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THE SYSTEMATIC POSITION OF AN AUSTRALIAN MANGROVE CRAB *HELOECIUS CORDIFORMIS* (CRUSTACEA: DECAPODA: BRACHYURA)

MICHAEL TÜRKAY

Forschungsinstitut Senckenberg

Senckenberganlage 25, D-6000 Frankfurt/M.-1, W. Germany

SUMMARY

Males of *Heloecius* possess a coxo-sternal genital opening. This character suggests that *Heloecius* is the most primitive crab within the classical Ocypodidae. It is therefore excluded from the Ocypodinae and a new subfamily, the Heloecinae, is proposed for it. The relationships of this subfamily are discussed and *Ucides*, an American genus of mangrove crab, is provisionally included in the new subfamily.

Introduction

The name *Heloecius* was introduced by Dana (1852a: 248) for *Gelasimus cordiformis* H. Milne-Edwards 1837. Dana (1852b: 319) identified the main characteristic of the species as follows: "Second joint of male abdomen narrower than sternum behind". He also stated that *Gelasimus* was significantly different in this and in other respects. However, the general appearance of the species as well as several other similarities in position and direction of antennal and antennular appendages, led him to conclude that *Heloecius* might be closely allied to *Gelasimus*. Therefore, he left the former in subfamily Ocypodinae.

The position of the genus in the subfamily Ocypodinae has remained unquestioned by subsequent workers. For example Alcock (1900) and Borradaile (1907) left *Heloecius* with *Ocypode* and *Uca* in the subfamily. This classification was also used by Tesch (1918), who, however, used the ratio abdomen:sternum to separate *Heloecius* from the two other Ocypodinae genera. Balss (1957) also accepted the mentioned classification without change.

A number of characters have been used for distributing the ocypodid genera to subfamilies. Many of these, however, are only applicable to certain genera within each subfamily and are of no help in differentiating between the subfamilies. There are, however, three characters which together have historically been used to separate the subfamilies: the mode of folding of the antennules, the breadth of the interantennular septum, and the existence and position of the supplementary respiratory openings. The latter have hair-tufts at their sternal ends, which have been found to function as organs of moisture uptake from damp substrata (see Verwey, 1930 and Bliss, 1968). The three subfamilies of the Ocypodidae were defined as follows:

	Ocypodinae	**Scopimerinae**	**Macrophthalminae**
1)	Antennules folded lengthwise or oblique.	Antennules folded lengthwise or oblique.	Antennules folded transversely or slightly oblique.
2)	Interantennular septum broad.	Interantennular septum broad.	Interantennular septum very narrow.
3)	A hairy-edged pouch leading into the branchial cavity between the bases of third and fourth pereiopods.	A hairy-edged pouch between bases of second and third pereiopods or none at all.	No hairy-edged pouch present at the base of of any pereiopod.

This classification is not satisfactory, as the main characters of the frontal appendages (1 and 2 above) do not clearly differentiate the subfamilies. The remaining character (3) will be discussed later.

The basic trend in evolution of crabs is the adjustment to a construction permitting highly efficient and rapid locomotion. This led to the evolution of such advanced forms as *Ocypode* and other terrestrial crabs. It must be concluded that the direction of evolution of the group is dominated by the enlargement of the sternum. This modification results in the distribution of the body weight on a larger surface and the movement of the centre of gravity farther back between the walking legs. As a result, the whole locomotory system becomes more efficient as the body can be more easily balanced and, at the same time, there is more room in the enlarged thoracic system for a more complex endoskeletal musculature. This trend seems basic in the evolution of the Decapoda and Brachyura, though it takes place along different phylogenetic lines. Many of these evolutionary lines and the effect of the enlargement of the sternum on the external reproductory system have been discussed by Guinot (1969, 1978, 1979).

Because of these circumstances, the classification of the grapsoid crabs must be revised, largely on the basis of evolutionary characters drawn from the thoracic and genital configuration. A new classification for the Brachyura has been recently outlined by Guinot (1978), but the grapsoid groups within this revision still need further investigation.

These considerations led me to reexamine the status of *Heloecius* and the results lead to some surprising conclusions.

Structure of the male reproductive system of *Heloecius cordiformis*

(Figs 1–3)

Superficially, the male genital opening seems to be coxal as the base of the penis is connected with the coxa of the fifth pereiopod (Fig. 2). The eighth sternite does not meet the seventh above the penis so that there is no purely sternal arrangement. But when the penis is removed it becomes apparent that the genital opening is not merely coxal, but coxo-sternal (Fig. 3). That is, the lateral part of the genital opening arises from the coxa, while the medial and caudal part is bordered by the eighth sternite at the fronto-lateral border where the genital opening is situated. The border between the seventh and eighth sternite forms the frontal margin of the opening. This configuration is much more primitive than that ordinarily encountered in the Ocypodidae. The latter are normally advanced forms with a clearly sternal genital opening. For this reason, the abdomen covers nearly the whole space between the coxae of the fifth pereiopods in *Heloecius*, while it is much narrower in comparison to the hind part of the sternum in all other ocypodids.

The first male pleopod of *Heloecius* has a unique shape and construction. Evidently there is a torsion of the distal part, as the sperm channel begins dorso-laterally, then turns to dorsal, and just behind the palp passes to the ventral side where it enters the terminal horny piece and meets the distal opening terminally (Fig. 1). The terminal piece is thus fronto-laterally directed.

Discussion

Since the genus *Heloecius* shows primitive features that are unique among the Ocypodidae and never encountered in *Ocypode* and *Uca* s.l., and as its first male pleopod shows a particular construction, the genus must be excluded from the Ocypodinae. However, it can not be included in any other classic subfamily. Therefore, a new subfamily is proposed.

Heloecinae n. subfam.

Type genus: *Heloecius* Dana, 1852

This subfamily clearly differs from the other generally recognised subfamilies by its posteriorly narrow sternum, which must be considered a more primitive catometopan feature. Supplementary characters, such as the obliquely folded antennulae and the tufts of setae between the coxae of the third and fourth pereiopods, may be used to distinguish the subfamily from the Scopimerinae and Macrophthalminae.

With the exclusion of *Heloecius* from the Ocypodinae, the classical characters of this subfamily must be discussed. The main characters also shared by *Heloecius* are listed in this paper. The obliquely folded antennulae are also shared with the Scopimerinae and some Macrophthalminae so that it would be more accurate to state that the latter have more transversely oblique folding, while the former two may have more lengthwise folding. In practice, there is no problem distinguishing between these two kinds of obliqueness but it is questionable whether such intergrading characters are of sufficient significance to be used for the definition of such high ranks. In any case, they can not outweigh the

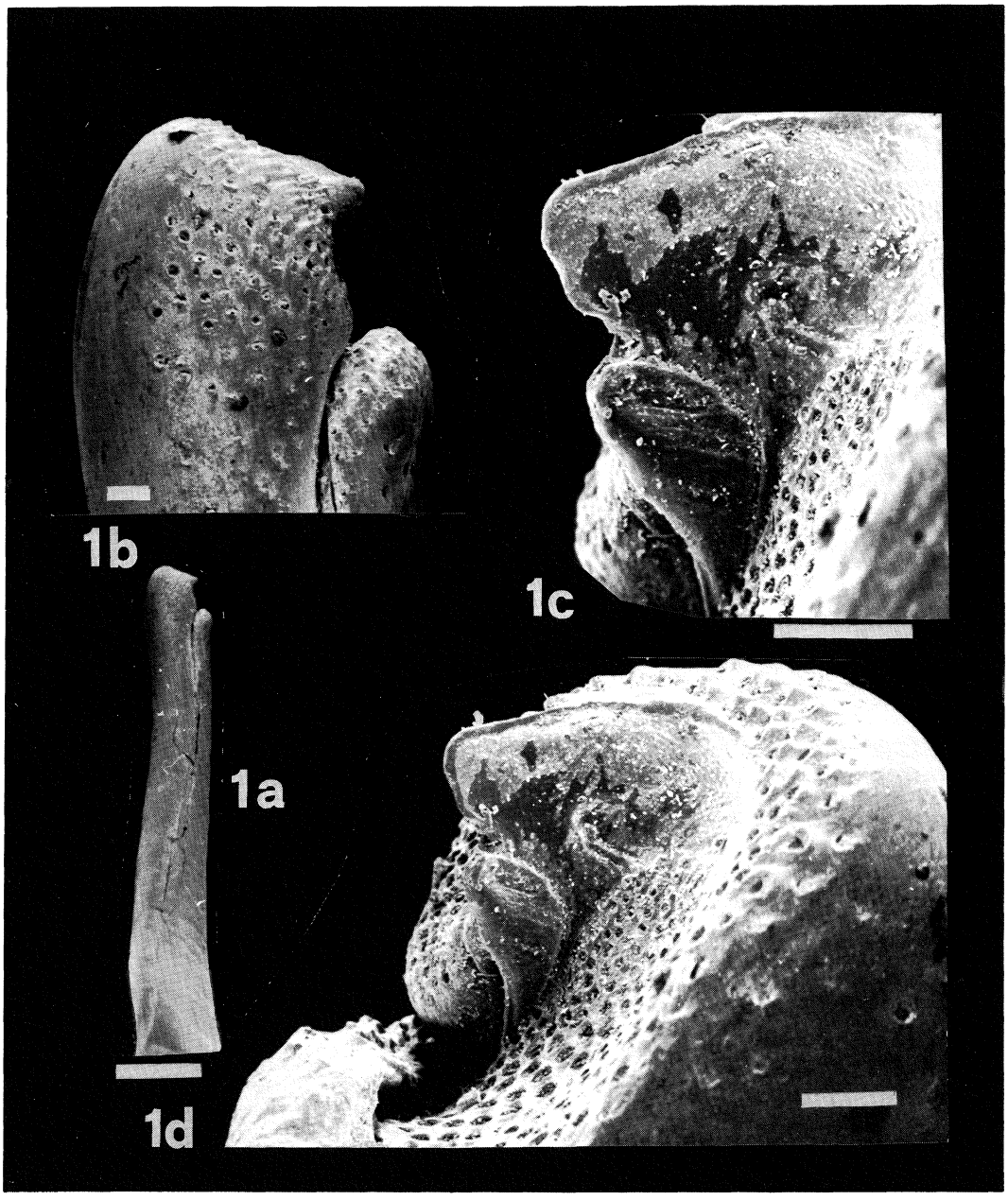

Fig. 1. *Heloecius cordiformis* (H. Milne-Edwards, 1837), right first male pleopod (from specimen in Australian Museum, Sydney, catalogue number P. 3839): **a**, total organ, dorso-lateral aspect; **b**, distal part, dorso-lateral aspect; **c**, horny terminal piece, ventral aspect; **d**, distal portion, ventral aspect. (Scales: total organ, 1 mm; all others, 1/10 mm).

importance of structural differences in the male genital system between *Heloecius* and the remaining Ocypodinae.

The same applies to several other characters which I believe represent convergence due to adaptations to certain common modes of life and not to phylogenetic relationships, or which upon further analysis are not diagnostic. For example, the breadth of the interantennular septum does not show significant

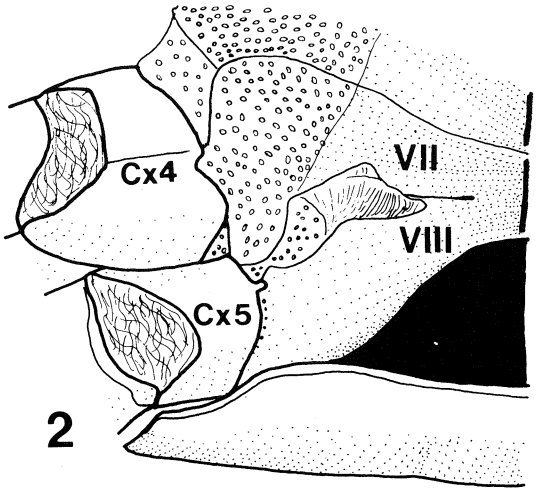

Fig. 2. *Heloecius cordiformis* (H. Milne-Edwards, 1837), latero-caudal part of sternum showing the coxae of the fourth (Cx 4) and fifth (Cx 5) pereiopod and the penis. VII and VIII indicate the last two thoracic sternites.

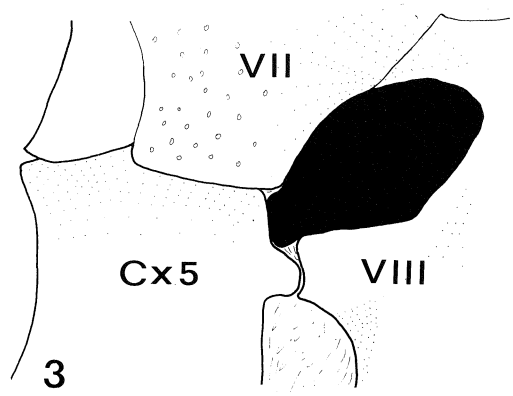

Fig. 3. *Heloecius cordiformis* (H. Milne-Edwards, 1837), situation of the male genital opening (black) after the removal of the penis. All symbols as in Fig. 2.

differences between the subfamilies. The tuft of setae between the coxae of the third and fourth pereiopods occurs not only in *Ocypode*, *Uca* and *Heloecius*, but also in several grapsid genera such as *Geograpsus* and *Goniopsis* (see Balss, 1944: 557). They also occur in *Scopimera*, where they are situated between the coxae of the second and third pair of pereiopods, but are absent in all other crabs actually grouped in the Scopimerinae, a fact ignored when the latter genera are included in this subfamily. At the same time, the tufts have been considered reliable characters for the remaining subfamilies. Griffin (1968) mentioned some common features in the behaviour of *Heloecius* and the two other ocypodine genera. However, none of these are restricted to this genus and thus they cannot form a basis for relationships (Crane, 1975).

As stated above, *Heloecius* is not only distinct from the other classical ocypodine genera, but also from the Scopimerinae and the Macrophthalminae which have a typical, highly advanced, catometope organisation.

The American genus *Ucides* is another group of species with an uncertain position within the Ocypodidae. It was transferred from the Gecarcinidae to the Ocypodidae by Chace & Hobbs (1969: 219-223), a view which I also support (Türkay, 1970: 350). The former authors mentioned several similarities between *Ucides* and *Heloecius*, but stated that there was no pronounced tuft of hairs at the base of the third and fourth pereiopods. Therefore, they did not include the genus in the Ocypodinae. A close examination of the male reproductive system shows several similarities to *Heloecius*, but also some differences. The male genital opening in this genus is sternal, but the sternum is oval and narrowed behind. This means that the eighth sternites is much narrower than in typical ocypodid crabs. Thus, the abdomen, as in *Heloecius*, covers nearly the whole space between the coxae of the fifth pereiopods. In spite of this difference in the position of the male genital opening, *Ucides* does in fact show a similar configuration to *Heloecius* in that the sternal position of the former is the result of the meeting of the seventh and eighth sternites over the base of the penis, while both sternites are already apporoximated in *Heloecius*. Thus, *Ucides* is more advanced in that the hind part of the sternum is a little broader than in *Heloecius*. In this respect, the gap between the two genera is less than that between *Ucides* and the remaining Ocypodidae. In addition, the first male pleopods of *Ucides* show considerable resemblance to *Heloecius*, i.e. the parts of the organ are oriented in nearly the same plane. This is also reflected by the directions of the slits of the female vulvae which are identical in both genera. However, the torsion of the distal part of the pleopod is much stronger in *Heloecius*, where the sperm channel is fronto-ventrally situated, while it remains rather dorsal in *Ucides*. Otherwise, the torsion of the pleopod is identical in both, as shown by the direction of the sperm channel.

In evaluating these differences, I conclude that *Ucides* is more closely related in evolutionary rank to *Heloecius* than to other ocypodid genera. It should therefore be provisionally included in the Heloecinae, which would then contain the more primitive members of the family. These are characterised by a male abdomen which covers nearly all the space between the coxae of the fifth legs. However, the different torsion of the distal part of the first male pleopods is a difficulty which can not be overlooked. As, at the moment, there is no functional or evolutionary explanation for pleopod torsion, either in the *Ucides-Heloecius* complex or in such genera as *Uca* s.l., the question must be left open. For this reason, I stress the provisional character of the inclusion of *Ucides* in the Heloecinae. A more detailed study of the male reproductive system, and of the sternal construction of the grapsoid crabs, will enable us to answer these questions more definitely than is now possible. Such studies could, of course, also lead to the creation of a new group for *Ucides*, as apart from the different torsion of the male pleopod tips, there are other differences in gross morphology, e.g. the folding mode to the antennulae, which must also be resolved.

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REFERENCES

Alcock, A. 1900. Materials for a carcinological Fauna of India. No. 6. The Brachyura Catometopa or Grapsoidea. *J. asiat. Soc. Bengal* 69 (2,3): 621-798.

Balss, H. 1941-1944. Decapoda. III. Morphologischer Teil. in: Bronn, Klassen und Ordnungen des Tierreichs, 5 (I, 7, 1-5): 1-669, figs 1-740.

———— 1957. Decapoda. VII. Systematik. in: Bronn, Klassen und Ordnungen des Tierreichs, 5 (I, 7, 12): 1505-1672, figs 1131-1199.

Bliss, D. E. 1968. Transition from Water to Land in Decapod Crustaceans. *Am. Zoologist* 8: 355-392.

Borradaile, L. A. 1907. On the Classification of Decapod Crustaceans. *Ann. Mag. nat. Hist.* (7) 19: 457-486.

Chace, F. H. & H. H. Hobbs, 1969. The Freshwater and Terrestrial Decapod Crustaceans of the West Indies with Special Reference to Dominica. *Bull. U.S. natn. Mus.* 292: 1-258.

Crane, J. 1975. Fiddler Crabs of the World. Ocypodidae: Genus *Uca*. Princeton University press. Princeton, New Jersey. Pp. XXIII, 736, 101 figs 21 maps, 50 pls, 24 tables.

Dana, J. D. 1852a. Conspectus Crustaceorum quae in Orbis Terrarum Circumnavigatione, Carolo Wilkes e Classe Reipublicae Foederatae Duce, lexit et descripsit. *Proc. Acad. nat. Sci. Philad.* 5: 246-254.

———— 1852b. Crustacea. U.S. explor. Exped. 1838, 1839, 1840, 1841, 1842, 13(1): 1-685, 1 map.

Griffin, D. J. G. 1968. Social and maintenance behaviour in two Australian ocypodid crabs (Crustacea: Brachyura). *J. Zool. London* 156: 291-305.

Guinot, D. 1969. Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyoures. VII. Les Goneplacidae. *Bull. Mus. natn. Hist. nat.* (2) 41: 241-265, 507-528, 688-724, figs 1-146, pls 1-5.

———— 1978. Principes d'une Classification évolutive des Crustacés Décapodes Brachyoures. *Bull. biol. Fr. Belg.* (N.S.) 112(3): 211-292.

———— 1979. Morphologie et phylogenèse des Brachyoures. *Mem. Mus. natn. Hist. nat.* (N.S., A) 112: 1-354.

Tesch, J.J. 1918. The Decapoda Brachyura of the Siboga Expedition. I. Hymenosomidae, Retroplumidae, Ocypodidae, Grapsidae and Gecarcinidae. *Siboga Exped.* 39c (82): 1- 148, pls 1-6.

Türkay, M. 1970. Die Gecarcinidae Amerikas. Mit einem Anhang uber *Ucides* Rathbun (Crustacea: Decapoda). *Senckenberg. biol.* 51 (5/6): 333-354.

Verwey, J. 1930. Einiges über die Biologie Ost-Indischer Mangrovekrabben. *Treubia* 12: 167-261.