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Contribution to the knowledge of European Liljeborgiidae (Crustacea, Amphipoda), with considerations on the family and its affinities

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Abstract

An examination of morphological characters of the Liljeborgiidae reveals that these uncalceolated gammaromorphic amphipods share a number of putative plesiomorphic characters with the Melphidippoidea and the Oedicerotoidea. The Liljeborgiidae are subdivided in two subfamilies: the Idunellinae subfam. nov. for *Idunella* G.O. SARS, 1894 sensu lato (including *Listriella* J.L. BARNARD, 1954) and *Sextonia* CHEVREUX, 1920, and the Liljeborgiinae STEBBING, 1899 for *Liljeborgia* BATE, 1862 sensu lato (including *Isipingus* J.L. BARNARD & KARAMAN, 1987). A list of all known Liljeborgiidae is given. *Idunella aeqvicornis* (G.O. SARS, 1877) (the type species of the genus), *Idunella picta* (NORMAN, 1889) (a species partly agreeing with the characters of the genus *Listriella*, which is provisionally treated as a junior synonym of *Idunella*) and *Sextonia longirostris* CHEVREUX 1920 (the most plesiomorphic Liljeborgiidae known to date) are re-described. *Idunella* proves to be morphologically very diverse but the splitting of the genus appears premature. Three groups are recognized within the genus *Liljeborgia*. Groups 1 and 2, which are cosmopolitan, speciose and well represented in Europe, are considered as separate subgenera: *Liljeborgia* BATE, 1862 and *Lilljeborgiella* SCHELLENBERG, 1931. Group 3, which was not available for study, includes a few little-known Northwestern Pacific species and the very insufficiently described South African *L. epistomata* K.H. BARNARD, 1932 (= *Isipingus epistomatus*). The North East Atlantic and Mediterranean species of the subgenus *Liljeborgia* are revised and the following taxa are separately treated: *Liljeborgia brevicornis* (BRUZELIUS, 1859), *L. dellavallei* STEBBING, 1906, *L. inermis* CHEVREUX, 1920, *L. kinahani* (BATE, 1862), *L. macronyx* G.O. SARS, 1894, *L. mixta* SCHELLENBERG, 1925, *L. pallida* (BATE, 1857), *L. psaltrica* KRAPP-SCHICKEL, 1975 and *Liljeborgia* sp. 4. These species include the type species of the genus *Liljeborgia*: *L. pallida*. Remaining difficulties to separate *L. brevicornis*, *L. dellavallei*, *L. kinahani*, *L. mixta*, *L. pallida* and *Liljeborgia* sp. 4 are pointed out and the validity of some of these taxa remains questionable. The rare *L. inermis*, which was previously only known from Mauritania and the Cape Verde Islands, is now recorded from South Portugal. The close similarities between the Scandinavian upper-bathyal species *Liljeborgia macronyx* and the lower-bathyal Antarctic species *L. cnephatis* D'UDEKEM D'ACOZ, 2008 (both eyeless species) are pointed out, and it is suggested that the ancestors of *L. macronyx* could have lived in the Southern Ocean. In the subgenus *Lilljeborgiella*, *Liljeborgia caliginis* D'UDEKEM D'ACOZ & VADER, 2009 is considered as a probable synonym of *L. charybdis* D'UDEKEM D'ACOZ & VADER, 2009. An identification key and a checklist are provided for all known Mediterranean and North East Liljeborgiidae. It is pointed out that the names with 'qv' introduced by G.O. SARS, like *Idunella aeqvicornis* (G.O. SARS, 1877) have to retain their original spelling and that the 'qv' may not be converted into 'qu' as it is usually done in literature. In an appendix to the present paper, two melphidippoid families, cited in literature but previously nomenclaturally invalid, are herein valided: the Cheirocratidae fam. nov. and the Hornelliidae fam. nov.

Key-words. Crustacea, Amphipoda, Liljeborgiidae, Liljeborgiinae, Idunellinae subfam. nov., *Liljeborgia*, *Lilljeborgiella*, *Idunella*, *Sextonia*, Cheirocratidae fam. nov., Hornelliidae fam. nov., Europe, Arctic, Atlantic, Mediterranean, Systematics.

Résumé

Un examen des caractères morphologiques des Liljeborgiidae révèle que ces amphipodes gammaromorphes non calcéolés partagent un nombre important de caractères supposés plésiomorphiques avec les Melphidippoidea et les Oedicerotoidea. Les Liljeborgiidae sont subdivisés en deux sous-familles: les Idunellinae subfam. nov. pour *Idunella* G.O. SARS, 1894 sensu lato (incluant *Listriella* J.L. BARNARD, 1954) et *Sextonia* CHEVREUX, 1920 et les Liljeborgiinae STEBBING, 1899 pour *Liljeborgia* BATE, 1862 sensu lato (incluant *Isipingus* J.L. BARNARD & KARAMAN, 1987). Une liste de toutes les espèces connues de Liljeborgiidae est donnée. Une redescription est donnée pour *Idunella aeqvicornis* (G.O. SARS, 1877) (l'espèce type du genre), *Idunella picta* (NORMAN, 1889) (une espèce dont les caractères coïncident partiellement avec ceux de *Listriella*, genre provisoirement traité comme un synonyme plus récent d'*Idunella*) et *Sextonia longirostris* CHEVREUX 1920 (le Liljeborgiidae le plus plésiomorphique connu à ce jour). Le genre *Idunella* s'avère morphologiquement particulièrement divers mais le démembrement de ce dernier semble prématuré. Trois groupes sont reconnus au sein même de *Liljeborgia*. Les groupes 1 et 2, qui sont cosmopolites, riches en espèces et bien représentés dans les eaux européennes, sont considérés ici comme des sous-genres distincts: *Liljeborgia* BATE, 1862 et *Lilljeborgiella* SCHELLENBERG, 1931. Le groupe 3, qu'il n'a pas été possible d'étudier, comprend un petit nombre d'espèces peu connues du Pacifique nord occidental et l'espèce sud-africaine très insuffisamment caractérisée *L. epistomata* K.H. BARNARD, 1932 (= *Isipingus epistomatus*). Les espèces nord-est atlantiques et méditerranéennes du sous-genre *Liljeborgia* sont révisées et les taxa suivants sont traités séparément: *Liljeborgia brevicornis* (BRUZELIUS, 1859), *L. dellavallei* STEBBING, 1906, *L. inermis* CHEVREUX, 1920,

L. kinahani (BATE, 1862), *L. macronyx* G.O. SARS, 1894, *L. mixta* SCHELLENBERG, 1925, *L. pallida* (BATE, 1857), *L. psaltrica* KRAPP-SCHICKEL, 1975 et *Liljeborgia* sp. 4. Ces espèces comprennent l'espèce type du genre *Liljeborgia*: *L. pallida*. Les difficultés éprouvées à séparer *L. brevicornis*, *L. dellavallei*, *L. kinahani*, *L. mixta*, *L. pallida* et *Liljeborgia* sp. 4 sont soulignées et la validité d'une partie de ces taxons demeure incertaine. Une espèce rare, *L. inermis*, qui n'était précédemment connue qu'en Mauritanie et aux Iles du Cap Vert, est maintenant signalée dans le sud du Portugal. Les étroites similitudes entre *Liljeborgia macronyx* de la zone bathyale supérieure de Scandinavie et *L. cnephatis* D'UDEKEM D'ACOZ, 2008 de la zone bathyale inférieure antarctique (espèces toutes les deux dépourvues d'yeux) sont mises en évidence, et il est suggéré que les ancêtres de *L. macronyx* pourraient avoir vécu dans l'Océan Austral. Dans le sous-genre *Lilljeborgiella*, *Liljeborgia caliginis* D'UDEKEM D'ACOZ & VADER, 2009 est considéré comme un probable synonyme de *L. charybdis* D'UDEKEM D'ACOZ & VADER, 2009. Une clé d'identification et une liste d'inventaire sont proposées pour tous les Liljeborgiidae connus de la Méditerranée et de l'Atlantique Nord Oriental. Enfin, on signale en passant que les noms avec 'qv' introduits par G.O. SARS (par exemple *Idunella aeqvicornis* (G.O. SARS, 1877)) doivent conserver leur orthographe originale et que le 'qv' ne peut en aucun cas être converti en 'qu' comme on le fait habituellement dans la littérature. Dans un appendice au présent article, deux familles de Melphidippoidea, en usage dans la littérature mais à ce jour invalides au point de vue de la nomenclature, sont validées et décrites comme «nouvelles»: les Cheirocratidae fam. nov. et les Hornelliidae fam. nov.

Mots-Clés. Crustacea, Amphipoda, Liljeborgiidae, Liljeborgiinae, Idunellinae subfam. nov., *Liljeborgia*, *Lilljeborgiella*, *Idunella*, *Sextonia*, Cheirocratidae fam. nov., Hornelliidae fam. nov., Europe, Arctique, Atlantique, Mediterranée, Systematique.

Introduction

The present work, which is focused on the Northeastern Atlantic and Mediterranean amphipods of the family Liljeborgiidae, is a follow-up of the paper by D'UDEKEM D'ACOZ & VADER (2009) on the European *Liljeborgia* of the subgenus *Lilljeborgiella* SCHELLENBERG, 1931. Herein, the species of the second subgenus, *Liljeborgia* BATE, 1862 (including the type species of the genus, *L. pallida* (BATE, 1857)) are revised. Since good quality material of some interesting European Liljeborgiidae belonging to other genera (*Idunella* and *Sextonia*) was available, these species are re-described as well. An identification key and a checklist are also provided for all known Liljeborgiidae of the North East Atlantic and the Mediterranean.

The subgenus *Liljeborgia* includes rather characteristic species like *Liljeborgia inermis* CHEVREUX, 1920, *L. macronyx* G.O. SARS, 1894 and *L. psaltrica* KRAPP-SCHICKEL, 1975 but also a group of ill-defined species, here designed as the group *pallida*. These taxa are treated separately, although the validity of some species is questionable. At this stage, it is considered more important to try to understand to which specimens the names proposed in literature do apply than to speculate on the validity of pseudo-cryptic species on the basis of hard to delineate characters examined for a limited number of specimens.

When studying the subgenus *Lilljeborgiella*, D'UDEKEM D'ACOZ & VADER (2009) postulated that the occurrence of anophthalmous amphipod species in the photic zone of Arctic and sub-Arctic seas resulted from a colonisation of shallow seas by species of abyssal origin, and they considered the possibility that the ancestors of such deep-sea species could have lived on the continental shelf of the Southern Ocean. The same question is considered for the subgenus *Liljeborgia*, with *L. macronyx*.

Besides alphataxonomic and biogeographic aspects, some higher systematic questions are briefly touched upon. The affinities of *Liljeborgia* and its relatives has been a source of continued debates over the past 150 years, resulting in a range of conflicting and often inconsistent proposals. The possible affinities of the Liljeborgiidae with the Melphidippoidea, suggested by recent molecular data, are explored in scrutinizing morphological data. Different generic level subdivisions of the family Liljeborgiidae have been proposed in the past, but none appear adequate. New subfamilial, generic and subgeneric divisions are herein proposed, and characters potentially important for further investigations in the study of the family are pointed out.

Finally, the comparison of the Liljeborgiidae with the Melphidippoidea obliges us to describe as 'new' two melphidippoid families, cited in literature but previously invalid: the Cheirocratidae fam. nov. and the Hornelliidae fam. nov.

Material and methods

Complete specimens and appendages were examined in temporary glycerin slides with a DML Leica compound microscope equipped with a drawing tube. Pencil drawings were scanned and afterwards inked with the software ADOBE ILLUSTRATOR 11.0.0 on an A3 drawing table (Wacom Intuos3 12 x 19), using the method described by COLEMAN (2003, 2009c). Ratios are given to 2 decimal places, in anticipation of a future cladistic study, which may require various forms of rescaling. The following abbreviations are used: A1, antenna 1; A2, antenna 2; Ep1–Ep3, epimeral plates 1–3; Gn1, gnathopod 1; Gn2, gnathopod 2; Md, mandible; Mx1, maxilla 1; Mx2, maxilla 2; Mxp, maxilliped; P3–P7,

pereiopods 3–7; U1–U3, uropods 1–3. Nomenclature of the setae of the mandibular palp follows Lowry & Stoddart (1993). In the descriptions, the term "tooth" is used for non-articulated, pointed ectodermic structures, the term 'acicula' for any articulated structure, 'spine' for stout, inflexibly articulated structures (i.e. robust aciculae), the term 'seta' for slender, flexibly articulated structures (i.e. slender aciculae), the term 'spinule' for very short spines and for inflexible lateral profections of setae, and the term 'setule' for very short setae and for flexible lateral projections of setae.

Watling (1989) proposed to use of the term 'setae' for any articulated structure (including broadly conical or ovoid structures) in crustaceans, and he was followed by many recent amphipodologists (e.g. Zimmer *et al.*, 2009). The use of a general term for any articulated structure can be considered as legitimate in anatomical or morpho-functional studies, because slender and robust articulated chitinous extensions are sometimes homologous and because intermediates exist in some cases (Oshel & Steele, 1988; Watling, 1989). However the compulsory and exclusive use of such a term in all fields of amphipodology is not justified and coining the term 'seta' for it may have been unfortunate. The new definition of 'seta' proposed by Watling (1989) conflicts both with the concept of seta used in the human language (long flexible or hair-like structure) and with its definition in classical amphipod literature (e.g. Barnard & Karaman, 1991, p. 806: a bristle, a weakly articulated chitinous extension, which is flexible). The current coexistence of two conflictive definitions of the term seta in literature has also probably become a source of confusion for non-specialists, who have to identify amphipods. This is the reason why the term 'acicula', plural 'aciculae' for any articulated chitinous extension is used herein. This term, which is the diminutive of 'acus' (= needle in Latin), is not used in the English language nor in previous amphipod literature. However, it is used in other groups of invertebrates, and Magenti & Gardner (2005) defines it as 'a slender needle-like process; a spine or a bristle; something larger than a seta or chaeta', which complies reasonably well with its proposed usage in amphipodology. It should also be realized that, if an exclusive term has to be used for any articulated structure, then a longer and more complex terminology is necessary when precise descriptions are required. So, Lowry & Stoddart (1995: 8), who applied the system of Watling (1989) to alphataxonomy, used the term 'slender setae' and 'robust setae' for the structures traditionally named 'setae' and 'spines'. This considerably lengthens alphataxonomical descriptions when fine descriptions are required ('slender setae' have to be subdivided into 'thin slender setae' and 'stout slender setae, etc) or have to be replaced by the acronyms SS and RS (e.g. Lörz, *et al.*, 2007), which decreases the abstractness of descriptions. The use of the terms 'spine' and 'seta' in their traditional sense seems therefore more practical for the descriptions of species. Lowry & Stoddart (1995: 8) also proposed to use the term spine for the structures traditionally called teeth in older literature: "what we previously referred mainly as teeth (non-articulating extrusions of the cuticle), are now referred to as spines". This substitution is also herein rejected, firstly because it was proposed without argumentation, and secondly because it is likely to lead to further trouble for non-specialists, who largely rely on classical literature (using traditional morphological nomenclature) for identifying their amphipods.

The following acronyms are used for scientific institutions: NHM: the Natural History Museum, London, UK (previously British Museum, Natural History); MCSN: Museo Civico di Storia Naturale, Verona, Italy; RBINS: Royal Belgian Institute of Natural Sciences, Brussels, Belgium; TSZCr, Tromsø Samlinger Zoologi Crustacea, UBZM, Universitetet i Bergen, Zoologisk Museum.

Systematics

Superfamily Liljeborgioidea Stebbing, 1899

Composition: herein restricted to the family Liljeborgiidae. Bousfield (1982, 1983) and Bousfield & Shih (1994) also included the Paracrangonyctidae Bousfield, 1982, the Sebidae Walker, 1907, the Colomastigidae Stebbing, 1899 and the Salentinellidae Bousfield, 1977, which are specialized families strongly departing from the typical liljeborgiid body plan. A relationship between these families and the Liljeborgiidae cannot not be ruled out, but further evidence is required before accepting this scheme.

Family Liljeborgiidae Stebbing, 1899

Family Liljeborgiidae Stebbing, 1899: 211 (type genus: *Liljeborgia* Bate, 1862; type species of the type genus: *Gammarus pallidus* Bate, 1857)

Description: Body elongate, laterally compressed, gammaromorphic in shape.

Head: Eye in normal position, present or absent; when present, eye usually elliptic or subquadrate,

rarely circular; rostrum short; anterior lobe moderately developed, rounded to bluntly angular, never acute; antennal concavity broad and very shallow; posterior lobe obtuse and in posterior position.

A1: equal or shorter than A2 (very rarely longer: male *Idunella chilkensis* CHILTON, 1921), not unfrequently shorter than peduncle of A2; peduncle short and stout, with very few spines and setae; article two of peduncle slightly to significantly shorter than article one, a bit narrower than article one; article three much shorter than article 1, usually short and stout; accessory flagellum present, well developed, with at least 2 articles, inserted dorsomedially; calceoli absent; callynophore absent.

A2: ornamentation of peduncle variable; articles four and five of peduncle subequal; flagellum about as long as sum of articles four and five of peduncle; calceoli absent; brush of setae absent.

Upper lip: short, truncate or weakly incised, symmetrical or not.

Lower lip: soft and fragile (difficult to dissect without damage); inner lobe scarcely developed; outer lobes ovate.

Md: rectangular, with hollow part narrowly triangular and long; incisor process well developed and toothed; left and right laciniae mobiles well developed, square, flattened, and morphologically distinct; left one with 4-6 (normally 5) large teeth, and right one with medial strong flattened tooth often posteriorly overlapping the rest of the lacinia (which is smooth to minutely denticulate); raker spine row well developed; molar process variably developed: fully triturative with one posterior gnathobasic molar seta (genus *Sextonia*) or forming a small projection with a cluster of long and stout setae (other genera); articulated with carapace with lateral or posterior hinge; palp well developed, with first article usually long, without tooth on posterodistal corner, with second article straight and long (longer than article one and article three); morphology and ornamentation of article three variable.

Mx1: left and right palps identical; palp 2-articulated, second article distally not truncate, with or without anteromedial setae, with row of posterior/distal smooth spines and with longitudinal row of facial setae; outer plate with 7-10 strong spines, which are smooth or with short lateral denticles, never furcate; inner plate poorly setose; when there are several setae they form a simple row.

Mx2: plates elliptic subequal (inner plate very slightly broader than outer plate); outer plate with posterior border straight or convex, with facial setae often few in number, often submarginal, irregularly distributed, not forming a row, or rarely forming an irregular row;.

Separate intermaxillar apodemes with simple medial margins (at least in *Liljeborgia*) (COLEMAN, 2002).

Mxp: plates and palp normally developed; outer plate not reaching tip of article two of palp; article four of palp with distinct unguis; inner plate with 1-7 anterior spines, which are not all clustered on anteromedial corner, usually without inner margino-facial spine (but such a spine present in *Idunella aeqvicornis*).

Coxae: never ventrally serrate; coxae 1-4 long to very long; coxa 1 more or less trapezoidal and usually somewhat anteriorly produced; coxae 2-3 more or less quadrato-elliptic; coxae 1-3 with small posterior (and often small anterior) ventral notch or tooth; coxa 4 square to rectangular, almost always excavate posterodorsally, often with anteroventral tooth, with several teeth or serrations on posterior border; ventral margin of coxa 1-4 usually not setulose, except for seta associated with anterior and posterior notch or tooth (setae arising from medial surface can be present) [exceptionally ventral margin of coxa 4 setulose]; coxae 1-4 of *Isipingus* departing from usual morphology; coxae 5-7 short, sometimes with posterior denticle; coxae 5-6 subequal and coxa 7 a bit shorter; anterior and posterior lobes of coxa 5 subequal.

Gills: coxal gills on Gn2-P6: elliptic and simple.

Oostegites: on Gn2-P5: very narrow, not especially large.

Gnathopods: subchelate, strong, similar, moderately different or strongly different; either Gn1 or Gn2 can be the strongest; merus often with small acute posterodistal tooth (tooth sometimes duplicated); carpus with or without long posterodistal process; palm well defined; outer border of palm with row of short hooked spines and often (especially on Gn2) with strong setae; medial border of palm either with 2 indistinct rows of strong setae armed with a few lateral spinules (Liljeborgiinae), or with 1 row of short stout spines and 1 row of strong setae armed with a few lateral spinules (Idunellinae); dactylus of Gn1-Gn2 toothed or not; no setae in interdental notches; dactylus of Gn1 without medial setae; dactylus of Gn2 with or without medial setae; dactylus of Gn1-Gn2 with 1 seta on anterior border, in very proximal position; dactylus of Gn1-Gn2 without distal unguis..

P3-P4: ordinary; propodus longer or slightly shorter than merus; dactylus either with vestigial unguis associated with 2 microscopical setules (*Sextonia*), or without unguis and without posterior ornamentation (other genera).

P5-P7: slightly to significantly dissimilar in structure; morphologically basal or rather basal; P5 < P6 < P7; basis often expanded; dactylus of very variable length,

with or without terminal unguis; dactylar ornamentation reduced to 1 proximal posterior seta and sometimes 1-2 subdistal tiny anterior setules.

Pleonites: ordinary, with or without posterodorsal small tooth/teeth, unpaired ventrofacial spines or setae sometimes present (but often absent); posterior border of epimeral plates usually smooth, rarely serrate or crenulate.

Pleopods: well developed with elongate peduncle (with 2 coupling hooks), with long rami.

Urosomite 1: with or without ventrofacial spine(s), with or without posterodorsal tooth or teeth; dorsal spination/setation usually absent, very reduced if present.

Urosomite 2: with or without posterodorsal tooth or teeth; dorsal spination/setation usually absent, very reduced if present.

Urosomite 3: with or without pair of posterodorsal spines.

U1-U2: peduncle of U1 with several ventrofacial spines in *Sextonia*, without ventrofacial spines in other genera; peduncle of U2 without ventrofacial spines; peduncle of U1 normally with several dorsolateral spines, with 1 distal dorsomedial spine or with several dorsomedial spines, without interramal tooth; lateral distal tooth (spur) of peduncle of U1 medium-sized, not more ventrolateral than dorsolateral (forming an angular discontinuity with both borders); U1 with rami subequal; U2 with outer ramus slightly shorter than inner ramus; tip of rami either broad and spinose (Idunellinae), or pointed (then tip either without spines or with trace of spine fused with tip) (Liljeborgiinae).

U3: strongly attached to urosome (never falling apart in preserved specimens, and hard to remove); peduncle medium-sized, about 2 x as long as broad; rami well developed (sometimes broader and larger in males than in females), most commonly subequal, with tip acute (without apical spines or setae); borders of rami always with spines (on at least one ramus), rarely with setae; outer ramus with 1 or 2 articles; the frequent disappearance of the second article results from its fusion with the first article, not from atrophy.

Telson: cleft and usually deeply cleft; one or several spines (sometimes associated with very short setae or setules) in the notch formed by the 2 apical teeth; telson without dorsal spines, but a group of 2 tiny equal pappose setules is sometimes observed on the surface of each lobe.

DISTRIBUTION: Cosmopolitan, polar to tropical, 0 to 6156 m depth.

REMARKS:

PUTATIVE SYNAPOMORPHIES OF THE LILJEBORGIIDAE: The Liljeborgiidae consist of two markedly distinct subfamilies (see further down). While the two subfamilies also share many characters, most of those are either presumably plesiomorphic or widely distributed amongst amphipods, albeit not in the same combination. However the occurrence of long lateral spinules on the margino-medial setae of the palm of the gnathopods, the absence of unguis on the dactylus of the gnathopods, and the absence of setae (except anteroproximal slender seta) on the dactylus of gnathopod 1 are candidate character states for synapomorphies uniting all the Liljeborgiidae. The flat left lacinia mobilis with a posterior tooth often overlapping the rest of the lacinia is perhaps also a synapomorphy of the Liljeborgiidae, but it is impossible to be certain, as the laciniae mobiles are often inadequately illustrated (or illustrated for one side only) in existing literature.

PREVIOUS INVESTIGATIONS ON THE SYSTEMATIC POSITION OF THE LILJEBORGIIDAE: The Liljeborgiidae are uncalceolated gammaromorphic amphipods, just like the Melphidippoidea STEBBING, 1899 and the Hadzioidea S. KARAMAN, 1943 and are often referred to 'primitive' in literature. Their affinities have long been debated but are not yet clear. After a review of earlier classificatory proposals, the morphology of the Liljeborgiidae is compared with that of some similar amphipods and possible relatives.

The oldest known species currently assigned to the family Liljeborgiidae is *Gammarus ? pallidus*; BATE, 1857 (see BATE, 1857: 145). The genus *Liljeborgia* was erected by BATE (1862: 118), with *Liljeborgia pallida* (BATE, 1857) as type species. BATE (1862) put *Liljeborgia* in his subfamily of the 'Phoxides BATE, 1857' and obviously considered it as closely allied to *Urothoe* as he compared the two genera. BATE & WESTWOOD (1862: 206) described the species *Liljeborgia shetlandica* BATE & WESTWOOD, 1862, which turned out to be a junior synonym of *Cheirocratus sundevallii* (RATHKE, 1843). Afterwards the genus *Cheirocratus* was assigned to Gammaridae LEACH, 1814 and Melitidae BOUSFIELD, 1973, before the 'creation' of its own family Cheirocratidae by BOUSFIELD & SHIH (1994)[1]. Hence BATE & WESTWOOD (1862) should be credited as the first authors to connect *Liljeborgia* with *Cheirocratus*.

[1] The term Cheirocratidae has been introduced by BOUSFIELD & SHIH (1994), albeit without respecting the provisions of ICZN (1994). It is described as 'new' for validation at the end of the present paper.

BOECK (1871: 154) had another opinion concerning the affinities of *Liljeborgia* (which he erroneously spelled *Lilljeborgia* with two 'L'), which he transferred to the subfamily Leucothoinæ DANA, 1852. He put '*Cheirocratus Sundevalli*' (p. 213) in the subfamily Gamarinæ [sic].

STEBBING (1888) restricted the Leucothoidae (elevated to the rank of family) to the genus *Leucothoe* (p. 771) and *Seba* (p. 782), and created the family Eusiridae STEBBING, 1888 (p. 953), to which he transferred *Liljeborgia*. (p. 980).

The idea to create a family for the genera *Liljeborgia* and *Idunella* was proposed by G.O. SARS (1894: 530), who nevertheless refrained to take any formal action, retained them in the Gammaridae and treated them immediately after the genus *Cheirocratus* in his monograph. The comments by G.O. SARS are interesting and some of them are pertinent to the present discussion. "The systematic position of this genus [*Liljeborgia*], established by Sp. BATE, appears somewhat doubtful. (...) Mr. STEBBING, having restricted the family *Leucothoidae* to the genus *Leucothoë*, retained the present genus within the remnant of BOECK's family Leucothoidae, for which he proposed the name of *Eusiridae*. The very fully developed accessory appendage of the superior antennae, as also the more or less conspicuous sexual difference in the structure of the gnathopoda, would, however, seem to remove this genus rather widely both from the genus *Eusirus* and *Rhachotropis*, and to bring it nearer to the family *Gammaridae*, its species having, indeed, an unmistakable resemblance, at least in external appearance, to those of the genus *Cheirocratus*. In the structure of the oral parts it differs, however, considerably both from this genus and the other Gammaridae, and in this respect it exhibits in fact a close resemblance to the genus *Leucothoë*. Perhaps therefore, the genus should more properly be regarded as the type of a separate family, and such a view is in fact supported by the existence of a very nearly-allied genus, *Idunella*, to be described below."

The formal, rather laconic erection of the family Liljeborgiidae was made by STEBBING (1899: 211) and runs as follows: "Here it may be mentioned that I find expedient definitely to establish the family (...) Liljeborgiidae, in accordance with a suggestion made by Professor SARS ('Crustacea of Norway', vol. i. p. 430) to receive the genera *Liljeborgia*, Bate, and *Idunella*, Sars".

DELLA VALLE (1893: 657) puts *Liljeborgia* in synonymy with the genus *Nicippe* (now in the Pardaliscidae BOECK, 1871). The possible affinity of these two genera has not been considered by subsequent authors. However NOTEBOOM (1986) pointed out that the Pardaliscidae could have affinities with *Sensonator*, which exhibits some vague similarities with the Liljeborgiidae.

J.L. BARNARD (1969b: 291) made the following comments (which are not always correct) about the affinities of the Liljeborgiidae. "In the Gammaridae only the genus *Parelasmopus* has an elongate mandibular palp article 1 but its mandibular molar has a well-developed grinding surface, unlike that of Liljeborgiidae. Apart from the mandible the Liljeborgiidae are like the Gammaridae. The Astyridae differs from the Liljeborgiidae by the overall appearance and the presence of inner lobes or a broad medial space on the lower lip. Astyrids have feeble gnathopods, whereas those of liljeborgiids are powerfully developed. The rami of uropod 3 of Astyridae are much more elongate than those of Liljeborgiidae. Some genera of Pleustidae have poorly developed mandibular molars as in Liljeborgiidae and the lower lips are similar. Pleustids, however, have a vestigial or no accessory flagella and usually have uncleft telsons, but one species of *Austropleustes* confounds the definition. The Eusiridae always have the accessory flagellum 2-articulated or less and this conflicts only with the genus *Listriella* in the Liljeborgiidae. But in contrast to the Eusiridae, *Listriella* usually has a 2-articulated outer ramus of uropod 3 with an elongated article 1 of the mandibular palp. *Eusirella* and *Eusiropsis* are the only eusirids having an obsolescent mandibular molar and they are clearly eusirids for their possession of calceoli. Eusirids have the outer ramus of uropods 1 and 2 shortened; in liljeborgiids this shortening is slightly evident only on uropod 2. One genus of Amphilochidae, *Pseudamphilochus* presumably lacks an accessory flagellum, has a large rostrum, and nonbifid apices of the telson." J.L. BARNARD & KARAMAN (1991: 413) gave a similar account, which adds little to the debate.

In a new system of classification, BOUSFIELD (1982, 1983) and BOUSFIELD & SHIH (1994) placed the Liljeborgiidae in the superfamily Liljeborgioidea, along with the Paracrangonyctidae BOUSFIELD, 1982, Sebidae WALKER, 1907, Colomastigidae STEBBING, 1899 and Salentinellidae BOUSFIELD, 1977. While a phyletic link between the Liljeborgiidae and these other families (which are morphologically highly derived) cannot be ruled out, BOUSFIELD did not argue convincingly. So, JAUME *et al.* (2004: 276) discuss the case of the Sebidae and, while they recognize a superficial similarity between *Idunella* (Liljeborgiidae) and *Seborgia* (Sebidae), they provide sound arguments for a close relationship between the Sebidae and the Leucothoidae, rather than between the Sebidae and the Liljeborgiidae.

BOUSFIELD (1982, 1983) and BOUSFIELD & SHIH (1994) also recognized the superfamily Melphidippoidea, where they put the Cheirocratidae, the Hornelliidae[2], the Megaluropidae THOMAS & J.L. BARNARD, 1986 and the Melphidippidae STEBBING, 1899. With some hesitation, they also included the Phreatogammaridae BOUSFIELD, 1982, which is accepted neither by WILLIAMS & BARNARD (1988) nor by BRÉHIER *et al.* (2010). When introducing the name Hornelliidae, BOUSFIELD & SHIH (1994: 128), considered it as a synonym of the Cheirocratidae, but this family should be understood as consisting of the genera *Hornellia* and *Metaceradocus* only. On the other hand, BOUSFIELD & SHIH (1994) placed the Melitidae BOUSFIELD, 1973 (a family previously including the Cheirocratidae) in the superfamily Hadzioidea. These actions actually refined proposals previously made by J.L. BARNARD & C.M. BARNARD (1983: 593), who discussed a loose, 'polyphyletic cheirocratid group', which also includes the 'maerellid group' and several genera with very little similarities with *Cheirocratus*. The grouping of the Cheirocratidae, Hornelliidae, Megaluropidae and Melphidippidae seems credible (albeit not fully resolved) since representatives of these families exhibit overlapping characters. It is herein accepted, but only as a working hypothesis. BOUSFIELD & SHIH (1994) formally considered the Melphidippoidea as belonging to their supposedly plesiomorphic 'natant grade' (amphipods mating in the water column), although they never have calceoli, a putatively plesiomorphic sensorial organ frequent in the 'natants'. The plesiomorphic nature of the occurrence of calceoli is supported by the works of ENGLISCH (2001) and ENGLISCH *et al.* (2003), who investigated the phylogeny of amphipods, using small subunit rDNA gene sequences. Indeed, these authors indicate that there would be a very high support for a basal phylogenetic position of the Oedicerotidae LILLJEBORG, 1865 (which include some calceolated forms) amongst amphipods. While the concept of 'natant' versus 'reptant' amphipods is somewhat debatable and is certainly an over-simplification, it seems reasonably applicable in the present restricted context. The inclusion of the Melphidippoidea amongst the 'natant' grade makes sense despite their lack of calceoli because some representatives of the Cheirocratidae, Megaluropidae, Melphidippidae (e.g. POULET *et al.*, 1996) and of the Hornelliidae (e.g. ALLDREDGE & KING, 1980, 1985) have been found in planktonic samples (however, in the cheirocratid *Casco bigelowi* (BLAKE, 1929) both sexes cohabit in the same burrow, where mating presumably occurs (THIEL, 1998)). To some extent, the Melphidippoidea could be transitional between calceolated 'natant' amphipods and fully benthic uncalceolated gammaromorphic amphipods like the Melitidae (Hadzioidea).

As far as is known, Liljeborgiidae have never been recorded in plankton samples, but they are able to 'move by rapid swimming' (ENEQUIST, 1949), and are often found in the upper net (epinet) of epibenthic sledges. So, at least some species could be swimming just above the sea bottom and would not be complete creepers like most Melitidae sensu lato (Melitidae and Maeridae KRAPP-SCHICKEL, 2008) and Corophioidea LEACH, 1814 (= Corophiidea sensu MYERS & LOWRY, 2003). In other words, they would be more benthic than the Melphidippoidea but less than the Melitidae/Maeridae and the Corophioidea.

In her thesis on the molecular phylogeny of amphipods, ENGLISCH (2001) obtained a very high support for a sister relationship between *Liljeborgia* and *Megaluropus* (Melphidippoidea). This would suggest that the aforementioned ecological gradation could have a phylogenetic background. These results would also suggest that the old intuition of BATE & WESTWOOD (1862) to relate *Liljeborgia* with *Cheirocratus* (Melphidippoidea, just like *Megaluropus*) should seriously be reconsidered. On the other hand, the data presented in the thesis of ENGLISCH (2001) are rather inconclusive concerning the systematic position of other uncalceolated gammaromorphic amphipods (*Maera* and *Paraceradocus*), which are scattered across different unstable positions on her various trees (which include many more species than those given in the more official publication of ENGLISCH *et al.*, 2003). Interestingly, they also suggest that major calceolated gammaromorphic superfamilies (Crangonyctoidea, Gammaroidea and Niphargoidea) are related to each others but not to uncalceolated gammaromorphic amphipods.

COMPARISON OF THE LILJEBORGIIDAE WITH OTHER AMPHIPOD TAXA: The traditional separation of the Liljeborgiidae from other uncalceolated gammaromorphic amphipods concerns the usual condition of the molar process of their mandible, which is non-triturative, reduced and is adorned with strong setae. For example, J.L. BARNARD (1959: 13) states "Liljeborgiid amphipods are quite plain and "normal" in the sense that they represent the typical textbook definition and figures of generalized amphipods. In this respect they resemble the family Gammaridae, but differ from that family

[2] The term Hornelliidae has been introduced by Bousfield & Shih (1994), albeit without respecting the provisions of ICZN (1994). It is described as 'new' for validation at the end of the present paper.

principally by the mandibular structure." However, this argument is not completely valid because there is one known liljeborgiid species, *Sextonia longirostris* CHEVREUX, 1920, which has a fully triturative molar process (CHEVREUX, 1920b; CHEVREUX & FAGE, 1925; present paper). The incorporation of *Sextonia* within the Liljeborgiidae is justified, for in most other respects, it is very similar to *Idunella*.

Ideally, affinities between Liljeborgiidae and other amphipods should be established by the discovery of unmistakable morphological synapomorphies with no trend for homoplasy (i.e. something equivalent to the fleshy telson of the Corophioidea). While in many respects, the morphology of ancestral amphipods remains debatable, it is probable that the Oedicerotoidea (which obviously themselves are highly derived) are the sister clade of all other amphipods (ENGLISCH, 2001; ENGLISCH *et al.*, 2003). So, it is a priori possible that this superfamily has retained unusual plesiomorphic traits, and it would be judicious to compare it with the Liljeborgiidae and its potential relatives. Another point to bear in mind when trying to place the Liljeborgiidae is that, amongst amphipods, evolution seems to frequently progress towards simplification of structures (loss or fusion of article two of outer ramus of the third uropod, loss or reduction of accessory flagellum, calceoli, setae, spines, teeth, etc) and it can be assumed that some losses are irreversible or at least difficult to reverse.

In the different trees of ENGLISCH (2001), *Liljeborgia* (Liljeborgioidea) and *Megaluropus* (Melphidippoidea) always form a highly supported clade. Therefore, a close relationship between the Liljeborgiidae and the Melphidippoidea (Cheirocratidae, Hornelliidae, Megaluropidae and Melphidippidae) should be considered as a good hypothesis for further examination. Similarities and dissimilarities observed between the Liljeborgiidae, the Melphidippoidea, the supposedly basal Oedicerotidae, and sometimes other taxa are enumerated and discussed hereafter, with the phylogenetic relationships suggested by ENGLISCH's (2001) trees as background.

HEAD: The antennal concavity of head is shallow in the Liljeborgiidae, as it is in the Hornelliidae, Megaluropidae and Melphidippidae, but it forms a narrow slit in some Cheirocratidae like *Cheirocratus* spp., as it is also the case in *Sensonator* and many Melitidae/Maeridae. The anterior lobe of head is always blunt (round or bluntly angular) in the Liljeborgiidae. This is also the case in many Melphidippoidea, but in species like *Megaluropus agilis* HOEK, 1889 and *Melphidippella macra* (NORMAN, 1889) it is distally pointed (with the eye in a much lower position), as it is the case in some Dexaminidae LEACH, 1814 and Photidae BOECK, 1871. The posterior lobe of the head is always blunt in the Liljeborgiidae, as in the Megaluropidae, but it is pointed in the Hornelliidae and often so in the Cheirocratidae.

CALCEOLI: they are absent in the Liljeborgiidae and Melphidippoidea as in the 'maerellids', the Hadzioidea and in the Corophioidea. On the other hand, they are present on the antennal flagella and on the peduncle of A2 in *Sensonator*.

A1: In Liljeborgiidae it is usually distinctly shorter than A2, sometimes equal to A2, very rarely longer than A2 (male *Idunella chilkensis* CHILTON, 1921); A1 is also distinctly shorter than A2 in the Cheirocratidae, Megaluropidae, *Sensonator* (and in many Oedicerotidae). A1 and A2 are subequal in Hornelliidae and Melphidippidae. On the other hand, A1 is normally longer than A2 in the Melitidae/Maeridae, the Phreatogammaridae, Crangonyctoidea, Gammaridoidea and Niphargoidea. Article three of the A1 peduncle is normally short and stout in Liljeborgiidae as in most Melphidippoidea, the Phreatogammaridae, *Sensonator*, *Bathyceradocus* (see J.L. BARNARD, 1961: 109-110; LEDOYER, 1983: 424-427) and many 'natant' families. The length of article three is variable in the Melitidae/Maeridae but it is normally more slender. The accessory flagellum is always present and usually well developed in the Liljeborgiidae as in the Melphidippoidea and many other gammaromorphic amphipods, but it is absent or truly vestigial in the Oedicerotoidea (Oedicerotidae, Exoedicerotidae J.L. BARNARD & DRUMMOND, 1982 and Paracalliopiidae J.L. BARNARD & KARAMAN, 1982). Neither the Liljeborgiidae nor the Melphidippoidea have a callynophore, a putatively plesiomorphic structure (according to BOUSFIELD & SHIH, 1994) frequent in natant groups like the Oedicerotidae.

A2: In the Liljeborgiidae there is no setal brush. The antennal brush of setae is a putatively plesiomorphic character (according to BOUSFIELD & SHIH, 1994) frequent in 'natant' amphipods like the Oedicerotoidea. In the Melphidippoidea, it has been observed in the Megaluropidae (drawings by LINCOLN, 1979: 387; THOMAS & BARNARD, 1986a: 455).

MD (MOLAR PROCESS): With the exception of *Sextonia*, which has a large triturative (usually considered a plesiomorphic condition) mandibular molar process with a single posterior gnathobasic seta, the Liljeborgiidae have a reduced, non-triturative molar process, adorned with long and smooth strong setae (this is usually considered an apomorphic condition). In some representatives of other families like the Dexaminidae, Hyperiopsidae BOVALLIUS, 1886, and Aoridae STEBBING, 1899 the molar process is fully triturative but its

posterior border can be adorned with a posterior row of long setae (e.g. J.L. BARNARD, 1972a: various figures; ANDRES, 1977: 59; COLEMAN & LÖRZ, 2010: 35). The same co-occurrence of a triturative molar process and molar setae was possibly also present in the ancestors of the Liljeborgiidae. In some lineages, the triturative surface would have disappeared, while in *Sextonia*, it was the row of setae, which would have vanished. This is of course speculative, but there is considerable evidence that such scenarios indeed happened in the Oedicerotidae, where both extreme and intermediate conditions have persisted into the modern fauna. In this family, most genera have a fully triturative mandible without posterior setae, but some have a reduced non-triturative mandible with strong setae: e.g. *Perioculodes* and *Synchelidium* (WATLING, 1993) and some have an intermediate condition with a triturative mandible and several posterior strong setae: e.g. *Monoculodes latissimanus* STEPHENSEN, 1931 (see drawings of LEDOYER, 1993) and *Paramonoculopsis acuta* ALONSO DE PINA, 1997 (see ALONSO DE PINA, 1997). In the Melphidippoidea, the molar is fully triturative without a posterior row of long setae, but published illustrations of some Cheirocratidae, such as *Cheirocratella thori* STEPHENSEN, 1940 and *Casco bigelowi* (see KRAPP-SCHICKEL & VADER, 2002 and SHOEMAKER, 1930) and of Megaluropidae such as *Megaluropus agilis* HOEK, 1889 (see LINCOLN, 1979), suggest that the posterior border of the molar process bears a row of strong denticles, which are perhaps homologous to the long posterior setae found in other families. However this morphological trait is far from rare and is also observed in some Melitidae/Maeridae. In other words, the strongly modified molar of most Liljeborgiidae is by no way unique and mysterious, and it neither supports nor refutes the possibility of a link between the Liljeborgiidae and the Melphidippoidea.

MD (LACINIA MOBILIS): In the Liljeborgiidae, the number of teeth on the left lacinia mobilis is 5 (rarely 4 or 6). This number is usually 3 or 4 in the Melphidippoidea but 5 in *Cheirocarpochela sinica* REN & ANDRES in REN, 2006 and *Hornellia incerta* WALKER, 1904 (if the drawings of REN (2006) are correct). This number is normally 4 in the Phreatogammaridae and the Melitidae/Maeridae, and 1 in *Sensonator*. BOUSFIELD (1983) considered that a left pentacuspate lacinia mobilis would be the plesiomorphic condition in amphipods (his opinion is not universally accepted, see WILLIAMS & BARNARD, 1988 for instance) and he also indicated this is the condition observed in the Oedicerotidae. It must be noticed that a pentacuspate left lacinia mobilis is also observed in the Sebidae (JAUME *et al.*, 2009). The right lacinia mobilis of the Liljeborgiidae is peculiar, being flattened, and often with an anterior major and minor posterior blades, but there is a paucity of data on the morphology of this lacinia in other families, preventing a systematic comparison.

MD (PALP): The first article of the mandibular palp is usually (but not always) long in the Liljeborgiidae and the Cheirocratidae (but not in the Hornelliidae, Megaluropidae and Melphidippidae). Interestingly, a long article 1 is also observed in *Maerella* (KARAMAN, 1981) and *Jerbarnia* (CROKER, 1971), which J.L. BARNARD & C.M. BARNARD (1983) placed in the 'maerellid' subgroup of their 'cheirocratids'. One or several setae on article 1 of the mandibular palp are observed in a few Liljeborgiidae (setation especially important in *Sextonia*), some Melphidippoidea and Phreatogammaridae (HURLEY, 1954a) and also in the 'maerellids' (CROKER, 1971; KARAMAN, 1980). The articulation between article 1 and 2 is geniculate in the Idunellinae (see present paper), several Cheirocratidae (actually subgeniculate) and *Hornellia incerta* WALKER, 1904 (see drawings in REN, 2006), while this articulation is rectilinear in the Liljeborgiinae and the rest of the Melphidippoidea. In a few Liljeborgiidae, article two is very setose, the setae being often divided in a large posterolateral row and a reduced posteromedial proximal row (e.g. *Idunella aeqvicornis* (G.O. SARS, 1877) and *I. pirata* KRAPP-SCHICKEL, 1975). It must be stated that in some Melphidippidae, like *Melphidippa willemiana* D'UDEKEM D'ACOZ, 2006, it is slightly curving convexly posteriorly and bears 2 well-developed longitudinal rows of strong setae (see D'UDEKEM D'ACOZ, 2006: 492), as is frequently the case in Oedicerotidae (e.g. drawings by J.L. BARNARD, 1961; LEDOYER, 1993). However such a disposition, albeit infrequent, is not unique, and an article two curving convexly posteriorly has been observed for example in the Pardaliscidae (e.g. HENDRYCKS & CONLAN, 2003b: 2347). Article three of the mandibular palp exhibits different character states in the Liljeborgiidae. In the putatively plesiomorphic *Sextonia*, it is falciform, with combed posterior setae (D3-setae) and long isolated anteromedial setae (B3-setae). This disposition approaches that one observed in the Hornelliidae, the Megaluropidae and the cheirocratid *Casco*. However this condition is far from unique and is also observed in several other groups of amphipods, including some Oedicerotidae.

MX1: In *Liljeborgia* (but not in other liljeborgiid genera), the anterior margin of the palp has one or more setae. This putatively plesiomorphic character (usual in the Oedicerotidae and not uncommon in other 'natant' families like the Eusiridae or the Gammarellidae) is rare in uncalceolated gammaromorphic amphipods (e.g.

not observed in the Melitidae/Maeridae sensu stricto). *Liljeborgia* shares it with the Cheirocratidae (not with other Melphidippoidea) and the '*Paraceradocus/ Ceradocoides* group' (ANDRES, 1984; NICHOLLS, 1938). The setation of the inner plate of Liljeborgiidae is variable but usually reduced, as in many Oedicerotoidea but unlike the Melphidippoidea and most other uncalceolated gammaromorphic amphipods, where it is well furnished with setae.

MX2: The Liljeborgiidae are rather unusual for uncalceolated gammaromorphic amphipods in that the facial row of the inner plate is usually absent, reduced and if present irregular. The facial row of setae is well developed and regular in the Melphidippoidea and the Phreatogammaridae but often absent in the Oedicerotoidea. This character is variable in the Hadzioidea.

MXP: The outer plate of the Melphidippoidea is rather basal, typically with true marginal aciculae (mostly spines) all around the inner, distal and distolateral border, and with inner margino-facial setae. In the Liljeborgiidae, this ornamentation is variously reduced: distolateral marginal aciculae missing in the genus *Liljeborgia*, and either the inner marginal or the inner margino-facial ornamentation is missing in the Idunellinae. The inner plate of the Liljeborgiidae usually has no inner margino-facial spine. In the Melphidippoidea, at least some Melphidippidae (e.g. D'UDEKEM D'ACOZ, 2006: 492 fig. 1i), Cheirocratidae (*Cheirocratus sundevallii* (RATHKE, 1843), personal observation: narrowly styliform spine on 0.6 of inner plate) and Hornelliidae (THOMAS & J.L. BARNARD, 1986b: 479 fig. 1SI, 484 fig. 4S) have such a spine.

GILLS AND OOSTEGITES: The Liljeborgiidae and the Melphidippoidea have slender oostegites on Gn2-P5, as in the Oedicerotidae, *Sensonator*, and the Melitidae/ Maeridae. STEELE (1990, 1991) considers slender oostegites as an apomorphic character state, but his main argument (occurrence of broad oostegites in non-amphipod peracarids) is far from convincing. The shape of the oostegites is also a priori easily reversible. The Liljeborgiidae have a simple coxal gill on the Gn2-P6, as it is the case in the Cheirocratidae, Hornelliidae, the Melphidippidae and *Sensonator*. The Megaluropidae and sometimes the Phreatogammaridae have a small gill on P7 (BOUSFIELD, 1982). The presence of a gill on P7 is usually considered as a plesiomorphic condition and is present in some Oedicerotoidea (STEELE & STEELE, 1991).

GN1-GN2 DOMINANCE: The dominance of the first gnathopod in some Liljeborgiidae (mostly Idunellinae) is rather unusual for amphipods (but this can be a family level character, as in the Aoridae), and especially unusual for gammaromorphic amphipods. In the Melphidippoidea the first gnathopod is normally smaller or subequal to the second, but the first gnathopod is stouter than the second in some species such as *Melphidippa goesi* STEBBING, 1899 (see G.O. SARS, 1890-1895, plate 169, as *M. spinosa* GOËS) and *M. willemiana* (see D'UDEKEM D'ACOZ, 2006: 493). Furthermore, a remarkable condition is observed in *Prosocratus butcheri* J.L. BARNARD & DRUMMOND, 1982. In this cheirocratid species the two gnathopods are subpediform in the female (the second being the largest). On the other hand, in the male the first gnathopod exhibits a grasping subchelate morphology, being enlarged and stronger than the second gnathopod (J.L. BARNARD & DRUMMOND, 1982). This suggests a predisposition in the Melphidippoidea for an inversion of the dominance of the gnathopods.

GN1-GN2 MORPHOLOGY: In the Liljeborgiinae, the carpus is produced into a long posterior lobe. This condition is not observed in the Idunellinae, although a tiny lobe independent from the carpus is sometimes present (Gn1 of *Sextonia longirostris* and of male *Idunella aeqvicornis*). With the exception of male *Cheirocarpochela sinica* (see REN, 2006), a pointed carpal lobe is observed neither in the Melphidippoidea nor in other gammaromorphic amphipods. A broad and angular carpal lobe is however commonly observed in the Megaluropidae. On the other hand, a long produced carpal lobe is observed in some 'natant' groups like many Oedicerotidae and some Eusiridae (e.g. *Rhachotropis*), and also in the Leucothoidae, many Amphilochidae and a few corophioids like male *Erichtonius*. It is not clear whether the long carpal lobe of *Liljeborgia* is a plesiomorphic or an apomorphic condition, due to the patchy distribution of this character state amongst amphipods. The gnathopods are always subcheliform in the Liljeborgiidae, usually subcheliform in the Melphidippidae and the Hornelliidae (where they are rather weak, with a palm poorly defined), but they are often subpediform in the Cheirocratidae and the Megaluropidae, especially in females. The ornamentation of the dactylus is usually rather rich in the Melphidippoidea and in some gammaromorphic amphipods of uncertain affinities like *Bathyceradocus* (see DAHL, 1959: 239; LEDOYER, 1983: 426 as *Benthedius*) and *Paraceradocus* (ANDRES, 1984), where they can have teeth, spines and/or setae in interdental notches and a terminal unguis. The dactylus of gnathopods of the Melitidae/Maeridae sensu stricto is most commonly toothless, but setae and an unguis can be present. Richly ornamented dactyli of gnathopods are not uncommon in 'natant' families (e.g. Dexaminidae) and are also

present in some corophioids like *Gammaropsis*. The dactyli of the Oedicerotoidea are usually illustrated as smooth, albeit minute denticles and a small unguis can be present (JAUME *et al.*, 1998: 348). Dactylar teeth are usually present in the Liljeborgiinae and sometimes in the Idunellinae. The Liljeborgiidae have no terminal unguis on the gnathopods. Setae are not present on the dactylus of gnathopod 1 (except for anteroproximal slender seta). They are however present on gnathopod 2 in the Liljeborgiinae (but not in the Idunellinae), where they arise from the medial surface and are not inserted in the interdental notches. Interestingly, the presence/absence of long dactylar setae on the gnathopods is also an important taxonomic character in the Maeridae (KRAPP-SCHICKEL & JARRETT, 2000). In the Liljeborgiidae the palm is usually smooth, or presents an ornamentation consisting of low lobes or low crenulations. However, in some Idunellinae like *I. picta* (see present paper) or *I. mollis* (see DAUVIN & GENTIL, 1983 as *I. dentipalma*) the palm presents minute but sharp proximal serrations. This kind of serrations, albeit very small, is also present in some Cheirocratidae, like *Cheirocratella thori* STEPHENSEN, 1940 (see KRAPP-SCHICKEL & VADER, 2002: 12). The posteromedial surface of gnathopod 2 is furry in the male of some Liljeborgiinae like *Liljeborgia georgiana* SCHELLENBERG, 1931 (see D'UDEKEM D'ACOZ, 2008: 174) and this condition is also observed in the male of some Cheirocratidae like *Cheirocratus* spp. (see G.O. SARS, 1894, pl. 185).

COXAE 1-4: these coxae are quite long, the fourth one normally bearing an upper posterior excavation in the Liljeborgiidae and the Megaluropidae. However the coxae of the Megaluropidae are marginally strongly setose (reminiscent of the Oedicerotidae), which is not at all the case in the Liljeborgiidae. In this family, marginal setae (not to be confused with setae sometimes arising from the medial surface of the coxa) are few in number and always arise from notches. The coxae are somewhat shorter (and not strongly setose) and coxa 4 has no strong posterodorsal excavation in the Cheirocratidae, Hornelliidae and Melphidippidae. The shape of the coxae is variable in the Melitidae/Maeridae, where they are usually not strongly setose.

DACTYLUS OF P3-P4: in the Liljeborgiidae, the posterior border is smooth, without unguis and without aciculae, except for *Sextonia*, which has a reduced unguis and 2 very small subdistal setules. The occurrence of a well-developed unguis is the rule in the Melphidippoidea and the Melitidae/Maeridae. Subdistal setules are also observed in the Cheirocratidae, Hornelliidae, the Megaluropidae, as in many other gammaromorphic amphipods (e.g. Melitidae/Maeridae). In the Melphidippidae there are often several isolated posterior (and sometimes anterior) setae. In *Sextonia*, the dactylus of pereiopods 3-4 exhibits a strange tiny distal anterior spoon-like process, which is distinct from the terminal unguis. The same structure (here named 'ungial hood') has been observed in *Bahadzia jaraguensis* JAUME & WAGNER, 1998 (see JAUME & WAGNER, 1998), *Seba* spp. (see JAUME *et al.*, 2009 as 'distal dactylar hyaline sheath'), several genera of Oedicerotidae: *Bathymedon* (JAUME *et al.*, 1998), *Monoculodes* (BOUSFIELD & CHEVRIER, 1996; HENDRYCKS & CONLAN, 2003a; HUGHES & LOWRY, 2009), *Oedicerina* (see HENDRYCKS & CONLAN, 2003b: 2360), *Oediceroides* (this paper, fig. 20; J.L. BARNARD, 1961: 91 as 'apical bubble'), and *Synchelidium* (JO, 1990).

Relative size of P5-P6-P7: In Liljeborgiidae, P5 < P6 < P7; in Cheirocratidae and Hornelliidae, P5 = P6 < P7; in Megaluropidae, P5 = P6 < P7 or P5 very slightly < P6 < P7; in Melphidippidae P5 = P6 = P7 or P5 = P6 very slightly < P7.

P7: the propodus presents very long slender posteromedial setae in *Liljeborgia* but not in the Idunellinae and Melphidippoidea. Such setae are not unique, and are present in a very similar disposition in *Sensonator* (NOTEBOOM, 1986), where these setae are plumose as in some Oedicerotidae (JO, 1990: 171), but unlike those in *Liljeborgia*. The length of the dactylus is remarkably variable in the Liljeborgiidae, from short to extremely long. A long dactylus is also observed in some Megaluropidae like *Megaluropus agilis* HOEK, 1889 but neither in the Cheirocratidae, the Hornelliidae and the Melphidippidae, nor in the Melitidae/Maeridae s.l. and the Corophioidea. A long dactylus on P7 is not a frequent character in amphipods, but this is the rule for the Oedicerotoidea. However the long dactylus of P7 observed in some Liljeborgiidae is hairless (proximal posterior setule excepted), while it is strongly setose in the *Megaluropus agilis* (see LINCOLN, 1979: 387) as in most Oedicerotoidea, a few Eusiridae of the genus *Rhachotropis* (BOUSFIELD & HENDRYCKS, 1995). Some subterranean fresh-water Ingolfiellidea, Hadzioidea, Niphargidoidea species (e.g. KARAMAN, 1993: 156, 212, 222, 228, 241, 314) and Crangonyctoidea (e.g. WILLIAMS & J.L. BARNARD, 1988: 89, 98, 137, 174, 177; HOLSINGER, 1992: 118; KRISTJÁNSSON & SVAVARSSON, 2004: 1888) have anterior spines or stout setae on the dactylus of pereiopod 7 but their dactyli are much shorter, stouter and markedly different from that of the aforementioned families; it is not at all sure that such structures are homologous. The similar dactylar setation shared by the Oedicerotidae and some Megaluropidae merits attention and it would be interesting to establish whether it is the outcome of convergent evolution or if

it is symplesiomorphic in nature.

PLEONITES 1-3: the armature of the posterodorsal border is rather variable in the Liljeborgiidae, the Melphidippoidea and the Melitidae/Maeridae. Toothed posterodorsal borders are rare in Oedicerotidae, e.g. *Acanthostepheia* (GURJANOVA, 1951: 549) and *Oedicerina* (HENDRYCKS & CONLAN, 2003b: 2360). The ventrofacial surface of the epimeral plates of the Liljeborgiidae is often completely smooth, but this condition is variable and in the putatively plesiomorphic *Sextonia*, all are furnished with isolated spines as in most Melphidippoidea and many other gammaromorphic amphipods. It can be noticed that the posteroventral angle of epimeral plates is often scarcely acute in the Megaluropidae and are therefore somewhat reminiscent of the Oedicerotidae where this angle is commonly totally rounded. This angle is pointed in other Melphidippoidea and in the Liljeborgiidae.

UROSOMITES: In the Liljeborgiidae, urosomites 1-2 usually have 0-1 posterodorsal teeth but *Sextonia* has 3 such teeth. The occurrence of postero-transversally polydentate urosomites is the usual condition in the Melphidippoidea as it is the case in many other gammaromorphic amphipods. Urosomites 1-2 are smooth in the Oedicerotidae. On the other hand the dorsal spination of the urosomites is much reduced or absent in the Liljeborgiidae. The occurrence of posterodorsal spines on urosomites 1-2 is frequent in the Melphidippoidea and the Melitidae/Maeridae. Urosomite 1 can have one, several or no ventrofacial spines in the Liljeborgiidae. These three conditions are also observed in the Melphidippoidea.

U1-2: In the Liljeborgiidae, several ventrofacial spines are present on uropod 1 in *Sextonia* but such spines are absent in all other known genera. There are no ventrofacial spines in the Cheirocratidae but there are several ones on the peduncle of U1 in the Megaluropidae, Melphidippidae and some Hornelliidae. There are also several ventrofacial spines in the 'maerellids' (e.g. KARAMAN, 1981), in *Bathyceradocus* (see J.L. BARNARD, 1961; LEDOYER, 1983 as *Benthedius*), *Paraceradocus* (ANDRES, 1984), a few Corophioidea like *Camacho* (COLEMAN & LÖRZ, 2010) and also in many 'natant' families like the supposedly basal Oedicerotidae. Normally only one (very strong) spine is present in the Melitidae/Maeridae sensu stricto. Interestingly, ventrofacial spines are also present on the peduncle of uropod 2 in *Melphidippa willemiana* (D'UDEKEM D'ACOZ, 2006: 495), as is frequently the case in Oedicerotidae (e.g. LEDOYER, 1993: 590, 597, 608; BOUSFIELD & CHEVRIER, 1996: 112; JAUME *et al.*, 1998: 352; JANSEN, 2002: 101; HENDRYCKS & CONLAN, 2003a: 57), sometimes (one small spine) in *Paraceradocus* (ANDRES, 1984: 105, fig. 9F) and rarely in the Eusiridae (BOUSFIELD & HENDRYCKS, 1995: 46). The first uropod of the Liljeborgiidae has no interramal tooth, an unusual structure observed in some Hornelliidae and Megaluropidae (THOMAS & J.L. BARNARD, 1986a, 1986b) and several genera of Corophioidea. The rami of uropods 1-2 are pointed with a trace of terminal tooth fused with the ramus in the Liljeborgiinae, distally broad with a cluster of spines (up to 4) in the Idunellinae subfam. nov. The latter plesiomorphic condition is observed in the Melphidippoidea and many other gammaromorphic amphipods, but the uropods are pointed and without distal spines in the Oedicerotoidea.

U3: The outer ramus is entire in the Liljeborgiinae, entire or 2-articulated in the Idunellinae (article two has a trend for fusing with article one, not to reduce in size until complete atrophy). In the Cheirocratidae the outer ramus is usually entire, but this is not the case in *Incratella inermis* (LEDOYER, 1968), where a second article (apparently partly fused to the first one) is present (LEDOYER, 1983: 452-453) and in *Incratella unidentatus* (LEDOYER, 1979), where a well-individualized second article is present (LEDOYER, 1983: 454-455). The outer ramus is entire in many Melphidippidae and Megaluropidae, but a small second article is present in *Melphidippa willemiana* (see D'UDEKEM D'ACOZ, 2006: 495), *Melphisana madagascariensis* LEDOYER, 1984 (see COLEMAN, 2009b), *Hornellia whakatane* (J.L. BARNARD, 1972) (see J.L. BARNARD, 1972b: 120-121, as *Metaceradocus whakatane*) and *H. incerta* WALKER, 1904 (see LEDOYER, 1983: 508-509). The outer ramus is always entire in the Oedicerotoidea. In the Liljeborgiinae, the ornamentation of the rami always consists of spines only. In the Idunellinae, this is also the most common condition, although a few species like *Idunella albina* can have long setae (J.L. BARNARD, 1959: 26, as *Listriella albina*). Rami of uropod 3 with spines but no setae are observed in the Cheirocratidae, the Oedicerotidae and in many Melitidae/Maeridae. However, some Hornelliidae like *Metaceradocus atlanticus* THOMAS & J.L. BARNARD, 1986 have plumose setae, isolated and paired with spines (THOMAS & J.L. BARNARD, 1986b: 486). Setae can also be present in the Megaluropidae, e.g. drawings of *Resupinus visendus* THOMAS & BARNARD, 1986 given by THOMAS & J.L. BARNARD (1986a: 452) and sometimes in the Melphidippidae, e.g. drawings of *Melphidippa goesi* STEBBING, 1899 given by LINCOLN (1979: 383).

Telson: In the Liljeborgiidae, it is typically deeply cleft, with each lobe terminated by 2 teeth; there is one or several spines in the interdental notch but no spines elsewhere on the telson. A similar condition is usually

observed in the Cheirocratidae (where the medial tooth occasionally disappears) and the Melphidippidae. In the Hornelliidae, this basic pattern persists, but in addition dorsal and lateral spines can be present (see THOMAS & J.L. BARNARD, 1986b: 481, 286). In the Megaluropidae, the telson is typically completely cleft with the tip of the lobe rounded or truncated; apical and non-apical spines can be present. In the Melitidae/Maeridae it is usually deeply cleft but rather variable in shape and ornamentation. In the Oedicerotidae it is broad, entire, or with a broad shallow distal concavity and with a reduced ornamentation.

In addition to this discussion, it must be pointed out that the Liljeborgiidae exhibit some intriguing similarities with the Perthiidae WILLIAMS & J.L. BARNARD, 1988, which is a minor epigean freshwater crangonyctoid family of Western and Southern Australia (see illustrations given by WILLIAMS & J.L. BARNARD, 1988). In the Perthiidae, antenna 1 is not longer than antenna 2, and has a stout peduncle; the mandibular molar process is reduced, non triturative with a cluster of slender spines and 1 long molar seta; the right lacinia mobilis has two unequal blades and seems very similar to that of the Liljeborgiidae; the inner plate of Mx1 has only 2 setae; the gnathopods are elliptic and quite strong, with a dactylus devoid of unguis; coxa 1-4 are very high and coxa 4 is absolutely identical to that of typical Liljeborgiidae; the telson is deeply cleft. However, the Perthiidae also exhibit profound differences with the Liljeborgiidae, such as the occurence of sternal gills, broad oostegites and a spinose dactylus on P3-P7. Therefore, these similarities are most probably the result of convergence.

To summarize this long list of observations, a significant number of similarities are observed between taxa belonging to the Liljeborgiidae and Melphidippoidea. However, there are also many differences, and no clear synapomorphies between the Liljeborgiidae and them or between the Liljeborgiidae and any other family of amphipod emerge, as it was hoped. This probably reflects the unspecialized liljeborgiid morphology. It seems that several changes happened many times independently within the (supposed) clades considered, or across them. In other words, in the taxa examined, the distribution of apomorphic and plesiomorphic character states presents a mosaic distribution obscuring the general evolutionary pattern. This is not really surprising because amphipods are well known for their predisposition for rampant homoplasy (e.g. J.L. BARNARD & DRUMMOND, 1978: 7, 16; MYERS & LOWRY, 2003: 458). Nevertheless, it should be noticed that the Liljeborgiidae share more putatively plesiomorphic characters with the Melphidippoidea than with the Melitidae/Maeridae group, the latter being in some respects more advanced. Interestingly, both the Liljeborgiidae and the Melphidippoidea share a number of unusual and putatively plesiomorphic characters with the Oedicerotoidea, which would be the sister clade of all other amphipods according to molecular data (ENGLISCH *et al.*, 2003). So, a rather basal position for the Liljeborgiidae and Melphidippoidea is suggested by their large number of putatively plesiomorphic character states, but the present empirical observation of morphological data can neither confirm nor reject the idea that they are related. A well-constructed cladistic analysis of morphological characters could be an interesting test, notwithstanding the fact that the experience has shown that this time-consuming exercise often yields disappointing results in amphipods (e.g. BERGE *et al.*, 2000). Molecular approaches using a larger number of species and gene fragments than ENGLISCH (2001) will probably also contribute to slowly disentangle the situation. However with the current techniques, it is unlikely they will solve all the problems all at once like a *deus ex machina*, as some people expect. Indeed it could be difficult to get adequately fixed material of some rare taxa of pivotal importance (e.g. some relict subterranean freshwater forms); the DNA of amphipods is easily degraded; this approach remains expensive and time-consuming, and even in using several gene fragments, there is no certainty in obtaining highly supported trees.

REMARKS ON THE MAJOR LINEAGES OF LILJEBORGIIDAE: The Liljeborgiidae consist of an *Idunella/Sextonia*-like group and a *Liljeborgia*-like group, which are separated by pronounced differences and are here considered as separated subfamilies, the Idunellinae subfam. nov. and the Liljeborgiinae. The following differences have been detected.

The articulation between articles 1 and 2 of the mandibular palp is geniculate in the Idunellinae, rectilinear in the Liljeborgiinae.

The hinge articulating the mandible with the carapace is posterior in the Idunellinae, lateral in the Liljeborgiinae.

The posterior border of the third article of the mandibular palp has setae in a comb-like disposition in the Idunellinae, irregularly disposed in the Liljeborgiinae.

The third article of the mandibular palp is flattened (and often falciform) in the Idunellinae, circular in cross section in the Liljeborgiinae.

The outer distal part of the mandible is pointed in the Idunellinae, not or scarcely pointed in the

Liljeborgiinae.

The molar process is triturative with a single molar seta (*Sextonia*) or reduced and multi-setaceous in the Idunellinae, always reduced and multi-setaceous in the Liljeborgiinae.

The second article of the palp of maxilla 1 is usually (always?) devoid of anterior setae in the Idunellinae, while there is always one or several such setae in the Liljeborgiinae.

The outer plate of maxilla 1 apparently always has 7 spines in the Idunellinae, whereas there are 7 to 10 spines in the Liljeborgiinae.

The inner plate of maxilla 1 always bears short setae (albeit combined with long setae in *Sextonia*) in the Idunellinae, one (rarely several) long setae in the Liljeborgiinae (the rare occurrence of an accessory short seta seems to be teratological).

In the Idunellinae, the inner marginal border of the outer plate of the maxilliped includes only one kind of aciculae, which can be either marginal or margino-facial, while in the Liljeborgiinae there is both a marginal row of spines and a margino-facial row of strong setae. In the Idunellinae the difference of strength between the apical and inner marginal aciculae is always more pronounced that in the Liljeborgiinae.

In the Idunellinae, the outer plate of the maxilliped bears aciculae on the inner margin, the apical margin and to various extents on the distal part of the outer margin (these aciculae being narrower than the apical ones), whereas there are only inner and inner-apical spines in the Liljeborgiinae.

Coxa 1 has no anterior notch or tooth in the Idunellinae, whereas it usually has such a notch or tooth in the Liljeborgiinae.

Gnathopod 1 is dominant or very slightly weaker than gnathopod 2 in the Idunellinae, whereas gnathopod 1 is always (in females) or almost always (in males) weaker than gnathopod 2 in the Liljeborgiinae.

The two gnathopods are sometimes markedly different from each other (even in females) in the Idunellinae, while they are always very similar in females and often in males in the Liljeborgiinae.

The number and the disposition of spinules on the mediomarginal strong setae of the gnathopods is variable in the Idunellinae (there are often more than 2 spinules and they are often present on both sides of the setae), whereas there are almost always only 2 spinules (always in anterior position) in the Liljeborgiinae.

The carpus of the gnathopods has no long posterior process in the Idunellinae, while such a process is present in the Liljeborgiinae.

In the Idunellinae, the dactylus of gnathopod 2 has no setae (except usual proximal anterior slender seta), whilst there are several medial setae in the Liljeborgiinae.

In the Idunellinae, the palm of gnathopod 1 can bear outer setae, a long outer row of hooked spines (always in females), a row of medial hooked spines (always in females), and a row of spinose setae (always in females); in the Liljeborgiinae, it bears no outer setae, has a long outer row of hooked spines, no medial hooked spines, but spinose setae.

In the Idunellinae, the palm of gnathopod 2 bears outer setae (disposed in short longitudinal rows in *Sextonia*; isolate in *Idunella*), a long outer row of hooked spines, a row of medial stout (and often hooked) spines, and a row of spinose setae; in the Liljeborgiinae, it bears isolate outer setae, a long outer row of hooked spines, no medial hooked spines, but spinose setae.

In the Idunellinae, the dactylus of pereiopods 3 and 4 can have an unguis and tiny subapical setules (*Sextonia* only), whilst unguis and setules are never present in the Liljeborgiinae.

In the Idunellinae, the medial setae of the propodus of P7 are usually shorter than in the Liljeborgiinae.

In the Idunellinae the posterodistal border of urosomites 1 and 2 sometimes have 3 teeth (*Sextonia*) or sometimes have spinules/setules (e.g. *Idunella janisae* IMBACH, 1967; see IMBACH, 1967: 145), while there is at most 1 tooth and never spinules/setules in the Liljeborgiinae.

In the Idunellinae, there are no ventrofacial spines on urosomite 1, while such spines are often present in the Liljeborgiinae.

In the Idunellinae, ventrofacial spines can be present on the peduncle of uropod 1 (*Sextonia*), whilst this is never the case in the Liljeborgiinae.

In the Idunellinae, the tip of the dorsolateral border of the peduncle of uropod 1 bears a long spine pointing backwards paired with a short spine pointing upwards; in the Liljeborgiinae, only the long spine pointing backwards is present.

In the Idunellinae, the tip of the rami of uropods 1-2 is broad or fairly broad, and is terminated by a cluster of spines (up to 4 spines), whilst in the Liljeborgiinae, the rami are gradually tapering and apically acute, and there is just a trace of spine fused with the tip of the ramus.

In the Idunellinae, the outer ramus of uropod 3 is either entire or 2-articulated, whilst it is always entire in the Liljeborgiinae.

In the Idunellinae, it is not uncommon to have spines on both sides of the outer ramus of uropod 3, whilst, in the Liljeborgiinae, spines (if present) are almost invariably restricted to the outer border.

In the Idunellinae, a ventral proximal spine is

sometimes present on the inner ramus of uropod 3; such a spine is never present in the Liljeborgiinae.

In the Idunellinae, the rami of uropod 3 sometimes (rarely) have setae; in the Liljeborgiinae they never have setae.

Amongst the differential characters, it is not always possible to guess which condition is apomorphic or plesiomorphic. However, in the Liljeborgiinae the cylindrical article 3 of the mandibular palp without a regular row of D3-setae and the pointed non-spinulose tip of the rami of uropods 1-2 are obviously apomorphic. In the Idunellinae, this is possibly the case of the absence of anterior notch or tooth on coxa 1 and the absence of medial setae on the dactylus of gnathopod 2.

Subfamily Idunellinae subfam. nov.

Type genus: *Idunella* G.O. Sars, 1894; type species of the type genus: *Lilljeborgia æqvicornis* G.O. Sars, 1877.

Description: Articulation between articles 1 and 2 of Md palp geniculate. Hinge articulating Md with carapace in posterior position. Article three of palp of Md flattened, with setae in a comb-like disposition on posterior border (D3-setae), with group of apical E3-setae, with or without isolate anterior B3-setae. Outer distal part of Md pointed. Molar process either basal and fully triturative (*Sextonia*) or reduced and bearing strong setae. Article two of the palp of Mx1 usually (always?) devoid of anterior setae. Outer plate of Mx1 with 7 spines. Part or all setae of inner plate of Mx1 short. Inner marginal border of the outer plate of Mxp with only one kind of aciculae, which can be either marginal or margino-facial. Coxa 1 without anterior tooth or notch. Gn1 dominant to slightly weaker than Gn2. Gn1 and Gn2 either fairly similar or markedly different (both sexes). Carpus of Gn1-Gn2 without long posterior process (tiny postrior process present on carpus of Gn1 in *Sextonia*). Palm of Gn1 with outer setae disposed in short longitudinal rows or without outer setae, with a long outer row of hooked spines, with a medial row of stout spines, and with a medial row of spinose setae. Palm of Gn2 with outer setae (disposed in short longitudinal rows in *Sextonia*), a long outer row of hooked spines, a row of medial hooked spines, and a row of spinose setae. Dactylus of Gn2 without setae (except for 1 proximal anterior slender seta). Margino-medial setae of palm of Gn1-Gn2 with variable number of anterior spinules; posterior spinule(s) can also be present. Dactylus of P3-P4 with or without unguis (if present, unguis vestigial), with or without tiny subapical setules. Posterodistal border of urosomites 1 and 2 with 0-3 teeth, rarely with spinules. No ventrofacial spines on the urosomite 1. Peduncle of U1 with or without ventrofacial spines. Tip of dorsolateral border of peduncle of U1 with a long spine pointing backwards paired with a short spine pointing upwards. Tip of rami of U1-2 usually broad, always terminated by a cluster of spines (up to 4 spines). Outer ramus of U3 either entire or 2-articulated. Rami of U3 with spines, and sometimes (rarely) also with setae. Outer ramus of U3 with spines either on both margins or on outer margin only. Ventral proximal spine sometimes present on inner ramus of U3.

Distribution: Mostly tropical and warm-temperate with only one Arctic/sub-Arctic species and no Antarctic or sub-Antarctic species; 0 to 1288 m

Generic divisions: G.O. Sars (1894) created the genus *Idunella* for the first known idunellin species, which was originally described as *Lilljeborgia æqvicornis* G.O. Sars, 1877, and which has a dominant gnathopod 1. J.L. Barnard (1959) created the genus *Listriella* for five Californian Idunellinae in which gnathopod 2 is dominant. As the discovery of new Idunellinae accumulated, Karaman (1980) observed a complete range of transition between species with dominant gnathopods 1 or 2 and concluded that *Listriella* should be considered as a junior synonym of *Idunella*. This opinion was followed by a number of authors like Krapp-Schickel (1989). Later on, J.L. Barnard & Karaman (1991) proposed a radically different definition of *Idunella*, which is largely based on the shortness of article 1 of the mandibular palp. With this new definition, they considered that only *Idunella aeqvicornis* (G.O. Sars, 1877) and *I. pirata* Krapp-Schickel, 1975 should be retained in the genus *Idunella* and they transferred all other *Idunella* species to *Listriella*. Surprisingly they retained *Listriella spinifera* Dauvin & Gentil (1983) in the genus *Listriella*, although it has a very short article 1 on the mandibular palp (Dauvin & Gentil, 1983). The opinion of J.L. Barnard & Karaman (1991) has been accepted by some authors like Othman & Morino (2006), who described *Listriella longipalma* Othman & Morino, 2006, with a dominant gnathopod 1, i.e. with the original main diagnostic character of *Idunella* proposed by J.L. Barnard (1959). According to Bousfield (in lit.), the complex *Idunella/Listriella* includes more than two subgroups deserving a generic rank. Examination of illustrations in literature suggests this could indeed be the case. However, many species (including the type species of *Listriella*) are only known by rather

imprecise illustrations and a generic re-arrangement of the species of the complex would require the detailed examination of a large number of species (according to BOUSFIELD, in lit. there could be many undescribed species). Since the differential definition of *Idunella* and *Listriella* proposed by J.L. BARNARD & KARAMAN (1991) is inconsistent, all the species of the *Idunella/ Listriella* complex are provisionally reassigned to the genus *Idunella*.

The genus *Sextonia* was created by CHEVREUX (1920b) for *Sextonia longirostris* CHEVREUX, 1920, as unlike other Liljeborgiidae this species has a fully triturative molar process on the mandible. Despite this remarkable character, several authors, like J.L. BARNARD (1959), IMBACH (1967), SIVAPRAKASAM (1972) and KRAPP-SCHICKEL (1989) considered *Sextonia* as a junior synonym of *Idunella*. While the affinities of *Sextonia* with *Idunella* are unequivocal, the unique characteristics of the molar process have been considered by KARAMAN (1980) and J.L. BARNARD & KARAMAN (1991) as sufficient to accept the validity of *Sextonia*. Their opinion is here considered as justified.

Genus *Idunella* G.O. SARS, 1894

Idunella G.O. SARS, 1894: 536 (type species = *Lilljeborgia æqvicornis* G.O. SARS, 1877; gender feminine)
Listriella J.L. BARNARD, 1959: 14 (type species = *Listriella goleta* J.L. BARNARD, 1959; gender feminine)
Ronconoides LEDOYER, 1973: 59 (type species = *Ronconoides brevicornis* LEDOYER, 1973; gender feminine)
Indunella HIRAYAMA, 1985: 176 (erroneous spelling for *Idunella*)

ETYMOLOGY: diminutive of Iðunn (sometimes spelled Iduna), goddess of the Norse mythology.

DIAGNOSIS: Anterior border of article three of Md either without B3-setae or with subdistal B3-setae. Molar process of Md reduced, non triturative and bearing strong setae. Inner plate of Mx1 with short setae only. Gn1 >, =, or < Gn2. Dactylus of P3-P4 without unguis, without subdistal setules, without microscopical distal anterior spatulate process (unguial hood). Peduncle of U1 without ventrofacial spines. Outer ramus of U3 1- or 2-articulated.

COMPOSITION: *Idunella aeqvicornis* (G.O. SARS, 1877); *Idunella albina* (J.L. BARNARD, 1959); *Idunella andresi* MARTIN, ORTIZ & ATIENZA, 2000; *Idunella bahia* (MCKINNEY, 1979); *Idunella barnardi* (WIGLEY, 1963); *Idunella bowenae* KARAMAN, 1979; *Idunella brevicornis* (LEDOYER, 1973); *Idunella carinata* (MCKINNEY, 1979); *Idunella chilkensis* CHILTON, 1921; *Idunella clymenellae* (MILLS, 1962); *Idunella curvidactyla* NAGATA, 1965; *Idunella dahli* SCHELLENBERG, 1938; *Idunella demersalis* SIVAPRAKASAM, 1972; *Idunella diffusa* (J.L. BARNARD, 1959); *Idunella eriopisa* (J.L. BARNARD, 1959); *Idunella excavata* KRAPP-SCHICKEL, 1975; *Idunella goleta* (J.L. BARNARD, 1959); *Idunella janisae* IMBACH, 1967; *Idunella kensleyi* ORTIZ & MORINO, 1996; *Idunella lindae* (GRIFFITHS, 1974); *Idunella longipalma* (OTHMAN & MORINO, 2006); *Idunella melanica* (J.L. BARNARD, 1959); *Idunella melanica lazaris* (J.L. BARNARD, 1969); *Idunella mollis* (MYERS & MCGRATH, 1983) [= *Listriella dentipalma* DAUVIN & GENTIL, 1983]; *Idunella nagatai* KARAMAN, 1979; *Idunella nana* SCHIECKE, 1973; *Idunella orientalis* (HIRAYAMA, 1985); *Idunella pauli* IMBACH, 1967; *Idunella picta* (NORMAN, 1889); *Idunella pirata* KRAPP-SCHICKEL, 1975; *Idunella quintana* (MCKINNEY, 1979); *Idunella saldanha* (GRIFFITHS, 1975); *Idunella serra* IMBACH, 1967; *Idunella similis* (RABINDRANATH, 1971); *Idunella sinuosa* (GRIFFITHS, 1974); *Idunella sketi* KARAMAN, 1980; *Idunella smithi* LAZO-WASEM, 1985; *Idunella spinifera* DAUVIN & GENTIL, 1983; *Listriella titinga* (WAKABARA, TARARAM, VALERIO-BERARDO & LEITE, 1988).

REMARKS: *Idunella* will probably have to be dismembered into several genera, but such an action will only be possible after the careful study of many species. In the present paper, the type species of the genus, *I. aeqvicornis* and a very different species, *I. picta*, are redescribed in detail. Characters of probable importance for a hypothetic future review and splitting of the genus are pointed out in the sections treating these two species.

Idunella aeqvicornis (G.O. SARS, 1877)
(Figs 1-6)

Lilljeborgia æqvicornis G.O. SARS, 1877: 355; 1883: 106 [remarks on sexual dimorphism]; 1885: 192, pl. 16 fig. 2, 2a
Lilljeborgia aeqvicornis; DELLA VALLE, 1893: 657
Idunella æqvicornis; G.O. SARS, 1894: 537, pl. 190
Idunella aequicornis; STEBBING, 1906: 234; CHILTON, 1921a: 527; STEPHENSEN, 1938: 194, 198; GURJANOVA, 1951: 517, fig. 339 (after G.O. SARS, 1895); IMBACH, 1967: 79, 80, 81; KARAMAN, 1980: 414, 415; J.L. BARNARD & KARAMAN, 1991: 414, fig. 85c (after G.O. SARS, 1894); WATLING, 1993: 844, fig. 3

Idunella aeqvicornis; D'UDEKEM D'ACOZ, 2008: 49 (correction of spelling)

MATERIAL: **Norway**, R/V Johan Ruud, sta. 1085-98, Stjernsundet near Gavlodden, 70°12.96'N 023°00.52'E, 455 m, Beyer sledge, 24.09.1998: 14 specimens (of which 1 adult male and 1 ovigerous female have been dissected and mounted in Euparal each, on 8 slides), leg. Wim VADER, TSZCr. 10892; R/V Johan Ruud, sta. 1083-98, Norway, Vargsundet, 70°18'N 023°21.40'E, 276 m, 24.09.1998: 12 specimens (previously mixed with 2 *Liljeborgia* sp.: possibly juvenile *L. fissicornis* sensu stricto), leg. Wim VADER, TSZCr. 10876; R/V Håkon Mosby, sta. 81.6.6.7, Norwegian Sea, 65°43.0'N 005°14.3'E, 794 m, T = -0.9°C, 06.vi.1981: 3 specimens (no adult male), UBZM nr. 86426; R/V Håkon Mosby, sta. 81.6.7.1, Norwegian Sea, 65°41.8'N 004°22.9'E, 1211 m, T = -1°C, 7.vi.1981: 67 specimens, UBZM nr. 86427; R/V Håkon Mosby, sta. 81.8.13.2, Norwegian Sea, 63°25.4'N 004°05.4'E, 1288 m, T = -0.9°C, 13.viii.1981: 17 specimens (incl. 1 adult male), UBZM nr. 86428; R/V Håkon Mosby, sta. 81.8.16.3, Norwegian Sea, 62°48.0'N 001°02.6'E, 1009 m, T = -1°C, 16.viii.1981: 45 specimens, UBZM nr. 86429; R/V Håkon Mosby, sta. 81.8.16.4, Norwegian Sea, 62°48.4'N 001°02.7'E, 1003 m, T = -1°C, 16.viii.1981: 11 specimens, UBZM nr. 86430; R/V Håkon Mosby, sta. 82.1.21.6, Norwegian Sea, Trough off, 62°48.2'N 001°05.3'E, 984 m, T = -0.9°C, 21.i.1982: 4 specimens including an immature male, UBZM nr. 86431; R/V Håkon Mosby, sta. 82.8.23.1, Norwegian Sea, 63°12.8'N 003°07.3'E, 1003 m, T = -1°C, 23.viii.1982: 1 adult male, UBZM nr. 86432; R/V Håkon Mosby, sta. 82.11.27.1, Norwegian Sea, 62°59.1'N 003°13.1'E, 804 m, T = -1°C, 27.xi.1982: 9 specimens (incl. 1 large female (8.5 mm)), 2 vials, UBZM nr. 86433; R/V Håkon Mosby, sta. 83.6.2.1, Norwegian Sea, Trough off, 62°11.9'N 000°00.2'W, 708 m, T = -0.3°C, 02.vi.1983: 4 specimens (including 3 adult males), UBZM nr. 86434; R/V Håkon Mosby, sta. 85.1.8.3, Norwegian Sea, 62°54.7'N 000°55.7'E, 1112 m, T = -0.9°C, 08.i.1985, epibenthic sledge: 1 adult male, UBZM nr. 86435.

DESCRIPTION: Head: eye indistinct in alcohol [consisting of a small oval patch of a whitish pigment, without any trace of visual elements (G.O. SARS, 1894)]; rostrum short, blunt; epistome truncated, not protruding, anterior and upper border forming a right angle.

A1: article one 2.33 x as long as wide; article three of peduncle 0.53 x as long as article two; major flagellum with 12 to 13 articles; accessory flagellum with 4 to 5 articles; ratio length of accessory flagellum / length of major flagellum: 0.36; ratio major flagellum / article one of peduncle: 1.80.

A2: about as long as A1 (or even very slightly shorter); article 3 without spines and setae; article four of peduncle 4.38 x as long as wide, with setae and 1 very slender anteromedial spine; article five of peduncle 5.17 x as long as wide, with setae, without spines; flagellum distinctly shorter than peduncle, with 8 to 9 articles.

Upper lip not notched.

Lower lip: distal part of lobes without tooth.

Md: distolateral corner forming a tooth; hinge process on proximolateral corner; left lacinia mobilis with 6 rounded teeth; right lacinia mobilis with anterior margin distinctly and sharply denticulate and with one especially large medial triangular tooth; largest tooth of incisor process of right Md long and acute; raker spines of incisor process smooth; molar process small but distinct, with 3 strong spines, of which the longest is barely longer than the longest spines of incisor process; article one of palp without setae, with anterior border slightly concave, forming a geniculate articulation with article two, considerably shorter than article two (ratio length article one / article two = 0.34); article one 1.94 x as long as wide; article two with row of setae almost all along anteromedial border and with 3 isolated setae on proximal 0.4 of anterolateral border, 5.00 x as long as wide; article three strongly curved (in a plane perpendicular to the broad side of the article), 5.20 x as long as wide, 0.74 x as long as article two, with posterior row of D3-setae (which are not of increasing length towards tip), with 1 subdistal B3-seta on anterior border, with distal group of E3-setae.

Mx1: article two of palp without setae on anterior margin, with 7 spines of normal stoutness on ventral and apical margin, and 4 well-developed facial setae; outer plate with 7 smooth spines; inner plate with 2 short apical setae.

Mx2: setae not very numerous and rather slender; outer plate with 4 very long setae on anterior margin; inner plate with 4 facial setae.

Mxp: article one of palp without distal outer seta (but with distal medial seta), article two without non-distal setae on outer margin and with well-developed tuft of long distolateral setae; article three with 2 transverse pairs of setae (of normal stoutness) on dorsal border and with setae all along ventral border; article four (dactylus) slender, with long unguis, with anterior and posterior margins straight and 0.92 x as long as article three; outer plate with medial and anteromedial border weakly crenulate to denticulate, with 5 well-developed slender, well-spaced strong setae on medioventral border and 3 anterior spines; inner plate with 1 long

stout anterolateral seta, 3 anterior spines (that one on the anteromedial corner can probably be considered as ventrofacial), and 2 dorsomedial setae.

Gn1: with very strong sexual dimorphism; coxa broad and anteriorly rounded, with posterior border straight, without anterior notch, with posterior tooth; basis with longitudinal row of setae on anteromedial border and proximal half of posterior border; merus with distal group of setae, without distal tooth; carpus without posterodistal process, without small anterodistal notch, with 1 (male) or 2 (female) anterodistal tuft of setae; propodus with anterior and posterior border nearly straight, diverging towards tip, 1.60 (male) or 1.78 (female) x as long as wide; usually 2 transverse groups of posteromedial setae anterior to palm; palm defined by 2 unpaired anteromedial spines (one spine lost on chela illustrated on fig. 3B); most distal anteromedial spine arising from proximal 0.26 (male) or 0.47 (female) of propodus; these spines consist of a small one and a larger one, the largest one being quite long in the female but rather short in the male; border of propodus without denticulate crest at the level of distal spine; palm border forming a pronounced regular curve and without teeth in female, deeply concave and defined by a strong proximal tooth and a well-developed distal tooth in adult male [concavity regularly curved or very vaguely sigmoid]; palm of female with broad cylindrical spines on lateral border (33 lateral spines + 4 setae), with another row of straight spines on medial border (about 9 spines); with a row of backwardly-curved setae on medial border, each of this setae presenting several anterior spinules (usually 2 or 3), without proximal strong seta, with distal non-spinulose seta; dactylus toothless, without medial setae.

Gn2: weakly sexually dimorphic; coxa quadratoelliptic, narrow, with lateral borders parallel, with anteroventral notch and posterior tooth (the notch and the tooth are very close to each other), posteromedial surface of coxa with row of setae; basis without anterodistal setae and with well-developed posterior row of setae, with distal part of anterolateral border not forming a short process; ischium without anteromedial setae, with 0 to 1 posterior short seta; merus with 5 to 6 isolate or loosely paired setae, and with 1 or 2 acute distal teeth; carpus without posterodistal process, with distal expanded part about as long as proximal narrow part (i.e. part connecting with merus), without anterodistal shallow notch, without setae on anteromedial and distomedial borders, with 3 to 4 tufts of setae on posterior border of distal expanded part; propodus with anterior and posterior border nearly straight, very slightly divergent, 1.84 (male) or 1.58 (female) x as long as wide, with 3 to 6 poorly developed anteromedial groups of setae, with 6 to 7 transverse groups of posterior and posteromedial setae; palm defined by a pair of anteromedial spines (a small lateral and a longer medial one), which are associated with 1 long seta; most distal anteromedial spine emerging on the proximal 0.56 (male and female) of propodus; border of propodus without denticulate crest at the level of distal spine; palm border forming a curve and without teeth or protrusions; palm with broad cylindrical spines (30 lateral spines + 4 lateral small setae in female; 23 lateral spines + 2 short setae in male), with another row of straight spines on medial border; with a row of backwardly-curved setae on medial border, each of this setae presenting several anterior spinules (usually 2 or 3), dactylus without teeth, without medial setae, 0.68 (male) or 0.72 (female) x as long as propodus.

P3: coxa subquadrate, narrow, with lateral borders parallel, with anteroventral notch and posterior tooth (the notch and the tooth are close to each other), posteromedial surface of coxa with row of setae; leg very slender; merus 1.15 x as long as carpus and 0.91 x as long as propodus; merus with 1 short anterodistal and 1 short posterodistal setae and no other ornamentation; carpus with 1 short anterodistal and 2 groups of 1 or 2 short posterior setae; propodus with 4 tufts of long slender posteromedial setae (length of longest propodal setae about 3.11 x as long as width of propodus); anterior border of propodus with 1 very short distal seta and no ornamentation in more proximal position; dactylus very long and very slender, with anterior and posterior borders distinctly curved, 0.98 x as long as carpus and 0.78 x as long as propodus.

P4: coxa narrow (1.41 x as long as wide), with anterior and posterior border parallel and very straight, with ventral border slightly convex, with 4 medium-sized serrations on posterior border and no anterior or medioventral tooth, notch or seta; leg very slender; merus 1.21 x as long as carpus and 0.97 x as long as propodus; merus with 1 short anterodistal and 2 very short isolated posterior setae; carpus with 1 short anterodistal and 3 groups of 1 or 2 short posterior setae; propodus with 4 tufts of long slender posteromedial setae (length of longest propodal setae about 2.92 x as long as width of propodus); anterior border of propodus with 1 very tiny distal seta and no ornamentation in more proximal position; dactylus very long and very slender, with anterior and posterior borders distinctly curved, 0.89 x as long as carpus and 0.71 x as long as propodus, without unguis.

P5: coxa with posterior tooth, without setae; basis broad (1.43 x as long as wide), anteriorly strongly and

regularly convex, posteriorly weakly convex (almost straight); anterior border with 7 well-developed spines, posterior border with 8 normally developed serrations, distal border rounded, produced into a regularly curved lobe; ischium with a well-developed spine and 2 short setae on anterodistal corner; merus 4.0 x as long as broad, with 3 anterior groups of 1-2 short to normally developed spines, with 2 posterior groups of 1-2 medium-sized spines; carpus with 3 anterior groups of 1 to 4 medium-sized spines (not intermixed with setae) and 1 posterodistal group of spines; carpus 0.84 x as long as merus and 0.94 x as long as propodus; carpus + propodus 1.69 x as long as merus; propodus with 4 isolated short conical spines on anterior border, 1 pair of long setae on middle of medial surface and well-developed propodal apical tuft of setae; dactylus scarcely curved, slender, 0.30 x as long as propodus.

P6: coxa with posterior tooth, without setae; basis broad (1.39 x as long as wide), anteriorly strongly and regularly convex, posteriorly weakly convex; anterior border with 8 well-developed styliform spines, posterior border with 8 serrations (normally developed except distal one, which is reduced), distal border rounded, produced into a regularly curved lobe; ischium with well-developed styliform spine and small seta on anterodistal corner; merus with 3 anterior groups of slender medium-sized spines, with 2 isolated medium-sized posterior spines + distal group of 4 well-developed posterodistal spines; carpus with 3 anterior groups of 2 medium-sized spines and 2 posterior groups of 1-3 medium-sized spines; carpus 1.00 x as long as merus and 0.93 x as long as propodus; propodus with 2 tiny isolated anterior spines (not associated with setae), 1 long posteromedial seta and a posterodistal cluster of articulated structures including 2 small spines and 2 long setae; dactylus almost straight, slender, with anterodistal tiny setule (but without real notch), 0.40 x as long as propodus.

P7: coxa without setae; basis broad (1.43 x as long as wide), anteriorly and posteriorly distinctly and regularly convex (basis symmetrically elliptic), anterior border with 8 well-developed styliform spines, posterior border with 9 normally developed serrations, distal border rounded, produced into a regularly curved lobe; ischium with well-developed styliform spine but without seta on anterodistal corner; merus with 3 groups of anterior spines (2 with rather small spines and one with well-developed spines) and 4 groups of 1-4 long slender posterior spines; merus 3.59 x as long as wide and 0.86 x as long as basis; carpus with 2 groups of rather small anterior spines, with 3 groups of posteromedial long slender spines; carpus 1.15 x as long as merus and 0.92 x as long as propodus; propodus of P7 1.26 x as long as propodus of P6; propodus with 1 anterior tiny conical spine, and 4 groups of 1 or 2 medium-sized posteromedial spines; dactylus straight, long, slender, not notched, 0.33 x as long as propodus.

Pleonite 1: posterodorsal area without tooth; Ep1 with small posteroventral tooth, with posterior border weakly convex; without ventrofacial spines; pleopod 1 with peduncle 2.46 x as long as broad, with rami 1.13 x as long as peduncle.

Pleonite 2: posterodorsal area with 1 rather small tooth; Ep2 with 3 small ventrofacial spines, with well-developed sharp posteroventral tooth, with posterior border nearly straight.

Pleonite 3: posterodorsal area without tooth, without shallow notch on each side; Ep3 with 2 small ventrofacial spines, with normally developed posteroventral tooth followed upwards by a notch, with posterior border strongly convex in its lower part.

Urosomite 1 without posterodorsal tooth; ventrofacial border without spines; peduncle of U1 without ventrofacial spines, with 8 dorsolateral spines: 8 normally developed regularly spaced spines followed by a pair of spines consisting of a small one pointing upwards and a long distal spine pointing backwards, with 11 well-developed and regularly spaced dorsomedial spines of which the distal one is by far the longest; outer ramus with 2 small stout outer and 1 small stout medial spines, with 2 spines on tip (which is notched); inner ramus with 1 small stout spine on outer border and with 5 rather long stout spines on medial border, with 2 spines on tip (which is notched).

Urosomite 2 without posterodorsal tooth; peduncle of U2 with 1 distal dorsolateral spine and 1 distal dorsomedial spine; outer ramus with 2 well-developed outer spines and 1 medial spines, with 2 or 3 spines on tip (which is notched); inner ramus with 1 medium-sized spine on outer border and with 3 well-developed stout spines on medial border, with 2 spines on tip (which is notched).

Urosomite 3 without posterolateral tooth on each side, with a pair of medium-sized posterodorsal spines; U3 distinctly shorter than U1 and slightly shorter than U2; outer ramus and inner ramus of U3 subequal, outer ramus 2-articulated, with article one with 2 to 4 isolated small slender spines on outer side and without spines on medial side, article two 0.33 (male) or 0.40 (female) x as long as article one; inner ramus 1.30 x as long as peduncle, with 2 tiny spines on outer border, without ventral spine, with 1 to 2 spines on medial border.

Telson: cleft to 0.80 of its length; medial tooth of each lobe distinctly overreaching of outer tooth (1.75 x

as long as outer tooth); each lobe with 2 (sometimes 3) spines of size increasing in a medial direction; longest interdental spine overreaching outer tooth by 0.64 of its length, 0.37 x as long as telson; telson without setae.

COLOUR PATTERN: Uniformly pale yellow; consisting of a small oval patch of a whitish pigment, without any trace of visual elements (G.O. SARS, 1894). The few living specimens seen by the author were almost colourless.

TOTAL LENGTH: Up to 8.5 mm.

DISTRIBUTION: Greenland (OLDEVIG, 1959; BRANDT, 1997), Svalbard (OLDEVIG, 1959; GULLIKSEN *et al.*, 1999; WĘSŁAWSKI *et al.*, 2003), Jan Mayen (STEPHENSEN, 1931), Barents Sea (G.O. SARS, 1885; OLDEVIG, 1959), Siberian Arctic (OLDEVIG, 1959); Norwegian Sea (G.O. SARS, 1885), Northern Norway (G.O. SARS, 1885, 1890-1895; NORMAN, 1902; NORDGAARD, 1905), North of Iceland (STEPHENSEN, 1931; BRANDT, 1997), between Iceland and the Faeroe (STEPHENSEN, 1931). From 100-120 m (STEPHENSEN, 1931) to 1288 m, between -1.0°C (G.O. SARS 1885) and +2.5°C (STEPHENSEN, 1931), on sandy clay (STEPHENSEN, 1938). The Mediterranean records of *I. aeqvicornis* by LEDOYER (1968) and BELLAN-SANTINI & LEDOYER (1973) are almost certainly based on another species.

SYSTEMATIC REMARKS: As previously mentioned, the genus *Idunella* is heterogeneous and will have to be subdivided sooner or later. A number of character states observed in *I. aeqvicornis* (i.e. the type species of the genus), which should probably be taken into account when this happens, are listed below:

Eye vestigial, non ommatidian; antennae subequal; accessory flagellum of A1 with about 5 articles; peduncle of A2 slender, with setae, without spines (except 1 slender anteromedial spine on article four); article one of mandibular palp short; article two of mandibular palp strongly setose; article three of mandibular palp falciform and with anterior subdistal B3-seta; lobes of lower lip without medial tooth; outer plate of Mxp with inner margin slightly crenulate (not smooth); aciculae of inner margin of outer plate of Mxp arising facialo-medially (not truly marginal); article two of palp of Mxp with long and strong setae on anterolateral corner; Gn1 > Gn2; palm of Gn1 of adult male deeply and regularly concave, with reduced setation/spination; carpus of Gn2 medium-sized, with several posterior groups of setae and no anterior setae; outer border of palm of Gn2 not with many long and stout setae in males; dactylus of Gn1-Gn2 not toothed; posterior border of propodus of P3-P4 with long setae disposed in tufts; ventral margin of coxa 4 smooth and without setae or setules; basis of P6-P7 with about 10 posterior serrations; P7 slender, with slender dactylus; posterior border of pleonites and of epimeral plates not serrate; Ep2-Ep3 with ventrofacial spines; urosomites 1-2 posterodorsally toothless and without spinules or setules; dorsomedial border of peduncle of U1 with many (short) spines; rami of U1-U3 slender; outer ramus of U3 biarticulated; inner ramus of U3 without ventral spine; rami of U3 subequal and without setae; telson deeply cleft.

NOMENCLATURAL REMARKS: In his original description, G.O. SARS (1877) spelled the name of this species as '*æqvicornis*', but modern authors usually use the spelling '*aequicornis*' (see synonymy). The International Code of Zoological Nomenclature, 4th edition (ICZN, 1999) edicts the following rules. Art. 32.2 states: "The original spelling of a name is the "correct original spelling" as provided in Article 32.5". Art. 32.5.1 states: "If there is in the original publication itself, without recourse to any external source of information, clear evidence of an inadvertent error, such as a lapsus calami or a copyist's or printer's error, it must be corrected. Incorrect transliteration or latinization, or use of an inappropriate connecting vowel, are not to be considered inadvertent errors." Hence 'qv' may not be converted into 'qu'. On the other hand, Art 32.5.2 states: "A name published with a diacritic or other mark, ligature, apostrophe, or hyphen, or a species-group name published as separate words of which any is an abbreviation, is to be corrected". Hence 'æ' should lose its ligature and must be converted in 'ae'. The correct spelling is thus *Idunella aeqvicornis*. A similar case has been treated by KOMAI (1999), who restored the original name '*propinqvus* G.O. SARS, 1870' for the caridean shrimp, which was previously named as *Pandalus propinquus* and which is now called *Atlantopandalus propinqvus*. G.O. SARS used 'qv' in the original spelling of several other species of crustaceans, which has been converted in 'qu' in subsequent literature. In all cases the original spelling has to be restored. The following cases are known: *Haplomesus qvadrispinosus* (G.O. SARS, 1879) (original combination = *Ischnosoma qvadrispinosum* G.O. SARS, 1879) (Isopoda), *Eusirus propinqvus* G.O. SARS, 1893, *Halirages qvadridentatus* G.O. SARS, 1877, *Harpinia propinqva* G.O. SARS, 1891, *Hippomedon propinqvus* G.O. SARS, 1890, *Metopa aeqvicornis* G.O. Sars, 1879, and *Metopa propinqva* G.O. SARS, 1892 (Amphipoda). On the other hand the conversion by G.O. SARS of 'qu' in 'qv' of the names of species described by earlier authors is of course unacceptable.

***Idunella picta* (NORMAN, 1889)**
(Figs 7-12)

Lilljeborgia picta NORMAN 1889: 116, pl. 10 fig. 5-9; DELLA VALLE, 1893: 658
Idunella picta; STEBBING 1906: 235; CHEVREUX, 1920a: 81, fig. 5 (mandible); CHEVREUX & FAGE, 1925: 158, fig. 158-159; GURJANOVA, 1951: 517 (key); KARAMAN, 1980: 423
Listriella picta; J.L. BARNARD, 1959: 14 (genus transfer, no description); LINCOLN, 1979: 392-393, fig. 186; LEDOYER, 1979: 112; MYERS & MCGRATH, 1983: 348-350, fig. 1B (habitus with colour pattern), fig. 2; DAUVIN & GENTIL, 1983: 434, 438, 440

MATERIAL: **France**, western part of the English Channel, Bay of Morlaix, East side of Ile Callot, at the level of the ford connecting Ile Callot and Ile Le Cerf, 48°41'23"N 003°55'12"W, bottom consisting of a mixture of gravel and small stones covered by calcareous algae, coarse sand, and mud, besides beds of *Zostera marina* L., extreme lower shore, sampled in sieving the substrate, 12.iii.2009: about 40 specimens including ovigerous females, coll. C. D'UDEKEM D'ACOZ, IRScNB, Inv. 67.745.

DESCRIPTION: Head: eye present, well developed, rounded, with ommatidia well developed, strongly pigmented; rostrum short, acutely triangular; epistome rounded, not protruding.

A1: article one 2.46 x as long as wide; article three of peduncle 0.53 x as long as article two; major flagellum with 8 articles; accessory flagellum with 3 articles; ratio length of accessory flagellum / length of major flagellum: 0.29; ratio major flagellum / article one of peduncle: 1.19.

A2: longer than A1 (1.42 x as long as A1); anterodistal corner of article 3 with 2 spines; article four of peduncle 3.3 x as long as wide, with a few setae, with 2 short anterior spines; article five of peduncle 3.0 x as long as wide, with setae, without spines; flagellum distinctly shorter than peduncle, with 8 articles.

Upper lip with shallow notch, each lobes being very slightly asymmetrical.

Lower lip: distal part of lobes with short tooth.

Md: distolateral corner forming a tooth; hinge process on proximolateral corner; left lacinia mobilis with 5 teeth; right lacinia mobilis with anterior margin distinctly denticulate and with one especially large medial triangular tooth; largest tooth of incisor process of right Md long and acute; raker spines of incisor process smooth; molar process small but distinct, with 4 to 7 stout setae, which are less than 2 x as long as longest spines of incisor process; article one of palp without setae, with posterior border slightly concave, forming a geniculate articulation with article two, distinctly but not considerably shorter than article two (ratio length article one / article two = 0.63); article one 2.93 x as long as wide; article two with 1 median and 6 subdistal setae (all these setae on posterolateral border), 5.04 x as long as wide; article three not curved, 5.78 x as long as wide, 0.79 x as long as article two, with posterior row of D3-setae of increasing length towards tip, without anterior B3-setae.

Mx1: article two of palp without setae on anterior margin, with 5 spines of normal stoutness on ventral and apical margin, and about 4 well-developed facial setae; outer plate with 7 smooth spines; inner plate with 2 short apical setae.

Mx2: setae not numerous and rather stout; outer plate with 3 very long setae on anterior margin; inner plate with 1-2 facial setae.

Mxp: article one of palp without distal outer setae, article two without non-distal setae on outer margin and without setae on distolateral corner; article three with 2 transverse pairs of setae (of normal stoutness) on dorsal border and without setae on proximal half of ventral border; article four (dactylus) slender, with very long unguis, with anterior and posterior margins straight and 0.71 x as long as article three; outer plate with medial and anteromedial margin smooth, with 9 well-developed slender and well-spaced spines on medial and anterior margin; inner plate with 1 long anterior seta, 1 slender anterior spine, and 1 dorsomedial seta.

Gn1: similar in both sexes; coxa narrowly triangular, with concave posterior border, without anterior notch, with posterior tooth; basis with longitudinal row of setae on anteromedial border and with isolate small seta on posterodistal angle; merus with distal group of setae, without distal tooth; carpus without posterodistal process, with small posterodistal shallow notch, with posterodistal tuft of setae; propodus with anterior and posterior border nearly straight, slightly diverging towards tip, 1.83 (male) or 1.71 (female) x as long as wide; 5 (male) or 4 (female) transverse groups of posteromedial setae anterior to palm; palm defined by 2 unpaired posteromedial spines, of which one is associated with a long seta; most distal posteromedial spine emerging on the proximal 0.64 (male) or 0.55 (female) of propodus; these spines are well developed and rather stout; border of propodus with small denticulate crest at the level of distal spine; palm border forming a pronounced regular curve, without teeth; palm with broad cylindrical spines on lateral border (19

to 22 lateral spines), with another row of straight spines on medial border; with a row of backwardly-curved setae on medial border, each of these setae presenting several anterior spinules (usually 4 or more), with one proximal nearly spiniform setae with setules on both sides, with distal pappose seta; dactylus with 4 teeth, without medial setae; dactylar teeth situated on second 1/4 of dactylus.

Gn2: coxa triangulo-elliptic, broad, with lateral borders converging downwards, with anteroventral slit and posterior tooth (the slit and the tooth are close to each other), posteromedial surface of coxa without row of setae; basis with 1 anteromedial and 2 anterodistal setae and with posterior loose row of setae, with distal part of anterolateral border forming a short process, which is acute in the male and blunt in the female; ischium without anteromedial setae, with 1 to 3 medium-sized posterior setae; merus with 3 to 5 isolate or paired setae, and with acute distal tooth; carpus without posterodistal process, with distal expanded part shorter than proximal narrow part (i.e. part connecting with merus), with small posterodistal shallow notch, without setae on anteromedial and distomedial borders, with 1 posterodistal tuft of setae; propodus with anterior and posterior border nearly straight, nearly parrallel, 1.84 (male) or 1.95 (female) x as long as wide, with 3 to 4 normally developed anteromedial groups of setae, with 6 transverse groups of posterior and posteromedial setae; palm defined by 2 unpaired anteromedial spines, which are associated with 2 long setae; most distal anteromedial spine emerging on the proximal 0.63 (male) or 0.56 (female) of propodus; these spines are well developed and rather stout; border of propodus with small denticulate crest at the level of distal spine; palm border forming a curve and without teeth or protrusions; palm with broad cylindrical spines associated with setae (scarce and small in females, numerous and very long in males) on lateral border (16 lateral spines + 4 small setae in females; 11 lateral spines + 11 long setae in male), with another row of straight spines on medial border; with a row of backwardly-curved setae on medial border, each of this setae presenting several anterior spinules (usually 4 or more), with one proximal nearly spiniform seta with spinules on both sides, with distal pappose seta; dactylus with 7 to 8 teeth, without medial setae; dactylar teeth situated on proximal 0.8 of dactylus, 0.59 (male and female) x as long as propodus.

P3: coxa elliptic, of normal width, with lateral borders slightly converging downwards, with anteroventral slit and posterior tooth (the slit and the tooth are close to each other); posteromedial surface of coxa with 2 setae close to tip; leg of normal stoutness; merus 1.13 x as long as carpus and 0.74 x as long as propodus; merus with 2 short anterodistal and 2 short posterodistal setae and no other ornamentation; carpus with 1 short anterodistal and 2 short posterodistal setae and no other ornamentation; propodus with 6 isolate setae and a distal pair of small spines on posterior border (length of longest propodal setae about 0.94 x as long as width of propodus); anterior border of propodus with distal group of 2 very short setae and no ornamentation in more proximal position; dactylus of normal length and stoutness, with anterior and posterior borders slightly curved, 0.64 x as long as carpus and 0.41 x as long as propodus.

P4: coxa broad (1.22 x as long as wide), with anterior and posterior border parallel, with ventral border nearly straight (barely convex), with 2 medium-sized serrations on posterior border and no anterior or medioventral tooth, notch or seta; leg of normal stoutness; merus 1.10 x as long as carpus and 0.77 x as long as propodus; merus with 2 short anterodistal and 1 short posterodistal setae and no other ornamentation; carpus with 1 short anterodistal and 1 short posterodistal setae and no other ornamentation; propodus with 5 isolate setae and a small spine on posterior border (length of longest propodal setae about 1.00 x as long as width of propodus); anterior border of propodus with distal group of 2 very short setae and no ornamentation in more proximal position; dactylus of normal length and stoutness, with anterior and posterior borders slightly curved, 0.61 x as long as carpus and 0.42 x as long as propodus.

P5: coxa with posterior tooth, with 1 well-developed seta on ventral border of posterior lobe; basis broad (1.56 x as long as wide), anteriorly strongly and regularly convex, posteriorly weakly convex; anterior border with 7 small conical spines, posterior border with 8 normally developed serrations (often no serrations on proximal 0.4), distal border rounded, produced into a weak lobe; ischium with tiny spine and short seta on anterodistal corner; merus 2.69 x as long as broad, with 2 anterior groups of 1-2 short spines, with 2 posterior groups of 1-2 spines (1 median very short spine, and a well-developed + a very short distal spine); carpus with 3 anterior groups of small to medium-sized spines (not intermixed with setae) and no posterior spines (except apical group); carpus 0.79 x as long as merus and 0.84 x as long as propodus; carpus + propodus 1.69 x as long as merus; propodus with 3 groups of 1-2 short and rather slender spines on anterior border and no spines or setae on posterior border except propodal apical tuft (the latter consisting of 1 spine and 2 long but stout setae); dactylus slightly curved and notched (setule in notch), of normal stoutness, 0.28 x as long as propodus.

P6: coxa with one well-developed posteroventral and one anterior setae; basis broad (1.57 x as long as wide), anteriorly strongly and regularly convex, posteriorly weakly convex; anterior border with 7 small conical spines, posterior border with 10 serrations (normally developed except proximal one and distal one, which are reduced), distal border rounded, produced into a weak curved lobe; ischium without spine, with pair of setules on anterodistal corner; merus with 3 anterior groups of 1 or 2 slender spines (two proximal groups short; distal one well developed), with 2 isolated small posterior spines + distal group of 3 medium-sized posterodistal spines; carpus with 3 anterior groups of well-developed spines and 1 posterodistal group of well-developed spines; carpus 0.81 x as long as merus and 0.83 x as long as propodus; propodus with 4 anterior groups of 1 to 3 well-developed slender spines (not associated with setae), and 3 groups (including apical tuft) of well-developed posteromedial slender spines; dactylus slightly curved and notched (setule in notch), of normal stoutness, 0.18 x as long as propodus.

P7: coxa with one well-developed anterior seta and a posterior setule; leg stout; basis broad (1.55 x as long as wide), anteriorly and posteriorly slightly and regularly convex (basis symmetrically elliptic), anterior border with only 3 small conical spines + distal angle with a long spine associated with a tiny spinule, posterior border with 12 normally developed serrations, distal border rounded, produced into a regularly curved lobe; ischium without spine, with small seta on anterodistal corner; merus with 3 groups of anterior and posterior medium-sized spines; merus 3.56 x as long as wide and 0.82 x as long as basis; carpus with 3 groups of well-developed anterior spines, with posterodistal group of spines and no other ornamentation on posterior border; carpus 0.91 x as long as merus and 0.78 x as long as propodus; propodus of P7 1.06 x as long as propodus of P6; propodus with 4 anterior groups of 1-3 fairly slender and well-developed spines, and 4 well-developed groups of posteromedial slender spines; dactylus straight, short and notched (setule in notch), of normal stoutness, 0.29 x as long as propodus.

Pleonite 1: posterodorsal area with small tooth (which can be very difficult to see); Ep1 with normally developed posteroventral tooth, with posterior border strongly convex; anteriorly with 2 thin setae; pleopod 1 with peduncle 2.60 x as long as broad, with rami 1.28 x as long as peduncle

Pleonite 2: posterodorsal area with 3 small equal teeth; Ep2 without ventral spines or setae, with well-developed sharp posteroventral tooth, with posterior border barely convex.

Pleonite 3: posterodorsal area without tooth, but with a shallow notch on each side; Ep3 without ventral spines or setae, with normally developed posteroventral tooth followed upwards by a notch, with posterior border distinctly convex in its lower half.

Urosomite 1 with 1 small posterodorsal tooth directed backwards; ventrofacial border without spines; peduncle of U1 without ventrofacial spines, with 6 dorsolateral spines: 4 normally developed regularly spaced spines followed by a larger space + a pair of spines consisting of a small one pointing upwards and a long distal spine pointing backwards, with 5 well-developed and regularly spaced dorsomedial spines; outer ramus with 2 small stout outer spine and no medial spines, with 4 spines on tip (which is blunt); inner ramus with 1 small spine on outer border and with 3 rather long spines on medial border, with 4 spines on tip (which is emarginate).

Urosomite 2 with 1 small posterodorsal tooth directed backwards; peduncle of U2 with 1 distal dorsolateral spine and 1 distal dorsomedial spine; outer ramus with 2 normally developed outer spines and no medial spines, with 4 spines on tip (which is emarginate); inner ramus with 1 spine on outer border and with 3 well-developed stout spines on medial border, with 4 spines on tip (which is emarginate).

Urosomite 3 without posterolateral tooth on each side but with posterolateral lobes bluntly angular, with a pair of medium-sized posterodorsal spines; U3 distinctly shorter than U1 and a bit longer than U2; outer ramus and inner ramus of U3 subequal, outer ramus 2-articulated with article one with 2 groups of 1-2 well-developed stout spines on outer side and 1 distal spine on medial side, article two 0.64 x as long as article one; inner ramus 1.45 x as long as peduncle, with 1 spine on outer border, with 2 spines on medial border, with 1 spine on ventral carina.

Telson: cleft to 0.78 of its length; medial tooth of each lobe distinctly overreaching of outer tooth (1.40 x as long as outer tooth); each lobe with 3 spines of size increasing in a medial direction; longest interdental spine overreaching outer tooth by 0.82 of its length, 0.45 x as long as telson; outer apical teeth of telson with 1 very short setule.

COLOUR PATTERN: Eye black. Dark brown pigmentation forming a regular colour pattern on a colourless background. Article one of A1 dark. Article five of A2 dark. Head colourless except for dark patch on the posteroventral corner. Segments of pereion totally dark, except for the last one, which presents dark pigmentation only on its anterior 0.3. Coxae 1-6 dark; coxa 7 colourless. Mxp, Gn1, Gn2 dark. Merus and carpus of P3-P4 dark.

Basis of P5 dark, except posterodistal 0.2. Basis of P6 dark on its anteroproximal 0.2. P7 and rest of P5-P6 colourless. Pleonite 2 with dark pigmentation on dorsal area. Pleonite 3 with a lateral and a ventrolateral dark patches. Urosomite 1 with a lateral and a ventrolateral dark patches. U1 and U2: tip of peduncle and entire rami dark. U3: peduncle and proximal part of rami dark.

LENGTH: About 6 mm.

DISTRIBUTION: Guernsey (NORMAN, 1889), France: west part of the coasts of the English Channel and Bay of Biscay (CHEVREUX, 1900; CHEVREUX & FAGE, 1925; TOULMOND & TRUCHOT, 1964; DE MONTAUDOUIN & SAURIAU, 2000); Spanish coasts of the Bay of Biscay (MARTÍNEZ & ADARAGGA, 2001); West Africa (CHEVREUX, 1925; REID, 1951; LE LŒUFF & INTÈS, 1993). Intertidal (CHEVREUX & FAGE, 1925; present material) to 50 m (REID, 1951). The material examined was collected by the author on a bottom consisting of a mixture of gravel and small stones covered by calcareous algae, coarse sand and mud, close to beds of *Zostera marina* L. CHEVREUX (1900) found the species on a bottom of 'nullipores', i.e. presumably on maerl.

SYSTEMATIC REMARKS: *Idunella picta* is very different from the type species of the genus *Idunella* (*I. aeqvicornis*) and its generic affiliation will undoubtedly have to be closely scrutinised at some time in the future. It is more similar to the type species of the genus *Listriella* (*L. goleta* J.L. BARNARD, 1959) and its related species: *L. albina* J.L. BARNARD, 1959, *L. diffusa* J.L. BARNARD, 1959, *L. eriopisa* J.L. BARNARD, 1959, and *L. melanica* J.L. BARNARD, 1959. *Listriella* is here provisionally placed in the synonymy of *Idunella*, but this genus will probably have to be reestablished (and redefined) when the subfamily Idunellinae will be revised and its internal phylogeny better understood. At that time, *L. picta* will possibly have to be retransferred to the genus *Listriella*, but not before. Important similarities but also differences are observed between *I. picta* and *I. goleta* (in assuming that J.L. BARNARD's (1959) drawings are exact):

Shared characters: strong pigmentation; A1 < A2; lobes of lower lip with medial tooth; article one of palp of Md long or fairly long; article three of Md with posterior D3- and distal E3-setae only, without anterior B3-setae; outer plate of Mxp with inner margin straight and smooth (not crenulate or irregular); aciculae of inner margin of outer plate of Mxp truly marginal (not arising facialo-medially); article two of palp of Mxp without setae on distolateral corner; Gn1 < Gn2; carpus of Gn2 short, with only one posterior group of setae, without anterior setae; outer border of palm of Gn2 with long and stout setae in males; posterior border of propodus of P3-P4 with short setae not disposed in tufts; ventral margin of coxa 4 smooth and without setae or setules; Ep1-Ep3 without ventrofacial spines; urosomites 1-2 without posterodorsal spinules; dorsomedial border of peduncle of U1 with a few (6 to 7) spines, which are long; outer ramus of U3 bi-articulated; rami of U3 without setae.

Differences: article two of palp of Md weakly setose in *I. picta*, strongly setose in *I. goleta*; dactylus of Gn1-Gn2 strongly toothed in *I. picta*, absolutely toothless in *I. goleta*; pleonites 1-2 posterodorsally toothed in *I. picta*, toothless in *I. goleta*; urosomites 1-2 with posterodorsal tooth in *I. picta*, without tooth in *L. goleta*; dorsomedial border of peduncle of U2 with distal spine only in *I. picta*, with 12 spines in *I. goleta*; inner ramus of U3 with ventral spine in *I. picta*, without ventral spine in *L. goleta*; rami of U3 equal in *I. picta*, inner ramus slightly longer than outer one in *I. goleta*.

Genus *Sextonia* CHEVREUX, 1920

Sextonia CHEVREUX, 1920a: 76 (type species: *Sextonia longirostris* CHEVREUX, 1920; gender feminine)

ETYMOLOGY: genus dedicated to Mrs Elsie SEXTON (née WING), 1868-1959, English amphipodologist.

DESCRIPTION: A2: 2 x as long as A1; peduncle of A2 well furnished with spines. Md: molar process well developed, fully triturative, with flat grinding surface and a single posterior gnathobasic seta; articulation with carapace in posterior position; anterolateral extremity of Md pointed; articulation between articles 1 and 2 of palp forming a right angle (geniculate); all articles of palp well furnished with setae; article three of palp curved, with row of short D3-setae on posterior border, with long E3-setae on tip, with long isolate B3-setae near anterior border. Lobes of lower lip without medial tooth. Mx1: article two of palp without setae on anterior margin; outer plate with 7 spines; inner plate both with short and long setae. Mxp: article two of palp with outer distal long and strong setae; outer plate with medial margin crenulate, with lateral setae, apical spines, medioventral setae but without medial spines. Gn1: carpus very short, with minute narrow posterior process, propodus much longer than in Gn2, with several group of setae on the part of posterior border proximal to palm; palm with 4 rows of articulated structures: outer side

with sparse setae (isolate or forming loose groups) and row of narrow hooked spines; medial side with row of bigger and stouter hooked spines and a row of spinulose long and stout setae (most of these spinulose setae have 3 anterior and 1 posterior strong spinules); dactylus with 1 proximal anterior seta and no medial setae. Gn2: carpus long (as long as propodus), strongly setose both on anterior and posterior margin; anteromedial border of propodus strongly setose; part of posterior border of propodus proximal to palm strongly setose; palm with 4 rows of articulated structures: outer side with sparse group of setae and row of narrow hooked spines; medial side with row of stout spines and row of spinulose stout setae (these spinulose setae have 1 to 3 strong spinules on anterior border); dactylus less than 0.5 x as long as propodus. P3-P4 sparsely setose, without spines; dactylus with vestigial unguis and unguial hood associated with 2 tiny setules. P5-P7 well furnished with spines. Pleonites 1-3 with ventrofacial spines. U1: peduncle with ventrofacial spines, with several spines on dorsolateral and dorsomedial borders, with distal spine of dorsolateral border paired with a subdistal shorter spine; inner ramus of U1 with proximal small ventral seta; tip of rami blunt and with several distal spines. U2: tip of rami blunt and with several distal spines. U3: outer ramus 2-articulated and with spines on both sides; inner ramus with spines on both sides and with long proximal spine arising from ventral surface. Telson: deeply cleft; medial tooth of each lobe much longer than lateral tooth; 2 or 3 spines in the notch formed by the medial and the lateral lobe.

REMARK: The genus *Sextonia* includes a single known species, *S. longirostris* CHEVREUX, 1920, from the Northeastern Atlantic.

Sextonia longirostris CHEVREUX, 1920
(Figs 13-19)

Sextonia longirostris CHEVREUX, 1920a: 77, fig. 2-3; CHEVREUX & Fage, 1925: 159, fig. 152, 160, 161; KARAMAN, 1980: 431
Idunella longirostris; J.L. BARNARD, 1959: 14; IMBACH, 1967: 80, 81 (discussion); MARTÍNEZ *et al.*, 2005: 55, fig. 25 (photograph in colour)
Not *Idunella longirostris* BOUSFIELD, 1973: 71

MATERIAL: **France**, western part of English Channel, Le Dossen, 48°42'10"N 004°03'59"W, intertidal, fine non-muddy sand, sieving sediment, 10-14.iii.2009: 6 specimens (1 ovigerous female fully dissected and mounted on 14 slides in Euparal and 1 male partly dissected and mounted on 4 slides), coll. C. D'UDEKEM D'ACOZ, RBINS, Inv 67.743.

Description: Head: eye medium-sized, elliptic, with very distinct ommatidiae, very dark in alcohol, but white in living specimens (labile white pigment hiding stable black pigment); rostrum long (for Liljeborgiidae), narrow, with tip not sharp; epistome pointed, protruding.

A1: article one of peduncle 1.77 x as long as wide; article three 0.36 x as long as article two; major flagellum with 13 articles; accessory flagellum with 5 articles; ratio length of accessory flagellum / length of major flagellum: 0.30; ratio length of major flagellum / length of article one of peduncle: 1.52.

A2: considerably longer than A1 (about 1.8 x as long as A1); article 3 with antrodistal and posterodistal spines; article four of peduncle 3.14 x as long as wide, with anterior and posterior spines; article five of peduncle 3.55 x as long as wide, with anterior spines (associated with setae) and posterior spines; flagellum slightly shorter than peduncle, with 13 articles.

Upper lip notched (notch asymmetrical).

Lower lip: distal part of lobes without tooth.

Md: distolateral corner forming a tooth; hinge process on proximolateral corner; left lacinia mobilis with 5 teeth of which the 3 median ones are triangular and narrow and the external ones are broad and blunt; right lacinia mobilis with anterior margin distinctly denticulate and with one large medial triangular tooth overlapping the blade of the lacinia; largest tooth of incisor process of right Md of normal size and blunt; raker spines of incisor process smooth; molar process large, fully triturative, with only 1 posterior molar seta; distal half of article one of palp with numerous lateral setae, with posterior border slightly concave, forming a geniculate articulation with article two, slightly shorter than article two (ratio length article one / article two = 0.74); article one 3.23 x as long as wide; article two with sparse A2- and B2-setae on most of its length (more abundant near tip), 5.14 x as long as wide; article three slightly curved, 4.69 x as long as wide, 0.69 x as long as article two, with posterior row of D3-setae (which are not of increasing length towards tip), with group of distal E3-setae, with 3 isolated anterior B3-setae.

Mx1: article two of palp without setae on anterior margin, with 7 slender blunt spines on ventral and apical margin, and 4 well-developed facial setae; outer plate with 7 spines; inner plate with 4 apical setae (2 short and 2 long ones).

Mx2: setae in normal number and rather slender; outer plate with 4 well-developed setae on anterior margin; inner plate without facial setae.

Mxp: article one of palp without distal outer setae, article two without non-distal setae on outer margin and with 3 long distolateral setae; article three with 3 loose transverse groups of setae (of normal stoutness) on dorsal border and with setae along the largest part of the ventral border; article four (dactylus) slender, distinctly curved, with long unguis, 0.71 x as long as article three; outer plate with medial and anteromedial border distinctly crenulate, with 6 to 7 well-developed slender and well-spaced strong setae on mediofacial border, 3 anterior spines, and 2 to 3 strong setae on lateral border; inner plate with 3 to 4 long stout anterolateral setae, 4 to 5 very short and stout anterior spines, and 3 dorsomedial setae.

Gn1: coxa broad and anteriorly rounded (broader and anteriorly more elongate in male than in female), with nearly straight posterior border, without anterior notch, with posterior tooth; basis with longitudinal row of setae on anteromedial, anterolateral and posterior borders; merus with 3 groups of 1 to 2 setae, with distal tooth; carpus with tiny posterodistal process, without small posterodistal notch, with 1 posterodistal tuft of setae; propodus with anterior and posterior border slightly convex, not diverging towards tip, 2.41 (male) or 2.46 (female) x as long as wide; about 6 transverse groups of posteromedial setae proximal to palm; palm defined by a cluster of 4 (male) to 6 (female) posterior and posteromedial spines associated with a few setae; most distal posteromedial spine arising from proximal 0.38 (female) of propodus; some of these spines are rather long; border of propodus without denticulate crest at the level of distal spine; palm border weakly convex (male) or straight (female), with isolated tiny blunt teeth in both sexes, without proximal and distal tooth; palm of female with broad hooked spines on lateral border (24 lateral spines forming loose groups + 8 groups of 1 to 5 lateral setae in male; 31 regularly spaced lateral spines + 5 groups of 1 to 3 setae in female), with another row of broader and longer hooked spines on medial border (21 spines in female); with a row of backwardly-curved setae on medial border, each of these setae presenting several anterior spinules (usually 3 to 4) and usually 1 posterior spinule, without proximal strong seta, with distal non-spinulose seta; dactylus toothless, without medial setae.

Gn2: coxa elliptic, narrow, with lateral borders converging downwards, without anteroventral notch or tooth, with posterior tooth, posteromedial surface of coxa without row of setae, but ventromedial surface with short slender setae; basis with well-developed anterolateral, anteromedial and posteromedial row of setae, with distal part of anterolateral border not forming a short process; ischium with several anteromedial and posterior long setae; merus with 5 to 6 isolate or loosely paired setae, and with 1 acute posterodistal tooth; carpus very long, without posterodistal process, with distal expanded part longer than proximal narrow part (i.e. part connecting with merus), without anterodistal shallow notch, with row of long setae on anteromedial and distomedial borders, with 7 tufts of setae on posterior border; propodus with anterior border distinctly convex, with posterior border nearly straight (the two borders are not divergent), 1.78 (male) or 1.80 (female) x as long as wide, with 10 well-developed anteromedial groups of setae, with 6 transverse groups of posterior and posteromedial setae; palm defined by a single anterior spine (a second spine is present well behind the palm, on the medial surface); anterior spine emerging on proximal 0.62 (female) of propodus; border of propodus without denticulate crest at the level of spine; palm border forming a curve and without teeth or protrusions; palm with broad cylindrical spines (19 lateral spines + 2 longitudinal rows of 3 to 4 stout and long setae), with row of spines on medial border; with a row of backwardly-curved setae on medial border, each of these setae presenting usually 2 anterior spinules, without proximal very strong, nearly spiniform seta with setules on both sides, with distal non-spinulose seta; dactylus without teeth, without medial setae, 0.54 (male) or 0.50 (female) x as long as propodus.

P3: coxa elliptic, narrow, with lateral borders almost parallel, without anteroventral notch or tooth, with posterior tooth, posteromedial surface of coxa with 3 setae forming a row; leg rather slender; merus 1.33 x as long as carpus and 0.93 x as long as propodus; merus with 3 groups of 1 to 2 anterior medium-sized setae and 3 isolated short posterior setae; carpus with 1 short anterodistal and 4 groups of 1 or 2 short posterior setae; propodus with 4 groups of 1 to 2 short slender posterior setae (length of longest propodal setae about 0.42 x as long as width of propodus); anterior border of propodus with 1 very short seta on 0.7 and 2 very short distal setae; dactylus very long and fairly slender, with anterior and posterior borders distinctly curved, 1.17 x as long as carpus and 0.81 x as long as propodus; dactylus with anterior spatulate process hooding reduced unguis and 2 microscopical setules at the basis of the unguis.

P4: coxa broad (1.07 x as long as wide), with anterior and posterior border straight and slightly diverging downwards, with ventral border scarcely convex, with 5 normally developed serrations on posterior border and with inconspicuous trace of very shallow anterior notch; leg slender; merus 1.32 x as long as carpus and 0.97 x as long as propodus; merus with 3 groups of 1

to 2 short anterior setae and 4 short isolated posterior setae; carpus with 1 short anterodistal and 4 groups of 1 or 2 short posterior setae; propodus with 5 isolated short slender posterior setae (length of longest propodal setae about 0.36 x as long as width of propodus); anterior border of propodus with 1 very short seta on 0.7 and 2 very short distal setae; dactylus very long and fairly slender, with anterior and posterior borders distinctly curved, with spoon-like process and 2 microscopical setules on tip, 1.17 x as long as carpus and 0.83 x as long as propodus; dactylus with anterior spatulate process hooding reduced unguis and 2 microscopical setules at the basis of the unguis.

P5: coxa without posterior tooth, with 1 ventral seta and 1 posterior minute setule on posterior lobe; basis broad (1.31 x as long as wide), anteriorly strongly and regularly convex, posteriorly weakly convex; anterior border with 9 groups of 1 to 3 spines, posterior border with 11 normally developed serrations, distal border rounded, produced into a low lobe; ischium with 1 long and 2 short spines on anterodistal corner; merus very stout, 2.87 x as long as broad, with 7 anterior groups of 2 to 4 spines (including 1 long and 1 to 3 short spines), with 4 posterior groups of 1 to 3 well-developed slender spines; carpus with 4 anterior groups of 2 to 4 well-developed slender spines (not intermixed with setae) and 1 posterodistal group of spines; carpus 0.67 x as long as merus and 0.97 x as long as propodus; carpus + propodus 1.32 x as long as merus; propodus with 5 groups of 1 to 3 medium-sized spines on anterior border, 3 isolated long setae on medial surface and well-developed propodal apical tuft of setae; dactylus weakly curved, slender, with protrusion (with 2 tiny setules) just before minute terminal unguis, 0.43 x as long as propodus.

P6: coxa with posterior tooth, with 4 anterior setae on anterior lobe and 3 ventral setae on posterior lobe; basis broad (1.41 x as long as wide), anteriorly strongly and regularly convex, posteriorly nearly straight; anterior border with 9 isolated spines or distally group of 3 spines (of which one is long), posterior border with 15 serrations, distal border rounded, produced into a low lobe; ischium with 1 long and 2 short spines on anterodistal corner; merus with 6 anterior groups of slender medium-sized spines, with 5 groups of 1 (4 proximal groups) to 4 (distal group) of well-developed slender posterior spines; carpus with 4 anterior groups of 1 to 5 well-developed spines and posterodistal group of 3 well-developed spines; carpus 0.80 x as long as merus and 0.96 x as long as propodus; propodus with 5 groups of 1 to 3 small anterior spines (not associated with setae), 5 posteromedial (including distal one) groups of well-developed setae, of which none are associated with a spine; dactylus scarcely curved, rather slender, with anterodistal tiny setule, 0.30 x as long as propodus.

P7: coxa with 5 anterior setae, leg stout; basis broad (1.36 x as long as wide), anteriorly strongly and regularly convex, posteriorly straight; anterior border with 9 spines (or sometimes groups of 2 o 3 spines), posterior border with 16 serrations, distal border rounded, produced into a low lobe; ischium with 1 long and 2 short spines on anterodistal corner; merus with 5 anterior groups of slender medium-sized spines, with 6 groups of 1 to 5 short to medium-sized posterior spines; merus 2.86 x as long as wide and 0.94 x as long as basis; carpus with 3 anterior groups of 3 to 5 well-developed spines and 4 posterior groups of 1 to 5 well-developed spines; carpus 1.16 x as long as merus and 0.94 x as long as propodus; propodus of P7 1.43 x as long as propodus of P6; propodus with 5 anterior pairs of small slender spines, and 5 groups of 2 to 4 medium-sized posteromedial setae (of which some are associated with a spine); dactylus straight, short, rather stout, not notched, 0.22 x as long as propodus.

Pleonite 1: posterodorsal area without tooth; Ep1 with normally developed posteroventral tooth, with posterior border distinctly convex; with 1 ventrofacial seta; pleopod 1 with peduncle 2.78 x as long as broad, with rami 1.56 x as long as peduncle.

Pleonite 2: posterodorsal area without tooth; Ep2 with 7 well-developed ventrofacial setae, with well-developed posteroventral tooth, with posterior border distinctly convex.

Pleonite 3: posterodorsal area without tooth, without shallow notch on each side; Ep3 with 6 medium-sized ventrofacial setae, with strong and sharp posteroventral tooth followed upwards by a notch, with posterior border strongly convex in its lower part.

Urosomite 1 with 3 posterodorsal teeth (median tooth the longest); ventrofacial border without spines; peduncle of U1 with 3 ventrofacial spines, with 6 dorsolateral spines: 4 normally developed regularly spaced spines followed by a pair of spines consisting of a small one pointing upwards and a long distal spine pointing backwards, with 9 well-developed and regularly spaced dorsomedial spines of which the distal one is slightly longer than others; outer ramus with 4 medium-sized outer and 2 well-developed medial spines, with 4 spines on tip; inner ramus with 2 small spines on outer border, with 4 long stout spines on medial border, with small proximal ventral seta, with 3 spines on tip.

Urosomite 2 with 3 posterodorsal teeth (median tooth the longest); distal half of peduncle of U2 with 3 long dorsolateral spines and 1 distal dorsomedial spine;

outer ramus with 4 well-developed outer spines and no medial spines, with 4 spines on tip; inner ramus with 2 medium-sized spines on outer border and with 3 long spines on medial border, with 4 spines on tip.

Urosomite 3 without posterolateral tooth on each side, with a pair of well-developed posterodorsal spines; U3 sexually dimorphic, distinctly shorter than U1, but longer than U2; outer ramus and inner ramus of U3 subequal, outer ramus 2-segmented with article one with 4 groups of 2 to 3 well-developed stout spines on outer side and with 4 to 5 spines on medial side, article two 0.21 (male) or 0.23 (female) x as long as article one; inner ramus with border parallel on most of their length but terminated in a point in male, with borders regularly converging towards tip in female, 1.52 (male) or 1.50 (female) x as long as peduncle, with 5 groups of 1 spine (4 proximal groups) or 6 spines (distal group) on outer border, with large ventral spine, with 2 subdistal groups of 1 to 2 spines on medial border.

Telson: cleft to 0.74 of its length; medial tooth of each lobe considerably overreaching of outer tooth (3.20 x as long as outer tooth); each lobe with 1 tiny setule, with 2 spines of which the medial one is slightly longer than the outer one; longest interdental spine overreaching outer tooth by 0.80 of its length, 0.22 x as long as telson.

Colour pattern (after photographs of a male made by the author): Colour pattern made of brown, grey, yellowish grey, whitish and white, the different colours intergrading without sharp contrasts. Head whitish-grayish, with white eyes [when preserved in alcohol, the white pigment disappears and the eyes become black]. Thoracic segments, except last one, grayish (light brown near the posterior and ventral border, dorsally with a diffuse white patch); last thoracic segment dark brown, posteriorly with a narrow diffuse grayish transversal stripe and posterior border light brown. Segments of pleon whitish with pleonites becoming light brown near their posterior border; first pleonite whitish-grayish with posterior border light brown, dorsally with large diffuse white patch, broadening posteriorly; second pleonite whitish-grayish with posterior border light brown, dorsally with small central dark brown spot, posteriorly followed by diffuse white patch; pleonite 3 whitish-grayish with posteroventral and ventral borders light brown, dorsally with medium-sized anterior elongate dark brown spot followed by medium-sized posterior elongate diffuse white spot. Urosome with whitish and white hues; the first urosomite dorsally with small very diffuse pale brown marks. Telson white. A1 with peduncle brown and flagella colourless. A2 with article three brown, with article four brown on its proximal 0.7 and gradually becoming white towards tip; article five white; flagellum colourless. Coxae with central part whitish, with marginal and ventral part brown. Gn1 whitish. Gn2 with the last 4 articles brown. P3-P4 with basis, ischium and merus brown, with carpus, propodus and dactylus whitish. P5 with basis, ischium, merus and carpus brown, with propodus and dactylus whitish. P6 with basis brown, ischium white, merus brown on the middle and proximally and distally white, with carpus, propodus and dactylus white. P7 with basis whitish and marginally brown, ischium whitish, merus brown on the middle and whitish on both extremities; carpus and propodus whitish with very faint brownish hue on the middle; dactylus white. U1-3 entirely white.

Total length: The largest specimen examined during this study, which is a non-terminal male (it was preparing a moult), was 10 mm long. According to Chevreux & Fage (1925), males can reach up to 14 mm.

Distribution and ecology: NW France: Saint-Lunaire, Portrieux, Morgat (Chevreux, 1920; Chevreux & Fage, 1925), Le Dossen (Toulmond, 1964; Toulmond & Truchot, 1964; present material), Bay of Douarnenez (Deniel, 1975; Blanchet *et al.*, 2004); North Spain: Ría de Ares-Betanzos (Sanchez-Mata *et al.*, 1993); San Sebastián (Martínez & Adarraga, 2001), between Getaria and Zarautz (Martínez *et al.*, 2005, 2007b), near Laga and San Juan de Gastelugache (Martínez *et al.*, 2006), continental shelf of Guipúzcoa and Od Bizkaia (Martínez *et al.*, 2007a), Playa América (Galicia) (Moreia *et al.*, 2008), Ría de Aldán (Lourido *et al.*, 2008); Portugal (Marques & Bellan-Santini, 1993; Cunha *et al.*, 1997); Atlantic coast of Morocco: region of Sidi Boulbra (Fadlaoui & Rétière, 1995). Bousfield (1973: 71) mentions *Sextonia longirostris* (as *Idunella longirostris*) in his key to American species of *Idunella*, but gives no further information on the species. He was probably referring to an apparently undescribed species of *Idunella*, of which he kindly sent me drawings, and which shares some characters with *Sextonia*.

Fine sand (Toulmond & Truchot, 1964; Deniel, 1975; Martínez & Adarraga, 2001; present material). Toulmond (1964) indicates that the species prefers *Bathyporeia* sands, i.e. well-sorted sands with a unimodal curve and a maximum between 90 and 200µ. On the sandy shore of Le Dossen, at the same level as *S. longirostris*, the most common crustaceans found by the author were the amphipods *Bathyporeia elegans* Watkin, 1938, *B. pelagica* (Bate, 1856), *Hippomedon denticulatus* (Bate, 1857), *Urothoe pulchella* (Costa,

1853) and especially the cumacean *Eocuma dolfussi* CALMAN, 1907. Intertidal (CHEVREUX, 1920; CHEVREUX & FAGE, 1925; TOULMOND & TRUCHOT, 1964; present material) to 34 m (MARTÍNEZ *et al.*, 2005). CHEVREUX & FAGE (1925) considered the species as very rare, and the sampling carried out by the present author confirms that it is not common in north Brittany, where three days of intensive sand sieving on the shore yielded only 6 specimens.

REMARKS: *Sextonia longirostris* exhibits several characters, which are unique for the Liljeborgiidae, most of them being probably plesiomorphic: molar part of mandible fully triturative and with single setulose posterior gnathobasic seta; article three of mandibular palp with several setae on anterior border; dactyli of pereiopods 3-4 with vestigial terminal unguis associated with 2 tiny setules and ungial hood; urosomites 1 and 2 posterodorsally tridentate; peduncle of uropod 1 with several ventrofacial spines, a proximal ventral seta on the inner ramus of uropod 1. A reduced, non-triturative molar on the mandible with a cluster of strong setae is observed in all other Idunellinae and in all Liljeborgiinae (a presumably advanced condition). At the same time, it is difficult to derive the Liljeborgiinae from *Sextonia*, because the first ones have medial setae on the dactylus of gnathopod 2 (a presumably plesiomorphic character state), whereas *Sextonia* has no such setae (presumably an advanced condition). Possibly, ancestral Liljeborgiidae had a triturative molar associated with several strong setae, a condition which exists in representatives of the Dexaminidae, Hyperiopsidae and some Oedicerotidae (see section on the affinities of the Liljeborgiidae). In the Liljeborgiinae and in advanced Idunellinae, the triturative part would have independently disappeared, whereas in *Sextonia*, it would have been the strong setae, which would have regressed.
The occurrence of a spoon-like process 'hooding' a reduced unguis on the dactylus of pereiopods is a condition rarely recorded in amphipods except for Oedicerotidae, where it is of common occurrence. As an example, a figure of this structure in *Oediceroides lahilhei* CHEVREUX, 1911 is given on figure 20.

Subfamily Liljeborgiinae STEBBING, 1899.

Type genus: *Liljeborgia* BATE, 1862; type species of the type genus: *Gammarus pallidus* BATE, 1857.

DESCRIPTION: Articulation between articles 1 and 2 of Md palp rectilinear. Article three of Md palp not flattened, without D3-setae in a comb-like disposition on posterior border. Hinge articulating Md with carapace in lateral position. Outer distal part of Md not pointed. Molar process always reduced, non triturative, and bearing strong setae. Article two of the palp of Mx1 with 1 or several anterior setae. Outer plate of Mx1 with 7 to 10 spines. Inner plate of Mx1 with 1 (more rarely several) long setae [accessory short setae only present in teratological specimens]. Inner marginal border of the outer plate of the maxilliped with marginal spines and margino-facial setae. Coxa 1 usually with anterior tooth or notch. Gn2 dominant (except in male *Liljeborgia prionota* D'UDEKEM D'ACOZ, 2008, in which the reverse is true). Gn1 and Gn2 always fairly similar in females and often also in males. Carpus of Gn1-Gn2 with long posterior process. Palm of Gn1 without outer setae, with a long outer row of hooked spines, never with a row of medial hooked spines, and with medial spinose medial setae apparently forming two loose rows. Palm of Gn2 with outer setae (sometimes just a few, sometimes many; usually more numerous and longer in males than in females), with a long outer row of hooked spines, never with a medial row of hooked spines, and with medial spinose setae apparently forming two loose rows. Dactylus of Gn2 with some strong setae on medial surface (in addition to proximal anterior short seta). Margino-medial setae of palm of Gn1-Gn2 almost always with 2 anterior spinules and no posterior spinules. Dactylus of pereiopods 3 and 4 without unguis, spinules or setules. Posterodistal border of urosomites 1 and 2 with 0-1 teeth, without spinules. Urosomite 1 with or without ventrofacial spines. Peduncle of U1 without ventrofacial spines. Tip of dorsolateral border of the peduncle of U1 with a long spine pointing backwards not paired with a short spine pointing upwards. Rami of U1-2 tapering distally, with tip pointed and narrow, without spines or with trace of a spine fused with tip. Outer ramus of uropod 3 entire. Outer ramus of U3 almost always with spines on outer margin only. Ventral proximal spine never present on inner ramus of U3. Rami of U3 with spines only, never with setae.

DISTRIBUTION: Cosmopolitan (speciose at all latitudes), 0 to 6156 m depth.

REMARKS: For the time being, the Liljeborgiinae are considered as including only one genus, *Liljeborgia* BATE, 1862, but subgeneric divisions are recognized. The subdivisions of the subfamily will have to be reconsidered when the *Liljeborgia* species of group 3 will be better known.

Genus *Liljeborgia* BATE, 1862

Liljeborgia BATE, 1862: 118 (type species: *Gammarus pallidus* BATE, 1857; gender feminine)
Not *Liljeborgia* CLAUS, 1866: 22 (Copepoda, type species: *Liljeborgia linearis* CLAUS, 1866: 22)

DESCRIPTION: As for subfamily Liljeborgiinae.

SUBDIVISIONS OF THE GENUS *LILJEBORGIA*: When studying Antarctic and sub-Antarctic *Liljeborgia* species, D'UDEKEM D'ACOZ (2008) observed that all the species of the Southern Ocean and most species from other seas could be assigned to a group 1 and a group 2, and D'UDEKEM D'ACOZ (in press) indicated that a few unusual *Liljeborgia* species would form a group 3.

Liljeborgia species of groups 1 and 2 have only one distal spine on the lobes of the telson (there are at least two spines in the group 3) and include the vast majority of known *Liljeborgia* species. Since they exhibit clear-cut constant differences, it is proposed to consider them as distinct subgenera. The species of group 1 are put in the subgenus *Liljeborgia* BATE, 1862 (type species: *Gammarus pallidus* BATE, 1857, re-described in the present paper) and the species of group 2 in the subgenus *Lilljeborgiella* SCHELLENBERG, 1931 (type species: *Lilljeborgiella longicornis* SCHELLENBERG, 1931; see SCHELLENBERG, 1931 and D'UDEKEM D'ACOZ, 2008 & 2009 for description). Note that the second 'L' is doubled in *Lilljeborgiella* but not in *Liljeborgia*. See D'UDEKEM D'ACOZ (2008: 49) for an explanation of this unfortunate difference of spelling. The following differences have been detected:

The outer plate of the first maxilla has 7 to 8 (most commonly 7) spines in *Liljeborgia* (except for '*L. akaroica* sensu LEDOYER, 1986' which has 9 spines); 9 to 10 (most commonly 10) spines in *Lilljeborgiella*.

There are no anterior outer setae on the dorsal side of article one of the palp of the maxilliped in *Liljeborgia*, whilst such setae are present in *Lilljeborgiella*.

The setae of the anterior border of article three of the palp of the maxilliped are never forming pairs or groups in *Liljeborgia*, whilst some or all the setae of the anterior border of article three of the palp of the maxilliped are forming pairs or transverse groups in *Lilljeborgiella*.

When present, the ventral tooth of coxa 4 is situated near anterior 0.6 or 0.7 in *Liljeborgia*, whereas it is close to the anteroventral angle in *Lilljeborgiella*.

The posterior border of the propodus of pereiopods 3 and 4 has setules or small spines, never long setae in *Liljeborgia*, whereas the ornamentation of the posterior border of the propodus of the pereiopods 3 and 4 most commonly consists of long or rather long (stout or slender) setae in *Lilljeborgiella*.

The posterolateral lobe of urosomite 3 is always rounded in *Liljeborgia*, rounded or with a tooth in *Lilljeborgiella*.

On urosomite 3, a posterodorsal pair of spines is present or absent in *Liljeborgia*, always present in *Lilljeborgiella*.

There is only one (distal) spine on the dorsomedial border of the peduncle of uropod 1 (except very rare teratological cases) in *Liljeborgia*, whilst there are several spines on the dorsomedial border of the peduncle of the uropod 1 in *Lilljeborgiella*.

The spines of the rami of uropod 3 never form transverse pairs or triplets in *Liljeborgia*, whilst this is sometimes the case in *Lilljeborgiella*.

Both groups are cosmopolitan, but *Liljeborgia* is perhaps more diverse in warm waters and *Liljeborgiella* in cold (shallow or deep) waters.

Liljeborgia has been recorded between 0 and 3700 m, *Liljeborgiella* between 4 and 6156 m.

Group 3, which has not been available for study, is possibly heterogeneous. It includes a few species from the Northwestern Pacific, *L. serrata* NAGATA, 1965, *L. hwanghaensis* KIM & KIM, 1990 and *L. sinica* REN, 1992, which have two or more spines in the distal notch of the telson instead of one (NAGATA, 1965; KIM & KIM, 1990; REN, 1992). With the data at hand, it is impossible to establish the subgeneric position of these species. The poorly known *L. epistomata* K.H. BARNARD, 1932 from South Africa is also integrated into the catch-all group 3 (see K.H. BARNARD, 1932, 1940, 1955 for descriptive data). A separate genus, *Isipingus* J.L. BARNARD & KARAMAN, 1987, was proposed for *L. epistomata* by J.L. BARNARD & KARAMAN (1987: 864), on the basis of two, presumably autapomorphic, characters: very pointed epistome and enlarged coxa 1, and one presumably plesiomorphic character, the multispinose lobes of the telson (as in the Asian *Liljeborgia* of the group 3). Since the available descriptions of the species are very fragmentary, its precise systematic position remains unresolved. However, there are so far no objective reasons to remove it from the genus *Liljeborgia*, as currently defined. For practical reasons, *Isipingus* is here provisionally considered as a subgenus of *Liljeborgia*. If *Isipingus* is revalidated as a full genus in the future, after a careful re-description, the correct name of its type species would be *Isipingus epistomatus* and not *Isipingus epistomata*, because *Isipingus* is masculine (J.L. Barnard & Karaman, 1987: 864) and *epistomatus* is clearly an adjective.

The subgeneric/group affiliation of the known

Liljeborgia species runs as follows.

Group 1 (= subgenus *Liljeborgia*): *L. aequabilis* STEBBING, 1888; *L. aequabilis* sensu HURLEY, 1954 (= undescribed species according to VADER, 1995), *L. akaroica* SENSU LEDOYER, 1986 (presumably an undescribed species); *L. bousfieldi* MCKINNEY, 1979; *L. bousfieldi* sensu LEDOYER, 1986 (presumably an undescribed species; clearly different from the true *L. bousfieldi*); *L. brevicornis* BRUZELIUS, 1859; *L. capensis* K.H. BARNARD, 1932; *L. chevreuxi* SCHELLENBERG, 1931; *L. cnephatis* D'UDEKEM D'ACOZ, 2008; *L. cryptothrix* D'UDEKEM D'ACOZ, 2008; *L. dellavallei* STEBBING, 1906; *L. enigmatica* LEDOYER, 1986; *L. geminata* J.L. BARNARD, 1969; *L. georgiensis* K.H. BARNARD, 1932; *L. gloriosae* LEDOYER, 1986; *L. heeia* J.L. BARNARD, 1970; *L. inermis* CHEVREUX, 1920; *L. japonica* NAGATA, 1965; *L. joergpeteri* COLEMAN, 2009; *L. kerguelensis* BELLAN-SANTINI & LEDOYER, 1974; *L. kinahani* (BATE, 1862); *L. laniloa* J.L. BARNARD, 1970; *L. macronyx* G.O. SARS, 1894; *L. mixta* SCHELLENBERG, 1925; *L. octodentata* SCHELLENBERG, 1931 (= *L. falklandica* K.H. BARNARD, 1932); *L. pallida* (BATE, 1857); *L. petrae* LYONS & MYERS, 1991; *L. polonius* HUGHES & LOWRY, 2006; *L. proxima* CHEVREUX, 1907; *L. psaltrica* KRAPP-SCHICKEL, 1975; *L. pseudomacronyx* BELLAN-SANTINI & LEDOYER, 1986; *L. serratoides* TZVETKOVA, 1967, *Liljeborgia* sp. 1 D'UDEKEM D'ACOZ, 2008; *Liljeborgia* sp. 4 (this paper).

Group 2 (= subgenus *Lilljeborgiella*): *L. abyssotypica* D'UDEKEM D'ACOZ, 2008; *L. akaroica* HURLEY, 1954 (peduncle of U1 apparently with 1 dorsolateral distal spine and 5 dorsomedial spines in original description); *L. anepsia* D'UDEKEM D'ACOZ, 2009; *L. barhami* HURLEY, 1954; *L. bathysciarum* D'UDEKEM D'ACOZ, 2009; *L. bythiana* D'UDEKEM D'ACOZ, 2008; *L. caeca* BIRSTEIN & VINOGRADOVA, 1960; *L. charybdis* D'UDEKEM D'ACOZ & VADER, 2009; *L. charybdis* forma *caliginis* D'UDEKEM D'ACOZ & VADER, 2009; *L. consanguinea* STEBBING, 1888; *L. cota* J.L. BARNARD, 1962; *L. dubia* (HASWELL, 1879) (= *L. affinis* HASSELL, 1885); *L. eurycradus* THURSTON, 1974; *L. fissicornis* (M. SARS, 1858); *L. georgiana* SCHELLENBERG, 1931; *L. hansoni* HURLEY, 1954; *L. homospora* D'UDEKEM D'ACOZ, 2008; *L. longicornis* (SCHELLENBERG, 1931); *L. macrodon* SCHELLENBERG, 1931; *L. marcinabrio* J.L. BARNARD, 1969; *L. maria* HURLEY, 1954; *L. mojada* J.L. BARNARD, 1961; *L. mozambica* LEDOYER, 1986; *L. nesiotica* D'UDEKEM D'ACOZ, 2008; *L. ossiani* D'UDEKEM D'ACOZ & VADER, 2009; *L. palmata* GRIFFITHS, 1974; *L. permacra* D'UDEKEM D'ACOZ, 2008; *L. polosi* J.L. BARNARD & KARAMAN, 1991 (= *L. dubia* KAMENSKAYA, 1980, not HASWELL, 1879); *L. polydeuces* D'UDEKEM D'ACOZ, 2009; *L. prionota* D'UDEKEM D'ACOZ, 2008; *L. quadridentata* SCHELLENBERG, 1931; *L. quinquedentata* SCHELLENBERG, 1931; *L. rauscherti* D'UDEKEM D'ACOZ, 2008; *L. semperhiemalis* D'UDEKEM D'ACOZ, 2008; *L. zarica* J.L. BARNARD, 1962; *Liljeborgia* sp. 2 D'UDEKEM D'ACOZ, 2008; *Liljeborgia* sp. 3 D'UDEKEM D'ACOZ, 2009; *Liljeborgia* n. sp. D'UDEKEM D'ACOZ, in press

Group 3 (subgenus *Isipingus* and species of indeterminate subgeneric position): *L. epistomata* K.H. BARNARD, 1932; *L. hwanghaensis* KIM & KIM, 1990; *L. serrata* NAGATA, 1965; *L. sinica* REN, 1992.

Besides the species listed above, J.L. BARNARD & KARAMAN (1991) cited an enigmatic Mediterranean species called *Liljeborgia bispinosa* (A. COSTA, 1853). Its original description (A. COSTA, 1853) is not available to me but I have seen the paper of A. COSTA (1857), which also describes the species. The figure of A. COSTA (1857) is difficult to interpret and does not agree with any known Mediterranean *Liljeborgia* species. Actually it is dubious if it is a *Liljeborgia* at all and DELLA VALLE (1893) thought it could be *Gammarus locusta* (LINNAEUS, 1758).

Finally, REN (2006: 47-48) lists *Liljeborgia crasspalmata* [sic] REN, *L. longidactyla* REN, *L. podocristata* REN and *L. unidentata* REN, which are nomina nuda, and STRANSKY & BRANDT (2010) cite a '*Liljeborgia* sp. 1' from South Greenland, of which the identity has not yet been established.

Subgenus *Liljeborgia* BATE, 1862

Iduna BOECK, 1861: 656 (type species: *Gammarus brevicornis* BRUZELIUS, 1859) [homonym of *Iduna* KEYSERLING & BLASISUS, 1840: Aves]
Liljeborgia BATE, 1862: 118 (type species: *Gammarus pallidus* BATE, 1857; gender: feminine)
Microplax LILLJEBORG, 1865a: 11; 1865b: 18 [= 18bis] (type species: *Gammarus brevicornis* BRUZELIUS, 1859) [new name for *Iduna* but homonym of *Microplax* FIEBER, 1861: Heteroptera]
Lilljeborgia GOËS, 1866: 529 (erroneous spelling for *Liljeborgia* BATE, 1862)
Heeliljeborgia LEDOYER, 1986: 691 (type species: *Liljeborgia heeia* J.L. BARNARD, 1970)
Not *Liljeborgia* CLAUS, 1866: 22 (Copepoda; type species: *Liljeborgia linearis* CLAUS, 1866: 22)

ETYMOLOGY: taxon dedicated to Dr. Vilhelm LILJEBORG (William LILLJEBORG), Swedish zoologist (1816-1908).

DESCRIPTION: Article five of peduncle of A1 without

anteromedial spines (only with setae); outer plate of Mx1 with 7-9 spines (most commonly 7, rarely 9). No anterior outer setae on the dorsal side of article one of the palp of Mxp. Setae of the anterior border of article three of the palp of Mxp never forming pairs or groups. Ventral tooth of coxa 4 (if present) situated near the distal 0.6 or 0.7. Posterior border of the propodus of P3-P4 with setules or small spines, never with long setae. Only 1 (distal) spine on the dorsomedial border of the peduncle of uropod 1 (very rare teratological specimens excepted). Urosomite 3, with posterolateral lobe of urosomite 3 rounded (without tooth), with or without posterodorsal pair of spines. Spines of the rami of U3 never forming transverse pairs or triplets. Tip of lobes of telson with only 1 spine (except for very rare teratological specimens).

REMARKS: The species of the subgenus *Liljeborgia* have a remarkably uniform morphology. On a global scale, the following characters (non exhaustive listing) seem important for separating species or complexes of pseudocryptic species: colour pattern of living specimens; presence/absence of eyes; colour of eyes in alcohol; length and stoutness of articles of mandibular palp; presence/absence of seta(e) on article one of mandibular palp; article two of mandibular palp with setae all along its length, versus restricted to tip; sometimes (rarely) the shape of the propodus of the gnathopods; sometimes the number of teeth on the dactylus of the gnathopods (character to be used with caution; number increasing with size!); sometimes setation of basis and merus of P3-P4; presence of spines versus setules on the posterior border of the propodus of P3-P4; when propodus of P3-P4 adorned with posterior spines, significant increase in length and stoutness of them towards tip, versus spines of homogeneous length and stoutness; length and slenderness of dactylus of P3-P4; stoutness of basis of P7; ornamentation of propodus of P7 (outer and medial sides); length of dactylus of P7; presence/absence of posterodorsal tooth/teeth on pleonites 1-2; size of the posteroventral tooth of Ep3; relative length of spines of dorsolateral border of peduncle of U1 in fully adult males; urosomites 1-2 with or without posterodorsal tooth; spination of peduncle of U2 (both sides); urosomite 3 with or without pair of posterodorsal spines (and length of these spines when present); relative size of teeth and spines of tip of telson; presence/absence of setules on tip of telson. The presence of 1 versus 3 posterodorsal teeth on pleonites 1-2 is sometimes important but this character should be considered with caution, because it is sometimes variable and when small, the lateral teeth can be extremely difficult to see.

Difficulties in separating species are especially acute in the case of *pallida* (BATE, 1857) species complex. The species of this group, which is apparently widely distributed, exhibit the following combination of characters: eye present and ommatidian; dactylus of Gn1 toothed; posterior border of propodus of P3-P4 with spines (rarely with spiniform setules); pleonites 1-2 with 1 to 3 posterodorsal teeth; urosomite 1-2 with posterodorsal tooth; uropod 2 normally with one (distal) spine on dorsolateral and dorsomedial border of peduncle; urosomite 3 without posterodorsal pair of spines. The following northeastern Atlantic and Mediterranean taxa belong to this group: *L. brevicornis* (BRUZELIUS, 1859), *L. dellavallei* STEBBING, 1906, *L. kinahani* (BATE, 1862), *L. mixta* SCHELLENBERG, 1925, *L. pallida* (BATE, 1857) and *Liljeborgia* sp. 4. Earlier descriptions of these taxa are inadequate and sometimes erroneous. They are treated separately in the present paper, and with the exception of the West African *L. mixta*, which was not available for study, a new descriptive account is provided. I have tried to provide illustrations as precise as possible. However, it must be noticed that some apparent differences could be attributed to size differences, individual variability or the state of preservation of the material. *Liljeborgia* species are indeed fragile and are prone to lose the long medial setae of the propodus of the posterior pereiopods, and sometimes lose spines. It is also not impossible that the colour of the eyes is partly related to depth. These taxa are treated separately to make the meaning of the different names explicit, i.e. to explain to which specimens of *Liljeborgia* these different names apply to. This does not mean that these taxa should definitely be accepted as valid, as the morphological differences between them are sometimes so elusive, that in several cases this question remains entirely unresolved. The comparison of DNA sequences could possibly help to improve the understanding of this situation. In case of uncertain identification, it appears desirable to label specimens as *Liljeborgia* group *pallida* (BATE, 1857).

Liljeborgia (*Liljeborgia*) *brevicornis* (BRUZELIUS, 1859)

(Figs 21-26)

Gammarus brevicornis BRUZELIUS, 1859: 62, pl. 3 fig. 11

Iduna brevicornis; BOECK, 1860: 656

Lilljeborgia pallida; BOECK, 1871: 177 (in part); 1876: 497 (in part), pl. 8 fig. 9; G.O. SARS, 1894: 530, pl. 187; SCHELLENBERG, 1931: 129, 130, 133, 135 (in part)

Lilljeborgia brevicornis; STEPHENSEN, 1929: 111, 112 (in part), fig. 27.169; 1931: 221-222 (in part); STEPHENSEN,

1938: 194-196 (in part); GURJANOVA, 1951: 515, fig. 337 (after G.O. SARS, 1895); TZVETKOVA, 1967: 69
Liljeborgia brevicornis; STEBBING, 1906: 230, 231 (in part); HURLEY, 1954b: 791; NAGATA, 1965: 47
Not *Gammarus pallidus* (*Lilljeborgia*); GOËS, 1866: 529, pl. 40 fig. 27 (= *Liljeborgia fissicornis* (M. SARS, 1858))
Not *Lilljeborgia brevicornis*; CHEVREUX & FAGE, 1925: 153, 155, fig. 155 (= *L. pallida* (BATE, 1857))
Not *Liljeborgia brevicornis*; HOLMES, 1909: 526; CHILTON, 1921b: 64 (= *L. aequabilis* STEBBING, 1888); REID, 1951: 232 (= *L. mixta* SCHELLENBERG, 1925); J.L. BARNARD, 1962: 83, 86

MATERIAL: **Norway**, R/V August Brinkmann, sta. E43-73, Brattholmen Hjeltefjorden, 60°24'27"N 005°06'33"E, 80-120 m, triangular dredge, 21.i.1973: 3 large specimens (up to 8 mm), leg. Anders WARÉN, TSZCr 15377; R/V August Brinkmann, sta. E100-70, Korsfjord, 60°12'48"N 005°11'06"E, 140-200 m, Ockelmann sledge, 27.iv.1970: 2 specimens, leg. W. VADER, TSZCr 11198; R/V Ottar, sta. 217921, Steinavær, 69°14'N 016°41'E, coral reef, 270-360 m, triangular dredge, 21.vii.1992, coral: 1 specimen (note in the vial indicating it had white eyes), leg. W. VADER, TSZCr 10000; R/V August Brinkmann, sta. E65-73 Marsteinen, 60°07'15"N 004°52'50"E, 306-308 m, epibenthic sledge, 9.ii.1973: 4 specimens, leg. Anders WARÉN, TSZCr 15352; R/V August Brinkmann, sta. 79-73, Marsteinen, 60°06'50"N 004°53'32"E, 265-275 m, epibenthic sledge, 13.ii.1973: 4 specimens, leg. Anders WARÉN, TSZCr 15404; R/V Johan Ruud, sta. 303-05, West Finnmark, SW Magerøya, 71°00.26'N 025°21.56'E, 161 m, sand with tunicates and hydroids, RP sledge, 13.iv.2005: 7 specimens (1 female dissected, mounted on 9 slides and illustrated; 1 specimen mounted in toto), coll. C. D'UDEKEM D'ACOZ, TSZCr. 14025; Trondheimsfjord near Biological station, 10-200 m, shell and coral, 01.ix.1961: 1 specimen (previously identified as *Liljeborgia kinahani* by W. VADER. UBZM nr 58950.

DESCRIPTION: Head: rostrum pointed, with acute tip, curving downwards, rather broad and short; eye large, with well-developed ommatidia, blackish in life, colourless or pale brown in alcohol.

A1: major flagellum with 15 articles; accessory flagellum with 9 articles.

A2: article four of peduncle with a few slender dorsomedial and ventrolateral spines; article five with dorsomedial setae but without dorsomedial spines, with only one (distal) ventrolateral spine; flagellum with 13 articles.

Epistome: rounded, protruding in lateral view.

Md: left lacinia mobilis large with anterior margin with 5 triangular teeth; right lacinia mobilis slightly smaller than left one, with anterior margin distinctly denticulate and with one medium-sized medial triangular tooth; ultimate raker spine of incisor process rather stout (but not stouter than more proximal ones); article one of palp distinctly shorter than article two (ratio length article one / article two = 0.66); article one 2.57 x as long as wide; article two with setae on tip only, 4.14 x as long as wide; article three 2.90 x as long as wide, 0.50 x as long as article two.

Mx1: article two of palp with 3 long setae on anterior margin, 6 spines on posterior and apical margin (all of medium stoutness) and 6 facial setae; outer plate with 7 spines, of which some are distinctly denticulate; inner plate with a single seta.

Mx2: outer plate with 2 well-developed setae on anterior margin.

Mxp: article one of palp without distal outer dorsal setae, article two without non-distal setae on outer margin; article three with 3 isolated setae on anterior border, article four (dactylus) distally slender, with anterior and posterior margins distinctly curved and 0.93 x as long as article three; outer plate with 6 well-spaced spines on medial border (these spines are of normal stoutness and length), and 6 to 7 slender medio-facial setae; inner plate with 2 to 3 rather slender anterior spines (of normal size) and 5 setae.

Gn1: coxa trapezoidal and narrow, not pilose on medial surface, with posterior border concave, with small posterior and anterior tooth; merus with 3 groups of setae and distal tooth; carpus process with 3 to 5 groups of setae, tip of carpus reaching 0.26-0.27 of propodus, far from reaching propodal group of strong spines; propodus 2.17 (male) or 1.93 (female) x as long as wide; group of spines on proximal 0.39-0.41 of propodus (most distal spine used as reference point); these spines being rather small; palm border forming a regular curve, without teeth; with hooked spines on outer row narrowly spaced (41 (male) or 26 (female) hooked outer spines, and no outer setae); dactylus with 4 to 7 (most commonly 5) teeth.

Gn2: coxa quadrato-elliptic, of normal width (1.51 x as long as wide), with anterior and posterior tooth (teeth very distant); merus with 3 groups of setae and with distal tooth; carpus process with 5 to 6 groups of setae; tip of carpus reaching 0.29 (male) or 0.24 (female) of propodus, not reaching propodal group of strong spines; propodus 2.06-2.14 x as long as wide; group of spines on the proximal 0.38 (male) or 0.34 (female) of propodus

(most distal spine used as reference point); these spines are of normal length; palm border curved and convex, medial margin smooth (female) or with very low distal projection (male); lateral margin sometimes presenting distal low crenulations; palm with hooked spines of outer row widely spaced (12 to 13 outer hooked spines and 15 (male) or 9 (female) outer setae); dactylus of normal width, with 11-14 (most commonly 12) teeth. Gn2 larger than Gn1; ratio length of propodus of Gn2 / length of propodus of Gn1: 1.32 (male) or 1.33 (female), surface of propodus of Gn2 / surface of propodus of Gn1: 1.75 (male) or 1.70 (female).

P3: coxa elliptic and narrow (2.06 x as long as wide), with anterior and posterior tooth (teeth rather close to each other); merus 1.23 x as long as carpus and 0.80 x as long as propodus; posterior border of merus with 4 isolated setules and anterior border with 1 distal setule; posterior border of carpus with 2 isolated non-distal setules and 1 fairly long distal seta paired with a setule; anterior border of carpus with 2 isolated setules; propodus with 4-10 posterior isolated spines, of which the length is not strongly increasing towards tip (length of longest posterior propodal spines 0.66 x as long as width of propodus); anterior border of propodus with 1 to 2 isolated non-distal setules + group of 1-2 distal setules; dactylus of normal length, slender with its two borders weakly curved, 0.63 x as long as carpus and 0.41 x as long as propodus.

P4: coxa of normal width (1.30 x as long as wide), with anterior and posterior border parallel, with ventral border weakly convex, with 4 normally developed serrations on posterior border and 1 normally developed ventral tooth; merus 1.24 x as long as carpus and 0.82 x as long as propodus; posterior border of merus with 4 isolated setules and anterior border hairless; posterior border of carpus with 2 isolated non-distal setules and 1 fairly long distal isolated seta; anterior border of carpus with 1 isolated setule; propodus with 8 to 11 posterior isolated spines, of which the length is not strongly increasing towards tip (length of longest posterior propodal spines 0.59 x as long as width of propodus); anterior border of propodus with 2 isolated setules; dactylus of normal length, slender with its two borders weakly curved, 0.56 x as long as carpus and 0.37 x as long as propodus.

P5: coxa without posterior notch; basis broad (1.51 x as long as wide), with anterior and posterior border convex; anterior border with 11 small conical spines (distal one paired with a medium-sized spine), posterior border with 9 low serrations, distal border produced into a rounded lobe; ischium with medium-sized spine on anterodistal corner; merus with 3 isolated short anterior spines, and 4 isolated posterior spines (small spines except distal one, which is medium-sized); carpus with 3 anterior groups of 1 to 3 medium-sized spines; carpus 0.74 x as long as merus; carpus + propodus 1.63 x as long as merus; propodus with 6 to 8 anterior small spines or pairs of spines; dactylus almost straight and slender, with tip entire, 0.29 x as long as propodus.

P6: coxa with small posterior tooth; basis broad (1.51 x as long as wide), with anterior and posterior border convex; anterior border with 9 small conical spines, posterior border with 12 normally developed serrations, distal border produced into a rounded lobe; ischium with setule on anterodistal corner; merus with 4 groups of 1-3 spines (2 proximal ones short, 2 distal ones well developed) and 4 posterior spines (3 proximal ones short, distal one long); carpus with 3 anterior groups of medium-sized spines, with posterodistal group of spines; carpus 0.76 x as long as merus; propodus with 6 anterior spines or pairs of spines, and 6 to 8 posterior groups of long thin setae (easily rubbed off); dactylus scarcely curved, slender, with tip entire, 0.38 x as long as propodus.

P7: coxa without posterior tooth; basis broad (1.33 x as long as wide), with anterior and posterior border convex; anterior border with 7 small conical spines (distal one paired with medium-sized spine), posterior border with 10 low serrations, distal border produced into a low rounded lobe; ischium with small spine paired with setule on anterodistal corner; merus with 4 anterior groups of 2 to 4 spines (long except those of proximal group, which are short) and 4 posterior groups of 1 to 4 long spines; merus 3.50 x as long as wide and 0.86 x as long as basis; carpus 1.06 x as long as merus; propodus of P7 1.25 x as long as propodus of P6; propodus with 6 to 8 slender spines (most of them long) or pair of spines, and 8 to 9 groups of posteromedial setae associated with a long slender spine; dactylus straight, long and very slender, entire, > 0.57 x as long as propodus (small part of dactylus missing in illustrated specimen).

Pleonite 1: posterodorsal area produced into 3 small teeth of which the median one is the longest (lateral teeth sometimes indistinct); Ep1 with normally developed posteroventral tooth, with posterior border distinctly convex; without anterior setae.

Pleonite 2: posterodorsal area produced into 3 small teeth of which the median one is the longest (lateral teeth sometimes indistinct); Ep2 with normally developed posteroventral tooth, with posterior border weakly convex.

Pleonite 3: posterodorsal area toothless; Ep3 with small posteroventral tooth, with posterior border nearly

straight.

Urosomite 1 with small posterodorsal tooth; ventrofacial border with 1 spine; peduncle of U1 with medial distal corner rounded, with 4 to 6 dorsolateral spines of which the 2 or 3 proximal ones are moderately long in males, and with 1 dorsomedial distal spine; outer ramus with 3 to 5 short stout outer spines and 1 to 2 short stout medial spines; inner ramus with 1 to 3 short stout outer spines and 5 to 6 stout medium-sized medial spines.

Urosomite 2 with small posterodorsal tooth; peduncle of U2 with 1 well-developed dorsolateral distal spine, with 1 dorsomedial distal spine; outer ramus with 3 to 5 short stout outer spines and 1 medial spine; inner ramus without 1-2 short stout spines on outer border and with 6 to 8 stout medium-sized spines on medial border.

Urosomite 3: without posterolateral tooth on each side, without posterodorsal spine on each side; outer ramus of U3 with 1 to 2 short outer spines; inner ramus with 2 short spines on outer border, with 3 medium-sized spines on medial border; rami subequal and 1.35 x as long as peduncle.

Telson: cleft to 0.75 of its length; medial tooth of each lobe either a bit longer or a bit shorter than outer tooth; interdental spine overreaching outer tooth by 0.63 of its length, 0.38 x as long as telson; medial apical teeth of telson with 1 setule.

COLOUR PATTERN: Almost colourless; viscera pale yellowish/brownish; pereiopods very faintly tinged with yellowish/brownish; eyes blackish in life condition (photograph made by the author after a specimen from Magerøya). The eyes become colourless or pale brown in alcohol.

SIZE: At most 10 mm.

BIOLOGY: ENEQUIST (1949) made the following observations: "In *Lilljeborgia fissicornis*, *L. brevicornis*, *L. kinahani* and *L. macronyx* the alimentary canal usually contains an abundance of clay particles, so all of them can be assumed to be detritus-feeders. In an aquarium I had the opportunity of observing *L. brevicornis* and *L. macronyx*. These move by rapid swimming or creeping in a lateral position on the bottom with the aid of the five pairs of pereiopods and with the gnathopods drawn up under the head. When feeding they remain by collections of detritus close to or under shells or irregularities of the bottom and seem mainly with the help of the mandibular palps to scrape together detritus from the surface of the bottom. In this connection the current created by the pleopods seems to be of no consequence for feeding. Strangely enough, the gnathopods do not appear to take an active share in the feeding process either. During the experiments the animals were not observed to show any tendency to dig." W. VADER (in lit.) made the following observations: "I have had *L. brevicornis* and *L. fissicornis* s.l. (probably *L. ossiani*) in small aquaria when I lived in Bergen, and my observations completely agree with those of ENEQUIST. *Liljeborgia* spp. are really fast swimmers, but they do not swim often, it seems to me. I have no obervations of feeding".

DISTRIBUTION: All along the coasts of Norway (STEPHENSEN, 1938; OLDEVIG, 1959; BUHL-JENSEN, 1986; BRATTEGARD & HOLTHE, 2001), Spitsbergen, Iceland, Barents Sea (STEPHENSEN, 1931, 1938 as *L. pallida*), Sweden (OLDEVIG, 1959). Records from the British Isles and France (e.g. CHEVREUX & FAGE, 1925; LINCOLN, 1979) are presumably based on *L. pallida*. The specimens from Senegal recorded by CHEVREUX (1925), STEPHENSEN (1931) and REID (1951) are presumably referable to *L. mixta* SCHELLENBERG, 1925. The specimens from Greenland recorded by STRANSKY (2007), STRANSKY & SVAVARSSON (2010) and STRANSKY & BRANDT (2010) are possibly true *L. brevicornis* but their identity needs confirmation. The specimens used by BRUZELIUS (1859) for his original description were collected from western Finnmark (the northernmost county of Norway) and Bohuslän (SW Sweden). Depth range: 25 m (STEPHENSEN, 1938) to 1130 m (STEPHENSEN, 1938).

REMARKS: Some authors like BRUZELIUS (1859) and BOECK (1876) indicate the occurrence of a posterodorsal tooth on pleonite 3. There is no such tooth in any of the specimens examined by me and the statements of these authors are probably erroneous. The same kind of erroneous descriptions was also encountered with *L. dellavallei* (see this paper, section on that species) and *L. chevreuxi* SCHELLENBERG, 1931 (see D'UDEKEM D'ACOZ, 2008, 2009).

The Norwegian *L. brevicornis* are very similar to the British *L. pallida* examined. However the Norwegian specimens have unpigmented or barely pigmented eyes in alcohol, whilst preserved British specimens have completely black eyes. Furthermore, the number of teeth on the dactylus of gnathopod 1 and to a lesser extent of gnathopod 2 is consistently smaller in the Norwegian specimens than in British specimens of the same size (this character has been systematically controlled). Interestingly the reduced number of teeth in the Scandinavian form was already indicated in the original description by BRUZELIUS (1859), who noted the

occurrence of 4 teeth on the dactylus of gnathopod 1 and 7-8 teeth on that of gnathopod 2 in his description in Swedish. The British specimens usually also have a higher number of anterior spines on the propodus of pereiopod 7 and on the dorsolateral border of the peduncle of uropod 1 than in Norwegian specimens, but these differences are small and are here considered as of little significance. The spines of the telson can be long both in Norwegian and British specimens but they are usually slightly longer in Norwegian specimens. However this character is very variable in British specimens and in one male examined, the spines of the telson are very short (see fig. 55E). The relative length of the outer and inner tooth of the tip of the lobe of the telson exhibits the same range of variation in the specimens of the two origins. The teeth are usually subequal and either the outer or the inner can be the longest. Finally, Norwegian specimens are almost colourless and without red marks (personal observations), whilst British specimens are said to exhibit conspicuous red marks (BATE, 1862).

Small differences between Scandinavian and other Northwestern European populations have been recorded in at least another amphipod, *Bathyporeia elegans* WATKINS, 1938 (see d'UDEKEM d'ACOZ, 2004). It remains unresolved question whether the differences in eyes colour and in the number of dactylar teeth between *L. brevicornis* and *L. pallida* are really of a specific nature or not. However in the absence of evidence to the contrary, it seems preferable to keep them as separate for the time being.

Liljeborgia (*Liljeborgia*) *dellavallei* STEBBING, 1906
(Figs 27-32)

Nicippe pallida; DELLA VALLE, 1893: 658 (in part), pl. 1 fig. 1, pl. 19 fig. 35-52
Lilljeborgia pallida; CHEVREUX, 1902: 695 (list)
Liljeborgia dellavallei STEBBING, 1906: 230, 234; SCHELLENBERG, 1925: 144; J.L. BARNARD, 1962: 86, table 1; GELDIAY *et al.*, 1971: 375, fig. 1-3; KRAPP-SCHICKEL, 1975: 455, fig. 1; 1989: 465, fig. 315; LYONS & MYERS, 1991: 610; COSTA *et al.*, 2009: 53, fig. 77, 78 (photograph in colour)
Lilljeborgia Della Vallei; CHEVREUX, 1911: 201, pl. 13 fig. 7-11; 1927: 85; CECCHINI & PARENZAN, 1935: 181-182, fig. 22
Lilljeborgia Della-Vallei; CHEVREUX & FAGE, 1925: 153, fig. 153-154;
Liljeborgia mixta; KRAPP-SCHICKEL, 1969: 294 (list)
Lilljeborgia mixta; RUFFO, 1946: 56 (list)
Liljeborgia della-vallei; HURLEY, 1954b: 791
Lilljeborgia (cfr. [sic] *mixta*; RUFFO, 1959: 405
Lilljeborgia dellavallei; TZVETKOVA, 1967: 69

MATERIAL: **NW Greece**, Ionian Sea, Lygia, 39°09'47"N 020°33'24"E, 2.5 m, *Posidonia* growing on rocks, snorkeling, hand net, August 2002: 1 adult male (dissected and mounted on 10 slides in Euparal), coll. C. d'UDEKEM d'ACOZ, TSZCr 13935; **Sardinia, Tavolara-Punta Coda Cavallo**, sample "(1) SC5C Ld", 40°51'36.6"N 009°43'23.1"E, *Posidonia* bed, 11 m, SCUBA diving, air-lift sampler, 12.viii.2007: 1 specimen, coll. Nicolas STURARO, RBINS, INV.93165; sample "(2) SC6D Ld", 40°51'36.6"N 009°43'23.1"E, *Posidonia* bed, 12 m, SCUBA diving, air-lift sampler, 11.viii.2007: 1 specimen, coll. Nicolas STURARO, RBINS, INV.93166; sample "(3) SC8C Ld", 40°51'39.8"N 009°43'14.3"E, *Posidonia* bed, 12 m, SCUBA diving, air-lift sampler, 04.viii.2007: 1 specimen, coll. Nicolas STURARO, RBINS, INV.93167; sample "(4) SC8C Ld2", 40°51'39.8"N 009°43'14.3"E, *Posidonia* bed, 12m, SCUBA diving, air-lift sampler, 04.viii.2007: 1 specimen, coll. Nicolas STURARO, RBINS, INV.93168; sample "(5) SC9D Ld ", 40°51'34.7"N 009°41'08.5"E, *Posidonia* bed, 12 m, SCUBA diving, air-lift sampler, 02.viii.2007: 1 specimen, coll. Nicolas STURARO, RBINS, INV.93169; sample "(6) SC10B Ld", 40°51'34.7"N 009°41'08.5"E, *Posidonia* bed, 13 m, SCUBA diving, air-lift sampler, 31.vii.2007: 1 specimen, coll. Nicolas STURARO, RBINS, INV.93170; sample "(7) SC10D Ld ", 40°51'34.7"N 009°41'08.5"E, *Posidonia* bed, 13 m, SCUBA diving, air-lift sampler, 31.vii.2007: 1 specimen, coll. Nicolas STURARO, RBINS, INV.93171; sample "(8) SC11A Ld ", 40°51'37.0"N 009°41'05.1"E, *Posidonia* bed, 12 m, SCUBA diving, air-lift sampler, 28.vii.2007: 1 specimen, coll. Nicolas STURARO, RBINS, INV.93172; sample "(9) SC11A Ld2", 40°51'37.0"N 009°41'05.1"E, *Posidonia* bed, 12 m, SCUBA diving, air-lift sampler, 28.vii.2007: 1 specimen, coll. Nicolas STURARO, RBINS, INV.93173; sample "(10) SC11B Ld", 40°51'37.0"N 009°41'05.1"E, *Posidonia* bed, 12 m, SCUBA diving, air-lift sampler, 28.vii.2007: 1 specimen, coll. Nicolas STURARO, RBINS, INV.93174; sample "(11) SC11B Ld2", 40°51'37.0"N 009°41'05.1"E, *Posidonia* bed, 12 m, SCUBA diving, air-lift sampler, 28.vii.2007: 1 specimen, coll. Nicolas STURARO, RBINS, INV.93175; sample "(12) SC11D Ld", 40°51'37.0"N 009°41'05.1"E, *Posidonia* bed, 12 m, SCUBA diving, air-lift sampler, 28.vii.2007: 1 specimen, coll. Nicolas STURARO, RBINS, INV.93176; **Malta**, Malta Island, Mellieha Bay, 35°59'N 014°22'E, *Posidonia* bed, 10 m, August 1998: about 30 specimens, coll. J.A. BORG, RBINS, INV.93160; Malta Island, Mellieha

Bay, 35°59'N 014°22'E, *Posidonia* bed, 11-12 m, September 1998: 3 specimens, coll. J.A. Borg, RBINS, INV.93161; Malta Island, Mellieha Bay, 35°59'N 014°22'E, *Posidonia* bed, 9-12 m, September 1999: 10 specimens, coll. J.A. Borg, RBINS, INV.93162; Malta island, White Rocks, 35°56'N 014°28'E, *Posidonia* bed, 9-12 m, September 1999: 5 specimens (including a large male), coll. J.A. Borg, RBINS, INV.93163; Gozo Island, Ramba Bay, 36°04'N 014°17'E, *Posidonia* bed, 9-12 m, September 1999: 4 specimens, coll. J.A. Borg, RBINS, INV.93164.

Description: Head: rostrum acute, sometimes produced into a styliform process, pointing downwards; eye large, of variable shape, with well-developed ommatidia, eye usually black in alcohol.

A1: major flagellum with 16 to 17 articles; accessory flagellum with 10 to 11 articles.

A2: article four of peduncle with a few slender dorsomedial spines, some ventrolateral setae and one distal ventrolateral spine; article five with dorsomedial setae but without dorsomedial spines, with a distal ventrolateral spine; flagellum with 15 articles.

Epistome: rounded, protruding in lateral view.

Md: left lacinia mobilis large with anterior margin with 5 teeth (rounded except the medial one, which is triangular); right lacinia mobilis distinctly smaller than left one, with anterior margin distinctly denticulate and with one medium-sized medial triangular tooth; ultimate raker spine of incisor process of normal stoutness; article one of palp a bit shorter than article two (ratio length article one / article two = 0.81); article one 2.79 x as long as wide; article two with setae on tip only, 3.58 x as long as wide; article three 2.62 x as long as wide, 0.54 x as long as article two.

Mx1: article two of palp with 2 long setae on anterior margin, 6 spines on posterior and apical margin (all of medium stoutness) and 5 facial setae; outer plate with 7 spines, which do not seem to be denticulate; inner plate with a single seta.

Mx2: outer plate with 3 well-developed setae on anterior margin.

Mxp: article one of palp without distal outer dorsal setae, article two without non-distal setae on outer margin; article three with 2 isolated setae on anterior border, article four (dactylus) distally slender, with anterior and posterior margins distinctly curved and 0.86 x as long as article three; outer plate with 7 well-spaced spines on medial border (these spines are narrow and rather long), and 4 slender medio-facial setae; inner plate with 2 rather slender anterior spines (of normal size) and 5 setae.

Gn1: coxa trapezoidal and rather narrow, with anterior medial setae, with posterior border weakly concave, with small posterior tooth and inconspicuous anterior notch; merus with 2 to 3 groups of setae and distal tooth; carpus process with 2 groups of setae, tip of carpus reaching 0.24-0.29 of propodus, not reaching propodal group of strong spines; propodus 1.90 (male) or 1.88 (female) x as long as wide; group of spines on proximal 0.24-0.30 of propodus (most distal spine used as reference point), these spines being rather small; palm border forming a regular curve, without teeth; with hooked spines on outer row narrowly spaced (27 to 29 (male) or 26 (female) hooked outer spines, and no outer setae); dactylus with 5 to 7 teeth.

Gn2: coxa triangulo-elliptic, broad (1.16 x as long as wide), with anterior and posterior notch (notches not very distant); merus with 2 to 3 groups of setae and with distal tooth; carpus process with 5 groups of setae; tip of carpus reaching 0.24-0.27 of propodus, not reaching distal propodal group of strong spines; propodus 1.94 (male) or 1.88 (female) x as long as wide; group of spines on the proximal 0.36 (male) or 0.32 (female) of propodus (most distal spine used as reference point); these spines are of normal length; palm border curved and convex, medial margin smooth; lateral margin sometimes presenting distal low crenulations; palm with hooked spines of outer row widely spaced (16 (male) to 14 (female) outer hooked spines and 9 (male) or 6 (female) outer setae); dactylus of normal width, with 10 to 13 teeth. Gn2 larger than Gn1; ratio length of propodus of Gn2 / length of propodus of Gn1: 1.40 (male) or 1.34 (female), surface of propodus of Gn2 / surface of propodus of Gn1: 1.94 (male) or 1.67 (female).

P3: coxa elliptic and narrow (2.08 x as long as wide), with anterior and posterior notch (notches very close to each other); merus 1.15 x as long as carpus and 0.84 x as long as propodus; posterior border of merus with 4 isolated setules and anterior border with distal setule; posterior border of carpus with 2 isolated non-distal setules and a third distal setule paired with a medium-sized seta; anterior border of carpus with 3 isolated setules; propodus with 8 posterior isolated spines, of which the length is significantly increasing towards tip (length of longest posterior propodal spines 1.15 x as long as width of propodus); anterior border of propodus with 2 isolated non-distal setules and a pair of distal setules; dactylus of normal length, slender with its two borders weakly curved, 0.58 x as long as carpus and 0.43 x as long as propodus.

P4: coxa of normal width (1.31 x as long as wide), with anterior and posterior border parallel, with ventral

border distinctly convex, with 3 normally developed serrations on posterior border and 1 ventral notch associated with a seta; merus 1.12 x as long as carpus and 0.83 x as long as propodus; posterior border of merus with 4 isolated setules and anterior border with distal setule; posterior border of carpus with 3 isolated non-distal setules and a fourth distal setule paired with a medium-sized seta; anterior border of carpus with 2 isolated setules; propodus with 6 to 7 posterior isolated spines, of which the length is significantly increasing towards tip (length of longest posterior propodal spines 1.00 x as long as width of propodus); anterior border of propodus with 3 isolated setules; dactylus of normal length, slender with its two borders slightly curved, 0.57 x as long as carpus and 0.42 x as long as propodus.

P5: coxa with small posterior tooth; basis broad (1.42 x as long as wide), with anterior and posterior border convex; anterior border with 9 small conical spines (distal one paired with a medium-sized spine), posterior border with 13 well-developed serrations, distal border produced into a rounded lobe; ischium with medium-sized spine paired with a spinule on anterodistal corner; merus with 4 groups of 1-2 rather short anterior spines, and 4 short posterior spines (distal one paired with a spinule); carpus with 3 anterior groups of articulated structures including long setae and 1-4 medium-sized spines, and with posterodistal pair of spines; carpus 0.76 x as long as merus; carpus + propodus 1.75 x as long as merus; propodus with 8 groups of 1-2 small anterior spines and long medial setae; dactylus distinctly curved and of normal stoutness, with tip entire, 0.28 x as long as propodus.

P6: coxa with small posterior tooth; basis broad (1.47 x as long as wide), with anterior and posterior border convex; anterior border with 9 small conical spines (distal one paired with a medium-sized spine), posterior border with 13 strong serrations, distal border produced into a rounded lobe; ischium with medium-sized spine paired with a spinule on anterodistal corner; merus with 4 anterior groups of 1-2 spines (two proximal ones short, two distal ones including a well-developed spine) and 5 posterior spines or pairs of spines; carpus with 3 anterior medium-sized spines or groups of spines associated with long setae arising more medially, with posterodistal group of spines; carpus 0.71 x as long as merus; propodus with 8 anterior spines or pairs of spines, with about 7 posterior groups of long thin setae; dactylus slightly curved, of normal width, with tip entire, 0.21 x as long as propodus.

P7: coxa without posterior tooth; basis broad (1.22 x as long as wide), with anterior and posterior border convex; anterior border with 9 small conical spines (distal one paired with medium-sized spine), posterior border with 14 strong serrations, distal border produced into a low rounded lobe; ischium with small spine paired with spinule on anterodistal corner; merus with 5 anterior groups of long spines and 5 posterior groups of 1 to 2 long spines; merus 3.47 x as long as wide and 0.90 x as long as basis; carpus 0.96 x as long as merus; propodus of P7 1.32 x as long as propodus of P6; propodus with 7 anterior well-developed spines or pair of spines, and 10 posterior slender spines associated with group of posteromedial setae (easily rubbed off); dactylus straight, very long and slender, entire, 0.76 x as long as propodus.

Pleonite 1: posterodorsal area produced into 3 small teeth of which the median one is the longest; Ep1 with normally developed posteroventral tooth, with posterior border weakly convex; without anterior setae.

Pleonite 2: posterodorsal area produced into 3 small teeth of which the median one is the longest; Ep2 with normally developed posteroventral tooth, with posterior border distinctly convex.

Pleonite 3: posterodorsal area toothless; Ep3 with small posteroventral tooth, with posterior border nearly straight.

Urosomite 1 with small posterodorsal tooth; ventrofacial border with 1 spine; peduncle of U1 with medial distal corner rounded, with 5 to 6 dorsolateral spines of which the proximal one is extremely long in adult male (but not in females), and with 1 dorsomedial distal spine; outer ramus with 3 to 5 medium-sized stout outer spines and 0 to 2 short stout medial spines; inner ramus with 1 to 3 short stout outer spines and 5 stout medium-sized medial spines.

Urosomite 2 with small posterodorsal tooth; peduncle of U2 with 1 long dorsolateral distal spine, with 1 dorsomedial distal spine; outer ramus with 4 well-developed stout outer spines and 0 to 1 medial spine; inner ramus with 2 to 3 short stout spines on outer border and with 5 to 6 stout medium-sized spines on medial border.

Urosomite 3: without posterolateral tooth on each side, without posterodorsal spine on each side; outer ramus of U3 with 4 short outer spines; inner ramus with 2 medium-sized stout spines on outer border, with 3 well-developed spines on medial border; rami subequal and 1.27 x as long as peduncle.

Telson: cleft to 0.80 of its length; medial tooth of each lobe either a bit longer or a bit shorter than outer tooth; interdental spine overreaching outer tooth by 0.49 of its length, 0.21 x as long as telson; medial apical teeth of telson with 1 or 2 setules.

COLOUR PATTERN: "DELLA VALLE describes gray and ruby-coloured varieties. I could observe (...) specimens (...) bright coral-red from head until metasome, with white stripes all over body; eye totally chalky-white" (GELDIAY *et al.*, 1971). The specimen on the photograph by COSTA *et al.* (2009) is weakly pigmented, with the anterior half of body, the gnathopods and to a lesser extent the pleon pinkish; the eye is white. The white pigments of the eyes obviously disappear in alcohol, where they become black.

TOTAL LENGTH: 7 mm.

DISTRIBUTION AND ECOLOGY: Widely distributed in all the Mediterranean Sea (KRAPP-SCHICKEL, 1989) up to the coasts of Libya (ORTIZ & PETRESCU, 2007); recorded from the Strait of Gibraltar (CONRADI & LÓPEZ-GONZÁLEZ, 1999). On mud and sand, *Peyssonnelia*, *Zostera*, *Posidonia*; from 0 to 105 m (KRAPP-SCHICKEL, 1989), sometimes on *Dictyopteris* (KRAPP-SCHICKEL, 1993). Also recorded on coralligenous bottoms (BELLAN-SANTINI, 1998) and on hard substrates (CHINTIROGLOU *et al.*, 2004; MANOUDIS *et al.*, 2005). Frequently found in the shell of the hermit crab *Dardanus arrosor* (HERBST, 1796) (CUADRAS & PEREIRA, 1977), who state "The amphipod *L. Della-Vallei* (present in 10/50 associations) was always found on the inside, within the last spires of the whelk, by groups of 4 or 5 individuals." Also recorded in 2% of the shells occupied by the hermit crabs *Pagurus cuanensis* BELL, 1845 and *Paguristes eremita* (LINNAEUS, 1767) (as *P. oculatus* (FABRICIUS, 1775)) by STACHOWITSCH (1980). Sometimes eaten by the sea anemone *Cereus pedunculatus* (PENNANT, 1777) (CHINTIROGLOU & KOUKOURAS, 1992). If *Liljeborgia* sp. 4 treated elsewhere in this paper proves to be a species distinct from *L. dellavallei*, then the bathymetric and ecological distribution of *L. dellavallei* given in literature will have to be reconsidered. In this context, it must be pointed out that DELLA VALLE (1893) recognized a form with red pigmentation observed in the military harbour of Naples and a more slender uniformly grey form found on sandy bottoms in front of the zoological station of the same town.

REMARKS: The specimens identified as *L. dellavallei* agree well with the figures of DELLA VALLE (1893), as *Nicippe pallida*. STEBBING (1906) and CHEVREUX & FAGE (1925) state that *Liljeborgia dellavallei* has a posterodorsal tooth on the third pleonite, but this is not true.

SCHELLENBERG (1925) described *Liljeborgia mixta* SCHELLENBERG, 1925 from Senegal, without giving any illustration. The name *L. mixta* has sometimes been applied to the Mediterranean form considered in the present section (e.g. RUFFO, 1946), and more recently, GELDIAY *et al.* (1971) set *L. mixta* SCHELLENBERG, 1925 in the synonymy of *L. dellavallei* STEBBING, 1906. From SCHELLENBERG's (1925) account, it can be assumed that *L. mixta* belongs to the complex *pallida* and is therefore related to *L. dellavallei*. However I feel that putting the two forms into synonymy without direct examination is going a step too far. In the absence of further evidence, *L. mixta* is therefore provisionally retained as a separate species.

The significant increase in the length and stoutness of the posterior spines of the propodus of pereiopods 3-4 observed in *L. dellavallei* also occurs in the West Atlantic species *L. bousfieldi* MCKINNEY, 1979 (MCKINNEY, 1979), the Indo-Pacific species *L. enigmatica* LEDOYER, 1986 (see LEDOYER, 1986), *L. heeia* J.L. BARNARD, 1970 (see LEDOYER, 1986), *L. joergpeteri* COLEMAN, 2009 (see COLEMAN, 2009a) and the East Pacific species *L. geminata* J.L. BARNARD, 1969 (J.L. BARNARD, 1969a).

Liljeborgia (*Liljeborgia*) *inermis* CHEVREUX, 1920
(Figs 33-38)

Lilljeborgia inermis CHEVREUX, 1920a: 7; 1927: 83, pl. 6 fig. 11-22
Liljeborgia inermis; J.L. BARNARD, 1962: 86, table 1

MATERIAL: **Portugal**, Algarve, Ferragudo, 37°08'N 008°32'W, net refuse of fishermen (small boat), 02.iv.2004: 1 male, anterior half of body crimson and posterior half white (dissected and mounted on 11 slides in Euparal), coll. C. D'UDEKEM D'ACOZ & MARCO FAASSE, TSZCr 13901; Algarve Armação de Pêra, 37°06'N 008°22'W, net refuse of fishermen (small boat), 27.iii.2004: 1 male, coll. C. D'UDEKEM D'ACOZ & Marco FAASSE, IRScNB, INV.93152.

DESCRIPTION: Head: rostrum acute, triangular, short, with dorsal margin pointing downwards; eye very large, of somewhat irregular form, with well-developed ommatidia, black in alcohol.

A1: major flagellum with 17 articles; accessory flagellum with 11 articles.

A2: article four of peduncle with a few slender dorsomedial spines and some ventrolateral setae; article five with dorsomedial setae but without dorsomedial spines, ventrolateral setae, with a distal ventrolateral spine; flagellum broken in the two specimens available.

Epistome: rounded, protruding in lateral view.

Md: left lacinia mobilis large with anterior margin with 5 rounded teeth; right lacinia mobilis distinctly smaller than left one, with anterior margin distinctly denticulate and with one medium-sized medial triangular tooth; ultimate raker spine of incisor process of rather stout but not much stouter than more proximal ones; article one of palp shorter than article two (ratio length article one / article two = 0.81); article one with a distal seta, 3.09 x as long as wide; article two with setae on tip only, 3.52 x as long as wide; article three 3.17 x as long as wide, 0.61 x as long as article two.

Mx1: article two of palp with 3 long setae on anterior margin, 6 spines on posterior and apical margin (all of medium stoutness) and 5 facial setae; outer plate with 7 spines, of which one is denticulate; inner plate with a single seta.

Mx2: outer plate with 2 well-developed setae on anterior margin.

Mxp: article one of palp without distal outer dorsal setae, article two without non-distal setae on outer margin; article three with 3 isolated setae on anterior border, article four (dactylus) distally slender, with anterior and posterior margins distinctly curved and 0.93 x as long as article three; outer plate with 5 to 8 well-spaced spines on medial border (these spines are very narrow (except for the two distal ones, which are fairly narrow) and rather long), and 2 to 3 medio-facial setae; inner plate with 1 anterior spine (of normal size and stoutness) and 9 to 10 setae.

Gn1: coxa triangular, of normal stoutness, without anterior medial setae, with posterior border distinctly concave, with small posterior and inconspicuous anterior notch; merus with 3 groups of setae and distal tooth; carpus process with 3 groups of setae, tip of carpus reaching 0.30 of propodus, not reaching propodal group of strong spines; propodus 1.97 x as long as wide; group of spines on proximal 0.44 of propodus (most distal spine used as reference point), these spines being medium-sized; palm border forming a regular curve, without teeth; with hooked spines on outer row narrowly spaced (32 hooked outer spines, and no outer setae); dactylus with 7 teeth.

Gn2: coxa elliptic, rather broad (1.28 x as long as wide), with anterior and posterior notch (notches widely separated); merus with 2 groups of setae and with distal tooth; carpus process with 5 groups of setae; tip of carpus reaching 0.42 of propodus, not reaching distal propodal group of strong spines; propodus 1.71 x as long as wide; group of spines on the proximal 0.40 of propodus (most distal spine used as reference point); these spines are of normal length; palm border curved and convex, medial margin smooth; lateral margin presenting low crenulations; palm with hooked spines of outer row widely spaced (14 outer hooked spines and 11 outer setae); dactylus rather stout, with 11 teeth. Gn2 larger than Gn1; ratio length of propodus of Gn2 / length of propodus of Gn1: 1.33, surface of propodus of Gn2 / surface of propodus of Gn1: 1.97.

P3: coxa elliptic and narrow (1.91 x as long as wide), with anterior and posterior notch (notches rather close to each other); merus 1.40 x as long as carpus and 0.95 x as long as propodus; basis with a few anterior setules and setae and only one posterior (distal) setule; posterior border of merus with 4 isolated setules, and anterior border with distal short seta; posterior and anterior border of carpus with 1 isolated distal setule; propodus with 8 posterior isolated spines, of which the length is not significantly increasing towards tip (length of longest posterior propodal spine 0.56 x width of propodus); anterior border of propodus with 2 isolated setules; dactylus rather short and stout, with its two borders weakly curved, 0.58 x as long as carpus and 0.40 x as long as propodus.

P4: coxa of normal width (1.31 x as long as wide), with anterior and posterior border nearly parallel, with ventral border distinctly convex, with 1 small notch on posterior border and 1 ventral notch associated with a seta, with posteroventral corner strongly curved and not at all angular; merus 1.32 x as long as carpus and 0.93 x as long as propodus; posterior border of merus with 4 isolated setules, and anterior border with distal short seta; posterior border of carpus with 4 isolated non-distal setules and a fourth distal setule paired with a fairly long seta; anterior border of carpus with 2 isolated setules; propodus with 8 posterior isolated spines (length of longest posterior propodal spines 0.62 x width of propodus); anterior border of propodus with 4 isolated setules; dactylus rather short and stout with its two borders slightly curved, 0.54 x as long as carpus and 0.38 x as long as propodus.

P5: coxa with small posterior tooth; basis broad (1.49 x as long as wide), with anterior and posterior border convex; anterior border with 12 small conical spines (distal one paired with a medium-sized spine), posterior border with 12 well-developed serrations, distal border distally almost straight but with posterior corner rounded; ischium with medium-sized spine paired with a spinule on anterodistal corner; merus with 5 anterior groups of 1-2 rather short or very short spines, and 4 posterior groups of 1-2 rather short spines; carpus with 3 anterior groups of aciculae including long setae and 1-3 medium-sized spines, and with posterodistal group of spines; carpus 0.76 x as long as merus; carpus

+ propodus 1.70 x as long as merus; propodus with 8 groups of 1-2 small anterior spines, and with long medial setae; dactylus distinctly curved and rather stout, with tip entire, 0.28 x as long as propodus.

P6: coxa with small posterior tooth; basis broad (1.53 x as long as wide), with anterior and posterior border convex; anterior border with 11 small (distal one medium-sized) conical spines, posterior border with 15 well-developed serrations, distal border produced into a very low lobe; ischium with medium-sized spine paired with a spinule on anterodistal corner; merus with 4 anterior groups of 1-3 short to medium-sized spines and 5 posterior spines or groups of spines; carpus with 2 groups of anterior medium-sized spines and with several long setae arising more medially, with posterodistal group of spines; carpus 0.72 x as long as merus; propodus with 9 anterior spines or pairs of spines, with posteromedial well-developed groups of long thin setae; dactylus almost straight, slender, with tip entire, 0.27 x as long as propodus.

P7: coxa without posterior tooth; basis broad (1.34 x as long as wide), with anterior and posterior border convex; anterior border with 7 small conical spines (distal one paired with medium-sized spine), posterior border with 14 strong serrations, distal border produced into a very low lobe; ischium with small spine paired with spinule on anterodistal corner; merus with 4 anterior groups of medium-sized spines and 5 posterior groups of 1 to 3 long spines; merus 3.49 x as long as wide and 0.95 x as long as basis; carpus 1.00 x as long as merus; propodus of P7 1.42 x as long as propodus of P6; propodus with 9 anterior well-developed spines or pair of spines, and 9 posterior long slender spines associated with group of posteromedial setae; dactylus straight, long and slender, > 0.34 x as long as propodus (tip broken).

Pleonite 1: posterodorsal area toothless; Ep1 with normally developed posteroventral tooth, with posterior border strongly convex; without anterior setae.

Pleonite 2: posterodorsal area toothless; Ep2 with well-developed posteroventral tooth, with posterior border distinctly convex.

Pleonite 3: posterodorsal area toothless; Ep3 with well-developed posteroventral tooth, with posterior border straight.

Urosomite 1 without posterodorsal tooth; ventrofacial border with 1 spine; peduncle of U1 with medial distal corner rounded, with 5 to 6 normally developed slender dorsolateral spines, and with 1 dorsomedial distal spine; outer ramus with 5 to 6 small slender outer spines and 3 to 4 small slender medial spines; inner ramus without outer spines and with 5 slender medium-sized medial spines.

Urosomite 2 without posterodorsal tooth; peduncle of U2 with 1 normally developed dorsolateral distal spine, with 1 dorsomedial distal spine; outer ramus with 5 medium-sized slender outer spines and 2 medial spines; inner ramus with 2 medium-sized spines on outer border and with 6 stout and fairly long spines on medial border.

Urosomite 3: without posterolateral tooth on each side, without posterodorsal spine on each side; outer ramus of U3 with 3 rather short outer spines; inner ramus with 2 medium-sized slender spines on outer border, with 5 well-developed slender spines on medial border; rami subequal and 1.45 x as long as peduncle.

Telson: cleft to 0.80 of its length; medial tooth of each lobe 1.34 x as long as outer tooth; interdental spine overreaching outer tooth by 0.73 of its length, 0.21 x as long as telson; medial apical teeth of telson with 1 setule.

COLOUR PATTERN: Anterior half of body crimson and posterior half white (observations by the author).

SIZE: 8 mm.

DISTRIBUTION: Southern Portugal (Algarve) (present material); Mauritania (Banc d'Arguin), Cape Verde Islands, between 75-90 m and 888 m (CHEVREUX, 1920a, 1927). The material examined has been obtained in the net refuse of very small fishing boats (less than 6 m long) and has presumably been caught at depths of less than 100 m. Recorded from greenish muddy sand and bottoms of sand and shells (CHEVREUX, 1927).

REMARKS: The finding of the rarely recorded *L. inermis* in the nets of Portuguese fishermen is intriguing. Perhaps they came from the shells of the hermit crabs, which were caught in large numbers in those nets. Indeed several other species of *Liljeborgia* have been recorded in the shells of hermit crabs (VADER, 1995; WILLIAMS & MCDERMOTT, 2004).

Liljeborgia (*Liljeborgia*) *kinahani* (BATE, 1862)

(Figs 39-44)

Phaedra kinahani BATE, 1862: 119, pl. 21 fig. 1; BATE & WESTWOOD, 1862: 211, unnumbered fig.; ROBERTSON, 1888: 50

Lilljeborgia kinahani; CHEVREUX, 1888b: 665; G.O. SARS, 1894: 532, pl. 188 fig. 1; CHEVREUX & FAGE, 1925: 153, 157, fig. 157; STEPHENSEN, 1927: 111, 112:, fig. 27.170; 1938: 194, 197; GURJANOVA, 1951: 515 (key); TZVETKOVA, 1967: 69

Liljeborgia kinahani; STEBBING, 1906: 233; SCHELLENBERG, 1925: 144; K.H. BARNARD, 1932: 142; NAGATA, 1965: 164; J.L. BARNARD, 1969a: 167; GELDIAY *et al.*, 1971: 377; LINCOLN, 1979: 388, 390, fig. 184b-i
Not *Liljeborgia kinahani*; J.L. BARNARD, 1962: 83, 86; 1964: 228 (list) (= *L. geminata* J.L. BARNARD, 1969); GRIFFITHS, 1974: 304

MATERIAL: **Norway**, Lille Fugløya, Drivsundet, B.S. 335-65, shell sand, 27 m, 9.viii.1965: 1 large male (4 mm), UBZM nr 58945; Store Risøya, West of Tofterøya, B.S. 343-65, fine shell sand, 5-8 m, 12.viii.1965: 8 specimens (1 female dissected and mounted on 13 slides), UBZM nr 58946; Liholmene, Liholmsrennen, Raunefjorden, E 51-72, 130 m, 05.iv.1972: 1 ovigerous female with 3 eggs close to hatching, UBZM nr 58949; Raunefjorden, 40 m, 13.ix.1985: 1 specimen, coll. R.J. LINCOLN & G.A. BOXSHALL, NHM 1986:678:1; **United Kingdom**, survey EHSWFD07, Ballygally Bay, sample BGB-a (0.5), 54.9066°N 005.8488°W, Day Grab, 30.vii.2007, RefCol 73920: 2 specimens (previously identified as *L. pallida*), RBINS, INV.93177.

DESCRIPTION: Head: rostrum acute, short and pointing downwards; eye rather small, usually rounded but sometimes broadly elliptic, with well-developed ommatidia, pigmentation variable in alcohol.

A1: major flagellum with 10 articles; accessory flagellum with 6 articles.

A2: article four of peduncle with a slender dorsomedial spine and a well-developed distal ventrolateral spine; article five with dorsomedial setae but without dorsomedial spines; flagellum with 9 articles.

Epistome: triangular, protruding in lateral view.

Md: left lacinia mobilis large with anterior margin with 6 broad rounded teeth; right lacinia mobilis a bit smaller than left one, with anterior margin looking smooth (but observation difficult due to its small size); ultimate raker spine of incisor process of normal stoutness; article one of palp distinctly shorter than article two (ratio length article one / article two = 0.58); article one 1.64 x as long as wide; article two with setae on tip only, 3.14 x as long as wide; article three 1.67 x as long as wide, 0.41 x as long as article two.

Mx1: article two of palp with 1 long seta on anterior margin, 5 spines on posterior and apical margin (all of medium stoutness) and 3 facial setae; outer plate with 7 spines, of which some are weakly denticulate; inner plate with a single seta.

Mx2: weakly setose; outer plate with 2 well-developed setae on anterior margin.

Mxp: article one of palp without distal outer dorsal setae, article two without non-distal setae on outer margin; article three with 1 isolated seta on anterior border, article four (dactylus) distally slender, with anterior and posterior margins distinctly curved and 0.93 x as long as article three, with unguis unusually long; outer plate with 3 to 4 well-spaced spines on medial border (these spines are narrow and very long), and 4 slender medio-facial setae; inner plate with 1 rather slender anterior spine (of normal size) and 4 setae.

Gn1: coxa rectangular and very narrow, with anterior medial setae, with posterior border scarcely concave, with small posterior and anterior notch, with ventral margin slightly concave; merus with 2 groups of setae and distal tooth; carpus process with 2 groups of setae, tip of carpus reaching 0.28 of propodus, far from reaching propodal group of strong spines; propodus 1.83 x as long as wide; group of spines on proximal 0.40 of propodus (most distal spine used as reference point); these spines being rather small; palm border forming a regular curve, without teeth; with hooked spines of outer row narrowly spaced (15 hooked outer spines, and no outer setae); dactylus with 2 teeth.

Gn2: coxa quadrato-elliptic, of normal width (1.40 x as long as wide), with anterior and posterior tooth (teeth fairly distant); merus with 2 groups of setae and with distal tooth; carpus process with 3 groups of setae; tip of carpus reaching 0.28 of propodus, not reaching distal propodal group of strong spines; propodus 2.00 x as long as wide; group of spines on the proximal 0.36 of propodus (most distal spine used as reference point); these spines are of normal length; palm border curved and convex, smooth; palm with hooked spines of outer row widely spaced (6 outer hooked spines and 5 outer setae); dactylus of normal width, with 5 teeth. Gn2 larger than Gn1; ratio length of propodus of Gn2 / length of propodus of Gn1: 1.27 (female), surface of propodus of Gn2 / surface of propodus of Gn1: 1.51 (female).

P3: coxa elliptic and narrow (1.90 x as long as wide), with anterior and posterior very weak notches (notches very close to each other); merus 1.21 x as long as carpus and 0.80 x as long as propodus; posterior border of merus with 2 isolated setules; anterior border of merus with 1 isolated setule; posterior border of carpus with posterodistal setule paired with a medium-sized seta and no anterior setules; propodus with 4 posterior isolated very slender spinules or setules, of which the length is not significantly increasing towards tip (length of longest posterior propodal setule 0.69 x width of propodus); anterior border of propodus with 1 isolated non-distal setule; dactylus of normal length, slender, weakly curved, 0.63 x as long as carpus and 0.42 x as long as propodus.

P4: coxa of normal width (1.57 x as long as wide), with anterior and posterior border almost parallel (very slightly converging downwards), with ventral border straight, with 3 weak notches on posterior border and 1 ventral notch; merus 1.18 x as long as carpus and 0.79 x as long as propodus; posterior and anterior border of merus with distal setule; posterior border of carpus with a pair of distal short setae; anterior border of carpus without ornamentation; propodus with 4 posterior isolated very slender spinules or setules, of which the length is not significantly increasing towards tip (length of longest posterior propodal setule 0.77 x width of propodus); anterior border of propodus with distal setule; dactylus of normal length, slender with its two borders weakly curved, 0.70 x as long as carpus and 0.46 x as long as propodus.

P5: basis fairly broad (1.76 x as long as wide), with anterior and posterior border convex; anterior border with 4 spines (3 small conical spines followed by a medium-sized spine), posterior border with 7 well-developed serrations, distal border produced into a strong rounded lobe; ischium with medium-sized spine on anterodistal corner; merus with 3 groups of 1-2 rather anterior and posterior spines; carpus with 2 anterior groups of 2 to 3 spines and posterodistal group of 3 spines; carpus 0.80 x as long as merus; carpus + propodus 1.74 x as long as merus; propodus with 4 anterior spines, with a few long medial setae; dactylus slightly curved and of normal stoutness, with tip entire, 0.30 x as long as propodus.

P6: coxa narrow, without small posterior tooth; basis broad (1.60 x as long as wide), with anterior and posterior border convex; anterior border with 6 spines (5 small conical spines followed by a medium-sized spine), posterior border with 7 rather strong serrations, distal border produced into a well-developed rounded lobe; ischium with medium-sized spine on anterodistal corner; merus with 3 anterior and posterior groups of 1-2 spines (distal group including a quite long spine); carpus with 2 anterior pairs of spines (each group including a short and a quite long spines), with posterodistal pair of spines; carpus 0.75 x as long as merus; propodus with 5 anterior spines, with at least 1 long thin seta [such setae are easily lost]; dactylus distinctly curved, rather narrow, with tip entire, 0.32 x as long as propodus.

P7: coxa narrow, without posterior tooth; basis broad (1.31 x as long as wide), with anterior and posterior border convex; anterior border with 6 spines (5 small conical spines followed by medium-sized spine), posterior border with 7 rather strong serrations, distal border produced into a well-developed rounded lobe; ischium with small spine paired with setule on anterodistal corner; merus with 4 anterior groups of long spines and 3 posterior groups of 1 to 2 very long spines; merus 3.11 x as long as wide and 0.89 x as long as basis; carpus 0.95 x as long as merus; propodus of P7 1.22 x as long as propodus of P6; propodus with 5 well-developed anterior spines or pair of spines, and 6 posteromedial groups of aciculae including long setae and usually a long slender spine; dactylus nearly straight, very long and slender, entire, 0.59 x as long as propodus.

Pleonite 1: posterodorsal area produced into 3 small teeth of which the median one is the longest; Ep1 with normally developed posteroventral tooth, with posterior border distinctly convex; without anterior setae.

Pleonite 2: posterodorsal area produced into 3 small teeth of which the median one is the longest; Ep2 with normally developed posteroventral tooth, with posterior border weakly convex.

Pleonite 3: posterodorsal area toothless; Ep3 with small posteroventral tooth, with posterior border nearly straight.

Urosomite 1 with small posterodorsal tooth; ventrofacial border without spine; peduncle of U1 with medial distal corner rounded, with 3 to 4 well-developed slender dorsolateral spines, and with 1 dorsomedial distal spine; outer ramus without spines; inner ramus without outer spines and 3 strong medial spines.

Urosomite 2 with small posterodorsal tooth; peduncle of U2 with 1 long dorsolateral distal spine, with 1 dorsomedial distal spine; outer ramus with 1 well-developed outer spine and no medial spines; inner ramus without spines on outer border and with 4 stout medium-sized spines on medial border.

Urosomite 3: without posterolateral tooth on each side, without posterodorsal spine on each side; outer ramus of U3 without spines; inner ramus without spines on outer border, with 1 well-developed spine on medial border; rami subequal and 1.16 x as long as peduncle.

Telson: cleft to 0.82 of its length; medial tooth of each lobe a bit shorter than outer tooth; interdental spine overreaching outer tooth by 0.61 of its length, 0.48 x as long as telson; medial apical teeth of telson without setules.

COLOUR PATTERN: Pale orange (ROBERTSON, 1888). Anterior part of body tinged with purple, whilst the posterior half is pinkish white (CHEVREUX, 1888b); eyes black (CHEVREUX & FAGE, 1925). W. VADER (in lit.) kindly provided me with a colour description of specimens from Western Norway. 'From Drivsundet (E335-65) I have a colour description. Female with eggs. Mostly glassy transparent, but distally on coxal plates, on gnathopods, epimeral plates and pleopods orange-red pigment; these parts are also transparent. Eyes

dull white with c 20 red small facets. Eggs yellowish. Antennae, P3-P7 almost colourless (a few small dots on P6-P7). There is an indication of a vague pattern of transverse stripes proximally and distally on each segment, but this is far from clear. Samples from Store Risøya (E343-65) were similar, while in other samples (loc. uncertain, but in the same area) the animals were two-coloured: mesosomites 1-6 with reddish pigment, mesosomite 7, and metasome and urosome colourless. Eggs vividly orange-yellow. Gnathopods with red pigment on basis and carpus, P3-P6 colourless, but gills and maxilliped red. In different animals the intensity of the red pigmentation is quite variable, but the pattern is quite constant. A few specimens have no red pigment at all!'

SIZE: 4 mm.

DISTRIBUTION: Western Norway (G.O. SARS, 1894; BUHL-JENSEN, 1986; BUHL-MORTENSEN, 1996); British Isles (LINCOLN, 1979); western France (CHEVREUX & FAGE, 1925); Portugal (MARQUES & BELLAN-SANTINI, 1993); northwestern Mediterranean (?) (HARMELIN, 1964; MUNILLA & SAN VINCENTE, 2005). Beds of maerl (ROBERTSON, 1888 [nullipora]; CHEVREUX & FAGE, 1925 [*Lithothamnium*]; HALL-SPENCER *et al.*, 2006), shell sand (CHEVREUX, 1888b), pink gravel (CHEVREUX & FAGE, 1925), coarse sand (DAUVIN & GENTIL, 1983), rarely below boulder (TRUCHOT, 1963; TOULMOND & TRUCHOT, 1964). Rarely intertidal (TRUCHOT, 1963; TOULMOND & TRUCHOT, 1964) to 130 m (present material).

REMARKS: On the illustrations given in the present paper, *L. kinahani* may look quite different from the sympatric *L. brevicornis* and *L. pallida*. However a large part of the differences can probably be attributed to size difference. Indeed, *L. kinahani* reaches at most 4 mm, whilst the two other species can reach up to 10 mm. It would be useful to compare *L. kinahani* with juveniles of its two relatives, when more comprehensive material becomes available.

Liljeborgia (*Liljeborgia*) *macronyx* G.O. SARS, 1894
(Figs 45-50)

Lilljeborgia macronyx G.O. SARS, 1894: 533 pl. 188 fig. 2; STEPHENSEN, 1929: 111, 112, fig. 27.171; 1938: 194, 197; GURJANOVA, 1951: 515 (key)
Liljeborgia macronyx; STEBBING, 1906: 231; HURLEY, 1954b: 791; J.L. BARNARD, 1962: 85, 86, table 1; NAGATA, 1965: 164; BELLAN-SANTINI & LEDOYER, 1987: 405

MATERIAL: **Norway**, R/V Harry Borthen, sta. 29, Tautra, Trondheimsfjorden, 63°35'N, 010°30'E, depth not recorded, triangular dredge, 04.vii.1963: 1 adult male, leg. Lita GREVE, TSZCr 15180; R/V Johan Ruud, sta. 177, Humpen, Solbergfjorden, 69°08'N 017°38'E, 351 m, RP sledge, 04.v.2004: 1 specimen, leg. W. VADER, TSZCr 14629; R/V Johan Ruud, sta. 273, Buvika, Malangen, 69°31.23'N 018°03.84'E, 358 m, Beyer sledge, 03.v.2004: 1 male, leg. W. VADER, TSZCr 14550; AKVAPLAN-NIVA, sta. 7-2, Visund, 61°22'11"N, 002°28'33"E, 334 m, grab, 28.v.1999: 1 specimen, leg. R. PALERUD, TSZCr 17374; AKVAPLAN-NIVA, sta. 8-5, Troll vest, 60°45'01"N 003°27'05"E, 337 m, grab, 27.v.1991: 1 male and 1 mature female with fully grown oostegites (only 4.5 mm), TSZCr 18992; AKVAPLAN-NIVA, sta. 15-2, Troll øst, 60°33'20"N 003°43'28"E, 308 m, grab, 27.v.1994: 1 mature female, TSZCr 18998; AKVAPLAN-NIVA, sta. 33-3, Snorre, 61°28'51"N 002°12'54"E, 327 m, grab, 04.vi.1999: 1 specimen in poor condition, leg. R. PALERUD, TSZCr 17539.

DESCRIPTION: Head: rostrum acute, narrow, of normal shape, pointing downwards; eye absent.

A1: major flagellum with 13 articles; accessory flagellum with 8 articles.

A2: article four of peduncle with a few slender dorsomedial spines and one distal ventrolateral spine; article five with dorsomedial setae but without dorsomedial spines; flagellum with 9 articles.

Epistome: rounded, protruding in lateral view.

Md: left lacinia mobilis large with anterior margin with 6 bluntly triangular teeth; right lacinia mobilis distinctly smaller than left one, with anterior margin almost smooth and with one medium-sized medial triangular tooth; incisor process with only 2 raker spines of normal stoutness; molar process with only 3 spines or stout setae, which are short and stout; article one of palp shorter than article two (ratio length article one / article two = 0.75); article one 2.94 x as long as wide; article two with only one seta, on tip, 2.93 x as long as wide; article three 2.44 x as long as wide, 0.63 x as long as article two.

Mx1: article two of palp with 1 seta on anterior margin, 5 slender spines on posterior and apical margin and 3 facial setae; outer plate with 7 spines, which do not seem to be denticulate; inner plate with a single seta.

Mx2: outer plate with 2 well-developed setae on anterior margin.

Mxp: article one of palp without distal outer dorsal setae, article two without non-distal setae on outer margin; article three with 1 isolated seta on anterior

border, article four (dactylus) stout, with anterior and posterior margins slightly curved and exactly as long as article three, with unguis short; outer plate with 8 well-spaced spines on medial border (these spines are very narrow and rather long), and 5 stout medio-facial setae; inner plate with 1 spine (of normal size and stoutness) and 2 setae.

Gn1: coxa triangular and of normal width, with anterior medial setae, with posterior border distinctly concave, with small posterior tooth and anterior notch; merus with only 1 group of setae and distal tooth; carpus process with only 1 (distal) group of setae, tip of carpus reaching 0.27 to 0.28 of propodus, not reaching propodal group of strong spines; propodus 2.06 to 2.08 x as long as wide; group of spines on proximal 0.38-0.39 of propodus (most distal spine used as reference point); these spines being rather small; palm border forming a regular curve, without teeth; with hooked spines on outer row narrowly spaced (19 hooked outer spines, and no outer setae); dactylus with 2 teeth.

Gn2: coxa elliptic, broad (1.67 x as long as wide), with anterior notch and posterior tooth (notch and tooth fairly distant); merus with 1 to 2 groups of setae and with distal tooth; carpus process with 4 groups of setae; tip of carpus reaching 0.35-0.38 of propodus, not reaching distal propodal group of strong spines; propodus 2.08 to 2.14 x as long as wide; group of spines on the proximal 0.52 (male) or 0.42 (female) of propodus (most distal spine used as reference point); these spines are small; palm border curved and convex, medial margin smooth; lateral margin sometimes presenting distal low crenulations; palm with hooked spines of outer row widely spaced (9 (both sexes) outer hooked spines and 17 long (male) or 3 short (female) outer setae); dactylus of normal width, with 6 teeth. Gn2 larger than Gn1; ratio length of propodus of Gn2 / length of propodus of Gn1: 1.52 (male) or 1.31 (female), surface of propodus of Gn2 / surface of propodus of Gn1: 2.26 (male) or 1.59 (female).

P3: coxa quadrato-elliptic and narrow (2.17 x as long as wide), with anterior notch and posterior tooth (notch and tooth very close to each other); basis ornamentation reduced to a few short setae on distal 0.8 of anterior border and 1 posterodistal setule; merus 1.23 x as long as carpus and 1.03 x as long as propodus; merus without ornamentation; posterior border of carpus with a pair of short subdistal setae; anterior border of carpus with 1 distal setule; propodus with 4 posterior isolated setule and 1 posterodistal spinule (length of longest posterior propodal setule 0.55 x width of propodus); anterior border of propodus with 1 distal setule; dactylus very long, very slender with its two borders slightly curved, 0.92 x as long as carpus and 0.76 x as long as propodus.

P4: coxa of normal width (1.21 x as long as wide), with anterior and posterior border parallel, with ventral border weakly convex, with 4 well-developed serrations on posterior border and 1 ventral notch associated with a seta; basis ornamentation reduced to a few short setae on distal 0.8 of anterior border and 1 posterodistal setule; merus 1.40 x as long as carpus and 0.89 x as long as propodus; merus without ornamentation; posterior border of carpus with 2 isolated short setae; anterior border of carpus with 1 distal setule; propodus with 4 posterior setules (length of longest posterior propodal setule 0.33 x width of propodus); anterior border of propodus with 1 distal setule; dactylus very long, very slender, with its two borders slightly curved, 0.95 x as long as carpus and 0.61 x as long as propodus.

P5: coxa with small posterior tooth; basis broad (1.39 x as long as wide), with anterior and posterior border convex; anterior border with 10 isolated small conical spines (distal one paired with a longer spine), posterior border with 11 well-developed serrations, distal border produced into a rounded lobe; ischium with pair of short spines on anterodistal corner; merus with 3 groups of 1-2 rather short anterior and posterior spines; carpus with distal group of 5 spines and with 2 long posterior setae; carpus 0.75 x as long as merus; carpus + propodus 1.58 x as long as merus; propodus with 4 isolated anterior spinules, with 4 posteromedial setae (distal one associated with a spine); dactylus slightly curved and very slender, with tip entire, 0.52 x as long as propodus.

P6: coxa with small posterior tooth; basis broad (1.50 x as long as wide), with anterior and posterior border convex; anterior border with 9 small conical spines (distal one paired with a longer spine), posterior border with 11 well-developed serrations, distal border produced into a rounded lobe; ischium with pair of short spines on anterodistal corner; merus with 4 anterior and posterior groups of 1-2 short spines; carpus with 3 anterior groups of 1 or 2 short to medium-sized spines (distal one associated with a long seta), with posterodistal group of rather short spines; carpus 0.67 x as long as merus; propodus with 4 anterior spinules, with 5 posteromedial groups of 2 or 3 long setae (distal group also including a spine); dactylus slightly curved, very slender, with tip entire, 0.52 x as long as propodus.

P7: coxa without posterior tooth; basis broad (1.38 x as long as wide), with anterior and posterior border convex; anterior border with 7 small conical spines, posterior border with 10 normally developed serrations, distal border produced into a low rounded lobe; ischium with small spine on anterodistal corner;

merus with 4 anterior groups of medium-sized slender spines and 5 posterior groups of 1 to 3 medium-sized spines; merus 3.54 x as long as wide and 0.83 x as long as basis; carpus 0.94 x as long as merus; propodus of P7 1.24 x as long as propodus of P6; propodus with 3 anterior spinules, and 6 posteromedial groups of long setae, most of them associated with a medium-sized spine (distal group with 2 spines); dactylus almost straight, extremely long and slender, entire, 1.53 x as long as propodus.

Pleonite 1: posterodorsal area produced into 1 small tooth; Ep1 with normally developed posteroventral tooth, with posterior border distinctly convex; without anterior setae.

Pleonite 2: posterodorsal area produced into 3 small teeth of which the median one is by far the longest; Ep2 with normally developed posteroventral tooth, with posterior border straight.

Pleonite 3: posterodorsal area toothless; Ep3 with very small posteroventral tooth, with posterior border curved in its lower part, sometimes with 1 setule.

Urosomite 1 with small posterodorsal tooth; ventrofacial border without spine; peduncle of U1 with medial distal corner rounded, with 4 dorsolateral spines (quite short except for distal one), and with 1 dorsomedial distal spine; outer ramus with 2 short slender outer and medial spines; inner ramus with 1 very short outer spine and 3 medium-sized slender medial spines.

Urosomite 2 without posterodorsal tooth; peduncle of U2 with 1 dorsolateral and 1 dorsomedial distal spines (none is very long); outer ramus with 3 short slender outer spines and no medial spines; inner ramus with 1 short slender spine on outer border and with 5 slender medium-sized spines on medial border.

Urosomite 3: without posterolateral tooth on each side, but posterolateral area bluntly angular, with medium-sized posterodorsal spine on each side; outer ramus of U3 with 1 spinule on each side; inner ramus with 2 small spines on outer border, with 3 medium-sized spines on medial border; rami subequal and 1.23 x as long as peduncle.

Telson: cleft to 0.65 of its length; medial tooth of each lobe a bit shorter than outer tooth; interdental spine very short, either slightly shorter or very slightly longer than outer tooth, 0.088 x as long as telson; medial apical teeth of telson without setules.

COLOUR PATTERN: Completely colourless, whitish; viscera with a greenish/grayish hue; no trace of eyes (photograph in colour of a Norwegian specimen made by the author). VADER (in lit.) also provided me with the following notes. 'For *L. macronyx* I have also a few data from Bergen (Byfjorden and Korsfjorden). The first specimen was colourless and transparent. The only pigment observed was clear pink on the mouthparts and a light pink tinge on the gnathopods. The second specimen, which was an adult male, was colourless and quite transparent. Its mouthparts (mandibles, maxillae and maxilliped) were conspicuously reddish.'

SIZE: A small species, reaching at most 6 mm (G.O. SARS, 1894) but usually smaller.

DISTRIBUTION: Northern Norway (northwards to 69°31'N) (present material), Western Norway (BUHL-JENSEN, 1986; BUHL-MORTENSEN, 1996), Southern Norway: Chritianafjord (G.O. SARS, 1894), Sweden (ENEQUIST, 1949; OLDEVIG, 1959). STRANSKY (2007) and STRANSKY & BRANDT (2010) record a *Liljeborgia* cf *macronyx* from Greenland. The identity of their material needs confirmation. From 130 m (OLDEVIG, 1959) to 732 m (G.O. SARS, 1894).

REMARKS: In many respects the Scandinavian *Liljeborgia macronyx* G.O. SARS, 1894 is similar with the Antarctic *L. cnephatis* D'UDEKEM D'ACOZ, 2008: e.g. absence of eye, dorsal dentition of the urosome, small size of the tooth of the third epimeral plate, short length of the distal spines of the telson, posterior ornamentation of the propodus of pereiopods 3 and 4 with setules (see D'UDEKEM D'ACOZ, 2008). *L. cnephatis* exhibits the following rather minor differences: no posterodorsal tooth on pleonite 1, more setae and setules on the proximal articles of pereiopods 3 and 4, shorter dactylus on the same pereiopods, and occurrence of a setule on the tip of the lobe of the telson (there is none in *L. macronyx*). *L. cnephatis* was also found below 2000 m, whilst *L. macronyx* has been recorded between 100 and 800 m. One can wonder if these species from the cold waters of the two hemispheres are not related. In a recent paper, D'UDEKEM D'ACOZ & VADER (2009) suggested that the Scandinavian *Liljeborgia* of the group *fissicornis* could be related to the similar but less apomorphic Antarctic and sub-Antarctic *Liljeborgia* of the group *georgiana*. The ancestor of the group *fissicornis* would have lived on the Antarctic shelf, descended into the deep-sea and migrated northwards through the cold abysses of the Atlantic before reaching the Scandinavian continental shelf, where the waters are cold enough for emergence from the depths. They pointed out that this hypothesis was supported by the Antarctic origin of the deep-sea water masses, which move in a northwards direction (e.g. TOMCZAK & GODFREY, 2005; RAHMSTORF, 2006), and that this has recently been verified for deep-sea

octopuses (Strugnell *et al.*, 2008). *L. cnephatis* and *L. macronyx* are very different from the *Liljeborgia* of the *georgiana* group and the *fissicornis* group (they don't belong to the same subgenus). So, if *L. macronyx* is indeed related to *L. cnephatis*, this would suggest a replication of the phylogeographic scenario already proposed for the *georgiana* and *fissicornis* groups. This seems plausible as there is apparently an evolutionary progression between the species of different origins and depth. In Antarctica, there are eyed shelf species like *L. chevreuxi* Schellenberg, 1931 and *Liljeborgia* sp. 2, which are fairly similar to the blind deep-sea Antarctic *L. cnephatis* (see d'Udekem d'Acoz, 2008, 2009), supporting the idea that the colonization of the abysses did occur in the cold parts of the southern hemisphere. Furthermore, when comparing the southern *L. cnephatis* with the northern *L. macronyx,* it seems that the second species is more apomorphic, by the elongation of its dactylus of pereiopods 3 and 4 and by the reduction of the setation of the same pereiopods. The existence of distinct albeit similar species in Antarctic and Arctic waters is not unusual and is the basis of the concept of 'relaxed bipolarity' implicitly proposed by Ekman (1953: 250). The colonization of the Arctic shelf by the offspring of deep-sea species of Antarctic origin is a process which possibly happened many times during the Cenozoic era.

Liljeborgia (*Liljeborgia*) *mixta* Schellenberg, 1925

Liljeborgia mixta Schellenberg, 1925: 144; J.L. Barnard, 1962: 86, table 1; Nagata, 1965: 164
Lilljeborgia brevicornis; Chevreux, 1925: 301; Stephensen, 1931: 221-222 (in part)
Liljeborgia brevicornis; Reid, 1951: 232
Lilljeborgia mixta; Tzvetkova, 1967: 69

Distribution: West Africa: Senegal (Chevreux, 1925; Schellenberg, 1925; Stephensen, 1931) and Guinea (Reid, 1951). From 10 m (Stephensen, 1931) to 65 m depth (Reid, 1951).

Remarks: Literature data indicates that a *Liljeborgia* species of the *pallida* group is present off West Africa and that the name *L. mixta* Schellenberg, 1925 is available for it. This non-European form, which is only known by brief accounts without illustrations, has not been examined during the present study. It is therefore impossible to say if *L. mixta* is identical to *L. pallida* sensu stricto, to *L. dellavallei* or if it is a separate species. In such a situation, it is preferable to provisionally retain *L. mixta* as a valid species, rather than elaborating speculations as Geldiay *et al.* (1971) did. The name *L. mixta* has erroneously been applied to *L. dellavallei* by Ruffo (1946) and Krapp-Schickel (1969).

Liljeborgia (*Liljeborgia*) *pallida* (Bate, 1857)
(Figs 51-56)

Gammarus ? *pallidus*; Bate, 1857: 145; White 1857: 185
Lilljeborgia brevicornis; Chevreux & Fage, 1925: 153, 155, fig. 155; Chevreux, 1927: 85; Geldiay *et al.* 1971: 377-378
Liljeborgia pallida; Bate, 1862: 118, pl. 20 fig. 5; Bate & Westwood, 1862: 203, unnumbered fig.; Stebbing, 1906: 230; Lincoln, 1979: 388, 390, fig. 184a, 185
Lilljeborgia pallida; Chevreux, 1888b: 665; 1900: 87; 1927: 85; Schellenberg, 1931: 129, 130, 133, 135 (in part)

Material (details of stations missing): **United Kingdom**, Survey IOW95, LabRef # 8421, area: SE Isle of Wight, sample 123-124, Hamon Grab, 17.ix.1995, RefCol # 7663: 6 specimens, RBINS, INV.93144; Survey IOW95, LabRef # 8494, area: SE Isle of Wight, sample 034, Hamon Grab, 15.ix.1995, RefCol # 7690: 1 large ovigerous female, RBINS, INV.93145; Survey IOW98, LabRef # 13886, area: SE: Isle of Wight, sample G47-A, Hamon Grab, 07.vi.1998, RefCol # 18412: 2 fine large specimens, (1 male, RBINS, INV.93178 a-i and 1 female, RBINS, INV.93180 a-k; fully dissected and respectively mounted on 9 slides (male) and 11 slides (female); Survey B3722, LabRef # 5347, area: Selsey, sample 41, dredge, 05.xi.1994, RefCol # 4918: 2 specimens, RBINS, INV.93146; Survey CEFWHENG05, LabRef # 37925, area: Wight, sample 226-B, Hamon Grab, 01.ix.2005, RefCol # 47188: 1 specimen, RBINS, INV.93147.

Description: Head: rostrum pointed, with acute tip, curving downwards, rather broad and short; eye large, with well-developed ommatidia, completely black in alcohol.

A1: major flagellum with 25 articles; accessory flagellum with 13 articles.

A2: article four of peduncle with several slender dorsomedial and ventrolateral spines; article five with dorsomedial setae but without dorsomedial spines, without ventrolateral spine; flagellum with 23 articles.

Epistome: triangular, protruding in lateral view.

Md: left lacinia mobilis large with anterior margin with 5 sharp triangular teeth; right lacinia mobilis distinctly smaller than left one, with anterior margin

distinctly denticulate and with one medium-sized medial triangular tooth; ultimate raker spine of incisor process of rather stout (but not much stouter than more proximal ones); article one of palp distinctly shorter than article two (ratio length article one / article two = 0.68); article one 3.05 x as long as wide; article two with setae on tip only, 4.11 x as long as wide; article three 2.42 x as long as wide, 0.39 x as long as article two.

Mx1: article two of palp with 3 long setae on anterior margin, 11 spines on posterior and apical margin (all of medium stoutness) and 9 facial setae; outer plate with 7 spines, which do not seem to be denticulate; inner plate with a single seta.

Mx2: outer plate with 2 well-developed setae on anterior margin.

Mxp: article one of palp without distal outer dorsal setae, article two without non-distal setae on outer margin; article three with 4 isolated setae on anterior border, article four (dactylus) distally slender, with anterior and posterior margins distinctly curved and 0.76 x as long as article three; outer plate with 10 to 14 well-spaced spines on medial border (these spines are narrow and rather long), and 5 to 9 slender medio-facial setae; inner plate with 1 to 2 rather slender anterior spines (of normal size) and 5 to 6 setae.

Gn1: coxa trapezoidal and rather narrow, with anterior medial setae, with posterior border weakly concave, with small posterior tooth and anterior notch; merus with 2 groups of setae and distal tooth; carpus process with 5 groups of setae, tip of carpus reaching 0.29-0.32 of propodus, not reaching propodal group of strong spines; propodus 2.47 (male) or 2.29 (female) x as long as wide; group of spines on proximal 0.38-0.40 of propodus (most distal spine used as reference point); these spines being rather small; palm border forming a regular curve, without teeth; with hooked spines on outer row narrowly spaced (27 (male) or 33 (female) hooked outer spines, and no outer setae); dactylus with 8 to 12 teeth.

Gn2: coxa quadrato-elliptic, of normal width (1.78 x as long as wide), with anterior and posterior notch (notches very distant); merus with 2 groups of setae and with distal tooth; carpus process with 6 to 8 groups of setae; tip of carpus reaching 0.32 (male) or 0.27 (female) of propodus, not reaching propodal group of strong spines; propodus 2.13 (male) or 2.33 (female) x as long as wide; group of spines on the proximal 0.42 (male) or 0.33 (female) of propodus (most distal spine used as reference point); these spines are of normal length; palm border curved and convex, medial margin smooth; lateral margin sometimes presenting distal low crenulations; palm with hooked spines of outer row widely spaced (10 (male) to 17 (female) outer hooked spines and 9 (both sexes) outer setae); dactylus of normal width, with 10-11 (small specimens) or 14-16 (large specimens) teeth. Gn2 larger than Gn1; ratio length of propodus of Gn2 / length of propodus of Gn1: 1.34 (male) or 1.31 (female), surface of propodus of Gn2 / surface of propodus of Gn1: 1.96 (male) or 1.70 (female).

P3: coxa elliptic and narrow (2.13 x as long as wide), with anterior and posterior shallow notches (notches very close to each other); merus 1.11 x as long as carpus and 0.78 x as long as propodus; posterior border of merus with 6 isolated setules and anterior border with 1 distal setule; posterior border of carpus with 4 isolated non-distal setules and 1 fairly long distal seta; anterior border of carpus with distal setule; propodus with 12 to 13 posterior isolated spines, of which the length is not strongly increasing towards tip (length of longest posterior propodal spines 0.52 x width of propodus); anterior border of propodus with 5 to 7 setules; dactylus of normal length, slender with its two borders weakly curved, 0.47 x as long as carpus and 0.33 x as long as propodus.

P4: coxa of normal width (1.36 x as long as wide), with anterior and posterior border parallel, with ventral border weakly convex, with 3 crenulations on posterior border and 1 ventral notch associated with a seta; merus 1.14 x as long as carpus and 0.80 x as long as propodus; posterior border of merus with 3 isolated setules and anterior border with distal setule; posterior border of carpus with 5 isolated non-distal setules and a sixth distal setule paired with a medium-sized seta; anterior border of carpus hairless; propodus with 11 to 14 posterior isolated spines, of which the length is not strongly increasing towards tip (length of longest posterior propodal spines 0.33 x width of propodus); anterior border of propodus with 5 to 6 isolated setules; dactylus of normal length, slender with its two borders slightly curved, 0.47 x as long as carpus and 0.33 x as long as propodus.

P5: coxa without posterior notch; basis broad (1.78 x as long as wide; measurement imprecise due to distortion of the basis; basis probably a bit broader), with anterior and posterior border convex; anterior border with 10 small conical spines (distal one paired with a medium-sized spine), posterior border with 9 normally developed serrations, distal border produced into a rounded lobe; ischium with medium-sized spine paired with a spinule on anterodistal corner; merus with 4 pairs of medium-sized anterior spines, and 3 posterior groups of 1-2 rather short spines; carpus with 4 anterior groups of aciculae including long setae and 0-3

medium-sized spines; carpus 0.67 x as long as merus; carpus + propodus 1.69 x as long as merus; propodus with 7 anterior small spines and ant least 6 groups of long medial setae (some can be rubbed off in illustrated specimen), with posterodistal spine; dactylus almost straight and slender, with tip entire, 0.27 x as long as propodus.

P6: coxa with small posterior tooth; basis broad (1.72 x as long as wide; measurement imprecise due to distortion of the basis; basis probably a bit broader), with anterior and posterior border convex; anterior border with 9 small conical spines (distal one paired with a medium-sized spine and a setule), posterior border with 11 normally developed serrations, distal border produced into a rounded lobe; ischium with setule on anterodistal corner; merus with 4 groups of 1-3 spines (proximal one short, 3 distal ones well developed) and 5 posterior spines or pairs of spines; carpus with 3 anterior medium-sized or groups of spines, with medial groups of setae and 1 posterior spine; carpus 0.72 x as long as merus; propodus with 9 to 10 anterior spines or pairs of spines, 7 to 11 posterior groups of long thin setae and posterodistal spine; dactylus weakly curved, of normal width, with tip entire, 0.44 x as long as propodus.

P7: coxa without posterior tooth; basis broad (1.26 x as long as wide; measurement not made after illustrated specimen), with anterior and posterior border convex; anterior border with 6 small conical spines (distal one paired with medium-sized spine), posterior border with 11 normally developed serrations, distal border produced into a low rounded lobe; ischium with small spine paired with spinule on anterodistal corner; merus with 5 anterior groups of spines (long except those of first group, which are short) and 5 posterior groups of 1 to 3 long spines; merus 3.50 x as long as wide and 0.81 x as long as basis; carpus 1.02 x as long as merus; propodus of P7 1.39 x as long as propodus of P6; propodus with 9 to 12 well-developed spines or pair of spines, and 9 to 11 groups of posteromedial setae associated with a long slender spine; dactylus straight, rather long and rather slender, entire, 0.44 to 0.62 x as long as propodus.

Pleonite 1: posterodorsal area produced into 3 small teeth of which the median one is the longest; Ep1 with normally developed posteroventral tooth, with posterior border distinctly convex; without anterior setae.

Pleonite 2: posterodorsal area produced into 3 small teeth of which the median one is the longest; Ep2 with normally developed posteroventral tooth, with posterior border distinctly convex.

Pleonite 3: posterodorsal area toothless; Ep3 with small posteroventral tooth, with posterior border nearly straight.

Urosomite 1 with small posterodorsal tooth; ventrofacial border with 1 spine; peduncle of U1 with medial distal corner rounded, with 6 to 8 dorsolateral spines of which the 2 or 3 proximal ones are rather long (especially in males), and with 1 dorsomedial distal spine; outer ramus with 4 to 6 short stout outer spines and 4 to 5 short stout medial spines; inner ramus with 1 to 3 short stout outer spines and 6 stout medium-sized medial spines.

Urosomite 2 with small posterodorsal tooth; peduncle of U2 with 1 well-developed dorsolateral distal spine (especially long in male), with 1 dorsomedial distal spine; outer ramus with 4 to 5 short stout outer spines and 0 to 2 medial spines; inner ramus without 1-3 short stout spines on outer border and with 5 to 7 stout medium-sized spines on medial border.

Urosomite 3: without posterolateral tooth on each side, without posterodorsal spine on each side; outer ramus of U3 with 4 to 5 short outer spines; inner ramus with 0 to 3 medium-sized stout spines on outer border, with 3 to 5 medium-sized stout spines on medial border; rami subequal and 1.40 x as long as peduncle.

Telson: cleft to 0.79-0.80 of its length; medial tooth of each lobe either a bit longer or a bit shorter than outer tooth; interdental spine overreaching outer tooth by 0.56 (female) or 0.15 (male) of its length, 0.25 (female) or 0.078 (male) x as long as telson; medial apical teeth of telson with 1 setule.

Colour pattern: "The colour of this animal is white, with a rich crimson blotch near the middle which is very conspicuous, and readily enabled me to identify every specimen I took. The propoda on the gnathopoda are of a rosy hue, and a tinge of the same colour may be observed at several of the articulations of the pereiopoda" (Bate, 1862). "Eye tolerably round, and black" (Bate & Westwood, 1862). The eye remains completely black in alcohol (present material).

Size: Up to 10 mm.

Type material: In the collections of the Natural History Museum (London), there is a tube labeled "*Liljeborgia pallida*, 1952.7.5.177, Plymouth, holotype". However this vial only contains woody particles, which are probably the remains of an old corky plug. In an e-mail dated November 18th, 2009, Miranda Lowe, informed me about the existence of 3 slides, which she first believed to include parts of the type specimen. However, in a letter dated December 2nd, 2009, she told me that these slides, which are in very poor condition, are actually not based on the type.

DISTRIBUTION: British Isles (LINCOLN, 1979); French coasts of the English Channel and of the bay of Biscay (CHEVREUX & FAGE, 1925, as *L. brevicornis*); North Spain (MARTÍNEZ *et al.*, 2007a); Portugal (MARQUES & BELLAN-SANTINI, 1993). The recent record from Libya by ORTIZ & PETRESCU (2007) seems dubious, and that from Florida (CAMP *et al.*, 1998) and from India (ANONYM, 2003) extremely unlikely. The type locality is Plymouth (BATE, 1857). Intertidal (LINCOLN, 1979) to 180 m (CHEVREUX, 1900). LINCOLN (1979) indicates that the species can be found down to 600 m depth but he possibly refers to non-British and non-French *L. pallida*, i.e. to misidentified specimens. Bottoms of maerl [corallines] (CHEVREUX, 1887); on a bottom of sand, pebbles and broken shells, and on a bottom of muddy sand (CHEVREUX, 1888a, 1900), on a block of coral of the genus *Dendrophyllia* overgrown by tunicates (CHEVREUX & FAGE, 1925); sometimes in holdfasts of the kelp *Laminaria hyperborea* (GUNNERUS) FOSLIE (MOORE, 1978, as *L. brevicornis*); beds of *Limaria hians* (GMELIN, 1791) (HALL-SPENCER & MOORE, 2000).

REMARKS: BATE & WESTWOOD (1862) do not indicate the number of teeth on the gnathopods (and their drawing is very imprecise) but noticed that the *Gammarus brevicornis* as described by BRUZELIUS (1859) differs from *L. pallida* by "the less ornate character of the serrature of the fingers of the hands". They attribute this apparent difference to inadequate observations by BRUZELIUS (1859). However, the present study confirms that this difference is real (see account on *L. brevicornis*).

A specimen examined had two spines (instead of one) in one of the distal notches of the telson, which is obviously teratological in nature.

Liljeborgia (Liljeborgia) psaltrica KRAPP-SCHICKEL, 1975

(Figs 57-62)

Liljeborgia psaltrica KRAPP-SCHICKEL, 1975: 464, fig. 6-8; 1989: 465, 467, fig. 316-317

MATERIAL: **Adriatic Sea, Croatia**, 43°38'25"N 015°55'24"E, 46 m: holotype (sex unknown) mounted on two slides in Faure's liquid, MCV slides 1365 and 1366; **Aegean Sea, Greece**, Thermaikos Gulf, muddy bottom, 22-40 m depth, year 1970: 1 male (6 mm long; dissected and mounted on 12 slides, RBINS, INV.93181a-l) and 1 female (5 mm long; dissected and mounted on 4 slides, RBINS, INV.93182 a-d), specimens received from A. KOUKOURAS and previously (correctly) identified by D. STEFANIDOU.

DESCRIPTION: Head: rostrum triangular, acute and short; eye medium-sized, broadly elliptic, with well-developed ommatidia, pigmentation in alcohol moderate to absent.

A1: major flagellum with 10 articles; accessory flagellum with 6 articles.

A2: article four of peduncle with several slender dorsomedial spines and one distal ventrolateral spine; article five with dorsomedial setae but without dorsomedial spines; flagellum with 8 articles.

Epistome: rather rounded, protruding in lateral view.

Md: left lacinia mobilis large with anterior margin with 6 (one is reduced) bluntly triangular teeth; right lacinia mobilis distinctly smaller than left one, with anterior margin distinctly denticulate and with one medium-sized medial triangular tooth; ultimate raker spine of incisor process quite stout (but not stouter than more proximal ones); article one of palp shorter than article two (ratio length article one / article two = 0.72); article one 2.23 x as long as wide; article two with a median seta and several setae on tip, 3.09 x as long as wide; article three 3.07 x as long as wide, 0.68 x as long as article two.

Mx1: article two of palp with 2 long setae on anterior margin, 6 spines on posterior and apical margin (all rather slender) and 4 facial setae; outer plate with 7 denticulate or setose spines; inner plate with a single seta.

Mx2: outer plate with 2 well-developed setae on anterior margin.

Mxp: article one of palp without distal outer dorsal setae, article two without non-distal setae on outer margin; article three with 2 isolated setae on anterior border, article four (dactylus), with anterior and posterior margins distinctly curved and 0.75 x as long as article three; outer plate with 4 well-spaced spines on medial border (the two proximal ones are short and stout; the two distal ones are long and of normal stoutness), and 7 strong medio-facial setae; inner plate with 2 rather anterior spines (of normal size and stoutness) and 5 setae.

Gn1: coxa trapezoidal (nearly triangular) and narrow, with anterior medial setae, with posterior border scarcely concave, with small posterior and anterior notch; merus with 2 groups of setae and distal tooth; carpus process with 2 groups of setae, tip of carpus reaching 0.21 (male) or 0.14 (female) of propodus, very far from reaching propodal group of strong spines; propodus extremely elongate, 2.81 to 2.89 x as long as wide; group of spines on proximal 0.47-0.50 of propodus (most distal spine used as reference point); these spines being rather small;

palm border forming a regular curve, without teeth; with hooked spines on outer row narrowly spaced (22 to 23 hooked outer spines, and no outer setae); dactylus without teeth.

Gn2: coxa quadrato-elliptic, broad (1.54 x as long as wide), with anterior and posterior notch (notches moderately distant); merus with 3 groups of setae and with distal tooth; carpus process with 5 to 7 groups of setae; tip of carpus reaching 0.22-0.27 of propodus, not reaching distal propodal group of strong spines; propodus 2.10 (male) or 2.28 (female) x as long as wide; distal group of spines on the proximal 0.41 (male) or 0.47 (female) of propodus (most distal spine used as reference point); these spines are of normal length; palm border curved and convex, margin smooth in female, nearly smooth except for 2 very low distal crenulations in male; palm with hooked spines of outer row widely spaced (16 (male) to 12 (female) outer hooked spines and 17 (male or 3 (female) outer setae); dactylus of normal width, with 6 teeth. Gn2 slightly longer (but distinctly stouter) than Gn1; ratio length of propodus of Gn2 / length of propodus of Gn1: 1.23 (male) or 1.07 (female), surface of propodus of Gn2 / surface of propodus of Gn1: 1.80 (male) or 1.28 (female).

P3: coxa nearly rectangular and narrow (1.85 x as long as wide), with anterior notch and posterior tooth (notch and tooth very close to each other); basis well-furnished with medium-sized setae all along its anterior border and with short setae along the distal 0.6 of its posterior border; merus 1.05 x as long as carpus and 0.69 x as long as propodus; posterior border of merus with 4 isolated setules and anterior border with distal setule; posterior border of carpus with 1 isolated non-distal setule and a distal setule paired with a medium-sized seta; anterior border of carpus with 2 isolated setules; propodus with 5 posterior setules and 1 posterodistal spinule (length of longest posterior propodal setules 0.38 x width of propodus); anterior border of propodus with 2 isolated setules; dactylus very long and very slender with its two borders distinctly curved, 0.89 x as long as carpus and 0.59 x as long as propodus.

P4: coxa of normal width (1.36 x as long as wide), with anterior and posterior border almost parallel (slightly diverging downwards), with ventral border slightly convex, with anteroventral and posteroventral corner distinctly angular, with 3 small teeth or notches on posterior border and 1 anteroventral notch; basis well furnished with medium-sized setae all along its anterior border and with a few short setae on its posterior border; merus 1.11 x as long as carpus and 0.75 x as long as propodus; posterior border of merus with 4 isolated setules and anterior border with distal setule; posterior border of carpus with 1 isolated non-distal setule and a distal setule paired with a medium-sized seta; anterior border of carpus with 2 isolated setules; propodus with 5 posterior setules and 1 posterodistal spinule (length of longest posterior propodal setules 0.32 x width of propodus); anterior border of propodus with 2 isolated non-distal setules and 1 pair of distal setules; dactylus very long and very slender with its two borders distinctly curved, 0.87 x as long as carpus and 0.59 x as long as propodus.

P5: coxa with small posterior tooth; basis broad (1.53 x as long as wide), with anterior border distinctly convex and posterior border nearly straight; anterior border with 8 small conical spines (distal one can be paired with a medium-sized spine), posterior border with 7 to 10 normally developed serrations, distal border produced into a rounded lobe; ischium with or without medium-sized spine on anterodistal corner; merus with 3 groups of 1-2 rather short anterior spines, and 3 posterior spines; carpus with 2 anterior groups of 1 to 2 medium-sized spine and a pair of posterodistal spines (one long and one short); carpus 0.83 x as long as merus; carpus + propodus 1.83 x as long as merus; propodus with 3 very slender single spines (one rubbed off in illustrated specimen) and long posterodistal seta; dactylus long, distinctly curved and of rather slender, with tip entire, 0.60 x as long as propodus.

P6: basis broad (1.56 x as long as wide), with anterior border convex distinctly convex, with posterior border scarcely convex; anterior border with 8 small conical spines, posterior border with 9 normally developed serrations, distal border produced into a rounded lobe; ischium with medium-sized spine paired with a setule on anterodistal corner; merus with 2 anterior groups of 1-2 short spines and 4 posterior spines or pairs of spines; carpus with 2 anterior short to medium-sized spines or pairs of spines, with posterodistal group of spines (scars also suggest the presence of 2 non-distal isolated posterior spines); carpus 0.81 x as long as merus; propodus with 4 very slender anterior spines or pairs of spines, with 1 non-distal posterior short seta, with posterodistal tuft of long setae; dactylus long and slender, scarcely curved, with tip entire, 0.61 x as long as propodus.

P7: coxa without posterior tooth; basis broad (1.32 x as long as wide), with anterior and posterior border convex; anterior border with 4 isolated small conical spines followed by a distal pair of spines, posterior border with 9 normally developed serrations, distal border produced into a low rounded lobe; ischium with small spine; merus with 3 anterior groups of 1 to 3 spines and 4 posterior groups of 1 to 3 medium-sized

spines; merus 2.59 x as long as wide and 0.70 x as long as basis; carpus 1.31 x as long as merus; propodus of P7 1.31 x as long as propodus of P6; propodus with 4 anterior slender isolated spines, and 10 posterior slender spines associated with a setule [it is likely that long setae were present and have been rubbed off]; dactylus straight, extremely long and slender, entire, 1.43 x as long as propodus [at least in juveniles; length of dactylus not known for adults].

Pleonite 1: posterodorsal area produced into 3 small teeth of which the median one is the longest; Ep1 with small posteroventral tooth, with posterior border distinctly convex; without anterior setae.

Pleonite 2: posterodorsal area produced into 3 small teeth of which the median one is the longest; Ep2 with normally developed posteroventral tooth, with posterior border almost straight and with 1 setule.

Pleonite 3: posterodorsal area toothless; Ep3 with quite small posteroventral tooth, with posterior border straight and with 1 setule.

Urosomite 1 with small posterodorsal tooth; ventrofacial border without spine; peduncle of U1 with medial distal corner rounded, with 4 to 5 slender and rather short dorsolateral spines, and with 1 dorsomedial distal spine [1 specimen also had second spine on the middle of the medial border, but this is probably a teratological condition]; outer ramus with 4 to 5 small outer spines and 1 small medial spines; inner ramus with 2 to 3 small outer spines and 3 to 4 medium-sized and rather slender medial spines.

Urosomite 2 with small posterodorsal tooth; peduncle of U2 with 1 dorsolateral distal spine, with 1 dorsomedial distal spine; outer ramus with 4 small outer spines and no medial spines; inner ramus with 1 small spine on outer border and with 4 medium-sized spines on medial border.

Urosomite 3: without posterolateral tooth on each side, without posterodorsal spine on each side; outer ramus of U3 with 2 short spines in females, with 2 setules in male; inner ramus broader in male than in female, with 2 medium-sized spines (female) or 1 setule and 1 spinule (male) on outer border, with 3 medium-sized spines on medial border; rami subequal and 1.04 to 1.32 x as long as peduncle.

Telson: cleft to 0.79 of its length; medial tooth of each lobe slightly longer than outer tooth; interdental spine overreaching outer tooth by 0.64 of its length, 0.30 x as long as telson; medial apical teeth of telson with 1 setule.

COLOUR PATTERN: Unknown.

SIZE: 6 mm (present material).

DISTRIBUTION: Northwestern Mediterranean (KRAPP-SCHICKEL, 1989); Adriatic Sea (KRAPP-SCHICKEL, 1975); Aegean Sea, at 30-40 m, 21-36 m and 38 m (STEFANIDOU & VOULTSIADOU-KOUKOURA, 1995). From 46 to 100 m, on mud with detritus (KRAPP-SCHICKEL, 1989). Also found with the invasive red alga *Womersleyella setacea* (HOLLENBERG) R.E. NORRIS (ANTONIADOU & CHINTIROGLOU, 2007) and on hard substrates (CHRYSSANTHI, 2004). CARTES & SORBE (1999) recorded *L. psaltrica* between 396 and 601 m on the Catalan Sea slope. However such an important depth is somewhat surprising and I feel that the identity of these *Liljeborgia* should be re-controlled.

REMARKS: The accounts on *L. psaltrica* by KRAPP-SCHICKEL (1975, 1989) are based on 2.5 mm long juveniles. The present study demonstrates that the species can become considerably larger (6 mm). KRAPP-SCHICKEL (1975, 1989) illustrated the right eye of the holotype as round. I have re-examined her microscope slide and I found that the real shape of the right eye is difficult to establish. On the same microscope slide, the left eye appears broadly elliptic. However this could results from distortion artifacts during the mounting of the slide and uncertainties on the shape of the eyes remain. The eyes could not be observed on the Greek specimens examined, which were not in a very good condition.

The slender propodus of gnathopod 1 in *L. psaltrica* is somewhat reminiscent of that of *L. japonica* (see NAGATA, 1965: 162).

Liljeborgia (*Liljeborgia*) sp. 4

(Fig 63)

? *Lilljeborgia* cf. *brevicornis*; LEDOYER, 1968: 194, pl. 1
? *Liljeborgia dellavallei*; LEDOYER, 1977: 371

MATERIAL: **Italy**, Naples area, Vervece, *Corallina*, 55-60 m, no date: 5 specimens, with eyes unpigmented, leg. G. KRAPP-SCHICKEL, RBINS, Inv. 69584.

MORPHOLOGICAL NOTES: Eyes large, fully ommatidian but not pigmented in alcohol. Gn1: dactylus with 4-7 teeth. Gn2: dactylus with 10-12 teeth. P3-P4: propodus more slender than in *L. dellavallei* with posterior spines more slender than in *L. dellavallei* and not significantly increasing in size distally. Posterior serrature of basis of P7 strong, as in *L. dellavallei*. Three distal articles of P7 missing in all specimens. Pleonite 1-2 with

3 posterodorsal teeth of which the median one is the longest (these teeth are weaker than in *L. dellavallei*). Apical spines of the lobes of the telson longer than in *dellavallei*.

TOTAL LENGTH: 6 mm.

NOMENCLATURE: In previous papers (D'UDEKEM D'ACOZ, 2008, 2009), the names *Liljeborgia* sp. 1, sp. 2 and sp. 3 were used for distinctive taxa, which could be neither assigned with certainty to a known species nor described as new. Following this, the present form is recorded as *Liljeborgia* sp. 4.

REMARKS: The identity of the specimens here named *Liljeborgia* sp. 4 is problematic. At first they were considered somewhat atypical *L. dellavallei*. However, a second examination reveals they could belong to a separate albeit very closely related species. The posterior ornamentation of the propodus of periopods 3 and 4 is different, the spines being more slender (especially the distal ones) and not significantly increasing in size towards the tip as in *L. dellavallei*. The present specimens are actually remarkably similar to the Scandinavian form, *L. brevicornis*. However, the examination of a larger number of specimens of Mediterranean *Liljeborgia* of the group *pallida*, not coming from *Posidonia* beds or found below 30 m, would be necessary for confirming the existence of a second species of that group in the Mediterranean Sea.

Interestingly, DELLA VALLE (1893) recognized two Mediterranean forms of '*Nicippe pallida*', with different colour patterns, different ecological preferences and minor morphological differences. LEDOYER (1968) and BELLAN-SANTINI & LEDOYER (1973), who had access to living or freshly preserved material, recognized a common Mediterranean *Liljeborgia* species, which they considered as distinct from *L. dellavallei* and which they called *L.* cf. *brevicornis*. There is no doubt that the *L. dellavallei* of LEDOYER (1968) are properly identified. Indeed, he considered the species as typical of *Posidonia* beds and the numerous *Liljeborgia* from *Posidonia* beds examined during the present study conform to the illustrations by DELLA VALLE (1893), on which STEBBING (1906) based his description. LEDOYER (1968) considered his *L.* cf. *brevicornis* as a circalitoral species with a wide ecological distribution and he indicated that he found the species on coralligenous bottoms. The depth ranges of the *Liljeborgia* sp. 4 examined corresponds to the circalitoral and the indication '*Corallina*' possibly refers to coralligenous bottoms rather than to red algae of the genus *Corallina*. Therefore it is plausible that *Liljeborgia* sp. 4 is identical to the *L.* cf. *brevicornis* of LEDOYER (1968). In a more recent paper, LEDOYER (1977) put his *L.* cf. *brevicornis* in the synonymy of *L. dellavallei*, referring to the paper by KRAPP-SCHICKEL (1975). However, the illustrations given in that paper are not precise enough to show the subtle differences observed between *L. dellavallei* sensu stricto and *Liljeborgia* sp. 4; hence the question remains unresolved.

IDENTIFICATION KEY TO NORTH-EAST ATLANTIC AND MEDITERRANEAN LILJEBORGIIDAE

1.- Carpus of Gn1-Gn2 without long posterodistal process; tip of rami of U1-U2 broad and with cluster of 2-4 spines; large distal dorsolateral spine of peduncle of U1 pointing backwards paired with small spine pointing upwards (subfamily Idunellinae) 2

\- Carpus of Gn1-Gn2 with long posterodistal process; tip of rami of U1-U2 gradually tapering towards tip and terminated in a distal tooth without cluster of spines; large distal dorsolateral spine of peduncle of U1 pointing backwards not paired with small spine pointing upwards (subfamily Liljeborgiinae: genus *Liljeborgia* BATE, 1862) 9

2.- Carpus of Gn2 anteriorly not setose; peduncle of U1 without ventrofacial spines; Md with molar process reduced, non triturative, but with a cluster of well-developed stout setae (NE Atlantic and Mediterranean species of *Idunella* G.O. SARS, 1894) 3

\- Carpus of Gn2 anteriorly strongly setose; peduncle of U1 with ventrofacial spines; Md with molar process well developed and fully triturative, with 1 slender posterior seta (genus *Sextonia* CHEVREUX, 1920) .... *Sextonia longirostris* CHEVREUX, 1920

3.- Posterodorsal border of urosomite 1 without tooth; article 2 of palp of Mxp with distolateral setae; Gn1 > or = Gn2; carpus of Gn2 medium-sized with at least 2 posterior groups of setae; article 1 of mandibular palp short; dorsomedial border of peduncle of U1 with about 10 or more spines 4

\- Posterodorsal border of urosomite 1 with tooth; article 2 of palp of Mxp without distolateral setae; Gn1 slightly < Gn2; carpus of Gn2 short with only 1 posterior group of setae; article 1

of mandibular palp long; dorsomedial border of peduncle of U1 with or without non-distal spines (if spines present, their number is about 5 or less) 6

4.- Posterodorsal border of pleonite 2 with tooth; Gn1 slightly > Gn2 in females, significantly > Gn2 in males 5

- Posterodorsal border of all pleonites toothless; Gn1 = Gn2 in females, condition in male unrecorded [dorsomedial border of peduncle of U1 with about 20 spines]; NW Atlantic species ..... *I. spinifera* (DAUVIN & GENTIL, 1983)

5.- Gn1 of adult male with palm deeply and regularly concave; propodus of P3-P4 with posterior tufts of long setae; posterodorsal border of pleonite 1 smooth; dorsomedial border of peduncle of U1 with about 11 spines; Arctic and sub-Arctic species ..... *I. aeqvicornis* G.O. SARS, 1877

- Gn1 of adult male with palm convex with distinct notch on distal 0.6; propodus of P3-P4 with isolated long setae; posterodorsal border of pleonite 1 with tooth; dorsomedial border of peduncle of U1 with about 15-17 spines; Mediterranean species .... *I. pirata* KRAPP-SCHICKEL, 1975

6.- Dactylus of Gn2 not toothed 7

- Dactylus of Gn2 strongly toothed [some parts of the body with dark brown pigmentation persisting in alcohol; dorsomedial border of peduncle of U1 with about 5 long spines] .... *I. picta* (NORMAN, 1899)

7.- Pleonites 1 and 2 with 1 posterodorsal tooth; pleonite 3 with 1 to 3 posterodorsal teeth 8

- Pleonite 2 with posterodorsal tooth; pleonite 1 and 3 toothless [dorsomedial border of peduncle of U1 with 1 (distal) spine; rami of U3 with fairly strong spination] .... *I. mollis* MYERS & MCGRATH, 1983

8.- Gn2 of male with distal 0.5 of palm deeply concave; P3-P4 with posterior border of propodus with about 5 medium-sized isolated setae; peduncle of U1 with about 5 dorsomedial spines; U3 with inner ramus spinose; telson 0.8 cleft..... ..... *I. excavata* SCHIECKE, 1973

- Gn2 of male with palm devoid of concavity; P3-P4 with posterior border of propodus with single seta [or very scarcely setose]; peduncle of U1 with 1 (distal) dorsomedial spine; U3 with inner ramus without spines; telson 0.6 cleft .... *I. nana* (SCHIECKE, 1973)

9.- Dorsomedial border of peduncle of U1 with only one (distal) spine; article 1 of palp of Mxp without dorsal distal setae; article 3 of palp of Mxp with dorsal setae always isolated; posterior border of propodus of P3-P4 with spines or tiny setules; eye present or absent (NE Atlantic and Mediterranean species of the subgenus *Liljeborgia* BATE, 1862) 10

- Dorsomedial border of peduncle of U1 with several spines; Article 1 of palp of Mxp with dorsal distal seta(e); article 3 of palp of Mxp with at least some of the dorsal setae forming pairs or transverse groups; posterior border of propodus of P3-P4 with long and strong setae; eye absent (NE Atlantic and Mediterranean species of the subgenus *Lilljeborgiella* SCHELLENBERG, 1931) 18

10.- Pleonites 1-2 each with 1 to 3 posterodorsal teeth; urosomite 1 and in several species also urosomite 2 with posterodorsal tooth 11

- None of the pleonites and none of the urosomites with posterodorsal tooth [posterior border of propodus of P3-P4 with spines]..... ..... *L. inermis* CHEVREUX, 1920

11.- Propodus of Gn1 not elongate, with group of spines defining the palm moderately to weakly distant from tip of carpal posterodistal process; dactylus of Gn1 with at least 2 teeth 12

- Propodus of Gn1 very elongate, with group of spines defining the palm very distant from tip of carpal posterodistal process; dactylus of Gn1 without teeth [posterior border of propodus of P3-P4 with true setules] .... *L. psaltrica* KRAPP-SCHICKEL, 1975

12.- Eye present; dactylus of P3-P4 of normal length (< half of propodus) and stoutness; posteroventral tooth of Ep3 normally developed; urosomite 2 with posterodorsal tooth; urosomite 3 without pair of posterodorsal spines; apical spine of lobes of telson usually well developed and usually distinctly longer than distal teeth (rarely reduced); posterior border of propodus of P3-P4 with spines (sometimes very slender and looking as setules at low magnification): *Liljeborgia* group *pallida* 13

- Eye absent; dactylus of P3-P4 very long (> half of propodus) and very slender; posteroventral tooth of Ep3 very small; urosomite 2 without posterodorsal tooth; urosomite 3 with pair of well-developed posterodorsal spines; apical spine of lobes of telson very short (about as long as distal teeth); posterior border of propodus of P3-P4 with true setules .... *L. macronyx* G.O. Sars, 1894

13.- Forms of the Mediterranean, and the temperate and cold parts of NE Atlantic 14
- West African form..... .....*L. mixta* Schellenberg, 1925

14.- Eye large, elliptic or irregular-shaped, rarely circular; coxa 1 not especially narrow and ventrally not concave; coxa 4 not especially narrow; posterior border of propodus of P3-P4 with stout spines; spines of merus of P7 normally developed; outer ramus of U1 usually with spines; U3 rami normally with several spines; total length up to 6-10 mm 15
- Eye small, circular or sometimes weakly elliptic; coxa 1 very narrow and ventrally concave; coxa 4 unusually narrow; posterior border of propodus of P3-P4 with small and extremely slender spines (looking as setules at low magnification); spines of merus of P7 very long; outer ramus of U1 without spines; U3 rami with a single spine (on medial border of inner ramus); maximum total length up to 4 mm ..... *L. kinahani* (Bate, 1862)

15.- Posterior border of propodus of P3-P4 with spines weakly increasing or not increasing in length towards tip, not increasing in stoutness towards tip 16
- Posterior border of propodus of P3-P4 with spines distinctly increasing in length and stoutness towards tip [Eye usually black in alcohol; dorsolateral border of peduncle of U1 of adult male with one spine immensely elongated and the other ones short; Mediterranean form] .... *L. dellavallei* Stebbing, 1906

16.- Eye colourless or weakly pigmented in alcohol; dactylus of Gn1 with 4-7 teeth 17
- Eye black in alcohol; dactylus of Gn1 with 8-12 teeth [Atlantic coasts of Europe excluding Scandinavia] ..... *L. pallida* (Bate, 1857)

17.- Scandinavian form .... *Liljeborgia brevicornis* (Bruzelius, 1859)
- Mediterranean form ..... *Liljeborgia* sp. 4

18.- Gn2 of male without distinct distal protrusion on palm, with dactylus with sigmoid (i.e. normal) teeth and without proximal protrusion; propodus of P3 stout, with most setae arranged in pairs or in triplets; only inner ramus of U3 with spines, these spines being small; telson with rather short apical spines; large species (total length sometimes > 25 mm] 19
- Gn2 of male with distinct distal protrusion on palm (rest of palm in male absolutely straight), with dactylus with small irregular proximal denticulations followed by low protrusion; propodus of P3 slender with posterior setae usually unpaired; both rami of U3 with spines, these spines being strong; telson with very long apical spines; small species (total length up to 10 mm) [pleonite 3 with posterodorsal tooth; Posterodistal corner of basis of P5–P7 blunt] ..... *L. ossiani* d'Udekem d'Acoz & Vader, 2009

19.- Posterodistal corner of basis of P5-P7 forming a tooth; Ep3 with small posteroventral tooth; pleonite 3 with or without posterodorsal tooth; deep-sea forms recorded below 700 m depth at negative temperatures 20
- Posterodistal corner of basis of P5–P7 blunt; Ep3 with strong posteroventral tooth; pleonite 3 without posterodorsal tooth; form recorded at depth shallower than 500 m, usually at positive temperatures ..... *L. fissicornis* (M. Sars, 1858)

20.- Pleonite 3 with posterodorsal tooth..... *L. charybdis* d'Udekem d'Acoz & Vader, 2009
- Pleonite 3 without posterodorsal tooth ..... *L. charybdis* forma *caliginis* d'Udekem d'Acoz & Vader, 2009

Checklist of North-East Atlantic and Mediterranean Liljeborgiidae

Subfamily Idunellinae

Idunella aeqvicornis G.O. Sars, 1877: Northern Norway, Svalbard, Faeroe Islands, Iceland, Greenland, Barents Sea, Siberian Russia; 120 m to 1288 m, between -1.0°C and +2.5°C (see present paper).

Idunella excavata Schiecke, 1973: Western Mediterranean Sea, fine sand, 140-190 m (Schieke, 1973; Krapp-Schickel, 1989).

Idunella mollis (MYERS & MCGRATH, 1983) (= *Listriella dentipalma* DAUVIN & GENTIL, 1983): Ireland, 15 m depth (MYERS & MCGRATH, 1983 as *Listriella mollis*); SW English Channel, no depth indication (DAUVIN & GENTIL, 1983).

Idunella nana SCHIECKE, 1973: NW Mediterranean Sea, coarse sand, 6-30 m (SCHIECKE, 1973; KRAPP-SCHICKEL, 1975, 1989); also recorded in the Western Mediterranean by TODARO & KRISTENSEN (1998) and DE BIASI *et al.* (2003); Aegean Sea, 31 to 51 m, coarse sand, or amongst algae (SEZGIN *et al.*, 2007); Strait of Gibraltar, *Caulerpa prolifera* (FORSSKÅL) J.V. LAMOUROUX beds, and on sandy bottoms, at a depth of 30 m (CONRADI & LÓPEZ-GONZÁLES, 1999); Strait of Gibraltar on coarse and fine sand (GUERRA-GARCÍA & GARCÍA-GÓMEZ, 2004, 2006).

Idunella picta (NORMAN, 1899): Channel Isles to Guinea; extreme lower shore to 50 m (see present paper).

Idunella pirata KRAPP-SCHICKEL, 1975: Mediterranean; on mud, between 110 and 870 m (KRAPP-SCHICKEL, 1975, 1989; KARAMAN, 1975; LEDOYER, 1977), recorded down to 1263 m by CARTES & SORBE (1999). It should be noticed that the ventral border of coxa 4 is illustrated as weakly crenulated with several setules by KRAPP-SCHICKEL (1975, 1989), whereas it is shown as smooth with a single seta on anterior 0.3 by KARAMAN (1975). The posterior border of the third epimeral plate is illustrated as scarcely protruding by KRAPP-SCHICKEL (1975, 1989), as strongly convex and protruding by KARAMAN (1975) and LEDOYER (1977).

Idunella spinifera (DAUVIN & GENTIL, 1983): SW English Channel; 15 m depth (DAUVIN & GENTIL, 1983, as *Listriella spinifera*).

Sextonia longirostris CHEVREUX, 1920: SW English Channel to Morocco; on fine sand, intertidal to 34 m (see present paper).

SUBFAMILY LILJEBORGIINAE

Liljeborgia (*Liljeborgia*) *brevicornis* (BRUZELIUS, 1859): Norway Sweden, Spitsbergen, Iceland, Barents Sea, 25 to 1135 m (present paper).

Liljeborgia (*Liljeborgia*) *dellavallei* STEBBING, 1906: Mediterranean, *Posidonia* beds, 2 to 13 m; records outside *Posidonia* beds need confirmation (present paper).

Liljeborgia (*Liljeborgia*) *inermis* CHEVREUX, 1920: South Portugal to Mauritania and Cape Verde Islands, 75-90 m to 888 m (present paper).

Liljeborgia (*Liljeborgia*) *kinahani* (BATE, 1862): Western Norway to Portugal, dubiously recorded from the Mediterranean, rarely intertidal to 130 m (present paper).

Liljeborgia (*Liljeborgia*) *macronyx* G.O. SARS, 1894: Norway and SW Sweden, 130 to 732 m (present paper)

Liljeborgia (*Liljeborgia*) *mixta* SCHELLENBERG, 1925: West Africa, 10 to 65 m (present paper).

Liljeborgia (*Liljeborgia*) *pallida* (BATE, 1857): British Isles, North and West France, North Spain, Portugal, rarely intertidal to 180 m (present paper)

Liljeborgia (*Liljeborgia*) *psaltrica* KRAPP-SCHICKEL, 1975: Mediterranean, 36-601 m (present paper).

Liljeborgia (*Liljeborgia*) sp. 4: Western Mediterranean, 55-60 m (present paper).

Liljeborgia (*Lilljeborgiella*) *charybdis* D'UDEKEM D'ACOZ & VADER, 2009: Norwegian Sea, possibly West Greenland and South West Iceland, 1700 m (D'UDEKEM D'ACOZ & VADER, 2009).

Liljeborgia (*Lilljeborgiella*) *charybdis* forma *caliginis* D'UDEKEM D'ACOZ & VADER, 2009: Svalbard, Norwegian Sea between 740 and 2500 m. Abundant material of *Liljeborgia* from the Norwegian deep sea examined after the publication of the paper by D'UDEKEM D'ACOZ & VADER (2009) indicates the existence of transitional forms between *L. charybdis* and *L. caliginis*. Specimens with and without a posterodorsal tooth on pleonite 3 were found in the same sample and the development of this tooth (when present) proved to be very variable in these samples. Therefore the two species are probably identical. It is here decided to give precedence to the name *L. charybdis* over *L. caliginis* (principle of the first revisor, ICZN, 1999, Art. 24.2). The name *caliginis* is provisionally retained as a form for the specimens without posterodorsal tooth on pleonite 3.

Liljeborgia (*Lilljeborgiella*) *fissicornis* (M. SARS, 1858): Northern Norway, Svalbard, Barents Sea, probably Jan Mayen, probably New Siberian Islands, possibly West Greenland, 93 to 458 m (possibly as shallow as 9 m) (D'UDEKEM D'ACOZ & VADER, 2009).

Liljeborgia (*Lilljeborgiella*) *ossiani* D'UDEKEM D'ACOZ & VADER, 2009: Northern Norway (probably all the coasts of Norway and possibly Svalbard), 55 to 446 m (G.O. SARS, 1894 as *L. fissicornis*; D'UDEKEM D'ACOZ & VADER, 2009). The '*Liljeborgia fissicornis*' from the Bay of Biscay and the Azores recorded by CHEVREUX (1900) clearly belong to the subgenus *Liljeborgiella*. The small illustration of the Azorean specimen found at 1372 m given by CHEVREUX (1900: 88, pl. 14 fig. 5, in colour) is compatible with *L. ossiani* but its specific identity cannot be established without direct examination.

Appendix: formal description of the family Cheirocratidae fam. nov. and Hornelliidae fam. nov.

The discussion on the systematic affinities of the Liljeborgiidae required a comparison with the 'Cheirocratidae' and the 'Hornelliidae'. These family names were introduced by Bousfield & Shih (1994), without complying with the provisions of ICZN (1999) and were therefore invalid. Since it is improper to refer to nomenclaturally invalid families, there was no other option than validating them here, as an appendix to the present study.

Superfamily Melphidippoidea Stebbing, 1899

Family Cheirocratidae fam. nov.

Cheirocratids J.L. Barnard & C.M. Barnard, 1983: 597, fig. 15 (invalid: vernacular name)
Cheirocratidae Bousfield & Shih, 1994: 128 (invalid: nomen nudum)
Cheirocratidae Ren, 2006: 259 (invalid: not considered as new)
Cheirocratidae Coleman & Lowry, 2009: 334 (invalid: not considered as new)

Description: Body elongate, laterally compressed, gammaromorphic in shape.

Head: Eye present, in normal position, small to medium-sized, round, fully ommatidian; rostrum short; anterior lobe moderately developed, rounded to bluntly angular, never acute; inferior antennal concavity broad or forming a narrow slit; posterior lobe anteriorly produced and often acute.

A1: not longer than the peduncle of A2; peduncle with very few spines and setae; article one moderately to much stouter than article two; length of article one of peduncle subequal to length of article two; article three much shorter than article one, short but not especially stout; accessory flagellum present but short, with at least 2 articles; calceoli absent; callynophore absent.

A2: ornamentation of peduncle reduced; articles 4 and 5 of peduncle subequal; article four with spines and setae, article five with setae only; flagellum about as long as sum of articles four and five of peduncle or longer; calceoli absent; brush of setae absent.

Upper lip: short, entire, symmetrical.

Lower lip: inner lobe normally developed; outer lobes ovate.

Md: incisor process well developed and toothed; laciniae mobiles well developed, moderately unequal, left flattened, right one thin, with 3-4 large teeth (apparently 5 in *Cheirocarpochella*); raker spine row well developed; molar process fully triturative with one posterior gnathobasic seta; posteriorly articulated with carapace; palp well developed, with article one long (about 3 x as long as broad or longer), often setose, sometimes with tooth on posterodistal corner; articulation between article one and two typically subgeniculate; article two usually straight (convex on both sides in *Incratella*), usually distinctly longer than article one and two (shorter than article one in *Incratella*), with posterior border setose at least on distal half; article three with comb of setae on posterior border (D3-setae) and with or without anterior B3-seta(e).

Mx1: palp 2-articulated, second article distally truncate, usually with anteromedial setae, with row of distal spines (which are often strongly denticulate or even furcate) and with longitudinal row of facial setae; outer plate with 6-11 strong spines, usually strongly denticulate, sometimes furcate; inner plate strongly setose (setae on two rows).

Mx2: plates elliptic and subequal (inner plate very slightly broader than outer plate); inner plate with posterior border straight or concave, with facial setae forming a regular oblique row.

Mxp: outer plate large, reaching or overeaching tip of article two of palp, longer than article three; article four of palp with distinct unguis; inner plate with 0-3 distal stout and fusiform spines (when present near medial corner of anterior border), margino-facial spine present at least in *Cheirocratus sundevallii* (Rathke, 1843), where it is small, narrowly styliform and situated on 0.6 of inner plate (personal observation).

Coxae: not serrate, with few setae (which are sometimes stout); coxae 1-4 sometimes with posteroventral small tooth or notch (sometimes a setule on anteroventral corner of coxae 2-4, not inserted in distinct notch); coxae 1-4 rather long, equal in length or coxa 3-4 shorter than coxa 1-2; coxa 1 more or less trapezoidal and sometimes anteriorly produced; coxae 2-4 more or less quadrate; coxa 4 not excavate posterodorsally (but the whole border can be slightly concave), without row of teeth or serrations on posterior border; coxae 5-7 of decreasing length; anterior lobe of coxa 5 longer than posterior lobe.

Gills: on Gn2-P6: elliptic and simple.

Oostegites: on Gn2-P5: very narrow, not especially large.

Gnathopods: pediform or subchelate, dissimilar in male, usually similar in female; usually (but not always) Gn2 is the strongest; merus often with posterodistal

blunt tooth; carpus without posterodistal process (except for *Cheirocarpochela sinica* REN & ANDRES, 2006); palm weakly or not clearly defined; ornamentation of palm variable (spines often few in number or even absent, setae often abundant; sexual dimorphism often important); dactylus of Gn1-Gn2 without true medial setae; the cutting edge of Gn1-Gn2 can be toothed and with setae and spines; distal unguis frequently (possibly always) present.

P3-P4: ordinary; propodus shorter than merus; dactylus with unguis associated with setule(s).

P5-P7: similar in structure, morphologically basal; P5 < P6 = P7; basis weakly to moderately expanded; propodus with spines, without setae; dactylus short, with terminal unguis; dactylar ornamentation reduced to 1 proximal posterior seta and sometimes 1-2 subdistal tiny anterior setules.

Pleonites: ordinary, with or without posterodorsal tooth/teeth (posterodorsal border never serrate), with ventrofacial spination usually well developed; posterior border of epimeral plates smooth.

Pleopods: well developed with elongate peduncle, with long rami.

Urosomite 1: with or without ventrofacial spine(s) [when present it/they is/are usually long], often with (strong) posterodorsal tooth or teeth; dorsal spination present or absent.

Urosomite 2: with or without posterodorsal tooth or teeth; dorsal spination/setation variable.

Urosomite 3: with or without pair of posterodorsal spines.

U1-U2: peduncle of U1-U2 without ventrofacial spines; peduncle of U1 with row of dorsolateral and dorsomedial spines; lateral distal tooth of peduncle of U1 long; tip of dorsolateral border of the peduncle of U1 with a long spine pointing backwards paired with a short spine inserted immediately behind it; tip of rami (fairly) broad and spinose (typically with 4 spines).

U3: not strongly attached to urosome (can be lost in preserved specimens); peduncle long, at least 2 x as long as broad; rami well developed, equal in length, with tip acute, always with spines (on both rami), without setae; outer ramus with 1 or 2 articles (most commonly with 1 article); the frequent disappearance of the second article results from its fusion with the first article, not from atrophy.

Telson: deeply to completely cleft; each lobe often with 2 apical teeth, but medial one can be reduced or absent; 0 to several spines and 1 or a few short setae in the notch formed by the 2 apical teeth (or positioned more medially than the remaining tooth); telson without dorsal spines, but a group of 2 setulose (sometimes equal but usually unequal) setae (of which at least one is well developed) on the surface of each lobe.

COMPOSITION: *Casco* SHOEMAKER, 1930; *Cheirocarpochela* REN & ANDRES in REN, 2006; *Cheirocratella* STEPHENSEN, 1940; *Cheirocratus* NORMAN, 1867; *Degocheirocratus* G. KARAMAN, 1985; *Incratella* BARNARD & DRUMMOND, 1982; *Prosocratus* BARNARD & DRUMMOND, 1982. *Indiocratus* LEDOYER, 1983 is a junior synonym of *Incratella* BARNARD & DRUMMOND, 1982 (see COLEMAN & LOWRY, 2009: 334).

TYPE GENUS: *Cheirocratus* NORMAN, 1867, p. 12; etymology (according to NORMAN, 1867): χείρ and χρατέα, strong in the hand; type species, *Cheirocratus mantis* NORMAN, 1867: 13, pl. 7 fig. 14, 15 (= junior synonym of *Cheirocratus assimilis* (LILJEBORG, 1852).

REMARKS: This description is largely based on the species descriptions and figures given by G.O. SARS (1890-1895), SHOEMAKER (1930), BARNARD & DRUMMOND (1982), KARAMAN (1982, 1985), LEDOYER (1983), KRAPP-SCHICKEL & VADER (2002), REN (2006) and COLEMAN & LOWRY (2009).

BARNARD & BARNARD (1983) introduced the concept of 'cheirocratid' as a vernacular name, which is invalid since it does not respect the provisions of article 11 of ICZN (1999)

11.7.1. A family-group name when first published must meet all the following criteria. It must:

11.7.1.1. be a noun in the nominative plural formed from the stem of an available generic name [Art. 29] (...).

Later on, BOUSFIELD & SHIH (1994) introduced the term 'Cheirocratidae' in respecting the provisions of article 11. However, this name is also invalid because these authors failed to give any formal description as required by article 13.

13.1. Requirements. To be available, every new name published after 1930 must satisfy the provisions of Article 11 and must

13.1.1. be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon, or

13.1.2. be accompanied by a bibliographic reference to such a published statement, even if the statement is contained in a work published before 1758, or in one that is not consistently binominal, or in one that has been suppressed by the Commission (unless the Commission has ruled that the work is to be treated as not having been published [Art. 8.7]), or

13.1.3. be proposed expressly as a new replacement

name (nomen novum) for an available name, whether required by any provision of the Code or not.

REN (2006: 259) described the family 'Cheirocratidae J.L. BARNARD & C.M. BARNARD, 1983' and COLEMAN & MYERS (2009) the family 'Cheirocratidae REN, 2006'. Despite the explicit descriptions of these authors, the name 'Cheirocratidae' remains unavailable, this time because they do not respect some provisions of article 16 requiring the explicit intention to describe the family as new. Furthermore, COLEMAN & MYERS (2009) did not refer to a type genus, as required by ICZN (1999):

Article 16. Names published after 1999.

16.1. All names: intention of authors to establish new nominal taxa to be explicit. Every new name published after 1999, including new replacement names (nomina nova), must be explicitly indicated as intentionally new.

Recommendation 16A. Means of explicitly indicating names as intentionally new. To avoid uncertainty about their intentions, authors proposing new names (nomina nova), including new replacement names, are advised to make their intentions explicit by using in headings, or at first use of new names in proposals, appropriate abbreviations of Latin terms such as "fam. nov.", "g. nov.", "sp. nov.", "ssp. nov.", or some strictly equivalent expression such as "new family", "new genus", "new species", "new subspecies", "n. fam.", "n. g.", "n. sp.", "n. ssp.", "nomen novum". The abbreviation "nom. nov." should only be used to indicate a new replacement name.

16.2. Family-group names: type genus to be cited. In addition to satisfying the provisions of Articles 13-15, a new family-group name published after 1999 must be accompanied by citation of the name of the type genus (i.e. the name from which the family-group name is formed).

The family Cheirocratidae fam. nov. is now finally validated in respecting all the provisions of ICZN (1999).

Family Hornelliidae fam. nov.

Hornelliids J.L. BARNARD & C.M. BARNARD, 1983: 600 (invalid: vernacular name)
Hornelliidae BOUSFIELD & SHIH, 1994: 128 (invalid: nomen nudum)

DIAGNOSIS: Body elongate, laterally compressed, gammaromorphic in shape.

Head: Eye present, in normal position, large, elliptic to subreniform, fully ommatidian; rostrum short; anterior lobe broad and rounded; inferior antennal concavity shallow; posterior lobe anteriorly produced and often acute.

A1: much longer than the peduncle of A2 (the two antennae can be subequal); peduncle with rather few spines and setae; article one much stouter than article two; length of article one of peduncle subequal to length of article two; article three much shorter than article one, short but not especially stout; accessory flagellum present, short to medium-sized, with at least 2 articles; calceoli absent; callynophore absent.

A2: ornamentation of peduncle moderate; articles four and five of peduncle subequal; flagellum about as long as sum of articles four and five of peduncle or longer; calceoli absent; brush of setae absent.

Upper lip: very short, notched, asymmetrical.

Lower lip: inner lobe normally developed; outer lobes ovate.

Md: incisor process well developed and toothed; laciniae mobiles well developed, with 3-4 large teeth (apparently 5 in *Hornellia incerata* WALKER, 1904; see REN, 2006: 264); raker spine row well developed; molar process well developed and fully triturative; palp well developed, with first article short or fairly short (about 1-2 x longer than broad), setose or not, without tooth on posterodistal corner; articulation between article one and two rectilinear or geniculate; article two more or less straight (slightly curved in *Metaceradocus vesentiniae* RUFFO, 1969), considerably longer than article one, about as long as article two, with posterior border setose (at least on distal half); article three with comb of setae on posterior border (D3-setae), with apical tuft of E3-setae, and with or without isolated anterior B3-seta(e).

Mx1: palp 2-articulated, second article distally truncate, without anteromedial setae, with row of distal spines (which are apparently smooth) and with longitudinal row of facial setae; outer plate with 10-12 strong spines, usually strongly dentate; inner plate strongly setose (setae on one row; those on anterodistal corner sometimes much shorter than others).

Mx2: plates elliptic and subequal (inner plate very slightly broader than outer plate); inner plate with posterior border straight or convex, with facial setae forming a regular oblique row.

Mxp: outer plate normally developed, not reaching tip of article two of palp, longer than article three; article four of palp with distinct unguis; inner plate with 3 distal spines (not all clustered on medial corner of anterior border), with inner margino-facial (subdistal) spine (at least in *Hornellia incerta* WALKER, 1904, *Metaceradocus atlanticus* THOMAS & BARNARD, 1986

and *M. tequestae* THOMAS & BARNARD, 1986).

Coxae: serrate or not, with few setae; antero- and postero-ventral corners of coxae 1-4 usually with small tooth or notch; coxae 1-4 rather long, equal in length or coxa 3-4 shorter than coxa 1-2; coxa 1 more or less trapezoidal and sometimes anteriorly produced; coxae 2-4 more or less quadrate; coxa 4 not excavate posterodorsally (but the whole border can be slightly concave), without row of teeth or serrations on posterior border; coxae 5-7 of decreasing length; anterior lobe of coxa 5 longer than posterior lobe; coxae 6-7 sometimes with posterior tooth.

Gills: on Gn2-P6: elliptic and simple.

Oostegites: on Gn2-P5: very narrow, not especially large.

Gnathopods: subchelate, not very strong, not strongly sexually dimorphic; Gn2 is the strongest; Gn1 and Gn2 similar or fairly similar; merus often with posterodistal blunt tooth; carpus without or with short blunt posterodistal process; palm weakly or not clearly defined; palm with few long spines and setae; dactylus of Gn1-Gn2 without true medial setae; the cutting edge of Gn1-Gn2 can be toothed and adorned with setae; dactylus of Gn1-Gn2 with 1 seta on anterior border, in very proximal position; distal unguis frequently (possibly always) present.

P3-P4: ordinary; propodus a bit longer than or as long as merus; dactylus with unguis associated with 2 setules.

P5-P7: similar in structure, morphologically basal; P5 < P6 = P7; basis weakly to moderately expanded; propodus with long aciculae; dactylus short, with terminal unguis; dactylar ornamentation reduced to 1 proximal posterior seta and 1-2 subdistal setules; orientation of dactylus often inverted.

Pleonites: posterodorsal border serrate (except for *Metaceradocus inermis* LEDOYER, 1983, where this border is smooth), with ventrofacial spination usually well developed; posterior border of third and often other epimeral plates serrate (only in *Metaceradocus inermis*, all the epimeral plates are smooth).

Pleopods: well developed with elongate peduncle, with long rami.

Urosomite 1: ventrofacial spine present at least in some species, with strong posterodorsal serrations; dorsal spination and setation present.

Urosomite 2: with strong posterodorsal serrations; dorsal spination and setation present.

Urosomite 3: often with one pair (sometimes two pairs?) of posterodorsal spines.

U1-U2: peduncle of U1-U2 with or without ventrofacial spines; peduncle of U1 with row of dorsolateral and dorsomedial spines; lateral distal tooth of peduncle of U1 short, in dorsolateral position; interramal tooth can be present; tip of dorsolateral border of the peduncle of U1 with a long spine pointing backwards not paired with a short spine inserted immediately behind it; tip of rami (fairly) broad and spinose (up to 4 spines).

U3: peduncle long, about 3-4 x as long as broad; rami well developed, equal in length, with tip acute, always with spines (on both rami), sometimes with plumose setae; outer ramus with 1 or 2 articles (most commonly with 1 article); the frequent disappearance of the second article results from atrophy, not from fusion with the first article.

Telson: deeply or completely cleft; each lobe with 2 apical teeth (3 teeth in *Metaceradocus vesentiniae* RUFFO, 1969), but medial one sometimes reduced; one or several apical spines; telson with dorsal spine(s) or stout setae.

COMPOSITION: *Hornellia* WALKER, 1904; *Metaceradocus* CHEVREUX, 1925.

TYPE GENUS: *Hornellia* WALKER, 1904, p. 268; etymology (after WALKER, 1904): 'named after Mr. JAS. HORNELL, F.L.S., Marine Biologist to the Ceylon Government'; type species, *Hornellia incerta* WALKER, 1904: 269, pl. 4 fig. 27.

REMARKS: The present description is based on the species descriptions and figures given by STEBBING (1910), CHEVREUX (1925), J.L. BARNARD & REISH (1959), RUFFO (1969), J.L. BARNARD (1972b), LEDOYER (1983), THOMAS & BARNARD (1986b), LYONS & MYERS (1993) and REN (2006).

The name 'Hornelliidae' was introduced by BOUSFIELD & SHIH (1994) (who condidered it themselves as a junior synonym of the Cheirocratidae), without description, hence without fulfilling the provisions of article 13 of ICZN (1999). The family Hornelliidae fam. nov. is here officially validated.

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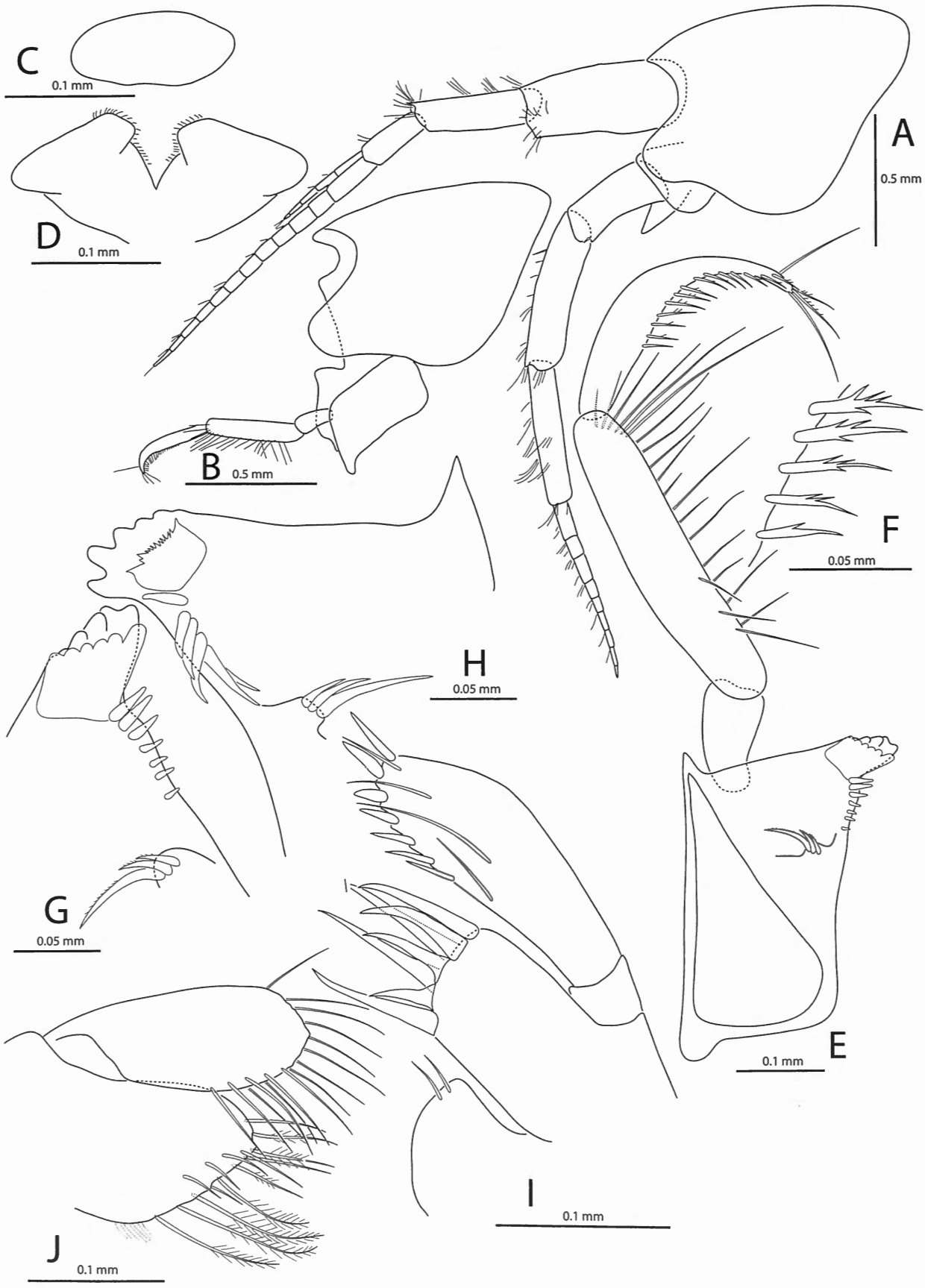

Fig. 1. – *Idunella aeqvicornis* (G.O. Sars, 1877), Norway, R/V Johan Ruud, sta. 1085-98. A, B, ovigerous female (8.5 mm); C-J, adult male (7 mm). A, head and antennae; B, head, epistome and mandible; C, upper lip; D, lower lip; E, left Md; F, proximal D3-setae of article 3 of palp of left Md; G, distal part of left Md; H, distal part of right Md; I, left Mx1; J, right Mx2.

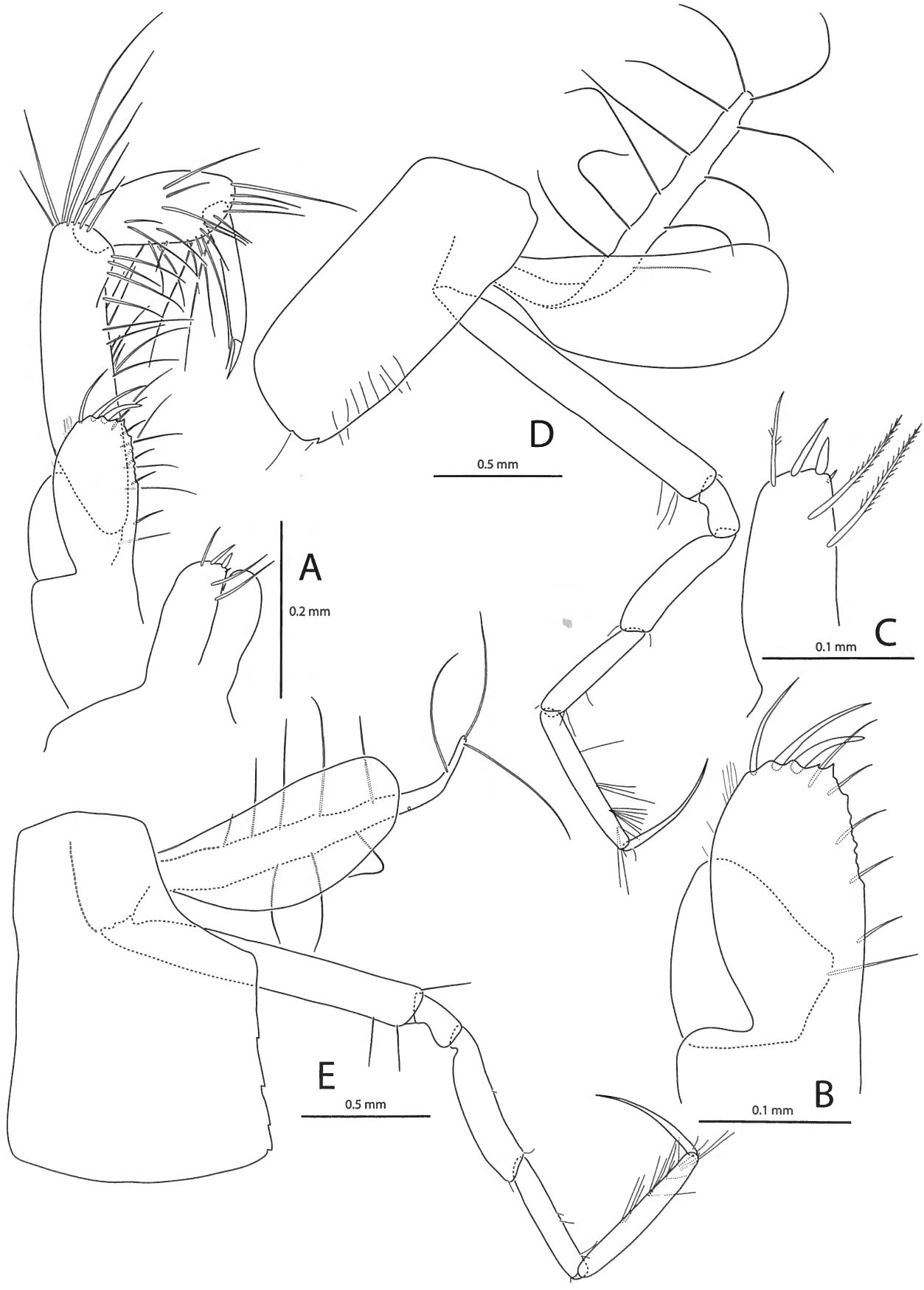

Fig. 2. – *Idunella aeqvicornis* (G.O. SARS, 1877), Norway, R/V Johan Ruud, sta. 1085-98. A, B, C, adult male (7 mm); D, E, female (8.5 mm). A, Mxp; B, left outer plate and article 1 of palp of Mxp; C, left inner plate of Mxp; D, left P3; E, left P4.

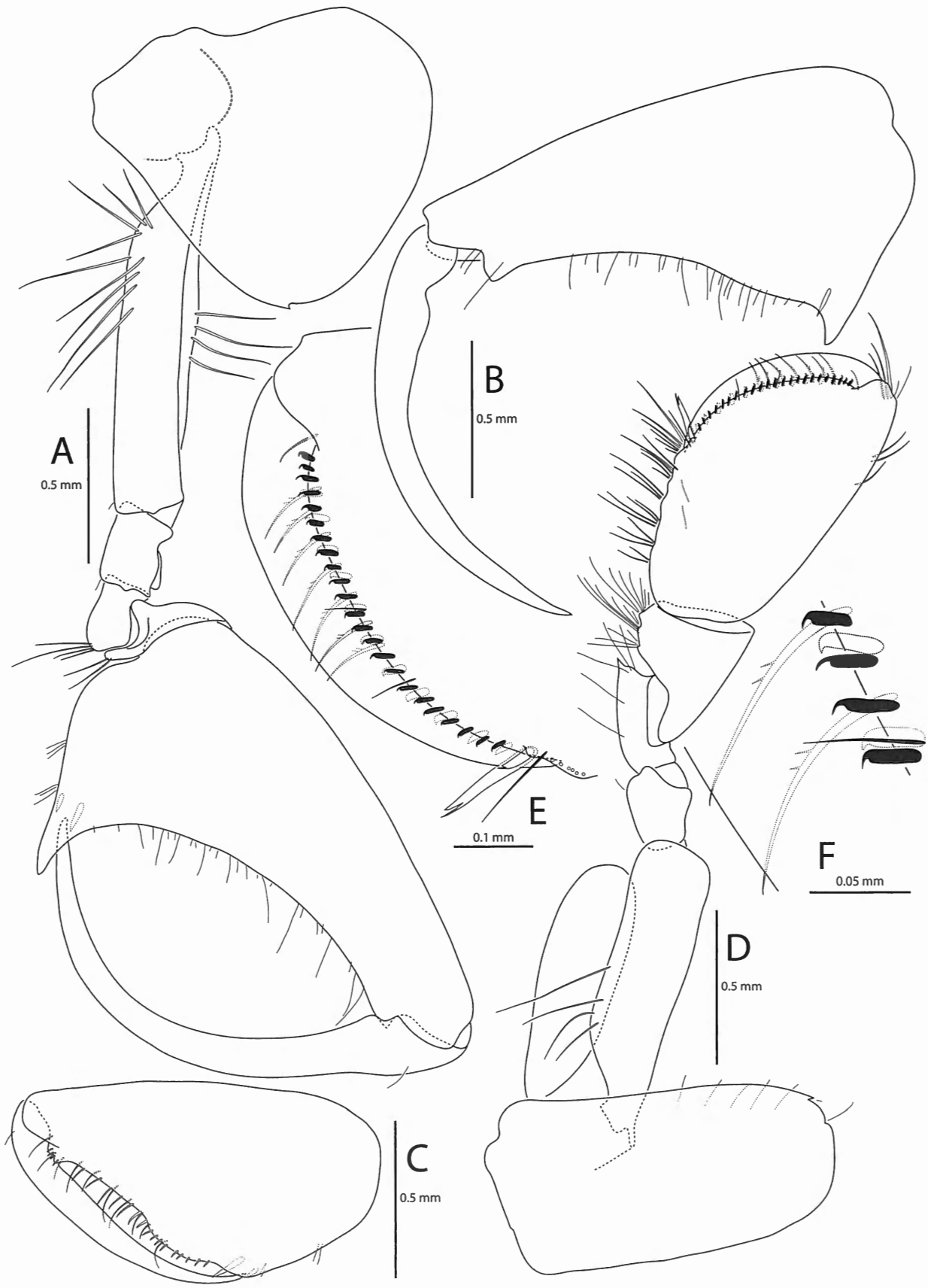

Fig. 3. – *Idunella aeqvicornis* (G.O. Sars, 1877), Norway; A, D, E, F, adult male (7 mm), R/V Johan Ruud, sta. 1085-98; B, adult male (about 7 mm), R/V Håkon Mosby, sta. 85.1.8.3; C, immature male, R/V Håkon Mosby, sta. 82.1.21.6. A, right Gn1 (outer view); B, chela of right Gn2 (medial view); C, chela of left Gn1 (outer view); D, left Gn2 (outer view); E, palm and dactylus of left Gn2; F, detail of the same.

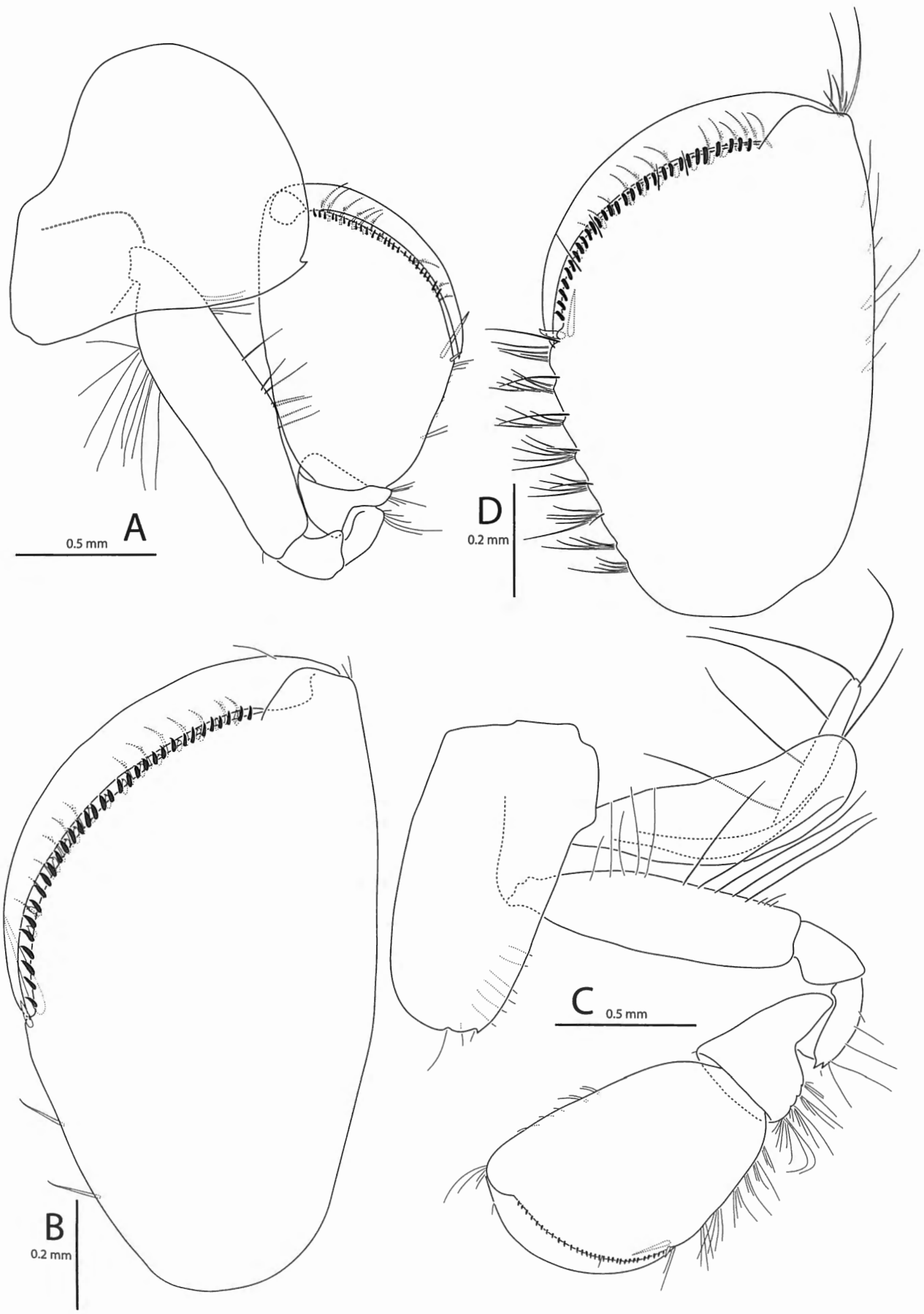

Fig. 4. – *Idunella aeqvicornis* (G.O. SARS, 1877), Norway, adult females (about 8 mm). A, C, R/V Johan Ruud, sta. 1085-98; B, D, R/V Håkon Mosby, sta. 82.11.27.1. A, right Gn1; B, chela of left Gn1; C, left Gn2; D, chela of left Gn2.

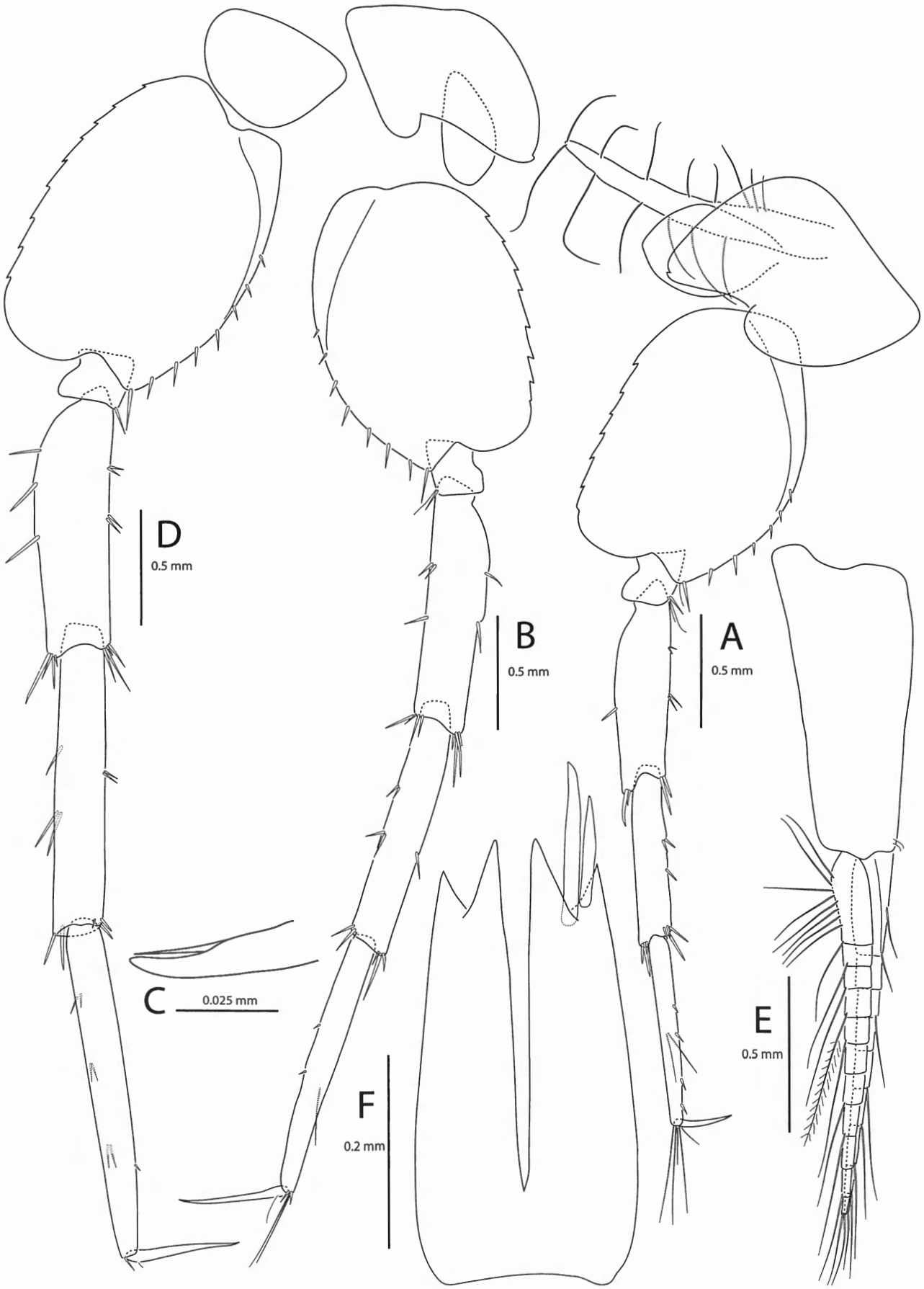

Fig. 5. – *Idunella aeqvicornis* (G.O. Sars, 1877), Norway, R/V Johan Ruud, sta. 1085-98. A-E, ovigerous female (8.5 mm); F, adult male (7 mm). A, right P5; B, left P6; C, tip of dactylus of left P6; D, right P7; E, right pleopod 1; F, telson.

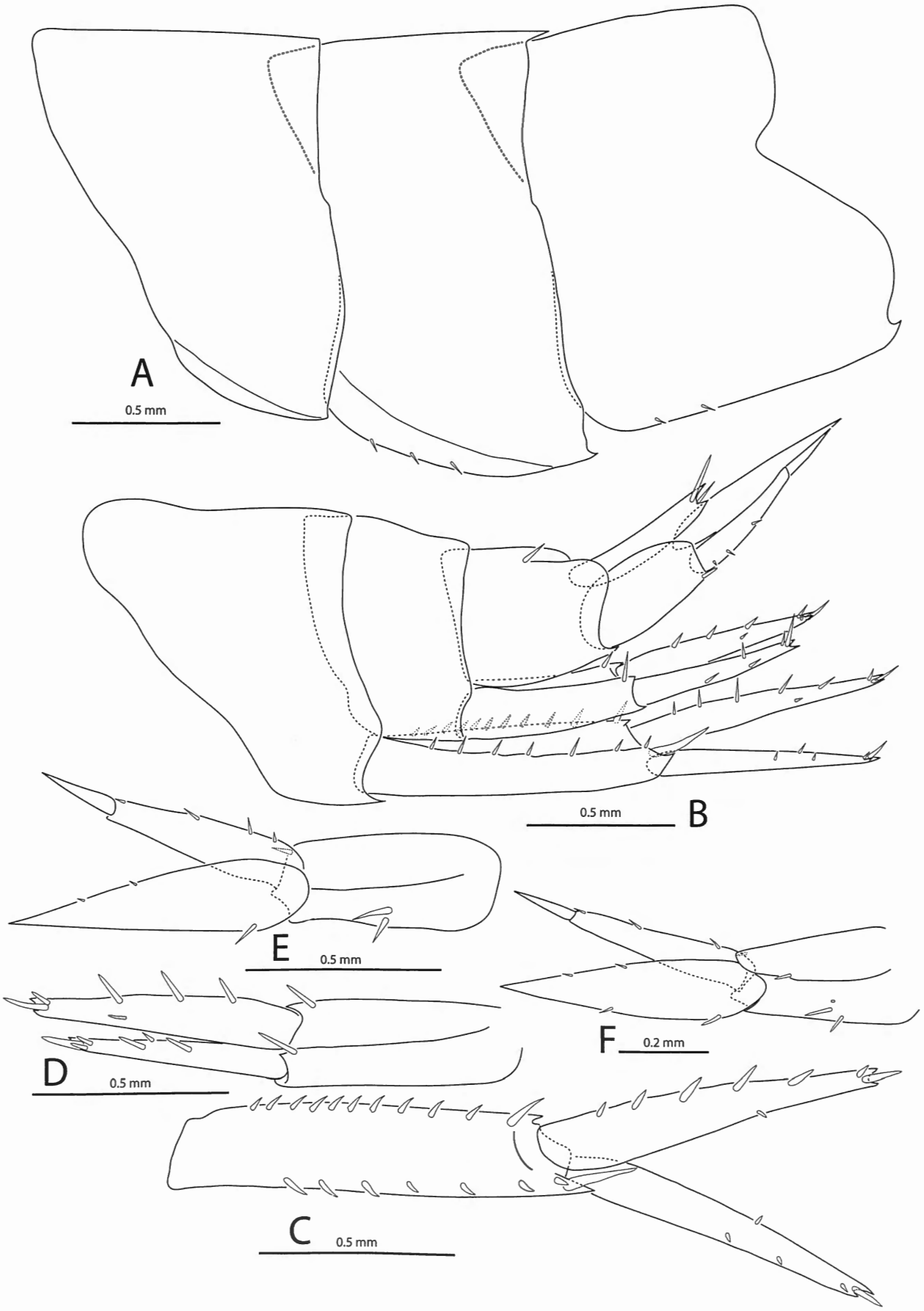

Fig. 6. – *Idunella aeqvicornis* (G.O. SARS, 1877), Norway, R/V Johan Ruud, sta. 1085-98. A-E, ovigerous female (8.5 mm); F, adult male (7 mm). A, pleosome; B, urosome; C, left U1; D, right U2; E-F, left U3.

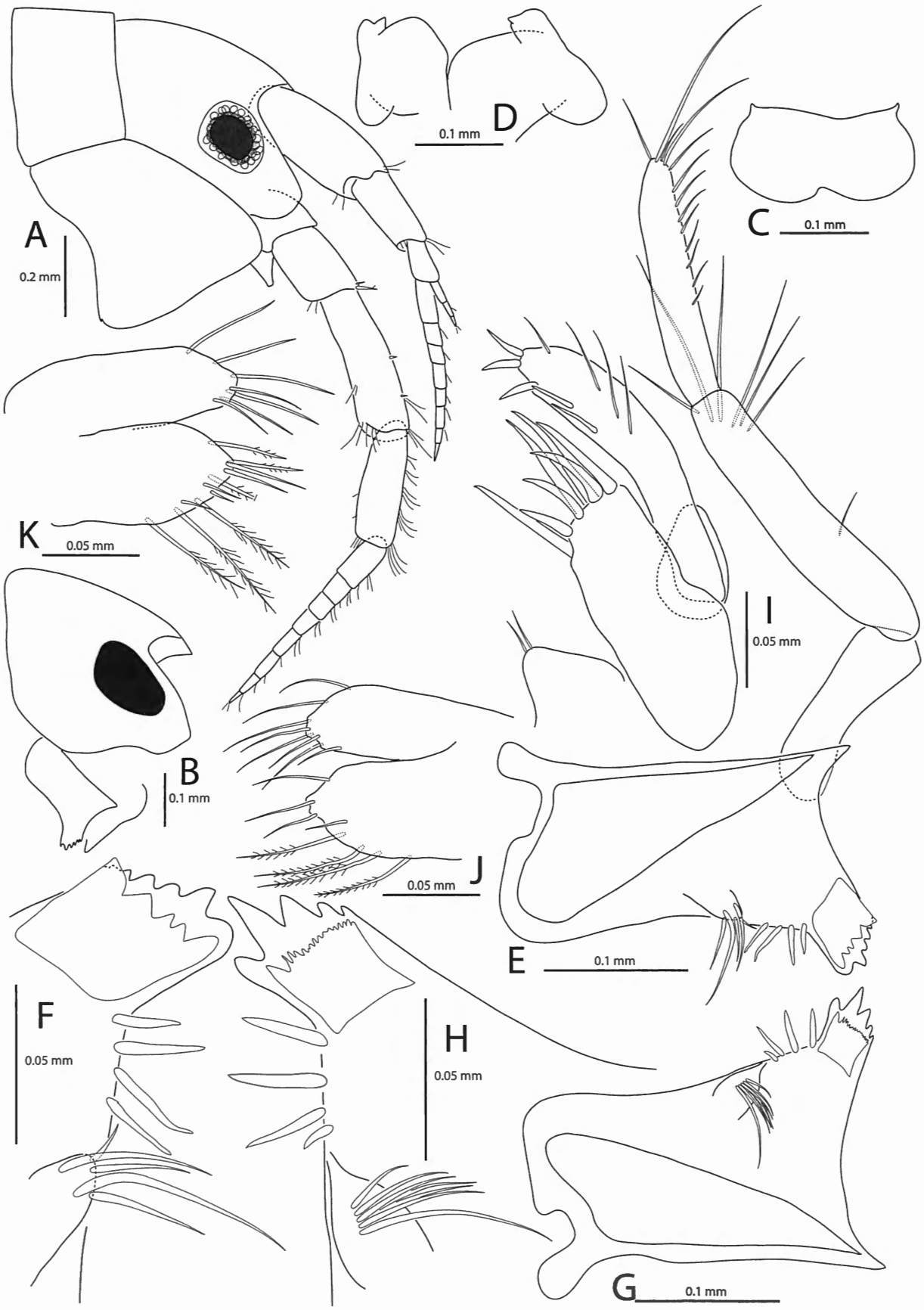

Fig. 7. – *Idunella picta* (Norman, 1889), W France, Ile Callot (5 mm). A, I, K, female 1; B, male 2; C-H, J, male 1. A, head, antennae, first free thoracic segment; B, head, epistome, and mandible in lateral view; C, upper lip; D, lower lip; E, left Md; F, distomedial part of left Md; G, right Md; H, distomedial part of right Md; I, left Mx1; J, left Mx2; K, right Mx2.

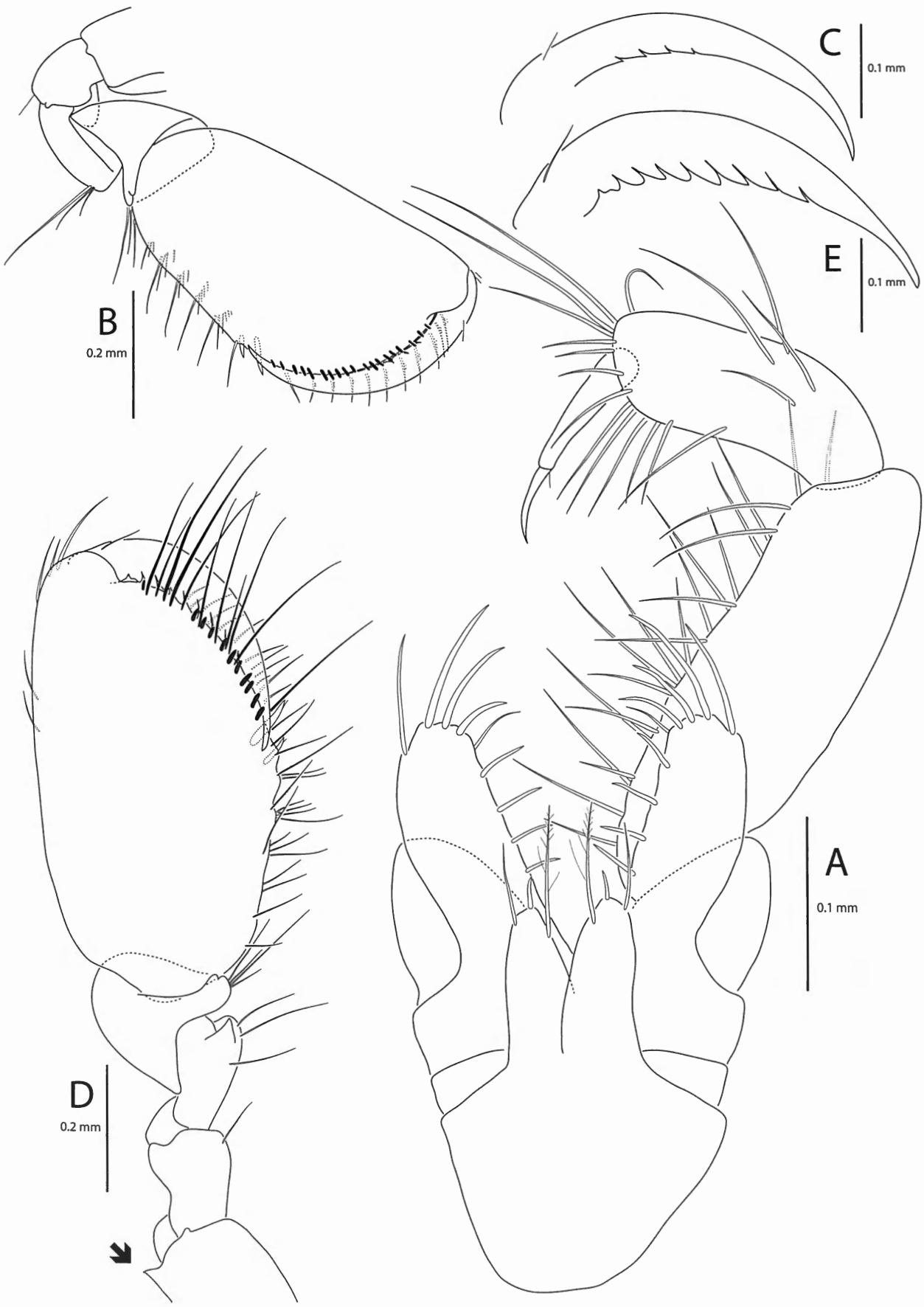

Fig. 8. – *Idunella picta* (Norman, 1889), W France, Ile Callot (5 mm). A, female 1; B-E, male 1. A, Mxp; B, right Gn1; C, dactylus of right Gn1, D, right Gn2; E, dactylus of right Gn2.

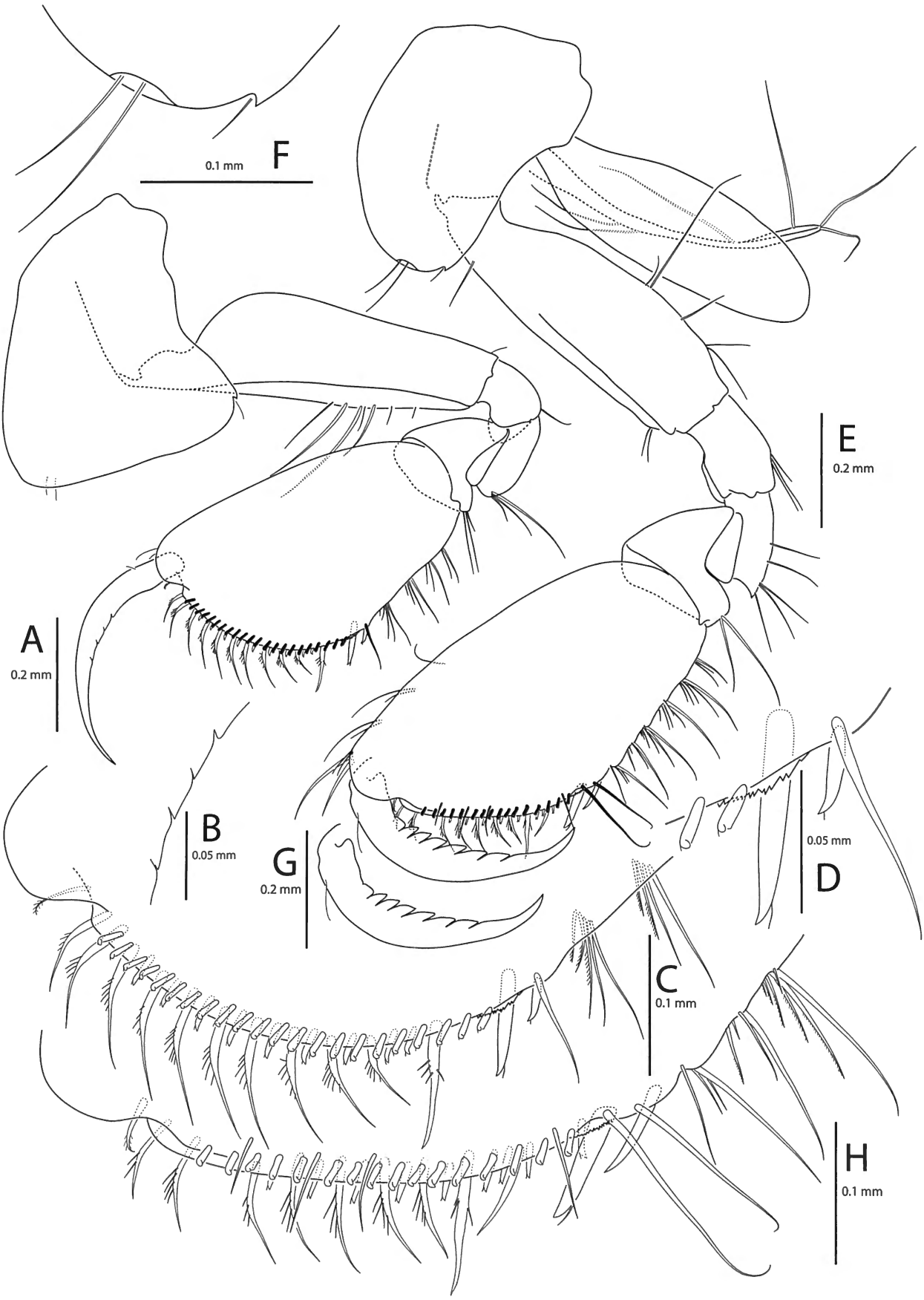

Fig. 9. – *Idunella picta* (Norman, 1889), W France, Ile Callot, female 1 (5 mm). A, left Gn1; B, teeth of dactylus of left Gn1; C, posterodistal border of propodus of left Gn1; D, proximal part of palm of left Gn1; E, left Gn2; F, ventral border of left coxa 2; G, dactylus of left Gn2; H, posterodistal border of propodus of left Gn2.

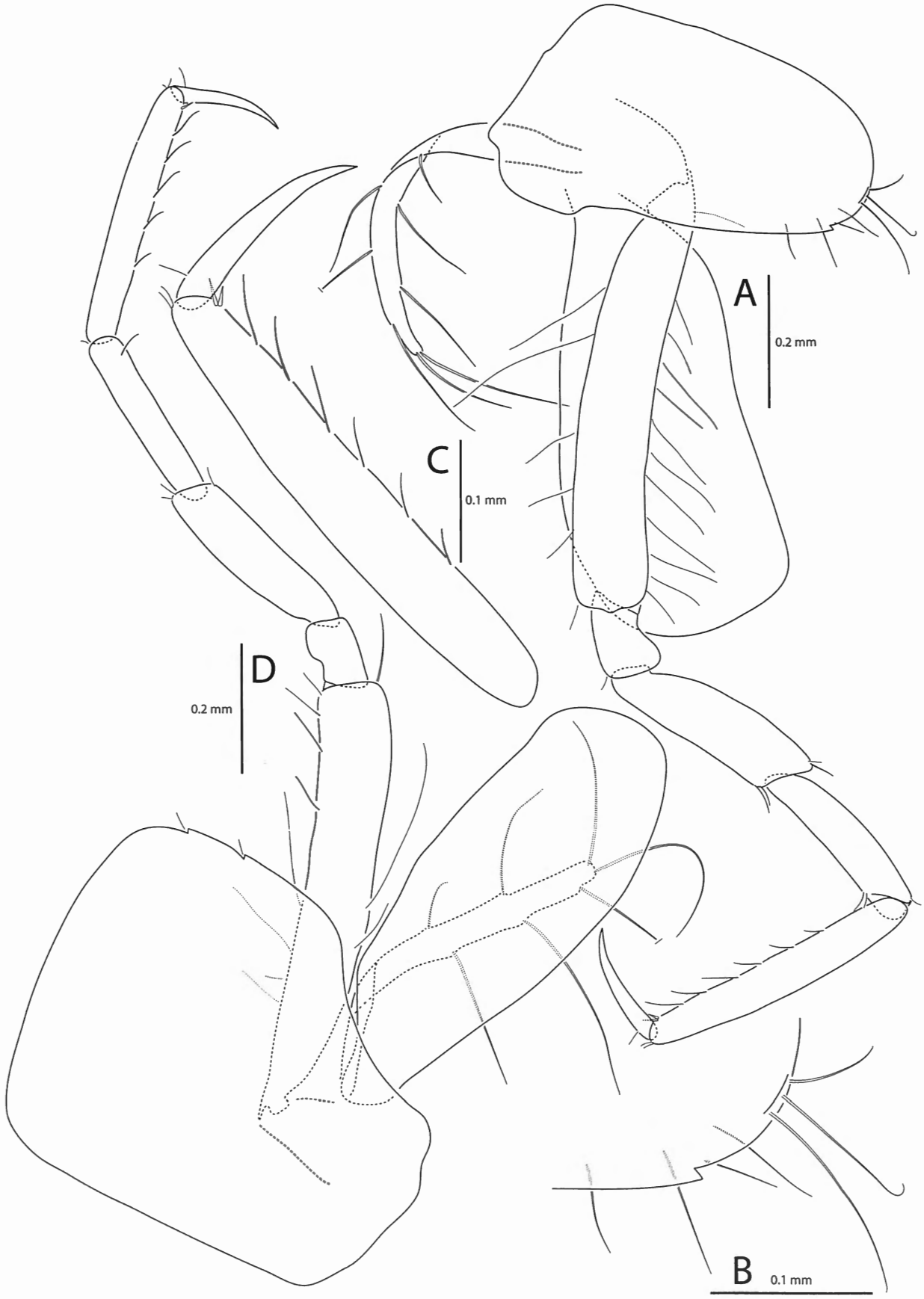

Fig. 10. – *Idunella picta* (NORMAN, 1889), W France, Ile Callot, female 1 (5 mm). A, right P3; B, ventral border of right coxa 3; C, propodus and dactylus of right P3; D, right P4.

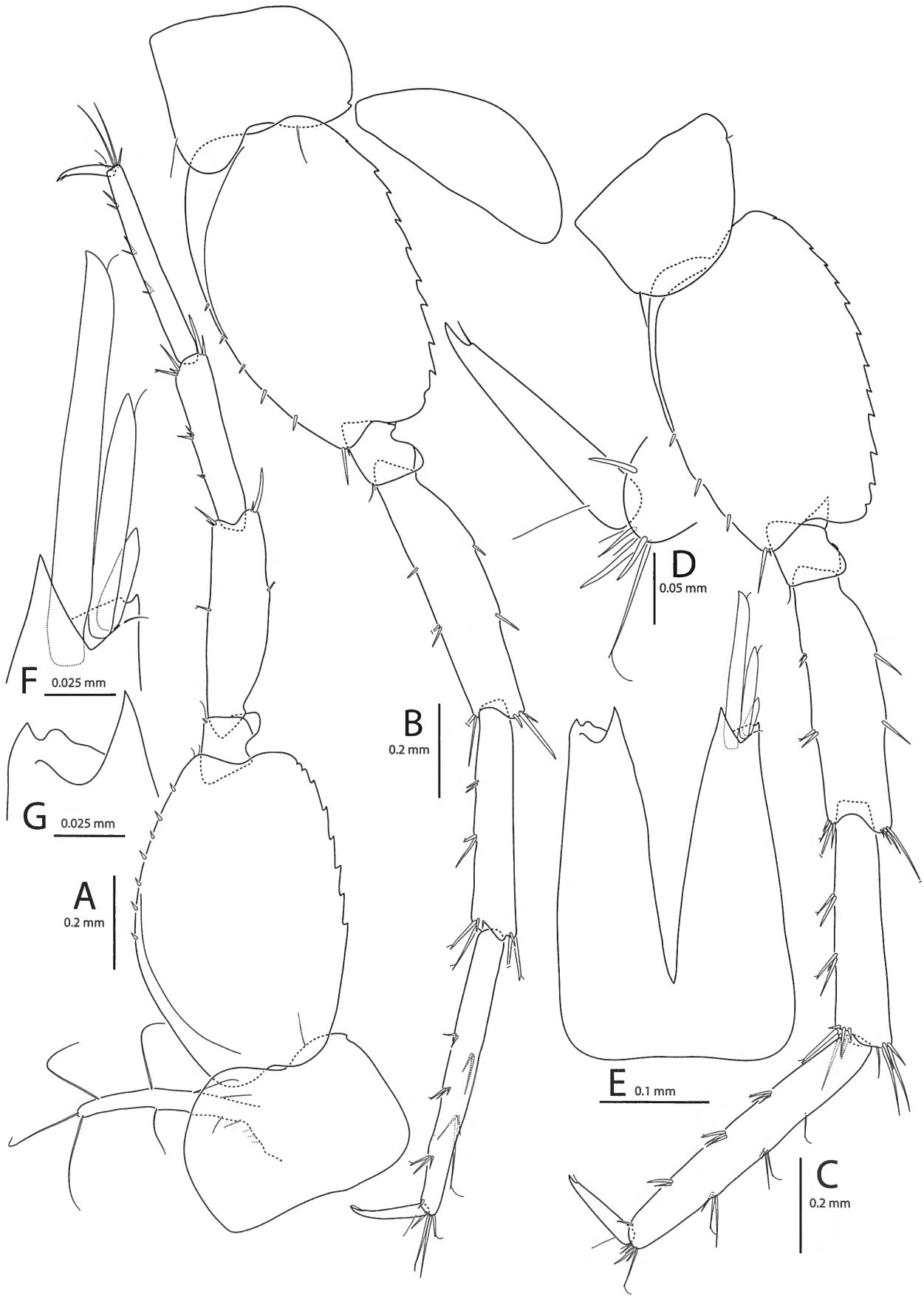

Fig. 11. – *Idunella picta* (Norman, 1889), W France, Ile Callot (5 mm). A-D, female 1; E-G, female 2. A, right P5; B, left P6; C, left P7; D, dactylus of left P7; E, telson; F, tip of left lobe of telson; G, tip of right lobe of telson (spines not shown).

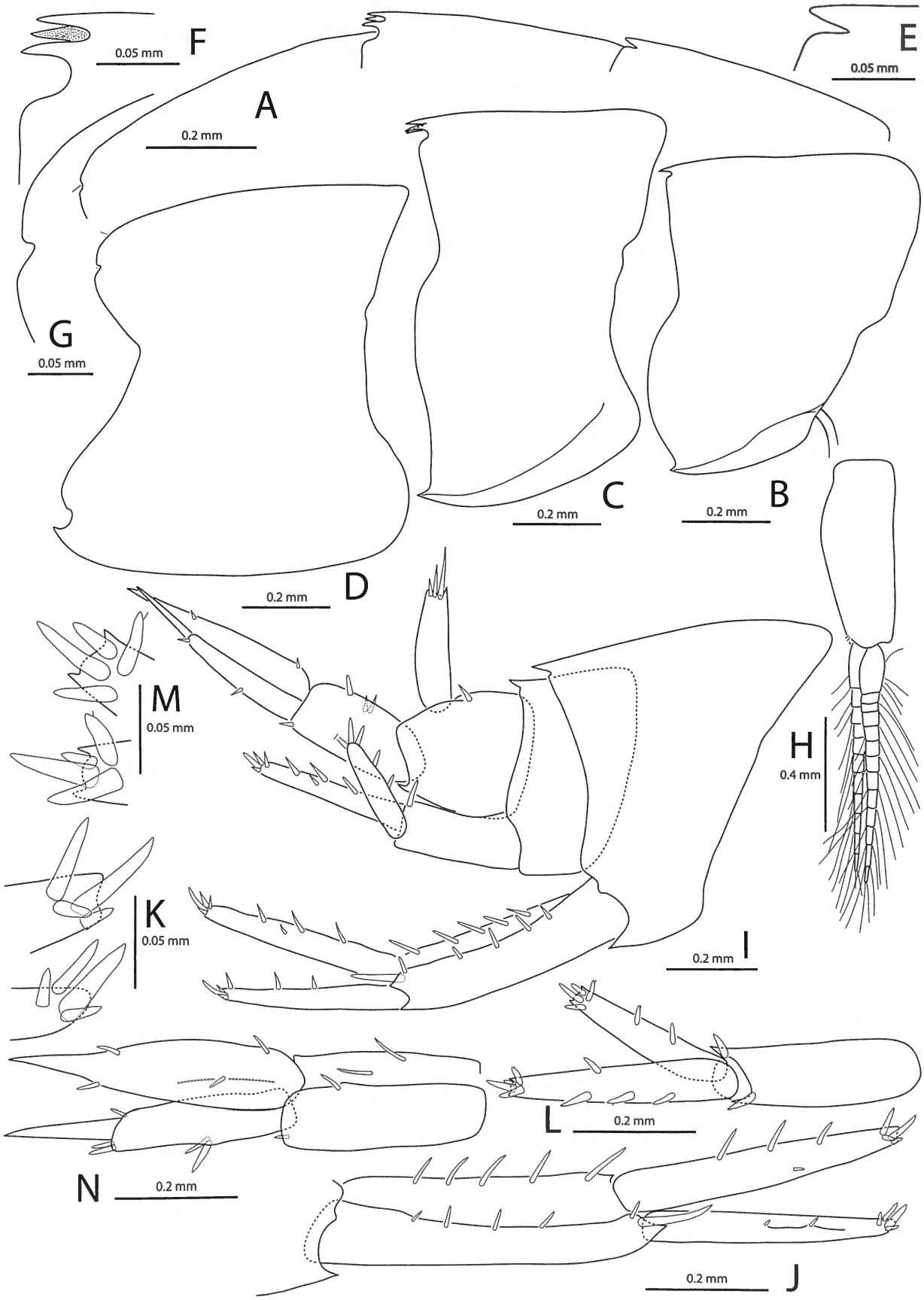

Fig. 12. – *Idunella picta* (Norman, 1889), W France, Ile Callot (5 mm). I-N, female 1; A, E, F, H, female 2; B, C, D, G, male 1. A, dorsal border of pleosome in lateral view; B, pleonite 1; C, pleonite 2; D, pleonite 3; E, posterodorsal corner of pleonite 1; F, posterolateral corner of pleonite 2; G, posterolaterodorsal corner of pleonite 3; H, right pleopod 1; I, urosome; J, left U1; K tip of rami of left U1; L, left U2; M, tip of rami of left U2; N, right U3.

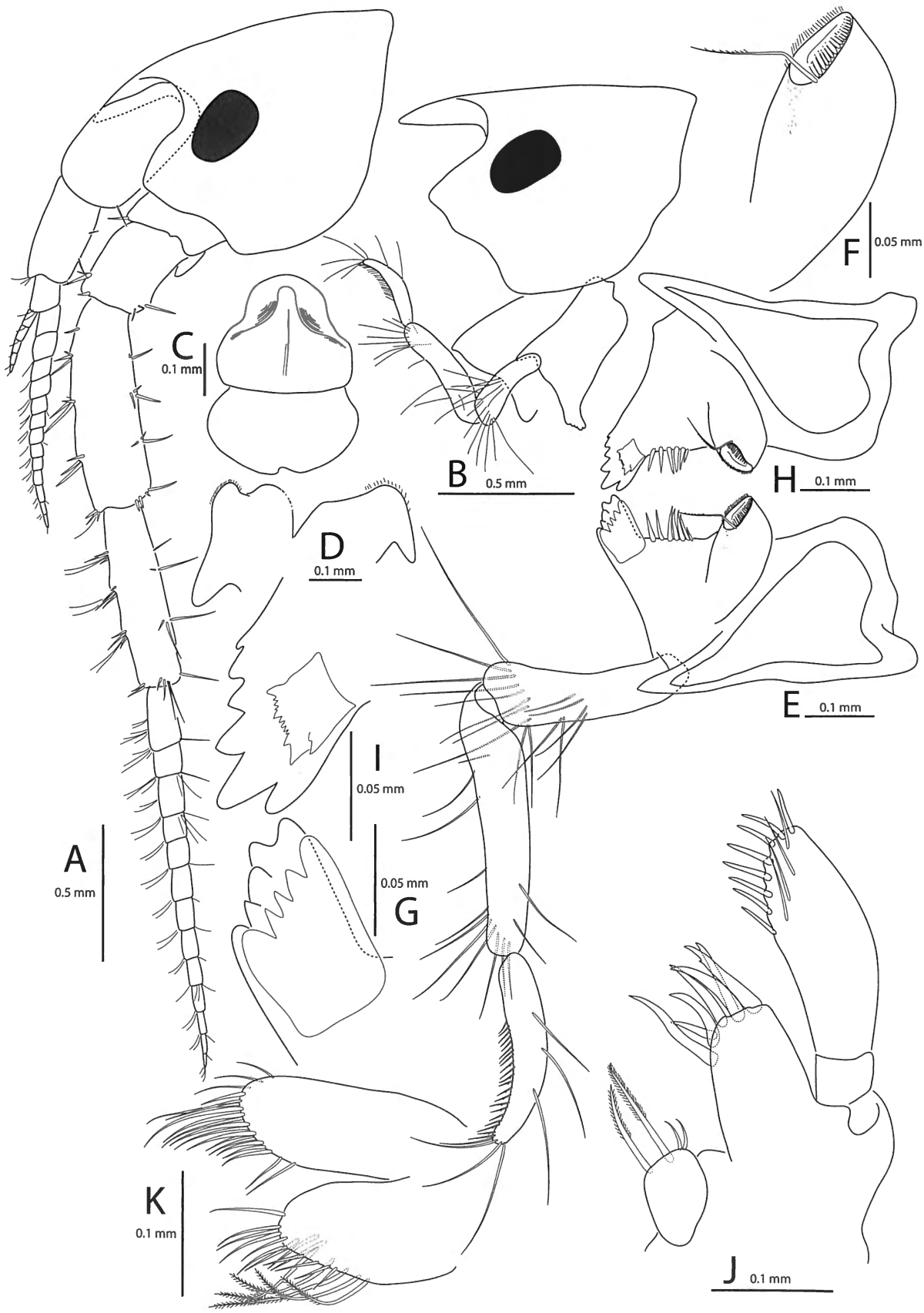

Fig. 13. – *Sextonia longirostris* Chevreux, 1920, ovigerous female, W France, Le Dossen (9 mm). A, head with antennae; B, head with left Md and epistome; C, epistome and upper lip in frontal view; D, lower lip; E, left Md; F, molar process of left Md; G, incisor process and lacinia mobilis of left Md; H, right Md; I, incisor process and lacinia mobilis of right Md; J, left Mx1; K, left Mx2.

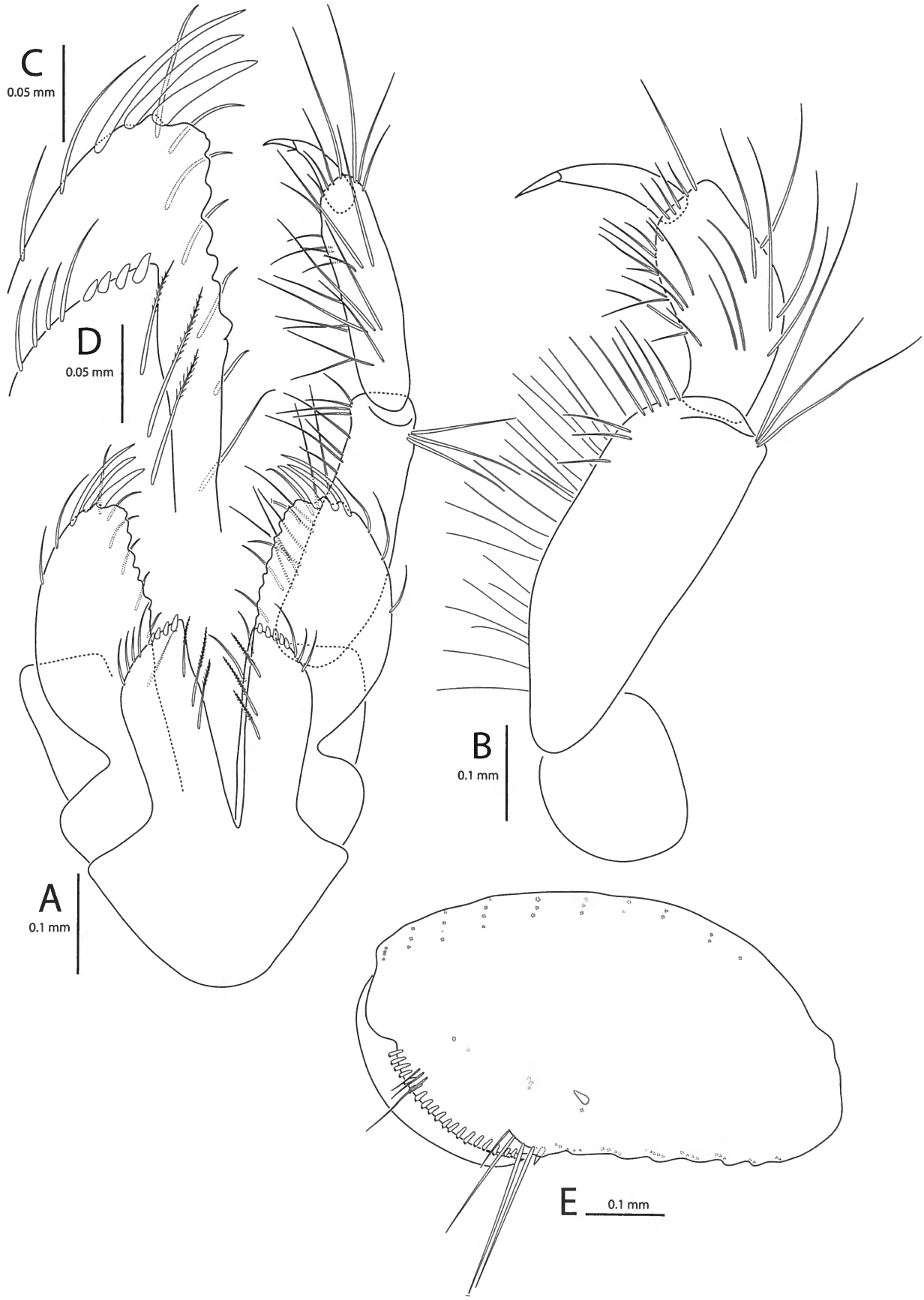

Fig. 14. – *Sextonia longirostris* CHEVREUX, 1920, W France, Le Dossen; A, C, D, E, ovigerous female (9 mm); B, male (10 mm). A, Mxp; B, right palp of Mxp (in flattened position); C, distal part of left outer plate of Mxp; D, distal part of left inner plate of Mxp; E, chela of left Gn2 (position of medial setae indicated by disk of insertion).

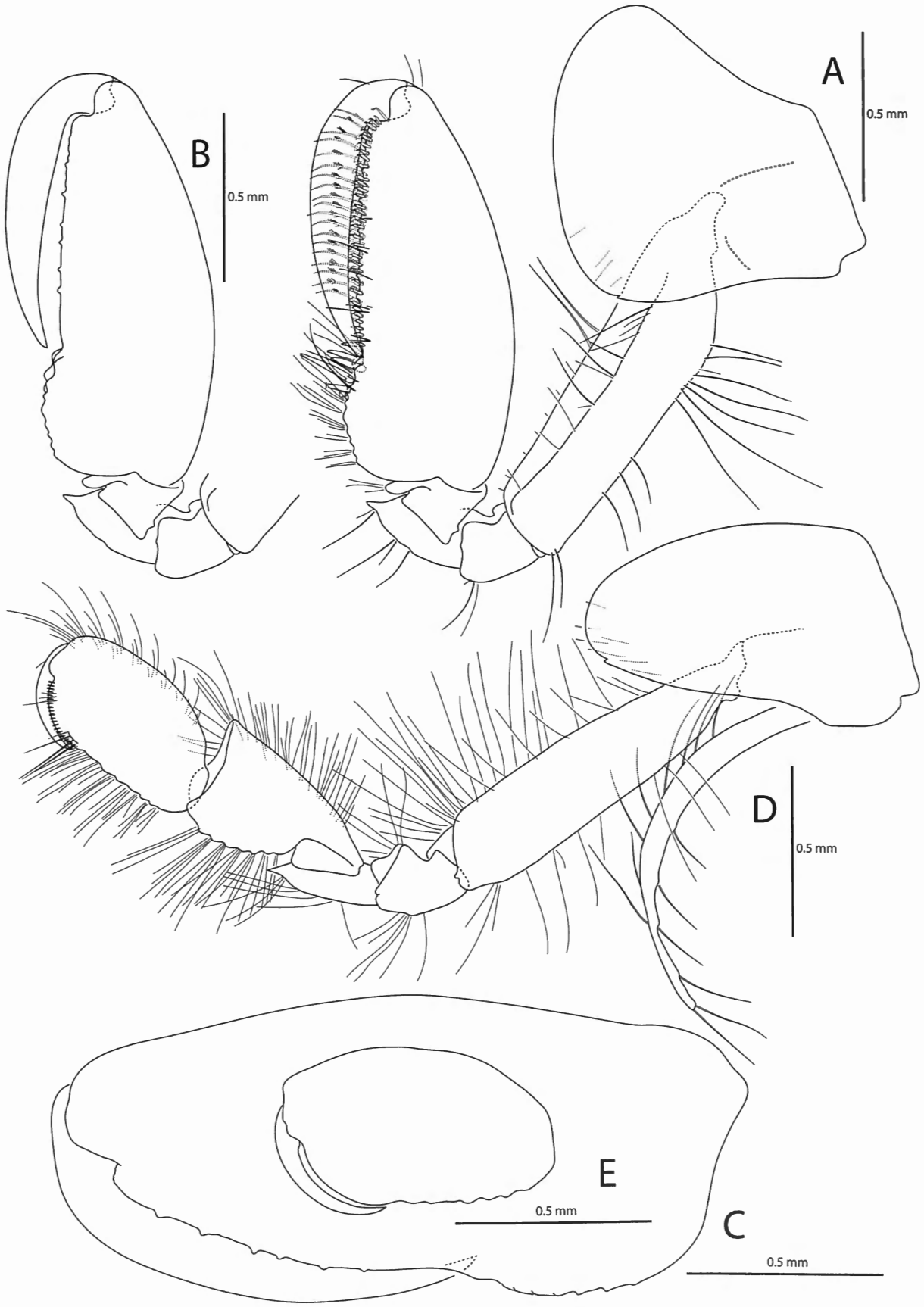

Fig. 15. – *Sextonia longirostris* Chevreux, 1920, W France, Le Dossen; A, B, D, ovigerous female (9 mm); C, E, male (10 mm). A, left Gn1; B, distal part of left Gn1 (ornamentation not shown); C, chela of left Gn1; D, left Gn2; E, chela of left Gn2.

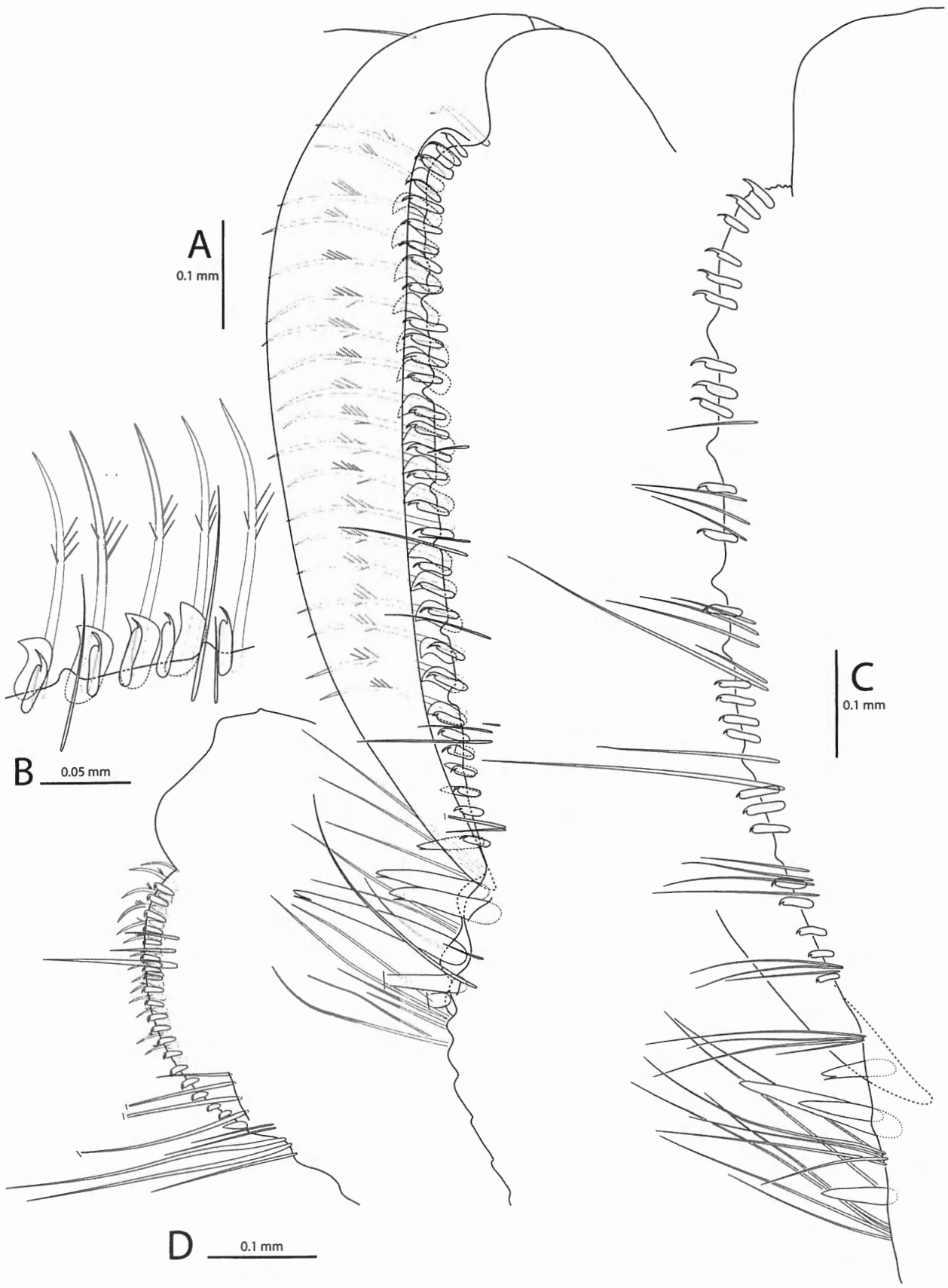

Fig. 16. – *Sextonia longirostris* CHEVREUX, 1920, W France, Le Dossen; A, B, ovigerous female (9 mm); C, D, male (10 mm). A, posterodistal part of chela of left Gn1; B, detail of the palm of left Gn1; C, palm of left Gn1 (medial hooked spines and medial spinose setae not shown); D, posterodistal border of propodus of left Gn2.

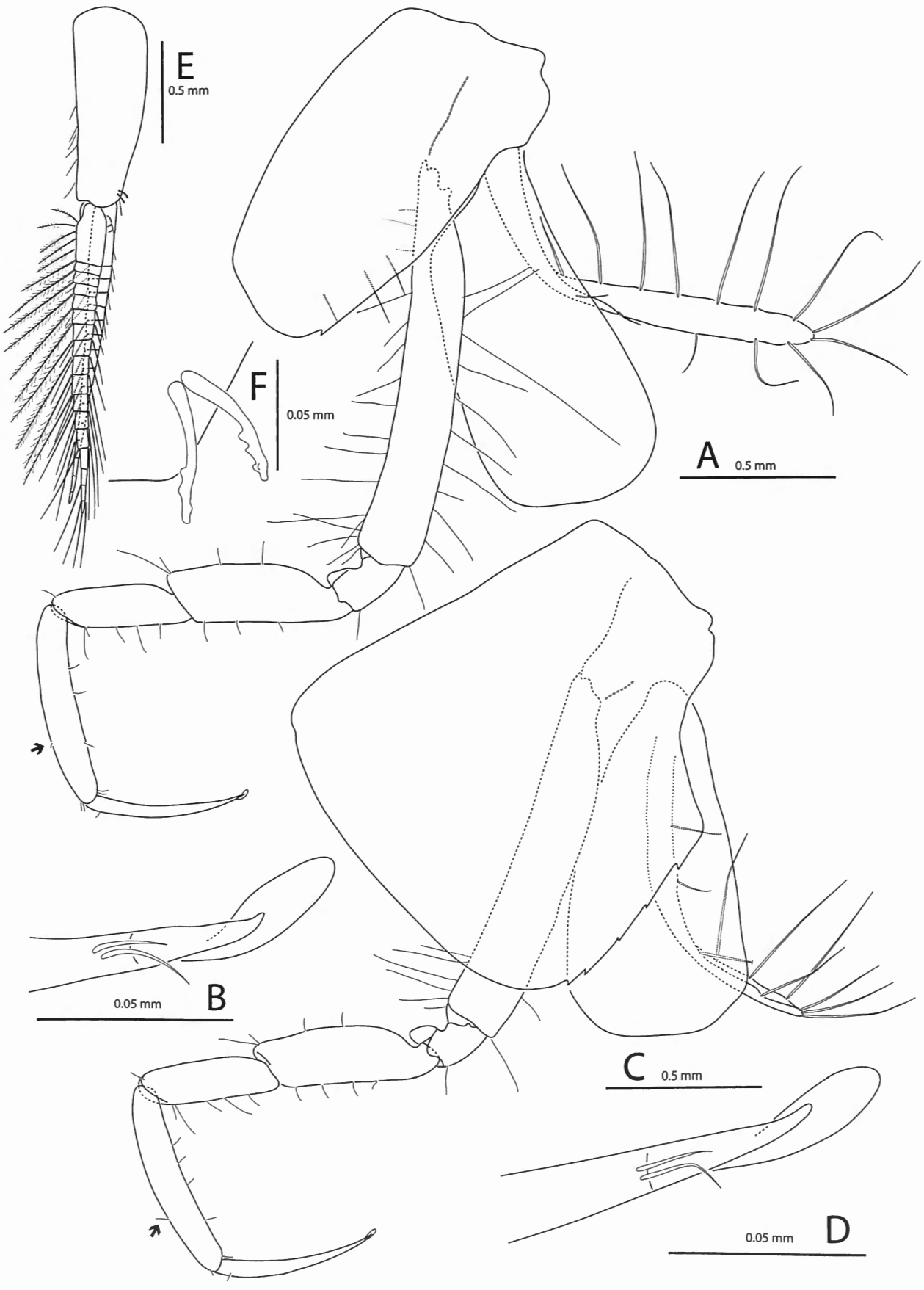

Fig. 17. – *Sextonia longirostris* Chevreux, 1920, ovigerous female (9 mm), W France, Le Dossen. A, left P3; B, tip of dactylus of left P3; C, left P4; D, tip of dactylus of left P4; E, right pleopod 1; F, coupling hooks of right pleopod 1.

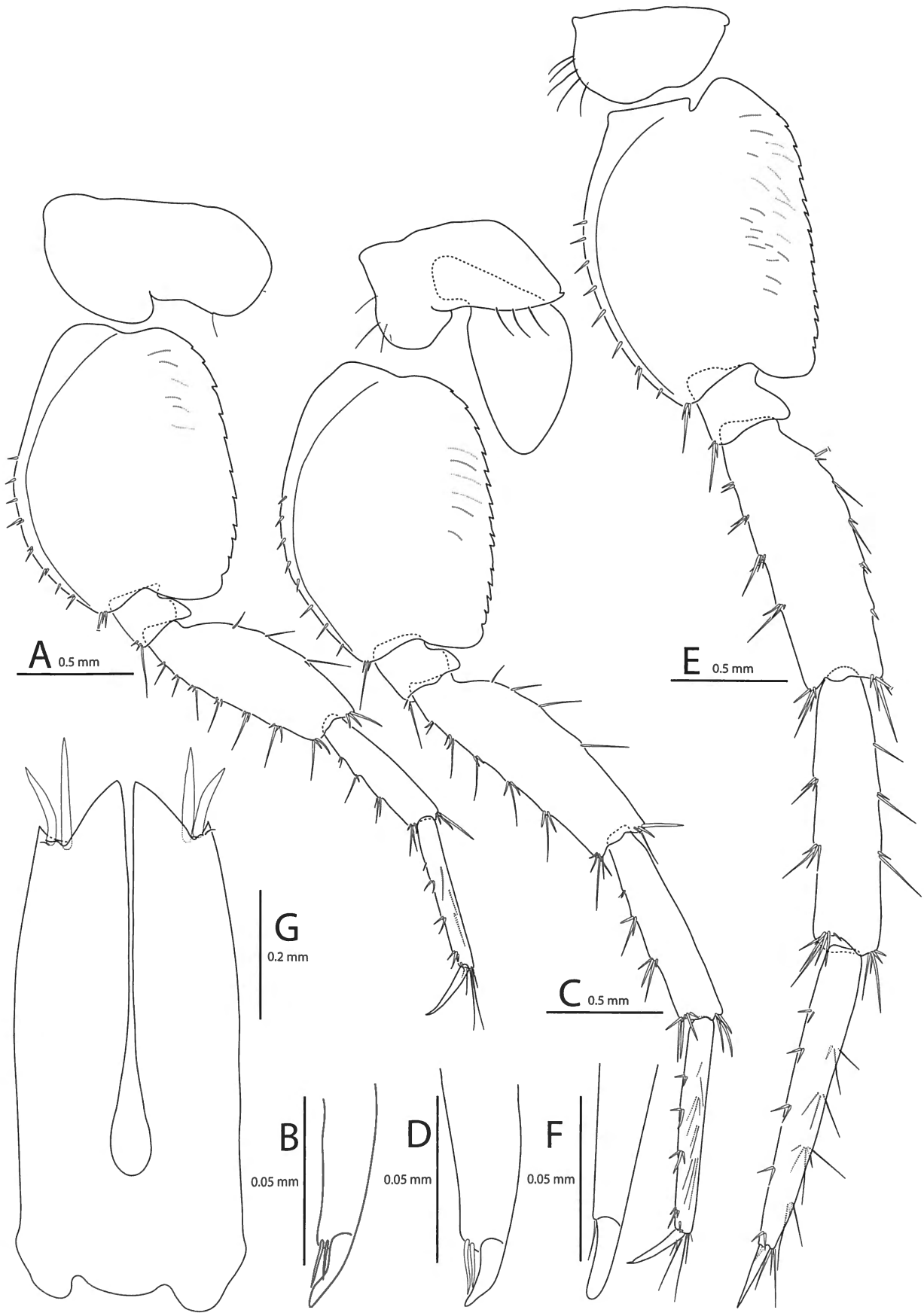

Fig. 18. – *Sextonia longirostris* Chevreux, 1920, W France, Le Dossen; A-F, ovigerous female (9 mm); G, male (10 mm). A, left P5; B, tip of dactylus of left P5; C, left P6; D, tip of dactylus of left P6; E, left P7; F, tip of dactylus of left P7; G, telson.

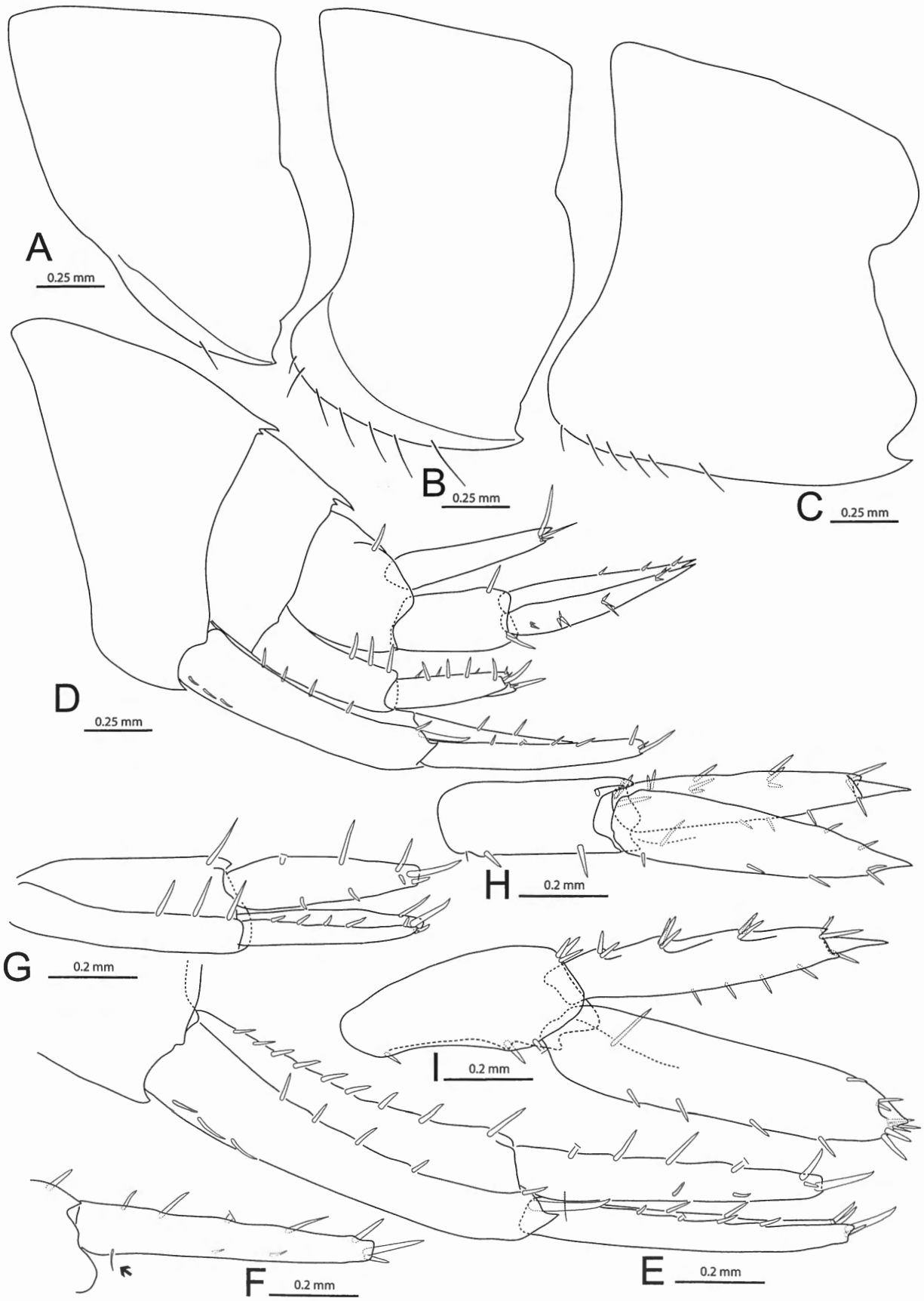

Fig. 19. – *Sextonia longirostris* Chevreux, 1920, W France, Le Dossen; A-H, ovigerous female (9 mm); I, male (10 mm). A, pleonite 1; B, pleonite 2; C, pleonite 3; D, urosome; E, left U1; F, inner ramus of right U1 (ventral view); G, left U2; H, I, right U3.

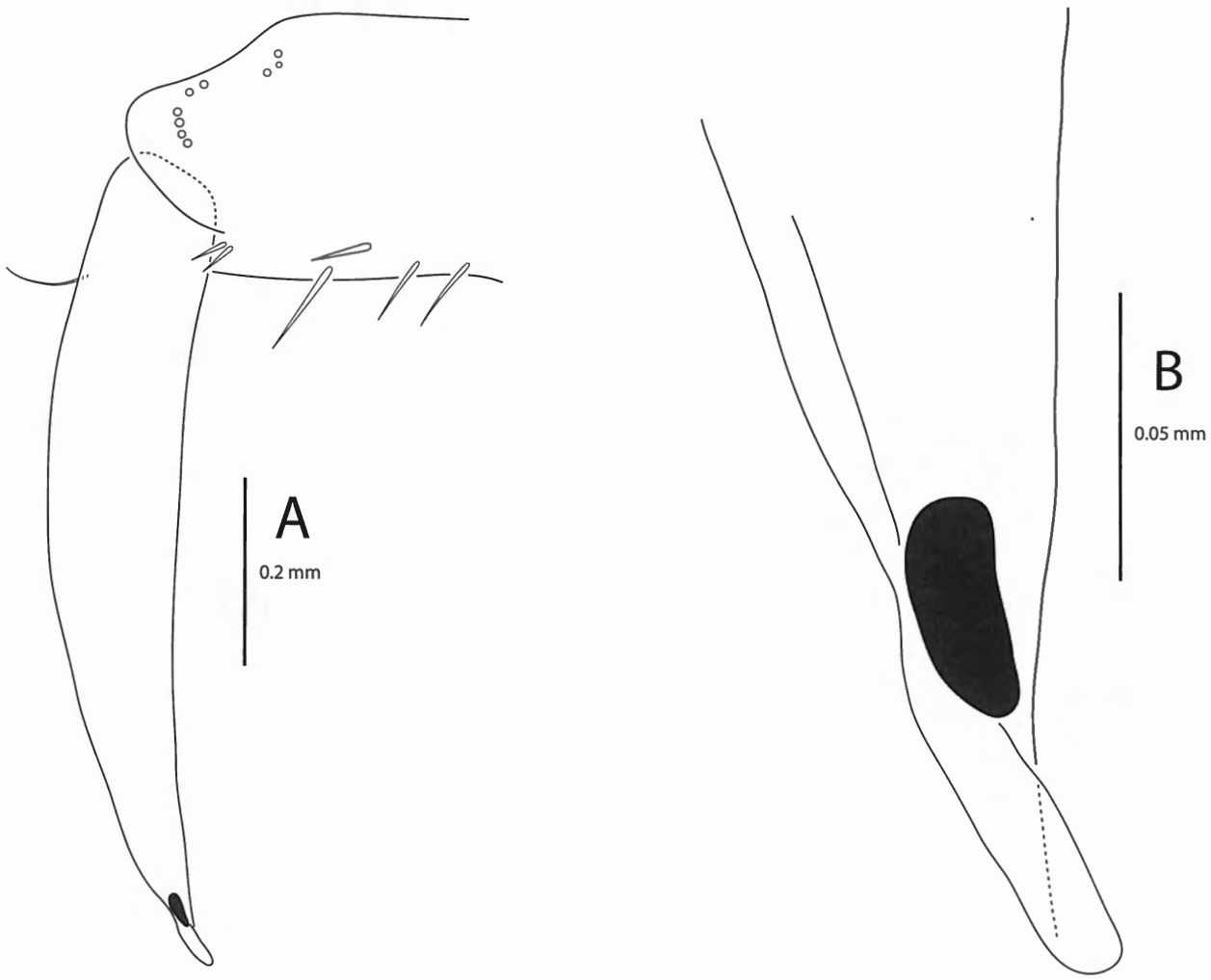

Fig. 20. – *Oediceroides lahilhei* CHEVREUX, 1911, female (about 22 mm), W Antarctica, R/V Polarstern, cruise ANTXXIII-8, station, 654-6, 61°22.80'S 056°03.84'W to 61°23.35'S 056°04.89'W, 341-342 m, Agassiz trawl, 29.xii.2006, coll. C. D'UDEKEM D'ACOZ & H. ROBERT, RBINS I.G. 31.071. A, dactylus of left P3; B, tip of dactylus of left P3 (unguis in black).

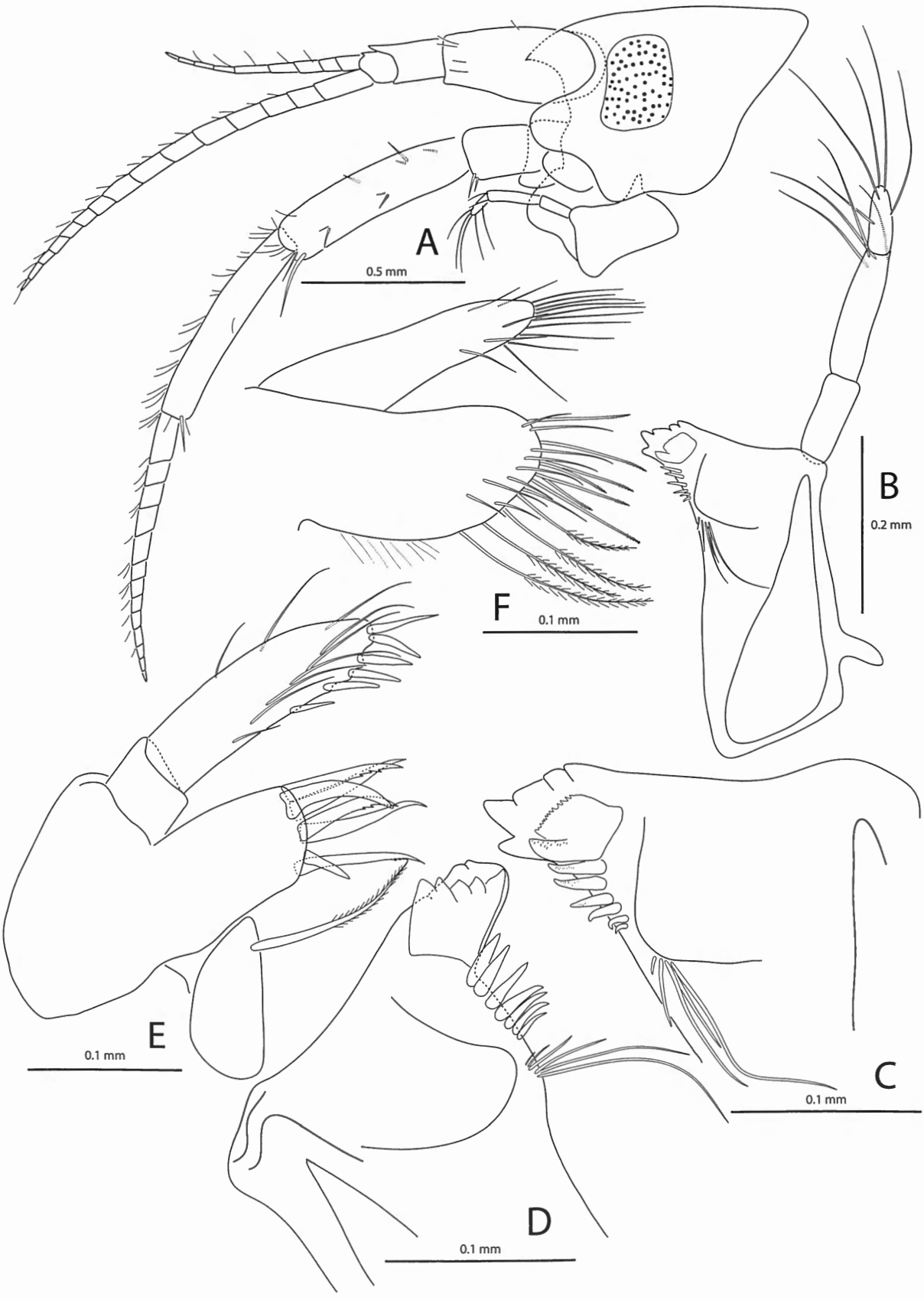

Fig. 21. – *Liljeborgia* (*Liljeborgia*) *brevicornis* (Bruzelius, 1859), ovigerous female (7 mm), R/V Johan Ruud sta. 303-05, N Norway, SW Magerøya. A, head with appendages; B, right Md; C, tip of right Md; D, tip of left Md; E, right Mx1; F, right Mx2.

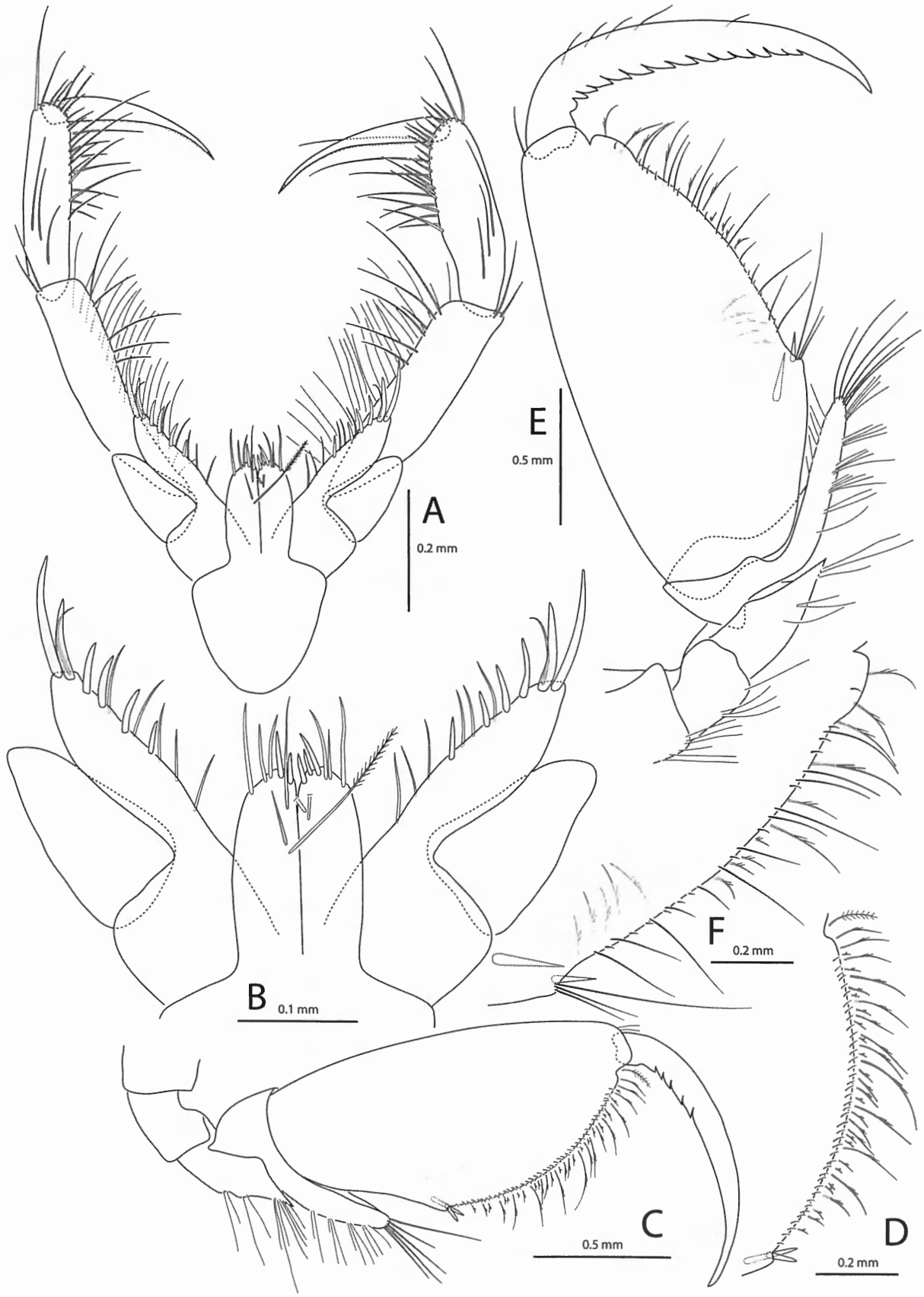

Fig. 22. – *Liljeborgia* (*Liljeborgia*) *brevicornis* (BRUZELIUS, 1859), A, B, ovigerous female (7 mm), R/V Johan Ruud sta. 303-05, N Norway, SW Magerøya; C-F, male (8 mm), R/V August Brinkmann, sta. E43-73, Brattholmen Hjeltefjorden. A, Mxp; B, plates and article 1 of palp of Mxp; C, right Gn1; D, palm of right Gn1; E, right Gn2; F, palm of right Gn2.

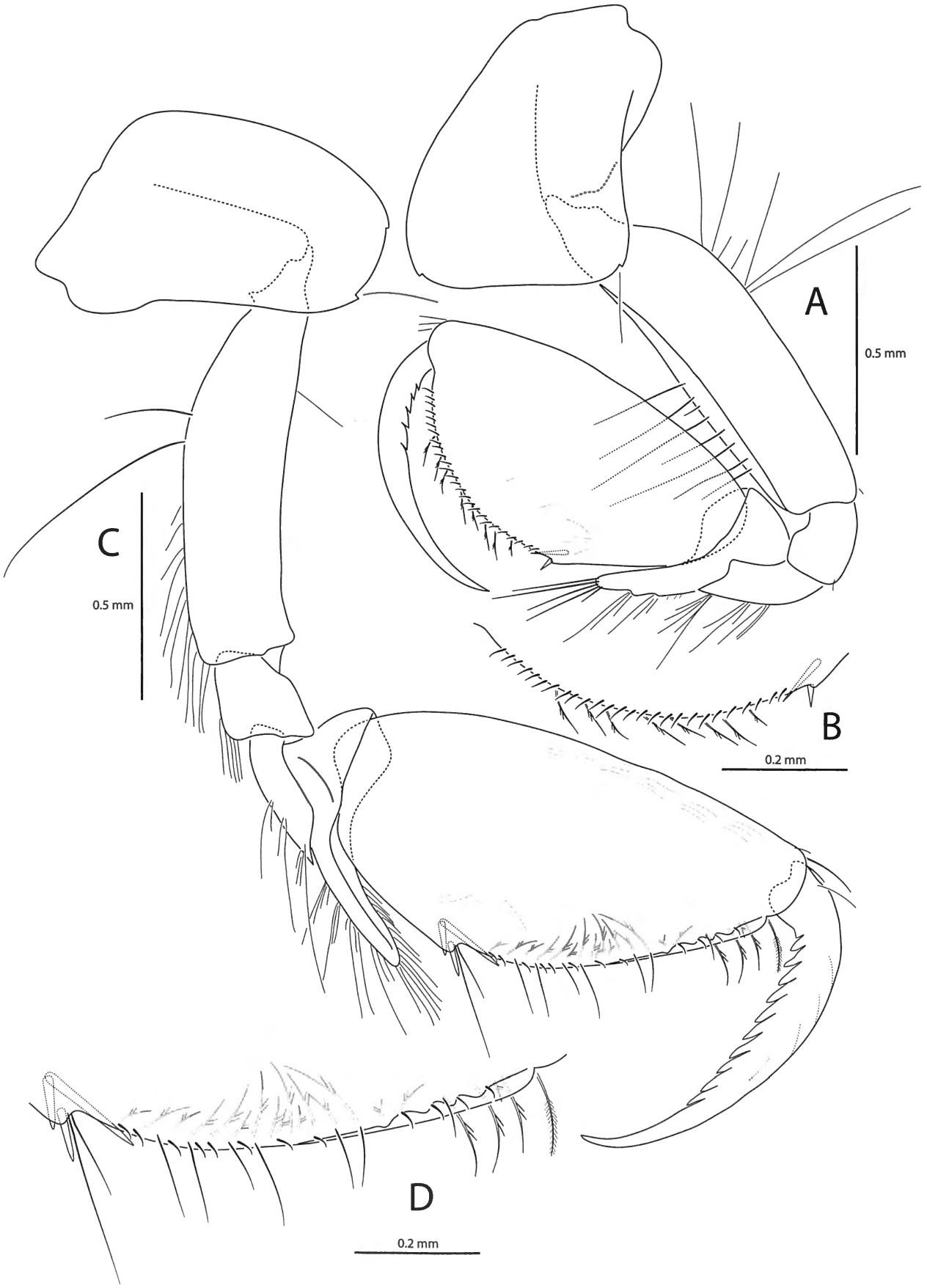

Fig. 23. – *Liljeborgia* (*Liljeborgia*) *brevicornis* (Bruzelius, 1859), ovigerous female (7 mm), R/V Johan Ruud sta. 303-05, N Norway, SW Magerøya. A, left Gn1; B, palm of left Gn1; C, right Gn2; D, palm of right Gn2.

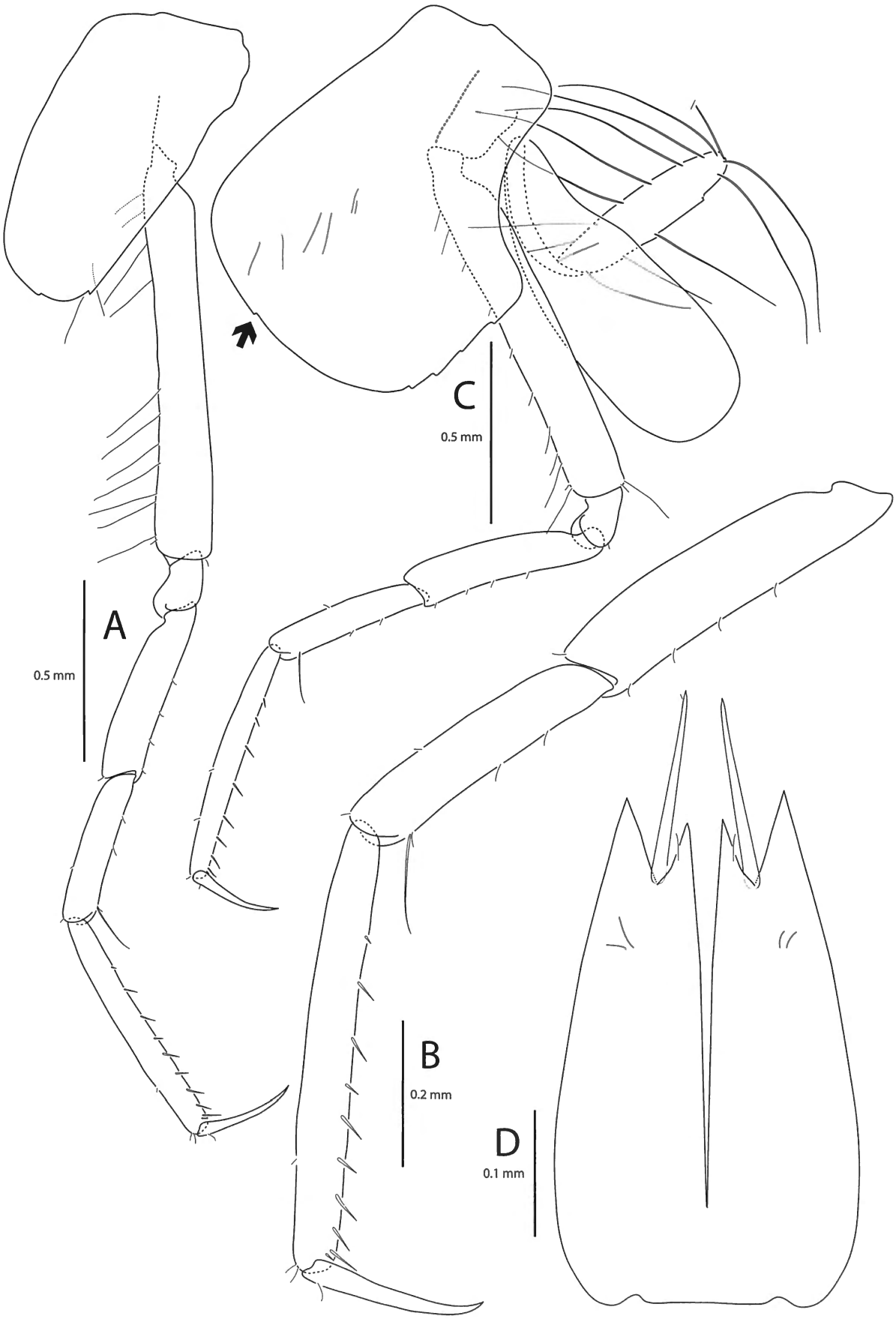

Fig. 24. – *Liljeborgia* (*Liljeborgia*) *brevicornis* (BRUZELIUS, 1859), ovigerous female (7 mm), R/V Johan Ruud sta. 303-05, N Norway, SW Magerøya. A, left P3; B, distal 4 articles of left P3; C, left P4; D, telson.

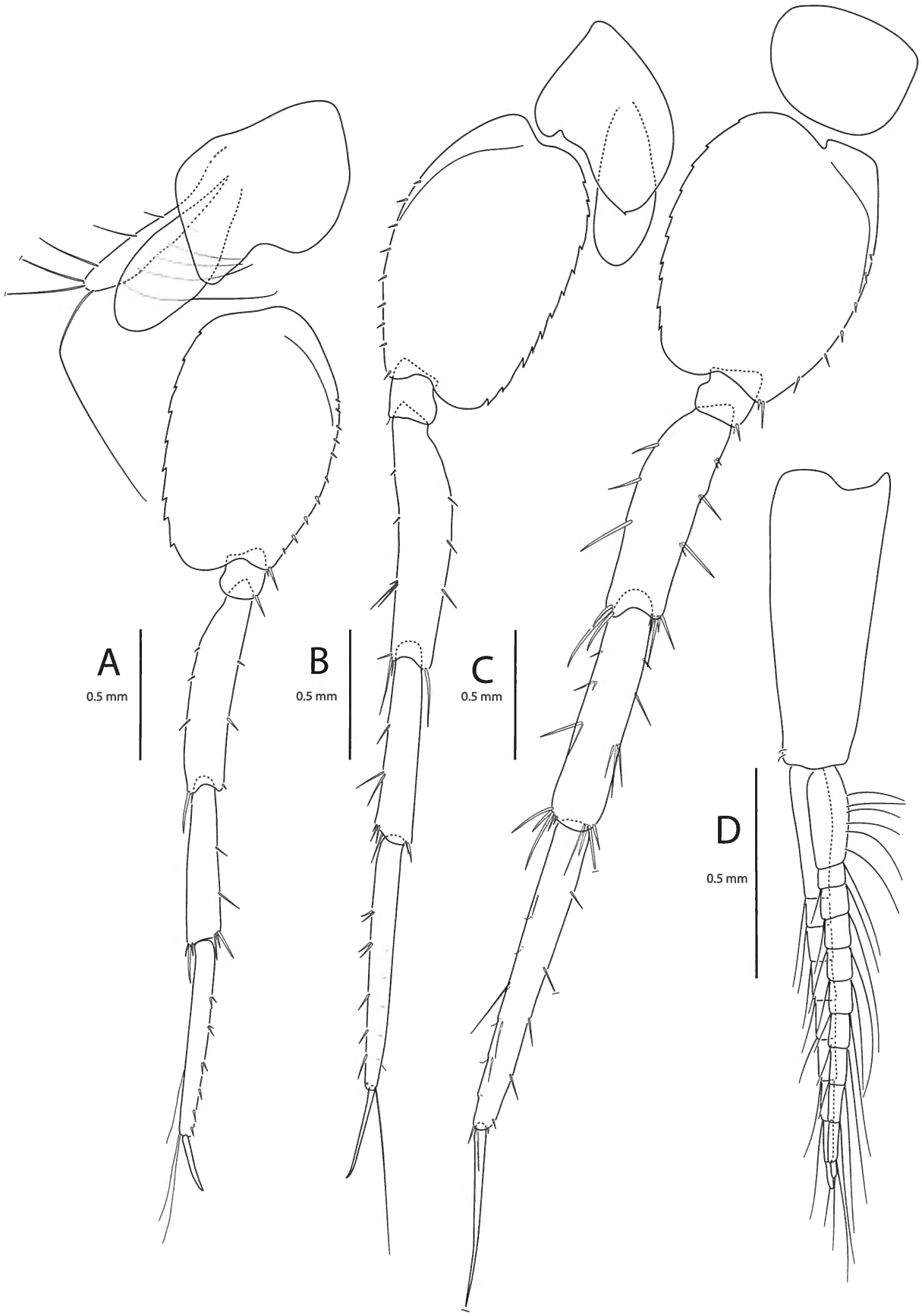

Fig. 25. – *Liljeborgia* (*Liljeborgia*) *brevicornis* (Bruzelius, 1859), ovigerous female (7 mm), R/V Johan Ruud sta. 303-05, N Norway, SW Magerøya. A, right P5; B, left P6 (posterior setae of propodus rubbed off); C, right P7 (most posterior setae of propodus rubbed off); D, detached pleopod.

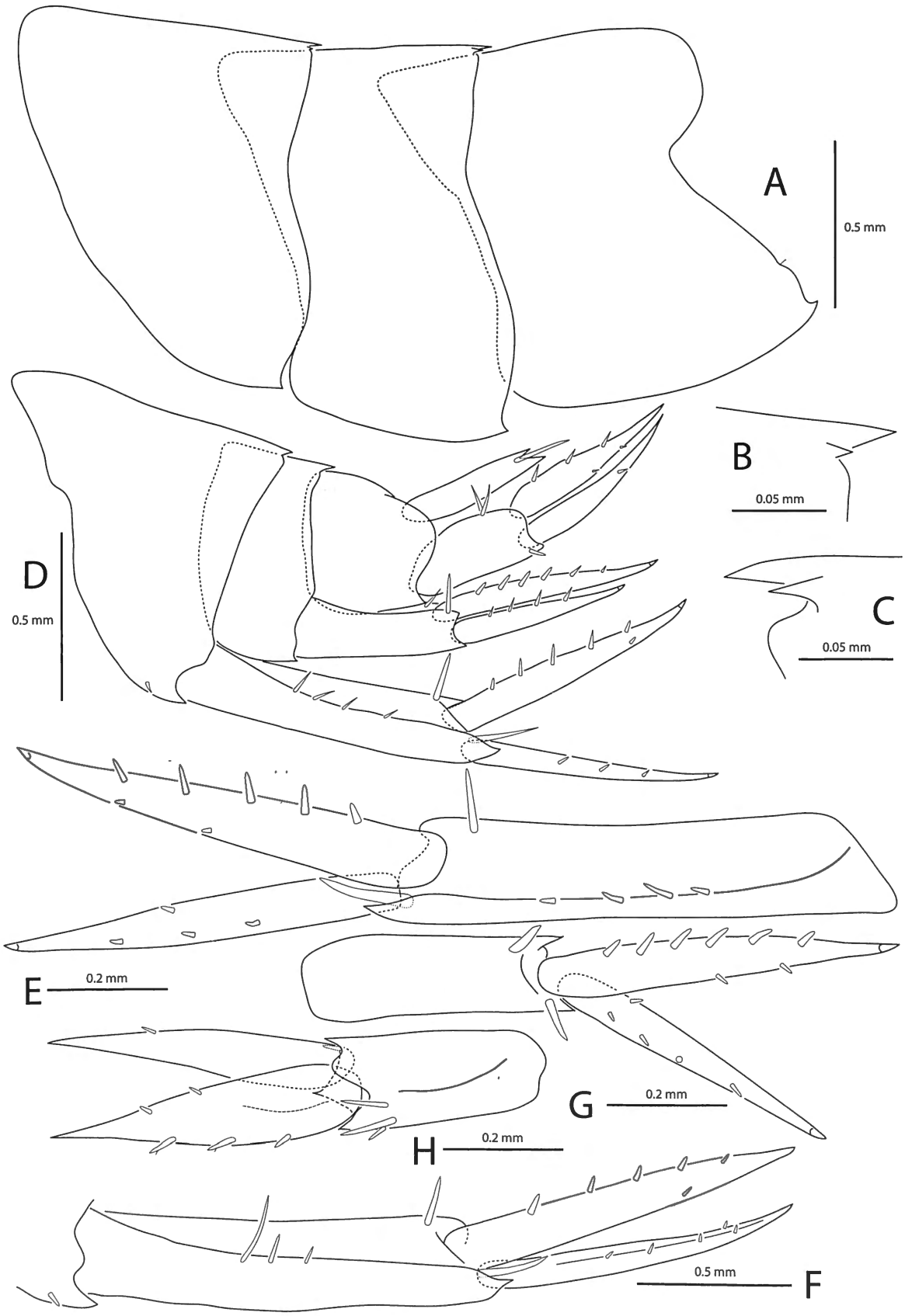

Fig. 26. – *Liljeborgia* (*Liljeborgia*) *brevicornis* (Bruzelius, 1859), A-E, G, H, ovigerous female (7 mm), R/V Johan Ruud sta. 303-05, N Norway, SW Magerøya; F, male (8 mm), R/V August Brinkmann, sta. E43-73, Brattholmen Hjeltefjorden. A, pleosome; B, posterodorsal border of pleonite 1 (lateral view); C, posterodorsal border of pleonite 2 (lateral view); D, urosome; E, right U1; F, left U1; G, left U2; H, left U3.

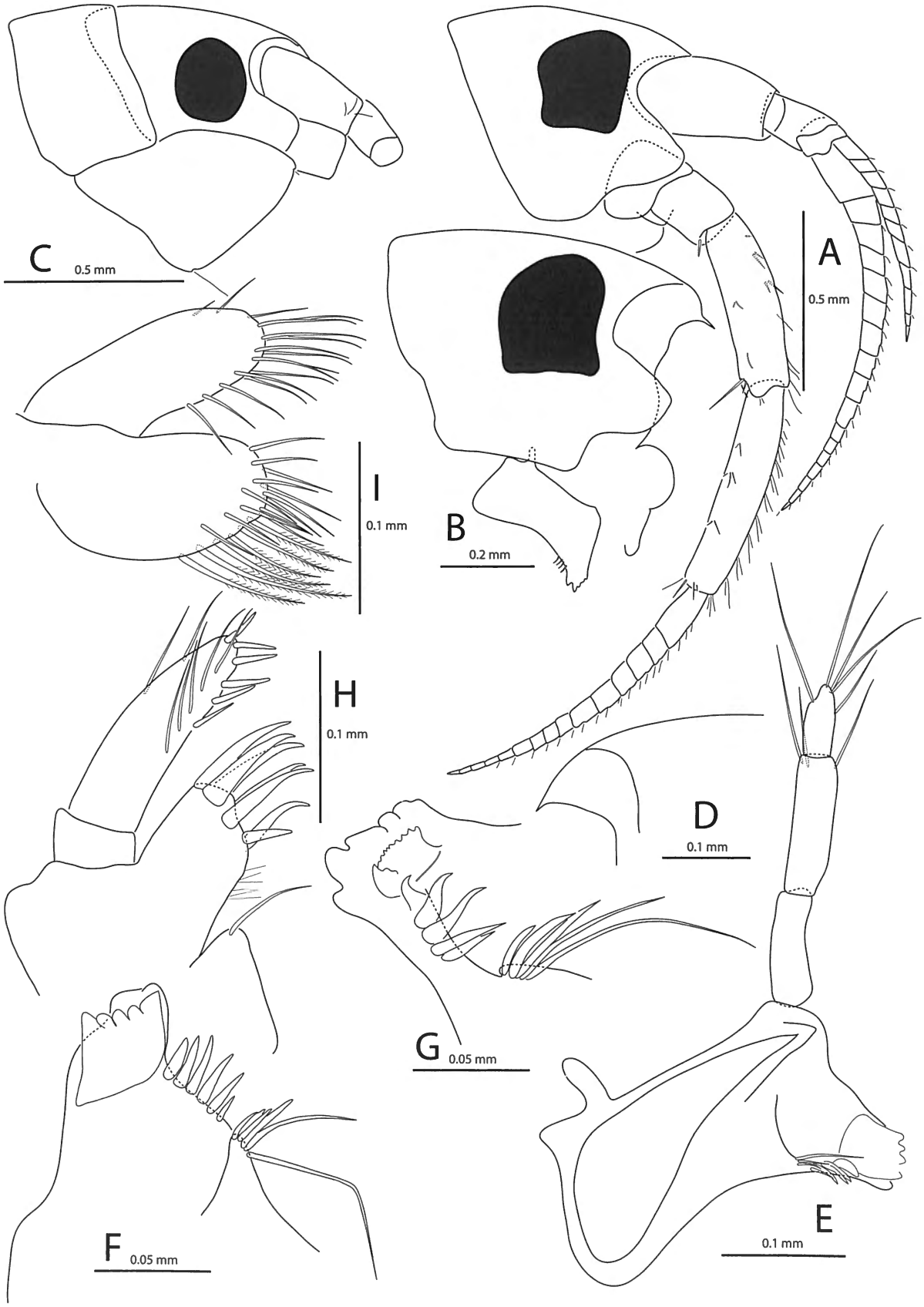

Fig. 27. – *Liljeborgia* (*Liljeborgia*) *dellavallei* Stebbing, 1906, A, B, E, H, I, adult male (6 mm), NW Greece, Lygia; C, F, G, ovigerous female (6 mm), sample "(10) SC11B Ld", Sardinia, Tavolara-Punta Coda Cavallo; D, ovigerous female (6 mm) "(7) SC10D Ld", Sardinia, Tavolara-Punta Coda Cavallo. A, head with antennae; B, head with epistome and mandible; C, head and surrounding structures; D, rostrum; E, left mandible; F, tip of left mandible; G, tip of right mandible; H, right Mx1; I, right Mx2.

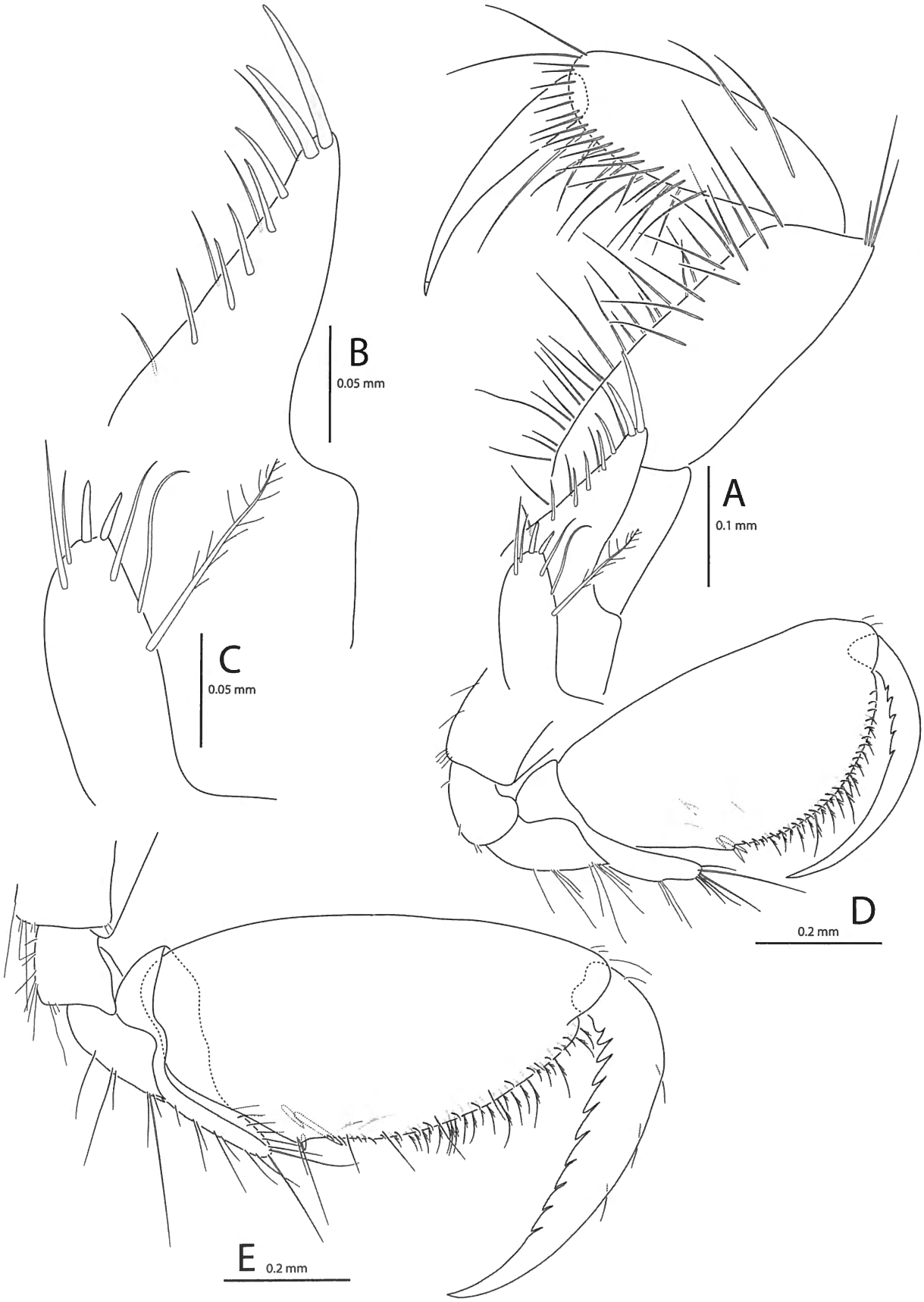

Fig 28. – *Liljeborgia* (*Liljeborgia*) *dellavallei* STEBBING, 1906, A-C, adult male (6 mm), NW Greece, Lygia; D-E, ovigerous female (6 mm), sample "(10) SC11B Ld", Sardinia, Tavolara-Punta Coda Cavallo. A, Mxp; B, right outer plate of Mxp; C, left inner plate of Mxp; D, right Gn1; E, right Gn2.

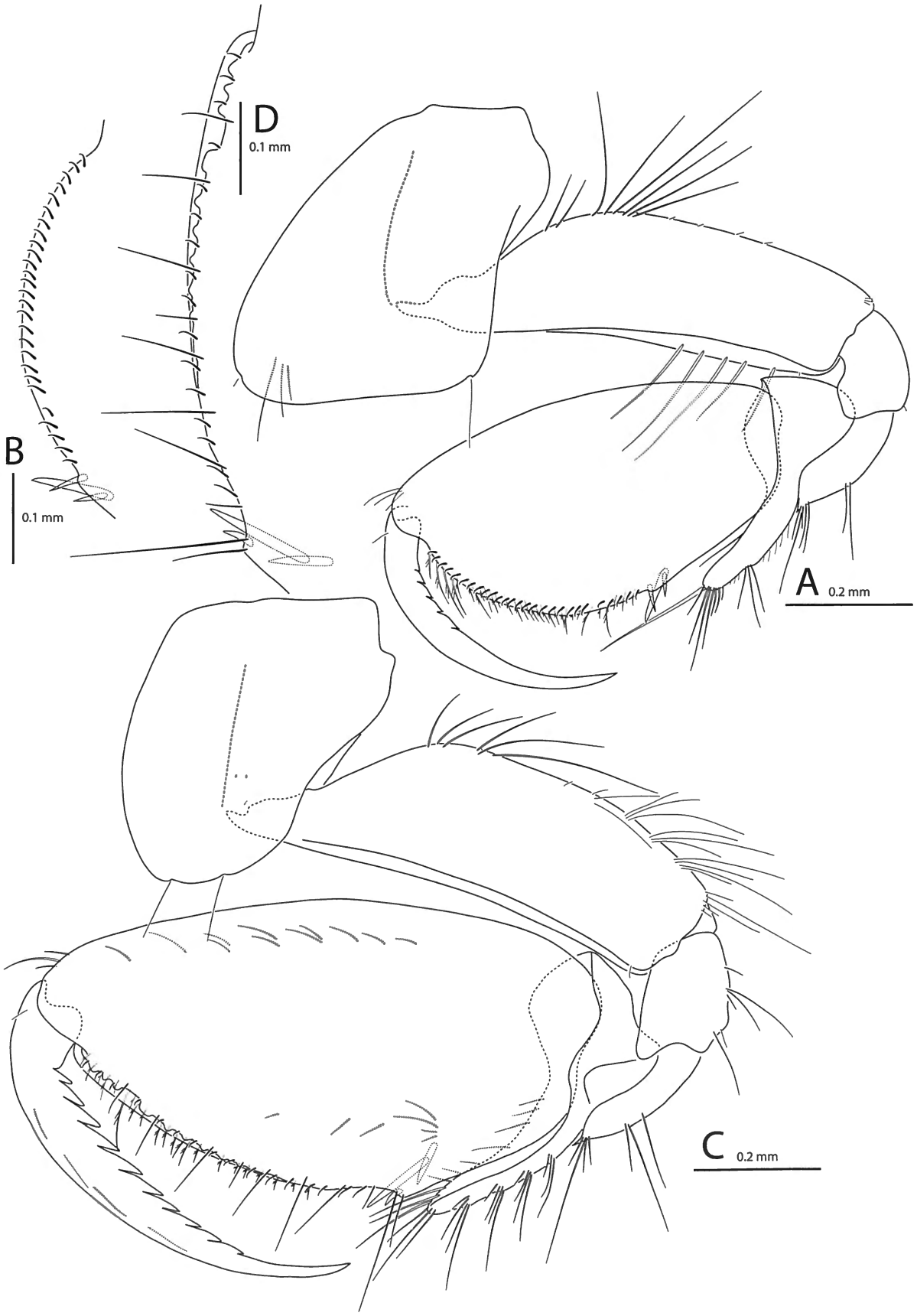

Fig. 29. – *Liljeborgia* (*Liljeborgia*) *dellavallei* Stebbing, 1906, A-D, adult male (6 mm), NW Greece, Lygia. A, left Gn1; B, palm of left Gn1 (medial setae not shown); C, left Gn2; D, palm of left Gn2 (medial setae not shown).

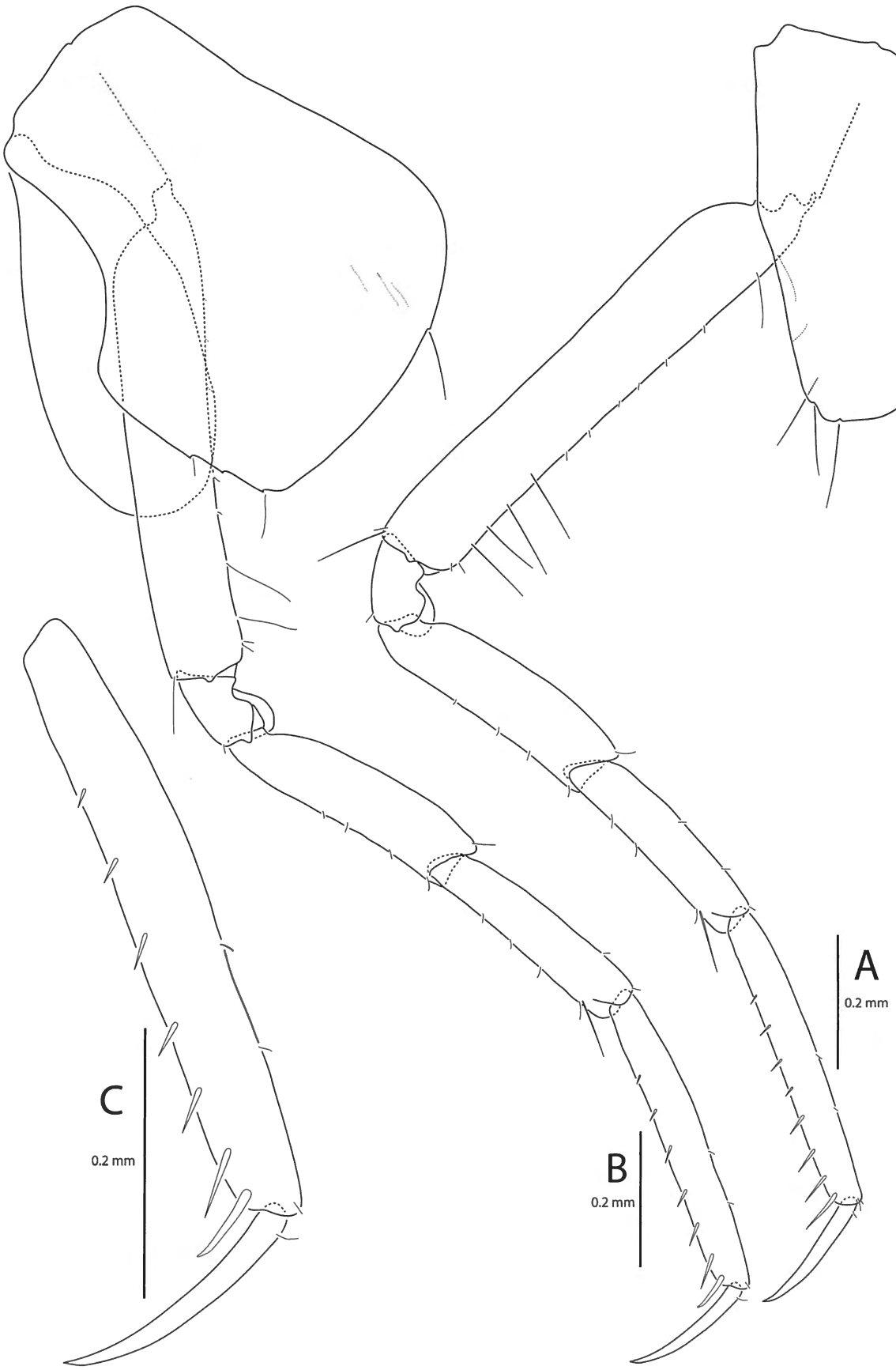

Fig. 30. – *Liljeborgia* (*Liljeborgia*) *dellavallei* STEBBING, 1906, A-C, adult male (6 mm), NW Greece, Lygia. A, right P3; B, right P4; C, propodus and dactylus of right P4.

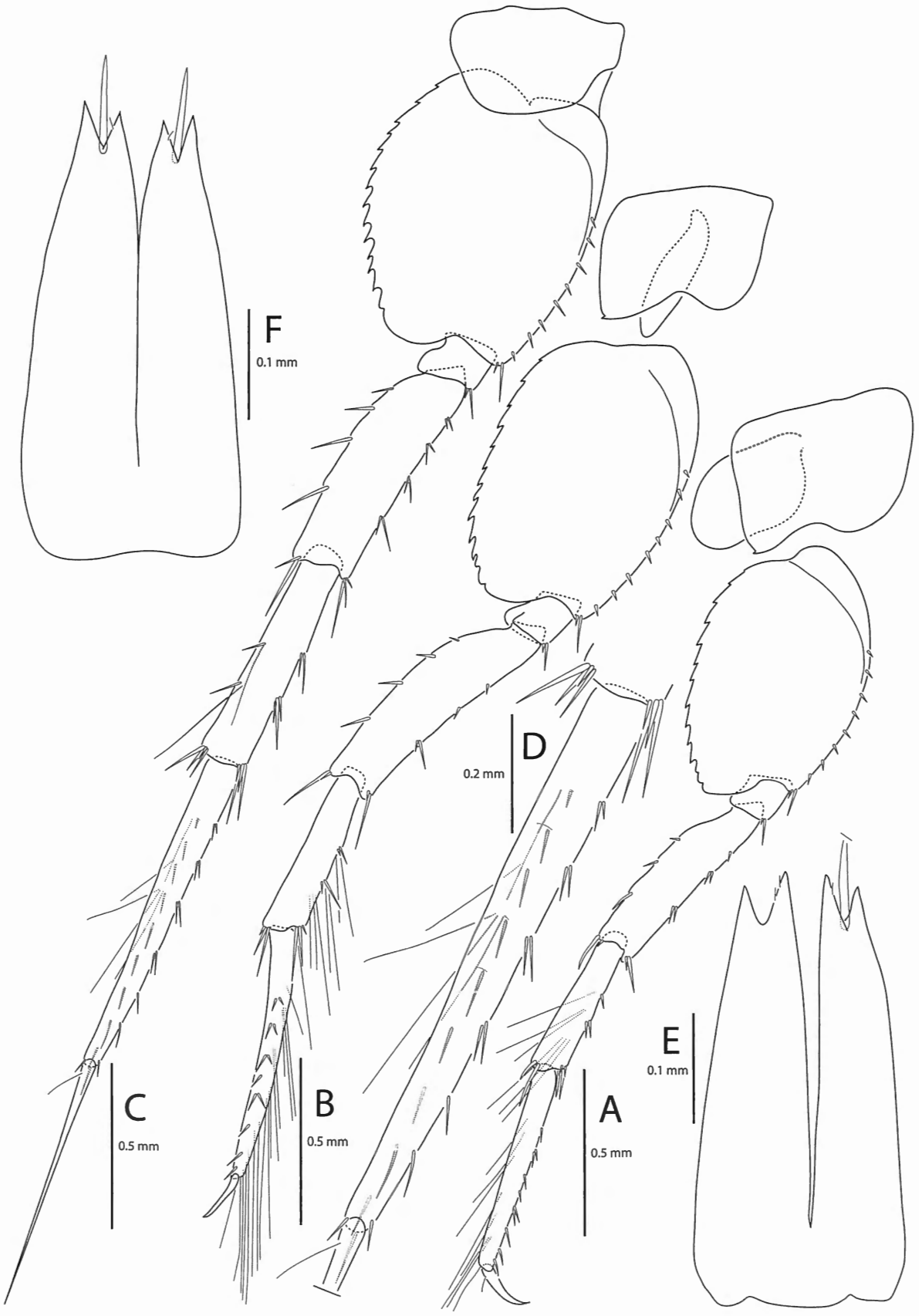

Fig. 31. – *Liljeborgia* (*Liljeborgia*) *dellavallei* Stebbing, 1906, A-E, adult male (6 mm), NW Greece, Lygia; F, ovigerous female "(10) SC11B Ld", Sardinia, Tavolara-Punta Coda Cavallo. A, right P5; B, right P6; C, right P7; D, propodus of right P7; E-F, telson.

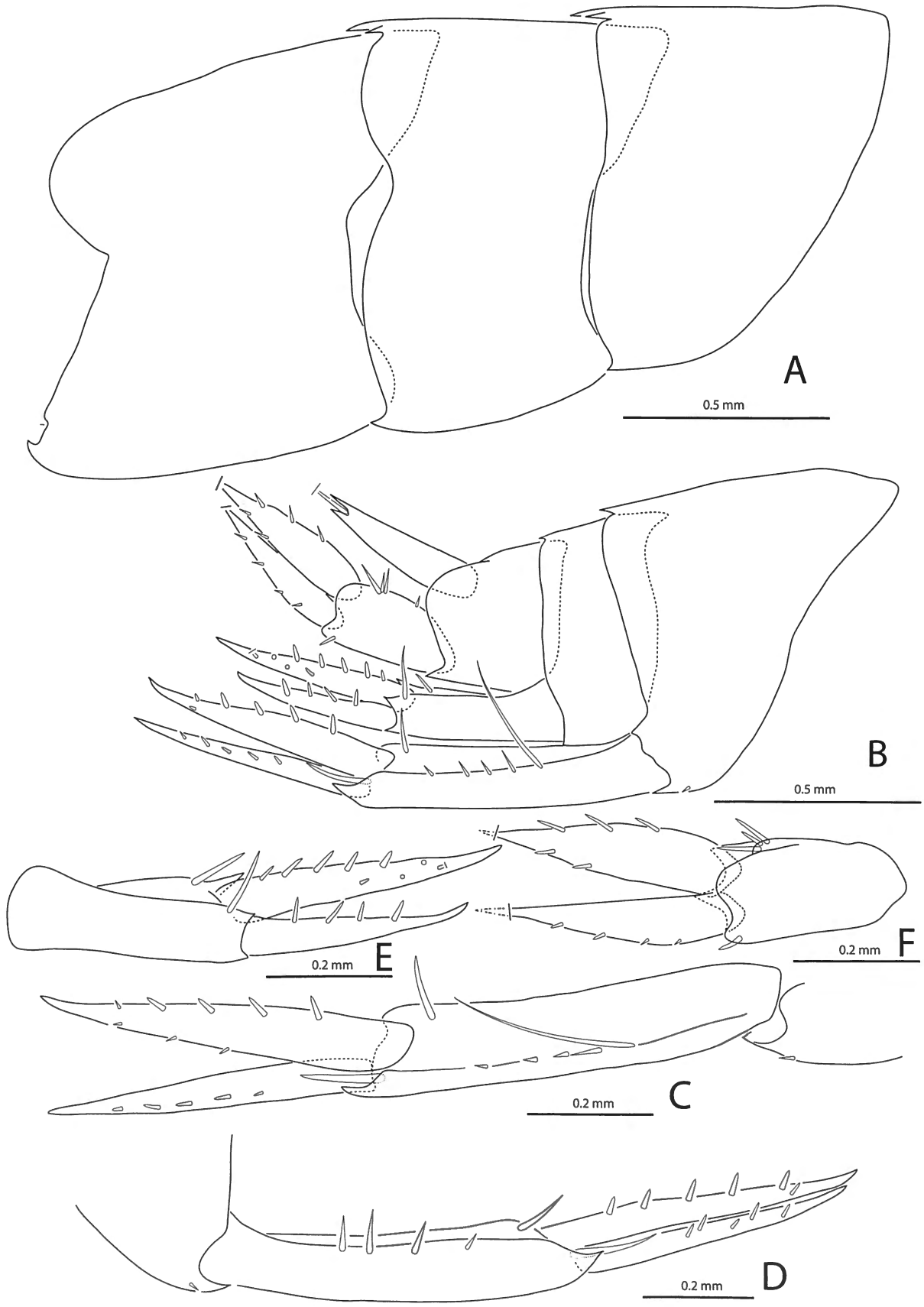

Fig. 32. – *Liljeborgia* (*Liljeborgia*) *dellavallei* Stebbing, 1906, A-C, E-F, adult male (6 mm), NW Greece, Lygia; D, ovigerous female (6 mm) "(10) SC11B Ld", Sardinia, Tavolara-Punta Coda Cavallo. A, pleosome; B, urosome; C, right U1; D, left U1; E, left U2; F, right U3.

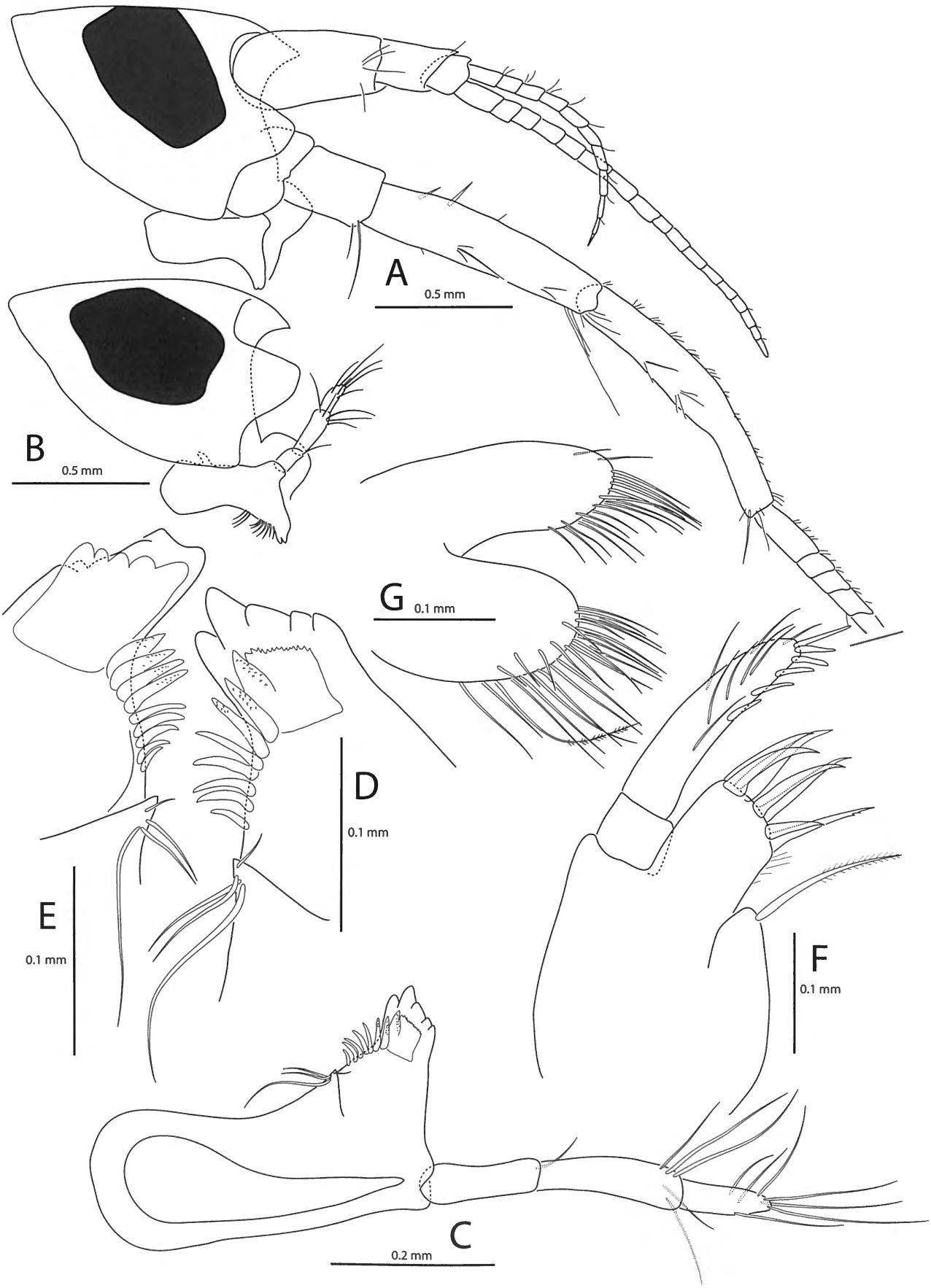

Fig. 33. – *Liljeborgia* (*Liljeborgia*) *inermis* Chevreux, 1920, male (8 mm), S Portugal, Ferragudo. A, head with antennae; B, head with mandible and epistome; C, right Md; D, tip of right Md; E, tip of left Md; F, right Mx1; G, right Mx2.

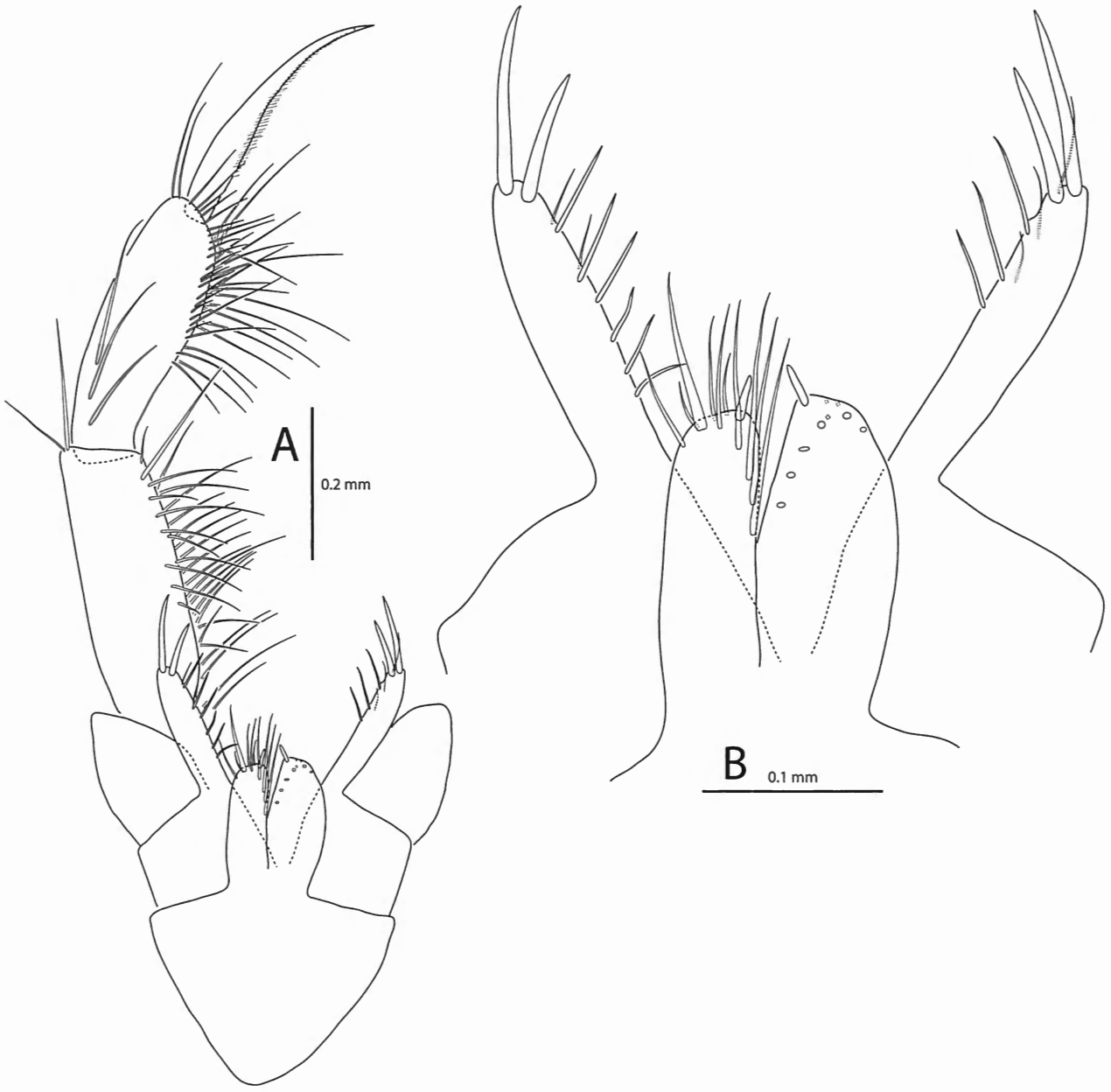

Fig. 34. – *Liljeborgia* (*Liljeborgia*) *inermis* CHEVREUX, 1920, male (8 mm), S Portugal, Ferragudo. A, Mxp; B, plates of Mxp.

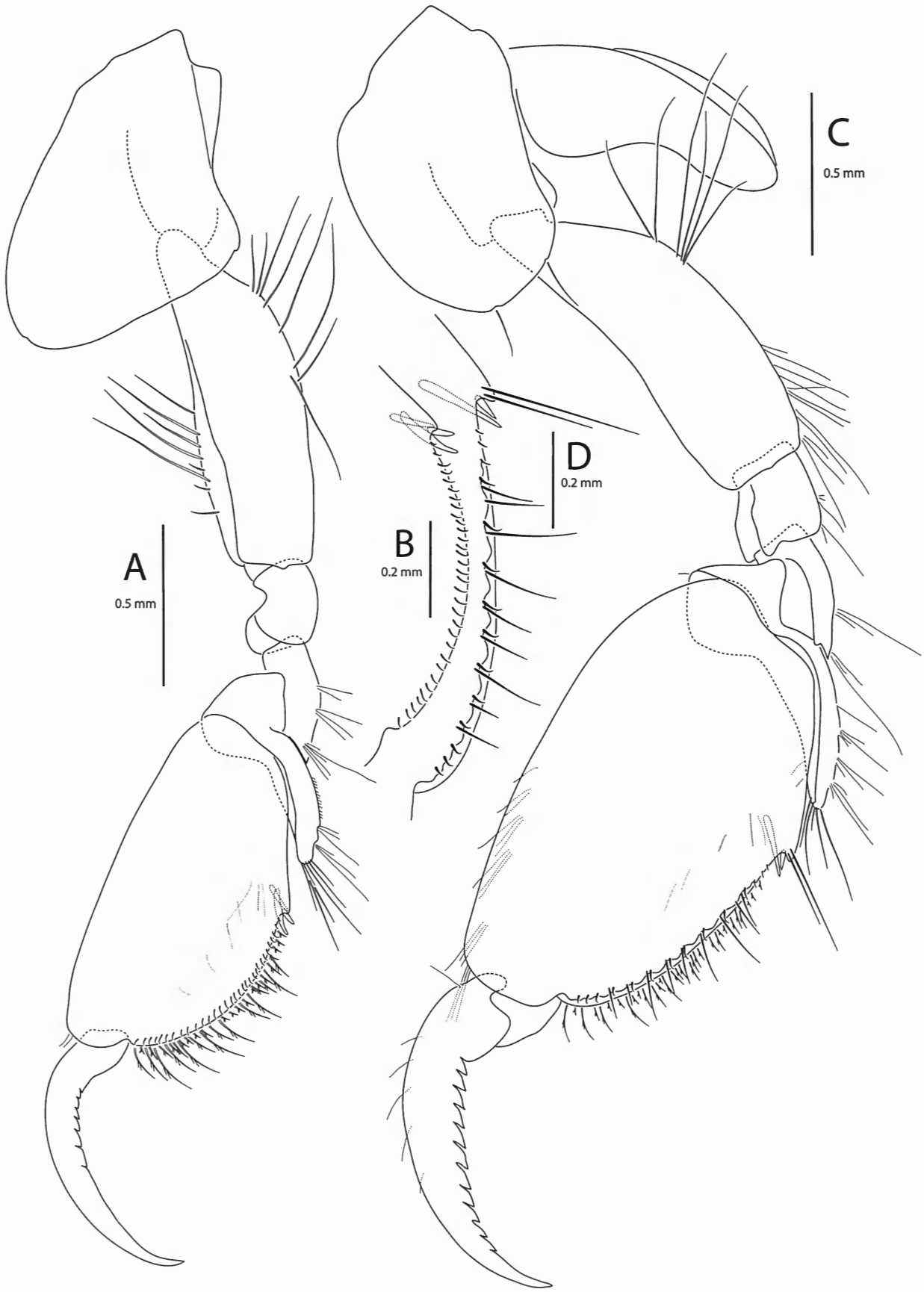

Fig. 35. – *Liljeborgia* (*Liljeborgia*) *inermis* Chevreux, 1920, male (8 mm), S Portugal, Ferragudo. A, left Gn1; B, palm of left Gn1 (medial setae not shown); C, left Gn2; D, palm of left Gn2.

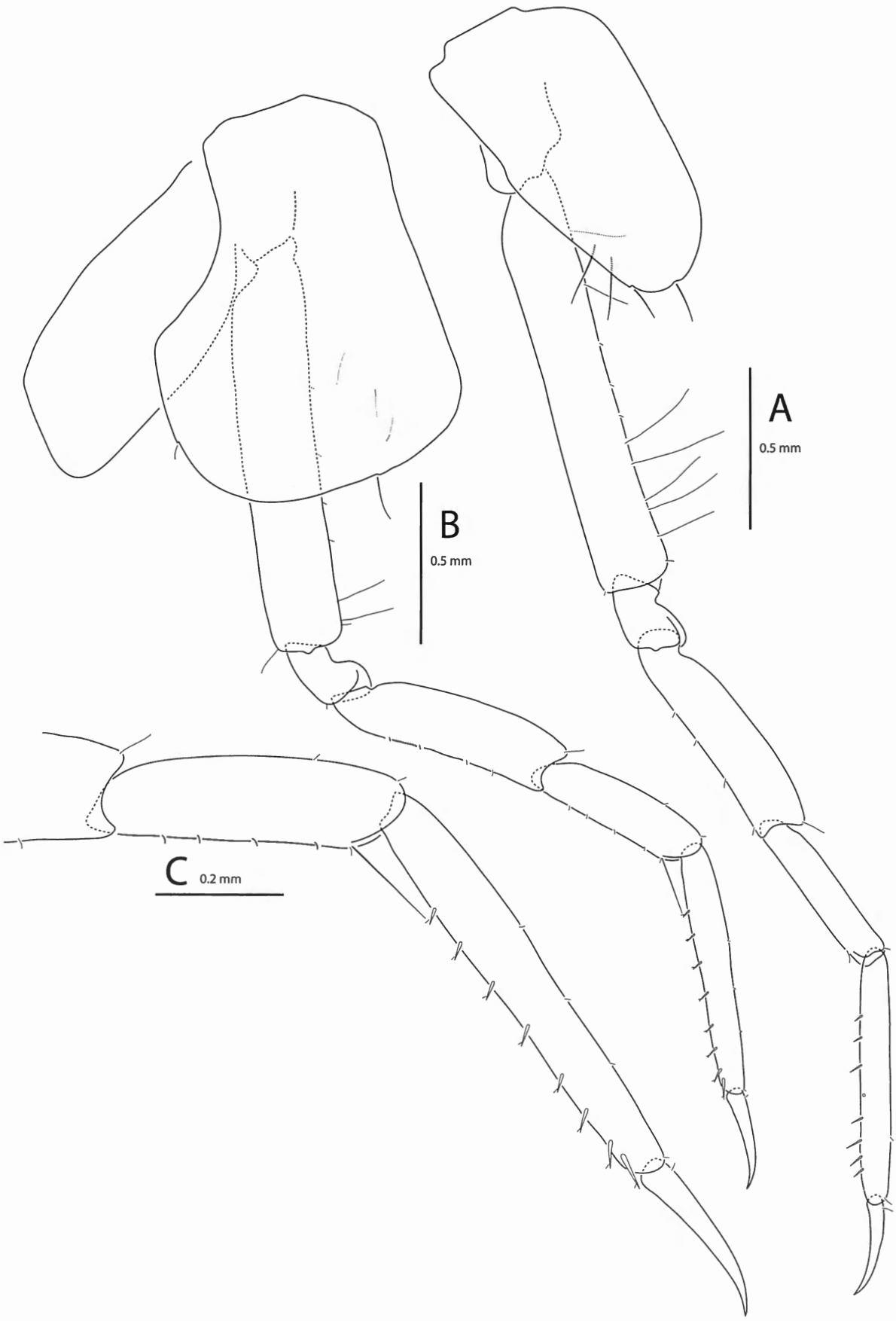

Fig. 36. – *Liljeborgia* (*Liljeborgia*) *inermis* CHEVREUX, 1920, male (8 mm), S Portugal, Ferragudo. A, right P3; B, right P4; C, distal 3 articles of right P4.

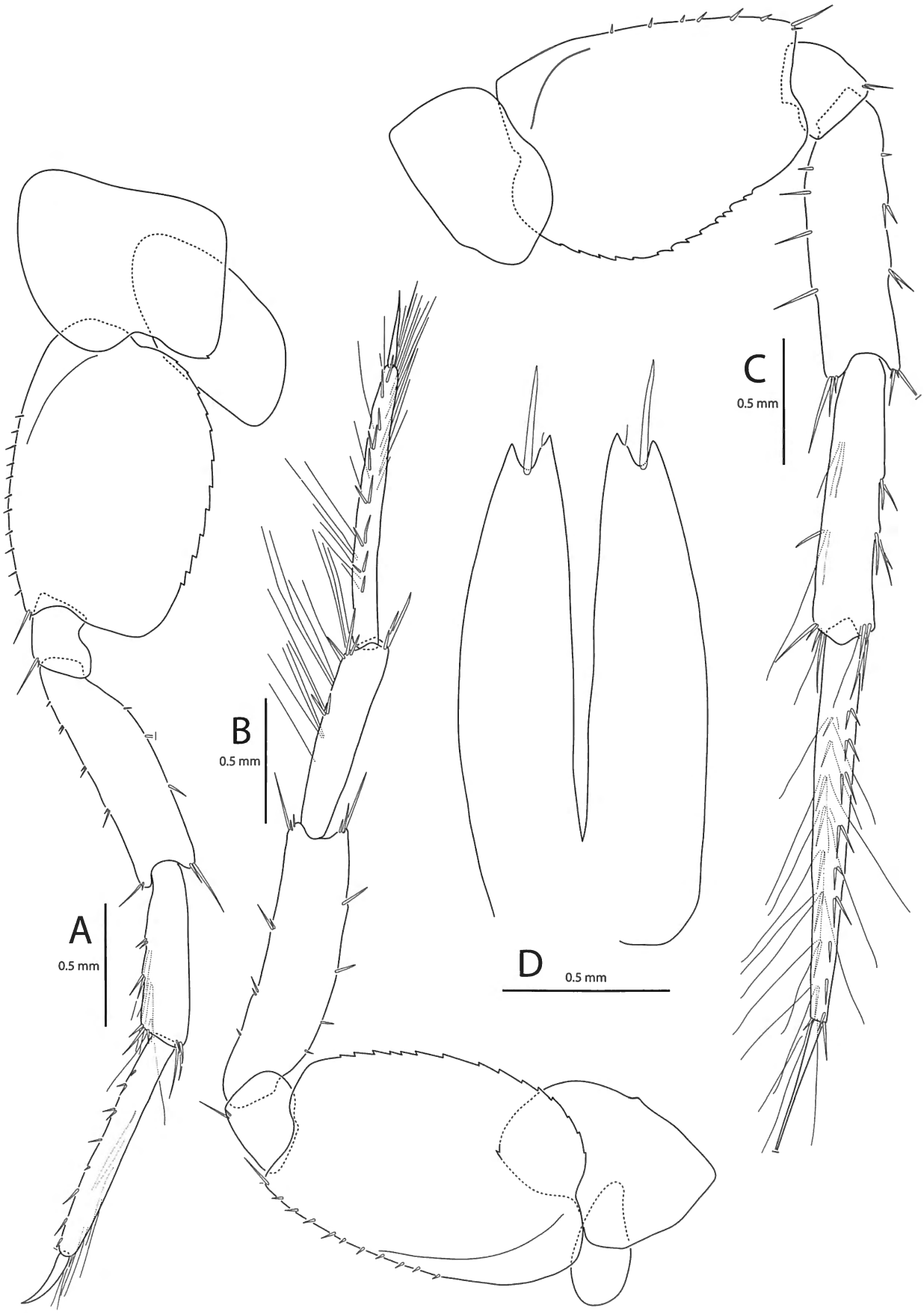

Fig. 37. – *Liljeborgia* (*Liljeborgia*) *inermis* Chevreux, 1920, male (8 mm), S Portugal, Ferragudo. A, left P5; B, right P6; C, right P7; D, telson.

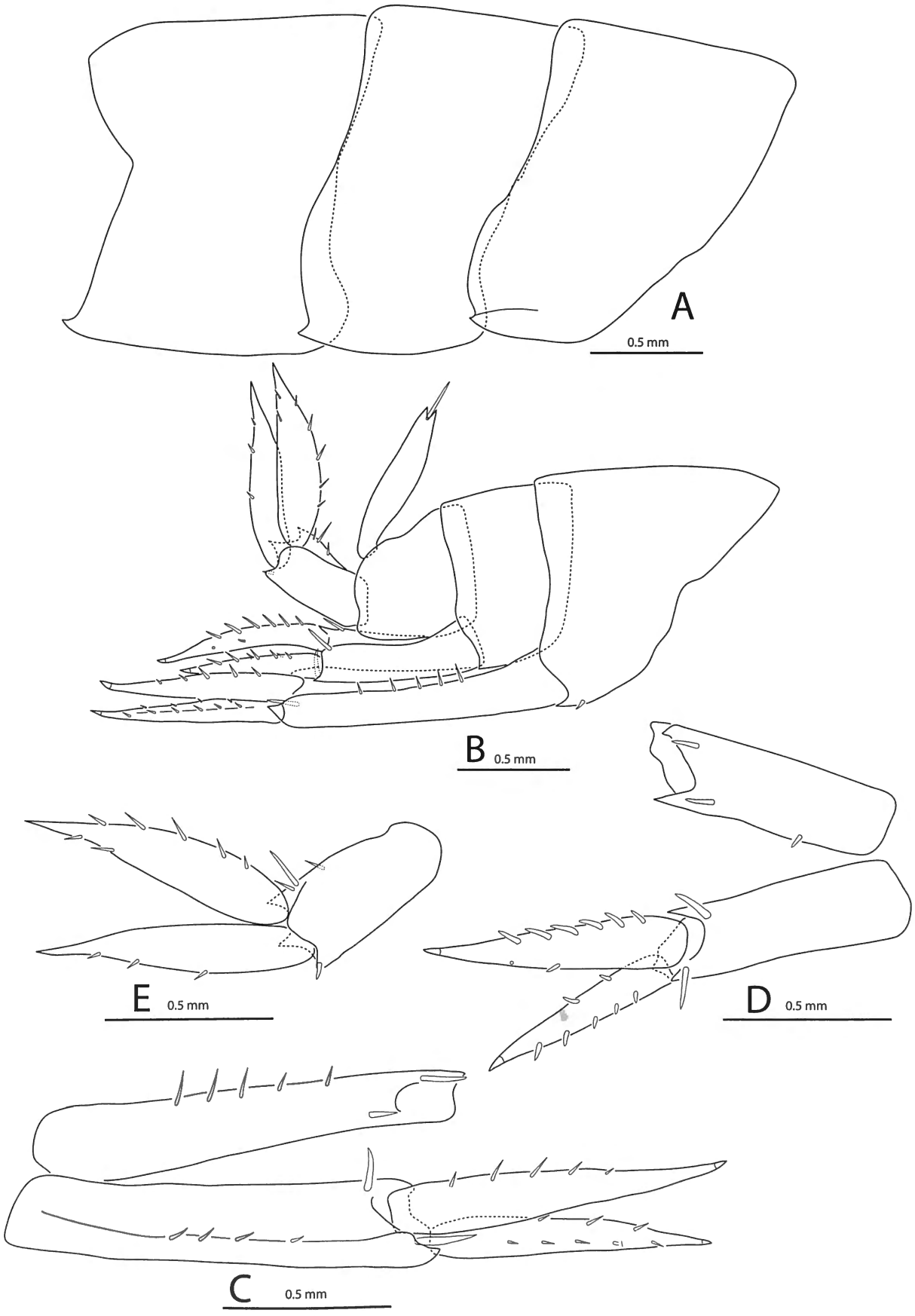

Fig. 38. – *Liljeborgia* (*Liljeborgia*) *inermis* CHEVREUX, 1920, male (8 mm), S Portugal, Ferragudo. A, pleosome; B, urosome; C, left U1 and peduncle of right U1; D, right U2 and peduncle of left U2; E, right U1.

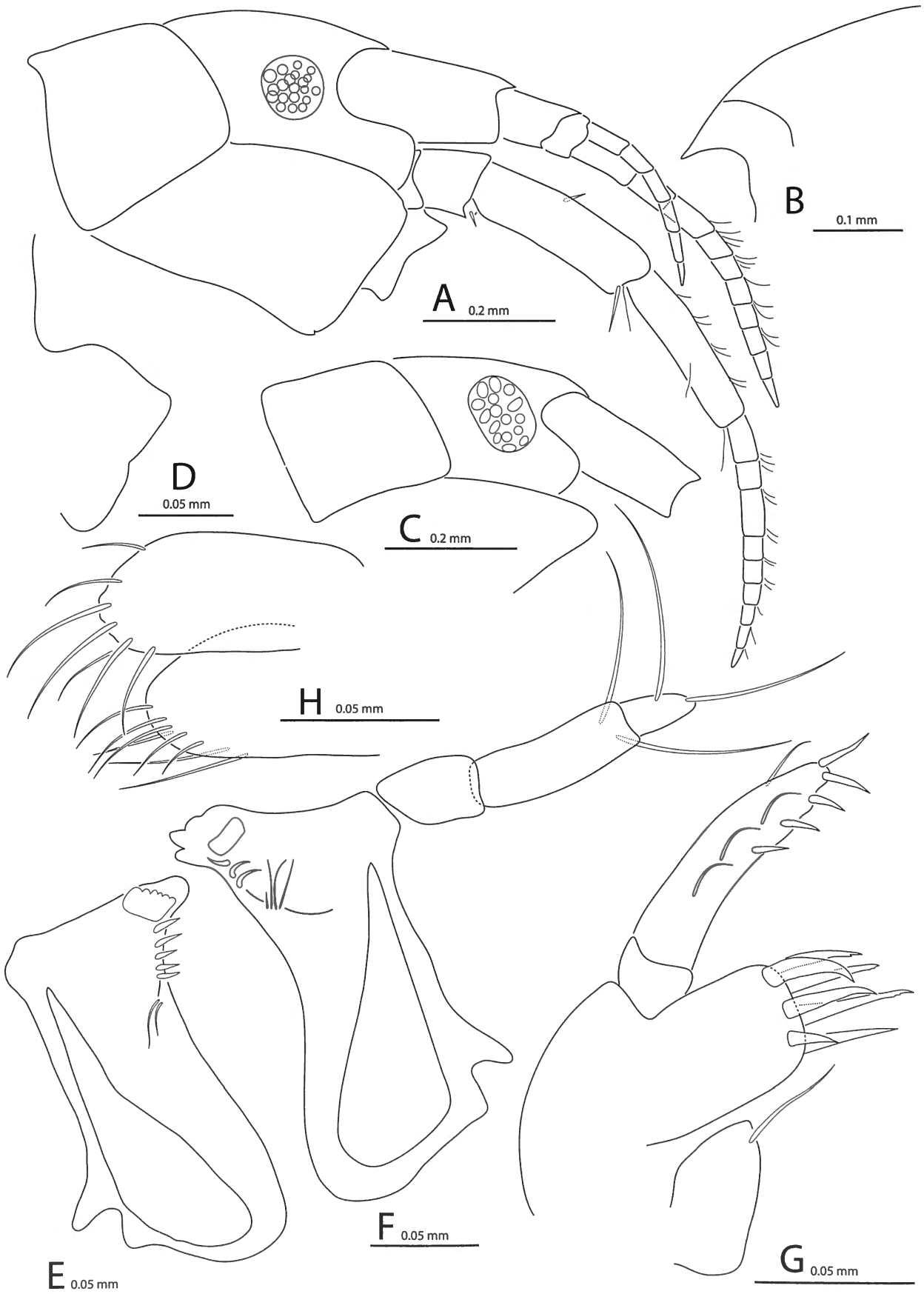

Fig. 39. – *Liljeborgia* (*Liljeborgia*) *kinahani* (Bate, 1862), females (3 mm); A-B, female 2, W Norway, Rissøya; C, female 3, Liholmene; D-H, female 1, Rissøya. A, head and surrounding structures; B, rostrum; C, head with surrounding structures; D, epistome in lateral view; E, left Md; F, right Md; G, right Mx1; H, left Mx2.

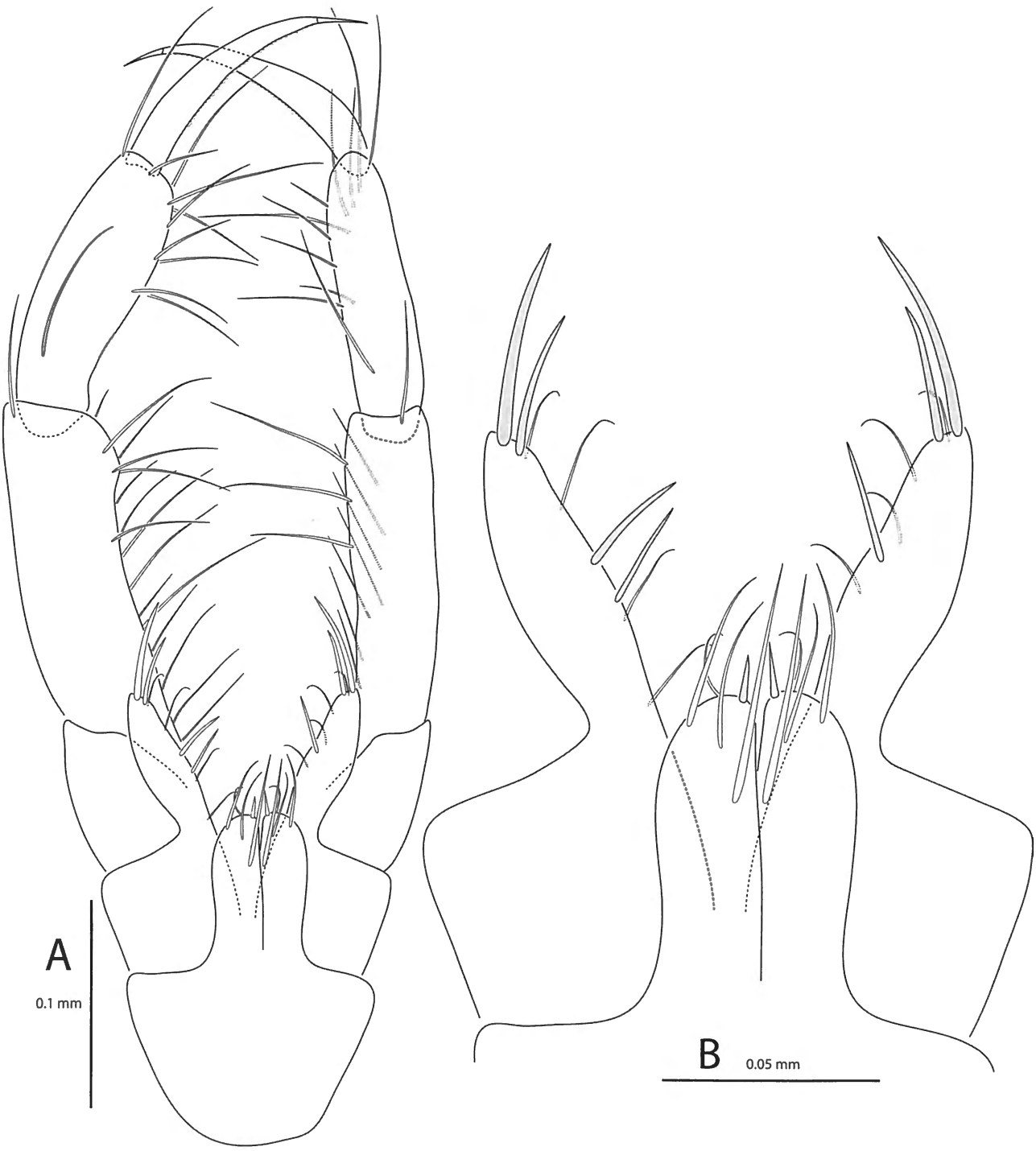

Fig. 40. – *Liljeborgia* (*Liljeborgia*) *kinahani* (Bate, 1862), female 1 (3 mm), W Norway, Rissøya. A, Mxp; B, Mxp plates.

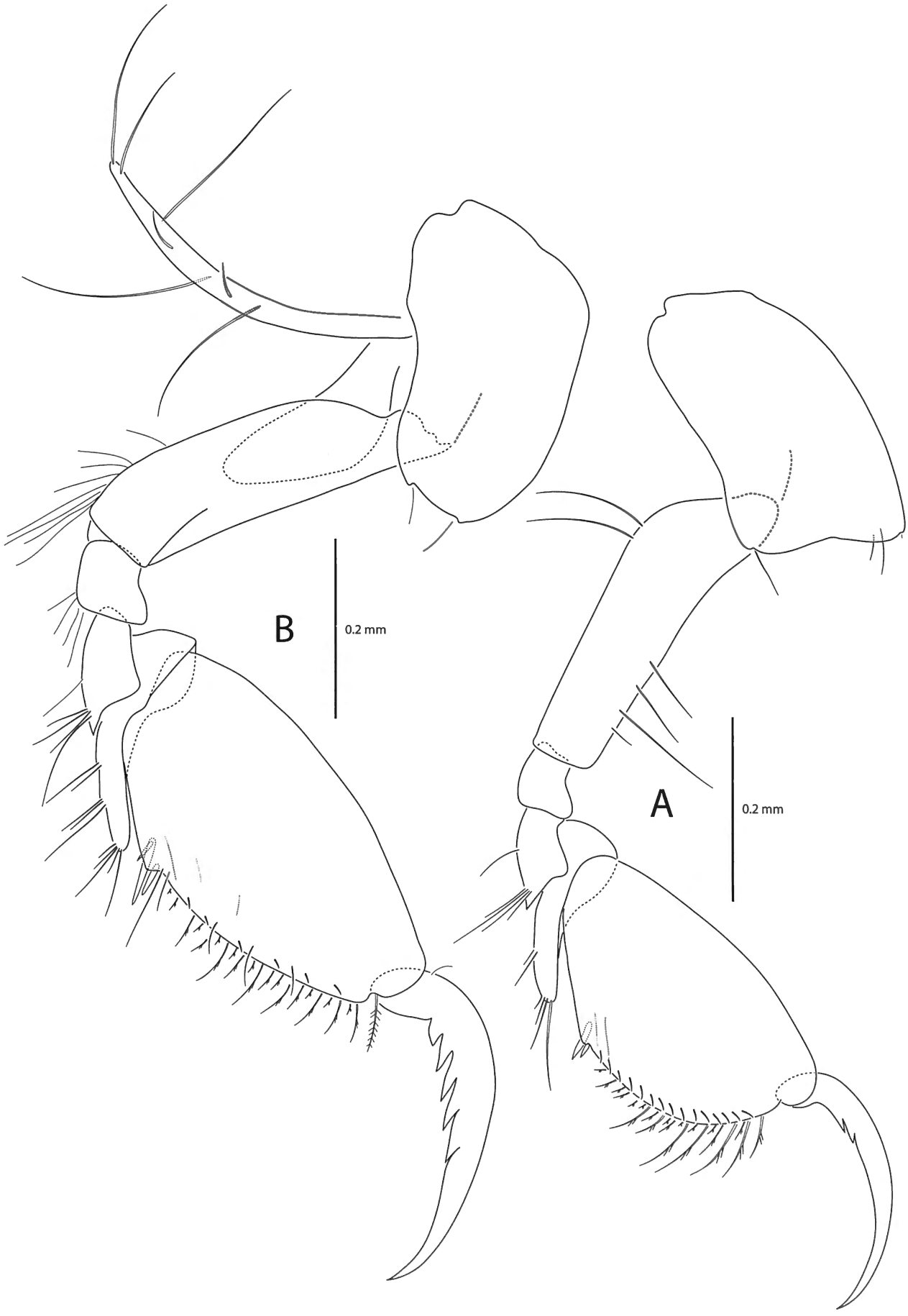

Fig. 41. – *Liljeborgia* (*Liljeborgia*) *kinahani* (Bate, 1862), female 1 (3 mm), W Norway, Rissøya. A, right Gn1; B, right Gn2.

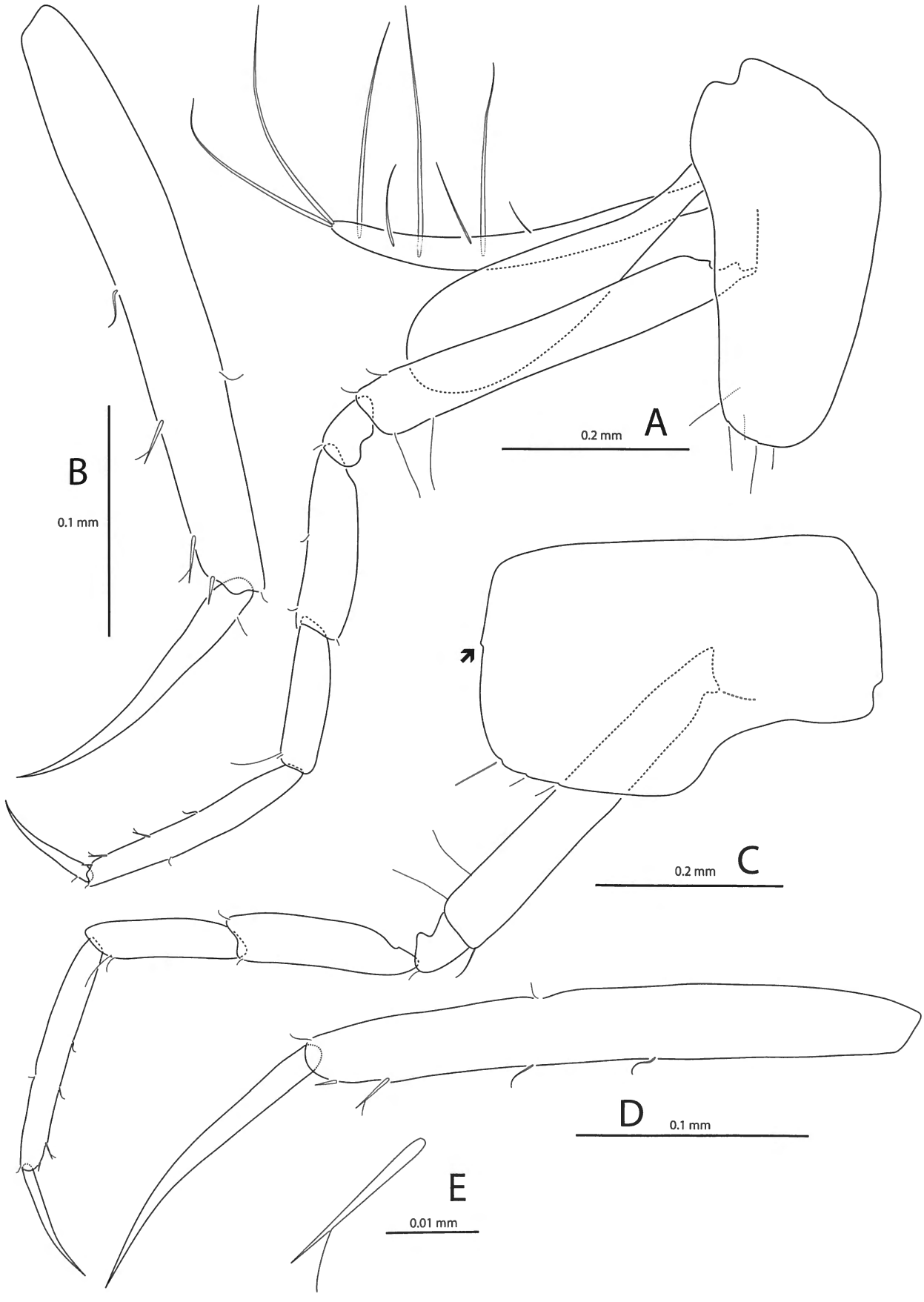

Fig. 42. – *Liljeborgia* (*Liljeborgia*) *kinahani* (Bate, 1862), female 1 (3 mm), W Norway, Rissøya. A, right P3; B, propodus and dactylus of right P3; C, left P4; D, propodus of left P4; E, third acicula of left P4.

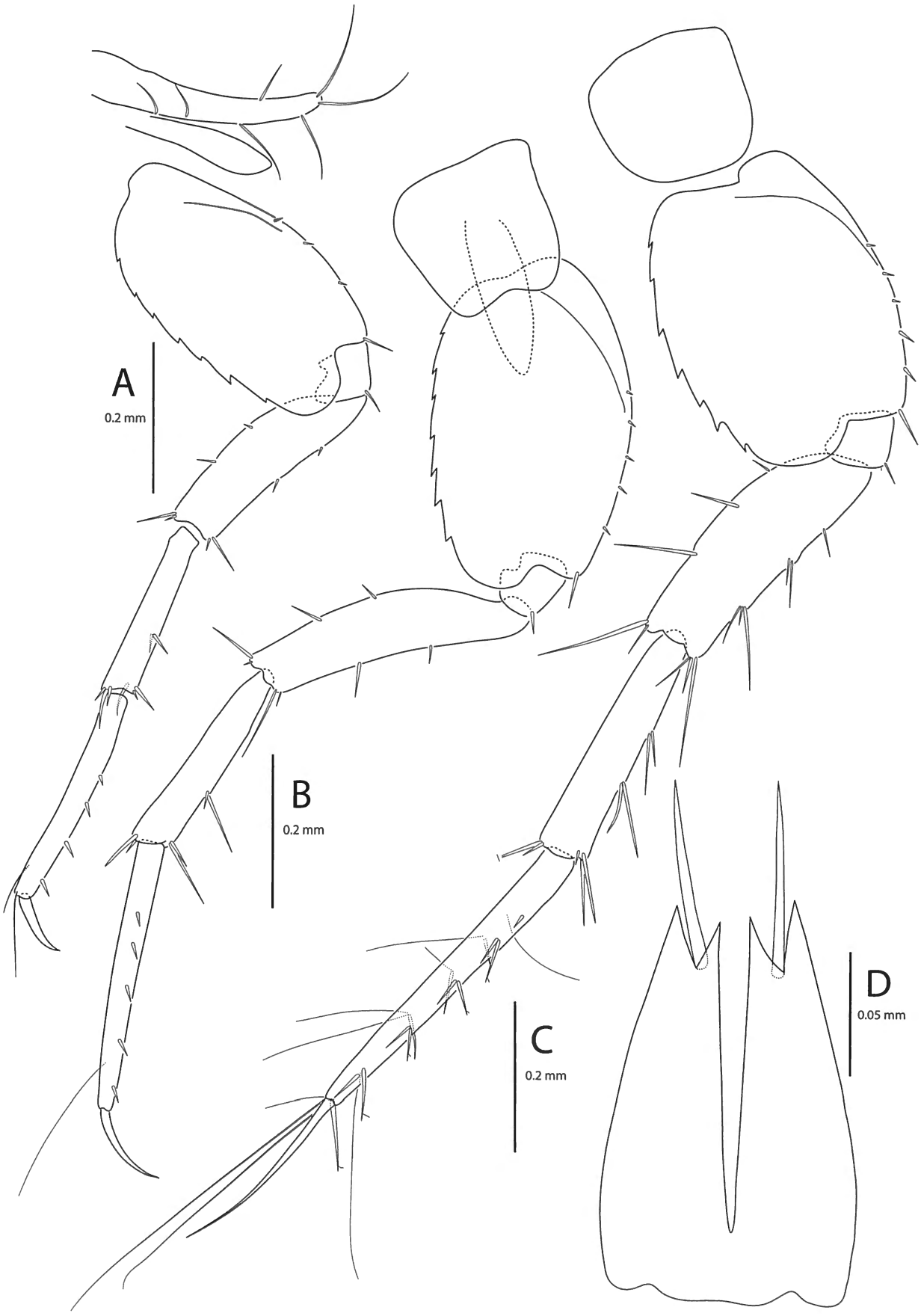

Fig. 43. – *Liljeborgia* (*Liljeborgia*) *kinahani* (Bate, 1862), female 1 (3 mm), W Norway, Rissøya. A, right P5; B, right P6; C, right P7; D, telson.

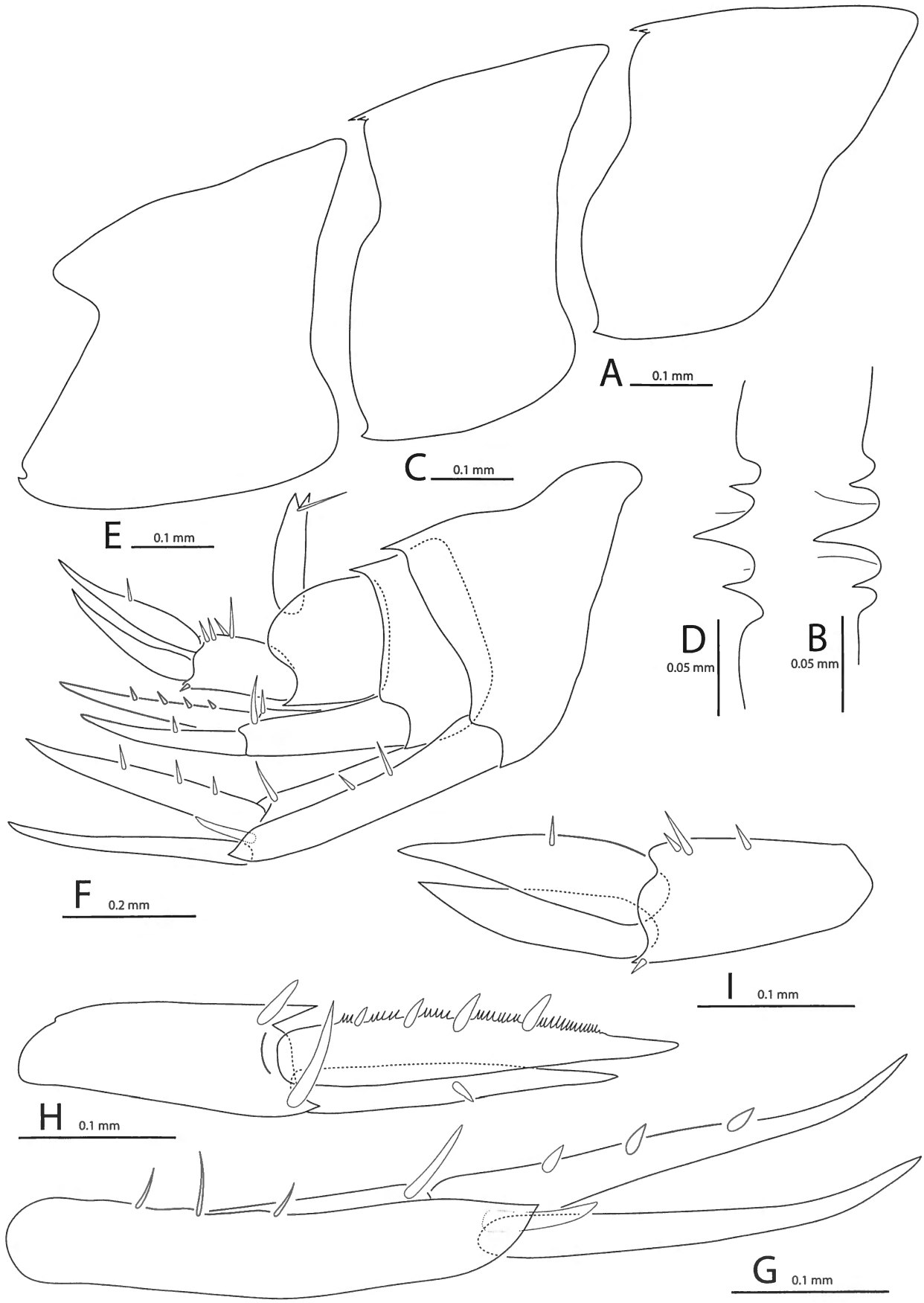

Fig. 44. – *Liljeborgia* (*Liljeborgia*) *kinahani* (Bate, 1862), female 1 (3 mm), W Norway, Rissøya. A, pleonite 1; B, posterodorsal border of pleonite 1 in dorsal view; C, pleonite 2; D, posterodorsal border of pleonite 2 in dorsal view; E, pleonite 3; F, urosome; G, left uropod 1; H, left uropod 2; I, right uropod 3.

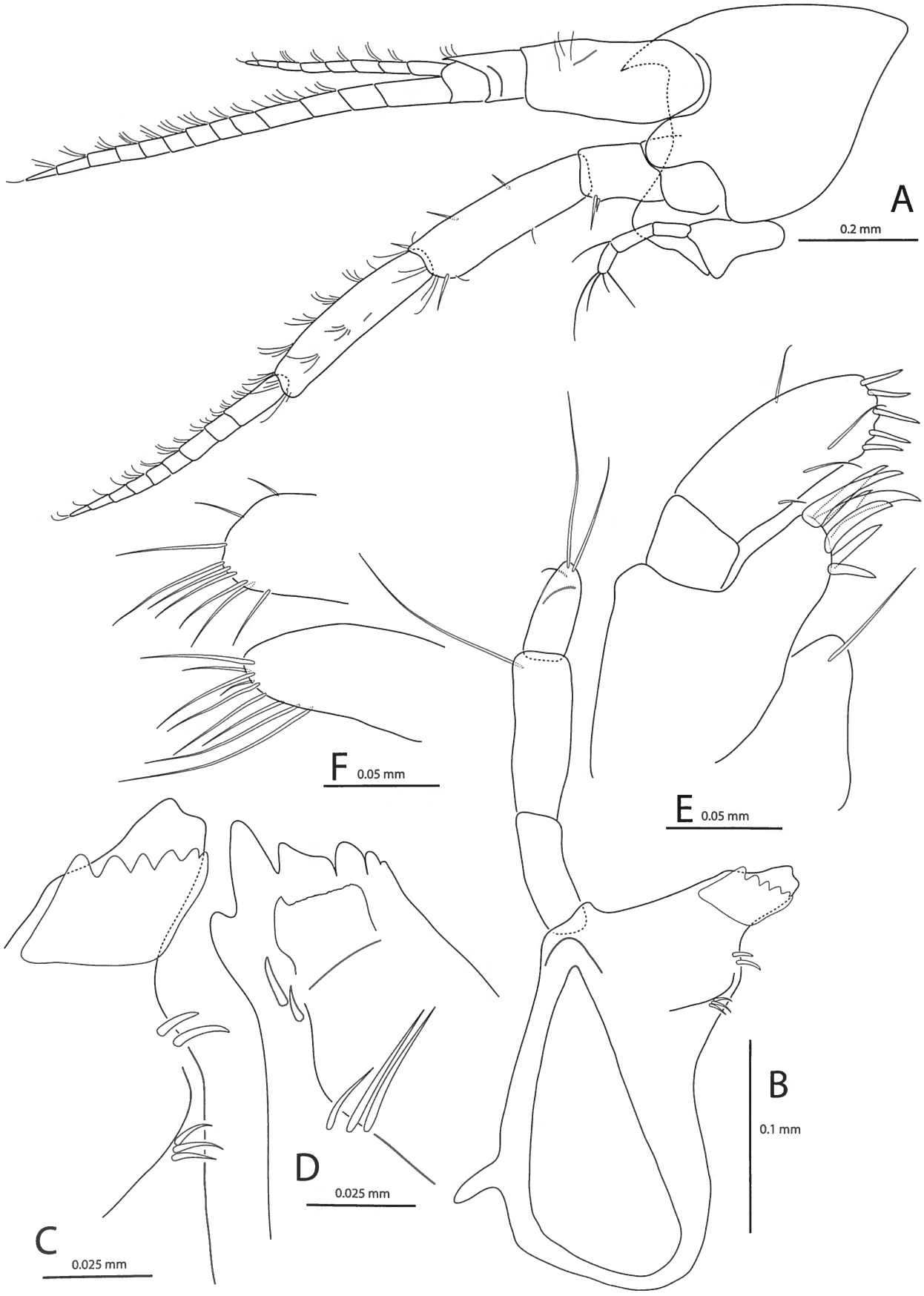

Fig. 45. – *Liljeborgia* (*Liljeborgia*) *macronyx* G.O. Sars, 1894, male (5 mm), W Norway, Trondheim area, L. Greve sta. 29. A, head with antennae and Md; B, left Md; C, tip of left Md; D, tip of right Md; E, right Mx1; F, left Mx2.

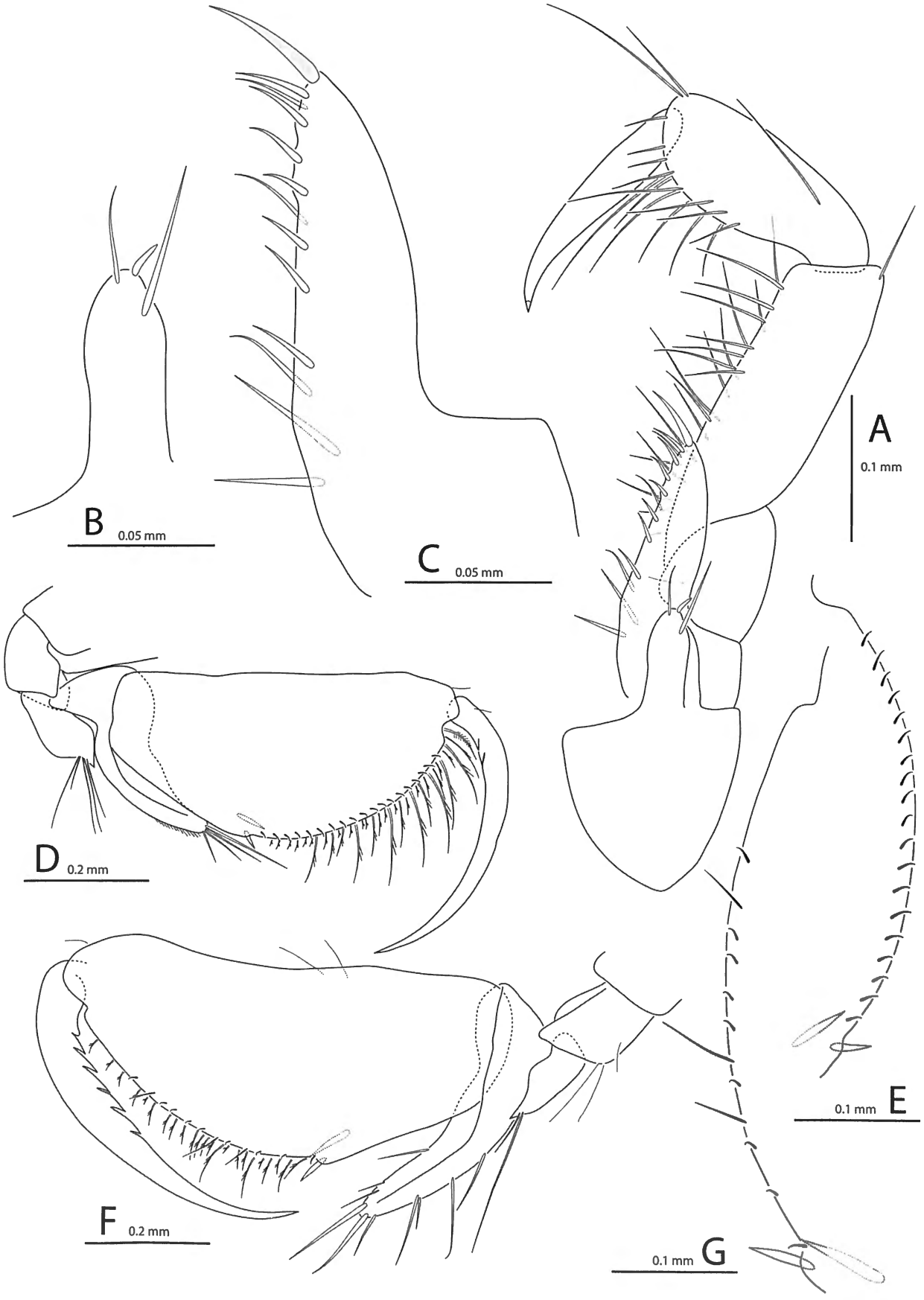

Fig. 46. – *Liljeborgia* (*Liljeborgia*) *macronyx* G.O. SARS, 1894, A-C, male (5 mm), W Norway, Trondheim area, L. GREVE sta. 29; D-G, female, sta. 8-5, Troll vest. A, Mxp; B, left inner plate of Mxp; C, right outer plate of Mxp; D, right Gn1; E, palm of right Gn1 (medial setae not shown); F, left Gn2; G, palm of left Gn2 (medial setae not shown).

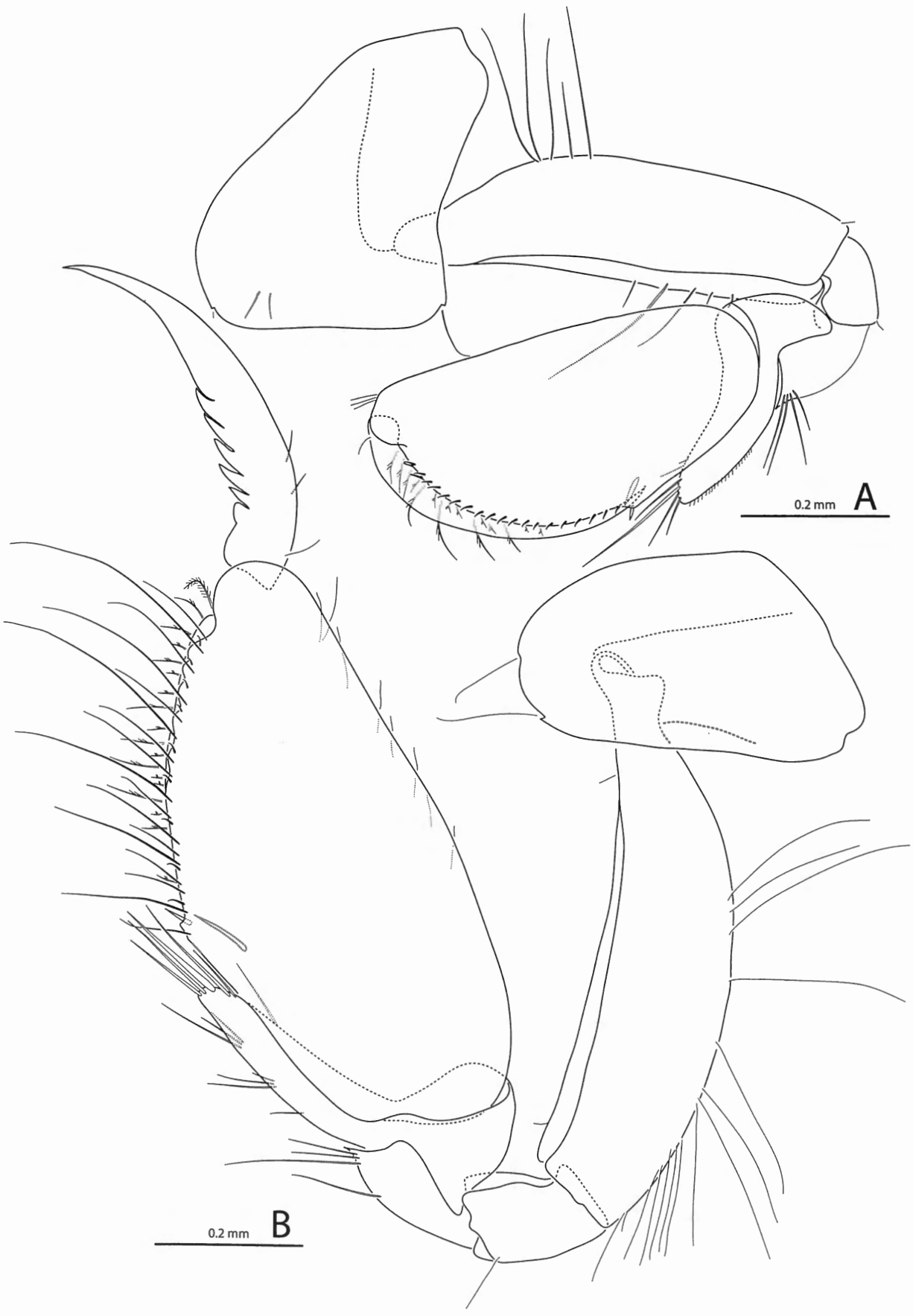

Fig. 47. – *Liljeborgia* (*Liljeborgia*) *macronyx* G.O. Sars, 1894, male (5 mm), W Norway, Trondheim area, L. Greve sta. 29. A, left Gn1; B, left Gn2.

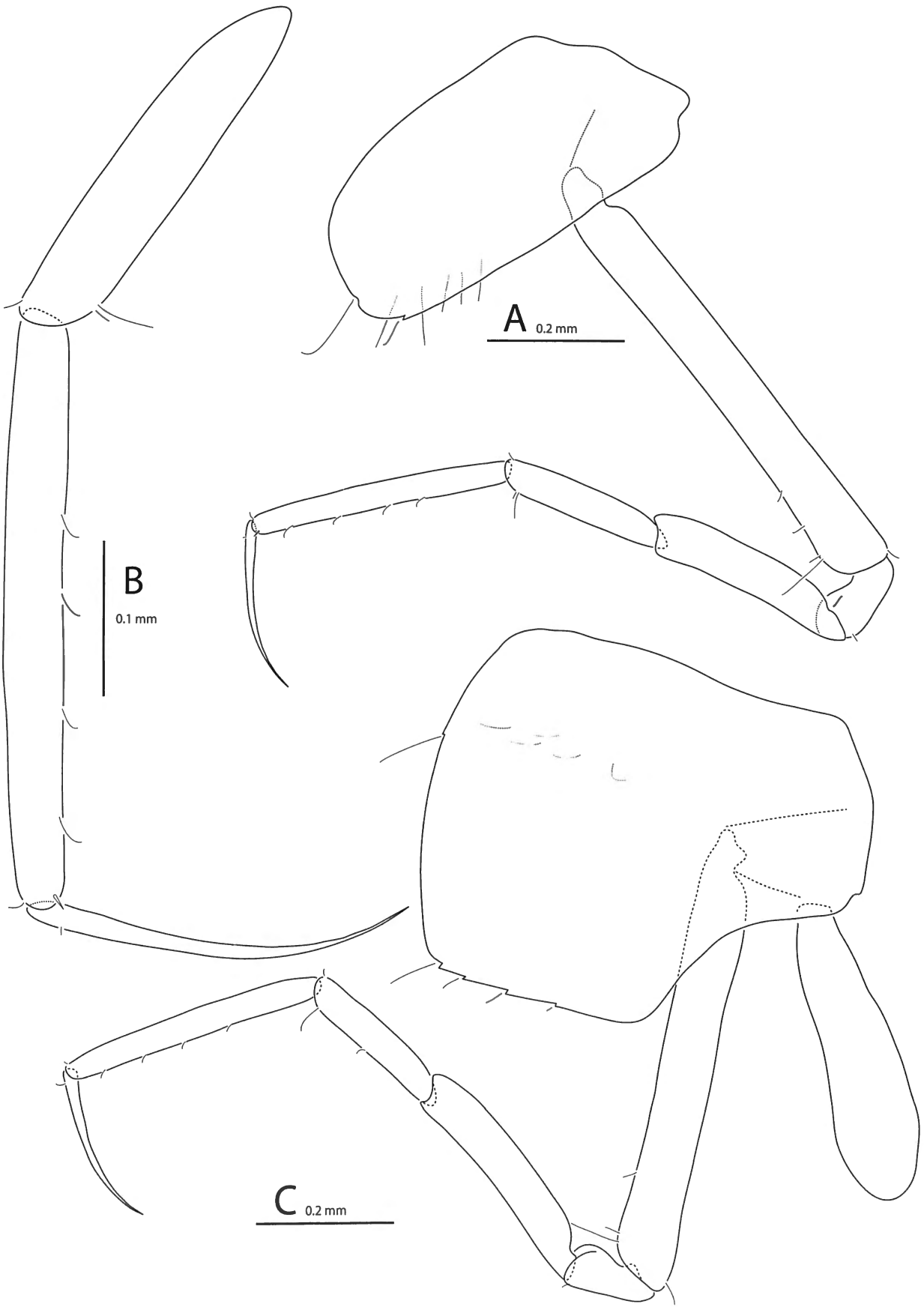

Fig. 48. – *Liljeborgia* (*Liljeborgia*) *macronyx* G.O. SARS, 1894, male (5 mm), W Norway, Trondheim area, L. GREVE sta. 29. A, left P3; B, carpus, propodus and dactylus of left P3; C, left P4.

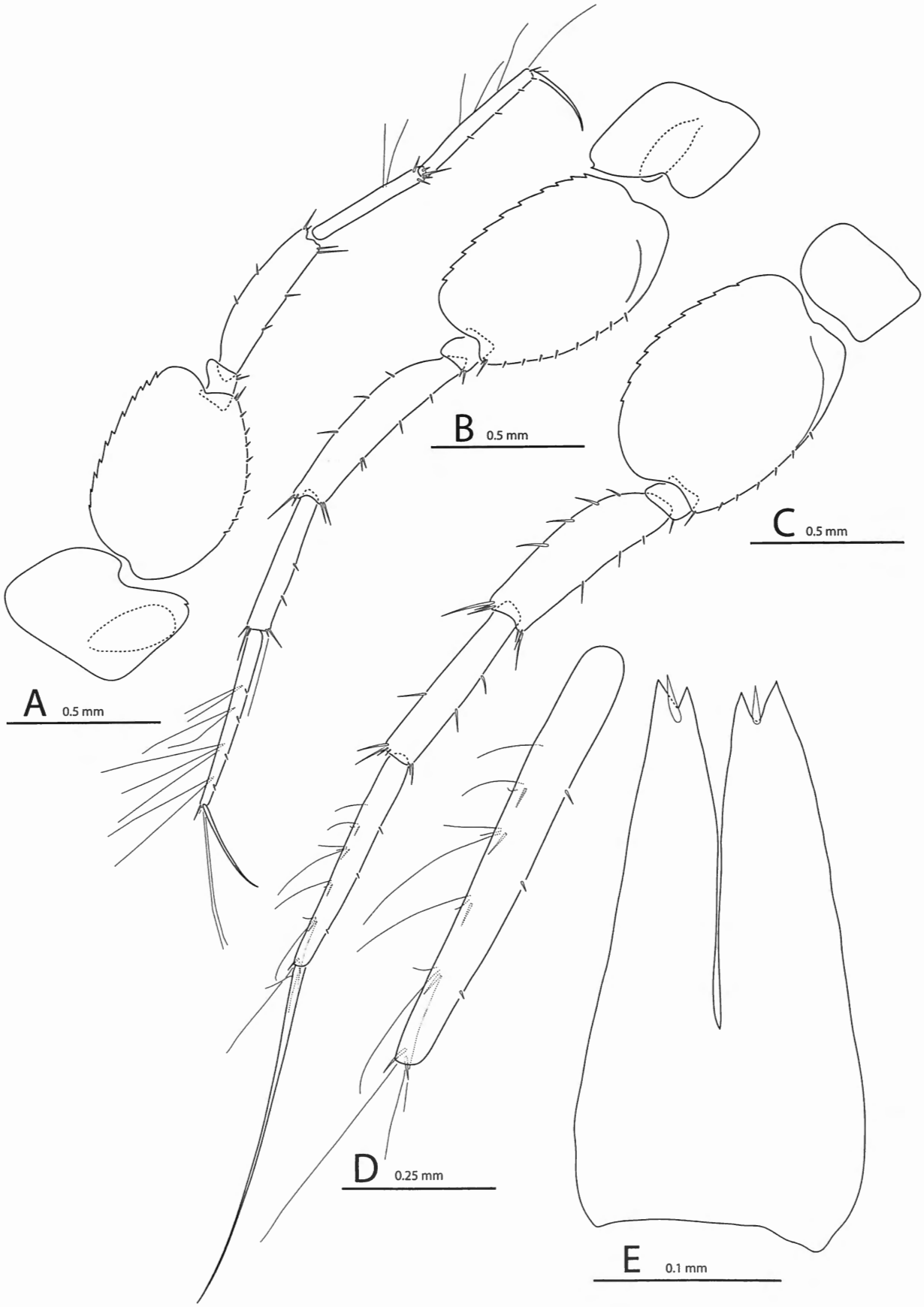

Fig. 49. – *Liljeborgia* (*Liljeborgia*) *macronyx* G.O. Sars, 1894, male (5 mm), W Norway, Trondheim area, L. Greve sta. 29. A, left P5; B, right P6; C, right P7; D, propodus of right P7; E, telson.

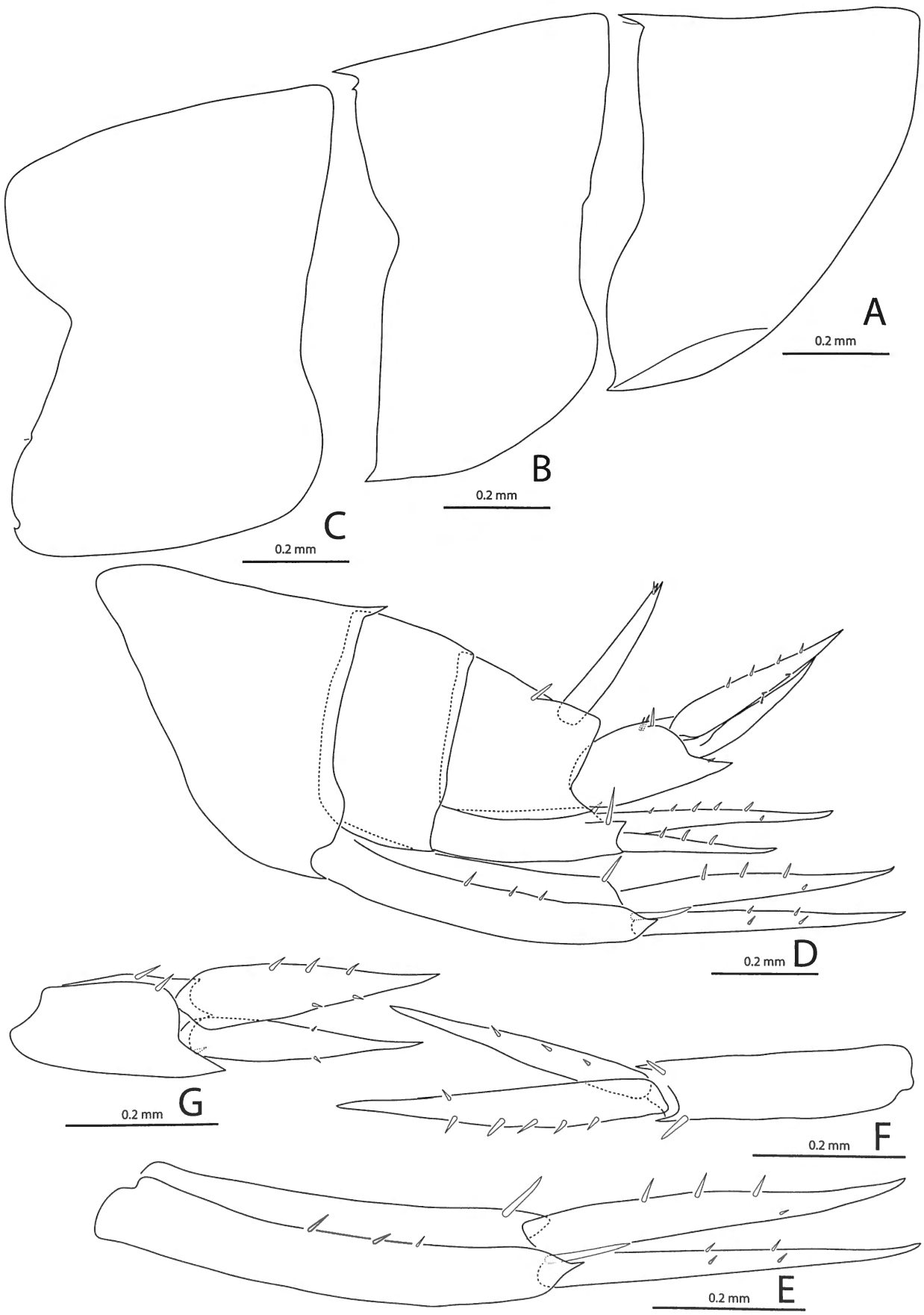

Fig. 50. – *Liljeborgia* (*Liljeborgia*) *macronyx* G.O. SARS, 1894, male (5 mm), W Norway, Trondheim area, L. GREVE sta. 29. A, pleonite 1; B, pleonite 2; C, pleonite 3; D, urosome; E, left U1; F, left U2; G, left U3.

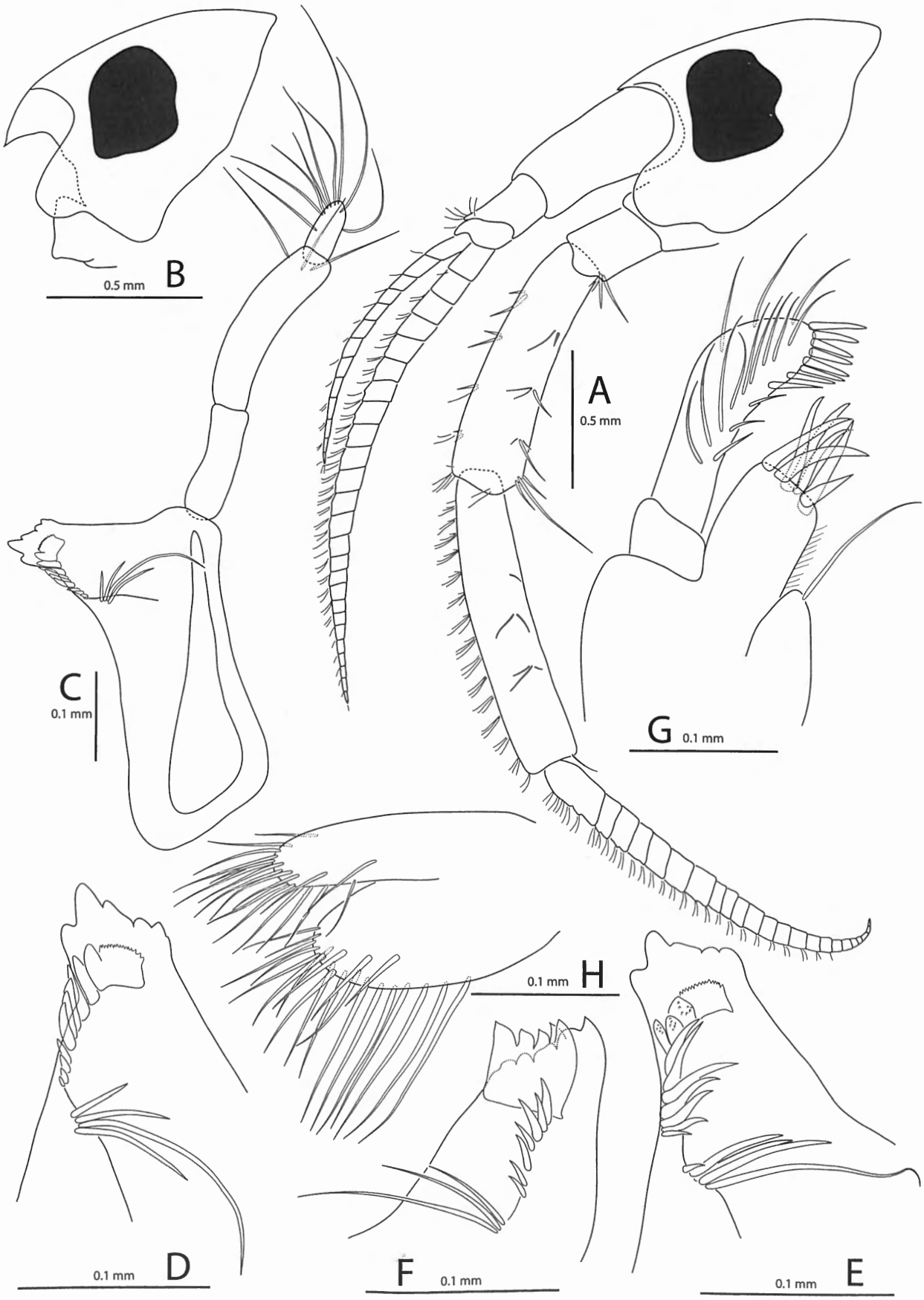

Fig. 51. – *Liljeborgia* (*Liljeborgia*) *pallida* (Bate, 1857), S England, SE Isle of Wight, sample G47-A. A-D, male (10 mm); E-H, ovigerous female (10 mm). A, head with antennae; B, head with epistome; C, right Md; D, E, tip of right Md; F, tip of left Md; G, right Mx1; H, left Mx2.

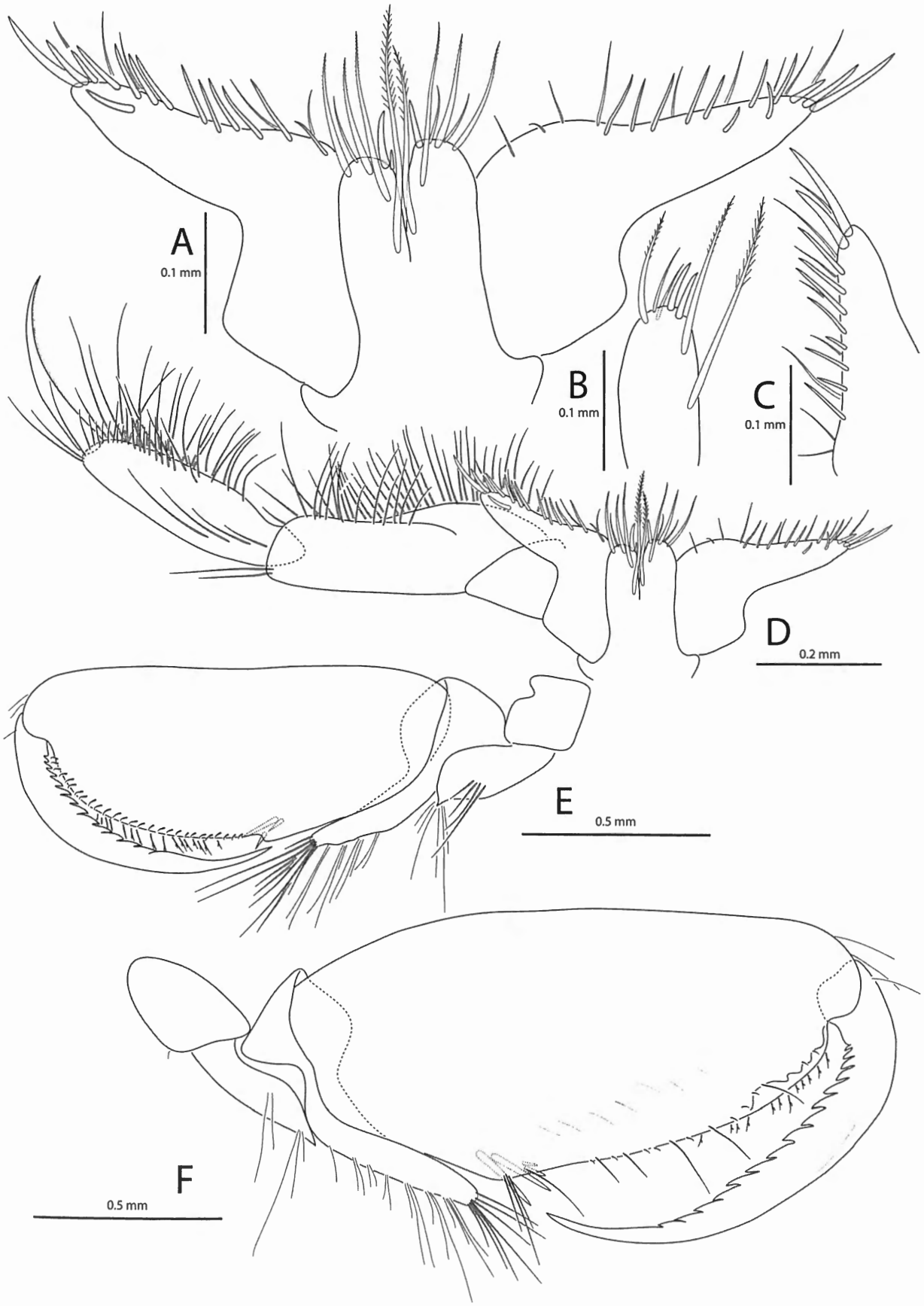

Fig. 52. – *Liljeborgia* (*Liljeborgia*) *pallida* (Bate, 1857), S England, SE Isle of Wight, sample G47-A. A, D, ovigerous female (10 mm); B, C, E, F, male (10 mm). A, plates of Mxp; B, left inner plate of Mxp; C, right outer plate of Mxp; D, Mxp; E, left Gn1; F, right Gn2.

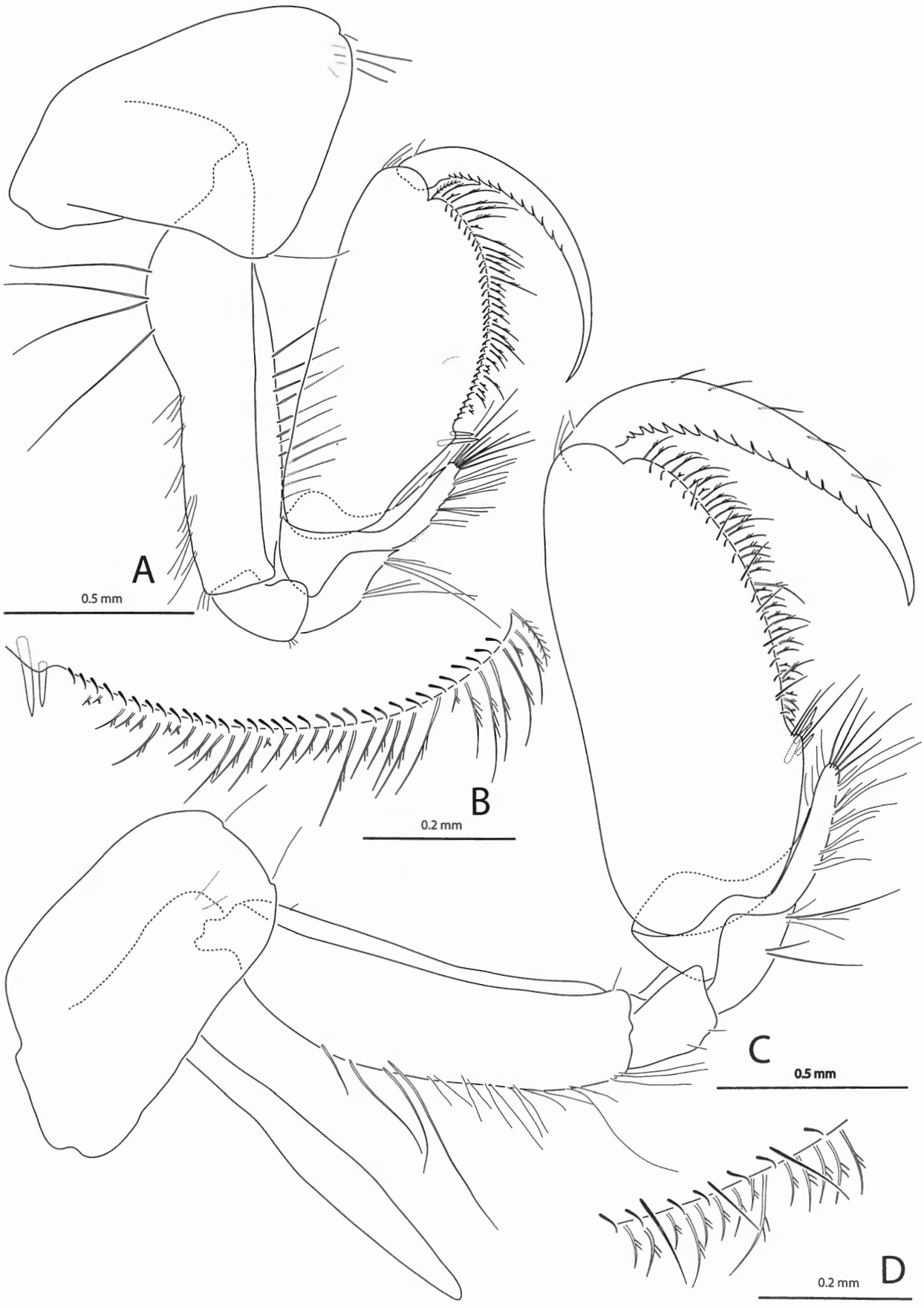

Fig. 53. – *Liljeborgia* (*Liljeborgia*) *pallida* (Bate, 1857), S England, SE Isle of Wight, sample G47-A, ovigerous female (10 mm). A, right Gn1; B, palm of right Gn1; C, right Gn2; D, detail of palm of right Gn2.

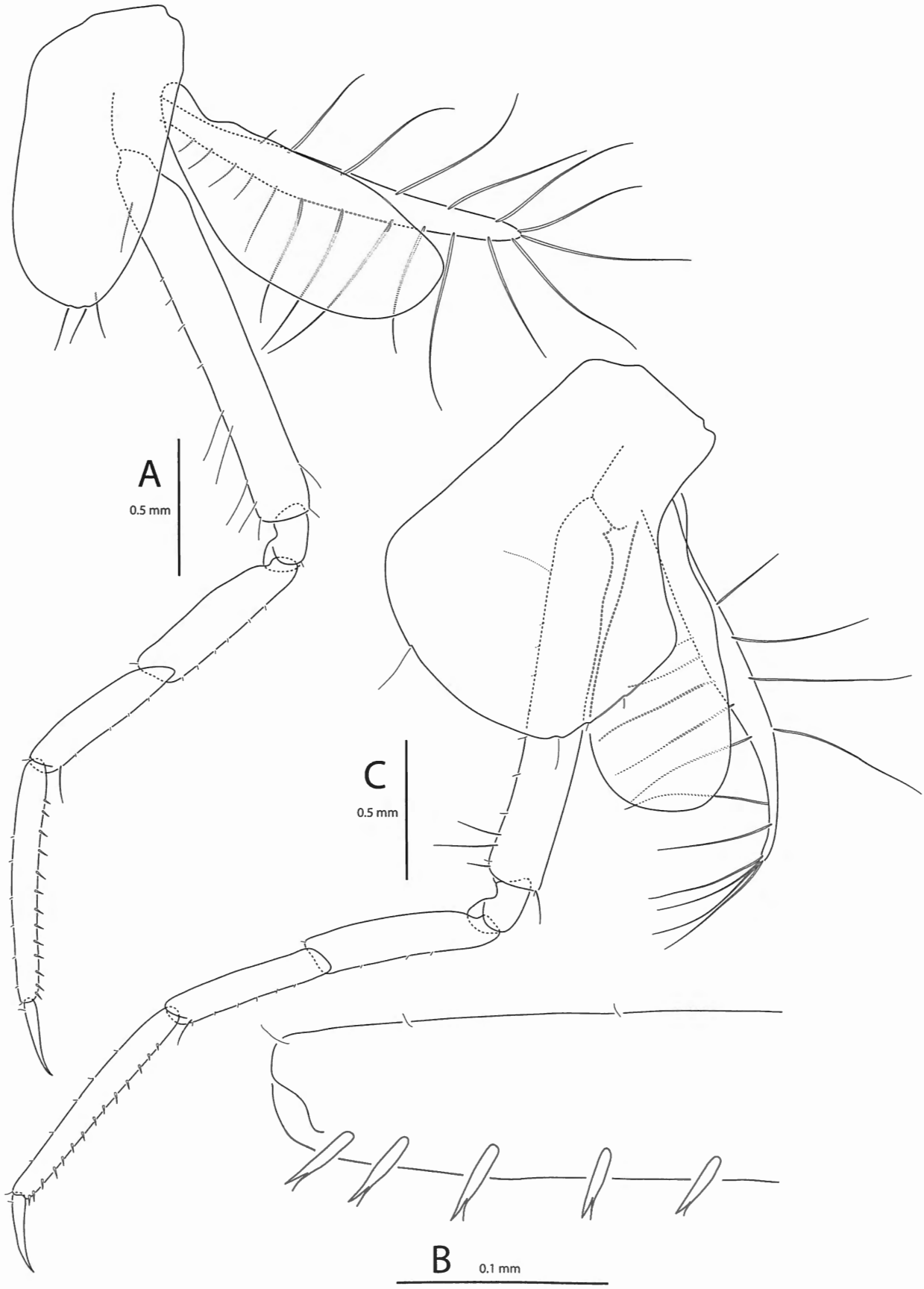

Fig. 54. – *Liljeborgia* (*Liljeborgia*) *pallida* (BATE, 1857), S England, SE Isle of Wight, sample G47-A, ovigerous female (10 mm). A, left P3; B, tip of propodus of left P3; C, left P4.

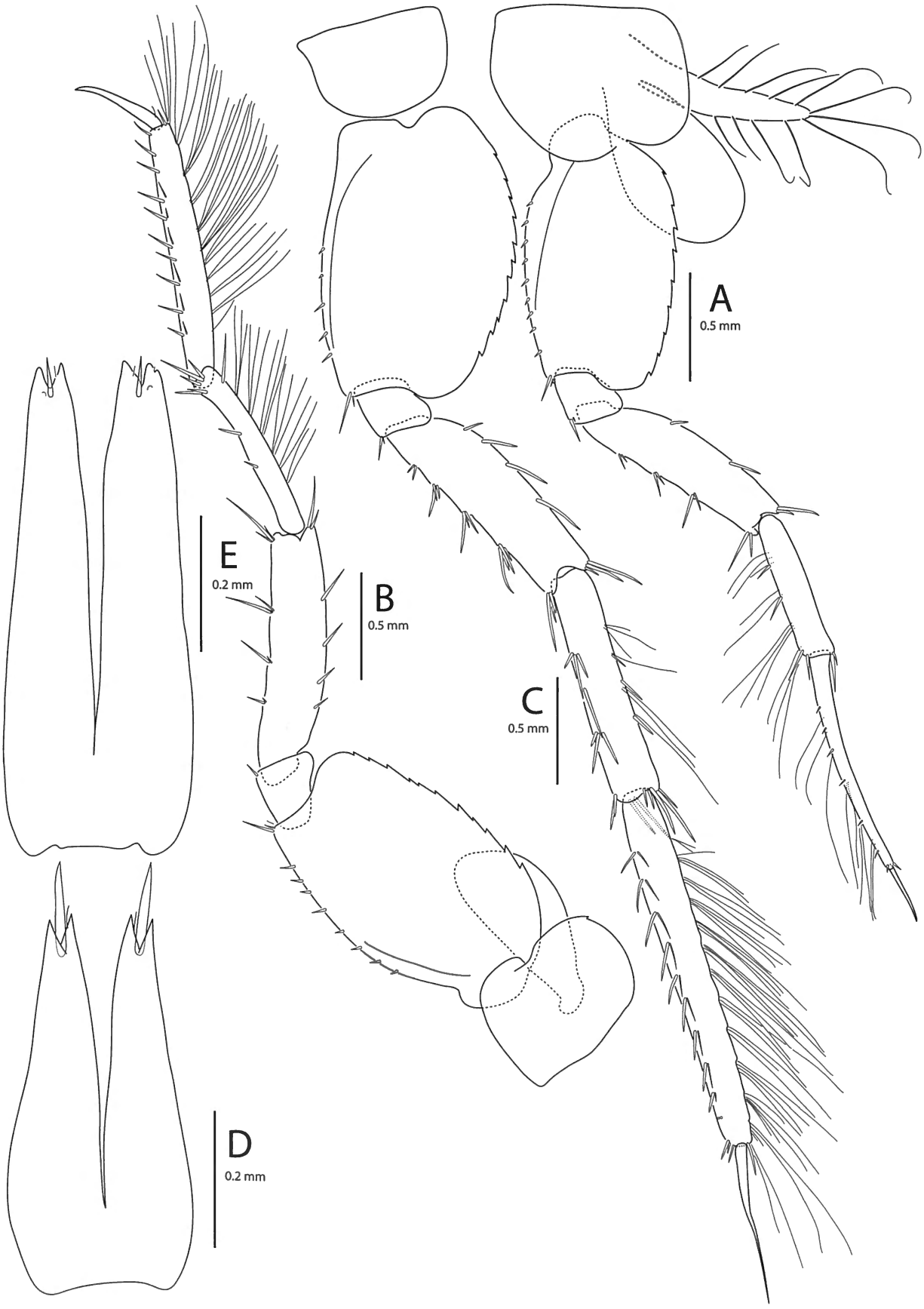

Fig. 55. – *Liljeborgia* (*Liljeborgia*) *pallida* (Bate, 1857), S England, SE Isle of Wight, sample G47-A. A-D, ovigerous female (10 mm); E, male (10 mm). A, left P5; B, right P6; C, left P7; D-E, telson (D, normal specimen; E, specimen with abnormally short distal spines).

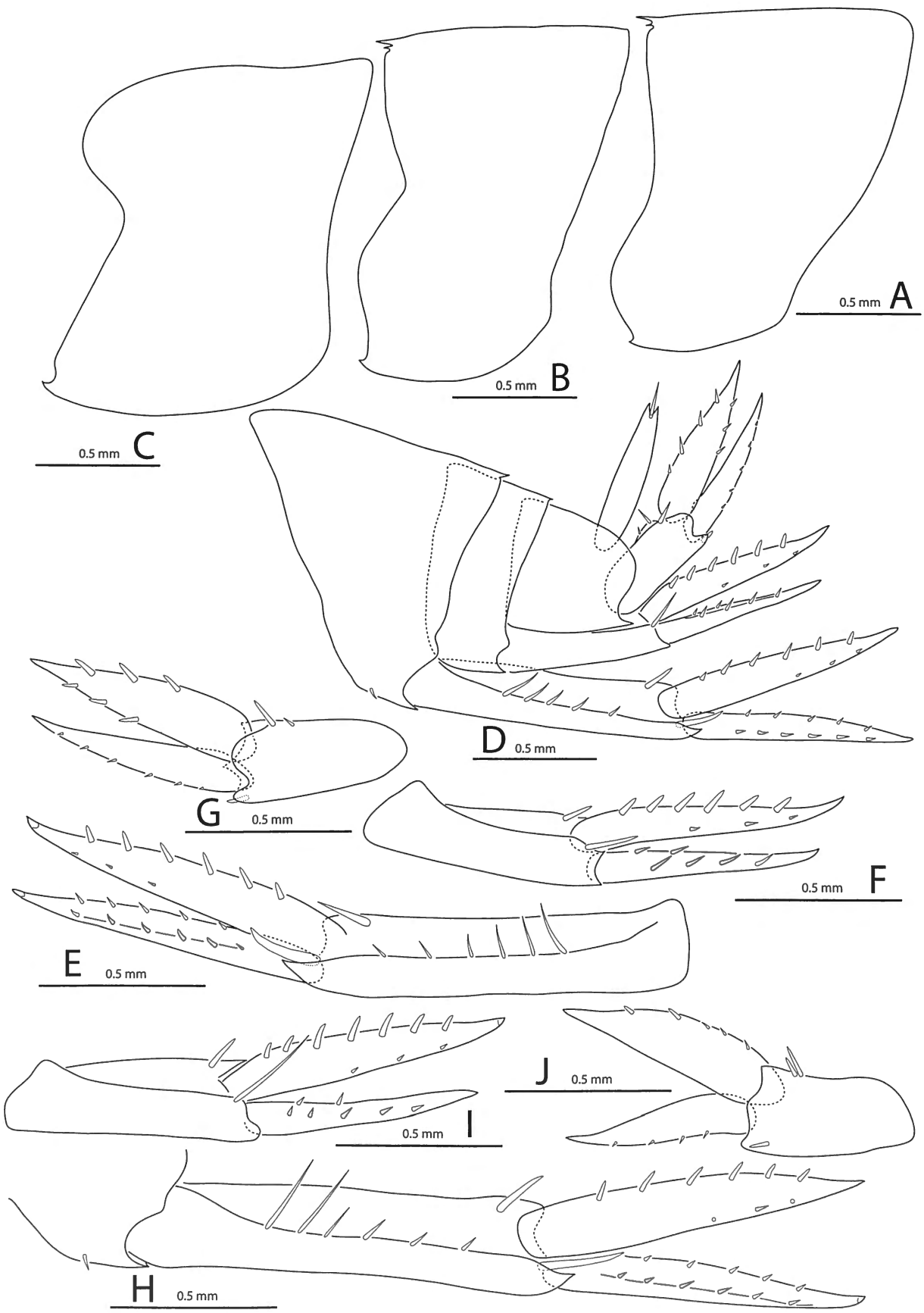

Fig. 56. – *Liljeborgia* (*Liljeborgia*) *pallida* (Bate, 1857), S England, SE Isle of Wight, sample G47-A. A-G, ovigerous female (10 mm); H-J, male (10 mm). A, pleonite 1; B, pleonite 2; C, pleonite 3; D, urosome; E, right U1; F, left U2; G, right U3; H, left U1; I, left U2; J, right U3.

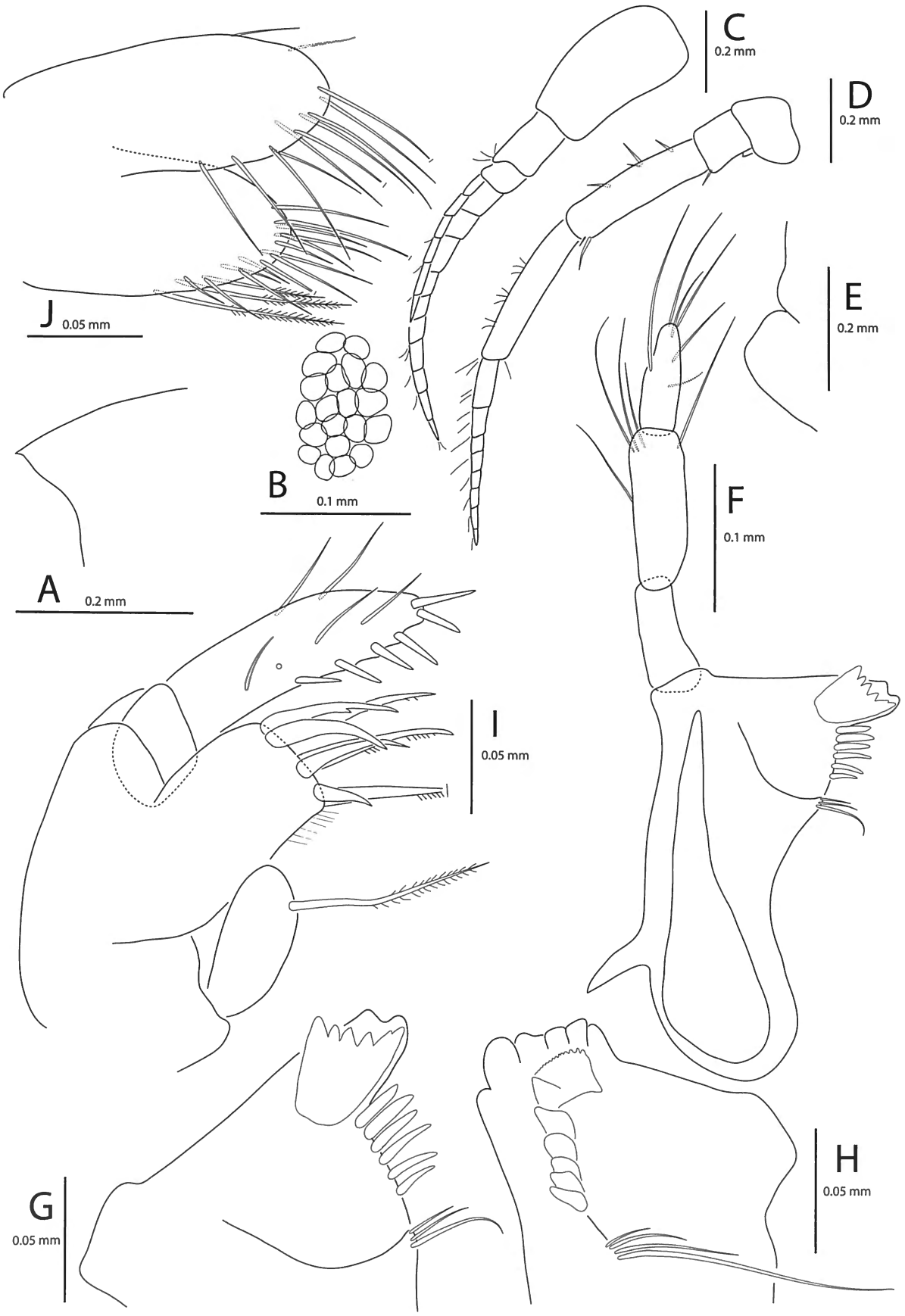

Fig. 57. – *Liljeborgia* (*Liljeborgia*) *psaltrica* KRAPP-SCHICKEL, 1975. A, female, C-J male, NE Greece, Thermaikos Gulf; B, holotype, sex unknown, Croatia. A, rostrum; B, left eye; C, left A1; D, left A2; E, epistome in lateral view; F, left Md; G, tip of left Md; H, tip of right Md; I, right Mx1; J, right Mx2.

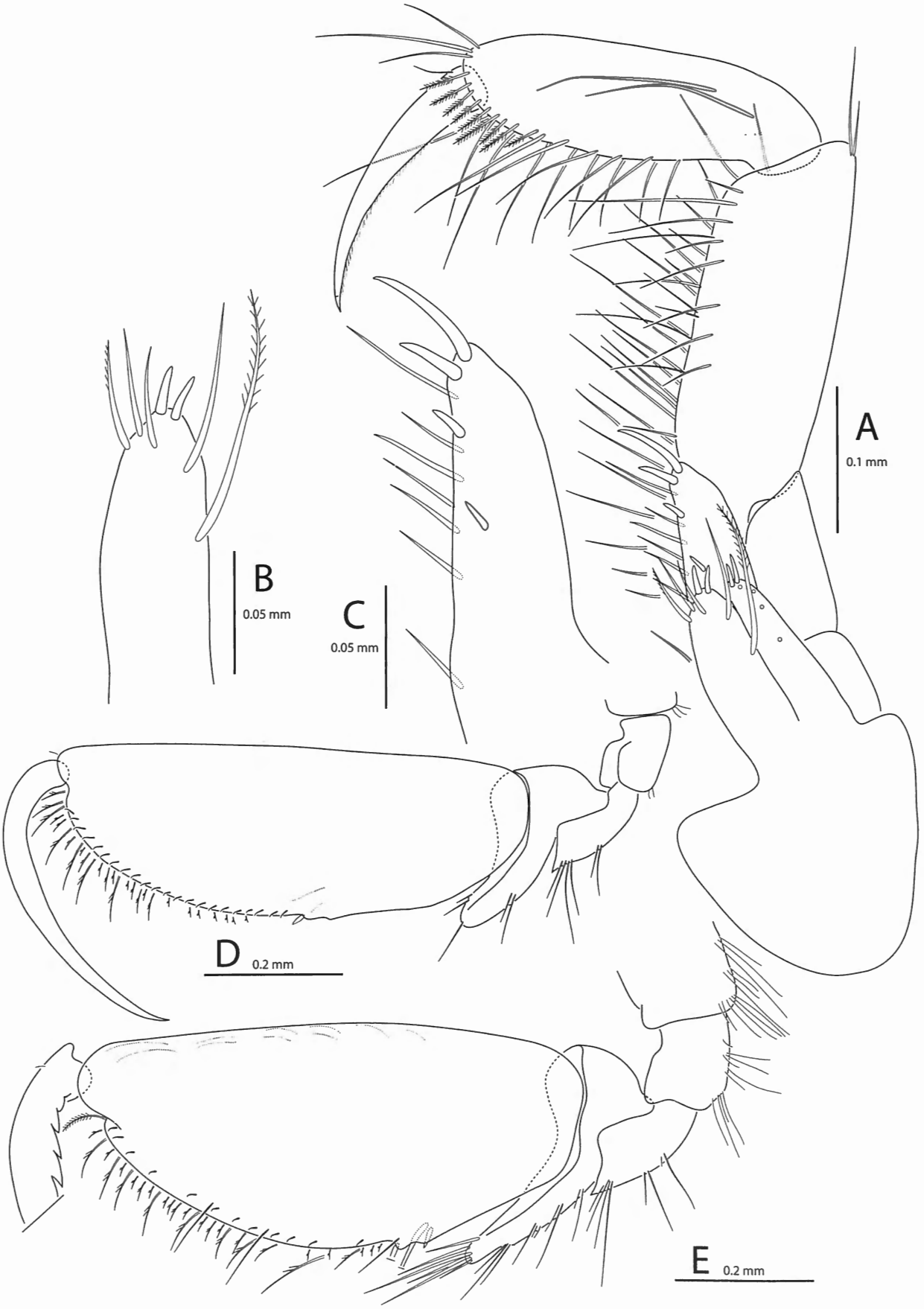

Fig. 58. – *Liljeborgia* (*Liljeborgia*) *psaltrica* KRAPP-SCHICKEL, 1975, NE Greece, Thermaikos Gulf. A, B, C, male (6 mm); D, E, female (5 mm). A, Mxp; B, left inner plate of Mxp; C, right outer plate of Mxp; D, left Gn1; E, left Gn2.

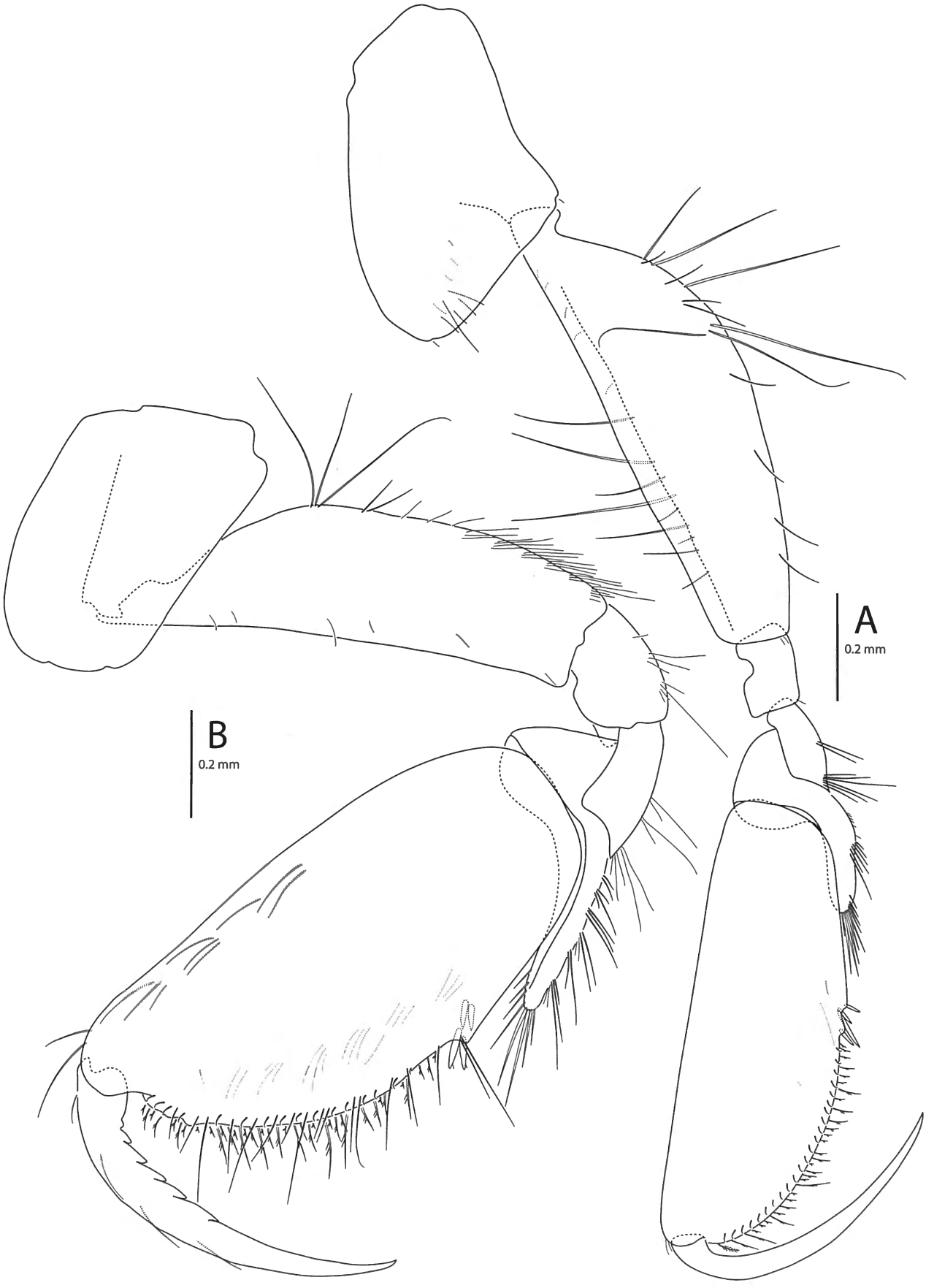

Fig. 59. – *Liljeborgia* (*Liljeborgia*) *psaltrica* KRAPP-SCHICKEL, 1975, male (6 mm), NE Greece, Thermaikos Gulf. A, left Gn1; B, left Gn2.

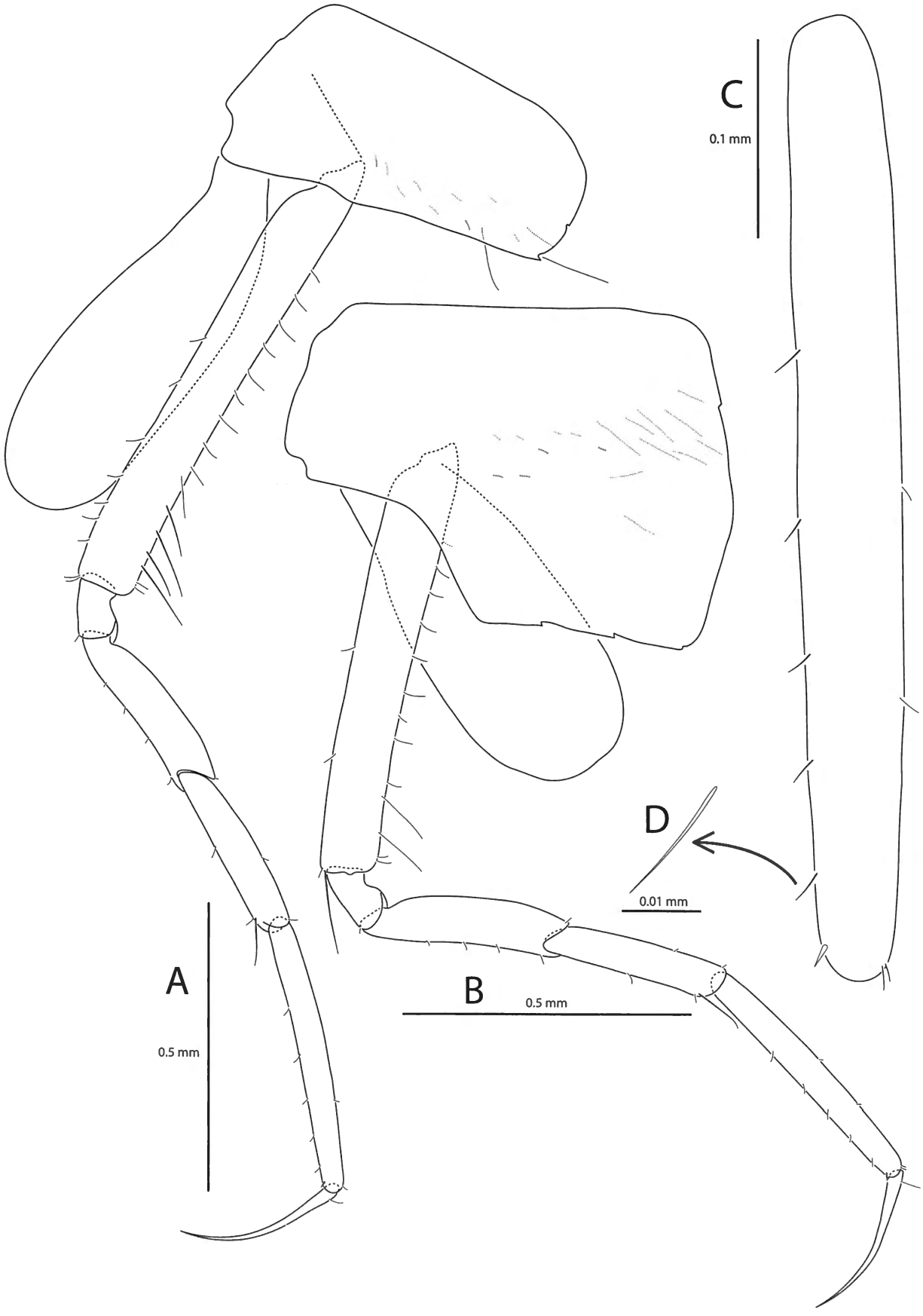

Fig. 60. – *Liljeborgia* (*Liljeborgia*) *psaltrica* KRAPP-SCHICKEL, 1975, male (6 mm), NE Greece, Thermaikos Gulf. A, right P3; B, right P4; C, propodus of right P4; D, 5th setule of posterior border of propodus of P4.

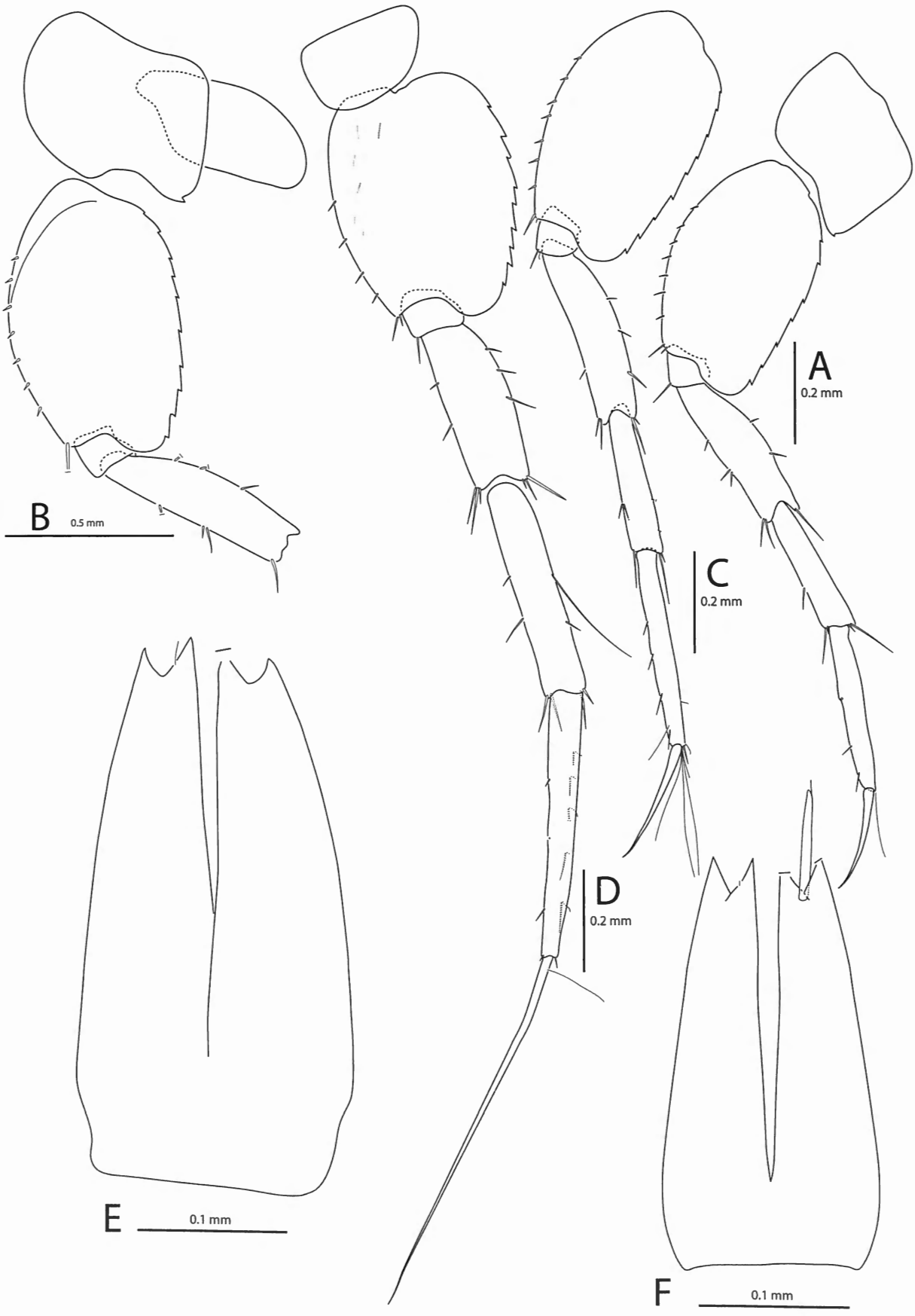

Fig. 61. – *Liljeborgia* (*Liljeborgia*) *psaltrica* KRAPP-SCHICKEL, 1975. A, C, D, holotype, sex unknown (2.5 mm), Croatia; B, E, male (6 mm); F, female (5 mm), NE Greece, Thermaikos Gulf. A, B, left P5; C, left P6; D, left P7; E, F, telson.

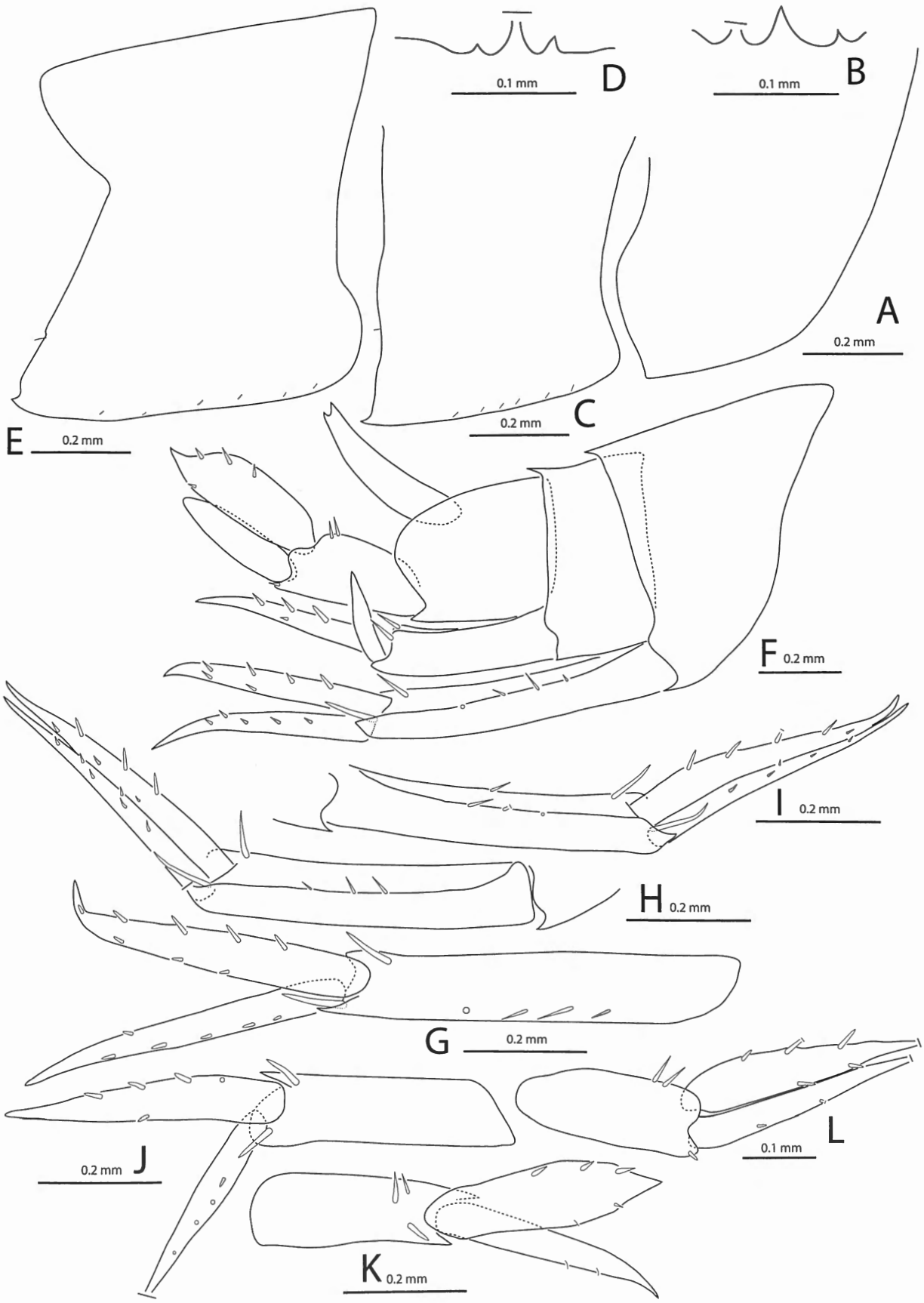

Fig. 62. – *Liljeborgia* (*Liljeborgia*) *psaltrica* KRAPP-SCHICKEL, 1975, NE Greece, Thermaikos Gulf; A-F, G, J, K, male (6 mm); I, L, female (5 mm). A, Ep1; B, posterodorsal border of pleonite 1 in dorsal view; C, Ep2; D, posterodorsal border of pleonite 2 in dorsal view; E, pleonite 3; F, urosome; G, H, right U1, I, left U1 (the occurence of a dorsomedial median spine on the peduncle is presumably abnormal); J, right U2; K, L, left U3.

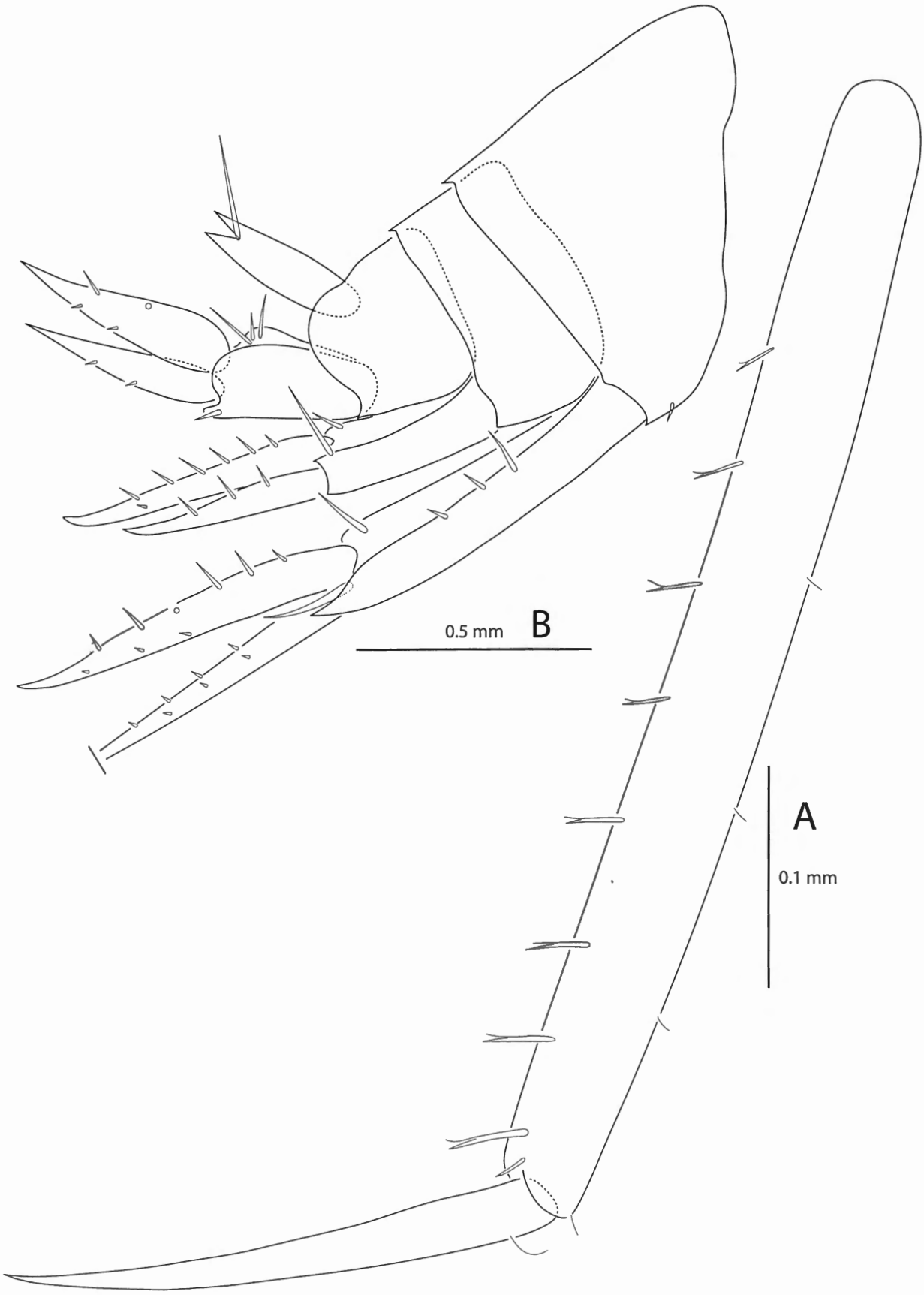

Fig. 63. – *Liljeborgia* (*Liljeborgia*) sp. 4, ovigerous female (6 mm), Italy, Naples area, Vervece, 55-60 m. A, propodus and dactylus of right P3; B, urosome.