

FRESHWATER CRABS AS POOR ZOOGEOGRAPHICAL INDICATORS: A CRITIQUE OF BĂNĂRESCU (1990)

BY

PETER K. L. NG

Department of Zoology, National University of Singapore, Kent Ridge, Singapore 0511, Republic of Singapore

and

GILBERTO RODRIGUEZ

Instituto Venezolano de Investigaciones Científicas (IVIC), Centro de Ecología y Ciencias Ambientales, Apartado 21827, Caracas 1020-A, Venezuela

ABSTRACT

A critique of Bănărescu's (1990) ideas and hypotheses regarding the importance of freshwater crabs in zoogeography is presented. We contend that many of Bănărescu's generalizations are too simplistic and do not agree with our observations and findings about freshwater crabs. The value of freshwater crabs in zoogeography is briefly discussed.

RÉSUMÉ

Critiques des idées et hypothèses de Bănărescu (1990) sur l'importance des crabes d'eau douce en zoogéographie. Nous soutenons que beaucoup des généralisations de Bănărescu sont trop simplistes et ne s'accordent pas avec nos observations et constatations sur les crabes d'eau douce. La valeur des crabes d'eau douce en zoogéographie est brièvement discutée.

The recent synopsis and analysis of the significance of freshwater crabs in zoogeography by Bănărescu (1990: 223-225, 247-249) requires detailed discussion. Although he notes that he follows Bott's hypotheses (see Bott, 1969, 1972, 1974) on their zoogeography and that the various freshwater crab higher taxa had separate marine ancestors, most of Bănărescu's extrapolations seem unfounded and most unlikely. There are also numerous inaccuracies. As Bănărescu's book is the most significant contribution to the use of freshwater animals in biogeography in recent years, it is necessary to discuss the validity of his conclusions regarding freshwater crabs, especially of the Asian and American fauna, which the authors have been studying for many years.

After presenting the published data (mostly Bott's series of papers), Bănărescu (1990: 224, 225) concluded by writing "no species within these families is known to occur in sea water, but the presence of Sundathelphusidae in New Guinea and Australia, a family also living in western Indonesia and Ceylon, as well as the occurrence of Pseudothelphusidae both on the American mainland and the West Indies, demonstrate that at least two families either are

(or were until recently) able to cross salt water barriers, or are derivatives of not too distant marine ancestors. Large-sized freshwater crabs can also survive outside water ... having thus the possibility to disperse short distances by land in humid atmosphere ... Because of these ecological and geographical peculiarities, freshwater crabs are zoogeographically less significant than crayfishes and can be ascribed to a biogeographical category more or less corresponding to the secondary-division freshwater fishes." Never has a large group of wholly freshwater animals been dismissed as zoogeographical indicators so sweepingly. One gets the impression that because the zoogeographical data from freshwater crabs do not appear to agree with those from crayfish and primary freshwater fish, something must be "special" about them.

We cannot agree with Bănărescu's logic behind these statements. Freshwater crabs have been used as suitable zoogeographical subjects in several recent studies which combine the more classical methods of comparative anatomy with cladistic taxonomy and palaeo-geographic data to falsify vicariant or dispersalist hypotheses. The presence of freshwater groups on islands and from scattered localities need not necessarily imply they originally had the ability to cross sea water barriers. It might simply mean these land masses had been connected during an earlier geological period. Rodriquez (1986) suggested that the Pseudothelphusidae of South and Central America are perhaps related to those from West Africa and Asia (Gecarcinoidea) (see also Ng et al., 1995). Work on the Asian fauna seems to support this idea (PKLN, unpubl. data). This would mean that freshwater crabs (and possibly the Brachyura) are older than previously believed. There are very few published data to show that freshwater crabs can tolerate sea water for long periods. Ng (1990) noted that some very adaptable lowland and open-country parathelphusids (e.g., *Parathelphusa maculata* De Man, 1879) can survive in well oxygenated sea water for up to 24 hours, but highland taxa like gecarcinucids and potamids die within an hour when immersed in salt water (PKLN, unpubl. data). The habits of the Central and South American pseudothelphusids parallel those of the potamids, as well as many terrestrial gecarcinucids and parathelphusids in South and Southeast Asia, and they would probably not survive long in salt water as well.

Bott's contention that there are parathelphusid and sundathelphusid genera occurring both in Sri Lanka (Ceylon) and Sundaic Southeast Asia is based on his taxonomic interpretation that the Sri Lanka and Sundaic freshwater crabs are closely related. Even in Bott's (1970) monograph, only one genus, *Perbrinckia*, is actually "shared" between Southeast Asia (Java and Borneo) and Sri Lanka. Ng (1989) showed that the Southeast Asian species should be referred to a separate genus (*Terrathelphusa*), with *Perbrinckia* restricted to the single known Sri Lankan species. Recent studies of *Perbrinckia enodis* (Kingsley, 1880) and allied undescribed species (Ng, 1995a) from Sri Lanka, confirm the hypothesis that the Sri Lankan and Southeast Asian genera are distinct and not closely related. Bott (1970) explained the disjunct distribution of these species on the

premise that there had been a landbridge spanning the Andaman Sea, from Sri Lanka to the northern tip of Sumatra. This landbridge hypothesis, however, has not been generally accepted for some time (see de Beaufort, 1951).

Bănărescu's recognition of freshwater crabs as only "... corresponding to the secondary-division freshwater fishes" and of equivalent value is a very sweeping and over-simplified generalisation to say the least. The freshwater crabs are a very diverse group with a large number of species and ecological niches, and the uncritical dismissal of the group as a whole is unacceptable. While some freshwater crabs are generalists and quite adaptable (especially the lowland parathelphusids, see Ng, 1988, 1990), most species (especially the gecarcinucids and potamids) are very fastidious in their habitat requirements and have very localized distributions, including semiterrestrial or terrestrial taxa.

Bănărescu makes far too many sweeping statements about freshwater crabs, and he has tended to ignore other views. For example, he writes that "It can be accepted that each family of freshwater crabs has distinct marine ancestors" (p. 247). This is certainly not the view of most carcinologists, or even among those actually working on freshwater crabs (see Holthuis, 1974, 1979; Rodriguez, 1986, 1992; Ng, 1988). Bott's hypotheses about their polyphyletic origins is one possibility: that is all. A non-carcinologist could be very easily misled to think that Bănărescu's hypothesis is now a well established theory.

Because some members of the Parathelphusidae are present in Sulawesi and happen to have crossed Wallace's Line, Bănărescu writes that "It can be assumed that the species of the family, like those of the Sundathelphusidae, are more salt-tolerant (or more recent derivation of marine intruders) than other freshwater crabs" (p. 230). While it is true that some lowland *Parathelphusa* species can tolerate salt water for short periods as mentioned earlier, several species in Sulawesi are terrestrial or live in isolated lakes and are unable to tolerate salt water.

Regarding a presumed polyphyletic origin for freshwater crabs, comparative anatomy provides a first insight into the origin of the Old and New World families and serves to test Bănărescu's contention that "It can be accepted that each family of freshwater crabs has distinct marine ancestors" (p. 247). The presence of species with reduced exognaths (an apomorphy connected with their advanced adaptation to fresh water life) in America, Africa and India is a strong argument for a monophyletic origin of several families of these same species, is also evidence of a former Gondwanan distribution, and shows that the transformation of buccal appendages had already begun in mid-Cretaceous times in a basic group whose modern representatives are the American Pseudothelphusidae and the African Gecarcinucidae. The Trichodactylidae, in which buccal reaccomodation does not appear, are derived from a separate basic group and probably related to the Eupotamonea of western Africa (Rodriguez, 1986).

This hypothesis of two monophyletic groups for the origin of the majority of freshwater crabs is further supported by the study of the structure of their sexual openings (Rodriguez, 1992), a character of fundamental phylogenetic significance in the Brachyura (Guinot, 1977, 1978, 1979). All the freshwater crabs formerly grouped in the "Potamonidae" by Rathbun (1904-1906) belong in the section Heterotremata Guinot, 1977, i.e., brachyuran crabs in which the female opening is sternal but the male opening is either coxal or coxo-sternal. The heterotrematous condition suggests an evolutionary process beginning with the location of the penis in the coxa of the fifth pereopod; in successive stages, the penis is lodged in a sternal groove which later forms a channel due to the disposition of the sternites in this area; finally sternites 7 and 8 completely cover the channel and the penis is embedded under the sternal plates, although the duct still reaches the coxa.

All freshwater crabs can be placed at the beginning of this process, but whereas in the Pseudothelphusidae the penial groove is located between the posterior margin of episternite 7 and the anterior margin of sternite 8, probably a first stage in the process leading to the orifices located near sternal suture 7/8, as in the *Ocypodidae* and *Pinnotheridae*. In the *Trichodactylidae*, as well as in some freshwater crabs like *Somanniathelphusa sexpunctata* (Lanchester, 1906) (Parathelphusidae), the penial groove is located along sternite 8. This last disposition is also found in some members of the superfamily Portunoidea with which the *Trichodactylidae* share other autapomorphies, such as the presence of the so-called "portunid lobe" on the endopodite of the first maxilliped.

Bănărescu's belief that freshwater crabs also are able to cross salt water barriers is based partially on the occurrence of the family Pseudothelphusidae being present both on mainland South America as well as in the West Indies. However, an alternative hypothesis is more plausible (Rodriguez, 1986). This family displays two disjunctions in the land masses surrounding the Caribbean. The first disjunction concerns the two subfamilies of Pseudothelphusidae in the Antilles and mainland South America, and can be resolved according the vicariance model proposed by Rosen (1976), namely that the present Antillean biota are descendants of an ancestral stock which occupied a Proto-Antillean archipelago situated between North and South America during the Mesozoic. The islands moved to their present location during the late Mesozoic and Cenozoic when a portion of the Eastern Pacific seafloor wedged itself between North and South America, carrying the archipelago with it. During a still undetermined period of time, the Antillean and South American landmasses were continuous and presumably shared common biota which at a later stage became disjunct. The second disjunction concerns only one species of Pseudothelphusidae, *Guinotia dentata* (Latreille, 1825), found in some Windward Islands and whose nearest relative seems to be located in the Guianas. Rafting, which is not uncommon in this area of the Caribbean, could account for this peculiar distribution.

As an alternative to cross salt water barriers, Bănărescu mentions the possibility that freshwater crabs were derived from "... not too distant marine ancestors". The studies mentioned earlier imply a pre-Tertiary origin for the basic groups. A confirmation of the antiquity of these crabs (and an interesting case of stasigenesis) is found in the fossil record of the common South American trichodactylid *Sylviocarcinus piriformis* (Pretzmann, 1968) found in the Miocene outcrops in Colombia (Rodriguez, 1993).

Examples of the relevance of freshwater crabs or general biogeographical theories could also be found in the recent literature. The distribution of some Pseudothelphusidae in South America have been used to give support to a vicariance hypothesis modelled after the generalised tracks of Croizat (see Croizat et al., 1974). Based on cladistic analyses, Rodriguez & Campos (1989) have postulated that the crabs of the tribe Strengerianini were widespread in the area of northwestern South America in Miocene times. Later, the uplifting and displacement of the Santa Marta Massif led to disruption of the ancestral Strengerianini stock to form the actual pattern of distribution of two disjunct groups in the Sierra de Santa Marta and the Colombian Andes.

Another example of the relevance of freshwater crabs in general to biogeographical problems is afforded by the distribution of the pseudothelphusid genus *Fredius* in the Guianas, where it has been shown by "area cladograms" that most of the species were present in a hypothetical major basin comprising the present Orinoco, Essequibo and Cuyuni Rivers, and that much of the evolution of the genus occurred there (Rodriguez & Pereira, 1992).

Bănărescu's explanations for the distributions of many of the taxa sound "glib", too simplistic and not based on any "hard data" at all. For example, he notes that "The range of the Parathelphusidae includes only a rather small part of southern Asia mainland. Both families have hence a "marginal" range in Asia and they may have been "pushed" by the more competitive Potamonoidea" (p. 248). We would certainly not consider a distribution that covers the whole of southern India, Sri Lanka, Burma, Indo-China, Southeast Asia and southern China as "marginal". Even without considering what Bănărescu really means by "pushed", most potamids and parathelphusids have very different niches and habitats. Potamids (and many gecarcinucids) generally prefer higher altitudes whilst many parathelphusids are lowland species. Many gecarcinucids also have semiterrestrial to terrestrial habits (see Holthuis, 1979; Collins, 1980; Ng, 1986, 1987, 1988, 1989, 1991; Naiyanetr, 1978, 1988). In a similar vein, Bănărescu writes: "The Isolapotamidae have, like the Parathelphusidae and Sundathelphusidae, [have] a "marginal" range, occurring mainly on the islands of the Asian shelf (but without crossing Wallace's Line). They may have also been "pushed" by the more competitive Potamonidae and Sinopotamidae" (p. 248). Is it not possible, even assuming the family classifications are accepted (see however, Ng, 1988, 1995b), that the isolapotamids evolved through prolonged insular isolation of an original ances-

tral potamid stock? After all, there is at least one known potamid genus in Borneo, *Cerberusa* (cf. Holthuis, 1979), or that the isolapotamids are a recently evolved group and are only recently beginning to expand their range? In fact, reading through these hypotheses of Bănărescu's, one cannot help but get the idea that groups which have a continental distribution are "fitter" and "more competitive" than the insular ones.

There are also a significant number of taxonomic and other errors, some of which are based on incorrect interpretation of published data. The absence of references in the volume is very irritating. It is obvious that some references have been incorrectly cited but this cannot be checked at all due to the structure of the series (i.e., references will only be listed in the final volume). Some of the errors are:

1. The use of the name Potamonoidea (p. 230) is incorrect. It is also incorrect to say that the Potamonidae can also be spelt Potamidae (p. 231). The original spelling of the family, Potamonidae, was shown to be grammatically incorrect by Holthuis (1964) and was corrected to Potamidae. The grammatically correct name, Potamidae Ortmann, 1896, is now placed on the "Official List of Family Names in Zoology". On the basis of this, the spelling of the superfamily is Potamoidea, not Potamonoidea.

2. Holthuis (1979) had already stated that the correct name for the superfamily Parathelphusoidea (p. 225) should be Gecarcinucoidea Rathbun, 1904, by priority.

3. There is no such genus called "*Megapotamon* from Madagascar" (p. 231). Bănărescu is almost certainly referring to the potamonautid genus *Madagapotamon* Bott, 1965, instead (Bott, 1965).

4. The genus *Utica* belongs to the family Grapsidae, not Ocypodidae (p. 244).

5. The genus *Baruna* does not belong to the family Grapsidae (p. 244) but to the family Ocypodidae.

6. The brief treatment of the freshwater family Hymenosomatidae makes no mention whatsoever of the important monograph by Lucas (1980) on the family, in which a new freshwater genus, *Amarinus*, is dealt with.

7. The brief discussion of freshwater Grapsidae makes no mention of the wholly land and freshwater genera *Sesarmoides* and *Geosesarma*. Although some authors prefer to regard both genera as synonymous with *Sesarma* sensu lato, there are a good number of these species, especially *Geosesarma*, which are wholly freshwater, occur in mountains far from the coast and have abbreviated larval developments without connections to the sea (see Hartnoll, 1964, 1971; Serène, 1968; Ng, 1988).

8. There are many spelling mistakes which can be quite confusing. The potamid genus is *Cerberusa*, not "*Cerberussa*" (p. 231), the sundathelphusid species is *Perbrinckia enodis* (nec *P. enolis*) (p. 227), the hymenosomatid species is *Neorhynchoplax introversus* (nec *N. ontroversus*) (p. 244), the xanthoid genera are

Rhithropanopeus and *Panopeus* (nec *Rhithropanpaesus* and *Panopaesus*) (p. 244), the ocypodid species is *Potamocypoda pugil* (not *P. pugila*) (p. 244).

Several of the maps contain distributional errors which have arisen from misinterpretations of the published literature on crabs as well as unwarranted extrapolations of the published data. This is a very serious problem as it not only obscures disjunct distributions, but gives the reader the impression that the distributions of the various genera are actually continuous and in accordance with the prescribed hypothesis. For example:

1. Bănărescu notes in his caption for the map of the potamid genera *Potamiscus*, *Ranguna* and *Larnaudia* that their ranges are “largely overlapping” (p. 230, fig. 3/10) and include Peninsular Malaysia. Even if Bott’s (1970) system of classification is followed strictly, Bott does have any records of *Potamiscus* and *Larnaudia* from Peninsular Malaysia, and in his distribution listings for both genera, does not include this area.

2. In his map on the distribution of the potamoid family Isolapotamidae, the range of *Malayopotamon* includes the whole of Java (p. 232), but there are no reports of potamids other than from west Java. The genus *Malayopotamon* is only known to occur in Sumatra and west Java (Bott, 1968a). While one might logically expect the genus to be present in east Java, one cannot exclude the possibility that the absence of potamid crabs from central and east Java is a real phenomenon. Certainly, the latter seems to be true.

3. The range of the potamid genus *Nanhaipotamon* (p. 232, fig. 3/11) is “all encompassing”, ranging from China through to Taiwan and the northern half of the Philippines (Bott, 1968a, 1970). But this ignores the fact that the genus is not known from Luzon. The only record of this genus in the Philippines is the description of *N. balssi* Bott, 1968, from the island of Mindoro (Bott, 1968a). Again, the range of the genus has been incorrectly extrapolated. A disjunct distribution often indicates that the taxonomy of the group needs to be re-examined. In this case, the taxonomy proved to be faulty. In any event, the genus *Nanhaipotamon* is a heterogeneous grouping (see Ng & Dudgeon, 1991), and Ng & Takeda (1992) recently established a new genus, *Mindoron*, for *N. balsii* and a second new species from Mindoro.

4. The distribution of the genus *Phricotelphusa* (not spelt *Phricothelphusa*) is not restricted to Burma (p. 225, fig. 3/5). It is also present in western Thailand and northwestern Peninsular Malaysia (see Ng, 1986, 1988).

5. The distribution of the genus *Spiralothelphusa* Bott, 1968 (with three recognised species) (p. 228, fig. 3/8), includes Sri Lanka, southern India, southern Burma and Nicobar Islands. There are however, no records of the genus from mainland Burma (see Bott, 1968b; Ng, 1994). In fact, it remains to be seen if the record of *S. wuellerstorfi* (Heller, 1862) from the Nicobars is valid.

6. The statement that the genus *Parathelphusa* occurs in “Malay Peninsula, Djawa, Sumatra, Lombok Island — apparently not Bali — and Sulawesi” (p. 229) is erroneous. It is definitely found in Bali (PKLN, unpublished data).

7. The genus *Mainitia* Bott, 1969, is mapped as being present in the area of Sabah or northeastern Kalimantan (p. 226, fig. 3/6). But Bott (1979: 82) described the only Bornean species, *M. nieuwenhuisi* Bott, 1970, from the Kajan and Kapuas areas in central Borneo (near the headwaters of the Kapuas and Mahakam Rivers). One of us (PKLN) has examined the types and the species is actually very distinct from *Mainitia* s. str. and belongs to its own genus (unpublished data).

8. The map for the genus *Perbrinckia* (p. 226, fig. 3/6) incorrectly includes Sumatra. Bott (1969, 1970) established the genus for *P. enodis* (from Sri Lanka), *P. kuhli* (De Man, 1883) (from Java), *P. modesta* (De Man, 1892) (from Java) and *P. loxophthalma* (De Man, 1892) (from Borneo), and there are no known records of the genus from Sumatra. It is of course logical to assume that a genus which occurs in Sri Lanka, Java and Borneo should also be expected to be present in Sumatra, but it is wrong to state it as a matter of fact. As it turned out, the Javan and Bornean species were recently shown to belong to a separate genus from *Perbrinckia* (cf. Ng, 1989).

While it is always useful (and often invaluable) to compile and discuss the data from all groups in compiling a treatise on zoogeography, uncritical interpretation and extrapolation of another person's data is a very dangerous exercise, especially if it is not a group one is familiar with. Bănărescu would have done a greater service to zoogeography if he had only compiled the information of freshwater crabs, discussed Bott's ideas as regards their distributions, compared it with other groups, noting the discrepancies, and left it at that.

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