

THE PRESUMED DECAPOD, *PALAEOPEMPHIX* GEMMELLARO, 1890, IS A UNIQUE MEMBER OF THE PHYLLOCARIDA (PALAEOPEMPHICIDA: PALAEOPEMPHIDAE)

RODNEY M. FELDMANN,¹ ALESSANDRO A. GARASSINO,² AND CARRIE E. SCHWEITZER³

¹Department of Geology, Kent State University, Kent, Ohio 44242, <rfeldman@kent.edu>,

²Museo di Storia Naturale di Milano, Milano, Italy, <a.garassino@tin.it>, and

³Department of Geology, Kent State University Stark Campus, Canton, Ohio 44720, <cschweit@kent.edu>

ABSTRACT—Reevaluation of 21 specimens of Permian crustaceans from near Palermo, Italy, referred to *Palaeopemphix* Gemmellaro, 1890, has resulted in transfer of the genus from the decapod Crustacea to a new suborder, the Palaeopemphida, and a new superfamily, Palaeopemphidae, of the archaostrocan Phyllocarida.

INTRODUCTION

THE SEARCH for the rootstock of the decapod Crustacea has resulted in the discovery of numerous Paleozoic organisms that bear some similarity to Mesozoic and Cenozoic shrimp, lobsters, and crabs. Several of these decapodlike creatures have been suggested to be early representatives of the group (Gemmellaro, 1890; Schram et al., 1978; Schram and Mapes, 1984); however, the vagaries of preservation of arthropods has made it difficult to ascertain ancestry of the Decapoda with any degree of certainty. Herbig (1993) suggested that Late Devonian coprolites from Morocco exhibited distinctive internal morphology that confirmed the presence of decapods in those rocks; however, this suggestion is conjectural because no remains of hard parts were associated with the coprolites. Because crustaceans tend to fragment upon death and decomposition, often only the more durable, isolated fragments are preserved. The appendages tend to be more fragile and less calcified than the carapace, and they and the abdominal somites are often not preserved. Conclusions about ancestry, therefore, are often drawn only from carapace material. Such is the case with *Palaeopemphix* Gemmellaro, 1890. It is the purpose of this work to reexamine the type material of *Palaeopemphix*, a Permian arthropod originally assigned to the Decapoda, and to reevaluate its systematic position.

Gemmellaro described the new genus *Palaeopemphix* based upon a large, but now indeterminate, number of specimens collected from allochthonous blocks of limestone (Gemmellaro, 1890) found in the Pietra di Salamone, along the Sosio River, Palermo Province, Italy (Catalano et al., 1992). The Pietra di Salamone (“Rock of Solomon”) is a large rock (200 m × 84 m × 30 m; Miller, 1933, p. 409) associated with two other large blocks of limestone found in the Sosio Klippe (Miller, 1933; Catalano et al., 1992). Miller (1933) corroborated the Permian age of the Pietra di Salamone based upon ammonoids and nautiloids; he also suggested that the unit was correlative with the Word Formation of Texas (p. 423).

Later, the names Lercara and Mufara formations were applied to the rocks exposed in the Sosio blocks (Schmidt di Friedberg, 1964–1965). However, Catalano et al. (1992) suggested abandoning the term “Lercara Formation” based upon the variable lithology of these rocks. The Lercara Formation, as originally defined, included Early Permian flysch, Middle Permian olistostromal limestones, and Late Permian claystones. The Mufara Formation appears to be Late Triassic in age (Catalano et al., 1992). It seems most likely that the phyllocarids described herein were collected from the olistostromal limestone member of the “Lercara Formation,” based upon their presence in a vuggy, fossiliferous, calcareous matrix with small solution pits that are

filled with secondary calcite crystals. The phyllocarids were associated with *Fusulina* sensu lato, cephalopods and gastropods, which led Gemmellaro (1890, p. 1) to conclude that the rocks were Permian in age. Based upon more recent work, the fossils are most likely Middle Permian in age (Catalano et al., 1992).

The specimens were associated with a wide range of arthropods, including trilobites, ostracodes, and two strange hemispherical forms which he assigned to the Decapoda, *Paraprosopon* Gemmellaro, 1890 and *Oonocarcinus* Gemmellaro, 1890. These latter two genera were considered to be related to the Brachyura by Gemmellaro; however, they neither bear resemblance to true crabs nor to decapods in general. Glaessner (1928, p. 394; 1969, p. R569) placed both taxa in the enigmatic superfamily Cycloidea Glaessner, 1928, and considered *Paraprosopon* to be the junior synonym of *Cyclus* de Koninck, 1841. Based upon a cladistic analysis of the type genus, *Cyclus* de Koninck, 1841, Schram et al. (1997) elevated the superfamily Cycloidea to ordinal rank and referred it to the Class Maxillopoda Dahl, 1956. These taxa will not be considered further.

SYSTEMATIC PALEONTOLOGY

Subclass PHYLLOCARIDA Packard, 1879

Order ARCHAEOSTRACA Claus, 1888

Discussion.—The Phyllocarida historically has been subdivided in several different ways. Rolfe (1969) subdivided the group into three orders, of which two are extinct. The extant Leptostraca Claus, 1880 and the extinct Hymenostroaca Rolfe, 1969 are both characterized by possession of relatively simple, thin, flexible carapaces that lack a hinge line (Rolfe, 1969; Martin and Davis, 2001). In contrast, the Archaostroaca, members of which range from the Early Ordovician to Late Triassic (Rolfe, 1969), exhibit hinged carapaces that may be simple or highly complex and tend to be thick and durable. Subsequent to Rolfe’s work, Schram (1986) recognized two additional orders, the Canadaspidida Novozhilov, 1960 and the Hoplostraca Schram, 1973. The Canadaspidida, characterized by a bivalved carapace lacking both a rostral and a dorsal plate, is a Cambrian group. The Hoplostraca is a small, enigmatic group of Carboniferous arthropods with a distinctly elongate carapace drawn out into a narrow front.

The carapace of *Palaeopemphix* is highly complex; a series of grooves, swollen regions, and marginal thickenings distinguish the genus from known genera within the Leptostraca, Hymenostroaca, Canadaspidida, or the Hoplostraca. Although there is no decisive evidence for the existence of a true hinge in specimens of *Palaeopemphix*, a hinge structure can be inferred. All specimens of *Palaeopemphix* are preserved as single right and left valves only, with no vestige of other fragments attached, strongly suggesting that it was bivalved. The specimens available for study

are preserved as molds of the interior of the carapace. Because of the historic value and type status of the specimens, it was not possible to prepare them further. The carapace is presumed to be rigid because the molds are never distorted. Thus it is probable that the carapace of *Palaeopemphix* was thick, rigid, and quite possibly calcified. This combination of characters is found only within the Archaeostraca. The carapace size, ranging from 6.2 to 15 mm, is small-sized for archaeostracans.

Taken as a group, the Archaeostraca are probably the most variable of the phyllocarids with regard to size, carapace outline, and carapace ornamentation. Species within the order range in carapace length from 4 mm (Hannibal and Feldmann, 1997) to at least 93 mm (Stumm and Chilman, 1969). Carapace outline varies from a smoothly rounded outline as in, for example, *Aristozoe* Barrande, 1872, to the elongate, triangular form of *Tropidocaris* Beecher, 1884 and *Elymocarid* Beecher, 1884. Some taxa bear spines along the margin as seen on *Pephricarid* Clarke, 1898. However, of all the morphological variables, carapace surface ornamentation is most variable. Several genera are characterized by possession of smooth carapaces, whereas others have one or more transverse or longitudinal ridges. Swollen areas variously interpreted as adductor muscle scar attachment sites or sessile eyespots have been described in other taxa. Although groove patterns are less common in phyllocarids than they are in the macruran decapod crustaceans, several genera do exhibit distinctive groove patterns. Perhaps the most heavily ornamented phyllocarid is the Middle Devonian to Late Mississippian *Echinocaris* Whitfield, 1880, within the archaeostracan suborder Ceratiocarina. Nodose ridges, groove patterns, and swollen regions are diagnostic of this genus (Hannibal, 1990; Rode and Lieberman, 2002) (Fig. 1.6). Thus *Palaeopemphix* lies well within the range of variation of characters observed in the order. However, it cannot be referred to any of the existing suborders.

It is important to note that the Phyllocarida has, to some extent, served as a catch-all taxon. For example, Rolfe (1969) recognized more genera (24) of uncertain order and family than he did genera within the Archaeostraca (21). The latter number is probably inflated. For example, Pinna et al. (1982) erected a new crustacean class, the Thylacocephala Pinna, Arduini, Pesarini, and Teruzzi, 1982, and suggested that the genera *Austriocaris* Glaessner, 1931 and *Concavicularid* Rolfe, 1961 could be referred to that class. These two genera were previously considered to be archaeostracans. Although it is not the purpose of this work to reexamine the entire order, it is interesting to note that Schram (personal commun., 2003) noted that if the Phyllocarida contain taxa that are better placed elsewhere, there is equal likelihood that taxa erroneously assigned elsewhere could better be referred to the Phyllocarida.

Suborder PALAEOPEMPHIDA new suborder

Included family.—Palaeopemphidae, new family.

Diagnosis.—Archaeostracan with robust, convex carapace; anterior margin with concave re-entrant at presumed site of eyestalk; carapace groove pattern consisting of one, or in some species two, anteroventrally directed grooves and one posteroventrally directed groove; possibly an intercalated rostral plate; and a well-developed lateromarginal carina (doublure).

Discussion.—Rolfe (1969) recognized two suborders within the Archaeostraca, the Ceratiocarina Clarke in Zittel, 1900 and the Rhinocarina Clarke in Zittel, 1900. With regard to characters of the carapace, these two suborders are readily distinguished on the basis of presence, in the Rhinocarina, or absence, in the Ceratiocarina, of a median dorsal plate. Both typically possess a rostral plate. The morphology and relative position of these plates is well illustrated by Rolfe (1969, fig. 146.1, 146.4). Possession of a rostral plate in *Palaeopemphix* is inferred from the form of the dorsal

margin; a concavity along the anterior end of the dorsal margin is interpreted to be the site of insertion of the rostral plate. *Palaeopemphix* is more closely allied to the Ceratiocarina s. Rolfe (1969) because there is no evidence of a median dorsal plate.

Recently, Rode and Lieberman (2002) provided a concise history of classification of the Phyllocarida, focusing on the Archaeostraca, and conducted a cladistic analysis of the Devonian phyllocarids. In so doing, they rearranged the subordinal categories of the Archaeostraca. Their rearrangement reduced the Ceratiocaridina to include only the family Ceratiocarididae Salter, 1860; created the Pephricaridina Van Straelen, 1933, by bringing together the Ohiocaridae, Rolfe, 1962 (removed from the Rhinocarina), and the Pephricarididae Van Straelen, 1933; placed essentially the remainder of the Ceratiocarina, s. Rolfe (1969) in the Echinocaridina Clarke in Zittel, 1900; and retained the Rhinocaridina sans Ohiocarididae more or less in the sense of Rolfe (1969).

Examination of the diagnoses of these suborders s. Rode and Lieberman suggests that it may be difficult to unequivocally distinguish members of the Pephricaridina because the diagnoses of the suborders are not parallel. Some of the characters used to define the Pephricaridina, such as the shape of the posterior margin, are shared with genera in other suborders. In addition, the Ohiocarididae exhibit a large mid-dorsal plate and a very long hinge line, and the Pephricarididae lack a mid-dorsal plate and have a very short hinge line. These would appear to be major morphological differences. The most diagnostic and unifying feature of the Pephricaridina is the oblique fold that crosses most of the carapace from near the anterodorsal margin to near the posteroventral corner. No comparable feature is seen on any other phyllocarid to our knowledge; however, the suborder is not sufficiently differentiated by just one character.

Palaeopemphix cannot be referred to the Ceratiocarina, considered either in the sense of Rolfe (1969) or of Rode and Lieberman (2002), without expanding the concept of the taxon markedly. *Palaeopemphix* bears a distinctive, well-developed pattern of transverse grooves that distinguish it from all other phyllocarids as well as from the Decapoda. The absence of any archaeostracans with morphologies similar to, or intermediate between, the defined suborders, either in the sense of Rolfe or Rode and Lieberman, and *Palaeopemphix* supports the introduction of a new suborder.

The most distinctive features of the Palaeopemphida are the groove extending posteroventrally across the carapace, the well-developed carapace re-entrants that are in the inferred position of the eyestalks, and the well-developed lateromarginal carina or doublure. This combination of features clearly distinguishes palaeopemphids from all other archaeostracans and precludes placement within the Decapoda.

Family PALAEOPEMPHIDAE new family

Included genus.—*Palaeopemphix* Gemmellaro, 1890, p. 17.

Diagnosis.—As for suborder.

Genus PALAEOPEMPHIX Gemmellaro, 1890

Palaeopemphix GEMMELLARO, 1890, p. 17.

Type species.—*Palaeopemphix sosisiensis* Gemmellaro, 1890, by subsequent designation herein.

Other species.—*Palaeopemphix meyeri* Gemmellaro, 1890; *Palaeopemphix affinis* Gemmellaro, 1890.

Diagnosis.—Small-sized phyllocarids, carapace length ranges from 6.2 to 15 mm; carapace bivalved; slightly longer than high; preserved dorsal margin slightly arched with concavity at anterior end and shallow indentations where posterior and, when present, medial grooves intercept margin; posterior margin recurved with strong marginal carina and deep postmarginal groove; ventral

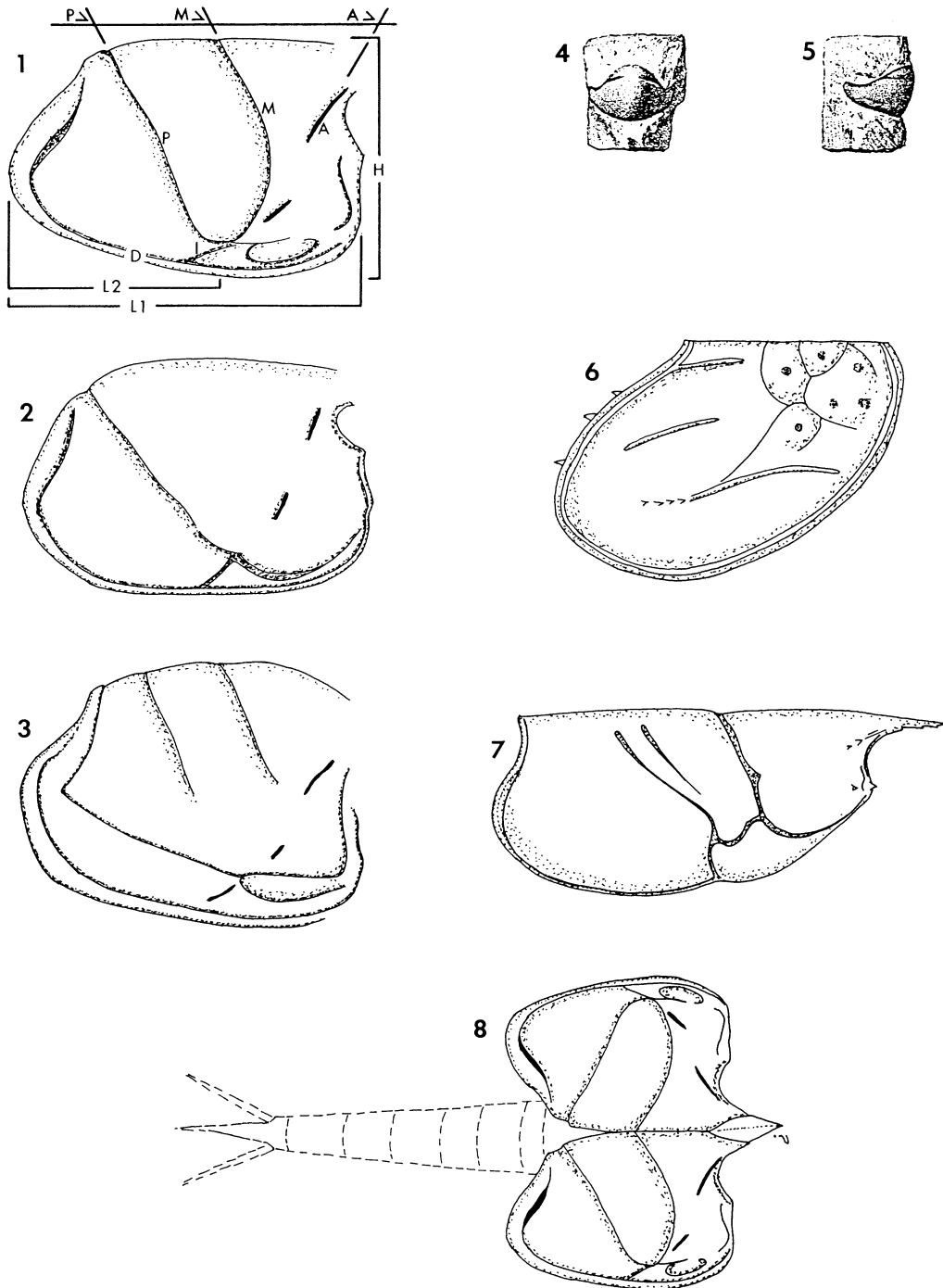


FIGURE 1—1, *Palaeopemphix sosisiensis* Gemmellaro, 1890, approximately $\times 5$. The position and orientation of measurements recorded in Table 1 are indicated. A = anterior groove, D = doublure, M = medial groove, P = posterior groove. 2, *Palaeopemphix meyeri* Gemmellaro, 1890, approximately $\times 5$. 3, *Palaeopemphix affinis* Gemmellaro, 1890, approximately $\times 5$. 4, 5, Reproductions of the illustrations of the sole pleon preserved with *Palaeopemphix* and attributed to *P. sosisiensis* by Gemmellaro (1890, pl. 4, figs. 8, 9), dorsal and right lateral views, $\times 2$. The specimen has apparently been lost. 6, Line drawing of a generalized carapace of *Echinocaris* Whitfield, 1880 illustrating the position of ridges, grooves, and swollen regions observed in the genus, approximately $\times 5$. Modified from Hannibal, 1990. 7, Line drawing of a generalized carapace of *Eryma* illustrating the typical groove pattern exhibited by primitive decapod crustaceans, approximately $\times 1.25$. Modified from Förster, 1966. 8, Hypothetical reconstruction of *Palaeopemphix sosisiensis*, approximately $\times 3$. Morphology of the rostral plate, anterodorsal margin of the carapace, and abdomen is conjectural.

margin convex with broad, strong lateromarginal carina (double—D); anterior margin convex ventrally, weakly concave medially, and with rimmed orbital concavity dorsally. Carapace surface with prominent posterior groove (P) extending from near posterodorsal corner anteroventrally and curving anteriorly across about 85 percent of height of carapace; medial groove (M), paralleling posterior groove may be present or absent. Anterior groove (A) extends from upper corner of orbital rim posteroventrally as deep, narrow groove or as two deep, disjunct, linear depressions. Anterior and posterior grooves intersect at triple junction with short, arcuate inferior groove (I) extending posteroventrally to doubleure.

Discussion.—The material basis for restudy of this genus consists of 21 carapaces from the series originally studied by Gemmellaro. He implied that there were abundant specimens available for his study but gave no actual numbers. It is clear that some of the specimens available to him have subsequently been lost. Of the 18 illustrations of carapaces of *Palaeopemphix* (Gemmellaro, 1890, pl. 4), 14 could be matched with specimens now curated in the Museo Geologico of the Università di Palermo. An additional seven specimens that were not illustrated are in the museum collection, and four carapace specimens and one specimen of a pleon, illustrated by Gemmellaro (Fig. 1.4, 1.5), are apparently lost. Despite the loss of some specimens, the present collection is robust and contains representatives of the three species Gemmellaro named. The specimens were originally catalogued as numbers 13, 14, 15, and 16. To be certain that individual specimens in these lots are identifiable and assignable to the appropriate species, the individuals were assigned letter designations, 13a–f, 14a–e, 15a–h, and 16a and b.

Palaeopemphix was originally assigned to the decapod Crustacea and, based upon the comparisons Gemmellaro made with decapods, he recognized some similarities between the new genus and Triassic representatives of *Pemphix* von Meyer, 1840 within the Pemphicidae van Straelen; *Litogaster* von Meyer, 1847 (erroneously called *Lithogaster* by Gemmellaro), within the Glypheidae; and *Lissocardia* von Meyer, 1851, within the Erymidae. However, he also pointed out that the new genus was substantially different from these genera and that it was distinctly different from Carboniferous Eocarida. “The specimens ascribed to *Anthropalaemon*, *Palaeocarabus*, *Pseudogalatea*, *Crangopsis*, and *Pygocephalus* of the Carboniferous Period, and the specimens ascribed to *Pemphix*, *Lithogaster* [sic], and *Lissocardia* of the Triassic Period, have carapaces completely different from those of the study specimens. . . . The study carapaces are completely different from those of *Pemphix* because the gastric region lacks the swollen tubercles typical of this Triassic genus. The abdominal somites are also different from those of *Pemphix*, lacking the typical articulation present in this genus. . . . *Lithogaster* [sic], *Lissocardia*, and *Pemphix* differ from the study carapaces in ornamentation and in the arrangement of the grooves” (translated from Gemmellaro, 1890, p. 17, 18 by AG).

Placement of *Palaeopemphix* within the Decapoda was undoubtedly based upon the development of the transverse grooves that, in some regards, are similar to those in some Mesozoic lobsters. However, there are enough differences in the groove patterns and other features to separate the genus from the Decapoda. The posteriormost groove extends posterodorsally almost to the posterodorsal corner and the anteriormost groove extends in a posteroventral direction, neither of which is observed in the lobsters. The groove patterns of *Palaeopemphix* (Fig. 1.1–1.3) are not that of decapods (Fig. 1.7). It should be noted that the terminology of the grooves—posterior, median, anterior, and inferior—refers only to the position of the grooves and is not intended to suggest any homology. This procedure is in contrast to the

naming of grooves in the Decapoda, which does carry implications of homology. The position and symbols used for the grooves in *Palaeopemphix* are illustrated in Figure 1.1.

Other aspects of the morphology of *Palaeopemphix* that separate it from the Decapoda include the bivalved nature of the carapace and the strong development of the lateromarginal carina, or doubleure. Decapods, particularly lobsters, commonly exhibit a suture along the dorsal margin of the carapace that facilitates molting and might result in preservation leading to the conclusion that the specimen was bivalved. However, examination of a large number of fossil lobsters by the authors confirms that the two halves of the carapace are rarely, if ever, completely separated during burial and preservation. Thus, lobsters are seldom preserved in separated halves so as to appear bivalved. Specimens may be distorted, flattened, or compressed, but the carapace remains intact. Although there may be a very narrow marginal carina in some lobsters, it typically becomes reduced in size and disappears at about the midlength. Very strong, persistent lateromarginal carinae are not developed in lobsters. These groove patterns and the presence of a doubleure are not those of decapods.

The first recognition that *Palaeopemphix* probably was not a decapod was that of Glaessner (1969, p. R435). His conclusion was based upon the nature of the groove pattern, as discussed above. However, in that same work, the Treatise on Invertebrate Paleontology, Brooks (1962, p. R339) apparently did consider *Palaeopemphix* to be a decapod and commented on the development of three transverse grooves as a distinctly decapod character. The comments of Brooks did include recognition that only some species of *Palaeopemphix* bore three grooves but did not note the unique development of the anterior groove.

PALAEOPEMPHIX SOSIENSIS Gemmellaro, 1890
Figures 1.1, 1.8, 2

Palaeopemphix sosisiensis GEMMELLARO, 1890, p. 19, pl. 4, figs. 1–9, 12, 15.

Palaeopemphix affinis GEMMELLARO, 1890 (part), p. 20, fig. 10.

Description.—Carapace with well-developed continuous or discontinuous median groove curving ventrally to join posterior groove in a smooth arc. Anterior groove extends from near dorsal end of orbit posteroventrally as narrow, well-defined groove. Elongate, anteriorly tapering swelling extends along anteroventral part of carapace from near intersection of posterior and medial grooves nearly to anteroventral corner; swelling prominent to subtle. Surface of mold of interior of cuticle smooth to finely punctate.

Measurements.—Measurements taken on this species are given in Table 1. Orientation of the measurements is shown in Figure 1.1.

Material examined.—Thirteen specimens from the Gemmellaro collection in the Museo Geologico of the Università di Palermo. On the original labels, specimens 14a–14e and 15b–15h were identified as *Palaeopemphix sosisiensis* and specimen 16b was labeled as *P. affinis*.

Designation of type specimen.—Gemmellaro did not clearly designate type specimens for the new species he named. However, in the case of *P. sosisiensis*, there is sufficient indication to be assured that a single specimen (Gemmellaro, 1890, pl. 4, fig. 1), constituted the primary basis for his concept of the species. Therefore, that specimen, 14e, is identified as the holotype by original designation. Comparison of the surviving specimens with the illustrations of the species on Gemmellaro's plate 4 indicate that specimens illustrated as figures 2, 6, 8, and 9 are not available for study. The specimen in figures 8 and 9, unfortunately, is the only described abdominal somite (Fig. 1.4, 1.5). Because that abdominal somite is not associated with a specific carapace, its assignment to *P. sosisiensis* must be considered conjectural.

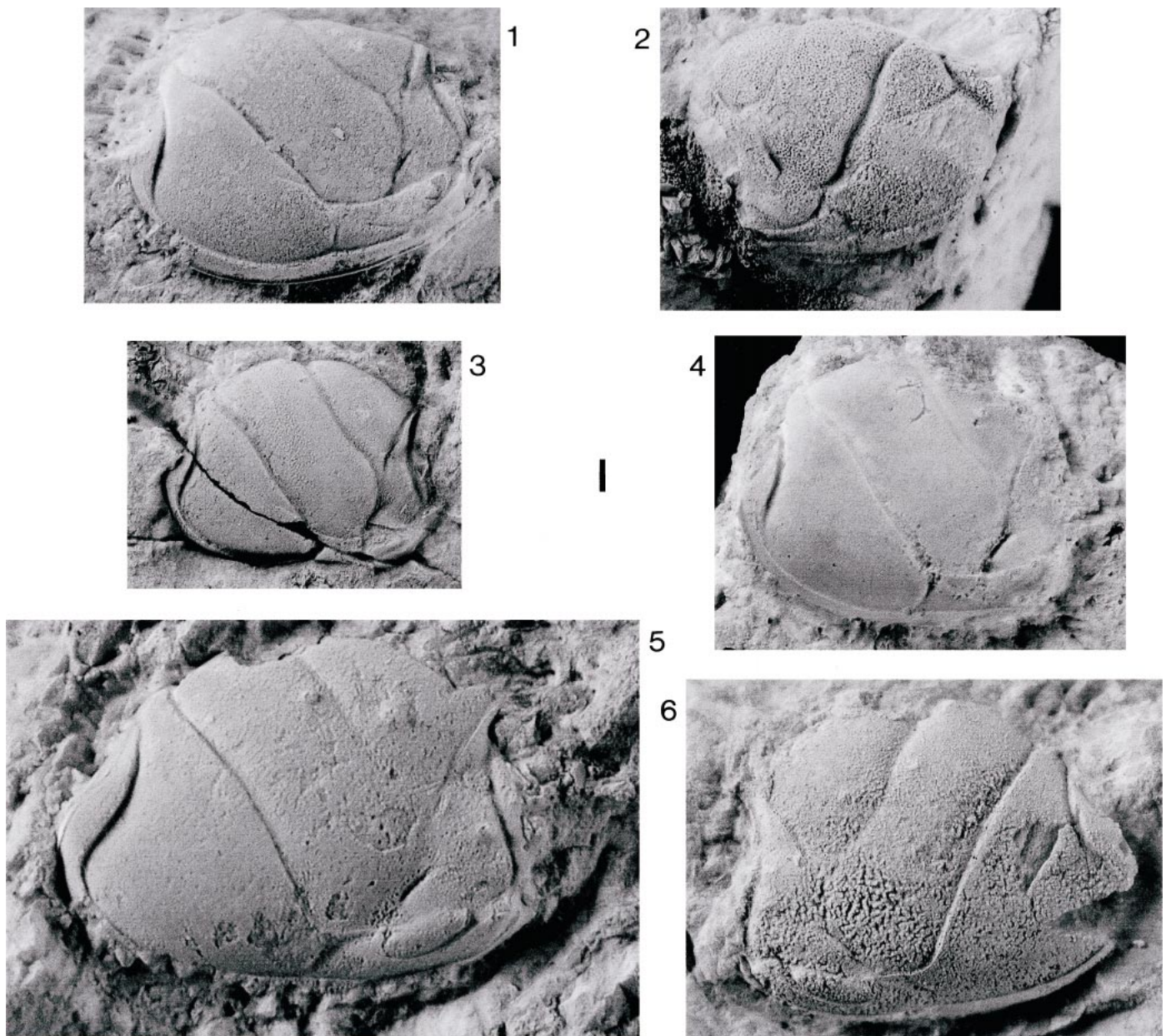


FIGURE 2—*Palaeopemphix sosiensis* Gemmellaro, 1890. 1, specimen 15h, right valve; 2, specimen 14a, left valve; 3, specimen 15e, right valve; 4, specimen 15g, right valve; 5, holotype, specimen 14e, right valve; 6, Specimen 15b, left valve. Scale bar equals 1 mm.

Discussion.—*Palaeopemphix sosiensis* is represented by 13 specimens, of which eight are right valves and five are left valves. The morphology of the carapace of this species provides the best basis for judging the general array of grooves and marginal structures typifying the genus. All three major grooves are developed and the lateromarginal carina, or doublure, is prominent. The development of the three transverse grooves and the absence of a longitudinal groove clearly distinguish this species from the other two.

The morphology of the other two species can be contrasted to this species. The ornamentation on the carapace is intermediate in strength within the three species. Ornamentation, as interpreted from the mold of the interior, ranges from nearly smooth to finely punctate in *P. sosiensis* whereas that of *P. affinis* is smooth on the sole specimen and the ornamentation is coarsely punctate on *P. meyeri*. The transverse grooves are well established and the

posterior and medial grooves join one another on *P. sosiensis*, whereas the medial groove is totally absent on *P. meyeri*. Although the posterior and medial grooves are present on *P. affinis*, they do not extend ventrally beyond the midline. *Palaeopemphix affinis* also bears a longitudinal groove that is unique among members of the family.

PALAEOPEMPHIX MEYERI Gemmellaro, 1890
Figures 1.2, 3

Palaeopemphix meyeri GEMMELLARO, 1890, p. 20, pl. 4, figs. 16–22.
Palaeopemphix sosiensis GEMMELLARO, 1890, part, p. 20.

Description.—As in *P. sosiensis*, except median groove absent. Anterior groove composed of two elongate, straight or slightly curved depressions; dorsalmost depression shorter, arising behind

TABLE 1.—Measurements taken on specimens of *Palaeopemphix* sp. Gemmellaro, 1890. Orientation of the measurements is given in Figure 2.1. Angular measurements are given in degrees and linear measurements are given in millimeters.

Specimen	Valve	Posterior angle	Medial angle	Anterior angle	Length 1	Length 2	Height
<i>Palaeopemphix sosisiensis</i>							
14E-Holotype	Right	57		119	15	9.2	11.4
14A	Left						7.5
14B	Right					3.7	4.8
14C	Right					4.2	4.7
14D	Left						5.2
15B	Left	63	59	122	12.7	7.9	10
15C	Left	45	50	117		3	4.2
15D	Left	59	61	116	12.1	7.5	9.4
15E	Right	54	55	113	8.5	6	7
15F	Right	51	51	110	6.4	4.2	5.2
15G	Right	57	60	104	10.6	7.3	8.3
15H	Right	42	45	104	11.3	7.3	8.1
16B	Right					3.7	5.8
<i>Palaeopemphix meyeri</i>							
13C-Lectotype	Right	54		103	6.8	4.1	5.1
13A	Left	50		118	8	4.9	4.3
13B	Left					4.8	4.1
13D	Right	45		103	6.2	3.9	4.6
13E	Right	53		111	5.9	3.9	4.7
13F	Right	50		110	7.1	4.6	5.1
15A	Left	47		106	8.8	5.5	6.4
<i>Palaeopemphix affinis</i>							
16A-Lectotype	Right	58	55	110	7.6	4.8	5.6

orbit; ventralmost depression longer, narrower, extending to or nearly to junction with posterior and inferior grooves. Surface of mold of interior of cuticle coarsely punctate.

Measurements.—Measurements taken on *Palaeopemphix meyeri* are given in Table 1. Orientation of the measurements is shown in Figure 1.1.

Material examined.—Seven specimens from the Gemmellaro collection in the Museo Geologico of the Università di Palermo. On the original labels, specimens 13a–13f were labeled as *Palaeopemphix meyeri* and specimen 15a was identified as *P. sosisiensis*.

Designation of type specimen.—Gemmellaro made no indication of which of the specimens of *P. meyeri* should serve as the type specimen. Comparison of the surviving specimens with the type description and Gemmellaro's illustrations (pl. 4, figs. 16–20) indicate that three of the illustrated specimens survive (specimen 13d, fig. 16; specimen 13e, fig. 18; and specimen 13c, fig. 19). The most complete of the specimens, 13c (pl. 4, fig. 19) is therefore designated the lectotype.

Discussion.—*Palaeopemphix meyeri* is the second most common species in the genus. Seven specimens have been assigned to this species, of which four are right valves and three are left valves. The total absence of the medial groove readily distinguishes members of this species from the other two.

PALAEOPEMPHIX AFFINIS Gemmellaro, 1890
Figures 1.3, 4

Palaeopemphix affinis GEMMELLARO, 1890, p. 4, fig. 11.

Description.—Like *P. sosisiensis* but with subtle longitudinal ridge extending from junction of posterior and inferior grooves and terminating near posterior margin; deeper groove extending from posterior termination of subtle longitudinal groove dorsally arching to posterodorsal corner, almost parallel to posterior margin. Surface of mold of interior of cuticle very finely granular to smooth.

Measurements.—Measurements taken on the sole specimen are given in Table 1. Orientation of the measurements is shown in Figure 1.1.

Material examined.—One specimen from the Gemmellaro collection in the Museo Geologico of the Università di Palermo. On the original label, the specimen was identified as *Palaeopemphix affinis*.

Designation of type specimen.—No type was originally designated for this species; however, based upon the description of the species, it is clear that specimen 16a (pl. 4, fig. 11) most closely conforms to the description. Therefore, it is herein designated the lectotype. The other specimen originally designated as *P. affinis*, specimen 16b (pl. 4, fig. 10), has been reassigned to *P. sosisiensis*.

Discussion.—*Palaeopemphix affinis* is represented by only one specimen, a right valve. The distinctive longitudinal groove is unlike anything seen on the other specimens of *Palaeopemphix* and readily documents the distinctness of the specimen. Because the species is represented by just one specimen whereas several specimens document the other species, it is possible that the longitudinal structure is a taphonomic or pathologic feature and that the specimen should be referred to *P. sosisiensis*. That possibility was considered and rejected because the longitudinal groove is very precisely formed and because no taphonomic processes could be thought of that would produce such a structure.

DISCUSSION

The establishment of a new suborder cannot occur without careful consideration. Assigning a new taxon to an existing suborder can be done only under the condition that the taxon meets the definition of the group or that expansion of the definition of the group does not destroy its integrity. As has been discussed above, placement of *Palaeopemphix* in the Decapoda, as was done originally, would necessitate expanding the definition of the order to include weakly hinged, bivalved creatures with a broad doublure. The integrity of the Decapoda would be seriously eroded. It is much more reasonable to place *Palaeopemphix* within the Phyllocarida based upon the bivalved nature of the carapace, development of a pattern of grooves and elevations on the carapace that are uncharacteristic of any decapod (but within the range of characters of the Phyllocarida), and development of a prominent doublure. When that is done, the genus does not fall within the

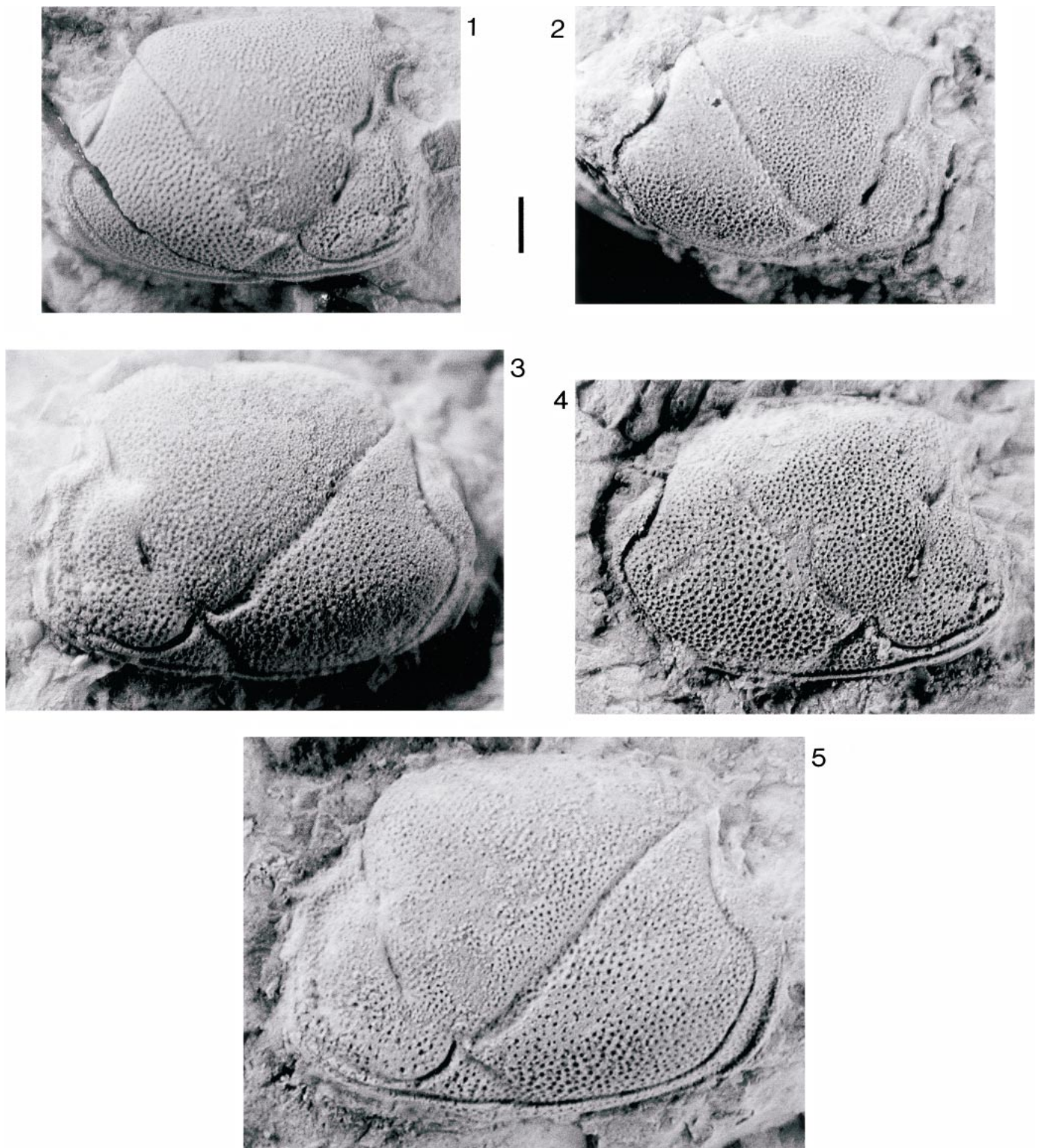


FIGURE 3—*Palaeopemphix meyeri* Gemmellaro, 1890. 1, lectotype, specimen 13c, right valve; 2, specimen 13e, right valve; 3, specimen 13a, left valve; 4, specimen 13f, right valve; 5, specimen 15a, left valve. Scale bar equals 1 mm.

definition of any established suborder. Thus, creation of the new higher taxon is warranted.

Paleozoic arthropods, particularly the phyllocarids, are an extremely variable group. However, when surveying the known

forms, none has a pattern of grooves even remotely like that on *Palaeopemphix*; none has the distinctive swollen region near the anteroventral corner of the carapace; and none has a hinge structure that is so weak that the right and left valves were dissociated



FIGURE 4—*Palaeopemphix affinis* Gemmellaro, 1890. Lectotype, specimen 16a, right valve. Scale bar equals 1 mm.

upon death in all specimens available for study. Definition of a new suborder appropriately places the organisms within the classification hierarchy and reflects their relationship to other phyllocarids.

ACKNOWLEDGMENTS

Specimens forming the basis for this study were loaned by Museo Geologico of the Università di Palermo. D. A. Waugh, Kent State University, read a draft of the manuscript and assisted with preparation of the graphical material. An earlier draft of the manuscript was read by J. Hannibal, Cleveland Museum of Natural History, and G. Teruzzi, Museo di Storia Naturale di Milano. Careful reviews by Hannibal, F. R. Schram, University of Amsterdam, and B. S. Lieberman, University of Kansas, substantially improved the manuscript. Our thanks to these individuals.

REFERENCES

- BARRANDE, J. 1872. Système Silurien du Centre de la Bohême, supplement au, Volume 1, Trilobites, Crustacés, divers et Poissons, 647 p.
- BEECHER, C. E. 1884. Ceratiocaridae from the Chemung and Waverly groups of Pennsylvania. Second Geological Survey of Pennsylvania, Report of Progress, PPP:1–22.
- BROOKS, H. K. 1962. The Paleozoic Eumalacostraca of North America. Bulletin of American Paleontology, 44(202):1–338.
- BROOKS, H. K. 1969. Eocarida, p. R332–345. In R. C. Moore (ed.), Treatise on Invertebrate Paleontology, Part R, Arthropoda 4(1). Geological Society of America and University of Kansas Press, Lawrence.
- CATALANO, R., P. DI STEFANO, AND H. KOZUR. 1992. New data on Permian and Triassic stratigraphy of Western Sicily. Neues Jahrbuch für Geologie und Paläontologie, 184(1):25–61.
- CLARKE, J. M. 1898. Notes on some crustaceans from the Chemung Group of New York. I. A singularly ornamented phyllocarid genus, *Pephricaris*. New York State Museum, Forty-ninth Annual Report of the Regents, 1895, 2:731–733.
- CLAUS, C. 1880. Grundzüge der Zoologie. Volume 4. N. G. Elwert, Marburg, 438 p.
- CLAUS, C. F. W. 1888. Ueber den Organismus der Nebaliden und die systematische Stellung der Leptostraken. Arbeiter der Zoologische Institut. Wien, 3:1–148.
- DAHL, E. 1956. Some crustacean relationships. Bertil Hanström, Zoological Papers in Honor of his Sixty-Fifth Birthday November 20, 1956, Lund University, 138–148.
- FÖRSTER, R. 1966. Über die Erymiden, eine alte konservative Familie der mesozoischen Dekapoden. Palaeontographica, 125(A):62–175.
- GEMMELLARO, G. G. 1890. I crostacei dei calcari con *Fusulina* della valle del fiume Sosio nella Provincia di Palermo in Sicilia. Memorie della Società Italiana delle Scienze, 8(1):1–40.
- GLAESSNER, M. F. 1928. Zur Frage der ältesten fossilen Krabben. Centralblatt für Mineralogie, Geologie, und Paläontologie, B(6):388–398.
- GLAESSNER, M. F. 1931. Eine Crustaceen fauna aus den Lunzer Schichten Niederösterreichs. Jahrbuch der Geologischen Bundesanstalt, 81:467–486.
- GLAESSNER, M. F. 1969. Decapoda, p. R399–R533. In R. C. Moore (ed.), Treatise on Invertebrate Paleontology, Part R, Arthropoda 4(2). Geological Society of America and University of Kansas Press, Lawrence.
- HANNIBAL, J. T. 1990. *Echinocaris*, a mid-Paleozoic crustacean. Unpublished Ph.D. dissertation, Kent State University, Kent, Ohio, 362 p.
- HANNIBAL, J. T., AND R. M. FELDMANN. 1997. Phyllocarid crustaceans from a Middle Ordovician black shale within the Ames Structure, northwest Oklahoma. Oklahoma Geological Survey Circular, 100:370–373.
- HERBIG, H.-G. 1993. First Upper Devonian crustacean coprolites: *Favreina prima* from northern Morocco. Journal of Paleontology, 67:98–103.
- KONINCK, L. G. DE. 1840–1842. Description des animaux fossils qui se trouvent dans le terrain carbonifère de Belgique. H. Dessain, Liège, 650 p.
- MARTIN, J. W., AND G. E. DAVIS. 2001. An updated classification of the Recent Crustacea. Natural History Museum of Los Angeles County Science Series, 39:1–124.
- MEYER, H. VON. 1840. Neue Gattungen fossiler Krebse aus Gebilden vom bunten Sandstein bis in die Kreide. [Zoological Museum], Stuttgart, 28 p.
- MEYER, H. VON. 1847. *Halicyne* und *Litogaster*, zwei Crustaceen gattungen aus dem Muschelkalke Württembergs. Palaeontographica, 1:134–140.
- MEYER, H. VON. 1851. Fische, Crustaceen, Echinodermen und andere Versteinerungen aus dem Muschelkalk Oberschlesiens. Palaeontographica, 1:216–279.
- MILLER, A. K. 1933. Age of the Permian limestones of Sicily. American Journal of Science, 5th series, 154(26):400–427.
- NOVIZHILOV, N. I. 1960. Crustacés bivalves [Conchostraca de la série Diado de l'Asie orientale dans le trias surérieur de Madygen (Kirghizie occidentale)]. Annales de la Société Géologique du Nord, 80:177–186.
- PACKARD, A. S. JR. 1879. The nebalid Crustacea as types of a new order. American Naturalist, 13:128.
- PINNA, G., P. ARDUINI, C. PESARINI, AND G. TERUZZI. 1982. Thylaccephala: una nuova classe di crostacei fossili. Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano, 123:469–482.
- RODE, A. L., AND B. S. LIEBERMAN. 2002. Phylogenetic and biogeographic analysis of Devonian phyllocarid crustaceans. Journal of Paleontology, 76:271–286.
- ROLFE, W. D. I. 1961. *Concavicaris* and *Quasicaris*, substitute names for *Colpocaris* Meek, 1872 and *Pterocaris* Barrande, 1872. Journal of Paleontology, 35:1243.
- ROLFE, W. D. I. 1962. A new phyllocarid crustacean from the Upper Devonian of Ohio. Breviora, 151:1–7.
- ROLFE, W. D. I. 1969. Phyllocarida, p. R296–R331. In R. C. Moore (ed.), Treatise on Invertebrate Paleontology, Part R, Arthropoda 4(1). Geological Society of America and University of Kansas Press, Lawrence.
- SALTER, J. W. 1860. On new fossil Crustacea from the Silurian rocks. Annals and Magazine of Natural History, series 3, 5:153–162.
- SCHMIDT DI FRIEDBERG, P. 1964–1965. Litostratigrafia petrolifera della Sicilia. Rivista Mineraria Siciliana (Palermo), 88–90, 91–93, 88 p.
- SCHRAM, F. R. 1973. On some phyllocarids and the origin of the Hoplocarida. Fieldiana: Geology, n.s., 26:77–94.
- SCHRAM, F. R. 1986. Crustacea. Oxford University Press, Oxford, 606 p.
- SCHRAM, F. R., AND R. H. MAPES. 1984. *Imocaris tuberculata*, n. sp. (Crustacea: Decapoda) from the upper Mississippian Imo Formation, Arkansas. Transactions of the San Diego Society of Natural History, 20:165–168.
- SCHRAM, F. R., R. M. FELDMANN, AND M. J. COPELAND. 1978. The Late Devonian Palaeopalaemonidae and the earliest decapod crustaceans. Journal of Paleontology, 52:1375–1387.
- SCHRAM, F. R., R. VONK, AND C. H. J. HOF. 1997. Mazon Creek Cycloidea. Journal of Paleontology, 71:261–284.
- STUMM, E. C., AND R. B. CHILMAN. 1969. Phyllocarid crustaceans from

- the Middle Devonian Silica Shale of northwestern Ohio and southeastern Michigan. Contributions from the Museum of Paleontology, University of Michigan, 23:53–71.
- VAN STRAELEN, V. 1933. Note sur les Phyllocarides paléozoïques ou *Archaeostraca* de la Belgique et remarques sur la systématique de ces Crustacés. Bulletin du Musée Royal d'Histoire naturelle de Belgique, 9:9–10.
- WHITFIELD, R. P. 1880. Notice of new forms of fossil crustaceans from the upper Devonian rocks of Ohio, with descriptions of new genera and species. American Journal of Science, Third series, 19:33–42.
- ZITTEL, K. A. 1900. Text-book of Palaeontology, Volume 1, edited by C. R. Eastman. Macmillan, New York, 706 p.

ACCEPTED 26 JULY 2003