

New subterranean Sebidae (Crustacea, Amphipoda, Gammaridea) from Vietnam and SW Pacific

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ABSTRACT

Three new species of the stygobiotic genus *Seborgia* (Amphipoda, Sebidae) are described from anchialine waters on the Loyalty Islands and on Vanuatu (Melanesia), and from slightly brackish groundwaters in the Gulf of Tonkin (Vietnam). *Seborgia sanctensis* n. sp. displays a biramous third uropod, a feature never previously reported in sebidids. The same species is also noteworthy in having a bilobed maxilla, a trait currently regarded as diagnostic of the Sebiinae. Even though these features could be interpreted as evidence supporting the establishment of a separate, new genus for this taxon, its overall similarity with the other *Seborgia* species is striking, and we prefer to consider it as the representative of the genus exhibiting the most plesiomorphic character states. The other *Seborgia* species display a relatively derived, regressive condition in both of these characters. The biramous third uropod of *Seborgia sanctensis* n. sp., the posterior part of the body strongly reflexed beneath the pereion when alive, the fusion of the basis segments of the paired maxillipeds in *S. kanaka* n. sp., and the entire telson, all lend additional support to previous suggestions that the sebidids should be included among the leucothoideans. The discovery of *Seborgia sanctensis* n. sp. and *S. kanaka* n. sp., two species retaining the visual apparatus or at least traces of it, in anchialine pools located on coarse non-consolidated sediments suggests that this type of crevicular habitat is the primary habitat for the genus, and leads us to infer that *Seborgia* has probably come to occupy inland subterranean habitats by way of marine regressions.

KEY WORDS

Crustacea,
Amphipoda,
Gammaridea,
Seborgia,
anchialine caves,
Tethyan distributions,
biogeography,
Loyalty Islands,
Lifou,
Vanuatu,
Espíritu Santo,
new species.

RÉSUMÉ

Nouveaux Sebidae souterrains (Crustacea, Amphipoda, Gammaridea) du Vietnam et du Pacifique sud-ouest.

Trois nouvelles espèces du genre *Seborgia* (Amphipoda, Sebidae) sont décrites des eaux anchialines des Îles Loyauté et du Vanuatu (Mélanésie), et des eaux souterraines légèrement saumâtres du Golfe du Tonkin (Vietnam). *Seborgia sanctensis* n. sp. possède un troisième uropode biramé, caractère qui n'avait jamais été mentionné chez un Sebidae. Cette même espèce se distingue aussi par une maxille bilobée qui est considérée comme diagnostique des Sebinae. Ces caractères pourraient justifier l'établissement d'un nouveau genre, cependant la similarité globale de cette espèce avec les autres *Seborgia* est frappante et nous préférons la considérer comme le représentant du genre ayant les états de caractères les plus plésiomorphes. Les autres espèces de *Seborgia* présentent une condition relativement dérivée, régressive pour ces caractères. Le troisième uropode biramé de *Seborgia sanctensis* n. sp., la partie postérieure du corps fortement repliée sous le péréion chez l'animal vivant, la fusion de la base des segments des maxillipèdes pairs chez *S. kanaka* n. sp., et le telson entier, étayent les suggestions d'inclure les Sebidae dans les Leucothoidea. La découverte de *Seborgia sanctensis* n. sp. et *S. kanaka* n. sp., deux espèces conservant un appareil visuel ou au moins des traces, dans des mares anchialines situées sur des sédiments grossiers non consolidés, suggère que ce type d'habitat de crevasses est l'habitat primaire du genre et nous amène à déduire que *Seborgia* est venu occuper des habitats souterrains terrestres par suite de régressions marines.

MOTS CLÉS

Crustacea,
Amphipoda,
Gammaridea,
Seborgia,
grottes anchialines,
distributions
téthysiennes,
biogéographie,
Îles Loyauté,
Lifou,
Vanuatu,
Espírito Santo,
espèces nouvelles.

INTRODUCTION

The Sebidae Walker, 1907 is a small family of primarily marine amphipods currently comprising 18 species in three genera, arranged in two subfamilies (Shaw 1989; Holsinger 1992; Larsen 2007). The Sebinae Walker, 1907, comprising *Seba* Bate, 1862 (13 species) and the monotypic *Caribseba* Shaw, 1989, is exclusively marine and almost cosmopolitan, extending from shallow waters to the deep sea; most living as commensals with invertebrate hosts. The Seborgiinae Holsinger, 1980 comprises *Seborgia* Bousfield, 1970 only (four species), and occurs in groundwater habitats ranging from the littoral interstitial medium to freshwater aquifers located far inland. *Seborgia relicta* Holsinger & Longley, 1980 is limited to a freshwater aquifer in south-central Texas (Holsinger & Longley 1980), and *S. hershleri* Holsinger, 1992 occurs in the same Texan aquifer (Holsinger 1992) as well as,

apparently, in a freshwater cave in Tamaulipas, NE Mexico (Pesce & Iliffe 2002). The other two *Seborgia* species retain ties to the sea: *S. minima* Bousfield, 1970 occurs in an anchialine lake on Rennell Island which is in connection with an anchialine system (Solomon Islands, SW Pacific; Bousfield 1970), and *S. schieckei* Ruffo, 1985 was found (probably in brackish water) in the interstitial medium at the mouth of a coastal stream in the Andaman Islands (Indian Ocean; Ruffo 1985).

The biogeography of *Seborgia* is remarkable since it is indicative of an ancient origin for the genus because, assuming a direct, shallow-water marine derivation, there are species located around the Gulf of Mexico occupying areas not covered by the sea at least since the Late Cretaceous (Holsinger 1986). However, the existence of the Indo-West Pacific species leads us to infer that the origin of the genus is even older, perhaps Early Cretaceous, prior to the opening of the Atlantic, when the fragmentation of

the shallow-water, Tethyan circum-tropical pathway commenced (Sclater *et al.* 1977; Stock 1993).

Here we describe three additional *Seborgia* species, two from anchialine waters on the Loyalty Islands and Vanuatu (Melanesia, SW Pacific), the third from slightly brackish groundwaters in the Gulf of Tonkin (Vietnam). One of the new species displays a biramous third uropod, a feature never previously reported in sebids. The same species is also noteworthy in possessing a bilobed maxilla, a trait supposed to be diagnostic of the subfamily Sebinae.

MATERIAL AND METHODS

The animals were collected with a hand-held plankton net attached to an extensible handle, or using baited traps set in the lakes for several days. Drawings were prepared using a camera lucida on Olympus BH2 and Leica DM 2500 microscopes equipped with Nomarski differential interference contrast. Material examined on glass slides was mounted in lactophenol and the coverslips sealed with nail varnish. Body measurements were derived from the sum of the maximum dorsal dimensions of somites. Material is deposited in the Crustacea collections of the Muséum national d'Histoire naturelle, Paris (MNHN), of The Natural History Museum, London (BMNH), and at the zoological collection of Oddelek za biologijo, Biotehniška fakulteta, Univerza v Ljubljani, Ljubljana (OB BF UL).

NOTE ON TERMINOLOGY

Following Boxshall (2004), a distinction is made in the antennules and antennae between articles (corresponding to subdivisions of true segments by the formation of annuli, each lacking intrinsic musculature) and segments (possessing intrinsic musculature). The so-called (medial and lateral) lobes and palp of the amphipod maxillule are identified as the coxal and basal endites, and the endopod, respectively, after comparison with the basic pattern exhibited in malacostracan crustaceans, where

this limb is biramous and comprises a protopod divided into coxa and basis, each with a single endite, an up to 3-segmented endopod, and an unsegmented exopod (cf. Boxshall 1998). With regard to the segmentation of the maxilliped, it is homologised with that of the other thoracopods (the pereopods); the so-called palp corresponds to the merus-dactylus part, and the inner and outer lobes are identified homologues of the basal and ischial endites, respectively. This anatomical precision is necessary following the recent discovery of stygobiotic amphipods that possess a supplementary, innermost lobe on the maxilliped as well as the normal two enditic lobes (see Iannilli *et al.* 2006 and references therein). The additional lobe represents a coxal endite. Following Watling (1989), the term "spine" is restricted to rigid armature elements with a hollow central core that do not articulate basally with the body integument.

SYSTEMATICS

Order AMPHIPODA Latreille, 1816
Suborder GAMMARIDEA Latreille, 1802

Family SEBIDAE Walker, 1907
emend. Bousfield 1970

ADDITIONAL DIAGNOSTIC CHARACTER. — Uropod III uni- or biramous.

Subfamily SEBORGIINAE Holsinger, 1980

Genus *Seborgia* Bousfield, 1979 emend.

DIAGNOSIS. — Antennule short, less than half body length, longer than or equal to antenna, with more distal peduncle segments progressively shorter; accessory flagellum of antennule 1-articulate; flagellum of antenna shorter than corresponding peduncle. Incisor of both mandibles 5-dentate; lacinia mobilis present on both sides, left 5-dentate, similar to incisor, right reduced, multidentate; molar reduced to lappet crowned with single seta. Paragnaths with well-developed inner lobes, latter separated or fused proximally; outer lobes each with tubular pore presumably associated with salivary gland (see Barnard 1969: 11). Maxillule coxal endite

(= inner lobe) unarmed; endopod (= palp) 2-segmented. Maxilla uni- or bilobed. Maxilliped basal endite (= inner plate) reduced, finger-like, with two simple setae distally; merus (= palp segment 1) short. Coxal plates I-IV much longer than broad, all about same length, larger than corresponding pereionites; coxa I broadly overlapping head, expanded anterodistally; coxae II and III narrow, subrectangular; coxa IV subrectangular with square excavation proximally on posterior margin. Coxal gills present on pereiopods II-VI, stalked, ovoid and smooth. Oostegites on pereiopods II-VI, long and slender, each with 2-4 simple marginal setae. Gnathopod I of similar size or, rarely, larger than gnathopod II, both with propodus widest distally; first gnathopod sub- or parachelate, second gnathopod parachelate; basis of gnathopod I longer than in gnathopod II; carpus of both gnathopods articulating on distolateral surface of merus, that of gnathopod II short. Urosomites separate. Margins of tergite of urosomite III produced posterolaterally into triangular process on each side covering origin of third uropods. Rami of uropods I and II notched subterminally; exopod of uropod III 1-segmented.

Seborgia sanctensis n. sp.

(Figs 1-6)

TYPE MATERIAL. — **Vanuatu**. Espiritu Santo, anchialine pool located outside entrance to Loren cave (14°58'49.2"S, 167°3'28.08"E), G. A. Boxshall and D. Jaume coll., 8.IX.2006, holotype brooding ♀ 1.90 mm preserved in 70% ethanol in single vial (MNHN-Am7544).

Paratypes: same data as holotype, 7 brooding ♀♀ 1.63, 1.92, 1.71, 1.65, 1.81, 1.83 and 1.68 mm, plus additional 11 brooding ♀♀, 4 specimens of unknown sex, and 19 juveniles, not measured, all preserved in 70% ethanol in single vial (MNHN-Am7545); 10 specimens, none measured, preserved in 100% ethanol in single vial (BMNH 2009.28-37).

DIAGNOSIS. — Flagellum of antennule longer than corresponding peduncle. Fifth peduncle segment of antenna elongate, longer than first peduncle segment of antennule. Mandibular palp segment 3 rhomboid, with several D-setae (*sensu* Stock 1974). Maxilla bilobed. Unguis of gnathopod I elongate. Uropod III biramous.

ETYMOLOGY. — The species name refers to the type locality on the island of Espiritu Santo (Vanuatu).

DESCRIPTION OF BROODING FEMALE

(MALE UNKNOWN)

Body (Fig. 1A) compact, with integument covered with densely set microspinules (partially shown in some figures); colourless; eyes lateral, fully developed

and pigmented (pigment not shown in figures). Head (Fig. 1B) with triangular rostrum in lateral aspect, not over-reaching distally proximal half of first segment of antennular peduncle; head lobe well developed, evenly rounded, extending slightly beyond tip of rostrum; antennary sinus broad, shallowly excavated. Hyaline frill along posterodorsal margin of each pleonite with four large triangular serrations (Fig. 1A). Epimeral plates (Fig. 6A) with posterodistal angle weakly produced into pointed process; plates progressively larger towards posterior, with armature reduced to 0 or 1 robust seta on distal margin of second plate only; distal margin of third plate straight. Urosomites II and III strongly telescoped, with third virtually hidden beneath second (Fig. 6C, F).

Antennule (Fig. 1A, B) peduncle segments length ratio 44: 29: 27. Peduncle-to-main flagellum length ratio 45: 55. Main flagellum 7-articulate, article 5 longest; three distal articles each bearing aesthetasc, that on distal article reduced (Fig. 1C). Accessory flagellum bearing two simple slender setae plus one shorter penicillate seta (Fig. 1D).

Antenna (Fig. 1A, B, E) shorter than antennule. Gland cone short, directed posteriorly. Peduncle segments 4 and 5 length ratio 47: 53; fifth peduncle segment longer than first peduncle segment of antennule. Flagellum 4-articulate, shorter than fifth peduncle segment, with short aesthetasc on first, second and fourth articles only (Fig. 1E).

Labrum (Fig. 2A) with slightly produced epistome; anterior margin with sparsely-set, long and stout, simple setules; both lobes of bilobed distal margin microspinulate medially. Paragnaths (Fig. 2B) inner lobes shorter than outer, separate; both inner and outer lobes covered with sparsely-set short setules distally.

Right mandible (Fig. 2C) spine row comprising three elements with brush-like setules between. Molar process distal seta slender, pappose; anterior margin of process covered with sparsely-set microspinules. Palp segments length ratio 28: 43: 29; second segment with cluster of 3 or 4 setae on distomedial margin. Distal segment rhomboidal, sparsely ornamented with long spinules and armed with three D-setae and four E-setae (*sensu* Stock 1974). Left mandible (Fig. 2D, E) as right counterpart except

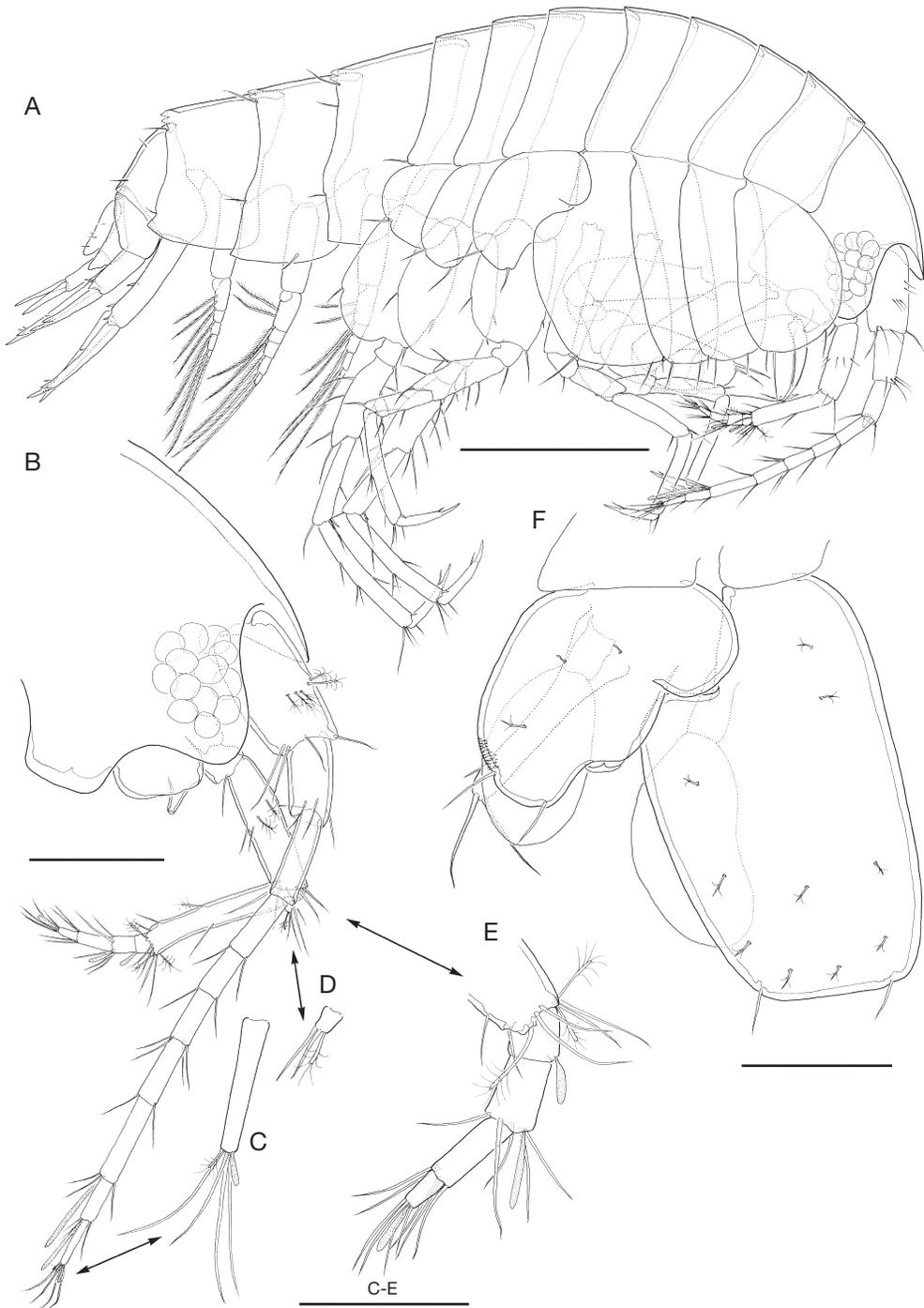


FIG. 1. — *Seborgia sanctensis* n. sp., brooding ♀ paratype 1.68 mm: **A**, body, lateral; **B**, head with right antennule and antenna attached, lateral; **C**, detail of tip of antennule; **D**, inset of accessory flagellum; **E**, flagellum of antenna; **F**, detail of right coxal plates IV-V, lateral (oostegite on coxal plate IV omitted). Scale bars: A, 0.25 mm; B, F, 0.1 mm; C-E, 0.05 mm.



FIG. 2. — *Seborgia sanctensis* n. sp., brooding ♀ paratype 1.68 mm: **A**, labrum, anterior; **B**, paragnaths, posterior; **C**, right mandible; **D**, left mandible with palp omitted; **E**, inset of incisor of latter; **F**, inset of lacinia; **G**, left maxilliped, posterior. Scale bar: 0.05 mm.

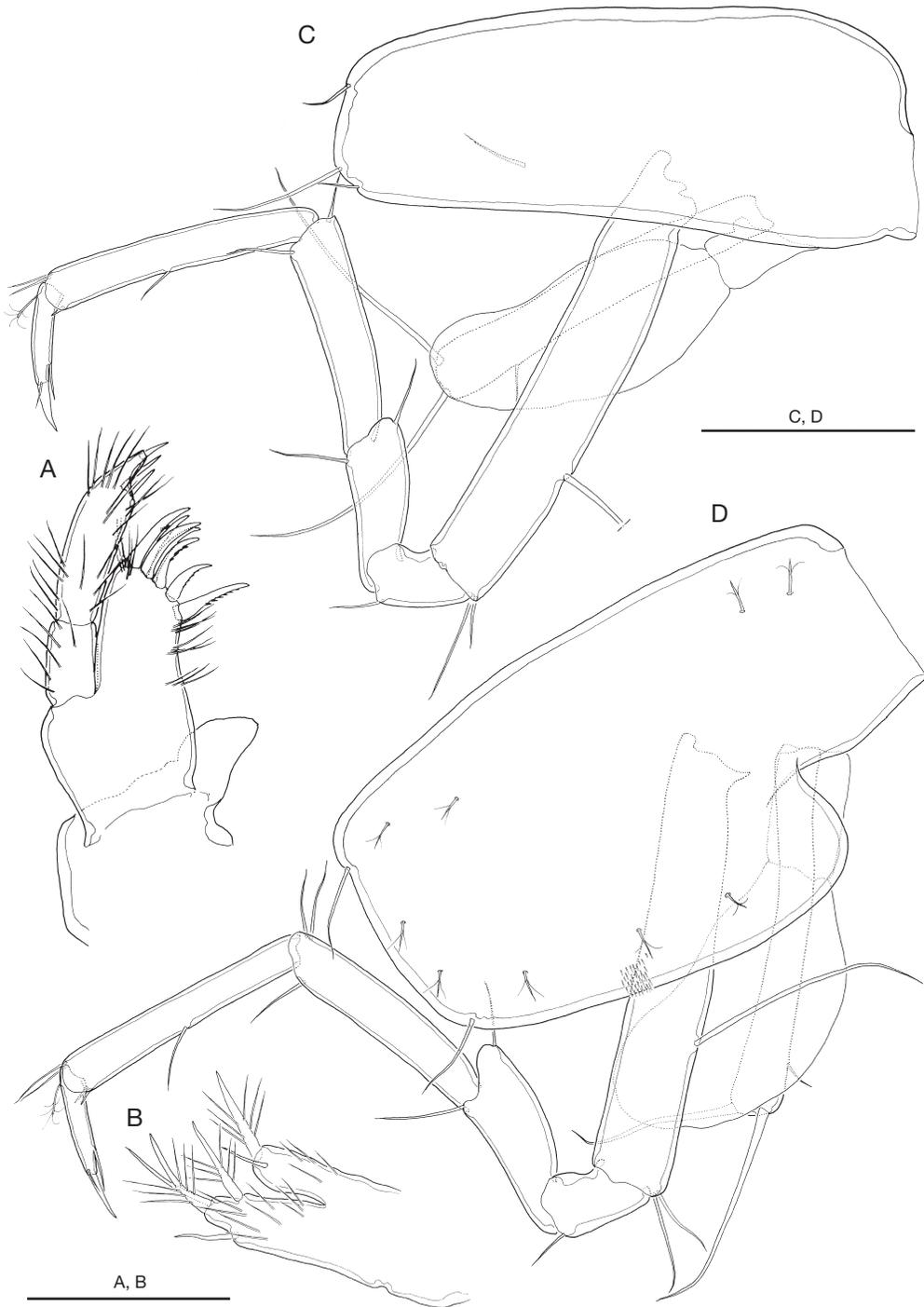


FIG. 3. — *Seborgia sanctensis* n. sp., brooding ♀ paratype 1.68 mm: **A**, maxillule; **B**, maxilla; **C**, left pereopod III, lateral; **D**, left pereopod IV, lateral. Scale bars: A, B, 0.05 mm; C, D, 0.1 mm.

for lacinia (Fig. 2F), and with anterior margin of molar process covered with densely-set setules.

Maxillule (Fig. 3A) with smooth conical coxal endite (= inner plate). Endopod with three short stiff simple setae on distal segment; latter longer than proximal segment (relative proportions of segments 20: 80). Basal endite (= outer plate) and endopod sparsely covered with long simple setules.

Maxilla (Fig. 3B) bilobed, outer lobe with four setae, inner lobe with two; outer element on each lobe simple and reduced; one of two terminal elements on outer lobe simple; remaining elements on lobes stout, smooth distally but ornamented with stout pinnules proximally. Long setules sparsely-set on both lobes as figured.

Maxilliped (Fig. 2G) palp relative length of carpus: propodus: dactylus: unguis as 40: 31: 20: 9. Maxillipedal segments from ischium (included) onwards ornamented with long simple spinules as figured; dactylus with conspicuous transverse comb row of long spinules subdistally.

Coxal plate IV (Figs 1F; 3D) about 1.6 times longer than broad, widest just below square posterior excavation; anterior and posterior margins of plate slightly convex; excavation occupying proximal 26% of posterior margin. Coxal plate V (Figs 1F; 5A) bilobed, smaller anterior lobe covering square posterior excavation of coxa IV.

Gnathopod I (Fig. 4A) subchelate, propodus about 1.5 times longer than broad, palm angle evenly rounded, located at 47% of maximum length of segment. Palm margin slightly convex, covered with short stout triangular denticles and with single flagellate robust seta located submarginally (Fig. 4B); palm angle with two stout robust bifid setae, one either side of angle, that on lateral side longer. Dactylus with terminal spine on medial margin. Unguis long and slender, about 33% length of dactylus.

Gnathopod II (Fig. 4C) propodus subrectangular, about 1.3 times longer than broad; palm angle armed with single long, stout simple robust seta; palm margin (Fig. 4D) covered with stout triangular denticles and with three flagellate robust setae submarginally. Dactylus with two short terminal robust setae on medial margin; unguis short, about 15% length of dactylus.

Pereiopods III and IV (Fig. 3C, D) slender, similar, with unguis not incorporated into dactylus, i. e. articulating basally with it; dactylus with subterminal simple seta on medial margin and shorter simple seta on distal margin.

Pereiopods V-VII (Fig. 5) bases about 1.6, 1.5 and 1.4 times longer than broad, respectively, progressively broader towards posterior, with anterior and posterior margins displaying 1 or 2 simple slender setae at most; posterior margins evenly convex and virtually smooth (displaying 1 or 2 shallow notches at most).

Pleopods (Fig. 6B) with protopod smooth, lacking setulation, each with subparallel margins except pleopod I (not figured; but see Fig. 11A), which bears swelling proximally on lateral margin. Protopods each with two retinacles.

Uropods progressively shorter towards posterior (Figs 1A; 6C). Uropod I (Fig. 6D) protopod as long as rami, with robust flagellate seta on both posterolateral and posteromedial distal angles, plus another about midway along posterolateral margin. Rami about equal in length; endopod armed with flagellate robust seta; exopod with pair of robust setae, one simple, other flagellate; setae on both rami located around subterminal notch. Uropod II (Fig. 6E) similar to uropod I except for length of protopod, shorter than rami and lacking seta on lateral margin, and for relative length of rami, with exopod clearly shorter than endopod. Uropod III (Fig. 6F) protopod longer than rami, thick; rami unarmed, endopod longer.

Telson (Fig. 6F) with evenly rounded distal margin; armature comprising two pairs of penicillate setae plus five trifid setae distributed as figured.

REMARKS

Seborgia sanctensis n. sp. is the only sebid possessing a biramous third uropod, and the bilobed state of its maxilla is also noteworthy since it was previously known to occur only in the Sebinae. Even though these features provide some evidence to support the erection of a separate, new genus for this taxon, its overall similarity with the other *Seborgia* species is striking, and we prefer here to treat it as the representative of the genus exhibiting the most plesiomorphic character states. The other

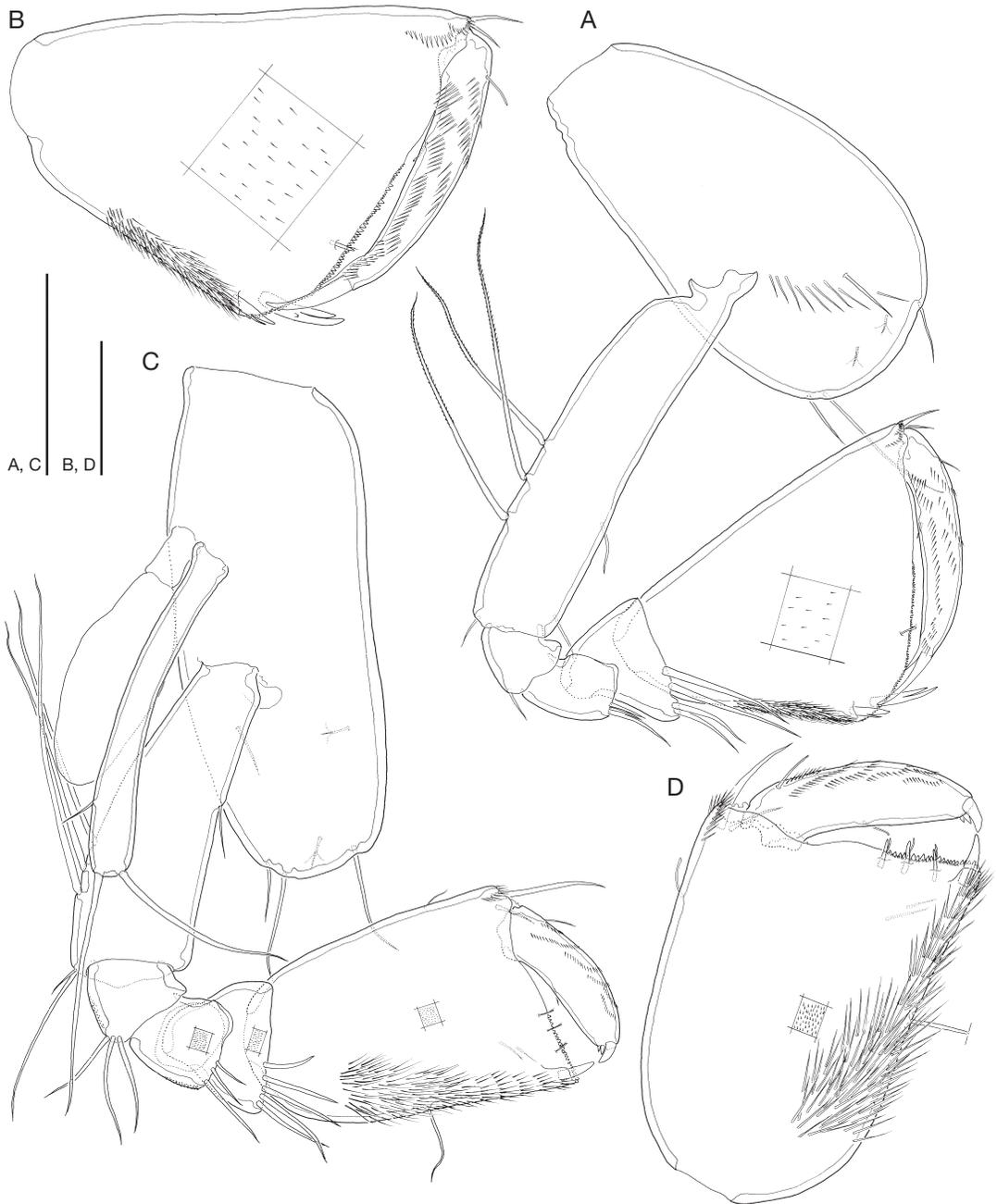


FIG. 4. — *Seborgia sanctensis* n. sp., brooding ♀ paratype 1.68 mm: **A**, left gnathopod I, medial; **B**, detail of propodus + dactylus, medial; **C**, left gnathopod II, medial; **D**, detail of propodus + dactylus, medial. Scale bars: A, C, 0.1 mm; B, D, 0.05 mm.

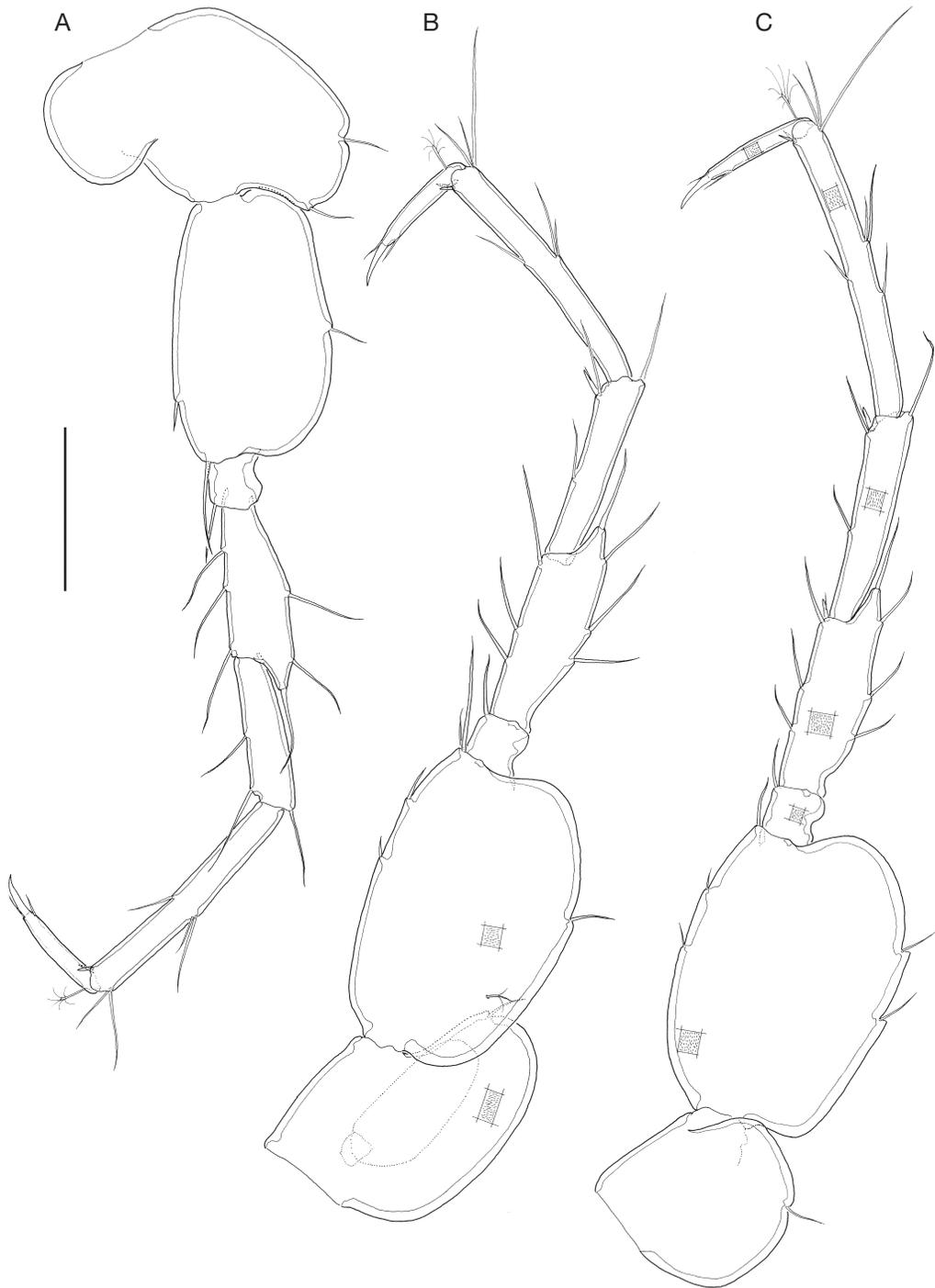


FIG. 5. — *Seborgia sanctensis* n. sp., brooding ♀ paratype 1.68 mm: **A**, left pereopod V with oostegite and coxal gill omitted, lateral; **B**, right pereopod VI, lateral; **C**, right pereopod VII, lateral. Scale bar: 0.1 mm.

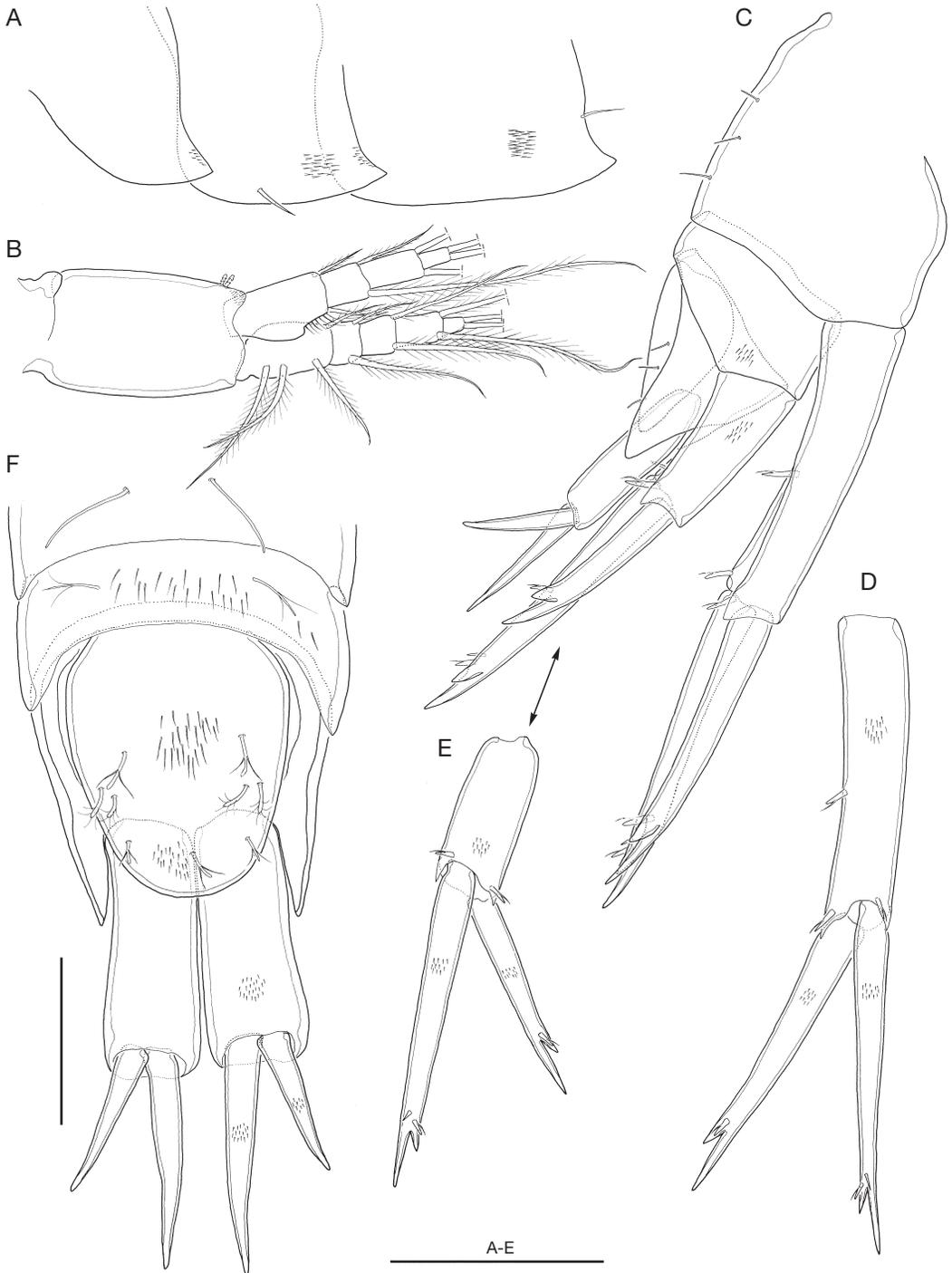


FIG. 6. — *Seborgia sanctensis* n. sp., brooding ♀ paratype 1.68 mm: **A**, left epimeral plates, lateral; **B**, left pleopod III, posterior; **C**, urosome, lateral; **D**, left uropod I, posterior; **E**, right uropod II, posterior; **F**, dorsal view of urosome with third uropods and telson attached. Scale bars: A-E, 0.1 mm; F, 0.05 mm.

Seborgia species display a secondarily reduced state for both of these characters. By analogy, the validity of the monotypic *Caribseba* Shaw, 1989 within the Sebinae should be questioned, since the unique traits distinguishing this taxon from the extremely similar *Seba* are also reductions, such as the absence of the accessory flagellum from the antennule and the loss of certain setae on the appendages (see Shaw 1989: 1889), and so *Caribseba* might represent a terminal branch arising within the genus *Seba*.

Additional unique features of the new taxon compared to other *Seborgia* species (Table 1) include: the flagellum of the antennule longer than the corresponding peduncle; the elongated antennal peduncle segment 5; the presence of several D-setae on the third segment of the mandibular palp; the outline of the latter segment (rhomboidal vs. slender and subparallel in other species); and the elongated unguis of the gnathopod I.

ECOLOGY, ETHOLOGY

The new species was discovered in a small anchialine pool (about 5 m in diameter and 0.5 m deep) located about 30 m inland from the shore. An active spring discharged into the pool during low tide but at high tide the water flow was greatly reduced and the water became slightly brackish (3.2 ppt). The pool is formed on coarse coral rubble and is locally surrounded by dense forest. This pool may well be connected to the nearby Loren cave system, the entrance of which is located about 50 m away. In addition to the new species, there were many tanaids in this pool, living within a thick blackish mat of algae/bacteria that coated the surface of the submerged stones and boulders.

Specimens of *Seborgia sanctensis* n. sp. were observed alive under the stereo-microscope in the laboratory. The animals moved ventral side down, not upside-down or on one side. The stance of the animals is quite unusual for an amphipod, vaguely resembling an isopod due to their slightly dorso-ventrally depressed body. It maintains the pleo- and urosome strongly reflexed beneath the pereion, having a short and “tail-less” appearance when viewed in dorsal aspect. Two embryos were invariably carried in the brood pouch of brooding females.

Seborgia vietnamica n. sp.

(Figs 7-11)

TYPE MATERIAL. — Vietnam. Vinh Ha Long (Ha Long Bay), Gulf of Tonkin, phreatic lake in cave Đông Duc Tiên (GPS coordinates: 20°50.34'N, 107°16.77'E), island Đảo Van Giò, P. Trontelj & B. Sket coll., 17.VI.2003, holotype brooding ♀ (oostegites developed, setose) 2.76 mm, completely dissected and mounted on single slide (BMNH2009.38).

Paratypes same data as holotype: 18 specimens (BMNH2009.39-48) including 7 brooding ♀♀, of which 5 measured (2.55, 2.55, 2.53, 2.60 and 2.88 mm); 32 specimens, sex unknown (OB BF UL).

OTHER MATERIAL EXAMINED. — Polje Viêt Hải headwater, between rootlets in spring (20°48'08"N, 107°02'29"E; coordinates approximate, derived from Google Earth), Đảo Cát Bà island, B. Sket & P. Trontelj coll., 15.VI.2003, 2 specimens, one clearly juvenile (OB BF UL).

DIAGNOSIS. — Posterior margin of coxa of female pereopod IV strongly oblique. Mid-lateral armature of protopod of uropod I comprising several flagellate robust setae.

ETYMOLOGY. — Species name derived from Vietnam, where it was found.

DESCRIPTION OF BROODING FEMALE

(MALE UNKNOWN)

Body (Fig. 7A) completely unpigmented, eyeless, similar to *S. sanctensis* n. sp. except for narrow triangular head lobe (Fig. 8A), variably produced rostrum (cf. Figs 7A; 8A), and posterodorsal margin of pleonites lacking serrations (Fig. 11C, F). Outline of epimeral plates variable, from all with posterodistal angle distinct and produced into pointed process to only angles of plate II produced into pointed process (Fig. 19G).

Antennule (Figs 7A; 8A) peduncle segments length ratio 44: 33: 23. Peduncle-to-main flagellum length ratio 64: 36. Main flagellum 4-articulate, proximal article longest, all articles with aesthetasc. Accessory flagellum with three slender simple setae, one shorter simple robust seta and one penicillate seta.

Antenna (Figs 7A; 8A) differing from *S. sanctensis* n. sp. in gland cone, directed laterally (vs. posteriorly); in length ratio of peduncle segments 4-5 (57.5: 42.5; vs. 47: 53 in *S. sanctensis* n. sp.); in length of peduncle segment 5 relative to first peduncle segment of antennule (segment shorter;

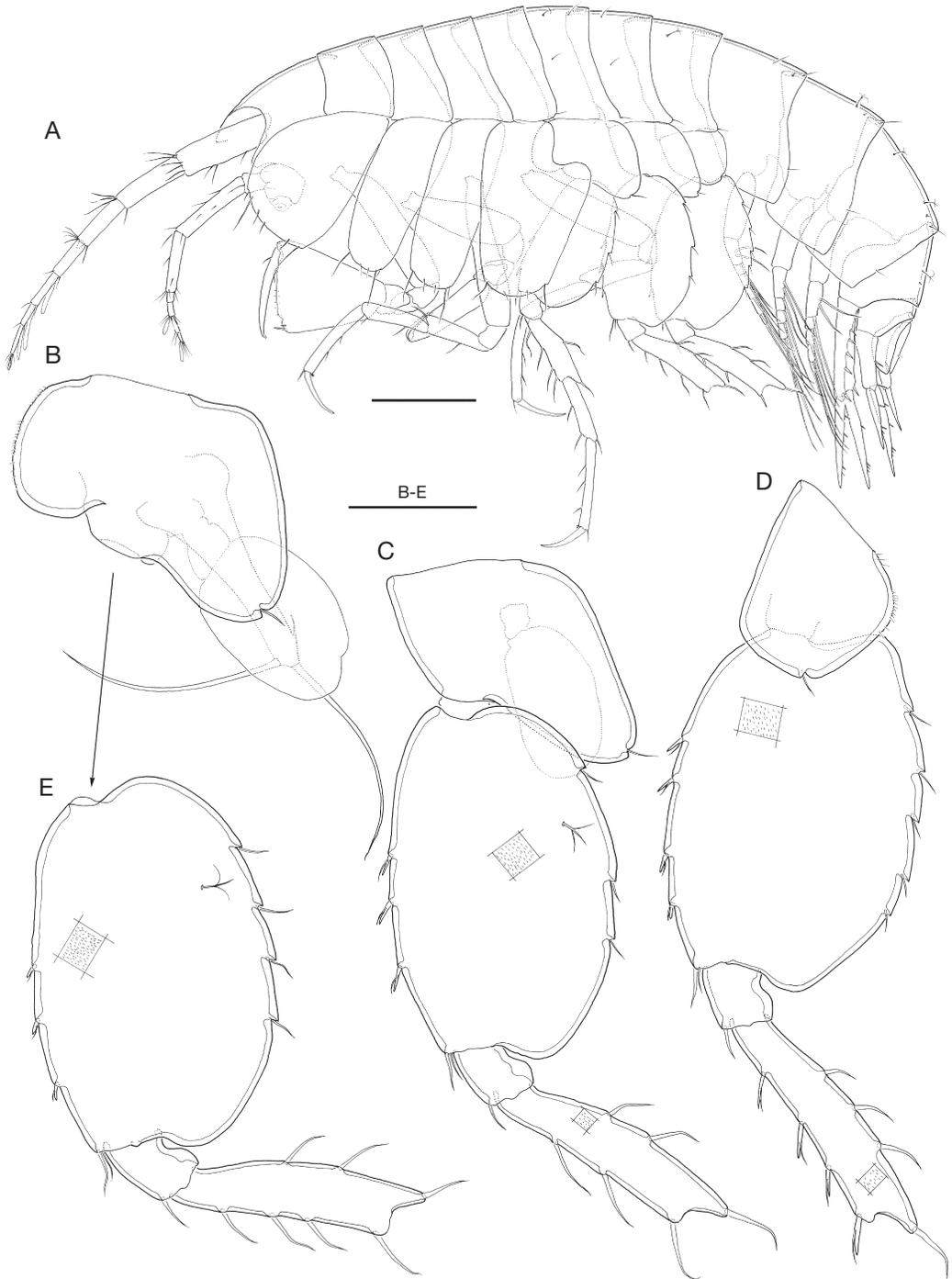


FIG. 7. — *Seborgia vietnamica* n. sp., ♀ paratype 2.88 mm: **A**, habitus, lateral; **B**, left pereopod V, lateral; **C**, left pereopod VI, lateral; **D**, **E**, left pereopod VII, lateral. Distal parts of pereopods V-VII omitted. Scale bars: A, 0.25 mm; B-E, 0.125 mm.

vs. longer in *S. sanctensis* n. sp.); and in articles of flagellum, all approximately similar in length, with short aesthetasc present on articles 2 and 4 only.

Labrum (Fig. 9A) as in *S. sanctensis* n. sp. Paragnaths (Fig. 8C) with inner lobes longer than outer lobes (reverse of *S. sanctensis* n. sp.).

Right mandible differing from *S. sanctensis* n. sp. in composition of spine row, with series of buds probably corresponding to additional spines located proximal to three well-defined, ordinary distal spines (Fig. 8B); left mandible spine row with similar buds, although here there are four rather than three well-defined distal spines (Fig. 9B). Molar process of both mandibles with smooth anterior margin (vs. margin ornamented with setules or microspinules in *S. sanctensis* n. sp.) and distal seta smooth with trifid tip (vs. pappose and unicuspid in *S. sanctensis* n. sp.). Mandibular palp (Fig. 9C) differing in relative proportions of segments (22: 52: 26; vs. 28: 43: 29 in *S. sanctensis* n. sp.), demonstrating elongation of segment 2 in *S. vietnamica* n. sp., and in segment 3 narrow and subrectangular instead of rhomboidal; in addition, armature of distal segment reduced to four E-setae only (cf. D-setae also present on medial margin of segment in *S. sanctensis* n. sp.).

Maxillule (Fig. 9D) differing from *S. sanctensis* n. sp. in ornamentation of coxal endite, covered with long simple setules (vs. endite smooth in *S. sanctensis* n. sp.), in having only two setae instead of three on distal segment of endopod, and in much shorter endopod segment 2 (relative proportions of segments 50: 50; vs. 20: 80 in *S. sanctensis* n. sp.).

Maxilla (Fig. 8D) reduced to single lobe equivalent to outer lobe of *S. sanctensis* n. sp. based on common display of four armature elements; ornamentation of elements different; two medial elements tricuspidate, two lateral elements simple. Protuberance covered with weak setules positioned close to base of lobe on medial side presumably equivalent to inner lobe of maxilla.

Maxilliped (Fig. 8E) differing from *S. sanctensis* n. sp. in relative proportions of carpus-to-unguis of palp (41: 34: 19: 6; vs. 40: 31: 20: 9 in *S. sanctensis* n. sp.), especially on proportionately longer propodus (= palp segment 3) and noticeably shorter and more slender unguis; and in absence of trans-

verse comb of long spinules on dactylus, among other features.

Coxa IV (Fig. 9F) with portion of posterior margin below proximal square excavation strongly oblique; anterior margin of plate straight.

Gnathopod I (Fig. 10A) subchelate, propodus about 1.3 times longer than broad (vs. 1.5 times longer in *S. sanctensis* n. sp.), with pointed palm angle located at 54% of maximum length of segment (vs. at 47% in *S. sanctensis* n. sp.). Palm margin convex, densely ornamented with slender triangular denticles and row of about five submarginal flagellate robust setae; palm angle (Fig. 10B) with two robust setae, one on each side of angle, that on lateral side shorter (vs. longer in *S. sanctensis* n. sp.) and bifid, other simple. Dactylus (Fig. 10C) with two tiny robust setae terminally on medial margin (vs. long spine in *S. sanctensis* n. sp.); unguis short and stout, about 12% length of dactylus (vs. 33% in *S. sanctensis* n. sp.).

Gnathopod II (Fig. 10D) propodus subquadrate, with convex palm margin covered with stout triangular denticles and submarginal row of about nine robust flagellate setae; palm angle with short and stout, hardly visible simple robust seta (Fig. 10F); dactylus with two short simple robust setae terminally on medial margin, and with hyaline sheath almost completely covering unguis (Fig. 10E); unguis tiny, about 3% length of dactylus.

Pereiopods III-IV (Fig. 9E, F) with unguis fully incorporated into dactylus; latter unarmed.

Pereiopods V-VII (Fig. 7B-D) bases each about 1.5 times longer than broad, that of pereiopod V longest (vs. basis of pereiopod V shortest in *S. sanctensis* n. sp.); anterior margin of bases provided with 3 or 4 flagellate robust setae; posterior margin evenly convex with 3-5 serrations each provided with slender simple seta.

Pleopods with protopod variably setulose (Fig. 11A, B); that of pleopod I with proximal swelling covered with long setules (Fig. 11A).

Uropods I and II (Fig. 11C-E) differing from *S. sanctensis* n. sp. in display of additional robust setae on posterolateral margin of protopod and on both rami. Uropod III (Fig. 11F) uniramous, with ramus considerably longer than protopod.



FIG. 8. — *Seborgia vietnamica* n. sp., ♀ paratype 2.88 mm: **A**, left antennule and antenna with head lateral lobe and rostrum, lateral; **B**, right mandible with palp omitted, medial; **C**, paragnaths, anterior (arrows pointing to presumed pore of salivary gland); **D**, left maxilla, lateral; **E**, left maxilliped plus coxa and basis of right counterpart, posterior. Scale bar: A, 0.125 mm; B-E, 0.05 mm.

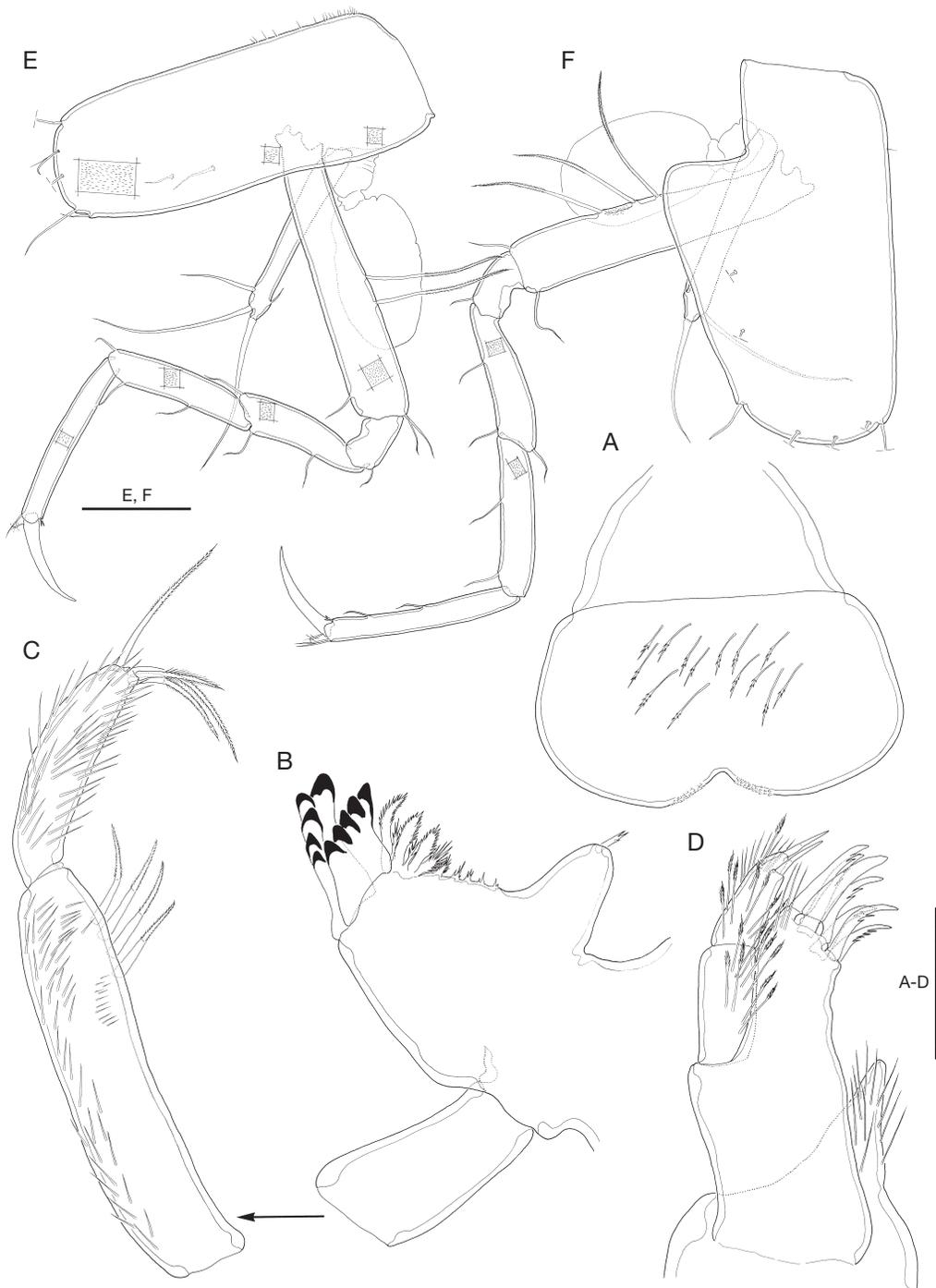


FIG. 9. — *Seborgia vietnamica* n. sp., ♀ paratype 2.88 mm: **A**, labrum with epistome, anterior; **B**, left mandible, medial; **C**, distal segments of palp; **D**, maxillule; **E**, left pereiopod III, lateral; **F**, right pereiopod IV, lateral. Scale bars: A-D, 0.05 mm; E, F, 0.125 mm.

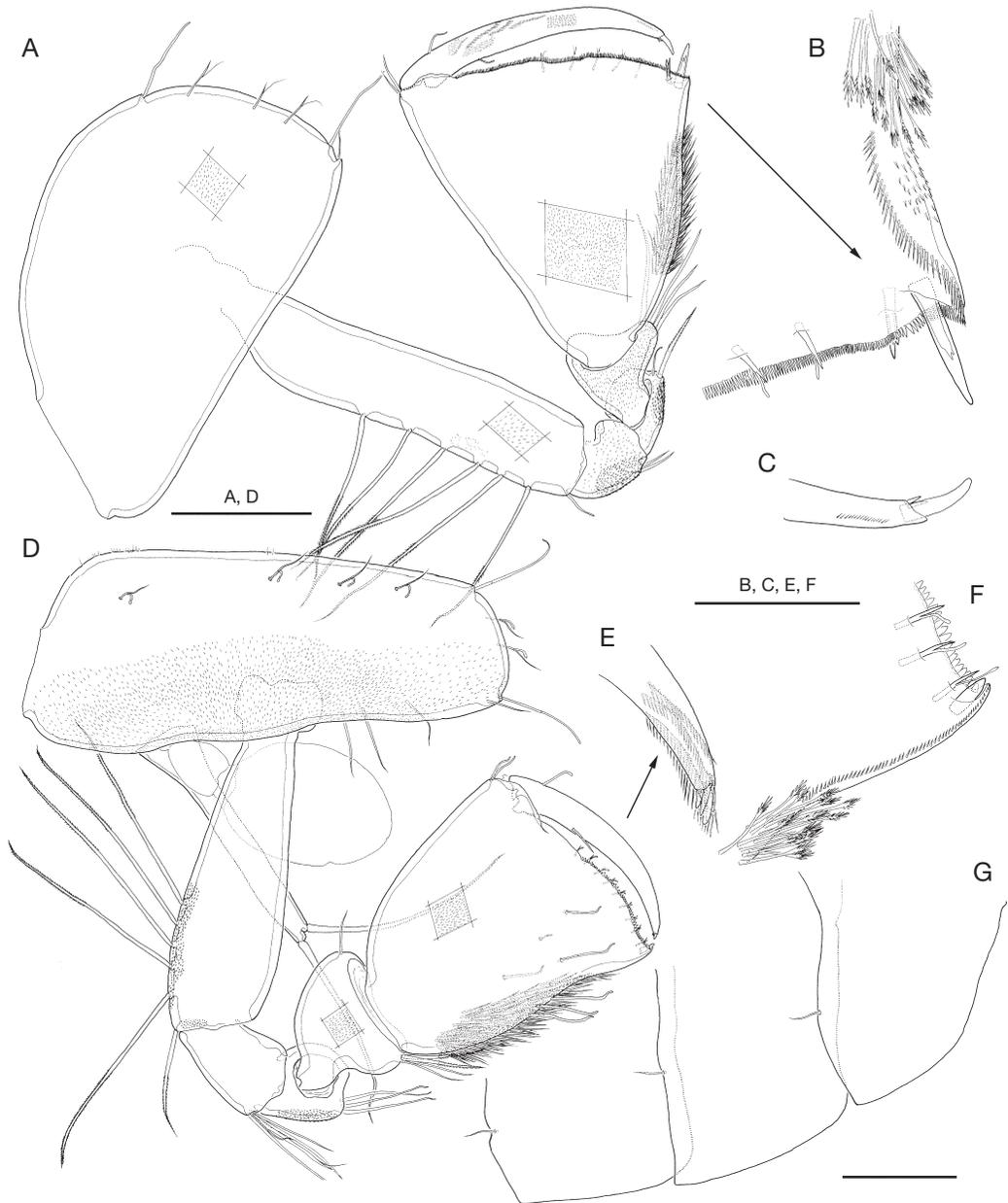


FIG. 10. — *Seborgia vietnamica* n. sp., ♀ paratype 2.88 mm: **A**, right gnathopod I, lateral; **B**, detail of palm angle, medial; **C**, detail of distal portion of dactylus and unguis, medial; **D**, right gnathopod II, lateral; **E**, detail of distal portion of dactylus and unguis, lateral; **F**, detail of palm angle of left gnathopod II, medial; **G**, right epimeral plates, lateral. Scale bars: A, D, G, 0.125 mm; B, C, E, F, 0.05 mm.

REMARKS

Seborgia vietnamica n. sp. is unique in the possession of a series of flagellate robust setae mid-laterally on the

protopod of uropod I. The other species of the genus have a single robust seta at most in the homologous position. The strongly oblique posterior margin of coxa

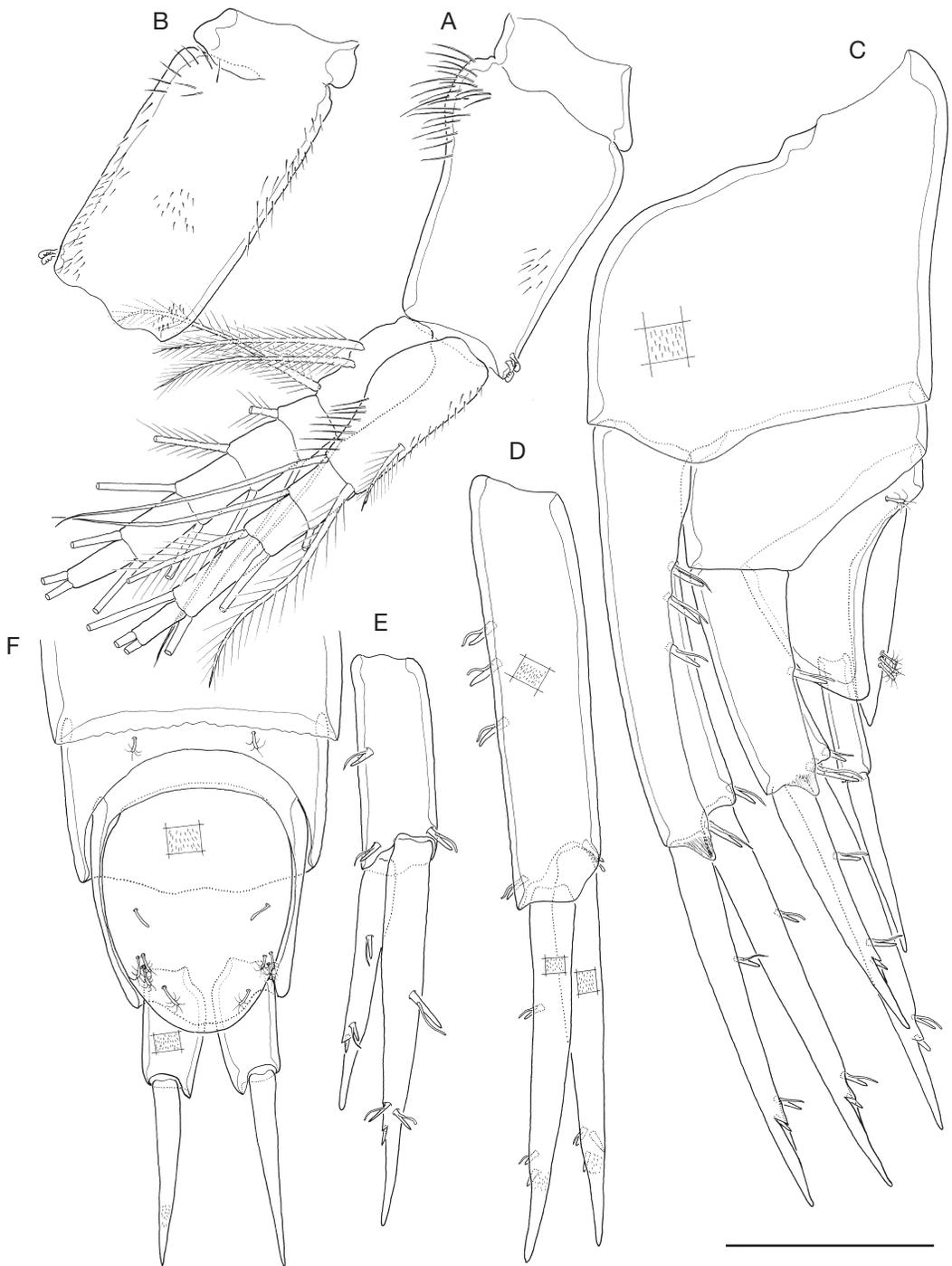


FIG. 11. — *Seborgia vietnamica* n. sp., ♀ paratype 2.88 mm: **A**, left pleopod I, posterior; **B**, protopod of left pleopod III, anterior; **C**, urosome, lateral; **D**, right uropod I, anterior; **E**, left uropod II, posterior; **F**, urosome with third uropods and telson attached, dorsal. Scale bar: 0.125 mm.

TABLE 1. — Main diagnostic differences between *Seborgia* Bousfield, 1979 species. Abbreviations: **A1**, antennule; **A2**, antenna; **Md**, mandible; **G1**, gnathopod I; **G2**, gnathopod II; **P5-P7**, pereopods V to VII; **U1**, **U3**, uropods I and III. Character states in parentheses for *S. kanaka* n. sp. indicating the uncertainty about sex of known specimens.

	<i>S. sanctensis</i> n. sp.	<i>S. vietnamica</i> n. sp.	<i>S. kanaka</i> n. sp.	<i>S. relicta</i> + <i>S. hershleri</i>	<i>S. minima</i>	<i>S. schieckei</i>
Eyes: either vestigial or fully developed (+) vs. absent (-)	+	-	+	-	-	+
Rostrum: well developed (+) vs. reduced (-)	+	+	-	+	-	+
Pleonites, posterodorsal margin: serrate (+) vs. smooth (-)	+	-	-	-	-	+
A1 flagellum: longer than peduncle (+) vs. shorter (-)	+	-	-	-	-	-
A2 peduncle segment 5: elongate (+) vs. ordinary (-)	+	-	-	-	-	-
Md palp segment 3 outline: rhomboidal (+) vs. slender subrectangular (-)	+	-	-	-	-	-
Md palp segment 3: number of E-setae	4	4	3	3	4	4
Md palp segment 3: number of D-setae	3	0	0	0	0	1
Paragnaths, inner lobes: separate (+) vs. partially fused (-)	+	+	-	-	-	?
Maxilla: bilobed (+) vs. unilobed (-)	+	-	-	-	-	-
Maxilliped: basis of left and right sides fused (+) vs. separate (-)	-	-	+	-	-	-
G1 propodus form: subchelate (+) vs. parachelate (-)	+	+	+	-	+	+
G1 female propodus proportions: longer than broad (+) vs. broader than long (-)	+	+	(-)	-	?	+
G1 propodus palm angle: number of robust setae	2	2	2	1	1	1
G1 unguis: elongate (+) vs. short (-)	+	-	-	-	?	-
G1-G2, relative size of propodus: strongly unequal (+) vs. equal (-)	-	-	-	+	-	-
G2 female, propodus proportions: longer than broad (+) vs. equal or broader than long (-)	+	-	(-)	-	?	+
G2 female, propodus palm angle: strongly protruded (+) vs. not protruded (-)	-	-	(+)	+	-	-
Coxa 4, posterior margin: strongly oblique (+) vs. subparallel to anterior margin (-)	-	+	(-)	-	-	-
P5, anterior lobe of coxa: present (+) vs. absent (-)	+	+	-	+	?	?
P5-P7, posterodistal margin of basis: profusely serrate (+) vs. hardly serrate or smooth (-)	-	-	-	+	-	-
P5-P7, posterior margin of basis: convex (+) vs. angled (-)	+	+	-	+	+	+
U1, length of rami: subequal (+) vs. distinctly unequal (-)	+	+	-	-	-	+
U1 protopod mid-lateral armature: several robust setae (+) vs. 1 robust seta at most (-)	-	+	-	-	-	-
U3 condition: biramous (+) vs. uniramous (-)	+	-	-	-	-	-
U3 rami: longer than peduncle (+) vs. shorter (-)	-	+	-	+	+	-

IV is also unique in *Seborgia*, although in *S. relicta* – where coxa IV is sexually-dimorphic – the margin in the female is slightly oblique (see Holsinger & Longley 1980: fig. 25d). The peculiar serrated tip of the long setules present on some limb segments is probably also characteristic of the species, although it is only visible under the highest magnification and could have been overlooked in the other species. Additional diagnostic features of the new taxon compared with other *Seborgia* species are given in Table 1.

ECOLOGY

A moderately dense population of these amphipods

was found in the cave lake in Đông Dục Tiên on the small island Đảo Vạn Giò (eastern part of Ha Long Bay, 15 km off the coast). At the time of the visit it was a water body up to 1.5 m deep and approximately 100 × 20 m in surface area, fragmented by large boulders into a system of interconnected basins with loamy bottom. Water was slightly brackish (4-5 ppt salinity). From the nature of its fauna, we infer that this body of water is, at least during highest levels, connected to and included in the general body of phreatic water of the island. The island is slightly over 1 km² in surface area, with a complex branching outline, its width in few

locations reaching as much as 400 m. Copepods and oligochaetes were extremely scarce. The lake is inhabited by a small population of a troglobiotic freshwater fish (Pisces, Balitoridae, Nemacheilinae). It is surprising that a freshwater fish could have survived on such a small island, possibly since the Pleistocene, when it was a continental hill.

Only a few specimens were found on the larger island Đáo Cát Bà, in an inland karst spring, most probably in the permanently freshwater zone.

Seborgia kanaka n. sp.
(Figs 12-17)

TYPE MATERIAL. — **Loyalty Islands.** Lifou, Grotte de Luengoni (20°58'38.5"S, 167°22'59.1"E), G. A. Boxshall and D. Jaume coll., 22.X.2000, holotype 1.71 mm, sex unknown (lacking oostegites or penile papillae), completely dissected and mounted on two slides (MNHN-Am7546).

Paratypes same data as holotype: 3 specimens of 1.77, 1.79 and 1.87 mm, former completely dissected and mounted on single slide (MNHN-Am7547); latter 2 preserved in 70% ethanol vial (MNHN-Am7548).

DIAGNOSIS. — Basis of maxillipeds fused to each other and incorporated into common segment with fused coxae. Posterior margin of basis of pereopods V-VII angled. Coxal gills bilobed.

ETYMOLOGY. — Species name derived from the Kanak, the original inhabitants of the Loyalty Islands.

DESCRIPTION OF HOLOTYPE

Body (Fig. 12A) unpigmented, micro-oculate, eyes faintly pigmented retaining about five facets (Fig. 12B). Differing from *S. sanctensis* n. sp. in conspicuously hispid condition (see Fig. 12E; short setules covering uniformly most of body integument omitted from most of figures) and in hardly developed rostrum (Fig. 12B). Posterodorsal margin of pleonites smooth (Fig. 12E), only epimeral plate II with posterodistal angle produced posteriorly into pointed process; plates I and III with groove immediately above angle (Fig. 13F).

Antennule (Figs 12A; 13A) peduncle segments length ratio 46: 29: 25. Peduncle-to-main flagellum length ratio 60: 40. Main flagellum 4-articulate, distal article longest, all articles with aesthetasc.

Accessory flagellum (Fig. 13B) with three simple slender setae and one shorter robust seta; penicillate seta apparently absent.

Antenna (Figs 12A; 13C) differing from *S. sanctensis* n. sp. in length ratio of peduncle segments 4-5 (57: 43 vs. 47: 53) and in length of peduncle segment 5 relative to first peduncle segment of antennule (segment shorter vs. longer in *S. sanctensis* n. sp.). In addition, proximal article of flagellum lacking aesthetasc (aesthetasc present in *S. sanctensis* n. sp.).

Labrum (Fig. 13A, D) virtually identical to *S. sanctensis* n. sp. Paragnaths (Fig. 13E) inner lobes fused proximally (lobes separated in *S. sanctensis* n. sp.).

Mandibles (Fig. 14A-E) differing from *S. sanctensis* n. sp. in presence of four elements in spine row instead of three, in smooth anterior margin of molar, and in simple condition of seta on latter process. Palp (Fig. 14D) segments almost identical in relative proportions in both species (23: 52: 25 vs. 22: 52: 26 in *S. sanctensis* n. sp.), although distal segment of *S. kanaka* n. sp. devoid of D-setae and with three E-setae (vs. four in *S. sanctensis* n. sp.).

Maxillule (Fig. 15A) as in *S. sanctensis* n. sp. except for sparsely setulose coxal endite and relative proportions of endopod segments (47: 53 vs. 20: 80 in *S. sanctensis* n. sp.).

Maxilla (Fig. 15B) reduced to single lobe with four simple setae; lobe equivalent to outer lobe of *S. sanctensis* n. sp., based on presence of same number of armature elements.

Maxillipeds (Fig. 14F) differing from *S. sanctensis* n. sp. in basis of each limb fused to opposite member of pair and incorporated into common compound segment with fused coxae. Relative proportions of carpus-to-unguis of palp 47: 33: 16: 4 (vs. 40: 31: 20: 9 in *S. sanctensis* n. sp.); transverse comb of long spinules on dactylus lacking.

Coxal plate IV (Fig. 15D) 2.2 times longer than broad (vs. 1.6 times in *S. sanctensis* n. sp.), with both anterior and posterior margins straight (vs. slightly convex in *S. sanctensis* n. sp.); excavation covering only proximal 13% of posterior margin (26% in *S. sanctensis* n. sp.). Coxa V (Fig. 17A) anterior lobe wanting. Coxal gills (Figs 15C, D; 16C) each with small sacciform protuberance posterolaterally on proximal part.

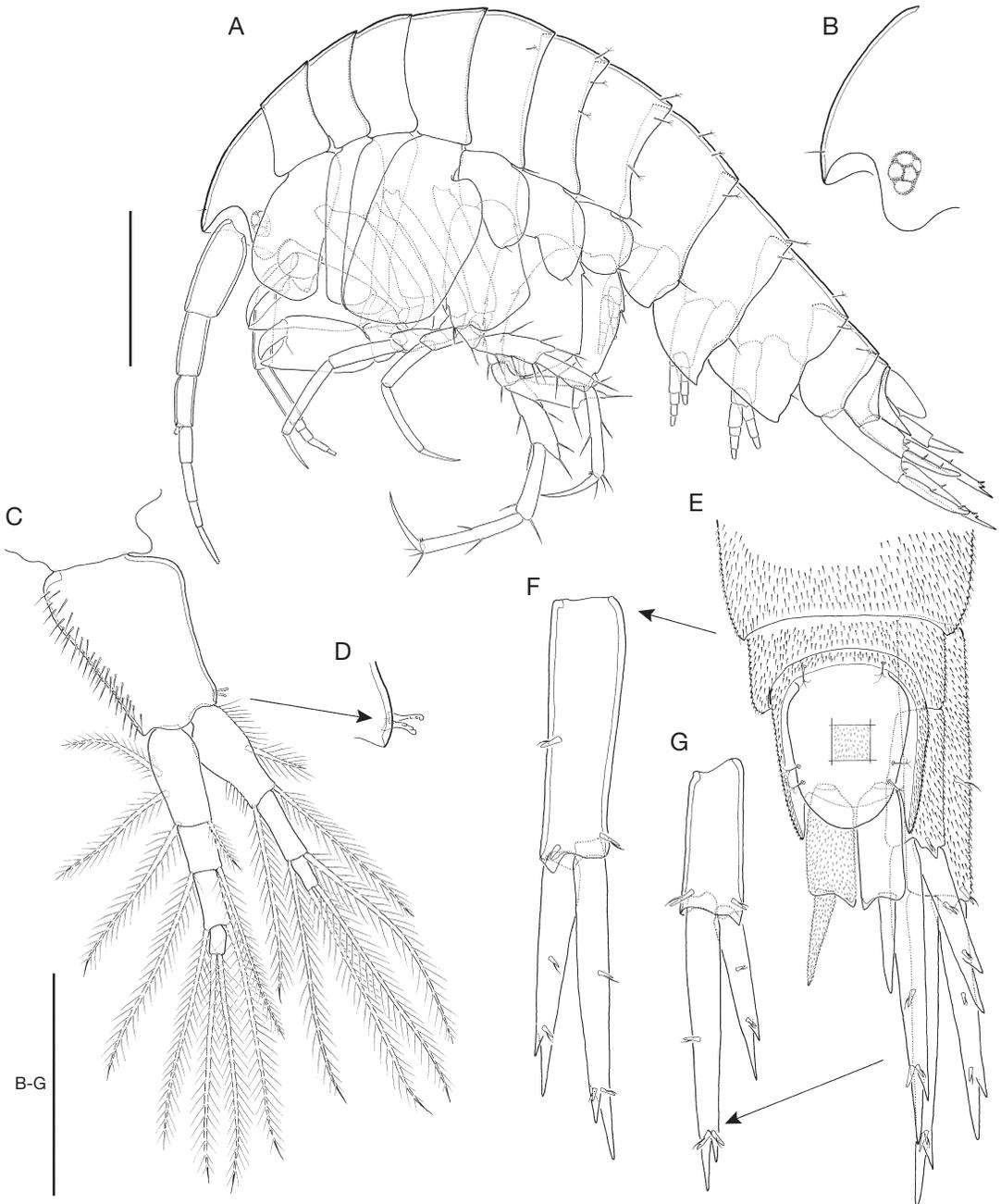


FIG. 12. — *Seborgia kanaka* n. sp., holotype: **A**, body, lateral; **B**, detail of rostrum, lateral lobe and eye; **C**, right pleopod I, anterior; **D**, detail of retinacles; **E**, urosome and telson, dorsal; **F**, left uropod I, posterior; **G**, right uropod II, posterior. Scale bars: A, B, 0.25 mm; C, E-G, 0.125 mm; D, 0.05 mm.

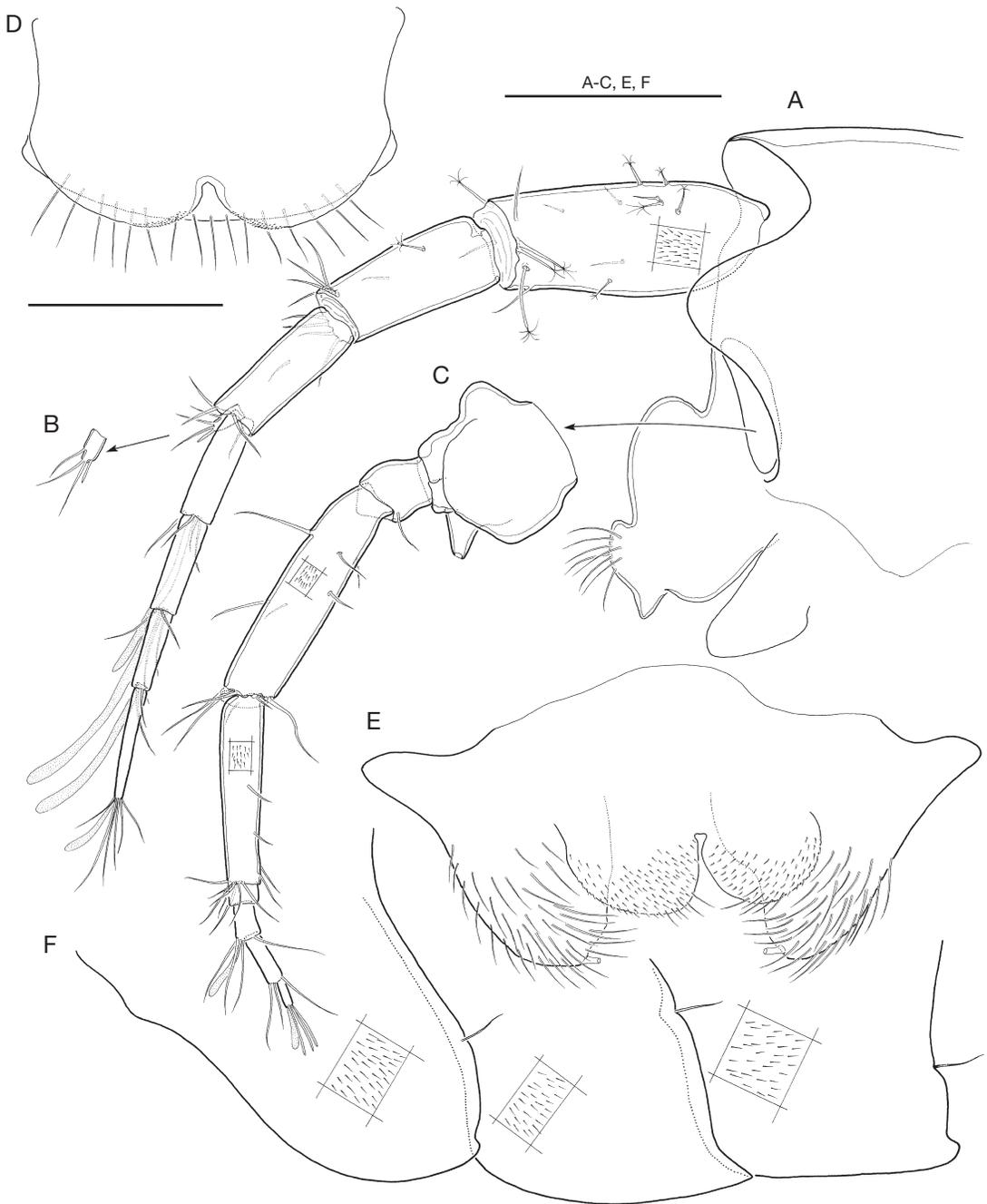


FIG. 13. — *Seborgia kanaka* n. sp., holotype: **A**, head, labrum, paragnaths and left antennule, lateral; **B**, detail of accessory flagellum of latter; **C**, left antenna, lateral; **D**, labrum, posterior; **E**, paragnaths, posterior; **F**, left epimeral plates, lateral. Scale bars: A-C, F, 0.125 mm; D, E, 0.05 mm.



FIG. 14. — *Seborgia kanaka* n. sp., holotype: **A**, left mandible with palp omitted, anteromedial view; **B**, detail of incisor; **C**, detail of lacinia; **D**, palp of left mandible, lateral; **E**, distal part of right mandible, medial; **F**, right maxilliped with proximal portion omitted, posterior (= ventral). Scale bar: 0.05 mm.

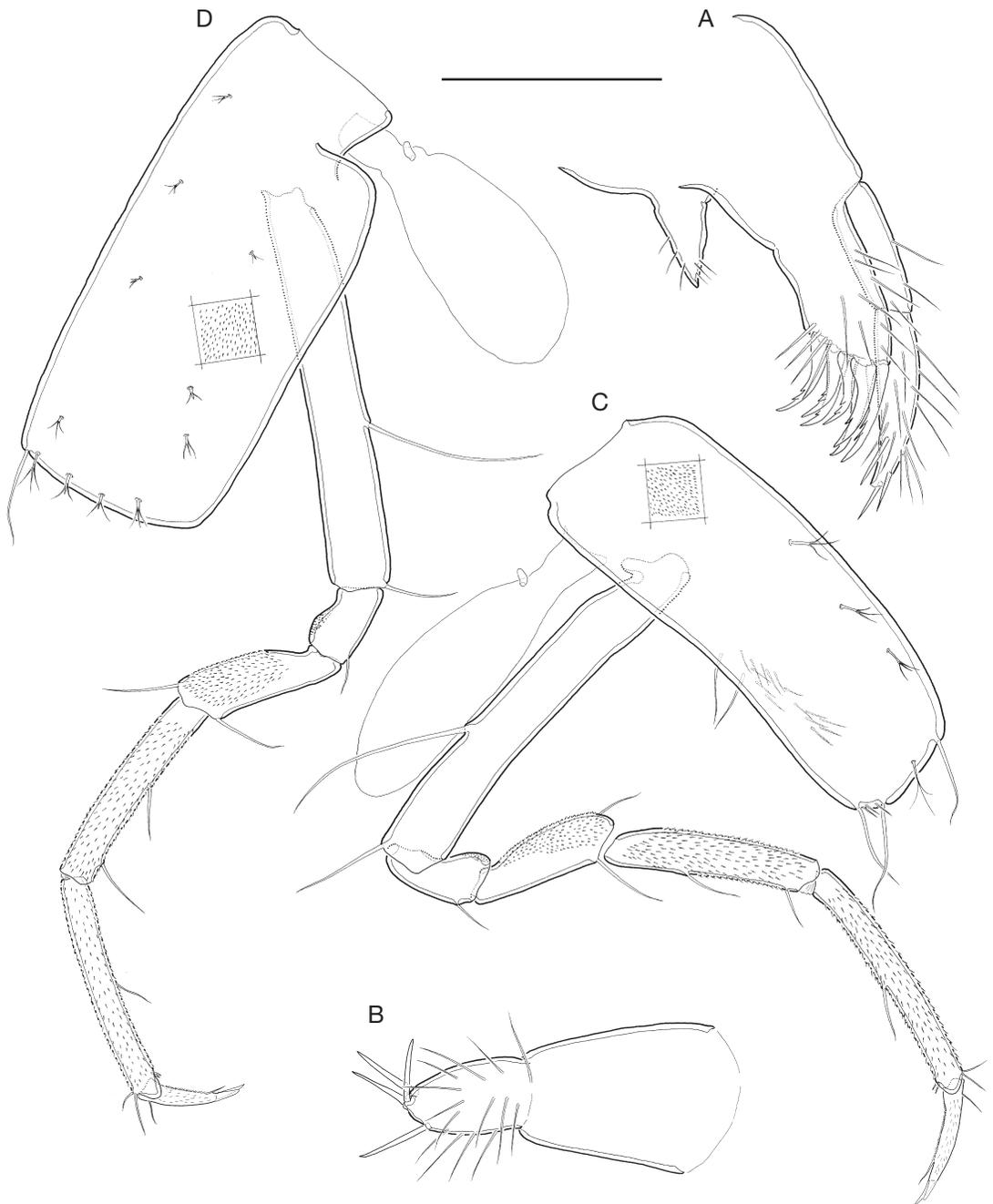


FIG. 15. — *Seborgia kanaka* n. sp., holotype: **A**, right maxillule, posterior; **B**, right maxilla, posterior; **C**, right pereopod III, lateral; **D**, left pereopod IV, lateral. Scale bar: A, B, 0.05 mm; C, D, 0.125 mm.

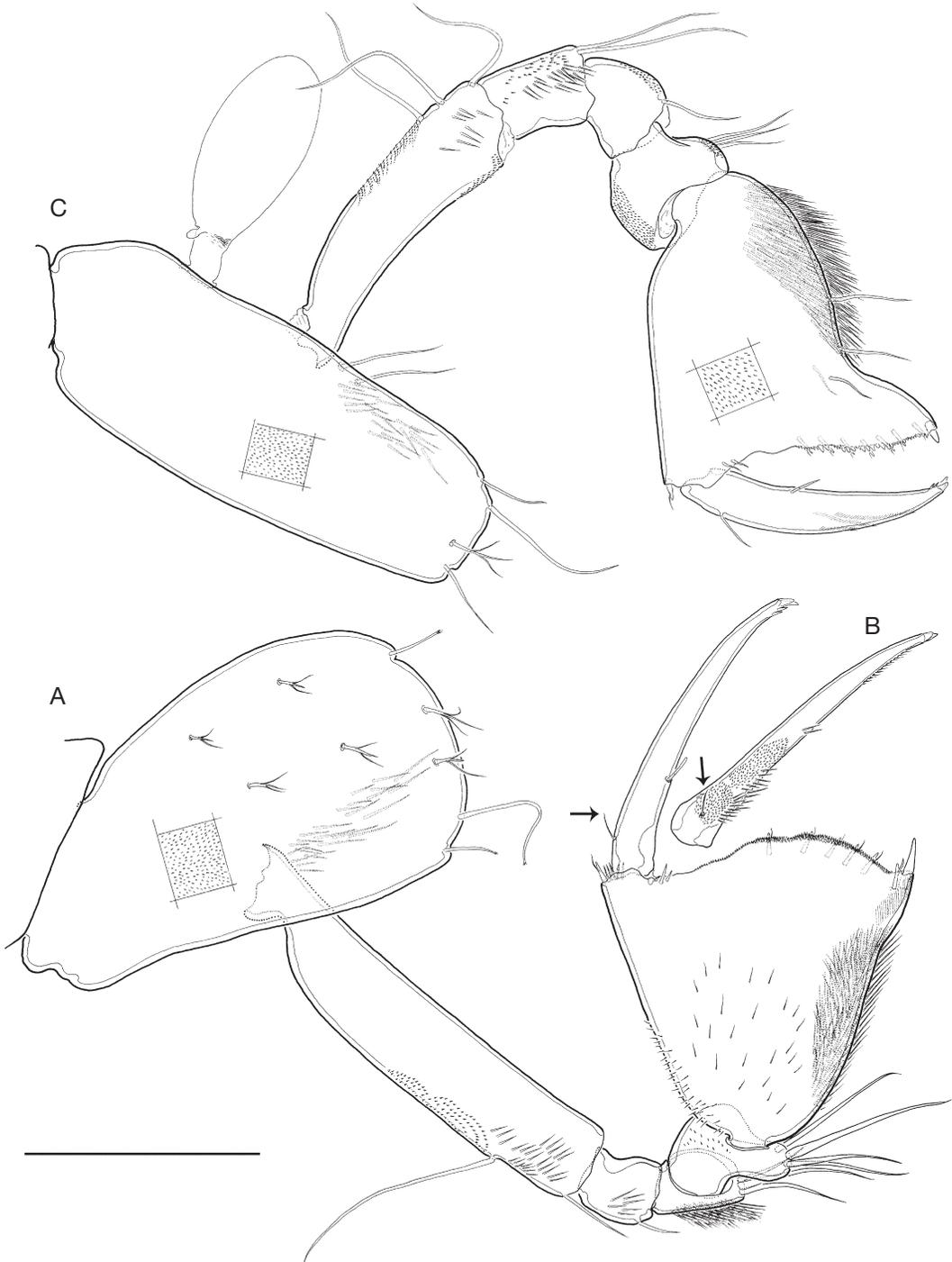


FIG. 16. — *Seborgia kanaka* n. sp., holotype: **A**, right gnathopod I, lateral (integumental microspinulation on surface of dactylus omitted; arrow indicating anteroproximal seta of dactylus); **B**, dorsomedial aspect of nail of left gnathopod I (arrow pointing to anteroproximal seta of dactylus); **C**, left gnathopod II, lateral. Scale bar: 0.125 mm.

Gnathopod I (Fig. 16A) subchelate, propodus about 1.1 times broader than long (vs. 1.5 times longer than broad in *S. sanctensis* n. sp.), with palm angle acute, located at 63% of maximum length of segment (vs. at 47% in *S. sanctensis* n. sp.). Palm margin broadly convex, covered with stout triangular denticles and with submarginal row of about five flagellate robust setae; palm angle with one long and stout simple robust seta on medial side, plus short and slender flagellate robust seta on lateral side. Dactylus (Fig. 16B) with two short robust setae terminally on medial margin, plus hyaline sheath almost completely covering unguis; latter minute, about 5% length of dactylus.

Gnathopod II (Fig. 16C) propodus about 1.2 times broader than long (vs. 1.3 times longer than broad in *S. sanctensis* n. sp.), with palm angle strongly protruded distomedially; palm angle armed with single short and stout simple robust seta; palm margin with row of stout triangular denticles and with submarginal row of about six flagellate robust setae. Dactylus with two tiny terminal robust setae on medial margin, plus hyaline sheath almost completely covering unguis; latter tiny, about 6% length of dactylus (vs. 15% in *S. sanctensis* n. sp.).

Pereiopods III and IV (Fig. 15C, D) each with unguis incorporated into dactylus, latter with single simple seta subterminally on medial margin; hyaline sheath on distal margin of dactylus covering unguis anteriorly; medial margin of dactylus with row of densely set spinules.

Pereiopods V-VII (Fig. 17B-D) each with basis about 1.5 times longer than broad; anterior margin with 2 or 3 robust setae; posterior margin produced into angle (margin evenly convex in other species), with 1-3 notches each provided with slender simple seta.

Pleopods (Fig. 12C, D) with protopod setulose along lateral margin only; proximal swelling on protopod I smooth.

Uropods I-II (Fig. 12F, G) differing from *S. sanctensis* n. sp. in possession of additional robust seta about midway along each ramus, and in relative length of rami of uropod I, with exopod clearly shorter than endopod (rami about equal in length in *S. sanctensis* n. sp.). Uropod III (Fig. 12E) uniramous, ramus shorter than protopod.

REMARKS

Seborgia kanaka n. sp. is unique in possessing an angled posterior margin of the basis of pereopods V-VII, all other *Seborgia* species have a bowed, variably convex posterior margin on this segment. The fusion of the basis of both maxillipeds into a common compound segment with the fused coxae is also a unique feature of the new species, although such a fusion apparently also occurs in at least some members of *Seba* (see Larsen 2007: fig. 8j). Another probable autapomorphic trait of the new species is the loss of the anterior lobe of the coxa of pereopod V; however, the state of this character is not indicated in the descriptions of *S. minima* Bousfield, 1970 and *S. schieckei* Ruffo, 1983. Additional diagnostic features of the new taxon are given in Table 1.

Seborgia kanaka n. sp. is, together with the female of *S. relictata* Holsinger & Longley, 1980, the only member of the genus displaying a strongly concave posterior margin of the propodus of gnathopod II, a by-product of the strong protrusion of the palm angle. Since the male of *S. relictata* does not display this feature, the morphology of the second gnathopod of the new species may provide evidence that the four specimens currently known are females.

ECOLOGY

Grotte de Luengoni – the type locality of the new species – lies about 2 km to the NE of the small village of Luengoni and opens in an upraised coral reef terrace via a sinkhole about 40 m in diameter and 30 m deep. A detailed description and topography of the cave appears in Thomas *et al.* (1995). There are two lakes, one in direct sunlight, the other fully subterranean. The surface water in both lakes is brackish, although the deepest parts (–31 m) of the cave lake may be fully marine. Three of the specimens of *Seborgia kanaka* n. sp. were captured with baited traps set at a depth of 4 m inside the cave, whereas the fourth was caught with a hand net in the dimly lit part of the outside lake, which is directly connected to the cave lake. The accompanying fauna in the cave lake consisted of *Stygocyclops* sp. (Copepoda, Calanoida, Pseudocyclopiidae Sars, 1902), *Josephosella microps* Stock & Iliffe, 1995 (Amphipoda, Melitidae Bousfield, 1973),

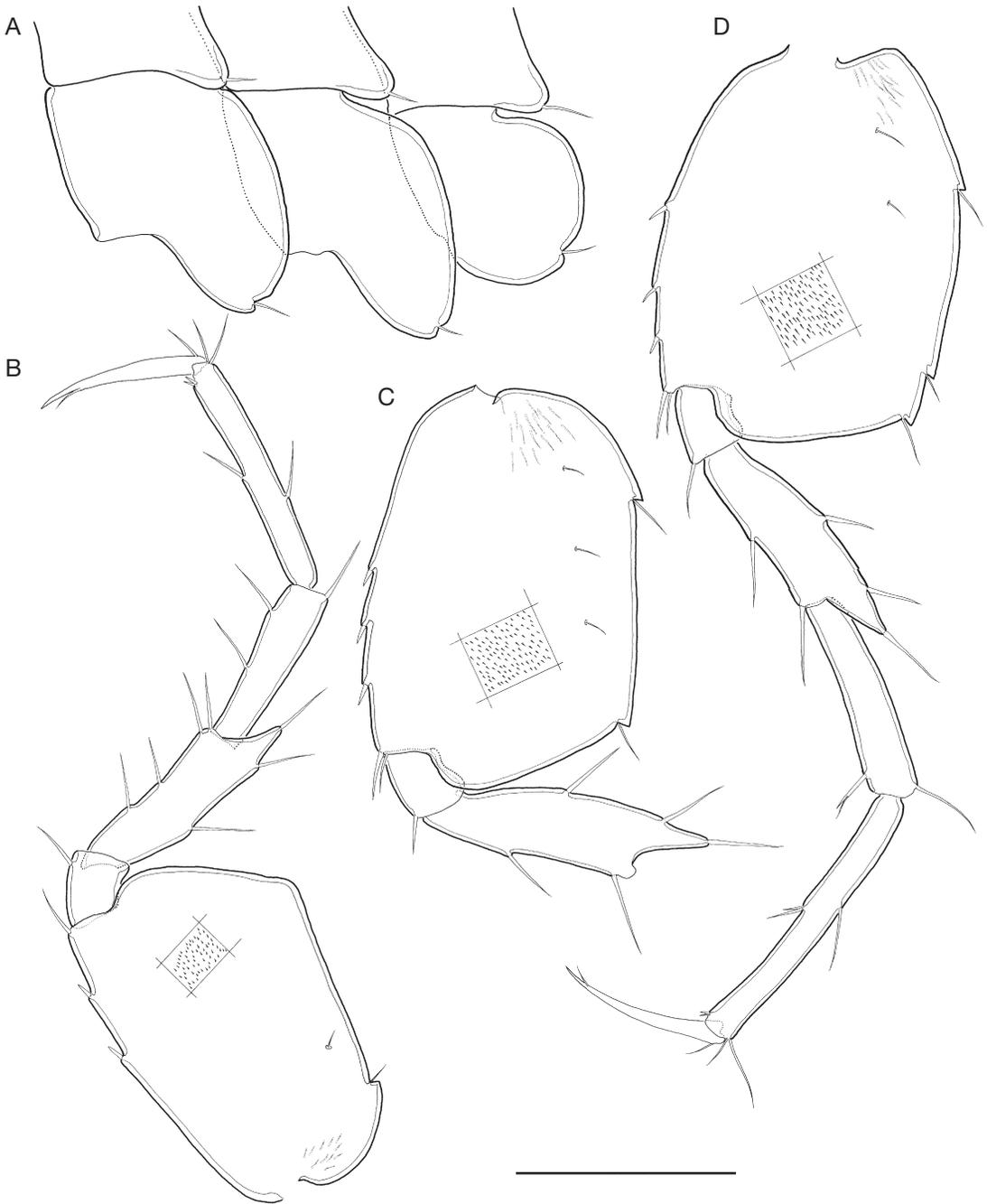


FIG. 17. — *Seborgia kanaka* n. sp., holotype: **A**, left coxal plates V-VII, lateral; **B**, left pereopod V, lateral; **C**, proximal segments of left pereopod VI, lateral; **D**, right pereopod VII, lateral. Scale bar: 0.125 mm.

Macrobrachium microps Holthuis, 1978 (Decapoda, Palaemonidae Rafinesque, 1815), eels and other fishes. In the exterior lake were harpacticoid and cyclopoid copepods plus undetermined polychaete worms.

DISCUSSION

The original classification of the genus *Seborgia* in the Sebidae Walker, 1908 by Bousfield (1970) was challenged by Ruffo (1985), who suggested that it should be treated as intermediate between the Sebidae and the Liljeborgiidae Stebbing, 1899, although he did not formally establish a new family to accommodate it. Holsinger & Longley (1980) had already noticed the peculiar characteristics of *Seborgia* compared with *Seba*, and they erected the subfamily Seborgiinae for the former. The discovery of the three new species described above has re-enforced the affinity between *Seborgia* and other sebidids (i.e. the bilobed maxilla of *Seborgia sanctensis* n. sp. is shared with members of *Seba*; the entire condition of the telson in all members of the family; the fusion of the bases of the paired maxillipeds in *Seborgia kanaka* n. sp. and in *Seba bathybia* Larsen, 2007), but there are no shared derived character states pointing towards a close relationship with liljeborgiids, the latter family being implicitly considered by Bousfield (1982) as a close relative of sebidids. Indeed, some liljeborgiids such as *Idunella* G. O. Sars, 1894 show a remarkable overall similarity to *Seborgia*, although their accessory flagellum of the antennule is multi-articulate, the rami of uropod III are lanceolate, and the telson is deeply cleft with each apex notched and bearing a robust seta. These remain significant differences between the sebidids and the liljeborgiids.

The biramous uropod III of *Seborgia sanctensis* n. sp. (as also found in the families Amphiloichidae Boeck, 1871, Anamixidae Stebbing, 1897 and Leucothoidea Dana, 1852), having the posterior part of the body strongly reflexed beneath the pereion (as in the Amphiloichidae), the fusion of the bases of the paired maxillipeds in *S. kanaka* n. sp. and *Seba bathybia* (as in many leucothoideans), and the entire telson, all lend additional support to the

suggestion of Barnard (1969), Bousfield (1979) and Shaw (1989) that sebidids should be included among leucothoideans on the basis of shared overall body facies, similar mouthparts, and the tendency to live in association with other invertebrates (as in *Seba*).

G. Karaman (1982) established a new genus, *Relictoseborgia*, for one of two species known at that time. As he stated: "is rather similar to genus *Seborgia* Bousf. but differs from latter in the non telescopic antenna 1, unequal gnathopods 1-2, large inner lobes of labium, shallow lateral cephalic lobes and obsolete ventroanterior sinus of head, shape of mandibular palp, uropod 3, etc." In most of the mentioned characters, the recently known species are in different positions between *S. minima* and *S. relictata*, and they might be difficult to classify in one of both genera. Considering also the small number of species, we do not think that a division of them on so minute differences is necessary.

The discovery of *Seborgia sanctensis* n. sp. and *S. kanaka* n. sp., two species which retain at least some vestige of the visual apparatus, in anchialine pools located on coarse unconsolidated sediments suggests that this type of crevicular habitat may be the primary habitat for the genus and, as proposed by Holsinger (1986), that occupation of inland subterranean habitats via marine regressions is the likely colonization route for *Seborgia*.

Acknowledgements

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