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DEVELOPMENTAL PATTERNS OF LARVAL SCAPHOGNATHITES: AN AID TO THE CLASSIFICATION OF ANOMURAN AND BRACHYURAN CRUSTACEA

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ABSTRACT

Analysis of 340 published descriptions of larval development in the Anomura and Brachyura reveals that the maxillary scaphognathite of the first zoeal stage can be classified into one of eight types. In addition, there are five sequences by which the diverse zoeal scaphognathites develop into the typical postlarval form. These features appear to be valuable taxonomic characters and provide relevant larval evidence concerning the lower limits of the Brachyura and affinities within the Anomura.

For over a century biologists have been collecting, rearing, and illustrating the larval stages of decapod crustaceans. In the Anomura and Brachyura alone, the complete or incomplete descriptions of the larval develpment of about 400 species (in approximately 30 families) can be found in the literature. Larval features have been generally ignored in the classification of most invertebrate groups. The published accounts of decapod crustacean development therefore offer a unique opportunity to analyze larval structure and to begin to construct a rational taxonomic scheme which takes into account larval features as well as the traditional adult characters. Despite this wealth of information, there have been few comparisons of larval morphology beyond the generic level, and those which do exist are primarily devoted to the Brachyura (Aikawa, 1929, 1937; Williamson, 1976; Rice, 1980). It has been argued that since all zoeae occupy the same pelagic habitat, they are presumably free of the convergent or divergent adaptations to specialized life styles exhibited by the adults; they thus have great potential to provide evidence for natural relationships within the Decapoda (Williamson, 1976; Rice, 1980). Whether or not this is true, available larval evidence should be considered in any scheme of crustacean classification. It has long been recognized that the larval maxilla, the third in a series of feeding appendages, is a valuable character at the lower taxonomic levels (Aikawa, 1929, 1937). This appendage is equipped with an endopodite and protopodal endites (which function as part of the larval feeding apparatus), and with a lateral lamellar expansion, or scaphognathite (which serves as a "gill-bailer" in the adult, but whose function is uncertain in the larva since the gills may be absent or rudimentary). Analysis of the literature and examination of representative specimens using a compound microscope reveal that the maxillary scaphognathite of the first zoeal stage in the Anomura and Brachyura can be classified into one of eight types using a combination of three features: the presence of an apical process or seta, the extent of development of the posterior lobe, and the degree of marginal setation. In addition, these eight types of scaphognathite appear to follow five basic developmental sequences, three of which occur in the Anomura (*sensu* Dana, 1852), one in the Brachyura (*sensu* Milne Edwards, 1837; i.e., excluding the Homolidae, Raninidae, Dromiidae, and Tymolidae), and one in which the structure of the scaphognathite does not clearly relate it to either the Anomura or Brachyura. This analysis, which uses zoeal morphology as well as developmental patterns, provides relevant larval evidence which should be considered in any resolution of the current controversy regarding the classification of the decapod Crustacea (Guinot, 1977, 1978; Fincham, 1980; Rice, 1980; Saint-Laurent, 1980a, b).

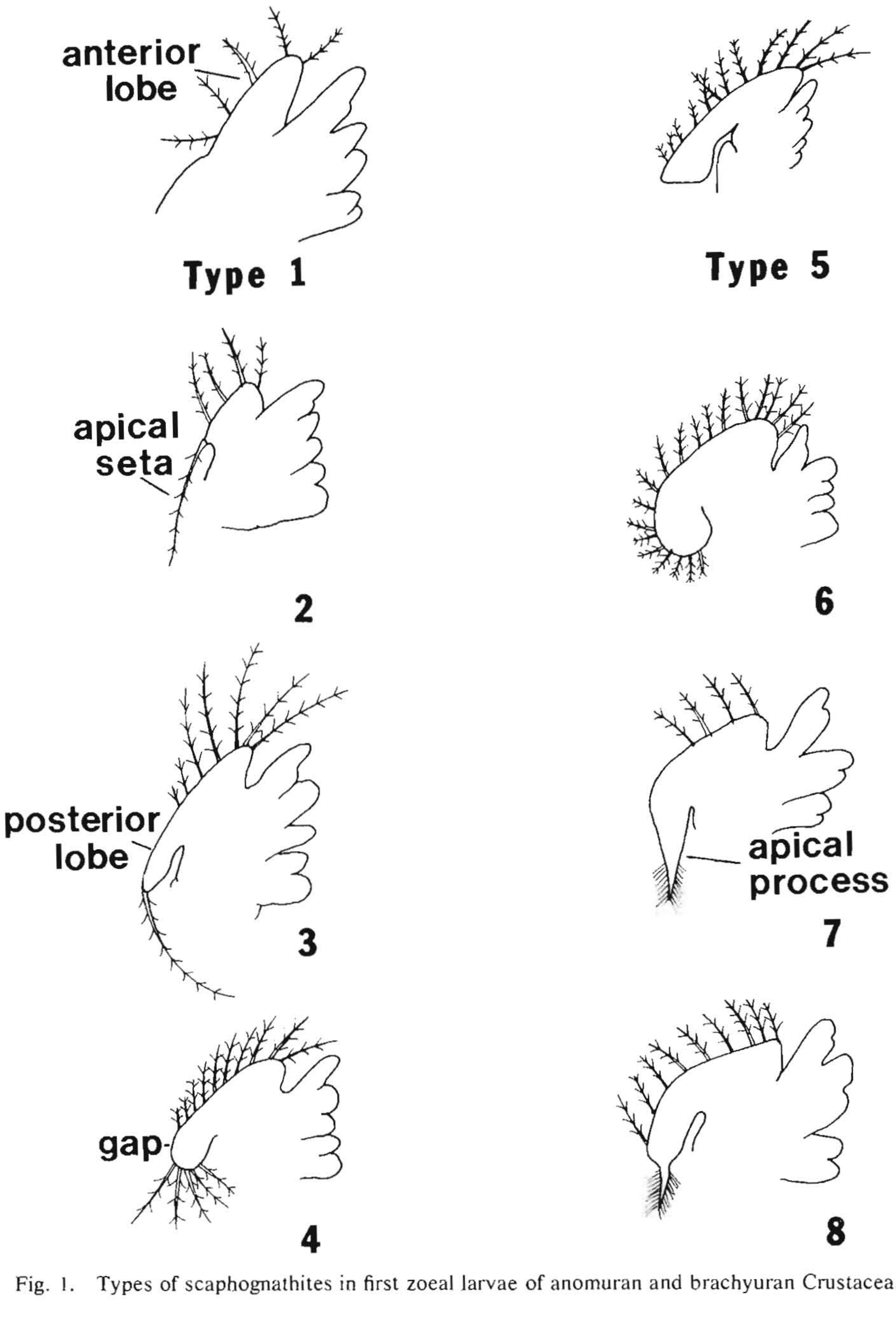

Fig. 1. Types of scaphognathites in first zoeal larvae of anomuran and brachyuran Crustacea.

Descriptions of the types of scaphognathite (Fig. 1) and the known larvae in which they occur follow.

Type 1: Small anterior (=distal) lobe extending from the basal region of the maxilla; posterior lobe absent; typically 5 marginal setae (range 3–10); Paguridae, Diogenidae, Coenobitidae, Lithodidae.

Type 2: Small anterior lobe separated from the maxilla at its proximal end; posterior lobe absent; apical seta at the proximal end; 4 (rarely 5) marginal setae; Galatheidae, Homolidae, Raninidae.

Type 3: Anterior and posterior lobes present; typically with 6–7 marginal setae (range 4–8) on the anterior lobe; posterior lobe naked except for an apical seta; nearly all known species of Porcellanidae.

Type 4: Anterior and posterior lobes present; apical seta absent; anterior lobe bearing 7–11 marginal setae and posterior lobe bearing 5 setae, with a distinct gap between these two groups of setae; so far known in two species of Porcellanidae (*Petrolisthes ornatus, P. elongatus*).

Type 5: Anterior and posterior lobes present (similar to Type 4); marginal setation complete (no gap) except at the truncate end of the posterior lobe; Albuneidae and Hippidae.

Type 6: Anterior and posterior lobes present; marginal setation complete (along entire margin of scaphognathite); Dromiidae, Tymolidae, one species of Galatheidae (*Munidopsis serricornis, =M. tridentata*), two species of Atelecyclidae (*Erimacrus isenbeckii, Telmessus cheiragonus*).

Type 7: Anterior lobe terminating in a stout, hairy apical process; typically 4 marginal setae (range 3–18); Xanthidae, Corystidae, Goneplacidae, Cancridae, Portunidae, Calappidae, Parthenopidae, Hymenosomatidae, Hapalocarcinidae, Grapsidae, Gecarcinidae, Geryonidae, Ocypodidae, Dorippidae, Leucosiidae, Pinnotheridae, Atelecyclidae.

Type 8: Anterior and posterior lobes present; apical process greatly reduced; Majidae.

Although the first *zoeal* scaphognathite may be one of eight known types, the scaphognathite of the first *postlarval* stage (the glaucothoe or megalopa) is remarkably uniform throughout the Anomura and Brachyura, consisting without exception of well developed anterior and posterior lobes with complete fringes of marginal setae. There are five basic developmental sequences (Fig. 2) in which the diverse zoeal scaphognathites assume the postlarval shape.

Sequence A: In this developmental sequence the posterior lobe first appears in the last zoeal stage (naked, or rarely with 1–2 setae) or in the first postlarval stage (setose). This pattern is found in the Paguridea, i.e., species with a Type 1 scaphognathite.

Sequence B: This developmental sequence is characterized by the gradual longitudinal expansion of the anterior lobe resulting in a scaphognathite with both anterior and posterior lobes; it is found in larvae with a Type 2 scaphognathite (Galatheidae, Homolidae, Raninidae). The porcellanid scaphognathites (Types 3 and 4) of the first zoeal stage appear to be intermediate and later developmental stages, respectively, of this sequence. This reflects the tendency of the scaphognathite to develop precociously in cases of abbreviated development (Makarov, 1968).

Sequence C: The posterior lobe is well developed in the first zoeal stages of species which follow this developmental sequence, but the setae do not occur along the entire margin until the postlarval stage. This pattern occurs in species with a Type 5 scaphognathite (Albuneidae, Hippidae).

Sequence D: The scaphognathite of the first and subsequent zoeae in this sequence is indistinguishable from that of the postlarva, although there may be an increase in the total number of marginal setae. Species with a Type 6 scaphognathite exhibit this developmental sequence (Dromiidae, Tymolidae, *Munidopsis serricornis, Erimacrus isenbeckii, Telmessus cheiragonus*).

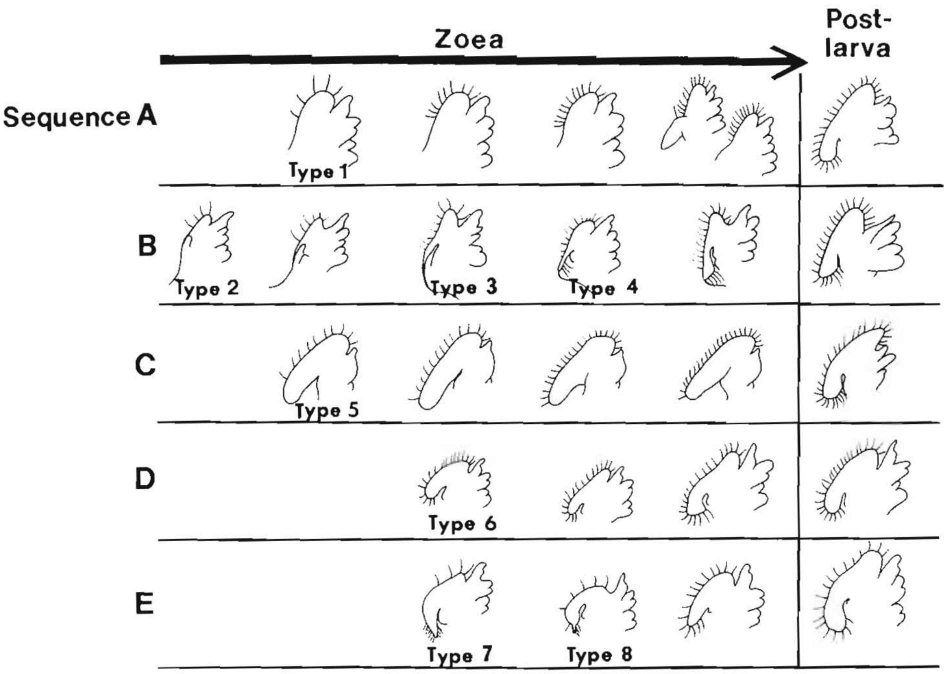

Fig. 2. Developmental sequences of larval scaphognathites of anomuran and brachyuran Crustacea.

Sequence E: In this developmental sequence, the apical process gradually expands laterally to form the posterior lobe. The Type 7 (brachyuran) scaphognathite follows this pattern of development; the Type 8 (majid) scaphognathite appears to be a later stage in this sequence, reflecting the abbreviated development among the Majidae.

Rice's (1980) recent review of larval structure and brachyuran classification identified a number of outstanding problems. The present study contributes additional evidence toward the resolution of several of these problems. Some clarification of the lower limits of the Brachyura and the relationships among the dromiids, homolids, raninids, and tymolids is provided by the structure and development of the scaphognathite (Table 1). The Homolidae and Raninidae are shown to have the same type of zoeal scaphognathite (Type 2) and pattern of development (Sequence B), and are also allied in this respect to the anomuran families Galatheidae and Porcellanidae. The Dromiidae and Tymolidae are likewise linked to each other (Type 6, Sequence D). The similarity of their scaphognathite to that of other families is not clear because the developmental pattern appears to be as closely related to Sequence B as it is to Sequence E; these families can be distinguished from other Anomura and Brachyura, however, by their type of scaphognathite. Additionally, the Brachyura (excluding the Homolidae, Raninidae, Dromiidae, and Tymolidae) are unified by the type of scaphognathite and its developmental pattern. The Majidae can be distinguished from the remaining brachyuran families on the basis of their type of scaphognathite, but the pattern of development is similar enough to be included in the same category.

Table 1. Larval scaphognathites and relationships of anomuran and brachyuran Crustacea.

Taxon	Scaphognathite type	Developmental sequence	Number of species considered
(Anomura)			
Paguridae	1		29
Diogenidae	1	A	15
Coenobitidae	1		2
Lithodidae	1		4
Galatheidae	2		9
Homolidae	2	B	5
Raninidae	2		3
Porcellanidae	3, 4		47
Albuneidae	5	C	6
Hippidae	5		6
(*incertae sedis*)			
Dromiidae	6		5
Tymolidae	6	D	1
plus 3 anomalous species	6		3
(Brachyura *sensu stricto*)			
Brachyura	7	E	168
Majidae	8		37

Finally, the anomuran families can be arranged into three groups based on scaphognathite structure and its development; this supports previous arguments (Williamson, 1976) for a re-evaluation of the Anomura as a coherent taxon.

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