

New genus and two new species of driftwood hoppers (Crustacea, Amphipoda, Talitridae) from northeast Atlantic and Mediterranean coastal regions

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Abstract

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A new specialist driftwood talitrid from the Swale, U.K., is figured and described as *Neotenorchestia kenwildishi* gen. n., sp. n. A further new driftwood talitrid, *Macarorchestia pavesiae* sp. n., is figured and described from coastal regions in the Adriatic Sea. *Orchestia microphthalma* Amanieu & Salvat, 1963 from the Atlantic coast of France is re-designated as *Macarorchestia microphthalma* (Amanieu & Salvat, 1963). A key is provided for the known species of driftwood talitrids in northeastern Atlantic and Mediterranean coastal regions.

Key Words

Neotenorchestia kenwildishi gen. n., sp. n.
Macarorchestia pavesiae sp. n.
Macarorchestia microphthalma (Amanieu & Salvat, 1963) comb. n.

Introduction

Driftwood specialist hoppers are a rare, difficult to find, ecological group of Talitridae which are virtually confined to rotting driftwood where they live in galleries, consuming rotting driftwood and reproducing with relatively small broods (1 to 19 ova per brood in the *Macarorchestia* so far described). The ova are incubated in the brood pouch formed by the oostegites on pereopod segments 2 through 5 and hatch as juvenile forms. Because talitrids have no larval stage their dispersal, particularly to distant oceanic islands, was seen as problematic. The general view was that some form of passive rafting dispersal was involved (Wildish 1988). In the lineal “island” theory (Wildish 2012) this view was focussed and the hypothesis proposed that driftwood hoppers, with near-permanent residence in driftwood, were important agents of long distance dispersal for talitrids, particularly to distant oceanic islands. Circumstantial evidence

supporting the lineal “island” theory was presented in Wildish (2012), showing that driftwood talitrids reached the northeast Atlantic islands on driftwood transports. After reaching the remote, recently-formed, volcanic islands they evolved further there into terrestrial or cavernicolous forms if sub-tropical rain forest or seashore caves were contiguous habitats with the supralittoral and also lacked a talitrid fauna. Alternatively driftwood specialists remained in place in their primary ecotope as supralittoral, driftwood hoppers if the supply of driftwood habitat was plentifully available.

Currently known driftwood taxa (Wildish et al. 2012) comprise 5 species presently grouped in 2 genera from the Mediterranean and northeast Atlantic (*Macarorchestia* and *Orchestia*), with another genus (*Platorchestia*) reported from the west coast of North America by Bousfield (1982). The preponderance of driftwood hoppers in the northeast Atlantic/Mediterranean coastal areas is suggested to be the result of more intensive sampling there.

Other geographic areas and particularly the southern hemisphere, where no driftwood hoppers have yet been found, have not been sampled intensively enough to conclude that they are without driftwood talitrid specialists.

As a result of molecular studies of *Macarorchestia remyi* it was suggested that two genetically distinguishable forms: one centred in the Tyrrhenian and the other in the Adriatic Sea were present (Pavesi et al. 2011). This result was confirmed with further relative growth studies (Wildish et al. 2012) and a new species referable to *Macarorchestia* is described herein. Molecular and relative growth studies (Wildish et al. 2012; Pavesi et al. 2014) determined the taxonomic identity of an unknown talitrid taxon found in a driftwood log which stranded in the Swale, U.K., and found morphological evidence supporting a generic level change in nomenclature for *Orchestia microphthalmia* Amanieu & Salvat, 1963. A formal presentation of the taxonomic changes outlined above is provided with a key for the currently known driftwood species from the Mediterranean and northeast Atlantic coastal region.

Material and methods

Slides were prepared as temporary mounts without staining and after dissecting mouthparts and limbs. Some were prepared as permanent mounts by Sara LeCroy, after staining with lignin pink and permanently mounted in CMCP-10 (Master's Company, Inc.).

Photographs of limb parts were made with a Carl Zeiss photomicroscope and digital Canon 990 camera. Adobe Photoshop (version 7.0), Illustrator (version 11.0) and a Wacom tablet were used to draw limb parts and prepare plates, essentially as outlined in Coleman (2003, 2006). Antenna, mouth and limb part abbreviations used throughout are: A1 = first antenna, A2 = second antenna, LL = lower lip (labium), UL = upper lip (labrum), RMnd = right mandible, LMnd = left mandible, Mx1 = first maxilla, Mx2 = second maxilla, Mxpd = maxilliped, Gn1 = first gnathopod, Gn2 = second gnathopod, P3 to P7 = peraeopods 3 through 7, P11 to P13 = pleopods 1 through 3, Up1 to Up3 = uropods 1 through 3, and T = telson. Body length was measured accurately from digital photographs of each individual pinned in a dissecting dish. The total body length (TBL) was measured from the most anterior part of the cephalon to the telson tip, on digital photographs with the aid of Image Pro Plus software. Limb ratios were calculated as P13/TBL, in units of mm.

Systematics

Genus Macarorchestia Stock, 1989

Stock 1989: 1109; Ruffo 1993: 738.

Type species. *M. martini* Stock, 1989

Component species. Currently includes five species: *M. martini*, *M. roffensis*, *M. remyi*, *M. pavesiae* sp. n., *M. microphthalmia* (Amanieu & Salvat, 1963) new comb.

Diagnosis. As in Stock (1989) except that the lacinia mobilis of the left mandible is 4 - 5 -dentate. The propodus of the seventh peraeopod carries distinctive tufts of long, slender setae, which are sexually dimorphic. The first antenna with up to 5 articles (versus 3 in Stock). The pleopods are biramous with a basis which is not reduced, but both rami are variously reduced dependant on the total body length of the largest adults of the species. Thus in the smallest species, *martini*, there is no segmentation in the rami and 1-3 plumose setae and in the largest, *microphthalmia*, there up to 5 segments and 11 plumose setae. The pleopod rami may be sexually dimorphic, as in male *M. remyi*, and the second antennal flagellum articles are sexually dimorphic in female *M. pavesiae* sp. n. In addition all species are small, that is to say < 15 mm in total body length and lack epidermal pigment patterns.

Macarorchestia martini Stock, 1989

Stock 1989: 1109.

Material examined. Male holotype and 8 females (allotype and paratypes) on loan from Zoological Museum of Amsterdam, Amsterdam, the Netherlands (AMPH. 108.57). Collected by J. Stock on 2 August, 1987 from Gruta das Agulhas in Porto Judeus on the island of Terceira, Azores archipelago.

Distribution. Known only from the type locality on the island of Terceira.

Epidermal pigment patterns. Not mentioned by Stock (1989).

Remarks. This is the type species and smallest *Macarorchestia*. Stock (1989) was equivocal about whether this was a recent troglobiont specialist or troglomenous form. I concur with the latter view and believe that the adaptations (small body length, body length greater in the female, small eyes, reduced pleopod rami and shortened length of the first 5 peraeopods) indicate that *M. martini* is a driftwood specialist.

Macarorchestia roffensis (Wildish, 1969)

Wildish 1969: 288; Lincoln 1979: 212; Wildish 1987: 571, as *Orchestia remyi roffensis* or *O. roffensis*; Ruffo 1993: 739.

Material examined. Male holotype (BMNH 1968:64), one female allotype (BMNH 1968:65) and 416 paratypes of all life history stages (BMNH 1968:66). Collected by D.J. Wildish (DJW) in August 1968, 0.2 km upstream from

Chatham Ness in Limehouse Reach, Medway estuary, near Rochester, Kent, U.K.

Distribution. Besides the type locality one other locality in the Medway estuary was found in 1968 with a few specimens in a driftwood log by DJW. The location was ~ 0.6 km upstream from the old Rochester Bridge in Tower Reach on the eastern shore. A few specimens collected by DJW in 1999 from the Swale, in Ferry Reach ~ 0.5 Km northwest of Kingsferry Bridge on the mainland shore.

Epidermal pigment patterns. Absent.

Remarks. This is the second smallest *Macarorchestia*. The type locality was destroyed during reclamation of Frindsbury marsh as an industrial estate.

Macarorchestia remyi (Schellenberg, 1950)

Schellenberg 1950: 325; Ruffo 1993: 739.

Material examined. Two males, 4 females, 1 juvenile (Crust. 25468) ZMB Museum für Naturkunde, Berlin. Collected by A. Schellenberg from a seashore cave at St. Barthelemy, Corisca. A total of 47 individuals (combined sample) of all life history stages, including females with ova, collected by L. Pavesi on 20 January and 15 April 2007 at Principina a Mare, Tyrrhenian Sea, Italy. Sample location co-ordinates: 42°41'18"N, 10°59'53"E. A further sample collected at Principina a Mare by L. Pavesi on 24 April 2011 consisted of 28 individuals of all life history stages, including females with ova. One individual from Corfù Island (Ionian Sea, Greece) collected by L. Pavesi in 2007 (Destructively used in DNA analysis).

Distribution. Besides the locations found by L. Pavesi for this species, published records include that of Ruffo (1960) in Sardinia and Ruffo (1993) in France, Greece and Italy. Possibly some of these records refer to the species described below.

Epidermal pigment patterns. Absent.

Remarks. This is the second largest *Macarorchestia*. In recent times the type locality has been destroyed by cleaning beaches for the benefit of tourists (L. Pavesi, pers. comm.).

Macarorchestia pavesiae sp. n.

<http://zoobank.org/42B57D1C-E898-408E-AA2F-0F7A27915691>

Pavesi et al. 2011: 220; Wildish et al. 2012: 2678, as *M. remyi*.

Type material. Holotype male of 8.0 mm TBL (NHMUK 2014. 408) and allotype female of 7.5 mm (NHMUK 2014. 409) collected by L. Pavesi on 31 October, 2006 at Lesina, Adriatic Sea, Italy. 13 paratypes collected on the same date (NHMUK 2014. 410 - 419). Paratypes have also been de-

posited in the Natural History Museum, Verona and Museum at Rome University, Rome, Italy by L. Pavesi.

Type locality. Lesina, Adriatic Sea, Italy (41°54'11"N, 15°26'50"E).

Other material examined. 17 individuals collected by L. Pavesi in April 2006 at Varano, Adriatic Sea, Italy (41°55'12"N, 15°47'29"E).

Diagnosis. *M. pavesiae* sp. n. is distinguished from its close relative, *M. remyi*, by its smaller size, sexually dimorphic second antennal flagellum articles in adult females and absence of sexual dimorphism in pleopod rami.

Description. Based on male paratypes: total body lengths in the range of 8.0 to 6.7 mm. Figs 1 and 2. The male holotype has similar morphology to male paratypes dissected in preparing the figures.

Head deeper than long (1: 0.7); eyes small, round, less than half the head length. Antenna 1 flagellum 5-articulate with tip just exceeding the junction of peduncle segments 4 and 5 of antenna 2. Antenna 2 short, flagellum 12-articulate, peduncle not incrassate.

Mouthparts. Lower lip with lateral lobes, minute setae on the inner clefts. Left mandible with a 4-dentate lacinia mobilis and large molar process. Right mandible with the tip of the dentate incisor bilobed, 6-dentate lacinia mobilis. Maxilla 1 inner plate narrow with 2 terminal plumose setae, inner margin with long, fine setae; outer plate with a palp, apical robust setae curved and serrated on the inner edge. Maxilla 2 both plates equal in size, inner with a single, plumose seta, with shorter robust setae on the distal edge; outer plate with simple robust setae. Maxilliped inner plates with 3 stout teeth apically, inner, outer and palp distal edges covered with robust setae; palp large and 3-articulated.

Peraeon. Gnathopod 1 weakly subchelate with palmate lobes on propodus and carpus; dactylus as long as propodus lobe; the largest robust setae are present on the posterior edge of the merus. Gnathopod 2 subchelate with propodus and dactylus massively enlarged, dactylus drawn out in a short, blunt tip, its inner surface lacking fine setae. Ventral edge of each coxal plate rounded and with fine robust setae. Peraeopods 3 to 5 short, peraeopods 6 and 7 longer, the latter just longer than uropod 1. Peraeopods 3 and 4 lack a dactylus notch ("pinched unguis"). Peraeopods 6 and 7 not sexually dimorphic in merus and carpus. Six distinctive tufts of long, slender setae originating from the propodus of peraeopod 7 as follows: anterodistal (2 setae), distal (6 setae), anterior side of peraeopod near the first insertion of robust, bifid-tipped setae (4 setae), then on the posterior side of the peraeopod: first insertion of robust, bifid-tipped setae (2 setae), second (4 setae) and third (3 setae). The maximum length of the longest seta from the distal tuft was 144 µm (Fig. 3).

Pleosome. Pleopod basis not reduced and with a pair of hooked coupling spines, robust setae and fine marginal setae absent. All rami are shorter than the basis. The second pleopod rami have 3 articles each bearing a pair of long, plumose setae: exopod -7, endopod -5.

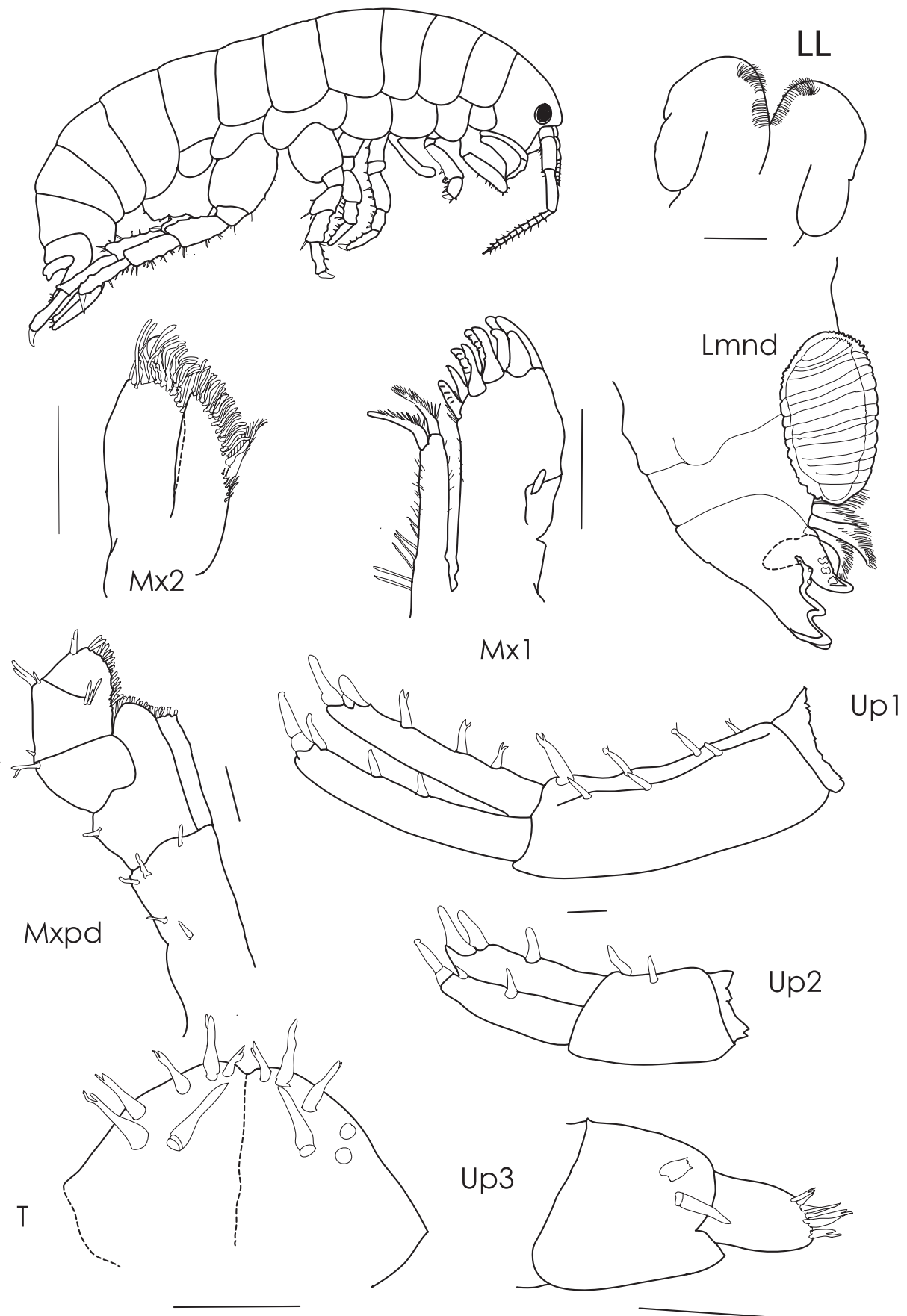


Figure 1. *M. pavesiae* sp. n. Habitus of female allotype total body length (TBL) = 7.5 mm. Mouthparts, telson and uropods from male paratype. Mouthparts, Up3 and telson, scale = 0.1 mm, except Lmnd, Up1 and Up2 = 0.25 mm.

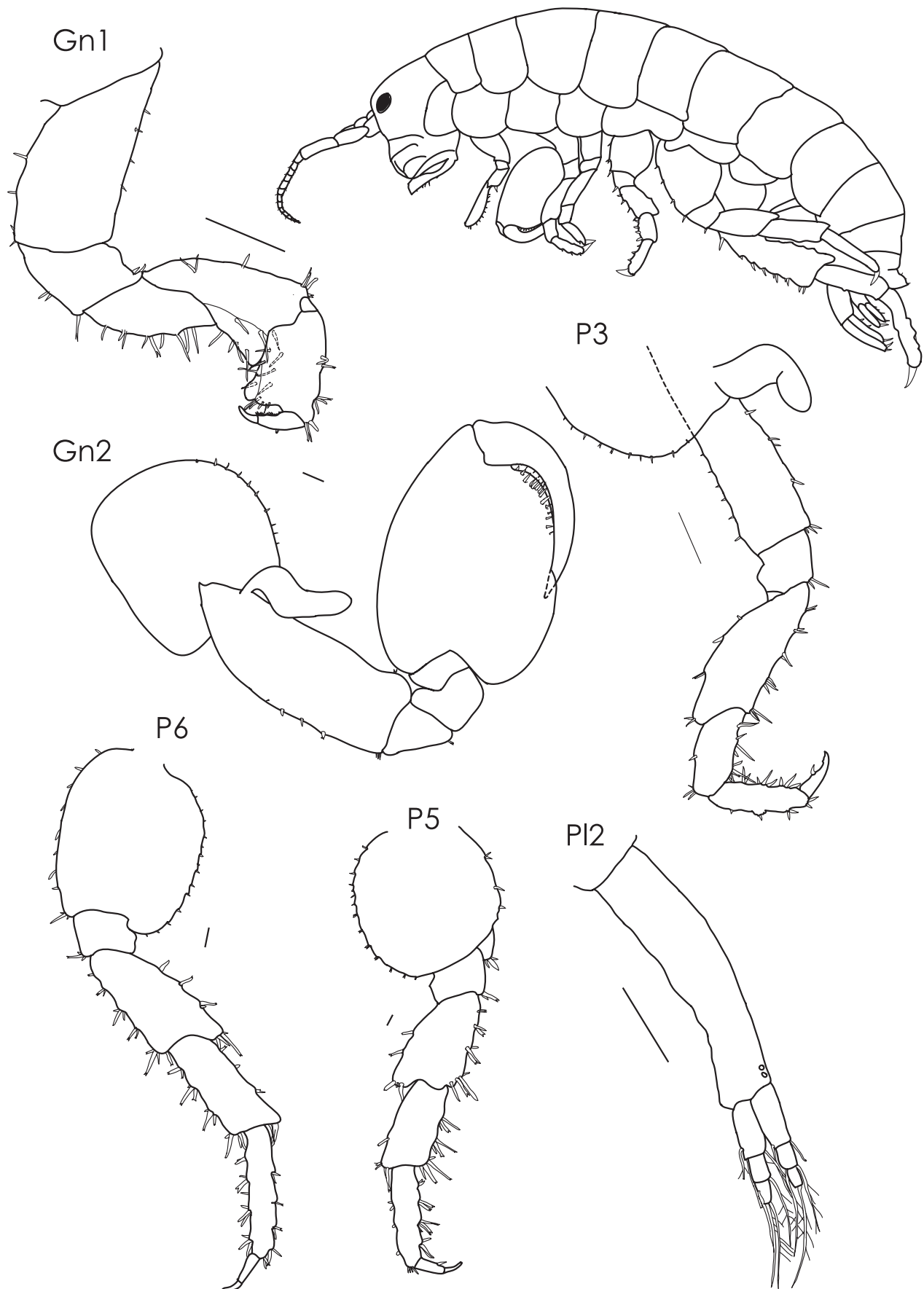


Figure 2. *M. pavesiae* sp. n. habitus of male holotype, TBL = 8.0 mm. Limb parts from male paratype. Scale = 0.25 mm.

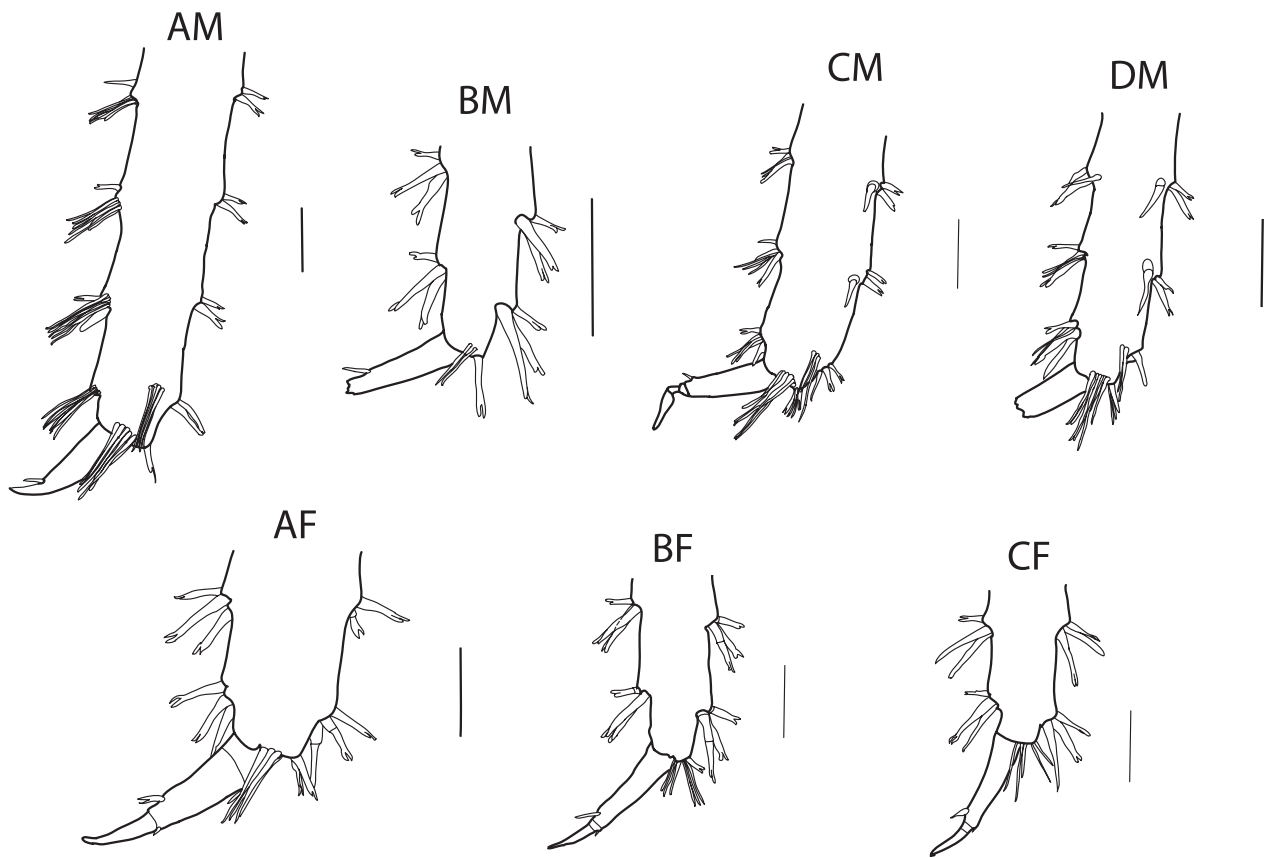


Figure 3. Peraeopod 7 tip (dactylus and part of propodus) in male (M) and female (F) *Macarorchestia*. **A.** *M. microphthalmalma*, **B.** *M. roffensis*, **C.** *M. remyi*, **D.** *M. pavesiae* sp. n. Scale = 0.1 mm.

Urosome. In uropods 1 and 2 the inner and outer rami are of similar length, with 2-4 apical robust setae and 1 or 2 inter-ramal robust setae, basis with 1 or 2 dorso-ventral, robust setae distally. Uropod 3 basis longer than the ramus and with 2 large, robust setae dorso-laterally. Smaller robust setae at the ramus tip but lacks inter-ramal robust setae. Telson with a mid-dorsal groove and 6-7 dorso-lateral robust setae on each lobe.

Sexually dimorphic differences. Based on non-breeding adult female paratype of 7.3 mm total body length.

Gnathopod 1 without palmate lobes on propodus and carpus. Gnathopod 2 basis slender and with weak robust setae. Palmate lobes present on merus, carpus and propodus, dactylus small (described as “miten-shaped” gnathopod 2). Pairs of non-ovigerous oostegites on peraeopods 2 to 5. Adult females greater than 7.5 mm body length with no more than 11 antennal flagellum articles (versus up to 13 in males). The 6 tufts of long, simple setae on the propodus of peraeopod 7 in males compares with 2 tufts, of sparser and shorter length setae in females.

Epidermal pigment patterns. Absent.

Etymology. The name honours Dr. Laura Pavesi who originally discovered and collected the new species during graduate studies at the University of Rome, Italy.

Distribution. There are three known locations for this species on the shores of the Adriatic Sea and one on Corfú Island, Ionian Sea.

***Macarorchestia microphthalmalma* (Amanieu & Salvat, 1963), comb. n.**

Amanieu and Salvat 1963: 390; Pavesi et al. 2014, as *Orchestia microphthalmalma*

Material examined. Male holotype (No. 5-1963) and paratypes in the Museum National d’Histoire Naturelle, Paris. Collected in 1962 by Mr. C. Caussanel from Cap Ferret Point near Arcachon on the Atlantic coast of France. Paratypes also in L’Institut de Biologie Marine at Arcachon. Collection by DJW in the type locality on 11th September 1967 and deposited in the Natural History Museum, London (BMNH 1967 10.6.1-75).

Diagnosis. *M. microphthalmalma* is distinguished from *M. remyi* and *M. pavesiae* sp. n., by:

- Sexually dimorphic tufts of long, slender, simple setae from the propodus of peraeopod P7, with no tuft at anterodistal position and 4 tufts on the posterior side of the propodus in males, versus a tuft at anterodistal position and 3 tufts on the posterior side of the propodus in males of *M. remyi* and *M. pavesiae* sp. n. (Fig. 3),

- its larger size, and
- lack of sexual dimorphism in pleopod and second antennal characters. Pleopod sexual dimorphism was discovered by Wildish et al. (2012) in *M. remyi* where males grew at the same rate as juveniles throughout life, whereas females grew at a slower rate. A2 flagellum article sexual dimorphism was present in *M. pavesiae* sp. n., where adult females grew at a slower rate than juveniles and males (Wildish et al. 2012).

Distribution. Known from the type locality and 3 other locations further south on the French Atlantic coast (Lagardere 1966).

Epidermal pigment patterns. Absent.

Remarks The largest species of *Macarorchestia*.

Orchestia Leach, 1814

Leach 1814: 402; Bousfield 1982: 22; Lowry and Fanini 2013: 205.

Type species. *Orchestia gammarellus* (Pallas, 1766).

Component species. Since the erection of *Orchestia* Leach, 1814 the genus has been uncritically used to include many new species from around the World. In more recent times genera have been split off from *Orchestia* including: *Platorchestia* by Bousfield (1982), *Palmorchestia* by Stock and Martin (1988) and *Macarorchestia* by Stock (1989). Bousfield (1982) re-defined the range of *Orchestia*, limiting species to those found in the Atlantic/ Mediterranean region. I have further limited the geographic range of this taxon to the northeast Atlantic, the Mediterranean and Black Seas, but excluding the western Atlantic coastline of North America. The northeast Atlantic islands including: Canary, Madeira and Azore archipelagos are also included in the region. The northerly limit is arbitrarily set at the Arctic Circle (thus including Iceland) and the southern one at the Tropic of Cancer. Circumstantial evidence (Henzler and Ingolfsson 2008) supports the presence of *Orchestia gammarellus* on northwest Atlantic coastlines (as far south as Maine), as a result of recent, post glacial, synanthropic, dispersal from the northeastern shores of the Atlantic.

Taking only *Orchestia* species which occur within this newly defined geographic range and excluding those outside it, synonyms, and where the taxonomic or ecological status is unclear (inclusive of *O. kosswigi* Ruffo, 1949-which is figured and described in Ruffo (1993) but its ecological status remains unclear); *O. guerni* Chevreux, 1889 and *O. gambierensis* Chevreux, 1908), leaving a total of 13 species (Table 1). The placement of these 13 species in five clearly separate habitats is consistent with a polyphyletic origin for them and that we can expect further generic splitting of *Orchestia*. In fact Lowry and Fanini (2013) have recently proposed a revision of the genus *Orchestia* in which all the species belonging to freshwater and terrestrial rain forest leaf litter of the northeast Atlantic islands (columns 3 and 4 in Table 1) were removed to a newly created genus *Cryptorchestia*. *O. kosswigi* is also transferred to the new genus and these authors describe a new species referable to *Orchestia*: *O. xylino* Lowry & Fanini from the Mediterranean Sea. Recent molecular evidence (Pavesi et al. 2014) does not support the close genetic relationship required by Lowry and Fanini's proposal between *cavimana* and the Atlantic islands endemic "*Orchestia*" listed in column 4 of Table 1. One of these taxa, *O. guancha*, was shown to be close genetically to *O. gammarellus*, confirming earlier work by Villacorta et al. (2008). Pavesi et al. (2014) also show that *O. montagui* and *O. stephenseni* are not closely linked genetically to the other species of *Orchestia* inclusive of the type species *O. gammarellus*, plus *O. mediterranea*, *O. aestuarensis* and *O. guancha*. With the transfer of *O. microphthalmia* to *Macarorchestia* herein, this reduces the habitats occupied by "*Orchestia*" to 4. The genetic findings of Pavesi et al. (2014) suggest the polyphyletic status of *Orchestia* and a generic level re-alignment like that shown in Table 2. Further genetic and taxonomic work is needed to include all the species listed in Tables 1 and 2.

Diagnosis. An interim diagnosis is provided based on the type species, *O. gammarellus* from the Medway estuary, U.K., as listed in Table 2. This is because of the demonstration of polyphyly (Pavesi et al. 2014) within the older view of the genus *Orchestia* and because of the resultant taxonomic uncertainty regarding which of the taxa in Table 1 should be included within *Orchestia*. A diagnosis of the 5 genera listed by letter in Table 2 is delayed because the current COI phylogeny (Pavesi et al. 2014) does not include 6 species of "*Orchestia*" (indicated by brackets in

Table 1. Ecological habitats occupied by species of *Orchestia* which are listed in WoRMS Editorial Board (2013) available from: World Register of Marine Species, <http://www.marinespecies.org>, accessed in 2013-06-26, and occurring in the northeast Atlantic (including offshore islands), Mediterranean and Black Sea region.

Marine/estuarine supralittoral wrack	Marine/estuarine eulittoral wrack	Freshwater supralittoral wrack	Terrestrial rain forest leaf litter	Marine driftwood
<i>gammarellus</i>	<i>mediterranea</i>	<i>cavimana</i>	<i>chevreuxi</i>	<i>microphthalmia</i>
<i>stephenseni</i>	<i>aestuarensis</i>	<i>monticola</i>	<i>guancha</i>	
<i>montagui</i>			<i>stocki</i>	
			<i>canariensis</i>	
			<i>gomeri</i>	

Table 2. Ecological habitats and proposed generic groupings of species listed in Table 1, based on the molecular phylogeny (COI) of Pavesi et al. (2014). ? before a species name indicates that the ecological habitat given has not been confirmed. Brackets indicates absence of COI data for that species.

Genus	Marine/estuarine supralittoral wrack	Marine/estuarine eulittoral wrack	Freshwater supralittoral wrack	Terrestrial rain forest leaf litter
<i>Orchestia</i>	<i>gammarellus</i>			
Genus A		<i>mediterranea</i> ?aestuarensis		
Genus B	<i>stephenseni</i> <i>montagui</i> ?(xyline)			
<i>Cryptorchestia</i>			<i>cavimana</i>	
Genus C			?(monticola)	
Genus D				?guancha ?(gomeri) ?(canariensis) ?(stocki)
Genus E				?(chevreuxi)

Table 2). This omission might change the final phylogenetic tree obtained with all species listed in Table 2 included.

Adult total body length up to 22 mm; dorsal pigment patterns present; eyes medium in size, approximately one quarter of head length; antenna 1 flagellum just reaching antenna 2 peduncle of article 4; antenna 2 sexually dimorphic, peduncle slightly incrassate in adult males and without ventral plate on peduncle article 3; upper lip without robust setae; mandible left lacinia mobilis 4 dentate; maxilliped palp 3 articulate, article 2 with well developed medial lobe; gnathopod 1 of male subchelate with palm equal to dactyl, carpus and propodus free and with rounded lobes covered with palmate setae; gnathopod 1 of female parachelate, without lobes on carpus and propodus; gnathopod 2 of male strongly subchelate, merus and carpus free, dactylus with blunted tip and is half the length of the enlarged propodus; gnathopod 2 of female, ovigerous oostegite long and wide with many, long, simple, marginal setae, basis expanded anteriorly; pereopods 3-7 cuspidactylate; pereopods 5-7 lack slender setae lining the anterior margin of the dactyl; pereopod 7 sexually dimorphic, adult males with merus and carpus enlarged; distinctive tufts of long simple setae on propodus of pereopod 7 absent in both sexes; pleon segments 1-3 lacking vertical slits; pleopod rami slightly, or not, reduced; uropods without apical, spade-like robust setae, uropod 1 not sexually dimorphic, peduncle lacking well developed dorsolateral robust setae distally, outer ramus with marginal robust setae, uropod 2 rami equal in length, uropod 3 ramus shorter than peduncle; telson apically notched with 6-8 robust setae per lobe and shorter than uropod 3.

Neotenorchestia gen. n.

<http://zoobank.org/D3C3762F-5DF0-47AD-9EC3-2DB079544F1E>

Wildish et al. 2012; Pavesi et al. 2014, as unknown taxon.

Type species. *Neotenorchestia kenwildishi* gen. n., sp. n.

Component species. Monotypic.

Diagnosis. As in *Orchestia* and specifically similar to *Orchestia mediterranea* A. Costa 1853 except for:

- lack of dorsal pigment patterns (versus dorsal pigment patterns in *O. mediterranea* as in Wildish, 1987).
- smaller size by neoteny (largest total body length estimated to be 12 to 16 mm, versus up to 20 mm in *O. mediterranea*)

Very similar to *Orchestia mediterranea* A. Costa 1853 and if characterization is limited to conventional morphological methods this species can easily be misidentified as a juvenile *O. mediterranea*. The use of relative growth methods and regression fitting predictions as found in Pavesi et al. (2014, see Table 3) are required for definitive identification.

Etymology. Refers to the origin of the new genus by a form of neoteny and combination of the stem of this word with the genus *Orchestia* to which it is closely related.

Neotenorchestia kenwildishi sp. n.

<http://zoobank.org/DD3AA445-5FAB-49FF-8D3E-84442454732C>

Wildish et al. 2012: 2677; Pavesi et al. 2014, as unknown taxon.

Type material. Holotype-immature male of 7.2 mm total body length (NHMUK 2014. 397) and slide preparation from this individual (NHMUK 2014. 397). Nine juvenile paratypes (NHMUK 2014. 398 - 406) and 2 immature females (destructively sampled for temporary slide mounts and mtDNA analysis) removed from a cast-up driftwood log resting at the base of the seawall in the *Enteromorpha* zone by K.J. Wildish. The driftwood log had been tethered to an old cattle fence on the shore, so it could not float away. It was sampled on 14th June 2011, 23rd July 2011 and 13th August, 2011 from the Swale, near Kingsferry Bridge, U.K.

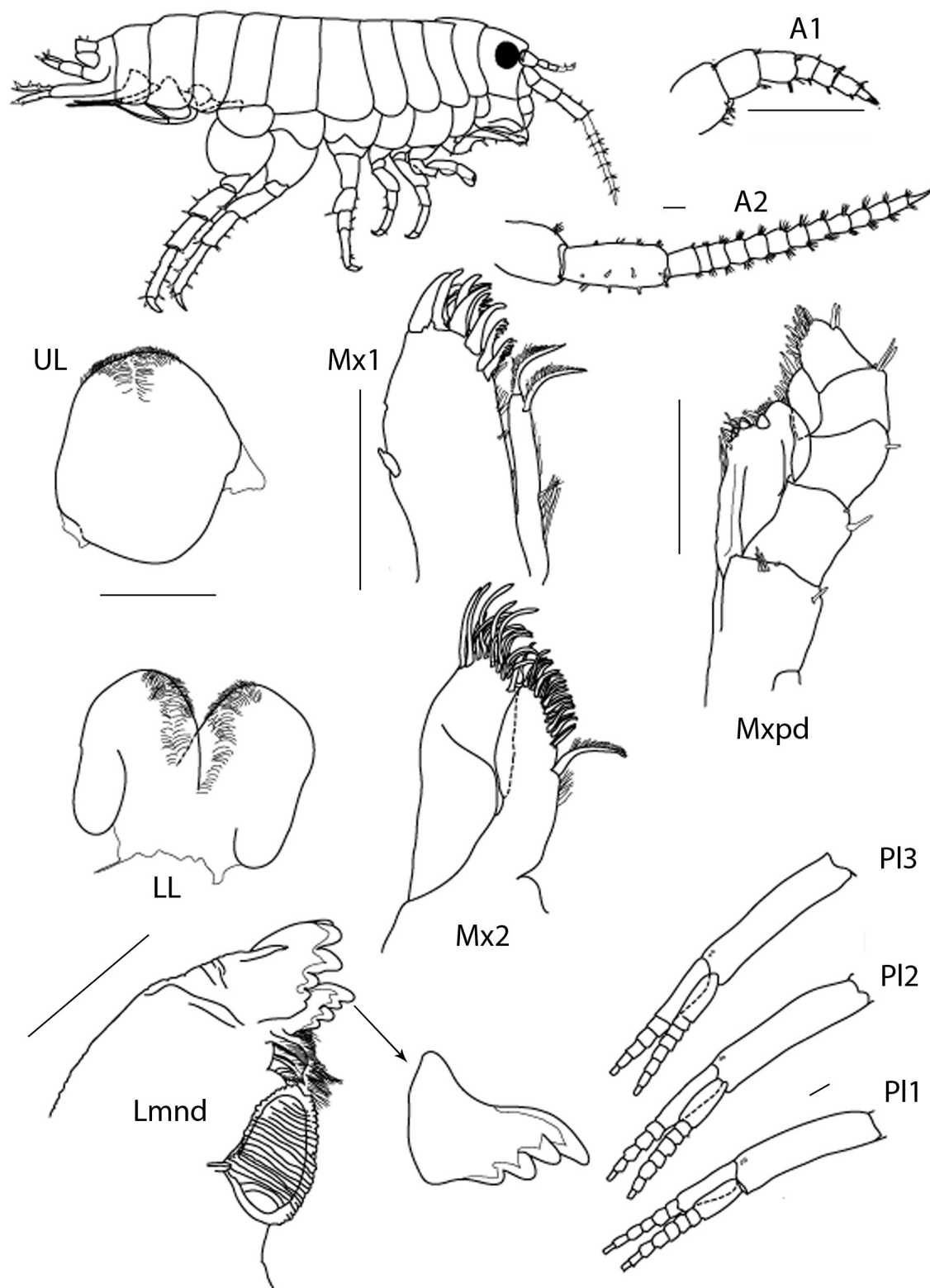


Figure 4. *Neotenorchestia kenwildishi* gen. n., sp. n. Habitus of juvenile paratype, total body length (TBL) = 3.7 mm. All other body parts from immature male holotype, TBL = 7.2 mm. Antennae and pleopod scale = 0.25 mm. Mouthparts, scale = 0.1 mm.

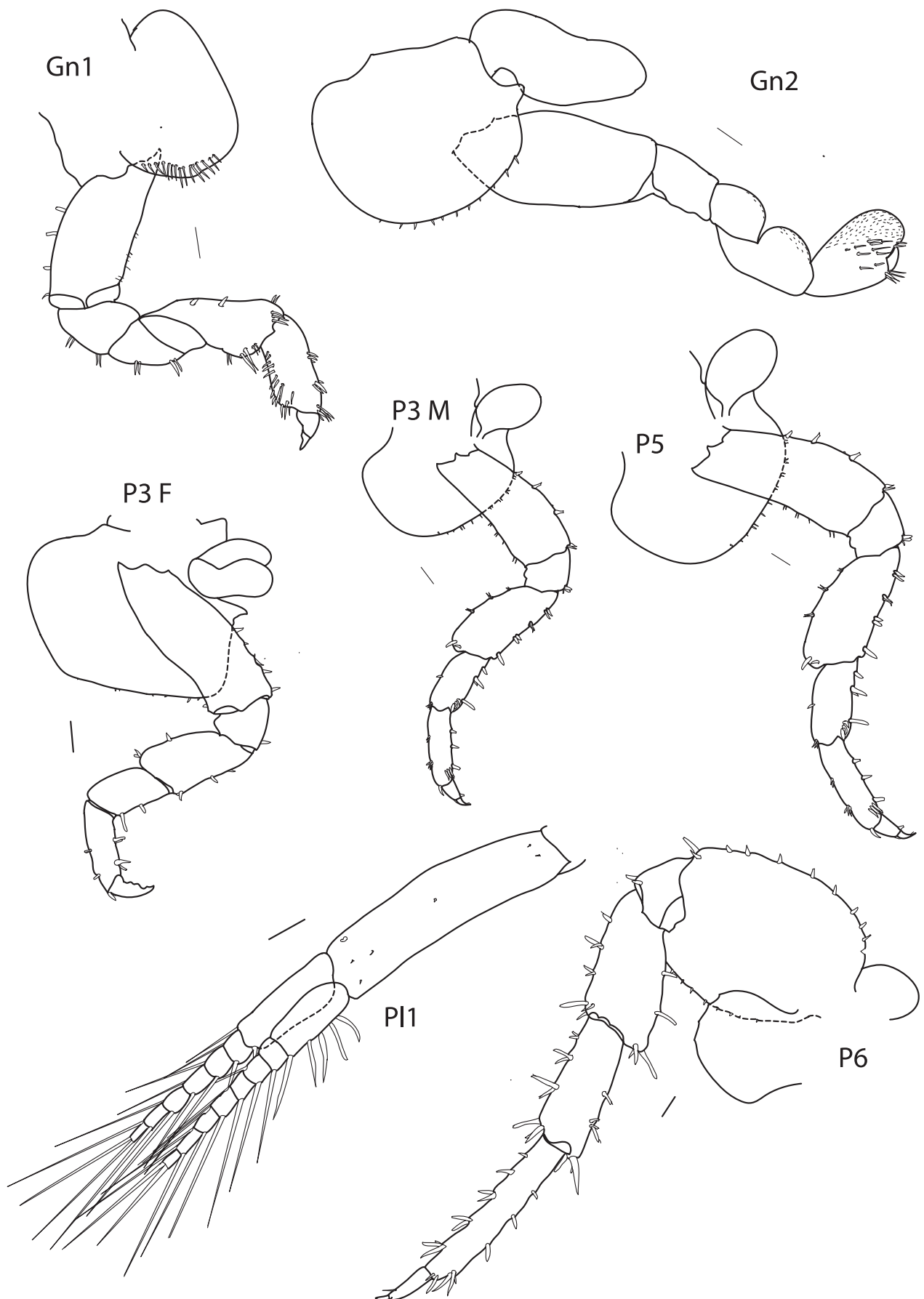


Figure 5. *Neotenorchestia kenwildishi* gen. n., sp. n. Immature male holotype as in Fig. 3, except pereopod 3 is from a female paratype of TBL = 8.3 mm. Scale = 0.25 mm.

Type locality. Approximately 0.5 km west of Kingsferry Bridge, The Swale on the mainland shore in a single rotting driftwood log ($\sim 3 \times 0.5 \times 0.5$ m) determined to be of Douglas fir by Dr. P. Gasson, Kew (Pavesi et al. 2014). GPS position: 51°23.97'N, 00°43.56'E.

Maximum body length. Unknown, the largest found was an 8.9 mm TBL immature female. Mature adults predicted by relative growth methods to be 12 to 16 mm total body length (Pavesi et al. 2014).

Diagnosis. *N. kenwildishi* sp. n., can readily be distinguished from other driftwood hoppers of the genus *Macarorchestia* by its medium size eyes (versus small) and unreduced pleopods (rami sub-equal to basis, versus rami shorter than basis).

Description. Based on immature male holotype of 7.2 mm total body length. Figs 4 and 5.

Head deeper than long (1 : 0.5); eyes medium/large, round and greater than half the head length. Antenna 1 flagellum 4-articulate. Antenna 2 flagellum 13-articulate. Peduncle not incrassate.

Mouthparts. Upper lip with minute setae on the apical margin. Lower lip deeply cleft and with minute setae on the inner face. Maxilla 1 inner plate slim and with two terminal, plumose setae; inner margin with long fine setae; outer plate with a vestigial palp, apical robust setae curved inwards, some simple and others serrated on the inner edge. Maxilla 2 with inner plate subequal to the outer, inner with a single, plumose seta and fine marginal setae below it; both inner and outer plates with long, simple robust setae which curve inwards. Left mandible with a 4-dentate lacinia mobilis, 6-dentate incisor, strong molar process and setose accessory blades. Maxilliped with 3 strong api-

cal teeth on the inner plate; inner, outer and palp edged with simple, robust setae; palp large and 3-articulated.

Peraeon. Gnathopod 1 weakly subchelate, palmate lobes on propodus and carpus. Gnathopod 2 weakly subchelate with dactylus shorter than the propodus lobe; palmate lobes on propodus, carpus and merus. Peraeopod 3 lacks a dactylus notch (“pinched unguis”), but this is present in an immature female. Peraeopod 5 shorter than peraeopods 6 and 7, the latter not sexually dimorphic in the immature male.

Pleosome. Pleopods large and well developed, with 6–7 ramal segments in the endopod, 8 segments in the exopod; rami subequal to basis with paired coupling spines on the inner, distal margin of the basis; 6 simple setae present on the basis of pleopod 1.

Urosome. Uropod 1 rami subequal to peduncle. Peduncle with 2 rows of 2 robust setae. Terminal setae on each ramus consists of 1 large and 1 or 2 smaller robust setae. 3 interramal robust setae on inner and 2 on outer ramus.

Sexually dimorphic differences. Based on immature female of 8.9 mm total body length.

In the absence of sexually mature males and females the only unique female characters found were: absence of palmate lobes on propodus and carpus of gnathopod 1, presence of pinched unguis on peraeopod 3, and presence of small, rudimentary oostegites on coxae of peraeopods 2–5.

Etymology. The name honours Kenneth J. Wildish who discovered and collected the new taxon in the Swale during the summer of 2011.

Epidermal pigment patterns. Absent.

Distribution. Known only from the type locality.

Key for northeast Atlantic/Mediterranean *Macarorchestia* and *Neotenorchestia* gen. n.

- | | | |
|---|---|------------------------------|
| 1 | Medium size eyes and pleopod rami > basis length | <i>N. kenwildishi</i> sp. n. |
| – | Small eyes and pleopod rami < basis length | 2 |
| 2 | Maximum adult size (TBL < 8 mm), female TBL > male | 3 |
| – | Maximum adult size (TBL > 8 mm), male TBL ≥ female | 4 |
| 3 | Third pleopod exopod length ratio > 0.16 | <i>M. martini</i> |
| – | Third pleopod exopod length ratio < 0.16 | <i>M. roffensis</i> |
| 4 | Maximum adult size (TBL = 15 mm), male TBL > female | <i>M. microphthalmia</i> |
| | Lacks sexual dimorphism in A2 and pleopods | |
| | Males with no tuft at anterodistal and 4 tufts of long, simple setae on posterior edge of P7 propodus | |
| – | Maximum adult size (TBL < 13 mm), male TBL ≤ female | 5 |
| | With sexual dimorphism either in pleopods or A2 flagellum articles | |
| | Males with a single tuft at anterodistal and 3 tufts of long, simple setae on posterior edge of P7 propodus | |
| 5 | Adult male TBL > 8 mm fit: $y = 0.050x + 0.159$ | <i>M. remyi</i> |
| – | Adult male TBL > 8 mm fit: $y = 0.026x + 0.024$ | <i>M. pavesiae</i> |
| – | Adult female TBL > 7.5 mm fit: $y_1 = 0.585x + 6.995$ | <i>M. remyi</i> |
| – | Adult female TBL > 7.5 mm fit: $y_1 = 0.130x + 9.248$ | <i>M. pavesiae</i> |
- (where x = TBL, y = PI3 Ex L, and y_1 = A2 FA)

Discussion

The following arguments were considered in deciding how to name the unknown taxon. Relative growth data was available to show that the unknown taxon fundamentally differed from juvenile *Orchestia mediterranea* (Wildish et al. 2012; Pavese et al. 2014). The relative growth of the unknown taxon differed from that in *O. mediterranea* by:

- being slower growing with a reduced terminal moult size,
- sexualization beginning at an earlier moult stage and with fewer moult stages per life history, and
- dorsal pigment patterns being absent.

The first two of these three phenotypic characters are described as neotenous dwarfism and are the basic adaptations possessed by all driftwood specialist talitrids of the genus *Macarorchestia* Stock. Because the unknown taxon clearly does not belong to *Macarorchestia*: by possession of fully developed eyes and pleopods, by COI divergence differences (Wildish et al. 2012) and because it is clearly a driftwood specialist, both in habitat and adaptive morphology, the unknown taxon should be placed in a new genus.

On the other hand molecular evidence suggests that the differences between the unknown taxon and *O. mediterranea* are small (Wildish et al. 2012; Pavese et al. 2014). Thus for the mitochondrial gene, COI, the difference for K2P = 2% with a divergence time of 0.83 ± 1.5 MYA (Pavese et al. 2014). The low K2P% would not reach species level difference (assumed to be K2P = 3% in Amphipoda, Radulovici et al. 2009; 4% in Wildish et al. 2012). It is hypothesized that the unknown taxon was formed from an *O. mediterranea* population which found itself in a secondary ecotope (driftwood) where a few, or single pleiotropic, nuclear gene mutations occurred which resulted in slower growth and sexualisation occurring at an earlier moult. Thereafter, the unknown taxon would follow life within driftwood and be unable to breed with *O. mediterranea* because of size and habitat differences. If this mutant form arose recently (in geological time), as the COI divergence time suggests, the magnitude of K2P differences may be an inapplicable measure of species or genus level difference. Clearly further genetic evidence to test this hypothesis is required: such as a search for the hypothesized nuclear gene(s) controlling neotenous dwarfism.

Pragmatically, and in the absence of conclusive molecular data, it is considered prudent to remove the unknown

taxon from *Orchestia*, a supralittoral wrack generalist genus and create a new driftwood specialist genus: *Neotenorchestia* for the unknown taxon. Finding adult males and females of the new genus is needed to complete the description and diagnosis of the new taxon.

Inclusive of the taxonomic actions taken above brings the total genera of driftwood talitrids to three: *Macarorchestia* Stock 1989, "*Platorchestia*" *chathamensis* Bousfield 1982 and *Neotenorchestia* gen. n. For the latter genus only one species is known and with the transfer of *microphthalma* Amanieu & Salvat, 1963 from *Orchestia* brings the species belonging to *Macarorchestia* to a total of 5. Thus the known driftwood specialist talitrids total to date is 7 species.

The scarce locality records for each species documented here suggest either rareness and/or that they are difficult to find on shores of the northeast Atlantic and Mediterranean seas. Further evidence for this is that 2 of the 6 driftwood taxa dealt with here are known only from the type locality and the rest from only a few locations. A problem for future discoveries of driftwood talitrids is that the habitats are fast being destroyed by human activities. Documented examples include the destruction of the type locations for two species as mentioned above.

Both *Macarorchestia* and *Neotenorchestia* gen. n. probably originated from ancestors that were larger and faster growing. The evolutionary process in these genera involves reductions in metabolic and growth rates as well as sexualization occurring at an earlier moult number (neotenous dwarfism). A recent, common ancestor gave rise to modern *O. mediterranea* and *N. kenwildishi* gen. n., sp. n., which is consistent with morphological (relative growth) and molecular genetic studies (Wildish et al. 2012; Pavese et al. 2014). The common ancestor of *Macarorchestia* is unknown, but within the genus of two lineages defined genetically (Wildish et al. 2012):

1. *roffensis* --- *martini*
2. *remyi* --- *pavesiae* sp. n.

evolution involves further neotenous dwarfism. Thus taxa to the left are larger and plesiomorphic, whereas those to the right are smaller and apomorphic. Neotenous dwarfism of this kind in driftwood talitrids poses a special challenge to taxonomy because many of the slope values between pairs of species are isometric. In these cases only regression constants, or plots, can be used to separate two species populations. Isometric relative growth is rare

Table 3. Summary of morphological and molecular data available for species of *Macarorchestia*. * Stock (1989), **Wildish et al. (2012).

Species	Lmnd lacinia mobilis dentition	Numbers of setae in tufts on male propodus of P7		Number of tufts on posterior side of male propodus of P7	Mt DNA COI**
		Distal	Anterodistal		
<i>M. microphthalma</i>	4	6	0	4	?
<i>M. roffensis</i>	4	2	0	0	Yes
<i>M. martini</i>	5*	?	?	?	Yes
<i>M. remyi</i>	4.5	6	2	3	Yes
<i>M. pavesiae</i> sp. n.	4	6	2	3	Yes

within the Amphipoda and where it does occur ratios cannot be used to express the relative growth differences and recourse to regression predictions appears to be the only way to handle the differences due to neotenus dwarfism.

Permanent slides of limb and mouth parts prepared by Sara LeCroy (Gulf Coast Research Lab, University of Southern Mississippi) of four species of *Macarorchestia* identified possible, taxonomically important, morphological differences between groups 1 and 2 as defined in the preceeding paragraph. Thus the left mandible lacinia mobilis in *Macarorchestia* appeared to be predominantly 4-dentate (Table 3). In an immature male *M. roffensis* the teeth were lateral to the viewing plane and consequently easy to count. In all other preparations, including temporary ones, the teeth were dorsal to the viewing plane (“end on”) making it necessary to focus up and down to see the teeth. An adult male of *M. remyi* appeared to be 5-dentate, whereas an immature female of this species was 4-dentate. Intraspecific variation of left mandible lacinia mobilis dentition has been recognized in other talitrids (Wildish and LeCroy 2014) and this may be the case in *Macarorchestia*, which renders this character of dubious value in taxonomic discrimination. Further studies are needed to resolve this point. The presence of long, simple, fine setae on the propodus of peraeopod 7 (“comb” setae) proved to be useful in distinguishing species of *Macarorchestia* (Fig. 3). Thus males of *M. microphthalmia* had groups of 6 tufts: one near the first insertion of bifid-tipped, robust spines on the anterior side of peraeopod 7 (5 setae), distal (6 setae of 192 µm), anterodistal (0 setae), then 4 setal tufts on the posterior side of the peraeopod at the first insertion of bifid-tipped, robust setae (5 setae), second (6 setae), third (5 setae) and fourth (4 setae). Setal length was approximately the same at each insertion, varying from 156 to 168 µm, except for the most proximal where it was 120 µm. Males of *M. remyi* and *M. pavesiae* sp. n., also had groups of 6 tufts on the propodus of peraeopod 7, but differed from *M. microphthalmia* in having a single tuft at anterodistal position (2 setae) and only 3 tufts on the posterior propodus. A subadult male *M. roffensis* had a single tuft (2 setae, length 70 µm). This character is sexually dimorphic in all species of *Macarorchestia* and females have only two tufts at distal and anterodistal positions on the propodus of peraeopod 7 (each of 3–6 setae), which are of smaller setal length than in males. The number of setae in each tuft is growth dependant, so the number of setae per tuft cannot be used as a definitive taxonomic character.

In considering current data of Table 3 and assuming that the left mandible lacinia mobilis dentition is not taxonomically useful, it is possible to propose a subgeneric split based on Atlantic versus Mediterranean coastal ranges of *Macarorchestia*. This is clearly premature because:

- of missing data as indicated by question marks in Table 3.
- The left mandible lacinia mobilis is 5 dentate according to Stock (1989), rather than 4 dentate, as would be the case if it were close to *M. roffensis* as the molecular

data indicates (see Table 5 in Wildish et al. 2012). If intraspecific variation in dentition (4 or 5 dentate) is common this might explain this apparent anomaly.

Further molecular and morphological studies are needed to resolve the subgeneric status of *Macarorchestia*.

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