The xiphosuran *Liomesaspis* from the Montceau-les-Mines Konservat-Lagerstätte, Massif Central, France

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With 7 figures and 1 table in the text


Abstract: *Liomesaspis laevis* Raymond, 1944 is described from Montceau-les-Mines, based on comparison with the type material of Raymond (1944). *Anacontium brevis*, *A. carpenteri*, *Palatinaspis beimbaueri*, *Pringlia bispinosa*, *P. demaisteri*, and *P. fritschi*, are junior synonyms of *Liomesaspis laevis*. *Veltheimia bicornis* is a nomen nudum, the described material belongs to *Liomesaspis laevis*. Previously cited taxonomic differences between these forms are due to inaccuracies in the original description of *L. laevis* and variable states of preservation in subsequently described material. *Liomesaspis* marks the incursion of euryhaline marine organisms into the Montceau-les-Mines basin.


Introduction

Xiphosurans (horseshoe crabs) are a common aquatic faunal element of many Late Palaeozoic Konservat-Lagerstätten. Deposits of Carboniferous age, where flora and fauna are preserved in sideritic concretions have so far...
yielded five genera of these aquatic chelicerates: *Bellinurus* Pictet, 1846, *Euproops* MeeK, 1867, *Liomesaspis* Raymond, 1944, *Paleolimulus* Dunbar 1923 (from the Essex biota of Mazon Creek, Illinois) and *Valloisella* Racheboeuf, 1992 (see Anderson & Horrocks 1995). Xiphosurans have previously been reported from the Stephanian of Europe by Remy & Remy (1959), Vandenberghhe (1960), Müller (1962) and Simon (1971). All of these finds were assigned to the genus *Pringlia* Raymond, 1944. Most recently, the new genus *Palatinaspis* was described by Malz & Poschmann (1993) from the Lower Permian of the Saar-Nahe-Basin, Germany.

This paper identifies and describes the xiphosuran species present in the Montceau-les-Mines biota (Stephanian B), France and its taxonomic relationship with the above finds. Secretan (1980), Pacaud et al. (1981), Rolfe et al. (1982) and Poplin & Heyler (1994, p. 145-146), provisionally identified the xiphosuran from Montceau as *Pringlia*. However, examination of this, along with the type material of *Liomesaspis* from Mazon Creek, Illinois prompted a detailed taxonomic study to re-assess its true identity.

The geological setting of Montceau-les-Mines was dealt with in great detail in a recent cumulative volume on the area by Poplin & Heyler (1994). In summary, the roof shales hosting the sideritic concretions from which these xiphosurans are derived are above the first coal seam (Premiere Couche de charbon) of Blanzy/Montceau (Pacaud & Sotty 1994). Coulie et al. (1994, p. 41) suggested that the sedimentological evidence from the site indicated a deltaic depositional setting, with fast burial inducing the necessary chemical conditions for sideritic nodules to form. This view is backed up by the excellent preservation state of the otherwise unmineralised cuticles of arthropods from the site including the first fossil mesothele spider (Selden 1996). The intense creasing apparent on many cuticles occurred whilst the cuticle was still flexible, i.e. prior to bacterial degradation.

Materials and methods

This study was based on the examination of xiphosuran material housed in the collections of the Museum d'Histoire Naturelle d'Autun, France (AM). Additionally, material in the collections of the Manchester Museum, Manchester (MM), The Natural History Museum, London (NHM), The Lapworth Museum, University of Birmingham (BU), and The Museum of Comparative Zoology, Harvard (MCZ) was examined for comparative purposes. Xiphosuran specimens from Montceau-les-Mines were cleaned by soaking the split nodules in dilute HCl acid for three minutes which dissolved out the calcite and loosened the white, powdery kaolinite from the mould, facilitating further preparation by vibro tool prior to examination. The material was examined under an Olympus SZH binocular microscope from which camera lucida drawings were prepared. Preserved specimens of the extant xiphosuran *Limulus polyphemus* were examined for comparative morphology.
Fig. 1. *Liomesaspis laevis* Raymond, 1944. a: MCZ 109536 (formerly 4698), holotype specimen (X 3). b: MCZ 109534 (formerly 4696a) (part) and MCZ 109534 (formerly 4696b) (counterpart), paratype (X 3). Both specimens from the Upper Carboniferous (Westphalian D) of Mazon Creek, Illinois. Scale bar = 1 cm.
Taphonomy of the Montceau-les-Mines xiphosurans

Recent studies have emphasised the importance of determining the taphonomic and preservational history of xiphosuran fossils prior to consideration of their taxonomy (Anderson 1994, Anderson & Horrocks 1995, Anderson 1996). This study adheres to the same line of inquiry in order to determine potentially useful taxonomic characters (both specific and generic) which are not affected by the variable preservation state present between both geographically disparate sites and individual specimens.

The vast majority of xiphosurans collected from Montceau-les-Mines are preserved in markedly spherical to sub-spherical siderite nodules. The distinctive shape of these nodules suggests that they were formed during very early diagenesis of the sediments, and as a result, preserve an excellent three-dimensional representation of the fossils. One specimen (AM 45689; Fig. 2f.) is preserved as a black compression fossil in a grey shale, presumably the roof shale of one of the exploited coal seams. Notably, specimens preserved in shale show signs of compressional deformation resulting in skewing of the midline and also a change in the shape of the opisthosoma from broadly triangular to slightly rounded, indicating pliability of the cuticular exoskeleton during burial compaction. Specimens preserved within nodules often contain white, powdery kaolinite and minor pyrite. At least one specimen (AM 33271) consists of a body fossil mould completely infilled by sparry calcite. Other infilling phases include minor sphalerite and galena. As is normally the case in sideritic concretions, the animals are relatively complete with the prosoma, opisthosoma and even the tail spine still articulated. Unusually, however, the majority of specimens from this site possess noticeable prosomal appendages. These are rarely preserved within sideritic concretions and are more often encountered within phosphatised deposits such as those hosting the Lower Carboniferous xiphosuran Rolfeia Waterston, 1985. In this respect, it would appear that the deposit represents an unusual preservation state. The unmineralised cuticle may have been subject to phosphatisation prior to burial and subsequent sideritic concretion formation. A good example of this is AM 50613 (Fig. 2e.).

Systematic Palaeontology

Phylum Chelicerata Heymons, 1901
Class Xiphosura Latreille, 1802
Order Xiphosurida Latreille, 1802
Suborder Bellinurina Zittel & Eastman, 1913

Emended diagnosis: Xiphosurida with fixed lateral opisthosomal spines, lacking a free lobe and movable, opisthosomal spines. Tergite 1 is reduced to a microtergite and lacks lateral fields. Posterior axial lobe triangular in shape. Ophthalmic ridges produced posteriorly to form sharp, carinate, ophthalmic spines (emended from Zittel & Eastman (1913)).
Included families: Bellinuridae Packard, 1885; Euproopidae Eller, 1938.

Discussion: This scheme follows the recent classification of Anderson & Selden (in press) which recognised the occurrence of a thoracetron of fused opisthosomal segments in the genus Bellinurus. Prior to the work of Anderson & Selden (in press) a thoracetron was considered a convergently evolved innovation of superfamilies Euproopacea and Limulacea.

Raymond (1944) defined the family Liomesaspidae as euproopceans without true dorsal furrows on the prosoma or lateral spines on the thoracetron. Dorsal furrows, or, in the terminology adopted here, cardiac furrows, are present on all specimens of Liomesaspis I have studied, and as such, I reject this character as being of use in defining the Family Liomesaspidae. Secondary loss of the lateral opisthosomal spines is an autapomorphy of Liomesaspis and I retain it to diagnose that genus. In the absence of any further autapomorphies for Family Liomesaspidae, I place Liomesaspis within Family Euproopidae (see below).

Family Euproopidae Eller, 1938

Emended diagnosis: Bellinurina with the bases of the opisthosomal lateral spines fused distally to form a lateral flange. Path of the ophthalmic eyes concave in outline posterior to the lateral compound eyes (emended from Raymond (1944)).

Type genus: Euproops Meeke, 1867; Upper Carboniferous, Westphalian D, Francis Creek Shale, Mazon Creek, Illinois, USA. By original designation.


Remarks: Eller (1938) originally created Euproopidae for the genus Euproops and included the apparently aberrant Euproops morani. At a later date, Raymond (1944) moved Euproops morani to the new, monotypic, genus Elleria morani (Eller, 1938) but retained it within the family Euproopidae. Examination of the holotype of Elleria morani by the author suggests that it in fact belongs to Kasibelinuridae as defined by Pickett (1993).

Raymond (1944) gave a description of the type species of the genus Euproops danae (Meeke & Worthen, 1865). Although he commented that this form was relatively well known, he did not indicate that he was describing the type material in the body of the text. This led Anderson (1994) to consider the type material of E. danae to be lost and to erect a neotype. It has since come to the attention of the author that the material described by Raymond (1944) was actually the type material of E. danae and is now housed in the collections of the Yale Peabody Museum (YPM 28140) (Dr. L. E. Babcock, pers. comm.). Any subsequent taxonomic work on this species should take note of this amendment.

Previous listings of genera belonging to Family Euproopidae have included Pringlia, Anacontinentum, Prolimulus and ?Palatinaspis. However, this study recognises Liomesaspis as the only other member of Euproopidae. All of the above named are considered congeneric with Liomesaspis. The details of the synonymy are given in the discussion of the species Liomesaspis laevis.
Genus *Liomesaspis* RAYMOND, 1944

Type species: *Liomesaspis laevis* RAYMOND, 1944; Upper Carboniferous, Westphalian D, Francis Creek Shale, Mazon Creek, Illinois, USA. By original designation.


**Diagnosis:** Euproopidae with a lateral opisthosomal flange which lacks lateral spines. Genal spines short and reduced, whilst the ophthalmic spines are highly inflated near their bases tapering to sharp carinate spines distally. Ophthalmic spines reach back as far as the posterior margin of the opisthosoma. Bases of ophthalmic spines may obscure the underlying genal spines. Slight, lateral flange may also be developed on the prosomal rim. Tail spine short and styliform (emended from RAYMOND (1944)).

**Discussion:** RAYMOND (1944) described *Liomesaspis* as having a rounded prosoma, lacking genal spines and a defined cardiac lobe, and possessing an axial lobe of the thoracetrtron which was clearly defined but obscurely segmented. In this study, genal spines have been positively identified on a number of specimens (e.g. NHM I. 13882 from Coseley, England). However, they are very reduced and are often hidden under the inflated bases of the ophthalmic spines (which are particularly well developed in NHM I. 13974, In 18495 and the material described by REMY & REMY (1959)). RAYMOND (1944, p. 475) commented that since the xiphosurans from Mazon Creek were preserved in siderite nodules, they had suffered relatively little distortion due to compaction and any distortion which had occurred was due to the thinness of the test (cuticle). However, he still insisted on setting up new species, genera and even families on poorly preserved or incomplete material. Re-examination of the type material revealed that it had obviously suffered some compression. Additionally, examination of Raymond's figures of *Liomesaspis* (p. 499, figs. 7-8 and also p. 500, figs. 9-10) suggest that a cardiac lobe is present in this form, a rather globose structure which appears to expand anteriorly. To further confuse the picture, this is the same structure which is evident in WOODWARD's original description (1868) of *Prestwichia birtwelli*, which Raymond failed to comment on. RAYMOND (1944) assigned *Prestwichia birtwelli* to *Pringlia* and also erected the new species *P. bispinosa*. In the accompanying text-figure (p. 503, fig. 11), he illustrated an isolated prosoma with ophthalmic spines, reduced genal spines and a cardiac lobe which appears to taper anteriorly, in the same manner as that of *Bellinurus* and *Euproops*. The same appearance of the cardiac lobe is seen in the material described by REMY & REMY (1959), VANDENBERGHE (1960) and MÜLLER (1962). Similar genal and ophthalmic spine configurations are also recorded in this material. The apparent anteriorly expanding cardiac lobe structure suggested by RAYMOND's figures is interpreted here as a misidentification of the inner margins of the raised ophthalmic spine bases.

FRIC (1899) described a xiphosuran from the Gaskohles of N'yrany as *Prolimulus woodwardi*. However, FRIC (1899) neglected to cite the specimen number(s) and repository of the type material. Examination of a syntype of *Prolimulus woodwardi* (NHM In 18588) suggests that the differences stated
Fig. 2. *Liomesaspis laevis* Raymond, 1944. a: AM 24824 (x 3). b: AM 5779 (x 3), c: AM 50613 (x 3), d: AM 50608 (x 3), e: AM 50613 (x 3), f: AM 45689 (x 3). Upper Carboniferous (Stephanian B) of Montceau-les-Mines, Massif Central, France. Scale bar = 1 cm.
between *Prolimulus* and *Liomesaspis* may be no more than preservational. Raymond (1944) listed *Prolimulus* as a liomesaspid on the basis of the lack of genal spines in one specimen which he had seen (MCZ 4694) and also a lack of lateral spines on the thoracetron. He commented that all specimens of this form were so badly preserved that the genus could hardly be said to have any distinguishing characteristics! Whilst *Liomesaspis* normally occurs in sideritic nodules, *Prolimulus* is always preserved in a sapropelic oil shale. As a result, it is extremely flattened and in most cases, preserved as a thin pyritised film. *Prolimulus* was formerly considered to be Stephanian B in age (Raymond 1944), however subsequent stratigraphic correlation dates the Nýřany site as Westphalian D (Opluštíl 1985). The specimens of *Prolimulus* that I have studied are too badly preserved to attempt a valid comparison with *Liomesaspis*. However, if new material which demonstrates the possible synonymy between *Liomesaspis* and *Prolimulus* is discovered, then Frick’s genus should have priority. It would be unfortunate if this synonymy proves to be the case as *Prolimulus* would belong to Suborder Bellinurina and not Suborder Limulina and therefore could not have given rise to any member of the Limulina contrary to what the generic name implies.

Rachboeuf (1992) described a new genus of Carboniferous xiphosuran, *Valloisella*, from the Westphalian B of France, comparing it to both *Euproops* and *Pringlia*. However, Anderson & Horrocks (1995) demonstrated that this form is in fact a paleolimulid on account of the presence of a free lobe and movable, opisthosomal spines.

Discussion of the species assigned to *Liomesaspis*: Woodward (1872) erected the species *Prestwichia birtwelli* for a new xiphosuran from the Soapstone Bed (Upper Carboniferous, Westphalian A), a siderite nodule band lying above the Lower Mountain Mine, exposed by opencast working at the Cornfield Pit on the south bank of the River Calder, Padiham, Lancashire, England, UK (Selden 1993). Associated nodules host the diagnostic zone fossil *Gastrioceras listeri*. Woodward (1872) stated that the original specimen upon which he had based his description was in the private collection of Mr. Thomas Birtwell of Gawthorpe Gardens, Padiham, Lancashire. However, he gave no formal diagnosis for this new species nor indicated where the ‘holotype’ material would finally be accessioned. There has been no subsequent indication of the whereabouts of the original holotype specimen, and as a result, I have not been able to study it, check its description or compare it with the type material of *L. laevis*. Woodward (1872) originally considered the lateral spines of this xiphosuran to have lain outside the margin of the nodule in which the fossil was preserved. On this basis, he assigned the specimen to the pre-existing genus *Prestwichia* and erected the new species *P. birtwelli* for it. However, careful preparatory excavation of a number of specimens by Fisher (1975) showed that this was not the case, and that lateral spines are truly absent from this form.
Interestingly, Raymond (1944) was also unable to locate the holotype and additional specimen of *P. birtwelli* which Woodward (1872) originally figured. However, he did point out that the proportions of *P. birtwelli* were "about the same as in *Liomesaspis laevis*”. As *P. birtwelli* was not formally diagnosed, described or accessioned to a museum collection, I consider the species name to be unavailable until either the original material which Woodward described is rediscovered, or a neotype based on material from the type locality and horizon is described. Without a type species for *Pringlia*, taxa previously assigned to this genus require revision (see below). *Pringlia leonardensis* was described from the Lower Permian of Annelly, Harvey County, Kansas by Tasch (1961). However, as I have not seen the specimen, I cannot give its specific diagnosis or how it differs from *L. laevis*. 

Fig. 3. *Liomesaspis laevis* Raymond, 1944. a: AM 41549 (x 3). b: AM 24825 (x 3). c: AM 6343 (x 3). d: AM 52688 (x 3). Upper Carboniferous (Stephanian B) of Montceau-les-Mines, Massif Central, France. Scale bar = 1 cm.
Liomesaspis laevis RAYMOND, 1944
Figs. 1a-c, Figs. 2a-f, Figs. 3a-d, Fig. 4, Figs. 5a-b, Fig. 7

Type material: RAYMOND (1944) originally designated the holotype of *Liomesaspis laevis* as MCZ 4698, and the following as paratypes: MCZ 4696 and YPM 16913. It is noted here that following re-numbering of the MCZ type and figured collections, the holotype of *L. laevis* is now MCZ 109536 and the paratype MCZ 109534.

Additional material: Autun Museum (AM) 5772, 5778, 6343, 24824-6, 50608 (enrolled), 50611, 24689, 41549, 45684, 33271, 59485-6, 50613, 52658-9, 51955-6 (enrolled) 45689, MCZ 109531 (previously 4724) and MCZ 109532 (previously 4725) (the holotype and paratype of *Anacontium carpenteri* RAYMOND, 1944), MCZ 109533 (previously 4726) (the holotype and only specimen of *Anacontium brevis* RAYMOND, 1944) YPM 16911 (holotype and only specimen of *Pringlia bispinosa* RAYMOND, 1944), NMM (Naturhistorisches Museum Mainz) 5825a, b, NMM 5824a, b SSN 11 NM 93 (Paläontologisches Museum Mainz).

Fig. 4. Camera lucida drawing of MCZ 109536 (holotype of *Liomesaspis laevis*); ca: carapace, ot: ocellar tubercle, opr: ophthalmic ridge, c lb: cardiac lobe, op s: ophthalmic spine, opi: opisthosoma, ax r: axial ridge, op f: opisthosomal flange.
Fig. 5. a: Camera lucida drawing of MCZ 109534 (paratype of Liomesaspis laevis). b: Camera lucida drawing of MCZ 109534 (paratype counterpart); le: lateral eye, op r: ophthalmic ridge, ca: carapace, c lb: cardiac lobe, op s: ophthalmic spine, opi: opisthosoma, ax r: axial ridge, sp b: spine boss, op f: opisthosomal flange, t sp: x 3.

Museum Nierstein, H. Stapf collection), SSN 11 NM 25 and SSN 11 NM 443 the holotype and paratypes of Palatinaspis beimbaueri MALZ & POSCHMANN, 1993, the holotype of Pringlia demaistrei, 583,15 the holotype of Pringlia fritschi, T/A2, T/A3, T/A4, T/A5, the co-types of Pringlia fritschi, Sigs.- Nr 30/31 in the Geologisches Institut der Bergakademie Freiberg (Sachsen) described by MÜLLER (1962), the unnumbered material described as Veltheimia bicornis by BEYSCHLAG & v. FRITSCH (1899), and the specimens described, but not numbered by SIMON (1971) as Pringlia ? fritschi.

Type locality: Upper Carboniferous, Westphalian D, Francis Creek Shale, Mazon Creek, Illinois, USA.

Diagnosis: As for the genus.
Description of the type material: The holotype of *L. laevis* (MCZ 109536) designated by RAYMOND (1944) consists of the part only (Fig. 1a, Fig. 4.). The counterpart of the nodule is missing. The specimen itself appears to have been extensively prepared subsequent to its collection. This is especially the case around the left hand lateral margin of the prosoma and the posterior margin of the opisthosoma. This has obliterated certain delicate structures such as the ophthalmic and genal spines and possibly also the tail spine. The carapace itself is relatively uncompressed and as a result, the dorsal topography is relatively clear. The most striking feature of the carapace are the paired ophthalmic ridges which commence at the posterior margin of the carapace and run forward in a concave manner before intersecting with the “M” shaped anterior expression of the ophthalmic ridges. At the junction between these two portions of the ridges are situated the lateral eyes. This is the same configuration as in the genus *Euproops*. Within the intercardiophthalmic region lies the cardiac lobe. In this specimen, the cardiac lobe is present but poorly defined as a result of its low topography. It is broadly triangular in shape and tapers anteriorly to the point at which it joins with the ophthalmic ridges. At this point, a small raised node marks the position of the median dorsal ocelli. Flanking the cardiac lobe on both sides are slight trenches. The surface then rises up to the level of the ophthalmic ridges. The topography falls away once more lateral to the ridges before encountering the lateral margins of the carapace. These are the inflated bases of the ophthalmic spines whose presence is hinted at in this specimen by the slight overlap of the carapace onto the opisthosoma on the left hand side of the specimen.

The thoracetron of the holotype specimen is rounded and is broader than it is axially long. Again, like the carapace, it is relatively uncompressed and its most noticeable feature is the base of an upstanding spine boss towards the posterior of the axial column. This spine boss has been fractured producing a circular breakage point in the cuticle, probably produced when the nodule was first opened. Anterior to the spine boss, the axial segments are all coalesced. Original segmentation lines are only hinted at by remnant structures and also by the positioning of entapophyses attachment points. Towards the posterior, the opisthosoma surface falls away before reaching the opisthosomal flange. There are no indications of lateral opisthosomal spines in this specimen or any other.

The paratype specimen MCZ 109534 consists of both part and counterpart of a relatively well preserved xiphosuran in a large siderite concretion (see Figs. 1 b-c, Figs. 5a-b). The carapace, opisthosoma and a small length of the terminal tail spine are visible. It should be noted that the original figure of this specimen given by RAYMOND (1944; fig. 7) is so poor that it hardly bears any resemblance to the actual specimen. The carapace is criss-crossed with creases formed as a result of compression of the unmineralised cuticle during the early stages of burial. However, the carapace in the main retains its original shape and dimensions. One point which should be noted though is that the
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The anterior section of the paired ophthalmic ridges appears to lie very close to the anterior of the carapace. This is not an original configuration but has come about as a result of buckling and compression of the anterior edge of the carapace. The prosoma is rounded and approximately equal in size, if not slightly larger than the opisthosoma. The ophthalmic ridges are poorly defined but again follow the same configuration as described in detail above for the holotype specimen. Two structures lying equidistant either side of the axis of the carapace, approximately one half the way down the axial length form conspicuous raised topography. These are not the lateral eyes, although they do lie along the line of the ophthalmic ridges. They are probably internal carapace structures and in fact appear to be also present in the Montceau-les-Mines material of *Liomesaspis laevis*. The cardiac lobe in this specimen is much clearer in outline. As before, it is a broadly triangular structure which tapers to a point anteriorly. However, in this specimen, the posterior of the lobe is broken off. The same is true of the posterior upper surface of the ophthalmic ridges. An apparent widening of the ridge suggests that ophthalmic spines were originally present but were broken off on opening of the nodule.

The opisthosoma of the paratype is relatively well preserved. The axial column is distinct and is comprised of five coalesced axial rings followed posteriorly by a rounded spine boss. Towards the left hand posterior margin of the opisthosoma of the counterpart, a small fragment of the lateral opisthosomal flange is visible. No trace of lateral opisthosomal spines is present. A short section of the tail spine is present. Judging from the degree of tapering and the initial basal width, it was probably originally as long as the combined axial length of the prosoma and opisthosoma.

In all of the type material, the small, inwardly facing genal spines identified in additional material appear to have been prepared off, or may lie below the surface of the carapace. This led Raymond (1944) to consider them absent in *Liomesaspis*. Their position and orientation are still evidenced by the fractured bases towards the posterior of the carapace (see Figs. 1 b-c).

Description of the Montceau-les-Mines material: The morphology of the xiphosurans from Montceau-les-Mines confirms closely to that observed in the type material of *Liomesaspis laevis*. However, as a result of peculiarities of preservation unique to this site, a number of morphological structures are identified which have previously not been recorded. A list of specimen numbers and size of individuals is given in Table 1. In the opisthosomal cavity of AU 24824 (Fig. 2a) there are radiating ridges of replaced cuticle which are interpreted as the remains of the book gills. Unfortunately, much of the area is covered by kaolinite and the lamellae themselves are so fragile that further removal of the kaolinite would damage the specimen. In the same specimen, the attachment point of the prosomal limbs are also seen remarkably well. This is due to the dorsal cuticular surface of the carapace having been removed allowing a view down into it. A kite-shaped region in
Table 1. The Montceau-les-Mines xiphosuran material. \( L \) = total combined axial length of the prosoma and opisthosoma.

| AM 5772-5773 (Part/counterpart) | Juvenile instar \( L = 6 \) mm |
| AM 5778-5779 (Part/counterpart) | \( L = 10 \) mm |
| AM 6442-6443 (Part/counterpart) | \( L = 10 \) mm |
| AM 24823-24824 (Part/counterpart) | \( L = 11 \) mm |
| AM 24825-24826 (Part/counterpart) | \( L = 10 \) mm |
| AM 41549 (part only) | \( L = 10 \) mm |
| AM 45684-45685 (Part/counterpart) | \( L = 11 \) mm |
| AM 45689 (part only) Juvenile instar | \( L = 7 \) mm |
| AM 50608 (part only) Partially enrolled | \( L \approx \) approx. |
| AM 50613 (Part only) Heavily phosphatised. | \( L = 10 \) mm |
| AM 51956 (Part/counterpart) Partially enrolled \( L \approx \) approx. |
| AM 52658 (part only) Juvenile instar | \( L = 4 \) mm |
| AM 59485 (part only) Juvenile instar | \( L = 7 \) mm |

the opisthosoma of AU 24824 is unusual, and its position is close to where the genital openings would be expected. In the proximal region of the tail spine of the same specimen is preserved in a position underneath where the boss-like fused posterior segments would have sat, is a strong articulation point. Specimens AU 50608 (Fig. 2d) and AU 51956 are loosely flexed at the prosomal/opisthosomal junction. This is quite different from the style of enrollment seen in specimens of *Bellinus* and *Euproops* which both coapt (see Anderson 1996 for details). Instead, the bulbous prosoma of *Liomesaspis* appears to be too large to permit this type of enrollment. In some respects, it is closer in functional morphology to flexing in extant *Limulus* than the other Carboniferous forms.

General description of *Liomesaspis laevis*: Moderately small xiphosurans ranging from 7 to 30 mm in length, including the tail spine. Prosoma rounded, with a semicircular outline. Prosomal margin sharply delineated from the cardiophthalmic region, producing a well-defined prosomal flange which is widest anteriorly before sweeping posteriorly to the inwardly-curved, minute genal spines. Cardiac lobe broad based near the posterior margin of the prosoma before tapering anteriorly. Cardiac lobe is flanked either side by deep furrows. On the posterior margin of the cardiac lobe, is a short, sharp spine. Genal spines small and inward facing, formed from continuations of the lateral marginal flange of the prosoma. Ophthalmic spines inflated, overlying and obscuring the small genal spines. Ophthalmic ridges carinate, bearing compound lateral eyes at the junction between the lateral portions. Ophthalmic ridges are commonly indistinct due to intense compression and creasing of the carapace cuticle. Prosomal appendages slender. First pair of appendages small chelicerae.

Opisthosoma sub-triangular in outline, and entirely fused to form a thoracevron, consisting of five axial segments and a posterior axial lobe of three seg-
ment. Some compressed specimens appear to have a rounder opisthosoma. Underlying the dorsal cuticle in the region of the three fully fused posterior segments is a thin sheet of cuticle which defines the posterior wall of the opisthosomal vault cavity. First segment lacks lateral fields, is reduced in size and forms an articulating microtergite. Last segment gives rise to a rounded spine boss, from which a posteriorly and upwardly facing axial spine projects. A well-defined lateral opisthosomal flange runs around the perimeter of the opisthosoma. Poorly defined transverse ridges cross this flange. The flange does not bear fixed lateral spines. Segmentation of the median column is distinct, however the topography of the transverse ridges of the opisthosomal fields is variable. Tail spine styliform, and approximately equal to, or slightly longer than the combined axial length of the prosoma and opisthosoma.

Discussion: The figures and specific diagnoses originally given by Raymond (1944) for species belonging to Liomesaspis, Pringlia and Anacontium were confusing and unspecific with some diagnoses applying equally well to different taxa. As a result, subsequent work on these taxa has reflected an initially poorly defined taxonomy. This, coupled with an apparent trend to describe new taxa whenever new specimens of these animals are encountered (presumably on account of their status as rare fossils although this is not necessarily the case) has resulted in a high degree of oversplitting. This study compares fossil material from geographically disparate but stratigraphically close localities and suggests that all of these forms belong to the type species Liomesaspis laevis. The discussion below deals with each species in alphabetical order. One point which should be noted is the apparent absence of genal spines in some specimens and their presence in others. This can be explained in relation to considering the sediment hosting the fossils. In siderite concretions, with little compression, the genal spines remain hidden below the bases of the ophthalmic spines and can only be seen by the removal of the latter. In specimens preserved in shale, compression tends to increase the angle that the genal spines make with the axis (Anderson 1994) and as a result, they appear displaced at the lateral margins of the carapace (see Fig. 6). A further consequence of compression is the appearance of the anterior pro­somal arch (see Fig. 6). In the most compressed material (the holotypes of Pringlia fritschi and Palatinaspis beimbaueri) this arch is quite conspicuous.

Raymond (1944) defined the new genus, Anacontium and the accompanying two new species A. brevis (Holotype and only known specimen MCZ 109533 (previously MCZ 4726)) and A. carpen­teri (Holotype MCZ 109531 (previously MCZ 4724) and paratype MCZ 109532 (previously MCZ 4725)) on fragmentary material from the Lower Permian Wellington Formation, Noble County, Oklahoma. He assigned Anacontium to Liomesaspidae. Bergström (1975) considered the genus Anacontium to be a synonym of Pringlia, and I agree with Bergström’s views.

Malz & Possmann (1993) erected the new genus and species Palatinaspis beimbaueri for a xiphosuran from the Lower Permian of the Saar-
Fig. 6. Diagram illustrating the relative positions of the genal and ophthalmic spines in relation to the degree of compaction of the carapace, which in turn relates to the enclosing sediment. A: Minimal compaction within a siderite concretion. B: Dorso-ventral compaction within shale, ophthalmic spines mould around the underlying opisthosomal topography. C: Dorso-ventral compaction within shale, genal and ophthalmic spines splayed outwards.

Nahe-Basin, Germany. They loosely assigned it to either Euproopidae or Liomesaspidae commenting that it was most closely related to the genera *Pringlia* and *Liomesaspis*. However, they considered both *Liomesaspis* and *Prolimulus* to lack genal and collar (ophthalmic) spines. As discussed above, the ophthalmic spines of the type material had been broken off although their presence is indicated by the broken bases of the spines still present at the posterior margin of the carapace. As REMY & REMY (1959) had assigned a Stephanian xiphosuran which possessed ophthalmic spines to the genus *Pringlia*, they considered *Palatinaspis* to be most closely related to *Pringlia*. However, they did not make reference to the work of SIMON (1971). Examination of their reconstruction (p. 28, fig. 5a-b) of *Palatinaspis beimbaueri* and the figure of *Pringlia fritschi* suggests that the only differences between them
The xiphosuran *Liomesaspis* from Montceau-les-Mines is the angle at which the genal spines are projected from the postero-lateral margins of the carapace. The magnitude of the angle made between the genal spines and the midline of the animal was shown by Anderson (1994) to be highly variable due to the effects of burial compression (see also Fig. 6). Consequently, I regard *Palatinaspis beimbaueri* to be a junior synonym of *P. fritschi*, which as detailed below is in turn a junior synonym of *L. laevis*.

*Pringlia demaistrei* and *P. fritschi* were both recorded as Stephanian B in age by Vandenberghe (1960) who cited the differences between *P. demaistrei* and *P. fritschi* as being due to nothing more than different dimensions, a different contour of the prosoma, and the orientation of the genal spines relative to the posterior prosomal margin. When studied in relation to taphonomic distortion by compression (Anderson 1994), it is apparent that these differentiating characteristics are both subject to alteration and as such are rejected as taxonomic characters in this study (see also Fig. 6.). It is therefore relevant to the discussion to consider the matrix in which the xiphosuran is preserved. All of the available specimens of *Liomesaspis* from Mazon Creek are preserved in the form of moulds in siderite concretions, however, the holotype of *P. demaistrei* is preserved in shale. It is reasonable to suspect that compression of such a vaulted prosoma, with its bounding prosomal flange would produce something similar to the plate which Vandenberghe (1960) figured. In addition, judging from his plates, the course of the ophthalmic spines has been influenced by the underlying opisthosomal topography. *P. fritschi* and *P. demaistrei* appear to be identical morphologically and are thus synonymised to *Pringlia fritschi*, on the basis of priority of publication date of *P. fritschi* over *P. demaistrei*. As I can find no good morphological characters with which to differentiate *Pringlia fritschi* from *Liomesaspis laevis*, I synonymise *P. fritschi* and *P. demaistrei* with *L. laevis*.

Simon (1971) also described new xiphosuran material from the Hallesche Mulde as *Pringlia f. fritschi* Remy & Remy, 1959. Recent stratigraphic revision suggests that this material was collected from within the Wettin subformation in the NE Saale Basin and is therefore Stephanian C in age (Schneider et al. 1995). However, the material appears to have been held in private collections as no museum numbers are associated with the xiphosurans he figured. The line drawings of Simon (1971; p. 54, figs.1-3) all show the presence of minute genal spines and enlarged ophthalmic spines projecting from the posterior of the carapaces. For this reason, I am satisfied that the specimens figured by Simon (1971) belong to *Liomesaspis laevis*.

*Pringlia bispinosa* was erected by Raymond (1944) for an isolated and incomplete prosoma. He designated YPM 16911 as the holotype and only known specimen. He differentiated *P. bispinosa* from *P. birtwelli* on the basis that in the former, the lateral eyes were positioned further back on the prosoma than in the latter species. As the apparent position of the lateral eyes on the dorsal surface of the carapace is related to the extent and angle of
compression of the carapace (c. f. the holotype of Liomesaspis laevis), I consider this an unreliable character upon which to erect a new species. Additionally, as the type species of Pringlia has been shown above to be an unavailable name, I synonymise P. bispinosa with L. laevis RAYMOND, 1944.

REMY & REMY (1959) regarded Veltheimia bicornis BEYSCHLAG & v. FRITSCH, 1899 as a nomen nudum, an assignment with which I agree. They indicated that no formal description of the species was given, merely rather poor line drawings (BEYSCHLAG & v. FRITSCH (1899, p. 180, fig. 8a, b.) which depicted two separate carapaces. MÜLLER (1962) agreed with REMY & REMY (1959) as to the status of Veltheimia bicornis. RAYMOND (1944) did not mention the work of BEYSCHLAG & v. FRITSCH (1899) in his treatment of Late Palaeozoic xiphosurans and neither did SIMON (1971) nor MALZ & POSCHMANN (1993). The specific name referred to the two, posteriorly directed ophthalmic spines present in the specimens. A reconstruction of Liomesaspis laevis is presented in Figure 7.

Occurrence: Liomesaspis laevis is a relatively widespread xiphosuran occurring at Mazon Creek, Illinois (Westphalian D), Montceau-les-Mines, France (Stephanian B), Hallesche Mulde, Germany (Stephanian C) and the Lower Permian of the Saar-Nahe-Basin, Germany. Current work in the Lancashire coal fields of England (ANDERSON et al. in press) suggest that it may also be present there in rocks of Westphalian A age.

Palaeoecology of Liomesaspis

Liomesaspis is the only xiphosuran recorded to date from the Montceau-les-Mines biota. Why should this be? Both Euproops and Paleolimulus are known to be present at this stratigraphic interval albeit at different localities, but as yet have not been found at Montceau. This apparent mismatch of taxa, stratigraphic interval and locality has been identified from other sites such as Writhlington where only Euproops has been found (ANDERSON 1994). Conventionally, the view has been taken that such monogenic occurrences result from niche partitioning within the various xiphosuran genera co-existing at any given stratigraphic range. That is, that certain genera such as Euproops and also Liomesaspis occur in a fresh to brackish water association (the Braidwood biota of Mazon Creek) whilst others such as Paleolimulus represent truly marine conditions (Essex biota of Mazon Creek). But this does not explain why the two fresh to brackish water components are not always found in close association. To further confuse the picture, reports of up to four genera of xiphosurans including both allegedly fresh to brackish water forms and marine forms from Bickershaw have been made (ANDERSON et al. in press). This obviously breaks the rules of the simple scheme outlined above.

ANDERSON et al. (in press) suggested a possible mechanism to explain this association. Different breeding seasons would bring certain genera into a certain area only at specific times. Consequently, if these breeding seasons...
The xiphosuran *Liomesaspis* from Montceau-les-Mines

Fig. 7. Morphological reconstruction of the xiphosuran *Liomesaspis laevis* RAYMOND, 1944. Note the minute and incurving genal spines apparent on the lateral view, but hidden by the inflated bases of the ophthalmic spines in the dorsal view.

coincided with a specific 'preservational window' within the depositional setting i.e. a variety of environmental conditions leading to the formation of siderite concretions, then only that species would be preserved. It seems likely therefore that the Montceau-les-Mines xiphosurans represent an influx of
euryhaline marine organisms at the precise time that depositional conditions were favourable to their preservation. So, although in a sense they were part of the freshwater biota, evidenced by the presence of syncarid shrimps (SECRETAN 1980), they were in fact truly marine animals.

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