

# A CARBONIFEROUS SYNZIPHOSURINE (XIPHOSURA) FROM THE BEAR GULCH LIMESTONE, MONTANA, USA

by RACHEL A. MOORE\*, SCOTT C. MCKENZIE† and BRUCE S. LIEBERMAN\*

\*Department of Geology, University of Kansas, 1475 Jayhawk Blvd, Lindley Hall, Room 120, Lawrence, KS 66045-7613, USA; e-mail: moorerach@gmail.com

†Geology Department, Room 206B, Zurn Hall of Science, Mercyhurst College, 501 East 38th St., Erie, PA 16546-0001, USA

Typescript received 21 November 2005, accepted in revised form 23 August 2006

**Abstract:** A new synziphosurine, *Anderella parva* gen. et sp. nov., extends the known range of this group from the Silurian to the Carboniferous and is the youngest known so far from the fossil record. Previously the youngest synziphosurine, *Kasibelinurus*, was from the Devonian of North America. *Anderella parva* has a semi-oval carapace with pointed genal regions, nine freely articulating opisthosomal segments and a long styliform tail spine. It is the third xiphosuran genus to be described from the Bear Gulch Limestone and its discovery highlights this deposit as containing an unusually diverse xiphosuran biota. It is also the only

known locality where synziphosurines occur alongside the more derived xiphosurids. Xiphosurans reached their greatest diversity in the Carboniferous when the xiphosurids began to occupy brackish and freshwater habitats and became dominant over the synziphosurines. The discovery of the only known Carboniferous synziphosurine in marine sediments may indicate their inability to exploit these same environments.

**Key words:** Mississippian, Serpukhovian, Chelicerata, Arthropoda, horseshoe crab, marine.

THE Carboniferous Bear Gulch Limestone of Montana, USA, is perhaps best known for its diverse chondrichthyan fauna (Lund and Poplin 1999) but it also yields a rich invertebrate fauna of worms, crustaceans and chelicerates (e.g. Schram and Horner 1978; Schram 1979a, b). To date, species of two genera of xiphosurids have been found at Bear Gulch: *Paleolimulus longispinus* and *Euproops* sp. (Schram 1979a). *P. longispinus* is known from over 15 specimens, while *Euproops* is only known from one identifiable specimen and two possible fragments (Schram 1979a). Xiphosurans are therefore rare elements of the Bear Gulch biota. Here we describe a new xiphosuran from this locality. It is the first synziphosurine from the Bear Gulch Limestone and extends the known range of synziphosurines from the Lower Silurian (Llandovery) to the Lower Carboniferous (Namurian).

## GEOLOGICAL SETTING AND ASSOCIATED FAUNA

The Bear Gulch Limestone is Namurian E<sub>2</sub>b in age (corresponding to the Late Mississippian or Serpukhovian of American usage) and occurs as one of a series of lenses within the Heath Formation of central Montana (Grogan and Lund 2002). The fossiliferous beds crop out over approximately 85 km<sup>2</sup> with a maximum thickness of

30 m at the north-eastern margin (Grogan and Lund 2002) and have been described as lithographic limestones, or Plattenkalken, similar in nature to those of Solnhofen, Germany (Feldman *et al.* 1994). The beds were deposited during a marine transgression when episodic seismic activity, resulting in subsidence of the basin and subsequent infilling, produced lenses of carbonate material (Feldman *et al.* 1994; Grogan and Lund 2002, fig. 4). The sediments are composed of fine lime silts and clays and accumulated as rhythmically alternating thick, dark coloured, massive to graded beds and thin, lighter coloured laminar beds with a higher clay content (Hagadorn 2002). This bedding structure, often described as ‘Flinz and Fäule’, is typified by that described at Solnhofen (Barthel *et al.* 1990). The thicker limestone units (Flinz) show evidence of deep-sea turbidity currents, while the thinner laminar beds (Fäule) were deposited during quieter, seasonal currents (Feldman *et al.* 1994).

Careful and in-depth sampling has revealed a diverse and exceptionally preserved fauna at Bear Gulch (Grogan and Lund 2002). Arthropods are represented by a variety of shrimps (Schram and Horner 1978), two genera of phyllocarids, a concavicularid, xiphosurans and ostracodes. Gastropods are quite rare but several bivalve genera are present. Coiled cephalopods are abundant and often show crop contents, while straight cephalopods are present in smaller numbers. Polychaetes, and other worms, are frequently

found and may preserve soft parts (Schram 1979b). The cnidarian *Sphenothallus* (Van Iten *et al.* 1992; Peng *et al.* 2005) is fairly common and sponges are moderately abundant, with *Arboraspongia* forming dense thickets in some parts of the basin (Rigby 1979). Phosphatic and calcareous brachiopods (Lutz-Garihan 1979), a sea salp (Tunicata: Thaliacea) and the enigmatic *Typhloesus* (Conway Morris 1990) are also present. The vertebrate diversity is dominated by Chondrichthyes including rare flying sharks (Iniopterygii) (Lund and Grogan 2005). Other fish include fusiform and deep-bodied paleoniscoids, coelacanth and a lamprey (Lund and Lund 1985; Lund and Poplin 1999). Plants are limited to rafted or blown-in land forms and a variety of algae including filamentous types, which are widespread in some sections of the limestone.

The Bear Gulch Limestone was deposited in a tropical marine bay and is characterized by up to five facies (Grogan and Lund 2002). The new specimens described here were found within the filamentous algal facies (R. Lund, pers. comm. 2005), which is typified by abundant algal filaments, small productid brachiopods and *Sphenothallus* (Grogan and Lund 2002).

## MATERIAL AND METHODS

Specimens are deposited at the Carnegie Museum, Pittsburgh, under catalogue numbers CM54200 (holotype, Text-fig. 1A–B) and CM54201 (paratype, Text-fig. 1C–D). An additional specimen (undescribed) is in the private study collection of the authors (SM). Counterparts of the two described specimens were not recovered. Photographs were taken with a Nikon D1H digital SLR and camera lucida drawings were prepared using a WILD stereomicroscope with a drawing tube attachment.

Systematic terminology follows Anderson and Selden (1997). While the term ‘synziphosurine’ does not define a natural group, it is used here to distinguish between the Xiphosurida and their stem-group that lack a thoracetron (Anderson and Selden 1997).

*Abbreviations.* ap, appendage; axn, axial node; cl, cardiac lobe; cm, carapace margin; f, furrow; mr, median ridge; opr, ophthalmic ridge; pcm, posterior carapace margin; r, ridge; tsp, tail spine; w, wrinkle; numbers 1–9 indicate opisthosomal segments.

## PRESERVATION

The quality of fossil preservation within Bear Gulch sediments is extremely variable. It ranges from disarticulated elements and scales to complete preservation of cartilaginous, soft-bodied and lightly sclerotized animals (Grogan and Lund 2002). In some vertebrates, skin outlines, pig-

mentation patterns, reproductive organs, internal organs and traces of the circulatory system have been reported (Grogan and Lund 1995). Invertebrates are preserved as external and internal moulds, casts, organic remains and as colour differences (Hagadorn 2002); soft-tissue preservation is common and in some cases the jaw apparatus, denticles, parapodia, acicula and gut contents of polychaetes survive (Hagadorn 2002).

Both new specimens described here are preserved on individual slabs and are not immediately associated with any other plants or animals, but CM54200 has a specimen of the branching sponge *Arborispongia* on the underside of the slab. CM54201 is preserved in an orange-tan limestone while CM54200 is in a light grey limestone. Both specimens are preserved as dorsoventrally flattened thin films that are slightly darker than the surrounding matrix. CM54200 is an internal mould with only a small amount of relief in the carapace whereas CM54201 is an external mould that preserves slightly more relief; the opisthosoma and tail spine in both specimens show little relief. Both specimens are complete apart from lacking the full length of the tail spine.

## SYSTEMATIC PALAEOLOGY

Phylum CHELICERATA Heymons, 1901

Class XIPHOSURA Latreille, 1802

Genus *Anderella* gen. nov.

*Derivation of name.* After Lyall Anderson, in recognition of his contribution to the systematic description of fossil xiphosuran taxa and their phylogenetic relationships.

*Type and only known species.* *Anderella parva* sp. nov.

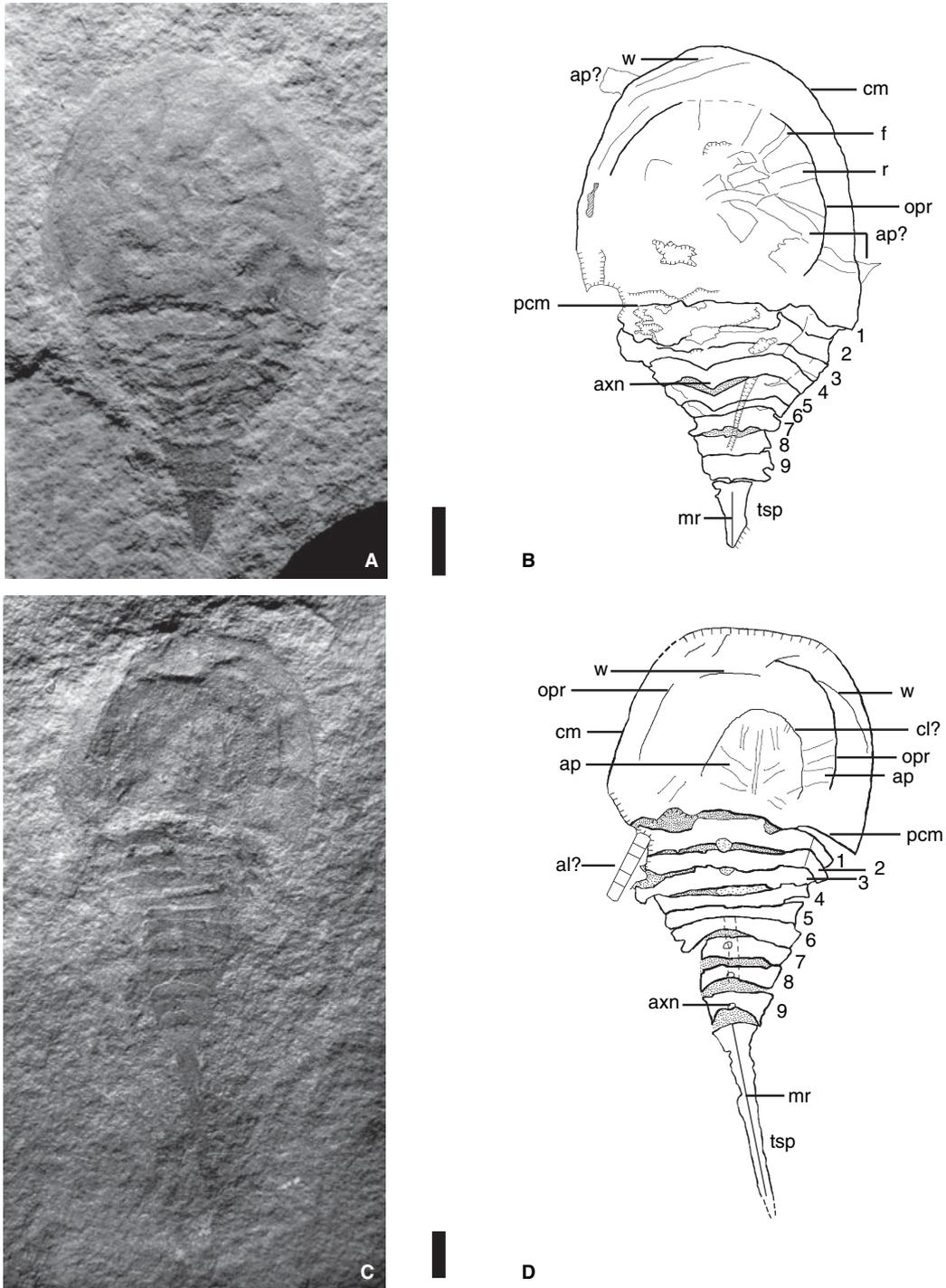
*Diagnosis.* Semi-oval carapace with pointed genal regions lacking true genal spines; nine freely articulating opisthosomal segments, six preabdominal and three postabdominal; first segment not reduced to a microtergite and second not hypertrophied; preabdominal segments with blunt pleura, postabdominal segments lacking pleura; axial nodes on all opisthosomal segments; tail spine styli-form with median ridge.

*Remarks.* *Anderella* is not assigned to a family here pending a revision of the synziphosurines.

*Anderella parva* sp. nov.

Text-figure 1; Table 1

*Derivation of name.* Latin, *parva*, young.



**TEXT-FIG. 1.** *Anderella parva* gen. et sp. nov. A–B, CM54200 (holotype), internal mould: photograph and camera lucida drawing. C–D, CM54201 (paratype), external mould: photograph and camera lucida drawing. Scale bars represent 5 mm.

*Types.* CM54200 (holotype), CM54201 (paratype).

*Occurrence.* Carboniferous, Namurian E2b (= Serpukovian), Bear Gulch Limestone, central Montana, USA.

*Diagnosis.* As for genus.

*Description.* The carapace is approximately 55 per cent of the total length (sag.) of the organism, excluding the tail spine. It is

**TABLE 1.** Measurements of holotype (h) and paratype (in mm).

Catalogue no.	Carapace length	Maximum carapace width (tr.)	Total length, excluding tail spine	Maximum preserved tail spine length	Width of ninth opisthosomal segment
CM54200 (h)	19	21	33	5	4
CM54201	17	22	35	18	5

semi-oval, lacks a marginal ridge and becomes acute at the genal region, but lacks true genal spines. It is most completely preserved in the holotype. The carapace of the paratype appears to be less rounded anteriorly because the matrix obscures this region. The ophthalmic ridge runs parallel to the margin of the carapace, becoming less pronounced anteriorly. No evidence for eyes or lensar structures can be found associated with the ophthalmic ridge. The topography of the cardiac lobe region is unclear although a region that may correspond to the edge of the cardiac lobe is present in the paratype (Text-fig. 1D, cl?). The interophthalmic area has a pattern of ridges and furrows; five distinct ridges are present on the right side of the holotype (Text-fig. 1B, r). Traces of appendages, indicated by raised and/or darker coloured regions, are also present but their morphology is unclear. In some cases possible segment boundaries can be determined (Text-fig. 1B). On the upper left and lower right side of the holotype a possible appendage can be seen to extend beyond the carapace margin (Text-fig. 1B, ap?). The posterior margin of the carapace is straight.

Nine opisthosomal segments are present, divided into six in the preabdomen and three in the postabdomen. Segments are discrete and separated by matrix. Preabdominal segments are divided into wide (tr.) axial regions bearing axial nodes and pleura. Pleura are rectangular and have blunt terminations. The first segment is not a microtergite but is almost as wide as the posterior margin of the carapace and the following opisthosomal segments narrow in width posteriorly towards the postabdomen. Postabdominal segments lack pleura and are narrower (tr.), yet longer (sag.) than those of the preabdomen. The postabdomen is best preserved in the paratype where it occupies 45 per cent of the total length (sag.) of the opisthosoma.

The original length of the tail spine is not exposed in the holotype or preserved in the paratype, but it is clear from the latter that it is long and styliform (Text-fig. 1, tsp). A pronounced median ridge on the tail spine is evident in both specimens.

*Remarks.* The disarticulated nature of the opisthosomal segments is a function of the lack of fusion together in life. As in other synziphosurine fossils, the relatively thin arthrodial membrane decomposed more rapidly than the tergites leading to separation of the elements and introduction of sediment between them. Unfused opisthosomal tergites are a characteristic of the synziphosurines, in contrast to the development of a thoracetrone (fused tergites) in the Xiphosurida (Anderson and Selden 1997).

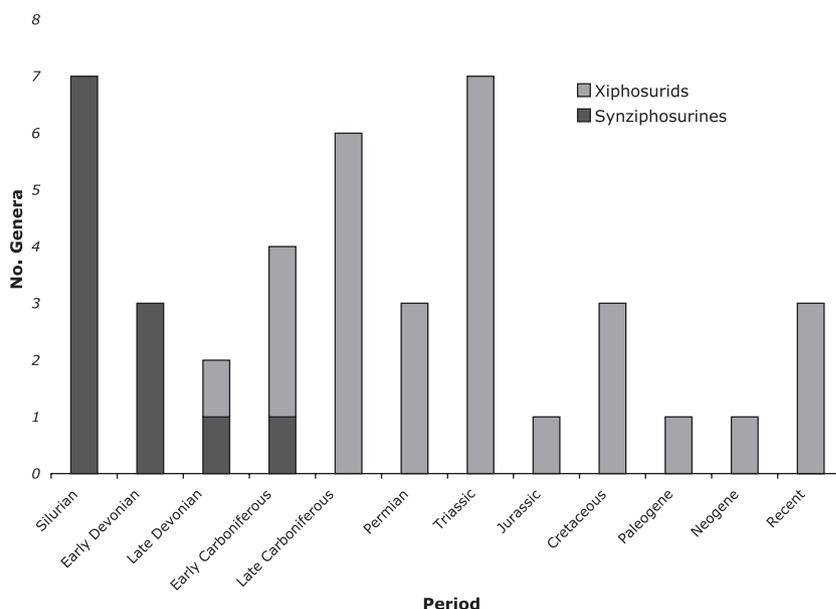
Synziphosurine relationships are often difficult to resolve because of the incomplete nature of many of the fossils and the rarity of specimens. The frequent compres-

sion of their non-mineralized cuticle when preserved also makes it difficult to identify characters such as the presence or absence of eyes, the topography of the carapace and the morphology of opisthosomal segments. Exceptions include *Weinbergina opitzi* Richter and Richter, 1929 from the Hunsrück Slate of Germany, which preserves fine details of the appendages in pyrite (Stürmer and Bergström 1981; Moore *et al.* 2005a) and both *Legrandella lombardii* Eldredge, 1974 from Bolivia and *Bunodes lunula* Eichwald, 1854 from Estonia, which are preserved in three dimensions.

The most basal synziphosurines have 10 or 11 freely articulating opisthosomal segments while *A. parva* resembles the most derived synziphosurine, *Kasibelinurus* Pickett, 1993, in having nine (Anderson and Selden 1997). *Kasibelinurus* is the only known Late Devonian synziphosurine since *Protolimulus eriensis* Packard, 1886 was shown to be a trace fossil rather than a body fossil (Babcock *et al.* 1995). *Kasibelinurus* resembles the Carboniferous taxa *Bellinurus* and *Euproops* in having, among other characters, an M-shaped configuration of the ophthalmic ridge and a carapace that is much wider (tr.) than it is long (sag.). These characters are absent in *A. parva* and in this respect it has a less derived morphology than *Kasibelinurus*. The wide axial regions of the opisthosomal segments, rectangular pleura and distinct division into a pre- and postabdomen bear most resemblance to *Venustus waukeshaensis* Moore, in Moore *et al.* 2005b, which is known from the Lower Silurian (Llandovery) Waukesha Lagerstätte, Wisconsin, USA. *Anderella parva* lacks a hypertrophied second opisthosomal segment that is a characteristic of the bunodids (*B. lunula*, *Bembicosoma pomphicus*, *Limuloides limuloides* and *Pasternakevia podolica*) and differs from the pseudoniscids (*Cyamocephalus loganensis* and *Pseudoniscus aculeatus*) in lacking a procurved posterior carapace margin and acutely pointed pleura. The presence of a clear division between pre- and postabdomen in *A. parva* is unlike that of the pseudoniscids and *W. opitzi*.

In summary, apart from the presence of nine opisthosomal segments and axial nodes in *A. parva* this taxon is similar to the oldest-known synziphosurine, *V. waukeshaensis*. However, the number of opisthosomal segments has previously been a key taxonomic feature of synziphosurines (Anderson 1996) and in this respect *Kasibelinurus* is the most similar. Pending a phylogenetic analysis of the

**TEXT-FIG. 2.** The number of genera of Xiphosura known from each time period. Subdivisions are shown for the Devonian and Carboniferous to improve resolution in the major faunal shift. No xiphosurids are known from the Silurian and Early Devonian but there was a major change during the Late Devonian–Early Carboniferous in the dominance of xiphosurids over synziphosurines. *Anderella parva* is the only synziphosurine known from the Carboniferous and none has been recorded from younger sediments.



Xiphosura, a family-level assignment of *Anderella* is not presented here.

## DISCUSSION

More genera of xiphosurans are known from the Carboniferous Period than from any other time in Earth history (nine; Text-fig. 2) and it was a key period in their evolution. The earliest xiphosuran with a thoracetron (= Xiphosurida) is *Bellinuroopsis rossicus* Chernyshev, 1933 from the Famennian of Russia (Anderson and Selden 1997), but by the Carboniferous the xiphosurids had become dominant and the synziphosurines are only represented by *A. parva* (Text-fig. 2). During the Early Carboniferous two groups of xiphosurids emerged, the Bellinurina Zittel and Eastman, 1913 and the Limulina Richter and Richter, 1929 (Anderson and Selden 1997). The latter group gave rise to the extant genera *Limulus*, *Carcinoscorpius* and *Tachypleus* (Anderson and Selden 1997).

There was also a shift in habitat preference at the end of the Devonian. Synziphosurines are found almost exclusively in marginal marine sediments, while the xiphosurids are often found in sediments deposited in deltaic or brackish environments. There is evidence from the Upper Carboniferous, Mazon Creek biota of Illinois, USA, that the Limulina and Bellinurina occurred preferentially in different habitats. While the marine Essex biota yields specimens of *Paleolimulus signatus* (Limulina) and rarely *Euproops*, the euproopids (Bellinurina) are the dominant group in the brackish–freshwater Braidwood biota (Schram 1979c). The Bear Gulch Limestone has been des-

cribed as forming a faunal continuum with the Essex biota (Schram 1979c). At first glance the presence of *Paleolimulus* in both the Bear Gulch and the Essex biota of Mazon Creek localities seems to support this suggestion. However, restudy of *Paleolimulus longispinus* by Anderson (1996) showed that the presence of a distinct opercular segment and six long, fixed spines and five short, moveable spines align these specimens with *Rolfeia* Waterston, 1985 rather than *Paleolimulus*. *Rolfeia* is known from the Tournaisian of Glencartholm, Scotland, and occurs in a marine–brackish depositional environment (Waterston 1985). The discovery of the youngest-known synziphosurine in marine sediments at a time when xiphosurans were diversifying into brackish waters may be significant. This may indicate the inability of synziphosurines to adapt to brackish–freshwater conditions.

The Bear Gulch Limestone contains an unusually diverse xiphosuran biota. Comparable xiphosuran diversity occurs in the Mazon Creek biota, deposits of similar age (Westphalian) in England (Anderson 1994; Anderson et al. 1999), and the Middle Triassic Montral-Alcover biota, Spain (Vía 1987). However, most xiphosuran-bearing localities yield only one or two genera. Bear Gulch is also the only locality where a synziphosurine occurs alongside xiphosurids.

The similarity of *A. parva* to *V. waukeshaensis* is surprising considering the c. 120 myr time gap between them. The discovery of a Carboniferous synziphosurine that is little changed from a Silurian genus may be a reflection of a slow rate of evolution in xiphosurans. Extant xiphosurans are often described as ‘living fossils’, showing morphological conservatism since at least the Late Jurassic (Fisher 1984). An explanation for the

absence of other examples of Carboniferous synziphosurines could be a reduction in their abundance to below the detection limit of the fossil record after the Late Devonian biotic crisis (Wignall and Benton 1999); they would only reappear when numbers had recovered sufficiently. This is the pattern shown by Lazarus taxa (Flessa and Jablonski 1983), but in this case the term does not strictly apply because taxonomic affiliation is unclear. Any discussion of xiphosuran abundance must contain the caveat that they are rare as fossils and their non-biomineralized cuticle requires special preservational conditions. The apparent absence of *Anderella*-like forms between the Emsian and Namurian (a period of c. 80 myr) is also likely to be a result of taphonomic control.

*Acknowledgements.* We thank A. Kollar at the Carnegie Museum, Pennsylvania, for access to specimens and arranging the cataloguing of new specimens. R. Lund provided valuable information and critical feedback. O. E. Tetlie is thanked for his useful remarks on the manuscript. J. Dunlop and one anonymous referee are thanked for their constructive reviews of the manuscript. Funding was provided by NSF EAR-0518976, NASA Astrobiology NNG4GMYIG and a Self Faculty Scholar Award to BSL.

## REFERENCES

- ANDERSON, L. I. 1994. Xiphosurans from the Westphalian D of the Radstock Basin, Somerset Coalfield and Mazon Creek, Illinois. *Proceedings of the Geologists' Association*, **105**, 265–275.
- 1996. Taphonomy and taxonomy of Palaeozoic Xiphosura. Unpublished PhD thesis, University of Manchester, 413 pp.
- DUNLOP, J. A., EAGAR, R. M. C., HORROCKS, C. A. and WILSON, H. M. 1999. Soft-bodied fossils from the roof shales of the Wigan Four Foot coal seam, Westhoughton, Lancashire, UK. *Geological Magazine*, **135**, 321–329.
- and SELDEN, P. A. 1997. Opisthosomal fusion and phylogeny of Palaeozoic Xiphosura. *Lethaia*, **30**, 19–31.
- BABCOCK, L. E., WEGWEISER, D., WEGWEISER, A. E., STANLEY, T. M. and MCKENZIE, S. C. 1995. Horseshoe crabs and their trace fossils from the Devonian of Pennsylvania. *Pennsylvania Geology*, **26**, 2–7.
- BARTHEL, K. W., SWINBURNE, N. H. M. and CONWAY MORRIS, S. 1990. *Solnhofen, a study in Mesozoic palaeontology*. Cambridge University Press, Cambridge, 246 pp.
- CHERNYSHEV, B. I. 1933. Arthropods from the Urals and other regions of the U.S.S.R. *Sbornik Tsentral'nogo Nauchno-Issledovatel'skogo Geologorazvedochnogo Instituta. Paleontologiya i Stratigrafiya*, **1**, 15–24. [In Russian].
- CONWAY MORRIS, S. 1990. *Typhloesus wellsi* (Melton and Scott, 1973), a bizarre metazoan from the Carboniferous of Montana, USA. *Philosophical Transactions of the Royal Society of London B*, **327**, 595–624.
- EICHWALD, E. 1854. Die Grauwackenschichten von Live-und Esthland. *Bulletin de la Société Impériale des Naturalistes de Moscou*, **27**, 1–211.
- ELDREDGE, N. 1974. Revision of the suborder Synziphosurina (Chelicerata: Merostomata), with remarks on merostome phylogeny. *American Museum Novitates*, **2543**, 1–41.
- FELDMAN, H., LUND, R., MAPLES, C. and ARCHER, A. 1994. Origin of the Bear Gulch beds (Namurian, Montana, USA). *Geobios, Mémoire Spécial*, **16**, 283–291.
- FISHER, D. C. 1984. The Xiphosurida: archetypes of bradytely? 106–212. In ELDREDGE, N. and STANLEY, S. M. (eds). *Living fossils*. Springer-Verlag, Berlin, 291 pp.
- FLESSA, K. W. and JABLONSKI, D. 1983. Extinction is here to stay. *Paleobiology*, **9**, 315–321.
- GROGAN, E. D. 2002. The geological and biological environment of the Bear Gulch Limestone (Mississippian of Montana, USA) and a model for its deposition. *Geodiversitas*, **24**, 295–315.
- and LUND, R. 1995. Pigment patterns, soft anatomy and relationships of Bear Gulch Chondrichthyes. *Geobios, Mémoire Spécial*, **19**, 145–146.
- HAGADORN, J. W. 2002. Bear Gulch: an exceptional Upper Carboniferous Plattenkalk. 167–183. In BOTTJER, D. J. and BAMBACH, R. K. (eds). *Exceptional fossil preservation: a unique view on the evolution of marine life*. Columbia University Press, New York, NY, 424 pp.
- HEYMONS, R. 1901. Die Entwicklungsgeschichte der Scolopender. *Zoologica*, **13**, 244 pp.
- LATREILLE, P. A. 1802. *Histoire naturelle, générale et particulière, des Crustacés et des Insectes*. Dufart, Paris, 467 pp.
- LUND, R. and GROGAN, E. D. 2005. Fossil fishes of Bear Gulch website: [http://www.sju.edu/research/bear\\_gulch/index.php](http://www.sju.edu/research/bear_gulch/index.php).
- and LUND, W. L. 1985. Coelacanth from the Bear Gulch Limestone (Namurian) of Montana and the evolution of the Coelacanthiformes. *Bulletin of the Carnegie Museum of Natural History*, **25**, 1–74.
- and POPLIN, C. 1999. Fish diversity of the Bear Gulch Limestone, Namurian, Lower Carboniferous of Montana, USA. *Geobios*, **32**, 285–295.
- LUTZ-GARIHAN, A. B. 1979. Brachiopods from the Upper Mississippian Bear Gulch Limestone of Montana. *Compte Rendu, Neuvième Congrès International de Stratigraphie et de Géologie du Carbonifère*, **5**, 457–467.
- MOORE, R. A., BRIGGS, D. E. G. and BARTELS, C. 2005a. A new specimen of *Weinbergina opitzi* (Chelicerata: Xiphosura) from the Lower Devonian Hunsrück Slate, Germany. *Paläontologische Zeitschrift*, **79**, 399–408.
- — BRADDY, S. J., ANDERSON, L. I., MIKULIC, D. G. and KLUESSENDORF, J. 2005b. A new synziphosurine (Chelicerata: Xiphosura) from the Late Llandovery Waukesha Lagerstätte, Wisconsin, USA. *Journal of Paleontology*, **79**, 242–250.
- PACKARD, A. S. 1886. On the Carboniferous xiphosurous fauna of North America. *Memoirs of the National Academy of Sciences*, **3**, 143–157.
- PENG, J., BABCOCK, L. E., ZHAO, Y. L., WANG, P. L. and YANG, R. J. 2005. Cambrian *Sphenothallus* from Gui-

- zhou Province, China: early sessile predators. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **220**, 119–127.
- PICKETT, J. W. 1993. A Late Devonian xiphosuran from near Parkes, New South Wales. *Memoirs of the Association of Australian Palaeontologists*, **15**, 279–287.
- RICHTER, R. and RICHTER, E. 1929. *Weinbergina opitzi*, n.g., n.sp. ein Schwerträger (Merost., Xiphos) aus dem Devon (Rheinland). *Senckenbergiana*, **11**, 193–209.
- RIGBY, J. K. 1979. The sponge fauna from the Upper Mississippian Bear Gulch Limestone of central Montana. *Compte Rendu, Neuvième Congrès International de Stratigraphie et de Géologie du Carbonifère*, **5**, 443–456.
- SCHRAM, F. R. 1979a. Limulines of the Mississippian Bear Gulch Limestone of central Montana, U.S.A. *Transactions of the San Diego Society of Natural History*, **19**, 67–74.
- 1979b. Worms of the Mississippian Bear Gulch Limestone of Central Montana. *Transactions of the San Diego Society of Natural History*, **19**, 107–120.
- 1979c. The Mazon Creek biotas in the context of a Carboniferous faunal continuum. 159–190. In NITECKI, M. H. (ed.). *Mazon Creek fossils*. Academic Press, New York, NY, 581 pp.
- and HORNER, J. R. 1978. Crustacea of the Mississippian Bear Gulch Limestone of central Montana. *Journal of Paleontology*, **52**, 394–406.
- STÜRMER, W. and BERGSTRÖM, J. 1981. *Weinbergina*, a xiphosuran arthropod from the Devonian Hunsrück Slate. *Paläontologische Zeitschrift*, **55**, 237–255.
- VAN ITEN, H., COX, R. S. and MAPES, R. H. 1992. New data on the morphology of *Sphenothallus* Hall: implications for its affinities. *Lethaia*, **25**, 135–144.
- VÍA, L. 1987. Arthropodos fosiles Triasicos de Alcover-Montral. II. Limulidos. *Cuadernos Geología Ibérica*, **11**, 281–282.
- WATERSTON, C. D. 1985. Chelicerata from the Dinantian of Foulden, Berwickshire, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **76**, 25–33.
- WIGNALL, P. B. and BENTON, M. J. 1999. Lazarus taxa and fossil abundance at times of biotic crisis. *Journal of the Geological Society, London*, **156**, 453–456.
- ZITTEL, K. A. VON and EASTMAN, C. R. 1913. *Textbook of palaeontology*. Second edition. Macmillan, London, 839 pp.