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Stephos (Copepoda: Calanoida: Stephidae) from Balearic caves (W Mediterranean)

Abstract A new species of the calanoid copepod genus *Stephos* is described from an anchialine cave on Majorca (Balearic Islands). It occurs in sympatry with *S. margalefi*, another Balearic endemic differing markedly in body size as well as in the morphology of the fifth legs of both sexes. The new species is extraordinary within its family, the Stephidae, and even within the entire superfamily Clausocalanoidea in displaying a paired arrangement of the reproductive system in the female genital double-somite. No other member of this cluster of 10 families displays such a primitive condition, all exhibiting different degrees of coalescence or reduction of the genital opercula, pores and ducts. We interpret the condition found in *Stephos vivesi* sp. nov. as secondary, perhaps derived by loss of the operculum concealing the paired apertures and their subsequent migration and separation on the ventral surface. We take advantage of this discovery to amend the diagnosis of *S. margalefi*, which was inaccurately described and of which the type material has been lost. This species is unique in the genus in expressing the basal exite seta on the maxillule and in having a 4-segmented (vs. 5-segmented) male left fifth leg; the latter condition is the result of the failure to express the inter-segmental articulation between ancestral segments 3 and 4. In addition, it is the only *Stephos* with the segment 3 of the male left leg 5 (fused to fourth segment) displaying any armature, viz. a tiny spine on the lateral margin, and a pointed process on the medial margin. We tentatively consider *S. balearensis*, a third cavernicolous species apparently endemic to Minorca, to be a junior synonym of *S. margalefi*. The disjunct distribution of this apparently stygobiont species, embracing three different islands of the Balearic archipelago, does not pose any biogeographical problem since all three comprised a single island as recently as 17000 yr BP, at the time of the last glacial maximum when a global marine regression of up to 140 m took place.

Key words taxonomy, new species, anchialine caves, *Stephos*, Mediterranean islands

Introduction

Recent explorations of the submarine and anchialine caves of the Balearic Islands have revealed a rich assemblage of new calanoid copepods (Riera *et al.*, 1991; Carola & Razouls, 1995, 1996; Jaume & Boxshall, 1995a, 1995b; Razouls & Carola, 1996; Jaume *et al.*, 1999, 2000). Some of these taxa belong to genera supposed to be strictly tropical and could consequently be considered as thermophilic relicts (e.g. *Exumella* Fosshagen, 1970, and *Ridgewayia* Thompson & Scott, 1903). Others occur also at higher latitudes (e.g. *Metacalanus* Cleve, 1901, *Paramisophria* T. Scott, 1897, *Pseudocyclops* Brady, 1872, *Stephos* T. Scott, 1892, *Stygocyclopia* Jaume & Boxshall, 1995, and *Thompsonopia* Jaume, Fosshagen & Iliffe,

1999), and their biogeographic interest is more limited. None of these genera is strictly stygobiont, but all utilise demersal (= hyperbenthic) habitats in shallow water, in the deep sea, or in both.

Stephos is a shallow-water taxon found from the tropics to the poles and is perhaps one of the most common calanoids in submarine caves. Two endemic species had been reported thus far from the Balearic archipelago. *Stephos margalefi* Riera, Vives & Gili, 1991 was described from a submarine cave on the NE coast of Majorca, and later reported from a nearby anchialine cave (Gràcia *et al.*, 2003). *Stephos balearensis* Carola & Razouls, 1996 is apparently restricted to a single submarine cave on the eastern coast of Minorca, about 65 km to the north of the type locality of *S. margalefi*. Here we describe a third,

new Balearic species. It occurs in a Majorcan anchialine cave in sympatry with *S. margalefi* in chambers close to the sea, whereas it is the only *Stephos* present in the innermost passages of this cave, up to 600 m inland. The species differ markedly in body size (cf. Fig. 9A, B), as well as in the morphology of the fifth legs of both sexes. We take advantage of this discovery to amend the diagnosis of *S. margalefi*, which was inaccurately described by Riera *et al.* (1991), and of which the type material has been lost.

The new species described herein is extraordinary within its family, the Stephidae, and even within the entire superfamily Clausocalanoidea in displaying a paired arrangement of the reproductive system in the female genital double-somite. No other member of this cluster of 10 families displays such a primitive condition, all exhibiting different degrees of coalescence or reduction of the genital opercula, pores and ducts. *Stephos vivesi* sp. nov. is the fifth *Stephos* known to occur in Mediterranean waters. Previous reports of the genus in the region include *S. gyrans* (Giesbrecht, 1892) (Gulf of Naples; Giesbrecht, 1892); *S. marsalensis* Costanzo, Campolmi and Zagami, 2000 and *S. cryptospinosus* Zagami, Campolmi and Costanzo, 2000 (Sicily; Costanzo *et al.*, 2000; Zagami *et al.*, 2000); and *S. margalefi* (Riera *et al.*, 1991). In addition, there is an unpublished record of a new, undescribed species from a submarine cave around Marseille (Pierre Chevaldonnée and Damià Jaume, pers. obs.).

Materials and methods

Cova des Coll is a typical mixing-zone cave excavated in an upper Miocene coral reef at Portocolom (Felanitx, Majorca; Fig. 1A, B), reaching a maximum depth of 15 m. It has a direct connection to the sea plus 3 additional subaerial entrances (two of them being artificial wells), and its total extent exceeds 6.5 km. The cave comprises: 5009 m of subaquatic passages, 765 m of aquatic passage but with air chambers, and 726 m of fully terrestrial passages (see Fig. 1C). The sector of the cave closest to the sea lies directly beneath the urban area and is exposed to strong hydrodynamic effects, with intermittent influx and reflux of water resulting from the combined action of lunar and barometric tides. The walls and tunnels of these passages are covered with a diverse array of sessile filter-feeding organisms, including sponges, tunicates, sabellid polychaetes and bivalve molluscs, which take advantage of the organic matter penetrating the cave with the inflowing sea water, plus that contributed by a cesspool that inputs directly into these passages (Fig. 1C). As usual for this type of cave, the water column is strongly stratified in the more isolated chambers, with low salinity water (8.5‰) overlying full-strength marine water (37.5‰; see Fig. 1D). These chambers remain at a stable temperature all year round, between 19 and 22 °C (see Fig. 1D), whereas minimum winter temperature in the sea outside falls to 14 °C. Gràcia *et al.* (2005) provided a thorough description of the cave and its fauna.

The copepods were caught using a hand-held plankton net or in traps baited with meat that were set for several days in the submerged passages using specialised cave diving techniques. Hauls of the plankton net were taken through narrow hori-

zontal and/or vertical ranges, which were precisely recorded during dives in order to detect any micro-habitat preferences of the species. Salinity and temperature profiles of the cave waters were produced with a SEABIRD SBE19 CTD oceanographic profiler programmed to take readings every 0.5 s. The descent of the profiler was controlled to a rate of *c.* 10 cm s^{-1}, and was held out in front by the diver to avoid disturbing the water column. Specimens were fixed in the field in formalin, and studied as temporary preparations in lactic acid under the microscope. Drawings were prepared using a camera lucida on an Olympus BH-2 microscope equipped with Nomarski differential interference contrast. Material for SEM was washed in distilled water, dehydrated through graded acetone series, critical point dried using liquid carbon dioxide as the exchange medium, mounted on aluminium stubs and sputter coated with palladium. Coated material was examined on a Phillips XL30 Scanning Electron microscope. Body length measurements include caudal rami, but not their setae. Material is deposited in the collections of the Department of Zoology, The Natural History Museum, London [BMNH], and in the IMEDEA Crustacea collection [MNCM]. The terminology used in the descriptions follows Huys and Boxshall (1991). U.T.M. coordinates of the caves are referred to Datum Europe 50.

Systematics

Subclass COPEPODA H. Milne Edwards, 1830
Order CALANOIDA G. O. Sars, 1903
Family STEPHIDAE G. O. Sars, 1902
Genus *Stephos* T. Scott, 1892
Stephos vivesi sp. nov. (Figures 2–9A)

Type material

Cova des Coll (Portocolom, Majorca, Balearic Islands), UTM coordinates: 31 4364500/522770. Holotype: male 0.45 mm [BMNH reg. no. 2005.2070]. Paratypes: 5 males of 0.45, 0.45, 0.45, 0.45 and 0.44 mm; 5 females of 0.45, 0.45, 0.45, 0.44 and 0.44 mm [BMNH reg. nos. 2005.2071–2080]; 126 specimens, both sexes, not measured [MNCM-367]. Collected by F. Gràcia and D. Jaume, 21 December 2004.

Description of adult male

Eyeless and completely unpigmented. Body (Figs 2A, 3A) tiny, 0.44–0.45 mm in length (based on 6 specimens). Cephalosome and first pedigerous somite separate except ventrolaterally (see Fig. 7B). Long sensilla present on each side of third pedigerous somite (Figs 2A, 3A, 7B). Somites 4 and 5 completely coalesced, with posterolateral corners rounded and slightly asymmetrical in dorsal aspect, extending posteriorly slightly further on right side (Fig. 3A); tiny spine located subterminally on inner surface of each posterolateral corner (Fig. 8). Rostrum hardly developed, rounded, with two bifid sensillae frontally (Figs 4A, 7A). Body widest at first
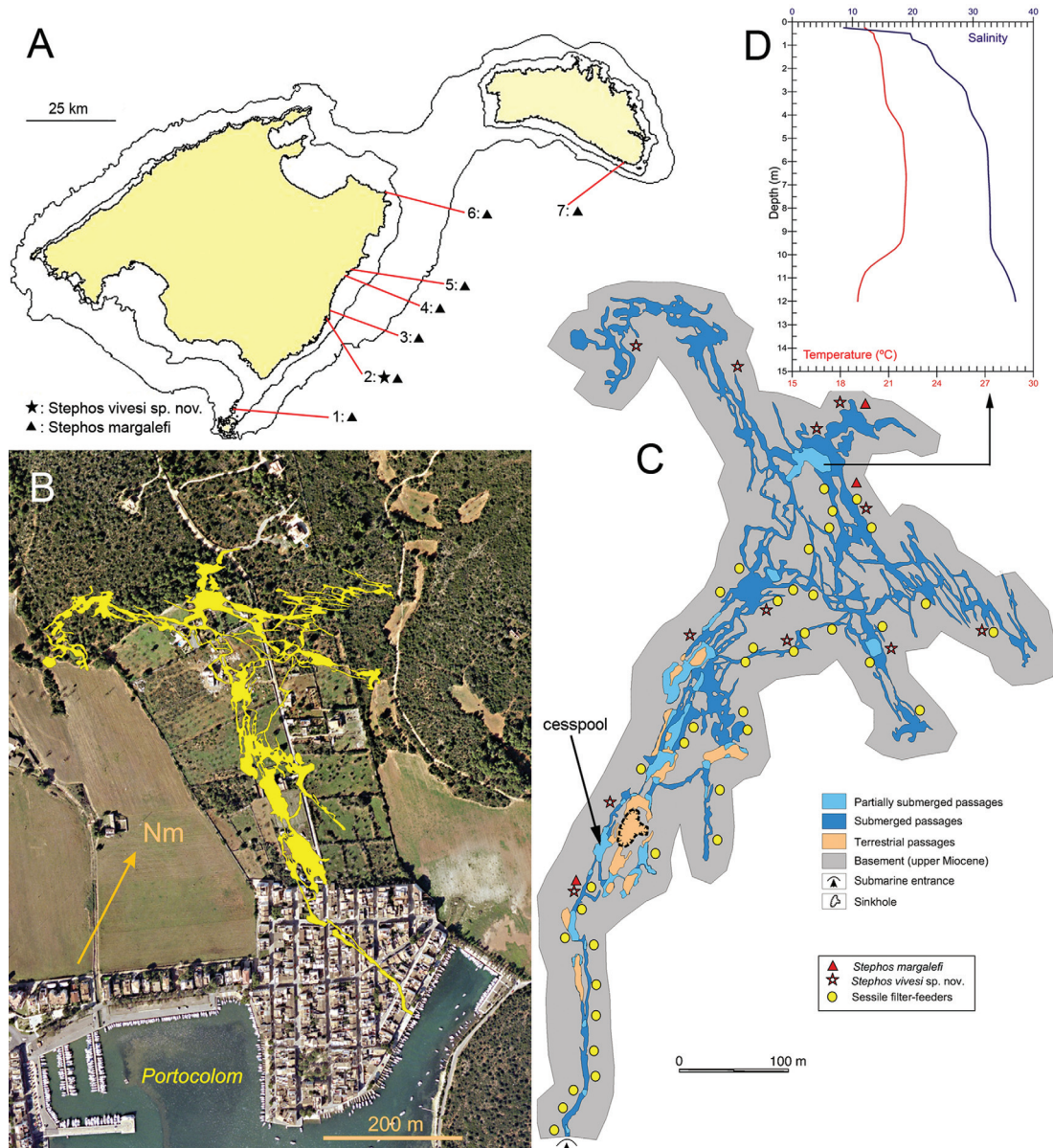
Figure 1 A, location of caves harbouring *Stephos* in the Balearic Islands; isobaths correspond to 50 and 100 m (1: Cova de sa Llumeta; 2: Cova des Coll; 3: Es Secret des Moix; 4: Cova Genovesa; 5: Cova del Dimoni; 6: Cova de la Catedral; 7: Cova de sa Gamba); B, aerial photograph of the zone of Portocolom (Majorca), with plan of Cova des Coll projected on it; C, plan of the cave showing microdistribution of *Stephos vivesi* and *S. margalefi*; D, temperature and salinity profiles in a permanently stratified chamber of the cave. Nm = magnetic North.

pedigerous somite, ratio of prosome to urosome length *c.* 2.5:1. Urosome 5-segmented, with all somites except anal somite about same length; genital somite slightly produced laterally on left side, with single gonopore opening posterolaterally on left side ventral surface; ornamentation of somite reduced to cluster of few short spinules anterodorsally on right margin of somite (Fig. 3B). Posterior hyaline frill of fourth urosomite transformed progressively into row of long spinules ventrally and ventrolaterally (as in female; Fig. 3D). Anal somite short, with scarcely developed, hyaline anal operculum. Caudal rami (Fig. 3A, C) symmetrical, 1.7 times longer than wide, with 4 distal setae and 1 reduced seta (seta VII) on outgrowth midway along medial margin; no trace of seta I. Cluster of short

filaments and processes present on lateral distal corner of each ramus, not homologous with seta II (Fig. 7C, D). Distal setae short (just longer than urosome) and stiff, spinulose, distolateral seta (seta III) slightly shorter than rest (Fig. 3A, C). Internal tissue of distal setae finely corrugated.

Antennules (Fig. 4B) long and symmetrical, extending beyond posterior margin of prosome (Fig. 2A), non-geniculate, 23-segmented with failure to express articulations between segments I–IV (although vestige of articulation between segments II and III expressed dorsally), X–XI and XXVII–XXVIII. Armature formula of segments as follows: segment 1 (corresponding to compound ancestral segment I–IV), 7 setae + 5 aesthetascs; segment 2 (V), 2 + ae; segment 3 (VI), 2 setae;
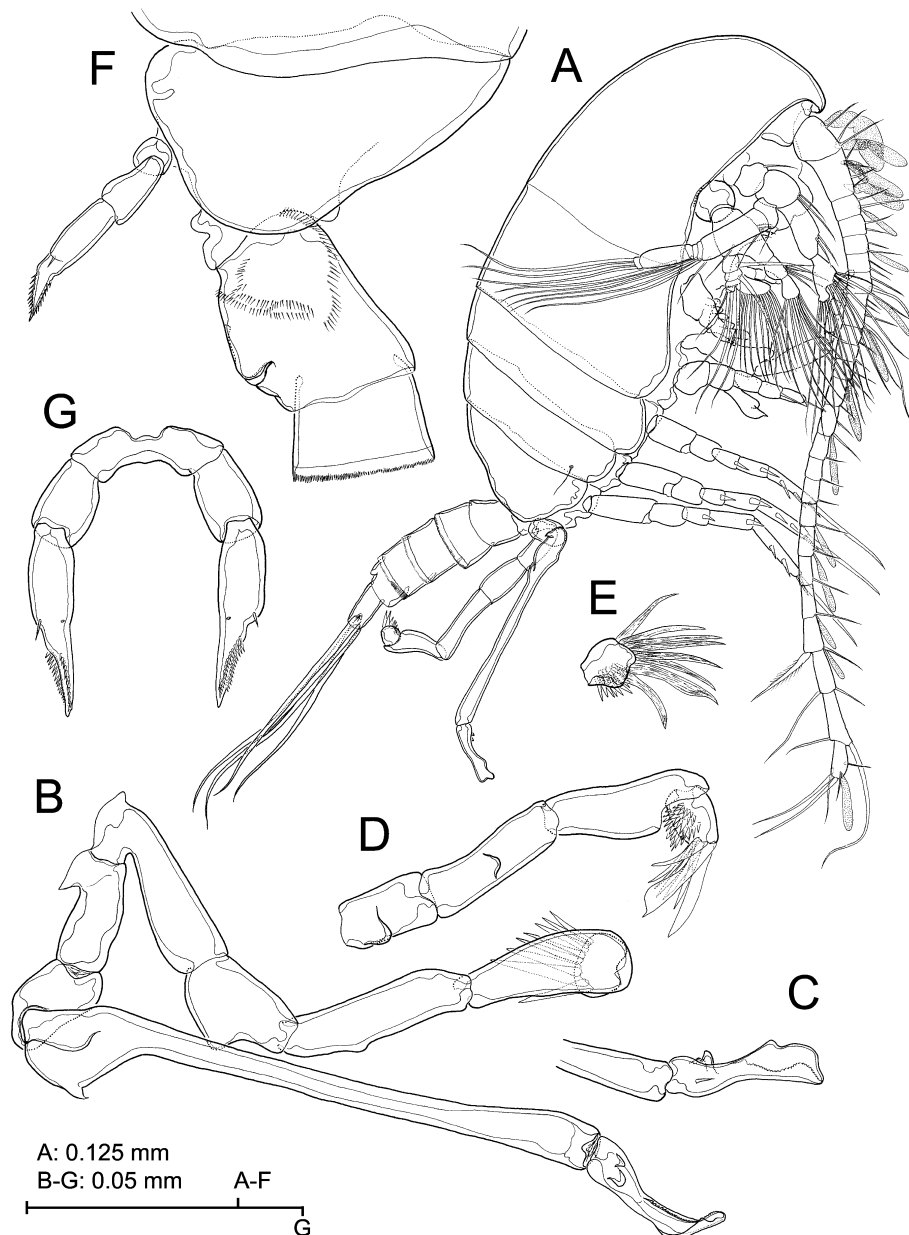
Figure 2 *Stephos vivesi* sp. nov. A, adult male body, lateral; B, male fifth legs, anterior; C, detail of distal segment of right leg, lateral; D, detail of distal segments of left leg, medial; E, detail of distal segment of left leg, ventral (= anterior). E, adult female last prosomite with attached fifth legs, genital double-somite, and first free abdominal somite, left lateral; F, detail of female fifth legs, anterior.

segment 4 (VII), 2 + ae; segment 5 (VIII), 2 setae; segment 6 (IX), 2 + ae; segment 7 (composed X-XI), 4 + ae; segments 8 (XII) and 9 (XIII), 1 seta each; segment 10 (XIV), 2 + ae; segment 11 (XV), 1 seta; segment 12 (XVI), 2 + ae; segments 13 (XVII) to 15 (XIX), 1 seta each; segments 16 (XX) and 17 (XXI), 1 + ae each; segment 18 (XXII), 1 seta; segment 19 (XXIII), 1 + ae; segment 20 (XXIV), 1 + 1 + ae; segments 21 (XXV) and 22 (XXVI), 1 + 1 setae each; segment 23 (composed XXVII-XXVIII), 5 + ae. Some setae with internal tissue finely corrugated; seta on posterior margin of segment 20 (XXIV) thicker than rest, pinnate proximally. Segments 11 to 22 each with small oblique spinulose comb on ventral surface. Segments 1 to 8 with spinulose combs also, but oriented

more perpendicular to posterior margin of respective segment and closer to it. One sensilla on dorsal surface of compound segment 1, probably corresponding to ornamentation of incorporated ancestral segment III.

Antenna (Fig. 5A) biramous. Coxa and basis with 1 and 2 setae on distomedial angle, respectively; coxa with patch of tiny denticles on anterior margin. Exopod indistinctly 7-segmented, with intersegmental articulation between segments 2 and 3 not completely expressed; setal formula as follows: segment 1 (corresponding to ancestral I), 1 seta; segment 2 (II–IV), 3 setae; segment 3 (V), 1 seta; segment 4 (VI–VII), 2 setae; segments 5 (VIII) and 6 (IX), 1 seta each; segment 7 (X), 3 setae. Setae on segments 1 and 2 more slender than
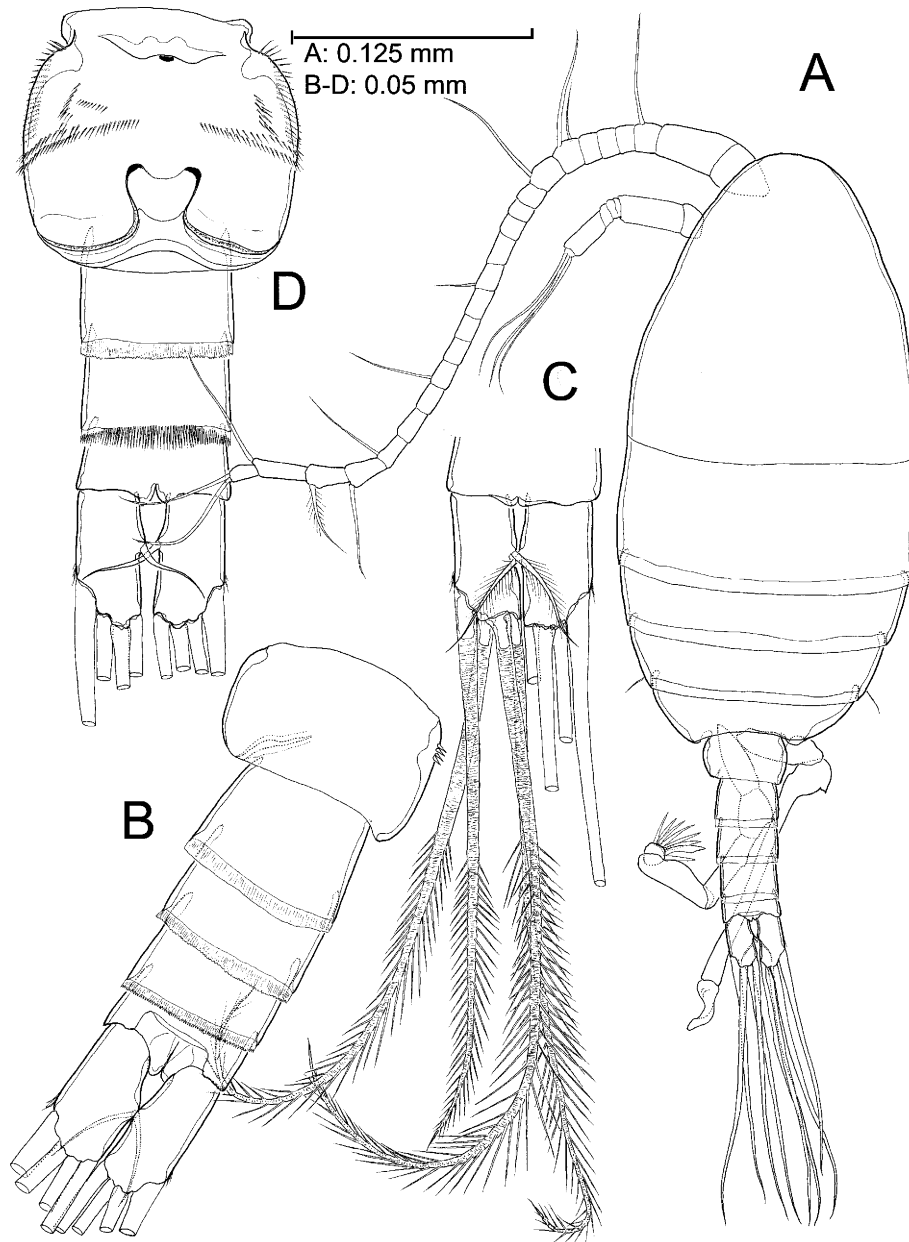
Figure 3 *Stephos vivesi* sp. nov. A, adult male body, dorsal; B, male urosome, dorsal; C, detail of caudal rami, ventral; D, adult female urosome, ventral.

rest. Segment 1 with row of sparsely set small denticles running parallel to distal margin on anterior surface. Endopod 2-segmented, proximal segment with 2 setae, distal segment expanded subdistally into medial lobe bearing 8 setae, and with distal portion crowned with 7 setae; transverse row of long spinules subdistally on lateral margin of segment.

Mandibular gnathobase (Fig. 5B) with row of spinules subdistally on ventral margin; cutting edge comprising 8 teeth plus dorsal spinulose seta; ventralmost tooth largest, smooth and unicuspid; 3 adjacent teeth with row of 3 small denticles, unicuspid; 4 dorsal teeth reduced, tricuspidate, with transverse comb of long spinules basally. Palp (Fig. 5C) biramous, basis with 4 setae on inner margin, proximalmost seta unipinnate, others smooth. Exopod indistinctly 5-segmented, setal formula 1,1,1,1,2. Proximal endopodal segment with 4

setae on distomedial angle; distal segment with 10 setae, one reduced.

Maxillule (Fig. 5D) with praecoxal arthrite carrying 8 marginal spines plus 4 stiff setae on posterior surface; 2 combs of short spinules located transversely on ventral margin of arthrite. Coxal epipodite with 9 setae; coxal endite with 3 stiff setae. Basis with cluster of 6–7 denticles on anterior surface; proximal basal endite with 4 setae; distal basal endite indistinct, with 5 setae; no trace of basal exite. Exopod with 11 marginal setae, and row of setules along distal portion of medial margin. Endopod not articulated to basis, indistinctly 3-segmented, setal formula 4,4,7.

Maxilla (Fig. 5E) indistinctly 6-segmented, comprising partially coalesced praecoxa and coxa, allobasis and 3-segmented endopod. Armature of praecoxal and coxal
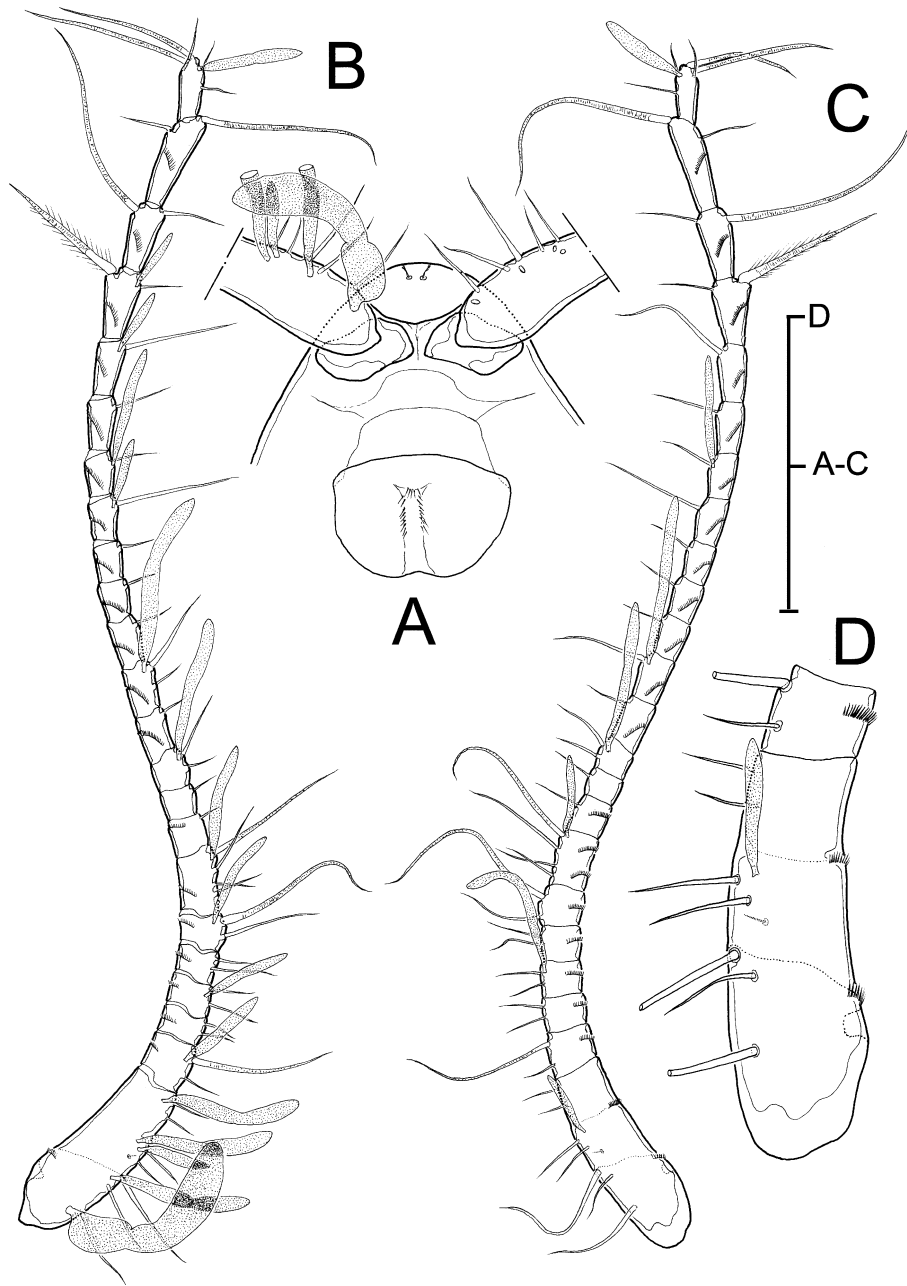
Figure 4 *Stephos vivesi* sp. nov. A, adult male rostrum and labrum, ventral; B, male right antennule, ventral; C, female left antennule, ventral; D, detail of proximal part of latter. Scale bar: 0.05 mm.

endites 5,3,3,3, respectively. Basal endite with 4 setae, 1 stouter than rest; endopodal endite with 1 seta on tip. Free endopod setal formula 1,1,3, respectively. Integument of praecoxa ornamented with patch of denticles on posterior margin. Praecoxal and coxal endites with cluster of long spinules subdistally on lateral surface; distal coxal endite with additional row of denticles proximally on medial surface.

Maxilliped (Fig. 5F) 7-segmented with syncoxa, basoendopod and free 5-segmented endopod. Syncoxa with 2,3,3 setae on medial margin, distalmost seta thorn-like with plumose tip, carried on outgrowth protruding from distomedial angle of segment; praecoxal endite unarmed. Basoendopod as long as preceding segment, with 3+2 setae; medial row of hy-

aline lamellae submarginally on anterior surface of segment. Free endopod setal formula: 4,4,3,3+1,3+1. Syncoxa ornamented with patch of short denticles and 2 rows of spinules on posterior surface, as figured.

Swimming legs 1–4 (Fig. 6) progressively larger towards posterior, each comprising coxa, basis and 3-segmented exopod; endopod of first leg (Fig. 6A) 1-segmented, that of second leg (Fig. 6C) 2-segmented; endopods of third and fourth legs (Fig. 6D, E) 3-segmented. Long setae on rami of legs short and stiff, spinulose except distalmost 3 on exopod of leg 4, apparently smooth. Seta on distomedial angle of basis of leg 1 setose on posterior surface only (Fig. 6B); outer spines on exopod slender, needle-like (Fig. 6A); endopod with rounded
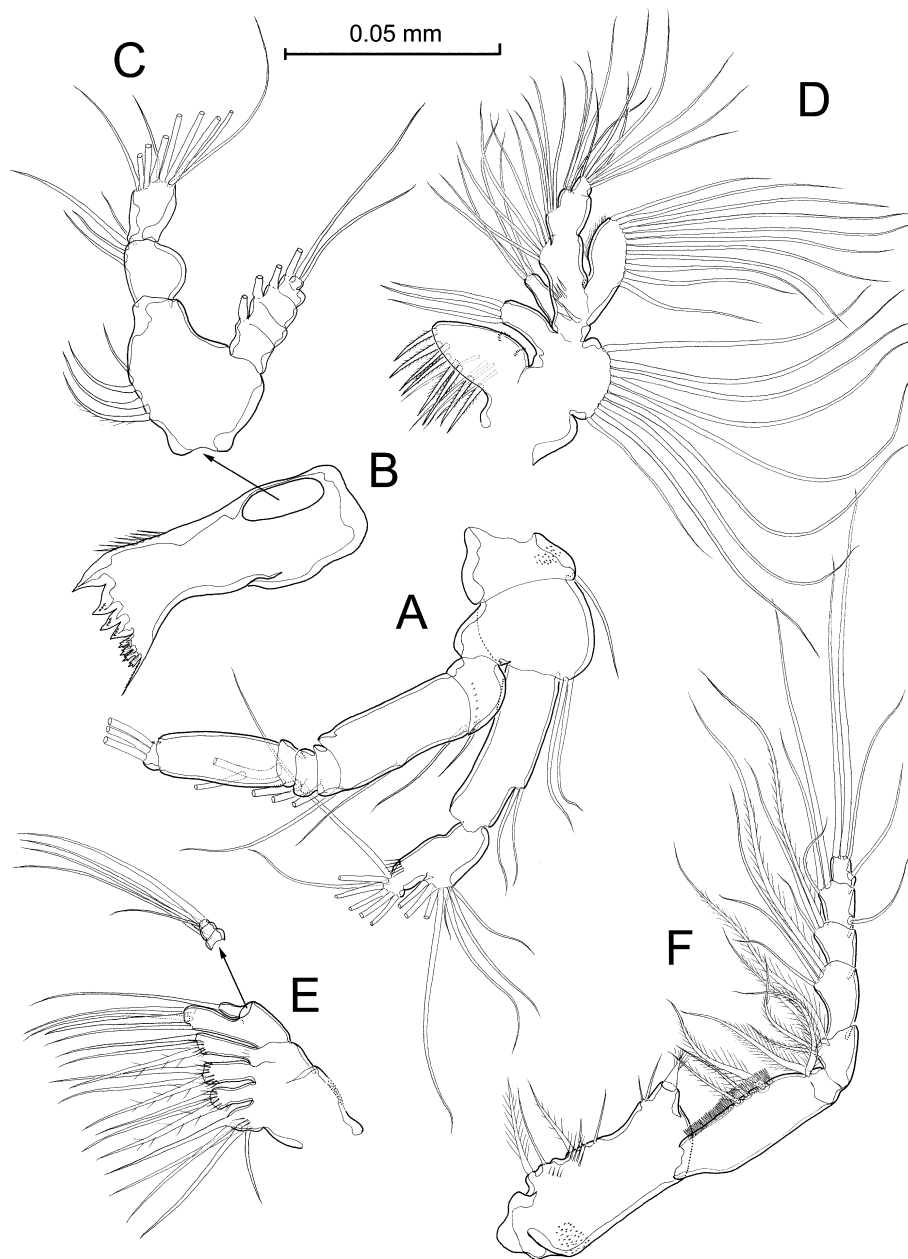
Figure 5 *Stephos vivesi* sp. nov., adult male. A, right antenna, lateral; B, mandibular gnathobase; C, mandibular palp; D, right maxillule, anterior; D, right maxilla with disarticulated free endopod, lateral; E, left maxilliped, anteromedial.

process anterolaterally (Fig. 6A). Most setae on all legs with internal tissue finely corrugated. Armature of legs as follows:

	Coxa	Basis	Exopod segment			Endopod segment		
			1	2	3	1	2	3
Leg 1	0–0	0–1	0–0	I–1	I,2,2	0,2,3		
Leg 2	0–1	0–0	I–1	I–1	III,I,4	0–1	1,2,2	
Legs 3 & 4	0–1	0–0	I–1	I–1	III,I,4	0–1	0–1	1,2,2

Fifth legs (Fig. 2B) strongly asymmetrical, uniramous and filiform, both longer than urosome (see Fig. 2A). Left leg 5-segmented, segments 2 and 3 each with rounded outgrowth on medial margin (see Fig. 2B, D); fifth segment short and rounded, reflexed posteriorly, with row of 8 unequal long

hyaline lamellae on distal margin and patch of short, stout spinules on posterior surface (Fig. 2E). Right leg 4-segmented; segment 3 very elongate, (segment longer than urosome), straight and slender except slightly expanded proximal part, with small pointed process proximally on lateral margin; segment 4 roughly spatulate, with 2 rounded outgrowths proximally on anterior surface, tiny spine proximally on lateral margin (see Fig. 2C), and finely denticulated distomedial margin.

Description of adult female

Similar in size and all major features to the male except for urosomal segmentation, armature of antennule and morphology of fifth legs. Urosome (Fig. 3D) 4-segmented, with symmetrical genital double-somite, adorned with several rows of ventrolateral and dorsolateral rows of spinules as in Figs 2F and
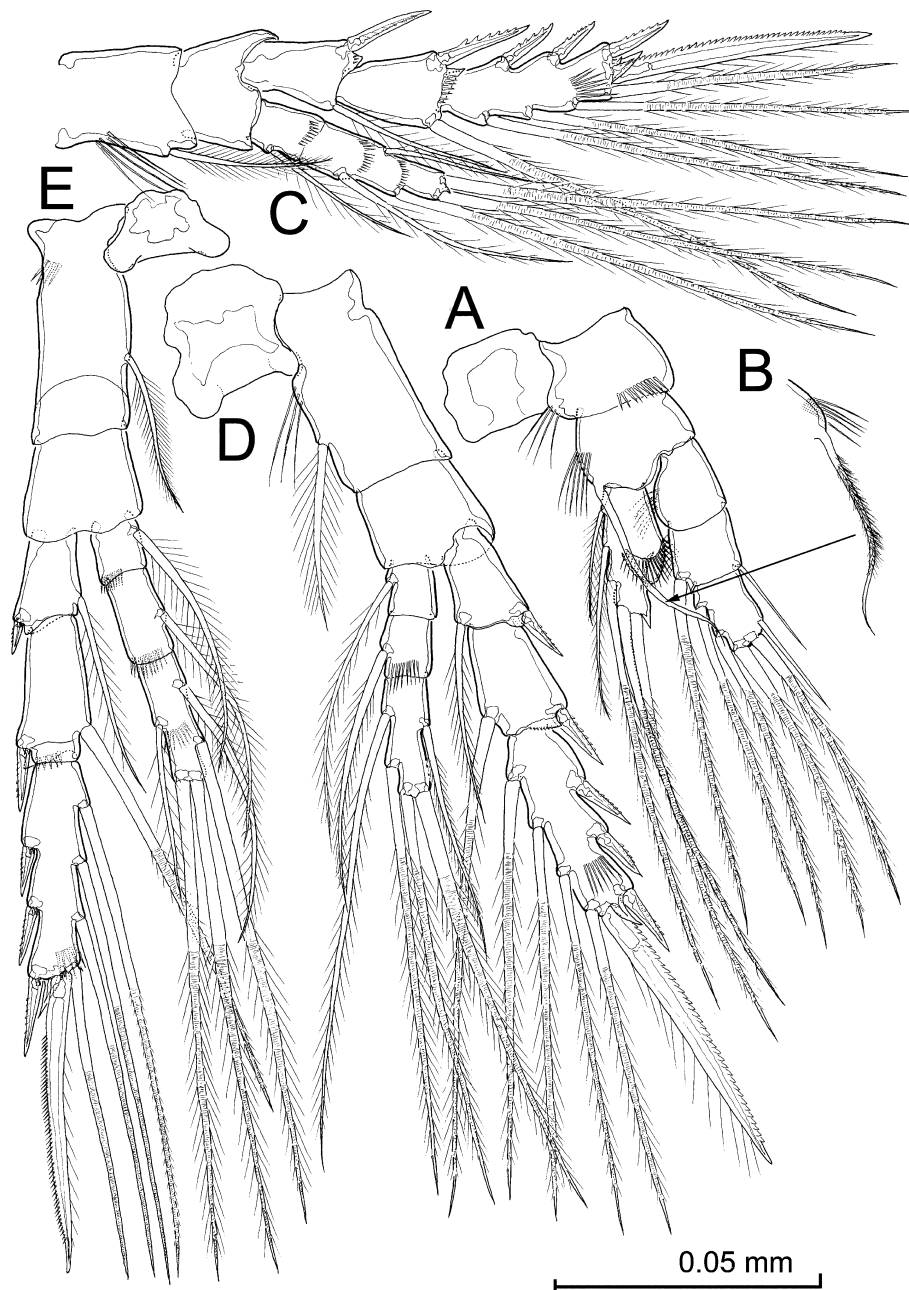
Figure 6 *Stephos vivesi* sp. nov., adult male. A, left leg 1, anterior; B, detail of ornamentation on posterior side of inner basal seta of latter; C, leg 2, anterior; D, leg 3, anterior; E, leg 4, posterior.

3D. Reproductive system showing paired arrangement (see Fig. 8), with paired genital opercular plates located ventrally, each partially concealing copulatory pore, placed ventromedially. Genital opercular plates capable of retraction, as shown in Fig. 8.

Antennule (Fig. 4C, D) differing from male in only 4 details: (1) fewer aesthetascs; (2) number of spinulose combs on compound segments 1 and 7 (2 combs per segment instead of only 1); (3) articulation between ancestral segments III and IV partially expressed dorsally (see Fig. 4D); and (4) only 1 seta on segment 12 (XVI) but 2 setae in male. Segments 6, 16, 19 and 20 lack aesthetascs (vs. 1 aesthetasc per segment in the male antennule), whereas segment 1 bears only 1 (vs. 5 aesthetascs in the male).

Fifth legs (Fig. 2F, G) symmetrical, uniramous, 3-segmented with proximal segment fused to intercoxal sclerite. First and second segments unarmed; third segment longer than previous 2 combined, with tapering distal half; tiny seta and pore positioned submarginally on anterior surface about midway along segment, seta close to lateral margin, pore close to medial margin; two rows of denticles along tapering portion of segment as figured.

Etymology

The species name honours the pioneering Majorcan copepodologist Dr Francisco Vives Galmés, in commemoration of his 80th birthday.
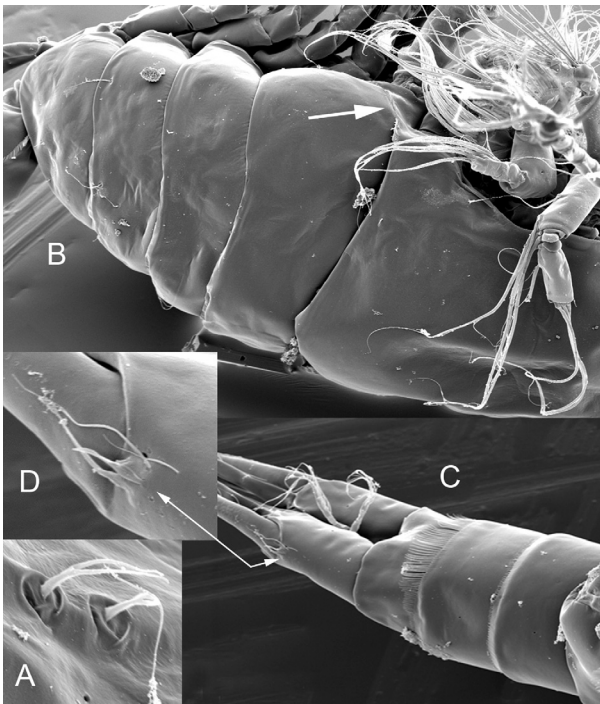
Figure 7 *Stephos vivesi* sp. nov., adult female, SEM micrographs. A, detail of frontal sensillae; B, left lateral view of prosome showing (arrowed) incomplete section of articulation between cephalosome and first pedigerous somite); C, detail of distal part of urosome showing spinulose ventral portion of posterior frill of third abdominal somite, ventrolateral; D, detail of lateral ornamentation of left caudal ramus (note scars left by several missing setules).

Remarks

The new species exhibits an external configuration of the female genital system that is unique for the genus *Stephos* and family Stephidae. All other stephids for which reliable information is available possess a single genital operculum covering both genital apertures. The common genital operculum may be located in the ventral midline and symmetrical, or positioned asymmetrically. The presence of a pair of widely separated genital apertures posterolaterally on the ventral surface of the genital double-somite is found in basal calanoid taxa such as the Pseudocylopidae and Boholinidae (Huys & Boxshall, 1991) but has not, to our knowledge, been reported from any member of the superfamily Clausocalanoidea. We interpret the condition found in *Stephos vivesi* sp. nov. as secondary, perhaps derived by loss of the operculum concealing the paired apertures and their subsequent migration and separation on the ventral surface. The sequence of SEMs (Fig. 8) demonstrates that the genital apertures can open by rotating anteriorly up into the double-somite, in order to allow the eggs to be laid.

Out of the 29 species comprising the genus *Stephos* (see Boxshall & Hasley, 2004) the new species falls within a group characterised by a 4-segmented male right fifth leg combined with a left leg in which segment 4 is not swollen. This group comprises six taxa from the Pacific and Atlantic (viz. *S. angulatus* Bradford-Grieve, 1999; *S. morii* Greenwood, 1978; *S.*
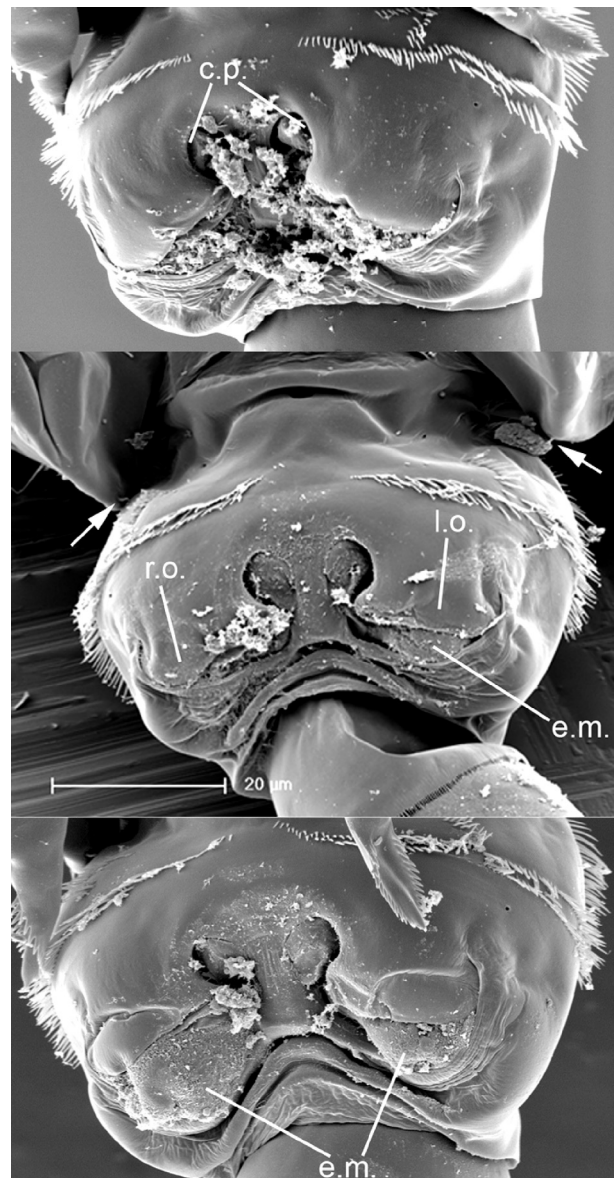

Figure 8 *Stephos vivesi* sp. nov., adult female, SEM micrographs. Views of the genital double-somite in different females showing sequence of stages of extrusion of an unidentified material. Arrows indicate the tiny terminal spinule on the inner margin of the last prosomite. (c.p.: copulatory pores; e.m.: extruded material; l.o.: left genital operculum; r.o.: right genital operculum).

pacificus Ohtsuka & Hiromi, 1987; *S. pentacanthos* Chen & Zhang, 1965; *S. rustadi* Strömgren, 1969; and *S. tsuyazakiensis* Tanaka, 1966; see Bradford-Grieve, 1999) plus the recently described Mediterranean *S. marsalensis*.

The male fifth legs are key to distinguishing *Stephos vivesi* sp. nov. from the other species in this group: it differs from *S. angulatus* in having a spatulate rather than bifid distal segment of the right male fifth leg (see Bradford-Grieve, 1999); in *S. marsalensis*, segment 4 of right male fifth leg is relatively longer, there are fewer (only 5) lamellate hyaline processes on segment 5 of left leg and, in addition, it displays asymmetrical female fifth legs (see Costanzo *et al.*, 2000); in
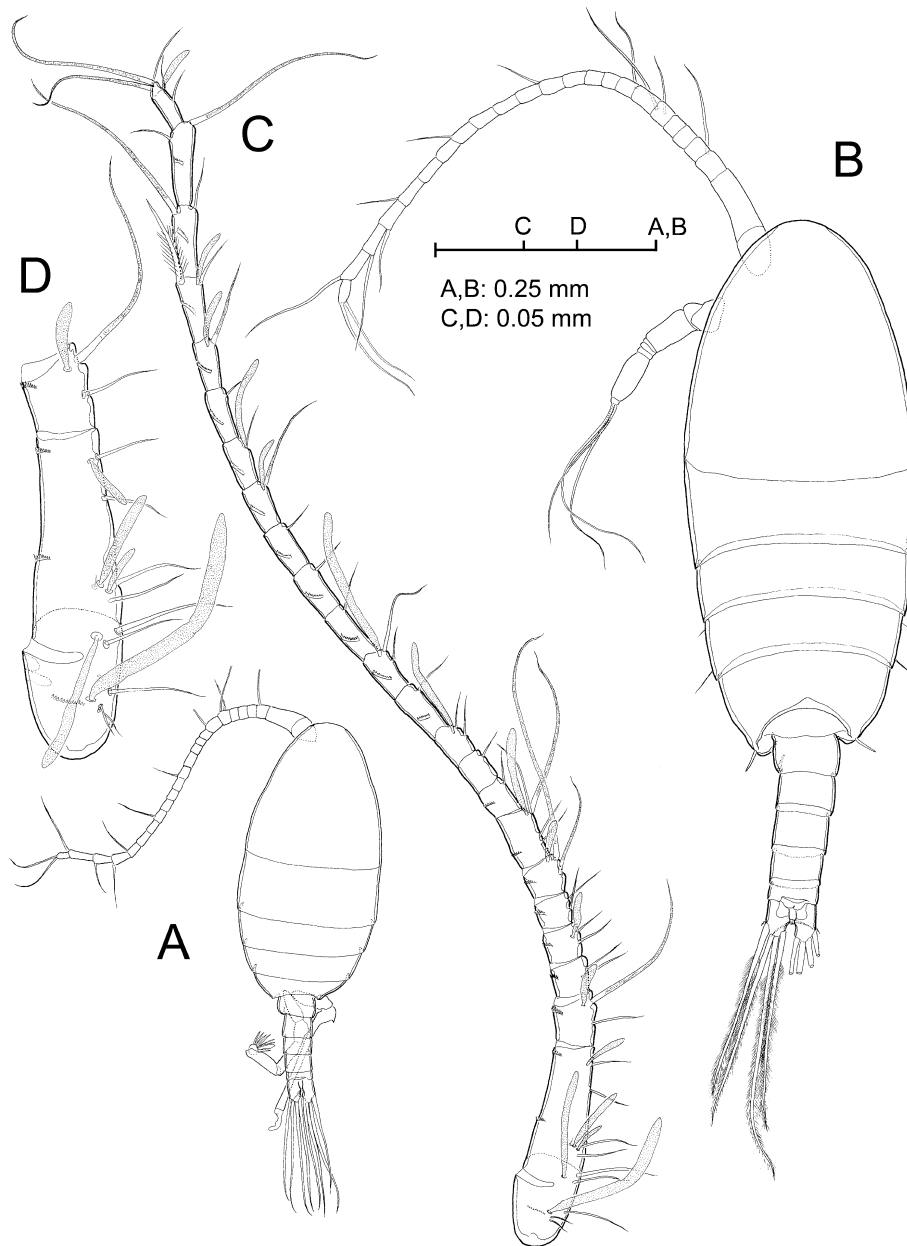
Figure 9 A, *Stephos vivesi* sp. nov., adult male body, dorsal; B, *Stephos margalefi* Riera, Vives & Gili, 1991, adult male, dorsal; C, right antennule of latter, ventral; D, detail of proximal part of antennule.

S. rustadi the right leg has segment 3 slightly shorter than segment 4 which terminates in a claw-like structure, and the left leg carries 2 strong hook-like processes on the fifth segment, the larger one bifid (see Strömgren, 1969); in *S. morii* the right leg is pseudochelate with a large proximal process on the tapering terminal segment and the left leg carries about 5 lamellate processes on the distal segment which is produced into a long spinous process about 1.6 times longer than the segment (see Greenwood, 1977 as *S. tropicus* Greenwood); in *S. pacificus* the right leg has an elongate fourth segment, more than half as long as the third, and the left leg carries 3 terminal and 2 subterminal lamellate processes on the distal segment (see Ohtsuka & Hiromi, 1987); *S. pentacanthos* and *S. tsuyazakiensis* both have a very similar fifth leg to *S. pacificus* also with an elongate fourth segment on the right side,

but it is curved in these two species, and both carry a total of 5 lamellate processes on the terminal segment of the left leg (cf. Chen & Zhang, 1965 and Tanaka, 1966).

Two species of *Stephos* are known only from the female so the differential diagnosis of the new species cannot only rely on features of the male fifth legs. *Stephos vivesi* sp. nov. can be separated from *S. exumensis* Fosshagen, 1970 in the absence of the characteristic dorsolateral process on the right side of the female genital double-somite of this species, among other features (see Fosshagen, 1970). *Stephos simillimus* Brady, 1918 is inadequately described (Brady, 1918), indeed Bradford-Grieve (1994: 133) commented that Brady's species is more likely a scolecitrichid than a stephid, although she subsequently (Bradford-Grieve, 1999) included *S. simillimus* in her list of species without comment. The maxilliped
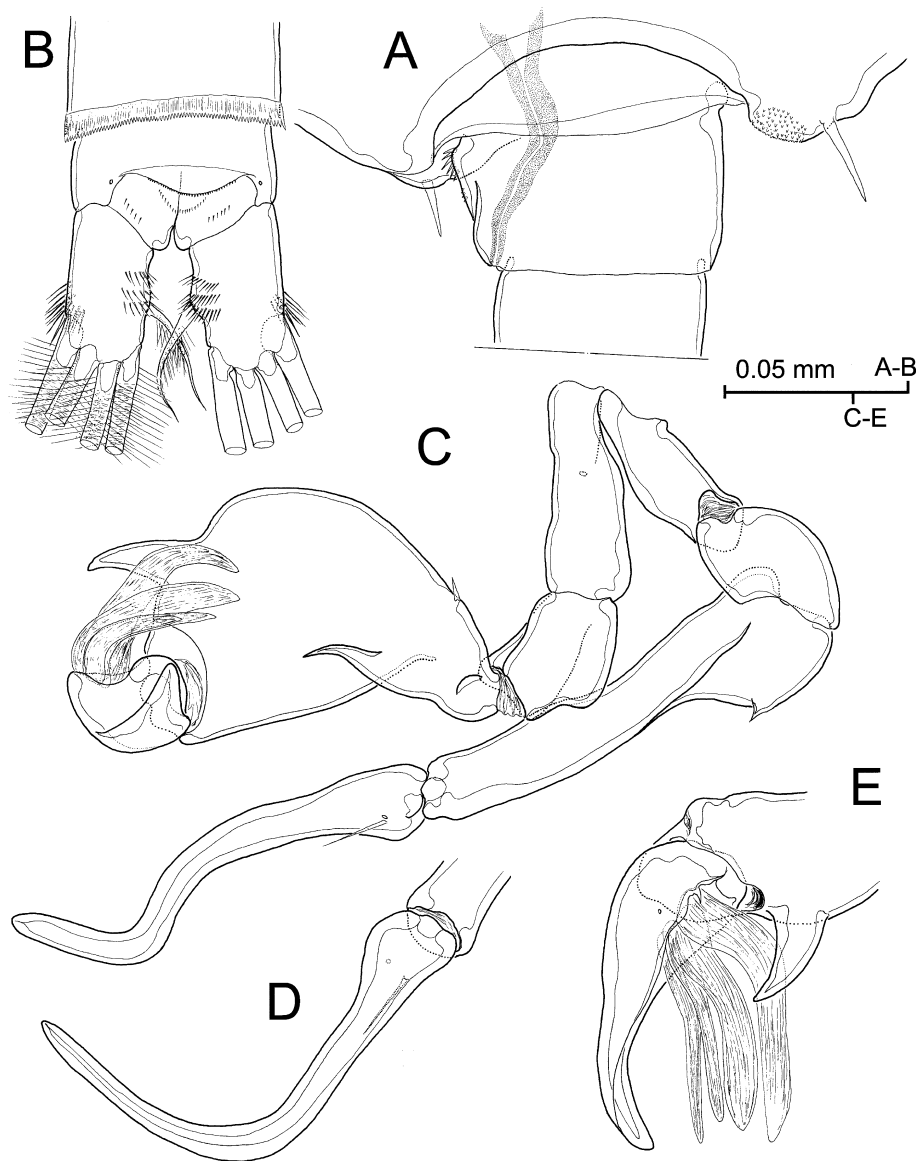
Figure 10 *Stephos margalefi* Riera, Vives & Gili, 1991, adult male. A, detail of last prosomal and genital somites, dorsal view showing functional genital duct on left side only; B, last two urosomites plus caudal rami, dorsal; C, fifth legs, posterior; D, detail of distal segment of right fifth leg, anteromedial; E, same for left leg, anterolateral.

of *S. simillimus* as illustrated by Brady (1918: Plate 9, fig. 15) is reflexed and does not resemble that of *Stephos*. We consider *S. simillimus* to be a *species inquirendum* and that its stephid affinities are doubtful.

Stephos vivesi sp. nov. shows a rather uniform distribution in the cave, occurring both in passages subjected to strong tidal currents as well as in permanently stratified waters of the more isolated chambers, located far inland (see Fig. 1C). It seems to be relatively euryhaline since it does not avoid the low salinity (8.5‰) zones of the water column but also occupies the full marine water of the deepest explored layers.

Cases of sympatry in *Stephos* have been reported before, some times involving up to 8 different species (Ohtsuka & Hiromi, 1987; Jacoby & Greenwood, 1991). Ohtsuka *et al.* (1996) analysed these and other cases of sympatric occurrence in hyperbenthic calanoids, and concluded that the generally high variability of benthic environments may allow the coexistence of several congeners. In Cova des Coll, the two species coexist in the hydrologically dynamic passages of the cave, where periods of marine intrusion irregularly alternate with periods of subterranean drainage towards the sea. The chambers located further inland, which are permanently stratified and free of sessile filter-feeders, seem to be occupied only by the new species (see Fig. 1C). In addition, it is noticeable that the degree of euryhalinity of the new species seems higher than in *S. margalefi*, the latter species having never been caught in water with salinity lower than 24‰ (Gràcia *et al.*, 2003, and current observations). There is a remarkable difference in body size between these congeners (cf. Fig. 9A and 9B) from which we could infer the existence of some type of resource partitioning between them. Although *Stephos* appear to be unspecialised particle feeders, the peculiar mandibular cutting edge of *S. margalefi* (see below) suggests it has a more specialised food regime than the new species.
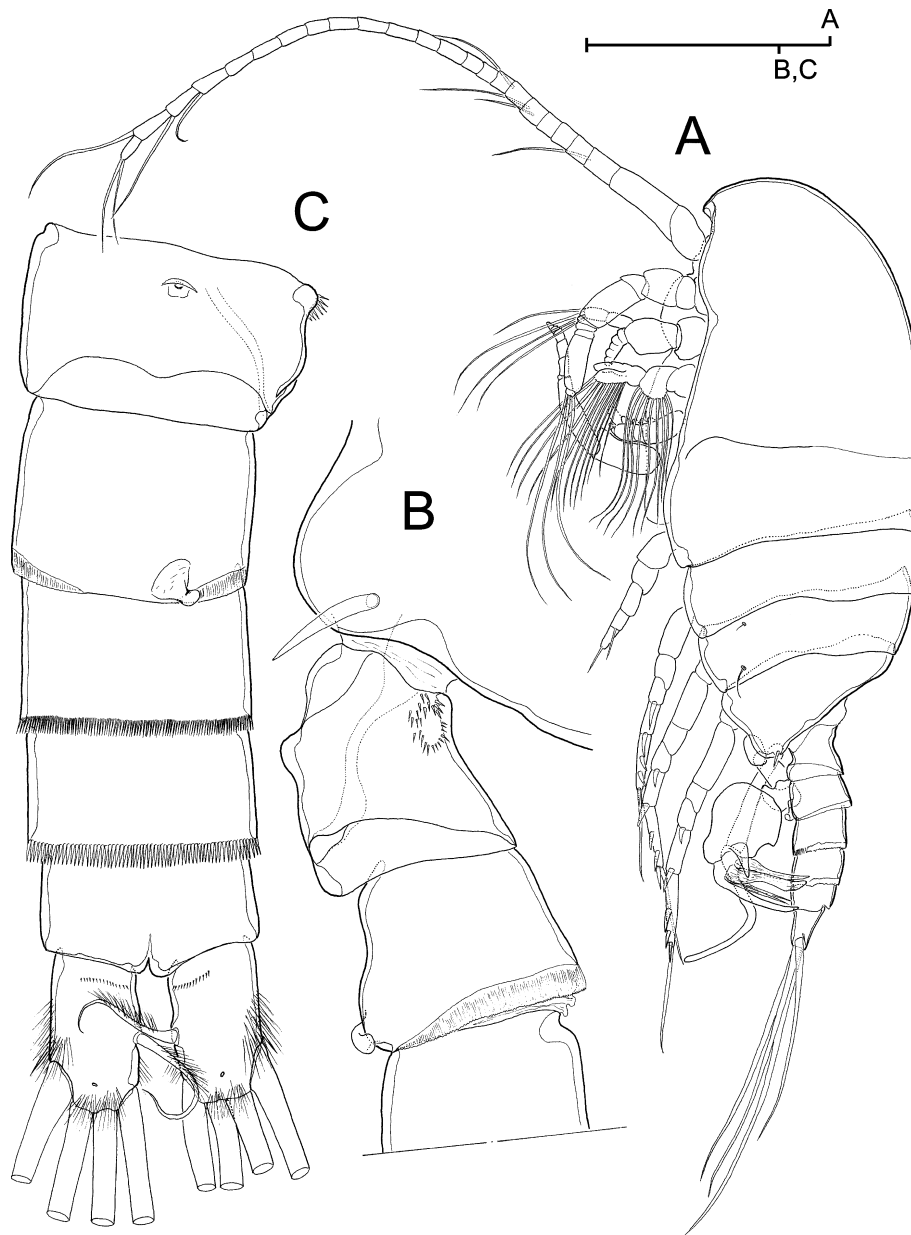
Figure 11 *Stephos margalefi* Riera, Vives & Gili, 1991, adult male. A, left lateral aspect; B, detail of proximal part of urosome and last prosomite, lateral view from left side; C, urosome, ventral. Scale bar: 0.25 mm (A); 0.05 mm (B, C).

Stephos margalefi Riera, Vives & Gili, 1991 (emend.),
(Figures 9B–15)
Stephos balearensis Carola & Razouls, 1996: 344–348;
Fig. 1
Stephos baleariensis Carola & Razouls, loc. cit.: 344.
Razouls, 2005: www.copepodes.obs-banyuls.fr

Material examined

Cova de la Catedral (Capdepera, Majorca; UTM coordinates: 539360/31 4394200). Two adult female topotypes [BMNH reg. nos. 2006.554–555]. Collected by F. Gràcia and D. Jaume, 2 April 2006.

Cova des Coll (Portocolom, Majorca): About 100 specimens, both sexes [MNCM-368]. Collected by F. Gràcia and D. Jaume, 21 December 2004.

Cova Genovesa (Portocristo, Majorca; UTM coordinates: 527170/31 4375440): several specimens of both sexes; material accidentally lost. Collected by F. Gràcia and D. Jaume, 28 July 2002.

Cova del Dimoni (Portocristo, Majorca; UTM coordinates: 530013/31 4377359): 2 males and 1 female (MNCM-206). Collected by G.A. Boxshall and D. Jaume, 21 August 1998.

Cova de na Mitjana (Capdepera, Majorca; UTM coordinates: 539010/31 4390710): 1 female (MNCM-364). Collected by G.A. Boxshall and D. Jaume, 24 July 1997.

Es Secret des Moix (Manacor, Majorca; UTM coordinates: 31 4365750/523925): At small lake directly connected to sea, 1 male and 1 female (MNCM-365). Collected by G.A. Boxshall and D. Jaume, 24 July 1997.
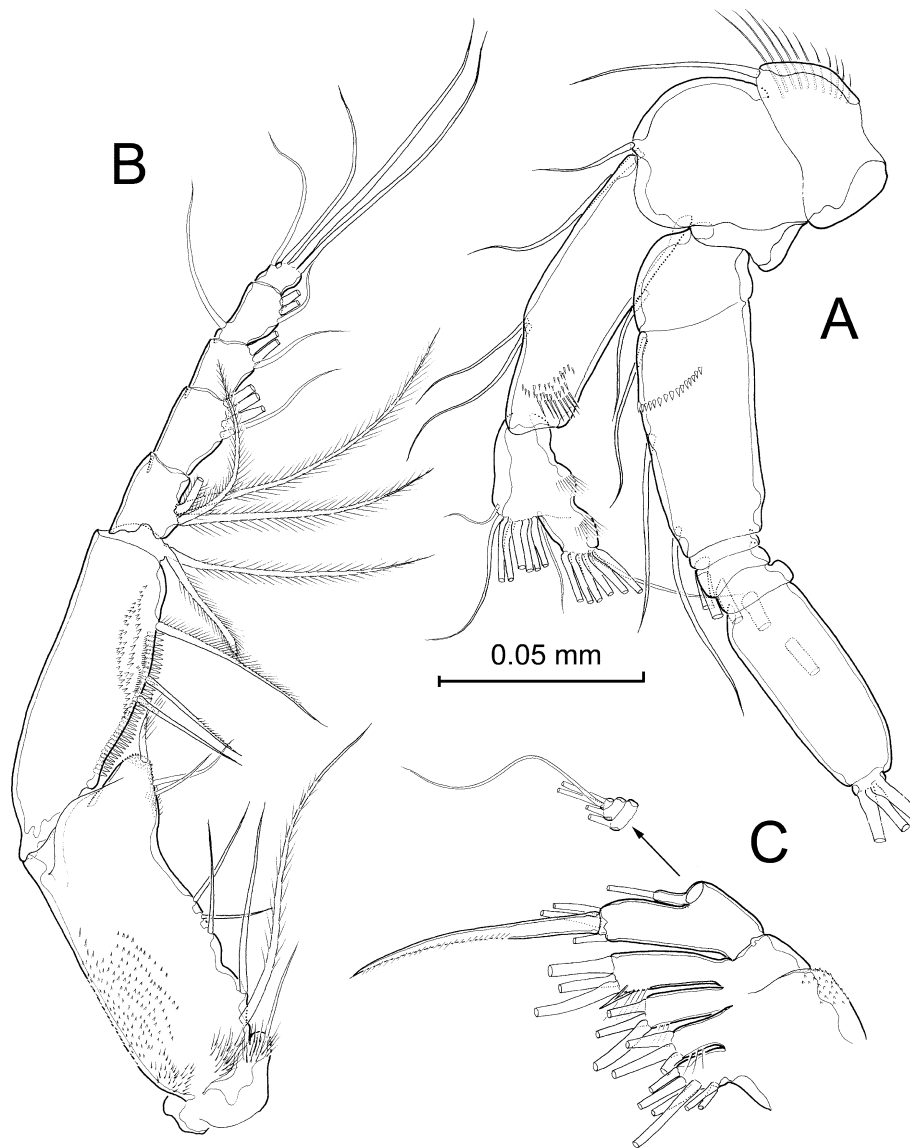
Figure 12 *Stephos margalefi* Riera, Vives & Gili, 1991, adult male. A, left antenna, lateral; B, right maxilla with disarticulated free endopod, lateral; C, right maxilliped, medial.

Cova de sa Llumeta (Conillera islet, Cabrera archipelago; UTM coordinates: 31 4337312/496567): 2 females (MNCM-366). Collected by D. Jaume, 10 August 1993.

Description of adult male

Body (Figs 9B, 11A) with a mean length of 0.77 mm (range 0.74 to 0.80 mm based on 5 specimens). Prosome similar in major features to preceding species, but widest at level of cephalosome (instead of at first pedigerous somite); asymmetry of last prosomite more pronounced, with left side (and not right) extended posteriorly; in addition, subterminal spines on last prosomite stout and conspicuous (Fig. 10A).

Urosome differing in presence of patch of spinules anterodorsally on left side of genital somite (right in preceding species; Fig. 11B, C) and of blunt recurved outgrowth ventrolaterally on left side of first free abdominal somite (see Fig. 11A–C). Hyaline anal operculum faintly serrate (Fig. 10B). Caudal rami (Fig. 10B) with 3 transverse rows

of spinules dorsomedially; seta V longer than rest; seta II apparently retained, partially hidden within patch of spinules at ventrolateral corner of ramus.

Antennules (Fig. 9C) similar to preceding species except for armature of segment 1, bearing 2 additional setae (corresponding to armature of ancestral segment I), and 2 combs of spinules instead of only 1; in addition, proximal aesthetasc more slender than in *S. vivesi*, and transverse row of triangular spinules located close to aesthetasc (see Fig. 9D). Spinules comprising oblique combs on all segments shorter, stouter and triangular in outline (Fig. 11D), differing from new species, in which they are needle-like.

Antennae (Fig. 12A) similar to preceding species except for: (1) presence of additional seta on subdistal lobe and 2 transverse rows of spinules on lateral margin of distal segment of endopod (cf. 1 in *S. vivesi*); (2) patch of spinules subdistally on lateral surface of proximal segment of endopod; (3) transverse row of triangular denticles proximally on medial
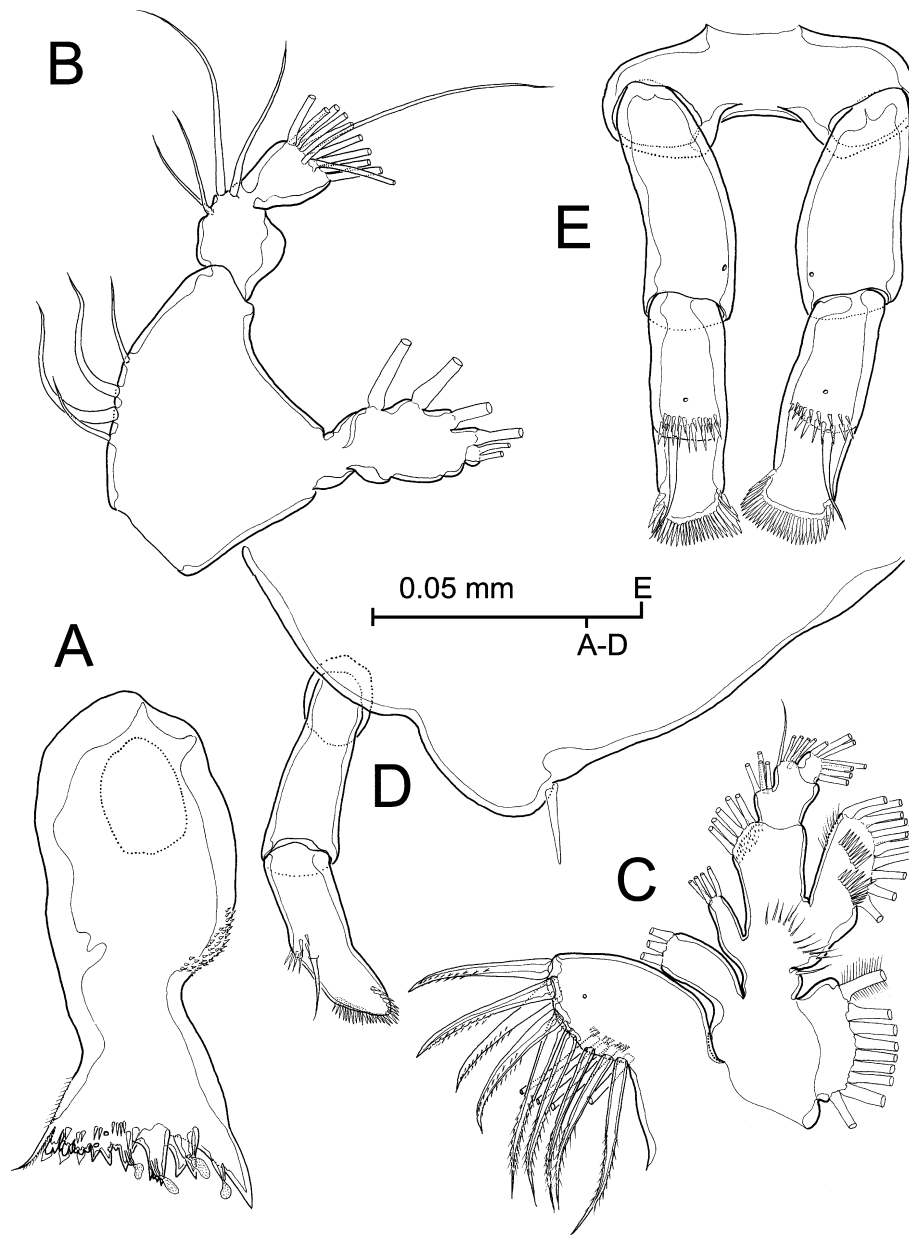
Figure 13 *Stephos margalefi* Riera, Vives & Gili, 1991. A, adult male mandible gnathobase (note drops of unidentified substance extruded from pores on cutting edge); B, mandibular palp; C, right maxillule, anterior; D, adult female lateral view of last prosomal somite and left fifth leg; E, adult female fifth legs, anterior.

margin of exopodal segment 2 (row on segment 1 in *S. vivesi*); and (4) comb of long spinules on coxa. Intersegmental articulations between exopodal segments 1–2 and between 6–7 not fully expressed.

Mandibular gnathobase (Fig. 13A) with spinules of subdistal row on ventral margin shorter than in preceding species. Patch of triangular denticles about midway along dorsal margin. Cutting edge comprising 9 unequal teeth, either uni-, bi- or tricuspidate (as figured). Four more dorsal teeth each with tubular extension ending in apparent secretory pore (still retaining drops of unidentified substance stippled in Fig. 13A). Three teeth situated more ventrally with hyaline tip. Two pores and several rows of spinules present proximally to ventral teeth. Mandibular palp (Fig. 13B) with 1 additional terminal seta on

endopod than in *S. vivesi*. Proximal seta on basis apparently smooth.

Maxillule (Fig. 13C) differing from preceding species in presence of 1 additional spine on praecoxal arthrite, in expression of basal exite seta, and in 1 additional seta subdistally on endopod. Integumentary ornamentation of segments differing also, as follows: 2 conspicuous oblique rows of stout spinules on anterior surface of exopod; patch of tiny denticles on anterior surface of distal basal endite; and 3 clusters of tiny denticles near insertion of 4 setae of praecoxal arthrite, on posterior surface.

Maxilla (Fig. 12C) differing from preceding species in display of additional seta on praecoxal endite and of acute pointed process on distal coxal endite.
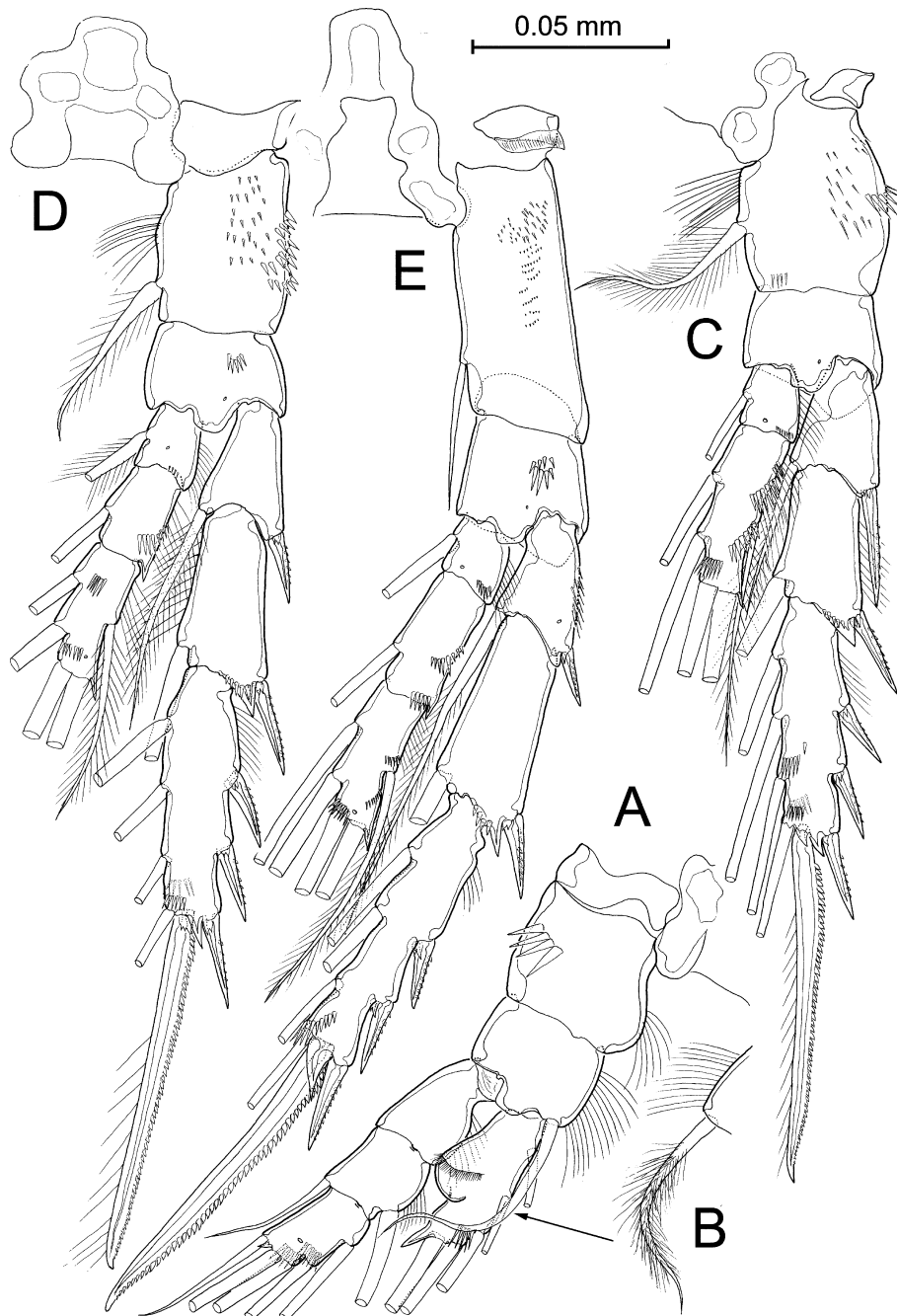
Figure 14 *Stephos margalefi* Riera, Vives & Gili, 1991, adult male. A, right leg 1, anterior; B, detail of posterior ornamentation on inner basal seta of latter; C, left leg 2, anterior; D, left leg 3, anterior; E, left leg 4, anterior.

Maxilliped (Fig. 12B) differing from *S. vivesi* in expression of seta on proximal syncoxal endite, morphology of brush-like seta on distal endite of latter segment (less stout), morphology of 1 seta on endopodal segment incorporated into basis (with spatulate tip), and by richer integumentary ornamentation on syncoxa and basoendopod (cf. Figs 12B and 5F).

Swimming legs 1–4 with armature formula as in preceding species. Differing mainly in details of integumentary ornamentation (cf. Figs 14 and 6).

Fifth legs (Figs 10C, 11A) asymmetrical, both uniramous and 4-segmented. Right leg rather filiform, with third segment slightly expanded basally, displaying pointed process on lateral margin; fourth segment S-shaped, with rounded tip, displaying short needle-like seta plus pore proximally on posterior surface (Fig. 10D). Left leg with proximal segment bearing pore on anterior surface; third segment globose, with 2 pointed processes, one recurved and acute proximally on medial margin, other stouter, placed subdistally on lateral margin (Fig. 10E); 1 reduced spine proximally on lateral margin of segment; fourth segment small, with stout pointed process curved posteriorly on medial margin, and 4 hyaline lamellae as in Fig. 10E.

Description of adult female

Body (Fig. 15A) apparently larger than male, with mean length of 0.82 mm, range 0.77 to 0.85 mm (based on 5 specimens) and similar to it in all major features except for urosomal
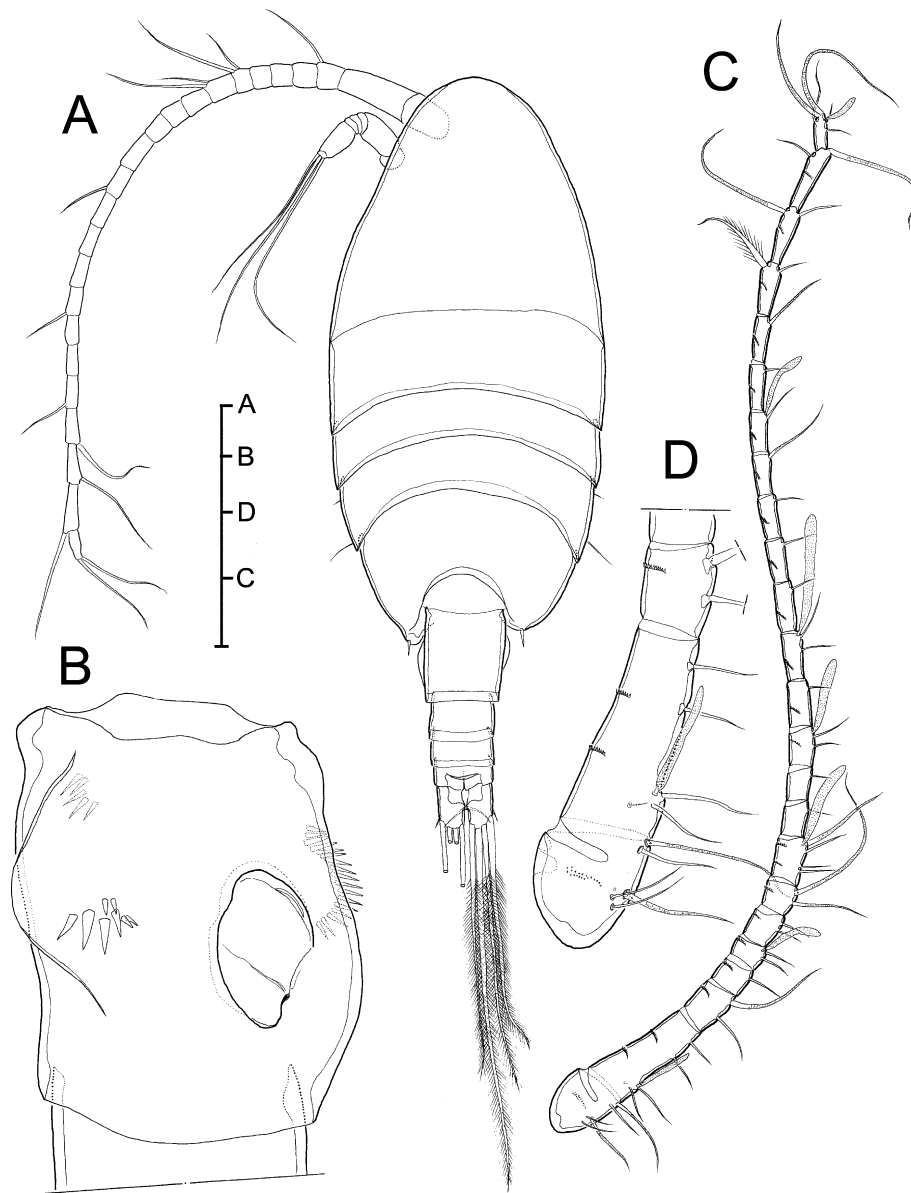
Figure 15 *Stephos margalefi* Riera, Vives & Gili, 1991, adult female. A, dorsal aspect; B, detail of genital double-somite, ventral; C, right antennule, ventral; D, detail of proximal part of latter, ventral. Scale bar: 0.25 mm (A); 0.05 mm (B–D).

segmentation, armature of antennule and morphology of fifth legs. Urosome (Fig. 15A) 4-segmented, genital double-somite asymmetrical, with ventrolateral bulge on right side and 3 rows of stout spinules as in Fig. 15B. Only single genital opening expressed externally, on left side, with single copulatory pore almost completely exposed anteriorly on margin of genital area, plus operculum placed ventrolaterally covering gonopore.

Antennule (Fig. 15C, D) differing from male (cf. Fig. 9) in displaying fewer aesthetascs (only 1 on segment 1, and none on segments 2, 6, 16, 19 and 20) and in presence of 2 spinulose combs on segment 7. In addition, distal spinulose comb on segment 1 is not positioned as far distally as in male, and 2 proximal setae on this segment are not as reduced (Fig. 15D).

Fifth legs (Fig. 13E) symmetrical, uniramous, 3-segmented with proximal segment fused to intercoxal sclerite. Legs truncate distally, although appearing misleadingly pointed when viewed in lateral aspect (cf. Fig. 13D and E). First and second segments unarmed, second with pore anteromedially; third segment slightly longer than preceding segment, with fan-like comb of spinules along truncate distal margin, seta, 2 parallel rows of spinules, and pore positioned on anterior surface about midway of segment; seta implanted towards lateral margin, not extending beyond segment distally.

Remarks

Stephos margalefi is unique in the genus in possessing the basal exite seta on the maxillule and in having a 4-segmented (vs. 5-segmented) male left fifth leg; the latter condition is the result of the failure to express the inter-segmental articulation between ancestral segments 3 and 4. In addition, it is the only *Stephos* with segment 3 of the male left leg 5 (fused to fourth segment) displaying any armature, viz. a tiny spine on the lateral margin, and a pointed process on the medial margin. Apart from these unique features, the new species can be

grouped within a species cluster characterised by having both male fifth legs 5-segmented, and the (ancestral) fourth segment of the left leg swollen. This cluster comprises 14 species (excluding *S. balearensis*; see below) occurring in all oceans except at high latitudes (see Bradford-Grieve, 1999; Zagami *et al.*, 2000). In the Mediterranean, the closest relative to *S. margalefi* is the Sicilian *S. cryptospinosus*, from which it differs in the morphology of the distal segment of both left and right male fifth legs (right bifid, left with about 14 hyaline lamellae in *S. cryptospinosus*; vs. right not bifurcate, left with only 4 hyaline lamellae in *S. margalefi*), among other features. *Stephos canariensis* Boxshall, Stock and Sánchez, 1990, from the nearby Canary Islands and which belongs to the same group of species, differs from *S. margalefi* in the bifid distal segment of the male right fifth leg, and in the lack of hyaline lamellae on the distal segment of the left leg (see Boxshall *et al.*, 1990).

The ventrolateral process on the first abdominal somite of the male *S. margalefi* is displayed in several other species, including *S. hastatus* Bradford-Grieve, 1999, *S. pacificus*, *S. morii* and *S. marsalensis*; its function is not known.

As mentioned above, two species of *Stephos* were described based on females only. *Stephos margalefi* can be separated from both as follows: it differs from *S. exumensis* in the absence of the dorsolateral process on the right side of the female genital double-somite, and in the morphology of the distal segment of fifth legs, which have a truncate and not acutely pointed distal margin, among other features (see Fosshagen, 1970). *Stephos simillimus* is a *species inquirendum* of doubtful stephid affinity.

The presence of pores on several of the teeth on the cutting edge of the mandible is interesting. Miller *et al.* (1990) noted pores opening on the mandibular cutting edge of suspension feeding copepods of the genera *Calanus* Leach, 1819 and *Neocalanus* Sars, 1925. They traced ducts from the pores to small subintegumentary glands and suggested that the exudates might be either toxins or aids to digestion. Nishida and Ohtsuka (1996) showed profound modifications to the mandibles in some carnivorous heterorhabdids. The ventralmost tooth formed a tubular hypodermic needle-like, delivery mechanism, which served to inject secretion, possible venom, into prey. However, the glands producing the secretion were contained within the labrum, rather than in the mandible itself. The function of the pores in *S. margalefi* is unknown.

Stephos margalefi was described based on material caught in a single submarine cave on the NE corner of Majorca (Riera *et al.*, 1991). The description was very basic, although it clearly depicted the diagnostic male fifth legs of the species, with a 4-segmented left ramus showing the penultimate (compound) segment inflated, and with the right ramus filiform, its distal segment not forked and bearing a tiny marginal seta proximally (see Riera *et al.*, 1991: fig. 6b). The species was later reported from an anchialine cave of the eastern coast of the island (Gràcia *et al.*, 2003), and was also known to occur (G.A. Boxshall and D. Jaume, pers. obs.) in other caves of the Majorcan SE littoral and the small islet of Conillera (Cabrera archipelago, off south Majorca; see Fig. 1A). All these specimens conform well to the description of *S. margalefi* regarding the male fifth legs, but the female fifth legs displayed a trun-

cated distal margin with a row of spinules (Fig. 13D, E) instead of the pointed tip shown in Riera *et al.* (1991: fig. 6a). In addition, none of these specimens displayed 2 inner coxal spines on leg 3 as shown for *S. margalefi* in the original description (Riera *et al.*, 1991: fig. 5) – a feature otherwise unknown in copepods, which display a maximum of 1 setal element at this position (see Huys & Boxshall, 1991). Instead, the putative *S. margalefi* specimens displayed an ordinary seta plus a transverse row of long and coarse setules along the inner margin of the coxa (Fig. 14D).

These differences raised the question of whether these specimens represented a new species or belonged to *S. margalefi*, the original description would then be shown to be inaccurate. Since the type material of *S. margalefi* is apparently lost (see Razouls, 2005), we re-sampled at the type locality (La Catedral cave in Capdepera) in search of topotypic material to make comparisons. Based on study of this supplementary material – now in the collections of the Zoology Department, The Natural History Museum, London – all the *Stephos* material from the Majorcan SE coast and from the neighbouring Cabrera archipelago is here assigned to *Stephos margalefi*.

Stephos balearensis, a second Balearic species of *Stephos*, was described from a single anchialine cave on the Minorcan SE littoral, about 65 km to the NE of the type locality of the Majorcan *Stephos margalefi* (Carola & Razouls, 1996; see Fig. 1A). Bradford-Grieve (1999: 15) noted that the mouthparts of this species apparently displayed unusually low numbers of armature elements compared to other representatives of the genus. However, the fifth legs of both sexes figured by Carola and Razouls (1996) in the original description appear identical to those of *S. margalefi* as described above. Indeed, the conspecificity of these two taxa was suspected by Razouls (2005), who could not confirm this since the type material of *S. margalefi* was lost. We were unable to locate the type material of either *S. margalefi* or *S. balearensis* but we also tentatively consider the latter to be a junior synonym of *S. margalefi*.

Stephos margalefi displays a broad distribution along the eastern coast of the so-called Balearic Promontory (see Fig. 1A). It seems to be a strict thalassostygobiont inhabiting caves with water that scarcely differs from the full marine salinity. It has never been caught in plankton or hyperbenthic hauls in Balearic coastal waters outside caves. In Cova des Coll, it is always found below 2 m depth, in water of salinity greater than 24‰, whereas at Cova Genovesa, an anchialine cave covering an almost full range of salinity from 4 to 37.5‰, it was found only in waters of salinity in excess of 34‰ (see Gràcia *et al.*, 2003).

The disjunct distribution of this apparently stygobiont species, embracing three different islands, does not pose any biogeographical problem since all three comprised a single island as recently as 17 000 yr BP, at the time of the last glacial maximum when a global marine regression of up to 140 m took place (see isobaths in Fig. 1A).

Acknowledgements

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