4580

Bruce & Holdich 2002

J. Mar. Biol. Ass. U.K. (2002), **82**, 51–68
Printed in the United Kingdom

Revision of the isopod crustacean genus *Campecopea* (Flabellifera: Sphaeromatidae) with discussion of the phylogenetic significance of dorsal processes

Niel L. Bruce* and David M. Holdich†

*Zoologisk Museum, University of Copenhagen, Universitetsparken 15, Copenhagen Ø, DK 2100, Denmark.
Present address: Marine Biodiversity and Systematics, National Institute of Atmospheric and Water Research,
PO Box 14-901, Kilbirnie, Wellington, New Zealand. E-mail: n.bruce@niwa.cri.nz
†School of Life and Environmental Sciences, University of Nottingham, Nottingham, NG7 2RD.
E-mail: david.holdich@ntlworld.com

The sphaeromatid crustacean isopod genus *Campecopea* is revised, a new diagnosis given and the genus *Anoplocopea* Racovitza, 1907, is placed in synonymy; the type species *Campecopea hirsuta* is redescribed and *Campecopea lusitanica* comb. nov. is recorded from the Canary Islands and Azores. The four species of *Campecopea* differ from each other principally in the presence or absence of a prominent posteriorly directed dorsal process on the male pereonite 6, the ornamentation of the posterior pereonites, the shape of the uropods and also the fine details of the dactylus accessory spine (smooth or serrate).

The phylogenetic significance of dorsal process is re-evaluated here, and the character discussed in relation to *Campecopea*, *Dynoides* and *Clianella*, and several other sphaeromatid genera. It is regarded that the interpretation of this character as being of intrinsic generic merit has resulted in the over splitting of several genera and also the creation of paraphyletic genera. It is suggested that reappraisal of sphaeromatid generic characters in cladistic terms is a necessary first step in terms of establishing the monophyly of many sphaeromatid genera.

INTRODUCTION

The genus *Campecopea* Leach, 1814, is one of the earliest described of the sphaeromatid genera. While relatively frequently recorded from western European coasts, other than the redescription by Tetart (1962, 1963), it has remained poorly described. Initially placed in the Cassidininae by Hansen (1905), Bruce (1994a) in revising the Cassidininae of Australia relegated it to the status of *incertae sedis*. The redescription of the genus *Anoplocopea* Racovitza, 1907 (Nolting et al., 1998) and the discovery of *Campecopea* on the Canary Islands has allowed for a critical appraisal of the genus, and for development of a redescription and diagnosis based on characters of perceived phylogenetic significance.

As part of a study into the geographical distribution of another sphaeromatid genus, *Dynamene* Leach (see Holdich, 1970, 1976; Holdich & Harrison, 1980), preliminary surveys of the rocky intertidal zone were carried out by D.M.H. on three islands in the Canaries group, Fuerteventura (1995), Lanzarote (1996) and Tenerife (1997). These surveys resulted in the collection of *C. hirsuta* for the first time from the Canaries and in the discovery of a clearly related species from the same habitat. In addition, a third isopod species was discovered in the same habitat as the *Campecopea* species on the islands of Lanzarote and Tenerife, a species of the enigmatic and poorly known genus *Paravireia* Chilton, 1925 (see Brökeland et al., 2001). The discovery of that genus, known previously only from New Zealand, and of a *Campecopea* in the Canary Islands, highlights the fact that more studies need to be undertaken on the cryptic isopod fauna of the upper zone of rocky shores of the north-eastern Atlantic.

A second part of this present work has been to attempt a reassessment of the significance of dorsal processes in the family, particularly whether or not the absence of such a character should be axiomatically regarded as of generic merit. In particular we discuss these processes for the generic pairs of *Dynoides* Barnard, 1914 and *Clianella* Boone, 1923, *Isocladus* Miers, 1876 and *Exosphaeroma* Stebbing, 1900, together with discussion of the distribution of these characters in other sphaeromatid genera. We conclude that the genus *Anoplocopea* Racovitza, 1907 (recently redescribed by Nolting et al., 1998) cannot be upheld, and it is here placed in synonymy with *Campecopea*.

MATERIALS AND METHODS

Isopods were collected from crevices in volcanic rock and from between and within empty barnacles (*Chthalamus stellatus*) on the middle and upper shore up to the upper limit of the barnacles. As pointed out by Lawson & Norton (1971) much of the littoral rock in Tenerife at least is weathered basalt, and this also appears to be the case for Fuerteventura and Lanzarote. Consequently, collecting in crevices requires the services of a strong crowbar (jemmy). The isopods often occurred as individuals in barnacle tests and small pits on the rock surface, but sometimes as groups of ten or more individuals of mixed age structure in rock crevices. The best way of collecting the isopods was to place pieces of rock with attached barnacles on a tray of tap water and wait for them to swim out. They could then be extracted with a pipette. Isopods collected in the field were preserved in 70% alcohol and others transported live in their natural habitat back to Nottingham, where, as long as they were kept cool they survived in seawater for two weeks.

For scanning electron microscopy (SEM), specimens were taken from alcohol and rehydrated through an alcohol series to distilled water. Specimens and dissected appendages were placed on glass cover slips, excess moisture blotted off with filter paper, and then air-dried at room temperature (20°C) for 24 h. They were then mounted on aluminium stubs using double-sided sticky tape or an epoxy resin glue, sputter coated with gold, and examined at an accelerating potential of 10–15KV with a JEOL JSM 840 SEM.

Terminology

In discussing the significance of dorsal processes to sphaeromatid taxonomy we employ the now widely used terminology of cladistic taxonomy, in particular the terms apomorphy (and its derivatives), plesiomorphy (and its derivatives) and synapomorphy. These words are generally accepted to indicate a character state derived from an ancestral character, the ancestral character state and diagnostic uniting character state respectively (e.g. Lincoln et al., 1983). We consider these character states as discussed here to be putative or potential apomorphic characters. While outgroup comparison has been used in our character assessment, and we discuss these character states in a cladistic context, we do not consider that our discussion of dorsal processes to be a cladistic or phylogenetic analysis nor obviate the need for such an analysis on the Sphaeromatidae.

Abbreviations

CP, circumplumose; PMS, plumose marginal setae; ZMUC, Zoologisk Museum, University of Copenhagen, Denmark.

SYSTEMATICS

Genus *Campecopea* Leach, 1814

Campecopea Leach, 1814:405, 1815:367, 1818:341; Milne Edwards, 1840:219; Dana, 1852:305; Bate & Westwood, 1868:433; Hansen, 1905:112, 139; Omer-Cooper & Rawson, 1934:46; Naylor, 1972:36; Kussakin, 1979:338; Harrison, 1984:373.

Anoplocopea Racovitza, 1907:LXXXIV; Harrison & Ellis, 1991:933; Harrison, 1984:370; Nolting, Reboreda & Wägele, 1998:19 (type species *Anoplocopea hanseni* Racovitza, 1907, by monotypy); **new synonymy**.

Type species

Oniscus hirsutus Montagu, 1804, by monotypy, Leach (1814).

Diagnosis of male

Head and pereonites without ornamentation. Coxae of pereonite 6 larger than 5 or 7, posteriorly produced and laterally overlapping pereonite 7. Pleon of 1 or 2 segments, without lateral or posterior sutures. Pleotelson posterior margin with partial (*Campecopea hirsuta*), or complete ventral exit channel, or with posteriorly enclosed foramen (*C. lusitanica*, Canary Islands). Antennule peduncle article 2 short, less than half as long as article 1. Maxilliped palp articles weakly lobate. Pereopods with accessory unguis multiply cuspid or smooth (*C. ischiana*); pereopod 7 ischium elongate, 1.2 to 1.3 times as long as basis, 5.4–6.0 times as long as wide. Pleopod 1 rami collinear; pleopod 2 appendix masculina basal; pleopod 3 exopod with entire weak transverse suture; pleopods 4 and 5 with both rami lamellar. Uropods articulating at anterior dorsolateral position, endopod completely absent, endopod and peduncle reduced, forming articulating knob.

Description of male

Dorsal surface of body increasingly granular towards posterior. Coxae not distinctly demarcated. Pereonite 6 with or without posteriorly directed dorsal process.

Antennule peduncle article 1 more than twice as long as 2, articles 1 and 2 robust, article 3 slender; articles collinear, flagellum shorter than peduncle. Antenna peduncle articles 1 and 2 short, partly fused, 3 slightly longer than 2, article 4 longer than 3 and 5 longest.

Epistome anteriorly rounded or truncate, with posteriorly directed lateral flanges. Mandible incisor 3- or 4-cuspid; molar process prominent, crushing surface with nodular ridges; left mandible with lacinia mobilis, both mandibles with spine row of four spines; palp 3-articled, article 1 longest, 3 shortest. Maxillule lateral lobe with about nine (visible) simple and weakly serrate robust setae on gnathal surface, medial lobe with three serrate plumose robust setae and one shorter simple spine. Maxilla with all articles well developed, with prominent setae on lateral and middle lobes, medial lobe with 4–6 prominent CP setae.

Pereopods all ambulatory, pereopods 1–3 subsimilar, pereopod 1 shorter and more robust than 2 and 3; pereopods 4–7 becoming increasingly slender; inferior margins of ischium to propodus with weak to dense setulose fringe; superior margins of ischium with proximal spine.

Penes paired, unfused, medially adjacent at posterior of pereonite 7, short, not extending to pleopod peduncles

Pleopods 1–3 both rami with PMS. Pleopod rami subequal in length, approximately collinear; exopod with proximolateral spine; peduncle with two coupling hooks on medial margin. Pleopod 2 appendix masculina extending beyond distal margin of endopod, distally bluntly rounded. Pleopods 4 and 5 exopods without transverse suture, lateral margins of either with or without short simple setae. Pleopod 5 exopod with two or three weak scale patches.

Female, ovigerous

Process on pereonite 6 (*C. hirsuta*) absent, coxae of pereonite 6 less large than in male. Generally less granular than male, with pleotelson exit channel (*C. lusitanica*) less developed in females. Brood pouch without pockets, oostegites arising from coxae of pereonites 1–4. Otherwise appendages are similar to those of the male.

Female, non-ovigerous and juveniles

Generally similar to ovigerous females, but lacking oostegites, and less swollen in body shape.

Composition

Campecopea hirsuta, type species; *Campecopea hanseni* (Racovitza, 1907), comb. nov.; *Campecopea ischiana* (Verhoeff, 1943), comb. nov.; and *Campecopea lusitanica* (Nolting, Reboreda & Wägele, 1998), **comb. nov.**

Remarks

The four species of this genus are extremely similar in most body and appendage characters (other than *C. hirsuta* having a prominent dorsal process on pereonite 6), some of which can be regarded as potential synapomorphies. These character states include: pereopod 7 ischium greatly elongated (1.2–1.3 times as long as basis, about 5–6 times as long as wide) and the uropod articulation anterior mediolateral (not ventrolateral as in most sphaeromatids), these characters being, as far is known, unique to the genus, and potential autapomorphies. Further, probably apomorphic, characters (although these are also known to occur in some other unrelated genera), are the large coxae of pereonite 6 which overlap pereonite 7 and extend to pleon in lateral view (also occurs in *Dynamenopsis*); pleon with only one or two (first+fused remainder) segments (the significance of this is difficult to assess as such reductions are widespread) and the uropod endopod totally reduced in both sexes, forming an articulating 'knuckle' [also found in the family Ancinidae, *Bathycopea* Tattersall, 1905 (see Bruce 1991), in the sphaeromatid genera *Pistorius* Harrison & Holdich, 1982 (which has a similar endopod, in the male) and in the stygial *Monolistra* Gerstaecker, 1856 (see Racovitza, 1910)]. Finally *Campecopea* has pleopods 4

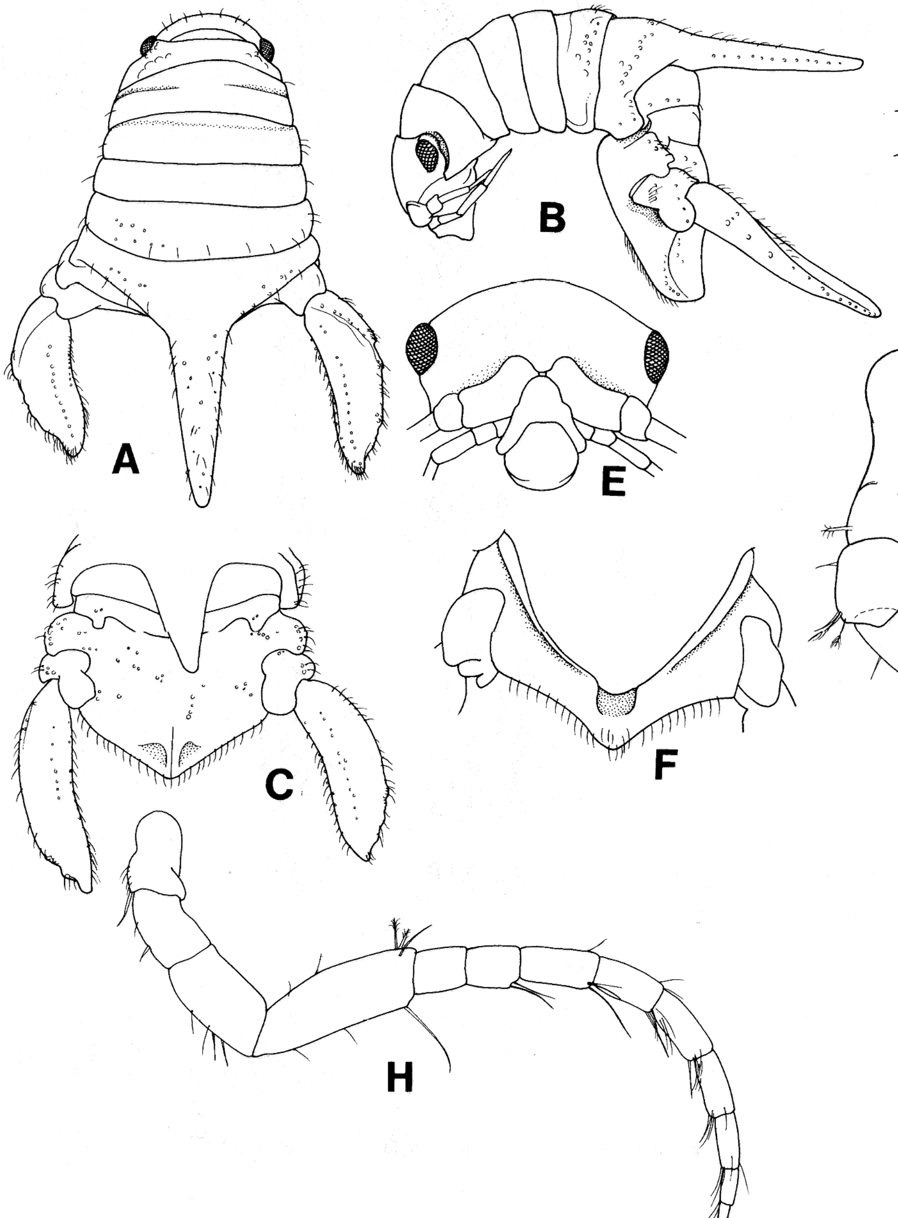

Figure 1. *Campecopea hirsuta*. (A–F) ♂ 3.3 mm, remainder ♂ 2.1 mm, Viana do Castelo, Portugal, ZMUC CRU2481. (A) Dorsal view; (B) lateral view; (C) pleonite 6 and pleon in dorsal view; (D) detail of pleon lateral margin; (E) frons; (F) pleon, ventral view; (G) antennule; (H) antenna. Scale bar: 1.0 mm.

4684

and 5 essentially lamellar, although this character state, being highly homoplasious in the Sphaeromatidae, is of little phylogenetic significance as has been repeatedly demonstrated (Bruce, 1993, 1994a,b, 1995, 1997).

Synonymy of Anoplocopea

Nolting et al. (1998) gave excellent figures for the several species that they regarded as belonging to the little-known genus *Anoplocopea*. Comparison of the generic diagnosis given here with those figures indicates that the sole distinguishing character for *Anoplocopea* is the absence of the dorsal process of on pereonite 6, and the genus is therefore probably paraphyletic. We discuss the significance of the dorsal processes as a character of intrinsic generic merit for genera other than *Campecopea* separately in the Discussion. Our conclusion, based on both the recognizable defining characters for *Campecopea* and of the lack of such defining characters for *Anoplocopea*, is that *Anoplocopea* is a junior synonym of *Campecopea*.

Distribution

Eastern North Atlantic and Mediterranean: the type species is known from the coasts of Europe, Atlantic northern Africa, and the Canary and Azores island groups, while *C. lusitanica* is known from the Canary Islands, the Azores and the Iberian Peninsula; in the Mediterranean *C. hanseni* is known from Corsica and *C. ischiana* from the Gulf of Naples.

Relationships

It is not immediately obvious which are the related or sister genera to *Campecopea*. Several groups of genera, all Dynameninae, can easily be eliminated on multiple character differences. Equally the genus does not belong in the Cassidininae (*sensu* Bruce, 1994a) in either the strict or broad sense of that subfamily. On that basis related genera to *Campecopea* should be sought in the Sphaeromatinae. The weakly-produced maxilliped palp lobes, together with the relatively simple pleotelson posterior margin eliminates those genera related to and including *Cymodoce*, while the posterior border of the pleotelson with an exit channel eliminates those genera allied to and including *Sphaeroma* (see Harrison & Holdich, 1984 for figures). Although the presence of a dorsal process in one of the species together with the loss of the uropodal endopod may suggest an affinity with the *Cilicaea–Cilicaeopsis–Paracilicaea* group of genera, those species that have a pleonal process, also have the uropodal

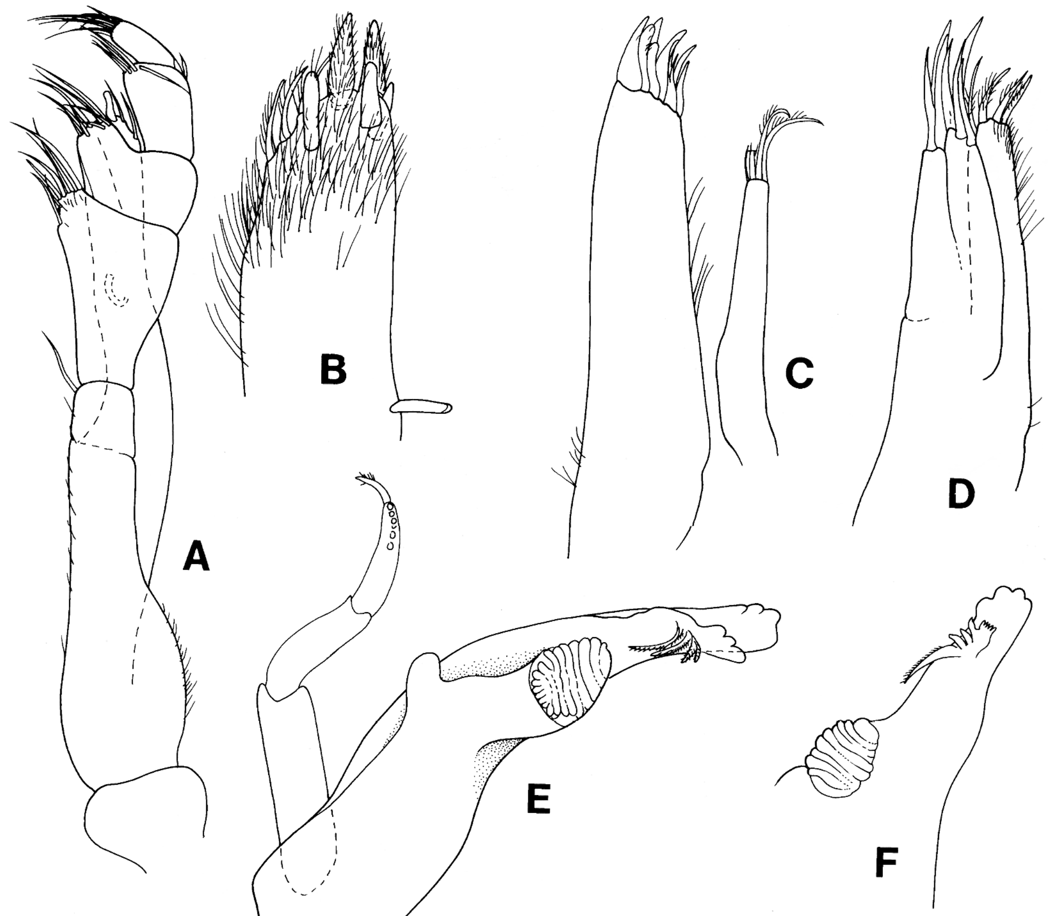

Figure 2. *Campecopea hirsuta* ♂ 2.1 mm, Viana do Castelo, Portugal, ZMUC CRU2481. (A) Maxilliped; (B) maxilliped endite, detail; (C) maxillule; (D) maxilla; (E) left mandible; (F) right mandible, distal part.

endopod variously reduced, and an affinity is furthermore not supported by differences in the morphology of the maxilliped, pereopods, pleopod 1 (exopod oblique) and pleopods 4 and 5 (exopods with entire transverse suture).

At present we regard the position of *Campecopea* as *incertae sedis* within the Sphaeromatinae. A more informative assessment of the phylogenetic position of this genus will only result from a critical phylogenetic and cladistic analysis of all the genera of the Sphaeromatidae.

Key to the species of Campecopea

1. Pereonite 6 with elongate posteriorly directed dorsal process; (males); pleotelson dorsal margin posteriorly entire (males and females) .... *Campecopea hirsuta*

—Pereonite 6 without elongate posteriorly-directed dorsal process; pleotelson dorsal margin posteriorly with foramen or open notch (males and females) 2

2. Pereopods with simple dactylus unguis..................... 3

—Pereopods with multicuspid dactylus unguis.............. 4

3. Posterior margin of pereonite 7 with two weak submedian lobes; uropod lateral margin distinctly sinuate .... *Campecopea hanseni*

—Posterior margin of pereonite 7 even; uropod lateral margin convex .... *Campecopea lusitanica* (male morph A)

4. Posterior margin of pleotelson with simple slit........... .... *Campecopea ischiana*

—Posterior margin of pleotelson with foramen widest anteriorly, nearly close posteriorly............................ .... *Campecopea lusitanica* (male morph B)

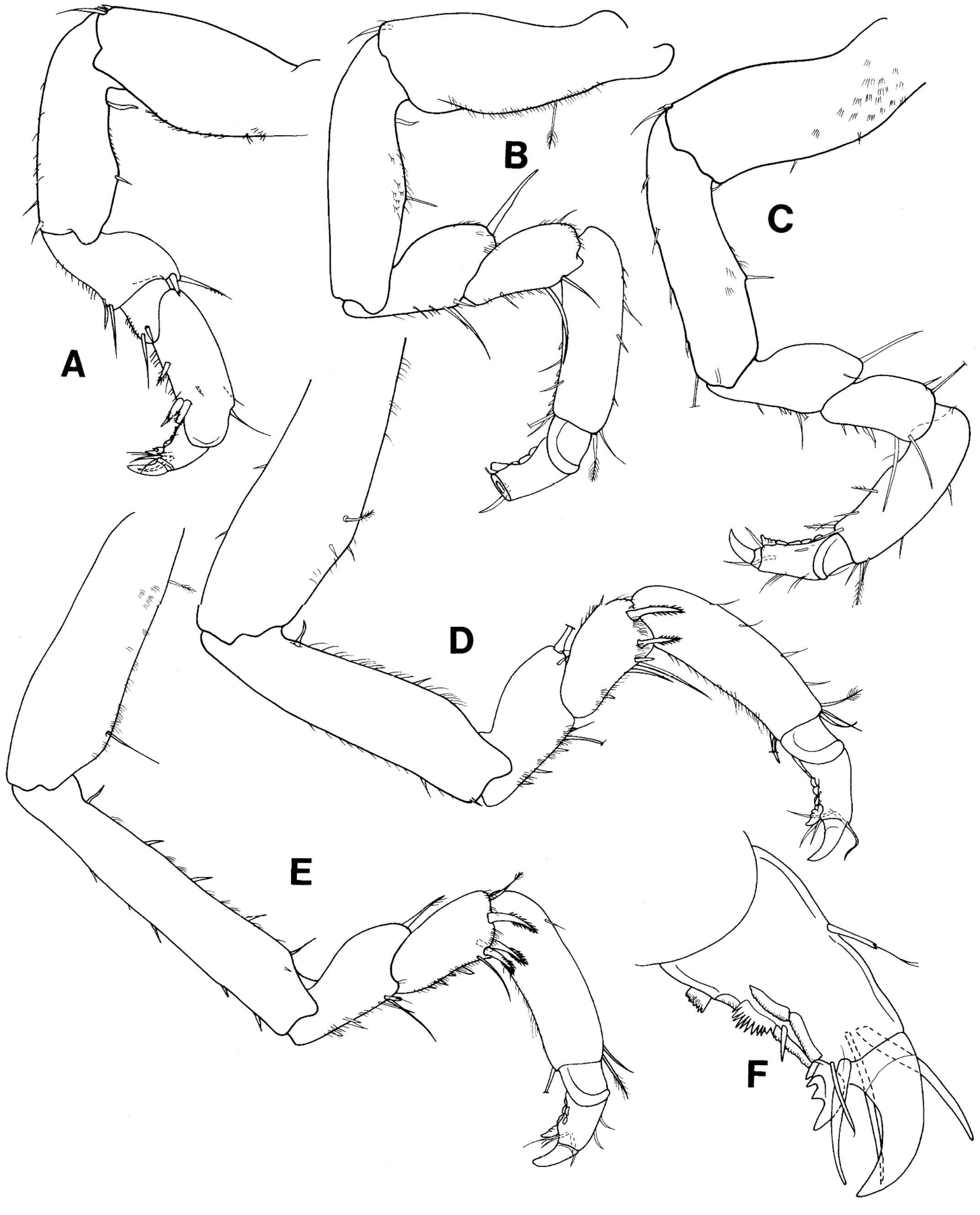

Figure 3. *Campecopea hirsuta*. ♂ 2.1 mm, Viana do Castelo, Portugal, ZMUC CRU2481. (A–E) Pereopods 1, 3, 2, 6 and 7 respectively; (F) dactylus of pereopod 1.

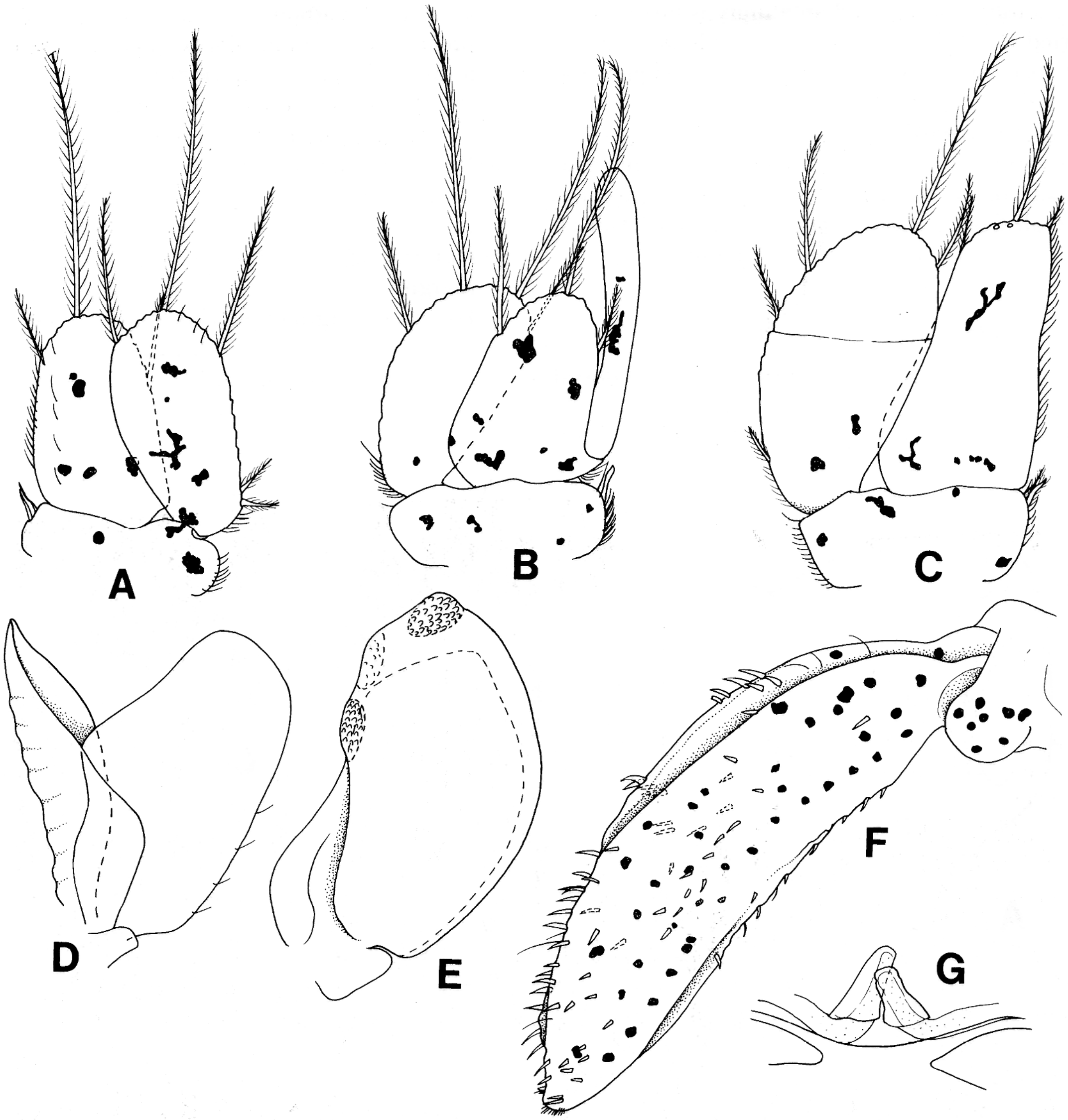

Figure 4. *Campecopea hirsuta*. ♂ 2.1 mm, Viana do Castelo, Portugal, ZMUC CRU2481. (A–E) Pleopods 1–5 respectively; (F) uropod; (G) penial processes.

Campecopea hirsuta (Montagu, 1804)
Figures 1–5, 12A–C

Oniscus hirsutus Montagu, 1804:71, plate 6, figure 7.

Campecopea hirsuta.—Leach, 1814:405.

Campecopea hirsuta.—Leach, 1815:367, 1818:341; Desmarest, 1825:294; Guérin-Méneville, 1837, plate 30, figure 3; 1840:32; Lucas*, 1840:254; Milne Edwards, 1840:220; White, 1847:105, 1850:78, 1857:248, plate 14, figure 2; Cocks, 1849:84; Goss, 1855:135, figure 238; Bate & Westwood, 1868:434; Bate, 1878:123; Gerstaecker, 1882:253; Bonnier, 1887:156; Dollfus, 1888:36; Bolivar, 1893:133; Norman, 1905:14; Thompson, 1910:27; Norman & Scott, 1906:43; Monod, 1923:95, 1931a:496, figures 4–6, 1931b:65, figures 60–61; Maury, 1929:156; Omer-Cooper & Rawson, 1934:46, plate 5, figures 3–6; Panouse, 1940:93; Tetart, 1962:159, plates 1–3, 1963:165; Harvey, 1968:761; Naylor, 1972:36, figure 11C,D, 1990:394, figure 9.11; Kussakin, 1979:338, figures 201–203; de Grave & Holmes, 1998:25 (Table 1).

Campecopea cranchii Leach, 1818:341; Desmarest, 1825:295; Milne Edwards, 1840:220; White, 1850:78; 1857:248; Gerstaecker, 1882:253; Bonnier, 1887:155.

Campecopea cranchii.—Bate & Westwood, 1868:436.

Sphaeroma hirsute.—Bosc, 1830:151.

Naesa angulosa Hesse, 1873:27, plate 3, figures 18–21.

Campecopea lineata Hesse, 1873:29, plate 3, figures 22–25.

Material examined

Six ♂ (2.1, 2.5, 2.5, 2.6, 2.8, 3.3 mm), four immature ♀ (2.3, 2.3, 2.6, 2.7 mm), two ovigerous ♀ (2.1, 2.3 mm), four non-ovigerous ♀ (2.1, 2.5, 2.5, 3.0 mm, + six tightly rolled), Viana do Castelo, Portugal, ~41°47′N 08°52′W, July 1993, coll. A. Murias (ZMUC CRU2481).

Additional material: ♂ (2.0 mm), three ♀ (2.3, 2.3, 2.5 mm), Costa Teguise, Lanzarote, Canary Islands, ~29°05′N 13°32′W, 26 March 1996, upper shore crevices and barnacles, coll. D.M. Holdich (ZMUC CRU2482). Two ♂ (2.8, 2.1 mm), two ♀ (2.2, 2.3 mm), Aqua d'Atto,

---

*, The paper by Lucas was printed three times, in 1840, 1842 and 1851, with identical pagination (L.B. Holthuis, personal communication). Only the first date is included here.

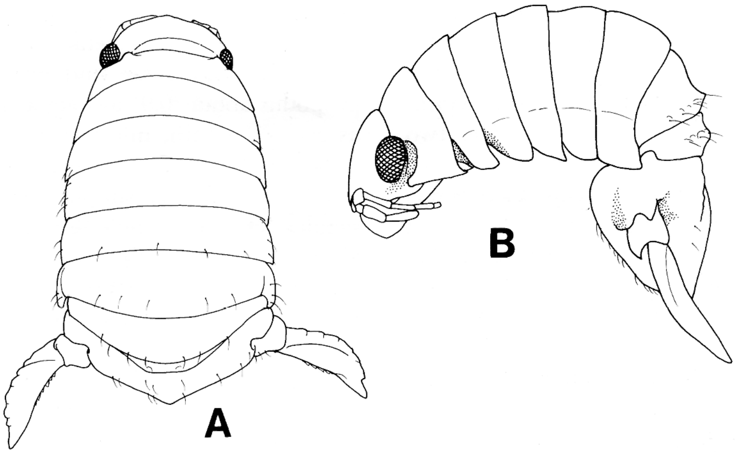

Figure 5. *Campecopea hirsuta*. ♀ 2.5 mm ovigerous, Viana do Castelo, Portugal, ZMUC CRU2481. (A) Dorsal view; (B) lateral view.

São Miguel, Azores, August 1994, from shells of *Chthalamus stellatus*, coll. B. Morton (ZMUC CRU2483). **England**: eight ♂, nine ♀, White Island, St Martin's, Isles of Scilly, exposed shore, empty *C. stellatus* on rocks (ZMUC CRU2476); two ♂, 14 ♀ and juveniles, Torquay, Torbay, Devon, empty *C. stellatus* on sheltered harbour wall (ZMUC CRU2477); six ♂, 11 ♀ and juveniles, Shoalstone Point, Brixham, Torbay, Devon, empty *C. stellatus*, fairly sheltered (ZMUC CRU2478); six ♂, two ♀, Ladram Bay, Devon, empty *C. stellatus*, fairly sheltered (ZMUC CRU2480); two ♂, seven juveniles, Saunton, North Devon, empty *C. stellatus*, exposed shore (ZMUC CRU2479); all coll. A.H. Clayton, 1995. **ZMUC Old Collections**: ♂, five ♀ and two juveniles, Torquay, Devon, 1902, A.M. Norman (ZMUC CRU3689, CRU3690). ♀, El Araish (Maros. So) (Morrocco), E.v. Benzon, IW, coll. W. Sørenson (ZMUC CRU3688).

Type locality

Montagu did not mention a specific location in his description, and as the publication deals with material from the Devonshire coast of England, the type locality is Devon.

Type material

The whereabouts of the type material is unknown, and is presumed lost. It is known that Montagu's description was based on a female specimen.

Description of male

Body about twice as long as greatest width, widest at point of insertion of uropods; lateral margins widening to pereonite 6; dorsal surfaces not polished, granular, with scattered setae. Cephalon dorsal surface smooth, not conspicuously granular, anterior margin without transverse ridge, with rostral process extending between antennule bases. Pereonites 1–4 unornamented; pereonite 5 with median process about as long as width of pereonite 6, extending posteriorly over pleotelson, surface finely granular with scattered short setae; pereonite 7 largely concealed in dorsal view by pereonite 6; coxae without sutures, those of pereonites 2–4 not posteriorly directed, those of pereonite 6 extending posteriorly to posterior of pereonite 7. Posterior of pleon with lock-and-key points. Pleotelson posterior margins straight, converging to distinct sub-acute apex; dorsally with indistinct distal median ridge running from posterior half of pleotelson to apex, with indistinct submedian depression either side of ridge; posterior margin with weakly developed fringe of setae; ventral margin with shallow exit channel not extending to posterior of pleotelson, mediolateral margins of pleotelson forming ridge.

Antennule peduncle article 1 twice as long as article 2, article 3 1.2 times as long as article 2; flagellum of six articles. Antenna peduncle articles 2 and 3 appearing fused, subequal in length to article 4; article 5 longest, 1.6 times as long as article 4; flagellum of 11 articles, extending to pereonite 2.

Epistome smooth, anteriorly rounded, with mediolateral stepped indentation. Left mandible incisor with four indistinct cusps, lacinia mobilis tricuspid, spine row of three serrate curved spines; right mandible with four cusps, spine row of one broad-based multi-digitate spine, three simple short blunt spines and one long pectinate spine; molar process with crushing surface distinctly ridged; palp article 1 longest, articles 1 and 2 without setae, article 3 with seven setae; terminal seta largest, apically plumose. Maxillule medial lobe with three long pectinate setae and one shorter simple seta, lateral lobe with ten robust setae on gnathal surface of which latter group are weakly serrate. Maxilla lateral lobe and middle lobe each with three curved robust setae, medial lobe with four CP robust setae. Maxilliped endite slender, extending about half way along palp article 3, distal margin one conical robust seta, two rounded robust setae, two cactus robust setae and two slender plumose robust setae; palp articles 2–5 with about seven, eight, six and eight setae respectively.

Pereopod 1 basis about twice as long as greatest width, anterodistal angle with two simple setae; ischium as long as basis, 3.0 times as long as greatest width, superior margin with one acute proximal robust seta, mid-superior margin with single acute robust seta, inferior margin with sparse small setae and single seta at distal angle; merus 0.4 as long as ischium, 1.2 times as long as greatest width, superior distal angle with two robust finely serrate setae, inferodistal angle with two simple elongate setae; carpus 0.6 as long as merus, 0.8 as long as wide, inferodistal angle with two simple elongate setae; propodus 0.7 times as long as ischium, 2.7 times as long as greatest width, inferior margin with single biserrate robust setae, two biserrate robust setae opposing base of dactylus, superior distal angle with single slender seta; dactylus 0.4 times as long as propodus, unguis about 50% entire length of dactylus, inferior margin with distinct serrate cuticular scales, secondary unguis recurved with three basal cusps. Pereopods 2 and 3 similar to pereopod 1 but more slender and with additional setae. Pereopod 2 ischium 0.9 as long as basis, 3.2 times as long as wide, merus about 0.4 as long as ischium, about as long as wide; carpus 1.2 times as long as merus, 1.8 times as long as wide; propodus 2.0 times as long as carpus, 4.8 times as long as wide. Pereopod 3 of similar proportions to pereopod 2, ischium slightly more elongate, 3.7 times as long as wide. Pereopods 5–7 similar, becoming progressively more slender. Pereopod 6 basis about 3.0 times as long as wide, superior margin with sensory seta at mid-point; ischium 0.8 long as basis, 3.6 times as long as greatest width, superior margin with one acute proximal robust seta, mid-superior margin with single acute robust seta, inferior margin with sparse small setae; merus 0.4 as long as ischium, 1.6 times as long as wide, superior distal angle with one robust rate seta, inferodistal margin with two simple elongate setae and three short setae; carpus about as long as merus, 1.9 as long as wide, distal margin with two biserrate robust setae, inferodistal angle with two simple elongate setae and one short acute robust seta; propodus about (0.9) as long as ischium, 4.0 times as long as greatest width, inferior margin with two robust setae opposing base of dactylus, superior margin with four evenly spaced sort simple setae, distal angle with two slender setae and single sensory seta. Pereopod 7 similar to 6, but ischium five times as long as wide, superior margin with five acute simple robust setae, inferior margin with four simple setae; merus distal margin with three biserrate setae.

Penial processes about 1.9 times as long as basal width, tapering to subtruncate apex.

Pleopod 1 exopod and endopod with ~20 and ~10 PMS respectively. Pleopod 2 exopod and endopod with ~20 and ~11 PMS respectively; appendix masculina about 7.8 times as long as wide, curving medially, apex bluntly rounded; widest at approximately three-quarters of its length. Pleopod 3 exopod and endopod with ~20 and ~8 PMS respectively. Pleopod 4 endopod with faint ridges, without transverse suture; exopod lateral margin with four fine setae. Pleopod 5 endopod without folds or ridges, without transverse suture; exopod with three scale patches. Uropod exopod robust, 3.9 times as long as greatest width, rami held well clear of pleotelson; dorsal with abundant scale-spikes, curves medially to narrowly rounded apex, lateral margin indistinctly serrate.

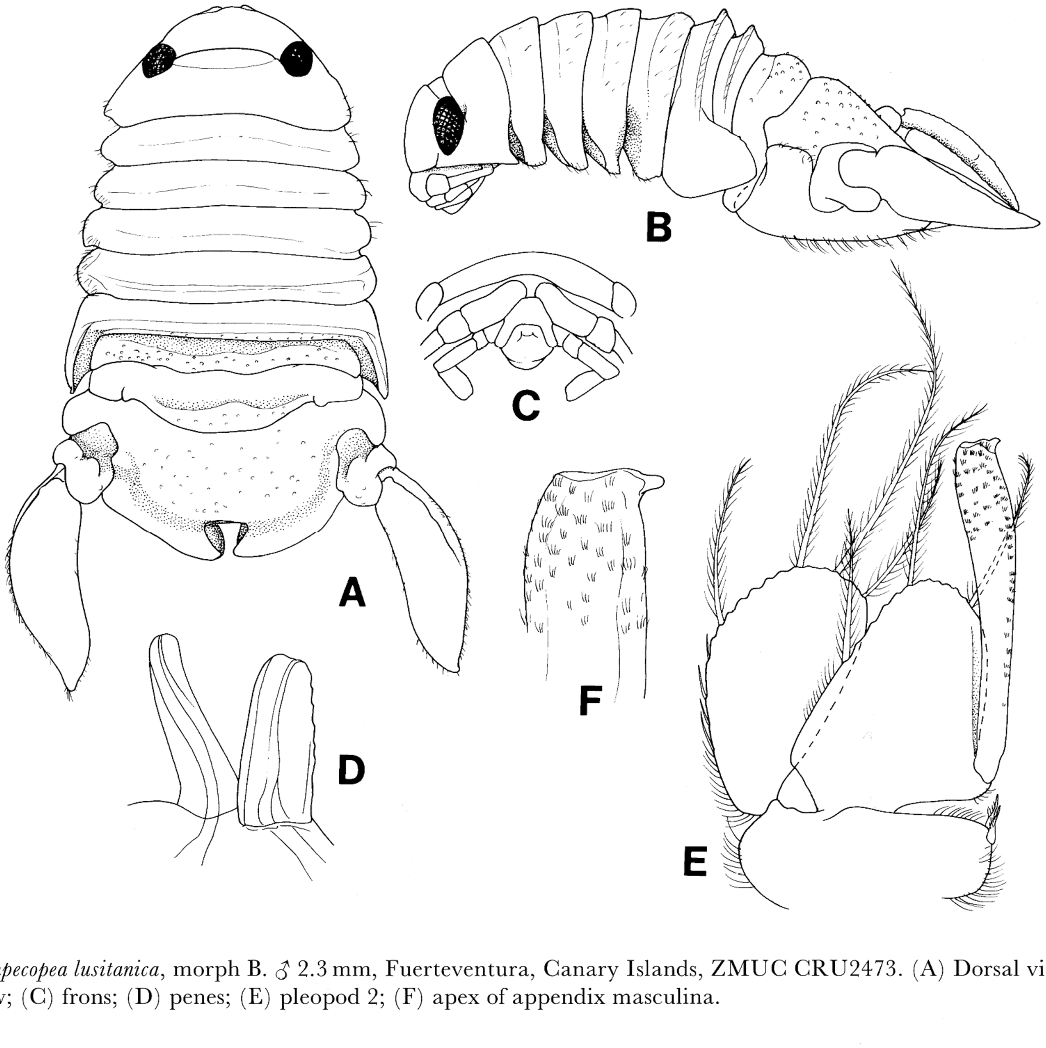

Figure 6. *Campecopea lusitanica*, morph B. ♂ 2.3 mm, Fuerteventura, Canary Islands, ZMUC CRU2473. (A) Dorsal view; (B) lateral view; (C) frons; (D) penes; (E) pleopod 2; (F) apex of appendix masculina.

Females

As for generic diagnosis; posterior margins of pereonites 6 and 7 with obscure transverse ridge, with scattered small setae.

Remarks

Males of *Campecopea hirsuta* are immediately recognized by the prominent posteriorly directed process on pereonite 6, and the pereopods of both sexes of *C. hirsuta* being far less setose than those of *C. lusitanica*. Females have the pleotelson entire, the uropodal lateral margin weakly serrate and the body surfaces largely smooth. The characters that separate *C. hirsuta* from *C. lusitanica* also serve to distinguish it from the other species of the genus—*C. hanseni* and *C. ischiana*. *Campecopea hanseni* is not well discriminated against *C. lusitanica*, the only apparent difference being that in the former the uropod is more strongly recurved distally and has a more acute apex. *Campecopea ischiana* is readily discriminated by being the only species with a simple accessory unguis on the dactylus in combination with a simple pleotelson sinus. Morph B males of *C. lusitanica* also have a simple accessory unguis to the dactylus, but have a prominent pleotelson sinus that is widest anteriorly and largely closed posteriorly.

Ecology

Found inhabiting the upper zones of exposed and semi-exposed rocky shores, sometimes down to mid-tide level (Harvey, 1968). Usually found associated with crevices, empty barnacle tests and lichens (e.g. *Lichina pygmaea*). It is well adapted for surviving extremes of the upper littoral zone, the conglobating habit helping to resist such extremes (Wieser, 1963; Kensler, 1967). *Campecopea hirsuta* can be abundant, with up to 300 per 10 g of lichen being recorded.

In the present study *C. hirsuta* was found occupying empty barnacle tests and small depressions in the basal rock of the upper shore on the north-eastern coast of Lanzarote.

Distribution

Despite being recorded from Wales and south-western England (Harvey, 1968), the Atlantic coasts of France (Hesse, 1873; Maury, 1929), Spain (Arrontes & Anadón, 1990), Portugal (present study), and north-west Africa (Monod, 1931a,b) only a few studies have been carried out on this species (Panouse, 1940; Tetart, 1962, 1963; Wieser, 1963; Harvey, 1968). No records are known from Madeira and *C. hirsuta* is recorded here for the first time from the Canary Islands and also from the Azores. As Omer-Cooper & Rawson (1934) pointed out, the fact that

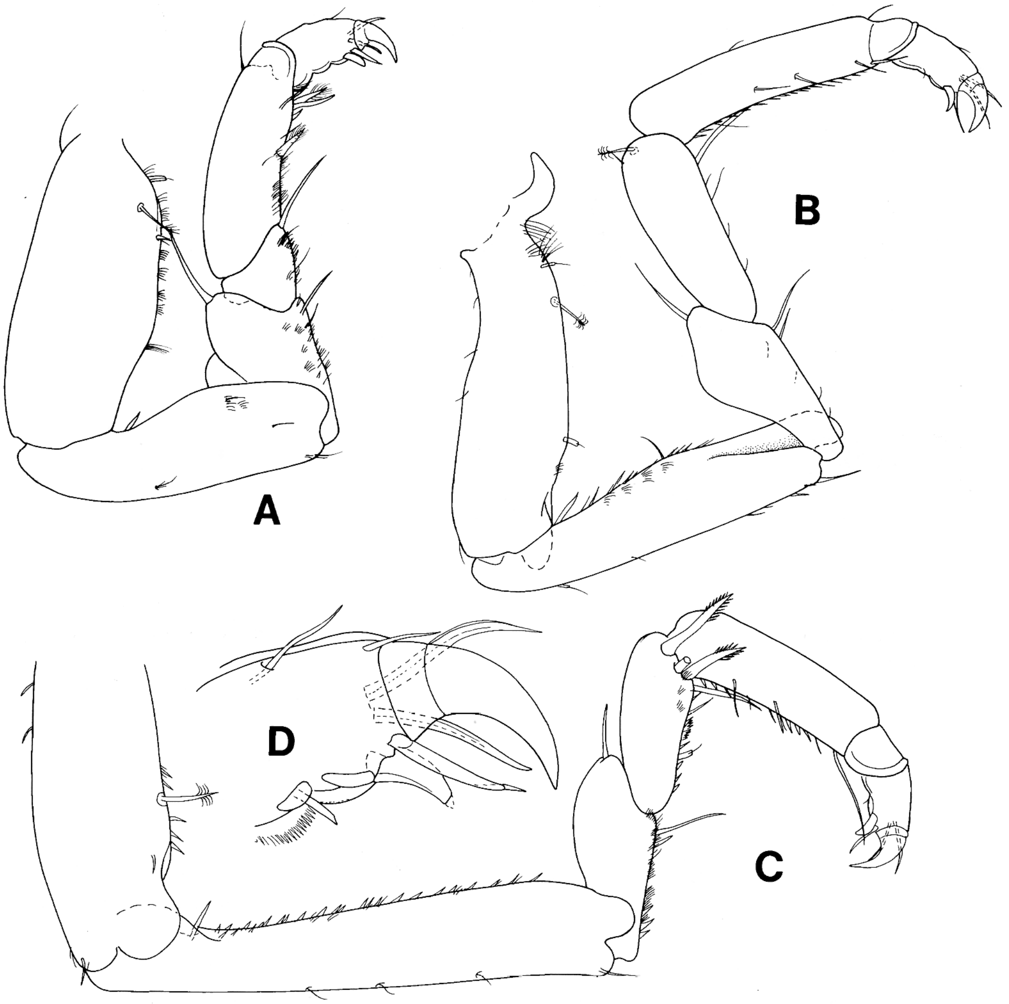

Figure 7. *Campecopea lusitanica*, morph B. ♂ 2.3 mm, Fuerteventura, Canary Islands, ZMUC CRU2473. (A) Pereopod 1; (B) pereopod 2; (C) pereopod 7; (D) dactylus, pereopod 1.

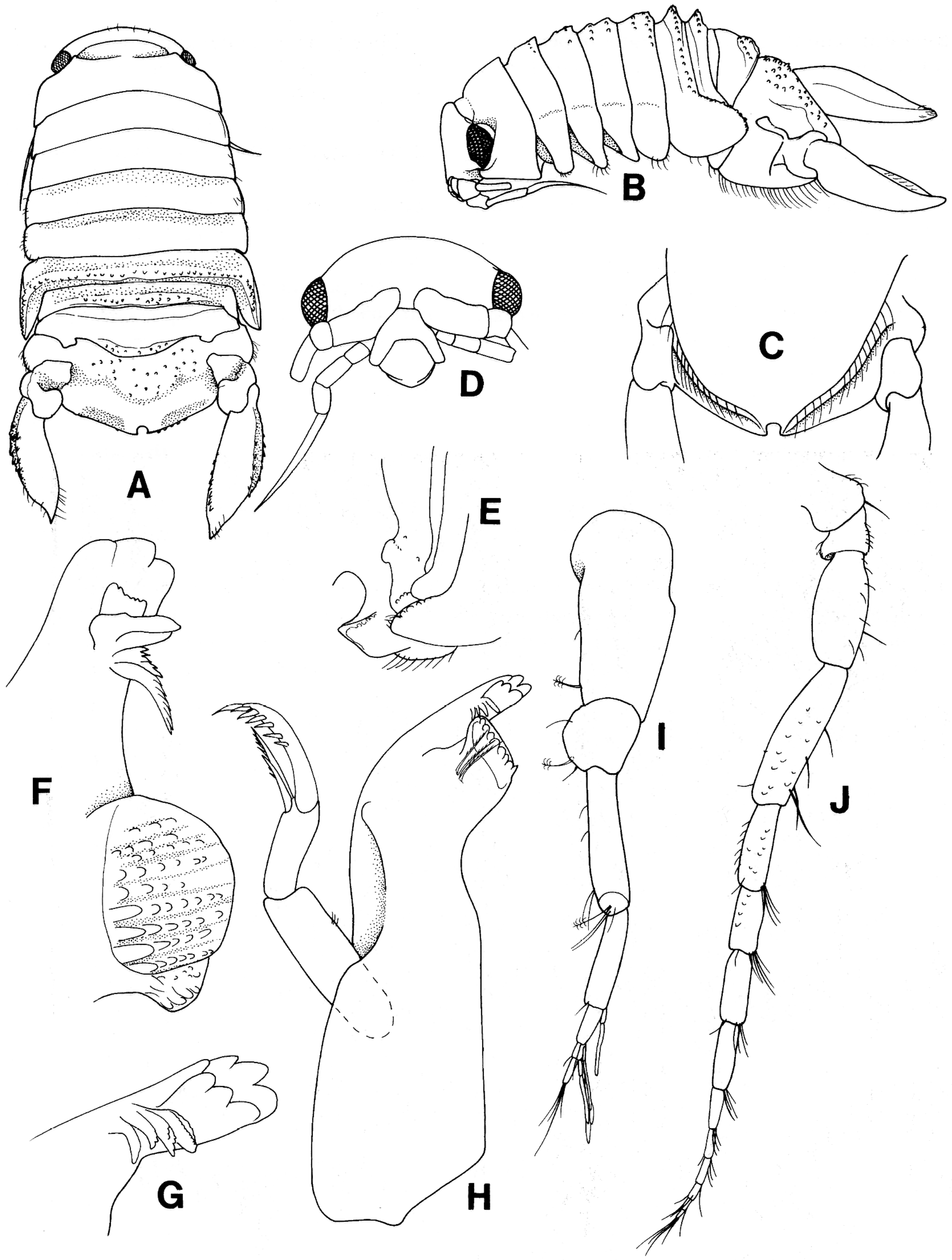

Figure 8. *Campecopea lusitanica*, morph A. (A–E) Specimen B, ♂ 2.8 mm; (F–J) specimen B1 ♂ 2.6 mm (dissected), Fuerteventura, Canary Islands, ZMUC CRU2607. (A) Dorsal view; (B) lateral view; (C) pleon posterior margin, ventral view; (D) frons; (E) lateral view of pleonites; (F) right mandible, distal part; (G) left mandible, distal part; (H) left mandible; (I) antennule; (J) antenna.

so few collectors work seriously in the region of the high-tide mark means that *C. hirsuta* has not been recorded in many surveys of the rocky littoral. Monod (1931b) mentions *C. hirsuta* as occurring in Ireland, but there were no published localities in his work or elsewhere, and Harvey (1968) failed to find the species in western Ireland. Alan Myers has informed us (personal communication) that *C. hirsuta* does occur on rocky shores at Tragumna, Talispeen and Dunmanus Bay, all County Cork, Ireland, and it has been recently recorded from Lough Hyne (de Grave & Holmes, 1998). Edward (1876) stated that *C. hirsuta* had been found in eastern Scotland, but this is unlikely, there being no known records even for the warmer coasts of western Scotland (P.G. Moore, personal communication). Harvey suggests that the species reaches the northern limit of its distribution in Ireland and southern Britain, and that its northwards spread is probably restricted by low temperature.

Size

Males 2–4 mm, females 2–3 mm.

Colour

Green or brown when alive, but this may be masked by various patterns of white, blue and yellow chromatophores; blue chromatophores may be particularly intense on the lateral body margins.

Campecopea lusitanica (Nolting, Reboreda & Wägele, 1998)

Figures 6–11, 12D–H

Anoplocopea lusitanica Nolting, Reboreda & Wägele, 1998:20, 1–10.

Material examined

Male (2.5 mm), Caleta de Fuste, Fuerteventura, Canary Islands, ~28°24′N 13°52′W, 17 April 1995, upper shore crevice, coll. D.M. Holdich (ZMUC CRU2473); 11 ♂ (2.3, 2.3[A], 2.4 keyhole telson; 2.3, 2.3, 2.4, 2.4, 2.5, 2.6[B1], 2.8[B], 3.1[senescent, slit pleotelson] mm), ovigerous ♀ (2.0 mm), four non-ovigerous ♀ (2.0, 2.3, 2.4, 2.9 mm), 27 mancas and immature (1.0–1.8 mm), same data as previous (ZMUC CRU2607). Two ♂ (2.2, 2.6 mm), two ♀ non-ovigerous (2.6, 3.0 mm), three immature (1.5, 1.7, 1.9, 1.9 mm), Costa Teguise, Lanzarote, Canary Islands, ~29°05′N 13°32′W, 26 March 1996, upper shore crevices and barnacles, coll. D.M. Holdich (ZMUC CRU2474). Two ♀, non-ovigerous (2.0, 2.2 mm), Caloura, St Miguel, Azores,

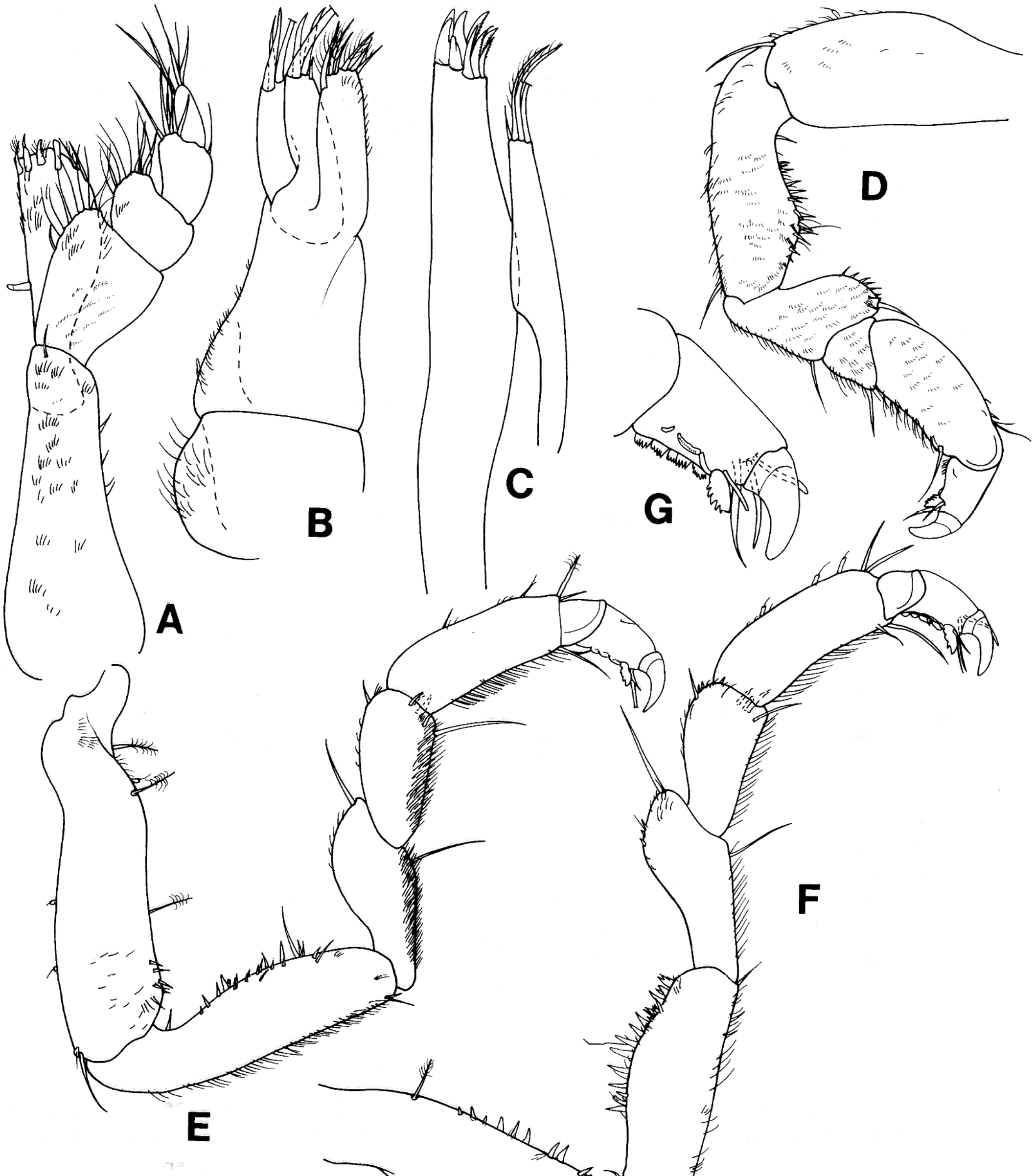

Figure 9. *Campecopea lusitanica*, morph A. ♂ specimen B1, Fuerteventura, Canary Islands, ZMUC CRU2607. (A) Maxilliped; (B) maxilla; (C) maxillule; (D–F) pereopods 1–3 respectively; (G) pereopod 1 dactylus.

4 February 1997, barnacles on eulittoral–infralittoral cobbles, coll. Ana Costa (ZMUC CRU2648).

Descriptive notes

Species of this genus are very similar, and as the Canary Islands specimens are distant to the original records of the species we have illustrated the specimens in detail. Of particular interest is that there are two male morphs, in which the supposed 'mature' morph presents a change in the pleotelson morphology from a simple short apical slit (male morph A) to a nearly enclosed foramen that is widest anteriorly males (male morph B, Figure 6). In addition the appendix masculina develops an acuminate tip and has more mictrotrichs than the more common morph A, and the accessory unguis to the dactylus is simple rather than multicuspid.

Variation

Male specimens in some cases have pleonite 1 clearly visible, as is illustrated here. In other specimens the first pleonite is impossible to see and appears to be genuinely absent. The males are dimorphic, both occurring together at the two localities: males with a small open pleotelsonic notch, and those with a prominent foramen. The latter morph also has a more prominent rim to the posterior margin of the pleotelson, and reduced setation on the pereopods; in addition the appendix masculina is more ornate, and this stage of male (morph B) is assumed to be the mature form. Females from the two islands are similar in appearance.

Remarks

The only difference between the insular and continental populations appears to be that the appendix masculina of those specimens from the Canary Islands is terminally spatulate in mature males while being straight-sided in Portuguese specimens, and that male morph B has not been recorded from continental coasts. At present we do not consider that this warrants the separation of the two distinct species.

Distribution

Eastern North Atlantic, here recorded from the Canary Islands and the Azores; previous records (Nolting et al., 1998) from the Atlantic coast of Portugal.

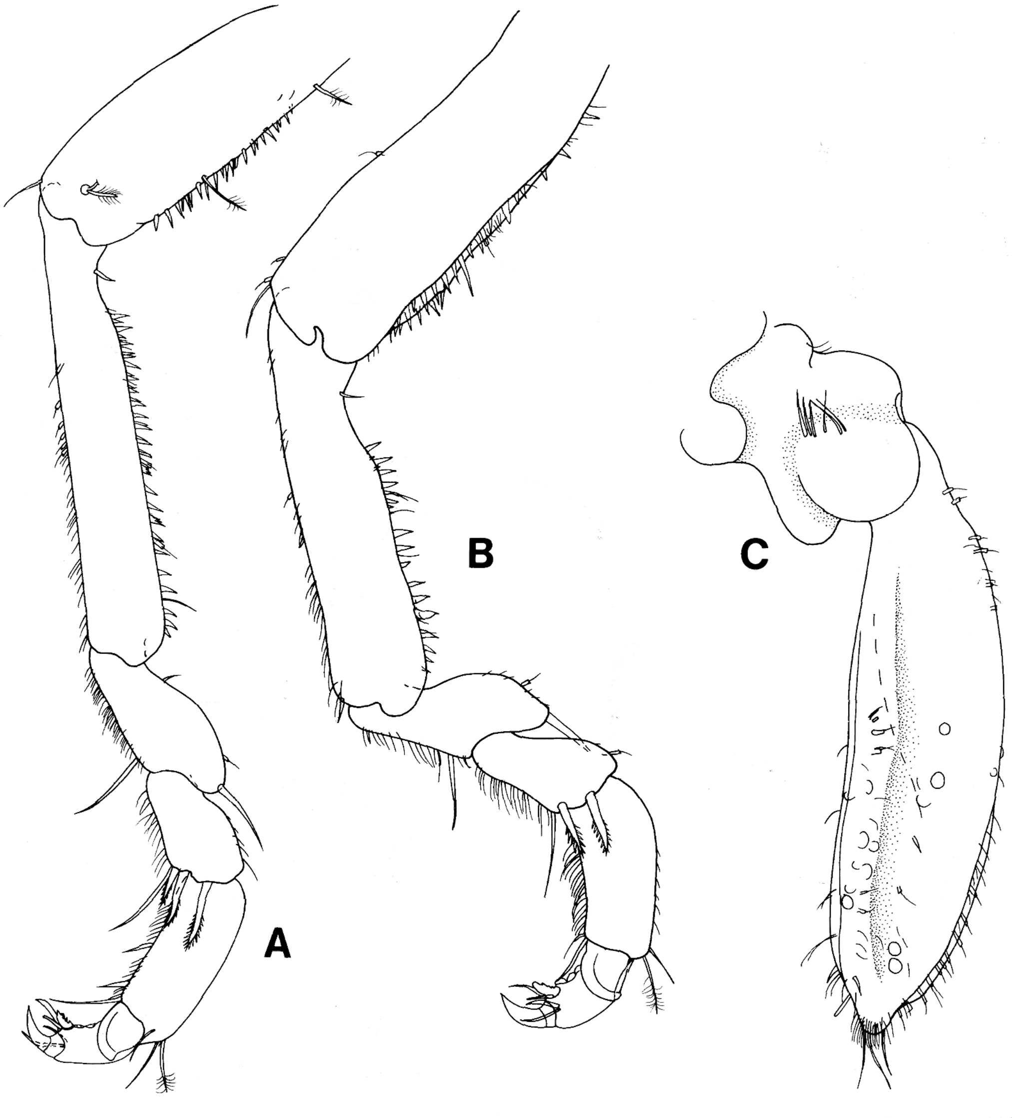

Figure 10. *Campecopea lusitanica*, morph A. ♂ specimen B1, Fuerteventura, Canary Islands, ZMUC CRU2607. (A) Pereopod 7; (B) pereopod 6; (C) uropod.

Table 1. *Occurrence of dorsal processes in the Sphaeromatidae.*

Genus	Position of process	'Twin' genus
Campecopea Leach, 1814 (one)	pereonite 6	none
Cassidias Richardson, 1906	pleotelson, single	none
Cilicaea Leach, 1818	pleon, single	*Paracilicaea* Stebbing, 1910
Cilicaeopsis Hansen, 1905	pleon, single	*Paracilicaea* Stebbing, 1910
Cymodoce Leach, 1814 (some)	pleon, single	none
Cymodopsis Baker, 1926 (some)	pleon, single and paired	none
Dynamene Leach, 1814	pereonite 6, paired	none
'Dynamenella' dioxus Barnard, 1914*	pereonite 7, paired	–
Dynoides Barnard, 1914	pleon, single	*Clianella* Boone, 1923
Haswellia Miers, 1884	pereonite 7, single	none
Isocladus Miers, 1876	pereonite 7, single	*Exosphaeroma* Stebbing, 1900
Oxinasphaera Bruce, 1997 (some)	pleon, paired	none
Zuzara Leach, 1818	pereonite 7, single	?*Exosphaeroma*

*, An *Ischyromene*-group species (*sensu* Bruce, 1995).

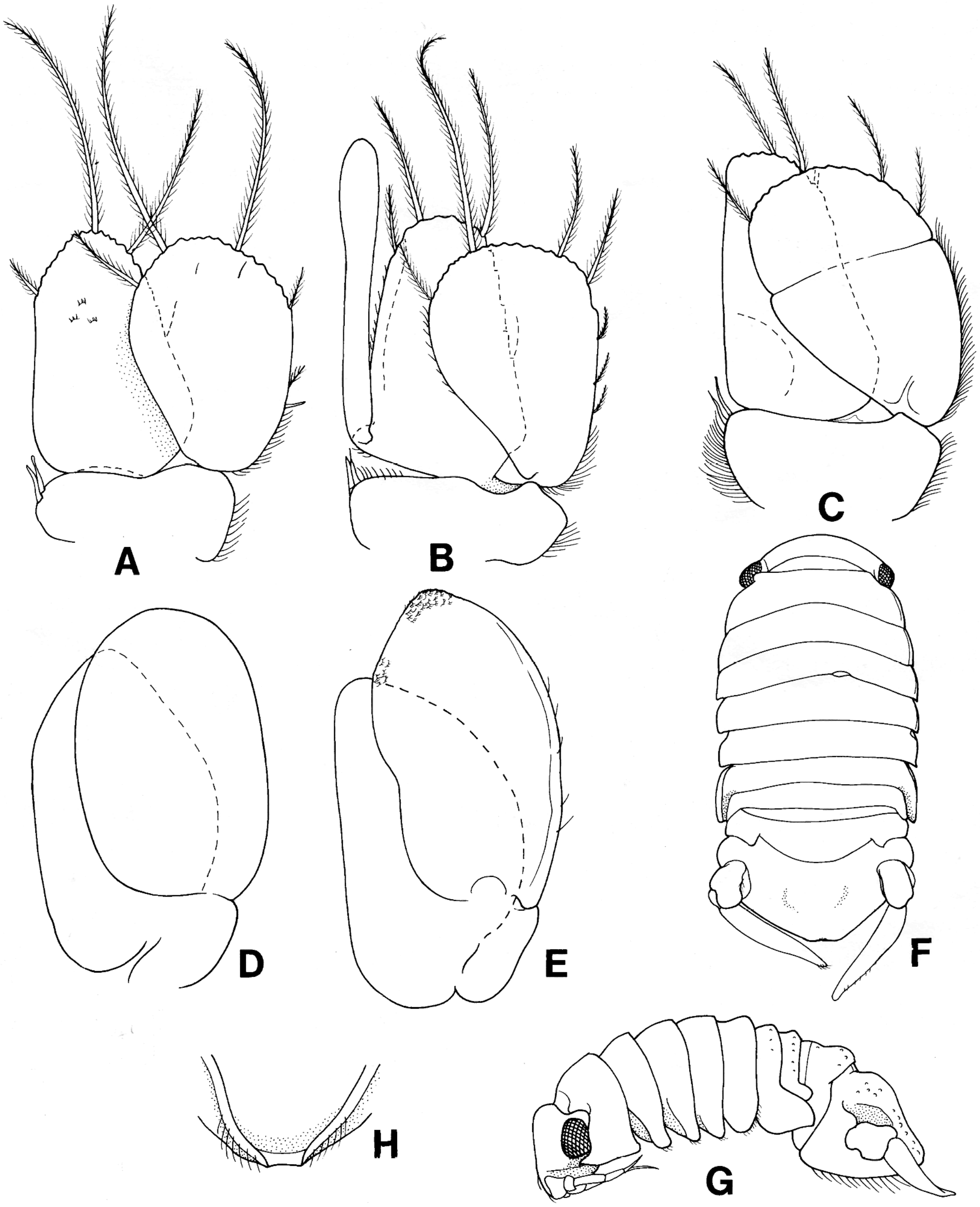

Figure 11. *Campecopea lusitanica*, morph A. Fuerteventura, Canary Islands, ZMUC CRU2607. (A–E), B1: pleopods 1–5 respectively; ♀ 2.0 mm: (F) dorsal view; (G) lateral view; ventral view, pleotelson distal margin.

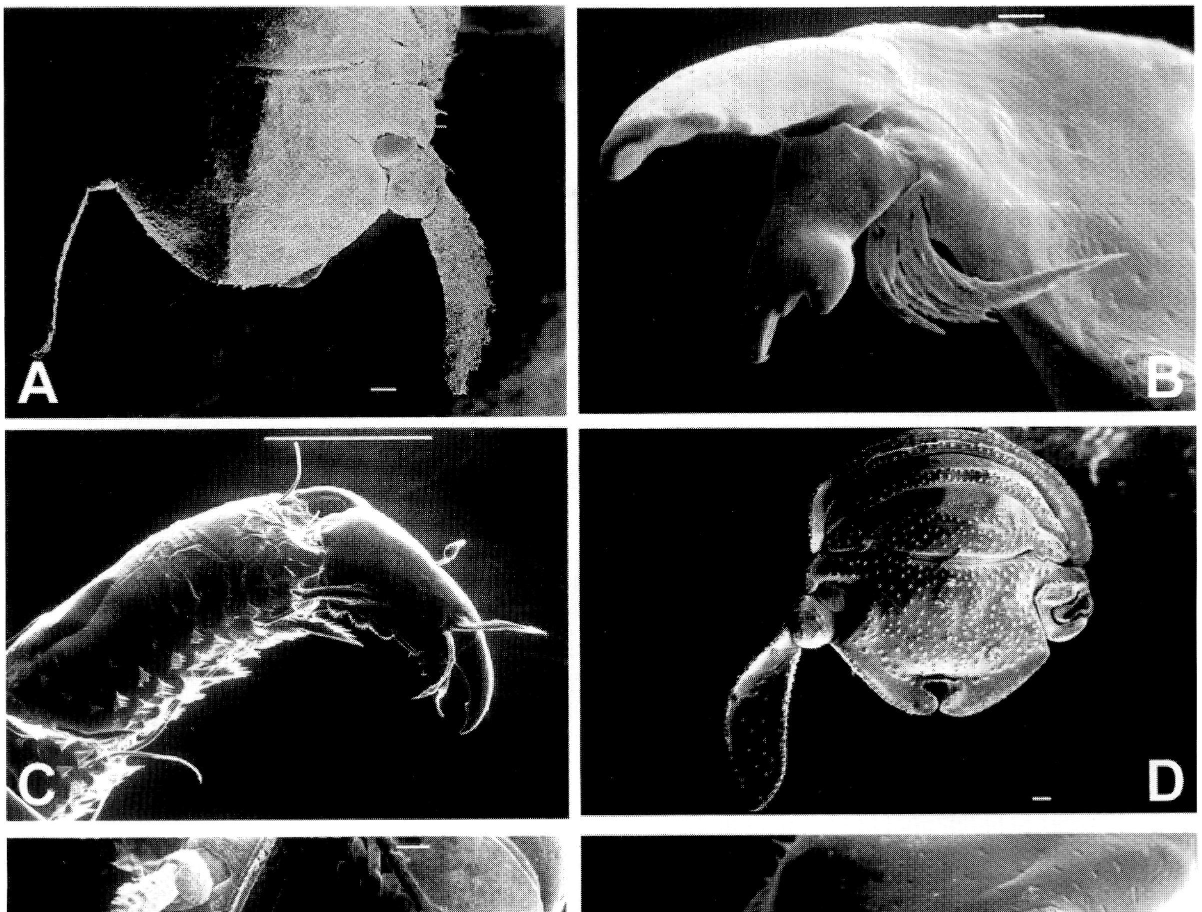

Figure 12. Scanning electron micrographs. (A–C) *Campecopea hirsuta*; (D–H) *Campecopea lusitanica*. (A) Dorsal view of pleotelson; (B) left mandible showing lacinia mobilis and spine row; (C) pereopod 1 dactylus; (D) male, morph B, dorsal view of pleotelson; (E) female, ventral view of pleotelson; (F) right mandible showing molar surface; (G) pereopod 1 dactylus; (H) pereopod 1 inferior margin, setulose scales.

DISCUSSION

Dorsal processes in the Sphaeromatidae

Sphaeromatids show a diversity of body form, from being dorsoventrally flattened ('scale-like'), slender to strongly vaulted. Species in many genera may be ornamented by tubercles, sculpting and also by having posteriorly produced processes. These processes are known to occur on the sixth pereonite, the seventh pereonite, the pleon and pleotelson, and may be simple or bifid (Table 1). There exist several instances of what we here call 'twin' genera in which the sole distinguishing and defining character for one of the genera is the absence of such a process (Table 1). Currently there exist four genera in which this type of character is polymorphic: *Cymodoce* Leach and *Cymodopsis* Baker—although the former is almost certainly not monophyletic—and two other genera which are polymorphic for dorsal processes, and which have good characters to support their monophyly: *Oxinasphaera* Bruce, 1997 and *Campecopea*.

Dynoides *Barnard, 1914 and* Clianella *Boone, 1923*

Dynoides Barnard, 1914, a strongly sexually dimorphic genus, has a complex synonymy, most recently reviewed in great detail by Harrison & Holdich (1984, pp. 364–366), when reinstating and redescribing the genus *Clianella* Boone, 1923. The two genera contain 14 and five species respectively. Summarizing, the conclusions of Harrison & Holdich were that 'the presence and absence of dorsal processes is an important generic character...' and '...the presence or absence of such a process should be a consistent generic character'.

This position with regard to generic characters is totally mechanistic, and begs the question of the phylogenetic significance of the character and of the monophyly of the genera involved. It needs to be realized that the sole distinguishing 'character' for *Clianella* is the absence of a putative apomorphic character state, and also that the character itself is of dubious value as it exists in varying degrees of development in mature males, from absent to elongate. In *Dynoides brevispina* Bruce, 1980 the pleon has a short and wide boss, while in *Dynoides brevicornis* Kussakin & Malyutina, 1987, the process is a blunt nodule. In *Dynoides saldanai* Carvacho & Haasmann, 1984 the posterior margin of the pleon very weakly lobate, while in *Dynoides hoonsooi* Kwon, 1990 it is equally too short to be termed a process. In other words, intermediate stages exist. Furthermore, ontogenic evidence suggests that it is of doubtful importance, as it is absent from juvenile males, and therefore immature specimens of the two taxa cannot be distinguished from one another. However, the two genera do share some unique characters that by simple outgroup comparisons can be interpreted as putative synapomorphies for the species of both genera. These characters are: (i) the pleonal sinus with an anterior lobe; (ii) the pleonal sinus with internal 'teeth'; (iii) penial processes basally fused for half their length; and (iv) appendix masculina elongate, twice as long as endopod, and strongly reflexed. There are some other characters that could be added but these are known to have a widespread homoplasious occurrence. These four characters could then be taken to define one genus containing those species currently housed in both *Clianella* and *Dynoides*. It is easy to see that *Clianella* is defined only by those putative apomorphic characters shared by both genera, and in being defined by a plesiomorphic character state is therefore a paraphyletic taxon. The conclusion can only be that *Clianella* is not a valid genus (i.e. is not a monophyletic taxon) and that *Dynoides*, an unambiguously definable genus and the senior name for the taxon, is polymorphic for that character. This interpretation has recently been acted on by Li (2000) who placed *Clianella* in synonymy with *Dynoides*.

Exosphaeroma *Stebbing, 1900 and* Isocladus *Miers, 1876*

A similar situation exists between these two genera as described for the two genera above. *Exosphaeroma*, however, contains a number of species that do not belong to the genus *sensu strictu*. At the moment, and in the absence of a critical generic revision, the relationship between these two genera is uncertain, as is their relationship to *Zuzara*, which differs in the morphology of the pleotelson posterior margin. As far as can be seen from contemporary and recent descriptions, upholding *Isocladus* results in *Exosphaeroma* being a paraphyletic taxon, characterized solely by the plesiomorphic state of lacking a process on pereonite 7. All of the three genera here have one potential synapomorphy, and that is the posterior margin of the first pleonite has two sub-medial curves rather than being even.

Oxinasphaera *Bruce, 1997*

This genus, recently distinguished (Bruce, 1997) and separated from *Cymodoce* Leach, contains about 29 species (Bruce, 1997; Benvenuti et al., 2000). As currently constituted, the monophyly of the genus is supported by several striking apomorphies (see Bruce, 1997) in the form of hardened cuticular spikes on the antennule peduncle, epistome and body segments and also the extreme development of finger like lobes on the maxilliped palp. The posterior margin of the pleotelson has two submedian slits, and may also have a dorsal lobe. The posterior margin of the pleon may be even, with a median boss, or formed into two prominent posteriorly directed processes. Among those species with a boss, a boss with prominent points is little removed for being interpreted as 'short posterior processes.' Removal of those species with processes to a separate genus, in the absence of a unique apomorphy (or apomorphies) for the remaining species would be unacceptable as, again, the putative sister genus would be definable only by the characters that it shares with the sister genus or therefore by the absence of a character. That absence being the plesiomorphic state, such a genus would be paraphyletic, and unacceptable by contemporary standards.

Cilicaea *Leach, 1818;* Cilicaeopsis *Hansen, 1905; and* Paracilicaea *Stebbing, 1910*

These three genera total about 50 species, many of which are probably incorrectly placed. *Paracilicaea* has recently been revised by Benvenuti & Messana (2000) and species of all three genera have been described by Harrison & Holdich (1984), together with detailed discussion of the genera and the species placed therein. The three genera (*sensu strictu*) share a very similar general somatic and appendage morphology. *Paracilicaea* and *Cilicaea* are effectively distinguished solely by the lack of a pleonal process in the former; *Cilicaeopsis* and *Cilicaea* by the latter having a medial lobe in the pleotelson notch as well as a recurved appendix masculina. Without a clear identification of the autapomorphies for each genus, or the synapomorphies between them, it is impossible to establish the monophyly of this group of genera or of the individual genera.

CONCLUSION

It is here considered that the presence or absence of a dorsal process in the Sphaeromatidae is of doubtful generic value, and of little phylogenetic significance. Such characters are distributed throughout the family and occur in several dissimilar genera in the Sphaeromatinae and Dynameninae (Table 1). In some genera, such as *Dynamene*, the presence of processes is consistent for the genus, but in other cases where genera have been defined by apomorphic character states, the presence or absence of such processes is of specific significance only. In the unrelated genus *Paracassidina* (see Bruce, 1994a) there are species with and without cephalic horns, and species with or without antennular horns, but the monophyly of the genus is not in question.

For the donation of specimens we thank the following: Dr Antonio Murias dos Santos, Instituto de Zoologia, Universidade do Porto, Portugal; Ms Ana Costa, St Miguel, Azores; D.I. de Pomerai (School of Life & Environmental Sciences, University of Nottingham, UK) for provision of additional specimens of *C. lusitianica* from Lanzarote; Professor Brian Morton, SWIRE Institute of Marine Science, University of Hong Kong; Dr Adrian H. Clayton, Department of Biological Sciences, University of Exeter, UK. Thanks are due to Professor A.A. Myers (University of Cork) for information on the Irish occurrence of *Campecopea hirsuta*, and similarly to Dr P.G. Moore (University Marine Biological Station Millport) for commentary on the absence of that species from Scottish coasts. We thank Ms Birgitte Rubæk (ZMUC) for her inking of the illustrations. We thank Professor L.B. Holthuis and Dr Charles Fransen for assistance with bibliographic details of some of the old literature records.

REFERENCES

Arrontes, J. & Anadón, R., 1990. Distribution of intertidal isopods in relation to geographical changes in macrofaunal cover in Biscay Bay. *Journal of the Marine Biological Association of the United Kingdom*, **70**, 283–293.

Baker, W.H., 1926. Species of the isopod family Sphaeromidae, from the eastern, southern and western Australian coasts of Australia. *Transactions of the Royal Society of South Australia*, **50**, 247–279, plates 83–53.

Barnard, K.H., 1914. Contribution to the crustacean fauna of South Africa. 3. Addition to the marine Isopoda with notes on some previously incompletely known species. *Annals of the South African Museum*, **10**, 325–442, plates 27–39.

Bate, C.S., 1878. Crustacea revised and added to. In *The Cornish fauna: a compendium of the natural history of the county.* Part 1. *Vertebrate animals and Crustaceans*, 2nd ed. (ed. J. Couch), pp. 56–127.

Bate, C.S. & Westwood, J.O., 1868. *A history of the British sessile-eyed Crustacea.* **II**, i–lvi, 1–536.

Benvenuti, D. & Messana, G., 2000. The sphaeromatid genus *Paracilicaea* Stebbing 1910 (Crustacea: Isopoda) from the western Indian Ocean with the description of five new species. *Tropical Zoology*, **13**, 181–217.

Benvenuti, D, Messana, G. & Schotte, M., 2000. On a new species of *Oxinasphaera* (Isopoda, Sphaeromatidae) from Somali and Yemeni coasts, western Indian Ocean. *Crustaceana*, **73**, 407–415.

Bolivar, J., 1893. Lista de la collección de Crustáceos de España y Portugal del Museo de Historia Natural dc Madrid. *Acta de la Sociedad Española de Historia Naturale*, **23**(3), 124–141.

Bonnier, J., 1887. Catalogue des crustacés malacostracés recueillis dans la Baie de Concarneau. *Bulletin Scientifique du Départment du Nord*, 2ème Série, Xème Année (1887), 1–190.

Boone, P., 1923. New marine tanaid and isopod Crustacea from California. *Proceedings of the Biological Society of Washington*, **36**, 147–156.

Bosc, L.A.G., 1830. *Manuel de l'histoire naturelle des Crustacés* etc. Edition mise au niveau des connaissances actuelles par A.G. Desmarest: **1**, 1–328, **2**, 1–306.

Brökeland, W., Wägele, J.-W. & Bruce, N.L., 2001. *Paravireia holdichi* n. sp., an enigmatic isopod crustacean from the Canary Islands with affinities to species from New Zealand. *Organisms, Diversity and Evolution*, **1**, 83–98.

Bruce, N.L., 1980. The systematics of some Japanese marine isopods (Family Sphaeromatidae) of the genera *Dynoides* Barnard, 1914 and *Cymodocella* Pfeffer, 1887, with descriptions of two new species. *Crustaceana*, **38**, 199–211.

Bruce, N.L., 1991. New records of marine isopod crustaceans (Sphaeromatidae, Cirolanidae) from south-eastern Australia. *Memoirs of the Museum of Victoria*, **52**, 263–275.

Bruce, N.L., 1993. Two new genera of marine isopod crustaceans (Flabellifera: Sphaeromatidae) from southern Australia, with a reappraisal of the Sphaeromatidae. *Invertebrate Taxonomy*, **7**, 151–171.

Bruce, N.L., 1994a. The Cassidininae (Crustacea, Isopoda, Sphaeromatidae) of Australia. *Journal of Natural History*, **28**, 1077–1173.

Bruce, N.L., 1994b. Four new genera of marine isopod crustaceans (Family Sphaeromatidae) from eastern and southern Australia. *Memoirs of the Museum of Victoria*, **54**, 399–437.

Bruce, N.L., 1995. The taxonomy and phylogeny of tube-tailed sphaeromatid isopods (Crustacea) with descriptions of new species and a new genus from southern Australia. *Ophelia*, **43**, 127–180.

Bruce, N.L., 1997. A new genus of marine isopod (Crustacea: Flabellifera: Sphaeromatidae) from Australia and the Indo-Pacific region. *Memoirs of the Museum of Victoria*, **56**, 145–234.

Carvacho, A. & Haasmann, Y., 1984. Isopodos litorales de Oaxaca, Pacifico Mexicano. *Cahiers de Biologie Marine*, **25**, 15–32.

Chilton, C., 1925. A new genus of Isopoda (Family Sphaeromidae). *Records of the Canterbury Museum*, **2**, 321–326.

Cocks, W.P., 1849. Contributions to the fauna of Falmouth. *Annual Report of the Royal Cornwall Polytechnical Society*, **17**, 38–102. [Reference not sighted.]

Dana, J.D., 1852. On the classification of the Crustacea Choristopoda or Tetradecapoda. *American Journal of Sciences and Arts*, **14**, 297–316.

Desmarest, A.G., 1825. *Considérations générales sur la classe des crustacés et description des espèces de ces animaux qui vivent dans la mer, sur les côtes ou dans les eaux douces de la France*, i–xix, 1–446.

Dollfus, A., 1888. Sur quelques crustacés isopodes du littoral des Açores. Troisième campagnc dc *l'Hirondelle*, 1887. *Bulletin de la Société Zoologique de France*, **13** (for 1887), 35–36.

Gerstaecker, A., 1856. Carcinologische Beiträge. *Archiv für Naturgeschichte*, **22**, 101–162, plates IV–VI.

Gerstaecker, A., 1882. Sechste Ordnung: Isopoda Asseln [Part]. In *Klassen und Ordnung des Their-Reichs, wissenschaftlich dardestellt in Wort und Bild. Fünfter Band II—Abtheilung Gleiderfussler: Arthropoda. Crustacea (Zweite Hälfte: Malacostraca), 4, 5, 6, 7, 8* (ed. H.G. Bronn), pp. 97–278. Leiferung.

Goss, P.H., 1855. *A manual of marine zoology for the British Isles*. Part I. London: John van Voorst.

Grave, S. de & Holmes, J.M.C., 1998. The distribution of marine Isopoda (Crustacea) in Lough Hyne. *Proceedings of the Royal Irish Academy* B, **98**, 23–30.

Guérin-Méneville, F.E., 1836–1844. Crustacés. In *Iconographie du Règne Animal de G. Cuvier, ou Représentation d'après Nature de l'une des espèces les plus remarquables et souvent non encore figurées de chaque genre d'animaux*, vol. **3** (1844) (ed. G. Cuvier), 48 pp., 35 plates (1837). Paris: Baillière.

Harrison, K., 1984. The morphology of the brood pouch (Crustacea: Isopoda: Sphaeromatidae). *Zoological Journal of the Linnean Society*, **82**, 363–407.

Harrison, K. & Holdich, D.M., 1982. New eubranchiate sphaeromatid isopods from Queensland waters. *Memoirs of the Queensland Museum*, **20**, 421–445.

Harrison, K. & Holdich, D.M., 1984. Hemibranchiate sphaeromatids (Crustacea: Isopoda) from Queensland, Australia, with a world-wide review of the genera discussed. *Zoological Journal of the Linnean Society*, **81**, 295–387.

Harvey, C.E., 1968. Distribution and seasonal population changes of *Campecopea hirsuta* (Isopoda: Flabellifera). *Journal of the Marine Biological Association of the United Kingdom*, **48**, 761–767.

Hesse, M., 1873. Mémoire sur des Crustacés rares ou nouveaux des côtes de France. *Annales Scientifiques et Naturelles de Zoologie*, **17**, 1–35.

Holdich, D.M., 1970. The distribution and habitat preferences of the Afro-European species of *Dynamene* (Crustacea: Isopoda). *Journal of Natural History*, **4**, 419–438.

Holdich, D.M., 1976. A comparison of the ecology and life cycles of two different isopods. *Journal of Experimental Marine Biology and Ecology*, **24**, 133–149.

Holdich, D.M. & Harrison, K., 1980. The sphaeromatid isopod genus *Dynamene* in Australia with description of a new species from coral reefs. *Memoirs of the Queensland Museum*, **10**, 163–170.

Kensler, C.B., 1967. Desiccation resistance of intertidal crevice species as a factor in their zonation. *Journal of Animal Ecology*, **36**, 391–406.

Kussakin, O.G., 1979. *Marine and brackish water like-footed Crustacea (Isopoda) from the cold and temperate waters of the northern hemisphere. Suborder Flabellifera*. Vol. 1. (Opredeliteli po Faune SSSR, Izdavaemye Zoologicheskim Institutom Akademii Nauk SSSR, 122.) Izdatel'stvo Nauka, Leningrad, pp. 472. [In Russian.]

Kussakin, O.G. & Malyutina, M.V., 1987. Morskie ravnogie rakoobraznye (Crustacea, Isopoda) litorali Zaliva Petra Velikogo. [=Marine Isopoda (Crustacea) from the shore of Zaliv Petra Velikogo.]. In *Issedovaniya litorali Dal'nevostochnogo morskogo zapovednika I soprede"nykh raionov* (ed. Gu"bin), pp. 47–67. Vladivostok: VV DVO AN, SSSR.

Kwon, D.H., 1990. A systematic study on the Korean marine isopod crustaceans. *Inje Journal*, **6**, 151–192.

Lawson, G.W. & Norton, T.A., 1971. Some observations on littoral and sublittoral zonation at Tenerife (Canary Islands). *Botanica Marina*, **14**, 116–120.

Leach, W.E., 1814. Crustaceology. In *The Edinburgh encyclopaedia*, 1st ed., vol. 7 (ed. D. Brewster), pp. 383–437. London: Baldwin.

Leach, W.E., 1815. A tabular view of the external characters of four classes of animals which Linné arranged under *Insecta* with the distribution of the genera composing three of these classes into orders, and description of several new genera and species. *Transactions of the Linnean Society of London*, **11**, 306–400.

Leach, W.E., 1818. Cymothoidées. In *Dictionnaire des Sciences Naturelles*, vol. 12 (ed. F. Cuvier), pp. 338–354. Paris and Strasbourg.

Li, L., 2000. A new species of *Dynoides* (Crustacea: Isopoda: Sphaeromatidae) from the Cape d'Aguilar Marine Reserve, Hong Kong. *Records of the Australian Museum*, **52**, 137–149.

Lincoln, R.J., Boxshall, G.A. & Clark, P.F., 1983. *A dictionary of ecology, evolution and systematics*. Cambridge: Cambridge University Press.

Lucas, H., 1840. Histoire naturelle des Crustacés. Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842. *Sciences Physiques et Zoologie*, **I**, 1–601.

Maury, A., 1929. Tanaidacés et isopodes des côtes normandes (excl. Epicarides) Crustacés marins d'eaux saumâtres et d'eaux douces. *Bulletin de la Société Linnéenne de Normandie*, **1**, 152–161.

Miers, E.J., 1876. Descriptions of some new species of Crustacea, chiefly from New Zealand. *Annals and Magazine of Natural History, Series 4*, **17**, 218–229.

Miers, E.J., 1884. Crustacea. In *Report on the Zoological collections made in the Indo-Pacific Ocean during the voyage of HMS "Alert", 1881–1882*, pp. 178–322, 513–575, plates 18–34. London: British Museum of Natural History.

Milne Edwards, H., 1840. *Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux*, vol. 3, 605 p. Paris: Roret.

Monod, T., 1923. Prodrome d'une faune Tanaidacea et des Isopoda (excl. Epicaridea) de côtes de France (excl. Méditerranée). *Annales de la Société des Sciences Naturelles de la Charente Inférieure (La Rochelle)*, **37**, 19–124.

Monod, T., 1931a. Faune de l'appontement de l'administration à Port Étienne (Afrique Occidentale Française). *Bulletin de la Société Zoologique Française*, **55**, 489–501.

Monod, T., 1931b. Tanaidacés et isopodes aquatiques de l'Afrique occidentale et septentrionale. 3ème partie (1). Sphaeromatidae. *Mémoires de la Société des Sciences Naturelles du Maroc*, **29**, 5–91.

Montagu, G., 1804. Description of several marine animals found on the south coast of Devonshire. *Transactions of the Linnean Society of London*, **7**, 61–85, plates 5–7.

Naylor, E., 1972. British marine Isopods. *Synopses of the British Fauna (New Series)*, **3**, 1–86.

Naylor, E., 1990. Isopoda. In *The marine fauna of the British Isles and north-west Europe*, vol. 1 (ed. P.J. Hayward and J.S. Ryland), pp. 387–405. Oxford: Oxford University Press.

Nolting, C., Reboreda, P. & Wägele, J.-W., 1998. Systematic revision of the genus *Anoplocopea* Racovitza, 1907 (Crustacea: Isopoda) with description of a new species from the Atlantic coast of the Iberian Peninsula. *Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologische, Reihe*, **74**, 19–41.

Norman, A.M., 1905. *Museum Normanianum* or *A catalogue of the invertebrata of the Arctic and North Atlantic temperate ocean and palearctic region which are contained in the collections of the Rev. Canon A. M. Norman. III Crustacea*, 2nd ed., Thos, i–vi, pp. 5–47. Durham: Caldeugh & Sons.

Norman, A.M. & Scott, T., 1906. *The Crustacea of Devon and Cornwall*. London: W. Wesley & Sons.

Omer-Cooper, J. & Rawson, J.H., 1934. Notes on British Sphaeromatidae (Crustacea: Isopoda). *Reports of the Dove Marine Laboratory*, **2**, 22–58.

Panouse, J.B., 1940. Notes biologiques sur les sphèromiens 1) *Campecopea hirsuta* Montagu. *Bulletin de la Société Zoologique de Française*, **65**, 93–98.

Racovitza, E.-G., 1910. Sphéromiens (première série) et révision des Monolistrini (Isopodes sphéromiens). *Archives de Zoologie Expérimentale et Générale, 5ème Série*, **4**, 625–758, plates 18–31.

Stebbing, T.R.R., 1900. On some crustaceans from the Falkland Islands, collected by Mr Rupert Vallentin. *Proceedings of the Zoological Society of London*, **1900**, 517–568.

Stebbing, T.R.R., 1910. Isopoda from the Indian Ocean and British East Africa. The Percy Sladen Trust Expedition to the Indian Ocean under the leadership of Mr J. Stanley Gardiner. Vol. III. *Transactions of the Linnean Society of London, Series Zoology*, **14**, 83–122.

Tattersall, W.M., 1905. *The marine fauna of the coast of Ireland*. Part V. *Isopoda. Great Britain*. Reports of the Department of Agriculture and Technical Instruction for Ireland, Scientific Investigations of the Fisheries Branch, 1904, **II**, 1–90.

Tetart, J., 1962. Étude morphologique de *Campecopea hirsuta* (Montagu). *Bulletin de la Société Linnéenne de Normandie*, **10**, 158–164.

Tetart, J., 1963. Description du polychromatisme de *Campecopea hirsuta* (Montagu). *Bulletin de la Société Linnéenne de Normandie*, **11**, 165–172.

Thompson, W. d'Arcy, 1910. *A catalogue of Crustacea and of Pycnogonida contained in the Museum of University College, Dundee*, pp. i–v, 1–56.

White, A., 1847. *List of the specimens of Crustacea in the collection of the British Museum, London*. London: British Museum.

White, A., 1850. *List of the specimens of British animals in the collection of the British Museum*. Part IV. *Crustacea*, pp. i–iv, 1–141.

White, A., 1857. *A popular history of British Crustacea*. London: Lovell Reeve.

Wieser, W., 1963. Adaptations of two intertidal isopods. II. Comparison between *Campecopea hirsuta* and *Naesa bidentata* (Sphaeromatidae). *Journal of the Marine Biological Association of the United Kingdom*, **43**, 97–112.

Submitted 8 May 2001. Accepted 26 November 2001.