

Revision of *Hermodice* Kinberg, 1857 (Polychaeta: Amphinomidae)

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SUMMARY: The genus *Hermodice* Kinberg, 1857 was established with the species *Aphrodita carunculata* Pallas, 1766, based on the shape and development of the caruncle. Several species were later described within the genus; however, it is currently regarded as monotypical, with *H. carunculata* as a widespread species. An evaluation of available type and non-type specimens together with observations of living specimens has allowed the diagnostic features to be refined, and two new features have been included: the number of branchial filaments and the anal lobe. Consequently, in this study we have been able to confirm the differences between *Hermodice* and *Pherecardia* Horst, 1886. The type species, *H. carunculata*, has been redescribed, and *H. nigrolineata* Baird, 1870 has been re-established. Further, *H. formosa* (Quatrefages, 1866) has been transferred to *Pherecardia*, together with *H. pennata* Treadwell, 1906 and *H. distincta* Hoagland, 1920.

Keywords: caruncle, fireworms, morphological variability, taxonomy, Grand Caribbean, eastern Atlantic, Mediterranean Sea.

RESUMEN: REVISIÓN DEL GÉNERO *HERMODICE* KINBERG, 1857 (POLYCHAETA: AMPHINOMIDAE). – El género *Hermodice*, Kinberg, 1857 se estableció con la especie *Aphrodita carunculata* Pallas, 1766, debido a la forma y desarrollo de la carúncula. Posteriormente, se describieron varias especies dentro del género. Sin embargo, actualmente se considera que el género es monotípico y que *H. carunculata* es una especie cosmopolita. La revisión de material tipo y especímenes adicionales, incluyendo ejemplares vivos, nos ha permitido redefinir las características diagnósticas e incorporar dos nuevos atributos: el número de filamentos branquiales y el lóbulo anal. Como consecuencia, ha sido posible confirmar las diferencias entre *Hermodice* y *Pherecardia* Horst, 1886. Así mismo, se redescrive la especie tipo *H. carunculata* y se reestablece *H. nigrolineata* Baird, 1870. Además, *H. formosa* (Quatrefages, 1866) se transfiere a *Pherecardia*, junto *H. pennata* Treadwell, 1906 y *H. distincta* Hoagland, 1920.

Palabras clave: carúncula, gusanos de fuego, variabilidad morfológica, taxonomía, Gran Caribe, Atlántico oriental, mar Mediterráneo.

INTRODUCTION

Amphinomid polychaetes are commonly known as fireworms because of the burning sensation caused by their chaetae breaking after penetrating human skin. They are brightly colored and may reach large sizes (>50 cm long, ≈2 cm wide), as in the cases of some *Eurythoe* Kinberg, 1857 and *Hermodice* Kinberg, 1857 species. Fireworms thrive in the intertidal and may be abundant in coral reef or rocky areas; there are also some deep-water genera. Although several species are

very large and colorful, the group has several taxonomic problems because its morphologic variability is poorly understood (particularly within closely related genera). In fact, several nominal species have been regarded as synonyms, often without an evaluation of the type materials. This might explain the presence of some widely distributed species (Salazar-Vallejo, 1997). Consequently, detailed revisions of species and even genera are needed (Kudenov, 1995), together with phylogenetic studies to clarify the affinities within the family (Wiklund *et al.*, 2008).

TABLE 1. – Taxonomic status of species considered in *Hermodice*.

Species	Author	Taxonomic status	In <i>Hermodice</i> by:	Described in the genus:
<i>H. carunculata</i>	(Pallas, 1766)	Valid	Kinberg, 1857, 1867, Baird, 1870	<i>Aphrodita</i>
<i>H. savignyi</i>	(Brullé, 1832)	junior synonym	Kinberg, 1867, Baird, 1870	<i>Amphinome</i>
<i>H. striata</i>	Kinberg, 1857	Belong to <i>Pherecardia</i>	Kinberg, 1857, 1867, Baird, 1870	<i>Hermodice</i>
<i>H. smaragdina</i>	(Schmarda, 1861)	junior synonym	Kinberg, 1867	<i>Amphinome</i>
<i>H. sanguinea</i>	(Schmarda, 1861)	junior synonym	Kinberg, 1867, Baird, 1870	<i>Amphinome</i>
<i>H. dydimobranchiata</i>	(Baird, 1864)	junior synonym	Baird, 1870	<i>Amphinome</i> after in <i>Amphibranchus</i>
<i>H. formosa</i>	(Quatrefages, 1866)	Belong to <i>Pherecardia</i>	Kinberg, 1867	<i>Amphinome</i>
<i>H. bruguieresii</i>	(Quatrefages, 1866)	Belong to <i>Pherecardia</i>	Kinberg, 1867	<i>Amphinome</i>
<i>H. picta</i>	Kinberg, 1867	<i>nomen nudum</i>	Kinberg, 1867	<i>Hermodice</i>
<i>H. nigrolineata</i>	Baird, 1870	Valid	Baird, 1870	<i>Hermodice</i>
<i>H. pennata</i>	Treadwell, 1906	Belong to <i>Pherecardia</i>	Treadwell, 1906	<i>Hermodice</i>
<i>H. distincta</i>	Hoagland, 1920	Belong to <i>Pherecardia</i>	Hoagland, 1920	<i>Hermodice</i>
<i>H. pennata tutuliensis</i>	Treadwell, 1926	Belong to <i>Pherecardia</i>	Treadwell, 1926	<i>Hermodice</i>

Kinberg (1857) proposed *Hermodice* for *H. striata* Kinberg, 1857, from the Pacific island of Moorea, and to include *Aphrodita carunculata* Pallas, 1766, from the Lesser Antilles (Antigua). Later, Kinberg (1867) wrongly recognized *Hermodice* as a new genus, now with eight species: the two preceding ones, a new one from the Mediterranean Sea, *H. picta* Kinberg, 1867, and five formerly described in *Amphinome* Bruguière, 1789: *H. savignyi* (Brullé, 1832) from Moorea, *H. smaragdina* (Schmarda, 1861) and *H. sanguinea* (Schmarda, 1861) both from Jamaica, *H. formosa* (Quatrefages, 1866) from the Sandwich Islands, and *H. bruguieresii* (Quatrefages, 1866) from the Seychelles Islands. Kinberg (1867) also proposed *Amphibranchus* as a new genus that includes two species: *A. occidentalis* newly described from the Antilles (Barthelemy) and *A. dydimobranchiata* (Baird, 1864) from Ascension Island. *Amphibranchus* was subsequently regarded as a junior synonym of *Hermodice*, and its two species were regarded as junior synonyms of *H. carunculata* by Baird (1870), Fauvel (1914, 1923) and Hartman (1949).

Baird (1870) recognized only six species in *Hermodice* and described *H. nigrolineata* from the Mediterranean Sea and the Canary Islands, which was later synonymized with *H. carunculata*, as was *H. savignyi* (Fauvel, 1923; Ebbs, 1966).

Horst (1886) proposed *Pherecardia* for a new species: *P. lobata*, which had a large, foliose caruncle resembling that in *Hermodice*, although the folds were divergent and included a conspicuous median keel. Later, Horst (1911) indicated that several amphinomid species, including *H. striata*, should be transferred to *Pherecardia*. Regrettably, this was overlooked and consequently other species with a *Pherecardia*-like caruncle were described within *Hermodice*: *H. pennata* Treadwell, 1906 (Hawaii), *H. distincta* Hoagland, 1920 (Philippines), and the variety *H. pennata tutuliensis* Treadwell, 1926 (Samoa). Augener (1927) considered all these species as junior synonyms of *H. striata* without noticing that they should belong to another genus. Hartman (1949) emphasized that *H. striata* belonged to *Pherecardia*, and in her 1959 catalogue she listed these three species as probable synonyms of *P. striata*. However, Hartman did not evaluate her proposal with material revision.

As a result, most species in *Hermodice* have been regarded as junior synonyms of *H. carunculata* (Fauvel, 1923; Ebbs, 1966) (Table 1). Fauchald (1977) recognized four species (i.e. *H. carunculata*, widely distributed in the Atlantic, and the three questionable species included in the catalogue in Hartman (1959)). Nonetheless, besides the original descriptions, most records for the genus belong to *H. carunculata* (Fig. 1), which has been reported from shallow reef zones down to 300 m deep on sand flats (Ehlers, 1887; Ebbs, 1966).

This complex taxonomic background relies on synonymies that have mainly been proposed based on the available descriptions and illustrations rather than studies of type materials. Old descriptions, however, often lack complete characterizations of diagnostic characters. Therefore, in this paper, we present a systematic revision based on studying the available type material and including comparisons with additional material from different locations to propose a valid taxonomy for *Hermodice* and related genus.

MATERIALS AND METHODS

Specimens were borrowed from the following collections: The Natural History Museum, London (BMNH); Departamento de Zoología, Universidad de la Laguna, Tenerife (DZUL); Colección de Referencia, El Colegio de la Frontera Sur, Chetumal (ECOSUR); Museum of Faculty of Fisheries, Ege University, Turkey (ESFM); Institut de Recherche Fondamentale et Appliquée, Université Catholique de l'Ouest, Angers (IRFA); Los Angeles County Museum of Natural History, Allan Hancock Foundation, California (LACM-AHF); Muséum National d'Histoire Naturelle, Paris (MNHN); Swedish Museum of Natural History, Stockholm (SMNH); Texas Cooperative Wildlife Collection, Texas (TCWC); Colección de Referencia, Universidad de Nuevo León, Monterrey (UANL); National Museum of Natural History, Smithsonian Institution, Washington (USNM); Zoologisch Museum, Universiteit van Amsterdam, Netherlands (ZMA).

Some standard measurements were made (body length, body width in chaetiger 10, and number of

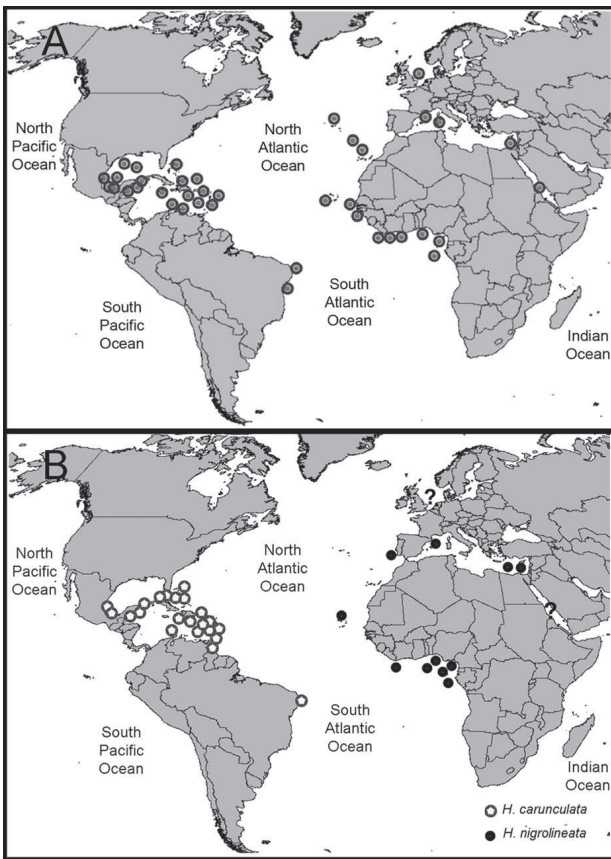


FIG. 1. – A, *Hermodice carunculata* records according to the literature. B, *Hermodice* species after this review, question marks indicate unavailable material.

chaetigers). Further, we assessed the diagnostic potential of the median antenna length (MA), lateral antennae length (LA), palp length (PL), caruncle length (CaL), caruncle width (CaW), caruncular folds (CaF), branchial filaments in the dorsal (DB) and lateral (LB) branches in chaetiger 10, cirrophore length (CpL), cirrostyle length (CsL), ventral cirri length (VC), and anal lobe length (ALL) and width (ALW) (Fig. 2). The variability against body size (as number of chaetigers) was evaluated using the Prism 5.0c for Mac OS X, GraphPad Software, based on log-transformed data, and a power regression model was used to calculate the parameters of allometric relationship (Harvey and Pagel, 1991). Since two tendencies for branchial filaments were identified, the slopes of DB were compared with ANCOVA using the above-mentioned software. Semi-permanent slides of parapodia from chaetigers 10, 30 and 50 (often including some additional parapodia because chaetae may show different levels of erosion) were prepared to describe the chaetal denticulation.

The morphology of the caruncle was first described on living specimens, which were then fixed to study the possible modifications. Further, some histological sections were made and stained with Hematoxylin and Eosin to show muscular fibers in the caruncle. To provide a precise description of the caruncle morphology and its diagnostic features in *Hermodice*, materials belonging to *Pherecardia* from the LACM-AHF and USNM collections were borrowed for comparison.

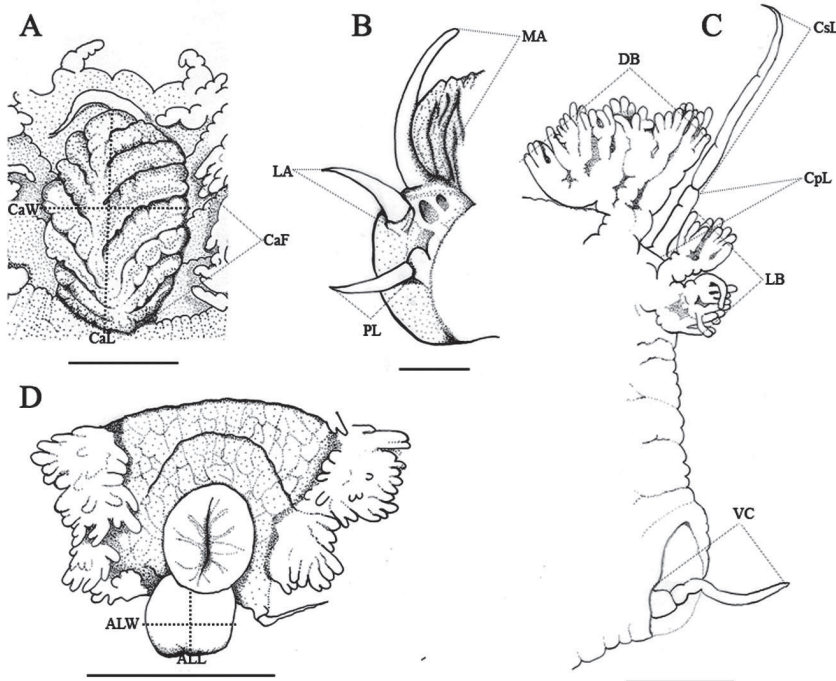


FIG. 2. – Morphological features evaluated in *Hermodice*: A, caruncle; B, protopodium; C, parapodium; D, pigydium. A scale: 1 mm; other scale: 0.5 mm. Abbreviations: ALL, anal lobe length; ALW, anal lobe width; CaF, caruncular folds; CaL, caruncle length; CaW, caruncle width; CpL, cirrophore length; CsL, cirrostyle length; DB, branchial filaments in the dorsal branch in chaetiger 10; LA, lateral antennae length; LB, branchial filaments in the lateral branch in chaetiger 10; MA, median antenna length; PL, palp length; VC, ventral cirri length.

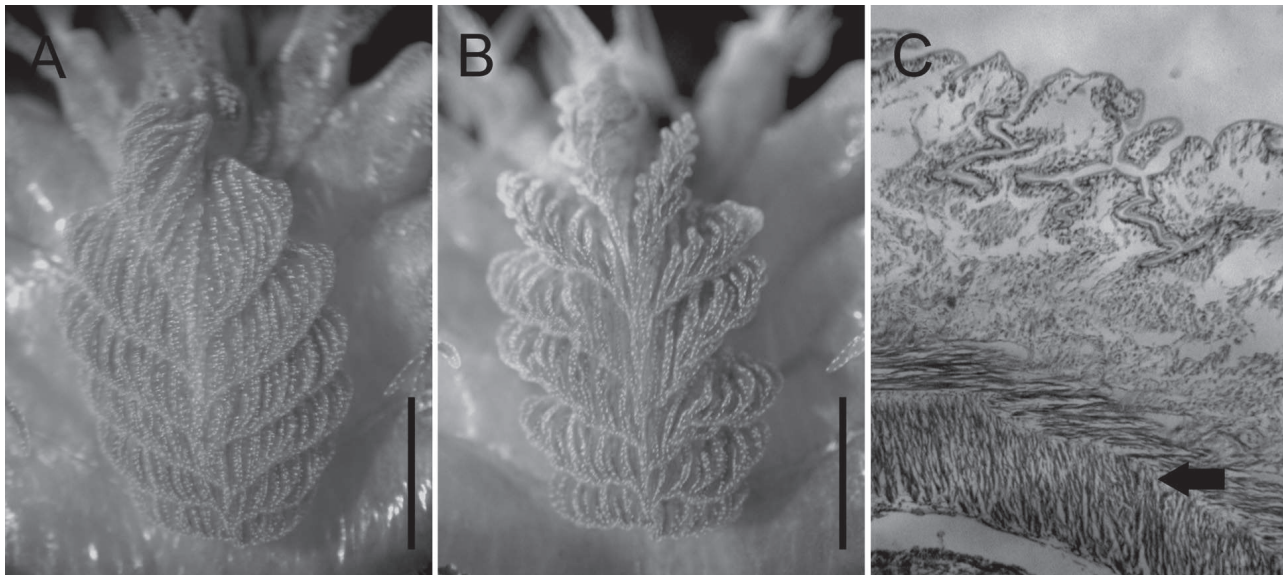


FIG. 3. – *Hermodice* caruncle: A and B same living worm; C, transverse section from median folds. Arrow: muscular fibers. Scale: 1 mm.

RESULTS

Morphological features

Prostomium

After fixation, the prostomium is usually covered by the contraction of the first three chaetigers. On living animals, however, the prostomium projects forward beyond these anterior chaetigers. Thus, the contraction affects the relative eye-size and arrangement, which can only be correctly perceived by comparing dorsal and lateral views. Dorsally, the eyes are similarly sized and arranged in the corners of a rectangle, whereas laterally the posterior ones appear about half as large as the anterior ones. *Hermodice* eyes are complex, with well-developed optical nerves, a pigmented retina, a relatively homogeneous lens, and the underlying cuticle as a corneal layer (Marsden and Galloway, 1968). This complex structure may explain the observed differences in size, and that the pigmented areas appear to differ when seen from a single plane due to the different orientation of the eyes.

Prostomial appendages such as palps and antennae often show transverse marks, but these are irregular and depend on the contraction, so they are considered smooth. They show allometric relationships with the number of chaetigers, and vary greatly ($MA=0.860x-1.442$, $R^2=0.688$, $n=115$; $LA=1.036x-1.964$, $R^2=0.758$, $n=139$; $PL=0.752x-1.553$, $R^2=0.467$, $n=86$). However, the median antenna always tends to be thicker and longer than laterals, and palps tend to be slightly smaller than lateral antennae.

Caruncle

This organ is widely employed to separate amphinomid genera and even species within the same genus.

However, the caruncle is made of a complex network of muscular filaments and nerves (Tovar-Hernández and Salazar-Vallejo, 2008), which is markedly altered during fixation (Fig. 3C). Living *Hermodice* specimens move the caruncle by contracting the longitudinal muscles, which makes the caruncular folds more prominent and better defined (Fig. 3A-B). Caruncle size depends on the number of chaetigers (Fig. 4A), and the length explains the variability better ($CaL=1.019x-1.430$, $R^2=0.901$, $n=130$) than either width ($CaW=1.067x-1.695$, $R^2=0.862$, $n=118$) or number of folds ($CaF=0.044x+0.041$, $R^2=0.692$, $n=133$). Thus, the relative shape of the caruncle, which is ovoid or trapezoidal due to the natural movement, the length, the relative thickness or number of folds should not be employed as diagnostic features.

Branchiae

In *Hermodice* the relative position of the main branchial branches and the branching type are variable, and these variations and the relative branchial length have been employed in the past to establish additional species. However, this character is strongly affected by the relative contraction of successive chaetigers, so that branching patterns can be evaluated better in non-contracted than in contracted chaetigers. Contracted specimens will tend to have thicker and shorter filaments than non-contracted ones, so the real branching pattern will be easier to detect in the latter. The first three chaetigers have less branchial filaments and their number increases towards median chaetigers. The number of branchial filaments has an allometric relationship with the number of chaetigers, with two distinct patterns ($A=1.614x-1.127$, $R^2=0.893$, $n=91$; $B=1.4x-1.337$, $R^2=0.576$, $n=23$) and the differences are more pronounced in the dorsal branch (Fig. 4B) ($F=25.8322$, $P<0.0001$).

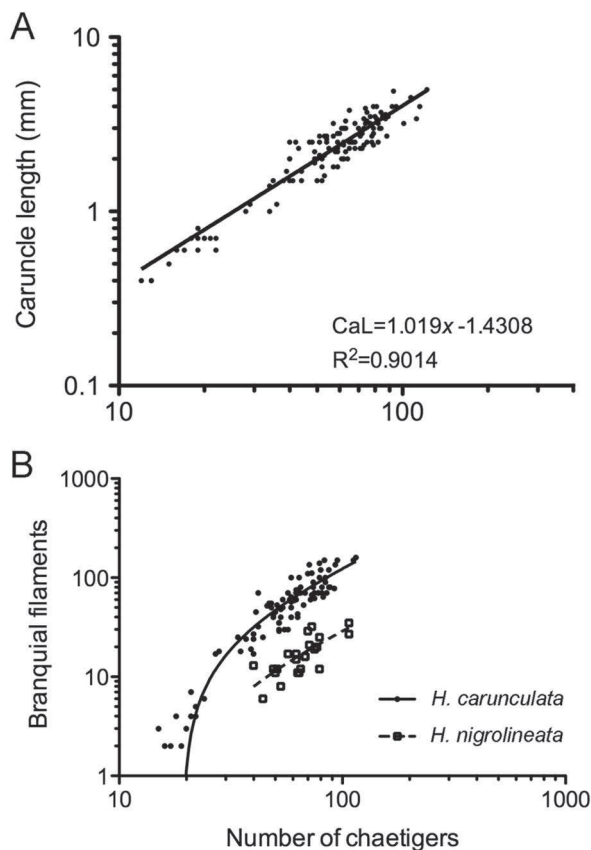


FIG. 4. – Morphological features in relation to the number of chaetigers: A, allometric relationship between caruncle and number of chaetigers; B, number of branchial filaments in the dorsal branchiae from two *Hermodice* species.

Dorsal cirri

Another usual diagnostic feature is the relative length of dorsal cirri in relation to chaetal length. However, chaetal sacs are retractable, which renders this attribute useless. Dorsal cirri length is also non-consistent because cirri are muscular and contractile. However, the relative length of the cirrophores is relatively constant despite that the cirrostyle varies.

Anal lobe

The relative development of the anal lobes has not been previously employed as a taxonomic feature. This is a terminal, fleshy outgrowth showing two consistent patterns: it may be short and round or large and distally cleft (Figs. 5H, 6F). This character allows us to separate two species (see below).

Chaetae

Since chaetae are calcareous, erodible and employed for self-defense, their relative proportion should not be employed as a diagnostic feature. Harpoon chaetae in particular may be easily lost when employed for

defensive purposes. Further, small variations in chaetal features must be used with caution because chaetal tips are easily eroded. Moreover, the traditional formalin-solution fixation becomes acidic, and thus alters the fine chaetal details (Fauvel, 1923). Consequently, the relevance of chaetae was considered to be rather minimal (Day, 1957). However, they could be employed after the variability along the body is defined. More specifically, the micro-scale regional differences in the distribution of each chaetal type in the chaetal lobe seem to be particularly relevant (Gustafson, 1930).

SYSTEMATICS

Family AMPHINOMIDAE Savigny in Lamarck, 1818
Genus *Hermodice* Kinberg, 1857

Hermodice Kinberg, 1857:12; Kinberg, 1910:35; Baird, 1870:219.
Amphibranchus Kinberg, 1867:90.

Type species. *Aphrodita carunculata* Pallas, 1766, by subsequent designation (Hartman, 1949:41).

Diagnosis. Body large, rectangular in cross-section. Prostomium with four eyes and three antennae. Peristomium with two palps over dorsal lips. Caruncle massive, extending over three chaetigers, with oblique, convergent folds, without median keel. Branchiae from chaetiger 1, branching. Parapodia biramous; notopodia with single cirri. Anus dorsal with a terminal lobe. Notochaetae include serrate, long or short, and harpoon chaetae. Neurochaetae with smooth or denticulate spur chaetae, and more than ten aciculae.

Remarks. Kinberg (1910) redefined *Hermodice* as a new genus, but only included *H. striata* as a new species because the compilation for the *Eugenie* expedition series was prepared by someone else. However, the genus was proposed before (Kinberg, 1857) and *H. carunculata* was already included, as stated by Baird (1870) who also regarded *Hermodice* as a valid genus. *H. carunculata* was finally designated as the type species by Hartman (1949). However, this was overlooked by Ebbs (1966:518) who stated “type fixation unknown to me”.

The alternating positions of parapodia along the body give the impression of duplicate branchiae (McIntosh, 1885), which might explain why Kinberg (1867) proposed including *Amphibranchus* based on Baird (1864)’s description of *Amphinome dydimobranchiata* as having a branchial pattern different enough to merit a distinct genus. However, Kinberg (1867)’s new genus overlooked its similarity to one of his previous genera. Baird (1870) noticed this problem, which might explain the omission of *Amphibranchus*, and the transfer of his own species to *Hermodice*.

Since the original proposal for *Hermodice*, the genus has not been rejected. However, it contains several species that might correspond to *Pherecardia* due to their caruncle type (Horst, 1911), which differs from

that of *Hermodice* in having diverging folds and a well developed median keel.

Accordingly, our revision of type and topotype materials, together with the original descriptions, indicates that the following nominal *Hermodice* species should be transferred to *Pherecardia*: 1) *H. pennata*, 2) *H. pennata tutuliensis*, 3) *H. formosa*, and 4) *H. bruguieresii*. However, *H. picta* should be regarded as a *nomen nudum* (Table 1).

***Hermodice carunculata* (Pallas, 1766)**
(Fig. 5)

Aphrodita carunculata Pallas, 1766:102-106, Fig. 12-13.

Amphinome carunculata Bruguère, 1789:46-47 (n. comb.); Audouin and Milne Edwards, 1833:197; Quatrefages, 1866:395-397.

Pleione carunculata Savigny, 1822:61-62 (n. comb.).

Hermodice carunculata Kinberg, 1857:13 (n. comb.); Kinberg, 1867:89; McIntosh, 1885:24-27; Ehlers, 1887:27-29; Treadwell, 1939:173-175, Fig. 8; Hartman, 1949:41-42; Hartman, 1951:22-25, Pl. 5, Fig. 1; Ebbs, 1966:518-524, Fig. 8; Ibarzábal, 1989:13-14, Fig. 7; Liñero-Arana, 1993:24, Pl. 6, Figs. 1-7; Salazar-Vallejo, 1997:383, Figs. 3, 9, 12 (all with descr.).

Amphinome smaragdina Schmarda, 1861:140, Pl. 34, Fig. 288; Quatrefages, 1866:405.

Amphinome sanguinea Schmarda, 1861:140, Pl. 34, Fig. 289; Quatrefages, 1866:405.

Amphinome dydimobranchiata Baird, 1864:449-450, Figs. 1-7.

Amphibranchus occidentalis Kinberg, 1867:90.

Type material: Holotype of *Amphibranchus occidentalis* Kinberg, 1867 [SMNH-1257]. Barthelemy. Syntypes of *Amphinome dydimobranchiata* Baird, 1864 [BMNH-1983.11.6.2]. Ascension Island, Coll. Mr. Watson: (4) damaged.

Additional materials. Netherland Antilles, [ZMA] Aruba: Sta. 1003, Lagoen Boekoeti, Oranjestad, sand-limestone, 1 m, 1930 (2); Sta. 1116B, Gallows Bay, rocky bottom, 1-2 m, 1949 (1). Bonaire: Sta. 1057a, Kralendijk, rocky shore, 1 m, 1930 (3). Curaçao: Boeke, 1905 (2); 1906 (1); Sta. 1323, Santa Marta Baai, lagoon, 1955 (3); Sta. 1029, Piscadera Baai, rocky shore, 1.5 m, 1949 (1); Sta. 1029A, tide-pool (9); Sta. 1453, Mouth NE, 3.5 m, 1964 (12); Sta. 1017, Knip Baai S, 0.5 m, 1949 (1) damaged; Sta. 1666A, Awa di Oostpunt, 30-50 m offshore, sand, 1 m, 1970 (1); [LACM-AHF] Sta. A46-39, shore, (1); [USNM-4643] (3); R/V Albatross, 1884 (4). [ZMA] Klein Bonaire: Sta. 1367 W, rocky shore, 1 m, 1955 (1). Saint Martin: Sta. 1125, Great Bay, rocky shore, 0.5 m, 1949 (2). Bahamas, Bimini: Sta. 1150A, Massy Creek S, sand, 1 m, 1949 (1). [USNM-3904] New Providence: R/V Albatross, 1886 (9). Barbados, [USNM-31034] 13.2°N, 59.5°W, coral rocks, 1-3 m, 1962 (3). Brazil, [USNM-15867] Alagoas, coral reefs, 1899 (1). British Overseas Territories, Anguila: [ZMA] Sta. 1142, rocky shore, 0.5 m, 1949 (2). Bermuda: [USNM-4781] 32.3°N, 64.8°W, 1876 (3). Colombia, [LACM-AHF] Honda Bay, 15 m (1); [USNM-20503] Providencia Island, Presidential Cruise Expedition, Sta. 30, 1938 (4). Florida, [LACM-AHF] Harbor Branch, 21.6 m, 1975 (2); Biscayne Bay, 1949 (1); St. Lucie, 27°11.6'N, 80°0.7'W, 41 m, 1976 (2); 1936 (1); Lake Worth, 1936 (1). Virgin Islands, [USNM-1656] St. Thomas, R/V Albatross, 1884 (4); [TCWC-1-2269] St. Croix, Isaac Bay, 1973 (1). Jamaica, [USNM-1646] R/V Albatross, 1884 (4); [USNM-31035] Kingston Harbour, Port Royal, 1961 (2); [ZMA] Sta. 1683, Drunkemans N, sand and debris, 1 m, 1973 (1). Mexico, [ECOSUR-AMPI-3] Quintana Roo: Ascension Bay, 19°36'N, 87°44'W, 1988 (2); Chichorro Cay, Sta. EL-2774, 18°45'N, 87°15'W, 52 m, 1990 (1); Contoy Island, 21°28'N, 86°47'W, 1999 (1); 2001 (8); Cozumel Island, 20°19'N, 87°02'W, 1960 (1); 2001 (4); Sta. EL-2772, 20°39'N, 86°49'W, 160 m, 1990 (1); Gavilan Point 18°21'N, 87°47'W, 1992 (1); Herrero Point S, Sta. EL-2789-4, 19°13'N, 87°30'W, 1990 (1); Indio River, 18°48'N, 87°40'W, reef lagoon, 1991 (1); Mahahual, 18°43'N, 87°42'W, 1981 (1); 1988 (2); 1989 (1); 1996 (3); 1997 (1); 1998 (1); 2000 (4); Sta. EL-2783, 18°41'N, 87°41'W, 58 m, 1990 (1); Morelos Port, 20°50'N, 86°52'W, 3-4 m, 1987 (1); 1988 (1); 1992 (1); Nizuc Point, 21°07'N, 86°44'W, 1997

(1); Xahuayxhol, 18°30'N, 87°45'W, 1999 (3); Xcaceel, 20°20'N, 80°20'W, 1992 (1); 1995 (1); 2005 (1); Xcalak, 18°15'N, 87°49'W, 1983 (2); 1990 (2); Xcaret, 20°33'N, 87°08'W, 2007 (23); Xocox or Chacom Point, Sta. EL-2784, 18°46'N, 87°34'W, 57 m, 1990 (1); 1991 (1); Xoquem Point, 19°49'N, 87°27'W, 1986 (1); 1991 (1). Veracruz, Santiaguillo, 1957 (1); [UANL-0016] Cazonez, 1973 (1); [UANL-0638] Tuxpan, 1974 (1); [UANL-0637] 1977 (1). Panama, [LACM-AHF] Bastimentos Island N, Sta. F-1001/BDT-3, coral rubble, 10 m, 2003 (3); Bocas del Toro, 9°13.34'N, 82°15.24'W, coral rubble, 16 m, 2003 (1); Caledonia Bay, Sta. A8-39, 1939 (2); Sta. A57-39 (4); Sta. A50-39 (1); Sta. A2-39 (3); Fort Randolph, reef lagoon, 1972 (2); San Blas, Porvenir, 1969 (1); Pina Beach, rocky shore, 1969 (1). Puerto Rico, [LACM-AHF] La Parguera, 16 m, 1955 (1); Mayaguez, 1945 (2). Saint Lucie, [ZMA-VPOL0421] Port de Castrie, Exp. Chazalie, 1906, (2). Trinidad and Tobago, [LACM-AHF] Tobago coast, Sta. A4139 (6).

Description. Body complete [Topotype ZMA-unnumb.], long, truncated at ends, 4.5 cm long, 0.6 cm wide, 62 chaetigers. Prostomium semicircular with four eyes, anterior larger, dark reddish. Median antenna (0.7 mm long) central, longer and thicker than lateral antennae (0.4 mm long), placed on anterior prostomial margin. Palps slightly smaller (0.3 mm) than lateral antennae, placed ventrally and externally to antennae in a swollen area running from lips (Fig. 5A). Mouth placed ventrally between chaetigers 3 and 4. Caruncle oval (2 mm long, 1.5 mm wide) with seven convergent folds, each carrying some irregular constrictions or striae (Fig. 5B).

Branchiae from chaetiger 1, present throughout body. Each branchia has two main branches, dorsal (DB) and lateral (LB), DB with more branchial filaments (Fig. 5D, E); total branchial filaments per chaetiger as follows: 1 with 7 (DB=4, LB=3); 2 with 15 (DB=10, LB=5); 3 with 26 (DB=17, LB=9); 10 with 87 (DB=72, LB=15); median chaetigers with approximately 94 (DB=80, LB=14); posterior chaetigers showing a decreasing trend in branchial filaments; far posterior chaetigers with 50 (DB=45, LB=5).

Parapodia biramous, massive, each ramus with a single cirrus (Fig. 5C). Dorsal cirri with long cirrophore (0.5 mm long), cirrostyle thinner, longer (1 mm long), becoming smaller and thicker in some chaetigers (Fig. 5I). Ventral cirri digitate, larger in anterior than in posterior chaetigers.

Pygidium truncate, anus dorsal, with a distal lobe wider than long (0.2 mm long, 0.3 mm wide), margin smooth (Fig. 5H).

Notochaetae as harpoon chaetae and simple capillaries with tiny denticles of varying shape: basal ones triangular, wide, short, widely separated from each other; distal ones sharper, abundant, forming irregular continuous rings (Fig. 5F, G). Neurochaetae with or without a spur, but with denticulated distal margin, with 4-25 denticles per chaetae. Neuroaciculae lance-shaped, in a single series.

Variation. Size range: 12-130 chaetigers, from 0.25 cm long and 0.15 cm wide up to 25 cm long and 2.5 cm wide. Prostomium: median antenna 0.1-2.0 mm long, lateral antennae 0.1-1.3 mm, palps: 0.1-0.8 mm. Caruncle: size dependent, having 3-10 folds (0.4-

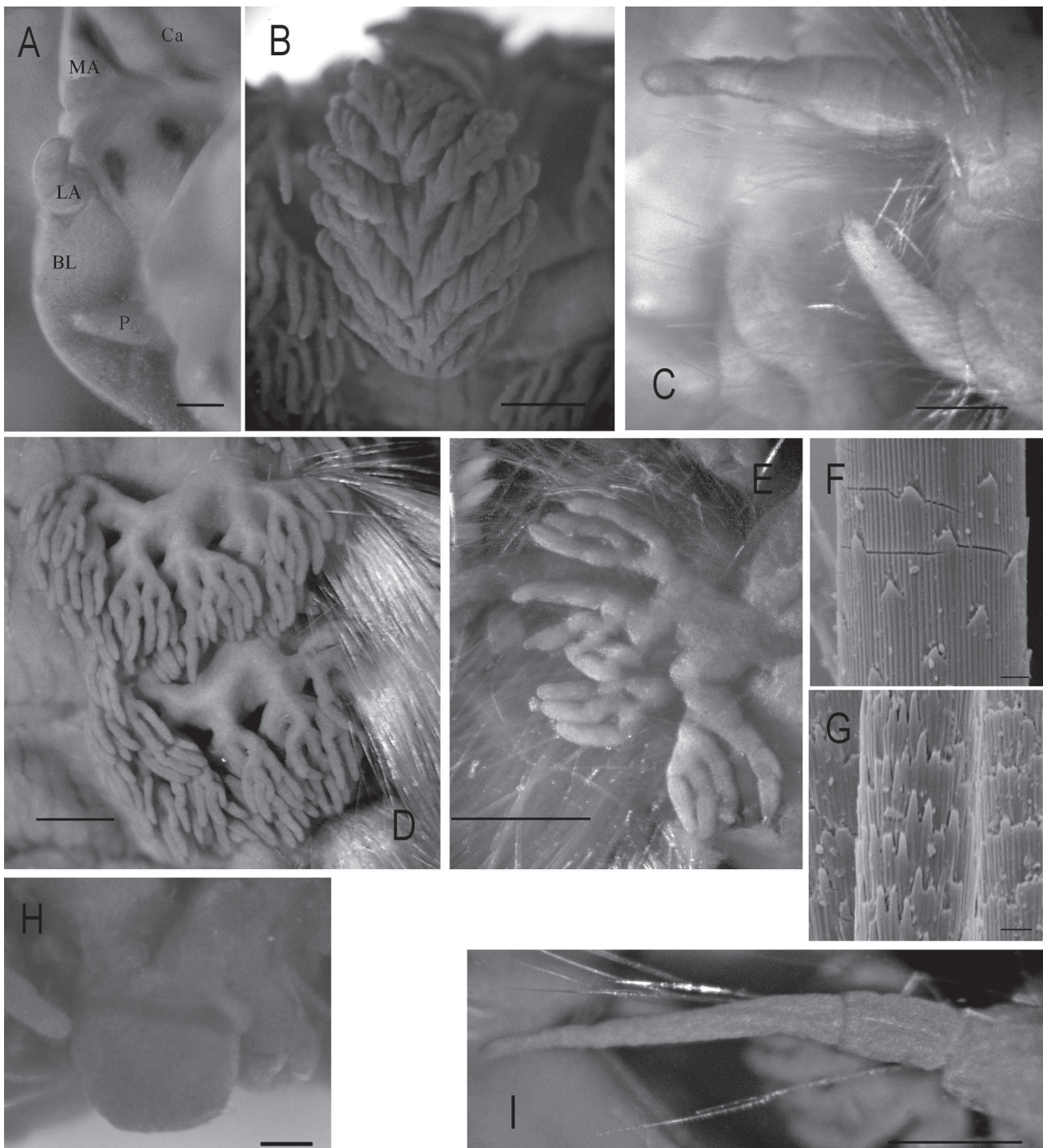


FIG. 5. – *Hermodice carunculata*: A, prostomium, lateral view; B, caruncle, dorsal view; C, parapodium; D, branchial dorsal branch; E, branchial lateral branch; F, distal surface of capillary notochaeta; G, basal surface of capillary notochaeta; H, anal lobe, view after displacement; I, dorsal cirrus. A and C scale: 0.2 mm; B, D, E, and I scale: 0.5 mm; F and G scale: 2 μ m; H scale: 1 mm. Abbreviations: BL, buccal lip; Ca, caruncle; LA, lateral antenna; MA, median antenna; and P, palp.

3.7 mm long, 0.1–2.7 mm wide); sometimes with a tenuous, thin, median elevation, but never with a well-developed median keel; oval to trapezoidal in shape, depending on fixation, since it is very muscular and movable. Branchiae: 12-chaetiger specimens with only 2–3 branchial filaments on chaetiger 10; >100-chaetiger specimens with over 150 filaments only on the dorsal

branch. A >50-chaetiger specimen (about 4 cm long) had about 70 filaments (DB=55, LB=15). Branchial branch separation varies and depend on the alternating elevation of successive chaetigers and specimen contraction. Only branchial bases were left on damaged specimens, they lost terminal filaments. Parapodia: Dorsal cirri along first chaetigers slightly thicker, es-

pecially in larger specimens, showing an irregularly wrinkled cirrophore. Cirrostyle length ranging from 0.6 to 2.7 mm long. Pygidium: Anal lobe often with a distal, median contraction, or with a diffuse dark pigmentation, always with abundant white or dark spots on living specimens (frequently lost after fixation). Chaetae: Relative size of notochaetae varying both in length and width. Neurochaetae with marked differences in number of marginal teeth, very often with a basal spur. Denticles on chaetal tips often blunt or even round due to erosion. Pigmentation: Living specimens vary from orange to dark red, purple or deep green, often with inter-segmental, dorsal lines surrounded by a thick yellow band (often lost after fixation), or with a longitudinal, mid-dorsal, darker brown band (also often lost after fixation). One specimen had a rather irregular pigmentation pattern probably due to an integument infection. Transverse black band absent in some specimens, as it may be lost after fixation but can be retained for as long as 10 to 20 yr. Living specimens with white spots in branchiae, prostomium and caruncle, absent from preserved worms.

Remarks. The descriptions of *A. smaragdina* and *A. sanguinea* from Jamaica (Schmarda, 1861) emphasized the color variations, especially on branchiae, as indicated by the species epithet: emerald green in the former, deep red in the latter. The names of these species were based on large specimens (>15 cm), but the caruncle shape and branching patterns were defined only for *A. sanguinea*. However, since there is wide variation in pigmentation, the caruncle can be modified by contraction, and the reviewed Jamaican specimens did not differ from *H. carunculata*, these nominal species are regarded as junior synonyms of this species.

A figure in the original description of *A. dydimobranchiata* (Baird, 1864) shows some small teeth under the spur of harpoon chaetae. However, these small denticles were not observed in the present study, and taking into account that physical or chemical damage can shatter chaetal surfaces and also due to the lack of other differences *A. dydimobranchiata* is also regarded as a junior synonym of *H. carunculata*.

The branchial pattern led Kinberg (1867) to propose *A. occidentalis*, but the similarity with the caruncle of *Hermodice* was overlooked. Lateral branchial branches may be difficult to observe as they might be hidden behind chaetal lobes and Baird (1870)'s revision disregarded *A. occidentalis* (it was probably regarded as invalid, but there were no further comments). Since the position and visibility of the lateral branchial branch is variable and the observed materials share all the morphological features of *H. carunculata*, *A. occidentalis* is regarded as a junior synonym.

Gametes. Gametes are present in the coelom in females once they have over 50 chaetigers, and in males that have more than 80 chaetigers; mature specimens were collected in February (1♀), March (1♀) and June

(9♀, 2♂). Oocytes were in various degrees of development, and were $97 \pm 16 \mu\text{m}$ in diameter ($n=100$). Spermatozooids were aggregated in masses, each had a protective shield, a spherical head plus mitochondria, and a long tail. This corresponds to a primitive type, probably related to external fertilization.

No sexual dimorphism was found. Gametes were seen in specimens with over 50 chaetigers. A previous account of sexual maturity in smaller specimens (Salazar-Vallejo, 1997) was incorrect; the specimen was re-analyzed and there were no oocytes or sperm. The observed particles were probably from the gut.

Pigmentation. Despite the different pigmentation patterns (Savigny, 1822; Ehlers, 1887; Ibarzabal, 1989) and their use to separate species (Schmarda, 1861), they do not correspond with a valid taxonomical explanation. Savigny (1822) noticed transverse black band in the largest specimens only, while Ehlers (1887) regarded pigment variations as age dependent. Kudenov (1974) found that *E. complanata* (Pallas, 1766) adult males were whitish whereas mature females were pink or reddish, which reflects the abundance of gametes. In *H. carunculata*, different colorations were found in animals of similar sizes or even in mature females. Thus, physiological or genetic studies are necessary to clarify the reasons behind this variability and determine its taxonomic usefulness.

Anomalies. Seventeen out of 198 specimens (8.5%) had malformations. Two had anterior eyes smaller than the posterior ones. Two had the pigment scattered in the eye area but no eyes. Several had some appendices doubled: lateral antenna (1), palps (1), dorsal cirri (10) and cirrophore (1). Double dorsal cirri are restricted to 1-5 chaetigers. Some specimens had a very small dorsal anal lobe, which could result from an incomplete regeneration. Malformations have been previously reported in other amphinomid, such as *E. complanata* (Barroso, pers. com.) as well as *H. carunculata* (a double ventral cirrus in Liñero-Arana, 1993). In addition, some irregular regeneration was indicated by double parapodia on one side of a single chaetiger.

Questionable records. After examining some deep-water material, the specimens were revealed to belong to different genera or even families, especially those collected below 100 m. The Fauvel and Rullier (1959) record of *H. carunculata* from 100-109 m corresponds to a *Linopherus* sp., and the *Hermodice* [MNHN] specimens from 850 m deep are actually aphroditids. The report of Ehlers (1887) from 323 m deep probably belongs to a juvenile specimen and must be regarded with care because the deepest record for a juvenile confirmed with the observed material is 70 m deep.

Hartman (1951) illustrated a *Pherecardia striata* probably collected in the Gulf of Mexico. However, *Pherecardia* is restricted to the Pacific Ocean while *Hermodice* is apparently restricted to the Atlantic Ocean. Further, Salazar-Vallejo and Londoño-Mesa

(2004) wrongly included two records of *H. carunculata* for the tropical eastern Pacific and the only previous record for this region, from Port Parker (10°55'N, 85°48'W) in Costa Rica (Treadwell, 1941), did not provide sufficient details and therefore it has been regarded as questionable (Dean, 2004).

***Hermodice nigrolineata* Baird, 1870**
(Fig. 6)

Hermodice nigrolineata Baird, 1870:220-221.

Hermodice carunculata Fauvel, 1914:88; Rullier, 1964:143-144 (partim, non Pallas, 1766).

Hermodice carunculata dydimobranchiata Fauvel, 1914:113-116; Monro, 1930:42; Tebble, 1955:83.

Type material. Holotype of *Hermodice nigrolineata* Baird, 1867 [BMNH-1887.7.27.72]. Egyptian coast, near Alexandria, Coll. R.M. Andrew; damaged material, five fragments, probably belonging to two specimens.

Additional material. Cape Verde, [MNHN] Without data (3), Calypso Sta. 34 (1), Sta. 50 (2), Sta. 69 (2). Gulf of Guinea, [MNHN] Gabou, 9-5 (1), Calypso Sta. 68, 0-6 m, 1956 (3), Sta. 127, 127 m, 1956 (1), Cape Lopez, 1989 (1), Gerard Tréca Sta. 42, 9°05'N, 15°W, 75-80 m, 1953 (1), São João dos Angolares, 1906 (1); [IRFA] Ombago, 30 m, 1960 (1), Uohomey, 45.5 m, 1964 (1). Egypt, [MNHN] Alexandria, 1933 (2). Spain, [DZUL] Canary Islands, Tenerife, Poni de Abona, 6 m, 2005 (1), Las Eras, 6.5 m, 2005 (6). Portugal, [MNHN] 200 m from Graciosa, Sta. 238, 95 m, 1998 (1). Turkey, [ESFM-POL-501] Kumluca Karaöz Limani 36°16'32"N, 30°24'15"E, rocks, 1-3 m, 2005 (8); [ZMA-unnumb.] the same data, donated by Melih Cinar.

Description. Body complete [Topotype ZMA-unnumb.], truncate at both ends, 7 cm long, 1 cm wide, 68 chaetigers. Prostomium semicircular with two pairs of dark eyes, anterior ones larger. Three antennae, median one longer and thicker (1 mm long) placed in anterior prostomial region; lateral antennae (0.7 mm long) placed on anterior prostomial margin. Palps slightly smaller (0.6 mm long), ventral and external to lateral antennae (Fig. 6A). Mouth ventral, between chaetigers 2 and 4. Caruncle oval (2.5 mm long, 2 mm wide), with seven convergent caruncular folds (Fig. 6B).

Branchiae from chaetiger 1, extending throughout the entire body; each branchia with a dorsal (DB) and a lateral branch (LB), both with a few filaments (Fig. 6D, E), gradually increasing in DB towards median region and remaining almost without change posteriorly; relatively constant in LB. Total branchial filaments per chaetiger as follows: 1 with 5 (DB=3, LB=2); 2 with 12 (DB=6, LB=6); 3 with 15 (DB=7, LB=6); 10 with 27 (DB=16, LB=11); median chaetigers with 26 (DB=18, LB=8); posterior region with about 30 filaments (DB=21, LB=7).

Parapodia biramous, massive, each ramus with one cirrus (Fig. 6C). Dorsal cirri with short cirrophore (0.3 mm long); cirrostyle thin, long (1.5 mm long) (Fig. 6G). Ventral cirri prominent.

Pygidium truncate, anus dorsal with an anal lobe markedly longer than wider (0.5 mm long, 0.2 mm wide), posterior margin with a distal notch, apparently bilobulate (Fig. 6F).

Harpoon and long or short capillary chaetae, with non-visible denticulation. Serrated notochaetae often with spur, with 3, 4 or up to 30 distal denticles. Aciculae in a single series.

Variation. Body size: 44 to 107 chaetigers and from 2 cm long, 3.5 mm wide to 25 cm long, 1.4 cm wide). Prostomium: median antenna: 0.5-2.8 mm long, lateral antennae: 0.4-1.5 mm long, palps: 0.3-1.3 mm long. Caruncle: With 6 or 7 folds (1.5-3.3 mm long, 1.0-2.4 mm wide); mostly oval; two specimens with more projected folds (probably resulting from regeneration). Branchiae: Branchial filaments less numerous than in *H. carunculata*. A 50-chaetiger specimen, about 4.5 cm long had 25 filaments (DB=18, LB=7), while a ≈ 100 chaetiger specimen about 17 cm long had about 30 filaments (DB=19, LB=9). Parapodia: Dorsal cirri 0.7-2 mm long. Dorsal cirrophore short, even in large specimens, reaching up to 0.4 mm in length; dorsal cirrostyle variable, although thinner than in *H. carunculata*, and often reflexed. Pygidium: regardless of their relative size, all specimens had a rectangular anal lobe, markedly longer than wider and with distal margin bilobed. Chaetae: besides varying in distal denticle number, chaetal tips are rounded, probably as a result of abrasion. Pigmentation: all specimens with a transverse, dorsal, intersegmental black line.

Remarks. The species name refers to the presence of a transverse, dorsal, intersegmental black line, which is not exclusive for the species (as noted above). The original description emphasized the caruncular resemblance to *H. carunculata* (Baird, 1870), and the species was regarded as a junior synonym of *H. carunculata* (Hartman, 1959; Ebbs, 1966), particularly after observing that some juvenile specimens from Florida have intersegmental black lines (Ebbs, 1966). However, Baird (1870) indicated that the branchiae were clearly less developed than in *H. carunculata*, as they have just a few branched filaments, although this feature has not been employed before to separate species.

All examined specimens had the dorsal, transverse, black line, which was previously reported for a few specimens collected in the Mediterranean or Azores (Fauvel, 1914). The specimens from Cabo Verde had a dorsal pigmentation ranging from a pale background with emerald-green transverse band to a metallic blue, including ochre or green variations, but all of them showed the transverse, dorsal, black, intersegmental band (Rullier, 1964). Other published photographs of *H. nigrolineata* show orange to a dark dorsal pigmentation, with a yellow and black complex, transverse, dorsal band (Monterroso *et al.*, 2004).

Fauvel (1914) found species up to 129 m deep, but only some of them from 95 m deep were analyzed here. Finally, some juveniles have been found in *Dendrophyllia* coral bottoms off the Canary Islands (Nuñez *et al.*, 1991) at 108 m deep.

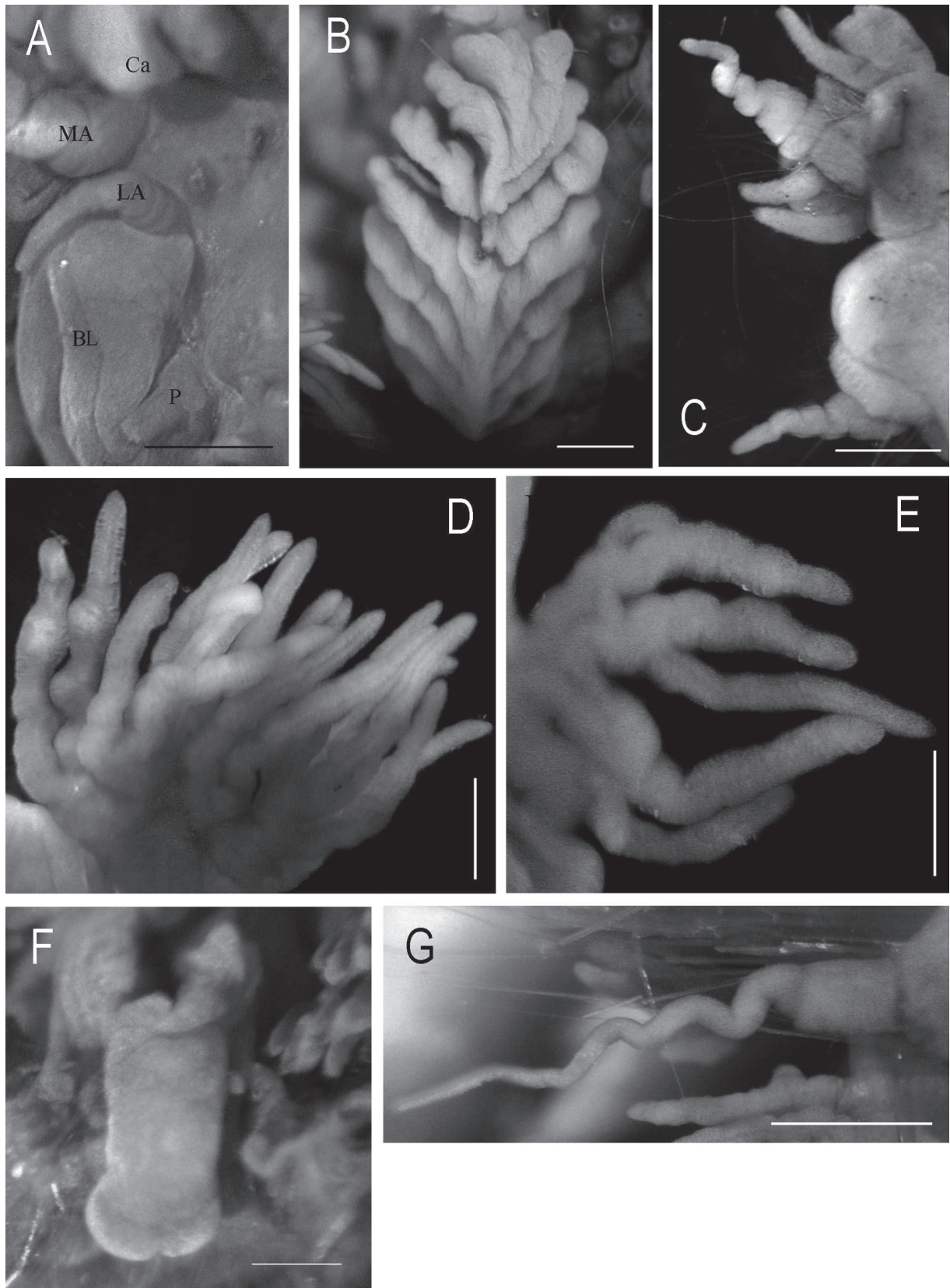


FIG. 6. – *Hermodice nigrolineata*: A) prostomium, lateral view; B, caruncle, dorsal view; C, parapodium; D, branchial dorsal branch; E, branchial lateral branch; F, anal lobe, view after displacement; G, dorsal cirrus. A, B, C and G scale: 0.5 mm; D, E and F scale: 0.2 mm. Abbreviations: BL, buccal lip; Ca, caruncle; LA, lateral antenna; MA, median antenna; and P, palp.

The proposal of *H. carunculata dydimobranchiata* Fauvel, 1914, based on specimens from the Gulf of Guinea lacking harpoon chaetae, might correspond to specimens without these chaetae because they have been used as defensive weapons, as some species from those examined here had harpoon chaetae.

Anomalies. Duplication of dorsal cirri (3/37), although one specimen had a triple dorsal cirrus with double cirrophore.

DISCUSSION

Quatrefages (1866) wondered whether the same species would live in the Caribbean Sea and in the Mediterranean Sea. Although he compared some specimens from the Gulf of Mexico, the Antilles and the Mediterranean coast of Portugal, he could not find any differences. The large, massively muscular body of *Hermodice* species, which is easily distorted during preservation, makes it quite difficult to observe most species-specific features. Further, as shown above, most useful taxonomic features for other genera are not appropriate for distinguishing between the *Hermodice* species.

However, our thorough evaluation of the relevant morphological features has allowed us to distinguish between *Hermodice carunculata* (redefined and restricted to the Grand Caribbean region) and *H. nigrolineata* (reinstated and distributed in the Mediterranean Sea and adjacent eastern Atlantic Ocean areas). This distinction could be made because, rather than carrying out standard detailed analyses of museum materials, we observed living specimens of *H. carunculata*. This provided information on the natural caruncle modifications, on the effect of preservation on the relative size of appendices, and on the changes in eye shape. Consequently, we could base our conclusions on new taxonomic features (such as the relative number of branchial filaments and the development of the anal lobe) to separate these two similar species.

A finer resolution could be achieved with a molecular approach, and therefore additional cryptic species could be determined. The teleplanic, rostraria larva typical of amphinomids apparently does not guarantee an effective long-distance dispersal and, according to the typical areas of polychaete endemisms (Glasby, 2005), other species might be hidden under the two morphological distinctions described here. A molecular approach might also enhance our understanding of the affinities between these postulated cryptic species, as demonstrated for at least three cryptic species of the fireworm *E. complanata* found by Barroso *et al.* (2010). Further relevant data could also be obtained by evaluating color polymorphisms in combination with reproductive biology.

The clear morphological distinction between *H. carunculata* and *H. nigrolineata* implies that a careful evaluation of additional features other than the classi-

cal ones could be potentially useful in future studies of the family. However, this type of approach apparently tends to remain in the background of current scientific interests, and is displaced by the growing number of molecular studies. Accordingly, we hope that our study will encourage similar evaluations of closely related species, since there are many pending issues in many problematic polychaete taxa.

Key for *Hermodice* Kinberg, 1857

- 1 Dorsal branchiae with many filaments in median chaetigers (more than 40 in worms with at least 50 chaetigers); anal lobe short, rounded; dorsal, intersegmental, black transverse band sometimes present *H. carunculata* (Pallas, 1766).
- Dorsal branchiae with few filaments in median chaetigers (less than 20 in worms with at least 50 chaetigers); anal lobe long, bilobed; dorsal, intersegmental, black transverse band always present
..... *H. nigrolineata* Baird, 1870.

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