On the taxonomy and biogeography of *Potamon atkinsonianum* (Wood-Mason, 1871) and *Potamon* (*Potamon*) *emphysetum* (Alcock, 1909)

Dirk Brandis

Forschungsinstitut Senckenberg, Senckenberganlage 25, D-60325 Frankfurt a. M., Germany
Zoologisches Institut I, Universität Heidelberg, Im Neuenheimer Feld 230, D-69120 Heidelberg, Germany
E-mail: dirk.brandis@urz.uni-heidelberg.de

Abstract

The Himalayas are known to be a geologically young and dynamic mountain range hosting an endemic flora and fauna. To date, for freshwater crabs, one endemic subgenus within the genus *Potamon, Potamon (Himalayapotamon)* Pretzmann, 1966, has been described from the Himalayas. This subgenus includes two species, *Potamon atkinsonianum* (Wood-Mason, 1871) and *Potamon emphysetum* (Alcock, 1909). The taxonomic position of these two species is reconsidered. The subgenus *Himalayapotamon* is raised to generic level and its systematic and zoogeographic position is discussed. Based mainly on the morphology of the male copulatory system, *Himalayapotamon* belongs to the family Potamidae. It is more related to the Eurasian genus *Potamon* Savigny, and is distinct from the South-East Asian genus *Potamiscus* as well as from the Indian freshwater crabs of the family Gecarcinucidae. Zoogeographically *Himalayapotamon* appears to be an endemic genus related to *Potamon*, both genera presumably being isolated during the Miocene when the Gangetic waters were separated from the western Eurasian river systems. Further speciation occurred during glacial periods.

Introduction

The Himalayan mountain range is geologically comparatively young and known to be one of the most dynamic mountain chains of the world, due to the ongoing collision of the Indian subcontinent with Asia (Shroder, 1993). The Himalayas are well known to host an endemic flora and fauna (Hora, 1955; Das, 1990; Banarescu, 1992). However, for most of the fauna, and especially invertebrate freshwater species, the zoogeographical relationships and histories are poorly known at present. For the freshwater crabs, for example, there is no recent available information on their taxonomic relations to other groups or distribution patterns. According to their last revision by Bott (1970), the Himalayan species belong to the genus *Potamon* and would thereby be part of the Eurasian fauna. This classification is very doubtful, however, as shown for *Potamon edwardsi* (Wood-Mason, 1871)

and *P. andersonianum* (Wood-Mason, 1871) from the eastern Himalayas, which belong in fact to the genus *Potamiscus* (Brandis, 2000). The main problem of this group is that presently only few specimens from these regions are available in museum collections and detailed information on their distribution is lacking due to inexact locality data of the material. Since freshwater crabs are considered conservative in their distribution patterns, they might be a good indicator for paleogeographical relationships and the history of river development in the Himalayan mountain range.

The first mention of freshwater crabs from the Himalayas was by Wood-Mason (1871), who described *inter alia Thelphusa atkinsonianum* Wood-Mason, 1871. Rathbun (1904–1906) placed this species in the genus *Potamon* (*Thelphusa* Latreille, 1819 being a junior synonym of *Potamon* Savigny, 1816). Six years later Alcock (1909, 1910) redescribed the species of Wood-Mason as *Potamon* (*Potamon*) *atkinsonianum*

and established several subspecies as *P. (P.) atkinsonianum emphysetum* Alcock, 1909 or as *P. (P.) atkinsonianum ventriosum* Alcock, 1909. Since that time, the systematics of freshwater crabs has 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; Bauer 1986). Bott (1966, 1970) also placed *P. atkinsonianum* in the genus *Potamon*.

Based on these new characters and on biogeographical observations, Pretzmann (1966a,b,c) established the subgenus *Potamon (Himalayapotamon)* for *Potamon atkinsonianum* and added some new subspecies.

Current systematics of freshwater crabs is mainly based on the revisionary work of Bott (1955, 1966, 1969, 1970), and confirmed by more recent studies in that the most important character for classification of the species and genera is the morphology of the first male gonopod (Bott, 1955, 1966, 1970; Pretzmann, 1966a,b,c; Türkay, 1975; Guinot, 1979).

However, Brandis et al. (1999) considered that the morphology of the second male pleopod possessed additional taxonomic information. Consequently, the purpose of this present study is to review the systematic position of *P. atkinsonianum* by predominantly using first and second male pleopod characters.

Material and methods

Fifty specimens from Central and Eastern Nepal and adjacent regions were collected in January 2000 by the author. In addition, material from the following collections has been examined: The Natural History Museum, London (NHM); U.S. National Museum of Natural History, Washington (USNM); Forschungsinstitut Senckenberg, Frankfurt a.M. (SMF); Naturhistorisches Museum Basel and Naturhistorisches Museum, Wien (NMW). For morphological studies, first and second gonopods were separated from the pleon, fixed in 10% formalin, embedded in SPURR, sectioned with glass-knifes and stained with Richardson stain (Brandis, 2000). Additional characters, such as the morphology of the carapace and the chelipeds was examined.

The terminology used for the gonopod descriptions follows Magalhães & Türkay (1996). In that, 'mesial' is defined as the part of the gonopod directed towards the sternal centre, 'lateral' the part facing the sides of the body, 'dorsal' the side facing the sternum, and 'ventral' the side facing the abdomen.

The first gonopod is 3-segmented, the distal article is called the terminal segment (Fig. 1a,b). It is divided into the more or less conical terminal and the subterminal joint. The terminal joint can be deflected at a flexible zone (Fig. 1b), situated on the dorsal side between terminal and subterminal joint. The lateral edges of the terminal segment form a tube by overlapping, and this overlapping zone faces the ventral side (arrows in Fig. 1a).

Measurements were made to the nearest 0.1 mm by calliper. 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; carapace height (CH), measured at the highest point of the carapace. Abbreviations used: juvenile(s)=juv. (s); Altitude=Alt.

Taxonomy

Himalayapotamon Pretzmann, 1966 grat. nov. (see Figs 2–4).

Potamon (Himalayapotamon) Pretzmann, 1966a: 4; 1966b: 343; 1966c: 299.

Type species: *Thelphusa atkinsonianum* Wood-Mason, 1871 (by original designation).

Diagnosis: Carapace smooth, anterolateral margin well developed, serrated with small regular teeth, cervical grooves S-shaped, deep and well developed, connected with deep, well developed cardiac groove, but distinctly separated from postfrontal lobe. Flagellum of exopodite of third maxilliped well developed. Pleon triangular, segments well separated. Terminal segment of first male pleopod divided into short terminal joint and much longer, sinuous subterminal joint. Terminal joint more or less triangular, bearing long stiff setae. Second gonopod strongly elongated, tube in cross-section with very narrow cuticular margins.

Distribution: From Punjab (western Himalayas) to Sikkim (Eastern Himalaya).

Remarks: *Potamon atkinsonianum* and *P. emphysetum* differ in certain carapace and gonopod characters from all *Potamon* species from the Mediterranean and the Middle East.

In all *Potamon* species from the Middle East and Mediterranean Europe, the cervical groove is straight
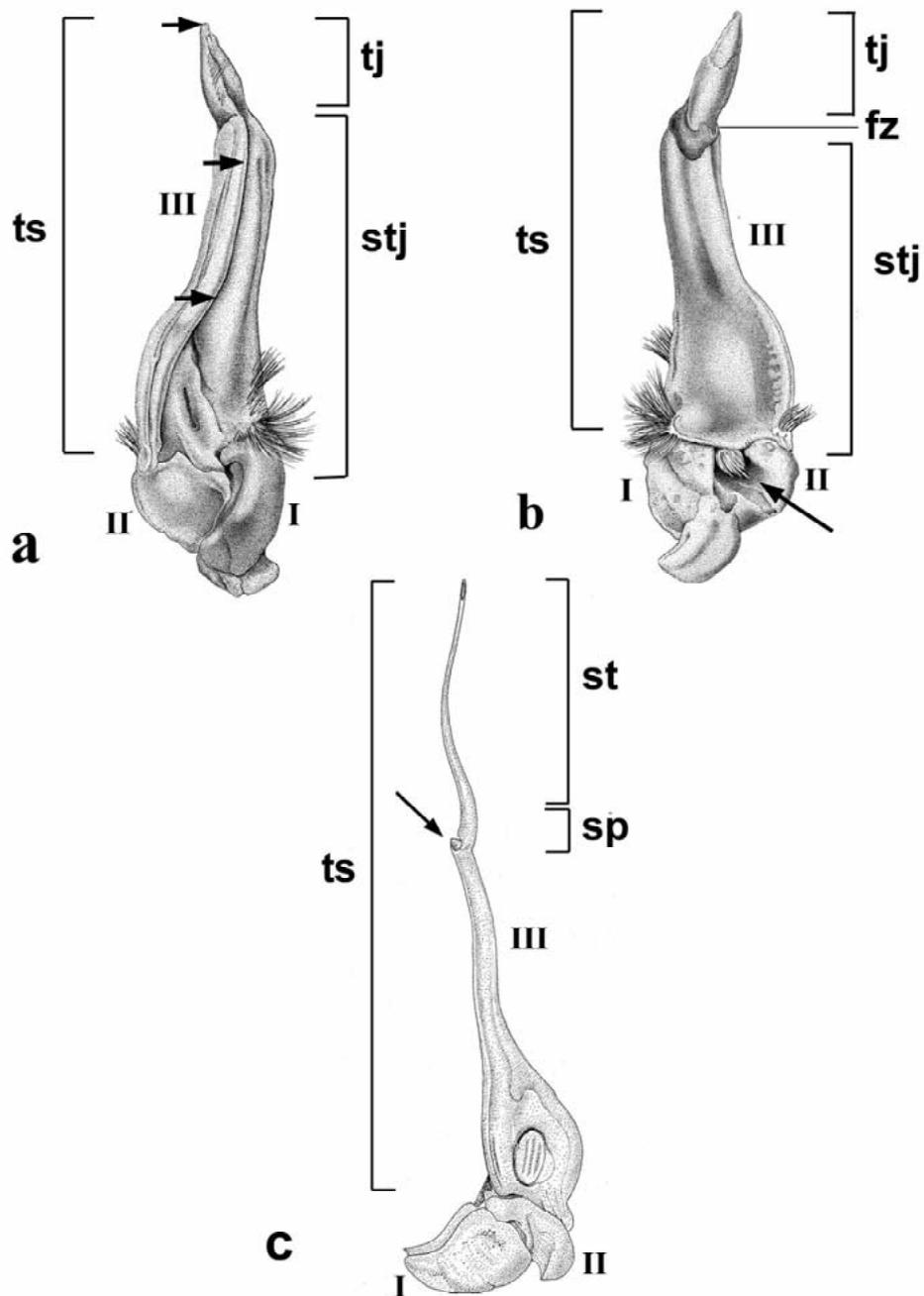
Figure 1. (a–c) Generalised morphology of potamid male gonopods 1 & 2 with explanation of morphological terms after Brandis et al., 1999: fz – flexible zone; sp – soft cuticulated part; st – sclerotized tube; stj – subterminal joint; tj – terminal joint; ts – terminal segment. I–III segments of first and second gonopod. Segment III of the gonopod 1 is divided into the more or less conical terminal – and the subterminal joint. The terminal joint can be deflected by a flexible zone (Fig. 1b), on the dorsal side between terminal and subterminal joint. The lateral edges of the terminal segment form a tube by overlapping and this overlapping zone is situated on the ventral side (arrows in Fig. 1a). (a) Gonopod 1 (ventral view) arrows in (a) indicate the overlapping zone of gonopodial groove. (b) Gonopod 1 (dorsal view) arrow indicates the insertion area for the penis. (c) Gonopod 2 arrow indicates the spoon like structure.
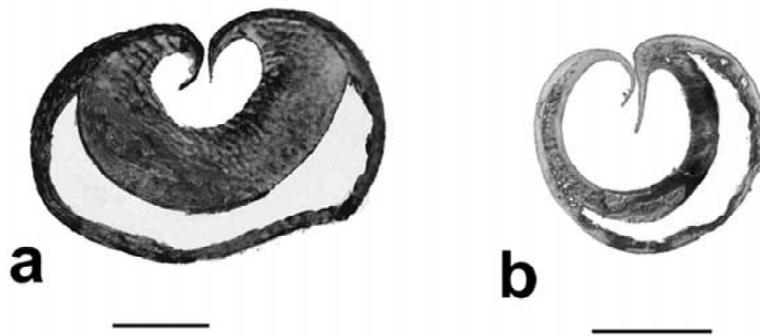
Figure 2. Transections of the terminal tube of the second gonopod. (a) *Potamon potamios* after Brandis et al., 1999, (b) *Himalayapotamon emphysetum* comb. nov. (♂ SMF 26069). Scale bar indicates 0.5 mm.

and only the frontal part is distinct and deep, becoming more indistinct in the posterior part. In *P. atkinsonianum* and *P. emphysetum*, this cervical groove is strongly S-shaped, deep in all parts and connected to the cardiac groove.

The morphology of the male copulatory apparatus differs distinctly from that of *Potamon*. The terminal joint of the first gonopod bears long, stiff setae in *P. atkinsonianum* and *P. emphysetum*, while in the *Potamon* species, the setae are short.

In all species of *Potamon*, the second gonopod has in cross-section a characteristically thickened, net-like structured cuticle, covering the base of the tube (Brandis et al., 1999). In *P. atkinsonianum* and *P. emphysetum*, this cuticle is thin and not net-like (Fig. 2).

Characters of the male copulatory apparatus and the carapace differ strongly between the species of *Potamon* and the Himalayan species, but within both groups the characters are constant (see Fig. 2a,b). Thus, the crabs from the Himalayan mountain range need to be assigned to a new genus. Pretzmann (1966a) established the subgenus *Potamon* (*Himalayapotamon*) for *P. atkinsonianum*. Therefore, *Himalayapotamon* has been given generic status to include *Himalayapotamon atkinsonianum* and *H. emphysetum*.

Himalayapotamon atkinsonianum (Wood-Mason, 1871) comb. nov. (see Fig. 3a–c).

Thelphusa atkinsonianum Wood-Mason, 1871: 205, pl. 14, Figs 12–16; Henderson, 1819: 385.

Potamon (Potamon) atkinsonianum – Rathbun, 1904: 271; Alcock, 1910: 26, pl. 10, Fig. 39; Bott, 1966: 474, text Fig. 4.

Potamon (Himalayapotamon) atkinsonianum – Pretzmann, 1966a: 4.

Potamon (Himalayapotamon) atkinsonianum janetschekii Pretzmann, 1966b: 343, Figs 1–4.

Potamon atkinsonianum – Bott, 1970: 140, pl. 37, Figs 14–15, pl. 44, Fig. 13.

Material examined: India: 1♂, 1♀ (USNM 42767) Runghee, Sikkim, India; 2♂ (NHM 1934.1.15.3-4) Runghee, Sikkim, India (exch. Indian Museum).

Nepal: 1♂ (NMW 3265) Nigale, leg. Janetschek 1♂, 6 juvs (SMF 2804) Balu Khola, Biratnagar, leg. Becker-Larssen; 1♂ (NHM 1977.242) Mabandra Gupha, Pokhara, Nepal; 1♂ (SMF 7071) Kathmandu Valley, 27° 45′ N, 085° 17′ E, Nagarjong, Nepal, Alt. 1600 m, leg. Dierl-Schacht (ex. Coll. Mus. München) IX.1967; 1♂ (SMF 5636) Chisapani Garhi SW Kathmandu, Bhainse Dobhan (tributary of Rapti river), 27° 34′ N, 085° 08′ E, 16–20. 07.1967, leg. Dierl Schacht ex. Coll. Museum München); 1♂ (SMF 24727) Nepal, Uyam, Juwa Khola, before mouth into Kabeli Khola (28° 09′ N, 084° 02′ E), 1400 m, 31.08.1983, leg. J. Martens; 4♂♂, 1♀, 4 juvs (SMF 26063) Pushre Khola, Chorepatan, Pokhara, Kaski district, Gandaki province, Western Region, 28° 11.114′ N, 083° 57.466′ E, Alt. 730 m, 9.01.00, leg Brandis and Sharma; 5♂♂, 1♀, 7 juvs (SMF 26059) Yamdi Khola, Hyanja, near Pokhara, Kaski district, Gandaki province, Western Region, 28° 15.360′ N 083° 57.676′ E, Alt. 970 m, 8.01.00, leg. Brandis and Sharma; 2♂♂ (SMF 26068) Yamdi Khola, Hyanja, near Pokhara, Kaski district, Gandaki province, Western Region, 28° 15.360′ N, 083° 57.676′ E, 30.03.99, leg. Sanjai; 2♂♂, 2♀, 2 juvs (SMF 26061) Sediya Khola, Sedi, Pokhara, Kaski district, Gandaki province, Western Region, 28° 13.449′ N 083° 57.121′ E, Alt. 912 m, 8.01.00, leg. Brandis and Sharma; 1♂ (juv.), 1♀ (SMF 26065) Biche Khola, Goda, Ilam, Ilam district, Mechi Province, Eastern Region. 18.01.00, leg. Brandis and
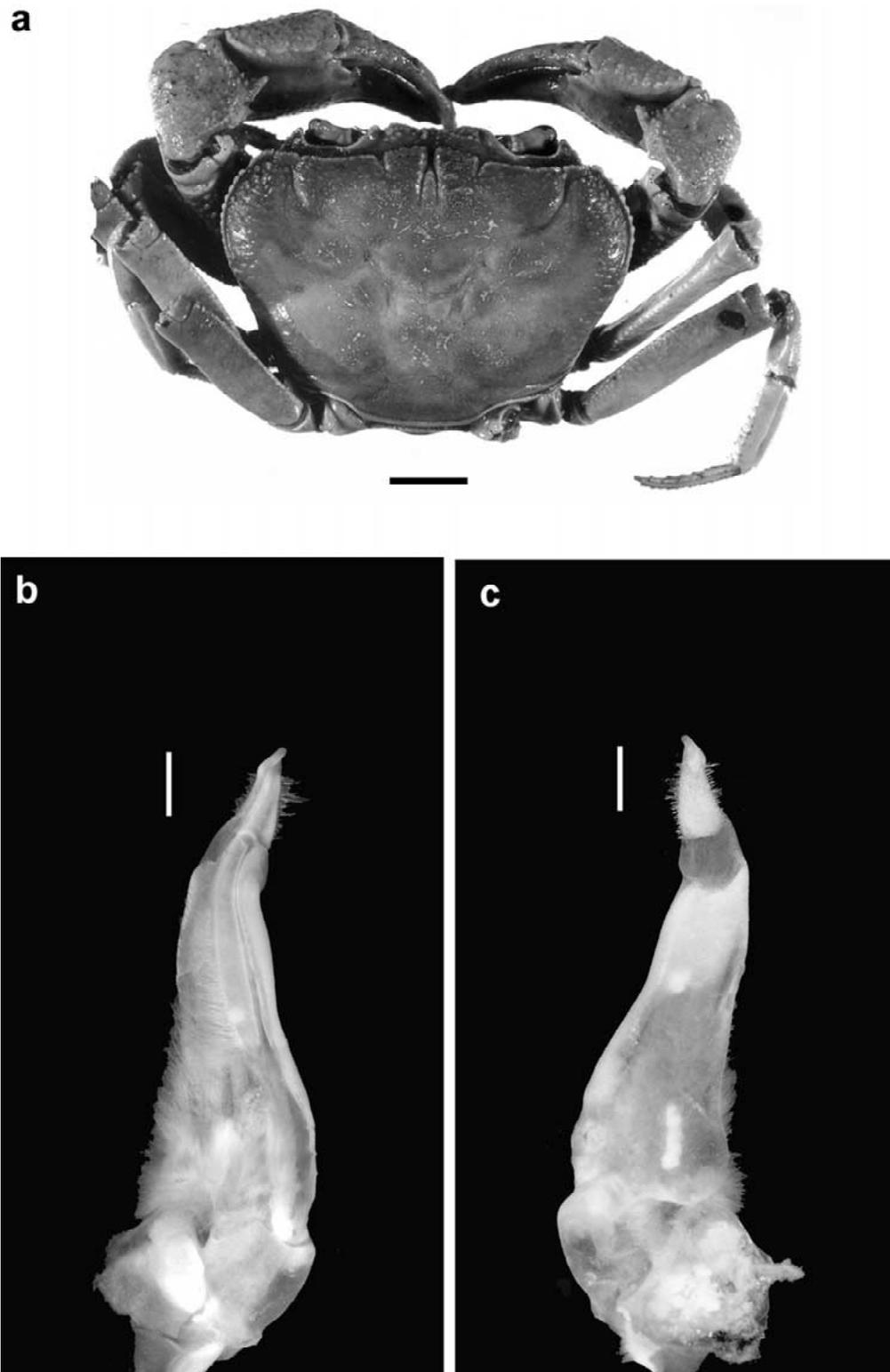
Figure 3. (a–c) *H. atkinsonianum* comb. nov.: Habitus and Gonopod 1 (♂ SMF 2804). (a) Habitus, dorsal. Scale bar indicates 1 cm. (b) Gonopod 1, ventral view. (c) Gonopod 1, dorsal view. Scale bars in (b, c) indicate 1 mm.
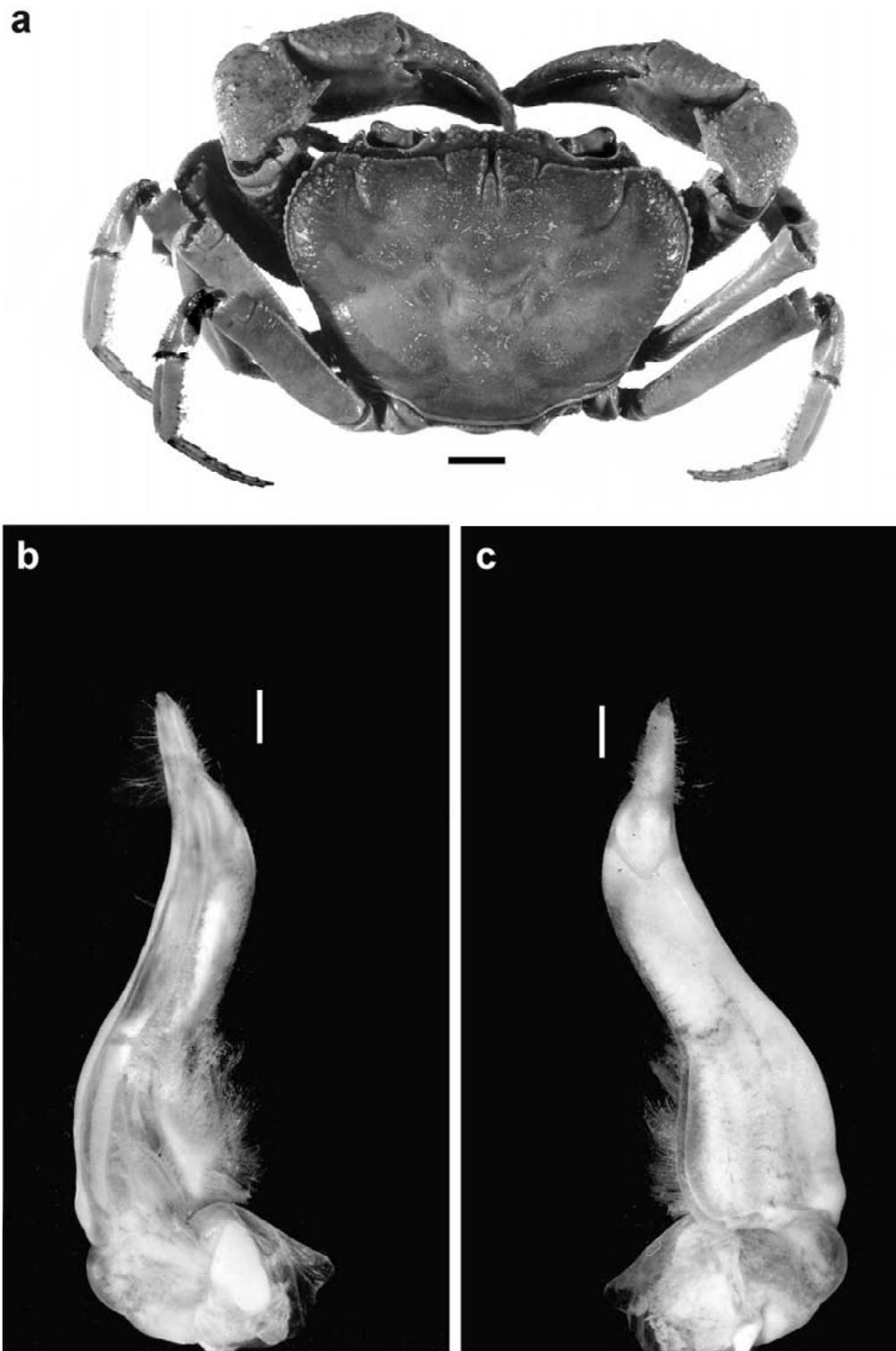
Figure 4. (a–c) *H. emphysetum* comb. nov.: Habitus and Gonopod 1 (♂ SMF 1762). (a) Habitus, dorsal. Scale bar indicates 1 cm. (b) Gonopod 1, ventral view. (c) Gonopod 1, dorsal view. Scale bars in b, c indicate 1 mm.

Sharma; 1♂, 1♀, 1 juv. (SMF 26067) right tributary to Mai Khola before bridge, Ilam, Ilam district, Mechi Province, Eastern Region. Alt. 500–700 m. 18.01.00, leg. Brandis and Sharma.

Diagnosis: Terminal joint of first male gonopod S-shaped, terminal tip dorsally elongated, crossing over ventral part, forming spoon-like structure; flexible zone distinctly asymmetric, mesially strongly elongated; subterminal joint sinuous, mesial margin well developed.

Type locality: Darjeeling.

Distribution: Sikkim, Darjeeling, eastern Nepal from 200 m upto 2000 m, central Nepal (distribution area ends west of Katmandu).

Measurements: CB: 40.2 CL: 30.7 FB: 12.8 CH:15.4 (male SMF 2804).

Remarks: The species is characterised by its gonopod morphology which showed no variation within the examined material. Distinct characters of the first gonopod are the asymmetric flexible zone and the S-shaped terminal joint with the crossed tip.

Previously, there was confusion about the taxonomy and the distribution of this species.

H. atkinsonianum was originally described as *Thelphusa atkinsoniana* by Wood-Mason (1871) based on material from Darjeeling and the so called Thankot Hills, Nepal (Thankot 27° 41′ N, 85° 11′ E, West of Katmandu). The species was mainly characterised by features of the carapace and the chelipeds.

Wood-Mason explicitly explained that the description was based on a specimen collected by Dr Stolizcka. The material from Thankot hills was, according to Alcock (1910), captured by a museum collector. Alcock (1910) listed only one sample donated by Stoliczka from Darjeeling. Even though Alcock (1910) labelled some specimens from Sikkim as probable types collected by Atkinson, this material was not mentioned by Wood-Mason and consequently it can not be type material. Therefore, Darjeeling is probably the type locality.

Rathbun (1904) assigned the species to the genus *Potamon* Savigny because *Thelphusa* Latreille, 1819 is a junior synonym of *Potamon* Savigny, 1816. Alcock (1909, 1910), and Kemp (1913, 1923) kept the species in *Potamon*, as did Bott (1966, 1970). Additionally, Alcock introduced several subspecies for *P. atkinsonianum*. From the Kumaon region (=Kumaun 29° 50′ N 79° 30′ E in Uttar Pradesh), he described *P. atkinsonianum ventriosum* Alcock, 1909 and from Punjab *P. atkinsonianum emphysetum*. As shown below, both

subspecies do not belong to *H. atkinsonianum* and are assigned to a separate species.

Bott (1966, 1970) followed Rathbun in the general classification of *P. atkinsonianum* and first described the male gonopods. Pretzmann (1966a) established a new subgenus *Himalayapotamon* for this species. Following Bott (1966, 1970) in using the first male gonopods for classification, Pretzmann (1966a,b,c) established two new subspecies: *Potamon (Himalayapotamon) atkinsonianum gordoni* and *Potamon (Himalayapotamon) atkinsonianum janetschekii*. However, the description of *P. janetschekii* was based mainly on characters of the carapace. According to Pretzmann (1966a,b,c), the main characters of this subspecies are the shorter and less curved anterolateral margin, the stronger bilobed frontal margin, the stronger projecting epigastrical lobes and the indistinct sculpture of the carapace. Additionally, the pleon has straight lateral margins, the seventh abdominal segment is broader than long and the sixth segment half as long as broad.

The re-examination of the type specimen of *P. (H.) janetschekii* shows that the morphology of the first gonopod is congruent to that of the nominate *H. atkinsonianum* from eastern Nepal and Darjeeling. The dorsally elongated tip, which crosses over the ventral part, forming a spoon-like structure, is characteristic. The comparison of the carapace and pleon structures described by Pretzmann with the specimens examined from Nepal and Darjeeling shows no special characters for the specimen from Nigale. There is, however, variability regarding the outer morphology and sculpture in all examined specimens. No population from Nepal or Darjeeling can be characterised by distinct carapace characters.

The anterolateral margin is variably curved and differs in length.

The sculpture of the carapace varies strongly in the examined specimens, ranging from roughly sculpturated specimens with deep grooves to specimens with smooth surfaces and indistinct grooves. This variability can be observed in single populations e.g. from Yamdi Khola, and thus has no taxonomic value.

The pleon has more or less straight margins and the sixth and seventh segment show no differences wthin all the examined material.

This means that characteristic morphologic differences of *P. (H.) atkinsonianum janetschekii* cannot be observed in comparison to the samples of *H. atkinsonianum*, and therefore this subspecies is synonymised with *H. atkinsonianum*.

Himalayapotamon emphysetum (Alcock, 1909) comb. nov. (see Fig. 4a–c).

Potamon (*Potamon*) *atkinsonianum* var. *emphysetum* Alcock, 1909: 243; 1910: 29, pl. 1, Fig. 2.

Potamon (*Potamon*) *atkinsonianum* var. *ventriosum* Alcock, 1909: 244; 1910: 29.

Potamon (*Himalayapotamon*) *atkinsonianum gordoni* Pretzmann, 1966a: 5; 1966c: 299, pl. 1, Figs. 1–4.

Potamon (*Potamon*) *emphysetum* – Bott, 1966: 472, Fig. 3.

Potamon emphysetum – Bott, 1970: 141, pl. 37, Fig. 17; pl. 44, Fig. 15.

Material examined: India: 1♂, 1♀ (SMF 1762) Dharampur near Simla, exch. Zoological Survey of India; 1♂ (NHM 1996.1407), Nepal, N-India, leg. J.J. Murray esq.

Nepal: 1♂ (NHM 1971.308) Silatpati, Sarda Khola, 3500 ft, Nepal, IX.1952, leg. L.A.P. Williams (Holotype of *Potamon* (*Himalayapotamon*) *atkinsonianum gordoni* Pretzmann, 1966); 5♂♂, 3♀♀, 10 juvs (SMF 26074) Dhadama Khola, Jarepipal, Palpa, Palpa district, Lumbini Province, Western Region, 27° 48.741′ N, 083° 31.433′ E, Alt. 764 m, 10.01.00, leg. Brandis & Sharma; 3♂♂, 16♀♀, 24 juvs (SMF 26069) Chundi Khola, Tanahu near Dumre, Tanahu district, Gandaki Province, Western Region, 27° 57.559′ N, 084° 24.891′ E, Alt. 450 m, 7.01.2000, leg. Brandis & Sharma; 2♂♂, 2 juvs ♂♂, 2♀♀ (SMF 26080) Daune Khola, Daune, Nawalparasi district, Lumbini province, Central region, 27° 33.336′ N, 083° 50.523′ E, Alt. 500 m, 27.01.00, leg. Brandis & Sharma; 1 juv. (SMF 26071) Phusre Khola (tributary of Buldi Khola) Ranigaon, Tanahu, Tanahu district, Gandaki Province, Western Region, 27° 59.409′ N, 084° 16.727′ E, Alt. 435 m, 7.01.00, leg. Brandis & Sharma; 1♂, 1♀ (SMF 26073) Tinau Khola at Phalebas, Palpa district, Lumbini Province, Western Region, 27° 48.894′ N, 083° 32.019′ E, Alt. 615 m., 10.01.00, leg. Brandis & Sharma; 1♂, 2 juvs (SMF 26072) Armadi Khola, Waling, Syangja district, Gandaki province, Western Region, 27° 59.625′ N, 083° 46.758′ E, Alt. 618 m, 9.01.00, leg. Brandis & Sharma; 4♂♂, 4♀♀, 17 juvs (SMF 26078) right tributary of Jugedi Khola, Jugedi, Chitawan, Makawanpur district, Narayani province, Central region, 27° 46.024′ N, 084° 28.182′ E, Alt. 285 m, 26.01.00, leg. Brandis & Sharma; 3♂, 1♀, 2 juvs (SMF 26076) Bhut Khola at Bhut Pul, Palpa, Palpa district, Lumbini Province, Western Region, 27° 44.743′ N, 083° 28.508′ E, Alt. 840 m (origin from Siwalik hills), 10.01.00, leg. Brandis & Sharma; 5♂♂, 1♀ (SMF 26077) Samari Khola, Samari bridge, Hetauda, Makawanpur district, Narayani province, Central region, 27° 27.383′ N, 08502.55′ E, Alt. 474 m, 25.1.00, leg. Brandis & Sharma.

Diagnosis: Terminal joint of first gonopod elongately triangular in shape, lateral margins straight, bearing long stiff setae; flexible zone elongated, V-shaped; subterminal joint sinuous, broadened, mesial margin well developed, broad.

Type locality: Bilaspur or Kangra, Punjab.

Distribution: Northwestern India, Punjab, Himachal Pradesh, western to central Nepal.

Measurements: CB: 57.2 CL: 48.8 FB: 13.6 CH: 23.6 (male SMF 1762).

Remarks: *Himalayapotamon emphysetum* is a species distinguishable from *H. atkinsonianum* by the morphology of the first male gonopod. The terminal joint of the first gonopod in *H. atkinsonianum* is S-shaped and has a distal tip where the elongated dorsal part crosses the ventral one, while the flexible zone is asymmetric. In *H. emphysetum*, the terminal joint is triangular with a normal shaped tip, while the flexible zone is V-shaped. *H. emphysetum* was originally described by Alcock (1909) as a new subspecies of *P. atkinsonianum* for specimens from Punjab due to "the very strong convexity of the antero-lateral and concomitant strong convergence of the postero-lateral borders". Additionally, Alcock (1909) designated a second subspecies, *Potamon* (*Potamon*) *atkinsonianum ventriosum* for one specimen from Sanesvar, Kumaon (=Kumaun 29° 50′ N, 79° 30′ E in Uttar Pradesh). The examination of material from Punjab and the comparison with the figures of Alcock (1909) shows that the populations from Punjab are morphologically identical with the nominate *H. emphysetum*. Therefore, both subspecies are synonymised with *H. emphysetum*.

Bott (1966) examined the first male gonopod morphology of *H. atkinsonianum* and *Potamon* (*Potamon*) *atkinsonianum emphysetum* characteristically different and consequently he gave the latter specific status. After the re-examination of the type of a new subspecies, *Potamon* (*Himalayapotamon*) *atkinsonianum gordoni*, Pretzmann (1966a), Bott (1970) assumed, *H. emphysetum* was only a subspecies or variation of *H. atkinsonianum*. Pretzmann (1966a) characterized this subspecies mainly by features of the carapace, the shaping of pleon and the length of the legs. According to Pretzmann (1966a), *P.* (*H.*) *gordoni* has a more curved carapace than the nominate *H. atkin-*

sonianum, the anterolateral margin is very short, the pleon has slightly concave margins and 6th abdominal segment is nearly quadrangular. The walking legs are more elongate than in *H. atkinsonianum*. The re-examination of the type specimen shows that the determination of Pretzmann (1966a) was wrong. The morphology of the first gonopod is identical with that of *H. emphysetum* from Punjab and western Nepal. Thus the specimens from Silatpati, Sarda river belong to *H. emphysetum*.

For *H. atkinsonianum*, there is a variability regarding outer morphology and sculpture within populations of Himalayan crabs. This applies also for populations of *H. emphysetum*, especially the anterolateral margins varies in curvation and length as well as the distinctness of sculpturation. The pleon shape shows no distinct variability in the examined material and there is no variation regarding the length of walking legs. These characters, however, do not allow a separation of the material from Sarda Khola and the subspecies *P. (H.) gordoni*, therefore, is synonymised with *H. emphysetum*.

Discussion

Himalayapotamon now belongs to the Potamidae and within that family it appears closest to the genus *Potamon*. *Himalayapotamon* is separable from *Potamon* mainly by features of the male copulatory apparatus, but also by the general structure of the carapace. Zoogeographically, the genus *Himalayapotamon* shows affinities to the Near East and the Mediterranean, being presumably related to the genus *Potamon*. The freshwater crab fauna of the central and western Himalayas thus shows affinities to Europe, while the eastern Himalayas have more affinities to Southeast Asia, where the genus *Potamiscus* is dominant (Brandis, 2000).

The general distribution pattern of the freshwater crabs corresponds well to the general biogeographic model on the Himalayas (see Fig. 5).

The major biogeographic division in the Himalayas is between an Eastern humid tropical fauna, derived from Indo-Chinese/Malaysian area and a western steppe fauna, derived from Ethiopian/Mediterranean area (Mani, 1974). According to Mani (1974), the boundary coincides precisely with the Sutlej gorge. Such a tropical fauna is represented in freshwater crabs by the genus *Potamiscus* with *P. koolooensis* occurring in the region of Simla (Brandis, 2000). The

distribution of this species ends in the region of Sutleij river (Brandis, 2000). On the other hand, the Mediterranean fauna in the western Himalayas is represented by the subgenus *Potamon* (*Centropotamon*) occurring in Iran, Afghanistan and the right tributaries of the Indus river (Brandis et al., 2000). *Himalayapotamon*, however, is restricted to the western and central Himalayas and thereby endemic to this region. The distribution pattern of the two known species of *Himalayapotamon* is also interesting with one species occurring mainly in the western part and another one occurring in the East (see Fig. 5).

Interpretation of the observed affinities and reconstruction of the zoogeographical history is difficult since almost any fossil record of freshwater crabs is lacking from the region. It is, however, worthwhile reviewing at the geological history of the rivers of the Himalayan region and to compare this with the observed zoogeographical affinities.

Geologically, it appears that some of the larger Himalayan rivers like the Indus, Brahmaputra and Ganges existed before the final elevation of the Himalayan mountains (Das, 1990; Shroder, 1993).

The regions of the present Himalayas range originally formed the bottom of the Tethys Sea, which separated the northern continent Laurasia from the southern continent Gondwana during the late Palaeozoic (Hall, 1998). About 80 million years BP, the southern continent broke and several parts started moving north, including India (Sinha, 1992). The initial mountain building process started about seventy million years ago during the Upper Cretaceous period, when the two land masses began to collide with each other. As a result, the already shallow seabed rapidly folded and was raised into longitudinal ridges and valleys.

About 65 m.y.a. (Upper Eocene Period), came the second phase of mountain building. The bed of the Tethys started rising again. The Northeastern part of the Tethys Sea retreated, and the ground changed into shallow lagoons and further into brackish water and freshwater lakes. Gradually this land-form changed by the ongoing elevation into a marshland, which allowed a faunal exchange (Sinha, 1992).

This process finally lead to the folding of the Himalayas. The main elevation took place during the Miocene and the early Pliocene when the marshlands were elevated into high mountain ranges (Dewey & Bird, 1970). At about 25 m.y.a. (Middle Miocene Period) came a special mountain building period which led to the formation of the low Sivalik ranges. After this, periodic mountain building phases occurred during the
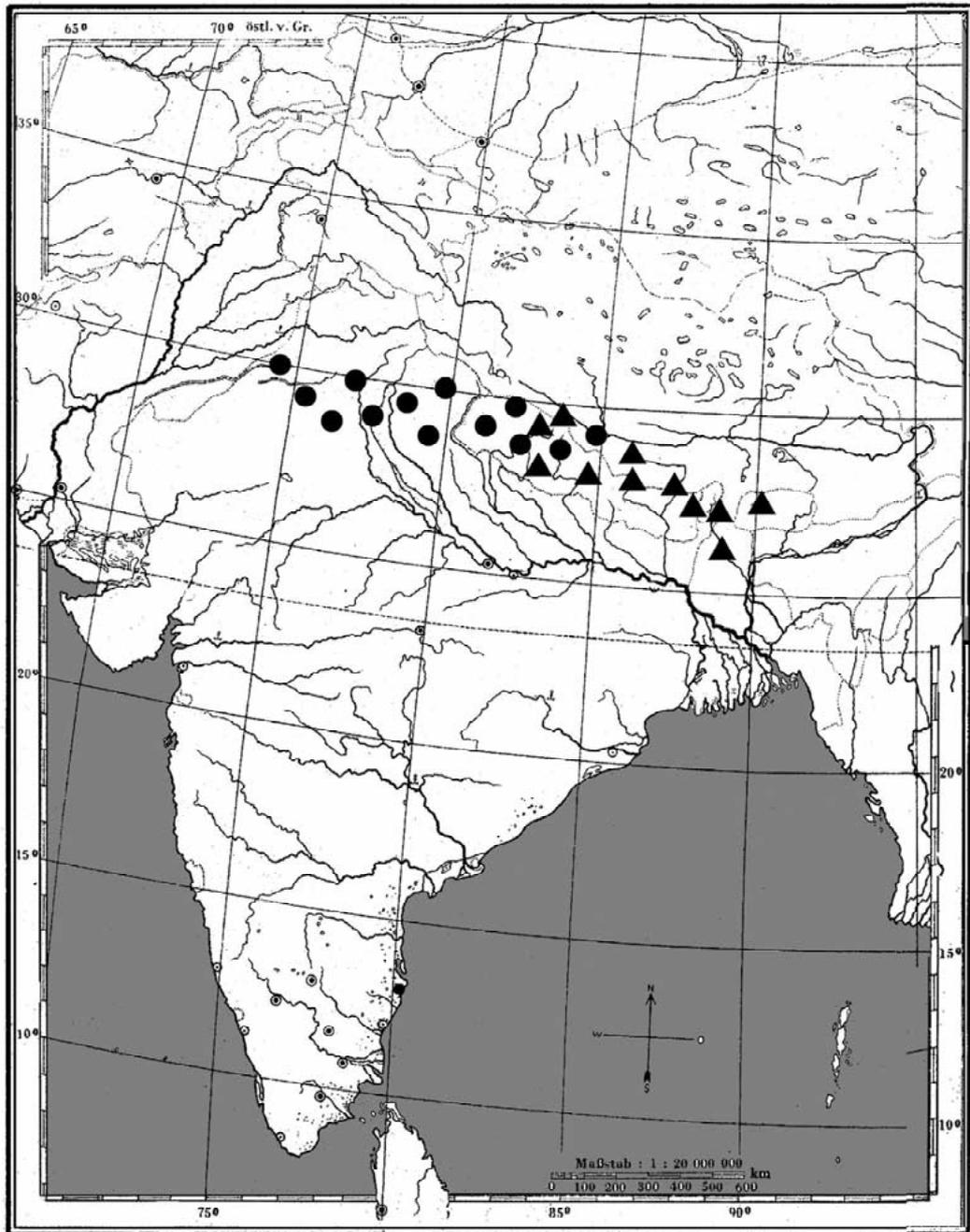
Figure 5. Distribution map of the genus *Himalayapotamon*, with indication of species distribution. The map includes India and the adjacent areas. ▲ – *H. atkinsonianum*; ● – *H. emphysetum*.

ongoing collision of the Indian plate with the Eurasian plates which led to the Himalayan ranges rising further. The last major phase occurred 600 000 years ago and is still ongoing. This means that the Himalayas is still rising and tectonically unstable.

Due to the ongoing tectonic activity of the Himalayan region, the understanding of the direction and currency of the river systems is complicated. Presently, four groups of rivers can generally be characterized (Seeber & Gornitz, 1983; Shroder, 1993):

1. One group of rivers existed before the elevation of the mountains. Such types of rivers are presumably the Indus-river, and the Ganges-Brahmaputra. For this theory the most striking fact is that these rivers rise near each other in the slopes of Mount Kailas in Tibet, 100–150 km north of the main Himalaya watershed. The Indus and Brahmaputra, after flowing parallel to the range in opposite directions along the rather straight watershed boundary for over 1000 km, both turn abruptly through it and escape southward (Shroder, 1993). The other odd fact is that most of the remaining larger rivers of the Himalayas start at the north of highest peaks and cut deep and narrow transverse gorges south through the range. According to Shroder (1993), both rivers originated when the Tethys Sea receded and an isthmus grew in its place. Both rivers eroded the ground faster than the mountains elevated and this resulted in deep valleys, which conserved their original course.

2. Another group of rivers is younger than the folding of the mountains and these formed valleys crosswise to the mountain range. They rise from the highest northern peaks.

3. A third group originated when active headwaters of early rivers cut down through drainage divides to capture parts of other rivers.

4. A fourth group was formed by periodic damming by ice, slope capture or faulting caused ponding and eventual overflow through low passes in different directions.

Due to the present distribution pattern of *Himalayapotamon* including more or less the tributaries of Ganges river, it is most important to understand the history of this river system.

The Ganges, Indus and Brahmaputra rise on the slopes of Mt. Kailas (6714 m) in the Gangdise range of Tibet (Allen, 1985). Two melting glaciers meet in the mountain village of Devaprayag to form river Ganges. From this confluence point, quite near the border of Tibet, the Ganges flows southwards to Rishikesh, and then travels hundreds of miles to eventually end up in the Indian Ocean at the Bay of Bengal. The Ganges presumably originated by the diversion of a large Proto-Indus river (Beck & Burbank, 1990).

According to Beck & Burbank (1990), a large sandy river similar to the modern Indus debouched from the mountain front at the same longitude as the modern river and flowed southwards towards the Arabian Sea from at least 13.5–11.5 m.y.a. Enhanced subsidence of the Gangetic foredeep, owing to accelerated loading by the Himalayas at 11 m.y.a. (Middle Miocene), seems it have diverted this large, south flowing Indus-like river eastwards into the Gangetic system and the Bay of Bengal (Beck & Burbank, 1990). This separation isolated the river-systems draining into the Ganges-system from the more western draining Indus tributaries. In consequence, the fauna of the Ganges system and the connected tributaries was isolated from the more western river systems and due to an increasing aridization during the Miocene, faunal exchange became problematic. This means that the separation of the Ganges system also isolated the freshwater fauna from the western river systems. This is very important for the understanding of freshwater crab history, since the first fossil records of Potamoidea date back only to the Miocene (Szombathy, 1916; Glaessner, 1928, 1929; Bachmayer & Pretzmann, 1971). The separation of one eastern and one western species dates most presumably back to the quaternary, when organisms were restricted to refugial centres during glacial periods. *Himalayapotamon atkinsonianum* and *H. emphysetum* reflect this situation; presently they are expanding from the old refugial centres, meeting finally in the region west of Kathmandu (see Fig. 5). Thus, it is probable that in the eastern part of central Himalayas and in the western part two refugial centres for freshwater organisms existed, leading to speciation in this region.

Acknowledgements

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