Revision of Selatium Serène & Soh, 1970 (Crustacea: Brachyura: Sesarmidae), with description of a new genus and two new species

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Abstract

The Indo-West Pacific sesarmid genus Selatium Serène & Soh, 1970, is revised, and two wide-ranging species are recognized, S. brockii (De Man, 1887) and S. elongatum (A. Milne-Edwards, 1869). A new genus, Lithoselatium, which superficially resembles Selatium, is described, and two new species are recognized: L. pulchrum n. sp. from Taiwan, and L. kusu n. sp. from Singapore and nearby areas. Their relationship is discussed using both morphological and molecular datasets.

Key words: Decapoda, Thoracotremata, crab, morphology, mtDNA, 16S rRNA

Introduction

In his synthesis of the Indo-West Pacific Sesarminae, Serène & Soh (1970) established a new genus, Neoepisesarma, for a group of common mangrove crabs, with four subgenera, Neoepisesarma s. str., Tiomanium, Muradium and Selatium. Holthuis (1977), however, showed that Episesarma De Man, 1895, was the older name for Neoepisesarma Serène & Soh, 1970. The general consensus is that all these subgenera should be regarded as distinct genera (see Ng et al., 2008a). Of these, Selatium is probably the most distinct. It originally included a single taxon, Sesarma brockii De Man, 1887, an obligate tree-climbing species. Hartnoll
(1975), Sivasothi et al. (1993), Tan & Ng (1994) and Ng & Sivasothi (1999) recognised Selatium as a distinct genus but without detailed explanations. Subsequently, another arboreal species, Sesarma elongatum A. Milne-Edwards, 1869, was also transferred to Selatium (see Hartnoll 1975; Vannini et al. 1997; Ng et al. 2008a). Fratini et al. (2005) and Schubart et al. (2006) demonstrated that both species are sister taxa and generically distinct from the closely related Episesarma, Neosesarma Serène & Soh, 1970, and Clistocoeloma A. Milne-Edwards, 1873, on the basis of evidence from two mitochondrial genes.

The present paper provides unambiguous morphological and molecular data justifying Selatium as a distinct genus from Episesarma, and discusses the affinities of S. brockii and S. elongatum. A new genus, morphologically and genetically allied to Selatium and Clistocoeloma, is also described, with two new species from Taiwan and Singapore, respectively. Unlike Selatium, this new genus lives under rocks and boulders in the supralittoral zone.

Material and methods

The abbreviations G1 and G2 are used for the male first and second gonopods (pleopods) respectively. Sutures between male thoracic sternites are denoted by “/” (e.g. suture 3/4 = suture between sternites 3 and 4). Measurements provided are of carapace width and length respectively. Specimens examined or used for molecular analysis are deposited in the National Taiwan Ocean University (NTOU), Keelung, Taiwan; Taiwan National Museum (TMCD), Taipei, Taiwan; Institute of Zoology, Academia Sinica (ASIZ), Taiwan; Muséum national d’Histoire naturelle (MNHN), Paris, France; Senckenberg Museum Frankfurt (SMF), Frankfurt a.M., Germany; and Zoological Reference Collection of the Raffles Museum of Biodiversity Research (ZRC), National University of Singapore, Singapore.

New mitochondrial DNA (mtDNA) sequences for this study were obtained at the University of Regensburg between 2000 and 2006 (Table 1). DNA extractions and selective amplification of the mitochondrial complex consisting of part of the large ribosomal subunit gene 16S rRNA were carried out as reported in Schubart et al. (2006). PCR-amplifications were run with four minutes denaturation at 94°C, 40 cycles with 45s 94°C, 1 min 48°C, 1 min 72°C and 10 min final denaturation at 72°C and the primers 16L2 and 1472 (see Schubart et al. 2006). PCR products were purified with Microcon 100 filters (Microcon) or Quick-Clean (Bioline) and subsequently sequenced with the ABI BigDye terminator mix followed by electrophoresis in an ABI Prism 310 Genetic Analyzer (Applied Biosystems, Foster City, USA). New sequence data were submitted to the European molecular database EMBL (see Table 1 for accession numbers). In addition, the following sequences archived in molecular databases were included in our analyses: Sesarma reticulatum (AJ130799), Chiromantes haematocheir (AJ308414), Clistocoeloma villosum from Kenya (AJ784018), Clistocoeloma merguense (AJ784019), Episesarma mederi (AJ784020), Episesarma versicolor (AJ784021), Neosesarma gemmiferum (AM180682), Neosesarma rectipectinatum (AM180682), Selatium brockii from Kenya (AJ784022) and Selatium elongatum from Kenya (AJ784023). Sequences were aligned with xESEE version 3.2 (Cabot & Beckenbach 1989). Of these, S. reticulatum and C. haematocheir are the only two species without a longitudinal pectinated crest on the propodi of the male chelae and were included as outgroup.

The model of DNA substitution that fitted our data best was determined using the software MODELTEST 3.6 (Posada & Crandall 1998). Two methods of phylogenetic inference were applied to our dataset: maximum parsimony (MP) using the software package PAUP* (Swofford 1998), and Bayesian analysis (BI) as implemented in MrBayes v. 3.0b4 (Huelsenbeck & Ronquist 2001). MP trees were obtained by a heuristic search with 100 replicates of random sequences addition and tree-bisection-reconnection as branch swapping options keeping multiple trees (MulTrees); gaps were treated as fifth character state. Subsequently, confidence values for the proposed groups within the inferred trees were calculated with the nonparametric bootstrap method (2000 pseudoreplicates, 10 replicates of sequence addition). Only minimal trees were retained and zero-length branches were collapsed. The BI trees were calculated using the suggested model of evolution.
The Bayesian analysis was run with four MCMC (Markov chain Monte Carlo) chains for 2,000,000 generations, saving a tree every 500 generations (with a corresponding output of 4,000 trees). The –lnL converged on a stable value between 2,000 and 5,000 generations (burn-in phase). The first 10,000 generations were thus excluded from the analysis to optimize the fit of the remaining trees. The posterior probabilities of the phylogeny were determined by constructing a 50% majority-rule consensus of the remaining trees. Consensus trees were obtained using the “sumpt” option in MrBayes.

**TABLE 1.** List of crab specimens for which 16SmtDNA was newly sequenced and used together with sequences from GenBank for phylogenetic reconstruction.

<table>
<thead>
<tr>
<th>Species</th>
<th>Collection Locality</th>
<th>date</th>
<th>collection #</th>
<th>accession #</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clistocoeloma villosum</td>
<td>Singapore: Labrador</td>
<td>19.3.2006</td>
<td>SMF-33843</td>
<td>FN295574</td>
</tr>
<tr>
<td>Lithoselatium kusu n. sp.</td>
<td>Singapore: Labrador</td>
<td>19.3.2006</td>
<td>SMF-33840</td>
<td>FN295569</td>
</tr>
<tr>
<td>Lithoselatium pulchrum n. sp.</td>
<td>Taiwan: Pingtung: Fontzueisha</td>
<td>27.8.1999</td>
<td>ZRC 2002.0152</td>
<td>FN295570</td>
</tr>
<tr>
<td>Selatium brockii</td>
<td>Singapore: Mandai mangrove</td>
<td>11.9.1999</td>
<td>MZUF 2497</td>
<td>FN295571</td>
</tr>
<tr>
<td>Selatium brockii</td>
<td>Singapore: Labrador</td>
<td>19.3.2006</td>
<td>SMF-33841</td>
<td>FN295571</td>
</tr>
<tr>
<td>Episesarma palawanense</td>
<td>Philippines: Palawan: Nakoda Bay</td>
<td>31.12.1908</td>
<td>USNM 45792</td>
<td>FN295576</td>
</tr>
<tr>
<td>Episesarma singaporense</td>
<td>Singapore: Sungei Buloh mangrove</td>
<td>10.3.2006</td>
<td>SMF-33842</td>
<td>FN295575</td>
</tr>
</tbody>
</table>

The molecular dataset consisted of 582 aligned characters, of which 408 were constant, 109 parsimony-informative and 174 variable. GTR+G was selected as the best-fitting evolutionary model by MODELTEST and implemented for subsequent Bayesian analysis. The MP analysis resulted in a tree of the length 358 with CI = 0.623, RI = 0.624, RC = 0.389 as tree scores. Tree topologies obtained by both methods were not in conflict, but MP was less resolved. The consensus tree with confidence values of both methods exceeding 50% is shown in Fig. 18.

**Systematic Account**

**Family Sesarmidae Dana, 1851**

**Selatium** Serène & Soh, 1970

**Type species.** Sesarma brockii De Man, 1887, by original designation; gender neuter.

**Diagnosis.** Carapace quadrate to longitudinally rectangular, lateral margins parallel to subparallel or gently divergent posteriorly; lateral margins of carapace with 1 distinct epibranchial tooth or almost entire; regions of carapace well defined by distinct grooves; frontal margin strongly deflexed; anterior frontal lobes prominent, posterior frontal lobes weakly demarcated; antennae entering orbits; basal segments of antennae, antennules mobile, not separated by a septum; Verwey’s groove (see Abele, 1992) delimited by dorsal and ventral rows of setae. Exopod of third maxilliped with long flagellum. Cheliped merus with expanded foliaceous distal margin, lined with prominent sharp spines and teeth. Chelae with stridulating structure: dorsal margin of palm with 1 longitudinal crest of tubercles, partly pectinated, with 33–37 teeth in males; dorsal margin of dactylus with ca. 30 dome-shaped tubercles; fingers relatively long, tips of fingers hoofed with sharp cutting edges; inner surface of palm convex, with raised transverse ridge of small or large granules. Ambulatory legs 1–4...
relatively short, dactylus about one third length of propodus. Coxae of ambulatory legs 1–3 with short setae around lateral margins, without tufts of long setae on ventral, lateral surfaces; dactylus about one-third length of propodus; propodal-dactylar condyle dactylus large. Thoracic sternal suture 1/2 completely fused; suture 3/4 separated by complete suture; sutures 4/5, 5/6, 6/7, 7/8 medially interrupted, separated by wide gap; deep longitudinal median groove present on sternites 7, 8; male sterno-abdominal cavity almost reaching suture of thoracic sternites 3, 4; sternite 8 not visible when male pleon fully closed. Penis proximally calcified, sternal. Male telson slightly longer than wide; all somites free. G1 stout, with sharp, tapering, pectinated tip; G2 short.

Selatium brockii (De Man, 1887)
(Figs. 1–4)


Type locality. Ambon (Indonesia).

Diagnosis. Carapace quadrate, wider than long; lateral margins gently diverging towards posterior margin, prominent sharp epibranchial tooth (Fig. 1A, B); chelipeds equal to subequal in males (Fig. 1A); chela and fingers relatively long (Fig. 2C); dorsal margin of palm with curved pectinated crest consisting of 37–39 teeth (Fig. 3A, B); dorsal margin of dactylus with row of 21–23 prominent tubercles (Fig. 3C); ambulatory
legs relatively long (Fig. 1A); anterior thoracic sternites and male abdomen relatively short longitudinally (Figs. 2A, 4C); distal part of G1 dilated with distinct triangular pectinated tip (Fig. 4D–G).

FIGURE 1. Selatium brockii (De Man, 1887). Male (29.2 x 26.9 mm) (ZRC 1989.2875), Mandai, Singapore. A, dorsal view; B, dorsal view of carapace; C, frontal view of carapace.
FIGURE 2. *Selatium brockii* (De Man, 1887). Male (29.2 x 26.9 mm) (ZRC 1989.2875), Mandai, Singapore. A, anterior sternum and abdomen; B, right propodus and dactylus of first ambulatory leg; C, outer view of right chela.
FIGURE 3. *Selatium brockii* (De Man, 1887). Male (29.2 x 26.9 mm) (ZRC 1989.2875), Mandai, Singapore. A, lateral view of pectinated ridge on dorsal margin of palm; B, dorsal view of pectinated ridge on dorsal margin of palm; C, ridge on dorsal margin of dactylus.

**Description.** Carapace quadrate, lateral margins slightly diverging posteriorly; dorsal surfaces relatively smooth, regions well defined by prominent grooves; surface adjacent to anterolateral margins lined with
strong, oblique striae; gastrocardiac surface with distinct groove. Postfrontal lobes prominent; 2 median lobes larger, with granular ridge just anterior to it; 2 lateral lobes with uneven margins; lobes separated by deep grooves. Front strongly deflexed downwards, with 2 prominent subtruncate lobes separated by broad, deep cleft, strongly produced anteriorly. Supraorbital margin entire. Anterolateral margin entire, confluent with posterolateral margin, with prominent epibranchial tooth, minute tubercle as rudiment of subsequent tooth. Posterolateral margin gently diverging towards weakly convex posterior carapace margin. Epistome with pronounced horizontal ridge, medially concave; posterior margin with prominent median triangular projection, lateral part with 2 concave indentations. Verwey’s groove delimited by dorsal and ventral rows of setae. Infraorbital ridge tuberculate, setose. Pterygostomial region weakly granular, covered by dense surface of distally curved setae. Antenna entering orbit; basal segments of antenna, antennule not separated by septum; basal antennal segment mobile. Ischium of third maxilliped with shallow submedian sulcus; merus bovate with distinct submedian longitudinal setose ridge extending to antero-external angle of ischium; exopod slender, with long flagellum.

Chelipeds equal to subequal in size and shape in adult males. Outer surface of chelae distinctly granular, inner surface with coarser granules, low submedian transverse ridge of granules closer to fingers; ventral border gently convex to straight; dorsal margin of palm with longitudinal crest of 25–27 low proximal granules, followed by slightly curved pectinated crest consisting of 37–39 teeth of varying sizes, median ones higher; scattered tubercles on inner side; fingers more than half length of palm; dorsal margin of dactylus with row of 21–23 tubercles, proximal ones rounder, otherwise transversely elongate with conical apex; cutting edge of dactylus with several teeth on distal two-thirds, distal one largest; cutting edge of pollex with several teeth, median and subdistal ones largest; tips of fingers hoofed (medially excavated) with sharp cutting edges. Outer surface of carpus rugose; inner distal angle produced, margins with sharp tubercles. Outer face of merus strongly convex, with rows of granules; inner face granular, strongly expanded distally forming foliaceous structure, with subdistal tooth on dorsal margin, distal margins lined with numerous large, sharp spines and teeth, distal part visible from dorsal view, even when chelipeds apposed tightly against carapace; inner face with 2 longitudinal rows of stiff setae. Basis, ischium immobile but separated by distinct suture, surface with scattered granules.

Ambulatory legs long, third pair longest. Coxae of ambulatory legs 1–3 with short setae around lateral margins, without tufts of long setae on ventral and lateral surfaces. Outer surfaces of meri, carpi, propodi rugose. Meri laterally flattened, foliaceous, margins finely granulated; with distinct subdistal dorsal spine; outer part of postero-distal margin expanded, anterior surface convex. Outer surface of carpi with 2 distinct carinae, 1 on inner surface. Distal third of propodi with short, stiff setae dorsally and ventrally; lower distal margins each with 4 or 5 short spines. Dactylo-propodal lock absent but propodal-dactylar condyle prominent. Dactyli very short, ca. one-third length of propodus, with 4 rows of setae.

Margins of anterior thoracic sternites and surfaces of sternites 1–4 setose. Stermites 1, 2 completely fused, suture concave toward buccal cavity; suture 3/4 separated by complete suture; sutures 4/5, 5/6, 6/7, 7/8 medially interrupted, separated by wide gap; deep longitudinal median groove present on sternites 7, 8; male sterno-abdominal cavity not reaching suture 3/4; sternite 8 not visible when male pleon fully closed. Penis proximally calcified, sternal. Abdomen triangular; lateral margins of abdominal somites 3, 6 convex, lateral margins of somites 4, 5 gently concave. Telson subcircular, slightly longer than wide, tip rounded. G1 very stout, distal part dilated, distinctly wider than median part, giving structure gently curved appearance from ventral view; distal part with short, triangular pectinated structure. G2 very short, distally spatuliform, no distal segment present.

**Female.** Chela generally smaller, pectinated crest on palm of cheliped replaced by tubercles.

**Remarks.** De Man (1887) briefly diagnosed this species without figures from a 26 by 23 mm male collected from Ambon in Indonesia. He subsequently provided a detailed description and excellent figures of the same specimen (De Man 1888). We have not been able to locate this specimen; it is not to be found in any of the repositories De Man was known to have deposited his material (see Fransen et al. 1997), and like much of the material from his 1887–1888 report, is almost certainly lost. We have also not been able to find another
specimen from Ambon. The detailed description and figures of De Man (1888), however, leave no doubt that our material belongs to this species. Since all the material we have examined from Kenya to the western Pacific is referable to one species and we have not seen any morphological or clearcut genetic data to suggest otherwise, we also do not see the immediate need to designate a neotype for it.

**FIGURE 4.** *Selatium brockii* (De Man, 1887). Male (29.2 x 26.9 mm) (ZRC 1989.2875), Mandai, Singapore. A, abdomen; B, right third maxilliped (denuded); C, left side of anterior thoracic sternum; D, dorsal view of left G1 (denuded); E, ventral view of left G1 (denuded); F, dorsal view of distal part of left G1 (denuded); G, ventral view of distal part of left G1 (denuded); H, left G2 (denuded).
Ecology. Selatium brockii is a tree-climbing species from coastal mangroves. It is most commonly found underneath the bark of dead trunks or inside hollow trees in Southeast Asian mangroves. The ecology of this species has been discussed at length by Sivasothi et al. (1993) and Sivasothi (2000).

Selatium elongatum (A. Milne-Edwards, 1869) (Figs. 5–8)


Sesarma latifemur Alcock, 1900: 421 (Andaman Islands). — Alcock & McArdle 1903: pl. 66, fig. 2 (Andaman Islands).


Sesarma (Holometopus) latifemur — Tesch 1917: 168 (no new locality).

Sesarma sp. — Fourmanoir 1954: 3 (Madagascar).

Sesarma (Holometopus) elongatum — Crosnier 1965: 49, figs. 63–67, 72, 84, pl. 4 fig. 1. — Serène 1968: 107 (no new locality).


Material examined. Madagascar: Lectotype male (34.4 x 36.2 mm) (MNHN-B3640).


Indonesia, Sulawesi: Tomini Bay: mangrove between Mapane and Poso, 1 male (40.1 x 40.9 mm), 1 juvenile female (24.6 x 24.7 mm) (ZRC 2000.1738), coll. C. D. Schubart et al., 20 January 2000 (DNA voucher); 4 males, 3 females, mangrove forest, on trees, Bunaken Island, off Manado, coll. N. K. Ng & J. Lai, September 2003.

Papua New Guinea: 1 male (40.7 x 42.0 mm) (ZRC 2009.0567), Oro Province, Tuti District, Tuti Wharf, on rope, coll. H. H. Tan, 10 December 2008.

Type locality. Madagascar.

Diagnosis. Carapace longitudinally rectangular, longer than wide; lateral margins subparallel or gently diverging towards posterior margin, entire, without epibranchial tooth, with only small notch marking rudimentary tooth (Fig. 5A, B); chelipeds unequal in adult males (Fig. 5A); chela with relatively short fingers (Fig. 6B); dorsal margin of palm with curved pectinated crest consisting of 43–48 teeth (Fig. 7A); dorsal margin of dactylus with row of 32–35 prominent tubercles (Fig. 7B); ambulatory legs relatively short (Fig. 5A); anterior thoracic sternites and male pleon relatively long longitudinally (Figs. 6A, 8C); distal part of G1 appears swollen, with short triangular pectinated tip (Fig. 8D–G).

Remarks. In naming this species, A. Milne Edwards (1869) did not state how many specimens he had nor did he select a holotype. As such, all his material must be regarded as syntypes. No subsequent author has selected a type specimen. We hereby designate the MNHN dried specimen (MNHN-B3640) (the only one that is still extant) as the lectotype of Sesarma elongatum. The material we have on hand from Madagascar to Sulawesi is clearly conspecific and we can find no significant morphological or genetic differences between them.

Ecology. Selatium elongatum is a tree-climbing species from mangroves. Hartnoll (1975) states that it can also be found sheltering beneath rocks and mentions that Fourmanoir (1954) records it from pools at the high water mark in Madagascar. However, we could not find this record by Fourmanoir despite careful reading of that source. The present specimens from Sulawesi were found in mangrove tree holes or climbing along the trunk slightly above sea water level. Cannicci et al. (1999) indicated that in Kenya this species is active at
FIGURE 5. *Selatium elongatum* (A. Milne-Edwards, 1869). Lectotype male (34.4 x 36.2 mm) (MNHN-B3640), Madagascar. A, dorsal view; B, dorsal view of carapace; C, anterior thoracic sternum and abdomen.
high tide and feeds on floating algae and mangrove leaves. These authors also found that males defend their activity areas from other large males. This explains the marked sexual dimorphism in cheliped size of this species, with prominent male chelae.

**Lithoselatium n. gen.**

*Type species.* *Lithoselatium pulchrum n. sp.*, by present designation.

*Diagnosis.* Carapace slightly trapezoidal, diverging towards posterior carapace margin; lateral margins entire, without epibranchial tooth (occasionally indicated by low granule); regions of carapace relatively well defined by distinct grooves; frontal margin deflexed; anterior frontal lobes prominent but relatively less strongly
produced anteriorly, posterior frontal lobes weakly demarcated; antennae entering orbits; basal segments of antennae and antennules mobile, not separated by septum; Verwey’s groove delimited by dorsal and ventral rows of setae. Exopod of third maxilliped with long flagellum. Cheliped merus with expanded foliaceous distal margin, lined with small tubercles or sharp granules. Chelae with stridulating structure: dorsal margin of palm with 1 longitudinal crest of tubercles, partly pectinated, with 33–37 teeth in males; dorsal margin of dactylus with ca. 30 dome-shaped tubercles; fingers relatively long, tips of fingers hoofed with sharp cutting edges; inner surface of palm convex, with no obvious transverse ridge or aggregation of prominent granules. Ambulatory legs 1–4 relatively long, dactylus distinctly longer than half propodal length. Coxae of ambulatory legs 1–3 lined with numerous short setae on lateral margins; lateral and ventral surfaces with dense tufts of long setae, densest on coxae of second leg; dactylus longer than half length of propodus; propodal-dactylar condyle prominent but relatively smaller than in Selatium. Thoracic sternal suture 1/2 completely fused; suture 3/4 separated by complete suture; sutures 4/5, 5/6, 6/7, 7/8 medially interrupted, separated by wide gap; deep longitudinal median groove present on sternites 7, 8; male sterno-abdominal cavity almost reaching suture of thoracic sternites 3, 4; part of thoracic sternite 8 visible, when male pleon fully closed. Telson of male abdomen with length subequal to width, all somites free. G1 stout, with bifurcated pectinated tip; G2 short.

**FIGURE 7.** *Selatium elongatum* (A. Milne-Edwards, 1869). Male (40.1 x 40.9 mm) (ZRC 2000.1738), Tomini Bay, Sulawesi. A, dorsal view of pectinated ridge on palm; B, ridge on dactylus of chela.

**Etymology.** The first part of the name is derived from the Greek *lithos* for rock, in reference to the preferred habitat of the genus. It is combined with the genus name *Selatium*, due to their overall similarities. The gender is neuter.

**Remarks.** See *General Discussion.*
FIGURE 8. Selatium elongatum (A. Milne-Edwards, 1869). Male (40.1 x 40.9 mm) (ZRC 2000.1738), Tomini Bay, Sulawesi. A, abdomen; B, left third maxilliped (denuded); C, left side of anterior thoracic sternum; D, dorsal view of left G1 (denuded); E, ventral view of left G1 (denuded); F, dorsal view of distal part of left G1 (denuded); G, ventral view of distal part of left G1 (denuded).
Lithoselatium pulchrum n. sp.
(Figs. 9–12)

Material examined. Taiwan: Holotype male (23.5 x 20.8 mm) (ZRC 2002.0152), Yakoulu, Manchou, Pingtung County, Taiwan, rocky shore with tide pools, coll. H.-C. Liu, 27 August 1999 (DNA voucher); paratypes: 1 female (23.2 x 20.1 mm with eggs) (ZRC 2002.0152), same data as holotype; 1 female (18.1 x 15.7 mm), Chuanfanshih, Hengchun, Pingtung County, Taiwan (ZRC 1999.0555), coll. P. K. L. Ng et al., 31 May 1997; 2 females (25.7 x 22.5 mm, 18.7 x 16.1 mm), 1 ovigerous female (25.1 x 22.1 mm) (HC Liu, to be deposited at TMCD), Yakoulu, Manchou, Pingtung County, Taiwan. coll. H.-C. Liu, 29 August 1999; 1 female (23.5 x 20.3 mm) (HC Liu, to be deposited at TMCD), Yakoulu, Manchou, Pingtung County, Taiwan. coll. H.-C. Liu, 25 May 1999; 3 females (23.3 x 19.9 mm, 22.3 x 19.5 mm, 19.3 x 16.2 mm), 1 ovigerous female (23.3 x 20.0 mm) (HC Liu, to be deposited at TMCD), Yakoulu, Manchou, Pingtung County, Taiwan. coll. H.-C. Liu, 27 August 1999; 1 male (18.1 x 15.1 mm) (NTOU), Chuanfanshih, Hengchun, Pingtung County, Taiwan, coll. P.-H. Ho, 2004.

Type locality. Taiwan, Pingtung County, Manchou.

Diagnosis. Carapace trapezoidal, lateral margins distinctly diverging posteriorly; lateral margins entire without epibranchial tooth, but occasionally 1 or 2 low granules (Fig. 10A, B); frontal margin with 2 low, gently convex lobes not produced anteriorly, posterior lobes distinct (Fig. 10A, B); outer inner surfaces of chelae finely granular (Fig. 11B); dorsal margin of palm with continuous longitudinal crest of proximal tubercles, followed by pectinated crest consisting of 36 or 37 teeth, approximately 5 distal tubercules; 3–5 short, oblique rows of tubercles on inner side (Fig. 11C); dorsal margin of dactylar finger with row of 34 or 35 tubercles; all tubercles broad with exception of proximal 2, dome-shaped, transversely striated with yellow apex in life, becoming more widely spaced towards distal (Fig. 11D); cutting edge of dactylus with 2 or 3 larger teeth proximally, larger tooth subdistally; cutting edge of pollex with 2 or 3 larger teeth medially, larger tooth subdistally (Fig. 11B); G1 with pectinated distal part; subtruncate tip with slight cleft, lower part larger than upper (Fig. 12D–G).

Description of male holotype. Carapace trapezoidal, lateral margins distinctly diverging toward posterior margin; dorsal surfaces smooth, regions well defined by distinct grooves; surface adjacent to anterolateral margins lined with weak, oblique striae; gastrocardiac surface with distinct groove. Postfrontal lobes distinct; 2 median lobes larger with finely granular margins, without clearly visible anterior ridge; 2 lateral lobes low with finely granular margins; lobes separated by distinct grooves. Front strongly deflexed downwards, with 2 low, gently convex lobes separated by broad, shallow cleft, not strongly produced anteriorly. Supraorbital margin entire. Anterolateral margin entire, confluent with posterolateral margin, without epibranchial tooth; 1 or 2 very low granules may mark rudimentary teeth. Supraorbital margin entire. Anterolateral margin entire, confluent with posterolateral margin, without epibranchial tooth; 1 or 2 very low granules may mark rudimentary teeth. Posterolateral margin gently diverging towards convex posterior carapace margin. Epistome with pronounced horizontal ridge, medially concave; posterior margin with median triangular projection, lateral part with 2 concave indentations. Verwey’s groove delimited by dorsal and ventral rows of setae. Infraorbital ridge tuberculate, evenly setose. Pterygostomial region tuberculate, covered by distally curved setae. Antenna entering orbit; basal segments of antenna and antennules not separated by septum; basal antennal segment mobile. Ischium of third maxilliped with shallow submedian sulcus; merus subovate with distinct submedian longitudinal setose ridge extending to anteroexternal angle of ischiium; exopod slender, with long flagellum.

Chelipeds equal in size and shape. Outer surface of chelae slightly granular, inner surface with fewer, somewhat coarser granules, without distinct transverse ridge; ventral border straight; dorsal margin of palm with continuous longitudinal crest of proximal tubercles, followed by pectinated crest consisting of 36 or 37 teeth and approximately 5 distal tubercules; 3–5 short, oblique subsidiary rows of tubercles on inner side; fingers long, more than half length of ventral margin of palm; dorsal margin of dactylus with row of 34 or 35 tubercles; all tubercles broad with exception of proximal 2, dome-shaped, transversely striated with yellow apex in life, becoming more widely spaced towards distal part; cutting edge of dactylus with 2 or 3 larger teeth proximally, larger tooth subdistally; cutting edge of pollex with 2 or 3 larger teeth medially, larger tooth subdistally; tips of fingers hoofed (medially excavated) with sharp cutting edges. Outer surface of carpus
FIGURE 9. Lithoselatium pulchrum n. sp., colour in life. A, B, holotype male (23.5 x 20.8 mm) (ZRC 2002.0152), Taiwan; B, C, paratype male (18.1 x 15.1 mm) (NTOU), Taiwan. A, B, dorsal views; C, ventral view.
FIGURE 10. *Lithoselatium pulchrum* n. sp. Holotype male (23.5 x 20.8 mm) (ZRC 2002.0152), Taiwan. A, dorsal view; B, dorsal view of carapace; C, frontal view of carapace.

rugose; inner distal angle not distinctly produced, margins weakly granulated. Outer face of merus strongly convex, with rows of granules; inner face granular, strongly expanded distally, appearing foliaceous, with
subdistal tooth on dorsal margin, distal margins lined with small granules or tubercles, distal portion dorsally visible, even when chelipeds apposed tightly against carapace; inner face with 2 longitudinal rows of stiff setae, ventral row continuous, with longer setae. Basis and ischium immobile but separated by distinct suture, surface with scattered granules.

Ambulatory legs long, third pair longest. Lateral margins of coxae of legs 1–3 with numerous short setae; lateral and ventral surfaces with dense long tufts of long setae; those on first leg concentrated on posterior portion, those of leg 3 on anterior portion, those of leg 2 densest and longest, covering surface. Outer surfaces of meri, carpi, propodi rugose. Meri laterally flattened, foliaceous, margins finely granulated; with low subdistal dorsal spine; outer part of postero-distal margin slightly expanded, anterior surface convex. Outer surface of carpi with 2 distinct carinae. Distal third of propodi with tufts of short setae dorsally and ventrally. Dactylo-propodal lock absent, propodal-dactylar condyle not enlarged. Dactylus elongate, distinctly longer than half length of propodi, densely setose dorsally and ventrally.

Margins of anterior thoracic sternites and surfaces of sternites 1–4 setose. Sternites 1, 2 completely fused, suture concave toward buccal cavity; suture 3/4 separated by complete suture; sutures 4/5, 5/6, 6/7, 7/8 medially interrupted, separated by wide gap; deep longitudinal median groove present on sternites 7, 8; male sterno-abdominal cavity almost reaching suture 3/4; part of sternite 8 clearly visible when male pleon fully closed. Penis partially calcified, sternal.

Abdomen triangular; lateral margins of abdominal somites 3 and 6 convex, lateral margins of somites 4, 5 gently concave. Telson subcircular, width and length subequal.

G1 relatively stout, subdistal part only slightly wider than median part, almost straight from ventral view; pectinated distal part prominently bifurcated, lower part larger than upper part. G2 very short, distally spatuliform, no distal segment present.

**Females.** Chelipeds of females also homochelous, but relatively small compared to male chelipeds; tubercles on dorsal margin of dactylus reduced. Pectinated crest on palm shorter with 16 or 17 broad teeth, longitudinal crest completed by row of tubercles. Margins of all abdominal somites in contact with bases of ambulatory legs; telson sunken into anterior margin of somite 6. Gonopores elevated, bilobed.

**Colour.** Carapace and legs purplish in life; carapace with yellowish-green mottling; chelae pink-red (Fig. 9).

**Ecology.** *Lithoselatium pulchrum* n. sp. has so far only been collected from rocky shores in southern Taiwan. It constructs burrows in sandy areas between the rocks and can often be found in tide pools. The preferred habitat seems to be the surge channels of eroded and rugged limestone with many crevices and rock pools. The crab usually lives in crevices close to the supralittoral zone. The salinity of tide pools close to the burrows inhabited by *L. pulchrum* ranges from 0–33‰. Only three mature males have been found thus far (one not preserved), although females and juveniles are often seen. During a two-week collecting trip in 2007 by the second author, three immature males and 14 females (11 of them adult) were collected and most subsequently released. The smallest ovigerous female had a carapace width of 18.9 mm and the smallest mature female (determined by the morphology of abdomen) measured 17.0 mm. Two ovigerous females were observed at the surf zone about to release their larvae. Another two females were collected from the surf zone with eggs about to hatch. Ovigerous females were found from July to October.

In laboratory conditions, females bred between April and October. Two captive females became ovigerous twice without mating. It appears that even after ecdysis, the female can lay fertilized eggs without mating. A female collected in September 2007 moulted in February 2008, and became ovigerous in captivity in June 2008, in the absence of a male. Eggs of *L. pulchrum* are large and yolky, and hatch as highly developed larvae. Eggs in an early stage of development are relatively large and have a diameter of 1.09 ± 0.02 mm (n = 10). These eggs reached their maximum size of about 1.25 ± 0.04 mm (n = 11) just before hatching. The incubation was about 43 days under laboratory conditions of 19°–28°C. Ovigerous females only released their larvae at night, with the entire release process lasting only a few seconds. The number of hatched larvae varied between 525 and 1158 (n = 5), and was dependent on the size of the females, with fecundity directly increasing with size (Kuo 2008).
FIGURE 11. Lithoselatium pulchrum n. sp. Holotype male (23.5 x 20.8 mm) (ZRC 2002.0152), Taiwan. A, anterior thoracic sternum and abdomen; B, outer view of right chela; C, dorsal view of ridge on palm; D, ridge on dactylus of palm.
**FIGURE 12.** Lithoselatium pulchrum n. sp. Holotype male (23.5 x 20.8 mm) (ZRC 2002.0152), Kenting, Taiwan. A, abdomen; B, left third maxilliped (denuded); C, left side of anterior thoracic sternum; D, dorsal view of left G1 (denuded); E, ventral view of left G1 (denuded); F, dorsal view of distal part of left G1 (denuded); G, ventral view of distal part of left G1 (denuded); H, left G2 (denuded).

**Etymology.** From Latin *pulcher* for “beautiful” used as an adjective, in reference to the pretty colour of the new species.
Lithoselatium kusu n. sp.
(Figs. 13–16)

Material examined. Singapore: Holotype male (16.0 x 14.35 mm) (ZRC 2002.0149), Singapore: Kusu Island: between loose rocks, coll. C. D. Schubart, 26 December 1999 (DNA voucher); paratypes: 1 male (16.8 x 14.95 mm), 2 juvenile females (14.15 x 12.4 & 11.95 x 10.3 mm) (ZRC 2002.0150), same collection data as holotype; 1 juvenile female (ZRC 2009.0568), Sentosa Island: rock jetty, coll. C. D. Schubart, 15 August 1999; 7 males (largest 29.0 x 25.8 mm), 9 females (largest 29.1 x 26.0 mm) (ZRC 2009.0569), Raffles Lighthouse, coll. H. H. Tan et al., 30 January 2002; 5 females (20.9 x 17.8, 19.2 x 16.2, 17.0 x 14.4, 17.0 x 14.5, 16.2 x 13.5 mm, smallest DNA voucher), 2 juvenile males (12.1 x 10.2, 11.31 x 9.64 mm), 1 juvenile female (11.34 x 9.72 mm) (SMF-33840), Labrador Beach, coll. C. D. Schubart, S. Klaus & P. Koller, 19

**FIGURE 14.** *Lithoselatium kusu* n. sp. Holotype male (16.0 x 14.35 mm) (ZRC 2002.0149), Kusu Island, Singapore. A, dorsal view; B, dorsal view of carapace; C, frontal view of carapace.
FIGURE 15. Lithoselatium kusu n. sp. Holotype male (16.0 x 14.35 mm) (ZRC 2002.0149), Kusu Island, Singapore. A, anterior thoracic sternum and abdomen; B, outer view of right chela; C, dorsal view of ridge on palm; D, ridge on dactylus of palm.
FIGURE 16. Lithoselatium kusu n. sp. Holotype male (16.0 x 14.35 mm) (ZRC 2002.0149), Kusu Island, Singapore. A, abdomen; B, left third maxilliped (denuded); C, dorsal view of left G1 (denuded); D, ventral view of left G1 (denuded); E, dorsal view of distal part of left G1 (denuded); F, ventral view of distal part of left G1 (denuded).

Type locality. Singapore, Kusu Island.

Diagnosis. Carapace slightly trapezoidal, diverging toward posterior margin; lateral margins entire, without trace of epibranchial tooth (Fig. 14A, B); frontal margin with anterior lobes prominent, posterior lobes weakly demarcated (Fig. 14A, B); outer and inner surfaces of chelae smooth (Fig. 15B); dorsal margin of palm with one continuous longitudinal crest of proximal tubercles, followed by a pectinated crest consisting of 33 or 34 teeth, and approximately 5 or 6 partly fused distal tubercles (fewer, broader and shorter teeth in females); 3–5 short and oblique subsidiary rows of tubercles on inner side (Fig. 15C); dorsal margin of dactylar finger with a row of 30–32 tubercles, with circular rings and a central conical apex, more widely spaced towards distal part (Fig. 15D); cutting edge of with 2 larger teeth proximally and one larger tooth subdistally; cutting edge of pollex with 2 larger teeth proximally to medially and one larger tooth subdistally (Fig. 15B); G1 with pectinated distal part subtruncate, tip gently clefted, lower part larger than upper part (Fig. 16C–F). Proportionally shorter legs compared to L. pulchrum.
Etymology. The name kusu is used as a noun and refers to the type locality of the new species, the small island south of Singapore. In Chinese kusu means “turtle”, describing the shape of the island.

Colour. In life, carapace and legs purplish; carapace with yellowish-green mottling; chelae orangish-red (Fig. 13).

Remarks. Lithoselatium kusu n. sp. can be morphologically separated from L. pulchrum n. sp. by its proportionately shorter ambulatory legs and, if alive, by the strikingly different colour pattern.

Ecology. Lithoselatium kusu is so far known from Labrador Beach, Kusu I., Sentosa I. and Raffles Lighthouse (Singapore) as well as from an island off Sabah. The species was found among coarse rock and coral rubble well above the water line in all localities. When chased, it moves rapidly between the rocks without necessarily seeking protection in the water.

General discussion

Although superficially similar, Lithoselatium n. gen. differs from Selatium sensu stricto in several key characters: distinctly more trapezoidal carapace (Figs. 10A, B, 14A, B) (quadrate to rectangular in Selatium, Figs. 1A, B, 5A, B); lower and less anteriorly produced frontal lobes (Figs. 10B, 14B) (more prominent frontal lobes in Selatium, Figs. 1B, 5B); expanded foliaceous distal margin of the cheliped merus being armed with small tubercles or sharp granules (Figs. 10A, 14A) (prominent spines or teeth in Selatium, Figs. 1A, 5A); inner surface of the palm being convex and having no obvious transverse ridge or aggregation of prominent granules (inner surface of the palm of the male cheliped has a raised transverse ridge lined with granules in Selatium, especially prominent in S. elongatum); proportionately longer dactylus of ambulatory legs 1–4, distinctly longer than half propodal length (Figs. 10A, 14A) (short, about one third length in Selatium, Figs. 1A, 2B, 5A); relatively smaller propodal condyle of ambulatory legs (relatively larger in Selatium); presence of a prominent tuft of setae between coxae of ambulatory legs 2 and 3 (Figs. 11A, 15A, 17B, C) (absent in Selatium, Figs. 2A, 5C, 6A, 17A); part of sternite 8 being exposed when male abdomen fully closed (Fig. 17B, C) (sternite 8 not visible, when male abdomen fully closed in Selatium, Fig. 17A); the male telson is relatively more squarish (Figs. 12A, 16A) (slightly longer than wide in Selatium, Figs. 4A, 8A); and by the tip of the pectedinated part of the G1 being bifurcated (Figs. 12F, G, 16E, F) (tapered and sharp in Selatium, Figs. 4F, G, 8F, G).

The visibility of the male thoracic sternite 8 when the abdomen is completely closed is a valuable character which has been occasionally used in brachyuran taxonomy, notably in a revision of the pilumnid genera Pilumnopeus and Heteropanope (see Davie 1989; Hsueh et al. 2009) as well as in studies of the goneplacoids (see discussion in Ng & Manuel-Santos 2007). Sternite 7 is the last visible thoracic sternite when the male abdomen is closed in Selatium, the episternite 7 being large, prominent and bracketing male abdominal somites 2 and 3. Sternite 8 is compressed by sternite 7 and pushed inwards, and is completely covered by the male abdomen. In Lithoselatium, however, a small portion of sternite 8 is still visible, and resembles a small plate present adjacent to sternite 8 and the abdominal margin.

The molecular evidence argues for the reciprocal monophyly of the genera Lithoselatium and Selatium (confidence values 99–100%, Fig. 18). At the same time, it is also evident that these two genera do not necessarily have to be sister taxa since the genus Clistocoeloma seems to be similarly close to Selatium and Lithoselatium. In contrast, members of two other common genera with a longitudinal pectinated crest on the carpus of the male chela (Episesarma and Neosesarma) are phylogenetically farther separated from Selatium and Lithoselatium. For Selatium, our genetic data allowed intraspecific comparisons of East African representatives with others from Southeast Asia as far east as Sulawesi (S. elongatum) and Philippines (S. brocki). For both species, very close genetic similarity or intraspecific identity of 16S rDNA haplotypes made it evident that no major phylogeographic break seems to be present within the Indian Ocean. The opposite has recently been shown for the mangrove sesarmid crab Neosarmatium meinerti (see Ragionieri et al., 2009). In contrast to the pronounced genetic differences between the two species of Selatium, genetic differences
between the two species of *Lithoselatium* are shallower, resulting in lower confidence values in the support of monophyletic species and suggesting a more recent speciation. It will be interesting to obtain new records from this genus between Singapore and Taiwan as well as other areas.

**FIGURE 18.** Bayesian Inference tree obtained with GTR+G model of nucleotide substitution and *Sesarma reticulatum* as outgroup (2 million generations, 4 chains). Confidence values shown (only >50): BI posterior probabilities / MP bootstrap values after 2000 pseudoreplicates.

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