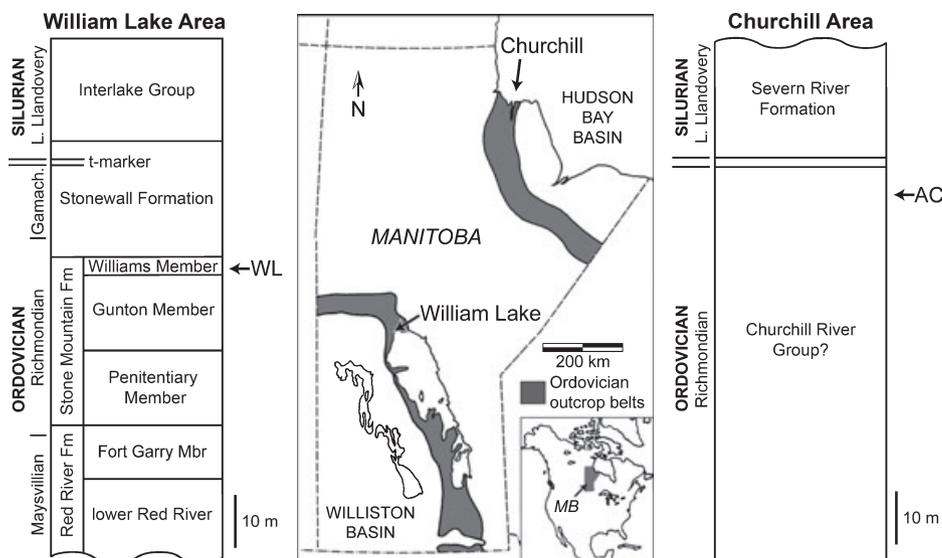
TEXT-FIG. 1. Geographic location and stratigraphic position of William Lake (WL) and Airport Cove (AC) Konservat-Lagerstätten horizons, central and northern Manitoba, Canada.

Lunataspis aurora sp. nov.
Text-figures 2–5

Derivation of name. Latin, *aurora*, dawn, and the eponymous mythological Roman goddess.

Holotype. MM (Manitoba Museum) I-4000A (Text-figs 2A–C, 4A–D), articulated exoskeleton from Airport Cove site, Churchill, Manitoba.

Localities and horizon. Upper Ordovician (Richmondian), Churchill River Group (?), Airport Cove site, east of Churchill, northern Manitoba; Upper Ordovician (Richmondian), Williams Member, Stony Mountain Formation, William Lake site, central Manitoba, Canada (Text-fig. 1) (Elias 1991; Elias *et al.* 1999; Young *et al.* 2007). Age of the Lagerstätten horizons containing *Lunataspis* and other non-biomineralized organisms is based upon a co-occurring conodont fauna that includes elements of *Rhipidognathus symmetricus* and *Aphelognathus*? species.

Other material. Paratype MM I-3989 (Text-fig. 2D–F), mould of an articulated exoskeleton from William Lake site, Manitoba. Additional specimens from Airport Cove site include MM I-3999A (incomplete articulated exoskeleton), MM I-3992–I-3997, I-3998A, I-3998B, and I-4000D (prosomal shields); from William Lake site, MM I-3990 (Text-fig. 3A, partial mesosomal thoracetron; Text-fig. 3B, associated telson), I-3991 (prosomal shield), and I-4036A (juvenile mesosomal thoracetron).

Diagnosis. As for the genus.

Preservation. Specimens of *Lunataspis aurora* from both localities are preserved as somewhat flattened mould impressions in laminated, fine-grained dolostone units, but show sufficient relief to suggest moderate vaulting of both prosomal shield and opisthosoma in life. Thin areas of translucent degraded exoskeletal cuticle remain on some specimens; small patches of dark oxidized pyrite are most frequently associated with axial muscle attachment areas and narrow marginal rims. The left lateral eye of the holotype specimen retains a crescentic patch of dark brown cuticle probably corresponding to degraded visual pigments (Text-fig. 4A–B); individual ommatidia not preserved. Darker, possibly pigment-rich patches of degraded cuticle are preserved at metasoma segment boundaries on the holotype specimen (MM I-4000A) and these show a fine reticulate pattern (Text-fig. 4C–D) comparable to that seen on the corresponding region of the posterior axial lobe in *Limulus*. Determination of the total number of segments (six or seven) in the mesosoma of articulated specimens is hampered by slight telescoping and crushing at the prosomal-opisthosomal junction. On the paratype (MM I-3989; Text-fig. 2D, F) and on MM I-3999A, very faint linear impressions beneath the prosomal shield may represent walking legs.

Description. Two nearly complete articulated individuals (holotype MM I-4000A; paratype MM I-3989) are closely similar in size and both consist of a large prosomal shield of nearly circular outline with a shallow U-shaped to subtriangular posterior embayment almost enclosing the mesosomal portion of opisthosoma; median depth of the embayment is *c.* 34 per cent of maximum shield length. The posterolateral corners of the prosomal shield are extended backwards and slightly inwards into broad-based, acutely pointed genal spines. Sagittal length of the paratype shield (the more easily measured of the two) is 16 mm with a maximum length (exsag.) of 24 mm; maximum width (at *c.* 75 per cent exsag. length) 26 mm, width between genal spine tips 14 mm. Total exposed opisthosomal length of the paratype is *c.* 12 mm, comprising a mesosoma of 8 mm and metasoma of 4 mm. Lateral compound eyes are small, length about 10 per cent of maximum prosomal shield length, and located on weakly developed ophthalmic ridges posterior to sagittal midlength, at *c.* 50 per cent of the maximum shield length, and about midway between the sagittal axis and lateral margin. The eye is semi-lunate in dorsal view with an abaxially convex visual surface; in lateral view the eye is teardrop-shaped, narrower anteriorly, and only slightly elevated above subophthalmic area. The course of the ophthalmic ridges is poorly demarcated, strongest between posterior margin of the prosomal shield and eye, and obscure anteriorly. The cardiac lobe is relatively narrow, indistinct, and only slightly inflated between the eyes; the course of short, anteriorly divergent longitudinal furrows is indicated by dark pyrite patches, possibly marking the linear trace of entapophyses, between the posterior margin of the prosomal shield and anterior limit of the eyes. The presence of dorsal median ocelli is suggested (in holotype MM I-4000A; Text-fig. 4A) by a small, subtle subcircular structure on the midline *c.* 40 per cent of sagittal prosomal shield length from the anterior margin. Anterior and lateral margins of the prosomal shield, as well as genal angles, are sharply defined by a distinct narrow rim; the shape and extent of the ventral doublure is unknown in the material available.

The opisthosoma is divided into two discrete units with an intervening articulation. A broad anterior mesosomal thoracetron is composed of six or seven fused tergites with a convex axial (cardiac) lobe and flattened, outwardly sloping, pleural (extracardiac) regions. The narrow parallel-sided metasoma comprises three fused tergites, approximately the same width as the posterior mesosomal axis; it lacks pleural fields. The mesosoma is roughly pentagonal in dorsal view, widest (trans.) anteriorly at or just behind the prosomal articulation (hinge), tapering steadily backwards to about 30 per cent of the maximum anterior width. Details of the anterior and posterior articulations (hinge structures), dorsolateral margins, tergite count, axial relief, and external topography not easily discerned in the articulated specimens. The general nature of segmentation is visible on the holotype (MM I-4000A; Text-fig. 2A) and a second specimen from Airport Cove (MM I-3999A) owing to pyrite mineralization presumably associated with serial muscle attachment sites and entapophyseal pits along longitudinal furrows. On the pleural (extracardiac) regions of both holotype and paratype, parallel linear features trending obliquely forward from the axial furrows may represent the posterior margins of book gills (branchial appendages). The faint suggestion of a lateral serrated margin on the left side of the paratype mesosoma (Text-fig. 2) may indicate the presence of fixed spines. A positive latex impression of an isolated partial mesosoma (MM I-3990, preserved as a mould of the ventral surface; Text-fig. 3A) reveals the following supple-
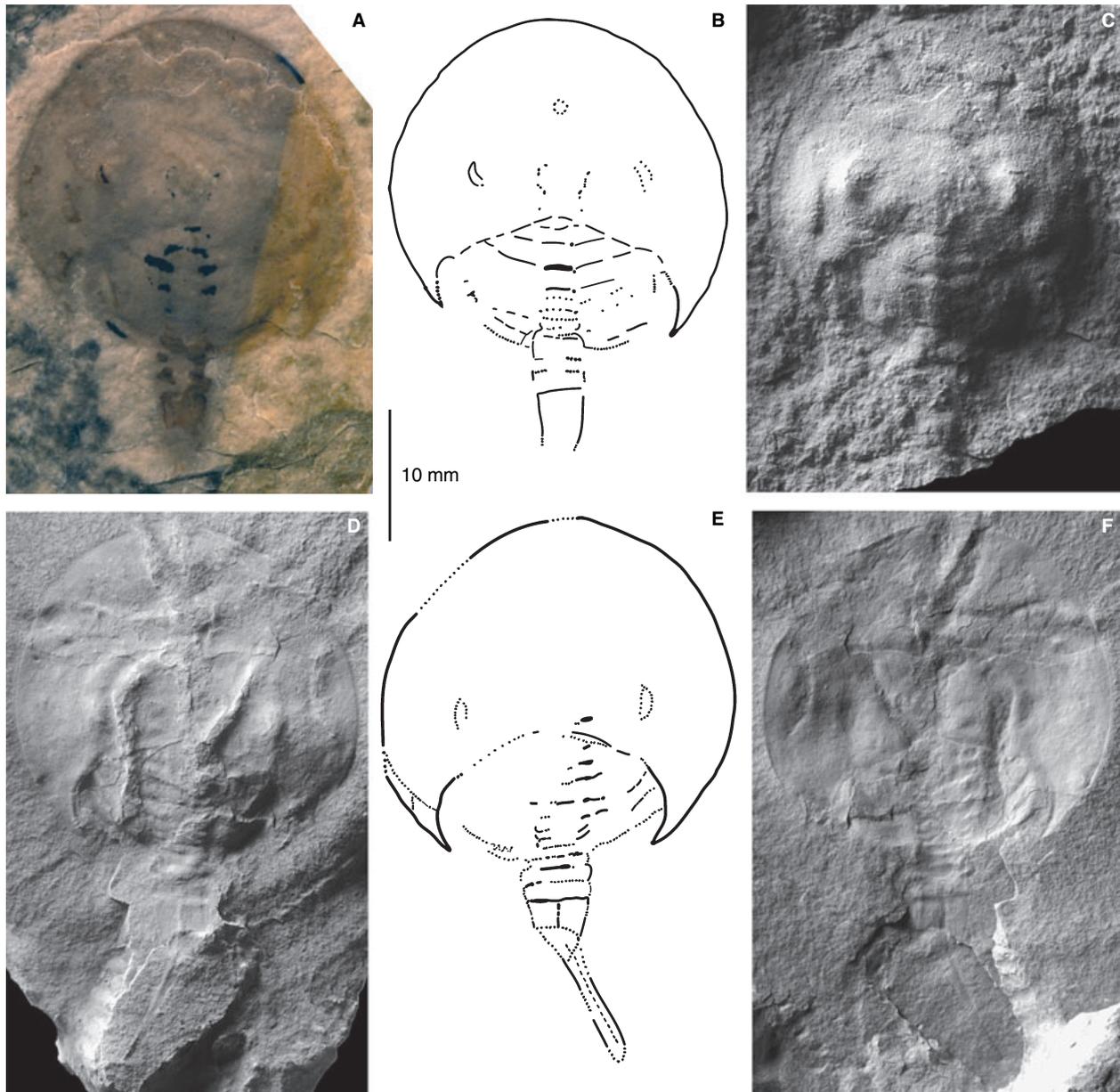
TEXT-FIG. 2. *Lunataspis aurora* gen. et sp. nov. A–C, holotype, MM I-4000A, Airport Cove; articulated exoskeleton. A, photographed under water to reveal local pyrite mineralization (small black patches) associated with marginal rim and axial furrows defining cardiac lobe of prosomal shield, and with serial ?opercular structures beneath mesosoma; yellow tone of right-hand side is the result of weathering. B, interpretive drawing showing outline and proportions of prosomal shield, mesosoma, metasoma, and anterior portion of telson. C, coated with ammonium chloride sublimate to show remnant relief. D–F, paratype, MM I-3989, William Lake; articulated exoskeleton. D, positive latex peel of negative counterpart, coated with ammonium chloride sublimate to highlight remnant relief: note faint radiating linear structures beneath prosomal shield that may represent walking legs. E, interpretive outline showing proportions of prosomal shield, mesosoma, metasoma, and telson. F, negative part of paratype specimen coated with ammonium chloride sublimate to show exoskeletal proportions and details of mesosomal and metasomal topography.

mentary details. The anterior margin is nearly transverse, with the middle third bowed gently forwards. The axial lobe is *c.* 33 per cent of the maximum mesosomal width anteriorly, tapering evenly backwards; it is only moderately inflated, consisting of at least six fused axial rings separated by shallow transverse furrows that arc smoothly forward mesially and terminate abaxially in shallow ovate depressions (muscle attachment sites). Each ring bears a blunt tubercle at the posterior midline and a pair of smaller nodes at the posterolateral corners. The inner surface of the pleural field shows at least five broad, flat 'ribs' fused along adjacent edges, marked by narrow ridges that are straight at first, then curve gently backwards abaxially.

TEXT-FIG. 3. *Lunataspis aurora* gen. sp. nov. A, latex impression of ventral surface of discrete mesosomal sclerite; MM I-3990, William Lake. B, negative impression (natural) of telson; MM I-3991 associated with MM I-3990, William Lake. A and B both coated with ammonium chloride sublimate).
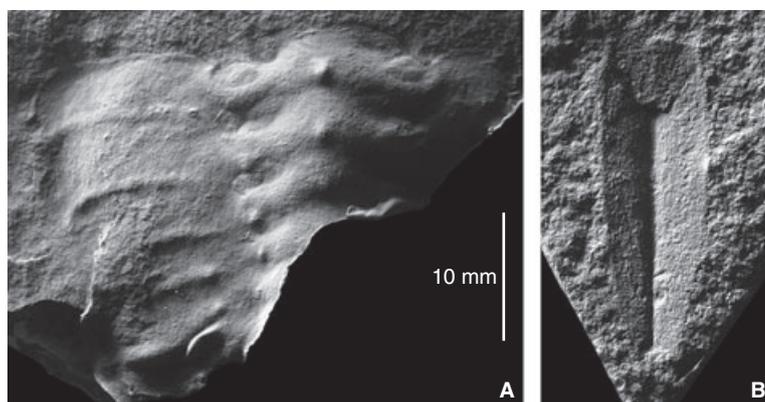
The metasoma is best observed in the holotype and paratype (Text-figs 2, 4C–D), in which it appears as a narrow, subcylindrical sclerite composed of three fused segments approximately corresponding in width (trans.) to the last axial ring (cardiac lobe) of the mesosoma; it forms a continuation of the cardiac region with no expansion into pleural fields (epimera) and little or no backwards taper. The nature of the posterior articulation with the telson is obscure, but apparently transverse and without a deep embayment.

A more or less complete telson (tail spine) is known from a latex impression of the prepared paratype counterpart (negative) (Text-fig. 2D), and the distal end from a single isolated negative mould associated with the discrete mesosoma specimen (MM I-3990; Text-fig. 3B); the anterior portion is seen on the holotype (Text-figs 2A, 4C–D). The dorsal outline of the telson is roughly lanceolate, resembling a classical Greek *xiphos* in shape. It is slightly shorter than the sagittal length of either the prosomal shield or opisthosoma and broadly triangular in cross-section, flat ventrally, with a low median dorsal keel. Maximum width (trans.) of the telson is at its articulation with the metasoma, narrowing evenly rearwards to about mid length where it expands slightly before curving smoothly back to a pointed apex. The nature of telson articulation, including range of lateral and vertical motion, is not discernible.

Discussion. Although the state of preservation of the fossils is remarkably good, details of opisthosomal segmentation and articulation in *Lunataspis* remain uncertain. For the two most complete specimens (MM I-3989, -4000A), crushing and telescoping preclude a definitive assessment of the expression of somites VII and VIII in particular. Based on relative proportions of the prosomal shield and opisthosoma (Text-fig. 5), however, it is apparent that *Lunataspis* possessed a segmentation pattern more closely comparable with that of Xiphosurida (nine fused or partially fused opisthosomal segments in total) than with that of well-documented synziphosurines, such as *Venustulus* (Moore *et al.* 2005*a*) and *Weinbergina* (Moore *et al.* 2005*b*), both with ten, or *Kasibelinurus* (Pickett 1993; Anderson and Selden 1997) and *Anderella* (Moore *et al.* 2007) with nine free segments. This in turn suggests that somite VII had already become fully encephalized (Fisher 1984; Selden and Siveter 1987), even though its ventral development (for instance, as a pair of chilaria in modern limulines) beneath the posterior of the prosomal shield in *Lunataspis* cannot be established. Likewise, the status of somite VIII remains unclear: if there are indeed only six segments in the mesosoma this would imply that the somite may already have been partially incorporated into the dorsal prosomal-opisthosomal hinge, and fully developed only ventrally on the opisthosoma (as is the genital operculum in modern forms). Vestiges of somite VIII are expressed dorsally in certain derived xiphosurids as so-called 'free lobes' fused to the anterolateral corners of the opisthosoma (Selden and Siveter 1987; Anderson and Selden 1997). Equivalent dorsal structures may be present in *Lunataspis*, but on articulated specimens the anterolateral angles of the opisthosoma are obscured beneath the genal spines; the single discrete mesosomal unit (MM I-3990; Text-fig. 3A) is an internal mould of the ventral surface and as such does not preserve the dorsal anterior corners. Alternatively, if the mesosomal segment count should ultimately prove to be seven, this 'extra' tergite could represent somite VIII still fully retained dorsally but fused within the opisthosoma. Issues of prosomal versus opisthosomal segment identity in various synziphosurine taxa have been resolved based on counts of paired prosomal appendages (Anderson *et al.* 1998; Moore *et al.* 2005*b*), but the present material of *Lunataspis* does not preserve unequivocal evidence of ventral limbs.

CONCLUSIONS

While *Lunataspis* is remarkably 'modern' in overall appearance (see reconstruction in Text-fig. 5), particularly with respect to prosomal morphology and possession of fused opisthosomal tergites, the bipartite thoracetron-like tagma sets it apart from all known post-Palaeozoic horseshoe crabs. We note that at least one species of *Paleolimulus*, an undoubted Carboniferous–Permian xiphosurid,
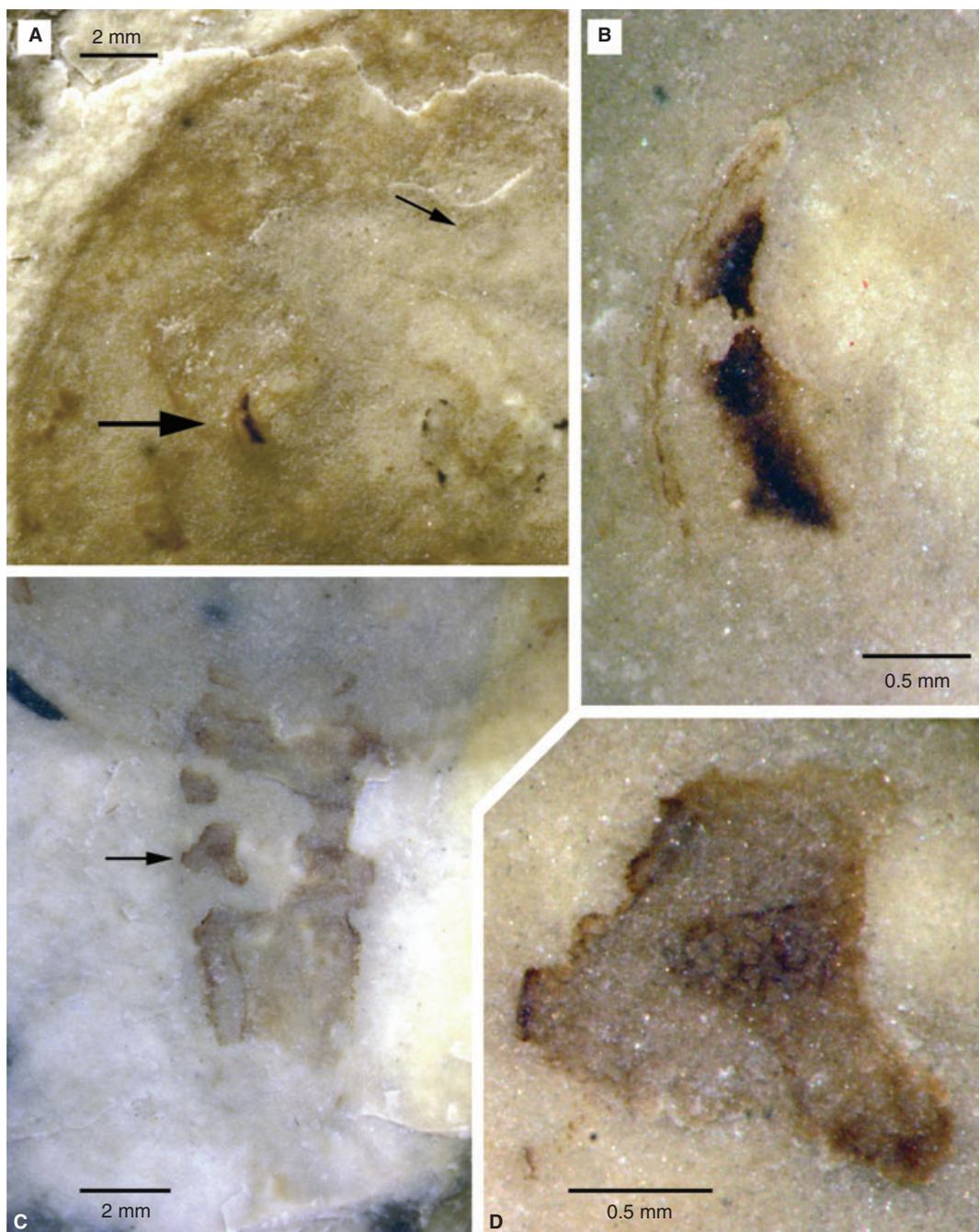
TEXT-FIG. 4. *Lunataspis aurora* gen. et sp. nov. Holotype, MM-I-4000A, Airport Cove; photographed under water. A, left anterior quadrant of prosomal shield; large arrow indicates left lateral eye, small arrow points to circular structure interpreted as location of median ocelli. B, pigmented cuticle on visual surface of left lateral eye, from area on prosomal shield indicated by large arrow in A. C, metasoma and anterior of telson. D, close-up detail of reticulate pattern in region of darker preserved cuticle, near segmental boundary of metasoma indicated by arrow on C.

has recently been redescribed as having a two-part opisthosoma: a broad anterior sclerite containing six fused segments and a posterior unit with two (Babcock *et al.* 2000, but see Allen and Feldmann 2005). It remains unclear whether in *Paleolimulus* the putative metasoma represents a modified plesiomorphic condition (with loss of one of three posteriormost tergites) or a secondary reversal from a fully fused nine-somite thoracetron. If the concept of a fused thoracetron, the primary synapomorphy uniting all members of the Xiphosurida, can be stretched to accommodate the two-part condition in *Paleolimulus*, then *Lunataspis* must also be included in

TEXT-FIG. 5. *Lunataspis aurora* gen. et sp. nov. Reconstruction of external exoskeletal morphology: left, dorsal view; right, lateral view; length *c.* 50 mm.
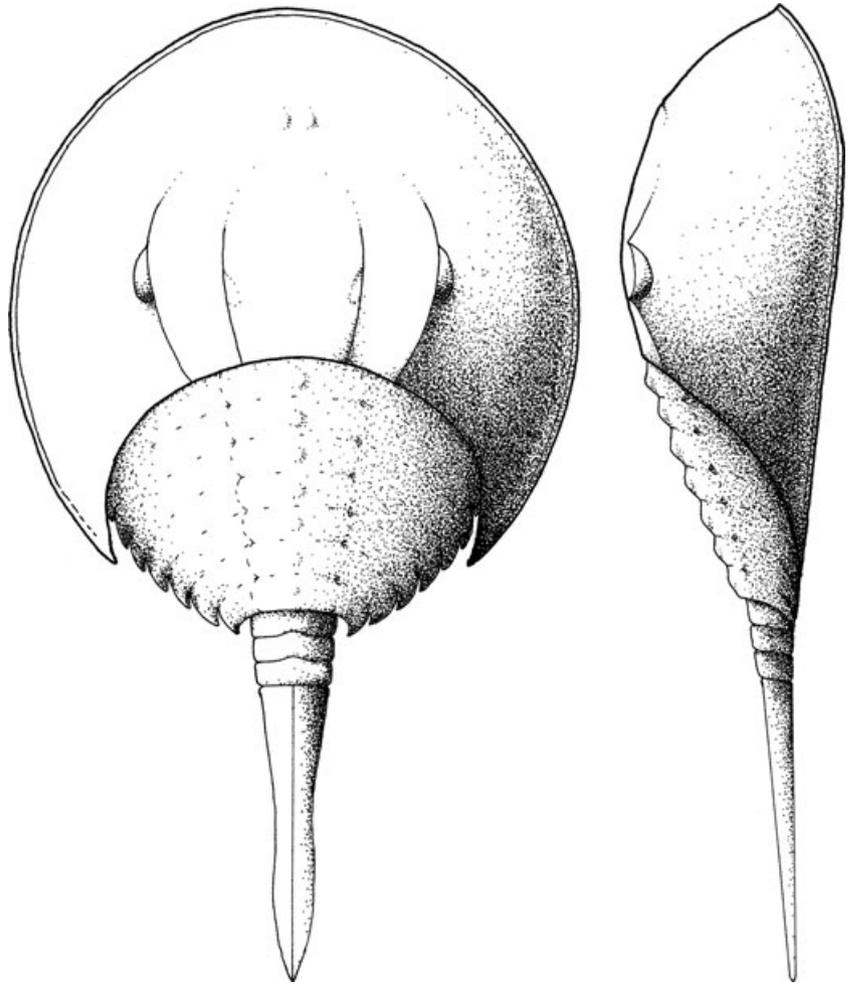
that group, as we propose herein. Alternatively, Xiphosurida must be redefined on other grounds, but this can only be undertaken as part of a comprehensive cladistic reappraisal of Xiphosura, a task well beyond the scope of this brief account.

Regardless of its ordinal-level status, *Lunataspis* is the oldest undoubted representative of the Xiphosura, yet its gross exoskeletal morphology is much closer to limulines than to any synziphosurine or even to many Late Palaeozoic xiphosurids. Extending the stratigraphic range of the xiphosurid body plan into the Late Ordovician in turn implies that its roots lie even deeper in the Cambro-Ordovician. The new minimum age will provide an important temporal benchmark for assessing a variety of recent and often conflicting hypotheses of euarthropod and chelicerate relationships, some based primarily on fossil and morphological data (Shultz 1990; Weygoldt 1998; Sutton *et al.* 2002; Cotton and Braddy 2004, for example), and others incorporating molecular sequence data and developmental studies (Wheeler and Hayashi 1998; Giribet *et al.* 2001; Angelini and Kaufman 2005;

Jager *et al.* 2006, among others). At the very least, this discovery will help constrain the timing of events in chelicerate evolution (Regier *et al.* 2005), and may in turn bear on such interesting issues as the advent of arthropod terrestrialization (Pisani *et al.* 2004). The presence of *Lunataspis* in the William Lake and Airport Cove Konservat-Lagerstätten, in sediments clearly representing near-shore restricted marine environments, establishes the earliest record of a long-term and persistent association between xiphosurids and shallow-marine coastal and littoral (marine, brackish, and fresh) ecozones (Bottjer *et al.* 2002; Anderson and Schuster 2003). While it is difficult to tease apart the strongly interwoven eco-evolutionary and taphonomic (Fisher 1979; Babcock *et al.* 2000; Scholtz and Edgecombe 2005) signals of this association, one clear implication is that still older fossil forms (ancestral to Xiphosurida and the paraphyletic synziphosurines, eurypterids for example) are likely to be found by searching for and carefully sampling similar shallow, near-shore palaeoenvironmental settings.

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