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THE OPHIACANTHID GENUS AMPHILIMNA (OPHIUROIDEA, ECHINODERMATA)

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Until recently Amphilimna Verrill, 1899 was considered an amphiurid genus and considerable confusion existed regarding the systematic characters of the type-species, Amphilimna olivacea (Lyman, 1869). Some of the mystery surrounding this species was cleared up when it was discovered (Thomas, 1967) that A. olivacea is not an amphiurid, and that a second nominal species, A. caribea (Ljungman, 1871), belongs in the ophiocomid genus Ophiopsila. Unfortunately, I considered Amphilimna reduced to monotypic status by my studies, overlooking a species described from the Philippines 45 years earlier (A. multispina Koehler, 1922). Consequently, as of 1967 Amphilimna actually included two nominal species, A. olivacea and A. multispina.

Thomas and Schoener (1972) suggested that Amphitarsus H. L. Clark, 1941, with two species, A. mirabilis H. L. Clark, 1941, and A. nike Schoener, 1967 should probably be considered a junior synonym of Amphilimna. Devaney (1974), describing a new species of Amphilimna from Pitcairn Island, acted upon this suggestion by making Amphitarsus a junior synonym of Amphilimna. Unfortunately, Devaney also overlooked Koehler's Pacific species, considering his own new one, A. tanyodes, the first known from the Pacific. Another species of Amphilimna, A. cribriformis was described from southern Africa by A. M. Clark in 1974 in a paper published about the same time as Devaney's. Finally, during a visit to the British

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Museum (Nat. Hist.) in the summer of 1974, I discovered, as A. M. Clark (1974) had suggested, that Anamphiura valida H. L. Clark is in fact an Amphilimna; thus, including the latter species as a new combination, there are now seven species in the genus Amphilimna: A. olivacea (Lyman, 1869), A. multispina Koehler, 1922, A. nike (Schoener, 1967), A. mirabilis (H. L. Clark, 1941), A. tanyodes Devaney, 1974, A. cribriformis A. M. Clark, 1974, A. valida (H. L. Clark, 1939) new combination.

In the following account I have included only selected references in the synonymies. These references should be consulted for more complete synonymies. The diagnoses have been deliberately kept short. As more material of the poorer known species becomes available, expanded diagnoses will undoubtedly appear. Similarly the keys to the species must be considered provisional, subject to future elaboration and revision.

Through the years, while working on Amphilimna and other genera, I have been assisted by Maureen Downey and David Pawson of the United States National Museum of Natural History (hereafter abbreviated USNM); Elizabeth Deichmann, H. Barraclough Fell, Charlene Long, and Amy Schoener of the Museum of Comparative Zoology at Harvard (MCZ); and Ailsa Clark of the British Museum (Natural History) (BM). Mary Anna Bogle assisted with most of the technical work for this paper, and Claire Ulanoff made the illustrations of A. nike. I am grateful to all for their long and valued assistance and friendship, and particularly for their patience when it appeared academic and other responsibilities would preclude my completing some of the research projects I had begun. I am also grateful to Linda Pequegnat of Texas A & M University who arranged for me to look at the collection in which a fine large specimen of A. nike was discovered and to Dennis Devaney who kindly edited my diagnosis of his new species.

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OPHIACANTHIDAE

Amphilimna Verrill, 1899

Amphilimna Verrill, 1899: 30.—Thomas, 1967: 123.—Devaney, 1974: 122.

Amphitarsus H. L. Clark, 1941: 83.

Diagnosis: The following is based upon consideration of the 7 nominal species listed above which presently constitute the genus Amphilimna. The differences between this diagnosis and Devaney's (1974) are discussed below: Disc notched at radial shields; radial shields variable in size and shape; disc scales covered to varying degrees by spines, spinelets, and/or granules. Two to 6 oral papillae at apex of jaw, 2 or 3 at or near distal end of jaw around second oral tentacle pore, 1 or more papillae (1 an oral tentacle scale?) between distal and apical clumps of papillae. Some arm spines under disc flattened and fused together forming peculiar "flanges" in the genital slits. Ventral arm plates abruptly widen distally. Proximal arm segments usually with 2, occasionally to 5, tentacle scales, 1 to 3 on lateral arm plate, 1 or 2 usually arising from middle of side of ventral arm plate; tentacle scales spiniform, round and flat, or some intermediate condition.

Discussion: Devaney's (1974) treatment and diagnosis of Amphilimna requires some modification and comment, partly because of the addition of more species to the genus. The following range of variation may be found if one considers all 7 species: The distal oral papillae, bordering the outermost tentacle pores, are not necessarily "squamiform," but may be either round and very flat, spiniform, or of some intermediate condition. There is, varying in expression from species to species, a tendency for the proximal oral papillae to occur in a distinct cluster at the jaw apex. The distal and proximal groups of papillae are usually separated from one another by 1 or more papillae (including what seem to be oral tentacle scales). The ventral arm plates of all species widen abruptly at their distal ends, a condition I consider of generic importance. With the addition of A. valida to Amphilimna the arm length to disc diameter ratio deviates considerably from Devaney's figure of "six or more times disc diameter." The arm length may be only 2 times the disc diameter in A. valida, and the ratio for ophiuroids in general is probably useful only within specific size classes of individual species.

Earlier (Thomas, 1967: 125) I discussed the dental plates of Amphilimna olivacea and pointed out their similarities with those of other ophiacanthid genera, but I also suggested that Ophioprium cervicorne (Lyman, 1883) was closely related to A. olivacea. After examining the holotype of O. cervicorne I still believe the 2 genera are quite closely related. Devaney has suggested that Amphilimna shows affinities with a group of 6 genera, with large tentacle pores, indicated by Matsumoto (1917) and (possibly?) with 2 genera included in that group by Fell (1960). Two of the genera Devaney lists seem to be synonyms of other

genera and the affinities of the 8 nominal genera with Amphilimna vary, in my opinion, from none whatsoever to a definite affinity in the case of Ophioprium. Considering the genera in question, Ophiopora Verrill, 1899 is treated by Fell (1960) as a synonym of Ophiotoma Lyman, 1883, whose type-species, Ophiotoma coriacea Lyman, 1883, except for lacking tentacle scales, looks vaguely like an Amphilimna. Ophiopristis Verrill, 1899 is considered a synonym of Ophiacantha Müller and Troschel, 1842 by Fell (1960) but it seems to be misplaced here, as the type-species of Ophiopristis, O. bartletti Lyman, 1883, has large tentacle pores and looks very much like an Ophiotoma. The remaining genera in Devaney's list are Ophiambix Lyman 1880, Ophiomedea Koehler, 1906, Ophiotrema Koehler, 1896, Ophiodelos Koehler, 1931, Glaciacantha Fell, 1961 and Ophioprium, Clark, 1915. The type-species of Glaciacantha, Ophiodelos, and Ophiambix, in my opinion, cannot be considered as having any "affinity" with Aphilimna. The type-species of Ophiomedea, O. duplicata Koehler, 1906, has a similar tentacle scale arrangement and in other ways looks vaguely similar to A. olivacea, as does the type-species of Ophiotrema, O. alberti Koehler, 1896, which has naked radial shields, spines on the disc, large tentacle pores with tentacle scales on both the lateral arm plates and ventral arm plates.

The major problem in determining relationships of other genera with Amphilimna appears to me to be in determining the generic characteristics of Amphilimna itself. Aside from the flattened fused arm spines under the disc, the features which seem to be most characteristic of this genus are the shape of the ventral arm plates and the arrangement of the tentacle scales around the large tentacle pores, the presence of the oral papillae, notches in the disc at each radial shield pair, and the presence of spines or granules on the disc. Characters which vary from species to species include the relative size and shape of the radial shields (these vary also with the size of the individual), the disc covering, the shape and numbers of oral papillae, the shape and numbers of tentacle scales, and the number of arm spines.

Amphilimna olivacea (Lyman, 1869)

Ophiocnida olivacea Lyman, 1869: 340.

Amphitarsus spinifer Schoener, 1967: 269.

Amphilimna olivacea: Thomas, 1967: 123, figs. 1-6.—Madsen, 1970: 163, fig. 5.—Tommasi, 1970: 32, figs. 30, 31—A. M. Clark, 1974: 444
[in discussion].—Devaney, 1974: 121 [in discussion].

Material Studied: 14 spec.; COSNOLD Sta. 1074; northeast of Hudson Canyon (39°43.0'N, 71°53.2'W), 225 m; 12 May 1963.—6 spec.; GOSNOLD Sta. 1261; Block Canyon (40°00.0'N, 71°16.8'W), 235 m; 4 October 1963.—4 spec.; GOSNOLD Sta. 1571; off Florida Keys (24°32.0'N, 81°16.5'W), 89 m; 31 May 1964.—6 spec.; GOSNOLD Sta. 1572; off Florida Keys (24°29.3'N, 81°27.7'W), 97 m; 31 May 1964.

Diagnosis: Jaws with 2 or 3 papillae at apex, 2 or 3 slender, pointed oral papillae bordering each oral tentacle pore; 1 papilla (probably an oral tentacle scale) separating infradental papillae and papillae arising from oral tentacle pore. Oral shield rhomboidal, wider than long; adorals meeting or nearly meeting proximally; arms slender, 6 times disc diameter in large specimen, 8 to 10 proximal arm plates with 2 tentacle scales at each tentacle pore, innermost attenuated, arising from middle of ventral arm plate; beyond tenth ventral arm plate innermost absent; 7 or 8 slender arm spines, ventralmost longest; all but ventral 2 or 3 arm spines of arm segments under disc greatly flattened, fused with others to form peculiar flanges occupying genital slits; dorsal arm plates slightly wider than long. Disc scales studded with slender spines. Radial shields narrow, about 3 times longer than wide, joined proximally, slightly separated distally; disc deeply notched at each pair of radial shields. Two slender spines at distal ends of genital plates near junction with radial shields. Color variable, disc gray, tan or brown, arms pink or orange.

Discussion: With its slender disc spines, attenuated inner tentacle scales, and slender oral papillae, O. olivacea appears to be most similar to A. cribriformis. It differs in having a rhomboidal oral shield, contiguous or nearly contiguous adorals, longer arm spines, and in a variety of other details discussed by A. M. Clark (1974: 444).

Distribution: Widespread in the Atlantic Ocean from 60 to 350 m. Perhaps extending to nearly 500 m (Verrill, 1899b: 377). Liberia to Angola in the eastern Atlantic, Massachusetts to Uruguay in the western Atlantic.

Amphilimna cribriformis A. M. Clark, 1974

Amphilimna cribriformis A. M. Clark, 1974: 442, Fig. 1.

Material Studied: None.

Diagnosis (modified after A. M. Clark, 1974): Jaws with 2 to 4 infradental papillae at apex, 3 slender, pointed oral papillae bordering each oral tentacle pore; one papilla (probably an oral tentacle scale) separating apical and distal oral papillae. Oral shields triangular, broadest distally; adoral plates separated at proximal angle of oral shield. First 8–10 arm segments bearing 2 tentacle scales, innermost arising from middle of ventral arm plate, initially long and slender; beyond tenth or twelfth ventral arm plate innermost absent; outermost arising from lateral arm plate, short, becoming flattened toward distal end of arm. Six or fewer arm spines each arm segment, under disc all but ventral spine flattened and fused to form peculiar flanges occupying genital slits; dorsal arm plates beyond first few ovate, broader than long, thin, semitransparent. Disc scales studded with slender spines. Radial shields long, narrow, joined proximally, slightly separated distally; disc somewhat notched at each pair of radial shields. Two spines

stouter than disc spines at distal ends of genital plates near junction with radial shields.

Discussion: A. M. Clark (1974) described this species in detail. It differs from O. olivacea, with which it seems most similar, in having triangular oral shields, slightly separated adoral shields, shorter arm spines which are never as long as an arm segment, 2–4 infradental papillae rather than 2–3, and in the oval shape and transparent, delicate nature of the dorsal arm plates.

Distribution: Known only from along the continental shelf of eastern South Africa and southern Mozambique, 86 to 200 m.

Amphilimna multispina Koehler, 1922

Figure 1

Amphilimna multispina Koehler, 1922: 183, p. 61, figs. 4-9, pl. 96, fig. 7

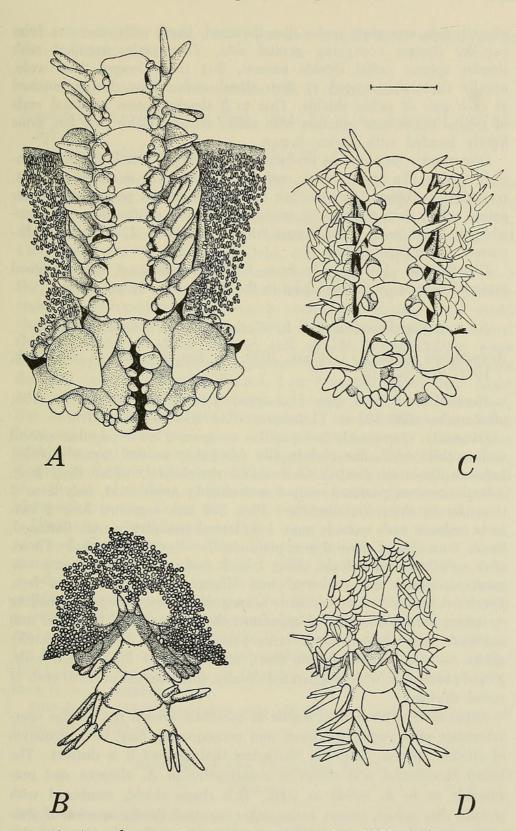
Material Studied: 1 spec. (paratype); ALBATROSS Sta. 5220; between Marinduque and Luzon, Philippines (13°38'00"N, 121°58'00"E), 91 m; 24 April 1908; USNM Cat. No. E 23.—13 spec. (paratypes); ALBA-TROSS Sta. 5221; between Marinduque and Luzon, Philippines (13°38'15"N, 121°48'15"E), 335 m; 24 April 1908; USNM Cat. No. E 26, E 27.—4 spec. (paratypes); ALBATROSS Sta. 5222; between Marinduque and Luzon, Philippines (13°38'30"N, 121°42'45"E), 357 m; 24 April 1908; USNM Cat. No. E 25.—1 spec. (paratype); ALBA-TROSS Sta. 5223; between Marinduque and Luzon, Philippines (13°36'00"N, 121°25'30"E), 357 m; 24 April 1908; USNM Cat. No. E 24.—4 spec. (paratypes); ALBATROSS Sta. 5375; Marinduque Island and vicinity, Philippines (13°42'15"N, 121°50'15"E), 196 m; 2 March 1909; USNM Cat. No. E 4.

Diagnosis: Jaws with one or 2–6 short blunt papillae at apex, 2 large broadly flattened papillae longer than wide bordering each oral tentacle pore, oral papilla (probably an oral tentacle scale) separating infradental papillae and papillae arising from oral tentacle pore. Oral shield almost twice longer than wide, arrowhead shaped, pointed proximally, broadly rounded distally. Adoral shields joined at distal end of oral papillae except in very large specimens. Arms slender, probably at least 6 times as long as disc diameter. Tentacle scales flattened, oval, scale arising from lateral arm plate largest, completely covering tentacle pore, smaller similarly shaped scale arising from side of ventral arm plate for first 8–10 segments; 6–9 arm spines, slender, flattened, dorsalmost longest, longer than an arm segment. All but ventral 2 or 3 spines

FIG. 1. A, Amphilimna nike, GOSNOLD Sta. 1580, oral view, two jaws and base of arm. B, A. nike, GOSNOLD Sta. 1580, radial shields and base of

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arm. C, A. multispina, Paratype, ALBATROSS Sta. 5221, oral view, two jaws and base of arm. D, A. multispina, Paratype, ALBATROSS Sta. 5221, radial shields and base of arm. Scale equals 1 mm.

of each side arm plate under disc flattened, fused with others to form peculiar flanges occupying genital slits. Disc scales studded with slender spines; radial shields narrow, 3–4 times longer than wide, usually slightly separated at their distal ends. Disc deeply notched at each pair of radial shields. One to 3 slender spines at distal ends of genital plates near junction with radial shields. Color pale tan, arms lightly banded with darker brown.

Discussion: Amphilimna multispina bears large, round, flattened tentacle scales like those of A. valida, A. nike, A. mirabilis, and A. tanyodes. It differs from the last three, however, in possessing slender spines rather than granules or granulose spinules on the disc. The possible relationship of A. multispina with A. valida or A. tanyodes is discussed under those species.

Distribution: Known only from Koehler's (1922, p. 183) original material near Marinduque Island in the Philippines, 91 to 357 m.

Amphilimna valida (H. L. Clark, 1939) new combination

Anamphiura valida H. L. Clark, 1939: 70, figs. 26a, 27.—A. M. Clark, 1974: 478, fig. 16.

Material Studied: 1 spec. (holotype); John Murray Exped. Sta. 105; off Zanzibar, 238–293 m; 11 January 1934; BM 1948.5.26.87.

Diagnosis: Jaws with 2–4 papillae at apex, 2 or 3 papillae around oral tentacle scale, one oral papilla (probably an oral tentacle scale) between the two groups. Oral shield rhomboidal, wider than long. Adorals meet at proximal end of oral shield. Arms short, only 2 or 3 times longer than disc diameter. First 3–6 arm segments bear 2 tentacle scales at each tentacle pore, 1 on lateral arm plate round, flattened, large, 1 on side of ventral arm plate smaller, round or conical. Thereafter only large outer scale. First 1 or 2 arm segments bear some arm spines flattened and coalesced into "flange," 2 ventral spines free. Five or 6 arm spines on segments nearest disc; lowest longest, equalling or longer than arm segment, uppermost shortest, one-half length of arm segment. Disc scales include large primitive plates, scattered slender spines on disc. Radial shields short, up to 2 times longer than wide, joined proximally, widely separated distally, disc notched at distal ends of radial shields.

Discussion: Although A. valida as presently known has all the characteristics of a young specimen and consequently may be a synonym of another species, there are characters that suggest it is distinct. The broad rhomboidal oral shield is conservative in A. olivacea and presumably so in A. valida as well. This shape shield, combined with slender disc spines, occurs in no other nominal Pacific species of Amphilimna. Otherwise A. valida appears most similar to A. multispina which has similar tentacle scales and slender disc spines.

Distribution: Known only from John Murray Sta. 105, Zanzibar area

238-293 m (H. L. Clark, 1939), and near Tugela River mouth, 350 m (A. M. Clark, 1974).

Amphilimna mirabilis (H. L. Clark, 1941)

Amphitarsus mirabilis H. L. Clark, 1941: 83, pl. 8.—Schoener, 1967: 2, fig. 1.

Amphilimna mirabilis: Devaney, 1974: 22.

Material Studied: 1 spec. (holotype); ATLANTIS Sta. 3402; off Cayo Coco, Camaguey Province, 420 m; MCZ 6232.—1 spec. (paratype); ATLANTIS Sta. 3332; Bahia de Cochinos, Santa Clara Province, Cuba, 320–412 m; MCZ 6398.—1 spec. (paratype); ATLANTIS Sta. 3422; off Caibarien, Santa Clara Province, Cuba, 430 m; MCZ 6399.

Diagnosis: Jaws with 3 or 4 oral papillae at apex of jaw, 2 or 3 flat, round papillae guarding oral tentacle pore; 2 groups of oral papillae separated by (probably oral tentacle scale) oral papilla. Oral shield rhomboidal, slightly wider than long with rounded angles. Adoral shields meeting at distal side of oral shields. Arms slender, more than 6 times disc diameter, segments under disc with arm spines flattened and fused forming flanges, 1 or 2 ventral spines free. Eight or 9 arm spines near disc, ventralmost longest. Tentacle scales round, flat, largest arising from lateral arm plate, 1 or 2 smaller ones arising from side of ventral arm plate of basal arm segments. Disc scales thickly studded with tiny spinules and granules. Radial shields narrow, 4 times longer than wide, separated their distal third, disc deeply notched at each pair of shields, several slender spines arising from each genital plate within notch. Color, disc grayish white, arms yellowish white.

Discussion: Amphilimna mirabilis seems to be most similar to A. nike and A. tanyodes, the only other species with granules or closely grouped spinules rather than slender spines on the disc. It differs from A. nike in having at least twice as many arm spines, a much more dense covering of granules, much longer radial shields and in the adoral shields meeting at the distal side of the oral shields. Amphilimna tanyodes appears to be more like A. mirabilis in the above and other characters but seems to have somewhat longer spinules on the disc. In view of the distribution of the 2 species, A. tanyodes, though similar, must be distinct from A. mirabilis.

Distribution: Has been taken only off the north and south coasts of Cuba, 320 to 430 m.

Amphilimna nike (Schoener, 1967) Figure 1

Amphitarsus nike Schoener, 1967: 2, fig. 2. Amphilimna niki: Devaney, 1974, p. 122 [lapsus].

Material Studied: 1 spec. (holotype); WHOI CHAIN cruise 35, Dredge Sta. 33; 140 miles north of Surinam (7°53.5'N, 54°33.3'W),

535 m; 25 April 1963; MCZ 6797.—1 spec.; disc diameter 10 mm; GOSNOLD Sta. 1580; off Florida Keys (24°10.0'N, 81°22.0'W), 681 m; 1 June 1964.—1 spec.; Texas A&M cruise 69A11, Sta. 58; off Veracruz, Mexico (19°02.6'N, 95°27.5'W), 476 m; no date (specimen returned to Texas A&M).

Diagnosis: Oral papillae varying from jaw to jaw, 2-4 small papillae at apex of each jaw, 1 or 2 large round flattened papillae distally at each oral tentacle pore, occasionally a smaller papilla also, apical and distal groups separated by 1 or 2 small papillae (probably oral tentacle scales). Oral shields slightly longer than wide, roughly pentagonal with proximolateral sides meeting at a rounded angle and distolateral sides meeting a distal side. Adoral shields widely separated by oral shields. Arms probably 6 or more times disc diameter; arm spines under disc flattened and fused to form flanges except ventralmost which is free. Large, round, flattened tentacle scale arising from lateral arm plate, 1 or 2 much smaller scales arising from sides of ventral arm plates of proximal arm segments for varying distances along arm. Three or 4 slender arm spines, longest about as long as arm segment. Dorsal arm plates wider than long, often slightly separated by lateral arm plates. Disc scales covered by scattered conical granules often as far apart as 2 or 3 times diameter of granule; granules giving way to spinules on ventral surface of disc. Radial shields separated, only one and one-half times longer than wide, broadest distally; disc notched at each pair of radial shields.

Discussion: Amphitarsus nike and A. mirabilis both display considerable variation in their oral armature. Fortunately they seem easily separable by other characters, particularly the number of arm spines and proportions of the radial shields. In addition to the smaller specimens of the type material, A. nike is now known from a specimen with a disc diameter of 10 mm (see material studied).

Distribution: Known from the type-material collected in the tropical Atlantic 140 miles north of Surinam at 535 m and other material from the Gulf of Mexico off Veracruz, Mexico at 476 m, and in the southern Straits of Florida at 681 m.

Amphilimna tanyodes Devaney, 1974

Amphilimna tanyodes Devaney, 1974: 116, figs. 1-5.

Material Studied: None.

Diagnosis (modified after Devaney, 1974): Two to 4 small papillae extending around proximal end of jaw; 2 large round or oval papillae at each oral tentacle pore; papillae of proximal end of jaw separated from group at oral tentacle pore by 2 or 3 papillae, one nearest those at oral tentacle pore largest. Oral shields about as wide as long, bluntly pointed proximally, slightly lobed distally. Adoral shields meeting (or nearly so) at proximal end of oral shields. Arms slender, long,

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more than 10 times disc diameter. At size of 6–7 mm, 2 tentacle scales regularly to ninth arm segment, irregularly to 17th segment, single scale beyond; outer scale largest, oblong with rounded tip, flat, arising from side arm plate; inner scale smaller, more tapering, arising from ventral arm plate. Seven to 8 arm spines near disc; 1 to 3 lower arm spines on each lateral arm plate under disc unmodified, upper spines flattened and fused to form flanges; spines forming flanges divided beyond base. Disc scales studded with granules above, more widely spaced spinules below. Radial shields 3 times longer than wide, slightly separated proximally, more widely separated distally; disc notched at each pair of radial shields; 2 to 4 bluntly tipped spines at junction of radial shield and genital plate.

Discussion: A. tanyodes, except for having granules and small spines (spinules) on the disc, appears rather similar to A. multispina Koehler.

REMARKS ON THE GENUS AMPHILIMNA

The seven nominal species of Amphilimna considered here seem to fall into three groups of similar species, one consisting of A. olivacea and A. cribriformis, one consisting of A. multispina and A. valida, and one consisting of A. nike, A. mirabilis and A. tanyodes. Unfortunately, so little is known about five of the seven species I feel it is impossible, at present, to construct a completely satisfactory key. The following provisional key may serve to assist in the identification of the species provided recourse to the diagnosis is made.

PROVISIONAL KEY TO THE SPECIES OF AMPHILIMNA

1.	On basal arm segment innermost tentacle scales (arising from
	ventral arm plates) long and slender, longer than outer scales
	arising from lateral arm plates 2
	On basal arm segments innermost tentacle scales round and
	flattened, or occasionally absent or granular, not long and
	slender, shorter than outer tentacle scale 3
2.	Oral shield rhombic with angular or curved distal side A. olivacea
	Oral shield triangular with straight distal side A. cribriformis
3.	Disc scales of upper surface bear scattered spinelets
	Disc scales of upper surface bear closely clustered tiny short
	spinelets and/or granules
4.	Oral shield longer than wide, 6-9 arm spines A. multispina
	Oral shield wider than long, 6 or fewer arm spines A. valida
5.	Four arm spines or fewer, radial shields oval or round, as wide
	as long A. nike
	Six or more arm spines, radial shields at least twice as long
	as wide 6
6.	Atlantic species
	Pacific species A. tanyodes

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