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ART. XXXVII.—*Kansas Permian Insects. Part 2. Paleolimulus, a New Genus of Paleozoic Xiphosura, with Notes on other Genera;* by CARL O. DUNBAR. (With Plate II.)

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The genus *Limulus* is a persistent type, appearing in the Triassic and enduring throughout the Mesozoic and Cenozoic into the present. It is, moreover, a singularly isolated race, so remotely related to all contemporary arthropods that it has been relegated to a distinct order, the Xiphosura, and since there are no other known xiphosurans in either Cenozoic or Mesozoic faunas, its isolation has not been recently acquired. In the Paleozoic there are a few related genera, of which *Belinurus* and *Prestwichia* are best known, but from the beginning of their fossil record the Xiphosura have been a small and specialized group whose relationships and ancestry remain a problem. Considerable interest attaches, therefore, to the discovery of a new generic type of these early merostomes, which is described in the following pages.

This small xiphosuran is one of the few invertebrate fossils associated with the Lower Permian insects of Kansas.[1] The Yale collection contains some exceptionally preserved specimens, one of which reveals the ven-

[1] The geologic occurrence and the living environment of this remarkable insect fauna will be fully discussed by the writer in an early number of this Journal. An exhaustive biologic study of the insects is in progress by the eminent paleoentomologist, Doctor R. J. Tillyard, director of the Cawthron Institute for Scientific Research, Nelson, New Zealand, and his studies will follow in a series of installments under the general title "Kansas Permian Insects." The present paper is No. 2 of the series, No. 1 being the general treatment of the geologic occurrence of the insects mentioned above.

tral thoracic limbs and thus makes possible a rather close comparison with the living king-crab. The correspondence is striking. The carapace of the fossil, however, bears strong impressions of the segmentation of the body, an ancestral feature significantly repeated in the "trilobite stage" in the ontogeny of *Limulus*. These indications of segmentation are shown in the pronounced annulation of the rachis of the abdomen, and in the cephalothorax take the form of "glabellar lobes." There are additional minor distinctions, but the lobation of the carapace alone is undoubtedly of generic importance, yet it is a character that does not pertain to any known genus. With a feeling of confidence that the new genus is the Paleozoic forebear of *Limulus*, I shall propose to name it *Paleolimulus*.

Paleolimulus, gen. nov.

Diagnosis: Body limuloid in shape. Cardiac lobe of the cephalothorax defined by converging longitudinal grooves, widest behind, and tapering anteriorly to a point where it joins the ophthalmic ridges in a small ocellar tubercle. Ophthalmic ridges prominent. The areas within these ridges, bordering the cardiac lobe on either side, are occupied by six low, rounded, "glabellar" lobes, of which the anterior three are progressively smaller and fainter, the sixth being visible only on very well preserved specimens. Lateral compound eyes and a median pair of ocelli are present.

Abdomen irregularly hexagonal, as in *Limulus*, and consisting of nine (?) fused segments plus a slender ensiform telson. Rachis elevated and strongly annulated except on the last two segments, where it is more depressed. Margins of the abdomen ornamented by scallops, within which were borne small articulated stylets as in *Limulus*.

Of the ventral appendages, the cheliceræ are unknown. The first four pairs of ambulatory legs are chelate, but the fifth pair ends in a whorl of slender plates.

Genotype.—P. avitus, sp. nov.

Paleolimulus avitus, sp. nov.

Description.—Small, limuloid in shape. Cephalothorax depressed convex, semi-elliptical in outline, its

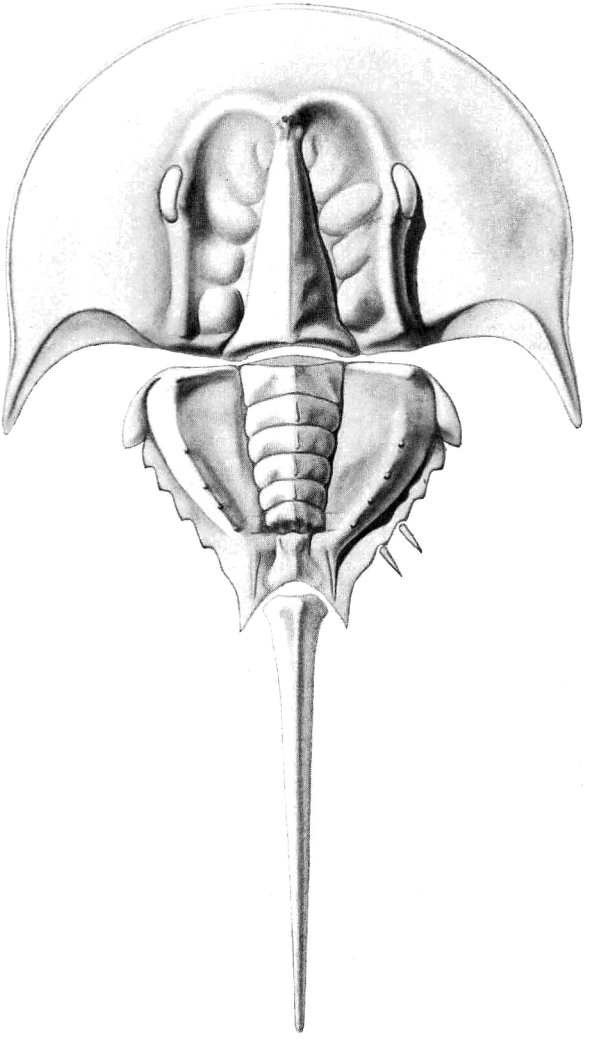

PLATE II (FIG. 1).—Restoration of *Paleolimulus avitus*, a new xiphosuran from the Permian of Kansas. Dorsal view. × 7.

length slightly exceeding its breadth. Genal spines moderately stout, their length about one-fourth as great as the breadth of the carapace in the largest specimens, but relatively shorter in the smaller ones. Central or cardiac lobe of the cephalothorax elevated, subangular along the middle line, widest behind, and tapering almost uni-

FIG. 2.

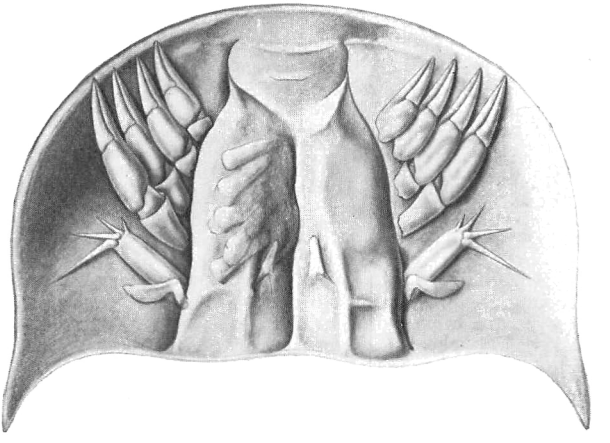

FIG. 2.—Restoration of *Paleolimulus avitus,* gen. et sp. nov., from the ventral side. × 7.

formly to its terminus at a point about two-thirds the distance from the front margin of the carapace. Prominent ophthalmic ridges beginning at points distant from the median line by about the width of the base of the cardiac lobe, running almost directly forward to the eyes, near the mid-length of the carapace, and then beginning to converge with an increasing curvature until they meet in a shallow reëntrant at the apex of the cardiac lobe. The blunt tubercle formed at this point is surmounted by a pair of ocelli.

Compound eyes as in *Limulus,* situated about the mid-length of the cephalothorax and on the outer margins of the ophthalmic ridges; oval in shape, depressed convex, and rather small. The individual facets are shown over a part of the area of one eye in the largest specimen in our collection, and from this portion it is estimated that the entire eye possessed about 450 lenses, a number that

agrees approximately with that of a very young *Limulus* of the size of the Permian fossil. In a mature individual of *Limulus polyphemus,* on the other hand, the facets are not only larger but more numerous, attaining almost double the number mentioned above. Phylogeny thus agrees with ontogeny in indicating that the number of facets of the limuloid eye has increased with time. The lenses are arranged in rather irregular oblique rows.

FIG. 3. FIG. 4.

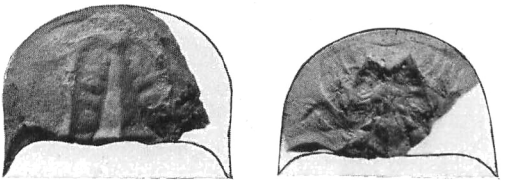

FIG. 3.—*Paleolimulus avitus,* gen. et sp. nov. Dorsal view of cephalothorax, showing "glabellar lobes" and other characteristic features. The compound eyes are broken off. × 2 ±.

FIG. 4.—Ventral view of a specimen of *Paleolimulus avitus,* gen. et sp. nov., showing distal portions of the thoracic limbs. × 2.

Depressed areas enclosed by the ophthalmic ridges on either side of the cardiac lobe each marked by six low, rounded, transverse nodes, of which the three posterior ones are most strongly marked and the anterior ones progressively smaller and fainter. The foremost of these is minute, situated close against the side of the ocellar tubercle, and may be seen only on well preserved specimens. These nodes correspond to the paired limbs beneath, and reflect the segmented character of the body.

Abdomen irregularly hexagonal and resembling in form that of *Limulus walchi* of the Jurassic. The number of segments is evidently the same as in modern *Limulus* and offers the same difficulties of interpretation. The rachis clearly shows eight segments. On the first six of these, it is elevated, subangular along its middle line, and rather strongly annulated, but it is more depressed on the posterior two, which are delimited only by a narrow depressed line. To the last segment is articulated a long, slender, ensiform telson. Uncertainty as to the number of abdominal segments arises from the fact that the large anterior lobes of the pleura appear to

be anterior to the front segments of the rachis. It has been suggested for *Limulus,* where the same condition presents itself, that these large pleural lobes belong to the opercular segment, which is suppressed in the rachis of the dorsal carapace. If this interpretation be correct, then the abdomen in *Paleolimulus* consists of nine segments plus the telson, but on the contrary, if the large anterior pleural lobes do not represent an additional segment, the number is eight.

FIG. 5.

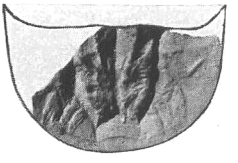

FIG. 6.

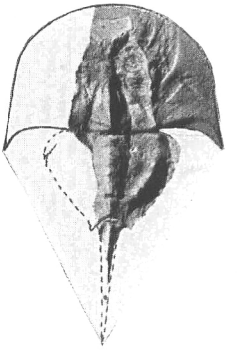

FIG. 5.—Identical view of the same specimen as in Fig. 4, with angle of oblique light reversed, showing better the right-hand limbs, especially the burrowing leg with its whorl of four terminal plates, and its exopodite below. × 2.

FIG. 6.—Obverse of the above specimen, showing an impression of the ventral structures of the cephalothorax, and the dorsal aspect of the abdomen and a part of the telson. × 2.

The pleura of the abdomen are divided longitudinally by a subangular ridge, inside of which is a flattened and depressed area bordering the rachis, and outside of which is a narrower steep slope down to the flattened margin. The annulations of the rachis do not cross the pleura of the abdomen, but along the ridges described above there is a row of five small rounded nodes which correspond to the first, third, fourth, fifth, and sixth segments of the rachis, that of the second being repressed.

The flattened margins terminate in a series of rather blunt and unsymmetrical points, directed obliquely caudad, separating cusps in which were lodged small articulated stylets. Seven such points and six cusps are present on the right-hand side of the specimen (fig. 6).

Two of the small slender stylets may be seen almost in place, and a third was accidentally destroyed in preparation of the specimen.

One of the type specimens reveals the thoracic limbs, which are impressed against the ventral side of the carapace (see figs. 4-6), and appear in low relief. The proximal portions of the limbs are very obscure, but the distal parts of five pairs of walking legs are clearly outlined.

FIG. 7.

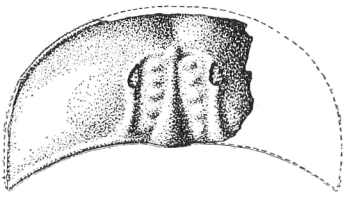

FIG. 7.—*Paleolimulus? randalli* (Beecher). Dorsal view of the type specimen, after Beecher. × 1.

Because of their very slight relief, the limbs can be seen to advantage only when illuminated by low oblique light. This fact will be evident upon comparing figures 4 and 5, which are identical views of the same specimen but with the direction of the light reversed. In the former, the left-hand limbs are well shown and those of the right side indistinct; in the latter the reverse is true. By the same token, no single photograph will show all the structures which can be observed when the specimen is rotated in oblique light under the binocular.

The cheliceræ are not shown in this specimen, and it is probable that they were very small. The succeeding four pairs of ambulatory legs are chelate, and of moderate size, reaching about to the margin of the carapace. As the joints of the limbs are very obscure, the length of the pincers is a matter of some uncertainty. With proper illumination, all the left-hand limbs seem to show joints as represented in figure 2, delimiting a rather small posterior ramus. On the other hand, a faint longitudinal groove can be seen extending further up the limb, which, at first, suggested that the pincer was long and the posterior ramus rather thicker than the anterior. After careful study, the former interpretation has been

tentatively adopted. The fifth limb is non-chelate, and, like the burrowing limb of *Limulus,* terminates in a whorl of slender diverging plates, of which four are visible in the type specimen. This limb also possessed an exopodite, the flabellum, very similar to that of *Limulus,*

FIG. 8.

FIG. 8.—*Paleolimulus signatus* (Beecher). Dorsal view of the type, after Beecher. × 1.

which arises from the outer end of the coxal segment. This structure is apparently a single segment consisting of a rounded shank which curves at a sharp right angle into a spatula-like distal blade.

The coxæ of the limbs are crowded closely together under the central portion of the cephalothorax, those of the posterior limbs appearing fully one-third the length of the carapace from its posterior margin. Accordingly, the area behind the last limbs is proportionately much larger than in the living *Limulus.* The small and obscure elevations shown here in figures 2 and 4 probably represent the chilaria.

The abdominal appendages are unknown.

Measurements.—The dimensions of the largest cephalothorax are: median length, 15 mm.; width, 24 mm. The most perfect specimen (fig. 3) is of average size,

measuring: length of cephalothorax, 6.5 mm.; width, 11 mm.; length of abdomen, 5 mm.; length of telson (estimated), 5-7 mm.

Habitat.—The habitat of this species will be discussed fully in a subsequent paper dealing with the environment of the entire fauna. It may be noted here, however, that it was associated with fragmentary plant remains, and with many remarkably preserved insects, both adults and aquatic larvæ, that no fishes were present, and that the only marine elements of the fauna are two species of the clam *Myalina*. The water must have been sweet or slightly brackish, and was probably a fresh lagoon at the head of an inland sea.

Horizon and Locality.—Elmo limestone member of the Lower Permian Wellington shale, near Elmo, Kansas. Types in the Peabody Museum, Yale University.

Congeneric Species.—In addition to the genotype, *Paleolimulus* will embrace Beecher's *Prestwichia signata*[2] and possibly also his *P. randalli*.[3] The former species is based upon a single very incomplete specimen (fig. 8), a natural mold of the interior of the cephalothorax. Nevertheless it shows the striking feature of the genus, the "glabellar" lobes of the prosoma. It was found at the base of the Permo-Carboniferous of Kansas, in the Fort Riley limestone, a horizon about 300 feet below that of *P. avitus*. So far as can be determined from Beecher's fragmentary type, it is very similar to the new species. It differs from the latter, however, in being much larger, having over three times the diameter of the largest specimen of *P. avitus*. Its ophthalmic ridges also are less pronounced, and the cardiac lobe is more slender and reaches nearer the front margin.

P. randalli is much older, being based upon a single rather well preserved carapace of the prosoma which was found in the Chemung sandstone of the Upper Devonian (fig. 7). It shows clearly a tapering cardiac lobe, bordered on either side by an area possessing five rounded nodes and circumscribed by raised ophthalmic ridges, all of which features ally it with *Paleolimulus*. On the other hand, the lateral portions of the carapace in this species are disproportionately large and wide as compared with the area within the ophthalmic ridges, and the genal

[2] C. E. Beecher, This Journal (4), **18**, 23, 1904.
[3] C. E. Beecher, Amer. Geol., **29**, 143, 1902.

angles are reduced and blunt. Of course, nothing is known of the abdomen or of any of the ventral appendages, hence the reference of the species to the genus *Paleolimulus* must be only provisional until its characters are more fully known. In any event, it seems more nearly allied to this genus than to *Prestwichia.*

Generic Characters of Belinurus and Prestwichia.

Upon attempting to compare the new Permian fossils with other genera of Xiphosura, it became evident that there has crept into the literature much divergence of opinion as to the generic characters of *Prestwichia* and *Belinurus,* and that American authors, misled by Packard, have a conception of *Belinurus* which does not accord with its genotype.

The generic term *Belinurus* was introduced by König[4] in 1825 for his species *B. bellulus,* which thus became the genotype. Some years later, Buckland,[5] unaware of König's work, described the same fossil under the name *Limulus trilobitoides,* a term subsequently used by Prestwich, Portlock, and Baily. However, in 1854, Pictet[6] revived König's name, and nine years later Baily,[7] without knowledge of Pictet's work, independently reverted to this name, under which he described two new species. By 1866 six species had been referred to *Belinurus,* and then Woodward[8] in his study of the Xiphosura was led to the conclusion that these species were "divisible into two well marked genera." His diagnosis of these two genera is appended, with brackets inserted for the sake of clarity, since it was his belief that the prosoma of the merostomes embraced only the head (instead of head and thorax), and that the body behind it (now known to be the abdomen only) included both the thorax and abdomen. He says:

"(*a*) Those having movable thoracic [i. e., the first five abdominal] segments and anchylosed abdominal ones [the posterior three abdominal ones only], to be included in the genus *Belinurus.*" To this group he

[4] C. König, Icones Fossilium Sectiles, pl. 18, fig. 230.
[5] W. Buckland, Bridgewater Treatise, vol. 1, 396, vol. 2, 77, 1836.
[6] F.-J. Pictet, Traité de Paléontologie, 2d ed., vol. 2, 538.
[7] W. H. Baily, Ann. Mag. Nat. Hist., 3d ser., 11, 107-114, 1863.
[8] H. Woodward, Quart. Jour. Geol. Soc., London, 23, 31-33, 1867.

referred *B. trilobitoides* [= *B. bellulus*], *B. reginæ*, *B. arcuatus*, and, with a query, *B. danæ*.

"(*b*) Those in which the thoracic and abdominal [all the abdominal] segments are not divided and in which the former [i. e., the anterior abdominal segments] appear to be anchylosed, to be included in a new genus, for which I venture to propose . . . the name of *Prestwichia*." To this genus he referred *P. anthrax* and *P. rotundata*, the latter of which is figured.

Woodward's sole criterion for distinguishing these genera was, therefore, that in *Prestwichia* the abdominal segments are firmly anchylosed as in the pygidium of a trilobite, whereas in *Belinurus* the anterior five segments are movably articulated like the trilobite's thoracic segments. His illustrations of representative species, *B. reginæ* and *P. rotundata*, clearly indicate this difference.

There seems no reason to doubt Woodward's observation that in the typical species of *Belinurus* the first five abdominal segments are movably articulated, since this observation was made also by Pictet, Baily, and others, was re-affirmed by Woodward in his "Monograph of British Fossil Crustacea, Order Merostomata," in 1878, and was accepted by Shipley in his treatise on the Arachnida in the Cambridge Natural History. Moreover, this character is strongly suggested in Woodward's illustration of König's original type and is clearly shown in the figures of *B. reginæ*.

As to the number of abdominal segments, Woodward stated that both genera had the same, although his figure of *B. reginæ* copied from Prestwich shows eight abdominal segments, instead of the seven possessed by *Prestwichia*. In view of the fact that the posterior segments are very small and the last three are anchylosed, it might be difficult to determine the number, whether seven or eight, unless the specimens were well preserved, but as Woodward's illustration shows eight segments and this number is accepted in the recent work of so great an authority as Shipley, it may be regarded as correct.

The shape of the abdomen is also highly distinctive in these genera. That of *Prestwichia rotundata* is a rounded, convex shield; in *Belinurus bellulus* (and the better known *B. reginæ*), it is triangular and possesses long lateral spines.

Undoubtedly the structures of the central region of the cephalothorax would show distinctive features of more fundamental significance if they were well known, but until more perfectly preserved specimens can be compared, we must rely upon abdominal characters, as Woodward did, to separate species of *Prestwichia* and *Belinurus*. These characters are three-fold: the presence or absence of articulation, the number of segments, and the shape of the abdomen. By way of summary, a brief diagnosis of each genus may therefore be given as follows:

Belinurus: Body limuloid in shape. Abdomen triangular, distinctly trilobed, consisting of eight segments plus a slender ensiform telson. The first five segments movably articulated, the last three anchylosed. Genotype, *B. bellulus* König.

Prestwichia: Body limuloid in shape. Abdomen a subrounded, depressed convex shield consisting of seven fused segments plus a slender ensiform telson. Genotype, *P. rotundata* Prestwich.

It follows from the above diagnoses that Packard's *Belinurus lacoei*[9] is a *Prestwichia*. He himself noted the resemblance of the species to *Prestwichia*, for he stated that "While having the same number of abdominal segments [as *Belinurus*], this species, the first representative of the genus which has occurred in America, differs from *B. reginæ* chiefly in the more rounded, less triangular outline of the abdomen, and in the smaller lateral abdominal spines." He relied entirely upon the number of abdominal segments in distinguishing the genera. Yet, strangely, the excellent figures in lithogravure on his Plate 5 show not only the same shape but the same number of segments for *Prestwichia danæ* and *B. lacoei*. There are in each the same seven lateral spines and the same number of raised lines crossing the pleural regions of the abdomen. The bead-like annulations of the rachis are clearly but seven in *B. lacoei*, and while only six in the figure of *P. danæ*, this is clearly because the last two failed to be normally separated, the last annulation being twice as long as the rest and bearing two crowning nodes, one near the front and one further back. While there are specific differences here in the relative width and

[9] A. S. Packard, Mem. Nat. Acad. Sci., vol. 3, pt. 2, 149, 1886.

shape of the rachis, the length of telson, outline of prosoma, etc., these species are certainly congeneric. In any event, the species *lacoei* can not be referred to *Belinurus*.

Summary.

The new genus *Paleolimulus* is readily distinguished from either *Prestwichia* or *Belinurus* not only by the pronounced lobation of the prosoma, but likewise by the shape and structure of its abdomen.

Mention should also be made of the genus *Protolimulus,* founded upon a single obscurely preserved specimen from the Chemung sandstone, since it has a limuloid shape and appearance; its detailed characters, however, are altogether too obscure to permit of close comparison with any other genus.

Closest resemblance is found with *Limulus,* with which it agrees in shape, number of segments, and structure of abdomen, and to which it even shows remarkably close resemblances in the form and structure of the thoracic limbs. On the other hand, the new genus differs from *Limulus* in its strongly marked traces of segmentation, particularly in the "glabellar lobes" of the prosoma and in the annulations of the rachis of the abdomen, as well as in the forward position of the mouth and ventral thoracic limbs. These are significant characters, and seem without doubt to be of generic value. Nevertheless, they are ancestral characters reviewed in the ontogeny of the living king-crab, for at the "trilobite stage," segmentation is strongly marked in the larval *Limulus.* Moreover, even though the king-crab does not have its carapace embellished with "glabellar lobes," there is still a lingering hint of them in the ill defined and somewhat irregular pits along the grooves beside the cardiac lobe. None of its characters seem to bar *Paleolimulus* from the direct ancestral lineage of *Limulus.* It follows that the contemporary genera, *Prestwichia* and *Belinurus,* were at most only side lines divergent from this ancient stock.

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