The Higher Taxonomy and Evolution of Decapoda (Crustacea)

Martin D. Burkenroad

Abstract. The decapods are herein divided into four suborders: Dendrobranchiata, Euzygida, Eukyphida, and Reptantia. Evidence for monophyly of these taxa is supplied by the adult morphology of characters of gill arrangement, modes of pleopodal incubation, patterns of overlap of abdominal pleura, pleural lock and hinge arrangements, chelation of legs, presence of appendix interna, and form of spermatozoa; the fossil record; and ontogeny. Some possible lines of investigation are outlined which might yield a more natural classification within the Eukyphida and Reptantia.

INTRODUCTION

The difficulty in devising a satisfactory general classification for the Decapoda arises from doubts concerning the higher relationships of the numerous well defined and more or less isolated groups relatively low in the taxonomic hierarchy. For example, Peneidea, Stenopodidea, and Caridea are regarded by Holthuis (1955) as members of a supersection Natantia of the suborder Macrura, which he distinguished from two other suborders Anomura and Brachyura. This classification was derived from Bouvier (1917) and Milne-Edwards (1837). The same three "natant" groups (Peneidea, Stenopodidea, and Eucyphidea) are regarded by Balss (1957) as forming the suborder Natantia, while the remaining decapods are grouped together as Reptantia (more or less after Borradaile, 1907; Ortmann, 1892a, 1892b, 1892c; and Boas, 1880). Glaessner (1960), a paleontologist, divides the same three "natant" groups between two different suborders. The Penaeidea and Stenopodidea together with reptant Nephropsidea form a suborder Trichelida, while the Caridea together with the reptant Thalassinidea and Paguridea form an infraorder Anomocarida of the suborder Heterochelida (the other infraorders being Palinura, Anomura, Brachyura, and the Glypheocarida). This is a modification of an earlier scheme proposed by Beurlen and Glaessner (1930). Gurney (1942) also restricted Natantia, placing the Euphausiacea among the Decapoda and the Stenopodidea among the Reptantia. Burkenroad (1963a) divided the natant groups still differently. Peneids and sergestids were placed in the suborder Dendrobranchiata while the Caridea and Stenopodida were placed with the other decapod groups in the suborder Pleocyemata, an arrangement essentially followed by Glaessner (1969).

The view of this paper is that the Decapoda are monophyletic and distinct from the Euphausiacea, but that most previous subordinal arrangements of the decapods are polyphyletic. It is suggested that the three traditional "natant" groups are not at all closely related to each other and must be regarded as three independent suborders comparable to the fourth homogeneous suborder, Reptantia. It is further suggested that the Reptantia are naturally divisible into several majòr groups, with the brachyuran forms distinct from all the rest. Within the non-brachyuran Reptantia, thalassinideans seem to be quite distinct from the anomuran, astacuran, and palinuran reptants and are treated in this paper as an independent supersection equal in status to the other three macruran and anomuran supersections.

The presence of chelate legs in the early Triassic reptant *Clytiopsis* seems to imply that differentiation within the Reptantia by the development of chelae was already then

advanced. Evidence from the structure and development of the living decapods suggests a "hump-backed" common ancestor of stenopodids and eukyphids. Eukyphids must have separated from an achelate stem having pleopodal incubation before the development of the definitive branchial characteristics of the Reptantia, in time before the subdivision of the Reptantia was established in early Triassic. Consequently, it seems that at least three main lines of decapods must have been distinct in the Permian. The many striking differences between the living stenopodids and eukyphids suggests that the divergence of these two lines from their common ancestor also may have occurred in the Paleozoic, soon after separation of their stem from the line which then gave rise to the reptants.

The formal classification here proposed is as follows:

Order Decapoda Latreille, 1803
    Suborder Dendrobranchiata Bate, 1888
        Superfamily Peneoidea Rafinesque, 1815
        Superfamily Sergestoidea Dana, 1852
    Suborder Euzygida nov.
        Family Stenopodidae Huxley, 1879
    Suborder Eukyphida Boas, 1880
        Several superfamilies with about 20 living families
    Suborder Reptantia Boas, 1880
      Supersection Thalassinida Boas, 1880
      Supersection Astacina H. Milne-Edwards, 1839
      Supersection Palinura Borradaile, 1907
      Supersection Anomala de Haan, 1841
      Supersection Brachyura Boas, 1880

SYSTEMATICS

Order Decapoda Latreille, 1803

Diagnosis.—Antennular peduncle with statocyst; maxilla with a large exite which draws respiratory water through the gill chambers; the first three thoracic appendages reduced and modified as mouth parts and the last five specialized as raptorial and walking legs; the exopodites when present taper throughout without an enlarged stalk; gills in three series, of which the distalmost (podobranch) forms part of a coxal exite and is lacking from the fifth thoracic leg (which often bears a pleurobranch); genital apertures coxal. (Exceptions to the above are secondary: statocyst, exopodites, gills and some legs may be lost; and genital aperture may migrate to sternum.)

Suborder Dendrobranchiata Bate, 1888

Diagnosis.—Eggs freely broadcast (or briefly hung from pereiopods as in *Lucifer*); hatched as nauplii (or protozoeas); pleurobranchs appear later during ontogeny than do the pairs of arthrobranchs, and are lost before the latter, when, during phylogeny, the branchial formula becomes impoverished; gill stems bear a double series of primary rami equipped with secondary filaments or plates; first three pairs of legs chelate, none much enlarged (except the first pair in adult males of *Heteropeneus*); pleopods without appendix interna (unless such is represented by hooks on endopod of male first pleopod, or by the unarmed blade on the male second pleopod of Aristeidae); first pair of pleopods in males with endopod much modified as a copulatory organ (reduced or absent in females); pleura of first pleonic somites overlap those of the second; pleonic somites locked to each other by mid-lateral hinges, which are usually exposed at the two anterior and the two posterior somite articulations but always hidden under the posterior margin of the third somite at the middle articulation (in Recent forms).

Etymology and remarks.—The name of the suborder refers to the compound branching of gills, unique among decapods. It is derived from Bate's "Macrura Den-

drobranchiata'' (1888), although present use applies only to Bate's "Dendrobranchiata Normalia" (his "Aberantia" comprised the mysids and euphausiids).

It has been traditional to use descriptive names rather than generic derivatives for the higher categories of Decapoda (e.g., Macrura and Brachyura of Latreille; Macrura, Anomura, and Brachyura of H. Milne-Edwards; Brachygnatha, Oxystomata, Anomala, and Carides [although Astacina from *Astacus*] of de Haan; Natantia and Reptantia of Boas; Trichobranchiata and Phyllobranchiata of Huxley; Trichelida and Heterochelida of Beurlen and Glaessner). In the case of Dendrobranchiata, desirability of a neutral name at the subordinal level is increased by the likelihood that a new section will have to be created for some of the fossils, Dana's section name Peneidea being best reserved for the living forms.

The superfamily names are simple promotions of two of Dana's three families of Peneidea (excluding *Stenopus* from his Peneidae and transferring *Lucifer* from his Mysidae to his Sergestidae). The spelling Peneoidea is here used in the view that since *Penaeus* has been placed on the Official List of Generic Names in Zoology by illegal means (so that the orthographic question remains an open one) *Peneus* is preferable for both etymological and practical reasons (Burkenroad, 1963*b*).

Suborder Euzygida nov.

Diagnosis.—Eggs hung from pleopodal setae; hatched as zoeas (or later); pleurobranchs appear before arthrobranchs during individual development, present on five somites when one of the two arthrobranchs per somite is missing in those few adults with an impoverished branchial formula; gill stems bear numerous simple filaments, not arranged in regular rows; three anterior pairs of legs chelate, the third being enlarged; pleopods entirely without appendix interna, first pair uniramous in both sexes; pleura of anterior pleonic somites usually not expanded, but when they are, enlarged enough so the first overlap the second; only the three posterior pleonic somites are hinged together by definite locking points.

Etymology and remarks.—This subordinal name comes from *eu-*, truly, and *zyg-ios*, yoked (from *Zygia*, Juno as the goddess of marriage), which refers to the well-known tendency of members of the group to live in couples even when not imprisoned in sponges (Limbaugh et al., 1961). It also refers to the presumptive Paleozoic conjunction of the group with the yoke-shaped (kyphonid) Eukyphida, from which time it retains a tendency to the bent posture (discussed below). The reasons for a descriptive name rather than using Stenopodida for the suborder are similar to those given above for Dendrobranchiata. It may be added that according to Holthuis (1947, 1955), *Stenopus* might fall prey to Rafinesque's prior use of the name *Byzenus*.

Suborder Eukyphida Boas, 1880

Diagnosis.—Eggs hung from pleopodal setae; hatched as zoeas (or later); pleurobranchs appear earlier than arthrobranchs during individual development; no more than one arthrobranch ever present on a somite and all may be absent even when pleurobranchs are still retained on all the legs; gill stems bear double series of plate-like rami without secondary branches; one or both of the two anterior pairs of legs chelate (except in *Procaris*), of which one or both of either pair may be enlarged; pleopods usually with appendix interna, the first pair with an endopod (usually reduced; typically not elaborately modified in males); pleura of the second pleonic somite overlap those of the first; the two anterior and two posterior pleonic somites are hinged together, but the middle articulation lacks a hinge; the pleon is often carried bent between the third and fourth somites (the first maxillipede usually with a setose expansion on the outer side of the base of the exopod, not found in the other suborders).

Etymology and remarks.—This name comes from Ortmann's modification (1890) of Boas's (1880) name Eukyphotes, employed by Balss (1927) in Kükenthal and Krumbach's Handbuch and (1957) in Bronn's Tierreich. Boas derives the name from *kuphos,*

crooked (which seems to be cognate with *kuphon*, a yoke). This usage is preceded in classical antiquity by Aristotle's, ". . . ton men karidon ai te kuphai . . ." in the *Historia Animalium* (*see* Thompson, 1910).

Boas made a new name for this group of his suborder Natantia because he felt that to follow Dana in restricting Latreille's "Carides" would result in confusion as to what was meant (because of persistent use of Latreille's name in its original polyphyletic sense). An analogous reason for now sustaining Boas's name is that "Caridea" in Dana's sense has of recent years been used chiefly by those who do not recognize the fundamental nature of Boas's revision and who continue to group long-tailed decapods together whether they are reptants or not. A desirable difference in nomenclature, corresponding to the difference in systems of classification, thus results from the present rejection of "Caridea" as a name for the suborder.

The broad use of *karis* (which was general, except for Dana, from Aristotle until 1907 when Borradaile revived "Carides" in Dana's restricted definition) is appropriately preserved in Calman's Eucarida, and in the term "caridoid facies of the Malacostraca" (which does not mean "eukyphid facies" [H. Milne-Edwards, 1837]).

The hump and flexure of the third and fourth pleonic somites, so characteristic of many eukyphids, seems to be the relic of an ancient conjunction of this suborder with the euzygids; and the latter name has accordingly been coined in reference to the former (the roots of both names having apparently originated in the terminology of the cattle yoke).

The Eukyphida contains some twenty more or less distinct living families, the relationships of which are in the main still so debatable that no generally accepted groupings between the subordinal and family levels have yet been proposed. Compare Holthuis (1955) with Balss (1957, who gives a good summary of the distribution of characteristics within the group) and note the remark by the former, p. 10: "I fully realize that the arrangement of the families given here is by no means a natural one . . . ."

The mentioned arrangement by Holthuis, including two new superfamilies and several more or less novel regroupings, is only sparsely characterized, discussed, or documented. It does not distinguish between arbitrary groupings by Holthuis, for which there seems nothing favorable to be said, and valid groupings developed by prior authors, e.g., p. 12, ". . . OPLOPHOROIDA . . . Three families are left in this superfamily"; but no reasons are given for retention of Nematocarcinidae when other families traditionally grouped with Hoplophoridae are removed. Of another sort is Holthuis' statement on p. 82, "In my opinion the Processidae are so closely related to the Hippolytidae . . . that they cannot be placed in a different superfamily. Both Borradaile and Balss assigned the Processidae to the superfamily Crangonoida, but this is certainly incorrect"; which is a conclusion evidently taken from Lebour (1936), who is not cited. Again, p. 117, ". . . Pandaloida . . . consists of the three families Pandalidae, Thalassocaridae, and Physetocaridae," but reasons for making *Thalassocaris* a family are not given, and the somewhat intricate reasons (Burkenroad, 1942) for regarding *Physetocaris* as a pandaloid are not cited. Holthuis states on p. 36, "The Bresiliidae generally were believed to belong to the Pasiphaeoida, the Eugonatonotidae and the Disciadidae were placed in the Oplophoroida, while the Rhynchocinetidae formed part of the Palaemonoida. . . . The Rhynchocinetidae and the Eugonatonotidae certainly are closely related . . . . The Disciadidae in several respects are intermediate between the Bresiliidae and the other two subfamilies . . . "; but compare this to Gurney (1939, 1941), Burkenroad (1939), or Lebour (1941), none of which are cited.

In effect, Holthuis seems to have employed only those selected results of others which are compatible with a simplified, artificial arrangement based almost entirely on the structure of the chelate legs (structures actually often intergradient, and apparently highly subject to convergence). His system thus seems unlikely to stand the test of monophyly.

Suborder Reptantia Boas, 1880

Diagnosis.—Eggs hung from pleopodal setae; hatched as zoeas (or later); arthrobranchs and pleurobranchs generally appear simultaneously in development, but pleurobranchs never occur anterior to the second leg (pleurobranchs seem to appear later than arthrobranchs in ontogeny of thalassinids that have any pleurobranchs, while arthrobranchs appear later than pleurobranchs or are absent on second to fourth legs of Brachyura); gill branches range from multiple filaments (trichobranchs like those in Euzygida) through quadruple or double rows of filaments or flattened, narrow plates, to fully developed phyllobranchs (like those in Eukyphida), but are never secondarily branched as in Dendrobranchiata; number of chelate legs ranges from none to all five pairs (and second and third maxillipedes are also occasionally chelate); first pair of legs enlarged; pleopods with, but more commonly without, appendix interna, first pair uniramous in both sexes and usually reduced, modified, or absent; pleura of second pleonic somite overlap those of first when pleura are sufficiently well developed; all five articulations between pleonic somites locked by mid-lateral hinge points when the pleon is large and strong, but pleon often reduced (the first somite always so) and the pleura often small even when pleon is well developed.

There are characteristics which distinguish most Reptantia from the other decapods and are appended here to the standard list above because the wide range among reptants in structure of gill rami, number of chelate legs, form of pleopods, etc., permits only a single completely diagnostic distinction from the other two incubatory suborders (lack of a pleurobranch on the first legs). Body never laterally compressed, too heavy for really effective pleopodal swimming; rostrum never laterally compressed as a serrate blade; antennule usually without a stylocerite; antennal exopodite never expanded disto-medially into a foliaceous blade (at least in living forms); basis and ischium of first legs usually immovably joined (as frequently in the other legs also); legs usually stout, with a breaking plane in the basis; propodus usually movable in only one plane; exopods usually entirely absent from the pereiopods (and never more than rudimentary in the adult); podobranchs often present on the third maxillipedes and the anterior four pairs of legs.

Beurlen and Glaessner's "infraorder" Glypheocarida does not appear to be comparable with the above five supersections, since distinctions between their Glypheidea and Thalassinidea seem rather obscure, while their Pemphicidea seem to be primitive Palinura (cf. Balss, 1957).

The names and authors here given for higher groups beyond the governance of the Rules are intended as the earliest corresponding to the present definitions. The name Anomala was coined by Latreille but unlike de Haan he excluded the lithodids. Astacini of Latreille was a melange, restricted in Milne-Edwards's "Famille des Astaciens." Eryonids and loricates were first united by Borradaile although Boas recognized their close relationship. Brachyura seems not to have been used in exactly the present sense from Latreille on until Boas; similarly, the "Famille des Thalassiens" of Milne-Edwards and the Thalassinidea of Dana included the pagurid *Glaucothoë*. The name Anomura, introduced by Milne-Edwards for those decapods which establish "le passage entre les Brachyures et les Macroures . . . ," has always included the thalassinids or dromiids etc., and it is not equivalent to de Haan's and Boas's Anomala either in composition or in connotation. It seems best dropped, along with the comparable grade-name Macrura Latreille.

DISCUSSION

In this section is given in some detail the reasoning behind the above proposed subdivision of the Decapoda, as based on a consideration of a broad range of decapod biological features.

Evidence from Morphology

Various features which heretofore have been regarded as characteristic of the Reptantia are either not so universal among them or not so limited to them as had been thought. First, a stylocerite is quite as well developed in the Stenopodidae as in the Anomala. Second, a two-hinged articulation of propodus and carpus which is usual in the pereiopods of Reptantia is lacking in the chelipeds of at least some Eryonidea (the chelae in that group being mobile in many directions, as is usual in dendrobranchiates and eukyphidans). Third, the basis and ischium are not fused in any pereiopods in at least some of the axiid Thalassinidea, whereas they are fused in alpheid eukyphidans as an exception to the natant rule. Fourth, the coxal position of the male genital apertures usual in Reptantia (sternal in the higher Brachyura) is matched by stenopodids as well as by the eukyphidan *Pandalus* (Boas, 1880). Fifth, the first pleonic somite is as much reduced in some stenopodids as in some Reptantia. Sixth, the pleopods of some thalassinid Reptantia are almost as well developed and used as much for swimming as are those of stenopodids.

Branchial pattern.—Reptantia do possess at least one characteristic unique among decapods which seems to demonstrate the homogeneity of the group and to emphasize its distinctness from the Euzygida, Eukyphida, and Dendrobranchiata. This character is that, in the Reptantia, pleurobranchs never occur on the first pereional somite, even when one occurs on all of the following pereional somites; whereas, in the other three groups, when a pleurobranch is present on the somite of the second leg it is preceded by a homologous gill on the first leg. It is difficult to avoid the conclusion that loss of the first pereional pleurobranch was a basic difference between the ancestral reptant and the ancestral decapod. Table 1 expands on this and compares the various decapod groups. It supplies strong evidence of a monophyletic origin of the Reptantia later in date than the separation of the eukyphid-euzygid line as discussed below.

The extreme formulae given in Table 1 are synthetic and do not necessarily represent any one species. If any gill is known to be present in any member of a given group, it has been entered in the "rich" or maximal formula; similarly, if any gill is known to be absent in any species which retains any gills, it has been omitted in the "impoverished" formula. For example, a dorsal arthrobranch of the second maxillipede is present in laomediid thalassinids, which lack pleurobranchs; whereas, in the axiid thalassinids, some of which have pleurobranchs, the dorsal arthrobranch of the second maxillipede is absent. In the maximal formula given here for thalassinids both the dorsal arthrobranch of the second maxillipede and the pleurobranchs are shown. Intermediate formulae are selected actual ones. However, it should be noted that relatively few branchial formulae have been determined; therefore, all statements concerning them should be understood as qualified by the phrase "as far as known."

The specific branchial formulae from which the present table has been prepared are given in compilations by Calman (1909), Gurney (1942) and Balss (1957), in part corrected or confirmed by my own published and unpublished observations. The principles employed in identifying those gills which are present on somites where the full complement is lacking are as follows: the *podobranchs* spring from (or at the base of) a stem, the epipodite, which has a coxal insertion, and which is often present without bearing branchial filaments; the *arthrobranchs*, primitively in pairs from narrowly separated insertions, spring from the body wall above the coxa and sometimes originate in larval development by the splitting of an unpaired rudiment (Burkenroad, 1945), with the posterior one of the pair usually quite appreciably dorsal to the ventral one and near the posterior margin of the somite; the *pleurobranchs* are never paired, and insert on the body wall above the arthrobranchs, near the anterior margin of the somite. When there are only two body gills on a somite, the homology of the dorsal-most has to be judged chiefly by its position anterior or posterior to the ventral one. Although the lack of three body gills on any somite of Eukyphida prevents complete certainty that the dorsal one is a pleurobranch, it seems likely from the euzygid pattern that the rule of position is applicable also to eukyphids.

TABLE 1. Maximal, intermediate and impoverished branchial formulae among the living decapod Crustacea. (r) rudimentary, (0) absence, (e) epipodite, (p) podobranch, (a) arthrobranch, (pl) pleurobranch.

Thoracic somite / Limb	1 (Maxillipede 1) e + p	a?	2 (Maxillipede 2) e + p	a	pl	3 (Maxillipede 3) e + p	a	pl	4 (Pereiopod 1) e + p	a	pl	5 (Pereiopod 2) e + p	a	pl	6 (Pereiopod 3) e + p	a	pl	7 (Pereiopod 4) e + p	a	pl	8 (Pereiopod 5) pl	Total exites e	p, a, pl
Dendrobranchiata	1 + 0	r	1 + 1	1	1	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1 + 0	2	1	1	7	24
	1 + 0	0	1 + 1	1	1	0 + 0	2	1	1 + 0	2	1	1 + 0	2	1	0 + 0	2	1	0 + 0	1 + r	0	0	4	17
	1 + 0	0	1 + 0	0	0	0 + 0	1	0	0 + 0	1	0	0 + 0	1	0	0 + 0	0	0	0 + 0	0	0	0	2	3
Euzygida	1 + 0	1	1 + 1	1	0	1 + 0	2	1	1 + 0	2	1	1 + 0	2	1	1 + 0	2	1	1 + 0	2	1	1	7	19
	1 + 0	r	1 + r	r	0	1 + 0	1	1	0 + 0	1	1	0 + 0	1	1	0 + 0	1	1	0 + 0	1	1	0	3	13
	1 + 0	0	1 + r	0	0	1 + 0	1	1	0 + 0	1	1	0 + 0	1	1	0 + 0	1	1	0 + 0	r	1	0	3	11
Eukyphida	1 + 0	0	1 + 1	0	0	1 + 0	1	1	1 + 0	1	1	1 + 0	1	1	1 + 0	1	1	1 + 0	1	1	1	7	12
	1 + 0	0	1 + 0	0	0	1 + r	0	r	0 + 0	r	1	0 + 0	r	1	0 + 0	r	1	0 + 0	r	1	1	3	11
	0	0	0 + 0	0	0	0 + 0	0	0	0 + 0	0	1	0 + 0	0	1	0 + 0	0	1	0 + 0	0	1	r	0	5
Reptantia — Homarida	1 + r	r	1 + 1	1	0	1 + 1	2	0	1 + 1	2	0	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1	7	23
	1 + 0	0	1 + 1	1	0	1 + 1	2	0	1 + 1	2	0	1 + 1	2	r	1 + 1	2	r	1 + 1	2	r	0	7	20
	r + 0	0	1 + 0	r	0	1 + 1	1	0	1 + 1	1 + r	0	1 + 1	1 + r	0	1 + 1	1 + r	0	1 + 1	1 + r	0	0	7	15
Reptantia — Palinura	1 + 0	0	1 + 1	1	0	1 + 1	2	0	1 + 1	2	0	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1	7	21
	1 + 0	0	1 + 0	0	0	1 + 1	2	0	1 + 1	2	0	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1	7	19
	1 + 0	0	0 + 0	0	0	r + 0	1	0	1 + 1	2	0	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1	6	17
Reptantia — Thalassinida	1 + 0	1	1 + 1	2	0	1 + 1	2	0	1 + 1	2	0	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	r	7	23
	1 + 0	0	1 + r	r	0	1 + 1	2	0	1 + 1	2	0	1 + 1	2	0	0 + 0	2	0	0 + 0	2	0	0	5	15
	0 + 0	0	1 + 0	0	0	0 + 0	2	0	0 + 0	2	0	0 + 0	2	0	0 + 0	2	0	0 + 0	2	0	0	1	10
Reptantia — Anomala	1 + 0	0	r + 0	0	0	1 + 0	2	0	1 + 0	2	0	1 + 0	2	1	1 + 0	2	1	1 + 0	2	1	1	7	14
	1 + 0	0	0 + 0	0	0	1 + 0	2	0	1 + 0	2	0	1 + 0	2	1	1 + 0	2	1	0 + 0	2	1	1	5	13
	1 + 0	0	0 + 0	0	0	0 + 0	1	0	0 + 0	2	0	0 + 0	2	0	0 + 0	2	0	0 + 0	2	0	1	1	10
Reptantia — Brachyura	1 + 0	0	1 + 1	1	0	1 + 1	2	0	1 + 1	2	0	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1	7	21
	1 + 0	0	1 + 1	0	0	1 + 0	2	0	0 + 0	2	0	0 + 0	0	1	0 + 0	0	1	0 + 0	0	1	0	3	8
	1 + 0	0	0 + 0	0	0	r + 0	1	0	0 + 0	2	0	0 + 0	0	0	0 + 0	0	0	0 + 0	0	0	0	2	3
Hypothetical Stem-decapod	1 + 1	1	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1 + 1	2	1	1	7	27

When there is only one body gill (as always on the first maxillipede and fifth leg) its homology is uncertain. Since the gill of the fifth leg appears after the arthrobranchs of preceding somites in Dendrobranchiata (like the pleurobranchs in this group), and before the arthrobranchs in the Euzygida and Eukyphida (like the pleurobranchs in these groups), I have called it a pleurobranch throughout the Decapoda. There is no reason to think that the body gill of the first maxillipede is not homologous in all decapods, but to call it an arthrobranch is a convention. It should be noted that this gill is a lamella fringed with filaments in Dendrobranchiata (the filaments tend to be separated into two groups in Solenocerinae, but this probably does not mean that they represent two distinct gills as thought by Kubo [1949] whose observations on branchiae seem erratic). In contrast, in the euzygidan *Stenopus* cf. *S. scutellatus* the gill of the first maxillipede is an ordinary one of large size (as well developed as that of the second maxillipede); and the gill of the first maxillipede is also normal in form, though minute, in the laomediid reptant *Axianassa* sp.

There are two body gills on the second maxillipede in many Dendrobranchiata and in reptant laomediid Thalassinida, but none elsewhere in the order. Holthuis (1947) has mistaken the gill of the first maxillipede of Euzygida for a second one on the second maxillipede, except in *Spongicoloides profundus* for which he evidently copied the correct formula from Hansen. There may be a real difference between Dendrobranchiata and Reptantia in homology of the dorsal of these two gills. The dorsal gill in Dendrobranchiata is clearly anterior to the ventral one, which inserts on the posterior margin of the somite. In *Axianassa* sp., the dorsal gill is directly above the ventral one, which is in the middle of the somewhat roomier lower part of the narrow somite. The dorsal gill appears to be the one missing in Euzygida, according to the low and medial emplacement of the one which is present.

The dorsal of the two body gills of the third maxillipede of Eukyphida has been termed an arthrobranch by some observers, a pleurobranch by others. Its position seems to be anterior to the ventral gill in all, so it is here considered a pleurobranch since in Burkenroad (1939) "somite VIII" is a *lapsus calami* for somite IX.

Gills absent in the adult seem never to be present in the larvae, although it is important to note that gills relatively weak in the earlier larva sometimes outgrow their previously larger neighbors (Burkenroad, 1945). In general, gills absent in adults with impoverished formulae are relatively delayed in the larval development of related forms with rich adult formulae (Burkenroad, 1934, 1939, and 1945).

It is most important to note the following. Inasmuch as any body gill on a somite can presumably serve the function of another, the differences among decapods in patterns of loss of gills from the primitive, maximal formula seem likely to be controlled chiefly by genetic accident in ancestral forms and not to be much subject to adaptive convergence. There are several significant features to be derived from Table 1. First, there is the tendency of dendrobranchiates to lose pleurobranchs in contrast to the preferential loss of arthrobranchs in euzygids and eukyphids. Second, there is the persistence of a podobranch on the first maxillipede and the fourth leg in some Reptantia (Calman, 1909, p. 278). Third, there is the total lack of pleurobranchs anterior to the second leg in any reptant (although pleurobranchs are present on the second and following legs in some members of all reptant supersections). Fourth, there is a total lack of podobranchs in all Anomala. Fifth, there is the total loss of arthrobranchs posterior to the first legs in all but the most primitive Brachyura despite the retention of pleurobranchs on posterior somites in most of the higher Brachyura. Any natural evolutionary system of decapod classification must give serious consideration to these features.

One conclusion that can be reached is that the gills of living Dendrobranchiata and Reptantia cannot be derived one from the other but only from a common ancestor with a richer formula than in any living form. That is, no dendrobranchiate has a podobranch on the first maxillipede or the fourth leg, and no reptant has a pleurobranch on the maxillipedes or the first pereiopods. Similarly, the branchial pattern in Brachyura cannot be derived from one like that in any living Anomala, since a podobranch is present

on at least one of the pairs of maxillipedes of some member of every brachyuran group. Therefore, it seems doubtful whether the podobranch-bearing ancestor of the Brachyura could be defined as an anomalan.

Pleopodal incubation.—The basic reason against accepting Boas's "Natantia" as a natural group is that it would require that pleopodal incubation of the eggs arose independently in at least two different decapod lines. The condition in the Dendrobranchiata, where the eggs are broadcast (or by exception briefly incubated under the thorax), must be regarded as a primitive characteristic correlated with eclosion in the naupliar (or by exception, the protozoeal) state, and almost certainly retained from the ancestral decapod. Therefore, if the dendrobranchiates, euzygids, and eukyphids had a common "natant" ancestor distinct from that of Reptantia, the euzygids and eukyphids must have invented pleopodal incubation and abbreviated development independently of the reptants—which is possible but seems improbable.

As shown by Burkenroad (1947), incubation in decapods is made possible by the temporary self-fusibility of the outermost of the three membranes secreted by the ovum. Essentially, the eggs can become attached to any structure around which their outer shells can meet to fuse. Although an enzymatic intensifier from pleopodal glands seems usually involved in the process, incubation appears to be more an invention in behavior—retention of the eggs in contact around suitable projections until the outer membranes have fused and hardened, together with an inhibition of subsequent cleaning behavior—than in structure.

Attachment of the eggs of the sergestoid dendrobranchiate *Lucifer* to spinules on the coxa of the third leg shows that the independent development of incubatory behavior can occur. It would, however, be surprising if the euzygids, eukyphids, and reptants had each independently developed not only behavior leading to egg attachment, but also egg attachment exclusively to special pleopodal setae. It is therefore probable that euzygids, eukyphids, and reptants had a common ancestor which diverged from the dendrobranchiates by developing pleopodal incubation. Pleopodal incubation made abbreviation of development possible by reducing larval mortality, thus permitting fewer and larger eggs. Abbreviated development facilitates change in the form and order of appearance of various structures since the embryonic structures no longer have to be functional as they were with naupliar eclosion, which characterized the decapod stem form and the Dendrobranchiata. Therefore, the development of pleopodal incubation may have been the crucial step that freed decapod evolution from the limitations of the caridoid facies.

Overlap direction of abdominal pleura.—Euzygida resemble Dendrobranchiata in having the first pleonic pleura overlapping the second. Eukyphida resemble Reptantia in that, when any overlap is detectable, the second pleuron overlaps the first (compare *Crangon* with the undoubtedly convergent *Naushonia*). It seems likely that the decapod stem form had unexpanded pleura with no decided overlap, as in many living Reptantia. However, the fact that the pleural overlap in reptants (when detectable) seems always to be of the second pleuron over the first suggests that the pleura of living Reptantia may have been reduced from an ancestral state of greater expansion and decided overlap. It is my view that the direction of overlap must have been variable in the common ancestor of the euzygids and eukyphids. The resemblance in pleural overlap of euzygids to dendrobranchiates and of eukyphids to reptants is, then, the result of independent development. If the directions of overlap were not independently derived, this would imply independent development of the peculiar euzygid-eukyphid branchial pattern and a multiple origin of pleopodal incubation (among other features), which seems unlikely.

Pleural lock and hinge arrangements.—In addition to the direction of overlap of the pleura, their contacts supply another distinctive set of patterns among the decapods. Euzygids are unique in having the anterior three pleonic segments more or less loosely and flexibly bound together, with a locking point present only between the fourth and fifth, and fifth and sixth somites. Reptants with well-developed pleura have, in contrast, all of the segments locked together by mid-lateral hinge points.

These reptant hinge points are exposed and strong in eryonids, scyllarids, and some homarids. They are present in *Cambarus,* but hidden under the pleura except between the fifth and sixth somites. They are present but hidden except between the first and second somites in *Upogebia.* They are exposed on all segments in *Munidopsis* but weak between the fifth and sixth somites. In raninids they grow stronger from front to rear.

Eukyphids have a still different pattern. In those I have examined there is no well-defined hinge point between the third and fourth somites. These somites are quite flexibly coupled although bound rather firmly in, e.g., *Spirontocaris.* The other pleonic somites are locked to each other, with all four pairs of hinges usually externally visible. The one between the second and third somites is sometimes weak and hidden under the pleura (e.g., in *Spirontocaris*).

Finally, the dendrobranchiates resemble the eukyphids in having well-developed hinges at the anterior two and posterior two pleonic joints. These hinges are externally visible except the anterior two in *Sicyonia* which are hidden under the pleura. No hinge is externally visible between the third and fourth somites. The dendrobranchiates differ from the eukyphids in having the third and fourth somites quite inflexibly coupled by a rather ill-defined hinge point hidden under the pleura.

It seems possible that the decapod stem form may have had all pleonic somites obviously hinged and that a tendency towards loss of pleonic hinges was a special characteristic of the hypothetical euzygid-eukyphid line. At any rate, it seems significant that the euzygids, although resembling the dendrobranchiates in direction of pleonic overlap, are far different in pleonic hinge pattern.

Pleonic hinge patterns can be observed in fossils. In *Aeger,* an available specimen of *A. tipularius* from Solenhofen shows the dendrobranchiate pattern including the covered locking-point in the joint between the third and fourth somites. It is also noted that the figures of *Acanthochirus* and *Dusa* by Balss (1922) suggest an exposed hinge in this position such as now occurs only in Reptantia.

Branchial development.—A fundamental feature in which the euzygids resemble the eukyphids, and the reptants resemble the dendrobranchiates, has been described by Burkenroad (1939). In the course of euzygid and eukyphid ontogeny pleurobranchs appear before arthrobranchs. When the gill formula of their thoracic somites three to seven (second maxillipede to fourth leg) is impoverished in an adult, it is one or both of the pair of arthrobranchs which is missing rather than the pleurobranchs, e.g., some species of the euzygids (*Spongicoloides* [Holthuis, 1947]) and in all Eukyphida. In contrast, in peneids and axiid reptants the pleurobranchs appear later in development than the arthrobranchs (Gurney, 1942). In adult peneids and reptants, pleurobranchs may be absent on thoracic segments three to seven even though paired arthrobranchs are present on all of them. The higher Brachyura, with greatly impoverished branchial formulae, differ from other reptants in that pleurobranchs may occur on the somites of the second and third legs although arthrobranchs are completely lacking there. It seems possible that the euzygids and the eukyphids had a remote common ancestor distinguished from the stem leading to the reptants by the precocious appearance of larval pleurobranchs.

Chelate legs and appendix interna.—The euzygids share with the dendrobranchiate and the astacuran reptants the characteristic of having chelae on the three anterior pairs of thoracic limbs, and with the dendrobranchiates the lack of the appendix interna. These similarities are probably not phylogenetically significant since the similarity to reptants in these same features has almost certainly not been the result of retention from a common ancestor. Likewise, certain thalassinids resemble eukyphids in possessing two pairs of chelate legs and sometimes the appendix interna, and this also seems unlikely to signify any special relationship.

The appendix interna is assuredly a primitive character, independently lost in a variety of groups (note its retention on the second male pleopod of aristeid peneoids and the astacine genus *Enoplometopus* [Barnard, 1950]).

The unknown ancestor of the decapods may have had no chelae at all, as in males of the living scyllarid Palinura. However, unless the decapod stem form had the posterior maxillipede and all five pairs of legs chelate, so that the differing patterns in various groups all represent reduction of the ancestral number, there must have been some independent development of chelae among decapods.

Spermatozoan construction.—Similarity of spermatozoa among "Natantia" has been cited as evidence of the unity of such a group by Balss (1957, p. 1515; "Die Natantia z. B. stimmen in Bau der Spermien überein . . . ."). This supposed uniformity does not in fact exist. There is as great a variation in gross form and structure among Dendrobranchiata as among Reptantia—from superficially simple ellipsoids in the sergestid *Lucifer faxoni* (comparable with the reptant *Callianassa seilacheri*) to subdivided cells with a seta-like, obliquely directed appendage in the peneoid *Trachypeneus birdi* (apparently comparable in complexity with the structure in such reptants as *Pagurus longicarpus*). In some dendrobranchiates (e.g., *Parapeneus longirostris, Hymenopeneus robustus*) the spermatozoa do show a resemblance in general form to those of some eukyphids, a more or less flattened head and a tapering central spike like a tack. However, there is no reason to think that these cells are any more like each other cytologically than they are like reptant spermatozoa. The tack-like form is not universal in eukyphids (there are exceptions such as *Xiphocaris elongata* and *Atya scabra*). Finally, the euzygids have still another type of spermatozoan according to my examination of unstained material from the jelly-column in the vas deferens of a formalin-fixed, alcohol-preserved male of *Stenopus* cf. *S. scutellus* (apparently the first spermatozoan from this group to be described). This cell is superficially like the diagram of a "*Squilla*" spermatozoan given by Nichols (1909). It is a slightly flattened spheroid, apparently lacking appendages, with a small refractile body in the middle of one side of the disc.

Before the various types of decapod spermatozoa can be interpreted in terms of relationship at the subordinal level, it will be necessary to have electron microscope studies of a variety of them, like those of Moses (1961a, 1961b) on *Procambarus clarki*. It would also be helpful to understand the functional significance of the differences in structure (*see* Burkenroad [1947] on the mechanism of fertilization in decapods). Despite the difficulty of interpretation of gross structure, the decapod spermatozoa might be of considerable use in distinguishing taxa. Burkenroad (1934, 1936) made routine descriptions intended as notes toward possible future use in setting generic limits.

Evidence from the Fossil Record

Not having examined much fossil material, I am not in a position to discuss with authority the compatibility of the fossil record with the foregoing hypotheses, but will venture a few remarks. Triassic dendrobranchiates include a form quite indistinguishable from the living *Peneus*—*Antrimpos*, known back to the lower Triassic (Burkenroad, 1936; Balss, 1922, 1957). There is also an extinct type perhaps representing the common ancestor of Peneoidea and Sergestoidea—*Aeger* (Burkenroad, 1936, 1945; Balss, 1957), which has a petasma which would ensure that it is not a euzygid.

Reptantia of the groups Astacina and Palinura Eryonidae, already with chelae like those of living members of these groups, were also present in the Triassic (Glaessner, 1969). Also known from the Triassic are the Glypheidae, without chelae and somewhat suggesting thalassinids, and the Pemphicidae, which suggest scyllarid Palinura but with rostrum, diaeresis, and rudimentary chelae on the second and third legs. The Glypheidae seem to have survived into the Recent without developing chelae. Thalassinida, Anomala, and Brachyura have not yet been found before the Jurassic. The Jurassic Anomala, however, included both pagurid and galatheid forms, implying that this supersection must have separated long before from the others. The earliest decapod, *Palaeopalaemon newberryi* from the Late Devonian, cannot be assigned with confidence to "any of the recognized infraorders" (Schram et al., 1978).

Eukyphida also have not yet been found before the Jurassic. *Adorella* is of special interest as apparently lacking chelae, all of the legs being subchelate with the dactyls folded against the body of the propodus (Balss, 1957).

Euzygidan fossils have not so far been recognized. However, the supposed dendrobranchiate *Acanthochirana* (Jurassic) evidently had the first pleonic somite rather reduced, the pleura narrow and spiny and the uropodal exopod lacking a diaeresis (Balss, 1922); thus it might be a euzygid.

Glaessner (1960) believes that Glypheidae gave rise to the Pemphicidae and to all of the extant reptant groups except the Astacina. He derives the Astacina separately with the dendrobranchiates and euzygids. However, he does not discuss the surprising similarity of the carapace of his stem astacine, *Lissocardia,* to that of the glypheids. In my judgement, a glypheid-like stem form, lightly built and without hypertrophied first legs, gave rise to all the reptant supersections. This would seem to imply that, despite its great age, *Palaeopalaemon* may be well advanced along the reptant line. It will have differentiated before the Late Devonian from a similarly achelate euzygid-eukyphid stem-form with large first pleonic somite, both of these being distinct from a dendrobranchiate stem-form already with chelae. Although the lack of fossils of higher Brachyura before the Cretaceous seems highly significant, the lack of early specimens of the lightly constructed and probably rather scarce eukyphids and euzygids need not be surprising. Fossils now being laid down in warm seas are probably also mostly heavily armored reptants, though in the modern fauna these may be fewer than the dendrobranchiates (the eukyphids and especially euzygids being sparser still).

Evidence from Ontogeny

Gurney's valuable but rather disappointing summary (1942) of knowledge of the larvae of the Eucarida does not attempt "to define the larval characters of the major groups." However, it does offer a brief estimate of certain relationships on p. 11–12, some further remarks and a table of characteristics helpful "in placing a larva" on p. 177–179, and a summary of the characteristics of caridean larvae on p. 192–193. Gurney indicates that "the primitive larval history which characterizes all Penaeidea distinguishes the group sharply from all others" among the decapods; that the larvae of Stenopodidea "are very peculiar, but suggest some relationship to the Anomura and Thalassinidea"; that the Eukyphida show a peculiar resemblance to the protozoea of dendrobranchiates in having only 6 pairs of spines on the embryonic telson; and that larval Reptantia are peculiar in having the antennal scale unsegmented, as well as in never having an exopod on the maxillule (indicated as present in all Dendrobranchiata and in a few Eukyphida and Euzygida). Gurney's chief reason for relating the Euzygida to the Reptantia is the hair-like form of the second spine of their telson, but on p. 239 he notes that "the possession of so primitive a maxillule in one species is difficult to reconcile with such a view." On p. 146–147 he seems to doubt the significance of the peculiar difference of euzygids and eukyphids from dendrobranchiates in order of development of the gills, and suggests that instead "the dorsal gills of Caridea may actually be arthrobranchs of the dorsal series." However, it must be noted that, whatever the homology of the dorsal gill of eukyphids, there is a real resemblance to euzygid development, and a real difference from dendrobranchiates (Burkenroad, 1945).

Gurney's (1942) pessimistic feeling that, "It must be confessed that the evidence from development so far accumulated has not produced any very serious contribution to the systematics of the group," seems to me simply a result of the natural reluctance of systematists to attempt to organize the mass of specialized information, difficult to check or extend, which has become available about the larvae; I should like to acknowledge here that the present revision of the Decapoda stems from an early collision with that stimulating work of Gurney, and to note again that the revision is directly dependent on the lead supplied by the peculiarities of branchial ontogenesis.

A larval pattern, the possible large scale significance of which has not been previously considered, is provided by the order of development of the pleopods. The first

pleonic somite of the reptant larvae never has pleopods until long after those of posterior somites are well developed and biramous (indeed, never until after metamorphosis, if then, except in eryonids). In euzygids the first pleopod "seems generally if not always to be delayed in appearance till the end of larval life" (Gurney, 1942). In eukyphids, all five pleopods usually appear together, but according to Gurney's account (1941) of *Rhynchocinetes* the first pleopod in it seems to be somewhat delayed after those of 2–5; and the first pleopod does not appear until post-larval stages in *Leptochela* (Gurney, 1938). In dendrobranchiates, the pleopods usually appear all together, but (in contrast to the incubatory groups) when the appearance is serial it is the anterior most pleopod which first develops (*Gennadas*) or is the best developed (*Acetes*). In this tendency to precociousness of the first pleopod, the dendrobranchiates seem to make some approach to the serial development found in euphausiids; and it seems possible that in the evolution of the incubatory decapods there was a more or less progressive tendency to increased delay of the first pair of pleopods.

Another larval feature, the possible phylogenetic significance of which has not been previously noticed, is the tendency for the pleon to be "bent at the third segment at almost a right angle" in the late larvae of euzygids (Lebour, 1941). This posture resembles that of eukyphid larvae and seems correlatable with the lack of a hinge between third and fourth somites in adults of both groups, since it does not seem to be found in other decapod larvae. It seems likely to have characterized the larvae if not the adults of the common ancestor of Euzygida and Eukyphida.

The hair-like second telson spine in larvae of Euzygida, Thalassinida, Anomala, and Dromiacea (and probably some Astacina: note that Gurney's remark in 1942, p. 227, that the telson is "normal for this stage" in his possible *Nephrops* from the Great Barrier Reef is quite different from his remark in 1938, p. 296, "The telson, indeed, is exactly the same as that of *Callianassa* . . .") seems to be a character of considerable significance, as Gurney thought. Rather than a mark of special relationship between euzygids and thalassinids, or dromiids and Anomala, however, it seems more likely to be a relic from the stem-form of the three incubatory suborders, never present in dendrobranchiates, and effaced in eukyphids, most Astacina, Palinura and the higher Brachyura.

A more thorough review of decapod development from a phylogenetic outlook might be fruitful.

Taxonomic Issues

In both the Eukyphida and the Reptantia there is a large number of more or less clearly distinguished living groups, the interrelationships of which are still poorly understood. I am not fully prepared to attempt a definitive arrangement of either of these two suborders, but will offer scattered remarks based on new but incomplete observations.

A) Among Eukyphida, the male genital aperture is in the articular membranes and definitely proximal to the coxa in a number of Palaemonidae (including Pontoniinae) and Alpheidae which I have examined. It is coxal in all others so far checked (several Hippolytidae, Atyidae, Hoplophoridae, Pandalidae, and Crangonidae). This coxal position is rather different from the coxal aperture in *Stenopus* and various Reptantia, being low on the segment instead of in the distal part. I believe the articular apertures probably indicate a close relationship (as concluded by Gurney from embryological evidence). This evidence would suggest that Holthuis's (1955) superfamilies overemphasize the relative dimensions of the chelate legs.

B) Like other authors after Borradaile (1907), Balss (1957) has stated, that in the Reptantia "der Stylocerit fehlt immer . . . ." However, later in that same work Balss says of the Eryonidea Palinura, "Antennula . . . manchmal mit Stylocerit." The basal joint of the antennule of *Polycheles typhlops* bears a pair of spines which may or may not be homologous with the stylocerite of dendrobranchiates, eukyphids, and euzygids. These resemble those of the galatheoid *Munidopsis* and pagurids in form and relation

to the statocyst. The galatheoid *Petrolisthes* has the statocyst expanded into a lateral projection of the base of the antennule which seems likely to be a homologue of the "natant" stylocerite. The hippid *Lepidopa* is comparable. The eryonids, then, probably do retain a stylocerite lost in the scyllarids.

The eryonids seem to differ from the scyllarids (Loricata) in a number of other features which seem of importance (as far as can be judged from my comparison of *Polycheles typhlops* with *Panulirus argus*). The eryonids have a less completely fused basis and ischium of the legs (Barnard, 1950; Balss, 1957). They lack a double hinge between carpus and propodus of the legs. They have chelae on the anterior four legs (Balss), and the base of the antenna is not fused to the carapace and epistome but is free. The fusion of carapace and epistome is concealed under the frons and visible only inside the branchial chamber as in homarids. Borradaile (1907) and subsequent authors are thus in error in distinguishing the eryonids as well as the scyllarids from the Astacina by "carapace fused at sides with epistome." The scyllarids are intermediate between eryonids and Astacina in grade of loss of appendix interna, which is present on the male second pleopod of *Enoplometopus,* which appears to be an astacine (Barnard, 1950). The living eryonids resemble the scyllarids and differ from the astacines in lacking a diaeresis on the uropodal exopod, but some fossil eryonids had a diaeresis (Balss, 1957). The loss must have occurred independently in the chelate and the achelate lines, unless the latter branched off from the eryonids and lost the chelae (which seems less likely than that the scyllarids stemmed from achelate pemphicids). In fact, it is not easy to define Borradaile's "Palinura" with precision except by their possession of a peculiar button fastening the carapace to the side of the last thoracic somite (presumably it necessitates special arrangements at the molt and therefore seems of considerable phylogenetic interest). The eryonids and scyllarids may not have had a common ancestor since the early Triassic (if the pemphicids were, as seems possible, ancestral to the scyllarid stem rather than to that of all Palinura).

C) The "Anomura" are said by Borradaile (1907) and subsequent authors to have "Carapace not fused with epistome." However, this is quite untrue of *Callianassa* and *Upogebia,* where the frons above the linea thalassinica is openly fused with an extension of the sternite behind the antenna. A similar fusion in some axiids at least seems to be indicated by Bouvier's remark (1925) that in *Calocaris aberrans* "Le bord anterieur de la carapace . . . au dessous des antennes . . . est fusionné avec l'epistome"; and this is probably also true of the laomediid *Naushonia,* according to Chace's figure (1939) of it.

The frons in other "Anomura" (the Anomala) is somewhat different, the fusion of carapace and epistome being shallowly concealed (Chace, 1939, Fig. 6a, b, c, d); and this, together with the presence of a stylocerite would seem to distinguish the Anomala as a unit from the Thalassinida. Gurney (1942) believes that the thalassinids are not homogeneous but include two groups, one (Axiidae and Callianassidae) shown by its development to be homarid in relationship and the other (Laomediidae and Upogebiidae) related to the Anomala. However, Gurney ultimately found the larval distinctions to be less absolute than he at first believed, and it is difficult to believe that the peculiar frons of *Callianassa* and *Upogebia* was independently invented (although it then seems surprising that in thalassinid larvae the frons is produced to conceal the point of fusion). It would be of great interest to know whether an exposed fusion of carapace with epistome might be combined with presence of a stylocerite in the glypheids.

D) The loss of arthrobranchs from pleurobranch-bearing thoracic somites posterior to the fourth is highly distinctive of Brachyura with a reduced gill complement. It therefore seems likely that there was a brachyuran stem form with a more or less complete branchial formula and coxal genital apertures which was distinguished from other reptant lines by delayed appearance of posterior arthrobranchs (relative to posterior pleurobranchs) during individual development. Although it is not completely certain that the dromiids qualify as true Brachyura by delayed development of the posterior arthrobranchs, this seems probable from Gurney's account (1924) of the gills
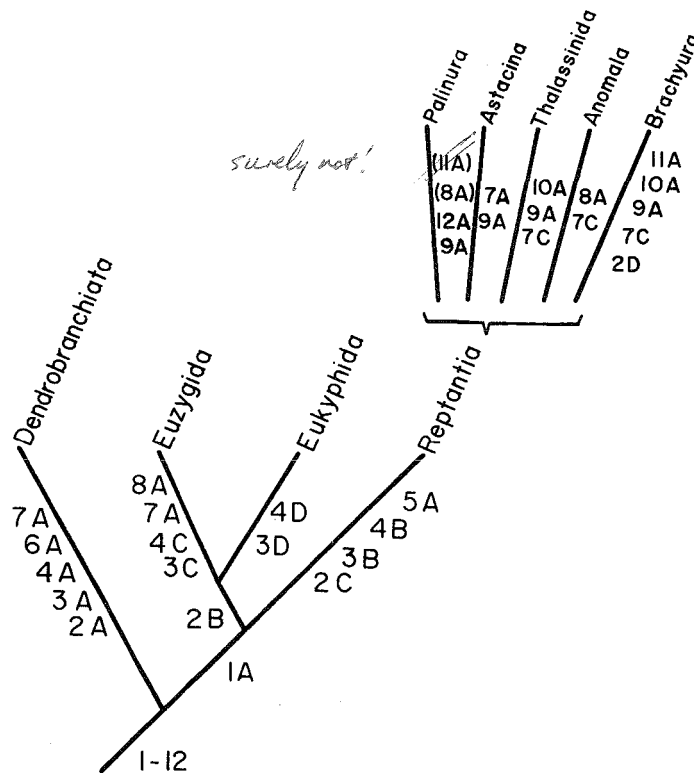
Fig. 1. Cladogram of relationships of decapod suborders postulated in this paper. Reptant groups not arranged phylogenetically. Numbers and letters keyed to text. Parentheses indicate lack of the particular advanced character in important members of that group.

of what Lebour (1934) agrees must be a *Dromia*. Gurney describes the third zoea as having the paired arthrobranchs already present on thoracic somites 3 and 4, while unpaired rudiments occur on "each of the following limbs." In the fourth zoea, there are pleurobranchs on each of the legs 2–5, and an unpaired arthrobranch has appeared on legs 2–4. In Lebour's fifth zoea, the adult complement has been completed by the addition of a second arthrobranch on legs 2 and 3. It thus seems that the gills on legs 2–5 in Gurney's third zoea were pleurobranchs, and that *Dromia* possesses the developmental pattern to be expected of the brachyuran stem form. The combination in *Dromia* of unique larval characteristics and brachyuran features with others found in thalassinids and in Anomala (which Lebour thinks make it necessary to "remove the Dromiacea from the Brachyura" to "a separate group") seems likely to result from the retention of larval characteristics from the common reptant stem in this surviving representative of the primitive Brachyura.

E) The possibility that the linea "thalassinica," "anomurica," "dromidica," and "homolica" are homologous and retained from a common ancestor rather than, as suggested by Glaessner (1960), acquired independently in different lineages, is of considerable interest (Burkenroad, 1963a). This is especially so since the Late Devonian *Palaeopalaemon* seems to possess a linea.

CONCLUSIONS

A diagram showing the presumptive order of appearance of the characteristics of the suborders of Decapoda, up to the differentiation of the supersections of Reptantia

in the Triassic, is presented in Figure 1. Changes from a hypothetical ancestor are shown at each branching of the lines by code numbers which are explained in the chart below, primitive characteristics being retained except as indicated. (In some of the ultimate branches, characteristics different from those shown in their hypothetical stems have since appeared.)

DECAPOD CHARACTERISTICS (see Fig. 1)	
Primitive	Advanced
1. Eggs set free; eclosion naupliar.	1A. Pleopodal incubation; development abbreviated.
2. Thoracic somites 3–7 each with a podobranch-bearing epipodite, two arthrobranchs and a pleurobranch, which appear more or less simultaneously during individual development.	2A. Pleurobranchs delayed. 2B. Arthrobranchs delayed. 2C. Anterior pleurobranchs omitted. 2D. Posterior arthrobranchs delayed.
3. First pleonic somite large; first and second pleura not expanded enough to overlap; all pleonic somites hinged together by an exposed diarthrosis.	3A. First pleura expanded and overlapping the second; hinge between third and fourth pleomeres covered. 3B. First somite reduced; second pleura slightly expanded to overlap the first. 3C. First somite somewhat reduced; its pleura somewhat expanded and overlapping the second; hinge between third and fourth pleomeres lost. 3D. Second pleura expanded to overlap the first; hinge between third and fourth pleomeres lost.
4. All pleopods large, biramous and with an appendix interna which couples each pair together.	4A. Appendix interna lost except traces in male first and second pleopod. 4B. First pleopods reduced and uniramous; appendix interna on the rest. 4C. First pleopods more or less reduced: uniramous; no appendix interna. 4D. First pleopod with endopod usually reduced, appendix interna on all pleopods usually.
5. Legs with propodus movable in more than one plane; all seven joints free.	5A. Carpal-propodal joint with two hinges, restricting propodus to movement in a single plane.
6. Trichobranchiae.	6A. Dendrobranchiae.
7. Legs not chelate.	7A. First three pairs chelate. 7B. First four pairs chelate. 7C. First pair chelate.
8. Diaeresis on uropodal exopod.	8A. No diaeresis.
9. Antennular stylocerite present.	9A. No stylocerite.
10. Attachment of carapace to anterior sternite (epistome) hidden under the produced frontal margin.	10A. Fusion of carapace to epistome exposed.
11. Pleon large and extended.	11A. Pleon reduced.
12. Carapace not fastened down posteroventrally (unless by overlap of anterior margin of first pleonic pleuron).	12A. Posteroventral sides of carapace held in place by a projection of the last thoracic pleura which engages inner side of carapace.

ACKNOWLEDGMENTS

had survived, and deleted and updated it to accord with some of the findings in the 17 years since most of the manuscript was written (although surprisingly they did not find a great deal to change). Without their efforts this product of my more active carcinological days would never have reached print. Deanne Deméré acted as patient typist through several revisions.

LITERATURE CITED

Balss, H. 1922. Studien an fossilen Decapoden. Palaeont. Zeitschr. 5:123–147.

———. 1927. Decapoda. *In* W. Kükenthal and T. Krumbach, Handbuch der Zoologie 3(1):840–1038. de Gruyter, Berlin.

———. 1957. Decapoda. Systematik. *In* H. G. Bronn, Klassen and Ordnungen des Tierreichs Bd. 5, Abt., Buch 7, Lief. 12:1505–1672. Academische Verlagsgesellschaft, Leipzig.

Barnard, K. H. 1950. Descriptive catalogue of South African Decapod Crustacea. Ann. S. Afr. Mus. 38:1–837.

Bate, C. S. 1888. Report on the Crustacea Macrura collected by the H.M.S. Challenger during the years 1873–1876. Rept. Scientific Results Voyage H.M.S. Challenger. Zoology 24:1–942.

Beurlen, K., and M. F. Glaessner. 1930. Systematik der Crustacea Decapoda auf Stammesgeschichtlicher Grundlage. Zool. Jahrb. Abt. f. Syst. 60:49–84.

Boas, J. E. V. 1880. Studier over Decapodernes Slaegtskabsforhold. Vidensk. Selsk. Kristiania, Skrifter (5)6:25–210.

Borradaile, L. A. 1907. On the classification of the Decapod Crustaceans. Ann. Mag. Nat. Hist. London (7)19:457–486.

Bouvier, E. L. 1917. Crustacés decapodes (macroures marcheurs) provenant des campagnes des yachts Hirondelle et Princesses Alice (1885–1915). Res. Camp. Sci. Monaco 50, 104 p.

———. 1925. Les Macroures Marcheurs. *In* Reports of the results of dredging under the supervision of Alexander Agassiz in the Gulf of Mexico by the U.S. Steamer "Blake." Mem. Mus. Comp. Zool. Cambridge, Mass. 47:401–472.

Burkenroad, M. D. 1934. The Penaeidea of Louisiana with a discussion of their world relationships. Bull. Amer. Mus. Nat. Hist. 68:61–143.

———. 1936. The Aristaeinae, Solenocerinae and Pelagic Penaeinae of the Bingham Oceanographic collection. Materials for a revision of oceanic Penaeidae. Bull. Bingham Oceanogr. Coll. New Haven 5(2):1–151.

———. 1939. Further observations on Penaeidae of the Northern Gulf of Mexico. Bull. Bingham Oceanogr. Coll. New Haven 6(6):1–62.

———. 1942. The development and relationships of *Glyphocrangon* (Crustacea, Decapoda, Caridea). Amer. Nat. 76:421–425.

———. 1945. A new Sergestid shrimp with remarks on its relationships. Trans. Conn. Acad. Arts Sci. 36:553–593.

———. 1947. Reproductive activities of Decapod Crustacea. Amer. Nat. 81:392–398.

———. 1963a. The evolution of the Eucarida (Crustacea: Eumalacostraca) in relation to the fossil record. Tulane Studies in Geology 2(1):3–16.

———. 1963b. Comments on the petition concerning peneid names (Crustacea: Decapoda) (Z.N.(S.) 962). Bull. Zool. Nom. 20:169–174.

Calman, R. T. 1909. Crustacea. *In* A treatise on zoology. Part VII (R. Lankester, ed.). Adam and Charles Black, London.

Chace, F. A. 1939. On the systematic status of the crustacean genera, *Naushonia, Homoriscus* and *Coralliocrangon*. Ann. Mag. Nat. Hist. 11:524–530.

Glaessner, M. F. 1960. The fossil decapod Crustacea of New Zealand and the evolution of the order Decapoda. New Zealand Geo. Surv. Paleont. Bull. 31:1–63.

———. 1969. Decapoda. *In* Arthropoda 4. Part R. Vol. 2. Treatise on Invertebrate Palaeontology (R. C. Moore, ed.), p. R399–R533. Geol. Soc. Am. Univ. of Kansas Press, Lawrence.

Gurney, R. 1924. Crustacea. Part IX. Decapod Larvae. British Antarctic Terra Nova Expedition (Zoology) 8:37–202.

———. 1938. Larvae of Decapod Crustacea. Part V. Nephropsidae and Thalassinidea. Discovery Rept. 17:291–344.

———. 1939. A new species of the decapod genus *Discias* Rathbun from Bermuda. Ann. Mag. Nat. Hist. (11)3:388–393.

———. 1941. On the larvae of certain Crustacea Macrura, mainly from Bermuda. J. Linn. Soc. 11:89–181.

———. 1942. Larvae of Decapod Crustacea. Ray Society, London.

Holthuis, L. B. 1947. Biological results of the Snellius Expedition. XIV. The Decapoda Macrura of the Snellius Expedition. I. The Stenopodidae, Nephropsidae, Scyllaridae and Palinuridae. Temminckia 7:1–178.

———. 1955. The recent genera of the caridean and stenopodidean shrimps (Class Crustacea, Order Decapoda, Supersection Natantia) with Keys for their determination. Zool. Verhandl. 26:1–157.

Kubo, I. 1949. Studies on Penaeids of Japan and its adjacent waters. J. Tokyo Coll. Fish. 36:1–467.

Lebour, M. V. 1934. The life-history of *Dromia vulgaris*. Proc. Zool. Soc. London 1934:241–249.

———. 1936. Notes on the Plymouth *Processa* (Crustacea). Proc. Zool. Soc. London 1936:609–617.

———. 1941. Notes on Thalassinid and Processid larvae (Crustacea: Decapoda) from Bermuda. Ann. Mag. Nat. Hist. (11)7:402–420.

Limbaugh, C., H. Pederson, and F. A. Chace.

268

1961. Shrimps that clean fishes. Bull. Mar. Sci. Gulf and Caribbean 11:237–257.

Milne-Edwards, H. 1837. Histoire naturelle des Crustaces comprenant l'anatomie, la physiologie et la classification de ces animaux, Vol. II. Paris.

Moses, M. J. 1961a. Spermatogenesis in the crayfish (*Procambarus clarki*) Part I. Structural characteristics of the mature sperm. J. Biophys., Biochem., Cytol. 9:222–228.

———. 1961b. Spermatogenesis in the crayfish (*Procambarus clarki*) Part II. Description of stages. J. Biophys., Biochem., Cytol. 10:301–333.

Nichols, M. L. 1909. Comparative studies in Crustacean spermatogenesis. J. Morph. 20:461–478.

Ortmann, A. 1890. Die Decapoden-Krebse de Strassburger Museums mit besonderer Berücksichtigung der von Herrn. Dr. Döderlein bei Japan und bei den Lui-Kui-Inseln gesammelten und z. Z. im Strassburger Museum aufbewahrten Formen. Zool. Jahrb. (Abt. f. Syst.) 5:437–540.

———. 1892a. Die Decapoden-Krebse des Strassburger Museums. III. Die Abtheilungen der Reptantia, Boas: Homaridae, Loricata and Thalassinidea. Zool. Jahrb. Syst. 6:1–57.

———. 1892b. Die Decapoden-Krebse des Strassburger Museums. IV. Die Abtheilungen Galatheidea und Paguridea. Zool. Jahrb. Syst. 6:241–326.

———. 1892c. Die Decapoden-Krebse des Strassburger Museums. V. Die Abtheilungen Hippidea Dromidea und Oxystomata. Zool. Jahrb. Syst. 6:532–588.

Schram, F. R., R. M. Feldman, and M. J. Copeland. 1978. The late Devonian Palaeopalaemonidae and the earliest decapod crustaceans. J. Paleo. 52:1375–1387.

Thompson, D. W. 1910. Historium Animalium (transl.). *In* The Works of Aristotle, (J. A. Smith and W. D. Ross, eds.), Vol. 4. Clarendon Press, Oxford.

Department of Geology, San Diego Natural History Museum, P.O. Box 1390, San Diego, California 92112 USA.