Fossil brachyuran crabs from the Jambusan Caves (Bau, Sarawak), collected by A.H. Everett in 1878-1879

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Crustacean subfossils from the Jambusan Caves in Bau (Sarawak), collected by the late A.H. Everett are assigned to two relatively large species of potamid freshwater crabs (Brachyura) that are still extant in the area, viz. *Isolapotamon bauense* Ng, 1987 and *I. consobrinum* (De Man, 1899). While *I. bauense* is known to occur naturally in the caves, *I. consobrinum* is a primarily riverine species. On the basis of the available archaeological evidence, the two species were probably collected for food by early human inhabitants of Sarawak. Characters that are useful to identify the chelae and fingers of Bornean freshwater crabs are also discussed.

Contents

Introduction

The palaeontological collections (Quaternary Mammals) of The Natural History Museum in London hold a mixed assemblage of animal remains identified on accompanying cards and paper slips as the zoological collections obtained 'from Borneo caves' by Alfred Hart Everett in 1878-1879. The lot numbers under which the specimens are boxed correspond with those appearing in Everett's published list (Everett *in* Evans *et al.*, 1879) and reports of his fieldwork and the finds authenticate their origin (Anonymous, 1879; Everett *et al.*, 1880). During 2003-2011, this collection was preliminarily catalogued with mammal specimens entered on the palaeontology register (M series). The remains of vertebrates of other classes and animals of other phyla were labelled with reference to Everett's listed lots (thus: Ev26.01, 02 ... denotes lot #26, items 1, 2 etc.), and entered with the mammal specimens in a common inventory (see Cranbrook, 2013). These non-mammalian specimens include subfossil parts of freshwater crabs that form the basis of the present note.

The caves investigated by Everett occur in the limestone-rich Bau area of western Sarawak, about 25 km southwest of the town of Kuching (Wilford, 1964). Everett undertook what he termed 'partial excavations' in 12 caves in this area. In four instances (Caves V, XIII, XXI and XXIII), he found 'a regular series of deposits', characteristically consisting of four stratigraphic elements. All the crab remains reported below stem from Cave V. The biodiversity of Bau was surveyed in recent years (see Yong *et al.*, 2004), including freshwater decapod crustaceans (Ng & Grinang, 2004; see also Ng, 1987, 1989a, b; Ng & Tan, 1998).

Specimens examined are held in The Natural History Museum (NHM), London, UK and Zoological Reference Collection (ZRC) of the Raffles Museum of Biodiversity Research, National University of Singapore. As to comparative material of the various Sarawak crabs used in this study from the ZRC and Sarawak Museum (Kuching), these have previously been listed in Ng (1987), Ng & Tan (1998) and Ng & Grinang (2004), and these data are not repeated here. Measurements of the fragments are of the maximum length (ML) (in millimetres). Carapace measurements of extant specimens, in millimetres, are of carapace width and length, respectively.

Everett's Cave V and his excavations

Cave V was the first in which Everett noted stratified deposits. Information on the first stage of his excavation of Cave V has been lost, with his first report. The opening narrative of his second quarterly report picks up in the middle of his investigation of this cave: 'As mentioned in my first Report, I was still occupied at the date of its despatch in the examination of this cave' [Everett *in* Evans *et al.*, 1879, p. 150]. 'Excavation B was continued across the low-level chamber to its left-hand wall, where the earth attained a thickness of about 5 feet [1.5 m]. The contents preserved the character already noted throughout, and they yielded no sign of organic remains of any kind whatever. Excavation C, situated half-way up the steep entrance talus was carried to a depth of 4 feet only. The contents were washed … with the result that a few bones of bats and small rodents, together with the abundance of the usual land and fresh-water snails were met with; but nothing to warrant an extended working until the remains sent from the D excavation shall have been examined and reported upon.' In his final report, Everett described the 'talus' or second stratigraphic layer of this cave as rising to a summit 'nearly 50 feet above the floor of the cave'. This deposit was rich in archaeological

Table 1. Summary of Everett's notes on excavation sites

Lot	Everett's published notes	Reg. no	Item
18	Teeth, &c. Cave V. Excavation D. Found about 18 inches below the surface	Ev 18.02	Crab: partial chela
30	Miscellaneous bones, jaw of rodent &c. Excavation D, Cave V. Nearly 3 feet below the surface.	Ev 30.07	Crab: broken chela
74	Various teeth. Cave V. Excavation D.	Ev 74.02	Crab: broken chela
76	Vertebrae, chelae of crustacea, fish scales, &c. Cave V. Excavation D.	Ev 76.16	Crab: 6 chelae
82	Miscellaneous remains. Cave V. Excavation D.	Ev 82.19	Crab: 4 chelae

remains, providing 29 lots in Everett's report, about a quarter of the total list. Crab remains consisted of detached, and often fragmentary chelae, from six lots (Table 1).

It is clear from the reports of Everett's work (Evans *et al.*, 1879; Everett *et al.*, 1880) that the huge volume of freshwater shells (listed by Everett as *Potamides*), all recognized human remains and all artifacts, including a large number of potsherds, were either discarded on site by Everett or, after receipt in London; and subsequently diverted to others for study. The NHM collection therefore consists only of residual land molluscs and remains of other animal classes. Moreover, as Cranbrook (2013) showed, Everett was selective in his choice of vertebrate remains that he recovered by wet-sieving. There may therefore be bias in the composition of the associated fauna that formed the NHM collection. The present contents are shown semi-diagrammatically in Table 2, in which the frequency of specimens of each category is indicated by the size of the filled circle.

Numerically predominant are the cranial elements of naturally occurring speliobionts, notably fruit bats (Pteropodidae) and large roundleaf horseshoe bats (Hipposideridae, cf. *Hipposideros diadema*). Other vertebrates that naturally frequent caves are also present, including, among mammals, rats and porcupines, although the latter may represent the quarry of human hunters. Most of the bird remains recognized are identifiable as cave swiftlets (Collocaliinae, cf. *Aerodramus* sp.). However, monkey remains (Cercopithecidae, cf. *Macaca* sp.), teeth of tapir (Tapiridae, *Tapirus indicus*), bearded pig (Suidae, *Sus barbatus*) and sambar deer (Cervidae, *Rusa unicolor*) provide certain evidence of casual use of the cave by human hunters. Also likely to have been consumed

Table 2. Associated fauna in Everett's excavation site (Cave V).

	Cave													
Lot	Stratum	Monkey	Civet	Tapir	Deer	Pig	Rat	Squirrel	Porcupine	Bat	Bird	Varanus	Turtle	Snake
20	Surface of inner talus									●	•			
21	Surface of inner talus									●	•			
26	Cave-earth of Excavation B	•		•					•	•			•	•
27	Upper part of the deposit in Excavation D						•			•	•	•	•	
24	Excavation D. Uppermost foot-level of the deposit	•												
74	Excavation D							•						•
75	Excavation D													
76	Excavation D											•		•
82	Excavation D	•	•			•	•			•	•		•	•
18	Excavation D. About 18 inches below the surface	•									•			
19	Excavation D. About 2 inches below the surface						•			●				
22	Excavation D. About 2 inches below the surface					•				•				
23	Excavation D. About 2 inches below the surface									•				
28	Excavation D. About 2 inches below the surface									•	•		•	
37	Excavation D. Between 2 to 3 feet below the surface						•		•	•	•			
30	Excavation D. Nearly feet below the surface						●			●	•	•	•	
X	Excavation D. 3 feet below the surface						•							
46	Excavation E						•	•		●				
86	Excavation G				•					●				
87	Excavation G						•			●			•	
98	Excavation G					•	•			•	•			

by people in the cave are the remains of tortoises or terrapins, and monitor lizard (Varanidae, *Varanus* sp.). That human visitors exploited the aquatic environment is confirmed by the presence of fish bones.

Everett's Cave V has not been re-investigated archaeologically, but later excavations have been conducted in his cave XIII, known as Gua Tupak, by Gani *et al.* (2009). Their preliminary report provided illustrations and a description of the soil profile of the cave that matched Everett's summary of the stratification. Of the excavated materials (bulked), 65 per cent by weight consisted of 15,216 riverine gastropod shells including the thiarids *Thiara variabilis* and *Melanoides tuberculata*, and pachychilids *Brotia episcopalis* and *B. costula* concentrated at depths of 3-60 cm (1-2 feet). This record therefore established without doubt that Tupak had been occupied by people who depended heavily on the freshwater environment; non-molluscan animal remains comprised 7,332 pieces, mainly fragmented bat bones, mostly found at levels 60-80 cm in trench A, i.e., corresponding to Everett's Stratum 3. Radiocarbon dates obtained from charcoal samples gave calibrated ages of AD 1480-1680 for trench A, layer 4, 30-40 cm, and AD 1650-1890 for trench B, layer 4, 50-60 cm. This deposit therefore reflected human activity of the historic period.

Similar dates are likely to be reflected in the material from Cave V. Although the tapir is now extinct in Borneo, Cranbrook & Piper (2013) noted that this large mammal certainly survived into the nineteenth and even into the early twentieth century. The presence of domestic pig, although not yet evaluated in relation to local breeds, serves to confirm that the deposit is not of great antiquity. Yet, the cave was clearly visited by people of the time, who hunted wild game, ate fish, and, evidently, local freshwater crabs as well. The results therefore provide a further instance of the versatility of early human food-gathering behaviour in the equatorial rainforest environment, including freshwater, additional to the archaeological discoveries at the important Sarawak site of Niah Caves (Barker *et al.*, 2011; Barker, 2013).

The crabs: taxonomy using cheliped characters

Identifying fossil and subfossil crab fragments is always a challenge. Invariably, the parts that are often excavated are parts of the pincers (chelipeds) or legs; characters that are not always used to identify genera or even families. Students of subfossils have often generalized, with inaccurate identifications, even describing new genera and species based on sparse fragments and incomplete anatomical comparison (see Ng *et al.*, 2008, pp. 8, 9). Pretzmann (1971) presented a terminology for the dentition of the chelae of European freshwater crabs of the genus *Potamon* to help with fossil identifications (see Bachmayer & Pretzmann, 1971) and, while most of the features he noted are also generally applicable for *Isolapotamon*, his nomenclature is unnecessarily complicated and there is too much variation in some aspects to be useful.

Having recent comparative collections from the study area is of great help. In the context of the present study, recent material from Jambusan is available in the ZRC for comparative work, as well as a good series of other species from Borneo.

The Bau area in western Sarawak has 11 known species of freshwater and semiterrestrial brachyuran crabs from three families:

- Sesarmidae: *Geosesarma bau* Ng & Grinang, 2004;
- Gecarcinucidae: *Stygothelphusa bidiensis* (Lanchester, 1900), *Coccusa cristicervix* Ng & Grinang, 2004, *Lepidothelphusa cognetti* (Nobili, 1903), *Parathelphusa oxygona* Nobili, 1901, *Parathelphusa sarawakensis* Ng, 1986, *Perithelphusa borneensis* (Von Martens, 1868) and *Terrathelphusa kuchingensis* (Nobili, 1901);
- Potamidae: *Isolapotamon bauense* Ng, 1987, *Isolapotamon consobrinum* (De Man, 1899) and *Ibanum pilimanus* Ng & Grinang, 2004 (compare Ng & Grinang, 2004).

The archaeological crab material in the Everett Collection is a composed solely of fingers of the chela or claw (Pls. 1-3). This is not surprising because the fingers are the hardest part of the pincer and most readily preserved. The pattern of pits and grooves on the outer surface as well as the structure of the teeth and the tip of the finger leave no doubt that all specimens belong to the family Potamidae. Sesarmids are distinct in that the fingers of the chelae are usually strongly curved with tubercles on the dorsal margin of the dactylar finger, the cutting margins have strong teeth and the tips of the fingers are slighty scalloped and pectinated (see Ng, 1988, 2004). In any case, all adult true freshwater and inland sesarmids are relatively small (less than 20 mm in carapace width), their chelae are not more than 10-15 mm in total length and their fingers less than half this length (Ng, 1988, 2004). Gecarcinucids and potamids can grow much larger and include some of the largest freshwater crabs in Asia (e.g., *Isolapotamon bauense* reaches carapace widths of more than 80 mm; see Ng, 1987). With regard to the chelae, gecarcinucids have very similar fingers but the surfaces are less pitted and the cutting teeth have a different arrangement, usually being distinctly separated from each other and generally more conical in shape. In potamids, the pits on the outer surface are deep, and form two distinct longitudinal rows; and the teeth are usually more blade like. Both gecarcinids and potamids have heteromorphic chelae (*i.e.*, one is larger with the palm more swollen; Pls. 4, 5), and in adults, the major or larger one often has a large tooth (usually molariform or submolariform) at the base of the dactylar finger. This is probably used for crushing freshwater molluscs (see Ng, 1988, 1989a, b; Chia & Ng, 2006).

In gecarcinucids only males have prominently asymmetrical chelae (the larger may be 1.5-2 times larger than the smaller one), while females generally have equal and similarly structured chelae and fingers. In potamids on the other hand, while asymmetrical, the difference in size between the major and minor chelae is generally less dramatic, with the former only slightly more swollen. However, the cutting margins of the fingers are different. The dactylar finger of the major chelae usually has a molariform or submolariform tooth (larger in large individuals) at the base, with the rest of the cutting margin having closely appressed blade-like teeth (Pl. 5, figs. 1a, 2a, 3a, 4a). The propodal finger of the major chela often has the basal part of the cutting margin flattened, usually with low teeth (opposing the molariform tooth on the dactylar finger), with the rest of cutting margin lined with variously sized but closely appressed blade-like teeth (Pl. 5, figs. 3a, 4a). On the minor chelae, the cutting margins of both the dactylar and propodal fingers are lined with closely appressed blade-like teeth (Pl. 5, figs. 1b, 2b, 3b, 4b).

Cheliped structures are not used to separate genera and species, with the form of the carapace, male abdomen and male reproductive structures (gonopods) the most useful (see Ng, 1988, 2004). For the potamid fossils studied here, it is clear that they all belong to *Isolapotamon* rather than *Ibanum*. The fingers of *Ibanum* are relatively shorter and stouter (see Ng, 1995; Ng & Grinang, 2004). In any case, all adult *Ibanum* are relatively small species not exceeding 20 mm in carapace width with the chelae not exceeding 15 mm in total length and the fingers are only about half this length (see Ng, 1995). Adults of species of *Isolapotamon* on the other hand, are all large, exceeding 50 mm in carapace width with chelae longer than 20 mm in total length (Ng, 1987; Ng & Tan, 1998). As to species differentiation, there is too much variation in the chelae among the 18 known species of *Isolapotamon* (all from Borneo and Mindanao) (Ng *et al.*, 2008) to use this character effectively to separate them. Fortunately, in the Bau area, only two species of *Isolapotamon* are present, and their chelae are quite different (Pl. 5).

The dactylar fingers of *Isolapotamon bauense* are proportionately stouter and less strongly curved; with the teeth along the cutting margins of both fingers are generally smaller (Pl. 5, fig. 1a, b). The molariform tooth on the dactylar finger is also usually medially clefted (Pl. 5, fig. 1a). In *Isolapotamon consobrinum*, the dactylar fingers are relatively more slender, more strongly curved, and the teeth along the cutting margins of both fingers are proportionately larger, especially in the case of the propodal finger (Pl. 5, figs. 2-4). The molariform tooth on the dactylar finger is also more entire (Pl. 5, figs. 2a, 3a, 4a).

The specimens in the Everett Collection all belong to relatively large individuals. Using the length of fingers of fresh ZRC specimens as a guide; the two smallest fossil specimens – a finger of *I. bauense* 13.8 mm (NHM Ev82.19) (Pl. 1, fig. 5) and a finger of *I. consobrinum* 13.8 mm (NHM Ev82.19) (Pl. 3, fig. 3), belong to individuals about 35 mm in carapace width, which is already adult size. The largest fossil, a finger of *I. consobrinum* measuring 25.8 mm (NHM Ev82.19) (Pl. 2, fig. 2), would belong to a very large individual at least 60 mm in carapace width.

Species accounts

Isolapotamon bauense Ng, 1987

Pl. 1; Pl. 4, fig. 1; Pl. 5, fig. 1.

Material examined – NHM Ev76.16, left propodal finger; NHM Ev82.19, left propodal finger, tip broken; NHM Ev76.16, left dactylar finger; NHM Ev76.16, left dactylar finger, tip broken; and NHM Ev82.19, left dactylar finger.

Remarks – This is arguably the largest freshwater crab in Borneo, perhaps even Asia, with the largest known specimen from the Bau area reaching 85.1 mm in carapace width (Ng, 1987) (Pl. 4, fig. 1). The preferred habitat of this species is at the edge of waterfalls or riparian systems, usually hiding in burrows under large rocks during the day. They are semiterrestrial although they usually live close to streams, and have also been found in more swampy areas some distance from the streams (see also Ng & Grinang, 2004; Grinang *et al.*, 2013). Significantly for this study, they have been collected inside caves in the Bau area as well as nearby Gua Sireh, Serian. It is not always easy to sample as they tend to be cryptic, and they are never present in large numbers in any one area (Ng, 1987; Ng & Tan, 1998; Ng & Grinang, 2004; Grinang *et al.*, 2013).

Isolapotamon consobrinum (De Man, 1899)

Pls. 2, 3; Pl. 4, fig. 2; Pl. 5, figs. 2-4.

Material examined – NHM Ev76.16, left propodal finger; NHM Ev82.19, right propodal finger; NHM Ev74.02, right propodal finger; NHM Ev76.16, right dactylar finger, tip broken; NHM Ev76.16, right dactylar finger, distal half broken; NHM Ev82.19, left dactylar finger; NHM Ev30.07, left dactylar finger; NHM Ev21.3, right dactylar finger; and NHM Ev18.02, right dactylar finger.

Remarks – This is a common species in western Sarawak (Pl. 4, fig. 2). Ng (1987, p. 42) noted that the species was, 'usually found under rocks in fast flowing waterfalls and highland streams.' Additional collections and observations over the years indicate it is also present in lowland areas as long as there is clear fast-flowing water with a rocky substrate (see also Ng & Grinang, 2004). It can be present in large numbers hiding under rocks or among submerged vegetation and accumulated debris. This is a primarily aquatic species that is rarely observed outside water. It prefers habitats with sandy/rocky substrates, and is found in almost all the waterways in the Bau limestone area (Ng, 1987; Ng & Tan, 1998; Ng & Grinang, 2004).

Among specimens examined, NHM Ev30.07 (Pl. 3, fig. 4) is heavily eroded so that most of the distinguishing features are not clearly visible. In general proportions, this particular specimen is closer to *I. consobrinum* and is therefore referred here. The same is true for specimen NHM Ev21.3 (Pl. 3, fig. 5), which is even more heavily eroded.

Discussion

Fossils of freshwater decapod crustaceans are relatively rare. Best known perhaps are those from Europe, with a good number of well-preserved Neogene fossils of *Potamon* reported (for a review, see Klaus & Gross, 2007, 2010). Fossil *Potamon bilobatum* Brandis, Storch & Türkay, 2000 have also been recorded from Iran (Limondin-Lozouet *et al.*, 2014). The study by Ashkenazi *et al.* (2005) is noteworthy as those authors conducted a detailed morphometric analyses on a large deposit of subfossil Middle East potamids of Early-Middle Pleistocene age which they identified as close to *Potamon potamios* (Olivier, 1804) (see also Ashkenazi *et al.*, 2007; Horwitz & Garfinkel, 1991). In Asia, considering the size of the continent and substantial diversity of species present today (see Cumberlidge & Ng, 2009), surprisingly few fossils have been recorded. Glaessner (1933) reported on fossil (Middle Miocene-Pliocene) '*Potamon*' (probably what is known today as *Himalayapotamon*) from the Siwalik Hills in India and Klaus *et al.* (2011) have recently recorded an unidentified Neogene potamid from Laos. An unidentified gecarcinucid, possibly *Sartoriana*, from the Siwalik Hills has been documented by Klaus & Gross (2010). More recent material includes Late Pleistocene *Geothelphusa* (Potamidae) from Japan (Karasawa, 1997; Naruse *et al.*, 2003, 2006) and unidentified potamids from Holocene sites in Vietnam (Rabett *et al.*, 2008, 2011).

The recognition of potamid chelipeds among archaeological deposits in Sarawak is notable as it represents the first such examples from Borneo. Although the age of these specimens is likely to be historic or prehistoric, i.e., Late Holocene, the study is a useful exercise, showing that the taxa can be identified by cheliped characters, by comparison with extant species in the area.

In archaeological terms, the results emphasize the significance of the freshwater environment as an essential food source for human foraging and food-gathering in the equatorial rainforest environment of Borneo. In the Middle East, burn marks on some fossil fragments of *Potamon* have been suggested as evidence that these crabs were consumed by early occupants (Horwitz & Garfinkel, 1991; Ashkenazi *et al.*, 2007). The present material from Borneo, however, shows no signs of burning.

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Plate 1

Isolapotamon bauense Ng, 1987

Fig. 1a, b. NHM EV76.16, ML = 19.8 mm, left propodal finger, in outer and inner views, respectively.

Fig. 2a, b. NHM EV82.19, ML = 21.4 mm (tip broken), left propodal finger, in outer and inner views, respectively.

Fig. 3a, b. NHM EV76.16, ML = 21.8 mm, left dactylar finger, in outer and inner views, respectively.

Fig. 4a, b. NHM EV76.16, ML = 21.6 mm (tip broken), left dactylar finger, in outer and inner views, respectively.

Fig. 5a, b. NHM EV82.19, ML = 13.8 mm, left dactylar finger, in outer and inner views, respectively.

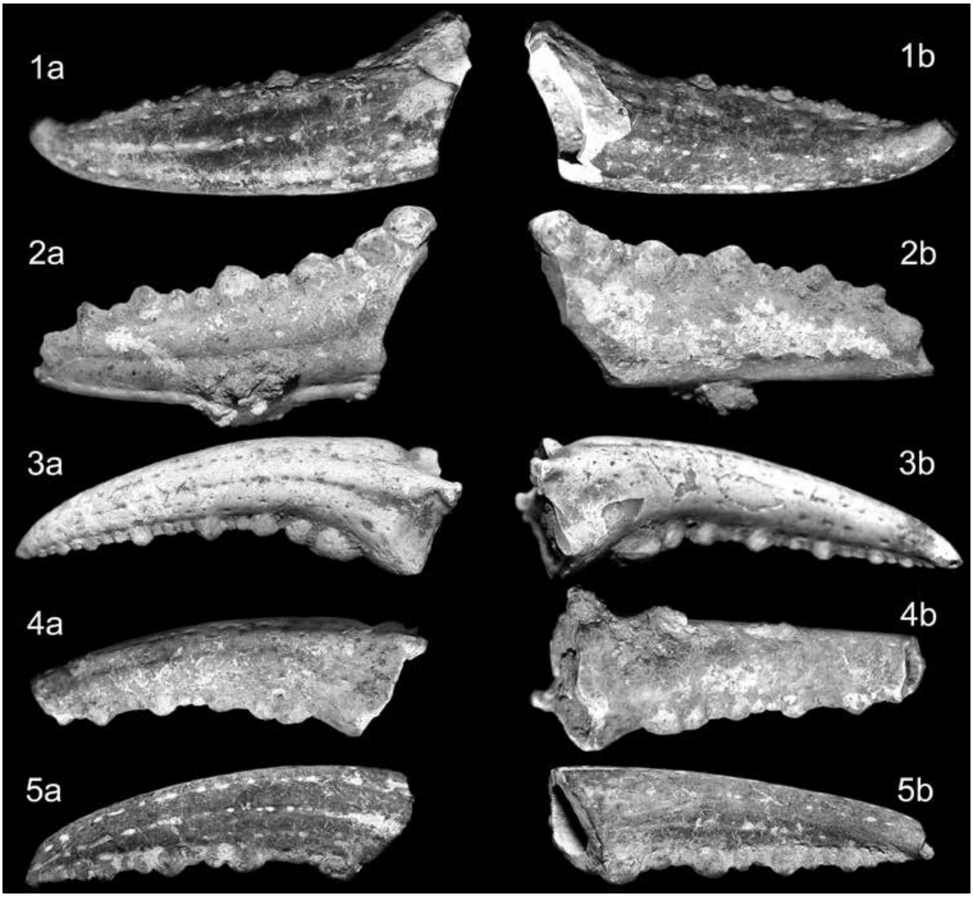
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Plate 2

Isolapotamon consobrinum (De Man, 1899)

Fig. 1a, b. NHM EV76.16, ML = 21.8 mm, left propodal finger, in outer and inner views, respectively.

Fig. 2a, b. NHM EV82.19, ML = 25.8 mm, right propodal finger, in outer and inner views, respectively.

Fig. 3a, b. NHM EV74.02, ML = 19.3 mm, right propodal finger, in outer and inner views, respectively.

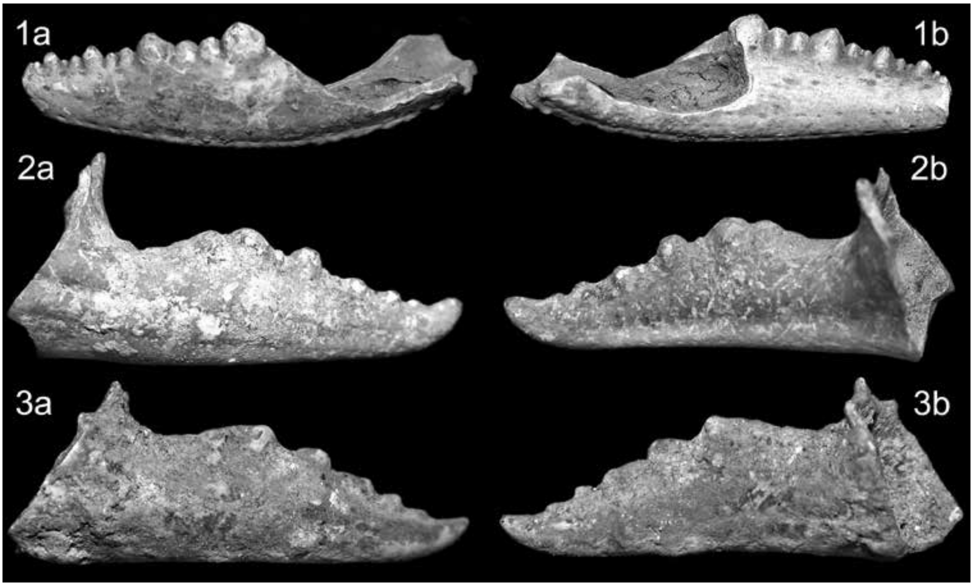
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Plate 3

Isolapotamon consobrinum (De Man, 1899)

Fig. 1a, b. NHM EV76.16, ML = 19.4 mm (tip broken), right dactylar finger, in outer and inner views, respectively.

Fig. 2a, b. NHM EV76.16, ML = 14.2 mm (distal half broken), right dactylar finger, in outer and inner views, respectively.

Fig. 3a, b. NHM EV82.19, ML = 13.8 mm, left dactylar finger, in outer and inner views, respectively.

Fig. 4a, b. NHM EV30.07, ML = 22.1 mm, left dactylar finger, in outer and inner views, respectively.

Fig. 5a, b. NHM EV21.3, ML = 14.6 mm, right dactylar finger, in outer and inner views, respectively.

Fig. 6a, b. NHM EV18.02, ML = 18.9 mm, right dactylar finger, in outer and inner views, respectively.

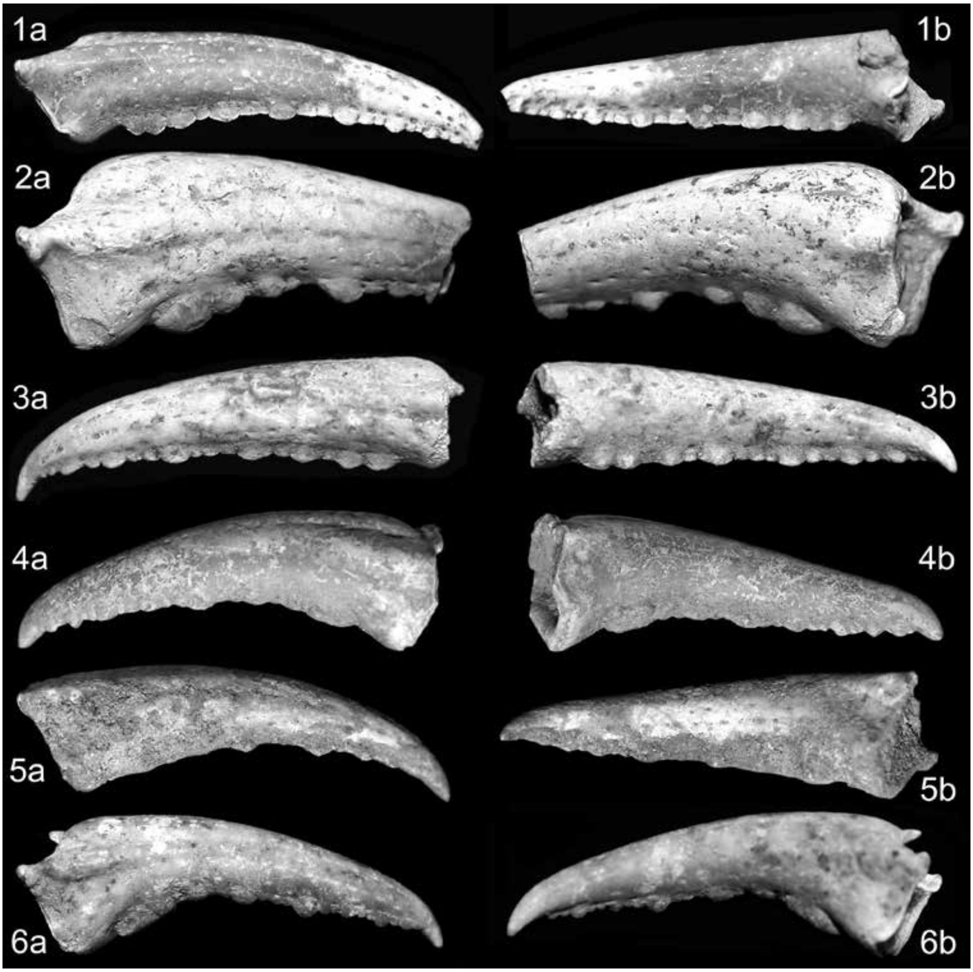
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Plate 4

Overall habitus of extant representatives

Fig. 1. *Isolapotamon bauense*, male, 58.9 × 45.4 mm (ZRC 1997.782), Gua Sireh, Serian, Sarawak, collected 19 October 1982.

Fig. 2. *Isolapotamon consobrinum*, female, 49.5 × 37.3 mm (ZRC 2013.1857), Kampung Tembawang Kuching, Sarawak, collected 14 September 2013.

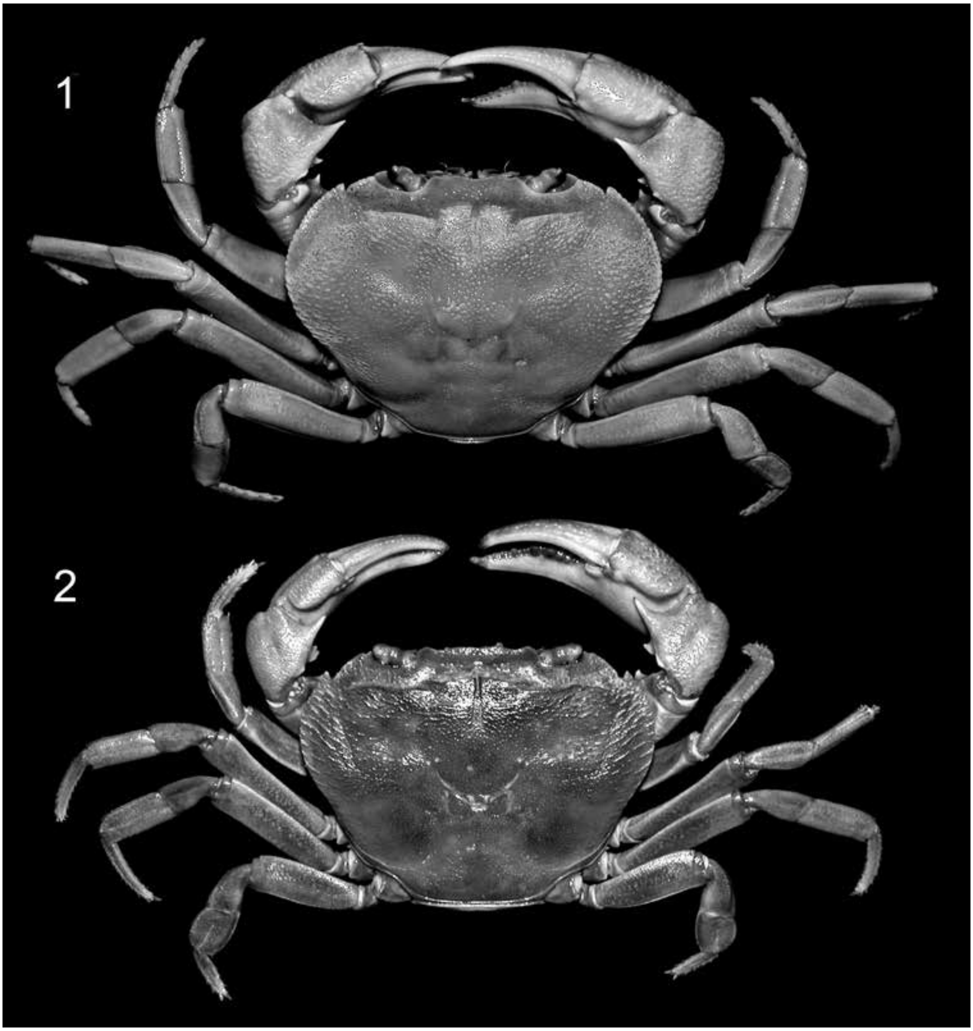
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Plate 5

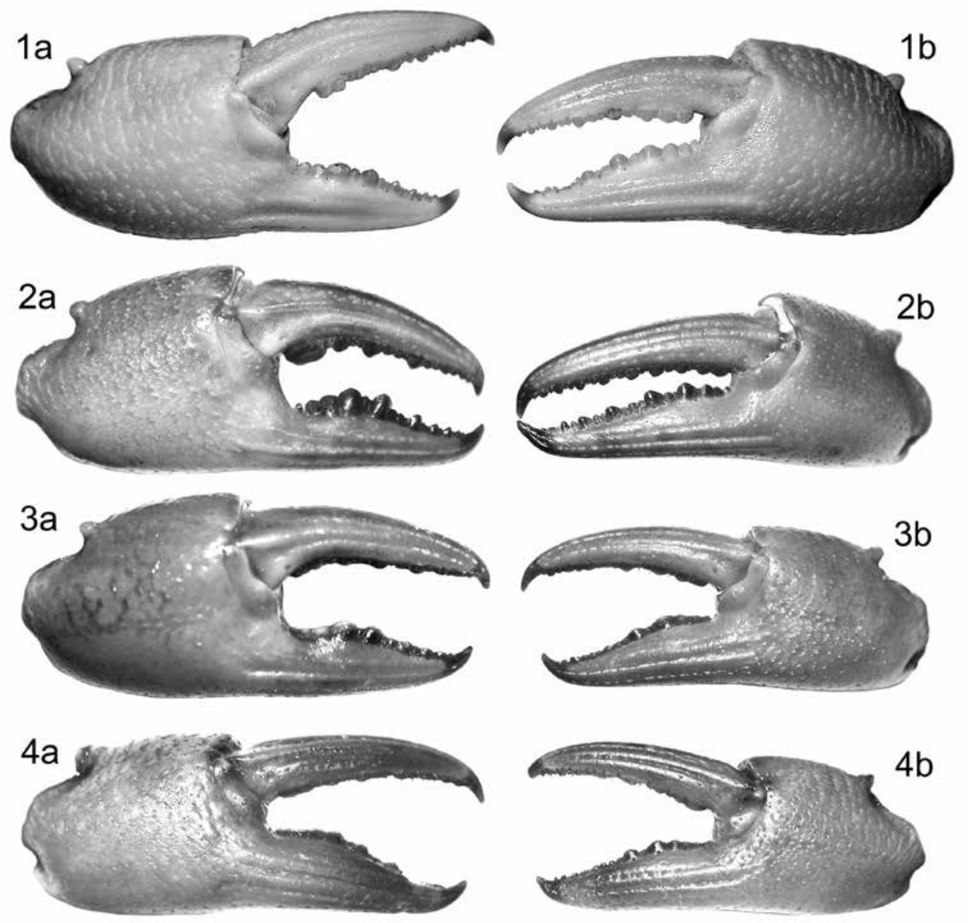
Outer surfaces of chelae of extant representatives

Fig. 1. *Isolapotamon bauense*, male, 58.9 × 45.4 mm (ZRC 1997.782), Gua Sireh, Serian, Sarawak, collected 19 October 1982. a, right chela; b, left chela.

Fig. 2. *Isolapotamon consobrinum*, female, 49.5 x 37.3 mm (ZRC 2013.1857), Kampung Tembawang Kuching, Sarawak, collected 14 September 2013. a, right chela; b, left chela.

Fig. 3. *Isolapotamon consobrinum*, female, 42.3 × 33.5 mm (ZRC 1998.537), Sungai Kuhas, Sarawak, collected 25 June 1998. a, right chela; b, left chela.

Fig. 4. *Isolapotamon consobrinum*, male, 35.3 × 27.1 mm (ZRC 2013.1858), Sungai Aman, Penrissen (Borneo Highlands), Sarawak, collected 16 September 2013. a, right chela; b, left chela.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