Paleolimulus, an early limuline (Xiphosurida), from Pennsylvanian–Permian Lagerstätten of Kansas and taphonomic comparison with modern Limulus

LOREN E. BABCOCK, DANIEL F. MERRIAM AND RONALD R. WEST

LETHAIA

Horseshoe crabs, or xiphosurids, are a small clade of chelicerate arthropods that have a stratigraphic record ranging from the Paleozoic to the present. Approximately 30 valid genera and approximately 50 species of these animals are known, of which four species, belonging to three genera, are extant.

The purposes of this paper are: (1) to clarify the concept of the type species of Paleolimulus from upper Paleozoic rocks of Kansas (Figs 1, 2); and (2) to provide information on taphonomic conditions leading to the exceptional preservation of specimens in those rocks. Paleolimulus has been recognized (Bergström 1975; Störmer 1952, 1955; Fisher 1982, 1984; Waterston 1985; Selden & Siveter 1987; Anderson & Horrocks 1995; Anderson & Selden 1997) as one of the earliest limulines, or so-called modern horseshoe crabs. A putative Paleolimulus from Wales indicates that this genus dates from the Middle Pennsylvanian (or Upper Carboniferous; Westphalian B; Bergström, 1975; Fisher 1984; Waterston 1985; Anderson & Horrocks 1995). Other early examples of limulines are Xaniopyramis from the upper Mississippian (or Lower Carboniferous; Namurian) of England (Siveter & Selden 1987), and Valloisella from the middle Pennsylvanian (or Upper Carboniferous; Westphalian B) of England (Dix & Jones 1932; Anderson & Horrocks 1995). Understanding the evolution of limulines depends on elucidation of the relationships among species attributed to Paleolimulus and other early forms. In this context, we provide new information on the type species of Paleolimulus that will help facilitate comparison with early species.

The second important aspect of this work is that it represents a further step in our understanding of the taphonomic conditions under which non-mineralized arthropods are preserved as fossils. Lack of a mineralized cuticle, possession of a rather generalized arthropod morphology, and occurrence of morphologically similar living and fossil representatives, makes these xiphosurids excellent subjects for understanding taphonomic processes affecting various non-mineralized arthropods. Actualistic experiments can

be conducted on living representatives and applied to fossil representatives that seem to have similar taphonomic histories. Results of such experiments, as shown here, can have important implications for the morphologic and even systematic interpretation of non-mineralized arthropods from Palaeozoic Lagerstätten. In addition to demonstrating that some non-mineralized arthropod exoskeletons are resistant to preburial disarticulation, these experiments demonstrate that distortion without breakage of the exoskeleton is related to pliability of that exoskeleton after death or moulting. Specimens showing similar distortion have been illustrated from most Palaeozoic Konservat-Lagerstätten representing aquatic environments (e.g. see Schram 1979; Conway Morris et al. 1982; Baird et al. 1985; Mikulic et al. 1985; Whittington 1985; Hou & Bergström 1990; Robison 1990; Babcock & Chang 1997).

Repositories. - Fossil specimens cited herein are deposited in the following institutions: Peabody Museum of Natural History, Yale University, New Haven, Connecticut (YPM); U.S. National Museum of Natural History, Washington, D.C. (USNM); University of Kansas Natural History Museum (Division of Invertebrate Paleontology), Lawrence, Kansas (KUMIP); and Orton Geological Museum, The Ohio State University, Columbus, Ohio (OSU).

Late Palaeozoic xiphosurids from Kansas

Six genera and eight species of real or supposed xiphosurids were named from specimens collected from Permian rocks of eastern Kansas (Beecher 1904; Dunbar 1923; Tasch 1961, 1963, 1964; Babcock 1990). This number is mitigated, however, by the subsequent reassignment of five genera and five species described by Tasch (1961, 1963, 1964) from the Wellington Formation (Middle Permian) to other arthropod groups (Bergström 1975). One species described by Tasch (1961) from the Wellington Formation at Annelly, Harvey County, Pringlia leonardensis, appears from published illustrations (Tasch 1961, pl. 98, figs. 4a, b) to be a genuine xiphosurid.

The valid horseshoe crab genus Paleolimulus Dunbar, 1923, was described using P. avitus Dunbar, 1923 (Fig. 3D–G), from the Wellington Shale (Middle Permian) at 'Insect Hill', near Elmo, Dickinson County, as the type species. Prestwichia signata Beecher, 1904 (Fig. 3A–C), which was previously described from the Fort Riley Limestone Member of the Barneston Limestone (Lower Permian) near Stockdale, Riley County, was transferred to Paleolimus by Dunbar (1923). As revised herein, P. signatus is a senior synonym of P. avitus.
In addition to taxa named from Kansas, one euproooid xiphosurid, *Euproops danae* (Meek & Worthen) also occurs in the state. A studied specimen of this species (YPM 35153) was collected from a Mazon Creek-type assemblage (Braidwood biota) in the Lawrence Formation (Douglas Group; Upper Pennsylvanian) near Lawrence, Douglas County.

Other evidence of the existence of xiphosurids in Kansas is in the form of trace fossils. Bandel (1967) reported trails putatively produced by xiphosurids (= *Kouphichnium*) from the Tongonoxie Sandstone Member of the Stranger Formation (Douglas Group; Upper Pennsylvanian), near Ottawa, Franklin County. Here, we illustrate an indistinct, bilobed trace fossil (Fig. 4I), one of many at locality 4 (Figs 1, 2). The traces are inferred to have been produced by xiphosurids (presumably *P. signatus*), although they do not exactly conform in shape to either *Kouphichnium* or *Protolimulus* traces described from other localities and ages (e.g. Caster 1938; Malz 1964; Hardy 1970; Miller 1982; Chisholm 1985; Babcock et al. 1995). The bilobed ploughing traces are similar to bilobed traces produced by modern *Limulus* in wet, soupy mud (Fig. 5). Of particular note is the general lack of distinct scratch marks left by the appendages in both the ancient and modern traces. Indistinct impressions may be the result of burrowing into a relatively fluid-rich sediment.

Geographic and stratigraphic occurrences

*Paleolimulus* is known from four localities in Kansas (Fig. 1). A generalized stratigraphic column, showing productive intervals, is given in Fig. 2. Additional stratigraphic information concerning the units from which *P. signatus* has been collected was provided by Zeller (1968).

Locality 1. – Fort Riley Limestone Member of the Barneston Limestone (Chase Group; Lower Permian); from about 4.8 km (3 miles) west of Stockdale, Riley County (Beecher 1904). This is the type locality for *P. signatus* (USNM 483405; casts YPM 26319, 26319A). The location of this site relative to present-day geography is uncertain because Stockdale no longer exists. According to an early gazetteer (Gannett 1898), Stockdale was a post office and station on the Blue Valley and Manhattan Railway in Grant Township, Riley County, altitude 340 m. The most likely locality is west of the Stockdale Recreation Area (near Tuttle Creek Lake) in the south half of sec. 33, T. 8 S., R. 7 E., Riley County (Oldsburg SW, Kansas 7.5’ topographic quadrangle, U.S. Geological Survey 1964, photorevised 1978).

Locality 2. – Crouse Limestone (Council Grove Group;
Lower Permian); from Carnahan Creek Recreation Area on the east side of Tuttle Creek Lake, west side of sec. 23, T. 8 S., R. 7 E., Pottawatomie County; Tuttle Creek Dam, Kansas 7.5’ topographic quadrangle (U.S. Geological Survey 1964, photorevised 1978). One specimen, USNM 484412, was collected from this site.

**Locality 3.** Insect Hill Konservat-Lagerstätte. Elmo
Depositional environments and xiphosurid habitats. – Among the localities yielding *Paleolimulus* in Kansas, only localities 3 and 4 have yielded multiple specimens, so it is for these localities that the interpretation of depositional environments is most meaningful for understanding the habitat preferences of *Paleolimulus*. The insect beds of the Wellington Formation (locality 3) were evidently deposited in a lacustrine setting (Dunbar 1923; Brooks 1957; Tasch 1958, 1961, 1963); adjacent rocks, which are rich in conchostracan crustaceans (Tasch 1958, 1961, 1963), represent freshwater lake or brackish water lagoonal deposits (Dunbar 1923; Brooks 1957).

Xiphosurids from the Pony Creek Shale (locality 4) occur within a succession of strata that has been interpreted (West & Matsumoto 1989) to represent a marine-to-non-marine transition. Our observations of paired, mm-scale, light-dark lamination in the Pony Creek Shale Member at the site suggest tidally influenced sedimentation (see Feldman et al. 1993) for the beds yielding *Paleolimulus* and the xiphosurid trace fossils. The Pony Creek Shale at this locality is interpreted to have been either an estuary or tidal flat. Walking or burrowing traces of xiphosurids, in particular, are usually associated with tidal-flat lithofacies (Caster 1938; Brooks 1957; Miller 1982; Babcock et al. 1995), although they are not restricted to them.

An estuarine, tidal-flat, or lacustrine habitat for *P. signatus* is compatible with the general range of habitats expected of xiphosurids (e.g. Rudloe 1979; Miller 1982; Pickett 1984; Fisher 1984; Baird et al. 1985; Chisholm 1985; Boucot 1990; Babcock et al. 1995). However, paleolimulids from Carboniferous coal swamp settings have been inferred to have been distinctly marine in habitat (Schram 1979; Fisher 1984), compared to euryopoids, which are interpreted as nearer the brackish water-freshwater-partly terrestrial end of the spectrum of environments represented in coal swamps (Fisher 1984). Permian paleolimulids similarly were inferred (Fisher 1984) to have tended toward marine habitats. Oddly, other marine-influenced Pennsylvanian or Permian Konservat-Lagerstätten (Mapes & Mapes 1988; Maples & Schulze 1988) in the same general region of the USA have not yielded *Paleolimulus*.

Preservational circumstances and taphonomy

Xiphosurid diversity and preservation. – The fossil record of xiphosurids, although it extends to the early Paleozoic, is rather meagre (Fisher 1984). Xiphosurids are one of the least diverse groups of arthropods known from fossil remains, and they seem to have had a genuine low diversity of species through time (see Fisher 1984). The accepted diversity of present-day xiphosurids world-wide is four species, *Carcinoscorpius rotundicauda*, *Limulus polyphemus*, *Tachypleus gigas*, and *T. tridentatus* (Sekiguchi & Sugita 1980; Fisher 1984). A fifth described species, *T. hoeveni* (Pocock 1902) has not been recognized by most workers (Waterman 1958; Fisher 1984). This is a marked departure from the diversity of most other arthropod groups, which together have a present-day diversity numbering in the millions of species, and which account for more than 75% of living animal species (Hickman et al. 1982).

The low observed diversity of ancient xiphosurids probably is enhanced by two additional factors. One factor is the lack of a mineralized exoskeleton, which limits their preservation potential. The second factor is the role of habitat in limiting the preservation of taxa. Marginal-marine through brackish water, freshwater, and partly terrestrial settings, which represent the depositional environments where most fossil xiphosurid remains occur (Fisher 1979; Pickett 1984), generally are not well represented in the stratigraphic record.

Despite the rather sporadic stratigraphic occurrence of horseshoe crabs, specimens from some localities are so well preserved that we can obtain from them an excellent morphological understanding of not just the...
Fig. 4. A–H. *Paleolimulus signatus* (Beecher) in different stages of disarticulation. A. External mould of specimen in stage 1 of disarticulation, retaining appendages but lacking gills; note the split along the anterolateral margin of the prosoma; locality 3; YPM 16156; ×4. B. Internal mould of specimen apparently buried before reaching stage 1 of disarticulation, preserved in a small limestone concretion; the telson and the posterior part of the posterior opisthosomal sclerite were outside the concretion and not preserved or collected; note the book gills attached to the opisthosoma; locality 4; USNM 465528; ×1.25. C. Internal mould of specimen in stage 2 of disarticulation, in which the book gills have been lost and most of the appendages have been broken along joints; the anterior part of the telson is attached to the posterior opisthosomal sclerite but most of the telson was not collected; locality 4; USNM 465528; ×1.25. D. Internal mould of specimen in stage 3 of disarticulation, in which the telson has been lost; little remains of the appendages; note loose folding of the exoskeleton, especially along the opisthosoma; also note the joint between anterior and posterior abdominal sclerites (arrow); locality 4; USNM 484408; ×1. E. External mould of specimen in stage 3 of disarticulation (the unfigured part of the specimen, which preserves only the most posterior part of the specimen, demonstrates that the telson was disarticulated); locality 4; USNM 484409; ×1. F. Internal mould of separate prosoma in stage 4 of disarticulation; note strong wrinkling of the exoskeleton; locality 4; USNM 484410; ×1. G. Internal mould of separate prosoma in stage 4 of disarticulation; note remains of the intestinal diverticula; locality 4; USNM 484411; ×0.75. H. Internal mould of separate opisthosoma, retaining both sclerites, in stage 4 of disarticulation; locality 2; USNM 484412; ×1. I. Incomplete ploughing trace from an inferred tidal-flat lithofacies; occurs in association with, and thought to have been produced by, *P. signatus*; locality 4; USNM 484413; ×1.
dorsal surface, but also the appendages and book gills (Dunbar 1923; Raymond 1944; herein). In a few Konservat-Lagerstätten such as the Solnhofen Limestone of Germany (Barthel 1978; Barthel et al. 1990), the Insect Hill deposit (Dunbar 1923, 1924; Carpenter 1930; Raymond 1944) of Kansas, and the Pony Creek Shale of Kansas (herein), specimens are also moderately abundant. This apparent paradox seems to be explainable partly by a slow preburial disarticulation rate of xiphosurid exoskeletons, and partly by the exclusion or near-exclusion of scavengers, sediment bioturbators, and effective microbial decomposers from some postburial depositional settings that yield xiphosurid remains (see Barthel 1978; Barthel et al. 1990; Babcock & Chang 1997). Fluctuating salinity conditions (Babcock & Chang 1997; Babcock 1998) and possibly desiccating conditions are probably mostly responsible for limiting these organisms from preburial and postburial environments; anoxic sediments could have limited further destructive organisms from postburial environments. High sedimentation rates, which are characteristic of some tidally influenced environments that are potential xiphosurid-bearing Lagerstätten (Feldman et al. 1993; Babcock et al. 1995; herein), may also partly account for the exceptional preservation of unmineralized, chitinous xiphosurid exoskeletons.

**Actualistic taphonomic experiments.** – *Paleolimulus signatus* specimens from the Pennsylvanian–Permian of eastern Kansas represent the full range of taphonomic states from individual, disarticulated sclerites to articulated exoskeletons that retain the ventral appendages and gills (Fig. 4). To better understand the early taphonomic history (necrolysis through biostratinomy) of these fossils, comparative actualistic experiments were performed on *Limulus polyphemus*. Most of these results were reported earlier (Babcock & Chang 1997), but additional information is presented here. The results show that preburial disarticulation of xiphosurid remains (Fig. 6) is a relatively slow process, a discovery that is in general agreement with actualistic data on other marine arthropods and polychaete worms (Allison 1986, 1988; Plotnick 1986; Plotnick et al. 1988; Allison & Briggs 1991a, b; Briggs & Kear 1993). Disarticulation of *Limulus*, however, seems to proceed at a slower rate than disarticulation of previously studied arthropods.

**Comparative taphonomic experiments** were performed on small specimens of the Holocene *L. polyphemus*. Specimens were approximately 7–13 cm long, which is the general size range of most observed *P. signatus*. Three different experiments were conducted on dead specimens kept in oxygenated, artificial seawater inoculated with bacteria. Specimens

---

*Fig. 5.* Ploughing traces produced by extant *Limulus polyphemus* in wet mud, St. Catherines Island, Georgia, USA. Note indistinct scratch marks left by the appendages. Centimetre scale is on camera lens cap.
were: (1) tumbled shortly after death (to simulate transport in a nearshore marine or estuarine setting); (2) tumbled beginning one week after death (following decay of all internal soft parts); or (3) left undisturbed in a tank. The tumbling of specimens was carried out in an ordinary lapidary tumbler with inoculated artificial seawater and no sediment; specimens were tumbled at a rate equivalent to transport of about 3 km/day.

A small, freshly dead specimen of *L. polyphemus* floats for a few hours to two days. The carcass initially curls somewhat as rigor mortis begins but becomes entirely limp or pliable in 1–48 hours. If handled, the exoskeleton can be compressed and wrinkled or bent to a considerable extent without rupturing. The joints are soft, and major sclerites flop about loosely. When allowed to settle through water and come to rest on the sediment, the major tagmata (prosoma, opisthosoma, and telson) can fold loosely in a way that mimics incomplete enrollment. Usually, the prosoma flops forward a little compared to the opisthosoma.

Internal soft parts of *L. polyphemus* decay in seven days in oxygenated, inoculated, artificial seawater, but sclerites tend to remain articulated for a longer time whether the carcass is left undisturbed or is vigorously tumbled in seawater. Tumbled specimens show perforation of the ventral exoskeleton and loss of some book gills (Fig. 6A), beginning with the posterior ones, after about 7 days. Thus, after this time, a carcass effectively becomes a sedimentary particle that is hydrodynamically similar to, if not indistinguishable from, a moulted exoskeleton. Vigorously tumbled specimens have most of their appendages broken after 10 days (Fig. 6B), and the telson detaches after 14 days (Fig. 6C). Finally, the prosoma separates from the opisthosoma after 27–40 days. (Fig. 6D). At a tumbling rate of 3 km/day, this is the equivalent of being transported approximately 81–120 km in a unidirectional current system. Major sclerites of undisturbed (untumbled) specimens can remain articulated in normally oxygenated seawater for at least 64 days under experimental conditions when scavengers and sediment bioturbators are excluded.

Taphonomic comparison. – In Holocene *Limulus* and Pennsylvanian–Permian *Paleolimulus*, five distinct stages of progressive disarticulation are recognizable (Figs 4, 6). These stages, as indicated here, can be equated with an elapsed time of decay and disarticulation in *Limulus*, and, by inference, in *Paleolimulus*. They bracket the time of final burial of *Paleolimulus* or other xiphosurid remains relative to the time of death.

Stage 0: Specimen is fully articulated.

Stage 1: Most of the book gills become detached (Figs 4A, 6A). Stage 1 is reached in about 7 days if the specimen is tumbled and after 53 days if the specimen is untumbled.

Stage 2: Most of the legs become broken (Fig. 4C). Stage 2 is reached in 10–18 days if the specimen is tumbled, and after 62 days if the specimen is untumbled.

Stage 3: The telson becomes detached (Figs 4D, 4E, 6C). Stage 3 is reached after 14 days; it is not always recognizable as distinct from stage 4 because all of the major sclerites may disarticulate at nearly the same time.

Stage 4: The prosoma and opisthosoma become detached (Figs 4F–H, 6D). Stage 4 is reached between about 27 and 40 days if the specimen is tumbled, and after 64 days (quickly following stage 2 or 3) if the specimen is untumbled.

Pliability of *Limulus* exoskeletons in water also seems to have parallels among ancient specimens. All specimens of *P. signatus* illustrated here (Fig. 3, 4A–H)
show some post-mortem distortion. Distortion ranges from simple compression (Fig. 4H) through minor (Figs 3G, 4E) or major (Fig. 4F) wrinkling, to folding (Fig. 4D) of the exoskeleton. With one exception (Fig. 4A), distortion has occurred without obvious rupturing of the exoskeletal margin. Evidently, illustrated *P. signatus* specimens (with the possible exception of the one in Fig. 4A) had pliable exoskeletons at the time of burial, just as small *L. polyphemus* specimens do if they are kept in water until burial. The exoskeleton of *L. polyphemus* becomes brittle upon desiccation, and dorsoventrally oriented pressure can cause rupturing at the margin. The large marginal rupture on the anterolateral part of the prosoma of the specimen in Fig. 4A suggests that it was at least partly dried out at the time of burial.

Variable compression of a pliable exoskeleton in water is here interpreted to be responsible in part for the expression of lobation on the intra-opthalmic areas of the prosoma of *P. signatus* (see Dunbar 1923; Raymond 1944). Dunbar (1923) considered the lobation of this area to be the most distinguishing character of the genus *Paleolimulus*. Although the intra-opthalmic area of the prosoma of *Paleolimulus* is undoubtedly lobed, just as the homologous area in extant *Limulus* is lobed (Fig. 7A, B), available specimens show considerable variability in that character (cf. Figs 3C, 3F, 3G, 4D–G). All known specimens of *P. signatus* are compressed to some extent. Upon moderate compression in soft sediment, a pliable prosoma is expected to show enhancement of the lobation because the exoskeleton originally would have been corrugated at the boundaries between the lobes (cf. Pickett 1984, pl. 56, fig. 1). There is no reason to think, however, that the lobes were more strongly expressed on living specimens of *P. signatus* that they are on *L. polyphemus*.

**Comparison with the taphonomy of other arthropods.** – The preburial disarticulation rates of present-day xiphosurids (Babcock & Chang 1997; herein) and other arthropods (Allison 1986, 1988; Allison & Briggs 1991a, b) are relatively slow. Actualistic experiments help us to more accurately specify at what rates arthropod exoskeletons disarticulated after death (cf. Speyer & Brett 1985, 1986; Speyer 1987), and, in general, those rates are somewhat slower than previously assumed. Aquatic arthropods seem to disarticulate more slowly than do echinoderms kept in warm water (see Kidwell & Baumiller 1990; Baumiller & Ausich 1992). This demonstrates that not all organisms having multipart skeletons can be construed as equivalent in terms of disarticulation rates.

The relatively slow disarticulation rates of present-day aquatic arthropods have important implications for the fossil record of arthropods. Prior to burial,
some ancient arthropods may have remained articulated or partly articulated for somewhat longer lengths of time than earlier assumed. Arthropods that have mineralized exoskeletons (e.g. trilobites and ostracodes) are more abundant in the stratigraphic record as a whole, and articulated or partly articulated specimens are moderately abundant in places. Mineralized sclerites of arthropods are held together at joints by unmineralized cuticle. Slow preburial disarticulation rates in environments having few scavengers, low rates of bioturbation, and possibly low rates of microbial decay (in some situations related to fluctuating salinity), can help to explain the abundant occurrence of articulated arthropods in some places.

Pliability of the sclerites or joints of arthropods soon after death also has important implications for the fossil record of aquatic arthropods, particularly as it affects our interpretation of life habits. Among arthropods lacking a mineralized exoskeleton, post-mortem or post-moulting distortion has been discussed for various arthropods including xiphosurids (herein) and naraoiids (Babcock & Chang 1997), and the phenomenon probably affected a wide variety of non-mineralized arthropods from Lagerstätten deposits. As examples among arthropods having mineralized sclerites, agnostoid trilobites have been inferred to have lived in an enrolled condition (Robison 1972; Müller & Walossek 1987), yet articulated specimens usually occur outstretched (e.g. Robison 1982, 1984). The outstretched condition of these animals (which could be misinterpreted as a life posture) may be attributable to post-mortem or post-moulting pliability of the cuticle at the arthrodial membranes. Pliability of the arthrodial membranes also raises questions about the flexed condition in which trilobites such as calymenids may occur (e.g. Whittington 1992; Mikulic 1994; Babcock 1997). As suggested by Mikulic (1994), they may be preserved in a moulting posture. It is also possible that some moults or carcasses were deposited in slightly flexed position following transport by currents.

Systematic palaeontology

Order Xiphosurida Latreille, 1802
Superfamily Paleolimuloidea Anderson & Selden, 1997
Family Paleolimulidae Raymond, 1944
Genus *Paleolimulus* Dunbar, 1923

Type species. – *Paleolimulus avitus* Dunbar, 1923, by original designation (Dunbar 1923, p. 444).

*Paleolimulus signatus* (Beecher, 1904)

Figs 3, 4

1904 *Prestwichia signata* Beecher, p. 24, fig. 1.

1923 *Paleolimulus avitus* Dunbar - pp. 444–451, figs. 1–6.

1923 *Paleolimulus signatus* (Beecher) – Dunbar, p. 450, Fig. 8.

1944 *Paleolimulus avitus* Dunbar – Shimer & Shrock, p. 707, Pl. 300, figs. 1, 2.

1952 *Palaeolimulus [sic] avitus* Dunbar – Størmer, fig. 1.

1955 *Paleolimulus avitus* Dunbar – Størmer, pp. P21, P22, Fig. 15C, 16,1.

1963 *Paleolimulus avitus* [sic] Dunbar – Tasch, p. 1247, pl. 173, fig. 1.

1987 *Paleolimulus* [sp.] Robison – Fig. 13.46, A.

1991 *Paleolimulus* [sp.] Eldredge – pl. 90.

1991 *Paleolimulus avitus* Dunbar – Novozhilov, Fig. 1183.

Types. – Holotype prosoma of *P. signatus*, USNM 483405, from locality 1; plaster casts, YPM 26319, 26319A. Lectotype of *P. avitus* (selected here), part and counterpart, YPM 26324; paralecotypes, YPM 26317, 26325, all from locality 3.

Discussion. – The holotype prosoma of *P. signatus* was originally illustrated by only a restored plaster cast (Beecher 1904, fig. 1; reillustrated by Dunbar 1923, Fig. 8). The actual fossil was not illustrated, and it probably remained for years in the collection of J.W. Beede. We have identified an unlabeled specimen, apparently the holotype, in the collections of Kansas State University. The specimen has been transferred to the U.S. National Museum of Natural History (USNM 48305; Fig. 3C). Although broken along pre-existing cracks, the pattern of anastomosing lines and cracks in the fossil is identical with those in the YPM casts (cf. Fig. 3A, B). The original fossil is a large prosoma preserved as an internal mould. Examination of it (Fig. 3C) and the slightly restored cast (Fig. 3B) shows that not only were the lateral regions of the prosoma restored on the illustrated cast (Fig. 3A), a part of the posterior margin was also restored. Grooves on the dorsal surface seem to have been subtly enhanced by mechanical preparation of Beecher’s illustrated plaster cast.
Dunbar (1923) erected *Paleolimulus avitus* using specimens from the Insect Hill Lagerstätte (locality 3). Three syntypes (Fig. 3D–G) were identified; the most complete of these (Fig. 3D, E; original of Dunbar 1923, figs. 4–6) is here selected as the lectotype of *P. avitus*.

Characters used to distinguish *P. avitus* from *P. signatus* seem to be trivial and attributable to individual or ontogenetic variation, rather than to species differences; for this reason, *P. avitus* is regarded as a junior synonym of *P. signatus*. Dunbar (1923, p. 450) stated that *P. signatus* differs from *P. avitus* in being of larger size; having less pronounced ophthalmic ridges, a more slender cardiac lobe, and a longer cardiac lobe. The three-fold size difference between Beecher’s specimen and Dunbar’s specimens reasonably can be attributed to ontogenetic differences. Ophthalmic ridges are defined slightly better in Dunbar’s (1923) specimens of *P. avitus* than in Beecher’s (1904) specimen of *P. signatus*. Judging from the new collections (e.g. Fig. 4D–G), distinctness of the ophthalmic ridges is largely taphonomically related, with comparatively more compressed specimens exhibiting more poorly defined ophthalmic ridges. Comparison of the length of the cardiac lobe to total prosomal length (Table 1) indicates that the cardiac lobe is proportionately shorter, although only slightly so, in Beecher’s specimen (YPM 26319A) than in any of Dunbar’s specimens. This difference is attributable to ontogenetic or individual variation. Finally, comparison of the width of the cardiac lobe at the posterior margin to total prosomal length (Table 1) indicates that the proportionate width of that character in Beecher’s specimen falls well within the range of variation of Dunbar’s specimens.

The opisthosoma of *Paleolimulus* is divided into two sclerites (e.g. Figs 3H, 4D, E, H). Previously, the smaller posterior sclerite was homologized with the transverse area at the anterior of the telson of *Limulus* (Raymond 1994; but see Anderson & Selden 1997). Based on new collections, we concur with Anderson & Selden (1997) and interpret the posterior opisthosomal sclerite (‘posterior axial lobe’ of Anderson & Selden 1997) as homologous with the posterior part of the opisthosoma of *Limulus*. Evidence for this interpretation is the presence in *L. polyphemus* of a distinct, although subtle, fused joint between a larger anterior area and a smaller posterior area of the opisthosoma (Fig. 7A). This fused joint is presumed to be homologous with the joint between the two opisthosomal sclerites of *P. signatus* (Fig. 4D). The larger anterior sclerite of *P. signatus* contains six segments, the smaller posterior segment two segments. The anterior part of the opisthosoma (forward of the fused suture) of *L. polyphemus* contains six segments and the posterior part two segments.

Anastomosing lines on the prosoma of *P. signatus* are interpreted to be impressions left in the exoskeleton by intestinal diverticula. The anastomosing lines, which closely resemble the pattern of the intestinal diverticula impressed on the ventral side of the dorsal surface in extant *L. polyphemus* (Fig. 7B) are well expressed in the holotype (Fig. 3A–C). Another specimen of *P. signatus* (Fig. 4G) shows a mosaic of polygonal bumps over the surface of the internal mould left as the result of the dissolution of the anastomosing lines.

**Occurrence.** – Upper Pennsylvanian to Middle Permian of northeastern Kansas; Middle Pennsylvanian of northeastern Illinois.

**Acknowledgements.** – We thank R.D. White (Peabody Museum, Yale University) for lending xiphosurid specimens for study, and for providing much valuable information about the specimens. The late A.S. Horowitz (Indiana University) provided information about J.W. Beebe’s collections. H.R. Feldman (Shell Oil Company) helped with some field work. C.G. Maples (Indiana University) provided helpful information about Upper Pennsylvanian–Permian stratigraphy of Kansas. G.J. Wasserman (Ohio State University) printed many of the photographs used herein. Betty Heath (Ohio State University) keyboarded the manuscript. Karen Tyler (Ohio State University) drafted some figures. The manuscript has benefited from reviews by R.M. Feldmann (Kent State University) and three anonymous reviewers. This work was partly supported by grants from the Kansas Geological Survey and the U.S. National Science Foundation (EAR-9405990) to Babcock.

**References**


