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Revision of Family Megacalanidae (Copepoda: Calanoida)

JANET M. BRADFORD-GRIEVE[1,5], LEOCADIO BLANCO-BERCIAL[2,3] &
GEOFFREY A. BOXSHALL[4]

[1]*National Institute of Water and Atmospheric Research, Private Bag 14901, Wellington 6241, New Zealand.*
E-mail: janet.grieve@niwa.co.nz
[2]*Department of Marine Sciences, University of Connecticut, 1080 Shennecossett Road, Groton, 06340 CT, USA.*
[3]*Present address: Bermuda Institute of Ocean Sciences, St George's GE 01, Bermuda. leocadio@bios.edu*
[4]*Department of Life Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, U.K. E-mail: G.Boxshall@nhm.ac.uk*
[5]*Corresponding author*

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JANET M. BRADFORD-GRIEVE, LEOCADIO BLANCO-BERCIAL & GEOFFREY A. BOXSHALL
Revision of Family Megacalanidae (Copepoda: Calanoida)
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Elenacalanus princeps **(Brady, 1883).** (© David Shale, UK.).

This volume is dedicated to the memory of
Dr Sigrid Schiel
(1946–2016)

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Abstract

The Megacalanidae were revised based on new and archived material. Taxonomic confusion that has existed in the family is discussed and a method is suggested for stabilising names. A detailed examination of the morphology of this family, using the light microscope, has added further useful characters that distinguish genera and species. The added, hitherto undescribed species include character states incompatible with aspects of previous generic definitions (e.g. presence or absence of setae on the maxillule coxal endite). Nevertheless, the cladistic and molecular analyses confirmed that there are at least four monophyletic clades mostly with high bootstrap support. These clades represent already defined genera, one of which [*Elenacalanus* nom. nov. (*nomen novum*)] replaces the preoccupied name *Heterocalanus* Wolfenden, 1906. Four previously described species have been re-assigned to *Elenacalanus* in new combinations: *E. princeps* (Brady, 1883), *E. eltaninae* (Björnberg, 1968), *E. sverdrupi* (Johnson, 1958) and *E. inflatus* (Björnberg, 1968). Eleven new species are described: three *Megacalanus*, one *Bradycalanus*, six *Bathycalanus*, and one *Elenacalanus* nom. nov. *Bradycalanus pseudotypicus enormis* Björnberg, 1968 has been raised to species status based on genetic data although it can be only be distinguished morphologically from *Br. typicus* by its large size. All four genera are differentially diagnosed and keys are provided to the genera and species. We confirm that all male right antennules are geniculate in the Megacalanidae. Thirteen males are known. Of these males, eight are newly described (*M. frosti* **n. sp.**, *M. ericae* **n. sp.**, *M. ohmani* **n. sp.**, *Bathycalanus bradyi* (Wolfenden, 1905a), *Ba. dentatus* **n. sp.**, *Ba. milleri* **n. sp.**, *Ba. unicornis* Björnberg, 1968, and *Elenacalanus tageae* **n. sp.**). We cannot be absolutely certain that the correct males have been assigned to the appropriate female so our decisions await testing with new data. The cladistic analysis provides the first morphology-based phylogeny. This scheme served as a working hypothesis which was tested and corroborated using the newly gathered molecular data. Vertical and horizontal distributions are summarised.

Key words: *Megacalanus, Bradycalanus, Bathycalanus, Elenacalanus* nom. nov., key, morphology, genes, phylogeny, Atlantic, Indian, Pacific, bathypelagic, abyssopelagic, *Megacalanus frosti* **n. sp.**, *M. ericae* **n.sp.**, *M. ohmani* **n. sp.**, *Bradycalanus abyssicolus* **n. sp.**, *Bathycalanus dentatus* **n. sp.**, *Ba. milleri* **n. sp.**, *Ba. tumidus* **n. sp.**, *Ba. adornatus* **n. sp.**, *Ba. pustulosus* **n. sp.**, *Ba. bucklinae* **n. sp.**, *Elenacalanus tageae* **n. sp.**

Introduction

The Megacalanidae are large (9−17 mm long), predatory to detrital-feeding (Arashkevich 1969), red-pigmented, bathy- to abyssopelagic calanoid copepods with a wet weight of up to 0.09 g (Thuesen *et al*. 1998). They are widespread and sparsely distributed in the deep sea and some species have been taken only rarely (Michel 1994). The vertical distribution of megacalanids may vary with developmental stage (Sewell 1947, Gueredrat & Friess 1971) but few studies have recorded the developmental stage and precise depth of capture.

Knowledge of Megacalanidae systematics comes mainly from a few historical collections where net hauls were deployed below 1000 m although the exact vertical range of occurrence is usually unknown since opening-closing nets were not used (Brady 1883; Scott 1909; Wolfenden 1911; Sars 1924/25; Vervoort 1946; Sewell 1947). Subsequently, megacalanid collections have been made with Issacs-Kidd Midwater trawls, also with habitats unconstrained vertically (Johnson 1958; Bjornberg 1968; Grice & Hulsemann 1968; Michel 1994). It is only recently that opening-closing nets have been used although only a few collections have been made to the deepest depths of the ocean. The Census of Marine Zooplankton (CMarZ) collaboration (Wiebe *et al.* 2010) and resulting sampling of the deep Atlantic down to at least 4000 m using MOCNESS 1 m^2 and 10 m^2 nets (Wiebe *et al.* 1976) has greatly improved our knowledge of the diversity and vertical distribution of megacalanids.

To date, no attempt has been made to formulate phylogenetic hypotheses for the Megacalanidae. Studies of the taxonomy and phylogeny are now using molecular tools to test hypotheses derived from morphological approaches. This combined approach has had much to offer: 1) where differentiation of species is challenging because of character variability and the presence of cryptic species; 2) where rare taxa have insufficient individuals to establish delimiting characters; and 3) where the taxonomy is not properly established and under debate. The Megacalanidae can benefit from the latter two types of molecular approaches. Molecular-based contributions to the phylogeny of a number of different taxonomic groups within Copepoda include studies which made use of one or two genes (Braga *et al.* 1999; Bucklin *et al.* 2003; Taniguchi *et al.* 2004), but the field is moving to multi-gene studies (Blanco-Bercial *et al.* 2011; Bradford-Grieve *et al.* 2014). In addition, publications integrating, or comparing genetic data with, morphological traits (Bucklin & Frost 2009; Cornils & Blanco-Bercial 2013; Goetze & Bradford-Grieve 2005; Huys *et al.* 2007; Wyngaard *et al.* 2010), have provided a better understanding of the relationships among the taxa, and have established a framework for future research on the evolution and relationships of the groups of interest.

Our approach to a phylogeny of the Megacalanidae has been hindered by an unstable taxonomy and nomenclature. The reasons for this state of affairs are partly historical because past descriptions were not complete and may have also been due to the occurrence of cryptic species not previously recognised. As Damkaer (2000) explains, near simultaneous publications by Wolfenden, Farran and G.O. Sars, sometimes on the same species, led to taxonomic complications. This resulted in synonyms with ambiguous priorities that were "tangled even as they were introduced" with some still unresolved (Damkaer 2000). This situation was compounded by Wolfenden's private publication of *Plankton Studies* with a limited circulation over the years 1904–1906. Damkaer (2000) could not determine exactly when part I of *Plankton Studies* was published although he documented the circulation of volumes to a limited number of workers (eight examples of part I and four examples of part II). Furthermore, after initially distributing Part 1 (Wolfenden 1905a), Wolfenden found he had made technical errors in the nomenclature of three nominal *Megacalanus* species and decided to change the manuscript resulting, effectively, in a second publication (Wolfenden 1905b), further compounding the taxonomic problems (Damkaer 2000).

Very few genetic sequences for members of the Megacalanidae have been deposited in GenBank as at May 2015 and then only for nuclear 18S and 28S rRNA. Here, we have an opportunity to enhance knowledge of a family of calanoid copepods that are sparsely distributed in their remote environment and therefore difficult to sample. The most commonly employed technique is DNA Barcoding (Hebert *et al.* 2003, 2004) which usually includes use of the mitochondrial cytochrome *c* oxidase subunit I as a genetic marker for metazoans (including copepods: Blanco-Bercial *et al.* 2014). Other markers such as the mitochondrial ribosomal 16S (Bucklin *et al.* 1992; Goetze 2010; Linsay *et al.* 2015) and 12S subunits (Böttger-Schnack & Machida 2011; Machida *et al.* 2012) as well as many of the nuclear ribosomal regions (Hirai *et al.* 2013; Lindeque *et al.* 2013; Zagoskin *et al.* 2014) have also been successfully applied. Within Copepoda, multiple examples have proved the strength of combining molecular markers and morphological characters to clarify the taxonomy of different groups (Böttger-Schnack 2009; Cornils & Blanco-Bercial 2013; Goetze & Bradford-Grieve 2005; Goetze & Ohman 2010; Gollner *et al.* 2011; Huys *et al.* 2006; Thum 2004).

This monograph aims to: revise the family Megacalanidae, describe all known species, including those previously unrecognised, provide genetic markers for a selection of species, derive a phylogenetic hypothesis based on morphological data and test it using genetic data, and provide an analysis of our current understanding of the horizontal and vertical distribution of selected Megacalanidae.

Material and methods

Specimens. This study of the Megacalanidae was based on material collected in the Atlantic Ocean during a CMarZ (http://www.cmarz.org/) Cruise ANT XXIV/1 aboard the Alfred Wegener Institute vessel Polarstern using MOCNESS nets (Wiebe *et al.* 2010) (Table 1). Material from this cruise was preserved in both 95% ethanol and 4% formalin. A typical 1 m^2 MOCNESS tow took about 3 hours to complete down to 1000 m and a typical 10 m^2 MOCNESS tow down to 5000 m (Table 2) took 10 hours to complete. Each sampling interval of the 10 m^2 MOCNESS filtered 38,000-54,000 m^3 to obtain sufficient individual zooplankters for study (Wiebe et al. 2010). The time that deep ocean sampling takes should be kept in mind when considering the physical state of some specimens and possible problems caused in sequencing some genes.

A large collection of material preserved in formalin was also examined from the plankton archive of Scripps Institution of Oceanography, made available by Prof. Mark Ohman, as well as material from R/V Oceanus Cruise #473 "Ocean Acidification Pteropod Study", preserved in 95% ethanol (Table 1). Material deposited in the Natural History Museum, London was re-examined by one of us (GAB) and also listed in Table 1. Additional material was examined from the Smithsonian Institution, and National Institute of Water and Atmospheric Research, New Zealand to improve the description of geographic ranges. For some collections made with an Isaccs Kidd Midwater Trawl (IKMT) the depth fished was not given, rather, 'metres of wire out'. Here, it is assumed that the trawl angle was 45º to work out an approximate fishing depth.

TABLE 1. Station data and capture circumstances for Megacalanidae newly studied here. BN = Benthic net; EBS-S = Epibenthic Sledge – supranet (top); IKMT = Isaacs-Kidd Midwater Trawl; MN = Multinet; MOC 10 = 10 m^2 MOCNESS net; MOC 1 = 1 m^2 MOCNESS net; mwo = metres of wire out; N100 = 1 m diameter net with stramin mesh (Sewell 1935); N200 = 2 m diameter net with graded mesh; AT = Agassiz Trawl; PMT = Petersen Mesoplankton Trawl; RMT = Rectangular Midwater Trawl; * Tow net attached to various depths on sounding line (Brady (1883).

Cruise name	Station #	Gear	Depth /Wire out	Latitude°	Longitude °	Date	Species	Sequence catalogue number / series #
Alfred Wegener Institute of Polar Research / Woods Hole Oceanographic Institution / Census of Marine Zooplankton								
ANT XXIV/I	2	MOC10	4000–3000 m	11.683 N	20.419 W	8 Nov 2007	*Bradycalanus typicus*	Co303.1.1, Co303.1.2
ANT XXIV/I	2	MOC10	3000–2000 m	11.683 N	20.419 W	8 Nov 2007	*Bathycalanus richardi* *Bathycalanus bradyi* *Megacalanus princeps* *Bathycalanus tumidus*	Co022.4 Co375.1.2, Co376.1.1 Co375.1.1, Co375.1.3
ANT XXIV/I	2	MOC10	2000–1000 m	11.683 N	20.419 W	8 Nov 2007	*Megacalanus princeps*	
ANT XXIV/I	3	MOC10	3999–2993 m	03.510 N	15.008 W	11 Nov 2007	*Bathycalanus bradyi*	
ANT XXIV/I	3	MOC10	2993–1957 m	03.510 N	15.008 W	11 Nov 2007	*Bathycalanus bradyi* *Bradycalanus typicus*	
ANT XXIV/I	3	MOC10	1957–998 m	03.510 N	15.008 W	11 Nov 2007	*Bathycalanus bradyi*	
ANT XXIV/I	6	MOC10	0–5038 m	13.155 S	0.316 E	17 Nov 2007	*Bathycalanus adornatus* *Bradycalanus enormis* *Bradycalanus typicus*	 Co360.1.1
ANT XXIV/I	6	MOC10	5110–3993 m	13.155 S	0.316 E	17 Nov 2007	*Bathycalanus adornatus*	Co022.3.1
ANT XXIV/I	6	MOC10	3886–1987 m	13.155 S	0.316 E	17 Nov 2007	*Bradycalanus typicus* *Bathycalanus bradyi*	Co384.1.1
ANT XXIV/I	6	MOC10	1985–998 m	13.155 S	0.316 E	17 Nov 2007	*Bathycalanus milleri*	
ANT XXIV/I	8	MOC10	4390–3992 m	25.082 S	09.584 E	21 Nov 2007	*Bathycalanus adornatus*	
ANT XXIV/I	8	MOC10	3992–2990 m	25.082 S	09.584 E	21 Nov 2007	*Bradycalanus typicus* *Bradycalanus gigas* *Bathycalanus unicornis*	
ANT XXIV/I	8	MOC10	2990–2062 m	25.082 S	09.584 E	21 Nov 2007	*Bathycalanus bucklinae*	
ANT XXIV/I	2	MOC 1	800–1000 m	11.379 S	20.350 E	5 Nov 2007	*Megacalanus princeps*	Co119.2.1
ANT XXIV/I	9	MN	0–940 m	23.240 S	08.238 E	20 Nov 2007	*Bathycalanus bradyi*	
Scripps Institution of Oceanography								
Francis Drake III	2	IKMT	0–3000 m	46.617 S	75.800 W	10 Apr 1975	*Elenacalanus princeps* *Elenacalanus eltaninae* *Bathycalanus milleri* *Bathycalanus richardi*	
Francis Drake III	4	IKMT	0–3000 m	02.867 N	80.850 W	8 May 1975	*Bathycalanus milleri* *Megacalanus frosti*	

……*continued on the next page*

TABLE 1. (Continued)

Cruise name	Station #	Gear	Depth /Wire out	Latitude°	Longitude °	Date	Species	Sequence catalogue number / series #
Southtow IV MV72-11	36	IKMT	0–2000 m	13.867 S	77.717 W	12 May 1972	*Megacalanus princeps* *Megacalanus frosti* *Bradycalanus typicus* *Bathycalanus milleri*	
Circe II	15T-1	IKMT	0–3000 mwo	06.000 N	122.600 E	21 Apr 1968	*Megacalanus ericae* *Bathycalanus richardi* *Bathycalanus bradyi*	
Indopac VII	5	IKMT	0–3000 mwo	04.517 S	125.583 E	26 Aug 1976	*Megacalanus princeps* *Megacalanus ericae*	
Indopac VIII	6	IKMT	0–2964 mwo	05.350 S	133.583 E	19 Sep 1976	*Megacalanus princeps* *Megacalanus ohmani*	
MV66-11	5	IKMT	0–5500 mwo	38.033 N	124.183 W	24 May 1966	*Megacalanus princeps* *Megacalanus frosti* *Bradycalanus typicus* *Bathycalanus bradyi* *Bathycalanus pustulosus* *Bathycalanus dentatus* *Bathycalanus richardi* *Bathycalanus milleri*	
MV73-1	53	IKMT	0–2000 m	13.32 N	92.033 W	14 Apr 1973	*Megacalanus frosti* *Bathycalanus unicornis* *Elenacalanus eltaninae* *Bathycalanus tumidus* *Bathycalanus richardi* *Bradycalanus typicus* *Bradycalanus enormis*	
Antipode IV	52D	IKMT	0–1900 m	29.533 N	137.233E	30 Aug 1970	*Megacalanus ericae* *Bathycalanus tumidus* *Bathycalanus bradyi* *Bathycalanus dentatus* *Bathycalanus richardi*	
Antipode IV	53A	IKMT	0–2000 m	27.133 N	138.233E	31 Aug 1970	*Megacalanus ericae* *Bathycalanus tumidus* *Bathycalanus richardi* *Bathycalanus bradyi*	
Antipode IV	53D	IKMT	0–2500 m	26.441 N	139 03.7E	1 Sep 1970	*Megacalanus ericae* *Elenacalanus tageae* *Bathycalanus richardi* *Bathycalanus tumidus*	

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TABLE 1. (Continued)

Cruise name	Station #	Gear	Depth /Wire out	Latitude°	Longitude °	Date	Species	Sequence catalogue number / series #
Antipode IV	55D	IKMT	0–2000 m	20.933 N	138.533E	4 Sep 1970	*Megacalanus ericae* *Elenacalanus tageae* *Bathycalanus bradyi* *Bathycalanus richardi* *Bradycalanus typicus*	
CCE P0810	Cycle 1 tow 1/1	MOC1	500–700 m	34.13 N	120.97W	4 Oct 2008	*Megacalanus frosti*	
University of Hawaii								
OCN 627		IKMT	1000 m	21.376 N	158.307 W	14 Feb 2009	*Megacalanus ericae*	Co439.2.1, 439.2.2
Woods Hole Oceanographic Institution								
Oceanus Cr 473	1	MOC1	100–866 m	34.996N	52.027 W	11 Aug 2011	*Megacalanus princeps*	Co119.3.1
Oceanus Cr 473	8	MOC1	1001–801 m	38.503N	51.900 W	15 Aug 2011	*Megacalanus princeps* *Elenacalanus princeps*	Co119.4.1 Co024.2.1
Oceanus Cr 473	21	MOC1	798–600 m	44.933N	41.996 W	19 Aug 2011	*Megacalanus princeps* *Elenacalanus princeps*	Co119.5.1 Co024.3.1, Co024.3.2
Oceanus Cr 473	26	MOC1	1001–798 m	47.490N	41.986 W	23 Aug 2011	*Elenacalanus princeps*	Co024.5.1
Oceanus Cr 473	26	MOC1	600–400 m	47.490N	41.986 W	23 Aug 2011	*Elenacalanus princeps*	Co024.6.1
Oceanus Cr 473	31	MOC1	797–599 m	49.993N	41.983 W	23 Aug 2011	*Elenacalanus princeps*	Co024.7.1
NH1208	11	MOC1	399–598 m	45.046 N	141.447 W	4 Sep 2012	*Megacalanus ericae*	Co439.4.1
NH1208	11	MOC1	599–797 m	45.046 N	141.447 W	4 Sep 2012	*Megacalanus ericae*	Co439.3.1, Co439.3.2
NH1208	18	MOC1	399–600 m	41.533 N	135.786 W	7 Sep 2012	*Megacalanus frosti*	Co439.5.1
NH1208	18	MOC1	600–800 m	41.720 N	135.823 W	7 Sep 2012	*Megacalanus ericae*	Co439.6.1
NH1208	24	MOC1	200–400 m	38.623 N	135.062 W	9 Sep 2014	*Megacalanus ericae*	Co439.7.1
NH1208	27	MOC1	400–600 m	37.0231 N	135.129 W	10 Sep 2012	*Megacalanus ericae*	Co439.8.1
NH1208	32	MOC1	0–1000 m	34.501 N	135.000 W	12 Sep 2012	*Megacalanus ericae*	Co439.9.1
NH1208	34	MOC1	400–600 m	33.505 N	135.000 W	13 Sep 2012	*Megacalanus frosti*	Co439.10.1
RHB0603	1	MOC1	200–400 m	33.524 N	69.961 W	13 Apr 2006	*Elenacalanus princeps*	Co024.1.1,Co024.1.2, Co024.1.4
RHB0603	3	MOC1	1000–3000 m	24.791 N	60.364 W	20 Apr 2006	*Megacalanus princeps*	
RHB0603	5	MOC1	600–799 m	14.003 N	54.999 W	25 Apr 2006	*Bathycalanus richardi*	Co022.2.1
Senckenberg Forschungsinstitut und Naturmuseum								
ANT XIX/4	135-4	EBS-S	4678 m	64.999 S	43.020 W	11 Mar 2002	*Bradycalanus abyssicolus*	

……*continued on the next page*

TABLE 1. (Continued)

Cruise name	Station #	Gear	Depth /Wire out	Latitude°	Longitude °	Date	Species	Sequence catalogue number / series #
ME 63-2	40-S	EBS-S	5055 m	28.051 S	07.330 E	4 Mar 2005	*Bradycalanus gigas*	
ME 79-1	534	EBS-S	4605–4585 m	36.010 S	49.026 W	16 Jul 2009	*Bradycalanus abyssicolus*	
ME 79-1	537	EBS-S	4605–4585 m	36.010 S	49.026 W	17 Jul 2009	*Bradycalanus abyssicolus*	
ME 79-1	605	EBS-S	5168–5184 m	03.958 S	28.078 W	6 Aug 2009	*Bradycalanus abyssicolus*	
ANT52 Russ Hopcroft								
Umitaka Maru	16	RMT-8D2	500–1000 m	63.000 S	140.000 E	30 Jan 2008	*Bathycalanus bradyi*	Co411.1.1
Umitaka Maru	18	RMT-8D2	500–1000 m	64.010 S	140.01 E	1 Feb 2008	*Bathycalanus milleri*	Co411.2.1
University of Connecticut								
LMG11-10	11	MOC1	1500–2000 m	60.737 S	54.942 W	13 Nov 2012	*Elenacalanus princeps*	Co441.3.1
John Murray Expedition								
	96	N100	390–635 m	10.911– 0.888 N	61.348 – 61.373 E	19 Dec 1933	*Megacalanus princeps*	
	98	N200	0–2800 m	6.978 N	55.683 E	22 Dec 1933	*Megacalanus princeps*	
	120	AT	2926 m	5.820–5.873 S	41.470 – 41.670 E	20 Jan 1934	*Bradycalanus gigas*	
	131	N100	0–500 m	1.65 S	61.23 E	11 Feb 1934	*Megacalanus frosti*	
	131D	N100	0–1500 m	1.652–2.125 S	61.230 –61.353 E	11 Feb 1934	*Megacalanus princeps*	
	131D	N200	0–2500 m	1.652–2.125 S	61.230 –61.353 E	11 Feb 1934	*Megacalanus princeps*	
	172	N100	0–850 m	9.673–9.705 N	54.560 –54.650 E	29 Apr 1934	*Megacalanus princeps*	
	172	N200	0–2091 m	9.673–9.705 N	54.560 –54.650 E	29 Apr 1934	*Megacalanus princeps*	
R.R.S. Discovery								
	7089	RMT8	800–900 m	18.00 N	25.00W	14 Nov 1969	*Bathycalanus richardi*	Series #12
	7406	RMT8	900–1000 m	40.00N	20.00 W	2 Oct 1970	*Bathycalanus richardi* *Elenacalanus princeps*	Series #6
	7406	RMT8	600–700 m	40.00N	20.00 W	4 Oct 1970	*Megacalanus princeps*	Series #24
	7406	RMT8	990–1250 m	40.00N	20.00 W	6 Oct 1970	*Elenacalanus princeps* *Elenacalanus inflatus*	Series #33
	7478	RMT8	1500–2000 m	40.00N	20.00 W	6 Nov 1970	*Elenacalanus eltaninae*	Series #1
	7480	RMT8	1250–1500 m	40.00N	20.00 W	7 Nov 1970	*Elenacalanus princeps*	
	7482	RMT8	2000–2500 m	40.00N	20.00 W	7 Nov 1970	*Bradycalanus typicus*	
	7709	RMT8	1010–1250 m	60.00 N	20.00 W	29 Apr 1971, 5 May 1971	*Bathycalanus richardi* *Elenacalanus princeps*	Series #35, #63

……*continued on the next page*

TABLE 1. (Continued)

Cruise name	Station #	Gear	Depth /Wire out	Latitude°	Longitude °	Date	Species	Sequence catalogue number / series #
	7709	RMT8	1250–1500 m	60.00 N	20.00 W	30 Apr 1971, May 1971	*Bathycalanus bradyi* *Elenacalanus princeps* *Elenacalanus eltaninae* *Elenacalanus inflatus*	Series #44, #76
	7709	RMT8	1520–2000 m	60.00 N	20.00 W	8 May 1971	*Bathycalanus bradyi*	Series #91
	7711	RMT8	800–900 m	53.00 N	20.00 W	17 May 1971	*Elenacalanus princeps*	Series #4
	7711	RMT8	1260–1500 m	53.00 N	20.00 W	25 May 1971	*Bathycalanus bradyi* *Elenacalanus eltaninae*	Series #47, #56
	7711	RMT8	1500–2000 m	53.00 N	20.00 W	27 May 1971	*Bradycalanus typicus* *Bathycalanus bradyi* *Elenacalanus princeps*	Series #39, #61
	8507	RMT8	1250–1500 m	44.00 N	13.00 W	10 Apr 1974	*Bathycalanus bradyi* *Elenacalanus princeps*	Series #72
	8507	RMT8	1500–2000 m	44.00 N	13.00 W	10 Apr 1974	*Bathycalanus richardi* *Elenacalanus princeps* *Elenacalanus eltaninae*	Series #3, #73
	8508	RMT8	1000–1250 m	44.00 N	13.00 W	12 Apr 1974, 13 Apr 1974	*Bathycalanus richardi*	Series #1, #3
	8508	RMT8	2000–2500 m	44.00 N	13.00 W	20 Apr 1974	*Bradycalanus typicus* *Bathycalanus bradyi*	Series #76
	8508	RMT8	2500–3100 m	44.00 N	13.00 W	20 Apr 1974	*Bradycalanus typicus* *Bradycalanus enormis* *Bathycalanus bradyi* *Bathycalanus unicornis*	Series #78
	8509	RMT8	2000–2500 m	44.00 N	13.00 W	27 Apr 1974	*Bradycalanus typicus* *Bathycalanus bradyi*	Series #15
	8509	RMT8	3000–3500 m	44.00 N	13.00 W	28 Apr 1974	*Bradycalanus typicus* *Bradycalanus enormis* *Bathycalanus bradyi* *Bathycalanus unicornis*	Series #20
	8509	RMT8	3500–4000 m	44.00 N	13.00 W	29 Apr 1974	*Bathycalanus unicornis*	Series #27
	8512	BN	2281–2465 m	42.31 N	11.44 W	7 May 1974	*Bradycalanus typicus*	Series #4
	11261	RMT8	910–1000 m	21.34 N	25.29 W	27 June 1985	*Bathycalanus bradyi*	Series #8, #9
Challenger Expedition								
	45	Tow net*	2275 m	38.57 N	72.17 W	3 May 1873	*Elenacalanus princeps*	
	50	Tow net	2294 m	42.00 N	63.65 W	21 May 1873	*Elenacalanus princeps*	
	Sr224	PMT	1284 m	53.12 N	15.10 W	12 May 1905	*Megacalanus princeps*	

TABLE 2. Net haul statistics for a 10 m^2 MOCNESS tow on 8 November 2007 (http://cmarz.whoi.edu/jg/info/CMarZ/mocness_tabs_PS24%7Bdir=www.cmarz.org/jg/dir/CMarZ/,data=www.cmarz.org/jg/serv/CMarZ/mocness_tabs_PS24.html0%7D).

Time (local)	Depths sampled	Volume filtered.
Start—0832 h	Net 0: 0000–4795 m	54166 m^3
End—1850 h	Net 1: 4795–4000 m	52253 m^3
	Net 2: 4000–3000 m	59461 m^3
Elapsed time	Net 3: 3000–2000 m	47091 m^3
10.3 h	Net 4: 2000–1000 m	37795 m^3

The habitus of individuals was illustrated under low power on a cavity slide in water and covered by a coverslip propped up by small pieces of water repellent modelling clay. Limbs were then dissected off and mounted in gum-chloral (Pantin 1964). Mounted specimens were drawn using a drawing tube and 'inked' digitally (Coleman 2003). Aesthetascs, especially in males, were often damaged with either only the stiffened border evident, the proximal part present or completely absent but represented by the region of attachment. Therefore aesthetascs have been illustrated in a stylised manner with a minimum length indicated. Their shape on the drawings should not be interpreted as an accurate representation.

The system of morphological nomenclature used in the systematic account is based mainly on that of Huys & Boxshall (1991) but the major body segments are referred to as "somites" and the somites bearing legs are "pedigerous somites". Most observations were made with a microscope fitted with Nomarski differential interference optics and a drawing apparatus although some structures were difficult to see using this method, especially hair sensilla. Figures 1–6 illustrate features appearing in descriptions and the cladistics analysis.

Measurements were made as indicated on Fig. 1. Total length was measured from any anterior protrusions to the posterior border of the caudal rami and was arrived at by adding the "prosome" length (as measured along the mid-line from any anterior protrusions to the anterior border of the genital double-somite) to the length of the urosome because many of the animals were too large to be measured with the techniques available in one measurement. Measurements of selected proportions of male urosomites were made to test whether or not the ratios from small samples of three species of *Bathycalanus* could be distinguished statistically using pair-wise PERMANOVA in PRIMER 7 (Anderson *et al.* 2008).

In the systematic account, higher taxa (families and genera) were first differentially diagnosed then described. The differential diagnosis of the Megacalanidae contains a combination of character states that distinguish the Megacalanidae from all other families in the Calanoida. The generic differential diagnoses contain key character states that, in combination, distinguish each genus within the Megacalanidae. Each genus is fully described and stands alone. Descriptions of species contain only those elements that distinguish species within their genera.

Most species were fully illustrated. In a few cases, where species are well known or species are very similar to one another, not all limbs were illustrated. For example, *Megacalanus* species are very similar to one another. *Megacalanus ohmani* **n. sp.** was chosen for full illustration whereas the other three species were illustrated by those aspects that serve to distinguish the species. In the case of the species pair, *Bradycalanus typicus* and *Br. enormis*, which are very alike morphologically, the male of *Br. typicus* and female of *Br. enormis* are fully illustrated. Their opposite sexes are illustrated by sexually dimorphic features. Furthermore, a number of males are illustrated by the sexually dimorphic characters alone since many of their limbs are identical to those of the female.

The synonymies below include only those references where enough evidence is presented to allow confirmation of the identity of each species being evaluated.

Morphological data for cladistics analysis. The character set chosen for the cladistic analysis differs in a number of respects from the character set used conventionally for calanoid taxonomic description. That is, some characters used in taxonomic descriptions represent an amalgam of several characters that would be used separately in a cladistics analysis. For example, in a taxonomic description of the maxillule of *Megacalanus*, the posterior surface of the praecoxal arthrite would be described as having 4 setae, whereas, in the cladistic analysis, each seta is considered to be a character in its own right—either present or absent. For this reason, it is not expected that taxonomic descriptions and the character set for cladistics analysis would be exactly the same.

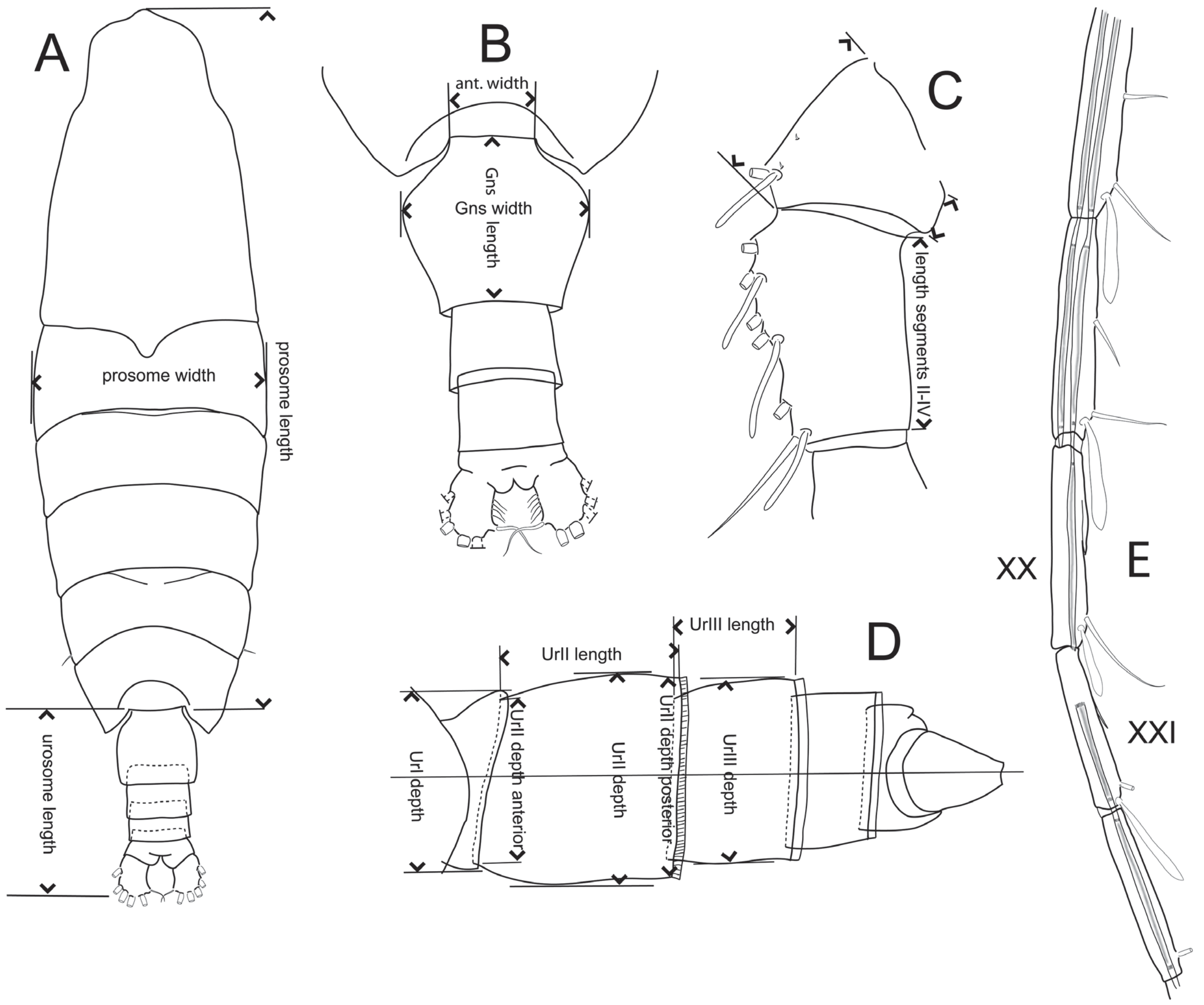

FIGURE 1. Diagram illustrating how measurements were made: A, dorsal view of female *Megacalanus princeps*; B, dorsal view of urosome of female *Bathycalanus tumidus* (Gns = genital double-somite); C, female antennule ancestral segments I–IV of *Megacalanus ohmani*; D, lateral view of urosome (Ur) of male *Bathycalanus bradyi*. E, intrinsic musculature of male *Megacalanus princeps* right antennule, ancestral segments XVIII–XXIII.

A character/state set was chosen based on defensible hypotheses of primary homology. Hypotheses of primary homology relating to the presence of arthrodial membranes and setae employed our current understanding of development in the Calanidae and other families with some corroborating evidence from the Megacalanidae. We used copepodite development and topographical position of characters. Some evidence comes from a copepodite stage II (CII) of *Megacalanus princeps* examined during this study. Other evidence comes from the literature (Heron & Bowman 1971; McKinnon & Arnott 1985; Lawson & Grice 1973; Bradford *et al*. 1988; Ferrari 1995).

Characters (Char.) and their states are listed in Table 3 and the data matrix is given in Table 4. On figures 1–6 specific "characters : states" are indicated in the form '◄ 3:2', that is, character 3, state 2. Some characters in the species descriptions, not found to be useful for the phylogenetic analysis, are also discussed.

Anterior head (Figs 1A, 2A–E). The anterior head viewed dorsally has a shape which partly reflects the position of the base of the rostrum. In *Megacalanus* and *Bradycalanus* the rostrum usually lies directly ventral to the main frontal outline of the anterior head so the base of the rostrum is not visible from above. In most *Bathycalanus* the rostral base is set anteriorly on a narrow projection which appears as a small rounded knob in dorsal view (Fig. 2A). The anterior margin of the head may be undecorated (Fig. 1A), bear 2 small spine-like processes (Fig. 2A), bear 1 spine-like process (Fig. 2B) or may be crested (Fig. 2C) (Chars 1–3).

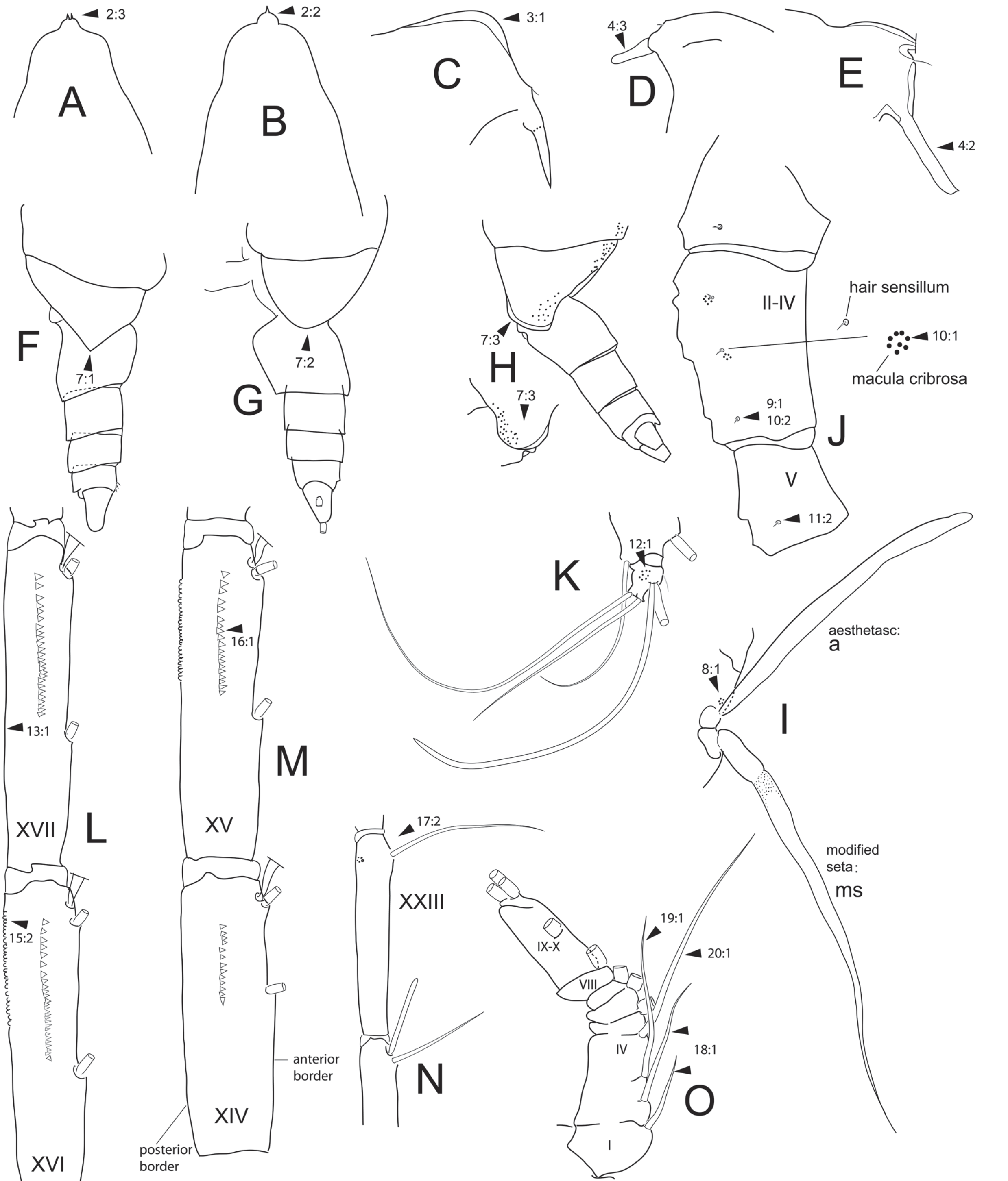

FIGURE 2. Selected characters and their states as detailed in Table 3. A, anterior head of *Ba. richardi*; B, anterior head of *Ba. unicornis*; C, anterior head of *M. frosti* **n. sp.**; D, anterior head of *E. eltaninae*; E, anterior head in lateral view of *Ba. bradyi*; F, urosome and pedigerous somite 5 of *M. frosti* **n. sp.**; G, urosome and pedigerous somite 5 of *M. ohmani* **n. sp.**; H, urosome and pedigerous somite 5 (right and left) of *Ba. pustulosus* **n. sp.**; I, detail of aesthetasc (a) and modified setae (ms) distally on antennule ancestral segments XXV of *M. ohmani* **n. sp.**; J. dorsal view of female antennule ancestral segments I–V of *M. princeps* showing position of hair sensilla and maculae cribrosae; K, female antennule ancestral segment XXVIII of *M. ohmani* **n. sp.**; L, female antennule ancestral segments XVI and XVII of *M. princeps***;** M, female antennule ancestral segments XIV and XV of *M. princeps***; N,** female antennule ancestral segment XXIII of *M. ohmani* **n. sp.**; O, antenna exopod of *M. ohmani* **n. sp.** Specific 'character : state' is indicated in the form '◄ 3:2'.

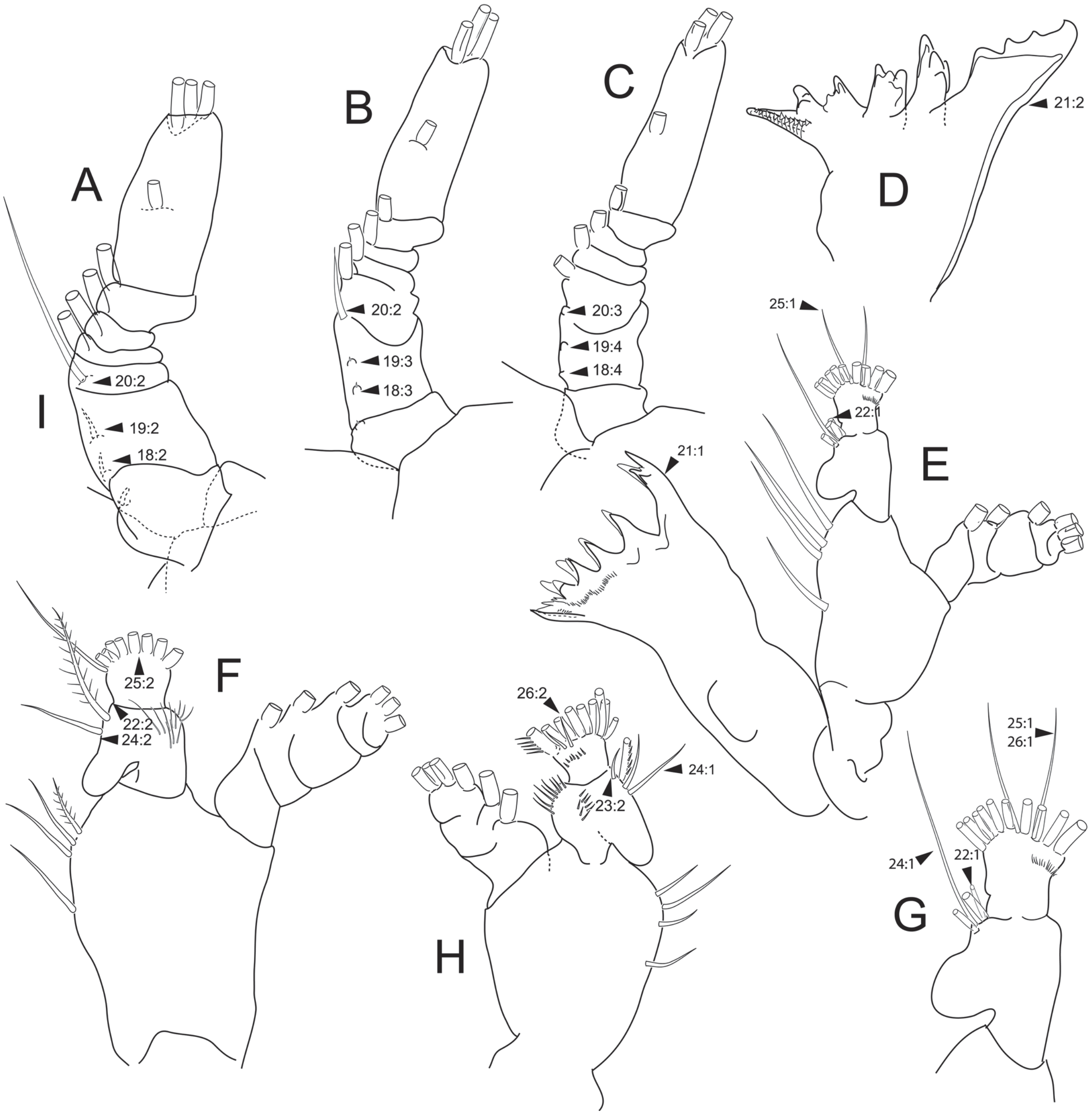

FIGURE 3. Selected characters and their states as detailed in Table 3. A, antenna exopod of *Br. abyssicolus* **n. sp.**; B, antenna exopod of *Ba. richardi*; C, antenna exopod of *E. princeps*; D, cutting edge of mandibular gnathobase of *Br. enormis*; E, mandible of *M. ohmani* **n. sp.**; F, mandibular palp of *E. princeps*; G, mandibular endopod of *M. ohmani* **n. sp.**; H, mandibular palp of male *Br. typicus*; Specific 'character : state' is indicated in the form '◄ 3:2'.

Rostrum (Fig. 2C–E). The ventroanterior margin of the head extends to form a pair of ventrally directed branches tapering a point in *Megacalanus* and *Bradycalanus* (Fig. 2C). In *Bathycalanus* the rostrum is short with a pair of distinctive parallel-sided (sausage-shaped) sensory filaments (Fig. 2E) and in *Elenacalanus* nom. nov. the rostral filaments are bluntly tapering (Char. 4) (Fig. 2D).

Female urosome (Figs 1B, 2F–H). In many species the genital double-somite in dorsal view has lateral swellings that are usually situated at about the anterior one third in dorsal view. Some species have other proportions. Genital double-somite length : maximum width (Char. 5) in dorsal view (Fig. 1B) and the anterior—posterior location of the lateral genital bulge (Char. 6) were characterised. Analysis of the ratios calculated for Char. 5 determined that clusters of ratios were separated by gaps. These clusters were treated as characters states. Seminal receptacles were inferred to be present in all Megacalanidae based on the observations of Barthélémy (1999) for *Megacalanus princeps* and *Bathycalanus bradyi* and the present observation of *Bradycalanus enormis* (see Fig. 24C). The presence of seminal receptacles was not observed in all examined species because of the opaque nature of most specimens that was not susceptible to clearing. The shape, in lateral view, of the corners of pedigerous somite 5 may be bluntly triangular (Fig. 2F), rounded (Fig. 2G) or be extended as irregularly-shaped lappets (Fig. 2H) (Char. 7).

TABLE 3. Morphological characters/states used for phylogenetic analysis (Figs 1–6) followed by the consistency index and rescaled consistency index (**bold**). Characters are those of the female. A1 = antennule; A2 = antenna; B = basis; B1 = basal endite 1; B2 = basal endite 2; Be = basal exite; C = coxal endite; C1 = coxal endite 1; Ce = coxal epipodite; Gns = genital double-somite; Mn = mandible; Mx1 = maxillule; Mx2 = maxilla; Mxp = maxilliped; P1 = leg 1; Pa = praecoxal arthrite; Pd5 = pedigerous somite 5; Pe1, 2 = praecoxal endite 1, 2; ReII, III, IV = ancestral exopod segments II, III, IV; Ri1–5 = endopod segment 1–5.

1. Anterior head decoration in dorsal view (absent, present): 0.50, **0.44**
2. Anterior head spine-like processes (0, 1, 2): 1.00, **1.00**
3. Head crest (present, absent): 0.33, **0.00**
4. Rostral filaments (tapering to a point, sausage-shaped, bluntly tapering): 1.00, **1.00**
5. Gns length : widest width in dorsal view (less than 0.73, 0.83–1.15, greater than 1.2): 0.50, **0.17**
6. Gns widest width in dorsal view (at anterior one eighth; at about anterior one third, at about midlength): 0.40, **0.16**
7. Posterior borders of Pd5 (blunt triangle, rounded, irregular-shaped lappets): 0.30, **0.11**
8. A1 ancestral segment I macula cribrosa adjacent to aesthetasc (present, absent): 0.50, **0.38**
9. A1 ancestral segment IV dorsal hair sensillum (present, absent): 1.00, **1.00**
10. A1 ancestral segment IV macula cribrosa adjacent to hair sensillum (present, absent): 0.33, **0.11**
11. A1 ancestral segment V macula cribrosa adjacent to hair sensillum (present, absent): 1.00, **1.00**
12. A1 ancestral segment XXVIII macula cribrosa (present, absent): 0.50, **0.38**
13. A1 ancestral segments XVI–XX anterior border (smooth, toothed): 1.00, **1.00**
14. A1 ancestral segment XV posterior border (smooth, toothed): 1.00, **1.00**
15. A1 ancestral segment XVI posterior border (smooth, toothed): 0.50, **0.25**
16. A1 ancestral segment XIV–XVII ventral surface tooth row (present, absent): 1.00, **1.00**
17. A1 ancestral segment XXIII aesthetasc (present, absent): 1.00, **1.00**
18. A2 ReII and III seta (developed—longer than its segment, reduced—shorter than its segment, vestigial—minute spinule on raised projection, absent—only raised projection present): 1.00, **1.00**
19. A2 ReIII seta (developed—longer than its segment, reduced—shorter than its segment, vestigial—minute spine on raised projection, absent—only raised projection present): 1.00, **1.00**
20. A2 ReIV seta (developed—extends beyond distal border of exopod, short—extends short of distal border of exopod, absent): 1.00, **1.00**
21. Mn gnathobase ventral tooth (at right angles to main plane of gnathobase, at oblique angle to main plane of gnathobase): 0.50, **0.38**
22. Mn Ri1 small distal seta (present, absent): 1.00, **1.00**
23. Mn Ri1 small distal seta (developed, vestigial): 1.00, **1.00**
24. Mn Ri1 small proximal seta (present, absent): 1.00, **1.00**
25. Mn Ri2 surface setae (present, absent): 1.00, **1.00**
26. Mn Ri2 surface setae (developed, vestigial, absent): 1.00, **1.00**
27. Mx1 Be seta (present, absent): 1.00, **1.00**
28. Mx1 Pa posterior distal seta (present, absent): 0.50, **0.44**
29. Mx1 Pa posterior second most distal seta (present, absent): 0.50, **0.44**
30. Mx1 C with (0, 1, 2, 4, 5 setae): 1.00, **1.00**
31. Mx1 B1 with (2, 4 setae): 1.00, **1.00**
32. Mx1 B2 with (2, 3, 4 setae): 0.50, **0.33**
33. Mx1 Ri1 with (1, 2, 3, 4 setae): 0.80, **0.64**
34. Mx1 Ri2 with (0, 1, 2, 4 setae): 0.75, **0.64**
35. Mx1 Ri3 posterior surface seta (developed, short—about or less than length of endopod): 1.00, **1.00**
36. Mx1 Ri3 seta 6 (present, absent): 1.00, **1.00**
37. Mx1 Ri3 seta 7 (present, absent): 1.00, **1.00**
38. Mx2 Ce seta (developed, vestigial): 1.00, **1.00**
39. Mx2 setae of Pe1 and 2 and C1 with long sparse auxilliary spinules (present, absent): 1.00, **1.00**
40. Mx2 Ri setae with long sparse auxilliary spinules (present, absent): 1.00, **1.00**
41. Mx2 Ri1 smallest setae (developed, vestigial): 1.00, **1.00**
42. Mx2 Ri2 proximal inner seta (developed, small and finely tapering, vestigial and composed of oval base drawn out to curved point): 1.00, **1.00**
43. Mx2 Ri2 distal inner seta convex border (naked, bearing spinules): 1.00, **1.00**

44. Mx2 terminal setae (gently curving along whole length, curling distally in semicircle, completely curled on themselves distally): 1.00, **1.00**
45. Mxp Ri3 seta 2 (present, absent): 1.00, **1.00**
46. Mxp Ri3 seta 2 (fully developed, small): 1.00, **1.00**
47. Mxp Ri3 seta 3 (present, absent): 1.00, **1.00**
48. Mxp Ri3 seta 3 (fully developed, small): 1.00, **1.00**
49. Mxp Ri3 seta 4 (present, absent): 1.00, **1.00**
50. Mxp Ri4 seta 3 (present, absent): 1.00, **1.00**
51. Mxp Ri5 inner seta 2 (present, absent): 1.00, **1.00**
52. Mxp Ri5 inner seta 2 (fully developed, small): 1.00, **1.00**
53. Mxp Ri5 outer seta (present, absent): 1.00, **1.00**
54. P1 B anterodistal hook-like process (present, absent): 1.00, **1.00**
55. P1 B inner distal seta (straight to curved, S-shaped): 0.50, **0.38**
56. P1 Re1 and 2 outer distal spine (present, absent): 1.00, **1.00**
57. P1 Re3 proximal outer spine 1 (present, absent): 1.00, **1.00**

TABLE 4. Morphological data matrix of character state scores.

Calanus helgolandicus	1123322212	2211122111	2111111114	2344111111	1121111111	1112211
Megacalanus princeps	1123221112	2112212111	1111111115	2334111111	1121111111	1111111
Megacalanus ericae **n. sp.**	1123221111	2111112111	1111111115	2334111111	1121111111	1111111
Megacalanus frosti **n. sp.**	1113221112	2112212111	1111111115	2334111111	1121111111	1111111
Megacalanus ohmani **n. sp.**	1123222111	2111112111	1111111115	2334111111	1121111111	1111111
Bradycalanus typicus	1121221212	2211121112	2121121115	1323212212	2211121211	1212211
Bradycalanus enormis	1121221212	2211121112	2121121115	1323112212	2211121211	1212211
Bradycalanus abyssicolus **n. sp.**	1111231212	2211121222	2121121113	1323212212	2211121211	1212211
Bradycalanus gigas	1121212212	2211121112	2121121115	1323212212	2211121211	1212211
Bathycalanus richardi	2322322122	1111121332	1121121221	1223112122	2323121211	1212122
Bathycalanus bradyi	2322222122	1111121332	1121121221	1223112122	2323121211	1212122
Bathycalanus dentatus **n. sp.**	2322222122	1121121332	1121121221	1123112122	2323121211	1212122
Bathycalanus milleri **n. sp.**	2322222122	1121221332	1121121221	1123112122	2323121211	1212122
Bathycalanus tumidus **n. sp.**	2322223122	1111121332	1121121221	1323112122	2323121211	1212122
Bathycalanus adornatus **n. sp.**	2322323122	1?1112?332	1121121221	1222112122	2323121211	1212122
Bathycalanus unicornis	2222212122	1111121332	1121121211	1333112122	2323121211	1212122
Bathycalanus bucklinae **n. sp.**	2322232122	1111121332	1121121112	1323112122	2323121211	1212122
Elenacalanus eltaninae	2112132111	1111121443	12?2232221	11(12)(12)1221 22	23222?2?22	2?22121
Elenacalanus princeps	1122232111	1111121442	12?2232221	1212122122	23222?2?22	2?22121
Elenacalanus tageae **n. sp.**	1122232111	1?1112?442	12?2231221	1112122122	23222?2?22	2?22121

Female antennule (Fig. 2I–N). A hair sensillum is found on the dorsal surface of ancestral segments I–V and these may or may not be accompanied by a macula cribrosa (Fig. 2J). We use the term 'hair sensillum' because there is no adjacent pore to an integumental gland (Fleminger 1973); in some species the sensillum is very small. On the antennules of female *Calanus helgolandicus* (Claus, 1863), hair sensilla were difficult to see and were examined using a bench top scanning electron microscope (Fig. 4). Here, the presence or absence of a hair sensillum on segment IV was chosen (Char. 9). Maculae cribrosae were first mentioned by With (1915) and interpreted as being "a group of delicate filaments projecting through minute pores (?)". The scanning electron micrographs of Miller (2002, p. 136) showed, however, that the dots represent small raised thickenings on the cuticle surface connected to the interior by a "neural nexus". The ultrastructure and function of this organ is not known. Sewell (1929) details the presence of maculae cribrosae in *Megacalanus* and *Bathycalanus*. Those in *Megacalanus* are the most easily seen, whereas in *Bathycalanus* they are sometimes difficult to observe and in

Bradycalanus they appear to be absent. Presence or absence of a macula cribrosa adjacent to the aesthetasc on ancestral segments I, IV and XXVIII (Chars 8, 9, 12) (Fig. 2I, K) and adjacent to the hair sensillum on segments IV and V (Fig. 2J) (Chars 10, 11) have been selected for this analysis. Various segments carry rows of spinules in different locations in *Megacalanus* and *Bathycalanus*: the anterior border of ancestral segments XVI–XX may be smooth or toothed (Char. 13) and the posterior border of ancestral segments XV and XVI may be smooth or toothed (Fig. 2L, M) (Chars 14, 15). The ventral surface of ancestral segments XIV–XVII has a longitudinal row of small spinules in *Megacalanus* (Char. 16) (Fig. 2L, M). Aesthetascs (a) are conservatively located on most antennular segments in this family apart from on segment XXIII (Fig. 2N) where an aesthetasc may be present or absent (Char. 17). Most setae on the antennule appear to be of the bi-modality type (Lenz *et al.* 1996), here called modified setae (ms) (see Fig. 5I).

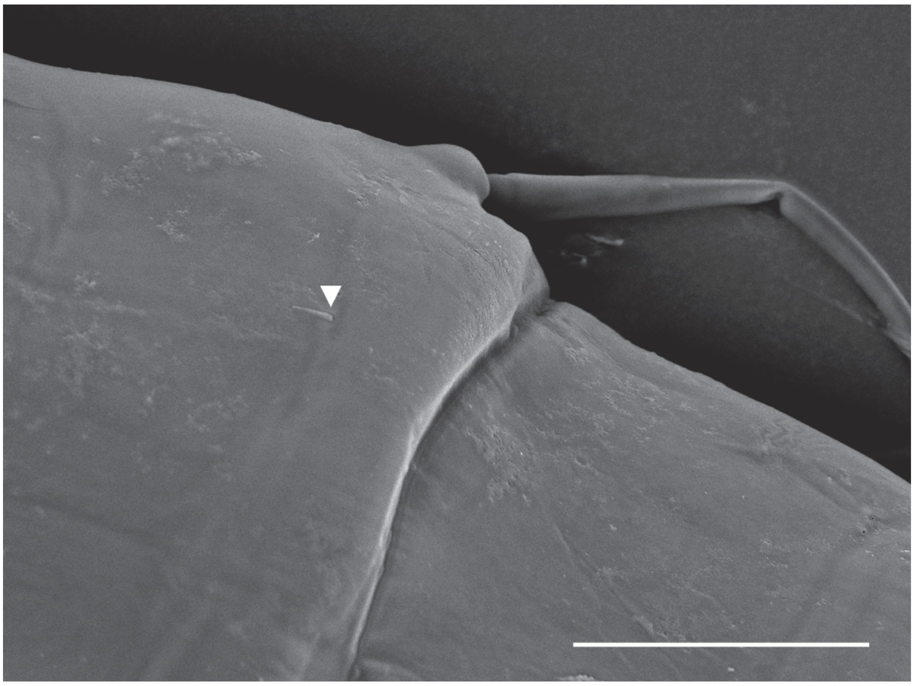

FIGURE 4. Scanning electron micrograph of female antennule ancestral segments IV and V of *Calanus helgolandicus*. White arrow indicates dorsal hair sensillum but no macula cribrosa on segment IV. Scale bar represents 50 µm.

Male antennule (Fig. 1E). The presence of a right side geniculation was tested by examining the intrinsic musculature. There was an expected break in muscle bundles such that they did not pass through the joint between segments XX and XXI (Fig. 1E). The posterior muscle attaches to the proximal border of segment XX and the anterior muscle passes through the joint between segments XIX and XX and attaches to the proximal border of segment XXI. The right antennule geniculation of *Bradycalanus* and *Bathycalanus* appears to have the same type of muscle arrangement; *Elenacalanus* nom. nov. was not checked. We noted that the musculature of the joints around the geniculation differs slightly from that of *Euaugaptilus* Sars, G.O., 1920 (Boxshall 1985). In *Euaugaptilus*, the posterior muscle inserts on the proximal rim of ancestral segment XXI whereas, in *Megacalanus* this muscle inserts on the proximal rim of segment XX. That is, in *Megacalanus*, there is no antagonistic muscle opposing the action of the anterior muscle which is inserted on the proximal rim of segment XXI therefore abduction must be effected by cuticular elasticity—probably a weaker system than in *Euaugaptilus*. Geniculation of the right male antennule was not used in this cladistic analysis since it is a synapomorphy for the whole family.

Antenna (Figs 2O, 3A–C). The form of exopod setae on ancestral segments I to III differs among genera: ranging from a relatively well developed seta that is longer than its segment (Fig. 2O), to one that is shorter than its segment (Fig. 3A), a vestigial remnant on a raised projection (Fig. 3B), or absent (Fig. 3C) (Chars 18, 19). Ancestral segment IV may have a seta that extends beyond the distal border of the exopod (Fig. 2O), extends short of this border (Fig. 3A, B), or is completely absent (Fig. 3C) (Char. 20).

Mandible (Fig. 3D–H). The large ventral tooth of the coxal gnathobase may differ in orientation relative to the main plane of the gnathobase. This large ventral tooth is usually orientated at right angles to the main plane thus appearing to taper when the gnathobase is mounted flat (Fig. 3E). In *Bradycalanus* this tooth is oriented at an oblique angle to the main plane such that it presents as having a very broad base (Fig. 3D) (Char. 21). Endopod segment 1 bears a large lobe which plesiomorphically has 4 setae the proximal-most of which is added last (Ferrari 1995). In nauplius VI (NVI) of *Megacalanus princeps* (see Fig. 10E), 4 setae are already present so we do not have evidence in this family as to which seta appears last. It is only in *Elenacalanus* nom. nov. that this number is reduced to 2. Here we suggest that it is the 2 shortest setae of *Megacalanus* (Fig. 3G) that are absent in *Elenacalanus* nom. nov. (Chars 22, 24). Additionally, the short distal seta may be well developed in *Megacalanus* (see Fig. 3G) or short to vestigial as in *Bradycalanus* (Fig. 3H) and *Bathycalanus* (Char. 23). Endopod segment 2, plesiomorphically, has 11 setae. The 2 shorter setae appear at copepodite 1 (CI) in *Ridgewayia klausruetzleri* (Ferrari & Dahms 2007), one on each surface, whereas these setae are present at NVI in *M. princeps* and are on the same surface in the adult but may be present or absent (Char. 25) (Fig, 3F, H) and when present either well-developed or vestigial (Char. 26) (Fig. 3G, H).

Maxillule (Fig. 5A, B). The basal exite usually carries one seta but may be absent in some species (*Ba. eltaninae* and *Ba. princeps*) (Char. 27). Homologies among other setae that vary in numbers in the Megacalanidae were investigated using copepodite development and topographical position. Some evidence comes from a CII of *Megacalanus princeps*, examined during this study. Other evidence comes from the literature (Heron & Bowman 1971; McKinnon & Arnott 1985; Lawson & Grice 1973; Bradford *et al.* 1988; Ferrari 1995). The maxillule praecoxal arthrite posterior surface has 4 posterior surface setae plesiomorphically (Fig. 5A). Two posterior surface setae on the praecoxal arthrite are usually found at copepodite stage I (CI), 3 at CII (see Fig. 11) and 4 at CIV with the extra seta at each stage being added at the distal end of the row. Therefore, we assume that it is the 2 distal-most setae that are absent when there are only 2 posterior surface setae present (Chars 28–29). Apart from the posterior surface setae, the setation of the praecoxal arthrite is evolutionarily conservative in the Megacalanidae as is the setation of the exopod (11 setae) and coxal epipodite (7 long + 2 short setae). The setation of the rest of this limb varies with species and genus. The coxal endite plesiomorphically has 5 setae but may have 0, 1, 2 or 4 setae; basal endite 1 may have 2 or 4 setae; basal edite 2 may have 2, 3, or 4 setae; endopod segment 1 may have 1, 2, or 3 setae; and endopod segment 2 may have 0, 1, 2 or 4 setae. At present, it is impossible to establish setal homologies based on developmental data. Therefore, we assume, that where numbers of setae are equal then it is the same setae that have failed to develop (Chars 30–34). Homologies amongst setae on endopod segment 3 were assumed to be related to setal position (Chars 35–37) (Fig. 5B). Maximum numbers of setae found on endopod segments 1, 2 and 3 in *Megacalanus* are: 3 (2 anterior and 1 posterior), 4 (3 anterior and 1 posterior), and 6 + 1 small posterior seta, respectively.

Maxilla (Figs 5C–J, 6A, B). The number of setae on the maxilla is conservative within the Megacalanidae, although the overall development of this limb and its setae varies among genera. In *Megacalanus* the maxilla is developed similarly to *Calanus.* The coxal epipodite seta is usually present (Fig. 5F) but is vestigial in *Bradycalanus* (Char. 38). In *Megacalanus*, all setae (apart from the claw-like seta on the basal endite), as well as having very small closely spaced spinules, are bordered by long, widely spaced auxiliary spinules (Char. 40) (Fig. 5C). In *Bradycalanus* the maxilla is relatively enlarged and only the setae of praecoxal endites 1 and 2 and coxal endite 1 have auxiliary spinules (Char. 39). None of the maxilla setae in *Bathycalanus* or *Elenacalanus* nom. nov has auxiliary spinules (see Fig. 5D). The longer, stiffly curving setae of coxal endite 2 have a concave border differing in appearance compared with the convex border. In *Bradycalanus* there is a row of long, closely spaced soft setules along more than ½ of the distal concave surface (Fig. 5G). In *Bathycalanus*, the longest maxillary setae are greatly enlarged, finely tapering and completely curled back on themselves distally (Char. 44) (Fig. 5I). These setae usually extend to and beyond the rostrum and are bordered along the distal half of the concave border by one row of fine, long setules. In the renamed genus (*Elenacalanus* nom. nov.), these longest maxilla setae curl slightly in a semicircle (Fig. J). The terminal setae of *Megacalanus* and *Bradycalanus* curve gently along their length (Fig. 5H). Endopod segment 1 has 4 setae although only one seta is well-developed; the smallest setae may be developed (Fig. 5E) or vestigial (Fig. 6A) (Char. 41). The 2 inner setae of endopod segment 2 are differently developed in each genus (Char. 42) (Fig. 5F, 6A, B) and the convex border may be naked or spinulose (Char. 43). In *Megacalanus* both inner setae are well-developed (Fig. 5F) with each side lined with small spinules along the distal ¾ and also have long, sparse, auxiliary setules along each seta. In *Bradycalanus* the proximal inner seta of endopod segment 2 is reduced to a slim vestige (Fig. 6A), while the long seta is curved and naked. In the other genera the concave border is lined by long spinules along the distal 2/3 and the convex border is naked. In *Bathycalanus* the proximal inner seta is represented by a vestige which takes the form of an oval basal part drawn out into a curved spinule (Fig. 6B) and the convex surface of the distal seta is lined by long spinules.

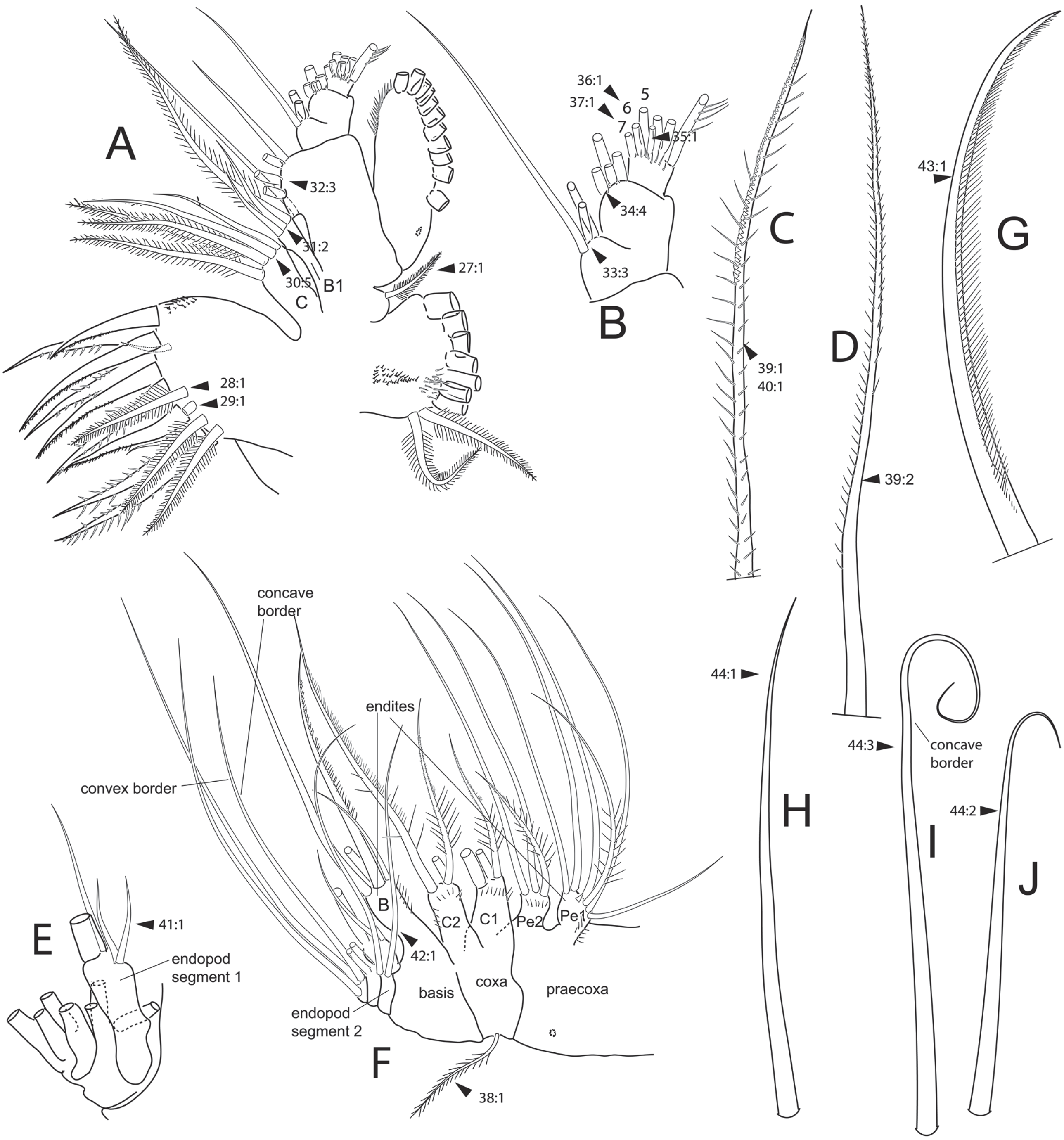

FIGURE 5. Selected characters and their states as detailed in Table 3. A, maxillule of *M. ohmani* **n. sp.** (C = coxal endite, B1 = basal endite 1); B, endopod of maxillule of *M. ohmani* **n. sp.**; C, maxilla praecoxal endite 1 seta of *M. princeps*; D, seta from praecoxal endite 1 of maxilla of *Ba. richardi*; E, maxilla endopod of *M. ohmani* **n. sp.**; F, maxilla of *M. ohmani* **n. sp.** (B = basal endite, C1, 2 = coxal endite 1 and 2, Pe1, 2 = praecoxal endties 1, 2); G, seta of coxal endite 2 of maxilla of *Br. enormis*; H, terminal maxilla seta from *Megacalanus* and *Bradycalanus*; I, terminal maxilla seta from a *Bathycalanus*; J, terminal maxilla seta from a *Elenacalanus* nom. nov. Specific 'character : state' is indicated in the form '◄ 3:2'.

Maxilliped (Fig. 6C). The maximum number of setae (found in *Megacalanus, Bradycalanus* and *Bathycalanus*) on endopod segments 2–6 is 4, 4, 3, 3+1 outer, 3+1 outer, respectively, numbered from proximal to distal (Fig. 6C). The setae on endopod segments 1 and 2 are conservative throughout the family. During development, e.g. *Clausocalanus* Giesbrecht, 1888 (Clausocalanoidea) (Heron & Bowman 1971), setae are added proximally on endopod segments during development. Therefore, where there are fewer than the maximum number of setae, it is assumed that they fail to develop in reverse order to their addition (Chars 45–53). The proximal setae may be well-developed or small (s) (Chars 46, 48, 52).

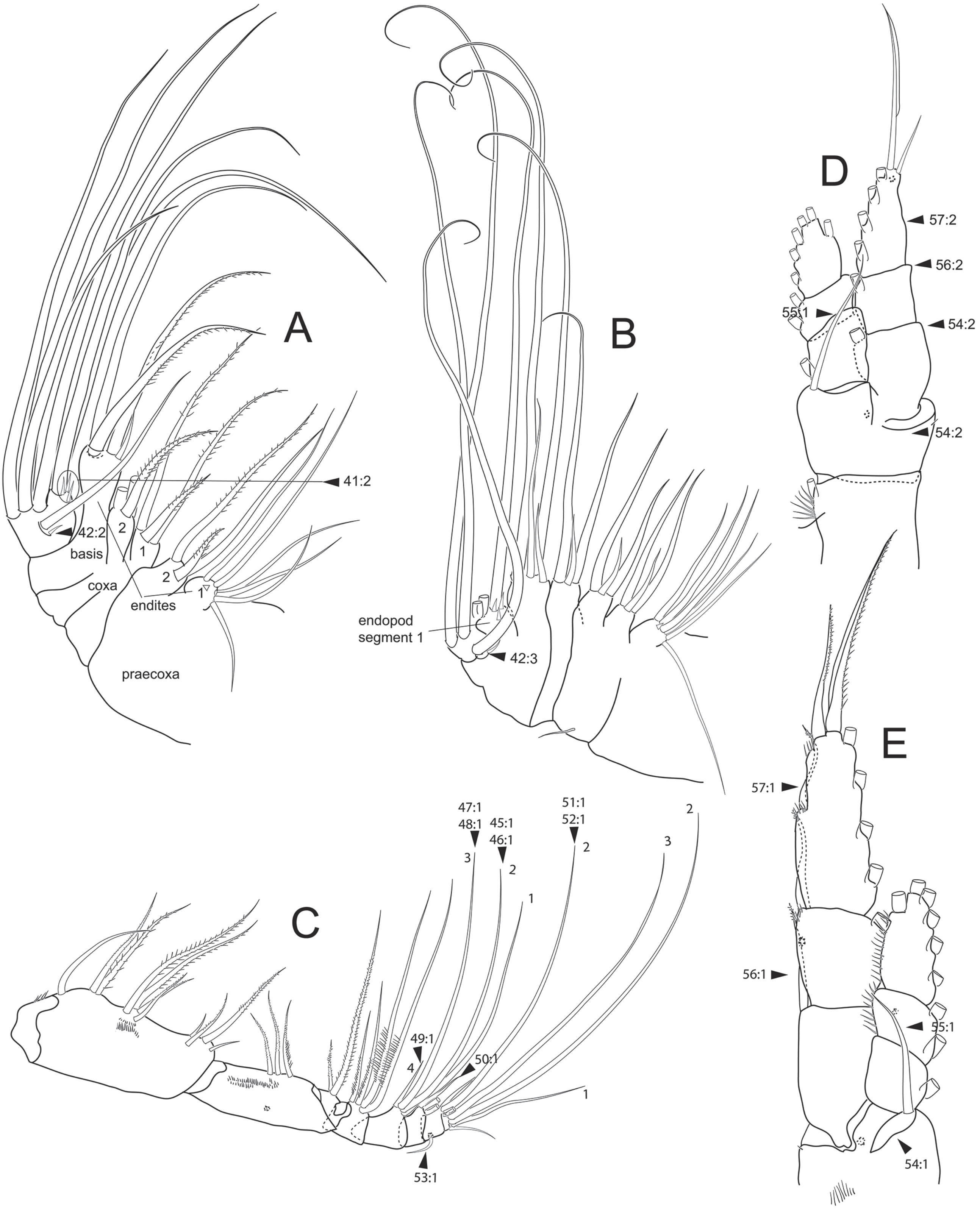

FIGURE 6. Selected characters and their states as detailed in Table 3. A, maxilla of *Br. abyssicolus* **n. sp.**; B, maxilla of *Ba. bradyi*; C, maxilliped of *M. ohmani* **n. sp.**; D, leg 1 of *Ba. dentatus* **n. sp.**; E, leg 1 anterior view of *M. ohmani* **n. sp.** Specific 'character : state' is indicated in the form '◄ 3:2'.

Leg 1 (Fig. 6D, E). The basis may or may not have a proximally-directed anterodistal hook-like process (Fig. 6D, E) (Char. 54), the inner distal seta may be straight or slightly curved (Fig. 6D, E), or S-shaped (Char. 55), and the distolateral corners of exopod segments 1 and 2 and the mid outer border of segment 3 may be with (Fig. 6E) or without (Fig. 6D) a spine (Chars 56, 57).

Outgroup taxon. The aim in choosing an outgroup in a cladistic analysis is to select an taxon the character states of which help to polarise character state transformations in the ingroup taxa and identify transformational sequences of character states. The current phylogenetic hypothesis concerning calanoid copepod families (Bradford-Grieve *et al.* 2014) has the Calanidae as sister to the Megacalanidae. The exemplar chosen is *Calanus helgolandicus* because this is one of the taxa used in the outgroup for the genetic analysis. Other exemplars were considered (*Disseta* Giesbrecht, 1889—Augaptiloidea, *Centropages* Krøyer, 1849—Centropagoidea, and *Paracalanus* Boeck, 1865—Megacalanoidea) but aspects of the morphology of these taxa are derived relative to the most plesiomorphic ingroup taxon. In the first two genera there are fewer setae on the endopod of the maxillule. In the last case, while some features are plesiomorphic, leg 1 endopod is 2-segmented (instead of 3-segmented as in the Megacalanidae) and leg 5 in both sexes is highly modified compared with the Megacalanidae, thus it is impossible to reliably identify certain homologies.

Morphology-based phylogenetic analysis. Initially, a database of 24 taxa and approximately 70 morphological characters was created using the DELTA software (Dallwitz *et al.* 1993; Coleman *et al.* 2010) and output as a nexus file. Preliminary analysis showed that missing data had a big impact on the results with many trees with ambiguous character state changes. Therefore, species with some unknown characters states (*Bathycalanus eximius*, *Ba. pustulosus, Ba. sverdrupi* and *Ba. inflatus*) were omitted along with male characters since males are not known for a number of species. Thus, a data matrix of 20 taxa and 57 morphological characters (Tables 3, 4) was used in the phylogenetic analysis. The majority of characters are binary, although ten have three states, three have 4 states and 1 has five states. Inapplicable characters were coded '?'. Characters are unordered and equally weighted. Since characters are unordered, the scores given for each state (1, 2, 3 etc.) imply nothing about polarity or order.

Phylogenetic analysis of the data matrix (Table 4) under maximum parsimony (MP) was conducted in PAUP 4.0b10 (Swofford 2002). Character states were polarised using *Calanus helgolandicus,* since the Calanidae is sister to the Megacalanidae (Bradford-Grieve *et al.* 2014). *Calanus helgolandicus* is designated as outgroup, and cladograms were rooted with the single outgroup. Analyses were conducted using the heuristic search (1000 replicates with random input order; branch swapping: tree-bisection-reconnection). Strict consensus and majority-rule consensus trees were computed. Bootstrap support on unweighted data was determined in PAUP* (heuristic search; random addition sequence; 50% minimum bootstrap partition frequency; 1000 bootstrap replicates). The dataset was then analysed under a single round of successive weighting using the rescaled consistency index (Farris 1969). Character state distributions were studied in MacClade 4.0 (Maddison and Maddison 2000).

Genetic data. Specimens for genetic analysis were obtained from live animals and from samples preserved in 95% ethanol collected from various locations (Table 1). Ethanol was changed every 24 h, until the ethanol remained clear and colourless. DNA was obtained from two legs (one from each of the 2nd and 3rd pairs to avoid the potential loss of diagnostic characters), that were excised from each individual under the stereomicroscope. Preserving the integrity of the individual allowed the direct correspondence between gene sequences and the morphological description for each single individual. DNA was extracted using the DNeasy Blood & Tissue Kit (QIAGEN) or the E.Z.N.A.® Mollusc DNA Kit (OMEGA) following manufacturer instructions. Elution volumes ranged from 50 to 100 µL.

PCR reactions were carried out to amplify the genes for the mitochondrial cytochrome c oxidase I (COI), the nuclear genes for the Histone 3 (H3), the 5' end region for the ribosomal subunits 18S and 28S, as well as the region of the ribosomal transcription unit comprising the Internal transcribed spacer 1 (ITS1), the 5.8S ribosomal subunit and the Internal transcribed spacer 2 (ITS2). PCR amplifications were performed in a total volume of 25 µL, including 5 µL of 5x Green GoTaq Flexi Buffer, 2.5 µL of 25 mM $MgCl_2$, 1 µL of dNTPs (final concentration 0.2 mM each), 1 µL of each primer (10 µM), 0.75 units of GoTaq Flexi DNA Polymerase (Promega) and 3 µL of DNA sample. 35 cycles were used for all PCR reactions. Primers used and annealing temperatures are described in Table 5. PCR products were run in a 1.5 % agarose gel, and the product band was excised and purified using the QIAquick Gel Extraction Kit (QIAGEN). Both strands of the marker were sequenced using the same set of primers as in the original amplification and Big Dye Terminator Ver. 3.1 (Applied Biosystems Inc., ABI), and run on an ABI 3130 Genetic Analyzer capillary DNA sequencer.

Gene-based analysis. Sequences from both strands were compared using MEGA ver. 6 (Tamura *et al*. 2013). Alignment of the strands was carried out in ClustalW (Thompson *et al.* 1994) as implemented in MEGA, and refined by eye to minimise the effect from the insertions and deletions typical from the transcribed spacers. In the case of the amplified product comprising the ITS1, ITS2 and 5.8S regions, the ITS1 and ITS2 were considered as independent evolutionary units. Final alignments of all sequences were carried out in MAFFT (Katoh & Standley 2013) using the l-insi option, with the exception of the ITS-2 region, for which the secondary structure was taken into consideration using RNAsalsa (Stocsits *et al*. 2009). The amplified region for 18S was found to be conserved within genera, and therefore is not further analysed. Alignment and ML and Bayesian trees can be accessed on TreeBASE (Bradford-Grieve *et al.* 2016a).

TABLE 5. PCR and sequencing primer names, sequences and annealing temperature (A.T.), as well as approximate marker length (in bp). Abbreviations are: forward primer (F); reverse primer (R); base-pairs (bp).

Gene	Primer name, sequence, reference		A.T.	Length (bp)
18S	18SE (F) 18SL (R)	CTGGTTGATCCTGCCAGT (Hillis and Dixon 1991) CACCTACGGAAACCTTGTTACGACTT (Hamby and Zimmer 1988)	52°C	1650
28S	28S F1a 28S R1a	GCGGAGGAAAAGAAACTAAC (Ortman 2008) GCATAGTTTCACCATCTTTCGGG (Ortman 2008)	50°C	850
COI	LCO1490 (F) HCO2198 (R)	GGTCAACAAATCATAAAGATATTGG (Folmer *et al.* 1994) TAAACTTCAGGGTGACCAAAAAATCA (Folmer *et al*. 1994)	45°C	
H3	H3AF H3AR	ATGGCTCGTACCAAGCAGACVGC (Colgan *et al.* 1998) ATATCCTTRGGCATRATRGTGAC (Colgan *et al.* 1998)	60°C	326
ITS1, 5.8S, ITS2	ITS1 ITS4	TCCGTAGGTGAACCTGCGG (White *et al.* 1990) TCCTCCGCTTATTGATATGC (White *et al*. 1990)	50°C	289 (ITS1) 352 (ITS2)

Molecular diagnosis. Since all sequences for each marker had the same length, genetic distances within-species and between species were calculated as number of base pair differences. Amplification of COI was only successful for the few *Megacalanus* individuals obtained from shallow samples, likely due to primer mismatch and/or degradation of mitochondrial DNA during the deep net sampling process (Table 2). The between-species genetic differences cut-offs for markers other than COI were established by direct comparison on individuals for which both COI and the other markers (H3 and the multiple ribosomal markers) were available.

Molecular phylogeny. Initially, phylogenetic analyses included only individuals from the Megacalanidae. Maximum Likelihood phylogenetic analyses on the partitioned data were run in RAxML ver. 7.5.5 (Stamatakis 2006, 2014) under the GTRGAMMA option and complete random starting tree, and confidence values were obtained after 10,000 bootstrap replicates. Neighbor-Joining analyses were carried out in MEGA ver. 6 (Tamura *et al.* 2013) with evolutionary distances computed using the Maximum Composite Likelihood method (Tamura *et al.* 2004), and confidence values obtained after 10,000 bootstrap replicates. Maximum Parsimony phylogeny was reconstructed in MEGA ver. 6 (Tamura *et al.* 2013), using the TBR algorithm; initial trees were obtained by random addition of sequences (100 replicates). Bayesian inference of the phylogeny was obtained using the parallel version of MrBayes ver. 3.2.1 (Altekar *et al.* 2004; Ronquist *et al.* 2012) under the GTR+G evolutionary model with unlinked parameters across the markers (mirroring the RAxML approach). The analysis was run to 3,000,000 generations, and it was sampled every 1000 generations. Convergence was assessed according to the Estimated Sample Size (EES) and the Potential Scale Reduction Factor (PSRF; Gleman & Rubin 1992) values. The majority-rule phylogenetic tree and Bayesian posterior probabilities (BPP) were calculated after discarding the first 500 sampled trees (Burn-in). Sequences for *Paraheterorhabdus* (*Antirhabdus*) *compactus* (Sars), *Centropages violaceus* (Claus), and one representative for each of the other families belonging to the Megacalanoidea (Sewell, 1947), *Paracalanus aculeatus* (Giesbrecht) and *Calanus helgolandicus*, were included as outgroups for the phylogenetic analyses (Table 6). Due to the gap-rich characteristic of these spacers, the ITS1 region was impossible to unambiguously align when including the outgroup species even after using gap-rich region oriented alignment methods in MAFFT (Katoh & Standley 2013), and therefore was coded as missing data for the analyses to avoid spurious results.

TABLE 6. Individual taxa, gene sampling and GenBank accession numbers of each sequence used for the molecular study. In italics, sequences from previous studies downloaded from GenBank.

Species	Voucher #	COI	28S	H3	ITS1-5,8-ITS2
Paraheterorhabdus compactus		-	*HM997026*	*HQ263667*	KU053642
Centropages violaceus		-	*HM997030*	*HQ263668*	KU053643
Calanus helgolandicus		-	*HM997038*	*HQ263670*	KU053641
Paracalanus aculeatus		-	*AF385459*	*JQ912007*	-
Megacalanus princeps	Co119.5.1	-	KU053519	KU053565	KU053614
	Co119.4.1	-	KU053520	KU053566	KU053617
	Co119.2.1	-	KU053521	KU053567	KU053615
	Co119.3.1	-	KU053522	KU053568	KU053616
Megacalanus frosti	Co439.2.2	KU053559	KU053523	KU053569	KU053632
	Co439.2.1	-	KU053524	KU053570	KU053631
	Co439.10.1	KU053560	KU053525	KU053571	KU053630
	Co439.5.1	KU053558	KU053526	KU053572	KU053636
	Co439.1.2	-	KU053527	KU053573	KU053629
Megacalanus ericae	Co439.1.1	-	KU053528	KU053574	KU053628
	Co439.7.1	-	KU053529	KU053575	KU053638
	Co439.8.1	-	KU053530	KU053576	KU053639
	Co439.4.1	KU053563	KU053531	KU053577	KU053635
	Co439.3.2	KU053564	KU053532	KU053578	KU053634
	Co439.3.1	KU053561	KU053533	KU053579	KU053633
	Co439.6.1	KU053562	KU053534	KU053580	KU053637
Elenacalanus princeps	Co24.3.2	-	KU053535	KU053581	KU053610
	Co24.5.1	-	KU053536	KU053582	KU053611
	Co24.1.1	-	KU053537	KU053583	KU053605
	Co24.7.1	-	KU053538	KU053584	KU053613
	Co24.1.4	-	KU053539	KU053585	KU053607
	Co24.1.2	-	KU053540	KU053586	KU053606
	Co24.2.1	-	KU053541	KU053587	KU053608
	Co24.3.1	-	KU053542	KU053588	KU053609
	Co24.6.1	-	KU053543	KU053589	KU053612
Bradycalanus typicus	Co303.1.1	-	KU053544	KU053590	KU053618
	Co303.1.2	-	KU053545	-	KU053619
	Co384.1.1	-	KU053546	-	KU053625
Bradycalanus enormis	Co360.1.1	-	KU053547	KU053591	KU053620
Bathycalanus tumidus	Co375.1.3	-	KU053548	KU053592	KU053623
	Co375.1.1	-	KU053549	KU053593	KU053621
Bathycalanus richardi	Co22.2.1	-	KU053550	KU053594	KU053602
	Co22.4.1	-	KU053551	KU053595	KU053604
Bathycalanus milleri	Co411.1.2	-	KU053552	KU053596	KU053627

......continued on the next page

TABLE 6. (Continued)

Species	Voucher #	COI	28S	H3	ITS1-5,8-ITS2
Bathycalanus brady	Co375.1.2	-	KU053553	KU053597	KU053622
	Co376.1.1	-	KU053554	KU053598	KU053624
	Co411.1.1	-	KU053555	KU053599	KU053626
	Co441.3.1	-	KU053556	KU053600	KU053640
Bathycalanus adornatus	Co22.3.1	-	KU053557	KU053601	KU053603

Systematic account

Family MEGACALANIDAE Sewell, 1947

Differential diagnosis. Large copepods > 8 mm long. Female urosome of 4 free somites, of male 5 free somites. 'Cephalic dorsal hump' present in male. Female antennule with segments I and II separate, at least segments II–III, III–IV, X–XI fused. Hair sensilla on dorsal surface of all or some of ancestral segments I–V. Right antennule of male geniculate between ancestral segments XX and XXI, segments I and II usually separate, at least segments II–III, III–IV, IX–XI and XXII–XXIII fused, segments around geniculation (XIX–XXI) with gripping elements. Clavate (club-shaped) seta present on ancestral segment XI on both male antennules. Aesthetascs larger than in female, and longest on proximal segments (longer than the width of segments). Antenna exopod 10-segmented with ancestral segments I and II separate, segments II–IV and IX–X fused. Male mouthpart setation not reduced (except in *Elenacalanus* nom. nov.). Mandible endopod segment 1 with large inner lobe. Maxillule basal exite usually with 1 seta (except in some *Elenacalanus* nom. nov.). Maxilla coxal epipodite with 1 seta. Maxilliped ancestral endopod segment 5 without enlarged outer setae in male. Legs 1–5 with 3-segmented rami in both sexes. Exopod segment 3 of legs 2–4 with 3 outer edge spines and terminal spine with serrated outer border. Legs 1–5 basis with outer distal seta or spine. Leg 5 of male and female similar to other legs; inner distal border of male left exopod segment 2 with specialised seta.

Description. Large calanoid copepods up to 17 mm total length, pedigerous somites 1 to 5 all separate. Pair of rostral filaments of varying form; anterior head in dorsal view of varying shapes. 'Cephalic dorsal hump' present in male. Urosome of female comprising 4 free somites, genital double-somite with small anteroventral genital operculum covering genital atrium into which opens pair of seminal receptacles and gonopores (Barthélémy 1999); male with 5 free urosomites. Caudal rami with seta I absent, setae II and III lateral, setae IV–VI terminal (seta V longest), seta VII inserted at inner distal corner on small projection. Mouthparts usually identical in both sexes, setation not reduced except in *Elenacalanus* nom. nov.

Antennule of female usually extending well beyond caudal rami. Female with ancestral segments II–IV, X–XI fused, segments XXVII and XXVIII separate. Most setation elements modified setae (ms) or aesthetascs (a), very few of naked simple type (ss). Setation of segments as follows: I—1ms, 1a, 2ss (varying in size), II to XXI—2ms, 1a; XXII—1 ms, 1a; XIII—1ms, 1/0a; XXIV to XXV—2ms 1a; XXVI—2 ms; XXVII—2 ms; XXVIII—3ms, 1a, 1ss. Male antennule geniculate on right. Left antennule with ancestral segments II–IV, IX–XI fused, XXVII and XXVIII separate, aesthetascs doubled on at least segments III, V, VII, IX, XI–XIV. Right antennule with ancestral segments II–IV fused, IX–XI, XIV–XV fused or separate, XXI/XXII–XXIII fused, XXVII and XXVIII separate, aesthetascs doubled on at least segments III, V, VII, IX, XI–XIII/XIV.

Antenna with separate coxa and basis, coxa with 1 inner plumose seta and basis with 2 inner setae, each ornamented with short setules. Exopod and endopod approximately equal in length. Endopod 2-segmented although line of fusion between segments 2 and 3 visible on posterior surface; segment 1 with 2 inner setae and short longitudinal row of outer setules, terminal segment with 9+7 setae. Exopod ancestral segment I separate from segment II, segments II–IV and IX–X fused; compound terminal segment IX–X with 1 + 3 terminal setae, segments V–VIII each with long plumose seta, ancestral segments I–IV each with seta of variable development.

Mandible coxal gnathobase with five complex teeth with opaline tips. Largest tooth ventrally situated, separated from adjacent tooth by wide gap, form and orientation of which varies with genus; 4 following teeth progressively decreasing in size, followed by 3 simpler teeth, dorsal-most tooth longest; and finally, 1 long, lash-like element situated dorsally, bordered with wide setules. Basis with 4 inner setae; endopod 2-segmented, segment 1 with large inner lobe and 4 distal inner setae (1 or 2 setae may be very small or absent), segment 2 with up to 11 terminal setae, 2 of them short on one surface or absent; exopod 5-segmented with 1, 1, 1, 1, 2 setae.

Maxillule praecoxal arthrite with up to 15 setae (up to 2 of the 4 ancestral posterior surface setae may be absent in *Bathycalanus* and *Elenacalanus* nom. nov.); coxal endite with 0, 1, 2, or 5 terminal setae, coxal epipodite with 9 setae (2 proximal setae shorter, vestigial or absent); basal endites 1 and 2 with 2–4 and 2–4 setae respectively, exite usually represented by 1 seta except for some *Elenacalanus* nom. nov.; basis and endopod separate or fused; endopod with segments 1 and 2 fused—fusion line visible on anterior surface, segment 3 separate, setation of endopod segment varying with genus and species, with 1–3; 0, 1, 2, 4; 5–6 + 1 small anterior surface seta, respectively; exopod usually with 11 setae.

Maxilla praecoxal endites 1 and 2 with 6+1 small, spine-like seta and 3 setae, respectively; coxal endites 1 and 2 each with 3 setae, coxal epipodite with 1 seta (vestigial in *Bradycalanus*); basal endite longest, with 4 setae; endopod segment 1 with short lobe bearing 3 small + 1 large setae, endopod segments 2–4 apparently with 2 (1 often vestigial), 2, 3 setae. Inner surfaces of praecoxal to basal endites each with 1 seta shorter and more densely lined with long spinules; longer setae of at least basal endite and endopod of form varying with genus.

Maxilliped directed ventrally so that setae on syncoxa and basis directed towards midline; syncoxa with 1, 2, 4, 4 setae; basis with 3 setae, patch of setules on anteroproximal surface. Endopod segment 1 usually separate, bearing 2 setae; endopod segments 2–6 plesiomorphically with 4, 4, 3, 3+1 (outer seta directed proximally), 4 setae (some setae reduced in size or absent in different genera), respectively.

Legs 1–5 biramous, each ramus 3-segmented with setal formula (Roman numerals indicate spines, Arabic numerals setae, outer border setation listed to left in each group separate by ';') as follows:

Leg 1 (Coxa 0-1. Basis 1-1. Exopod 0/I-1; 0/I-1; I/II,1,4. Endopod 0-1; 0-2; 1,2,3);

Leg 2 (Coxa 0-1. Basis I-0. Exopod I-1; I-1; III,1,5. Endopod 0-1; 0-2; 2,2,4);

Leg 3 (Coxa 0-1. Basis I-0. Exopod I-1; I-1; III,1,5. Endopod 0-1; 0-2; 2,2,4);

Leg 4 (Coxa 0-1. Basis 1-0. Exopod I-1; I-1; III,1,5. Endopod 0-1; 0-2; 2,2,3);

Leg 5♀ (Coxa 0-0. Basis 1-0. Exopod I-0; I-1; II,1,4. Endopod 0-1; 0-1; 2,2,2);

Leg 5♂ left (Coxa 0-0. Basis 1-0. Exopod I-0; I-1; II,1,0. Endopod 0-0; 0-1; 2,2,2);

Leg 5♂ right (Coxa 0-0. Basis 1-0. Exopod I-0; I-0/1; II,1,0. Endopod 0-0; 0-1; 2,2,2).

Leg 1 with inner seta on coxa, outer distal seta of basis vestigial, basis anterodistal surface usually naked but with hook-like process in *Megacalanus*. Distolateral corner of endopod segment 1 rounded, spine usually present on outer distal corners of exopod segments 1 and 2 except in *Bathycalanus* and *Elenacalanus* nom. nov. Legs 2–4 with seta on inner margin of coxa; basis with outer distal spine; pore openings located on anterior surfaces at base of outer edge spine of exopod segments 1–3. Leg 5 of female with outer distal corner of endopod segment 1 rounded; pore openings on anterior surface at base of outer border spines. Leg 5 of male slightly asymmetrical because of specialised seta on inner distal corner of left side exopod segment 2 (on exopod segment 2 on both sides in *Bathycalanus unicornis*), setulose inner border of left exopod segment 3, and asymmetrically placed spine on inner borders of exopod segment 3 on both sides, interpreted here as being the terminal spine of other legs.

Type genus. *Megacalanus* Wolfenden, 1904

Remarks. Sewell (1947) implies the type genus for the Megacalanidae is *Megacalanus* Wolfenden, 1904 because the family name is formed from this genus (ICZN 1999, Article 63).

Genus Megacalanus Wolfenden, 1904

Macrocalanus Sars, 1905, p. 26.
?Pseudolovenula Marukawa, 1921, p13, pl. 1 figs 10–13, pl. 2 figs 1–4.

Differential diagnosis. As for Megacalanidae plus following character states: Anterior head without spine-like processes, rostral filaments tapering to point. Female antennule ancestral segment XXIII without aesthetasc, and segments XIV–XVII have ventral surface tooth row. Female and male ancestral segments I–V each with very small hair sensillum on dorsal surface. Right male antennule segments XIV–XV and XXII–XXIII fused, at least segments XX and XXI with fused gripping elements. Antennal exopod ancestral segments I–IV bearing relatively well-developed setae, on segments 1-III each seta longer than its segment, on segment IV seta extends beyond distal border of exopod. Mandibular gnathobase with ventral tooth set at right angles to main plane of gnathobase therefore appears tapering and similar to other teeth; endopod segment 1 with 4 setae, endopod segment 2 with 9 large and 2 short proximal setae. Maxillule praecoxal arthrite with 4 posterior surface setae, coxal endite with 5 setae, basal endites 1 and 2 with 4 setae each, endopod segment 2 with 4 setae. Maxilla modestly developed; longest setae extend as far as anterior labrum; most setae bear auxilliary setules. Maxilliped modestly developed, longest setae extending to rostrum, endopod segments 3–5 with proximal seta shortest. Leg 1 basis usually with anterior inner surface bearing large hook-like process onto which straight inner seta inserted, exopod segments 1 and 2 each bear distolateral articulated spine, segment 3 with 2 outer border spines. Specialised seta on male left leg 5 with base greatly enlarged into outer border bulge then tapering into short terminal section bordered by long setules. Circular or oval distoanterior 'macula cribrosa' present: between rostral points; at base of all antennular aesthetascs, associated with some dorsal surface hair sensilla on ancestral segments I–V depending on species, and distoposteriorly on ancestral segment XXVIII; on mandibular gnathobase, proximally near insertion of basis; on maxillule outer proximal surface of exopod; on maxilliped inner surface of basis and endopod segment 5; on anterior surface of basis of legs 1–5 adjacent to insertion of exopod segment 1; and leg 1 exopod segment 2.

Type species. *Megacalanus princeps* Wolfenden, 1904

Type locality. 51–60°, 6–13°W.

Description. Female: Anterior margin of head rounded or crested without anterior spine-like processes. Rostrum ventroposteriorly-directed, extending into two long cuticular extensions, tapering to point, 1 macula cribrosa situated at base, between rostral points. Urosome of four free somites. Genital double-somite symmetrical in dorsal view, approximately as long as wide with widest width at about anterior one third; with small anteroventral genital operculum and pair of seminal receptacles. Posterior borders of pedigerous somite 5 bluntly triangular or rounded in lateral view. Caudal rami with seta I absent, setae II and III lateral, setae IV–VI terminal (seta V longest), seta VII inserted at inner distal corner on small projection.

Antennule extending up to 8 segments beyond caudal rami, ancestral segments II–IV, X–XI fused; XXVII and XXVIII separate. Most setation elements modified setae (ms), aesthetascs (a), or few naked simple setae (ss); proximal setae on ancestral segment I small but developed. Posterior setae on ancestral segments XXIV to XXVI pseudoannulate as well as plumose, and posteriormost seta of terminal pair on segment XXVIII, pseudoannulate. Setation of segments as follows: I—1ms, 1a, 2 ss; II to XXI—2ms, 1a; XXII—1ms, 1a; XXIII—1ms; XXIV to XXV—1+1ms, 1a; XXVI—1+1ms; XXVII—1+1ms; XXVIII—3ms, 1ss, 1a. Distoanterior maculae cribrosae located at base of all aesthetascs and also distoposteriorly on ancestral segment XXVIII. Dorsal surface of ancestral segments I–V each with hair sensillum which may or may not be accompanied by macula cribrosa, depending on species (see Figs 7H, 20G). Ventral surface of ancestral segments XIV to XVII with longitudinal distoventral row of small teeth, distoposterior border of segments XV and XVI may or may not be lined by blunt teeth.

Antenna with separate coxa and basis; coxa with 1 long inner plumose seta and inner tuft of setules, basis with 2 inner setae each ornamented with rows of short setules. Exopod slightly longer than endopod; endopod 2-segmented although line of fusion between segments 2 and 3 visible on posterior surface; segment 1 with 2 inner, almost naked setae and short longitudinal row of outer setules, terminal segment with 9+7 setae and patch of long setules; exopod in anterior view with segments I and II separate, segments II–IV fused, although ancestral segments I–IV appear to be fused in posterior view; terminal segment IX–X with 1 + 3 terminal setae, segments V–VIII each with long plumose seta, ancestral segments II–IV with 3 short but well developed setae bearing short setules and segment I with 1 short but well developed seta.

Mandible coxal gnathobase with five complex teeth oriented at right angles to main plane of gnathobase, with opaline tips, largest tooth ventrally situated, tapering when viewed at right angles to broad plane of gnathobase, separated from adjacent tooth by wide gap; 4 following teeth progressively decreasing in size; then, 3 simpler, asymmetrically bicuspid teeth without opaline tips follow, dorsal-most tooth longest; and finally, 1 long, lash-like element situated dorsally, bordered by wide setules; macula cribrosa situated proximally on gnathobase near insertion of basis; rows of setules lying on both distal anterior and posterior surfaces at bases of dorsal-most 6 teeth. Basis with 4 inner setae; endopod 2-segmented, segment 1 with large inner lobe and 4 distal inner setae distal of which well-developed, segment 2 with 9 terminal setae plus 2 short setae both on the same surface and transverse row of setules; exopod 5-segmented with 1, 1, 1, 1, 2 setae.

Maxillule praecoxal arthrite with full complement of 15 setae (4 of them on posterior surface); coxal endite with 5 terminal setae, epipodite with 7 long and 2 short setae; basal endites 1 and 2 with 4 and 4 setae, respectively;

exite with 1 seta; basis and endopod separate; endopod with ancestral segments 1 and 2 fused—fusion line visible on anterior surface, with 3, 4, 6 + 1 small posterior surface seta, segment 3 with row of anterior surface setules; exopod with 11 setae, 1 macula cribrosa on outer proximal surface.

Maxilla modestly developed, longest setae extend as far as anterior labrum, praecoxa with macula cribrosa on outer surface. Praecoxal endites 1 and 2 with 6+1 small and 3 setae, respectively; coxal endites 1 and 2 with 3 setae each, coxal epipodite with 1 long plumose seta; basal endite longest with 4 setae, one of them more heavily developed than others; endopod segment 1 with short lobe bearing 1 large plus 3 short, but well developed setae, endopod segments 2–4 with 3, 2, 2 setae, respectively, setae bordered by two rows of moderately spaced long spinules and distal part of concave border differs in appearance from convex border, possibly ridged. Inner surfaces of praecoxal endite 2, coxal endites 1 and 2 and basal endite each with 1 seta that is shorter and more densely lined with long spinules; endopod segments 2 and 3 with inner setae shorter than outer setae, segment 2 inner proximal seta well-developed, inner distal seta convex border bearing spinules. Terminal setae gently curving along whole length. All setae (apart from heavily built seta on basal endite), as well as having very small closely spaced spinules, bordered by long, widely spaced auxiliary spinules; distal seta on coxal endite 2 similar although closely spaced spinules much longer than on remaining setae.

Maxilliped directed ventrally so that setae on syncoxa and basis directed into animal's midline; syncoxa with 1, 2, 4, 4 setae, longest seta of endite 4 extending short of distalmost border of basis and lined by very short small spinules; basis with 3 setae, patch of bifurcate setules on anteroproximal surface; endopod segment 1 separate bearing 2 setae; endopod segments 2–6 with 4, 4, 3, 3+1 (outer seta directed proximally), 4 setae; endopod segments 3–5 with proximal seta shortest. One macula cribrosa on inner surface of basis and on endopod segment 5.

Legs 1–5 biramous, each ramus 3-segmented with following setal formula (Roman numerals indicate spines, Arabic numerals setae, outer border setation listed to left in each group separated by ';'):

Leg 1 (Coxa 0-1. Basis 1-1. Exopod I-1; I-1; II,1,4. Endopod 0-1; 0-2; 1,2,3);

Leg 2 (Coxa 0-1. Basis I-0. Exopod I-1; I-1; III,1,5. Endopod 0-1; 0-2; 2,2,4);

Leg 3 (Coxa 0-1. Basis I-0. Exopod I-1; I-1; III,1,5. Endopod 0-1; 0-2; 2,2,4);

Leg 4 (Coxa 0-1. Basis 1-0. Exopod I-1; I-1; III,1,5. Endopod 0-1; 0-2; 2,2,3);

Leg 5♀ (Coxa 0-0. Basis 1-0. Exopod I-0; I-1; II,1,4. Endopod 0-1; 0-1; 2,2,2).

Leg 1 coxa and basis with long setules on anterior surface, basis usually with large anterodistal hook-like process from which straight short seta arises, macula cribrosa situated on anterior surface adjacent to articulation socket of exopod segment 1. Distolateral corner of endopod segment 1 rounded. Exopod segment 2 with macula cribrosa on lateral surface at base of outer distal spine and macula cribrosa also on anterior surface of endopod segment 2. Legs 2–4 with maculae cribrosae on: basis adjacent to region of articulation of exopod segment 1, at base of outer spines on exopod segments 1 and 2, at base of 2 proximal outer edge spines on exopod segment 3, and on endopod segment 2; pore openings (presumably of bioluminescence glands, see Herring 1988) located on anterior surfaces at base of outer edge spines of exopod segments 1–3; endopod segment 1 outer distal corner extends into sharp point. Leg 5 extending just beyond third free urosomite, with outer distal corner of endopod segment 1 rounded; pore openings on anterior surface at base of outer border spines; maculae cribrosae on anterior surface of basis near articulation with exopod segment 1, on endopod segment 2, and just proximal to pore on exopod segments 1–3.

Male: Anterior margin of head rounded or crested, without anterior spine-like processes. Rostrum extending into two long, ventroposteriorly- or ventrally-directed, tapering points that appear to be direct extensions of cuticle. Urosome of five free somites, genital somite short. Posterior borders of pedigerous somite 5 bluntly triangular or rounded in lateral view. Caudal rami seta I absent, setae II and III lateral, setae IV–VI terminal (seta V longest), seta VII inserted at inner distal corner onto small projection; tufts of setules decorate inner border, row of setules located at base of seta VII, and tufts on lateral border between setae II and III.

Antennules asymmetrically developed, geniculate on right. Aesthetascs larger than in female with stiffened posterior border. Left antennule with ancestral segments II–IV, IX–XI fused, segments XXVII and XXVIII separate, with aethetascs doubled on segments III, V, VII, IX, XI–XIV. Most setal elements modified setae (ms) or aesthetascs (a); plus few naked simple setae (ss). Setation of segments as follows: I—1ms, 1a, 2ss; II–IV—6ms, 4a; V—2ms, 2a; VI—2ms, 1a; VII—2ms, 2a; VIII—2ms, 1a; IX–XI—5ms, 5a, 1 clavate (club-shaped) seta (on segment XI, damaged in specimen figured); XII—2ms, 2a; XIII—2ms, 2a; XIV—2ms; 2a; XV to XXI—2ms, 1a;

XXII to XXIII—1ms, 1a; XXIV—1+1ms, 1a; XXV—1+1ms, 1a; XXVI—1+1ms; XXVII—1+1ms; XXVIII—3ms, 1a, 1ss. Segments XIV and XV with row of distoventral teeth. Maculae cribrosae at base of every aesthetasc including on segment XXVIII. Right antennule geniculate between segments XX and XXI, with ancestral segments II–IV, IX–XI, XIV–XV, XXI–XXII fused on ventral surface with arthrodial membrane present on dorsal surface; XXII–XXIII completely fused, XXVII and XXVIII separate. Setation of segments as follows: I—1ms, 1a, 2ss; II–IV—6ms, 4a; V—2ms, 2a; VI—2ms, 1a; VII—2ms, 2a; VIII—2ms, 1a; IX–XI—5ms, 5a, 1 clavate seta (on segment XI based on *M. ohmani* and *M. princeps*); XII to XIII—2ms; 2a; XIV–XV—4ms, 3a; XVI to XVIII—2ms, 1a; XIX—2ms, 1a or 1ms, 1 fused gripping element, 1a; XX—1ms, 1 fused gripping element, 1a; XXI—1ms, 1 fused gripping element, 1a or 2 gripping elements, 1a; XXII–XXIII—1ms, 1ss; XXIV to XXV—1+1ms, 1a; XXVI—1+1ms; XXVII—1+1ms; XXVIII—3ms, 1a, 1ss. Marker seta interpreted as indicating fusion of segments XXII–XXIII minute, proximally-inserted at first 1/6th of this double segment. Maculae cribrosae located at base of all aesthetascs, and distally on segments XXIV and XXVI. Fused segments XIV and XV on right antennule each with longitudinal row of teeth on ventral surface.

Antenna, mandible, maxillule, maxilla, maxilliped and legs 1–4 as in female. Leg 5 with following setal formula (Roman numerals indicate spines, Arabic numerals setae, outer border setation listed to left in each group separated by ';'):

Leg 5♂ left (Coxa 0-0. Basis 1-0. Exopod I-0; I-1; II,1,0. Endopod 0-0; 0-1; 2,2,2);

Leg 5♂ right (Coxa 0-0. Basis 1-0. Exopod I-0; I-0; II,1,0. Endopod 0-0; 0-1; 2,2,2).

Leg 5 almost symmetrical apart from specialised seta on inner distal border of left exopod segment 2 and asymmetrically inserted single spine on inner border of exopod segment 3 (homologous with terminal spine of female). Male left leg 5 exopod segment 2, specialised seta composed of two sections: wide basal part and lash arising from proximodistal border of basal part. Basal part of variable proportions and bearing pit on anterodistal corner. Lash bearing longitudinal rows of long setules extending onto basal part and tuft of setules arising from pit. Outer distal corner of endopod segment 1 rounded. Pore openings on anterior surface at base of outer spines. On posterior surface, 1 macula cribrosa on endopod segment 3 and just proximal to each outer spine on exopod segments 1 to 3. Basis inner distal border naked or with patch of elongate setules.

Type species. *Megacalanus princeps* Wolfenden, 1904

Remarks. Type species. The identity and nomenclature of Atlantic Ocean *Megacalanus* had not been stabilised when this work began. A great deal of confusion was caused by the incomplete description of *Calanus princeps* by Brady (1883), making its true identity the subject of ongoing speculation. Also the generic diversity of the Megacalanidae was not recognised until A. Scott's (1909) description of *Bradycalanus*, a genus which is morphologically closer to *Megacalanus* than to *Bathycalanus*.

Damkaer (2000) concluded that the correct name for Atlantic *Megacalanus* is *M. longicornis* (Sars, 1905, as *Macrocalanus*) although the first recognisable description of this species was actually *Megacalanus princeps* Wolfenden, 1904; the presence of the anterodistal hook-like process on the basis of leg 1 clearly indicates Wolfenden's species is a *Megacalanus*. The most important question requiring an answer to untangle this confusion is: should *Megacalanus princeps* Wolfenden, 1904 be considered to be a homonym of *Calanus princeps* Brady, 1883? Our answer is 'no' based on the following reasoning.

Wolfenden (1904) reported on page 113 that: "the only described copepod at all resembling it [*Megacalanus princeps* Wolfenden, 1904] is *C. princeps* of Brady … in which the feet are very similar, but there are not such setae on the anterior foot jaws as Brady figures, the maxilla is totally different as regards its bristles, and the segmentation of the anterior antennae and abdomen is also different. It is therefore certainly not Brady's species."

In using the same species name as Brady (1883), Wolfenden implied his *Megacalanus princeps* was not in the same genus as Brady's species. Nevertheless, he did not resolve the issue of generic affinities of *C. princeps* Brady, 1883 except to say that, in his opinion, Brady's species was not a *Calanus* because of the extra outer border spine on exopod segment 3 of legs 2–4. Thus, it was Sars' (1905) opinion, a year later, which erroneously designated *Megacalanus princeps* Wolfenden, 1904 as a junior homonym of *Megacalanus princeps* (Brady, 1883).

By 1906, Wolfenden (P. 4) had examined Brady's type specimen of *Calanus princeps* and again recognised it was not a *Megacalanus* and concluded it resembled *Heterocalanus* Wolfenden, 1906 although the totality of his comments are contradictory. We agree with Wolfenden's (1906) concept of a separate genus to take *C. princeps* Brady, 1883 and develop this idea further in a later section along with a discussion of the need for a replacement name.

One of us (GAB) recently examined two of Brady's type specimens of *Calanus princeps* Brady, 1883 (BMNH 1884.4. c.c.2/5), each dissected on two slides, and found that most limbs were in good condition. The maxillule setal formula is: praecoxal arthrite, coxal endite and basal endite 1 with 11, 0, 2 setae, respectively; basal endite 2 with 2 setae, and endopod segments with 1, 1, 4+1 setae. The first endopod segment carried 1 seta on one side of the body but 2 setae on the other side. Leg 1 exopod segments 1 and 2 both lack an outer border spine and exopod segment 3 has 2 outer border spines.

We propose that there is no value in attempting to untangle all the opinions expressed concerning synonymies between the dates of 1905–1925. We recommend the use of Wolfenden's (1904) name *Megacalanus princeps* since his is the first recognisable description of this species and it is clearly not in the same genus as *C. princeps* Brady, 1883.

Species. Four species of *Megacalanus* are now included in this genus: the type species and three new species described herein: *Megacalanus frosti* **n. sp.** is the crested form recorded by Miller (2002) and *M. ohmani* **n. sp.** and *M. ericae* **n. sp.** These species may be distinguished by a combination of female and male characteristics relating to: the general shape of the posterior borders of pedigerous somite 5 in the female, the shape of the anterior head and rostrum in lateral view, the presence or absence of small blunt teeth on the distoposterior border of antennular segments XV and XVI in the female, the shape of the specialised seta on the male left leg 5 inner distal corner of exopod segment 2, and the armature of the right male antennular segments XIX to XXI.

Vervoort (1949) considered a copepodite stage IV, described as *Pseudolovenula magna* by Marukawa (1921) and placed in the Centropagidae, to be a *Megacalanus.* Marukawa's (1921) figure (plate 1 fig. 13) of leg 1 does not have a large hook-like process on its basis which is present in at least copepodite stage II (see Fig. 11J). Therefore, it is not possible to be certain it is a *Megacalanus* and the species name *magna* is available for use.

The mouthparts and legs of *Megacalanus* species are generally indistinguishable. Thus, these limbs are fully illustrated for *M. ohmani* alone. Distinguishing features only, are illustrated for the other three species.

Distribution. The type species was found in the Atlantic and Indian Oceans, the southwest Pacific close to Chile, and strays have been found in the Celebes and Banda Seas and the tropical Central Pacific (see Fig. 9, Table 1). *Megacalanus frosti* **n. sp.** is the crested form recorded by Miller (2002) from the eastern Pacific, another new species is found east of Irian Jaya (*M. ohmani* **n. sp.**), and *M. ericae* **n. sp.** is widespread in the Pacific and Indian Oceans.

Megacalanus princeps Wolfenden, 1904

(Figs 7–9)

Megacalanus princeps Wolfenden, 1904, p. 112–113, pl. ix, fig. 1.
Macrocalanus longicornis Sars, 1905, p. 26.
Megacalanus longicornis: Farran, 1908, p. 21.
Megacalanus princeps: Wolfenden, 1911, p. 196–198, fig. 1.
Megacalanus princeps: With, 1915, p. 41–44, pl. 1, figs 3a–i, textfig. 8a–d.
Megacalanus longicornis: Sars, 1924–25, p. 11–14, pls I–II.
Megacalanus princeps var. *inermis* Sewell, 1947, p. 25–27, text-fig. 2.
Non *Calanus princeps* Brady, 1883, pp 36–37, pl. x, figs 3–7.
Non *Megacalanus princeps* Wolfenden, 1905b, p. 1–3, pl. I, figs 1–6.

Type locality. 51–60º N, 6–13º W.

Material examined. Oceanus Cr 473, MOC1: Stn 1, 100–866 m, 1♀ (8.8 mm), Co119.3.1; Stn 8, 801–1001 m, 1♂ (9.7 mm), Co119.4.1; Stn 21, 600–798 m, 2♀ (9.1, 9.5 mm), Co.119.5.1. ANTXIV/1, Stn 2, MOC10: 2000–3000 m, 1♀ (10 mm), 1♂ (10.4 mm); 1000–2000 m, 1 NVI (2.56 mm), 1 CII (4.0 mm), 2 CV (7.8, 8.0 mm). MOC1: 797–1003 m, 1♀ (10.5 mm), Co119.2.1; 399–500 m, 2♀ (9.7, 9.1 mm), 1CV, 1CIV. RHB0603, Stn 3, MOC10, 1000–3000 m 1♂. Indopac VII, Stn 5, IKMT, 0–2121 mwo, 5♀ (9.1–9.8 mm), 2♂ (9.5, 9.7 mm). Indopac VIII, Stn 6, IKMT, 0–2096 mwo, 1♂ (9.6 mm). Southtow IV, Stn 36, IKMT, 0–2000 m, 2♂ (9.8, 10.2 mm). Records from Natural History Museum, London: Sr 224, off Ireland, 700 fathoms, 3♀ (see Farran 1908—as *Megacalanus longicornis*), BMNH 1908.7.6.1-3. John Murray Expedition: Stn 96, 1CV, BMNH 1949.12.31.24; Stn 98, 1♂, BMNH 1949.12.31.25; Stn 131D, 1♂, BMNH 1949.12.31.27, 1♀, 3CV, 2CIV, BMNH 1949.12.31.28; Stn 172, 2665 mwo, 1CV, BMNH 1949.12.31.29; Stn 172, 1500 mwo, 1♂, 1CV, BMNH 1949.12.31.30. Discovery

Stn 7406#24, BT8, 600–700 m, 3♀ (8.6, 8.5, 8.5 mm), BMNH 1994.5752-5755. Additional records from Smithsonian Institution, USNM numbers: 69930, 262489, 262491, 298332, 299632, 1027487–89, 1027491, 1027492, 1027514–21, 1027685, 1027688–92, 1027731–37, 1027740, 1027741, 1207752

Genetic material. Co119.2.1, Co119.3.1, Co119.4.1, Co119.5.1. GenBank numbers in Table 6.

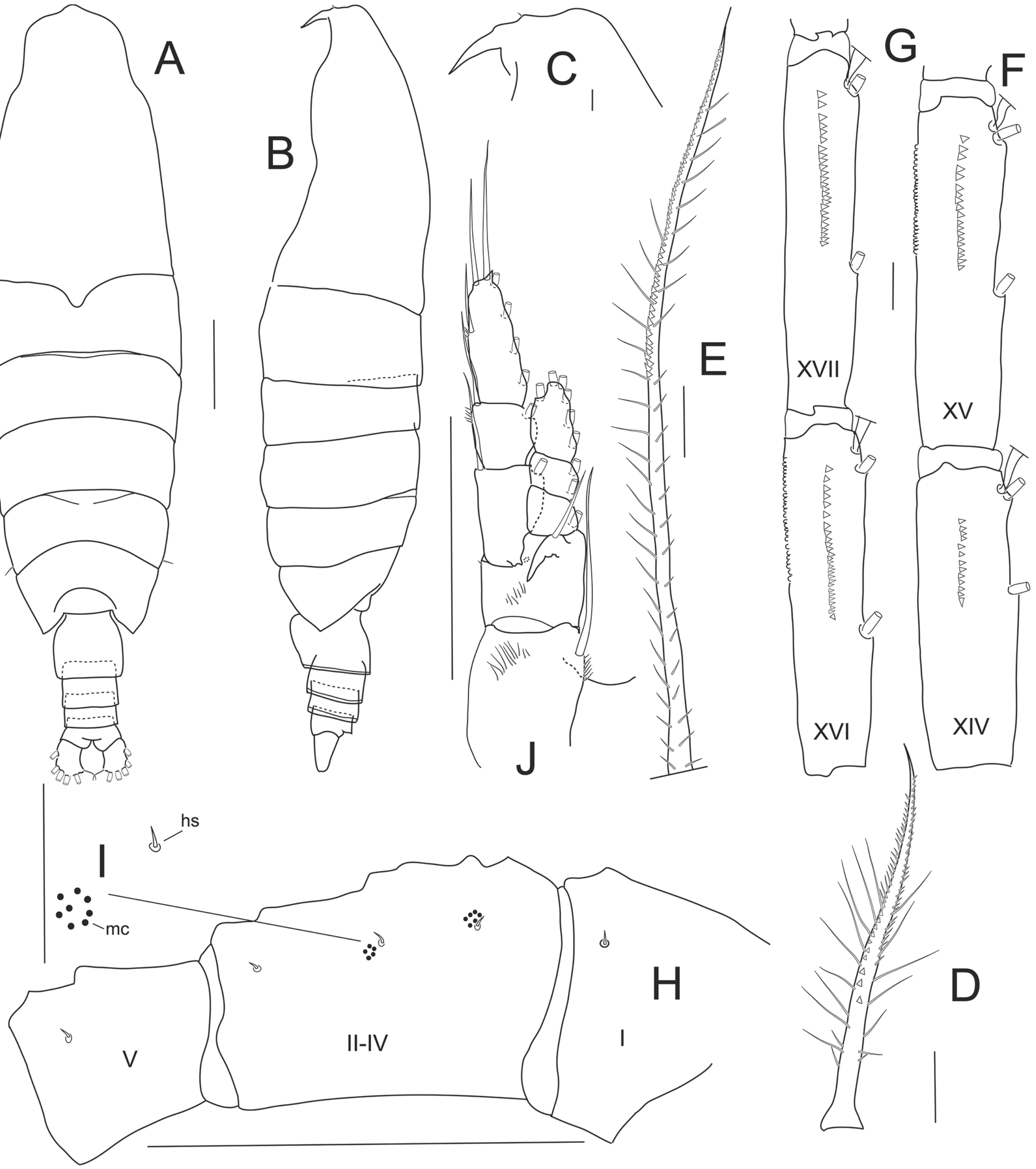

FIGURE 7. *Megacalanus princeps* Wolfenden, 1904 Female: A, dorsal view; B, lateral view; C, lateral view of anterior head; D, inner seta of maxilla praecoxal endite 2; E, seta of maxilla praecoxal endite 1 (and most of other setae on maxilla); F, antennule ancestral segments XIV–XV; G, antennule ancesstral segments XVI–XVII; H, antennule ancestral segments I–IV, dorsal view; I, hair sensilla (hs) and macula cribrosa (mc) on ancestral segment III; J, leg 1. Scale bars represent: 1.0 mm on figures A, B, H, J; 0.1 mm on remaining figures. Illustrated specimen from Oceanus Cr473, 100–866 m (A–C).

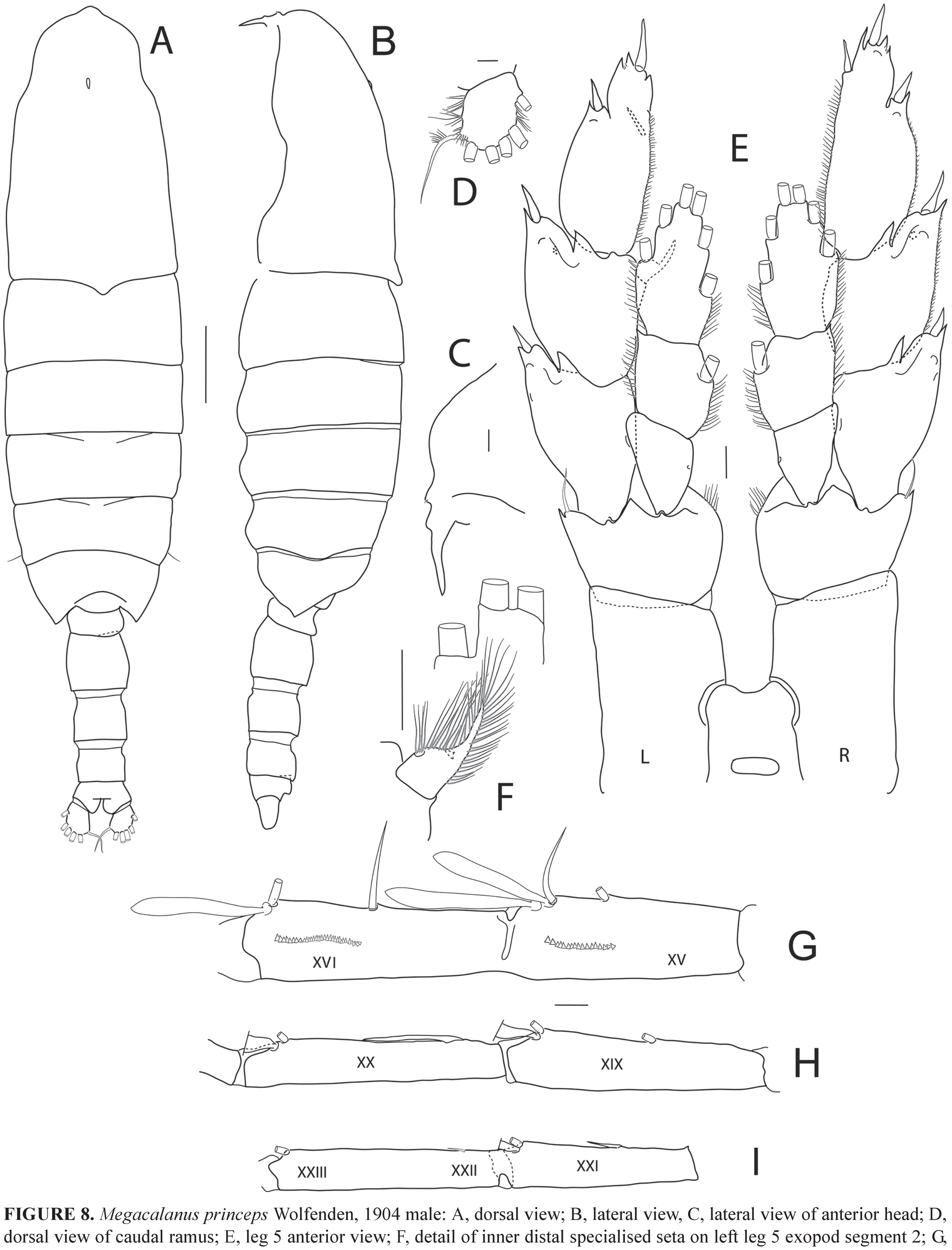

FIGURE 8. *Megacalanus princeps* Wolfenden, 1904 male: A, dorsal view; B, lateral view, C, lateral view of anterior head; D, dorsal view of caudal ramus; E, leg 5 anterior view; F, detail of inner distal specialised seta on left leg 5 exopod segment 2; G, antennule ancestral segments XV–XVI; H, antennule ancestral segments XIX–XXI; I, antennule ancestral segments XXI-XXIII. Scale bars represent 1.0 mm on figures A, B; 0.1 mm on remaining figures. Illustrated specimen from ANTXXIV/1, Stn 2, 1000–2000 m.

Morphological description. Following description based on specimens from Oceanus 473, 100–866 m and ANTXXIV/1 Stn 2. As for genus with following specific characters.

Female (Fig. 7). Total length 8.5–10.5 mm (mean 9.3 mm, n=12). Anterior margin of head in dorsal view slightly produced into short rounded projection dorsal to base of rostrum (Fig. 7A–C). Posterior borders of pedigerous somite 5 (Fig. 7B) extend into triangular lappets reaching one third of way along genital double-somite, in dorsal view (Fig. 7A) lappets appear pointed.

Antennule length of segments (µm) as follows (note last few segments missing). Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements are taken of ancestral segment I: I (676, 228); II–IV (654); V (329); VI (314); VII (366); VIII (379); IX (389); X–XI (814); XII (545); XIII (567); XIV (681); XV (787); XVI (765); XVII (782); XVIII (834); XIX (871); XX (881); XXI (884); XXII (646). Dorsal surface of ancestral segments I–V each with very small hair sensillum of which those on segments II and III accompanied by macula cribrosa (Fig. 7H); ancestral segments XIV–XVII with 13/13, 20/21, 25/26, 24/26 distoventral teeth, respectively, distoposterior borders of segments XV and XVI with 26/32 and 29/33 minute blunt teeth, respectively; in some specimens, observed in dish without coverslip, these blunt teeth appear to be cross-section of posterior border ridges that run at right angles to main axis of segment.

Leg 1 (Fig. 7J) outer spines on exopod segments 1 and 2 extend half way between bases of following 2 more distal spines; 1 macula cribrosa at base of outer spine on exopod segment 2.

Male (Fig. 8). Total length 9.5–10.4 mm (mean 9.8 mm, n=7). Anterior margin of head in dorsal view slightly produced into short rounded projection dorsal to base of rostrum which extends into two long, ventroposteriorly-directed, tapering points that appear to be direct extensions of cuticle (Fig. 8A–C).

Antennule right ancestral segment XIX without fused gripping element (Fig. 8H), instead, 2ms, 1a; XXI—1 short fused element (arising just proximal to midlength but fused to its segment only at its base), 1ms, 1a (Fig. 8I); fused segments XV–XVI (Fig. 8G) on right antennule each with longitudinal row of 16, 32 ventral teeth, respectively.

Leg 5 inner distal border of basis with setules, specialised seta on inner distal border of exopod segment 2 on left with basal part longer than wide and lash longer than basal part (Fig. 8E, F). Right exopod segment 3 inner border completely lined with fine spinules to just short of inner articulated spine.

Remarks. The possibility there may be another species of *Megacalanus* was considered because Sewell (1947) described *Megacalanus princeps* var. *inermis*: p. 25–27, text-fig. 2. This female, from the John Murray Expedition Stn 98 in the Arabian Sea, did not have an anterodistal hook-like process on the basis of leg 1 and was also characterised by the presence of macula cribrosa on the anterior surface at the base of the outer distal spine on exopod segments 1 and 2. In *M. princeps, M. frosti* **n. sp.**, *M. ericae* **n. sp.** and *M. ohmani* **n. sp.** there is a macula cribrosa only on exopod segment 2, but in the first three species the macula cribrosa is situated close to the base of the distolateral spine on the anterior surface, whereas, in *M. ohmani* **n. sp.** the macula cribrosa is situated more proximally on the lateral border. Re-examination of leg 1 of Sewell's specimen (GAB) revealed that there is no macula cribrosa on exopod segment 1, contrary to the original observation (Sewell 1947). The general shape of the head and the nature of antennular ancestral segments XIV–XVII are consistent with *M. princeps.* We also note Gueredrat's (1969) observation that a number of *Megacalanus* from the tropical western Pacific do not have an anterodistal hook-like process on the basis of leg 1 or have various versions of reduction or atrophy. Therefore, we consider var. *inermis* to be a deformed *M. princeps.*

Distribution. *Megacalanus princeps* is a bathypelagic species that also extends into the mesopelagic zone (see also Mauchline & Gordon 1991). It is known mainly from the Atlantic and Indian Oceans based on presently examined specimens. It extends into the Pacific Ocean since it has been recorded from the Celebes Sea and a few specimens have been found in the eastern Pacific as well as one in the tropical Pacific at 150º W (Fig. 9, Table 1). The vertical distribution of *M. princeps* extends from 500–2800 m.

Species comparisons. Both Wolfenden (1911) and Sewell (1947) mention the presence of a row of very small teeth on the distal part of the posterior border of the female antennular segments XV and XVI in *M. princeps.* The female of *M. princeps* shares this character with the female of *M. frosti* **n. sp.**, nevertheless, *M. princeps* can be distinguished from *M. frosti* **n. sp.** by the absence of a crest on the head, a characteristic found only in *M. frosti* **n. sp.** (Table 7). *Megacalanus princeps* males may be distinguished from males of all other species by the absence of a gripping element on ancestral segment XIX of the right antennule.

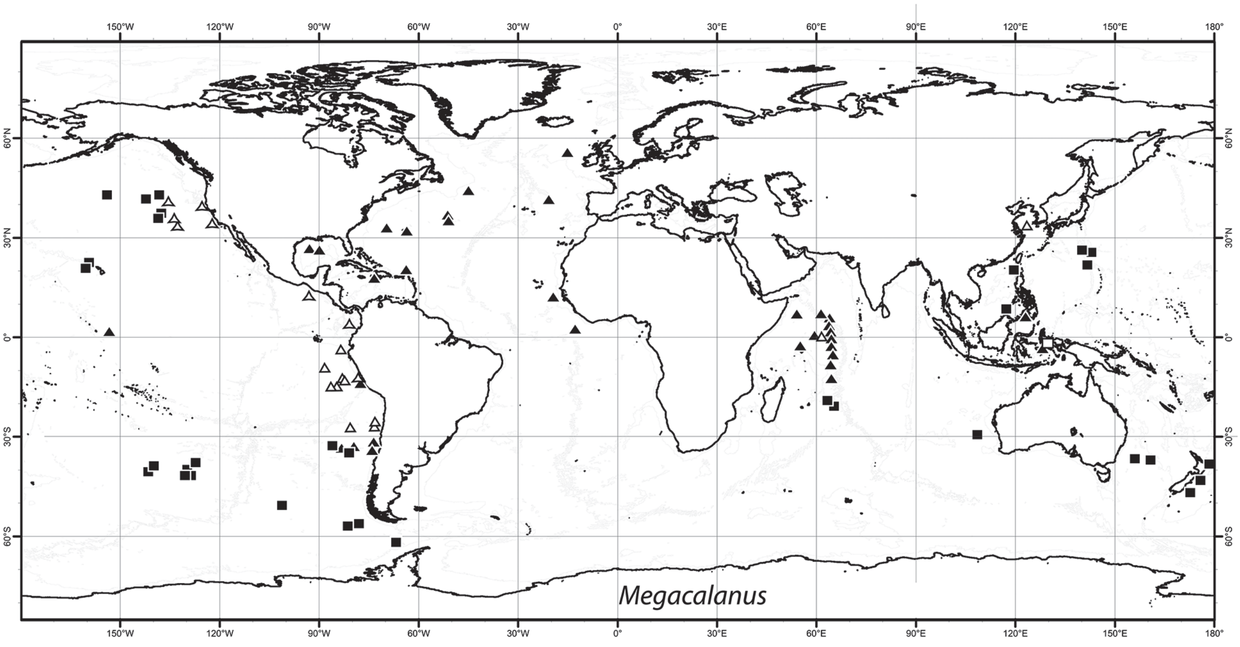

FIGURE 9. Distribution of *Megacalanus* species: filled triangle = *Megacalanus princeps*; open triangle = *M. frosti* **n. sp.**; filled square = *M. ericae* **n. sp.**; open square = *M. ohmani* **n. sp.**.

Nauplius VI

Description. Total length 2.56 mm. Typical nauplius stage VI (NVI) with well-developed antennule, antenna and mandible and with limb buds apparent for the maxillule, maxilla and maxilliped (Fig. 10A, B).

Antennule (Fig. 10C) with proximal pedestal naked, segment 1 with 1 seta, segment 2 with 2 setae, and segment 3 with 5 inner border setae and 12 setae along outer to terminal border (1 terminal seta very short).

Antenna (Fig. 10D) coxa with 1 short inner spine-like element; basis with 2 proximal and 2 distal short, inner, spine-like elements; endopod with 5 terminal setae (3 of these well-developed) and 4 inner setae (only 1 of these well-developed); exopod with 6 developed arthrodial membranes, terminal segment with 3 terminal setae, 5 more proximal segments each with 1 well-developed seta, and 1 large proximal segment with 1 well-developed distal segment, 1 moderately-developed penultimate segment and 2 very small spine-like elements.

Mandible (Fig. 10E) with short coxal gnathobase bearing very rudimentary teeth and 1 short, spine-like element; basis armed with 4 short, spine-like elements; endopod with 6 terminal setae (4 well-developed) and 4 inner setae (3 represented by very short, spine-like elements); exopod with 3 completely developed arthrodial membranes, terminal segment with 2 setae, 2 more proximal segments with 1 seta each and proximal segment with 2 setae, all setae well-developed.

Proto-urosome (Fig. 10F) slightly bifurcate and decorated with short spines: 4 inserted laterally on each side and 2 inserted more ventrally on inner surface of bifurcation.

Remarks. On this red-pigmented NVI, not all setae are completely intact but as far as can be deduced, this is a stage VI nauplius of *Megacalanus* as it is very similar to those of the Calanidae (Bradford *et al*. 1988). The taxonomic identity of this NVI is not entirely certain although setation of the antenna exopod places it clearly in either the Centropagoidea or the lineage containing the Megacalanidae, Calanidae, Eucalanidae, Spinocalanidae, Clausocalanoidea or Paracalanidae. The size of the NVI (2.5 mm) makes it unlikely to be anything other than a megacalanid. Additionally, the NVI was taken with a CII which is clearly a *Megacalanus*, identified by the leg 1 basis hook-like process and the long antennule relative to the total body length.

The antenna and mandible have the elements, presumably related to feeding in the Calanidae, either absent or reduced; 2 elements are missing from the antennal coxa, 1 element is missing from the proximal basis, and elements on the inner border of the endopod are relatively reduced in size. On the mandible, the gnathobase seta is not as well-developed as in the Calanidae; the basis has 3 fewer, reduced elements compared with the Calanidae that has 5 well-developed setae; and the endopod has 1 fewer elements compared with the Calanidae and 5 elements are much less well-developed compared with the Calanidae. The posterior part of the NVI differs from that of the Calanidae in not having a pair of terminal, elongate fine setae. It is deduced that the naupliar stages of *Megacalanus* are non-feeding stages.

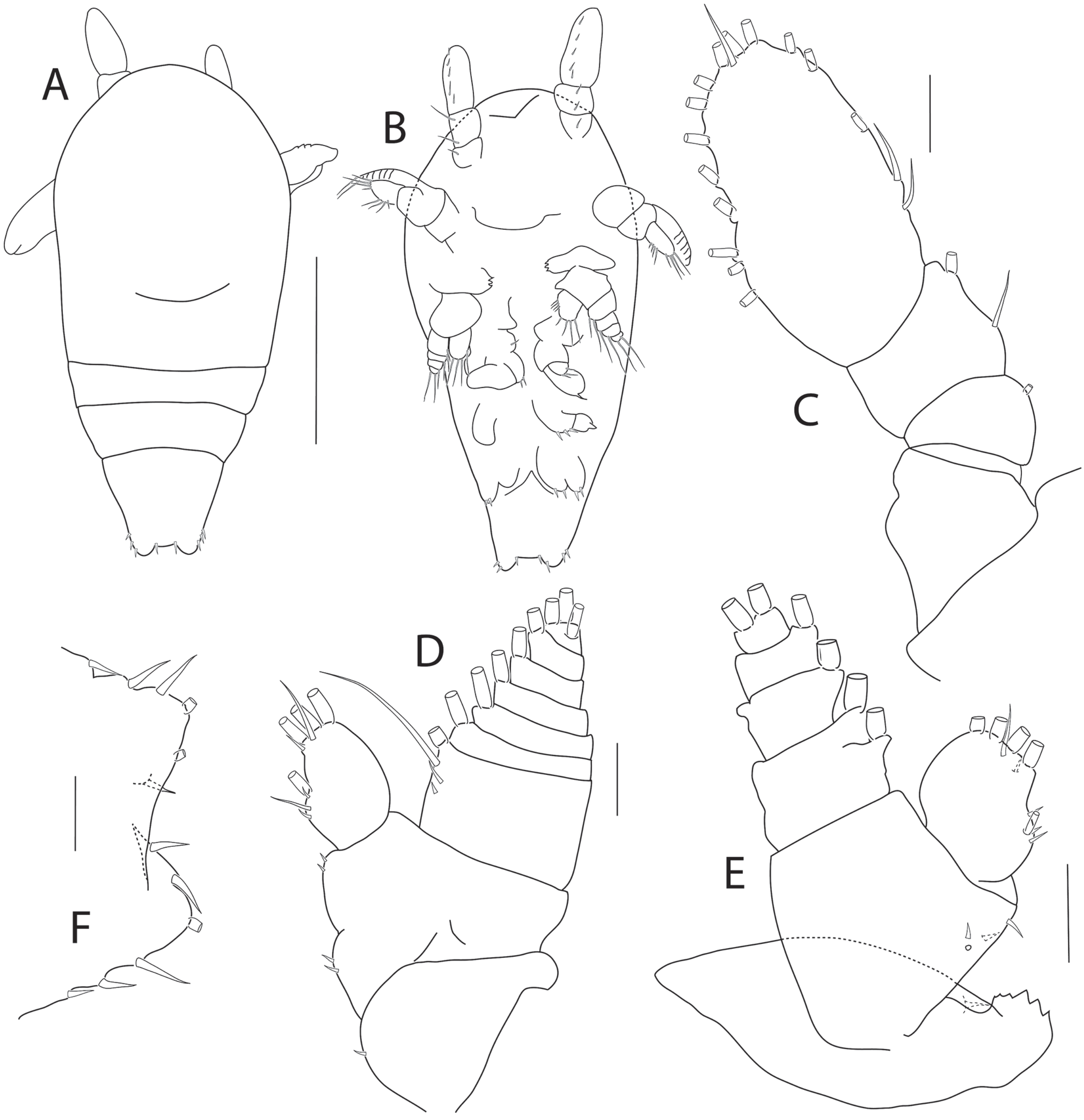

FIGURE 10. *Megacalanus princeps* Wolfenden, 1904 nauplius VI: A, dorsal view; B, ventral view; C, antennule; D, antenna; E, mandible; F, posterior body, dorsal view. Scale bars represent 1.0 mm on figure A, B; 0.1 mm on remaining figures. Illustrated specimens from ANTXXIV/1, Stn 2, 1000–2000 m.

Copepodite II

Description. Total length 4.0 mm. Copepodite stage II typical of Calanoida in having 2-segmented urosome and 3 pairs of legs as well as bud of leg 4 (Fig. 11A, B). Rostrum of 2 tapering points (Fig. 11D). Caudal rami damaged—definitely 1 small, plumose inner distal seta, several large setae.

Antennule extending beyond caudal rami by about last 5 segments, 17-segmented (Fig. 11C); setation as follows: I–V—2ms; VI–XI—2ms +2a; XII–XIII—0; XIV—1ms; XV— 0; XVI—1ms, 1a; XVII— 0;

XVIII—1ms; XIX— 0; XX—1ms; XXI—1ms, 1a; XXII —1ms; XXIII—1ms; XXIV— 1+1; XXV—1+1, 1a; XXVI—1+1; XXVII–XXVIII—5+1a.

Antenna (Fig. 11E, F) with 1 seta on coxa, 2 setae on basis, 7-segmented exopod apparently with adult setation, endopod segment 1 with 2 setae, segment 2 with 6+4 setae.

Mandible coxal gnathobase with well-developed teeth; 4 setae on basis; endopod segment 1 with 4 setae (Fig. 11G), segment 2 with 7 setae, 2 of which small; exopod segments 1–4 each with 1 seta, segment 5 with 2 setae.

Maxillule (Fig. 11H) praecoxal arthrite with 12 setae and spines 3 of which on posterior surface; coxal endite with 4 setae; basal endites 1 and 2 with 4 and 3 setae, respectively; endopod segments 1, 2, 3 with 2, 3, 5 setae, respectively; exopod with 7 setae; basal exite with 1 seta, coxal epipodite with 6 setae.

Maxilla praecoxal endites 1 and 2 with 5 and 3 setae, respectively; coxal endites 1 and 2 with 3, 3 setae, respectively; basal endite with 4 setae; and endopod segment 1 with 3 setae, segments 2–4 with total of 7 setae.

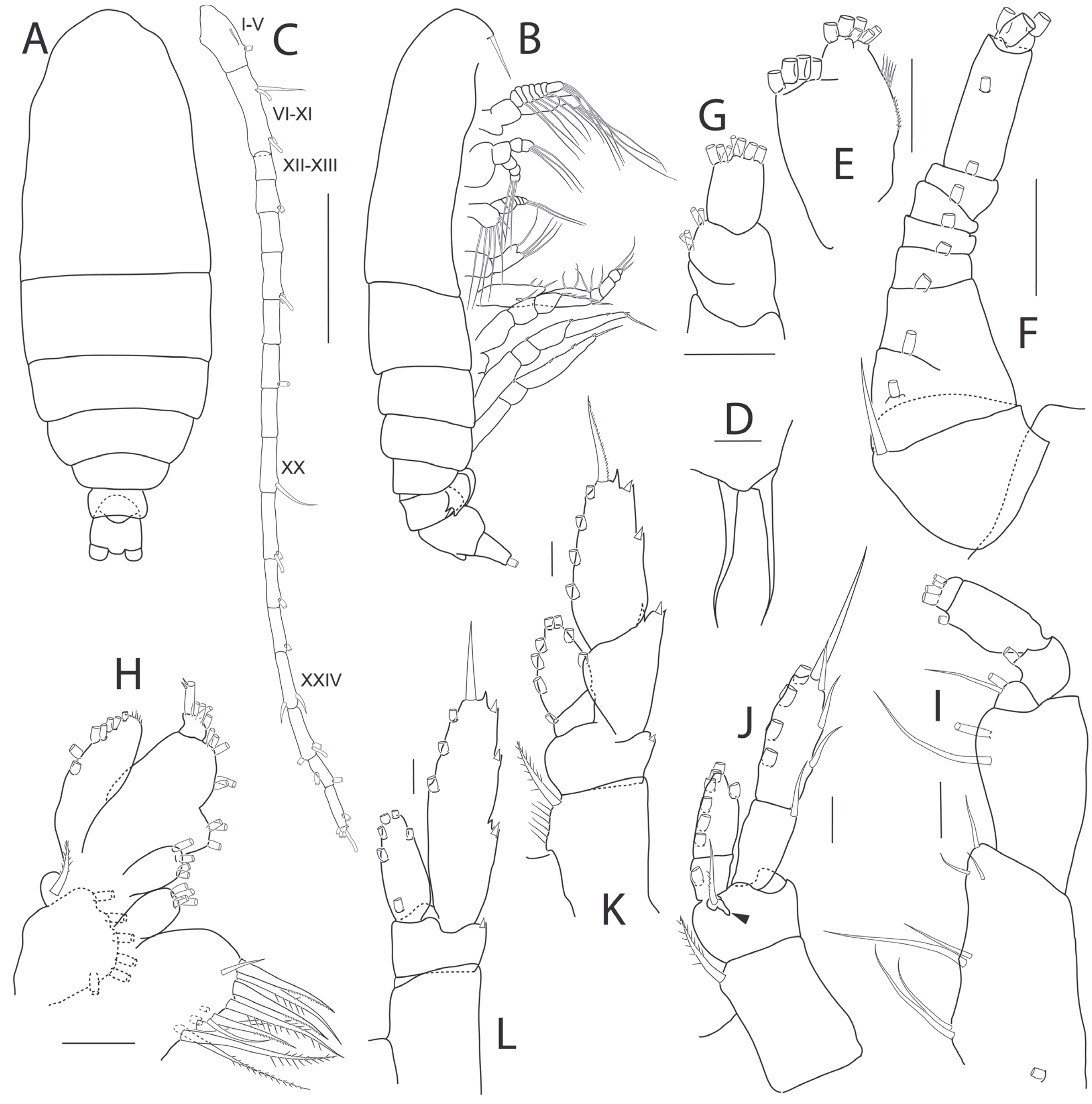

FIGURE 11. *Megacalanus princeps* Wolfenden, 1904 copepodite II: A, dorsal view; B, lateral view; C, antennule; D, rostral filaments; E, antenna endopod segment 2; F, antenna exopod; G, mandible endopod; H, maxillule; I, maxilliped; J, leg 1—arrow indicates hook–like process; K, leg 2; L, leg 3. Scale bars represent: 1.0 mm on figures A–C; 0.1 mm on remaining figures. Illustrated specimens from ANTXXIV/1, Stn 2, 1000–2000 m.

Maxilliped (Fig. 11I) syncoxal inner lobes 1–4 with 1, 2, 2, 3 setae, respectively; basis with 2 setae; endopod segment 1 with 2 setae; putative endopod segment 5 with 1 seta, endopod segment 6 with 4 setae.

Legs 1–3 (Fig. 11J-L) similar to those of Calanidae with following setal formula (Roman numerals indicate robust setae, Arabic numerals setae, outer border setation listed to left in each group separated by ';'):

Leg 1 (Coxa 0-1; Basis 0-1; Exopod I-0, III,1,4; Endopod 0-1; 1,2,4);

Leg 2 (Coxa 0-1; Basis I-0; Exopod I-0, II,1,4; Endopod 0-1; 2,2,3);

Leg 3 (Coxa 0-0; Basis I-0; Exopod III,1,3; Endopod 1,2,3).

Leg 1 basis with anterodistal hook-like process on inner distal border on anterior surface and bearing plumose seta, and leg 3 basis with rudiment of outer distal articulated spine.

Remarks. This red-pigmented stage II copepodite of *Megacalanus* is very similar to that of the Calanidae (Bradford *et al.* 1988) differing only in the following respects: maxillule praecoxal arthrite has 1 more seta and there is 1 more seta on endopod segment 2; leg 1 basis has an anterodistal hook-like process as in adult *Megacalanus.* The details of antennular setation appear to be exactly the same as in some other Calanoida that have been studied in detail (Boxshall & Huys 1998).

***Megacalanus frosti* n. sp.**
(Figs 9, 12–14)

Megacalanus longicornis: Miller, 2002, pp 129–142, figs 2–10.
Megacalanus princeps: Sewell, 1947, p. 25, Stn 131, female 8.53 mm.

Type locality. 2.867º N, 80.850º W.

Material examined. Francis Drake III, Stn 4, 8 May 1975, IKMT, 0–3000 m, 11♀ (9.3–10.7 mm), 6♂ (9.5–10.4 mm), holotype female (10.5 mm), paratypes. Southtow IV, Stn 36, IKMT, 0–2000 m, 7♀ (10.1–11.0 mm), 7♂ (10.5–11.2 mm), 1CV (8.9 mm). MV66-II, Stn 5, IKMT, 0–3889 mwo, 6♀ (10.6–11.0 mm), 2♂ (10.9, 10.6 mm). MV73-I, Stn 53, IKMT, 0–1900 m, 12♀ (9.9–11.0 mm), 5♂ (10.6–11.2 mm), 1CV (8.3 mm). CCE PO810 Cycle 1 Tow 1, Net 1, 500–700 m, 1♀, Co439.2.1, Co439.2.2. NH1208, MOC1: Stn 18, 399–600 m 1♀, Co439.5.1, NIWA105276; Stn 34, 400–600 m, 1♀, Co439.10.1. Record from Natural History Museum, London: John Murray Expedition, Stn 131, 0–500 m, 1♀ (8.53 mm), BMNH1949.12.13.26. Additional records from Smithsonian Institution, USNM numbers: 67211, 67213, 67218–24, 299531, 310291, 310301–03, 1027730, 1027738.

Type specimens. Deposited in the collection of the Scripps Institution of Oceanography, California: Holotype female: PIC-140409-0001-HT; Paratype male: PIC-140409-0002-PT; Paratype lot of 9 females and 4 males PIC-140409-0003-PT.

Genetic material. Co439.2.1, Co439.2.2, Co439.5.1, Co439.10.1. GenBank numbers in Table 6.

Morphological description. Following description based on holotype and paratype specimens from Francis Drake III, Stn 4. As for genus with following specific level features.

Female. Total length 10.5 mm (mean 10.2 mm, range 8.53–11.0 mm, n = 9) (Fig. 12A, B). Anterior head with low crest produced into short triangular projection extending beyond rostrum (Fig. 12A–C). Posterior borders of pedigerous somite 5 extending into triangular lappets reaching one third of way along genital double-somite, in dorsal view, lappets appearing pointed (Fig. 12A).

Length of antennule segments (μm) as follows. Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements taken of ancestral segment I. I (260, 688); II–IV (765); V (394); VI (379); VII (433); VIII (433); IX (465); X–XI (913); XII (619); XIII (631); XIV (738); XV (847); XVI (829); XVII (866); XVIII (904); XIX (891); XX (931); XXI (965); XXII (728); XXIII (654); XXIV (644); XXV (644); XXVI (371); XXVII (433); XXVIII (63). Dorsal surface of segments I–V each with very small hair sensillum of which those on segments I–III each accompanied by macula cribrosa (Fig. 12E); ancestral segments XIV to XVII with 15, 21, 32, 25 ventral teeth, respectively (Fig. 12F, G); and segments XV and XVI with variable numbers of blunt teeth along distoposterior border.

Leg 1 outer spines on exopod segments 1 and 2 extending half way between bases of following 2 more distal spines; 1 macula cribrosa at base of outer spine on exopod segment 2.

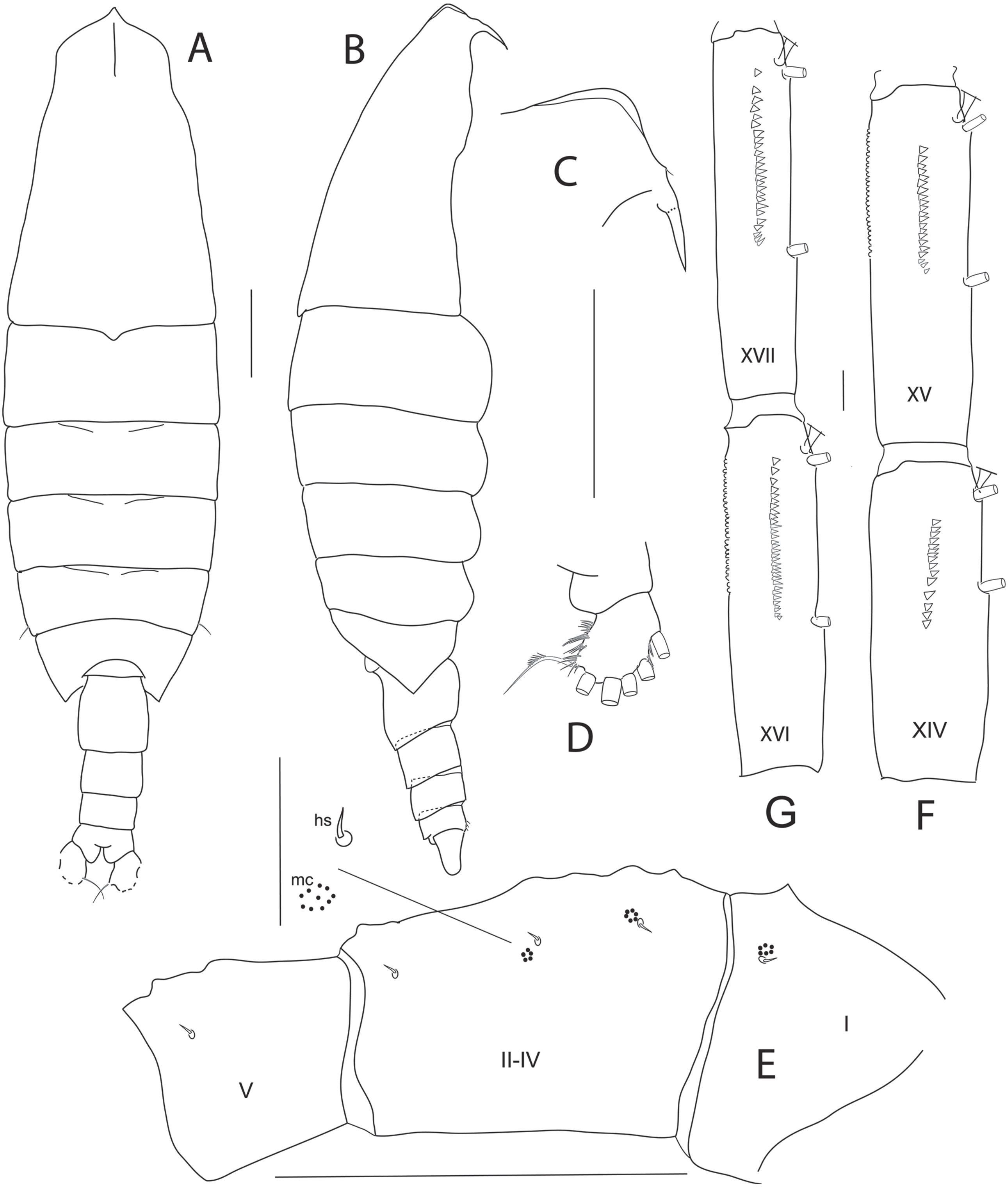

FIGURE 12. *Megacalanus frosti* **n. sp.** female: A, dorsal view; B, lateral view; C, lateral view of head; D, dorsal view of caudal ramus; E, antennule ancestral segments I–V (hs = hair sensillum, mc = macula cribrosa), dorsal view; F, antennule ancestral segments XIV–XV; G, antennule ancestral segments XVI–XVII. Scale bars represent: 1.0 mm on figures A–E, 0.1 mm on remaining figures. Illustrated specimen from Francis Drake III, Stn 4.

Male (Fig. 13A, B). Total length 10.4 mm (mean 10.6 mm, range 9.5–11.2 mm, n=8). Head with low crest (Fig. 13A–C). Posterior borders of pedigerous somite 5 extending as short triangular lappets, in lateral view, as far as posterior border of urosomite 1 (Fig. 13B).

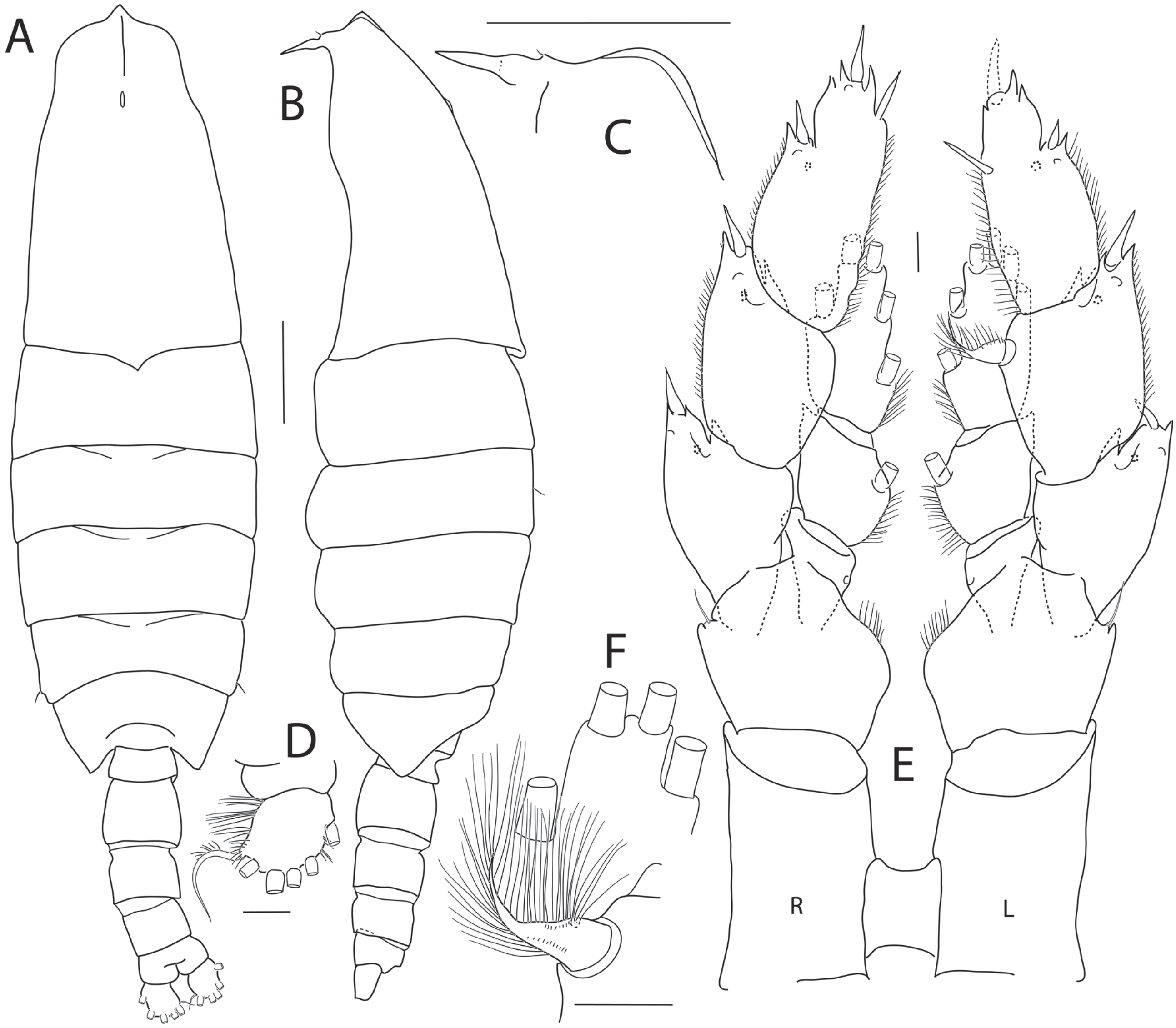

FIGURE 13. *Megacalanus frosti* **n. sp.** male: A, dorsal view; B, lateral view; C, lateral view of anterior head; D, dorsal view of caudal ramus; E, posterior view of leg 5; F, inner distal margin of exopod segment 2 of left leg. Scale bars represent 1.0 mm on figures A–C; 0.1 mm on remaining figures. Illustated specimen from Francis Drake III, Stn 4.

Antennule (Fig. 14A–D) on right with ancestral segment XIX with 1 fused griping element extending beyond base of aesthetasc, 1ms, 1a; XXI with 1 short gripping element at about midlength fused only at its base, 1ms, 1a.

Leg 5 as in generic description, inner distal border of basis with setules, left exopod segment 2 specialised seta with basal part usually longer than wide, lash longer than basal part; right exopod segment 3 with inner border completely lined with fine setules to just short of inner border articulated spine (Fig. 13E, F).

Morphological variation. Crest usually prominent, but sometimes small. Ancestral segments XIV to XVII of female antennules with 15–18, 20–26, 24–28, 24–32 ventral teeth, respectively (n=6 antennules). Male leg 5 left specialised seta with lash of variable length, sometimes shorter than basal part. Male ancestral segments XIV–XV ventral teeth with 17–29 and 35–39, respectively (n=4).

Distribution. *Megacalanus frosti* **n. sp.** is a bathypelagic species that extends into the mesopelagic zone from depths < 500 m to > 2000 m. It is known mainly from the eastern Pacific Ocean from off California to off Chile just south of 45ºS and extends westwards at least to about 135ºW at mid latitudes in the North Pacific (Fig. 9, Table 1) (see also Miller 2002). A single stray female was found in the Arabian Sea during the John Murray Expedition (Stn 131).

Species comparisons. Females of *M. frosti* **n. sp.** and *M. princeps* are similar in that antennule ancestral segments XV and XVI have a distoposterior row of blunt teeth, a feature not found in *M. ericae* **n. sp.** or *M.*

ohmani **n. sp.** (Table 7). Both sexes of *M. frosti* **n. sp.**, nevertheless, are easily distinguished by their crested heads whereas both sexes of *M. princeps* lack crests. Also, males of *M. frosti* **n. sp.** can be distinguished from the males of *M. princeps* by the presence of a fused gripping element on ancestral segment XIX on the right antennule (this element is not present in *M. princeps*).

The single crested female from the John Murray Expedition, examined by GAB, corresponds well to the description of *M. frosti* **n. sp.** It has ventral teeth on antennule segments XIV to XVII inclusive, and has blunt teeth on the posterior margin of XV and XVI, as figured for *M. frosti* **n. sp.** The posterior borders of pedigerous somite 5 are as figured. The crest is prominent. The body length for this adult female is only 8.53 mm total length which is small although specimen was from the "southern area of the Arabian Sea" (Stn 131).

Etymology. At the suggestion of Professor Charlie Miller of Oregon State University, who first recognised this form of *Megacalanus*, this species is named in honour of Professor Bruce Frost.

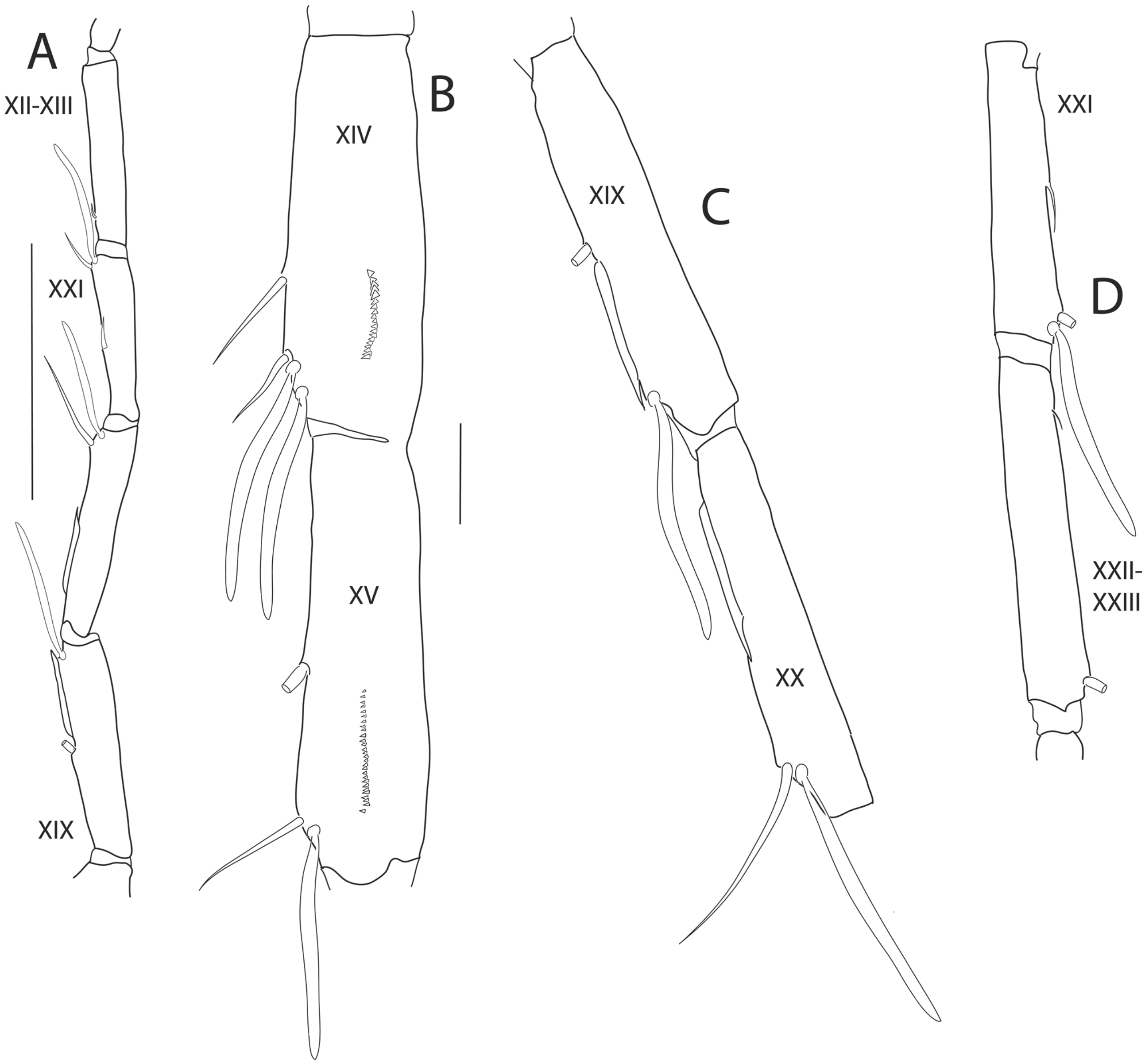

FIGURE 14. *Megacalanus frosti* **n. sp.** male, details of selected right antennule ancestral segments: A, segments XIX–XXIII; B, segments XIV–XV; C, segments XIX–XX; D, segments XXI–XXIII. Scale bars represent 1.0 mm on figure A; 0.1 mm on remaining figures. Illustrated specimen from Francis Drake III, Stn 4.

***Megacalanus ericae* n. sp.**
(Figs 9, 15–16)

Megacalanus princeps: Tanaka, 1956, pp 262–264, fig. 3.
Megacalanus princeps: Brodsky *et al.* 1983, pp 197–198, fig. 87.
Megacalanus princeps: Bradford-Grieve, 1994, pp 18–20, figs 4, 5.

Type locality. 21.376º N 158.307º W.

Material examined. OCN 627, University of Hawaii, IKMT, 1000 m, 7♀ (7.8–9.3? mm), 4♂ (9.6–10.4 mm), holotype female 9.3 mm, paratypes, Co439.1.1, Co439.1.2. Indopac VII, Stn 5, IKMT, 0–2121 mwo, 5♀ (10.1–10.9 mm), 14♂ (9.6–11.2 mm). Circe II, Stn 15T-1, IKMT, 0–2121 mwo, 3♀ (9.6–10.9 mm), 7♂ (9.6–11.2 mm). Antipode IV, IKMT: Stn 52D, 0–1900 m, 3♀ (10.5–10.9 mm), 3♂ (10.6–10.9 mm); Stn 53A, 0–2000 m, 5♂ (9.9–11.0 mm); Stn 53D, 0–2500 m, 1♀ (10.2 mm), 4♂ (10.2–11.0 mm); Stn 55D, 0–2000 m, 2♀ (9.6–10.4 mm), 4♂ (9.6–10.6 mm). VUW, ring net: Stn VUZ93, 0–1097 m, 1♀ (9.7 mm), NIWA60235; Stn VUZ105, 0–914 m, 1♀ (9.3 mm), 1♂ (8.5 mm), NIWA60236. MAF, Jco7014/76, plankton net, 1♂. NIWA: Stn F745, ring net, 0–1170 m, 1♀ (9.8 mm), NIWA60234; Stn F946, Bé net, 200–500 m, 1CV (8.3 mm), NIWA60233; X468h, MOC1, 0–1000 m, 1♂, NIWA91280. NH1208, MOC1, Stn 11: 797–599 m, 1♂ Co439.3.1, 1♂ Co439.3.2; 399–598 m, 1♀ Co439.4.1; Stn18, 600–800 m, 1♀ Co439.6.1; Stn 24, 200–400 m, 1♀ Co439.7.1; Stn 27, 400–600 m, 1♂ Co439.8.1; Stn 32, 0–1000 m, 1♀ Co439.9.1. Additional records from Smithsonian Institution, USNM numbers: 73658, 73988, 73989, 74394, 79819, 262464, 262478, 262479, 262481–83, 262485–87, 262490, 262492–94, 299636–38, 102686, 1027687, 1027692, 1027732, 1027739.

Type specimens. Deposited in the collection of the National Institute of Water and Atmospheric Research, New Zealand: Holotype female: NIWA 85195; Paratype male: NIWA 85196; Paratype lot of 6 females and 3 males NIWA 85197.

Genetic material. Co439.1.1, Co439.1.2, Co439.3.1, Co439.3.2, Co439.4.1, Co439.6.1, Co439.7.1, Co439.8.1, Co439.9.1,

Morphological description. Following description based on holotype and paratype specimens from OCN 627. As for genus with following specific level features.

Female (Fig. 15). Total length 9.3 mm (mean 9.9 mm, range 7.8–11.0 mm, n=16). Head bluntly rounded, base of rostrum hardly visible in dorsal view. Posterior corners of pedigerous somite 5 in female with triangular lappets extending more than half way along genital double-somite in dorsal view and beyond ventral genital bulge in lateral view; in dorsal view, lappets pointed (Fig. 15A–C).

Antennule ancestral segments XIV to XVII with 21, 39, 41, 36 teeth on ventral surface, respectively; hair sensillum on dorsal surface of segments I–IV each accompanied by macula cribrosa (Fig. 15D); segments XV and XVI smooth, without distoposterior row of teeth (Fig. 15E). Lengths of antennule segments (μm) as follows. Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements taken of ancestral segment I. I (178, 701); II–IV (738); V (375); VI (390); VII (442); VIII (452); IX (457); X–XI (924); XII (625); XIII (654); XIV (773); XV (886); XVI (894); XVII (933); XVIII (963); XIX (1003); XX (995); XXI (1035); XXII (1032); XXIII (684); XXIV (706); XXV (644); XXVI (420); XXVII (440); XXVIII (52).

Leg 1 outer spine on exopod segments 1 and 2 extend not quite half distance between bases of following two spines; 1 macula cribrosa at base of outer spine on exopod segment 2.

Male (Fig. 16). Total length 9.7 mm (mean 10.2 mm, range 8.5–11.0 mm, n=13). Rostral points directed ventrally (Fig. 16B). Posterior borders of pedigerous somite 5 extend slightly beyond posterior border of urosomite I, lappets short and triangular in lateral view (Fig. 16B).

Antennule right ancestral segment XIX with fused gripping element extending slightly beyond base of aesthetasc, 1ms, 1a (Fig. 16E); and segment XXI with 1 small fine gripping element, 1ms and 1a (Fig. 16F). Left antennule with clavate seta on ancestral segment XI apparently broken off leaving short setal vestige.

Leg 5 inner distal border of basis with setules, left exopod segment 2 specialised seta with basal part squat, usually wider than long, and lash shorter than basal part (Fig. 16C, D). Right exopod segment 3 of leg 5 inner border completely lined by fine spinules as far as inner articulated spine (Fig. 16C).

Morphological variation. Ancestral segments XIV to XVII of female antennules with 16–21, 34–39, 34–41, 31–36 ventral teeth, respectively (n=4 antennules). Proportions of basal part of male left leg 5 specialised seta variable but lash appears to be consistently short. Male ancestral segments XIV–XV on right with 27–31 and 34–49 ventral teeth, respectively (n=5). Right antennule ancestral segment XXI gripping element usually small but a specimen from cruise Circe II has this element larger and stronger, similar to that of *M. frosti* **n. sp.** although the specialised seta on the left leg 5 exopod segment 2 is squat with a short lash as in other *M. ericae* **n. sp.**

Distribution. *Megacalanus ericae* **n. sp.** is a bathypelagic species which extends into the mesopelagic zone from < 500 to > 2000 m. It is known from the Pacific Ocean (in the northeast Pacific it is known to overlap in distribution with *M. frosti*) and the Indian Ocean (Fig. 9, Table 1).

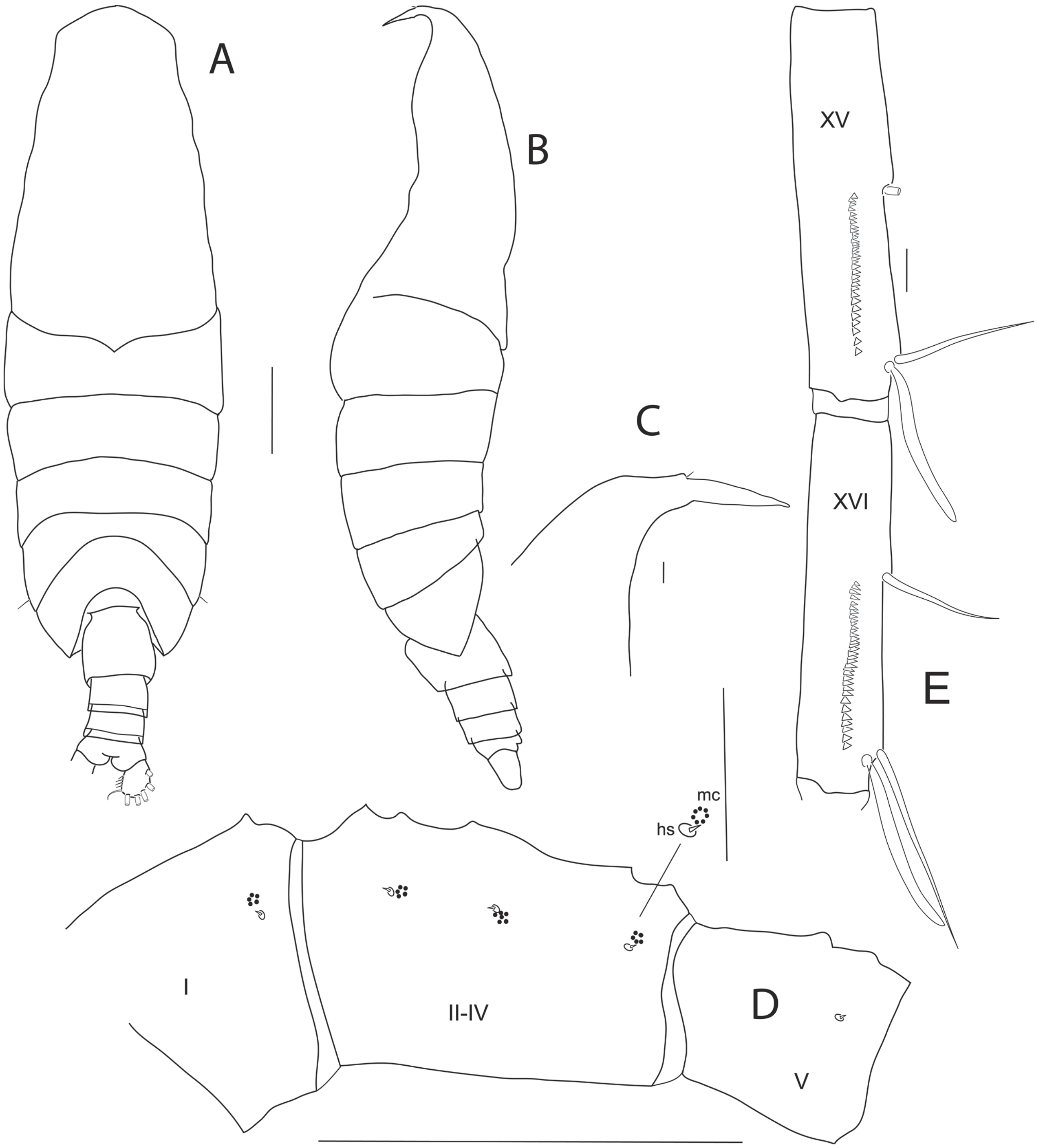

FIGURE 15. *Megacalanus ericae* **n. sp.** female: A, dorsal view; B, lateral view; C, lateral view of anterior head; D, ancestral segments I–V, dorsal view (hs = hair sensillum, mc = macula cribrosa); E, ancestral segments XV–XVI of antennule. Scale bar represents 1.0 mm on figures A, B, D; 0.1 mm on remaining figures. Illustrated specimen from OCN627.

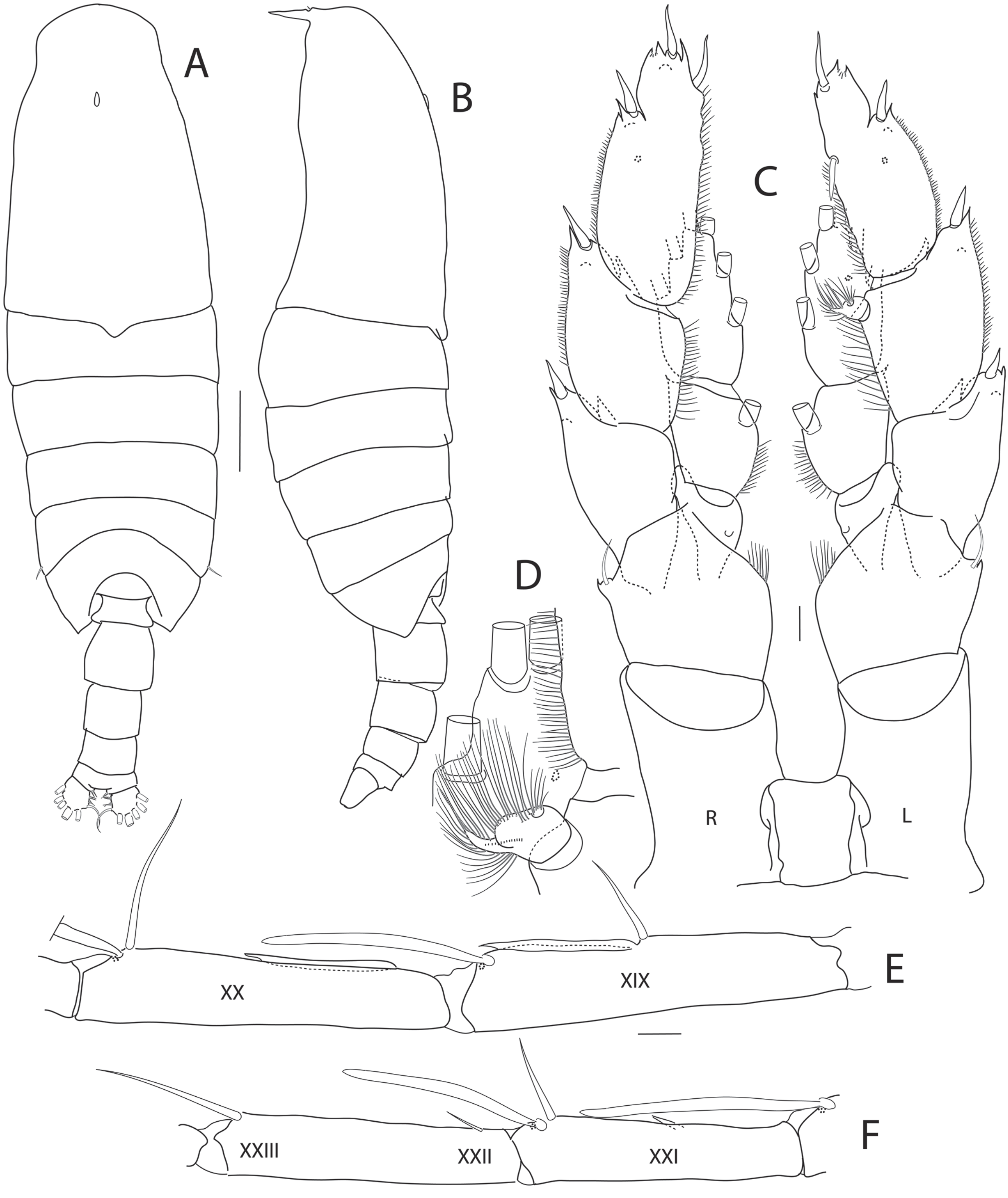

FIGURE 16. *Megacalanus ericae* **n. sp.** male: A, dorsal view; B, lateral view; C, posterior view of leg 5; D, inner distal margin of exopod segment 2 of left leg; E, ancestral segments XIX–XX of right antennule; F, ancestral segments XXI–XXIII of right antennule. Scale bars represent 1.0 mm on figures A, B; 0.1 mm on remaining figures. Illustrated specimen from OCN627.

Species comparisons. Females of *M. ericae* **n. sp.** and *M. ohmani* **n. sp.** are similar in that ancestral segments XV and XVI of the antennule have a smooth distoposterior border (compared with congeners that have a distoposterior row of blunt teeth, Table 7). Females can be distinguished by differences in the shape of the posterior borders of pedigerous somite 5 in lateral view. In *M. ericae* n. sp these borders are triangular and extend beyond the genital double-somite ventral bulge in lateral view; in *M. ohmani* **n. sp.**, these borders are shorter and rounded. Males of *M. ericae* **n. sp.** are easily distinguished from males of *M. ohmani* **n. sp.** by the presence, on the male right antennule ancestral segments XXI, of a single gripping element, whereas *M. ohmani* **n. sp.** has 2 long overlapping gripping elements. The right leg 5 exopod segment 3 inner border of *M. ericae* **n. sp.** is completely setulose as far as the inner spine. The specialised seta on the male left leg 5 exopod segment 2 has a uniquely short and squat form unlike that of any other species of *Megacalanus*.

Etymology. This species is named for Dr Erica Goetze (University of Hawaii, USA) who made specimens available for the genetic and morphological analysis.

***Megacalanus ohmani* n. sp.**
(Figs 9, 17–23)

Type locality. 5.350º S, 133.583º E.

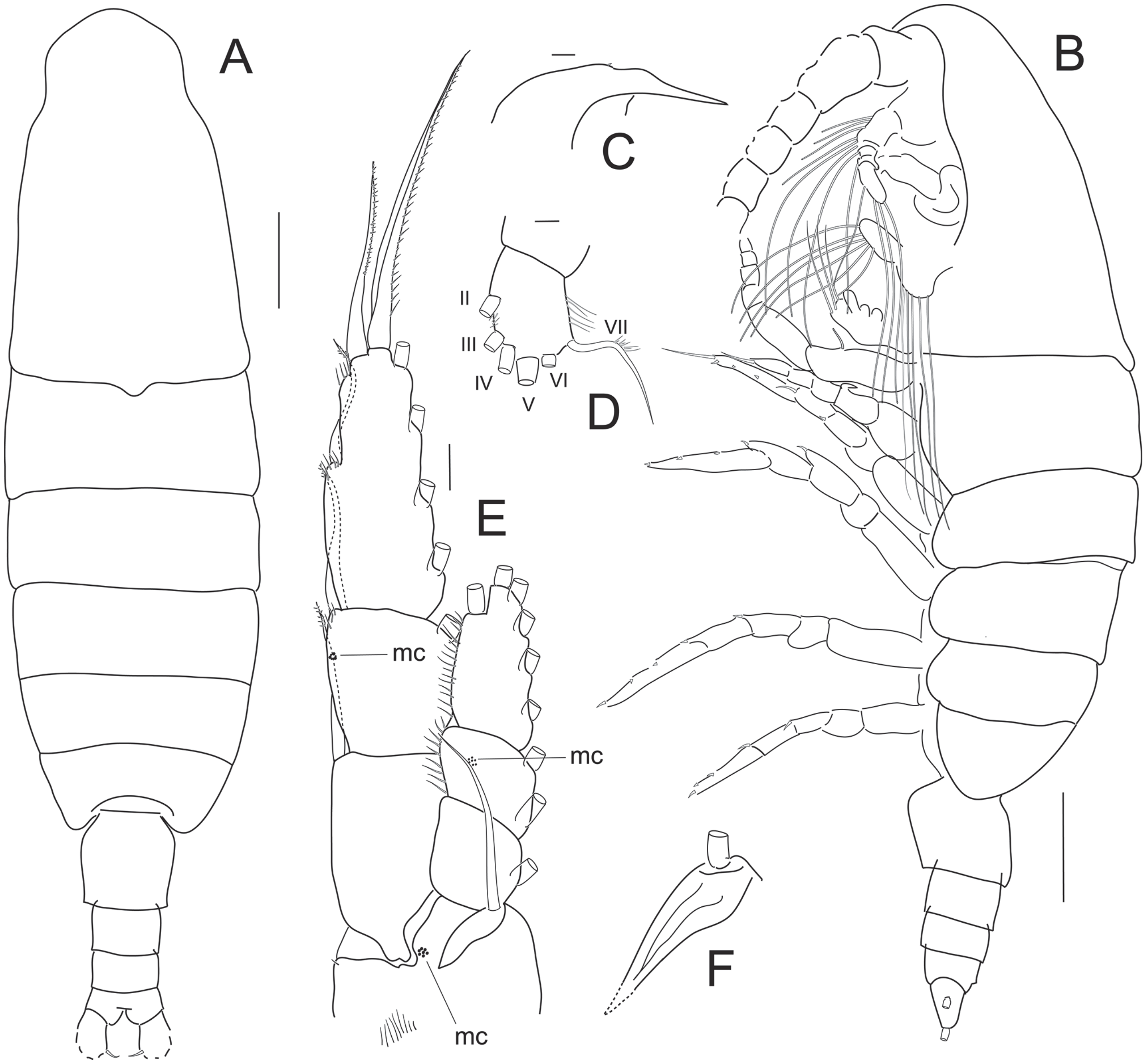

FIGURE 17. *Megacalanus ohmani* **n. sp.** female: A, dorsal view; B, lateral view; C, lateral view of anterior head; D, dorsal view of caudal ramus; E, anterior view of leg 1 (mc = macula cribrosa); F, detail of large spine on anterior surface of leg 1 basis. Scale bars represent 1.0 mm on figures A, B; 0.1 mm on remaining figures. Illustrated specimen from Indopac VIII, Stn 6.

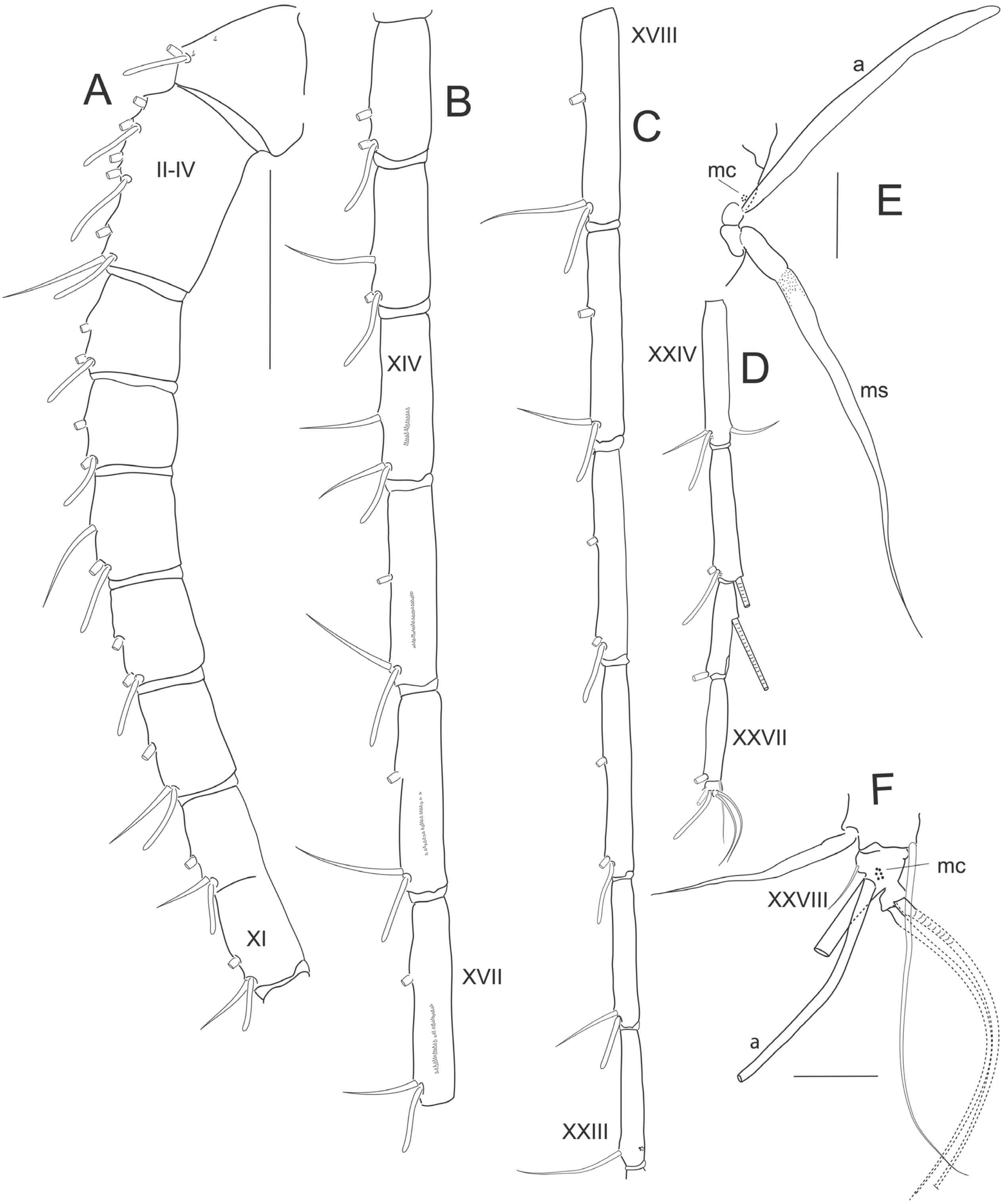

FIGURE 18. *Megacalanus ohmani* **n. sp.** female antennule ancestral segments: A, ventral surface of segments I–XI; B, segments XII–XVII; C, segments XVIII–XXIII; D, segments XXIV–XXVIII; E, detail of aesthetasc (a), modified setae (ms) and macula cribrosa (mc) distally on segments XXV; F, detail of terminal part of antennule (a = aesthetasc, mc = macula cribrosa). Scale bars represent 1.0 mm on figures A–D; 0.1 mm on remaining figures. Illustrated specimen from Indopac VIII, Stn 6.

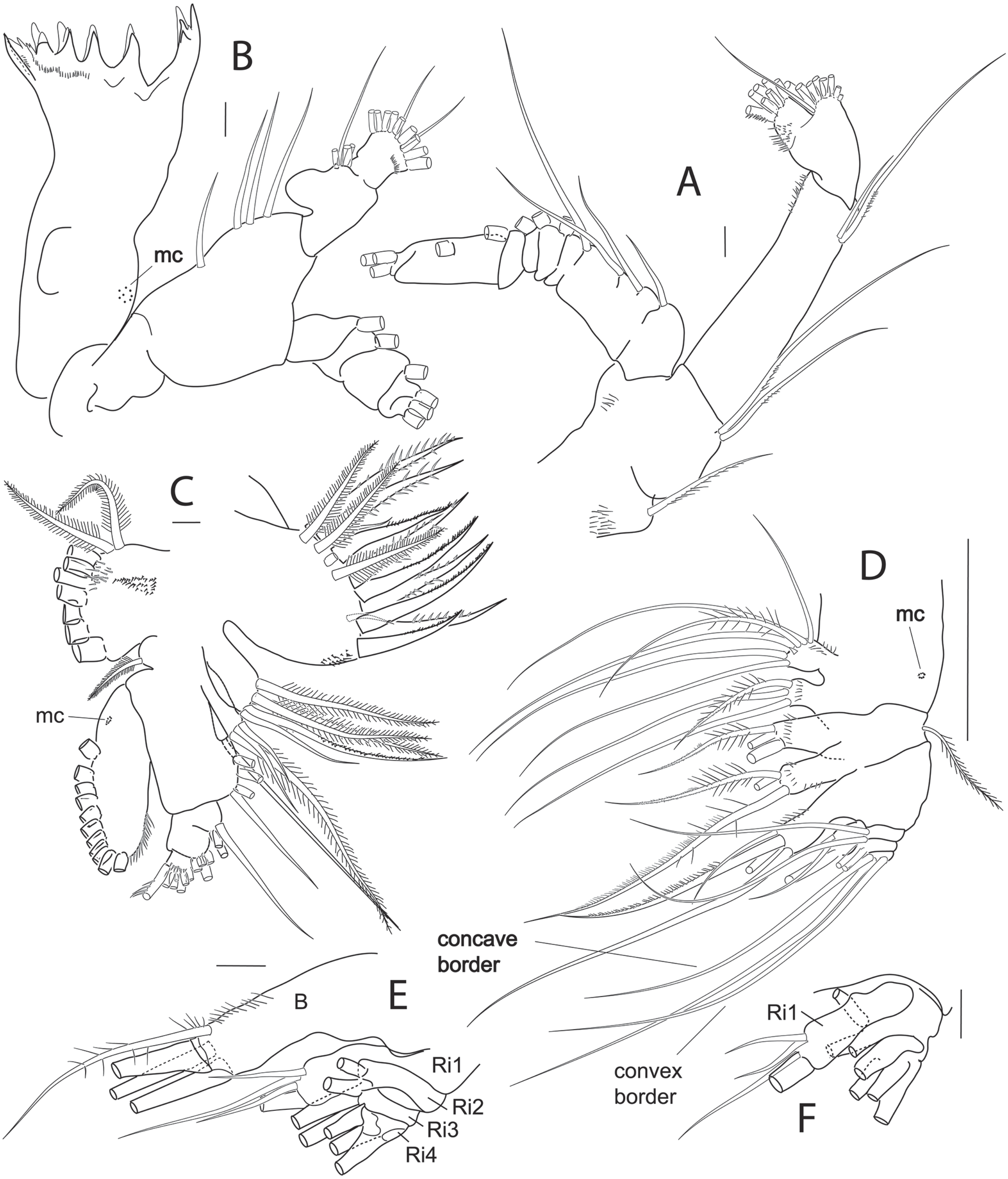

FIGURE 19. *Megacalanus ohmani* **n. sp.** female: A, antenna; B, mandible; C, maxillule (mc = macula cribrosa); D, inner view of maxilla; E, detail of inner view of terminal part of maxilla (B = basal endite, Ri 1–4 = endopod segments 1–4); F, outer view of endopod of maxilla. Scale bars represent 1.0 mm on figure D; 0.1 mm on remaining figures. Illustrated specimen from Indopac VIII, Stn 6.

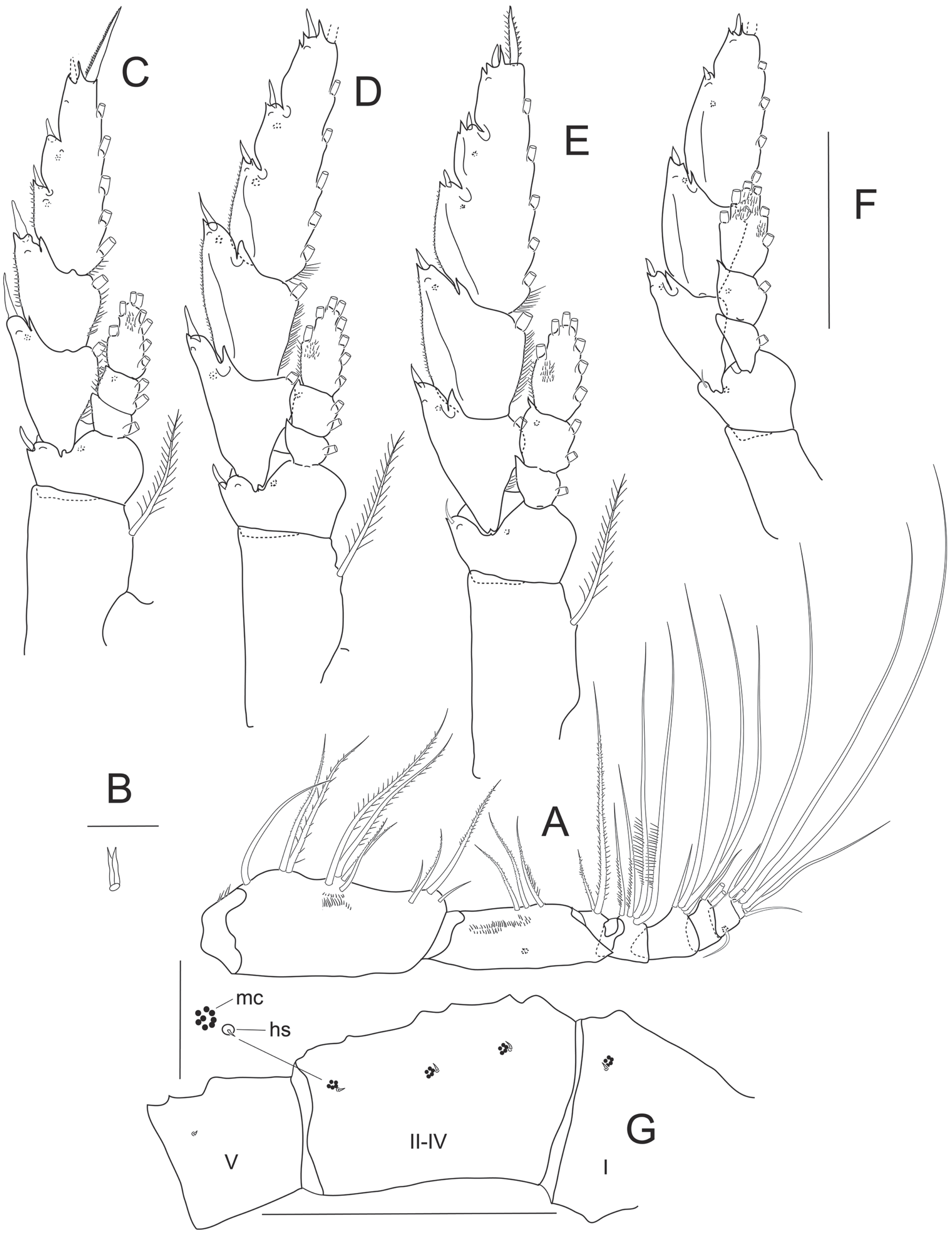

FIGURE 20. *Megacalanus ohmani* **n. sp.** female: A, maxilliped; B, detail of bifurcate spinule from basis of maxilliped; C, leg 2; D, leg 3; E, leg 4; F, leg 5; G, dorsal view of antennule ancestral segments I–V showing hair sensilla (hs) and maculae cribrosae (ms). Scale bars represent 1.0 mm on figures A, C–G; 0.1 mm on remaining figures. Illustrated specimen from Indopac VIII, Stn, 6.

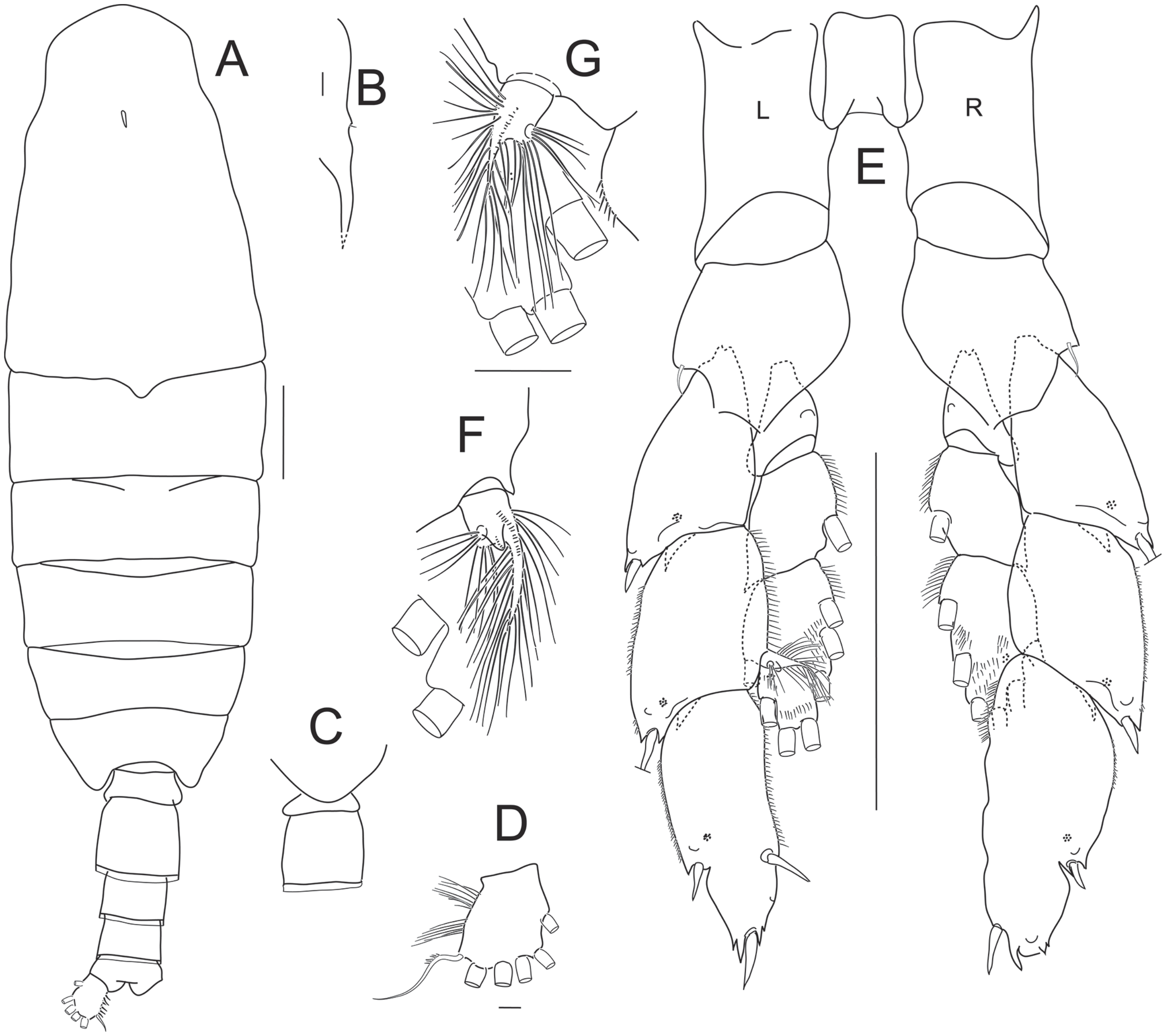

FIGURE 21. *Megacalanus ohmani* **n. sp.** male: A, dorsal view; B, lateral view of anterior head; C, lateral view of posterior corners of pedigerous somite 5; D, dorsal view of caudal ramus; E, posterior view of leg 5; F, distal inner corner of left exopod segment 2; G, distal inner corner of left exopod segment 2 of another specimen. Scale bars represent 1.0 mm on figures A, C, E; 0.1 mm on remaining figures. Illustrated specimen from Indopac VIII, Stn 6.

Material examined. Indopac VIII, Stn 6, IKMT, 0–2096 mwo, 33♀ (9.5–11.0 mm), 8♂, holotype female 11.0 mm, paratypes.

Type specimens. Deposited in the collection of the Scripps Institution of Oceanography, California: Holotype female: PIC-140409-0004-HT; Paratype male: PIC-140409-0005-PT; Paratype lot of 33 females and 7 males PIC-140409-0006-PT.

Morphological description. Following description based on holotype and paratype from Indopac VIII, Stn 6. As for genus with following specific level features.

Female (Figs 17–20). Total length 11.0 mm (mean 10.4 mm, range 9.5–11.0 mm, n=10). Head bluntly rounded, posterior corners of pedigerous somite 5 with short bluntly rounded posterior borders extending one quarter of distance along genital double-somite in dorsal view and only as far as genital bulge of genital double-somite in lateral view, posterior borders appearing rounded in dorsal view.

Antennule (Fig. 18) segment length (µm) as follows. Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements taken of ancestral segment I. I (441, 691); II–IV (765); V (376); VI (371); VII (418); VIII (418); IX (483); X–XI (928); XII (654); XIII (666); XIV (787); XV (938); XVI (951); XVII (968); XVIII (1020); XIX (1020); XX (1012); XXI (1005); XXII (708); XXIII (651);

XXIV (691); XXV (658); XXVI (431); XXVII (503); XXVIII (67). Dorsal surface of segments I–V each with very small hair sensillum of which those on segments I–IV each accompanied by macula cribrosa (Fig. 20G); ventral surface of ancestral segments XIV to XVII with distal row of 19/20, 31/31, 30/36, 30/30 teeth, respectively (Fig. 18B); ancestral segments XV and XVI smooth, without distoposterior row of blunt teeth.

Leg 1 (Fig. 17E, F) outer spines on exopod segments 1 and 2 extending only slightly beyond base of following, more distal spine and exopod segment 2 has macula cribrosa located at distal one third from base of distolateral spine on lateral border.

Male (Figs 21–23). Total length 10.7 mm. Anterior margin of head bluntly rounded in dorsal view.

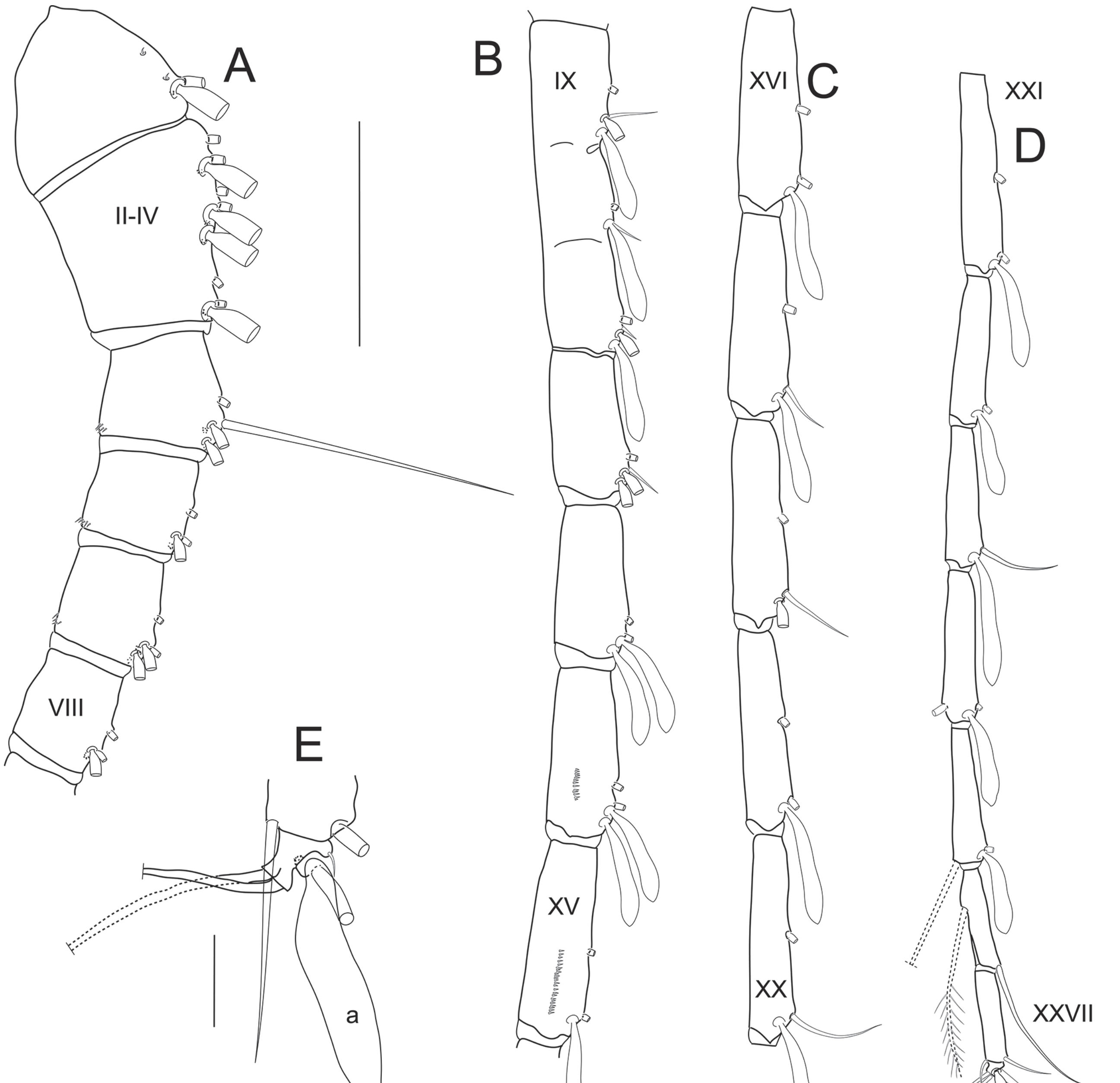

FIGURE 22. *Megacalanus ohmani* **n. sp.** male left antennule ancestral segments: A, segments I–VIII; B, segments IX–XV, note clavate seta on segment XI apparently knocked off but present in other specimens; C, segments XVI–XX; D, segments XXI–XXVIII. Scale bars represent 1.0 mm on figures A–D; 0.1 mm on figure E. Illustrated specimen from Indopac VIII, Stn 6.

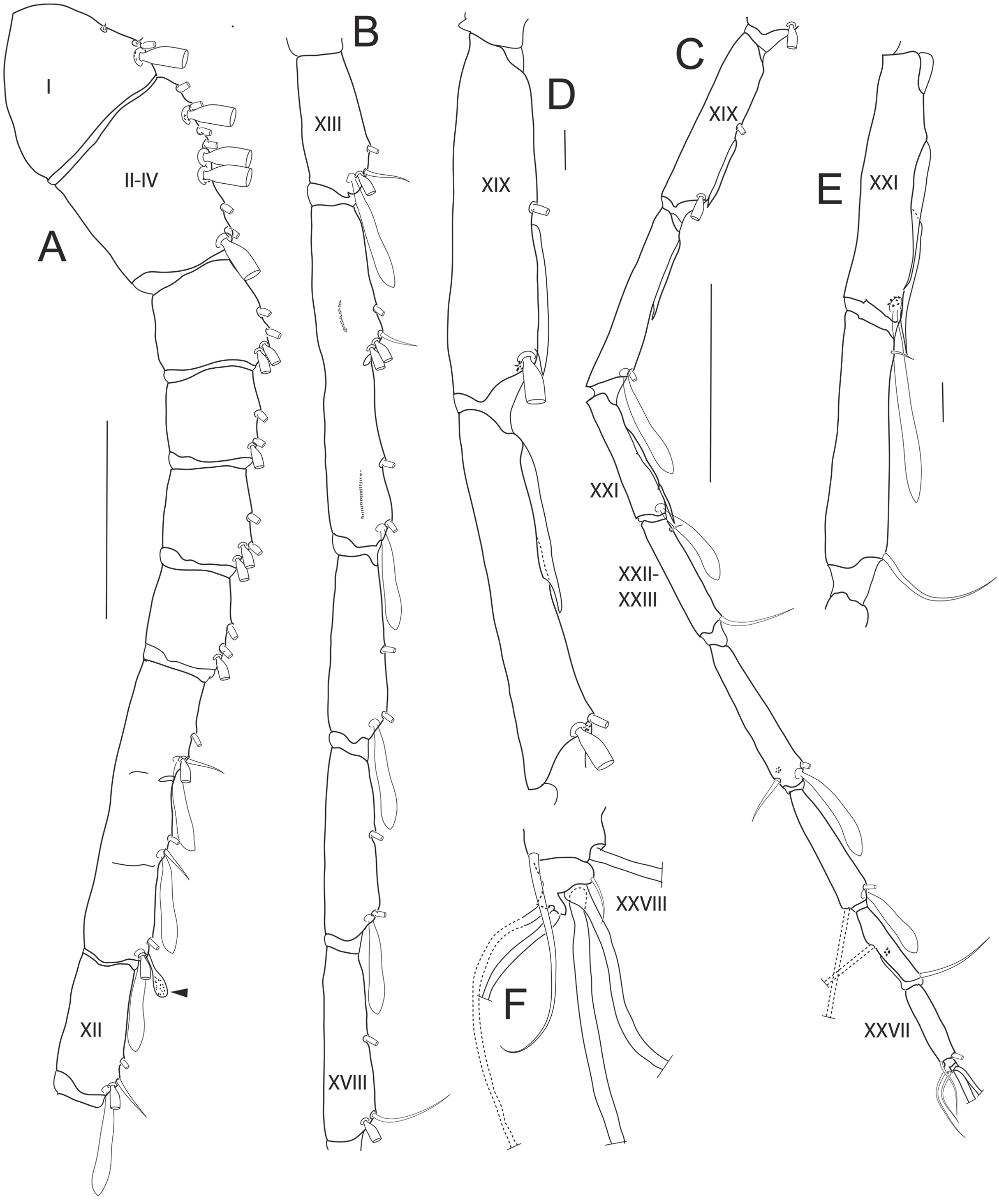

FIGURE 23. *Megacalanus ohmani* **n. sp.** male right antennule ancestral segments: A, segment I–XII, arrow indicates 'clavate seta'; B, segments XIII–XVIII; C, segments XIX–XXVIII; D, detail of segments XIX–XX; E, detail of segments XXI–XXIII; F, detail of terminal part. Scale bars represent 1.0 mm figures A–C; 0.1 mm on remaining figures. Illustrated specimen from Indopac VIII, Stn 6.

Right antennule ancestral segment XI with distal clavate (club-shaped) seta (indicated by arrow) (Fig. 23A); ancestral segment XIX with 1 fused gripping element extending beyond base of aesthetasc, 1ms, 1a (Fig. 23C, D); and segment XXI with 2 long overlapping gripping elements (proximal element with tip extending to base of aesthetasc, distal element extending well beyond distal border of segment), 1a (Fig. 23C, E). Left antennule (Fig. 22) with clavate seta broken off ancestral segment XI in figured specimen leaving setal vestige, but present in other specimens.

Leg 5 inner distal border of basis without setules, left leg 5 exopod segment 2 specialised seta with basal part longer than wide and lash longer than basal part (Fig. 21 E–G). Right exopod segment 3 inner border with series of hyaline ridges along distal two thirds, proximal one third lined with fine setules (Fig. 21E).

Distribution. *Megacalanus ohmani* is a bathypelagic species known so far only from east of Irian Jaya (Fig. 9, Table 1).

Species comparisons. Female of *M. ohmani* **n. sp.** and *M. ericae* **n. sp.** are similar in that ancestral segments XV and XVI of the antennule have a smooth distoposterior border (Table 7). Females (and males) of these two species may be distinguished by the shape of the posterior borders of pedigerous somite 5: in *M. ohmani* **n. sp.** these borders are short and round and in *M. ericae* **n. sp.** longer and triangular. Male *M. ohmani* **n. sp.** is easily distinguished from males of all other species by the pair of overlapping fused gripping elements on right antennule ancestral segment XXI and the inner border of the right leg 5 exopod segment 3 which is setulose only on the proximal one third and has a series of hyaline ridges along the remainder of the inner border—no other species has these features.

The specialised seta on the male left leg 5 exopod segment 2 is similar to that of *M. princeps* and *M. frosti* **n. sp.** but differs from the Pacific species *M. ericae* **n. sp.** which has a much stumpier specialised seta with a lash that is shorter than the basal part. Leg 1 of *M. ohmani* **n. sp.** has two unique features: the outer spines on exopod segments 1 and 2 extend only slightly beyond base of following, more distal spine (in the other species these outer spines are longer); and exopod segment 2 has the macula cribrosa located at distal one third from base of distolateral spine on lateral border (whereas in the other species the macula cribrosa is situated close to the base of the outer border spine and on the anterior surface).

Etymology. This species has been named for Professor Mark Ohman who made available the extensive collection of Megacalanidae from the Scripps Institution of Oceanography (USA) collection of pelagic invertebrates, on which this work is partly based.

Genus *Bradycalanus* A. Scott, 1909

Differential diagnosis. As for Megacalanidae plus following character states: Anterior head rounded or crested. Rostral filaments slender and tapering to point. Female antennule ancestral segment XXIII with aesthetasc. Dorsal surface of antennular ancestral segments I–V each with small hair sensillum without maculae cribrosae. Right male antennule ancestral segments XXI–XXIII fused, segments XIX, XX and XXI with gripping elements. Antennal exopod ancestral segments I–III each bearing relatively well-developed seta each longer than its segment, or shorter than its segment (*Br. abyssicolus* n.sp.), seta on segment IV extending short of distal border of exopod. Mandibular gnathobase with ventral tooth set at oblique angle to main plane of gnathobase therefore appearing broader than other teeth, remaining tooth row more or less in line (not set anterior and posterior as in *Bathycalanus*); endopod segment 1 with 4 setae, endopod segment 2 with 9 large setae and 2 vestigial setae. Maxillule praecoxal arthrite with 4 posterior surface setae, coxal endite with 4 + 1 small or 2 setae (*Br. abyssicolus*); basal endites 1 and 2 with 2, 4 setae, respectively; endopod segments 1–3 usually with 2, 1 + 1 vestigial, 5 + 1 small posterior surface setae, respectively. Maxilla relatively enlarged compared with other megacalanids; longest setae extend as far as mid labrum and only setae of praecoxal endites 1 and 2 and coxal endite 1 with auxiliary setules; proximal inner seta of endopod segment 2 vestigial, convex border of distal inner seta of endopod segment 2 naked. Maxilliped not enlarged compared with other megacalanids, longest setae extend to rostrum, endopod segments 3–5 with variable numbers of setae poorly developed. Leg 1 basis without hooked process, exopod segments 1 and 2 each bearing distolateral articulated spine, segment 3 with 2 outer border spines. Maculae cribrosae absent. Male leg 5 specialised seta on left leg tapering evenly, bordered by very long setules.

Type species. *Bradycalanus typicus* A. Scott, 1909.

Type locality. 0º 17.6'S, 129º 14.5'E.

Description. Female. Anterior margin of head in dorsal view rounded or crested, rostrum extending into two long, ventroposteriorly-directed, tapering points that appear to be direct extensions of cuticle. Pedigerous somites

1–5 separate, posterior border of somite 5 rounded or extended into small, sharp or obtuse projections in lateral view. Urosome of four free somites. Genital double-somite symmetrical in dorsal view, lateral borders slightly convex, approximately as long as wide and widest at variable locations anterior to posterior; in lateral view distinct ventral genital bulge anteriorly placed or with posterior ridge (*Br. abyssicolus* **n. sp.**). Caudal rami with seta I absent, setae II and III lateral, setae IV–VI terminal (seta V longest), seta VII inserted at inner distal corner on small projection.

Antennule extending as far as posterior border of caudal rami or several segments beyond; ancestral segments II–IV and X–XI fused, segments XXVII and XXVIII separate. Most setae modified; one plumose or naked seta on segment I and naked seta on segment XXVIII. Segments I–V each with dorsal surface hair sensillum, without maculae cribrosae. Setation of segments as follows (based on *Br. abyssicolus* because specimens of other species not in good condition): I—1ms, 1a, 2 ss (or 1 ss and 1 plumose setae); II to XXI—2ms + 1a; XXII to XXIII—1ms + 1a; XXIV —1ms + 1a anteriorly, 1 ms posteriorly; XXV —1 ms + 1a anteriorly, 1 large ms posteriorly; XXVI to XXVII—1ms + 1; XXVIII—3ms, 1a, 1ss, no maculae cribrosae present.

Antenna with separate coxa and basis; coxa with 1 inner plumose seta with very long setules along both sides and inner tuft of setules, basis with 2 inner setae each with 2 rows of short setules. Exopod slightly longer than endopod; endopod 2-segmented although line of fusion between ancestral segments II and III visible on posterior surface; segment 1 with 2 inner naked setae and short longitudinal row of outer setules, terminal segment with 9+7 setae; exopod ancestral segment I separate from ancestral segment II, usually with 1 inner disal seta longer than its segment (in *Br. abyssicolus* **n. sp.** shorter than its segment). Segment IV seta extends short of distal border of exopod. Segments II–IV fused on posterior surface although line of demarcation visible on anterior surface; segments V–VIII separate, each with long plumose seta; segments IX–X fused, segment X bearing 3 terminal setae.

Mandible coxal gnathobase heavily sclerotised, without macula cribrosa, very broad terminally with six large, complex teeth; largest ventral tooth oriented obliquely to plane of gnathobase thus appearing very wide at base; teeth 2–5 at right angles to main plane of gnathobase, dorsal-most teeth not complex: 2 small and 1 large tooth adjacent to non-articulated lash-like element bordered by 2 tooth rows; basis with 4 inner setae; endopod 2-segmented, segment 1 bearing large inner lobe and 4 distal inner setae (distalmost seta small), segment 2 with 11 terminal setae, 2 of them on one surface, vestigial; exopod 5-segmented with 1, 1, 1, 1, 2 setae.

Maxillule praecoxal arthrite with full complement of 15 setae, 4 of these on posterior and 2 on anterior surface; coxal endite with 5 or 2 setae, epipodite with 7 long and 2 proximal short setae; basal endites 1 and 2 with 2 and 4 setae, respectively, exite with 1 seta; basis and endopod segment 1 fused or separate; endopod with ancestral segments I and II fused, with 2, 1 + 1 vestigial, and 5 + 1 small seta, respectively; exopod with 11 setae, without macula cribrosa.

Maxilla enlarged relative to other megacalanids, longest setae extend as far as mid labrum. Praecoxal endite 1 with 6 setae plus 1 small triangular spine, praecoxal endite 2 with 3 setae; coxal epipodite with 1 vestigial seta; coxal endites 1 and 2 with 3 setae each; basal endite longest with 4 setae; endopod segment 1 with lobe bearing 3 vestigial + 1 large seta, endopod segments 2–4 with 3 (inner proximal seta vestigial, distal seta naked), 1, 2 setae, respectively, most of them strong and curved along whole length. One seta on inner surface of praecoxal endite 1 and coxal endites 1 and 2 shorter and more densely lined with long spinules; longest setae of praecoxal endite 2 and coxal endites 1 and 2 with closely spaced short setules as well as long sparse auxiliary setules. Basal endite and endopod setae strong and spine-like with distal two thirds of concave border lined with closely spaced setules; inner distal long seta of endopod segment 2 with fine spinules on distal proximal-facing (concave) border and naked distally-facing (convex) border.

Maxilliped directed ventrally so that setae on syncoxa and basis directed into animal's midline; syncoxa with 1, 2, 4, 3 short + 1 long setae, respectively (on endite 4, long seta toothed and extending as far as third basal seta); basis with 3 setae and with or without long row of very small spinules; endopod segment 1 bearing 2 setae, longer seta plumose along both borders, shorter seta with smooth basal part and tapering distal part bordered by 2 rows of spinules, separate from or partially incorporated into basis; endopod segments 2–6 with 4, 1+3 small, 1+2 small, 1+2 small +1 outer, 2+2 small setae, respectively, 3 of 4 setae on endopod segment 2 with long setules along one border, distal-most seta longest, bordered by short spinules along distal two thirds of one border.

Legs 1–5 biramous, each ramus 3-segmented with following setal formula (Roman numerals indicate spines, Arabic numerals indicate setae; outer border setation listed first):

Leg 1 (Coxa 0-1. Basis 1-1. Exopod I-1; I-1; II,1,4. Endopod 0-1; 0-2; 1,2,3);
Leg 2 (Coxa 0-1. Basis I-0. Exopod I-1; I-1; III,1,5. Endopod 0-1; 0-2; 2,2,4);
Leg 3 (Coxa 0-1. Basis I-0. Exopod I-1; I-1; III,1,5. Endopod 0-1; 0-2; 2,2,4);
Leg 4 (Coxa 0-1. Basis 1-0. Exopod I-1; I-1; III,1,5. Endopod 0-1; 0-2; 2,2,3);
Leg 5♀ (Coxa 0-0. Basis 1-0. Exopod I-0; I-1; II,1,4. Endopod 0-1; 0-1; 2,2,2);

Leg 1 inner seta on coxa arising from inner posterior surface; basis without macula cribrosa, with inner distal S-shaped seta arising on anterior surface and curving across distal border of endopod segment 1, outer seta vestigial; distolateral corner of endopod segment 1 rounded; distolateral exopod spines of various lengths and exopod segments of varying length : width proportions. Legs 2–4 coxal seta on inner margin; pore openings located on anterior surface at base of outer edge spines of exopod segments 1–3, and endopod segment 1 outer distal corners with small rounded or pointed protrusions. Leg 5 with outer distal corner of endopod segment 1 rounded; pore openings on anterior surface at base of outer border spines. On legs 2–5 outer borders of endopod segments 1–2 and proximal outer border of segment 3 lined with fine setules, apart from leg 5 endopod segment 1; proximal inner border of endopod segments 2 and 3 lined with fine setules. Fine setules line outer border of exopod segment 2 and proximal outer border of exopod segment 3 of legs 2–5; fine setules line inner borders of exopod segments 1 and 2 and proximal inner border of segment 3 of legs 2–5, except for naked inner border of exopod segment 1 of leg 5.

Male. Anterior margin of head similar to that of female. Rostrum extending ventroposteriorly into two long, tapering points appearing to be direct extensions of cuticle. Urosome of five free somites, genital somite short. Caudal rami seta I absent, setae II and III lateral, setae IV–VI terminal (seta V longest), seta VII inserted at inner distal corner onto small projection; setules decorating inner border.

Antennules asymmetrical, geniculate on right. Aesthetascs larger than in female with stiffened posterior border. Left antennule with ancestral segments II–IV, IX–XI fused, segments XXVII and XXVIII separate, with aethetascs doubled on segments I, III, V, VII, IX, XI–XIV. Most setae of modified (ms) type, or aesthetascs (a); and few naked simple setae (ss). Setation of segments as follows: I—1ms, 2a, 2ss; II–IV—6ms, 4a; V—2ms, 2a; VI—2ms, 1a; VII—2ms, 2a; VIII—2ms, 1a; IX–XI—6ms, 5a; XII to XIV—2ms; 2a; XV to XXI—2ms, 1a; XXII to XXIII—1ms, 1a; XXIV to XXV—2ms, 1a; XXVI—1 + 1ms; XXVII—1 + 1ms; XXVIII—3ms, 1a, 1ss. Right antennule geniculate between segments XX and XXI, with ancestral segments II–IV, IX–XI, XXI–XXIII fused; XXVII and XXVIII separate. Setation of segments as follows: I—2ss, 2a; II–IV—6ms, 4a; V—2ms, 2a; VI—2ms, 1a; VII—2ms, 2a; VIII—2ms, 1a; IX–XI—6ms (presence of clavate seta could not be confirmed because of damage to setae), 5a; XII to XIII—2ms; 2a; XIV to XVIII—2ms, 1a; XIX—1ms, 1 gripping element, 1a; XX—1 gripping element, 1ms, 1a; XXI–XXIII—2 gripping elements, 1a, 1ms; XXIV to XXV—2ms, 1a; XXVI—2ms; XXVII—2ms; XXVIII—3ms, 1a, 1ss.

Antenna, mandible, maxillule, maxilla, maxilliped and legs 1–4 similar to those of female, although setae on antenna exopod segments I–IV shorter.

Leg 5 with following setal formula (Roman numerals indicate spines, Arabic numerals setae, outer border setation listed to the left in each group separate by ';'):
Leg 5♂ left (Coxa 0-0. Basis 1-0. Exopod I-0; I-I; II,1,0. Endopod 0-0; 0-1; 2,2,2);
Leg 5♂ right (Coxa 0-0. Basis 1-0. Exopod I-0; I-0; II,1,0. Endopod 0-0; 0-1; 2,2,2).

Leg 5 almost symmetrical apart from specialised seta on inner distal border of left exopod segment 2 and asymmetrically inserted single seta on inner border of exopod segment 3 (these homologous with terminal spine of female). Male left leg 5 exopod segment 2, specialised seta evenly tapering bearing dense longitudinal rows of long setules not extending onto basal part; outer proximal border bearing small tapering lobe. Outer distal corner of endopod segment 1 rounded. Pore openings on anterior surface at base of outer spines. Basis inner distal border with patch of elongate setules.

Remarks. Four species have been included in this genus: *Bradycalanus typicus* A. Scott, 1909; *Br. gigas* Sewell, 1947; *Br. pseudotypicus* Björnberg, 1968; and *Br. pseudotypicus enormis* Björnberg, 1968.

Bradycalanus enormis Björnberg, 1968
(Figs 24–29)

Bradycalanus pseudotypicus enormis Björnberg, 1968, pp 85–89, figs 64–77.

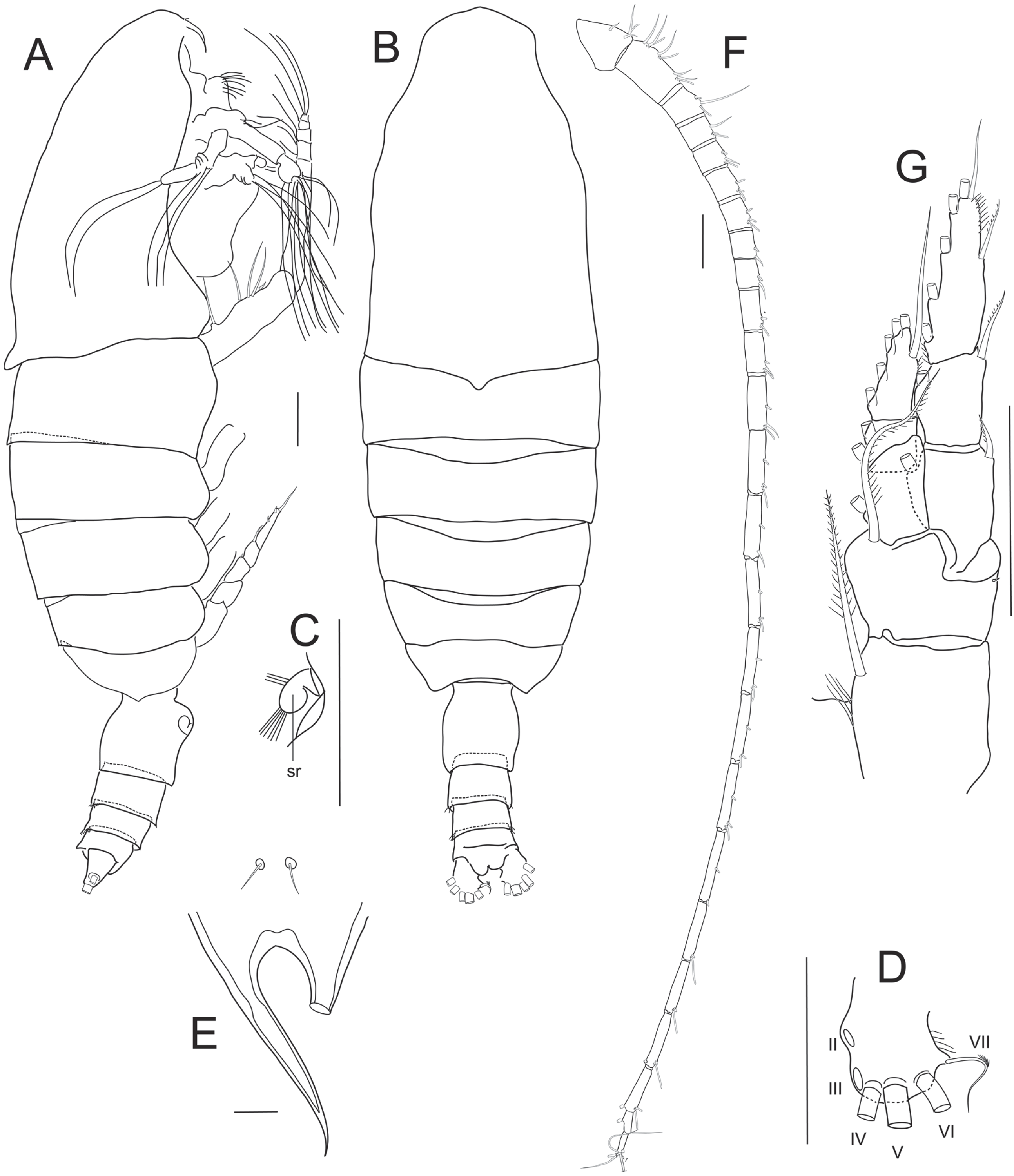

FIGURE 24. *Bradycalanus enormis* Björnberg, 1968 female: A, lateral view; B, dorsal view; C, detail of genital double-somite showing seminal receptacle (sr); D, dorsal view of caudal ramus; E, anterior view of rostral filaments; F, antennule; G, leg 1. Scale bars represent 1.0 mm on figures A, B, D, F, G; 0.1 mm on remaining figures. Illustrated specimens from: ANTXXIV/1, Stn 6, 0–5038 m (A–D, F, G); MV73-1, Stn 53 (E).

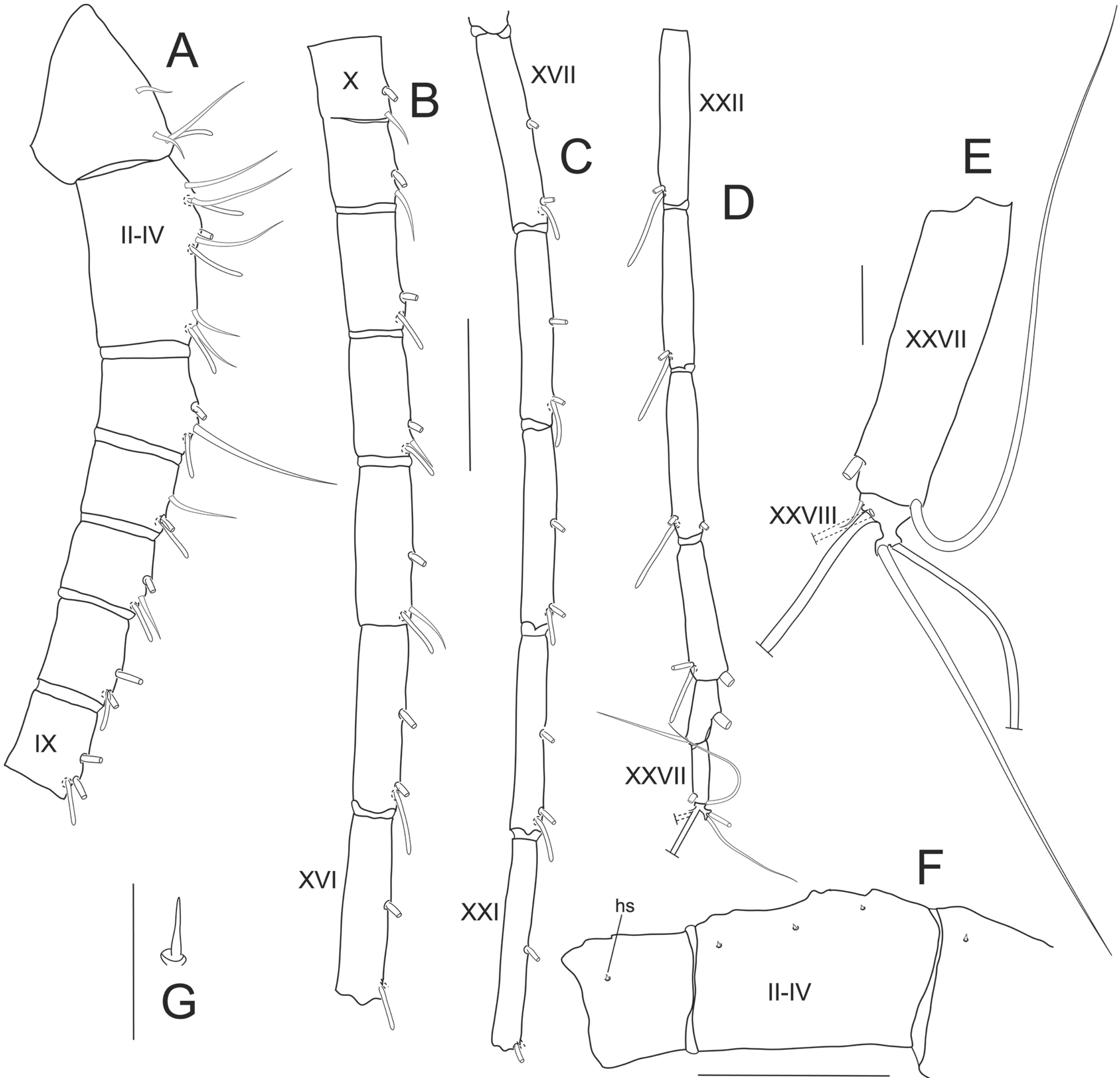

FIGURE 25. *Bradycalanus enormis* Björnberg, 1968 female antennule ancestral segments: A, segments I–IX; B, segments X–XVI; C, segments XVII–XXI; D, segments XXII–XXVIII; E, detail of terminal segments; F, detail of dorsal surface of segments I–V showing positions of hair sensilla (hs); G, detail of hair sensillum from segment I. Scale bars represent 1.0 mm on figures A–D, F; 0.1 mm on remaining figures. Illustrated specimen from ANTXXIV/1, Stn 6, 0–5038 m.

Type locality. 40.766ºS 76.800ºW.

Material examined. ANTXXIV/1, Stn 6, MOC10, 0–5038 m, 1♀ (16.5 mm), Co360.1.1. Eltanin Stn 175, IKMT, 2893 m, 1♂ (13.0 mm), Holotype USNM122577. MV73-1, Stn 53, IKMT, 0–2000 m, 7♀ (15.8–17.1 mm). Records from Natural History Museum, London: Discovery Stns, RMT8: 8508#78, 2500–3100 m, 1♀ (15.8 mm), BMNH 2015.2936; 8509#20, 3000–3500 m, 1♀ (15.3 mm), BMNH 1993.1462. Additional records from Smithsonian Institution, USNM numbers: 122577, 302082, 299634, 269510.

Genetic material. Co360.1.1. GenBank numbers in Table 6.

Morphological description. As for genus with following specific level features.

Female (Fig. 24–28). Total length 16.36 mm, (mean 15.5 mm, range 14.1–17.1 mm, n = 8). Anterior margin of head in dorsal view rounded, without projection (Figs 24A, B). Pedigerous somite 5 in lateral view extended into triangular lappets terminating in short point or triangular spine (Fig. 24A). Genital double-somite in dorsal view widest at anterior one third.

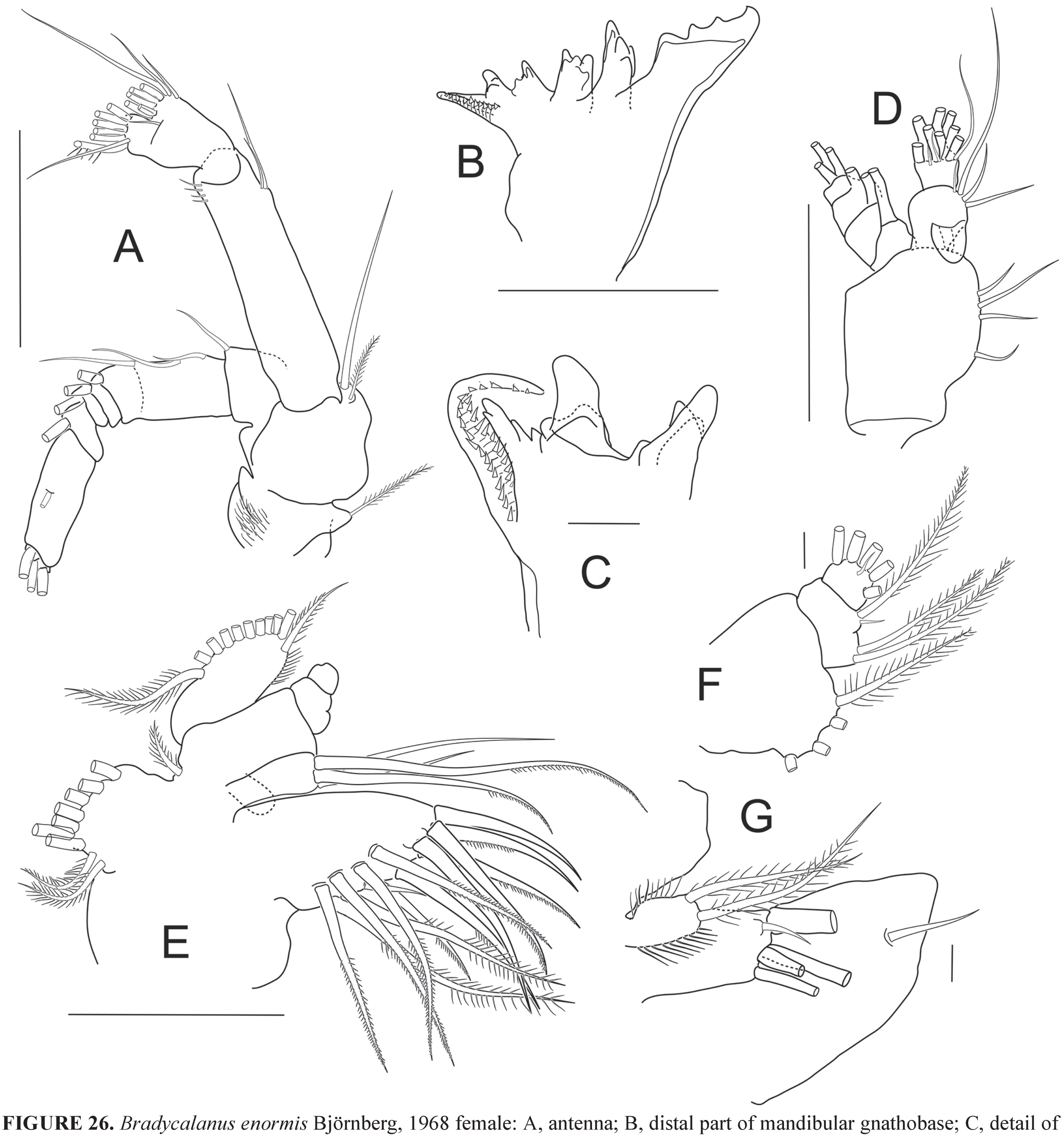

FIGURE 26. *Bradycalanus enormis* Björnberg, 1968 female: A, antenna; B, distal part of mandibular gnathobase; C, detail of dorsal border of mandibular gnathobase; D, mandibular palp; E, maxillule; F, basal endite 2 and endopod of maxillule; G, coxal endite and basal endite 1 of maxillule. Scale bars represent 1.0 mm on figures A, B, D, E; 0.1 mm on remaining figures. Illustrated specimen from ANTXXIV/1, Stn 6, 0–5038 m.

Antennule (Figs 24F, 25) extending about 7 segments beyond caudal rami; lengths of antennule segments (µm) as follows. Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements taken of ancestral segment I. I (370, 1101); II–IV (1101); V (407); VI (443); VII (512); VIII (500); IX (505); X–XI (948); XII (751); XIII (782); XIV (979); XV (1115); XVI (1160); XVII (1223); XVIII (1220); XIX (1268); XX (1273); XXI (1376); XXII (1069); XXIII (1000); XXIV (1005); XXV (866); XXVI (421); XXVII (-); XXVIII (-).

Antenna (Fig. 26A) exopod segments I–III each with short but well-developed seta, segment IV with well-developed seta extending as far as distal border of segment VIII.

Maxillule (Fig. 26E–G) coxal endite with 5 setae, one of them short; endopod segment 2 with one long and 1 vestigial seta, segment 3 with posterior surface seta short.

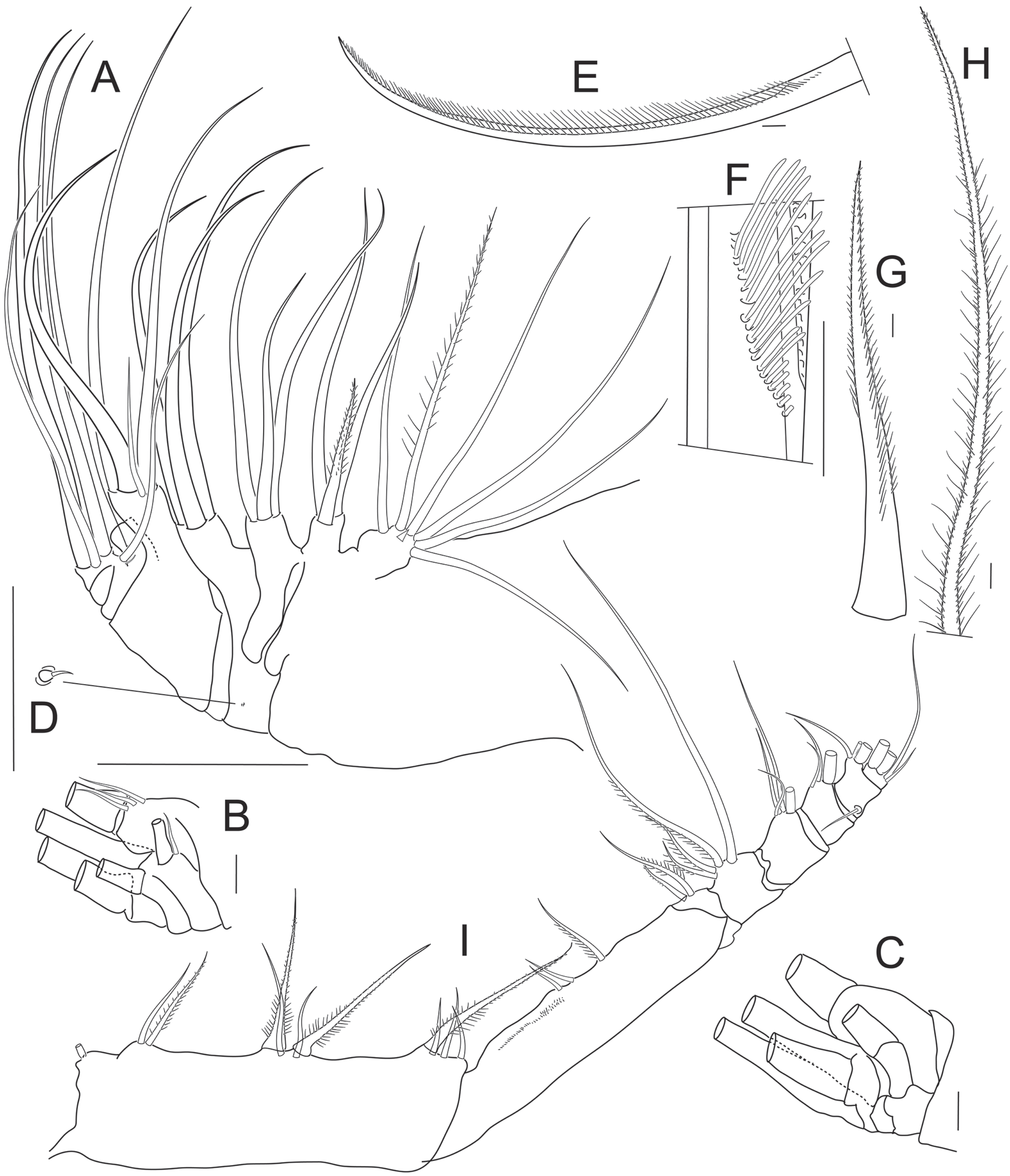

FIGURE 27. *Bradycalanus enormis* Björnberg, 1968 female: A, maxilla; B, detailed inner view of endopod of maxilla; C, detailed outer view of endopod of maxilla; D, detail of vestigial seta of coxal epipodite; E, seta of coxal endite 2 of maxilla; F, detail of seta of coxal endite 2 of maxilla; G, inner seta of praecoxal endite 2 of maxilla; H, seta of praecoxal endite 1 of maxilla; I, maxilliped. Scale bars represent 1.0 mm on figures A, I; 0.1 mm on remaining figures. Illustrated specimen from ANTXXIV/1, Stn 6, 0–5038 m.

Leg 1 (Fig. 24G) exopod segment 3, about 2.7 times as long as maximum width; distal border of endopod segment 1 extends as far as distal border of exopod segment 1; exopod outer spines: on segment 1 extends less than half way along segment 2; on segment 2 extends half distance to first spine on segment 3; segment 3 proximal spine extends almost to base of distal spine.

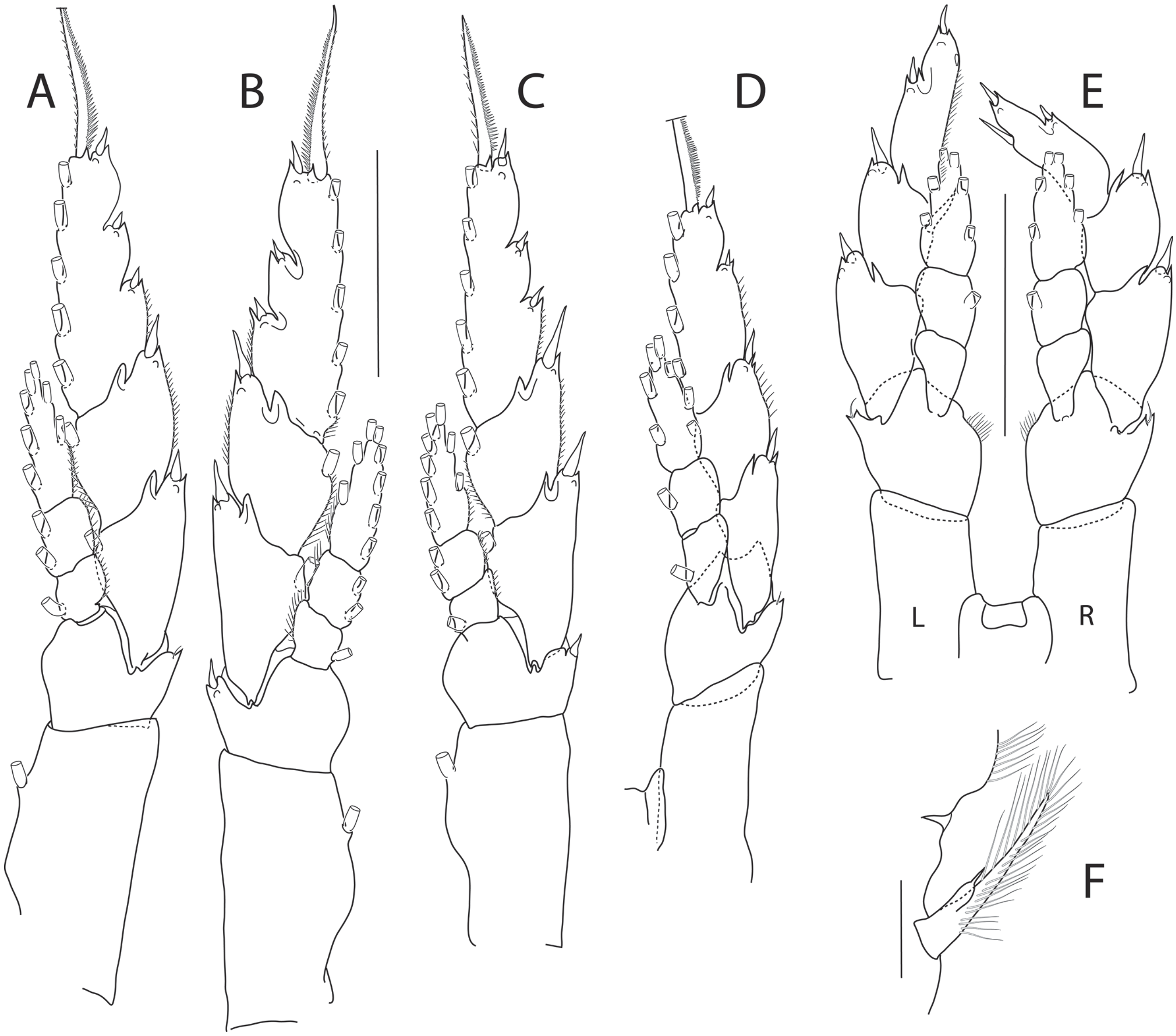

FIGURE 28. *Bradycalanus enormis* Björnberg, 1968 female: A, leg 2; B, leg 3; C, leg 4; D, leg 5. Male: E, leg 5, anterior view; F, distal inner corner of left leg 5 exopod segment 2. Scale bars represent 1.0 mm on figures A–E; 0.1 mm on remaining figure. Illustrated specimens A–D from ANTXXIV/1, Stn 6, 0–5038 m and E, F from USNM122577 (*Br. pseudotypicus enormis* Björnberg, 1968).

Male (Figs 31–34: *Br. typicus*). Total length 13.0 mm. Anterior head rounded in dorsal view. Pedigerous somite 5 in lateral view slightly pointed.

Antennule could not be checked as the holotype slide of *Br. pseudotypicus enormis* (USNM122577) does not have the antennules.

Antenna exopod segments I–IV each with less well-developed setae than in female; maxillule endopod segment 1 with 2 setae, segment 2 with 1 seta.

Leg 1 could not be checked because the holotype slide of *Br. pseudotypicus enormis* (USNM122577) does not have leg 1.

Leg 5 (Fig. 28E, F) left exopod segment 2 specialised seta tapering, with small proximal tapering projection on outer margin; specialised seta in form of long setulose lash extending short of distal border of endopod segment 3; inner border of left exopod segment 3 setulose with inner articulated spine inserted just proximal to second outer (terminal) spine; inner border of right exopod segment 3 naked and without notches, inner articulated spine inserted distal of first outer border spine.

Remarks. The description of Björnberg (1968) differs from the present description in some details but examination of the variety *Br. pseudotypicus enormis* (USNM122577) revealed that the mouthparts and leg 1 are identical to the specimens examined here; the holotype slide of *Br. pseudotypicus enormis* (USNM122577) does not have the antennules, nor leg 1 so these could not be checked. Based on the genetic distance data for ITS1 and ITS2 markers (see Tables 16, 17), this variety has been raised to specific rank.

Distribution. *Bradycalanus enormis* is an abyssopelagic species taken from 2000 m to < 5000 m. It is has been found in the southeastern Pacific and Atlantic Oceans (Fig. 29, Table 1).

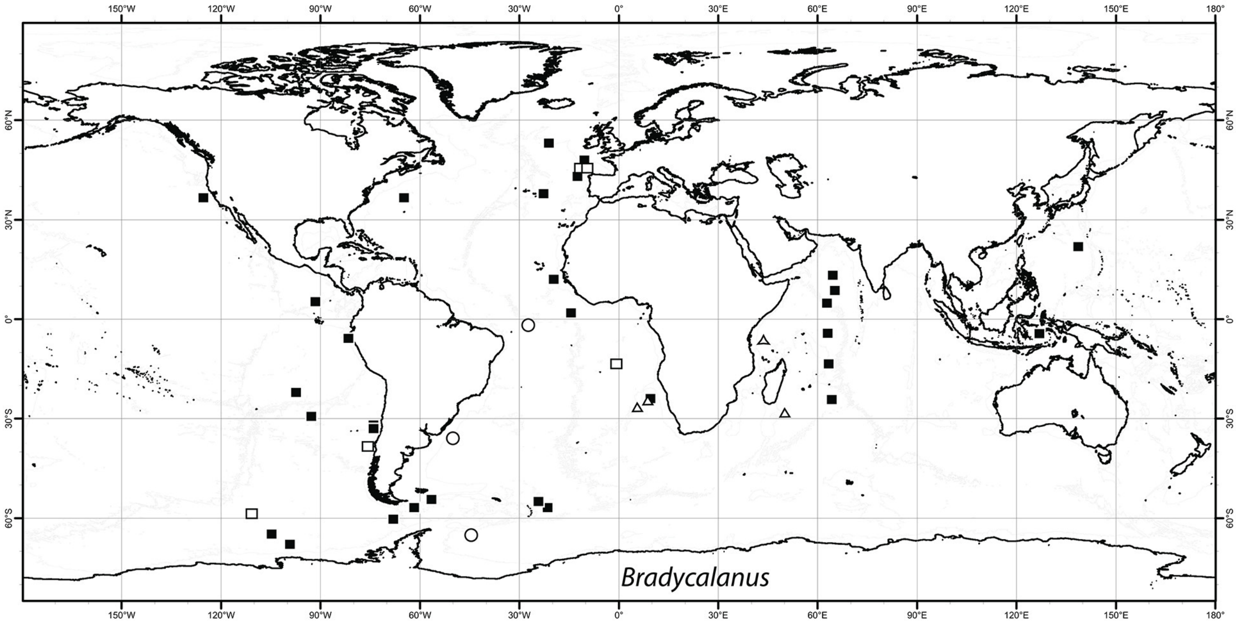

FIGURE 29. Distribution of *Bradycalanus* species: open square = *Bradycalanus enormis*; filled square = *Br. typicus*; open triangle = *Br. gigas*; open circle = *Br. abyssicolus* **n. sp.**.

Species comparisons. Females of *Br. enormis* are distinguished morphologically from their closest relative, *Br. typicus*, only by their large size. *Bradycalanus enormis* appear to be greater than 15 mm long but we cannot be certain of the identity of specimens between 13–15 mm total length. The majority of female *Br. typicus* are 11–12 mm long with fewer specimens 12–13 mm and longer. Females of *Br. enormis* and *Br. typicus* have the same mouthpart setation (Table 8).

Males similarly vary in length (*Br. enormis*: 13.0 mm, *Br. typicus*: 11.0–11.3 mm). Males are possibly distinguished by the more distal insertion of the inner spine on the right leg 5 exopod segment 3 relative to the outer spine and the lack of a notch in the inner border (*Br. typicus* has inner spine inserted opposite the outer spine and the inner border is notched).

Females of *Br. enormis* can be distinguished from *Br. gigas* by its triangular to pointed posterior corners of pedigerous somite 5 (rounded in *Br. gigas*), by its long antennule extending about 7 segments beyond the caudal rami (3 segments in *Br. gigas*) and leg 1 outer border spines of exopod segments 1 and 2 which are short and not extending as far as the base of following spine (long in *Br. gigas*, extending to the base of the following spine).

Bradycalanus typicus A. Scott, 1909

(Figs 29–34)

Bradycalanus typicus A. Scott, 1909, pp 14–16, pl.I, figs 1–11.
Megacalanus princeps (Brady, 1883): Sars, 1924, 1925, pp 14–15, pl. III, figs 1–12.
Megacalanus sarsi Farran, 1939, pp 355–356.
Megacalanus typicus: Vervoort, 1949, pp 58–62, fig. 5.
Bradycalanus pseudotypicus Björnberg, 1968, pp 82–85, figs 55–63.
Bradycalanus sarsi: Brodsky *et al*. 1983, p. 199, fig. 88.
Bradycalanus typicus: Michel, 1994, pp 180–181.
Non *Megacalanus princeps* Wolfenden, 1904

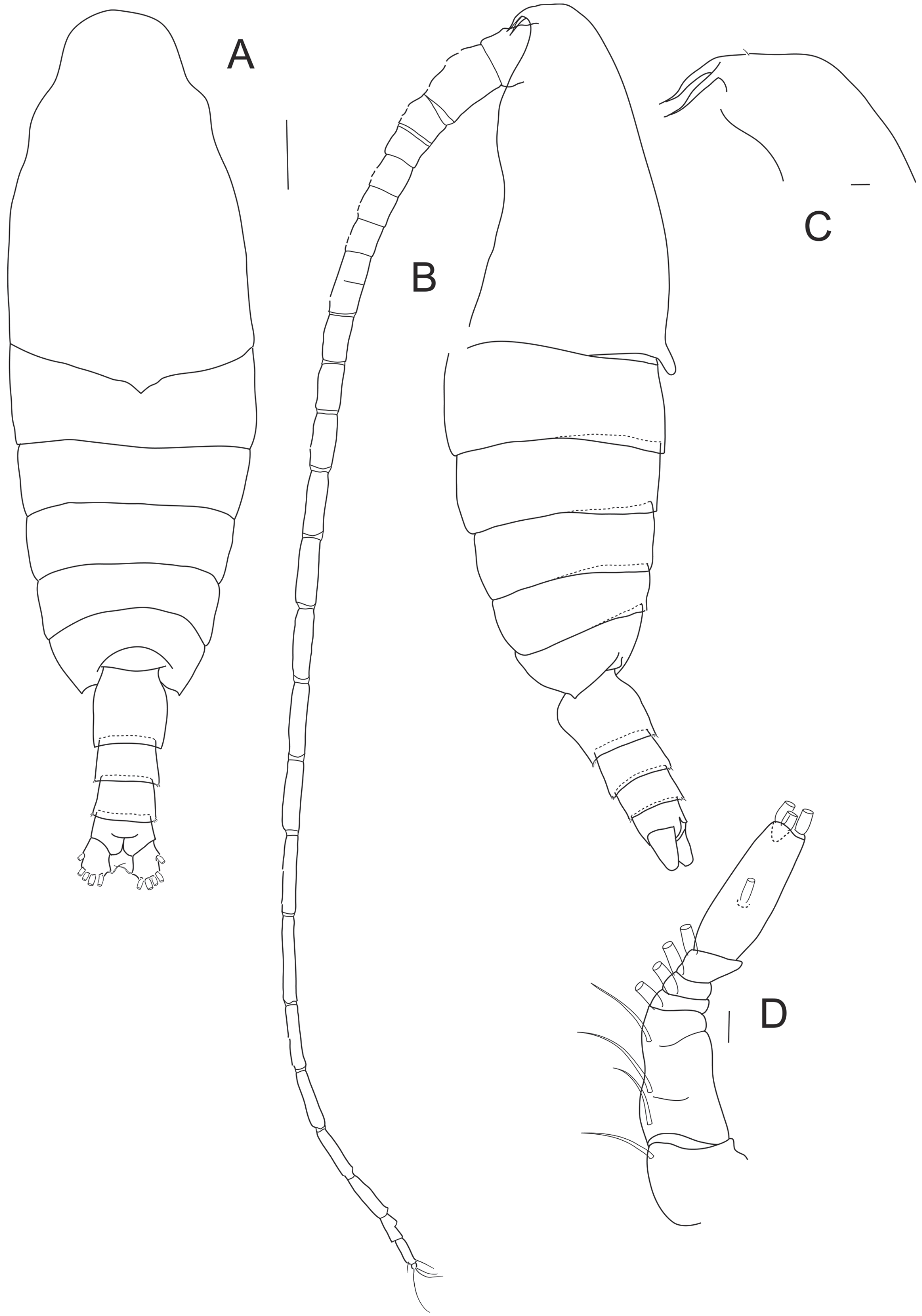

FIGURE 30. *Bradycalanus typicus* A. Scott, 1909 female: A, dorsal view; B, lateral view; C, lateral view of anterior head; D, exopod of antenna. Scale bars represent 1.0 mm on figures A, B; 0.1 mm on figures C, D. A–C illustrated from specimens from Antipode IV, Stn 55D and D is illustrated from specimen from ANT XXIV/I Stn 8, 2990–3992.

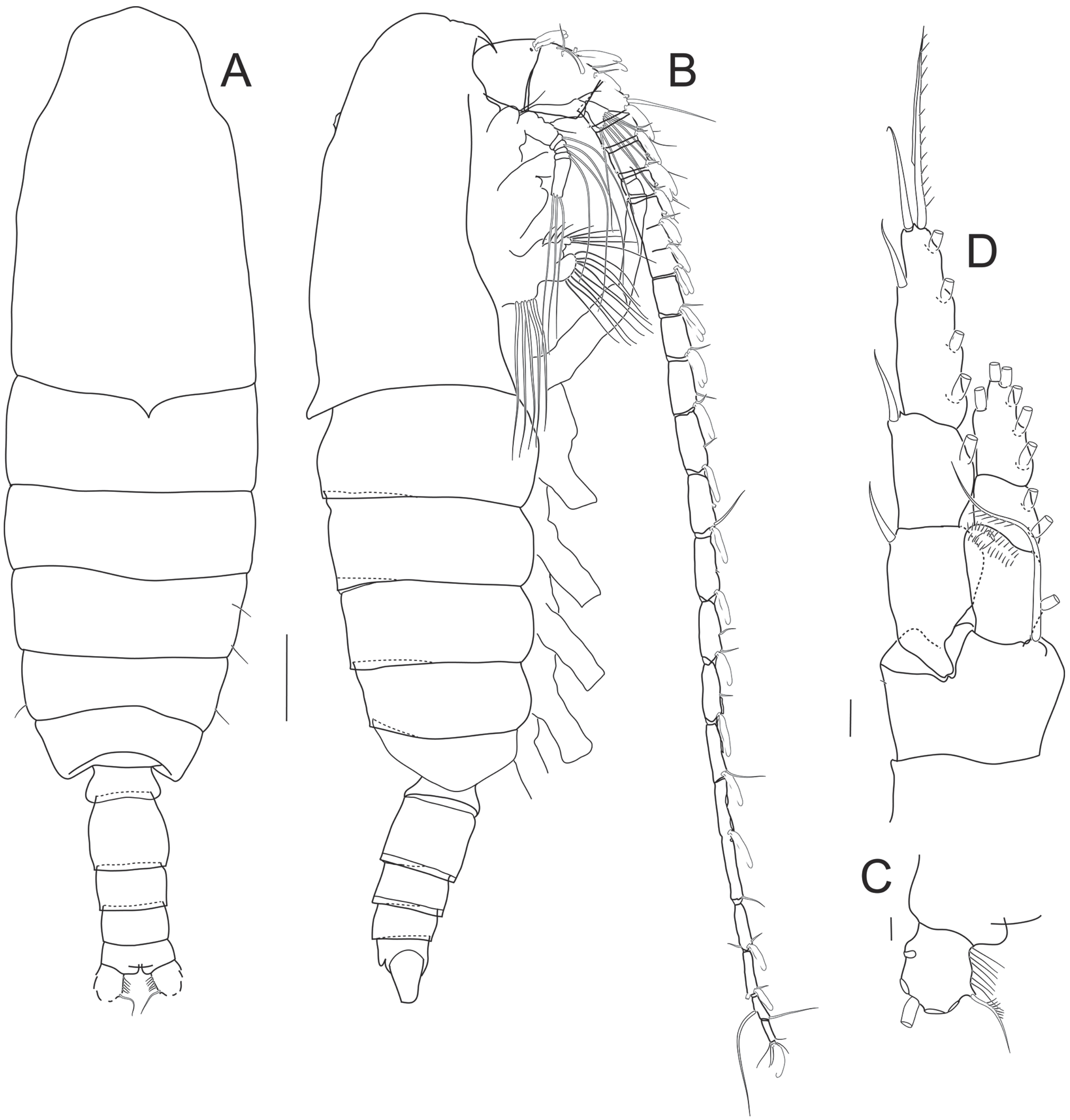

FIGURE 31. *Bradycalanus typicus* A. Scott, 1909 male: A, dorsal view; B, lateral view; C, dorsal view of caudal ramus; D, leg 1. Scale bars represent 1.0 mm on figures A, B; 0.1 mm on remaining figures.

Type locality. 0.293º S 129.242º E.

Material examined. ANTXIV/1, MOC10, Stn 2, 3000–4000 m, 1♀ (11.8 mm), Co303.1.1, Co303.1.2; Stn 3, 1957–2993 m, 1♀ (12.6 mm); Stn 6, 0–5038 m, 1♀ (11.5 mm); 1987–3886 m, 1♀, Co384.1.1; Stn 6, 1987–3886 m, 1♀ (12.4 mm); Stn 8, 2990–3992 m, 1♀ (12.0 mm). MV66-11, Stn 5, IKMT, 0–3889 mwo, 1♂ (11.3 mm). MV73-1, Stn 53, IKMT, 0–2000 m, 5♀ (13.0–13.9 mm). Southtow IV, Stn 36, IKMT, 0–2000 m, 2♀ (13.0, 13.0 mm). Antipode IV, Stn 55D, IKMT, 0–2000 m, 1♀ (12.6 mm), 1 Copepodite. Eltanin, Stn 125, IKMT, 1830 m, 1♀ (13.75 mm), Holotype *Br. pseudotypicus* USNM122574. Eltanin 11, Stn 898, 1♀, 1♂, USNM1208943 *Br. typicus.* Records from Natural History Museum, London: Discovery Stns, RMT8: 8508#76, 2000–2500 m, 21♀ (12.4, 12.2, 11.8, 12.0, 12.5, 12.0, 12.4, 12.5, 12.0, 12.5, 12.1, 11.5, 11.7, 12.6, 12.2, 12.0, 11.9, 12.1, 12.2, 12.2, 12.4 mm), BMNH 1993.1472-1481; 8508#76, 2000–2500 m, 1♂ (9.4 mm), BMNH 1993.785; 8508#78, 2500–3100 m, 16♀ (12.4, 12.9, 13.1, 12.5, 12.8, 12.3, 12.0, 12.2, 12.6, 12.4, 12.6, 12.7, 12.6, 12.2, 12.4, 12.4 mm), BMNH 1993.1446-

1455; 8509#15, 2000–2500 m, 10♀ (11.9, 12.1, 12.0, 12.6, 12.2, 12.5, 12.9, 11.7, 12.4 mm), BMNH 1993.1463-1471; 8509#20, 3000–3500 m, 6♀ (12.5, 12.2, 12.3, 12.7, 13.0, 12.1 mm), BMNH 1993.1456-1461; 7482, 2000–2500 m, 2♀ (12.0, 12.7 mm), BMNH 1993.1443-1445; 7711#39, 1520–2000 m, 7♀ (12.2, 12.0, 12.4, 12.3, 12.3, 12.2 mm, 1 damaged), BMNH 1994.659-665; 7711#61, 1500-2000 m, 3♀ (12.6, 12.4, 12.7 mm), BMNH 1994.780-782; 7711#61, 1520–2000 m, 1♂ (10.1 mm), BMNH 1993.784; 8512#4, BN, 2281–2465 m, 4♀ (12.0, 12.1, 11.8, 11.8 mm), BMNH 1994.5759-5762. Additional records from Smithsonian Institution, USNM numbers: 67214, 232143, 232145, 122574–76, 262467, 269501–09, 269512, 302079–82.

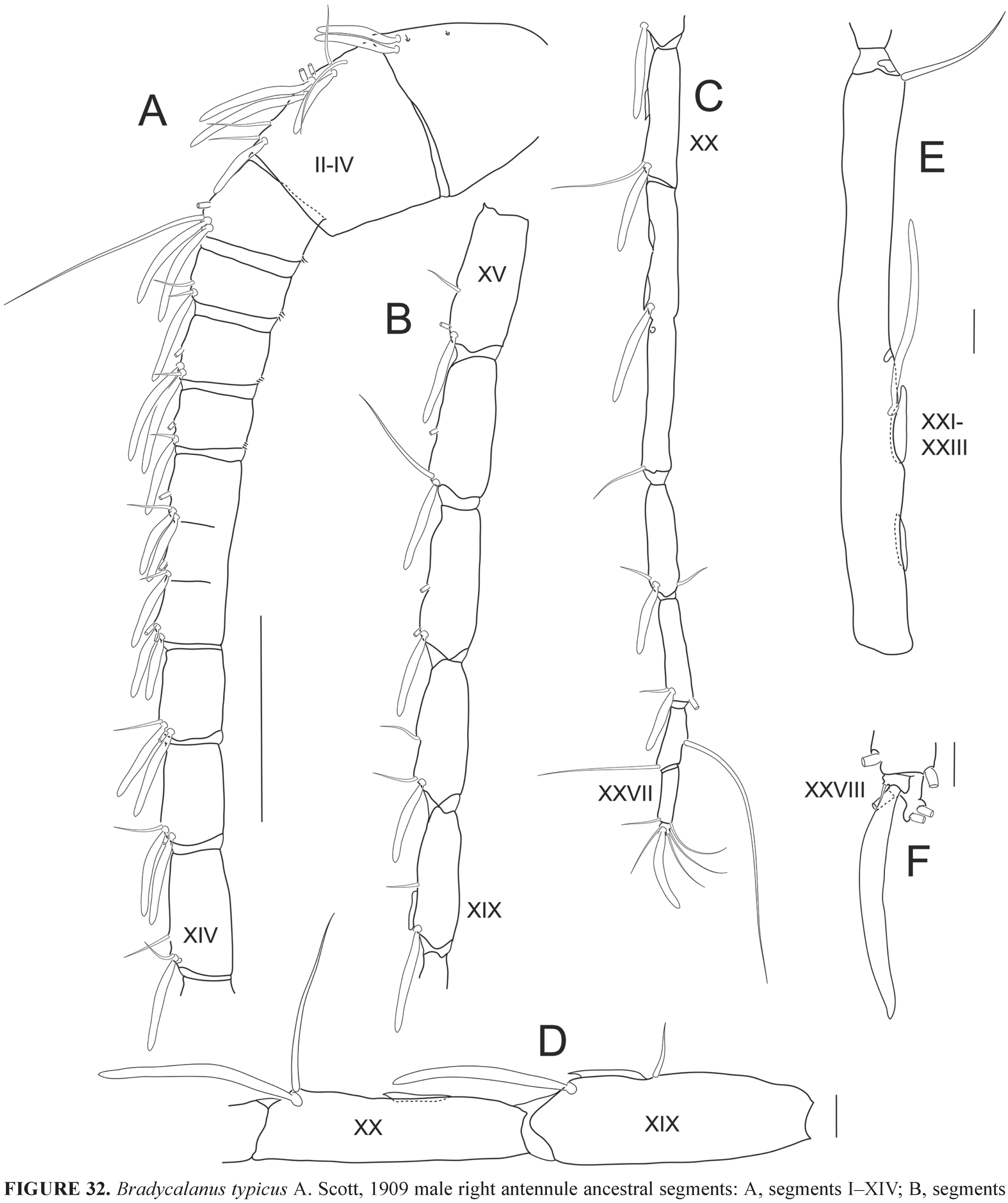

FIGURE 32. *Bradycalanus typicus* A. Scott, 1909 male right antennule ancestral segments: A, segments I–XIV; B, segments XV–XIX; C, segments XX–XXVIII; D, detail of segments XIX–XX; E, detail of segments XXI–XXIII; F, detail of segment XXVIII. Scale bars represent 1.0 mm on figures A–C; 0.1 mm on remaining figures. Illustrated specimens from MV66-11.

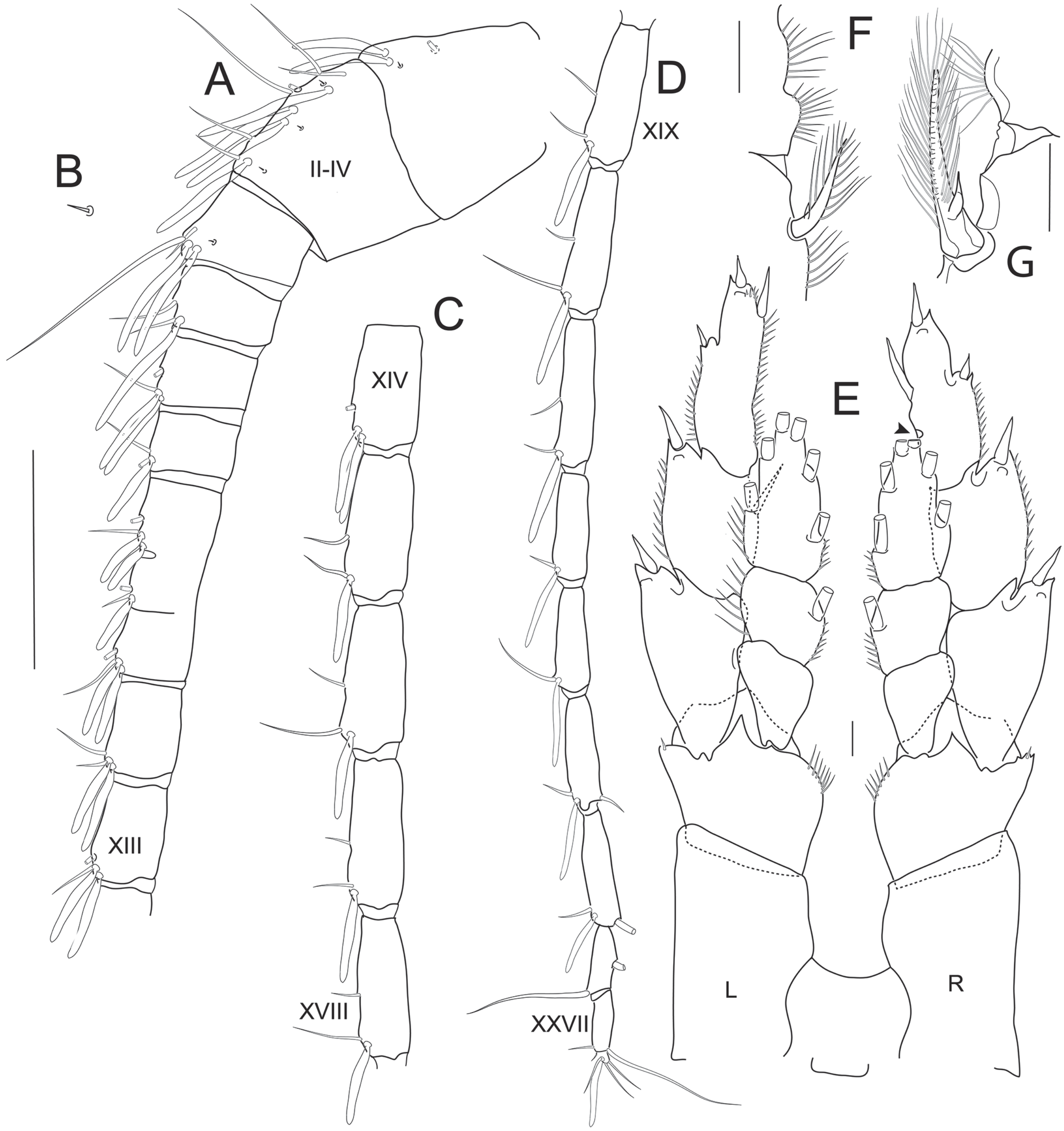

FIGURE 33. *Bradycalanus typicus* A. Scott, 1909 male: A, left antennule ancestral segments I–XIII; B, hair sensilla of dorsal surface of ancestral segment V; C, left antennule ancestral segments XIV–XVIII; D, left antennule ancestral segments XIX–XXVIII; E, anterior view of leg 5, arrow indicates notch; F, distal inner corner of left leg 5 exopod segment 2. G, distal inner corner of left leg 5 exopod segment 2 of specimen USNM1208043, Scale bars represent 1.0 mm on figures A, C, D; 0.1 mm on remaining figures. Illustrated specimens from MV66-11, USNM1208943.

Genetic material. Co303.1.1, Co303.1.2, Co384.1.1. GenBank numbers in Table 6.

Morphological description. As for genus with following specific level features.

Female (Fig. 30). Total length 12.4 mm, (mean = 12.3 mm, range = 10.3–13.9 mm, n = 93). Anterior margin of head in dorsal view rounded, without projection. Pedigerous somite 5 in lateral view extended into triangular lappets terminating in short point or triangular spine. Genital double-somite in dorsal view widest at anterior one third.

Antennule (Fig. 30B) extending about 7 segments beyond caudal rami and length of antennule segments (µm) as follows. Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements taken of ancestral segment I. I (223, 743); II–IV (805); V (327); VI (319); VII (347); VIII (349); IX (359); X–XI (705); XII (569); XIII (584); XIV (710); XV (802); XVI (842); XVII (894); XVIII (911); XIX (936); XX (970); XXI (1057); XXII (844); XXIII (792); XXIV (671); XXV (629); XXVI (322); XXVII (344); XXVIII (56).

Antenna exopod (Fig. 30D) segments I–III each with short but well-developed seta, segment IV with well-developed seta extending as far as distal border of segment VIII.

Maxillule with coxal endite with 5 setae, one of them short; endopod segment 2 with one long and 1 vestigial seta.

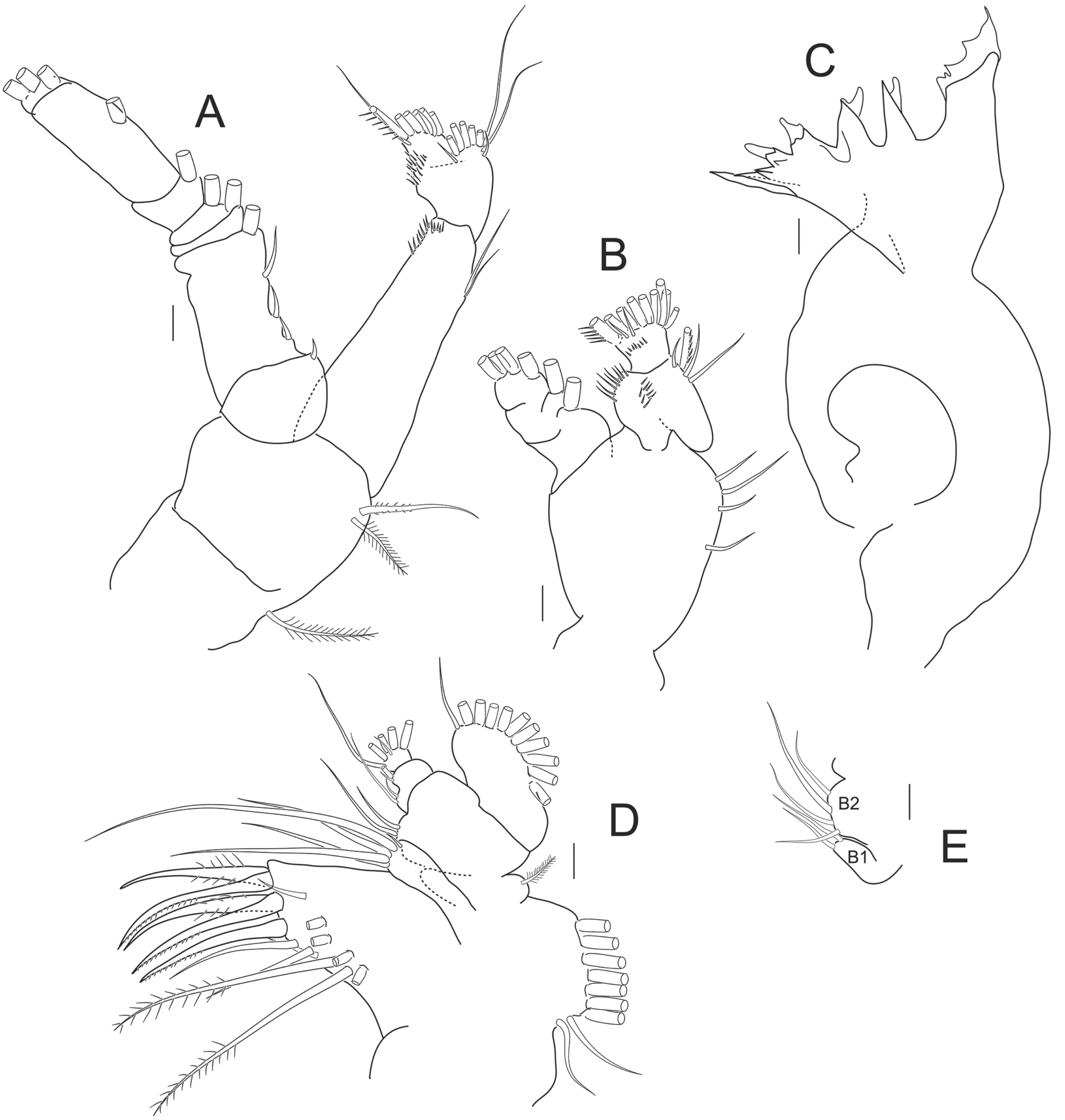

FIGURE 34. *Bradycalanus typicus* A. Scott, 1909 male: A, antenna; B, mandibular palp; C, mandibular gnathobase; D, maxillule; E, details of basal endites 1 and 2 (B1, 2) of maxillule. Scale bars represent 0.1 mm on all figures. Illustrated specimens from MV66-11.

Leg 1 exopod segment 3, about 2.7 times as long as maximum width; distal border of endopod segment 1 not extending beyond exopod segment 1; exopod outer spines: on segment 1 extends less than half way along segment 2; on segment 2 extends half distance to first spine on segment 3; segment 3 proximal spine extends almost to base of distal spine.

Male. Total length 11.3 mm, (mean = 10.7 mm, range = 9.4–11.8 mm, n = 4). Anterior head rounded in dorsal view (Fig. 31A, B). Pedigerous somite 5 in lateral view rounded.

Antennule (Figs 32, 33A–D) extending about 2–3 segments beyond caudal rami (Fig. 31B), ancestral segments II–IV, IX–XI and XXI–XXIII fused, double aesthetascs on ancestral segments I, III, V, VII, IX, XI–XIV. Right antennule geniculate between ancestral segments XX and XXI, setation of gripping elements: XIX—1 fused gripping element extending as far as base of aesthetasc, 1ms, 1a; XX—1 gripping element, 1ms, 1a; XXI–XXIII—2 short gripping elements, second extending slightly beyond base of aesthetasc, 1a, 1 unknown element, 1ms.

Antenna (Fig. 34A) exopod segments I–IV each with less well-developed seta than in female. Maxillule (Fig. 34D, E) endopod segment 1 with 1 large and one vestigial seta, segment 2 with 1 seta.

Leg 1 (Fig. 31D) outer border spines on exopod segments 1 and 2 extend half way to base of following spine; first outer spine inserted at two thirds distance along outer border of exopod segment 3 and extending beyond base of outer distal spine; distal border of endopod segment 1 level with distal border of exopod segment 1.

Leg 5 (Fig. 33E–G) left exopod segment 2 specialised seta tapering, extending short of distal border of endopod segment 3, with small proximal tapering projection; inner border of left exopod segment 3 setulose with inner articulated spine inserted just proximal to second outer (terminal) spine; inner border of right exopod segment 3 naked, inner articulated spine inserted opposite first outer border spine, small notch in inner border level with distal border of right endopod.

Remarks. Currently three species names exist in the literature which could be assigned to this species, in chronological publication order: *Br. typicus* A. Scott, 1909, *Br. sarsi* Farran, 1939, and *Br. pseudotypicus* Björnberg, 1968. Björnberg's (1968) description of *Br. pseudotypicus* differs from the present description in some details. Nevertheless, examination of the holotype of *Br. pseudotypicus* (USNM122574) revealed that the mouthparts and leg 1 are identical to the specimens examined here suggesting that *Br. pseudotypicus* is a junior synonym of *Br. typicus*. Likewise, Sars' (1924/25) description of *Megacalanus princeps* (later named *Bradycalanus sarsi* by Farran, 1939) appears to be identical to *Br. typicus* A. Scott, 1909. Specimens of the *typicus-enormis* complex have identical mouthpart setation.

The only male known for *Bradycalanus* was that of *Br. pseudotypicus enormis*. The right antennule was described (Björnberg 1968) as "show[ing] no change into a grasping organ". The specialised seta on the left leg 5 was not described in detail and the leg 1 exopod segment 1 was illustrated as not having an outer border spine. The single male, found here, is of a size that is consistent with the smaller females—*Br. typicus*. It is clear that the male from MV66-11 has a geniculate right antennule, the specialised seta of the left leg 5, although similar to that of other megacalanids, does not have a swollen basal part but does have a small outer proximal tapering projection and leg 1 exopod segment 1 has an outer border spine. Damaged specimens, identified as *Br. typicus*, included both a male and female (USNM1208043). The male leg 5 proved to be very similar to the male described here (Figs 31–34); the right antennule was not intact, only ancestral segments I to XIII were present.

Morphological variation. All females examined (including those held by the Smithsonian Institution) vary from about 10.3 mm to about 14 mm. There was very little variability in the morphology of *Br. typicus* apart from slight differences in the form of the posterior border of pedigerous somite 5 which ranges from rounded to bluntly triangular through to a pointed triangle. On leg 1, the outer border spines of the exopod segments vary in length although the outer border spines of exopod segments 2 and 3 never extend beyond the base of the spine more distal to it.

Distribution. *Bradycalanus typicus* is an abyssopelagic species taken from about 1500 m to about 4000 m. It is widely distributed from the Pacific, Indian, Atlantic and Southern Oceans based on specimens examined here (Fig. 29, Table 1).

Species comparisons. Females of *Br. typicus* are distinguished from their closest relative *Br. enormis* by their smaller size (*Br. typicus* (10–14 mm) vs *Br. enormis* (15–17 mm)) and their genetic characteristics (ITS1 and ITS2 markers, see Tables 16, 17). Because of the limited amount of genetic information we cannot be certain that the size ranges of these two species do not overlap (Table 8).

TABLE 7. Comparison of key differences among *Megacalanus* species. A1 = antennule; B = basis; P1, 5 = leg 1, 5; Pd5 = pedigerous somite 5; post. = posterior; Re1–3 = exopod segments 1–3; seg(s) = segment(s).

Species	Head crest	♀ A1 segs XV, XVI, post. border	♀ A1 segs with dorsal macula cribrosa	♀♂ shape Pd5 lateral view	P1 Re1,2 outer spines extend:	♂ A1 seg XIX gripping element	♂ right A1 seg XXI no. gripping elements	♂ P5 B inner distal border setules	♂ P5 left Re2 specialised inner distal seta, basal part	♂ P5 left Re2 specialised inner distal seta: lash	♂ P5 right Re3 inner border
M. princeps	No	**Toothed**	II, III	Triangular	Well beyond base of following spines	**No**	1	Yes	Longer than wide	Longer than basal part	Completely lined with fine spinules
M. frosti n. sp.	**Yes**	**Toothed**	I, II, III	Triangular	Well beyond base of following spines	Yes	1	Yes	Usually longer than wide	Usually longer than basal part	Completely lined with fine spinules
M. ericae n. sp.	No	Smooth	I, II, III, **IV**	Triangular	Well beyond base of following spines	Yes	1	Yes	**Squat, usually wider than long**	**Shorter than basal part**	Completely lined with fine spinules
M. ohmani n. sp.	No	Smooth	I, II, III, **IV**	**Rounded**	**Just beyond base of following spine**	Yes	**2**	**No**	Longer than wide	Longer than basal part	**Proximal 1/3rd with fine setules, distally hyaline ridges**

TABLE 8. Comparison of key differences among *Bradycalanus* species. A1 = antennule; A2 = antenna; Mx1 = maxillule; C = coxal endite; P1, 5 = leg 1, 5; Re1–3 = exopod segments 1–3; Re I–III = exopod ancestral segments I–III; Ri1, 3 = endopod segments 1, 3.

Species	Head crest	♀ Size (mm)	♀ A1 length	♀ A2 Re I–III: setal length	♀ Mx1 C: number setae	♀ Mx1 Ri3: posterior surface seta	♀ P1 Re3 length : width	♀ P1 Re1 length outer spine	♀ P1 Ri 1 distal border extends	♂ P5 right Re3 inner spine insertion
Br. enormis	No	**14.1–17.1**	Extends 7 segments beyond CR	Longer than its segment	4 + 1 small	Vestigial	2.7	Extends less than half way along Re2	Extends to distal border of Re1	Distal to outer spine
Br. typicus	No	10.5–13.9	Extends 7 segments beyond CR	Longer than its segment	4 + 1 small	Vestigial	2.7	Extends less than half way along Re2	Extends to distal border of Re1	Opposite outer spine
Br. gigas	No	13.7	**Extends slightly beyond CR**	Longer than its segment	4 + 1 small	Vestigial	2.6	**Extends almost to base of spine on Re2**	**Extends beyond distal border of Re1**	♂ unknown
Br. abyssicolus n. sp.	**Yes**	11.0–11.8	Extends 5–7 segments beyond CR	**Shorter than its segment**	**2**	**Small**	**5.0**	Extends to 1/3rd distance to spine on Re2	Extends to distal border of Re1	♂ unknown

Males of *Br. typicus* may possibly be distinguished by the inner spine on the right leg 5 exopod segment 3 which is inserted opposite the outer spine and the inner border is notched (in *Br. enormis* the inner spine is more distally inserted relative to the outer spine on the right leg 5 exopod segment 3 and there is no notch in the inner border). Females of *Br. typicus* can be distinguished from *Br. gigas* by its triangular to pointed posterior corners of pedigerous somite 5 (rounded in *Br. gigas*), by its long antennule extending about 7 segments beyond the caudal rami (3 segments in *Br. gigas*) and leg 1 outer border spines of exopod segments 1 and 2 are short, not extending as far as base of following spine (long in *Br. gigas* extending to base of following spine).

Bradycalanus gigas **Sewell, 1947**
(Figs 29, 35, 36)

Bradycalanus gigas Sewell, 1947, pp 28–30, text-fig. 3.

Type locality. 5.820ºS 41.470ºE.

Specimens examined. DIVA III, Stn 40-S, EBS-S, 5055 m, 1♀ (12.48 mm), ZMH K-44185. ANTXIV/1, Stn 8, MOC10, 3992–2990 m, 1CV. Records from Natural History Museum, London: Holotype ♀ (14.9 mm), John Murray Expedition, Stn 120, BMNH 1949.12.31.31 [with dissection slides of mouthparts and leg 1, BMNH 1963.6.28.39-40]. Additional records from Smithsonian Institution, USNM number: 269500.

Morphological description. Following description based on specimens from DIVA III, Stn 40. As for genus with following specific level features.

Female (Fig. 35). Total length 12.4 and 14.9 mm. Anterior head bluntly rounded (Fig. 35A–C). Pedigerous somite 5 rounded with short lappets. Genital double-somite in dorsal view with slight bulge at about anterior one quarter.

Antennule (Figs 35B, 36A–F) extending to caudal rami or slightly beyond; length of antennule segments (µm) as follows. Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements taken of ancestral segment I. I (228, 748); II–IV (831); V (315); VI (289); VII (316); VIII (319); IX (303); X–XI (587); XII (379); XIII (392); XIV (482); XV (615); XVI (648); XVII (731); XVIII (719); XIX (751); XX (717); XXI (694); XXII (524); XXIII (506); XXIV (545); XXV (534); XXVI (274); XXVII (362); XXVIII (46). Hair sensilla, one each on ancestral segments I–V, conspicuous.

Antenna (Fig. 35D) inner surface of coxa and outer distal border of endopod segment 1 apparently without spinules; exopod segments I–III each with moderately well-developed setae, seta on segment IV extending beyond distal border of segment VIII.

Maxillule (Fig. 36G) coxal endite with five setae, one of them very short; endopod segment 3 with vestigial posterior surface seta.

Maxilliped second most proximal seta on endopod segments 3–5 half length of longest seta.

Leg 1 (Fig. 35F) exopod segment 3 about 2.6 times as long as maximum width; distal border of endopod segment 1 extends well beyond distal border of exopod segment 1; outer articulated spines on exopod segments 1 and 2 extend as far as base of more distal spine, proximal spine of exopod segment 3 extends beyond base of distal spine by about half its length.

Male. Unknown.

Remarks. The present specimens agree in most respects with the original description by Sewell (1947) of *Bradycalanus gigas*. Re-examination of the dissected holotype confirmed that the basis and endopod segment 1 of the maxillule are fused, endopod segment 2 has a small vestigial seta in addition to the long seta, coxal endite 1 of the maxilla has 3 setae (one was broken off the dissected limb of the holotype but its detachment scar was clearly visible), the basal endite has 4 setae, and the first endopod segment lobe bears 1 large seta and 3 vestigial setae.

Distribution. *Bradycalanus gigas* is a deep abyssopelagic species taken from < 3000 m to > 5000 m. It has been taken in the South Atlantic and the Indian Ocean off Zanzibar (Fig. 29, Table 1) (Sewell 1947).

Species comparisons. *Bradycalanus gigas* females are distinguished from all other species in this genus by their short antennules extending, at most, 3 segments beyond the caudal rami whereas, in other species, the female antennules extend 6–7 segments beyond the caudal rami (Table 8). The distolateral spines of exopod segments 1 and 2 of leg 1 in *Br. gigas* extend to the bases of the following more distal spine (in the remaining species these spines do not extend to the bases of the more distal spines.)

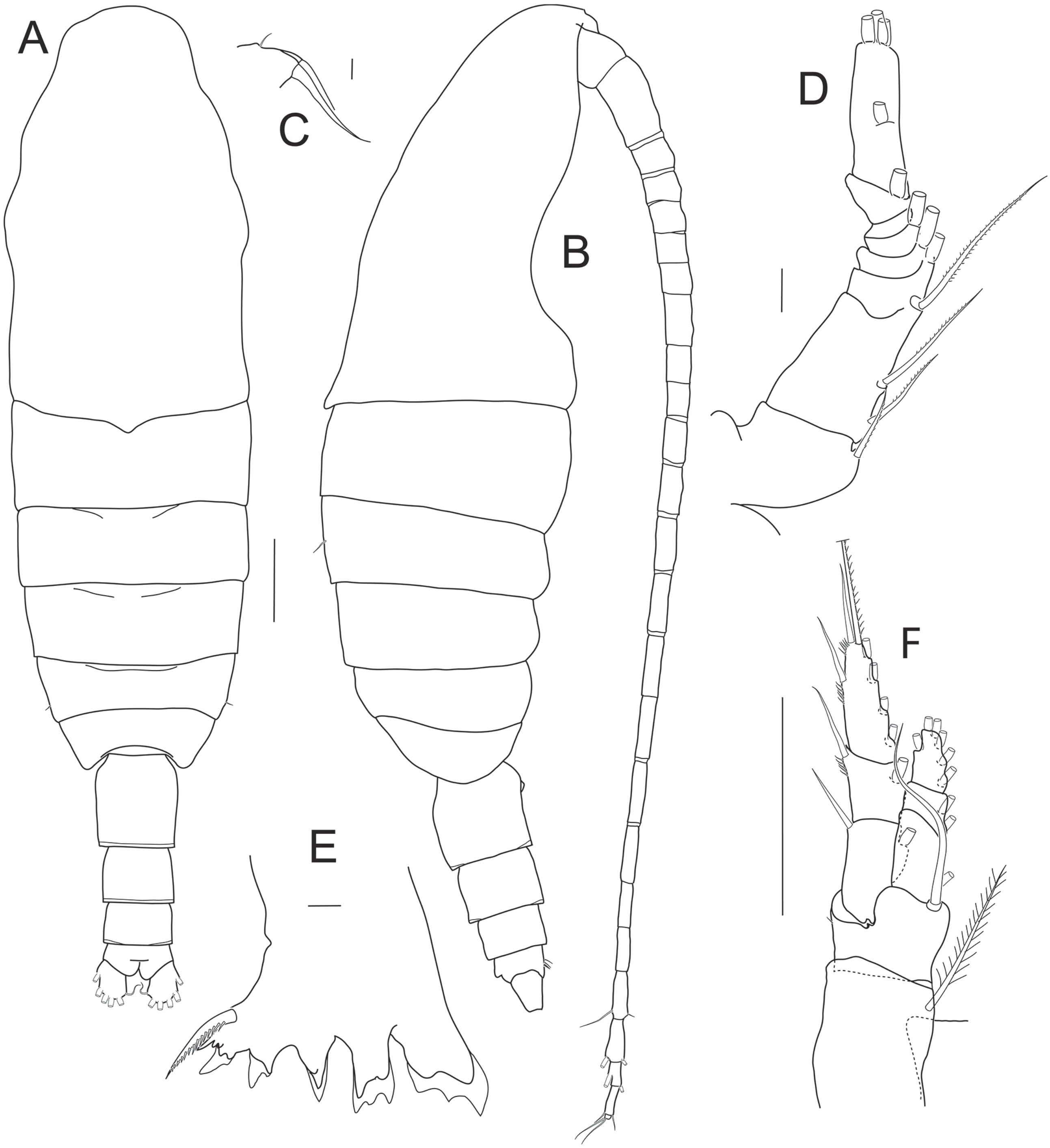

FIGURE 35. *Bradycalanus gigas* Sewell, 1947 female: A, dorsal view; B, lateral view; C, lateral view of anterior head; D, exopod of antenna; E, mandible gnathobase; F, anterior view of leg 1. Scale bars represent 1.0 mm on figures A, B, F; 0.1 mm on remaining figures. Illustrated specimen from DIVA III, Stn 40-S.

Bradycalanus abyssicolus **n. sp.**
(Figs 29, 37–40)

Type locality. 64.999º S, 43.020º W.

Material examined. ANTXIX/4, Stn 135-4, EBS-S, 4678 m 1♀ (11.0 mm) holotype; paratypes: DIVA III, EBS-S: Stn 534, 4605–4585 m, 1♀ (11.5 mm); Stn 537, 4605–4585 m, 1♀ (11.8 mm); Stn 605, 5168–5184 m, 1♀ (11.8 mm).

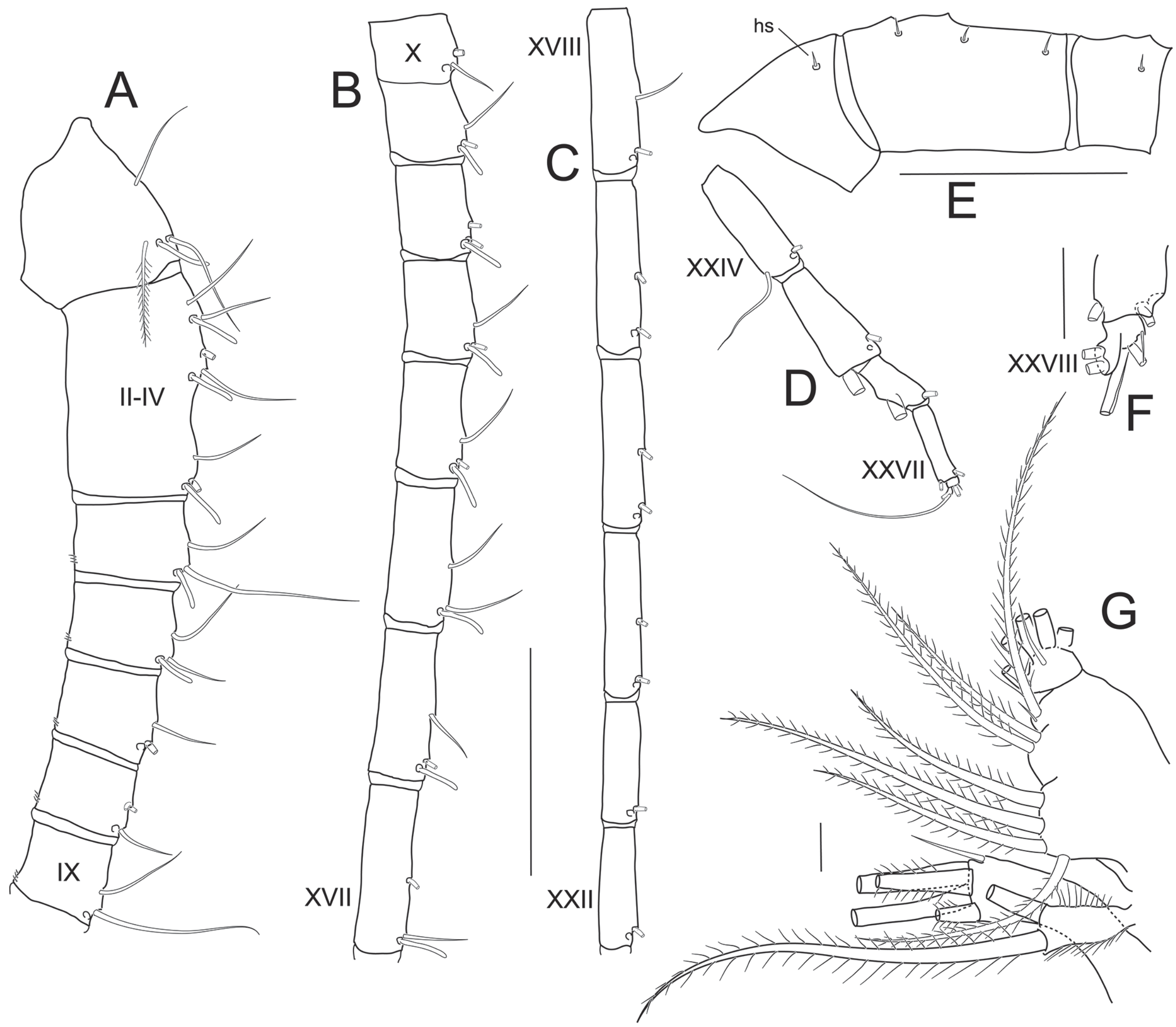

FIGURE 36. *Bradycalanus gigas* Sewell, 1947 female antennule ancestral segments: A, segment I–IX; B, segments X–XVII; C, segment XVIII–XXIII; D, segments XXIV–XXVIII; E, detail of dorsal surface of segments I–V (hs = hair sensillum); F, detail of segment XXVIII. Maxillule: G, coxal endite, basal endites 1 and 2 and endopod. Scale bars represent 1.0 mm on figures A–E; 0.1 mm on remaining figures. Illustrated specimen from DIVA III, Stn 40-S.

Type specimens. Deposited in the collection of the Zoological Museum, University of Hamburg. Holotype female: ZMH K-44181; Paratype series: ZMH K-44182-ZMH K-44184.

Morphological description. Following description based on holotype and paratype specimens from ANTXIX/4, Stn 135-4. As for genus with following specific level features.

Female (Fig. 37A–E). Total length 11.1 mm (mean = 11.5 mm, range, 11.0–11.8 mm, n = 4). Anterior head crested, rostral base thick, rostrum directed posteriorly in lateral view with pair of curled tapering filaments. Pedigerous somite 5 with short, symmetrical posterior lappets with posteroventral extension usually directed posteriorly (bent ventrally in illustrated specimen); lappets extending less than one third of way along genital double-somite. Genital double-somite in dorsal view with slight bulge at about midlength; in lateral view, genital area with posterior tranverse ridge giving ventral outline flattened appearance.

Antennule (Figs 37B, 38A–F) extends about 5–6 segments beyond caudal rami and length of antennule segments (µm) as follows. Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements taken of ancestral segment I. I (371, 775); II–IV (1064); V (280); VI (277); VII (322); VIII (322); IX (332); X–XI (636); XII (460); XIII (458); XIV (555); XV (631); XVI (661); XVII (745); XVIII (792); XIX (777); XX (795); XXI (782); XXII (542); XXIII (550); XXIV (542); XXV (537); XXVI (376); XXVII (438); XXVIII (10).

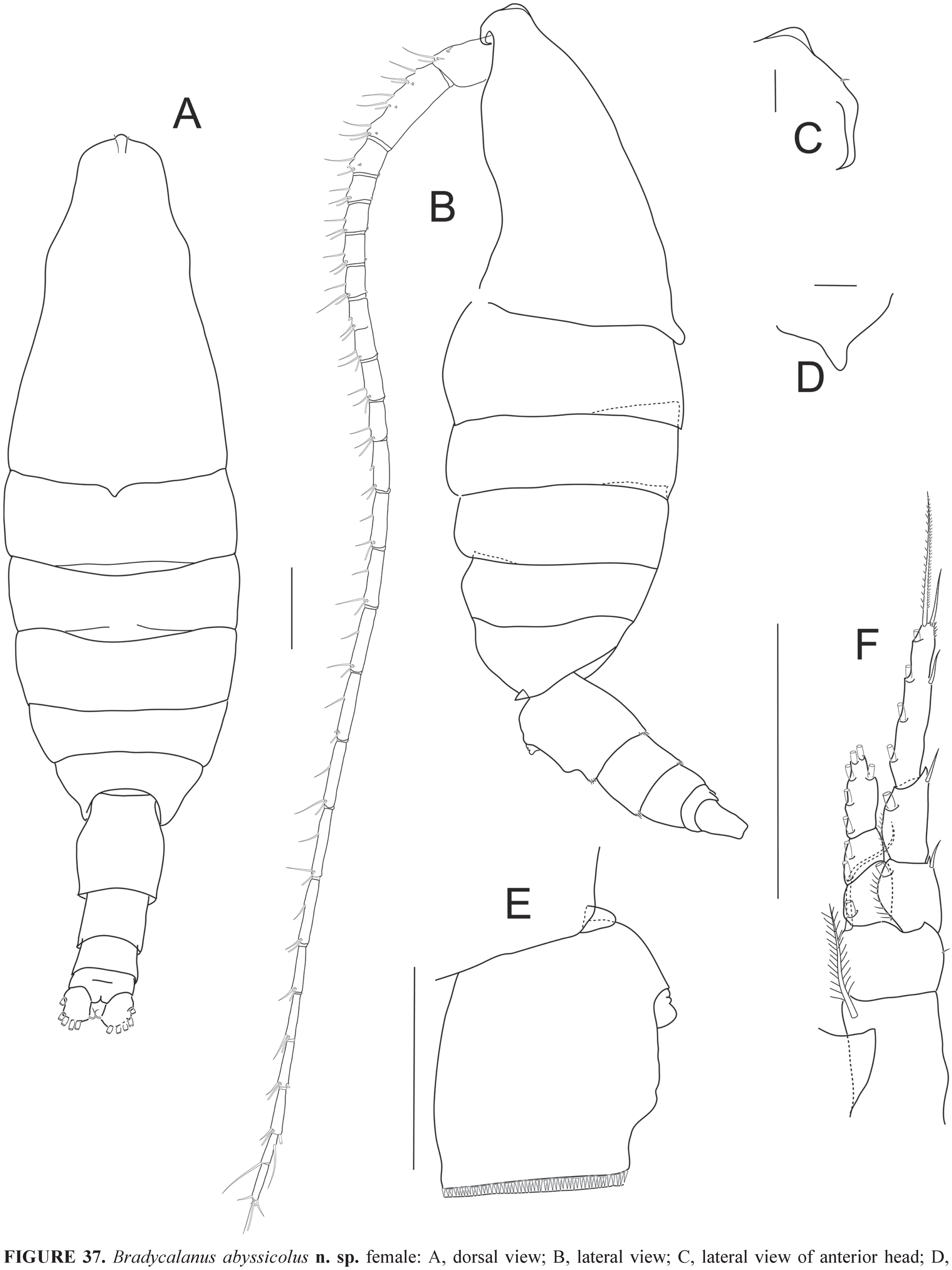

FIGURE 37. *Bradycalanus abyssicolus* **n. sp.** female: A, dorsal view; B, lateral view; C, lateral view of anterior head; D, lateral view of posterior pedigerous somite 5; E, lateral view of genital double-somite; F, posterior view of leg 1. Scale bars represent 1.0 mm on figures A, B, E, F; 0.1 mm on remaining figures. Illustrated specimen from ANDEEP II, ANTXIX/4, Stn 135-4.

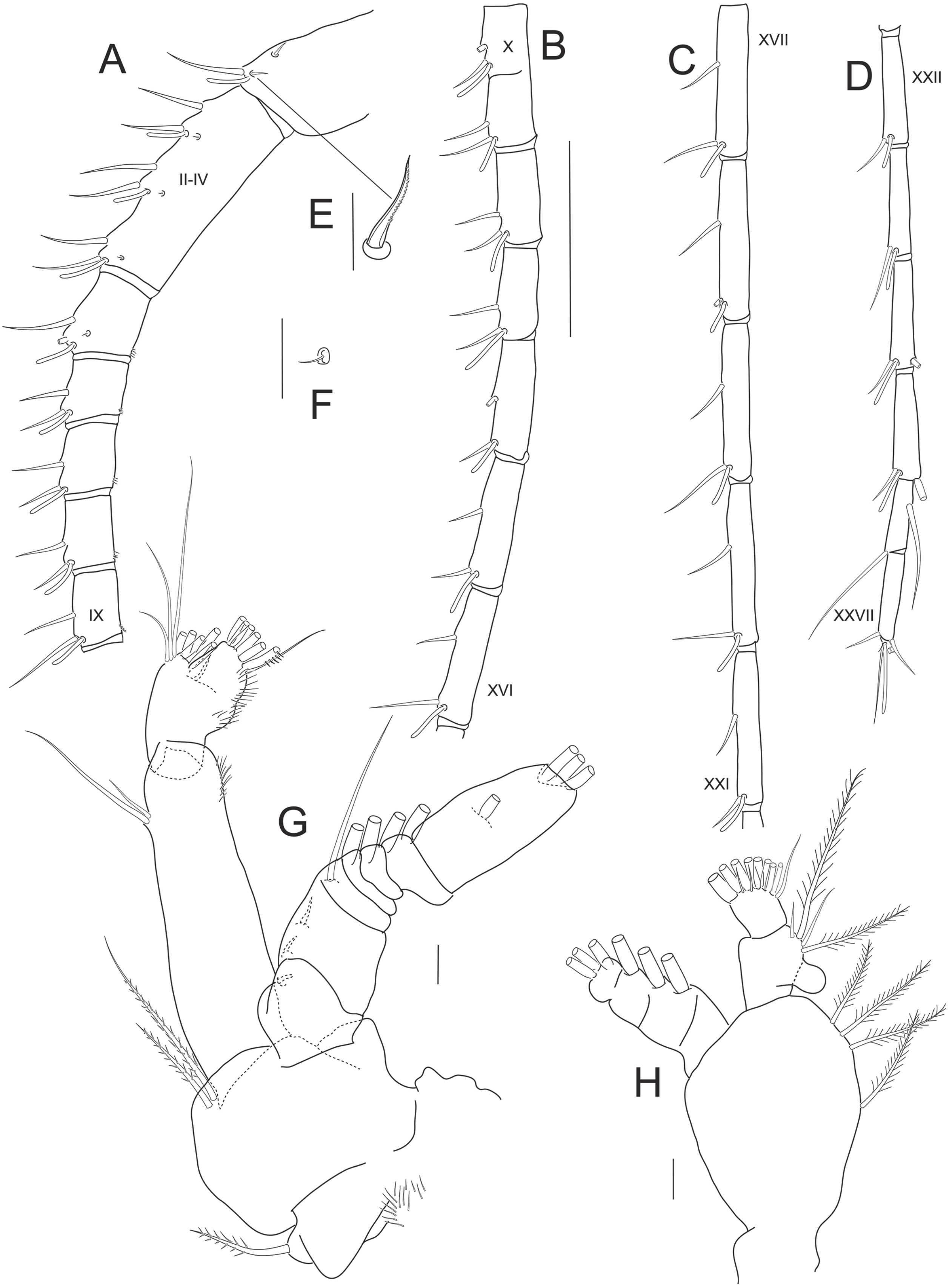

FIGURE 38. *Bradycalanus abyssicolus* **n. sp.** female antennule ancestral segments: A, segments I–IX; B, segments X–XVI; C, segments XVII–XXI; D, segments XXII–XXVIII; E, reduced setae of segment I; F, hair sensillum on dorsal surface of segment III. Mouthparts: G, antenna; H, mandibular palp. Scale bars represent 1.0 mm on figures A–D; 0.1 mm on remaining figures. Illustrated specimen from ANDEEP II, ANTXIX/4, Stn 135-4.

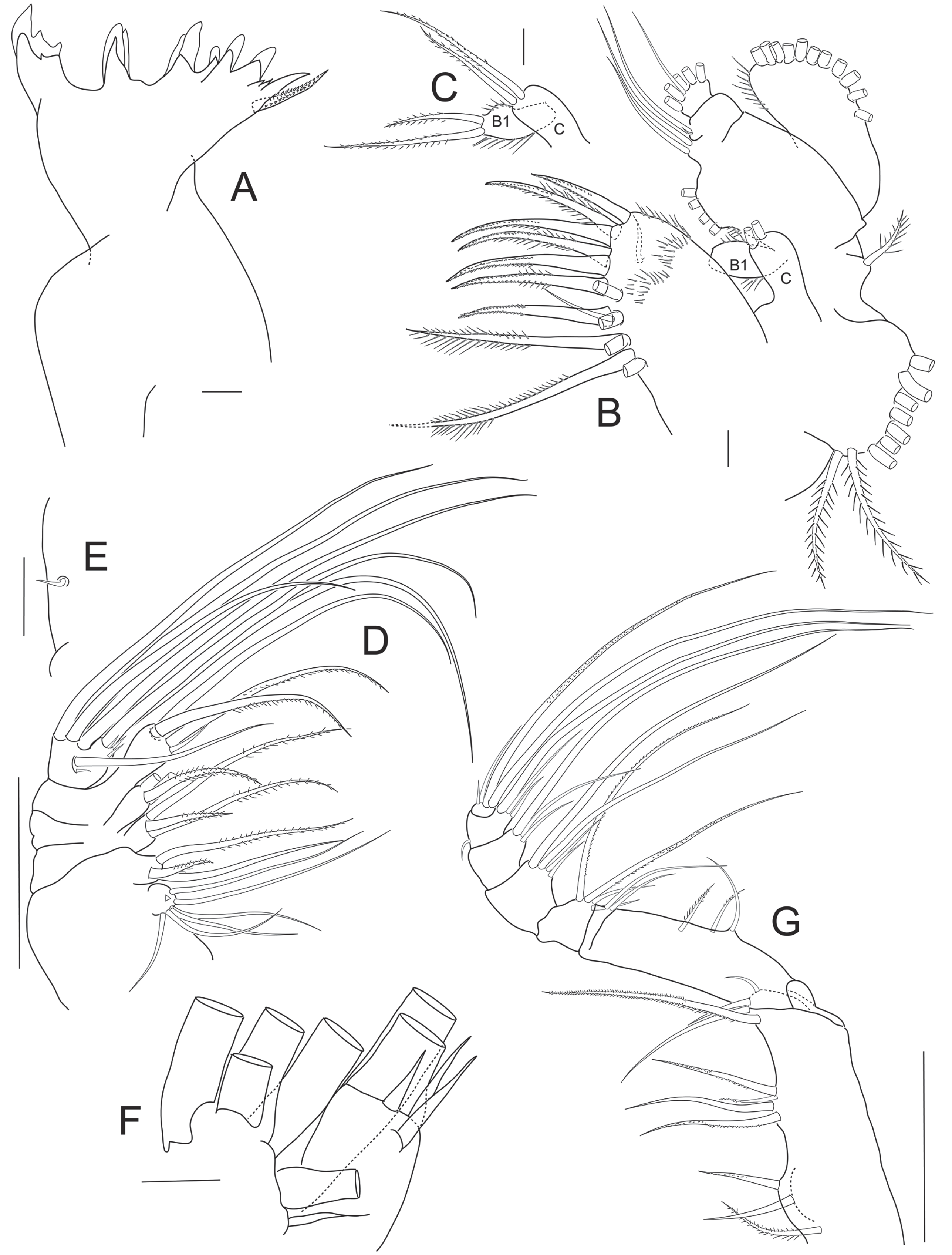

FIGURE 39. *Bradycalanus abyssicolus* **n. sp.** female: A, mandibular gnathobase; B, maxillule (B1 = basal endite 1, C = coxal endite); C, coxal endite (C) and basal endite 1 (B1) of maxillule; D, maxilla; E, detail of vestigial coxal epipodite; F, detail of endopod of maxilla; G, maxilliped. Scale bars represent 1.0 mm on figures D, G; 0.1 mm on remaining figures. Illustrated specimen from ANDEEP II, ANTXIX/4, Stn 135-4.

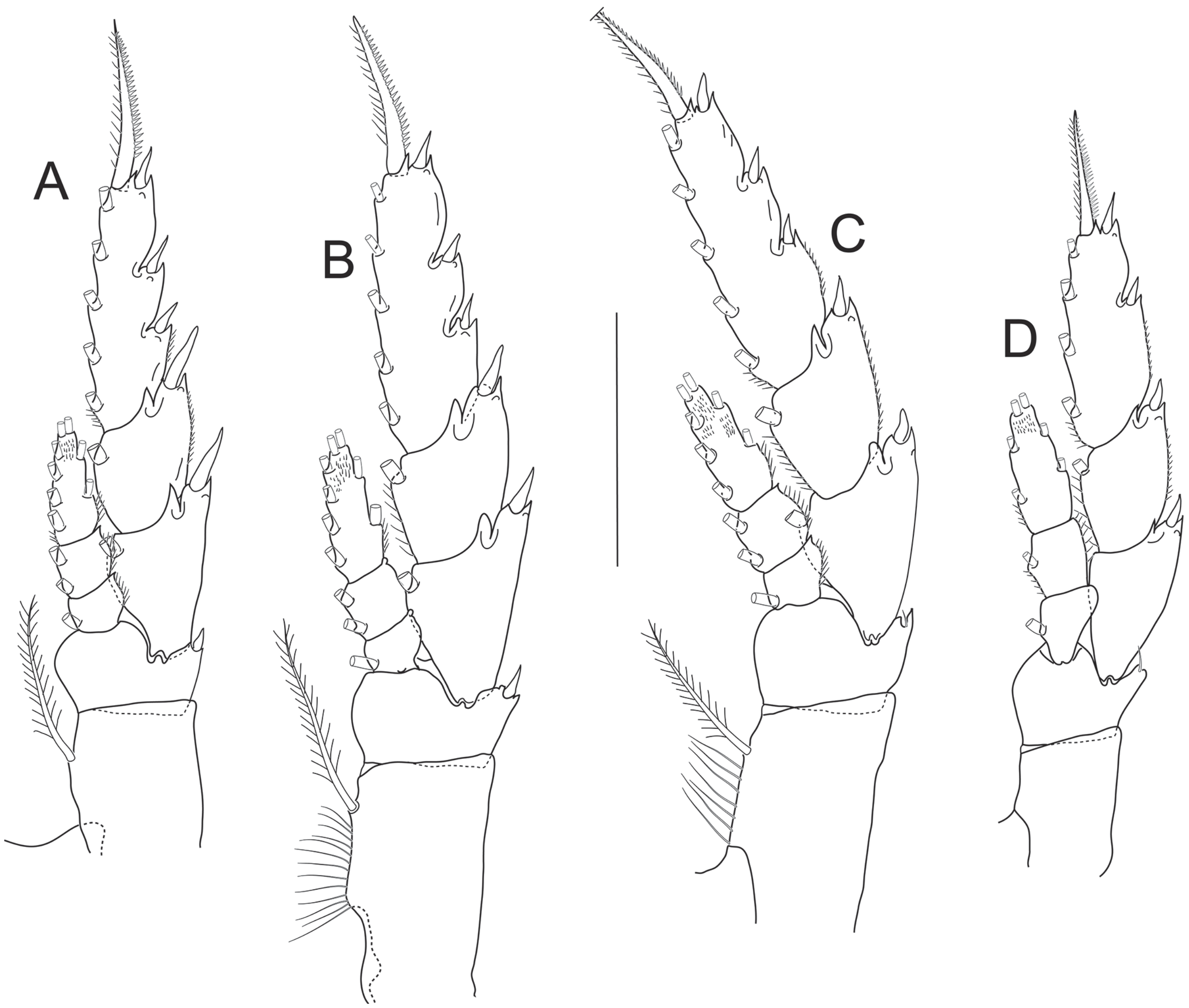

FIGURE 40. *Bradycalanus abyssicolus* **n. sp.** female, anterior views of: A, leg 2; B, leg 3; C, leg 4; D, leg 5. Scale bar represents 1.0 mm on all figures. Illustrated specimen from ANDEEP II, ANTXIX/4, Stn 135-4.

Antenna (Fig. 38G) exopod segments I–III each with vestigial seta, segment IV with relatively well-developed seta extending as far as base of seta on segment IX.

Maxillule (Fig. 39B, C) coxal endite with only 2 setae; endopod segment 3 with posterior surface seta moderately long.

Maxilliped (Fig. 39G) second most proximal seta on endopod segments 3–5 one third length of longest seta.

Leg 1 (Fig. 37F) exopod segment 3 elongate and narrow, nearly 5 times as long as maximum width; distal border of endopod segment 1 extends to distal border of exopod segment 1; exopod outer spines: on segment 1 extends one third distance to outer spine on segment 2; on segment 2 extends about one third distance to proximal outer spine on segment 3; segment 3 proximal spine extends half distance to outer distal spine.

Male. Unknown

Etymology. The species name is derived from the Latin words *abyssus* = 'deep sea' and *colus* = 'dwelling in', gender masculine. This name refers to the discovery of this species at depths greater than 4000 m.

Distribution. *Bradycalanus abyssicolus* n.sp. is an abyssopelagic species living at depths > 4000 m. It has been found in the Argentine Basin, the Central Weddell Sea and the equatorial Atlantic Ocean (Fig. 29, Table 1).

Species comparisons. This species is easily distinguished from other described *Bradycalanus* as it is the only species that has a crested head, a reduced number of setae on the coxal endite of the maxillule, and a narrow leg 1 exopod, in particular, exopod segment 3 which is nearly 5 times its maximum width (Table 8).

Genus *Bathycalanus* Sars, 1905

Differential diagnosis. As for Megacalanidae plus following character states: Rostral filaments usually parallel-sided, sausage-shaped (tapering to point in *Ba. unicornis*). Anterior head with small rounded protrusion on which sits pair of spine-like processes or single anteriorly-directed spine-like process. Genital double-somite with variable length : width characteristics, widest width, in dorsal view at variable positions anterior to posterior. Pedigerous somite 5 posterolateral corners of variable shape. Female antennule ancestral segment XXIII with aesthetasc, spines may be present along anterior and posterior borders of some segments in some species; female and male ancestral segments I, II, III, and V with dorsal surface hair sensillum, usually with adjacent macula cribrosa. Right male antennule segments XIV–XV and XXI–XXIII fused, segments XIX, XX, XXI and sometimes XVIII with fused gripping elements. Antennal exopod ancestral segments I–III with vestigial seta, seta on segment IV extends short of distal border of exopod. Mandibular gnathobase with ventral tooth set at right angles to main plane of gnathobase therefore appearing tapering, similar to other teeth; endopod segment 1 with 4 setae (distal seta very small), endopod segment 2 with 9 long setae and 2 vestigial setae. Maxillulary setation species specific. Setae of maxilla endopod curled completely in on themselves and with row of fine, long dense setules along distal half of concave surface; long setae extending anteriorly beyond rostrum, inner proximal seta of endopod segment 2 vestigial. Maxilliped with some endopod setae of reduced size. Leg 1 basis without anterodistal hook-like process, exopod segments 1 and 2 without outer border spines, exopod segment 3 with 1 distal outer border spine.

Description. Female. Anterior margin of head in dorsal view usually with pair of small spine-like processes (*Ba. unicornis* with 1 spine-like process). Rostrum extending into two long, ventrally-directed, parallel-sided, sausage-shaped filaments. Urosome of four free somites. Genital double-somite in dorsal view usually as long as wide (three species longer than wide), widest width in dorsal view variable in location anterior to posterior, and paired seminal receptacles present (Barthélémy 1999). Posterolateral borders of pedigerous somite 5 usually rounded but may be irregularly shaped (*Ba. bucklinae* **n. sp.**, *Ba. adornatus* **n. sp.**, and *Ba. pustulosus* **n. sp.**). Caudal rami with seta I absent, setae II and III lateral, setae IV–VI terminal (seta V longest), seta VII inserted at inner distal corner on small projection.

Antennule with ancestral segments II–IV, X–XI fused, XXVII and XXVIII separate. One macula cribrosa at base of each aesthetasc: most setae of modified type (ms) or aesthetascs (a), longest modified setae on at least segments I, V, IX, XXV, and XXVI. Setation of segments as follows: I—1ms, 2ss (vestigial), 1a; II to XXI—2ms, 1a; XXII to XXIII—1ms, 1a; XXIV to XXV—1+1ms, 1a; XXVI—1+1ms; XXVII—1+1ms; XXVIII—3ms, 1a, 1ss. Oblique row of small setules on posterodistal border of segments V–IX; segments I, II, III, and V with dorsal surface hair sensillum and usually adjacent macula cribrosa; ventral surfaces of ancestral segments XIV to XVII without teeth, and anterior and posterior borders of segments smooth or with teeth.

Antenna with separate coxa and basis; coxa with 1 short inner plumose seta and inner tuft of setules, basis with 2 inner setae one bordered by 2 rows of short setules. Exopod about same length as endopod; endopod 2-segmented although line of fusion between segments 2 and 3 visible on posterior surface; segment 1 with 2 inner setae (one naked and one plumose) and short longitudinal row of outer distal setules; terminal segment with 9+7 setae and lined with long outer setules; exopod with arthrodial membrane present between ancestral segments I and II, arthrodial membrane between ancestral segments II–III, III–IV and IV–V not developed although signs of demarcation between ancestral segments III and IV and IV and V may be visible; ancestral segments VI, VII and VIII expressed and segments IX and X fused. Terminal segment IX–X with 1 + 3 terminal setae, segments V–VIII each with long plumose seta, ancestral segments I–III each with 1 vestigial seta and segment IV with short seta bearing short setules extending, at most, just beyond exopod segment VIII.

Mandible coxal gnathobase with five complex teeth with opaline tips, largest tooth set at right angles to main plane of gnathobase, ventrally situated, tapering when viewed at right angles to broad plane of gnathobase, separated from adjacent tooth by wide gap; 4 following teeth progressively decreasing in size, but 2 teeth immediately adjacent to large ventral tooth not in same plane, one being more anterior, other posterior appearing to lie nearly on top of one another when mounted; 3 simpler teeth without opaline tips follow, dorsal-most tooth longest; and finally, 1 lash-like element situated dorsally, bordered by wide setules. Basis with 4 inner setae; endopod 2-segmented, segment 1 with large inner lobe and 4 (including 1 sometimes vestigial) distal inner setae, segment 2 with 9 + 2 vestigial terminal setae; exopod 5-segmented with 1, 1, 1, 1, 2 setae, respectively.

Maxillule praecoxal arthrite with 13–15 setae, 2–4 posterior surface setae present and 2 distoanterior surface seta; coxal endite poorly developed, usually without seta (1 seta in both *Ba. tumidus* **n. sp.** and *Ba. pustulosus* **n. sp.**), coxal epipodite with 7 long and 2 short setae; basal endites 1 and 2 with 2 and 2–4 setae respectively, exite with 1 seta; basis and endopod segments 1 and 2 fused, segment 3 expressed; endopod with 2–3, 2, 5 + 1 small posterior surface seta; exopod with 11 setae.

Maxilla praecoxal endites 1 and 2 with 6+1 small and 3 setae, respectively; coxal endites 1 and 2 with 3 setae each, coxal epipodite with 1 small seta; basal endite longest with 4 setae; endopod segment 1 with short lobe bearing 3 vestigial + 1 large seta, endopod segments 2–4 apparently with 3 (proximal seta vestigial), 2, 2 setae, respectively. Inner surfaces of praecoxal endite 2, coxal endites 1 and 2 and basal endite each with 1 shorter seta lined with 2 rows of spinules along distal half whereas other setae ornamented with one row of spinules; coxal endite 2 usually with short setae, only 1 of them curled distally; basal endite and endopod segments 1–4 with very long setae, distally very thin, curling completely on themselves distally, lined along more than distal half with very fine spinules. None of setae on maxilla with auxiliary spinules although inner distal seta of endopod segment 2 has row of spinules along convex, distal-facing surface. Longest setae extend beyond rostrum when maxilla directed ventroanteriorly, and appear to function as mechanical tangling devices.

Maxilliped directed ventrally so setae on syncoxa and basis directed into animal's midline; syncoxal endites with 1, 2, 4, 4 setae; basis with 3 setae and elongate patch of setules on anteroproximal surface. Endopod segment 1 mostly separate from basis and bearing 2 setae, 1 longer seta with long spinules along one edge, short seta with smooth, wide basal part then rapidly tapering and lined distally by 2 rows of long spinules; endopod segment 2 with 4 setae, 3 setae bordered on one side by long spinules, 1 seta with much shorter spinules; endopod segments 3–6 with 1 large + 3 small, 1 large + 2 small, 1 large + 2 small + 1 small outer seta, 2 large + 1 small + 1 small outer seta, respectively.

Legs 1–5 biramous, each ramus usually 3-segmented (apart from leg 1 exopod in *Ba. richardi*) with following setal formula (Roman numerals indicate spines, Arabic numerals setae, outer border setation listed to left in each group separated by ';'):

Leg 1 (Coxa 0-1. Basis 1-1. Exopod 0-1; 0-1; I,1,4. Endopod 0-1; 0-2; 1,2,3);

Leg 2 (Coxa 0-1. Basis I-0. Exopod I-1; I-1; III,1,5. Endopod 0-1; 0-2; 2,2,4);

Leg 3 (Coxa 0-1. Basis I-0. Exopod I-1; I-1; III,1,5. Endopod 0-1; 0-2; 2,2,4);

Leg 4 (Coxa 0-1. Basis 1-0. Exopod I-1; I-1; III,1,5. Endopod 0-1; 0-2; 2,2,3);

Leg 5♀ (Coxa 0-0. Basis 1-0. Exopod I-0; I-1; II,1,4. Endopod 0-1; 0-1; 2,2,2).

Leg 1 basis inner distal seta almost straight, hook-like process absent, outer distal seta rudimentary, macula cribrosa on anterior surface adjacent to insertion of exopod segment 1 although sometimes difficult to see, exopod segments 1 and 2 without outer distal spine, segment 3 with 1 outer distal spine, distolateral corner of endopod segment 1 rounded. Legs 2–4 with coxal seta on inner margin; pore openings located on anterior surface at base of outer edge robust setae of exopod segments 1–3, outer border of exopod segment 2 and outer distoproximal border of exopod segment 3 extending into thin flange bordered by short setules; endopod segment 1 outer distal corner rounded. Leg 5 with outer distal corner of endopod segment 1 rounded; pore openings on anterior surface at base of outer border spines; outer border of exopod segment 2 and outer distoproximal border of exopod segment 3 extending into thin flange bordered by short setules.

Male. Anterior margin of head and rostrum similar to that of female. Urosome of five free somites, urosomite II of various proportions relative to other somites.

Antennule asymmetrically developed, geniculate on right. Aesthetascs larger than in female with stiffened posterior border. Left antennule with ancestral segments II–IV and IX–XI fused, XXVII and XXVIII separate with aesthetascs doubled on segments, III, V, VII, IX, XI–XIV. Most setae of modified type (ms) or aesthetascs (a). One macula cribrosa present at base of each aesthetasc. Setation of segments as follows: I—1ms, 2ss (vestigial), 1a; II–IV—6ms, 4a; V—2ms, 2a; VI—2ms, 1a; VII—2ms, 2a; VIII—2ms, 1a; IX–XI—6ms, 5a; XII to XIV—2ms, 2a; XV to XXI—2ms, 1a; XXII to XXIII—1ms, 1a; XXIV to XXV— 1+1ms, 1a; XXVI—1+1ms; XXVII—1+1ms; XXVIII— 3ms, 1 enlarged ss, 1a. Right antennule geniculate between segments XX and XXI, with ancestral segments II–IV, IX–XI, XXI–XXIII fused, XIV–XV fused or separate, XXVII and XXVIII separate. Setation of segments as follows: I—1ms, 2ss (vestigial), 1a; II–IV—6ms, 4a; V—2ms, 2a; VI—2ms, 1a; VII—2ms, 2a; VIII—2ms, 1a; IX–XI—6ms, 5a (clavate seta not observed—damaged?); XII to XIV—2ms, 2a; XV to XVIII—2ms, 1a; XIX—1ms, 1 fused gripping element, 1a; XX—1 fused gripping element, 1ms, 1a; XXI–XXIII—2 fused gripping elements, 1a, 1 small fused gripping element, 1ms; XXIV to XXV— 1+1ms, 1a;

XXVI—1+1ms; XXVII—1+1ms; XXVIII—2ms, 2a, 1ss. Segments 1, II, III, and V with dorsal surface hair sensilla and adjacent macula cribrosa.

Antenna, mandible, maxillule, maxilla, maxilliped and legs 1–4 as in female. Leg 5 with following setal formula (Roman numerals indicate spines, Arabic numerals setae, outer border setation listed to left in each group separated by ';'):

Leg 5♂ left (Coxa 0-0. Basis 1-0. Exopod I-0; I-1; II,1,0. Endopod 0-0; 0-1; 2,2,2);

Leg 5♂ right (Coxa 0-0. Basis 1-0. Exopod I-0; I-0/1; II,1,0. Endopod 0-0; 0-1; 2,2,2).

Leg 5 almost symmetrical, apart from specialised seta on inner distal border of left exopod segment 2 and sometimes on right leg exopod segment 2 (*Ba. unicornis*). Outer distal corner of endopod segments 1 and 2 rounded; pore openings on anterior surface of exopod segments at base of outer border spines; outer border of exopod segment 2 and outer proximal border of exopod segment 3 extending into thin flange. Left leg 5 exopod segment 2, specialised seta composed of two sections: wider basal part and lash arising from distal border of basal part. Exopod segment 3 on both sides with analogue of terminal spine on other legs located on distal inner border; on left bordered by setules, on right with or without bordering setules.

Type species. *Bathycalanus richardi* Sars, 1905

Remarks. The phylogenetic analyses (see Figs 112, 113) clearly identify two separate clades within what was previous called *Bathycalanus.* When Sars (1905) described this genus, *Ba. richardi* was the only included species. Thus, the name *Bathycalanus* is retained for the group of species without reduced numbers of setae on mouthparts of both sexes and with one outer border spine on leg 1 exopod segment 3. Here, we designate, by original monotypy (ICZN 1999, Article 68.3), *Bathycalanus richardi* Sars, 1905 as the type species of the genus *Bathycalanus*. This genus currently contains the following species: *Ba. richardi* Sars, 1905; *Ba. bradyi* (Wolfenden, 1905); *Ba. unicornis* Björnberg, 1968 and *Ba. eximius* Markhaseva, 1983, to which are added a further six new species.

The morphology of some *Bathycalanus*, as defined here, supported by limited molecular data, suggests that this genus might be further subdivided in the future. In the morphology-based cladistic analysis (see Fig. 112), the genus *Bathycalanus* has little bootstrap support and relationships among species are unresolved. In the limited molecular data, both the topology of the phylogenetic tree, and the genetic distances of *Ba. tumidus* **n. sp.** from *Ba. milleri* **n. sp.**, *Ba. richardi, Ba. bradyi* and *Ba. adornatus* **n. sp.** would support the subdivision of this genus (see Fig. 113; Tables 14–17). The setation of parts of the maxillule (see Table 18) indicates the range of combinations of setation on the posterior of the praecoxal arthrite, coxal endite, basal endite 2 and endopod segment 1 although it is not clear which characters would be aligned with a monophyletic genus containing *Ba. tumidus* **n. sp.**

Bathycalanus richardi Sars, 1905

(Figs 41–46)

Bathycalanus richardi Sars, 1905, p. 7, 8.
Bathycalanus richardi: Wolfenden, 1911, p. 200, pl. 23, fig. 8.
Bathycalanus richardi: Sars, 1924, 1925, pp 16–19, pls 14, 15.
Bathycalanus richardi: Sewell, 1929, p. 31.

Type locality. West and south of the Azores to Bay of Biscay (Sars 1925). 45.50ºN 5.83ºW to 36.28ºN 28.88ºW (Sars 1905).

Material examined. Antipode IV, IKMT: Stn 52D, 0–1900 m 2♀ (9.5, 9.9 mm); Stn 53A, 0–2000 m, 4♀ (9.8–10.4 mm); Stn 53D, 0–2500 m, 1♀ (10.6 mm) 1♂ (9.2); Stn 55D, 0–2000 m 1♂ (8.9 mm). ANTXIV/1, Stn 2, MOC10, 2000–3000 m, 1♂ (8.8 mm), Co022.4. RHB0603, Stn 5, 600–799 m, 1♀, Co022.2.1. Circe II, Stn 15T-1, IKMT, 0–2121 mwo, 5♀ (8.6–10.6). MV66-II, Stn 5, IKMT, 0–3889 mwo, 1♂ (8.9 mm). MV73-I, Stn 53, IKMT, 0–2000 m, 1♀ (10.0 mm). Francis Drake III, Stn 2, IKMT, 0–3000 m 1♀ (10.0 mm). Records from Natural History Museum, London: Discovery Stns, RMT8: 7089#12, 800–900 m, 1♀ (9.1 mm), BMNH 1994.5790; 7406#6, 900–1000 m, 1♀ (9.4 mm), BMNH 1994.5749; 7709#63, 1000–1250 m, 1♀ (9.5 mm), 1♂ (9.7 mm), BMNH 1993.871-872; 8508#1, 1000–1250 m, 6♀ (9.0, 9.2, 9.1, 9.5, 9.6, 9.4 mm), BMNH 1993.865-870; 8508#3, 1000–1250 m, 1♀ (9.0 mm), BMNH 1993.864; 8508#3, 1000–1250 m, 1♀ (9.0 mm), BMNH 1994.831. Additional records from Smithsonian Institution, USNM numbers: 67308, 72406, 262452–56, 262465, 262494, 269458, 269471–73, 269511.

Genetic material. Co022.4.1, Co022.2.1. GenBank numbers in Table 6.

Morphological description. Following description based on specimen from Antipode IV, Stn 53A. As for genus with following specific characters.

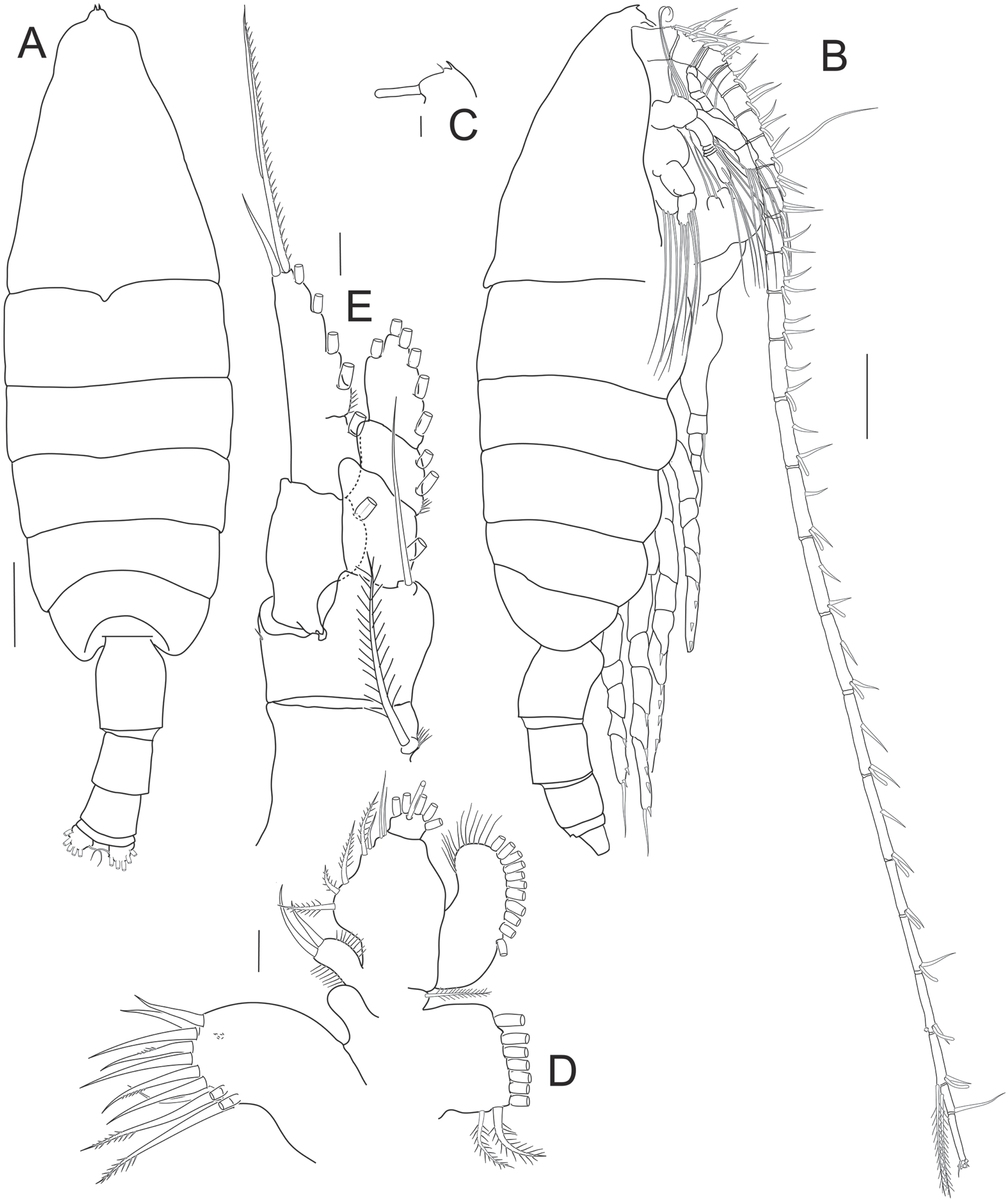

FIGURE 41. *Bathycalanus richardi* (Sars, 1905) female: A, dorsal view; B, lateral view; C, lateral view of anterior head; D, maxillule; E, anterior view of leg 1. Scale bars represent 1.0 mm on figures A, B; 0.1 mm on remaining figures.

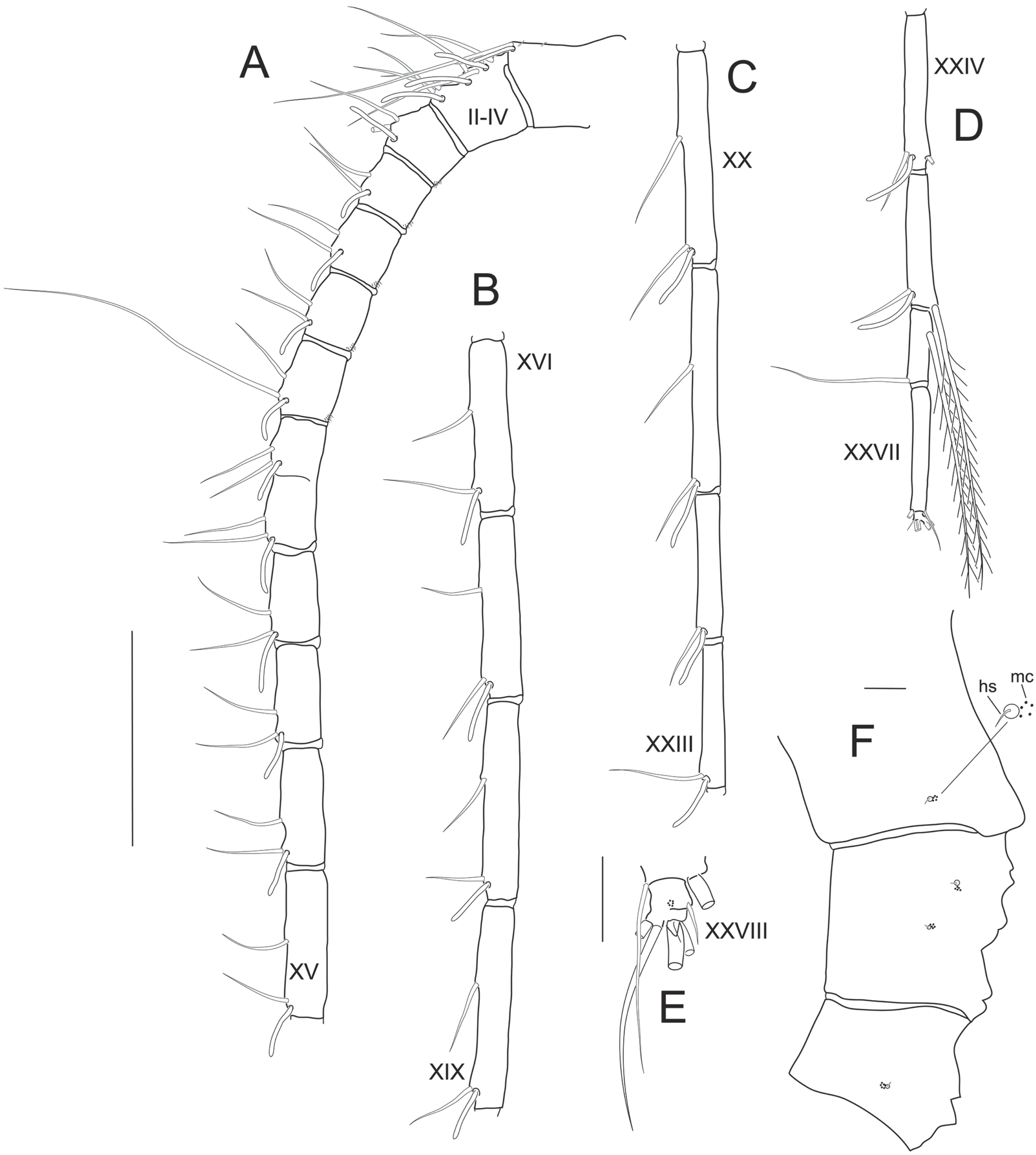

FIGURE 42. *Bathycalanus richardi* (Sars, 1905) female antennule ancestral segments: A, segments I–XV; B, segments XVI–XIX; C, segments XX–XXIII; D, segments XXIV–XXVIII; E, detail of segment XXVIII; F, dorsal surface of segments I–V (hs = hair sensillum, mc = macula cribrosa). Scale bars represent 1.0 mm on figures A–D; 0.1 mm on remaining figures. Illustrated specimen from Antipode IV, Stn 53A.

Female (Fig. 41A, B). Total length 10.3 mm (mean = 9.51 mm, range = 8.8–10.6 mm, n = 19). Anterior head in dorsal view with rounded prominence extending into pair of small anteriorly-directed spine-like processes. Pedigerous somite 5 with short, symmetrical, rounded posterior lappets extending one quarter of way along genital double-somite. Genital double-somite in dorsal view widest at anterior one third, length about 1.4 times widest width.

Antennule (Figs 41B, 42) extends about 7 segments beyond caudal rami. Lengths of antennule segments (µm) (below) taken from specimen from Antipode IV, Stn 53D. Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements taken of ancestral segment I. I (249, 625); II–V (336); V (205); VI (237); VII (294); VIII (296); IX (277); X–XI (578); XII (422); XIII (435); XIV (548); XV (716); XVI (812); XVII (869); XVIII (943); XIX (946); XX (1017); XXI (1049); XXII (719); XXIII (699); XXIV (726); XXV (657); XXVI (351); XXVII (640); XXVIII (45). Anterior and posterior borders and ventral and dorsal surfaces of ancestral segments XVI–XXI smooth.

Antenna (Fig. 43A) exopod segment IV with short seta, not extending beyond distal border of segment VI, lined with spinules.

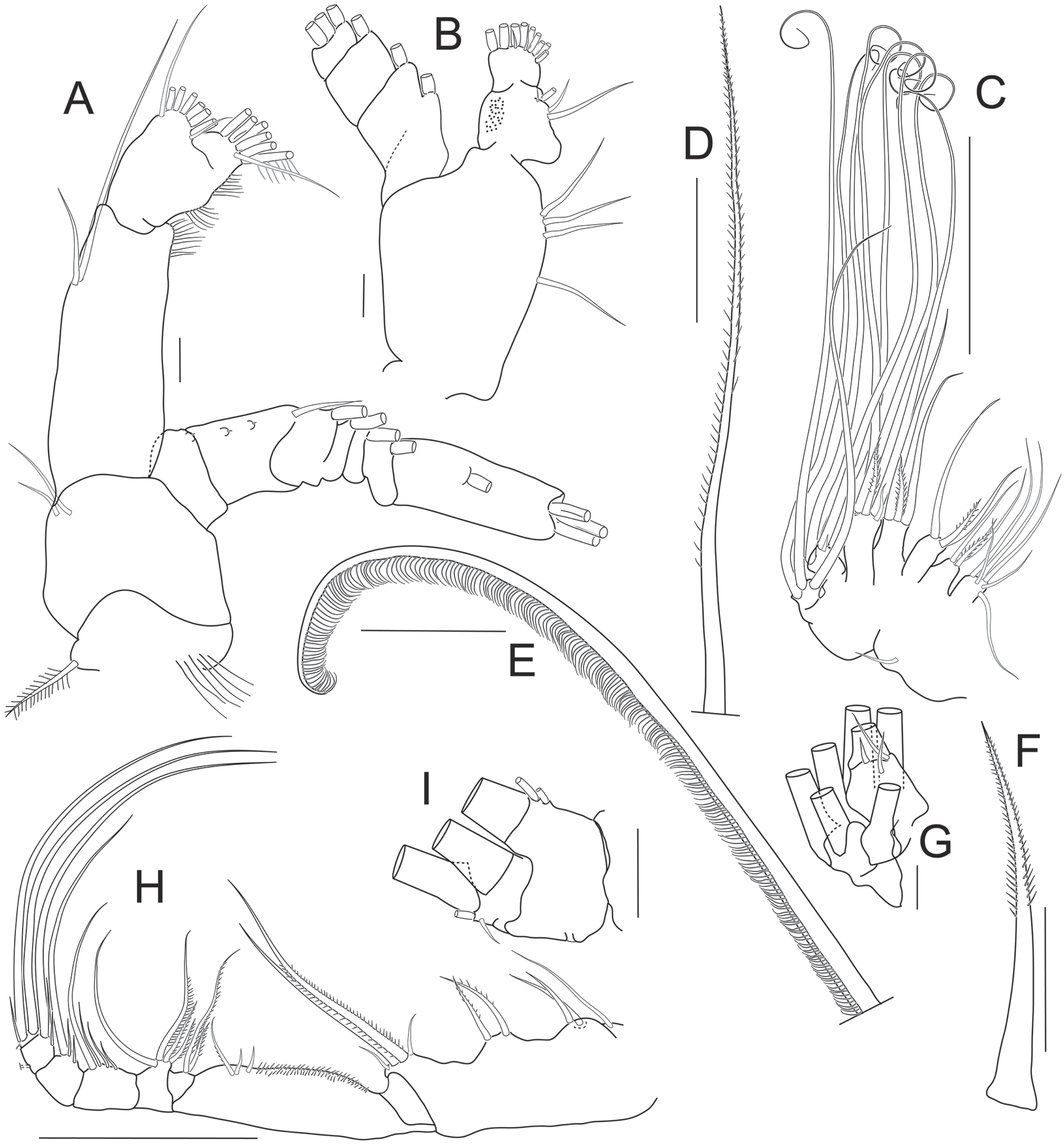

FIGURE 43. *Bathycalanus richardi* (Sars, 1905) female: A, antenna; B, mandibular palp; C, maxilla; D, seta from praecoxal endite 1 of maxilla; E, part of seta from coxal endite 2 of maxilla; F, inner seta of praecoxal endite 2 of maxilla; G, detail of endopod of maxilla, inner surface; H, maxilliped; I, terminal part of endopod of maxilliped—note outer seta of endopod segment 5 (Ri5) knocked off. Scale bars represent 1.0 mm on figures C, H; 0.1 mm on remaining figures. Illustrated specimen from Antipode IV, Stn 53A.

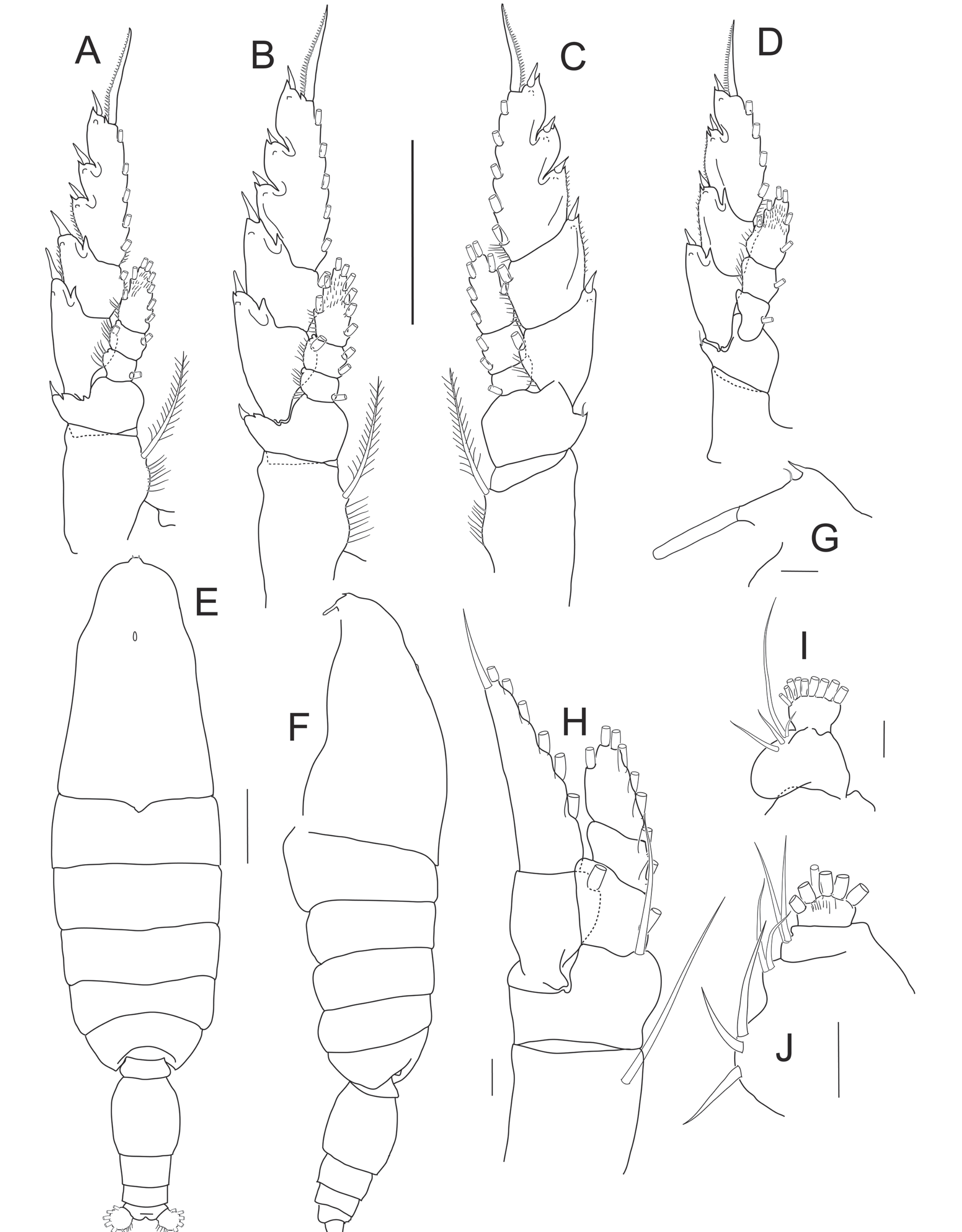

FIGURE 44. *Bathycalanus richardi* (Sars, 1905) female: A, anterior view of leg 2; B, anterior view of leg 3; C, posterior view of leg 4; D, anterior view of leg 5. Illustrated specimen from Antipode IV, Stn 53A. Male: E, dorsal view; F, lateral view; G, lateral view of anterior head; H, anterior view of leg 1; I, endopod of mandibular palp; J, basal endite 2 and endopod of maxillule. Illustrated specimens from: MV66-II , Stn 5. (E); ANTXXIV/1, Stn 2 (F–J). Scale bars represent 1.0 mm on figures A–F; 0.1 mm of remaining figures.

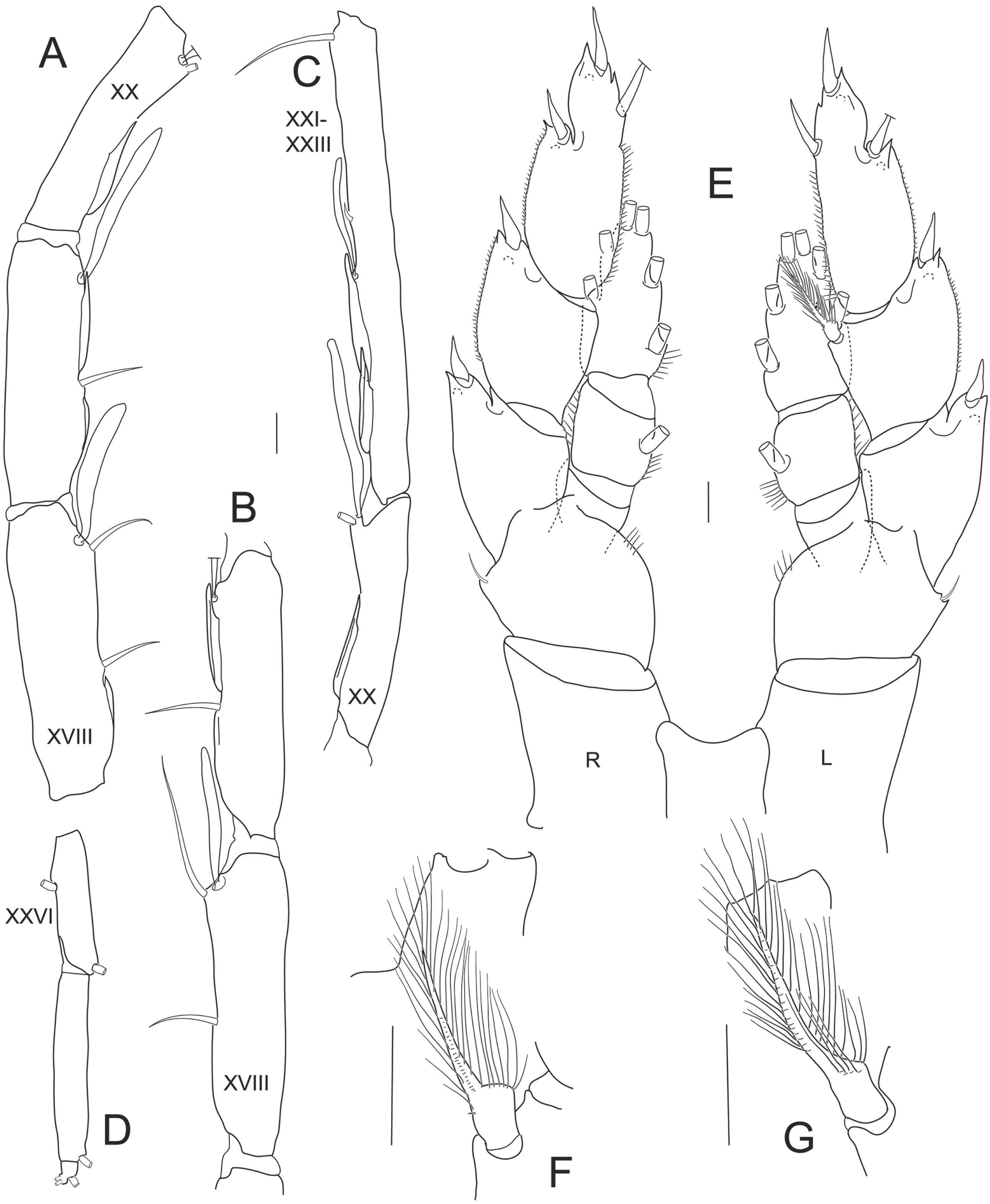

FIGURE 45. *Bathycalanus richardi* (Sars, 1905) male right antennule ancestral segments: A, segments XVIII–XX; B, segments XVIII–XIX; C, segments XX–XXIII; D, segments XXVI–XXVIII. Scale bar represents 0.1 mm for all figures. Illustrated specimens from: ANTXXIV/1, Stn 2, 2000–3000 m (A); MV66-11, Stn 5 (B–D). Male: E, posterior view of leg 5; F, detail of inner distal corner of left exopod segment 2; G, detail of inner distal corner of left exopod segment 2 of another specimen. Illustrated specimens: ANTXXIV/1, Stn 2, 2000–3000 m (E, F); MV66-11, Stn 5 (G). Scar bars represent 0.1 mm for all figures.

TABLE 9. Proportions of male urosomites of *Bathycalanus*.

Sample location	Species	TL mm	Length UII/UIII	$Depth_{mx}$ UI/UII	$Depth_{max}$ UII/UIII	Length/depth UII	Depth UII_{ant}/UII_{post}	Notes
Antipode IV Stn 53D	*Ba richardi*	9.8	**2.17**	0.71	1.31	**1.18**	**0.65**	
MV66-11	*Ba richardi*	9.8	**2.36**	0.72	1.27	**1.18**	**0.64**	
ANTXIV/1 Co022.4	*Ba richardi*	8.8	**2.58**	0.73	1.29	**1.21**	**0.69**	
Antipode IV Stn 55D	*Ba richardi*	8.9	**2.35**	0.77	1.20	**1.15**	**0.68**	
MV66-11	*Ba bradyi*	9.4	1.66	0.85	1.17	1.00	0.79	
Antipode IV Stn 55D	*Ba bradyi*	9.5	1.54	0.92	1.08	0.91	0.80	A1 absent
Circe II	*Ba bradyi*	9.9	1.80	0.89	1.18	0.98	0.81	No thickenings on leg exopods
ANTXIV/1 Stn 4	*Ba bradyi*	9.0	1.57	0.94	1.15	0.94	0.83	A1 absent
Antipode IV Stn 55D	*Ba bradyi*	9.9	1.62	0.86	1.20	0.96	0.85	
MV66-11	*Ba dentatus*	**11.7**	1.58	0.79	1.20	0.86	0.73	
MV66-11	*Ba milleri*	9.4	1.55	0.84	1.22	0.85	0.78	
MV66-11	*Ba milleri*	9.7	1.70	0.84	1.22	0.85	0.79	
ANTXIV/1 Stn 6	*Ba milleri*	9.5	1.55	0.84	1.22	0.74	0.74	
Southtow IV	*Ba milleri*	9.5	1.52	0.84	1.23	0.95	0.73	
USNM262488	*Ba milleri*	9.2	1.62	0.91	1.19	0.95	0.88	

Maxillule (Fig. 41D) praecoxal arthrite with 13 setae and spines, including 2 setae on posterior surface; coxal endite without setae; basal endite 2 with 3 short setae; endopod segments with 2 (subequal), 2 (subequal), 6 setae (including 1 smaller seta arising from posterior surface), respectively.

Maxilliped (Fig. 43H, I) syncoxal endite 4 with longest spinulose seta extending to distal border, or beyond, of endopod segment 1.

Leg 1 (Fig. 41E) exopod with articulation between exopod segments 2 and 3 undeveloped.

Male (Fig 24E, F). Following description based on specimens from MV66-II, Stn 5 and ANTXXIV/1, Stn 2. Total length 9.2 mm (mean = 9.1 mm, range 8.8–9.2 mm, n = 5). Anterior head in dorsal view with rounded prominence extending into pair of small anteriorly-directed spine-like processes. Pedigerous somite 5 with short, rounded posterior lappets. Urosomal measurements made in lateral view as in Fig. 1 are tabulated in Table 9. In lateral view urosomite II (UrII) of enlarged and swollen appearance, constricted anteriorly: UrII 2.17–2.58 (mean = 2.37, S.D. = 0.17, n = 4) times longer than UrIII and constricted anteriorly such that ratio $UrII_{ant}$ / $UrII_{mx}$ = 0.64–0.68 (mean = 0.67, S.D. = 0.03, n = 5).

Right antennule (Fig. 45A–D) ancestral segments (completely intact only on MV66-11 specimen)**:** XIX—1ms, 1 fused gripping element extending beyond base of aesthetasc, 1a; XX—1 gripping element, 1ms, 1a; XXI–XXIII—2 gripping elements extending well beyond base of following element, 1a, 1 short fused gripping element, 1ms (segments XVIII—XX from males from ANTXXIV/1, Stn 2, 2000–3000 m; segments XXI–XIII from MV66-II, Stn 5).

Leg 5 (Fig. 45E–G) left exopod segment 2 specialised seta with long lash extending almost to distal border of endopod segment 3, basal part rectangular in shape; inner border of right exopod segment 3 lined with setules.

Remarks. Male specimens taken from the Atlantic Ocean are clearly *Bathycalanus richardi* Sars, 1905 in that they have a 2-segmented leg 1 exopod. These specimens allow some details of Sars' (1924/25) description and figures to be augmented. The right antennule, ancestral segment XIX, was drawn by Sars (1924, pl. 5, fig. 3) as having 2 fused gripping elements whereas, in the specimens examined here, the proximal-most gripping element is not present although there is a short, low ridge on the anterior border that is additional to the normal complement of setae. A number of setae were apparently missed by Sars (1924, pl. 5, figs 6, 7, 9) from female mandibular endopod segment 1, maxillule endopod segment 2, and maxilliped endopod segments 4 to 6.

There is some uncertainty over the previous identifications of *Bathycalanus* that have a pair of small spine-like processes on the rostral base. Among the present specimens there are three additional, previously unrecognised, morphological species that are superficially similar to *Ba. richardi*. However, these all have leg 1 with 3 exopod segments and there are also features of the female antennules that serve to distinguish these species from *Ba. richardi*. In addition, there are several types of males, differing from that described by Sars (1924/25) with urosomites of varying proportions and subtle differences in the fifth legs. Here it is assumed that Sars' (1924/25) assignment to *Ba. richardi* of a male with a very long, wide urosomite II that is constricted anteriorly, is correct.

Morphological variation. Leg 1 usually does not have a functional articulation expressed between exopod segments 1 and 2 although some specimens have these segments more or less expressed. Male leg 5 left exopod segment 2 inner distal border specialised setulose seta is of variable length ranging from extending short of the distal border of endopod segment 3 to beyond it; sometimes, but not always, there is a small outer border spinule on the basal part of the setulose seta. There were slight differences in the male right antennule between the specimen from ANTXXIV/1, Stn 2 (Atlantic Ocean) and specimens from the Pacific Ocean (MV66-11, Stn 5 and USNM269458). Ancestral segments XVIII and XIX had a proximal ridge in the Atlantic specimen but were without such a ridge in Pacific specimens.

Distribution. *Bathycalanus richardi* is a bathy- to abyssopelagic species taken from < 1200 m (Sars 1924; Sewell 1929) or deeper; it was taken between 2000–3000 m, above the Cape Verde Abyssal Plain during ANTXIV/I and 800–2000 m in the north Atlantic Ocean. It appears to be widespread being distributed in the Atlantic, Pacific and Indian Oceans (present data) (Fig. 46, Table 1).

Species comparisons. Among *Bathycalanus* that have two small anterior spine-like processes on the rostral prominence and bluntly rounded posterolateral corners of pedigerous somite 5 (*Ba. richardi, Ba. bradyi, Ba. dentatus* **n. sp.**, *Ba. milleri* **n. sp.** and *Ba. tumidus* **n. sp.**), *Ba. richardi* may be distinguished by the following combination of character states (Table 10): 1) the female genital double-somite in dorsal view is widest at anterior one third; 2) the female antennular segments XII–XVII are without surface thickenings and segments XVI–XXI are without anterior or posterior teeth; 3) the maxillule second basal endite has 3 setae; 4) the leg 1 exopod is 2-segmented in both sexes; 5) the male leg 5 left exopod segment 2 inner distal specialised setulose seta of variable length, extending just short of, to just beyond, the distal border of endopod segment 3, and the inner border of the right exopod segment 3 is bordered by setules; 6) the length proportions of the male urosomites UrII/UrIII in *Ba. richardi* are significantly different from those of *Ba. bradyi* (pair-wise PERMANOVA (P) = 0.006) and *Ba. milleri* **n. sp.** (P = 0.01); and 7) in lateral view the ratio of anterior/posterior depth of UrII is significantly different from that of *Ba. bradyi* (P = 0.014) and *Ba. milleri* **n. sp.** (P = 0.014).

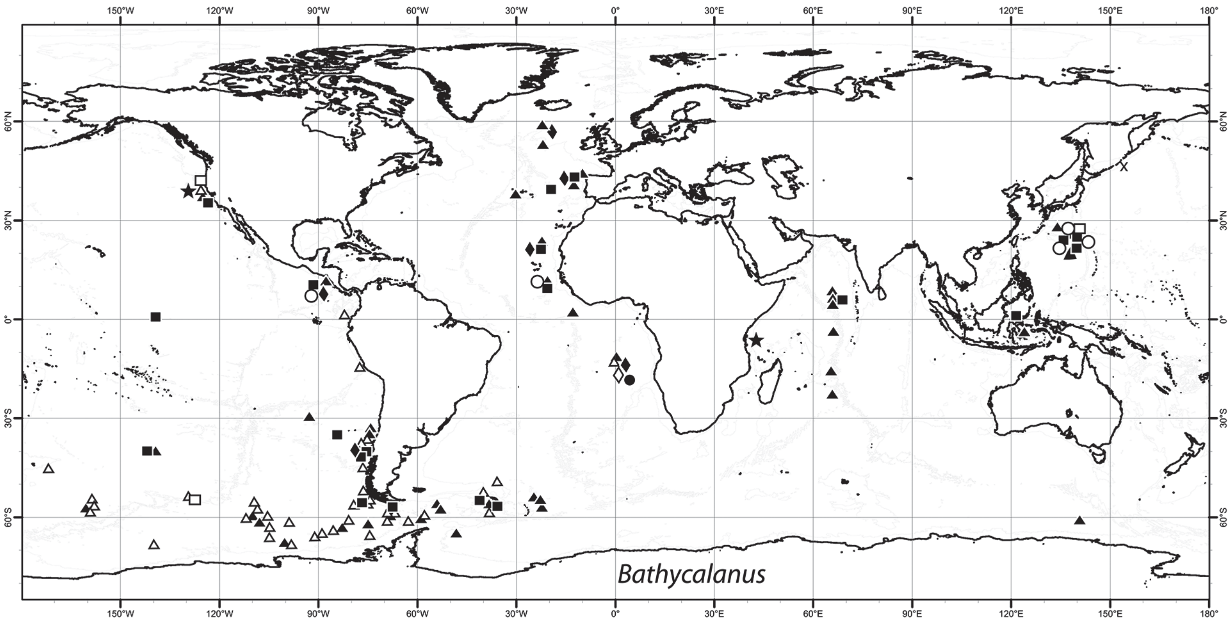

FIGURE 46. Distribution of *Bathycalanus* species: filled triangle = *Bathycalanus bradyi*; open triangle = *Ba. milleri* **n. sp.**; filled square = *Ba. richardi*; open square = *Ba. dentatus* **n. sp.**; open circle = *Ba. tumidus* **n. sp.**; open diamond = *Ba. adornatus* **n. sp.**; filled star = *Ba. pustulosus*; filled diamond = *Ba. unicornis*; filled circle = *Ba. bucklinae* **n. sp.**; cross = *Ba. eximius*.

Bathycalanus bradyi (Wolfenden, 1905)
(Figs 46–51)

Megacalanus bradyi Wolfenden, 1905a, p. 3, pl. I, figs 7–9.
Megacalanus princeps: Wolfenden, 1905b, p. 3, pl. I, figs 7–9.
Bathycalanus maximus Wolfenden, 1911, p. 189, pl. xxiii, figs 1–7, text-fig. 2a, b.
Bathycalanus bradyi: Sewell, 1947, pp 32–34, text-fig. 4.

Type locality. Apparently no type locality was identified. Originally taken in the mid Atlantic Ocean: "it is in abundance in the *Gauss* collections made in the Atlantic traverse" (Wolfenden 1905a). This is between the Cape Verde Islands, through the equatorial Atlantic to the South Atlantic at 36ºS and in the southern Indian Ocean near Kerguelen Islands (Wolfenden 1911, as *Ba. maximus*).

Material examined. ANTXIV/1, MOC10: Stn 2, 2000–3000 m, 1♀ (11.2 mm) Co375.1.2, 1CV Co376.1.1; Stn 3, 2992–3999 m, 1♀ (10.9 mm); Stn 3, 1957–2993 m, 1♂ (9.2 mm); Stn 3, 998–1957, 1♀ (11.2 mm); Stn 6, 1987–3886 m, 1♂ (9.2 mm). ANTXIV/1, MN, Stn 9, 0–940 m, 1♀ (11.0 mm). MV66-II, IKMT, Stn 5, 0–3889 mwo, 4♀ (11.5–12.8 mm), 1♂ (9.3 mm). Antipode IV, IKMT: Stn 53A, 0–2000 m, 2♀ (11.6, 11.9 mm); Stn 52D, 0–1900 m, 1♀ (12.0 mm); Stn 55D, 0–2000 m, 1♀ (11.7 mm), 1♂ (9.9 mm). Circe II, IKMT, Stn 15T-1, 0–2121 mwo, 1♀ (11.1), 1♂ (9.9 mm). Umitaka Maru, RMT-8D2, Stn 16, 1♀ (13.0 mm) Co411.1.1. University of Connecticutt, Stn 11, 1500–2000 m, Co441.3.1. Records from Natural History Museum, London: Discovery Stns, RMT8: 7709#44, 1250–1500 m, 11♀ (10.0, 10.0, 10.1, 10.3, 9.9, 10.2, 10.2, 9.9, 10.4, 10.1, 10.1 mm), BMNH 1993.1385-1394; 7709#91, 1520–2000 m, 1♂ (9.5 mm), BMNH 1993.792; 7711#39, 2000–1520 m, 6♂ (9.5, 9.5, 9.9, 9.4, 9.6, 9.7 mm) BMNH 1993.841-846; 7711#56, 1500–1250 m, 7♂ (9.7, 10.2, 9.9, 9.1, 10.0, 9.4, 9.4 mm) BMNH 1993.834-840; 7711#61, 1500–2000 m, 4♂ (8.9, 9.3, 8.9, 9.0 mm), BMNH 1993.815-818; 8507#72, 1250–1500 m, 1♂ (8.4 mm), BMNH 1993.874; 8508#76, 2000–2500 m, 5♀ (10.7, 10.6, 10.8, 11.6, 11.5 mm), BMNH 1993.847-851; 8508#76, 2000–2500 m, 1♂ (10.0 mm), BMNH 1993.791; 8508#78, 2500–3100 m, 3♂ (9.0, 9.1, 9.0 mm), BMNH 1994.824-826. 8509#15, 2000–2500 m, 6♀ (12.5, 11.8, 11.5, 9.8, 11.6, 9.7 mm), BMNH 1993.852-857; 8509#15, 2000–2500 m, 1♂ (10.0 mm), BMNH 1993.790; 8509#20, 3000–3500 m, 2♂ (10.1, 10.1 mm), BMNH 1993.807-808; 11261#8/9, 1♀ (9.2 mm), BMNH 1985.308. Additional records from Smithsonian Institution, USNM numbers: 232144, 232146, 262445–47, 262457, 269443–45, 269447–50, 269452, 269454–57, 269459, 299521, 299523, 302049, 302051, 302060, 302064, 302066, 302068, 302074, 1132629, 1132634.

Genetic material. Co375.1.2, Co411.1.1, Co376.1, Co441.3.1. GenBank numbers in Table 6.

Morphological description. Following description based on specimen from ANTXXIV/1, Stn 9, 0–940 m. As for genus with following specific level features.

Female (Fig. 47A–D). Total length 11.5 mm (mean = 10.93 mm, range = 9.9–13.0 mm, n = 35). Anterior head in dorsal view with rounded prominence extending into pair small anteriorly-directed divergent spine-like processes. Pedigerous somite 5 with symmetrical, short, rounded posterolateral corners extending one quarter of way along genital double-somite. Genital double-somite symmetrical in dorsal view, about as long as wide, with small anteroventral genital operculum, seminal receptacles not observed.

Antennule (Figs 47B, 48A–E) extending about 6 segments beyond caudal rami. Lengths of antennule segments (µm) as follows. Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements taken of ancestral segment I. I (318, 592); II–IV (345); V (242); VI (281); VII (340); VIII (352); IX (355); X–XI (665); XII (482); XIII (523); XIV (650); XV (809); XVI (927); XVII (939); XVIII (1044); XIX (1081); XX (1210); XXI (1257); XXII (878); XXIII (856); XXIV (890); XXV (844); XXVI (391); XXVII (736); XXVIII (40). Ancestral segments XII–XVII sometimes with surface thickenings but not always. Anterior and posterior borders of ancestral segments XVI–XXI smooth.

Antenna (Fig. 48F) exopod segment IV with short seta extending to distal border of segment VIII, lined with spinules.

Maxillule (Fig. 49C) praecoxal arthrite with 13 setae and spines, including only 2 setae on posterior surface; coxal endite without setae; basal endite 2 with 3 short setae; endopod segments with 2 (subequal), 2 (subequal), 6 setae (1 smaller one arising from posterior surface), respectively.

Maxilliped (Fig. 47G) syncoxal endite 4 with longest spinulose seta extending to distal border or beyond, of endopod segment 2; endopod segments 3–6 with 4 (3 very short), 3 (2 short), 3 (2 short) + 1 outer, 3 setae (1 short) + 1 outer seta, respectively.

Leg 1 (Fig. 47F) exopod with articulation between exopod segments 2 and 3 expressed, exopod segment 3 with 1 distal outer spine.

Legs 2–5 (Fig. 50A–E) exopod surfaces usually bearing small thickenings.

Male (Fig. 50F–J). Total length 9.0 and 9.5 mm (mean = 9.45 mm, range = 8.4–10.2 mm, n = 39). Anterior head in dorsal view with low rounded prominence extending into pair of small, slightly divergent, anteriorly-directed spine-like processes and parallel sided rostral filaments. Pedigerous somite 5 with short, rounded posterior lappets not extending as far as posterior border of urosomite I. Urosomal measurements made from lateral view, as in Fig. 1, are tabulated in Table 9. In lateral view urosomite II (UrII) not enlarged and swollen: UrII 1.54–1.80 (mean = 1.64, S.D. = 0.10, n = 5) times longer than UrIII and not constricted anteriorly such that ratio $UrII_{ant}$ / $UrII_{mx}$ = 0.79–0.85 (mean = 0.82, S.D. = 0.02, n = 5).

Antennules (Fig. 51A–D) not well known as specimens damaged. Left antennule illustrated by Wolfenden (1911) as *Ba. maximus* reaches beyond caudal rami when extended. Some parts of right antennule (similar to those of *Ba. richardi*) were present in specimen from Circe II but this specimen was atypical in that it did not have thickenings on leg exopods.

Antenna, mandible, maxillule, maxilla, maxilliped and legs 1–4 similar to those of female.

Leg 5 (Fig. 51F–H) basis with long setules on inner distal border. Exopod segments 1–3 with thickenings on outer cuticle. Left exopod segment 2 specialised seta with long lash extending almost to distal border of endopod segment 3, basal part rectangular in shape with outer distal spine. Left exopod segment 3 with inner spine inserted opposite first outer border spine, inner border of segments proximal to inner spine entirely lined with long setules. Right exopod segment 3 with inner spine inserted just proximal to level of insertion of first outer spine, inner border mostly naked apart from short region of setules proximally.

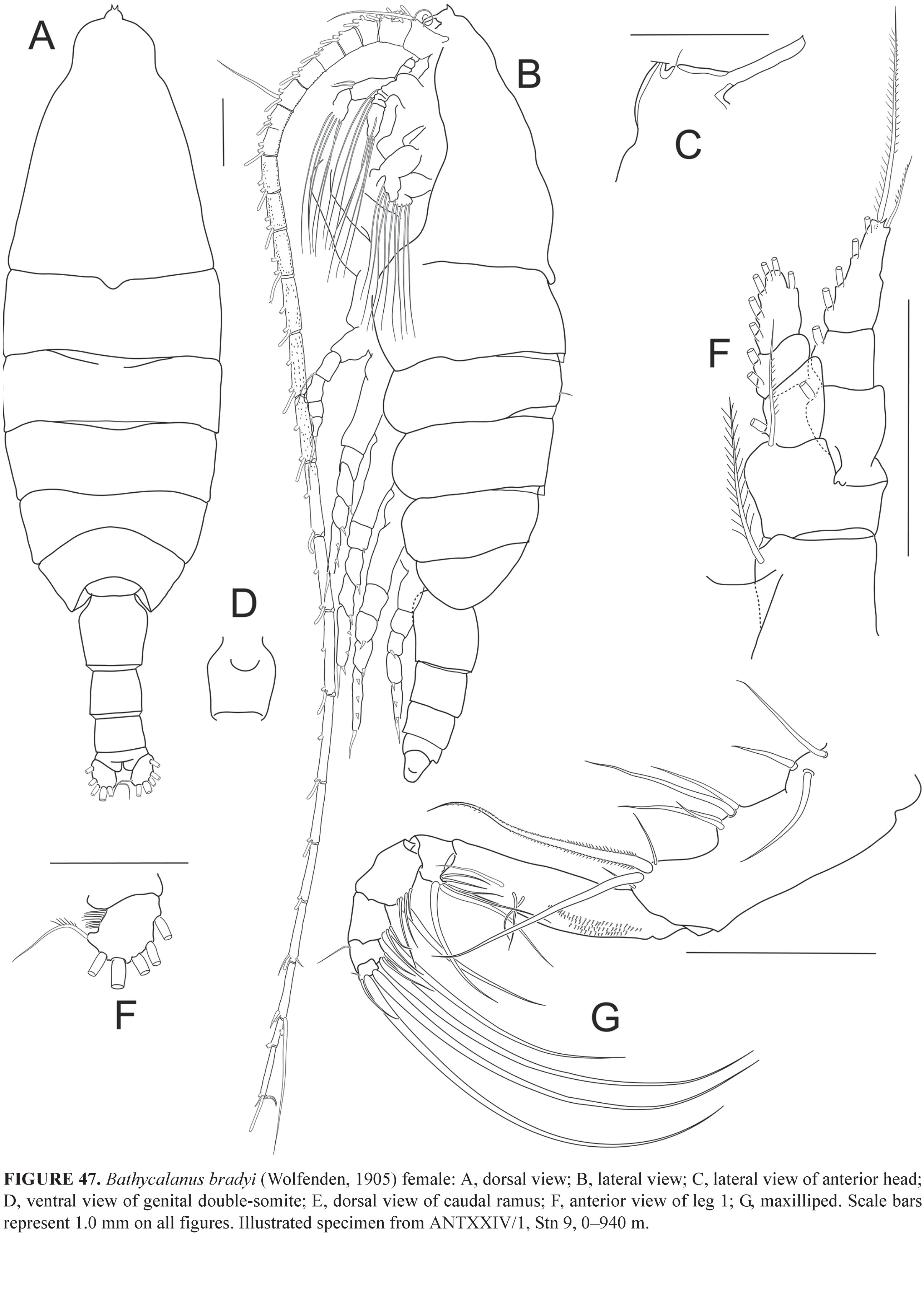

FIGURE 47. *Bathycalanus bradyi* (Wolfenden, 1905) female: A, dorsal view; B, lateral view; C, lateral view of anterior head; D, ventral view of genital double-somite; E, dorsal view of caudal ramus; F, anterior view of leg 1; G, maxilliped. Scale bars represent 1.0 mm on all figures. Illustrated specimen from ANTXXIV/1, Stn 9, 0–940 m.

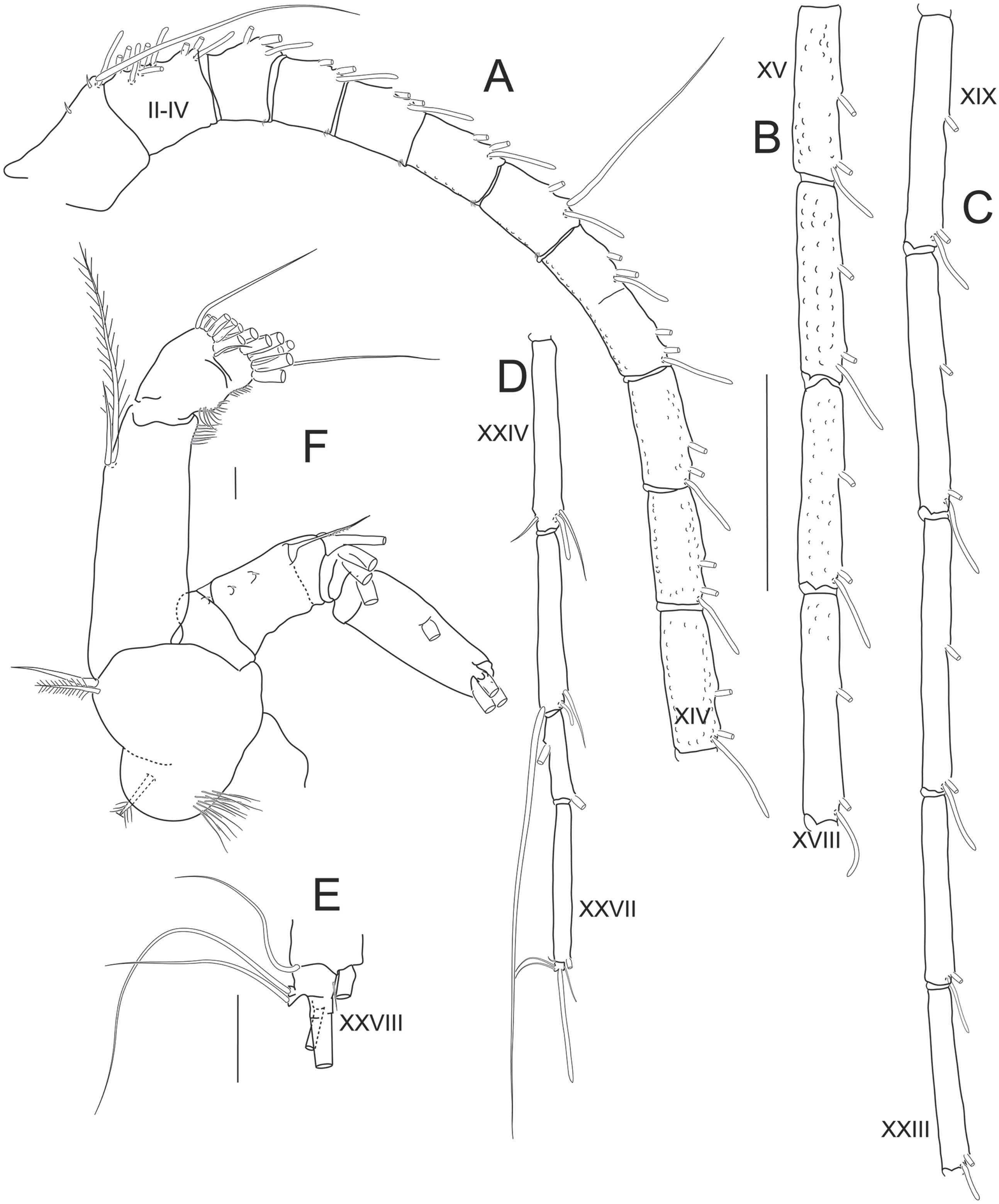

FIGURE 48. *Bathycalanus bradyi* (Wolfenden, 1905) female antennule ancestral segments: A, segments I–XIV; B, segments XV–XVIII; C, segments XIX–XXIII; D, segments XXIV–XXVIII; E, detail of segment XXVIII. Mouthpart: F, antenna. Scar bars represent 0.1 mm on figures A–D; 0.1 mm for remaining figures. Illustrated specimen from ANTXXIV/1, Stn 9, 0–940 m.

Remarks. Farran (1939, p. 357) points out that the specimens that Wolfenden (1905a) named *Megacalanus bradyi* Wolfenden, 1905 stand as a valid description of a species, clearly a *Bathycalanus*, that differs from *Ba. richardi* in having a 3-segmented leg 1 exopod. In 1911, Wolfenden described *Bathycalanus maximus* Wolfenden, 1911, clearly the same species as the specimens recorded here. Wolfenden's (1911) figure of the maxillae (pl. 23, fig. 4) and male left leg 5 (pl. 23, fig, 6) agree with the present specimens. Also the urosome of the male, illustrated on pl. 23, fig. 1, has similar proportions to the males described here in that they do not have the elongate, anteriorly constricted, swollen urosomite II typical of *Ba. richardi*. Wolfenden (1911) however does not mention the distinctive thickenings usually present on the female antennule segments XII–XVII or legs.

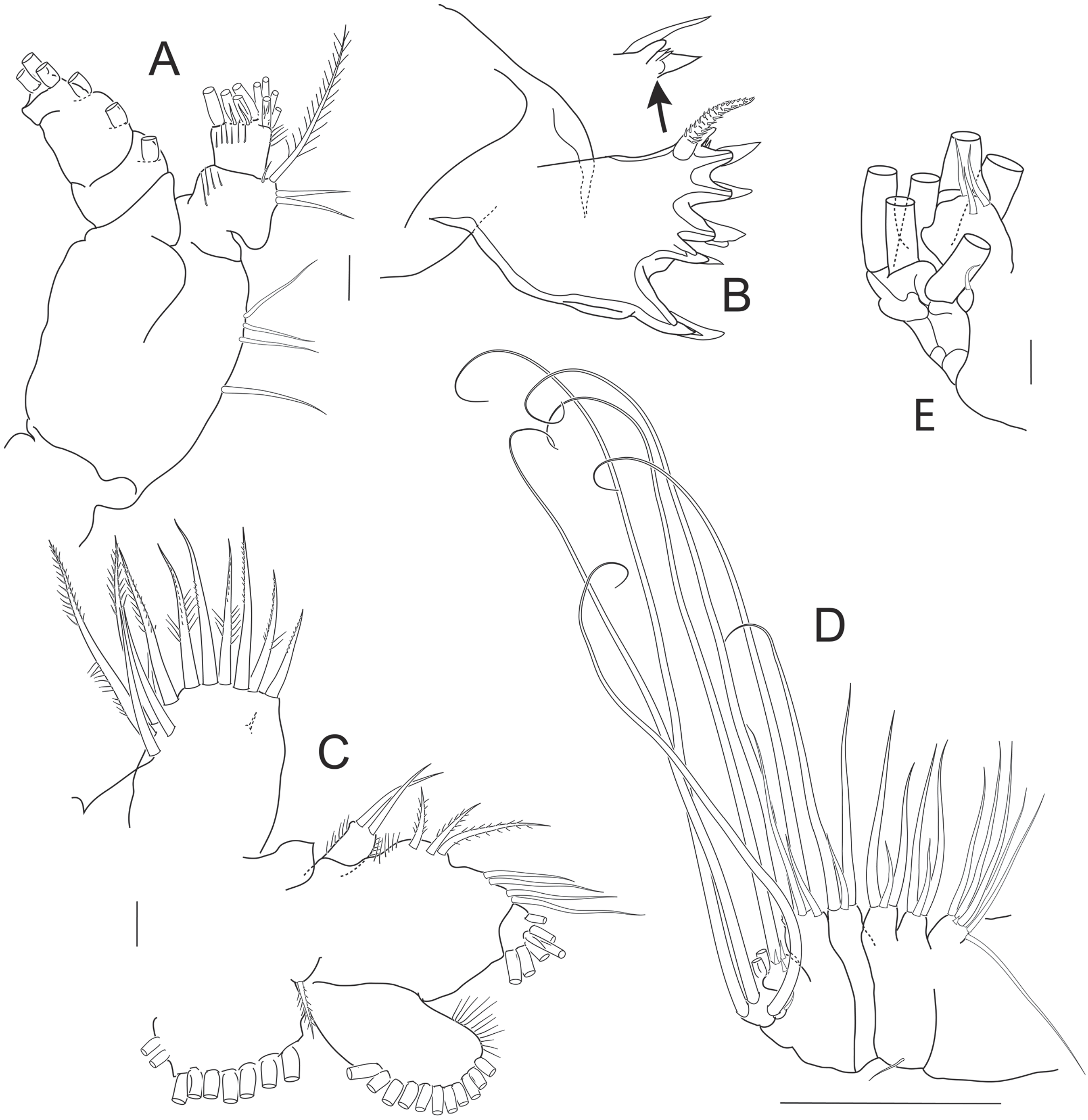

FIGURE 49. *Bathycalanus bradyi* (Wolfenden, 1905) female: A, mandibular palp; B, mandibular gnathobase; C, maxillule; D, maxilla; E, detail of inner view of endopod of maxilla. Scar bars represent 0.1 mm on figure D; 0.1 mm on remaining figures. Illustrated specimen from ANTXXIV/1, Stn 9, 0–940 m.

We note that what we are calling *Ba. bradyi* may be a complex of more than one species. Not only is there morphological variation but the molecular data are also ambiguous (see Tables 14–17, Fig. 113). The molecular data suggest a couple of clades may exist in the *Ba. bradyi* data and one specimen of the newly described morphological species (*Ba. adornatus* **n. sp.**) also groups with one of these clades. These observations suggest that the gene regions employed in this study are not sufficient to distinguish species unambiguously in *Bathycalanus.*

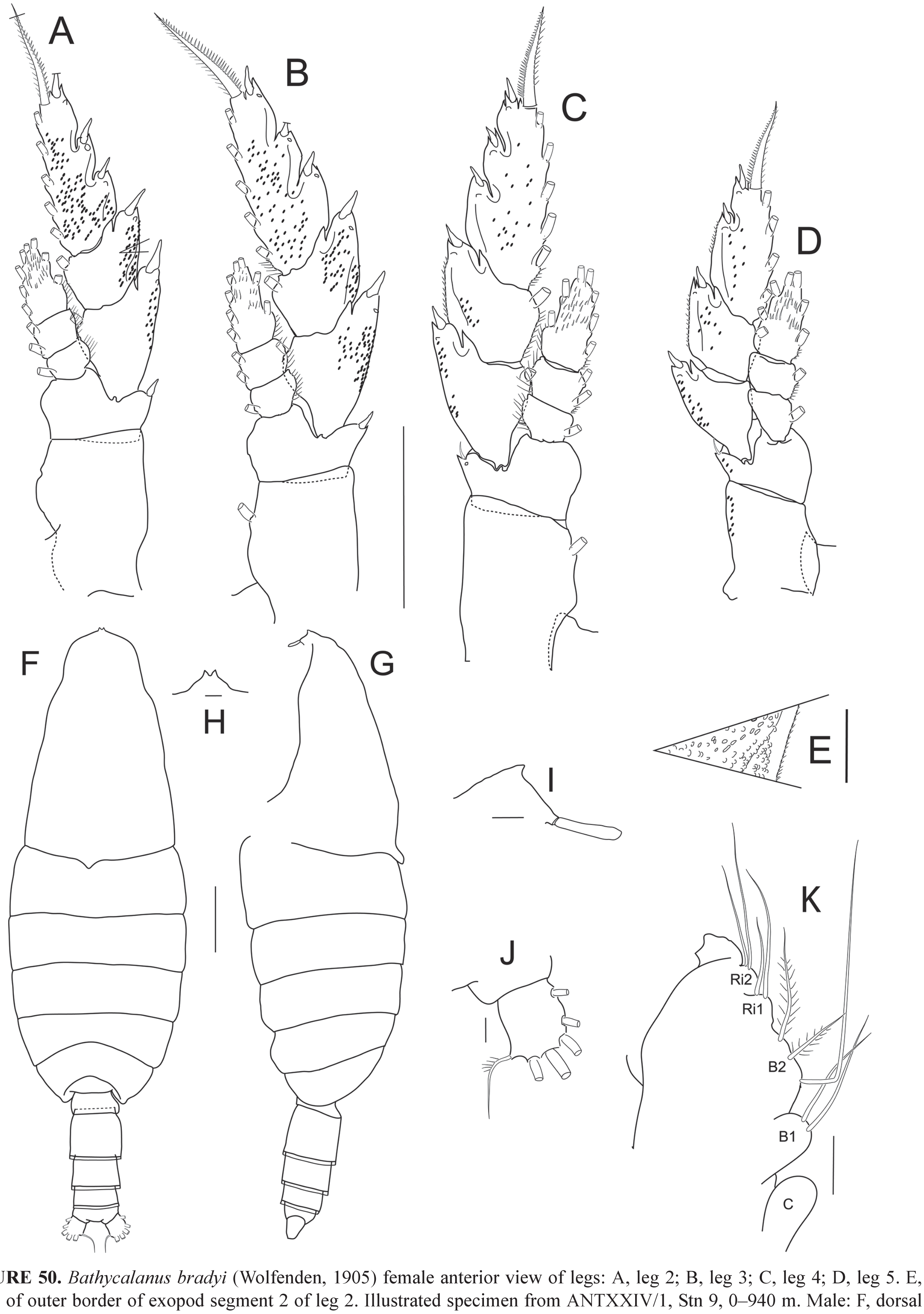

FIGURE 50. *Bathycalanus bradyi* (Wolfenden, 1905) female anterior view of legs: A, leg 2; B, leg 3; C, leg 4; D, leg 5. E, detail of outer border of exopod segment 2 of leg 2. Illustrated specimen from ANTXXIV/1, Stn 9, 0–940 m. Male: F, dorsal view; G, lateral view; H, dorsal view of anterior head; I, lateral view of anterior head; J, dorsal view of caudal ramus; K, coxal endite (C), basal endites 1 and 2 (B1, 2), endopod segments 1 and 2 (Ri1, 2) of maxillule. Illustrated specimen from Antipode IV, Stn 55D. Scale bar represents 1.0 mm on figures A–D, F, G; 0.1 mm on remaining figures.

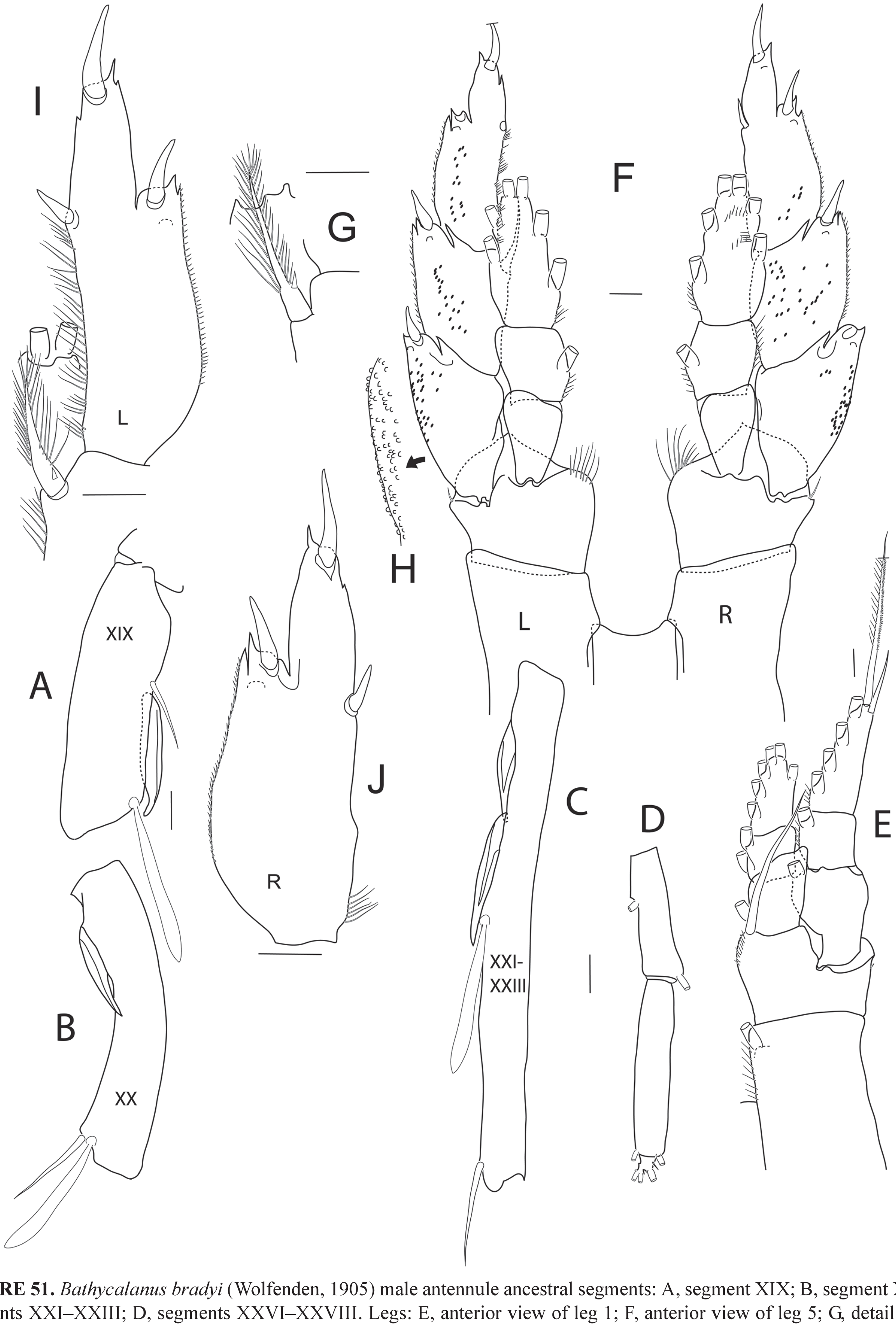

FIGURE 51. *Bathycalanus bradyi* (Wolfenden, 1905) male antennule ancestral segments: A, segment XIX; B, segment XX; C, segments XXI–XXIII; D, segments XXVI–XXVIII. Legs: E, anterior view of leg 1; F, anterior view of leg 5; G, detail of left inner distal corner of exopod segment 2; H, detail of outer border of exopod segment 1; I, left exopod segment 3 of leg 5 from another specimen; J, detail of right exopod segment 3 of leg 5 from another specimen. Scale bar represents 0.1 mm on all figures. Illustrated specimens from Circe II, Stn 15T-1 (A–D), from Antipode IV, Stn 55D (E–H); ANTXXIV/1, Stn 6, 1987–3886 m (I, J).

TABLE 10. Comparison of key differences among female *Bathycalanus* species. A1 = antennule; B2 = basal endite 2; C = coxal endite; Gns = Genital double-somite; Mx1 = maxillule; no. = number; Pa = praecoxal arthrite; Pd5 = pedigerous somite 5; P1 = leg 1; Re2–3 = exopod segments 2–3; seg(s) = segment(s).

Species	Anterior head spine-like processes	Gns widest part in dorsal view	Pd5 symmetry	Pd5 shape, lateral view	A1 segs XV–XX anterior border	A1 seg XVI posterior border	Mx1 Pa posterior setae	Mx1 C, no. of setae	Mx1 B2 setae	P1 Re 2–3: fusion
Ba. richardi	2	Anterior 1/3rd	Symmetrical	Bluntly rounded	Smooth	Smooth	2	0	3	**Fused**
Ba. bradyi	2	Anterior 1/3rd	Symmetrical	Bluntly rounded	Smooth	Smooth	2	0	3	Separate
Ba. dentatus n. sp.	2	Anterior 1/3rd	Symmetrical	Bluntly rounded	**Toothed**	Smooth	2	0	2	Separate
Ba. milleri n. sp.	2	Anterior 1/3rd	Symmetrical	Bluntly rounded	**Toothed**	**Toothed**	2	0	2	Separate
Ba. tumidus n. sp.	2	**Midlength**	Symmetrical	Bluntly rounded	Smooth	Smooth	**4**	**1**	4	Separate
Ba. adornatus n. sp.	2	Anterior 1/3rd	Symmetrical?	**Extended into irregular-shaped lappets**	Smooth	Smooth	2	0	3	Separate
Ba. pustulosus n. sp.	2	**Midlength**	**Asymmetrical**	**Rounded lappet on right, rectangular on left**	?	?	2	**1**	2	Separate
Ba. bucklinae n. sp.	2	Anterior 1/3rd	**Asymmetrical**	**Irregularly-shaped lappets**	Smooth	Smooth	2	0	4	Separate
Ba. unicornis	**1**	**Anterior 1/8th**	Symmetrical	Bluntly rounded	Smooth	Smooth	**3**	0	4	Separate
Ba. eximius	2	**Midlength**	Symmetrical	Bluntly rounded	Smooth	Smooth	**3**	0	4/5	Separate

TABLE 11. Comparison of key differences among *Elenacalanus* species. A2 = antenna; B = basis; B2 = basal endite 2; Be = basal exite; Ce = coxal epipodite; Mn = mandible; Mx1 = maxillule; Mxp = maxilliped; P5 = leg 5; no. = number; Pa = praecoxal arthrite; Re2, 3 = exopod segments 2, 3; ReIV = ancestral exopod segment IV; Ri 6 = endopod segment 6.

Species	Head crest	Rostral filaments directed	♀ A2 ReIV seta	♀ Mn B: no. of setae	♀ Mx1 B2 no. of setae	♀ Mx1 Pa posterior: no. setae	♀ Mx1 Ce proximal seta	♀ Mx1 Be seta	♀ Mxp Ri6: no. of seta	♂ P5 right Re3 inner border	♂ P5 left specialised seta of Re2
E. princeps	**Yes**	Ventrally	**Absent**	4	1–2	2	**Absent**	Absent	**3**	**Proximal tuft of setules**	Wide basal part + long inner lash
E. eltaninae	No	Ventrally	Present	4	**2–3**	2	Present	Absent	4	Naked	Wide basal part + long inner lash
E. tageae n. sp.	No	Ventrally	Present	4	2	2	Present	**Present–vestigial**	4	Naked	**Basal part + 2 equal short lashes**
E. sverdrupi	No	**Antero-ventrally**	Present	**3?**	**1**	**3**	Present	Absent	**2?**	♂ unknown	♂ unknown
E. inflatus	No	Ventrally	**Absent**	4	2	2	Present	Absent	4	♂ unknown	♂ unknown

Morphological variation. Two males from Circe II, and Antipode IV, 55D differ slightly from the two males described above. The proportions of urosomites measured in lateral view are slightly different: UrII 1.62, 1.80 times longer than UrIII (Table 9). The male legs do not have thickenings on the surface of the exopod segments, the proximal inner border of right leg 5 exopod segment 3 is naked in one specimen and has a tuft of proximal setules in the other, but the left leg 5 exopod segment 2 inner setulose seta has an outer distal spinule on the basal part in one specimen (in the other from Circe II exopod segments 2 and 3 are missing). Most of the specimens identified as *Ba. bradyi* in the collection of the Smithsonian Institution also did not have thickenings on the antennules and legs of females. Both types of specimens (with and without thickenings) are here assigned to *Bathycalanus bradyi* in this work awaiting genetic information that evaluates this conclusion.

Distribution. *Bathycalanus bradyi* is a bathypelagic species that has been taken from about 900 m to > 3000 m and was taken between 2000–3000 m, above the Cape Verde Abyssal Plain during ANTXIV/I. It is distributed in all oceans (Fig. 46, Table 1): the North and South Atlantic as far south as 65ºS (Wolfenden 1911, present data), in the Pacific Ocean (present data), Indian Ocean at 65ºS (Vervoort 1957), and the Gulf of Oman (Sewell 1947).

Species comparisons. Among female *Bathycalanus* that have two small anterior spine-like processes on the anterior head and bluntly rounded posterolateral corners of pedigerous somite 5 (*Ba. richardi, Ba. bradyi, Ba. dentatus* **n. sp.**, *Ba. milleri* **n. sp.**, *Ba. tumidus* **n. sp.**), *Ba. bradyi* may be distinguished by the following combination of character states (see Table 10): 1) leg 1 exopod segments 2 and 3 separate; 2) the female genital-double-somite in dorsal view is widest at the anterior one third; 3) the basal endite 2 of the maxillule has 3 setae; 4) surfaces of legs 2–5 exopods usually, but not always, bearing small thickenings; and 5) female antennular segments XVI–XXI anterior border smooth.

Known males that have two small anterior spine-like processes on the anterior head (*Ba. richardi, Ba. bradyi, Ba. dentatus* **n. sp.**, *Ba. milleri* **n. sp.**) may be distinguished partly by the proportions of the urosomites. Only one specimen of *Ba. dentatus* **n. sp.** was available so could not be included in a statistical comparison, whereas there were four or five specimens of the remaining species. Therefore, only three species can be compared statistically below.

Male *Ba. bradyi* may be distinguished from male *Ba. richardi* as follows: 1) segment XX curved and with smaller radius of curvature in *Ba. bradyi* than in *Ba. richardi*; 2) two fused elements on segments XXI–XXIII overlap very slightly in *Ba. bradyi* whereas in *Ba. richardi* the proximal element overlaps the distal element by about ¼ of length of distal element; 3) surfaces of leg 5 exopod segments usually, but not always, bearing small thickenings; 4) the length proportions of the male urosomites UrII/UrIII of *Ba. bradyi* are significantly different from those of *Ba. richardi* (P = 0.006) but not *Ba. milleri* **n. sp.** (P = 0.428) (Table 9) and 4) in lateral view, the ratio of anterior/posterior depth of UrII of *Ba. bradyi* is significantly different from that of *Ba. richardi* (P = 0.014) but not *Ba. milleri* **n. sp.** (P = 0.342).

Bathycalanus dentatus n. sp.
(Figs 46, 52–59)

Type locality. 38.033º N, 124.183 W.

Material examined. MV66-II, IKMT, Stn 5, 0–3889 mwo, 1♀ (13.4 mm, holotype), 1♂ (11.8 mm, paratype). Antipode IV, Stn 52D, IKMT, 0–1900 m, 5♀ (11.4–13.1 mm), 2CV (9.9, 10.2 mm).

Type specimens. Deposited in the Scripps Institution of Oceanography collection: Holotype female: PIC-140409-0007-HT; Paratype male: PIC-140409-0008-PT; Paratype lot of 4 females and 2 CV: PIC-140409-0009-PT.

Morphological description. Following description based on holotype specimen from MV66-11, Stn 5. As for genus with following specific level features.

Female (Fig. 52A–D). Total length 13.4 mm (mean = 12.1 mm, range = 11.1–13.4 mm, n = 5). In lateral view anterior head with curved hump just posterior to rostral projection, anterior head in dorsal view produced into distinct rounded projection bearing pair of very small rounded processes. Pedigerous somite 5 with short, rounded posterior lappets, extending one quarter of way along genital double-somite. Genital double-somite with slight anterolateral bulge in dorsal view at anterior one third, length about 1.1 times maximum width.

Antennule (Figs 52B, 53) extending 5–6 segments beyond caudal rami. Lengths of antennule segments (µm) as follows. Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements taken of ancestral segment I. I (305, 700); II–IV (457); V (265); VI (295); VII (346); VIII (359); IX (364); X–XI (791); XII (540); XIII (558); XIV (683); XV (855); XVI (934); XVII (1054); XVIII (1125); XIX (1160); XX (1182); XXI (1224); XXII (835); XXIII (813); XXIV (779); XXV (668); XXVI (415); XXVII (-); XXVIII (-). Distoanterior and borders of segments XVI–XXI with about 6, 13, 13, 13, 7 (some may be broken off), 13 unevenly spaced teeth, respectively, lining slight excavation just distal to seta; all teeth slightly on ventral surface; posterior borders of these segments smooth.

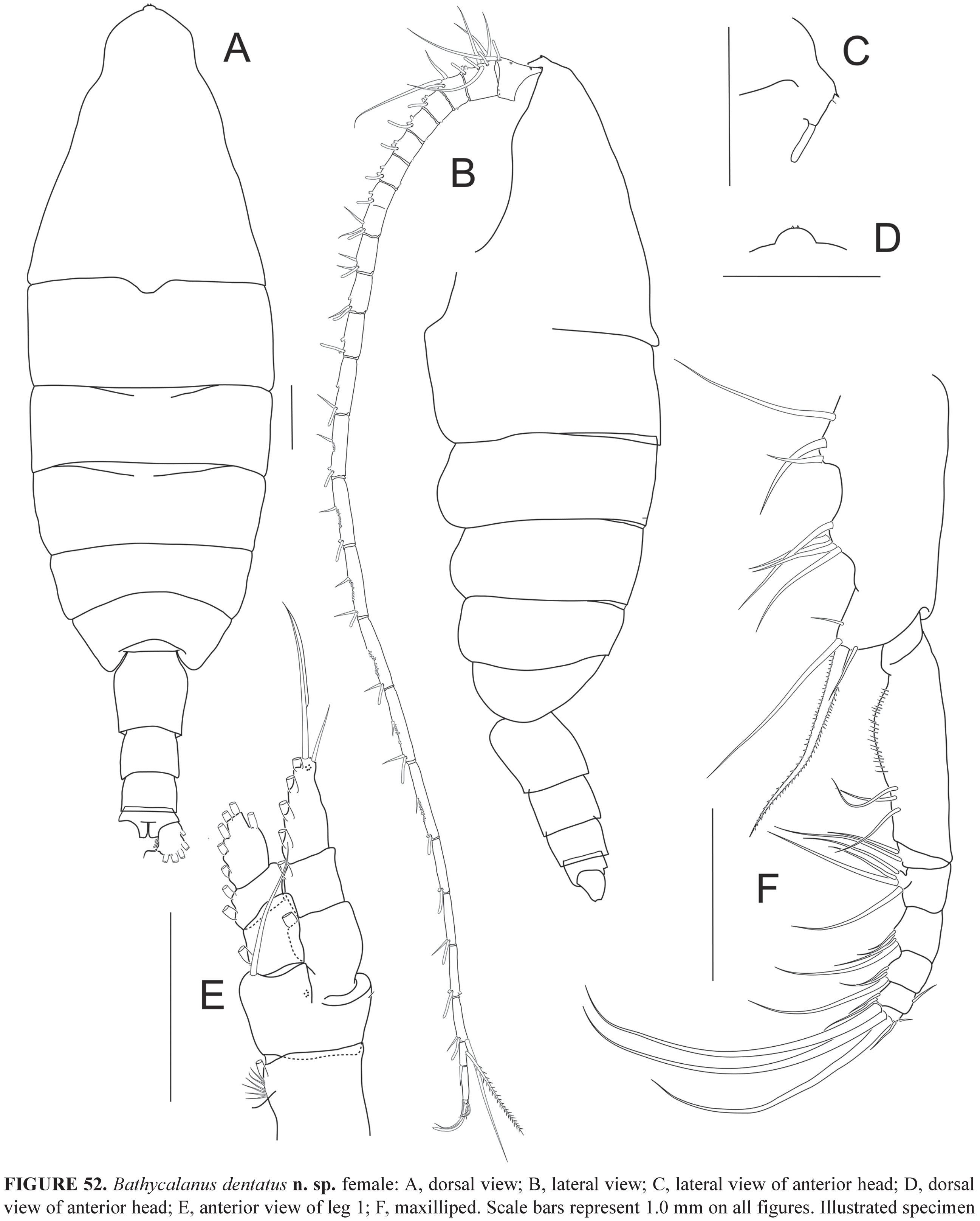

FIGURE 52. *Bathycalanus dentatus* **n. sp.** female: A, dorsal view; B, lateral view; C, lateral view of anterior head; D, dorsal view of anterior head; E, anterior view of leg 1; F, maxilliped. Scale bars represent 1.0 mm on all figures. Illustrated specimen from MV66-11, Stn 5.

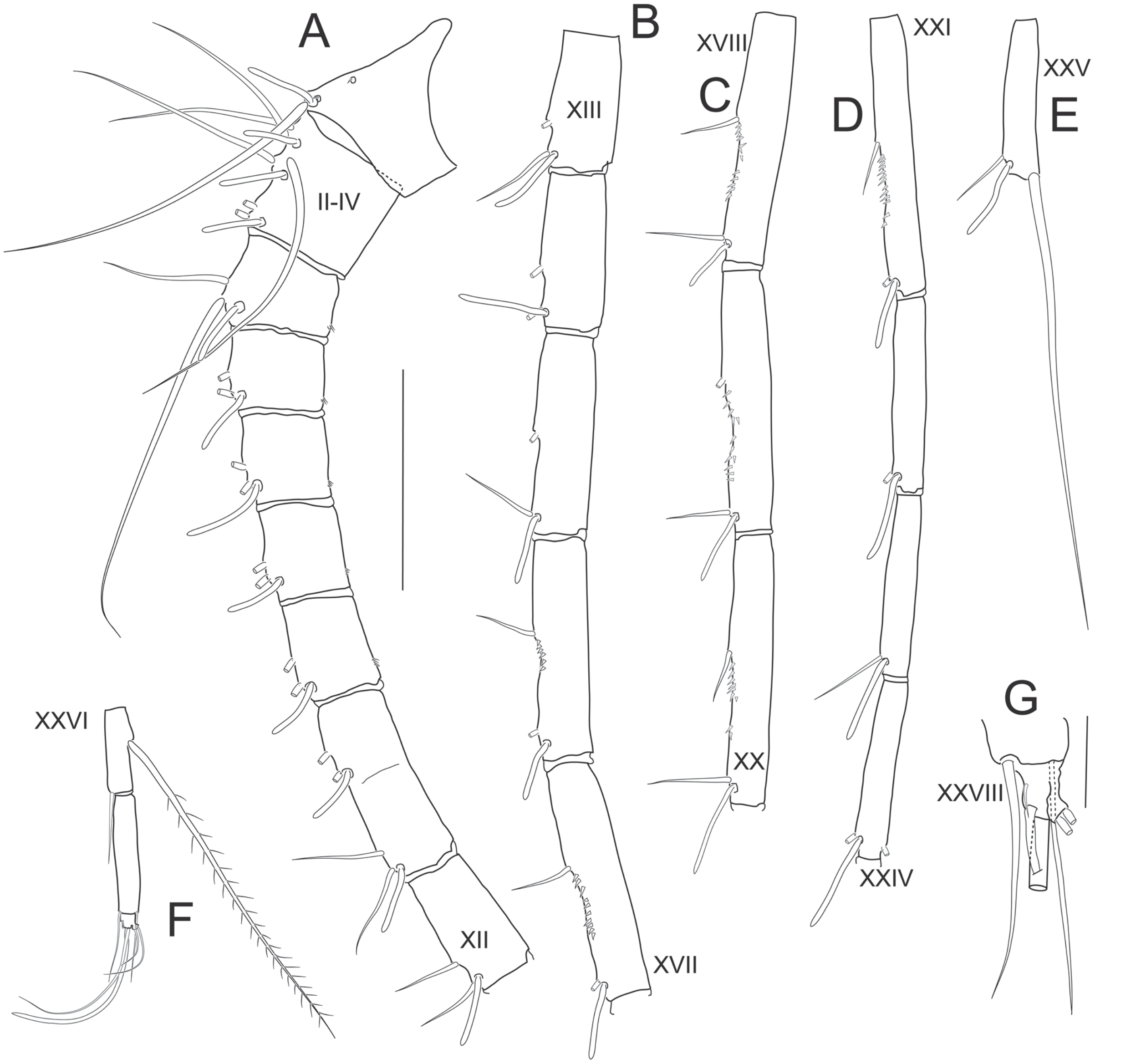

FIGURE 53. *Bathycalanus dentatus* **n. sp.** female antennule ancestral segments: A, segments I–XII; B, segments XIII–XVII; C, segments XVIII–XX; D, segments XXI–XXIV; E, segment XXV; F, segments XXVI–XXVIII; G, detail of segment XXVIII. Scale bars represent 1.0 mm on figures A–F; 0.1 mm on remaining figure. Illustrated specimen from MV66-11, Stn 5.

Antenna (Fig. 54A, B) exopod segment IV with short seta extending slightly beyond distal border of segment VIII, lined with spinules.

Maxillule (Fig. 54E) praecoxal arthrite with 13 setae and spines, including 2 setae on posterior surface, 1 distoanterior seta small; coxal endite without setae; basal endite 2 with 2 short setae; endopod segments with 2 (subequal), 2 (subequal), 6 setae (including 1 smaller seta arising from posterior surface), respectively.

Maxilliped (Fig. 52F) syncoxal endite 4 with longest spinulose seta extending to distal border of endopod segment 1.

Leg 1 (Fig. 52E) exopod with articulation between exopod segments 2 and 3 well developed. Maculae cribrosae present on anterior surfaces of basis and exopod segments 1–3 of legs 2–4 (Fig. 55) and basis and exopod segment 3 of leg 1.

Male (Fig. 56A, B). Total length 11.8 mm. Pedigerous somite 5 with short rounded lappets not reaching posterior border of urosomite I. Urosome measurements made from lateral view, as in Fig. 1 and tabulated in Table 9. Urosomite II 1.58 times longer than urosomite III and in lateral view and not constricted anteriorly such that ratio $UrII_{ant}$ / $UrII_{mx}$ = 0.73.

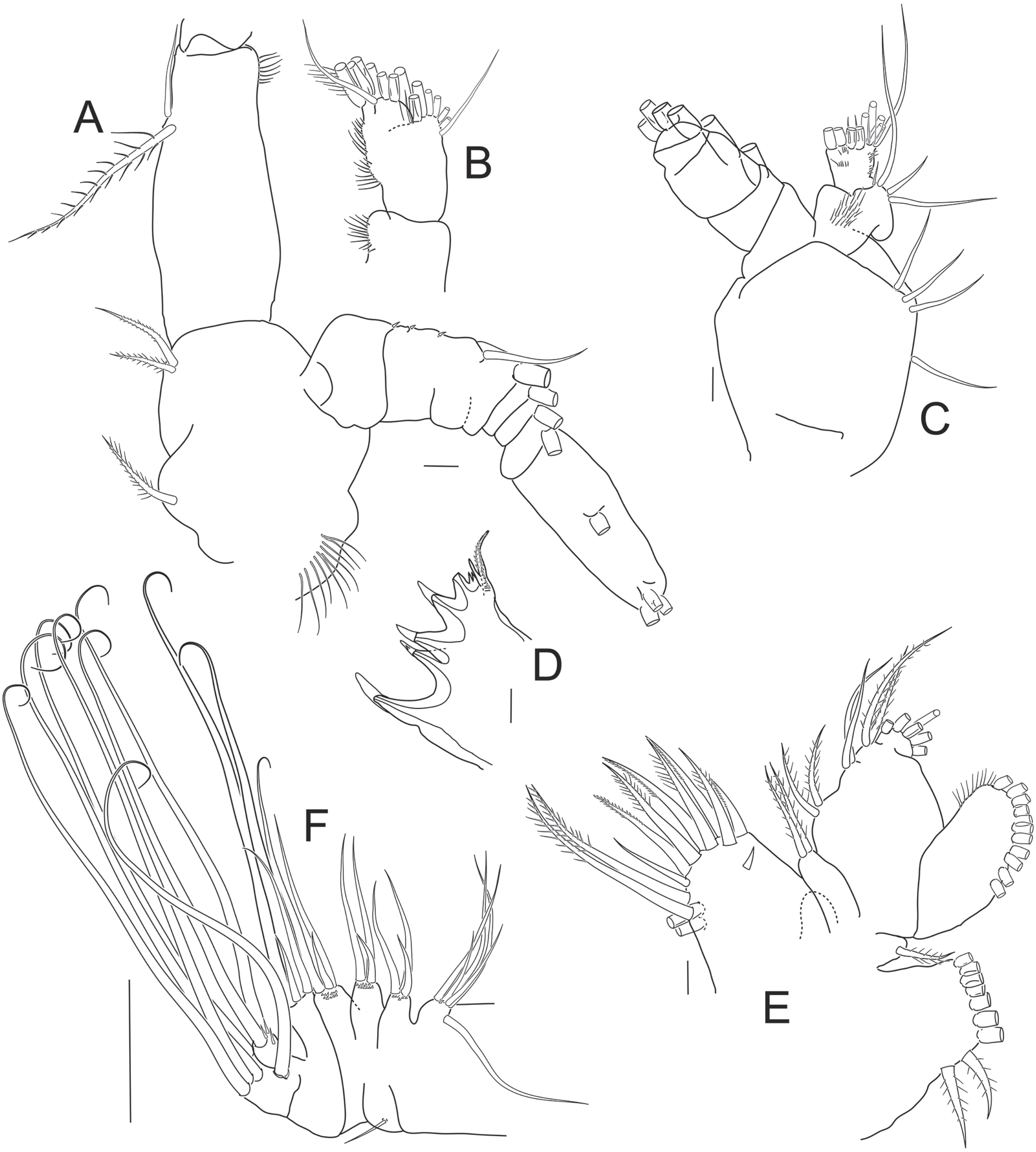

FIGURE 54. *Bathycalanus dentatus* **n. sp.** female: A, antenna minus terminal endopod segment; B, terminal endopod segment of antenna; C, mandibular palp; D, mandibular gnathobase; E, maxillule; F, maxilla. Scale bars represent 1.0 mm on figure F; 0.1 mm on remaining figures. Illustrated specimen from MV66-11, Stn 5.

Antennule (Figs 56B, 57, 58) right gripping elements around geniculation very similar to those of *Ba. richardi*.

Leg 5 (Fig. 59C–E) left exopod segment 2 specialised seta with long lash extending well beyond distal border of endopod segment 3 and densely covered in long setules, basal part elongate; inner border of right exopod segment 3 lined with patches of setules, proximal part of border naked.

Remarks. *Bathycalanus dentatus* **n. sp.** is one of a group of species that are closely related to *Ba. richardi* and *Ba. bradyi* in that it also has a pair of small spine-like processes on the anterior head. Females of this species have possibly been identified as *Ba. bradyi* in the past. The male has been assigned, here, to *Ba. dentatus* **n. sp.** mainly on the basis of its large size and the fact that it had only 2 setae on the second basal endite of the maxillule. Nevertheless, a final conclusion probably has to await genetic analysis because the left antennule does not carry the teeth characteristic of the female.

Morphological variation. Only one male is known. Females have variable numbers of teeth on the antennules although the teeth seem to be easily dislodged.

Distribution. *Bathycalanus dentatus* **n. sp.** is an upper abyssopelagic species taken in hauls 0–1900 and 0–3889 m. It is known from the type locality in north eastern Pacific, south of Japan, south eastern Pacific and off California (Fig. 46, Table 1).

Species comparisons. Among *Bathycalanus* that have two small anterior spine-like processes on the anterior head and bluntly rounded posterolateral corners of pedigerous somite 5 (*Ba. richardi Ba. bradyi, Ba. dentatus* **n. sp.**, *Ba. milleri* **n. sp.**, *Ba tumidus* **n. sp.**) *Ba. dentatus* **n. sp.** is distinguished by the following combination of character states (Table 10): 1) the basal endite 2 of the maxillule has 2 setae; 2) leg 1 exopod segments 2 and 3 separate in both sexes; 3) the female antennular segments XVI–XXI each have their distoanterior borders lined with unevenly-spaced teeth located in a slight excavation; 4) posterior border on antennule segment XVI smooth; 5) the male leg 5 left exopod segment 2 inner distal setulose seta is very long, extending well beyond the distal border of endopod segment 3 and the basal part is elongate; 6) male leg 5 inner border of right exopod segment 3 is bordered by tufts of setules.

Etymology. The specific name refers to the teeth found on the anterior border of some antennule segments in the female.

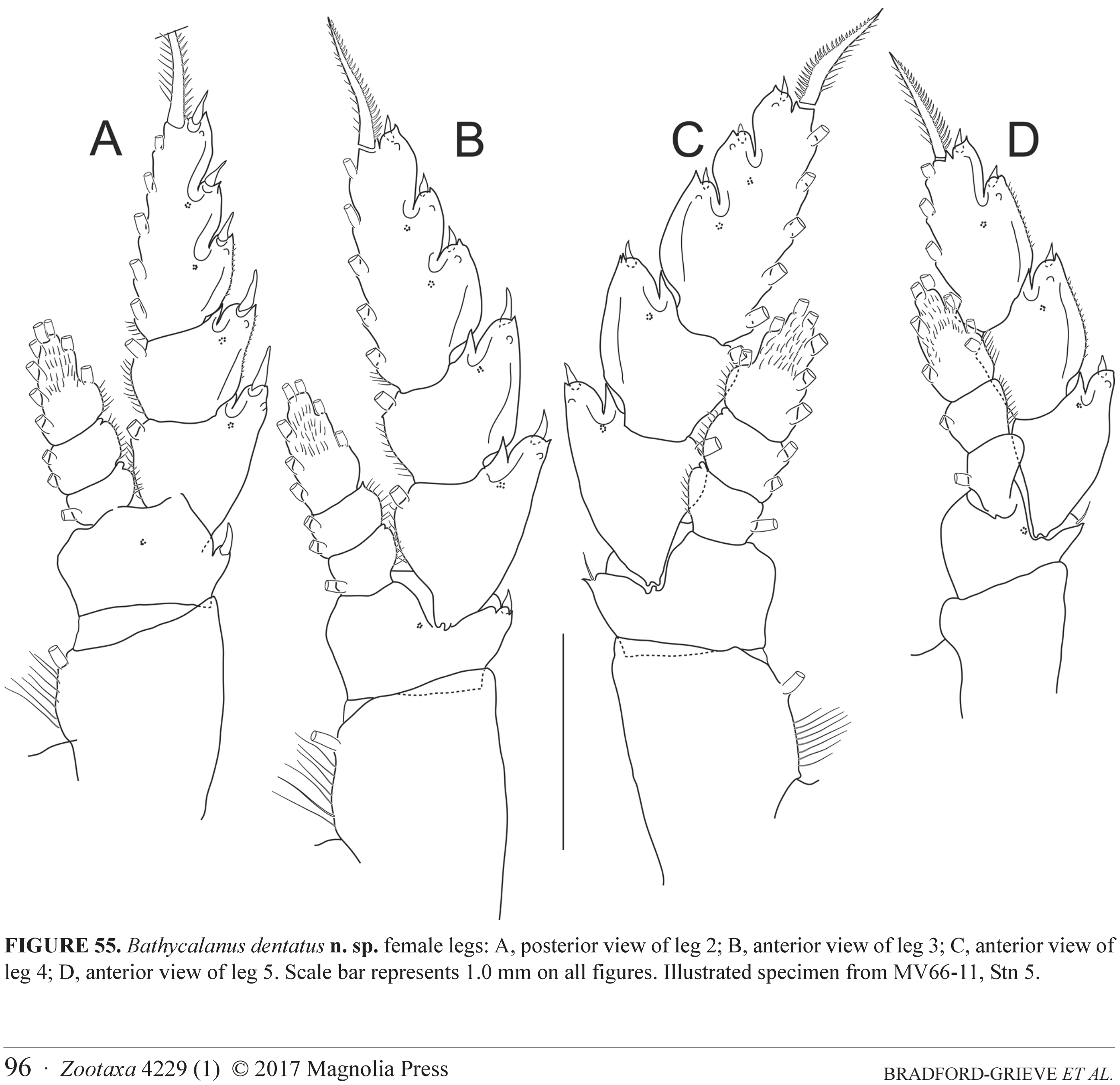

FIGURE 55. *Bathycalanus dentatus* **n. sp.** female legs: A, posterior view of leg 2; B, anterior view of leg 3; C, anterior view of leg 4; D, anterior view of leg 5. Scale bar represents 1.0 mm on all figures. Illustrated specimen from MV66-11, Stn 5.

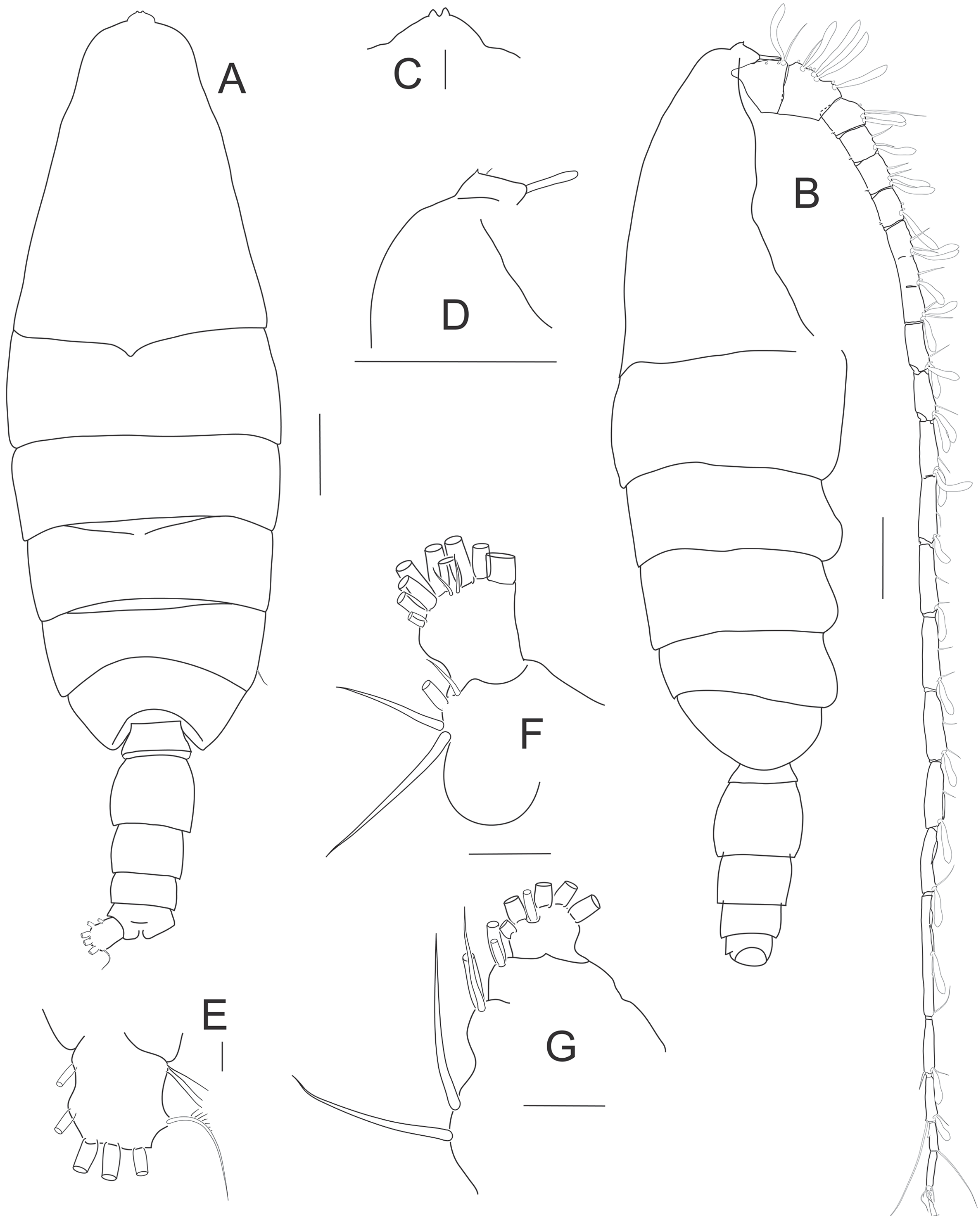

FIGURE 56. *Bathycalanus dentatus* **n. sp.** male: A, dorsal view; B, lateral view; C, dorsal view of anterior head; D, lateral view of anterior head; E, dorsal view of caudal ramus; F, endopod of mandible; G, basal endite 2 and endopod of maxillule. Scale bar represents 1.0 mm on figures A, B, D; 0.1 mm on remaining figures. Illustrated specimen from MV66-11, Stn 5.

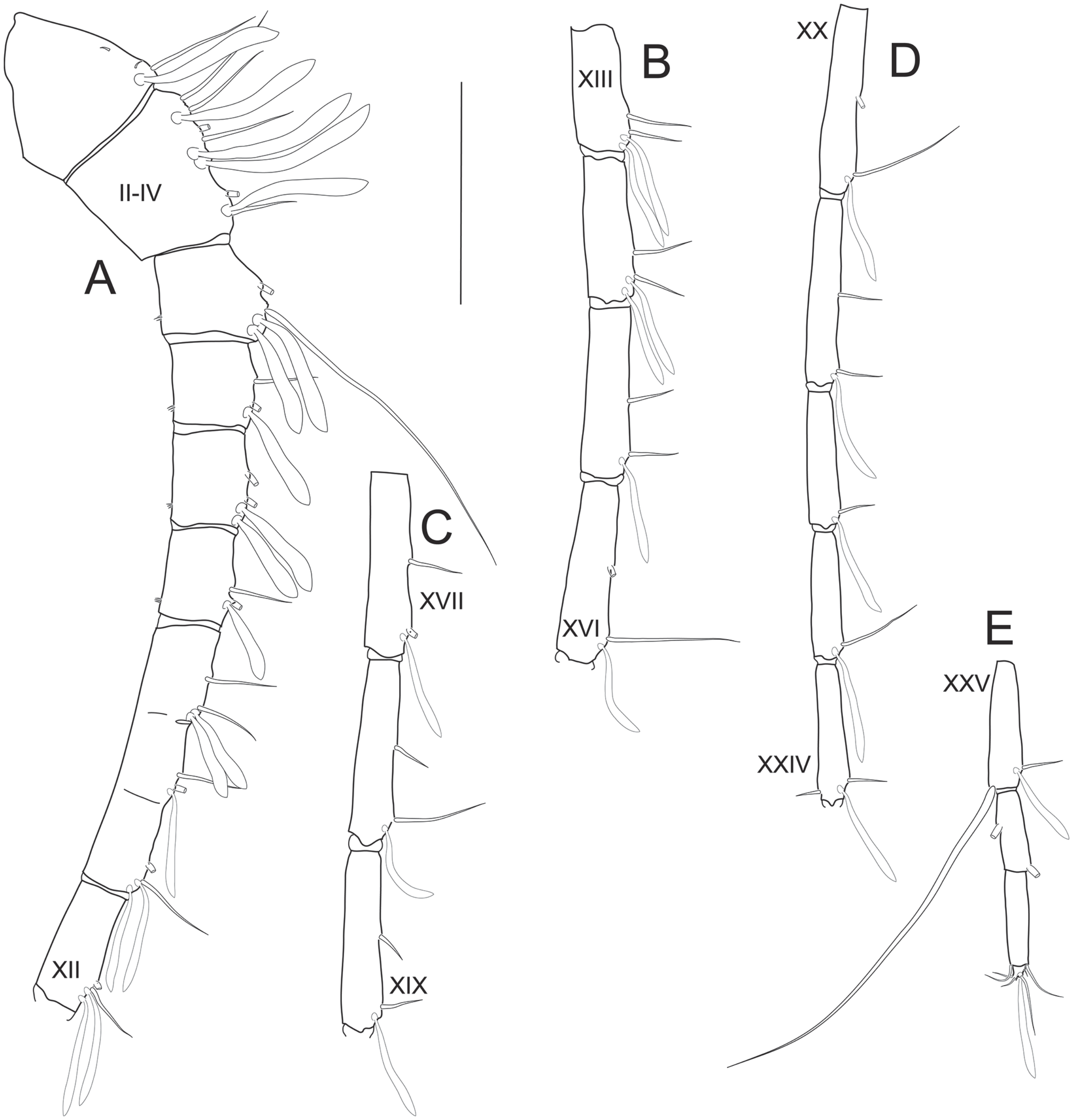

FIGURE 57. *Bathycalanus dentatus* **n. sp.** male left antennule ancestral segments: A, segments I–XII; B, segments XIII–XVI; C, segments XVII–XIX; D, segments XX–XXIV; E, segments XXV–XXVIII. Scale bar represents 1.0 mm on all figures. Illustrated specimen from MV66-11, Stn 5.

Bathycalanus milleri **n. sp.**
(Figs 46, 60–66)

Type locality. 02.867º N. 80.850º W.

Material examined. Francis Drake III, IKMT: Stn 4, 0–3000 m, 1♀ (10.0 mm), holotype; Stn 2, 0–3000 m, 1♀ (11.2 mm). MV66-II, IKMT, Stn 5, 0–3889 mwo, 3♀ (10.7–11.0 mm), paratypes, 2♂ (9.4, 9.7 mm). ANTXIV/1, Stn 6, MOC10, 998–1985 m, 1♀ (9.5 mm), 1♂ (9.5 mm). ANT52, RMT, Stn 18, 500–1000 m, 1♀ (11.5 mm), Co411.1.2. Southtow IV, IKMT, Stn 36, 0–2000 m, 1♀ (9.1 mm), 1♂ (9.1 mm), Umitaka Maru, RMT-8D2, Stn 18,

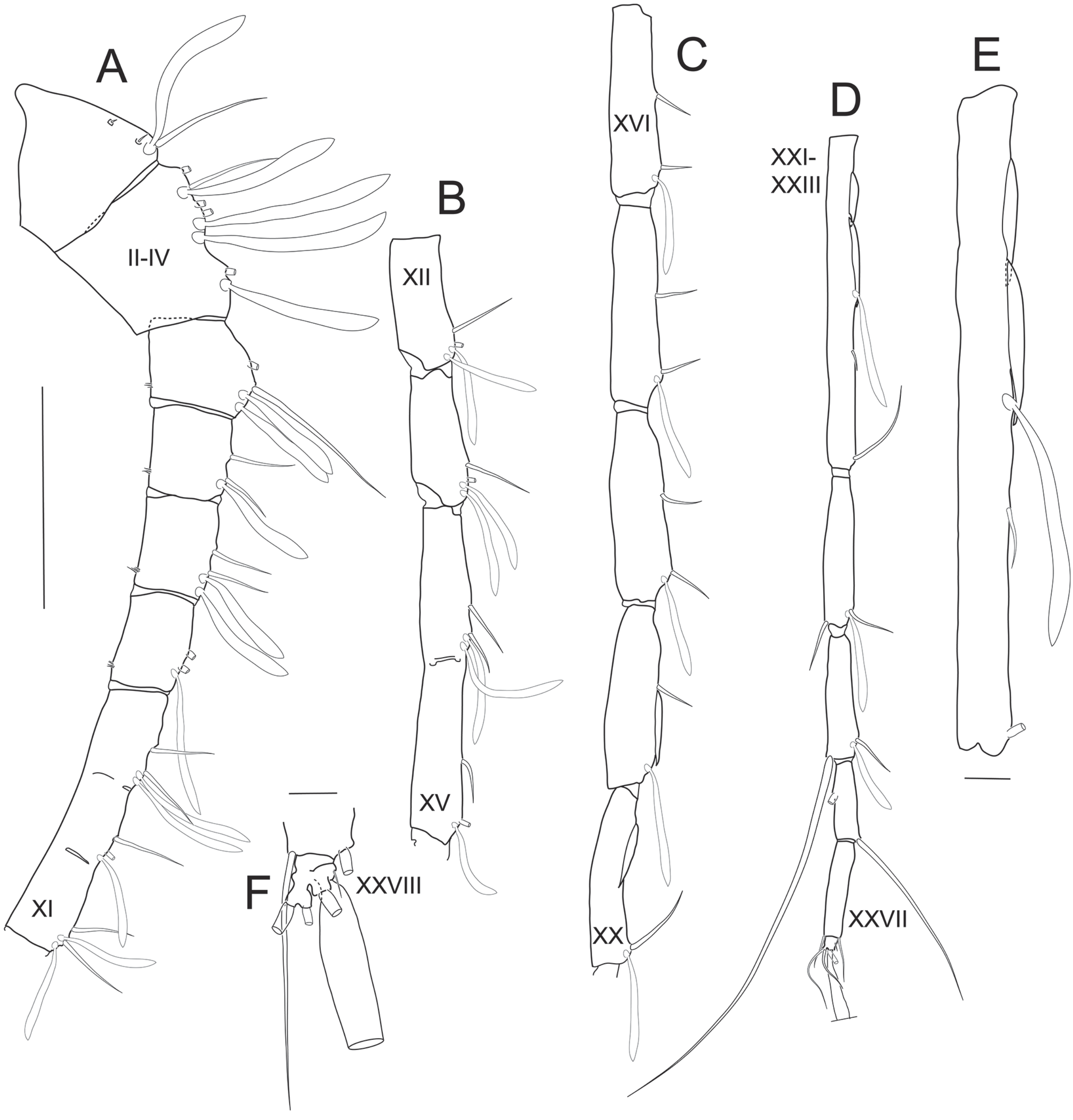

FIGURE 58. *Bathycalanus dentatus* **n. sp.** male right antennule ancestral segments: A, segments I–XI; B, segments XII–XV; C, segments XVI–XX; D, segments XXI–XXVIII; E, detail of segments XXI–XXIII; F, detail of segment XXVIII. Scale bar represents 1.0 mm on figures A–D; 0.1mm on remaining figures. Illustrated specimen from MV66-11, Stn 5.

1♀ Co411.2.1. Additional records from Smithsonian Institution, USNM numbers: 298331, 262439–40, 262443–44, 262448–51, 262458–61, 262466, 262488, 299518–23, 299527–28, 302050, 302052–53, 302055, 302057, 302059, 302062–64, 302066, 302068, 302071, 302074, 302078, 1132628, 1132632, 1132629.

Type specimens. Deposited in collection of the Scripps Institution of Oceanography, California: Holotype female: PIC-140409-0010-HT; Paratype lot of 3 females: PIC-140409-0011-PT. Deposited in the collection of the National Institute of Water and Atmospheric Research, Wellington: Paratype male: NIWA 85232 (1 vial, 2 slides); Paratype female: NIWA 85231 (1 vial, 1 slide).

Genetic material. Co411.1.2. GenBank numbers in Table 6.

Morphological description. Following description based on holotype specimen from Francis Drake III, Stn 4. As for genus with following specific level features.

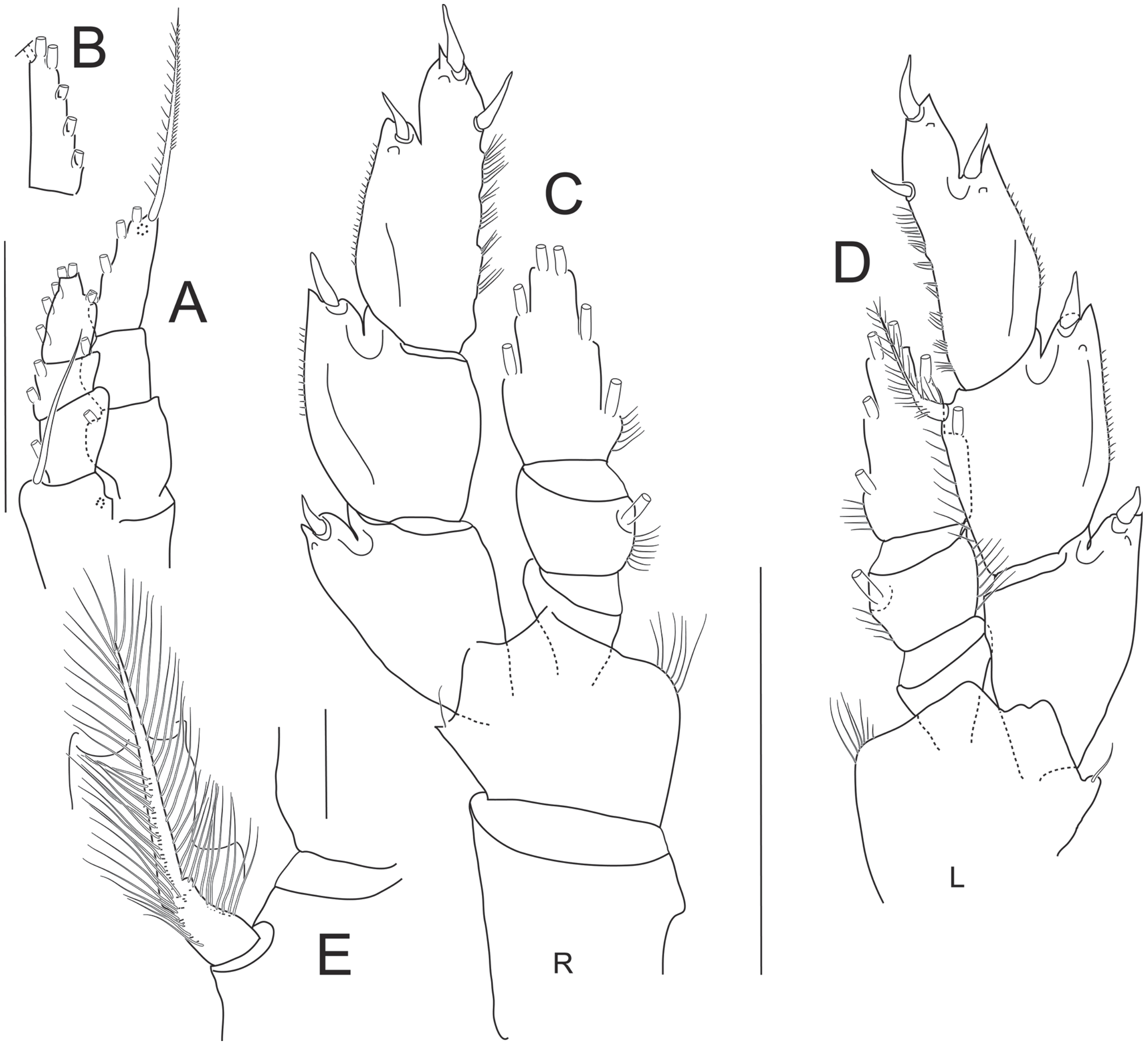

FIGURE 59. *Bathycalanus dentatus* **n. sp.** male: A, anterior view of leg 1; B, exopod segment 3 of leg 1 (other side); C, posterior view of right leg 5; D, posterior view of left leg 5; E, inner distal corner of left leg 5 exopod segment 2. Scale bar represents 1.0 mm on figures A–D; 0.1mm on remaining figure. Illustrated specimen from MV66-11, Stn 5.

Female (Fig. 60A–E). Total length 10.5 mm (mean = 10.5 mm, range = 9.1–11.5 mm, n = 7). In lateral view anterior head with curving hump just posterior to rostral projection, anterior margin of head in dorsal view produced into distinct short rounded projection bearing pair of very small spine-like processes. Pedigerous somite 5 with symmetrical, short, rounded posterolateral corners extending less than one quarter of way along genital double-somite. Genital double-somite widest in dorsal view at anterior one third, length about as long as widest width.

Antennule (Figs 60B, 61, 62A–C) extending about 5–6 segments beyond caudal rami. Lengths of antennule segments (µm) as follows. Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements taken of ancestral segment I. I (265, 679); II–IV (355); V (213); VI (238); VII (304); VIII (321); IX (336); X–XI (652); XII (458); XIII (476); XIV (596); XV (757); XVI (811); XVII (876); XVIII (922); XIX (951); XX (1032); XXI (1101); XXII (765); XXIII (748); XXIV (777); XXV (743); XXVI (365); XXVII (703); XXVIII (49). Distoanterior borders of segments XVI–XX with about 23, 21, 21, 22, 24, teeth, respectively, lining border just distal to seta; posterior borders of these segments lined distally with 14, 30, 31, 19, 0 teeth, respectively; all teeth slightly on ventral surface.

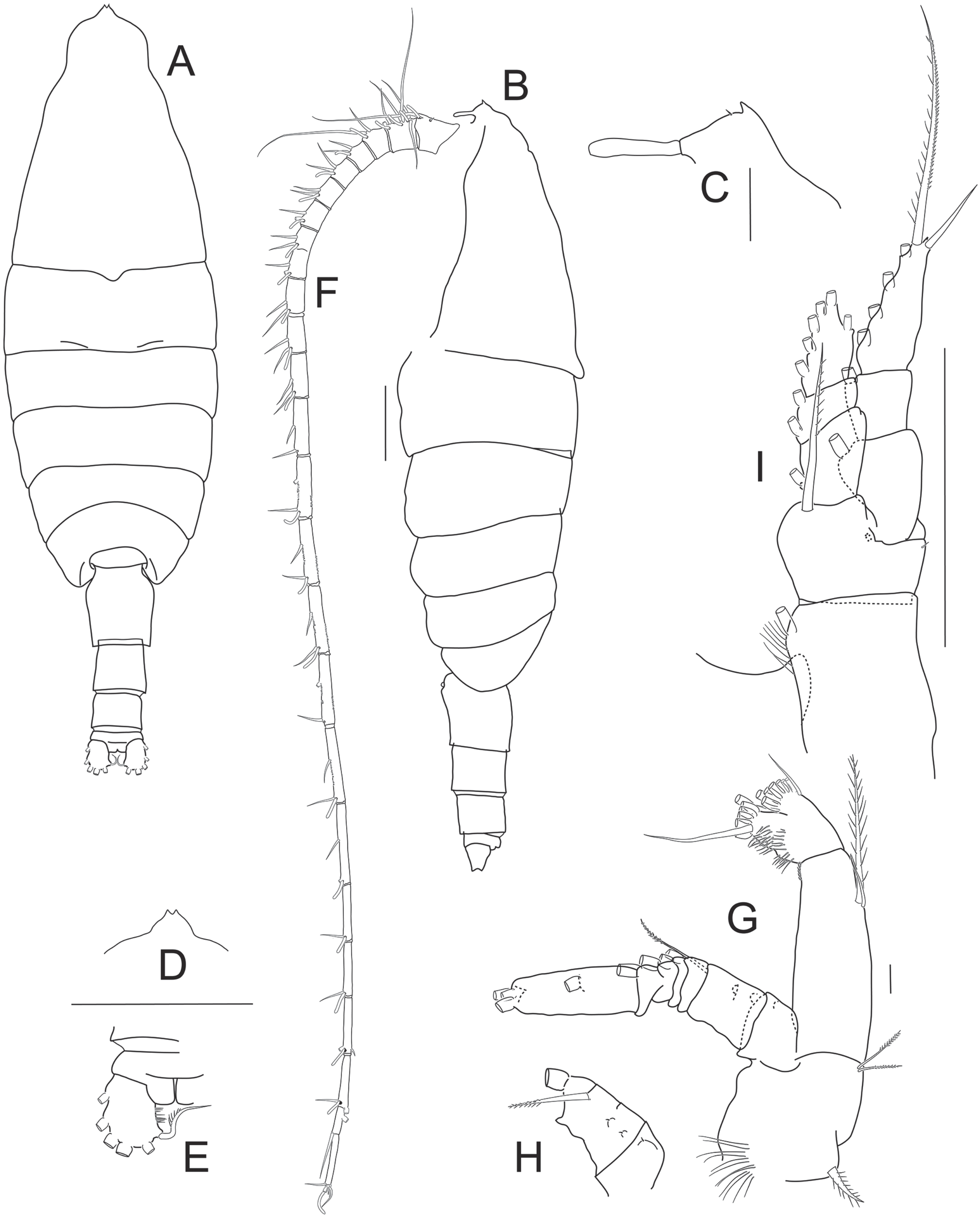

FIGURE 60. *Bathycalanus milleri* **n. sp.** female: A, dorsal view; B, lateral view; C, lateral view of anterior head; D, dorsal view of anterior head; E, dorsal view of caudal ramus; F, antennule; G, antenna; H, proximal part of exopod of antenna, another view; I, anterior view of leg 1. Scale bar represents 1.0 mm on figures A, B, F, I; 0.1mm on remaining figures. Illustrated specimen from Francis Drake III, Stn 4.

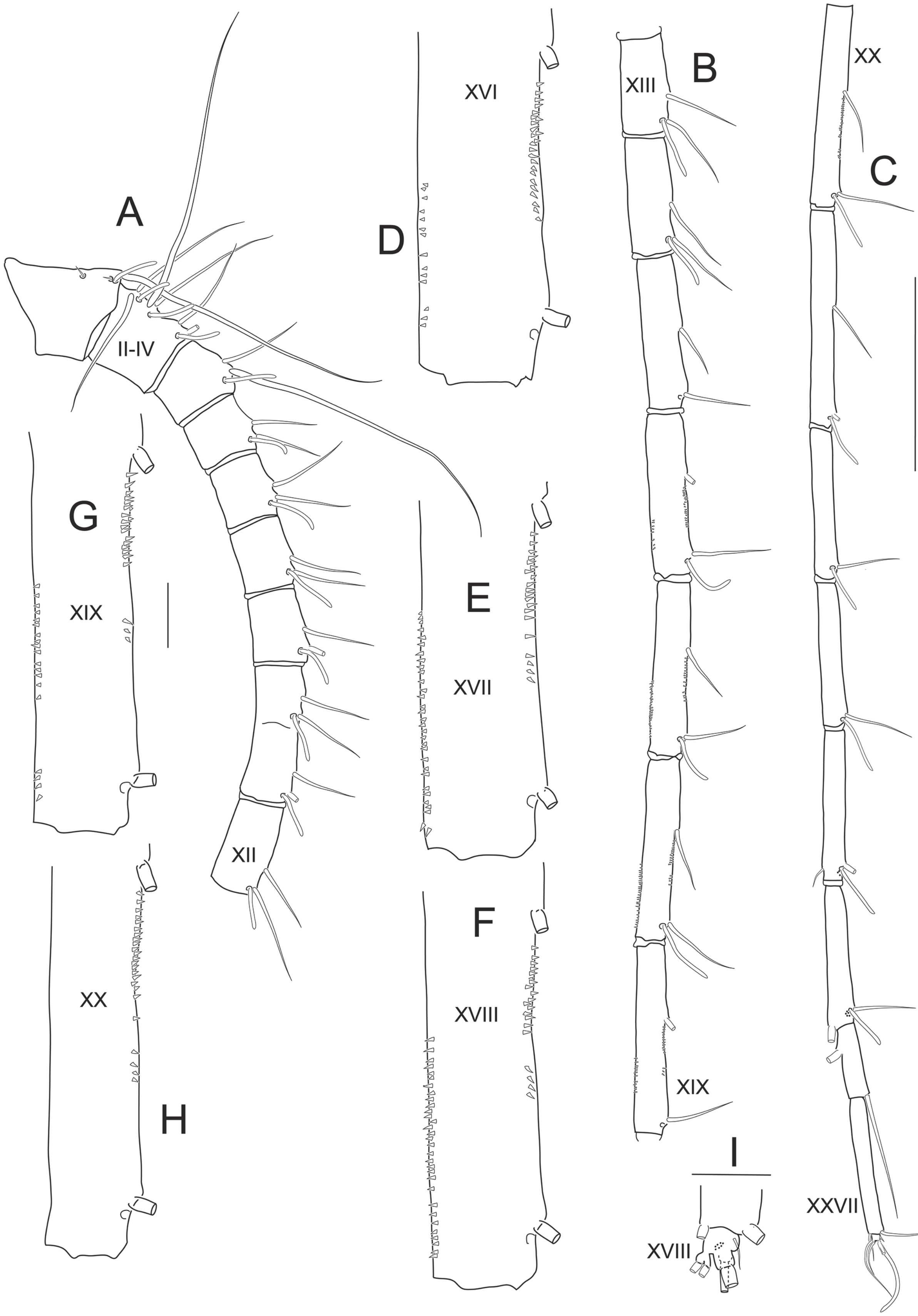

FIGURE 61. *Bathycalanus milleri* **n. sp.** female antennule ancestral segments: A, segments I–XII; B, segments XIII–XIX; C, segments XX–XXVIII; D, distal part of segment XVI; E, distal part of segment XVII; F, distal art of segment XVIII; G, distal part of segment XIX; H, distal part of segment XX; I, detail of segment XXVIII. Scale bars represent 1.0 mm on figures A–C; 0.1mm on remaining figures. Illustrated specimen from Francis Drake III, Stn 4.

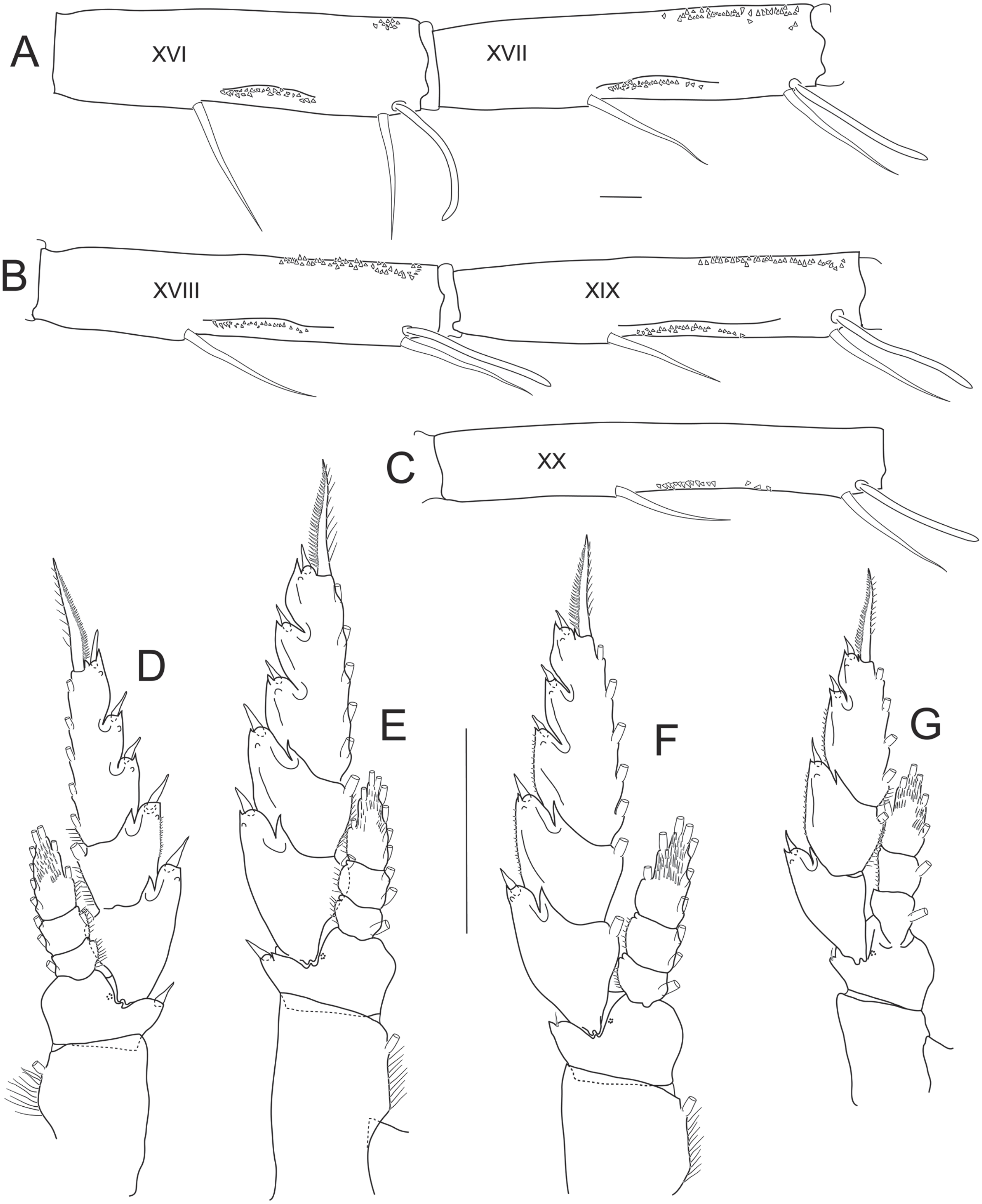

FIGURE 62. *Bathycalanus milleri* **n. sp.** female antennule ancestral segments: A, segments XVI–XVII; B, segments XVIII–XIX; C, segment XX. Illustrated specimen from ANT52 (Co411.2). Female legs, anterior view: D, leg 2; E, leg 3; F, leg 4; G, leg 5. Illustrated specimen from Francis Drake III, Stn 4. Scale bar represents 1.0 mm on D–G; 0.1 mm on remaining figures.

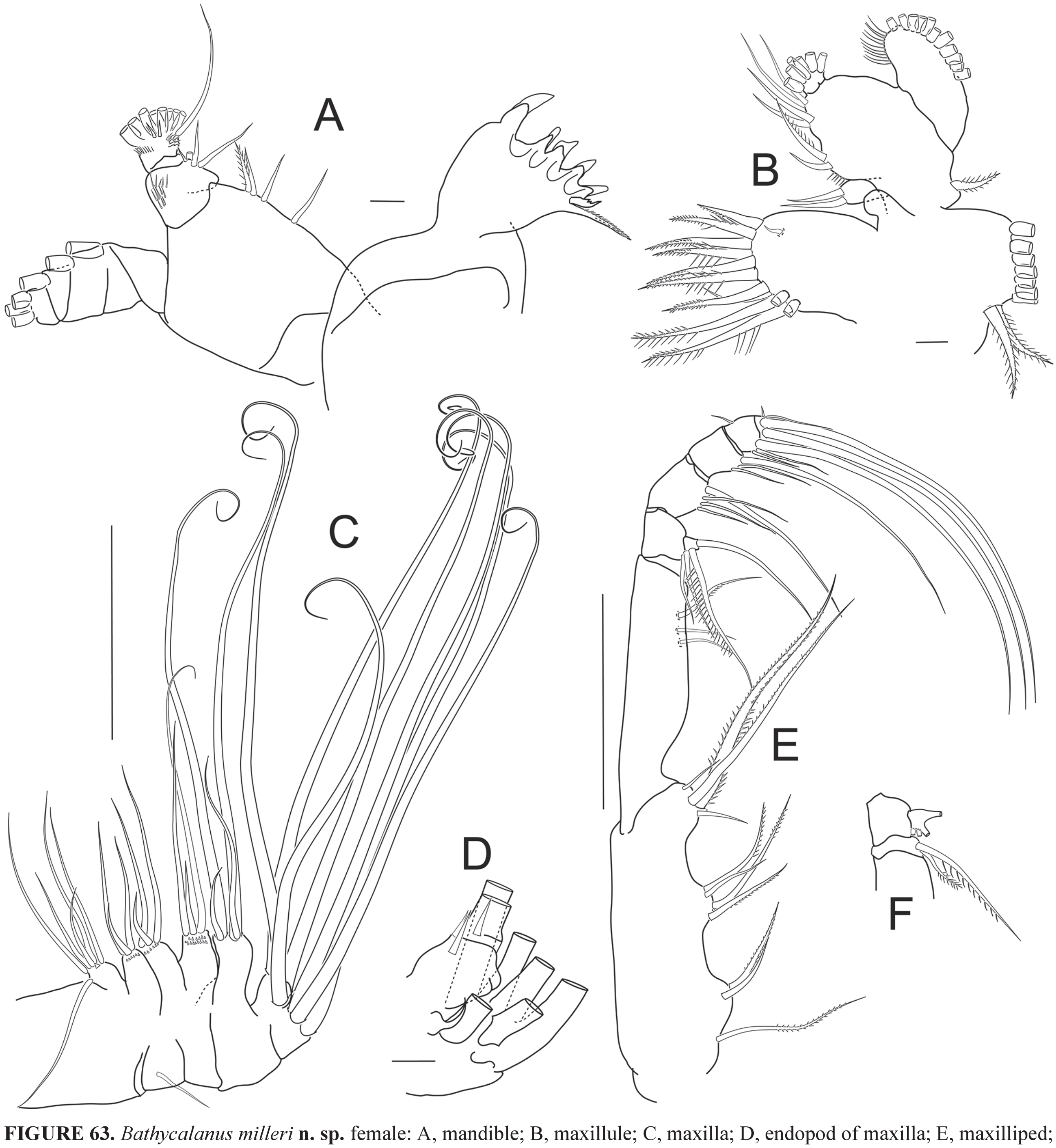

FIGURE 63. *Bathycalanus milleri* **n. sp.** female: A, mandible; B, maxillule; C, maxilla; D, endopod of maxilla; E, maxilliped; F, another view of endopod segments 1 and 2 of maxilliped. Scale bar represents 1.0 mm on figures C, E, F; 0.1mm on remaining figures. Illustrated specimen from Francis Drake III, Stn 4.

Antenna (Fig. 60G, H) exopod segment IV with short seta extending slightly beyond distal border of exopod segment VIII, bordered by spinules.

Maxillule (Fig. 63B) praecoxal arthrite with 13 setae and spines, including 2 setae on posterior surface, 1 distoanterior seta small; coxal endite without setae; basal endite 2 with 2 short setae; endopod segments with 2 (subequal), 2 (subequal), 6 setae (including 1 smaller seta arising from posterior surface), respectively.

Maxilliped (Fig. 63E, F) syncoxal endite 4 with longest spinulose seta extending short of distal border of endopod segment 2.

Leg 1 (Fig. 60I) exopod with articulation between exopod segments 2 and 3 well developed.

Male (Fig. 64A–C). Total length 9.2 mm (mean 9.4 mm, range = 9.1–9.7 mm, n = 4). Pedigerous somite 5 with short rounded lappets not reaching posterior border of urosomite I. Proportions of male urosomites, viewed laterally, as follows, location of measurements illustrated in Fig 1 (Table 9). In lateral view urosomite II (UrII) not enlarged and swollen: UrII 1.52–1.70 (mean = 1.59, S.D. = 0.10, n = 5) times longer than UrIII and not constricted anteriorly such that ratio $UrII_{ant}$ / $UrII_{mx}$ = 0.73–0.79 (mean = 0.78, S.D. = 0.02, n = 5).

Antennule (Figs 64F, 65A–I) right gripping elements around geniculation (Fig. 65F, H, I) very similar to those of *Ba. richardi*.

Leg 5 (Fig. 66) left exopod segment 2 specialised seta with moderately lengthened lash extending well short of distal border of endopod segment 3 and densely covered in long setules, basal part swollen, bearing spinule; inner border of right exopod segment 3 naked.

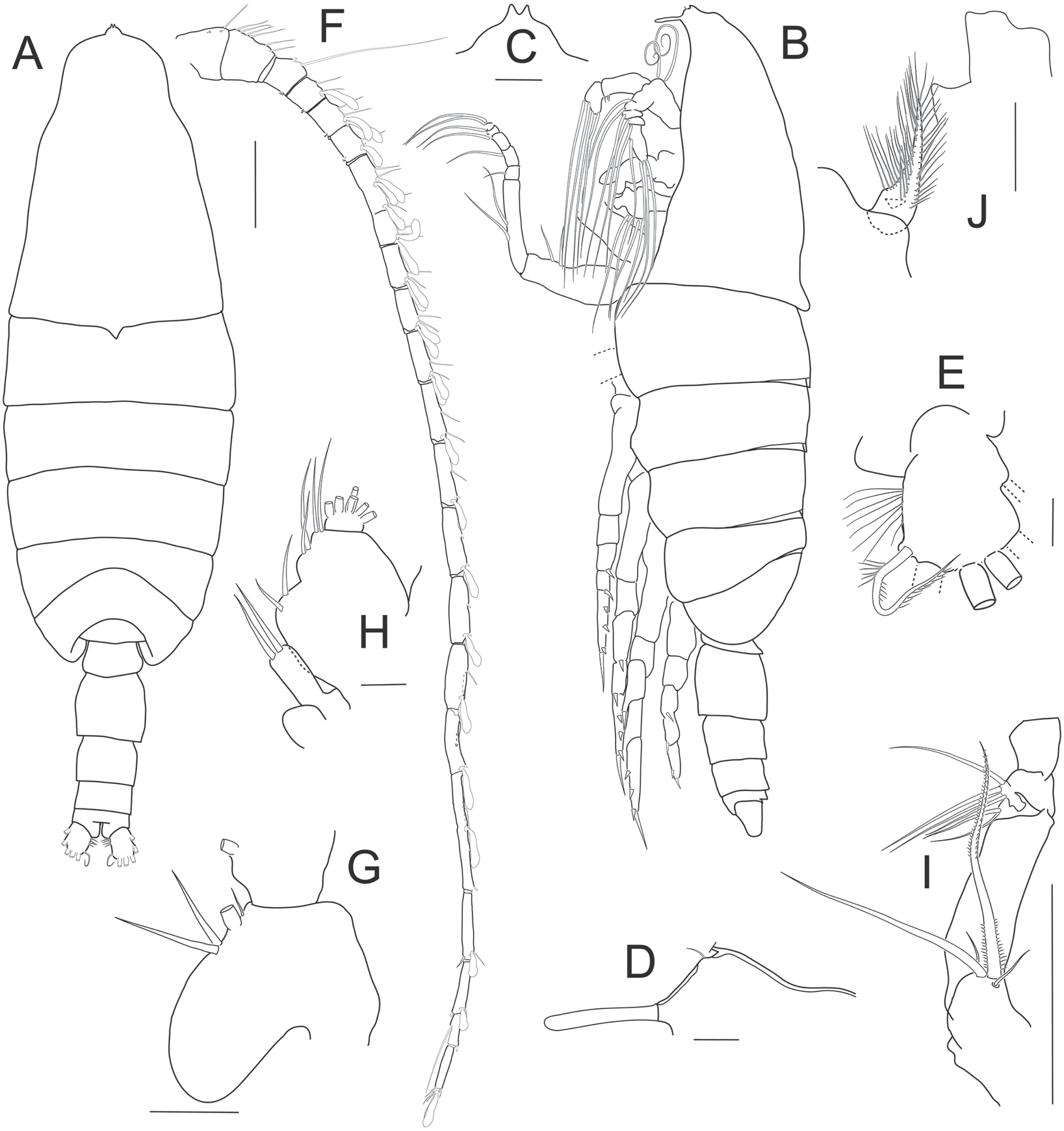

FIGURE 64. *Bathycalanus milleri* **n. sp.** male: A, dorsal view; B, lateral view; C, dorsal view of anterior head; D, lateral view of anterior head; E, dorsal view of caudal ramus; F, right antennule; G, endopod segment 1 of mandible; H, coxal endite, basal endites 1 and 2 and endopod of maxillule; I, middle part of maxilliped; J, inner distal corner of left exopod segment 2 of leg 5. Scale bar represents 1.0 mm on figures C, B, F, I; 0.1mm on remaining figures. Illustrated specimen from ANTXXIV/1 Stn 6, 998–1985 m.

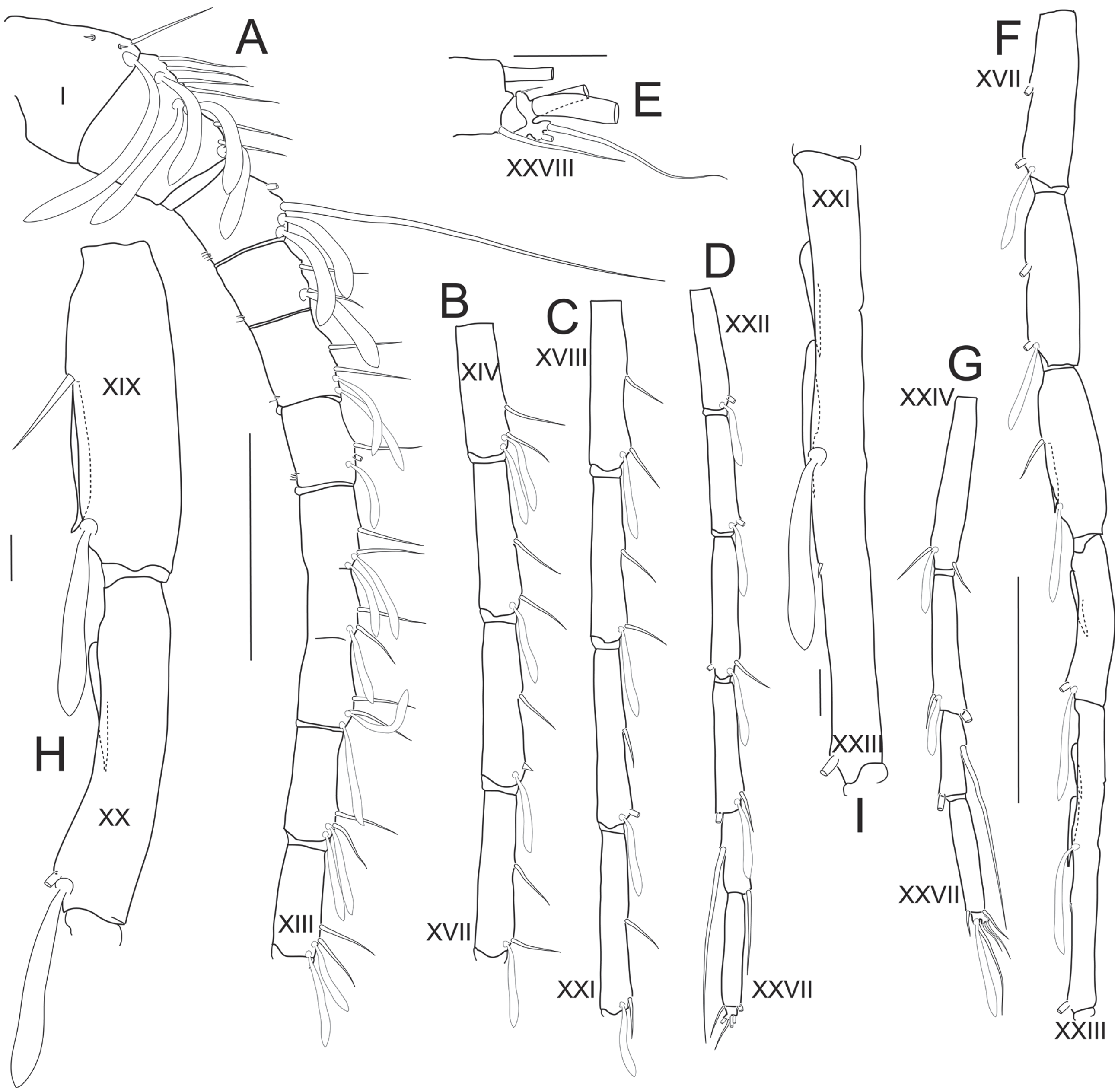

FIGURE 65. *Bathycalanus milleri* **n. sp.** male left antennule ancestral segments: A, segments I–XIII; B, segments, XIV–XVII; C, segments XVIII–XXI; D, segments XXII–XXVIII; E, detail of segment XXVIII. Right antennule ancestral segments: F, segments XVII–XXIII; G, segments XXIV–XXVIII; H, detail of segments XIX–XX; I, segments XXI–XXIII. Scale bar represents 1.0 mm on figures A–D, F, G; 0.1mm on remaining figures. Illustrated specimen from ANTXXIV/1 Stn 6, 998–1985 m.

Morphological variation. The female specimen taken by Southtow IV agrees with the description of *Ba. milleri* **n. sp.** in that it has 2 setae on the second basal endite of the maxillule but the antennule is completely free of spinules on segments XVI–XX. The male found with it has urosome proportions that fit with the males assigned here to *Ba. milleri* **n. sp.**, the right exopod segment 3 of leg 5 is completely naked, and the specialised seta on the inner distal corner of left exopod segment 2 extends short of the distal border of endopod segment 3 as in *Ba. milleri* **n. sp.**

The spinules found on the anterior and posterior borders of most of antennule segments XVI–XX are diagnostic for this species (Fig. 61), along with the 2 setae on the second basal endite of the maxillule (Fig. 63B). Nevertheless, among the three specimens that were examined in detail, one specimen from ANTXXIV/1 Stn6, 998–1985 m also had spinules on the distoposterior border of segment XV. The specimens from ANT52 (Co411.2)

(Fig. 62A–C) have segment XVI with very few posterior border spinules and the anterior border spines appear to be situated in an excavation distal to midlength seta. In general, the numbers and locations of spinules are variable.

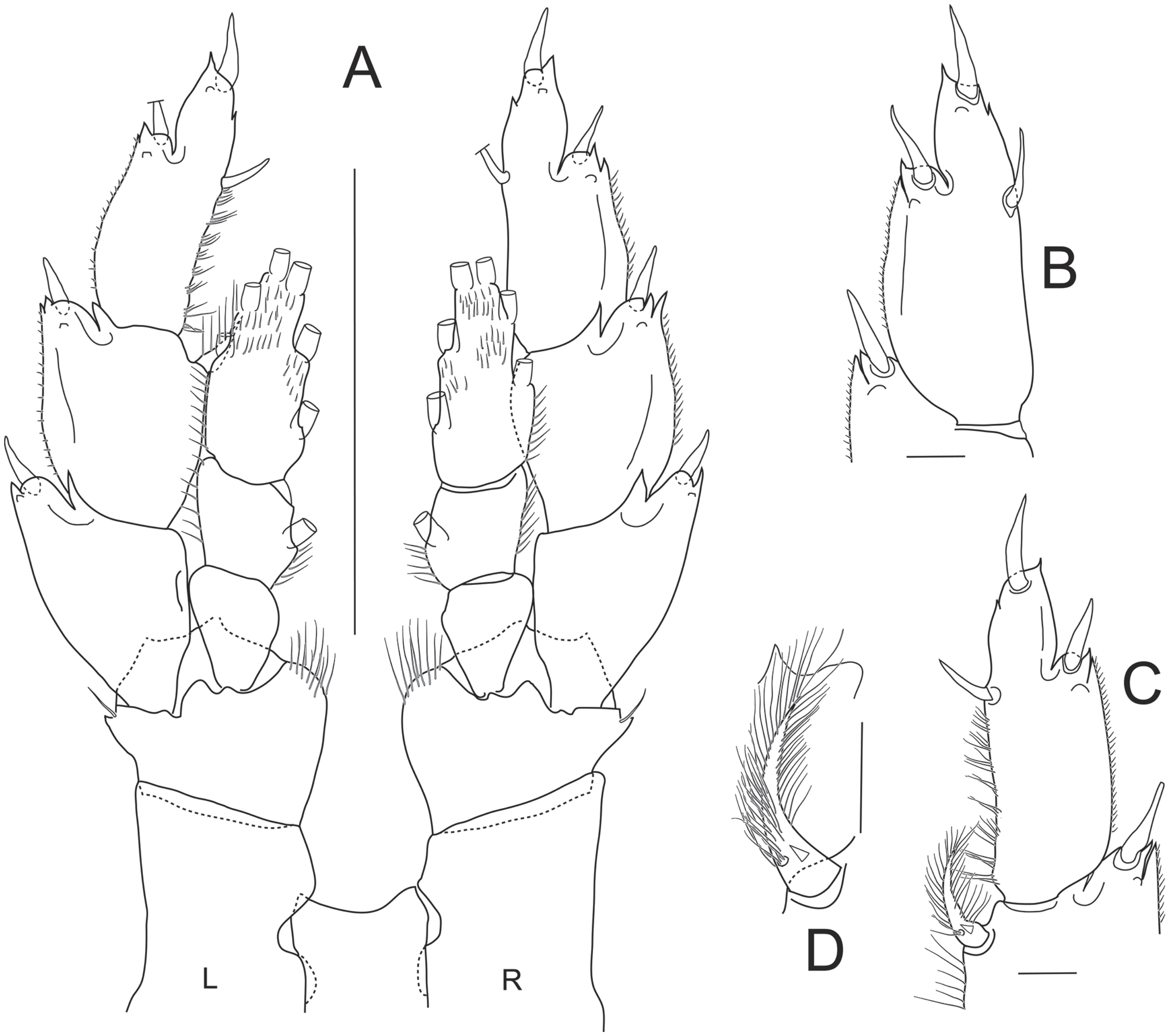

FIGURE 66. *Bathycalanus milleri* **n. sp.** male: A, anterior view of leg 5. Another specimen: B, right exopod segment 3 of leg 5; C, left exopod segment 3 of leg 5; D, inner distal corner of left exopod segment 2 of leg 5. Scale bar represents 1.0 mm on figure A; 0.1mm on remaining figures. Illustrated specimens: Figure A from ANTXXIV/1 Stn 6, 998–1985 m; figures B–D from MV66-11, Stn 5.

Distribution. *Bathycalanus milleri* **n. sp.** is a bathy- to abyssopelagic species taken in hauls between 0–4000 m (including 500–1000 and 1000–2000 m). It is known from the eastern Pacific off Ecuador and California, as well as in the Pacific and Atlantic sectors of the Southern Ocean (Fig. 46, Table 1).

Species comparisons. Among *Bathycalanus* that have two small anterior spine-like processes on the rostral prominence and bluntly rounded posterolateral corners of pedigerous somite 5 (*Ba. richardi*, *Ba. bradyi, Ba. dentatus* **n. sp.**, *Ba. milleri* **n. sp.** and *Ba tumidus* **n. sp.**) *Ba. milleri* **n. sp.** may be distinguished by the following combination of character states (Table 10): 1) the second basal endite of the maxillule has 2 setae; 2) leg 1 exopod segments 2 and 3 separate (both sexes); 3) female antennule segments XVI–XX with anterior border toothed; 4) female antennule segments XVI–XIX posterior border toothed; 5) the length proportions of the male urosomites UrII/UrIII of *Ba. milleri* **n. sp.** are significantly different from those of *Ba. richardi* ($P = 0.01$) but not *Ba. bradyi* ($P = 0.428$) and 6) in lateral view, the ratio of anterior/posterior depth of UrII of *Ba. milleri* **n. sp.** is significantly different from that of *Ba. richardi* ($P = 0.014$) but not *Ba. bradyi* ($P = 0.342$).

Etymology. This species is named after Professor Charlie Miller of Oregon State University, who first recognised the eastern Pacific form of *Megacalanus* and has made many insightful contributions to biological oceanography of the north east Pacific Ocean.

***Bathycalanus tumidus* n. sp.**
(Figs 46, 67–70)

Type locality. 29.5333º N, 137.233º E.

Material examined. Antipode IV, IKMT: Stn 52D, 0–1900 m, 1♀ (10.9 mm) holotype; Stn 53A, 0–2000 m, 2♀ (10.0, 10.5 mm) paratype; Stn 53D, 0–2500 m, 1♀ (10.2 mm). ANTXIV/1, MOC10, Stn 2, 2000–3000 m, 1♀ (9.5 mm) Co375.1.1, 1♀ (9.3 mm) Co375.1.3, paratype. MV73-I, IKMT, Stn 53, 0–2000 m, 1♀ (10.4 mm).

Type specimens. Deposited in the collection of the Scripps Institution of Oceanography, California. Holotype female: PIC-140409-0012-HT; Paratype series: PIC-140409-0013-PT. Deposited in the collection of the National Institute of Water and Atmospheric Research, Wellington: NIWA 85230 (Co375.1.3) 1 vial plus 1 slide.

Genetic material. Co375.1.1, Co375.1.3. GenBank numbers in Table 6.

Morphological description. Following description based on holotype specimen from Antipode IV Stn 52D. As for genus with following additional specific level features.

Female (Fig. 67A–F). Total length 10.6 mm (mean = 10.11 mm, range = 9.3–10.9 mm, n = 7). Anterior margin of head, in dorsal view, produced into distinct short rounded projection located dorsal to base of rostrum and bearing pair of small stout divergent spine-like processes. In lateral view, posterolateral corners of pedigerous somite 5 symmetrical, rounded. Genital double-somite bulbous, symmetrical in dorsal view, slightly wider than long, widest width at approximately midlength, with small anteroventral genital operculum, seminal receptacles not observed.

Antennule (Figs 67F, 68) lengths of antennule segments (µm) as follows. Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements taken of ancestral segment I. I (327, 644); II–IV (478); V (268); VI (288); VII (673); VIII (384); IX (357); X–XI (587); XII (406); XIII (406); XIV (495); XV (618); XVI (692); XVII (766); XVIII (819); XIX (878); XX (951); XXI (998); XXII (760); XXIII (703); XXIV (782); XXV (772); XXVI (372); XXVII (-); XXVIII (-). Anterior and posterior borders of antennule ancestral segments XVI–XXI smooth.

Antenna (Fig. 69A) exopod segment IV with short seta extending beyond distal border of segment VIII and bearing short setules.

Maxillule (Fig. 69C) praecoxal arthrite with 15 setae including 4 on posterior surface and 2 small anterior surface setae; coxal endite with 1 seta, basal endites 1 and 2 with 2 and 4 setae respectively, basis and endopod segments 1 and 2 fused although demarcation between segments visible, segment 3 separate; endopod segments with 2 (subequal), 2 (subequal), 5+1 smaller anterior surface seta.

Maxilliped (Fig. 69E) syncoxal endite 4 with large toothed seta extending half way along endopod segment 2.

Leg 1 (Fig. 67G) exopod with articulation between exopod segments 2 and 3 well developed.

Male. Unknown.

Distribution. *Bathycalanus tumidus* **n. sp.** is an upper abyssopelagic species taken in the eastern and western North Pacific and the Atlantic off West Africa near the Cape Verde Islands where it was found at depths between 2000 and 3000 m (Fig. 46, Table 1).

Species comparisons. This species is very like *Ba. richardi* except the genital double-somite is of a bulbous shape in dorsal view, widest at midlength and wider than long. The maxillule praecoxal arthrite has 4 posterior surface setae, unlike any other species of *Bathycalanus*; the coxal endite has one relatively well-developed seta unlike most other known *Bathycalanus* except *Ba. pustulosus* **n. sp.**; and basal endite 2 has 4 setae whereas in *Ba. pustulosus* it has only 2 setae (Table 10). The genetic distance data suggest that this species may represent an as yet unrecognised genus (see Tables 14–17).

Etymology. The species name is derived from the Latin adjective "*tumidus*" meaning swollen, referring to the shaped of the genital double-somite.

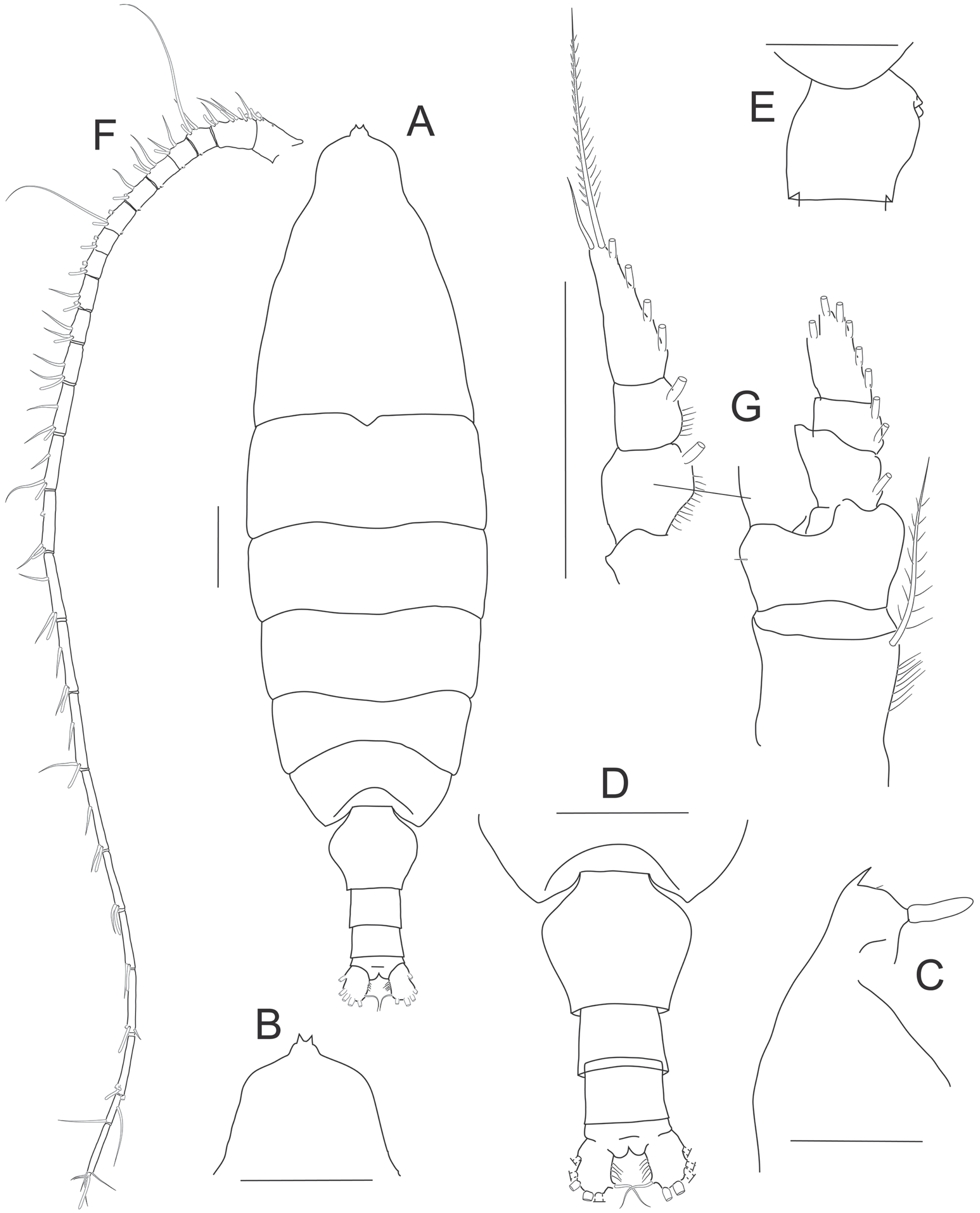

FIGURE 67. *Bathycalanus tumidus* **n. sp.** female: A, dorsal view; B, dorsal view of anterior head; C, lateral view of anterior head; D, dorsal view of urosome; E, lateral view of genital double-somite; F, antennule; G, posterior view of leg 1. Scale bar represents 1.0 mm on all figures. Illustrated specimen from Antipode IV, Stn 52D.

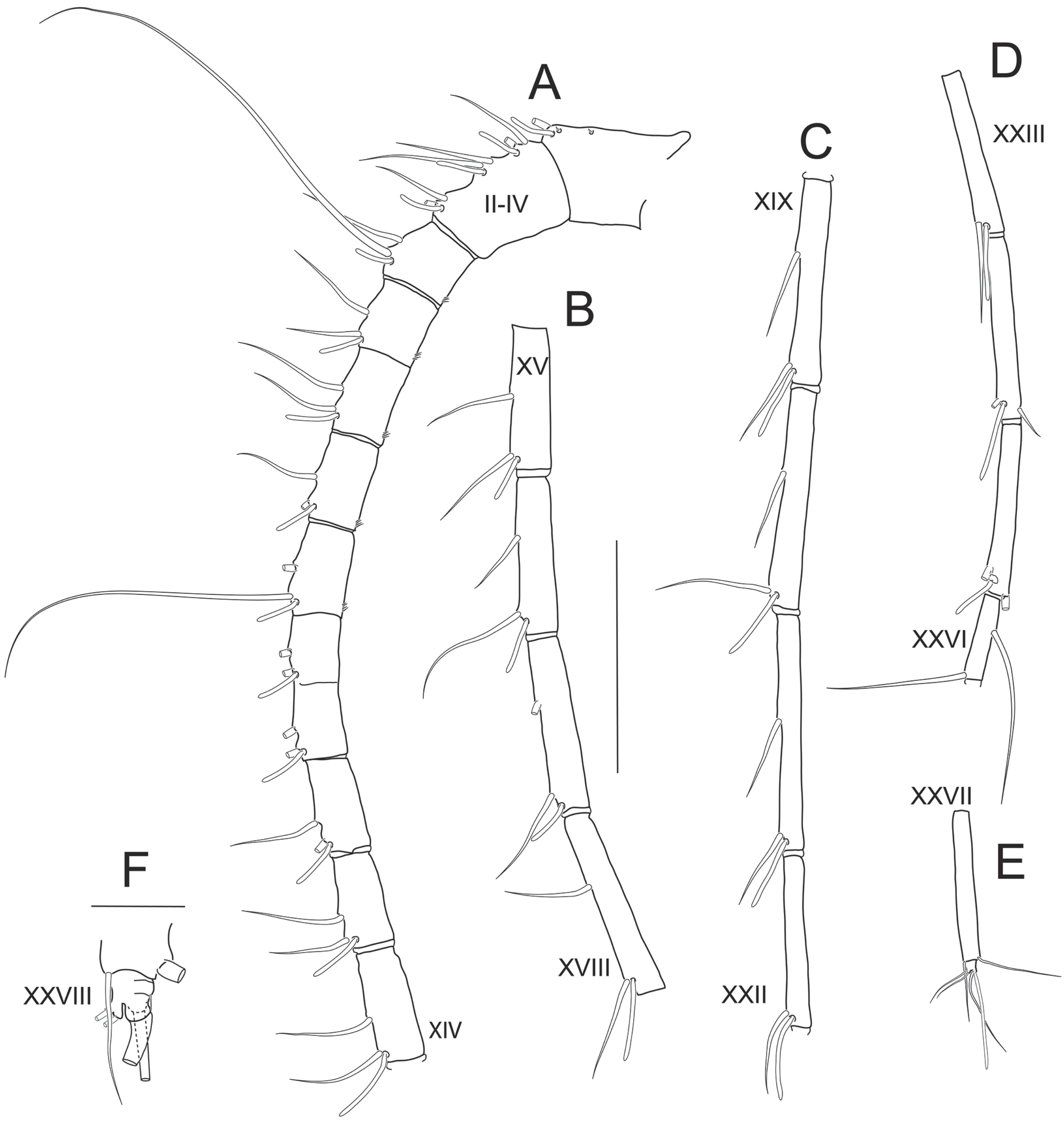

FIGURE 68. *Bathycalanus tumidus* **n. sp.** female antennule ancestral segments: A, segments I–XIV; B, segments XV–XVIII; C, segments XIX–XXII; D, segments XXIII–XXVI; E, segments XXVII–XXVIII; F, detail of segment XXVIII. Scale bar represents 1.0 mm on figures A–E; 0.1mm on remaining figure. Illustrated specimen from Antipode IV, Stn 52D.

***Bathycalanus adornatus* n. sp.**
(Figs 46, 71–73)

Type locality. 25.082º S, 09.584º E.

Material examined. ANTXIV/1, MOC10: Stn 8, 3992–4390 m, 1♀ (10.9 mm) Co441.1.1, holotype; Stn 6, 3993–5110 m, 1♀ (11.8 mm) Co022.3.1, paratype.

Type specimens. Deposited in the collection of the National Institute of Water and Atmospheric Research, New Zealand: Holotype female: NIWA 85234 Co441.1.1 (1 vial, 2 slides). Paratype female: NIWA 85235 Co 022.3.1 (1 vial, 1 slide).

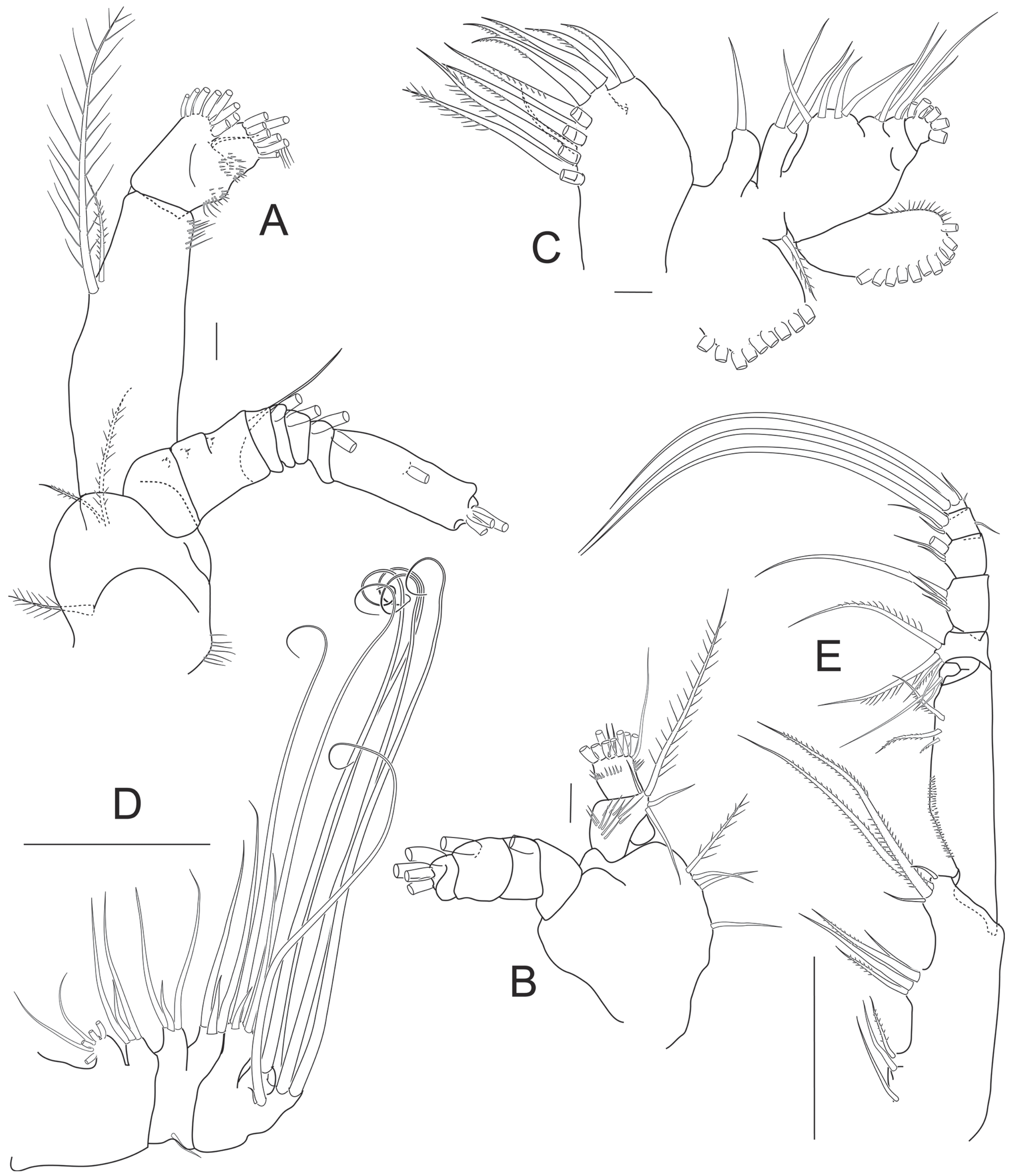

FIGURE 69. *Bathycalanus tumidus* **n. sp.** female: A, antenna; B, mandibular palp; C, maxillule; D, maxilla; E, maxilliped. Scale bar represents 1.0 mm on figures D, E; 0.1mm on remaining figures. Illustrated specimen from Antipode IV, Stn 52D.

Genetic material. Co022.3.1. GenBank numbers in Table 6.

Morphological description. Following description based on specimen from ANTXXIV/1, Stn 8. As for genus with following specific level features.

Female (Fig. 71A–D). Total length 11.8 mm (mean = 11.4 mm, range = 10.9–11.8 mm, n = 2). Anterior margin of head in dorsal view produced into distinct short rounded projection dorsal to base of rostrum bearing pair of stout small spine-like processes. In lateral view posterior corners of pedigerous somite 5 extended into irregularly-shaped, lightly sclerotised lappets that appear asymmetrical in illustrated specimen, but possibly symmetrical.

Posterolateral borders of pedigerous somite 4 also extended into symmetrical, irregularly-shaped, lightly sclerotised lappets. Genital double-somite symmetrical in dorsal view, with pair of small dorsolateral papillae and ventrolateral swelling; together these features contribute to lateral borders appearing angular when viewed dorsally. Genital double-somite wider than long (length : width = 0.86), widest at anterior one-third, with small ventral genital operculum just anterior to midlength, seminal receptacles not observed.

Antennule (Figs 71B, 72A–C) broken, longest remnant with ancestral segment XIX present. Lengths of antennule segments (μm) as follows. Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements taken of ancestral segment I. I (315, 734); II–IV (421); V (261); VI (276); VII (658); VIII (386); IX (388); X–XI (685); XII (478); XIII (488); XIV (612); XV (744); XVI (822); XVII (901); XVIII (990); XIX (1030); XX (-); XXI (-); XXII (-); XXIII (-); XXIV (-); XXV (-); XXVI (-); XXVII (-); XXVIII (-). Anterior and posterior borders on ancestral segments XVI–XIX naked.

Antenna (Fig. 73A) exopod ancestral segment IV with short seta extending short of distal border of exopod segment VIII and bearing short setules.

Maxillule (Fig. 73 D, E) praecoxal arthrite with 13 setae including 2 on posterior surface and 2 setae on anterior surface, 1 of them small; basal endite 2 with 3 setae; endopod segments with 2 (unequal), 2 (unequal), 5+1 anterior surface seta.

Maxilliped (Fig. 73I) syncoxal endite 4 with longest seta extending beyond distal border of endopod segment 2.

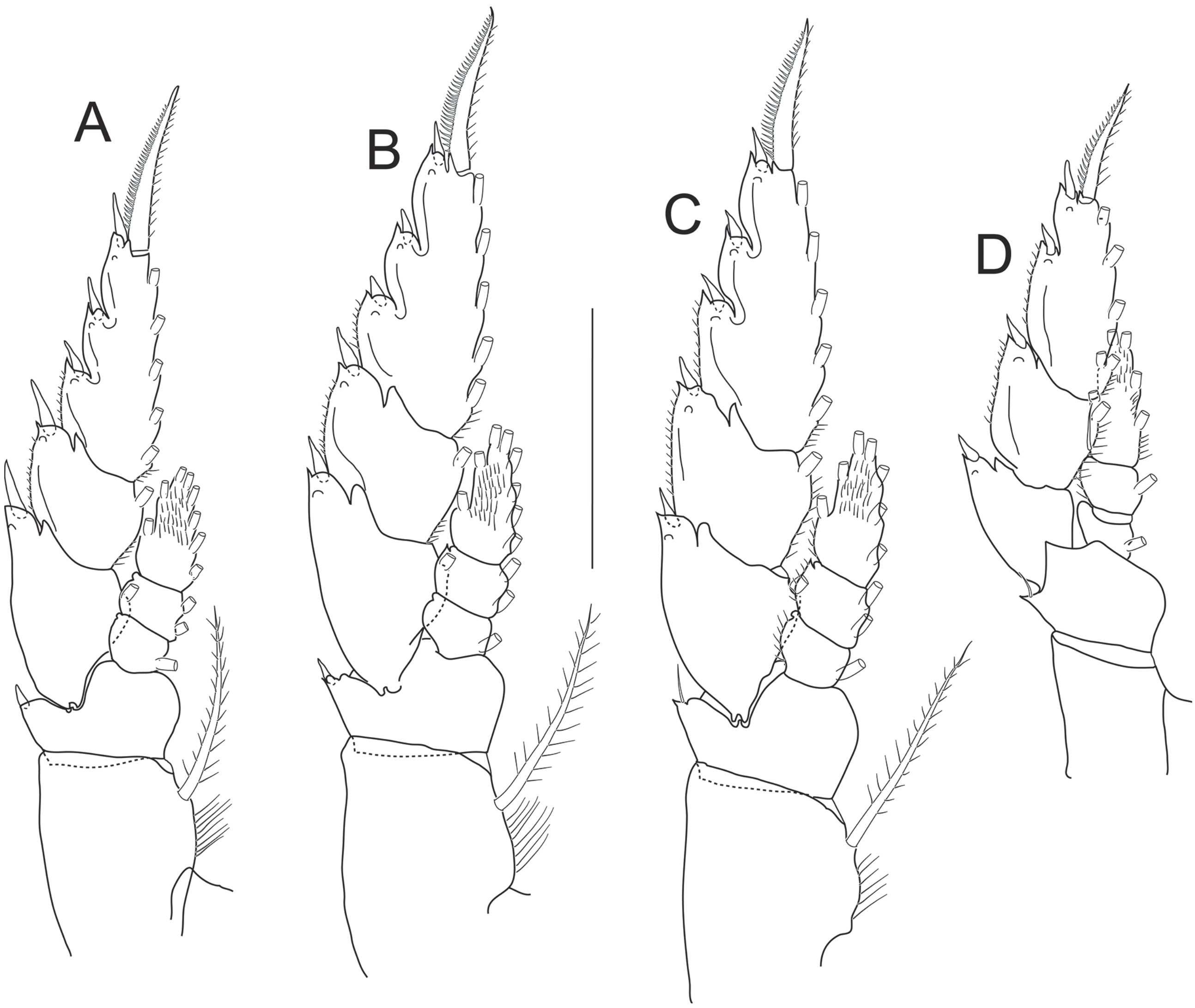

FIGURE 70. *Bathycalanus tumidus* **n. sp.** female: A, anterior view of leg 2; B, anterior view of leg 3; C, anterior view of leg 4; D, posterior view of leg 5. Scale bar represents 1.0 mm on all figures. Illustrated specimen from Antipode IV, Stn 52D.

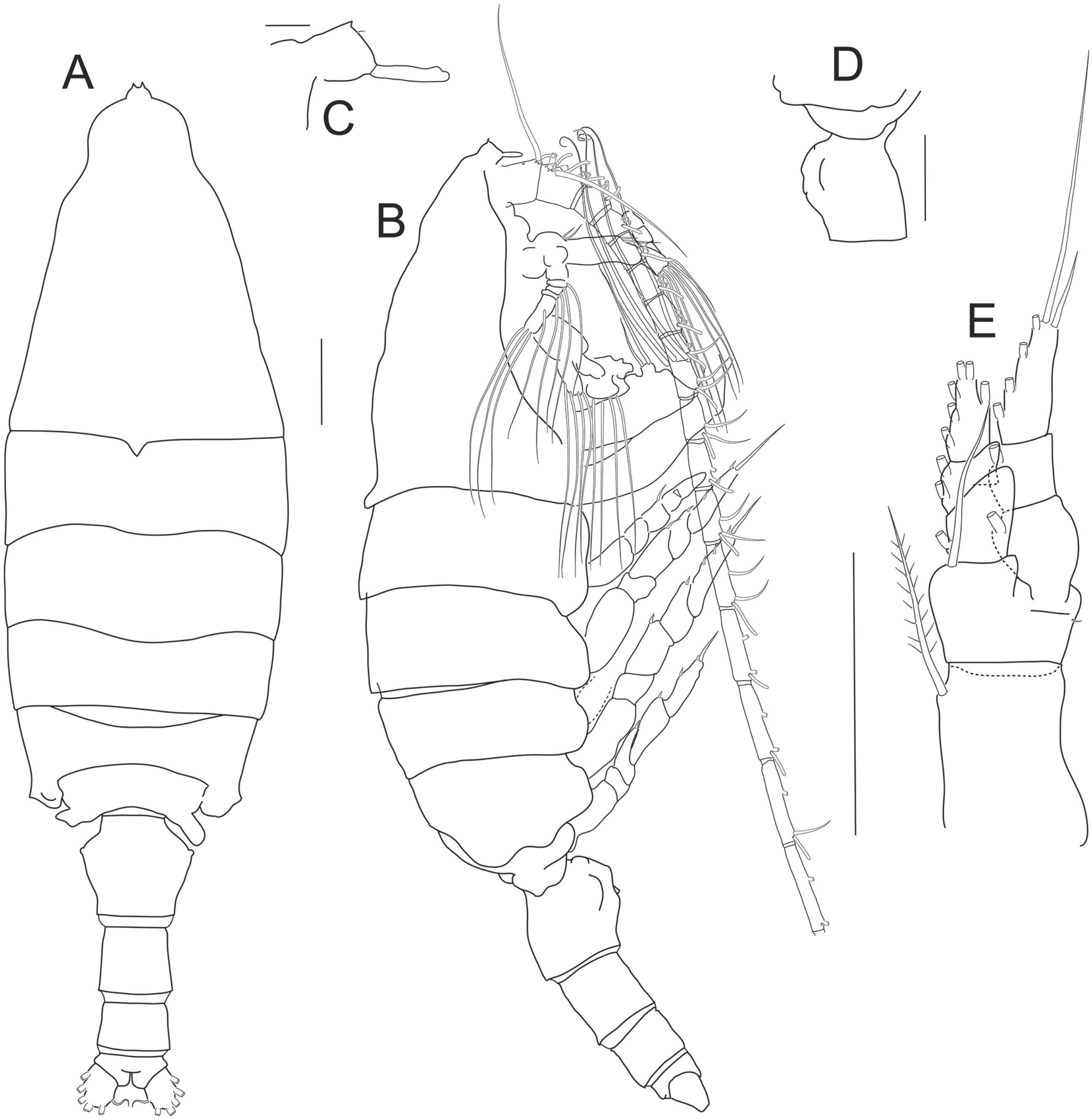

FIGURE 71. *Bathycalanus adornatus* **n. sp.** female: A, dorsal view; B, lateral right view; C, lateral view of anterior head; D, lateral left view of genital double-somite; E, anterior view of leg 1. Scale bar represents 1.0 mm on figures A, B, D, E; 0.1mm on remaining figure. Illustrated specimen from ANTXXIV/1, Stn 8, 3992–4390 m.

Leg 1 (Fig. 71E) exopod with articulation between exopod segments 2 and 3 well developed.

Male. Unknown

Distribution. *Bathycalanus adornatus* **n. sp.** is an abyssopelagic species so far found only in the southeastern Atlantic over the abyssal plains off Namibia and Angola (Fig. 46, Table 1). It was taken in hauls between approximately 4000 and 5000 m.

Species comparisons. *Bathycalanus adornatus* **n. sp.** is very like *Ba. richardi* except the genital double-somite in dorsal view is wider than long, with angular corners at the anterior one third, and the posterolateral borders of pedigerous somites 4 and 5 are extended into irregularly shaped, conspicuous lappets (Table 10). Genetic data suggest that this species is indistinguishable from some specimens of *Ba. bradyi* (see Fig. 113, Tables 14–17). Nevertheless, we do not hesitate to describe it as 'new' because of its morphological distinctness.

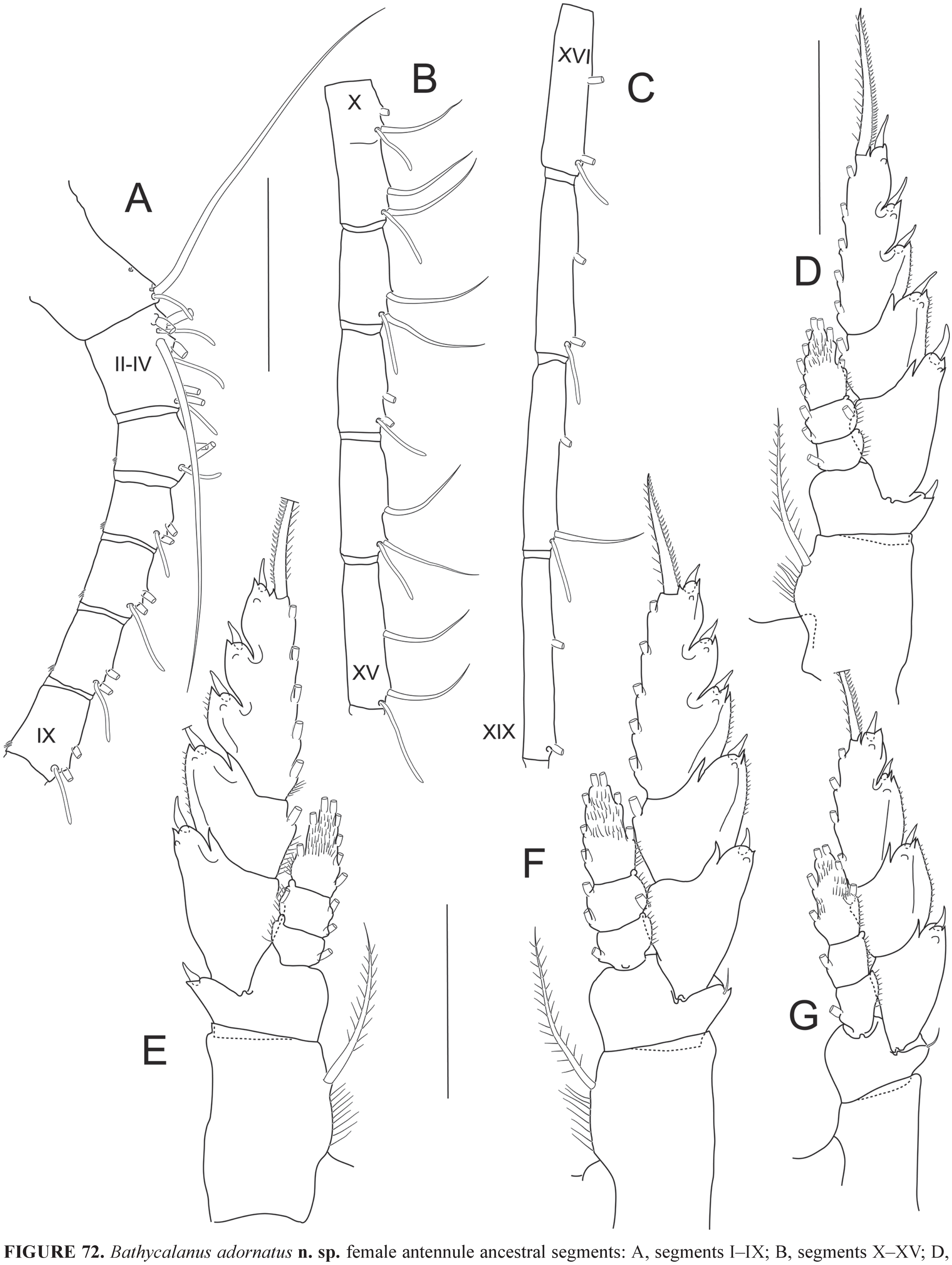

FIGURE 72. *Bathycalanus adornatus* **n. sp.** female antennule ancestral segments: A, segments I–IX; B, segments X–XV; D, segments XVI–XIX. Legs, anterior view: D, leg 2; E, leg 3; F, leg 4; G, leg 5. Scale bar represents 1.0 mm on all figures. Illustrated specimen from ANTXXIV/1, Stn 8, 3992–4390 m.

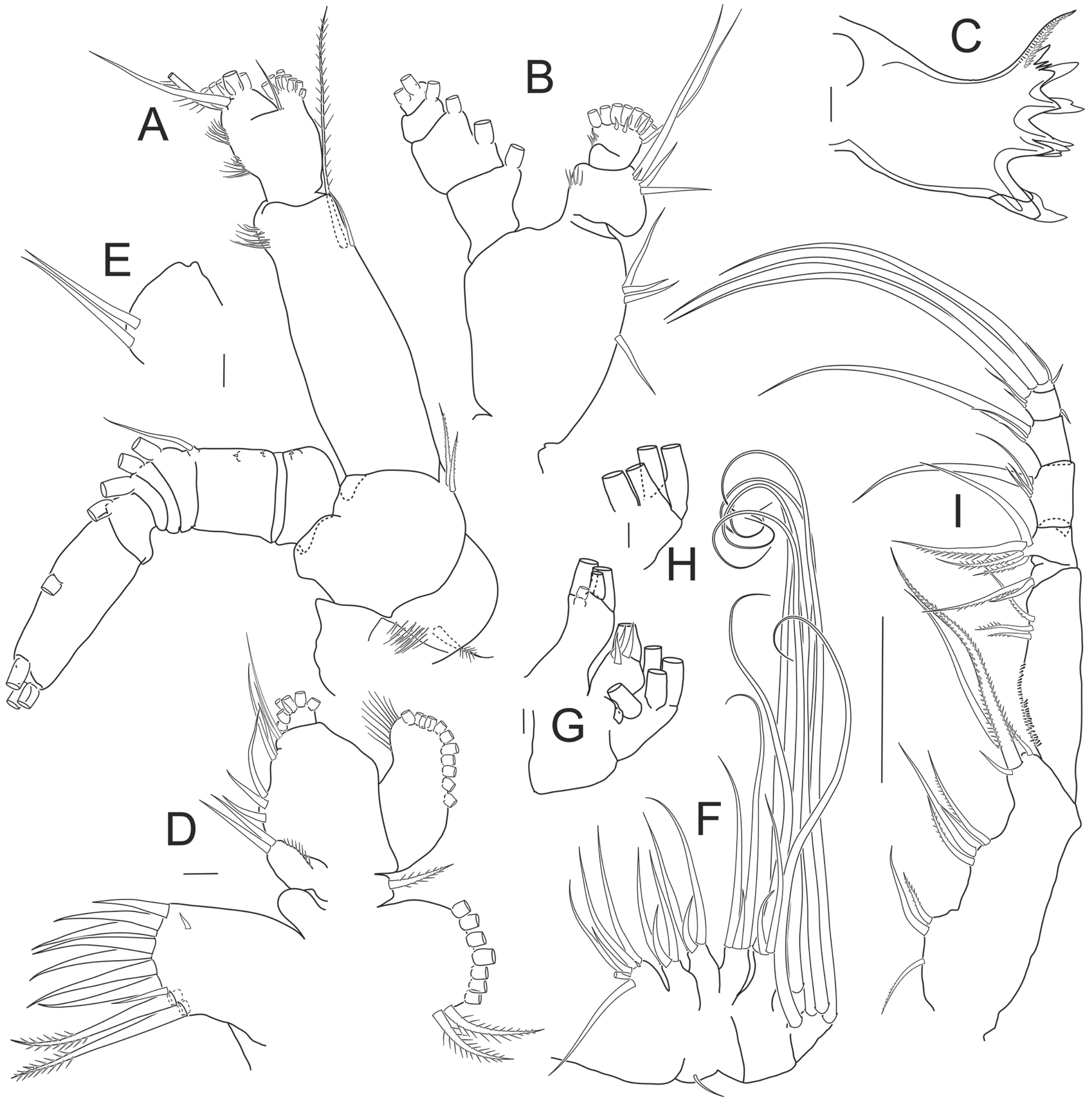

FIGURE 73. *Bathycalanus adornatus* **n. sp.** female: A, antenna; B, mandibular palp; C, mandibular gnathobase; D, anterior view of maxillule; E, posterior view of praecoxal arthrite of maxillule to show 2 posterior surface setae; F, maxilla; G, inner view of distal part of maxilla; H, outer view of endopod of maxilla; I, maxilliped. Scale bar represents 1.0 mm on figures F, I; 0.1mm on remaining figures. Illustrated specimen from ANTXXIV/1, Stn 8, 3992–4390 m.

Etymology. Species name derived from Latin adjective "*adornatus*" meaning decorated, embellished, referring to the lappets on the posterolateral borders of pedigerous somites 4 and 5.

Bathycalanus pustulosus **n. sp.**
(Figs 46, 74–76)

Bathycalanus sp.? Sewell, 1947, p. 34, fig. 5.

Type locality. 38.033º N, 124.183º W.

Material examined. MV66-II, Stn 5, IKMT, 0–5500 mwo, 1♀ (9.7 mm) holotype.

Type specimens. Deposited in the collection of the Scripps Institution of Oceanography, California: Holotype female: PIC-140409-0014-HT.

Morphological description. Following description based on holotype specimen from MV66-II, Stn 5. As for genus with following additional specific level features.

Female (Fig. 74A–F). Total length 9.7 mm. Whole body covered in small pustules easily observed in profile. Anterior margin of head in dorsal view produced into distinct short rounded projection located dorsal to base of rostrum and bearing pair of stout small spine-like processes. In lateral view, posterolateral corners of pedigerous somite 5 produced into left rectangular and right rounded, asymmetrical lappets extending half way along genital double-somite in dorsal view. Genital double-somite symmetrical in dorsal view, about as wide as long, widest at midlength, with small genital operculum anteriorly situated, seminal receptacles not observed.

Antennules broken off.

Antenna (Fig. 75A, B) exopod segment IV with short setae not extending as far as distal border of segment VII and bearing short setules.

Maxillule (Fig. 75E, F) praecoxal arthrite with 13 setae including 2 on posterior surface and 2 setae on anterior surface, one of them very small; coxal endite with one seta, basal endites 1 and 2 with 2 subequal setae each; endopod segments with 2 (subequal), 2 (subequal), 5+1 anterior surface seta, respectively.

Maxilliped (Fig. 75I) syncoxal endite 4 with longest toothed seta extending beyond distal border of endopod segment 2.

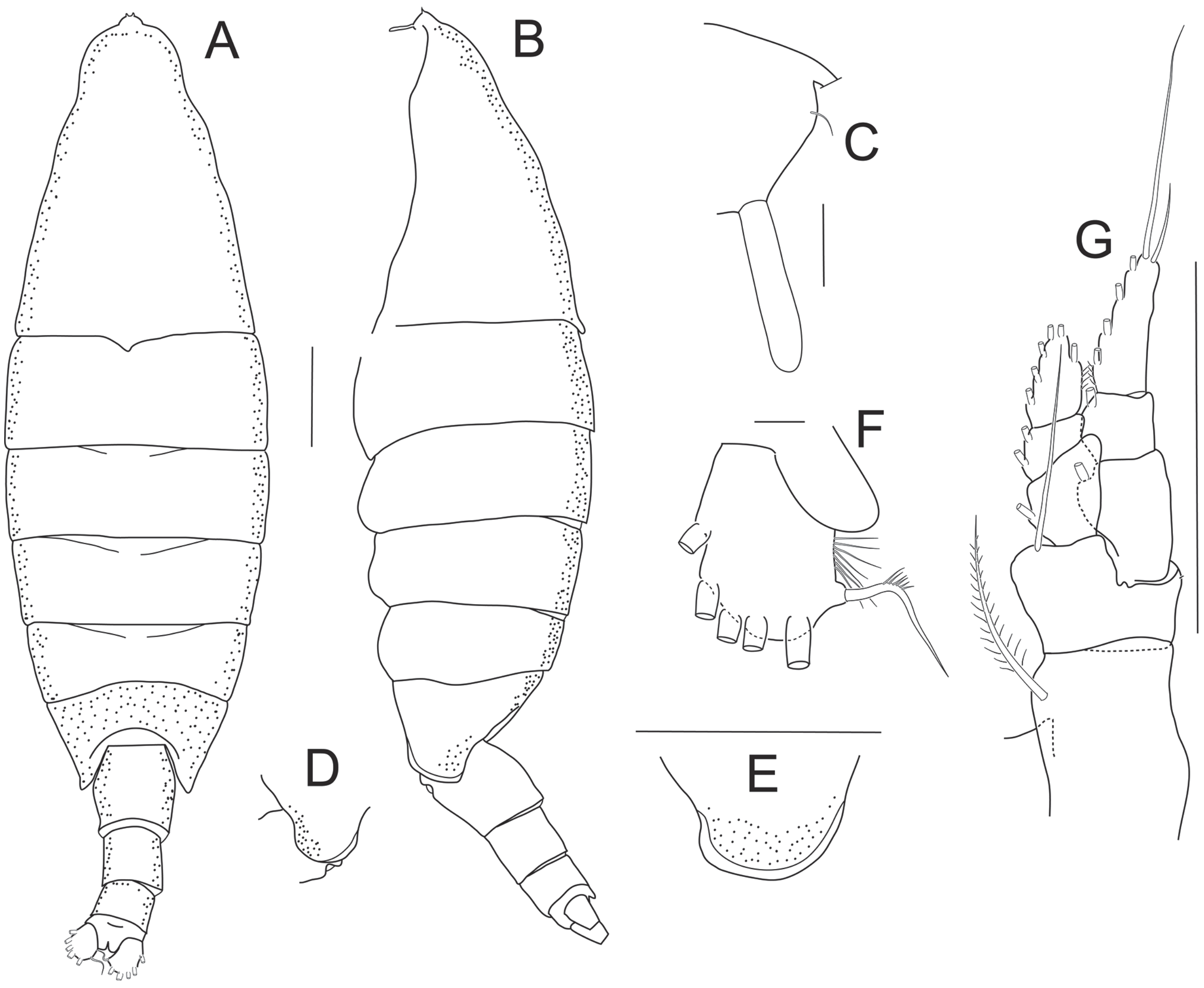

FIGURE 74. *Bathycalanus pustulosus* **n. sp.** female: A, dorsal view; B, lateral left view; C, lateral view of anterior head; D, right lateral view of posterior lappet of pedigerous somite 5; E, detail of lateral left posterior lappet of pedigerous somite 5; F, dorsal view of caudal ramus; G, anterior view of leg 1. Scale bars represents 1.0 mm on figures A, B, D, E, G; 0.1 mm on remaining figures. Illustrated specimen from MV66-11, Stn 5.

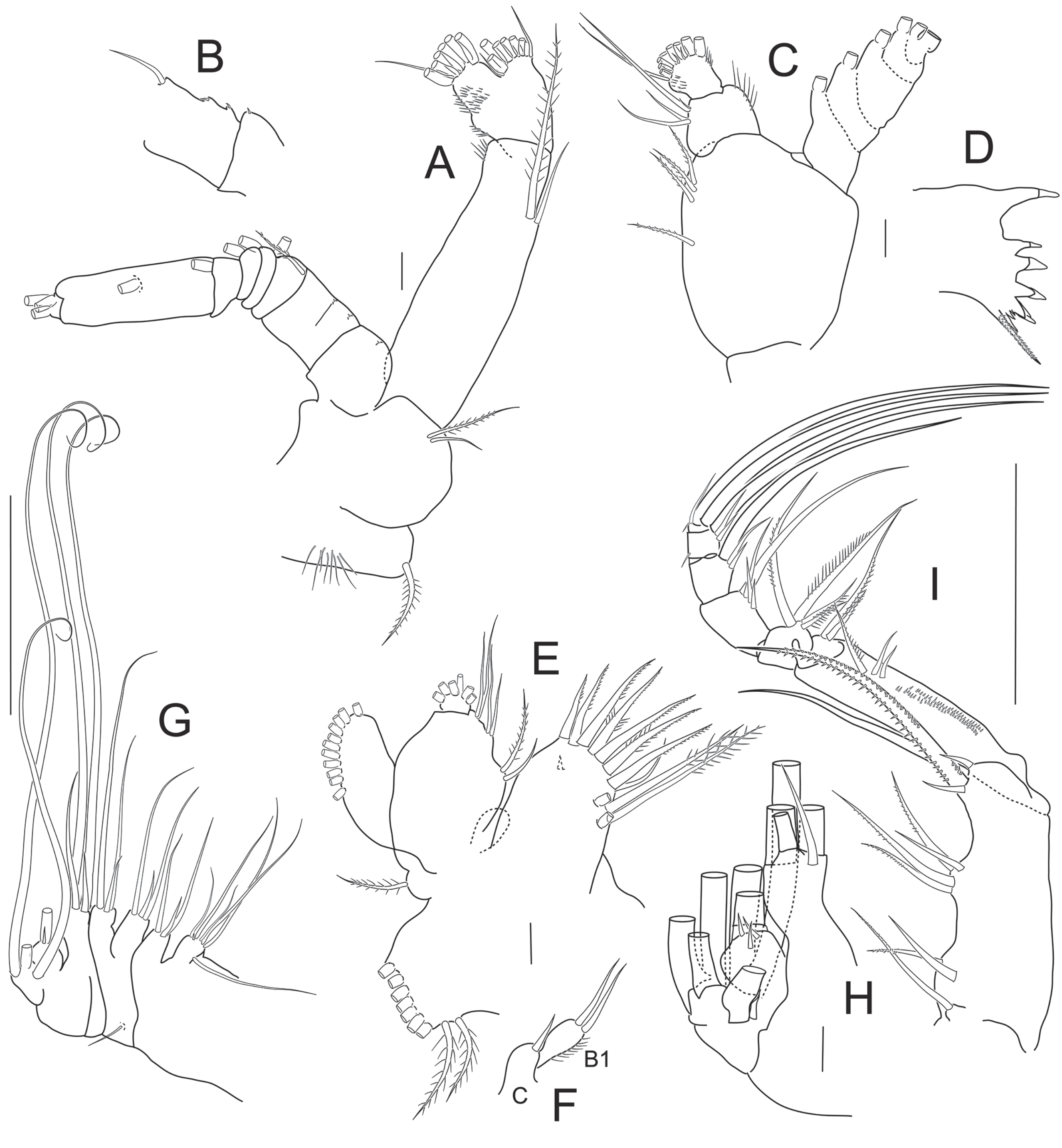

FIGURE 75. *Bathycalanus pustulosus* **n. sp.** female: A, antenna; B, proximal part of exopod of antenna from another view; C, mandibular palp; D, mandibular gnathobase; E, maxillule; F, coxal endite (C) and basal endite 1 (B1) of maxillule; G, maxilla; H, terminal part of maxilla; I, maxilliped. Scale bars represents 1.0 mm on figures G, I; 0.1 mm on remaining figures. Illustrated specimen from MV66-11, Stn 5.

Leg 1 (Fig. 74G) exopod with articulation between exopod segments 2 and 3 well developed.

Male. Unknown.

Remarks. It is possible that Sewell (1947) found a stage V individual (7.9 mm) in the Arabian Sea 0–1500 m. This possibility is based on the fact that the body of Sewell's specimen was covered by 'short ridges', the right posterolateral corner of pedigerous somite 5 is drawn out into a rounded lappet, and there were two subequal setae on the basal endite 2 of the maxillule. Nevertheless, Sewell (1947) does not record a seta on the coxal endite of the maxillule as is present in *Ba. pustulosus* **n. sp.**

Distribution. *Bathycalanus pustulosus* **n. sp.** is probably an abyssopelagic species. The present specimen was taken at the type locality off California (Fig. 46, Table 1).

Species comparisons. This species is related to *Ba. richardi* in that it has a pair of small anterior spine-like processes on the anterior head. Nevertheless, *Ba. pustulosus* **n. sp.** can be distinguished from all other species by a combination of 1) having thickenings covering the whole body; 2) the distinctive left rectangular and right rounded posterolateral lappets of pedigerous somite 5, viewed laterally; and 3) having 1 seta on the coxal endite and 2 setae on the second basal endite of the maxillule (Table 10).

Etymology. The specific name is derived from the Latin adjective *pustulosus* meaning "full of blisters" referring to the nature of the surface of the body.

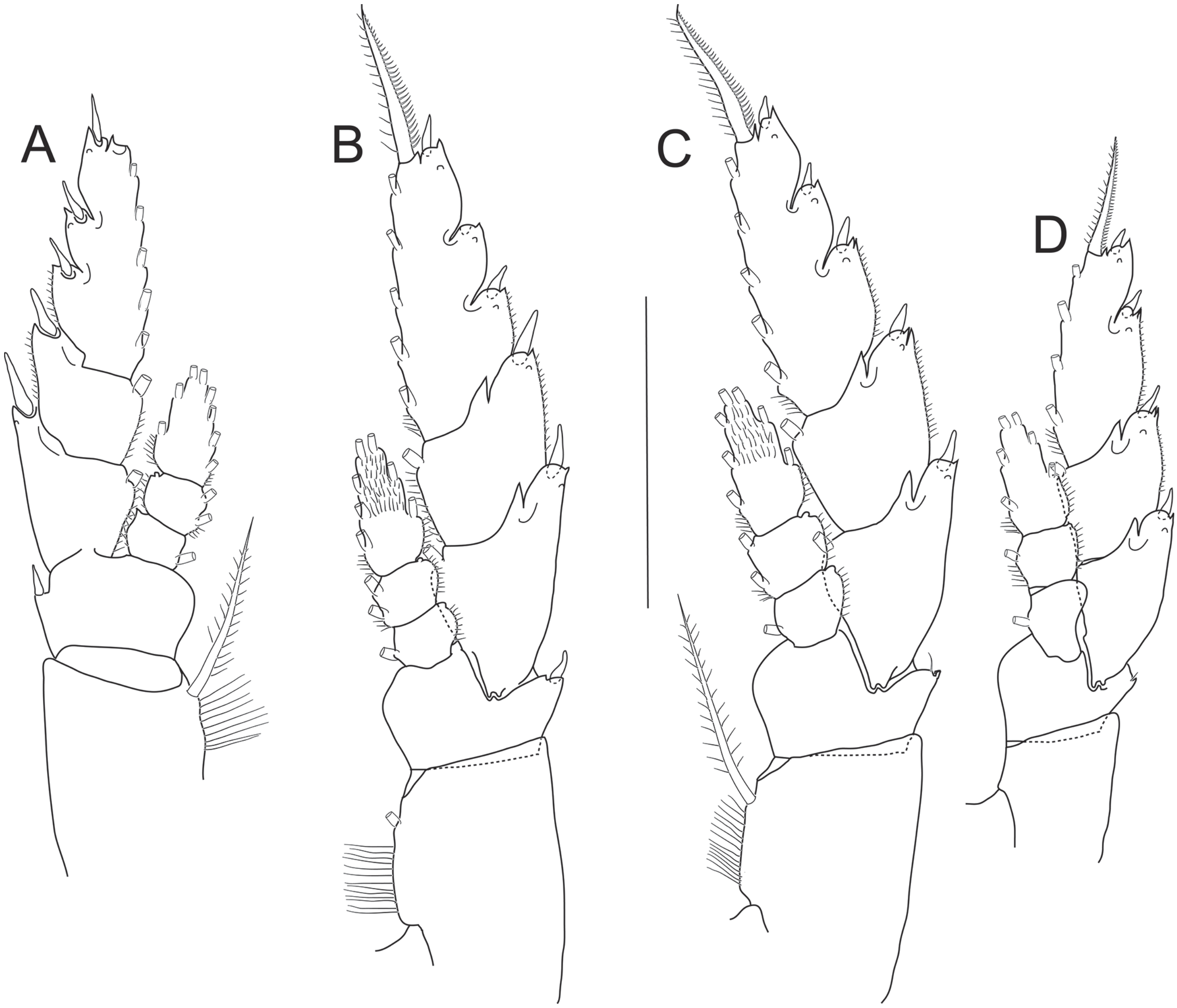

FIGURE 76. *Bathycalanus pustulosus* **n. sp.** female legs, anterior view: A, leg 2; B, leg 3; C, leg 4; D, leg 5. Scale bar represents 1.0 mm on all figures. Illustrated specimen from MV66-11, Stn 5.

***Bathycalanus bucklinae* n. sp.**
(Fig. 46, 77–80)

Type locality. 25.082º S, 9.584º W.

Material examined. ANTXXIV/1, Stn 8, MOC10, 2062–2990 m, 1♀ (11.2 mm), holotype.

Type specimens. Deposited in the collection of the National Institute of Water and Atmospheric Research, New Zealand: Holotype female: NIWA85233 (1 vial, 2 slides).

Morphological description. Following description based on holotype specimen from ANTXXIV/1, Stn 8. As for genus with following specific level features**.**

Female (Fig. 77A–E). Total length 11.2 mm. Anterior margin of head in dorsal view produced into rounded protrusion dorsal to base of rostrum and extending into pair of small divergent spine-like processes. In dorsal view, posterior border of pedigerous somite 5 extending into transparent, asymmetrical lappets, slightly longer on right. Genital double-somite symmetrical in dorsal view, widest at about anterior one third, 1.21 times longer than wide, seminal receptacles not observed.

Antennule (Fig. 78) extending beyond caudal rami by about 4 segments. Lengths of antennule segments (µm) as follows. Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements taken of ancestral segment I. I (320, 655); II–IV (399); V (209); VI (266); VII (330); VIII (367); IX (367); X–XI (695); XII (525); XIII (530); XIV (650); XV (818); XVI (916); XVII (978); XVIII (1071); XIX (1101); XX (1278); XXI (1296); XXII (897); XXIII (855); XXIV (934); XXV (877); XXVI (458); XXVII (823); XXVIII (47). Anterior and posterior borders of ancestral segments XVI–XXI smooth. Hair sensillum on ancestral segment II not accompanied by macula cribrosa (Fig. 78E).

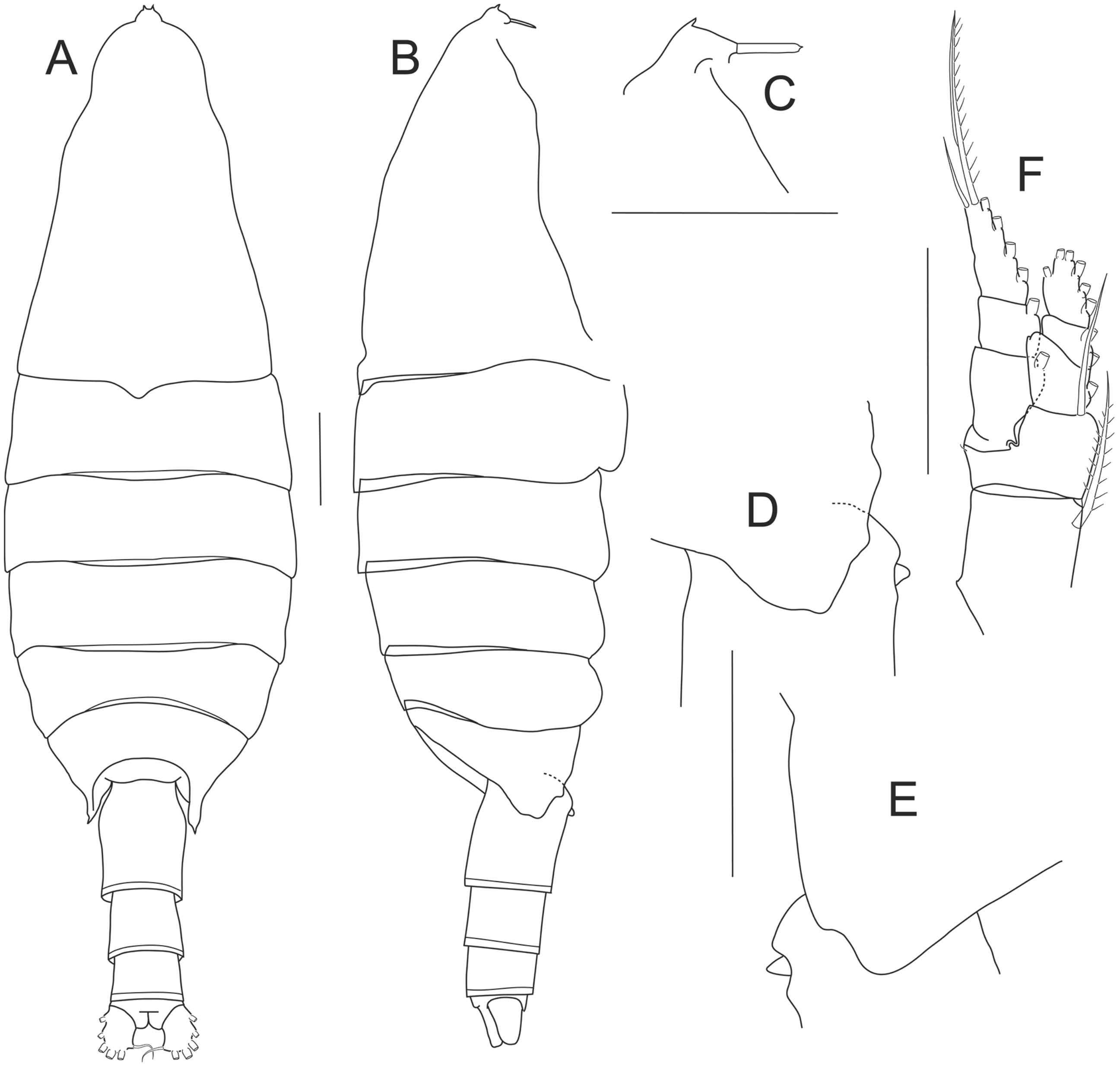

FIGURE 77. *Bathycalanus bucklinae* **n. sp.** female: A, dorsal view; B, lateral view; C, lateral view of anterior head; D, right lappet of pedigerous somite 5; E, left lappet of pedigerous somite 5; F, anterior view of leg 1. Scale bars represent 1.0 mm on all figures. Illustrated specimen from ANTXXIV/1, Stn 8, 2062–2990 m.

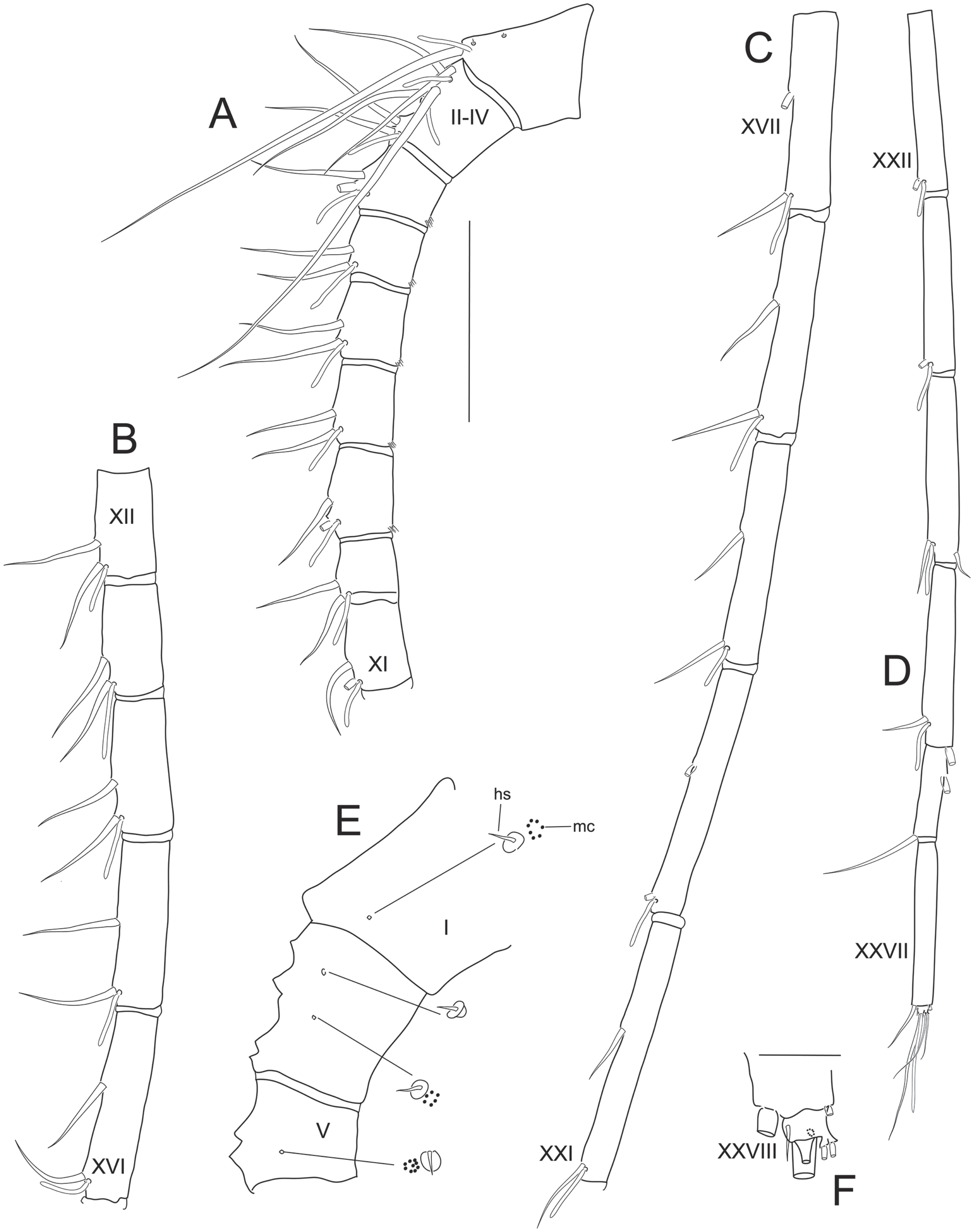

FIGURE 78. *Bathycalanus bucklinae* **n. sp.** female antennule ancestral segments: A, segments I–XI; B, segments XII–XVI; C, segments XVII–XXI; D, segments XXII–XXVIII; E, dorsal surface of segments I–V showing position of hair sensilla; F, detail of segment XXVIII. Scale bars represent 1.0 mm on figures A–E; 0.1 mm on remaining figure. Illustrated specimen from ANTXXIV/1, Stn 8, 2062–2990 m.

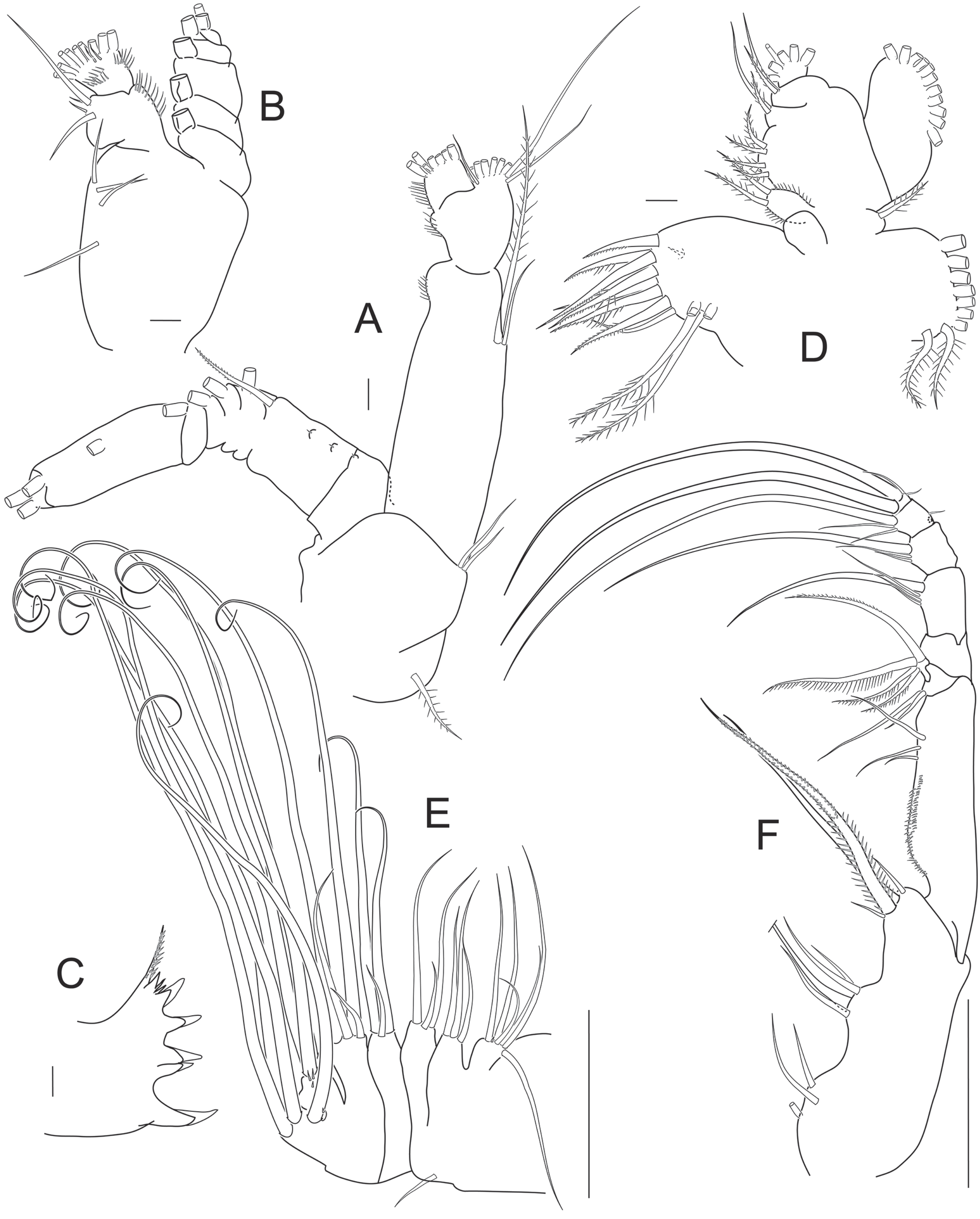

FIGURE 79. *Bathycalanus bucklinae* **n. sp.** female: A, antenna; B, mandibular palp; C, mandibular gnathobase; D, maxillule; E, maxilla; F, maxilliped. Scale bars represent 1.0 mm on figures E, F; 0.1 mm on remaining figures. Illustrated specimen from ANTXXIV/1, Stn 8, 2062–2990 m.

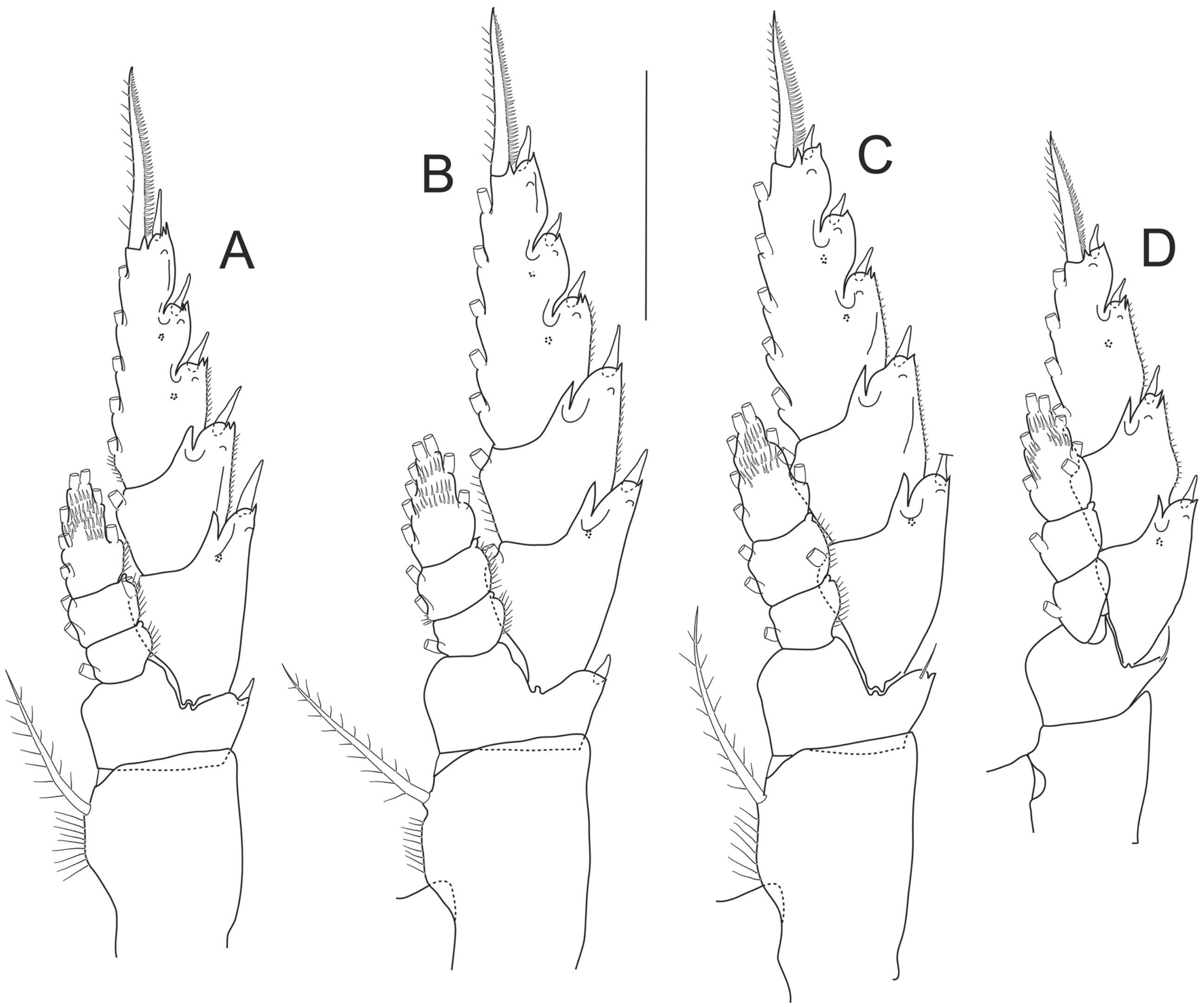

FIGURE 80. *Bathycalanus bucklinae* **n. sp.** female legs, anterior view: A, leg 2; B, leg 3; C, leg 4; D, leg 5. Scale bar represents 1.0 mm on all figures. Illustrated specimen from ANTXXIV/1, Stn 8, 2062–2990 m.

Antenna (Fig. 79A) exopod segment IV with short seta extending to distal border of segment VIII and bearing short setules.

Maxillule (Fig. 79D) praecoxal arthrite with 13 setae including 2 on posterior surface and 2 setae on anterior surface, one of them small; coxal endite without setae, basal endites 1 and 2 with 2 and 4 setae respectively; endopod segments with 2 (subequal), 2 (subequal), 5+1 smaller anterior surface seta.

Maxilliped (Fig. 79F) syncoxal endite 4 longest, toothed seta extending half way along endopod segment 2.

Leg 1 (Fig. 77F) exopod with articulation between exopod segments 2 and 3 well developed; distolateral corner of endopod segment 1 bilobed.

Male. Unknown.

Etymology. This species is named for Professor Ann Bucklin, University of Connecticut, who conceived and led the CMarZ programme.

Distribution. *Bathycalanus bucklinae* **n. sp.** is an upper abyssopelagic species taken from the type locality south of the Walvis Ridge over the Namibia Abyssal Plane in the South Atlantic at greater than 2000 m depth (Fig. 46, Table 1).

Species comparisons. This species is related to *Ba. richardi* in that it has a pair of small anterior spine-like processes on the head. Nevertheless, *Ba. bucklinae* can be distinguished from any other *Bathycalanus* species by a combination of having 1) pedigerous somite 5 with long asymmetrical posterolateral lappets; 2) body somites smooth and without pustules; 3) a genital double-somite with its widest part, in dorsal view, at one third the distance from the anterior border; 4) female antennule ancestral segment II hair sensillum not accompanied by macula cribrosa; and 5) 4 setae on the second basal endite of the maxillule (Table 10).

Bathycalanus unicornis Björnberg, 1968
(Figs 46, 81–86)

Bathycalanus unicornis Björnberg, 1968, pp 73–75, figs 1–14.

Type locality. 40.767º S, 76. 800º W**.**

Material examined. MV73-I, Stn 53, IKMT, 0–2000 m, 2♀ (9.8, 10.2 mm), 2♂ (8.3, 8.8 mm). ANTXXIV/1, Stn 8, MOC10, 2990–3992 m, 2♀ (9.3, 9.6 mm). Eltanin, Stn 175, IKMT, 2893 m, 1♀ Holotype USNM122566. Records from Natural History Museum, London: Discovery Stns, RMT8: 8508#78, 2500–3100 m, 3♀ (9.3, 9.3, 9.4 mm) BMNH 1993.859-861; 8509#20, 3000–3500 m, 1♀ (9.35 mm), BMNH 1993.858; 8509#27, 3500–4000 m, 2♀ (10.0 mm, 1 damaged) BMNH 1993.862-863.

Morphological description. Following description based on specimen from MV73-1, Stn 53. As for genus with following specific level features.

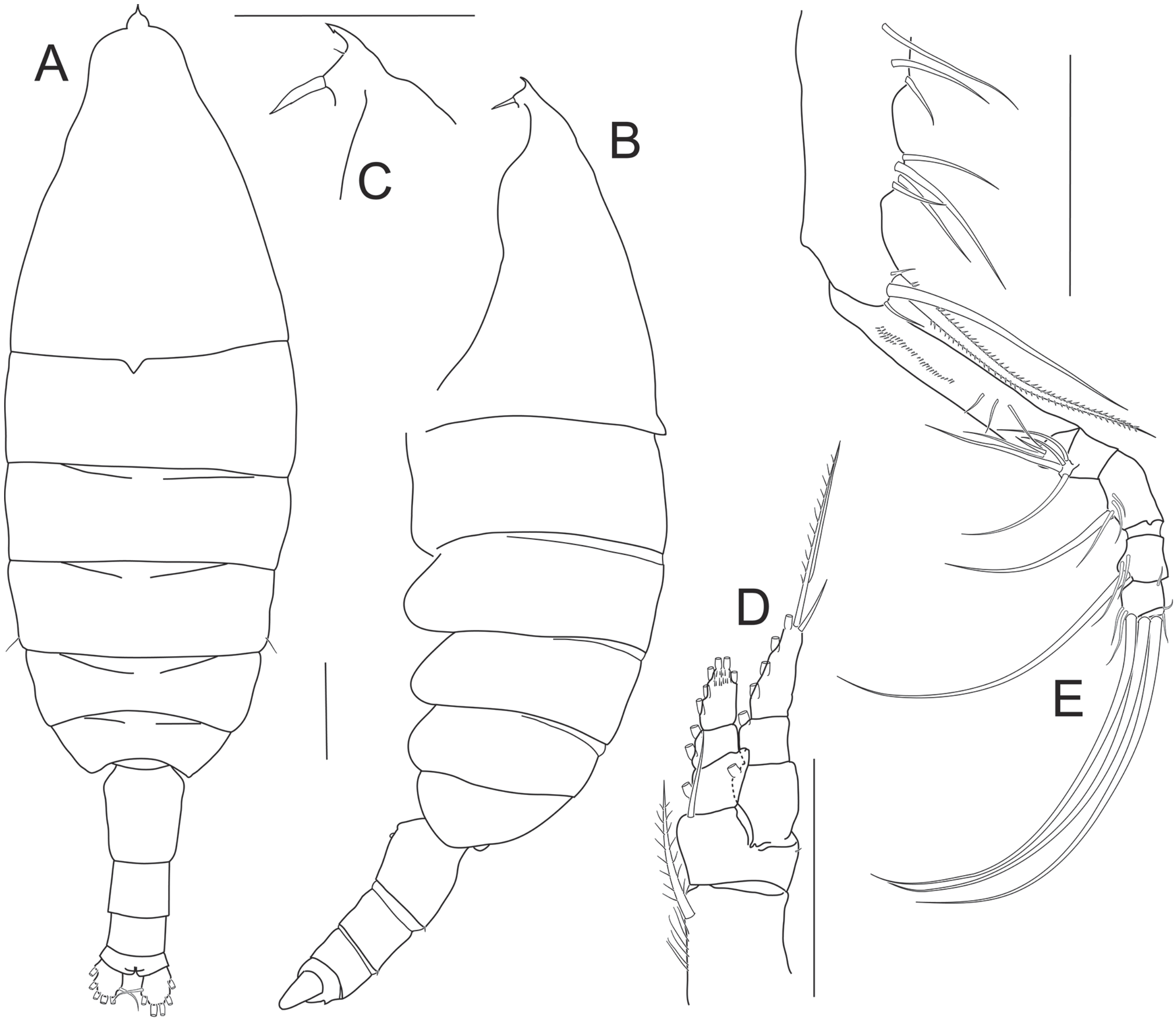

FIGURE 81. *Bathycalanus unicornis* Björnberg, 1968 female: A, dorsal view; B, lateral view; C, lateral view of anterior head; D, anterior view of leg 1; E, maxilliped. Scale bars 1.0 mm on all figures. Illustrated specimen from MV73-1, Stn 53.

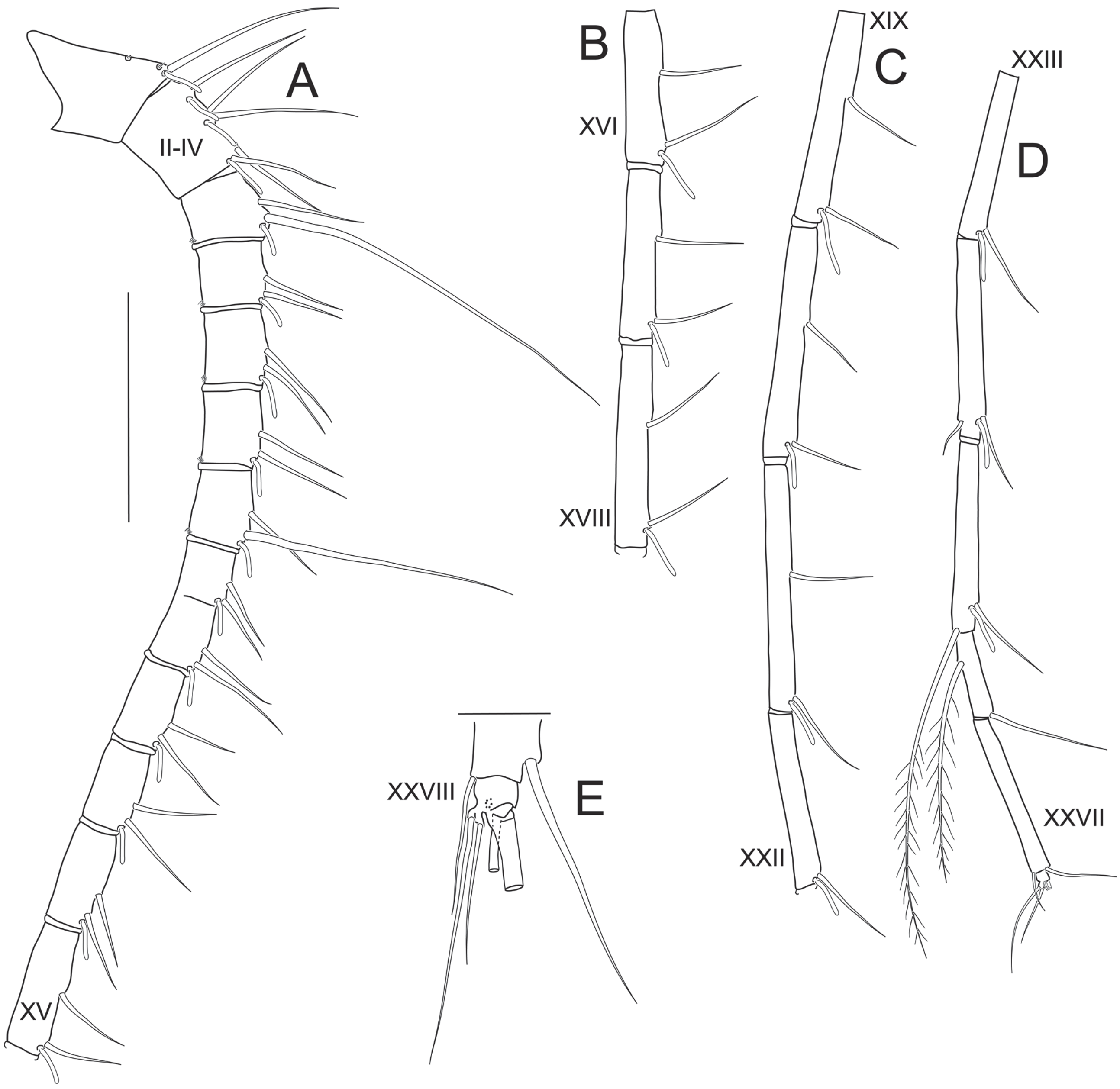

FIGURE 82. *Bathycalanus unicornis* Björnberg, 1968 female antennule ancestral segments: A, segments I–XV; B, segments XVI–XVIII; C, segments XIX–XXII; D, segments XXIII–XXVIII; (E) detail of segment XXVIII. Scale bars represent 1.0 mm on figures A–D; 0.1 mm on remaining figure. Illustrated specimen from MV73-1, Stn 53.

Female (Fig. 81A–C). Total length 10.5 mm (mean = 9.6 mm, range = 9.3–10.2 mm, n = 9). Anterior margin of head in dorsal view produced into single spine-like process, curved ventrally with ventral barb near tip. In lateral view, posterolateral corners of pedigerous somite 5 symmetrical, short and rounded, not extending posterior to widest part of genital double-somite. Genital double-somite symmetrical in dorsal view, widest at about anterior one eighth, 1.2 times longer than wide, seminal receptacles not observed.

Antennule (Fig. 82) extending beyond caudal rami by about 5–6 segments. Lengths of antennule segments (µm) as follows. Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements taken of ancestral segment I. I (308, 623); II–IV (365); V (217); VI (256); VII (315); VIII (305); IX (303); X–XI (537); XII (345); XIII (367); XIV (429); XV (552); XVI (675); XVII (737); XVIII (892); XIX (926); XX (1032); XXI (1059); XXII (778); XXIII (727); XXIV (872); XXV (842); XXVI (389); XXVII (741); XXVIII (38). Anterior and posterior borders of ancestral segments XVI–XXI smooth.

Antenna (Fig. 83A) exopod segment IV with short seta extending to distal border of segment VIII and bearing short setules.

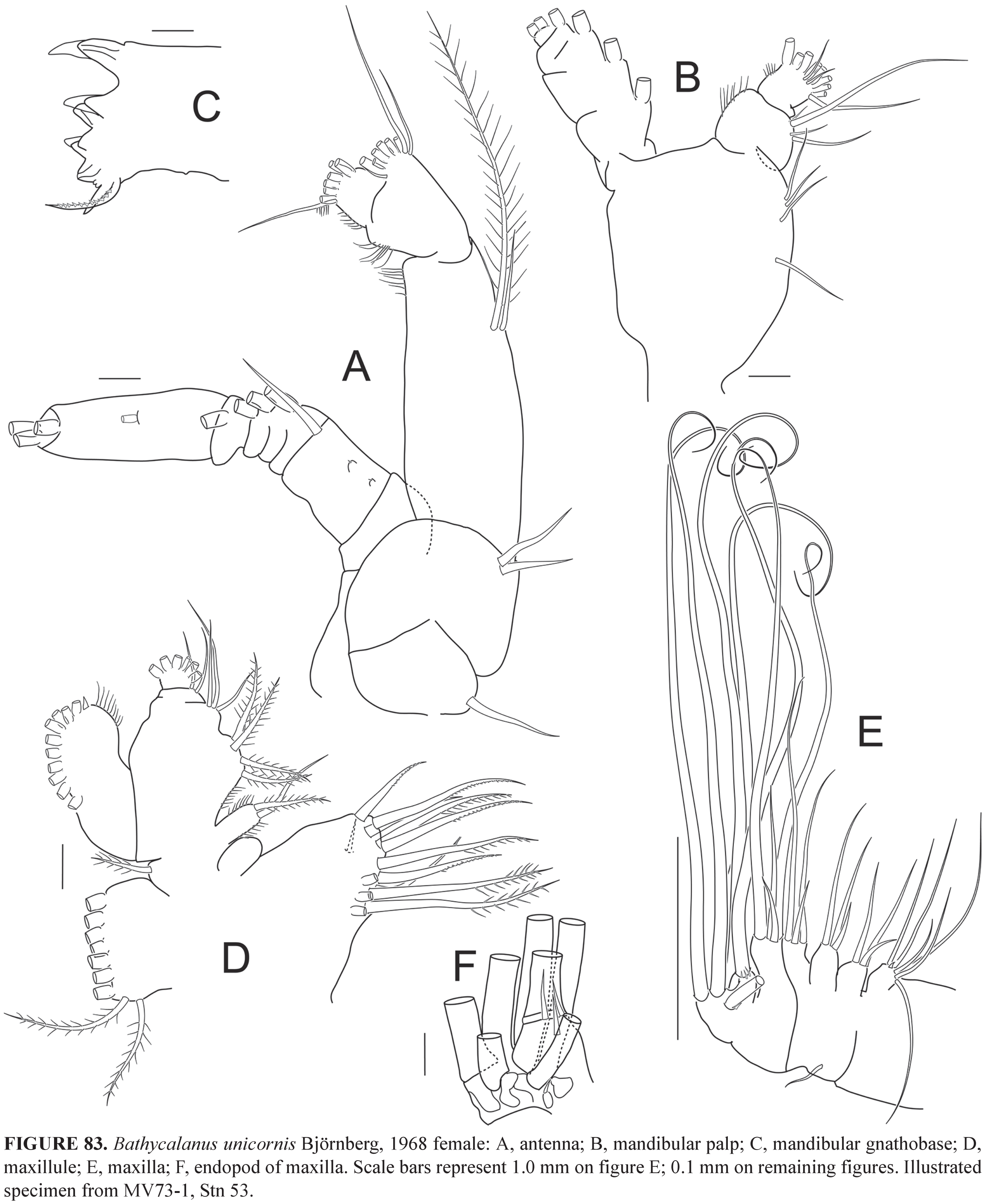

FIGURE 83. *Bathycalanus unicornis* Björnberg, 1968 female: A, antenna; B, mandibular palp; C, mandibular gnathobase; D, maxillule; E, maxilla; F, endopod of maxilla. Scale bars represent 1.0 mm on figure E; 0.1 mm on remaining figures. Illustrated specimen from MV73-1, Stn 53.

Maxillule (Fig. 83D) praecoxal arthrite with 14 setae including 3 on posterior surface and 2 setae on anterior surface, one of them small; coxal endite without setae, basal endites 1 and 2 with 2 and 4 setae respectively; endopod segments with 2/3, 2, 5+1 smaller anterior surface seta.

Maxilliped (Fig. 81E) syncoxal endite 4 longest, toothed seta extending beyond distal border of endopod segment 2.

Leg 1 (Fig. 81D) exopod with articulation between exopod segments 2 and 3 well developed; distolateral corner of endopod segment 1 bilobed.

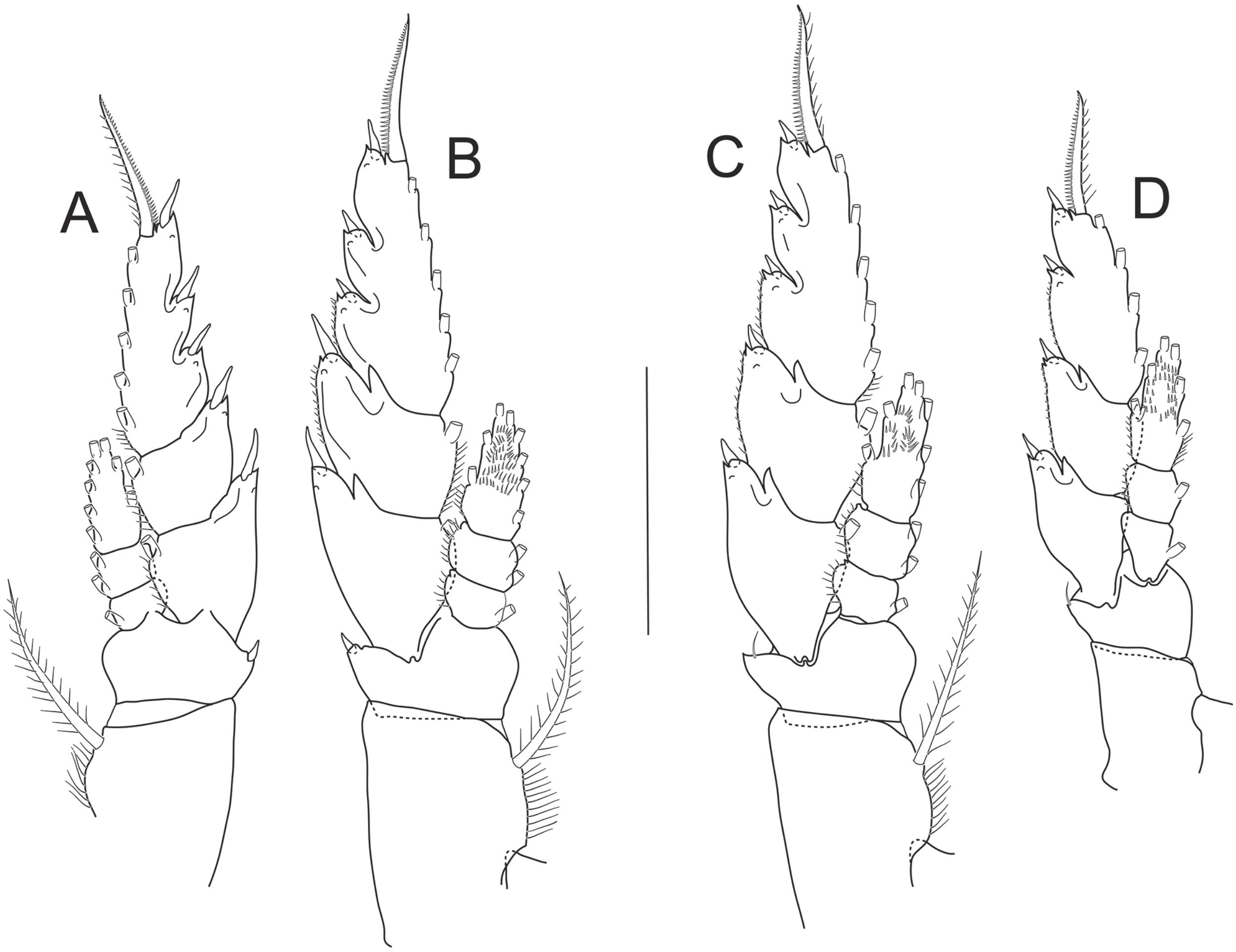

FIGURE 84. *Bathycalanus unicornis* Björnberg, 1968 female: A, posterior view of leg 2; B, anterior view of leg 3; C, anterior view of leg 4; D, anterior view of leg 5. Scale bar represents 1.0 mm on all figures. Illustrated specimen from MV73-1, Stn 53.

Male (Fig. 85A–C). Total length 8.8, 8.3 mm. Anterior margin of head in dorsal view produced into single spine-like process curved ventrally, with ventral barb near tip. In lateral view, posterior corners of pedigerous somite 5 rounded, extending almost to posterior border of urosomite I.

Antennule (Figs 85D, 86) extends beyond caudal rami by about 5–6 segments on left. Left antennule similar to that of female. Right ancestral segment XVIII widened by anterior border ridge—2ms, 1a; XIX with proximal ridge—1ms, 1 fused element with free tip, 1a; XX—with 1 long fused element with free tip, 1ms, 1a; XXI–XXIII—2 fused elements with free tips (proximal element largely overlapping distal element), 1a, 1 vestigial s?, 1ms.

Leg 5 (Fig. 85E–G) extending just beyond third free urosomite, asymmetrically developed; left leg slightly longer than right leg, outer borders of exopod segments without surface thickenings. Right exopod segment 2, inner border seta in form of short thickened proximal part and apparently articulated tapering distal part. Inner border of right exopod segment 3 naked apart from proximal setules. Left exopod segment 2 inner border specialised seta in form of spherical proximal part with outer naked rounded lobe and inner pair of long lashes clothed in very long setules. Inner border of left exopod segment 3 irregular in shape, bordered by setules from proximal to near inner spine.

Remarks. This is the second time *Ba. unicornis* has been recorded since its original discovery off Valdivia, Chile (Björnberg 1968). Here, we have corrected some observations, highlighted additional characters distinguishing the female of this species from other *Bathycalanus* and added a description of the male.

Morphological variation. There appears to be some variation in the setation of the maxillule as there may be 2 or 3 setae on endopod segment 1 in the same individual, although it is not possible to be sure if this observed variation is due to damage.

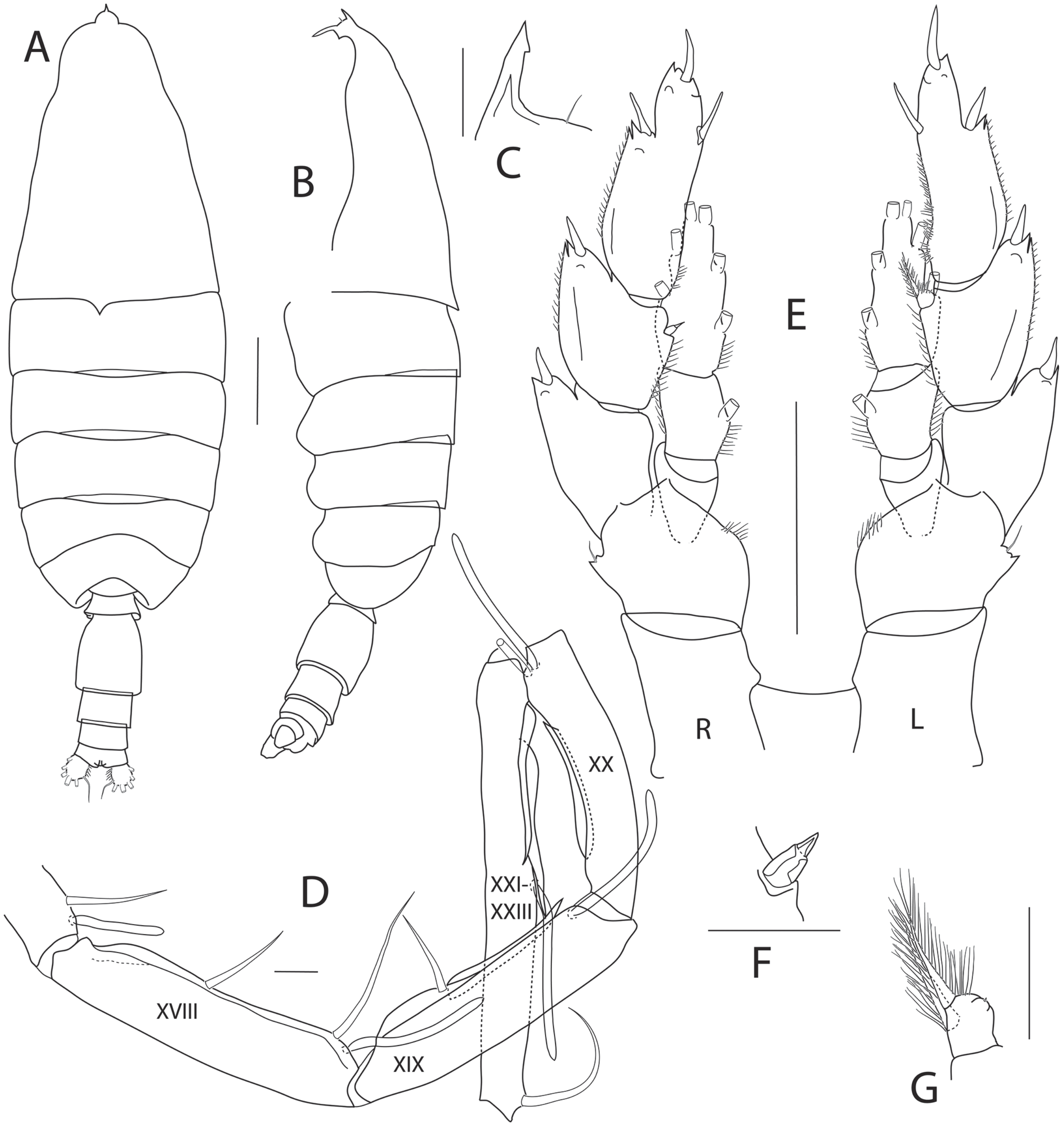

FIGURE 85. *Bathycalanus unicornis* Björnberg, 1968 male: A, dorsal view; B, lateral view; C, lateral view of anterior head; D, ancestral segments XVIII–XXIII of right antennule; E, posterior view of leg 5; F, inner distal corner modified seta of right exopod segment 2 of leg 5; G, inner distal specialised seta of left exopod segment 2 of leg 5. Scale bars represent 1.0 mm on figures A, B, E; 0.1 mm on remaining figures. Illustrated specimen from MV73-1, Stn 53.

Distribution. The present records extend the distribution into the Atlantic Ocean over the abyssal plain off Namibia and northwards into the eastern Pacific to off the coast of Mexico (Fig. 46, Table 1) (Björnberg 1968). *Bathycalanus unicornis* is an upper abyssopelagic species taken from depths < 2000 to > 3000 m.

Species comparisons. *Bathycalanus unicornis* is unique amongst *Bathycalanus* in several respects (Table 10): 1) the anterior head has 1 large barbed spine-like process projecting anteriorly and curving ventrally; 2) the genital double-somite, in dorsal view, is 1.2 times longer than wide and the widest part is at the anterior one eighth; 3) the posterolateral borders of pedigerous somite 5 are very short and rounded in lateral view; 4) the maxillule has 3 posterior surface setae on the praecoxal arthrite; 5) the male leg 5 is unique among currently known *Bathycalanus* in having a setal remnant on the inner border of the right exopod segment 2; and 6) in having 2 moderately long setulose lashes on the inner specialised seta of left exopod segment 2.

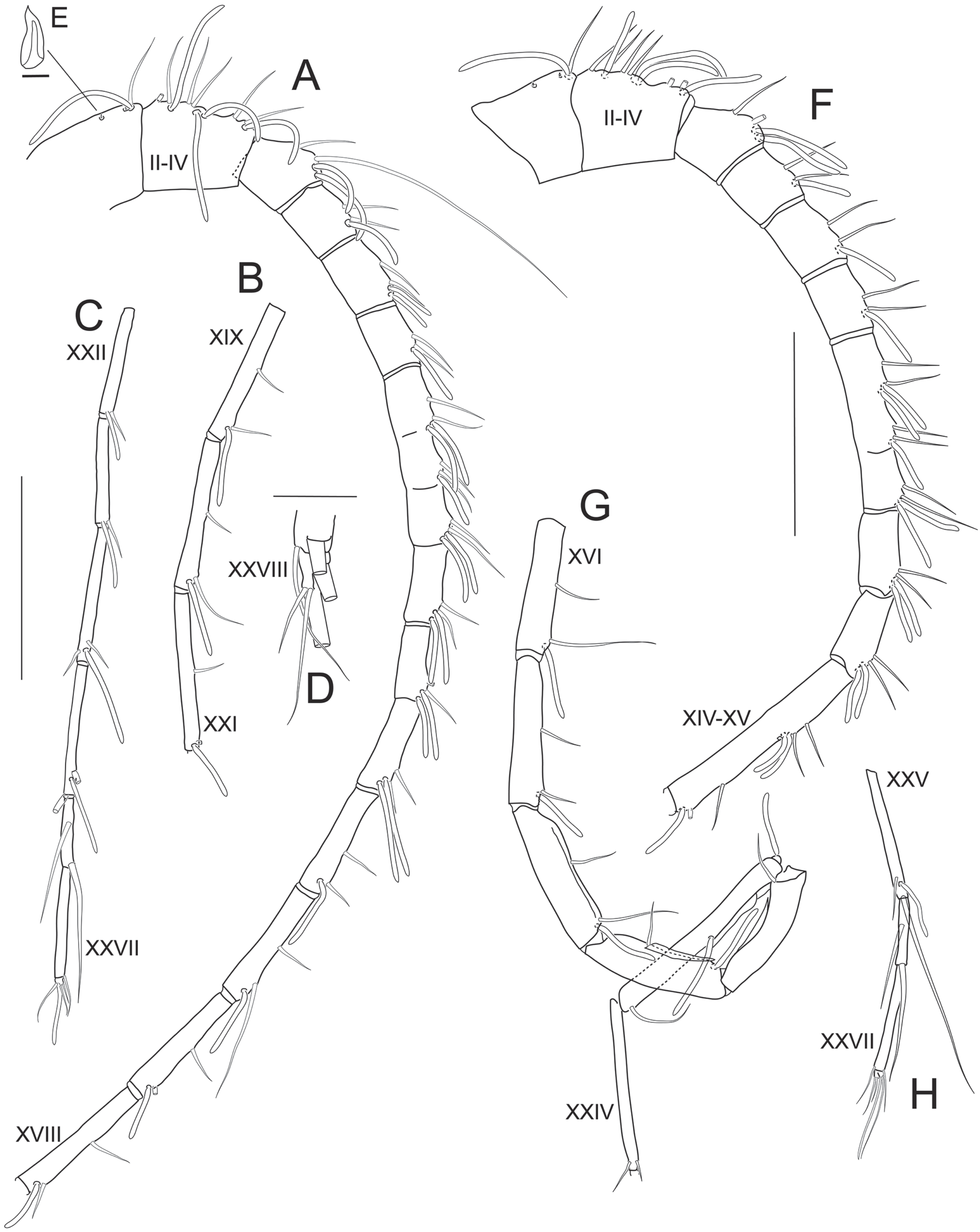

FIGURE 86. *Bathycalanus unicornis* Björnberg, 1968 male ancestral antennule segments. Left antennule: A, segments I–XVIII; B, segments XIX–XXI; C, segments XXII–XXVIII; D, detail of segment XXVIII. Right antennule: F, segments I–XV; G, segments XVI–XXIV; H, segments XXV–XXVIII. Scale bars represent 1.0 mm on figures A–C, F–H; 0.1 mm on remaining figure. Illustrated specimen from MV73-1, Stn 53.

***Bathycalanus eximius* Markhaseva, 1983**
(Fig. 46)

Bathycalanus eximius Markhaseva, 1983, pp 197–198, fig. 87.

Type locality. Kurile-Kamchatka Trench.

Material examined. Dr Elena Markhaseva, Institute of Zoology, St Petersberg, Russia, kindly re-examined the holotype material of this species and has augmented her original description with the following additional observations.

Morphological description. As for genus with following specific level features.

Female. Total length 11.9 mm. Anterior margin of head in dorsal view with low projection bearing pair of small spine-like processes. In lateral view posterior corners of pedigerous somite 5 symmetrical, rounded, but slightly pointed in dorsal view. Genital double-somite markedly swollen and symmetrical in dorsal view, wider than long, with lateral surfaces ornamented with large spinules.

Antennule extending beyond caudal rami by 4–6 segments. Anterior and posterior borders of ancestral segments XVI–XXI smooth.

Antenna exopod ancestral segment III with small seta and segment IV with short seta extending beyond segment VIII, no sign of setae on ancestral segments I and II.

Maxillule praecoxal arthrite with 14 setae including 3 on posterior surface and 1 longer and 1 smaller on anterior surface; coxal endite without setae, basal endites 1 and 2 with 2 and 4/5 setae respectively; endopod segments with 2, 2, 5+1 small anterior surface seta**;** basal exite with 1 seta, epipodite with 7 long and 2 short, reduced setae.

Maxilliped syncoxa endite 4 longest seta extending beyond distal border of endopod segment 2; endopod segments 2–6 with 4 (including 3 small), 3 (including 2 small), 3 (including 2 small) + 1, 4 setae (2 large and 2 very small of which one on outer border), respectively.

Leg 1 exopod segment 3 with 1 outer border spine.

Male. Unknown

Distribution. *Bathycalanus eximius* is probably a deep abyssopelagic species and is known only from the Kurile-Kamchatka Trench in a haul with 7040 metres of wire out at approximately 5000 m depth.

Species comparisons. *Bathycalanus eximius* is distinguished from all other *Bathycalanus* by (Table 10): 1) having a very swollen genital double-somite bearing lateral spinules; and 2) having the second basal endite of the maxillule with 4 setae.

Genus *Elenacalanus* nom. nov.

Differential diagnosis. As for Megacalanidae plus following character states. Anterior head usually rounded and without anterior spine-like processes but may be crested (*E. princeps*). Rostral filaments bluntly tapering. Genital double-somite bulbous, widest in dorsal view at about midlength, usually as wide as long. Posterolateral corners of pedigerous somite 5 usually bluntly triangular or rounded in *E. sverdrupi*. Female antennule ancestral segment XXIII with aesthetasc; female and male ancestral segments I–V with hair sensillum on dorsal surface and adjacent macula cribrosa except sometimes on segment IV. Right male antennule segments XIV–XV and XXI–XXIII fused, segments XIX, XX and XXI with fused gripping elements. Antennal exopod ancestral segments I–III without seta, on segment IV seta absent (*E. princeps*) or, more usually, extending short of the distal end of exopod. Mandibular gnathobase with ventral tooth set at right angles to main plane of gnathobase therefore appearing tapering, similar to other teeth; endopod segment 1 with 2 setae, endopod segment 2 with 9 setae. Maxillule with 2 or 3 posterior surface setae on praecoxal arthrite, coxal endite without setae, basal endites 1 and 2 with 2, 1–3 setae, respectively, endopod segments 1 and 2 with 1 seta each at most, endopod segment 3 with 4 + 1 small setae (often 4 in male), basal exite with or without seta, coxal epipodite usually with 7 + 2 proximal reduced setae (sometimes absent). Setae of maxilla endopod curled into semicircle distally but not completely curled on themselves, with row of fine, long dense setules along distal half of concave surface; long setae extend anteriorly as far as rostrum, none of setae with auxiliary spinules; 1 inner seta of endopod segment 2 vestigial. Maxilliped endopod segments 2–6 with 4, 1, 1, 1 (outer seta absent), 2 long + 0-2 small setae (sometimes outer setae absent). Leg 1 basis without anterodistal hook-like process, exopod segments 1 and 2 without outer border spines, exopod segment 3 with 2 outer border spines. Setae on some male mouthparts reduced in size.

Description. Female. Anterior margin of head in dorsal view rounded and without spine-like processes but may be crested (*E. princeps*); posterolateral borders of pedigerous somite 5 bluntly triangular in lateral view (or rounded in *E. sverdrupi*). Rostrum extending into two long, ventrally-directed, bluntly tapering filaments. Urosome of four free somites, genital double-somite bulbous with smoothly curving lateral, dorsal and ventral borders usually as wide as long, or wider than long. Caudal rami with seta I absent, setae II and III lateral, setae IV–VI terminal (seta V longest), seta VII inserted at inner distal corner on small projection.

Antennule with ancestral segments II–IV, X–XI fused, XXVII and XXVIII separate. Most setae of modified type (ms) or aethetascs (a), longest setae on at least segments V, VI, XVIII, XXV, and XXVI. Setation of segments as follows: I—1ms, 2ss (vestigial), 1a; II to XXI—2ms, 1a; XXII to XXIII—1ms, 1a; XXIV to XXV—1+1ms, 1a; XXVI—1+1ms; XXVII—1+1ms; XXVIII—3ms, 1a, 1ss. Oblique row of small setules on posterodistal border of ancestral segments V–IX; dorsal surface hair sensillum and macula cribrosa on variable numbers of segments I–V; ventral surfaces of ancestral segments XIV to XVII without teeth, and anterior and posterior borders of segments smooth. Maculae cribrosae present at base of all aesthetascs including segment XVIII.

Antenna with separate coxa and basis; coxa with 1 short inner seta and inner tuft of setules, basis with 2 inner setae, one plumose, other bordered by 2 rows of short setules. Exopod about same length as endopod; endopod 2-segmented although line of fusion between ancestral segments II and III visible on posterior surface; endopod segment 1 with 2 inner setae (one naked and one plumose) and short distal longitudinal row of outer setules, terminal segment with 9+7 setae and lined with long outer setules; exopod with arthrodial membrane present between ancestral segments I and II, arthrodial membranes between ancestral segments II–III, III–IV, IV–V not completely developed although signs of partial demarcation between some or all of ancestral segments II and III, III and IV, and IV and V sometimes visible; ancestral segments VI–VIII expressed and segments IX and X fused. Terminal segment IX–X with 1 + 3 terminal setae, segments V–VIII each with long plumose seta, ancestral segments I–III without setae, segment IV with or without seta.

Mandible coxal gnathobase with five complex teeth with opaline tips, largest tooth set at right angles to main plane of gnathobase, ventrally situated, tapering when viewed at right angles to broad plane of gnathobase, separated from adjacent tooth by wide gap; 4 following teeth progressively decreasing in size, but 2 teeth immediately adjacent to large ventral tooth not in same plane, one being more anterior, other posterior thus appearing to lie nearly on top of one another when mounted; 3 or fewer simpler teeth without opaline tips follow, dorsal-most tooth longest; and finally, 1 lash-like element situated dorsally, bordered by wide setules. Basis usually with 4 inner setae (3 in *E. sverdrupi*); endopod 2-segmented, segment 1 with large inner lobe and 2 distal inner setae (apparently distal and proximal setae of *Megacalanus* absent), segment 2 usually with 9 terminal setae (2 surface setae absent); exopod 5-segmented with 1, 1, 1, 1, 2 setae.

Maxillule praecoxal arthrite with 13 or 14 setae including 2 posterior surface setae (or 3 in *E. sverdrupi*) and 1 distoanterior surface seta; coxal endite poorly developed, without setae, epipodite with 7 long setae and with 2 proximal setae either very reduced or absent; basal endites 1 and 2 with 2 and 1–3 setae, respectively; coxal exite seta absent or present as vestige; basis and endopod segments 1 and 2 fused, segments 2 and 3 expressed; endopod segments with 1, 0–1, 4+1 posterior surface setae, respectively; exopod with 11 setae.

Maxilla praecoxal endites 1 and 2 with 6 setae + 1 small spine and 3 setae, respectively; coxal endites 1 and 2 with 3 setae each, coxal epipodite with 1 vestgial or relatively well-developed seta; basal endite longest with 4 setae (2 of them short); endopod segment 1 with short lobe bearing 3 vestigial + 1 large seta, endopod segments 2–4 apparently with 3 (1 proximal inner seta vestigial), 2, 2 setae, respectively. Inner surfaces of praecoxal endite 2, coxal endites 1 and 2 and basal endite each with 1 short seta lined with 2 rows of spinules along distal half whereas other setae with rows of spinules; coxal endite 2 usually with short setae, also only 1 seta curled distally (hardly curled in *E. inflatus*); basal endite and endopod segments 1–4 with very long setae (stiffer than in *Bathycalanus*), curling distally (but not curling completely back on themselves as in *Bathycalanus*), lined along more than half distal part with very fine long spinules. None of setae on maxilla with auxiliary spinules although inner distal seta of endopod segment 2 bears row of spinules along convex, proximal-facing surface in addition to fine spinules along concave, distal-facing border. Longest setae extend to rostrum when maxilla directed ventroanteriorly.

Maxilliped directed ventrally so setae on syncoxa and basis directed into animal's midline; syncoxa endites with 1, 2, 4, 4 setae, longest seta of endite 4 rarely extends beyond endopod segment 1. basis with 3 setae, elongate patch of possibly bifurcate setules on anteroproximal surface, endopod segment 1 mostly separate from basis and bearing 2 setae, 1 longer seta with long spinules along one edge, short seta with smooth, wide basal part then rapidly tapering and lined distally by 2 rows of long spinules; endopod segment 2 with 4 setae, 3 of them bordered on one side by long spinules, 1 seta with much shorter spinules; segments 3–6 with 1, 1, 1, 2 long + 0/1/2 small setae, endopod segment 5 without outer border seta.

Legs 1–5 biramous, each ramus 3-segmented with following setal formula (Roman numerals indicate spines, Arabic numerals setae, outer border setation listed to left in each group separate by ';'):

Leg 1 (Coxa 0-1. Basis 1-1. Exopod 0-1; 0-1; II,1,4. Endopod 0-1; 0-2; 1,2,3);

Leg 2 (Coxa 0-1. Basis I-0. Exopod I-1; I-1; III,1,5. Endopod 0-1; 0-2; 2,2,4);

Leg 3 (Coxa 0-1. Basis I-0. Exopod I-1; I-1; III,1,5. Endopod 0-1; 0-2; 2,2,4);

Leg 4 (Coxa 0-1. Basis 1-0. Exopod I-1; I-1; III,1,5. Endopod 0-1; 0-2; 2,2,3);

Leg 5♀ (Coxa 0-0. Basis 1-0. Exopod I-0; I-1; II,1,4. Endopod 0-1; 0-1; 2,2,2).

Leg 1 basis inner distal seta curved in *E. inflatus* but almost straight in other species, outer distal seta rudimentary, macula cribrosa on anterior surface adjacent to insertion of exopod segment 1 although sometimes difficult to see, exopod segments 1 and 2 without outer distal spines, segment 3 with 2 outer border spines, distolateral corner of endopod segment 1 rounded. Legs 2–4 with pore openings located on anterior surfaces at base of outer edge spine of exopod segments 1–3, outer border of exopod segment 2 and outer proximal border of exopod segment 3 extends into thin flange bordered by short setules; endopod segment 1 outer distal corner rounded. Leg 5 with outer distal corner of endopod segment 1 rounded; pore openings on anterior surface at base of outer border spines; outer border of exopod segment 2 and outer proximal border of exopod segment 3 extends into thin flange bordered by short setules.

Male. Anterior margin of head and rostrum similar to that of female. Urosome of five free somites.

Antennule asymmetrically developed, geniculate on right; aesthetascs larger than in female, doubled on both sides on at least segments III, V, VII–IX, XI–XIII. Right antennule geniculate between segments XX and XXI, with ancestral segments I/II–IV, XIV–XV, XXI–XXIII fused, IX–XII fused or separate, but XXVII and XXVIII separate. Most setae of modified type (ms) or aesthetascs (a). Setation I–IV—7ms, 1s, 5a; V—2ms, 2a; VI—2ms, 1a; VII—2ms, 2a; VIII—2ms, 2a; IX–XII—8ms, 7a; XIII—2ms, 2a; XIV–XV— 4ms, 2a; XVI to XVIII—2ms, 1a; XIX—1ms, 1 fused gripping element, 1a; XX—1 fused gripping element, 1ms, 1a; XXI–XXIII—2 fused gripping elements, 1a, 1s, 1ms; XXIV—1+1ms, 1a; XXV—1+1s, 1a?; XXVI—1+1; XXVII—1+1ms; XXVIII—3ms, 1a, 1ss. Left antennule with I–IV, IX–XII fused; proximal setation same as right antennule; XX to XXI—2ms, 1a; XXII and XXIII—1ms, 1a; XXIV—1+1ms, 1a; remaining segments probably same as in female (antennule broken). Oblique row of small setules on posterodistal border of segments V–IX.

Antenna, mandible, maxillule, maxilla, maxilliped and legs 1–4 as in female although some setae on mouthparts may be reduced in size and number relative to female.

Leg 5 with following setal formula (Roman numerals indicate spines, Arabic numerals setae, outer border setation listed to the left in each group separate by ';'):

Leg 5♂ left (Coxa 0-0. Basis 1-0. Exopod I-0; I-1; II,1,0. Endopod 0-0; 0-1; 2,2,2);

Leg 5♂ right (Coxa 0-0. Basis 1-0. Exopod I-0; I-1; II,1,0. Endopod 0-0; 0-1; 2,2,2).

Leg 5 almost symmetrical, apart from left exopod segment 2 specialised seta on inner distal border, composed of two sections: basal part and 1 setulose, curved lash (or 2 equal lashes in *E. tageae*). Exopod segment 3 on both sides with analogue of terminal spine of female leg 5 located on distal inner border; on left exopod segment 3 inner border lined with setules, right exopod segment 3 naked or with patch of inner proximal setules (known from 3 species).

Type species. *Heterocalanus medius* Wolfenden, 1906, designated here.

Etymology. The replacement genus name is for Dr Elena Markhaseva in honour of her substantial contributions to calanoid copepod taxonomy.

Remarks. The morphology-based cladistic analysis (see Fig. 112) and the molecular-based analysis (see Fig. 113) clearly identify two separate monophyletic clades within what was previously called *Bathycalanus.* The name *Bathycalanus* is retained, above, for the group of species, including the type species *Ba. richardi*, with a maximal number of setae on the endopod of the mandible, maxillule and maxilliped and one outer border spine on leg 1 exopod segment 3. Wolfenden (1906) recognised that a new genus was needed for the species that have reduced numbers of setae on some parts of the mouthparts and 2 outer border spines on exopod segment 3 of leg 1 and gave this genus the name *Heterocalanus*. Nevertheless, the genus name *Heterocalanus* was preoccupied by *Heterocalanus* T. Scott, 1894 which was applied to what proved to be a species of *Pseudodiaptomus* Herrick, 1884, of which *Heterocalanus* is a junior subjective synonym and is therefore not available for the current megacalanid genus.

Heterocalanus medius Wolfenden, 1906 is clearly described and appears to be a junior synonym of *Calanus princeps* Brady, 1883 since *H. medius* has a head crest and leg 1 exopod segment 3 has 2 outer spines. Thus, we propose the genus name *Elenacalanus* nom. nov. as the replacement name for *Heterocalanus* in the sense of Wolfenden (1906) and designate *Heterocalanus medius* Wolfenden, 1906 as the type species (see Recommendation 60A: ICZN 1999), noting that *H. medius* is a junior synonym of *Calanus princeps* Brady, 1883. This genus now contains *Elenacalanus princeps* (Brady, 1883) new combination [= *H. medius* Wolfenden, 1906; = *Ba. rigidus* Sars, 1920 (see Farran 1939)]; *E. sverdrupi* (Johnson, 1958) n. comb.; *E. eltaninae* (Björnberg, 1968) n. comb., *E. inflatus* (Björnberg, 1968) n. comb. and *E. tageae* **n. sp.**

***Elenacalanus princeps* (Brady, 1883) new combination**
(Figs 87–94)

Calanus princeps Brady, 1883, pp 36–37, pl. IV, figs 3–7.
Heterocalanus medius Wolfenden, 1906, pp 201–202, pl. XL, fig. 1–5.
Megacalanus princeps: Farran, 1908, p. 21.
Macrocalanus princeps: With, 1915, pp 37–40, pl. 1, figs 2a, 2b, textfig. 7.
Bathycalanus rigidus Sars, 1920, p. 2.
Bathycalanus rigidus: Sars, 1924/25, pp 19–20, pl. 5, figs 7–15.
Bathycalanus rigidus: Rose, 1929, pp 9–14, pl. 1, 25 figs.
Bathycalanus princeps: Farran, 1939, pp 357–359.
Bathycalanus princeps: Grice & Hulsemann, 1967, p. 13.

Type locality. 38.567º N, 72.167º W (Stn 45 of HMS Challenger Expedition, designated here).

Material examined. RHB0603, Stn 1, MOC1, 200–400 m, 3♀ Co024.1.1, Co024.1.2, Co024.1.4. Francis Drake III, Stn 2, IKMT, 0–3000 m, 2♀ (12.4, 12.6 mm). Oceanus Cr 473, MOC1: Stn 8, 801–1001 m, 1♀ (damaged) Co024.2.1; Stn 21, 600–798 m, 1CV (9.6 mm) Co024.3.1, Co024.3.2; Stn 26, 798–1001 m, 1♀ (12.6 mm) Co024.5.1; Stn 26, 400–600 m, 1♀ (12.9 mm) Co024.6.1; Stn 31, 400–600 m, 1♀ (13.4 mm) Co024.7.1. LMG11-10, MOC1, Stn 11, 1500–2000 m, 1♀ Co441.3.1. Eltanin Cr 15, 23 Jan 1964, 1♂ (8.9 mm) USNM299526. Records from Natural History Museum, London: Syntypes; 2♀ (each dissected on 2 slides) Challenger Expedition Stn 50 and Stn 45, BMNH 1884.4 c.c.2/5. Discovery Stns, RMT8: 7406#6, 900–1000 m, 3♀ (11.6, 12.3, 12.1 mm), 1CV (10.3 mm), BMNH 1994.5748; 7406#33, 990–1250 m, 5♂ (9.1, 9.3, 9.1, 9.2, 9.1 mm), BMNH 1993.809-813; 7480, 1250–1500 m, 1♂ (9.4 mm), BMNH 1993.875; 7709#35, 1010–1250 m, 2♀ (11.5, 11.9 mm), 2♂ (9.3, 9.4 mm), BMNH 1993.786-789; 7709#76, 1250–1500 m, 9♂ (9.9, 9.6, 9.8, 9.7, 10.0, 9.6, 9.8, 9.7, 9.8 mm), BMNH 1993.819-827; 7711#4, 800–900 m, 2♀ (11.9, 12.9 mm), BMNH 1994.5757-5758; 7711#61, 1500–2000 m, 1♂ (9.9 mm), BMNH 1993.814; 8507#72, 1250–1500 m, 1♂ (9.8 mm), BMNH 1993.873; 8507#73, 1500–2000 m, 8♂ (9.0, 9.8, 9.0, 9.1, 9.4, 9.2, 9.0, 9.5 mm), BMNH 1993.1435-1442; 8507#73, 1500–2000 m, 21♂ (9.6, 9.7, 9.5, 9.5, 9.8, 9.8, 9.5, 9.7, 9.6, 9.8, 9.9, 9.6, 9.6, 9.4, 9.7, 10.0, 9.7, 9.6, 9.5, 9.8 mm), BMNH 1993.1395-1404. Additional records from Smithsonian Institution, USNM numbers: 58954, 58955, 67211, 232142, 262439, 262441–42, 262461, 262468–73, 262475–77, 262484, 262488, 269442, 269446, 269460–70, 299520, 299523, 299526, 302048, 302050, 302061–62, 302067, 302070, 302072, 302074, 1132629.

Genetic material. Co024.1.1, Co024.1.2, Co024.1.4, Co024.2.1, Co024.3.1, Co 024.3.2, Co024.5.1, Co024.6.1, Co024.7.1. Genbank numbers in Table 6.

Morphological description. Following description based on female specimen from Francis Drake III, Stn 2. Male description based on that of Rose (1929) (as *Ba. rigidus*), and male, USNM122568, augmented by observations made on material held at the Natural History Museum, London. As for genus with following specific level features.

Female (Fig. 87A–C). Total length 12.4 mm (mean = 12.5 mm, range = 11.5–13.4 mm, n = 15). Anterior margin of head in dorsal and lateral views with low crest. In lateral view, posterior corners of pedigerous somite 5 short and rounded. Genital double-somite symmetrical in dorsal view, bulbous, wider than long.

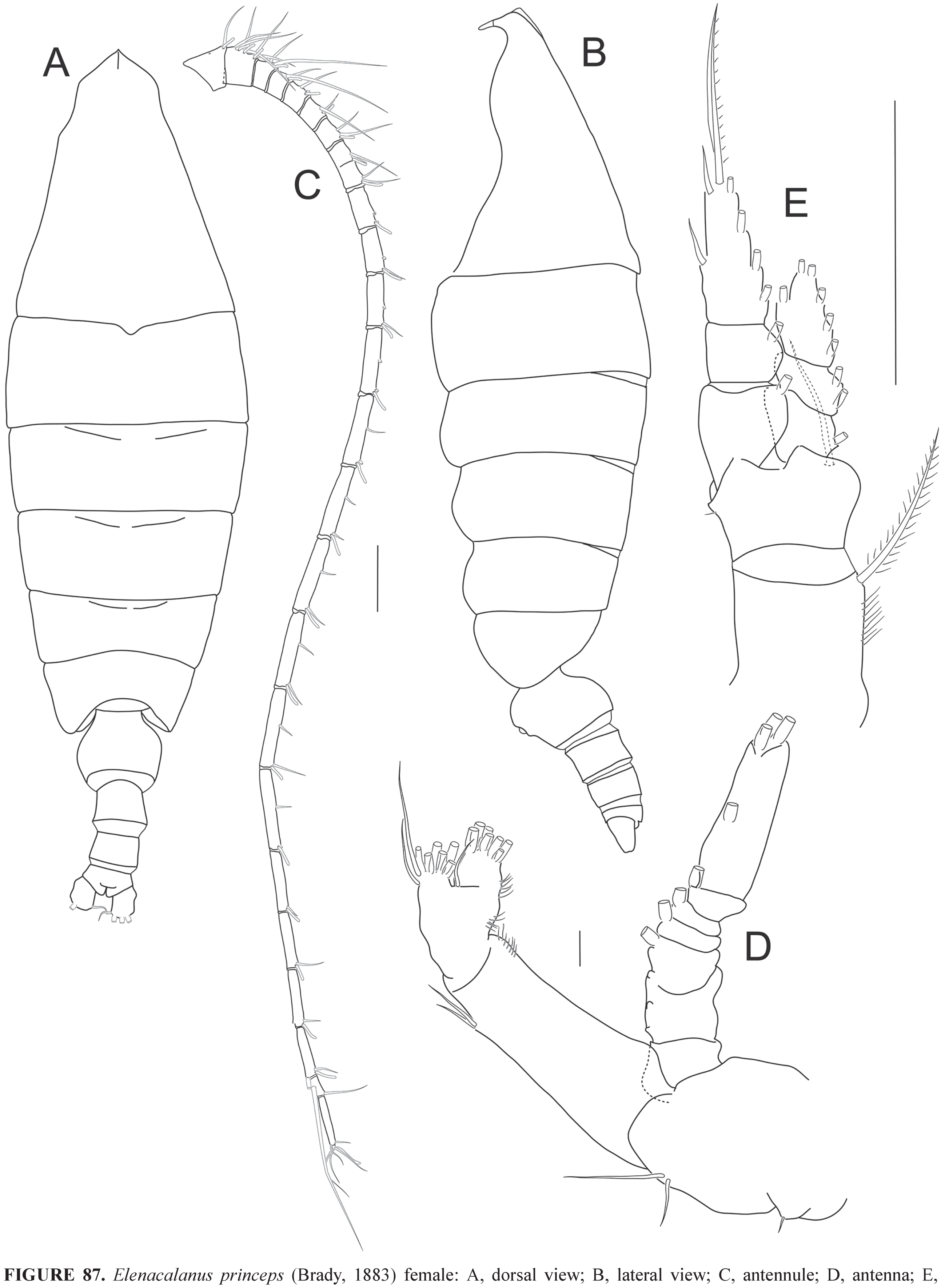

FIGURE 87. *Elenacalanus princeps* (Brady, 1883) female: A, dorsal view; B, lateral view; C, antennule; D, antenna; E, posterior view of leg 1. Scale bars represent 1.0 mm on figures A–C, E; 0.1 mm on remaining figure. Illustrated specimen from Francis Drake III, Stn 2.

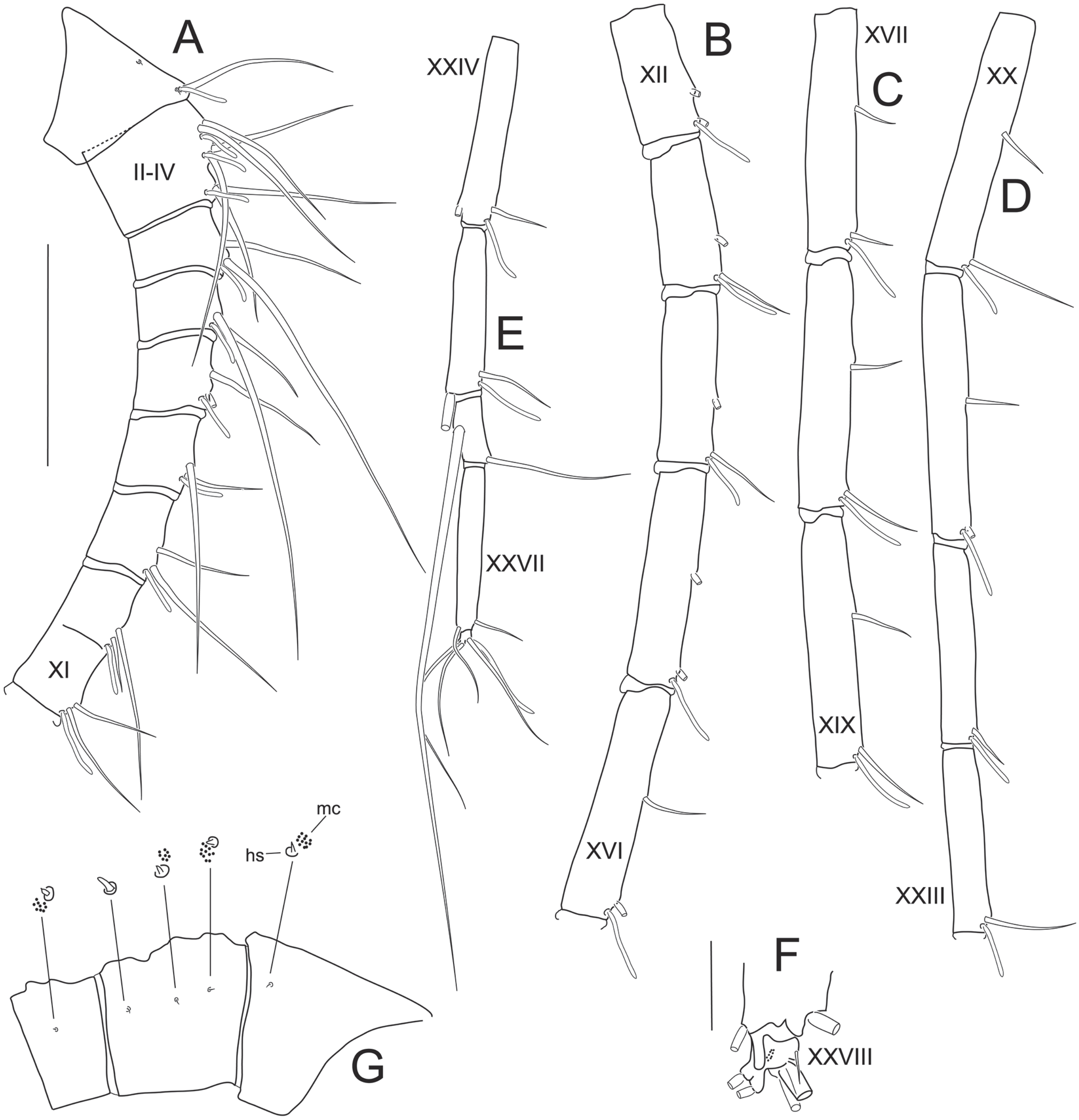

FIGURE 88. *Elenacalanus princeps* (Brady, 1883) female antennule ancestral segments: A, segments I–XI; B, segments XII–XVI; C, segments XVII–XIX; D, segments XX–XXIII; E, segments XXIV–XXVIII; F, detail of segment XXVIII; G, ancestral segments I–V dorsal surface showing distribution of hair sensilla (hs) and maculae cribrosae (mc). Scale bars represent 1.0 mm on figures A–E; 0.1 mm on remaining figure. Illustrated specimen from Francis Drake III, Stn 2.

Antennules (Figs 87C, 88) extending beyond caudal rami by 6 segments. Lengths of antennule segments (µm) as follows. Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements taken of ancestral segment I. I (207, 569); II–IV (429); V (244); VI (261); VII (283); VIII (308); IX (330); X–XI (638); XII (603); XIII (621); XIV (761); XV (975); XVI (1015); XVII (1089); XVIII (1143); XIX (1143); XX (1214); XXI (1196); XXII (906); XXIII (840); XXIV (850); XXV (764); XXVI (315); XXVII (734); XXVIII (39). Segments I, II, III, and V with dorsal surface hair sensillum and adjacent macula cribrosa, segment IV has only hair sensillum.

Antenna (Fig. 87D) ancestral exopod segment IV without seta.

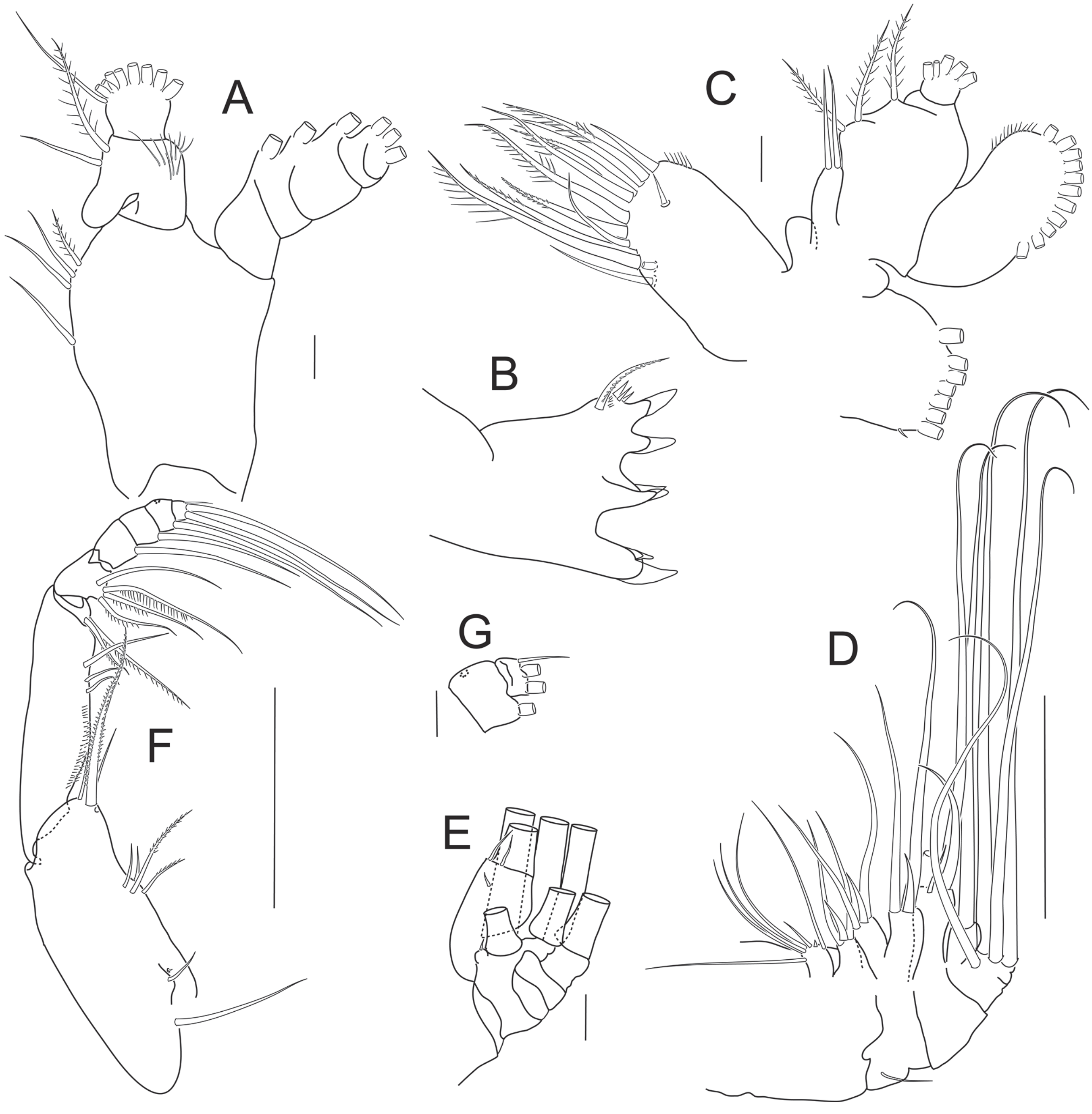

FIGURE 89. *Elenacalanus princeps* (Brady, 1883) female: A, mandibular palp; B, mandibular gnathobase; C, maxillule; D, maxilla; E, endopod of maxilla; F, maxilliped; G, terminal part of maxilliped. Scale bars represent 1.0 mm on figures D, F; 0.1 mm on remaining figures. Illustrated specimen from Francis Drake III, Stn 2.

Maxillule (Fig. 89C) basal endites 1 and 2 with 2 and 2 setae, respectively; endopod segments with 1–2, 0–1, 4+1 small anterior surface seta; basal exite without seta, epipodite with 7 long and 2 vestigial setae.

Maxilliped (Fig. 89F) syncoxal endites with 1, 2 (1 vestigial), 4, 4 (one vestigial) setae, longest seta on endite 4 extending as far as distal border of basis; endopod segments 3–6 with 1, 1, 1 (no outer border seta but 1 macula cribrosa), 3 terminal setae (2 large and 1 small, no seta on outer border), respectively.

Male (Fig. A–D). (From Rose, 1929, pp. 9–14, Pl. 1, 25 figs (as *Ba. rigidus*) and male USNM122568, augmented by observations made on material held at the Natural History Museum, London). Total length: mean = 9.6 mm, range = 8.9–11.0 mm, n = 50. Anterior margin of head in dorsal and lateral views rounded, without crest. Rostrum ventrally-directed, bluntly tapering.

Antennule (Figs 91D, 92) ancestral segments 1 and II fused. On right side (Fig. 92D–G), segments XVI to XIX with narrow proximal anterior border ridge; fused gripping element on segment XIX extending distally well beyond insertion of aesthetasc; segment XX curved on shorter radius than in *E. eltaninae*; proximal fused gripping element of fused segments XXI–XXIII overlapping second fused gripping element by about 40% of its length and gripping element 2 extending distally beyond base of small seta of incorporated segment XXII. Left antennule (Fig. 92A–C) segments XXV–XXVIII broken off.

Antenna (Fig. 93A) ancestral exopod segments I–IV without setae.

Mandible basis with 3 setae, endopod segment 2 with 9 setae (Fig. 91E, F).

Maxillule (Fig. 93B, C) praecoxal arthrite with about 10 reduced setae, apparently none on posterior surface, basal endites 1 and 2 with 2, 0 setae, respectively; endopod segments with 1/0, 0, 4 setae, exopod with 11 setae; basal exite without seta, epipodite with 7 long setae, proximal 2 setae absent.

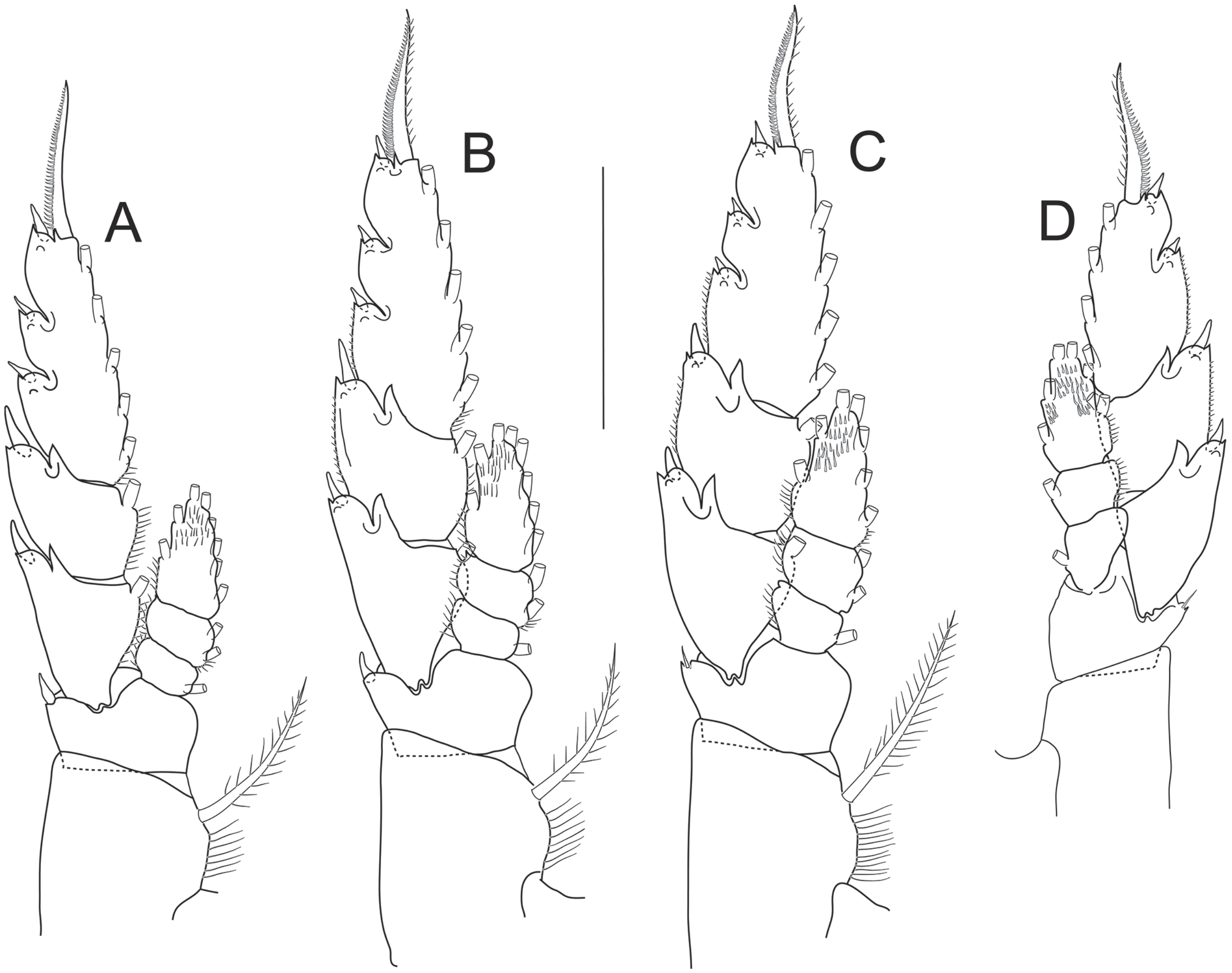

FIGURE 90. *Elenacalanus princeps* (Brady, 1883) female legs, anterior view: A, leg 2; B, leg 3; C, leg 4; D, leg 5. Scale bar represents 1.0 mm on all figures. Illustrated specimen from Francis Drake III, Stn 2.

Maxilla (Fig. 93D) as in female but setae weakly developed; 2 setae of basal endite and setae of endopod segments 1–4 very long, distally weak and narrow therefore not holding their distal curl, lined distally with very dense, fine spinules.

Maxilliped (Fig. 93E) syncoxal endites with 1, 2 (1 vestigial), 4, 3 setae, respectively, longest seta on endite 4 extending to distal seta of basis; endopod segments 3–6 with 1, 1, 1 (no outer border seta), 2 large setae and 1 short seta, respectively.

Leg 1 (Fig. 91G) exopod segment 2 proximal outer spine not extending to base of terminal outer spine.

Leg 5 (Fig. 91H–N) slightly asymmetrical. Right exopod segment 3 with tuft of proximal setules on inner border whereas left exopod segment 3 inner border densely setulose. Exopod segment 2 on left variable with characteristic specialised inner distal seta made of 2 parts: basal part and setulose lash; basal part usually rectangular, distally setulose (in some specimens base slightly drawn out) and with setules at base of lash; setulose

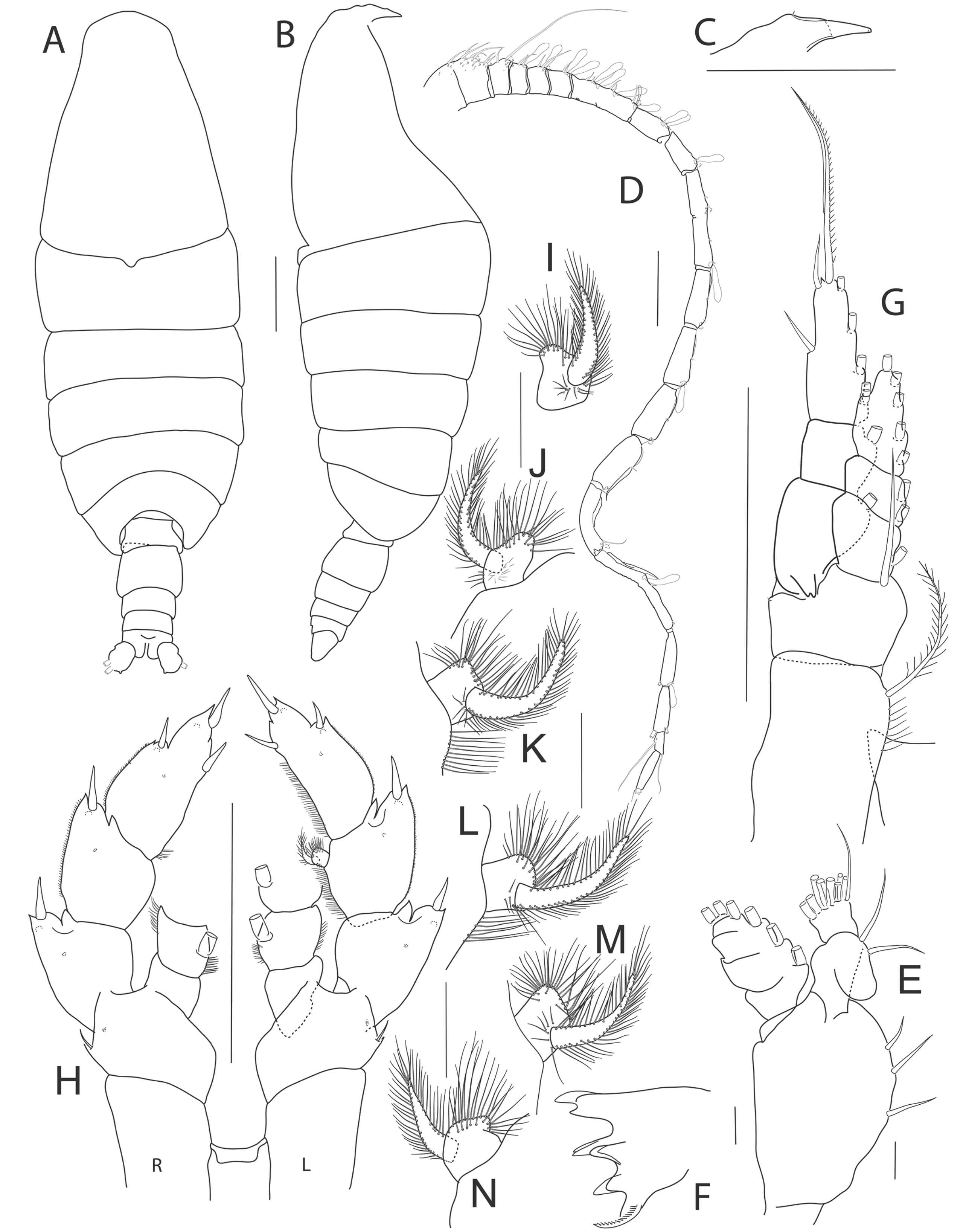

FIGURE 91. *Elenacalanus princeps* (Brady, 1883) male from 57.7º S, 138.1º W, USNM299526: A, dorsal view; B, lateral view; C, detail of rostrum in lateral view; D, right antennule; E, mandibular palp; F, distal part of mandibular gnathobase; G, anterior view of leg 1. Male from 60ºN 20'W BMNH1993.819–827: H, posterior view of leg 5. Specialised seta on left exopod segment 2 of North Atlantic specimens: I, K, from 60ºN 20'W, #63, #76, respectively; J, L, from 44ºN 13'W, #73, #72, respectively; M, from 53ºN 20'W, #61; N, from 40ºN 20'W, #33. Scale bars represent 1.0 mm on figures A–D, G, H; 0.1 mm on remaining figures.

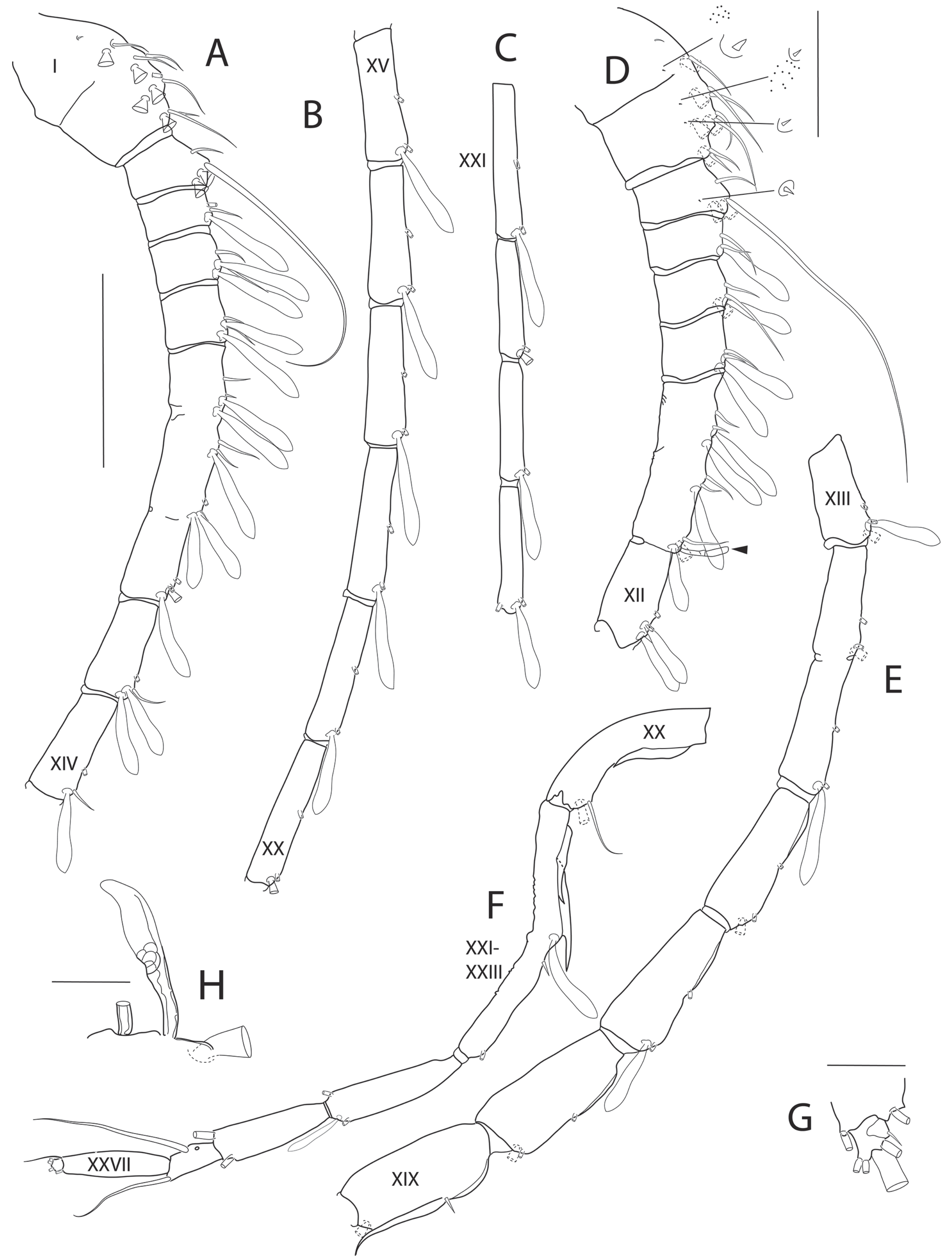

FIGURE 92. *Elenacalanus princeps* (Brady, 1883) male: Left antennule ancestral segments: A, segments I–XIV; B, segments XV–XX; C, XXI–XXIV. Right antennule: D, segments I–XII (arrow indicates clavate seta); E, XIII–XIX; F, segments XX–XXVIII; G, detail of segment XXVIII; H, clavate seta on segment XI. Scale bars represent 1.0 mm on figures A–F; 0.1 mm on remaining figures. Illustrated specimen from 57.7º S, 138.1º W, USNM299526.

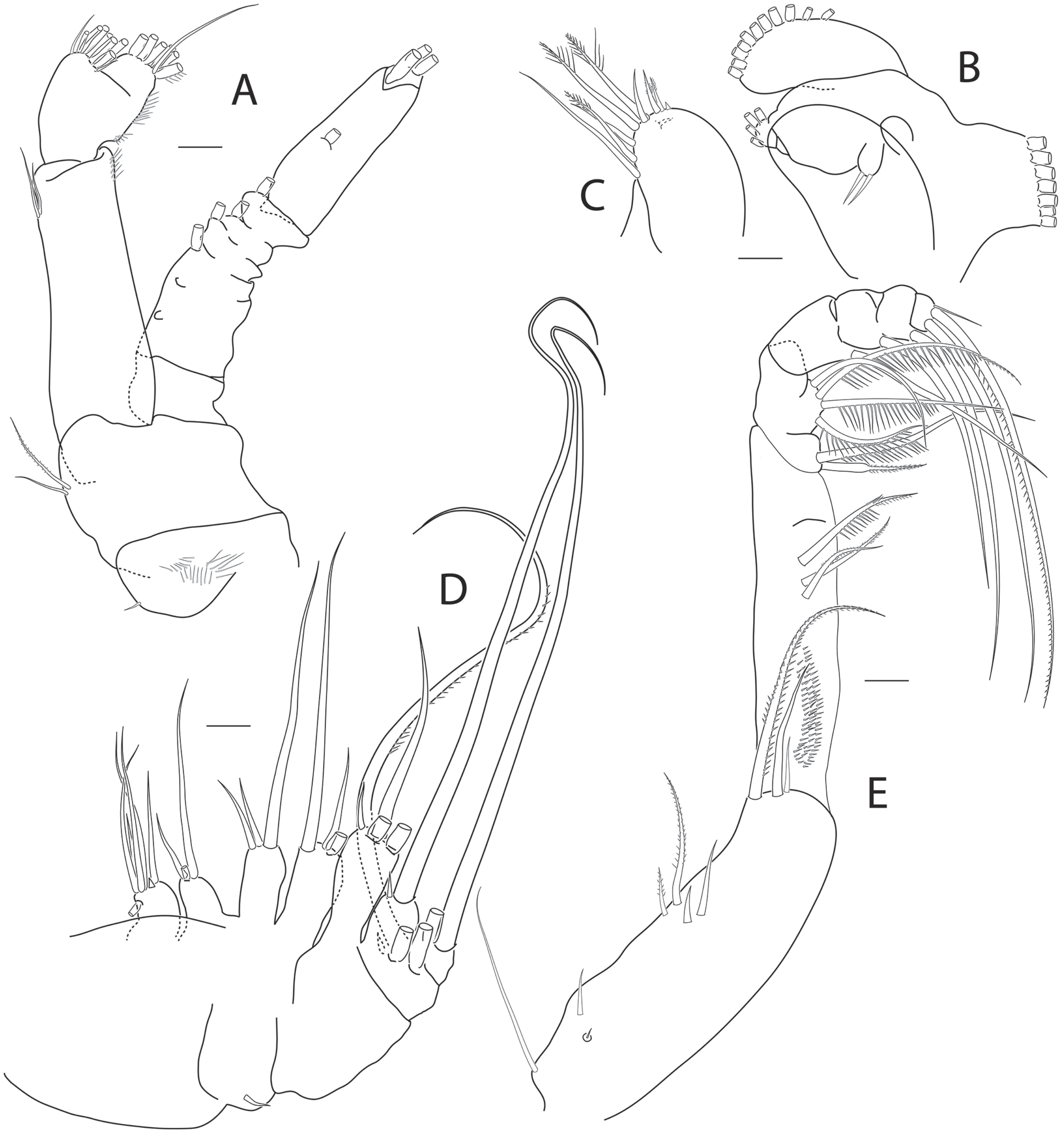

FIGURE 93. *Elenacalanus princeps* (Brady, 1883) male: A, antenna; B, maxillule; C, maxillule praecoxal arthrite; D, maxilla; E, maxilliped. Scale bar represents 0.1 mm on all figures. Illustrated specimen from 57.7º S, 138.1º W, USNM299526.

lash arising from proximal border of basal part. Left exopod segment 3 carrying 1 terminal, 1 inner (at about distal ¼) and 1 outer border spine (at distal 1/3rd); right exopod segment 3 with 1 terminal spine, 1 inner and 1 outer border spine positioned opposite each other. Macula cribrosa present on each of basis and exopod segments 1–3.

Remarks. There has been much previous confusion about the identity of this species because Brady's (1883) description and drawings were sufficient only to place this taxon in the Megacalanidae. That is, the maxillule was not accurately described, only a seta from the maxilla was illustrated and leg 1 was not described. One of us (GAB) recently re-examined two of Brady's type specimens, each dissected on two slides. Most of the limbs are in good condition in the female from Stn 50 (BMNH 1884.4 c.c.2) although not perfectly orientated. The maxillule formula is: coxal endite without setae, basal endites 1 and 2 with 2, 1 setae respectively, endopod with 1, 1, 4+1. Leg 1 exopod segments 1 and 2 lack outer border spines, while segment 3 has 2 outer spines. These character states confirm that *Calanus princeps* Brady, 1883 belongs to a genus separate from *Megacalanus, Bradycalanus* and *Bathycalanus.* Brady does not mention the crest on the head of the female but With (1915) and Wolfenden (1906) do. Brady (1883) does not describe the structure of leg 1, but we confirm that exopod segment 3 of leg 1 of the type specimens possesses 2 outer border spines in addition to a long terminal element and 4 inner setae, as illustrated by Rose (1929) and Wolfenden (1906). With (1915) states that leg 1 exopod segment 3 has only 1 outer border spine, but two spines are present in the types. The slide of the mouthparts of the syntype from Challenger Stn 50 has 7 + 2 short setae on the coxal epipodite of the maxillule on one side but 7 + 3 short setae on the other side. This is interpreted here as an aberrant state, given that the total of 9 setae is the maximum known anywhere in the Copepoda (Huys & Boxshall 1991).

Farran (1939) recognised that the specimens called *Calanus princeps* by Brady (1883) were the same as the specimen described as *Bathycalanus rigidus* and illustrated by Sars (1924/25). *Bathycalanus rigidus* consequently becomes a junior subjective synonym of *Elenacalanus princeps* (Brady, 1883).

The present female specimens agree with the description *Bathycalanus rigidus* of Sars (1924, 1925), although some details differ from the present description. His illustration of the maxilla has 5 setae on praecoxal endite 1 whereas presently examined specimens have 6 + 1 small seta. In the text, Sars (1925) says that the antenna, mandible and maxillule show no differences from the preceding species (*Ba. richardi*) which is not true. Sars' (1924) illustrations of these limbs of *Ba. richardi* omit several of the smaller setae that are present in currently examined specimens. For example, mandible endopod segments 1 and 2 are illustrated as having 3 and 8 setae, respectively; actually 4 and 11 setae, respectively, in currently examined specimens. Lack of this detail obscured differences from *E. princeps* where these mandible endopod setae are 2 and 9 respectively, a consistent characteristic of all *Elenacalanus*.

Rose (1929) contains the only description of a male to date. Among the specimens examined at the Smithsonian Institution there was one male (USNM299526) that agrees with most details given by Rose (1929) although leg 5 was not intact (the two left terminal exopod segments are missing) so the hook on the specialised seta could not be confirmed. Examination of males held by the Natural History Museum, London does not corroborate the presence of a hook on the basal part. Rather, the basal part is of variable shapes although one specimen examined (BMNH1993.809-813, Fig. 91N) had a slight distal notch. Males were assigned to females mainly based on the fact that *E. princeps* females were the most common *Elenacalanus* species in the R.R.V. Discovery material as were the males (total length: range 9–10 mm; mean 9.5 mm) which are slightly smaller on average than in *E. eltaninae* (total length: range 10–10.5 mm; mean 10.2 mm).

Sexual dimorphism of the limbs appears to be more extensive in *E. princeps* than in most other Megacalanidae. Compared with the female, the male, in addition to the antennules and leg 5, has 1 fewer setae on the mandible basis, fewer setae on the praecoxal arthrite, basis and endopod segments 1 and 2 of the maxillule; and the distal parts of the long setae of the maxilla are more weakly developed.

Morphological variation. The setation of the endopod of the female maxillule was variable on each side of the same individual examined here. The shape of the male inner distal specialised seta of left leg 5 exopod segment 2 is variable; the base may be very rectangular (Fig. 91K–M), drawn out distally (Fig. 91I, J) or with a slight notch (Fig. 91 N).

Distribution. *Elenacalanus princeps* seems to be a bathypelagic species that extends into the mesopelagic zone in the North Atlantic Ocean (800–2000 m (With 1915), and Natural History Museum, London records), in the southeastern Pacific off Chile (present results), the southern Indian Ocean 350–2394 m (Grice & Hulsemann 1967) and Atlantic sector of the Antarctic 366–3074 m (Michel 1994). Specimens held by the Smithsonian Institution are from the Atlantic and the Antarctic sector of the Pacific, and Indian Oceans (Fig. 94, Table 1). Michel (1994) summarises its depth of occurrence as 366–3074 m.

Species comparisons. Females of *Elenacalanus princeps* are closely related to *E. eltaninae, E. sverdrupi*, *E. inflatus* and an undescribed species from the northwest Pacific. *Elenacalanus princeps* may be distinguished from the other four species (Table 11) by the crested head of the female (head rounded in the other four species), proximal seta of maxillule coxal epipodite absent (present in all other species), and the maxilliped endopod segment 6 with 3 setae (4 in most other species).

Males are known for *E. princeps, E. eltaninae* and *E. tageae* **n. sp.**. The male leg 5 of *E. princeps* has the right exopod segment 3 inner border with a proximal tuft of setules (in the other known species this border is naked). The specialised seta on the left exopod segment 2 of leg 5 in *E. princeps* is rather variable and the form of this seta on *E. eltaninae* fits within the range of variability found in *M. princeps* (compare Fig. 91I–N and Fig. 100H). Males of *E. princeps* and *E. eltaninae* are also without a seta on exopod segment 4 of the antenna. The male geniculate antennule of *E. princeps* has ancestral segments IX–XI fused but segment XII separate (in *E. eltaninae* segments IX–XII are fused), the radius of curvature of segment XX of *E. princeps* is shorter than in *E. eltaninae* and the anteroproximal border of segments XVII–XIX are thickened into flange-like extensions (these are absent in *E. eltaninae*).

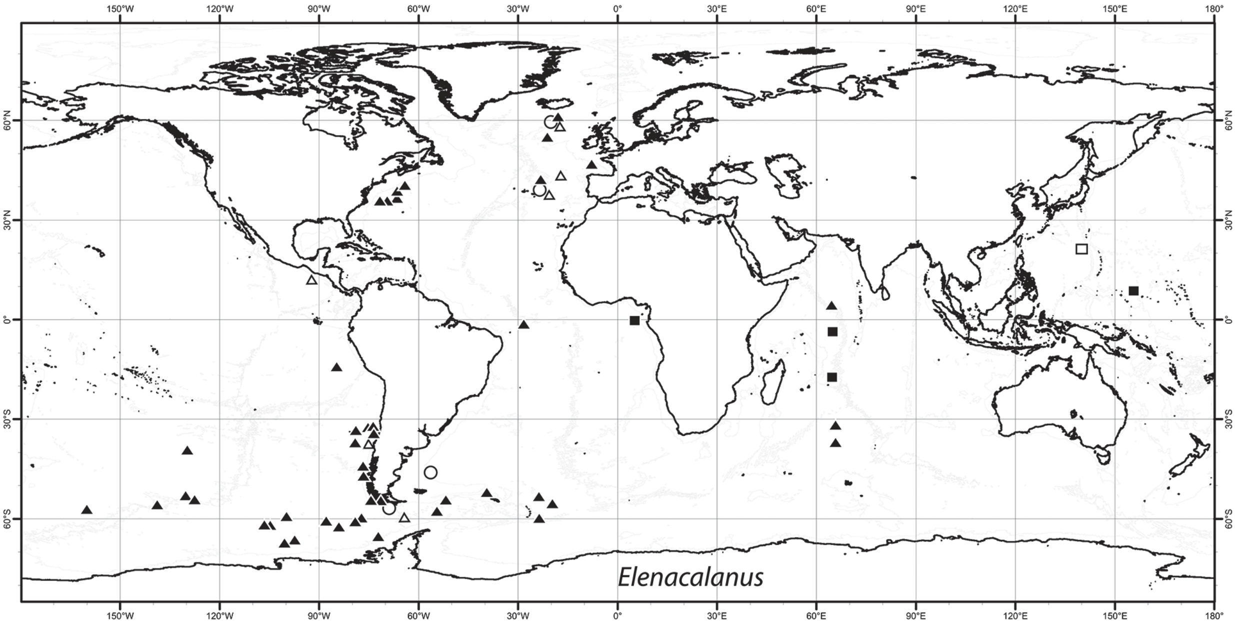

FIGURE 94. Distribution of *Elenacalanus* nom. nov. species: filled triangle = *Elenacalanus princeps*; open trangle = *E. eltaninae*; open square = *E. tageae* **n. sp.**; filled square = *E. sverdrupi*; open circle = *E. inflatus*.

Elenacalanus eltaninae **(Björnberg, 1968) new combination**
(Figs 94–100)

Bathycalanus eltaninae Björnberg, 1968, pp 75–81, figs 15–41.

Type locality. 38.150º S, 74.517º W.

Material examined. Francis Drake III, Stn 2, IKMT, 0–3000 m, 1♀ (14.5 mm). MV73-1, Stn 53, IKMT, 0–2000 m, 1♀ (14.8 mm). Records from Natural History Museum, London: Discovery Stns, RMT8: 7709#44, 1250–1500 m, 2♀ (11.8, 12.3 mm), BMNH 1993.793-794; 7709#76, 1250–1500 m, 1♀ (12.4 mm), BMNH 1993.796; 7478#1, 1500–2000 m, 2♀ (11.8, 12.2 mm), BMNH 1993.797-798; 8507#3, 1500–2000 m, 3♀ (11.8, 12.8, 12.3 mm), BMNH 1993.799-801; 7711#47, 1260–1500 m, 2♀ (12.7, 12.3 mm), BMNH 1993.802-803, 5♂ (10.0, 10.4, 10.3, 10.0, 10.5 mm), BMNH 1993.829-833; 7711#56, 1250–1500 m, 3♀ (12.7, 12.5, 12.4 mm), BMNH 1993.804-806. Additional records from Smithsonian Institution, USNM numbers: 122568–70.

Morphological description. Following description based on specimens from MV73-1. Stn 53 and Francis Drake III, Stn 2. Male description based on male holotype USNM122568 of *Bathycalanus eltaninae* Björnberg, 1968 and specimens from the Natural History Museum, London. As for genus with following specific level features.

Female (Fig. 95A–D). Total length 14.5 mm (mean = 12.7 mm, range 11.8–14.5 mm, n = 16). Anterior margin of head in dorsal view with low projection dorsal to base of rostrum. In lateral view, posterior corners of pedigerous somite 5 rounded.

Antennule (Fig. 96) extends beyond caudal rami by at least 7 segments. Lengths of segments (µm) as follows. Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements taken of ancestral segment I. I (253, 682); II–IV (612); V (307); VI (329); VII (455); VIII (479); IX

(518); X–XI (1049); XII (875); XIII (921); XIV (1170); XV (1339); XVI (1408); XVII (1452); XVIII (1521); XIX (1536); XX (1560); XXI (1477); XXII (1010); XXIII (1044); XXIV (1042); XXV (971); XXVI (386); XXVII (998); XXVIII (38). Segments I–V with dorsal surface hair sensilla and adjacent macula cribrosa (Fig. 96A).

Antenna (Fig. 95E) exopod segment IV with very short seta not extending beyond segment V.

Maxillule (Fig. 97D) praecoxal arthrite with 13 setae including 2 on posterior surface and 1 longer and 1 smaller seta on anterior surface; coxal endite without setae, basal endites 1 and 2 with 2 and 3 setae respectively; endopod segments with 1, 1, 4+1 smaller anterior surface seta; basal exite without seta, epipodite with 7 long and 2 very short, reduced setae.

Maxilla (Fig. 97E) longest setae extend short of rostrum.

Maxilliped (Fig. 95F) syncoxal endite 4 longest seta not extending as far as distal border of basis; endopod segments 2–6 with 4 subequal, 1, 1, 1 (no outer border seta but 1 macula cribrosa), 4 setae (2 large and 2 very small, of which one on outer border), respectively.

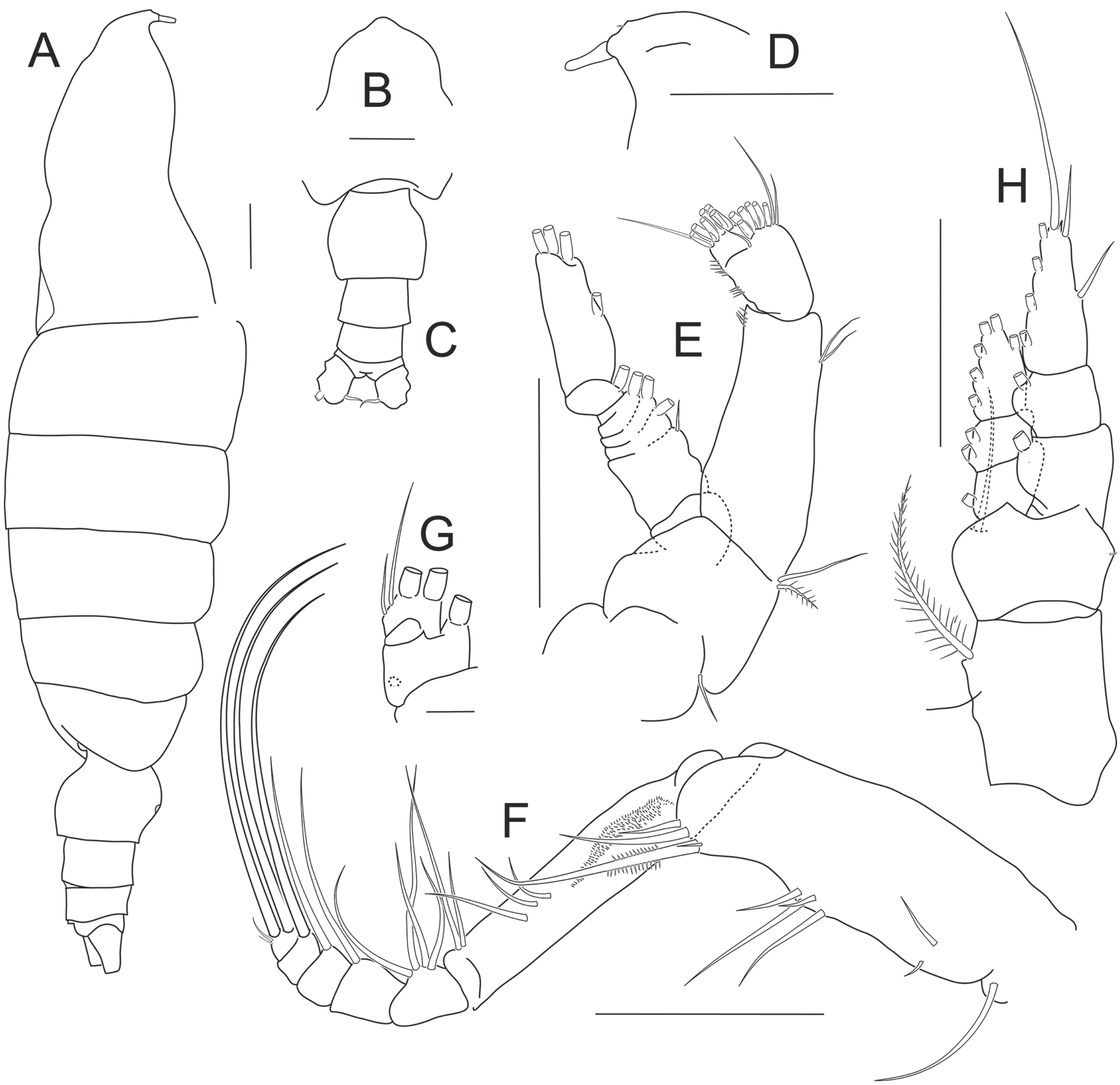

FIGURE 95. *Elenacalanus eltaninae* (Björnberg, 1968) female: A, lateral view (note damage to dorsal surface of posterior head); B, dorsal view of anterior head; C, dorsal view of urosome; D, lateral view of anterior head; E, antenna; F, maxilliped; G, detail of terminal part of maxilliped; H, posterior view of leg 1. Scale bars represent 1.0 mm on figures A–F, H; 0.1 mm on remaining figure. Illustrated specimens from MV73-1, Stn 53 (A); from Francis Drake III, Stn 2 (B–H).

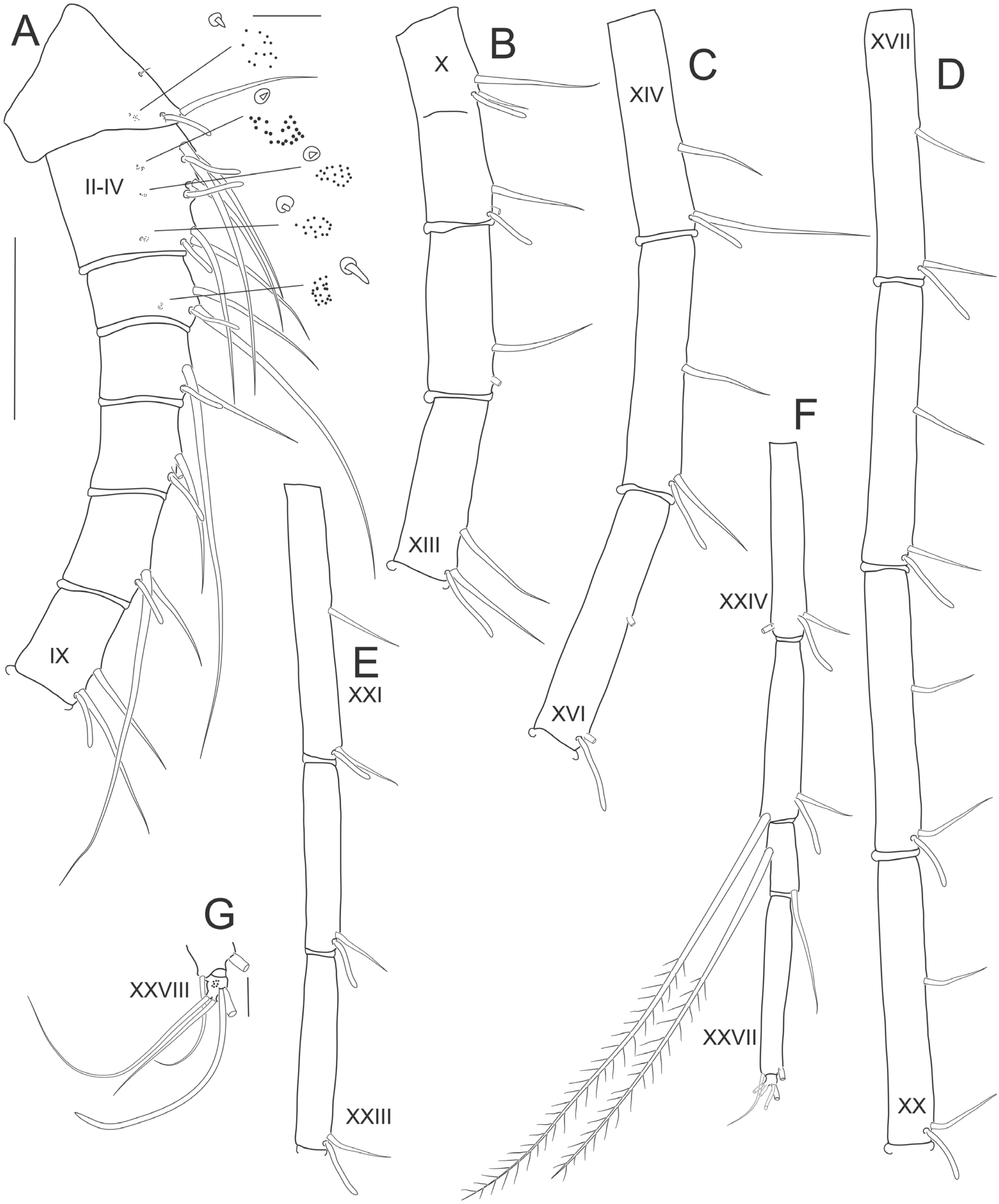

FIGURE 96. *Elenacalanus eltaninae* (Björnberg, 1968) female antennule ancestral segments: A, segments I–IX (hs = hair sensillum, mc = macula cribrosa); B, segments X–XIII; C, segments XIV–XVI; D, segments XVII–XX; E, segments XXI–XXIII; F, segments XXIV–XXVIII; G, detail of segment XXVIII. Scale bars represent 1.0 mm on figures A–F; 0.1 mm on remaining figure. Illustrated specimen from Francis Drake III, Stn 2.

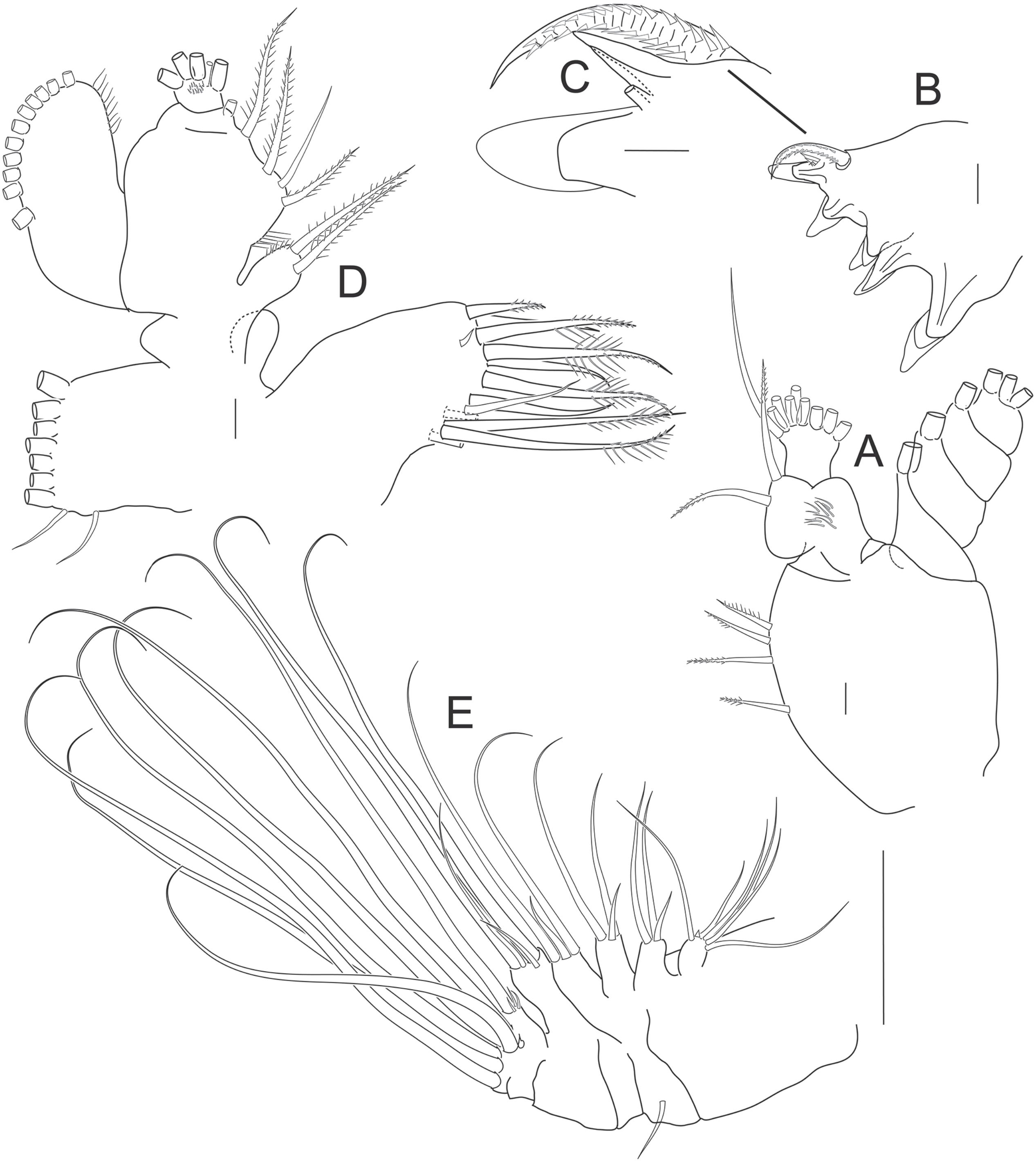

FIGURE 97. *Elenacalanus eltaninae* (Björnberg, 1968) female: A, mandibular palp; B, mandibular gnathobase; C, detail of dorsal part of mandibular gnathobase; D, maxillule; E, maxilla. Scale bars represents 1.0 mm on figure E; 0.1 mm on remaining figures. Illustrated specimen from Francis Drake III, Stn 2.

Male. From decription of Björnberg (1968) and holotype male slide USNM 122658.

Total length 12.7 mm. Anterior margin of head in dorsal and lateral views rounded, without crest. In lateral view, posterior corners of pedigerous somite 5 short and rounded.

Antennule (Fig. 99) ancestral segments 1 and II separate. Right antennule extending 5 segments beyond caudal rami; fused gripping element on segment XIX extending as far as insertion of aesthetasc; segment XX curved on longer radius than in *E. princeps*; proximal fused gripping element of fused segments XXI–XXIII overlapping second fused gripping element by about 24% of its length and gripping element 2 extending distally short of base of small seta of incorporated segment XXII; segments XXVII–XXVIII broken off.

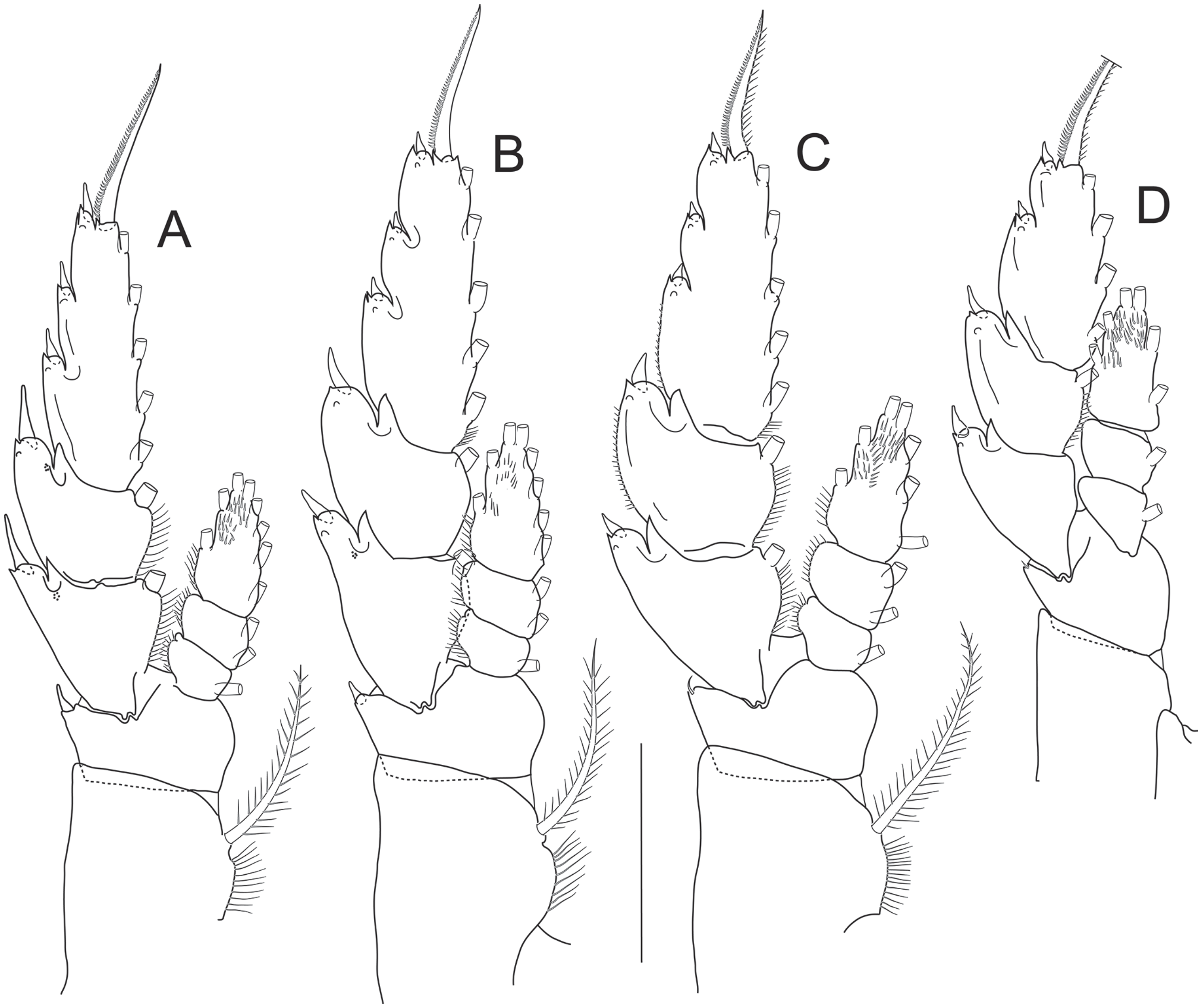

FIGURE 98. *Elenacalanus eltaninae* (Björnberg, 1968) female legs, anterior view: A, leg 2; B, leg 3; C, leg 4; D, leg 5. Scale bar represents 1.0 mm on all figures. Illustrated specimen from Francis Drake III, Stn 2.

Antenna ancestral exopod IV without seta.

Mandible basis with 4 setae.

Maxillule (Fig. 100A) setation slightly reduced compared with female. Praecoxal arthrite with 13 setae, 2 on posterior surface; basal endites 1 and 2 with 2 and 2 setae, respectively; endopod segments with 1, 1, 4 setae, respectively; exopod with 11 setae; basal exite with vestigial seta, epipodite with 7 long setae.

Maxilla setation slightly reduced compared with female, longest setae weakly developed.

Maxilliped (Fig. 100B, C) syncoxal endites with 1, 2 (1 vestigial), 4, 4 setae (longest seta on endite 4 extending to distal seta of basis, 1 seta vestigial**),** respectively; endopod segments 3–6 with 1, 1, 1 (no outer border seta), 2 large setae and 2 vestigial setae, respectively.

Leg 1 (Fig. 100D) exopod segment 3 proximal outer spine extending short of base of terminal outer spine.

Leg 5 (Fig. 100E–H) slightly asymmetrical (from USNM122658). Right exopod segment 3 with naked inner border whereas left exopod segment 3 densely setulose. Exopod segment 2 on left with characteristic inner distal specialised seta comprising 2 parts: large, outer, setulose basal lobe, distally rounded and inner, soft, densely setulose lash. Left exopod segment 3 carrying 1 terminal, 1 inner (at about distal one quarter) and 1 outer border spine (at distal one third); right exopod segment 3 with at least 1 terminal spine and scars denoting position of 1 inner and 1 outer border spine positioned as on left leg. Endopod as in generic description.

Remarks. The present female specimens agree with the written description of *Bathycalanus eltaninae* by Björnberg (1968) apart from the following details. The female antennules have ancestral segments X and XI fused, but segments XXVII–XXVIII are separate. The praecoxal arthrite of the maxillule has 13 spines and setae including 1 short spine on anterior surface and 2 setae on the posterior surface (not 10 or 11 as in the original description), basal endite 2 has 3 setae (not 1–3 as in the original description), and endopod segment 3 bears 5 setae (including 1 small seta) (4/5 setae in the original description) (the number of setae could not be checked as this limb was not mounted on the paratype slide, USNM122569). The maxilla basal endite has 4 setae (3 in original description) and endopod segment 1 has 4 setae, 3 of them vestigial (2 setae in original description). The maxilliped endopod segment 6 has 4 setae, two of them small (3 setae in original description).

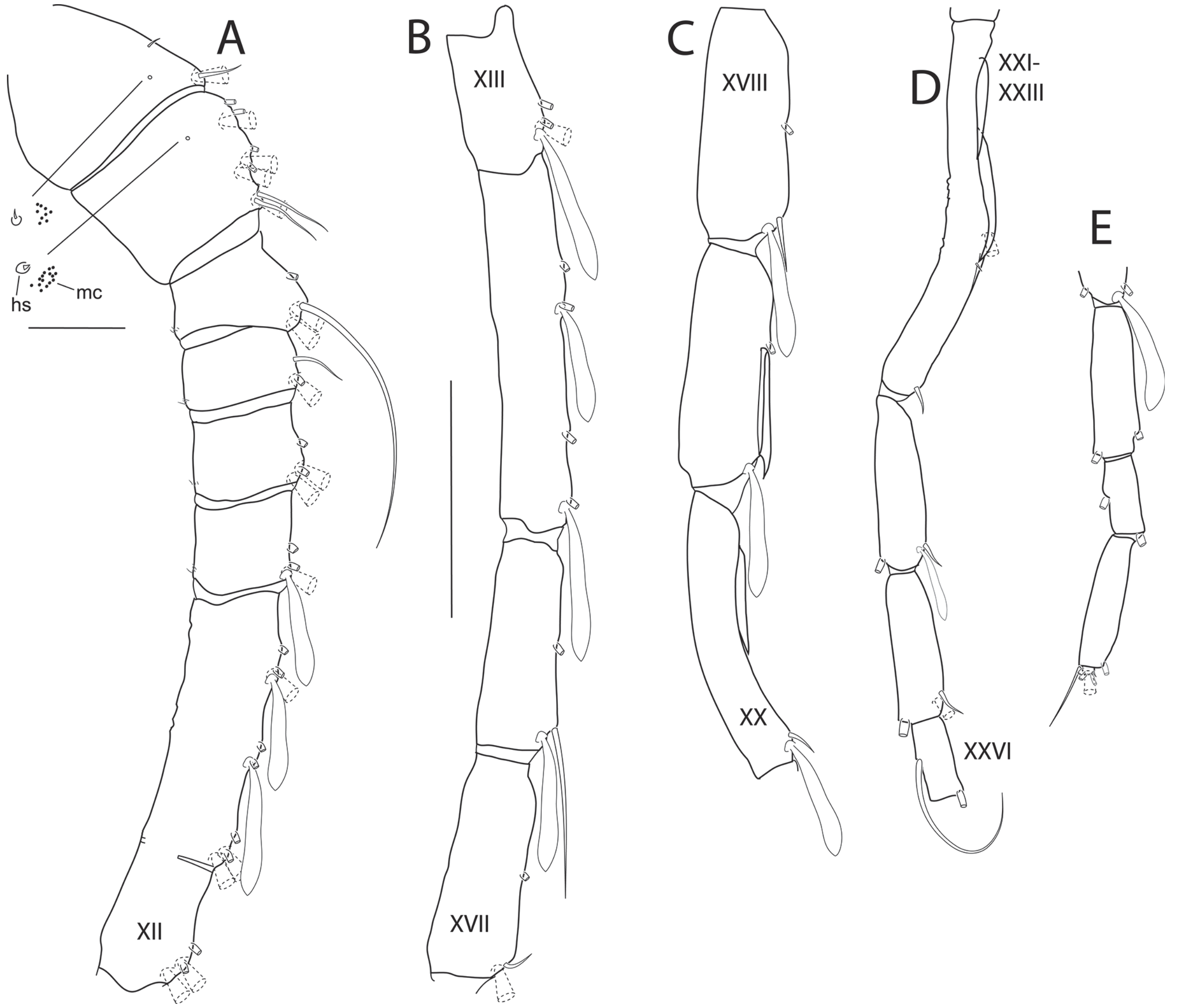

FIGURE 99. *Elenacalanus eltaninae* (Björnberg, 1968) male right antennule: A, ancestral segments I–XII (hs = hair sensillum, mc = macula cribrosa); B, segments XIII–XVII; C, segments XVIII–XX; D, segments XXI–XXVI. Left antennule: E, segments XXV–XXVIII. Illustrated specimen is holotype USNM122568. Scale bar represents 1.0 mm on all figures.

The male right antennule up to ancestral segment XVI has segments IX–XII and XIV–XV fused (these appear to be separate in the original description). We believe that the males we have assigned to female of *E. eltaninae* are correct because they co-occurred with female of *E. eltaninae* at Stn 7711#47 in the Discovery material and are slightly larger on average (total length: range 10–10.5 mm; mean 10.2 mm) than *E. princeps* (total length: range 9–10 mm; mean 9.5 mm).

Distribution. *Elenacalanus eltaninae* is an upper abyssopelagic species found so far in the Pacific Ocean off Chile (Björnberg 1968), the tropical eastern Pacific off Mexico, northeastern Atlantic and Atlantic sector of the Antarctic (present results) (Fig. 94, Table 1). Taken in hauls between 1250 and 3000 m.

Species comparisons. *Elenacalanus eltaninae* females may be distinguished from other members of the genus by a combination of the following characters: head not crested; maxillule praecoxal arthrite has 2 setae on the posterior surface, basal endite 2 with 2–3 setae, coxal epipodite with 9 setae; maxilliped endopod segment 6 with 4 setae (Table 11); and leg 1 exopod segment 3 proximal outer spine does not extend as far as the base of the terminal outer spine.

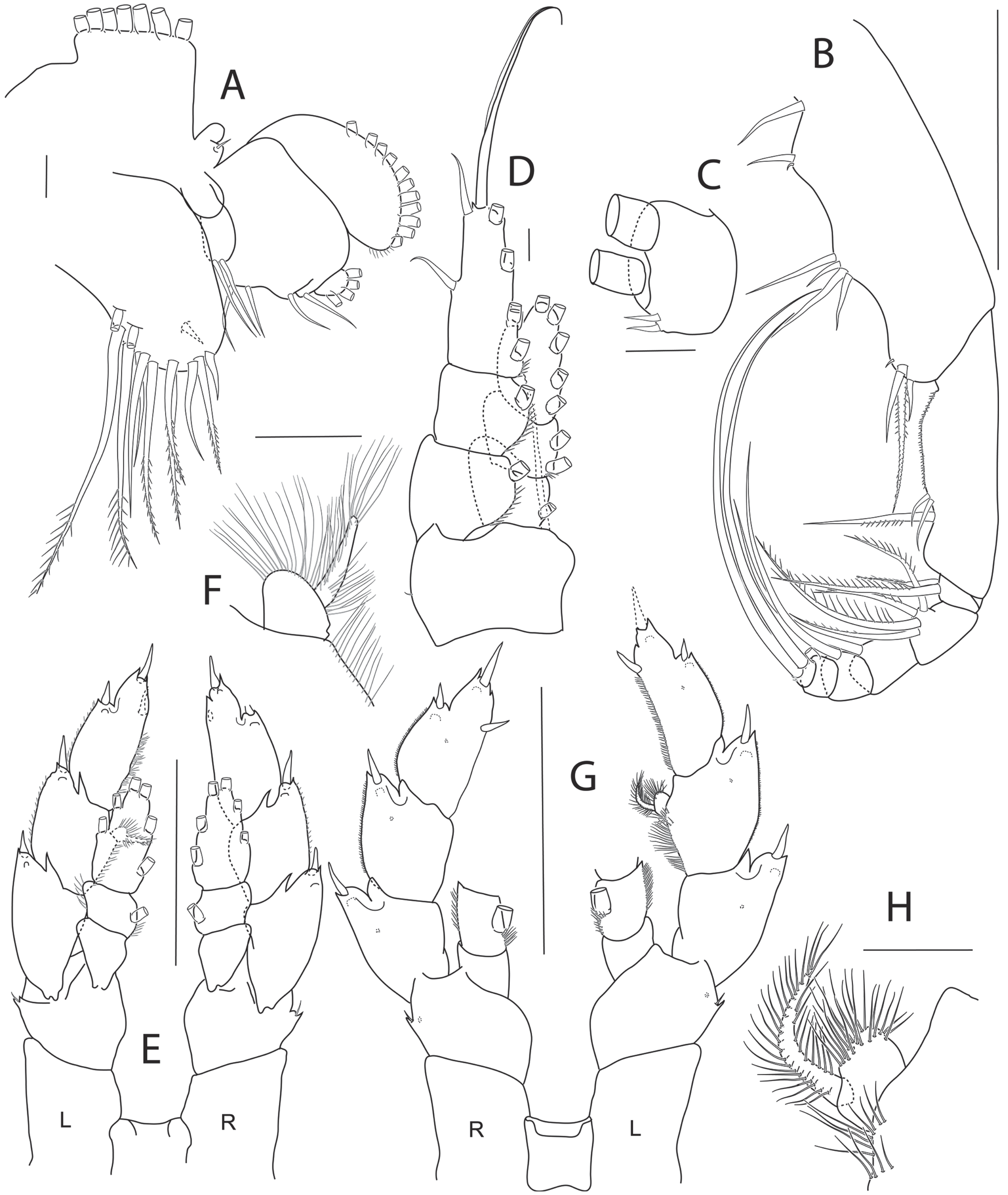

FIGURE 100. *Elenacalanus eltaninae* (Björnberg, 1968) male holotype USNM122568: A, maxillule; B, maxilliped; C, detail of terminal segment of maxilliped. D, posterior view of leg 1; E, anterior view of leg 5; F, specialised seta of left leg 5 exopod segment 2. Male BMNH1993.829–835 #47: G, posterior view of leg 5; H, specialised seta of left leg 5 exopod segment 2. Scale bars represent 1.0 mm on figures B, E, G; 0.1 mm on remaining figures.

The male leg 5 specialised seta of *E. eltaninae* has a large squat rectangular basal part that fits within the range of variability demonstrated by *E. princeps* and both have a curved elongate inner lash. The only difference between leg 5 of *E. eltaninae* and *E. princeps* is the naked inner border of right exopod segment 3 in the former and presence of a small proximal tuft of setules in the latter. The male right geniculate antennule of *E. eltaninae* may be distinguished from that of *E. princeps* because ancestral segment XX is much less curved (i.e. has a larger radius of curvature) than in *E. princeps*, and ancestral segment XII is fused to segments IX–XI (in *E. princeps* segment XII is separate).

Elenacalanus tageae **n. sp.**

(Figs 94, 101–106)

Type locality. 26.441º N 139.037º E.

Material examined. Antipode IV, IKMT: Stn 53D, 0–2500 m, 1♀ (13.4mm) holotype, 1CV; Stn 55D, 0–2000 m, 1♂ (12.7 mm) paratype.

Type specimens. Deposited in the collection of the Scripps Institution of Oceanography, California: holotype female: PIC-140409-0015-HT; paratype male: PIC-140409-0016-PT.

Morphological description. Following description based on holotype and paratype specimens from Antipode IV, Stns 53D and 55D. As for genus with following specific level features.

Female (Fig. 101A–C). Total length 13.4 mm. Anterior margin of head in dorsal view with low projection dorsal to base of rostrum. In lateral view, posterior corners of pedigerous somite 5 rounded. Genital double-somite symmetrical in dorsal view, bulbous, about as long as wide, in lateral view bulging both ventrally and dorsally, and is much deeper than following somite.

Antennule (Figs 101D, 102A–C) extending beyond caudal rami by at least 7 segments (segments XXI–XXVIII broken off). Lengths of segments (µm) as follows. Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements taken of ancestral segment I. I (211, 603); II–IV (534); V (265); VI (294); VII (341); VIII (365); IX (380); X–XI (750); XII (632); XIII (711); XIV (917); XV (1125); XVI (1216); XVII (1262); XVIII (1309); XIX (1319); XX (1370); XXI (-); XXII (-); XXIII (-); XXIV (-); XXV (-); XXVI (-); XXVII (-); XXVIII (-). Segments I–V each with dorsal surface hair sensillum and adjacent macula cribrosa.

Antenna (Fig. 102D) exopod ancestral segment IV with very short seta not extending beyond segment V.

Maxillule (Fig. 102G) praecoxal arthrite with 13 setae including 2 on posterior surface and 1 longer and 1 smaller seta on anterior surface; coxal endite without setae, basal endites 1 and 2 with 2 setae each; endopod segments with 1, 1, 4+1 small anterior surface seta; basal exite with vestigial seta, epipodite with 7 long and 2 very small setae.

Maxilliped (Fig. 103A) syncoxal endite 4 longest seta broken off—probably extending as far as distal basal seta as in male; endopod segments 2–6 with 4 subequal, 1, 1, 1 (no outer border seta but 1 macula cribrosa), 4 setae (2 large and 2 small, of which one on outer border), respectively.

Leg 1 (Fig. 101E) exopod segment 3 proximal outer spine extends beyond base of terminal outer spine.

Male (Fig. 104A–C). Anterior margin of head similar to that of female. Total length 10.8 mm. Urosomite II length 0.8 times its width in dorsal view; urosomite II is 1.5 times as long as urosomite III. In lateral view, posterior corners of pedigerous somite 5 rounded.

Antennules (Fig. 104D, E) not entire; left antennule absent; right antennule first 16 ancestral segments remaining, ancestral segments IX–XI fused and XIV–XV fused on right.

Antenna (Fig. 105A) exopod ancestral segments I–IV without setae.

Mandible (Fig. 105B) basis with 4 (2 very small) inner setae.

Maxillule (Fig. 105D, E) setation reduced in number and size relative to female: basal endites 1 and 2 with 2 and 1 reduced seta, respectively; endopod segments with 1 reduced, 1 reduced**,** 4+1 anterior surface seta; basal exite without seta, epipodite with 7 long setae.

Maxilla (Fig. 106A, B) with longest setae extending only as far as anterior part of labrum.

Maxilliped (Fig. 106C) similar to that of female; syncoxal endite 4, longest seta extending to distal basal seta.

Legs 1–4 similar to those of female, especially exopod segment 3 of leg 1 which has proximal outer spine extending beyond base of distal outer spine.

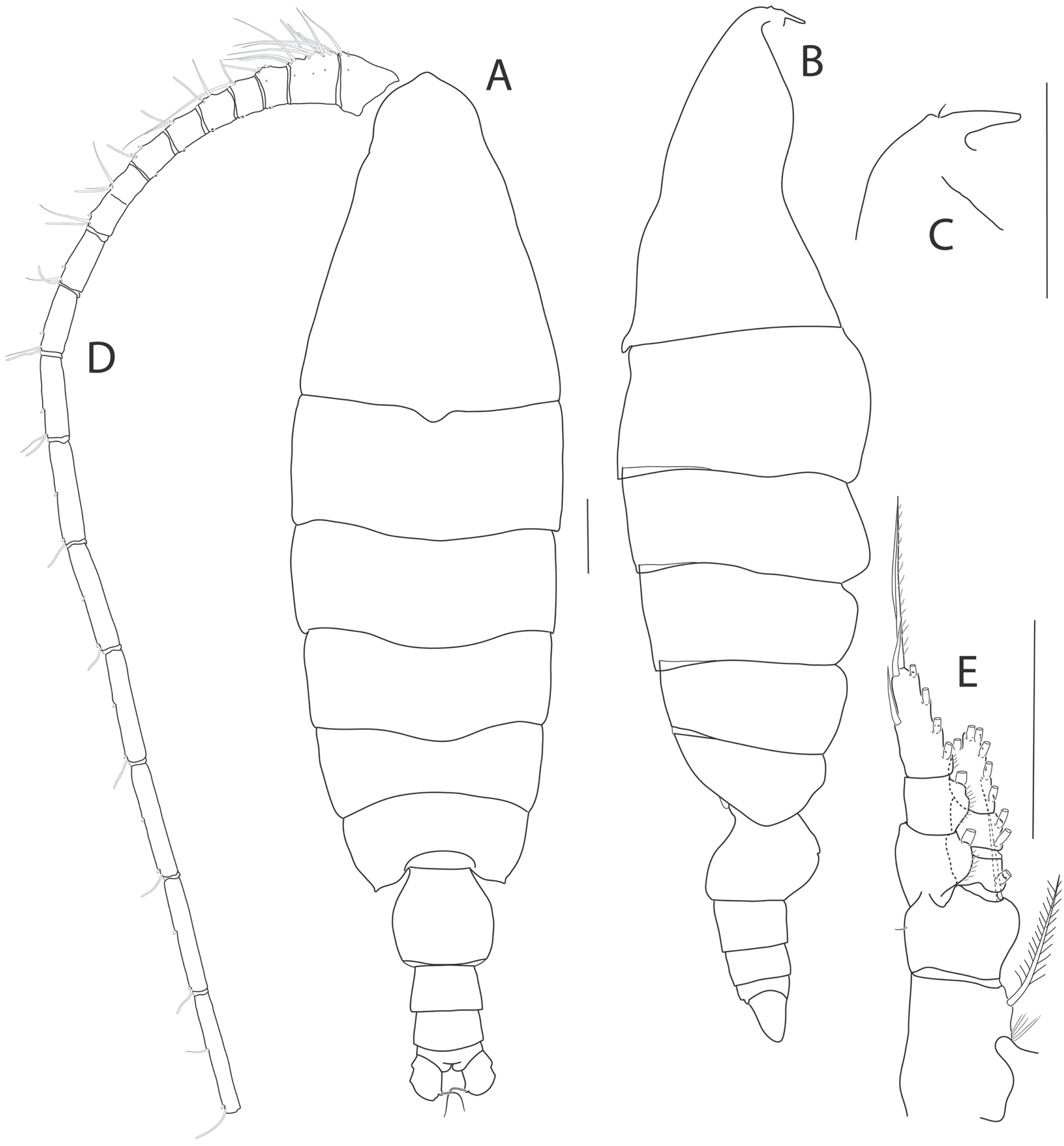

FIGURE 101. *Elenacalanus tageae* **n. sp.** female: A, dorsal view; B, lateral view; C, lateral view of rostrum; D, left antennule; E, posterior view of leg 1. Scale bar represents 1.0 mm on all figures. Illustrated specimen is from Antipode IV, Stn 53A, 0–2000 m.

Leg 5 (Fig. 106D, E) slightly asymmetrical, left leg slightly longer than right leg; left exopod segment 2 inner distal corner bearing bifurcate specialised seta with 2 short setulose lashes arising from proximal part; inner border of exopod segment 3 naked on right, irregularly shaped and lined with setulues on left.

Etymology. This species is named for Professor Tagea Björnberg the discoverer of the closely related species *E. eltaninae*.

Distribution. *Elenacalanus tageae* is probably a bathypelagic species and has been taken only in the northwest Pacific Ocean 0–2500 m, south of Japan (Fig. 94, Table 1).

Species comparison. The female of *E. tageae* is very like *E. eltaninae* differing only the longer proximal outer spine on leg 1 exopod segment 3 (extends beyond base of distal outer spine in *E. tageae* but short of this spine in *E.*

eltaninae) (Table 11). The main difference between *E. tageae* and *E. eltaninae* is the nature of the male leg 5 left specialised seta on exopod segment 2: in *E. tageae* it is bifurcate with each short lash approximately equal in length while in *E. eltaninae* this seta is composed of a large rounded outer lobe and an elongate inner lash.

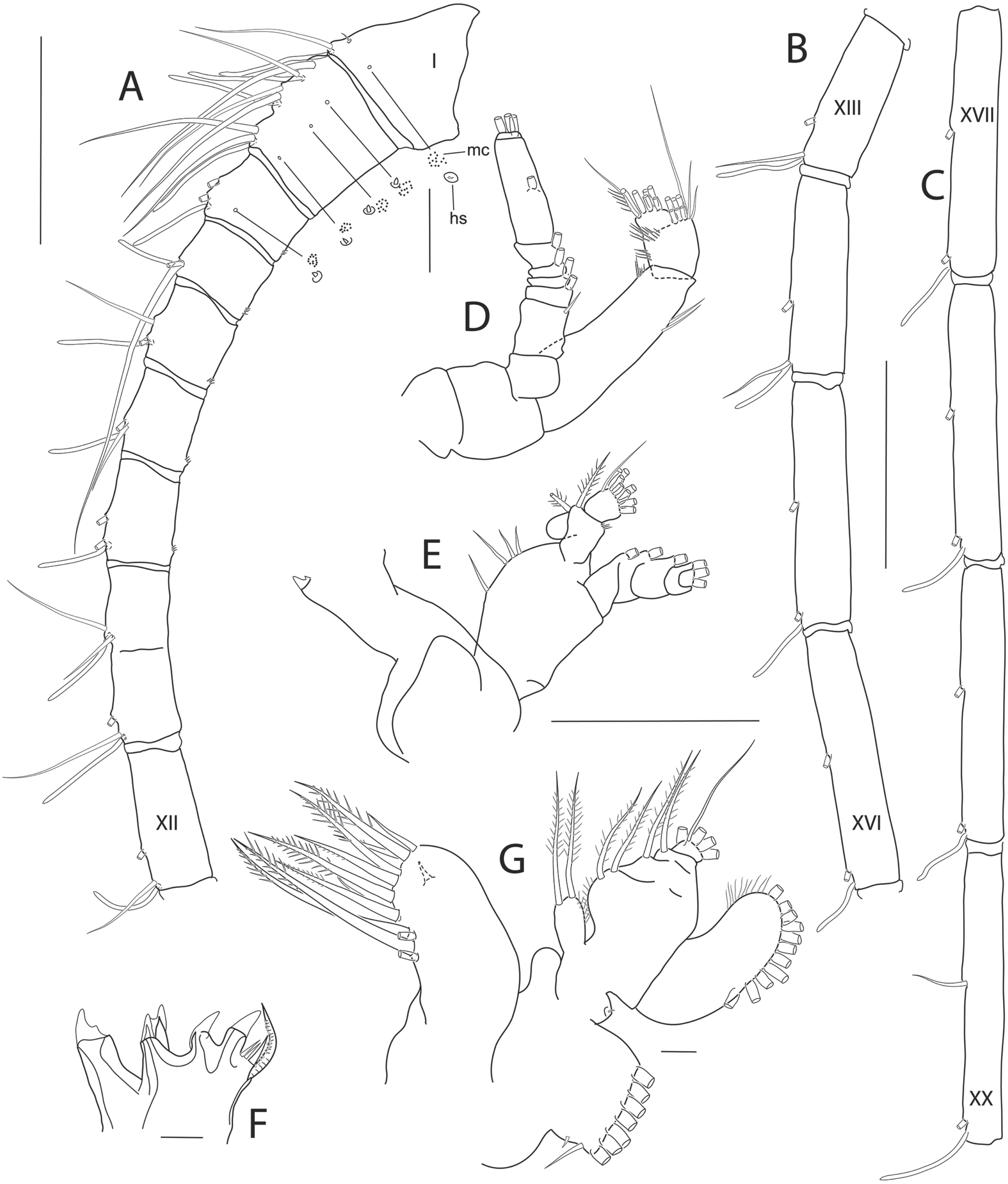

FIGURE 102. *Elenacalanus tageae* **n. sp.** female: A, antennule ancestral segments I–XII (hs = hair sensillum, mc = macula cribrosa); B, antennule segments XIII–XVI; C, antennule segments XVII–XX; D, antenna; E, mandibular palp; F, distal part of mandibular gnathobase; G, maxillule. Scales bars represent 1.0 mm on figures A–E; 0.1 mm on remaining figures. Illustrated specimen is from Antipode IV, Stn 53A, 0–2000 m.

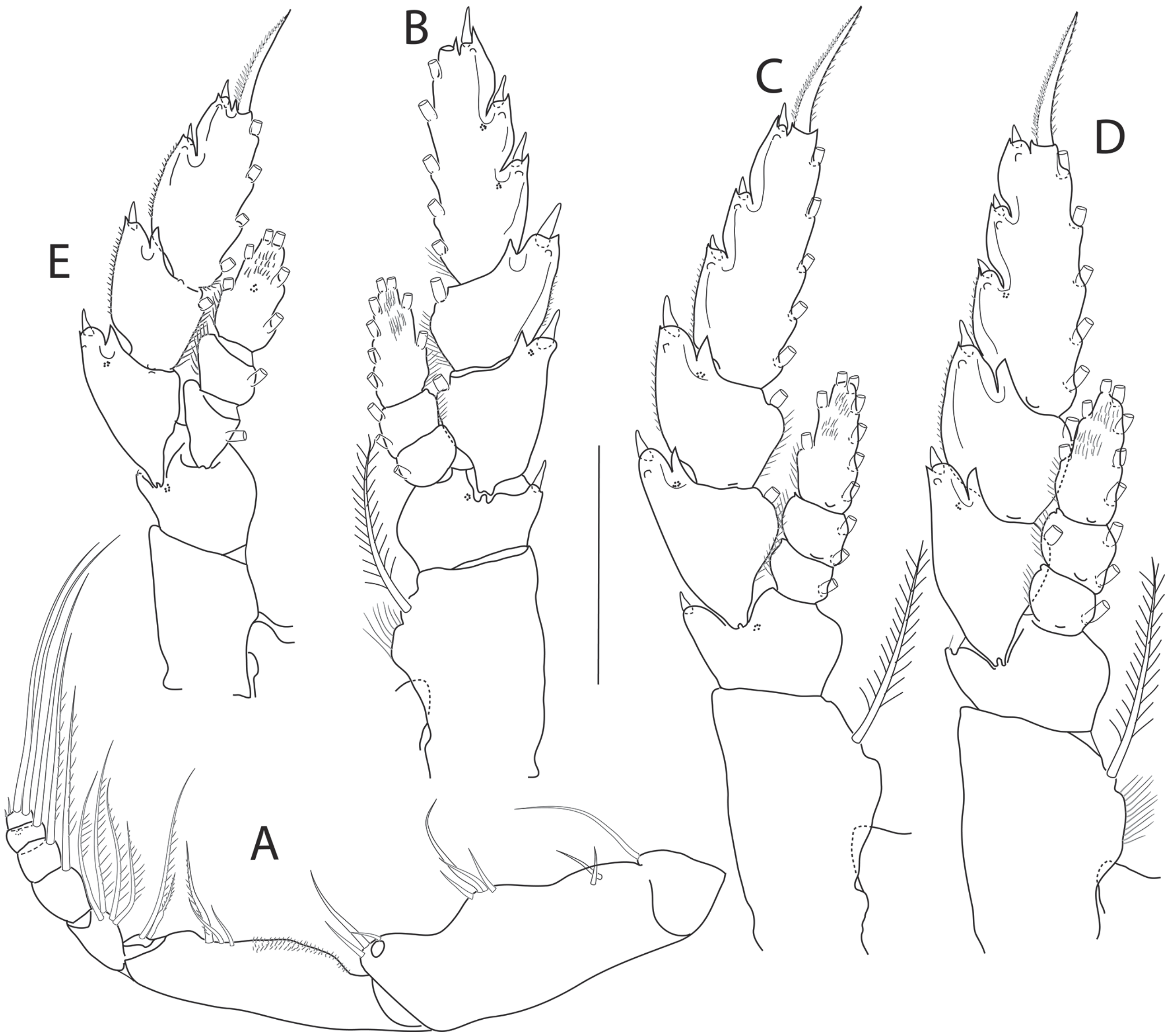

FIGURE 103. *Elenacalanus tageae* **n. sp.** female: A, maxilliped; B, anterior view of leg 2; C, anterior view of leg 3; D, anterior view of leg 4; E, anterior view of leg 5. Scale bars represent 1.0 mm on all figures. Illustrated specimen is from Antipode IV, Stn 53A, 0–2000 m.

Elenacalanus sverdrupi (Johnson, 1958) new combination

(Figs 94, 107)

Bathycalanus sverdrupi Johnson, 1958, pp 257–265, figs 1–14
Bathycalanus sverdrupi: Grice & Hulsemann 1967, p. 13.

Type locality. 12.550º N, 164.817º E.

Material examined. Holotype examined USNM101078. Additional records from Smithsonian Institution, USNM numbers: 259717, 272745–46.

Morphological description. As for genus with following specific level features.

Female. Total length 16.8–17.0 mm. Anterior margin of head in lateral view projecting forwards and in dorsal view rostral branches partially visible. In lateral view posterior corners of pedigerous somite 5 rounded. Genital double-somite swollen, symmetrical in dorsal view, much wider than long.

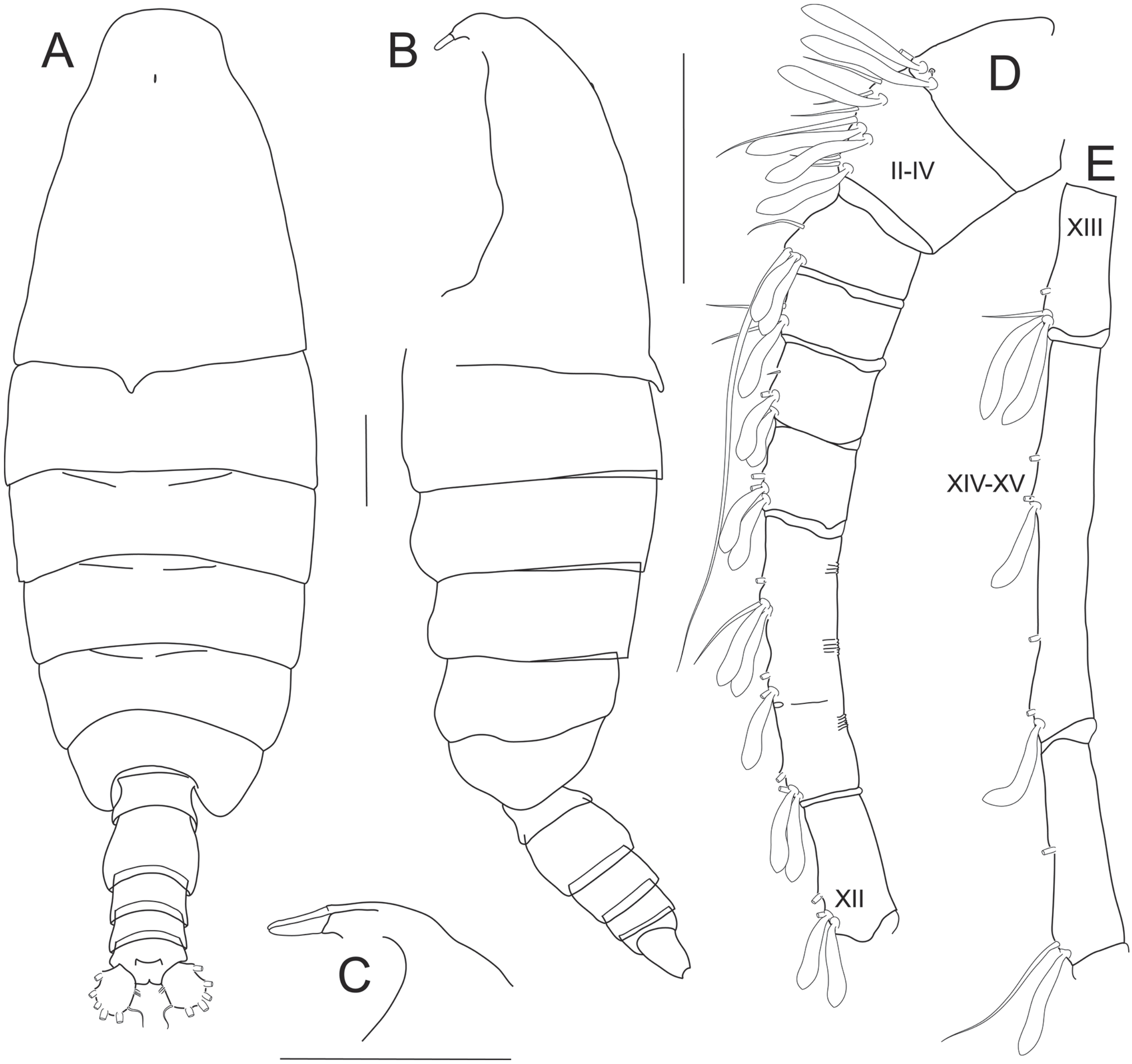

FIGURE 104. *Elenacalanus tageae* **n. sp.** male: A, dorsal view; B, lateral view; C, lateral view of anterior head; D, right antennule ancestral segments I–XII; E, right antennule ancestral segments XIII–XVI. Scale bars represent 1.0 mm on all figures. Illustrated specimen from Antipode IV, Stn 55D.

Antennule not extending to caudal rami. Antennule not mounted on holotype slide so not checked.

Antenna exopod ancestral segment IV bearing short seta extending to segment VIII.

Mandible basis with 3 setae (Johnson 1958).

Maxillule (Fig. 107A, B) praecoxal arthrite with 14 setae including 3 setae on posterior surface and 1 moderately long seta on anterior surface; coxal endite without setae, basal endites 1 and 2 with 2 and 1 seta respectively; endopod segments with 1, 1, 4+1 small setae; basal exite without seta, epipodite with 7 long and 2 very short, reduced setae.

Maxilla with terminal setae curled distally in semicircle and extending beyond rostrum, setae on coxal endite 2 particularly well developed, curled in semicircle and of similar length to terminal setae.

Maxilliped syncoxa endite 4 longest seta extending beyond distal border of endopod segment 2; endopod segments 3–6 with 1, 1, 1, 2, respectively, apparently without any outer border setae on endopod segments 5 and 6. [after Johnson 1958—limb not on slide therefore not checked]

Leg 1 (Fig. 107C) exopod segment 3 with 2 outer border spines, proximal spine broken on mounted leg and probably longer than that illustrated by Johnson (1958).

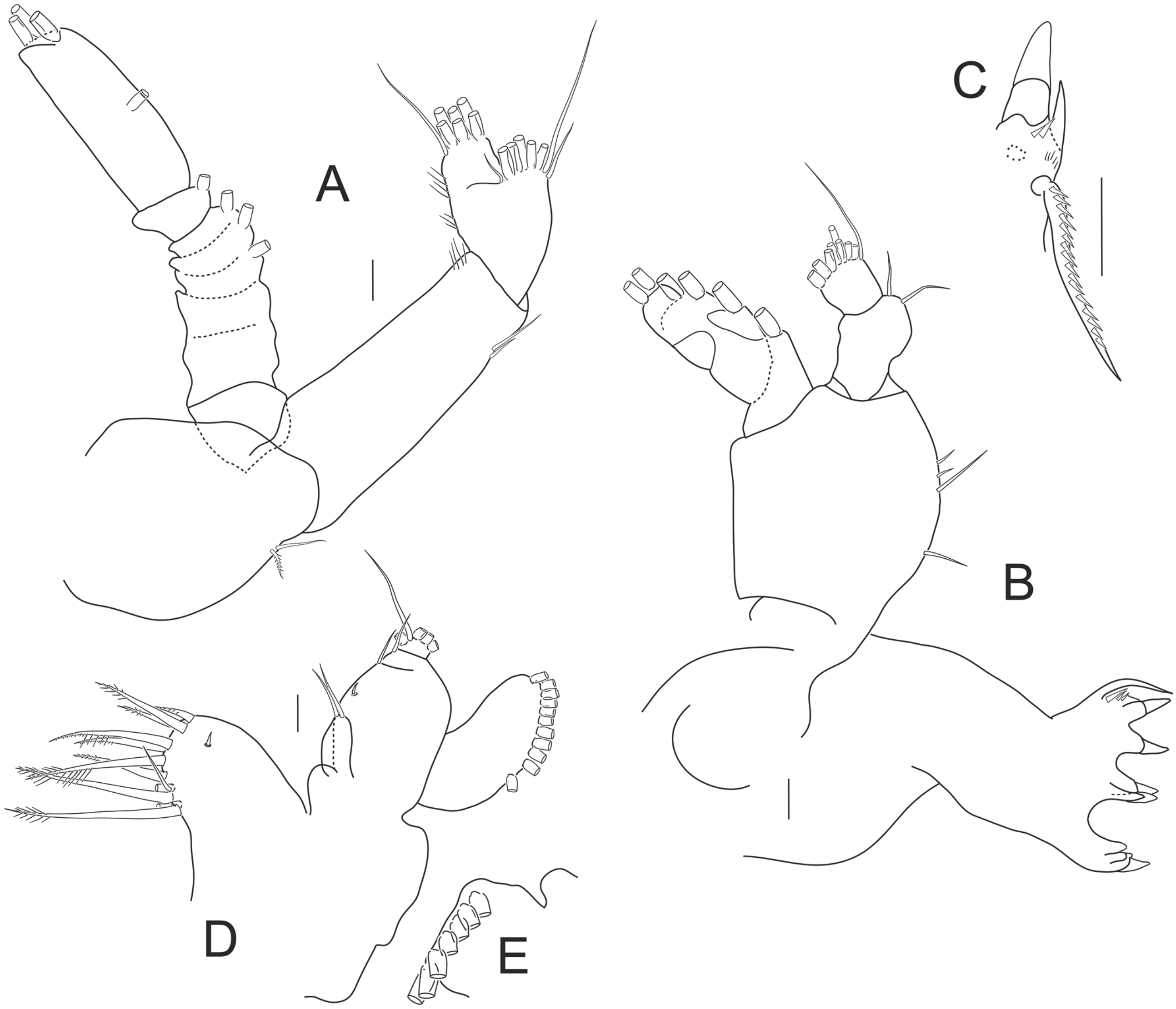

FIGURE 105. *Elenacalanus tageae* **n. sp.** male: A, antenna; B, mandible; C, dorsal part of mandibular gnathobase; D, maxillule; E, coxal epipodite of maxillule. Scale bars represent 0.1 mm on all figures. Illustrated specimen from Antipode IV, Stn 55D.

Male. Unknown**.**

Distribution. *Elenacalanus sverdrupi* is an upper abyssopelagic species known only from the tropical west Pacific from a tow at 2103 m (Johnson 1958), the Indian Ocean at 275–2080 m (Grice & Hulsemann 1967) and the Gulf of Guinea (Owre & Foyo 1967) (Fig. 94, Table 1).

Species comparisons. *Elenacalanus sverdrupi* is very like other members of this genus, nevertheless, it is distinguished by: the short bluntly tapering rostral points directed slightly anteriorly, the very short antennules not extending beyond the caudal rami, the single seta on the maxillule second basal endite, and the unusually long curled setae on maxilla coxal endite 2 (Table 11).

Elenacalanus inflatus (Björnberg, 1968) new combination

(Figs 94, 108–111)

Bathycalanus inflatus Björnberg, 1968, pp 81–85, figs 42–54.

Type locality. 56.108S 71.233W.

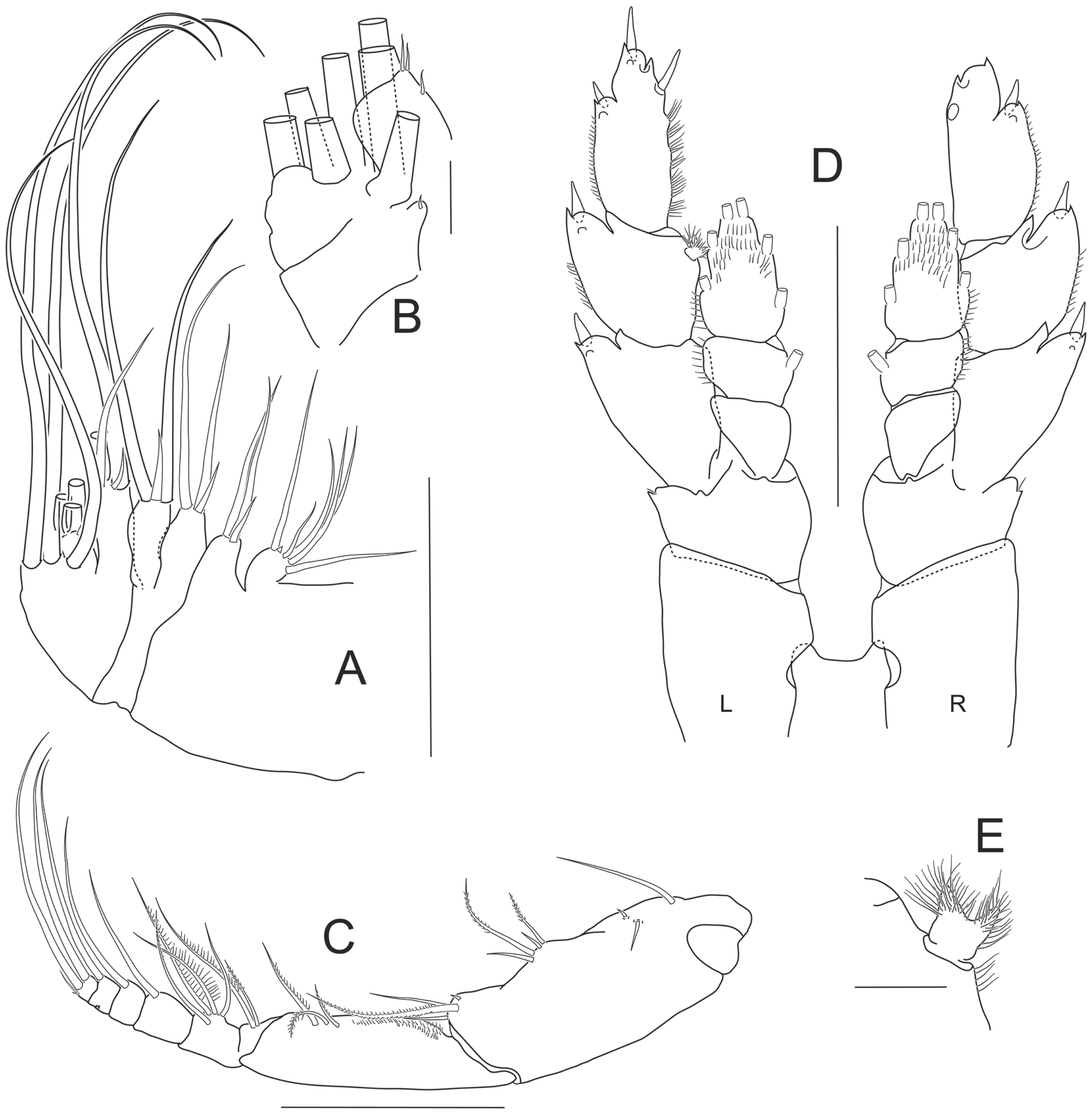

FIGURE 106. *Elenacalanus tageae* **n. sp.** male: A, maxilla; B, endopod of maxilla; C, maxilliped; D, anterior view of leg 5; E, inner distal corner of left exopod segment 2 of leg 5. Scale bars represent 1.0 mm on figures A, C, D; 0.1 mm on remaining figures. Illustrated specimen from Antipode IV, Stn 55D.

Material examined. Holotype specimen USNM122572 and specimen USNM122573. Records from Natural History Museum, London: Discovery Stns, RMT8: 7406#33, 990–1250 m, 1♀ (13.5 mm), BMNH 1993.876; 7709#44, 1250–1500 m, 2♀ (12.4, 13.0 mm), BMNH 1993.877-878.

Morphological description. Following description based on specimen from Discovery Stn 7406 (BMNH 1993.876). As for genus with following specific level features.

Female (Fig. 108A–E). Total length 12.9 mm (range = 12.40–13.85 mm). Body of 'stout' appearance such that depth of somites in lateral view, relative to the length of the whole animal or individual somites, is greater than in other species; Ur2/Gns = 0.93, where Ur2 is the midlength depth of free urosomite 2 and Gns is the posterior depth of the genital double-somite, in lateral view. In lateral view, posterolateral corners of pedigerous somite 5 bluntly triangular. Genital double-somite approximately as wide as long, symmetrical in dorsal view; in lateral view dorsal and ventral profile of second and third free urosomites convex.

Antennule (Figs 108B, 109A–C) broken, ancestral segments I–XVIII, only, available; Measurements taken along posterior border of each segment but two (posterior (shortest) and anterior) measurements taken of ancestral segment I. I (249, 815); II–IV (617); V (281); VI (300); VII (389); VIII (373); IX (398); X–XI (776); XII (646); XIII (673); XIV (834); XV (971); XVI (1037); XVII (1081); XVIII (1185). Dorsal surface of ancestral segments I, II, and III, only, with dorsal surface hair sensillum and adjacent macula cribrosa.

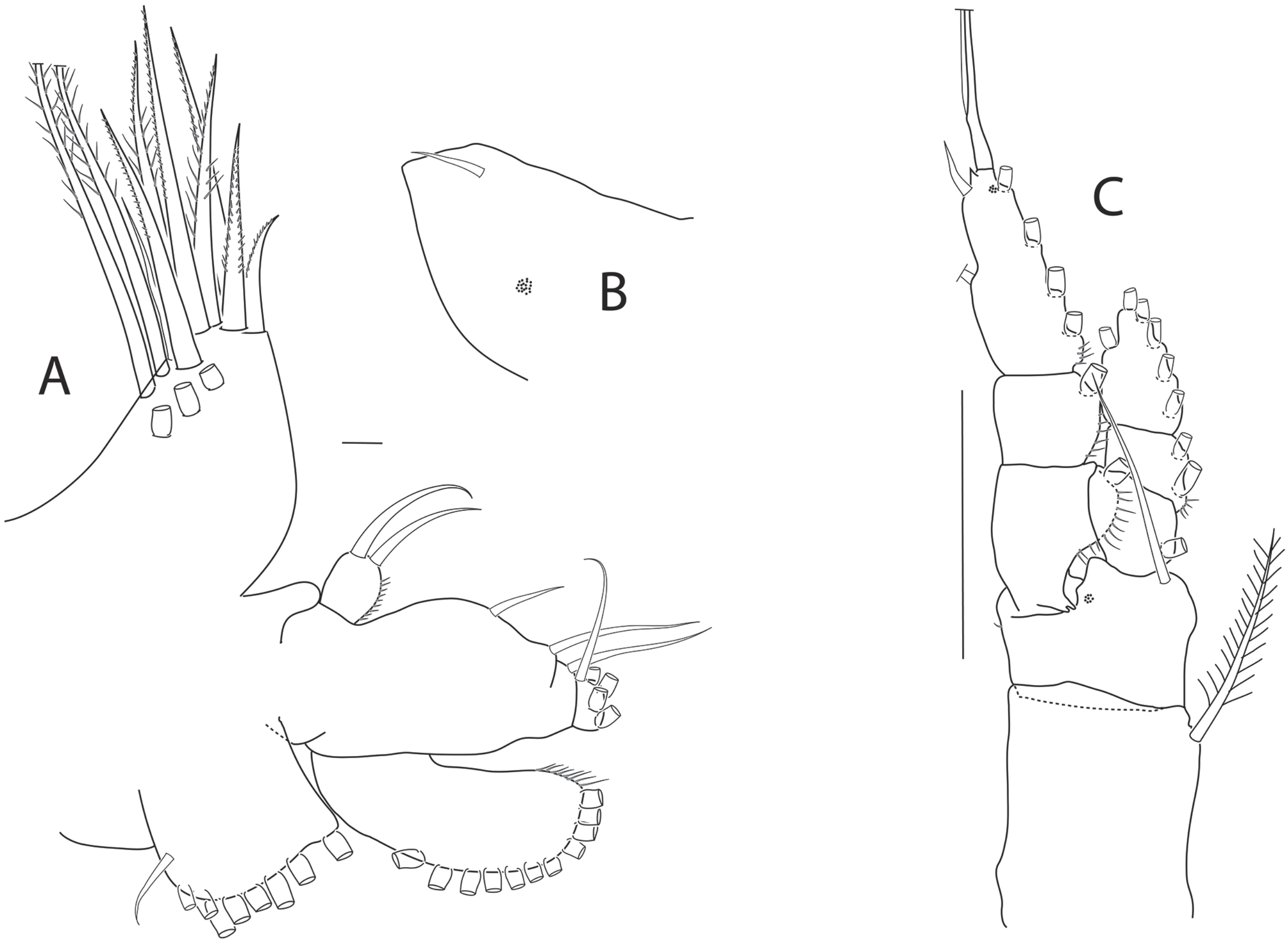

FIGURE 107. *Elenacalanus sverdrupi* (Johnson, 1958) female: A, maxillule, posterior surface; B, maxillule praecoxal arthrite, anterior surface; C, leg 1 anterior surface. Scale bars represent 1.0 mm on figure C; 0.1 mm on figures A, B. Illustrated specimen from type specimen USNM101078.

Antenna (Fig. 109D) exopod ancestral segment IV without seta.

Mandible (Fig. 110A) basis with all 4 setae inserted on distal inner border; that is, proximalmost seta inserted well distal to midlength of basis inner border.

Maxillule (Fig. 110B) praecoxal arthrite with 13 setae including 2 on posterior surface; coxal endite without setae, basal endites 1 and 2 each with 2 setae; endopod segments with 1, 1, 4+1 anterior surface seta; basal exite without seta, epipodite with 7 long and 1 vestigial setae.

Maxilla (Fig. 110C–H) terminal setae only slightly curved distally.

Maxilliped (Fig. 111A–C) syncoxal endite 4 longest seta extends to distal border of endopod segment 1.endopod segments 3–6 with 1, 1, 1, 4 setae (2 large and 2 very small), respectively.

Leg 1 (Fig. 108F) basis inner distal seta curved along distal border of endopod segment 1; exopod segment 3 with proximal outer spine not extending as far as base of distal outer spine.

Male. Unknown.

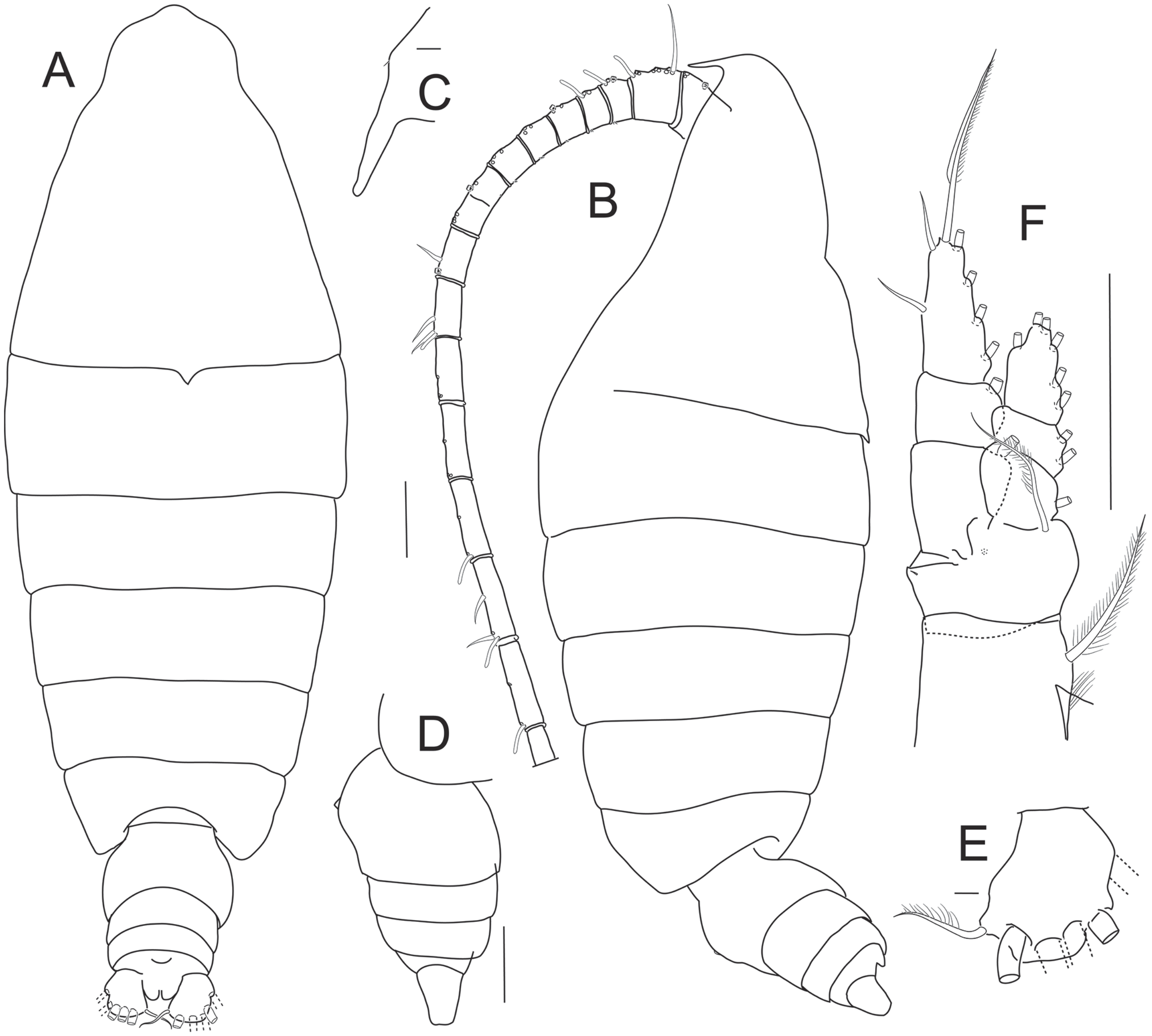

FIGURE 108. *Elenacalanus inflatus* (Björnberg, 1968) female: A, dorsal view; B, dorsolateral view; C, rostrum; D, urosome, lateral view; E, right caudal ramus, dorsoposterior view; F, leg 1. Scale bars represent 1.0 mm on figures A, B, D, F; 0.1 mm on remaining figures. Illustrated specimen is from Natural History Museum, London, 1993.876, Discovery Stn 7406, 990–1250 m.

Distribution. *Elenacalanus inflatus* is a bathypelagic species known from the Drake Passage and the Scotia Sea, 0–1867 m (Fig. 94) (Björnberg 1968) and the North Atlantic 900–1500 m (present data).

Remarks. Re-examination of the holotype slide (USNM122572) and examination of specimen from Discovery Station 7406 (BMNH 1993.876) confirms most of the written description of Björnberg (1968). Details of the setation of the maxillule and maxilliped are corrected above. It is noted that the leg labelled as leg 4 in the original description is leg 2 because it has 8 setae on endopod segment 3. Leg 4 endopod segment 3 has only 7 setae in North Atlantic material (BMNH 1993.876). Rostral filaments bluntly taper and the posterolateral corners of pedigerous somite 5 are bluntly triangular, therefore *E. inflatus* is the same as most other species in these respects.

Species comparisons. *Elenacalanus inflatus* is very like *E. princeps* and *E. tageae* **n. sp.** in that all three species have 2 setae on basal endite 2 of the maxillule and the posterolateral corners of pedigerous somite 5 are bluntly triangular. *E. inflatus* is distinguished by the distal placement of the four setae of the basis of the mandible, and the setae on the terminal part of the maxilla which are hardly curled. The dorsal surface of ancestral segments I, II, and III, only, have a dorsal surface hair sensillum and an adjacent macula cribrosa (in other species where these characteristics are known, *E. princeps, E. eltaninae* and *E. tageae* **n. sp.**, segment IV and V both have a hair sensillum which may not be accompanied by a macula cribrosa—Table 11). It is difficult to quantify the general description of *E. inflatus* as being 'stout' because the single specimen examined has the urosome tilted dorsally, its somites are telescoped and bounds could not be put on any measurements made. Nevertheless, we suggest *E. inflatus* may possibly be distinguished from other *Elenacalanus* in the future by the ratio between the depth at midlength of free urosomite 2 (Ur2) and the posterior depth of the genital double-somite (Gns): Gns/Ur2 = 0.93 (this ratio from a single specimen of: *E. princeps* = 0.76; *E. eltaninae* = 0.85; *E. tageae* **n. sp.** = 0.86).

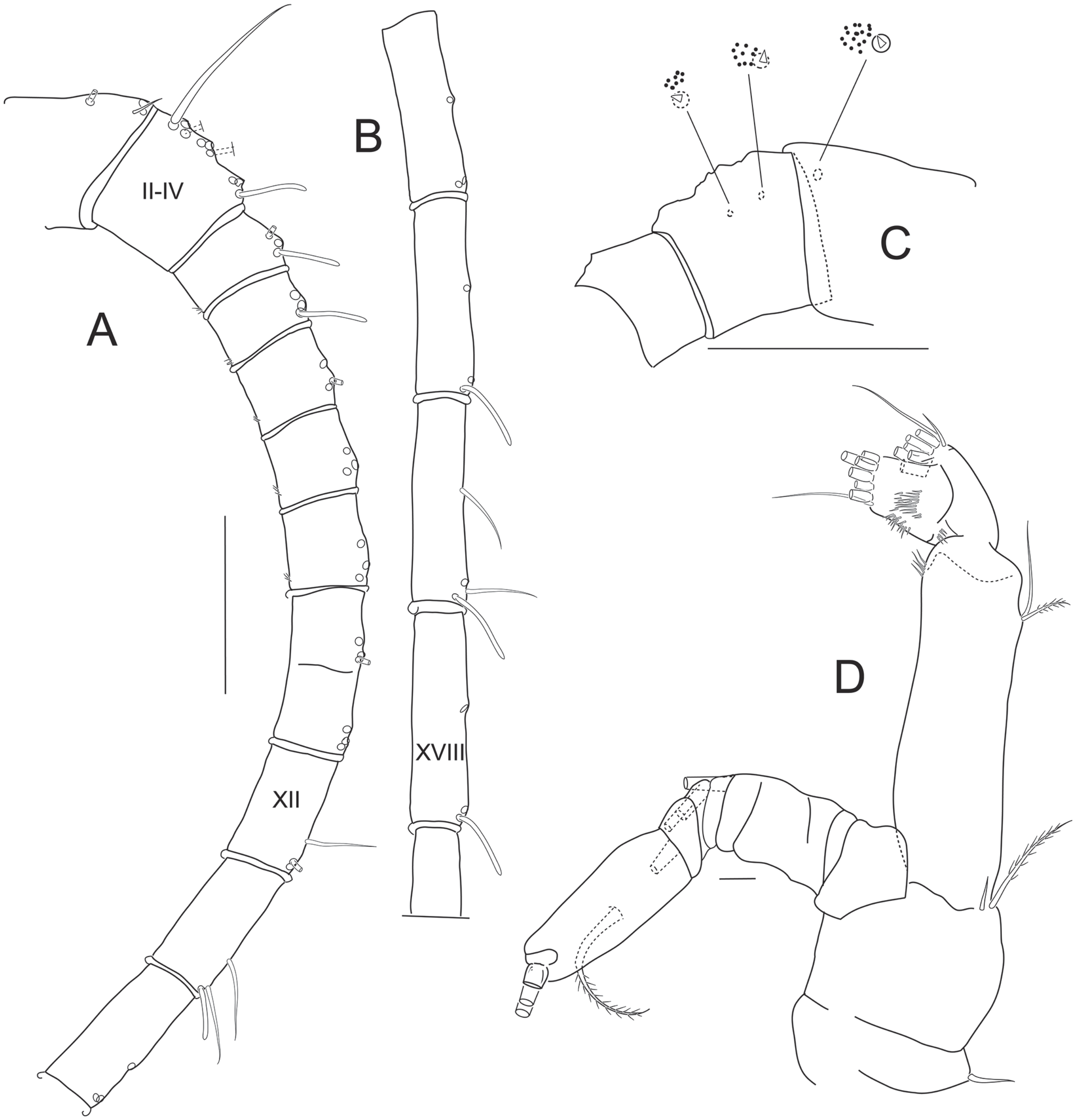

FIGURE 109. *Elenacalanus inflatus* (Björnberg, 1968) female: A, antennule, ancestral segments I–XIV; B, antennule, ancestral segments XV–XVIII; C, antennule, ancestral segments I–IV, dorsal view; D, antenna. Scale bars represent 1.0 mm on figures A–C; 0.1 mm on remaining figure. Illustrated specimen is from Natural History Museum, London, 1993.876, Discovery Stn 7406, 990–1250 m.

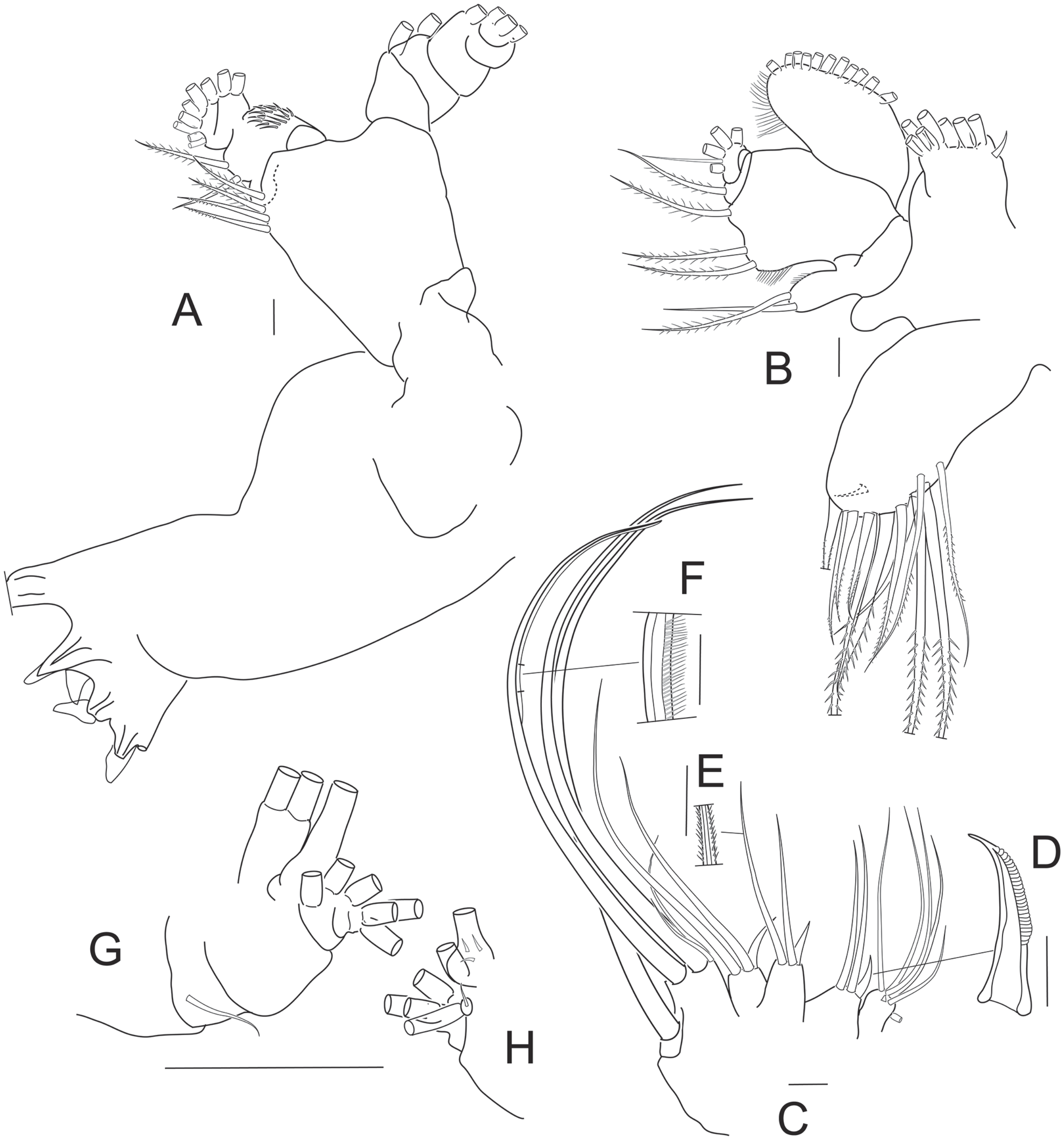

FIGURE 110. *Elenacalanus inflatus* (Björnberg, 1968) female: A, mandible; B, maxillule; C, maxilla praecoxal to basal endites; D, detail of small seta of praecoxal endite 2; E, detail of longest seta on coxal endite 1; F, detail of distal seta of basal endite; G, maxilla endopod and basal endite lateral view; H, maxilla endopod inner view. Scale bars represent 1.0 mm on figures G, H; 0.1 mm on remaining figures. Illustrated specimen is from Natural History Museum, London, 1993.876, Discovery Stn 7406, 990–1250 m.

Results

Morphology-based phylogeny

The heuristic search in PAUP4.0 retrieved 84 most parsimonious trees (length 102, consistency index 0.75, retention index 0.90). In the strict consensus tree there are more unresolved relationships than the 50% majority-rule tree (Fig. 112A, B). A monophyletic *Megacalanus* (Clade 1), *Bradycalanus* (Clade 3), *Bathycalanus* (Clade 5), and a renamed genus *Elenacalanus* (Clade 6) are recovered with bootstrap support of 92, 99, 90 and 100%, respectively.

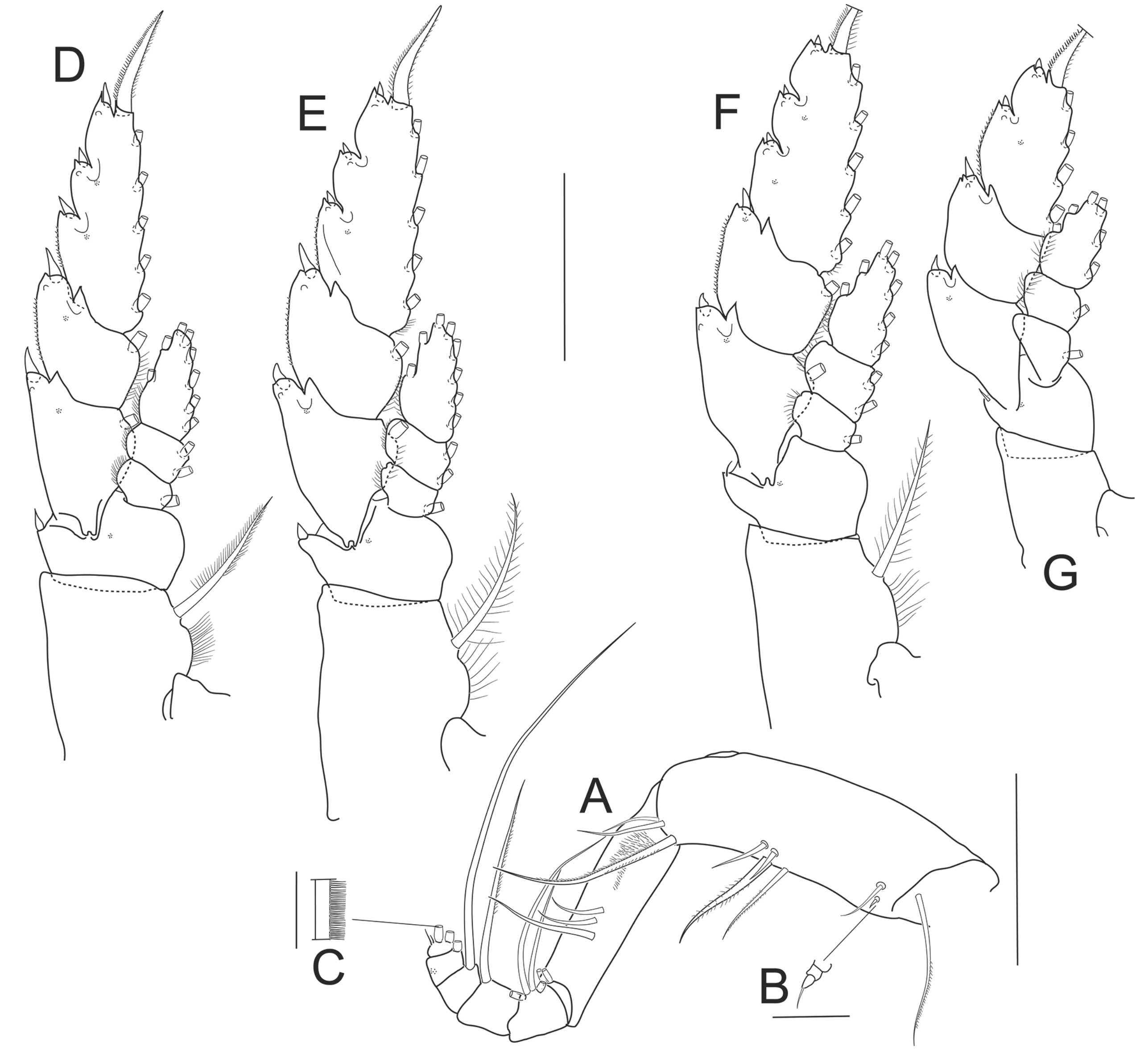

FIGURE 111. *Elenacalanus inflatus* (Björnberg, 1968) female: A, maxilliped; B, detail of small seta on syncoxal endite 2 of maxilliped; C, detail of terminal seta on endopod segment 6 showing long fine setules along concave border; D, leg 2; E, leg 3; F, leg 4; G, leg 5. Scale bars represent 1.0 mm on figures A, C–F; 0.1 mm on remaining figure. Illustrated specimen is from Natural History Museum, London, 1993.876, Discovery Stn 7406, 990–1250 m.

As indicated by the rescaled consistency index (*RC*) for each character (Table 3), four out of 57 characters made little contribution (*RC* < 0.20) to the resulting topologies. Among characters with a high *RC* (1.00) are several that are recognised here as defining the genera. For example, character 44 (terminal setae of maxilla: curled completely on themselves) defines *Bathycalanus*; characters 56 and 57 (outer spines of P1 exopod segments 1–3: present) and 54 (leg 1 basis anterodistal hook-like process: present) define *Megacalanus*; character 42 (proximal inner seta of endopod segment 2 of maxilla: vestigial with oval base) defines *Bradycalanus*; characters 56 and 57 (outer distal spines of leg 1 exopod segments 1 and 2: absent) define *Bathycalanus*; and a number of characters define the renamed genus *Elenacalanus*.

One round of successive weighting yielded 12 most parsimonious trees that are similar to the unweighted 50% majority rule concensus tree (Fig. 112B). Here we describe tree 1 of the weighted analysis which has a similar topology as the unweighted 50% majority rule tree. In tree 1, *Megacalanus* (Clade 1) is sister to the remaining members of the family. Clade 1 (92% bootstrap support) (Fig. 112B) is united by two unambiguous, unique characters that are uniform above the node in the tree (Char. 16: antennule segments XIV–XVII with ventral surface with row of teeth; and Char. 54: leg 1 basis with hook-like process) (Table 12).

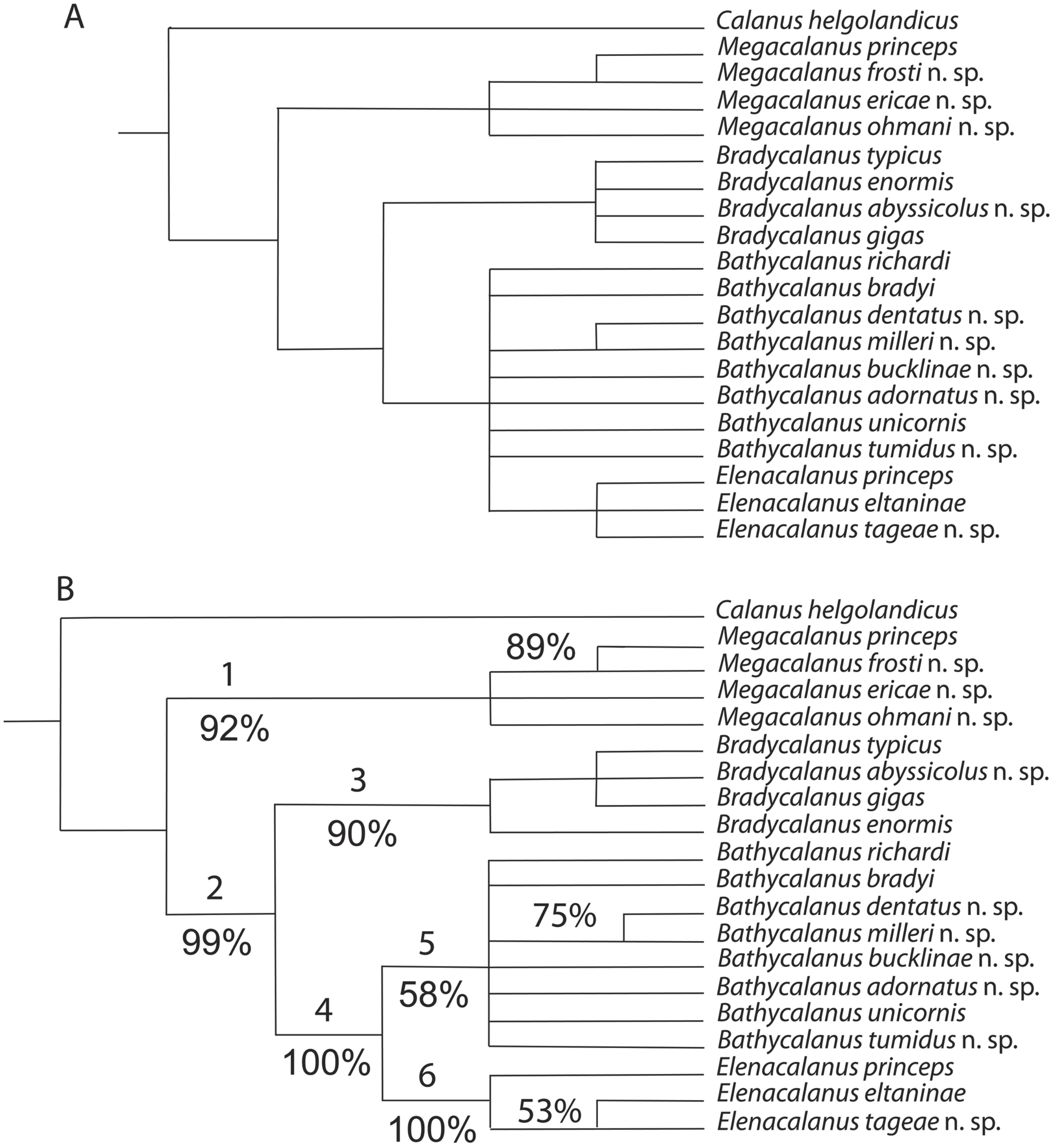

FIGURE 112. Strict consensus (A), 50% majority-rule (B) trees, of 84 trees, length 102, consistency index (*CI*) = 0.75, retention index (*RI*) = 0.90. After one round of successive reweighting (50% majority rule of 12 trees), the topology of tree 1 is same as unweighted 50% majority rule tree (B). The trees are rooted to the outgroup *Calanus helgolandicus*. Clade number above the line and bootstrap support below.

Clade 2 (99% bootstrap support) is united by four unique, unambiguous character changes that are uniform above in the tree (Table 12). On the maxillule, basal endite 1 with 2 setae (Char. 31) and endopod segment 3 lacks seta 7 (Char. 37). On the maxilla, the endopod setae do not have long sparse auxiliary spinules (Char. 40) and endopod segment 1 smallest setae are vestigial (Char. 41). Several other characters change unambiguously on a branch, change above the node in the tree, but are uniform outside the branch: An aesthetasc is present on female ancestral antennular segment XXIII (Char. 17). Antenna segment IV seta is short (Char. 20). On the mandible endopod segment 1 (Char. 23) and segment 2 the surface setae are vestigial (Char. 26). On the maxillule, endopod segment 2 has 2 setae (Char. 34). On the maxilliped endopod segment 3, setae 2 and 3 are reduced in size (Chars 46, 48) and on endopod segment 5 inner seta 2 is reduced in size (Char. 52).

Clade 2 divides into two sister clades—3 and 4. Clade 3 (*Bradycalanus*) has good bootstrap support (90%) and is united by two unique unambiguous characters that are uniform above. These are: the maxilla coxal epipodite seta is vestigial (Char. 38) and on endopod segment 2 the distal inner seta convex border is naked (Char. 43) (Table 12).

Clade 4 (100% bootstrap) is united by three unambiguous, unique changes uniform above: there is a macula cribrosa adjacent to the hair sensillum on ancestral segment V of the female antennule (Char. 11); the setae of praecoxal endites 1and 2 and coxal endite 1 of the maxilla are without sparse auxiliary spinules (Char 39) and there is no outer distal spine on exopod segments 1 and 2 of leg 1 (Char 56) (Table 12). Two characters that change unambiguously on its branch but are homoplasious above in the tree are: on the maxillule, the absence of the two distal-most setae on posterior surface and the presence of 2 setae on basal endite 2 (Chars 28, 29 and 32).

Within Clade 4 there are two sister clades (5 and 6) with variable bootstrap support. Clade 5 (*Bathycalanus*) has no bootstrap support (58%) and is united by two unambiguous, unique changes uniform above (Table 12): the hair sensillum on ancestral segment IV is absent (Char. 9) and leg 1 exopod segment 3 is without a proximal outer spine (Char. 57). One character changes above but not outside: anterior head with 2 spines (Char. 2), and one character is homoplasious outside: anterior head is decorated in dorsal view (Char. 1).

Clade 6 (100% bootstrap support) (the renamed genus *Elenacalanus* nom. nov.) is united by eleven unambiguous unique changes uniform above (Table 12): on mandibular endopod segment 1, the distal and proximal setae are absent (Chars 22, 24); endopod segment 2 both surface setae are absent (Chars 25, 26). On maxillule endopod segment 3, seta 6 is absent (Char. 36). On the maxilliped, setae 2, 3 and 4 of endopod segment 3 are absent (Chars 45, 47 and 49); seta 3 of endopod segment 4 is absent (Char. 50) and inner seta 2 of endopod segment 5 and the outer border seta are both absent (Chars 51, 53). Three other characters are homoplasious outside and one character that is homoplasious above also unite this clade.

Generally the present morphological data set is insufficient to resolve most relationships at the species level.

Molecular diagnosis

Amplification of the COI gene was successful only for individuals of *Megacalanus ericae* **n. sp.** and *M. frosti* **n. sp.** Within-species differences ranged from 0.2 to 4.5%, meanwhile differences between species ranged from 19.6 to 21% (Table 13). When compared against other genetic markers, H3 showed no variation within species and a single base pair change between the two species (Table 14), 28S showed 0 to 1 bp changes within species, and 2 to 3 between species (Table 15), ITS1 showed no changes within and 2 bp differences between species (Table 16), and ITS2 showed no changes between any of the individuals analysed for COI independently of the species (Table 17). The most consistent marker was ITS1 (0 to 1 bp differences within species, 2 or more between species), meanwhile H3 and 28S showed no clear differences between some species.

When the criteria, identified in the previous paragraph, of between-species distances were applied to the distances among all analysed individuals, the results supported the morphological assignments, with some exceptions within *Bathycalanus*. Within *Bradycalanus*, the ITS1 and ITS2 markers showed differences between *Br. enormis* and *Br. typicus* (Tables 16, 17) therefore, we infer that *Br. enormis* is a distinct species. Within *Bathycalanus*, *Ba. adornatus* **n. sp.** and *Ba. bradyi* are mixed although there are two genetic clusters that might be species (Tables 16, 17). One clade is composed of *Ba. adornatus* (22.3.1) and *Ba. bradyi* (36.1.1 and 375.1.2) which are genetically identical (Fig. 113). A related clade is formed from *Ba. bradyi* (411.1) and *Ba. bradyi* (441.3.1). In general, *Bathycalanus* was the genus with the most conflicts between morphological identifications and molecular data.

The designation of *Elenacalanus* nom. nov. based on molecular diagnosis showed that the distances between individuals belonging to *Elenacalanus* and *Bathycalanus* were intermediate between those obtained between species within genera and between the other genera (Tables 16, 17). Distances between *Bathycalanus tumidus* **n. sp.** and the other *Bathycalanus* were also closer to those obtained between genera than within genus for the ITS1 and ITS2 sequences (Tables 16, 17).

TABLE 12. Unambiguous character state changes for one (number 1) of 12 most parsimonious cladogram of the Megacalanidae phylogeny following successive weighting. Unique character changes not changing above are in **bold** type.

Clade 1	**16: 2→1, 54: 2→1**
Clade 2	17: 2→1, 20: 1→2, 23: 1→2, 26: 1→2, **31: 1→2,** 34: 4→3, **37: 1→2, 40: 1→2, 41: 1→2,** 46: 1→2, 48: 1→2, 52: 1→2
Clade 3	**38: 1→2, 43: 2→1**
Clade 4	**11: 2→1,** 28: 1→2, 29: 1→2, 30: 5→1, 32: 4→2, **39: 1→ 2, 56: 1→2**
Clade 5	1: 1→2, 2: 1→3**, 9: 1→2, 57: 1→2**
Clade 6	6: 2→3, **22: 1→2, 24: 1→2, 25: 1→2, 26: 2→3,** 33: 2→1, 34: 3→2, **36: 1→2, 45: 1→2, 47: 1→2, 49: 1→2, 50: 1→2, 51: 1→2, 53: 1→2**

TABLE 13. Genetic distances (uncorrected p-value) between individuals within the analysed COI region region. Sequences from COI were obtained from freshly fixed *M. frosti* and *M. ericae* only. Co = catalogue numbers.

Megacalanus frosti	Co439.2.2						
	Co439.10.1	0.003					
	Co439.5.1	0.002	0.002				
Megacalanus ericae	Co439.4.1	0.205	0.205	0.196			
	Co439.3.2	0.199	0.202	0.196	0.043		
	Co439.3.1	0.210	0.210	0.205	0.045	0.025	
	Co439.6.1	0.207	0.207	0.201	0.045	0.025	0.007

TABLE 14. Non-corrected genetic distances (in bp) between individuals within the analysed H3 region. Co = voucher numbers.

Megacalanus princeps	Co119.5.1																																						
	Co119.4.1	0																																					
	Co119.2.1	0	0																																				
	Co119.3.1	0	0	0																																			
Megacalanus frosti	Co439.2.2	0	0	0	0																																		
	Co439.2.1	0	0	0	0	0																																	
	Co439.10.1	0	0	0	0	0	0																																
	Co439.5.1	0	0	0	0	0	0	0																															
Megacalanus ericae	Co439.1.2	0	0	1	1	1	1	1	1																														
	Co439.1.1	0	0	1	1	1	1	1	1	0																													
	Co439.7.1	0	0	1	1	1	1	1	1	0	0																												
	Co439.8.1	0	0	1	1	1	1	1	1	0	0	0																											
	Co439.4.1	0	0	1	1	1	1	1	1	0	0	0	0																										
	Co439.3.2	0	0	1	1	1	1	1	1	0	0	0	0	0																									
	Co439.3.1	0	0	1	1	1	1	1	1	0	0	0	0	0	0																								
	Co439.6.1	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0																							
Elenacalanus princeps	Co24.3.2	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7																						
	Co24.5.1	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	1																					
	Co24.1.1	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7	0	0																				
	Co24.7.1	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	1	0	0																			
	Co24.1.4	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7	0	1	0	1																		
	Co24.1.2	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7	0	1	0	1	0																	
	Co24.2.1	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7	0	1	0	1	0	0																
	Co24.3.1	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7	0	1	0	1	0	0	0															
	Co24.6.1	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7	0	1	0	1	0	0	0	0														
Bathycalanus tumidus	Co375.1.3	8	8	8	8	8	8	8	8	9	9	9	9	9	9	9	9	5	6	5	6	5	5	5	5	5													
	Co375.1.1	8	8	8	8	8	8	8	8	9	9	9	9	9	9	9	9	5	6	5	6	5	5	5	5	5	0												
Bathycalanus richardi	Co22.2.1	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	4	6	4	6	4	4	4	4	4	1	1											
	Co22.4.1	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	4	6	4	6	4	4	4	4	4	1	1	0										
Bathycalanus milleri	Co411.1.2	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	3	4	3	4	3	3	3	3	3	2	2	1	1									
Bathycalanus bradyi	Co375.1.2	8	8	8	8	8	8	8	8	9	9	9	9	9	9	9	9	3	5	3	5	3	3	3	3	3	1	1	0	0	2								
	Co376.1	8	8	8	8	8	8	8	8	9	9	9	9	9	9	9	9	3	5	3	5	3	3	3	3	3	1	1	0	0	2	0							
	Co411.1.1	8	8	8	8	8	8	8	8	9	9	9	9	9	9	9	9	3	5	3	5	3	3	3	3	3	2	2	0	0	1	1	1						
	Co441.3.1	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	3	5	3	5	3	3	3	3	3	1	1	0	0	1	0	0	0					
Bathycalanus adornatus	Co22.3.1	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	3	5	3	5	3	3	3	3	3	1	1	0	0	1	0	0	0	0				
Bradycalanus typicus	Co303.1.1	5	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	5	6	5	6	5	5	5	5	5	5	5	3	3	4	4	4	4	3	3			
	Co303.1.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
	Co384.1.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Bradycalanus enormis	Co360.1.1	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	6	8	6	8	6	6	6	6	6	6	6	4	4	6	5	5	5	4	4	1	-	-

TABLE 15. Non-corrected genetic distances (in bp) between individuals within the analysed 28S region. Co = voucher numbers.

Megacalanus princeps	Co119.5.1																																						
	Co119.4.1	0																																					
	Co119.2.1	0	0																																				
	Co119.3.1	0	0	0																																			
Megacalanus frosti	Co439.2.2	6	6	6	6																																		
	Co439.2.1	6	6	6	6	0																																	
	Co439.10.	5	5	5	5	1	1																																
	Co439.5.1	6	6	6	6	0	0	1																															
Megacalanus ericae	Co439.1.2	1	1	1	1	5	5	4	5																														
	Co439.1.1	2	2	2	2	4	4	3	4	1																													
	Co439.7.1	2	2	2	2	3	3	3	3	1	0																												
	Co439.8.1	1	1	1	1	3	3	2	3	0	0	0																											
	Co439.4.1	2	2	2	2	2	2	2	2	1	0	0	0																										
	Co439.3.2	2	2	2	2	3	3	2	3	1	0	0	0	0																									
	Co439.3.1	2	2	2	2	3	3	2	3	1	0	0	0	0	0																								
	Co439.6.1	2	2	2	2	4	4	3	4	1	0	0	0	0	0	0																							
Elenacalanus princeps	Co24.3.2	16	16	16	16	16	16	17	16	17	16	14	15	13	15	15	16																						
	Co24.5.1	16	16	16	16	16	16	17	16	17	16	14	15	13	15	15	16	0																					
	Co24.1.1	16	16	16	16	16	16	17	16	17	16	14	15	13	15	15	16	0	0																				
	Co24.7.1	16	16	16	16	16	16	17	16	17	16	14	15	13	15	15	16	0	0	0																			
	Co24.1.4	16	16	16	16	16	16	17	16	17	16	14	15	13	15	15	16	0	0	0	0																		
	Co24.1.2	16	16	16	16	16	16	17	16	17	16	14	15	13	15	15	16	0	0	0	0	0																	
	Co24.2.1	16	16	16	16	16	16	17	16	17	16	14	15	13	15	15	16	0	0	0	0	0	0																
	Co24.3.1	16	16	16	16	16	16	17	16	17	16	14	15	13	15	15	16	0	0	0	0	0	0	0															
	Co24.6.1	16	16	16	16	16	16	17	16	17	16	14	15	13	15	15	16	0	0	0	0	0	0	0	0														
Bathycalanus tumidus	Co375.1.3	18	18	18	18	18	18	19	18	19	18	15	17	14	17	17	18	6	6	6	6	6	6	6	6	6													
	Co375.1.1	18	18	18	18	18	18	19	18	19	18	15	17	14	17	17	18	6	6	6	6	6	6	6	6	6	0												
Bathycalanus richardi	Co22.2.1	17	17	17	17	17	17	18	17	18	17	14	16	13	16	16	17	5	5	5	5	5	5	5	5	5	4	4											
	Co22.4.1	17	17	17	17	17	17	18	17	18	17	14	16	13	16	16	17	5	5	5	5	5	5	5	5	5	4	4	0										
Bathycalanus milleri	Co411.1.2	15	15	15	15	15	15	16	15	16	15	12	14	11	14	14	15	3	3	3	3	3	3	3	3	3	4	4	2	2									
Bathycalanus bradyi	Co375.1.2	14	14	14	14	14	14	15	14	15	14	11	13	10	13	13	14	4	4	4	4	4	4	4	4	4	5	5	3	3	1								
	Co376.1	14	14	14	14	14	14	15	14	15	14	11	13	10	13	13	14	4	4	4	4	4	4	4	4	4	5	5	3	3	1	0							
	Co411.1.1	18	18	18	18	18	18	19	18	19	18	13	17	12	17	17	18	8	8	8	8	8	8	8	8	8	9	9	7	7	5	4	4						
	Co441.3.1	8	8	8	8	9	9	9	9	9	9	9	8	8	8	8	9	3	3	3	3	3	3	3	3	3	3	3	3	3	1	0	0	1					
Bathycalanus adornatus	Co22.3.1	14	14	14	14	14	14	15	14	15	14	11	13	10	13	13	14	4	4	4	4	4	4	4	4	4	4	4	2	2	1	0	0	4	0				
Bradycalanus typicus	Co303.1.1	19	19	19	19	19	19	20	19	20	19	17	18	16	18	18	19	15	15	15	15	15	15	15	15	15	16	16	16	16	14	13	13	17	10	13			
	Co303.1.2	19	19	19	19	19	19	20	19	20	19	17	18	16	18	18	19	15	15	15	15	15	15	15	15	15	16	16	16	16	14	13	13	17	10	13	0		
	Co384.1.1	20	20	20	20	20	20	21	20	21	20	17	19	16	19	19	20	16	16	16	16	16	16	16	16	16	17	17	17	17	15	14	14	18	10	14	1	1	
Bradycalanus enormis	Co360.1.1	19	19	19	19	19	19	20	19	20	19	16	18	15	18	18	19	15	15	15	15	15	15	15	15	15	16	16	16	16	14	13	13	17	9	13	2	2	1

TABLE 16. Non-corrected genetic distances (in bp) between individuals within the analysed ITS1 region. Co = voucher numbers.

Megacalanus princeps	Co119.5.1																																						
	Co119.4.1	0																																					
	Co119.2.1	0	0																																				
	Co119.3.1	0	0	0																																			
Megacalanus frosti	Co439.2.2	2	2	2	2																																		
	Co439.2.1	2	2	2	2	0																																	
	Co439.10.1	2	2	2	2	0	0																																
	Co439.5.1	2	2	2	2	0	0	0																															
Megacalanus ericae	Co439.1.2	5	5	5	5	2	2	2	2																														
	Co439.1.1	5	5	5	5	2	2	2	2	0																													
	Co439.7.1	5	5	5	5	2	2	2	2	0	0																												
	Co439.8.1	5	5	5	5	2	2	2	2	0	0	0																											
	Co439.4.1	5	5	5	5	2	2	2	2	0	0	0	0																										
	Co439.3.2	5	5	5	5	2	2	2	2	0	0	0	0	0																									
	Co439.3.1	5	5	5	5	2	2	2	2	0	0	0	0	0	0																								
	Co439.6.1	5	5	5	5	2	2	2	2	0	0	0	0	0	0	0																							
Elenacalanus princeps	Co24.3.2	35	35	35	35	34	34	34	34	37	37	37	37	37	37	37	37																						
	Co24.5.1	35	35	35	35	34	34	34	34	37	37	37	37	37	37	37	37	0																					
	Co24.1.1	35	35	35	35	34	34	34	34	37	37	37	37	37	37	37	37	1	1																				
	Co24.7.1	35	35	35	35	34	34	34	34	37	37	37	37	37	37	37	37	0	0	1																			
	Co24.1.4	35	35	35	35	34	34	34	34	37	37	37	37	37	37	37	37	0	0	1	0																		
	Co24.1.2	35	35	35	35	34	34	34	34	37	37	37	37	37	37	37	37	0	0	1	0	0																	
	Co24.2.1	35	35	35	35	34	34	34	34	37	37	37	37	37	37	37	37	0	0	1	0	0	0																
	Co24.3.1	35	35	35	35	34	34	34	34	37	37	37	37	37	37	37	37	0	0	1	0	0	0	0															
	Co24.6.1	35	35	35	35	34	34	34	34	37	37	37	37	37	37	37	37	0	0	1	0	0	0	0	0														
Bathycalanus tumidus	Co375.1.3	34	34	34	34	33	33	33	33	36	36	36	36	36	36	36	36	18	18	18	18	18	18	18	18	18													
	Co375.1.1	34	34	34	34	33	33	33	33	36	36	36	36	36	36	36	36	18	18	18	18	18	18	18	18	18	0												
Bathycalanus richardi	Co22.2.1	34	34	34	34	33	33	33	33	36	36	36	36	36	36	36	36	21	21	21	21	21	21	21	21	21	17	17											
	Co22.4.1	36	36	36	36	35	35	35	35	38	38	38	38	38	38	38	38	21	21	21	21	21	21	21	21	21	17	17	0										
Bathycalanus milleri	Co411.1.2	37	37	37	37	36	36	36	36	37	37	37	37	37	37	37	37	20	20	20	20	20	20	20	20	20	16	16	7	7									
Bathycalanus bradyi	Co375.1.2	35	35	35	35	34	34	34	34	35	35	35	35	35	35	35	35	19	19	19	19	19	19	19	19	19	15	15	6	6	1								
	Co376.1	36	36	36	36	35	35	35	35	36	36	36	36	36	36	36	36	19	19	19	19	19	19	19	19	19	15	15	6	6	1	0							
	Co411.1.1	37	37	37	37	36	36	36	36	38	38	38	38	38	38	38	38	17	17	17	17	17	17	17	17	17	17	17	8	8	5	4	4						
	Co441.3.1	36	36	36	36	35	35	35	35	38	38	38	38	38	38	38	38	18	18	18	18	18	18	18	18	18	18	18	7	7	6	5	5	1					
Bathycalanus adornatus	Co22.3.1	35	35	35	35	34	34	34	34	36	36	36	36	36	36	36	36	18	18	18	18	18	18	18	18	18	14	14	5	5	1	0	0	3	4				
Bradycalanus typicus	Co303.1.1	31	31	31	31	30	30	30	30	33	33	33	33	33	33	33	33	28	28	29	28	28	28	28	28	28	21	21	25	27	29	27	28	30	30	27			
	Co303.1.2	31	31	31	31	30	30	30	30	33	33	33	33	33	33	33	33	28	28	29	28	28	28	28	28	28	21	21	25	27	29	27	28	30	30	27	0		
	Co384.1.1	31	31	31	31	30	30	30	30	33	33	33	33	33	33	33	33	28	28	29	28	28	28	28	28	28	21	21	25	27	29	27	28	30	30	27	0	0	
Bradycalanus enormis	Co360.1.1	33	33	33	33	32	32	32	32	35	35	35	35	35	35	35	35	31	31	32	31	31	31	31	31	31	24	24	28	30	32	30	31	33	33	30	2	3	2

TABLE 17. Non-corrected genetic distances (in bp) between individuals within the analysed ITS2 region. Co = voucher numbers.

Megacalanus princeps	Co119.5.1																																						
	Co119.4.1	0																																					
	Co119.2.1	0	0																																				
	Co119.3.1	0	0	0																																			
Megacalanus frosti	Co439.2.2	2	2	2	2																																		
	Co439.2.1	2	2	2	2	0																																	
	Co439.10.1	2	2	2	2	0	0																																
	Co439.5.1	2	2	2	2	0	0	0																															
Megacalanus ericae	Co439.1.2	2	2	2	2	0	0	0	0																														
	Co439.1.1	2	2	2	2	0	0	0	0	0																													
	Co439.7.1	3	3	3	3	1	1	1	1	1	1																												
	Co439.8.1	3	3	3	3	1	1	1	1	1	1	0																											
	Co439.4.1	2	2	2	2	0	0	0	0	0	0	1	1																										
	Co439.3.2	2	2	2	2	0	0	0	0	0	0	1	1	0																									
	Co439.3.1	2	2	2	2	0	0	0	0	0	0	1	1	0	0																								
	Co439.6.1	2	2	2	2	0	0	0	0	0	0	1	1	0	0	0																							
Elenacalanus princeps	Co24.3.2	24	24	24	24	22	22	22	22	22	22	23	23	22	22	22	22																						
	Co24.5.1	24	24	24	24	22	22	22	22	22	22	23	23	22	22	22	22	0																					
	Co24.1.1	24	24	24	24	22	22	22	22	22	22	23	23	22	22	22	22	0	0																				
	Co24.7.1	24	24	24	24	22	22	22	22	22	22	23	23	22	22	22	22	0	0	0																			
	Co24.1.4	24	24	24	24	22	22	22	22	22	22	23	23	22	22	22	22	0	0	0	0																		
	Co24.1.2	24	24	24	24	22	22	22	22	22	22	23	23	22	22	22	22	0	0	0	0	0																	
	Co24.2.1	24	24	24	24	22	22	22	22	22	22	23	23	22	22	22	22	0	0	0	0	0	0																
	Co24.3.1	24	24	24	24	22	22	22	22	22	22	23	23	22	22	22	22	0	0	0	0	0	0	0															
	Co24.6.1	24	24	24	24	22	22	22	22	22	22	23	23	22	22	22	22	0	0	0	0	0	0	0	0														
Bathycalanus tumidus	Co375.1.3	41	41	41	41	41	41	41	41	41	41	42	42	41	41	41	41	29	29	29	29	29	29	29	29	29													
	Co375.1.1	41	41	41	41	41	41	41	41	41	41	42	42	41	41	41	41	29	29	29	29	29	29	29	29	29	0												
Bathycalanus richardi	Co22.2.1	36	36	36	36	34	34	34	34	34	34	35	35	34	34	34	34	23	23	23	23	23	23	23	23	23	23	23											
	Co22.4.1	36	36	36	36	34	34	34	34	34	34	35	35	34	34	34	34	23	23	23	23	23	23	23	23	23	23	23	0										
Bathycalanus milleri	Co411.1.2	32	32	32	32	30	30	30	30	30	30	31	31	30	30	30	30	20	20	20	20	20	20	20	20	20	21	21	5	5									
Bathycalanus bradyi	Co375.1.2	34	34	34	34	32	32	32	32	32	32	33	33	32	32	32	32	21	21	21	21	21	21	21	21	21	20	20	4	4	1								
	Co376.1	33	33	33	33	31	31	31	31	31	31	32	32	31	31	31	31	20	20	20	20	20	20	20	20	20	19	19	4	4	1	0							
	Co411.1.1	34	34	34	34	32	32	32	32	32	32	33	33	32	32	32	32	21	21	21	21	21	21	21	21	21	20	20	6	6	3	2	1						
	Co441.3.1	33	33	33	33	31	31	31	31	31	31	32	32	31	31	31	31	20	20	20	20	20	20	20	20	20	19	19	5	5	2	1	0	0					
Bathycalanus adornatus	Co22.3.1	34	34	34	34	32	32	32	32	32	32	33	33	32	32	32	32	21	21	21	21	21	21	21	21	21	20	20	4	4	1	0	0	2	1				
Bradycalanus typicus	Co303.1.1	17	17	17	17	17	17	17	17	17	17	18	18	17	17	17	17	15	15	15	15	15	15	15	15	15	35	35	31	31	28	29	28	29	28	29			
	Co303.1.2	17	17	17	17	17	17	17	17	17	17	18	18	17	17	17	17	15	15	15	15	15	15	15	15	15	35	35	31	31	28	29	28	29	28	29	0		
	Co384.1.1	16	16	16	16	16	16	16	16	16	16	17	17	16	16	16	16	14	14	14	14	14	14	14	14	14	34	34	30	30	27	28	27	28	27	28	0	0	
Bradycalanus enormis	Co360.1.1	18	18	18	18	18	18	18	18	18	18	19	19	18	18	18	18	15	15	15	15	15	15	15	15	15	36	36	32	32	29	30	29	30	29	30	3	3	2

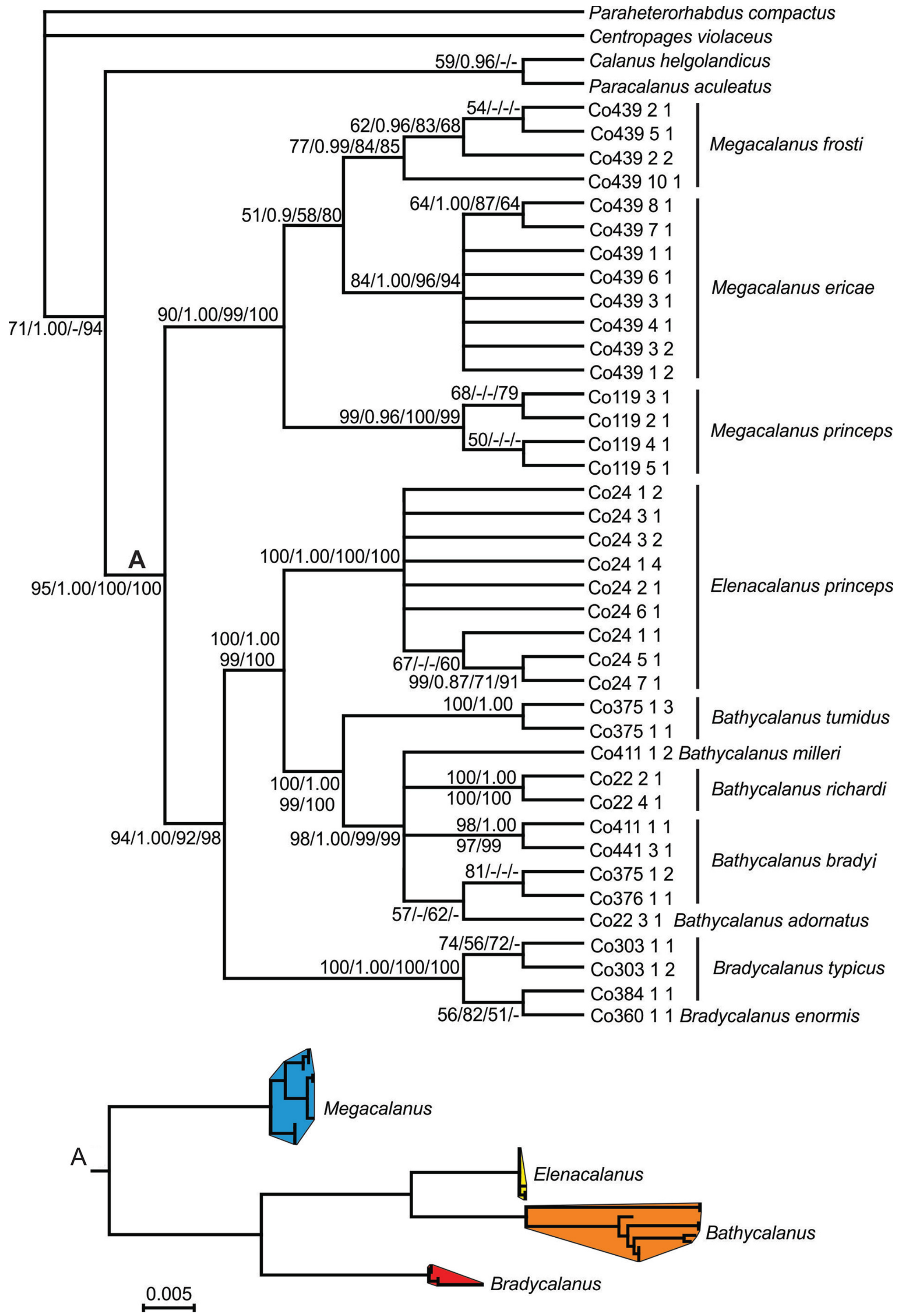

FIGURE 113. Reconstructed phylogeny trees of the Megacalanidae and out-groups, showing the topology (upper panel) and branch lengths (lower panel) corresponding to the ML analysis. Numbers at nodes indicate statistical support under ML/Bayesian/MP/NJ (bootstrap recovery when > 50%; Bayesian Posterior Probability when > 0.8). On the lower panel, ML distances are showed for branches within node "A", comprising the Megacalanidae. Each colour represents a different genus. All genera are recovered as monophyletic, and relationships between genera resemble the morphology-based phylogeny. ML = maximum likelihood; MP = maximum parsimony; NJ = neighbour joining.

Gene-based phylogeny

When the Megacalanidae was analysed within a broader context (with outgroups belonging to the other families within Megacalanoidea, as well as representatives of the two superfamilies basal to Megacalanoidea) (Fig. 113), the four tested methods recovered all the previously established genera, as well as *Elenacalanus* nom. nov., as monophyletic clades. The associated statistical support values for the genera were all high (Bootstrap / posterior probability > 90%. 0.9). The Maximum Parsimony method suffered from a major issue, i.e. a paraphyletic Megacalanoidea, in which the Paracalanidae and the Centropagidae (Centropagoidea) taxa formed a clade sister to the Megacalanidae + Calanidae (see http://dx.doi.org/10.5281/zenodo.46925).

Within the Megacalanidae, the tree topology indicated *Megacalanus* as the most basal genus. The three *Megacalanus* species included in the analyses were consistently recovered in all phylogenies, and indicated a closer relationship between *M. frosti* **n. sp.** and *M. ericae* **n. sp.** Within *Bathycalanus*, *Ba. tumidus* **n. sp.** is placed basal to all the other species of the genus. *Bathycalanus richardi* is recovered as monophyletic, meanwhile *Ba. bradyi* and *Ba. adornatus* **n. sp.** are recovered in a mixture of paraphyletic and polyphyletic groupings.

Identification tools

Several aids to identification of Megacalanidae genera and species are presented here: 1) keys to the genera and species are below; 2) tables of key differences among species in each genus are located in Tables 7, 8, 10, and 11; 3) tables of numbers of setae on selected parts of the antenna exopod, mandible endopod, maxillule and maxilliped of all species are located in Tables 18–21; and 4) interactive, multicharacter, illustrated electronic keys, constructed in DELTA and accessed by the IntKey program (see Coleman *et al*. 2010 and references therein) are available at http://niwa.co.nz/static/web/megacalanidae.zip [6MB ZIP] (Bradford-Grieve *et al.* 2016c). Abbreviations represent: A1 = antennule; Gns = genital double-somite; Mn = mandible; Mx1 = maxillule; Mx2 = maxilla; P1, 5 = leg 1, 5; Pd4, 5 = pedigerous somite 4, 5; Re1, 2, 3 = exopod segment 1, 2, 3; Ri2 = endopod segment 2; Ur II, III = urosomite II, III.

Key to Megacalanidae genera, females and males

1 Exopod of P1 in both sexes with 1,1,2 outer marginal spines; Mx2 terminal setae gently curving, extending short of mouth . 2
- Exopod of P1 in both sexes with different arrangement of outer marginal spines; Mx2 terminal setae, curled, extending to or beyond rostrum 3
2 P1 basis usually with inner anterodistal hook-like processes, Mx1 Ri2 with 4 setae, Mn gnathobase with ventral tooth set at right angles to main plane of gnathobase thus appearing narrow; male right A1 ancestral segments XXII–XXIII fused . . . . *Megacalanus*
- P1 basis without inner anterodistal hook-like process, Mx1 Ri2 with at most 2 setae, Mn gnathobase with ventral tooth set obliqely to main plane of gnathobase thus appearing broad; male right A1 ancestral segments XXI–XXIII fused . . . . *Bradycalanus*
3 Re of P1 in both sexes with 0,0,2 outer marginal spines; anterior margin of head of both sexes without pair of anteriorly-directed spine-like processes but female may be crested; Mx2 terminal setae curled distally into semicircle. . . . *Elenacalanus*
- Re of P1 in both sexes with 0,0,1 outer marginal spines; anterior head of both sexes with pair of anteriorly-directed spine-like processes or single spine-like process; Mx2 terminal setae curled completetely on themselves distally. . . . . *Bathycalanus*

Key to *Megacalanus*, females and males

1 Head with crest in females and males . . . . *Megacalanus frosti* **n. sp.**
- Head without crest in females and males 2
2 Posterolateral lappets of Pd5 rounded in females and males . . . . *Megacalanus ohmani* **n. sp.**
- Posterolateral lappets of Pd5 triangular in females and males 3
3 Female A1 ancestral segments XV and XVI posterior border smooth; male right A1 segment XIX with 1 distal fused gripping element . . . . *Megacalanus ericae* **n. sp.**
- Female A1 ancestral segments XV and XVI with posterior border blunt teeth; male right A1 segment XIX without distal fused gripping element . . . . *Megacalanus princeps*

Key to *Bradycalanus*, females and males

1 Head rounded; posterior Pd5 corners triangular in lateral view; Mx1 coxal endite with 5 setae 2
- Head crested; posterior Pd5 corners with posteroventral attenuated extension in lateral view; Mx1 coxal endite with 2 setae (male unknown) . . . . *Bradycalanus abyssicolus* **n. sp.**
2 Female A1 short extending no more than 3 segments beyond caudal rami; P1 Re1 and 2 with outer border spines extending to base of following spine (male unknown) . . . . *Bradycalanus gigas*
- Female A1 long extending about 6–7 segments beyond caudal rami; P1 Re1 and 2 with outer border spines short extending well short of base of following spine 3
3 Female total length < 13 mm; male right P5 Re3 inner border spine inserted opposite outer border spine, inner border with notch . . . . *Bradycalanus typicus*
- Female total length > 14 mm; male right P5 Re3 inner border spine inserted distal to level of outer border spine insertion, inner border without notch . . . . *Bradycalanus enormis*

Key to *Elenacalanus*, females and males

1 Head with crest in female, rounded in male; male P5 right Re3 inner border with patch of proximal setules. . . . . *Elenacalanus princeps*
- Head without crest; male P5 right Re3, where known, naked 2
2 Mx1 basal endite 2 with 1 seta (male unknown). . . . . *Elenacalanus sverdrupi*
- Mx1 basal endite 2 with 2 or more setae. 3
3 Mn B proximal seta placed distal to midlength; Mx1 basal endite 2 with 2 setae . . . . *Elenacalanus inflatus*
- Mn B proximal seta placed approximately at midlength; Mx1 basal endite 2 with 2–3 setae 4
4 Mx1 basal endite 2 with 3 setae in female, 2 in male; female P1 Re3 proximal outer spine extends short of base of distal outer spine; male P5 left Re2 specialised seta with large rounded outer lobe and attenuated setulose inner lash. . . . . *Elenacalanus eltaninae*
- Mx1 basal endite 2 with 2 setae in female, 1 in male; female P1 Re3 proximal outer spine extends beyond base of distal outer spine; male P5 left Re2 specialised seta with 2 equal, short setulose lashes . . . . *Elenacalanus tageae* **n. sp.**

Key to *Bathycalanus*, females and males

1 Mx1 coxal endite with 1 seta. 2
- Mx1 coxal endite without setae. 3
2 Mx1 praecoxal arthrite with 4 posterior surface setae, basal endite 2 with 4 setae (male unknown). . . . . *Bathycalanus tumidus* **n. sp.**
- Mx1 praecoxal arthrite with 2 posterior surface setae, basal endite 2 with 2 setae (male unknown) . . . . *Bathycalanus pustulosus* **n. sp.**
3 Anterior margin of head with one barbed spine-like process in both sexes; male left P5 Re2 specialised seta with 2 setulose inner lashes, right Re2 with rudimentary inner distal seta . . . . *Bathycalanus unicornis*
- Anterior margin of head with 2 very small spine-like processes 4
4 P1 Re2 and 3 fused in both sexes; male UrII in lateral view enlarged and swollen: UrII 2.17–2.58 times longer than UrIII . . . . *Bathycalanus richardi*
- P1 Re2 and 3 separate; males, where known, with UrII < 1.70 times longer than UrIII 5
5 Pd4 and 5 with laterally extended lappets; Gns with angular anterolateral borders in dorsal view (male unknown) . . . . *Bathycalanus adornatus* **n. sp.**
- Pd4 and 5 without laterally extended lappets; Gns otherwise shaped. 6
6 Gns very swollen in dorsal view, decorated with spinules (male unknown) . . . . *Bathycalanus eximius*
- Gns hardly swollen, without spinules 7
7 Pd5 extended posteriorly into asymmetrical, irregularly shaped lappets (male unknown) . . . . . *Bathycalanus bucklinae* **n. sp.**
- Pd5 hardly extended posteriorly, symmetrical, short and rounded in lateral view 8
8 Female A1 anterodistal borders of ancestral segments XVI–XXI with teeth, posterior borders smooth. Male left P5 Re2 specialised seta very long, extended beyond distal border of Ri, right P5 Re3 inner border setulose … *Bathycalanus dentatus* **n. sp.**
- Female A1 anterodistal borders of ancestral segments XVI–XX and distoposterior borders of segments XVI–XIX with teeth. Male P5 Re2 specialised seta not extended beyond distal border of Ri, right P5 Re3 inner border naked . . . . *Bathycalanus milleri* **n. sp.**
- Female A1 segments XII–XVIII without bordering teeth, may be covered or partly covered in thickenings. Male P5 left Re2 specialised seta extended to distal border of Ri, right P5 Re3 inner border with small patch of proximal spinules . . . . *Bathycalanus bradyi*

TABLE 18. Setation of selected parts of maxillule of *Bathycalanus* s.l. species. B1, 2 = basal endite 1, 2; C = coxal endite; Pa = praecoxal arthrite; Ri1, 2, 3 = endopod segment 1, 2, 3. *species for which there are genetic sequences.

Species	Pa posterior	C	B1	B2	Ri1	Ri2	Ri3
*Ba. adornatus**	2	0	2	3	2	2	6
*Ba. bradyi**	2	0	2	3	2	2	6
Ba. bucklinae	2	0	2	4	2	2	6
Ba. dentatus	2	0	2	2	2	2	6
*Ba. milleri**	2	0	2	2	2	2	6
Ba. pustulosus	2	1	2	2	2	2	6
*Ba. richardi**	2	0	2	3	2	2	6
*Ba. tumidus**	4	1	2	4	2	2	6
Ba. unicornis	3	0	2	4	3	2	6

Discussion

Data characteristics. The results presented here, based on morphological and genetic characteristics, are limited by both the number of morphological characters / states with well-supported hypotheses of homology and the number of species with available molecular markers.

Morphological characters. When the family Megacalanidae was erected it was noted (Sewell 1947) there were characters that tied the family together but there were few characters in the literature that separated the genera. Sewell (1947) observed that the absence of setae on the coxal endite of the maxillule was a characteristic of *Bathycalanus*. He noted the presence of 1 seta on endopod segment 2 of the maxillule, a characteristic of *Bradycalanus* (here we correct this to 2 setae, one of them vestigial), compared with 4 setae in *Megacalanus*, and he noted the presence of maculae cribrosae on various limbs and the body in *Megacalanus* and the antennules of *Bathycalanus*. In his key to the genera and species of the Megacalanidae, as then known, he also added the presence or absence of outer border articulated spines on the leg 1 exopod (1, 1, 2 for *Megacalanus* and *Bradycalanus*, and 0, 0, 2 for *Bathycalanus*). This latter conclusion missed the fact that the type species of *Bathycalanus*, *Ba. richardi*, has 0, 0, 1 outer spines on the leg 1 exopod. Sewell also clarified the nature of the terminal setae on the maxilla: in *Megacalanus* these are “armed with moderately spaced spinules”, in *Bradycalanus* these are “scythe-like and are densely ciliated” and in *Bathycalanus* these are “ribbon-like and are densely clad with spinules”. He also noted the nature of the rostral filaments which he described as slender and tapering in *Megacalanus* and *Bradycalanus*, but stout and sausage-like in *Bathycalanus*. To the above list we have added a number of other characters and extended our knowledge of the distribution of character states through megacalanid species (Tables 18–21).

In spite of extended knowledge of characters / states within the Megacalanidae a few important characters lack well-supported hypotheses of homology and seem to be a source of conflicting data thus impacting the strength of our taxonomic and phylogenetic conclusions at the species level. An example is found in maxillule characters, especially among *Bathycalanus* species. Two species (*Ba. tumidus* **n. sp.** and *Ba. pustulosus* **n. sp.**) have 1 seta on the maxillule coxal endite when all other species assigned to this genus are without any setae on this endite (Table 20); it was impossible to determine the homologies of this seta relative to the 5 setae found in *Megacalanus* and *Bradycalanus*. This character and the number of setae on the maxillule second basal endite are included in analyses on the assumption that the same total numbers of setae are strictly homologous. Similarly, three other species (*Ba. eximius, Ba. tumidus* **n. sp.** and *Ba. unicornis*), rather than having 2 distal posterior surface setae on the maxillule praecoxal arthrite, as in other *Bathycalanus*, have 3 setae in the case of *Ba. eximius* and *Ba. unicornis* and 4 setae in the case of *Ba. tumidus* **n. sp.** This character is used in the analysis and is semicongruent with there being 4 setae on the second basal endite.

Molecular data. The present lack of success in amplification of COI is not new to the field, being one of the most prominent criticisms of this molecule. One of the causes could be primer mismatch, a known problem of the

Folmer primers, and in general within the whole Folmer region (Leray *et al.* 2013). In our study, COI sequences were obtained only from live individuals caught in the upper layer (0–1000 m) of the ocean (belonging to *Megacalanus*). Individuals from other genera inhabiting deeper waters were likely dead (in many cases certainly dead—author's personal observation) for a long time (up to 10 h) before preservation. Therefore, mitochondrial DNA degradation after cell death probably caused the lack of success amplifying the COI marker. Nuclear genes, more protected from oxidative DNA degradation were successfully amplified from most individuals. The variation of most of these markers was however too low to differentiate closely-related species that were otherwise differentiated by the COI (i.e., *M. ericae* **n. sp.** and *M. frosti* **n. sp.**). Two of the initially chosen markers, 5.8S and 18S, had very few changes across all individuals analysed. Both markers are known to be very conservative, but some degree of variation was expected as has been reported in other groups of copepods, even within a genus (Cornils & Blanco-Bercial 2013). The low levels of differentiation found here may be related to multiple, possibly co-occurring, reasons. One reason could be that differentiation might be slowed down by the much longer life cycles of the megacalanid copepods. Megacalanidae probably have multiyear life cycles compared with the Paracalanidae which have multiple cycles per year (e.g. Huntley & Lopez 1996). Thus the number of generations since divergence would have been fewer. Another reason may be a lack of recognizable physical barriers in the environment of the Megacalanidae in the bathy- and abyssopelagic ocean; the associated high genetic flow throughout the distribution range of a number of species might have reduce the rate of the genetic drift.

TABLE 19. Summarised setation, at a glance, of selected parts of the antenna and mandible. *C.* = *Calanus*, *M.* = *Megacalanus*, *Ba.* = *Bathycalanus*, *Br.* = *Bradycalanus*, *E.* = *Elenacalanus*. Re1–4 = exopod segments 1–4; Ri 1, 2 = endopod segments 1, 2; s = small; v = vestigial seta.

Antenna					Mandible	
Species	Re1	Re2	Re3	Re4	Ri1	Ri2
C. helgolandicus	1	1	1	1	4	9+2s
M. princeps	1	1	1	1	4	9+2s
M. frosti	1	1	1	1	4	9+2s
M. ericae	1	1	1	1	4	9+2s
M. ohmani	1	1	1	1	4	9+2s
Br. typicus	1	1	1	1	4	9+2v
Br. enormis	1	1	1	1	4	9+2v
Br. gigas	1	1	1	1	4	9+2v
Br. abyssicolus	1	1	1	1	4	9+2v
Ba. richardi	v	v	v	1	4	9+2v
Ba. bradyi	v	v	v	1	4	9+2v
Ba. dentatus	v	v	v	1	4	9+2v
Ba. milleri	v	v	v	1	4	9+2v
Ba. tumidus	v	v	v	1	4	9+2v
Ba. adornatus	v	v	v	1	4	9+2v
Ba. pustulosus	v	v	v	1	4	9+2v
Ba. bucklinae	v	v	v	1	4	9+2v
Ba. unicornis	v	v	v	1	4	9+2v
Ba. eximius	0	0	v	1	4	9+2v
E. princeps	0	0	0	0	2	9+0
E. eltaninae	0	0	0	1	2	9+0
E. sverdrupi	0	0	0	1	2	9+0
E. inflatus	0	0	0	1	2	9+0
E. tageae	0	0	0	1	2	9+0

TABLE 20. Summarised setation, at a glance, of selected parts of maxillule. *C.* = *Calanus*, *M.* = *Megacalanus*, *Ba.* = *Bathycalanus*, *Br.* = *Bradycalanus*, *E.* = *Elenacalanus*. B1, 2 = basal endites 1, 2; Be = basal exite; C = coxal endite; Pa = praecoxal arthrite posterior setae; Ri 1–3 = endopod segments 1–3; s = small seta; v = vestigial seta.

Maxillule								
Species	Pa	C	B1	B2	Ri1	Ri2	Ri3	Be
C. helgolandicus	4	4	4	4	4	4	6+1s	1
M. princeps	4	5	4	4	3	4	6+1s	1
M. frosti	4	5	4	4	3	4	6+1s	1
M. ericae	4	5	4	4	3	4	6+1s	1
M. ohmani	4	5	4	4	3	4	6+1s	1
Br. typicus	4	5	2	4	2	1+1v	5+1s	1
Br. enormis	4	5	2	4	2	1+1v	5+1s	1
Br. gigas	4	5	2	4	2	1+1v	5+1s	1
Br. abyssicolus	4	2	2	4	2	1+1v	5+1s	1
Ba. richardi	2	0	2	3	2	2	5+1s	1
Ba. bradyi	2	0	2	3	2	2	5+1s	1
Ba. dentatus	2	0	2	2	2	2	5+1s	1
Ba. milleri	2	0	2	2	2	2	5+1s	1
Ba. tumidus	4	1	2	4	2	2	5+1s	1
Ba. adornatus	2	0	2	3	2	2	5+1s	1
Ba. pustulosus	2	1	2	2	2	2	5+1s	1
Ba. bucklinae	2	0	2	4	2	2	5+1s	1
Ba. unicornis	3	0	2	4	3	2	5+1s	1
Ba. eximius	3	0	2	4	2	2	5+1s	1
E. princeps	2	0	2	2	1	0/1	4+1s	0
E. eltaninae	2	0	2	3	1	1	4+1s	0
E. sverdrupi	3	0	2	1	1	1	4+1s	0
E. inflatus	2	0	2	2	1	1	4+1s	1
E. tageae	2	0	2	2	1	1	4+1s	1

Phylogeny. The general agreement between the morphological and the molecular phylogenetic reconstructions at the generic level strengthens the newly named genus and some species. The only disagreement was a paraphyletic Megacalanoidea found in the Maximum Parsimony (MP) tree. This might have resulted from artifacts such as long-branch attractions (LBA), since MP is particularly sensitive to this error (Anderson & Swofford 2004; Bergsten 2005). Within the (by nature) long outgroup branches, the Paracalanidae and Centropagoidea representatives showed significantly longer branches even when compared to the most distant taxa, the Augaptiloidea. This result weakened our global confidence in the MP reconstruction (see Bradford-Grieve *et al.* 2016b).

Comparisons at the species level are difficult to make because of incomplete coverage of the taxa known from their morphology. One example of non-congruence within genera is that between species of *Megacalanus*. The morphological data suggest *M. princeps* and *M. frosti* are the most closely related whereas the molecular data suggests *M. ericae* and *M. frosti* are the most closely related. We have no way of determining the effect of the absence of sequences for *M. ohmani* on conclusions about relationships among species of *Megacalanus*.

Most of the morphological characters and their states used in this revision, have a strong influence on the high support for monophyletic clades representing each genus or groups of genera (Fig. 112). This, along with support from the genetic data (Fig. 113), led to the reinstatement of a genus with the new name, *Elenacalanus*, which includes some species previously assigned to *Bathycalanus*. The only genus with low support was the *Bathycalanus* clade. The low bootstrap support for this clade (58%) may be real or an artifact of the bootstrap method applied to morphological data and the way it interacts with characteristics of the data set (Table 4). That is, the *Bathycalanus* node may be overly influenced by the quantity of conflicting data and the large amount of compatible, but not informative, data relevant to the *Bathycalanus* node. Soltis & Soltis (2003, p. 261) point out that the addition of irrelevant characters for a node in question increases the pool of characters that may be selected for a bootstrap pseudoreplicate, thus decreasing the chance that a given relevant character will be selected.

TABLE 21. Summarised setation at a glance, of selected parts of maxilliped and leg 1. *C.* = *Calanus*, *M.* = *Megacalanus*, *Ba.* = *Bathycalanus*, *Br.* = *Bradycalanus*, *E.* = *Elenacalanus*. Re1–3 = exopod segments 1–3; Ri 3–6 = endopod segments 3–6; s = small seta; * = both segments fused. Roman numerals represent spines, Arabic numerals represent setae. In setation formula for leg 1 exopod segments, left hand item is on outer border and right hand item is on inner border.

Maxilliped					Leg 1		
Species	Ri3	Ri4	Ri5	Ri6	Re1	Re2	Re3
C. helgolandicus	3+1s	3+1s	3+1	3+2s	I-1	I-1	II,I,4
M. princeps	3+1s	2+1s	2+1s+1	2+2s	I-1	I-1	II,I,4
M. frosti	3+1s	2+1s	2+1s+1	2+2s	I-1	I-1	II,I,4
M. ericae	3+1s	2+1s	2+1s+1	2+2s	I-1	I-1	II,I,4
M. ohmani	3+1s	2+1s	2+1s+1	2+2s	I-1	I-1	II,I,4
Br. typicus	1+3s	1+2s	1+2s+1	2+2s	I-1	I-1	II,I,4
Br. enormis	1+3s	1+2s	1+2s+1	2+2s	I-1	I-1	II,I,4
Br. gigas	1+3s	1+2s	1+2s+1	2+2s	I-1	I-1	II,I,4
Br. abyssicolus	1+3s	1+2s	1+2s+1	2+2s	I-1	I-1	II,I,4
Ba. richardi	1+3s	1+2s	1+2s+1	2+2s	0-1	0-1*	I,I,4*
Ba. bradyi	1+3s	1+2s	1+2s+1	2+2s	0-1	0-1	I,I,4
Ba. dentatus	1+3s	1+2s	1+2s+1	2+2s	0-1	0-1	I,I,4
Ba. milleri	1+3s	1+2s	1+2s+1	2+2s	0-1	0-1	I,I,4
Ba. tumidus	1+3s	1+2s	1+2s+1	2+2s	0-1	0-1	I,I,4
Ba. adornatus	1+3s	1+2s	1+2s+1	2+2s	0-1	0-1	I,I,4
Ba. pustulosus	1+3s	1+2s	1+2s+1	2+2s	0-1	0-1	I,I,4
Ba. bucklinae	1+3s	1+2s	1+2s+1	2+2s	0-1	0-1	I,I,4
Ba. unicornis	1+3s	1+2s	1+2s+1	2+2s	0-1	0-1	I,I,4
Ba. eximius	1+3s	1+2s	1+2s+1	2+2s	0-1	0-1	I,I,4
E. princeps	1	1	1+0	2+1s	0-1	0-1	II,I,4
E. eltaninae	1	1	1+0	2+2s	0-1	0-1	II,I,4
E. sverdrupi	1	1	1+0	2+0	0-1	0-1	II,I,4
E. inflatus	1	1	1+0	2+2s	0-1	0-1	II,I,4
E. tageae	1	1	1+0	2+2s	0-1	0-1	II,I,4

We must consider that the lack of support is real and related to the possibility that another as yet unnamed genus could be involved. The limited evidence for this comes from variability in maxillule setal characteristics among species (Table 20) coupled with the genetic distance of *Ba. tumidus* (Tables 14–17) from the rest of *Bathycalanus* for which there are sequences (Table 6). Unfortunately, we do not have enough data to unambiguously diagnose another genus.

Morphological trends. Several trends are evident moving from the *Megacalanus* clade through *Bradycalanus* to *Bathycalanus* and *Elenacalanus* nom. nov. One trend is a reduction and loss of setae on antenna exopod segments I–IV, various parts of the maxillule, the maxilla endopod segment 2 proximal inner seta, the maxilliped endopod segments 3–6, and leg 1 exopod outer border spines. Other trends are seen in novelties relating to, for example, the nature of the terminal setae of the maxilla trending from stiff, slightly curved with sparse spinules in *Megacalanus* to slightly curved, strong setae lined with dense setules in *Bradycalanus* to long setae, curled in a semicircle, lined with densely spaced setules in *Elenacalanus* and finally to elongate setae tightly curled on themselves and lined with densely spaced setules in *Bathycalanus*. Character-state-change novelties, evident in the phylogeny presented here, are far outweighed by the reduction in setal elements. Character novelties are: char. 9 (presence of a hair sensillum on the female antennule ancestral segment V), char. 11 (presence of macula cribrosa adjacent to hair sensillum on antennule ancestral segment V), char. 16 (presence of ventral surface tooth row on female antennule ancestral segments XIV–XVII), char. 39 (presence of long sparse auxiliary spinules on setae of maxilla praecoxal endites 1 and 2 and coxal endite 1), char. 40 (presence of long sparse auxiliary spinules on maxilla endopod setae), char. 43 (presence of spinules on convex border of maxilla endopod segment 2 distal inner seta), char. 54 (presence of leg 1 basis anterodistal hook-like process). These are all unambiguous character state changes. These novelties are 29% of all unique unambiguous character state changes at the genus level in one of the twelve most parsimonious trees.

Taxonomy. The molecular results supported the status of the newly described taxa for which data were available. For the two new *Megacalanus* species, *M. ericae* and *M. frosti*, genetic distances between them or to any other species corresponded to what is found between copepod species for both COI and ITS1 (Blanco-Bercial *et al.* 2014; Zagoskin *et al.* 2014), upholding the conclusions drawn from the morphological study.

The status of *Elenacalanus* nom. nov. is also supported by the molecular data, in terms of genetic distances from each individual marker (larger than those found within genera, especially for the ITS regions, Tables 16, 17) and also by the reconstructed phylogenies, where it is placed in a clade with *Bathycalanus* (Fig. 113), but forms a monophyletic clade sister to all *Bathycalanus* species. Despite lower genetic distances between *Elenacalanus* and *Bathycalanus* individuals, in some cases, than those between *Megacalanus, Bradycalanus* and *Bathycalanus*, there is no universal fixed genus-level cut off that can be established. Furthermore, raw distances between species for the ITS2 region (Table 17) showed a closer relationship of *Elenacalanus* to *Bradycalanus*, indicating a significant divergence from the other *Bathycalanus*. This molecular evidence, together with the robust synapomorphies shared by all the species of the genus, provides strong grounds for accepting the renamed *Elenacalanus.*

Although the approach taken here has unambiguous results in distinguishing genera we still had problems dealing with the historical confusion caused by the incomplete description of *Calanus princeps* by Brady (1883), which made its true identity the subject of ongoing speculation. We have re-examined Brady's type material and, in order to stabilise the nomenclature of this family, we propose that there is no value in trying to untangle all the opinions expressed concerning synonymies between the dates of 1905–1925 because the true diversity of megacalanids was unrecognised at that time. During this period the distinctions between *Megacalanus*, *Bradycalanus* and *Bathycalanus* were not completely recognised, the true identity of Brady's (1883) *Calanus princeps* was not settled, and *Megacalanus* and *Bradycalanus* are easily confused if care is not taken. In works where the nature of the maxillule and leg 1 were not explicitly alluded to, it is impossible to be certain of the identity of the genus and species being referred to. Therefore, *Megacalanus princeps* Wolfenden, 1904 is confirmed as the type species of *Megacalanus* since his is the first recognisable description of this species and genus and it is clearly not in the same genus as *C. princeps* Brady, 1883. The latter species was previously placed in the genus *Heterocalanus* Wolfenden, 1906, a name that is not available as it is a homonym of *Heterocalanus* T. Scott, 1894 and is thus here renamed *Elenacalanus* nom. nov.

Even though we have clarified the distinctions between megacalanid genera, some of the eleven new species reported here have blurred the distinction between *Bradycalanus* and *Bathycalanus*. Nevertheless, all species can still be assigned, with confidence, to one of the differentially diagnosed genera. The one new species of *Bradycalanus, Br. abyssicolus* **n. sp.** has the proximal setae of the antenna exopod reduced in size and the maxillule coxal endite has only 2 setae compared with the 5 setae present in other *Bradycalanus*. Nevertheless, this species has a mandibular gnathobase characteristic of *Bradycalanus* and is unambiguously located within the *Bradycalanus* clade (Fig. 112). Of the six new species of *Bathycalanus* that have been described, two have the maxillule coxal endite with 1 rudimentary seta of unknown homology (*Ba. tumidus* **n. sp.** and *Ba. pustulosus* **n. sp.**) which also blurs the distinction between *Bradycalanus* and *Bathycalanus*. Nevertheless, these two species have a mandibular gnathobase and maxilla terminal setae characteristic of *Bathycalanus* and are unambiguously located within the *Bathycalanus* clade in the cladistic analysis (Fig. 108).

Vertical distribution. The distribution of Megacalanidae in relation to a depth classification into bathypelagic and abyssopelagic zones, in the sense of Vinogradov & Tseitlin (1983), is approximate because the number of stations at which zooplankton sampling has been undertaken to really deep depths is small, the volume of water filtered is usually low relative to the concentrations of animals and the extent of vertical sample partitioning has been limited.

From what data are available, *Megacalanus* and *Elenacalanus* are mostly confined to bathypelagic (600–2800 m) depths (Fig. 114). *Megacalanus* has mouthparts that suggest a predatory life style whereas *Elenacalanus* have maxillary endopod setae reminiscent of those of *Bathycalanus* but are curled in a semicircle distally (not completely curled on themselves as in *Bathycalanus*) and are not as extremely adapted as entangling devices as *Bathycalanus*. These species are probably adapted to the macroscopic particulate matter that is formed in greatest concentrations in the mesopelagic zone (e.g. Bochdansky *et al.* 2010).

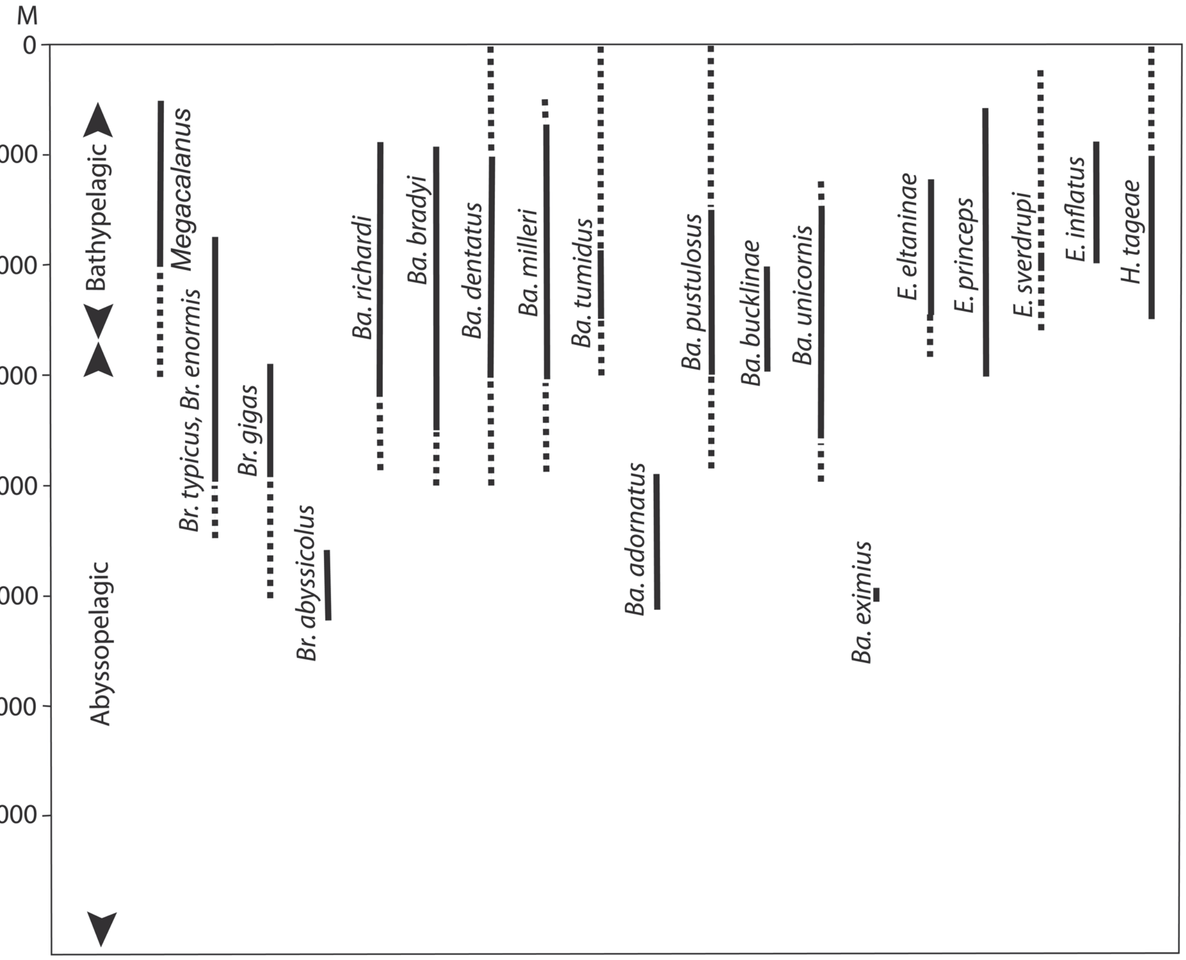

FIGURE 114. Known vertical distribution of megacalanid species estimated from current information, Smithsonian Institution records and other collections (Table 1). The vertical classification of the pelagic environment on the figure is after Vinogradov & Tseitlin (1983).

Many *Bathycalanus* (e.g. *Ba. richardi, Ba. bradyi, Ba. milleri* **n. sp.** and others) have a bathypelagic to abyssopelagic distribution (Fig. 114). Their specially modified maxillary endopod setae as tangling devices suggest a detritivorous life style. This mode of feeding makes particular sense in the case of the wholly abyssopelagic species (*Ba. adornatus* **n. sp.** and *Ba. eximius*). If the vertical distribution of macroscopic organic particles (marine snow) down to 5500 m in the tropical Atlantic (Bochdansky *et al.* 2010) is reflective of the, as yet, unknown distribution in other oceans, then there are likely to be vertical maxima and minima in various water masses in other oceans with a general relationship to surface primary production in source waters (Vinogradov 1968, p. 157).

Similarly, *Bradycalanus* species seem to exhibit two types of vertical distribution: *Br. typicus* and *Br. enormis* have a bathypelagic to abyssopelagic distribution and *Br. gigas* and *Br. abyssicolus* have an abyssopelagic distribution. Based on the form of the mouthparts, this genus appears to be predatory and not adapted to feeding on detritus, unlike *Bathycalanus*, and therefore probably did not radiated extensively into bathypelagic to abyssopelagic depths.

Geographic distribution. Taking an overview of the global megacalanid fauna, superficial examination of species richness at specific well-sampled locations, suggests that certain regions may be less species rich than others. ANTXXIV/1 Station 6 in the South Atlantic and Antipode IV Station 52D in the northwest Pacific both had 5 species (Table 1). On the other hand MV66-11 Station 5 in the eastern Pacific off California had 8 species. Nevertheless, differences in mouth opening of the nets used (MOC10—10 m^2 and IKMT—7–8 m^2) and the vertical extent of sampling (Tables 1, 2), and therefore the likely volume of water filtered, may account for differences in observed species richness.

For those species whose distributions are well enough known, several are widespread (*Bradycalanus typicus*, *Bathycalanus richardi*, and *Ba. bradyi*) (Figs 29, 46). It is likely that *E. sverdrupi, Bradycalanus gigas, Bathycalanus tumidus* **n. sp.**, *Ba. dentatus* **n. sp.** and *Ba. unicornis* will also prove to be widespread. It is noted that these species have distributions that extend well below 2000 m and are apparently not restricted by deep sea ridges marked by the 800–3500 m isobath (Watling *et al.* 2013). Species of *Megacalanus*, on the other hand, are the only species confined to bathypelagic depths that have distributions that are focused mainly on a particular ocean. *Megacalanus frosti* **n. sp.** has been found principally along the eastern boundary of the Pacific Ocean, whereas *M. ericae* **n. sp.** is more widespread in the Pacific and co-occurs with *M. frosti* **n. sp.** at about 38ºN 135ºW (Fig. 9). *Megacalanus princeps* has a distribution centred on the Atlantic and Indian Oceans but has been found in East Indies waters and in the south-eastern Pacific with a stray being recorded from the mid tropical Pacific.

Three species have distributions in the Southern Hemisphere linked to more limited distributions in other Oceans. For example, *E. princeps* is found in the Atlantic and the Southern Hemisphere, *M. ericae* **n. sp.** is found in the western and central Pacific and the Southern Hemisphere, and *Ba. milleri* **n. sp.** is found in the eastern Pacific and Southern Hemisphere.

Differences between the types of distribution mentioned above are possibly related to ocean circulation combined with the vertical distribution of the species. The surface circulation of the oceans is wind-driven and dominates in the upper few hundred metres while, away from the wind-driven circulation, density-driven (thermohaline) circulation dominates (Toggweiler & Key 2001).

Megacalanus is within the influence of the wind-driven circulation since the circulation at 900 m is very similar to that at the surface (Davis 2005). That is, the surface, wind-driven ocean circulation (Tomczak & Godfrey 1994 p. 119) probably maintains *M. ericae* **n. sp.** in the Pacific Ocean and ensures circumglobal population continuity via the southern hemisphere and the Indian Ocean (Fig. 9). Likewise, *M. princeps* probably has population continuity with the Indian Ocean via the southern Hemisphere although it is not so obvious how populations extend into the southeastern Pacific and the East Indies against the mean flow (Tomczak & Godfrey 1994, p. 199).

Conversely, deeper living Megacalanidae are probably distributed, at relevant depths, by the thermohaline circulation (Toggweiler & Key 2001). Some species may even be restricted to certain ocean basins when the upper limit to their vertical distribution is deeper than the marginal boundaries to that basin (e.g. *Bradycalanus abyssicolus* **n. sp.**, *Bathycalanus adornatus* **n. sp.** and *Ba. eximius*) but such a conclusion awaits more extensive exploration at abyssal and hadal depths. The thermohaline circulation connects all oceans (over about 600 years) through the formation, spreading and mixing of deep water, mainly from the North Atlantic and Antarctic, upwelling mainly in the Antarctic Circumpolar Current aided by the wind, and through near-surface return currents closing the flow (Toggweiler & Keys 2001).

Summary

The Megacalanidae have been revised based on new material collected during the CMarZ cruise XXIV/1 in the Atlantic Ocean aboard the Alfred Wegener Institute vessel Polarstern in 2007; material loaned from the plankton repository of Scripps Institution of Oceanography; material from R/V Oceanus Cruise #473 and RV New Horizon #1208 and material lodged in the Natural History Museum, London. Distributional records were augmented from material held in the Smithsonian Institution and National Institute of Water and Atmospheric research, New Zealand.

Taxonomic confusion that has existed in the family is discussed and a method selected for stabilising names. A detailed examination of the morphology of this family, using the light microscope, has added additional useful characters that were employed in a cladistics analysis of morphological data.

The genus *Elenacalanus* nom. nov. is established based on the generic concept of the unavailable *Heterocalanus* Wolfenden, 1906, supported by the results of the cladistic analysis and the molecular phylogeny. Four previously described species have been re-assigned to *Elenacalanus* as new combinations: *E. princeps* (Brady, 1883), *E. eltaninae* (Björnberg, 1968), *E. sverdrupi* (Johnson, 1958) and *E. inflatus* (Björnberg, 1968).

Eleven new species are described: three *Megacalanus*, one *Bradycalanus*, six *Bathycalanus*, and one *Elenacalanus*. All four genera are diagnosed and keys are provided to the genera and species. We confirm that male right antennules of all genera are geniculate. Thirteen males have been described. Of these species, eight are newly described (*M. frosti* **n. sp.**, *M. ericae* **n. sp.**, *M. ohmani* **n. sp.**, *Bathycalanus bradyi* (Wolfenden, 1905), *Ba. dentatus* **n. sp.**, *Ba. milleri* **n. sp.**, *Ba. unicornis* Björnberg, 1968, and *Elenacalanus tageae* **n. sp.**). We cannot be absolutely certain that the correct males have been assigned to the appropriate female so our hypotheses await testing with new data.

The proposed phylogenetic hypothesis, based on both morphological and molecular data, estimates relationships among the genera and provides the first phylogeny for the Megacalanidae.

Vertical and horizontal distributions are summarised although conclusions are tentative, given there has been very limited sampling of depths deeper than 1000 m, a limited number of samples have been taken between known depth strata, and there is a limited geographic coverage, biased towards ocean margins, with large areas of all oceans not represented in the samples examined. Thus, even though we have added eleven new species, it is probable that more undescribed abyssopelagic species will be discovered and knowledge of the vertical distribution of all species improved as more depth-stratified deep sampling down to at least 6000 m is undertaken.

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