A new species of freshwater crab (Crustacea: Brachyura: Potamidae) from Socotra Island and description of *Socotrapotamon* n. gen.

Michael Apel and Dirk Brandis

**Abstract:** Socotra Island has been separated from the mainland of the Arabian Peninsula since the late Tertiary and hosts a highly endemic flora and fauna. To date, only a single species of freshwater crab, usually referred to as *Potamon socotrensis* (Hilgendorf, 1883), has been recorded from the island. Here, the taxonomic position of this species is reconsidered, a lectotype is designated and a new genus, *Socotrapotamon*, proposed for it.

From material collected on Socotra Island in spring 1999, a second species of freshwater crab, *Socotrapotamon nojidensis* n. sp., is described. It differs from *S. socotrensis* mainly in the shape of the first gonopod's terminal joint, the distinctly elongated and strongly curved terminal tube of the second gonopod and the conspicuously longer and more slender walking legs. The systematic position of the new genus is discussed, primarily on the basis of the morphology of the male copulatory system. *Socotrapotamon* clearly belongs to the family Potamidae and appears to be most closely related to the Asian genus *Potamiscus* Alcock, 1909. It is very distinct from the African freshwater crabs of the family Potamonautidae. Zoogeographically *Socotrapotamon* appears to be a relic of a group of Potamidae related to *Potamiscus*, which most likely inhabited south-western Arabia, Iran and northern Pakistan during the Miocene and invaded Socotra during this period.

(Socotra: Brachyura: Potamidae: ObjJlJlJlJl)

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*Socotrapotamon* n. gen.

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INTRODUCTION

Socotra is the largest and most easterly of four islands of a small archipelago in the north-western Indian Ocean, some 400 km south of the Arabian Peninsula and about 200 km east of Cape Guardafui, the tip of the Horn of Africa.

The exact geological and biogeographical history of the island is still uncertain. However, the very high levels of endemism, with for example 40% of higher plants being endemic (Mies & Zimmer 1993), indicate that it has been isolated for a long time. Until the late Cretaceous or possibly the early Tertiary, Socotra formed part of the large southern continent Gondwana and most of the flora of the island dates back to that time (Mies 1998). During the mid-Tertiary period most of north-east Africa was covered by an ocean, while the centre of Socotra remained an island until the surrounding sea floor was uplifted and surfaced again during the Miocene (Mies 1998).

For most of the fauna, especially freshwater species, zoogeographical relations and history are poorly known at present. For the freshwater crabs, for example, no information on their taxonomic relations to other groups is available. Since freshwater crabs are considered very conservative in their distribution patterns, they might, however, be a good indicator for paleogeographical relations of the island.

The first mention of a freshwater crab from Socotra was by Hilgendorf (in Taschenberg 1883), who described *Telphusa socotrensis* from material collected in 1881 by E. Riebeck and G. Schweinfurth. One year later Koelbel (1884) described *Telphusa granosa* from material collected during the same expedition that was given by Riebeck to the Natural History Museum in Vienna (P. Dworschak, pers. comm.). According to Pocock (1903), however, B. Balfour and A. Scott, carrying out zoological and botanical studies on the island in 1880, were actually the first collectors to bring Socotran freshwater crabs to Europe, but this material was never systematically worked up. Further collections of freshwater crabs from the island were carried out by H. Forbes and W.R. Ogilvie-Grant in 1898 and were identified as *Potamon socotrensis* by Pocock (1903) – *Thelphusa* Latreille, 1819 (or *Telphusa*, as it was spelled by several authors) being a junior synonym of *Potamon* Savigny, 1816.

Systematically, Rathbun (1905) placed *P. socotrensis* in the subgenus *Geothelphusa* Stimpson, 1858, and thus followed Hilgendorf (in Taschenberg 1883) who compared his species to *Geothelphusa berardi* (Audouin, 1826) from Egypt. This view, however, was opposed by Balss (1929). He mentioned a much closer resemblance in general appearance and morphology of the male abdomen and third maxillipeds to *Potamon potamios* (Olivier, 1804) and referred it to the subgenus *Potamon* instead.

Since then, the systematics of freshwater crabs have changed considerably and new characters, such as the morphology of the male copulatory organs, have become important for taxonomic classification (Balss 1940-1961, Bott 1955, Türkay 1975, Guinot 1979). Today, the classification system of freshwater crabs is mainly based on the revisionary work of Bott (1955, 1965, 1969, 1970), but in none of these monographic volumes does he mention the species from Socotra. Subsequently, no reconsideration of the systematic affinities of *P. socotrensis* has been published and it was not even clear within which family of freshwater crabs the species should be placed. In the present paper, the systematic position of *P. socotrensis* is reconsidered, mainly on the basis of the morphology of the male copulatory system, and a second species from the island is described from material collected by the first author in the southern part of Socotra in spring 1999.
Figs 1-3: Generalised morphology of potamid male pleopods 1 and 2 (gonopods) with explanation of morphological terms (after BRANDIS et al. 1999). 1: Go/1, ventral aspect. 2: Go/1, dorsal aspect. 3: Go/2, dorsal aspect. I-III = segments of first and second gonopod, arrows in Fig. 1 indicate the overlapping zone of the gonopodial groove. It is divided into the more or less conical terminal and the subterminal joint. The terminal joint can be deflected by a flexible zone on the dorsal side between the terminal and subterminal joint (Fig. 2).

**MATERIALS AND METHODS**

Freshwater crabs were collected at several localities on Socotra in March and April 1999 by the first author. All the material obtained was immediately fixed in 4% formalin, before being shipped to the laboratory. Here the material was watered and transferred to 70% ethanol for examination and long-term storage. Half of the material from this collection is permanently deposited in the Senckenberg Museum, Frankfurt, while the other half will be deposited at the Environmental Protection Council, Yemen. Selected specimens were photographed in the field to document the colour of live animals.

In addition to these new collections, the type specimens of *Telphusa socotrensis* Hilgendorf, 1883 and *Telphusa granosa* Koelbel, 1884 from the Zoological Museum of Hamburg University and the Natural History Museum, Vienna were examined and lectotypes designated.

For histology, gonopods were embedded in SPURR-Medium after dehydration and sectioned with glass knives at 50-70 nm. For general tissue differentiation Richardson-staining (ROMEIS 1989) was used.

Measurements were made to the nearest 0.1 mm using callipers. The following measurements are provided: total carapace breadth (CB), measured across the widest point; total carapace length (CL), measured from the anterior margin of the front to the posterior border of the carapace; frontal breadth (FB), measured between the lateral margins of the front; fronto-orbital breadth (FOB), measured between the exorbital teeth; carapace height (CH), measured between the highest point of the carapace and the fourth sternite.
Further abbreviations used in the text are:

- **EPC** Environmental Protection Council, Yemen
- **Go/1:** First gonopod (= first pleopod of male)
- **Go/2:** Second gonopod (= second pleopod of male)
- **HLMD** Hessisches Landesmuseum, Darmstadt
- **Mxp 3:** Third (= outer) maxilliped
- **NHMW** Naturhistorisches Museum, Wien
- **SMF** Senckenberg Museum, Frankfurt
- **ZMH** Zoologisches Museum der Universität Hamburg

**SYSTEMATIC ACCOUNT**

*Socotrapotamon* n. gen.

*Type species:* *Telphusa socotrens* Hilgendorf, 1883 (by present designation).

*Diagnosis:* Carapace subrectangular, anterolateral margin short and rounded, smooth or minutely granular, but with small, distinct epibranchial tooth. Postorbital margin indistinct, almost absent, postfrontal lobes rounded without distinct anterior ridge. Chelipeds unequal, smooth or finely granular; walking legs long, slender. Mandibular palp 3-segmented, terminal segment simple, undivided (Fig. 4). Exopodite of Mxp 3 with well-developed flagellum. Go/1 with long terminal joint, subterminal joint S-shaped, flexible zone well developed, gonopodial groove reaching mesial margin of terminal joint, forming a projecting ridge. Go/2 with a long, laterally compressed terminal tube formed by fused lateral edges without any overlap (Fig. 5), fused zone situated laterally.

*Remarks:* *Socotrapotamon* clearly belongs to the family Potamidae and not to the Potamonautidae. The main argument for this placement is the morphology of the male copulatory appendages and in particular the way the terminal tube of the second gonopod is formed. As is typical for the Potamidae, this long and thread-like terminal tube is formed by the infolded edges, which are fused without any overlapping (BRANDIS et al. 1999). In contrast, for the Potamonautidae, these edges show a clear overlapping zone. Moreover, the mandibular palp is 3-segmented with a simple terminal segment, as is characteristic for Potamidae, while in the Potamonautidae it is only 2-segmented.

Within the Potamidae, the new genus resembles *Potamiscus* Alcock, 1909 in having the terminal tube of the second gonopod laterally compressed, a feature which has so far only been found for *Potamiscus* (BRANDIS in press). The arguments not to include the species from Socotra Island within *Potamiscus*, however, are based on external morphology and in particular the subrectangular carapace, the exceptionally long and slender walking legs and the indistinct postorbital margin. Since none of the known species of *Potamiscus* share a similar suite of these characters, which are very uniform within the genus, we consider it justified to separate the species from Socotra by placing it in a separate genus.

*Etymology:* The name *Socotrapotamon* is derived from Socotra Island where the genus occurs exclusively and from *Potamon* which is the oldest generic name used for freshwater crabs. The gender is neuter as in *Potamon*.

*Socotrapotamon socotrens* (Hilgendorf, 1883)


Figs 4-10, Plate 1
Fig. 4: *Socotrapotamon socotrensis*, ♂ specimen, SMF 25276, right mandibular palp, anterior aspect.

Fig. 5: *Socotrapotamon socotrensis*, SMF 25276, Go/2, cross-section through terminal tube.


_Telphusa granosa_: Yemen, Socotra Island, 1881, E. Riebeck (don. Steindachner), NHMW 18354. — Non-type material: Yemen, Socotra Island: 1 ♂, 3 ♀♀, Wadi Daneghan, 12°36′57″N 54°03′48″E, 150 m, 27.III.1996, W. Schneider & F. Krupp, HLMD EA 39-42; 2 ♂♂, Wadi Fahuh, 12°26′46″N 54°09′35″E, 12.III.1999, M. Apel, SMF 25272; 2 ♂♂, 2 ♀♀, 2 juvs, wadi near Hadibo, 13.III.1999, N. Simões, SMF 25273; 2 ♂♂, 2 ♀♀, 1 juv, 1 damaged specimen, same data, EPC; 9 ♂♂, 8 ♀♀, 1 juv., Wadi Ayhaft, 12°36′46″N 53°59′26″E, 5.IV.1999, M. Apel, SMF 25274; 9 ♂♂, 7 ♀♀, 1 juv., same data, EPC; 6 ♂♂, 3 ♀♀, 1 juv., Wadi Ayhaft, 12°36′40″N 53°59′44″E, 5.IV.1999, M. Apel, SMF 25275; 5 ♂♂, 3 ♀♀, same data, EPC; 2 ♂♂, 2 ♀♀, same data, SMF 25276.

*Diagnosis:* Carapace almost smooth over complete surface; branchial and postorbital regions with very low transverse ridges or rows of granules. Eyes with cornea occupying about half of total length of eyestalk or less. Chelae unequal, upper surface of palm smooth or very minutely granulated; in large males fixed finger usually deflexed and cutting edges not closing in proximal half; in females fixed finger almost straight, cutting edges closing over entire length. Walking legs long and slender, second one longest. Go/1 with terminal joint evenly curved laterally (Fig. 8).
Flexible zone asymmetric with lateral part strongly elongated (Fig. 9). Subterminal joint with curved lateral margin rounded, not forming a crest and mesial margin strongly convex distally. Go/2 as long as, or slightly shorter than first with terminal tube almost straight (Fig. 10).

**Colour:** In general the colour appears to be quite variable. The colour of the dorsal face of the carapace ranges from dark orange through light brownish to a dark violet or blue (Plate 1). The lateral side is usually somewhat lighter in coloration, the ventral surface is pale yellowish or violet. The colour of chelae and walking legs ranges from a very pale yellow through bright orange to dark red or purple.

**Measurements:** CB 23.2, CL 18.6, FB 6.7, FOB 17.3, CH 10.6 (lectotype of *T. socotrensis*)

**Habitat and distribution:** *Socotrapotamon socotrensis* is endemic to Socotra where it is common in freshwater streams and wadis throughout the island from the low coastal areas in the north to the mountainous parts of the Haggier. It is usually found in shallow water or on river banks where it builds burrows.

**Remarks:** The species is well characterised by its gonopod morphology, showing no variation within the examined material. There is, however, substantial variability with regards to the external morphology and coloration. One of these variable characters is the shape of the chelae, which ranges from having an almost straight fixed finger and completely closed cutting edges to a strongly deflexed fixed finger and widely gaping cutting edges. Such variability in chela morphology, however, was only observed in male specimens and is at least partly correlated with the size of the specimen. Similar variation of chela morphology occurs for example in *Potamon mesopotamicum* Brandis, Storch & Türkay, 1998, and is not unusual within the Potamidae.

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*Socotrapotamon nojidensis* n. sp. Figs 11-14, Plates 2-4

**Holotype:** ♀, Yemen, Socotra Island, waterfall in the western part of the Nojid plane at the escarpment, 12°20.271'N 53°37.894'E, 8.IV.1999, M. Apel, SMF 25277. — **Paratypes:** Yemen, Socotra Island: 4 ♀♀, 4 ♂♂, same data as holotype, SMF 25278; 3 ♀♀, 5 ♂♂, same data as holotype, EPC.

**Diagnosis:** Branchial and postorbital regions of carapace with numerous well-developed short transverse ridges and rows of granules. Eyes with large cornea, occupying more than half the total length of eyestalk. Chelae slightly unequal, upper surface of palm finely granulated; fixed finger straight, cutting edges closing over entire length. Walking legs very slender, long, second one longest. Go/1 with elongated conical terminal joint, tip distinctly curved mesially (Fig. 12). Flexible zone very narrow without distinct extension basally, situated on collar formed by cuticular bulge of subterminal joint (Fig. 13). Subterminal joint with curved lateral margin distally forming a ventral crest that reaches base of terminal joint. Go/2 longer than first with terminal tube distinctly curved laterally (Fig. 14).


Eyes with large cornea, occupying more than half the total length of eyestalk.
Mxp 3 with deep median longitudinal sulcus on ischium; exopod with well-developed flagellum. Mandibular palp 3-segmented, terminal segment simple, undivided.

Chelipeds unequal, outer surfaces of palm, carpus and merus slightly rugose, covered with small granules. Fingers slender, slightly shorter than palm. Fixed finger not deflexed. Cutting edges of both fingers with distinct serration and rows of conical teeth. Carpus with one long spine at proximal mesial angle and a small supplementary tooth near its base. Mesioventral margin of merus with row of granules and one, rarely two, distinct teeth at proximal end; triangular prominence present between mesioventral and dorsal margins.
Pereiopods 2-5 very long and slender, P 3 longest. Merus of P 3 between 3.7 and 4.6 times as long as high. Carpus of P 2-5 with elevated median ridges on posterior face. Propodus with pair of well-developed spines at ventro-distal end and rows of small, almost indistinct spines on ventral margin. Dactylus very slender, slightly curved, about as long as propodus or longer, with four rows of acute, distally directed spines.

Abdomen 7-segmented, triangular with almost straight lateral margins. First segment short, segments 2-6 progressively longer. Seventh segment longer than sixth, margins slightly convex with rounded tip.

Go/1 sinuous, terminal joint conical with tip elongated and distinctly curved mesially (Figs 12-13). Gonopodial groove reaching the mesial margin at base of terminal joint, forming a projecting ridge in its proximal half. Flexible zone very narrow, without distinct extension basally, situated on collar formed by cuticular bulge of subterminal joint (Fig. 13). Subterminal joint with curved lateral margin distally forming a ventral crest reaching base of terminal joint (Fig. 12). Go/2 with a short flexible zone, followed by a long terminal tube distinctly curved laterally (Fig. 14). Tube laterally compressed, formed by fused lateral edges without any overlap, fusing zone situated laterally.

Colour: Dorsal surface of carapace dark greenish-brown, lateral faces light creamish, ventral side pale with light orange spotting (Plates 2-4). Chelae bright orange with white tips. Walking legs bright orange at base of ischium, greenish-brown over most of their length and with orange dactylus.

Measurements: CB 36.6, CL 30.9, FB 8.3, FOB 27.6, CH 16.8 (holotype)

Habitat and distribution: To date, the new species has only been recorded from the type locality, which is a series of waterfalls and rock pools at the base of the escarpment in the western part of the Nojid plane on the south coast of Socotra Island. The specimens were collected in shallow water (less than 1 m deep) between rocks and plants.

Etymology: The specific name nojidensis is derived from the Nojid plain in the southern part of Socotra Island, where the type locality of the species is situated.

Affinities: Even though the new species appears to be similar in outer morphology to S. socotrensis, it is clearly distinguishable from the latter by the morphology of the male copulatory appendages. In particular the terminal joint of the Go/1 differs considerably between the two species. In S. socotrensis the terminal joint is evenly curved laterally ending in a short, stout and straight tip (Figs 8-9). In S. nojidensis the terminal joint is almost straight with the distal tip elongated and distinctly curved mesially (Figs 12-13). Additionally, the flexible zone in S. socotrensis is asymmetric with the lateral part strongly elongated basally (Fig. 9), while in S. nojidensis this zone is very narrow without any basal extension (Fig. 13). A very distinct character of S. nojidensis is the presence of a prominent cuticular bulge proximally from the flexible zone, which is absent in S. socotrensis. The Go/2 also differs considerably between the species, being longer than Go/1 with a strongly curved terminal tube in S. nojidensis (Fig. 14), while it is not longer than Go/1 with an almost straight and much shorter terminal tube in S. socotrensis (Fig. 10).

DISCUSSION

As described above, it is obvious that Socotrapotamon belongs to the family Potamidae and within that family it appears to be closest to the genus Potamiscus. Thus, the freshwater crabs of Socotra show zoogeographical affinities to those of Eurasia and in particular those of the Himalayas and south-eastern Asia. The type species of Potamiscus, P. annandalii (Alcock, 1909), had been de-
New freshwater crab from Socotra Island

Plates 1-4: 1: Socotrapotamon socotrensis, dorsal aspect. 2-4: Socotrapotamon nojidensis n. sp. 2: Dorsal aspect, SMF 25277, holotype. 3: Ventral aspect, SMF 25277, holotype. 4: Dorsal aspect, paratype.

scribed from Cachar (north-east India) and a limited distribution of the genus in the eastern Himalayas was assumed (Bott 1970). The taxonomic delineation of the genus, however, was considered unsatisfactory (Ng & Naiyanetr 1993) and its exact distribution thus remained uncertain. The second author recently redefined the genus Potamiscus and, due to great similarities in the morphology of the male reproductive system, enclosed a number of species from north-western India, Burma, Thailand and Malaysia formerly placed in Dromotelphusa, Potamon, and Terrapotamon (Brandis in press).

In contrast, Socotrapotamon bears little or no resemblance to the family Potamonautidae. The freshwater crabs of Socotra thus have no affinities to the African fauna which is dominated by the Potamonautidae (Cumberlidge 1987), but is devoid of Potamidae except for Potamon algeriense Bott, 1967. The latter species, however, is restricted to north-western Africa. It presumably invaded Africa from Italy during the Messinian crisis in the late Miocene, about 5-7 million years b.p. when the Mediterranean Sea dried up (Hsiu 1972, Hsiu et al. 1973). Likewise, there is no close relationship between the Socotran freshwater crabs and those from Madagascar and the Seychelles, where the families Potamonautidae, Gecarcinucidae and Deckeniidae occur (Bott 1965, Ng et al. 1995, Cumberlidge 1996).

Interpretation of the observed affinities and reconstruction of the zoogeographical history is difficult since we lack almost any fossil record of freshwater crabs from that region. It is, however,
worthwhile to look at the geological history of the Socotran region and to compare this with the observed zoogeographical affinities.

Geologically it appears that there is a closer fit between Socotra and the Dhofar – Kuria Muria area of southern Arabia than with Somalia (Laughton 1966, Beydoun & Bichan 1970). Prior to the opening of the Gulf of Aden during the Miocene, north-east Africa, south-west Arabia and the Socotran shelf formed an Afro-Arabian land mass separated from Asia by the Tethys Sea (Swartz & Arden 1960). According to Reed (1949), the islands on the Socotran shelf were separated from the mainland of the present Arabian Peninsula in late Tertiary times. Prior to this separation, large parts of north-east Africa and the Socotran shelf had been covered by a mid-Tertiary ocean before the sea floor was uplifted again during the late Miocene (Mies 1998).

The flora of Socotra mainly dates back to the late Cretaceous and early Tertiary and thus relates to that of ecologically comparable zones in north-east Africa, Arabia, southern Africa, Madagascar and India, representing descendants of a continuous arid southern Tethys belt of Gondwana (Mies 1998). Colonisation of Socotra Island by freshwater crabs, however, most probably took place later, since the first fossil records of Potamoidea date back only to the late Miocene (Glaessner 1929, Bachmayer & Pretzmann 1971). Furthermore no close taxonomic relation to Africa, Madagascar and India are apparent, thus making a Gondwana origin of the freshwater crabs on Socotra improbable.

In the early Miocene, the Arabian Peninsula first had contact with the Asian continent, thus providing a route for the interchange of terrestrial and freshwater organisms (Briggs 1995, Neubert 1998). An invasion of Asian fauna into the Arabian Peninsula during that period was demonstrated for freshwater fishes (Krupp 1983, Krupp & Schneider 1988), as well as land and freshwater molluscs (Brown & Wright 1980, Neubert 1998) and amphibians (Balletto et al. 1986). The most probable scenario of colonisation of the Socotran island by freshwater crabs thus is immigration during the Miocene from the Asian continent via the eastern Arabian mainland, which at this time was close to Socotra and, at least for certain periods, was connected with the Socotran shelf by land bridges.

At present no freshwater crabs are known from the Arabian Peninsula and the genus Potamiscus occurs only east of the Indus river to Malaysia, but not in Iran and north-western Pakistan (Brandis in press). Socotrapotamon thus appears to be a relic of a group of potamids of Asian origin closely related to Potamiscus, which presumably inhabited south-western Arabia, Iran and northern Pakistan during the late Miocene. Provided that there are no currently undescribed species of Potamidae allied to Potamiscus still present in these regions, it appears that this group became extinct due to climatic changes during the post-Miocene periods and was partly replaced by the genus Potamon.

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REFERENCES


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Authors’ addresses:
Michael Apel, Forschungsinstitut Senckenberg, Sektion Crustacea, Senckenberangasse 25, D – 60325 Frankfurt am Main, Germany; e-mail: mapel@sng.uni-frankfurt.de

Dr. Dirk Brandis, Zoologisches Institut der Universität Heidelberg, Im Neuenheimer Feld 230, D – 69120 Heidelberg, Germany; e-mail: dirk.brandis@urz.uni-heidelberg.de