

A new species of *Gebiacantha* Ngoc-Ho, 1989 (Decapoda: Gebiidea: Upogebiidae) from Hainan Island, China

Qi Kou^{1,2,3}, Gary C. B. Poore⁴ & Xuefeng Fang^{5*}

Abstract. A new species of mud shrimp, *Gebiacantha sinica*, new species, is described based on two specimens collected from Sanya, off the south coast of Hainan Island, northern continental shelf of the South China Sea, at a depth of 50–70 m. *Gebiacantha sinica*, new species, appears closest to *G. monoceros* (De Man, 1905) and *Gebicula irawadyensis* Sakai, 2006, both of whose type locality is Java, Indonesia. The new species can be distinguished from these two species in the ventral margin of antennal peduncle article 4 with 2 spines and the lateral surface of pereopod 1 carpus with a shallow longitudinal carina bearing 1 or more spinules. *Gebiacantha* Ngoc-Ho, 1989 is revised and now comprises 22 extant species, including the new species and *G. irawadyensis* (Sakai, 2006), new combination. The multi-gene phylogenetic tree supports the monophyly of *Gebiacantha*, despite limited taxon sampling, but does not support the validity of *Austinogebia* Ngoc-Ho, 2001, which should be synonymised with *Upogebia* Leach, 1814.

Key words. *Gebiacantha sinica*, *Gebicula*, molecular phylogeny, mud shrimp, revision, South China Sea, West Pacific

INTRODUCTION

Ngoc-Ho (1989) established a new upogebiid genus *Gebiacantha* including eleven species, with *Upogebia talismani* Bouvier, 1915 as the type species. After that, more species were described (Sakai, 1993; Ngoc-Ho, 1994a, b, 2005) and this genus was rediagnosed accordingly (Ngoc-Ho, 1994b, 2001, 2003). Sakai (2006) doubted the validity of *Gebiacantha* and synonymised it with *Upogebia* Leach, 1814. However, because Sakai's argument was actually unjustified (Ngoc-Ho, 2007; Poore, 2008; Komai, 2020), this synonymy was not accepted by other authors in subsequent works (e.g., Ngoc-Ho, 2007, 2014; Liu, 2010; Garassino et al., 2012; Komai, 2017, 2020; Dworschak, 2019). Currently, this genus contains 20 extant species distributed in the intertidal to subtidal zones of the western and central Indo-Pacific (18 spp.) and the subtropical Atlantic (2 spp.) (Komai, 2020; Poore & Ah Yong, 2023; DecaNet, 2026). Among these, only two species, *G. acanthochela* (Sakai, 1967) and *G. lagonensis* Ngoc-Ho, 1989, have been reported from Chinese

seas (Sakai, 1967; Liu, 2010; Komai, 2020). Recently, two upogebiid mud shrimps collected from Sanya, off the south coast of Hainan Island, northern continental shelf of the South China Sea, revealed the presence of an undescribed species of this genus. The new species is described and illustrated herein. Despite limited taxon sampling, multi-gene analyses on the monophyly and phylogenetic position of *Gebiacantha* is provided.

MATERIAL AND METHODS

Two individuals of the mud shrimps were collected by a fishing vessel using a bottom trawl off the south coast of Hainan Island in December 2024. The specimens were fixed and preserved in 99.5% ethanol on board. After the specimens were unloaded and carried to laboratory, preservation solution was replaced with 75% ethanol.

The specimens were examined and illustrated using a Zeiss SteREO Discovery V8 stereo microscope with a camera lucida attachment. Unimportant setae were omitted from illustrations for clarity. Local images were captured under a Nikon SMZ25 stereomicroscope. Stacks of frames of different focal planes were combined using NIS-Elements. Carapace length (cl) was measured from the tip of the rostrum to the posterior end of the carapace. Total length (tl) was measured from the tip of the rostrum to the posterior end of the telson, with the body stretched. The mandible, maxillule, and maxilla, which provide limited taxonomic information at the generic level, were not dissected. Maxillipeds 1 and 2 of the female specimen were photographed but not further illustrated.

Accepted by: Yang Chien-Hui

¹Institute of Oceanology, Chinese Academy of Sciences, Qingdao, Shandong 266071, China

²Laboratory for Marine Biology and Biotechnology, Laoshan Laboratory, Qingdao, Shandong 266237, China

³University of Chinese Academy of Sciences, Beijing 100049, China

⁴Museums Victoria, Melbourne, Vic. 3001, Australia

⁵National Marine Environmental Monitoring Center, Dalian, Liaoning 116023, China; Email: xffang@nmemc.org.cn (*corresponding author)

Table 1. Species used in molecular phylogenetic analyses with NCBI accession numbers. New nucleotide sequences are in bold.

Family	Species	Voucher ID	12S	16S	COI	18S	H3
Laomedidae Borradaile, 1903	<i>Axianassa australis</i> Rodrigues & Shimizu, 1992	NMV-J44613	MH234568	MH234568	MH234568	a*	a*
	<i>Axianassa intermedia</i> Schmitt, 1924	SAMN10953848	b*	b*	b*	b*	b*
	<i>Jaxea nocturna</i> Nardo, 1847		N/A	AF436046	AF436030	AF436006	N/A
	<i>Jaxea novaezealandiae</i> Wear & Yaldwyn, 1966	MTS-72593	PZ383222	PZ383225	PZ405947	PZ383228	PZ398375
Laomedidae	<i>Laomedea astacina</i> De Haan, 1841	MBM-Xinying	PV801420	PV816549	PV801007	PV801318	PV818843
	<i>Laomedea healyi</i> Yaldwyn & Wear, 1970	AM-P41482	MH234569	MH234569	MH234569	c*	c*
	<i>Naushonia</i> sp. indet.	SAMN10953849	d*	d*	d*	d*	d*
	<i>Thalassinia anomala</i> (Herbst, 1804)	SAMN44790395	e*	e*	e*	e*	e*
Thalassinidae Latreille, 1831	<i>Thalassinia kelanang</i> Moh & Chong, 2009		JN897378	JN897378	JN897378	N/A	N/A
	<i>Thalassinia squamifera</i> De Man, 1915	SAMN09789139	MG551498	MG551498	MG551498	f*	f*
	<i>Austinogebina edulis</i> (Ngoc-Ho & Chan, 1992)		JN897376	JN897376	JN897376	N/A	KJ133064
	<i>Austinogebina monospina</i> Liu & Liu, 2012	MBM-D7	PZ383223	PZ383226	PZ405948	PZ383229	PZ398376
Upogebiidae Borradaile, 1903	<i>Austinogebina narutensis</i> (Sakai, 1986)	NTOU-A00416	N/A	EF585443	AB771730	EF585454	N/A
	<i>Austinogebina wuhshienweni</i> (Yu, 1931)	MBM-Zhangjiang2	PV801421	PV816550	PV801008	PV801319	PV818844
	<i>Gebiacantha plantae</i> (Sakai, 1982)	NMV-J44914	MG551492	MG551492	MG551492	g*	g*
	<i>Gebiacantha sinica</i> , new species	MBM-304657	PZ383224	PZ383227	PZ405949	N/A	N/A
	<i>Upogebia affinis</i> (Say, 1818)	NMV-J40668	MH234572	MH234572	MH234572	h*	h*
	<i>Upogebia africana</i> (Ortmann, 1894)	SAMN15945744	i*	i*	i*	i*	i*
	<i>Upogebia bowerbankii</i> (Miers, 1884)	NMV-J53465	MG551499	MG551499	MG551499	j*	j*
	<i>Upogebia major</i> (De Haan, 1841)	MBM-B2882	PV801422	PV816551	PV801009	PV801320	PV818845
	<i>Upogebia pusilla</i> (Petagna, 1792)		KC107815	KC107815	KC107815	N/A	N/A
	<i>Upogebia yokoyai</i> Makarov, 1938		KM886610	KM886610	KM886610	N/A	N/A

a*: sequences recovered from WGS data of SRR7698901; b*: sequences recovered from WGS data of SRR8705899; c*: sequences recovered from WGS data of SRR7698907; d*: sequences recovered from WGS data of SRR8705898; e*: sequences recovered from WGS data of SRR8705898; f*: sequences recovered from WGS data of SRR7698904; g*: sequences recovered from WGS data of SRR7698906; h*: sequences recovered from WGS data of SRR7698905; i*: sequences recovered from WGS data of SRR12572948; j*: sequences recovered from WGS data of SRR7698908. Abbreviations: Australian Museum, Sydney (AM); Marine Biological Museum, Chinese Academy of Sciences, Qingdao (MBM); the Marine Invasives Taxonomic Service from National Institute of Water and Atmospheric Research, Wellington (MTS); Museums Victoria, Melbourne, Australia (NMV); National Taiwan Ocean University, Keelung (NTOU); BioSample accessions in NCBI database (SAMN).

A small piece of muscle tissue was taken from the paratype for total genomic DNA extraction. Five genes, mitochondrial COI, 16S rRNA and 12S rRNA plus nuclear H3 and 18S rRNA, were amplified and sequenced for phylogenetic tree building. The molecular procedures employed in this study followed Kou et al. (2025). Specimens of the new species are deposited in the Marine Biological Museum, Chinese Academy of Sciences, Qingdao, China (MBM). Additional specimens used for phylogenetic analyses are deposited in MBM and National Institute of Water and Atmospheric Research, Wellington, New Zealand (NIWA) provided from the Marine Invasives Taxonomic Service (MITS). Nucleotide sequences of 19 additional gebiidean species from NCBI database, that we were confident on their reported identifications were included in the analyses (Table 1). All newly generated DNA sequences have been deposited in the NCBI database.

TAXONOMY

Family Upogebiidae Borradaile, 1903

Genus *Gebiakantha* Ngoc-Ho, 1989

Gebiakantha Ngoc-Ho, 1989: 118. – Sakai, 1993: 98. – Ngoc-Ho, 1994b: 59. – Poore, 1994: 105 (key). – Ngoc-Ho, 2001: 54. – Davie, 2002: 481. – Ngoc-Ho, 2003: 505. [– Liu, 2010: 220.] – Poore & Ah Yong, 2023: 243.
Gebicula. – Sakai, 2006: 24 (part). [– Liu, 2010: 225 (part).] – Sakai, 2011: 1127 (part).
Upogebia. – Sakai & Türkay, 1995: 198 (part). – Sakai, 2006: 38 (part). – Sakai, 2011: 1130 (part).

Type species. *Upogebia talismani* Bouvier, 1915, by original designation.

Species included. *Gebiakantha acanthochela* (Sakai, 1967), *G. acutispina* (de Saint Laurent & Ngoc-Ho, 1979), *G. albengai* Ngoc-Ho, 2005, *G. arabica* Ngoc-Ho, 1989, *G. bermudensis* (Williams, 1993), *G. ceratophora* (De Man, 1905), *G. dampieri* Ngoc-Ho, 2007, *G. fortispinata* Komai, 2020, *G. irawadyensis* (Sakai, 2006), new combination, *G. lagonensis* Ngoc-Ho, 1989, *G. laurentae* Ngoc-Ho, 1989, *G. lifuensis* Ngoc-Ho, 1994a, *G. monoceros* (De Man, 1905), *G. multispinosa* Ngoc-Ho, 1994a, *G. plantae* (Sakai, 1982), *G. poorei* Ngoc-Ho, 1994b, *G. priochea* Sakai, 1993, *G. reunionensis* Ngoc-Ho, 1989, *G. richeri* Ngoc-Ho, 1989, *G. sagamiensis* Komai, 2017, *G. sinica*, new species, *G. talismani* (Bouvier, 1915).

Remarks. For recent diagnoses of *Gebiakantha* Ngoc-Ho, 1989, see Ngoc-Ho (2003) and Poore & Ah Yong (2023). Ngoc-Ho (2001) considered *Gebiakantha* to have a close affinity with *Austinogebina* Ngoc-Ho, 2001, both sharing: (1) one or more infrarostral spines; (2) numerous spinules on anterolateral margin of carapace; (3) prominent spines along upper margin of pereopod 1 carpus and propodus; (4) uropodal exopod not significantly longer than telson. However, *Gebiakantha* can be easily distinguished from *Austinogebina* by: (1) lateral ridges of gastric region not

forming strong projections; (2) maxilliped 1 without epipod; (3) lower margin of pereopod 1 propodus with large spine posterior to fixed finger; (4) posterior margin of telson medially concave; (5) lateral margin of uropodal exopod without prominent knob proximally. In fact, their close relationship is not supported by recent molecular data, as *Austinogebina* is always deeply embedded in *Upogebina*, and they form a clade which is sister to *Gebiakantha* in the phylogenetic trees (Fig. 9; Kou et al., 2025: fig. 3).

Another upogebiid genus potentially closely allied with *Gebiakantha* is *Gebicula* Alcock, 1901, exhibiting similar chelipeds. *Gebicula* was established based on a single specimen of *Gebicula exigua* Alcock, 1901 collected from the Andaman Sea at a depth of 485 m. *Gebicula exigua* is distinctive in having only one proximal spine on each side of dorsolateral margin of the rostrum and the dorsal surface and ventral margin unarmed; lower margin of pereopod 1 propodus with one large subdistal tooth and several small teeth posteriorly; upper and lower margins of pereopod 3 carpus and lower margin of pereopod 4 merus armed; and uropodal exopod more than twice as long as telson (cf. Alcock, 1901). Sakai (1982) synonymised *Gebicula* with *Upogebia*, and transferred *G. exigua* into his new genus *Wolffogebia* Sakai, 1982. He also described a male specimen collected from the Irrawaddy Delta, Myanmar, as *Wolffogebia exigua* (Alcock, 1901). In addition, Sakai (1982) maintained that *U. monoceros* De Man, 1905 was a junior synonym of *G. exigua* in spite of numerous significant differences between the two species (e.g., armature of the rostrum, antennal peduncle, carapace and chelipeds, length of uropodal exopod, and depth range of habitat). Ngoc-Ho (1989) did not accept Sakai's (1982) synonymies, but acknowledged that the male specimen from Myanmar belonged to *U. monoceros* and transferred this species into *Gebiakantha*. Sakai & Türkay (1995) thought *Gebiakantha* was not a well-defined genus and Sakai (2006: 39) synonymised it with *Upogebia*. Meanwhile, Sakai (2006: 24) realised that his specimen from Myanmar was different from the holotype of *Gebicula exigua*, and he revived *Gebicula*. In addition, Sakai (2006: 25) described a new species of *Gebicula*, inexplicably named *G. irawadyensis*, based on two male specimens from the shallow water (18 m) of Batavia Bay, Indonesia. Although he asserted that these two specimens and the single male specimen previously identified as *Wolffogebia exigua* from Myanmar were the same, the Irrawaddy Delta is not the type locality as Sakai (2006: 28) stated. Given that Sakai's (2006) synonymy of *Gebiakantha* with *Upogebia* is not widely accepted, and following Ngoc-Ho (1989) it is possible that the two male specimens from Batavia Bay are *Gebiakantha monoceros* (De Man, 1905), or at least, belong to *Gebiakantha* rather than *Gebicula*.

Indeed, there are some subtle differences between the specimens of *Gebicula irawadyensis* and the original description of *Upogebia monoceros* (cf. Table 2). However, since these specimens are very old, it is not feasible to verify whether these morphological differences represent intraspecific variation through using a molecular approach. Taking all of the above into consideration, we propose

Table 2. Comparison between *Gebiacantha sinica*, new species, and two morphologically similar species.

Species	<i>G. monoceros</i> (De Man, 1905)	<i>G. irawadyensis</i> (Sakai, 2006), new combination	<i>G. sinica</i> , new species
Specimens	holotype (female), northeast of Java, Indonesia	holotype and paratype (2 males), Batavia Bay, Indonesia	holotype and paratype (1 male, 1 female), south of Hainan, China
Ventral margin of rostrum	with 1 spine	with 3 spines	with 3 spines
Anterolateral margin of carapace	with 3 teeth	with 2 teeth	with 4 teeth
Pterygostomial angle	unarmed	unarmed	with 5 spinules
Ventral margin of antennal peduncle article 4	with 1 spine	with 1 spine (absent in Sakai's illustration)	with 1 spine
Scaphocerite	bifurcate	bifurcate	monospinous
Ischium of pereopod 1	lower margin with 1 spinule distally	lower margin with 1 spinule distally (absent in Sakai's illustration)	lower margin with 1 sharp spine distally
Carpus of pereopod 1	upper surface with 7 spines; lateral surface unarmed	upper surface with 3 spines; lateral surface unarmed	upper surface with 6 spines; lateral surface unarmed
Propodus of pereopod 1	mesial surface with 1 or 2 spines	mesial surface with longitudinal row of tubercles	mesial surface smooth
Fixed finger of pereopod 1	with a sharp tip	with a blunt tip	with a sharp tip
Merus of pereopod 2	lower margin with 2 spines	lower margin with 1 spine	unknown
Carpus of pereopod 2	upper margin with 4 spines	upper margin with 3 spines	unknown
Merus of pereopod 3	lower margin with 2 spines	unknown	unknown
Telson	lateral margin with 1 movable spinule	lateral margins unarmed	lateral margins unarmed
References	De Man (1905, 1928)	Sakai (2006)	Sakai (1982)

retaining *Gebicula irawadyensis* but place it in the genus *Gebiacantha*. The revised genus *Gebicula* is monotypic and confined to deep water, while *Gebiacantha* presently includes a total of 22 species generally inhabiting water shallower than 100 m. Our taxonomic treatment and the phylogenetic relationship between *Gebicula* and *Gebiacantha* are expected to be tested with additional genetic data from new materials in the future.

***Gebiacantha sinica*, new species**
[Chinese name: 中华棘螯蛄虾]
(Figs. 1–8)

Gebicula irawadyensis. [– Liu, 2010: 225–227, fig. 137. vii E, F (Not *Gebicula irawadyensis* Sakai, 2006)]

Type material. Holotype: Male (cl 4.3 mm, tl 12.5 mm), Sanya, off south coast of Hainan Island, northern continental shelf of the South China Sea, Northwest Pacific, 18°09'12"N, 109°41'42"E, 50–70 m depth, fishing vessel, bottom trawl, 3 December 2024, MBM 304656.

Paratype: Female (carapace and telson incomplete, size similar to male), same collecting information as holotype, MBM 304657.

Etymology. The species name indicates the locality of origin, China.

Diagnosis. Rostrum almost reaching distal end of article 4 of antennal peduncle, dorsolateral margins with 4–6 spiniform



Fig. 1. *Gebiacantha sinica*, new species, holotype, MBM 304656 (male, cl 4.3 mm, tl 12.5 mm), habitus in lateral view, 75% alcohol preserved specimen. Scale = 1 mm.

teeth, ventral margin with 1 or 2 spines. Carapace with hepatic spine and 4 teeth on anterolateral margin. Antennal peduncle article 3 with 1 ventral spine, article 4 with 2 ventral spines; scaphocerite monospinous. Pereopod 1 coxa with 1 prominent ventral spine; basis unarmed; ischium lower margin with 1 spine at midlength; merus upper margin with 1 subdistal spine, lower margin with row of 4 or 5 recurving spines; carpus upper surface with 7 or 8 irregularly arranged spines of various sizes, lateral surface with low longitudinal carina bearing 1 or several spinules, distomesial margin with 1 large spine, lower margin with 1 subdistal spine; propodal palm upper margin with row of 8–12 strong spines, submesial lower margin with 1 strong spine, mesial surface with longitudinal row of 5 or 6 spines; fixed finger inner margin unarmed; dactylus unarmed. Pereopod 2 merus upper margin with 1 subdistal spine, lower margin with 2 proximal spines; carpus upper margin with 4 spines, lower margin with 1 subdistal spine. Pereopod 3 merus upper margin with 1 subdistal spine, lower margin with 3 spines; dactylus lower margin with 5 spiniform setae. Pereopod 4 dactylus lower margin with 6 spiniform setae. Pereopod 5 dactylus lower margin with 7 spiniform setae. Uropodal endopod subtrapezoidal, with small knob-like tubercle proximally; exopod teardrop-shaped, 1.7 times as long as greatest width. Telson as wide as long, lateral margins armed with 1 movable spinule distally on each side, posterior margin slightly concave at median part.

Description of male holotype. Small upogebioid shrimp. Body weakly calcified. Pleon and telson together 1.8 times as long as carapace.

Rostrum almost reaching distal end of article 4 of antennal peduncle, subtriangular in dorsal view, 1.2 times as long as basal width, straight and flattened in lateral view, apex rounded in dorsal and lateral view; dorsal surface setose, dorsolateral margins with 4 (left) and 6 (right) spiniform teeth; ventral surface nearly straight, armed with 2 strong, anteriorly directed spines in distal half, distal spine larger, reaching apex of rostrum. Carapace somewhat compressed dorsoventrally; lateral gastric ridges nearly parallel, bearing row of 10 (left) and 12 (right) spiniform teeth decreasing in size posteriorly; gastric region flanked by shallow grooves

running along gastric lateral ridges and having 2 irregular, longitudinal rows of 12 tiny tubercles, extending anteriorly to rostral base on each side of midline; median naked area acutely triangular, flat, unarmed; anterolateral margin with 4 teeth, posterior-most indistinct; lateral postorbital region unarmed; pterygostomial margin rounded, unarmed; cervical groove distinct, extending to anterolateral notch; linea thalassinica interrupted by cervical groove, extending from anterolateral notch to posterodorsal margin of carapace, with prominent hepatic spine near intersection of linea thalassinica and cervical groove; branchiostegite unarmed.

Thoracic sternites 4–6 narrow, each separated by median slit forming pair of finger-like projection; sternite 7 broad, shield-shaped, with distinct groove in midline, anterolateral angles blunt.

Pleonites smooth, unarmed, slightly flattened; pleonites 1–5 tergites with distinct longitudinal groove on lateral surfaces, extending through whole somite; pleonite 1 narrow, posteroventral angle rounded; pleonite 2 1.1 times as long as pleonite 1 posterolateral margin rounded; pleonites 3–5 subequal in length, 0.8 times as long as pleonite 2, each posterolateral margin rounded, ventral margin with long setae; pleonite 6 longest, 1.7 times as long as pleonite 5, 1.2 times as wide as long (greatest width at 0.7 length of somite), with incomplete longitudinal groove on lateral surfaces, ventral margin almost straight, with small rounded posterolateral projection.

Eyestalk stout, subcylindrical, unarmed, reaching midlength of rostrum, widened basally; cornea pigmented, narrower than diameter of eyestalk.

Antennular peduncle overreaching distal margin of antennal peduncle article 4; article 1 subequal in length to distal 2 articles combined, with acute ventrodistal spine directed anteriorly, reaching midlength of article 2, statocyst lobe inflated; article 2 shortest, slightly widened distally, unarmed, 1.3 times as long as wide; article 3 cylindrical, unarmed, 3.0 times as long as article 2. Upper flagellum shorter than peduncle, of 10 articles; lower flagellum much more slender than upper flagellum, of about 9 articles.

Antennal peduncle article 1 widest, faintly granulate on distoventral margin; article 2 with 1 blunt distolateral tooth, dorsal margin unarmed; article 3 armed with 1 subdistal spine on ventral margin; article 4 with 2 spines on ventral margin, left side more separated, proximal spine larger, distal spine larger on right side; article 5 about half-length of article 4, unarmed; scaphocerite clearly demarcated basally, ending in 1 acute tooth (= monospinous). Flagellum about as long as carapace.

Maxilliped 1 without epipod. Maxilliped 2 without distinctive features. Maxilliped 3 endopod extending to distal margin of antennal peduncle article 4, ischium to dactylus unarmed, with dense long setae on lower margins; dactylus tapering, slightly shorter than propodus; exopod slender, not reaching midlength of merus, flagellum 0.6 times as long as basal

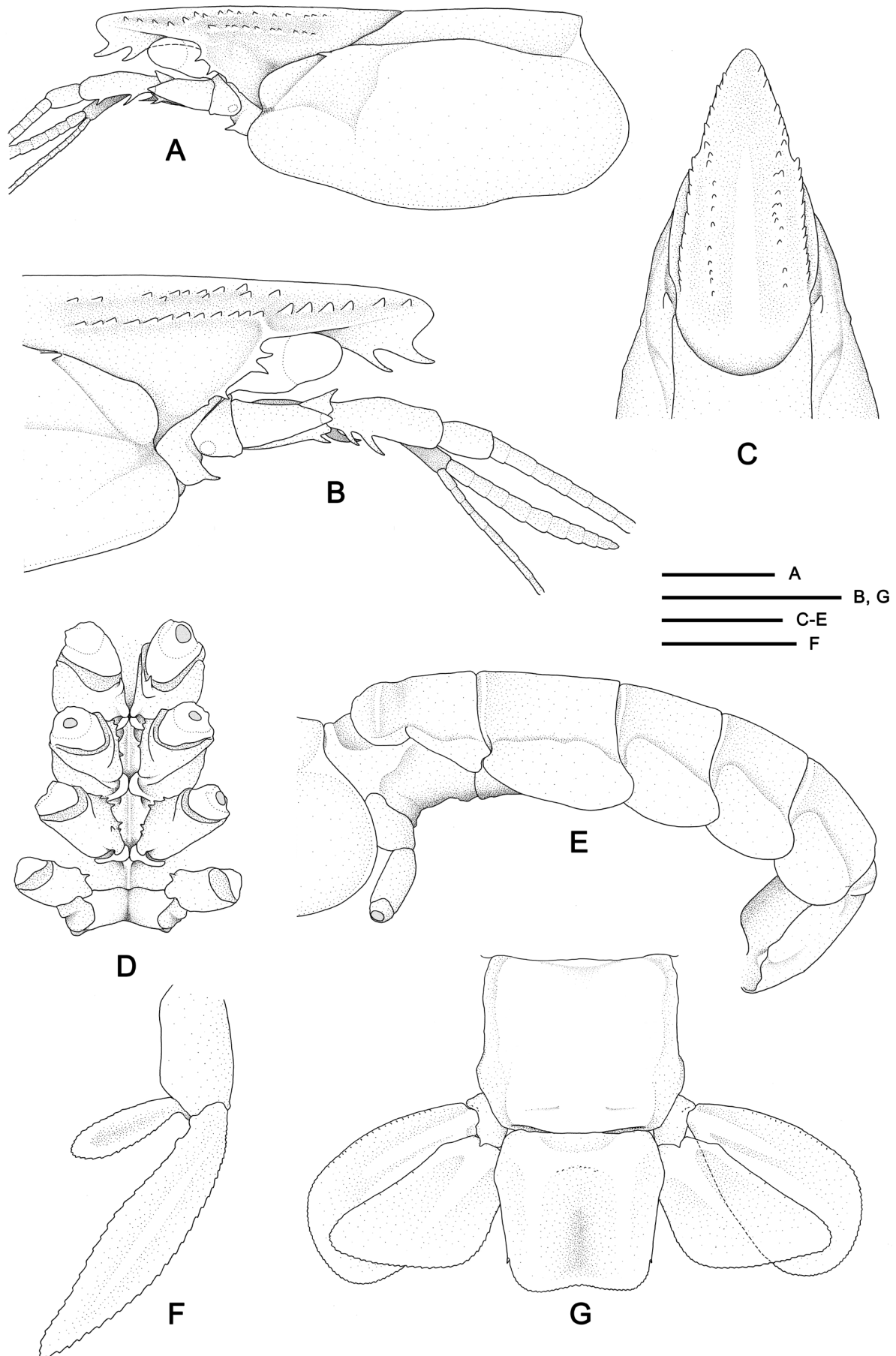


Fig. 2. *Gebiacantha sinica*, new species, holotype, MBM 304656 (male, cl 4.3 mm, tl 12.5 mm): A, carapace, eyestalk, antenna, antennule, left lateral view, flagella partially omitted; B, anterior carapace, eyestalk, antenna, antennule, right lateral view, flagella partially omitted; C, anterior carapace, dorsal view; D, sternites 4–7, pereopodal coxae 1–4, ventral view; E, posterior carapace, pleon, left lateral view; F, right pleopod 2, posterior view; G, pleonite 6, telson, uropods, dorsal view. Scales = 1 mm.

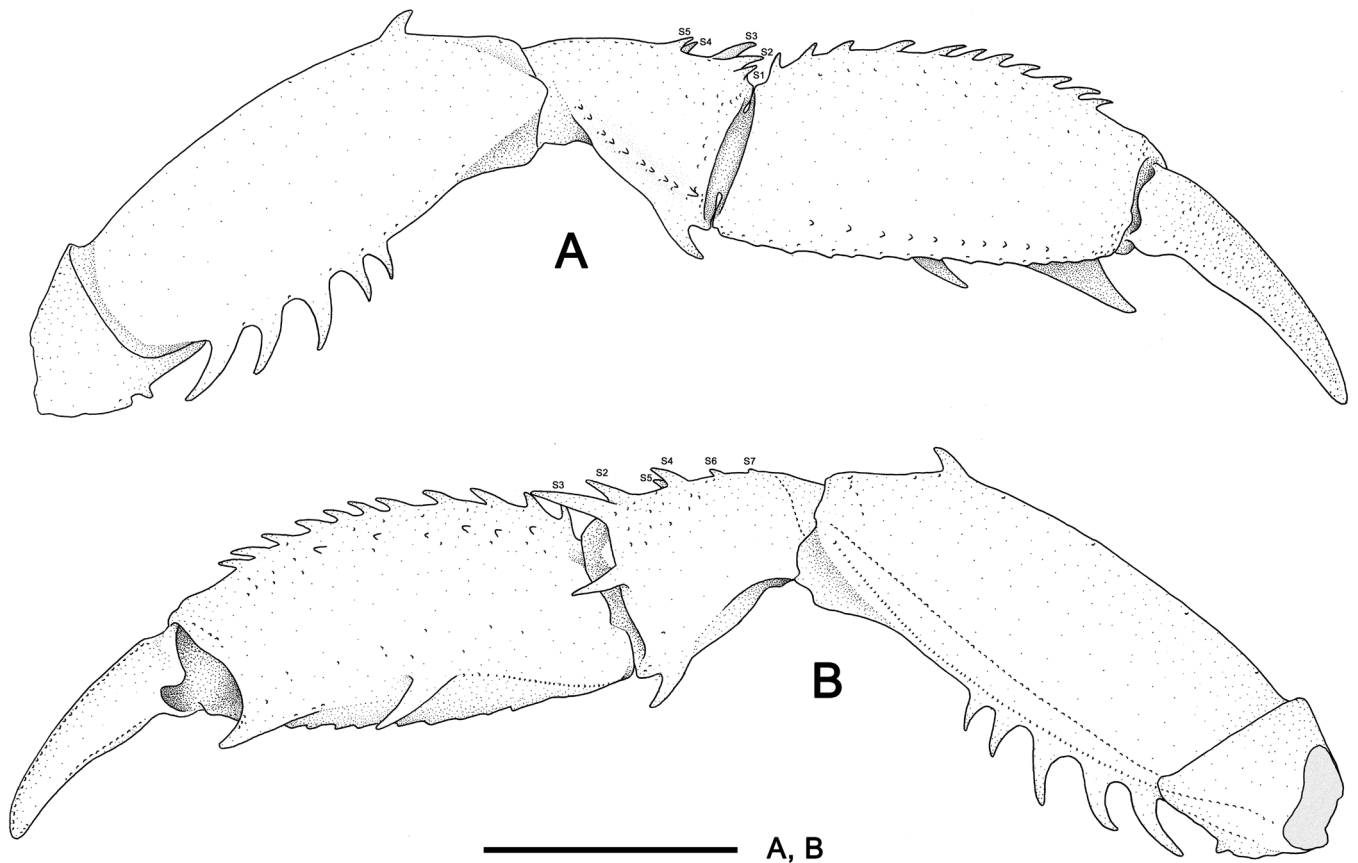


Fig. 3. *Gebiacantha sinica*, new species, holotype, MBM 304656 (male, cl 4.3 mm, tl 12.5 mm): A, right pereopod 1, lateral view; B, same, mesial view. Scale = 1 mm. Spines on the dorsal surface of the carpus are labelled as S1–S7 for ease of differentiation.

article, consisting of 3 articles, with long terminal setae. Epistome with 1 acute ventrodistal spine.

Pereopod 1 robust, symmetrical, subchelate, setation typical of upogebiids. Coxa with 1 prominent anteriorly directed spine on ventral surface. Basis unarmed. Ischium compressed laterally, as long as greatest width at distal end; upper margin unarmed; lower margin with 1 small, blunt spine at midlength. Merus compressed laterally, 3.0 times as long as ischium; upper margin arcuate, armed with 1 prominent subdistal spine, directed anteriorly; lower margin slightly convex, with row of 5 evenly spaced, large, recurved spines along proximal 0.6, increasing in size proximally. Carpus cup-shaped, slightly longer than half-length of merus; upper surface with 8 (left) and 7 (right) irregularly arranged spines of various size, distomesial spine strongest; lateral surface with shallow longitudinal carinate bearing row of 10 spinules, distalmost largest; mesial surface smooth, distal margin with 1 large spine; lower margin with 1 prominent subdistal spine. Propodal palm slightly swollen, 1.8 times as long as carpus, 2.2 times as long as wide; upper margin arcuate, armed with row of 12 (left) and 11 (right) strong spines of subequal size along proximal 0.8; lower margin convex, denticulate, lateral surface unarmed, with longitudinal row of 9 (left) and 10 (right) tiny tubercles superior to lower margin; mesial surface armed with longitudinal row of 6 spines inferior to upper margin, with 1 strong inferior spine at midlength, as long as fixed finger; fixed finger triangular, distinctly shorter than dactylus, inner margin unarmed. Dactylus 0.7 times as long as palm, unarmed, terminating in minute corneous

claw; outer margin evenly arcuate; inner margin rounded in proximal 0.2, slightly convex from proximal 0.2 to midlength, distal half evenly concave; lateral surface with longitudinal carina slightly superior to midline, extending through entire dactylus; mesial surface smooth.

Pereopod 2 with coxa bearing 3 (left) or 4 (right) spinules on mesial surface. Basis unarmed. Ischium widened distally, unarmed. Merus 4.5 times as long as ischium; upper margin straight, armed with 1 prominent subdistal spine, directed anteriorly; lower margin slightly convex, with 1 large proximal spine and 1 small spine in proximal 0.2. Carpus slightly shorter than half-length of merus; upper margin with row of 3 evenly spaced spines in midlength, increasing in size distally and 1 large distal spine; lower margin with 1 subdistal spine. Propodus subequal in length to carpus, unarmed; upper margin slightly convex; lower margin straight. Dactylus tapering to minute corneous tip, 0.85 times as long as propodus.

Pereopod 3 with coxa bearing 5 (left) or 6 (right) spinules on mesial surface. Basis and ischium unarmed. Merus straight, with 3 small spines on lower margin in proximal 0.7; upper margin armed with 1 subdistal spine. Carpus cup-shaped, unarmed, slightly shorter than half-length of merus. Propodus 0.8 times as long as carpus, unarmed; upper margin arcuate; lower margin almost straight. Dactylus slightly longer than propodus, terminating in acute tip; upper margin unarmed; lower margin with 5 closely set spiniform setae in distal one-third.

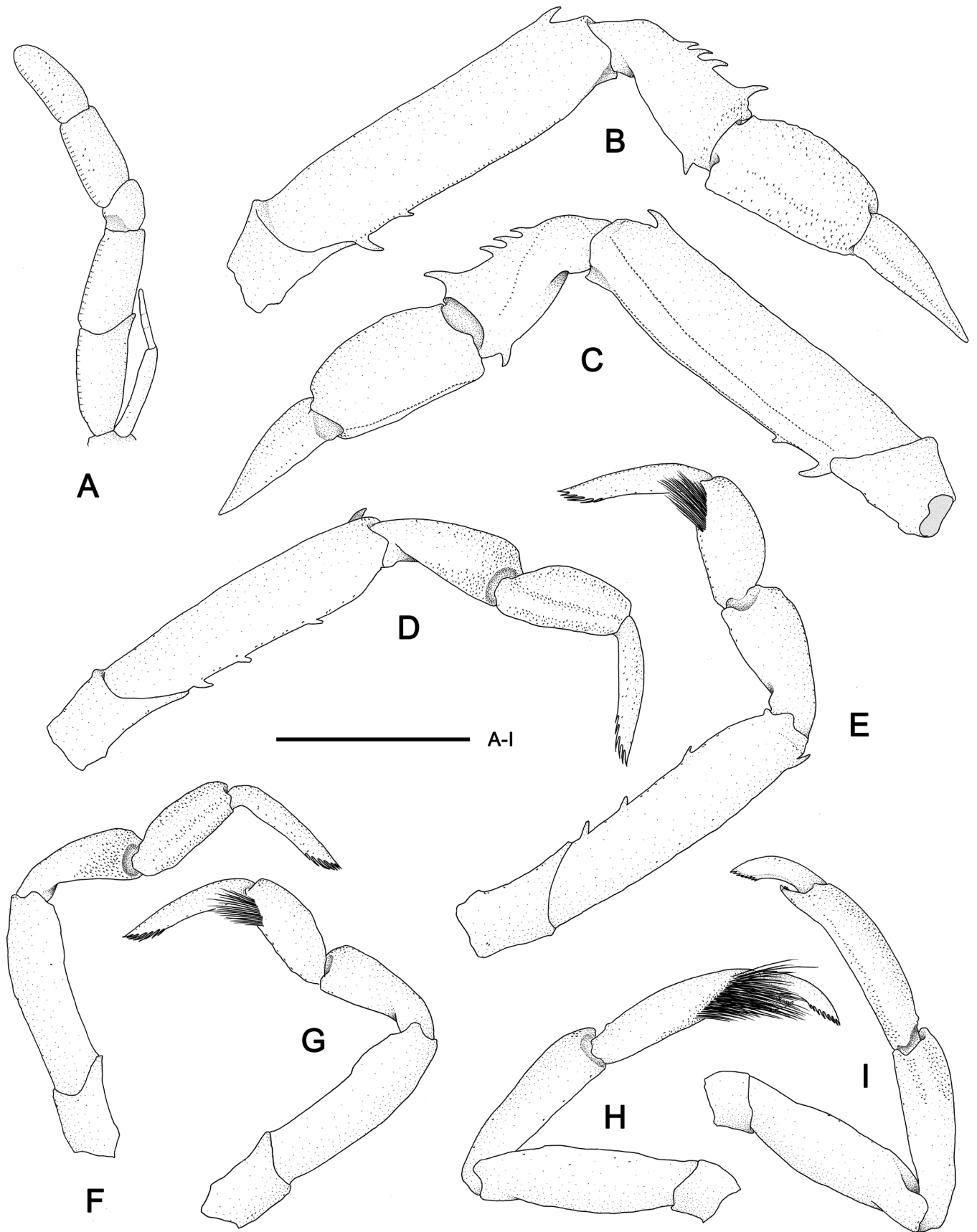


Fig. 4. *Gebiacantha sinica*, new species, holotype, MBM 304656 (male, cl 4.3 mm, tl 12.5 mm): A, left maxilliped 3, outer view; B, right pereopod 2, lateral view; C, same, mesial view; D, right pereopod 3, lateral view; E, same, mesial view; F, right pereopod 4, lateral view; G, same, mesial view; H, right pereopod 5, lateral view; I, same, mesial view. Scale = 1 mm.

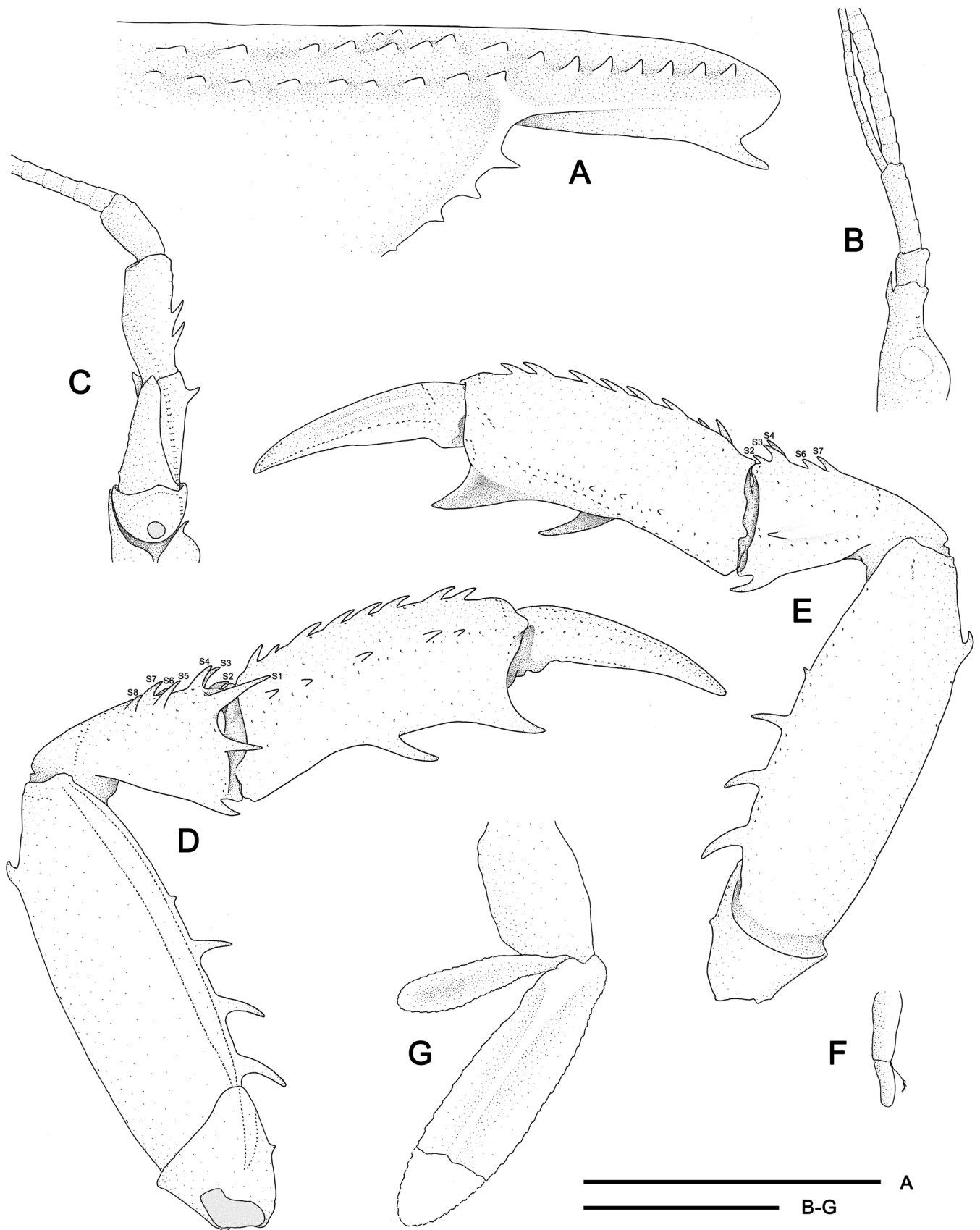


Fig. 5. *Gebiacantha sinica*, new species, paratype, MBM 304657 (female): A, anterior carapace, right lateral view; B, right antennule, mesial view; C, epistome, right antenna, lateral view; D, left pereopod 1, mesial view; E, same, lateral view; F, right pleopod 1, anterior view; G, right pleopod 2, posterior view. Scales = 1 mm. Spines on the dorsal surface of the carpus of pereopod 1 are labelled as S1–S8 for ease of differentiation.

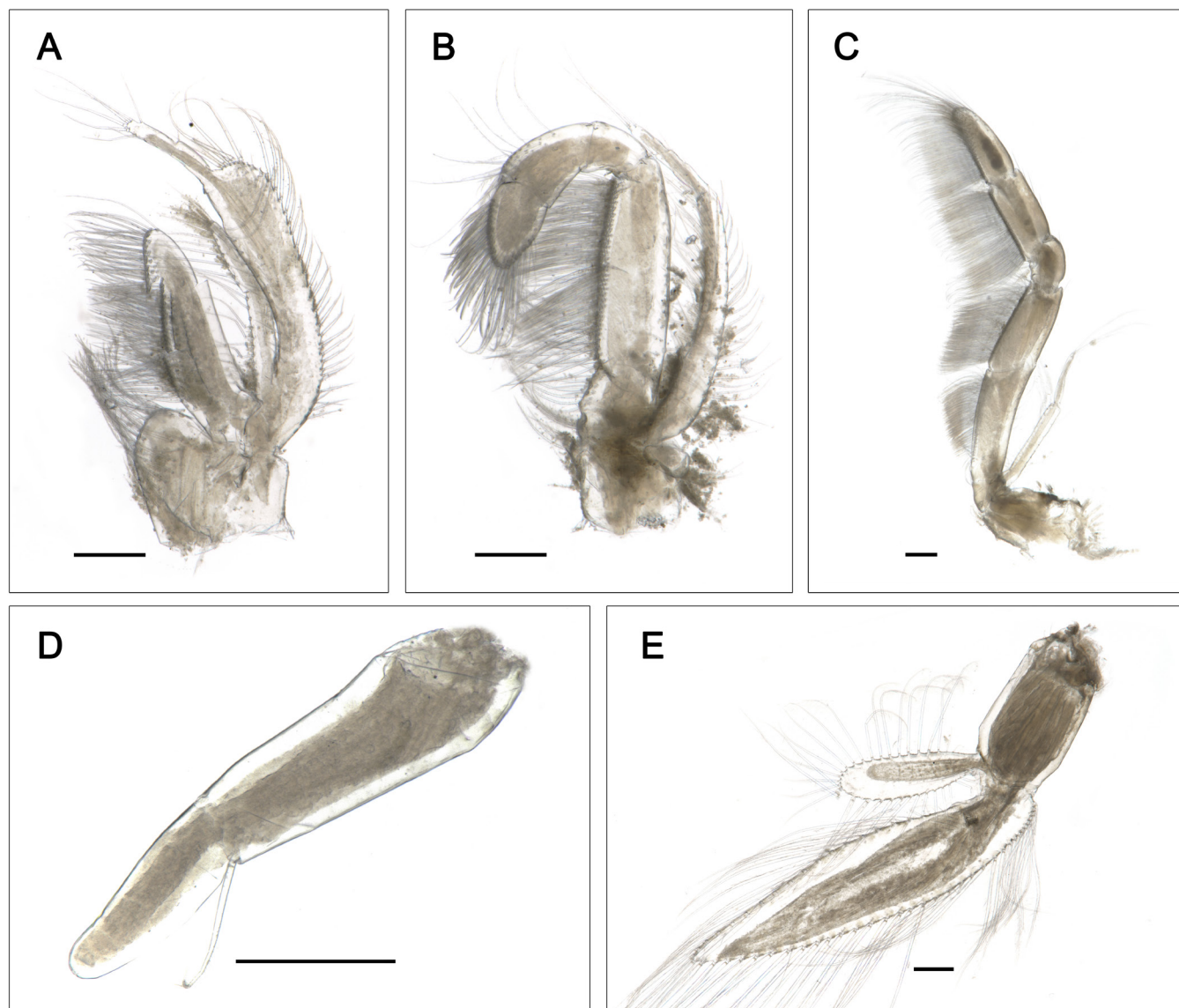


Fig. 6. *Gebiakantha sinica*, new species, A–D, paratype, MBM 304657 (female); E, holotype, MBM 304656 (male, cl 4.3 mm, tl 12.5 mm): A, left maxilliped 1, outer view; B, left maxilliped 2, outer view; C, left maxilliped 3, outer view; D, right pleopod 1, anterior view; E, right pleopod 2, posterior view. Scales = 200 μ m.

Pereopod 4 with coxa bearing 1 spinule on mesial surface. Basis to propodus unarmed. Dactylus slightly longer than propodus, terminating in acute tip; upper margin unarmed; lower margin with 6 closely set spiniform setae in distal one-third.

Pereopod 5 subchelate. Coxa with gonopore on both sides. Basis to carpus unarmed. Propodus as long as carpus, slightly curved; short fixed finger terminating in corneous tip and with 4 spinules on inner margin. Dactylus curved, about half-length of propodus, terminating in acute tip; upper margin unarmed; lower margin with 7 closely set spiniform setae in distal 0.4.

Pleopods 1 absent. Pleopods 2–5 biramous, generally similar; endopod suboval, short and slender, about 0.4 times as long as exopod; exopod lanceolate, 4.0 times as long as greatest width.

Uropod with protopod armed with small blunt tooth on posterior margin above base of endopod. Endopod not reaching posterior margin of telson, subtrapezoidal, with rounded distomesial angle and somewhat produced distolateral angle; inner and posterior margins almost straight; outer margin slightly concave, with small knob-like tubercle proximally; dorsal surface with median carina. Exopod overreaching posterior margin of telson, teardrop, 1.7 times as long as greatest width, distal margin rounded, dorsal surface with 2 longitudinal carinae.

Telson subrectangular, 1.1 times as long as greatest width at anterior 0.3; dorsal surface with U-shaped carina, medially concave in distal 0.8; lateral margins armed with 1 movable spinule at anterior 0.8 of telson length; posterolateral angle rounded, posterior margin slightly concave at median part, without median spine.

Female paratype. Generally similar to male holotype. Rostrum with ventral surface armed with 1 strong, anteriorly

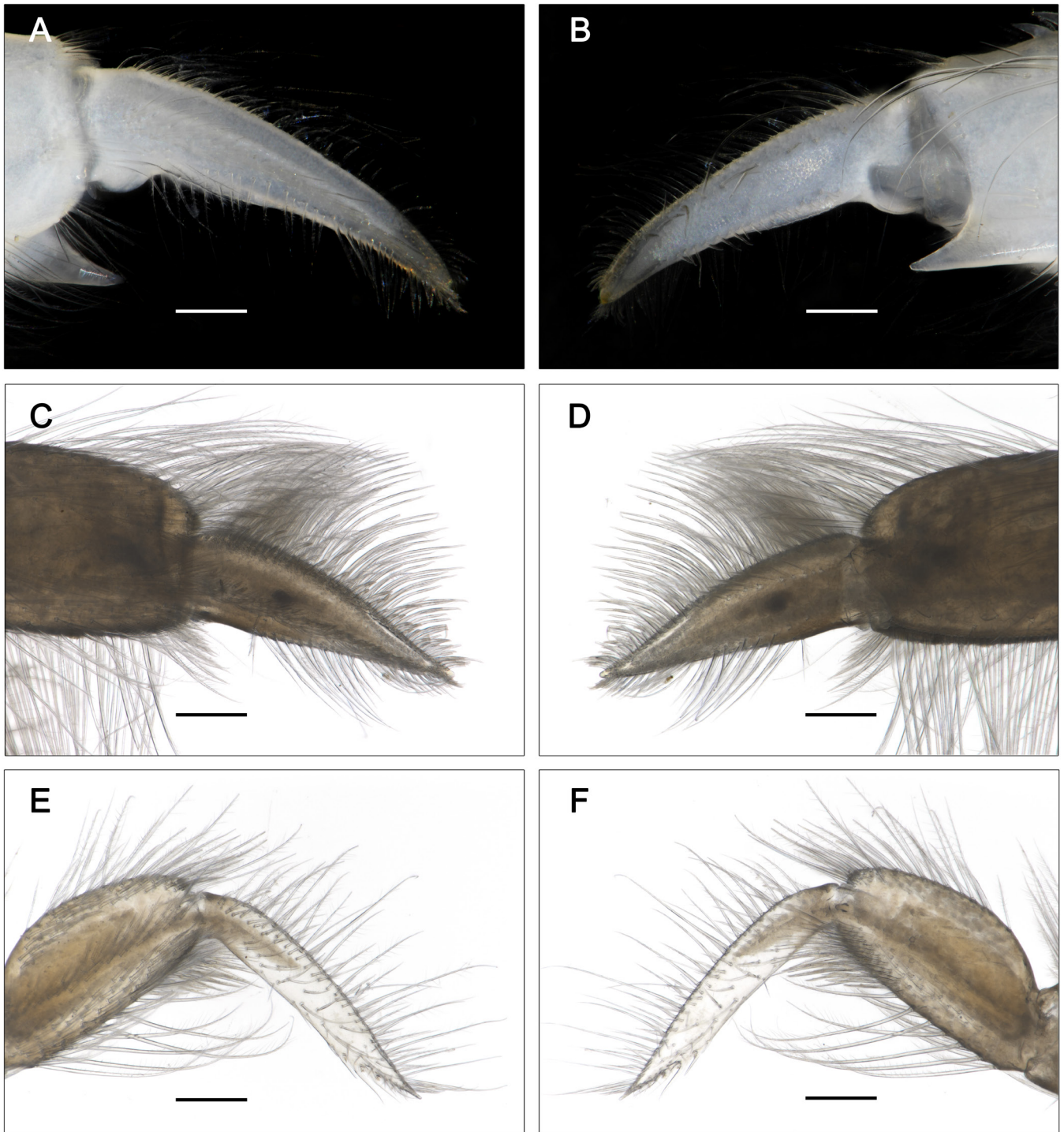


Fig. 7. *Gebiacantha sinica*, new species, holotype, MBM 304656 (male, cl 4.3 mm, tl 12.5 mm): A, right pereopod 1, detail of fixed finger and dactylus, lateral view; B, same, mesial view; C, right pereopod 2, detail of propodus and dactylus, lateral view; D, same, mesial view; E, right pereopod 3, detail of propodus and dactylus, lateral view; F, same, mesial view. Scales = 200 μ m.

directed spines in distal 0.3, almost reaching apex of rostrum, dorsolateral margins with 6 spiniform teeth. Carapace with lateral gastric ridges bearing row of 9 spiniform tubercles; gastric region with 2 irregular, longitudinal rows of 11 (left) and 10 (right) tiny tubercles. Pereopod 1 more slender than in male. Merus lower margin slightly convex, with row of 4 evenly spaced, spines along proximal 0.6, increasing in size proximally, distalmost tiny. Carpus upper surface with 8 (left) and 7 (right) irregularly arranged spines of various sizes; lateral surface with shallow longitudinal carinae ending

in 1 subdistal spine. Propodal palm upper margin arcuate, with row of 8 (left) and 10 (right) strong spines of subequal size along proximal 0.9; lower margin smooth, concave, with prominent spine at midlength; lateral surface with longitudinal row of 3 tiny tubercles superior to lower margin; mesial surface with longitudinal row of 5 spines inferior to upper margin. Pleopod 1 uniramous, short, 2-segmented, digitiform, with 1 marginal seta.

Colour in life. Unknown.

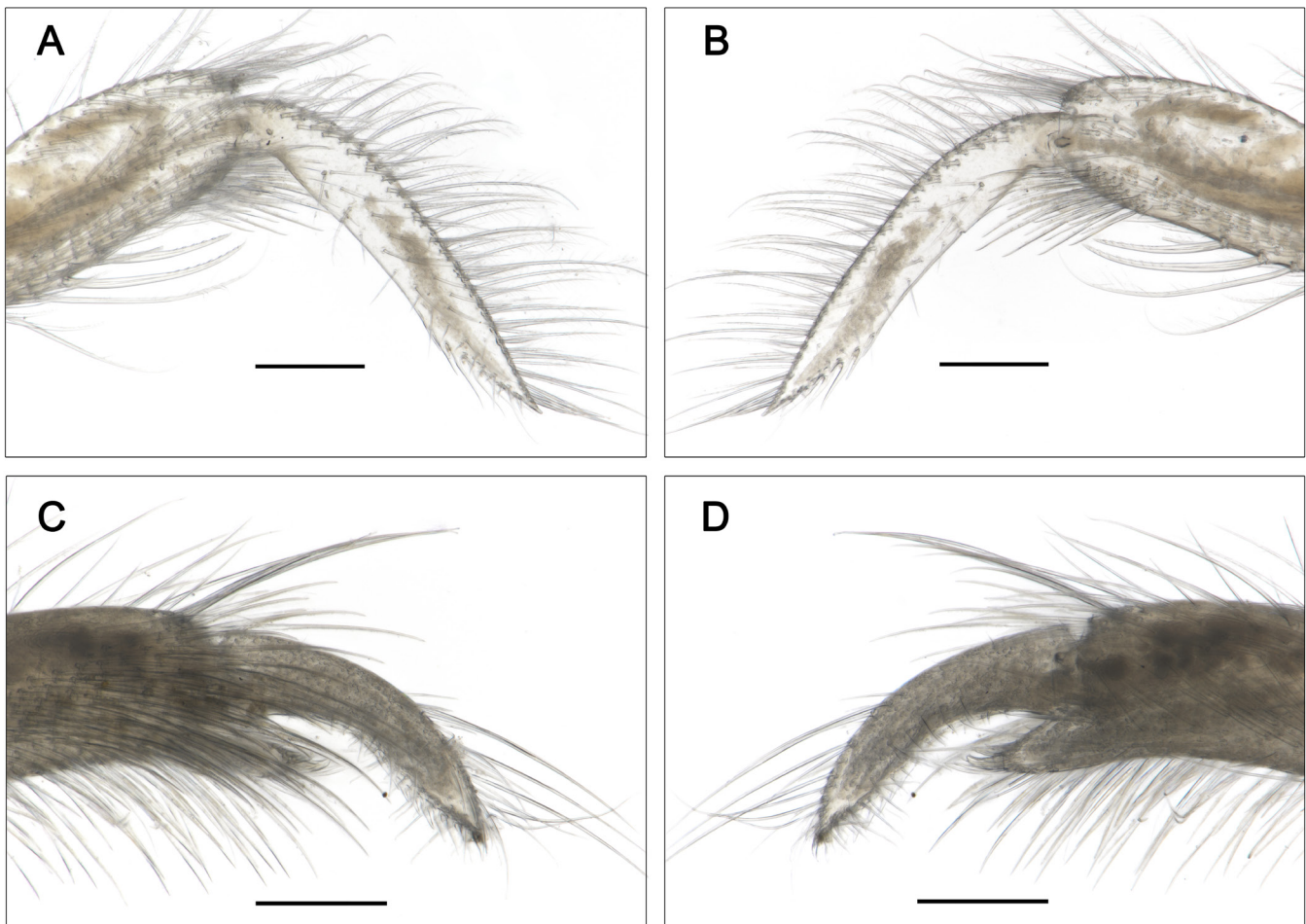


Fig. 8. *Gebiakantha sinica*, new species, holotype, MBM 304656 (male, cl 4.3 mm, tl 12.5 mm): A, right pereopod 4, detail of propodus and dactylus, lateral view; B, same, mesial view; C, right pereopod 5, detail of propodus and fingers, lateral view; D, same, mesial view. Scales = 200 μ m.

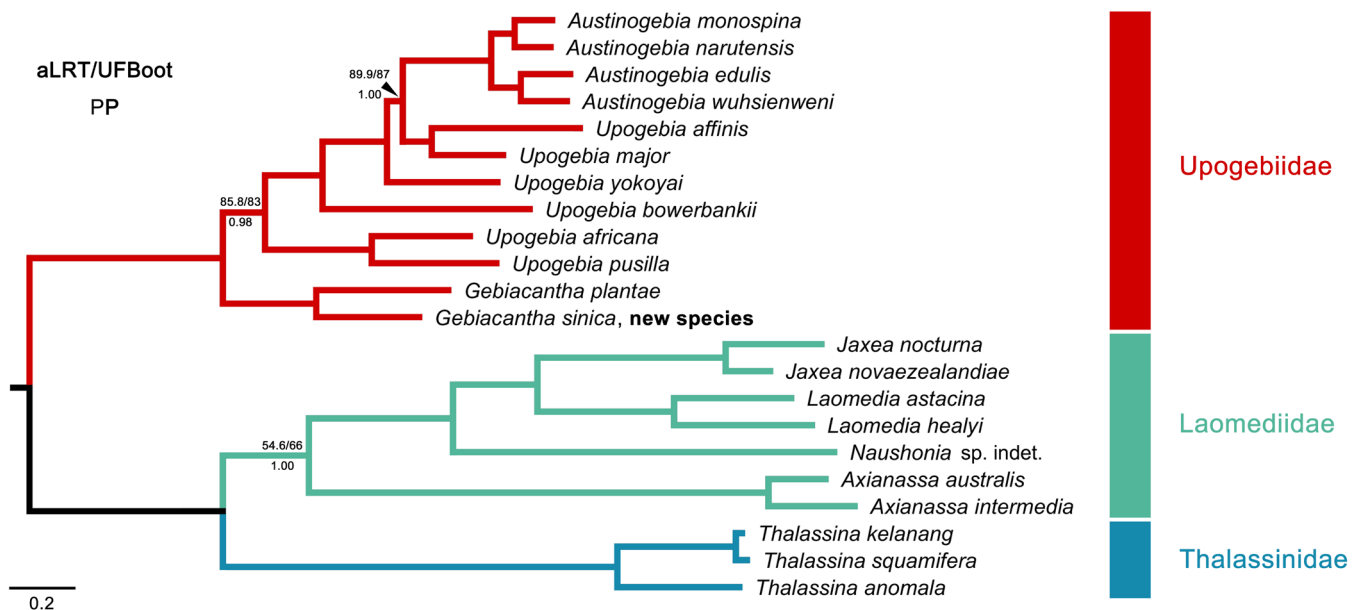


Fig. 9. Bayesian inference phylogenetic tree of Gebiidea de Saint Laurent, 1979 based on the concatenated five-gene dataset (5,641 bp) partitioned by gene and codon. SH-like approximate likelihood ratio test (aLRT, upper left) values, maximum likelihood ultrafast bootstrap scores (UFBboot, upper right) and Bayesian posterior probabilities (PP, below) are indicated adjacent to the nodes. Unlabelled nodes indicate aLRT value $\geq 90\%$, UFBboot $\geq 95\%$, and PP ≥ 0.99 .

Table 3. Alignment information and selected DNA substitution model in this study.

Gene and codon position	Partition delineation	Subset	Subset partitions	Model selected by ModelFinder and implemented in IQ-TREE 2.2.0.3	Model selected by ModelFinder and implemented in MrBayes 3.2.6
12S rRNA	1–730	1	12S rRNA + 16S rRNA	TVM+F+I+G4	GTR+F+I+G4
16S rRNA	731–1829				
18S rRNA	1830–3670	2	18S rRNA + COI-2 nd + H3-1 st + H3-2 nd	K2P+I+G4	K2P+I
COI-1 st codon	3671–5230\3				
COI-2 nd codon	3672–5230\3	3	COI-1 st	GTR+F+I+G4	GTR+F+I+G4
COI-3 rd codon	3673–5230\3				
H3-1 st codon	5231–5641\3	4	COI-3 rd	GTR+F+I+G4	GTR+F+I+G4
H3-2 nd codon	5232–5641\3				
H3-3 rd codon	5233–5641\3	5	H3-3 rd	TVM+F+G4	GTR+F+G4

Distribution. Off the south coast of Hainan Island and Beibu Gulf, the South China Sea, Northwest Pacific, 15–70 m depth.

DISCUSSION

Morphological comparisons. In his unpublished doctoral thesis, Liu (2010) reported two species belonging to the genus *Gebiakantha* from the China seas, *G. acanthochela* from the Yellow Sea and East China Sea and *G. lagonensis* from the South China Sea. *Gebiakantha sinica*, new species, can be immediately distinguished from the other two species in the weakly dentate rostrum, carapace and pereopod 1. In addition, the new species has a moderately concave posterior margin of telson, which is deeply concave, forming a distinct median notch in the other two species (cf. Sakai, 1967; Ngoc-Ho, 1989; Komai, 2020).

Of the other *Gebiakantha* species, *G. monoceros* and *G. irawadyensis* (Sakai, 2006), new combination, are the most morphologically similar to *G. sinica*, new species, in the weakly dentate dorsal surface of rostrum, the anterolateral margin of carapace with 2–4 spinules, the mesial surface of chela unarmed or only with few weak spines, the fixed finger unarmed on cutting edge, the telson with a moderately concave posterior margin, and the uropodal exopod less than twice as long as greatest width. However, *G. sinica*, new species, can be distinguished from *G. monoceros* in the monospinous scaphocerite (vs bifid scaphocerite), the mesial surface of propodus of pereopod 1 armed with longitudinal row of 5 or 6 spines (vs with 1 or 2 spines) and the lower margin of pereopod 3 merus with 3 spines (vs with 2 spines) (cf. De Man, 1905, 1928). *Gebiakantha sinica* differs from the Indonesia specimens (holotype and paratype) of *G. irawadyensis* in the monospinous scaphocerite (vs bifid scaphocerite), the upper surface of pereopod 1 carpus with 7 or 8 spines (vs with 3 spines), the fixed finger with a sharp tip (vs with a blunt tip), the upper margin of pereopod 2

carpus with 4 spines (vs with 3 spines), the lower margin of pereopod 2 merus with 2 spines (vs with 1 spine) and the lateral margin of telson armed with 1 movable spinule on each side (vs unarmed) (cf. Sakai, 2006); from the Burma specimen (non-type) in the pterygostomial angle unarmed (vs armed with 5 spinules), the mesial surface of chela armed with longitudinal row of 5 or 6 spines (vs smooth) and the lateral margin of telson armed with 1 movable spinule on each side (vs unarmed) (cf. Sakai, 1982). In addition, the new species is distinguishable from the two morphologically similar species by the ventral margin of antennal peduncle article 4 with 2 spines and the lateral surface of pereopod 1 carpus with shallow longitudinal carinate bearing 1 or more spinules. Differentiating characters among the three species are summarised in Table 2.

Liu (2010) also reported specimens identified as *Gebicula irawadyensis* from Beibu Gulf, the South China Sea at a depth of 15–34 m. The illustrations and photos of his specimens show that there are 2 spines on the ventral margin of antennal peduncle article 4, 3 spines on the lower margin of pereopod 3 merus and a longitudinal row of spines on the mesial surface of chela (Liu, 2010: figure 137). Based on these characteristics, we conclude that his specimens are actually *Gebiakantha sinica*, new species, rather than *G. irawadyensis*, new combination.

It is noteworthy that the spiniform setae on the lower margin of dactylus of pereopods 3–5 have long been overlooked by most taxonomic studies of *Gebiakantha*. However, we found that the number and arrangement of these spiniform setae seem to vary among different species of this genus (cf. Komai, 2017, 2020), suggesting that this trait might serve as a diagnostic character for species delimitation.

Molecular analyses. A total of 20 12S rRNA, 22 16S rRNA, 17 18S rRNA, 22 COI and 16 H3 sequences were obtained and included in our analyses. The final concatenated five-

gene dataset consisted of 5,641 bp (~92.89% of the original 6,073 bp alignment) after the alignments were trimmed with GBLOCKS 0.91b (original alignment 12S/16S/18S = 879/1,312/1,911 bp, trimmed alignment 12S/16S/18S = 730/1,099/1,841 bp). The optimum partitioning scheme and the best-fit models for each partitioned subset selected by ModelFinder are listed in Table 3. After 10 million iterations, the average standard deviation of split frequencies in BI analysis reached below 0.001, and the ESS values for all sampled parameters were above 1,000 for each run.

The phylogenetic trees inferred from both ML and BI analyses were totally congruent and generally well-supported (Fig. 9). At the family level, the monophyly of Thalassinidae Latreille, 1831 and Upogebiidae was fully supported in both analyses (aLRT & UFBoot = 100.0%, PP = 1.00), and the grouping of Laomediidae Borradaile, 1903 received full support in BI (PP = 1.00) but with low support in ML analysis (aLRT = 54.6%, UFBoot = 66.0%). At the genus level, except for *Upogebia*, the other six genera (*Austinogebia*, *Axianassa* Schmitt, 1924, *Gebiakantha*, *Jaxea* Nardo, 1847, *Laomedia* De Haan, 1841, and *Thalassina* Latreille, 1806) represented by more than one species were strongly supported as monophyletic (aLRT & UFBoot $\geq$ 99.0%, PP = 1.00). Within Upogebiidae, *Austinogebia* was deeply embedded in *Upogebia*, rendering the latter a paraphyletic group (aLRT = 85.8%, UFBoot = 83.0%, PP = 0.98). These two genera formed a big clade which was sister to *Gebiakantha* in both analyses (aLRT & UFBoot = 100.0%, PP = 1.00). In summary, the current molecular evidence does not support the validity of *Austinogebia*, and the genus should be synonymised with *Upogebia*. The monophyly of *Gebiakantha* and other gebiidean genera is generally supported although Sakai (2006) placed both *Austinogebia* and *Gebiakantha* in synonymy with *Upogebia* on the basis of morphological evidence. An unpublished study by Robles et al. (2011) placed both *G. plantae* and *Pomatogebia operculata* (Schmitt, 1924) outside all remaining 17 upogebiid species in their 16S rRNA phylogenetic tree, but included both species and *A. narutensis* (Sakai, 1986) within *Upogebia* in a phylogenetic tree based on 18S rRNA gene.

Admittedly, taxon coverage of this study is limited. It is anticipated that future studies incorporating a more comprehensive taxon sampling and an extended set of molecular markers will elucidate the validity and phylogenetic relationships across gebiidean families and genera.

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