

Redescription of *Hipponoa gaudichaudi* Audouin & Milne-Edwards, 1830 (Polychaeta, Amphinomidae)

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ABSTRACT

The genus *Hipponoa* (Polychaeta, Amphinomidae) is monotypic. *Hipponoa gaudichaudi* Audouin & Milne-Edwards, 1830, probably represents a highly specialized species whose affinities to amphinomids has been questioned. As part of an on-going study of Amphinomida, both the genus *Hipponoa* and species *H. gaudichaudi* are redescribed and emended. Affinities with other taxa of the order are briefly discussed.

RÉSUMÉ

Redescription d'*Hipponoa gaudichaudi* Audouin & Milne-Edwards, 1830 (Polychaeta, Amphinomidae)

Redescription de *Hipponoa gaudichaudi* Audouin & Milne-Edwards, 1830 (Polychaeta, Amphinomidae). Le genre *Hipponoa* est monotypique. *Hipponoa gaudichaudi* Audouin & Milne-Edwards, 1830, représente probablement une espèce très spécialisée dont les affinités avec les Amphinomidae sont discutées. Comme partie d'une étude en cours sur les Amphinomida, le genre *Hipponoa* et l'espèce *H. gaudichaudi* sont redécrits et émendés. Les affinités avec les autres taxa de l'ordre sont brièvement discutées.

INTRODUCTION

On-going studies on the phylogenetic systematics of the polychaete Order Amphinomida (cf. KUDENOV, 1994) have revealed both historical questions and undescribed features for the amphinomid *Hipponoa gaudichaudi* Audouin & Milne-Edwards, 1830. For example, MCINTOSH (1885) suggested that the setae of this species are not calcareous. This feature, coupled to the fact that *H. gaudichaudi* lacks a caruncle, led MCINTOSH and others to suspect that it was improperly assigned to the Amphinomidae. Indeed, the Order Amphinomida is highly diverged in the Class Polychaeta (DALES, 1962; CLARK, 1969). Removal of *Hipponoa* from the Amphinomidae may result in establishing another polychaete family (for which precedents exists, see CARUS, 1863; BAIRD, 1870). This decision cannot be made lightly. The purpose of this paper is to redescribe and emend the original of

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Hipponoa gaudichaudi, and to address the question by McINTOSH and others about the affinity of this species with the Amphinomidae.

MATERIALS AND METHODS

Materials of *Hipponoa gaudichaudi* were obtained both from the Smithsonian Institution (USNM) and the Allan Hancock Foundation Polychaete collection of the Los Angeles County Museum of Natural History (LACM-AHF). Tissue sections were made following specifications noted by KUDENOV (1977). Preliminary SEM work was performed at the USNM on preserved specimens held in the general collection.

Family Amphinomidae Lamarck, 1818

Genus *Hipponoa* Audouin & Milne-Edwards, 1830, emended

Hipponoa AUDOUIN & MILNE-EDWARDS, 1830: 156. — CUVIER, 1831: 18; MILNE-EDWARDS, 1838: 464. — COSTA, 1841: 270. — FAUCHALD, 1977: 102.

Hipponoe CARUS, 1863: 28. — QUATREFAGES, 1865: 409-410. — TREADWELL, 1939: 177. — GARDINER, 1975: 103. — *Non* TREADWELL, 1931: 3-4, figs. 10-12.

Hipponoe AUDOUIN & MILNE-EDWARDS, 1834: 116. — HOEVEN, 1850-1856: 244. — GRUBE, 1850: 289. — SCHMARDA, 1861: 134. — BAIRD, 1870: 239-240. — FAUVEL, 1913: 32; 1923: 132. — HORST, 1886: 170. — AMOUREUX, 1972: 51.

Hyponnë AUDOUIN & MILNE-EDWARDS, 1834: 117.

Metamphinome TREADWELL, 1940: 1.

Emended Diagnosis. — Body of adult fusiform, dorsoventrally flattened, with up to 105 setigers. Prostomium with five antennae, two pairs of eyes. Caruncle absent. Nuchal organ present. Mouth ventral. Notopodia on laterum. Neuropodia on ventrum. Dorsal cirri numbering one per notopodium. Ventral cirri papilliform. Notosetae all capillaries. Neurosetae retractile, hooks generally bidentate; may be unidentate. Branchiae planar, bipinnate. Anus terminal.

Remarks. — This emended diagnosis differs from those presented previously in that a nuchal organ is present, branchiae are planar and bipinnate, and the anus is terminal. Neurosetal hooks are generally bidentate in specimens with around 30 or fewer segments, and unidentate in a single specimen with 105 segments.

Hipponoa gaudichaudi Audouin & Milne-Edwards, 1830, emended

Figs 1-2

Hipponoa gaudichaudi Audouin & Milne-Edwards, 1830: 156-159, Pl. III, fig. 4-4a-4b. — AUDOUIN & MILNE-EDWARDS, 1834: 128-129, Pl. II, fig. 10-10 bis. — GUÉRIN, 1829-1843: 1-14, Pl. IV, fig. 3, 3A-3D. — CUVIER, 1831: 19. — IBAÑEZ, 1973: 124.

Hipponoa gaudichaudi agulhana DAY, 1967: 122, fig. 3.1 a-e.

Hipponoa gaudichaudii CUVIER, 1831: 18. — MILNE-EDWARDS, 1838: 464.

Hipponoe gaudichaudi BAIRD, 1870: 239-240. — McINTOSH, 1885: 30-33, Pl. I, fig. 5, Pl. IV, fig. 3, Pl. IIIA, figs. 13-17. — HORST, 1886: 170-171. — FAUVEL, 1913: 32; 1914: 89, Pl. I, fig. 2, 12; 1923: 132, Fig. 47 l-p; 1936: 19. — PETTIBONE, 1963: 57-59, fig 13 a-b. — FAUVEL & RULLIER, 1959: 510. — AMOUREUX, 1972: 51.

Hipponoe gaudichaudi HOEVEN, 1850-56: 244. — GRUBE, 1850: 289.

Hipponoe Gaudichaudi STOP-BÖWITZ, 1948: 15.

Hipponoe Gaudichaudi CUVIER, 1830: 199. — MILNE-EDWARDS, 1836: 31-32, Pl VIII, fig 4, 4a,b. — CARUS, 1863: 28. — QUATREFAGES, 1865: 410. — MOORE, 1903: 793. — WILLEY, 1910: 180. — SUMNER, OSBURN & COLE, 1913: 619. — AUGENER, 1922: 39. — OKUDA, 1950: 49, figs a-b. — GARDINER, 1975: 103, fig. 5 l-m.

Hipponoe gaudichaudi gigantea Hartmann-Schröder, 1981: 24-25, figs. 1, 2.

Hipponoe multibranchiata Hartman 1951: 29, Pl. 8, figs. 1-2.

Non Metamphinome multibranchiata Treadwell, 1940: 1-2, figs. 1-3.

Hipponoe cranchii Baird, 1870: 240, Pl. VI, figs. 7-14.

Non Hipponoe elongata Treadwell, 1931: 3-4, fig. 10-12; 1939: 177-178, Fig. 11.

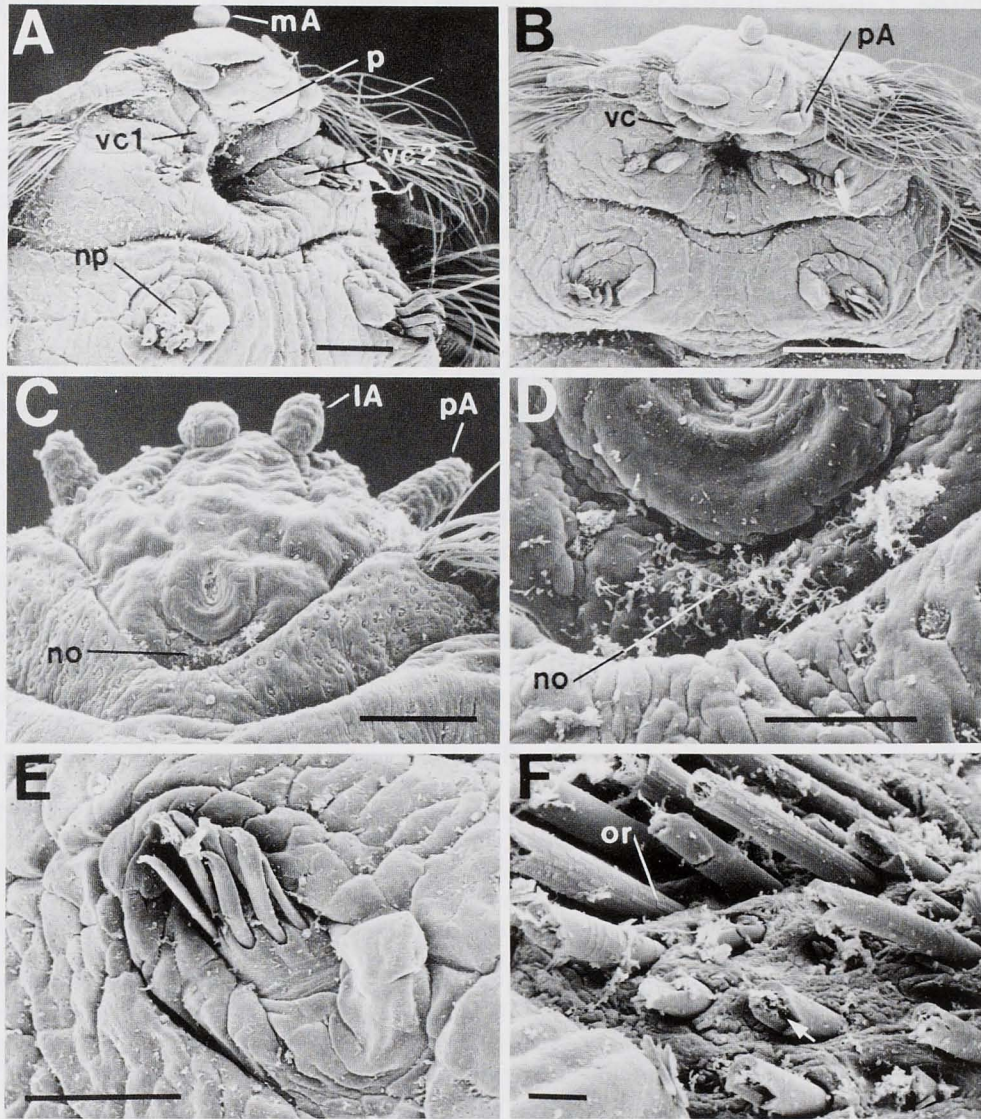


FIG. 1. — *Hipponoa gaudichaudi* Audouin & Milne-Edwards : A, prostomium and anterior segments of adult, ventrolateral view. —B, same, anteroventral view. —C, same of juvenile lacking median antenna, dorsal view. —D, same, detail of nuchal organ, dorsal view. —E, neuropodium, ventral view. —F, sheared capillary notofascicle revealing hollow core (arrow). Abbreviations: lA, lateral antenna; mA, median antenna; no, nuchal organ; np, neuropodium; or, notosetal ornamentation; p, palps; pA, palpal antenna; vc, ventral cirrus; vc 1, padlike ventral cirrus of setiger 1; vc 2, ventral cirrus of setiger 2. Scales : A = 0.2 mm; B = 0.4 mm; C = 0.1 mm; D = 20 μ m; E = 0.2 mm; F = 10 μ m.

Material examined. — North Atlantic Ocean, Gulf Stream, Surface, R/V *Albatross*, coll. J.E. BENEDICT, 20 specimens (USNM 16311); 3 specimens (USNM 32374). — Bermuda, south shore, 5 Aug 1948, coll. H. Ris, three specimens (LACM-AHF, n5858 from HARTMAN ledger).

Caribbean Ocean, Panama, Galeta Point, 14 Jul 1976, in sargassum rafts washed onto reef flats, coll.

G. HENDLER, 1 specimen (USNM 58724). — Louisiana, Grand Isle, coll. H. BENNETT, 4 (LACM-AHF, n10183 from HARTMAN ledger).

North Pacific Ocean, 30°50'N, 121°35'W, 29 May 1954, in *Lepas fascicularis* Ellis & Solander, coll. D. HENRY, 19 specimens (USNM 32366); 27°56'N, 119°36'W, 23 Apr 1954, in *L. anatifera* Linnaeus, two specimens (USNM 32367); 27°56'N, 119°36'W, 23 Apr 1954, in *L. fascicularis* Ellis & Solander, six specimens (USNM 32368); 28°40'N, 129°35'W, Jun 1955, in *L. anatifera* Linnaeus, two specimens (USNM 32369); 30° N, 118° W, 4 May 1954, one specimen (USNM 32370); 26°12'30" N, 118°27' W, 24 Aug 1954, in *L. fascicularis* Ellis & Solander, two specimens (USNM 32371); 30° 50'N, 121°35'W, 29 May 1954, in *L. pectinata* Spengler, one specimen (USNM 32372); 27°56'N, 119°36'W, 23 Apr 1954, in *L. anatifera* Linnaeus, 5 specimens (USNM 32373); Off Japan, 28°02'N, 155°58'E, 29 Apr 1970, coll. G. CHASE, 2 specimens (USNM 43205). —?Pacific Ocean, 9 Jun 1961, coll. D. DAVENPORT, seven adults + numerous juveniles (LACM-AHF).

Description. — Body of adults fusiform, dorsoventrally flattened, 24-105 mm long, 5-18 mm wide without setae, totalling 20-46 setigers; dorsum broadly exposed. Color in life bright orange.

Prostomium a small, single, rhomboid-shaped lobe, with 5 cirriform antennae (Fig. 1c-d). Median antenna about as long as prostomium, lacking ceratophore (Fig. 2a). Lateral antennae arising from frontal, dorsomedial surface, about 0.6 times length of median antenna (Fig. 2a). Palpal antennae arising from anterolateral surfaces of palps, somewhat more stout and shorter than lateral antennae (Figs 1a-b; 2b). Eyes numbering two pairs, located anterior to median antenna, where prostomium is widest, all small, inconspicuous. Caruncle absent. Nuchal organ present as ciliated patch on posterior prostomium, best observed in specimens with fewer than 15-18 setigers (Figs 1c-d; 2a). Palps fused into single lobe, forming upper lip of mouth and short midventral groove (Figs 1a-b; 2b). Mouth ventral, opening between setigers 1-2; setigers 1-2 forming lateral lips of mouth; setiger 2 posterior lip (Figs 1a-b; 2b).

Setiger 1 with setigerous notopodia, neurosetae absent, neuropodia only represented by pad-shaped ventral cirri (Figs 1a-b; 2b). Parapodia biramous, setigerous from setiger 2 to end of body; rami more widely separated from one another compared to setiger 1. Notopodia as transverse ellipses in outline in dorsal view, confined to extreme dorsolaterum; notopodial lobes not raised above general body surface. Neuropodia circular to slight transverse ellipses in outline in ventral view, confined to ventrum (Fig. 1e); neuropodial lobes resembling retractable papillae surrounded by thick, glandular collars of tissue (Fig. 1e) with papilliform ventral cirri.

Parapodial cirri present on all setigers. Dorsal cirri cirriform, with basal cirrophore two times longer than wide, distal style about 2-3 times longer than cirrophore; arising from body wall behind inferior notosetal fascicle margin, not within notosetal fascicle. Ventral cirri papilliform, lacking basal cirrophores, slightly longer than wide; arising medially from collar of neuropodium that encircles neurosetal fascicles (Figs 1a-b, e; 2b).

Notosetal fascicles with numerous setae directed laterally in all setigers. Notoetae hollow (Fig. 1f, arrow), slender capillaries with file-like teeth on shafts (Fig. 1a-b, f), calcareous, accessory subdistal spurs absent, tapering distally to fine, entire tips (Fig. 1a-b). Neurosetae from setiger 2 of one kind; chitinous, solid, distally bidentate hooks with longitudinal striae, numbering around 10 per fascicle (Fig. 1e). Notoaciculae inconspicuous, capillariform, numbering 3-5 per fascicle, limited to posterior notopodial margin. Neuroaciculae from setiger 2 distally curved, distally embedded in clear cuticular matrix, non-emergent, numbering 8 per fascicle, in single, long, dorsal rows along superior or outer lateral margins of neuropodia (Fig. 2c).

Branchiae bipinnate, pinnae branching alternately off primary branchial axis, each pinna in turn branching up to 6 times basally and having fewer branches distally (Fig. 2d-e); pattern more conspicuous in small specimens. Branchiae present from setiger 3 to end of body, numbering 1 pair per segment, tending to be planar, particularly in small specimens (Fig. 2d) than in larger ones (Fig. 2e). Branchial bases broad, arising posterodorsally to dorsal cirri, not extending beyond notosetae. Branchiae gradually increasing in length and development to midbody, gradually becoming shorter, less developed to end.

Pygidium with terminal anal cirrus; anus opening through anal cirrus (Fig. 2f).

Distribution. — Cosmopolitan in tropical and warm temperate oceans.

Remarks. — *Hippinoa gaudichaudi* has been reported from numerous localities throughout the world, and its description has not significantly changed since AUDOUIN & MILNE-EDWARDS (1830) first described and BAIRD (1870) later emended it. As presently understood, *H. gaudichaudi* appears to be a highly modified and specialized member of the Amphinomidae, probably reflecting the fact that it is an inquiline of barnacles (*Lepas* species;

BAIRD, 1870; AUGENER, 1910; KUDENOV, 1977). Although *H. gaudichaudi* retains many features of the Amphinomida, it is generally quite unlike most amphinomids (GUSTAFSON, 1930 ; KUDENOV, 1994).

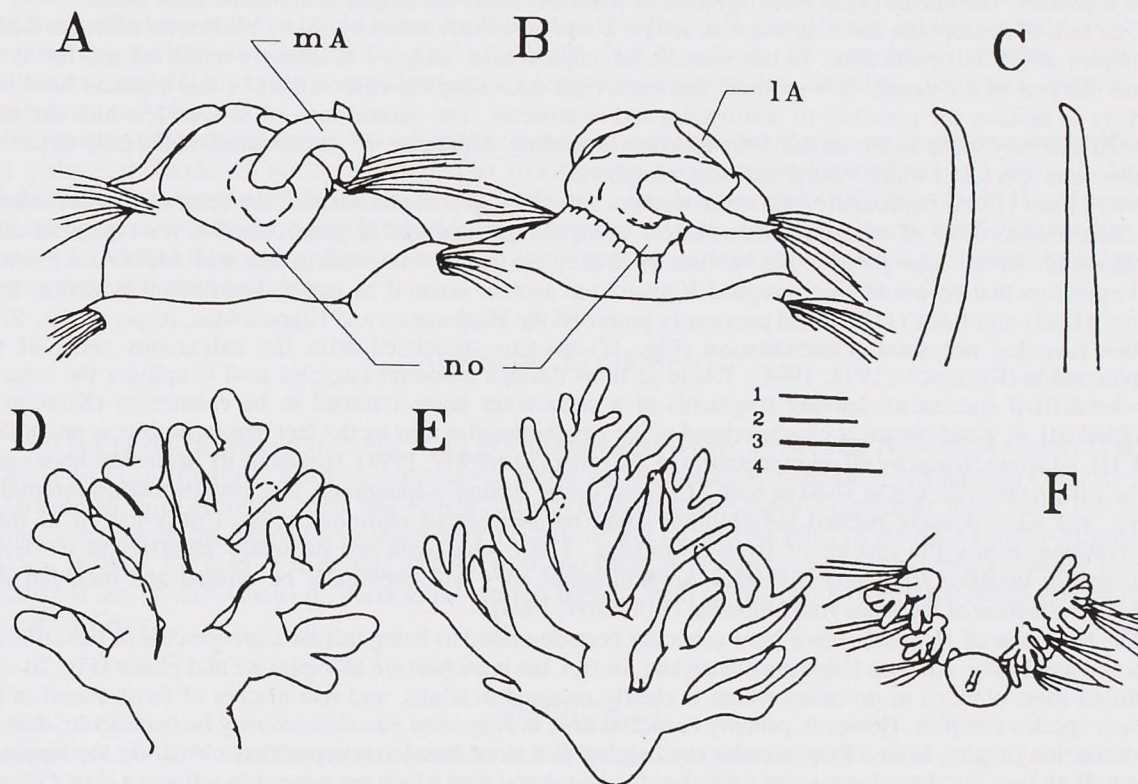


FIG. 2. — *Hipponoa gaudichaudi* Audouin & Milne-Edwards: A — B, Prostomium showing only three of five antennae and setiger 1, dorsal view. — C, neuroaciculae. — D, bipinnate branchia from right setiger 10, anterior view. — E, same, from left setiger 13, anterior view. — F, pygidium, dorsal view. Abbreviations : see legend for Fig. 1. Scales : 1 = 0.25 mm, F; 2 = 10 μ m, D; 3 = 30 μ m, E and 5 μ m, C; 4 = 0.2 mm, A, B.

For example, *H. gaudichaudi* differs from the general amphinomid pattern in that its body is strongly flattened and fusiform, and is the only known genus with a continuous midventral groove. Its prostomium is strongly reduced to a single lobe with palpal antennae arising from the anterolateral margins of the prostomium. Palps are extremely short, narrow, and fused medially, and are confined to the ventral area lying between the mouth and prostomium (Fig. 2b; KUDENOV, 1993). The mouth is present very close to the prostomium at the junction of setigers 1-2 (Fig. 2b). Setiger 1 is dorsally complete, and is not interrupted by a caruncle. Notopodia arise from the extreme dorsolaterum; neuropodia from the ventrum. The notosetae are entirely nonspurred capillaries; it is the only presently known genus of the family in which the notosetae are represented solely by capillaries. The dorsal cirri arise directly from the body wall as they do in the Euphrosinidae, and not from within the notopodial field as is typical of Amphinomidae. Obviously, *H. gaudichaudi* is quite unlike the Amphinomidae sensu lato in many of its features.

Additional traits either confirmed or newly discovered as part of this study can be added to this list. *H. gaudichaudi* is characterized by the: 1) lack of a caruncle; 2) a poorly ciliated, mound-shaped nuchal organ; 3) absence of both neuropodia and neurosetae in setiger 1; 4) reduced dorsal cirri in setiger 1; 5) lack of cirriphores on ventral cirri; 6) hollow calcareous notosetae; 7) solid neurosetae that may be chitinous; 8) planar, bipinnate branchiae; and 9) a terminal anus opening through an anal cirrus. All except the first and third of these traits are newly reported.

The nuchal organ is poorly ciliated, and more conspicuous as a mound-shaped lobe on the posterior prostomium in juveniles and subadults than in larger individuals, such as functionally mature females. This finding

may be expected, given the fact that *H. gaudichaudi* is a protandric hermaphrodite (KUDENOV, 1977). It is hypothesized that immature individuals rely on nuchal organs and chemical senses to a much greater extent compared to mature worms to maintain body contact with their brooder, to obtain food, and to subsequently locate other barnacles. The nuchal organ must therefore be relatively better developed in immature individuals.

The lack of neuropodia and neurosetae in setiger 1 was previously noted by DAY (1967) who made no further comments about its significance. In this specialized amphinomid, setiger 1 is strongly modified and forms the lateral margins of the mouth. It is so small that most light microscopical observations of this segment have lead workers to assume the presence of neuropodia and neurosetae. The ventral cirri of setiger 1, which are both reduced and very close to the mouth, may function in feeding. Moreover, *H. gaudichaudi* is the only described amphinomid species in which ventral cirri lack cirriphores.

McINTOSH (1885) particularly, and other workers generally, questioned whether the setae of *H. gaudichaudi* are calcareous as those of other amphinomids. He strongly suggested that *H. gaudichaudi* is not typical of other amphinomids whose setae produce gas bubbles when they are treated with weak acetic acid. McINTOSH conveys the impression that he would have assigned *Hipponoa* to another taxon if he had had additional evidence. Both CARUS (1863) and BAIRD (1870) had previously proposed the Hipponacea and Hipponoidae, respectively. SEM studies revealed notosetal ornamentation (Fig. 1f) usually associated with the calcareous setae of the Amphinomida (KUDENOV, 1993, 1994). Tissue sections through notosetal fascicles tend to splinter the setae of non-decalcified specimens, leaving fragments of a clear outer layer assumed to be calcareous (KUDENOV, unpublished). *H. gaudichaudi* is clearly related to the Amphinomidae also by the fact that its notosetae are hollow (Fig. 1f), a feature shared by all other members of the order (KUDENOV, 1994). However, its neurosetal hooks may not be calcareous. All appear solid in both SEM and tissue section preparations, lack ornamentation referred to above, and have densely packed longitudinal striae reminiscent of chitinous setae. Confirmation of these observations awaits the receipt of fresh specimens. These setal data are presently insufficient to define relationships between *Hipponoa* and other Amphinomida; they will eventually be refined and included in a cladistic evaluation of the order Amphinomida (KUDENOV, 1994).

The branchiae of *H. gaudichaudi* have generally been described as being tuft-like, arborescent or dendritically branched and bushy. All such terms are misleading. In fact, the branchiae are all bipinnate and planar (Fig. 2d-e), a condition most obvious in juveniles which is clearly retained in adults, and reminiscent of those found in the *Chloeia* species complex. However, primary branchial axes in *Hipponoa gaudichaudi* may be contractile; degrees of contraction ranging from a long, slender zig-zagging to a stout, basal axis sometimes obscuring the bipinnate pattern. Both taxa also have lateral cirri (mistaken for true dorsal cirri which are present in setigers 1-4 of *Chloeia*) arising directly from the body wall and outside the notopodial field. No attempt to imply common ancestry between these taxa is intended.

Another overlooked character in *H. gaudichaudi* is the presence of a terminal anus that opens through the anal cirrus (the presence of a dorsal anus has been assumed [e.g., FAUVEL, 1923]). In other members of the Amphinomidae, the anus opens on the dorsum of the last few body segments, above an associated, unpaired anal papilla. The anus of Euphrosinidae is terminal, and opens between or above paired anal cirri (KUDENOV, 1994). The unusual anus of *H. gaudichaudi* presumably reflects its highly specialized life style, enabling it to void its feces without fouling either itself or its host. This point can only be answered by studying live specimens of both the worm and its host.

The synonymies listed above are not intended to be exhaustive. Analysis of the earliest literature shows AUDOUIN & MILNE-EDWARDS (1830) original record from Port Jackson, Australia, was quoted by subsequent workers. BAIRD (1870) published what appears to be the second record of the species from the eastern equatorial Atlantic and Madeira. He described a second species, *H. cranchii*, which his illustrations show to be a juvenile *Amphinome* (?rostrata), and not a second species of *Hipponoa*. The third record of *H. gaudichaudi* was from the *Challenger* expedition, and McINTOSH (1885) provided extensive observations about it, including the presence of capillary notosetae having distally forked ends. Such notosetae have not been reported for *H. gaudichaudi* at any other time prior or subsequent to his work. HORST (1886) represents the fourth record, after which time the species was more commonly encountered. DAY (1967, Fig. 3.1.a-e) later described the subspecies, *H. gaudichaudi agulhana*, based on the absence of notosetae as described by McINTOSH (1885). It is suggested that McINTOSH observed frayed or damaged notosetae that appeared distally forked. Another, *H. gaudichaudi gigantea* Hartmann-Schröder (1981) was distinguished on the basis of body size and hook morphology. Although the specimens she examined were up to 105 mm long, neurosetal hook morphology may reflect size-dependent relationships instead of polyploidy, as implied by HARTMANN-SCHRÖDER. Moreover, distinction between the terms "Normalform" and

"Riesenform" used by HARTMANN-SCHRÖDER to describe *H. gaudichaudi gigantea* are typological, and seem to preclude a continuum of morphological change associated with allometric growth.

The genus *Hipponoa* supposedly represents three described species (FAUCHALD, 1977) including *H. gaudichaudi*, *H. cranchii* Baird, 1870, and *H. elongata* Treadwell, 1931. *Metamphinome multibranchiata* Treadwell, 1940 was referred to *Hipponoa* by HARTMAN (1951) and *H. gaudichaudi* by PETTIBONE (1963). All previous descriptions and illustrations are sufficiently clear to indicate *H. cranchii* is probably a juvenile *Amphinome*, and *H. elongata* is most certainly a *Linopherus*-like species. Therefore, the genus *Hipponoa* is presently monotypic.

In summary, the species description of *Hipponoa gaudichaudi* is emended with certain observations confirmed and additional characters newly reported. The species seems to be highly specialized and derived; departs substantially from the general features normally attributed to the Amphinomidae (KUDENOV, 1994); and seems to be cosmopolitan in tropical, subtropical and warm-temperate oceans. But is this taxon truly cosmopolitan and monotypic? Only a thorough systematic study involving specimens from various points throughout its range can answer these and other questions.

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