REDESCRIPTION OF *LYSMATA INTERMEDIA* (KINGSLEY, 1879) BASED ON TOPOTYPICAL SPECIMENS, WITH REMARKS ON *LYSMATA SETICAUDA* (RISSO, 1816) (DECAPODA, CARIDEA, HIPPOLYTIDAE)

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ABSTRACT

In older literature, it has been claimed that the West Indian shrimp *Lysmata intermedia* also exists at Faial Island, in the Azores. It is now demonstrated here that these Azorean records of *L. intermedia* are actually based on *L. seticaudata*. Previous confusion probably arose from the very close similarity between the two species. *L. intermedia* is here redescribed on the basis of topotypical specimens (Dry Tortugas, Florida). It is shown that *L. seticaudata* displays significant geographical variations, the Atlantic specimens and particularly those of the Azores being more robust than those from the Mediterranean Sea. In *L. seticaudata*, the number of segments on the accessory branch of the outer antennular flagellum also increases with total body size. A synonymy and a brief account on their geographical distribution and their ecology are given for both species.

RÉSUMÉ

Dans la littérature ancienne, la crevette caraïbe *Lysmata intermedia* a été signalée à l’île de Faial, dans l’archipel des Açores. Nous montrons ici que ces signalements sont erronés et résultent d’une confusion avec *L. seticaudata*. L’extrême similitude entre les deux espèces explique aisément ces identifications antérieures incorrectes. *L. intermedia* est redécrite à partir de spécimens de la localité-type (Dry Tortugas, Florida). Il appert que *L. seticaudata* présente certaines variations géographiques, les spécimens atlantiques, et tout spécialement ceux des Açores, étant plus robustes que ceux de la Méditerranée. Chez *L. seticaudata*, il ressort aussi que le nombre de segments de la branche accessoire du flagelle antennulaire externe augmente avec la taille de la crevette. Une synonymie est donnée pour les deux espèces, de même qu’un résumé des informations disponibles sur leur distribution géographique et leur écologie.

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INTRODUCTION

*Lysmata intermedia* (Kingsley, 1879) has originally been described, without illustration, from Dry Tortugas, Florida by Kingsley (1879), as *Hippolysmata intermedia*. Kingsley (1882) gives a figure of this species, but only of the carapace, probably based on a syntype. Both Kingsley’s accounts are incomplete. Rathbun (1901) gives a further description, without illustrations, based on West Indian and Azorean material. Sivertsen (1933) reports the occurrence of *Lysmata intermedia* in the Galapagos Islands, and gives figures of moderately good quality of his material. The identity of Sivertsen’s material has never been really contested, although his illustrations suggest significant differences with accounts based on topotypical (tropical northwestern Atlantic) material. Chace (1969) records a specimen of *L. intermedia* from Venezuela and indicates that it significantly differs from a specimen from the Azores, obviously the Azorean specimen already recorded by Rathbun (1901). Chace (1972) gives an excellent key of western Atlantic *Lysmata* and obviously used topotypical (West Indian) *L. intermedia* for constructing that key. However, he gives neither an illustration nor a formal description of *L. intermedia*. Rodriguez (1980) redescribes and illustrates the supposed Venezuelan *L. intermedia* already recorded by Chace (1969); his figure shows an undivided accessory antennular branch, in discordance with previous accounts dealing with *L. intermedia*. Wicksten (1983, 1990) and Kerstitch (1989) again report *L. intermedia* in the Eastern Pacific but give no detailed descriptive accounts. Finally, Manning & Chace (1990) reexamine the Azorean *Lysmata* of Rathbun (1901) and accept her identification as *L. intermedia*; they also record *L. intermedia* on Ascension Island, without giving any descriptive information on their material.

So, literature data suggest an unusually wide distribution for *L. intermedia*, and the descriptive accounts based on specimens from various geographical areas are all very incomplete and comprise divergent information.

Finally, from the published data, and particularly the keys of Chace (1972, 1997), it appears that *L. intermedia* (Kingsley, 1878) is apparently closely related to the European species *L. seticaudata* (Risso, 1816) and *L. nilita* Dohrn & Holthuis, 1950.

*Lysmata* from the Azores have recently been collected for me by Prof. Dr. Peter Wirtz (Funchal, Madeira). Their colour pattern and their morphology were very similar to the common northeastern Atlantic and Mediterranean species *Lysmata seticaudata*, although several appendages of Azorean *Lysmata* were much more robust than in toptotypical (West-Mediterranean) *L. seticaudata*. So, at first, I have considered the possibility that my Azorean specimens could belong to the insufficiently described *L. intermedia*. 
Through the courtesy of Dr. R. B. Manning (Washington, D.C., U.S.A.), a large sample of topotypical *L. intermedia* was made available to me for comparison. It allowed me to conclude that Azorean *Lysmata* are not *L. intermedia* but *L. seticaudata*, such despite significant differences in robustness with Mediterranean specimens of the latter species. Previous confusion can easily be explained by the extreme similarity between *L. intermedia* and *L. seticaudata*.

As a consequence of the above considerations, the following aspects are developed in the present paper. Topotypical specimens of *L. intermedia* are redescribed and illustrated. *L. intermedia* (Kingsley, 1878) is compared with *L. seticaudata* (Risso, 1816) and with *L. nilita* Dohrn & Holthuis, 1950. The geographical and individual variability of *L. seticaudata* is also briefly discussed.

**SYSTEMATICS**

*Lysmata intermedia* (Kingsley, 1879) (figs. 1, 2A-C, E-G, 3)

*Hippolyssmata intermedia* Kingsley, 1879: 90 [Fort Jefferson and Tortugas, Florida]; 1882: 126, pl. 1 fig. 4 [no list of material, drawing of carapace probably based on type]; Rathbun, 1901: 115 (key), 116, in part: West Indian material only [specimens from Pim Bay, near Horta, Faial Island, Azores = *L. seticaudata*]; Schmitt, 1924: 69 (possibly only in part) [Curaçao].


? Not *Hippolyssmata intermedia* — Sivertsen, 1933: 5, pl. 2 figs. 9-15 [Galapagos].


Not *Lysmata intermedia* Manning & Chace, 1990: 23 [Pim Bay, near Horta, Faial Island, Azores and Ascension Island] (at least the Azorean specimens = *L. seticaudata*) [no description].

Not *Lysmata* sp. — Chapman & Santler, 1955: 373 [Horta Harbour, Faial Island, Azores] (= *L. seticaudata* (Risso)).

Fig. 1. *Lysmata intermedia* (Kingsley, 1879). Dry Tortugas, female, USNM 127791. Scale: 5 mm.
Description. — Rostrum fairly high, straight, 0.6 times as long as carapace, reaching 0.5 to 0.8 of third segment of antennular peduncle. Rostrum with 6 to 7 dorsal teeth: 2 to 3 in postrostral position and 3 to 4 (sometimes 5) in rostral position; 2 (sometimes 3, rarely 1) ventral teeth close to rostrum tip. Antennal tooth long and sharp, not separated from ventral angle of orbit. Pterygostomian tooth well developed and acute. Pleura of 4th pleonite usually terminated by a small tooth but sometimes rounded, pleura of 5th pleonite with a well developed
terminal tooth. Ratio dorsal length/height of 6th pleonite = 1.2. Ratio dorsal length of 6th/5th pleonite = 1.3 to 1.4. Ratio dorsal length of 6th pleonite/length of telson (not including terminal spines) = 0.6 to 0.8. Lateral margins of telson with many long setae on distal half. First pair of dorsolateral spines usually on 0.3 and second on 0.6 of telson (but variability important). Telson tip with well developed blunt apical tooth, and with 6 terminal spines: outer spines short; submedian spines long and strong; median spines thin and extremely long, pectinate, over twice as long as submedian spines (one telson tip examined). Antennular peduncle with stylocerite usually distinctly overreaching outer border of basal segment (sometimes just reaching). Dorsal antennular flagellum with accessory branch of 3 to 4 articles; 9-17 segments before bifurcation. Ratio length of accessory branch/length of flagellum before bifurcation = 0.13 to 0.15. Antennular peduncle overreached by 0.3 of scaphocerite. Scaphocerite slender with outer margin slightly concave; outer distal tooth very distinctly overreaching blade. Scaphocerite 4.4 times as long as wide (distal tooth included) in dissected scaphocerite. Mxp3 normally with 6 distal and 2 subdistal spines; exopodite reaching 0.8 of antepenultimate segment; normally at least 0.25 of ultimate segment overreaches scaphocerite. Ratio ultimate/penultimate segment of Mxp3 (dorsolaterally measured) = 2.0. Epipod on P1 to P4. P1 reaching tip of scaphocerite; P1 carpus reaching tip of antennular peduncle. Ratio length of merus/length of propodus in P1 = 1.2. Ratio length of propodus/length of carpus in P1 = 0.9 to 1.2 (longest carpus in small shrimps). Ratio length of dactylus/length of propodus in P1 = 0.3. P2 with merus subdivided in 14 to 17 inconspicuous segments and carpus in 25 to 31 (usually 28 to 30) distinct segments. P3-P5 with sparse long setae. P3 merus reaching middle of scaphocerite. P3 merus with 6 to 9 spines: 4 to 6 lateral or ventrolateral + 2 (occasionally 3) ventral [the distal spine is considered as lateral]. P4 merus with 5 to 8 spines: 3 to 5 lateral + 2 (occasionally 3) ventral. P5 merus with 2 to 4 spines (all lateral). P3 propodus with about 10 (sometimes 14) ventral spines or group of spines. P3-P5 dactylus with 5 (rarely 4 or 6) spines. Endopod of first male pleopod elongate. Appendix masculina (spines not included) nearly as long as endopod of second pleopod; approximately 0.5 to 0.6 of appendix masculina overreaches appendix interna; appendix masculina with terminal and lateral setae. Colour pattern: striped (cf. note within the vial USNM 127794).

Length. — Total length of females up to 22 mm and carapace length without rostrum up to 5 mm.

Geographical distribution and ecology. — Western Atlantic: Florida Keys to Tobago and Curaçao; mainly on grass flats studded with Porites and Pocillopora, also associated with algae on rocky shores and more rarely between reef corals; intertidal to 22 m deep (Chace, 1972). Only the largest L. intermedia (Kingsley,
REDESCRIPTION *LYSMATA INTERMEDIA*

Fig. 3. *Lysmata intermedia* (Kingsley, 1879), Dry Tortugas: A, female, USNM 127787; B-D, sex unknown (detached appendages), USNM 127794. A, first left pereiopod; B, second left pereiopod; C, fourth left pereiopod; D, dactylus of the same. Scales: A-C, 1 mm; D, 0.5 mm.

1878) examined by me are females, which suggests that it is a protandrous species, just like the two closely related species *L. seticaudata* (Risso, 1816) and *L. nilita* Dohrn & Holthuis, 1950 (cf. Dohrn & Holthuis, 1950).
Type material. — R. B. Manning (in litt.) wrote me: “So far I know, Kingsley’s types are not extant”.

Erroneous and uncertain records. — The identity of the Eastern Pacific *Lysmata* identified by Sivertsen (1933) as *L. intermedia* is questionable. Indeed, the ptery-gostomian area of Sivertsen’s illustrated shrimp is bluntly angular and devoid of the tooth characteristic of totopypical *L. intermedia*. In Sivertsen’s illustration, the accessory branch of outer antennular flagella have 6 segments (he indicated that there are 5 segments in the text) while there are 3 or 4 in totopypical *L. intermedia*. In Sivertsen’s shrimp, the rostrum has 3 ventral teeth, a feature that is not very frequent in totopypical *L. intermedia*. In Sivertsen’s shrimp the merus of third pereiopod has 3 ventral spines, another feature that is not very frequent in totopypical *L. intermedia*. I suspect that the Eastern Pacific form belongs to a closely related undescribed species. The identity of Chace’s (1969) and Rodriguez’s (1980) Venezuelan specimen identified as *L. intermedia* is also unclear. Although its general appearance agrees rather well with totopotypical *L. intermedia*, the accessory branch of its outer antenna consists of a unique segment, and not 3 or 4 as in totopypical *L. intermedia*. The unusual morphology of Rodriguez’s specimen cannot result from its small size (total length = 15 mm), since West Indian specimens of the same dimensions examined by me have 3- or 4-segmented accessory antennular branches. The Brazilian *L. intermedia* recorded by Ramos-Porto et al. (1995) have probably been identified correctly, although the description and figures given by these authors are insufficiently detailed to definitely confirm the identity of their specimens.

Nothing can be said as regards the identity of the supposed *L. intermedia* from Brazil reported by Christoffersen (1998), since this author gives no morphological account of his material.

The record of *L. intermedia* from Ascension Island reported by Manning & Chace (1990) is based on a misidentification and the specimen is probably *L. seticaudata* (cf. R. B. Manning, in litt.).

All shallow-water *Lysmata* from the Azores, examined by me prove to be *L. seticaudata* (as characterized here below) and not *L. intermedia*. Having established this, it gave me serious doubts as to the real identity of the Azorean *L. intermedia* reported by Rathbun (1901) and Manning & Chace (1990). On my request, Dr. Manning reexamined Rathbun’s (1901) specimen once more and informed me that it is a *L. seticaudata*, as characterized in the present paper. The previous confusions between the two species by highly qualified carcinologists are easily explained by their extreme similarity.

Distinction between *L. intermedia* and most related species. — In order to prevent further confusion, the western Atlantic *Lysmata intermedia* (Kingsley, 1879) has to be compared with its close relative *L. seticaudata* (Risso, 1816)
and *L. nilita* Dohn & Holthuis, 1950 from the northeastern Atlantic and the Mediterranean Sea. The other described Atlantic *Lysmata* are not closely related; they are listed by Fransen (1991).

First of all, it is important to point out that *L. intermedia* is much smaller than the other two species. The maximal total length is approximately 22 mm in *L. intermedia* (present material), 67 mm in *L. seticaudata* (see Smaldon et al., 1993), and 38 mm in *L. nilita* (see Dohrn & Holthuis, 1950).

The most important differentiating character concerns the outer antennular flagellum. In adult *L. intermedia*, the accessory branch consists of 3 or 4 segments. In adult *L. seticaudata*, it consists of 8 to 15 segments (Dohrn & Holthuis, 1950). However, in young *L. seticaudata* from Calvi, Corsica examined by me, and of a size comparable to adult *L. intermedia*, there are only 5 segments in the accessory branch. Adult *L. nilita* have 4 to 7 segments in the accessory branch (Dohrn & Holthuis, 1950); data on young specimens are not available. The ratio length of the accessory branch/length of the flagellum before bifurcation, is the best discriminating character. It is approximately 0.13-0.15 in adult *L. intermedia* (present material), 0.5 to 0.6 in adult *L. seticaudata* (see Dohrn & Holthuis, 1950) and 0.4 in young *L. seticaudata* of a comparable size to *L. intermedia* (present material). The ratio is 0.2-0.3 in adult *L. nilita* (see Dohrn & Holthuis, 1950).

The number of segments of the antennular flagellum prior to its bifurcation is a character of limited value. There are 9-17 segments in *L. intermedia* (present material), 20 to 38 in adult *L. seticaudata* (see Dohrn & Holthuis, 1950) but only 15 in a young *L. seticaudata* of the size of adult *L. intermedia* (material examined personally), 21 to 27 in adult *L. nilita* (see Dohrn & Holthuis, 1950).

In *L. intermedia*, the merus of the third pereiopod has usually 2 ventral spines, sometimes 3 (the ultimate spine being not considered as a ventral spine but as a lateral spine). In *L. seticaudata* examined by me there are always 3 spines. According to Dohrn & Holthuis (1950), there are 3 to 6 ventral spines in *L. nilita*.

In *L. intermedia*, the rostrum reaches 0.5 to 0.8 of the third segment of the antennular peduncle. The length of the rostrum is more variable in *L. seticaudata*: the rostrum often reaches the middle of the third segment but occasionally fails to reach the basis of the third segment (present material). In *L. nilita*, the rostrum slightly overreaches the tip of second segment (description of Dohrn & Holthuis, 1950) or almost reaches the tip (fig. 1a of Dohrn & Holthuis, 1950).

In *L. intermedia* and *L. seticaudata*, the distal tooth of the scaphocerite distinctly overreaches the blade and follows the concave curvature of the outer margin of the scaphocerite (present material), while in *L. nilita* the distal tooth is often poorly developed, sometimes hardly overreaches the blade, and is slightly curved towards the blade (Dohrn & Holthuis, 1950).
Diurnal colour patterns: possibly longitudinally striped in *L. intermedia*, with longitudinal stripes and a few discrete white dots in *L. seticaudata*, without longitudinal stripes but with broad ill-defined transverse stripes in *L. nilita* (at night, *L. seticaudata* also presents broad ill-defined transverse stripes, in addition to the longitudinal stripes). For good colour photographs of *L. seticaudata*, see synonymy of the species here below. For a sketch of colour pattern of *L. nilita*, see Dohrn & Holthuis (1950).

The climatic affinities of the West-Atlantic and East-Atlantic species are different. *L. intermedia* is a tropical/subtropical species while *L. seticaudata* and *L. nilita* are warm-temperate species.

Finally, it should be pointed out that in his worldscale key of the genus *Lysmata*, Chace (1997) indicates that the lateral margin of scaphocerite is straight in *L. seticaudata* and concave in *L. intermedia*. In the material available to me, the lateral margin is faintly concave in both species. As concerns this appendage, the only difference I see concerns the ratio length/width, the scaphocerite being somewhat narrower, particularly in its distal part, in *L. intermedia* than it is in *L. seticaudata*.

**Lysmata seticaudata** (Risso, 1816) (figs. 2D, 4, 5)


*Palemon Cognetii* Risso, 1816: 106.

*Melicerta Seti Caudata* Risso, 1816: 110, pl. 2 fig. 1 [precedence given over *Palemon Cognetii* by Holthuis (1977)].


*Alpheus Cogneti* — Risso, 1827: 76.

*Lysmata aberrans* Czerniavsky, 1884: 63, pl. 3 fig. 7a-k; Băcescu, 1937: 5, fig. 4.

*Miersia clavigera* Chun, 1888: 34, pl. 4 fig. 6 (possibly in part).

*Hippolysmata intermedia* — Rathbun, 1901: 115 (key), 116, in part: only material from Pim Bay [near Horta], Faial Island, Azores [not *Lysmata intermedia* (Kingsley, 1879)].

*Lysmata intermedia* — Chace, 1967: 149, in part: only material from the Azores; Manning & Chace, 1990: 23: material from the Azores and probably also material from Ascension Island (no description) [not *Lysmata intermedia* (Kingsley, 1879)].
Fig. 4. *Lysmata seticaudata* (Risso, 1816), females, third left pereiopod. A, Azores, Horta; B, Madeira, Baia d’Abra; C, Bay of Biscay, Spain, Cabo Oyambre; D, western Mediterranean, Corsica, Calvi; E, Aegean Sea, Lesbos Island, Anaxos. Scale: A-E, 2 mm.
Fig. 5. *Lysmata seticaudata* (Risso, 1816), females; A, C, Azores, Horta; B, D, western Mediterranean, Corsica, Calvi. A, B, left scaphocerite; C, D, left side of sixth pleonite. Scales: 2 mm.


Distribution and ecology. — Eastern Atlantic from Western part of English Channel (Norman, 1907; Sinel, 1907; Dauvin et al., 1991) to Morocco (Lagardère, 1971), the Azores (Barrois, 1888; Rathbun, 1901 as Hippolysmata intermedia Kingsley; Chapman & Santler, 1955 as Lysmata sp.; Manning & Chace, 1990 as Lysmata intermedia (Kingsley); Wirtz, 1995; Morton et al., 1998), Madeira (Wirtz, 1997), Canary Islands (González Pérez, 1995), ? Ascension Island (Manning, in litt.), the whole Mediterranean Sea (d’Udekem d’Acoz, 1999), Black Sea (Băcescu, 1967). Sometimes between the rhizomes of Posidonia oceanica (Linnaeus) Delile (Zariquiey Alvarez, 1968); mainly on hard bottoms, particularly in anfractuosities, nocturnal (Couturier-Bhaud, 1974a). Intertidal (Barrois, 1888) to 60 m (Holthuis, 1987). Often associated with the moray Muraena helena Linnaeus, 1758 which it cleans of its parasites (Baensch & Debelius, 1992). Cleaning behaviour common only in areas where it is not in competition with Lysmata grabhami (Gordon, 1935) (cf. Wirtz, 1995). Sometimes associated with the sea anemone Telmatactis cricoides (Duchassaing, 1850) (cf. Wirtz, 1997). Data on larval development summarized by Couturier-Bhaud (1974c) and Barnich (1996). L. seticaudata is a protandrous species (Dohrn, 1950; Charniaux-Cotton, 1958, 1961; Couturier-Bhaud, 1974a, b).

Remarks. — Two diagnostic characters of L. seticaudata given in Chace’s (1997) worldscale key of the genus Lysmata are incorrect. In opposition to Chace’s account, I observe that in L. seticaudata the outer border of its scaphocerite is slightly concave and not straight, and its distal spine overreaches the blade.

Geographical variations. — As indicated above, Azorean L. seticaudata are much more robust than specimens from the western Mediterranean Sea. This robustness difference affects various structures and is particularly evident in pereiopods (fig. 4A, D) and in scaphocerites (fig. 5A, B), less in 6th pleonite (fig. 5C, D).

I have compared specimens from various areas available to me as concerns the third pereiopod, making a drawing of an adult female of every distant locality examined (fig. 4). It appears that the most slender third pereiopods are found in the western Mediterranean (Corsica) and the most robust in the Azores. The specimens from the Bay of Biscay and from Madeira have an intermediate robustness, which suggests a clinal variation, the robustness increasing westwards. However, this general trend is not absolute and the specimen from the eastern Mediterranean (Lesbos) is more robust than those from Corsica. It is, however, important to notice that the number of available specimens is too small to allow very precise comparisons.

Interestingly, it appears that the pattern of geographical variations is different in some other hippolytid shrimps. For instance, in Hippolyte complex varians Leach,
1814, the most slender form does occur in the Mediterranean Sea, as in *L. seticaudata*, but the most robust form is found along the continental Atlantic coast of Europe, the specimens from Madeira being more or less intermediate, although closer to the Atlantic continental form (d’Udekem d’Acoz, 1996). Furthermore there is an abrupt passage between the Mediterranean form and the Atlantic continental near Gibraltar (García Raso et al., 1998).

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REDESCRIPTION LYSMATA INTERMEDIA


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