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CONTENTS

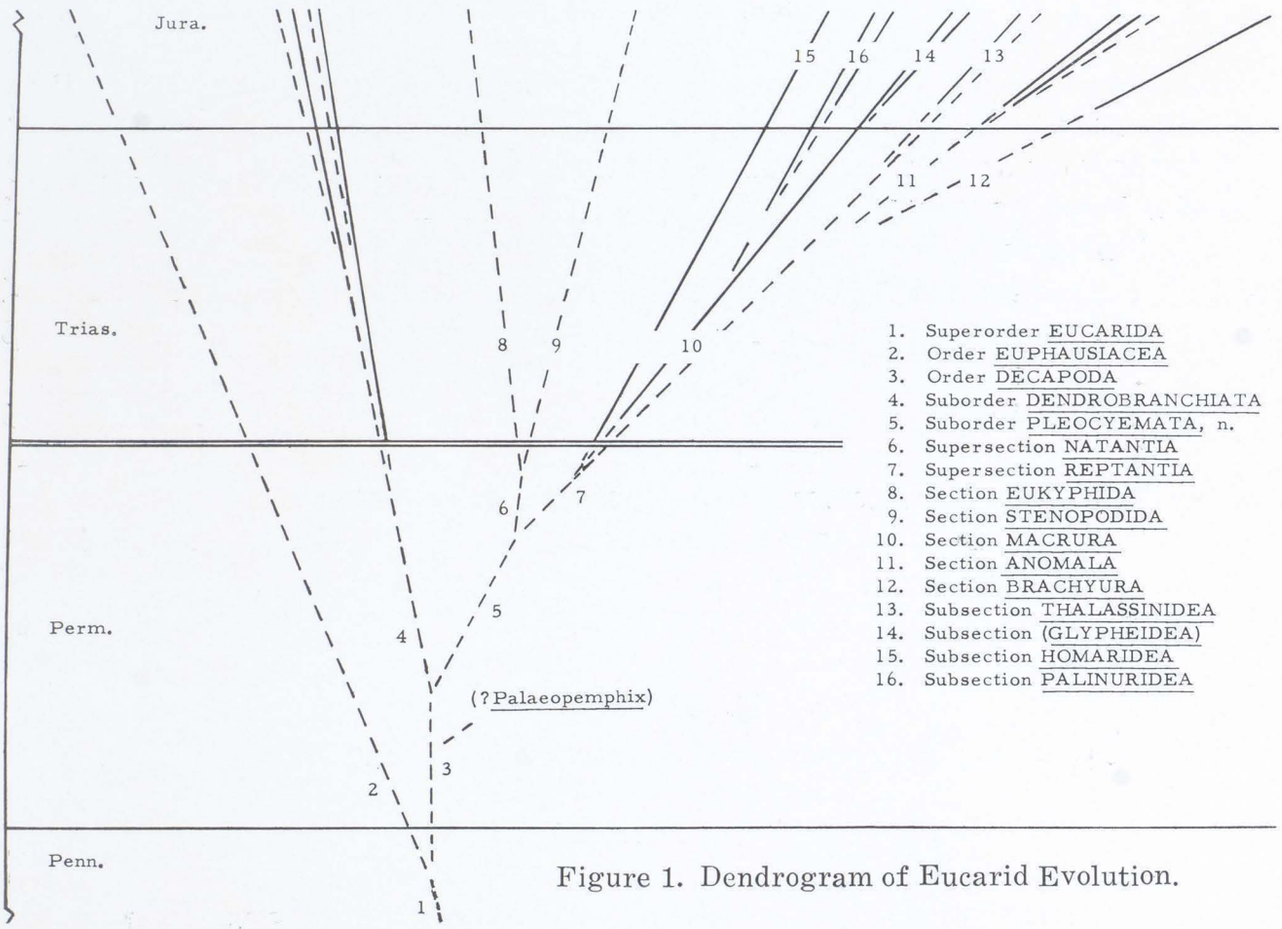

Figure 1. Dendrogram of Eucarid Evolution.

THE EVOLUTION OF THE EUCARIDA, (CRUSTACEA, EUMALACOSTRACA), IN RELATION TO THE FOSSIL RECORD

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ABSTRACT

Eumalacostracan fossils from the Mississippian indicate the beginnings of Recent superorders other than the Eucarida; which latter probably also differentiated around this time, from a primitive shrimp with carapace sculpture like that of *Palaeopalaemon,* in a marine form not yet discovered There is no valid evidence to suggest Eucarid polyphyly. The only Paleozoic record of the superorder seems to be the peculiar form *Palaeopemphix* from the Permian, which is certainly not a Glypheid but may represent an early, calcified offshoot of the stem-form of the order Decapoda (the family PALEOPEMPHICIDAE, n.). In the early Triassic, not only are the known Eucarids definitive Decapods, but this order was already differentiated into the suborders Dendrobranchiata and PLEOCYEMATA (n.), which were themselves already subdivided (*e.g.,* the Peneidae were presumably already separated from the AEGERIDAE, n. fam.). The available Mesozoic representation undoubtedly includes a disproportionate frequency of forms specialized by calcification; and this record seems too late, fragmentary and non-consecutive to supply crucial evidence either for or against the present view of Decapod phylogeny founded on evidence from Recent forms. The habits and characteristics to be expected of Paleozoic fossils representing the hypothetical stems of Eucarid groups are outlined.

I. INTRODUCTION

A new consideration of the adult and the developmental characteristics of Recent Eucarid Crustacea indicates that all previously-proposed systems of classification of the members of the order Decapoda are in various degrees polyphyletic (in the sense of grouping taxa together some of which are more closely related to members of other groups given equal rank; *cf.* Simpson, 1961, p. 120 ff.). This conclusion (for which the evidence is given in detail in a forthcoming treatment of the Recent Eucarida) necessitates a critical examination of paleontological findings, since the primary test of any phylogenetic hypothesis is its compatibility with the fossil record. The present paper is, then, a review of current paleontological ideas from the new point of view, and is offered in advance of detailed evidence from the Recent in order to secure comment on its weaknesses from specialists in fossils.

The Recent evidence indicates that the following more or less widely-accepted major taxa are monophyletic: (1) the superorder Eucarida Calman (carapace fused with all thoracic tergites, probably in relation to the habit of jumping backward; appendix masculina on male second pleopod); (2) the Eucarid order Euphausiacea Boas (body-gills entirely lost but podobranchs including that of the eighth thoracic appendage retained; specializations for sperm-transfer and for

pelagic life; (3) the Eucarid order Decapoda Latreille (loss of the eighth epipodite and podobranch, enclosure of all gills in the branchial chamber and enlargement of the maxillary pump with correlated reduction of the muscular basal part of the pereiopodal expodites; attenuation of the endopod of the first thoracic appendage and permanent flexure of that of the second one); (4) the Decapod supersection Reptantia Boas (loss of all pleurobranchs anterior to the fifth thoracic somite; specializations for benthonic life).

The Recent evidence unequivocally indicates that the "suborder Natantia" of Boas is polyphyletic. The Peneids represent one of two major branches of the order Decapoda and require separation as the suborder Dendrobranchiata (Bate, redefined). They retained dendrobranchiae and a non-incubatory habit with naupliar eclosion from the generalized Eumalacostracan that also gave rise to the marsupial superorder Peracarida; but differentiated from the ancestral Decapod by a few unique specializations, as well as by developing chelae on the fourth to sixth thoracic legs. The other major branch of the Decapoda, for which the new suborder PLEOCYEMATA is required, lost the secondary rami of the gills and developed pleopodal incubation with zoeal eclosion, but apparently continued at first to be achelate. This incubatory branch appears to have divided early into two stems. The first-differentiated of these two, which was especially characterized by delay in appearance of the arthrobranch gills during ontogeny (supersection Natantia Boas, as here restricted) soon divided further into two highly divergent lines nowadays represented by the sections Stenopodida Huxley and Eukyphida Boas. The other offshoot of the Pleocyemate ancestor is the benthonic supersection Reptantia Boas, of which the Recent Thalassinidea (some still achelate and most still little-calcified and with a longitudinal suture on the carapace) seem on the whole to have differentiated least decisively from the Reptant ancestor (although conservative features are scattered among all Reptant groups, along with specialized ones).

The present somewhat superficial examination of the Paleozoic and Mesozoic record does not reveal any decisive evidence in favor of the above phylogenetic hypotheses, but does seem to show that the conflicting previous deductions from the known fossils are not required by the evidence. A final section of the paper outlines the probable characteristics of Paleozoic Eucarid fossils which (according to the present view) are to be hoped for in the gap between the early, generalized Eumalacostraca known from the Devonian and the specialized Decapod genera (Peneine, Glypheid and Homaridean) so far recorded from the Permo-Trias and the early Triassic.

II. The Fossil Record

A. *Paleozoic:*

1. *Devonian and Carboniferous:* The Paleozoic Eumalacostraca have recently been extensively revised by Brooks (1962). According to him, the fossil record begins in the Devonian with three shrimplike genera believed all to have had a more or less enlarged antennular peduncle, undifferentiated biramous thoracic limbs with an undivided sympod, furcal plates on the telson (however, *cf. l.c.,* Plate 52, fig. 2; and also Howell, 1957, fig. 1) and a well-developed carapace, shorter than the pleon but covering although not fused to all thoracic tergites. Oöstegites have not been seen, although this might be "due to a deficiency of the fossils" (*l.c.,* p. 224).

One of these Devonian genera (*Palaeopalaemon*) extended into the Lower Mississippian; and during the later Mississippian and the Pennsylvanian there have been found five other shrimplike genera assigned to the same order (Eocaridacea Brooks). In Brooks's material of these later genera also, "oöstegites have not been seen . . ., but Peach . . . claimed they were present on *Crangopsis.* This needs reinvestigation" (p. 266. However, on p. 205 Brooks says that the *Crangopsis* "marsupium . . . may have been similarly developed on *Anthracophausia*"; and on p. 206, "It is inferred that a marsupium may have been present as one has been reported on a closely related genus").

During the Mississippian, fossils of a variety of other sorts of Eumalacostraca appear. One of these groups, the Palaeocaridacea Brooks, had no carapace and is assignable to the extant superorder Syncarida. A second had only a vestige of carapace (covering no more than the first two

thoracic somites) and, although tentatively assigned to the Peracarida (after Calman), is noted by Brooks, p. 268, to be a possible ancestor of, *e. g.,* the Pancarida. A third group, the Palaeostomatopoda Brooks, seems Hoplocarid (if, as stated by Brooks on p. 211, "Peach . . . mistook remains of the jointed endopods for a brood pouch in *Perimecturus elegans* . . . and the broad lobes shown on *P. pattoni* as a 'broodpouch' are probably the remains of pleopods"; which would remove the objection by Tiegs and Manton, 1958, p. 336, that "Few will support Glaessner in . . . placing the fossil Perimecturidae, possessing a typical peracaridan brood pouch, on the ancestry of the Hoplocarida").

A fourth group, which is first known from the Mississippian but mostly from the Pennsylvanian and the Permian (Pygocephalomorpha Beurlen as restricted by Brooks), consists of forms distinguished from Brooks's Eocaridacea by having a cephalothorax at least no shorter than the pleon and a "Branchiostegal development of the pleura of the carapace" (described for *Anthracaris,* p. 177, as an infolding of the lower edge of the broadened carapace, which fits "against the flanks of the thoracic somites just above the coxa of the legs to form a crablike branchial chamber"). Of these forms, *Anthracaris* had a sperm-receptacle on the last thoracic sternite of the female (p. 184, pl. 2 and 39) and no oöstegites (pp. 173, 265). *Tealliocaris* had oöstegites and no sperm-receptacle (p. 265 and pl. 7). *Pygocephalus* "not only has a peracarid marsupium, but the seminal receptacle diagnostic of syncarids and decapods" (p. 265. However, Woodward's figure of *Pygocephalus,* in which Brooks recognizes a sperm-receptacle, is said not to show oöstegites; and Brooks, p. 198, says that Woodward interpreted the "receptacle" as a "doubtful (anal?) plate displaced"). In the other five Pygocephalomorph genera listed by Brooks, it does not seem to be known whether the female had either oöstegites or a sperm-receptacle. In the Pygocephalomorphs from the southern hemisphere, the pleon was flexed under the cephalothorax, a crab-like convergence.

Brooks unites the Devonian and Carboniferous forms having a well-developed carapace as the superorder Eocarida Brooks, since "a vertical classification . . . would obscure the tenuousness of the inferred phylogenetic relationships" (p. 274). The members of this new superorder are "unique in that all have biramous thoracic appendages with a single joint in the sympods and furcal lobes and a median spine on the telson" (p. 265). However, since the six-jointed anterior thoracic appendages described for the Paleostomatopod *Archaeocaris* are neither biramous nor unique but would resemble those of the Recent Hoplocarida, it might be better not to include Brooks's Palaeostomatopoda in the same superorder with his Eocaridacea and Pygocephalomorpha.

The described distinctions between Eocaridacea and Pygocephalomorpha seem of doubtful significance when considered in relation to the diversity within these two groups. The Eocaridacean *Paleopalaemon,* with cephalothorax "only slightly reduced in length" and "an incipient branchiostegal development of the pleurae of the carapace" may, as Brooks thinks, represent the type from which "the Pygocephalomorpha evolved" (p. 266); but some Eocaridacea possess, whilst others seem to lack, the definitive Peracarid specialization (brood-lamellae). It seems more likely that Pygocephalomorpha with oöstegites were an offshoot of some similarly marsupial Eocaridacea such as must also have given rise to the Mysidacean Peracarida (since an oöstegite-formed marsupium is presumably correlated with abbreviated development, and such a trait seems too complex to have much probability of appearing more than once; although it can be lost, *cf.* Bovallius, 1890, p. 31). The sperm-receptacle on the last thoracic sternite of *Anthracaris* suggests that this form might have descended from some Eocaridacea which similarly lacked oöstegites but had a sperm-receptacle, other descendants of which lost the carapace (by hysterotely?) and gave rise to the Syncarida (although sperm-receptacles are not very safe indicators of relationship, having been independently developed many times on various somites of Malacostraca; *cf.* Andrews, 1905, pp. 48-9, on Homaridea and Burkenroad, 1936, pp. 62-3 on Peneids). It thus seems possible that the distinction made by Brooks between Pygocephalomorpha and Eocaridacea is between polyphyletic grades (like the original Decapod

suborders "Macrura" and "Brachyura") rather than between homogeneous taxa, and that his restricted "Pygocephalomorpha" are merely "the Paleozoic benthonic Eumalacostracans" (p. 265), convergent from diverse natant "Eocaridacea."

Brooks then suggests polyphyletic descent of the Eucarida from members of his "Eocaridacea" and "Pygocephalomorpha," as follows: (1) "Recent euphausids have retained the primitive telson and are probably specialized pelagic descendants of" the "Eocaridacea" (p. 266). (2) "The Penaeidae may have evolved from the Eocaridacea" (p. 270; and *cf.* Brooks's phylogenetic diagram, plate 16, where the line with a question mark, which evidently represents the differentiating Peneids, is drawn entirely independent of the Euphausiid and Reptant lines). (3) "Though *Anthracaris* from the Pennsylvanian has some characteristics of the eryonid decapods, it is a pygocephalomorph" (p. 269); and "It should be noted that the Decapoda may be polyphyletic. . . . The Eryonidae probably evolved from the Pygocephalomorph" (p. 270).

Brooks's suggestion of Eucarid polyphyly would imply that the definitive Eucarid specialization (carapace fused to all thoracic tergites) arose convergently on several occasions. However, this seems improbable; especially because Euphausiids and Decapods have in common a second, independent, peculiar specialization, not previously taken into consideration by taxonomists; namely, the bifurcation of the appendix interna of the second male pleopod to form an appendix masculina. A rigorous examination of Brooks's evidence thus seems to be required, as follows:

(a) The stated reason for deriving the Euphausiids from the "Eocaridacea" directly rather than as a branch of the Eucarid line (their "primitive telson") is elaborated by Brooks on p. 168, as follows: "all fossils except the syncarids have a pair of furcal lobes and a median spine on the telson. A furca is known in adult Recent Eumalacostraca only on euphausids and the syncarids of the Order Bathynellacea. The median spine is known only in the adults of euphausids. Gurney (1942, pp. 116-123) noted the occurrence of these structures of the telson in ontogenetic stages of the Eumalacostraca and concluded they are relics of a 'primitive form of telson preserved from a predecapod ancestor'. The paleontological evidence presented herein proves his deduction". However, Gurney, in the quoted suggestion ("It is possible that it is a primitive form of telson . . ."), was not referring to furcal rami, or to median spine as such, but to a peculiar pattern of telson common to some adult Mysids and Euphausiids and to some Eukyphid Decapod larvae. What he says about Euphausiacea (p. 119) is that they "afford no evidence as to the origin of the telson". The median spine, contrary to Brooks's generalization, is widely distributed; being found in some adult Mysids and Decapods (as is also an enlarged pair of spines like those of the Euphausiids, or a terminal fork suggestive of those in some of the larvae). What Gurney (1942, pp. 116-7) identified with the furcal rami of Branchiopoda, Copepoda, Leptostraca and embryonic Mysids were the forks of the larval telson of Peneid and Brachyuran Decapods, not the spines or setae borne on these forks (which he says, p. 119, "may be retained" while the forks are "absorbed into the telson and lose their individuality altogether"; *cf.* also Calman, 1909, p. 244, and Tiegs and Manton 1958, p. 295). The large "Eocarid" furcal plates shown by Brooks (setose in the restorations of the Pygocephalomorphs *Anthracaris, Mamayocaris* and *Tealliocaris;* pl. 2, 5, 7) suggest the Leptostraca, whereas the enlarged pair of spines of Euphausiids arises by hypertrophy of one previously undistinguished pair among the multiple larval spinules, and does not seem especially significant.

Brooks (p. 202) says of *Anthracophausia* that "The generic name . . . is most appropriate as far as superficial resemblances to the Recent euphausids are concerned. Peach . . . presented reliable evidence that the carapace was not fused with the posterior thoracic segments, but this primitive characteristic is to be expected of the ancestral euphausids. Most disconcerting, however, is the presence of a marsupium on females of the closely related contemporaneous fossil *Crangopsis* . . .". One might go further and say that if oöstegites were in fact present in these genera, their members seem most unlikely to have been ancestral to the Euphausiids or Peneids; and that they ought to be

regarded as primitive Peracarida (in the manner of Calman, 1909, p. 181).

(b) Brooks gives no reason why the Peneids should be thought to have arisen directly from Pennsylvanian Eocaridacea, independently both of the Euphausiids and of the other Decapods. Presumably, he was influenced by the remarkably *Peneus*-like outline and posture of the pleon in *Anthracophausia* (pl. 48). However, the intestine of *Anthracophausia* is shown by his photographs to have run along the middle of the pleon, rather than at the dorsal third as in Euphausiids or above the dorsal fifth as in Peneids and other Decapods. The position of the intestine relatively low in the body presumably indicates that the pleonic flexor muscles of *Anthracophausia* were not enlarged relative to the extensors; hence, that the organization of its pleon was more like that of Lophogastrid Mysidacean Peracarida than of the back-jumping Eucarids.

(c) The only Pygocephalomorph feature which Brooks specifically states to be like that of Eryonids is a sternal structure on the last thoracic somite of presumptive females of *Anthracaris* which "is reminiscent of the sperm receptacle of the syncarids and eryonid decapods" (p. 184). However, as pointed out by Andrews (1911), Eryonids do not have a sperm receptacle; instead, a pair of spermatophores is applied by the male to the surface of the hinder sternites of the female (mistaken by Geoffrey Smith for a receptacle like that of Recent Syncarids). Brooks regards the mandible of *Anthracaris* as "characteristic of decapods" in having a second articulation hinging it to a strongly developed epistome (pp. 181, 183, 265); but according to Snodgrass (1951, pp. 23, 41, 44-5, 46; 1952, pp. 182-3), a double-hinged mandible and a well-developed epistome are characteristic also of Peracarids and Hoplocarids. The resemblance of *Anthracaris* to Eryonids in habitus is surely convergent, since its free thoracic tergites are obviously pre-Eucarid, whereas the Eryonids are specialized chelate Reptants, not even primitive among Eucarida Decapoda Pleocyemata (the stem-form of which was almost certainly natant).

Consequently, paleontological evidence of Eucarid polyphyly is in fact completely lacking. What is instead to be deduced about the ancestor of the Euphausiids and Decapods from the characteristics of the available Paleozoic Eumalacostraca is as follows: It seems most unlikely that any of the ancient forms with reduced, depressed or heavy carapace, reduced or permanently flexed pleon, oöstegites, uniramous or raptorial legs, or a sperm-receptacle, could have given rise to the Eucarids. The three known Devonian genera seem to have lacked all these specializations, but seem in this to have been primitive, generalized Eumalacostraca showing little to connect them more closely with one rather than another of the extant superorders. Syncarid, Peracarid, Hoplocarid and possibly Pancarid specializations are all known in the Mississippian; and it would not be too surprising if a marine shrimp of similar date should ultimately be found, which had developed the definitive Eucarid specializations. Of the relatively unspecialized ancient forms, the one perhaps closest to such a direction of development might be *Palaeopalaemon,* which has carapace sculpture suggestive of that both of Mysids and of Decapods. The extremely hypertrophied antennular peduncle of *Palaeopalaemon* is, however, a specialization which seems to disqualify it as a direct ancestor of the Eucarida.

Brooks's restoration of *Palaeopalaemon* (pl. 9, fig. a) shows a system of carapace grooves resembling those of the Recent Mysid *Anchialina typica.* The groove marked "cvg" in the restoration ("cervical groove", p. 170) appears on Brooks's beautiful photographs (pl. 50, fig. 5; pl. 51, fig. 2) as deep and narrow, faintly turning to the dorsum at its upper end. Just below and parallel to it is a longer ridge, separated from it by a shallow trough which reaches the dorsum behind the middle of the carapace. The groove shown in the restoration as running in a rostral direction from a mid-lateral junction with "cvg", anterior to the level of an excavation of the dorsum, might be the homologue of Boas's groove *d* in Decapods (*cf.* p. 8 below). The dorsal notch might mark Boas's groove *e,* the cervical in the sense of Glaessner (*cf.* Brooks's pl. 14, fig. C, of a Recent Lophogastrid, where the groove marked "cvg" is the one described by Glaessner, 1960, p. 43, as "the last transversal furrow of the Mysidacea . . . [which] extends backward in a narrow U-shaped loop . . . [and] is undoubtedly homologous with the

branchio-cardiac groove of the Decapoda." Brooks's "cvg" in *Palaeopalaemon* might be equivalent to the "intermediate transverse furrow" which Glaessner notes for the Recent Lophogastrid *Eucopia* and evidently regards as homologous with Boas's groove *c,* the post-cervical of Decapods). Although the homologies cannot be regarded as certain, it would seem possible to derive the quadruple system of dorsum-attaining carapace grooves (*a, c, e, d*) which can be postulated for the stem-Eucarid from something like that in *Palaeopalaemon.*

The sharply-marked, midlateral, longitudinal ridge of the carapace of *Palaeopalaemon* is of special interest, because of the suture along its crest which is suggested by Brooks's photographs (pl. 50, fig. 7 and 51, fig. 3). If this suture existed in life, it would suggest that the midlateral ridge of *Palaeopalaemon* might be homologous with the unridged longitudinal suture which is found scattered in a few Recent Peneids, one Recent Eukyphid and many Recent Reptants of various sections (linea thalassinica, 1. anomurica, 1. homolica).

It is worth special note that Brooks (pp. 221, 258-9, 260) finds *Palaeopalaemon* unusual among available Paleozoic forms both in having had a somewhat calcified exoskeleton and in having been fully marine (*cf.* end of next section).

2. *Permian:* In the early (or early-Middle; or middle Upper) marine Permian (Sosio beds of Sicily; *cf.* Gignoux, 1950, and Neaverson, 1955; but note Montanaro Gallitelli, 1956, pp. 878, 882) Brooks recognizes a Decapod. He says, "the only Paleozoic fossil that may be a true decapod is *Palaeopemphix sosiensis* . . . and related species. . . . The carapaces figured by Gemmellaro . . . have cervical, post-cervical, and branchiocardiac sulci comparable to those of *Pseudoglyphea spinosus* and *Pseudopemphix albertii* . . . from the Triassic . . ." (pp. 269-70). On p. 274, he goes farther and assigns *Palaeopemphix* to the Glypheidae (which were almost certainly definitive Reptants closely related to the Recent Homaridea and Palinuridea).

In my opinion, Brooks's identification in *Palaeopemphix* of a post-cervical sulcus (groove *c* in the notation of Boas) is incorrect, and *Palaeopemphix* is a peculiar form with no close relation to the Glypheids or any other Reptant. However, I believe him to be right in assigning Gemellaro's genus to the Decapoda; on the grounds that it has a cardiacobranchial sulcus reaching the dorsum near the posterior margin of the carapace (groove *a* or *o* in the notation of Boas), and that the posterior margin of the carapace has the dorsal concavity characteristic of Eucarids.

What Brooks presumably regards as a cervical sulcus extends anterodorsally from the middle of the side on to the short rostrum of *Palaeopemphix,* and appears to represent the complete, primitive form of Boas's groove *d.* A complete groove found in the Triassic *Pemphix* anterior to *e* (but crossing the dorsum far posterior to the rostrum) is identified as *d* by Glaessner (1960, fig. 19, 4), but this primitive Palinuran Reptant has so many sulci that their homologies are unclear. In a few Recent Euphausiids, Peneids and Eukyphids (*e.g., Euphausia, Haliporous, Glyphocrangon*), a groove identifiable as *d* runs anterodorsally from a midlateral origin on the cervical to the rostrum, somewhat as in *Palaeopemphix.*

What Brooks evidently considers as the "post-cervical" of *Palaeopemphix* seems to be Boas's groove *q* or *e* (the cervical); not *c,* which according to Gemmellaro's figures seems to be missing. The deep, oblique groove (*a*) which runs from below the juncture of *d* and *e* to near the posterodorsal margin of the carapace (where it crosses the dorsum) resembles the cardiacobranchial of *Haliporus* (the Recent Peneid which seems in several respects the nearest of these to the stem-form of the relatively primitive suborder Dendrobranchiata); except that the cardiacobranchial of *Haliporus* sends off a posteroventral branch (as well as groove *c*). The extreme posterior crossing of the dorsum by groove *a* in *Palaeopemphix* is particularly reminiscent of *Haliporus* (and some species of the related *Hymenopeneus;* as well as the Reptant *Thalassina*). It is not exactly matched by any of the forms of groove *a* diagrammed by Glaessner (1960).

A number of Gemmellaro's specimens are figured as with a tubercle between *d* and *e,* and another behind *e.* These (although also reminiscent of, *e.g.,* the Pygocephalomorph *Anthracaris*) might be homologous with the postorbital spine characteristic of all

Solenocerine Peneids as well as some Sergestids and the Triassic-Jurassic *Aeger,* and with the postcervical spine found in a few Recent Solenocerinae.

The short, high carapace of *Palaeopemphix* and the absence of groove *c* seem surprisingly specialized for a primitive Decapod; although its short rostrum, complete groove *d,* groove *a* crossing the dorsum near the posterior margin, and postorbital tubercle might be primitive Decapod features (the whole peculiar combination requiring taxonomic distinction, which is here instituted by proposal of PALEOPEMPHICIDAE, new family). If the longitudinal ridge of *Palaeopalaemon* and the longitudinal sutures scattered among the Recent Decapoda are in fact homologous, as here suggested, *Palaeopemphix* seems disqualified as the stem-Decapod by loss of the suture. I would guess that when its pleon and appendages become known, it will prove to have been an achelate, calcified, benthonic offshoot of the hypothetical natant stem-Decapod.

Since it is here suggested that there was a varied fauna of Eucarids in the Paleozoic, culminating in the differentiation of the two Pleocyemate supersections of the Decapoda before the end of the Permian, the question arises why the only available traces of such a fauna are the somewhat debatable carapaces of *Palaeopemphix* (when, in contrast, a number of upper Paleozoic non-Eucarid Eumalacostraca are known, as well as a variety of Ostracods, Trilobites and other aquatic arthropods). Brooks has pointed out (1957, pp. 895-6; 1962, pp. 258-262) that marine arthropods with unmineralized exoskeletons are not, under usual conditions, likely to remain intact long enough for fossilization. Fresh- and brackish-water forms, such as the majority of known Paleozoic Eumalacostraca, are more frequently exposed to catastrophes (floods and sudden silting; drying-up and hypersalinity of lagoons; anaerobic conditions brought about by influx of organic material, stagnancy or stratification of water-layers; etc.) which enhance the likelihood of preservation of uncalcified kinds. Natant Crustacea are unlikely to have heavy shells. Scarce forms have (*ceteris paribus*) correspondingly less probability of being preserved than do abundant ones. There are several reasons (indicated at the end of Section IIB2 and in Section III below) for thinking that the Paleozoic Eucarida were, like the Recent ones, preponderantly uncalcified, shrimp-like, marine forms; and it also seems possible that, until the capacities latent in the Eucarid type of organization had begun to be successfully realized through the evolutionary accumulation of further specializations, no dense populations were produced (especially, not benthonic ones, so long as sea-bottom niches were still occupied by long-adapted Trilobites). As regards the frequent fossilization of marine Trilobites and Ostracods in the later Paleozoic, Brooks (1957, p. 896) points out that they "possessed exoskeletons fortified with calcium carbonate. . . ." Likewise, Harrington (1959, pp. O43, O76, O85) states that "The exoskeleton of trilobites consists both of hard mineralized integument and comparatively soft chitinous parts. . . . Ventral appendages of trilobites are very rarely preserved. . . . Parts of the integument were mineralized and hard. . . . This mineralization gave a high rigidity to the test, rendering it easily fossilizable". Benson (1961, p. Q56) says that "pelagic Ostracodes are rare as fossils", and Scott (1961, p. Q21) says that the carapace of ostracods "is composed of two parts: (1) a hard layer of calcium carbonate, and (2) a soft layer, the epidermis. The hard shell substance is preserved in fossils. . . ." Thus, scarcity of Paleozoic Eucarid fossils is conclusive evidence only against abundance of calcified kinds.

B. *Mesozoic:*

1. *Triassic:* The phylogeny of the Mesozoic Decapods has recently been discussed from a paleontological point of view by Glaessner (1957, 1960). Balss (1957) treats the fossils along with the Recent Decapods, and Balss and Gruner (1961) give a paleontological and phylogenetic summary.

Remains of only a few Decapods have been found in the Lower Triassic or Permo-Trias. Two species are referred to the genus *Antrimpos,* some members of which are thought to be very closely related to the recent Peneine *Peneus* (*cf.* Burkenroad, 1936, p. 127, on the Upper Jurassic *Atrimpos speciosus*); indeed, Balss (1922, p. 131) places the Lower Triassic species *atavus* in *"Penaeus"* with the statement, "mit Sicher-

heit hiergehört". In a lower Triassic setting, *Antrimpos* cannot be regarded as primitive; since the Peneinae have undoubtedly evolved from the upper end of a Solenocerine lineage, the lower end of which must have differentiated from a stem which also gave rise to the very primitive Aristeinae; and since this stem seems to have evolved from a common ancestor with the Sergestids, probably resembling *Aeger.* Thus, even without considering the differentiation of the ancestral Dendrobranchiate from the probably achelate, petasma-lacking, appendix-interna-bearing stem-Decapod, an early Triassic Peneine Peneid implies a long series of Decapod predecessors.

A second early *Triassic* form is referred to the Glypheid genus *Litogaster* (with a question mark by Glaessner, 1929; but without a question by Balss and Gruner, 1961). If it is indeed a Glypheid, it is presumably a Reptant Decapod; and evidence from the Recent unequivocally indicates that the Reptantia must have differentiated not only after separation of the incubatory Decapoda Pleocyemata from the Dendrobranchiata, but after separation of the Pleocyemate Natantia from the lineage that later gave rise to the Reptantia. This is shown by the combination of specializations accompanying the benthonic habit in all Recent Reptants (reduced first pleonic somite overlapped by the pleurite of the second when that is expanded; loss of exopodite of the first pleopod, loss of pereiopodal exopodites, etc.; and especially, loss of pleurobranchs anterior to the fifth thoracic somite), which must in all probability have been established in a common ancestor before subdivision of the group, rather than by convergence afterwards. The reason for thinking that the Natant group of incubatory Decapods (Stenopodida and Eukyphida) must have branched off before the definitive Reptant specializations were established is that the Natantia not only have pleurobranchs anterior to the second leg as adults but develop them before the arthrobranchs as larvae (*cf.* Burkenroad, 1939, pp. 316-8). Thus, if the Glypheids are Reptantia, they are not primitive Decapods.

A third early Triassic form is *Clytiopsis,* with two species, classed as a primitive and extinct but Homaridean Reptant group by Balss (1957, pp. 570-1, fig. 1164); the related *Protoclytiopsis* has recently been described from the Permo-Trias of Siberia. It is the present view that the Homaridea must have been derived from an achelate stem, so that *Clytiopsis* cannot even be regarded as primitive among the Pleocyemata Reptantia. Glaessner (1960, p. 48) groups the Homarids with the Peneids (and Stenopodids), citing Beurlen as having shown that the "three pairs of chelate legs in the Trichelida . . . could not have been acquired by primarily benthonic forms"; but against this view that the third legs would have to be reserved exclusively for walking, one might argue that the Eryonids could not have arisen from the achelate Glypheids through *Pemphix* (as proposed by Glaessner, 1960, fig. 19) without benthonic development of chelae on *all* walking legs, not merely the first three. Also, the number of true chelae among Recent Homaridea varies from one pair to four or five, and, as will be shown in the forthcoming review of Recent Decapods, chelae seem to have been independently developed by Eumalacostraca on numerous occasions and on various thoracic appendages including the second and third. Chelae must therefore be regarded as a feature highly subject to convergence, and the wide variation in number of them among different Pleocyemata strongly suggests that the stem-forms both of this suborder and of its supersections had none. A comparison of Glaessner's figures 18 and 19 (1960) shows a remarkable similarity in carapace between the trichelate Triassic Homarids and the achelate Glypheids, consonant with the present suggestion that these two groups are closely related to each other, rather than the Homarids to the Peneids (which have a quite different style of carapace sculpture).

Although I concur fully in Glaessner's observation (1960, p. 36) that "the paleontologist contributes one criterion of incontestable significance, the appearance of various taxa in time . . .," it has to be emphasized that the date of a fossil fixes only the minimal age of the taxon represented, leaving open the possibility that it had differentiated much earlier. The (somewhat questionable) evidence supplied by *Palaeopemphix,* combined with the degree of divergence among early Triassic forms, leaves little room for doubt that direct evidence of the primary evolution of the major

Decapod subdivisions has to be sought in the Permian.

In the Middle Triassic, in addition to further Glypheids and Erymaid Homaridea, the Glypheid-like *Pseudopemphix* and the Palinurid-like *Pemphix* have been found (*cf.* Balss, 1957, pp. 1562, 1577), both with rudimentary chelae. Glaessner (1960) shows that there would be no great difficulty in deriving the carapace of *Pseudopemphix* from that of the Glypheid *Litogaster,* that of *Pemphix* from *Pseudopemphix,* and that of Upper Triassic Eryonid Palinuridea from *Pemphix* (note that the fact that *Pemphix* had begun to develop chelae would seem to exclude it from the direct ancestry of the Scyllarid Palinuridea, despite its resemblance in habitus to the more primitive of the latter).

The Middle and the Upper Triassic yield remains attributed to the peculiar shrimp *Aeger,* which is shown by beautifully preserved late Jurassic material to have been a Peneid, not a Stenopodid. In addition to its three pairs of chelate legs (the third longest, but not stouter) and its first pleonic pleurite overlapping the second, Balss reports a petasma (1957, p. 1559), and I have been able to determine that the pleonic hinges are of a pattern characteristic of Recent Peneids (exposed condyles at the first two and the last two articulations, and a pleurite-covered but well-developed condyle at the third articulation). It is, however, a most peculiar form, as pointed out by Burkenroad (1936, pp. 1-2; 1945, pp. 562, 579). The absence of hepatic spine in most species, the usual presence of a postorbital spine, the ventral tooth of the rostrum, the densely pubescent integument etc., variously suggest Recent Aristeinae, Solenocerinae and some Peneinae; whilst the hypertrophied third maxillipeds and the dorsally-unarmed rostrum suggest certain Recent adult or larval Sergestids. The somewhat reduced first pleonic somite is unlike that of any Recent Dendrobranchiates but comparable with that of the peculiar Upper Jurassic *Acanthochirus* and *Dusa* as figured by Balss (1922). This mixture of characteristics in *Aeger* suggests that its lineage goes back to the undifferentiated Dendrobranchiate stem; and the new family AEGERIDAE is herewith proposed for it. It almost certainly cannot be derived from Peneinae such as *Antrimpos,* although the latter could be derived from something like a generalized form of it. The order of occurrence of the earliest known fossils of *Antrimpos* and *Aeger* thus appears to be the reverse of that in which their lineages differentiated.

2. *Jurassic:* From the Lower Jurassic, there has been reported a variety of Pleocyemate groups not known from the Triassic. These include Eukyphida, Mechochirid Glypheids, Axiid Thalassinidea, Scyllarid Palinuridea, Pagurid (and possibly the Galatheid) Anomala, and Dromiacean Brachyura; as well as a peculiar genus, *Uncina,* which Balss (1957, p. 1560) classifies (after Beurlen and Glaessner, 1930, p. 52) as the Natant "Tribus Uncinoidea . . . Den Stenopodidea nahestehend". What are indicated as unquestionable remains of Galatheids, the Thalassinid *Callianassa* (sensu lato) and Eukyphids have been found later in the Jurassic, strengthening the identifications of less well-preserved Lower Jurassic finds referred to these incubatory sections.

Evidence from the Recent indicates that the Anomala (of de Haan and Boas, comprising the Pagurids, Galatheids and Hippids and excluding the Dromiacea and the Thalassinidea, one or the other of which has customarily been included under the name Anomura H.M.-E.) constitute a monophyletic taxon (antennular stylocerite, peculiar antennal region of the carapace, posterior part of longitudinal suture low on the carapace, reduced fifth leg, medially placed aperture of antennal gland, no podobranchs, etc.). The presence of differentiated Pagurids and Galatheids in the Lias would thus mean that the definitive stem of the Anomala had arisen earlier, presumably in the Triassic.

The Lower Jurassic Scyllarid Palinuridea are presumably derived from an achelate ancestor, therefore perhaps from a time before the appearance of rudimentary chelae in the middle Triassic *Pemphix.* It must be granted that chelae can be lost as well as gained (as shown by, *e.g.,* the aberrant Sergestid *Lucifer* and by Pandalid Eukyphids; in which, however, the retrogression has been accomplished by loss of the dactyl); and Recent Scyllarids have a more advanced development of the diagnostic Palinuridean specialization (the thoracic condyle that en-

gages a depression on the underside of the carapace) than do the Eryonids, as well as various other marked peculiarities such as fusion of the basal joint of the antenna with carapace and epistome. Nevertheless, it would not be surprising to find a primitive achelate Scyllarid, resembling *Pemphix* in habitus, earlier in the Triassic than the Eryonids.

Derivation of the Axiids, in the Lower Jurassic, as "direct descendants of the extinct Glypheocarida" (Glaessner, 1960, p. 48), is at first glance plausible but seems to create phylogenetic difficulties. The distribution of adult and larval characteristics among Recent Thalassinidea suggests that the Axiids (without linea thalassinica), the Callianideids (some with remnants of the linea) and the Callianassids (with linea) had an ancestor with two pairs of chelae, appendices internae and a suture on the carapace; and that this group arose from a common ancestor with the Recent series comprising *Thalassina,* the Laomediids and the Upogebiids, which have a suture although no appendix interna, and have developed only one pair of chelae or none at all (*cf.* Gurney, 1938, pp. 339-343 and 1942, p. 240). It thus seems likely that the achelate ancestor of the Jurassic Axiids had a linea thalassinica, which would exclude the Glypheids. The latter (which are placed close to the Thalassinidea by Balss, 1957) might well be an early, calcified offshoot of the uncalcified, achelate Thalassinid-like Reptant stem, paralleled later from the same stem by the chelate, superficially Homaridean-like Axiids rather than ancestral to them. Such a possibility cannot be dismissed as improbable in the lack of sutured fossils, because the great Tertiary abundance of Callianassid remains consisting almost exclusively of major chelae shows that uncalcified, sutured, achelate Thalassinid-like forms would have had infrequent chances of fossilization. It is therefore here suggested that fossil stem-Reptants have not been found, that Recent Thalassinids have diverged only gradually and incompletely from this stem; and that the fossil Reptants have been preserved because they had become calcified (a specialization with which was correlated a loss of the longitudinal suture).

The Lower Jurassic Brachyuran (*Eocarcinus*), a Dromiacean in which the pleon is "relative gut entwickelt, nicht unter den Carapax geschlagen" (Balss, 1957, p. 1601), may nevertheless in certain respects be less conservative than some of the forms found later in the Jurassic (*e.g.,* it lacks vestiges of the uropods; and according to the present view that the linea homolica is probably homologous with the linea anomurica and the linea thalassinica, it has lost this primitive feature). The distinctive characteristic of the higher Brachyura (loss of arthrobranchs behind the first leg) is foreshadowed in Recent *Dromia,* which still develop posterior arthrobranchs, by a peculiar delay in the appearance of these during ontogeny. Therefore, although Gurney's view of the derivation of the Dromiacea seems sound (1942, p. 270: "it is probable that . . . the Dromiacea sprang" from a stock represented by Recent Laomediid and Upogebiid Thalassinidea), his disagreement with "the general conviction that the Brachyura are descended from the Dromiacea" and his opinion that "the Dromiacea should be excluded altogether from the Brachyura" seem to overemphasize the primitive ontogenetic features of these crabs. In contrast, although exception is here taken to Glaessner's view (1960, fig. 19, p. 45) that the connection of *Eocarcinus* with the unsutured *Pseudopemphix* (classed by Balss, 1957, p. 1577, as a Glypheid) is "beyond doubt", his statement that "It seems to have taken the Brachyura the long span of Jurassic time . . . to consolidate their organization on the level of the Dromiacea" appears to describe a fact (since the higher Brachyura of the Cretaceous must have had calcified ancestors, the lack of Jurassic traces of which would be inexplicable).

Uncina from the Lower Jurassic is believed by Balss (*l.c.*) to have been near the Stenopodida, but if its first chelipeds were the largest and its enlarged second pleonic pleurite overlapped the reduced first segment, it sounds more like an aberrant Homaridean which had lost the uropodal diaeresis like some Recent *Nephropsis* (as also suggested by the presence of chelae on its fourth and possibly on its fifth legs, described by Beurlen, 1928; *cf.* the multichelate Recent Homaridean *Thaumastocheles*).

The Solenhofen quarries have supplied a marvellous array of thin-shelled Upper Jurassic shrimp, among which *Udorella* is of especial interest to the present discussion. This form, as reconstructed by Balss (*cf.* 1957, fig. 1131), evidently had a pleon with expanded second pleura widely overlapping the large first somite, and with strong condyles exposed at the first two and the last two pleonic articulations but none at the third. Such a pleon is characteristically Eukyphid. In contrast to all Recent Eukyphida, however, *Udorella* had all five pairs of legs subchelate (like the middle six thoracic endopods of the Mysidacean *Eucopia*) instead of having the last three pairs simple and the first two chelate or, as in Crangonoids, the second pair chelate and the first subchelate. The presence of long exopodites on all the legs, and the unreduced first pleonic somite, demonstrate that *Udorella* can not have been a Reptant (despite its resemblance in habitus to the Recent Thalassinid *Naushonia; cf.* Chace, 1939 and Thompson, 1903).

As has already been indicated in Section II, B, 1 above, the fact that the Eukyphida must be derived from an ancestor with pereiopodal exopodites, unreduced first pleonic somite and biramous first pleopod, and with pleurobranchs on the second through eighth thoracic somites, means that they are derived from an incubatory lineage that had not yet developed definitive Reptant characteristics. The Eukyphid (and Stenopodid) line must therefore have already been separated from the Peneid and the Reptant lines at the start of the Mesozoic; despite the lack of any record until the Jurassic. It seems possible that the ancestors of *Udorella* never had chelae (and that the first legs of Recent Crangonoids are also relics from the Permian).

All of the major Recent Eucarid taxa except the Stenopodida and the Euphausiacea (which are not known at all as fossils) are represented in the Jurassic; but comparison with the Recent suggests that the Jurassic representation may be strongly biased toward forms fossilized because they had developed calcified arms and (or) armor. The Eucarid group with the greatest Recent population-mass is the Euphausiacea; and next most abundant (in biomass) are very probably the ancient, natant groups Dendrobranchiata and Eukyphida. Even though it includes so exceptional a deposit as Solenhofen, the available Jurassic record hardly suggests enormous success for these primitive, uncalcified adaptations; yet the strong persistence of bottom-living though natant Peneids and Eukyphids into the Recent despite the increasing pressure of radiation of the Reptantia surely implies a great predominance of such unarmed and unarmored forms in most niches of the Jurassic seas. By analogy, the known Triassic and Jurassic Reptants may have been those relatively scarce but readily fossilizable offshoots which had developed from a persistently abundant, uncalcified Reptant stem-lineage, by way of repeated, independent steps toward the hard-shelled, pincer-armed adaptations conducive to free-ranging benthonic survival in a world of predatory vertebrates.

The sutured ancestors of the Anomala and the Brachyura probably arose in the Triassic from the same conservative, unarmed and unarmored Reptant lineage that had earlier given rise to the calcified, unsutured Glypheids from which the Homarids and Palinurids arose; presumably by way of the habit of carrying shelter with them in forays for food out of reach of their crevices (a habit that would favor modification of the posterior legs and the pleon). The habits and structure of some of the Recent Thalassinids may be quite close to those of the hypothetical stem Reptant and its conservative descendants from which the Anomala and Brachyura seem to have arisen.

A diagrammatic representation of what seems likely to have been the order and time of appearance of the different Eucarid groups is given in Figure 1. The names there applied to the different taxa are discussed in the account of Recent Eucarida now being tidied for publication, but a brief explanation of the present acceptance of a tripartite subdivision of the Reptantia under the ancient names Macrura, Anomala and Brachyura seems needed here. A more natural grouping might be achieved by separation of the Glypheidea, together with their presumptive early offshoot the Homaridea and their presumptive later offshoot the Palinuridea, as the section Trichobranchida (restricted, from Huxley): forms lacking a longitudinal suture, and with the filaments of the gills arranged on the axis in pairs of

multiple series or in disorder (assuming that the extinct Glypheids would in this feature have resembled their presumptive early and late offshoots). The remaining three Reptant subsections Thalassinidea, Anomala and Brachyura would be grouped together as the section Phyllobranchida (redefined; from Huxley), probably having had a common ancestor (subsequent to the separation of the Trichobranchida) which retained the longitudinal suture and had the gill-filaments disposed feather-like in uni- or bi-serial pairs along the stem. Although the gills of the more primitive members of all three Phyllobranchid taxa have been classed as "trichobranchiae", and although the expansion of the filaments into flattened leaves was evidently developed independently on various occasions (and not only among Reptantia), Huxley's name seems appropriate enough.

Such a grouping of the Reptants into Trichobranchida and Phyllobranchida would have several disadvantages. First, it would constitute a radical departure from all the current classificatory modes; whereas one such departure (the present suborders Dendrobranchiata and Pleocyemata) seems enough to introduce at one time. Second, the traditional name Macrura, dispensed with by Boas in his great revision, keeps being piously restored to use, and might better be anchored in a more or less acceptable, restricted fashion (as by Waterman and Chace, 1960, p. 25) than left unassigned for attempts at revival in the ancient sense by non-evolutionary systematists (as Holthuis, 1955, p. 4). Third, poorly-known or early Reptant fossils could safely be reported as Macrura, when their classification as Glypheids, Homarids, Thalassinids, Trichobranchids or Phyllobranchids would not be assured. Fourth, further hierarchic downgrading of the taxa Anomala and Brachyura would over-cramp the subdivision of these latest-differentiated but highly-successful, numerous and varied groups. Accordingly, Chace has for the present been followed in grouping the long-tailed Reptantia which have normal uropods and fifth legs as the Macrura; with the reservation that their phylogenetic relationships, as indicated in Figure 1, might be better expressed by a different arrangement.

III. Summary of Probable Characteristics of Fossils of the Hypothetical Ancestors of Major Eucarid Taxa

The foregoing discussion of the fossil record of Eucarid evolution has followed the order of that fragmentary selection; but has been written from a view-point largely based on Recent evidence concerning phylogeny. Many of the crucial characteristics are unlikely ever to become known in fossils (even if deposits like the Burgess shale and the Solenhofen limestone should be located in the Carboniferous, Permian and early Triassic). In the present section, therefore, some deductions are offered concerning possibly recognizable features of undiscovered key fossils of the Eucarida, in the order in which they are here presumed to have evolved (Figure 1).

1. It seems likely that the Eucarid stem-form developed from a primitive Eumalacostracan shrimp with four carapace grooves crossing the dorsum and a longitudinal lateral suture, which lacked brood-lamellae and sperm-receptacle. It may have differentiated about as early as did the progenitors of other Recent Eumalacostracan superorders (in the Mississippian). It was probably a fairly large prawn; since if the branchiae of Lophogastrid Mysids are homologous with the body-gills of Decapods (as seems likely), the ancestral Eucarid must have had both these body-gills and podobranchs; and even though its water-pumping system may have been inefficient, so extensive a set of gills suggests a high volume-to-surface ratio for the body. It was probably a strong swimmer (large pleon and pleopods), a weaker walker (adequate but unspecialized thoracic endopodites) and a back-jumper with the intestine placed above the middle of the pleon to give room for enlarged flexor muscles (since use of the uropods for retrograde evasive propulsion, rather than for forward jumping or mere steering, seems a probable correlate of the diagnostic fusion of the carapace to the thoracic dorsum, presumably required for streamlining during rapid backward motion). It seems likely to have been a detritus-feeder (no chelae) which travelled and spawned off the bottom like some Recent Peneids (since the lack of fossils suggests a thin shell). The habitat was probably marine, like that of the great majority of

Recent Eucarids (note that although the nursery grounds of the juveniles of many Peneinae are in the estuaries of the warmer regions, the adolescents of almost all of these return to the sea to mature and spawn. Only a few species of one Sergestid genus have achieved completely fresh-water life. Investigators of crustacean excretion, osmoregulation and ionic balance seem generally to believe that Recent brackish- and fresh-water Eukyphids and Reptants are likewise invaders from the sea; *cf.* Robertson, 1960, p. 335 and Parry, 1960, pp. 360-1).

Features at all likely to be detectable in fossils and to distinguish the Eucarid stem-form from the Eumalacostracan ancestor are: (a) carapace fused to all thoracic tergites; (b) spines, rather than furcal lobes, flanking an unarticulated telson point; (c) coxa distinct from basis of thoracic appendages; (d) intestine fairly high in the pleon.

2. The stem-form of the Euphausiacea probably differentiated from the Eucarid ancestor fairly soon after that arose (perhaps in the Pennsylvanian), by completely abandoning contact with the bottom, as a feeder on suspended detritus, like some Recent coastal forms. Characteristics that might be detectable in fossils and would distinguish the Euphausiid stem from its Eucarid ancestor are (a) thoracic endopods weaker, especially posteriorly, and set closer together; (b) male genital aperture shifted from limb-base to sternite; (c) a branch of the appendix interna of the first male pleopod enlarged as a spermatophore-handling organ; (d) branchiostegite of carapace reduced (in correspondence with loss of the body-gills); (e) reduction of sculpture of the carapace including loss of the postcervical and cardiacobranchial sulci and of the longitudinal suture (the primitive function of which latter was probably as a spring to extend the branchiostegites again, after these had been clapped down to eject foreign matter from the gill-chamber).

3. The stem-form of the Decapoda may have differentiated from the primitive Eucarids early in the Permian, by improved adaptation to scavenging on the bottom. In particular, the gills became wholly enclosed by the carapace, and the maxillary pump greatly enlarged. Features possibly detectable in fossils, which would distinguish the stem-Decapod from both the Eucarid ancestor and the Euphausiid branch are: (a) cardiacobranchial sulcus crossing the dorsum near the posterodorsal margin of the carapace; (b) well-spaced and strong though unspecialized walking legs on the posterior five thoracic segments, with reduced exopodites of which the basal part was not enlarged, and with the coxal exite of the posteriormost thoracic leg completely lost; (c) endopodite of first thoracic appendage greatly reduced, that of the second one reduced and flexed, and that of the third turned forward and not used for walking; (d) intestine high in the pleon (in relation to improved back-jumping); and (e) development of an antennular statocyst with a statolith composed of sand-grains (probably independent of the Syncarid organ; needed for precise orientation in a natant bottom-feeder which has to avoid unexpected grounding during rapidly repeated jumps). The Permian Paleopemphicidae seem likely to have been a calcified offshoot of the early Decapod stem.

4. The stem-form of the Dendrobranchiata probably differentiated from the Decapod ancestor in the middle of the Permian, by specializations of which those likely to be detectable and diagnostic in fossils are: (a) development of small chelae on the first three pairs of walking-legs (used for picking out and seizing small benthos such as annelids, the setae of which might conceivably be recognizable in a fossilized gut); (b) uncoupling of the pleopods of the three posterior pairs, by loss of the appendix interna; (c) shift of the endopod of the first pleopod proximally from the tip of the protopodite, its reduction in the female, and enlargement of the entire ramus in the male to form a spermatophore-handling organ (the *petasma,* not homologous with the Euphausiid organ derived from a branch of the appendix interna, nor with the also independently-modified first endopods in various Reptant Decapods; about which Siewing, 1956, pp. 135-6, 157, 159, seems quite mistaken).

5. The common stem of the Eukyphids, Stenopodids and Reptantia (Pleocyemata) probably differentiated from the Decapod stem during the middle of the Permian, by developing pleopodal incubation (which probably replaced an earlier habit of scattering the eggs by off-bottom spawning; and

so permitted the beginning of Decapod evolution toward completely benthonic life). It is possible that ovigerous setae might be recognized in fossils; otherwise the incubatory stem-form might be hard to distinguish from the stem Decapod.

6. The stem-form of the Eukyphids and Stenopodids (Natantia, sensu restricto) probably arose from the incubatory branch during the Upper Permian, by loss of the hinges at the third pleonic articulation (permitting a humped posture). The diagnostic specialization, delay in development, or loss, of arthrobranchs, would not be detectable in fossils. The more benthonic Stenopodid line probably soon differentiated from the Eukyphids (according to the scarcity of adult or larval diagnostics common to their Recent representatives, and the numerous striking differences between the two). Among features that might be seen in fossils, the early Eukyphids (a) probably retained pereiopodal exopodites and did not develop true chelae for some time (and then perhaps at first only on the second walking-leg), whereas the Stenopodids probably soon lost the pereiopodal exopodites entirely and developed chelae on the first three pairs of walking-legs, with the third pair enlarged (perhaps the first Eucarid weapons); the Eukyphids (b) retained a biramous first pair of pleopods and the appendices internae, whilst the Stenopodids lost the coupling of the pleopods and the exopodite of the first one; the Eukyphids (c) developed expanded pleonic pleura with the second overlapping the first, whilst the Stenopodid pleura remained small (and when at all expanded, overlapped from front to rear); the Eukyphids (d) retained a large first pleonic somite, which in the Stenopodids tended to become reduced; the Eukyphids (e) lost the condyle only at the third pleonic articulation, whilst the Stenopodids lost those of the anterior articulations as well (according to an as yet incomplete survey of the Recent forms).

7. Finally, the stem-form of the Reptantia probably developed the definitive characteristic of that supersection (loss of the anterior pleurobranchs, undetectable in fossils) in the Upper Permian and became specialized but still thin-shelled crawlers on the bottom (probably crevice-dwellers until the evolution of armor, arms and shelter-carrying and fossorial habits). Recognizable distinctions of fossils of the stem-Reptant would probably be (a) strong achelate legs without exopodites; (b) exopodite of the first pleopods lost and the rest not large enough for effective swimming although still coupled by an appendix interna; (c) the first pleonic somite reduced and the second pleonic pleura somewhat overlapping the first; (d) the anterodorsal part of the carapace with spiny longitudinal ridges instead of the simple postorbital spine of the stem Decapod. The earliest offshoot of this Thalassinid-like Reptant stem was probably Glypheid, in the late Permian; and these (like their early derivatives, the chelate Homarids) would be distinguishable by calcification and the loss of the lateral longitudinal suture of the carapace.

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