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# **Rediagnosis of** *Palaemon* **and differentiation of southern Australian species** (Crustacea: Decapoda: Palaemonidae)

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Abstract

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Examination of the morphology of palaemonine shrimps from Tasmania and south-eastern Australia, and molecular analyses by other authors, necessitated an examination of the validity of some characters used for generic differentiation within the Palaemoninae and a redefinition of the genus *Palaemon*. A new species, *Palaemon dolospina* sp. nov., is described from Margate Beach in south-eastern Tasmania. *Palaemon intermedius* (Stimpson, 1860) is redescribed. Both species vary between localities across southern Australia. Keys are presented for the small estuarine and marine shrimps of Palaemoninae in south-eastern Australia belonging to genera, *Palaemon* and *Palaemonetes*. One species of *Palaemon* has been introduced to Australia from overseas.

Key words Crustacea, Caridea, Palaemonidae, Palaemon, new species, Australia

#### Introduction

An investigation of Tasmanian palaemonids shrimps usually known as *Macrobrachium intermedium* from the North West Bay River Estuary and D'Entrecasteaux Channel in southeastern Tasmania revealed not only the presence of two forms in these environments but also the presence of a similar new species in the estuary. Both species are common in seagrass and, in eastern and south-eastern Tasmania, occur sympatrically in the seagrasses *Zostera muelleri* and *Heterozostera tasmanica*. Further study showed that the first is widespread in marine and estuarine waters from Western Australia to Queensland. The new species has not been located outside South Australia, Tasmania and Victoria. It is generally found in estuarine waters or, in Tasmania, in shallow marine waters where the other is absent.

Neither species complies well morphologically with the generic diagnoses of *Macrobrachium* or the alternative, *Palaemon*. Analyses using allozymes and molecular information from 16S rRNA strongly suggested that *M. intermedium* was more closely related to *Palaemon serenus* (Heller, 1862) (Murphy and Austin, 2002) or to *Palaemonetes australis* Dakin, 1976 (Boulton and Knott, 1984; Murphy and Austin, 2003) than to other species of *Macrobrachium*. This paper re-examines morphological characters used in generic classification within the subfamily Palaemoninae and redefines

Palaemon. Both species are described and assigned to Palaemon, henceforth P. intermedius (Stimpson, 1860) and P. dolospina sp. nov.

We follow Bruce (1992) in treating the gills of maxilliped 3 as two arthrobranchs (one rudimentary) rather than one pleurobranch, said by Holthuis (1993) and earlier workers to define the subfamily Palaemoninae.

Palaemon is separated from Palaemonetes, Macrobrachium and other palaemonine genera principally on the basis of the presence and form of the branchiostegal groove, the presence or absence of branchiostegal and hepatic spines, the form of the second pereopods and the presence or absence of a mandibular palp. Problems with the use of these characters were noted previously by Fujino and Miyake (1968), Chace (1972), Bray (1976) and Boulton and Knott (1984). We reviewed these characters in eight southern Australian species (Table 1).

Palaemon is said to be separated from Macrobrachium by the presence of a branchiostegal spine and smooth second pereopods while Macrobrachium has an hepatic spine and spinulose second pereopods in males of many species. In Palaemon, adult females are larger than males while males are usually larger in Macrobrachium.

Most species of *Macrobrachium* have an hepatic spine set well back from the carapace edge on or just below the ridge of the antennal spine (Fig. 1). The branchiostegal groove is short,

	Palaemon	Palaemon	Palaemon	Palaemon	Palaemonetes	Palaemonetes	Macrobrachium	Macrobrachium
	intermedium	dolospina	serenus	debilis	australis	atrinubes	novaehollandiae	rosenbergii
Carapace spine	open posteriorly; migrates from carapace edge in early post-larval stages	set back from (tip just reaching) carapace edge; migrates from	set on carapace edge, just below start of branchiostegal groove	set on carapace edge, short distance below start of branchiostegal	set well back from (tip not reaching) carapace edge; migrates from	set on carapace edge, just below start of branchiostegal groove	closed posteriorly; migrates from carapace edge in early post-larval	closed posteriorly; migrates from carapace edge in early post-larval
		carapace edge in early post-larval stages		groove	carapace edge in early post-larval stages		stages	stages
Branchiostegal groove	running up to spine and stopping at dorsoposterior edge	running up to spine, looping over it and sweeping down posteriorly	starting on top of spine, sweeping to posterior in shallow arc	starting above spine, sweeping to posterior in shallow arc	sweeping to posterior in shallow arc, may deviate slightly over	starting on top of spine, sweeping to posterior in shallow arc	running up to spine and stopping	running up to spine and stopping
Mandibular palp	present in adults, 3 articles (absent in first postlarva)	present in adults, 3 articles (absent in first postlarva)	present in adults, 3 articles	present in adults, 3 articles	spine usually absent, if present of 1 or 2 articles	absent	present in adults, 3 articles	present in adults, 3 articles (absent in first postlarva)
Pereopod 2 of adult	~equal, same in both sexes, smooth	~equal, same both sexes, smooth	~equal, same in both sexes, smooth	~equal, same in both sexes, smooth	~equal, same in both sexes, smooth	~equal, same in both sexes, smooth	?equal, larger in males, spinulose	?equal, larger in males, spinulose
Larger sex	Female	Female	Female	Female	Female	Female	Male	Male

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Figure 1. SEMs of carapace spines. a, Macrobrachium rosenbergii; b, Palaemon serenus; c, Palaemonetes australis; d, Palaemon intermedius; e, Palaemon dolospina.

and runs from the carapace edge to the front of the base of the spine and stops there. The back of the spine is closed with a suture line surrounding the spine where it makes contact with the carapace and it is usually flattened dorsoventrally. The hepatic spine is well removed from the anterior edge of the carapace (Holthuis, 1950) by a distance greater than its length.

In most species of *Palaemon* (and *Palaemonetes*) there is a branchiostegal groove running back from the anterior edge of the carapace in a shallow arc near the junction of the branchiostegite and the thorax (Fig. 1). Its length generally varies from a quarter to a half of the carapace length. A branchiostegal spine is found below this groove, usually on the carapace edge close to the start of the groove. However, the spine may be found removed ventrally from the groove somewhat and set back a little from the carapace edge. In Australian material, the spine is usually rounded rather than flattened and there is no distinct suture line where it is in contact with the carapace.

Within Australia, there is a continuum of spine/groove patterns between those typically found in Palaemon and Macrobrachium. Palaemon serenus, Palaemon litoreus (McCulloch, 1909), Palaemon macrodactlyus (Rathbun, 1902) and Palaemonetes atrinubes Bray, 1976 have a typical branchiostegal groove and the spine on the edge of the carapace (Fig. 1b). Palaemonetes australis has the branchiostegal spine set well back from and not overlapping the carapace edge, with the groove of the usual form passing over it (Fig. 1c). Palaemon dolospina has a unique arrangement where a circular spine is set back from the carapace edge, but with the tip just overlapping it in some individuals (Fig. 1e). The spine is displaced dorsally to an almost hepatic position. The branchiostegal groove runs back into the spine but is then displaced dorsally, loops over the spine and runs past it in a ventroposterior direction for a distance equal to about twice the length of the spine. As the spine is below the branchiostegal groove, it can considered to be branchiostegal.

Palaemon intermedius possesses what appears to be an hepatic spine, but it is not set as far back from the carapace edge as is usual in that genus, and is lower on the carapace, being nearer the junction of the branchiostegite and thorax (Fig. 1d). The groove runs into the front of the spine but the latter is open posteriorly, having no suture line where it meets the carapace at that point. The groove or suture line dorsal to the spine extends further posteriorly than that ventral to it and may represent a short extension of the branchiostegal groove over the spine. The spine is flattened dorsoventrally.

*Macrobrachium rosenbergii* (De Man, 1879) (Fig. 1a), *M. lar* (Fabricius, 1798) and other Australian species of this genus have a typical hepatic spine set high up on the carapace with the branchiostegal groove running up into it and stopping. The spine is surrounded by a suture line where it joins the carapace, and its tip is well removed from the anterior carapace edge.

The intermediate nature of the two species can be appreciated by examination of post-larvae and juveniles. Both species have no branchiostegal groove and a branchiostegal spine on the edge of the carapace (Fig. 2). Over a series of moults, the spine migrates away from the carapace edge to its final adult position as the branchiostegal groove forms. This was also found to occur in *Macrobrachium australe* (Guérin-Méneville, 1838), *M. latimanus* (Von Martens, 1868) and *M. lar* by Holthuis (1950). Other species are similar: *M. nipponense* (De Haan, 1849) (Kwon and Uno, 1969), *M. rosenbergii* (see Uno and Kwon, 1969), *M. australiense* Holthuis, 1950 (Fielder, 1970), *M. niloticum* (Roux, 1833) (Williamson, 1972), *M. novaehollandiae* (De Man, 1938) (Greenwood et al., 1976), *M. equidens* (Dana, 1852) (Ngoc-Ho, 1976) and *M. lar* (see Atkinson, 1977).

Thus it appears that the "hepatic" spine of *Macrobrachium* and "branchiostegal" spine of *Palaemon* and related genera are homologous. An "hepatic" spine appears to be a branchiostegal spine that has migrated during post-larval and juvenile development. The groove appears to be displaced upwards and remains developed only between the carapace edge and the spine. One exception is found in *M. palaemonoides* Holthuis, 1950, where the spine is in an hepatic position but the groove passes below the spine (Holthuis, 1950). A consequence of this realisation is that while adults of *Macrobrachium* and *Palaemon* can be assigned to to their respective genera on this character, juveniles cannot and other characters must be applied to distinguish juveniles.

This ontological process appears to be arrested in *Palaemon intermedius* and *P. dolospina* but other characters such as features of pereopod 2 place them clearly in *Palaemon*.

Palaemonetes differs from Palaemon solely by the absence of a mandibular palp. Incidentally, the same character differentiates *Pseudopalaemon* Sollaud, 1911 from *Macrobrachium*. Most specimens of the two Tasmanian species have a threearticled palp. Boulton and Knott (1984) noted difficulties identifying the joint between the second and third article in *Palaemon intermedius* from Swan River, WA. The palp is absent in the first post-larval stage and present as a small bump in the second post-larval stage, developing into its normal form over the next few moults (Fig. 4m). This developmental change is widespread in *Palaemon, Macrobrachium* and *Leptocarpus* (e.g. Ngoc-Ho, 1976).

The mandibular palp varies in adults of some species or in some populations of some species. Chace (1972) reported specimens of *Palaemon debilis* Dana, 1852 from Hawaii with between one and three articles or no mandibular palp at all. Fujino and Miyake (1968) found the same for five species of *Palaemon* from Japan, and the same discrepancy between two sides of a single individual. Among 20 specimens of *Palaemon* cf. *debilis* from Coila Lake, NSW, the number of palp articles ranged from none to two (65%). Bray (1976) found *Palaemonetes australis* Dakin, 1915 from WA with a mandibular palp of one or two articles or without a palp.

The doubtful status of *Palaemonetes* has been noted previously on grounds of morphology (Chace, 1972; Bray, 1976), morphology and allozymes (Boulton and Knott, 1984) and mitochondrial genes (Murphy and Austin, 2003). Placing it in synonymy with *Palaemon* may not be appropriate since the form of the mandibular palp is consistent once adult state is achieved in at least some Australian species, *Palaemonetes atrinubes* and the two described below. Nevertheless, it is

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variable in *Palaemonetes australis* and *Palaemon* cf. *debilis*. A final decision on the synonymy would require a more thorough examination of species beyond Australia.

The second percopods of most, though not all, species of *Macrobrachium* (and *Chryphiops* Dana, 1852) are larger and often spinulose in adult males. This is a useful character for the generic identification of sexually mature males, but it is of no use in juveniles or females which resemble members of other genera such as *Palaemon* and *Palaemonetes*.

Pending a major revision of the Palaemoninae, Australian species may be divided into three groups. The first includes all species of Macrobrachium sensu stricto, which occupy freshwater or estuarine habitats, have markedly sexually dimorphic second percopods, larger males than females and the hepatic spine/groove arrangement typical of that genus. The second group is Palaemon serenus, P. litoreus, P. macrodactylus (introduced), P. dolospina and P. intermedius. These occupy marine and estuarine habitats, are robust, females are larger than males, the second percopods are similar in both sexes, a proximal tuft of setae is present dorsally on the telson and they always possess a mandibular palp of three articles. The third group contains Palaemonetes atrinubes, Palaemonetes australis, Palaemon debilis and possibly another species close to P. debilis. These occupy marine and estuarine habitats, are less robust than those of the second group, have more slender percopods, have larger females than males, the second pereopods are similar in both sexes, there is no proximal tuft of setae on the telson, and the number of articles in the mandibular palp appears to be variable with a tendency to be reduced or absent.

In spite of the shortcomings of the characters discussed above, it is possible to redefine *Palaemon* around the second and third groups of species and include the following two species.

#### Palaemon Weber, 1795

Palaemon Weber, 1795: 94.—Holthuis, 1950: 42–44 (extended diagnosis).—Holthuis, 1993: 112–114 (synonymy).

Diagnosis. Rostrum well developed, toothed dorsally and ventrally, without an elevated basal crest; upper margin bearing single row of setae between dorsal teeth. Carapace smooth, bearing distinct branchiostegal spine and groove; branchiostegal spine usually situated on carapace edge but may be set back; groove usually running straight back from carapace edge in a shallow arc but may rise upwards and over spine before continuing posteriorly or, in P. intermedius, into and over but not past its posterior edge. Antennal spine generally strong, on anterior margin of carapace some distance below rounded lower orbital angle. Mandibular palp usually of 2 or 3 articles, but may be absent. Eyes distinctly pigmented, cornea well developed. Anterior margin of antennular peduncle rounded, anterolateral spine small. First pleopod of male without or with rudimentary appendix interna on endopod. Propodus of fifth percopod with several transverse rows of setae on distal part of the posterior margin. Telson with 2 slender median setae on posterior margin. Pleura of fifth abdominal somite usually ending in small sharp point.

*Remarks.* The revised diagnosis allows for the variable position of the branchiostegal spine and accommodates the hepatic position of this spine seen in some Australian species.

#### Palaemon intermedius (Stimpson)

#### Figures 1d, 2a-e, 3a, 3b, 4, 5

Leander intermedius Stimpson, 1860: 41.—Haswell, 1882: 195.— Whitelegge, 1889: 224 (record in Port Jackson).—Thomson, 1893: 51 (record in Tas.).—Stead, 1898: 210.—Sayce, 1902: 155 (record in Port Phillip Bay).—McCulloch, 1909: 309, pl. 89 figs 13, 14.—Hale, 1927a: 58–59, fig. 53 (record in SA).—Hale, 1927b: 309.—Anderson, 1938: 351 (record in Spencer Gulf).—Mack, 1941: 108 (diet of cormorants, Gippsland Lakes).—Thomson, 1946: 59, 67 (record in WA).—Holthuis, 1950: 20.

Palaemon (Leander) intermedius.-Miers, 1884: 295.

*Macrobrachium intermedium.*—Holthuis, 1952: 207–209 (redescription).—Poore et al., 1975: 35, 71 (distribution in Port Phillip Bay).—Walker, 1979 (redescription and ecology in Tas.).—Boulton and Knott, 1984: 769–784 (ecology in WA).—Davie, 2002: 296.

*Material examined for redescription.* 15 males, 12.7–27.3 mm body length, 20 females including 7 ovigerous, 12.7–34.5 mm body length, Margate Beach, mouth of North West Bay River Estuary, Tasmania, T. Walker, 1975. 4 adult females, D'Entrecasteaux Channel, Middleton, 14 m, Tasmania, T. Walker, Khin Khin U and T. Sward, 11 Apr 1975. 4 ovigerous females, 2 mature males, Western Port, Victoria, Fisheries and Wildlife Department, Victoria, 29 Nov 1973. 3 ovigerous females, 1 mature male, Spalding Cove, 4–12 m, South Australia, 5 Nov 1969.

Additional material. Numerous sites in Tasmania, Victoria, South Australia, Western Australia, New South Wales, Queensland; including many lots registered in Museum Victoria,

*Diagnosis.* Carapace smooth; branchiostegal spine set back from anterior edge of carapace and open posteriorly; branchiostegal groove running from carapace edge upwards and posteriorly to dorsoposterior edge of the spine where it stops. Rostrum upper border with 7–10 teeth (usually 8 or fewer, commonly 9); 2–3 of these (usually 2) postorbital; dorsal teeth evenly spaced although proximal 3 or 4 often closer together than remainder and incompletely articulated; ventral rostral border with 4–6 teeth (usually 5) evenly spaced over distal twothirds;

Description. (based on 15 males, 20 females from Margate Beach, Tasmania) Maximum body length (orbit to telson tip) c. 30 mm in males, c. 40 mm in females.

Carapace smooth; antennal spine strong and marginal; branchiostegal spine set back from anterior edge of carapace and open posteriorly; branchiostegal margin rounded, branchiostegal groove running from carapace edge upwards and posteriorly to dorsoposterior edge of the spine where it stops.

Eyes well developed, with ocellus; interocular tooth well developed.

Rostral tip level with or exceeding terminal setae of scaphocerite; length:depth ratio 6.9-10.0 in males, 6.2-8.8 in females; upper border straight to concave; body length:rostral length ratio 2.5-3.1 in males, 2.8 - 3.6 in females; lateral carina gently and concavely curved, degree of curvature variable; third to half rostrum above lateral carina; upper border with 7-10 teeth (usually 8 or less commonly 9); 2-3 of these (usually 2) postorbital; dorsal teeth evenly spaced although



Figure 2. Migration of the carapace spine during growth to final position. a–e, *Palaemon intermedius*; f–j, *Palaemon dolospina*. Body lengths of shrimps (mm): a, 6.0; b, 6.2; c, 6.5; d, 6.6; e, 6.6; f, 6.3; g, 6.2; h, 6.3; i, 6.8; j, 8.4.

proximal 3 or 4 are often closer together than remainder and incompletely articulated; rostral tip usually bifid but may be trifid or a single point; single row of plumose setae along upper border between but not on teeth; ventral rostral border with 4–6 teeth (usually 5) evenly spaced over distal two-thirds; 2 rows of plumose setae on ventral border between but not on teeth.

Antennule well developed, article 1 of peduncle about 2.5 times length of articles 2 and 3; article 2 slightly longer than 3, bearing elongate, blunt projection on medial edge; basal article elongate and rectangular, about 2.3 times as long as wide, expanded and flattened on its inner edge, bearing several transverse and longitudinal rows of plumose setae, including subapical row extending across dorsal surface; setae longer over inner half of this row; basolateral spine slender, sharply pointed, reaching over half article 1; outer flagellum of antennular exopod much longer than inner flagellum; inner flagellum fused with outer usually over basal third of its length, about 13 articles in adult, fused up to half its length in juvenile; each free article of inner flagellum with medial and terminal transverse row of sensory setae, medial row bearing 3-4 setae and transverse row 4 setae in males, both rows bearing 3 setae in females.

Antenna with well developed peduncle with strong distolateral tooth, well developed flagellum and scaphocerite; proximal article of flagellum with blunt anteroventral projection; flagellum naked. Scaphocerite elongate, rectangular, extending well beyond peduncle, widest just anterior to its base, about one quarter of body length, 3.3–4.3 times as long as wide; distal and inner lateral edges bearing row of long plumose setae; outer edge naked, slightly concave, ending distally in well developed tooth that just fails to overlap anterior edge of lamella; inside edge straight or slightly concave.

Mandible- incisor of one side with 3 teeth (either side), incisor of the other usually with 4; palp with 3 articles; article 3 longest, with 3 terminal setae longer than article.

Maxillule endopod with bifid tip; distal lobe acute, naked; proximal lobe bearing 1 plumose seta; coxal endite with long setae and terminally 4–5 stout setae; basal endite with 3 rows of stout setae along terminal, inner edge extending down proximal margin as longer setae.

Maxilla basal endites elongate, nearly rectangular, both bearing long, stout setae terminally, distal endite with row of 5 setae along distal margin near its base; endopod with 3 short setae; scaphognathite proximal lobe wider and shorter than distal; coxa with small expansion near base (?epipod).

Maxilliped 1 with rectangular coxa with endite and bilobed epipod; basis with endite; endopod with 1 long, subterminal seta; well developed exopod with prominent lateral lobe; endites with stout setae along mesial edges, and distal on basal endite; both with single row of similar setae on posterior face.

Maxilliped 2 with well developed exopod; coxa with poorly developed endite (on its outer edge), epipod and podobranch; ischiobasis about twice as long as wide, with scattered setae; endopod merus half length of ischiobasis, carpus about half length of merus, propodus expanded, about as long as merus but twice as wide, dactylus short and wide; anterior and mesial margin of propodus bearing rows of setae, some on anterior margin strong.

Maxilliped 3 epipod, medial margin setose; exopod extending beyond article 1 of endopod. Endopod ischio-merus 1.4–2 times as long as propodo-dactylus; carpus 1.2–1.6 times as long as latter; ischio-merus with 2 rows of long setae, one on each of posterior and anteromesial margins; carpus with similar rows and additional row on lateral surface; propodo-dactylus with stout terminal seta and numerous plumose and serrate setae, parallel rows of shorter, serrate setae across anteromesial surface and longer plumose setae elsewhere. Two arthrobranchs, one rudimentary and obscured by the larger; maxilliped endopod relatively shorter in males than females. Body length: maxilliped 3 length ratio 3.7–4.5 in males, 3.5–4.3 in females.

Pereopod 1 articles smooth; reaching approximately to level of scaphocerite spine; tufts of serrate setae on posteroproximal region of palm and distomesial surface of carpus; outer surface of propodal finger with tufts of serrate setae, simple setae on both fingers; posteromesial ridge of ischium and merus with single row of long setae; fingers with simple cutting edge, 0.8–1.2 times as long as palm; carpus 1.5–2.5 times as long as chela and 1.1–1.4 times as long as merus; merus 1.1–1.9 times as long as ischium. Body length:pereopod 1 ratio 2.5–3.1 in males, 2.0–2.6 in females.



Figure 3. Habitus with colour pattern. a, Palaemon dolospina; b, telson of P. dolospina; c, Palaemon intermedius.

Pereopods 2 equal, similar in males and females, articles smooth, usually exceeding scaphocerite by all of palm; fingers slender, curved, with small tooth at base, cutting edges serrate, sometimes one or both smooth, particularly in smaller individuals; palm swollen, laterally flattened, 2.8-3.4 times as long as wide; palm 0.9-1.2 as long as fingers, usually longer; carpus long and slender, narrow proximally, 6.0-8.5 times as long as wide at that point, distally 1.7-2.4 times as wide as at base, length 6.0-8.5 times distal width; chela 0.9-1.4 times as long as carpus and 1.2-1.5 times merus; merus 1.0-1.3 times as long as ischium. Body length:pereopod 2 ratio 1.6-1.9 in males, 1.3-1.8 in females.

Pereopods 3–5 progressively longer, mainly owing to increase in lengths of propodi.

Pereopod 3 simple, slightly less than half body length; dactylus with small cutting edge on posterior border; propodus with 2 rows of long setae anteriorly, 2 variable rows of short plumose setae, outer row with 5–9 setae; propodus 2.0-2.5 times as long as dactylus and 1.5-1.9 times as long as carpus in males, 1.6-2.4 in females; merus 1.1-1.3 times as long as propodus and 1.1-1.5 times as wide; merus 1.9-2.4 times as long as lon

Pereopod 4 similar to 3, but slightly longer; propodus length about 2.5 times as long as dactylus, about twice as long as carpus; merus about same length as propodus and twice as long as ischium. Pereopod 5 similar to 3 and 4, slightly longer than 4; row of 5-7 short setae on lateral posterior margin of propodus with 5-7 parallel rows of serrate setae distally; mesial posterior edge with row of 7-10 short setae. Propodus 2.6–3.1 times as long as dactylus in male, 2.0–2.8 in female.

Branchial formula (r = rudimentary).

	Maxillipeds			Pereopods					Total gills
and the second	1	2	3	1	2	3	4	5	
Pleurobranchs	-	-	-	1	1	1	1	1	5
Arthrobranchs	-	-	1+1r	-	-	-	-	_	1 + 1r
Podobranchs	-	1	-	-	-	-	_	-	1
Exopods	1	1	1	1.00	-	-	÷.,	н	3
Epipods	1	1	1	Η	-	Η	-	$\exists$	3

Pleopod 1 with well developed exopod and smaller endopod; appendix interna absent. Endopod of male little more than half as long as exopod, with convex outer edge, concave inner edge, about 4 times as long as wide. Endopod of female smaller, about one third as long as exopod, about 3 times as long as wide.

Pleopods 2–5 with equally developed exopod and endopod; endopod with appendix interna. Endopod of male pleopod 2 with appendix masculina, longer than appendix interna, usually with 22 setae along its length, 6 of which are apical or subapical; each seta up to half as long as appendix masculina.



Figure 4. *Palaemon intermedius*. a, rostrum (female, 33.2 mm); b, rostrum (male, 20.8 mm); c, carapace spine (female, 30.2 mm); d, e, antennule and scaphocerite (female, 30.2 mm); f, scaphocerite (male, 28.0 mm); g, mandible; h, maxillule; i, maxilla; j–l, maxillipeds 1–3; m, mandible of post-larva (all mouthparts, female, 30.2 mm).

Pleopods 1–2 and to a lesser extent 3–5 with keel-shaped, flattened extension on lateral edge, smaller in male than female.

First abdominal pleuron about 2–3 times as long as wide; second abdominal pleuron about 1.5 times as long as wide; apex of fifth pleuron acute, with short terminal spine; sixth abdominal article 1.4–1.8 times as long as fifth. Ventral edges of abdominal pleura with row of short, plumose setae.

Telson 2.0–2.5 times wider at base than apex, length 2.9–4.2 times basal width; 1.1–1.4 times as long as sixth abdominal somite; with 2 pairs of dorsal stout setae and larger inner and smaller outer terminal pair; apex produced into acute spine flanked by a 1 simple seta on each side and occasionally a shorter second pair; apical spine much shorter than the terminal setae; tuft of long plumose setae dorsomedially near base of telson.

Uropods endopod elongate, fringed with long plumose setae; exopod rectangular; transverse suture on exopod about two-thirds of distance from base; outer edge of exopod entire, ending at suture line in an immovable spine; second movable seta often present inside spine; remainder of margin fringed by row of long plumose setae; posterior to immovable spine, dorsally and ventrally, a row of about 12 long, non-plumose setae set back from margin, extending almost to apex of exopod; ventrally, outer margin from base of the exopod to the immovable spine with row of stout, simple setae just inside the margin.

*Colour pattern.* Carapace chromatophore lines usually red; abdominal markings generally olive green, black and red; accessory flagellum distinctly marked with alternate red and white bands.

*Sexual dimorphism in adults.* Males are smaller than females; with larger sternal process on the eighth thoracomere; smaller keel-like expansion on outer edge of peduncles of pleopods; appendix masculina on pleopod 2; significantly larger endopod on pleopod 1; 4 setae in distal sensory row on each article of antennular inner flagellum (3 in adult female); rostrum more slender and longer; longer carpus in pereopod 2; maxilliped 3, pereopods 1 and 3 shorter relative to body length; the ratio of length of propodus and dactylus of pereopod 5 significantly greater.

Females ovigerous from 19.5 mm body length; bearing approximately 100–700 ovoid eggs, larger females bearing more eggs; egg size 0.55–1.0 mm depending on developmental stage, 0.9–1.0 mm when ready to hatch.

*Ontogenetic changes.* Some characters alter as the size of males and females increases. In females, the scaphocerite becomes stouter and shorter relative to body length; the number of articles over which the antennular flagella are fused increases; the carpus and merus of pereopod 1 become longer relative to other articles; the number of parallel rows of setae on the propodus of pereopod 5 increases, and pereopod 2 becomes longer. In males, the number of articles over which the antennular flagella are fused increases; length ratios between articles of pereopods 1–5 differ; pereopod 1 becomes slightly shorter relative to body length.

In early post-larval stages, the mandibular palp and the branchiostegal groove are absent and a branchiostegal spine is present on the edge of the carapace. Over a series of moults, a palp of three articles and the branchiostegal groove form and Palaemon and its southern Australian species



Figure 5. *Palaemon intermedius*. a–f, percopods 1–5; b details of chela of percopod 1 (male, 28.0 mm). g, h, pleopods 1, 2 (male); i, j, pleopods 1, 2 (female). k, telson. l, appendix masculina.

the branchiostegal spine migrates posteriorly and upwards to its final position in adults.

*Variation.* The type or types of *Leander intermedius* Stimpson, 1860 are lost. They were collected from Port Jackson, NSW. Examples of the species from nearby Port Hacking most resemble the typical Tasmanian form from Margate Beach but examples from other locations including Tasmania differ.

Deep-water form (5 adult females, 29.3–36.6 mm, D'Entrecasteaux Channel). More slender and longer legged than shallow water form. Scaphocerite more slender, rostrum with 2–3 but usually 3 postorbital teeth rather than 2; Pereopods 1, 3, 5 longer, body length 2.2–2.3 times as long as pereopod 1, 1.7–1.9 times as long as pereopod 2, 1.5–1.6 times as long as pereopod 5; carpus of pereopod 2 longer, carpus length 2.0–2.3, 3.7–4.7, 1.2–1.4 and 1.9–2.1 times as long as chela, fingers, merus and ischium respectively; palm more swollen, length 2.6–2.8 times its maximum width; apex of carpus more expanded; pereopods 3 and 5 with longer propodus; telson stouter, at least at its base, 2.2–3.8 times as long as basal width.

Intermediate form (4 ovigerous females, 21.2–33.0 mm, 2 adult males 26.2 mm, Western Port, Vic.). More similar to the deep-water form particularly in number of postorbital rostral teeth, length of percopods 2, 3, 5, and the degree the palm is swollen on percopod 2.

South Australian form (3 females (2 ovigerous) 21.9–35.9 mm, 1 adult male 20.8 mm, Spalding Cove, Port Lincoln. SA). Resembles closely Tasmanian material except for 3 postorbital rostral teeth and a more swollen palm on pereopod 2.

*Remarks. Palaemon intermedius* bears what appears to be an hepatic spine but it is set lower down and not as far back from the carapace edge as is usual in *Macrobrachium*, the genus to which it was assigned by Holthuis (1952). The branchiostegal groove appears to run back to the spine and over it, but ceasing at the back of the spine. The spine is open posteriorly, having no suture line between it and the carapace in that region. The migration of the branchiostegal spine from the carapace edge during ontogeny is arrested partly completed and the value of this character for generic assignment is therefore limited. Generic assignment is based principally on the other characters.

#### Palaemon dolospina sp. nov.

Figures 1e, 2f-j, 3c, 6, 7

Palaemon sp.-Walker, 1979.

*Material examined.* Holotype. Margate Beach, North West Bay, Tas. (lat long) in *Zostera muelleri* and *Heterozostera tasmanica* on sand, 0.2–1 m, T. Walker, 12 Dec 1973, NMV J52659 (male, 6.5 mm postorbital carapace length, 42 mm total length).

Allotype. Collected with holotype, NMV J52660 (ovigerous female, 8.9 mm postorbital carapace length, 45 mm total length)

Paratypes. Collected with holotype, NMV J52661 (92 specimens, 4.7–9.0 mm postorbital carapace length)

Material described. 26 males, 12–35 mm body length, 28 females, including 6 ovigerous, 12.6–40 mm body length, Margate Beach and in brackish water from North West Bay River Estuary, Margate, Tasmania, in seagrasses *Zostera muelleri* and *Heterozostera tasmanica*, T. M. Walker, 1975. 1 ovigerous female, 32.1 mm body length, Western Port, Victoria, intertidally on mud, Fisheries and Wildlife



Figure 6. *Palaemon dolospina*. a, rostrum (female, 31.8 mm); b, rostrum (male, 32.8 mm); c, carapace spine (female, 31.8 mm); d, e, antennule and scaphocerite (female, 31.8 mm); f, scaphocerite (male, 31.8 mm); g, mandible; h, maxillule; i, maxilla; j–l, maxillipeds 1–3 (all mouthparts, female, 31.8 mm).

Department, Victoria, 8 Jan 1974. 8 females, 2 ovigerous 13.9–34.6 mm, 6 males, 15.3–23.8 mm, ICI Saltfields, Port Gawler, South Australia, ICI staff ,13 Jan 1973. 6 ovigerous females, 37.7–50.7 mm, Newport Power Station, Victoria. H.A. Morrison, 21 July 1949.

Additional material from 50 sites in Tasmania (including Flinders and King Islands), 2 in Victoria, 3 in South Australia.

*Diagnosis.* Carapace smooth; branchiostegal spine set back from and its tip barely reaching anterior carapace edge, set high up on brachiostegite; branchiostegal groove runs up to, loops over the spine and sweeps down again posteriorly. Rostrum upper border with 6–9 teeth; 1–2 of these (usually 2) postorbital; dorsal teeth unevenly spaced, first set back from rest on carapace, next 3 or 4 evenly spaced, incompletely articulated, increasingly longer gap between next 3 until penultimate tooth close to distal tooth; ventral rostral border with 3–6 teeth (usually 4), evenly spaced over distal two-thirds.

Description. (based on 26 males, 28 females from Margate Beach, Tasmania. Characters resembling P. intermedius not described) Maximum body length (orbit to telson tip) c. 42 mm in males, c. 51 mm in females.

Carapace smooth; antennal spine strong and marginal; branchiostegal spine set back from and its tip barely reaching anterior carapace edge, set high up on brachiostegite; branchiostegal groove runs up to, loops over the spine and sweeps down again posteriorly.

Eyes well developed, with ocellus; interocular tooth well developed.

Rostral tip exceeding lamella of scaphocerite; length:depth ratio 6.5–9.3 in males, 5.3–7.6 in females; upper border straight

to concave; body length:rostral length ratio 2.4–3.6 in males, 2.5–3.5 in females; lateral carina gently concave and directed upwards at tip; third to half rostrum above lateral carina; upper border with 6–9 teeth; 1–2 of these (usually 2) postorbital; dorsal teeth unevenly spaced, first set back from rest on carapace, next 3 or 4 evenly spaced, incompletely articulated, increasingly longer gap between next 3 until penultimate tooth close to distal tooth; rostral tip appears bifid; single row of plumose setae along upper border between but not on teeth; ventral rostral border with 3–6 teeth (usually 4), evenly spaced over distal two-thirds; 2 rows of plumose setae on ventral border between but not on teeth.

Antennule well developed; basal article bearing subapical transverse row of 10 plumose setae, not extending onto stylocerite; basilateral spine moderately slender, sharply pointed, reaching over half basal article of peduncle; inner flagellum fused with outer usually over basal third of its length, about 11–12 articles in male and 14–15 in female, fused up to half its length in juveniles; each free article of inner flagellum with mesial and terminal transverse row of sensory setae, mesial row of 3–4 and distal of 4 setae in female, mesial row of 4 and distal of 5 (occasionally 4) setae in male; sensory setae noticeably shorter than those in *P. intermedius*.

Antennal scaphocerite elongate, rectangular, widest near base, 3.2–4.1 times as long as wide; outer edge slightly convex to slightly concave, with terminal spine that just fails reach anterior edge of lamella; inside edge straight or concave over distal two thirds, convex proximally.

Mandible incisor of one side with 3 teeth (either side), incisor of the other usually with 4; palp with 3 articles; article



Figure 7. *Palaemon dolospina*. a–f, percopods 1–5; b details of chela of percopod 1 (male, 32.8 mm). g, h, pleopods 1, 2 (male); i, j, pleopods 1, 2 (female). k, telson. l, appendix masculina.

2 with 10 or more setae; article 3 slightly swollen, setose including 3 terminal and 2 subterminal setae; article 3 length about twice article 2, article 1 about 1.5 times article 2. Maxillule endopod with bifid tip, naked, distal lobe acute. Maxilla endopod with 2 short setae on inner edge and about 10 on proximal half of outer edge. Maxilliped 1 endopod without seta.

Maxilliped 3 epipod, mesial margin setose; exopod extending to end of article 1 of endopod. Endopod ischio-merus 1.3–2 times as long as propodo-dactylus; carpus 1.2–1.6 times as long as latter; ischio-merus with 2 rows of long setae, one on each of posterior and anteromesial margins; propodo-dactylus with stout terminal seta Body length:maxilliped 3 length ratio 3.8–4.5 in both sexes.

Pereopod 1 articles smooth; reaching approximately to tip of scaphocerite lamella; tufts of serrate setae on posteroproximal region of palm and distomesial surface of carpus; outer surface of propodal finger with tufts of serrate setae, simple setae on both fingers; posteromesial ridge of ischium and merus with single row of long setae; fingers with simple cutting edge, 0.8–1.4 times as long as palm; carpus 1.3–2.2 times as long as chela and 1.0–1.4 times as long as merus; merus 1.3–1.8 times as long as ischium. Body length:pereopod 1 ratio 2.4–2.9 in both sexes.

Pereopods 2 equal, similar in males and females, articles smooth, usually exceeding scaphocerite by at least fingers; fingers slender, curved, with small tooth at base, cutting edges serrate, sometimes one or both smooth, particularly in smaller animals; palm slightly swollen, laterally flattened, 2.6–4.0 times as long as wide; palm 1.0–1.4 as long as fingers; carpus long and slender, narrow proximally, thickens distally to be 1.5–2.5 times wider than at base, length:apical width ratio

6.4-8.8 in males, 5.2-7.7 in females; chela 0.8-1.2 times as long as carpus and 1.0-1.4 times merus; merus 1.0-1.5 times as long as ischium. Body length:pereopod 2 ratio 1.6-2.2 in both sexes.

Pereopods 3–5 progressively longer, mainly due to increase in lengths of propodi. Pereopod 3 reaching about end of scaphocerite; dactylus with small cutting edge on posterior border; propodus with 2 rows of long setae anteriorly, 2 variable rows of short flagellate setae, outer row usually with 4–5 setae in male, 5–6 in female, inner row usually with 3–5 in male, 5 in female; propodus 1.5–2.1 times as long as dactylus and 1.4–1.8 times as long as carpus in males, 1.6–2.0 in females; merus 1.0–1.4 times as long as propodus and 0.9–1.5 times as wide; merus 1.8–2.4 times as long as ischium; 1.6–2.2 times as long as carpus in male, 1.8–2.4 in female.

Pereopod 4 similar to 3, but slightly longer. Pereopod 5 similar to 3 and 4, slightly longer than 4.

Branchial formula as for P. intermedius.

Pleopod 1 with well developed exopod and smaller endopod; appendix interna absent. Endopod of male little more than half as long as exopod, with convex outer edge, concave inner edge, about 4 times as long as wide. Endopod of female smaller, about one third as long as exopod, about 3 times as long as wide.

Pleopods 2–5 with equally developed exopod and endopod; endopod with appendix interna. Endopod of male pleopod 2 with appendix masculina, longer than appendix interna, usually with 24 setae along its length, 6 of which are apical or subapical; each seta less than third as long as appendix masculina. Pleopods 1–2 and to a lesser extent 3–5 with keelshaped, flattened extension on lateral edge, smaller in male than female. First abdominal pleuron about 2–3 times as long as wide; second abdominal pleuron about 1.5 times as long as wide; apex of fifth pleuron acute, with short terminal spine; sixth abdominal article 1.3–1.9 times as long as fifth. Ventral edges of abdominal pleura with row of short, plumose setae.

Telson 2.0–2.8 times wider at base than apex, length 3.0–4.3 times basal width; 1.0–1.3 times as long as sixth abdominal somite; with 2 pairs of dorsal stout setae and larger inner and smaller outer terminal pair; apex produced into acute spine flanked by 1 simple seta on each side and occasionally a shorter second pair; apical spine much shorter than terminal setae; tuft of long plumose setae dorsomedially near base of telson.

Uropods endopod elongate, fringed with long plumose setae; exopod rectangular; transverse suture on exopod incomplete laterally, about two-thirds of distance from base; outer edge of exopod entire, ending at suture line in an immovable spine; second movable seta often present inside spine; remainder of margin fringed by row of long plumose setae; posterior to immovable spine, dorsally and ventrally, a row of about 9 long, non-plumose setae set back from margin, extending almost to apex of exopod; ventrally, outer margin from base of the exopod three quarters of the way to the immovable spine with row of stout, simple setae just inside the margin.

*Colour pattern.* Carapace chromatophore lines red; distinct transverse abdominal bars generally red but may be olive green; abdominal bars present on first post-larva as single lines of orange or yellow chromatophores; lateral carina of rostrum often with row of large, white chromatophores; hexagonal matrix of abdominal segments most distinct in large females, made up of small, olive green and some scattered white chromatophores; viewed dorsally, tail fan with white, transverse bands or patches.

Sexual dimorphism in adults. Males are smaller and more slender than females; with larger sternal process on the eighth thoracomere (almost absent in female); smaller keel-like expansion on outer edge of peduncles of pleopods; appendix masculina on pleopod 2; significantly larger endopod on pleopod 1; 5 setae in distal sensory row on each article of antennular inner flagellum (3–4 in adult female); rostrum more slender and longer; broader carpus in pereopod 2; longer carpus in pereopod 3; ratio of length of propodus and dactylus of pereopod 5 greater.

Females ovigerous from 25 mm body length; bearing approximately 140-840 ovoid eggs, larger females bearing more eggs; egg size 0.65-1.15 mm depending on developmental stage, 0.9–1.15 mm when ready to hatch.

*Ontogenetic changes.* Some characters alter as the size of recognisably male and female animals increases. In females, the rostrum and scaphocerite becomes stouter and shorter relative to body length; the number of articles over which the antennular flagella are fused increases; pereopods 2, 3, 5 become longer relative to the body; the fingers of pereopod 1 become shorter relative to other articles; the palm of pereopod 2 becomes less swollen, the carpus more expanded and fingers shorter; the number of parallel rows of setae on the propodus of pereopod 5 increases; and the telson becomes stouter. In males,

the number of articles over which the antennular flagella are fused increases; length ratios between articles of pereopods 1–5 differ; carpus of pereopod 1 becomes relatively longer; pereopod 2 palm becomes less swollen and fingers shorter.

In early post-larval stages, the mandibular palp and branchiostegal groove are absent and a branchiostegal spine is present on the edge of the carapace. Over a series of moults, a palp of 3 articles and branchiostegal groove form and the branchiostegal spine migrates posteriorly and upwards to its final position in adults.

*Etymology.* From Latin, *dolus* meaning deceit and *spina*, a spine, alluding to the deceptive position of the branchiostegal spine.

*Remarks. Palaemon dolospina* bears a branchiostegal groove looping over a spine set back from the carapace edge albeit displaced dorsally somewhat. Consequently, although the spine is situated unusually high on the carapace between the usual branchiostegal and hepatic position, it can be defined as branchiostegal. Females are larger than males and the second pereopods of males are not spinulose or markedly sexually dimorphic. The mandibular palp is of three articles. In spite its unusual branchiostegal spine/groove arrangement, this species clearly belongs to *Palaemon*.

## Keys to species of *Palaemon* and *Palaemonetes* from southern Australia

The shallow marine and estuarine Australian palaemonid fauna includes eight, possibly nine, species distributed as follows:

Palaemon debilis Dana, 1852 – Widespread in Indo-West Pacific, Qld, redescribed by Holthuis (1950) and Chace (1972).

Palaemon cf. debilis Dana, 1852 – NSW, eastern Vic., also similar to Palaemonetes atrinubes but its status remains unresolved.

Palaemon dolospina sp. nov. - Vic., Tas., SA.

Palaemon intermedius (Stimpson, 1860) – Qld (N to Moreton Bay), NSW, Vic., Tas., SA, WA.

Palaemon litoreus (McCulloch, 1909) – NSW, Vic., SA, WA. Palaemon serenus and P. litoreus have in the past, been separated on the basis of the carpus exceeding the palm of pereopod 2 in P. serenus but being shorter in P. litoreus (McCulloch, 1909; Hale, 1927b; Bray, 1976). Examination of material of both species from Western Australia has shown that, the carpus exceeds the palm in both species.

Palaemon macrodactylus Rathbun, 1902 – NSW, SA [native to Japan, Korea, northern China, introduced to San Francisco Bay and two Australian localities (Buckworth, 1979; Walker, 1979). Identifications of Australian material confirmed by TW and L. Holthuis, 1976].

Palaemon serenus (Heller, 1862) – southern Qld, NSW, Vic., Tas., SA WA.

Palaemonetes australis Dakin, 1915 – WA. Palaemonetes atrinubes Bray, 1976 – NT, Qld, Vic, WA

 Carapace spine set back from carapace edge by less than its length and situated between branchiostegite and ridge of antennal spine; open posteriorly; branchiostegal groove runs up to dorsoposterior edge of spine but not past it (Figs 2.

3.

4.

5.

6

7.

1d, 4c); pereopod 2 smooth and equal; rostrum with 7-10 1. dorsal teeth, usually 8, 2-3 postorbital, proximal 4 incompletely articulated; 4-6, usually 5, ventral teeth ..... 2. .....Palaemon intermedius Carapace spine set below branchiostegal groove which \_ may deviate up and over the spine; spine may be on or set 3. back from edge of carapace; pereopod 2 and rostrum not as Branchiostegal spine set back from the carapace edge, Branchiostegal spine at or very near carapace edge just under start of branchiostegal groove; groove running back 4. from carapace edge in a shallow arc, not upwards sharply Branchiostegal spine almost or just reaching carapace edge with tip only; set above level of starting point of branchiostegal groove which runs upwards to front of spine, loops sharply over it and sweeps down again posteriorly (Figs 1e, 6c); percopod 2 carpus 1-1.5 times as long as merus; mandibular palp with 3 articles ..... 5. .....Palaemon dolospina Branchiostegal spine set well back from the carapace edge which it never overlaps; branchiostegal groove deviating only slightly as it passes over spine (Fig 1c); pereopod 2 carpus 1.3-1.5 times as long as merus; mandibular palp absent ..... Palaemonetes australis 6. Antennule inner flagellum fused for greater than half of its length, usually over about two thirds, 16-20 articles fused in adults; mandibular palp absent ..... Antennule inner flagellum fused for half or usually less of 7. its length, less than 15 articles fused in adults .....5 Pereopods slender (carpus of pereopod 2 1.5-2.0 times as long as chela, 1.4–1.7 times as long as merus) ......6 Pereopods not unusually slender (carpus of pereopod 2 shorter than chela, 0.9–1.1 times as long as merus .... 7 Rostrum exceeding scaphocerite by at least quarter of its length; proximal 2 dorsal teeth fully articulated; 5-7 8. ..... Palaemon debilis ventral teeth Rostrum exceeding scaphocerite by less than quarter of its length; no fully articulated dorsal teeth; 3-4 ventral teeth ..... Palaemon cf. debilis Pereopod 2 stout but short, 0.4-0.5 times body length 

- articulated; about one third of antennule inner flagellum fused (about 12 articles in adults) .... Palaemon serenus

In fresh material, pigmentation pattern can help separate species in this alternative key. The colour description for *Palaemon litoreus* was taken from a description by McNeill in Holthuis (1952) and those for *Palaemonetes australis* and *P. atrinubes* from Bray (1976).

Without dorsal hump on abdominal somite 3 .....2 Distinct dorsal hump on abdominal somite 3 ..... 4 Long, slender rostrum, substantially exceeding scaphocerite ..... Palaemon debilis Distinct black spot at posterolateral end of sixth abdominal somite; 3 distinct red and blue lines on carapace; 1 transverse line across posterior edge of third abdominal somite ......Palaemonetes atrinubes Without black spot at base of sixth abdominal somite .... ......Palaemon cf. debilis Broad, red band across most of palm of pereopod 2; fingers white; abdomen with longitudinal rows of few large spots of red, blue and black chromatophores; distinct longitudinal stripes on carapace ..... Palaemon serenus Without wide red band or only a narrow one across palm of pereopod 2; if narrow red band present, abdomen with saddle stripes of red on dorsal and lateral Grey or olive-green; distinct wide, grey band across palm of percopod 2; diffuse longitudinal and oblique rows on carapace; diffuse transverse lines on posterior edges of abdominal articles ..... Palaemon macrodactylus Without wide grey or olive-green band on palm of Saddle stripes of red across back and sides of whole body; less distinct on carapace; palm of pereopod 2 with narrow red band; fingers with similar band half way along ..... Without longitudinal stripes on abdomen .....7 Distinct red lines either obliquely on carapace or trans-Overall olive-green or brown due to red, white, yellow and blue chromatophores; carapace with diffuse dorsal and anterior bands and indistinct mottling posteriorly; antennule inner flagellum pale red ..... ..... Palaemonetes australis Distinct transverse red and/or occasionally olive stripes across all abdominal somites; less distinct longitudinal and oblique red stripes on carapace (Fig. 2a, b); antennule inner flagellum pink with few white flecks; often row of white chromatophores along lateral carina of the Distinct oblique and transverse red lines on carapace; few scattered red, olive and black chromatophores forming indistinct transverse lines on abdominal segments (Fig. 2c); antennule inner flagellum with definite red and white bars, persisting as purple bars in ethanol-preserved 

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