

THE DIPHYLETIC NATURE OF THE INFRAORDER THALASSINIDEA (DECAPODA, PLEOCYEMATA) AS DERIVED FROM THE MORPHOLOGY OF THE GASTRIC MILL

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ABSTRACT

A comparison of the gastric mill in some representative species of the Thalassinidea, indicates that the Thalassinidea are possibly diphyletic, consisting of the superfamily Callianassoidea Dana, 1852, including the families Callianassidae Dana, 1852, Axiidae Huxley, 1879, Callianideidae Kossmann, 1880, Ctenochelidae Manning & Felder, 1991, and Gourretiidae Sakai, 1999, in which the propyloric ossicle is simple and has a smooth posterior surface; and the superfamily Thalassinoidea Latreille, 1831, including the Thalassinidae Latreille, 1831, Upogebiidae Borradaile, 1903, and Laomediidae De Haan, 1849, in which the propyloric ossicle is triangularly protruded downwards and has a series of fine, transverse septa on its posterior face.

ZUSAMMENFASSUNG

Ein Vergleich der Kaumägen ausgewählter Arten der Thalassinidea deutet an, dass die Thalassinidea möglicherweise diphyletisch sind. Sie bestehen aus zwei Überfamilien, einerseits den Callianassoidea Dana, 1852, bei denen der propylorische Mittelzahn einfach und dessen Rückseite glatt ist, andererseits den Thalassinoidea, bei denen dieser Zahn dreieckig vorragt und auf der Rückseite transversale Septen trägt. Zu den Callianassoidea gehören die Familien Callianassidae Dana, 1852, Axiidae Huxley, 1879, Callianideidae Kossmann, 1880, Ctenochelidae Manning & Felder, 1991 und Gourretiidae Sakai, 2004; zu den Thalassinoidea die Familien Thalassinidae Latreille, 1831, Upogebiidae Borradaile, 1903 und Laomediidae De Haan, 1849.

INTRODUCTION

An extensive anatomical investigation of the gastric mill in the family Penaeidae was made by Kubo (1949: 157). However, a comparison of the characters of this complex structure and an application to the taxonomy of the infraorder Thalassinidea Latreille, 1831 have never been attempted to date. The study of the characters of the gastric mill in the Thalassinidea reported herein, however, has shown

that this organ is much differentiated, and that the elements in question imply many significant criteria for the classification and phylogeny of the Thalassinidea.

Gurney (1938: 330, 340; 1942: 240) mentioned, based on the characters of the known larvae of species representing all families of the Thalassinidea [except the Thalassinidae and Axianassidae (the Axianassidae Schmitt, 1924; syn. of Laomediidae Borradaile, 1903)] that there is a fundamental cleavage between the Callianassidae and the Upogebiidae, i.e., a “Homarine Group”: Axiidae and Callianassidae, and an “Anomuran Group”: Upogebiidae and Laomediidae.

Recently, Poore (1994: 79) presented a tentative phylogeny of the Thalassinidea with keys to families and genera. He mentioned that “The generally high values of *ci* and *ri* give considerable confidence in the structure of the cladograms and it is used to hypothesise a classification”. The significant taxonomic changes he proposed are: “1. Definition of the Thalassinidea as a monophyletic taxon distinct from the Anomura; and 2. Division of the Thalassinidea into three monophyletic superfamilies, Thalassinioidea Dana, 1852, Callianassoidea Dana, 1852, and Axioidea Huxley, 1879”.

However, a comparison of the gastric mills in some representative species of the Thalassinidea now indicates, that the Thalassinidea should not be divided into three superfamilies, but into two instead. The nature of the infraorder, as derived from this character complex, thus is shown to be diphyletic, consisting of the Callianassoidea Dana, 1852 and Thalassinioidea Latreille, 1831. Gurney’s (1938, 1942) taxa derived from the characters of the larvae closely corroborate the present author’s diphyletic classification, derived from features of the gastric mill. On the basis of this set of characters, a monophyletic nature of the Thalassinidea can not be confirmed, nor rejected.

Abbreviations used in the text: BLT, Biological Laboratory, Shikoku University, Tokushima; CL, carapace length; MNHN, Muséum national d’Histoire naturelle, Paris; NSMT, National Science Museum, Tokyo; SMF, Forschungsinstitut Senckenberg, Frankfurt am Main; TL, total length, from the tip of the rostrum to the end of the telson; Usa MBS, Usa Marine Biological Station, Kochi University, W. Kochi; ZLUA, Zoological Laboratory, Department of Biology, University of Athens, Athens.

MATERIAL AND METHODS

Representative species from each superfamily and family of the Thalassinidea, as well as from representatives of most of the other decapod infraorders currently recognized, have been examined for the structure of the median tooth and of the lateral tooth plates of the gastric mill. The median and lateral tooth plates, dissected

from each specimen, have been observed under the compound microscope. The specimens of the various species used for the analysis of ossicles and teeth are as follows:

Infraorder THALASSINIDEA Latreille, 1831

Callianassa subterranea (Montagu, 1808); SMF 18046, male, German Bight, North Sea, 54°01.000'N 07°45.000'E, 35 m, DG, R/V "Valdivia", 03.ii.1989.

Callianassa japonica Ortmann, 1891; BLT Cr 18228, Jatani, blackish area of the Katsuura-gawa, Tokushima, 29.iv.1990, leg. K. Sakai.

Calliax punica De Saint Laurent & Manning, 1982; ZLUA, Salamis, Saronikos Gulf, Greece, 14.ix.1994, leg. M. Legaki.

Axius stirhynchus Leach, 1815; MNHN Th 202, Paris.

Neaxius acanthus (A. Milne-Edwards, 1878); BLT 18243, Iriomote, 13.vi.2003, leg. Hirano et al.

Callianidea typa H. Milne Edwards, 1837; BLT 18238, Mitara, Iriomote-jima, Ryukyu Islands, 15.vi.2003, leg. H. Saigusa and O. Gusev.

Ctenocheles balsi Kishinouye, 1926; BLT Cr 18239, Form II female with the genital pore on the coxae of P3 and P5, but bearing a three-segmented Plp1 as in the normal form I females (Sakai, 1999; Sakai et al., 2004), TL/CL, 87.0/22.3 mm, None, Tōyo-cho, E. Cap Muroto, Kochi Prefecture, 29.iii.1998, leg. and det. K. Matsuzawa.

Gouretia denticulata (Lutze, 1937); SMF 28785, anterior part of carapace with appendages, including both chelipeds, around Marseille, France, 1.8 m depth, sediment with *Posidonia*, 28.v.1983, leg. A. Willsie.

Laomedea astacina De Haan, 1841; BLT 2964, Jatani, blackish area, Katsuura-gawa, Tokushima, 29.iv.1990, leg. K. Sakai.

Upogebia major De Haan, 1839; BLT 18241, Akkeshi, Hokaido, ca. 1982, leg. H. Mukai.

Thalassina anomala (Herbst, 1804); BLT 18240, Savu, Fiji, 3.xi.1992, leg. H. Mukai.

Infraorder ASTACIDEA Latreille, 1802

Procambarus (Scapulicambarus) clarkii (Girard, 1852); BLT 18233, bought from commercial crayfish shop, Tokushima, ca. 1995.

Pacifastacus (Pacifastacus) leniusculus (Stimpson, 1857); NSMT Cr. 1243, Akan-Ko Lake, Hokkaido, 10.vii.1987, contributor: Hitachinomiya.

Homarus americanus H. Milne Edwards, 1837; BLT 18230, bought on fish market, Tokushima.

Enoplometopus debelius Holthuis, 1983; BLT 18234, Philippines, 11.vii.1985, bought from T. Iwao, Osaka.

Thaumastocheles japonicus Calman, 1913; BLT 18235, Takaoka, Muroto, Japan, by deep-sea pump, 6.vi.2004, leg. K. Matsuzawa.

Metanephrops japonicus (Tapparone-Canefri, 1873); BLT 18232, Mimase, Kochi, from the coast of Tosa Bay, 10.iii.1988, leg. K. Sakai.

Infraorder PALINURA Latreille, 1802

Polycheles amemiyai Yokoya, 1933; BLT 18236, Mimase, Kochi, from the coast of Tosa Bay, 10.iii.1988, leg. K. Sakai.

Panulirus interruptus (Randall, 1840); BLT 18231, brought from a restaurant, Tokushima, ca. 1999.

Panulirus argus (Latreille, 1804); BLT 18244, Cuba, bought on fish market, Kochi, 16.v.1979, det. L. B. Holthuis.

Scyllarus martensii Pfeffer, 1881; BLT 1532, Asakawa, Kainancho, Tokushima, iv.1983, leg. K. Sakai.

Infraorder ANOMURA MacLeay, 1838

Albunea occultus Boyko, 2002; BLT 18229, shallow water off the coast of Usa MBS, W. Kochi, 29.iv.2003, leg. K. Sakai.

Cervimunida princeps Benedict, 1902; BLT 18242, Mimase, Kochi, off the coast of Tosa Bay, ca. 1980, leg. K. Sakai.

Dardanus impressus (De Haan, 1849); BLT 1832, Mimase, Kochi, off the coast of Tosa Bay, 12.ix.1983, leg. K. Sakai.

RESULTS AND DISCUSSION

The lateral tooth plate and the median tooth plate, with its propyloric ossicle, were examined in the species of the infraorder Thalassinidea and, for comparative reasons, in the representatives of three other infraorders of the Decapoda. It was found that these structures are to be divided into two types, by the structure of the propyloric ossicle, viz., whether that is simple or armed with a series of transverse septa on its posterior surface.

Type I. — The propyloric ossicle is simple, lacking a series of transverse septa on its posterior surface. This type is further subdivided into four subtypes, 1-4.

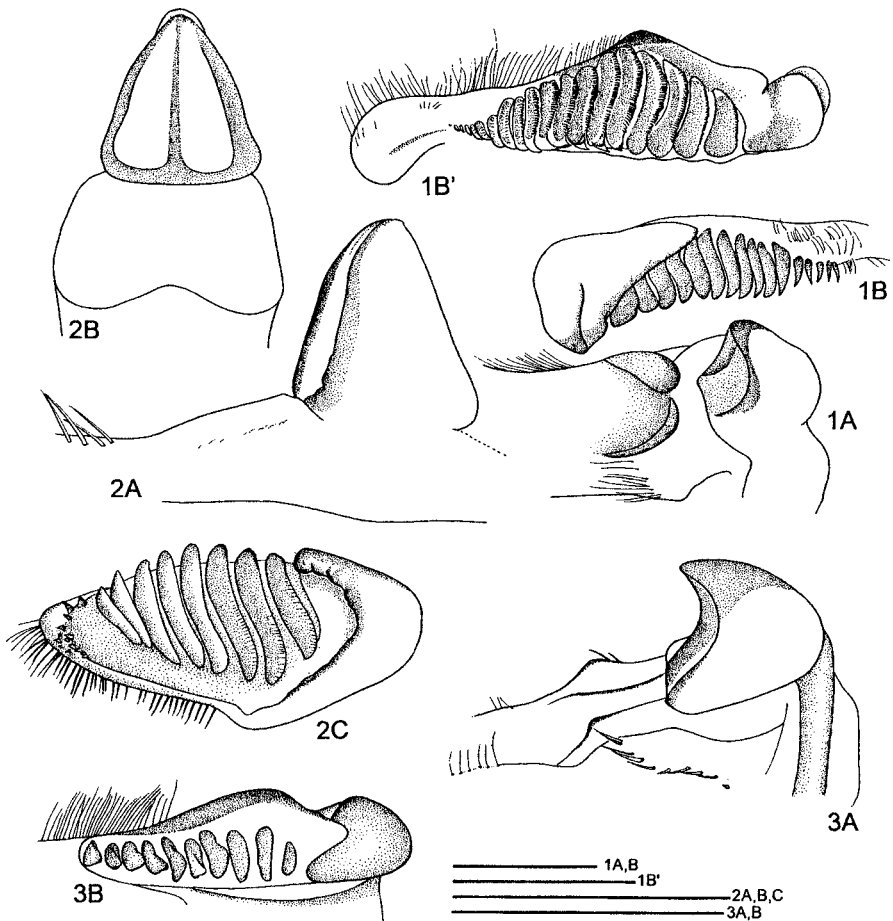
Subtype 1. — The propyloric ossicle is triangularly protruded ventrally, bending backward distally, or forward as in *Callianassa subterranea*, and its posterior surface is smooth, concave, and with a smooth, longitudinal median carina; the lateral tooth is oval to elongate in form, and armed with fine, transverse septa.

The species with this subtype include: (1) *Axius stirhynchus* Leach, 1815 (fig. 1A, B, B'); and (2) *Neaxius acanthus* (A. Milne-Edwards, 1878) in the Axiidae Huxley, 1879. (3) *Callianassa subterranea* (Montagu, 1808) (fig. 2A-C); and (4) *Callianassa japonica* Ortmann, 1891 in the Callianassinae Dana, 1852; (5) *Calliax punica* De Saint Laurent & Manning, 1982 (fig. 3A, B) in the Eucalliinae Manning & Felder, 1991, of the Callianassidae Dana, 1852.

Subtype 2. — The propyloric ossicle is triangularly protruded ventrally, and its posterior surface is concave with a longitudinal median carina; the lateral tooth is armed with two posterior molar teeth, and anterior to the secondary tooth an elongate, narrow, smooth, boat-shaped plate is developed without a series of transverse septa, though it is armed with a row of denticles on its ventral margin.

The species with this subtype include: *Callianidea typa* H. Milne Edwards, 1837 (fig. 4A, B, C) in the family Callianideidae Kossman, 1880.

Subtype 3. — The propyloric ossicle is highly protruded ventrally as in subtypes S 1, 2 (see figs. 1A, 3A, 4A), and its posterior surface bears a low, longitudinal median carina. The lateral tooth is thickened at the anterior end to form a molar protrusion, and posterior to it a smooth, lower median carina that extends backward to a secondary molar protrusion.



Figs. 1-3. *Axius stirhynchus* Leach, 1815 (Axiidae Huxley, 1879), *Callianassa subterranea* (Montagu, 1808), and *Calliax punica* De Saint Laurent & Manning, 1982 (Callianassidae Dana, 1852), respectively. 1, *Axius stirhynchus*: 1A, propyloric ossicle, left aspect; 1B, same, posterior aspect; 1B', left lateral tooth, mesial aspect; 2, *Callianassa subterranea*: 2A, propyloric ossicle, lateral aspect; 2B, same, posterior aspect; 2C, left lateral tooth, mesial aspect; 3, *Calliax punica*: 3A, propyloric ossicle, lateral aspect; 3B, right lateral tooth, mesial aspect. Scales: 1 mm.

The species with this subtype include: *Ctenocheles balssi* Kishinouye, 1926 (fig. 5A-C) in the family Ctenochelidae Manning & Felder, 1991.

Subtype 4. — The propyloric ossicle is projected forwards. The lateral tooth bears two thickened molar teeth at the anterior end.

The species with this subtype include: *Gourretia denticulata* (Lutze, 1937) (fig. 6A-C) in the Gourretiidae Sakai, 1999.

Type II. — In the infraorder Thalassinidea, the propyloric ossicle is triangularly protruded downward, and its posterior surface is concave, with a longitudinal median carina, both surfaces of which are provided with a row of fine, transverse

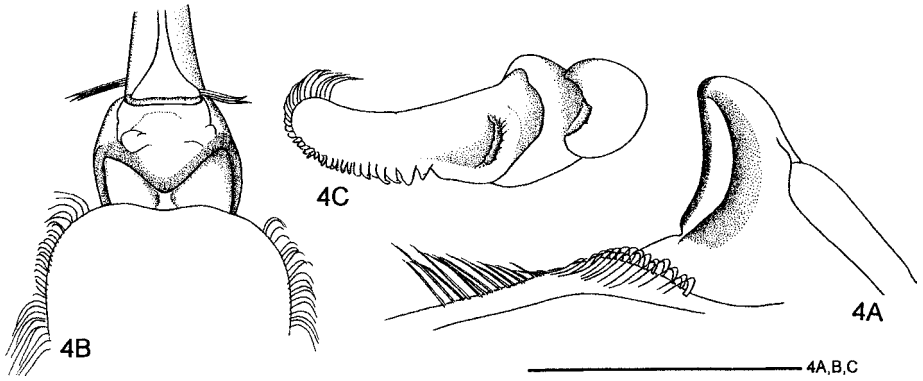


Fig. 4. *Callianidea typa* H. Milne Edwards, 1837 (Callianideidae Kossmann, 1880): 4A, propyloric ossicle, lateral aspect; 4B, same, ventral aspect; 4C, right lateral tooth, mesial aspect. Scale: 1 mm.

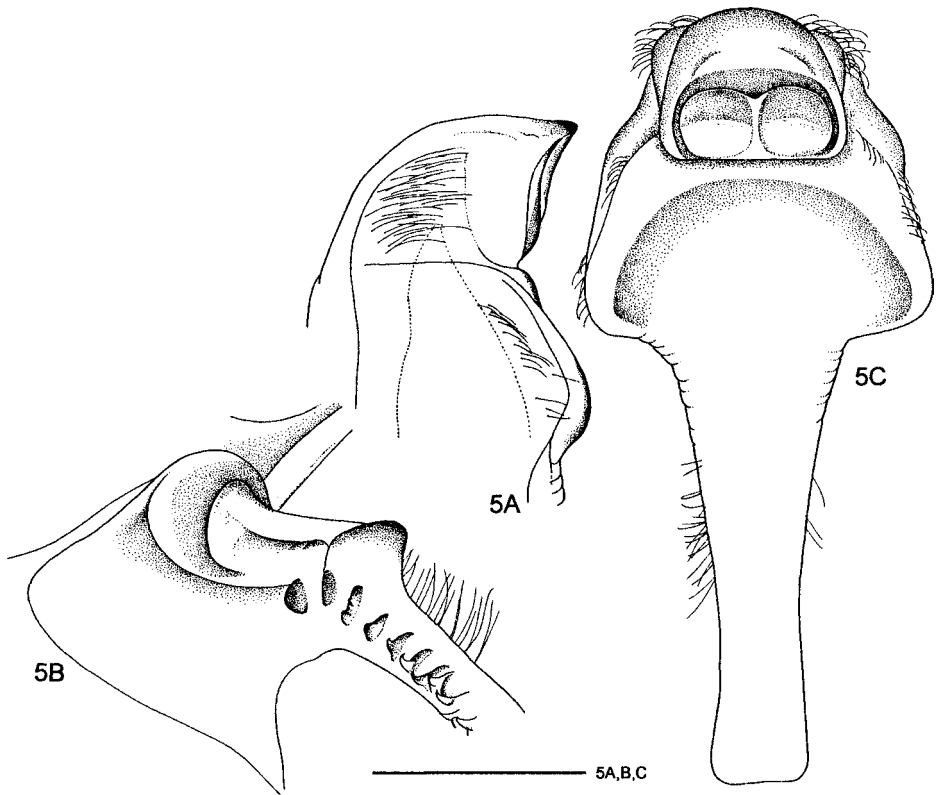


Fig. 5. *Ctenocheles balssi* Kishinouye, 1926 (Ctenochelidae Manning & Felder, 1991): 5A, propyloric ossicle, lateral aspect; 5B, same, ventral aspect; 5C, left lateral tooth, mesial aspect. Scale: 1 mm.

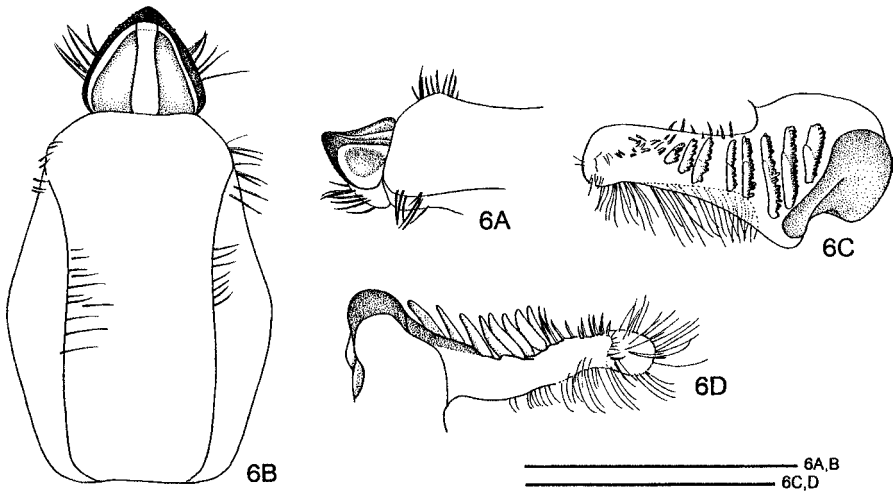
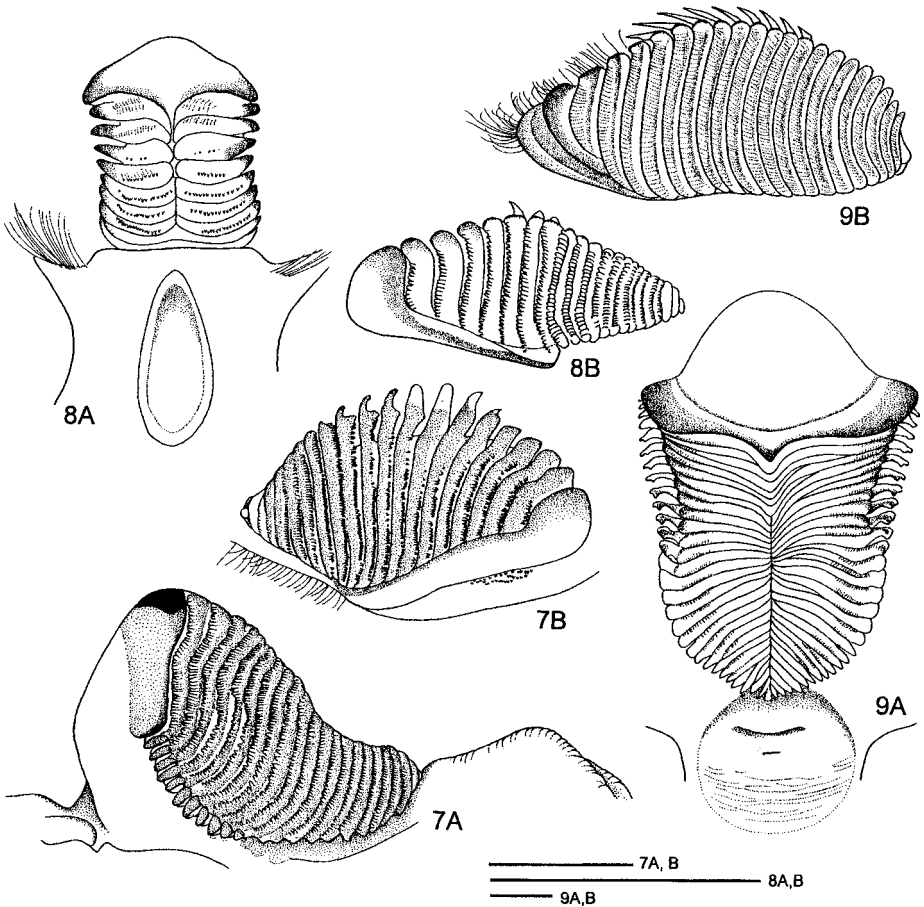


Fig. 6. *Gourretia denticulata* (Lutze, 1937) (Gourretiidae Sakai, 1999): 6A, propyloric ossicle, lateral aspect; 6B, same, posterior aspect; 6C, right lateral tooth, mesial aspect; 6D, same, lateral aspect. Scales: 6A, B, 1 mm; 6C, D, 0.5 mm.

septa; the lateral tooth is oval, and armed with a row of fine, transverse septa as well.

The species with this type include: *Upogebia major* (De Haan, 1839) (fig. 7A-B) in the Upogebiidae Borradaile, 1903; *Laomedea astacina* De Haan, 1841 (fig. 8A-B) in the family Laomediidae De Haan, 1849; *Thalassinia anomala* (Herbst, 1804) (fig. 9A-B), in the family Thalassinidae Latreille, 1831.

Poore (1994) gave a phylogeny of the Thalassinidea with keys to families and genera, and divided the infraorder as follows: "1. Definition of the Thalassinidea as a monophyletic taxon distinct from the Anomura; and 2. Division of the Thalassinidea into three monophyletic superfamilies, Thalassinioidea Dana, 1852, Callianassoidea Dana, 1852, and Axioidea Huxley, 1879." However, this theory is not compatible with the structures found in the gastric mill. In the present study, the median teeth of the species belonging to four decapod infraorders, i.e., Thalassinidea Latreille, 1831, Astacidea Latreille, 1802, Palinura Latreille, 1802, and Anomura MacLeay, 1838 were compared, and it was found that only in the infraorder Thalassinidea there are two different types of propyloric ossicle: that is either with (Type II) or without (Type I) a series of transverse septa on its posterior surface. In the other three infraorders Astacidea, Palinura, and Anomura, the propyloric ossicle is simple, and considered to be equivalent to Type I, Subtype 1, of the Thalassinidea. As a result, it is possible to propose that, based on this character, the infraorder Thalassinidea may have a diphyletic nature and should thus be divided into two superfamilies by the form of the propyloric ossicle. Type I can be further divided into four subtypes, 1-4, which



Figs. 7-9. 7, *Upogebia major* (De Haan, 1839) (Upogebiidae Borradaile, 1903); 8, *Laomedea astacina* De Haan, 1841 (Laomediidae De Haan, 1849); 9, *Thalassinina anomala* (Herbst, 1804) (Thalassinidae Latreille, 1831). 7, *Upogebia major*: 7A, propyloric ossicle, lateral aspect; 7B, right lateral tooth, mesial aspect; 8, *Laomedea astacina*: 8A, propyloric ossicle, posterior aspect; 8B, left lateral tooth, mesial aspect; 9, *Thalassinina anomala*: 9A, propyloric ossicle, posterior aspect; 9B, right lateral tooth, mesial aspect. Scales: 1 mm.

is compatible with recognizing four (groups of) families (see Conclusions, below) in the Thalassinidea. Type II of the Thalassinidea differs from Type I, by a series of septa on the posterior surface of the propyloric ossicle.

Gurney (1938, 1942) showed that the families of the suborder Thalassinidea except the Thalassinidae and Axianassidae (syn. of Laomediidae) have a fundamental division between the Callianassidae and the Upogebiidae, i.e., a Homarine Group: Axiiidae and Callianassidae, and an Anomuran Group: Laomediidae and Upogebiidae. However his theory of this basic dichotomy is, though compatible, not exactly the same as the present one, derived from the structure of the gastric mill.

From the distribution of the two recognized character states of the propyloric ossicle, i.e., Type I and Type II, among the infraorders of the Decapoda examined in this study, it could be deduced that Type I/Subtype 1 is the primitive (plesiomorphic, in cladistic terminology) state and Type II is the advanced (apomorphic) state. In a cladistic analysis, this would imply that the group with Type II, i.e., the superfamily Thalassinioidea, could be considered a monophyletic taxon, by virtue of the allegedly synapomorphic condition of the transverse septa on the propyloric ossicle in the families contained (i.e., Thalassinidae, Laomediidae, and Upogebiidae). On the other hand, it is clear that the taxonomic structure of the Callianassoidea cannot be reconstructed from this character, but that it can only be stated that this superfamily comprises four groups of families, based on the four Subtypes recognized, as outlined further, below.

CONCLUSIONS

It is concluded, that the infraorder Thalassinidea and its contained families might be assumed to be of a diphyletic nature, based on the structure of the propyloric ossicle, as follows:

Infraorder THALASSINIDEA Latreille, 1831

I. Superfamily CALLIANASSOIDEA Dana, 1852 [Type I]

- Families included: Callianassidae Dana, 1852 and Axiidae Huxley, 1879 [Subtype 1];
 Callianideidae Kossmann, 1880 [Subtype 2];
 Ctenochelidae Manning & Felder, 1991 [Subtype 3];
 Gourretiidae Sakai, 1999 [Subtype 4].

II. Superfamily THALASSINOIDEA Dana, 1852 [Type II]

- Families included: Thalassinidae Dana, 1852; Laomediidae Borradaile, 1903; Upogebiidae Borradaile, 1903.

The taxa of the Thalassinidea examined can thus be listed as follows:

Infraorder THALASSINIDEA Latreille, 1831

Superfamily CALLIANASSOIDEA Dana, 1852 (new sense)

- Family Callianassidae Dana, 1852 — *Callianassa subterranea* (Montagu, 1808); *C. japonica* Ortmann, 1891; *Calliax punica* De Saint Laurent & Manning, 1982.
 Family Axiidae Huxley, 1879 — *Axiis stirhynchus* Leach, 1815.
 Family Callianideidae Kossmann, 1880 — *Callianidea typha* H. Milne Edwards, 1837.
 Family Gourretiidae Sakai, 1999 — *Gourretia denticulata* (Lutze, 1937).
 Family Ctenochelidae Manning & Felder, 1991 — *Ctenocheles balssi* Kishinouye, 1926.

Superfamily THALASSINOIDEA Dana, 1852

- Family Thalassinidea Dana, 1852 — *Thalassina anomala* (Herbst, 1804).
 Family Laomediidae De Haan, 1849 — *Laomedea astacina* De Haan, 1841.
 Family Upogebiidae Borradaile, 1903 — *Upogebia major* (De Haan, 1839).

The representatives of the (three) other decapod infraorders examined can then be listed as:

Infraorder ASTACIDEA Latreille, 1802

Family Astacidae Latreille, 1802 — *Procambarus clarkii* (Girard, 1852); *Pacifastacus (Pacifastacus) leniusculus* (Stimpson, 1857).

Family Enoplometopidae De Saint Laurent, 1988 — *Enoplometopus debelius* Holthuis, 1983.

Family Thaumastocheilidae Bate, 1888 — *Thaumastocheles japonicus* Calman, 1913.

Family Nephropidae Dana, 1852 — *Metanephrops japonicus* (Tapparone-Canefri, 1873).

Infraorder PALINURA Latreille, 1802

Family Polychelidae Wood-Mason, 1875 — *Polycheles amemiyai* Yokoya, 1933.

Family Palinuridae Latreille, 1802 — *Panulirus interruptus* (Randall, 1840); *Panulirus argus* (Latreille, 1804).

Family Scyllaridae Latreille, 1825 — *Scyllarus martensii* Pfeffer, 1881.

Infraorder ANOMURA MacLeay, 1838

Family Albuneidae Stimpson, 1858 — *Albunea occultus* Boyko, 2002.

Family Galatheidae Samouelle, 1819 — *Cervimunida princeps* Benedict, 1902.

Family Paguridae Latreille, 1802 — *Dardanus impressus* (De Haan, 1849).

Remarks. — In the species of the family Astacidae, the propyloric ossicle shows an exceptional form, as it has a Y-shaped ventral tip. In the species of the family Palinuridae, the median tooth shows a transverse carina posterior to the propyloric ossicle.

Based on the character of the propyloric ossicle, and applying an interpretation in the sense of classical taxonomy, the structure of the infraorder Thalassinidea can thus be observed to be diphyletic, comprising a superfamily Callianassoidea with five families, Callianassidae, Axiidae, Callianideidae, Ctenochelidae, and Gourretiidae (in which Callianassidae and Axiidae might be grouped together), and a superfamily Thalassinioidea with three families, Thalassinidae, Laomediidae, and Upogebiidae. Yet, it is acknowledged that the structure of the propyloric ossicle represents only one character, and that, of course, many more characters will have to be taken into consideration before a truly reliable statement about the phylogenetic structure of the infraorder can be made. Therefore, pending a comprehensive analysis of the distribution of a larger number of morphological characters (or character states), the inclusion of the Callianideidae and Axiidae in the superfamily Callianassoidea cannot yet be proposed with certainty, but is here all the same advocated provisionally, instead.

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