

IN SITU OBSERVATIONS TEST HYPOTHESES OF FUNCTIONAL MORPHOLOGY IN MASTIGOTEUTHIS (CEPHALOPODA, OEGOPSIDA)

C.F.E. ROPER¹, M. VECCHIONE²

¹ Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA

² National Marine Fisheries Service, Systematics Laboratory, National Museum of Natural History, Washington, D.C. 20560, USA

CEPHALOPODS
SQUID
SUBMERSIBLE
DEEP SEA
BEHAVIOR
FUNCTIONAL MORPHOLOGY

ABSTRACT. – *Mastigoteuthis magna* observed *in situ* has a characteristic “tuning fork” posture that can be used as an aid for identification, even for very small squids. Observations of living *Mastigoteuthis* from submersibles in the western Atlantic Ocean enabled us to test formerly proposed hypotheses concerning functional morphology of these deep sea squids. Hypotheses supported by observations on live animals include: 1) *The large fins provide propulsion*; simple and double sinusoidal waves move anteriorly or posteriorly, fins flap powerfully, fins roll together ventrally to squeeze water out anteriorly or posteriorly. 2) *Tentacular suckers have weak release mechanism*; tentacular clubs on live animals feel very sticky, like fly paper, and must be firmly pulled off observer’s skin and aquarium wall. 3) *Tentacular suckers have sensory function*; tentacular tips skim along bottom to allow animal to maintain position in food-rich benthic boundary layer. Observations do not support these hypotheses: 1) *Vacuolated arms and head induce head-upwards posture*; observations confirm a head-downwards posture maintained by constantly maneuvering fins. 2) *Ventral arms lock together to form “gutter” for feeding*; live animals hold long ventral arms far apart with proximal part of tentacles enveloped in tentacular sheaths, allowing them to serve as non-tangling trolling lines fishing for minute prey. 3) *Well developed eyes and ink sac indicate photic zone habitat*; all observations of *Mastigoteuthis* from submersibles are close to the bottom below 500 m, never in photic zone. We suggest *Mastigoteuthis* evolved from a *Chiroteuthis*-like ancestor; its adaptive characters enable it to inhabit the unique trophic zone immediately above the deep sea bottom, feeding on small zooplankters with trolled, non-tangling tentacles.

CÉPHALOPODES
CALMAR
SUBMERSIBLE
EAUX PROFONDES
COMPORTEMENT
MORPHOLOGIE FONCTIONNELLE

RÉSUMÉ. – *Mastigoteuthis magna* se présente *in situ* en posture de “diapason” caractéristique permettant l’identification de l’espèce, même lorsqu’il s’agit d’individus de petite taille. L’observation de *Mastigoteuthis* à partir d’un submersible mis en action dans l’Atlantique occidentale a permis de tester certaines hypothèses avancées précédemment, relatives à la morphologie fonctionnelle de ces Calmars des eaux profondes. Les hypothèses confortées par nos observations sont: 1) Les très grandes nageoires servent à la propulsion: des ondes sinusoidales simples et doubles se propagent en direction antérieure ou postérieure, les nageoires battent vigoureusement, et s’enroulent du côté ventral en chassant l’eau vers l’avant ou vers l’arrière. 2) Les ventouses des tentacules ont un faible mécanisme de relaxation: les massues tentaculaires d’individus vivants sont très adhésives, comme du papier collant (“bandes à mouches”), et résistent fortement à toute traction exercée pour les détacher de la peau d’un observateur ou de la paroi d’un aquarium. 3) Les ventouses tentaculaires ont une fonction sensorielle: les extrémités des tentacules sont traînées au contact du fond permettant ainsi à l’animal de se maintenir dans la couche limite du benthos, riche en nourriture. Les observations ne confortent pas les hypothèses suivantes: 1) Les bras et la tête contenant des vacuoles causent l’orientation de la tête vers le haut: les observations mettent en évidence une position dans laquelle la tête est orientée vers le bas, maintenue ainsi par le mouvement continu des nageoires. 2) Les bras ventraux sont réunis pour former une “gouttière” canalisant la nourriture vers la bouche: les animaux vivants tiennent leurs bras ventraux écartés l’un de l’autre, les parties proximales des tentacules étant enveloppées dans des gaines tentaculaires, de sorte que les tentacules servent de lignes de pêche traînées pour

la capture de proies minuscules. 3) Les yeux et la poche d'encre bien développés témoignent d'un habitat en zone euphotique: toutes les observations sur *Mastigoteuthis* ont été faites près du fond, à des profondeurs dépassant 500 m, donc en aucun cas dans la zone euphotique. Nous pensons que *Mastigoteuthis* s'est développé à partir d'un ancêtre de type *Chiroteuthis*; ses caractéristiques adaptatives lui permettent de vivre dans la zone trophique très particulière qui se trouve juste au-dessus du substrat des grands fonds, et de consommer du zooplancton de petite taille à l'aide de tentacules séparés et traînés.

INTRODUCTION

Direct observations on the functional morphology of deepsea cephalopods always have been hampered by the difficulty of access to animals that are functioning normally. As a result, most inferences about function have been based on studies of the anatomy of dead specimens. Ongoing exploration of deepsea environments using submersibles is slowly overcoming this problem by allowing accumulation of observations on cephalopods *in situ* and by enabling their gentle capture for prolonged observation in shipboard aquaria.

The research reported here continues the series of studies we are conducting on deep sea cephalopods observed *in situ* from manned and unmanned submersibles, e.g., Vecchione and Roper (1992), Vecchione *et al.* (1992), Roper and Vecchione (1996). We have compiled from a number of sources several detailed observations on *Mastigoteuthis* spp, especially *M. magna* Joubin, 1913. A submersible cruise off North Carolina in 1994 provided a particularly rich source of *M. magna* behavior captured on video tape.

Chun (1910) first described the internal anatomy of several species of immature *Mastigoteuthis*; Dilly *et al.* (1977) provided excellent detailed observations on the anatomy of trawl-captured *Mastigoteuthis* sp. from which they inferred functional capabilities. Our observations from submersibles on living *Mastigoteuthis* in their natural habitat enable us to test several hypotheses concerning functional morphology proposed by Dilly *et al.* (1977), most notably the following:

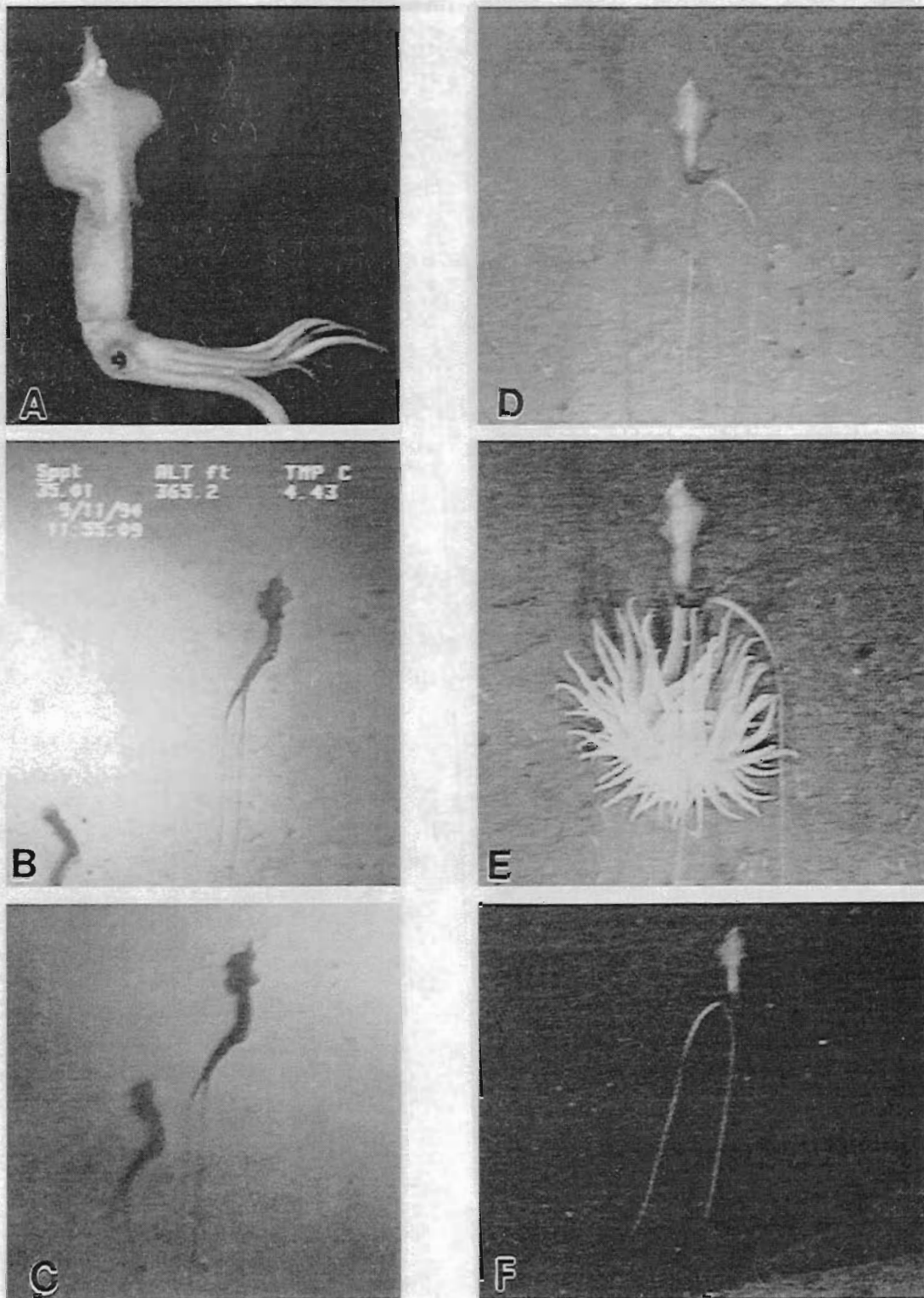
1. Based on the vacuolated tissue of the arms, the squid probably lives with its head upwards.
2. Because of the large and complex magno-cellular lobe of the brain, it is likely that propulsion is accomplished mainly by the large fins.
3. The large ventral arms may be held together to form a "gutter" for feeding.
4. The tentacular suckers probably have a poor or slowly acting release mechanism.
5. The multitude of minute tentacular suckers may have a sensory function.
6. The well-developed eyes and ink sac suggest that at least some of the adult life is spent in the photic zone where the eyes are used for the detection of prey.

MATERIALS AND METHODS

The information on *M. magna* was gathered from several sources, principally from video tapes taken during dive cruises in the western Atlantic Ocean using the *Johnson-Sea-Link I* and *II* submersibles. Also, specimens were captured and identified after having been observed *in situ*. The most extensive observations and videos were made during the cruise to "The Point" area near Cape Hatteras, North Carolina in September 1994. The bottom topography in the region of the dive sites at The Point at 700-1 000 m consists of soft sediments in a series of ridges and canyons that fan out into deeper water. Temperatures at the bottom in the canyons were generally 4.5°C. Details of the dive sites and ecosystem in relation to the cephalopod project are given in Roper and Vecchione (1996). Eight separate *in situ* video sequences that range in duration from a few seconds to about 15 minutes were recorded during the 1994 cruise. Also during this cruise, one of the specimens observed *in situ* was captured by the submersible, maintained alive and videotaped for several hours in a 1 m diameter plankton kreisel aquarium (Hamner, 1990).

OBSERVATIONS

The accumulation of video sequences of *Mastigoteuthis magna* during the past several years has revealed a strikingly habitual posture consistently seen in this species. This posture typically consists of the animal hanging or hovering head downward with the mantle vertical, posterior upward, head oblique, arms I through III held at an oblique angle toward the horizontal (approximately 45°); the ventral arms (IV) and the tentacles, their proximal sections tightly wrapped in the tentacular sheaths of arms IV, hang down vertically in a tuning fork (inverted Y with curved arms) configuration so that the arms and tentacles are rather widely separated (Plate I. A-F). The tentacle length of the seven specimens that could be measured extended 3-4 times the length of the mantle (Plate I. B,C,F). No active swimming or jetting is associated with the hovering posture, which appears to be held for extended periods of time. Specimens are in that posture when first encountered, continue through periods of observation and filming of up to 15 minutes, and remain essentially immobile as the submersible departs.



Pl. I. - *Mastigoteuthis magna*: A. In typical head-down posture. Fins show double sine wave undulation. Mucous strands (white blobs) attached to posterior end of mantle. B. In typical head-down, tuning fork posture with tips of elongate tentacles hanging close to bottom. Fins show non-synchronous double sine wave undulation. Note shadow on bottom. C. Drifting just above bottom in typical head-down, tuning fork posture. Elongate tentacles and their shadow on bottom are converging. Fins in double sine wave undulation. D. Drifting just above bottom in typical head-down, tuning fork posture with elongate tentacles and their shadows converging on the bottom. E. Drifting in typical tuning fork posture through expanded tentacles of anemone. F. In typical tuning fork posture with tentacles greatly elongate as animal suddenly drifts over steep drop-off of sea floor.

The animal's position in the water column and its vertical orientation are maintained by either simple or complex undulations of the fins. The undulations of the fins may take one of several forms, depending on the correction required to maintain vertical orientation, elevation above the bottom and, perhaps, orientation relative to the current. These include single sinusoidal undulations that originate at the anterior end of the fins and proceed posteriorly to the posterior end (Plate II. A), and those that originate at the posterior tip of the fins and proceed in a single wave to the anterior edge of the fins (Plate II. B). A new undulation begins after the completion of the preceding one. Each fin seems individually controlled, because the frequency and amplitude on one fin is different from that of the other. Complex undulations include a double sine wave progressing along the fin simultaneously (Plate I. A,B,C); these tend to be much more rapid than the single waves, and they may move either posteriorly or anteriorly. The undulations are used for relatively gentle motions that are positional corrections, not substantial locomotion. The fins also can be flapped in a strong dorsalventral beat (Plate II. C), apparently with a posterior to anterior gradient, that imparts a tailfirst locomotion that can be relatively strong when only the fins are involved; a very rapid escape reaction occurs when strongly flapped fins are combined with water ejected (jetted) from the funnel.

Another, previously unknown, function was observed for the fins. The fins sometimes are rolled together ventrally so that they overlap along the ventral midline and squeeze the water between the fins and mantle out anteriorly or posteriorly, providing a sort of low-velocity jet propulsion (Plate I. D,E).

The *M. magna* we have observed in the typical tuning fork posture have nearly always been located near the sea floor (Plate I. B-F). The animals drift along slowly above the bottom with their tentacles trailing down towards the substrate, and occasionally the tentacular tips touch the bottom. This is clear in several video sequences in which the tentacular tips and their shadows converge on the bottom sediment (Plate I. C,D). One sequence recorded over a bottom that steeply deepens shows the animal elongating its tentacles to twice their length as the sea floor drops off below it (Plate I. F). In cases where the bottom is not seen in the video, dive data show that the submersible and the *Mastigoteuthis* are just a few meters above the substrate. In the kreisel, the tentacular clubs of the squid stuck tenaciously to the glass, even when the animal vigorously tried to swim away, stretching the tentacles to many times the length of the mantle before they pulled free. When an animal is not drifting along the bottom with tentacles extended, the tentacles are contracted

almost completely into the tentacular sheaths of arms IV (Plate II. A,F), possibly for protection, to reduce drag and to avoid tangling.

An observation for which we have as yet no satisfactory explanation is the occurrence of what appear to be mucus strands attached principally, but not exclusively, around the posterior end of the mantle (Plate I. A, II. B). While this is not observed on every specimen, it occurs frequently enough on *Mastigoteuthis*, as well as on *Histioteuthis*, to draw our attention.

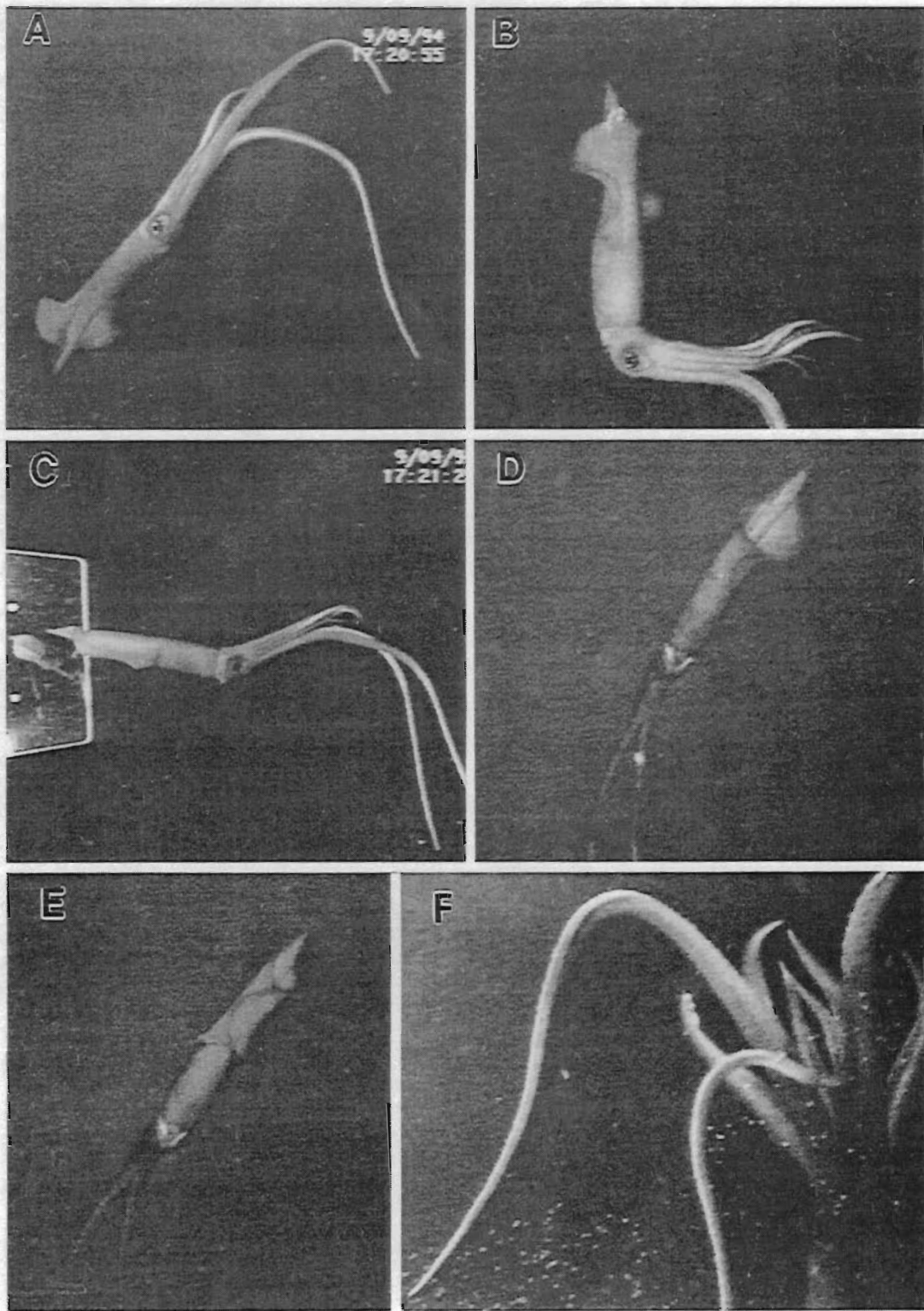
The stomach contents of several museum specimens were examined. The stomach is lined with a very heavy, rugose, cuticular lining. Several stomachs contained a large quantity of yellow oil. Some stomachs contained a few bits and pieces that consisted of the cephalothorax and spines of unidentified copepods. The caecum is a very large, long organ in comparison to the size of the stomach and does not have a similar lining.

DISCUSSION

The work of Dilly *et al.* (1977) provides an excellent platform from which to discuss the *in situ* observations of *Mastigoteuthis magna*. These authors give a detailed description of the histology of the brain and aspects of the external and internal anatomy of *Mastigoteuthis* sp., and they utilize these data to formulate hypotheses about its habits and mode of life. Our observations on living animals enable us to test their hypotheses about functional morphology.

1. *Vacuolated tissues of arms and head induce head upwards posture.* – Most of the tissues of *Mastigoteuthis*, especially the arms, head and mantle are vacuolated and contain lightweight ammonium ions as an aid to buoyancy (Denton and Gilpin-Brown 1973). Because the ventral arms are so very large, consequently buoyant, Dilly *et al.* (1977) hypothesized that these animals live with their heads and arms vertically upwards when they are not swimming. The tentacles, on the other hand, are not vacuolated but have dense tissue, so they hang downwards. Our observations on live animals do not support the headup posture. Instead, *Mastigoteuthis* consistently use their fins actively to maintain the inverse position, with head, arms and tentacles downwards. One squid that had ceased undulating its fins briefly began rotating toward a headup position, but this was an exception, possibly caused by the squid being in water disturbed by the submersible's maneuvering.

2. *Propulsion by large fins.* – Because the magnocellular lobe of the brain is extremely welldeveloped with its motor control output going to the large fins, Dilly *et al.* (1977) deduced that the



Pl. II. — *Mastigoteuthis magna*: A, With single sinusoidal undulation of fins originating at anterior end. Animal somewhat above bottom with tentacles contracted into tentacular sheaths of arms IV. B, With single sinusoidal undulation originating at posterior end. Mucous strands (white blobs) attached to posterior tip of mantle. C, With fins overlapping ventrally and motionless. Note rotation of head upward. D, With fins rolling together along ventral midline, squeezing water out posteriorly in a low-velocity jet. E, With fins overlapping along ventral midline at completion of low-velocity jetting stroke. F, In non-trolling mode off the bottom with right tentacle (left in photo) nearly completely contracted into tentacular sheath of right arm IV and left tentacle being contracted and enveloped into left arm IV tentacular sheath

fins are the main source of propulsion for *Mastigoteuthis*. This inference is further supported by the very well-developed fin lobe that receives connections from the magnocellular lobe (Young 1977; Maddock and Young 1987). Our *in situ* observations strongly support this hypothesis and demonstrate the numerous, complex, and varied fin functions. Single and double sinusoidal wave undulations sweep anteriorly or posteriorly along the fins; fins flap powerfully in escape maneuvers; fins roll together ventrally to squeeze water out both anteriorly or posteriorly. Jet propulsion does occur through the funnel, but the fins always seem active and are dominant in both locomotion and position-holding.

3. *Ventral arms form gutter for feeding.*— Following the suggestion of Rancurel (1971), Dilly *et al.* (1977) concur that the large ventral arms may be held together by the suckers to form a gutter that captures prey. The observations and videos of live animals show that the arms virtually always are held far apart. The tentacular sheaths along the entire length of the ventral arms envelop the proximal section of the tentacles, holding them far apart, perhaps so the tentacles will not become entangled and stuck together with their multitude of minute suckers. Therefore, the large, long arms function to control the position of the tentacles, holding them as far apart as possible while they drift along near the bottom like sticky trolling lines fishing for minute prey.

4. *Tentacular suckers have weak release mechanism.*— Dilly *et al.* (1977) suggest that the extremely numerous, minute, pedunculate tentacular suckers that consist primarily of cuticular tissues with very little soft or muscular tissue, function to mechanically attach to prey, but that they are very weak and slow to release their grip. This would explain why many trawlcaptured specimens have their tentacles missing; they have been pulled off in the webbing of the net from which they could not be released. When a live *Mastigoteuthis* is handled, its tentacles feel very sticky, reminiscent of fly paper, and they have to be firmly pulled off the skin, as they do not release themselves. The hypothesis is further borne out by our observations in the shipboard kreisel aquarium, where the clubs stuck tenaciously to the glass while the animal tried to move away, stretching the tentacles to many times the length of the mantle before they release. While other squids show this sticking phenomenon, e.g., *Chiroteuthis*, they do not appear to do so to the extreme that *Mastigoteuthis* does (M. Vecchione, C.F.E. Roper, pers. observ.).

5. *Tentacular suckers have sensory function.*— A very large axial nerve along the tentacle connects directly into the large ventral magnocellular lobe, the complexity of which suggests a chemotactile function. Dilly *et al.* (1977) proposed that tentacular suckers may contain sensory

cells that detect prey and direct it to the arms for transfer to the mouth. We have no observations on actual prey capture, but we observed one animal drifting just above the bottom in the feeding mode we hypothesize; it seemed to monitor its distance above the bottom with its tentacles. When the bottom dropped off suddenly, the tentacles immediately elongated to twice their length. This may result from a strong neural association between the tentacular suckers, the magnocellular lobe and the fins (Dilly *et al.* 1977; Young 1977), and it would keep the animal in the feeding zone of concentrated zooplankton in the benthic boundary layer (Dauvin *et al.*, 1995).

6. *Well-developed eyes and ink sac indicate photic zone habitat.*— Dilly *et al.* (1977) hypothesize that the large, well-developed eyes and an ink sac indicate that these animals undergo diel vertical migration into the photic zone in search of prey. None of the numerous *in situ* observations we now have on several species of *Mastigoteuthis* have occurred in the photic zone; all observations from submersibles are very close to the bottom. Roper and Young (1975) presented data on vertical distribution of trawl-captured mastigoteuthids, some by closing nets, and no captures of adults occurred in the photic zone. Shea (1995) showed the same pattern for paralarval mastigoteuthids caught in closing plankton nets. Mastigoteuthids always have been considered deep-sea inhabitants, mesopelagic to bathypelagic in vertical distribution. The first hint we had that at least some species are in fact benthopelagic came when stomach contents of macrourid rattail fishes (*Coryphenoides*) were shown regularly to include *Mastigoteuthis* and *Histioteuthis* beaks and remains (C.F.E. Roper, pers. observ.). These fishes are benthic/nearbottom feeders that do not venture far off the bottom. This revelation that mastigoteuthids are nearbottom dwellers, in spite of the longheld assumption of their midwater habitat, shows that caution is required when inferring function from anatomy in the absence of ancillary data on habitat, behavior or ecology.

An alternative explanation for the large eyes could be that vision is used to detect bioluminescence stimulated by movement of predators. It is not known yet if the ink sac secretes luminescent ink as has been observed in some other deep sea cephalopods (Herring 1977), or if the ink sac merely is a remnant of a shallow water ancestor (Vecchione 1994).

It seems counterintuitive that these squids typically are seen in a posture in which the center of gravity is higher than the center of buoyancy, because of the energy required to maintain this position. We suggest the possibility that the Mastigoteuthidae evolved from a *Chiroteuthis*-like ancestor. We have seen *Chiroteuthis*, which has smaller fins than *Mastigoteuthis* and vacuolated tis-

sues in its large head and arms, floating in an oblique head-upward orientation with the tentacles trailing downward. The mastigoteuthids have developed large, dexterous fins and complex magnocellular lobes to reverse the passive *Chiroteuthis* posture resulting from buoyancy. This allows them to use the sheathed ventral arms for better control of the tentacles with their extremely numerous, highly sensitive suckers. This complement of characters enables the mastigoteuthids to inhabit the unique trophic zone immediately above the deepsea bottom and to take advantage of the small zooplankters concentrated there (Wishner, 1980) while avoiding accidental entanglement of the tentacles.

It is acceptable, even necessary, to infer function based on morphology of dead specimens, but in order to inspire confidence, these inferences must be treated as hypotheses to be tested. Observations of live animals in their natural habitat allow tests of such hypotheses.

Because of the characteristic posture reported here, animals seen at the limits of vision from the submersible and in videotapes and photographs can now easily be identified as mastigoteuthids, even very small juveniles. In one instance, we have a one-second sequence from a transect reported on by Felley and Vecchione (1995) of a squid in the typical position that allows us to identify it as a *Mastigoteuthis*. One sequence is available on video because the observer in the submersible thought that, from a distance, the very small juvenile *Mastigoteuthis* was a cydippid ctenophore with its two tentacles hanging downward.

Portions of the video sequences upon which this paper are based are presented in the "Cephalopods in Action" web pages at the following URL on the Internet. <http://www.nmnh.si.edu/cephs>.

ACKNOWLEDGMENTS. - We gratefully acknowledge the following people and organizations for their significant contributions to this work: Drs. E. Widder, T. Frank, and T. Bailey for inviting one of us (CFER) to participate in their cruise (National Science Foundation Grant Number OCE-9313872, National Underwater Research Program Grant Numbers UNCW 9410 and UNCW 9406); the scientific, submersible and ship's crews; Harbor Branch Oceanographic Institution, Ft. Pierce, Florida, which owns and operates the submersible and its mother ship, R/V Edwin C. Link; Woody Lee, Smithsonian Marine Station; Dane Penland, Office of Photo Services, Smithsonian Institution; the Smithsonian Marine Station, Dr. M. Rice, Director; M.J. Sweeney prepared the plates and reviewed the manuscript. Two anonymous reviewers are acknowledged with thanks. This paper is Smithsonian Marine Station Contribution Number 397.

LITERATURE CITED

CHUN C. 1910. Die Cephalopoden. 1. Teil: Oegopsida. Wissenschaftlichen Ergebnisseder Deutschen Tiefsee Expedition "Valdivia" 18: 1-402.

- DAUVIN J.-C., SORBE J.-C. and LORGERE J.-C. 1995. Benthic boundary layer macrofauna from the upper continental slope and the Cap Ferret canyon (Bay of Biscay). *Oceanologica Acta* 18: 113-122.
- DENTON E.J. and GILPIN-BROWN J.B. 1973. Flootation mechanisms in modern and fossil cephalopods. *Adv. mar. Biol.* 11: 197-268.
- DILLY P.N., NIXON M. and YOUNG J.Z. 1977. *Mastigoteuthis* - the whip-lash squid. *J. Zool., Lond.* 181: 527-559.
- FELLEY J.D. and VECCHIONE M. 1995. Assessing habitat use by nekton on the continental slope using archived videotapes from submersibles. *Fish. Bull.* 93: 262-273.
- HERRING P.J. 1977. Luminescence in Cephalopods and Fish. In: Nixon M. and Messenger J.B., Eds. *The Biology of Cephalopods. Symp. Zool. Soc. Lond.* 38: 127-160.
- HAMNER W.M. 1990. Design development in the plankton kreisel, a plankton aquarium for ships at sea. *J. Plank. Res.* 12 (2): 397-402.
- MADDOCK L. and YOUNG J.Z. 1987. Quantitative differences among the brains of cephalopods. *J. Zool., Lond.* 212: 739-767.
- RANCUREL P. 1971. *Mastigoteuthis grimaldi* (Joubin, 1895). Chiroteuthidae peu connu de l'Atlantique tropicale (Cephalopoda-Oegopsida). *Cah. O.R.S.T.O.M. sér. Océanogr.* 9 (2): 125-145.
- ROPER C.F.E. and VECCHIONE M. 1996. *In situ* observations on *Brachioteuthis beanii* Verrill: paired behavior, probably mating (Cephalopoda, Oegopsida). *Am. Malac. Bull.* 13: 55-40.
- ROPER C.F.E. and YOUNG R. 1975. Vertical distribution of pelagic cephalopods. *Smiths. Contr. Zool.* 209: 1-51.
- SHEA E.K. 1995. The Early Life Histories of Three Families of Cephalopods (Order Teuthoidea) and an Examination of the Concept of a Paralarva. Masters Thesis, School of Marine Science, College of William and Mary, Virginia, 133 p.
- VECCHIONE M. 1994. Systematics and the lifestyle and performance of cephalopods. *Mar. Fresh. Behav. Physiol.* 25: 179-191.
- VECCHIONE M., ROBISON B.H. and ROPER C.F.E. 1992. A tale of two species: tail morphology in paralarval *Chiroteuthis* (Cephalopoda: Chiroteuthidae). *Proc. Biol. Soc. Wash.* 105 (4): 683-692.
- VECCHIONE M. and ROPER C.F.E. 1992. Cephalopods observed from submersibles in the Western North Atlantic. *Bull. Mar. Sci.* 49 (1-2): 433-445.
- WISHNER K.F. 1980. Aspects of the community ecology of deep-sea, benthopelagic plankton, with special attention to gymnopleid copepods. *Mar. Biol.* 60: 179-187.
- YOUNG J.Z. 1977. Brain, Behavior and Evolution of Cephalopods. In Nixon M. and Messenger J.B., Eds. *The Biology of Cephalopods. Symp. Zool. Soc. Lond.* 38: 377-434.

Reçu le 14 février 1996; received February 14, 1996
 Accepté le 3 juin 1996; accepted June 3, 1996