THE SYSTEMATICS OF THE PELAGIC SQUID
GENUS OCTOPOTEUTHIS RÜPPELL, 1844
(Cephalopoda: Teuthoidea) WITH EMPHASIS
ON SPECIES IN THE NORTH ATLANTIC

CENTRE FOR NEWFOUNDLAND STUDIES

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STEPHEN J. STEPHEN







The Systematics of the Pelagic Squid Genus Octopoteuthis Rüppell, 1844 (Cephalopoda; Teutholdea) with Emphasis on Species in the North Atlantic



Stephen J. Stephen, B. Sc.

A Thesis Presented to the School of Graduate Studies in Partial Fulfillment of the Degree of Master of Science.

> Memorial University of Newfoundland, 'St. John's, Newfoundland August 31, 1985

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Dedication

To my parents, Joseph and Della Stephen

ABSTRACT

The systematics of the pelágic squid genus Octopoteuthis Rüppell, 1844 is reviewed. Four hundred and fifty-six specimens were examined from museum sources worldwide ranging in size from 1.3 mm - 240 mm dorsal mantle length (ML). Of the nine nominal species five are found to be invalid or considered nomina dubia. All species are found to bear photophores in a variety of body locations. Characters used to separate species include presence or absence of anterior eyelid photophores; presence or absence of an eyeball photophore; and presence or absence of accessory cusps (hooklet) on the arm hooks. Larval specimens (those less than approximately 25 mm ML and still bearing tentacles or remnants of them) could not be separated into species at present because of the late development of the characters defined above. Discriminant analysis run on morphometric data on each specimen supported the species separation proposed here. Geographic and vertical distribution is also discussed.

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Chapter 1 INTRODUCTION

The squid family Octopoteuthidae Berry, 1912 is comprised of two genera, Octopoteuthia Rippell, 1844 and Taningia Joubin, 1931. The genus Octopoteuthia is represented by nine nominal species presently known to occurricumglobally. All species appear to be mesopelagic as adults (Lu and Clarke, 1975; Lu and Roper, 1977), 1978, 1981; Young and Roper, 1977.

Many of the earliest species descriptions were very brief with few or no illustrations. This made it very difficult to separate species. Octopoleuthis adult and larger juveniles differ considerably in appearance from the larvae and smaller juveniles (25-30mm). Also adults and larger juveniles bear distinct photophore patterns and numbers which were neither recognized nor recorded in the earliest species. The logs of many of the species holotypes precluded their reexamination to verify the presence or absence of characters. As a result, considerable confusion has developed in species separation because of inadequate original descriptions, descriptions of species based on larval or juvenile specimens, loss of type material, and the continued addition of new species without clarification of the status of previous/ones.

These problems became apparent when the writer was preparing an annotated checklist/key to cephalopods of the Canadian Atlantic for the Huntsman Marine Labbratory, St. Andrews, N. B. (Stephen, 1982, MS). At that time none of the Octopoteuthis specimens examined could be assigned to any of the three species reported, in the literature, to occur in the Western North Atlantic. Correspondence with several cephalopod systematists failed to indicate any means to accurately identify specimens of Octopoteuthis.

After being accepted to the Masters degree program at Memorial University the writer proposed a project to carry out a systematic revision of the genus Oclopoteuthis in the North Atlantic. Discussion with my supervisor, Dr. F. A. Aldrich, and correspondence with Dr. C. F. E. Roper, United States National Museum and Dr. G. L. Voss and Mrs. N. A. Voss, Rosenstiel School of Marine and Atmospheric Science, University of Miami, reinforced my idea for the project.

Such a revision required the examination of the largest possible number of specimens from the widest possible distributional range. Since Octopoteuthis specimens are caught infrequently, it was necessary to obtain specimens from several institutions. To mable the revision to be comprehensive for the genus, specimens representing Atlantic, Indias and Pacific Ocean species were obtained.

Chapter 2 HISTORICAL RESUME

Rüppell' described the first octopoteuthid in 1844 from a young specimen collected off Messina, Italy. He named it Octopoteuthis-sicul. Krohn (1846), expanded Rüppell's brief description and provided the first illustrations of the species, which showed total dornal and ventral views, the head and the hooks. In the paper Krohn changed the generic spelling to Octopodeteuthis following Rüppell's suggestion: "Nach Rüppell's Vorschlage nenne ich das Genus wozu die beschriebene. Species gehort, Octopodeteuthis (P. 49). In 1847, Krohn again changed the generic name to Verania after samining a well-preserved specimen which bore small tentacles. He placed his Verania in a family Onycholeuthiden, along with the genus Enoploteuthis d'Orbigny, 1839.

In 1849, Gray placed Octopodoteuthis sicula in his new family Onychoteuthidae. Verany (1851) made Verania a subgenus of Onychoteuthia Lichtenstein, 1818. Along with a description and a narrative of Ruppell's and Krohn's accounts of the species, Verany provided a ventral view of the gladius. For the next few years the genus was placed in the Onychoteuthidae but the generic spelling varied: Veranya (Fischer, 1887; Koferstein, 1888; Pelsencer, 1894; and Tiberi, 1880) and Verania (Tryon, 1879; and Weiss, 1889). Pieffer (1884) used the name Octopoteuthie sicula. Woodward (1871) in his *A Manual of the Mollusca* included Octopodoteuthis and Verania as synonyms of Ernopoteuthis.

Verrill (1882) included Verania in the family Teuthidae Gray, 1840. He assified the genus a non-supportable characteristic, however, when he listed it as having; "Tentacular club with hooks, ..." (p.280). In 1885, Verrill described a new species, Ancistrocheirus megaptera.

Steenstrup 1861. The two species were listed as Verania sicula and Ancistrocheirus megaptera.

Appellof (1889) gave a detailed description of a larval Octopoteuthis and provided some detailed illustrations of the arms, tentacular club, internal viscera, digestive system and optic ganglia. His illustrations clearly showed the photophores on the ink sac and at the ends of the arms although he did not recognize them as such. During the same year Ernest Weiss examined and illustrated a specimen with a mantle length of 7 mm. Weiss misinterpreted the arm tip photophores as hectocotylized or modified portions of the arm of male cephalopods used in spermatophore transfer.

Goodrich, in his 1892 paper, provided a table of chief characters of recent oegopsid cephalopods. His diagnosis of Verania was:

. Arms with 2 rows of hooks. Tentacles short suckers few. Pen slender, cartilaginous. Fins somewhat rounded, terminal. (p.320). In the 1896 Monograph by Jatta, the author placed Veranya sicula in the Onychii, reviewing the findings of most of the earlier workers who had looked at

it. He was the first to illustrate the radula

In 1899, Ficalbi verified the 1844 date of Rüppell's description of Octopoleuthis sicula thereby validating the correct authority for the species. He also reproduced Rüppell's paper in it's entirety, ensuring a larger audience for what had first appeared as a letter from Ruppell to one "m. le Coco".

Pfeffer, in his 1900 "Synopsis der oegopsiden Cephalopoden" assigned Octopodoteuthis to his family Enoploteuthidae. Hoyle (1904) maintained Pfeffer's classification and used the following as a diagnosis of the genus:

"Tentacles absent in the adult; in the young shorter than the arms and with but few suckers on the club; body stumpy and rounded behind: suckers extending to the tips of the arms. (p.11)

Most authors continued to adopt Pfeffer's classification for the next few years (Hoyle, 1909, 1910; Massy, 1909; Pfeffer, 1908; Thiele, 1921).

*Body gelatinous, without luminous organs. Arms with 2 rows of hooks. Tentacles small, deciduous. Club with a small number of bierial suckers. Six buccal pillars; 4th arms attached ventrally. Radula with 5 transverse rows of teeth. Funnel cartilage wide, with a shallow pit which widens posteriorly. Gladius as in Loligo. *(p.112)

Berry renamed the family Octopodoteuthidae in his July, 1912 paper on Japanese squids. It was not until November of that year that he explained his reasons for the change. He pointed out that Chun's Veranyidae was unacceptable because: "Verania is an exact synonym of Octopodoteuthidae (p. 645). Therefore, Veranyidae should be replaced by Octopoteuthidae of Octopodoteuthidae (if Krohn's emendation could be accepted). Several authors, however, continued to use Veranyidae as the family name (Chun, 1913; Murray and Hjort, 1912; Naef, 1916; Pearcy, 1965; and Voss, 1962; 1967).

Le Pfeffer's 1912 work Die Cephalopoden der Plankton-Expedition he called the group Octopodoteuthinae making it a subfamily of the Enoploteuthidae. He also included therein Verrill's Ancistrocheirus megaplera by creating a new genus for it called Octopodoteuthopsis.

Several authors, however, continued to use Pfeffer's classification (Joubin, 1920; Robson, 1924; Sasaki, 1916, 1929). Berry (1920a) continued to use the family Octopodoteuthidae but he did include Pfeffer's Octopodoteuthopsis in it. Berry's classification was used by the largest number of researchers (Akimushin, 1933; Bouxin and Legendre 1938; Degner, 1925; Johnson, 1934; Joubin, 1931; Naef, 1921, 1923; Silas, 1968; Thiele, 1933; and Voss, 1956, 1960, 1963.

Nael (1923), in his great monograph on the cephalopods, added two new, species of Octopodoteuthie to the list. Both his O, persics and O, indica were based on larval specimens first described by Chun in 1910. Joubin (1931), named the next species Octopodoteuthie danae, based on a specimen collected by the

In 1948, Robson added a sixth species by his description of Octopodoteuthis niclseni, illustrating the Junnel organ and a portion of the radula. Robson also questioned Pfeffer's separation of Octopodoteuthis and Octopodoteuthopsis. He combined these two genera into a single genus Octopodoteuthis.

Adam (1952), described a specimen which he identified as Octopoteuthis sicula. It bore two pairs of photophores, which he described as ocular and abdominal in their location. He provided illustrations of arm hooks bearing accessory cusps, subordinate to the main median hook, and a radula with nine rows of teeth. He also gave a good synopsis of the work of previous authors and agreed with Robson's consolidation of Pfeffer's adoption of two genera. In 1956(a & b). Voss described a specimen which he identified as Octopodoteuthopsis megaptera (Verrill, 1885) and placed in the family Octopodoteuthidae. He found three pairs of light organs; one pair on the recti abdominalis muscles, a second pair on the posterior ventrum of the mantle, and a third pair of ocula photophores. Voss maintained that Octopodoteuthis and Octopodoteuthopsis were distinct genera. Adam (1960), upon re-examining his 1952 specimens plus one other found the paired ventral mantle photophores similar to the ones decribed by Voss in his specimen of O. megaptera. Adam also listed the family to which they were to be assigned as Octopoteuthidae as did Clarke (1966), and Mercer (1968).

Several authors returned to Ruppell's original generic designation Octopoteuthis for the species O. sicula (Adam, 1952, 1960; Clarke, 1968; Mercer, 1968; Muus, 1963; Pearcy, 1965; Rancurel, 1970; and Voss, 1963).

In 1963, Akimushkin added the seventh species, Octopodoleuthis longiplera,

collected from a sperm whale (*Physeler catadon*) stomach. He compared O. sicula with his new species based on fin, mantle and funnel measurements, locking cartilage shape, and terminal swellings at the tips of the arms. The description of his species was brief and made no mention of photophores. No illustrations were provided.

Roper, Young and Voss (1989), offered a final solution to the problem of generic and familial spellings. The genera Verania (Veranya), Octopodoteuthis (Octopotheuthis, an incorrect spelling) and Octopodoteuthopsis were made synonyms of Rüppell's Octopoteuthis. Berry's Octopoteuthidae was sefected as the valid family name.

Young (1972), added an eighth species, Octopoteuthie deletron, to the genus. He provided a detailed description of it including information on its ontogeny. He was also the first to describe serial photophores along the course of the axial nerves in the arms. A thorough discussion of the sight-nominal species was included. Several species were eliminated or considered nomina dubia. O. persica was transferred to the species Taningia danae based on the specimen's distinct swellings on the tips of arms L and RII and it's extremely broad fins. Young ignored O. indica because its small size did not permit adequate comparison with other species. He termed O. longiptera a nomen dubium because of its inadequate original description and the loss of the holotype which prevented it's re-examination. He identified three species, O. megaptera, O. danae, and O. sp A, from the Atlantic and separated them using photophore patterns, hook structure and tail length: He suggested that one of the species was probably a synonym of O. sicula. In the Pacific, Young listed two species, his O. deletron and Robson's O. nicleani.

Lipka (1975), described brachial photophores from Western Atlantic specimens he identified as O. megaptera. His discussion reviewed much of Young's 1972 findings.

In 1980, Clarke named the ninth nominal species, O. rugosa, based on a complete female specimen collected from a sperm whale stomach. He reported that he found no light organs in his new species and that Young's suggestion that they were present in all members of the genus was_incorrect. Clarke reviewed Young's examination of the genus. Roper, Sweeney and Clarke (1985) also discussed rugoga in their work on Antarctic cephalopods.

Nesis (1982); recognized only seven identifiable Octopoteuthis species in a key to species of the genus; O. deletron, O. sp. A, O. danae, O. miegaptera, O. cicula, O. nieleeni, and O. rugosa. He commented that Akimuskin's O. longiptera was not included because of an extremely incomplete original description.

It is in this confusing state that we find ourselves at the beginning of this current review and, hopefully, rearrangement of the genus, with reference to the Atlantic specimens.

Chapter 3 MATERIALS AND METHODS

The bulk of specimens used in this study were obtained on loan from various institutions. Additional material was examined while on a Short-Term , Visitors Appointment to the United States National Museum of Natural History (Smithsonian Institution), Washington, D. C.. The following abbreviations are used to indicate the institutions from which specimens were borrowed:

- BMNH British Museum (Natural History), London
- CSI CSIRO (Commonwealth Scientific and Industrial Research Organization)
- IMPD Invertebrates and Marine Plants Division, Fisheries and Oceans, Canada, Halifax, N. S.
- INAP Instituto Nacional de Pesca, Montevideo, Uruguay.
- MUV Museum of Victoria (formally National Museum of Victoria), Melbourne, Australia.
- NMC National Museum of Natural History, a National Museums of Canada, Ottawa,
- RSM Royal Scottish Museum, Edinburgh, Scotland.
- SABS Biological Station, Fisheries and Oceans, Canada, St. Andrews, New

Brunswick.

- SAM South African Museum, Cape Town, South Africa.
- SBM Santa Barbara Museum, Santa Barbara,
- SIO Scripps Institute of Oceanography, University of California, La Jolla, California.
- SJBS Biological Station, Fisheries and Oceans, Canada, St. John's, Newfoundland.
- TAMU Texas A & M University, College Station, Texas.
- USC Allan Hancock Foundation, University of Southern California, Los Angeles.
- USNM United States National Museum of Natural History, Washington, D. C...
- ZMUC Zoologisk Museum, Universets of Copenhagen, Copenhagen, Denmark.
- ZMUB Zoologisk Museum, University of Bergen, Bergen, Norway
- ZMUH Zoologisches Museum der Universitat . Hamburg, Hamburg, Federal Republic of Germany.

In reference to ships the following designations apply:

ABM - R/V ALABAMA

ADO - R/V ANTON DOHRN

ADM - R/V ADMIRAL KING

AFR - R/V AFRICANA

AGA - R/V A. AGASSIZ

ALM - R/V. ALAMINOS

ALA - R/V ALASKA

.ALB - R/V ALBATROSS

ARC - R/Y ARCTURUS

ARG - R/V'ARGUS

ATC - R/V A. T. CAMERON

ATL - R/V ATLANTIS II

BAC - R/V BACHT

- BEL - R/V BELOGORSK

CLA - R/V T. CLARKE

CLI - R/V CLIMAX

COU - R/V COURAGEOUS

CRO - R/V T. CROMWELL

DAN - R/V DANA

DEL - R/V DELAWARE II

DIS - R/V DISCOVERY

DEJ - R/V DAVID STARR JORDAN

GAD - R/V GADUS

HAL - R/V HALCYON

HMA - RIV HAKUREI MARU

HUB - R/V C. L. HUBBS

TIL - R/V. ILLOVD

JOA - R/V JOAST

JWS - R/V. J. W. SCOGGAN

KMA - R/V KAIYA MARU

LHA - R/V LADY HAMMOND

MNA - R/V MEIRINE NAUDE

MSA - R/V MICHAEL SARS

PEN - R/V PENALBA

SAN - R/V SANDS

SMI - R/V H. M. SMITH

SOE - R/V SOELA

SPE - R/V SPENCER

SPR - R/V SPRIGHTLY

SWA - R/V SWAN

TAI - R/V TAIT
VEL - R/V VELERO-

WAS - R/V T. WASHINGTON

WHE - R/V WALTHER HERWIG

WIG - R/V WIGWAM

In reference to program the following designations apply:

EAS - R/V EASTROPAC plankton sampling program at

Gear employed in capturing the Octopoteuthis spp. reported herein are designated as follows:

BONG - Bongo

BT - Beam Trawl

COBB - Cobb Midwater Trawl

E300 - 3 metre Ring Trawl

EMT - Engels Midwater Trawl

IKMT - Issacs-Kidd Midwater Trawl

MOC - Multiple Opening-closing Net Environmental Sensing System

MOT - Monsoon Midwater Trawl

MWT - Midwater Trawl

NAN - Nanaimo Midwater Trawl

OTT - Otter Trawl

RMT - Rectangular Midwater Trawl

S150 - 1.5 metre Stramin Net

S200 - 2.0 metre Stramin Net

TUCK - Tucker Trawl

mw - metres of wire out

Measurements and counts are those recommended by Roper and Voss (1983). All measurements were taken by means of a steel centimeter rule or metric calipers, and are presented in millimeters (mm). The following abbreviations are the data categories measured or computed. The definitions of some of the actual measurements are inherent in the definition, of the indices. Figures 3-1, 3-2 and 3-3 illustrate where the measurements were taken on each specimen.

Figure 3-1: Generalized drawing of a squid of the genus Octopoteuthis (dorsal view) showing dimensions and structures measured in review of proposed diagnostic characters.

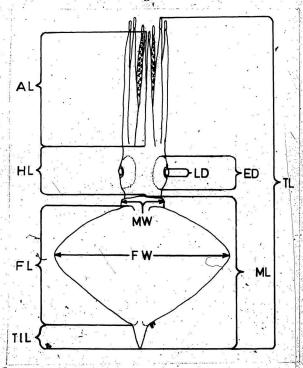


Figure 3-2: Generalized drawing of a squid at the genus Octopoleuthia (ventral view) showing position of photophores. ATP - arm tip photophore; AP- arm photophore; AEP anterior eyelid photophore; VHP - vientral head photophore; VP - vieral photophore; PVMP - posterior ventral mantle photophore.

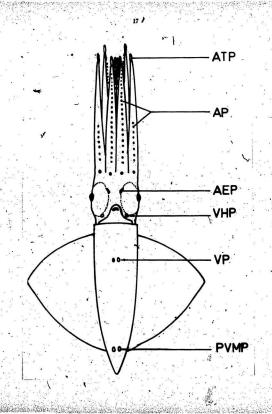
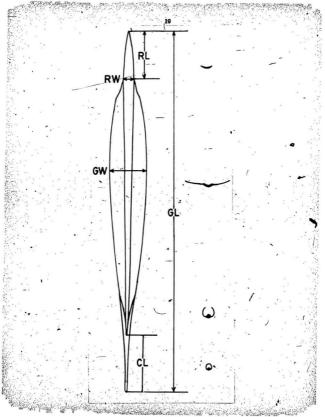


Figure 3-3: Generalized drawing of the gladius of Young's Octopoteuthis sp A showing, cross sectional configurations and the axes of which measurements were taken.



- AF Arm Formula: comparative length of arms expressed in decreasing order.
- HC Arm Hook Count: number of hooks on each designated arm.
- AL Arm Length (I, II, III, IV).
- ALI Arm Length Index: length of arm measured from the first basal (proximal-most) hook to the tip of the arm as a percentage of mantle length. (Arm I. dorsal; II. dorso-lateral; III. ventro-lateral; IV ventral)
- ED Eye Diameter.
- EDI Eye Diameter Index: greatest diameter of eye as a percentage of mantle length.
- FL Fin Length.
- FLI Fin Length Index: greatest length of fin (excluding tail) as a percentage of mantle length.
- FW Fin Width.
- FWI Fin Width Index: greatest width (dorsally) across both fins as a percentage of mantle length.
- GL Gladius Length: dorsal length of gladius along midline.
- GLI Gladius Length Index: length of gladius as a percentage of mantle length.
- GW Gladius Width.

- GWI Gladius Width Index: greatest width of gladius as a percentage of gladius length.
- HL Head Length.
- HLI Head Length Index: dorsal length of head measured from point of fusion of dorsal arms to anterior tip of nuchal locking cartilage as a percentage of mantle length.
- HW Head Width ..
 - HWI Head Width Index: greatest width of head at level of eyes as a percentage of mantle length.
- LD Lens Diameter.
- LDI. Lens Diameter Index: diameter of eye lens as a percentage of mantle length.
- ML Mantle Length: dorsal mantle length
 measured from anterior-most point
 of mantle to posterior apex of mantle.
- MW Mantle Width.
- (WI Mantle Width Index: greatest straightline (dorsal) width of mantle as a percentage of mantle length.
- RL _ Rachis Length.
- RLI Rathis Length Index: length of free rachis measured from anterior end of gladius to point where anterior end of vahe joins rachis, as a precentage of gladius length.
- RW Rachis Width.

- RWI Rachis Width Index: width of rachis measured at point where anterior edge of vane meets rachis as a percentage of gladius length.
- TlL Tail Length.
- TILI Tail Length Index: portion of the mantle measured from the posterior edge of fins to the distal tip of mantle as a percentage of mantle length.
- TtL Tentacle Length.
 - TtLI Tentacle Length Index: total length of tentacular stalk and club as a percentage of mantle length.
- TL Total Length: measured from the tip of club (or longest arm in juveniles and adults) to posterior-most point of mantle

Photophore numbers and placement were determined by minor microscope dissection. Axial nerve photophores were uncovered by making an incision along the length of all arms and by examining them using a dissecting microscope. Due to the extreme difficulty in determining arm photophore numbers without causing some damage to intact arms, specimens were X-rayed in an attempt to see if arm photophores could be seen on the film and counted. No photophores were visible on the film so after several attempts the procedure was abandoned.

The gladius was extracted for examination using the method described by Toll (1982), which requires displacement of viscera from the left side to the animal's right, slicing through the stellate ganglion thereby permitting easy removal of the gladius from the shell sac. The gladius thus acquired was stained by use of methylene blue and required measurements were taken with vernier calibers. Beaks and radula were removed for examination by existing the

complete buccal mass from the squid and then soaking the mass in a 10 percent solution of potassium hydroxide. The potassium hydroxide digested adhering tissue and after rinsing in distilled water the beaks were measured using Vernier calipers. The radula was photographed using a WILD Photomat MPS 55 dissecting scope/camera combination.

A number of additional characters were looked at including; funnel locking cartilage, nuchal cartilage and funnel organ sculpturing, and the number and type of brachial armature (ie. hooks and sucker counts).

Statistical analysis of the morphometrics was done using SAS software package (SAS, 1682) on the Memorial University YMS (DIGITAL) computing system. Initially, it was planned to analyze all morphometric and meristic variables but the loss of the arm tips of the majority of the specimens precluded the use of arm and total lengths, hook and sucker counts and axial photophore counts. Thus, only the following measurements were analysed statistically in individual species; mantle width, fin length, fin width, head length, head width, tail length, eye diameter, and lens diameter. Additional measurements analysed in larvae included tentacle length, and arm lengths.

Indices (means, maximum and minimum values) were calculated for the larvae, and individual species. The species indices were generated for size ranges of 25 mm ML intervals. Larval indices were generated for size ranges of 5 mm ML intervals.

Means comparisons, using the general linear models (GLM) procedure, were carried out on juvenile and maturing animals separated into 5 species defined by photophore position and number and hook structure. Each variable was analysed separately in individual GLM procedures. During each procedure the defined variable was compared for all species simultaneously. Each GLM indicated which means differed significantly (at the .05 per cent level) between species.

A Discriminant analysis was then run on the same morphometrics using the discriminant analysis (DISCRIM) procedure. The procedure classified specimens into one of the 5 defined species based on analysis of the morphometrics. It also reclassified any observations that speared to be misclassified originally and listed the number of observations and per cents classified into species. After the first DISCRIM procedure was completed it was found that one of the defined species —Q. sp A had very low numbers (5) and was not being treated with full matrix ranking. A second DISCRIM procedure was therefore run without the species.

Chapter 4 RESULTS

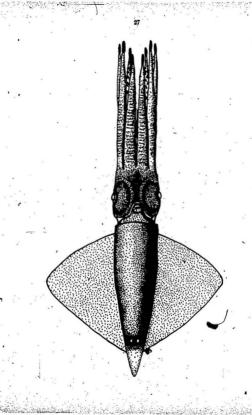
4.1. GENERAL MORPHOLOGY

Specimens of the genus Octopoteuthis, like other decapod squids, bear eight arms and two tentacles. The paired tentacles common to most squids are retained only during the larval period. By the time the animals have reached a dorsal mantle length of 25-30 mm, the tentacles are autotomized, the stumps being gradually resorbed. As adults the animals have large rhomboidal fins extending almost the total length of the mantle. Fin width is usually greater than mantle length (See Fig 4-1).

The mantle is conical, tapering gradually posteriorad. It is composed of layers of muscles internally and a gelatinous outer layer which contains ammonium and is thought to aid the animal in maintaining buoyancy (Clarke et al., 1969; Clarke et al., 1979; Denton and Gilpin-Brown, 1973). Both the gelatinous and muscular layers are heavily pigmented giving preserved specimens a rich purple-red colour. In mature females (of all species) the gelatinous layer at the anterior end of the mantle pear the funnel, becomes rugose.

The arms are nearly equal in length to the mantle and bear biserial hooks and suckers. These hooks, numbering around 40-90 per arm, are formed by the modified chitinous rings of the original arm suckers. A few (6-15) suckers remain near the distal end of each arm. The arms also have a relatinous outer layer Figure 4-1: Drawing of a Generalized Adult squid of the genus Octopoteuthie (ventral view).

(Scale = 10mm)



although most specimens lose much of this during capture. The gelatinous layer is not pigmented but underlying it on arms III and IV on most specimens is a layer of chromatophores arranged in parallel rows running across each arm. This has been previously noted only in Octopateuthia deletron Young, 1972; and O. rugosa Clarke, 1980.

Each species bears a number of photophores found in various locations on the body, ventrally on the posterior portion of the mantle, ventrally overlying the fink sac, one anteriorly on the tissue of the eyelid and another posterio-laterally to the eye between the eyelid and the olfactory papillae (and in some, on the eyeball as well), at the proximal base of each of the arms, and in a series paralleling the axial nerves of the ventral and two lateral pairs of arms. Elongate photophores are also found on the distal tips of each arm. Almost all of these photophores are situated in such a way that light they emit is directed ventrally (Young and Roper, 1977). The high incidence of arm tip loss eliminated the use of axial photophore counts as a possible aid in species identification.

The head is also covered by a gelatinous layer of tissue. The eyes are large, their diameter almost equal to the head length. There are two "olfactory" papillae, ventrally situated on the head, one on either side of the funnel. The funnel extends almost to the midpoint of the eye. The funnel locking apparatus is of a modified, simple, straight type which generally widens posteriorly. The funnel organ consists of an inverted Vishaped dorsal pad and two oval ventral pads. There is a papilla on a small ridge at the apex of the dorsal pad and longer ridges running partway down each side of the V. There was no discernable difference in the sculpturing of the funnel locking cartilage, the nuchal cartilage or the funnel organ in any of the species of Octopoteuthis examined.

Sexual maturity, in both sexes, seems to occur at a varying size range starting at around 80.0 mm mantle length (ML). Gravid females have very large indamental (85 mm in a 215 mm ML female) and oviducal glands. The mature exts are slightly oval and about 2 mm in diameter. In mature mides the penis is

very large extending, in some specimens examined, beyond the mantle cavity opening. Unlike the males of other teuthoid squids, those of Octopoteuthis lack a hectocotylus (the modified arm tip(s) used in spermatophore transfer).

The radula is composed of seven rows of teeth, one median row and three lateral rows to either side.

The gladii in the genus have been inaccurately described in the past. Most illustrations and descriptions were based on very small specimens and were drawn with little or no detail (Jatta, 1896; Adams and Adams, 1858). Structurally the gladius consists of a short free rachis, and wide vanes that join together posteriorly to form a conus (see Fig 4-2).

As stated earlier in this section, larvae differ from juveniles and adults in several ways. Fig 4-3 shows the ontogenetic development of three larvae from 5.0 to 10.9 mm ML. They bear very wide fins, like the adults, but the fin length is less than half that of the mantle. Photophores are nof present in the larval forms to the degree they are in the postlarval and adult configuration. An exception to this generalization is the case of the photophores found at the distal termination of the arms.

A total of 455 specimens of Octopoleuthie were examined representing collections from the North and South Atlantic, the NE Pacific, the Indian Ocean, the SW Pacific in the vicinity of Australia and from the Mediterranean Sea. Sizes of specimens ranged from larvae of L.Torm MI, to the largest adult of 240mm MI.

Of the nine nominal species described only four still have extant types; Octopoteuthia danae, O. nielseni, O. deletron, and O. rugosa. Only the O. deletron and O. rugosa holotypes are adult animals. Both the syntypes of O. nielseni and the holotype of O. danae are juveniles.

The following sections deal with each nominal species separately, giving

Figure 4-2: Drawings of (a.) the gladius and (b.) beaks of Octopoteuthis electron Young, 1972, and (c.) arm hooks (with and without cusps).

[Scale = 10mm]

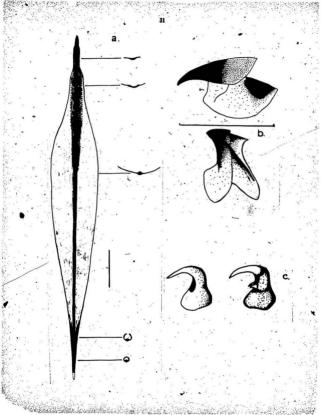
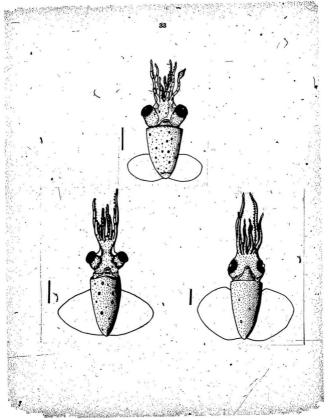


Figure 4-3: Drawings of larval squid of the genus Octopoteuthis showing ontogenetic changes in general morphology (Scale=2 mm).



information on the type specimen(s) followed by a full description of each species listing, characters of the species along with specific comments on the type(s). Where no type specimens exist the original description is given. Only two of the original nine nominal species could be clearly distinguished, dance and [deletron]. Three other species, temporarily designated as A, B, and C could be identified using the same criteria. To attempt to stabilize the systematics of the genus Octopoteuthis species B and C were used as the bases to redescribe the two oldest species, sicula and megaptera respectively. The reasoning for each choice will be discussed in the appropriate section below.

4.2. Octopoteuthis sicula Rüppell, 1844

SYNONYMY.

as Octopoteuthis sicula Rüppell, 1844; Pfeffer, 1884 Ficalbi, 1899; Degner, 1925; Adam, 1952, 1980; Clarke, 1986, 1980; Young, 1972; Nesis, 1982

as Octopodoteuthie sicula Krohn, 1845; Pfeffer, 1900; Hoyle, 1909; Pfeffer, 1908; Thiele 1921, 1935; Chun, 1910; Naef 1921, 1923;

as Verania sicula Krohn, 1847; Tryon, 1879; Verrill, 1882; Hoyle, 1886 a, b; Weiss, 1889; Goodrich, 1892;

as Octopodoteuthis sicula Gray, 1849

as Onychoteuthis (Verania) sicula Verany, 1861 as Veranya sicula Keferstein, 1866; Tiberi, 1880; Fischer,

1887; Pelseneer, 1894; Jatta, 1896;

as a synonym of Enoploteuthis in Woodward, 1871

Type: Juvenile, 44 mm ML, not extant.

Type Locality: From off Messina, Italy, 27 February 1844.

Material examined: see Appendices I and II.

DESCRIPTION.-Translated from Rüppell, 1844.

Finally, however, our honourable friend Dr. Krohn who is preparing the publication of a new genus of cephalopod, he recently uncovered, which I also collected and observed alive, permitted me the opportunity to give a short note calling it to the attention of Sicilian malacologists. This genus that is decreed to be called

Octopoteuthis.

combines the characteristics of the species Octopus, Loligo, and Enoploteuthis. In it, the head, the mouth of which is surrounded by eight tentacles equal in length and equipped with a double longitudinal set. of little hooks, rests on a visceral sac which is conical, funnel-shaped and supported by a very thin horny layer and which has on its dorsal side for two-thirds of its length towards the apex, a large fin-like subcordiform nembrane.

We call this species

Octopoteuthi siculiana

Octopoteuthis sicula

This has under the head a small, fleshy prolongation, thirty pairs of tiny hooks in alternate rows above each tentacle. The live animal is a translucent rosy colour, the ends of the tentacles a deep red.

In the dead animal the chromatophores produce many yellowish-red spots over the whole surface. The total length of the body and the tentacles is from 2.5 inches and the maximum transverse breadth of the fin is from 15 lines. (a line= one 12th of an inch)*

DESCRIPTION-O. sicula, an Atlantic and Mediterranean species, closely resembles Octopoteuthis dance although it does bear characters that separate the two.

The mantle is conical and covered with a gelatinous layer. The tail length is approximately 14 per cent of the ML.

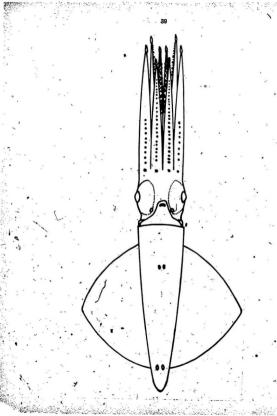
As in other species the fine are large and muscular. Fin length is 75 per cent of the ML while the fin width is 115 per cent of ML.

The head itself is robust with Thick outer gelatinous layer.

Figure 4-4: Photograph of Rüppell's original unpublished illustration of the holotype of *Octopoteuthis sicula*. (Courtesy of Ronald Jannsen, Curator of Invertebrates, Senckenberg Institut, Frankfurt, F. D. R.).

Octopolduthis s Nov. Genis. Then alt time just mil jeder pette the in though and grape field the the Marche 'min Kyafet de hellen to a les an nate de layer of the landinger on Kome Lay the Key 120. Prose 1 semo 72. 26 204. Maple 27/2 1844

Figure 4-5: Drawing of Octopoleuthie sicula Rüppell, 1844 showing photophore patterning.



The funnel is large and extends about half-way along the length of the head.

The arms have hooks which bear accessory cusps unlike the closely related species Octopoteuthis danae. The arm formula was II>III>IV>I in a 215 mm ML female.

A pair of photophores is found ventrally on the posterior portion of the mantle. There is a pair of photophores located ventrally adjacent to the ink sac, and a single photophore at the posterio-ventral position of each eye. The arms III and IV each have a series of axial photophores (43 and 25 respectively in a 215 mm ML female). (See Fig 4-5)

The gladius has a short, free rachis with RLI and RWI of 10 and 2 percent respectively. The rachis begins to form a dorsal keel about 1/3 of the way down its length. Anteriorly the vanes taper down to the rachis in a series of three gradual contractions. The vanes (GWI = 12 percent) begin to curl ventrally about 85 percent of the way down the gladius. The vanes which form the secondary conus (CLI = 2 percent) do not begin to fuse until the vanes have run together for a distance greater than the conus length. (See Fig 4-6)

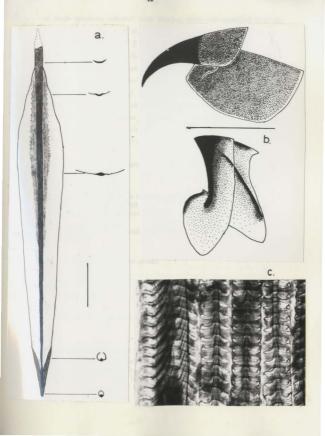
The radula has a tricuspid rachidian, bicuspid first lateral, and unicuspid second and third laterals. The outer cusps of the rachidian and first laterals are semall. The rostrum of the lower beak is about 1/3 the length of the wing. The rostral edge is almost straight with a hooked tip and the jaw angle is obtuse. The upper beak has a greatly curved rostrum and the jaw angle is acute.

DISCUSSION. The type specimen of sicula could not be traced; however Rüppell's original unpublished illustrations (see Fig 4-4) of the specimen were located at the library of the Senckenberg Institute in Frankfurt, Germany.

The illustrations give no indications of the photophore pattern of the specimen so little could be determined except the animal's basic habitus.

Figure 4-6: Drawings of (a.) gladius (with cross sections), (b.) beaks and a photograph of (c.) portion of radula from specimens of Octopoteuthis sicula Rüppell, 1844.

(Scale = 10 mm)



A single specimen collected from Messina, Italy was examined from the collections of the Royal Scottish Museum. It is a 28.3 mm ML animal bearing a pair of abdominal photophores. The hooks have all been dissolved away during preservation but it appears by the intact hook sheathing that accessory cusps were probably present. No photophores were visible on the eyeball or the anterior portion of the eyelid. The species B listed above bears paired abdominal photophores, no eyeball or eyelid photophores and hooks with accessory cusps. The similarity of the characters and the distribution of B throughout the North Atlantic including the Mauritanian subprovince associated with the Mediterranean subprovince (Backus and Craddock (1977) and Backus et al. (1977)) imply that species B is most probably Ruppell's sicula.

4.3. Octopoteuthis megaptera (Verrill, 1885)

SYNONYMY .-

as Octopoteuthis megaptera Clarke, 1986, 1980; Young, 1972; Linka, 1975; Nesis, 1982

as Ancistrocheirus megaptera Verrill, 1885; Hoyle 1886

as Octopodoleuthopsis megaptera Pfeffer, 1912; Berry 1920 a; Voss 1956 a, b;

Holotype: Juvenile, 44 mm ML, not extant.

<u>Type Locality: ALBATROSS</u>, Sta 2235, 39° 12'N, 72° 03'W, 500 mw, 09:49, 13 September 1884.

Material examined: Holotype not located. For other material see Appendices I and

ORIGINAL DESCRIPTION -

"Ancistrocheirus megaptera Verrill, sp. nov. Body small, rather short, with an acute posterior end, extending a little beyond the posterior border of the fin. Fins very large, thick and strong, attached nearly the entire length of the body, and together forming a broad,

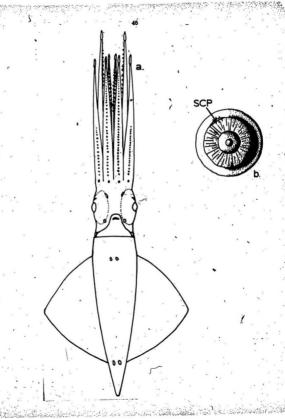
rhombic figure, with the outer angles behind the middle; anteriorly the attachment of the fin does not reach quite to the edge of the mantle. and the front edge forms a slightly rounded lobe in front of the attachment; posteriorly the fins are nearly united, across the back, but leave the acute, posterior tip of the body free for a short distance. The front edge of the mantle receeds in a broad curve ventrally, but has slightly prominent lateral lobes and a broad obtuse dorsal angle, which extends farther forward than the lateral does. The head is rather large, with large eyes, furnished with thin free lids. The siphon is rather large, with two small dorsal bridles. The connective cartilages on its base are rather smal, ear-shaped, such as in Ommastrephes. The arms are rather large, not very unequal in size, the dorsal ones slightly smaller than the others; all are unusually rounded and most of them, in our specimen, have lost their tips. They all bear two alternating rows of small prominent sharp claws, which are not very closely arranged. The inner face is not separated by a distinct margin. The tentacular arms are wanting. Color, in alcohol, orange-brown, due to nurmerous purple and brown specks scattered pretty uniformly over the surface. both above and below; the outer portions of the fins appear to have been transparent; the surface of the body appears to have been entirely smooth and destitute of tubercles, although the specimen is so much injured as to make this a little uncertain. Length of the body to front edge of mantle, 44 mm; length of free caudal portion, 8 mm; length of the attachment of fin, 34 mm; from front margin of fin to mantle edge, 3.5 mm; breadth across fins; 56 mm; length of head, from dorsal cartilage to base of dorsal arms, 19 mm; length of dorsal arms, 24 mm; diameter at base, 3.5 mm; diameter of lateral arms, 4 mm. A single mutilated specimen (No. 40,128) was taken at station 2235, 707 fathoms, 1884. This species closely resembles A. veranvi, recorded from the Indian Ocean, but it apparently differs from the latter by having larger fins and in being destitute of the rows of tubercles on the mantle: the arms also appear to differ in their proportions."

DESCRIPTION. The mantle is broadly conical with the tail making up approximately 14 per cent of ML in maturing adults.

The fins are large, their length being 71 per cent of ML while fin width equals_about 91 per cent of ML.

The head bears large eyes whose diameter nearly equals total head length.

Figure 4-7: Drawing of Octopoteuthis
megaptera (ventral view) showing
photophore patterning. EP - eye
photophore. (Scale = 10 mm)



The funnel projects about half-way along the length of the head. The dorsal pad of the funnel organ is an inverted V-shape with ridges running down each arm and a small papilla at the apex of the V.

The arms have hooks with accessory cusps. In a 113 mm ML female hook and sucker counts were as follows: LI - 50 hooks, 10 suckers; LIII - 53 hooks, 10 suckers; RII - 68 hooks, 12 suckers.

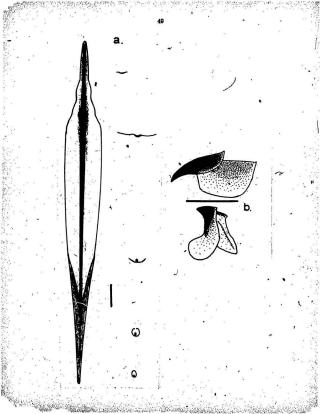
There are paired photophores on the ventral portion of the mantle. Paired photophores are also found adjacent to the ink sac. Single photophores are located at the anterior end of each eyeld. A crescent-shaped photophore is found on each eyeball, in an antero-dorsal position, at the junction of the iris and the sclera. These eye photophores are easily seen in specimens as small as 30 mm ML and are creamy white in colour (see Fig 4-7).

The gladius, like those of other species, is quite delicate (see Fig 4.8). There appears to be little or no free rachts with very narrow anterior vane extensions unning right up to the anterior tip of the gladius. The RLI and the RWI of the anteriormost portion of the gladius is 11.3 and .7 percent respectively. The rachis begins to form a dorsal keel about 1/3 of the way along its length. The vanes (GWI = 9.66 percent) begin to curl ventrally about one third of the way down the gladius. The fused portion of the vanes which form the secondary conus (CLI = 7.3) do not begin until the vanes have run together for a distance equal to the conus length.

The radula has a tricuspid rachidian, bicuspid first lateral, and unicuspid second and third laterals. The outer cusps of the rachidian and first laterals are small. The rostrum of the lower beak is about 1/3 the length of the wing. The rostral edge is almost straight with a hooked tip and the jaw angle is obtuse. The upper beak has a curved rostrum and the jaw angle is slightly acute.

DISCUSSION.-Although Verrill provided good morphometric measurements

Figure 4-8: Generalized diagram of (a.] gladius (with cross sections), (b.) beaks from specimens of Octopoteuthis megaptera.



he gave no indication of the presence of photophores or the structure of the hooks of his new species. With the holotype lost there can be no way of determining these characteristics. Four identifiable species of Octopoteuthis occur in the Northwest Atlantic, and with the exception of Young's O. sp A all have been collected near the type locality of O. megaptera. The long standing use of the species names sicula, megaptera and dance and the real need to stabilize the systematics of the genus warrant retention of megaptera as a valid species. Since sp C, listed earlier, remains the only species of the three in the area without a name it will be designated as megaptera.

4.4. Octopoteuthis indica (Naef, 1923)

SYNONYMY.-

as Octopodoteuthis indica Naef, 1923

as Octopoteuthis indica Young, 1972; Clarke, 1980

Holotype: Larva, 3.8 mm ML, not located.

<u>Type Locality</u>: VALDIVIA, Sta 102, 13° 2'N, 46° 41'W, vertical net, 0-1800 m, 1898-1899.

Material Examined: Holotype not located and no additional material found.

ORIGINAL DESCRIPTION - Translated from Naef:

• ...the larva described by Chun (1910, Plate XVII, Figures 3, 4, 9) from the Agulhas Current differs from the Mediterranean specimens. The stage of development is similar but the arm apparatus is markedly less developed. There are much fewer suckers and terminal swellings are absent, even-on the second pair, which is the longest. On the other hand, the tentacles are relatively strong. These are obviously two different species and I propose the name Cotpodictuitis indica now. spec. for this larva. It is significant that this larva already has a buccal funnel consisting of 6 parts at a dorsal mantle length of 3.8 mm.*

DISCUSSION. The holotype of this species could not be located so character examination was limited to the brief translated description and the few illustrations in Chun's monograph. Since none of the photophore patterns or the hook structure could be determined and basing species on larval specimens is at best risky Octopoteuthis indica should be considered a nomen dubium.

4.5. Octopoteuthis persica (Naef, 1923)

SYNONYMY.-Translated from Naef:

- as Octopodoteuthis persica Naci, 1923
- as Octopoteuthis persica Young, 1972

Holotype: Larva, 4.7 mm ML, not located.

<u>Type Locality: VALDIVIA</u>, Sta 271, 34° 31'S 26° 0'E, vertical net, 0-1200 m, 1898-1899.

Material Examined: Holotype not traced. No additional material found.

ORIGINAL DESCRIPTION.-

The oldest stage described by Chun (Plate XVII, Figures 1, 2, 7, 8) probably belongs to a third species. Although it is larger and more developed, it shows no evidence of conversion of suckers into hooks. I name this form Octopodoteuthis persica. The young O. persica has a mantle length of only 4.7 mm, compared with 6.5 mm of the specimen of O. sicula described below. The fins of the specimen of O. persica, however, are much larger, occupying 2/3 of the mantle length and their span is more tham 1.5 times that of the mantle length. On the other hand, the arm apparatus of O. persica is even less developed than that of the stage described above: the third and fourth arms are still shorter than the first, and terminal swellings fore only present on the second pair. All these differences are so marked that they cannot belong to the same species.

Discussion. The specimen Nacf described as a new species persica appears from all evidence to be a larval specimen of Taningia danae Joubin, 1931. Nacf's description and Chun's illustration of the terminal swellings of arms II is indicative of Taningia and not Octopoteuthie. This agrees with the findings of Clarke, 1980 and Young, 1972. O. persica must therefore be considered a nomen dublum.

4.6. Octopoteuthis danae (Joubin, 1931)

SYNONYMY.-

as Octopodoteuthis danae Joubin, 1931 as Octopoteuthis danae Young, 1972; Clarke, 1980;

Holotype: Juvenile female, 32 mm ML, in good condition in Zoologisk Museum, University of Copenhagen. (See Fig 4-9)

<u>Type Locality</u>: DANA Sta 1341 V, 33 * 15'N, 68 * 20'W, 1500 mw, S-200, 19:30, '

Material Examined: Holotype and additional material (See Appendices I and II).

DESCRIPTION. The mantle is conical in shape and somewhat gelatinous ending in a blunt point. The mantle projects beyond the posterior portion of the fins and forms a tail averaging about 16 per cent (18.7 per cent in the holotype) of the mantle length.

The fine are large, rhomboidal and their length is 77 per cent (71 per cent in the holotype) of the mantle length. Their posterior ends follow along the lateral edge of the tail in the form of narrow strips while the anterior edge of the fins form free lobes.

The head is large with the eyes occupying almost it's total length. The olfactory papilla lies posteriorly on the head, lateral to the base of the funnel. The head is encased in a thick gelatinous layer.

The funnel extends nearly to the midpoint of the eyeball. The funnel locking cartilage is a modified simple straight type. The actual shape is like an-elongate raindrop. The funnel organ is in three parts: a dorsal inverted V-shaped pad; and two ventral oral-shaped pads. The dorsal pad has a papilla resting on a

Figure 4-9: Photograph of the Holotype of Octopoteuthis danae (Joubin, 1931).



short anterior ridge. Other ridges run about halfway down each shoulder of the V. The sculpturing of the funnel organ can be highly variable. A funnel valve is present.

The arms are very brittle and are almost always broken distally. This makes determination of the arm formula difficult. In mature specimens they appear subequal. Larger specimens may have 50+ hooks and 6-10 suckers per arm. The hooks are alternating arranged in two rows and are enclosed in fleshy sheaths. The hooks have no accessory cusps. The distal arm tips are bare of hooks or suckers. At each arm tip there is a distinct swelling containing the subcutaneous elongate distal photophores. In the holotype only arms IV still intact. They are 19.0 and 20.0 mm long (right and left respectively). Each ventral arm bears about 45 hooks basally and approximately 9 suckers near each distal tip.

There are paired photophores on the ventrum of the mantle, another pair on the musculi recti abdominalis and a third pair on the ventral portion of the head near the olfactory papilla. There were no photophores on the eyeball or at the anterior of the eye orbit. There are approximately 24 photophores located along the axial nerve of each ventral arm. Photophores were found at the base of arm pairs II and III but none were found at the base of the dorsal arms. (See Fig 4-10)

The gladius has a short free rachis with RLI and RWI equal to 10 and 2 percent respectively. The rachis begins to form a dorsal keel about 1/3 of the way down its length. Anteriorly the vanes taper down to the rachis in a series of three gradual contractions with the final contraction before the free rachis being barely visible(see Fig 4-11). The vanes are widest at about the midpoint of the gladius (GWI = 6 percent) and begin to curl ventrally about 85 percent of the way down the gladius. The vanes do not begin to fuse until the vanes have run together for a distance greater than the comus length (CLV = 11 percent).

The radula has a tricuspid rachidian, bicuspid first lateral, and unicuspid

Figure 4-10: Drawing of Octopoteuthis danae
(Joubin, 1931) showing photophore patterning.

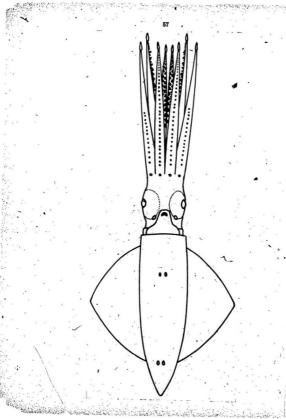
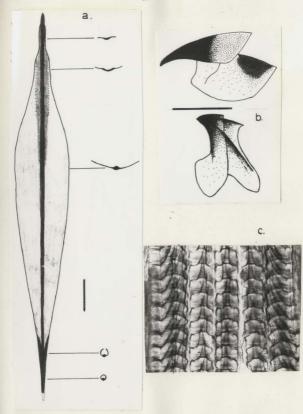


Figure 4-11: Drawings of (a.) a gladius (with cross sections), (b.) beaks and a photograph of (c.) portion of radula from specimens of Cotopoteulhis dance (Joubin, 1931) (Scale = 10mm)



second and third laterals. The outer cusps of the rachidian and) first laterals aresmall. The rostrum of the lower beak is about 1/3 the length of the wing. The rostral edge is almost straight and the jaw angle is slightly obtuse. The upper beak has a curved rostrum and the jaw angle is acute.

4.7. Octopoteuthis nielseni (Robson, 1948)

SYNONYMY.

as Octopodoteuthis nielseni Robson, 1948 as Octopoteuthis nielseni Young, 1972; Clarks, 1980; Nesis, 1982

Syntypes: Two juveniles, 28 mm ML (Robson, 1948) in extremely dehydrated condition, deposited in the British Museum (natural History), BM

Type Locality: ARCTURUS, Sta 74, 4 * 50'N, 87 * 00'W, near Cocos Island,
Pacific Ocean, 0-727 and 0-909 m, open townet, 14:30, 2 June 1925.

Material Examined. Syntypes.

ORIGINAL DESCRIPTION.-

In O. nielseni the suckers and hooks are arranged in a zig-zag about the median furrow. So much damage has been done to the arms that it is not easy to say how many hooks there were. On one arm there are at least 20 pairs.

The hooks are, as in sicula, sheathed in fleshy casings and are upright and columnar. The fins are 84% of the body-length and their total

span is 130% of the mastle-length (both figures are the same as in sicula). The cephalic component of the adhesive-organ is not like that of sicula as shown in Pfeffer's fig. 9, pl. 12 (1912); there is a far wider and less distinctly channelled groove. Unlike those of sicula the arms are rounded and have neither the "Schwimmsaume" nor the "Schwitzsaume" nor the "Schwitzsaume" nor the "Schwitzsaume" nor the properties of the state of sicula figured by Jatta (1896) though it is a little more like that shown by Sasaki (1929). The radula is quite unlike that of sicula (Jatta, 1889, pl. 1.3 fig. 8) in its rhachidian tooth, with an extraordinary small base and square admedian tooth.

w. The general shape and the form of the fins are not particularly different from those of sicula (e.g. as given by Pfelfer and Sasaki). The adhesive-organ, radula and the entire lack of membranes on the arms (which cannot be due to damage) are, however, features which preclude our ranking, it with sicula. The adhesive organ is of uncertain importance. Another point of diagnostic value is the great length of the third arms.

sicula. Jatta. Longest arms 25 mm. Pfeffer. Longest arms equal mantle. Sasaki. Longest arms slightly shorter than mantle.

nielseni. Longest arms 36 mm., mantle 26 mm.

DISCUSSION. The syntypes were borrowed from the British Museum (natural History) but were so severely dehydrated that no measurements or meristic could possibly be taken. The lack of knowledge about the photophore patterns and hook configuration of the syntypes inhibits any attempt to validate the species. The species C listed above has been assigned to Octopoteuthis' megaptra but appears to be found circum-globally. Future comparison of Atlantic and East Indian Ocean/West Pacific material may discern enough difference in characteristics to separate species C into two species the Pacific one being nicleent. Until that time nicleent must be considered a nomen dublum.

4.8. Octopoteuthis longiptera (Akimushkin, 1963)

SYNONYMY .-

as Octopodoleuthis longiptera Akimushkin, 1963

as Octopoteuthis longiptera Young, 1972; Clarke, 1980;

Nes18, 1982

Holotype: Adult, 590 mm ML, not extant (K. N. Nesis, personal communication).

Type Locality: From Sperm whale stomach, 20 ° S, 25 ° W.

Material Examined: None available.

DESCRIPTION.-Akimushkin's original description is as follows.

 ...head and arms had traces of a jellylike tissue which apparently covered the body of the live animal and had been partially digested.

Mantle, conical, 3 times as long as wide (c/l=33%). Dorsal margin of mantle protruding markedly forward to form an acute angle. Ventral incision inconspicuous. Fins long, extending from anterior margin of mantle (excluding the dorsal protuberance) along entire lateral surface to posterior and of mantle, where they narrow markedly to form a narrow border. Fins oval with the longer axis situated along the body, 38% longer than wide, 92% of the mantle length measured with the dorsal protuberance.

Head large but narrower than the mantle (o)c=70%). Eyes very large, convex but not stalked. Nuchal folds absent. Tuberculus colfactorius (airly long but thin and inconspicuous. Infundibular funnel of medium depth.

Funnel very long, terminally protruding beyond anterior margin of eyeball, though the eyes of this species are not small. Infundibular cartilage large, subtriangular, with narrow anterior and wide, obtuse posterior end. Central pit of infundibular cartilage deep, wide, pyriform.

Buccal membrane with 6 apexes and 7 rays. Two dorsal pairs of buccal darts attached dorsad to suckers of corresponding arms, two ventral ones ventrad. Arms of medium length (//L=47%). The tips of all but the second and third arms had been cut off, so their length is unknown. The second, however, is much longer than the third. Swimming carinas destroyed or absent. Fragments of protective membrane-show that these were well developed of the base of the arms (where they covered the hooks completely) and probably had an undulate margin. All arms bear two dense, rows of large hooks. Terminally the hooks diminish in size and the rows fuse into one zigas fine. Terminal part (7-8%) of arms covered with minute suckers disposed at first in a straight row but as the arm widens form a zigas pattern and terminally reappear in a straight row. The terminal swellings of the arms, typical of the genus Octopodoleithis, are almost imperceptible in our specimen; on the other hand, the tips of the preserved arms are somewhat compressed laterally.

Tentacles totally absent, without even a trace of their site of attachment. Beak with ventral mandible of highly characteristic form. Total length of specimen 590 mm.

DISCUSSION-ALthough Akimushkin described the largest Octopoteuthis specimen ever recorded in the literature the diagnosis of his new species lacked any good characters to separate his species with any others. Coupled with that that the holotype is no longer extant this species must be considered a nomen dubium. This agrees with the observations of Young, 1972; Clarke, 1980 and even Nesis, 1982.

4.9. Octopoteuthis deletron Young, 1972

SYNONYMY .-

as Octopoteuthis deletron Young, 1972

as Octopoleuthis sicula Pearcy, 1985; Okutani and acGowan, 1969

Holotype: Male, 109 mm ML, extant and in good condition, deposited in the Allan

Hancock Foundation, Los Angeles, California, Catalogue No. C-type#3.

Type Locality: VELERO, Sta 8716, 33 * 15'N, 118 * 37'W, 950 mw, IKMT, 7

June 1983.

<u>Material Examined</u>: Holotype and one paratype plus additional material. (See Appendices I and II)

DESCRIPTION.-The holotype of O. deletron is in the best condition of any of the existing species types (see Fig 4-12). It is a maturing male (100 mm ML) with several complete arms. The holotype has undergone some shrinkage (10-15 per cent) in most body measurements (see Table 4-1).

Table 4-1: Variation in body measurements in the holotype of Octopheuthis deletron after 15 years of preservation.

BODY LENGTH PRESENT MEASUREMENT ORIGINAL MEASUREMENT

(Young, 1972)

			(mm)
_			
	MI.	100.0	109.0
	MA	30.0	37.0
- 8 91	FL ,	· 80.0	94.0
	FW	96.0	104.0
	HW	29.3 .	33.0
	TIL	. 8.0	13.0

The mantle is conical with the posterior apex appearing very blunt due to ventral curving of the tail. The tail averages about 16 per cent of the mantle length in adults (8 per cent in the holotype).

The fine are large as in other species. Posteriorly, they appear to end short of the mantle but actually continue as reduced narrow strips along each lateral edge of the tail. The fin length averages 75.6 per cent (80 per cent in the holotype) of the mantle length.

The head is fairly large and the eyes extend almost the entire length of the

The funnel is fairly long extending almost to the midpoint of the head. The funnel lockingcartilage is a modified simple straight form which posteriorly curves slightly and flares. As in other Octopoteuthis species the dorsal pad of the funnel organ is an inverted V-shape with short ridges on the arms and a prominent papilla on a ridge at the apex. The ventral pads of the organ are oval.

There are two complete arms in the holotype, the ventral right (IV) and the ventral-lateral left (III). The second right arm (III) is regenerating but this will be discussed in a later section. Each arm has gelatinous aboral keels. The arms bear two rows of small hooks protected by fleshy sheaths. There are two distinct, small accessory cusps on each hook. There are 3-11 small suckers at the distal end of each arms (just before the distal elongate photophore).

There is a single photophore on the ventrum of the mantle (a character shared with only one other Octopotenthia species). Paired photophores are found lying ventrally on the ink sac, and two ventrally, one, on each side of the of the head near the olfactory papillae. Single photophores are found near the anterior medial margin of each eye and are obliquely orientated. The third and fourth arm pairs each have a series of photophores lying near the axial nerve. The basal photophore in each series is larger than those following it and is somewhat isolated from the others. In the holotype the arms IV bear about 25 photophores and arms III bear about 2 photophores. Arms II bear just the basal photophore while armq I lack any of the series. All four arm pairs bear the distal elongate photophores. (See Fig 4-13)

The gladius has a short free rachis with RLI and RWI equal to 4.6 and 1.6 percent respectively (see Fig 4.14). The rachis begins to form a dorsal keel about 1/3 of the way down its length. Anteriorly the vanes taper down to the rachis in a series of three gradual contractions with the final contraction before the free

Figure 4-12: Photograph of the Holotype of Octopoteuthis deletron Young, 1972.



Figure 4-13: Drawing of Octopoleuthis deletron Young, 1972 showing photophore patterning. (Scale = 10mm)

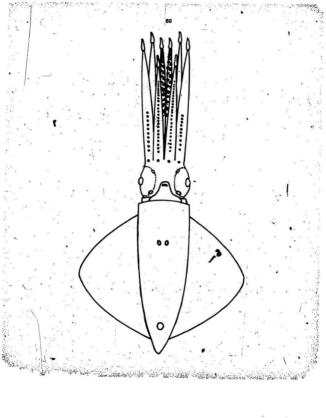
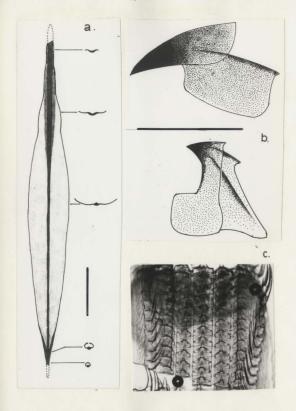


Figure 4-14: Drawings of (a.) a gladius (with cross sections), (b.) beaks and photograph of (c.) portion of radula from specimens of Octopoteuthia deletron Young, 1972

(Scale = 10mm)



rachis being barely visible. The vanes are widest about halfway down the gladius (GWI = 6.9 percent) and begin to curl ventrally about 85 percent of the way down the gladius. The vanes do not begin to fuse until the vanes have run together for a distance greater than the conus length (CLI = 5 percent).

The radula has a tricuspid rachidian, bicuspid first lateral, and unicuspid second and third laterals. The outer cusps of the rachidian and first laterals are small. The rostrum of the lower beak is about 1/3 the length of the wing. The rostral edge is almost straight with a hooked tip and the jaw angle is obtuse. The upper beak has a curved rostrum and the jaw angle is acute.

4.10. Octopoteuthis rugosa Clarke, 1980

SYNONYMY -

as Octopoteuthis rugosa Clarke, 1980, Nesis, 1982; Toll, 1982; Roper, Sweeney, and Clarke, 1985

<u>Holotype</u>: Mature female, 160 mm ML, in fair condition in the British Museum (natural History), BM 1973.100. Three paratypes also extant.

Type Locality: From sperm whale stomach, Donkergat, South Africa, 29 September 1963.

Material Examined: The holotype and a paratype (see Appendices I and II)

DESCRIPTION.-The holotype and a paratype of Octopoteuthis rugosa were examined. The holotype is a large mature female (see Fig 4-15) and the paratype is a male, both collected from a whale stomach.

The mantle is large and conical, tapering posteriorly into a large tail.

Although there is a considerable amount of digestion of the outer epithelium, the structure of the mantle can still be determined. There is found, both at the anterior and the posterior ends of the mantle, an outer gelatinous covering. In

Figure 4-15: Photograph of the holotype of Octopoteuthis rugosa Clarke, 1980 (arrows = 15 mm).





the holotype, the gelatinous layer at the anterior end bears longitudinal grooves.

The rugose mantle, for which the species was named, is a secondary sex character, as Clarke suspected. It is found in all fully mature female Octopoteuthie and is not species specific.

The fine are about 80 per cent of the ML in the holotype and 85 per cent in the paratype. The posterior end of the fins forms small lateral ridges on the tail of each specimen. The tail makes up about 16 per cent of the ML.

The head is large, with the eye diameter nearly equal to head length.

The funnel reaches nearly to the midpoint of the eye. The funnel locking cartilage is simple and straight but modified so that the posterior portion flares out slightly. The funnel organ has been dissolved in both specimens so that distinguishing characters have been obliterated.

There are only two intact arms in the holotype (arms III) and one in the paratype (right arm IV). Almost all of the hooks and suckers were lost from the arms so no accurate count could be taken.

In Clarke's (1980) description of his new species O. rigosa he expressly stated that he could find no photophores. Careful examination of both the holotype and the paratype revealed a number of photophores on both (although neither animal bore a complete set). There are paired photophores on the posterio-ventral side of both mantles (see Fig 4-16 for those of the female holotype), a pair of photophores on the recti abdominis muscles of the male, and eye orbit photophores on both. There were 12 photophores located along the axial nerves of arms III of the holotype and about 40 in the arms IV of the paratype. The condition of all but a few of these photophores was admittedly very poor but they are clearly demonstrable. It is not surprising that these organs, obviously missed by Clarke (1980), are in poor shape since these specimens were secured after having undergone partial digestion in a sperm whale stomach.



Figure 4-16: Photograph of the posterior ventral portion of the mantle of the holotype of *Octopoteuthis* rugosa Clarke, 1980 showing the paired photophores (arrows = 15 mm).

DISCUSSION-Clarke separates rugosa from other Octopoteuthis species by (1) lack of photophores on the mantle wall and ink sac, (2)a rugose mantle, in females and (3)lateral pigment bands on the ventral arms (first described in O. deletron by Young in 1972 is common to all species). Examination of Clarke's specimens show that photophores are present. The rugose mantle is found in all sexually mature female Octopoteuthis and the lateral pigment bands are present in all species. Thus there appear to be no characters by which rugosa can be identified as a distinct species and, as a result, it should be considered a nomen dublum.

4.11. Octopoteuthis sp A

DESCRIPTION. Young (1972) first used this designation for a species of Octopoteuthis found in the Atlantic that, like his O. deletron, bore a single ventral abdominal photophore on the mantle. (See Fig 4-17)

The mantle is conical with the tail portion averaging about 15 per cent of total mantle length. Like the other species of the genus, the mantle bears a gelatinous outer layer.

The fine are large and muscular, their length 77 per cent and their width about 104 per cent of ML.

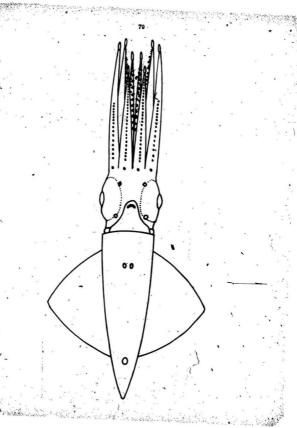
The head is large (37 per cent of ML) with the eye diameter almost equal to it's total length.

The funnel is relatively long, reaching nearly to the midpoint of the head. The inverted V-shaped dorsal pad of the funnel organ is, as in other species, highly variable in form. It generally has a small papilla on the apex of the dorsal pad with small to high ridges running down each arm.

The arms have hooks (65-70 per arm in an 84 mm ML specimen) which lack accessory cusps. The arms also bear several small pairs of suckers distally (7-10 in an 84 mm ML specimen).

Figure 4-17: Drawing of Young's

Octopoteuthis sp A showing
photophore patterning.



There is a single photophore found ventrally on the posterior portion of the mantle. As in all species there are paired photophores lying ventrally adjacent to the ink sac and at the posterior portion of the eye orbit. There is also a pair of anterior eyeball photophores as in O. deletron. These eyeball photophores are almost square. There are serial photophores along arms III and IV.

The gladius is fragile with the free portion of the rachis (RLI = 13.6 percent) being wider (RWI = 3 percent) than in other Octopoteuthia species. The vanes (GWI = 8.6 percent) are very thin and appear to tapper posteriorly. In effect the two vanes begin to curl ventrally about two-thirds of the way down the gladius until they touch and fuse; forming a long secondary conus (CLI = 15.9 percent), posteriorly. (See Fig 4-18)

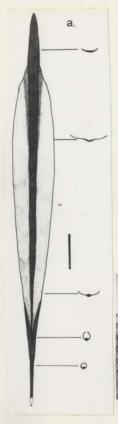
The radule has a tricuspid rachidian, bicuspid first lateral, and unicuspid second and third laterals. The outer cusps of the rachidian and first laterals are small as in other species. The rostrum of the lower beak is about 1/3, the length of the wing. The rostral edge is almost straight with hooked tip and the jaw angle is almost ninety degrees. The upper beak has a slightly curved rostrum and the jaw angle is acute.

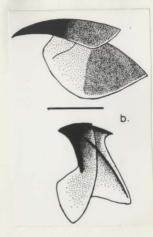
4.12. Statistical Analysis of Morphometric Data

The summary of indices for each species are presented below in a series of tables 4-3 to 4-7. Each index is handled in 25 mm ML intervals for the entire size range available for each species. Larval indices (see Table 4-2) are handled in 5 mm ML intervals although they cannot yet be identified to species. The arm length indices and the tentacular length indices are not presented for the individual species because of the very high percentage of loss of arms and total loss of tentacles in juveniles and adults.

The means comparisons of each variable gave an indication of differences between species presented in tables 4-8 through 4-15.

Figure 4-18: Drawings of (a.) gladius (with cross sections), (b.) beaks and photograph of (c.) portion of radula from specimens of Octopoteuthis sp A (Scale = 10mm)







C.

. 83

Table 4-2: Summary of indices for selected 5 mm increment series of Octopoteuthis spp larvae,

			14			
INDEX	N	- HEAN	· HINIHUH	- MAXIHUH VALUE	STD ERROR OF MEAN	DEVIATIO
		No. of London		-		
			AL	- 6-10 mm		
			4			
HWI .	35	0.48	0.26	0.49	0.01	0.09
FLI .	35 73	0.68	0.00	1.33	0.02	0.18
FWI .	67.	. 1.41	0.29	2.56	0.04	0.36
HLI	38	0.48	0.34	. 0.65	0.01	0.08
	34	0.57	0.40	0.69 .	9.01	0.08
	73	0.00	0.00	0.21	0.00	0.03
	35	0.20	. 0.06 .	0.33	. 0.01	0.04
	33	0.07	0.04	0.10	0.00	0.01
	13-	0.56	0.35	0.77	0.04	0.13
TLI	12	2.06	1.69	2.70	0.08	0.26
	73	0.02	0.00	0.78	0.01	0.12
	2	1.08	1.02	1.14	0.06	0.09
ALI.III	2	0.93	0.88	. 0.98	0.05	0.07
ALI IV	2	0.50	0.45	0.55	0.05	0.07
				L . 11-15 as		
	1 1	,		r - 11-13 mm	* .	
INI	16	0.41 -	0.30	0.50	0.01	0.06
	25	0.78	0.58	1.25	0.03	0.13
FUI	25	1,29	-0.46	2.00	. 0.06	7 0.32
	16	. 0.41	0.30	0.53	0.02	0.07
IWI	16	0.48	0.39	0.55	0.01	.0.05
TILI .	25	0.02	0.00	0.14	0.01	0.04
	16	0.18	0.10	0.25	0.01	. 0.04
	16	0.06	0.04	0.09	0.00	0.01
TtLI .	0					10.
TLI .	9 .	1.95	. 0.25	2.51	0.23	0.69
	25	.0.08	0.00	0.72	0.05	0.23
ALI II -	3	1.06	0.23	1.12	0.06	0.11
ALI III	6 -	0.78	0.83	. 0.93	0.05	0.12
ALI IV	6	0.63	0.08	0.79,	0.11	0.28
	,			L - 16-20 mm		
			,	- 10-10 44		
HUT	9.	. 0.39	0.31	0.51	0.02	0.06
FLI	15 .	0.77	0.42	1.06	. 0.03	0.13
	15	1.33	0.59	1.76	0.06	0.25
	10	0.38	0.27	0.45	0.02	0.05
	10	0.41	0.26	. 0.50	0.02	0.07
	15	0.05	0.00	. 0.19	- 0.01	0.06
	10	0.19	. 0.15	0.25	0.01	0.03
	10	0.06	. 0.04	. 0.08	0.00	0.01
TELI	0			2.44	• ` `	
TLI .	5	1 2.22	2.07		0.06	0.14
ALI II	15	0.18	0.00	0.79	0.08	0.31
ALI III	2 .	0.83	0.78	0.87	0.05	0.07
ALI IU	3 ,	0.67	0.49	0.60	0.00	0.01
			, 3.47	3.80	. 0.03	0.05
				-	1	

Table4-2, continued

* 4	INDEX	N	HEAN	HINIHUH	HAXINUH	STD ERR	OR · STANDARD
	JAPEX		HEAR	VALUE	VALUE	OF HEA	
				нь -	21-25		
5						- 0	
C	HWI	3	0.31	0.23	0.38	0.05	0.08
	FLI	4	0.64	0-37	0.76	0.09	0.18
	. FWI	4	1.16	0.74	1.40	0.14	0.29
	HLI	. 3	0.32	0.23	. 0.36	0.04	0.08
200	HUI	-3	0.35	0.26	0.41	0.05	0.08
	TILI	4	0.05	0.00	0.12	0.03	0+06
	EDI	. 3	0.17	0.10	0.21	0.04	0.04
	LDI	3 >	0.05	0.04	0.06	0.01	0.01
	TtLI	` ö			10000		
	TLI	.3	1.93	1.63	2.21	0.17	0.29
	ALI'I	4	0.34	. 0.00 -	0.49	0.19	0.39
	ALI II	2	0.81	0.71	0.90	0.09	0.13
	ALI III	1	0.40	0.40	0.40		
	. AL T TH					0.07	0.04

Table 4-3: Summary of indices for selected series Octopoteuthis sicula representing the entire size range available.

1	9	4000		2 6 6	**	
INDEX	N	MEAN	HINIHUH VALUE	HAXIMUM -	STD ERROR OF HEAN	STANDARD DEVIATION
			- 112 - 20 00 11			
HWI .	25	0.33	. 0.25	0.44	0.01	0.05
FLI	31	0.73	0.61	0.89	0.01	0.06
FUT	31 .	1.20	- 1.04	1.45	0.02	0.11
HLI	25	0.43	0.26	0.55	0.01	0.06
HWI	25	0.36	0.27	0.49	0.01.	0.05-
TILI	31	0.13	0.08	0.18	0.00	0.63
EDI	25	0.23	0.14	0.32	0.01	0.04
LDI	24	0.08	0.04	0.11	0.00	0.02
	24	0.00	0.04			0.02
			- HL = 51-75 m			
	2 10 1000	0.29	11 1		0.01	0.02
IWH	7	0.29	- 0.27	0.31	0.01	0.02
FLI	10.	0.76	0.71		. 0.01	
WI V	10	0.40	1.00	1.30	0:03	0.09
ILI .	7		0.35	Q.49	0.02	0.05
INI ,	7	0.34	0.27	. 0.38	0.01	. 0.04
TILI ,	10	0.18	0.10	0.31	0.02	0.07
IDI \	7 .	0 . 25	0.22	. 0.27	.0.01	0.02
.DI 1-	7	0.09	0.07	0.10	0.00	0.01
	1 1 1 1 1		- HL = 76-100 I			
WI .	5.	0.32	0.26	0.39	0.02	. 0.05
LI .	6	0.81	0.71	0.95	. 0.04	. 0.11
WI.	'6	1.13	1.00	1.34	0.05	0.13
LI	- 6	0.35	0.32	0.40	0.01	. 0.03
IWI	5 .	.0.32	0.25	0.39	0.03	0.06
TILI .	6	0.14	. 0.00	0.23	0.03	0.08
IDI ·	6 .	0.25	0.23	0.28	0.01	0.02
DI .	5	0.08	0.08	0.09	0.00	0.01
			HL = 101-125	n		
wi '		0.26	0.22	0.30	0.02	0.04
	. 12	0.75	0164	0.85	0.02	0.06
LI	12	0.75	0.90	1.15	0.02	0.07
	. 12		0.27	0.35		0.07
LI	5	0.29	0.27	0.35	0.01	0.03
IMI		0.27	0.09		0.01	
ILI .	12	0.16	0.09	0.23	0.01	0.04
DI .	5	. 0.21	0.18	0.22	0.01	0.02
DI		0.07	0.07	0.07	0.00	0.00
			HL - 126-150			
IWI	2	0.28	0.23	0.33	0.05	0.07
LI		0.28	0.73	0.84	0.04	0.04
WI .	m13	1.00	0.73	1.08	0.04	0.08
			0.72	0.29	0.01	0.01
LI	., 2	0.28	0.27	0.29		
HWI.	2	0.26			0.03	0.04
TILI		0.12	0.00	0.20	0.06	0.11
EDI	. 2	0.20	0.19	0.21	0.01	0.01
LDI	2	0.07	0.07	0.07	0.00	0.00

						190			10 ¹⁰		1	100	
INDEX		N	17	HEAN	§ .	HINIHUR		HAXIHUH VALUE	· *s	TD ERRO	R ST	ANDARD VIATION	į.
					HL	- 151-	75						
					1000	955					*		97
HWI	2.5	0	A.						100				
FLI		1		0.81		0.81		0.81					
FWI		1		1.03		1.03		1.03					
HLI .		0					100						
HWI		0					•						8 6
TILI		1		0.15		0.15	0.81	0.15					
EDI		0									13		
LDI .		. 0											
								9.19					. 1
					HL	a. 176-	200 .				*****		
	·	200						5.50	100				1.5
HWI		. 0 .	. "	15.60									
FLI	12	2	N.	0.80		0.79.		0.82		0:02		0.02 .	
FUI		2		0.98	•	0.92	5 X	1.03		0.05	1000	0.07	
·HLI	10.	0 .			Ø								
HUI.		0.	•						, ,		>-		5.00
TELI		2		0.19		: 0.17	- 3	0.22	100	0.03	100 E	0.043	
EDI		: 0							*				-
· LDI -		0										./	
	1000					41.00			100				n 5 1
				,	HL	- 201-2	25 RR						. 4
		18		2 3				2					
HUI :		. 1		0.25		0.25	* 3	0.25			25	ote nene	
FLI	V. B. S.	. 1 .		0.75	2.5	0.75		.0.75	3 %		100		· ·
FWI -		. 1		0.87	1000	0.87		0.87					0.00
HLI .		1		0.29	18.0	0.29	1	0.29	20.00				100
HWI		1		0.24		0.24	2	0:24					
+TILI		. 1		0.22		0.22	7	0.22				1	100
EDI .		1	13	0.14		0.14		0.14					
LDI		1.	-	0.06		0.06	10	0.06	100		0.1		•
4	5.5			8		× .		× ×				100	

97

Table 4-4: Summary of indices for selected series of Octopoteuthie megaptera representing the entire size range available.

					.4.	
INDEX :	MA.	HEAN .	VALUE	VALUE	OF HEAN	STANDARD DEVIATION
			HL = 25-50 as			
HWI	27	0.32	0.26	0.38	0.01	. 0.04
FLI	35	0.72	0.45	0.86	0.01	
FWI -		6.72	0.74	1.33	0.02	0.05
HLI	35	0.47	0.29	0.71	0.02	., 0.09
	27	0.74	0.22	0.41	0.02	0.07
TILI	35	0.16	. 0.00	0.28	0.01	0.05
EDI:			0.09	0.33	0:01	0.05
LDI .	27	0.23	0.02	0.11	0.00	0.02
		4.07.			. 0.00	
			HL 51-75 .			
		1				3
MMI	10 .	0.30	0.23	0.36	. 0.01	0.04
FLI .	. 11	0.71	0.23 0.62 0.84	0.78	0.01	. 0.05
FWI	11	1.02	0.84	1.22	0.03	0.10
HLI	10	. 0.39	0.31 . *	0.48	0.02	. 0.04
HWI	10	0.32	.0.26	. 0.38	0.01	0.04 0.06
TILI	11	0.19	0.06	0.26	0.02	0.00
EDI	10 11 11 10 10 11	0.25	0.20	. 0.31	0.01	. 0.04
LDI .	10	0.08	.0.05	. 0.10	0.00	0.01
			37 - 122-			
			HL = 76-100 :			
-HUI.	.11	0.28	0.24	0:33	0.01	. 0.03
FLI	13	0170	0.27	0.77	0.01	0.04
	12	0.72	0.63 0.88 0.31	1.05	0.02	0.06
	11	0:73	0.00		0.01	0.04
HWI		0.30	0.21	0.71	0.02	0.04
TILI	17	0.29	- 0.15	0.30	0.01	0.05
EDI	11	0.24	0.18	0.34	0.01	- 0.03
LDI	11 /	0.08	. 0.06	0.09	0.00	. 0.01
				,,		4102
			HL = 101-125			
HWI		0.31	0.20	0.49		0.17
FLI .	12 .	0.48	0.20	0.76	0.06	. 0.05
	12	0.91	0.77	1.04	0.01	0.08
HLI · · ·	12	0.35	0.27	0.40	0.02 0.02 0.02	0.05
HWI .	7	0.27	0.22	0.35	0.02	0.04
TILI	12	0.22	0.13	0.29	0.01	0.04
		0.20	0.13	0.27	0.01	0.02
EDI .		0.04	0.18	0.23	0.00	0.01
		0.00			. 0.00	0.01
			HL = 126-150			
			. 1			
HWI	. 5	0.27	0.21	0.30 .	0.02	0.04
FLI	8	0.73	0.67	0.85	0.02	. 0.05
FWI	.6	0.95	0.88	1.00	0.02	0.05
HLI	5	0.32	0.24		0.02	0.05
HWI	. 5	0.24	0.20	0.26	0.01	
	. 8	0.19	0.12	0.26	0.02	.0:05
EDI	5	0.18	- 0.16	0.20	0.01	0.02
LDI	. 5	0.04	0.04	: 0.08	0.01	0.01
		1 1 1 1				

			500						
	INDEX	N		HEAN	•.*.	HINIHUH VALUE,	MAXIMUH VALUE	STD ERROR OF MEAN	STANDARD DEVIATION
						HL . 151-17	5		
	HUI	3		0.25		9.22	0.28	0.02	0.03
	FLI /	. 5		0.71		.0.66	0.79	0.02	0.06
	FWI	5.		0.87		0.78	0.33	0.04	0.09
	HLI	3.		0.24		0.23	0.33	0.02	0.03
	TILI	5		6.22		0.14	0.26	. 0.02	0.05
	EDL	. 3		0.13		0.06	0.18	0.04	0.07
	LDI	3	×	0.04		0106	0.07	0.00	0 0.01
			**					1.	
÷						HL = 176-20	0 mg		
	7							. 1	3
٠,	HUI	1		0.24		0.24	.0.24	2: 1-	7"
	FLI:	. 1		0.64		0.64	0.64 .		
	FWI .	. 1		0.81		0.81	. 0.81		
. '	HLI	- 1		0.33		0.33	0.33	1	
	HMI	1		0.21		0.21	0.25		,
	TILI :	. 1	11	0.25		0.16 . +	0.16		1.0
1.	LDI	- 1		0.06		0.06	0.06		2 . Mil. 50
13								11	K
				*					
									1 114
						1 1	-		1 . 1, 1

Table 4-5: Summāry of indices for selected series of Octopoteuthis danae (Joubin, 1931) representing the entire size range available.

INDEX .	N.	. HEA	N .	HINIHUH	MAXIMUM	STD ERROR	STANDARD
					,	OF REAN	DEVINITON
				HL # 25-50	**		
INT .	17	0.3	4	0.31	0.36	0.01	0.02
LI	10	. 0.7		0.63	0.81	0.02	0.05
WI .	10	.1.2		1.09	1.49	. 0.03	0.10
LI	. 7	0.4		0.39	0.49	0.01	0.04
WI .	7	0.3		0.36	. 0.41		0.02
ILI -	10	0.1	2 .	0.00	0.23	0.03	0.09
DI	7	0.2		*0+21	1 0.30	0.01	0.03
DI .		0.0		0.08	0.11	0.00	0.01
				25 12			
				HL - 51-75			
		4 15	*				
WI .	12 .	0.3	3	0.22	0.40	:0.01	0.05
LI		0.7		0.67	1.09	- 0.03 -	0.11
WI:	18 .			1.02	1.25	0.01	0.06
LI	14	0.1		0.32	0.42	0.01	0.03
WI .	. 11	0.7	5 : .	0.28	0.50	0.02	0.07
ili .	18	0.1		0.00	0.23	0.02	0.07
DI .	-13	-0.2		0.22	0.30	0.01	0.02
DI	13	0.0	0	0.08	0.10	0.00	0.01
				4			
				HL - 76-100			
	٠.						
MI :	. 2	. 0.3	1	0:29	0.33	- 0.02	. 0.03
LI	. 2			:0.69	. 0.71	. 0.01	0.01
WI .			5	1.02	1.08	0.03	0.04
īi -	2 1		2	0.30 .	0.34	0.02	. 0.02
WI :	. 2	0.3		0.33	0.38	0.03	0.04
ILI .	. 2	0.1	7 .	0.12	0.21	0.05	0.06
DI .	2	. 0.2		.0.22	0.24	- 0.01	0.02
DI	- 2	-0.0		0.08	0.09	0.00	0.00 -
				U 101-125			
WI :	1	. 0.2		0.25	0.25		
Lī :	. 2	0.8	1	0.74	0.92	. 0.09	0.13
WI .	2	0.8		0.95	1.22 -	0:14	/ 0.19
LI.	1	0.3	1	0.31	0.31		, 0.17
NI.	i	0.2		0.24	0.24 .		
ili '		0.0		0.00	0.18	. 0.09.	0.12
DI -				/ 0.21	0.21	07	
DI	. 1	0.0		0.08	0108		
		. ,	04 3				

Table 4-6: Summary of indices for selected series of Octopoteuthis deletron Young. 1972 representing the entire size range available.

,						* *		4	
10	-	INDEX	N		HEAN	HINIHUH	HAXIHUH .	STD ERROR	STANDARD
e e						VALUE -	VALUE	OF HEAN	DEVIATION
				2	4 60	4 .			
						HL = 25-50 as			
9.8		1 Pun			0.31	0.28	0.33	0.02	0.03
		FLI	14		0.79	0.72	0.94	0.02	0.04
		FWI	. 14		1.19			0.02	- 0.04
		HLI	3	·	0.37	0.26	0.43	0.04	0.10
		TILI	14		0.07	0.00	0.15	0.01	- 0.02
		EDI	3		0.24	0.21	0.28	0.02	0.03
17.		LDI	3		0.08	0.07	0.09	. 0.01	0.01
				×	- 1	HL = 51-75 mm			100
	50 10			0 5		UF - 21-12 MW			
	-	HUI	2	9 0	0.34	0.33	0.35	0.01	0.01
	-	FLI .	. 4		0.74	0.69	0.82	0.03	0.03
	,	FWI	2		0.33	1.06	0.35	0.04	0.0B
with the te		HWI	. 2	•	0.33	0.32	70.41	0.02	0.03
		TILI	. 4		0-11	0.07	0.17	0.02	0.04
40.00		EDI	. 1	3	.0.26	0.26	0.26		S 45 10
		LDI	. 1	200	0.09	0.09	0.09		
250			3 7 . 1			L = 76-100 mm	1		
e de la	- /-	and a			·	r - 10-100 mm	1000		
		- NWI	3	-	0.30	0.26	0.33	0.02	. 0.04
		FLI	-3		0.81	0.80	0.82	0.01	0.01
		HLI	3		0.32	0.96	0.39	0.05	0.05
		HWI	. 3		0.30	0.28	0.34	0.02	0.03
25		TILI	. 3		0.08	0.04	0.08	0.01	0.01
100		EDI	3		0.21	0.20	0.22	0.01	0.01
		LDI	3		0.08	0.07	0.08	0.00	0.01
7 50					H	- 101-125 am			
*									
		HWI	1		0.27	0.27	0.27		
8		FLI	1		0.71	0.71	.0.71		
		FWI	. 1		0.30	0.30	1.07	•	
Took or		UUT			0.28	0.28	0.30		
1 m		FILI	i		0.17	0:17	0.28		100
		EDI	. 1		0.22	. 0.22	0.22		
100		LDI	. 1		80.0	0.08	0.08		
1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1						126-150 am			
	. 1								
e	/	HWI	. 0 .						.0.04
	1	FLI	3	· · · · · · · · · · · · · · · · · · ·	0.76	0.73	0.81	0.03	
F .	4	FUI HLI	. 3		0.86	0.83	0.897	0.02	0.03
	- 1	HHI		- 2	12 (7)	A		2.5	100
	. /	TILI	. 3		0.18	0.16	0.23	. 0.02	0.04
× 12 3	• /	EDI	. 0	100	. :				
	/~	LDI	0.				3.0		
Acres 1	- 1				6 . 1				2.0
71 .	1					(p) 4 B	1000		
100	-1-		. 99		5		4	n g 8	
9	1					. 57 8	1		
	1 .		75	590					200
Water Co.	.1-	1	1 .	100				1 1 1	
	1 .				y 500 cent	40'E 1 1 2	_	3 , 3	4 4 4
	1					Trul at	1 100	5 (10)	
100	25	•		1 m	20 B 10 15	Vie for an a	to William	دائر کی د	. W

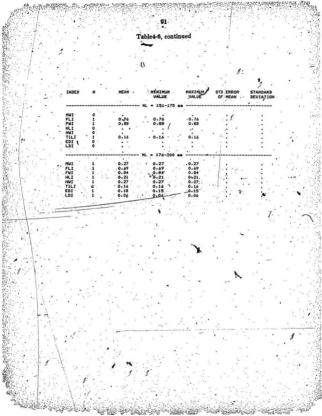


Table 4-7: Summary of indices for selected series of Octopoteuthis sp A Young, 1972 representing the entire size range available.

				27			a				
INDEX	N	MEAN	ĤINIHUH VALUE	,	VALUE		OF HEA			TANDAR	
			ML	25-50	· ·						
MI	1	0.27	0.27		0.27					100	
LI	1	0.87	0.87		0.87						
WI	1	1.26	1.26		1.26					· .	
LI	1	0.52	0.52		0.52						,
WI.	ì	0.32	0.32		0.32						
ILI	1	- 0.19	0.19	0.0	0.19			*			
DI .	1	0.24	0.24		0.24						
.DI	1	0.07	0.07		0.07						
				51-75							
				01.40		31					ć
WI	2 3	0.28	0.26		0.30		0.02	100		0.03	•
LI .	3	0.76	0170		0.83		. 0.04	2 3		0.07	
WI	3	1.11	0.99		1.30		. 0.10	40		0.17	
LI	2	0.42	0.41		0.43	5	0.01			.0.01	
NI.	2 .	0.29	0,25	3	0.33	. 3	0.04			0.06	200
	3	0.15	0.11		0,21		0.03			0.05	15
DI	2	0.22	0.21		0.23		. 0.01	1		0.01	
DI .	22	0.07	0.07		0.07	0.15	0.00			0.00	
			HL	76-10							
WI	0		1	-							
LI	4	0.76	0.69		0.84		- 0.04			0.07	
WI.	4	1.00	0.88	**	1.10		0.04			0.09	
LI	. 0	. /									
WI	. 0	. /	1000			40	1 200		-	A .	
ILI	. 4	0.15	0.08	8.0	0.20		0.03			0.05	
DI	0.	./	1								
DI	0	1			•						
			HL	101-1	25						
WI .		0.28	0.24		0.31		0.03			0.05	
LI	3 /	0.71	0.49		0.76		0.03			0.05	
LI	3 /	0.71	0.85		0.75		0.02			0.05	
LI	2/	0.71	0.35		0.41		0.03			0.04	
WI	2/	0.32	0.26	*	0.38		0.06	w 21		0.08	
1LT	3	0.20	0.15		0.24		0.03			0.05	
DI	/2	0.25	-0.24		0.26		.0.01			0.02	0
DI .	/2	0.10	0.09		040		0.01			0.01	
		4.1		126-1							
7	1,		AL	120-1							
WI /	. 0								-2		
LI/	1 .	0.75	. 0.75 -		0.75	4 9 90					
MI	. 1	0.94	0.94		0.94			1			
L/I	. 0					1					
INI	0										22
ILI	1	0.14	. 0.14		0.14						
DI	0 .				•		•			•	
DI	0	•			•					•	
	**										6
3											

02

Table4-7, continued

						- 0	
				1000000000			
INDEX	N	MEAN	HINIHUH	HAXIMUM	STD ERROR		STANDARD
			VALUE	VALUE	OF MEAN		DEVIATION
			ML 15	1-175 as			
4 .	8						
HWI .	1	0.26	0.26	0.26		51 (9)	
FLI	3	. 0.74	0.73	0.76	0.01		-0.02
FWI	3	05.87	0.82	0.92	. 0.03		0.05
HLI	2	0.34	0.33	0.34	. 0.00		0.01
HWI	1	0.20	0.20	0.20	. 2025		10000
TILI	-	0.14	0.12	0.16	0.01	9	0.00
EDI	ĭ	0.18	0.18	0.18	0.01		0.00
LDI		0.05	0.05	0.05			153
- DI	3	0.03	0.00	0.03	2.5	47	100
				6-200 an		mad ma	
. *			UL 1/	0-200 88			
	1950						
HMI	0				. 30	- 2	•
FLI .	1	0.74	0.74	0.74	•	•	
FWI	.1	0.90	0.90	0.90			
HLI	. 0			•*			
HWI	0						
TILI	. 1 /	0.14	0.14	0.14	0.00		
EDI	0						
LDI	0.				٠. ١		

Table 4-8: Means comparisons of mantle width between five species of Octopoteuthis.

ALPHA=.05 CONFIDENCE=0.95 DF=154 MSE=7709993 CRITICAL VALUE OF STUDENTIZED RANGE=3.904

COMPANISONS SIGNIFICANT AT THE .OS LEVEL ARE INDICATED BY ****

SIMULTANEOUS

LOWER DIFFERENCE UPPER

SPECIES		CONFIDENCE	BETWEEN	CONFIDENCE	
COMPARISON .		LIHIT	HEANS	LINIT	
	~~, -	Service our Service Service	-		
DANAE - SP A		-29.880	4.136	38.153	4
DANAE - DELETRON	CW.	-16.531	11.136	38.804	
DANAE - HEGAPTER	A	5.290	21.806	38.322	**
DANAE SICULA		14.577	32.062	49.548	**
SP A - DANAE		-38.153	-4.136	- 29.880	
SP A - DELETRON		-12.5BO	7.000	46.580	
SP A - HEGAPTER		-15.101	17.669	50.439	_
SP A SICULA		-5.343	27.926	61.195	Ø.
				4	1
DELETRON DANAE		-38.804	-11.136	16.531	•
DELETRON - SP A		-46.580	-7,000	32,580	
DELETRON - HEGAPTER		-15.450	10.669	36.789	
DELETRON - SICULA		-5.817	20.926	47.669	
DECEMBER - DACOEN		01017	201720	47.1007	
HEGAPTERA - DANAE		-38.322	-21.806	-5,290	**
HEGAPTERA - SP A		-50.439	-17.669	15, 101	***
HEGAPTERA & DELETRON		-36.789	-10.669	15,450	
HEGAPTERA - HEGAPTER		-4.659	10.257	25.172	
RECAPIERA - RECAPIER		P4.037	10.23/	23.1/2	
SICULA DANAE		-49.548	-32.062	-14.577	**
		-44.548	-32.082		**
				5.343	
		-47.669	-20.926	5.817	-
SICULA - HEGAPTER	A	-25.172	-10.257	4.659	

Table 4-9: Means comparisons of fin length between five species of Octopoteuthis.

ALPHA-.05 CONFIDENCE-0.95 DF-248 MSE-836.576 CRITICAL VALUE OF STUDENTIZED RANGE-3.886 COMPARISONS SIGNIFICANT AT THE .05 LEVEL ARE INDICATED BY ****

LOWER DIFFERENCE UPPER	
SPECIES CONFIDENCE BETWEEN CONFIDENCE	E
COMPARISON LIMIT MEANS LIMIT	
DANAE - SP A -16.433 7.519 31.471	
DANAE - MEGAPTERA 18.467 31.857 45.248	***
DANAE - DELETRON 18.007 - 35.944 53.880	***
DANAE - SICULA 22.991 . 36.332 49.673	***
And the second s	
SP A - DANAE31.471 -7.519 16.433	
SP A - HEGAPTERA 0.307 24.338 48.370	***
SP A - DELETRON 1.593 28.425 55.256	***
SP A - SICULA 4.809 28.813 52.817	***
	40.7
NEGAPTERA - DANAE -45.248 -31.857 -18.467	***
NEGAPTERA - SP A -48.370 -24.338 -0.307	***
HEGAPTERA - DELETRON -13.956 4.086 22.129	
HEGAPTERA -SICULA -9.009 - 4.475 17.958	
DELETRON - DANAE53.880 -35.944 -18.007	***
DELETRON - SP A -55.25628.425 -1.593	***
DELETRON - HEGAPTERA -22.129 -4.086 13.956	
DELETRON - BICULA17.618 0.388 18.395	11
The state of the s	0.00
SICULA - DANAE -49.67336.332 -22.991	. ***
SICULA - SP A -52.81728.913 -4.809	. ***
SICULA - HEGAPTERA -17.958 -4.475 . 9.009	
SICULA - DELETRON -18.395 -0.388 - 17.618	

Table 4-10: Means comparisons of lin width between five species of Octopoteuthia.

ALPHA=.05 CONFIDENCE=0.95 DF=244 M8E=627.639 . CRITICAL VALUE OF STUDENTIZED RANGE=3.887

COMPARISONS SIGNIFICANT AT THE .OS LEVEL ARE INDICATED BY "

CUMPA	KISU	45 SIGNIFICA	NT AT THE .O:	LEVEL ARE	INDICATED BY	
		A	STHULTANFOLD	9	SIMULTANEOUS	
			LOWER	DIFFERENCE		,
	SPEC	TES	CONFIDENCE	BETHEEN	CONFIDENCE	
	HPAR		LINIT	" MEANS	LIHIT	
CC	mran.	Laun	Linii	HEMMS	LINI)	
DANAE	-	SP A	-14.295	4.474	27,248	
DANAE	-	MEGAPTERA	20.976	32.749	44.521	***
DANAE	-	DELETRON	19.333	34,901	50.469	***
DANAE	_		23.492	35,289	46.887	***
PHILIP		SILULA	. 231072	331207	40.007	•••
SP A	· _	DANAE	-27,248	-A:47A	14,295	
SP A	-	MEDAPTERA	5.380	26.272	47.165	***
SP A			5,181	28,425	51.668	***
SP. A	- 1	SICULA	8.019	28.813	49.607	***
Jr., 11		STEULH	0.017	20.013	47.007	***
HEGAPTE	RA -	DANAE	-44.521	-32.749	-20.976	***
MEGAPTE	RA -	SP A -	-47.165	-26,272	-5.380	***
MEGAPTE	RA -	DELETRON	-13.577	2.152	17.882	
. HEGAPTE	RA -	SICULA	-9.272	2.541	14.354	
			V C			
DELETRO	ON -	DANAE	-50.469	-34.901 -	-19.333	***
DELETRO	ON	SP A	-51.668 .	-28,425	-5.181	***
DELETRO	N :-	HEGAPTERA	-17.682	-2.152	13,577	
DELETRO	IN -	SICULA	-15.210	0.388	15.987	
		0200011				100
SICULA	-	DANAE .	-46.882	-35,289	-23.692	***
SICULA		SP A	-49.607	-28.813	-8.019	***
SICULA	- 2	HEGAPTERA .	-14.354	-2.541	9.272	***
SICULA		DELETRON	-15.987	-0.388	15.210	

Table 4-11: Means comparisons of head length between five species of Octopoteuthis.

ALPHA=.05 CONFIDENCE=0.95 DF=158 MSE=660.67 CRITICAL VALUE OF STUDENTIZED RANGE=3.903

COMPARISONS SIGNIFICANT AT THE .05 LEVEL ARE INDICATED BY '***

		SIMULTANEOU		SIMULTANEO	US
		LOWER	DIFFERENCE	UPPER	
	SPECIES	CONFIDENCE	BETWEEN	CONFIDENC	E- ~
CC	HPARISON	LIMIT	MEANS	LIMIT	
SP A	- DANAE -	-18,261	11.039	40.339	
. SP A	- DELETRON	-16.455	18.500	53.455	
SP A	- HEGAPTERA	0.937	29.267	57.596	***
SP A	- SICULA	8.648	37.346	66.043	***
				AL COLUMN	100
DANAE	- SP A	40.339	-11.039	18.261	
DANAE	DELETRON	-17.894	7.461	32.816	
DANAE	- HEGAPTERA	3.274	18.228	33.181	***
DANAE	- SICULA	. 10.668	26.307	41.946	***
-		5 P		8 8 .	
DELETRO		-53.455	-18.500 -	16.455	(a) (b)
DELETRO		-32.816	7.461	17:894	
DELETRO		-13.461	10,767	34.994	E 10 8
DELETRO	N - SICULA	-5.810	18.846	43.502	· · · ·
		Account to the			
HEGAPTE		-57.596	-29.267	-0.937	***
HEGAPTE		-33.181	-18.228	-3,274	***
HEGAPTE		-34.994	T10.767	13.461	
HEGAPTE	RA - HEGAPTERA	-5.656	8.079	21.815	
				,	A
SICULA	- SP A	-66.043	-37.346	-8.648	***
BICULA	- DANAE	-41.946	-26.307 .	-10.668	***
SICULA	- DELETRON	-43.502	-18.846	5.810	

Table 4-12: Means comparisons of head width between five species of Octopoleuthis.

ALPHA .. 05 CONFIDENCE -0.95 DF-154 HSE-654.214

COMPARISONS SIGNIFICANT AT THE .05 LEVEL ARE INDICATED BY ***

	(F)		LOWER.	DIFFERENCE	UPPER	
	SPECIA	25	CONFIDENCE.	BETHEEN	CONFIDENCE	
	COMPAR		LIHIT	HEANS	LIMIT	
	CONFAR	Laun	LANA	. nema	CINI	
	DANAE ' -	SP A	-28.332	3.003	34.338	50.00
•	DANAE	DELETRON.	-15.483	10.003	35.489	
	DANAE -		5.926			10000000
	DANAE -	HEGAPTERA		21.183	36.440	***
	DANAE -	SICULA	13.587	29.622	45.657	***
	Section 1995	A CONTRACTOR OF THE PARTY OF TH	V 1970 CONT.		1	1500
	SP A -	DANAE	-34.338	-3,003	. 28.332	
	SP A -	DELETRON	-29.460	7.000	43.460	
	SP A	HEGAPTERA"	-12.028	18.180	48.389	
	SP A	SICULA .	-3.989	26.619	57.228	× 1
	27		"A 125" " 150			
	DELETRON	DANAE	-35 - 489	-10.003	15.483	1076
	DELETRON -	SP A	-43.460	-7.000	29.460	
	DELETRON -	HEGAPTERA	-12.907	. 11.180	35.268	
	DELETRON -	SICULA	-4.969	19.619	44.207	

	MEGAPTERA -	DANAE	-36 . 440 .	-21.183	-5.926	***
	MEGAPTERA -	SP A	-4B . 389	-18,180	12.028	
	HEGAPTERA -	DELETRON	-35.268	-11.180	12,907	
	MEGAPTERA -	SICULA	-5.265	8.439	22,142	
	SICULA -	DANAE	45 - 657	-29.622	-13.587	***
	SICULA -	SP A	-57 - 228	-26.619	3,989	****
	SICULA -	DELETRON	-44.207	-19.619	4.969	
	SICULA -	MEGAPTERA	-22.142	-8.439	5.265	

Table 4-13: Means comparisons of tail length between five species of Octopoteuthis.

ALPHA=.05 CONFIDENCE=0.95 DF=248 MSE=815.755 CRITICAL VALUE OF STUDENTIZED RANGE=3.886 COMPARISONS SIGNIFICANT AT THE .05 LEVEL ARE INDICATED

	- 4			
	SIHULTANEOUS	13	SIMULTANEOUS	3
	LOWER DI	FFERENCE	UPPER	-
SPECIES	CONFIDENCE '	BETHEEN -	CONFIDENCE	
COMPARISON	LIMIT	MEANS .	LIMIT	
COMPARADOR	- LANE	THE PRINT	name.	
DANAF - SP'A	-16.133	7.519	31.171	
	18.435	31.857	45.080	***
	18.232	35.944	- 53.655	***
DANAE - DELETRON			. 23.622	
DANAE SICULA .	23.158	36.332	49.506	***
the state of the s	1			
SP A - DANAE	-31.171	-7:519	16.133	
SP A : - MEGAPTERA	0.408	24.338.	48.069	. ***
SP A - DELETRON	1.929	28.425	54.920	***
SP A - SICULA	5.109	28.813	52.516	***
HEDAPTERA - DANAE	-45.080	-31.857 .	-18.635	***
HEGAPTERA - BP A	-48.069	-24.338	-0.408	***
	-13.730	4.086	21,903	
			17.789	
MEGAPTERA - SICULA	-8.840	4.475	17.767	
		Size areas	a marriada 1	1000
DELETRON - DANAE	-53.655	-35.944	-18.232	
DELETRON - SP A	-54.920	-28.425	-1.929	***
DELETRON - MEDAPTERA	-21.903	-4.086	13.730	
DELETRON - SICULA	-17.392	. 0.388	18.169	
STOULA - DANAE -	-49,506	-36.332	-23.158	
BICULA P- BP A	-52)516	-28.813	-5.109	***
SICULA - HEDAPTERA	-17.789	-4.475	8.840	

Table 4-14: Means comparisons of eye diameter between five species of Octopoleuthis.

ALPHA=.05 CONFIDENCE=0.95 DF=157 M8E=485.48 CRITICAL VALUE OF STUDENTIZED RANGE=3.903

OHPARISONS SIGNIFICANT AT THE .05 LEVEL ARE INDICATED BY '***

	SPECIES COMPARISON	SIMULTANEOUS LOWER CONFIDENCE LIMIT	DIFFERENCE BETWEEN MEANB	SIMULTANEOUS UPPER- CONFIDENCE LIMIT	
	DANA - SP A	-30.524	1.403	33,329	
.03	DANAF - DELETRON	-21.102	5,903	32.908	
-	DANAF - HEGAPTERA	. 1 3.538	18.814	34.091	***
	DANAE - SICULA	11.188	27,249	43.309	***
	THE RESERVE OF THE PARTY OF THE				
	SP A' DANAE	-33.329	-1.403	30.524	
2.0	SP A DELETRON	-33.502	4.500	42.582	
	SP A - HEGAPTERA	-13.481	17.411	48.304	
	SP A - SICULA	-5.442	- 25.846	57.133	-
1	100	41	4.	. / .	
	DELETRON - DANAE	-32.908	-5.903	21.102	1 0
	DELETRON - SP A	-42.582	-4.500 .	33.582	
	DELETRON - MEGAPTERA	-12.843	12.911	. 38.685	16
	DELETRON : - SICULA .	-4.900	21.346 .	47.592	
	and the second s	1 2 2 4 4			
20	HEGAPTERA - DANAE	-34.091	-18.814	-3.538	***
	HEDAPTERA - SP A	-48.304	-17.411	13.481	50
	HEGAPTERA - DELETRON	-38.685	-12.911 -	12.863	8 35
	HEGAPTERA - SICULA	-5.457	8.435	22.326	
1	and a first contract		-27.249		2
	SICULA - DANAE	-43.309		-11.188	***
	SICULA SP A	-57.133	·-25.846	5.442	100
	SICULA - DELETRON	-47.592	-21.346	4.900	
	SICULA - HEGAPTERA	-22.326	-8.435	5.457	

Table 4-15: Means comparisons of lens diameter between five species of Octopoteuthis.

ALPHA=.05 CONFIDENCE-0.95 DF=148 MSE=689.211 CRITICAL VALUE OF STUDENTIZED RANGE=3.906

COMPARISONS SIGNIFICANT AT THE .05 LEVEL ARE INDICATED BY ****

SPECIES COMPARISON	LOWER CONFIDENCE	DIFFERENCE BETWEEN HEANS	UPPER CONFIDENCE LIMIT	•
SP A - DELETRON	-33,712	4.500	42.712	hg.,
SP A - DANAF-	-25,824	6.600	39.024	
SP A - HEGAPTERA	-14.752	14.292	47.335	
SP A - SICULA	-5.436	26.035	57,505	-
and the second	and the second	1 5		
DELETRON - SP A	-42.712	-4.500	33.712	100
DELETRON - DANAE	-25.455	2.100	29.655	
DELETRON - HEGAPTERA	-14.125	11.792	37.709	200
DELETRON - SICULA	-4.891	21.535	47.961	
DANAE - SP A	-39.024	-6.600	25.824	
	-29.655	-2.100	25.455	3 10
				4 -
DANAE - HEGAPTERA	-4.520	9.692	25.904	
DANAE - SICULA	2.420	19.435	36.449	***
HEGAPTERA SP A	-47.335	-16.292	14.752	
HEGAPTERA - DELETRON	-37.709	-11.792	14.125	
HEGAPTERA - DANAE	-25.904	-9.692	6.520	
HEGAPTERA - SICULA	-4.466	9.743	23.952	-
	to the same of the same of			
SICULA - SP A	.: -57.505	-26.035	5.436	
SICULA DELETRON	-47.961	-21.535	4.891	
SICULA DANAE .	36.449	-19.435	-2.420	***
SICULA - HEGAPTERA	-23.952	-9.743	4.466	

The first DiSCRIM procedure produced a table giving the number of observations and the percents classified into species (see Table 4-18(a.)). Based on the analysis 73.7 per cent of the initial species assignments appeared correct. After removal one of the species with a very low sample number (O. sp A) the analysis recognized 78.1 per cent of the initial assignments correct (see Table 4-18.

Table 4-16: Discriminant analysis of species designation of (a.) live species of the genus Octopoleuthie and (b.) four species of the genus after removal of O. sp A.

DANAE DELETRON HEGAPTERA UNKNOWN 3.33 100.00 13.33 20.00 8.70 100.00 DANAE 82.61 0.00 DELETRON 77..78 11.11 100.00 - HEOAPTERA 5.36 17.86 100.00 SICULA 0:00 .83.33 100.00 169 0.2000 PRIORS

25				raconale contrata de la contrata de	Company of the Compan
FROM	OF OBSERVA	TIONS AND P	ERCENTS CLAS	SIFIED INTO	SPECIES:
SPECIES	DANAE	DELETRON-	HEGAPTERA	SICULA .	TOTAL
UNKNOWN	100 000		15	16	36
UNKNOWN	11.11	2.78	41.67	44.44	100.00
DANAE	. 20		7. 0	. 3	23
*,	86.96	0.00	0.00	13.04	100.00
DELETRON	. 1	. ,			. 9
and the second	11.11	77.78	0.00	11,11	100.00
HEGAPTERA 7	5	3	40	. 8	J 56 .
	8.93	5.36	71.43	14.29	100.00
SICULA	. 10		2	33	45
	22.22	. 0.00	14.44	73.33	100.00
TOTAL	40	. 11	57	61	169
PERCENT	23.67	6.51	33.73	36.09	100.00
PRIORS	0.2500	0.2500	- 0.2500	0.2500	50 K

4.13. Arm Regeneration in Octopoteuthis

Individuals of Octopoteuthie have very brittle arms, the tips of which are almost always lost when specimens are collected by standard gear types. This is particularly true of juveniles and adults. Arms commonly remain intact however when whole specimens are collected from the stomachs of farge predators, due to the manner of their being ingested whole.

Arm length ratios are commonly used as systematic characteristics (Roper and Voss, 1983). It was during the examination of complete arms on the specimens that arm regeneration was discovered. In all, 15 of the specimens examined showed evidence of one or more arms regenerating; including the holotype of Octopofeuthis deletron (see Fig. 4-19).

Arm and tentacle regeneration has been found in a number of different cephalopods (Adam, 1937, Aldrich and Aldrich, 1988, Lange, 1920) and Murata et al., 1981). A search of the pertinent literature revealed only one reference to this phenomenon in the genus Octopoteuthie. Rancurel, in his 1970 paper included but a single line with regards to regeneration, namely:

Sur l'echantillon no.21, les trois bras droits superiors ont eté rompus, anterieurement a la capture, et ont commende à regenerer sur une longeur de 2 a 3 mm.

Regeneration is easily identifiable by several means (see Figs 4-10 and 4-20).

First, the regenerated portions generally appear parrower than the basal (undamaged) portion of the arms (Fig 4-10 b). Second the normally encountered alternating pattern in the arm hooks is interrupted and there will be two or even three hooks produced in one row before another hook appears in the opposite row.

The arm and its accessory structure appear to have the ability to regenerate, including the hoold, the distal suckers, the spindle-shaped distal photophores and the photophores along the axial nerve. Injury or loss at any point along the arm can lead to regeneration of the missing portion or structures.



Figure 4-10: Photograph showing regeneration of arm RIII in the holotype of Octopoteuthis deletron Young, 1972. (Scale = 1 mm)

Figure 4-20: Photographs showing regeneration of arms in specimens of Octopoteuthis (a.) arm pair with one arm regenerating, (b.) diameter difference between basal and regenerating portion (Scale = 1 mm).





Figure 4-21: Photographs showing arm regeneration in Octopotenthia (a.) regenerating arm showing reformed spindle-shaped photophore at tip, (b.) change in armsture patterning on regenerating arm. (Scale in mm)





Chapter 5 Discussion

5.1. Species Validity

In the past several authors have attempted to clarify the status of the 0 nominal species. Young (1972) discussed the then 8 nominal species and considered the most important characters to be the presence of I or 2 ventral abdominal photophores, tail length, and presence or absence of accessory cusps on the arm hooks. He considered Octopoteuthis persica and O. indica to be nomina dubia because their small sire precluded accurate identification. He also believed that O. persica was really the young of Taningia danae based on the distinct swellings at the tips of arms II. Young questioned the validity of O. longiptera because the limited number of characters, used by Akimushkin, did not clearly separate it from other species. Although Young was unable to identify characters essential for a definition of O. niclseni he considered that it was a valid species. He thus considered the following species valid: O. danae, O. megaptera, and his O. sp A in the Atlantic, and O. deletron and O. niclseni in the Pacific. He suggested that one of the three Atlantic species, probably O. danae, was a synonym of O. sicuse.

Clarke (1980) agreed with Young's opinions on O. persies and O. indica but he considered O. longiptera to be a valid species based on it's size being considerably larger than that of any previous specimens captured. He also questioned Young's assumption that all Octopoleuthis species bear photophores. Clarke expressed some doubt on the distinction between O. sicula, O. megaptera and his new species O. rugosa, basing his opinion, at least in part, on incomplete.

data with respect to photophores in the two species. On the matter of *photophores Clarke is, at best, inconsistent.

Nesis (1983) produced a key to the genus Octopoteuthis and listed only seven species: O. danae, O. deletron, O. sicula, O. megaptera, O. rugosa, O. nielseni, and O. sp A. He made note that O. longiptera was lacking in good diagnostic characters.

The present study supports the validity of only four of the nine nominal species plus Young's as yet unnamed sp A (see Table 5-1). In addition, one other species is described here. Examination of specimens available have supported Young's assumption that all individuals greater than 20-25 mm ML bear photophores other than those at the arm tips. All species discussed below are determined by a combination of three photophore groups (ventral abdominal, anterior cyclid, and eyeball) and the presence or absence of accessory cusps on the arm hooks.

It should be noted that although all attempts were made to obtain representative specimens from all oceans several major areas were little, if at all represented. These include the Northwestern Pacific, Southeastern Pacific and Indian Oceans. The large Russian and Japanese collections of this genus (literature reports and personal communication - Yu. Froemah, K. N. Nesis and T. Okutanj) may possibly contain additional species and their re-examination based on this study's results will certainly improve our knowledge.

Young and Roper (4977) observed live specimens of what they identified as Octopoleuthis nicleeni and reported five small additional mantle photophores: one, located laterally, on either side of the mantle at the same level as the pair lying on the ventrum of the ink sac; a single photophore lying centrally and just anterior to the ventral abdominal pair; and one to each side of the single centre one and lying laterally. None of these five photophores could be found on any of the specimens examined in this study. Young also has been unable to find these

Table 5-1: Checklist of all names proposed for Octopoleuthis and their validity after this revision.

-	
<u> </u>	Validity after this Revision
FAMILIES: . ~	j
Veranyidae Chun, 1910	invalid.
Octopodoteuthidae Berry, July, 1912	Invalid
Octopoteuthidae Berry, November, 1912	Valid
GENERA:	
Octopoteuthis Rüppeli, 1844	Valid
Octopodoteuthis Krohn, 1845	Invalid
Verania Krohn, 1847	Invalid
Veranya Keferstein, 1866	Invalid.
Octopodoteuthopsis Pfeffer, 1912	Invalid
SPECIES (listed with the valid generic name):	
Octopoteuthis sicula Rüppell, 1844	Valid
O. megaptera Verrill, 1885	Valid
O. persica Naef, 1923	invalid
O. indica Naef, 1923	Invalid
O. danae Joubin, 1931	Valid
O. neilseni Robson, 1948	Invalid
O. longiptera Akimushkin, 1963	Invalid
O. deletron Young. 1972	Valic
O. rugosa Clarke, 1980	Invalid
O. sp A	Valid

photophores in any preserved specimens he has examined (personal communication). With the extremely dehydrated condition of the Robson's syntypes identification of characters is impossible.

All specimens collected in the eastern Pacific and originally thought to be Octopoteuthis nicleani have been found to bear eyeball and anterior eyelid photophores, paired abdominal photophores and cusps on their hooks. Based on those characters used in this study it would seem that the specimens examined, from the Pacific, are the same as those specimens described as species C, from the Atlantic, above and classified as Octopoteuthis megsptera. As more squid families are examined it becomes apparent that species squid have distribution patterns reflecting the geographic patterns of Backus and Oraddock, 1977 and others. It may turn out that Octopoteuthis niclseni may represent a valid Pacific form similar to the Atlantic megaptera but this remains questionable at the present time. On niclseni must at present be considered a normen dubium.

Originally it had been planned to obtain Mediterranean specimens in an attempt to clarify the identity of the type species O. sicula. Although over one hundred institutes and museums were contacted worldwide only a handful of Mediterranean specimens were obtained. These were all very young animals and only one specimen, from the type locality, had a discernable photophore pattern.

Nael's Octopoteuthie indica was a larval specimen and no taxonomically useful characters could be attributed to it. His second species Octopoteuthie pereica is actually a larval Taningia danae as both Young and Clarke had supposed. The two species named by Nael in 1923, and first described by Chun in 1910 as Octopodoteuthie sp. must then be considered nomina dubia.

The holotypes of Verrill's Octopoteuthis megaptera and Akimushkin's O. longitera have been lost and no photophore pattern has ever been described for either. To maintain longitera as valid on the basis of a few body measurements seems to be unjustifiable. There is absolutely no way to ascertain if it could be applied to any valid species to it seems wise to name longitera a nomen dubium.

As revealed in the results of this study both the holotype and paratype of Octopoteuthis rugosa were found to be characterized by widely distributed photophores. Specifically they are to be found on the posterior ventrum of the mantle, the posterior ventrum of the eyelid, along the axial nerves of at least the ventral arms and lying ventral to the ink sac and dorsal to the musculi recti abdominals. Unfortunately, because of partial digestion, it could not be determined if the specimens bore either the anterior cyclid or eyeball photophores. The complete photophore pattern was therefore unobtainable so O. rugosa can neither be placed within an existing species nor stand alone as a valid species. It must then be considered a nomina dubium.

The International Code of Zoological Nomenclature (International Commission for Zoological Nomenclature 1985) rules that changes in species validity, like those proposed above, are only legal if presented in a recognized publication (Article 11(a)). As a thesis is not a recognized publication (Article 19(11)) a manuscript is now in preparation for publication, which includes the above changes as well as a name for species A, all in accordance with the code.

5.2. An Artificial Key to the Species of Octopoteuthis

- A single photophore located ventrally and superficially on the posterior portion of the mantle at the muscle-gelatinous layers interface.

- Accessory cusps absent on arm hooks even in young stages (20-25 mm ML); species found primarily in the North Atlantic O. sp A

- Single crescent-shaped photophore absent on each eyeball; anterior eyelid photophore absent
- 4 a. Accessory cusps present on arm hooks even in young stages (20-25 mm ML) O. sicula
- 4 b. Accessory cusps absent on arm hooks even in young stages (20-25 mm ML) O. dance

Table 5-2 below lists the characters and character states of the five valid species.

Table 5-2: Characters and character state distribution of the five valid species of Octopoteuthie

Species			Abdominal Photophores	F.ye Photoghores	Accessory .	Eyelid. Photophores,
		•	1			
O. danae			2	absent	absent	absent
O. deletron		2	. 1 "	absent	present	present
O. sp A		*	1	absent	absent	present
O. sicula	×		. 2, . /	nosent	present	. absent
O. megaptera			2	present	present	present

5.3. Distribution

The distribution of the genus Octopoteuthie appears to be extremely widespread ranging from sub-Arctic to Antarctic waters. Most collections are from offshore locations but captures are recorded near continents where the continental shell is very close to shore.

Of the 285 juvenile and maturing specimens (identified and unidentified)
which had depth data, 194 (64.8 per cent) were collected in the first 500 metres of
water and a total of 250 (80.8 per cent) in the first 1000 metres.

The following sections describe the geographic and vertical distribution of each of the five species described above. The zoogeographic terms used for pelagic faunal regions in the Atlantic are those defined by Backus and Craddock (1977) and Backus et al. (1977).

Because of the problem of identifying Octopoteuthis larvae to species they are discussed as a group on their own. Unfortunately because of the large number of sources of specimens some data were unobtainable, particularly time of collection. This hindered somewhat the examination of vertical migration.

5.3.1. Octopoteuthis sicula

Geographic Distribution. Found primarily in the western North Atlantic in the slope water province of the North Atlantic temperate region (see Fig. 5-1). Also located in Gulf of Mexico and northen Sargasso Sea of the North Atlantic subtropical region and the Caribbean Sea and Apnazonian provinces of the Atlantic tropical region. Two specimens were collected, one from off of west Africa in the Northern Mauritanian upwelling province and the second from the Indian Ocean.

Vertical Distribution.-Of the 78 specimens of the species only 82 individuals had depth capture data available. All specimens were collected in the top 1000 metres of water at depths ranging between 24 and 1000m (see Fig 5-2). Nearly 81 percent of them were collected in the first 500 metres. Twenty-three animals were collected in the first 100 metres of water (17 from 2 tows). All known night captures (18) were found in the first 500 metres. Of the seven known daytime captures the deepest was collected from gear fishing at 800 metres.

Figure 5-1: Map showing distribution of the Octopoteuthis sicula Rüppell, 1844

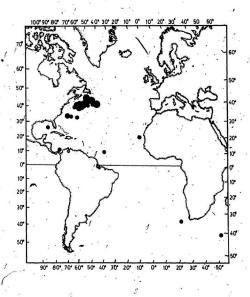
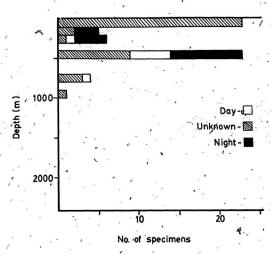


Figure 5-2: Vertical distribution of Octopoleuthis sicula Rüppell, 1844.



5.3.2. Octopoteuthis megaptera

Geographical Distribution. A very widespread species found throughout the Atlantic between 45 'N and 50 'S including: the slope water and Mediterranean outflow provinces of the North Atlantic temperate region; the Straits of Florida, Amazonian and Guinean provinces of the the Atlantic tropical region; the South Atlantic subtropical sea and off the coast of South Africa. Also found throughout the Indian Ocean and off Eastern Australia in the western Pacific. (See Fig 5-3)

Vertical Distribution-Fifty-seven specimens of megaptera were collected from gear fished from 25-4046 metres. MOCNESS captures were from 100 and 250 metres (see Fig 5-4). Eighty-eight percent of all captures were from the first 1000 metres (70 percent in the first 500 metres). All nighttime captures were in the first 1000 metres. The only known twilight capture was from a gear fished at 1000 metres.

Figure 5-3: Map showing distribution of Octopoteuthis megaptera (Verrill, 1885)

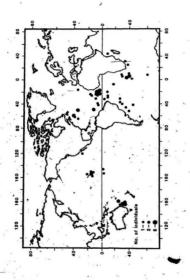
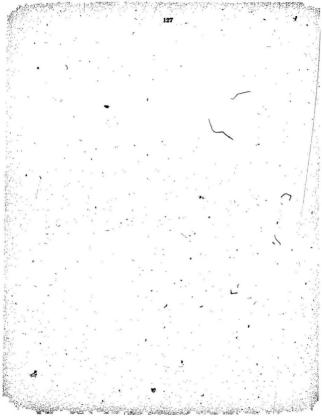


Figure 5-4: Vertical distribution of Octopoteuthis megaptera (Verrill, 1885)



5.3.3. Octopoteuthis danae

Geographic Distribution-Octopotesthis danae appears to be a Northwest Atlantic species collected between 35° and 45° N (see Fig 5-5). It is primarily found in the slope water of the North Atlantic temperate region. Several specimens have also been collected in the North Sargasso Sea province of the North Atlantic subtropical region. Single specimens have been collected from off west Africa in the southern Mauritanian appealing and from off South Africa. Two additional specimens were collected from off Eastern Australia. The identification of the Australian specimens is doubtful.

Vertical Distribution. Of the 33 individuals identified as dance only 21 had depth data available. Captures ranged from 100-4850 metres with 15 (60 per cent) of the captures coming from the first 500 metres (see Fig 5-8). There were 12 known nighttime captures, all above 1000 metres, with 11 of them in the top 500 metres. The two recorded daytime captures were from 200 and 500 metres respectively. The deepest capture using a MOCNESS closing net was at night while fishing at 441 metres denth.



Figure 5-5: Map showing distribution of Octopoleuthis danae Joubin, 1931.

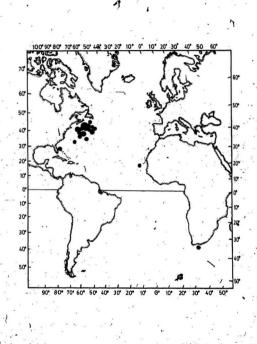
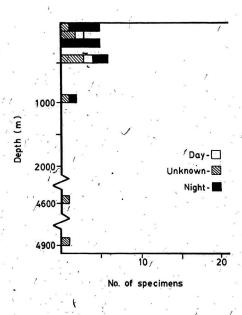


Figure 5-8: Vertical distribution of Octopoteuthis dance Joubin, 1931.

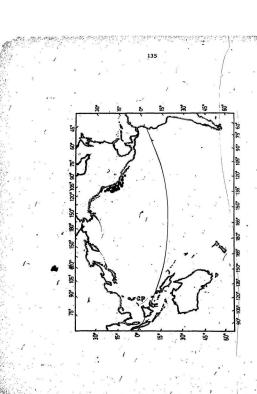


5.3.4. Octopoteuthis deletron

Geographic Distribution-Octopoteuthis deletron is found in the eastern Pacific primarily off California, Washington and Oregon 30° to 40° N and 118° to 128° W (see Fig 5-7).

Vertical Distribution. A total of 29 specimens (18 with depth data) of deletron were collected from gear fished at depths of 274-5500 metres (see Fig. 5-8). Seven were caught above 1000 metres and 14 were caught above 2000 metres. Of the remaining six specimens, three were collected from gear fished above 1000 metres and the remaining three were collected from gear fished at 3000, 4500, and 5500 metres and the remaining three were collected from gear fished at 3000, 4500, and 5500 metres from 2000 metres from above.

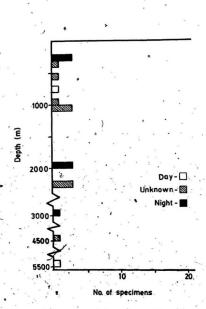
Figure 5-7: Map showing distribution of Octopoteuthis deletron Young, 1972.



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Figure 5-8: Vertical distribution of Octopoteuthis detectron Young, 1972.



5.3.5. Octopoteuthis sp A

Geographical Distribution. O. sp A is primarily distributed in the North Atlantic between 20° and 40° N in the north and south Sargasso Sea provinces of the Atlantic subtropical region (see Fig 5-9). Other specimens were collected from the northern and southern Mauritanian upwelling provinces of the North. African subtropical sea. A single specimen was collected from off South America in the South Atlantic subtropical sea.

Vertical Distribution. Only nine specimens of sp A had depth data available (see Fig 5-10). Six of the specimens were collected from 500 metres or less and all nine were collected from 800 metres or less. There were four known nighttime captures; one from 300, one from 500 and two from the 800 metre depth.



Figure 5-9: Map showing distribution of Young's Octopoteuthis sp A.

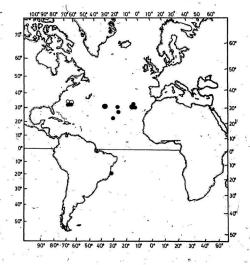
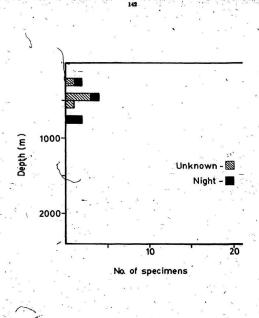


Figure 5-10: Vertical distribution of Young's Octopoteuthis sp A.



5.4. Larval Distribution

Geographical Distribution. In all, a total of 146 larval specimens were examined representing collections from the Atlantic, Indian, and Pacific Oceans and the Mediterranean Sea. The adult characters normally used to separate species (photophore patterns and number and the presence or absence of accessory cusps on arm hooks) do not develop early enough to be useful for species identification in larvae. At present no other characters have been identified that can accurately separate larval Octopoteuthis into species. All specimens discussed will, therefore be referred to as Octopoteuthis spp.

The largest number of specimens examined, totalling 108, came from the. Atlantic. Of those of were from the North Atlantic and a single specimen came from off the western coast of South Africa (see Fig 5-11). Atlantic specimens were collected in all months except December and January with highest catches in March, April and June (see Fig 5-12).

Only 40 other) specimens were examined, 6 and 29 from the Pacific and Indian Oceans respectively, and 5 from the Mediterranean Sea. To suppliment the sparse data the literature was searched for information on additional larvae (Mediterranean - Degner 1925, Issel 1925; Pacific - Okutani and McGowan 1989; and the Atlantic - Cairos. 1976. Massy 1999.

An attempt was made to compare these monthly distributions with those of mature and maturing adult specimens (ie. those showing evidence of gametes) of various species to aid in larval identification. All species of Octopoteuthis, however, seem to have a prolonged period of maturity that can span six to eight months of the year.

Vertical Distribution. Captures of specimens occurred using a variety of gear types fishing at depths of 23-3500 m (see Fig. 5-13). Only 13 specimens lacked year depth information (8 of those were from a single MOCNESS station).

Figure 5-11: Map of distribution of Octopoteuthis spp larvae.

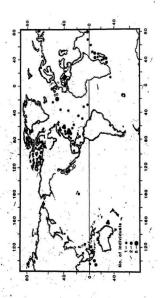
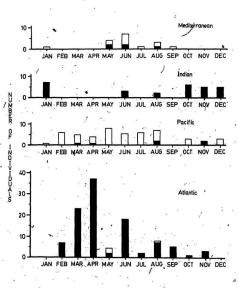


Figure 5-12: Monthly distribution of Octopoteuthis spp larvae based on catch data.



Of the 133 specimens with depth data 71 percent were collected in the first 500 m of depth and 90 percent in the first 1000 m (all gears combined).

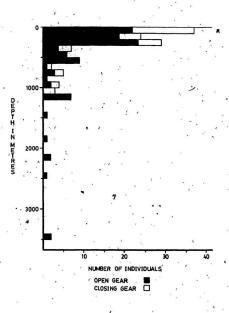
Daytime captures of larvae ranged from 55-1200 m for closing nets (55-1500 m for all gears). Of the 31 known daytime captures 18 were collected in the first 500 m and 15 in the next 1000 m. Night-time captures ranged from 50-1000 m for closing nets (50-3500 m for all gears). Fifty-four larvae were nighttime captures with 40 of those collected in the top 500 m. The heaviest nighttime concentration (31 individuals) was distributed between 100-400 m.

Although not closely looked at, size of individual animals (ML) did not seem to restrict vertical distribution. One daytime catch using a MOCNESS at 1050 m yielded a pair of larvae with MLs of 5.8 and 15.5 respectively. Two separate nighttime trawls in comparison, one at 23 and another at 50 m, yielded specimens of 16.8 and 1.9 mm ML.

Some of the present observations seem to agree with those of Roper and Young (1975). They reported day and night trawl catches of 60 and 81 percent respectively, of larvae of Octopoteuthie deletron Young, 1972 in the first 500 m of water. The remainder of their specimens were collected in the next 700 m. In comparison, only 4 specimens out of 148 reported on in this paper came from gear fished at depths greater than 1200 m. These deepwater records are probably the result of catches while the nets were being set.

Roper and Young also found that nighttime vertical distribution (near surface to 500, m) of Octopoteuthis deletron larvae encompassed and spread beyond their daytime distribution (200-400 m). O. deletron larvae were also absent from the upper 200 m of water. Unlike Roper and Young's observations however, a substantial number of larvae (one third of all day-time catches) were found to inhabit the top 200 metres. There also did 'not appear to be any substantial difference between day and nighttime range distribution (55-1200 and 50-1000 m respectively) when looking at results from closing gear.

Figure 5-13: Vertical distribution of Octopoteuthis spp larvae.



5.5. Gladius

Toll 1982) looked at the structure of the gladius in most of the teuthoid squids and laund it to be quite distinctive between families, some genera and somtimes even species specific. Due to a shortage of available specimens he was unable to determine the full structure of the gladius of the genus Octopoteuthia but he did report Clarke's 1980 comment that at least O. rugosa had a conus. The present study has verified the presence of what Toll (1982) calls a secondary conus in, all species of Octopoteuthia. This secondary conus is formed by the ventral fusion of the vanes of the gladius. The species of Octopoteuthia appear to have very different gladii but because of the small number examined (1-3) from each species inter- and intraspecific variability cannot be measured at this time. Examination should certainly be focussed in this area in any future studies in this genus.

5.6. Arm Loss and Regeneration

The loss of arms (at least the distal portion of them) is extremely common in the genus Octopoteuthia. So common in fact, that it is quite unusual to collect a specimen having more than one or two complete arms. Very few other groups of tetthoid squids, even the smallest species, undergo such loss during capture. Evidence that arm loss occurs during capture is supported by the frequent collection of detached arm tips with and without accompanying specimens (personal observation). The other valid genus in the family Octopoteuthia.

Taningia, rarely has incomplete arms, unlike the case in Octopoteuthis.

The causes of such arm loss may be several but one of the most probable reasons is due to the presence of photophores on all the arm tips and the behavioural and ecological consequences thereof. In an environment where available light levels are very low, such as is the case of the midwater depths usually inhabited by Octopoteuthia, any sources of light, no matter how faint, may serve as lures for prey or signals for species recognition. It may also

inadverticity attract predators to the animal and result in capture of the individual squid if some alternative action could not take place. The autotomy of one or several arms would leave a predator busy and allow the squid a chance to escape relatively unbarmed (much like some lizards that loose their tails when attacked). Of course, loss of parts of arms to predation may not be excluded.

Such action would be detrimental to the individual animal if no means were available to replace the lost parts. Arm regeneration would appear to be the natural physiological response to such a situation.

Lange (1920) was the first to study regeneration of cephalopods (primarily octopods) in detail. She noted that there was wound healing, in teuthoids but that the occasional case of regeneration is by what she labels "compensatory regulation". She stated that lost arms were replaced and not repaired "by developing that rudimentary buccal arm which was correlated to the lost arms". The "replaced arm" differs from the original in length and in that it occupies a position nearer the buccal membrane.

Aldrich and Aldrich (1968) disagreed with Lange in respect to the process of arm and tentacle regeneration of at least some of the teuthoids. Their examination of a specimen of Architeuthis dux Steenstrup, and review of the literature on regeneration in other species (Loligo pealei and Illex illeccerosus (Verrill, 1881); Architeuthis harvyi (Verrill, 1882); and Sepioteuthis teasoniana (Adam, 1937)) revealed that regeneration was certainly more complicated than Lange supposed.

Murata et al. (1981) looked at tentacle and arm regeneration in Ommastyches bartrami (Lesueur). They dound regenerated portions to be generally shorter and suckers on those portions to be smaller, fewer in number, and irregular in configuration. Percentages of captured squids with evidence of regeneration ranged form 0-17.1 per cent over a three year sampling period. The last two papers above corroborate the present findings of the degree of complexity that can occur in teuthoid arm (and tentacle) regeneration. The percentage of regeneration in Ommastrephes bartrami is approximately equal to the nearly 15 per cent found in the Octopoteuthis specimens examined here. It would certainly seem that regeneration is much more common in teuthoids than had previously been thought.

5.7. Photophores and Bioluminescence

It is surprising in a squid genus like Octopoteuthie, which bears many photophores, that the discovery of their bioluminescent function took so long. Nearly fifty years after O. sicula was first described Chun (1910) was one of the first researchers to suggest that the outgrowths located near the ink sac were photophores. In 1912 Pfeffer proposed two other possible photophore sites; at the distal extremities of the arm tips and on the ventral sides of the eye (lid ?). Berry (1920a and b) tentatively listed the genus as being bioluminescent. In 1923 Nacf accepted the presence of the arm tip photophores but doubted the nature of those organs lying ventrally against the ink sac.

Okada (1927) carried out the first histological study of the three supposed photophore groups. His conclusion was that the only photophores in Octopoteuthis were those located at the arm tips. In 1929 Pierantoni carried out a similar examination and appeared to be totally unaware of the work done two years earlier by Okada. Pierantoni found Octopoteuthis to be a luminescent species. In the same year, in Japan, Sasaki described arm tip photophores from specimens of Octopoteuthis specimens from Japan.

In 1931, Joubin described his new species Octopodoteuthis danae as having four pairs of photophores but was unable to conduct histological studies on them because of the poor condition of the specimen and its tissues.

Harvey (1952) in his classic text on bioluminescence listed Octopodoteuthis

and Octopodoteuthopsis as bioluminescent species. Both Adam (1952, 1980) and Voss (1956a) described photophores in specimens they described as Octopoteuthis sicula and O. megaptera respectively. Young (1972) was the first to find brachial photophores along the axial nerves of his new species O. deletron. In 1975 Lipka described brachial photophores from Octopoteuthis specimens in the North Atlantic.

Herring (1977) discussed bioluminescence in fish and cephalopods and presented a list of all known cephalopods bearing photophores including Octopeteuthis. Herring (1978a and b) again listed luminescent eephalopods and presented a table showing photophore distribution in each family.

Nearly all the photophores in Octopoteuthis species are directed ventrally (Young and Roper, 1977). During observations on live specimens of Octopoteuthis nielseni Young and Roper (1977) found that the squid could countershade themselves by using their body photophores to match the intensity of the level of light coming from an overhead light. The animals tested turned their photophores on in response to overhead illumination and reduced or turned them off when overhead light was extinguished.

5.8. Ecological and Economic Importance

While specimens of the genus Octopoteuthie are relatively rare in collections they have been collected from the stomachs of a large number of fish and cetacean species. Clarke (1980) has found members of the genus to account for up to 24 per cent of the buccal masses taken from sperm whale stomachs from off Durban, South Africa. Table 5-3 provides a list of predators from which Octopoteuthie specimens (or their beaks) have been collected and the literature reference.

It is obvious from the table that Octopoleuthis must play an important role as food for these predators. It should also be noted that the largest specimens we

Table 5-3: Predators from which Octopoteuthis specimens have been collected

PREDATOR	AUTHORITY

CETACEANS

Physeter catadon-Sperm whale Akimushkin, 1983; Clarke, 1986; Clarke, 1980; Clarke, and MacLeod, 1978; Clarke, MacLeod and Paliza, 1976; Okutani and Sataki, 1978; Okutani et al., 1978.

Hypercodon ampullatus-Clarke and Kristensen, 1980.
Northern bottlenosed whale

Tursiops truncatus Clarke, 1966; Rancurel, 1964.
Bottle-nosed dolphin

FISH

Thunnus alalunga-

Bouxin and Legendre, 1932.

Thunnus thynnus-Blue-fin tuna Data from specimens examined.

Alepisaurus ferox-

Rancurel, 1970.

Prionace glauca-Blue shark Clarke and Stevens, 1976.

have representing the genus generally come from the stomachs of large predators (Clarke, 1980). Indeed, the largest specimen examined in this study (240 mm ML) came from the stomach of a blue-fin tuna collected in South African waters.

The genus has little commercial value at present and the high ammonium content in its tissues would certainly detract from its palatability. Tomiyama and ~ Hibiya (1978) however listed it as being landed for use as food in Japan.

5.9. Statistical Analysis

Morphometrics have been used in taxonomic study since the late 1800's. Great emphasis has been placed on indices (ie. body measurements as a proportion of some standard body measure, most often the length of the mantle measured on the dorsum from the anterior-most point of the mantle to the posterior spex of the mantle, the mantle length) as a means to differentiate between cephalopod species. Roper and Voss (1983) call for an even greater emphasis. Little has been written however on the statistical testing of these indices and usually nothing is done other than to present their means, ranges and standard deviations.

Several authors have discussed the pros and cons of analysing derived variables, such as indices (ie. ratios), versus original measurements (Atchley et al., 1076; Blackwith and Reyment, 1971; Green, 1979; Marr, 1955; and Sokal and Rolf 1969, 1973). For the most part they considered the use of ratios to be statistically poor in morphometric analyses and recommended methods such as the analysis of covariance (ANCOVA) of the original measurements. One of the main reasons for the problem is that indices change with growth and it is sometimes diffiult to get specimens of equal size.

N. Voss (1985) has managed to get around this problem and retain the use of indices by summarizing them, for selected series, over an entire available size range. This method is certainly good when applied to a large and diverse sample size but it still does not statistically test the data.

A few cephalopod workers have used statistical analyses in their work.

Cohen, in her 1976 paper on the systematics of western North Atlantic species of

Loligo, used ANCOVA in her analysis. The ANCOVA allowed analysis of the

factors of sex and geographic location simultaneously and eliminated the need to

have samples of equal size.

The discriminant analysis used in this present review of the genus Octopoteuthis an ANCONVAs on the raw measurements of selected parameters of each of the species and recommended changes in classification based on those analyses. The growth factor was neutralized by making ML the independent variable and running all ANCOVAs against it. The discriminant analysis was, in fact, testing the usefulness of morphometries to distinguish a priori species based the characters defined above.

The initial discriminant analysis presented an a posteriori classification including a list of what it considered as 'misclassified specimens' and a table indicating the percentages of specimens classified into each a priori species. First results indicated an average of 73.7 per cent of classified specimens as correct. One species, O. sp A, had a very small sample population (5) with complete variable data. As a result the covariance matrix, was not of full value (ie. the analysis did not use two of the variables, eye diameter and lens diameter, of the species). O. sp A was therefore removed from the second discriminant analysis to see if the classification could be improved.

The second discriminant analysis resulted in an improved classification average of 78.1 percent of the original identifications correct. The overall result suggests that there is a good correlation between body measurements and the a priori defined species. One of the four species, Octopoteuthis danae had the highest correct classification of nearly 87 percent. The other three species deletron, sicula and megapters had lower classification percentages of 77.8, 73.3 and 71.4 per cent respectively.

Based on the a priori species classification it would be expected that sicula would be closest to danae in morphometrics since they differ only by the presence or absence of accessory cusps on the arm hooks. This is supported by the high percentage of sicula specimens (22.2 percent) that are placed into O. danae by the analysis.

The discovery that morphometrics appear to be useful in separating species in this genus is surprising in a group of squids that is generally very gelatinous. The specimens examined for this study were fixed for varying durations in formalin and preserved in a variety of alcohol types (70% ethanol, 50 % isopropanol) which would be expected to produce varying shrinkage results. Certainly with the very small number of specimens (160) with complete morphometric data the measurements seem to be species specific.

5.10. Conclusions

From this study I conclude that:

- There are 5 valid species of Octopéteuthis; 4 in the North Atlantic sicula, megaptera, dange, and sp A and 2 in the Pacific deletron and megaptera.
- 2. Species of Octopoteuthis may be separated using photophore patterns and hook structure making obvious therefore that intact complete specimens are necessary for proper analysis.
- Morphometric data alone are not sufficient criteria on which to base species differentiation.
- 4. Discriminant analysis is encouraged as a proper statistical means to test morphometries in a systematic paper such as this. The rate of success achieved in its use here exceeded all expectations and this technique should be used in cephalopod systematics where morphometries and resultant indices are so heavily relied upon.
- 5. With the co-occurence of 4 species in the North Atlantic and two in the Pacific one would expect that further close analysis of the two species presently recognized in the Pacific, supplemented by additional collections, would indicate multiple octopoteuthid fauna there as well.

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APPENDIX 1

This following appendix lists the collection and catalogue data for each specimen by species. See materials and methods for museum, gran and collector abreviations.

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APPENDIX 2

The following appendix includes the specimen morphometric and meristic data for each species listed. In the case of the measurements all 0.0 are missing a large data (except those in larval ie. < .25 mm ML specimens). The abdominal photophore (abdphot) column the numbers used equal the number of photophores present 2 or 1 (or 0 in larvae). In the other meristics (anteye, eyebal, and hook) 9 = missing data, 0 = absent, and 1 = present. See materials amd methods chapter for definition of abbreviations.

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