

CRUSTACEAN-BEARING CONTINENTAL DEPOSITS IN THE PETROLIA FORMATION (LEONARDIAN SERIES, LOWER PERMIAN) OF NORTH-CENTRAL TEXAS

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ABSTRACT—Numerous pygocephalomorph crustaceans occur with conchostracans, plants, fishes, amphibians, and amniotes in the Petrolia Formation (Leonardian Series, Lower Permian) of Baylor and Archer counties, Texas. Two pygocephalomorph species are represented; *Mamayocaris serendipitous*, new species, by hundreds of specimens that appear to be molted exoskeletons, and *Paulocaris schrami*, new species, by only a few specimens. *Mamayocaris* has been reported previously from the Lower Permian of Texas and South Dakota and the Upper Carboniferous of Illinois; *Paulocaris* was previously known only from South America. Associated plant assemblages are dominated by conifers accompanied by other Early Permian and some Late Carboniferous elements. Accompanying vertebrate remains include aquatic to fully terrestrial forms with close taxonomic ties to genera or families recorded in Upper Carboniferous deposits. The fossils are preserved in local deposits of thin (<2 cm), lenticular to nodular beds of limestone and thin (<15 cm) intervals of dark-gray claystone. These deposits accumulated in abandoned, standing-water segments of suspended-load fluvial channels. The archaic nature of these plant and animal assemblages supports previous interpretations that the Permian Petrolia Formation contains paleoenvironmentally isolated biotic elements characteristic of the Carboniferous and underscores prior depictions of the assemblages as relictual.

INTRODUCTION

THE TERRESTRIAL Lower Permian rocks of North-Central Texas are a well-known source of vertebrate remains, but few non-marine invertebrates have been reported from this region. However pygocephalomorph crustaceans, which are otherwise rare in the Permian (Brooks, 1962), have been found in abundance at several localities in the Petrolia Formation (Wichita Group, Leonardian Series) of Baylor and Archer counties (Fig. 1). These invertebrates are accompanied by plants and aquatic to terrestrial vertebrates, all preserved in a distinctive, recurring depositional setting. The purpose of this work is to describe two new pygocephalomorph crustacean species from the Petrolia Formation, record the associated biota, describe the geologic context of these deposits, and consider the paleoenvironmental and evolutionary significance of the biota.

A single pygocephalomorph, *Mamayocaris jepseni* Brooks, 1962, was described previously from the Lower Permian of Texas (Brooks, 1962). That specimen was from the middle Clear Fork Group of Taylor County, approximately 180 km south-southwest of our field area. Olson and Mead (1982) described the geology and diverse vertebrate assemblage of this deposit, and Mamay (1976) summarized associated plant remains.

GEOLOGY

The Petrolia Formation of the Wichita Group was established by Hentz and Brown (1987) for continental rocks that are approximate equivalents of the Elm Creek Formation and undivided Jagger Bend and Valera formations of the marine Albany Group (Hentz, 1988). Within our field area, the Petrolia Formation is identical to the more widely known but now obsolete Belle Plains Formation as mapped in detail by Romer (1974). The Petrolia Formation is regarded as early Leonardian in age mainly on the basis of ammonoids that occur in limestones at the base of the formation (Böse, 1917; Kemp, 1962). In a study of Late Paleozoic floral zones, Read and Mamay (1964) placed the Leonard-Wolfcamp boundary in North-Central Texas at the base of the Belle Plains Formation on the basis of the first occurrence of gigantopterid remains.

The sediments of the Petrolia Formation were deposited in a broad coastal plain along the landward margin of the Eastern Shelf of the Midland Basin. The approximately 130 m thick, mudstone-dominated Petrolia Formation is bounded by thin (<1 m) marine carbonates and consists mainly of paleosol sequences that include pedogenic carbonates. Sandstones are quartzose and restricted to fine to very-fine grained, high-sinuosity, suspended-load channel deposits and to minor tabular deposits of limited lateral extent (Hentz, 1988).

Seven pygocephalomorph-bearing localities were sampled in the Petrolia Formation of the Archer-Baylor county-line area (Fig. 1). These occur in local mudstone-dominated, channel-form deposits that are underlain by thin (<12 cm) channel-lag conglomerates. Localities 4, 5, and possibly 6, may represent coeval deposits, but their lateral continuity cannot be demonstrated. At all localities other than locality 3, numerous pygocephalomorphs are preserved in thin (<2 cm), resistant, lenticular to nodular beds of nonbedded, light- to dark-gray limestone that weathers to white, buff, or light brown. The upper surface of each bed is marked locally by small-scale cracks that may reflect synaeresis, and the limestone breaks with a conchoidal fracture. In thin section, the limestone is a pelmicrite that consists mainly of irregularly rounded grains that probably represent invertebrate fecal pellets. At localities 2 and 3, a few pygocephalomorphs were collected from finely laminated, gray to dark gray claystone units approximately 15 cm thick. Similar claystones found in association with the fossiliferous limestones at the other five localities did not yield pygocephalomorphs.

At locality 2, the most complete exposure (Fig. 2), the limestone extends laterally for approximately 30 m and is distinctively U-shaped in cross section. The fossiliferous limestone occurs within the lowermost storey of a repetitive, fluvial channel sequence. This storey begins with a basal conglomerate that scoured into red mudstones containing paleosol features. The conglomerate is overlain by a claystone-dominated fossiliferous interval, which contains spirorbid worm tubes, abundant conchostracans, plant debris, fusain, and a pygocephalomorph-bearing limestone. A second fossiliferous claystone interval coarsens upward to non-

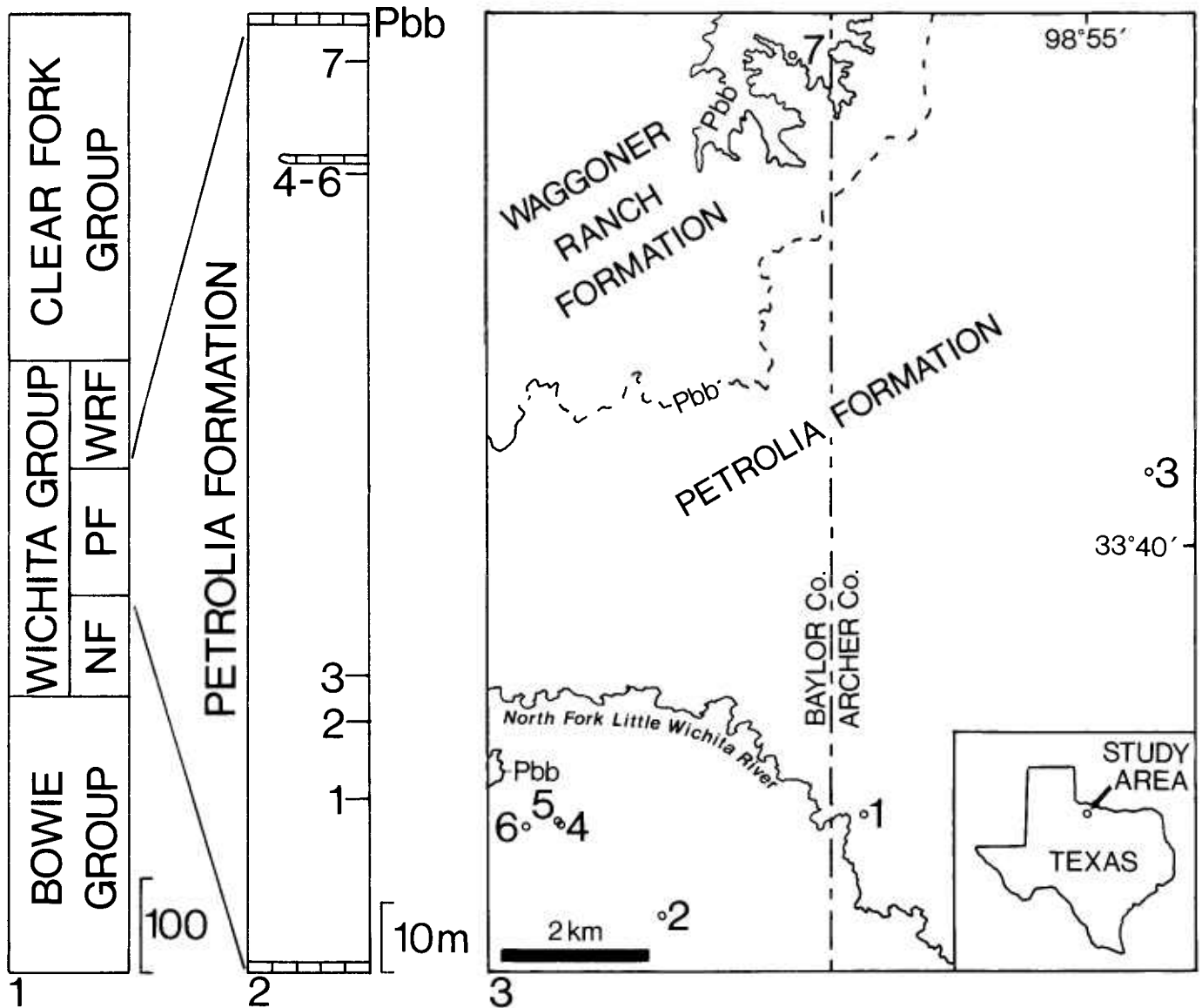


FIGURE 1—Lithostratigraphy and location of Lower Permian pygocephalomorph deposits in North-Central Texas. 1, Generalized stratigraphic column; Wichita Group formations abbreviated as NF, Nocona Formation, PF, Petrolia Formation, and WRF, Waggoner Ranch Formation; 2, generalized Petrolia Formation stratigraphic column with pygocephalomorph deposits (1–7) indicated; Pbb = Beavercreek Limestone; 3, map of study area; inset shows location within Texas. Geology adapted from Romer (1974) and Hentz and Brown (1987).

fossiliferous, gray siltstone. The overlying second storey fines upward from very fine grained sandstone to siltstone; it contains lateral-accretion bedding, and is nonfossiliferous. The capping third storey is a fine-grained, medium-scale trough-crossbedded, rippled sandstone that contains pectopterid impressions and small tetrapod trackways.

Many or all of the sedimentologic characteristics of the lower storey at locality 2 are found at the other pygocephalomorph deposits. Such organic-rich, claystone-dominated channel fills are interpreted as floodplain lakes that originated as cutoffs in high-sinuosity channel belts. Although deposits such as these comprise a minor fraction of the continental Lower Permian of North-Central Texas, they are the primary source of plant, invertebrate, and vertebrate remains in the region (Hook et al., 1989; DiMichele and Hook, 1992; Chaney et al., 1993, 1997; DiMichele et al., 1997).

SYSTEMATIC PALEONTOLOGY

Class MALACOSTRACA Latreille, 1802
Order PYGOCEPHALOMORPHA Beurlen, 1930
Family PYGOCEPHALIDAE Brooks, 1962

Discussion.—Transverse grooves characterize most of the pygocephalomorphs. Within this order, the Teallicaridae typically have longitudinal carinae in the branchial region and tend to lack anterolateral spines, and the Notocaridae are crab-like in outline with a nearly equidimensional carapace and an abdomen that is carried beneath the carapace. The Pygocephalidae, to which the Petrolia Formation specimens are referred, possess a broadened carapace with anterolateral spines and lacking longitudinal carinae.

Recently, Taylor et al. (1998) described some new pygocephalomorphs from China and performed a cladistic analysis of

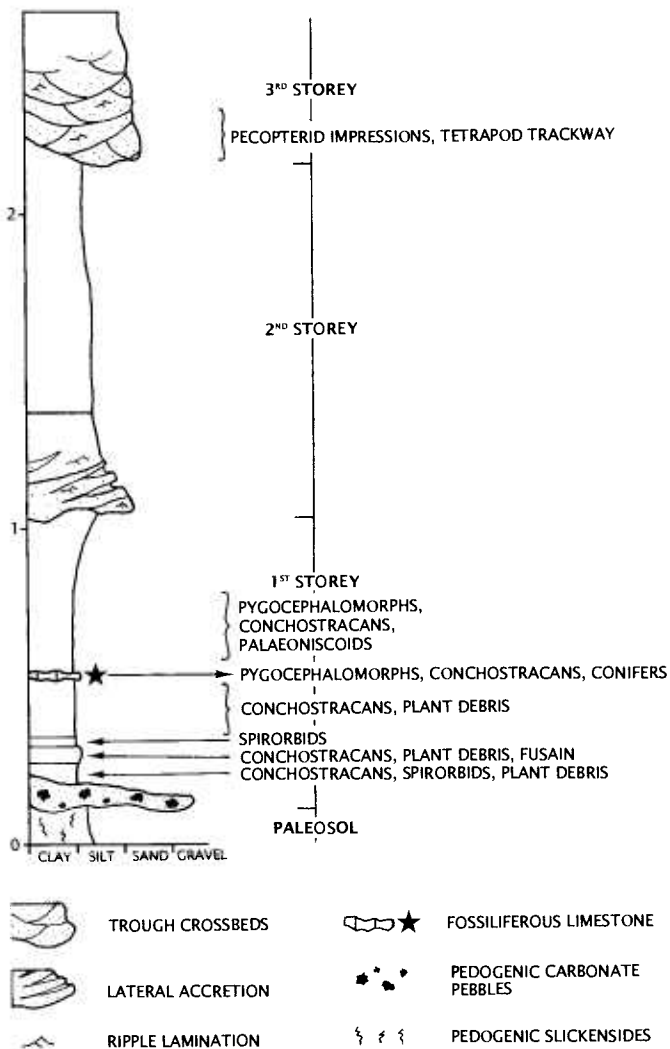


FIGURE 2—Measured section of locality 2. Left vertical scale is in meters.

the pygocephalomorphs and lophogastrids. Their results generally supported the unity of the Pygocephalidae as defined by Brooks (1962).

Genus MAMAYOCARIS Brooks, 1962

Type species.—*Mamayocaris jepseni* Brooks, 1962, p. 189, text pl. 5, pl. 44, figs. 1–3, pl. 45, fig. 5.

Diagnosis.—Pygocephalid with carapace lacking hepatic spines, dorsal carinae indistinct; short anterolateral spines followed by variable number of branchiostegal serrations; cervical groove directed posteriorly; telson subtriangular; females with seminal receptacles (Brooks, 1969; Schram, 1974).

Discussion.—The genus *Mamayocaris* Brooks, 1962, seems to be the most reasonable placement for this material. *Mamayocaris* is in many regards similar to *Pygocephalus*, but the descriptions

of *Pygocephalus* given by Brooks (1962) and Schram (1974) preclude placement in that taxon. *Pygocephalus* possesses a cervical groove that crosses the carapace at a high angle and a telson with small caudal furcae situated in the distalmost of two abrupt marginal steps. By contrast, the cervical groove of *Mamayocaris* crosses the midline at a low angle, and the telson bears a single pair of large furcae articulated at the position of the more proximal marginal step.

As noted above, a single specimen referred to this genus was reported from the middle Clear Fork Group, Leonardian Series, Lower Permian, of Taylor County (Brooks, 1962). He also noted a collection of 168 paratypes from the roughly correlative Opeche Shale of Pennington County, South Dakota. The South Dakota specimens are preserved as compressed, articulated individuals and do not appear to be exuviae. Attempts to recollect this site have been unsuccessful.

MAMAYOCARIS SERENDIPITOUS new species

Figure 3

Diagnosis.—Generally large *Mamayocaris*, with convex-forward cervical groove; strongly developed axial convergence; uropod base with deeply concave distal margin, posterolateral margins of telson with step-like taper; large furcae that extend beyond the tip of the telson spine, and lacking axial projection of the telson over the spine.

Description.—Carapace small, longer than wide, domed transversely in axial region; flaring anterolateral and lateral margins. Frontal margin gently convex forward. Anterolateral corner produced into acute spine, anterolateral margin with fine, forward-directed branchiostegal spines. Lateral margins gently arcuate, radius of curvature increasing posteriorly. Posteroventral corner rounded tightly, curving into concave posterior margin. Marginal furrow extends from anterolateral corner around perimeter of carapace defining a broad ventral ridge, not well expressed on mold of interior, and narrow posterior ridge. Dorsal midline occupied anteriorly by prominent medial crest, becoming narrower posteriorly, disappearing at cervical groove or continuing faintly nearly to posterior border; pronounced anterior definition of medial crest may be base of falciform rostrum. Gastric spines well defined, directed anteriorly, situated on broadly inflated gastric regions; remainder of carapace unadorned. Cervical groove well developed, originates at level of gastric spines, curves around lateral margin of gastric regions and continues as convex-forward arc to dorsal midline; intersects midline at approximately 20 degree angle at distance about two-fifths total carapace length from front margin. Antennules with at least two basal elements and two flagella. Antennae with at least four basal elements, a single long flagellum, and well-developed, acuminate antennal scale extending beyond distal-most basal element.

Thoracic somites well differentiated, covered completely by carapace but no dorsal fusion with carapace apparent. Somites VII–XIII bear equal-sized, narrow, biramous pereopods with propods directed anterolaterally.

Abdomen of six somites and telson, broadly arched. First somite shorter than others. Somites 2–6 subequal in length; width of somites 2–5 subequal, somite 6 slightly narrower. Terga smooth, with pair of slit-like setal pits on either side of midline

FIGURE 3—*Mamayocaris serendipitous* n. sp. 1, Partial remains of the cephalic region with antennules, antennae, and antennal scale, paratype (USNM 486026); 2, holotype (USNM 486025), nearly complete cephalothorax; 3, partially exposed cephalothorax with well-preserved gastric spines and anterolateral spines, paratype (USNM 486027); 4, partial thoracic and abdominal somites with proximal elements of pereopods, paratype (USNM 486028); 5, portion of abdomen, somites 3–6, and well-developed pleura, on same sample Figure 3.1, paratype (USNM 486026); 6, latex cast of complete abdomen and telson with numerous fecal pellets surrounding, paratype (USNM 486029). Bar scale equals 1 cm.

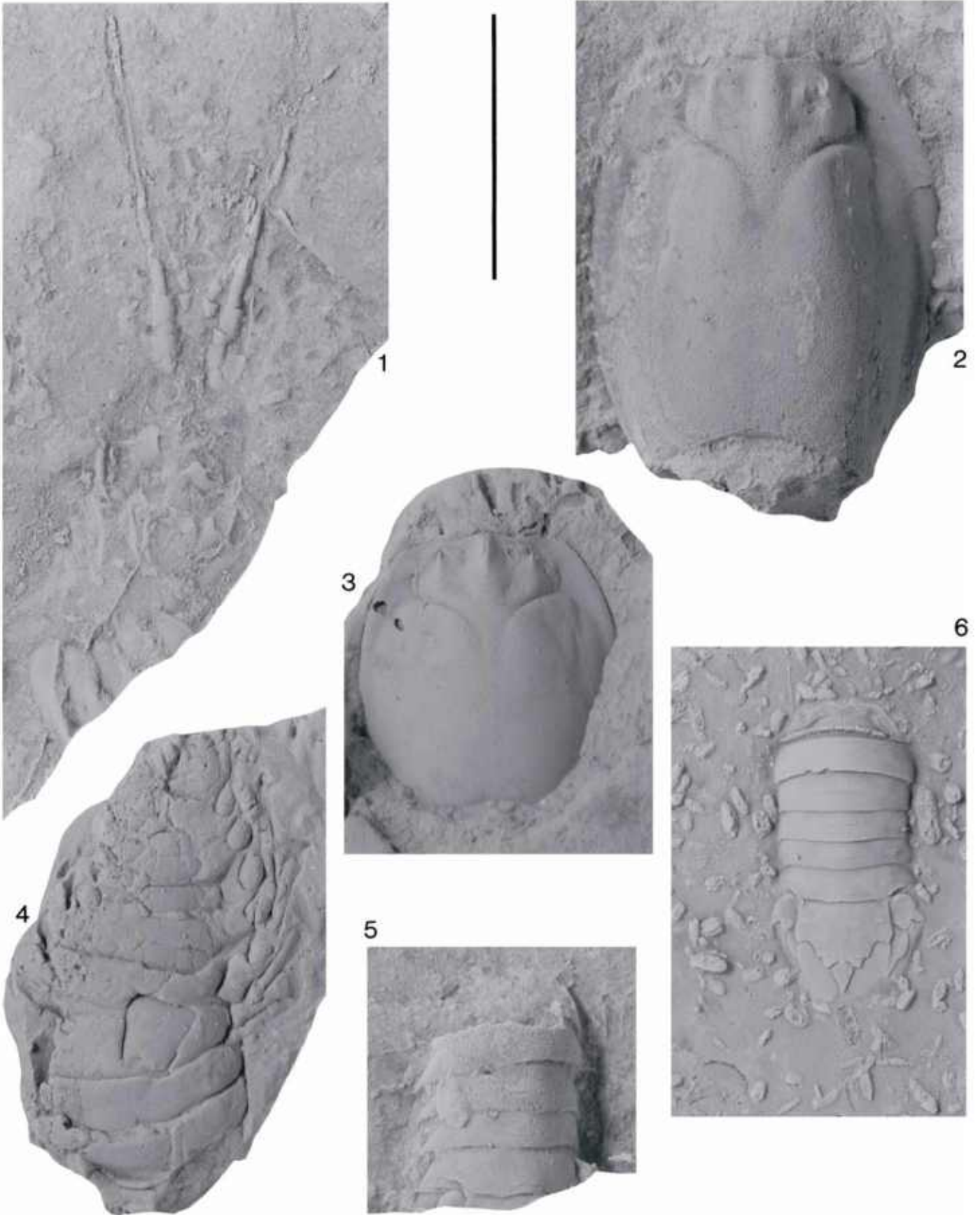


TABLE 1—Measurements (in mm) of *Mamayocaris serendipitous* n. sp. and *Paulocaris schrami* n. sp. from the Petrolia Formation. Abbreviations: Cl, carapace length; Cw, carapace width; Abl, length of abdominal somites; Tel, axial length of telson, including spine.

Taxon	USNM no.	Cl	Cw	Abl	Tel
<i>M. serendipitous</i>					
	486025	15.8	11.8	—	—
	486030	>10.2	8.9	—	—
	486027	>10.7	10.2	—	—
	486031	7.6	6.2	—	—
	486032	16.1	12.4	—	—
	486029	—	—	7.5	3.5
	486033	—	—	>4.2	2.0
	486034	—	—	10.6	—
<i>P. schrami</i>					
	486035	7.1	7.0	—	—
	486036	6.1	6.1	—	—
	486037	11.5	12.2	—	—

and between pleuron and tergum on somites 3–6; pleura 2–5 small, triangular, terminate in sharp apex directed toward posterior; pleuron of somite 6 more bluntly pointed, posterior margin of pleuron 6 with convex curve toward telson. Pleopods of somite 6 expanded into well-developed uropods with smooth, flattened endite and exite, both apparently with smoothly rounded margins. Telson smooth, straight-sided to about midlength, slightly wider posteriorly, becoming narrow posteriorly in two abrupt steps; anteriormost step most prominent, serving as point of attachment of flabellate furcal lobes; posteriormost step less well developed; posterior margin of telson a straight-sided concavity, in which is situated a prominent, elongate, articulating telson spine. At least three pairs of slit-like setal pits situated along margin of telson.

Etymology.—The trivial name alludes to the fortuitous discovery of the first specimen, a very small chip of material in a very small deposit.

Types.—Holotype, USNM 486025, a nearly complete cephalothorax (Fig. 3.2) from locality 5; paratypes, USNM 486026–486034 from locality 2 and locality 5 (Fig. 1).

Measurements.—Measurements are given in Table 1. The total length of the specimen (Cl) may be less than the true carapace length because the anterior margin is not exposed on any specimen. In most specimens, the carapace width (Cw) cannot be taken as the true width of the carapace because of post-mortem crushing. “Abl” is the length, measured along the axis, of abdominal somites 1–6; if fewer somites are preserved, the somites measured are indicated in parentheses. The axial length of the telson (Tel) includes the telson spine.

Occurrence.—Specimens were collected from the Petrolia Formation, Wichita Group, Leonardian Series, Lower Permian, at localities 1 (UTM [Universal Transverse Mercator coordinate] 14SNN04782132, Dundee 7.5' topographic quadrangle, Archer County), 2 (UTM 14SNN01951984, Dundee SW 7.5' topographic quadrangle, Baylor County), 3 (UTM 14SNN08542603, Dundee 7.5', Archer County), 4 (UTM 14SNN00562121, Dundee 7.5' topographic quadrangle, Baylor County), 5 (UTM 14SNN00542128, Dundee 7.5' topographic quadrangle, Baylor County), 6 (UTM 14SNN00142115, Dundee 7.5' topographic quadrangle, Baylor County), and 7 (UTM 14SNN03843164, Dundee 7.5' topographic quadrangle, Baylor County).

Discussion.—The morphologic terminology used herein is consistent with that of Brooks (1969). Although many of the terms refer to biological structures, this usage does not imply direct analogy with so-named structures in higher malacostracans because too little is known about *Mamayocaris serendipitous*.

Two species previously have been assigned to this genus. The type species, *Mamayocaris jepseni* Brooks, 1962, tends to be

smaller than *M. serendipitous* and exhibits several features in the region of the telson that serve to exclude the new species. The basis of the uropod on the type species has a convex distal margin whereas that of *Mamayocaris serendipitous* is scalloped. Similarly, the lateral margins of the telson of the type species is smoothly tapered posterior to the articulation of the furcae whereas that margin on the new species narrows in a step-like manner. *Mamayocaris jepseni* has been reported from the Leonardian Series (Permian) in the middle Clear Fork Group near Lawn, Texas, and from correlative rocks of the Opeche Formation near Rapid City, South Dakota (Brooks, 1962, p.192–193). The specimens were preserved as compressed, articulated individuals, making it difficult to compare aspects of convexity of the carapace of the two species.

Schram (1974) named *Mamayocaris jaskoskii* based upon numerous dorsoventrally compressed, articulated specimens from the Middle Pennsylvanian Essex fauna of Mazon Creek, Illinois. This extended the range of the genus downward into the Pennsylvanian. Several features of this animal distinguish it from *M. serendipitous*. The cervical groove on *M. jaskoskii* is nearly straight across the carapace laterally and becomes very faint and nearly parallel to the midline axially. That groove is convex forward laterally and convergent and strongly developed axially on *M. serendipitous*. The telson on *M. jaskoskii* bears caudal furcae that do not extend beyond the telson spine, and the telson spine is overlain axially by a projection of the telson. By contrast, the telson of *Mamayocaris serendipitous* bears furcae that extend well beyond the tip of the telson spine, and the axial termination of the telson does not exhibit a projection over the spine.

Over 100 specimens of *M. serendipitous* exhibit part or all of the dorsal carapace, the abdomen and telson, or the thoracic sternites with some attached pereopods. Many of the specimens, particularly the carapaces, have been crushed and distorted. Cuticle is present in only one specimen (USNM 486035, the obverse side of which preserves the holotype of a second new species described below), which is dorsoventrally compressed so that the lateral margins have been rotated into the plane of the dorsum. Because the integument appears to have been uniformly very thin and fragile, interior molds of the cuticle may be regarded as accurate expressions of surface morphology. Comparison of the features exhibited on these interior molds with those on the surface of the carapace indicates that surficial detail is expressed on the interior of the carapace. Many of the interior molds exhibit evidence of post-mortem distortion prior to preservation and solution of the carapace. Although remains of the cephalothorax, abdomen, and telson are preserved, none of the specimens is articulated. Thus, it is probable that most of the specimens represent molted individuals. There is no evidence that corpses are present in the sample.

Although Schram (1974) reconstructed *Mamayocaris jaskoskii* as having a cylindrical carapace in cross section, all specimens of *M. serendipitous* indicate that the anterolateral margins of the carapace were turned outward into the horizontal plane. Examination of the surfaces of the specimens gives no indication that they have been broken or distorted. This observation confirms the configuration of the carapace in the type species as described by Brooks (1962).

Family NOTOCARIDIDAE Brooks, 1962

Discussion.—Brooks (1962) included *Paulocaris* Clarke, 1920, and *Notocaris* Broom, 1931, in this family. The cladistic analysis of Taylor et al. (1998) does not support this arrangement; however, this part of their tree is poorly resolved. They noted (p. 830) that it would require better understanding of the southern hemisphere forms to clarify these relationships. Because a restudy of

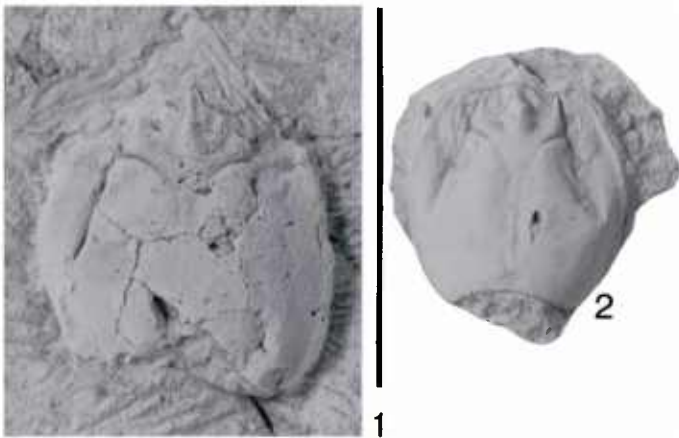


FIGURE 4—*Paulocaris schrami* n. sp. 1, Cephalothorax (holotype, USNM 486035); 2, cephalothorax (paratype, USNM 486036). Bar scale equals 1 cm.

these taxa is beyond the scope of the present work, the classification of Brooks (1962) is used to avoid unnecessary confusion.

Genus PAULOCARIS Clarke, 1920

Type species.—*Paulocaris pachoeoi* Clarke, 1920, p. 135, pl. 2, figs. 1–12, pl. 3, figs. 1–8.

Diagnosis.—Notocaridid with carapace as wide as long, prominent dorsal keel (Brooks, 1969).

Discussion.—The type species is represented by several specimens from the Irati Shale, Lower Permian, of Guarehy, São Paulo, Brazil.

The most useful morphological features serving to associate the specimen with *Paulocaris* include the length/width relationship which mimics that of the brachyurans, the vaulted dorsal surface, and development of the medial ridge and cervical groove. Although there is no evidence that the ventrolateral margins are recurved in the Texas specimens, the other characters so closely resemble those of *Paulocaris* that placement is relatively certain.

Pinto and Adami-Rodrigues (1996) reviewed the pygocephalomorphs from Brazil and South Africa and concluded that three species referred to *Paulocaris*, and all from the Irati Formation, were not referable to that genus. Both *Paulocaris clarkei* Beurlen, 1953, and *P. mariano* Beurlen, 1953, were said to lack the key characters of the genus. We concur. The third taxon, *Paulocaris brasiliensis* Beurlen, 1934, noted by Mezzalana (1971) was apparently a reference to a specimen that is neither *Pygaspis brasiliensis* Beurlen, 1934, nor a species of *Paulocaris* (Pinto and Adami-Rodrigues, 1996, p. 46, pl. 3, fig. 7). Thus, the genus *Paulocaris* includes only the type species and the new species described herein.

PAULOCARIS SCHRAMI new species Figure 4

Diagnosis.—*Paulocaris* with lateral margins becoming more convex anteriorly, strongly developed medial ridge, and lacking thickening of posterior carapace margin.

Description.—Carapace small, quadrate, maximum width slightly greater than length; vaulted with highest region along midline in posterior third of carapace. Lateral margins gently convex, increasing in convexity near the posterolateral corners. Posterior margin smoothly and deeply concave. Anterolateral margins inclined obliquely toward frontal region, which is broken. Dorsal surface divisible into four regions by medial ridge and cervical groove. Medial ridge narrow and prominent in cephalic region,

becoming less well defined near junction with cervical groove, terminating just in advance of posterior margin. Cervical groove deeply impressed, originating at midline near center of carapace, intercepting midline at approximately 35 degree angle, curving anterolaterally to point about three-fifths the distance from midline to lateral border, where it curves abruptly toward the anterior. Gastric region with anteriorly directed, nodose ridge. Branchial regions generally smooth, lateral margins of branchial regions folded tightly ventrally.

Abdominal region and appendages unknown.

Etymology.—In honor of Dr. Frederick Schram, who has contributed much to our understanding of North American malacostracans.

Types.—Holotype, USNM 486035, partial cephalothorax (Fig. 4.1) from locality 5 (UTM 14SNN00542128), Dundee 7.5' topographic quadrangle; paratypes, USNM 486036 (Fig. 4.2) and 486037, partial cephalothoraxes from locality 2 (UTM 14SNN01951984), Dundee SW 7.5' topographic quadrangle.

Measurements.—Measurements are given in Table 1. Carapace length (Cl) is less than the total length because the anterior of the carapace is not well preserved in any specimen.

Occurrence.—Specimens were collected from the Petrolia Formation, Wichita Group, Leonardian Series, Lower Permian at locality 2 (UTM 14SNN01951984, Dundee SW 7.5' topographic quadrangle, Baylor County), and locality 5 (UTM 14SNN00542128, Dundee 7.5' topographic quadrangle, Baylor County).

Discussion.—The material referred to this taxon consists of one inflated and one crushed mold of the interior of the dorsal carapace and several fragmentary specimens of the cephalothorax. Although the anterior margin is broken away or absent, the general outline and the convexity of the carapace are clearly shown on the inflated specimen. There is some evidence of distortion, particularly on the left lateral region, but the lateral compression of the region can clearly be identified when compared to the undistorted right side of the specimen. Because none of the specimens is articulated and the remains are limited to cephalothoraxes, it is probable that the specimens are from molted individuals.

Paulocaris has not been reported previously from deposits outside Brazil. Although the Texas specimens are few and incomplete, major features of the carapace are shared with those of the type species, *P. pachoeoi*. These include the general shape, vaulted dorsal surface, and development of the medial ridge and cervical groove. The recurved ventrolateral margins of *P. schrami* are not evident in *P. pachoeoi*.

Paulocaris pachoeoi is larger than *P. schrami* and has a more uniformly convex lateral margin and a smoother dorsal surface. The medial ridge of *Paulocaris pachoeoi* tends to be more strongly developed than that of *P. schrami*. The posterior margin of the type species is reported to be thickened and, occasionally, dissociated from the carapace (Clarke, 1920, pl. 3, figs. 6 and 7). No similar thickening is observed on *Paulocaris schrami*. There is little doubt that the two forms are distinct from one another but that, given the present classification of Paleozoic malacostracans, they are best assigned to the same genus.

ASSOCIATED BIOTA

Plants.—Plant assemblages of low diversity, ranging from four to 10 species, are preserved with the pygocephalomorph remains. Although conifer remains are common as three-dimensional impressions on the surface of the fossiliferous limestones, preservation is much better and floral diversity is greater in associated claystones that were excavated for plant collections at localities 2, 3, and 7 (Fig. 1, Table 2). At these localities, plant fossils are fragmentary and include both vegetative remains and reproductive organs. Conifers are the most commonly encountered fossils, with

TABLE 2—Plant taxa in rank-order abundance found in association with pygocephalomorphs of the Petrolia Formation at localities 2, 3, and 7; USNM collection numbers, total number of specimens per locality, and number of specimens per identification indicated.

Locality 2 (USNM 40032, 40033), 161 specimens total	
<i>Ernestiodendron</i> sp.	65
<i>Pecopteris</i> cf. <i>P. cyathea</i>	2
Calamite stem	1
Unidentified flabellate leaf	1
Locality 3 (USNM 40020), 264 specimens total	
<i>Ernestiodendron</i> sp.	106
<i>Walchia</i> cf. <i>schneiderii</i>	67
<i>Autunia conferta</i>	46
<i>Odontopteris</i> sp.	8
Unidentified flabellate leaves	5
<i>Taeniopteris</i> sp.	2
<i>Compsopteris</i> sp.	2
<i>Gigantopteridium americanum</i>	2
<i>Walchia pinniformis</i>	1
Calamite stem	1
Locality 7 (USNM 40626, 40627), 70 specimens total	
Unidentified conifer with long, broad, lax leaves	12
<i>Ernestiodendron</i> sp.	11
cf. <i>Culmitschia speciosa</i>	11
<i>Walchia</i> cf. <i>W. schneiderii</i>	8
Calamite stems	8
<i>Sphenopteridium</i> sp.	5
<i>Gigantopteridium americanum</i>	3
<i>Taeniopteris</i> sp.	3
<i>Walchia hypnoides</i>	2

only minor amounts of non-coniferous foliage. Fish scales or whole fish, spirorbids, myalinid pelecypods, and conchostracans are intermixed with plant remains at all three sites. Minor amounts of fusain also occur in association with the fossils.

Of the conifers, *Ernestiodendron* sp. occurs at all three sites and was the most common element at two of the localities. Other conifers include forms with long, lax leaves, one resembling *Walchia schneiderii*; an unattributed, rare specimen similar in form to *W. pinniformis* and *W. hypnoides*; and a conifer with foliage resembling *Culmitschia speciosa*. Calamite stems are rare at all three sites. Other plants that occur at two sites include *Taeniopteris* sp. and *Gigantopteridium americanum*. *Sphenopteridium* sp., *Autunia conferta*, *Odontopteris* sp., *Compsopteris* sp., and *Pecopteris* sp., and two kinds of unidentifiable flabellate foliage occur at one site only. A diversity of seeds, cone scales, and bracts occurred in each deposit, often in abundance.

Invertebrates.—Spirorbid worm tubes are preserved with the pygocephalomorphs in gray claystones at localities 2 and 3 (Fig. 1). Conchostracans occur in association with the pygocephalomorphs at localities 1, 2, 3, 6, and 7. A few poorly preserved conchostracans are found as impressions on the limestone bed. By contrast, abundant, well-preserved conchostracans occur in dark gray claystones that are associated with fossiliferous limestone beds at localities 2, 3, and 7, which were excavated for plant remains. Myalinid pelecypods also occur at these three localities.

Vertebrates.—Fish, amphibian, and reptile remains found associated with the pygocephalomorph-bearing beds reflect part of the diversity of vertebrate assemblages known from the Petrolia Formation (Table 3). Most of the specimens from localities 2, 3, and 7 were found in fossil-plant excavations of dark gray claystones associated with the fossiliferous limestone. The remaining localities were not excavated and their collections represent surface samples.

The acanthodian *Acanthodes*, the palaeoniscoid *Platysomus* [=

TABLE 3—Vertebrate taxa found in association with pygocephalomorphs of the Petrolia Formation. Numbers in parentheses indicate localities shown on Figure 1.

Chondrichthyes	
Undetermined hybodont spine	(1)
Acanthodii	
<i>Acanthodes</i>	(3)
Osteichthyes	
<i>Platysomus</i> sp.	(2)
<i>Sagenodus</i> sp.	(1)
<i>Spermatodus pustulosus</i>	(1)
Undetermined small fusiform palaeoniscoids	(1, 3, 7)
Amphibia	
<i>Diplocaulus</i> sp.	(1)
<i>Eryops megacephalus</i>	(1)
<i>Trimerorhachis insignis</i>	(1, 4, 5)
Reptilia	
<i>Ctenospondylus</i> sp.	(1)
<i>Dimetrodon</i> sp.	(1, 2, 5)

Schaefferichthys; see Zidek, 1992], and the fusiform palaeoniscoids are represented by small (<5 cm), nearly complete individuals. The hybodont spine, the lungfish *Sagenodus*, the coelacanth *Spermatodus*, the amphibians *Diplocaulus* and *Eryops*, and the pelycosaur *Ctenospondylus* are recorded by isolated elements found at the surface. Remains of the perennibranchiate amphibian *Trimerorhachis* and the pelycosaur *Dimetrodon* are preserved in the pygocephalomorph-bearing limestone at locality 5.

Two aspects of this vertebrate record are anomalous. First, the complete absence of xenacanth sharks is unusual because their remains, particularly teeth, are common to abundant in other channel-fill deposits within the Petrolia Formation in the field area. Second, the occurrence of the amphibian *Diplocaulus* is unexpected; although this genus is the most common amphibian found in the overlying Clear Fork Group, it is almost unknown in the Wichita Group (Hook, 1989). The identification of this taxon at locality 1 is based upon a highly distinctive tabular horn and diagnostic trunk vertebrae.

PALEOENVIRONMENTAL CONDITIONS

The sedimentologic aspects of the pygocephalomorph-bearing beds of the Petrolia Formation indicate that these deposits formed in standing-water conditions within abandoned segments of high-sinuosity, suspended-load, fluvial channels. The fossiliferous limestones and dark gray claystones record a range of paleoenvironmental conditions. Abundant invertebrate fecal pellets preserved in the limestone indicate that the cutoff lakes teemed with invertebrate life. The three-dimensional preservation of pellets and fossil remains in the limestones suggests that the carbonate muds were rapidly lithified, and that the limestones record minimal time averaging. In contrast, fossils in the claystones are flattened into two dimensions and occur in several bedding planes. Some bedding surfaces contain abundant conchostracan carapaces, which suggests intermittent anoxic conditions.

A lack of in situ pedogenic features in the fossiliferous first storey at locality 2 (Fig. 2) indicates that water depth in the small cutoff lake precluded plant growth. The actual channel depth cannot be determined because lateral-accretion beds of the second storey scoured down into the mudstones of the lower storey. Similar conditions existed at localities 4, 5, and 7, thus indicating the recurrence of small, permanent (for periods >100 yr; see Olson, 1977; Behrensmeier and Hook, 1992) floodplain lakes through an interval of approximately 100 m.

Previous occurrences of *Mamayocaris* and *Paulocaris* have

been attributed variously to marine, brackish, or freshwater settings without much site-specific sedimentologic data. Brooks (1962) strongly favored a lagoonal environment for *M. jepseni* and *Paulocaris* and regarded them as euryhaline. Schram (1981) considered *Paulocaris* to be a brackish to freshwater organism and *Mamayocaris* to be nearshore marine. *Mamayocaris jaskoskii* occurs in the Late Carboniferous marine to brackish water Essex assemblage of Mazon Creek, Illinois. The Essex assemblage, however, does include well-preserved fully terrestrial remains, notably the dissorophoid amphibian *Amphibamus*. In our collections, several fish taxa found in association with the pygocephalomorphs also are known from brackish as well as freshwater deposits. However, well-preserved terrestrial plants, amphibious to terrestrial vertebrate remains, and sedimentologic and stratigraphic data indicate that the *Petrolia* occurrences represent freshwater assemblages.

EVOLUTIONARY AND PALEOECOLOGICAL IMPLICATIONS

The biota and paleoenvironment of the pygocephalomorph-bearing deposits in the *Petrolia* Formation indicate that Lower Permian freshwater invertebrates of North-Central Texas mirror evolutionary and paleoecologic patterns found in coeval plant and vertebrate records. The earliest occurrence of *Mamayocaris* is in coal-bearing Upper Carboniferous rocks. Nearly all the plants and vertebrates found in association with the pygocephalomorphs in the *Petrolia* Formation likewise have generic or familial representation in coal-bearing Upper Carboniferous rocks of Texas, the Midcontinent, the Southwest, or the Dunkard Basin of the Appalachians. Vertebrate paleontologists have long recognized the relictual nature of assemblages from the Wichita Group (Romer, 1928, 1935; Olson, 1952, 1985), and ongoing paleobotanical studies have identified a similar pattern of Carboniferous-aspect plants in parts of the Wichita Group (DiMichele et al., 1991).

In North-Central Texas, the depositional context of these relictual plant and animal assemblages invariably is some variety of a local claystone-rich channel fill. These standing-water floodplain lakes probably represent the only preserved record of Early Permian environments that are somewhat comparable edaphically to the more extensive, poorly drained, peat-forming environments of the Late Carboniferous. The Early Permian plant record of the region suggests that the floodplain lakes and surrounding settings were evolutionary refugia during a time of floristic change in better-drained, nearby environments. In this regard, the new crustacean data from the *Petrolia* Formation corroborate the observations of Schram (1981, p. 132), who noted that Early Permian pygocephalomorph genera of his brackish water community, which included *Paulocaris*, persisted, "even at a time when the Paleozoic crustacean fauna was undergoing some cataclysmic changes." The youngest record of *Mamayocaris* is from the Clear Fork Formation of Taylor County, Texas; the sedimentologic context of this occurrence, which is remarkably similar to that of the fossiliferous claystones reported above, was interpreted as a small lake within a paralic setting by Olson and Mead (1982).

CONCLUSIONS

The discovery of abundant Early Permian pygocephalomorphs in association with well-preserved plants, conchostracans, fishes, amphibians, and reptiles in recurring claystone-dominated channel fills of the continental *Petrolia* Formation provide new information on the paleoenvironmental, paleoclimatic, and paleoecologic setting of the *Petrolia* Formation. The deposits originated as abandoned-channel segments that developed into floodplain lakes. These lakes supported a fairly diverse aquatic fauna and were flanked by streamside terrestrial plant and animal communities. Because the pygocephalomorphs, along with nearly all of the vertebrate and some of the plant taxa, have direct phylogenetic ties

to forms known from coal-bearing Upper Carboniferous rocks, these assemblages are regarded as relictual. Their occurrence in restricted, poorly drained floodplain settings indicates that they were ecologic refugia that resembled the edaphic conditions of earlier Permo-Carboniferous times.

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REFERENCES

- BEHRENSMEYER, A. K., AND R. W. HOOK (RAPORTEURS). 1992. Paleoenvironmental contexts and taphonomic modes, p. 15–136. In A. K. Behrensmeier, J. D. Damuth, W. A. DiMichele, R. Potts, H.-D. Sues, and S. L. Wing (eds.), *Terrestrial Ecosystems through Time*. University of Chicago Press, Chicago.
- BEURLEN, K. 1930. Vergleichende Stammesgeschichte Grundlagen, Methoden, Probleme unter besonderer Berücksichtigung der höheren Krebse. *Fortschrift der Geologie und Paleontologie*, 8:317–586.
- BEURLEN, K. 1934. Die Pygaspiden, eine neue Crustaceen-(Entomostraceen)-Gruppe aus den Mesosaurier führenden Iraty-Schichten Brasiliens. *Paläontologische Zeitschrift*, 16:122–138.
- BEURLEN, K. 1953. O gênero *Paulocaris* Clarke nas camadas Iratí do Brasil Meridional. *Notas Preliminares e Estudos, Divisão de Geologia e Mineralogia, DNPM*, 65:1–8, pl. 1.
- BÖSE, E. 1917. On some new ammonoids and the succession of the ammonoid-bearing horizons of the Permo-Carboniferous in Central Texas. *University of Texas Bulletin*, 1762:183–210.
- BROOKS, H. K. 1962. The Paleozoic Eumalacostraca of North America. *Bulletins of American Paleontology*, 44:163–338.
- BROOKS, H. K. 1969. Eocarida, p. R332–345. In R. C. Moore (ed.) *Treatise on Invertebrate Paleontology*, Pt. R, Arthropoda 4. Geological Society of America and University of Kansas Press, Lawrence.
- BROOM, R. 1931. On the *Pygocephalus*-like crustacean of the South African Dwyka. *Proceedings of the Zoological Society, Pt. II*, p. 571–573.
- CHANEY, D. S., W. A. DIMICHELE, R. W. HOOK, AND S. H. MAMAY. 1993. Paleocological implications of plant assemblages from red beds of the Arroyo Formation (Leonardian, Permian) of North-Central Texas. *American Journal of Botany*, 80(6):88.
- CHANEY, D. S., W. A. DIMICHELE, S. H. MAMAY, R. W. HOOK, AND W. J. NELSON. 1997. A new flora from the evaporite-bearing Blaine Formation (Pease River Group, Lower Permian) of King County, Texas. *American Journal of Botany* 84(6):131.
- CLARKE, J. M. 1920. Crustacea from the Permian of São Paulo, Brazil. *New York State Museum Bulletin*, 219–220:135–137.
- DIMICHELE, W. A., AND R. W. HOOK (RAPORTEURS). 1992. Paleozoic terrestrial ecosystems, p. 204–325. In A. K. Behrensmeier, J. D. Damuth, W. A. DiMichele, R. Potts, H.-D. Sues, and S. L. Wing (eds.), *Terrestrial Ecosystems through Time*. University of Chicago Press, Chicago.
- DIMICHELE, W. A., R. W. HOOK, AND D. S. CHANEY. 1997. Linking environmental and biotic change in the Late Paleozoic tropics: The record from North-Central Texas. *EOS Transactions* 78(17, Supplement):S178.
- DIMICHELE, W. A., R. W. HOOK, S. H. MAMAY, AND D. A. WILLARD. 1991. Paleocology of Carboniferous-Permian transitional vegetation in North-Central Texas. *American Journal of Botany*, 78(6):111–112.
- HENTZ, T. F. 1988. Lithostratigraphy and paleoenvironments of upper Paleozoic continental red beds, North-Central Texas: Bowie (new) and Wichita (revised) Groups. The University of Texas at Austin Bureau of Economic Geology, Report of Investigations, 170:1–55.
- HENTZ, T. F., AND L. F. BROWN, JR. 1987. Wichita Falls-Lawton Sheet.

- The University of Texas at Austin Bureau of Economic Geology, Geologic Atlas of Texas, scale 1:250,000.
- HOOK, R. W. 1989. Stratigraphic distribution of tetrapods in the Bowie and Wichita Groups, Permo-Carboniferous of North-Central Texas, p. 47–53. *In* R. W. Hook (ed.), *Permo-Carboniferous Paleontology, Lithostratigraphy, and Depositional Environments of North-Central Texas. Field Trip Guidebook 2, Annual Meeting of the Society of Vertebrate Paleontology, Austin, Texas.*
- HOOK, R. W., N. HOTTON, III, AND T. F. HENTZ. 1989. Paleoenvironmental analysis of Lower Permian vertebrate-bearing deposits in North-Central Texas: preliminary report. *Geological Society of America Abstracts with Program*, 21(1):15.
- KEMP, A. H. 1962. The stratigraphic and geographic distribution of cephalopod genera in the Lower Permian of Baylor County, North Central Texas. *Journal of Paleontology*, 36:1124–1127.
- LATREILLE, P. A. 1802–1803. *Histoire naturelle, général et particulière, des crustacés et des insectes. Volume 3.* F. Dufart, Paris, 468 p.
- MAMAY, S. H. 1976. Paleozoic origin of cycads. U.S. Geological Survey Professional Paper, 934, 49 p.
- MEZZALIRA, S. 1971. Contribuição ao conhecimento da geologia de sub-superfície e da paleontologia da Formação Irati no Estado de São Paulo. *Anais da Academia Brasileira de Ciências*, 43(suplemento):273–336.
- OLSON, E. C. 1952. The evolution of a Permian vertebrate chronofauna. *Evolution*, 6:181–196.
- OLSEN, E. C. 1977. Permian lake faunas: a study in community evolution. *Journal of the Palaeontological Society of India*, 20:146–163.
- OLSEN, E. C. 1985. Permo-Carboniferous vertebrate communities. Ninth International Congress of Carboniferous Stratigraphy and Geology, *Compte Rendu*, 5:331–345.
- OLSEN, E. C., AND J. G. MEAD. 1982. The Vale Formation (Lower Permian): its vertebrates and paleoecology. *Texas Memorial Museum Bulletin*, 29:1–46.
- PINTO, I. D., AND K. ADAMI-RODRIGUES. 1996. Pygocephalomorph Crustacea. New data and interpretations, with emphasis on Brazilian and South African forms. *PESQUISAS*, 23:41–50.
- READ, C. B., AND S. H. MAMAY. 1964. Upper Paleozoic floral zones and floral provinces of the United States. U. S. Geological Survey Professional Paper 454-K:K1–K35.
- ROMER, A. S. 1928. Vertebrate faunal horizons in the Texas Permo-Carboniferous red beds. *University of Texas Bulletin*, 2801:67–108.
- ROMER, A. S. 1935. Early history of Texas redbeds vertebrates. *Geological Society of America Bulletin*, 46:1597–1658.
- ROMER, A. S. 1974. The stratigraphy of the Permian Wichita redbeds of Texas. *Breviora*, 427:1–31.
- SCHRAM, F. R. 1974. Mazon Creek caridoid Crustacea. *Fieldiana: Geology*, 30:9–65.
- SCHRAM, F. R. 1981. Late Paleozoic crustacean communities. *Journal of Paleontology*, 55:126–137.
- TAYLOR, R. S., S. YAN-BIN, AND F. R. SCHRAM. 1998. New pygocephalomorph crustaceans from the Permian of China and their phylogenetic relationships. *Palaeontology*, 41:815–834.
- ZIDEK, J. 1992. Late Pennsylvanian Chondrichthyes, Acanthodii, and deep-bodied Actinopterygii from the Kinney Quarry, Manzanita Mountains, New Mexico. *New Mexico Bureau of Mines and Mineral Resources Bulletin*, 138:145–182.

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