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Crenoicus Nicholls, 1944 (Crustacea, Isopoda, Phreatoicidea): Systematics and Biology of a New Species from New South Wales

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ABSTRACT. The phreatoicidean isopod genus *Crenoicus* is found in upland swamps and springs throughout New South Wales and Victoria. We provide a new diagnosis of *Crenoicus* and review its 4 species, including one new species. As a benchmark for phreatoicidean external morphology, this paper provides a detailed description and illustrations of the new species found on the Boyd Plateau west of Sydney. Variation in some morphological features is high, with populations from separated swamps nearby showing localised differentiation. Measurements of large samples from two sites indicate that this species may reproduce continuously throughout the year, but with a substantial decrease during the winter.

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Crenoicus Nicholls, 1944 is known from the highlands of New South Wales and Victoria (Fig. 1). In New South Wales, species are found in *Sphagnum* swamps (discussed herein), spring-fed seeps (pers. obs.) and cavernicolous ground waters (S. Eberhard, pers. comm.). In Victoria, specimens are also found at lower altitudes among root masses in small streams. Where these habitats are undisturbed, localised population densities may exceed several hundred per square meter. Because of its relative abundance and ease of collection in the highlands of New South Wales, a new species (*Crenoicus buntiae* n.sp.) was chosen for our initial studies of the suborder Phreatoicidea.

First reviewed by Nicholls (1943, 1944), more recent publications on the suborder Phreatoicidea have dealt with their distribution (Knott, 1986; Banarescu, 1990; Eberhard *et al.*, 1991), specific aspects of morphology (Martin, Wägele & Knott, 1990; Wilson, 1991), or treatments of their phylogenetic position in the Isopoda (Wägele, 1989; Brusca & Wilson, 1991). Williams (1980, 1981) provides general accounts of the Phreatoicidea in Australian fresh waters. More recently Poore, Knott and Lew Ton (in press) revise the taxonomic names of the suborder and diagnose the families, primarily based on Knott (1975). Our paper provides an inventory of phreatoicidean external anatomy and

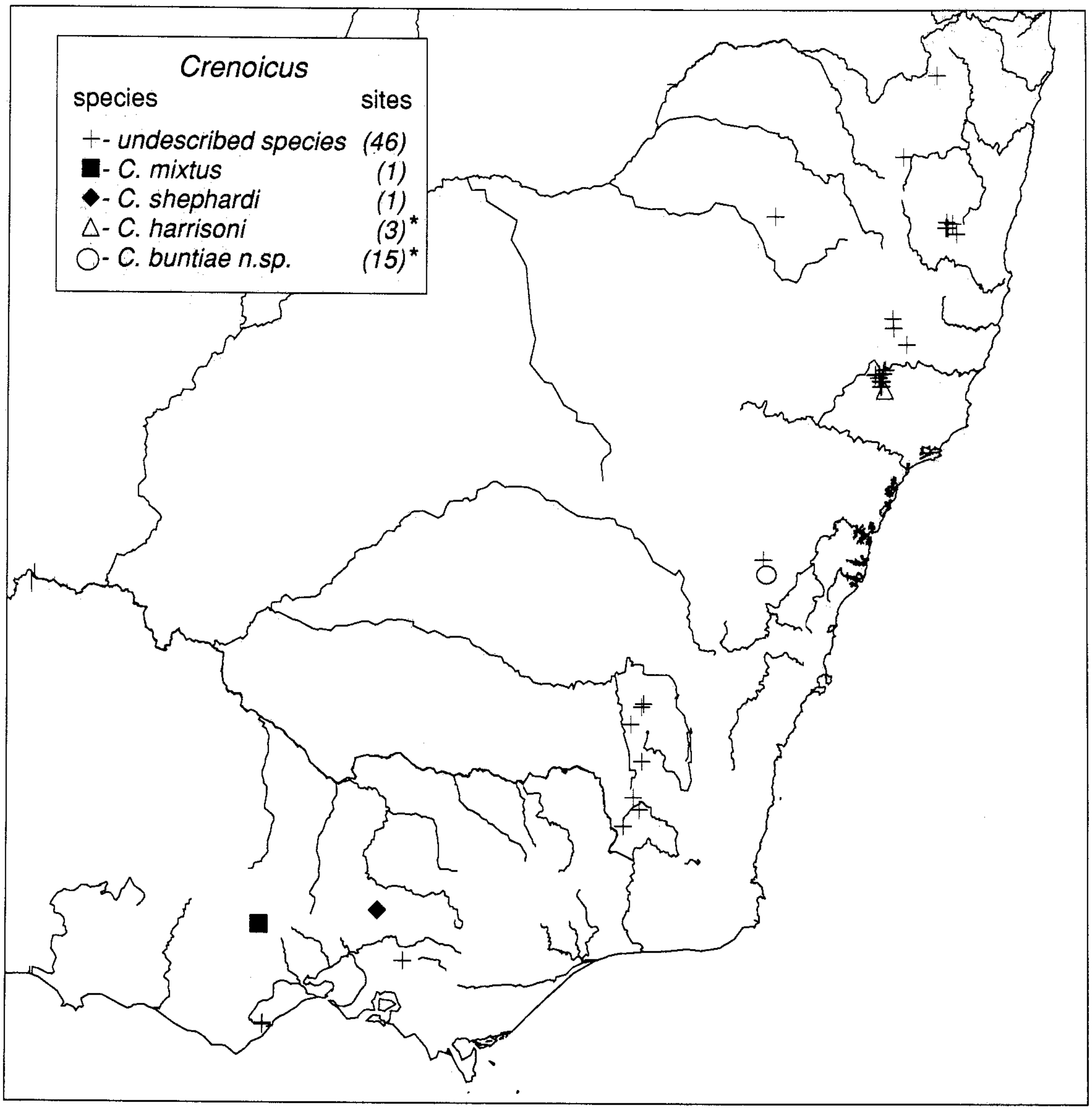

Fig. 1. Known distribution of species of *Crenoicus* in New South Wales and Victoria, Australia. Numbers within parentheses indicate the number of sites where specimens were found. Site numbers marked with an asterisk indicate overlapping sites, only one symbol shown in figure. Plus symbols may also overlap.

some information on variation in the species *Crenoicus buntiae* n.sp. The population biology of this species is also treated briefly. This work is part of a larger study of the Phreatoicidea of Australasia.

Methods

Crenoicus specimens were hand collected from moist seeps and from *Sphagnum* swamps. Positions were obtained using a portable GPS (Global Positioning System) instrument (radial accuracy 50–100 m). Specimens were found in localised concentrations amongst roots, stems and decaying vegetation, with all life stages occurring together. Once a clump of specimens was found, larger handfuls of material were washed with water and elutriated into hand sieves, or vegetation was preserved for sorting in the laboratory. As a consequence, the samples reported here are not quantitative with respect to area sampled. The samples, however, are qualitative, i.e. they recovered approximate proportions of life stages in the populations. Because we tended to hand pick adults during collection, these larger stages are somewhat accentuated numerically in the data over the mancas and juveniles. All specimens and associated material were fixed in approximately 10% formaldehyde solution buffered with sodium bicarbonate for at least one day, and then preserved in 70–80% ethanol.

Phreatoicideans are difficult to measure in dorsal view because most specimens preserve in a flexed position.

Therefore, we introduce a new method for length measurements. Body lengths were measured in lateral view as a series of line segments along the body axis. Nodal points were chosen close to the transverse axes of segmental rotation to minimise the effects of flexure. A specimen was arranged so that the antennular basal articles and the tip of the pleotelson were in the same plane. The specimens were measured using dissecting microscope images captured by a CCD camera attached to a Macintosh. The images were measured using NIH-Image (author, W. Rasband). Moving from the tip of the pleotelson (or the head), line segment selections were made along the body axis roughly parallel to the dorsal surface, from segment boundary to segment boundary. In the pereon, the axis was positioned above the insertions of the pereopods. In the pleon, the axis was positioned on a line extending midway between the dorsal and the ventral surfaces of the last pereonite. On pleonite 5, this point is at a marked angle of the articulation. The endpoint on the head was located at the dorsal insertion of the antenna. Head length was measured from this position to the dorsal insertion of the head into the pereon. Pleotelson length was measured from the tip of the pleotelson to the articular angle in the posterior margin of pleonite 5. Variation in line positioning was minimised by taking the median of 3 replicate readings. When repeated measurements were consistent within 0.05 mm, only single measurements were taken. The data were transferred to a spreadsheet program for graphic presentation and analysis.

Head and pleotelson lengths were measured to check for bias in the measured body lengths. Linear regressions of these parameters against body length were significant (R^2 = 0.95) at all sites indicating that preservation dependent changes in body length (particularly telescoping of the segments) did not greatly influence the results. Pleotelson length declined slowly relative to body length with increasing size suggesting that *C. buntiae* n.sp. did not grow in a completely linear fashion. This effect, however, was weak compared to the measurement variation. We do not report further on the head and pleotelson length data.

Populations, as defined in this study, are assumed to be contained within individual swamps, because the specimens of *Crenoicus* do not occur on the surrounding dry land or in the streams exiting the swamps. In studies of variation, mature specimens in each population were compared; maturity in males was assessed by the size of the first pereopod and the presence of penes with distal pores. A clear assessment of male maturity using the appendix masculina on the second pleopod requires the use of a compound microscope, so only the penes were used. In females, the presence of oostegites was used as a sign of maturity. Developmental stages were assessed independently from body size. Stages were identified as in previous studies (Forsman, 1944; Hessler, 1970; Wilson, 1981) as follows. Manca 1 individuals have no pereopod VII and pereonite 7 was much smaller than pereonite 6. Manca 2 individuals have a large pereonite 7 and pereopod VII was visible as a subcuticular anlagen. Manca 3 individuals have a pereonite 7 nearly same length as pereonite 6 and pereopod VII was expressed externally but rudimentary. Stage 4 individuals have a fully functional pereopod VII that was smaller than pereopod VI. Juveniles have a normal sized pereopod VII (larger than pereopod VI), but with no secondary sexual characters expressed (penes, oostegites). Juvenile males have rudimentary penes, defined as penes that have no distal opening and do not extend past the ventral margin of pereonite 7 posteriorly, on the coxae of pereopod VII. Adult males have fully developed penes (Figs 7C,D). Preparatory 1 females have small oostegal buds that do not extend more than halfway to the ventral midline. Preparatory 2 females have large oostegal buds, that extend to or nearly to the ventral midline. Brooding females have fully deployed oostegites, and may or may not have developing embryos. Although females rarely lost their brood during sample processing, embryonic stages were not assessed in this study.

Abbreviations: **AM**, Australian Museum; **NMV**, Museum of Victoria; **USNM**, United States National Museum of Natural History; **ZMUC**, Zoological Museum of the University of Copenhagen; **bl**, body length. Accession numbers beginning with "P" are from the Australian Museum Crustacea collection. In "Materials Examined" sections, samples collected on Australian Museum field trips are listed as "NSW *nnn*" where *nnn* is a sequential number, e.g., "NSW 485", one of two samples from Mumbedah Swamps designated as type material of *Crenoicus buntiae* n.sp. The style used for taxonomic descriptions of isopods is that of Wilson (1989).

Taxonomy

Crenoicus Nicholls, 1944

Crenoicus Nicholls, 1944: 21–23.

Type species. *Crenoicus mixtus* Nicholls, 1944.

Generic diagnosis. Eyes absent. Head length subequal to width in dorsal view, maxillipeds inserting near posterior margin of head. Dorsal surface with scattered fine setae, lacking tubercles or ridges. Pereonites lacking epimeral plates, all coxae visible in lateral view. Pereopodal coxae lacking distinct lateral projections. Gut with minimal typhlosole, "u" shaped in cross section. Pleonites with well-developed ventral epimera, pleopodal protopods not visible in lateral view. Pleotelson depth greater than length; posteriorly trilobed in dorsal or ventral view; medial tip not cleft, not distinctly longer than lateral lobes; ventral margin anterior to insertion of uropods with row of simple robust setae. Antennula terminal article shorter and narrower than subterminal articles, roughly globular. Right mandible lacking lacinia mobilis. Maxillula medial lobe narrower than lateral lobe, with 4 large plumose setae and 2 small simple setae (6 plumose setae sometimes occurring). Pereopod I male propodal palm with short, broadly conical, dorsally angled setae on low ridge; female propodal palm with row of broad based simple setae. Male pereopod

IV subchelate between dactylus and propodus, propodal palm with proximal large broad based setae. Penes smooth, lacking setae, strongly curved posteriorly, tapering distally to rounded point. Pleopod I exopod distally pointed, widest at midlength; endopod without setae. Male pleopod II appendix masculina curved, distally stylet-like, distal tip spatulate or spine-like with long single subdistal seta. Uropodal protopod distoventral margin with 1 robust distally spinose seta; propodal medial margin lacking distal projection; rami distally pointed, spine-like.

Remarks. Nicholls (1944) classified his genus *Crenoicus*, an exclusively Australian genus, in the subfamily Phreatoicinae which otherwise contains New Zealand forms. His subfamily concept may be too broad because the elongate subterranean genera *Phreatoicus* Chilton, 1883 and *Neophreatoicus* Nicholls, 1944 can be distinguished from the more typically shaped species of *Crenoicus* and *Notamphisopus* Nicholls, 1944. Nevertheless, Poore *et al.* (in press) expand the definition of the subfamily to include genera of Paraphreatoicinae Nicholls, 1944 plus *Uramphisopus* Nicholls, 1943, and raise this group to family level. We do not diagnose the family Phreatoicidae because the family level systematics of the Phreatoicidea should be revised using phylogenetic methods.

With this new composition of the Phreatoicidae, more genera must be compared with *Crenoicus*. The New Zealand species of *Phreatoicus* and *Neophreatoicus* are much more elongate than other Phreatoicidae and have a pleotelson whose length is greater than its depth. *Crenoicus* can be distinguished from *Colacanthotelson* Nicholls, 1944, *Mesacanthotelson* Nicholls, 1944 and *Onchotelson* Nicholls, 1944 by the lack of any unusual alterations of the dorsal cuticle, the pleotelson tip or the coxae (i.e. the cuticle is not rugose, the pleotelson does not have an elongate tip and the coxae are not laterally expanded). The other phreatoicid genera *Uramphisopus* Nicholls, 1943, *Colubotelson* Nicholls, 1944, *Metaphreatoicus* Nicholls, 1944, *Paraphreatoicus* Nicholls, 1944 and *Notamphisopus* Nicholls, 1944 are more similar to *Crenoicus*. Unlike Knott (1975) and Poore *et al.* (in press), we are uncertain whether the genera *Metaphreatoicus*, *Colubotelson* and *Paraphreatoicus* should be synonymised into *Uramphisopus*. *Uramphisopus pearsoni* Nicholls, 1943 has a large medial extension of the uropodal protopod, while none of the species attributed to other three genera have this feature. Other characters, such as the setation of the pleopodal endopods and the uropods, also suggest more diversity than a single genus should contain. Consequently, we prefer to recognise these genera until the suborder is revised. All of these genera, however, lack a distally pointed appendix masculina seen in *Crenoicus* and instead have a typically rounded tip with multiple setae. These genera also differ in other details such as the setation of the first pleopod and the number of spinose setae on the distal margin of the uropodal protopod. While most Australian Phreatoicidae have eyes, *Crenoicus* species are completely blind, although the head may have a cuticular remnant of the eyes. *Crenoicus* species also have a subcuticular white patch of unknown function in the ocular region of the head.

Species included. *Crenoicus mixtus* Nicholls, 1944; *C. shephardi* (Sayce, 1900); *C. harrisoni* Nicholls, 1944 and *C. buntiae* n.sp. Nicholls (1944: 31) noted another undescribed species from the New England region of New South Wales. The morphological conservatism of this genus coupled with substantial intrapopulation variation in some characters (discussed later in this paper) makes identification of species difficult. A complete species inventory for *Crenoicus*, therefore, will require careful morphometric and genetic studies.

Distribution of *Crenoicus* species. Throughout springs and swamps of Victoria and New South Wales: near Ballarat (*C. mixtus*), Plenty Range near Melbourne Vic. (*C. shephardi*), Barrington Tops NSW (*C. harrisoni*), Boyd Plateau NSW (*C. buntiae* n.sp.), Otway Range Vic. (*Crenoicus* sp.—undescribed). Our collecting activities have shown other undescribed species of *Crenoicus* to be widespread in NSW springs and marshes above 1000 m (see Fig. 1).

Crenoicus mixtus Nicholls, 1944

Crenoicus mixtus Nicholls, 1944: 23–27, figs 38–39.

Syntypes. Types not examined, apparently lost (Poore *et al.*, in press). Nicholls (1944) reported 1 male bl (body length) 14 mm, 6 females and 23 other specimens that he used for his description.

Type locality. "On Dividing Range near Ballarat [Victoria], in springs and soaks at the source of that city's water supply" (Nicholls, 1944: 27). Assuming that Winter Swamp near Ballarat is the type locality, this locality might be 37°33'S 143°48'E.

Diagnosis (derived from Nicholls, 1944: figs 38–39). Posterior robust seta on ventral margin of pleotelson subequal or shorter than more anterior robust seta. Maxillipedal epipod distally rounded. Male pereopod I basis anteroproximal surface with less than 5 setae, lacking dense group of setae. Male pereopod IV propodus not dorsally expanded, distal width less than palm length, anterior surface with distal indentation; ischium posterodistal margin with approximately 10 long setae. Pleopod I exopod proximally concave, widest point approximately midlength. Pleopod II appendix masculina with smooth tapering shaft, distal tip pointed (detail unknown, possibly with seta vis. Nicholls, 1944: fig. 39,13.2); endopod distally rounded, lacking indentation; distal segment of exopod longer than wide, lateral margin proximally straight sided.

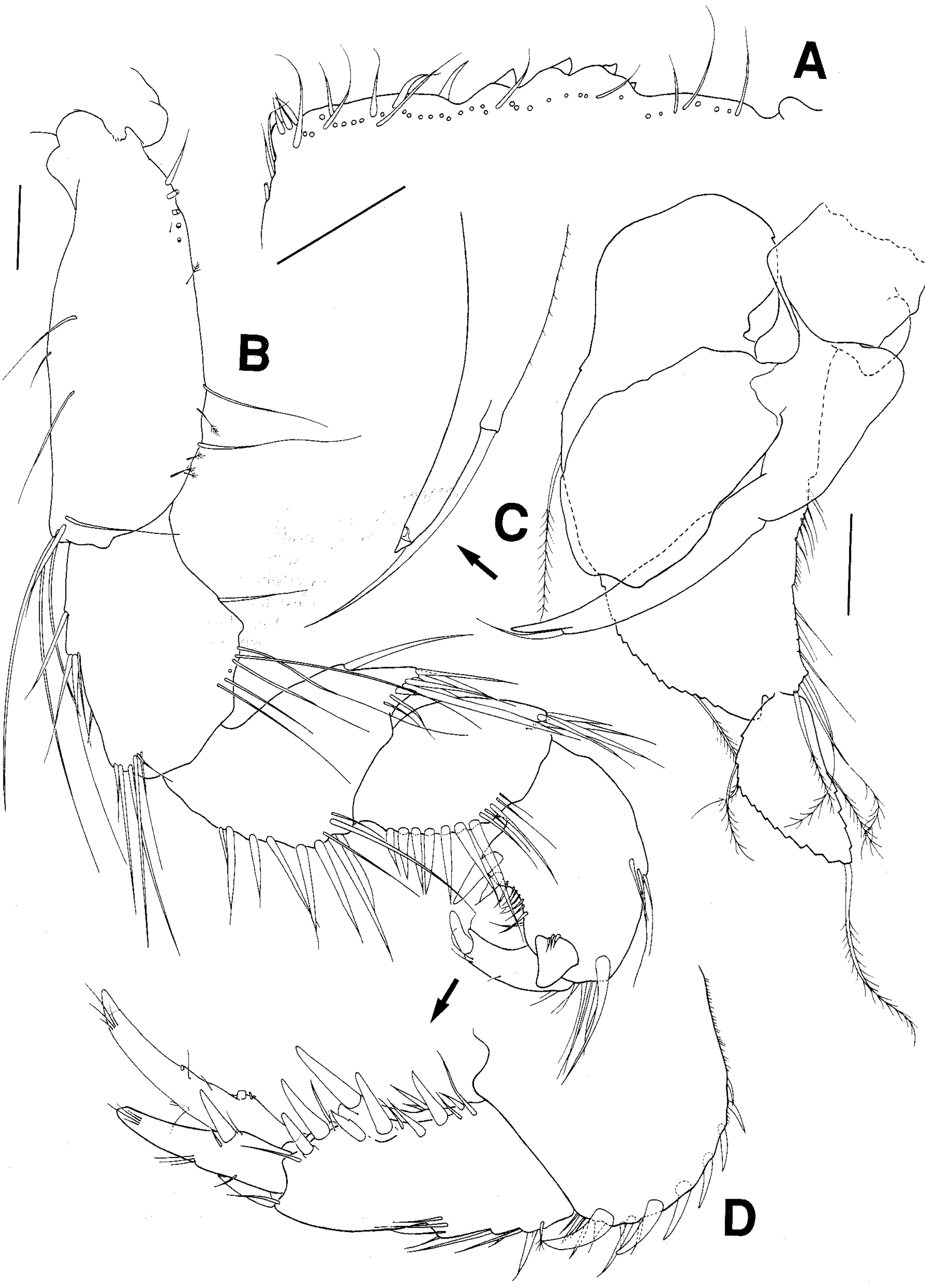

Fig. 2. *Crenoicus shephardi* Sayce, 1900. Limbs. NMV J213, holotype male, bl (body length) 11.3 mm. A, pereopod I, palm. B, pereopod IV. C, male pleopod II with distal enlargement of endopodal stylet. D, detached right pleuron of pleotelson with uropod in lateral view. Scale bar 0.2 mm.

Remarks. This diagnosis remains preliminary because we did not examine the types, which have been lost, depending only on Nicholls' description and illustrations. Some character states in the diagnosis depend on the accuracy of Nicholls' drawings. In most cases, we have found his rendition of shapes to be accurate, but setal details may be more fallible. Although Nicholls writes that "... penial stylet, unarmed terminally... " (Nicholls, 1944: 27), he illustrates it with a small distal split, suggesting that the stylet may have a seta as in other *Crenoicus* species. In any case, a pointed tip of the appendix masculina is a putative synapomorphy of the genus.

Crenoicus shephardi (Sayce, 1900)

Fig. 2

Phreatoicus shephardi Sayce, 1900: 25, pl. 3.
Phreatoicus shephardi. Sheppard, 1927: 112.
Crenoicus shephardi. Nicholls, 1944: 27–28.

Material Examined. HOLOTYPE male, NMV J213, bl 11.3 mm, collected 1899 by J. Shephard.

Type Locality. Source of a spring flowing into Wallaby Creek, Plenty Ranges, Victoria, approximately 37°24'S, 145°15'E.

Diagnosis. Posterior robust seta on ventral margin of pleotelson longer or subequal to more anterior robust seta. Maxillipedal epipod obtusely pointed distally. Male pereopod I basis anteroproximal surface with 5 or less setae, lacking dense group of setae. Male pereopod IV propodus not dorsally expanded, distal width less than palm length, anterior surface with distal indentation; ischium posterodistal margin with 4 long setae. Pleopod II appendix masculina with smooth shaft; distal tip laterally spatulate, medially thickened with no tiny denticles, distal seta basally narrower than distal tip; endopod with distal indentation; distal segment of exopod longer than wide, lateral margin proximally rounded.

Remarks. Only a single male specimen from the Museum of Victoria (NMV J213; Fig. 2) is known, from which the above diagnosis was derived. *Crenoicus shephardi* is largely similar to the other species of the genus, but the obtusely pointed maxillipedal epipod and the indented endopod of second pleopod should be sufficient to identify this species. The mouthparts are missing from the holotype, so the features of the mouthparts are obtained from Sayce's (1900) original description and figures. The details in our diagnosis should be checked against new material if available.

Crenoicus harrisoni Nicholls, 1944

Figs 3, 4

Crenoicus harrisoni Nicholls, 1944: 28–31, fig. 40.
Phreatoicus shephardi. Chilton, 1917: 91, fig. 13–17.

Material examined. P44459, adult male, bl 13.1 mm (Fig. 3, 4F–H) designated as NEOTYPE. P4076, 12 specimens; P4081, 1 specimen, 5 slides (prepared by C. Chilton); P4082, 1 specimen, 5 slides (prepared by C. Chilton). Other specimens not examined from AM P4076: NMV J13924, 6 specimens; specimens sent to G.E. Nicholls: 4 sent during 1926, 2 during 1928.

Neotype locality. Barrington Tops "near Dungog" (Chilton, 1917: 82) New South Wales, Australia, in roots and stems of moss in large swamp on plateau, 32°S, 151°27'E (position approximate), altitude 1400 m, collected by C. Hedley, December 1915.

Remarks on neotype designation. As with many of Nicholls' species, the types of *C. harrisoni* cannot be found. The collections of the Australian Museum contain specimens that were collected by C. Hedley during December 1915 (P44459, P4076, P4081, P4082). Poore *et al.* (in press) list these specimens as the syntypes of *C. harrisoni*. Nicholls (1944), however, based his descriptions on specimens given to him by Professor L. Harrison. He states in his text (Nicholls 1944: 31): "Occurrence. Collected by the late Professor Harrison at Mount Royal (Barrington Tops); *presumably* identical with that collected nearby some years earlier (Jan., 1916) by C. Hedley." [italics added]. The specimens reported from the vicinity of Mount Royal were probably obtained during 1925 when Harrison was actively collecting in the region (data from AM Crustacea collection database). The AM register entry of P4076—from which the neotype, P44459, comes—notes that Nicholls was sent 6 Hedley specimens, so that he may have compared the Hedley and the Harrison material, although his text suggests that he did not. The Harrison specimens are lost, along with many other phreatoicidean types that were held in Nicholls' collection at University of Western Australia (Jones, 1986; Poore *et al.*, in press). No populations of *Crenoicus* were found during a recent (January 1995) inspection of aquatic habitats around Mount Royal. The only active spring in this area was in a badly disturbed cattle handling area (altitude approximately 800 m, west of Mount Royal) that lacked *Sphagnum* moss. Moreover, the narrow ridge topography of Mount Royal is unlike other typical *Crenoicus* habitats in New South Wales, such as on the nearby Barrington Tops where known populations of *C. harrisoni* exist. Nicholls must have meant the Mount Royal Range, in which Barrington Tops is included. Therefore, we have selected a male neotype (P44459) from the Hedley collection from Barrington Tops which was described by Chilton (1917) as *Phreatoicus shephardi* Sayce. The chosen specimen is not a lectotype because Nicholls may

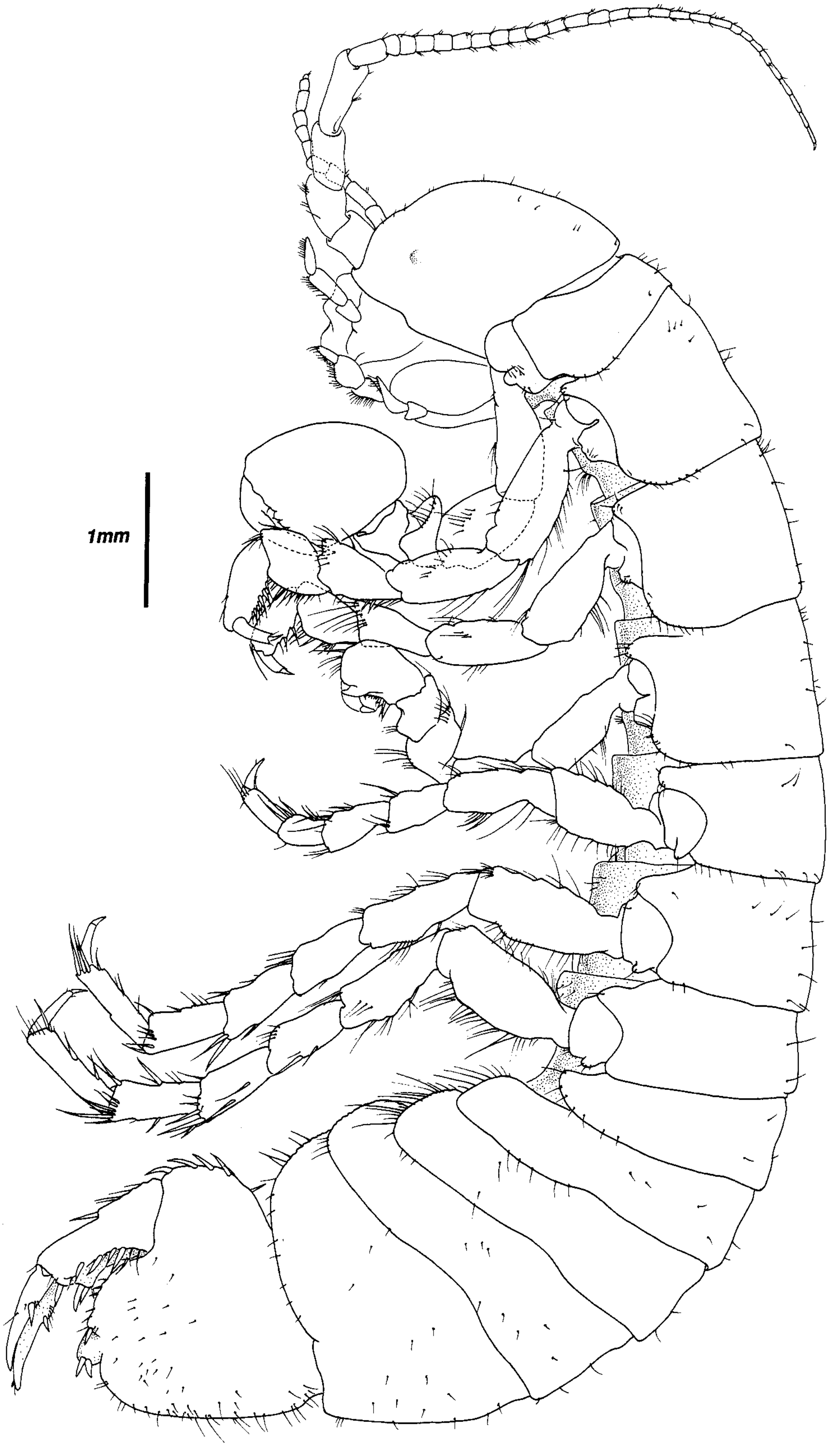

Fig. 3. *Crenoicus harrisoni* Nicholls, 1944. Body, lateral view. AM P44459, adult male neotype, bl 12.7 mm. Scale bar 1 mm.

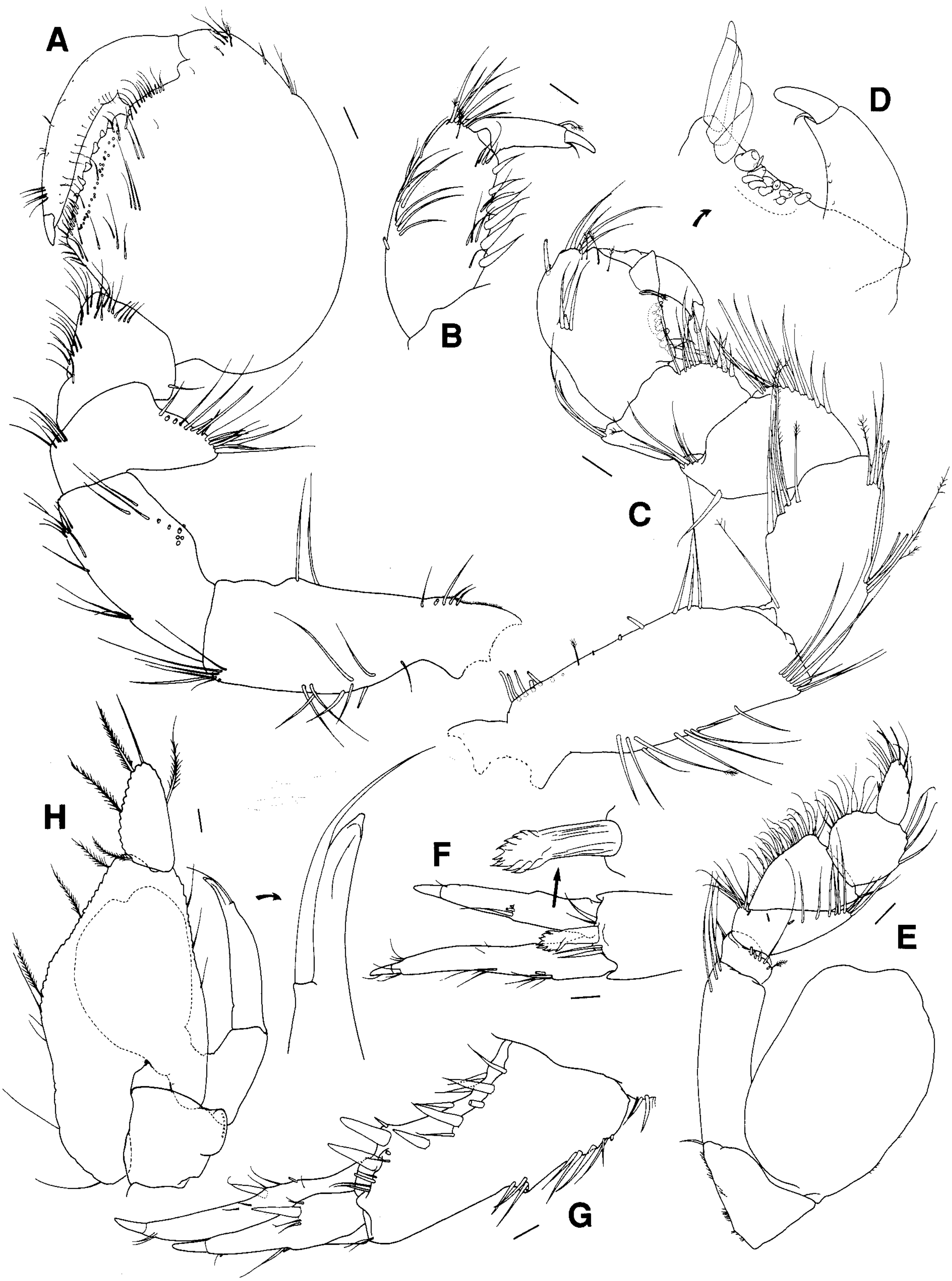

Fig. 4. *Crenoicus harrisoni* Nicholls, 1944. Limbs. A–E, AM P4076, adult male, bl 12.7 mm. G, H: AM P44459, adult male neotype, bl 13.1 mm. A, left pereopod I; B, right pereopod II, dactylus and propodus; C, D: right pereopod IV; C, whole limb lateral view; D, palm, medial view. Scale bar 0.1 mm.

not have used the Hedley collection for his description. Nevertheless, Hedley specimens have nomenclatural value because they agree in detail with Nicholls' illustrations (apparently he looked at them without changing their identification), and the specimens are from Barrington Tops, Nicholls' apparent type locality for the species. Of the material available at this time, only the Hedley specimens match Nicholls' description for *Crenoicus harrisoni*.

Diagnosis. Posterior robust seta on ventral margin of pleotelson subequal or shorter than more anterior robust seta. Maxillipedal epipod with concavity on distal margin. Male pereopod I basis anteroproximal surface with less than 5 setae, lacking dense group of setae. Male pereopod IV propodus dorsally expanded, distal width greater than palm length; ischium posterodistal margin with approximately 3–4 setae. Pleopod I exopod proximal part linear (not concave), widest point approximately midlength. Pleopod II appendix masculina with smooth shaft; distal tip laterally spatulate, medially thickened with 2–3 tiny rounded denticles, distal seta basally narrower than distal tip; endopod with distal indentation; distal segment of exopod longer than wide, lateral margin proximally rounded.

Remarks. This diagnosis will distinguish *Crenoicus buntiae* n.sp. from *C. harrisoni* Nicholls, as well as other undescribed species we have observed from New South Wales and Victoria. These two species, while being largely similar, are most easily separated using the shape of the male pereopod IV propodus, being dorsally expanded in *C. harrisoni* and evenly rounded in *C. buntiae* n.sp. Nicholls (1944: 29) remarked that the propodus lacked evident palm or "spines", differing from Chilton's (1917) account of the same species. We suspect that Nicholls missed the setae on the palm because they are strongly angled medially. Moreover, the propodus IV does have a small but well-developed palm, similar to other species. When making an identification of species of *Crenoicus*, one should be certain that a fully mature male is being used. Maturity in the male can be assessed by the size of the propodus of first pereopod.

Crenoicus buntiae n.sp.

Fig. 5–15

Type material. HOLOTYPE. P44348, adult male, bl 10.76 mm; NSW 758, Mumbedah Swamps, Kanangra-Boyd National Park, NSW, Australia; *Sphagnum* swamp at head of Mumbedah Creek, Boyd Plateau: NSW 758, 33°53.73'S, 150°4.05'E, 1200 m, 2/4/1992, collected by G. Wilson and party. PARATYPES from NSW 758: P44349, adult male, body length 10.8 mm, dissected; P44350, preparatory female, bl 8.25 mm, intact; P44351, preparatory female, bl 8.5 mm; P44352, brooding female, bl 6.35 mm, partially dissected; P44353, preparatory 2 females, bl 7.7 mm, intact; P44354, brooding female, bl 6.7 mm, intact; P44355, adult male, bl 10.4 mm, intact; P44356, adult male, cephalon only; P44394, preparatory female, bl 5.2 mm, partially dissected; P44359, adult male, bl 9.7 mm, partially dissected; P44395, adult male, bl 6.5 mm, partially dissected; P44396, brooding female, bl 6.2 mm, partially dissected; P44457, 303 specimens used for measurements. PARATYPES from NSW 485, 33°53.76'S, 150°3.92'E, 1200 m, 18/11/1992, collected by G.Wilson and party: P44463, 197 specimens used for measurements; NMV J40520 male, 2 females; USNM 253241, male, 2 females; ZMUC CRU1774, male, 2 females.

Other material: Kanangra-Boyd National Park, NSW. P44458, NSW 757: Luther's Creek near road, *Sphagnum* & sedge spring in old paddock, 33°52.78'S, 150°2.72'E, 1215 m, 2/4/1992. P44480, NSW 486: Luther's Creek near road, spring-fed swamp of *Sphagnum* and gelatinous algae in fresh water over silt, 33°52.82'S, 150°2.62'E, 1225 m, 19/11/1992. P44474, NSW 487: Roly Whalen Swamp, *Sphagnum* moss & mixed aquatic vegetation in fresh water 33°58.55'S, 150°3.30'E, 1180 m, 17/11/1992. P44475, NSW 478: Jensen's Swamp, *Sphagnum* moss & mixed aquatic vegetation in fresh water, 33°58.65'S, 150°2.76'E 1175 m, 17/11/1992. P44476, NSW 479: Jensen's Swamp, *Sphagnum* moss & mixed aquatic vegetation in fresh water, 33°58.59'S, 150°2.78'E 1175 m, 17/11/1992. P44460, NSW 480: Dingo Swamp, mixed sedge *Sphagnum* and sawgrass in fresh water, 33°59.34'S, 150°2.39'E 1180 m, 17/11/1992. P44477, NSW 482: Boyd Hill Swamp, downstream from clumps of *Sphagnum* & sedge in fresh water, 33°56.97'S, 150°1.44'E, 1225 m, 18/11/1992. P44478, NSW 483: "Oldmeadow Swamp," *Sphagnum* and mixed water plants in spring fed fresh water, 33°56.56'S, 150°2.48'E, 1211 m, 18/11/1992. P44479, NSW 484: Belarah Swamp, amongst *Sphagnum*, sticks & roots submerged in fresh water stream, 33°54.31'S, 150°4.65'E, 1185 m, 18/11/1992. All material collected by G. Wilson and party.

Other material, Council Creek population (*Crenoicus* sp. cf. *buntiae*). P44481, NSW 487: Swamp near road outside of Kanangra-Boyd National Park boundary, NSW, eastern headwaters of Council Creek, in *Sphagnum* & gelatinous algae over gravelly substrate, 33°50.51'S, 150°0.80'E, 1180 m, 19/11/1992, collected by G. Wilson and party.

Etymology. This species is named after Ms Bunty Oldmeadow, who accompanied us on a November 1992 field trip to collect isopods on the Boyd Plateau. Bunty aided our collecting effort and maintained a cheerful demeanour despite chilling rain and countless leeches. Ms Oldmeadow also suggested "friartuck" as a "common" name for phreatoicideans.

Diagnosis. Posterior robust seta on ventral margin of pleotelson subequal or shorter than more anterior robust seta. Maxillipedal epipod distally rounded. Male pereopod I basis anteroproximal surface with less than 5 setae, lacking dense group of setae. Male pereopod IV propodus not dorsally expanded, distal width less than palm length; ischium posterodistal margin with approximately 3–4 setae. Pleopod I exopod proximal part straight (not concave), widest point approximately midlength. Male pleopod II appendix masculina with smooth shaft; distal tip laterally spatulate, medially thickened with 2–3 tiny

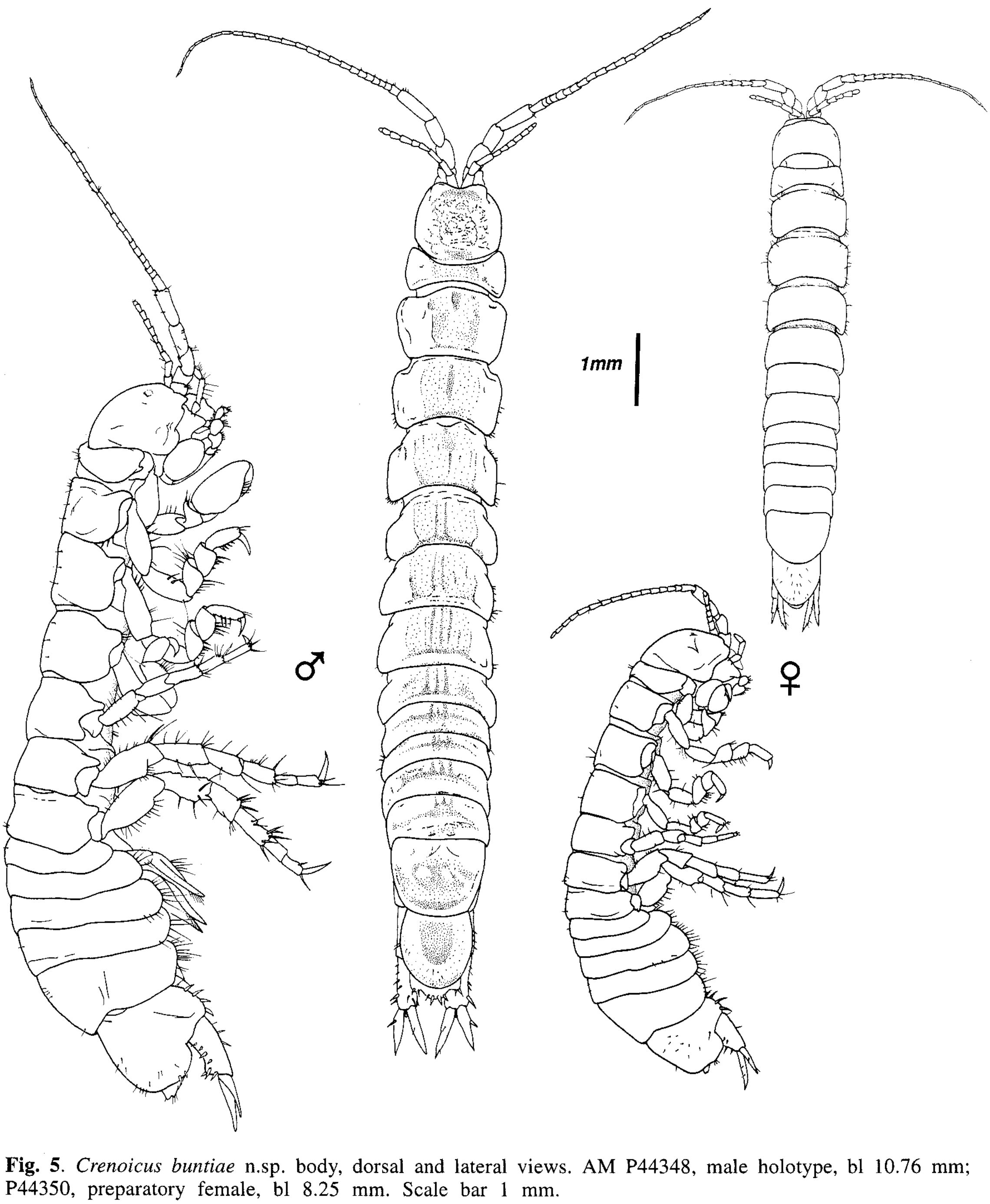

Fig. 5. *Crenoicus buntiae* n.sp. body, dorsal and lateral views. AM P44348, male holotype, bl 10.76 mm; P44350, preparatory female, bl 8.25 mm. Scale bar 1 mm.

rounded denticles, distal seta basally narrower than distal tip; endopod distal rounded, lacking indentation; distal segment of exopod longer than wide, lateral margin proximally rounded.

Description. *Head* (Fig. 5, 6A,E,F). Eye region roughly oval in shape, fully sessile, lacking pigment and ocelli, maximum diameter 0.09 head depth, orientation of longest axis vertical; living specimens with large dendritic subcuticular white patches in eye region. Cuticle of head smooth, tubercles absent, with few long scattered setae. Head shape in dorsal view roughly subcircular, only slightly wider than long, width 0.9 pereonite 1 width. Head lateral profile forming smooth open curve. Cervical groove straight, weakly indented, extending variably above anterolateral margin of pereonite 1. Mandibular groove absent. Mandibular notch present. Clypeal notch present. Antennal notch present. Frontal process above antennule absent. Mouth field adjacent to posterior margin of head, maxillipeds inserting 0.08 head length

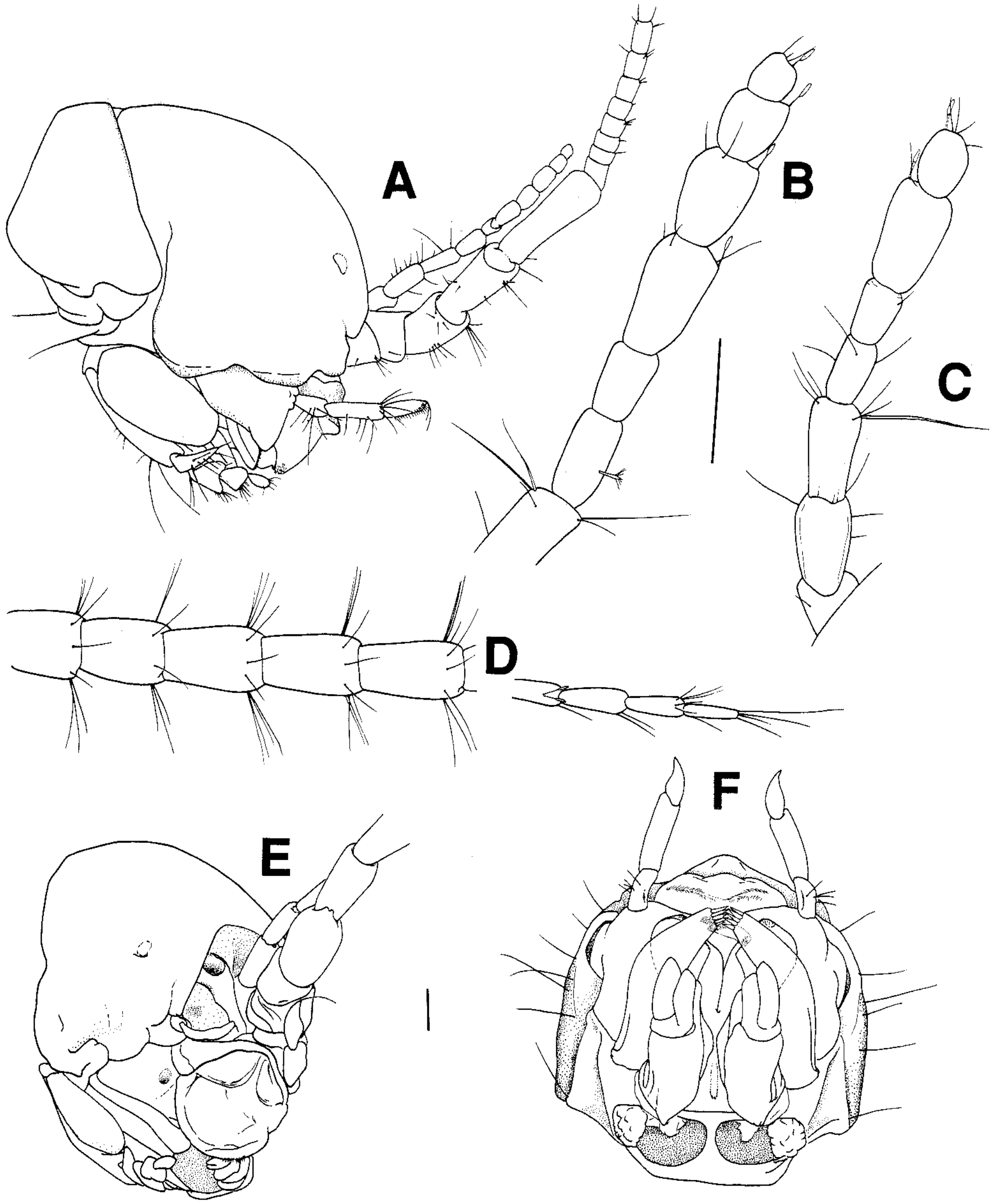

Fig. 6. *Crenoicus buntiae* n.sp. head, antennulae and antennae. A, E, F: P44349, adult male, bl 10.8 mm. B, D, P44348, holotype male, bl 10.76 mm. C, P44350, preparatory female, bl 8.25 mm. A, E–F, head: lateral, frontal oblique and ventral views, last with maxillipeds removed. B, C, male and female antennulae, proximal article truncated. D, antenna, flagellar segments, midlength and distally. Scale bar 0.2 mm.

from posterior margin of head.

Pereon (Fig. 5). Setation on dorsal surface sparse and scattered, seta thin and short. Dorsal surface of pereon smooth. Pereon only 10% wider than head. Pereonites much wider than long. Coxae on pereonites 2–7 with distinct sutures. Sternal processes absent. Gut with U-shaped typhlosole; hindgut caecae absent.

Pleonites (Figs 5, 7). Pleonites with large ventrolateral pleural plates extending well below level of pereonal coxae, basal region of pleopods not visible; pleonite 1 pleurae distinctly shorter than pleurae of pleonites 2–5. Pleonites 1–5 depth 1.2–1.3, 1.5–1.6, 1.7–1.8, 1.7–1.8, 1.3–1.4 pereonite 7 tergite depth, respectively. Pleonites 1–4 length subequal, less than half length of pleonite 5, width 0.68 total length in dorsal view.

Pleotelson (Fig. 7A–C,E). Lateral length 0.11–0.17 body length (mean = 0.14, N = 298), dorsal length 1.3 width (N = 2), lateral length 0.8–0.9 depth (N = 2), lateral median lobe length 0.1 pleotelson total length. Telsonic region distinct, trilobed, median lobe length 0.1

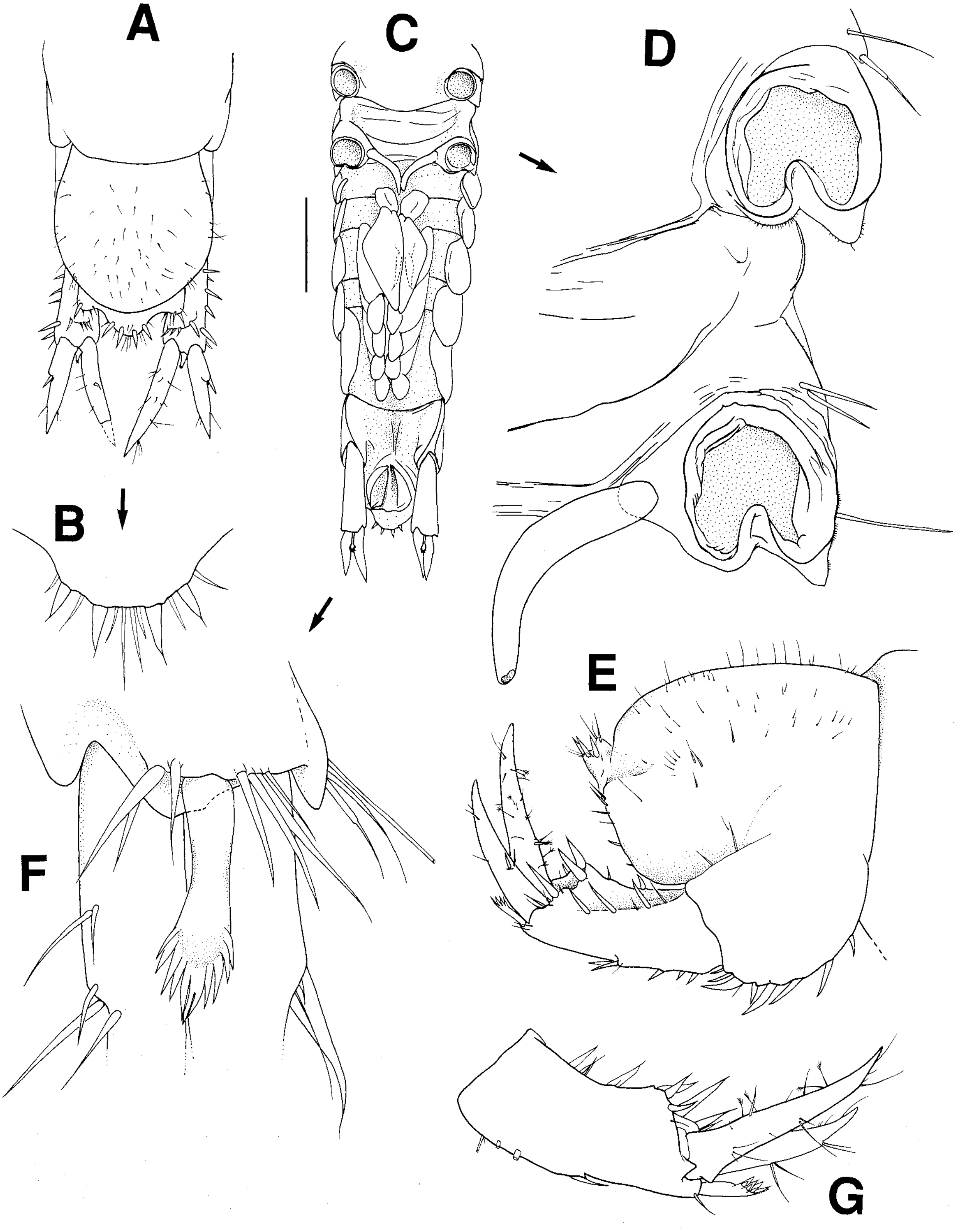

Fig. 7. *Crenoicus buntiae* n.sp. male pleon. AM P44349, adult male, bl 10.8 mm. A, pleotelson and uropods, dorsal view. B, pleotelson, median lobe. C, pereonites 6-7 and pleon, ventral view. D, coxae VI–VII, showing penes. E, pleotelson and right uropod, lateral view. F, right uropod, insertions of rami and robust distally spinose seta, ventral view. G, right uropod, medial view. Scale bar 1 mm.

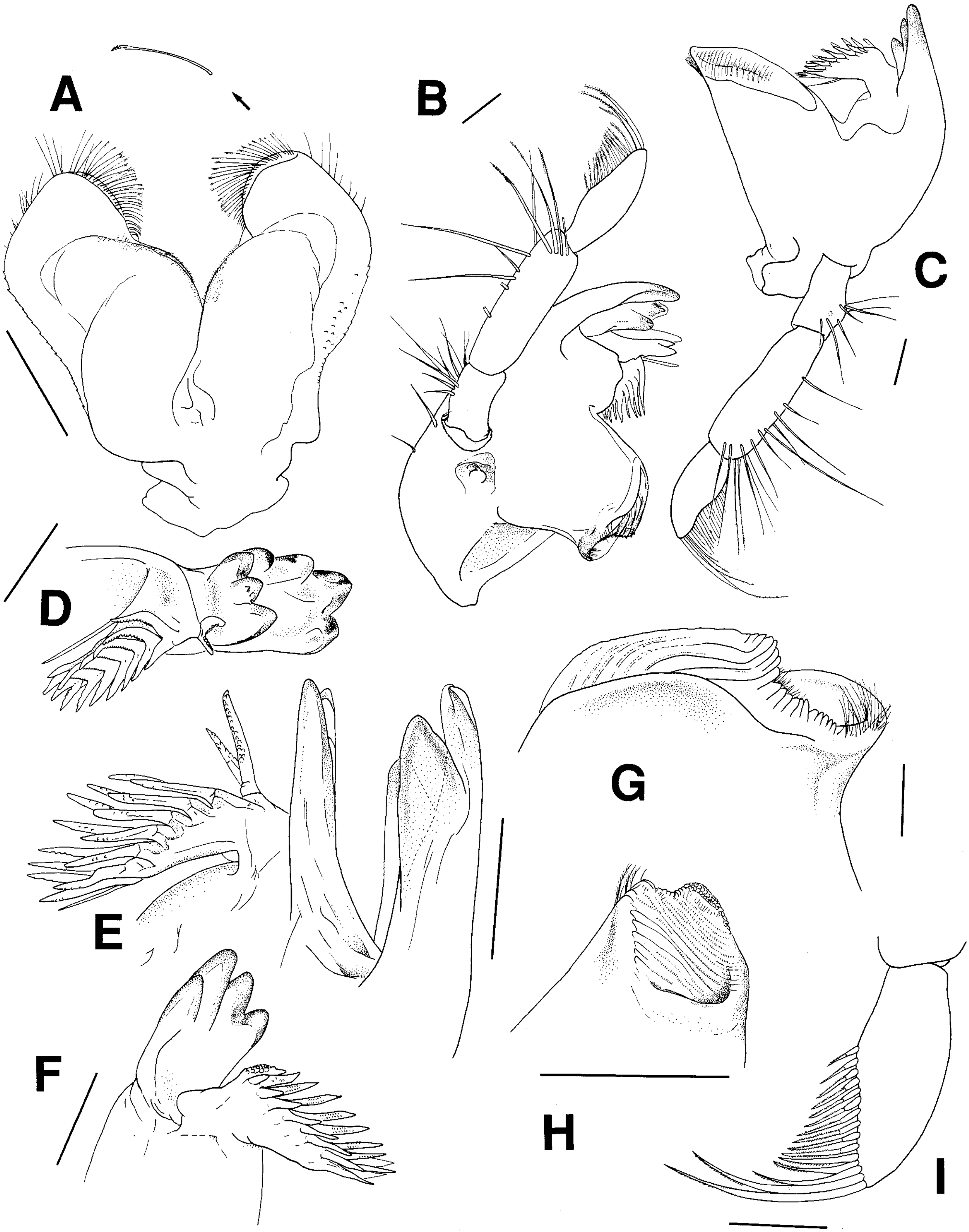

Fig. 8. *Crenoicus buntiae* n.sp. mouthparts. AM P44349, adult male, bl 10.8 mm. A, paragnaths, ventral view. B, left mandible, dorsal view. C, right mandible, dorsal view. D, E, left incisor, lacinia and spine row, medial and ventral views. F, right incisor process and spine row, ventral oblique view. G, H, left molar process, dorsal and ventral views. I, left palp article 3. Scale bar 0.1 mm.

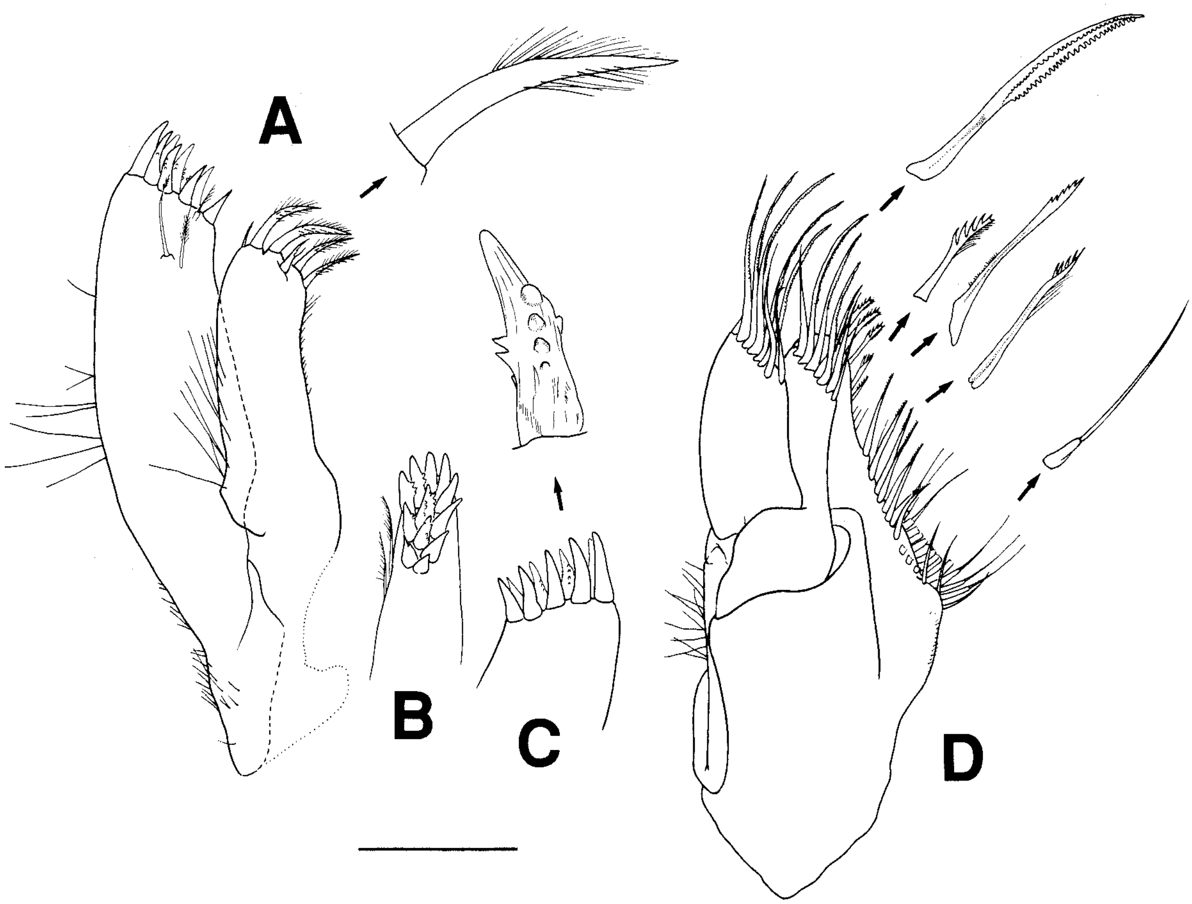

Fig. 9. *Crenoicus buntiae* n.sp. mouthparts. AM P44349, adult male, bl 10.8 mm. A–C, left maxillula, ventral view with enlargement of pappose seta, medial and dorsal views of lateral lobe with enlargement of denticulate seta; D, left maxilla with enlargements of various setal types. Scale bar 0.1 mm

pleotelson length, lateral lobes shorter than median lobe in dorsal view. Tailpiece lateral lobe with 1 strong sensillate setae, median lobe with 4 robust sensillate setae. Dorsal uropodal cleft present, with several fine setae. Ventral margin anterior to uropods with 4–5 strong setae.

Antennula (Figs 5, 6A–C). Length 0.1–0.13 body length, with 7–8 articles in adult females, 9–10 articles in largest adult males. Articles 4 distinctly shorter than article 3. Article 6 sometimes dividing into two articles. Single tiny aesthetascs on article 6 to terminal article distally. Terminal article approximately oval, shorter than penultimate article, length 1.2–1.4 width.

Antenna (Figs 5, 6A,D) length 0.46 body length in male, 0.38 in female. Flagellum length 0.70–0.73 antenna length, with 24–25 articles in largest males, 14–16 in females. Proximal propodal article absent, antennal scale absent on article 3. Article 5 subequal to article 4; article 6 subequal to articles 4 and 5.

Mouthfield (Fig. 6E,F). Clypeus consisting of broad bar, rounded laterally at mandibular fossae, width 0.69 head width. Labrum ventrally semicircular in anterior view, approximately same width as clypeus. Paragnaths (Fig. 8A) with distolaterally rounded lobes having medial setal row and thickened medial base covered with cuticular spinules.

Mandible (Fig. 8B–I). Palp length 0.88 mandibular body length; article 3 with (15–16) setae, setae finely setulate, lacking cuticular hairs or combs; articles 1–2 with groups of long setae (longer than half article length) on dorsolateral margins. Incisor process with 4 teeth or cusps, 3 distally and one on ventral margin. Left lacinia mobilis with 3 teeth or cusps. Right lacinia mobilis absent. Spine row on projection with 9 bifurcate spines on both sides, distalmost spine distinctly separated from remaining spines. Molar process stout, heavily keratinised, broader than long; triturating surface heavily ridged with single posterior rounded tooth and posterior row of fine simple setae.

Maxillula (Fig. 9A–C). Medial lobe length 0.75 lateral lobe length; medial lobe 0.77 width lateral lobe width. Medial lobe with 4 plumose seta and 2 distally denticulate "accessory" setae, one on distolateral margin and one between central plumose setae. Lateral lobe with 12 stout denticulate setae, ventral face with three thin distally plumose setae, 2 proximal and one adjacent to stout denticulate setae.

Maxilla (Fig. 9D). Medial lobe width subequal to width of lateral lobes, extending anteriorly approximately same distance as lateral lobes. Lateral lobes with 7–8

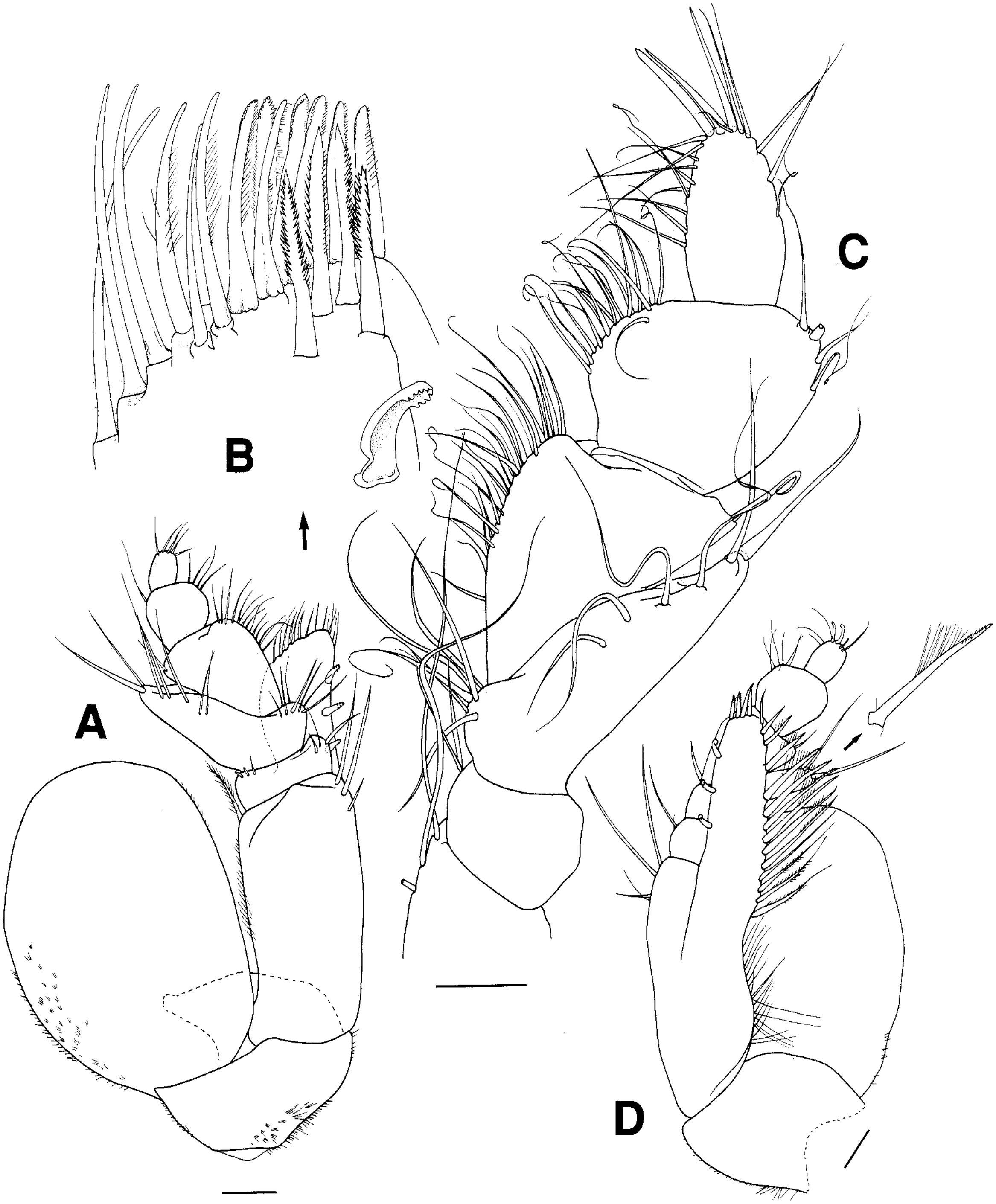

Fig. 10. *Crenoicus buntiae* n.sp. maxillipeds. A, D, P44395, adult male, bl 6.5 mm. B, C, AM P44349, adult male, bl 10.8 mm. A, left, ventral view. B, enlargement of endite ventral view. C, right palp, ventral view. D, left, medial view showing pappose denticulate setae on dorsal ridge. Scale bar 0.1 mm.

setae having two rows of denticles each. Medial lobe with two basal rows of setae separated from single distal row by distinct gap but otherwise smoothly continuous; setae in ventral basal rows with single row of fine setules; setae in dorsal basal row with distinct base and smooth shaft; setae in distal row with row of teeth and row of fine setules.

Maxilliped (Fig. 10). Epipod length 1.5 width, distal tip rounded, ventral surface and margins lacking setae, with lateral group of fine cuticular combs. Endite length 0.36 total basis length; distal tip with 4 subdistal biserrate setae on ventral surface; 3 coupling hooks (receptaculi) on medial margin; dorsal ridge with approximately 14 large, distally denticulate plumose

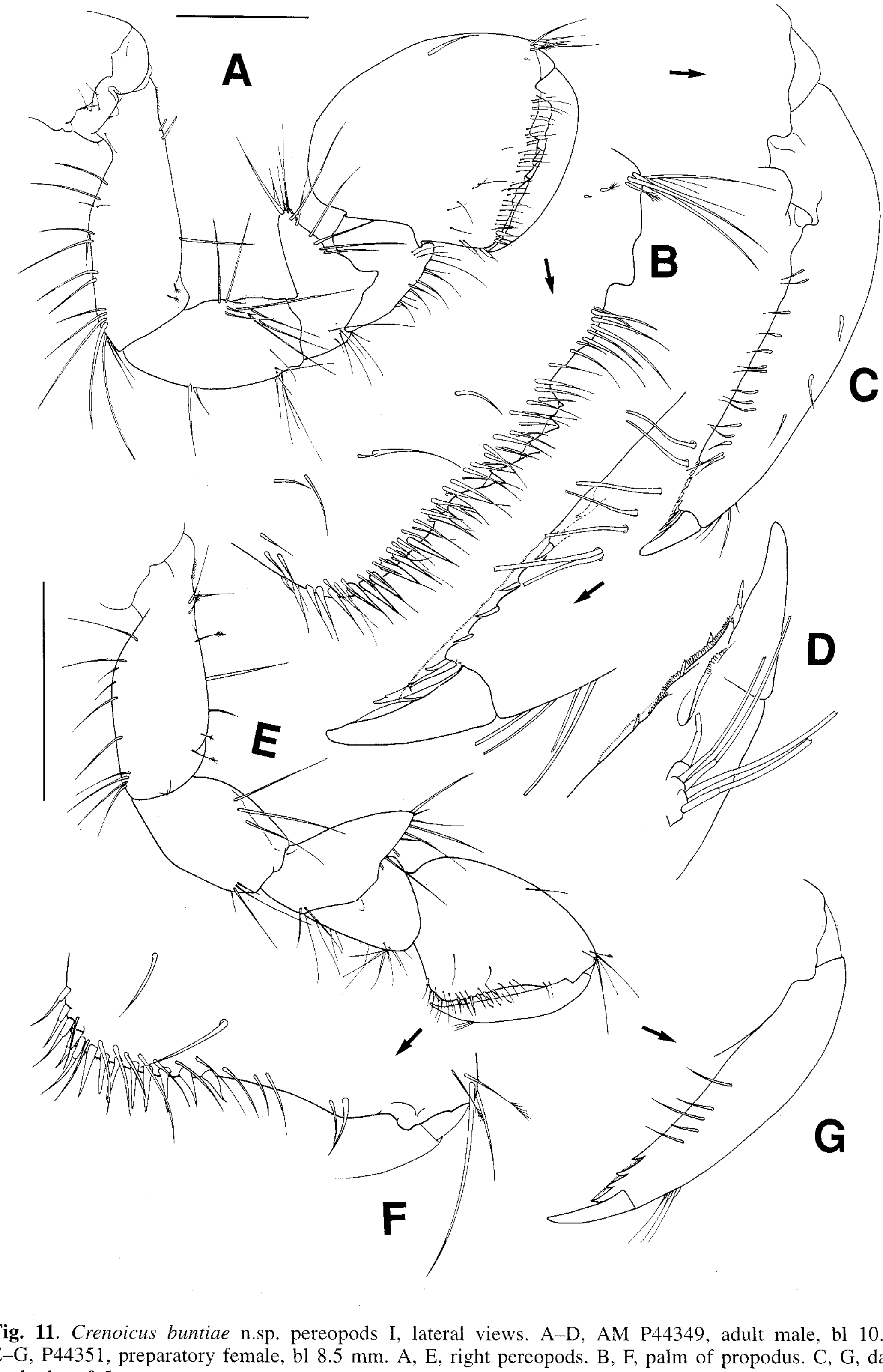

Fig. 11. *Crenoicus buntiae* n.sp. pereopods I, lateral views. A–D, AM P44349, adult male, bl 10.8 mm. E–G, P44351, preparatory female, bl 8.5 mm. A, E, right pereopods. B, F, palm of propodus. C, G, dactylus. Scale bar 0.5 mm.

setae. Palp insertion on basis with 1 plumose setae laterally, and 3 simple setae medially. Palp length 0.31 basis length, width (across article 2 & 3) 1.8 endite width; palp article 4 subcircular, length 1.1 width; palp article 5 length 0.87 width, length 0.8 article 4 length.

Pereopod I (Fig. 11). Sexually dimorphic, length 0.32 body length in adult male, 0.25 in preparatory female. Pereopod of juvenile males resembling female condition. Dactylus length subequal to palm length in both sexes; row of fine setae along lateral axis; ventral margin with

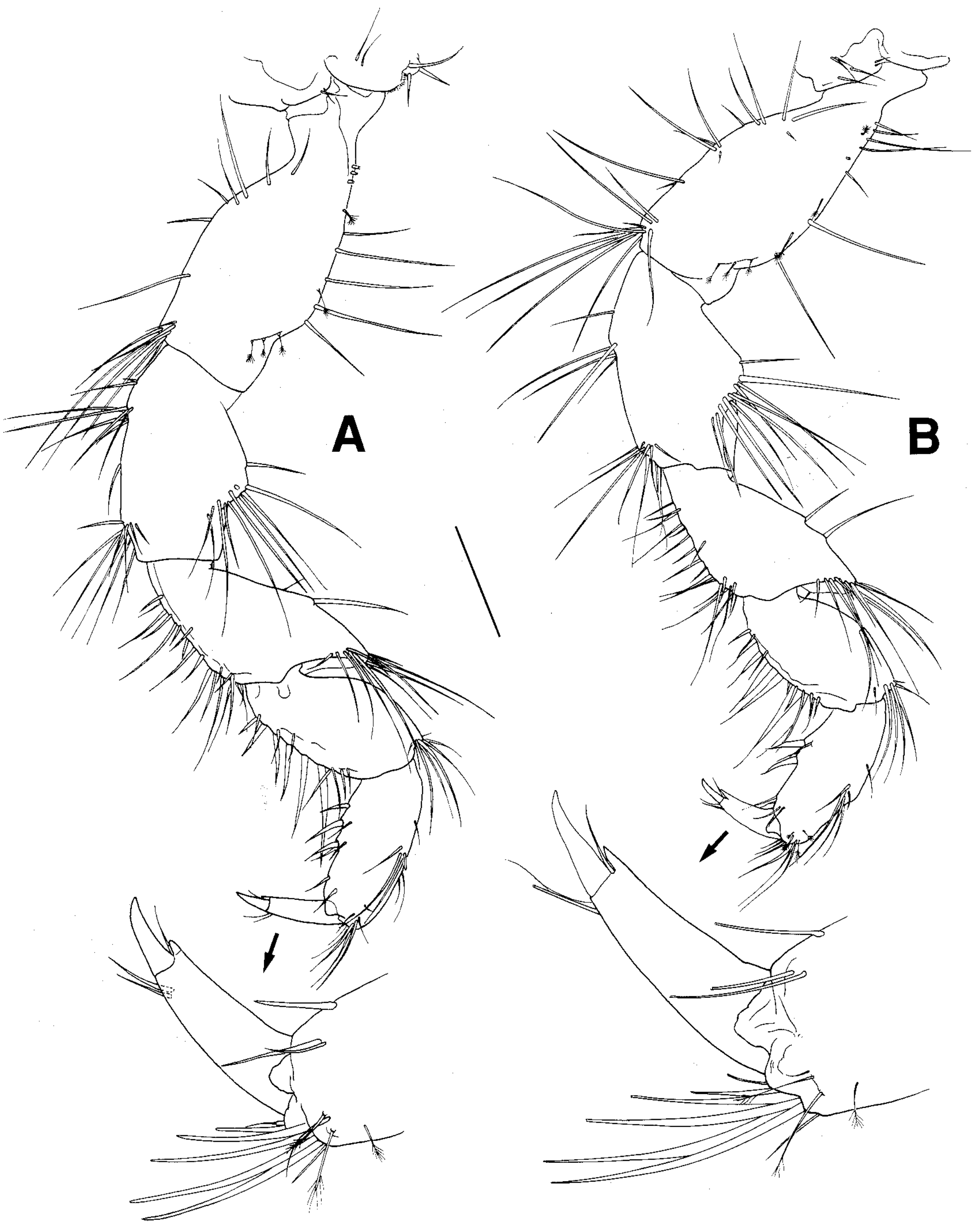

Fig. 12. *Crenoicus buntiae* n.sp. anterior pereopods. P44349, adult male, bl 10.8 mm. A, B, pereopods II–III, lateral view. Scale bar 0.4 mm.

curved setae and distal cuticular fringe; fringe length 0.14 total protopod length in male, 0.20 in female; dactylar distal tip with one large dorsal claw and 1–2 small accessory setae ventrally. Propodus length 0.24 pereopod length in adult male, 0.20 in female; length 1.0 width in adult male, 1.3 in female, dorsal margin protruding more in male. Propodus dorsal margin in male broadly rounded with proximally protruding section; in female, dorsal margin smoothly curving, not expanded proximally. Propodal palm without elongate spines or projections in both sexes. Propodal palm in male convex with 10–12 stout setae, 4 keratinised tooth-like setae on low humps and fringe of fine setae lateral to stout setae extending from dactylar insertion to ventral angle of palm. Propodal palm in female concave with 12–13 stout setae, no keratinised tooth-like setae and fringe of fine setae lateral to stout setae extending only half length of propodal palm. Basis length 2.5 width in males, 2.5

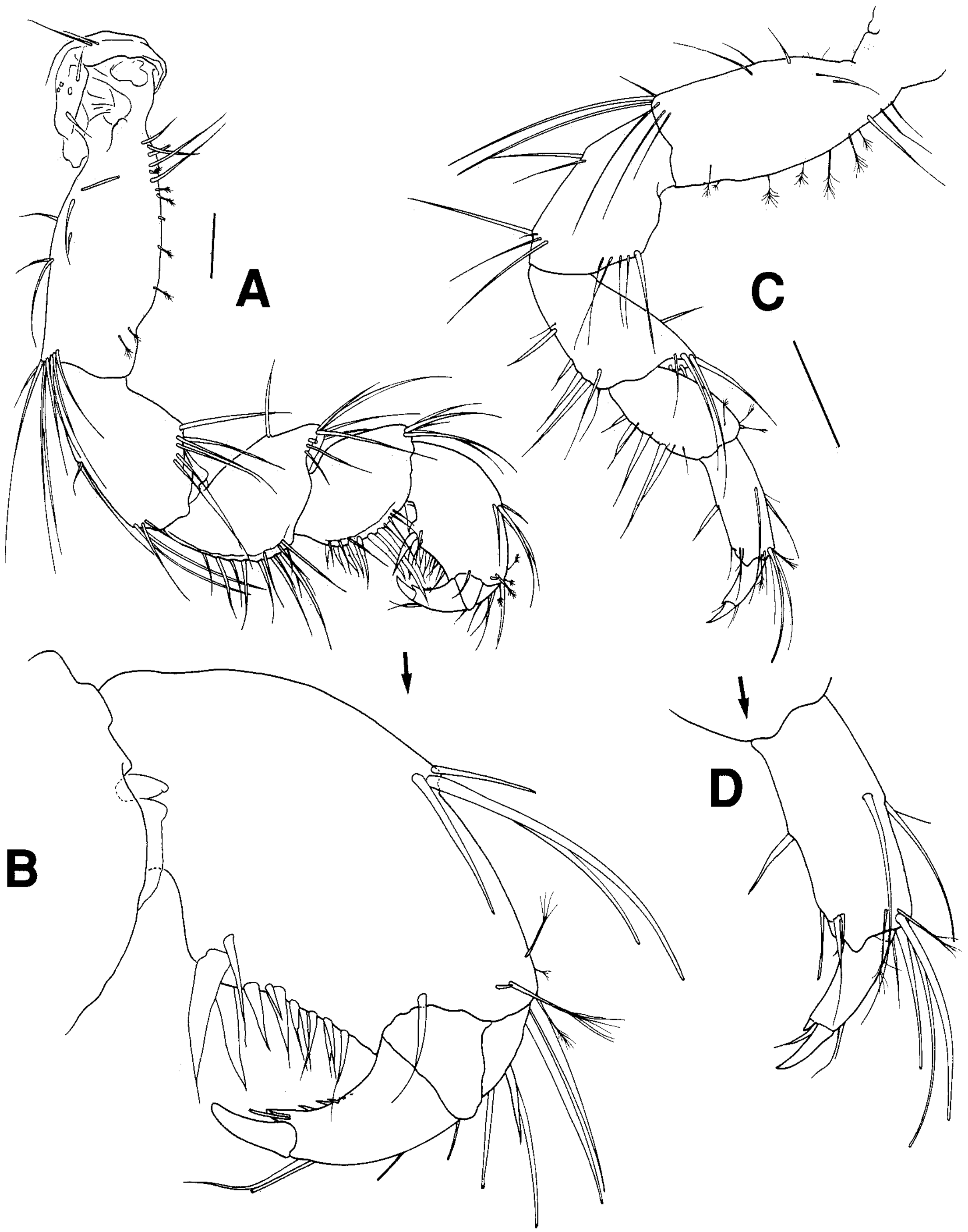

Fig. 13. *Crenoicus buntiae* n.sp. pereopods IV, with enlargements of dactylus and propodus, lateral view. A, B, AM P44349, adult male, bl 10.8 mm. C, D, P44351, preparatory female, bl 8.5 mm. Scale bar 0.2 mm.

in females; dorsal margin with 2–4 elongate setae positioned proximally; ventrodistal margin with group of 4–7 elongate setae distinctly shorter than ischium.

Pereopod II, III (Fig. 12). Length 0.32, 0.32 body length. Basis length 0.29, 0.30 pereopod II, III length; length-width ratio 2.5, 2.3; dorsal ridge with 7–9 large simple setae and scattered penicillate setae. Carpus 0.13, 0.13 pereopod length; length-width ratio 1.5, 1.5; margin with 6, 6 broad based setae. Propodus length 0.14, 0.14 pereopod length; length 2.1, 2.1 width; articular plate present on distolateral margin; ventral margin with 2–3, 2 broad based setae. Dactyli distal tip with ventral spine adjacent to claw.

Pereopod IV (Fig. 13). Sexually dimorphic, male pereopod IV subchelate with major hinges dactylus-propodus and propodus-carpus. Length 0.28 body length in male, 0.20 in female. Penicillate setae in male on dorsal margin of basis and anterodorsal margins of

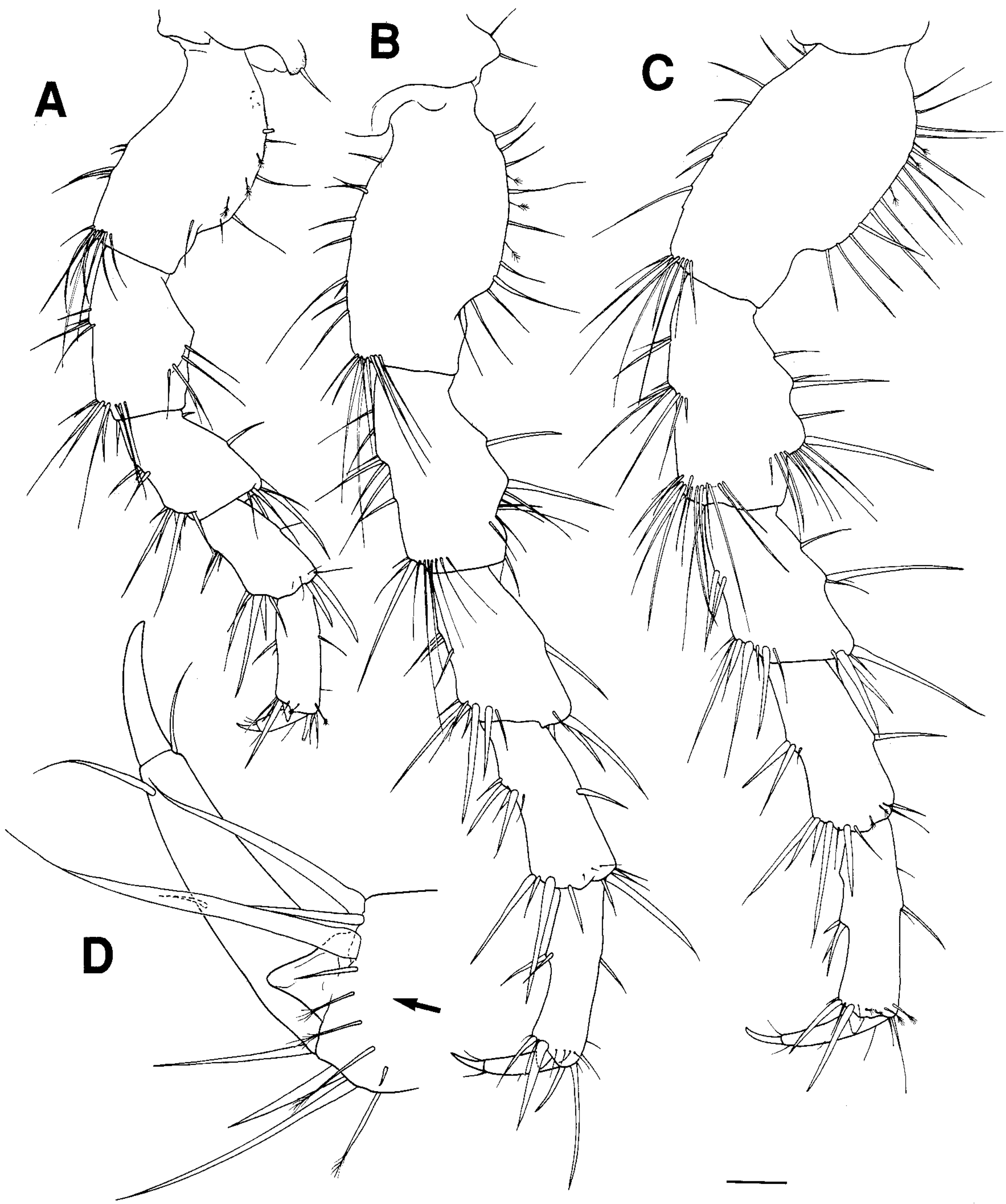

Fig. 14. *Crenoicus buntiae* n.sp. posterior pereopods. P44349, adult male, bl 10.8 mm. A–C, pereopods V-VII, lateral view. Scale bar 0.2 mm.

propodus, in female on dorsal margin of basis and anterodorsal margins of carpus and propodus. Dactylus in male subequal to propodal palm, with distal accessory spines in both sexes approximately one third length of primary claw in male, one fourth in female. Propodus length 0.14 pereopod length in male, 0.13 in female; articular plate present on posterior side of limb, length subequal to dactylar claw in male, shorter in female; approximately 9 broad based setae on ventral margin in male, two distinctly larger than others; female with only 1 broad based setae on ventral margin. Carpus length 0.13 pereopod length in male, 0.12 in female; approximately 7 broad based setae on ventral margin in male, 4 in female. Basis length 2.8 width in males, 2.6 in females; dorsal ridge rounded in cross section, with 3–5 setae positioned proximally.

Pereopods V, VI, VII (Fig. 14). Length 0.25, 0.34, 0.36 body length. Penicillate setae present on dorsal

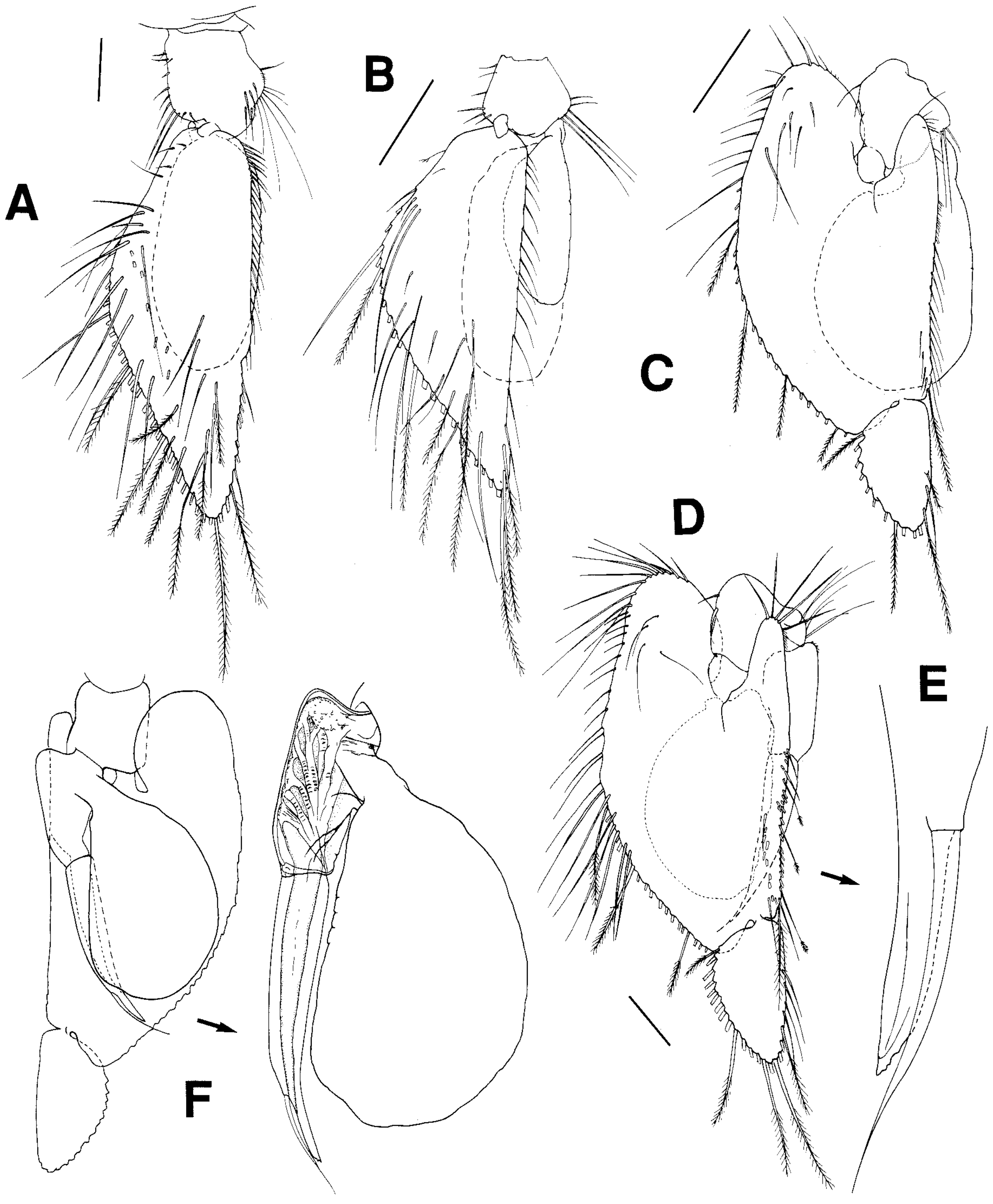

Fig. 15. *Crenoicus buntiae* n.sp. pleopods I–II. A, C–F, P44349, adult male, bl 10.8 mm. C, D, P44351, preparatory female, bl 8.5 mm. A, B, pleopod I, ventral view. C, D, pleopods II, ventral view. E, pleopod II endopod distal tip, ventral view. F, pleopod II, dorsal view with enlargement of endopod. Scale bar 0.2 mm.

ridge of basis, dorsodistal carpus, dorsodistal propodus. Dactylar claw length 0.38, 0.33, 0.30 dactylar length, distal accessory spines absent. Propodus length 0.14, 0.16, 0.16 pereopod length, articular plate on posterior side of limb present; distal margins with 2–4 elongate robust setae. Carpus length 0.14, 0.16, 0.16 pereopod length. Basis length 1.8, 1.6, 1.7 width; dorsal ridge not distinctly separated from basis shaft, in cross section rounded, with approximately 5, 10, 15 setae positioned along ridge.

Penes (Fig. 7C–D) strongly curved posteriorly, length 0.4 body width at pereonite 7, extending past midline and onto pleonite 1, shaft smooth, without setae, tapering, distally rounded.

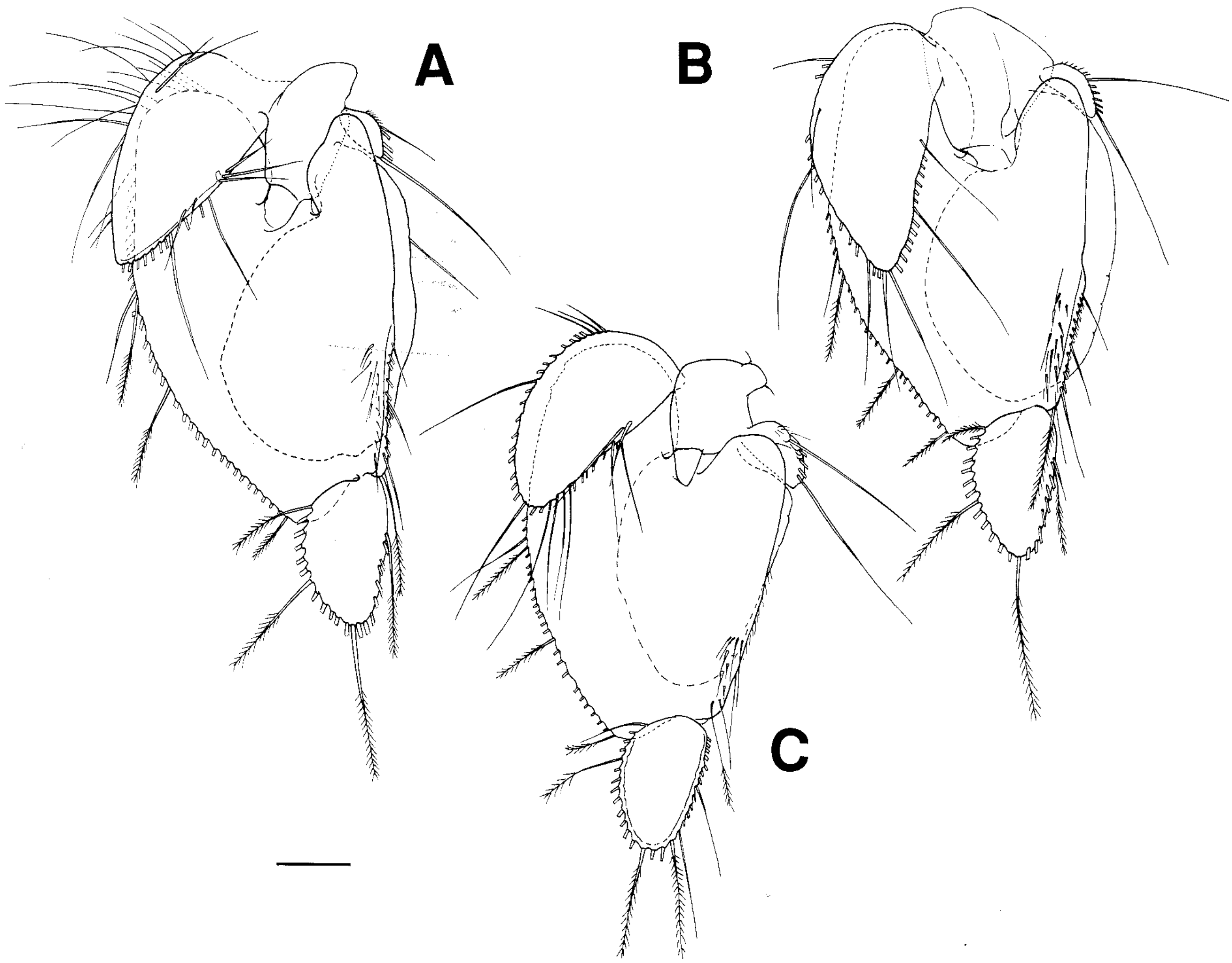

Fig. 16. *Crenoicus buntiae* n.sp. posterior pleopods. P44349, adult male, bl 10.8 mm. A–C, pleopods III–V, ventral view. Scale bar 0.2 mm.

Pleopods I–V (Figs 7C, 15, 16). Pleopods I–V lengths 0.15, 0.15, 0.15, 0.14, 0.13 body length in male; pleopods I–III lengths 0.11, 0.12, 0.10 body length in female. Exopods I–V length 2.6–2.7, 1.8–2.2, 1.5–1.7, 1.6, 1.6 width; exopod I uniarticulate; exopods II–V biarticulate, distal articles II–V length 0.36 [n = 2], 0.33–0.35, 0.37, 0.34 exopod length; exopod I with no lateral proximal lobes, exopods II–V with medial and lateral proximal lobes. Endopods I–V unilobed; length 2.4, 1.6–1.8, 1.6–1.8, 1.8, 1.4 width; length 0.59, 0.58–0.62, 0.69–0.54, 0.79, 0.60 exopod length; marginal setae absent. Protopods II–V with medial epipods, protopods III–V with lateral epipods. Pleopod I exopod in both sexes broadest at mid length, distally pointed, laterally broadly angular. Pleopod II endopodal appendix masculina (stylet) of male weakly curved, basal musculature pronounced; distal tip spatulate with 1 distal seta, length 0.38 pleopod II length.

Uropod (Fig. 7E–G). Total length 1.2 pleotelson length. Protopod length 0.32 width, length 0.47 uropod length; dorsomedial ridge not produced, dorsomedial ridge setae present, dorsolateral margin setae present, 1 robust distally spinose setae on distoventral margin. Rami distal tips pointed and entire (terminal setae absent), cross-sectional shape round; endopod subequal to protopod length, with no robust setae on dorsal margin; exopod 0.76 endopod length, exopod with 1 robust seta on dorsal margin.

Remarks. *Crenoicus buntiae* differs from *C. harrisoni* (see diagnosis for details) in the form of the mature male pereopod IV, with *C. buntiae* having a more typical limb (compare Figs. 4C,D and 13A,B). The second pleopod endopod also differs in males, and the maxillipedal epipod is also useful for identifying females or juveniles. The maxillipedal and pereopod IV setation can be used to separate *C. buntiae* from the Victorian species, with *C. mixtus* having many more setae on the pereopod IV ischium and *C. shephardi* having an obtusely pointed maxillipedal epipod. Certainty in identifying species of *Crenoicus* requires the inspection of adult males.

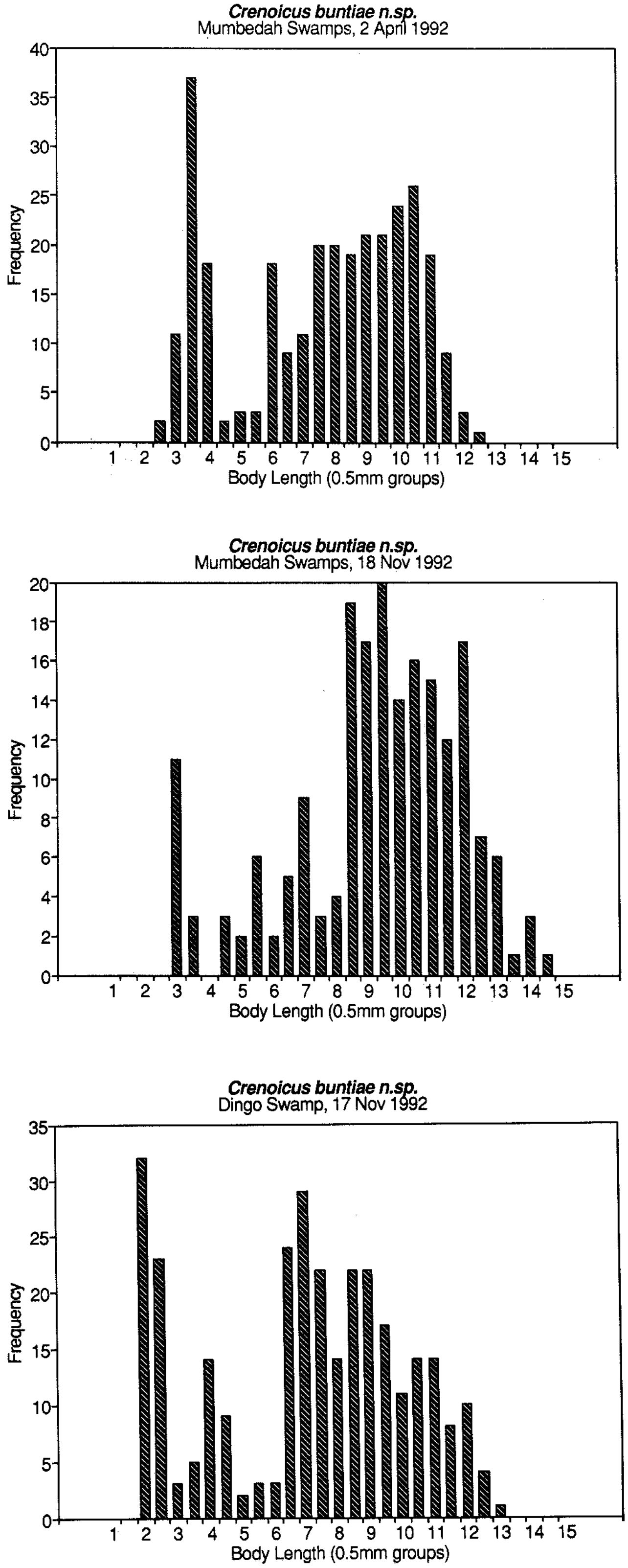

Fig. 17. *Crenoicus buntiae* n.sp. body length frequency classes.

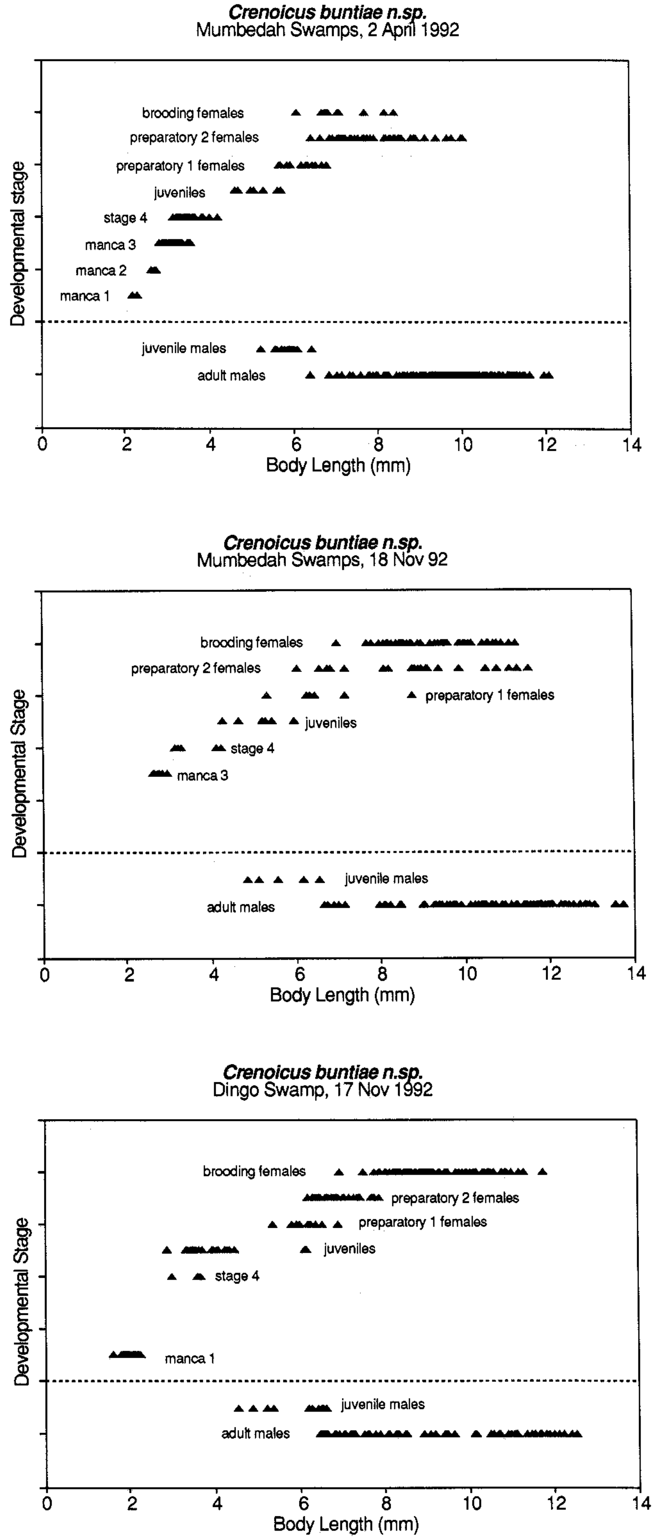

Fig. 18. *Crenoicus buntiae* n.sp. size range of developmental stages.

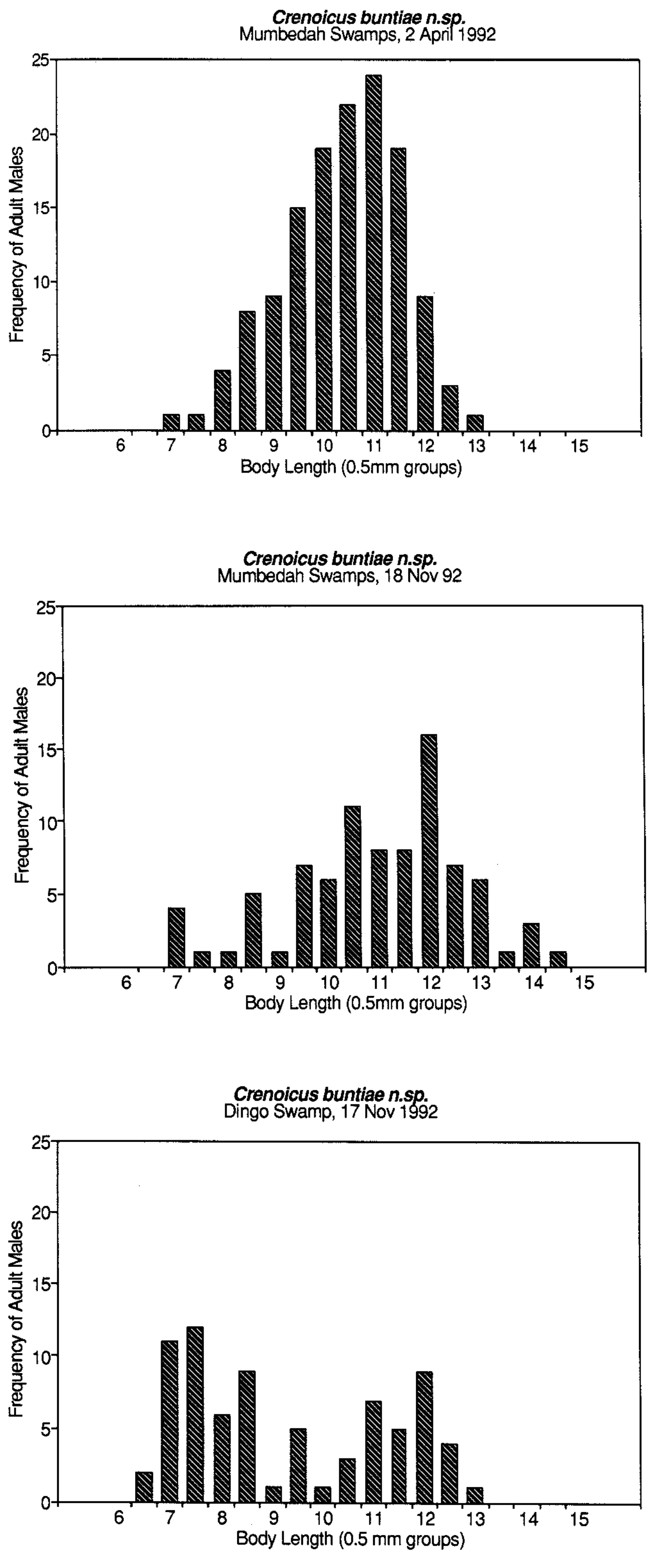

Fig. 19. *Crenoicus buntiae* n.sp. body length frequency classes of adult males.

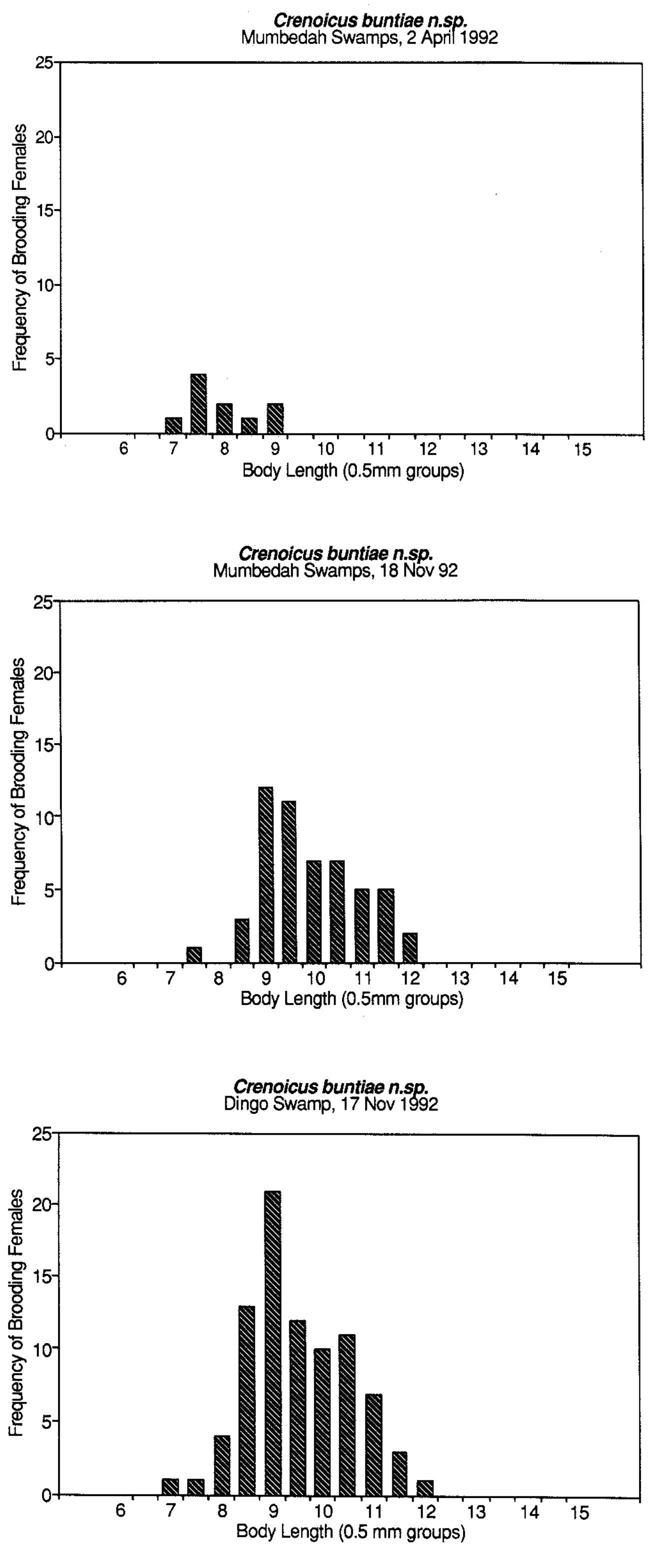

Fig. 20. *Crenoicus buntiae* n.sp. body length frequency classes of brooding females.

Small scale geographic variation. The description given above for *Crenoicus buntiae* n.sp. applies primarily to the populations found at Mumbedah Swamps, and is accurate for most non-cavernicolous specimens found on the Boyd Plateau. The description was taken from the holotype and paratypes that were dissected (see P numbers and figure captions). Populations on the Boyd Plateau can vary geographically in the relative proportions of particular characters. Although we have not made an exhaustive study of variation, some features differed among the sites (see Material Examined above). Populations at nearby localities (Belarah Swamp and Luther's Creek) showed the same variation seen at Mumbedah Swamps, and are not mentioned further.

The illustrated types lacked a robust seta positioned midlength on uropodal endopod (compare Figs 4G [identical to condition in *C. buntiae*] with 7G), while other mature specimens of the Mumbedah population had approximately equal numbers with and without this seta. Those with the seta varied in setal size, without regard to body size. All specimens at Roly Whalen Swamp and most specimens at "Oldmeadow Swamp" had a seta on the uropodal endopod. At Jensen's Swamp, on the other hand, few specimens had a stout seta on the endopod. Assuming that this variation is not an environmental phenotypic response, these data suggest that the populations at Jensen's Swamp and Roly Whalen Swamp may not intermix. This lack of mixing is surprising because the two populations are separated by only a low hill and less than a kilometre.

The propodal palm of pereopod II in adult specimens from Mumbedah Swamps had only 4 setae with a distinct gap between the distal two setae (Fig. 12A). A few specimens at this locality, however, had 5 setae at this position. At Dingo Swamp, many specimens had a pereopod II palm that lacked a gap and had 5 setae. Other sites showed mixtures of this situation. Five or 6 setae on the palm with no gap is a feature that is characteristic of *C. harrisoni*.

The propodal palm of the male pereopod IV varied in shape and position of 3 proximal broad-based setae (Fig. 13B). Most specimens at Mumbedah Swamps had these three setae in a row that was approximately parallel to the axis of the palm. In many specimens at Dingo Swamp, this row of three setae was rotated at an angle to the axis of the palm and the cuticle bearing the setae projected distinctly from the line of the palm. A reinspection of the Mumbedah Swamps population showed that a few adult males also had this condition. Males at Jensen's Swamp lacked this projecting condition, while some males at Roly Whalen Swamp had the three broad-based setal row at nearly a 90° angle to the axis of the palm.

Council Creek population. Most localities on the Boyd Plateau had specimens that attained maximum sizes of 12–14 mm in November, 1992. The largest size in April 1992 was smaller (maximum just over 12 mm), and less of the population was fully mature. The specimens collected in November 1992 near Council Creek (P44481, NSW 487, N = 136), however, were fully mature and copulatory with a maximum size of 10.1 mm (10 fully mature males observed). At the smallest sizes, manca 1 individuals had a median body length of 1.75 mm (N = 4, range 1.72–1.75 mm), which is distinctly smaller than other sites (Mumbedah Swamps, NSW 758, md bl = 2.2 mm, N = 2; Dingo Swamp, NSW 480, md bl = 1.99 mm, N = 55). The merus of the male pereopod IV was also longer than the propodus, whilst in other Boyd Plateau localities, the merus was subequal to the propodus. Other features showed variation similar to the Mumbedah Swamps population. Because the water flow from the *Sphagnum* swamp into Council Creek was small and near the main road, this population could be under more stress than sites within Kanangra-Boyd National Park. Alternatively, the Council Creek swamp is more isolated from the Park sites, so genetic differentiation may have taken place. We cannot distinguish these (or other) possibilities from a single sample.

Discussion. These observations suggest that significant small scale variation exists in the populations of *Crenoicus buntiae* n.sp. on the Boyd Plateau. Our survey shows that localised morphological differentiation may take place on an extremely small scale, e.g., over the distance separating Jensen's Swamp from Roly Whalen Swamp—less than a kilometre. We cannot assign any taxonomic status to these variants because each form is found in most populations in varying frequencies. Indeed, we are uncertain of conspecific status of the populations other than those that occur in Mumbedah Swamps. Whether the variation, especially that seen near Council Creek, is phenotypic or genotypic will require a more detailed morphometric and genetic survey of these populations.

Microhabitat. *Crenoicus buntiae* n.sp. and other species of *Crenoicus* are most commonly found in *Sphagnum* swamps, but not in an evenly dispersed fashion. The basal part of the *Sphagnum* must be submerged in clear flowing water, presumably ground water emerging at the surface. Most swamps with phreatoicids were the headwaters of streams flowing away from the highlands. *Sphagnum* without flowing water typically lacked any specimens. The green part of the *Sphagnum* moss exposed at the surface typically lacks phreatoicideans, while the subsurface pigmentless or brown decaying parts of the fronds will have specimens. Roots of other plants that may be mixed into the moss, such as sedges and *Myriophyllum*, may also provide a good substrate for the animals. Occasionally mounds of *Sphagnum* along slow flowing brooks or the edge of larger streams will have good assemblages on their interior, at or below the water line. Rarely, small numbers of other species have been found amongst the roots of grass along the margin of larger streams (e.g., above the falls on Guy Fawkes River, NSW). These collections were made after heavy rains, suggesting that the animals may have been washed from larger upstream populations.

Population Biology

Three samples of *Crenoicus buntiae* n.sp. were classified to life stages and measured for body length, head length and pleotelson length. The sites were Mumbedah Swamps (2 samples: NSW 758, 2 April 1992, N = 298; NSW 485, 18 November 1992, N = 196) and Dingo Swamp (NSW 480, 17 November 1992, N = 306) which are separated by a distance of 10.6 km and are part of different drainages (Cox River and Kowmung River, respectively). The results for all three samples are shown in Fig. 17 (length frequency, entire samples), Fig. 18 (the distribution of life stages), Fig. 19 (length frequency, adult males), and Fig. 20 (length frequency, brooding females). The body length data allow preliminary observations on the population biology of *Crenoicus buntiae* n.sp.

Life stages. Young are released from the brood pouch at body lengths between 1.8–2.2 mm and start differentiating into males and females at lengths between 4–6 mm. Maturity may be attained around 6–7 mm, and adults may reach lengths greater than 14 mm in the males, or 12 mm in females. Sex-related differences in sizes are consistently seen in species exhibiting mate guarding, precopula in this case (Ridley, 1983; Veuille, 1980; Wilson, 1991). Although not included in the measurement series, the largest brooding female observed (12.1 mm) was collected near Luther's Creek in sample number NSW 486 (P44480) and whose brood pouch contained nearly full term embryos. From the great disparity in the sizes of the adults and the earliest size of reproduction, we conclude that the females are probably iteroparous.

Timing of Reproduction. Brooding females were observed at all sites and times during this study. Males holding females in precopula were observed whenever *Crenoicus* species were collected. Moreover, distinct and narrow size modes of body lengths, which would indicate synchronised pulses of reproduction, do not appear in the data. This species, therefore, appears to reproduce asynchronously throughout the year.

The quantities of adults and young, however, varied in the samples, indicating that the frequency of reproduction may vary on a seasonal basis. The autumn sample (April 1992) had few brooding females of the smaller sizes only, while the spring samples (November 1992) had a broader range of brooding females (Fig. 20). Thus, the rate of reproduction appears to drop off during autumn, while in the spring more animals become fully reproductive. A decided gap also appears in the distribution of the mancas in both spring samples (November 1992), while the autumn sample (April 1992) had all sizes of mancas and juveniles. These data suggest that few young are released during the winter, but recruitment to the population takes place more or less continuously during the warm season.

The two spring samples are not identical in their distributions of mancas (Fig. 18): Mumbedah Swamps had no manca 1–2 stages, while Dingo Swamp has no manca 2–3 stages, but has numerous manca 1 stages. Moreover, Dingo Swamp had a distinct mode of young males, while Mumbedah Swamps were deficient in the smaller sized males (Fig. 19). The two sites thus appear to be out of synchrony with each other during the spring season.

Influences on reproduction. We suspect that these populations of *Crenoicus buntiae* n.sp. are not food limited because they live amongst their locally abundant food source (decaying vegetation). Moreover, asynchronous reproduction both within and between sites indicates that the populations are not cuing their reproduction to any specific environmental parameter, such as day length or rainfall. Nevertheless, we observe strong reproduction during the warm season, with hiatuses in recruitment during the winter. Thus, reproduction and recruitment in this species could be controlled by environmental temperature as a simple rate process. More data on populations and environmental parameters are needed before this can be shown with any certainty. Our preliminary data do not sample the entire seasonal cycle at several sites.

Summary

Although only four species of *Crenoicus* are now described, this genus will be found to be much more diverse when populations are investigated throughout its range. This study of *C. buntiae* demonstrates that phreatoicidean species may exhibit much morphological variation. The population biology of *C. buntiae* indicates that this species might breed year round, but with a peak of reproduction during the warmer part of the year and a hiatus during the winter.

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