

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

BY

CÉDRIC D'UDEKEM D'ACOZ<sup>1</sup>)

Avenue du Bois des Collines 34, B-1420 Braine-l'Alleud, Belgium

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 redécrise 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.

---

<sup>1</sup>) Research Associate at the Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium;  
e-mail: cdudekemda@be.packardbell.org

## 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 topotypical (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)**

*Hippolysmata 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].

*Lysmata intermedia* — Kemp, 1914: 112; Holthuis, 1947: 19, in part (list); Chace, 1972: 125 (key), 128 [West Indies]; Abele & Kim, 1986: 233, ? in part: key after Chace, 1972, ? not 243 fig. b-d (after Sivertsen, 1933); Fransen, 1991: 67 [West Indies]; ? Ramos-Porto et al., 1995: 107, fig. 1 [Brazil]; Chace, 1997: 72 (key); ? Christoffersen, 1998: 351 [Brazil] (list).

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

? Not *Lysmata intermedia* — Chace, 1969: 149 [Venezuela]; Rodriguez, 1980: 168, fig. 47 [Venezuela]; Wicksten, 1983: 22 (key), 28 (colour description) [Eastern Pacific]; Kerstitch, 1989: 81, fig. 199 (colour photograph) [Eastern Pacific]; Wicksten, 1990: 596 (key) [Eastern Pacific]; Debelius, 1999: 126, unnumbered colour photograph.

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)).

Material examined. — U.S.A., Florida, Dry Tortugas, Fort Jefferson, near intake pipes S.E. side, east of entrance, washed from seaweed, 04/viii/1924: 1 female, USNM 127787, Acc. no 84/129 — Dry Tortugas, Bird Key Reef, Sta. 34-32, 06/vi/1932: 3 males and 1 ovigerous female, USNM 127801 — Dry Tortugas, Sta. 25-5, 06/vi/1925: 1 ovigerous female, USNM 127790 — Dry Tortugas, East Side of Loggerhead Key, from two buckets of turtle grass, roots, etc., 17/vi/1925: 1 adult male and an ovigerous female, USNM 127791 — Dry Tortugas, Sta. 28-30, 22/vi/1930: 6 males and 1 ovigerous female, “Red striped yellow, legs reddish flagella, body trans.”, USNM 127794 [All material previously correctly identified in 1969 by Chace].

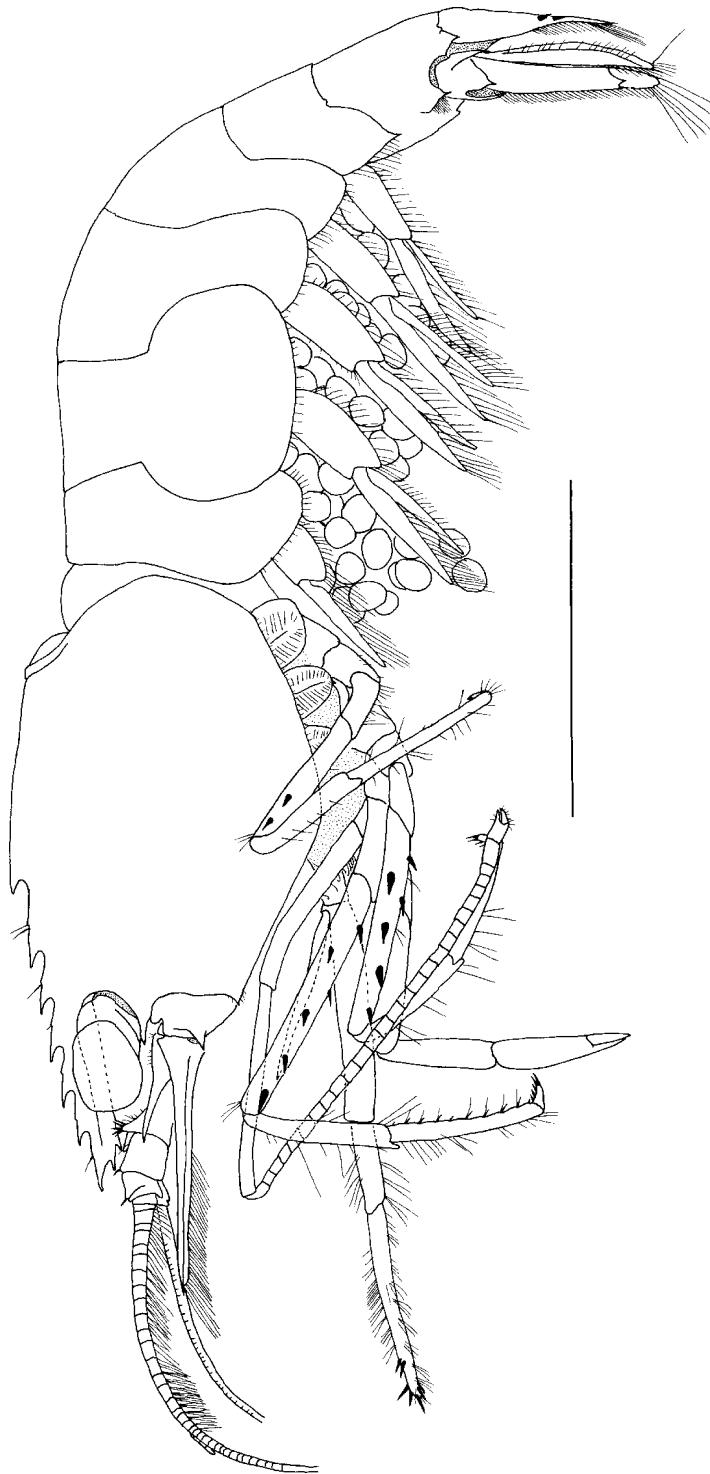


Fig. 1. *Lysmata intermedia* (Kingsley, 1879), Dry Tortugas, female, USNM 127791. Scale: 5 mm.

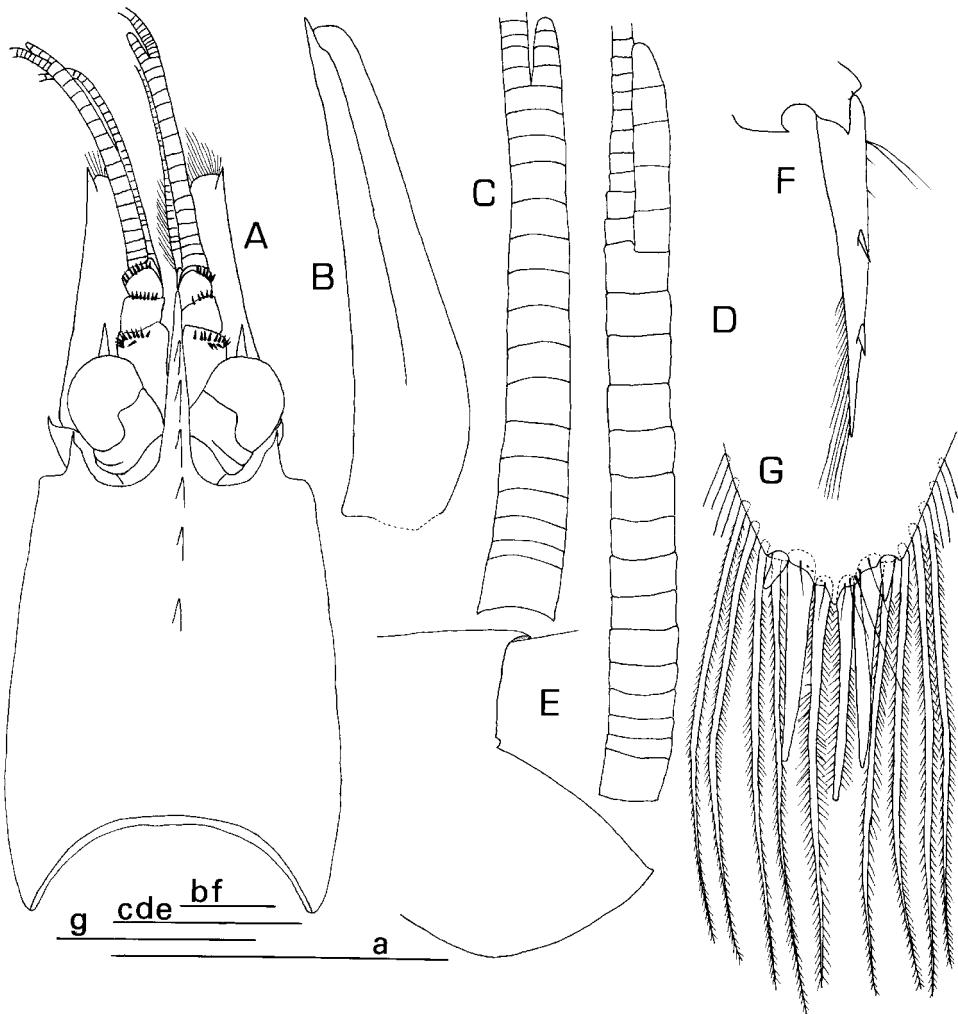


Fig. 2. A-C, E-G, *Lysmata intermedia* (Kingsley, 1879), Dry Tortugas, females: A, USNM 127791; B, E, F, USNM 127787; C, G, USNM 127790. D, *Lysmata seticaudata* (Risso, 1816), male, Corsica, Calvi. A, cephalothorax with cephalic appendages in dorsal view; B, left scaphocerite; C-D, left outer antennular flagellum; E, left side of fourth pleonite; F, left side of telson; G, tip of telson.

Scales: A, 5 mm; B-F, 1 mm; G, 0.5 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,

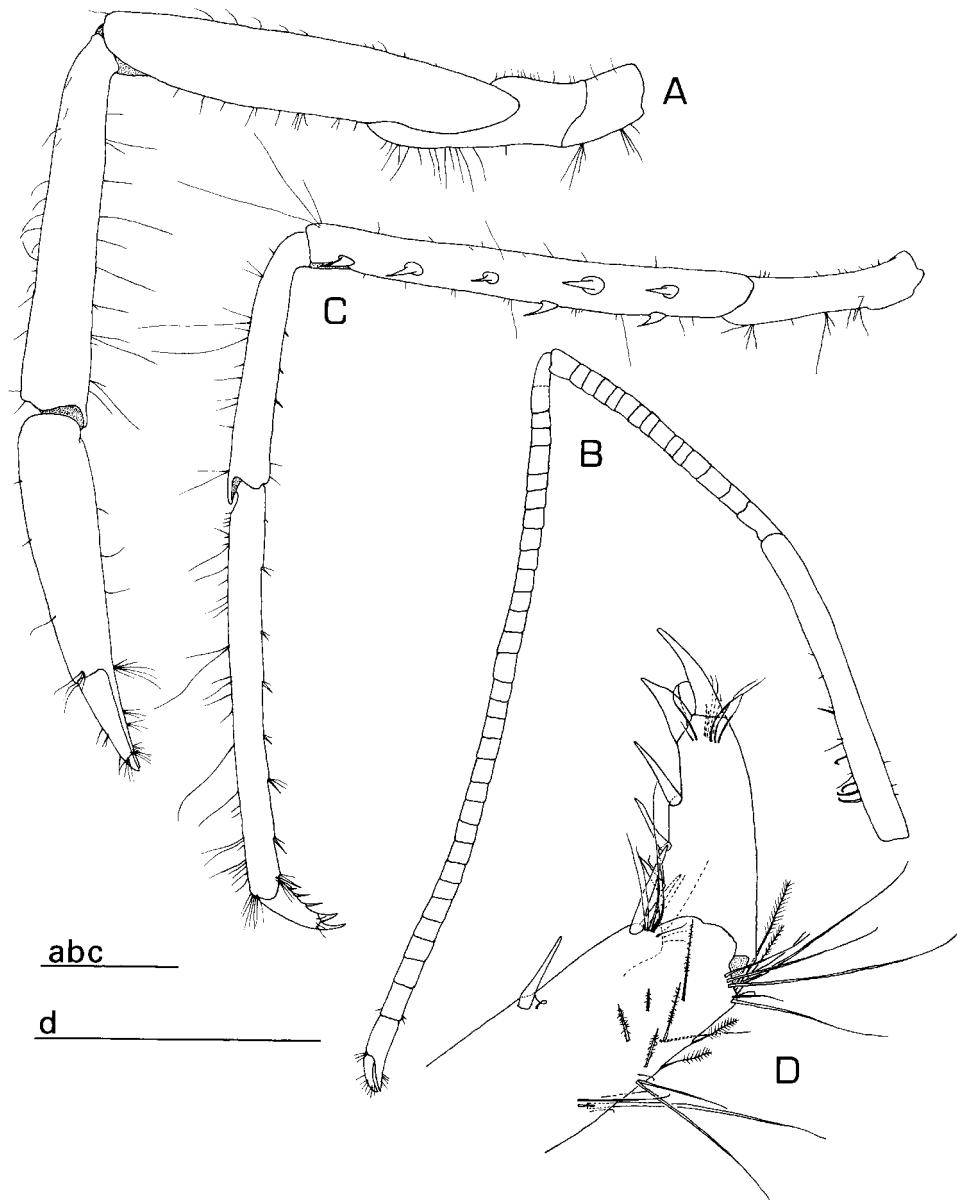


Fig. 3. *Lysmata intermedia* (Kingsley, 1879), Dry Tortugas: A, female, USNM 127787; B-D, sex unknown (detached appendages), USNM 127794. A, first left pereiopod; B, second left pereiopod; C, fourth left pereiopod; D, dactylus of the same. Scales: A-C, 1 mm; D, 0.5 mm.

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 pterygostomian area of Sivertsen's illustrated shrimp is bluntly angular and devoid of the tooth characteristic of topotypical *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 topotypical *L. intermedia*. In Sivertsen's shrimp, the rostrum has 3 ventral teeth, a feature that is not very frequent in topotypical *L. intermedia*. In Sivertsen's shrimp the merus of third pereiopod has 3 ventral spines, another feature that is not very frequent in topotypical *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 topotypical *L. intermedia*, the accessory branch of its outer antenna consists of a unique segment, and not 3 or 4 as in topotypical *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* Dohrn & 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 personnally), 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 occassionnally 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)**

*Aglaope striata* Rafinesque, 1814: 24; Holthuis, 1954: 19; 1956: 228; Opinion 522, 1958: 219 [name suppression].

*Palemon Cognetii* Risso, 1816: 106.

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

*Lysmata seticaudata* — Risso, 1827: 62; Roux, 1830: pl. 37 (in colour); H. Milne Edwards, 1837: 386, pl. 25 figs. 10-12; Heller, 1863: 234, pl. 8 fig. 1; Gourret, 1889: 129, pl. 10 figs. 8-23; Spitschakoff, 1912: 190, pls. 5-6; Pesta, 1918: 107, fig. 35; Holthuis, 1947: 19, 65; Dohrn, 1950: 257, fig. 2; Dohrn & Holthuis, 1950: 339, fig. 10-p, pl. 10; Holthuis & Maurin, 1952: 202; Opinion 522, 1958: 215 [placed on the Official List of Specific Names in Zoology]; Băcescu, 1967: 143, figs. 5, 29, 41, 74, 75, 76, 77, 78; Chassard-Bouchaud & Couturier, 1968a: 201; 1968b: 914; 1969: 173; Geldiay & Kocataş, 1968: 26, fig. 16, pl. 5 fig. 3; Zariquey Alvarez, 1968: 128, figs. 4a, 53, 54, 55, 56; Lagardère, 1971: 98, figs. 224-227; Holthuis, 1977: 53, pl. 4 fig. d; Holthuis, 1987: 227, unnumbered fig.; Fransen, 1991: 68; Grippa, 1991: 342, fig. 3b; Pérez Sánchez & Moreno Batet, 1991: 125, colour photograph; Baensch & Debelius, 1992: 478, unnumbered colour photographs; Falciai & Minervini, 1992: 104, unnumbered fig., pl. 6 fig. 1; Noël, 1992: 50 (key); Holthuis, 1993: 240, fig. 236; Smaldon et al., 1993: 86, fig. 32; González Pérez, 1995: 84, photographs 33, 34 (in colour); Moosleitner & Patzner, 1995: 114, unnumbered colour photograph; Chace, 1997: 72 (key); Debelius, 1999: 17, unnumbered colour photograph.

*Alpheus Cougneti* — 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)].

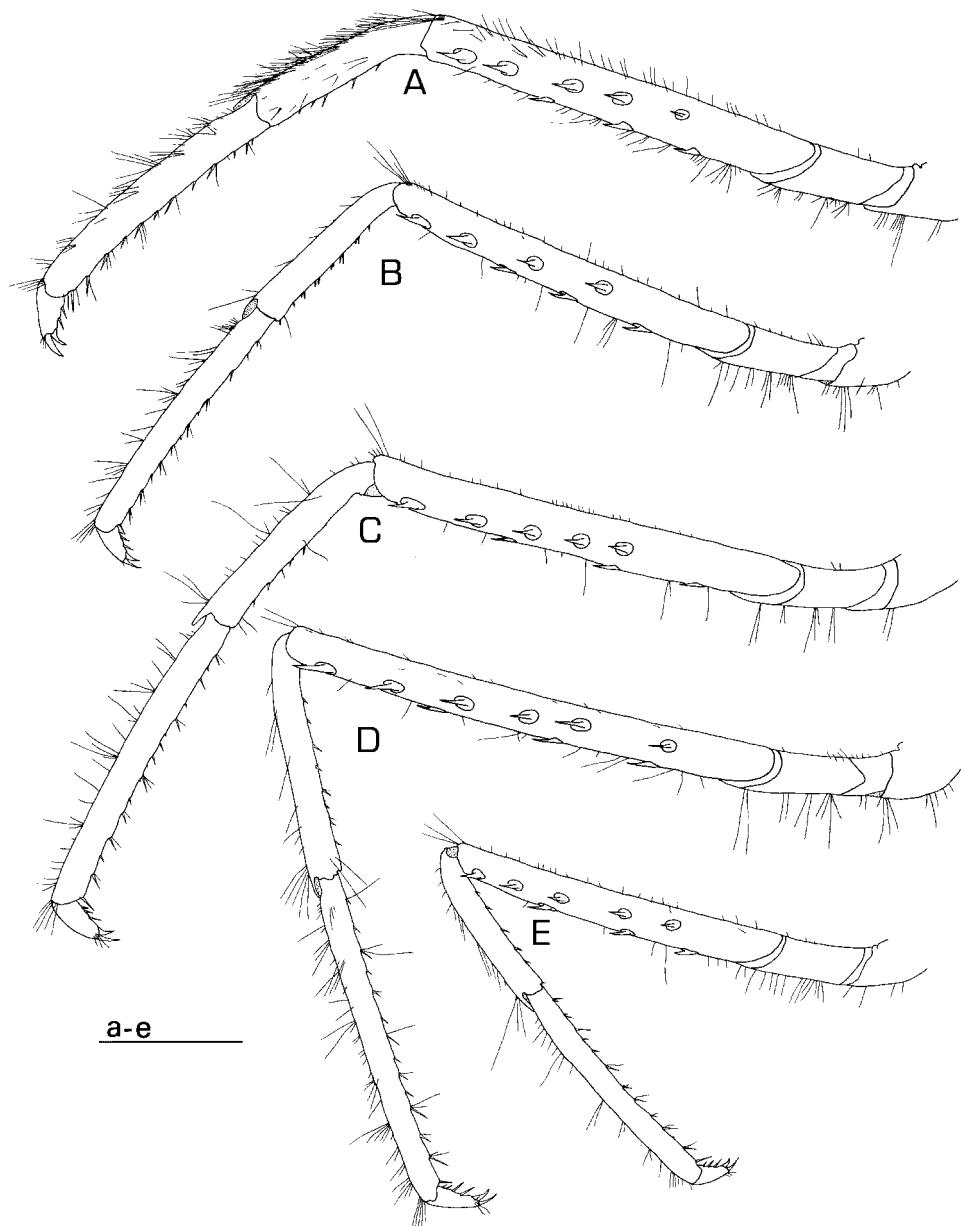


Fig. 4. *Lysmata seticaudata* (Risso, 1816), females, third left pereiopod. A, Azores, Horta; B, Madeira, Baia d'Abra; C, Bay of Biscay, Spain, Cabo Oyambre; D, western Mediterranean, Corsica, Calvi; E, Aegean Sea, Lesbos Island, Anaxos. Scale: A-E, 2 mm.

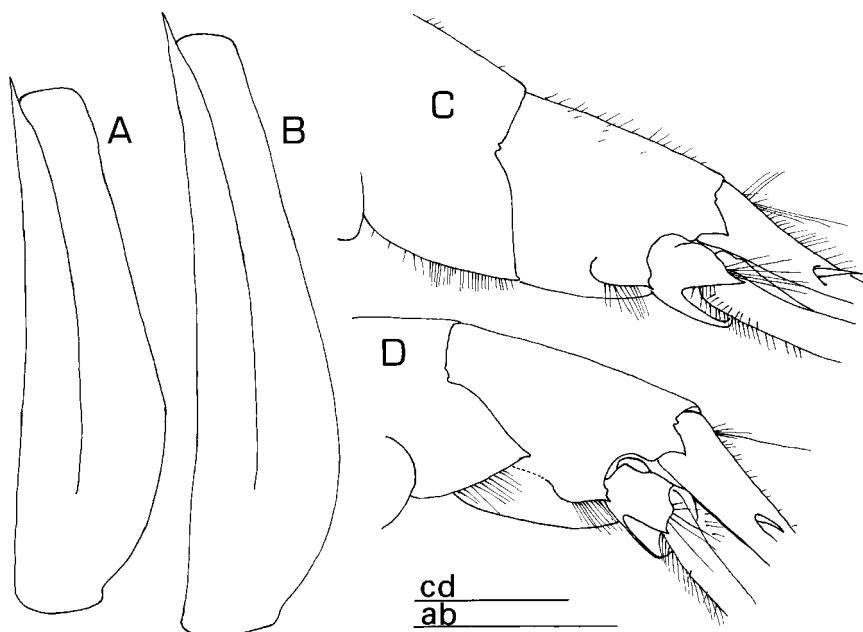


Fig. 5. *Lysmata seticaudata* (Risso, 1816), females; A, C, Azores, Horta; B, D, western Mediterranean, Corsica, Calvi. A, B, left scaphocerite; C, D, left side of sixth pleonite. Scales: 2 mm.

*Lysmata nilita* — González Pérez, 1995: 83, photograph 32 (in colour) [not *Lysmata nilita* Dohrn & Holthuis, 1950]; Debelius, 1999: 16, at least large colour photograph.

*Lysmata* sp. — Chapman & Santler, 1955: 373, Horta Harbour, Faial Island, Azores (no description).

Material examined. — Eastern Mediterranean, Aegean Sea, Samos Island, under stone, 0.1 m deep, C. d'Udekem d'Acoz coll., 06.vii.1984: 1 juvenile, collection Institut Royal des Sciences Naturelles de Belgique/Koninklijk Belgisch Instituut voor Natuurwetenschappen (IRScNB/KBIN) — Eastern Mediterranean, Aegean Sea, Lesbos Island, pebbles mixed with seagrasses, 1 m deep, night collecting, C. d'Udekem d'Acoz coll., 13.vii.1992: 1 ovigerous female, collection IRScNB/KBIN — Western Mediterranean, France, Corsica, Calvi bay, Stareso harbour, walls of the harbour, 1-2 m deep, night collecting, C. d'Udekem d'Acoz coll., May 1988: 1 ovigerous female and a small male (specimens used for illustrations), collection IRScNB/KBIN, 6 specimens, collection C. d'Udekem d'Acoz — S.E. of Madeira, Baia d'Abra, P. Wirtz coll., February 1999: 12 specimens, collection IRScNB/KBIN — Bay of Biscay, France, Guéthary, under a stone, lower shore, E. Dumoulin coll., 06.ix.1991: 1 specimen, collection IRScNB/KBIN — Bay of Biscay, Spain, eastern side of Cabo Oyambre, east of San Vincente de la Barquera, anfractuosity in rockpool, lower shore, C. d'Udekem d'Acoz coll., 13.xi.1997: 1 living specimen, morphological study based on exuvia obtained several months after capture, exuvia in collection IRScNB/KBIN. All specimens in the collection of the IRScNB/KBIN are registered under the number I. G. 28 688. — The Azores, Faial Island, Horta, from a mass of floating cables, P. Wirtz coll., 20.xi.1998: 2 large females, collection IRScNB/KBIN — Azores, Faial Island, Monte da Guia, rocks, 12 m deep, P. Wirtz coll., 21.viii.1999: 2 ovigerous females (seen when alive), collection IRScNB/KBIN — Azores, Pico Island, Madalena, 12.xi.1991: 9 adults, collection University of the Azores, Departamento Oceanografia e Pescas, Horta, CR 272.

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-Baud, 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 *Tellmatactis cricoides* (Duchassaing, 1850) (cf. Wirtz, 1997). Data on larval development summarized by Couturier-Baud (1974c) and Barnich (1996). *L. seticaudata* is a protandrous species (Dohrn, 1950; Charniaux-Cotton, 1958, 1961; Couturier-Baud, 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).

#### ACKNOWLEDGMENTS

I would like to sincerely thank the late Dr. Raymond B. Manning for lending me West Indian *Lysmata intermedia* and answering my numerous questions despite serious health problems, Prof. Dr. Peter Wirtz for giving me material of *Lysmata seticaudata* from Madeira and the Azores and for inviting me in August 1999 at Faial, and Dr. Helen Martins for access to the collection of the Department of Oceanography and Fisheries, University of the Azores.

#### BIBLIOGRAPHY

- ABELE, L. G. & W. KIM, 1986. An illustrated guide to the marine decapod crustaceans of Florida. State of Florida, Department of Environmental Regulation, Technical Series, **8**(1)(1, 2): 1-760.
- BĂCESCU, M. C., 1937. Căteva animale noi pentru fauna marină românească și unele date biologice asupra lor. Bul. Soc. Nat. România, București, **11**: 1-19.
- — —, 1967. Crustacea Decapoda. Fauna Republicii Socialiste România, **4** (9): 1-351, pls. 1-2.
- BAENSCH, H. A. & H. DEBELIUS, 1992. Meerwasser Atlas: 1-1216. (Mergus Verlag, Melle).
- BARNICH, R., 1996. The larvae of the Crustacea Decapoda (excl. Brachyura) in the plankton of the French Mediterranean coast (identification keys and systematic review): 1-189. (Cuvillier Verlag, Göttingen).
- BARROIS, TH., 1888. Catalogue des crustacés marins recueillis aux Açores: 1-110, pls. 1-4. (Le Bigot, Lille).
- CHASE, F. A., JR., 1969. Crustáceos decápodos y stomatópodos del Archipiélago de los Roques e isla de La Orchila. El Archipiélago de Los Roques y La Orchila: 145-168. (Sociedad de Ciencias Naturales La Salle, Caracas).
- — —, 1972. The shrimps of the Smithsonian-Bredin Caribbean expeditions with a summary of the West Indian shallow-water species (Crustacea: Decapoda: Natantia). Smithson. Contr. Zool., **98**: i-x, 1-179.
- — —, 1997. The caridean shrimps (Crustacea: Decapoda) of the Albatross Philippine expedition, 1907-1910, Part 7: families Atyidae, Eugonatonotidae, Rhynchocinetidae, Bathypalaemonellidae, Processidae, and Hippolytidae. Smithson. Contr. Zool., **587**: i-v, 1-106.
- CHAPMAN, G. & J. E. SANTLER, 1955. Aspects of the fauna and flora of the Azores V. Crustacea. Ann. Mag. nat. Hist., (12) **8** (89): 371-376.
- CHARNIAUX-COTTON, H., 1958. La glande androgène de quelques Crustacés Décapodes et particulièrement de *Lysmata seticaudata*, espèce à hermaphroditisme protéandrique fonctionnel. C. r. hebd. Séanc. Acad. Sci. Paris, **246** (19): 2814-2817.
- — —, 1961. Physiologie de l'inversion sexuelle chez la crevette à hermaphroditisme protéandrique fonctionnel *Lysmata seticaudata*. C. r. hebd. Séanc. Acad. Sci. Paris, **250** (24): 4046-4048.

- CHASSARD-BOUCHAUD, C. & Y. COUTURIER, 1968a. Etude des phénomènes chromatiques de *Lysmata seticaudata* Risso (Crustacés Décapode). I. Livrée chromatique et cycle nycthéméral. Cah. Biol. mar., **9**: 201-210.
- & —, 1968b. Données relatives à la physiologie chromatique de *Lysmata seticaudata* Risso (Crustacé Décapode). C. r. hebd. Séanc. Acad. Sci. Paris, **266**: 914-916.
- & —, 1969. Etude des phénomènes chromatiques de *Lysmata seticaudata* Risso (Crustacé Décapode). II. — Effets de l'ablation des pédoncules oculaires sur le cycle nycthéméral. Cah. Biol. mar., **10**: 173-180.
- CHRISTOFFERSEN, M. L., 1998. Malacostraca. Eucarida. Caridea. Crangonoidea and Alpheoidea (Except Glyphocrangonidae and Crangonidae). In: P. S. YOUNG (ed.), Catalogue of Crustacea of Brazil. Rio de Janeiro: Museu Nacional, (Livros) **6**: 351-372.
- CHUN, C., 1888. Die pelagische Tierwelt in grösseren Meerestiefen und ihre Beziehungen zu der Oberflächenfauna. Bibliotheca Zoologica, Cassel, **1**: 1-72, pls. 1-5.
- COUTURIER-BHAUD, Y., 1974a. Cycle biologique de *Lysmata seticaudata* Risso (Crustacé, Décapode) I. Cycle biologique des animaux adultes. Vie et Milieu, (A) **24** (3): 413-422.
- , 1974b. Cycle biologique de *Lysmata seticaudata* Risso (Crustacé, Décapode) II. Sexualité et reproduction. Vie et Milieu, (A) **24** (3): 423-430.
- , 1974c. Cycle biologique de *Lysmata seticaudata* Risso (Crustacé, Décapode) III. Etude du développement larvaire. Vie et Milieu, (A) **24** (3): 431-442.
- CZERNIAVSKY, V., 1884. Materialia ad zoogeographiam ponticam comparatam. II. Crustacea Decapoda Pontica littoralia. Trans. Soc. Univ. Kharkow, **13** (suppl.): 1-268, pls. 1-7. [Pages on *Lysmata* not seen].
- DAUVIN, J.-CL., A. IGLESIAS & F. GENTIL, 1991. Nouvelles espèces pour l'inventaire de la faune marine de Roscoff — Crustacés Amphipodes, Cumacés et Décapodes, Mollusques Gastéropodes et Ascidies. Cah. Biol. mar., **32**: 121-128.
- DEBELIUS, H., 1999. Crustacea guide of the world: 1-321. (IKAN-Unterwasserarchiv, Frankfurt).
- DOHRN, P. F. R., 1950. Studi sulla *Lysmata seticaudata* Risso (Hippolytidae [sic]). I. Le condizioni normali della sessualità in natura. Pubbl. Staz. zool. Napoli, **22** (3): 257-272.
- DOHRN, P. F. R. & L. B. HOLTHUIS, 1950. *Lysmata nilita*, a new species of prawn (Crustacea Decapoda) from the western Mediterranean. Pubbl. Staz. Zool. Napoli, **22** (3): 339-347, pls. 9-10.
- FALCIAI, L. & R. MINERVINI, 1992. Guida dei crostacei decapodi d'Europa: 1-282, pls. 1-18. (Franco Muzzio ed., Padova).
- FRANSEN, C. H. J. M., 1991. *Lysmata olavoi*, a new shrimp of the family Hippolytidae (Decapoda, Caridea) from the eastern Atlantic Ocean. Arquipélago, Life and Earth Sciences, **9**: 63-73.
- GARCÍA RASO, J. E., M. E. MANJÓN-CABEZA & J. C. MARTÍNEZ, 1998. Considerations on some species of *Hippolyte* (Decapoda, Caridea) from southern European waters, *H. niezabitowskii*, *H. holthuisi*, and *H. varians*. Crustaceana, **71** (4): 453-467.
- GELDIAY, R. & A. KOCATAŞ, 1968. Izmir körfesi ve civarında tespit edilen Natantia türleri (Crustacea Decapoda) [Report on a collection of Natantia (Crustacea Decapoda) from Izmir and its neighbourhood]. Scient. Rep. Fac. Sci., Ege Univ., **51**: 1-38, pls. 1-6.
- GONZÁLEZ PÉREZ, J. A., 1995. Catálogo de los crustáceos decápodos de las Islas Canarias. Gambas. Langostas. Cangrejos: 1-282. (Publicaciones Turquesa S. L., Santa Cruz de Tenerife).
- GORRET, P., 1889. Révision des Crustacés Podophthalmes du Golfe de Marseille, suivi d'un essai de classification de la classe des Crustacés. Ann. Mus. Hist. nat. Marseille, **3** (5): 1-212, pls. 1-18.
- GRIPPA, G. B., 1991. Note sui Crostacei Decapodi dell'isola del Giglio (Arcipelago Toscano). Atti Soc. Italiano Sci. Nat. Mus. civ. Stor. nat. Milano, **141** (24): 337-363.
- HELLER, C., 1863. Die Crustaceen des südlichen Europa. Crustacea Podophthalmia: 1-336, pls. 1-10. (Wilhelm Braumüller, Wien).

- HOLTHUIS, L. B., 1947. The Hippolytidae and Rhynchocinetidae collected by the Siboga and Snellius Expedition with remarks on other species. *Siboga Expeditie Monogr.*, **39a** (8): 1-100.
- —, 1954. C. S. Rafinesque as a carcinologist, an annotated compilation of the information on Crustacea in the works of that author. *Zool. Verh.*, Leiden, **25**: 1-43.
- —, 1956. Proposed suppression under the plenary powers (a) of certain names given by C. S. Rafinesque to genera and species of the order Decapoda and Stomatopoda (Class Crustacea) and (b) of certain specific names currently regarded as senior synonyms of the names of the type species of the genera "*Homola*" and "*Lissa*", both of Leach, 1815, belonging to the foregoing class. *Bull. zool. Nomencl.*, **12** (9): 227-239.
- —, 1977. The Mediterranean decapod and stomatopod Crustacea in A. Risso's published works and manuscripts. *Ann. Mus. Hist. nat. Nice*, **5**: 37-88.
- —, 1987. Crevettes. In: W. FISCHER, M. SCHNEIDER & M.-L. BAUCHOT (eds.), *Fiches FAO d'identification des espèces pour les besoins de la pêche. Méditerranée et Mer Noire. Zone de pêche 37. Révision 1. Volume 1. Végétaux et invertébrés: 189-292.* (FAO, Rome).
- —, 1993. The recent genera of the Caridean and Stenopodidean shrimps (Crustacea, Decapoda): with an appendix on the order Amphionidacea: 1-328. (Nationale Natuurhistorisch Museum, Leiden).
- HOLTHUIS, L. B. & C. MAURIN, 1952. Note sur *Lysmata unicornis* nov. spec. et sur 2 autres espèces intéressantes de crustacés décapodes macroures de la côte atlantique du Maroc. *Proc. Kon. Nederlandse Akad. Wetensch.*, Amsterdam, (C), **55** (2): 197-202.
- KEMP, S. W., 1914. Notes on Crustacea Decapoda in the Indian Museum. V. — Hippolytidae. *Records of the Indian Museum*, **10**: 81-129, pls. 1-7.
- KERSTITCH, A., 1989. Sea of Cortez marine invertebrates. A guide for the Pacific coast, Mexico to Ecuador: i-v, 1-114. (E. J. Brill, Leiden).
- KINGSLEY, J. S., 1879. Notes on the North American Caridea in the Museum of the Peabody Academy of Science at Salem, Mass. *Proc. Acad. Sci. Philadelphia*, **1878**: 89-98.
- —, 1882. Carcinological notes; number V. *Bull. Essex Inst.*, **14** (7-12): 105-132, pls. 1-2.
- LAGARDÈRE, J.-P., 1971. Les crevettes des côtes du Maroc. *Trav. Inst. Sci. Chérifien et de la Faculté des Sciences, Rabat, (Zool.)* **36**: 1-140.
- MANNING, R. B. & F. A. CHACE, JR., 1990. Decapod and stomatopod Crustacea from Ascension Island, South Atlantic Ocean. *Smithson. Contr. Zool.*, **503**: i-v, 1-91.
- MILNE EDWARDS, H., 1837. *Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux*, **2**: 1-531; atlas: 1-32, pls. 1-42. (Librairie encyclopédique de Roret, Paris).
- MOOSLEITNER, H. & R. PATZNER, 1995. Unterwasserführer Mittelmeer. *Niedere Tiere*: 1-214. (Delius Klasing, Edition Naglschmid).
- MORTON, B., J. C. BRITTON & A. M. DE FRIAS MARTINS, 1998. Coastal ecology of the Açores: i-viii, 1-247. (Sociedade Afonso Chaves, Associação de Estudos Açoreanos, Ponta Delgada).
- NOËL, P.-Y., 1992. Clé préliminaire d'identification des Crustacea Decapoda de France et des principales autres espèces d'Europe. *Secrétariat de la Faune et de la Flore. Collection Patrimoines Naturels*, **9**: 1-145. (Muséum National d'Histoire Naturelle, Secrétariat de la Faune et de la Flore, Paris).
- NORMAN, A. M., 1907. Notes on the Crustacea of the Channel Islands. *Ann. Mag. nat. Hist.*, (7), **20**: 356-371, pls. 16-17.
- OPINION 522, 1958. Suppression under the Plenary Powers (i) of certain names published by C. S. Rafinesque for genera and species of the Orders Decapoda and Stomatopoda (Class Crustacea) in the period 1814-1818 and (ii) of certain specific names currently regarded as senior subjective synonyms of the names of the type species of *Homola* Leach, 1815, and *Lissa* Leach, 1815 respectively being genera assigned to the first of the foregoing Orders. *Opin. Decl. int. Comm. zool. Nomencl.*, **19** (9): 209-248.

- PÉREZ SÁNCHEZ, J. M. & E. MORENO BATET, 1991. Invertebrados marinos de Canarias: 1-335. (Ediciones del Abildo Insular de Gran Canaria, Las Palmas de Gran Canaria).
- PESTA, O., 1918. Die Decapodenfauna der Adria: i-x, 1-500, 1 map. (Franz Deuticke, Leipzig and Wien).
- RAFINESQUE, C. S., 1814. Précis des découvertes et travaux somiologiques de Mr. C. S. Rafinesque-Schmaltz. entre 1800 et 1814. Ou choix raisonné de ses principales découvertes en zoologie et en botanique, pour servir d'introduction à ses ouvrages futurs: 1-55. (Palermo).
- RAMOS-PORTO, M., P. V. V. D. B. C. CARVALHO & M. L. BOTTER-CARVALHO, 1995. Registro de *Lysmata intermedia* (Kingsley, 1878) (Decapoda, Hippolytidae) no litoral Pernambucano. Trab. Oceanogr. Fed. Pernambuco, Recife, **23**: 107-111.
- RATHBUN, M. J., 1901. The Brachyura and Macrura of Porto Rico. Bull. U. S. Fish Comm. for 1900 [1902], **20** (2): 1-127, pls. 1-2.
- RISSO, A., 1816. Histoire naturelle des Crustacés des environs de Nice: 1-175, pls. 1-3. (Paris).
- —, 1827. Histoire naturelle des principales productions de l'Europe méridionale et particulièrement celles des environs de Nice et des Alpes maritimes, **5**: i-vii, 1-403, pls. 1-10. (Strasbourg).
- RODRIGUEZ, G., 1980. Los Crustáceos Decápodos de Venezuela: 1-494. (Instituto Venezolano de Investigaciones Científicas, Caracas).
- ROUX, [J. L. F.] P., 1828-1830. Crustacés de la Méditerranée et de son littoral: i-iv, 176 unnumbered pages, pls. 1-45. (Marseille). (1828: pls. 1-10; 1829: pls. 11-15; 1830: pls. 16-45).
- SCHMITT, W. L., 1924. The macruran, anomuran and stomatopod Crustacea. Bijdragen tot de kennis der fauna van Curaçao. Resultaten eener reis van Dr. C. J. van der Horst in 1920. Bijdr. Dierk., **23**: 61-81, pl. 8.
- SINEL, J., 1907. A contribution to our knowledge of the Crustacea of the Channel Islands. Rep. Trans. Guernsey Soc. nat. Sci. [Société Guernesiaise Transactions], **5** (year 1906): 212-225.
- SIVERTSEN, E., 1933. Littoral Crustacea Decapoda from the Galapagos Islands. Part VII. In: The Norwegian Zoological Expedition to the Galapagos Islands, 1925, conducted by Alf Wollebaek. Medd. zool. Mus., Oslo, **38**: 1-23, pls. 1-4.
- SMALDON, G., L. B. HOLTHUIS & C. H. J. M. FRANSEN, 1993. British coastal shrimps and prawns. Syn. British Fauna, (N.S.), (ed. 2) **15**: i-vii, 1-142. (Academic Press, London).
- SPITSCHAKOFF, T., 1912. *Lysmata seticaudata* Risso, als Beispiel eines echten Hermaphroditismus beiden Decapoden. Zeitschrift wiss. Zool., **100**: 190-209, pls. 5-6.
- UDEKEM D'ACOZ, C. d', 1996. The genus *Hippolyte* Leach, 1814 (Crustacea: Decapoda: Caridea: Hippolytidae) in the East Atlantic Ocean and the Mediterranean Sea, with a checklist of all species in the genus. Zool. Verh. Leiden, **303**: 1-133.
- —, 1999. Inventaire et distribution des crustacés décapodes de l'Atlantique nord-oriental, de la Méditerranée et des eaux continentales adjacentes au nord de 25°N. Collection Patrimoines Naturels, **40**: i-x, 1-383. (Muséum National d'Histoire Naturelle, Service du Patrimoine Naturel, Paris).
- WICKSTEN, M. K., 1983. Shallow water caridean shrimps of the Gulf of California, Mexico. Allan Hancock Foundation Monograph, **13**: 1-59.
- —, 1990. Key to the hippolytid shrimp of the eastern Pacific Ocean. Fish. Bull., U.S., **88**: 587-598.
- WIRTZ, P., 1995. Unterwasserführer Madeira, Kanaren, Azoren: 1-247. (Delius Klasing, Edition Naglschmid).
- —, 1997. Crustacean symbiont of the sea anemone *Telmatostichus cuniculus* at Madeira and the Canary Islands. Journ. Zool., London, **242**: 799-811.
- ZARIQUIEY ALVAREZ, R., 1968. Crustáceos Decápodos Ibéricos. Inv. Pesq., Barcelona, **32**: i-xv, 1-510.

First received 30 September 1999.  
Final version accepted 30 November 1999.