Centropages orsinii Giesbrecht, 1889 (Copepoda, Calanoida, Centropagidae) from an anchialine cave in Vanuatu

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Boxshall G. A. & Jaume D. 2012. — *Centropages orsinii* Giesbrecht, 1889 (Copepoda, Calanoida, Centropagidae) from an anchialine cave in Vanuatu. *Zoosystema* 34 (2): 377-387. http://dx.doi.org/10.5252/z2012n2a11

ABSTRACT
The adult male of *Centropages orsinii* Giesbrecht, 1889 is redescribed based on a single specimen collected in an anchialine cave on the island of Espiritu Santo in Vanuatu. The mouthparts of this species have never previously been described and figured. Males exhibit a remarkable asymmetry in the form of the basis of leg 4. On the right leg only the basis carries three processes on its posterior surface, a unique asymmetry for the entire Calanoida. Comparison with males from other locations in the Indo-Pacific reveals some variation in the precise form of these processes. Some other species of *Centropages* exhibit sexually dimorphic asymmetry, with modified setation elements present on the exopod of right leg 4 only in males. It is speculated that this might be correlated with the strong asymmetry exhibited in females of some species within the genus.

KEY WORDS
Centropages,
Vanuatu,
anchialine cave,
morphology,
male.

RÉSUMÉ
Centropages orsinii *Giesbrecht, 1889 (Copepoda, Calanoida, Centropagidae) originaire d'une grotte anchialine du Vanuatu.*
Le mâle adulte de *Centropages orsinii* Giesbrecht, 1889 est redécrit, à partir d'un spécimen unique, collecté dans une grotte anchialine de l'île d'Espiritu Santo, au Vanuatu. Les pièces buccales de cette espèce n'avaient jamais été décrites et illustrées auparavant. Les mâles possèdent une asymétrie remarquable de la forme de la base de la patte 4, unique pour tous les Calanoida. La patte droite porte à sa base trois protubérances sur sa face postérieure. La comparaison avec des mâles originaires d'autres localités dans la région indo-pacifique révèle quelques variations dans la forme précise de ces protubérances. D'autres espèces de *Centropages* possèdent un dimorphisme sexuel, avec une asymétrie des éléments de sétation modifiés présents sur l'exopode de la patte 4 droite, uniquement chez les mâles. Cela pourrait être lié à la forte asymétrie présente chez les femelles de certaines espèces de ce genre.

MOTS CLÉS
Centropages,
Vanuatu,
grotte anchialine,
morphologie,
mâle.

INTRODUCTION

Calanoid copepods are one of the dominant taxa in anchialine habitats around the coastal margins of tropical and subtropical islands. Recent studies on families such as the Epacteriscidae Fosshagen, 1973 and Ridgewayiidae Wilson, 1958 have revealed a rich assemblage of new genera and species from anchialine habitats (Fosshagen *et al.* 2001; Fosshagen & Iliffe 2003). Other calanoid families, for example, the Pseudocyclopiidae Sars, 1902, Arietellidae Sars, 1902 and Stephidae Sars, 1902, are also commonly represented in such habitats, but often by genera that are not strictly stygobiont, as they also utilise open marine hyperbenthic habitats typically in shallow-water (Ohtsuka *et al.* 1994; Jaume & Boxshall 1995; Jaume *et al.* 2008). Representatives of typical neritic zone planktonic calanoid families, such as the Acartiidae Sars, 1900, Centropagidae Giesbrecht, 1893, Pontellidae Dana, 1853, Temoridae Giesbrecht, 1893 and Tortanidae Sars, 1902, are rarely reported from anchialine caves.

During the SANTO 2006 expedition to the island of Espiritu Santo in Vanuatu (for a narrative and background of the expedition, see Bouchet *et al.* [2011a], and for a review of the geography and natural history of Santo, see Bouchet *et al.* [2011b]), the biodiversity inventory work of the karst team (Deharveng & Sémah 2011) provided the opportunity to collect copepod and other crustaceans in caves along the eastern part of the island. Only a single anchialine habitat, Loren cave, was explored in detail. Its opening is located at 14°58.850'S, 167°03.553'E on the east coast of Cape Queiros. The salinity-depth profile of Loren cave waters showed two haloclines: there was a surface layer of fresh to brackish water above a weak upper halocline at 8-10 m depth where salinity jumps from about 5 to 7 ppt, below which salinity gradually increases to about 10 ppt at a depth of 25 m where a second halocline exists marking an abrupt increase to 28 ppt (near full seawater) by 27 m depth (Bréhier *et al.* 2011). In the deep marine samples a single adult male calanoid copepod was collected by the dive team. This male was at first thought to represent a new species of *Centropages* Krøyer, 1849 (Boxshall & Jaume 2011), but is identified here as *Centropages orsinii* Giesbrecht, 1889. This species is widely distributed in the Indo-Pacific, from the Red Sea through the Indian Ocean to the Pacific, including Indonesian and Australian waters (summarised in Mulyadi 2004). The male is fully described here for the first time and the nature of the unique sexually dimorphic asymmetry of the fourth legs is characterised in detail.

MATERIAL AND METHODS

The male copepod was caught using a hand-held plankton net hauled through a narrow horizontal range. It was collected by the dive team of Franck Bréhier, Stefan Eberhard and Nadir Lasson, in September 2006 in the flooded section of Loren cave (Lotoror district), Espiritu Santo, Vanuatu. The entrance to the cave is located at 14°58.850'S, 167°03.553'E. The specimen was fixed in the field, transferred to 80% ethanol, and studied as a temporary preparation dissected in lactophenol. Drawings were prepared using a drawing tube on a Leitz Diaplan microscope equipped with differential interference contrast. Body length measurements include caudal rami, but not their setae. The male from Santo is deposited in the collections of the Department of Zoology, the Natural History Museum, London (BMNH). The terminology used in the description follows Huys & Boxshall (1991).

Comparative material of *Centropages orsinii* from the John Murray expedition and from the Great Barrier Reef expedition was examined from the collections of the Natural History Museum, London.

SYSTEMATICS

Order CALANOIDA G. O. Sars, 1903
Family CENTROPAGIDAE Giesbrecht, 1893
Genus *Centropages* Krøyer, 1849

Centropages orsinii Giesbrecht, 1889
(Figs 1-5)

NEW MATERIAL EXAMINED. — Vanuatu, Espiritu Santo, E coast of Cape Queiros, Loren cave, 14°58.850'S, 167°03.553'E, 1 ♂, IX.2006, F. Bréhier, S. Eberhard and N. Lasson (BMNH Reg. no. 2011.1266).

OTHER MATERIAL EXAMINED. — South Arabian coast, stn 56, John Murray expedition, surface net, 1 ♂, 4.XI.1933 (BMNH Reg. no. 1949.12.31.352). — Great Barrier Reef, 5 stations inside reef east of Low Island, stns 45 and 50 outside reef, 10 ♀♀, 8 ♂♂, Great Barrier Reef expedition (BMNH Reg. no. 1948.4.28.72)

TYPE LOCALITY. — Red Sea.

DESCRIPTION OF ADULT MALE

Body (Fig. 1A) 1.54 mm in length. Prosome comprising cephalosome and five pedigerous somites: cephalosome and first pedigerous somite separated by complete suture line. Functional articulation retained between somites 4 and 5, with posterolateral corners of pedigerous somite 5 slightly pointed and slightly asymmetrical in dorsal aspect, extending posteriorly further on left side (Fig. 1B). Rostrum weakly developed, broadly triangular, with large pair of frontal filaments directed postero-ventrally (Fig. 1C). Body widest at first pedigerous somite, ratio of prosome to urosome length *c.* 2.65: 1. Urosome 4-segmented; genital somite symmetrical, with single gonopore opening posterolaterally on left side ventral surface; somite lacking surface ornamentation. Ratio of lengths of urosomites and caudal rami: 1.00: 1.50: 1.23: 1.09: 1.66; anal somite slightly shorter than 2 preceding free abdominal somites; anus opening terminal, located between caudal rami, anal operculum absent. Caudal rami (Fig. 1B) symmetrical, 2.3 times longer than wide, with four long plumose setae along distal margin, one medium-length seta distally on outer margin, and one reduced seta (seta VII) located on dorsal surface near inner distal angle; seta I absent.

Antennules (Fig. 2) long and asymmetrical. Left antennule (Fig. 2A-C) non-geniculate, extending about to level of second urosomite (Fig. 1A), indistinctly 24-segmented with all articulations expressed, except between segments II-IV and XXVI-XXVIII; articulation between segments I and II incompletely expressed. Armature formula as follows: segment 1 (ancestral segment I), 2 + ae; segment 2 (corresponding to compound ancestral segments II-IV), 2 setae + 2 aesthetascs; segment 3 (V), 2 + ae; segment 4 (VI), 2 + ae; segment 5 (VII), 2 + ae; segment 6 (VIII), 1 + ae; segment 7 (IX), 2 + ae; segment 8 (X), 2 + ae; segment 9 (XI) 2 + ae; segment 10 (XII), 2 + ae; segment 11 (XIII), 1 + ae; segment 12 (XIV), 2 + ae; segment 13 (XV), 2 + ae; segment 14 (XVI) to 19 (XXI), 2 + ae, each; segment 20 (XXII), 1 + ae; segment 21 (XXIII), 1 seta; segment 22 (XXIV), 1 + 1; segments 23 (XXV), 1 + 1 + ae; segment 24 (composed XXVI-XXVIII), apical setation incomplete.

Right antennule (Fig. 2D-F) geniculate, 21-segmented, but with articulation between segments I and II incompletely expressed as in left antennule. Armature as follows: segment 1 (ancestral segment I), 2 + ae; segment 2 (corresponding to compound ancestral segments II-IV), armature incomplete; segment 3 (V), 2 + ae; segment 4 (VI), 2; segments 5 (VII) to 7 (IX), 2 + ae each; segment 8 (X), 1 + ae; segment 9 (XI) 2 + ae; segments 10 (XII) and 11 (XIII), 1 + ae each; segment 12 (XIV), 1 seta, 1 spine + ae; segment 13 (XV), 2 + ae; segment 14 (XVI), 1 seta, 1 spine + ae; segments 15 (XVII) and 16 (XVIII), 2 + ae, each; segment 17 (XIX), 1 + ae; segment 18 (XX), 1 seta; segment 19 (XXI-XXIII), 1 + 2 modified spines (but scars indicating 2 elements missing); segment 20 (XXIV-XXV), 2 + 2; segment 21 (XXVI-XXVIII), 6 + ae. Spinule rows present on segments XIX and XX, and on segment XXI, either side of geniculation.

Antenna (Fig. 1D) biramous. Coxa short, bearing plumose seta at distomedial angle. Basis with two subequal plumose setae on distomedial angle. Exopod indistinctly 7-segmented: segmental homologies I, II-IV, V, VI, VII, VIII, IX-X; intersegmental articulations between segments V to VII partially expressed; setal formula as follows: 1, 3, 1, 1, 1, 1, 1 + 3. All setae plumose. Endopod 2-segmented: proximal segment with two unequal, naked setae; compound distal segment expanded into medial lobe bearing seven setae, and with distal portion crowned with seven setae; segment ornamented with transverse row of long spinules subdistally on lateral margin.

Mandibular gnathobase (Fig. 3B) with cutting edge comprising eight cuspidate or simple teeth plus dorsal spinulose seta; ventralmost tooth largest, smooth and unicuspid. Ornamented with row of short spinules on surface near teeth. Palp (Fig. 3A) biramous, basis with four setae on inner margin, proximalmost seta unipinnate, other three setae naked. Exopod 5-segmented, setal formula 1, 1, 1,

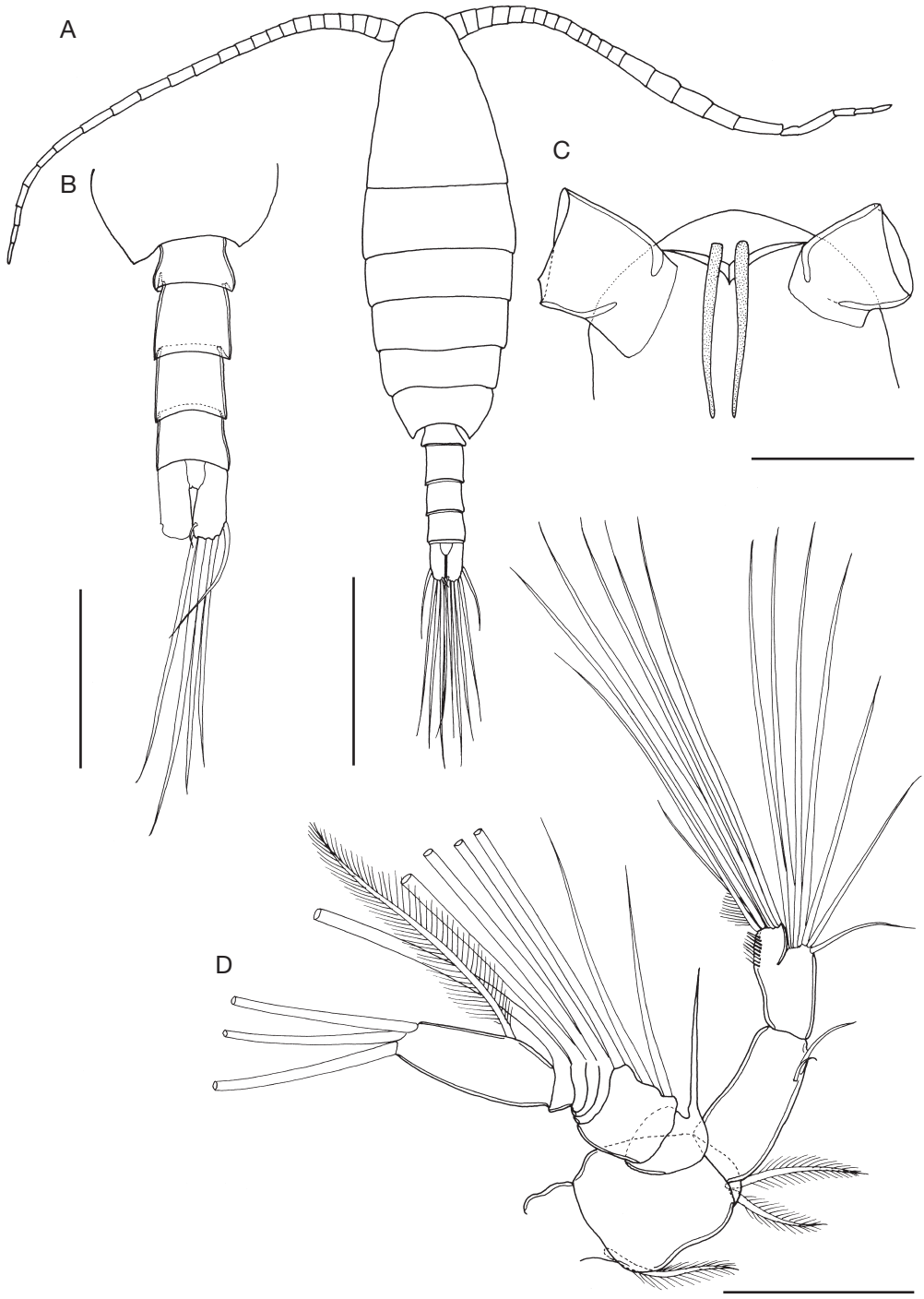

Fig. 1. — *Centropages orsinii* Giesbrecht, 1889 adult male: **A**, habitus, dorsal; **B**, last prosomite and urosome, dorsal; **C**, rostrum and frontal filaments, ventral; **D**, antenna. Scale bars: A, 0.05 mm; B, 250 µm; C, D, 100 µm.

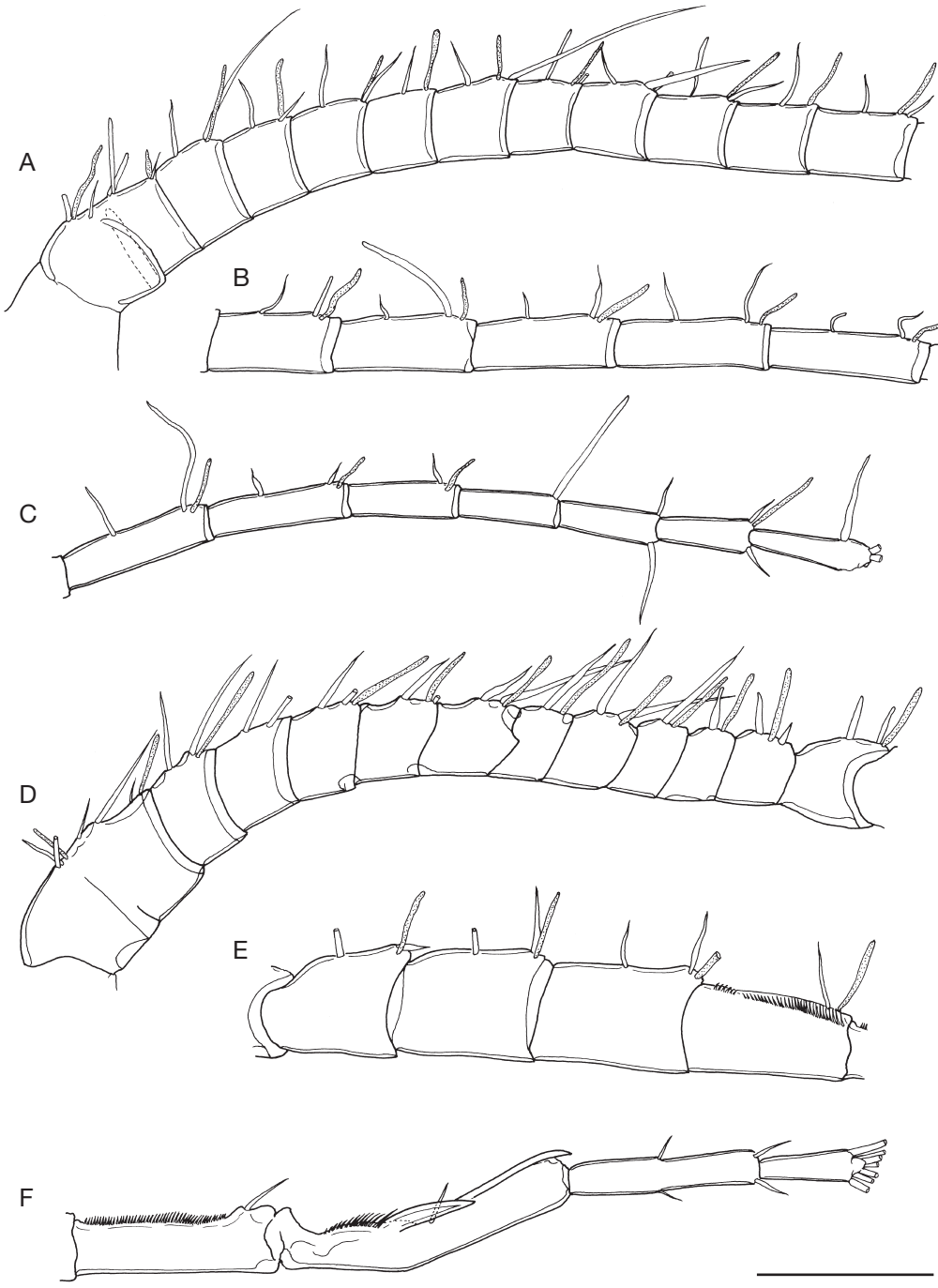

FIG. 2. — *Centropages orsinii* Giesbrecht, 1889 adult male: **A**, non-geniculate left antennule, expressed segments 1 to 12; **B**, left antennule, expressed segments 13 to 17; **C**, left antennule, expressed segments 18 to 24 (some setal elements missing from apex); **D**, geniculate right antennule, expressed segments 1 to 13; **E**, right antennule, expressed segments 14 to 17; **F**, right antennule expressed segments 18 to 21 (setal elements missing from segment 19, as indicated by scars). Scale bar: 100 µm.

TABLE 1. — Armature of legs of *Centropages orsinii* Giesbrecht, 1889.

	coxa	basis	exopodal segments	endopodal segments
Leg 1	0-1	0-I	I-1; I-1; II, I, 4	0-3; 1, 2, 3
Leg 2	0-1	0-0	I-1; I-1; III, I, 5	0-3; 2, 2, 4
Leg 3	0-1	0-0	I-1; I-1; III, I, 5	0-3; 2, 2, 4
Leg 4	0-1	0-0	I-1; I-1; III, I, 5	0-1; 0-2; 2, 2, 3

1, 2. Proximal endopodal segment with four setae at distomedial angle; distal segment with nine unequal setae, plus subapical transverse row of spinules.

Maxillule (Fig. 3C-D) with praecoxal arthrite carrying ten marginal spines plus four stiff setae on posterior surface. Coxal epipodite with nine setae; coxal endite with three spinulose setae. Basis fused to both rami: armed with four setae on proximal endite; distal basal endite with seven setae; basal exite represented by single vestigial seta. Exopod bearing eleven marginal setae. Endopod indistinctly 2-segmented, setal formula 4, 5.

Maxilla (Fig. 3E) indistinctly 7-segmented, comprising partially coalesced praecoxa and coxa, basis and 4-segmented endopod. Armature of praecoxal and coxal endites 5, 3, 3, 3, respectively; all bilaterally spinulate. Basal endite with four setae, one longer than others. Free endopod carrying seven setae in total. Long seta on basis and most setae on endopodal segments sparsely, bilaterally spinulate with spinules increasing in length distally.

Maxilliped (Fig. 3F) 7-segmented with syncoxa, basoendopod and free 5-segmented endopod. Syncoxa with 1, 2, 3, 4 setae on medial margin lobes, most setae sparsely bilaterally spinulate; small patch of denticles on medial surface proximal to seta of first syncoxal lobe. Basis about as long as syncoxa, with three plumose setae of basal origin plus two distal setae derived from incorporated first endopodal segment; row of strong spinules present along medial margin of segment proximal to basal setae. Free endopod setal formula: 4, 4, 3, 3 + 1, 4.

Swimming legs 1-4 (Figs 4A-C; 5A) biramous, with 3-segmented exopods: endopod 2-segmented in leg 1, indistinctly 2-segmented in legs 2 and 3, and 3-segmented in leg 4. Armature of legs: see Table 1.

Endopods of legs 2 and 3 with articulation between segments 1 and 2 only partially expressed. Inner basal seta on leg 1 short, only reaching to middle seta on compound proximal endopodal segment. Long setae on rami plumose; outer spines on distal exopodal segment of leg 1 flagellate; outer spines on legs 2 to 4 short and stout; terminal spine on exopod of each leg plumose internally and with marginal membrane externally. Outer margins of endopod segments with fine spinule rows; outer margins of second and third exopodal segments with row of fine spinules proximal to first spine. Leg 4 asymmetrical; basis of left leg unmodified, basis of right leg with three digitiform processes on outer and posterior surfaces (Fig. 5A, B).

Fifth legs (Fig. 5C) strongly asymmetrical. Left leg biramous, with relatively unmodified 3-segmented endopod, setal formula 0-1; 0-1; 2, 2, 2; exopod 2-segmented, heavily sclerotised; first segment with unilaterally serrate outer spine; second segment bearing 2 outer margin spines and with bilaterally serrate distal spine fused to segment; inner margin with spinule row. Right leg biramous, with endopod unmodified, exhibiting same setal formula as for left endopod; right endopod longer and wider than left. Exopod 3-segmented: first segment short, with outer spine and adjacent spinous process located at outer distal angle; second segment with large "thumb" process located proximally on inner margin – thumb process weakly-curved and about 10% longer than segment; outer spine very short and located on posterior surface of segment close to distal margin: third segment forming long, weakly-curved claw (often referred to as "terminal process") armed with slender seta on medial margin close to basal articulation.

DISCUSSION

There are currently 34 valid species of *Centropages* but only two, *C. orsinii* and *C. hyalinus* McKinnon & Kimmerer, 1988, share the possession of 2-segmented endopods on legs 1 to 3 whilst retaining 3-segmented endopods on legs 4 and 5. Both species also share the weakly asymmetrical and weakly pointed posterolateral angles on pedigerous somite 5; this character state is also shared with *C. sinensis* Chen & Zhang, 1965. However, *C. sinensis* has 3-segmented endopods

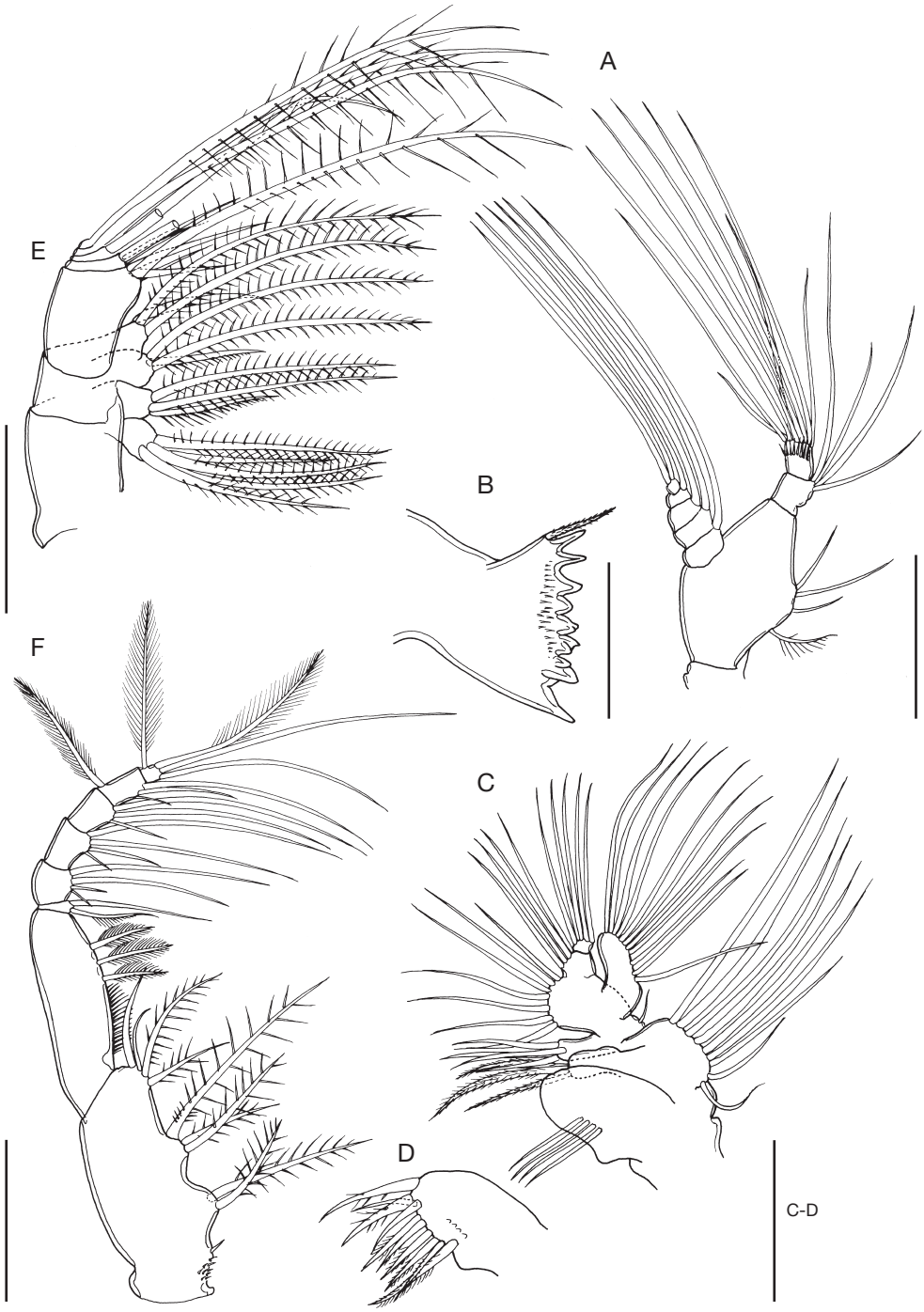

FIG. 3. — *Centropages orsinii* Giesbrecht, 1889 adult male: **A**, mandibular palp; **B**, mandibular gnathobase; **C**, maxillule, lacking marginal armature from praecoxal arthrite, posterior; **D**, praecoxal arthrite of maxillule showing margin setation (only insertion sites of posterior setae shown); **E**, maxilla (with two long endopodal setae drawn truncated for clarity); **F**, maxilliped. Scale bars: 100 µm.

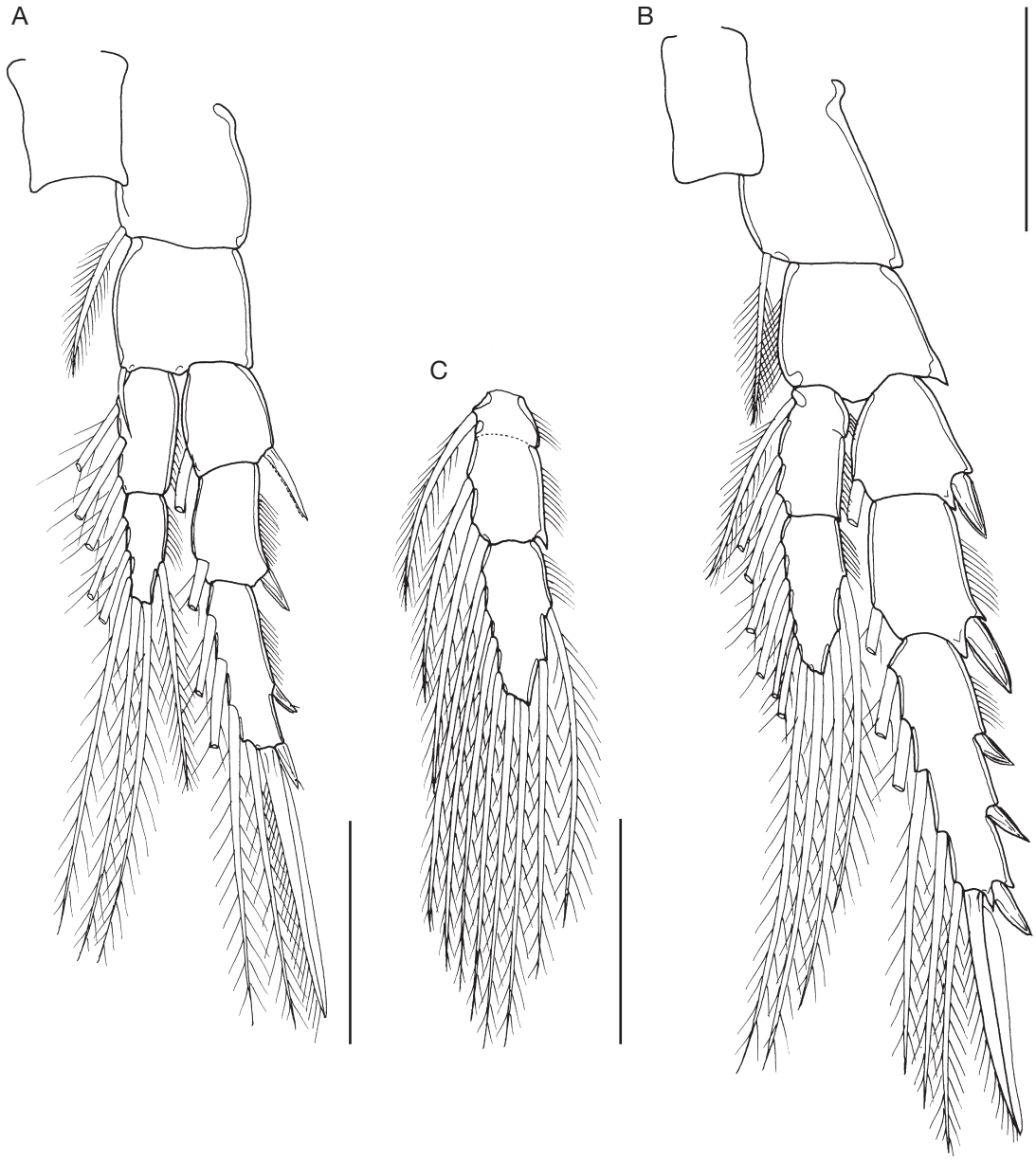

Fig. 4. — *Centropages orsinii* Giesbrecht, 1889 adult male: **A**, leg 1, anterior; **B**, leg 3, anterior; **C**, endopod of leg 2, anterior. Scale bars: 100 µm.

in legs 1 to 3 and possesses two terminal processes on the right fifth leg of the male.

On the basis of similarities in the male fifth legs, the specimen from Santo is identified as *C. orsinii* which was originally established from material collected from the Red Sea (Giesbrecht 1889). The original description was minimal comprising: "Ab omnibus generic speciebus differt primo cum secondo articulo rami 5^{ti} pedis interni conjuncto. ♀ 1,5-1,6 ♂ 1,25-1,3 mill." There were no illustrations.

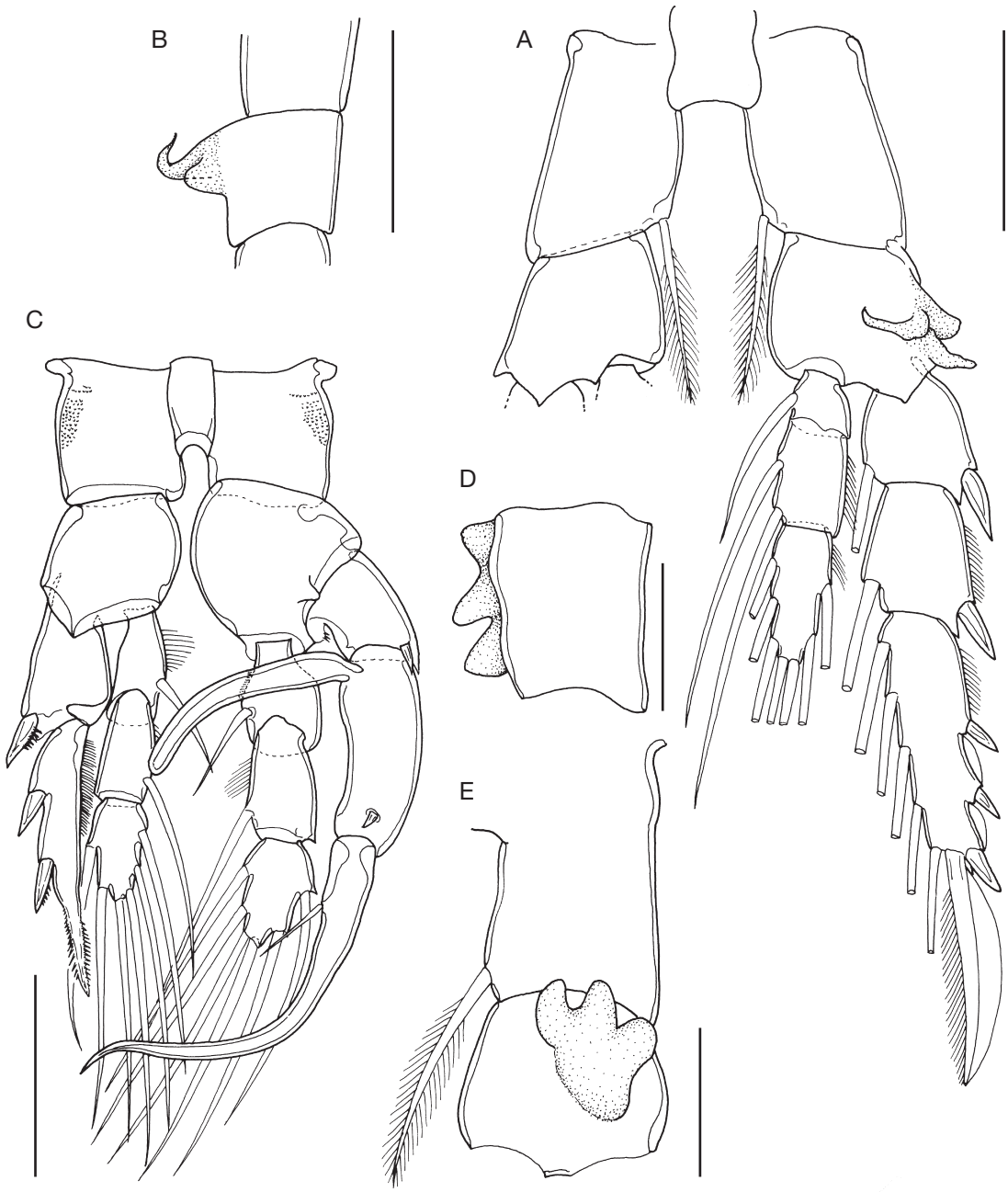

FIG. 5. — *Centropages orsinii* Giesbrecht, 1889 adult male: **A**, leg 4, posterior view showing right leg, with rami of left leg not drawn; **B**, basis of right leg 4, lateral view showing processes; **C**, leg 5, posterior view; **D**, basis of right leg 4 of male from John Murray expedition (BMNH 1949.12.31.352), lateral view showing processes; **E**, coxa and basis of right leg 4 of male from Great Barrier Reef expedition (BMNH 1948.4.28.72), posterior view showing processes on basis. Scale bars: A-C, 100 µm; D, E; 50 µm.

A more detailed description was published later by Giesbrecht (1893) who provided a formal diagnosis supported by figures of male habitus, female urosome, the fifth legs of both sexes, the male geniculate antennule and the female first leg. No modern full description has yet been published.

The most distinctive feature of *C. orsinii* has barely been mentioned in existing literature. The male exhibits a remarkable asymmetry in the fourth swimming leg: the basis of the right leg carries three digitiform processes on its posterior surface. No such processes are present on the left leg of the male or on either leg in the female. In his more detailed description of *C. orsinii*, Giesbrecht (1893: 321) noted the presence of these processes on the basis of male leg 4 stating "aber B 2 an der rechten Seite mit Fortsatz auf der Hinterfläche". The only illustration showing processes of the fourth leg is in Mulyadi (2004: fig. 75c) but it is labelled as a female leg 4. We presume that this is mislabelled since females from the Great Barrier Reef and John Murray expeditions in the collections of the Natural History Museum lack any such processes on leg 4.

In the male from Vanuatu (Fig. 5A) there are three processes and they are tapering in form. In contrast the three processes on males from the Great Barrier Reef expedition are more rounded and appear to originate on a common base on the posterior surface of the basis (Fig. 5E). In males from the John Murray expedition the three processes, in lateral view, appear more spread along the surface (Fig. 5D) than in the male from Vanuatu. There appears to be variability in the precise form of the processes.

While sexually dimorphic asymmetry of the fifth legs is almost a diagnostic feature of adult male calanoids, it is exceptionally rare for the fourth legs. *C. orsinii* is unique in possessing conspicuous processes on the basis of this leg, however, some other species of *Centropages* show asymmetry in the form or the size of the exopodal spines on male leg 4. In *C. sinensis*, for example, the distal spine on the outer margin of the third exopodal segment is enlarged and hook-like on the right side only (Chen & Zhang 1965), in *C. abdominalis* Sato, 1913 the same spine is about 4 times longer on the right leg 4 of the male than on the left (Mori 1964), and in both *C. tenuiremis* Thompson & Scott, 1903 and *C. uedai* El-Sherbiny, 2011 the outer spine on the second exopodal segment is enlarged and curved on the right side only in the male (Mori 1964: pl. 28, fig. 7, as *C. yamadai*; El-Sherbiny 2011). The functional significance of this asymmetry in males has not yet been elucidated but it seems likely to be correlated to the marked asymmetry of the genital double-somite and postero-lateral angles of the prosome apparent in the females of many species of this genus.

The discovery of *C. orsinii* in the deep marine water column of Loren cave on the island of Espiritu Santo is the first record of a centropagid from an anchialine habitat. The water level within the cave fluctuates with the tidal cycle and tidal flow is evident (Bréhier *et al.* 2011). The tidal amplitude of about 1 m and the presence of a widely distributed marine planktonic copepod in such a habitat indicates that there is a direct subterranean connection between the deep water column within the cave and the adjacent coastal waters.

Acknowledgements
Material from Vanuatu was collected during SANTO 2006, an international expedition organised by the Muséum national d'Histoire naturelle, Paris (MNHN), Pro-Natura International (PNI), and the Institut de Recherche pour le Développement (IRD). The expedition operated under a permit granted to Prof. Philippe Bouchet by the Environment Unit of the Government of Vanuatu. The specimens were collected during fieldwork carried out by the Santo Karst team, coordinated by Drs L. Deharveng and A. M. Sémah. We are grateful to Franck Bréhier, Stefan Eberhard and Nadir Lasson for undertaking the cave diving in Loren Cave. The authors are grateful to J. Bradford-Grieve, V. I. Ivanenko and A. Ohler for their careful reviews of this manuscript.

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Submitted on 31 October 2011;
accepted on 7 March 2012.