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SYSTEMATICS, DISTRIBUTION AND BIOLOGY OF THE CIRRATE OCTOPODS OF THE GENUS *OPISTHOTEUTHIS* (MOLLUSCA, CEPHALOPODA) IN THE ATLANTIC OCEAN, WITH DESCRIPTION OF TWO NEW SPECIES

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ABSTRACT

The systematics of the deep-sea cirrate octopod genus *Opisthoteuthis* Verrill in the Atlantic Ocean is reviewed. Comparisons, based on examination of all extant type material and new, reported and unreported material collected in recent years from the Atlantic, show the presence of five species: *Opisthoteuthis agassizii* Verrill 1883, *O. grimaldii* (Joubin, 1903), *O. massyae* (Grimpe, 1920) and two new species, *O. calypso* and *O. hardyi*, which are described. *Opisthoteuthis agassizii*, distributed only in the western North Atlantic, is redescribed, and a neotype is designated for the presumed lost holotype. *Opisthoteuthis grimaldii*, distributed in the East Atlantic and possibly also in the western North Atlantic, and *O. massyae*, distributed in the East Atlantic are also redescribed and junior synonyms listed. *Opisthoteuthis calypso*, found in the East Atlantic and *O. hardyi*, known only from a single specimen from the SW Atlantic are described. New morphometric data for *O. agassizii*, *O. massyae* and *O. grimaldii* are given. Illustrations, geographical distributions and a review of the biological information for all five species are provided.

The family Opisthoteuthidae comprises most of the known cirrate octopod species and within this family the genus *Opisthoteuthis* is the most diverse. This is probably due to the fact that *Opisthoteuthis* is the shallowest-distributed cirrate genus and that all the species are closely associated with the bathyal bottom, the most sampled of the deep water habitats. In contrast, other cirrate groups, such as the cirroteuthids, are less associated with the bottom and typically inhabit deeper bathyal and abyssal depths, thereby making collection more difficult. The delicate, gelatinous consistency of the cirrates, the few type specimens in good condition, the near absence of detailed comparative morphological studies, and, until recently, the relatively few collected specimens, have contributed to the existing confusion in the taxonomy of the group. Redescriptions, as done in recent studies, are a necessary first step to solving the problem (see among others, Aldred et al., 1983; Voss and Pearcy, 1990; Guerra et al., 1998; Collins and Henriques, 2000). In the Atlantic, the large number of recently collected specimens of *Opisthoteuthis*, both reported (see among others: Villanueva, 1992a; Daly et al., 1998) and unreported, together with our examination of all extant types have made it possible for us to herein define and review the systematics of the genus in the area.

Materials and Methods

Definitions of counts, measurements and indices used here follow Roper and Voss (1983), Toll (1988), Voss and Pearcy (1990), Villanueva (1992a) and Guerra el al. (1998). The dorsal mantle length (ML) was measured as for other octopods (Roper and Voss, 1983), and ventral mantle length

(VML) was obtained and indicated when dorsal was not possible. Fin length, fin width, and fin-length and fin-width indices are measured according to Voss and Pearcy (1990), where the length of the fin (in contrast to fin length in teuthoids) is measured from the midpoint of the base of the fin to the outer tip, and fin width is the greatest width across the fin measured perpendicular to the fin length. Finspan is according to Guerra et al. (1998), the distance between the apices of the fins, and Finspan Index (FSI), the ratio between the fin span and the total length (TL) multiplied by 100. Cirrus length index was obtained as in Guerra et al. (1998). The gill lamellae counts refer to the total number of lamellae on each gill; 7/6 means 7 lamellae on one gill and 6 on the other. Specimens were considered sexually mature on the basis of the presence of spermatophores in the seminal vesicle and/or penis of the males, and presence of eggs in the oviducts and/or oviducal gland of the females.

Abbreviations for the institutions that house the specimens examined here are: BMNH - Natural History Museum, London (formerly British Museum); HBOM - Harbor Branch Oceanographic Institution Museum, Fort Pierce, Florida; ICM - Instituto de Ciencias del Mar, Barcelona; MOM - Musée Océanographique, Monaco; MNHN - Muséum National d'Histoire Naturelle, Paris; NMI - National Museum of Ireland, Dublin; NMSZ - National Museum of Scotland, Zoology Department, Edinburgh; UMML - Marine Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami; USNM - National Museum of Natural History, Washington, DC. In the synonymy for each species, only references of systematic, distribution or biological significance are listed. Where recognized new distribution records occur in the synonymies, they are given in parentheses.

Systematics

Family Opisthoteuthidae Verrill, 1896
Genus *Opisthoteuthis* Verrill, 1883

Diagnosis.—Small to medium-size cirrate octopods of ovoid form in fresh specimens, with thick primary web, absence of intermediate web, and small fins. Shell simple with lateral wings tapering to acute points. Sucker enlargement pattern markedly sexually dimorphic. Mature males with a proximal, and usually a distal, enlarged sucker field on one to all arm pairs.

Opisthoteuthis agassizii Verrill, 1883
Figs. 1–5, 21, 22; Tables 1, 5–7

Opisthoteuthis agassizii Verrill, 1883: 113, pls. 1–2 (off Grenada, W.I.; type presumed lost); 1885: 408 (39°35′N, 70°03′W; specimen presumed lost); 1896: 74, figs. 1–2; - Berry, 1918: 289; - Robson, 1932: 167; - Voss, 1955: 106 (off Puerto Tánamo, Cuba); 1956: 156, fig. 14 (29°09′N, 87°55′W); - Cupka, 1970:1, figs 1–27 (28°33′-29°16′N, 86°54′-87°18′W; specimens lost); - Lipka, 1975: 266, fig. 30 c–d, f (28°00'N, 86°09′W; 16°11′N, 84°48′W; specimens presumed lost); - Voss, 1988a: 254, fig. 1m; 1988b: 298, fig. 3 (northeast of Bahamas); - Arocha et al., 1991: 231 (11°45′N, 63°05′W); - Vecchione and Roper, 1991: 433, fig. 4 (12°01′N, 61°45′W; off Key West, Florida; northwest Providence Channel, Bahamas); - Young and Vecchione, 1996: 91 (12°01′N, 61°57′W).

Material Examined.—CARIBBEAN: Johnson Sea-Link II : 1 immature female, approx. 25 mm VML, Dive 1746, off St. Vincent Island, 586 m, 25 Apr1989, HBOM 68:00086. - RV Oregon and RV Oregon II :1 ?sex immature, ? mm ML, Sta. 1902, 11°27′N, 83°11′W,

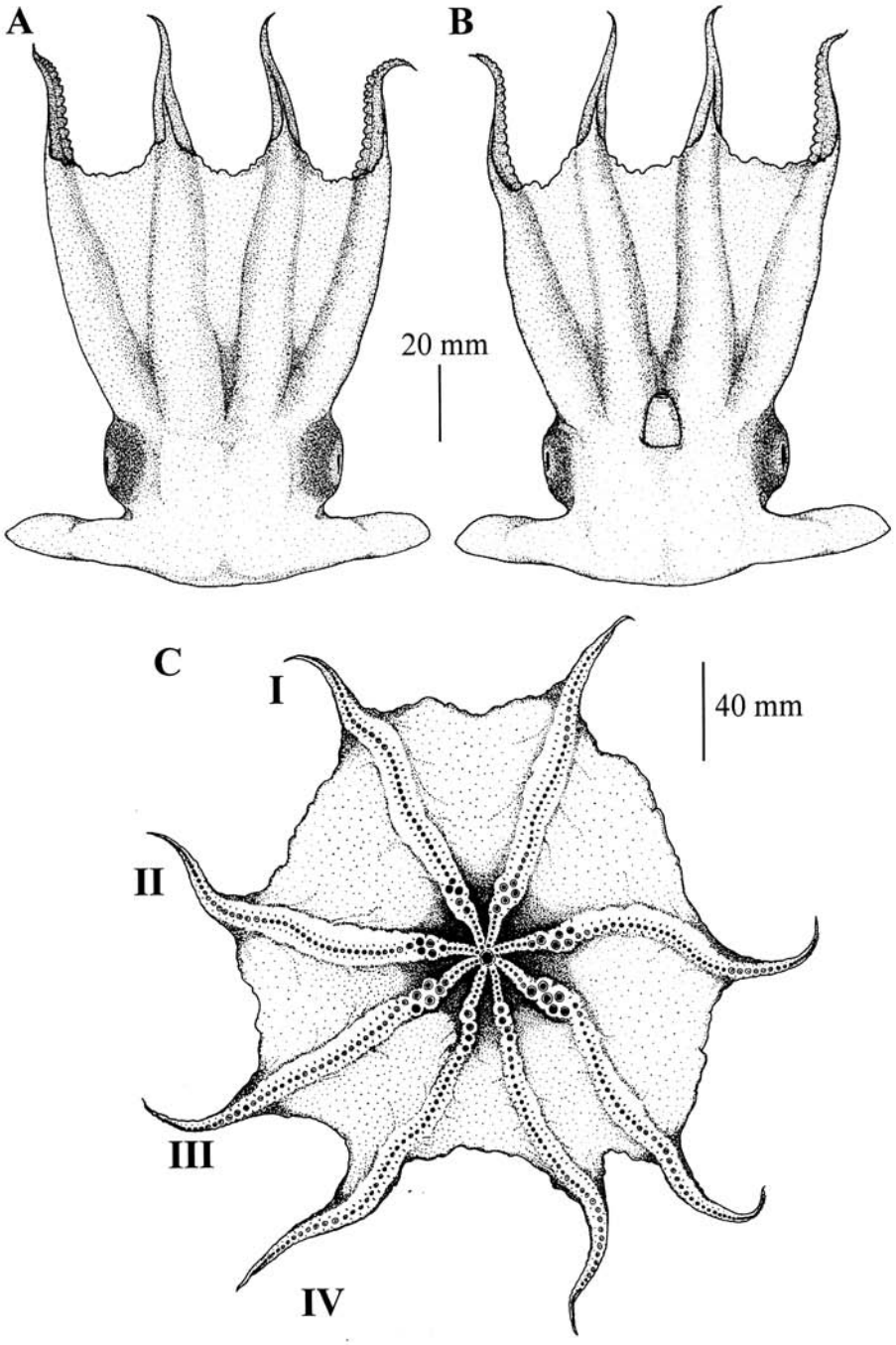

Figure 1. *Opisthoteuthis agassizii* (USNM 729079). Dorsal (A), ventral (B) and oral views of the Neotype, mature male 42 mm ML.

247 m, 9 Sep 1957, UMML 31.2889; 1 mature female, 23 mm ML, Sta. 1911, 12°44′N, 82°14′W, 640 m, 11 Sep 1957, UMML 31.2487; 3 mature males, 35, ?, ? mm ML, Sta. 1921, 13°33′N, 81°55′W, 503 m, 13 Sep 1957, UMML 31.2490; 1 mature male, approx 45 mm ML, 2 immature females, ? mm ML, 2 ? sex immatures, ? mm ML, Sta. 3565, 14°10′N, 81°55′W, 448 m, 21 May 1962, UMML 31.2887; 2 immature males, 22, 17 mm ML, 2 ? sex immatures, 17, 14 mm ML, Sta. 3575, 12°35′N, 82°19′W, 458 m, 23 May 1962, UMML 31.2888; 1 mature male, 40 mm ML, Sta. 3576, 12°25′N, 82°15′W, 567 m, 23 May 1962, UMML 31.2886; 2 mature females, 38, 37 mm ML, Sta. 3586, 09°20'N, 81°24′W, 888 m, 25 May 1962, UMML 31.2884; 1 maturing male, ? mm ML, Sta. 3616, 14°23′N, 81°45′W, 458 m, 5 June 1962, UMML 31.878; 1 mature male, 35 mm ML, 1 maturing male, 25 mm ML, 1 maturing female, 23 mm ML, Sta. 4882, 10°16′N, 75°54′W, 549 m, 25 May 1964, UMML 31.2488; 1 maturing female, 19 mm ML, Sta. 5722, 09°36′N, 76°22′W, 512 m, 16 Oct 1965, UMML 31.2891; 1 mature male, 44 mm ML, Sta. 5926, 15°36′N, 61°13′W, 503 m, 4 Mar 1966, UMML 31.1636; 1 mature male, 45 mm ML, Sta. 5928, 15°38′N, 6°12′W, 586 m, 4 Mar 1966, UMML 31.2491; 1 mature male, 42 mm ML, Sta. 10207, 12°24′N, 82°24′W, 613 m, 22 Nov 1968, NEOTYPE, USNM 729079; 1 immature male, 12 mm ML, Sta. 10207, 12°24′N, 82°24′W, 613 m, 22 Nov 1968, USNM 893732; 1 mature male, 43 mm ML, Sta. 10825, 15°42′N, 61°08′W, 641 m, 1 Dec 1969, USNM 729082; 1 mature male, 26 mm ML, 1 ? sex immature, ? mm ML, Sta. 11227, 09°12′N, 81°11′W, 555 m, 28 Oct 1970, UMML 31.2460; 1 immature female, 16 mm ML, Sta. 11244, 10°00′N, 76°10′W, 549 m, 6 Nov 1970, USNM 893729. - RV Pillsbury: 1 immature female, 18 mm ML, Sta. 1355,14°35′N, 81°32′W, 525–797 m, 31 Jan 1971, UMML 31.843.

GULF OF MEXICO: RV Oregon I and RV Oregon II: 1 mature male, approx 50 mm ML, Sta. 218, 23°27′N, 89°34′W, 227 m, 10 Jan 1951, UMML 31.2498; 1 immature male, ? mm ML, Sta. 3654, 29°08′N, 88°00′W, 732–750 m, 25 Jul 1962, UMML 31.921; 1 maturing male, 15 mm ML, Sta. 3656, 29°08′N, 87°58′W, 824–915 m, 26 Jul 1962, UMML 31.422; 1 mature male, 48 mm ML, 1 mature female, 36 mm ML, 1 maturing female, 33 mm ML, Sta. 4562, 23°53′N, 83°13′W,1098 m, 3 Dec 1963, USNM 893731; 1 maturing female, 32 mm ML, Sta. 4634, 27°30′N, 94°40′W, 915 m, 23 Jan 1964, UMML 31.2885; 1 immature female, 35 mm ML, Sta. 4730, 27°38′N, 92°24′W, 732 m, 27 Feb 1964, UMML 31.2493; 1 mature female, 45 mm ML, Sta. 4803, 25°05′N, 96°00′W, 1281 m, 7 Apr 1964, UMML 31.2489; 1 mature male, approx 45 mm ML, Sta. 4805, 23°28'N, 97°03'W, 915 m, 9 Apr 1964, UMML 31.2495; 1 immature male, approx 36 mm ML, Sta. 10637, 28°33′N, 86°54′W, 908 m, 21 Jun 1969, USNM 729078; 1 mature female, ? mm ML, 1 ? sex immature, ? mm ML, Sta. 10637, 28°33′N, 86°54′W, 908 m, 21 Jan 1969, USNM 729451; 1 ? mature male, 45+ mm ML, Sta. 10649, 29°04′N, 88°16′W, 717 m, 25 June 1969, USNM 729450; 1 mature female, 32 mm ML, Sta. 10955, 21°41′N, 96°55′W, 897 m, 3 Jun 1970, USNM 729080; 1 mature female, ? mm ML, Sta. 19°32′N, 93°46′W, 1098 m, 10 Jan 1970, USNM 729449; 1 maturing female, 33 mm ML, Sta. 13230, 29°02′N, 88°15′W, 732 m, 6 May 1973, USNM 893730. - RV Silver Bay: 2 mature males, 51, 46 mm ML, 1 mature female, 40 mm ML, Sta. 1181, 29°03′N, 88°20′W, 732 m, 3 Jun 1959, UMML 31.2473. NMS-NGOMCS: 1 maturing male, 38 mm ML, Cr. 3 Sta. C3, 27°49′N, 90°08′W, 841 m, 18 Nov 1984, USNM 815703.

BAHAMAS: RV Iselin: 1 immature male, 23 mm ML, Sta. 415, 23°33′N, 77°04′W, 1333–1342 m, 1 Mar 1976, UMML 31.2478. - RV Silver Bay: 2 maturing females, 34, 30 mm ML, Sta. 442, 27°53′N, 79°09′W, 686–760 m, 9 Jun 1958, UMML 31.2474.

Historical Resume.—Verrill (1883) described a new genus and species, *Opisthoteuthis agassizii*, based on a single specimen taken in the southeastern Caribbean off Grenada, West Indies. In the absence of a hectocotylus, Verrill believed it to be a female. However the text and illustrations describe and clearly show the pattern of enlarged proximal and distal suckers that indicates the specimen was a male, probably in the subadult stage. Unfortunately, the holotype could not be found by the collection managers at the Museum of Comparative Zoology, Harvard University (A. Baldinger, pers. comm., 1999), the Peabody Museum of Natural History, Yale University (E. Lazo-Wasem, pers. comm., 1999), or the National Museum of Natural History, Smithsonian Institution (M. Sweeney, pers. comm., 1999), so is presumed lost. Two years later, Verrill (1885) described and identified to the species a second, smaller specimen in poor condition taken in the northwestern Atlantic off New Jersey. Again, the specimen could not be located at the above museums, but judging from the described absence of a distal group of enlarged suckers on the arms and the small size, the specimen was either a female or an immature male. In this specimen, Verrill noted an additional feature that the present study recognizes as characteristic of the species, a series of stout, muscular web supports, which extend into the web along the ventral margins of the distal ends of the arms. Following Ijima and Ikeda's (1895) description of a second species belonging to the genus, *Opisthoteuthis depressa* from Japanese waters, which gave details of internal anatomy not permitted by the poor condition of Verrill's specimens of *O. agassizii*, Verrill (1896) assigned the genus to a new family Opisthoteuthidae.

In 1913, Chun mistakenly referred to the species four specimens taken off Ireland during the Michael Sars North Atlantic Deep Sea Expedition. These specimens and those subsequently misidentified to the species from the eastern Atlantic and Mediterranean by Bruun (1945), Morales (1959), Adam (1962) and others are assigned below to other species of the genus. The report by Voss (1955) of a juvenile in poor condition taken off Puerto Tanamo, Cuba, was the first record of *O. agassizii* from the northwestern Atlantic to appear since the holotype and Verrill's second specimen. The description and illustrations of a subadult female in fair condition taken in the northern Gulf of Mexico by Voss (1956) revealed the presence of seven gill lamellae, a 'semicircular shell vestige' and the absence of a radula, features not known for the species from the earlier reported three specimens. Fourteen years elapsed before the next report (Cupka, 1970) of *O. agassizii* in the Caribbean-Gulf of Mexico region where we now know the species to be broadly distributed. In his unpublished M.Sc. thesis, Cupka presented detailed descriptions and data analyses of the morphology and ecology of 46 specimens, including mature males and females, taken from the DeSoto Canyon region in the northeastern Gulf of Mexico. Unfortunately, all of the specimens are lost (D. Cupka, pers. comm., 1999), but the results of his work provided a wealth of information upon which we have heavily drawn in the present study. Another unpublished study, the PhD dissertation of Lipka (1975), reported the capture of two specimens in the northern Gulf of Mexico and the western Caribbean, and further described the sucker enlargement pattern of the adult male. Lipka (1975) also illustrated, for the first time, the stout muscular, web supports that extend into the web along the distal, ventral margins of the arms in this species. These specimens are also presumed lost as they could not be found in the Marine Organism's Systematic Collection, Texas A&M University (R. Cady, pers. comm., 1999).

Additional new records of the species were reported, but not described by Voss (1988a) from northeast of the Bahamas and northeastern Brazil, and by Arocha et al. (1991) from

off Venezuela. The undescribed material to which Voss referred from the former locality was found and is included in the present study, but no material was found from his latter locality. In a second paper in 1988, Voss (1988b) first illustrated the shell of the species. In 1991, Vecchione and Roper recorded the observations and collections of three specimens of *O. agassizii* from submersibles off Key West, Florida, Northwest Providence Channel, Bahamas, and St Vincent Island, Lesser Antilles. A photograph was given of the latter specimen on the bottom and its swimming behavior described. This paper also contains the first report of the rows of pigment-free spots along the arms and mantle, a feature illustrated and further described from the same specimen in the present paper. Briggs et al. (1996) gave the deepest capture depth for the species, 3411–3459 m in the eastern portion of the Venezuela Basin. However, the identification is suspect, and the specimen has been lost (K. Briggs, pers. comm., 2000). Finally, specimens identified to the species were used in two recent phylogenetic studies. Young and Vecchione (1996) examined a specimen from off Venezuela for 50 internal and external morphological characters for use in their study of relationships within coleoid cephalopods, and Voight (1997) examined two specimens from the northern Gulf of Mexico for 66 internal and external morphological characters in her cladistic analysis of the octopods. We regard the identification of the latter specimens as suspect (see Remarks section for this species).

Diagnosis.—Medium-sized species. No increased robustness of arms I in mature male. A series of stout, muscular, web supports extend from the ventral margins of all arms to web margin beginning at level of greatest depth of web, typically at sucker 26–32, and continuing distally to sucker 50–53. Arm sucker count in adults 58–80. Distal enlarged sucker field in male typically comprises eight to twelve suckers beginning at about sucker 30–33, with suckers 34, 35 or 36 usually largest. Sucker enlargement in distal field greatest on arms IV and III, least on I. Maximum distal enlarged sucker diameter exceeds that of proximal enlarged suckers only in older mature males. First cirri usually occur between suckers 3 and 4. Digestive gland entire (not divided into two lobes). Basal portion of shell with concave outer surface and convex inner surface. Pigment-free spots present on skin of head and all arms.

The following description is based primarily on the 56 specimens from the present study, which include 24 males (15 mature), 25 females (12 mature) and 7 immatures of unknown sex, taken over the wide geographic distribution of the species. Additional morphological data from Verrill (1883, 1885), Cupka (1970) and Lipka (1975) have also been used.

Description.—Medium-sized species, known maximum ML of males and females 63 mm and 56 mm respectively, with males maturing at 22 mm ML and above, and females at 23 mm ML and above. Entire body semi-gelatinous, ovoid in form in fresh specimens, with the eyes and fins superior. Mantle moderately short, about 21–28% TL, and broadly rounded posteriorly. Head slightly wider than mantle, with no discernable constriction between head and mantle. Pallial aperture small, closely surrounding funnel. Funnel flaccid, moderately long, averaging 65% ML. Funnel organ inverted V-shape. Olfactory organs rounded and prominent, located just within mantle aperture and to either side of funnel. Fins, widely set, posterolaterally positioned, small in relation to entire animal, averaging 86% ML in length and 48% ML in width. Anterior and posterior margins of fins thin, slightly convex, without lobe near the anterior insertion; fin tip rounded. Each fin supported by an internal, flexible, cartilage that extends from shell sac, to which it closely adheres, to approximately the middle of the fin. Fin cartilage thick basally, be-

coming progressively thinner and lanceolate as it extends out; cartilage tissue highly vacuolated. Eyes large, bulbous, averaging 66% ML, occupy entire sides of head. Optic lobes large, kidney-shaped, with 2–4 large bundles of optic nerves running to each eye. White body, closely associated with lobe, large, dark brown to purple. Optic lobes larger than semi-circular brain.

Arms enveloped in web except for short distal ends, moderately long, averaging 283–332% ML, and subequal in length, with no consistent length formula. Arms moderately stout, with no increased robustness of arms I in mature males. A series of stout, muscular, web supports extend from the ventral margins of all arms to web margin beginning at level of greatest depth of web, typically at sucker 26–32, and continuing distally to sucker 50–53. Supports frequently difficult to discern in intact web, but more easily seen when web is fragmented or in otherwise poor condition. Web deep, thick, occupying approximately 2/3 of arm length. Web formula not consistent, but sector E tends to be shallowest. Single row of suckers deeply set in semi-gelatinous tissue of all arms. Sucker count on each arm increases with growth to characteristic count of 58–80 in adults. Sucker enlargement pattern markedly sexual dimorphic. Mature males with two fields of markedly enlarged, bulbous, suckers on all arms. Proximally, suckers 6–10 typically enlarged, with suckers 7 or 8 usually the largest, but sometimes several suckers including suckers 7 and 8 equally enlarged. Sucker enlargement in proximal field approximately equal on all arms. Distal enlargement field typically comprises seven to eight suckers beginning at about sucker 30–33, just distal to level of greatest web depth, with suckers 34, 35 or 36 usually largest, but sometimes several suckers including one or more of these suckers equally enlarged. Sucker enlargement in distal field greatest on arms IV, moderate on arms II and III, and least on arms I. Initially, distal enlargement less than proximal, but with increased growth becomes equal, and in large males distal enlargement exceeds proximal enlargement. In mature females, same 5 or 6 suckers comprising proximal field of male show slight enlargement, with subsequent suckers gradually decreasing in size to tip of arm. Cirri short, first appear between suckers 3 and 4 on all arms (rarely between 2 and 3 or 4 and 5 on one arm). Longest cirri in middle of arms, length 1.7–5.0 mm or 4–9% ML.

Gills small, compact, spherical, with 7 lamellae (7/7 in 88% of 56 specimens present study, 83% of 43 specimens Cupka's study), rarely 6 (6/6 in 5% specimens present study, 2% Cupka's study), 8 (8/8 in 2% present study, 15% Cupka's study), or mixed 6/7 or 7/8 (5% present study, none Cupka's study). Gills relatively larger in juveniles than in adults. Entire outer surface of digestive system deeply pigmented. Buccal mass moderate in size. Rostrum of lower beak pointed, and with a small hood. Wings relatively long and narrow. No folds or ridges on lateral walls. Radula absent. Anterior and posterior salivary glands absent, but a glandular area in posterior region of buccal complex present. Esophagus of medium length, with chitinous lining and several longitudinal folds extending length of lumen. Posterior section of esophagus dilated into crop-like structure that empties into sac-like stomach. Stomach with weakly chitinized lining; proximal portion with numerous closely set, longitudinal, muscular folds; distal portion relatively thin-walled and smooth. Caecum walls with number of ciliated leaflets; without chitinous lining. Digestive gland large, dark-colored, with lighter-colored digestive duct appendages on ventral surface and enclosed within surrounding membrane. Digestive gland entire (not divided into two lobes), with depression on dorsal surface in which lies crop-like structure of esophagus. Bifurcate digestive ducts unite before emptying into caecum. Intestine long,

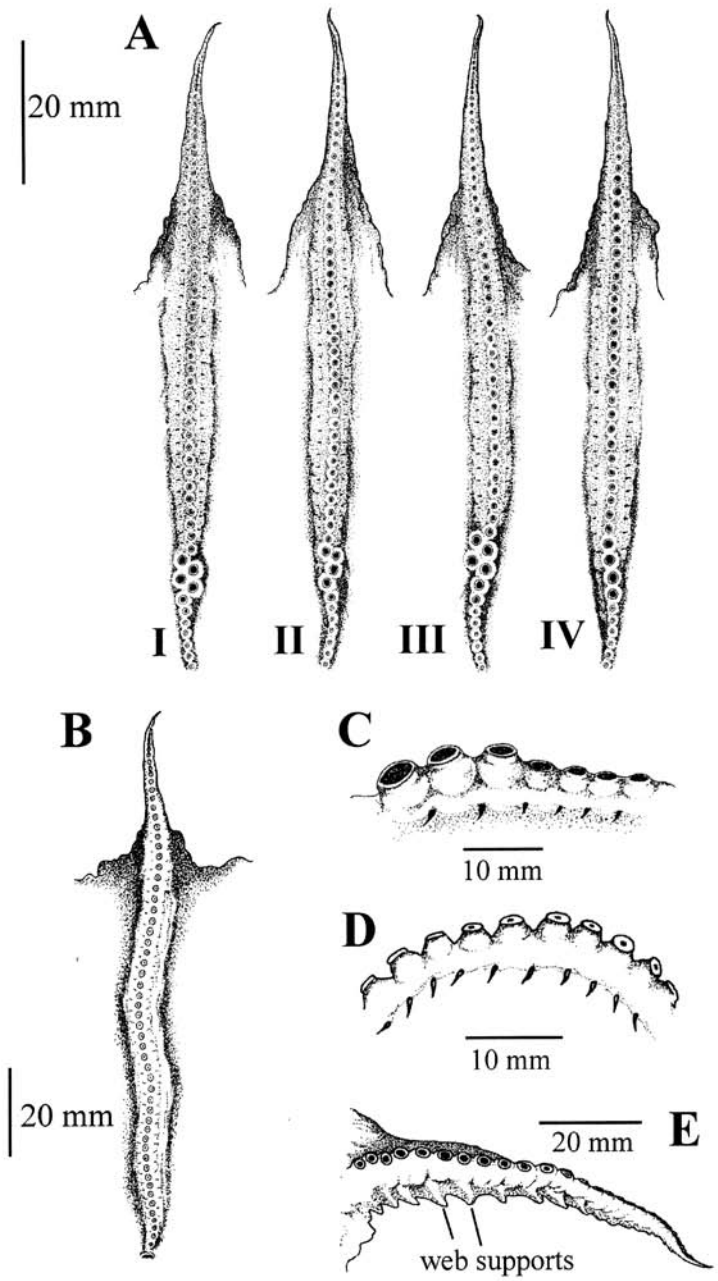

Figure 2. *Opisthoteuthis agassizii*. Sucker arrangement. A. Location of enlarged suckers on the left arms of the Neotype, mature male 42 mm ML (USNM 729079). B. First arm of mature female (UMML 31.2884). C. Lateral view of enlarged suckers and cirri of the Neotype. D. Lateral view of suckers and cirri of female (UMML 31.2884). E. Web supports of a maturing female 33 mm ML (USNM 893731).

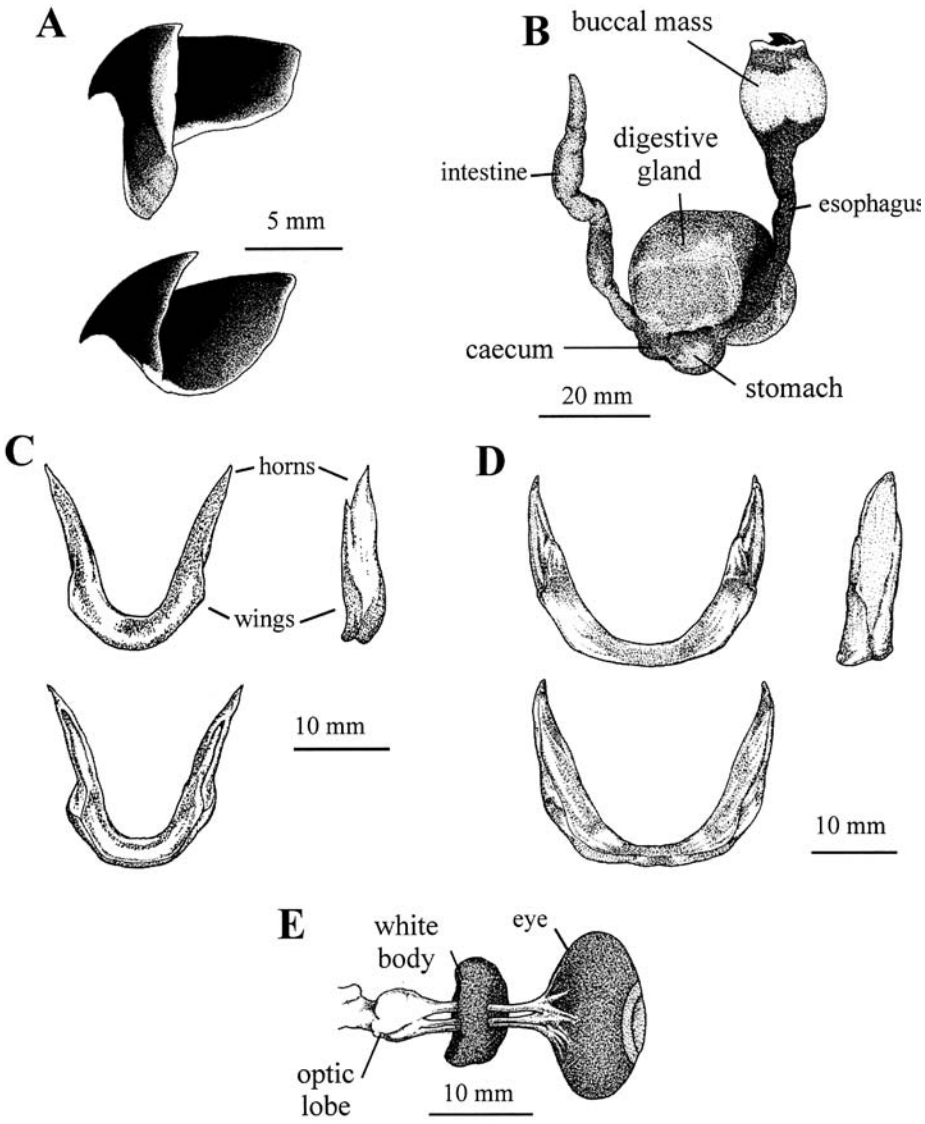

Figure 3. *Opisthoteuthis agassizii*. Internal anatomy. A. Lower (above) and upper beaks of a mature male 35 mm ML (UMML 31.2490). B. Digestive system of a mature male of approx. 50 mm ML (UMML 31.2498). C. Dorsal (upper), ventral (lower) and lateral views of the type A shell of the Neotype (male) (USNM 729079). D. Dorsal (upper), ventral (lower) and lateral views of the type B shell of a mature female (UMML 31.2884). E. Ventral view of the optic nerve complex of a maturing female 33 mm ML (USNM 893731).

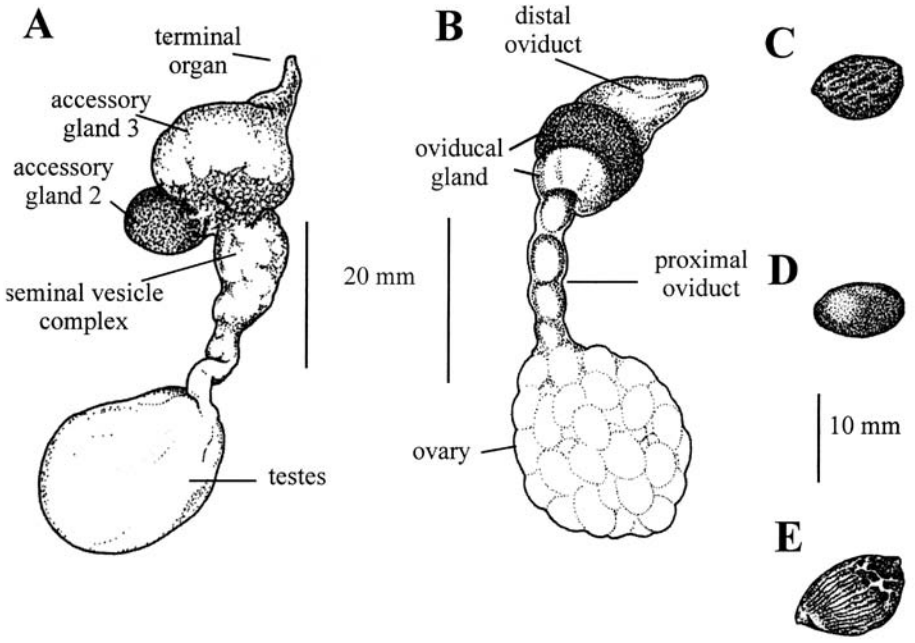

Figure 4. *Opisthoteuthis agassizii*. Reproductive anatomy. A. Reproductive tract of a mature male (UMML 31.2490). B. Reproductive tract of a mature female (UMML 31.2884). Eggs from ovary (C), proximal (D) and distal (E) oviducts (UMML31.2884).

about 1.5 times the length of esophagus, extends from caecum, describes an S-shape and ends in anus. Intestinal walls with four double, longitudinal folds that extend entire length; lacks chitinous lining. Ink sac absent.

Male genitalia composed of large, oval testis located in median portion of mantle cavity and dorsal in position; short vas deferens; large, convoluted seminal vesicle complex; large accessory gland complex dominated by accessory gland 3; terminal organ (penis) short. Spermatophores oval, with length range of 0.7–1.6 mm. Female genitalia large, approximately 50% of visceral mass in mature specimens, composed of large ovary, long proximal oviduct with thin walls that leads to large, two-chambered, acorn-shaped oviducal gland. Proximal chamber of gland striated, opaque in color, slightly shorter than striated, dark-colored distal chamber. Distal oviduct short to medium in length. Mature eggs (from oviducal ducts and oviducal gland), with size range of 7.7 × 5.8 – 10.2 × 7.7 mm. Eggs in proximal duct and posterior chamber of oviducal gland have smooth, opaque outer capsule. Eggs in distal oviducal duct and an egg found emerging from distal chamber of oviducal gland with brown, longitudinally striated, shell-like coating. Large ovarian oocytes with striated outer surface. Mature female of 54 mm ML contained approximately 320 oocytes (77 of 6 mm or greater length, approximately 250 of less than 6 mm) in ovary, and one egg each in proximal oviducal duct and gland (Cupka, 1970).

Shell stout, broadly U-shaped, with short, flaring lateral wings. Basal portion with outer surface concave, and inner surface convex. Lateral wings laterally compressed, taper to spike-like spine to relatively broad, pointed ends. Skin surface smooth, reddish-brown in preserved specimens. Pigment-free spots known only from single specimen,

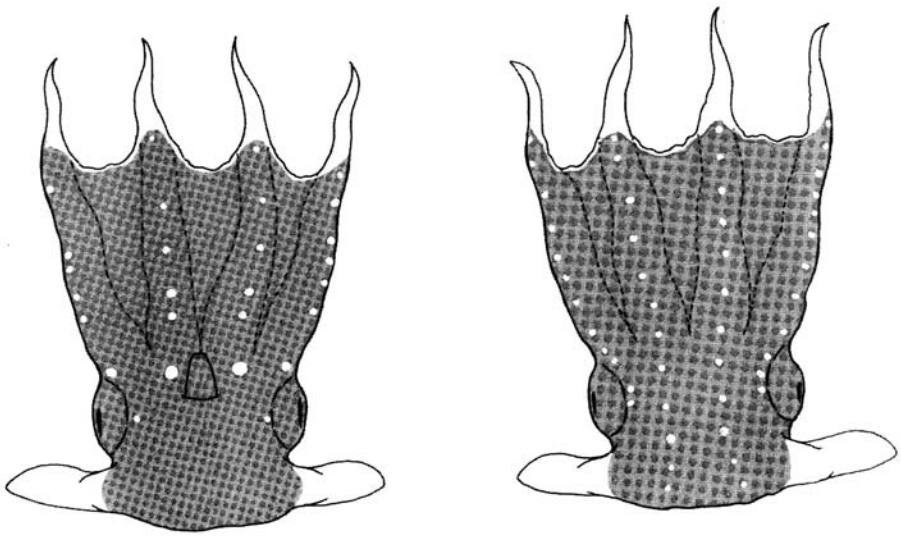

Figure 5. *Opisthoteuthis agassizii*. Dorsal and ventral view of immature female approx 25 mm VML (HBOM 68:00086) showing arrangement of pigment-free spots.

present on head and basal 2/3 of all arms (Fig. 5), arranged in 8 rows: the 2 median dorsal rows, comprising 12 spots, begin at the posterior end of the body and continue on each dorsal arm; the 4 lateral rows, comprising 8–12 spots, begin at mid-eye level and extend on each lateral arm; the 2 ventral rows, comprising 6 spots with the proximal pair enlarged, begin just lateral to the funnel and extend on each ventral arm.

Type Locality.—Grenada, West Indies, ca 12°00′N, 61°45′W, 532 m.

Distribution.—Known only from the western North Atlantic from around the perimeter of the Gulf of Mexico and Caribbean, and north in the Bahamas to 39°35′N, 70°03′W, off the coast of New Jersey, USA. The unreported specimen(s) mentioned by Voss (1988a) would extend the known distribution of *O. agassizii* to northeastern Brazil, but could not be located in the Marine Invertebrate Museum, RSMAS/Univ. of Miami. All specimens of the species were caught by trawls (except one collected by a submersible manipulator), fishing on or just off the bottom between 227 and 1935 m. Of 25 tows that captured the species and recorded bottom type and/or temperature, 23 were on mud or mud-and-stone bottom and 2 were made on rocky bottom. Recorded temperatures range from 4.2 to 12.8°C. In a study of the DeSoto Canyon in the northeastern Gulf of Mexico, 23 bottom-trawling stations were made between 366 and 1829 m, of these, Cupka (1970) reported that 10 (43%) were positive for *O. agassizii*, capturing a total of 46 specimens. All specimens were taken between 549 and 1207 m, with highest abundance between 732 and 914 m. Over the capture depth range, salinity ranged between 34.86 and 35.02‰, and density ranged between 27.25 and 27.8 sigma-t. Most interesting was Cupka's finding that dissolved oxygen concentration may affect the minimum depth for the species. In the canyon, the dissolved oxygen ranged in the vertical column between a minimum of 2.7 ml L^{-1} and a maximum of 4.62 ml L^{-1}. The oxygen minimum occurred between 400 and 500 m and thereafter, the dissolved oxygen concentration increased with depth. The shallowest capture depth, 549 m, was just below the oxygen minimum zone. Additionally, Cupka found that small specimens, which have relatively larger gills than adults, inhab-

Table 1. Indices of body proportions and counts of 15 mature males, 9 maturing males, 8 mature female and 12 maturing females of *Opisthoteuthis agassizii*. For each index or count, min–mean–max. values are indicated and standard deviation are shown between brackets. Measurements in mm.

Sex	M	M	F	F
Maturity	Mature	Maturing + immature	Mature	Maturing + immature
ML	32.0–43.5–55.0 (6.0)	12.0–27.3–38.0 (9.9)	23.0–34.3–40.0 (6.2)	15.0–24.8–35.0 (7.7)
TL	117.0–162.1–186.0 (25.2)	46.0–90.5–141.0 (39.0)	125.0–141.6–154.0 (13.1)	68.0–101.3–138.0 (30.9)
MWI	111.1	109.5	–	–
HWI	117.1–145.4–172.7 (19.5)	116.0–139.8–161.9 (18.8)	137.5–153.8–173.9 (18.5)	94.3–141.8–187.5 (28.6)
CiI	3.8–5.8–9.1 (1.9)	3.3–5.5–7.9 (2.3)	4.5–5.8–7.5 (1.3)	3.0–5.9–7.0 (1.4)
FLI	44.1–60.3–74.6 (11.2)	35.3–45.6–60.4 (10.6)	57.5–60.1–63.6 (3.2)	35.9–51.0–71.0 (13.1)
FWI	32.5–45.1–56.7 (8.6)	34.4–49.6–58.3 (10.8)	25.0–41.7–50.0 (9.7)	34.1–52.6–64.3 (10.2)
FSI	60.3–65.7–71.8 (4.8)	49.4–59.7–69.6 (10.1)	46.2–55.6–66.2 (10.1)	49.3–64.3–88.8 (14.2)
EDI	43.1–61.6–74.3 (11.7)	44.7–60.4–70.8 (11.1)	57.5–74.5–100.0 (18.4)	54.5–66.8–78.9 (8.4)
FuLI	41.9–57.3–68.8 (8.2)	56.7–61.9–68.0 (5.8)	64.9–74.0–83.3 (7.2)	48.6–67.3–91.7 (17.1)
FFuI	48.3–61.9–73.3 (8.5)	35.3–55.2–64.0 (13.5)	43.3–54.5–66.7 (8.3)	29.2–49.7–61.5 (10.9)
TOLI	5.7–9.0–13.0 (2.4)	8.0–13.2–18.3 (7.3)		
Gill LC	6–7.0–8 (0.4)	6–6.7–7 (0.5)	7	7–7.1–8 (0.3)
Egg length			7.7–8.9–10.2 (0.8)	
ALI-I	234.1–318.5–369.6 (40.8)	285.7–307.5–320.0 (18.9)	263.2–329.3–487.0 (81.2)	193.9–302.3–421.1 (78.7)
ALI-II	238.6–316.4–369.1 (41.6)	271.1–288.1–304.0 (1307)	278.4–326.9–456.5 (65.2)	193.9–306.7–431.6 (80.5)
ALI-III	238.6–317.3–371.4 (42.7)	290.5–299.2–308.0 (12.4)	286.8–329.8–439.1 (62.9)	203.0–320.2–478.9 (88.3)
ALI-IV	245.5–303.8–354.3 (36.2)	266.7–283.2–308.0 (21.9)	287.5–331.5–430.4 (53.4)	206.1–315.7–478.9 (87.5)
AWI-I	18.8–24.9–34.3 (6.2)			
AWI-II	18.8–23.5–31.4 (5)			
AWI-III	17.5–22.9–31.4 (5.4)			
AWI-IV	18.8–23.0–31.4 (5.2)			
SDI Proximal-I	8.6–10.0–12.6 (1.4)	6.4–8.1–10.8 (1.8)	4.5–5.4–6.5 (1.0)	5.9–6.6–7.4 (0.6)
SDI Proximal-II	8.5–10.1–12.3 (1.2)	6.4–8.4–10.8 (1.8)	5.0–5.6–6.5 (0.8)	5.6–6.6–7.4 (0.8)
SDI Proximal-III	8.4–10.3–12.3 (1.2)	6.4–9.7–14.2 (2.9)	3.9–4.9–5.5 (0.8)	5.0–6.1–7.4 (1.1)
SDI Proximal-IV	9.4–10.5–12.3 (1.0)	8.9–9.7–10.4 (0.7)	4.5–5.0–5.5 (0.5)	5.4–6.1–6.8 (0.7)
SDI Distal-I	5.8–7.4–8.9 (1.0)	5.6–5.8–5.9 (0.2)	–	–
SDI Distal-II	5.8–8.1–10.4 (1.5)	6.3	–	–
SDI Distal-III	5.6–9.1–10.3 (1.3)	5.6–5.9–6.3 (0.5)	–	–
SDI-IV Distal	5.6–9.2–10.8 (1.5)	6.0–6.4–6.9 (0.6)	3.8–4.3–4.8 (0.7)	–
Arm sucker count				
A I	64–67.4–71 (2.6)	43.0–57.5–66.0 (10.1)	59–66.2–71 (3.9)	57–68.3–77 (7.3)
A II	56–67.1–75 (6.0)	56.0–63.3–69.0 (6.7)	65–69.5–76 (3.8)	56–65.3–77 (7.7)
A III	58–66.5–77 (6.8)	64–66.5–69.0 (3.5)	65–71.8–77 (4.2)	57–68.6–78 (8.6)
A IV	63–69.8–78 (6.1)	60–64.5–69.0 (6.4)	66–70.8–78 (5.7)	58–68.9–80 (9.5)
AASC	58.3–67.0–74.8 (5.5)	43.0–59.2–68.3 (9.7)	64.0–69.5–75.0 (3.8)	57.3–67.3–77.7 (8.4)

ited the canyon's shallower, lower oxygen-content depths of 549–732 m, while 86% of the adults came from the higher oxygen-content depths below 732m. Combined data from the present and Cupka's studies indicate that *O. agassizii* occurs in considerable abundance over its geographic range in the Gulf of Mexico and Caribbean; data for the northern sector of the species range to north of the Bahamas is inadequate for drawing conclusions.

Biology.—That *O. agassizii* lives on and just above the bottom is well supported by the fact that all known trawl-caught specimens were taken in bottom trawls (none taken in the numerous mid-water trawls that have fished the waters within the known geographic and depth ranges of the species), and the observations made from a submersible reported by Vecchione and Roper (1991). Their paper contains a photograph of a specimen on the bottom off St. Vincent Island in the Lesser Antilles at 586 m, and described its subsequent swimming movement in which it beat its fins and used its arms and web for medusoid swimming. The specimen (HBOM 68:00086), collected in perfect condition by the submersible's manipulator, was examined in our study, and its pattern of pigment-free spots on the mantle and arms, first reported for the species in the above paper, is illustrated and further described in the above species description. These spots were not apparent in our trawl-caught, largely long-preserved specimens in which the fragile skin is mostly fragmented or absent. Referring to them as areolar spots, following Berry (1918), O'Shea (1999) considers their presence characteristic of the family Opisthoteuthidae. A detailed study is needed to determine their function. Vecchione et al. (1998) speculated that similar pigment-free spots in *Cirroctopus glacialis* gather and channel light.

Information on the food and feeding of the species is supplied by the analyses of stomach contents by Voss (1956), Cupka (1970) and Lipka (1975). Voss found the remains of numerous small crustaceans, including an amphipod and a mysid, together with polychaete bristles and appendages. Cupka reported finding polychaete bristles, cumaceans, amphipods, calanoid copepods, and the remains of various decapod crustaceans. In his 19 mm ML juvenile, Lipka found crustacean body parts and benthic foraminifera, and in his 55 mm adult found predominantly decapod crustacean parts, together with two sets of octopod beaks, and fragments of melanistic membranes. The results suggest that *O. agassizii* feeds both on and off the bottom.

Remarks.—Our study revealed a considerable degree of variation in the shape of the ends of the lateral wings of the shell in this species. Of 43 specimens examined for shell shape, 33 (from 21 lots; from the Gulf of Mexico, Caribbean and Bahamas) were classified as having type A or A-like wing ends (Fig. 3D); a spike-like pointed spine protruding from a shoulder that formed a distinct shelf), but the specimens showed varying degrees of development of the shoulder to form a distinct shelf, and of thickening and height of the shoulder. When the shoulder was low, the protruding, spike-like spine was long; when the shoulder was high, the spine was relatively short. The specimens comprised 8 mature males, 3 mature females, and 22 subadults/juveniles; 33% were mature. The remaining 10 (from 8 lots; from Gulf of Mexico and Caribbean) of the 43 specimens examined, were classified as having type B or B-like wing ends (Fig. 3C); taper to a relatively broad, pointed end, without a distinct, shelf-like shoulder). This group comprised 3 mature males, 4 mature females, and 3 subadults/juveniles; 70% were mature. We found no consistent differences in other characters between these two groups, and feel that we are dealing with a single species, *O. agassizii*, and that the variation found in the shape of the wing ends is maturity related. With maturity, the shoulder tends to thicken and merge with the

protruding spine, resulting in a stout, tapering point. Perhaps the stouter end affords a stronger base for the increased muscular development of the fins in the adult.

Two recent phylogenetic studies of coleoid cephalopods, Young and Vecchione (1996) and Voight (1997), included specimens identified to *O. agassizii* and described the presence or absence of several anatomical features in the species that are either verified or questioned by our findings. A fin cartilage forming the core support of each fin, formerly considered absent in cirrates, was reported present and described by Young and Vecchione (1996). The cartilage, easily seen in our dissections of the fin, was actually well described for the holotype by Verrill (1883), but his description of the 'separate internal cartilage' supporting each fin was misinterpreted by Berry (1918) as meaning a two-parted shell vestige. Subsequently, the necessary fin dissections were not made until Young and Vecchione's study, which confirmed Verrill's finding of a fin cartilage in the species. A posterior salivary gland, found by Voight in one of her two specimens attributed to *O. agassizii,* was not found in the specimens dissected in the present or Cupka's studies. Both latter studies did however show the presence of a glandular area in the posterior region of the buccal complex that remains unnamed. Also, the bilobed condition of the digestive gland reported for *O. agassizii* by Voight was not confirmed by our and Cupka's findings, which showed the digestive gland to be entire, and not divided into two lobes. Thus we regard the identification of Voight's specimens as suspect.

Opisthoteuthis calypso new species
Figs. 6–10, 21, 22; Tables 2, 3, 5–7

Opisthoteuthis agassizii (non Verrill 1883).- Chun 1913: 15 (off Ireland, 49°38′N, 11°35′W); - Morales: 1959: 113, figs. 1–3 (off Blanes, Mediterranean Sea); 1962: 98 (Mediterranean Sea); -?Adam 1962: 49°61′W of Cabinda, Angola); -?Alcázar and Ortea, 1981: 29, figs 1–5 (43°50′N, 05°05′ to 06°05′W; - Sánchez 1981: 33 (1837′S, 1122′E); -1988: 253, fig. 29; - Sánchez and Molí 1984: 20; -?Voss 1988a: 298 (05°05′N, 04°00′W); - Villanueva 1992a: 265, figs. 1, 2, 3d, 5, 6,7, 10 (off Namibia); - 1992b: 271 (NW Mediterranean, 40°30′N, 01°47′E); - Villanueva and Guerra 1991: 288, figs. 6–8, 9a–b; - Villanueva and Sánchez 1993: 18 (records off Namibian waters are from 18°37' to 29°39'S and 11°22' to 14°37'E); Quetglas et al. 2000: 741 (NW Mediterranean).

Material Examined.—Type material. HOLOTYPE, a mature male 38 mm ML from Cape Breton cruise Sta. CM08/CB87, Cantabric Sea, 43°34.64′N, 02°16.47′W, 495 m, Marinovich bottom trawl, 30 Jun 1987, fixed in formalin, preserved in 70% ethylalcohol, ICM199/2000. Paratypes: 2 mature males, 27 mm (MNHN3782) and 29 mm ML (USNM893733) collected from same trawl as holotype; 1 mature male, 45 mm ML, Cape Breton Cruise Sta. M27/CB88, Cantabric Sea, 43°43.19′N, 02°20.13′W, 917-954 m, Marinovich bottom trawl, 8 Jul 1988, UMML31.3137; 1 mature male 35 mm ML (NMSZ1999158.074) and 1 mature female 35 mm ML (NMSZ1999158.075), off Namibia, Freezer-trawler Janza, Sta. 250, 29°39.5′S, 14°37.2′E, 451 m, bottom trawl, 17 Sep 1989; 1 mature female, 39 mm ML off Namibia, Benguela IV Cruise, Chicha-Touza Sta. 82, 20°06′S, 11°47′E, 534 m, bottom trawl, 18 Apr 1981, UMML31.3138; 1 maturing male 28 mm ML, off Blanes, NW Mediterranean Sea, 670–-690 m, commercial bottom trawl, 12 Aug 1959, ICM530/1991, specimen refered as *O.agassizii* by Morales (1959); 1 mature female 26 mm ML, Benguela IV Cruise, Chicha-Touza Sta. 82, off Namibia, 18°37′S, 11°22′E, 522 m, bottom trawl, 17 Apr 1981, USNM893734; 1 mature female 29 mm ML, Benguela IV Cruise, Chicha-Touza Sta. 84, off Namibia, 19°08′S, 11°22′E, 531 m, bottom trawl, 17 Apr 1981, ICM200/2000.

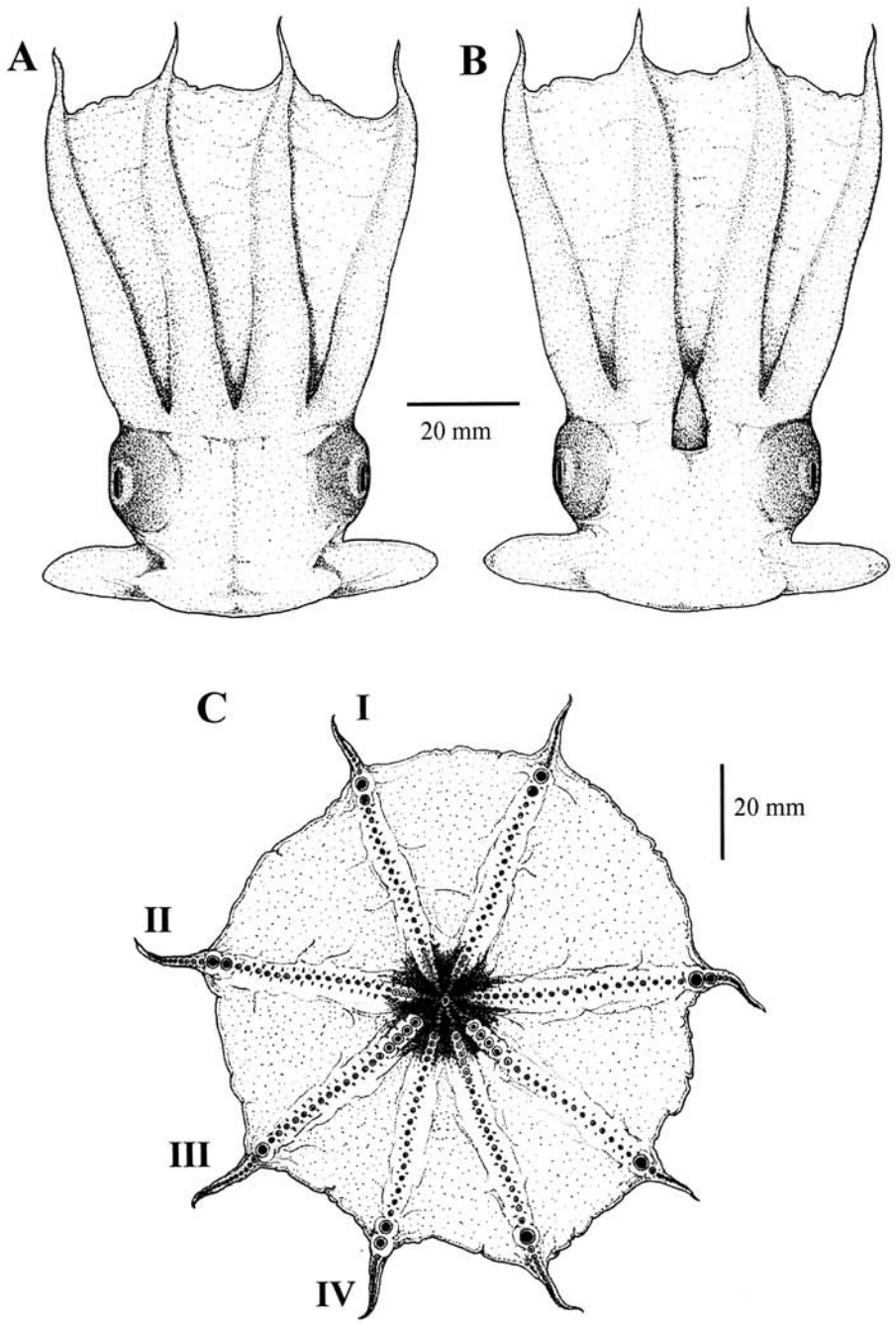

Figure 6. *Opisthoteuthis calypso* new species. Dorsal (A), ventral (B) and oral views of Paratype mature male 35 mm ML (NMSZ1999158.074).

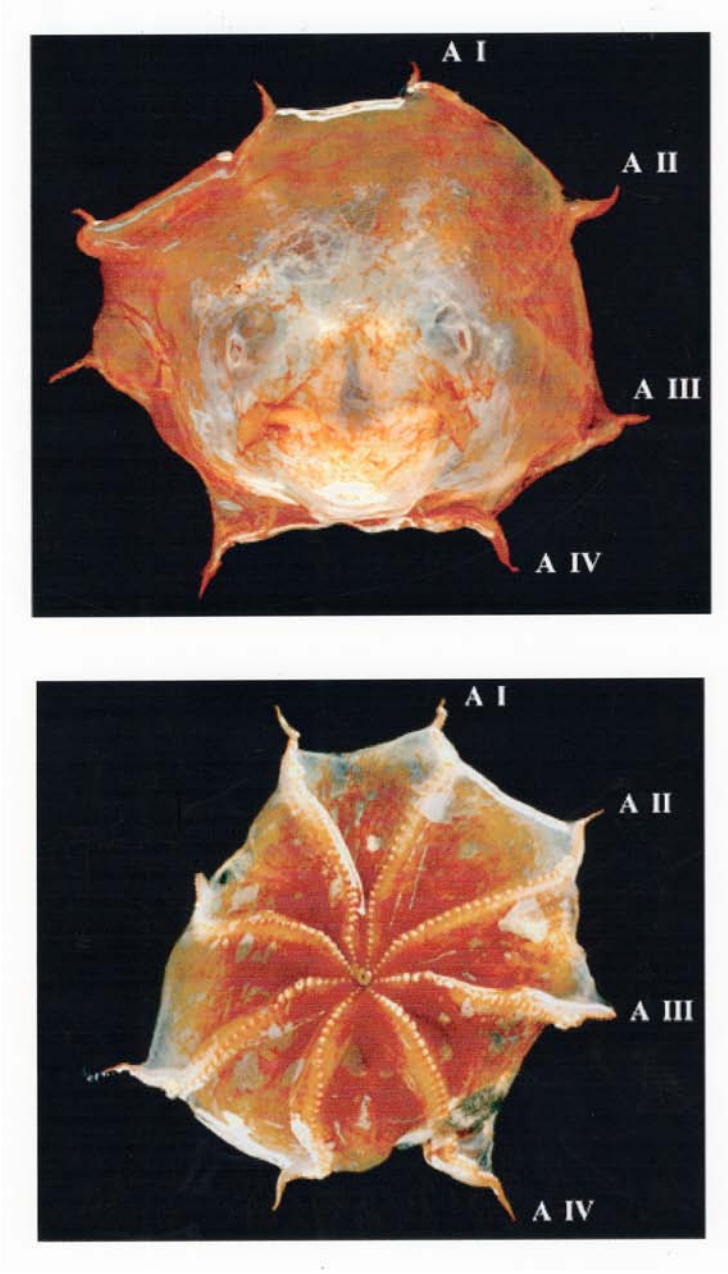

Figure 7. *Opisthoteuthis calypso* new species. Aboral (upper) and oral (lower) view of fresh specimens collected from Namibian waters (29º39.5′S, 14º37.2′E, 451 m), measured and photographed after thawing. Aboral view, mature female, 75 mm ML, 156 g TW (note the distinct contrast between the digestive system and the ovary); Oral view, mature male, 61 mm ML, 235 g TW.

Additional Material.—MEDITERRANEAN SEA.—1 immature female 13 mm ML off Blanes, commercial bottom trawl, 560–580 m, 13 Sep 1960, ICM531/1991, specimen reported as *O. agassizii* by Morales (1962); RV García del Cid: 1 immature male 19 mm ML, Bathos IV Cruise, Sta. 7, 41°11′N, 03°36′E, 2208 m, bottom trawl, 28 Jul 1988, ICM336/2000; 1 maturing male 21 mm ML, Bathos V Cruise, Sta. 2, 1585 m, bottom trawl, 25 Oct 1988, ICM337/2000; 1 immature male 18 mm and 1 immature female 13 mm ML, Bathos V Cruise, Sta. 8, 40°30′N, 01°47′E, 1588 m, bottom trawl, 27 Oct 1988, ICM338/2000; these last four specimens were reported as *O. agassizii* by Villanueva (1992b); 1 ?sex immature, 7 mm ML, Retro III Cruise, Sta. 8, 40°54′N, 02°05′E, 1290 m, bottom trawl, 12 Mar 1992, ICM341/2000; 1 immature female 9 mm ML, Retro IV Cruise, Sta. 8, 39°57′N, 02°18′E, 1293 m, bottom trawl, 27 Jul 1992, ICM339/2000; 1 maturing male 28 mm ML, off Barcelona, 40°50′N, 02°20′E, 1400 m, bottom trawl, 30 Sep 1998, ICM340/2000.

SOUTHEASTERN ATLANTIC, off Namibia.- Freezer-trawler Sueve: 1 maturing male 22 mm ML (ICM342/2000) and 1 mature female 31 mm ML (ICM343/2000), Sta. 194, 25°10′S, 13°38′E, 425 m, bottom trawl, 8 Jan 1988; 1 immature male 17 mm ML, Sta. 197, 24°51′S, 13°38′E, 420 m, bottom trawl, 9 Jan 1988, ICM344/2000; 2 mature females 34 (NMSZ1999158.089) and 34 mm ML (ICM345/2000), Sta. 198, 25°08′S, 13°39′E, 418 m, bottom trawl, 9 Jan 1988; 1 immature male 14 mm ML, Sta. 201, 25°36′S, 13°38′E, 422 m, bottom trawl, 10 Jan 1988, ICM346/2000; Freezer-trawler Hermanos Touza: 1 immature male 18 mm ML, Sta. 70, 25°49′S, 13°39′E, 480 m, bottom trawl, 29 Mar 1989, ICM347/2000; Freezer-trawler Janza: 1 mature female 27 mm ML, Sta. 53, 25°54′S, 13°44.5′E, 406 m, bottom trawl, 26 Jul 1989, ICM348/2000; 1 mature male 29 mm ML and 1 mature female 25 mm ML, Sta. 30, 26°48.8′S, 14°19.2′E, 365 m, bottom trawl, 20 Jul 1989, ICM349/2000; 1 immature male 11 mm ML (ICM359/2000), 5 mature males 30 (ICM350/2000), 32 (ICM351/2000), 34 (ICM352/2000), 35 (ICM353/2000), 35 mm ML (ICM354/2000) and 4 mature females 19 (ICM355/2000), 23 (ICM356/2000), 26 (ICM357/2000) and 27 mm ML (ICM358/2000), Sta. 250, 29°39.5′S, 14°37.2′E, 451 m, bottom trawl, 17 Sep 1989.

CENTRAL EASTERN ATLANTIC, Guinea Gulf.—These specimens are tentatively assigned to *Opisthoteuthis ?calypso*. No males are recorded from this area which complicates species identification. 1 mature female 34 mm ML, Sta. Thierry CR.No11. 61/8, 04°55′S, 11°20′E, 400 m, bottom trawl, 26 May 1964, USNM 893735; 1 female 28 mm ML, Pillsbury Sta. 44, Ivory Coast, 05º05′N, 04º00′W, 403 m, bottom trawl, 30 Jun 1964, UMML31.820.

Historical Resume.—The above study of *O. agassizii* Verrill shows the species to be restricted to the West Atlantic, and regards the previous reports of *O. agassizii* in the East Atlantic as misidentifications and attributable to other species of the genus. The first such report attributable to *Opisthoteuthis calypso* was by Chun (1913), who reported 4 unsexed specimens taken off Ireland by the Michael Sars Expeditions. In his work, Chun described the distal sucker enlargement pattern that we find below to be characteristic of mature males of *O. calypso*. The specimens from the Mediterranean Sea reported as *O. agassizii* by Morales (1959; 1962) and Villanueva (1992b) have been re-examined and identified in the present study as *O. calypso* (see material examined), and recently Quetglas et al. (2000) reported also *O. agassizii* for the Mediterranean. Adam (1962) reported two unsexed specimens of *O. agassizii* off Angola; the sucker size and counts of one of Adam's specimens appear to indicate that is a male of *O. calypso*. Voss (1966) reported, but did

not describe, 2 specimens of *Opisthoteuthis* sp. collected in the Gulf of Guinea. Voss later referred the specimens to *O. agassizii* (Cupka, 1970: 6; Voss, 1988a). The poor condition of the one specimen that could be located (UMML31.820), does not permit certain identification, but based on its sucker pattern and count, the specimen appears to be an immature female of *O. calypso*. Reports of *O. agassizii* by Alcázar and Ortea (1981) in the Cantabric Sea can be attributed to *O. calypso* on the basis of the description of the enlarged sucker pattern of males. A large number of specimens reported as *O. agassizii* have been taken in Namibian waters as part of faunistic (Sánchez, 1981; 1988; Sánchez and Molí, 1984; Villanueva, 1992c; Villanueva and Sánchez, 1993) and biological studies (Villanueva and Guerra, 1991; Villanueva, 1992a). This material collected during the Spanish Benguela scientific cruises in Namibian waters and stored in the ICM collections has been re-examined in the present study and reidentified as *O. calypso*. Other reported specimens of *O. agassizii* in the East Atlantic from north of Scotland and southeast of Ireland (Bruun, 1945), the Cantabric Sea (Olaso, 1990) and off South Africa (Roeleveld et al., 1992; Roeleveld, 1998) include published descriptions that are inadequate for accurate specific identification. These, which we have not examined, are considered to be *Opisthoteuthis* sp. (see Indeterminate Species section).

Diagnosis.—Medium to large-sized species. No increased robustness of arm I in mature male. From the ventral margins of all the arms, a single muscular nodule extends into the web to its outer edge at the approximate level of the maximum depth of the web between the arms, typically at sucker 22–27. Arm sucker count in adults 47–58. In mature males, sucker enlargement in proximal field greatest on arm III. The distal enlarged sucker field comprises two to three (exceptionally four) contiguous suckers, usually beginning at about sucker 23–24 with sucker 26 largest. In mature males, maximum distal enlarged sucker diameter equals or exceeds that of proximal enlarged suckers. Sucker enlargement in distal field greatest on arms III and IV. First cirrus usually occurs between suckers 1 and 2. Digestive gland entire. Basal portion of shell with slightly concave outer surface, and convex inner surface. Eggs relatively small, egg length from oviducal gland and distal oviduct ranges from 5.1 to 7.5 mm (mean: 6.5 mm). Pigment-free spots not known to occur on skin.

Description.—The following description is based on 21 males (11 mature), 17 females (14 mature) and 1 immature unsexed specimen. Additionally, morphometric data from Villanueva and Guerra (1991) and Villanueva (1992a) have been added to the text when necessary.

Medium to large-sized species. Males grow larger and heavier than females: TL and TW reaches 482 mm and 5400 g in males and 342 mm and 1650 g in females. The relationship between TW and TL is the same in both sexes: $TW = 2 \times 10^{-5} \times TL^{3.1}$ ($r = 0.96$, $n = 169$) (Villanueva and Guerra, 1991). Animals with soft body, semi-gelatinous consistency and ovoid appearance in fresh specimens. Mantle short, rounded posteriorly and little wider than long. Head width slightly greater than mantle width, with no discernible constriction between head and mantle. Pallial aperture small, closely surrounding the funnel. Funnel small, conical, free for about 2/3 of its length. Funnel organ with limbs separated, inverted \ / -shaped; discernible with difficulty. Olfactory organ unpigmented, rounded and prominent, located on each side of the funnel and just within the mantle aperture, measuring 0.5 mm in diameter in the holotype. From the olfactory organ a duct connects with the stellate ganglion, which is fusiform or ovoid in form, embedded in the mantle musculature, with 5 to 7 large nerves and more thin nerves on each side of the

ganglion. Two small fins, positioned posterolaterally on each side, are situated about halfway between the apex of mantle and the eye. Posterior margin of the fin nearly straight, only slightly curved near the posterior fin insertion. Fin tip rounded as a semicircle and anterior fin margin slightly convex, without lobe near the anterior insertion. Fins about twice as long as wide. Fin span about three times the fin length. Each fin supported by an internal, flexible cartilage that extends from shell sac to which it closely adheres to approximately mid length of fin. Fin cartilage thick basally, becoming progressively thinner and specimen only two nerves were observed passing through the white body.

Arms moderately long and subequal in length. No clear arm formula discernible, although arms I slightly larger and arms IV smaller than the others in medium-sized specimens. No increased robustness of arms I in mature males. From the ventro-lateral margins of all of the arms, a single muscular nodule extends into the web to its outer edge at the approximate level of the maximum depth of the web between the arms. In males, the nodule typically occurs at the level of sucker 24 to 27 (at sucker 27 in the holotype), and 1–2 suckers prior to the largest enlarged distal sucker. In females, the nodule is less pronounced and typically occurs at the level of sucker 22 or 23. The web is deep, occupying 2/3 of the arm. Web sectors extends equally, with a tendency for the sector E to be slightly smaller that the rest. Each arm bears a single row of suckers extending from the mouth to the tips of the arms. Average arm sucker count in mature males ranges from 48 to 58 suckers and in mature females from 47 to 54. Unmodified, normal suckers are of 2–3 mm in diameter, with a wide sucker peduncle deeply set into the semi-gelatinous tissue of the arm. Sucker rim and infundibulum less pigmented than peduncle (detailed description and illustration of the ultrastructure are in Villanueva and Guerra, 1991). Marked sexual dimorphism exists in sucker enlargement. Males have two fields of enlarged, bulbous-shaped suckers on all arms. On each arm of mature males, maximum distal enlarged sucker diameter is equal or (generally) exceeds that of proximal enlarged suckers. The

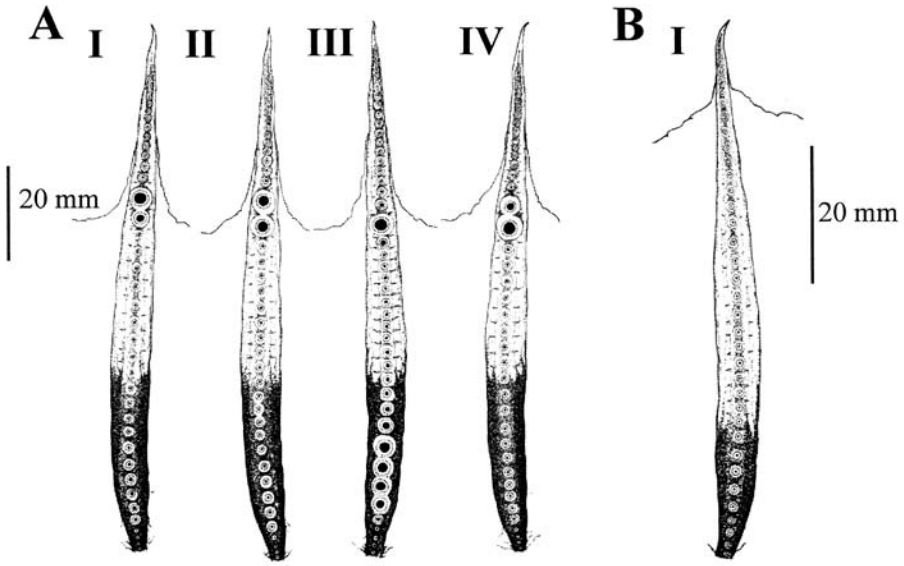

Figure 8. *Opisthoteuthis calypso* new species. Sucker arrangement. A. Location of enlarged suckers on the left arms of Paratype, mature male 35 mm ML (NMSZ1999158.074). B. First arm of Paratype, mature female 35 mm ML (NMSZ1999158.075).

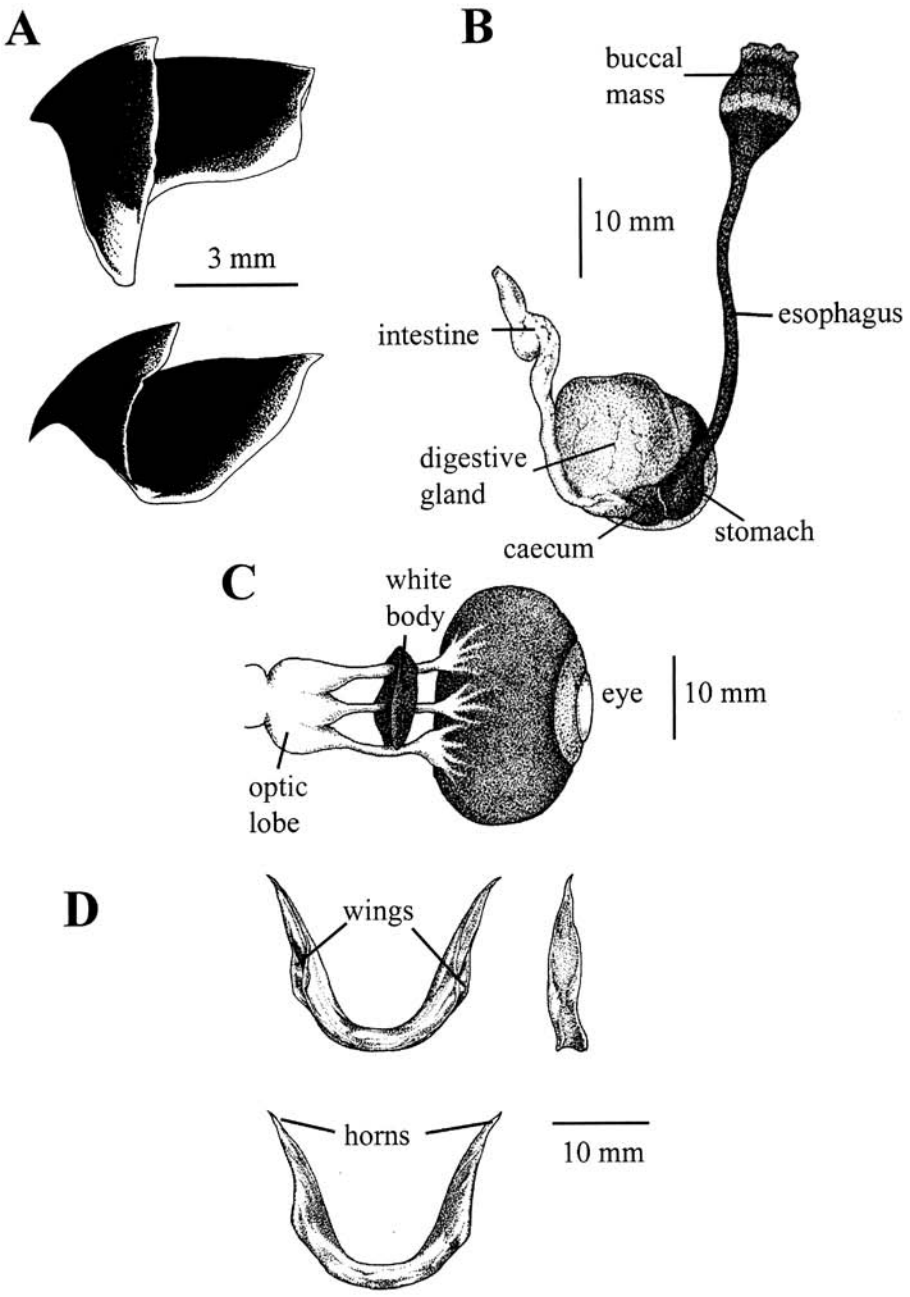

Figure 9. *Opisthoteuthis calypso* new species. Internal anatomy. A. Lower (above) and upper beaks of a mature male 37 mm ML. B. Digestive system of Paratype mature male 35 mm ML (NMSZ1999158.074). C. Ventral view of the optic complex of same (NMSZ1999158.074). D. Dorsal (upper), ventral (lower) and lateral views of the shell of a mature male 37 mm ML.

proximal enlarged sucker field is typically composed of four contiguous suckers (range 2 to 6) located from the 4–7th to the 6–9th suckers with maximum sucker diameter at the level of the 7th sucker. Arms III have the largest sucker diameter in this proximal field. The distal enlarged sucker field is composed of two to three (exceptionally four) contiguous, comparatively gigantic suckers, located at the level of the web margin, between the 23–28th and the 24–29th suckers, with sucker 26 usually having maximum sucker diameter. Arms III and IV have the maximum enlarged sucker diameter in the distal field. Females lack markedly enlarged suckers; suckers show the typical gradual increase and decrease in size observed in octopods. Typically, sucker diameter in females reaches its maximum at the 7th sucker, then gradually decreases to the tip of the arm. Cirri short, disposed in a single row on each side of the sucker row, alternating with the suckers. The first cirrus usually appears between the first and second suckers (59% of specimens), sometimes (in 35% of specimens) one or two arms have first cirrus between the second and third suckers and exceptionally (6%) between the third and fourth suckers. The longest cirri are found in the middle of the arm. Largest cirri in larger animals are 5 mm in length.

Gills compact, spherical, with seven lamellae (exceptionally, 6). Median pallial adductor muscle thin and narrow. Branchial heart rounded, approximately half the size of the gill. Buccal mass, esophagus, stomach and intestine deeply pigmented, dark purple. The buccal mass is relatively small. Relationships between the upper crest (UC) and lower crest (LC) of the beaks and specimen weight (TW) are: $\log UC = 0.46 + 0.22 \times \log TW$ ($r = 0.94$, $n = 58$) and $\log LC = 0.36 + 0.22 \times \log TW$ ($r = 0.99$, $n = 58$) (Villanueva and Guerra, 1991). There is no radula. Anterior salivary glands not discernible on the four specimens dissected, but a glandular tissue mass present on posterior region of buccal mass. Posterior salivary glands absent. No true crop present, but in some specimens the esophagus slightly distended near the stomach. Stomach oval shaped and muscular. Digestive gland large, connected to the caecum by two ducts. Digestive gland entire, with depression on dorsal surface in which lies crop-like structure of esophagus. Intestine wide and as long as esophagus. Anal flaps and ink sac absent.

Male genitalia located in the posterior mantle cavity. Testis large, oval and white in color, connected by a vas deferens to the seminal vesicle complex. Accessory glands also rounded and white, with accessory gland 2 largest. Terminal organ short, cylindrical and lightly pigmented at the end. Spermatophores small, rudimentary and located inside seminal vesicle and terminal organ. The total number of spermatophores in a specimen averaged 42 (range 15 to 103) (Villanueva, 1992a). Spermatophores are fusiform or ovate in shape, 1.5 to 2 mm in length. Two semispherical opercular structures are present, diametrically opposed at the anterior and posterior ends of the spermatophore. Each opercular structure consists of a spermatophoral pore, a crown attached to the end of the spermatophore, and a hinge extending from the crown that holds the operculum in place. The operculum has spiral groves on the surface. The spermatozoa have a conical acrosome at the anterior end of the oval nucleus and a flagellum axially (Villanueva, 1992a).

Female genitalia located in the posterior mantle cavity, unpaired, with only the left oviduct present. Ovary round, transparent, with ovarian oocytes of different size and development stage clearly visible inside. An average of 650 and 8 oocytes contained in the ovary and proximal oviduct respectively (Villanueva, 1992a). Largest ovarian oocytes display an average of 26 folicular folds (range 23 to 30). Proximal oviduct transparent in fresh specimens. The number of eggs in the proximal oviduct ranged between 2 and

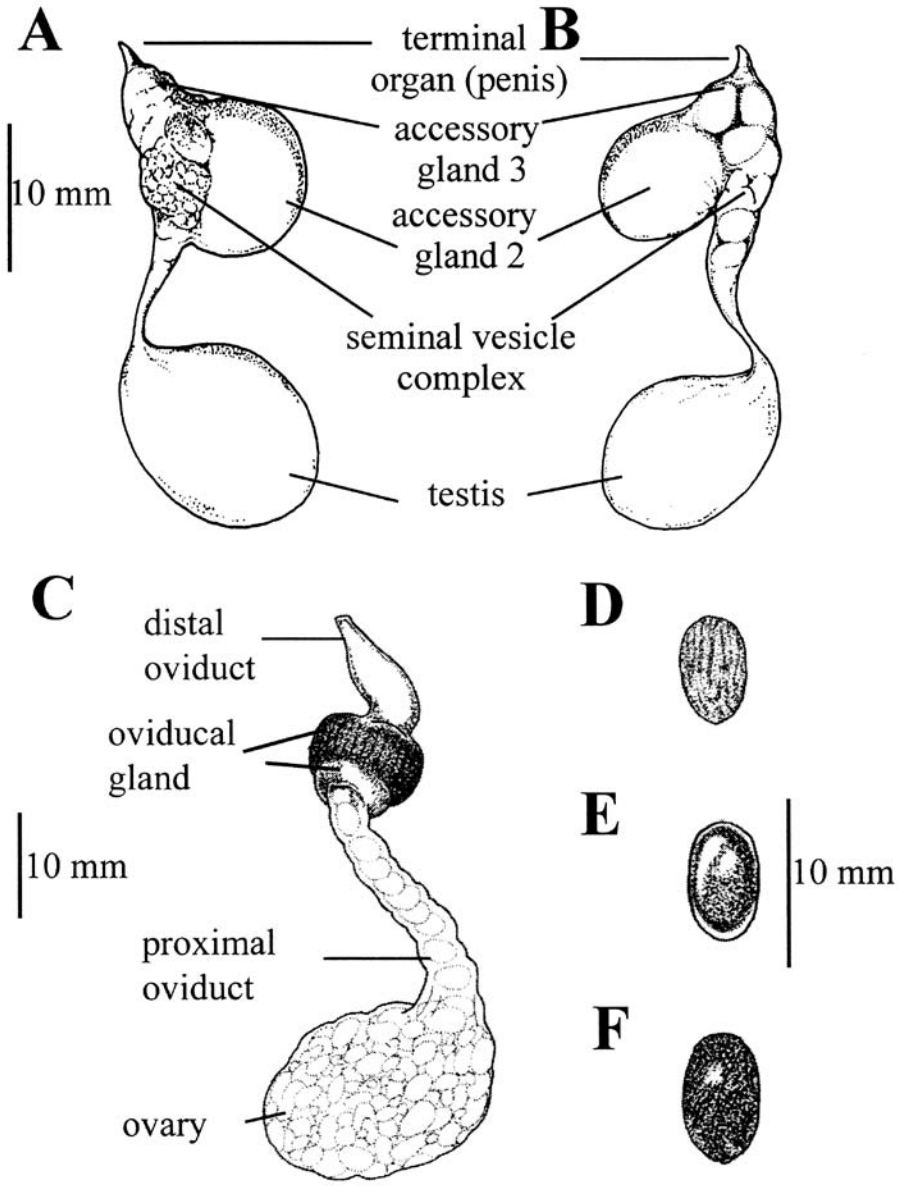

Figure 10. *Opisthoteuthis calypso* new species. Reproductive anatomy. Ventral (A) and dorsal (B) views of the reproductive tract of Paratype, mature male 35 mm ML (NMSZ1999158.074). C. Female reproductive tract of a mature female 34 mm ML (NMSZ1999158.089). Eggs from ovary (D), proximal (E) and distal (F) oviducts (NMSZ1999158.089).

17 (mean 8). Oviducal gland, two-chambered. The larger distal chamber, brown colored, with longitudinal striations parallel to the oviduct. On average, 3 (range 2 to 6) eggs inside the oviducal gland and one or two eggs inside the distal oviduct. In fresh specimens, eggs from proximal oviduct, oviducal gland and distal oviduct, pinkish in colour. Walls of distal oviduct muscular, opaque, with terminal part slightly pigmented. For ma-

Table 2. Counts and indices for holotype and paratypes of *Opisthoteuthis calypso* sp. nov. Measurements in mm.

Location	Barcelona	Paris	Washington	Edinburgh	Miami	Barcelona	Washington	Barcelona	Edinburgh	Miami
Specimen	ICM	MNHN	USNM	NMSZ	UMML	ICM	USNM	ICM	NMSZ	UMML
catalogue number	199/2000	3782	893733	1999158.074	31.3137	530/1991	893734	200/2000	1999158.075	31.3138
	HOLOTYPE	PARATYPE	PARATYPE	PARATYPE	PARATYPE	PARATYPE	PARATYPE	PARATYPE	PARATYPE	PARATYPE
Sex	M	M	M	M	M	M	F	F	F	F
ML	38	27	29	35	45	28	26	29	35	39
TL	202	176	148	130	206	117	105	115	105	137
MWI	113.2	138.7	155.2	68.6		82.1	142.3	148.3	80.0	
HWI	161.8	186.1	176.9	134.3	153.3	135.7	173.1	151.7	105.7	125.6
CiI	6.0	11.0	8.0	7.0	13.0	11.0	5.0	7.0	7.0	7.0
FLI	40.7	60.2	65.5	53.2	60.9	42.1	31.1	38.6	59.5	53.1
FWI	52.0	38.4	29.8	40.0	35.7	33.8	57.1	35.3	54.5	53.8
FSI	47.0	48.3	58.4	61.5	55.3	54.7	59.0	57.4	64.8	59.9
EDI	76.3	105.8	98.3	77.1	62.2	60.7	76.9	65.5	51.4	59.0
FuLI	77.1	93.4	76.6	57.1	68.9	50.0	57.7	65.5	62.9	59.0
FFuI	58.0	53.1	66.2	80.0	58.1	64.3	66.7	68.4	86.4	56.5
TOLI	9.2	14.6	6.6	11.4	6.4	8.6				
Gill LC	7	7	7	7	7	7	7	7	7	7
Web Formula	DBCAE	ABCDE	BA=DCE	B=C=DA=E	BCADE	BADEC	DECBA	DB=CA	A=B=CDE	DAB=CE
Egg length							5.8	5.6	6.5	6.6
ALI-I	384.2	470.8	420.7	300.0	357.8	325.0	303.8		214.3	233.3
ALI-II	321.1	478.1	434.5	300.0	351.1	303.6	300.0	303.4	228.6	248.7
ALI-III	334.2	459.9	441.4	300.0	346.7	314.3	326.9	310.3	242.9	251.3
ALI-IV	381.6	427.0	434.5	314.3	344.4	300.0	292.3	293.1	214.3	251.3
AWI-I	33	55	39	51		40				
AWI-II	32	55	28	44		38				
AWI-III	32	60	32	44		39				
AWI-IV	29	49	34	40		40				
SDI Proximal-I	12.9	15.0	15.2	11.1	10.7	14.6	6.5	7.6	5.4	6.2
SDI Proximal-II	11.8	15.0	12.1	10.3	11.8	13.9	6.9	7.6	5.4	6.2
SDI Proximal-III	18.2	25.5	20.7	14.0	15.8	14.3	6.5	7.2	5.4	6.2
SDI Proximal-IV	13.7	15.7	14.8	8.6	12.9	13.2	6.5	6.9	5.4	6.2
SDI Distal-I	19.2	21.9	21.7	16.9	16.2	16.1				
SDI Distal-II	19.7	23.4	20.7	16.6	15.8	15.7				
SDI Distal-III	22.1	25.5	20.7	18.9	18.9	16.4				
SDI-IV Distal	22.4	25.5	20.7	19.4	18.9	18.6				
AASC	54	55	54	50	55	47	51	51	40	50

Table 3. Indices of body proportions and counts of 11 mature, 3 maturing and 6 immature males and 14 mature females of *Opisthoteuthis calypso* sp. nov. For each index or count, min–mean–max. values are indicated and standard deviation are shown between brackets. Measurements in mm.

Sex	M	M	F
Maturity	Mature	Maturing + immature	Mature
ML	27.4–33.4–45.0 (5.0)	14.0–20.5–28.0 (5.1)	19.0–28.8–39.0 (5.5)
TL	130.0–168.2–206.0 (25.3)	50.0–73.5–117.0 (22.3)	105.0–116.3–137.0 (10.8)
MWI	68.6–122.0–155.2 (33.4)	82.1–114.5–150.0 (28.4)	80.0–120.8–148.3 (29.2)
HWI	134.3–162.5–186.1 (20.3)	85.7–123.0–164.7 (30.2)	105.7–132.4–173.1 (25.5)
CiI	4.0–7.4–13.3 (3.1)	4.3–6.7–10.7 (2.1)	4.0–6.2–9.3 (1.3)
FLI	40.7–56.1–65.5 (9.7)	27.8–37.5–47.8 (7.1)	31.1–46.4–59.5 (10.2)
FWI	29.8–38.0–52.0 (7.8)	33.8–46.3–67.5 (10.8)	33.3–49.3–66.7 (12.2)
FSI	47.0–54.1–61.5 (6.3)	44.1–56.1–80.0 (12.3)	50.0–57.5–64.8 (5.1)
EDI	48.6–74.1–105.8 (19.9)	31.4–54.4–85.7 (19.9)	51.4–62.1–76.9 (8.2)
FuLI	50.0–70.5–93.4 (15.5)	33.3–56.2–78.6 (16.6)	38.2–58.4–81.5 (14.2)
FFuI	53.1–63.4–80.0 (9.5)	58.3–71.7–85.7 (11.0)	56.5–68.2–86.4 (9.1)
TOLI	5.6–9.0–14.6 (2.9)	7.9–10.5–14.6 (1.8)	–
Gill LC	7	6–6.7–7 (0.5)	7
Egg length			5.6–6.3–7.0 (0.5)
ALI-I	300.0–367.7–470.8 (56.1)	194.4–258.1–325.0 (48.6)	214.3–297.7–442.1 (78.7)
ALI-II	300.0–374.5–478.1 (68.5)	144.4–229.7–308.1 (49.3)	182.4–292.8–421.1 (76.0)
ALI-III	291.2–358.0–459.9 (61.8)	166.7–245.4–314.3 (47.9)	197.1–301.8–410.5 (71.4)
ALI-IV	288.2–355.2–434.5 (54.0)	166.7–229.1–300.0 (44.5)	194.1–287.3–385.2 (62.7)
AWI-I	32.6–44.8–54.7 (8.0)		
AWI-II	27.6–42.0–54.7 (10.5)		
AWI-III	31.7–42.9–59.9 (10.6)		
AWI-IV	28.9–39.8–48.5 (7.7)		
SDI Proximal-I	10.7–13.7–16.3 (1.9)	6.1–11.3–14.7 (2.8)	5.4–7.5–10.0 (1.6)
SDI Proximal-II	9.7–12.7–15.0 (1.7)	7.1–11.2–14.5 (2.5)	5.2–6.9–10.0 (1.4)
SDI Proximal-III	14.0–19.9–25.5 (3.3)	8.2–11.7–14.3 (2.0)	5.2–7.0–11.2 (1.7)
SDI Proximal-IV	8.6–14.1–19.0 (2.7)	8.9–11.8–14.5 (2.0)	4.5–7.2–11.2 (2.2)
SDI Distal-I	15.6–18.8–23.5 (2.5)	6.7–10.6–16.1 (3.1)	–
SDI Distal-II	15.8–20.8–23.4 (2.7)	5.6–9.5–15.7 (3.1)	–
SDI Distal-III	18.9–21.6–25.5 (2.2)	7.1–12.1–16.4 (3.5)	–
SDI Distal-IV	18.9–23.1–27.4 (2.9)	7.2–12.4–18.6 (3.9)	–
Arm sucker count			
A I	49–52.2–55 (2.4)	33–42.0–49 (5.2)	46–49.8–52 (2.5)
A II	52–53.6–55 (1.5)	35–39.8–44 (3.5)	45–49.8–55 (3.6)
A III	48–53.6–61 (5.7)	38–42.8–47 (3.3)	45–49.7–52 (2.4)
A IV	48–53.0–56 (3.7)	37–41.6–47 (3.6)	47–50.8–53 (2.3)
AASC	48–53.2–58.0 (3.3)	34–40.4–46.8 (4.1)	46–50.4–54 (2.5)

ture eggs (found in oviducal gland or distal oviduct), lengths range from 5.1 to 7.5 mm (mean: 6.5 mm), widths from 3.6 to 4.0 mm. Egg shell highly irregular in shape with a rudimentary egg shell stalk (see photograph in Villanueva, 1992a: fig. 3d).

Shell small, broadly U-shaped, with the basal portion slightly concave on the outer surface, caused by slight inrolling, and convex on the inner surface, resulting in a weak U-shaped cross section. Lateral wings tapering to acute points. Skin surface smooth, no papillae observed. In fresh specimens, aboral and oral surfaces equally of reddish-brown color. No pigment-free spots observed on the skin.

Distribution.— Eastern Atlantic and Mediterranean species. From off Ireland 49°38′N, 11°35′W (Chun, 1913), Cantabric Sea (Alcázar and Ortea, 1981; and type material), northwestern Mediterranean Sea (Morales, 1959, 1962; Villanueva, 1992b; Quetglas et al., 2000), off Angola (Adam, 1962), Namibia (Sánchez, 1981; Sánchez and Molí, 1984; Villanueva, 1992a, 1992c; Villanueva and Guerra, 1991; Villanueva and Sánchez, 1993), and possibly to South Africa (Roeleveld et al., 1992; Roeleveld, 1998; specimens not examined).

Biology.—Species collected on muddy bottoms from 365 m (see additional material from SE Atlantic) to 2208 m depth in the Mediterranean (Villanueva, 1992b). In the south-eastern Atlantic *O. calypso* has been collected by trawl at densities of 6 to 23 individuals km^{-2} with no difference in day and night abundance. Stomach content analyses show a diet of small epibenthic and suprabenthic crustaceans (mostly amphipods and mysids) and polychaetes. No feeding rhythm has been detected (Villanueva and Guerra, 1991). Predators unknown. Mature individuals of both sexes are collected in all seasons of the year and all males from 95 to 5400 g and females from190 to1650 g TW are mature, indicating that considerable growth takes place after the onset of sexual maturity. Ovarian oocyte size-frequency analysis reveals continuous egg production over the entire adult life span (Villanueva, 1992a). The small number of eggs in the oviducts and oviducal gland indicates that eggs are probably released one or two at a time. Mineral composition of egg shell indicates that sulphur (32%) was the major element present (Villanueva, 1992a). Embryonic development and juvenile life unknown.

Etymology.—Calypso, from the Greek mythology, the marine nymph daughter of the Titan Atlas.

Opisthoteuthis grimaldii (Joubin, 1903)
Figs. 11–13, 21, 22; Tables 5–7

Cirroteuthis grimaldii Joubin, 1903: 100 (off Açores Islands); 1912: 1, figs.1-7; 1920: 7, Plates II-IV and Plate XV, fig. 1 (Gulf of Gascogne); - *Grimpoteuthis grimaldii* (Joubin), Robson 1932: 148, fig. 24; - *Opisthoteuthis grimaldi* (Joubin), Voss 1988b: 266; - non *Opisthoteuthis agassizii* Verrill, Boucher-Rodoni and Bonnaud 1996: 80 (off Cape Blanc).

Material Examined.—Type material.- HOLOTYPE, mature male 39 mm ML, Açores Islands, 55 mi NW of Fayal, Princesse Alice Sta. 1334, bottom trawl, 1900 m, 13 Aug 1902, MOM295148.

Other Material.— 1 mature male 50 mm ML, Açores Islands, Discovery Sta. 7422, BN 2.4 Trawl, 2287 m, 23 Oct 1970, British Museum; Freezer-trawler Chicha-Touza: two mature males, 31 (ICM197/2000) and 45 mm ML (ICM196/2000), off Namibia, Benguela IX Cruise, Sta. PP1, bottom trawl, 24°01.4′S, 12°57.4′E, 1142 m, 15 Feb 1986;

2 mature males of 42 (NMSZ1999158.090) and 45 mm ML (ICM198/2000), off Namibia, BENGUELA IX Cruise, Sta. PP2, bottom trawl, 24°05.2′S, 12°59.6′E, 1135 m, 15 Feb 1986; 1 mature male 33 mm ML, off Cape Blanc, Cruise Eumli2, RV ATALANTE, Sta. CPH05, 1795–1855 m, 20°31′N, 18°34′W, 6 Feb 1991, MNHN 2014, specimen reported as *O. agassizii* by Boucher-Rodoni and Bonnaud (1996); 1 mature male 45 mm ML, Rockall Trough, OTSB, 2165–2220 m, 23 Oct 1987, NMSZ1994128.45701.

Material tentatively identified to *Opisthoteuthis grimaldii*: 1 mature female, 54 mm ML, RV GILLISS Cr. 74-04, Sta. 71, 36°38'N, 74°28′W, 45' Otter Trawl, 1695–1734 m, 17 Nov 1974, USNM 1000565.

Historical Resume.—Joubin (1903) described *Cirroteuthis grimaldii* from a specimen captured off Açores Islands, NE Atlantic. Nine years later the same author (Joubin, 1912) redescribed and fully illustrated the unsexed holotype (examination during present study found it to be a mature male). Joubin (1920) reported a second specimen in poor condition captured in the Gulf of Gascogne, NE Atlantic. Both specimens are located at the Museé Océanographique de Monaco (Belloc, 1950) and no more specimens from near the type locality had been recorded (Gonçalves, 1991) until material from the Discovery Collections was examined during present study (see material examined). Following the work of Joubin*, C. grimaldii* was reported by Massy (1916) in the Indian Ocean (Gulf of Bengala, Ceylan and the Andaman and Arabian Seas). No illustrations were made on these specimens that Massy described to have "egg-shaped body, small fins" and we think they should be considered as *Opisthoteuthis* sp. until further examination. Robson (1932: 148) placed the species in the new genus *Grimpoteuthis,* considering *Cirroteuthis caudani* Joubin 1896 to be a conspecific of *G. grimaldii* and doubted Massy's (1916) identifications. Nesis (1987) concurred with Robson (1932) indicating *G. caudani* as a conspecific of *G. grimaldii*. Unfortunately, the *G. caudani* specimen could not be found and is presumed lost (P. Richoux, Museé de Zoologie de Lyon, pers. comm., 1997). Bruun (1945) reported *G. grimaldii* from off Iceland, and we regard these specimens as *Opisthoteuthis* sp. until reexamination of the specimens can be accomplished. Voss (1982) indicated the need for a redescription of *G. grimaldii*, subsequently considering *G. caudani* as *nomen dubium* (Voss, 1988a) and changing *G. grimaldii* to *Opisthoteuthis grimaldii*, new combination (Voss, 1988b). The two specimens of *Grimpoteuthis grimaldii* reported by Vecchione (1987) from north of the Bahamas, represent the only published report of the species in the Western Atlantic. These specimens were unfortunately not available for our study, and are here considered as *O. ?grimaldii*.

Diagnosis.—Medium to large-sized species. No increased robustness of arms I in mature males. From the ventro-lateral margins of all of the arms, a single muscular nodule extends into the web to its outer edge and typically occurs at the level of sucker 25 to 30, and 1–4 suckers prior to the largest enlarged distal sucker. Arm sucker count in adults 73 to 80. Distal sucker enlargement in mature males less than proximal. Distal enlarged sucker field typically comprises 9–10 suckers beginning at about sucker 22–31 and ending at sucker 31–39, with suckers 29–31 usually largest. Sucker enlargement in distal field approximately equal on all arms. First cirrus usually occurs between suckers 2 and 3. Digestive gland bilobed. Basal portion of shell with essentially flat outer surface, and convex inner surface. Pigment-free spots not known to occur on skin.

The following description is based on 8 mature male specimens. No females have been unquestionably identified to this species.

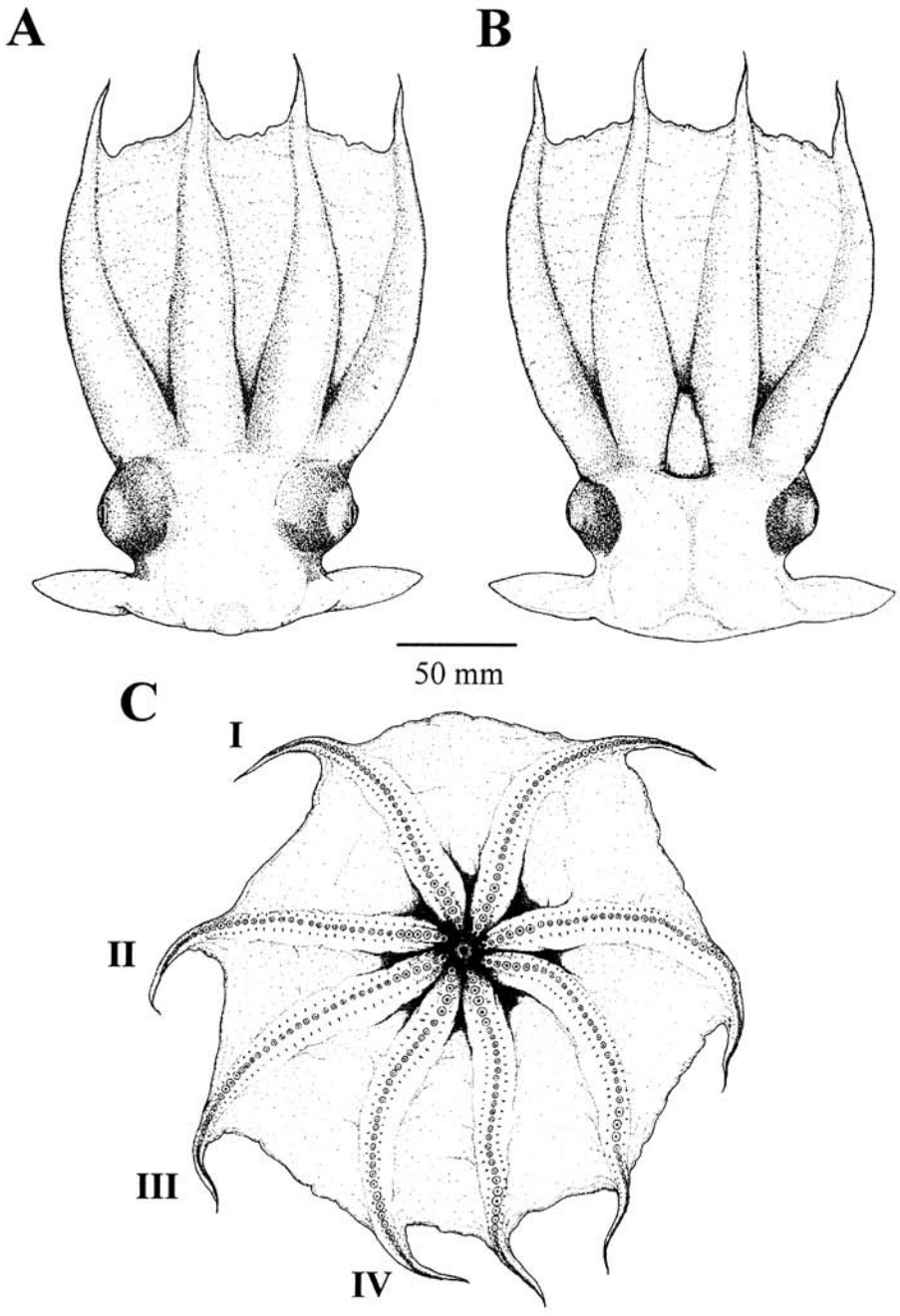

Figure 11. *Opisthoteuthis grimaldii*. Dorsal (A), ventral (B) and oral views of a mature male 45 mm (NMSZ1994128.45701).

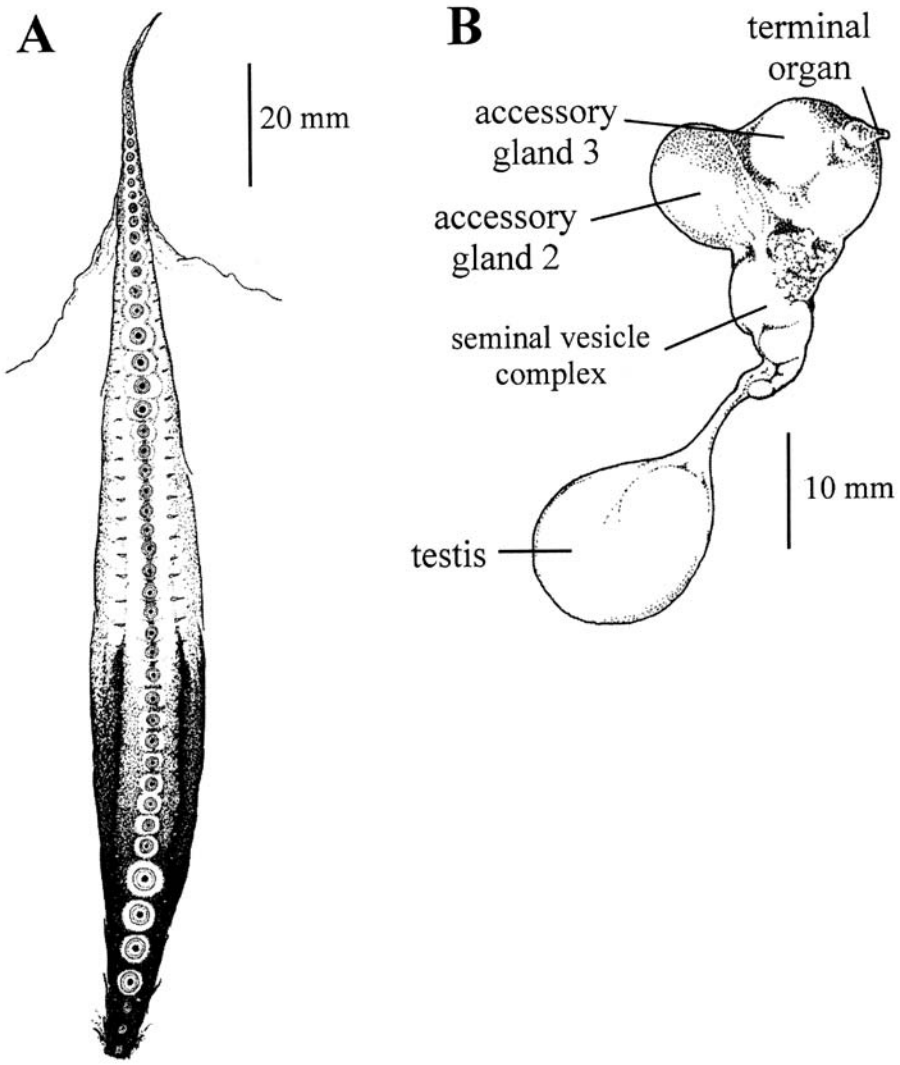

Figure 12. *Opisthoteuthis grimaldii*. A. Sucker arrangement on first arm of a mature male 45 mm ML (NMSZ1994128.45701). B. Reproductive tract of a mature male of 42 mm ML (NMSZ1999158.090).

Description.—Medium to large-sized species, known maximum ML 50 mm. Body semi-gelatinous, ovoid in form in fresh specimens, with the eyes and fins superior. Mantle moderately short, about 18–29% TL, and broadly rounded posteriorly. Head slightly wider than mantle, with no discernable constriction between head and mantle. Pallial aperture small, closely surrounding funnel. Funnel small, conical, free for about 2/3 of its length. Funnel organ with limbs separated, inverted \ / -shaped; difficult to discern. Olfactory organs rounded and prominent, located just within mantle aperture and to either side of funnel. Two small fins postero-laterally positioned, averaging 66% ML, and moderately wide, averaging 45% of fin length. Fin span about four times the fin length. Posterior

margin of the fin nearly straight, only slightly curved near the posterior fin insertion. Fin tip rounded and anterior fin margin slightly convex, without lobe near the anterior insertion. Each fin supported by an internal, flexible cartilage that extends from shell sac to which it closely adhers to approximately mid length of fin. Fin cartilage thick basally, becoming progressively thinner and lanceolate as it extends distally. Eyes large, bulbous, averaging 77% ML, occupy entire sides of head. Optic lobes large, kidney-shaped, with 2–3 large bundles of optic nerves running to each eye. White body, closely associated with optic lobe, large, dark brown to purple.

Arms enveloped in web except for short distal ends, moderately long, averaging 366–380% ML, and subequal in length, with no consistent arm formula. Arms moderately stout, with no increased robustness of arms I in mature males. From the ventro-lateral margins of all of the arms, a single muscular nodule extends into the web to its outer edge and typically occurs at the level of sucker 25 to 30, and 1–4 suckers prior to the largest enlarged distal sucker. Web deep, thick, occupying on average 57% of arm length. Web formula not consistent, but sector E tends to be shallowest. Single row of suckers deeply set in the semi-gelatinous tissue of all arms. Arm sucker count ranges from 73 to 80. Mature males with two fields of markedly enlarged, bulbous suckers on all arms. Proximally, suckers 4–11 typically enlarged, with suckers 6 or 7 usually the largest. Sucker enlargement in proximal field approximately equal on all arms. Distal enlargement field typically comprises 9–10 suckers beginning at about sucker 22–31 ending at 31–39, with suckers 29–31 usually largest. Sucker enlargement in distal field approximately equal on all arms. Distal enlargement less than proximal. Cirri short, first appear between suckers 2 and 3 on 40% of arms, between 3 and 4 on 32% and between 4 and 5 sucker in 27% of arms. Longest cirri on midportion of arms, length 2.5–4.7 mm or 5–10% ML.

Gills small, compact and spherical, with 8 lamellae in five specimens, 7 in two, and mixed 8/7 in one specimen. Branchial heart rounded, approximately half the size of the gill. Entire outer surface of digestive system deeply pigmented. Buccal mass moderate in size. Rostrum of lower beak pointed, with a small hood. No folds or ridges on lateral wall. Radula absent. Anterior and posterior salivary glands absent, but a glandular-like area in the posterior region of buccal mass present. Posterior section of long esophagus slightly dilated into crop-like structure that empties into a round or oval stomach. Digestive gland large, brown-grey colored, with lighter-colored digestive duct appendages on ventral surface and enclosed within surrounding membrane. Digestive gland bilobed. Intestine, which appears to be slightly shorter than esophagus, describes an S-shape and ends in anus without anal flaps. Ink sac absent.

Male genitalia white in color, composed of a large, oval testis located in median portion of mantle cavity and dorsal in position; short vas deferens; large, convoluted seminal vesicle complex; large, rounded accessory glands, with accessory glands 2 and 3 approximately equal in size. Relatively long, unpigmented terminal organ projects from the center of gland 3. Spermatophores oval, with length range of 1–2 mm. Female genitalia not known.

Shell stout, broadly U-shaped, with short, flaring lateral wings. Basal portion of shell with no inrolling of the edges, so outer surface is essentially flat, with inner surface convex. In cross section, basal portion is circular. Lateral wings tapering to acute points. Skin surface smooth, reddish-brown in preserved specimens. Pigment-free spots on the skin not observed.

Type Locality.—Açores Islands, 55 mi NW of Fayal, 1900 m.

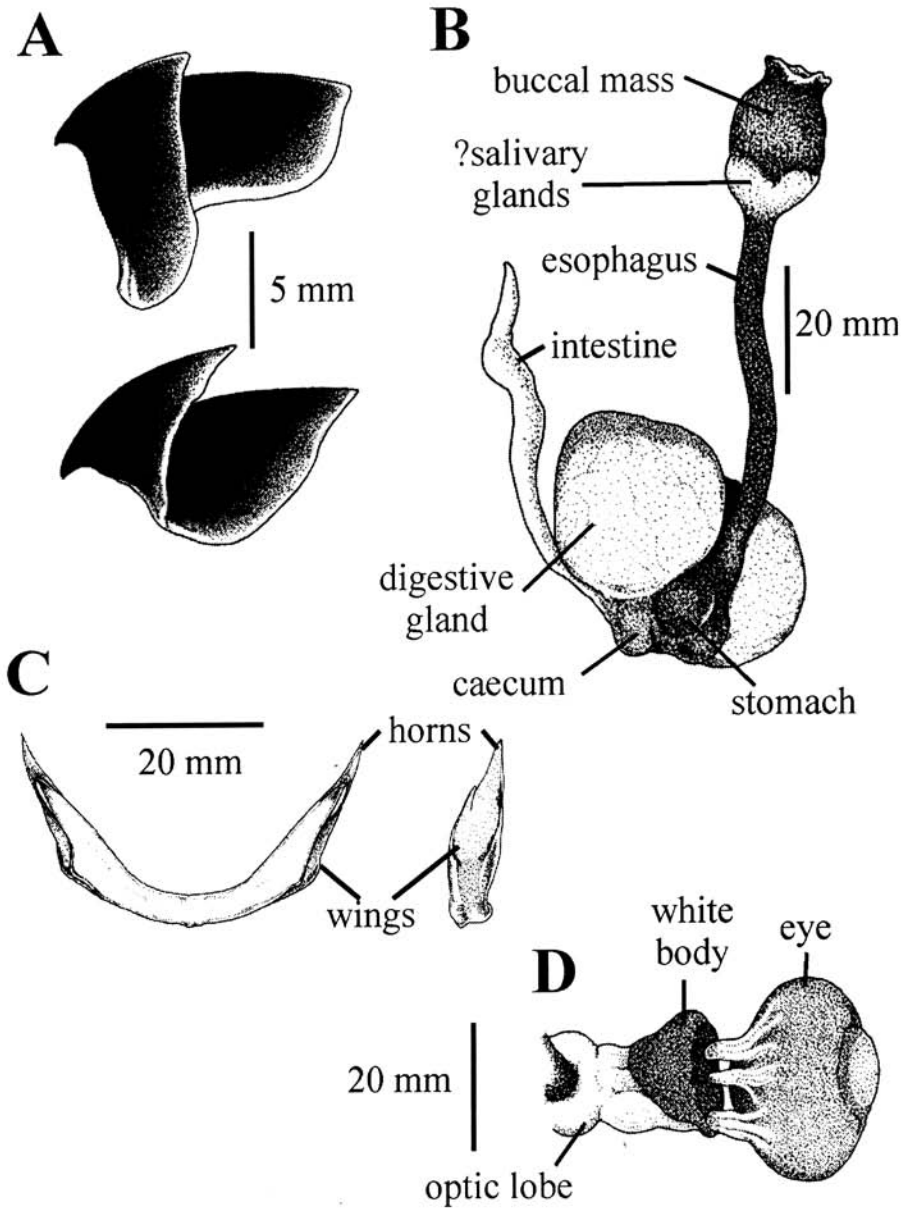

Figure 13. *Opisthoteuthis grimaldii*. Internal anatomy. A. Lower (above) and upper beaks of a mature male 42 mm ML (NMSZ1999158.090). B. Digestive system (NMSZ1999158.090). C. Dorsal and lateral views of the shell of a mature male 45 mm ML (NMSZ1994128.45701). D. Ventral view of the optic complex (NMSZ1999158.090).

Distribution.—Known for certain only from the eastern Atlantic: Rockall Trough, Açores Islands and off Cape Blanc in the North Atlantic; and off Namibia in the South Atlantic. A mature female taken northwest of Bermuda that is tentatively identified to the species (see Material Examined and distribution map of Fig. 20) indicates the possible presence of the species in the northwestern Atlantic. The species appears to be the deepest occurring *Opisthoteuthis* in the Atlantic, collected from 1135 to 2287 m depth.

Biology.—Not known

Opisthoteuthis hardyi new species
Figs. 14–16, 21, 22; Tables 5–7

Material Examined.—The species is known only from the HOLOTYPE, a mature male 45 mm ML, frozen before fixation, FV ARGOS GALICIA Sta. 97-25, near South Georgia (53°18'S, 42°12' W), pelagic trawl fished close to the sea-floor at 800–1000 m, 11 Sep 1997, NMSZ1999158.088.

Diagnosis.—Medium-sized species. Mature male with slight increased thickness of arms I. Single muscular nodule or multiple, muscular supports extending from ventral margins of arms absent. Arm sucker count in adult 60–67. Distal enlarged sucker field in male comprises 9–14 suckers beginning at about sucker 18 or 19, with suckers 22–24 largest. In mature male, sucker enlargement in distal field approximately equal on all arms. Maximum sucker diameter in distal and proximal fields approximately equal. First cirrus usually occurs between suckers 3 and 4. Digestive gland entire. Basal portion of shell with highly concave outer surface, and convex inner surface. Pigment-free spots not known to occur on skin.

Description.—Medium-sized species, known only from type specimen, a mature male with TL of 250 mm and ML of 45 mm. Fresh weight before fixation 1840 g. Body semi-gelatinous, ovoid in form. Eyes and fins superior. Mantle moderately short, 18% TL, and broadly rounded posteriorly. Head slightly wider than mantle, with no discernable constriction between head and mantle. Pallial aperture small, closely surrounding funnel. Funnel flaccid, moderately long, 64% ML and darkly pigmented. Funnel organ not discernible. Olfactory organs rounded and prominent, located just within mantle aperture and to either side of funnel. Fins contracted on preservation and appear short and positioned postero-laterally. Anterior and posterior margins of fins thin, slightly convex; without lobe near the anterior insertion; fin tip rounded. Each fin supported by an internal, flexible cartilage that extends from shell sac to which it closely adheres. Fin cartilage thick basally, becoming progressively thinner and lanceolate as it extends out the fin. Eyes of moderate size, bulbous, 38% ML, occupy entire sides of head. Optic lobes large, kidney-shaped, with 4 large bundles of optic nerves running to each eye. White body, closely associated with lobe, large, dark brown/purple. Optic lobes larger than semi-circular brain.

Arms long, 440–480% ML, and subequal in length, with arm formulae IV>I>II=III. Arms moderately stout, with slight increased thickness in arms I. Single muscular nodule or multiple, muscular supports extending into web from ventral margins of arms absent. Arms enveloped in web, occupying approximately 2/3 of arm length. Web extends further on the dorsal arms, formula A=B>C=D>E. Single row of suckers deeply set in semi-gelatinous tissue of all arms. Sucker count 60–67. Mature male with two fields of markedly enlarged, bulbous suckers on all arms. Proximally, suckers 4–9 typically enlarged, with suckers 6 or 7 the largest. Sucker enlargement in proximal field approximately equal on all arms. Distal enlargement field comprises 9 to 14 suckers beginning at about sucker 18 or 19, with suckers 22–24 the largest. Sucker enlargement in distal field, approximately equal on all arms. Sucker diameter approximately equal in proximal and distal fields. Cirri short, first appear between suckers 3 and 4 on most arms (between 2 and 3 only on Arm I right). Longest cirri on mid portion of arms, length 1.7–4.1 mm or 4–9% ML.

Gills, small, compact, spherical, with 7 lamellae. Median pallial adductor muscle thin and narrow. Branchial heart rounded, approximately half the size of the gill. Esophagus,

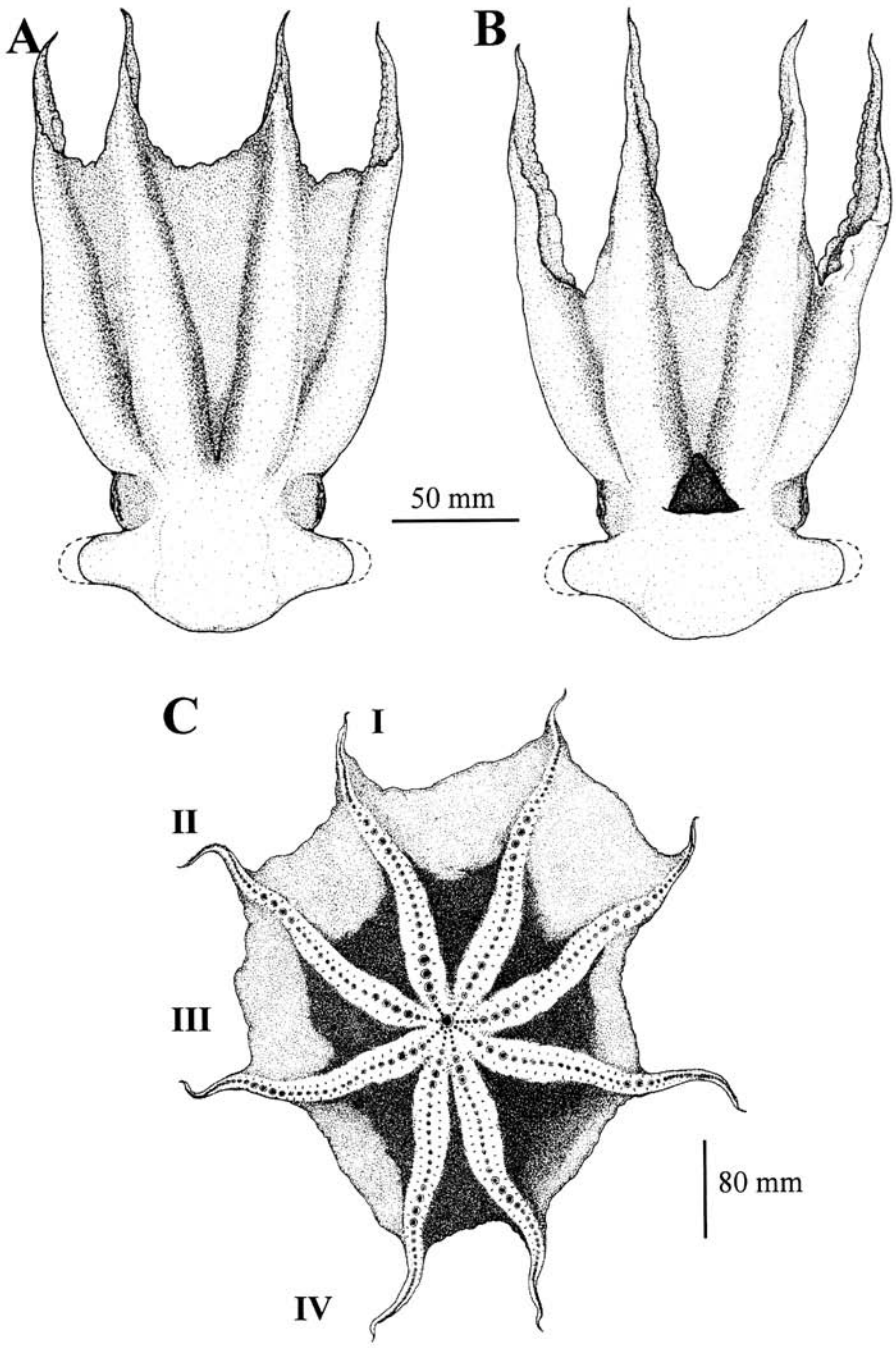

Figure 14. *Opisthoteuthis hardyi* new species. Dorsal (A), ventral (B) and oral views of the Holotype, mature male 45 mm ML (NMSZ1999158.088). Fins contracted on preservation, dotted lines indicate expected profile.

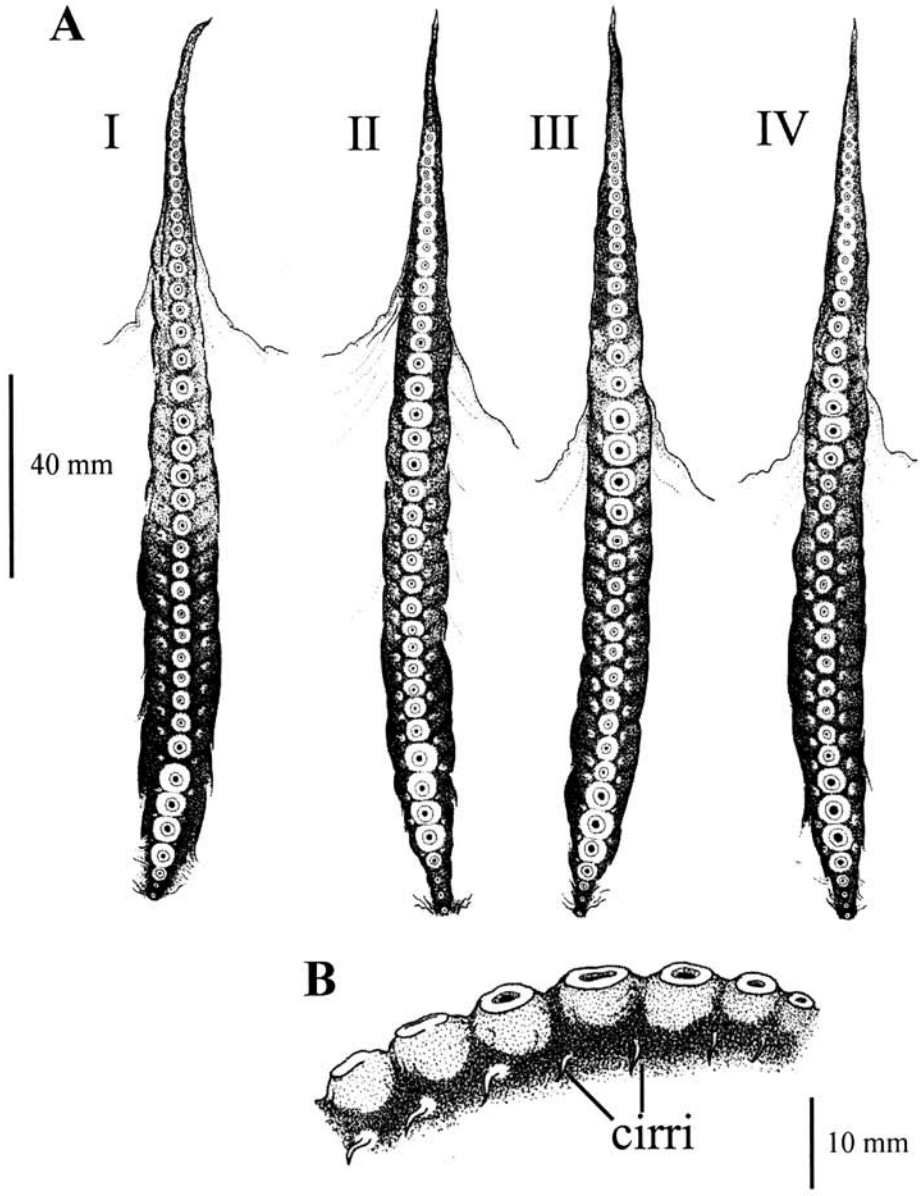

Figure 15. *Opisthoteuthis hardyi* new species. A. Sucker arrangement on the arms of the Holotype (NMSZ1999158.088). B Arrangement of suckers and cirri.

stomach and intestine deeply pigmented dark purple. Two digestive ducts unite before emptying into caecum. Intestine wide and approximately same length of esophogus. Anal flaps and ink sac absent. Digestive gland entire. Full digestive system in unique specimen not dissected. Male genitalia composed of large, oval testis located in median portion of mantle cavity and dorsal in position; short vas deferens; large, convoluted seminal vesicle complex; three accessory glands, with gland 2 the largest; and with a short terminal organ

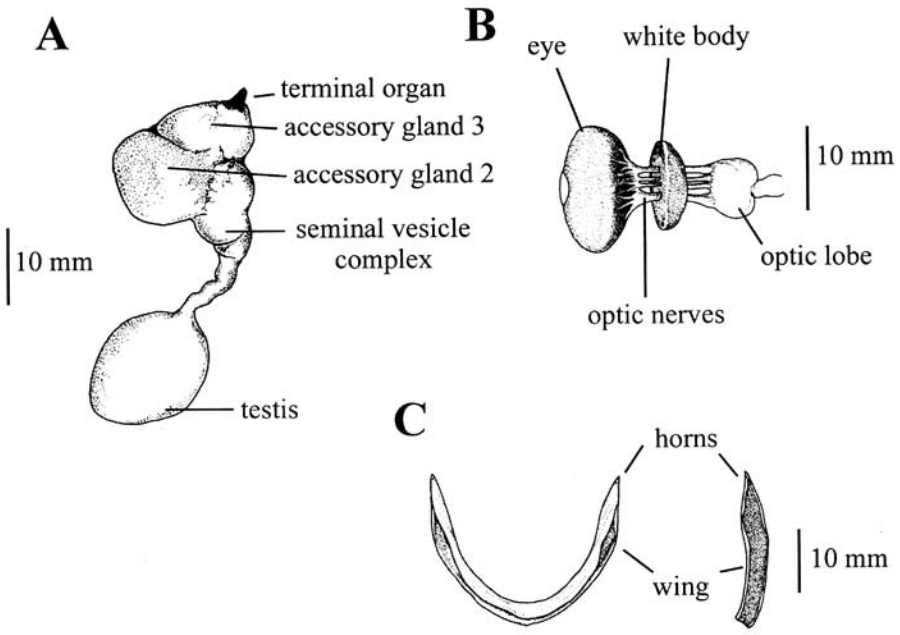

Figure 16. *Opisthoteuthis hardyi* new species. Internal anatomy of the Holotype (NMSZ1999158.088). A. Male reproductive tract. B. Ventral view of the optic complex. C. Dorsal and lateral views of the shell.

(penis) projecting from accessory gland 3. Spermatophores disc-shaped, with length range of 0.7–1.4 mm. Female genitalia not known.

Shell U-shaped, with short, flaring lateral wings. Basal portion with edges highly inrolled, making outer surface highly concave; inner surface convex; cross section U-shaped. Lateral wings with inrolled margins, tapering to acute points. However the extreme inrolling of the shell may be a consequence of freezing. Skin surface smooth, orange-brown in fresh specimens, becoming reddish-brown with preservation. Oral surface of the web deeply pigmented centrally, contrasting sharply with the less pigmented arms. Pigment-free spots on skin not apparent in only specimen.

Distribution.—Known only from the type locality, Shag Rocks, NW of South Georgia, South Atlantic (53°18′ S, 42°12′ W), 800–1000 m.

Biology.—Not known.

Etymology.—Named for Sir Alister Hardy, who worked extensively on the marine fauna of South Georgia and collected and drew the first cirrate (*Cirroctopus glacialis*) described in the area. He was briefly a Professor of Zoology at Aberdeen University.

Opisthoteuthis massyae (Grimpe, 1920)
Figs. 17–22; Tables 4–7

Cirroteuthis umbellata Massy 1909: 4 (off Ireland, 50°31′N, 11°31′W); - *Cirroteuthopsis massyae* Grimpe 1920: 233; - Robson 1932: 160; - *Opisthoteuthis* sp. Sánchez 1988: 255, fig.30; Daly et al. 1998: 187; - *Opisthoteuthis vossi* Sánchez and Guerra 1989: 1159, figs: 1 and 2 (2229′S, 0607′E, Valdivia Bank); - Villanueva and Guerra 1991: 288, figs. 3,5, 7d, 9c–d (off Namibia); -

Villanueva 1992a: 265, figs 3b–c, 4, 7b, 9, 10 (off Namibia); - Villanueva and Sánchez 1993: 18 (records off Namibian waters are from 23°30′ to 27°41′S); - non *Opisthoteuthis agassizi* Verrill, Clarke and Lu 1995: 194 (off Madeira Islands); - non *Opisthoteuthis grimaldii* (Joubin), Boyle et al. 1998: 1023; Boyle and Daly 2000: 317, figs. 1–10 (Hebrides Slope and off Scotland); Villanueva 2000: 555, fig. 1 (off Namibia, 23°39′N, 12°58′S)

Material examined.—Type material.—HOLOTYPE, mature male 66 mm ML, off Ireland, 50°31′N, 11°31′W, 1226–1450 m, 1 Aug 1908, bottom trawl, in good condition, NMI 459.1909.

Other material.—NORTHEASTERN ATLANTIC. West of Ireland: 1 mature male 65 mm ML (NMSZ1999158.084) and 1 maturing female (NMSZ1999158.083), trawl, 1053 m, 7 April 2000. West of Scotland: 1 mature male 65 mm ML and 1 mature female 76 mm ML (ICM190/2000), commercial trawl FV Bisson, depth unknown, 24 Jun 1995; 2 mature males 55 (NMSZ1999158.064) and 65 mm ML (NMSZ1999158.066) and 1 maturing female 46 mm ML (NMSZ1999158.070), commercial trawl, depth unknown, 12 Apr 1996; 1 maturing male 45 mm ML, commercial trawl, 900 m, 11 Jun 1997, NMSZ1999158.063. Rockall Trough: 1 mature male 68 mm ML, commercial trawl, depth unknown, 11 Feb 1997, NMSZ1999158.071; 1 maturing male 50 mm ML, commercial trawl, depth unknown, 25 May 1998, NMSZ1999158.067; 1 mature female 61 mm ML, OTSB, 1101–1118 m depth, 1 Jun 1999, NMSZ1999158.062; 1 mature male 75 mm ML (NMSZ1999158.072) and 1 maturing female 40 mm ML (NMSZ1999158.061), 1068–1080 m depth, OTSB, 6 Apr 1999; 1 mature female 62 mm ML, OTSB, 1025–1042 m, 6 Apr 1999, NMSZ1999158.060; 1 mature female 53 mm ML, OTSB, 877 m, 7 Apr 2000, NMSZ1999158.083.

AÇORES ISLANDS.1 maturing male 40 mm ML, Discovery Sta. 7857#5, 1356-1341 m, trawl BN 2.4, 12 Apr 1972.

MADEIRA ISLANDS: 1 mature male 48 mm ML, Discovery Sta. 8977, OTSB14 bottom trawl, 1032–924 m, 6 Aug 1976, specimen reported as *O. agassizii* by Clarke and Lu (1995).

SOUTHEASTERN ATLANTIC, off Namibia.- Freezer-trawler Chicha-Touza: 2 mature males 55 (ICM192/2000) and 59 mm ML (ICM191/2000), 1 maturing male 56 mm ML (UMML31.3119), 1 maturing female 50 mm ML (UMML31.3117), Valdivia Cruise, Sta. 10, 22°29′S, 06°07′E, 900 m, otter trawl, 21 May 1982, specimens reported as paratypes of *Opisthoteuthis vossi* Sánchez and Guerra 1989; 1 maturing male 52 mm ML (NMSZ1999158.068) and 1 maturing female 37 mm ML, Benguela XII Cruise, Sta. PP2, 23°34′S, 12°55′E, 952 m, bottom trawl, 1 Feb 1988, NMSZ1999158.073; 1 mature male 36 mm ML, Benguela XII Cruise, Sta. PP3, 23°32′S, 12°55′E, 869 m, bottom trawl, 1 Feb 1988, ICM193/2000); 1 immature female 32 mm ML, Benguela XVI Cruise, Sta. 105, 23°47′S, 13°07′E, 831 m, bottom trawl, 2 Mar 1990, ICM194/2000.

Historical Resume.—From collections made by the vessel Helga from west of Ireland, Massy (1909) described a specimen, caught at 670-690 fa (50°31′N, 11°31′W) which was tentatively assigned to *Cirroteuthis umbellata* Fischer, 1883. Later Grimpe (1920), based on Massy's description of the cirri disposition and apparently without examining the specimen, placed it in its own sub-genus, *Cirroteuthopsis*, with the specific name *massyae*. Nesis (1987) considered the species as *"C." massyae*, and Voss (1988) placed *C. massyae* as uncertain status. Following a thorough examination of type material in the present study, *massyae* is shown to be a valid species belonging to the genus *Opisthoteuthis*.

Sánchez and Guerra (1989) described *Opisthoteuthis vossi* from Namibian waters, SE Atlantic and examination during present study of the type material confirms that *O. vossi* is in fact a junior synonym of *O. massyae*. Records of *O. vossi*, mostly including biological studies based on a large collection of material, all from the SE Atlantic, are attributed now to *O. massyae*: Villanueva and Guerra (1991), Villanueva (1992a,c), Villanueva and Sánchez (1993). Reports of *O. vossi* off South Africa by Roeleveld et al. (1992) and Roeleveld (1998) probably belong also to *O. massyae* (specimens not examined). Also, specimens recently reported as *O. grimaldii* from the Hebrides Slope and off Scotland (Boyle et al., 1998; Daly et al., 1998; Boyle and Daly, 2000) and off Namibia (Villanueva 2000) have been re-examined during the present study and are re-identified as *O. massyae*. Yau (1994) assigned a small juvenile cirrate from the Rockall Trough to *Cirroteuthis massyae*, but on re-examination this specimen is probably a juvenile *Cirrothauma murrayi* Chun.

Diagnosis.—Medium to large-sized species. Marked increased thickness of arms I in mature male. A series of muscular, web supports, of which proximal support is stout and more distal ones weak, extend from the ventral margins of all arms to web margin beginning at level of greatest depth of web, typically at sucker 35–37, the level of first distal enlarged sucker in males. Arm sucker count in adults 82–106. In mature males, maximum proximal enlarged sucker diameter exceeds that of distal enlarged suckers. Distal sucker enlargement absent on arms I, slight on arms II, greatest on arms III and IV. Distal enlarged sucker field composed of 9 to11 contiguous suckers, beginning at about sucker 34–40, with suckers 40 or 41 usually largest. First cirri typically occur between suckers 3 and 4 or 4 and 5. Basal portion of shell with concave outer surface, and convex inner surface. Digestive gland bilobed. Pigment-free spots not observed.

Description.—The following description is based on 16 males (11 mature), and 3 mature, 5 maturing and 1 immature females. Additionally, morphometric data from Sánchez and Guerra (1989), Villanueva and Guerra (1991), Villanueva (1992a), Boyle et al. (1998), Daly et al. (1998) and Boyle and Daly (2000) have been added to the text when necessary.

Medium to large-sized species. Males grow larger and heavier than females: TW reaches 5750 g in males and 2959 g in females (Boyle et al.,1998). The relationship between TW and TL is the same in both sexes: $TW = 19 \times 10^{-5} \times TL^{2.7}$ ($r = 0.93$, $n = 117$) (Villanueva and Guerra, 1991). The body is semi-gelatinous in consistency and ovoid in form in fresh specimens. Mantle short, depressed and globose, rounded posteriorly and slightly longer than wide. Head is wider than the mantle, with no discernible constriction between regions. Pallial aperture small, closely surrounding the funnel. Funnel relatively long, conical, and narrow, free for about 1/2 of its length. Funnel organ with limbs separated, inverted \ / -shaped and discerned with difficulty. Olfactory organ unpigmented, rounded and prominent, located on each side of the funnel and just within the mantle aperture. From the olfactory organ a duct connects with the stellate ganglion, which is fusiform or ovoid in shape, embedded in the mantle musculature, with several large nerves and additional thin nerves on each side. Fins small in relation to the entire animal, averaging 72 % of ML in length, and moderately wide, averaging 52% of the fin length; laterally positioned on each side near the posterior end of the mantle. Anterior and posterior margins of the fin thin, slightly convex; the anterior border curved, without lobe near the anterior insertion. Each fin supported by an internal, flexible cartilage that extends from shell sac, to which it closely adheres, to approximately the middle length of the fin. Fin cartilage thick basally, becoming progressively thinner and lanceolate as it extends distally. Eyes

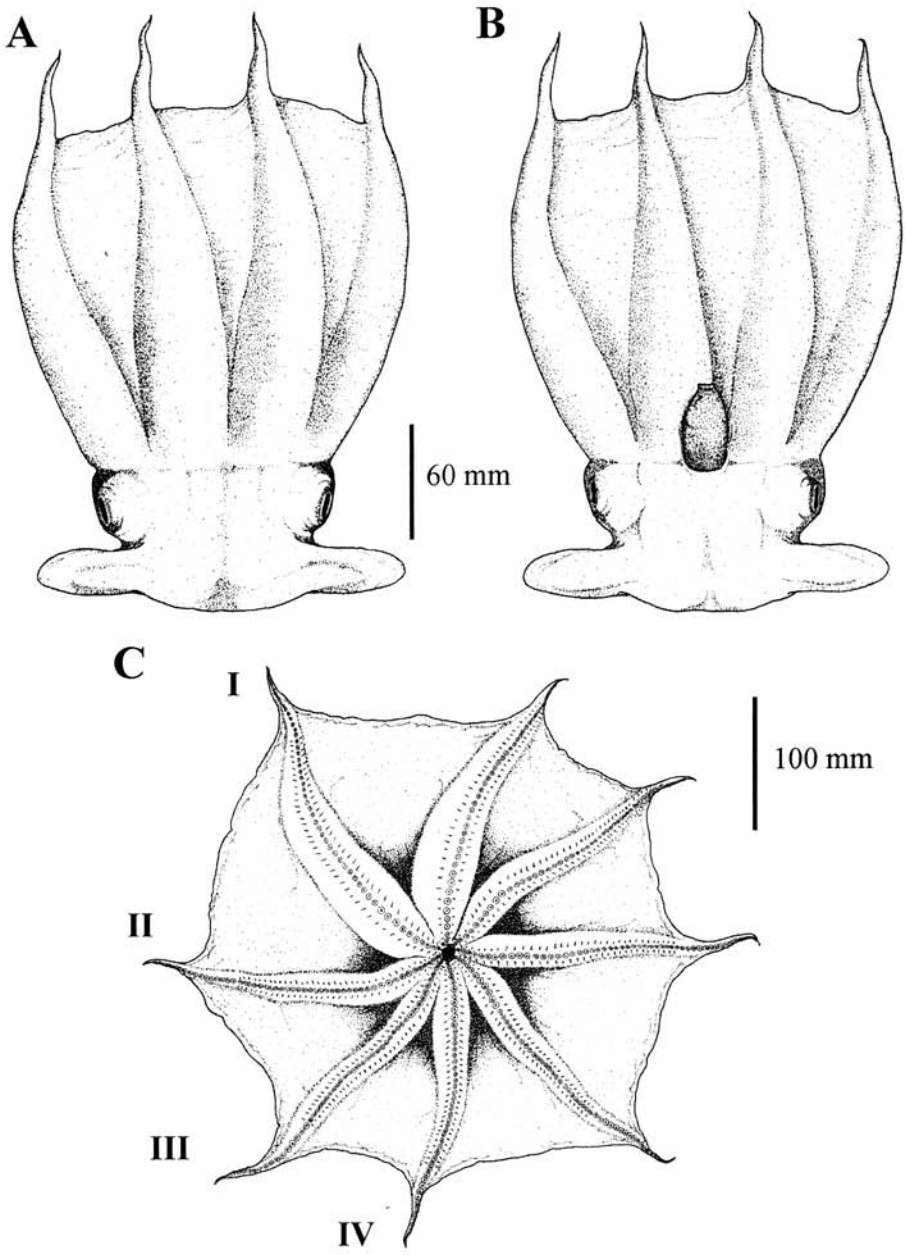

Figure 17. *Opisthoteuthis massyae.* Dorsal (A), ventral (B) and oral views of a mature male 75 mm ML (NMSZ1999158.072).

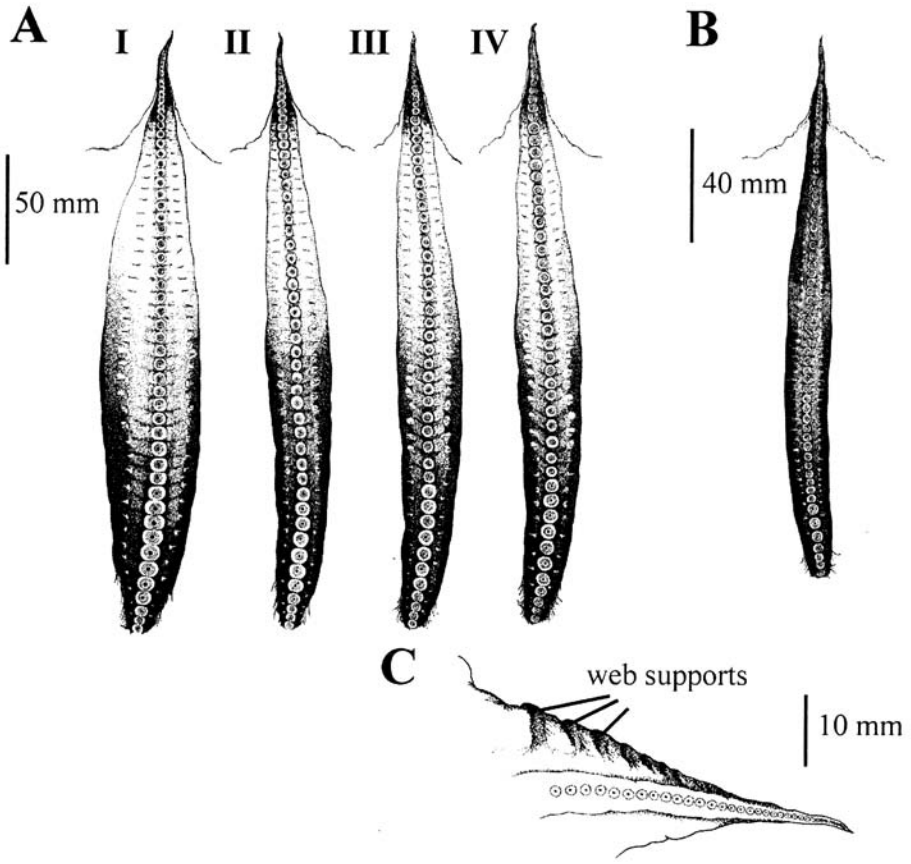

Figure 18. *Opisthoteuthis massyae.* Sucker arrangement. A. Location of enlarged suckers on the left arms of a mature male 75 mm ML (NMSZ1999158.072). B. First arm of a mature female 62 mm ML (NMSZ1999158.060). C. Location of the web supports at the tip of the 3rd arm.

large, somewhat protruding and ovoid; eye diameter about half the head width. The optic lobe is large, flattened and kidney-shaped. In two males examined, four large, thick nerve bundles pass through the white body, which is chocolate-colored, to the eyeball. In one female specimen only two large nerves were observed in the optic lobes of both eyes (Sánchez and Guerra 1989: fig. 2g).

Arms moderately long and subequal in length. In maturing and mature males, arms I become increasingly thick, more muscular and robust (AWI = 55.0 on average). In females, arms I are not modified as in males and are equal with the others. In both sexes, a series of muscular, web supports, of which the proximal support is stout and subsequent ones are weak, range in number from 7 to 20 (14 on average), and extend from the ventral margins of all arms to the web margin beginning at level of greatest depth of web, typically at sucker 35–37, the first distal enlarged sucker in males. The web is deep, occupying 1/2 of arm length. Web sectors extend approximately equally, with a tendency for sector E to be shallowest. Each arm bears a single row of suckers, deeply set into the arm, extending from the mouth to the tips of the arms. Average arm sucker count in mature males ranges from 82 to 106 suckers, and in the 3 mature females ranges from 85 to 87.

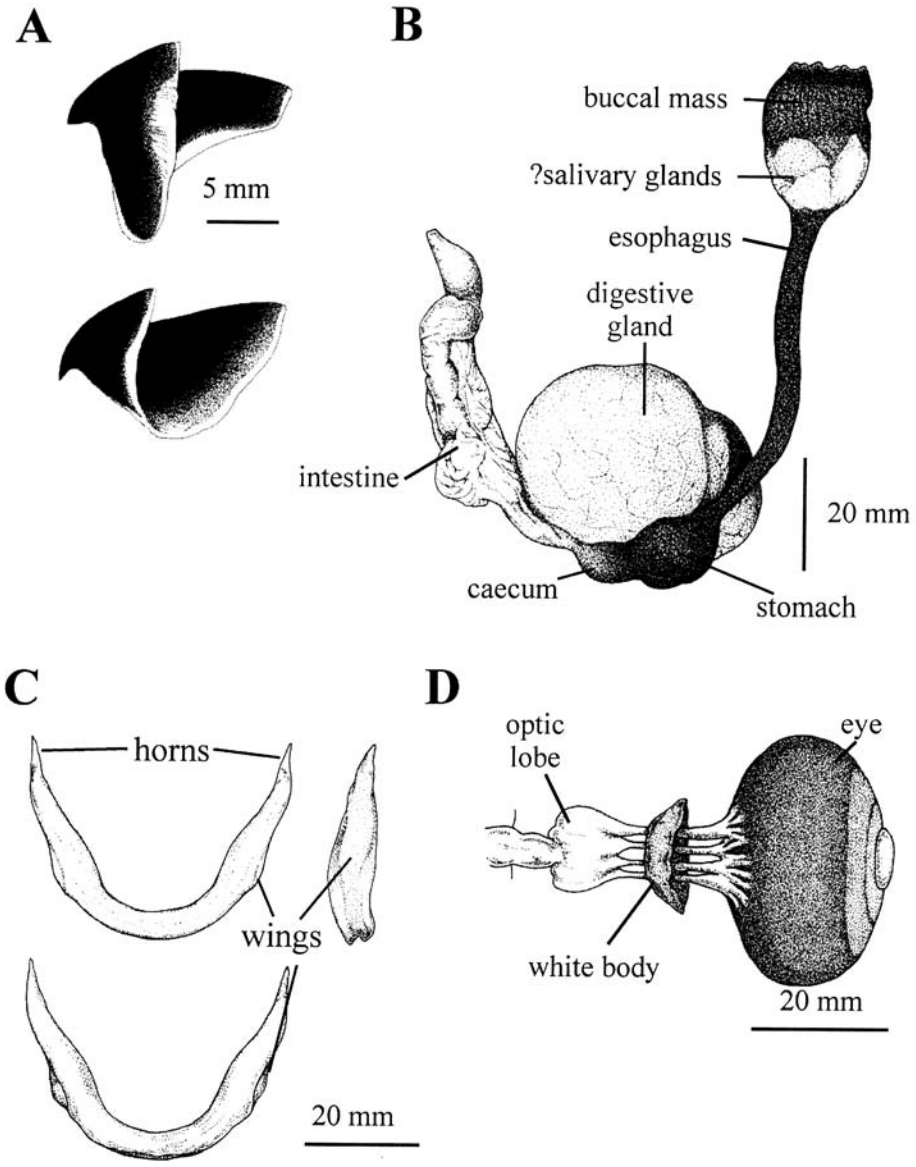

Figure 19. *Opisthoteuthis massyae.* Internal anatomy. A. Lower (above) and upper beaks of a mature male 75 mm ML (NMSZ1999158.072). B. Digestive system of a mature male 65 mm ML (NMSZ1999158.084). C. Dorsal (upper), ventral (lower) and lateral views of the shell (NMSZ1999158.084). D. Ventral view of the optic complex (NMSZ1999158.084).

Marked sexual dimorphism exists in sucker enlargement. Males have two fields of enlarged, bulbous-shaped suckers, that are absent in females. The proximal enlarged sucker field is typically composed of 7–8 contiguous suckers located from the 3–6th to the 8–12th suckers, with maximum sucker diameter usually at the level of the 7th sucker. Sucker enlargement in proximal field approximately equal on all arms. In mature males, maximum diameter of proximal enlarged sucker of the four arms exceeds that of the distal

enlarged suckers. Distal sucker enlargement absent on arms I, moderate on arms II, and maximum on arms III and IV. The distal enlarged sucker field is composed of 9–11 contiguous suckers, beginning at about sucker 34–40, with maximum sucker diameter, on average at the level of the 40–41st sucker. Females show the typical gradual increase and decrease in sucker size as observed in octopods, without markedly enlarged suckers. Cirri short, arranged in a single row on each side of the sucker row, alternating with the suckers. First cirri usually appear between suckers 3 and 4 or 4 and 5 (42% and 44%, respectively). The longest cirri are found in the middle of the arms; length 2.0–6.4 mm in all specimens, or 7.8% ML in mature males.

Gills compact, spherical, with 7 lamellae in 68% of specimens, 6 in 23%, 8 in 9%, and mixed 7/6 in one specimen. Median pallial adductor muscle thin and narrow. Branchial heart rounded, approximately half the size of the gill. Buccal mass, esophagus, stomach and intestine deeply pigmented dark purple. The buccal mass is relatively small. Relationships between the upper crest (UC) and lower crest (LC) of the beaks and the weight of the specimens (TW) are: $\log UC = 0.43 + 0.24 \times \log TW$ ($r = 0.87$, $n = 115$) and $\log LC = 0.38 + 0.23 \times \log TW$ ($r = 0.86$, $n = 115$) (Villanueva and Guerra, 1991). There is no radula. Anterior salivary glands may be represented by a glandular area on posterior region of buccal mass. Posterior salivary glands absent. No true crop, but in some specimens the esophagus is slightly distended near the oval-shaped, muscular stomach. Digestive gland large, bilobed. Bifurcate digestive ducts unite before emptying into caecum. Intestine wide and approximately same length as esophogus. Anal flaps and ink sac absent.

Male genitalia located in posterior mantle cavity. Testis oval and white in color, connected by vas deferens to seminal vesicle complex. Three accessory glands also rounded and white, with accessory gland 3 larger than the others. Terminal organ cylindrical and lightly pigmented at the end extends from accessory gland 3. Spermatophores small, rudimentary and located inside seminal vesicle and terminal organ. Total number of spermatophores averages 72 (range 2 to 172; 29 males examined; Villanueva, 1992a). Spermatophores fusiform or ovate in shape, 1 to 1.2 mm in length. Spermatophore with spermatophoral pores (200 microns in diameter) at both anterior and posterior ends. No associated opercular structures were observed. The spermatozoa have a conical acrosome with a ring around the basal portion at the anterior end of the cylindrical nucleus, and a flagellum located axially (Villanueva ,1992a).

Female genital complex in mature individuals averages 2.6% of TW of animal (range 1.5–7%) (Daly et al 1998). Ovarian oocytes of different size and development stage clearly visible inside large ovary (see photograph in Boyle and Daly 2000: fig. 5). From 137 to 2097 oocytes found in immature, and 897 to 2763 in mature females (Daly et al., 1998). In the ovary, the oocytes grow on short strings arising from a core of germinal epithelium, and at a final size of 10 mm the chorion is formed and the egg is released from the string and moves singly to the oviduct (Boyle and Daly, 2000). Largest ovarian oocytes displayed an average of 26 folicular folds (range 24 to 28). Long proximal oviduct with thin walls, transparent in fresh specimens, with 4–7 eggs inside (Villanueva, 1992a). Large oviducal gland, acorn-shaped and composed of two chambers. Proximal chamber smaller and lighter in color and distal chamber large and dark, with longitudinal striations parallel to the oviduct. One or two eggs found inside oviducal gland, and only one egg in distal oviduct. Distal oviduct short to medium in length, with muscular walls opaque and terminal portion slightly pigmented. Mature eggs (found in oviducal gland or distal oviduct)

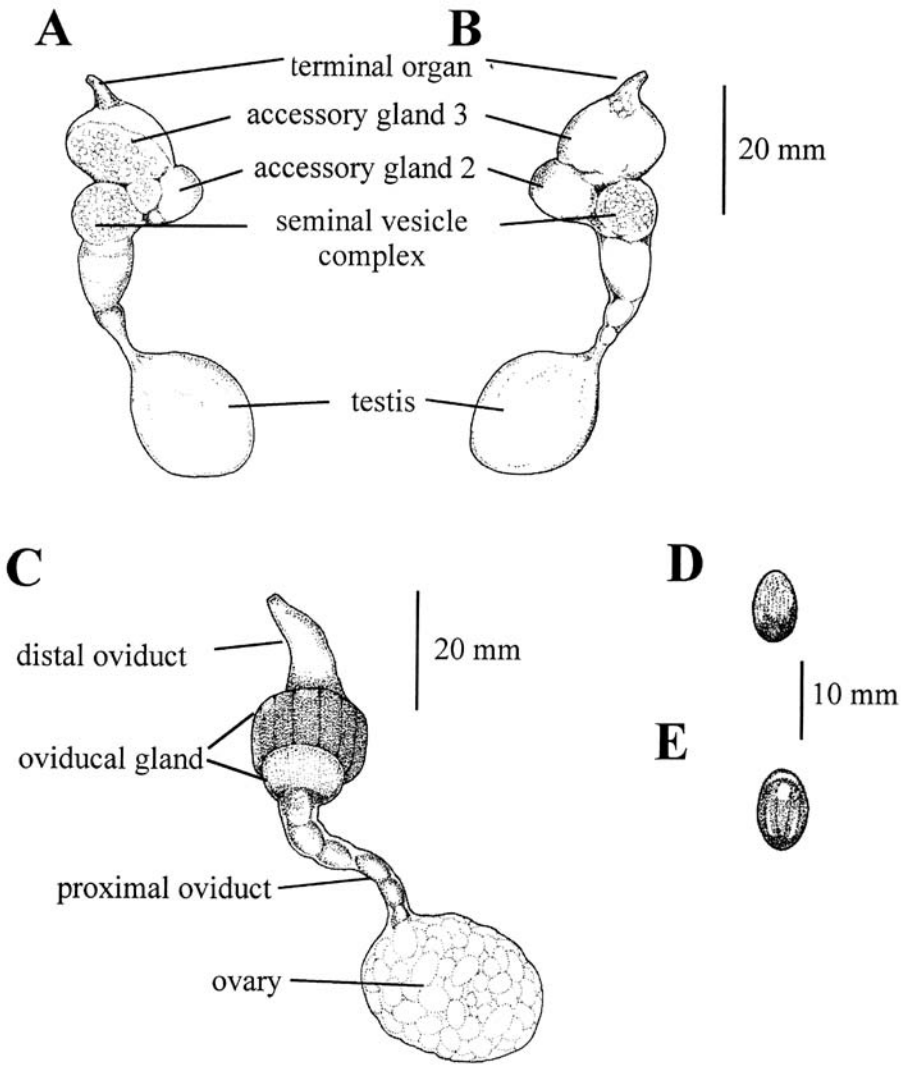

Figure 20. *Opisthoteuthis massyae.* Reproductive anatomy. Dorsal (A) and ventral (B) view of the reproductive tract of a mature male of 65 mm ML (NMSZ1999158.084). C. Reproductive tract of a mature female (NMSZ1999158.083). Eggs from ovary (D) and proximal (E) oviduct (NMSZ1999158.083).

with lengths from 9 to 11 mm (Villanueva, 1992a), and to 12.0 mm (Daly et al., 1998); widths from 4.8 to 5.0 mm. Egg shell with longitudinal striations and a short, rudimentary egg shell stalk (see photographs in Villanueva, 1992a: fig. 3c, Boyle and Daly, 2000: fig.6).

Shell, small, broadly U-shaped, with wings tapering to acute points. Edges of basal portion of shell slightly raised, making the outer surface concave, resulting in the basal portion being U-shaped in cross section. Inner surface of basal portion convex. Skin smooth, with poorly developed musculature. In preserved specimens, the color light red-

Table 4. Indices of body proportions and counts of 11 mature and 5 maturing males, 3 mature, 5 maturing and 1 immature females of *Opisthoteuthis massyae*. For each index or count, min–mean–max. values are indicated and standard deviation are shown between brackets. Measurements in mm.

	M	M	F	F
Sex	Mature	Maturing	Mature	Maturing + immature
ML	36.0–59.7–75.0 (10.8)	40.0–48.6–56.0 (6.2)	61.0–66.3–76.0 (8.4)	32.0–42.2–50.0 (7.0)
TL	210.0–287.7–350.0 (49.7)	175.0–213.4–292.0 (47.0)	275.0–280.0–285.0 (5.0)	166.0–202.2–250.0 (28.0)
MWI	60.0–102.0–175.0 (34.3)	68.0–80.5–100.0 (14.0)	77.0–93.5–104.8 (14.6)	86.5–106.1–125.0 (18.2)
HWI	116.4–141.0–177.8 (25.7)	111.5–133.6–165.0 (24.0)	101.3–117.7–137.1 (18.1)	110.0–148.6–193.8 (33.8)
CiI	4.5–7.0–9.2 (1.6)	5.8–7.8–11.0 (2.2)	5.2–6.4–8.4 (1.8)	5.2–6.8–10.0 (1.8)
FLI	32.8–53.6–75.1 (12.8)	47.2–60.4–74.1 (11.9)	31.4–35.9–40.0 (4.3)	33.3–45.6–67.3 (13.0)
FWI	38.5–51.8–71.4 (9.5)	33.3–42.3–50.0 (7.4)	42.9–46.6–50.0 (3.6)	48.4–55.5–70.0 (8.3)
FSI	37.7–49.0–66.2 (7.7)	33.1–47.3–52.6 (8.2)	33.3–36.7–40.0 (4.7)	35.5–43.9–48.2 (4.5)
EDI	30.8–59.6–91.7 (22.1)	38.0–53.3–70.0 (12.7)	29.0–34.5–43.4 (7.8)	36.0–58.1–81.3 (18.7)
FuLI	54.5–72.8–122.2 (18.8)	55.6–63.2–73.2 (8.4)	47.4–54.3–58.1 (6.0)	43.5–69.2–90.6 (16.7)
FfuI	38.5–58.8–82.2 (14.0)	58.5–67.1–71.4 (5.9)	54.3–58.8–61.1 (3.9)	44.4–61.9–73.3 (11.3)
TOLI	6.2–11.4–19.4 (5.0)	7		
Gill LC	6–6.9–8 (0.6)	6–6.6–7 (0.5)	7	6.0–7.0–8.0 (0.7)
Egg length			9.4–10.2–11.0 (1.1)	
ALI-I	263.6–394.9–516.7 (70.1)	320.0–355.0–394.6 (30.7)	330.6–357.0–377.0 (23.8)	347.8–405.6–453.1 (38.5)
ALI-II	263.6–382.9–488.9 (62.6)	320.0–347.7–400.0 (30.6)	338.7–355.4–385.2 (25.9)	314.0–385.8–437.5 (48.1)
ALI-III	309.1–389.8–511.1 (60.3)	310.0–348.6–401.8 (36.2)	335.5–345.0–360.7 (13.7)	310.0–388.9–437.5 (46.9)
ALI-IV	300.0–387.0–475.0 (53.7)	300.0–342.8–421.4 (48.7)	360.7	369.6–385.0–421.9 (24.9)
AWI-I	32.7–55.0–72.8 (15.0)	32.7–36.8–40.0 (3.7)	29.0–29.3–29.5 (0.3)	
AWI-II	25.5–43.1–58.9 (13.3)	28.6–37.4–44.1 (8.0)	26.2–32.2–38.3 (8.6)	
AWI-III	23.6–36.7–52.2 (9.3)	20.7–22.8–25.0 (3.0)	20.0–22.1–24.3 (3.0)	
AWI-IV	23.6–35.1–52.8 (10.4)	29.7–38.1–46.4 (11.8)	44.4–45.1–45.7 (0.9)	
SDI Proximal-I	7.4–10.3–15.0 (2.4)	7.1–8.9–12.1 (2.0)	5.1–5.8–7.2 (1.2)	5.4–6.3–7.2 (0.6)
SDI Proximal-II	7.8–10.0–15.0 (1.9)	6.9–8.6–12.1 (2.1)	4.9–5.4–5.7	5.4–6.2–7.2 (0.7)
SDI Proximal-III	7.5–10.3–15.3 (2.4)	8.0–9.4–13.8 (2.4)	4.8–5.8–7.5 (1.5)	5.5–6.2–7.8 (0.9)
SDI Proximal-IV	8.4–10.2–15.4 (2.1)	7.5–9.4–13.8 (2.5)	5.1–5.3–5.5 (0.2)	5.4–6.5–7.5 (0.7)
SDI Distal-I	3.3–4.4–5.6 (0.8)	3.2		
SDI Distal-II	3.6–5.8–8.3 (1.6)	3.4–5.1–7.0 (1.5)		
SDI Distal-III	5.2–7.9–9.7 (1.7)	3.3–6.0–9.1 (2.0)		
SDI-IV Distal	5.5–8.3–10.4 (1.9)	5.0–7.7–12.1 (3.2)		
Arm sucker count				
A I	78–86.1–96 (6.0)	80–88.5–97 (12.0)	82–84.3–88 (3.2)	76.0–84.0–94.0 (6.7)
A II	82–90.8–101 (6.1)	94–97.0–100 (4.2)	84–85.7–87 (1.5)	80.0–85.8–92.0 (4.4)
A III	80–92.2–108 (8.6)	95–101.0–107 (8.5)	85–86.5–89 (3.5)	77.0–82.6–88.0 (4.2)
A IV	82–89.6–105 (7.3)	82–95.7–107 (12.7)	–	78.0–83.0–90.0 (5.3)
AASC	81.7–89.5–102.5 (5.3)	93.3–92.7–102.8 (10.4)	85–85.8–87 (1.1)	79.5–84.9–90.0 (4.4)

Table 5. Min–mean–max. values and standard deviation (in brackets) of counts and indices of mature males of the Atlantic *Opisthoteuthis* species.

	O. agassizii 15 mature males	*O. calypso* sp. nov. 11 mature males	*O. grimaldii* 8 mature males	*O. hardyi* sp. nov. 1 mature male	*O. massyae* 11 mature males
ML	32.0–43.5–55.0 (6.0)	27.4–33.4–45.0 (5.0)	31.0–41.2–50.0 (6.5)	45	36.0–59.7–75.0 (10.8)
TL	117.0–162.1–186.0 (25.2)	130.0–168.2–206.0 (25.3)	126.0–199.5–250.0 (40.2)	250	210.0–287.7–350.0 (49.7)
MWI	111.1	68.6–122.0–155.2 (33.4)	71.0–118.8–160.0 (29.0)	97.8	60.0–102.0–175.0 (34.3)
HWI	117.1–145.4–172.7 (19.5)	134.3–162.5–186.1 (20.3)	132.3–163.7–211.1 (29.0)	140	116.4–141.0–177.8 (25.7)
CiI	3.8–5.8–9.1 (1.9)	4.0–7.4–13.3 (3.1)	4.9–7.8–10.4 (1.8)	9.1	4.5–7.0–9.2 (1.6)
FLI	44.1–60.3–74.6 (11.2)	40.7–56.1–65.5 (9.7)	20.0–40.0–49.4 (9.3)	–	32.8–53.6–75.1 (12.8)
FWI	32.5–45.1–56.7 (8.6)	29.8–38.0–52.0 (7.8)	28.6–44.6–60.6 (11.2)	–	38.5–51.8–71.4 (9.5)
FSI	60.3–65.7–71.8 (4.8)	47.0–54.1–61.5 (6.3)	32.7–50.6–70.3 (11.5)	–	37.7–49.0–66.2 (7.7)
EDI	43.1–61.6–74.3 (11.7)	48.6–74.1–105.8 (19.9)	62.0–76.7–95.2 (12.3)	37.8	30.8–59.6–91.7 (22.1)
FuLI	41.9–57.3–68.8 (8.2)	50.0–70.5–93.4 (15.5)	49.4–68.9–92.9 (18.1)	64.4	54.5–72.8–122.2 (18.8)
FFuI	48.3–61.9–73.3 (8.5)	53.1–63.4–80.0 (9.5)	46.2–61.3–71.0 (9.3)	–	38.5–58.8–82.2 (14.0)
TOLI	5.7–9.0–13.0 (2.4)	5.6–9.0–14.6 (2.9)	8.2–12.7–17.1 (4.1)	–	6.2–11.4–19.4 (5.0)
Gill LC	6–7.0–8 (0.4)	7	7–7.6–8 (0.5)	7	6–6.9–8 (0.6)
ALI-I	234.1–318.5–369.6 (40.8)	300.0–367.7–470.8 (56.1)	311.1–379.9–452.4 (60.8)	455.5	263.6–394.9–516.7 (70.1)
ALI-II	238.6–316.4–369.1 (41.6)	300.0–374.5–478.1(68.5)	230.0–378.5–440.5 (82.2)	422.2	263.6–382.9–488.9 (62.6)
ALI-III	238.6–317.3–371.4 (42.7)	291.2–358.0–459.9 (61.8)	220.0–372.2–460.6 (75.9)	433.3	309.1–389.8–511.1 (60.3)
ALI-IV	245.5–303.8–354.3 (36.2)	288.2–355.2–434.5 (54.0)	210.0–365.6–435.7 (82.9)	477.8	300.0–387.0–475.0 (53.7)
AWI-I	18.8–24.9–34.3 (6.2)	32.6–44.8–54.7 (8.0)	28.0–37.7–51.1 (7.5)	47.5	32.7–55.0–72.8 (15.0)
AWI-II	18.8–23.5–31.4 (5)	27.6–42.0–54.7 (10.5)	24.0–34.8–44.5 (7.4)	33.8	25.5–43.1–58.9 (13.3)
AWI-III	17.5–22.9–31.4 (5.4)	31.7–42.9–59.9 (10.6)	22.0–30.6–42.2 (8.4)	30.4	23.6–36.7–52.2 (9.3)
AWI-IV	18.8–23.0–31.4 (5.2)	28.9–39.8–48.5 (7.7)	20.0–30.6–42.2 (7.3)	33.3	23.6–35.1–52.8 (10.4)
SDI Proximal-I	8.6–10.0–12.6 (1.4)	10.7–13.7–16.3 (1.9)	6.0–12.4–17.0 (3.1)	15.3	7.4–10.3–15.0 (2.4)
SDI Proximal-II	8.5–10.1–12.3 (1.2)	9.7–12.7–15.0 (1.7)	6.2–12.1–16.7 (3.1)	16.2	7.8–10.0–15.0 (1.9)
SDI Proximal-III	8.4–10.3–12.3 (1.2)	14.0–19.9–25.5 (3.3)	6.0–11.3–15.2 (2.8)	16.2	7.5–10.3–15.3 (2.4)
SDI Proximal-IV	9.4–10.5–12.3 (1.0)	8.6–14.1–19.0 (2.7)	6.0–11.5–17.0 (3.1)	16	8.4–10.2–15.4 (2.1)
SDI Distal-I	5.8–7.4–8.9 (1.0)	15.6–18.8–23.5 (2.5)	5.5–9.4–13.9 (3.2)	13.8	3.3–4.4–5.6 (0.8)
SDI Distal-II	5.8–8.1–10.4 (1.5)	15.8–20.8–23.4 (2.7)	5.2–9.2–12.9 (3.0)	15.8	3.6–5.8–8.3 (1.6)
SDI Distal-III	5.6–9.1–10.3 (1.3)	18.9–21.6–25.5 (2.2)	5.8–9.6–14.2 (2.7)	14.2	5.2–7.9–9.7 (1.7)
SDI-IV Distal	5.6–9.2–10.8 (1.5)	18.9–23.1–27.4 (2.9)	6.0–10.1–14.2 (2.5)	14.2	5.5–8.3–10.4 (1.9)
Arm sucker count					
A I	64–67.4–71 (2.6)	49–52.2–55 (2.4)	74–77.2–82 (3.1)	60	78–86.1–96 (6.0)
A II	56–67.1–75 (6.0)	52–53.6–55 (1.5)	70–75.0–80 (3.9)	64	82–90.8–101 (6.1)
A III	58–66.5–77 (6.8)	48–53.6–61 (5.7)	73–78.0–83 (3.6)	67	80–92.2–108 (8.6)
A IV	63–69.8–78 (6.1)	48–53.0–56 (3.7)	68–75.5–81 (4.6)	64	82–89.6–105 (7.3)
AASC	58.3–67.0–74.8 (5.5)	48–53.2–58.0 (3.3)	73.0–76.1–80.3 (3.2)	64	81.7–89.5–102.5 (5.3)

dish brown; inside of web a dark chocolate brown with a slightly purplish hue on which the lighter-colored suckers and cirri are conspicuous. Pigment-free spots on skin not observed.

Distribution.—Eastern Atlantic species. From off Ireland, 50°31′N, 11°31′W (Massy, 1909); Hebrides Slope (Boyle et al., 1998); west of Scotland, and Rockall Trough (Daly et al., 1998; Boyle and Daly, 2000; present study); Açores Islands (present study); off Madeira Islands (Clarke and Lu, 1995); off Namibia (Sánchez and Guerra, 1989; Villanueva, 1992a,c; Villanueva and Guerra, 1991; Villanueva and Sánchez, 1993); and possibly to South Africa (Roeleveld et al., 1992; Roeleveld, 1998; specimens not examined).

Biology.—Species collected on muddy bottoms from 778 m off Namibia (Villanueva, 1992a) to 1300 m depth in NE Atlantic (Daly et al., 1998), and the holotype from 1226–1450 m. It is the most common cephalopod collected in bottom trawls on the Hebrides slope between 800-1300 m depth (Boyle et al., 1998; Daly et al., 1998; Boyle and Daly, 2000). In the southeastern Atlantic, *O. massyae* has been shown to undergo diel changes in abundance, collected by trawl at densities of 202–337 individuals km^{-2} during the daytime and 256–499 individuals km^{-2} during the nighttime (Villanueva and Guerra, 1991). Stomach content analyses show a diet composed of small epibenthic and suprabenthic crustaceans (mostly amphipods and isopods) and polychaetes. No conspicuous feeding rhythm has been detected, and males and females appear to feed on similar prey, regardless of size. The higher capture abundances recorded during nighttime could imply a change in activity independent of feeding (Villanueva and Guerra, 1991). Predators are unknown. Specimens observed in a shipboard aquarium displayed several behaviors such as bottom resting, flat-spreading, web-inversion and ballooning response (Villanueva, 2000). Mature individuals of both sexes are collected in all seasons of the year, both in the northern (Daly et al., 1998; Boyle and Daly, 2000) and southern Atlantic (Villanueva, 1992a). All of these studies of the reproduction of *O. massyae* show that considerable growth takes place after the onset of sexual maturity, and that egg release is continuous, without seasonal influence, over the entire adult life span. Follicular sheaths remaining in the ovary after egg release provided an estimate of potential fecundity with a maximum of 3202 eggs and a mean of 1396 eggs per female (Boyle and Daly, 2000). The small number of eggs in the oviducts and oviducal gland indicates that eggs are probably released one or two at a time. Mineral composition of egg shell shows that major elements were sulphur (27%) and phosphorus (20%) (Villanueva, 1992a). Embryonic development and juvenile life are not known.

Opisthoteuthis sp.

Specimens examined during the present study that probably belong to either *O. grimaldii* or *O. massyae*: 1 maturing female, 18 mm ML, Princesse Alice Sta. 1450, NE Atlantic, Gulf of Gascogne, bottom trawl, 1804 m, 24 Jul 1903, MOM295156, specimen in poor condition, reported by Joubin (1920); 1 immature female 17 mm ML off Namibia, 23°32′S, 12°55′E, bottom trawl, 952 m, 1 Feb 1988, ICM195/2000; 1 immature male 40 mm ML, West of Scotland, commercial trawl, ?depth, 12 Apr 1996, NMSZ1999158.065; 1 maturing male, 32 mm ML, PSB, OTSB, 1198 m, 14 Aug 1997, NMSZ1999158.039; 1 immature female, 40 mm ML, OTSB, Rockall, 1101–1118 m, 1 Jun 1999, NMSZ1999158.069.

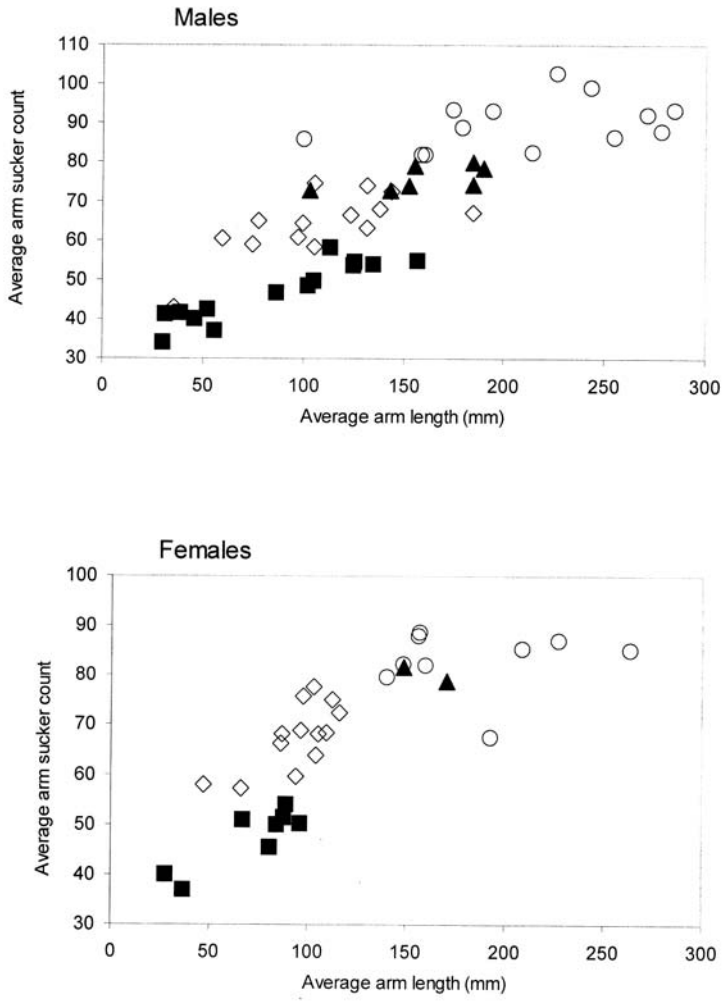

Figure 21. Relationship between average arm sucker count and average arm length in *Opisthoteuthis agassizii* ◇, *Opisthoteuthis calypso* ■, *Opisthoteuthis grimaldii* ▲ and *Opisthoteuthis massyae* ❍.

Comparative Material of Additional Species Examined from the Family Opisthoteuthidae

Opisthoteuthis californiana Berry, 1949, 1 mature male 52 mm ML, SW Colombia River mouth, 46°00.06′N, 124°50.48′W, RV Commando, 300 fm, Otter trawl, 9 May 1963, USNM 575641, good condition; *Opisthoteuthis depressa* Ijima and Ikeda, 1895, 1 immature female 27 mm ML, Atami, Japan, ?depth, 5 Apr 1907, BMNH 1925.3.6.1, poor condition; *Opisthoteuthis persephone* Berry 1918, 1 mature male 28 mm ML, RV Endeavour Sta. E5720, South Pacific Ocean, Australia, Victoria, Genoa Peak, 39°S, 150°E, 260 fm, 25 Jan 1917, USNM 816361, Paratype, poor condition; *Opisthoteuthis pluto*

Table 6. Comparison of the position of the enlarged sucker fields and number of suckers affected by arm in mature males of *Opisthoteuthis agassizii* (n = 15); *O. calypso* sp. nov. (n = 11); *O. grimaldii* (n = 8); *O.* hardyi sp. nov.(n = 1) and *O. massyae* (n = 11). PESF, Proximal enlarged sucker field; DESF, Distal enlarged sucker field.

Species	First sucker	last sucker	nº suckers (mean)	Mean position of the largest sucker	Range of the position of the largest sucker
Opisthoteuthis agassizii					
PESF- I	5–8	9–13	4	8	7–9
PESF- II	6–8	9–13	5	8	7–9
PESF- III	6–8	9–12	5	8	6–10
PESF- IV	6–8	9–12	5	8	6–10
DESF- I	26–37	34–45	7	36	33–38
DESF-II	26–38	35–44	7	35	33–39
DESF- III	25–36	34–44	7	34	29–39
DESF- IV	23–36	33–44	8	34	30–38
Opisthoteuthis calypso sp. nov.					
PESF- I	4–7	7–11	4	7	6–8
PESF- II	4–7	8–10	4	7	6–8
PESF- III	5–7	7–10	5	7	6–9
PESF- IV	5–7	7–10	5	7	6–8
DESF- I	24–28	26–29	2	27	25–29
DESF-II	23–28	25–29	2	26	24–28
DESF- III	23–28	25–29	3	26	24–28
DESF- IV	23–27	24–29	2	26	23–28
Opisthoteuthis grimaldii					
PESF- I	4–5	6–10	5	6	5–7
PESF- II	4–5	7–10	5	7	6–8
PESF- III	4–5	8–11	6	7	6–8
PESF- IV	4–5	8–11	6	7	6–8
DESF- I	24–31	31–39	9	31	27–34
DESF-II	22–28	31–37	9	30	27–32
DESF- III	23–28	33–36	10	30	26–32
DESF- IV	22–27	31–37	10	29	27–30
Opisthoteuthis hardyi sp. nov.					
PESF- I	4	7	4	6	
PESF- II	5	7	3	7	
PESF- III	5	8	4	7	
PESF- IV	5	9	5	7	
DESF- I	18	30	13	23	
DESF-II	19	30	12	23	
DESF- III	19	27	9	24	
DESF- IV	19	32	14	22	
Opisthoteuthis massyae					
PESF- I	3–5	8–11	8	6	4–7
PESF- II	3–6	9–11	8	7	5–8
PESF- III	4–6	9–12	7	7	5–8
PESF- IV	4–6	10–12	7	7	5–8
DESF- I	–	–	–	–	–
DESF-II	36–40	41–48	9	40	38–44
DESF- III	35–40	42–47	9	41	38–42
DESF- IV	34–40	43–49	11	41	37–44

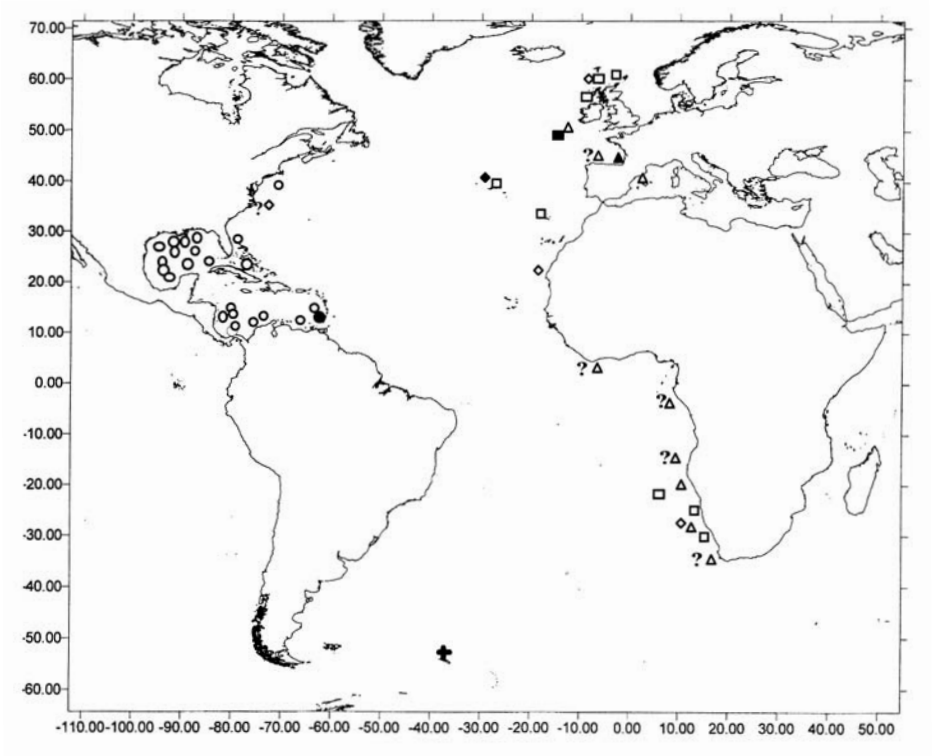

Figure 22. Distribution of Atlantic species of *Opisthoteuthis*. ❍*Opisthoteuthis agassizii* (●Type locality); △ *Opisthoteuthis calypso* new species (▲ type locality); ◇: *Opisthoteuthis grimaldii* (◆ type locality); + *Opisthoteuthis hardyi* new species; □: *Opisthoteuthis massyae* (■type locality). Each symbol in this map represents one or more specimens, from one or more stations reported in this paper; some stations that overlap greatly are not shown.

Berry 1918, 1 mature male 38 mm ML, Indian Ocean, Australia, Great Australian Bight, Eucla, RV Endeavour, Sta. E3632, 34°S, 130°10′E, trawl, 150 fm, no date capture, USNM 815830; 1 ?female 35 mm ML Indian Ocean, Australia, Great Australian Bight, Eucla, RV Endeavour Sta. E3629, 34S, 126°10′E, no depth data, 13 Jan 1917, USNM 815718, Paratype, poor condition; *Grimpoteuthis albatrossi* (Sasaki, 1920), 1 female, Bering Sea, R/V Albatross Sta. 4771, 54°30′N, 179°17′E, 12FT Tanner Beam, 426 fm, 4 Jun 1906, USNM 00332950, Paratype; 1 female, RV Albatross Sta. 5084, 34°N, 137°49′E, Agassiz trawl, 918 fm depth, 20 Oct 1906, USNM 00332948, Paratype; *Grimpoteuthis bruuni* Voss 1982, 1 male 25 mm ML, USNM 730616, HOLOTYPE, and 2 males 14 and 18 mm ML (USNM 730617, Paratypes), off Antofagasta, Chile, RV Anton Bruun Sta. 717, 23°41′S, 70°34′W, 57 FT Shrimp trawl, 250–360 m, 17 Aug 1966; *Cirroctopus glacialis* (Robson), 1 male 83 mm ML, Antarctica, RV Polarstern, EASIZ II Cruise, Sta. 48/338, 19 Mar 1998, Agassiz trawl, 61°39.9′S, 58°12.2′W, 417 m, ICM363/2000.

Discussion

The genus *Opisthoteuthis*. After the description of Verrill 1883, the diagnosis of this genus has been attempted by various authors (Robson, 1932; Nesis, 1987; Voss, 1988b; Hochberg et al., 1992; Voight, 1997; O'Shea, 1999). From our detailed study of the above species in the Atlantic and of the literature, we conclude that the genus *Opisthoteuthis* can be best diagnosed by the shared possession of three characters: (1) ovoid form of body and small fins, (2) U-shaped shell with lateral wings tapering to acute points and, (3) mature males with a proximal and usually a distal enlarged sucker field on one to all arms. In addition to these main characters that define the genus, two other, non-generic characters, help in the diagnosis, the shapes of the optic lobe and the fins. A kidney-shaped optic lobe is a common character for all the *Opisthoteuthis* species. Here it is not considered as a generic character because it is also present in *C. glacialis* (Kinney, 1988, and pers, observ.) and *Cirroctopus hochbergi* (O'Shea, 1999), species that can be easily separated from *Opisthoteuthis,* as *Cirroctopus* lacks enlarged suckers and the shell is V-shaped. On the basis of the shape of the optic lobe, Kinney (1988) and G. Voss (unpublished text of presentation made at 1988 CIAC workshop, Washington, D.C.) considered that *C. glacialis* may not belong to *Grimpoteuthis*, because they found the optic lobe to be round in all species of *Grimpoteuthis* examined. It should be pointed out, however, that *Grimpoteuthis bruuni* (Voss, 1982) matches the main *Opisthoteuthis* characters as here defined, but differs from other *Opisthoteuthis* species by the presence of a round optic lobe (as in the *Grimpoteuthis* genus). The generic status of *bruuni* needs clarification. In relation to the fin shape, the absence of a lobe near the anterior fin insertion is also a common character to the genus *Opisthoteuthis.* This character seems to occur also in *Grimpoteuthis abyssicola* (O'Shea, 1999), and without extensive examination of fin shape in other *Grimpoteuthis* and cirrate species, the character is not used here as generic. Future detailed studies and redescriptions of opisthoteuthids not examined in the present study and much-needed comparative morphological studies will surely add to the number of species of *Opisthoteuthis*, and produce additional distinct morphological differences between genera.

Comparison of Species.—In Table 7, we compare characters that we found to be most useful in separating *Opisthoteuthis* species. The five species that we know to occur in the Atlantic can be separated based on several external characters. The most useful proved to be the number and position of the enlarged suckers in maturing and mature males, these form a distinctive combination pattern for each Atlantic species (see Table 6), as well for other species of the genus. In contrast to common shallow-water octopods, the full sexual maturity, in at least two species of opisthoteuthids, *O. calypso* and *O. massyae*, appears to occupy the greater part of the life cycle (Villanueva, 1992a). Females, which lack enlarged suckers, are more difficult to identify. Among the Atlantic species, egg size was only distinctive for *O. calypso*, a small-egg species. However, the presence of either a single nodule or a series of muscular web supports on the ventrolateral margins of the arms, though sometimes difficult to detect, proved to be a good specific character for identifying both males and females. Additionally, arm sucker count in adults, the AL-AASC relationship (see Fig. 21), position of the first cirri, shape of the shell, and structure of the digestive gland are useful, to varying degrees, in identifying, both males and females to species. Other species attributed to *Opisthoteuthis* that are not listed in Table 7 such as *O. depressa*, *O. extensa*, *O. japonica*, *O. medusoides*, *O. persephone* and *O.*

Table 7. Comparison of the species of *Opisthoteuthis* (as herein diagnosed; see General Discussion)*. ASC, arm sucker count,; DESD, distal enlarged sucker diameter; DESF, Distal enlarged sucker field; PESD, Proximal enlarged sucker diameter. A kidney-shaped optic lobe and the absence of a lobe near the anterior fin insertion are also common characters for all the *Opisthoteuthis species*.

Geographical region	Species	Increased robustness of arms I in males	DESF, number of suckers	DESF, largest suckers	DESF, formula	DESD > PESD	Ventral web marginal supports	ASC in adults	Position of first cirrus between suckers	Shape of basal portion of shell surfaces	Digestive gland shape
Atlantic	*O. agassizii* Verrill, 1883	absent	7–8	34–36	IV.III.II.I	no (except in older males)	multiple (all stout)	58–80	3&4	outer concave, inner convex	entire
	O. calypso sp. nov.	absent	2–3	26–27	IV.III.II.I	yes	single	47–58	1&2	outer slightly concave, inner convex	entire
	O. grimaldii (Joubin, 1903)	absent	9–10	29–31	IV≥ III≥ I≥ II	no	single	73–80	2&3	outer flat, inner convex	bilobed
	O. hardyi sp. nov.	slight	9–14	22–24	IV≥ III=IV≥ I	no (coequal)	absent	60–67	3&4	outer highly concave, inner convex	entire
	O. massyae (Grimpe, 1920)	marked	9–11	40–41	IV.III.II.I	no	multiple (oral most stout, others weak)	82–106	3&4 or 4&5	outer strongly concave, inner convex	bilobed
Australasia	*O. chathamensis* O'Shea, 1999		6–8			no	absent	41–55	2&3 or 3&4	outer inner concave, convex	bilobed
	O. mero O'Shea, 1999					no		54–71	1&2		bilobed
	O. pluto Berry, 1918		3–4			no		80–85			
	O. robsoni O'Shea, 1999					no		74–89	2&3 or 3&4	outer concave,	entire
Pacific	*O. californiana* Berry, 1949		3–8		I	yes		60–70		inner convex	

(*) Other *Opisthoteuthis* species not listed such as *O. depressa*, *O. extensa*, *O. japonica*, *O. medusoides*, *O. persephone*, and *O. philippi* need additional studies to clarify their generic and/or species status.

philippi require additional studies to clarify their generic and/or species status. More detailed comparative morphological study of unexplored organ systems, as done by O'Shea (1999) with the shell and male reproduction tract, should enhance our understanding of the diversity of this fascinating family of cirrates.

DISTRIBUTION.—A species typically occurs over a broad depth range (see Distribution sections). Known depth ranges of these species are from about 500 m to greater than 1800 m. The shallowest known depth of capture of a species is 227 m for *O. agassizii* and the deepest 2287 for *O. calypso*. In the Atlantic, high abundance of *Opisthoteuthis* has been recorded on the Hebrides slope in the north (Boyle et al., 1998; Daly et al., 1998) and off Namibia and South Africa in the south (Villanueva, 1992a; Villanueva and Guerra, 1991; Roeleveld et al., 1992). Both are areas of intensive deep-sea fishing for Macrouridae and hake *Merluccius* spp., respectively, indicating that sampling effort probably largely defines our present picture of the geographic distributions of the various species of *Opisthoteuthis* and of other non-target cephalopod species. Maxim and Papadopol (1985) listed without an accompanying description, *Opisthoteuthis extensa* from the SE Atlantic in samples from 40°00′–55°00′S to 06°00′–20°00′E. Recognition of this additional species of *Opisthoteuthis* in the Atlantic requires the future confirmation of the identification of this material. In the Atlantic, the few records of *Opisthoteuthis* from the central region and no records from the southwestern regions will most likely change with increased sampling.

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