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THE SHELL IN VAMPYROPODA (CEPHALOPODA):

MORPHOLOGY, FUNCTIONAL ROLE AND EVOLUTION

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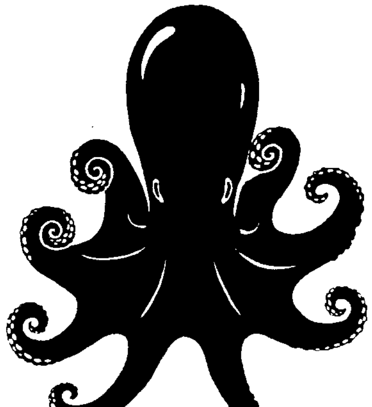

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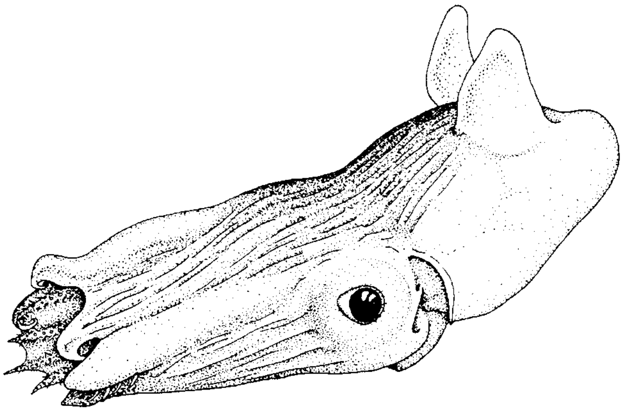
В.А. Бизиков

РАКОВИНА VAMPYROPODA (CEPHALOPODA): морфология, функциональная роль и эволюция



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The shell in Vampyropoda (Cephalopoda): morphology, functional role and evolution

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> *The shell of mollusks is the part that determines the whole.*
> Adolf Naef, 1921

ABSTRACT. Comparative functional morphology and microstructure of internal shell vestiges have been studied in 14 species of recent Vampyropoda including the single recent representative of vampire squids, *Vampyroteuthis infernalis* Chun, 1903, 3 species of Cirrata and 10 species of Incirrata. Relationship between the shell and the soft body was studied on total cross-sections of the mantle at different planes. The study shows that the shell plays different role in different groups of eight-armed Coleoidea, and evolution of the shell was stipulated by evolution of its function. In *Vampyroteuthis*, an early evolutionary offshoot of the Vampyropoda, the shell represents a typical gladius of the teuthoid type that provides attachment sites for the fins, mantle, funnel and head retractors, and the visceral sac. In cirrate octopods the gladius represents a remnant of cone flags, wings and lateral plates of vampyromorph gladius, which is transformed mostly into a 'fin support'. In the Incirrata the shell is reduced to paired rods, stylets, functioning as anchors supporting the funnel retractors. In several advanced lineages of Incirrata the shell has been lost completely.

Each lineage of recent octopodiforms — Vampyromorphida, Cirrata and Incirrata — has its own characteristic type of shell structure and shell-soft body relationships. Wide separation of stellate ganglia in all recent octopods presents morphological evidence that this group evolved from some vampyromorph-like ancestor with wide middle plate of gladius proostracum. Two crucial events took place in evolution of the shell in octopodian lineage: reduction of the middle plate of proostracum and conus resulting in transformation of vampyroteuthoid-like gladius into the gladius of the cirrate type; and reduction of the transversal connection (saddle) in the cirrate gladius resulting in its transformation into paired stylets of the Incirrata. In Incirrata the shell underwent gradual reduction until its complete loss in several evolved forms. This last event, complete disappearance of the shell, has occurred independently in all three principal lineages of Incirrata: Octopodoidea, Bolitaenoidea and Argonautoidea. In all cases the final loss of the shell was accompanied by the reduction of jet-swimming in connection with development of a 'walking' habit involving the arms (benthic Octopodoidea) or heavy reliance on passive floatation in pelagic Bolitaenoidea and Argonautoidea. The final loss of the shell vestiges in advanced Incirrata did not change their soft-body design, which remained generally the same as in primitive benthic Octopodoidea.

INTRODUCTION

Octopods have the most unusual shell among cephalopod mollusks. It differs greatly from the chambered, coiled shell of the pearly *Nautilus*, from the calcareous buoyant sepion of cuttlefishes, and from the chitinous supporting pen (gladius) of teuthids. Reduction of the shell that occurs in all groups of Coleoidea reaches its apex in the Octopoda. In finned octopods (suborder Cirrata) the shell is represented by a saddle-, butterfly- or U-shaped structure while in finless octopods (suborder Incirrata) it is reduced to a pair of widely separated spindle-like rods, or stylets, situated obliquely on the dorsal side of the mantle [Naef, 1921/23]. The stylets are very small: their mass comprises less than 0,004% of the body mass [Zuev, 1965]. But even these vestiges disappear in some octopod lineages: Bolitenoidea, Argonautoidea, some Octopodoidea [Robson, 1932; Voight, 1997].

Origin of octopod shell is obscure. Its morphological elements reveal no apparent homology to any part of the shell of other coleoids, both recent and fossil. There is no trace of a phragmocone or proostracum. The octopod shell is soft and cartilage-like, which differs from the hard, chitinous substance of the teuthoid gladius. Naef [1921/1923, p.657] noted, 'it has to be assumed, that the shell (of octopods) consists mainly of a remnant of the proostracum with a flattered cone'. However, even if Neaf is correct, we do not know, what parts of

Table 1. List of species examined in the study.

Таблица 1. Список исследованных видов.

ORDER FAMILY *Species*	Number of specimens examined		Mantle length range, mm	
	males	females	males	females
VAMPYROMORPHIDA				
VAMPYROTEUTHIDAE				
Vampyroteuthis infernalis Chun, 1903		3		53 — 70
CIRRATA				
OPISTHOTEUTHIDAE				
Opisthoteuthis californiana Berry, 1949	25	7	40 — 64	19 — 44
Grimpoteuthis umbellata (Fisher, 1883)		2		45 — 49
CIRROTEUTHIDAE				
Cirroteuthis muelleri Eschricht, 1838	1	4	80	65 — 128
INCIRRATA				
OCTOPODIDAE				
Enteroctopus dofleini (Wulker, 1910)	16	8	135 — 265	145 — 260
Benthoctopus sibiricus Loyning, 1930	16	9	60 — 175	83 — 200
Bathypolypus salebrosus (Sasaki, 1920)		4		47 — 56
Eledone messyae Voss, 1964	1	1	63	35
ALLOPOSIDAE				
Alloposus mollis Verrill, 1880	2	1	63, 67	57
TREMOCTOPODIDAE				
Tremoctopus violaceus Chiaie, 1830		2		57, 60
OCYTHOIDAE				
Ocythoe tuberculata Rafinesque, 1814		2		96, 103
ARGONAUTIDAE				
Argonauta nodosa Solander, 1786		2		94, 108
BOLITAENIDAE				
Japetella diaphana Hoyle, 1885		1		57
AMPHITRETIDAE				
Amphitretus pelagicus Hoyle, 1885	1		26	

the coleoid proostracum evolved into the octopod shell and why. We also do not know what the homology is between the U-shaped shell of Opisthoteuthidae, the saddle- or butterfly-shaped shell of the Cirroteuthidae and the dorsal stylets of finless octopods. Possible clues for understanding the origin and evolution of the shell in the Octopoda may come from its sister group, Vampyromorphida Pickford, 1939. The single living vampyromorph, *Vampyroteuthis infernalis* Chun, 1903, has a set of characters combining such 'teuthid' features as a well-developed, chitinous gladius with a generally octopod-like brachial crown [Pickford, 1949]. Vampyromorphida and Octopoda have long been united into a single taxon with different names, first on the basis of general similarity: Octobrachia [Young, 1989], later on the basis of morphological and genetic cladistic analyses: Vampyropoda [Boletzky, 1992; 1999], Octopodiformes [Berthold, Engeser, 1987; Young, Vecchione, 1996; Carlini, Graves, 1999; Haas, 2002]. The name Vampyropoda (Boletzky, 1992) seems to be the most appropriate and will be used in the present paper. It alludes to the vampyromorphs, on the one hand, and to the cirroctopods and octopods, on the other hand.

Knowledge of the highly variable morphology of the shell in the Octopoda is fragmentary. The shell is better known in those finned octopods where it is used in systematic analysis [Aldred *et al.*, 1983; Nesis, 1982/1987; Collins, Henriques, 2000; Villanueva *et al.*, 2002]. In finless octopods details of the shell vestiges have been traditionally absent from systematic descriptions, and their very presence is rarely mentioned [Akimushkin, 1963; Voight, 1997]. The inner structure of octopod shell and its growth pattern have not been studied.

Morphological variability of the octopod shell indicates variability of its function. In finned octopods the shell is commonly considered a fin support, its flattened lateral parts serving as the attachment sites for the fin bases [Robson, 1932; Aldred *et al.*, 1983]. The function of stylets in finless octopods is not clear. Akimushkin [1963] considered them as mere vestiges without any specific function. Naef [1921/1923, p. 676] believed the stylets 'serve mainly as points of attachment for the retractors of funnel and cephalopodium'. The shell is clearly not a useless vestige, at least in species where it is very large. If it is a supporting structure, how can support be provided when the shell disappears completely? While the general features of the shell in the Vampyropoda is known throughout the work of Naef [1921/1923], Pickford [1949] and others, no systematic study has been attempted to determine its structure, function and evolution.

The present paper describes morphology of the shell and its functional relationship with the soft body in all major groups of the Vampyropoda, and proposes hypothesis on possible evolution of the shell in Vampyropoda.

MATERIAL AND METHODS

Fourteen species representing most families of recent Vampyropoda, were studied. These include the single vampyromorph, *Vampyroteuthis infernalis*, 3 genera of cirrate octopods (*Opisthoteuthis, Grimpoteuthis* and *Cirroteuthis*) and 10 genera of incirrate octopods (*Octopus, Benthoctopus, Bathypolypus, Eledone, Alloposus, Tremoctopus, Ocythoe, Argonauta, Amphitretus* and *Japetella*) (Table 1). Only two rare families were beyond the scope of my study: the Stauroteuthidae (Cirrata) whose gladii were analyzed using literature data [Collins, Henriques, 2000], and the Viterledonellidae (Incirrata) that lack the shell completely [Nesis, 1982/1987; Voight, 1997].

Abbreviations for the institutes and museums that housed the octopods examined here are: VNIRO — Russian Federal Institute of Fishery and Oceanography, Moscow; SIORAN — P.P. Shirshov Institute of Oceanology, Moscow; AtlantNIRO — Atlantic Research Institute of Fisheries and Oceanography; ZMMU — Zoological Museum of Moscow State University; NSMT — National Science Museum, Tokyo; TIFA — Tromso Institute of Fisheries and Aquaculture, Norway. Other abbreviations used in the text are: ML — dorsal mantle length; TL — total length; GL — gladius length; SD — standard deviation; R/V — research vessel; F/V — fishery vessel.

Abbreviation used on figures

ac	axial cartilaginous core of the fins
afl	lateral funnel adductor
am	mantle artery
apl	apical line (in stylets of incirrate octopods and in gladii of some squids)
aur	auricle
bcf	basal cartilage of the fins
bnd	bend (morphologic part of the stylets of incirrate octopods)
bp	basal pockets
brht	brachial heart
car	cephalic cartilage
ce	caecum
cenp	central thickened part (in the shell of cirrate octopods
CF	cone flags
cfold	collar folds
cl	cartilaginous layer of the fin base
colf	collar fusion
CO	cone
colf	collar fusion
cont	cartilage filling the scars left by the stylets after their reduction
cp	collar pockets
crop	crop
d	dermis
da	dorsal aorta
dgd	dorsal groove on the mantle wall (in *Amphitretus*)
dgl	digestive gland
dgv	ventral groove on the mantle wall (in *Amphitretus*)
distl	distal transversal muscles (in fins of cirrate octopods)
dlm	dorsal longitudinal muscles (In fins of cirrate octopods)
dm	depressor muscles
dmad	anterodorsal mantle adductor
dml	dorsal intermediate muscular layer of fins
dr	dorsal ridge of the saddle (in the gladius of cirrate octopods)
dsm	surface layer of dense muscular tissue of fins (dorsal)
em	elevator muscle
eye	eye
fad	funnel adductors
fc	fin cartilage
fch	first check delimiting the postnuclear zone (in the gladius of cirrate octopods)
fb	fin base
fc	fin cartilague
fin	fins
fla	closer bond of the funnel
fo	funnel organ
fun	funnel
func	funnel corner
gl	gills
brgl	brachial gland
gon	gonad
gr	dorsal groove (in the shell of cirrate octopods)
gst	stellar ganglia
hydr	hydrostatic organ
hyp	hypostracum
inc1	1st order increments in the shell
inc2	2nd order increments in the shell
ink	ink sac
KA	marginal asymptote
kn	knob-like surface sculpture (in the stylets of incirrate octopods)
LA	lateral asymptote
lh	lateral horns of the shell (in cirrate octopods)
lig	visceral ligament connecting the funnel retractor with the visceral sac (in *Tremoctopus*)

LP	lateral plates
lw	lateral wings of the gladius
MA	median asymptote
mam	ventral median mantle adductor
mat	anterior extensions of ventral median mantle adductor muscles
mcart	mantle cartilage occupying position of the former stylets
mcd	mantle cavity dorsal
mcv	mantle cavity ventral
me	extraocular eye muscle
ml	muscular layer of the fin base
mla	closer bond of the mantle
mn	mantle
mnd	dorsal mantle wall
mnv	ventral mantle wall
mo	lateral openings of the mantle aperture (in *Amphitretus*)
mpa	median pallial artery
nfin	fin nerve
nmus	nuchal muscles (anterior mantle adductor)
np	pallial nerve
ns	Needham sac
nuf	nuchal fusion of the visceral sac with the mantle (in *Amphitretus*)
oe	esophagus
ost	ostracum
ova	ovary
ovi	oviduct
per	nephridial appendages
peri	periostracum
pz	postnuclear zone
Ra	rachis
rant	anterior retractors of fins
rc	cephalopodial (head) retractors
rfcart	cartilage at the inner margin of the funnel retractor
ren	renal appendages
rec	rectum
rf	funnel retractors (= posterodorsal mantle adductors in Octopodidae)
rm	cartilaginous rim of the shell sac
RO	rostrum
sant	anterior shoulder of the stylet (in incirrate octopods)
sca	mantle scars marking position of the former shell in some incirrate octopods
sdl	saddle (medial part of the gladius in cirrate octopods)
slg	salivary glands
spost	posterior shoulder of the stylet (in incirrate octopods)
sh	shell
sh sac	shell sac
shi	initial shell
soc	spermatophoric organs complex
st	stomach
stat	statocysts
sut	suture line of the visceral sac
test	testes
tun	collagen tunic
tub	tube-like extension of ventral mantle wall around the funnel (in *Cirroteuthis*)
vd	dermal vein
ven	vena cava
vlm	ventral longitudinal muscles (in fins of cirrate octopods)
vml	ventral intermediate muscular layer of fins
vpp	posterior pallial vein
vs	visceral sac
vsm	surface layer of dense muscular tissue of fins (ventral)
W	wings
wa	anterior parts of the wings in the shell of cirrate octopods
web	interbrachial web (in cirrate octopods)
wpo	water pores

***Vampyroteuthis infernalis* Chun, 1903.** Three specimens were studied. Two immature females (53 mm and 60 mm ML) were kindly provided by Dr. K.N. Nesis (SIORAN). The specimens were sampled from a catch of mid-water trawl during R/V *'Vityaz'* cruise № 17 in SW Indian Ocean, 9 December, 1988, in position 32°53'S, 44°12'E. Depth of place: 1280 m; fishing depth: 1260 m. The third specimen, maturing female, approx. 70 mm ML, was kindly provided by Dr. T. Kubodera (NSMT). The specimen was caught in West Pacific Ocean, 28 October, 1988, in position 31°03'S, 133°07'E, ?depth, Isaaks-Kidd mid-water trawl; reg. № NSMT-Mo66708.

***Opisthoteuthis californiana* Berry, 1949.** 32 specimens were studied. All specimens were collected during a survey onboard F/V *'Tenyu-Maru No 78'* in the Western Bering Sea in July, 1998. The specimens were sampled from the catches of two commercial bottom trawls. The trawl № 1 was performed 29 July, 1998 in position 59°58'N, 167°59'E at depth 450 m. It yielded 19 specimens including 2 mature females (36 mm and 41 mm ML), 1 immature female 19 mm ML and 16 mature males (42, 44, 44, 46, 46, 47, 48, 49, 50, 54, 54, 55, 58, 58, 62 and 64 mm ML). The trawl № 2 was made the same day in position 59°57'N, 167°57'E at depth 400 m. It yielded 13 specimens including 2 mature female (41 and 44 mm ML), 2 maturing females (35 and 36 mm ML) and 9 mature males (40, 42, 44, 47, 49, 50, 51, 53 and 54 mm ML).

***Grimpoteuthis umbellata* (Fisher, 1883).** Two immature females (49 and approx. 45 mm ML) were studied. Both specimens were kindly granted by Dr. K.N. Nesis (SIORAN). They were sampled and identified by Dr. Nesis from the same bottom trawl during R/V *'Vityaz'* cruise № 65, in Central Atlantic (Cape Verde Basin), 31 March, 1979, in position 41°14'N, 14°28'W, at depth 5310 m. The specimen 49 mm ML was in good condition while another specimen was badly damaged but was believed to belong to the same species. Total cross-sections were made from one of the specimens (49 mm ML), and the gladius was extracted from another.

***Cirroteuthis muelleri* Eschricht, 1836.** Five specimens (two samples) were studied. The first sample (1 maturing female: 78 mm ML) was kindly provided by Dr. K.N. Nesis (SIORAN). The specimen was sampled from a catch of pelagic trawl ('Agassiz' type) made onboard R/V *'Polar Stern'* (cruise ARK XI/1) in North Atlantic, 10, August, 1995, in position 68°14'N, 01°34'W. Depth of place: 3050 m; fishing depth: 1200 m. The second sample was kindly granted by Dr. H. S Björke (TIFA). The sample included 4 specimens: 1 immature female 65 mm ML; two maturing females (105 and 128 mm ML) and 1 maturing male 80 mm ML. All specimens were collected from the same pelagic trawl during R/V *'G.O. Sars'* cruise in the Norwegian Sea, 24, January, 1999, in position 69°57'N, 09°40'E. Depth of place: 2800 m; fishing depth: 1100 m. General view was drawn on immature female (65 mm ML) from the second sample. The gladius was extracted and drawn from two maturing females (65 and 128 mm ML), both from the second sample. Total cross-sections were made from maturing female (78 mm ML) from the first sample and maturing male (80 mm ML) from the second sample.

Enteroctopus dofleini **(Wulker, 1910).** 24 specimens were studied. All specimens were sampled from the catches of commercial bottom trawls during a survey onboard F/V *'Tenyu-Maru № 78'* in the Western Bering Sea in July, 1998. The samples included: 2 males (215 and 135 mm ML) captured 13 July, in position 60°57'N, 178°55'W at depth 206 m; 1 male (250 mm ML), and 1 female (210 mm ML) captured 14 July, in position 61°04'N, 178°30'W at depth 150 m; 1 female (260 mm ML) captured 15 July, in position 61°10'N, 178°37'W at depth 167 m; 4 males (138, 170, 205 and 210 mm ML) and 2 females (183 and 215 mm ML) captured 16 July, in position 60°56'N, 179°10'W at depth 355 m; 2 males (180 and 215 mm ML) captured 21 July, in position 60°56'N, 178°55'W at depth 200 m; 3 males (152, 190 and 253 mm ML) and 1 female (216 mm ML) captured 26 July, in position 60°32'N, 172°15'E at depth 400 m; 1 female (192 mm ML) captured 26 July, in position 60°42'N, 172°43'E at depth 310 m; 3 males (140, 142 and 228 mm ML) captured 27 July, in position 59°11'N, 170°15'E at depth 400 m; 1 male (265 mm ML) and 2 females (145 and 160 mm ML) captured 28 July, in position 60°02'N, 168°16'W at depth 365 m.

Benthoctopus sibiricus **Loyning, 1930.** 25 specimens were analyzed. All of these were collected from catches of commercial bottom trawls during a survey onboard F/V *'Tenyu-Maru № 78'* in the Western Bering Sea in July, 1998. The samples included: 1 male (173 mm ML) captured 13 July, in position 60°57'N, 178°55'W at depth 206 m; 1 male (150 mm ML) captured 14 July, in position 61°10'N, 178°30'W at depth 230 m; 2 males (150 and 155 mm ML) and 2 females (130 and 180 mm ML) captured 15 July, in position 61°10'N, 178°37'W at depth 167 m; 1 female (120 mm ML) captured 16 July, in position 60°56'N, 179°10'W at depth 355 m; 2 males (115 and 175 mm ML) captured 17 July, in position 61°10'N, 178°31'W at depth 158 m; 2 males (60 and 160 mm ML) captured 18 July, in position 61°23'N, 178°09'W at depth 148 m; 2 males (155 and 175 mm ML) and 1 female (200 mm ML) captured 19 July, in position 61°27'N, 177°46'W at depth 150 m; 5 males (103, 142, 145, 145 and 152 mm ML) and 3 females (115, 153 and 180 mm ML) captured 22 July, in position 61°25'N, 178°09'W at depth 155 m; 1 male (100 mm ML) captured 23 July, in position 61°16'N, 178°07'W at depth 150 m; 1 female (90 mm ML) captured 24 July, in position 61°09'N, 178°38'W at depth 170 m, and 1 female (83 mm ML) captured 26 July, in position 60°42'N, 172°43'E at depth 310 m.

Bathypolypus salebrosus **(Sasaki, 1920).** The description is based on 4 specimens, collected from catches of commercial bottom trawls during a survey onboard F/V *'Kayo-Maru № 28'* in the Western Bering Sea in December, 1999: 1 female (approx. 47 mm ML) captured 1 December, in position 60°01'N, 168°01'E at depth 250 m; 1 female (56 mm ML) captured 4 December, in position 61°04'N, 174°21'E at depth 130 m; 1 female (54 mm ML) captured 05 December in position 61°38'N, 175°01'E at depth 180 m. 1 female (approx. 50 mm ML) captured 10 December in position 61°10'N, 179°04'W at depth 230 m.

Eledone messyae **Voss, 1964.** Two specimens were studied: maturing female, 35 mm ML; and adult male, 63 mm ML. Both specimens were kindly granted by Dr. Ch. M. Nigmatullin (AtlantNIRO). They were sampled from a catch of the same bottom trawl during R/V *'Patriot'* cruise № 4, in SW Atlantic, 7 May, 1983; in position 46°04'S, 60°02'W. Depth of place: 680 m.

Alloposus mollis **Verril, 1880.** Three specimens were studied: immature female, 57 mm ML; immature male, 60 mm ML and immature male, 63 mm ML. They were kindly granted by Dr. Ch. M. Nigmatullin (AtlantNIRO). All three specimens were sampled from a catch of the same pelagic trawl (BPT-50 type) during R/V *'Gizhiga'* cruise in NW Atlantic, 25 May, 1983; in position 41°13'N, 64°21'W. Depth of place: 1200 m; trawling depth: unknown.

Tremoctopus violaceus **delle Chiaie, 1830.** The description is based on the two immature female (57 and 60 mm ML) obtained from cephalopod collection of ZMMU. Both specimens were sampled by Prof. A.P. Bogdanov in the region of Nice (France) in July, 1884.

Ocythoe tuberculata **Rafinesque, 1814.** Two immature females were studied: 103 mm ML and 96 mm ML. The first female (103 mm ML) was collected from a catch of pelagic trawl during R/V 'Odyssey' cruise in the central part of the Indian Ocean, 14 November, 1984, in position 22°47'S, 74°30'E. Depth of place: 4100 m; trawling depth: 100-0 m. The second female (96 mm ML) was sampled from pelagic trawl catch during R/V 'Vozrozshdenie' cruise in the SE Pacific Ocean 27 October, 1989, in position 26°00'S, 74°56'W. Depth of place: 3640 m; trawling depth: 10-0 m. Both females were kept in the cephalopod collection of VNIRO.

Argonauta nodosa **Solander, 1786.** Two mature females were studied: 94 mm ML and 108 mm ML. Both specimens were collected from catches of pelagic trawl during R/V 'Vozrozshdenie' cruise in the SE Pacific ocean in October-December, 1989. The first female (94 mm ML) was sampled 27 October, in position 26°00'S, 74°54'W. Depth of place 3900 m; trawling depth: 10-0 m. The second female (109 mm ML) was sampled 3 December, in position 31°09'S, 84°55'W. Depth of place 3850 m; trawling depth: 10-0 m. Both specimens were kept in the cephalopod collection of VNIRO.

Japetella diaphana **Hoyle, 1885.** The description is based on a single specimen, immature female, 57 mm ML kindly granted by Dr. G.M. Vinogradov. The specimen was sampled from a catch of planctonic net, during R/V *'Akademic M. Keldysch'* cruise № 49, in equatorial Eastern Pacific, 8 September, 2003; station № 4630, in position 09°50'S, 104°15'W. Depth of place: 2500 m; trawling depth range: 2160-0 m.

Amphitretus pelagicus **Hoyle, 1885.** The description is based on a single specimen, immature male, 26 mm ML kindly granted by Dr. K.N. Nesis (SIORAN). The specimen was sampled from a catch of pelagic trawl during R/V *'Akademic Kurchatov'* cruise № 11, in SW Atlantic, 31 December, 1971; station № 952; position unknown; depth of place unknown; trawling depth: 230 m.

Definitions of terms and measurements used here follow Robson [1929; 1932], Roper, Voss [1983] and Nesis [1982/1987]. The measurements of fin length and fin width were made according to Voss, Pearcy [1990]: fin width was the greatest perpendicular distance between anterior and posterior margins of the fin, and fin length was the distance from the middle of the fin base to the fin apex. In addition, fin span was measured according to Guerra *et al.* [1998] as the distance between the tips of the fins. Two basic measurements, length and width, were made for the gladius of cirrate octopods. The gladius width was measured as the distance between anterior margins of the wings, while the length was measured as the distance from posterior tip of the gladius to the line connecting anterior margins of the wings. Cross-sections of the shells of octopods and vampire squids were made according to the techniques elaborated by the author [Bizikov, 1990; 1991]. The shells were removed from fresh or formalin-preserved animals and stored in 4% buffered formalin. The inner structure of the shell was studied on cross-sections. To make cross-sections, the shell was squeezed by hand between two pieces of styrol foam and then cut manually using a microtome knife. Relationships of the shell with the soft body were studied on anatomical preparations and entire cross-sections. Entire cross-sections of octopods were made using the following procedure: an intact formalin-preserved specimen was soaked in fresh water, then spread on a flat surface and frozen at -24°C for 3-6 hours, depending on the animal size. After complete freezing the specimen was cross-sectioned manually with a sharp heavy knife with straight blade. The sections (0.5 mm to 1.0 mm thick) were thawed on a glass plate with water and drawn using a 'SZH-10 Olympus' zoom-microscope. In Vampyromorphida and Cirrata, the sections were made at the following levels: the funnel, behind the funnel, attachment of the funnel retractors, greatest width of the fins and behind the fins. In Incirrata, the sections were made at the level of the funnel, behind the funnel (ventral adductor), anterior dorsal adductors and posterior dorsal adductors (= funnel retractors).

RESULTS

Order Vampyromorphida Pickford, 1939

Vampyroteuthidae Thiele, in Chun, 1915

Vampyroteuthis infernalis Chun, 1903

HABITS AND HABITAT. *Vampyroteuthis*, or vampire squid, is a bathy- abyssopelagic species inhabiting tropical and temperate waters of all oceans at depths from 800 m to 2000 m [Nesis, 1982/1987; Young, 1998]. Underwater observations from submersibles [Hunt, 1996] showed that *Vampyroteuthis* can swim surprisingly fast for a gelatinous animal accelerating up to two body length/sec in about 5 sec. Fast swimming consists of quick movement of the fins toward the funnel alternating with a jet from the mantle. Swimming in this way, the vampire takes a series of quick turns in an erratic escape route [Hunt, 1996]. The vampire appears to orient most commonly in a horizontal attitude with the arms spread forward to form, together with the web, an umbrella-like posture [Hunt, -1996].

GLADIUS MORPHOLOGY. The gladius of *Vampyroteuthis* is a broad, chitinous, transparent plate lying along the dorsal surface of the body beneath the skin and a thick layer of loose connective tissue with a dermal network of muscle fibers (Fig. 1). It is thin and flat anteriorly, gradually becoming thicker and strongly arched posteriorly. Posterior to the fins, the gladius encircles the body for about 180° of its circumference then terminates in a broad conus and rostrum. The structure of vampire gladius is typically teuthoid: it is slightly longer than the mantle (the mantle terminates on the anterior edge of the conus), it consists of three morphological parts — dorsal plate (proostracum), conus and rostrum, and it is formed by three shell layers: middle layer (ostracum), inner layer (hypostracum) and outer layer (periostracum). Terminology of the gladius parts is given here according to Jeletzky [1966] and Bizikov [1996]. The problem of homological correspondence between structural parts of the same names in teuthoid and belemnitoid shells lies beyond the scope of the present study. The most developed layer in *Vampyroteuthis* is ostracum. Being composed of chitinous substance, it takes part in formation of the dorsal plate and the conus. Hypostracum and periostracum are somewhat cartilaginous: the former is laid down on the ventral side of the ostracum and provides the thickening of the posterior part of the gladius; the later lies dorsally and posteriorly and forms the small spine-shaped rostrum situated apically on the conus. The base of the rostrum forms a shallow thin-walled cup, the alveolus, over the apex of the conus and extends forward along the cone flag.

The proostracum consists of five longitudinal elements: the middle plate (rachis), two lateral plates, and two wings (Fig. 1A). All parts of proostracum are separated from each other by asymptotic lines formed by sharp bending of the gladius growth lines: a pair of median asymptotes separates the rachis from lateral plates, a pair of lateral asymptotes separates lateral plates from wings, and a pair of marginal asymptotes separates the wings from conus. The rachis is broad, uniformly widens anteriorly, with a broad, blunt anterior end. The dorsal surface of the rachis bears narrow parabolic growth lines repeating the shape of its anterior margin. The anterior part of the rachis, the free rachis, extends beyond the lateral plates. The free rachis in *Vampyroteuthis* comprises about 25% of the gladius length (GL). The lateral plates are narrow, with concave anterior margins and densely spaced hyperbolic growth lines. They are distinctly delineated from the rachis by median asymptotic lines but less clearly separated from the wings, as the lateral asymptotes, delimiting lateral plates from

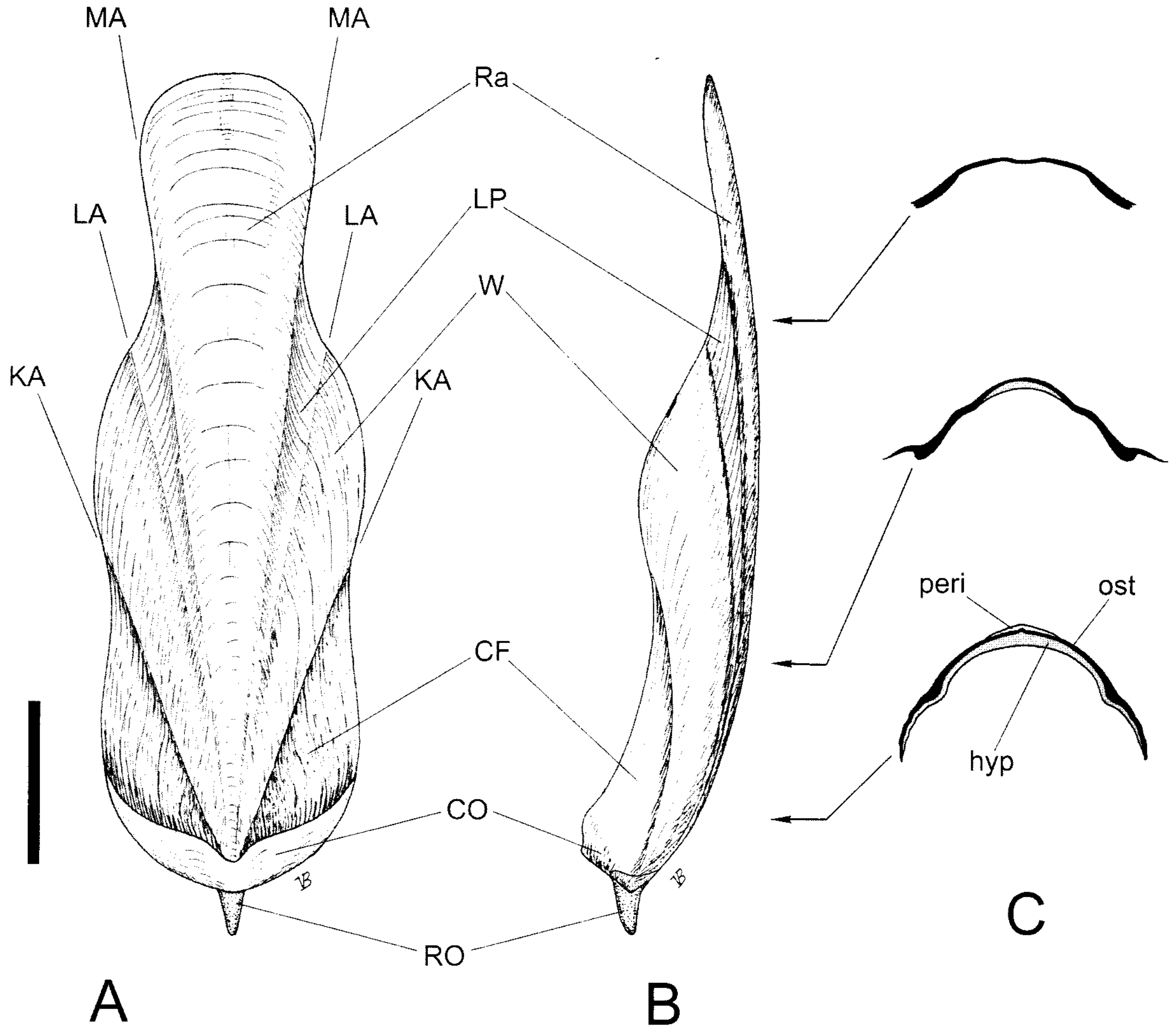


FIG. 1. Gladius of *Vampyroteuthis infernalis* (immature female: 53 mm ML). A. Ventral view. B. Lateral view. C. Cross-sections at different levels shown by arrows. Scale bar = 1 cm.

РИС. 1. Гладиус *Vampyroteuthis infernalis* (незрелая самка: 53 мм ДМ). А. Вид с вентральной стороны. В. Вид сбоку. С. Поперечные срезы на уровнях, указанных стрелками. Масштаб = 1 см.

the wings may be indistinct in some specimens [Pickford, 1949]. The wings are more than twice as wide as the lateral plates, uniformly convex (viewed dorsally), and make the greatest width of vampire gladius, approximately 31% of the GL. The dorsal surface of the wings bears convex oblique growth lines that are spaced more sparsely then those on the lateral plates.

The cone is a wide, shallow, cup-shaped structure enclosing the posterior apex of the viscera. It is separated from proostracum by the pair of marginal asymptotes. Junction of the conus with the wings is marked by slight constriction of the gladius that separates two almost equal maximums of the gladius width: anterior, formed by wings, and posterior, formed by the cone. The apical angle of the cone is broad. No trace of a chambered phragmocone exists. The ventral wall of the cone is short, with shallow incision in the middle. Dorso-lateral walls of the cone, or cone fields, according to Naef [1921/1923], are long and wide. They project anteriorly along the proostracum and form the posterior expansion of the gladius. The rostrum is a short, laterally compressed, cartilage-like spine tapering posterioly from the conus apex. Its length is about 5% of the proostracum length. The degree of rostrum development is variable in *Vampyroteuthis* and it may be absent in some specimens [Pickford, 1949].

RELATIONSHIP BETWEEN THE GLADIUS AND THE SOFT BODY. Typically in coleoids, the soft parts do not contact with the gladius directly but attach to the shell sac that surrounds the gladius. The outer side of the shell sac is formed by fibrous tissue while its inner side is lined by shell epithelium that secretes the gladius. When the shell sac is

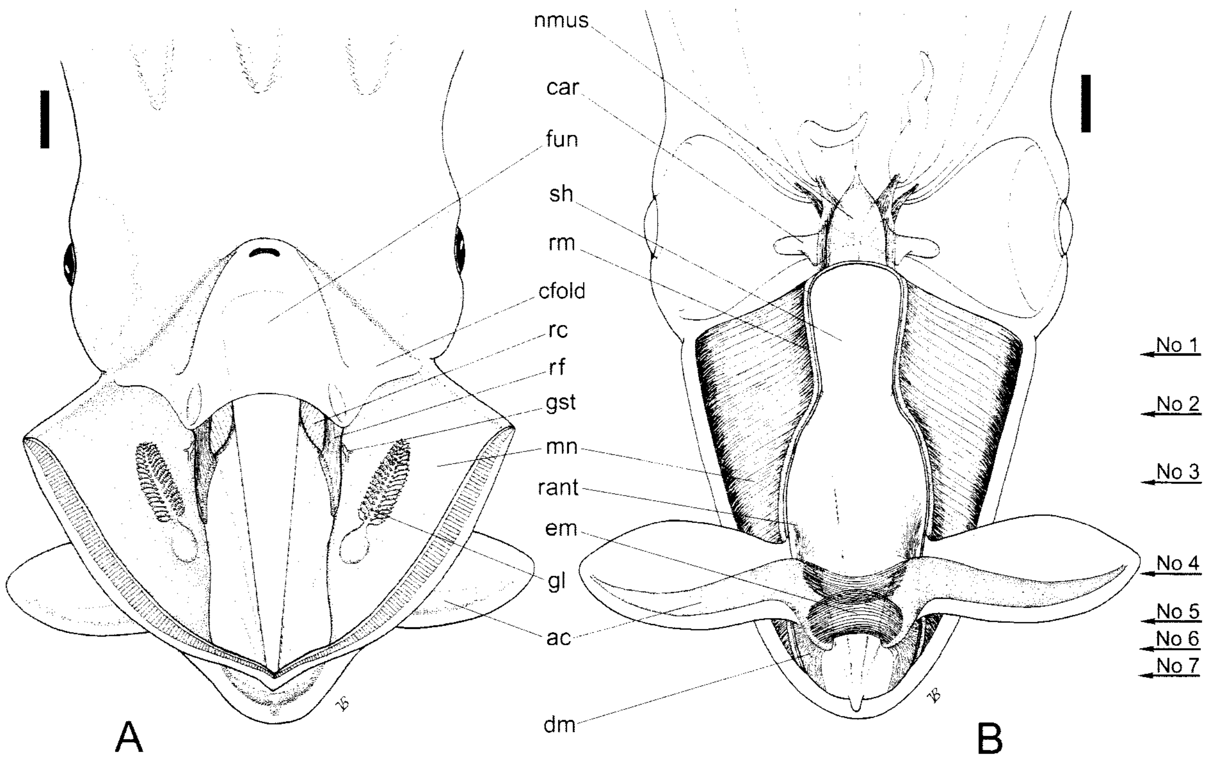


FIG. 2. Relationship between the shell and soft body in *Vampyroteuthis infernalis* (immature female; 53 mm ML). A. Ventral view, the mantle cavity is opened; the visceral organs are removed. B. Dorsal view, the skin is shown transparent. Arrows with numbers indicate the position of corresponding cross-sections (shown on Fig. 3 and Fig. 5). Scale bars = 1 cm.

РИС. 2. Взаимоотношение между гладиусом и мягким телом *Vampyroteuthis infernalis* (незрелая самка; 53 мм ДМ). А. Вид с вентральной стороны: мантийная полость вскрыта; висцеральные органы удалены. В. Вид с дорсальной стороны; кожные покровы показаны прозрачным контуром. Стрелки с цифрами указывают положения соответствующих срезов (показанных на Рис. 3 и Рис. 5). Масштаб = 1 см.

intact, it adheres to the gladius so tightly that attachment of soft parts to the sac is functionally equal to their attachment to the gladius itself.

In *Vampyroteuthis* the mantle muscles follow the contour of the gladius, attaching to its margin from ventral side (Fig. 2B). At site of mantle attachment, the shell sac is reinforced by cartilaginous rim first mentioned by Pickford [1949]. The head attaches to the gladius by paired cephalopodium retractors (head retractors), and nuchal muscles (Fig. 2B). Although the head and the mantle in adult *Vampyroteuthis* are fused, the means of fusion is unlike that of octopods. A vestigial nuchal cartilage is present in the head just under the anterior part of the free rachis. On the dorsal surface of the head there is complex nuchal muscle sheath including the fibers that pass from the shell sac to the cephalic cartilage, from the shell sac to the base of the arms and from the nuchal cartilage to the base of the arms. The head retractors are thin sheets. They pass from the cephalic cartilage, make a thin muscular envelope around the visceral sac and attach to the anterior margins of the lateral plates.

The funnel retractors are short, ribbon-like. They originate from the ventral posterior corners of the funnel, extend posteriorly along the visceral sac and attach to the anterior margins of the wings (Fig. 2A). The weakly-developed stellate ganglia appear as slightly enlarged knots on the pallial nerves and are situated laterally to the wide gladius at the level of its lateral plates (Fig. 2A). The fins attach near the dorsal side of the gladius, near cone fields. The fin bases are not fixed in their position rigidly, but are anchored by muscles (Fig. 2B). Vertical adjustment of the fins is accomplished by fin elevator and depressor muscles. Elevator muscles form thin muscular sheet, overlaying posterior axial part of the gladius, and unite the fin bases. Depressor muscles originate from the ventral side of the fin bases and run in a posteroventral direction, toward the margins of cone fields. Depressor muscles apparently serve to adjust the fins position in both vertical (ventral) and longitudinal (posterior) directions. Longitudinal adjustment in anterior direction is ensured by paired anterior retractor muscles radiating from the fin bases to the dorsal side of the gladius in the area of wings.

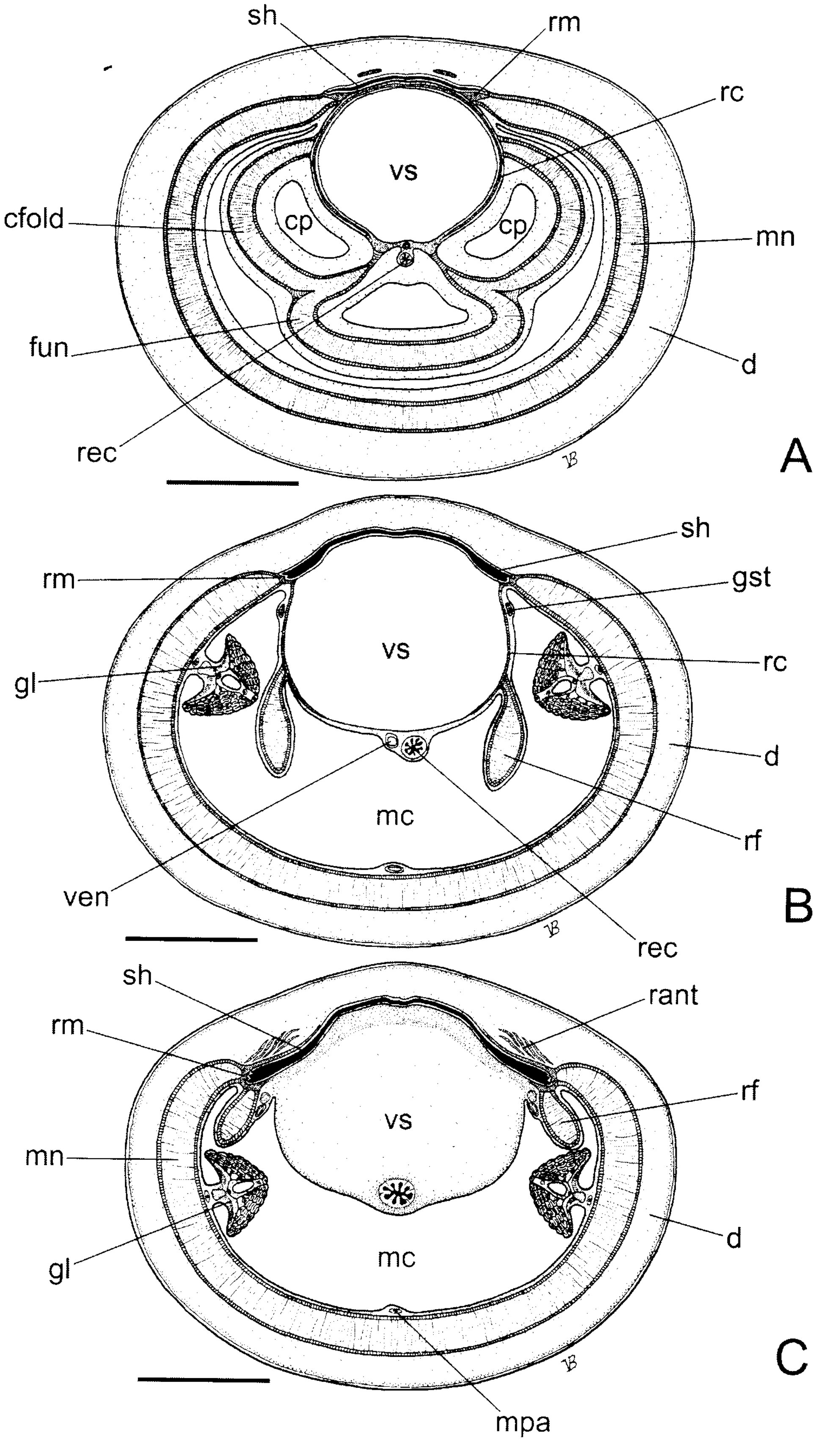


FIG. 3. Schematic cross-sections of the soft body of *Vampyroteuthis infernalis* (immature female; 60 mm ML). A. Section 1, at the level of the funnel. B. Section 2, immediately behind the funnel. C. Section 3, at the level of attachment of the funnel retractors. Position of the sections is indicated in Fig. 2. Scale bar = 1 cm.

РИС. 3. Срезы мягкого тела *Vampyroteuthis infernalis* (незрелая самка; 60 мм ДМ). А. Срез 1, на уровне воронки. В. Срез 2, позади воронки. С. Срез 3, на уровне прикрепления вороночных ретракторов. Положение срезов указано на Рис. 2. Масштаб = 1 см.

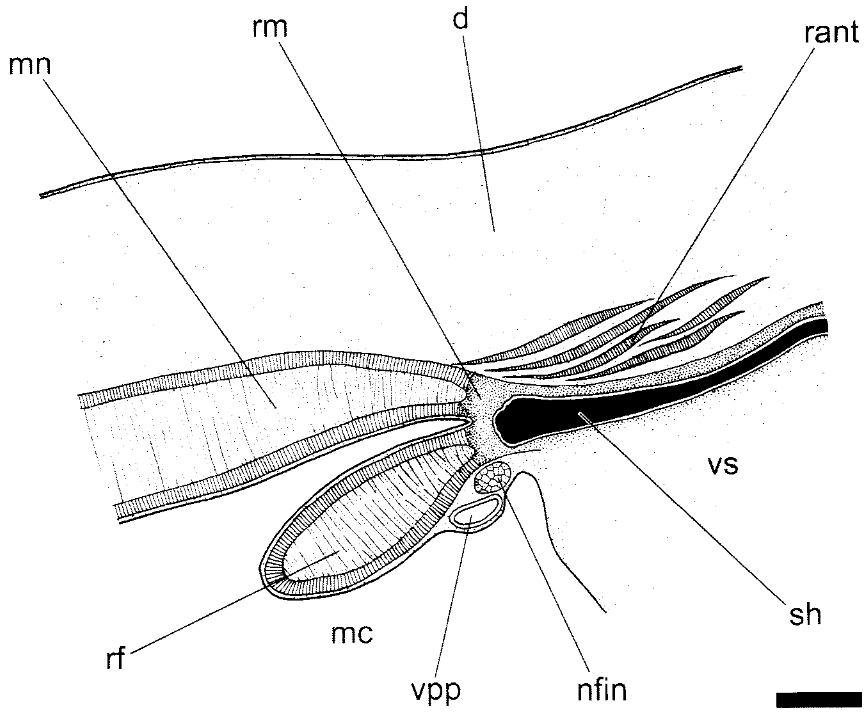


FIG. 4. *Vampyroteuthis infernalis*. Enlarged part of the section 3 (Fig. 3C) showing attachment of muscles to the gladius margin. Scale bar = 1 mm.

РИС. 4. *Vampyroteuthis infernalis*. Увеличенный фрагмент среза 3 (Рис. 3), показывающий прикрепление мускулов к краю гладиуса. Масштаб = 1 мм.

CROSS-SECTIONS (Figs. 3-5). Functional relationships between the gladius and soft body in *V. infernalis* are best understood from entire cross-sections of the body (Fig. 3-5). Position of the sections is shown by arrows in Fig. 2B. Section 1 (at the level of funnel) illustrates the attachment of soft parts to the free rachis (Fig. 3A). At this level the rachis is wide, thin and nearly flat without pronounced ribs. It is composed of the ostracum only. The visceral sac abuts the ventral side of the rachis, its dorsal wall being actually fused with the shell sac. Dorsal and lateral walls of the visceral sac are formed by thin head retractor muscles and collagen fibers. The ventral wall of the visceral sac serves for attachment of the funnel. At the sites of funnel attachment the ventral wall is thickened but no cartilage is present. Two muscular folds (collar folds) originate from lateral walls of the funnel. Upper margins of collar folds attach to the nuchal cartilage and the shell sac anteriorly and to the visceral sac posteriorly. The collar folds confine a pair of spacious cavities (collar pockets) on both sides of the visceral sac. The mantle attaches to the cartilaginous rim of the shell sac from the ventral side. The walls of the mantle, funnel and the collar, each consist of two thin muscular layers (inner and outer) separated by a thick highly vacuolated gelatinous core.

On the section 2, behind the funnel (Fig. 3B), the gladius is thicker, wider and slightly arched. Its section consists of a thin axial part corresponding to the rachis, and thickened lateral parts corresponding to the lateral plates on Fig. 1C. Margins of the lateral plates are encased in cartilage to which the mantle and head retractors attach. The mantle attaches laterally to the margins of the lateral plates while the head retractors attach to them from ventral inner side. The head retractors form the lateral walls of the visceral sac. The funnel retractors appear at this level as a pair of thick muscular flaps attaching to the lateral walls of the visceral sac.

Section 3, at the level of attachment of the funnel retractors (Fig. 3C), shows the gladius at the greatest width of the wings. The lateral regions of the gladius are thicker and wider here than in previous sections. The inner areas, corresponding to the lateral plates, are not distinctly separated from the outer areas, corresponding to the wings on Fig. 1C. All muscles at this level attach to the thickened lateral margins of the wings (Fig. 4). The mantle attaches to the dorsolateral side of the wings while the funnel retractors attach to their ventrolateral side. The dorsal side of the wings provides attachment for loose muscular fibers. These represent the anterior longitudinal retractors of the fins, shown

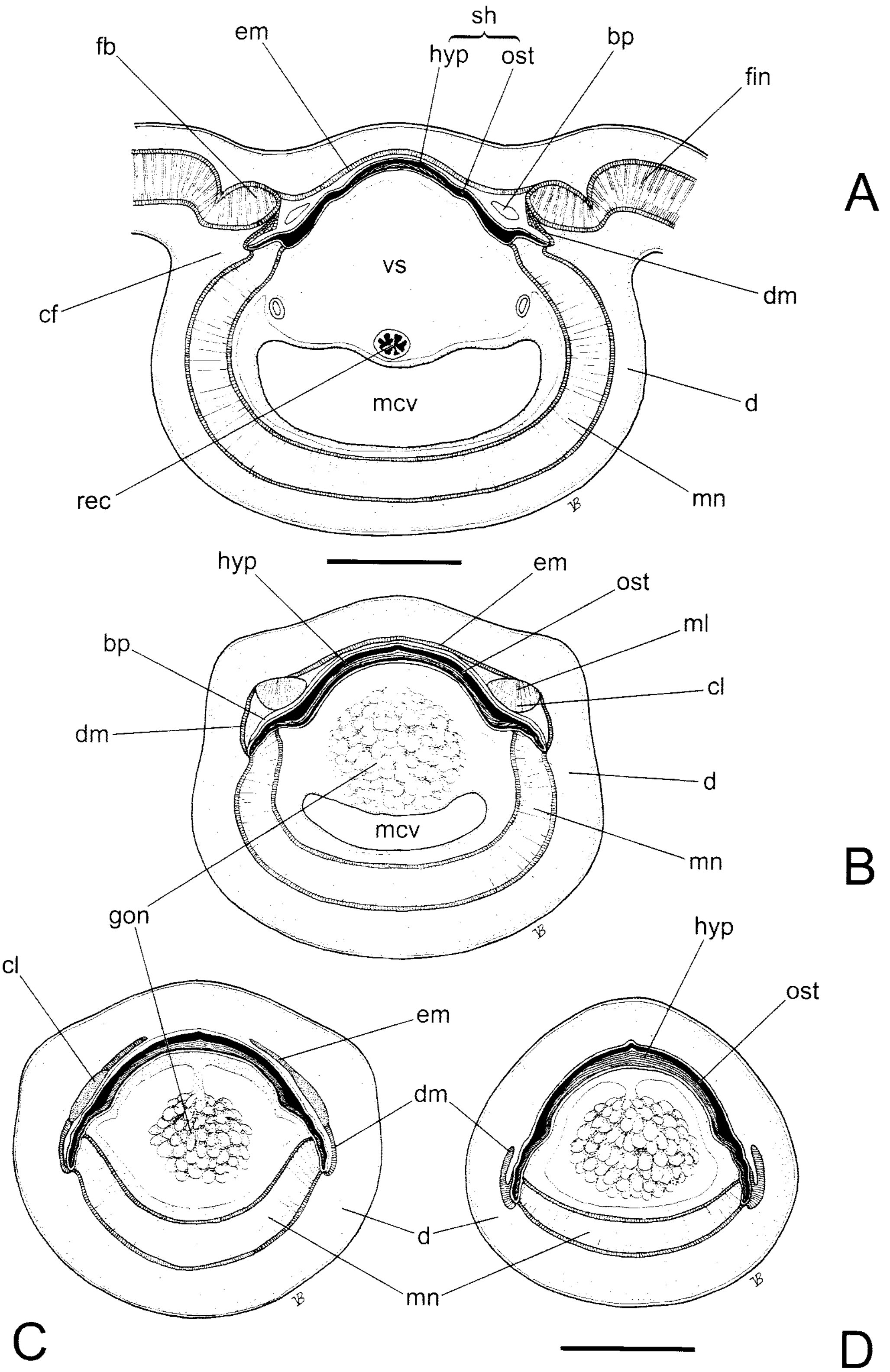


FIG. 5. Schematic cross-sections of the soft body of *Vampyroteuthis infernalis* (continued from Fig. 3). A. Section 4. at the greatest width of the fins. B. Section 5. at the middle part of the fin bases. C. Section 6. at the posterior parts of the fin bases. D. Section 7. through posterior part of the mantle behind the fin bases. Scale bars = 1 cm.

РИС. 5. Срезы мягкого тела *Vampyroteuthis infernalis* (продолжение Рис. 3). A. Срез 4. на уровне наибольшей ширины плавников. B. Срез 5. в средней части оснований плавников. C. Срез 6. в задней части основания плавников. D. Срез 7. в задней части мантии позади оснований плавников. Масштаб = 1 см.

also in Fig. 2B. At the site of muscular attachment, the shell sac is reinforced by cartilage which is thicker on the lateral side of the gladius than on its dorsal side. Inner structure of the visceral sac is not shown on this and the following sections due to its poor preservation in sectioned specimen.

At the level of the fins, the gladius provides indirect support for the fin bases and mantle (Fig. 5A). The gladius here is strongly arched and two-layered: the hypostracum appears on ventral side of the shell, increasing its thickness in axial region. In this section the thin marginal parts of the gladius correspond to the cone fields; the thickened lateral parts correspond to the wings fused with the lateral plates, and sharp change in thickness between them marks marginal asymptote. The ventral sides of the cone fields serve for attachment of the mantle. The fin bases lie on the dorsal side of the wings and cone fields. Sharp bends separate the base from the rest of the fin. Each base consists of two layers, approximately equal in thickness: a ventral cartilaginous layer, near the gladius, and a dorsal muscular layer. Elevator muscles connect the inner margins of the fin bases and overlay the dorsal surface of the gladius. Depressor muscles start originate on the ventral side of the fin bases and adhere to the margins of cone fields. Additional fixation is accomplished by bundles of connective-tissue fibers that bind the fin bases with lateral mantle walls. A pair of epithelial sacs (basal pockets), which may represent separated portions of the shell sac, are situated between the fin bases and the gladius. The sac walls presumably provide gliding surfaces during movement of the fins. According to Bandel and Boletzky [1979], basal pockets develop during embryogenesis as a differentiation of the secondary shell sac epithelium. At the level of greatest fin width the basal pockets occupy only part of the space between the gladius and fins bases, the rest is filled by highly vacuolated connective tissue.

At the level of posterior part of the fin bases epithelial basal pockets merge into one large basal sac spreading over the whole dorsal surface of the gladius (Fig. 5B). The posterior region of the fin bases are roughly triangular in cross-section, with cartilaginous ventral and muscular dorsal components. They occupy shallow concavities on the dorsal side of the cone fields and are held in position by elevator and depressor muscles. The elevator muscles attach to the muscular dorsal side of the fin bases while depressor muscles attach to their lateral side. Highly vacuolated connective tissue fills the space between the fin bases. The gladius is thicker where the hypostracum extends to the margins of the cone flags. The mantle attaches to ventral side of cone flags.

In the posterior part of the body, the gladius is arch-shaped, occupying dorsal half of the body circumference (Fig. 5C). The mantle attaches to the gladius ventrally, along the margins of the cone fields. The fins bases here are flat and wide and consist entirely of vacuolated cartilage. Basal pockets are absent. Elevator muscles are separated from one another in the axial region over the gladius. Depressor muscles connect the lateral sides of the fin bases with the outer margins of the cone fields. Depressor muscles spread posteriorly almost to the end of the gladius (Fig. 5D) and apparently act also as posterior longitudinal retractors of the fins. Posterior apex of the body is cupped by another muscle that is missing on my sections but was described in details by Young [1964]. According to Young, this muscle forms a cone of very delicate circular muscle fibers and covers the apex of the body except for a small pore at the most posterior point. The anterior edge of this muscle attaches to the border of the conus ventrally and the shell sac dorsally.

COMMENTS. Attachment of fins to the gladius in *Vampyroteuthis* is different from the one reported earlier. Pickford [1940, p. 176] wrote that in *Vampyroteuthis* "the fins rest directly on the shell sac whose wall is thickened to form what appear to be cartilaginous support." Apparently Pickford missed the basal pockets, which are difficult to see on gross anatomical preparations, but are clearly apparent on the cross-sections. Our data show that articulation of fins with the shell and mantle in *Vampyroteuthis* follows the same basic coleoid pattern described earlier in teuthids [Naef, 1921/1923: fig. 66] and sepiids [Naef, 1921/1923: fig. 290]. It is especially close to condition found in some oegopsid families, for example, Enoploteuthidae, where the gladius occupies superficial position and the fins bases rest on its dorsal side, separated from the shell sac by basal pockets [Naef, 1921/1923: fig. 66a].

Reported here for the first time, in addition to the more complete description of the muscular attachment to the gladius, are the presence and description of the three layers of the shell, the presence of the lateral plates of the gladius and their asymptotes, the three-dimensional shape of the gladius, the ventral incision of the conus, the presence of a basal pockets.

Order Octopoda Leach, 1818

Suborder Cirrata Grimpe, 1916

Family Opisthoteuthidae Verrill, 1896

Opisthoteuthis californiana Berry, 1949

GENERAL REMARK. Different terms are used in cephalopod literature for the shell of cirrate octopods: dorsal cartilage [Hoyle, 1886; Ijima, Ikeda, 1895]; internal shell [Appellöf, 1899]; shell vestige [Naef, 1921/1923; Robson, 1932]; gladius [Nesis, 1982/1987] or fin support [Aldred *et al.*, 1983]. I prefer to use 'gladius' to emphasize its origin from elongate internal shell of the early coleoids.

HABITS AND HABITAT. *Opisthoteuthis californiana*, or Californian flapjack devilfish, is a benthopelagic cirrate octopod inhabiting near-bottom waters of the outer shelf and continental slope (from 125 m to 1100 m) in the North Pacific, from the Bering Sea to the Sea of Okhotsk to off central Honshu in the northwestern Pacific and to off southern California in the northeastern Pacific [Nesis, 1982/1987; Vecchione *et al.*, 2003]. Swimming mode and behaviour of flapjack devilfishes were observed from a manned submersible in *O. californiana* [Alexeev *et al.*, 1989], and in similar species, *O. agassizi*, [Vecchione, Roper, 1991]. Observations showed that *Opisthoteuthis* swims mainly by contraction of the arm-web complex added by frequent fin strokes (2-3 fin strokes per every web contraction). During swimming the posterior apex of the mantle is oriented obliquely upward toward the direction of the swimming, and the octopod performs gentle thrusts by its arm-web complex, moving along a sinusoidal trajectory.

GLADIUS MORPHOLOGY. The gladius of *Opisthoteuthis* is a thick cartilage-like, broadly U-shaped structure laying transversally on the dorsal surface of the mantle (Fig. 6). Its width is much greater than its length. The gladius consists of a medial transverse part (saddle) and enlarged, thickened, lateral parts (wings). The wings terminate in pointed flexible lateral horns that protrude from ventral region of the wings in an anteroventral direction. Morphological parts of the gladius are not distinctly separated from one another. Asymptotic growth lines are absent. The saddle is rather thin, rounded in cross-section, with deep groove on the dorsal side. Low ribs are sometimes present on the dorsal convex side of the saddle and extend onto the lateral wings. Lateral wings are thicker and wider than the saddle. The outer sides of the wings are slightly concave; the inner sides are convex, strengthened by the low keels. The outer, concave sides of the wings are not parallel to one another but diverge toward the tips. The width of the gladius, measured between the tips of the horns, is 70-80 % of ML. The height of the gladius is about 33 %, and the anterior-posterior dimension of the saddle is 6-15 %. During growth the gladius becomes relatively thicker, its lateral horns become shorter, and the dorsal groove in the saddle becomes nearly flat.

MICROSTRUCTURE OF THE GLADIUS. At the midline of the gladius, cross-section is U-shaped, with the concave dorsal side corresponding to the dorsal groove (Fig. 6D). Numerous regular concentric increments of cartilage-like substance are seen in the sections. Each increment consists of a wide glass-like translucent zone and a peripheral narrow opaque zone. The center of growth (initial shell) is situated in the lower part of the section. It is a small flat body, 580-620 μm in width, 24-30 μm in height, and composed of an amorphous substance without any trace of growth increments. The initial shell is surrounded by a postnuclear zone (890-900 μm in width; 290-310 μm in height) separated from the outer zone by prominent line or first check (Fig. 6F). From 12 to 19 faint uniform increments were observed within postnuclear zone, each with a maximum width 15-20 μm. Beyond the postnuclear zone the increments become more distinct and their width gradually increases toward periphery up to 25-30 μm. In the outer zone the increments were clearly grouped into second-order cycles, from 7 to 25 increments in one cycle. The outline of the growth increments presumably repeats the shape of the gladius at earlier stages of its development. The microstructure of the gladius of *Opisthoteuthis* is very similar in the width and consistency of increments and in the second-order cycles to that of the inner shell layer, the hypostracum, in the gladius of recent squids [Arkhipkin, Bizikov, 1991]. In contrast to squids, however, the increments in the gladius of *Opisthoteutis* are continuous and each increment makes a closed envelop around the shell.

SOFT BODY MORPHOLOGY AND ITS RELATIONSHIP WITH THE GLADIUS. The cephalopodian Bauplan is difficult to recognize in the pancake-shaped body of adult *Opisthoteuthis* (Fig. 7A), but the young stages retain more features of the general cephalopod organization. During the cruise aboard the F/V *'Tenyu-Maru № 78'* in July, 1998, one specimen of *Opisthoteuthis* (immature female, 19 mm ML) was retrieved alive (trawl № 1), and observed and pictured in a shipboard aquarium. The main means of locomotions was swimming by medusoid contraction of the arm-web complex alternating periodically with short periods of fin-swimming. Similar behavior has been described for opisthoteuthids previously [Pereyra, 1965; Vecchione, Roper, 1991; Vecchione, Young, 1997; Villanueva, 2000; Hunt, 1999]. In producing the medusoid stroke, the animal brought the arms and web together, acquiring the position in which its cephalopodian plane of structure became apparent (Fig. 7B). The body of young *Opisthoteuthis* consists mainly of long arms united almost completely by a thick web. The head is small, confluent with the arms. The mantle has a shape of small conical cup on the posterior part of the body. Its length comprises 23-25% of the total length. On the dorsal side, the mantle is fused with the head. On the ventral side it forms small mantle aperture closely surrounding the funnel. The fins are relatively small, oar-shaped and set obliquely on the lateral sides of the mantle in its anterior part. The gladius lies obliquely in the man-

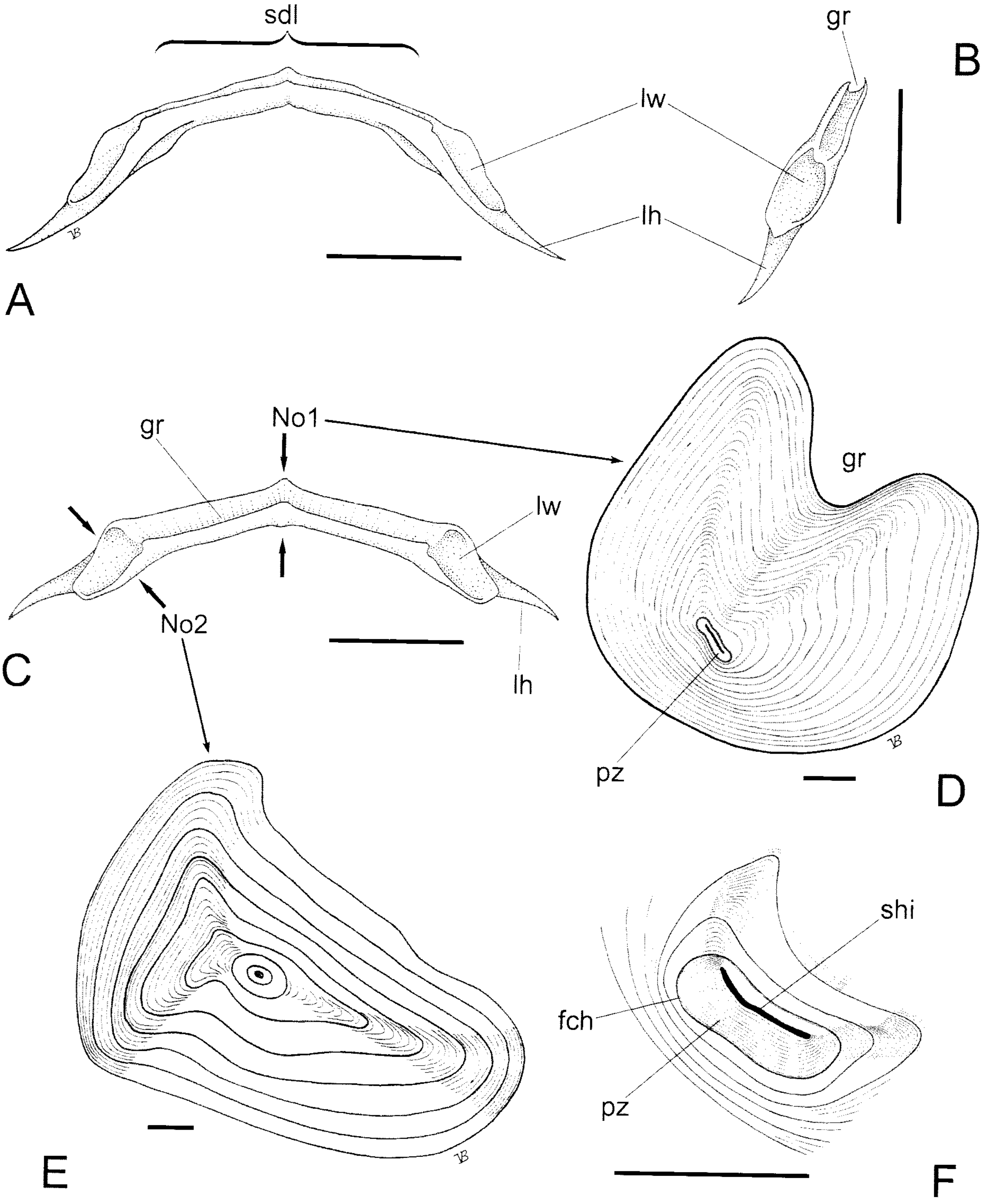
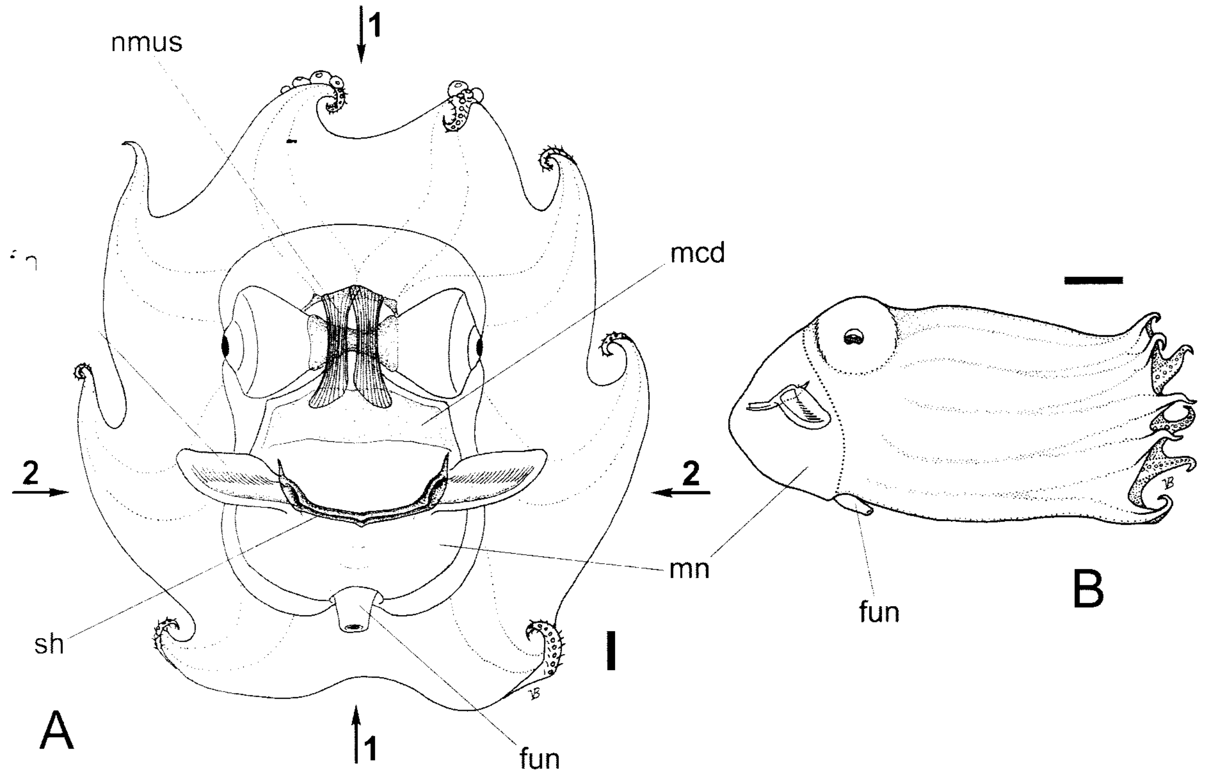


FIG. 6. Gladius of *Opisthoteuthis californiana*. A. Anterior view (dorsal side is up). B. Lateral view (anterior side is on the left). C. Dorsal view (posterior side is up). Bold arrows indicate the planes of the cross-section shown in D-F. D. Cross-section 1, through the middle part of the gladius (dorsal side is up; anterior side is on the left). E. Cross-section 2, through the middle part of the lateral wing (dorsal side is up; anterior side is on the right). F. Enlarged fragment of figure 'D' (section 1), showing initial shell and postnuclear zone. A-C: scale bar = 1 cm; D-F: scale bar = 1 mm.

РИС 6. Гладиус *Opisthoteuthis californiana*. А. Вид спереди (дорсальная сторона наверху). В. Вид сбоку (передняя сторона слева). С. Вид с дорсальной стороны (задняя сторона наверху). Стрелки указывают положение срезов, показанных на видах D-F. D. Срез 1, сагиттальный срез в средней части гладиуса (дорсальная сторона наверху; передняя сторона слева). E. Срез 2, в средней части латерального крыла (дорсальная сторона сверху; передняя сторона справа). F. Увеличенный фрагмент вида 'D' (Среза 1), показывающий зародышевую (?) раковину и постнуклеарную зону. A-C: масштаб = 1 см; D-F: масштаб = 1 мм.



IG. 7. *Opisthoteuthis californiana*. A. Dorsal view of a mature male; 49 mm DML. B. Lateral view of a swimming immature female: 19 mm DML. Arrows with numbers indicate the planes of corresponding cross-sections (see Figures 8 and 9). Scale bar = 1 cm.

ИС. 7. *Opisthoteuthis californiana*. А. Зрелый самец (49 мм ДМ); вид со спинной стороны. В. Плывущая незрелая самка (19 мм ДМ): вид сбоку. Стрелки с цифрами указывают положение соответствующих срезов (показаны на Рис. 8 и 9). Масштаб = 1 см.

le: its medial bridge is situated close to the apex while the lateral wings envelope the mantle like a horse-shoe with the lateral wings underlying the fins bases.

In adult *Opisthoteuthis* the very thick gelatinous integument disguises the outline of the body and makes it appear flat. The anterior dorsal margin of the mantle, which is tongue-shaped, almost reaches the bridge between eyes (Fig. 7A). The mantle is connected with the head by a pair of nuchal muscles running from its anterior dorsal mantle margin toward the arm bases.

TOTAL CROSS-SECTIONS. The section in sagittal plane (Fig. 8A,B) shows that adult *Opisthoteuthis* is flattened against its widely spread arms. Its mantle and viscera are reduced to a low hump above the arms and web. The muscular mantle is attached around the whole gladius but does not overgrow it (Fig. 7). The gladius divides the mantle dorsal (appearing anterior in the spread position) and ventral (appearing posterior in the spread position) parts. The long, tube-like funnel is turned 90° backward and fuses with the bases of arms IV along 2/3 of its length. The dorsally-positioned fins average 77% ML in length, and about two times the ML in their span. The head consists mainly of two large eyes. The brain is foreshortened and compressed between the arms bases and the digestive gland. Cephalic and ocular cartilages are absent. The head retractors lack muscles and are reduced to a film-like, collagen envelope of the visceral sac; they attaching to the dorsal and ventral margins of the gladius wings.

The posterior mantle wall is very thick. It consists of outer and inner muscular layers separated by thick gelatinous, highly vacuolated tissue. The posterior mantle wall attaches to the gladius along the dorsal groove of the saddle and the posterior sides of the wings. The anterior mantle wall, in contrast, is very thin, without distinct axial vacuolated tissue. It covers the dorsal side of the visceral sac and attaches to the anterior side of the gladius, merging with the posterior mantle beyond the tips of the horns. As a result, in the region between the fin bases the anterior and posterior mantles are separated from one another by the gladius. The visceral sac is large and occupies most of the visceral mass. The dorsal mantle cavity is a narrow slit between the anterior mantle wall and the digestive

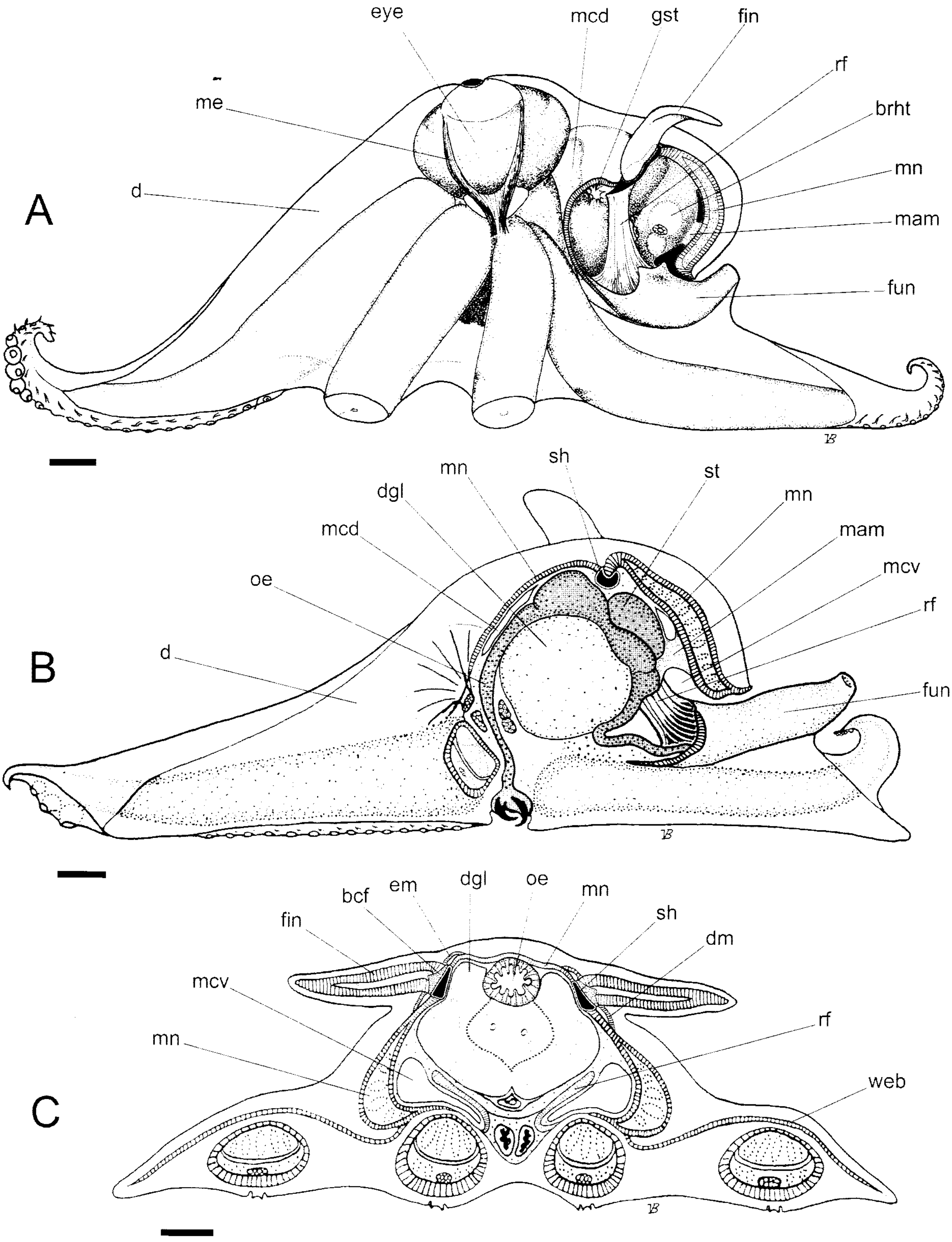


FIG. 8. General anatomy of *Opisthoteuthis californiana*. A. Lateral view of a maturing male (47 mm DML) after removal of the skin, arms, mantle wall and the gill from the left side. B. Sections 1, in median sagittal plane (maturing male: 49 mm DML). C. Section 2: transversal section at the greatest fins width (immature female: 43 mm DML). The position of the sections is indicated on Figure 7. Scale bar = 1 cm.

РИС 8. Строение *Opisthoteuthis californiana*. А. Вид сбоку (созревающий самец: 47 мм ДМ): с левой стороны удалены кожные покровы, руки, стенка мантии и жабра. В. Срез 1: сагиттальный срез в медиальной плоскости (созревающая самка: 49 мм ДМ). С. Срез 2: поперечный срез на уровне наибольшей ширины плавников (созревающая самка: 43 мм ДМ). Положение срезов показано на Рис. 7. Масштаб = 1 см.

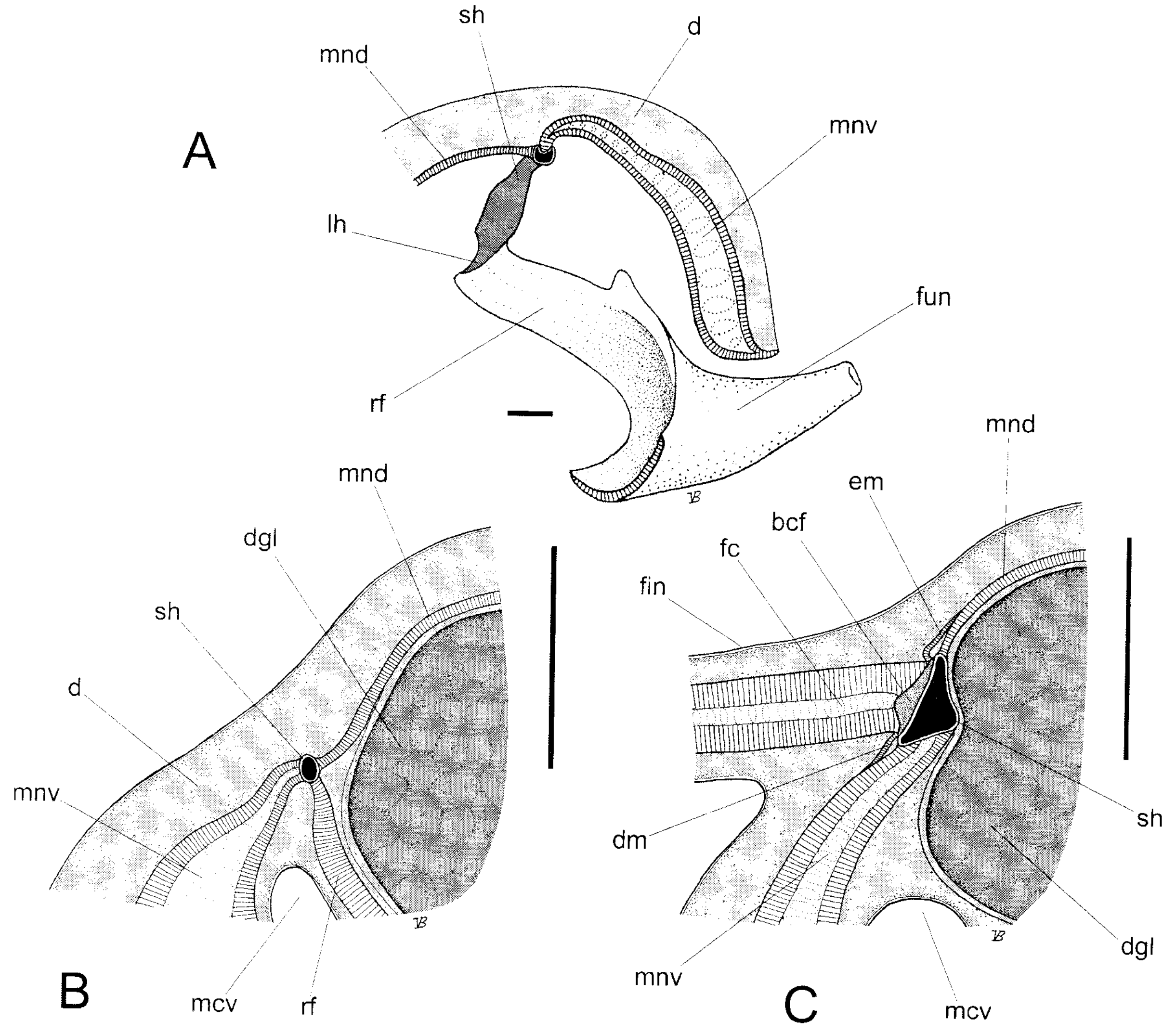


FIG. 9. Relationship of the gladius with the soft body in *Opisthoteuthis californiana*. A. Fragment of the median sagittal preparation, illustrating attachment of the mantle and funnel to the gladius (visceral organs and the left funnel retractor are cut away; only right part of the gladius is shown). B. Fragment of transverse section at the level of attachment of funnel retractors to the lateral horns of the gladius. C. Fragment of transverse section at the level of the greatest fins width (section 2; Fig. 8C). Scale bar = 1 cm.

РИС. 9. Взаимоотношение гладиуса и мягкого тела у *Opisthoteuthis californiana*. А. Фрагмент сагиттального препарата, показывающий прикрепление мантии и воронки к гладиусу (висцеральные органы и левый вороночный ретрактор удалены; показана только правая половина гладиуса). В. Фрагмент поперечного среза на уровне крепления вороночных ретракторов к латеральным рогам гладиуса. С. Фрагмент поперечного среза на уровне наибольшей ширины плавников (Срез 2; Рис. 8С). Масштаб = 1 см.

gland. The ventral mantle cavity is reduced to a small space between the visceral sac and the posterior mantle wall. The medium mantle septum is very thin. The funnel retractors are short and wide (Fig. 8). They originate from the inner wall of the funnel, pass along the visceral sac and attach to the lateral horns of the gladius (Fig. 9A).

The frontal section (Fig. 8C, 9C) illustrates the structure of the fins and their relationship with the gladius. Each fin, in this section, consists of two muscular layers (dorsal and ventral) separated by axial cartilage. The fin cartilage is a flexible supporting structure, thick and wide basally, gradually tapering distally. The basal part of the fin cartilage is separated from the rest of the cartilage as a more dense and stiff basal cartilage, triangular in cross-section. Apex of basal cartilage is inserted into the fin cartilage, while its base adheres tightly to the shell sac covering flat outer surface of lateral wings of the gladius (Fig. 9,C). Basal pockets are absent. Elevator and depressor muscles are thin and weakly developed. They originate on both sides of the fin base and attach to the mantle above and below the gladius. The function of these muscles is apparently to adjust position of the fins which otherwise is limited due to the absence of basal pockets and tight fusion of fin basal cartilage to the shell sac. The mantle attaches to lateral wings of the gladius from their sides and the digestive gland adjoins it from the inner side.

COMMENTS. Position of the gladius in *Opisthoteuthis* demonstrates its role as a supporting structure. The solid attachment of the fins to the shell is unique to the cirrates (with the possible exception of the paralarval fin of *Vampyroteuthis*) and is, apparently, needed for their flapping, bird-like strokes that differ from the undulatory fin motion seen in many decapodiforms and the more complex fin movement in *Vampyroteuthis*.

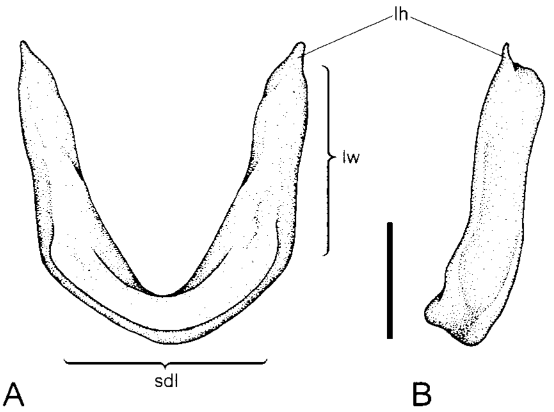


FIG. 10. Gladius of *Grimpoteuthis umbellata* (immature female; 46 mm DML). A. Anterior view (dorsal side down); B. Lateral view (anterior side right). Scale bar = 1 cm.

РИС. 10. Гладиус *Grimpoteuthis umbellata* (незрелая самка; 46 мм ДМ). А. Вид спереди (дорсальная сторона внизу); В. Вид сбоку (передняя сторона справа). Масштаб = 1 см.

Grimpoteuthididae O'Shea, 1999

Grimpoteuthis umbellata (Fisher, 1883)

HABITS AND HABITAT. Most species of the genus *Grimpoteuthis* are poorly known. They inhabit bottom and near-bottom waters of bathyal and abyssal zones of all oceans and mostly occur at depths below 1000 m [Nesis, 1982/1987]. *G. umbellata* is known from the tropical to temporal North Atlantic and the Caribbean Sea [Nesis, 1982/1987]. Direct underwater observations show that although *Grimpoteuthis*, like *Opisthoteuthis*, is closely associated with the bottom, the former is a much better swimmer than the latter [Villanueva *et al.*, 1997; Vecchione, Young, 1997; Vecchione *et al.*, 1998]. Fin swimming appears to be the dominant mode of locomotion in *Grimpoteuthis*, which is occasionally assisted by medusoid contraction of the arm/web complex [Vecchione, Young, 1997].

GLADIUS MORPHOLOGY. The gladius of *Grimpoteuthis* is thick, stout and deeply U-shaped (Fig. 10). Its width is slightly less than its length. The saddle is thick, short, somewhat compressed laterally. Dorsal (outer) side of the saddle is nearly flat; dorsal groove absent. Lateral wings long, laterally compressed, terminate in two lobes with small indistinct horns on ventral side. Outer flattened sides of the wings are nearly parallel to one another.

MICROSTRUCTURE OF THE GLADIUS in *Grimpoteuthis* is essentially the same as in *Opisthoteuthis*.

EXTERNAL MORPHOLOGY. Soft body of *Grimpoteuthis umbellata* (Fig. 11) has the same gelatinous consistency as in *Opisthoteuthis* but its form more closely resembles the typical cephalopod Bauplan. The mantle is bell-shaped, wide and confluent with the head. Its length averages 36% of the total length. The mantle cavity opening is reduced to a narrow slit around the ventral surface of the funnel. The funnel projects anteriorly from the mantle. The fins are large, oar-shaped, with small lobes at their anterior bases. They are set obliquely (slightly inclined anteriorly) on the lateral sides of the mantle in its anterior half. The fin length is 71-75% ML and the fin width is about 45% ML. The fin span is 1.8-2.0 times greater than the mantle length. The long arms (ca. two times the ML) are imbedded in the web except for short distal ends. The web between the arms in *Grimpoteuthis* is thinner than in adult *Opisthoteuthis*, enabling a more fusiform shape during fin swimming [Villanueva *et al.*, 1997]. The gladius occupies subterminal position on the dorsal side of the mantle, its saddle is visible through translucent skin between and posterior to the fins (Fig. 11B), while the wings project anteroventally along lateral sides of the mantle.

TOTAL CROSS-SECTIONS (Figs. 12,13). Mantle wall of *Grimpoteuthis* is thicker, more muscular and less gelatinous than in *Opisthoteuthis*. The relatively thick, muscular anterior margin of the mantle gradually becomes thinner posteriorly. The thickness of the mantle wall is approximately uniform around its circumference. The muscular mantle is attached around the whole gladius but does not overgrow it (Fig. 13A-C). Contrary to the descriptions by Vecchione and Young [1997], the posterior end of the gladius in *Grimpoteuthis* does not coincide with the posterior end of the mantle, but occu-

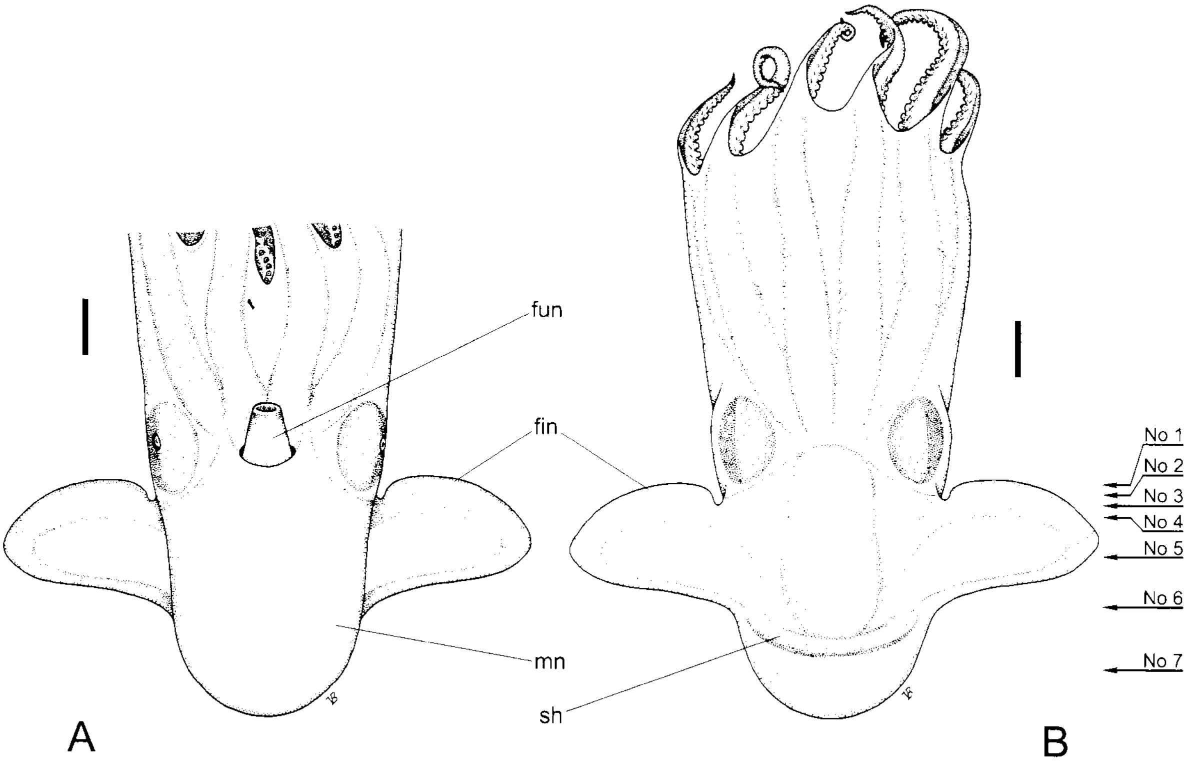


FIG. 11. *Grimpoteuthis umbellata* (immature female; 49 mm DML). A. Ventral view. B. Dorsal view. Arrows with numbers indicate the position of corresponding cross-sections shown in Fig. 12 and 13. Scale bar = 1 cm.

FIG. 11. *Grimpoteuthis umbellata* (незрелая самка; 49 мм ДМ). А. Вид с вентральной стороны. В. Вид с дорсальной стороны. Стрелки с цифрами указывают положение соответствующих срезов, показанных на Рис. 12 и 13. Масштаб = 1 см.

pies a subterminal position as in all octopods. The posterior extension of the thinning mantle surrounds a gelatinous core (Fig. 13D). The dorsal mantle cavity extends from the nuchal region to the level of anterior margins of the gladius wings. At the level of the funnel, the dorsal mantle cavity encircles the visceral sac for about 2/3 of its circumference (Fig. 12A). The ventral mantle cavity extends posteriorly to the level of saddle of the gladius (Fig. 14C).

The visceral sac is spacious and dominated anteriorly by the large digestive gland (Fig. 12). At the level of stellate ganglia, the visceral sac is broadly fused with the lateral mantle walls (Fig. 13C). In the middle of the mantle cavity, thick mantle septum containing the mantle adductor muscle is present (Fig. 13A). Posteriorly the sac is fused with the mantle and the shell sac (Fig. 13B). Between funnel and stellate ganglia, the visceral sac is suspended in the mantle cavity (Fig. 12B).

Structure of funnel is shown on the section 1 (Fig. 12A). Lateral walls of the funnel are thick and relatively muscular. Their inner parts attach to the visceral sac while the outer parts continue into thin collar folds and attach to the lateral walls of the mantle. At the sites of attachment of the funnel to the visceral sac, the funnel also fuses with the mantle forming the collar fusion. The ventral wall of the funnel is thin and less muscular. It joins with the lateral walls along the sides of the funnel. The cross-section shows the presence of a distinct junction formed by muscular fibers of different orientation between the ventral and lateral walls of the funnel. The dorsal wall of the funnel is lined with the thin muscular extension of ventral median mantle adductor.

The short, ribbon-like funnel retractors extend along ventral side of the visceral sac (Fig. 12B) and attach to lateral mantle walls at the level of stellate ganglia (Fig. 12C). Head retractors form the thin, muscular envelope of the visceral sac (Fig. 12A-C) and attach medially to the dorsal, ventral and anterior margins of the gladius wings (Fig. 13A).

The structure of fins is similar with that of *Opisthoteuthis* (Fig. 14). The basal fin cartilage is thick, but, unlike the cartilage in *Opisthoteuthis*, it is not clearly differentiated from the axial cartilage. The axial cartilage is thinner than in *Opisthoteuthis*. Widened base of the fin cartilage tightly adheres to the shell sac along outer flat sides of gladius wings (Fig. 13B). Epithelial basal pockets are absent.

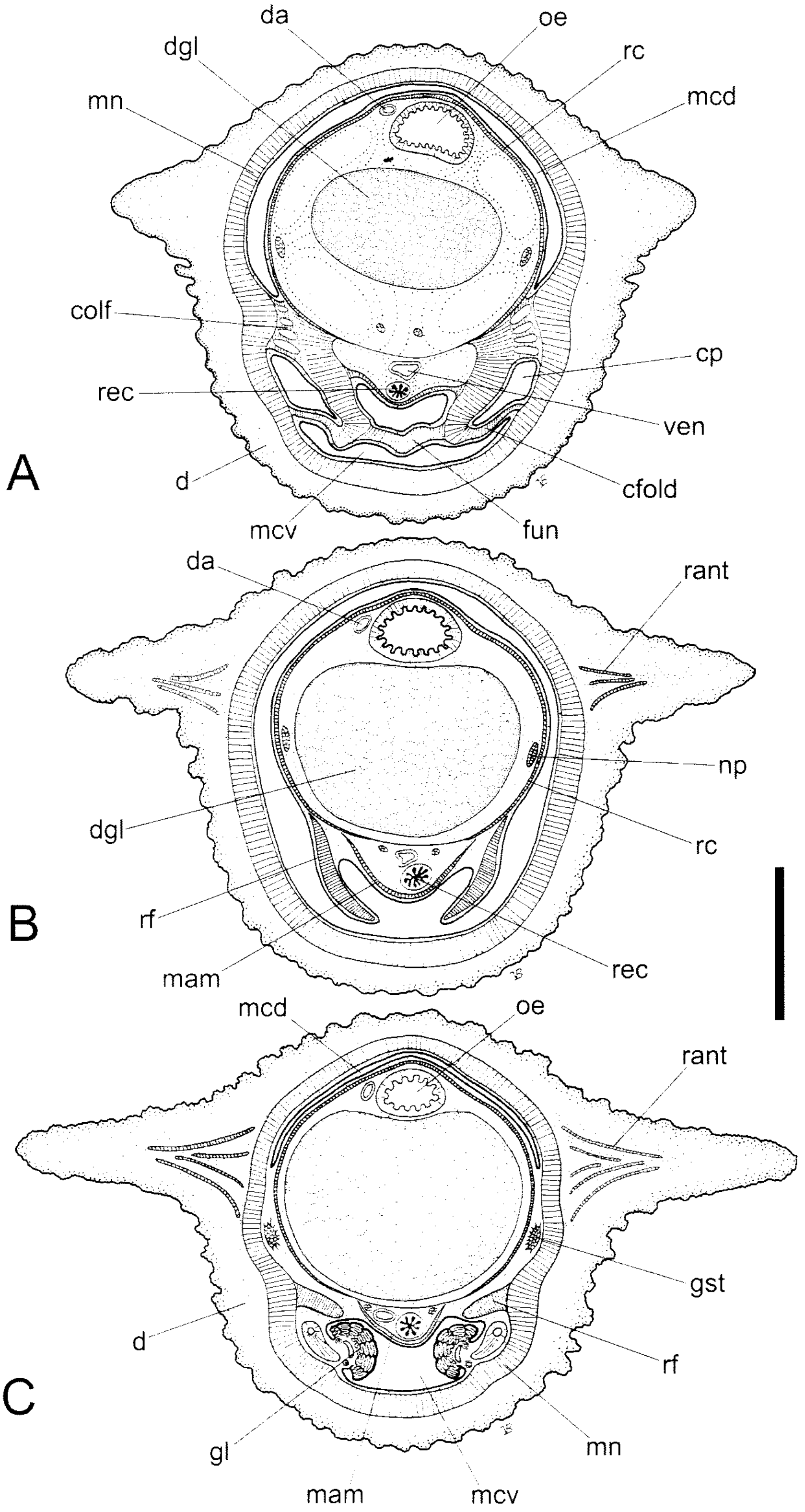


FIG. 12. Schematic cross-sections of *Grimpoteuthis umbellata* soft body (immature female: 49 mm ML). A. Section 1. at the level of the funnel. B. Section 2. immediately behind the funnel. C. Section 3. at the level stellar ganglia. The position of the sections is indicated in Fig. 11. Scale bar = 1 cm.

РИС. 12. Срезы мягкого тела *Grimpoteuthis umbellata* (незрелая самка: 49 мм ДМ). А. Срез 1. на уровне воронки. В. Срез 2. позади воронки. С. Срез 3. на уровне звездчатых ганглиев. Положение срезов показано на Рис. 11. Масштаб = 1 см.

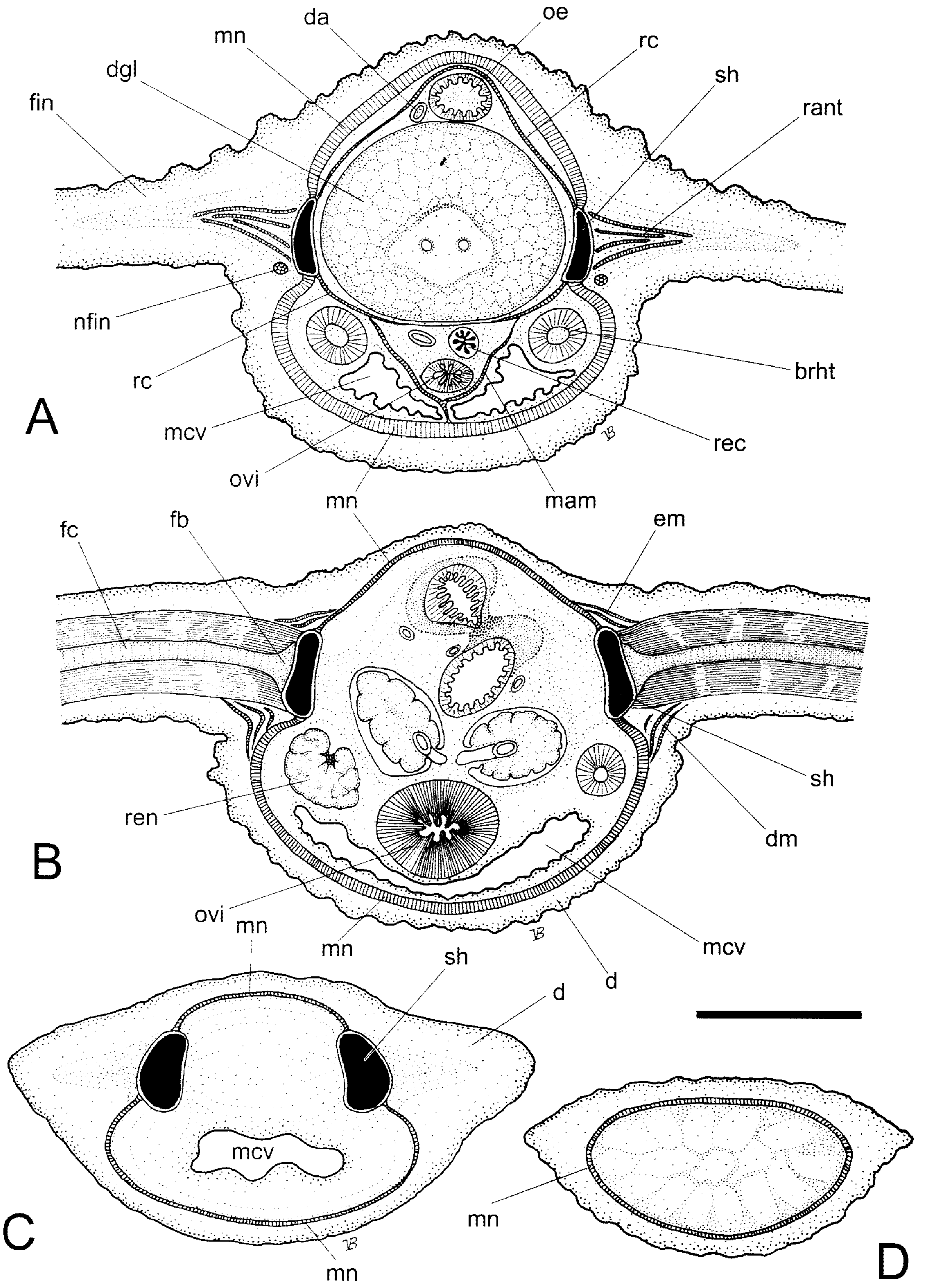


FIG. 13. Schematic cross-sections of *Grimpoteuthis umbellata* soft body (same specimen as in Fig. 12). A. Section 4, at the level of anterior margins of the gladius. B. Section 5. at the level of the greatest fins width. C. Section 6, behind the fins. D. Section 7. in the posterior part of the mantle. The position of the sections is indicated in Fig. 11. Scale bar = 1 cm.

РИС. 13. Срезы мягкого тела *Grimpoteuthis umbellata* (экземпляр тот же, что на Рис. 12). A. Срез 4, на уровне передних краев гладиуса. B. Срез 5. на уровне наибольшей ширины плавников. C. Срез 6, позади плавников. D. Срез 7. вблизи заднего апекса мантии. Положение срезов указано на Рис. 11. Масштаб = 1 см.

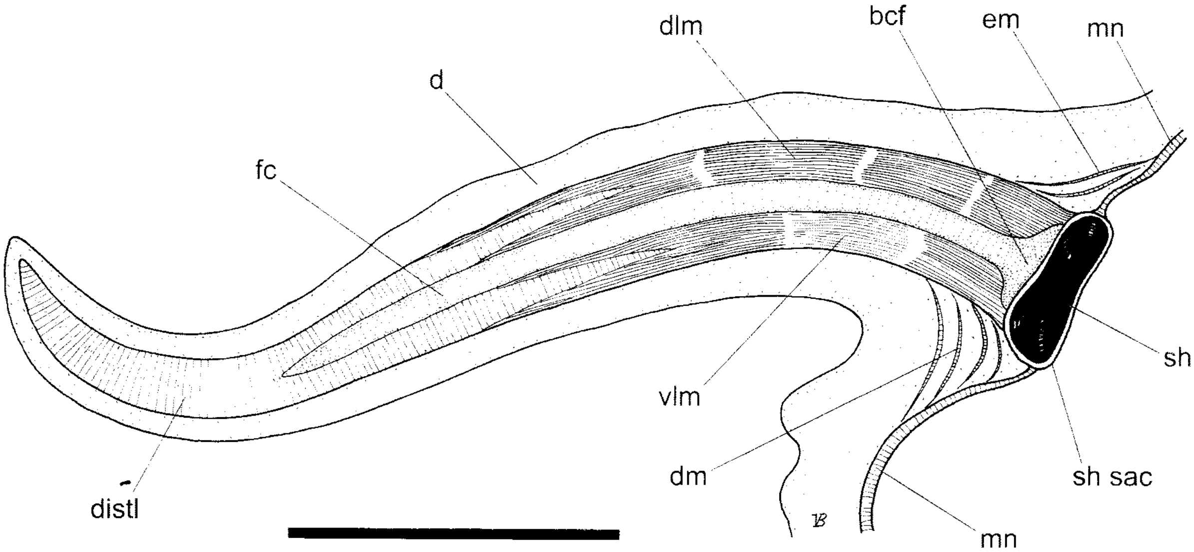


FIG. 14. *Grimpoteuthis umbellata*: section through the long axis of fin at the level of its greatest width. Scale bar = 1 cm.

РИС. 14. *Grimpoteuthis umbellata*: срез вдоль продольной оси плавника на уровне его наибольшей ширины. Масштаб = 1 см.

Muscles monitoring position of the fins on the mantle are weakly developed. Elevator and depressor muscles consist of dispersed muscular bundles originating on the fin base and attaching to the mantle above and below the fins (Fig. 14). Anterior retractors spread along the mantle from the fin bases to the level of the posterior end of the funnel (Fig. 12B,C). The muscular layers in the fins of *Grimpoteuthis* are morphologically differentiated into proximal and distal parts with different orientations of the muscle fibers (Fig. 14). In the proximal part, the dorsal and ventral muscular layers are composed predominantly of longitudinal fibers (parallel to the long axis of the fin) and to a lesser extend by oblique fibers. In the distal part of the fin, muscular layers consist mainly of transverse fibers oriented perpendicular to the fin surface.

COMMENTS. The gladius in *Grimpoteuthis* is thicker and bulkier than in *Opisthoteuthis*; its dorsal surface of the saddle is nearly flat; the lateral wings are relatively longer and laterally compressed; the lateral horns short and indistinct. The differences in gladius morphology reflect the differences in locomotion between the two species. The fins in *Grimpoteuthis* are much larger than in *Opisthoteuthis*. The fin bases in *Grimpoteuthis* are closer to one another than in *Opisthoteuthis*, and this is reflected in the shorter saddle of the former. The surfaces of the fin bases are greater in *Grimpoteuthis*, which corresponds to the larger outer surfaces of the lateral wings. The larger fins, presumably, are responsible for the thicker and stouter gladius. The weak development of the lateral horns in the gladius of *Grimpoteuthis* correlates with the weak funnel retractors, which do not attach to the gladius but to the mantle wall. Unlike the saddle groove of *Opisthoteuthis*, the gladius of *Grimpoteuthis* has no special adaptations for the attachment of the mantle muscles.

Cirroteuthidae Keferstein, 1866

Cirroteuthis muelleri Eschricht, 1836

HABITS AND HABITAT. *Cirroteuthis muelleri* is a benthopelagic cirrate octopod usually found in association with the ocean floor at great depth in the North Atlantic, Arctic Ocean [Nesis, 1982/1987], North Pacific [Guerra *et al.*, 1998] and off New Zealand [O'Shea, 1999]. In the North Atlantic it occurs at depth between 700 and 4854 m with the peak abundance at 3000-3500 m [Collins *et al.*, 2001]. Species of *Cirroteuthis* are the largest representatives of Cirrata reaching up to 1.5 m in length [Nesis, 1982/1987]. They are often found in deep water swimming or drifting near the ocean floor [Vecchione, Young, 2003a].

GLADIUS MORPHOLOGY. The gladius is a massive, translucent structure with a short, thick medial saddle and broad lateral wings (Fig. 15). The saddle has a wide ventral base and a narrow, dorsal longitudinal ridge. The wings are expanded both anteri-

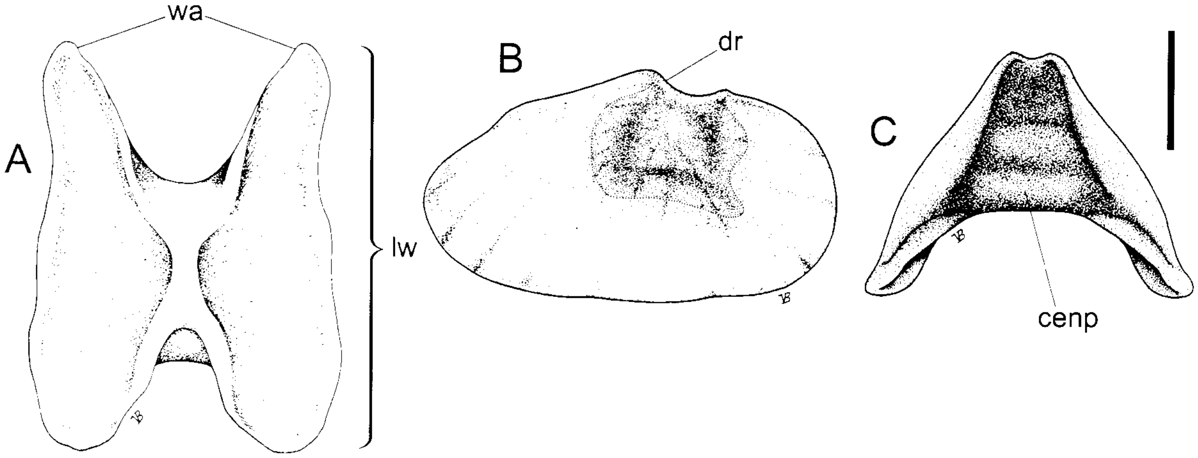


FIG. 15. Gladius of *Cirroteuthis muelleri* (maturing female; 128 mm ML). A. Dorsal view (anterior side is up). B. Lateral view (anterior side is on the left; dorsal side is up). C. Posterior view (dorsal side is up). Scale bar = 1 cm.

РИС. 15. Гладиус *Cirroteuthis muelleri* (созревающая самка; 128 мм ДМ). А. Вид с дорсальной стороны (передний конец сверху). В. Вид сбоку (передний конец слева; дорсальная сторона сверху). С. Вид сзади (дорсальная сторона сверху). Масштаб = 1 см.

orly and posteriorly. They are situated very close to one another and their ventrolateral margins are almost parallel. The anterior and posterior edges of the wings are bluntly rounded, and the wings are almost elliptical in lateral view. Lateral surface of each wing is slightly concave sloping downwards at an angle of approximately 60°.

MICROSTRUCTURE OF THE GLADIUS. Cross-section through the central part of the gladius is V-shaped, resembling the cross-sections of some teuthid gladii [Bizikov, 1996: Fig. 18C]. Center of growth is situated in the middle of the saddle. The growth increments are wide, united into second-order cycles. Microstructure of the gladius is similar to that of *Opisthoteuthis*.

EXTERNAL MORPHOLOGY. The body is gelatinous, very fragile, with short sac-shaped mantle and long arms (about twice the mantle length) embedded into a deep web except for the short distal ends (Fig. 16). The head is approximately the same width as the mantle, with small inconspicuous eyes. The mantle length comprises about 1/3 TL. Mantle aperture is reduced to narrow semicircular slit around the funnel. The fins are large, oar-shaped and set very close to one another on the dorsal side in the middle part of the mantle. Fin length is approximately equal to the mantle length, and the fin span is 1.9-2.0 times the mantle length. The anterior blade of each fin has a small lobe at the base. Long axes of fins are not parallel to each other but tilted anteriorly forming an angle about 135° between them. The funnel projects anteriorly from the mantle. It is long, tube-like and fused with the head on its dorsal side. The gladius occupies a subterminal position on the dorsal side of the mantle. The mantle bulges posterior to the gladius forming a dome-shaped apex. The axial part of the saddle and the dorsal margins of the wings can be seen through the gelatinous flesh on the dorsal side (Fig. 16B).

TOTAL CROSS-SECTIONS. The most striking feature about *Cirroteuthis* anatomy is the lateral fusion of its visceral sac with the mantle walls resulting in considerable decrease in size of the mantle cavity (Figs. 17B,C; 18A). This fusion starts at the level near the collar folds (Fig. 17B) and proceeds to the level of the gladius (Fig. 18A). The mantle in *Cirroteuthis* is rather thick anteriorly and gradually becomes thinner posteriorly. Part of the head extends into the body, so that its nuchal part, including statocysts, is covered by dorsal mantle wall (Fig. 17A). The mantle attaches to the gladius along the margins of the wings. The fin bases attach to the outer sides of the wings. On the dorsal side of the mantle, anterior and posterior parts of the mantle are fused over the dorsal ridge of the gladius (Fig. 18C). The thickness of mantle wall is approximately equal around its circumference except posterior to the gladius where the dorsal mantle wall is about two times thicker than the ventral wall (Fig. 18D). Subcutaneous gelatinous layer is about the same thickness as in *Grimpoteuthis*.

The funnel consists of a single muscular layer. Junctions of muscular layers between ventral and lateral walls are absent. The anterior part of the funnel is supported by paired funnel adductor muscles that pass from head retractors toward dorso-la-

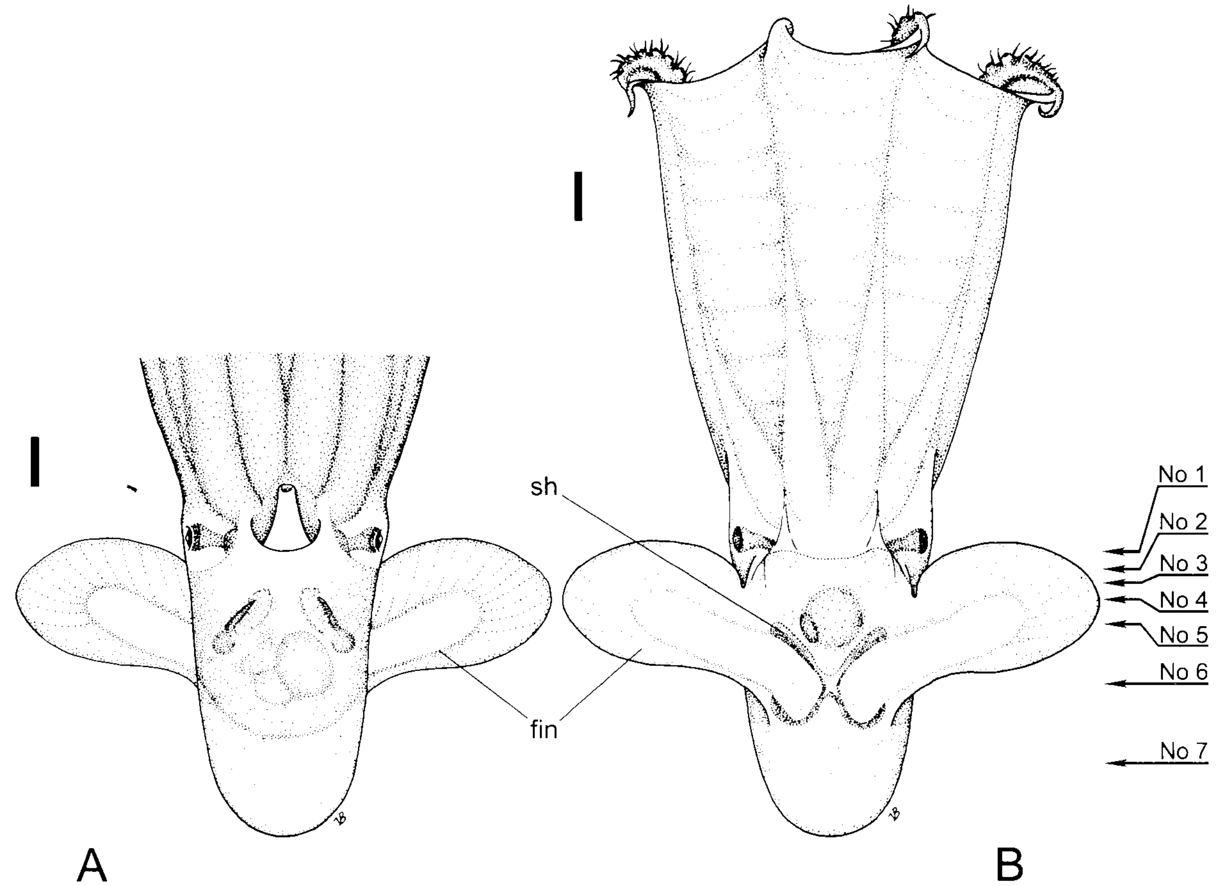


FIG. 16. *Cirroteuthis muelleri* (immature female; 65 mm DML). A. Ventral view. B. Dorsal view. Arrows with numbers indicate the planes of corresponding cross-sections (shown in Figures 17 and 18). Scale bar = 1 cm.

РИС. 16. *Cirroteuthis muelleri* (незрелая самка; 65 мм ДМ). А. Вид с вентральной стороны. В. Вид с дорсальной стороны. Стрелки с цифрами указывают положение соответствующих срезов, показанных на Рис. 17 и 18. Масштаб = 1 см.

teral walls of the funnel (Fig. 17A). Funnel orifice is extremely narrow and somewhat unusual in cross-section. In its anterior part a pair of coiled flaps (funnel organ?) protrudes inside the canal from the lateral walls (Fig. 17A). In the posterior part of funnel the flaps disappear, and funnel canal becomes triangular in cross-section (Fig. 17B). Collar folds are reduced to thin muscular strips originating from the ventrolateral sides of the funnel and attaching to the lateral walls of the mantle (Fig. 17B). Attachment sites of collar folds to the funnel are marked by junctions formed by muscular fibers with differing orientations. The funnel retractors are short and wide. They originate from posterior ventral corners of the funnel, follow the ventral side of the visceral sac and attach to lateral walls of the mantle at the level of stellate ganglia (Fig. 18A). At site of attachment the mantle walls are thickened. In their middle part the funnel retractors are muscular flaps hanging from the ventral wall of the visceral sac into the mantle cavity (Fig. 17C). The head retractors are thin, weak muscles. They form an envelope around visceral sac (Fig. 17B,C) and attach from inside to dorsal, ventral and anterior margins of gladius wings (Fig. 18B).

Mantle cavity is very small. The dorsal mantle cavity is a narrow slit in nuchal region (Fig. 17B,C). The short, thick saddle has shifted visceral organs ventro-anteriorly. Posterior part of ventral mantle cavity has a shape of narrow dorso-laterally squeezed tube. In contrast to *Grimpoteuthis*, ventral mantle cavity extends posteriorly beyond the gladius (Fig. 18D).

At the level of greatest fin width the V-shaped gladius is extremely thick and provides a rigid support for the fins (Fig. 18C). The fins in *Cirroteuthis* are larger than in *Grimpoteuthis* and *Opisthoteuthis*. A thick axial fin cartilage forms the core of each fin. The basal part of the fin cartilage is greatly expanded into wide flat base that adheres tightly to the shell sac along the flat outer sides of the wings (Fig. 18C). Elevator muscles originate on the dorsal

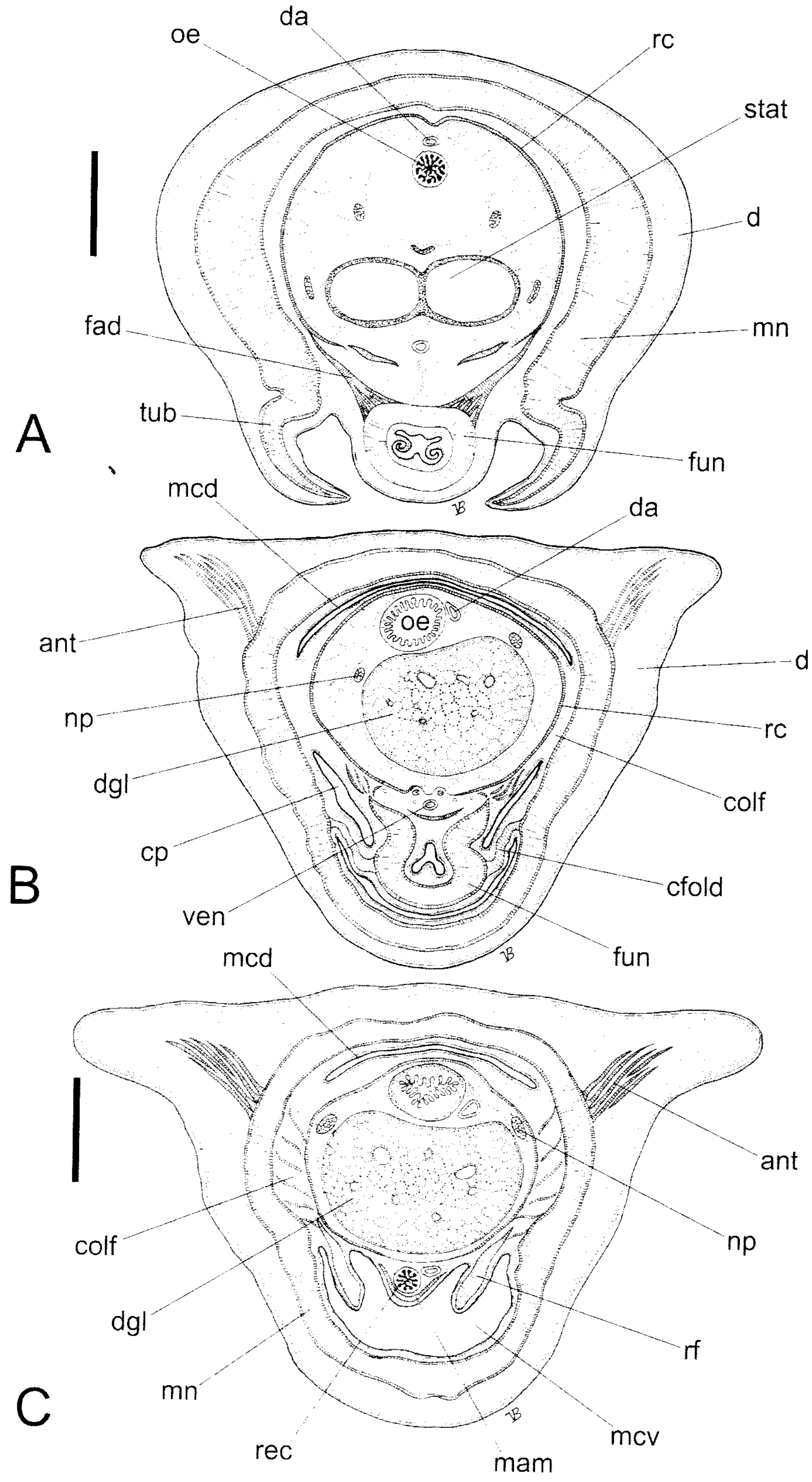


FIG. 17. Schematic cross-sections of *Cirroteuthis muelleri* soft body (maturing male; 80 mm ML). A. Section 1, at the level behind the eyes. B. Section 2, through the middle part of the funnel. C. Section 3, behind the funnel. The position of the sections is indicated on Fig. 16. Scale bar = 1 cm.

РИС. 17. Срезы мягкого тела *Cirroteuthis muelleri* (созревающий самец; 80 мм ДМ). А. Срез 1, позади глаз. В. Срез 2, в средней части воронки. С. Срез 3, позади воронки. Положение срезов указано на рис. 16. Масштаб = 1 см.

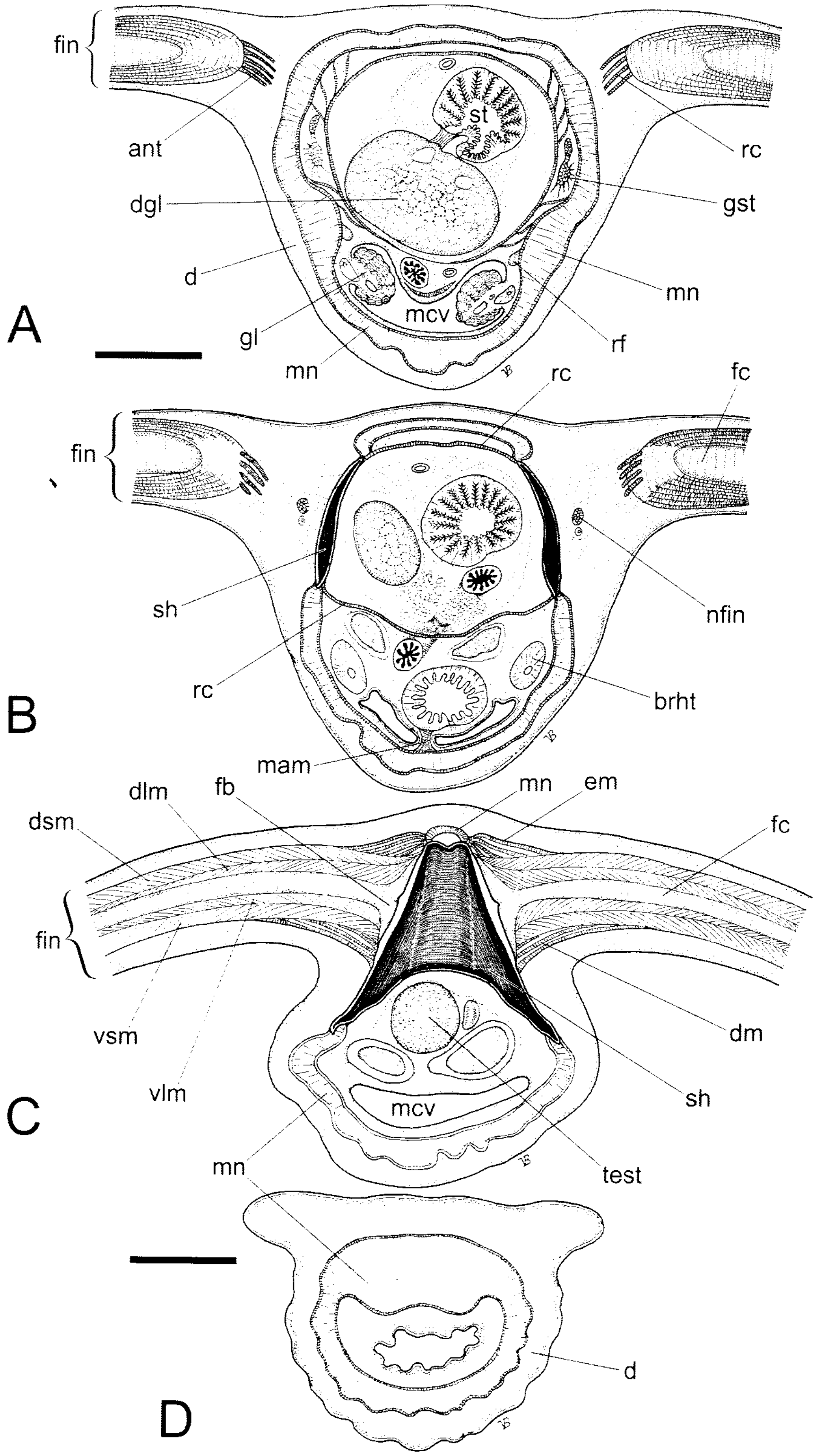


FIG. 18. Schematic cross-sections of *Cirroteuthis muelleri* soft body (same specimen as in Fig. 17). A. Section 4, at the level of anterior margin of the fins (level of stellar ganglia). B. Section 5, at the level of anterior wings of the gladius. C. Section 6, at the level of the greatest fins width. (The slit between fins bases and gladius on this section is an artifact of sectioning). D. Section 7, behind the gladius. The position of the sections is indicated on Fig. 16. Scale bar = 1 cm.

РИС. 18. Срезы мягкого тела *Cirroteuthis muelleri* (экземпляр тот же, что на Рис. 17). А. Срез 4, на уровне переднего края плавников (уровень звездчатых ганглиев). В. Срез 5, на уровне передних краев крыльев гладиуса. С. Срез 6, на уровне наибольшей ширины плавников. (Щель между основаниями плавников и гладиусом – артефакт, возникший при резке). D. Срез 7, позади гладиуса. Положение срезов указано на Рис. 16. Масштаб = 1 см.

surface of fins in their basal part and attach to the gladius wings in the region of medial dorsal ridge. Depressor muscles originate on the ventral surface of the fins in their basal part and attach to the gladius wings below the fins. The muscular layers in the fins of *Cirroteuthis* are more complex than in *Grimpoteuthis* and *Opisthoteuthis*. In the proximal part of the fins, both dorsal and ventral muscular layers consist of two layers each: an inner layer of longitudinal muscles, adhering to the axial cartilage, and an outer layer of oblique muscles covering dorsal and ventral sides of fin (Fig. 18C). In the distal part of the fin, the muscles consist mainly of transverse fibers, as in *Grimpoteuthis*.

COMMENTS. Prominent expansion of lateral wings in both anterior and posterior directions is one of two unique elements of the gladius in *Cirroteuthis*. The narrowing and increased depth of the saddle is the other. Both elements reflect an important change in the attachment of the fins to the gladius. In *Cirroteuthis*, the fins are set transversally on the wings and their bases are brought close together while in the other cirrates studied (*Opisthoteuthis* and *Grimpoteuthis*) the fins attach along the length of the wings and their bases are set wide apart (compare Figs. 16, 11 and 7). On one hand, the change in fin-attachment changed the angle of the fins with respect to the body axis: in *Opisthoteuthis* the fins bases attach to the wings at some angle to the body axis (Figs. 7, 8A), while in *Cirroteuthis* they attach along the body axis (Fig. 16). On the other hand, the gladius in *Cirroteuthis* also changed its orientation: the axis from the saddle to anteroventral tips of the wings makes a steeper angle with the body axis than in other cirrates studied. The depth of the saddle appears to be tied to the depth of the broad wings. Narrowing of the saddle and its increased depth transformed the middle part of the gladius into stout supporting beam, V-shaped in cross-section, with the fin attached to its sides (Fig. 18C).

Although the fins bases are fused with the shell sac, their position on the wings appears to be adjustable, perhaps through some elasticity in the shell sac. The possibility of adjustment is suggested by the vertical dimension of lateral wings, which is greater than the thickness of the fins bases attached to them. The flat, cartilaginous bases of the fins would conform well to outer surfaces of the wings over this range. In addition the elevator/depressor muscles are larger than in opisthoteuthids. The differentiation of the muscular layers in the fins indicates they are capable of more complex movements, perhaps an increased ability for anterior/posterior undulation. The gladius in *Cirroteuthis* has no special adaptations for the attachment of mantle or retractor muscles. The weak funnel retractors attach to the mantle walls, confirming the absence of jet-swimming. Indeed, the funnel reminds one more of a nostril than a jet nozzle.

Suborder Incirrata Grimpe, 1916

Octopodidae Orbigny, 1845

Octopodinae Orbigny, 1845

Enteroctopus dofleini (Wulker, 1910)

GENERAL REMARK. The shell in the Incirrata consists of a pair of narrow spindle-shaped cartilage-like rods embedded in the muscle tissue on dorsolateral side of the mantle. Although this unusual shell is termed sometimes 'gladius' [Nesis, 1982/1987], it differs from the typical teuthoid gladius in many aspects and deserves a special term: stylets [Robson, 1932; Voight, 1997].

HABITS AND HABITAT. Genus *Enteroctopus* as well as other closely related genera of Octopodinae includes familiar benthic muscular octopuses inhabiting a wide range of depths from intertidal pools to lower continental slopes down to 800 m [Nesis, 1982/1987]. They inhabit all oceans of the world from equator to high latitudes and occur on a wide range of habitats from coral and rocky reefs, seagrass and algal beds, to sand and mud substrates [Norman *et al.*, 1998]. Species of the genus *Enteroctopus* primarily move via two methods: (1) crawling over the substrate using the arms, and 2) jet propulsion using the mantle-funnel complex [Norman *et al.*, 1998]. *E. dofleini* is the largest representative of Octopodinae, reaching up to 5 m in total length (60 cm ML) and up to 150 kg in weight [Norman et al., 1998]. *E. dofleini* is found in the North Pacific, from the Bering Sea in the north to the Okhotsk Sea, the Sea of Japan and the Yellow Sea in the southwest and to California in the southeast [Nesis, 1982/1987]. The maximum depth of its occurrence is about 400 m [Filippova *et al.*, 1997].

SHELL MORPHOLOGY. The stylets in *Enteroctopus* are two thin translucent rods with pointed ends lying on dorsolateral side of the mantle at a sharp angle to longitudinal axis (Figs. 19A; 20A). Distance between stylets at the level of their anterior ends is about 50% ML. The stylets consist of a cartilage-like chitinous substance that is laid down in concentric layers. The length of stylets in adult octopuses ranges from 20.4% to 31.8% ML (mean length is 24.3%; SD=3.4). Each stylet is surrounded by a shell sac with dense connective tissue on the outer side of the sac and shell epithelium on the inner side. Each stylet has a bend

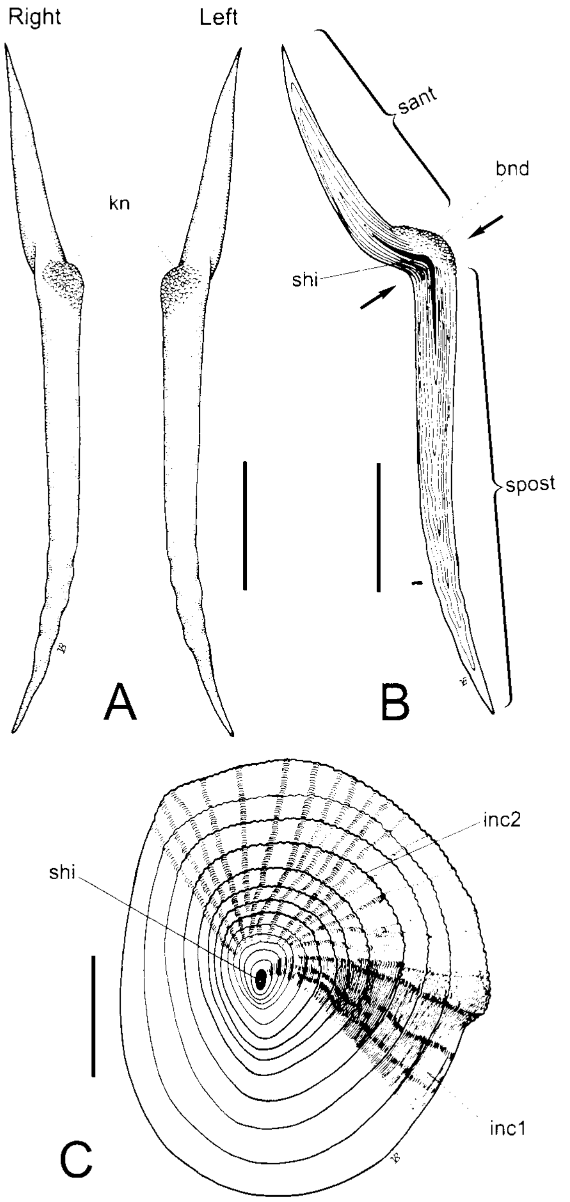


FIG. 19. Stylets of *Enteroctopus dofleini*. A. Ventral view of a pair of stylets from adult female (21 cm ML): right stylet is on the left: anterior end is up. The stylets are shown opaque to reveal their surface. B. Lateral view of the right stylet from the same specimen (ventral side if on the right). The stylet is shown naturally transparent to reveal its growth increments and the initial shell (shi). Bold arrows indicate the plane of the cross-section shown in 'C'. C. Cross-section through the angle of the stylet (ventral side is up: outer side is on the left). A.B: scale bar = 1 cm. C: scale bar = 1 mm.

РИС. 19. Стилеты *Enteroctopus dofleini*. А. Пара стилетов зрелой самки (21 см ДМ): вид с вентральной стороны (правый стилет слева: передняя сторона наверху). Стилеты изображены непрозрачными, чтобы показать рельеф их поверхности. В. Вид сбоку правого стилета той же особи (вентральная сторона справа). Стилет изображен естественно прозрачным, чтобы показать его линии нарастания и зародышевую раковину (shi). Стрелки указывают положение среза, изображенного на 'С'. С. Поперечный срез на уровне угла стилета (вентральная сторона наверху; внешняя сторона слева). А.В: масштаб = 1 см. С: масштаб = 1 мм.

in its anterior part that forms an obtuse angle (130°-145°) (Fig. 19B). At the bend the stylet reaches its greatestthickness that ranges from 5.1% to 8.4% of stylet length (ca. 6.6%; SD=0.86). The apex of bend is dome-shaped and its surface is covered with numerous minute knobs testifying the muscle attachment in this region. Indeed, during extraction of stylets, it is the bend that is the most difficult to separate from the soft tissues. The bend divides the stylet into anterior and posterior parts (shoulders). The anterior shoulder is short, about one half the length of posterior shoulder, and nearly straight. The posterior shoulder is long and slightly curved distally. The distal part of the posterior shoulder is often curved in a zigzag pattern, recalling the blade of a Malaysian 'Kris' dagger.

Although the general shape of the stylets in *E. dofleini* is rather conservative, their length, thickness and relative length of the shoulders show considerable ontogenetic and individual variability. The growth of stylets is negatively allometric. Their relative length decreases from 28-32% ML at 13-17 cm ML to 20-26% ML at 24-27 cm ML. Proportions of shoulders and thickness of stylets apparently do not change with age. The length of the anterior shoulder ranges from 28% to 43% of the stylet length, averaging 35.2% (SD=3.4). Stylet thickness varies from 5.1% to 8.4% of the stylet length, averaging 6.6% (SD=0.85). There is also considerable variability between left and right stylets of the same specimen. The length of stylets may differ up to 9% (average 4.3%; SD=4.1); the length of the shoulders may differ up to 11% (average 4.8%; SD=4.5), and the thickness of stylets may differ up to 33% (average 11.5%; SD=9.6). However, there is no consistent difference between left and right stylet: the average size of the left and right stylets is the same.

MICROSTRUCTURE OF THE STYLETS. The growth of stylet occurs in layers that are laid down on the outer surface of the previous layer. As a result, the shape of stylet at earlier stages may be reconstructed from its growth increments visible on intact stylet in transmitted light. The apices of previously formed layers form two thin apical lines diverging from the bend along the axes of both shoulders (Fig. 19B). In some stylets one or both apical lines becomes whitish and opaque, apparently due to some injury in the past. The stylet bend thus represents the center of growth and contains the earliest increments, including the embryonic shell.

A cross-section through the angle apex is roughly oval in shape (Fig. 19C). It is composed of numerous regular concentric increments. The widths of increments are 7-12 μm, averaging 9.2 μm. Each increment consists of a glass-like translucent zone confined by a distinct refracting border.

The width of each increment is approximately equal along its perimeter. The center of growth (initial shell) is situated close to the middle of the cross-section. It is an amorphous, opaque, oval body 170-190 µm in length, about 100 µm in width. The width of the growth increments does not vary significantly from the center toward periphery. The growth zones, similar to those described in statoliths, are absent [Clarke, 1978; Arkhipkin, Bizikov, 1991]. Primary increments are clearly grouped into second-order cycles, marked by prominent borders apparently reflecting some events in the animal's life. The number of first-order increments in one second-order cycle varied from 7-15 near the center to 25-33 in periphery. The minute knobs are located on the ventral (inner) side of the bend, while the dorsal (outer) side is smooth. The knobs can be traced on previously formed layers: their marks form twisted lines radiating from the center of growth.

EXTERNAL MORPHOLOGY. As *E. dofleini* is the first incirrate octopod to deal with in this study, this species will be used as an example in description of the general morphological Bauplan of the Incirrata.

The mantle in *E. dofleini* is muscular, wide, sac-shaped and broadly fused with the head on the dorsal side (Fig. 20A). Anterodorsal margin of the mantle can be seen after removal of the skin from dorsal side. The margin is nearly straight and reaches the posterior edge of the eyes. A wide nuchal muscle fastens the dorsal mantle wall to the head. This muscle extends from the dorsal mantle margin to the bases of arms I. Mantle is the most thick in its anterior part. Ventral mantle is thickest in the region of gills; the dorsal mantle wall is thickest in the region of the dorsal mantle cavity (Fig. 21A). Posteriorly the mantle becomes thinner and reaches its minimum thickness at the posterior apex. The mantle aperture is wide, extending laterally to the level of eyes. The mantle cavity is relatively spacious; the ventral part of the mantle cavity is distinctly larger than the dorsal one. The fins are absent. The stylets lie on the dorsolateral sides of the mantle in its posterior half. The anterior shoulder of each stylet lies superficially on the exterior surface of the mantle muscle, while its posterior shoulder is embedded in the mantle muscle.

The funnel is fused with the head and partly embedded in it (Fig. 20C). The middle part of the funnel is fastened to the head by a pair of lateral adductor muscles. The posterolateral walls of the funnel pass into muscular collar folds. The collar folds surround visceral sac like a wide bell-mouth jar and attach to the dorsal mantle wall. The funnel arises deep within the mantle cavity, and its posteroventral margin rests against the ventral mantle adductor (Fig. 21A). A funnel locking-apparatus is absent, but the posterior corners of the funnel bear small cup-like depressions caused by contraction of funnel wall over the head of the funnel retractors. The funnel retractors are thick and stout. They originate as wide posterior extensions of the dorsal wall of the funnel (Fig. 20C), run alongside visceral sac and adhere to the ventral sides of the stylets (Fig. 21A). Muscle fibers of axial part of funnel retractors attach to the stylet in the region of its angle, while peripheral fibers diverge in a fan-like fashion and attach along the anterior and posterior shoulders of the stylets (Fig. 21B).

Attachment of the visceral sac in the Incirrata is unique among cephalopods (Fig. 20B; 21A). The visceral sac, at its anterior end, is fused with the head and, at its posterior end, it adheres to the mantle. In the middle part the visceral sac is suspended inside mantle cavity by five adductor muscles: paired anterodorsal mantle adductors, paired posterodorsal mantle adductors (=funnel retractors) and an unpaired ventral median mantle adductor (=mantle septum). Anterodorsal mantle adductors are formed by the outer layer of the head retractors that branches off at the level of stellate ganglia. Each adductor undergoes an 180° twist so that the anterior-most margin at the visceral sac becomes the posterior-most margin at the attachment to the mantle wall (Fig. 20 B,C). The stellate ganglia are situated on the inner surface of the mantle just lateral to the attachment of the anterodorsal adductors. Among numerous nerves passing to and from the stellate ganglia, two are relevant to this study: a pallial nerve passing from the brain to each stellate ganglion through the anterodorsal adductors, and a "fin" nerve passing from each stellate ganglion posteriorly along the inner mantle wall to the stylets (Fig. 20C) and beyond. At the stylet, the "fin" nerve penetrates the mantle wall near the place of attachment of funnel retractor (Fig. 21B). Persistence of the "fin" nerves in incirrate octopods is quite remarkable, as they retain their original position in relation the shell, thus indicating the position of former fins. The posterodorsal adductors are formed by the funnel retractors. The ventral median-mantle adductor is a thick, wide muscular septum extending from the ventral mantle wall to the visceral sac (Fig. 21A). It is wide at the mantle wall and becomes progressively narrower toward the visceral sac. The median mantle adductor divides ventral mantle cavity into left and right parts. Posterior to the adductor, the mantle cavity is undivided.

CROSS-SECTIONS. A section at the level of the funnel shows that the visceral sac is enclosed by a thick muscular cover formed by the head retractors. The thickness of head retractors is greatest on the lateral sides of the sac and least on the dorsal side

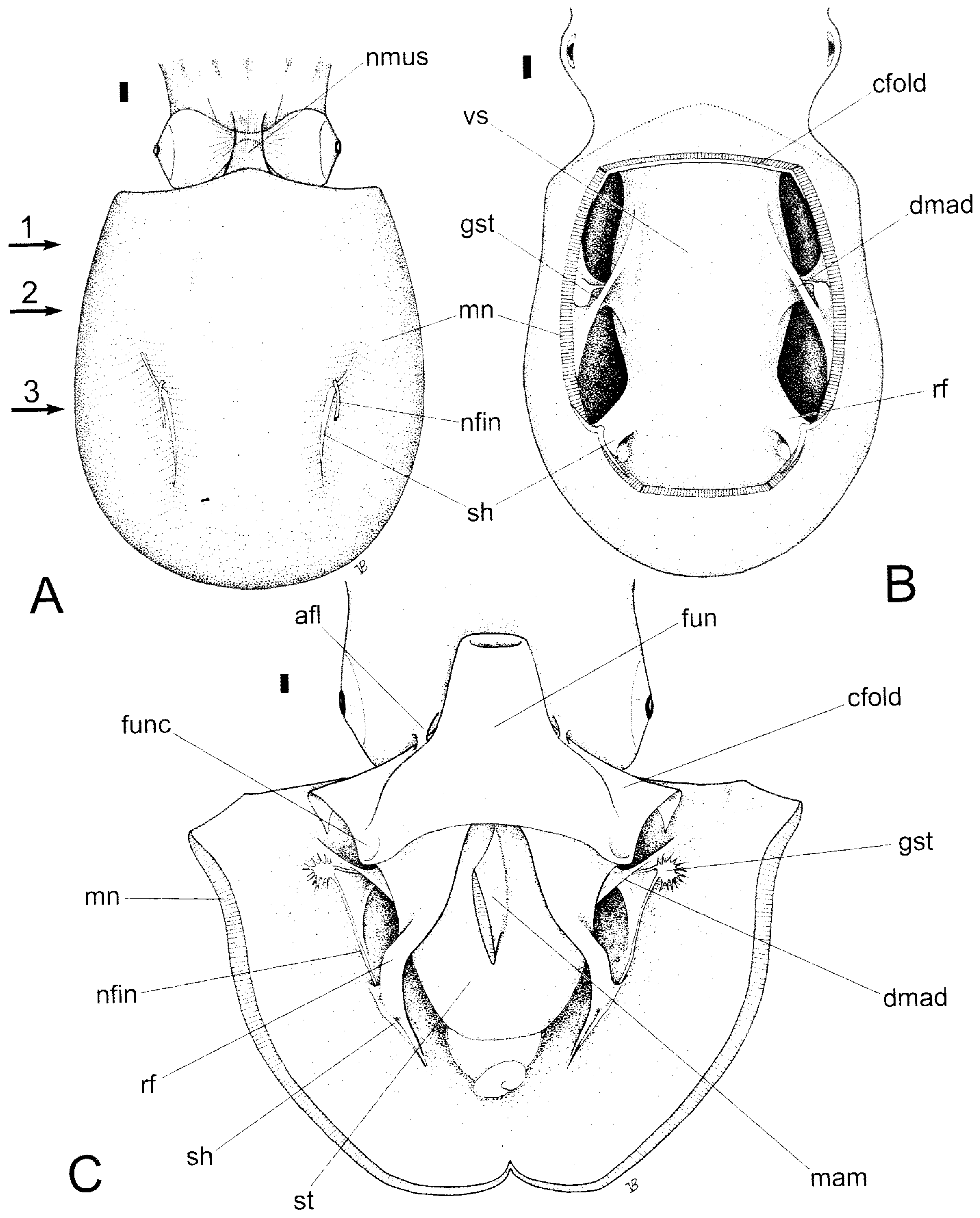
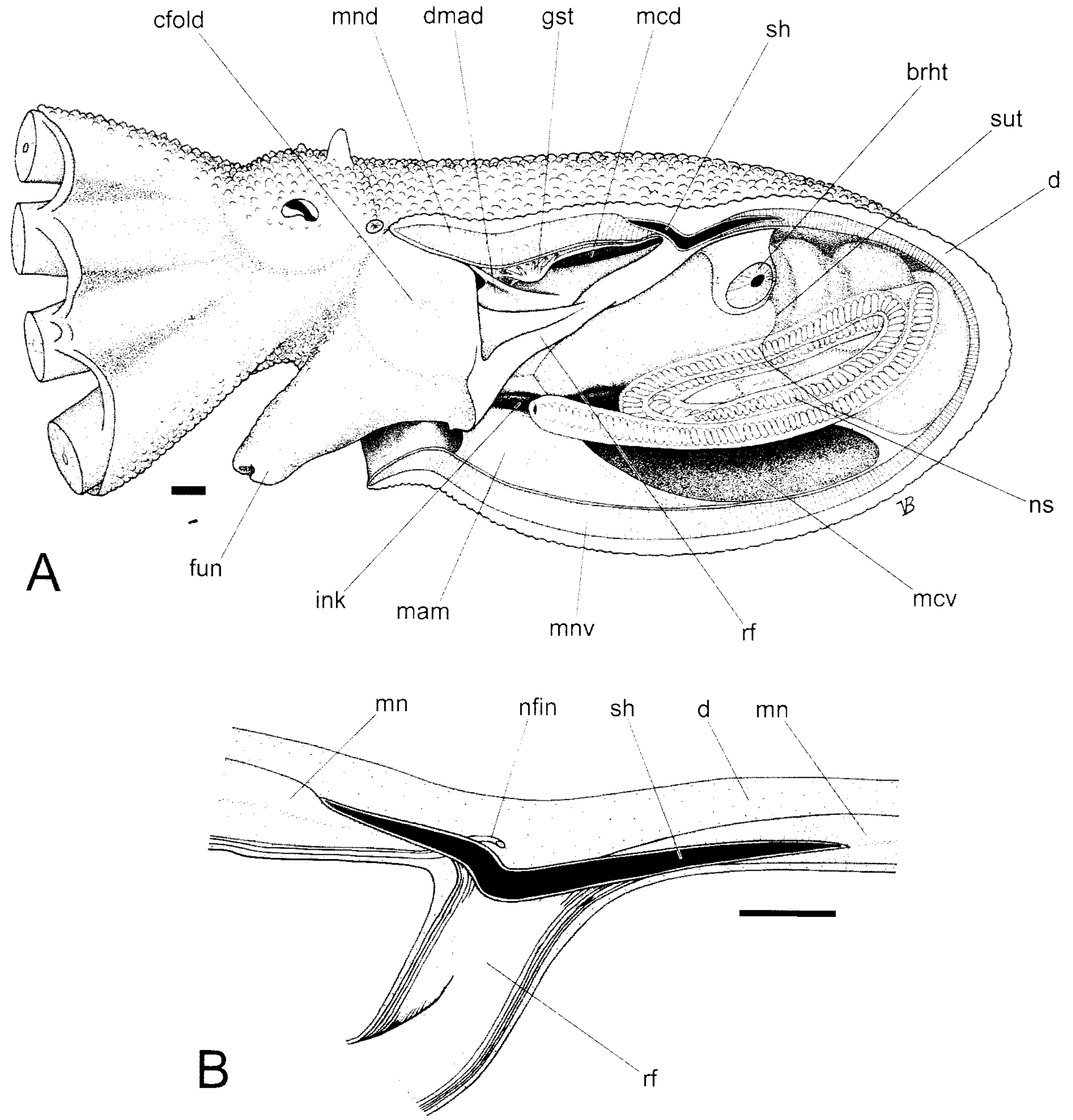


FIG. 20. General anatomy in *Enteroctopus* and *Octopus*. A. *E. dofleini*: dorsal view (female; 21 cm ML). The skin is removed to show the outline of the mantle and position of the shell vestiges. Bold arrows with numbers indicate the planes of corresponding cross-sections (shown in Figure 22). B. *O. vulgaris*: dorsal view of a half-grown animal. The muscular mantle is cut off from the dorsal side without changing natural topography [from Naef, 1923; modified]. C. *E. dofleini*, ventral view. The mantle is open at the insertion of the median mantle adductor and spread. The gills and visceral organs (except the digestive gland and stomach) are removed. Scale bar = 1 cm.

РИС. 20. Строение *Enteroctopus* и *Octopus*. A. *E. dofleini*: вид с дорсальной стороны (самка; 21 см ДМ). Кожа удалена, чтобы показать контур мантийных мышц и положение рудиментов раковины. Стрелки указывают положение соответствующих срезов (показаны на Рис. 22). B. *O. vulgaris*: вид молодого животного с дорсальной стороны. Дорсальная стенка мантии удалена без изменения положения внутренних органов [из Naef, 1923; с изменениями]. C. *E. dofleini*, вид с вентральной стороны. Мантия вскрыта с вентральной стороны вдоль средней линии, отделена от медиальной септы и расправлена, ventral view. Жабры и висцеральные органы удалены (кроме пищеварительной железы и желудка). Масштаб = 1 см.



IG. 21. Correlation of the shell vestiges with the soft parts in *Enteroctopus dofleini* (mature male: 180 mm ML). A. Lateral view. The skin, muscular mantle and the gill are removed from the left side. B. Enlarged fragment of figure 'A' showing attachment of muscles to the shell. Scale bar = 1 cm.

РИС. 21. Взаимоотношение между остатками раковины и мягким телом *Enteroctopus dofleini* (зрелый самец: 180 мм ДМ). А. Вид сбоку. С левой стороны удалены кожные покровы, мантия и жабры. В. Увеличенный фрагмент вида 'А', показывающий прикрепление мускулов к стилету. Масштаб = 1 см.

and along ventral midline. Pallial nerves are situated on dorsolateral sides of the visceral sac, between salivary glands and the head retractors (Fig. 22A). The mantle wall consists of two layers of muscular fibers separated by thin median layer of connective tissue. Ventrolateral walls of the mantle are slightly thicker than the dorsal wall. The funnel consists of three muscular folds: a ventral fold forming the ventral wall of the funnel, and a pair of lateral folds forming the dorsolateral walls of the funnel (Fig. 22A). Boundaries between ventral and lateral walls of the funnel are marked by the junction of muscular fibers of different orientation. The inner margins of dorsolateral walls of the funnel attach to collagen tunic of visceral sac. The muscular collar folds represent lateral extensions of the dorsolateral walls.

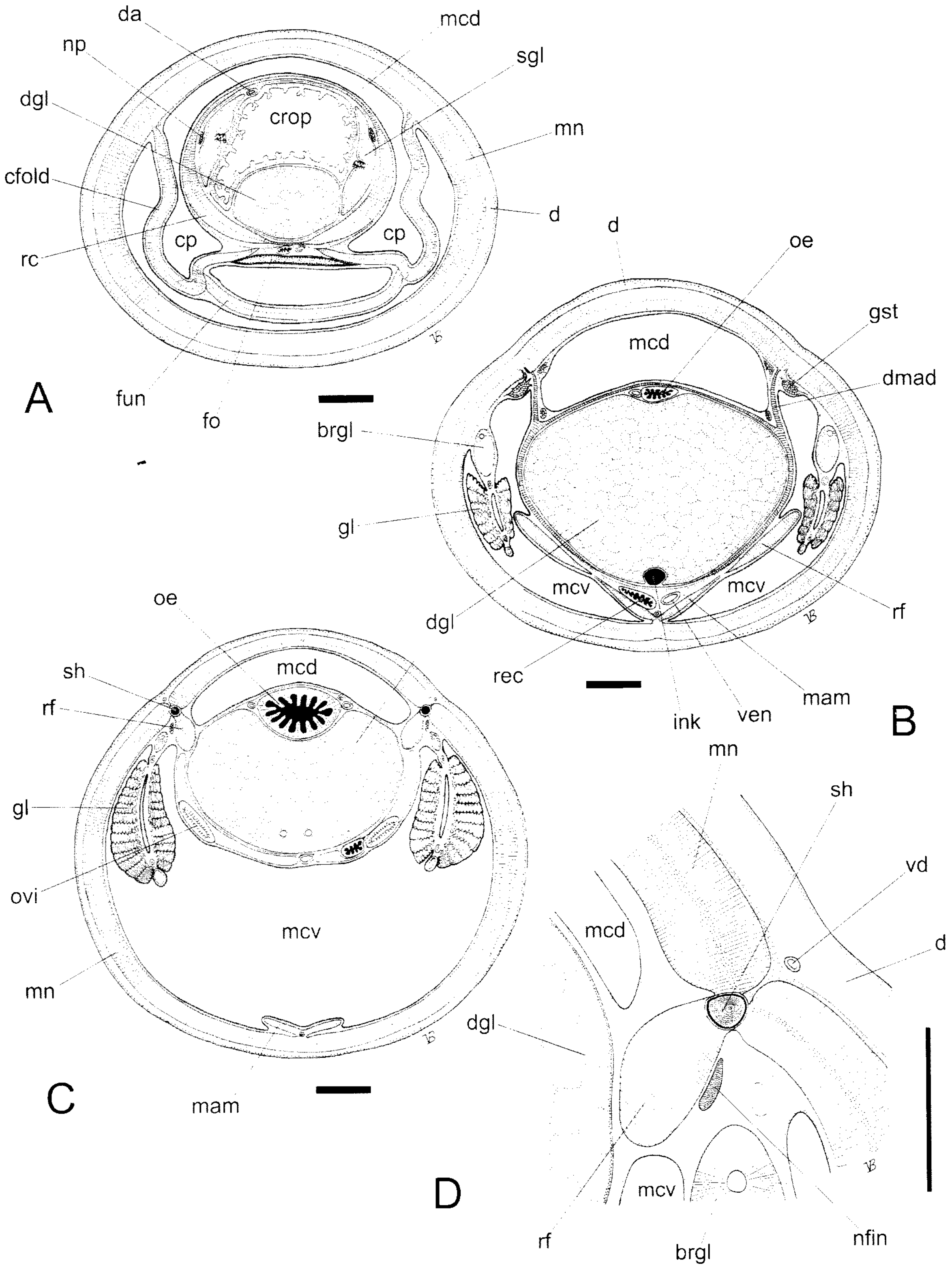


FIG. 22. Schematic cross-sections of *Enteroctopus dofleini* (female, 21 cm ML). A. Section 1, at the level of the funnel. B. Section 2, at the level of anterior dorsal mantle adductors. C. Section 3, at the level of attachment of the funnel retractors. D. Enlarged fragment of figure 'C' showing attachment of mantle and funnel retractor to the shell. The position of the sections is indicated on Fig. 20. Scale bars = 1 cm.

РИС. 22. Срезы мягкого тела *Enteroctopus dofleini* (самка: 21 см ДМ). А. Срез 1, на уровне воронки. В. Срез 2, на уровне передних дорсальных мантийных аддукторов. С. Срез 3, на уровне крепления вороночных ретракторов. D. Увеличенный фрагмент вида 'С', показывающий прикрепление мантийных мышц и вороночного ретрактора к стилету. Положение срезов показано на Рис. 20. Масштаб = 1 см.

They pass alongside the visceral sac and attach to dorsolateral walls of the mantle. Inner dorsal surface of the funnel canal is lined with a thick, glandular funnel organ.

At the level of anterodorsal adductors the head retractors are thinner, especially ventrally (Fig. 22B). The paired anterodorsal adductors are seen to arise from the head retractors. The anterodorsal adductors represent the only attachment sites of the head retractors to the mantle. Ventral median adductor is formed by two muscular layers diverging from the mantle wall to ventrolateral walls of the visceral sac. The ventral adductor straddle the rectum and vena cava. The funnel retractors are wide, flat and partly fused with ventrolateral walls of the visceral sac.

At the level of attachment of the funnel retractors the mantle reaches its greatest diameter. Visceral sac is relatively small here and occupies approximately half of the volume of the mantle cavity (Fig. 22C). Lateral sides of the visceral sac are fused with the funnel retractors which, in turn, attach to the stylets (Fig. 22D). The funnel retractors attach to the medial side of the stylets. Mantle walls attach to dorsal and ventrolateral sides of the stylets. The furrow between mantle muscles over the stylet is filled with dense connective tissue. Each "fin" nerve penetrates the mantle wall near the anterior shoulder of a stylet. The gill bases attach to mantle near the funnel retractors (Fig. 22D) and thus receive indirect support from the stylets.

COMMENTS. The most important function of stylets, one that determines their shape, is support of the funnel retractors. During contraction of the funnel retractors the bends of the stylets sustain the major load from the contraction forces. Visceral sac also receives indirect support from the stylets through the funnel retractors. The mantle attachment to the stylets apparently helps maintain some positioning between the viscera and the mantle.

Bathypolypodinae Robson, 1928

Benthoctopus sibiricus Loyning, 1930

HABITS AND HABITAT. Genus *Benthoctopus* includes about 26 species of deep-living, benthic octopods inhabiting continental shelf and slope of all oceans, from Arctic to sub-Antarctic [Nesis, 1982/1987]. Species of this genus occur at depths below 400 m in tropic and subtropic zones, while in the Arctic seas they ascend to the shelf and littoral [Nesis, 1982/1987]. Species of *Benthoctopus* are generally more fragile and less active animals than *Octopus*. *B. sibiricus* is the most cold-water and shallow-water species of this genus. It grows up to 180 mm ML and is known from the seas of Siberian Arctic and the Bering Sea [Nesis, 1982/1987].

SHELL MORPHOLOGY. Stylets in *Benthoctopus* are shorter, thicker and softer than in *Enteroctopus* (Fig. 23). They are embedded in dorsolateral mantle wall. The distance between anterior ends of the stylets is about 43% ML (Fig. 23A). Similar with *Enteroctopus*, the stylets consist of semi-transparent cartilage-like chitin laid down in concentric layers. The length of stylets ranges from 7.6% to 14% ML (mean length is 10%; SD=1.5), that is about two times smaller than in *Enteroctopus*. Each stylet has a bend in its anterior part that forms an obtuse angle (120°-130°). The bend is very prominent, thick, either dome-like or crest-shaped. At the bend the stylet reaches its greatest thickness that ranges from 8% to 30% of stylet length (mean ca. 16%; SD=4.6). The surface of the bend is faintly sculptured, while the rest surface of stylet is smooth. The anterior shoulder is curved, claw-like. Its length ranges from 16% to 46% of stylet length, averaging 33% (SD=6.3). The posterior shoulder is nearly straight, sharply pointed. The apical lines are rather distinct, especially in posterior shoulder.

The stylets in *Benthoctopus* exhibit greater variability in size and shape than in *Enteroctopus*. Among 25 specimens of *Benthoctopus* analyzed, three morphological types of stylets were found. The most abundant (14 specimens) were the stylets with high crest-like bend and long nearly straight anterior shoulder comprising 34% – 46% of stylet length (mean ca. 38%; SD=3.1) (Fig. 23D,E). The second in abundance (9 specimens) were thick stylets with massive dome-like bend and short anterior shoulder ranging from 25% to 35% of stylet length (mean ca. 31%; SD=3.3) (Fig. 23A). Rarely encountered (two specimens) were stylets with low bend and almost straight short anterior shoulder ranging from 16% to 18% of stylet length (Fig. 23C). Taxonomic status of above described morphological types is unclear. According to Nesis [1982/1987] and Kondakov et al. [1981], the genus *Benthoctopus* needs a revision, and *B. sibiricus* in the western Bering Sea may combine 2-3 undescribed species.

Variability between the left and the right stylets in *Benthoctopus* was also higher than in *Enteroctopus*. Although the average size of the left and the right stylets (in relation to the mantle length) was equal, the difference in length between them could reached up to 20%, difference in thickness — up to 21%, and difference in the length of anterior shoulder — up to 51%.

MICROSTRUCTURE OF THE STYLETS. Cross-sections of stylets at the level of the bend are roughly oval or slightly triangular in shape, consisting

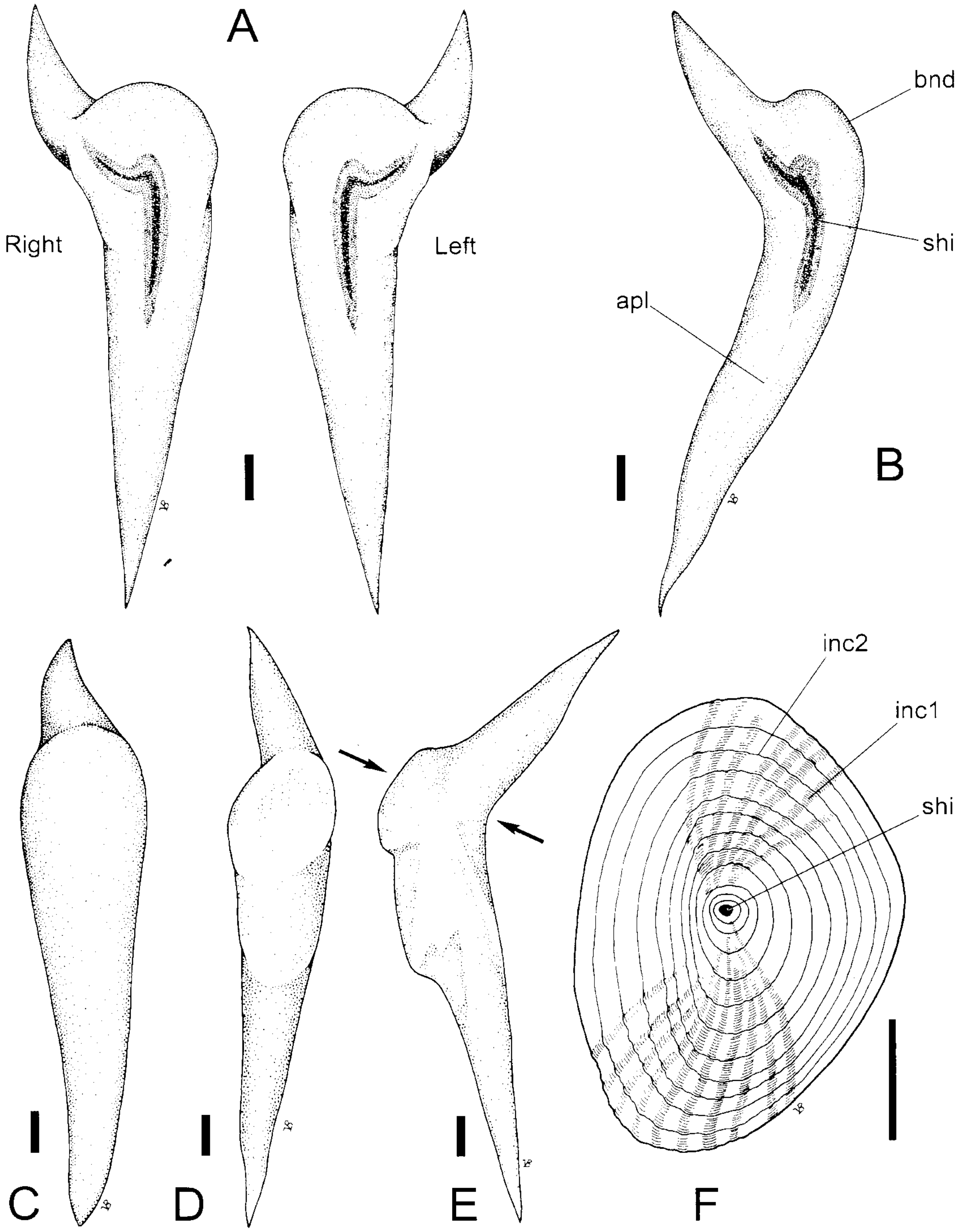


FIG. 23. Morphological variability of stylets in *Benthoctopus*. A. *B. sibiricus*. Ventral view of a pair of stylets from mature male (145 mm ML) (right stylet is on the left: anterior end is up). Note curvature of the stylets and conspicuous ventral angle in a shape of bulging dome. Dark initial shell is visible through semitransparent substance of the stylet. B. Left stylet from the same specimen: lateral view form the inner side (ventral side is on the right). C. *Benthoctopus sp.*: adult male (150 mm ML). Ventral view of a right stylet. D-F. Right stylet from *Benthoctopus sp.* adult male (173 mm ML). D.Ventral view (anterior end is up: outer side is on the left). E. Lateral view from the inner side (ventral side is on the left). Bold arrows indicate the plane of the cross-section shown in 'F'. F. Cross-section through the angle of the stylet (dorsal side is up: outer side is on the left). Scale bar = 1 mm.

РИС. 23. Морфологическая изменчивость стилетов *Benthoctopus*. A. *B. sibiricus*. Вид с вентральной стороны пары стилетов зрелого самца (145 мм ДМ): правый стилет слева: передняя сторона наверху. Угол стилета имеет вид широкого выпячивающегося купола. В центральной части стилета просвечивает темная зародышевая раковина. B. Левый стилет той же особи: вид сбоку с внутренней стороны (вентральная сторона справа). C. *Benthoctopus sp.*, взрослый самец (150 мм ДМ). Вид правого стилета с вентральной стороны. D-F. Правый стилет зрелого самца *Benthoctopus sp.* (173 мм ДМ). D. Вид с вентральной стороны (передний конец наверху: внешняя сторона слева). E. Вид сбоку с внутренней стороны (вентральная сторона слева). Стрелки указывают положение среза, изображенного на виде 'F'. F. Поперечный срез на уровне угла стилета (дорсальная сторона наверху: внешняя сторона слева). Масштаб = 1 мм.

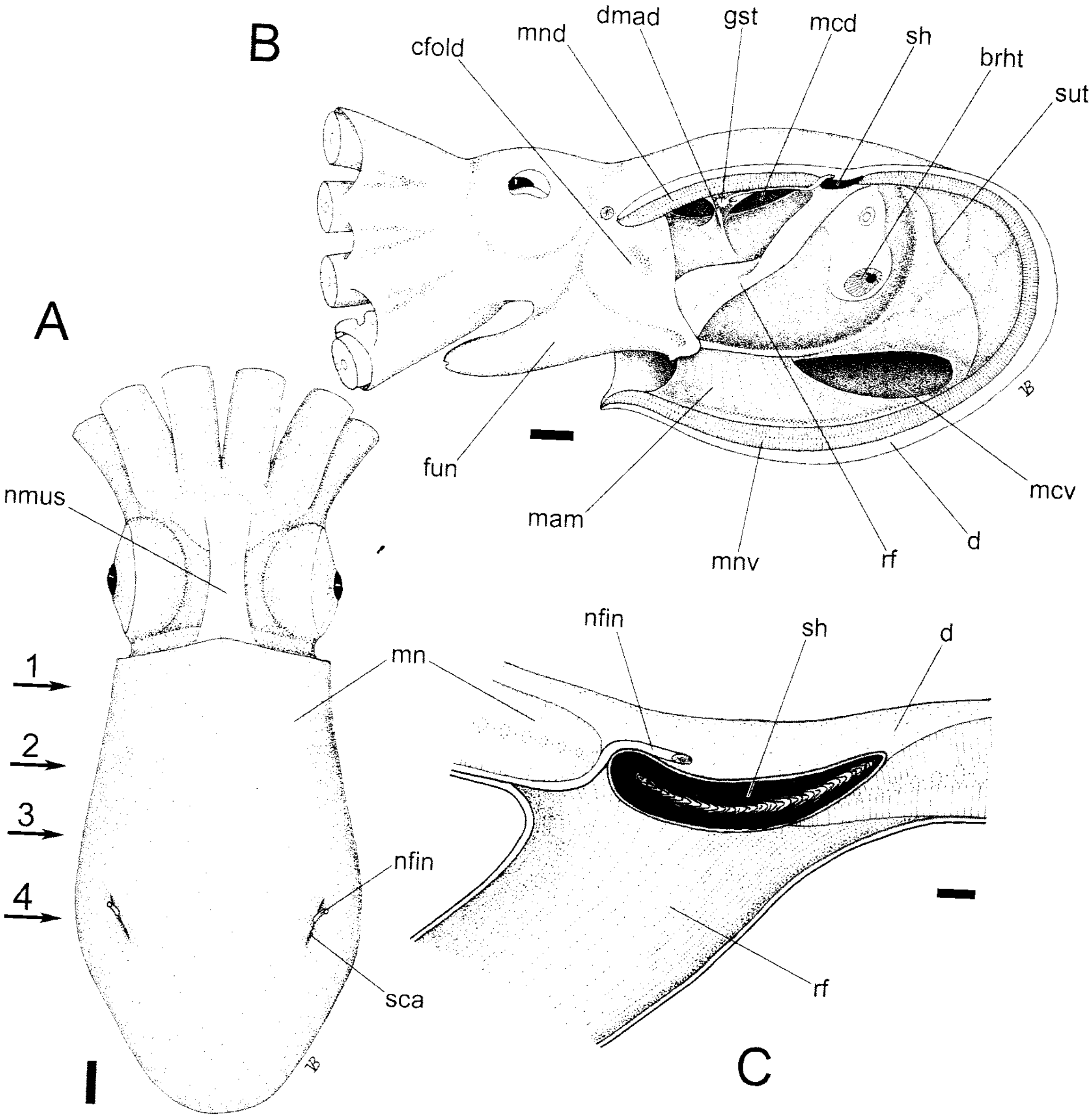


FIG. 24. General anatomy of *Benthoctopus sibiricus*. A. Adult male (115 mm ML), dorsal view. The skin is removed to show the outline of the mantle. Bold arrows with numbers indicate the planes of corresponding cross-sections (shown in Fig. 25). B. Same specimen: lateral view after removal of the mantle wall and the gill from the left side. C. Enlarged fragment of figure 'B' showing attachment of muscles to the left stylet. A and B: scale bar = 1 cm. C: scale bar = 1 mm.

РИС. 24. Строение *Benthoctopus sibiricus*. А. Взрослый самец (115 мм ДМ): вид с дорсальной стороны. Кожные покровы удалены, чтобы показать контуры мантии . Стрелки с цифрами указывают положение соответствующих срезов (показаны на Рис. 25). В. Вид сбоку той же особи (стенка мантии и жабры с левой стороны удалены). С. Увеличенный фрагмент вида 'В', показывающий крепление мышц к левому стилету. А и В: масштаб = 1 см. С: масштаб = 1 мм.

of numerous regular transparent concentric increments (Fig. 23F). Contours of previously formed increments are similar to the outer contour of the section, indicating that the stylet profile does not change significantly during growth. Microstructure of the increments is similar throughout the section. The growth zones are absent. Growth increments range in width from 6 to 14 μm, averaging 11 μm. The center of growth (initial shell) is situated close to the middle of the cross-section. It is round or oval, ranging from 80 to 160 μm in greater diameter. First-order increments are grouped into second-order cycles, from 8 to 35 increments in one cycle. Ventral side of the bend (in the bottom of the section) is covered by minute indistinct knobs. The knobs in *Benthoctopus* are less pronounced than in *Enteroctopus* and

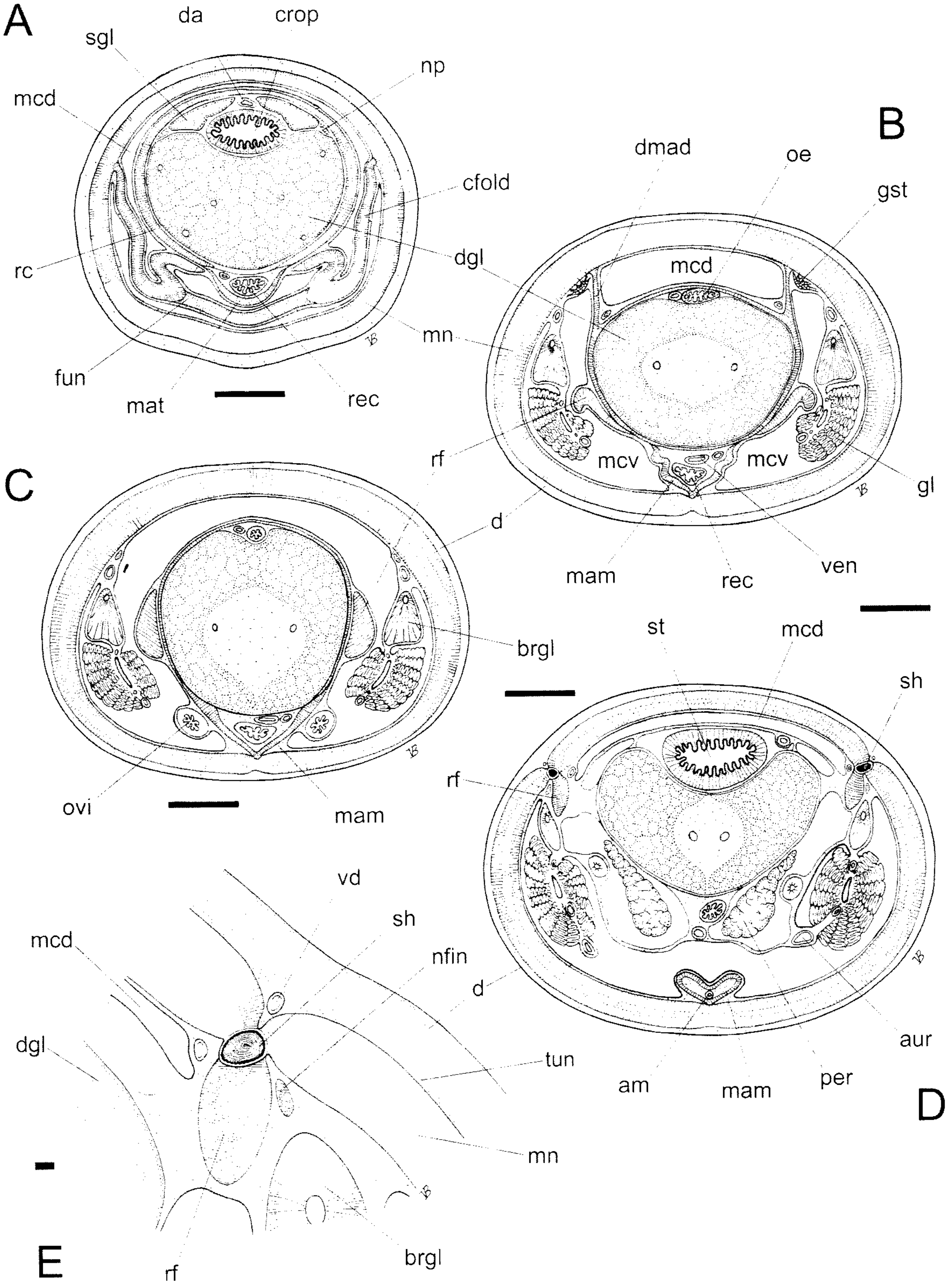


FIG. 25. Schematic cross-sections of the soft body in *Benthoctopus sibiricus* (maturing female: 90 mm ML). A. Section 1. at the level of the funnel. B. Section 2. at the level of dorsal mantle adductors. C. Section 3. behind anterior dorsal adductors. D. Section 4. at the level of attachment of the funnel retractors. E. Enlarged fragment of figure 'D' showing attachment of the mantle and funnel retractor to the shell. Position of sections is indicated on Fig. 24. A-D: scale bar = 1 cm. E: scale bar = 1 mm.

РИС. 25. Срезы мягкого тела *Benthoctopus sibiricus* (созревающая самка: 90 мм ДМ). A. Срез 1. на уровне воронки. B. Срез 2. на уровне дорсальных мантийных аддукторов. C. Срез 3. позади дорсальных мантийных аддукторов. D. Срез 4. на уровне пркрепления ретракторов воронки. E. Увеличенный фрагмент вида 'D', показывающий прикрепление мантии и ретрактора воронки к стилету. Положение срезов показано на Рис. 24. A-D: масштаб = 1 см. E: масштаб = 1 мм.

occupy minor part of the section. The knobs can be traced on previously formed increments as radial marks, forming a sector of about 60°.

EXTERNAL MORPHOLOGY. The body in *Benthoctopus* is more gentle and less muscular than in *Enteroctopus*. The mantle is elongated oval. The nuchal muscle is well developed spreading from the mantle margin toward the bases of arms I (Fig. 24A). The mantle wall is the most thick in anterior part, gradually becoming thinner posteriorly. The dorsal and the ventral mantle walls are approximately equal in thickness. The mantle aperture is narrower than in *Enteroctopus*, its lateral margins are situated below the eyes (Fig. 24B). Posteroventral margin of the funnel rests against the ventral mantle adductor. The mantle cavity is occupied almost entirely by the visceral sac. Free space of the ventral mantle cavity is greatly reduced as compared with *Enteroctopus*. The ventral median-mantle adductor is wide. The anterodorsal mantle adductors are situated at some distance from posterior margins of the collar folds. The funnel is narrow and long, reaching the bases of the ventral arms. A funnel locking-apparatus is absent. The funnel retractors are narrower and longer than in *Enteroctopus*. They attach to the stylets in a similar way as in *Enteroctopus* (Fig. 24C). The "fin" nerves start off the stellar ganglia, run posteriorly toward attachment of the funnel retractors and pierce the dorsal mantle wall near anterior ends of the stylets.

CROSS-SECTIONS. The mantle and the funnel consist of two surface muscular layers separated by thick middle layer of vacuolated connective tissue (Fig. 25). The dermal integument is smooth, thick and gelatinous, especially near the posterior apex of the mantle. The mantle cavity is relatively small; its ventral part is larger than the dorsal one. In the region between anterodorsal and posterodorsal adductors the dorsal and ventral parts of the mantle cavity merge alongside the visceral sac (Fig. 25C).

The visceral sac is large at the level of the collar folds, occupying most part of the mantle cavity (Fig. 25A). Pallial nerves are situated on dorso-lateral sides of the visceral sac, between salivary glands and the digestive gland (Fig. 25A). The rectum and the vena cava are situated on ventral side of the sac, projecting inside the funnel canal. The ink sac is absent.

The head retractors make muscular walls of the visceral sac at the level of the funnel (Fig. 25A). The thickness of head retractors is less than in *Enteroctopus*. The anterodorsal adductors differentiate from the head retractors at the level of the stellate ganglia (Fig. 25B). At this level the head retractors become thinner, especially on the ventral side of the visceral sac. The stellate ganglia are relatively small. They are situated on the mantle wall, laterally from the anterodorsal adductors. Posteriorly the head retractors extend to the level of the mantle septum (Fig. 25C).

The median mantle septum consists of two thin adductor muscles diverging in V-like pattern from the ventral mantle wall to ventro-lateral walls of visceral sac (Fig. 25B,C). Inner space between the adductor muscles contains the vena cava and the rectum. Anterior extensions of the adductors extend anteriorly forming a part of the dorsal funnel wall (Fig. 25A).

The muscular portion of the funnel in its anterior part consists of a single muscular layer. In posterior part of the funnel, boundaries between its ventral and lateral walls are marked by the junction of muscular fibers with different orientation (Fig. 25A). The muscular collar folds originate as extensions of dorsolateral walls of the funnel and attach to dorsolateral walls of the mantle.

The funnel retractors originate as posterior extensions of the dorsolateral walls of the funnel (Fig. 25B). They run obliquely alongside the visceral sac and attach to the stylets embedded in the dorsolateral walls of the mantle (Fig. 25D). The funnel retractors are wide and thick. Inner side of the funnel retractors attach to the lateral walls of the visceral sac along their entire length.

At the level of attachment of the funnel retractors the stylets, like in *Enteroctopus*, provide support for the mantle, funnel retractors and gills (Fig. 25D). The visceral sac is the largest here, occupying the mantle cavity almost entirely. The funnel retractors attach to the medial inner side of the stylets (Fig. 25E). Mantle walls attach to dorsolateral sides of the stylets, leaving narrow furrows over them. The visceral sac attach to inner side of the funnel retractors, while the gill bases attach to the outer side of the funnel retractors.

COMMENTS. Relative size of stylets in *Benthoctopus* is much smaller than in *Enteroctopus*, comprising in adults 7-14% ML and 20-31% ML, respectively. Adhesion of the funnel retractors to the stylets in *Benthoctopus* is weaker. If one tries to tear the funnel retractors off the mantle in fresh animals, in *Enteroctopus* they usually detach together with stylets attached to them, while in *Benthoctopus* the stylets as a rule remain inside the mantle wall. But the most important sign of vestigial state of the stylets in *Benthoctopus* is their high morphological variability, especially variability between left and right stylet of the same specimen. Such variability could not be possible in functionally important structure. It testifies that the stylets in *Benthoctopus* are not anymore the subjects for stabilizing pressure of natural selection. Thus, *Benthoctopus* represents an example of octopod with greatly reduced shell, which apparently was stipulated by the general decrease of animal activity.

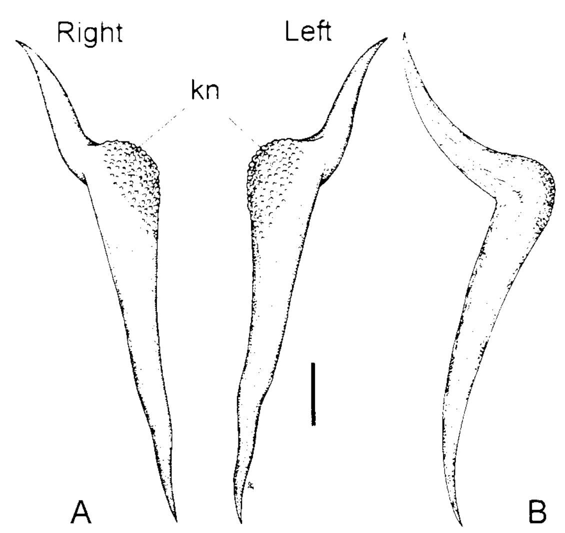


FIG. 26. Stylets in *Bathypolypus salebrosus* (female: 47 mm ML). A. Ventral view of a pair of stylets: right stylet is on the left: anterior end is up. B. Lateral (outer) view of the right stylet (ventral side if on the right: anterior end is up). Scale bar = 1 mm.

РИС. 26. Стилеты *Bathypolypus salebrosus* (самка: 47 мм ДМ). А. Вид пары стилетов с вентральной стороны: правый стилет слева: передняя сторона наверху. В. Вид с боку (снаружи) правого стилета (вентральная сторона справа: передний конец наверху). Масштаб = 1 мм.

Bathypolypus salebrosus (Sasaki, 1920)

HABITS AND HABITAT. *B. salebrosus* is a small (up to 50 mm ML) deep-water benthic octopus that is typically found at depths 150-600 m in the Okhotsk Sea, Bering Sea, off the eastern coasts of the Kurile Islands, Hokkaido and Honshu [Nesis, 1982/1987]. In the Bering Sea it mostly occurs on mud bottom of the continental shelf and slope. Biology and ecology of this species are poorly known.

SHELL MORPHOLOGY. Stylets in *Bathypolypus* are two cartilage-like chitin rods with prominent thickened bend in anterior part (Fig. 26). They lie on dorsolateral sides of the mantle at a sharp angle to the body axis (Fig. 27A). The length of stylets in adult octopuses comprises approximately 17% ML. Distance between stylets at the level of their anterior ends is about 52% ML. The bend between anterior and posterior shoulders is very prominent, ranging between 110° and 115°. Apex of the bend is thick, dome-shaped, bearing distinct knob-like sculpture. The greatest thickness of each stylet (at the level of the bend) comprises approximately 14% of stylets length. Anterior shoulder is about two times shorter than posterior. Both shoulders are thick, smooth and pointed. Posterior shoulder is faintly curved in zigzag pattern.

MICROSTRUCTURE OF THE STYLETS. The growth pattern of stylets is similar to that in *Enteroctopus* and *Benthoctopus*. The stylets grow by concentric layers. The initial shell is situated in the area of the bend. Apices of growth increments form apical lines visible through semitransparent substance of stylets.

EXTERNAL MORPHOLOGY. The mantle is wide, globular and covered by densely spaced dermal papillae (Fig. 27). It is the most thick in its anterior part, gradually becoming thinner posteriorly. Dorsal mantle wall is the thickest in the region of the dorsal mantle cavity; the ventral mantle wall is the thickest in the region of the ventral mantle adductor. Mantle aperture is wide. Its lateral margins are situated below the eyes. The ventral median-mantle adductor is thick, muscular and rather narrow. Its anterior margin is at some distance from ventral margin of the mantle (Fig. 27B). The funnel is short, conical. It arises deep within the mantle cavity, and its posteroventral margin rests against the ventral mantle adductor. A funnel locking-apparatus is absent. The posteriorlateral walls of the funnel pass into muscular collar folds. The funnel retractors are wide and ribbon-shaped. They run obliquely from posterior corners of the funnel toward the stylets embedded into dorsolateral walls of the mantle. Visceral sac is very large. The anterodorsal mantle adductors are shifted anteriorly to the level of collar folds (Fig. 27B). Each adductor undergoes an 180° twist so that the anterior-most margin at the visceral sac becomes the posterior-most margin at the attachment to the mantle wall.

CROSS-SECTIONS. The walls of mantle and funnel consist of two layers of muscular fibers separated by thin median layer of connective tissue (Fig. 28). The mantle and funnel are more muscular than in *Benthoctopus*. The lateral walls of the mantle are slightly thicker than the dorsal and ventral walls. The mantle cavity is approximately the same size as in *Benthoctopus*: its dorsal part is smaller than the ventral one. The dorsal mantle cavity is best developed in the area of collar folds, extending posteriorly to the level of the stylets (Fig. 28D). The ventral mantle cavity is the largest immediately behind the funnel (Fig. 28A,B) extending posteriorly to the level of gonads. In the region between the anterodorsal and posterodorsal adductors the dorsal and ventral parts of the mantle cavity merge alongside the visceral sac (Fig. 28C). The visceral sac occupies about of the mantle cavity reaching the greatest size at the level of attachment of the funnel retractors (Fig. 28D). The pallial nerves are very large, oval in cross-section and situated between salivary glands and the head retractors (Fig. 28A). Between the anterodorsal and posterodorsal adductors the visceral sac is occupied mainly by large digestive

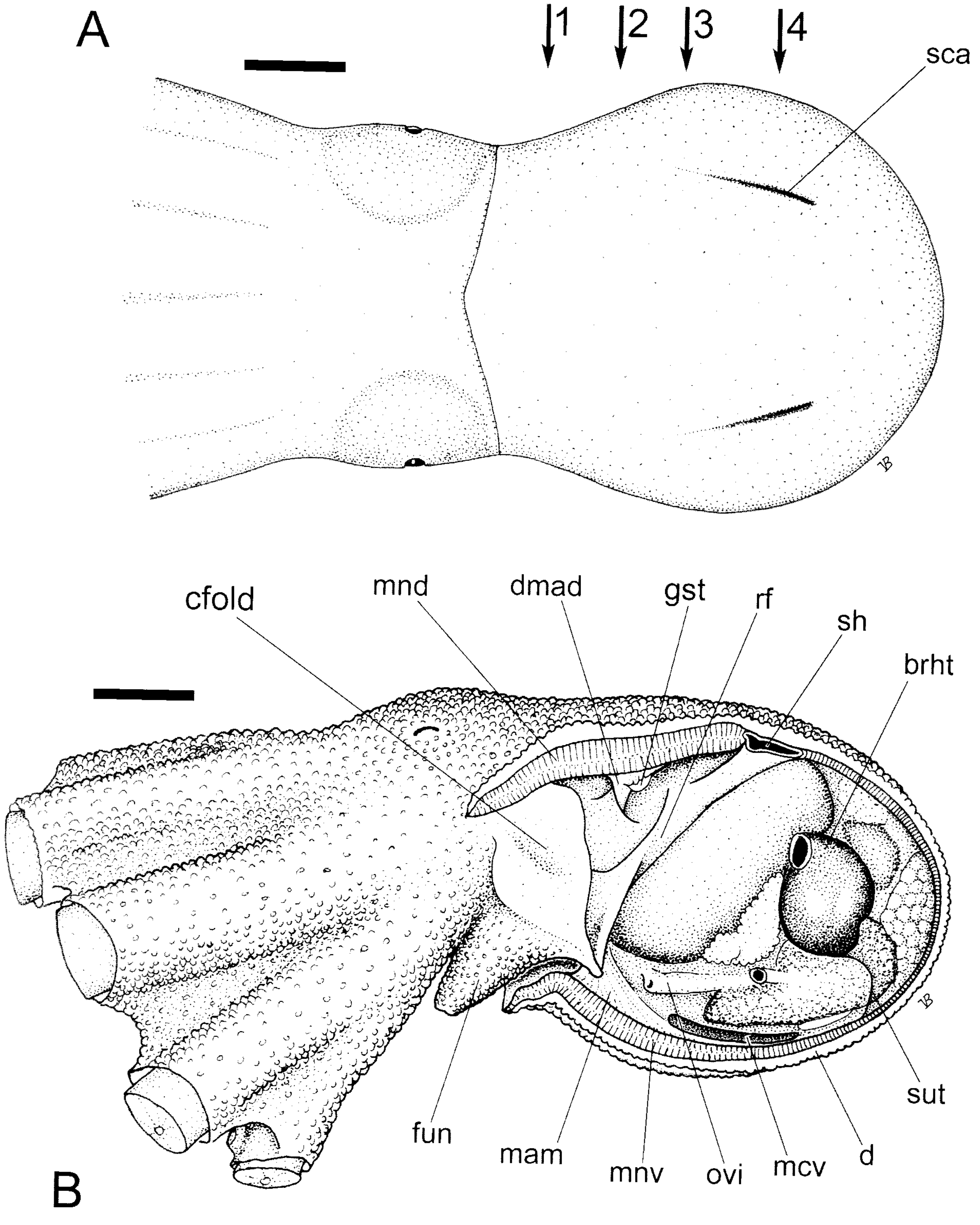


FIG. 27. General anatomy of *Bathypolypus salebrosus*. A. Adult female (47 mm ML), dorsal view. The skin is removed to show the outline of the mantle. Bold arrows with numbers indicate the planes of corresponding cross-sections (shown in Fig. 28). B. Adult female (50 mm ML), lateral view after removal of the mantle wall and gill from the left side. Scale bar = 1 cm.

РИС. 27. Строение *Bathypolypus salebrosus*. А. Взрослая самка (47 мм ДМ), вид с дорсальной стороны. Кожные покровы удалены, чтобы показать контуры мантии. Стрелки с цифрами указывают положение соответствующих срезов (показаны на Рис. 28). В. Взрослая самка (50 мм ДМ); вид сбоку после удаления мантии и жабры с левой стороны. Масштаб = 1 см.

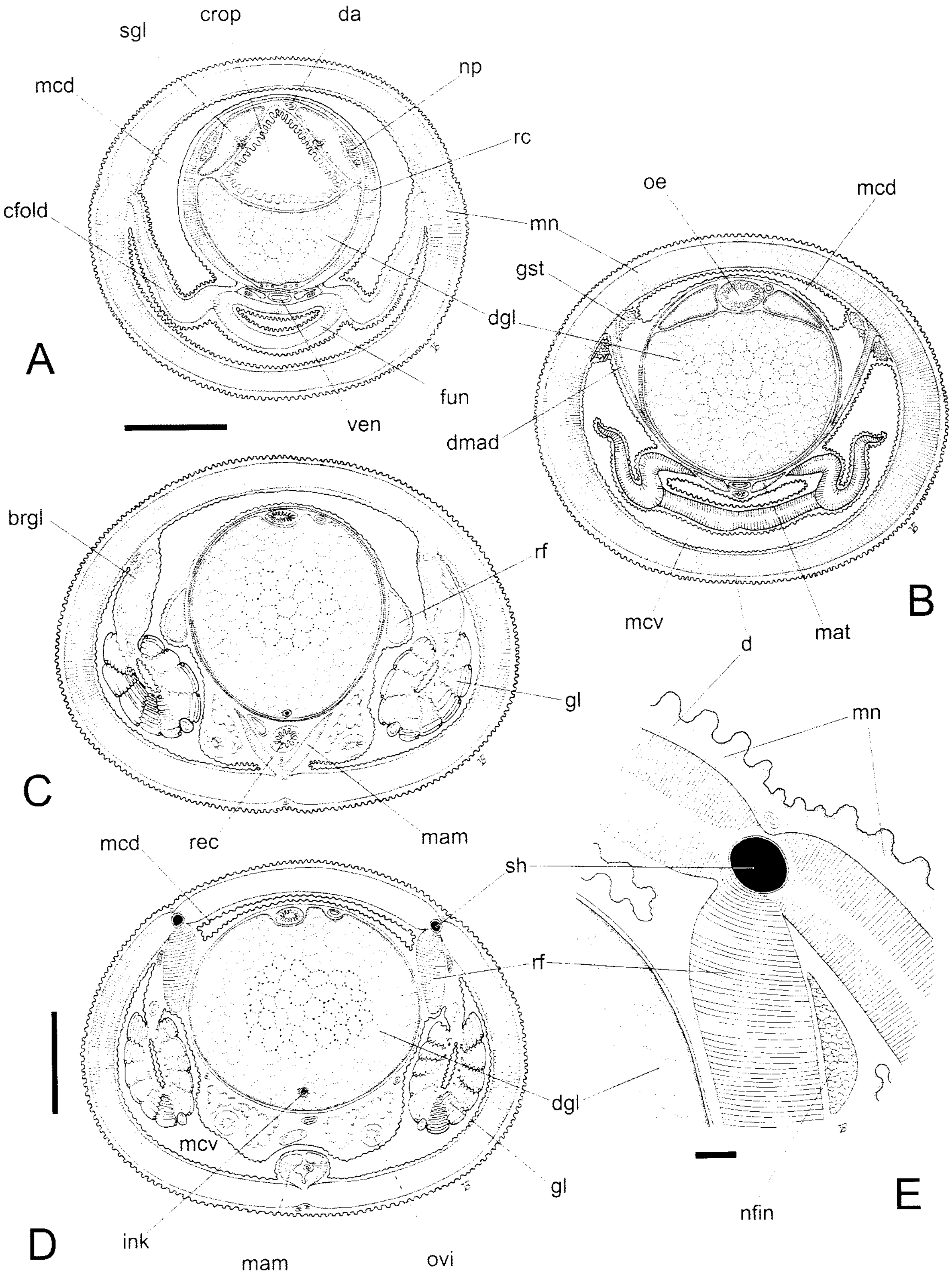


FIG. 28. Schematic cross-sections of the soft body in *Bathypolypus salebrosus* (adult female; 54 mm ML). A. Section 1, at the level of anterior part of the funnel. B. Section 2, at the level of anterior dorsal mantle adductors (posterior part of the funnel). C. Section 3, behind anterior dorsal mantle adductors. D. Section 4, at the level of attachment of the funnel retractors. E. Enlarged fragment of figure 'D' showing attachment of the mantle and funnel retractor to the shell. Position of sections is indicated on Fig. 27. A-D: scale bar = 1 cm. E: scale bar = 1 mm.

РИС. 28. Срезы мягкого тела *Bathypolypus salebrosus* (взрослая самка: 54 мм ДМ). А. Срез 1, на уровне передней части воронки. В. Срез 2, на уровне передних дорсальных мантийных аддукторов (задняя часть воронки). С. Срез 3, позади дорсальных мантийных аддукторов. D. Срез 4, на уровне прикрепления ретракторов воронки. Е. Увеличенный фрагмент вида 'D', показывающий прикрепление мантии и ретрактора воронки к стилету. Положение срезов указано на Рис. 27. A-D: масштаб = 1 см. Е: масштаб = 1 мм.

gland (Fig. 28C). The ink sac is absent. Posterior to the stylets the visceral sac is fused with the mantle.

The head retractors make thick muscular walls of the visceral sac at the level of the funnel (Fig. 28A). Posteriorly they gradually become thinner. The anterodorsal adductors separate from the head retractors at the level of the stellate ganglia (Fig. 28B). The stellate ganglia are larger than in *Benthoctopus*. They lie on the lateral mantle walls ventrally from the attachment of anterodorsal adductors. The anterodorsal adductors are unusually thick and run obliquely upward from ventrolateral sides of the visceral sac to the dorsolateral walls of the mantle. Each adductor is surrounded by thick gelatinous dermal integument. Posterior extensions of inner layers of the head retractors can be traced behind the anterodorsal adductors as thin muscular envelope of the visceral sac (Fig. 28C).

The median mantle septum consists of two thick adductor muscles diverging in a V-like pattern from the midline of the ventral mantle wall (Fig. 28C). Anterior extensions of the adductors extend anteriorly forming a part of the dorsal funnel wall and the wall of the visceral sac (Fig. 28B).

The muscular portion of the funnel in its anterior part consists of a single circular muscular layer (Fig. 28A). In posterior part of the funnel, boundaries between its ventral and lateral walls are marked by the junction of muscular fibers of different orientation (Fig. 28B). The collar folds originate as extensions of the dorsolateral walls of the funnel and attach to dorsolateral walls of the mantle. The funnel retractors originate as posterior extensions of dorsolateral walls of the funnel (Fig. 28B). They run obliquely alongside of the visceral sac and attach to the stylets embedded in the dorsolateral walls of the mantle (Fig. 28D). Inner sides of the funnel retractors attached to the lateral walls of the visceral sac along their entire length.

The stylets are enclosed into thick cartilaginous shell sac (Fig. 28E). The funnel retractors attach to the ventral side of the stylets, while the mantle attaches to their lateral sides leaving wide break on their dorsal surface. At the level of attachment of the funnel retractors the gills attach to the funnel retractors ventral to the stylets (Fig. 28D).

COMMENTS. The stylets in *Bathypolypus* fit well into the row of gradual reduction of the shell in Octopodidae occupying intermediate position between well developed stylets of *Enteroctopus* and vestigial ones of *Benthoctopus*. Relative length of the stylets in *Bathypolypus* (17%) is somewhere between that of *Enteroctopus* (20-32% ML) and *Benthoctopus* (7.6—14%). Sculptured knob-like surface of the bend in the stylets of *Bathypolupys* indicate that these structures provide substantial support for the funnel retractors, unlike soft and smooth stylets in *Benthoctopus*. On the other hand, the stylets in *Bathypolypus* could not be as effective supporting structures as in *Enteroctopus* due to their small size and softer consistency.

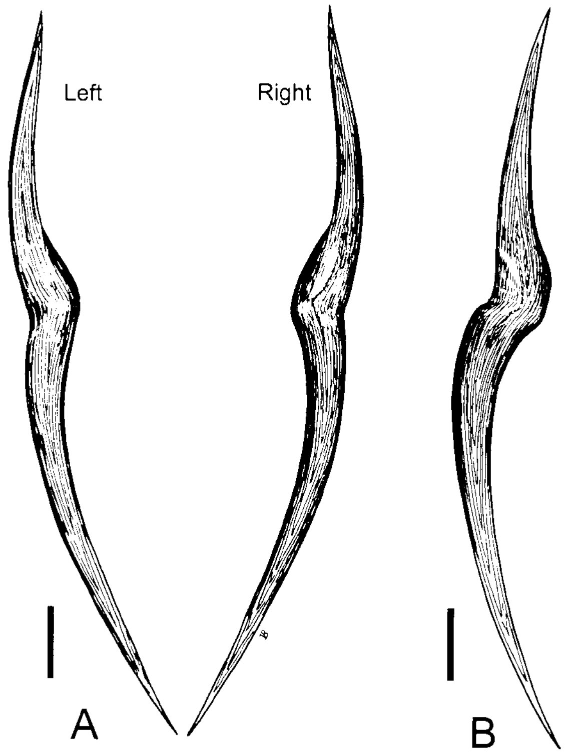


FIG. 29. Stylets in *Eledone messyae*. A. Dorsal view of a pair of stylets from adult male (63 mm ML); anterior end is up. B. Lateral (outer) view of the right stylet of the same specimen (ventral side if on the right; anterior end is up). Scale bar = 1 mm.

РИС. 29. Стилеты *Eledone messyae*. А. Вид с дорсальной стороны пары стилетов зрелого самца (63 мм ДМ); передняя сторона наверху. В. Вид сбоку (снаружи) правого стилета той же особи (вентральная сторона справа; передний конец наверху) Масштаб = 1 мм.

Eledoninae Grimpe, 1921

Eledone messyae Voss, 1964

HABITS AND HABITAT. Little is known about habitat and biology of *E. messyae*. According to Nesis [1982/1987], it is a benthic species inhabiting upper shelf of Brazil, Uruguay, Argentina and Trinidad Island in depth range from 30 m to 160 m. It is a small octopod, growing up to 75 mm in mantle length [Roper *et al.*, 1984].

SHELL MORPHOLOGY. The stylets are long, slender and needle-shaped chitin rods lying on the dorsolateral side of the mantle (Fig. 29). They are set widely apart from one another: distance between the stylets at the level of their anterior ends is about 80% ML (Fig. 30A). The length of stylets comprises approx-

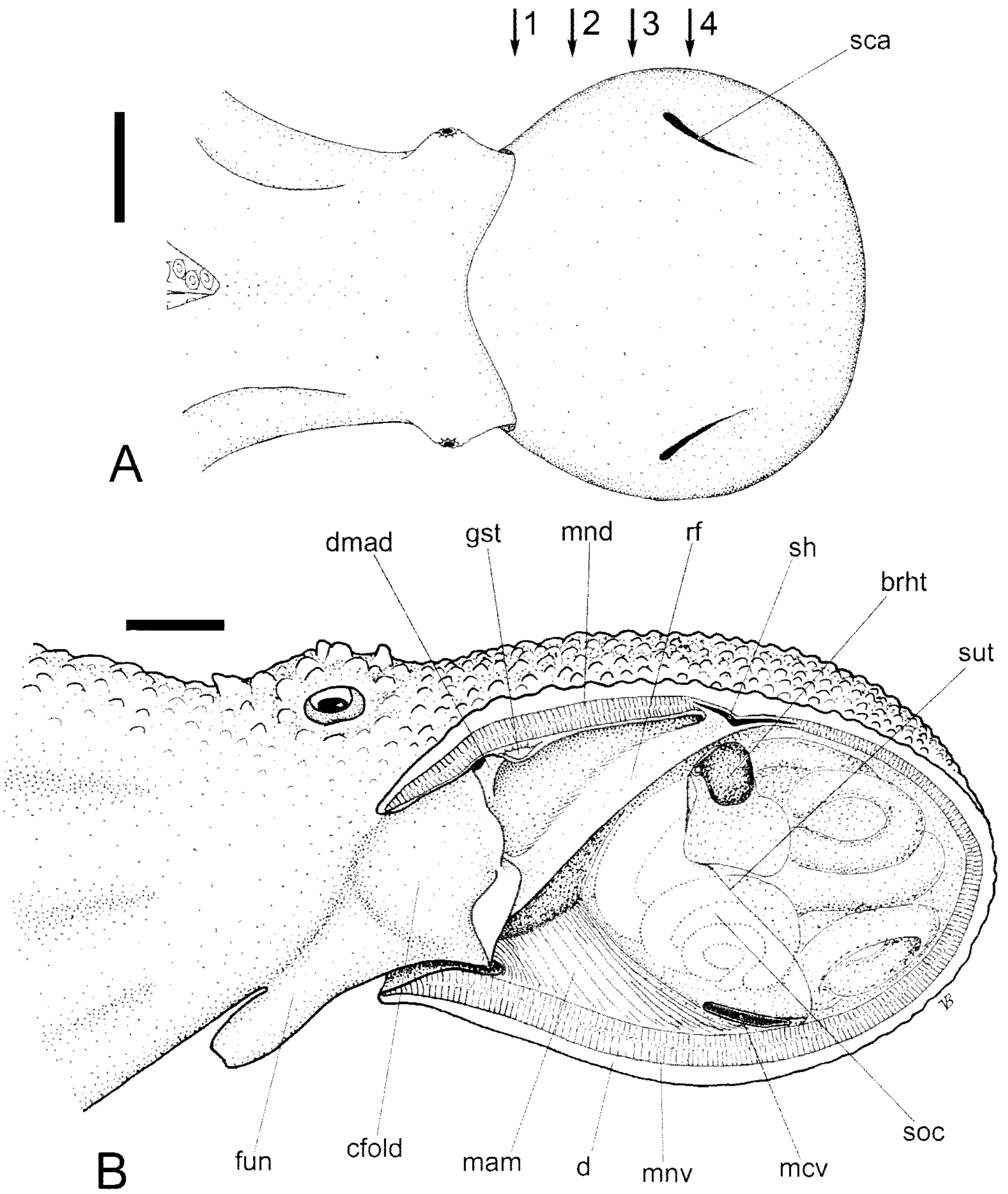


FIG. 30. General anatomy of *Eledone messyae*. A. Dorsal view of a maturing female (35 mm ML). The skin is removed to show the outline of the mantle. Bold arrows with numbers indicate the planes of corresponding cross-sections (shown in Fig. 31). B. Lateral view of an adult male (63 mm ML) after removal of the mantle wall and gill from the left side. Scale bar = 1 cm.

РИС. 30. Строение *Eledone messyae*. А. Дорсальный вид созревающей самки (35 мм ДМ). Кожные покровы удалены, чтобы показать контур мантии. Стрелки с цифрами указывают положение соответствующих срезов (показаны на Рис. 31). В. Вид сбоку (взрослый самец; 63 мм ДМ) после удаления стенки мантии и жабры с левой стороны. Масштаб = 1 см.

imately 17% ML. The bend is low, obtuse, ranging from 125° to 130°. Surface of the bend is smooth, as well as the rest of the stylets. Greatest thickness of stylets is situated at the level of the bend comprising about 7% stylet length. Anterior and posterior shoulders are slightly arched inside the mantle. The anterior shoulder is relatively long, approximately 40% of stylet length. The distal part of both shoulders is straight, without zigzag curvature.

MICROSTRUCTURE OF THE STYLETS. Microstructure of the stylets is essentially the same as in *Benthoctopus*. The stylets grow by concentric layers of semitransparent chitin. The initial shell is situated in the area of the bend. Growth increments and apical lines are clearly visible inside both shoulders in transmitting light.

EXTERNAL MORPHOLOGY. The mantle is wide, globular and covered by thick gelatinous dermal integument with prominent papillae on the dorsal side (Fig. 30). It is the most thick in its anterior

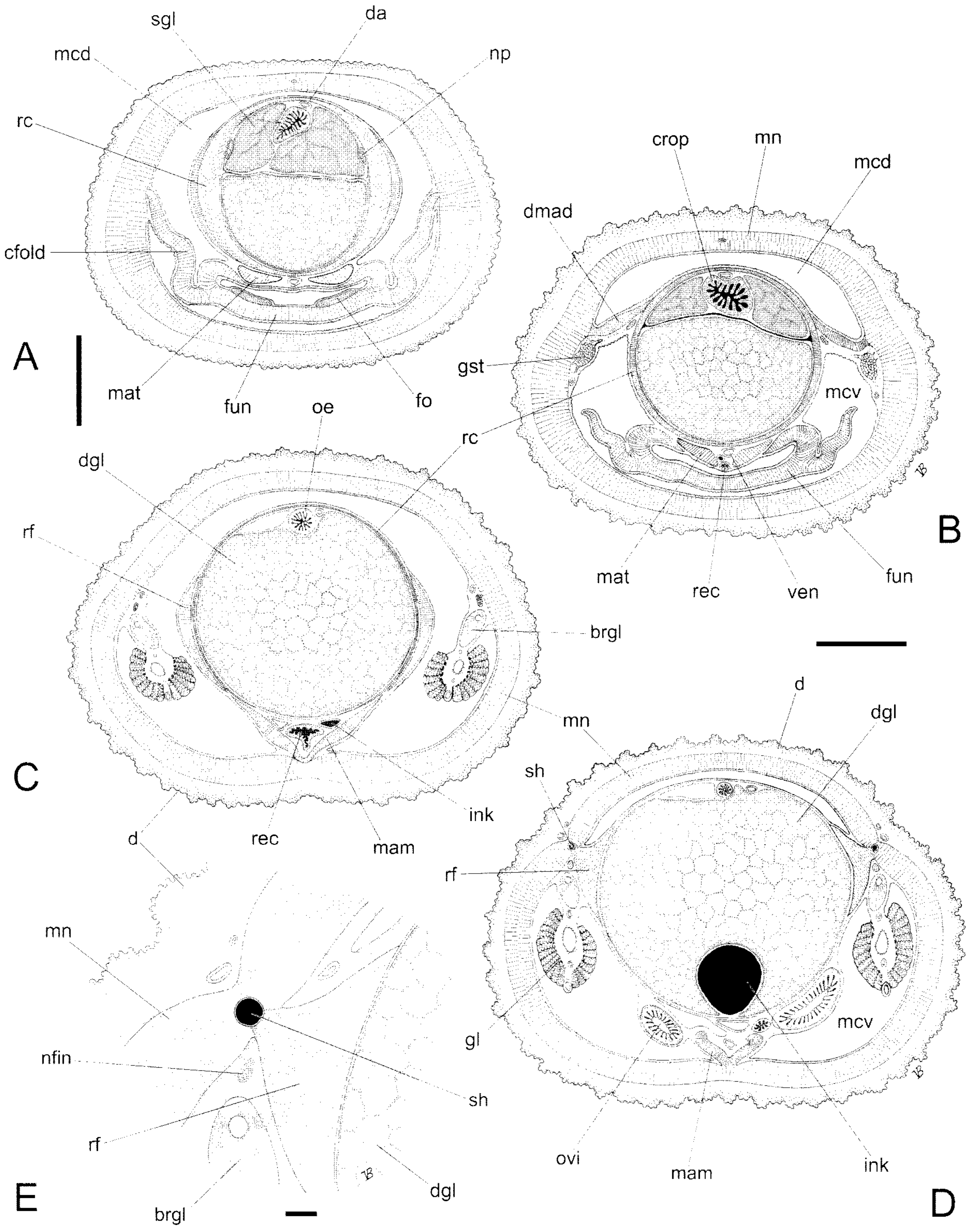


FIG. 31. Schematic cross-sections of the soft body in *Eledone massyae* (maturing female: 35 mm ML). A. Section 1, at the level of anterior part of the funnel. B. Section 2, at the level of anterior dorsal mantle adductors (posterior part of the funnel). C. Section 3, behind anterior dorsal mantle adductors. D. Section 4, at the level of attachment of the funnel retractors. E. Enlarged fragment of figure 'D' showing attachment of the mantle and funnel retractor to the left stylet. Position of sections is indicated on Fig. 30. A-D: scale bar = 1 cm. E: scale bar = 1 mm.

РИС. 31. Срезы мягкого тела *Eledone massyae* (созревающая самка; 35 мм ДМ). А. Срез 1, на уровне передней части воронки. В. Срез 2, на уровне передних дорсальных мантийных аддукторов (задняя часть воронки). С. Срез 3, позади дорсальных мантийных аддукторов. D. Срез 4, на уровне крепления ретракторов воронки. Е. Увеличенный фрагмент вида 'D', показывающий крепление мантии и ретрактора воронки к левому стилету. Положение срезов показано на Рис. 30. A-D: масштаб = 1 см. Е: масштаб = 1 мм.

part. gradually becoming thinner posteriorly. Lateral walls of the mantle are thicker than dorsal and ventral walls. The mantle aperture is relatively small: its lateral margins are situated well below the eyes. The ventral median-mantle adductor is thick and wide. It attaches to the visceral sac from the level of the anterodorsal adductors to the level of the stylets (Fig. 30B). Anterior margin of the ventral median-mantle adductor is at some distance from ventral margin of the mantle. The funnel is long, tube-like, fused with the head approximately along of its length. The funnel arises deep within the mantle cavity, and its posteroventral margin rests against the ventral mantle adductor. A funnel-mantle locking apparatus is absent. The funnel retractors are long, wide, ribbon-like. The anterodorsal adductors are situated at the level of posterior margins of the collar folds. They have a shape of short ribbon-like muscular ligaments twisted in the same way as in other Incirrata. The visceral sac is fused with the mantle posterior from the level of the stylets (Fig. 30B).

CROSS-SECTIONS. The walls of mantle and the funnel consist of two thick surface muscular layers separated by very thin layer of connective tissue (Fig. 31). In anterior part of the mantle its lateral walls are slightly thicker than dorsal and ventral walls. The dermal integument is very thick. Its surface bears prominent papillae covering the mantle entirely. The mantle cavity is relatively small. At the level of the funnel the dorsal mantle cavity is larger than the ventral one. Posterior from the funnel the dorsal mantle cavity is smaller than the dorsal one. Between the anterodorsal and posterodorsal mantle adductors both ventral and dorsal mantle cavities are fused together alongside the visceral sac (Fig. 31C). The visceral sac is relatively small in anterior part becoming very large posteriorly. Between the anterodorsal and posterodorsal mantle adductors the visceral sac is occupied mainly by large digestive gland (Fig. 31C,D). The ink sac is in unusual position, deeply embedded inside digestive gland from the ventral side.

Head retractors make thick muscular walls of the visceral sac at the level of the funnel (Fig. 31 A). At this level they consist of thick inner and thin outer muscular layers. The anterodorsal adductors differentiate from the outer layer of the head retractors at the level of the stellate ganglia (Fig. 31B). The anterodorsal adductors are unusually oriented running obliquely downward from dorso-lateral walls of the visceral sac to lateral walls of the mantle. The stellate ganglia are large, situated on lateral walls of the mantle just below the sites of attachment of the anterodorsal adductors. Posteriorly the head retractors extend to the level of the median mantle septum (Fig. 31C). The median mantle septum consists of two thick adductor muscles diverging in a V-like pattern from the midline of the mantle toward the visceral sac. Inner space between the adductor muscles contains the duct of the ink sac, vena cava and the rectum. Anterior extensions of the median mantle adductor form a part of the dorsal funnel wall (Fig. 31A,B).

The muscular portion of the funnel consists of single circular muscular layer (Fig. 31A,B). The collar folds originate as extensions of the lateral walls of the funnel and attach to lateral walls of the mantle. The funnel retractors originate as posterior extensions of dorsolateral walls of the funnel. They are thin, flat and ribbon-like in the middle part, gradually becoming thicker posteriorly (Fig. 31C). Inner side of the funnel retractors is attached to the visceral sac. At the sites of attachment to the stylets the funnel retractors are thick, wide and triangular in cross-section (Fig. 31D). The wide medial side of each base attaches to lateral side of the visceral sac, while the narrow outer apex attaches to the medial half of the stylet (Fig. 31D,E). The stylets are embedded deep inside the mantle wall. Their greatest diameter is about 1/3 the thickness of the mantle wall. The mantle attaches to the dorsolateral sides of the stylets while the funnel retractors attach to the ventral side of the stylets (Fig. 31E). The "fin" nerve is small, passing between the funnel retractor and mantle wall, ventrally from the stylets. The gills attach to the mantle wall ventral from the stylets.

COMMENTS. Extremely narrow needle-like shape differs the stylets in *Eledone* from those in other octopodids studied. At the level of the greatest diameter the stylets in *Eledone* comprise less than 1/3 of the mantle wall thickness. Weak expression of the bend, relatively small size and smooth surface of the stylets in *Eledone* indicate to the reduction of supporting role of the stylets in this species. On the other hand, the stylets in *Eledone* apparently retain their role of structural centers uniting the mantle, funnel retractors, visceral sac and the gills. Widened inner bases of the funnel retractors apparently ensure strong connection between the visceral sac and the mantle. Reduction of supporting role of stylets in *Eledone* may be caused by decrease of its swimming activity in the course of adaptation to benthic (crawling and hiding) behaviour.

Alloposidae Verrill, 1881

Alloposus mollis Verrill, 1880

HABITS AND HABITAT. *A. mollis* is a benthopelagic octopod, inhabiting near-bottom waters of continental slopes in all oceans, from tropical to high latitudes [Young, 1996]. Body tissues are gelatinous. Females are very large, reaching 400 mm ML or a total length up to 2 m [Nesis, 1982/1987].

Males are much smaller than females, but they are no dwarfs like in other representatives of argonautoid families [Young, 1996]. According to Nesis [1975], the deep umbrella formed by the arms and web serves *Alloposus* as its main organ of locomotion. Ability for the jet-swimming is apparently lost. Recently this was confirmed by direct submersible observations of *Alloposus* swimming with slow medusoid motion of its umbrella just above the ocean floor [Young, 1995].

SHELL MORPHOLOGY. Stylets in *Alloposus* were first discovered by Voight [1997] who described them as 'gelatinous masses', situated 'in the dorso-lateral mantle'. Stylets in *Alloposus* are unusual in their shape and structure (Fig. 32). They are relatively small, wide and thick drop-like bodies of soft consistency embedded in the lateral walls of the mantle. In formalin-stored specimens stylets are transparent, soft and flexible, like water-filled balloons. The lengths of stylets comprises about 10% ML. As the stylets lie on the lateral sides of the mantle, the distance between them equals the mantle width at that level, comprising about 54% ML. In each stylet the anterior and posterior shoulders form an obtuse angle of about 135^0-145^0 between them. The shorter anterior shoulder is rounded and wide; its length comprises about 33% of the stylet length. The posterior shoulder attenuates to a point. The bend is low and dome-shaped; its surface is smooth. The greatest width of the stylets (at the level of the bend) comprises approximately 46% of stylet length. The inner side of each stylet bears a prominent ridge ending in a prominent dome just above the nucleus (Fig. 33C). The surfaces of the stylets are smooth. Dorsal side of each stylet bears a shallow groove between the anterior and posterior shoulders.

MICROSTRUCTURE OF THE STYLETS. As in other incirrates, the stylets in *Alloposus* are composed of concentric layers growing around an initial shell. The latter is visible in transmitting light within the bend. However, all attempts to make cross-section of these structures failed, as the stylets lost their shape and released water when their surface is broken.

EXTERNAL MORPHOLOGY. The body is smooth and with gelatinous integument concealing the underlying musculature (Fig. 33). The mantle is short, wide and cup-shaped; its length averages 38% ML. Dorsal margin of the mantle forms wide tongue-like process projecting anteriorly. Ventral margin of the mantle is shallow concave. The mantle aperture is wide; its lateral margins are situated at the level of eyes. The long, wide, tube-like funnel is completely embedded in the head. Its wide nozzle opens anteroventrally to the eyes (Fig. 33B). A weak funnel locking-apparatus is present. It consists of hook-like muscular folds on the funnel corners

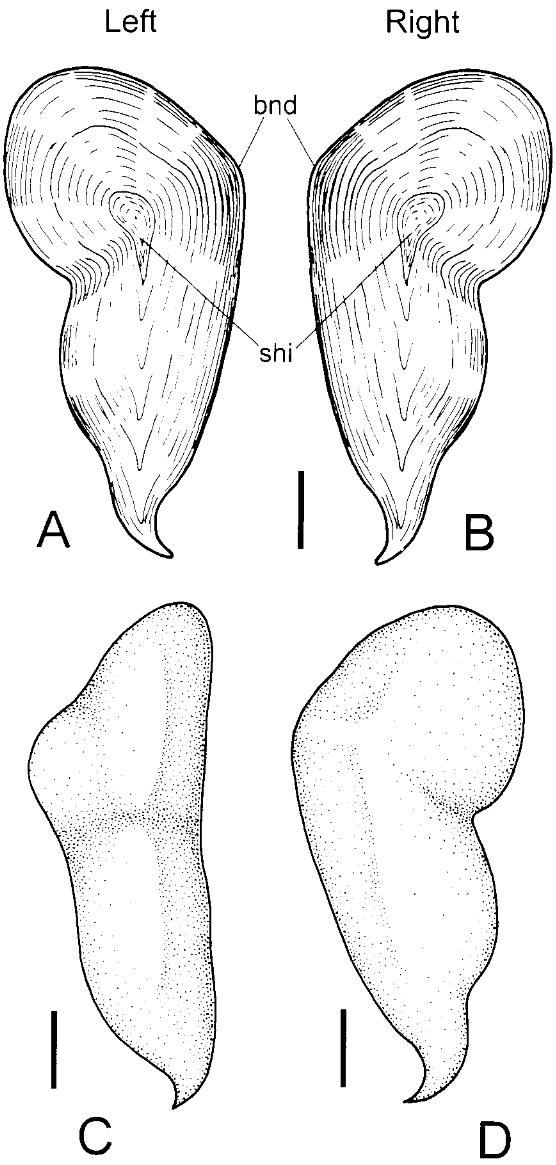


FIG. 32. Stylets of *Allopos mollis* (immature male: 60 mm ML). A. Inner lateral view of the left stylet (anterior end is up: ventral side is on the right). B. Inner lateral view of the right stylet (anterior end is up: ventral side if on the left). C. Dorsal view of the right stylet (anterior end is up: inner side is on the left). D. Inner lateral view of the right stylet (same orientation as in 'B'). A,B – the stylets are drawn naturally transparent to show their growth increments. C,D – the stylets are drawn opaque to reveal their surface. Scale bars = 1 mm.

РИС. 32. Стилеты *Allopos mollis* (незрелый самец: 60 мм ДМ). А. Вид левого стилета сбоку (изнутри): передний конец наверху; вентральная сторона справа. В. Вид правого стилета сбоку (изнутри): передний конец наверху: вентральная сторона слева. С. Вид правого стилета с дорсальной стороны (передний конец наверху; внутренняя сторона слева). D. Вид правого стилета сбоку (изнутри): ориентация та же, что на 'В'. А,В – стилеты изображены естественно прозрачными, чтобы показать их слои нарастания. C,D – стилеты изображены непрозрачными, чтобы показать рельеф их поверхности. Масштаб = 1 мм.

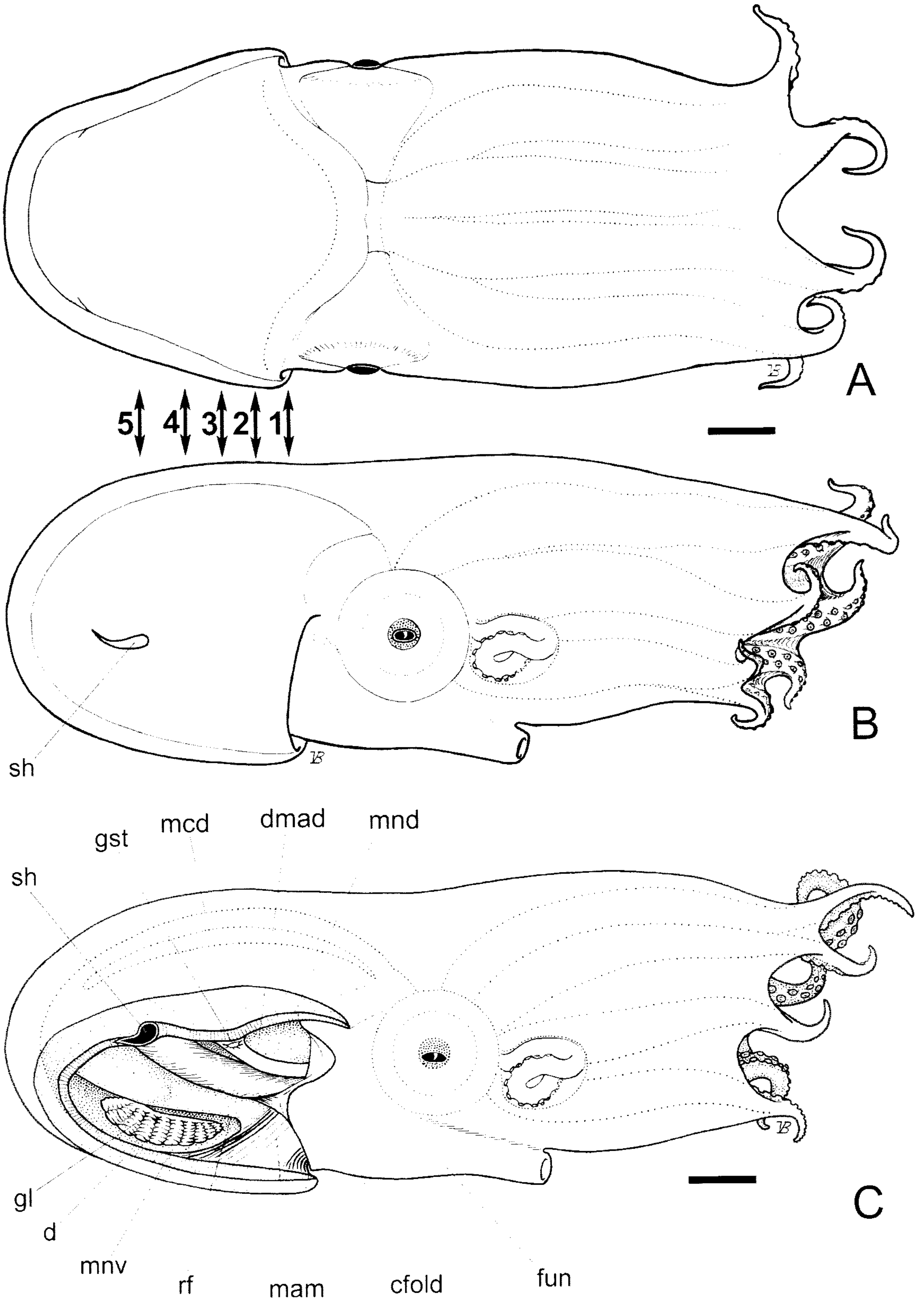


FIG. 33. General anatomy of *Alloposus mollis*. A. Dorsal view (immature male: 60 mm ML). B. Same specimen: lateral view. Bold arrows with numbers indicate the plane of corresponding cross-sections (shown in Fig. 34). C. Lateral view of a immature male (63 mm ML) after removal of mantle wall and gill from the right side. Scale bars = 1 cm.

РИС. 33. Строение *Alloposus mollis*. А. Вид с дорсальной стороны (незрелый самец: 60 мм ДМ). В. Тот же экземпляр: вид сбоку. Стрелки с цифрами указывают положение соответствующих срезов (показаны на Рис. 34). С. Вид сбоку после удаления стенки мантии и жабры с правой стороны (незрелый самец: 63 мм ДМ). Масштаб = 1 см.

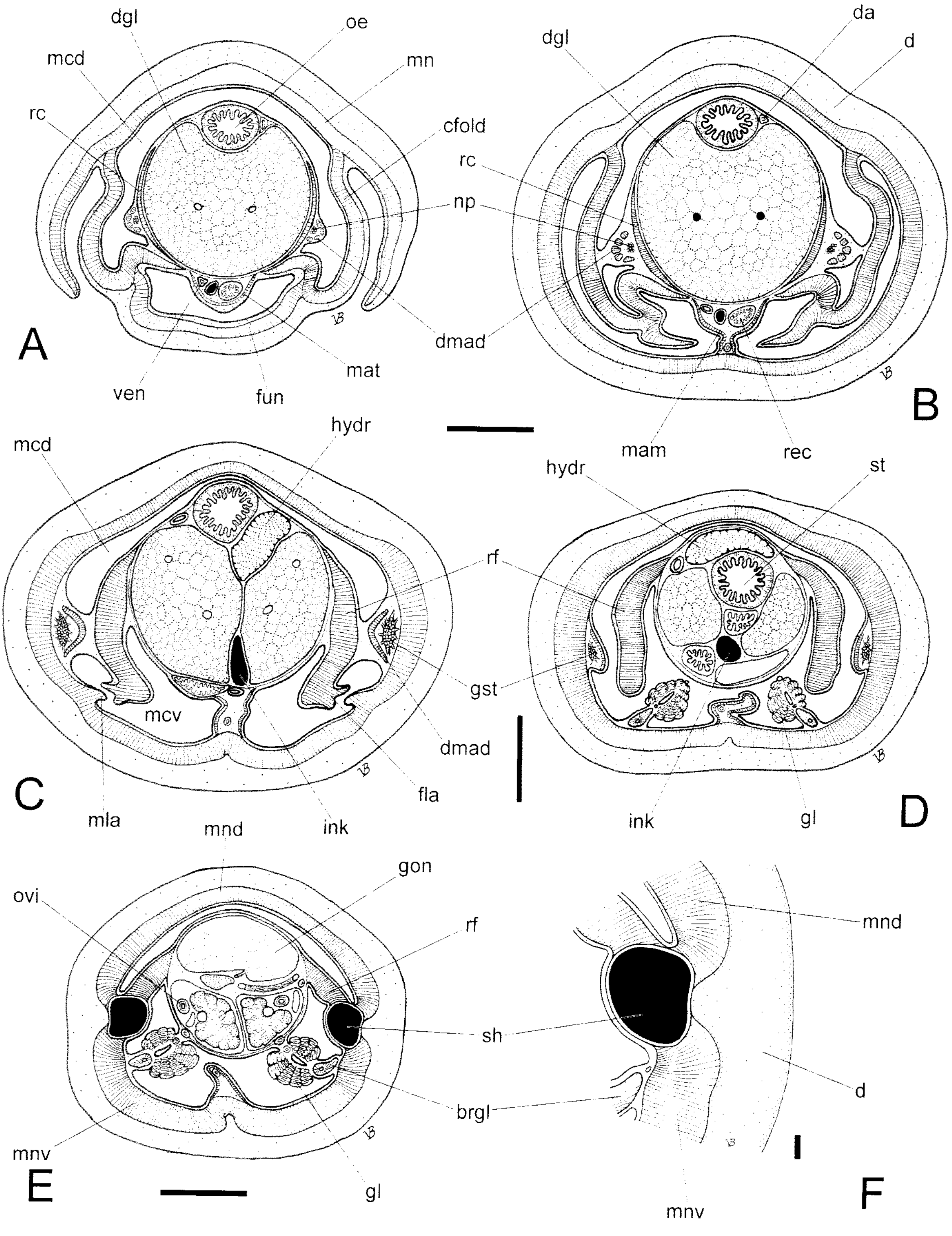


FIG. 34. Schematic cross-sections of the soft body in *Alloposus mollis* (immature female: 57 mm ML). A. Section 1, at the level of anterior dorsal margin of the mantle. B. Section 2, at the level behind the funnel. C. Section 3, at the level of anterior dorsal mantle adductors. D. Section 4, behind anterior dorsal mantle adductors. E. Section 5, at the level of attachment of the funnel retractors. F. Enlarged fragment of figure 'E' showing attachment of the mantle and funnel retractor to the left stylet. Position of sections is indicated on Fig. 33. A-E: scale bars = 1 cm. F: scale bar = 1 mm.

РИС. 34. Срезы мягкого тела *Alloposus mollis* (незрелая самка; 57 мм ДМ). А. Срез 1, на уровне переднего дорсального края мантии. В. Срез 2, позади воронки. С. Срез 3, на уровне передних дорсальных мантийных аддукторов. D. Срез 4, позади дорсальных мантийных аддукторов. Е. Срез 5, на уровне прикрепления ретракторов воронки. F. Увеличенный фрагмент вида 'Е', показывающий прикрепление мантии и ретрактора воронки к левому стилету. Положение срезов показано на Рис. 33. А-Е: масштаб = 1 см. F: масштаб = 1 мм.

and corresponding ridge/groove system on the mantle. Visceral sac is rather small. Ink sac is present. The median mantle septum is wide but feebly muscular. Its anterior margin is at the anterior ventral margin of the mantle. The funnel retractors pass nearly longitudinally along lateral sides of the visceral sac. The anterior dorsal mantle adductors are long and narrow, running almost parallel to the funnel retractors (Fig. 33C).

CROSS-SECTIONS. The walls of mantle and funnel are thin and weakly muscular. Dorsal wall of the mantle projects further anteriorly than the ventral wall, so that the latter is absent on the section at the level of the funnel (Fig. 34A). The dorsal mantle wall that confines the dorsal mantle cavity is conspicuously thinner than lateral and ventral walls confining the ventral mantle cavity (Fig. 34C,D). The mantle cavity is spacious; the dorsal part is larger than the ventral one. The dorsal mantle cavity is best developed in the area of collar folds, while the ventral part reaches the greatest size immediately behind the funnel (Fig. 35C,D). Visceral sac occupies about 2/3 of the mantle cavity. Posterior part of digestive gland is divided into left and right lobes (Fig. 34C,D). The ink sac is embedded between the two lobes of the digestive gland. An elongated hydrostatic organ lies in the middle part of the visceral sac, along its dorsal midline, next to digestive gland (Fig. 34C,D). Numerous folded and branched membranes project inside the organ from its walls.

Head retractors are thin, short and weak. They do not form a complete muscular envelope around the anterior part of the visceral sac, like in octopodids, but run along lateral sides of the visceral sac as a pair of thin muscular bands. Posteriorly the head retractors gradually become thinner and disappear by the level of stellate ganglia (Fig. 34A-C).

The anterodorsal mantle adductors are peculiar in shape and structure. They separate from the head retractors very early, at the level of the funnel. Here they have the shape of low ridges on the ventrolateral sides of the visceral sac (Fig. 34A). Each ridge consists of a series of muscular bundles surrounding a pallial nerve. The latter occupies unusual position in *Alloposus*, lying external to the head retractors. At the level of collar folds, the bridges containing the anterior adductors increase in size and their lateral sides fasten to the inner sides of the collar folds by thin ligaments thereby dividing the collar pockets into dorsal and ventral parts (Fig. 34B). Further posteriorly the bridges attach to the outer sides of the funnel retractors and the separated adductor bundles merge into single muscular layers that attach to the lateral mantle walls behind the stellate ganglia (Fig. 34C). They are situated so low in relation to the visceral sac that should be termed more correctly the 'anterolateral adductors'.

The median mantle septum consists of two thin adductor muscles running along the lateral sides of a gelatinous core containing the rectum, vena cava, mantle artery and the duct of the ink sac (Fig. 34B,C). Anterior extensions of the adductors form a low ridge that extends anteriorly forming part of the dorsal funnel wall and the ventral side of visceral sac (Fig. 34A).

The muscular portion of the funnel consists of one ventral and two dorsolateral muscular walls (Fig. 34A). Boundaries between these walls are marked by the junction of muscular fibers of different orientation. The collar folds originate from the lateral walls of the funnel, pass alongside the visceral sac and attach to dorsolateral walls of the mantle. The funnel retractors are thick and wide. They attach to the visceral sac along their dorsal margins, while the ventral margins hang free inside the mantle cavity (Fig. 34C,D). At the sites of attachment to the stylets, the funnel retractors are oriented obliquely from dorsolateral sides of the visceral sac to the dorsomedial sides of the stylets, which are situated low on lateral walls of the mantle (Fig. 34E). The stylets are much thicker than the muscles attaching to them. The mantle attaches to the dorsal and ventral sides of the stylets leaving wide break on their outer surface (Fig. 34F). The gills attach to the mantle wall ventral to the stylets.

COMMENTS. The stylets in *Alloposus* are unique among octopods in being soft, gelatinous and unusually large. Such structures could not provide support for the funnel retractors and apparently serve as a hydroskeleton, variable in shape but constant in volume, between the major muscles of the body. Reduction of the stylets in *Alloposus* was apparently stipulated by the loss of jet-swimming. However, the presence of a well-developed funnel locking apparatus in *Alloposus* suggests that it is derived from a more muscular ancestor.

Another characteristic feature of *Alloposus* is the presence of a hydrostatic organ, which is reported here for the first time. Until now, hydrostatic organ of similar structure was reported only for *Ocythoe* [Packard, Wurtz, 1994]. The presence of hydrostatic organ implies that *Alloposus* can attain neutral or near-neutral buoyancy passively. Development of a new septum between anterior dorsal adductors and the collar folds may support the anterodorsal adductor bridge.

Tremoctopodidae Tryon, 1879

Tremoctopus violaceus Chiaie, 1830

HABITS AND HABITAT. *Tremoctopus*, or blanket octopus, is an epipelagic octopod inhabiting tropical and subtropical surface waters of all oceans [Thomas, 1977; Nesis, 1975; 1985]. Females are large, up to 500 mm ML; the males are dwarf, about

15 mm ML. Direct underwater observations showed that this animal can jet-swim [Young, 1995]. In other cases *Tremoctopus* was found swimming near the shallow ocean floor with its long dorso-lateral arms and web spread wide apart [Mangold *et al.*, 1996a].

SHELL MORPHOLOGY. The stylets are straight, thick and relatively stiff sausage-shaped rods with slightly pointed ends (Fig. 35). They lie on the lateral sides of the mantle (Fig. 36A). Distance between the anterior ends of the stylets is about 45% ML. The stylets consist of cartilage-like chitin that is laid down by concentric layers. The center of growth (initial shell) is situated in anterior 1/3 of the stylets. Length of the stylets is about 1/6 ML. Each stylet is slightly compressed in its middle part and somewhat swollen in its anterior and posterior parts (Fig. 35A). The bend is absent. The surface of stylets is smooth. The greatest width is situated in the posterior 1/3 and comprises approximately 18% of their length.

MICROSTRUCTURE OF THE STYLETS. Cross-sections in the middle part of stylets are roughly oval in shape and consist of numerous regular, concentric, translucent layers (Fig. 35C). The center of growth is situated approximately in the middle of the section. Contours of the growth increments are similar throughout the section, indicating that the stylet shape does not change significantly during growth. Growth zones are absent. The width of growth increments ranges from 7 μm to 15 μm, averaging 9 μm. First-order increments are grouped into second-order cycles, from 5 to 32 increments in one cycle.

EXTERNAL MORPHOLOGY OF FEMALES. Body is dense, muscular and smooth. Mantle is elongated, rounded posteriorly (Fig. 36A). Anterior dorsal margin of the mantle forms wide tongue-shaped process, projecting to the level of eyes. Ventral anterior margin of the mantle is even. Mantle aperture is wide; its lateral margins are situated above the level of eye pupils (Fig. 36B). The position of the stylets is visible on intact animal as a pair of longitudinal grooves on lateral sides of the mantle. Dorsal arms I and II are very long (more than 2 times the mantle length) and connected by a large interbrachial web. Ventro-lateral arms III and IV are much shorter than the dorsal ones and not united by the web. A pair of water pores is situated at the bases of dorsal and ventral arms leading into large subcutaneous cephalic cavities. Funnel is long and tube-like, embedded in the head dorsally. The nozzle of the funnel is free, narrow and situated anteroventally from the eyes. Funnel corners are folded outward and form funnel locking-apparatus that fits into corresponding pocket-like slits in the mantle.

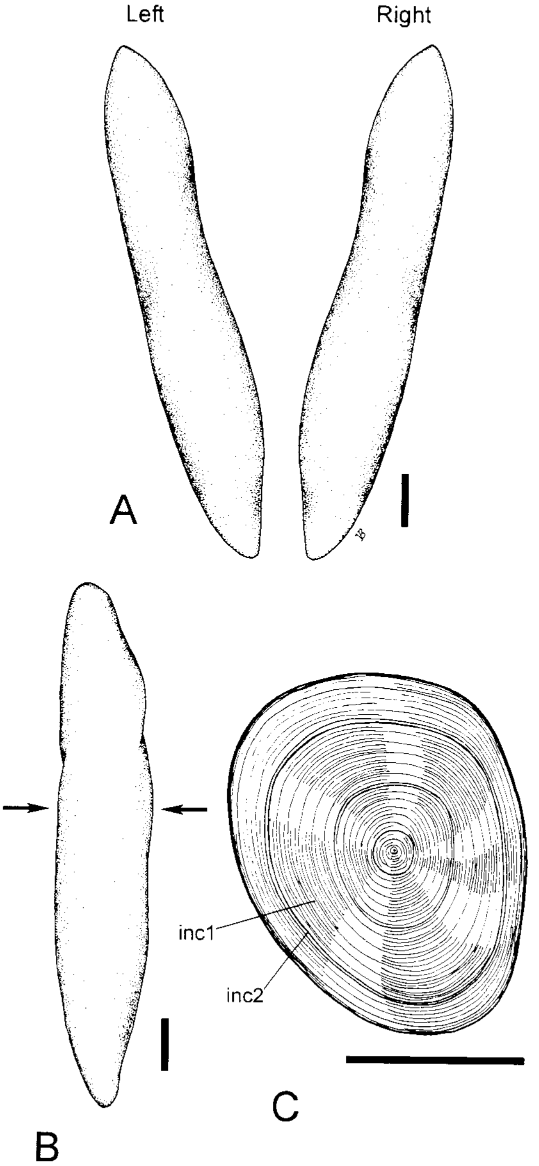


FIG. 35. Stylets in *Ttremoctopus violaceus*. A. Dorsal view of a pair of stylets from immature female (60 mm ML); anterior end is up. B. Lateral view from inner side of the right stylet (ventral side if on the left; anterior end is up). Arrows indicate the plane of the cross-section shown in 'C'. C. Cross-section of the right stylet (dorsal side is up; outer side is on the left). Scale bars = 1 mm.

РИС. 35. Стилеты *Ttremoctopus violaceus*. А. Вид с дорсальной стороны пары стилетов незрелой самки (60 мм ДМ); передняя сторона наверху. В. Вид сбоку с внутренней стороны правого стилета (вентральная сторона слева; передний конец наверху). Стрелки указывают положение среза, изображенного на виде 'С'. С. Поперечный срез правого стилета (дорсальная сторона наверху; внешняя сторона слева). Масштаб = 1 мм.

CROSS-SECTIONS OF FEMALES. The mantle wall is thick and muscular. Its outer and inner muscular layers are separated by a thin layer of connective tissue (Fig. 37). The lateral walls of the mantle are slightly thicker than the dorsal and ventral walls.

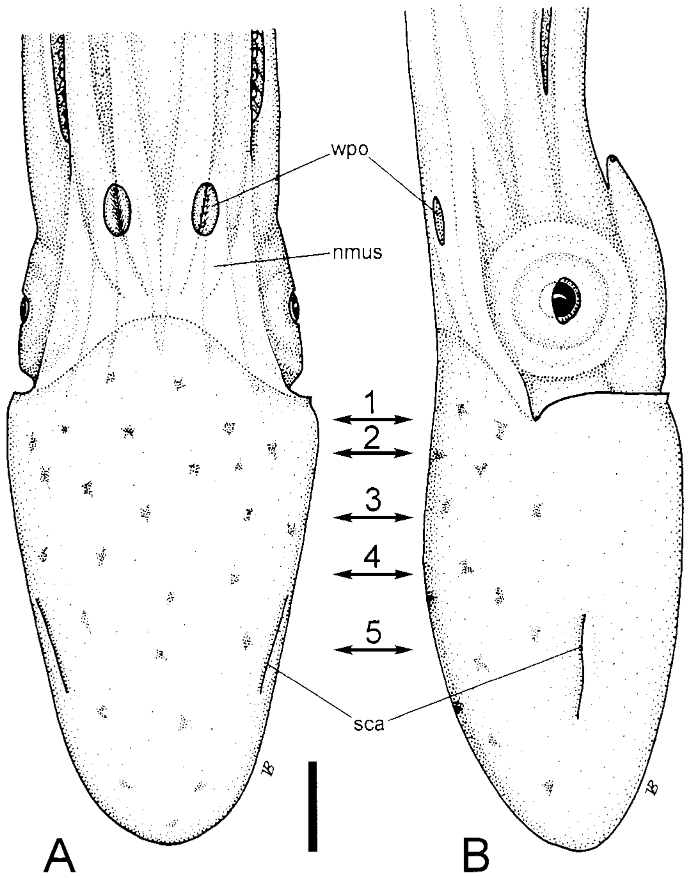


FIG. 36. General anatomy of *Tremoctopus violaceus* (immature female: 57 mm ML). A. Dorsal view. B. Lateral view. Bold arrows with numbers indicate the planes of corresponding cross-sections (shown in Fig. 37). Scale bar = 1 cm.

РИС. 36. Строение *Tremoctopus violaceus* (незрелая самка: 57 мм ДМ). А. Вид с дорсальной стороны. В. Вид сбоку. Стрелки с цифрами указывают положение соответствующих срезов (показаны на Рис. 37). Масштаб = 1 см.

Dermis is thin and smooth. The mantle cavity is relatively small; the dorsal part is larger than the ventral one. The visceral sac occupies about 2/3 of the mantle cavity. Digestive gland is not divided posteriorly and occupies most of the visceral sac anteriorly. Ink sac is large, triangular in cross-section, embedded deep into the digestive gland from ventral side (Fig. 37B-D). A hydrostatic organ is present in the middle part of the visceral sac on its dorsal side. It is situated posterior to the digestive gland and above the stomach and has the shape of a wide, flattened, muscular sac with numerous branched membranes projecting inside from its walls (Fig. 37E).

The head retractors are thin and wide. They form the muscular lateral walls of the visceral sac and almost merge dorsally and ventrally (Fig. 37A,B). Posteriorly the head retractors gradually become thinner and finally disappear at the level of the stellate ganglia. In the region of the funnel the head retractors consist of inner and outer layers with different orientation of their muscular fibers (Fig. 37A). The pallial nerves occupy position between layers of the head retractors on the lateral sides of the visceral sac. At the level of the collar folds, the outer muscular layer of the head retractors branches outward and forms anterior the anterodorsal mantle adductors containing the pallial nerve (Fig. 37B). Unlike *Alloposus*, anterodorsal adductors in *Tremoctopus* are not connected with the collar folds. Anterodorsal adductors attach to the mantle immediately behind the funnel (Fig. 37C). At the sites of attachment they are thicker and more muscular. The lateral end of each anterodorsal adductor attaches to the lateral mantle wall while the medial end attaches to the ventrolateral side of the visceral sac, close to the funnel retractors. The stellate ganglia are situated below and posteriorly the sites of attachment of the anterodorsal adductors.

Ventral median mantle septum is thick, muscular and Y-shaped in cross-section (Fig. 37B,C). Ventrally the septum is composed of a single, thick adductor muscle that attaches to the mantle wall.

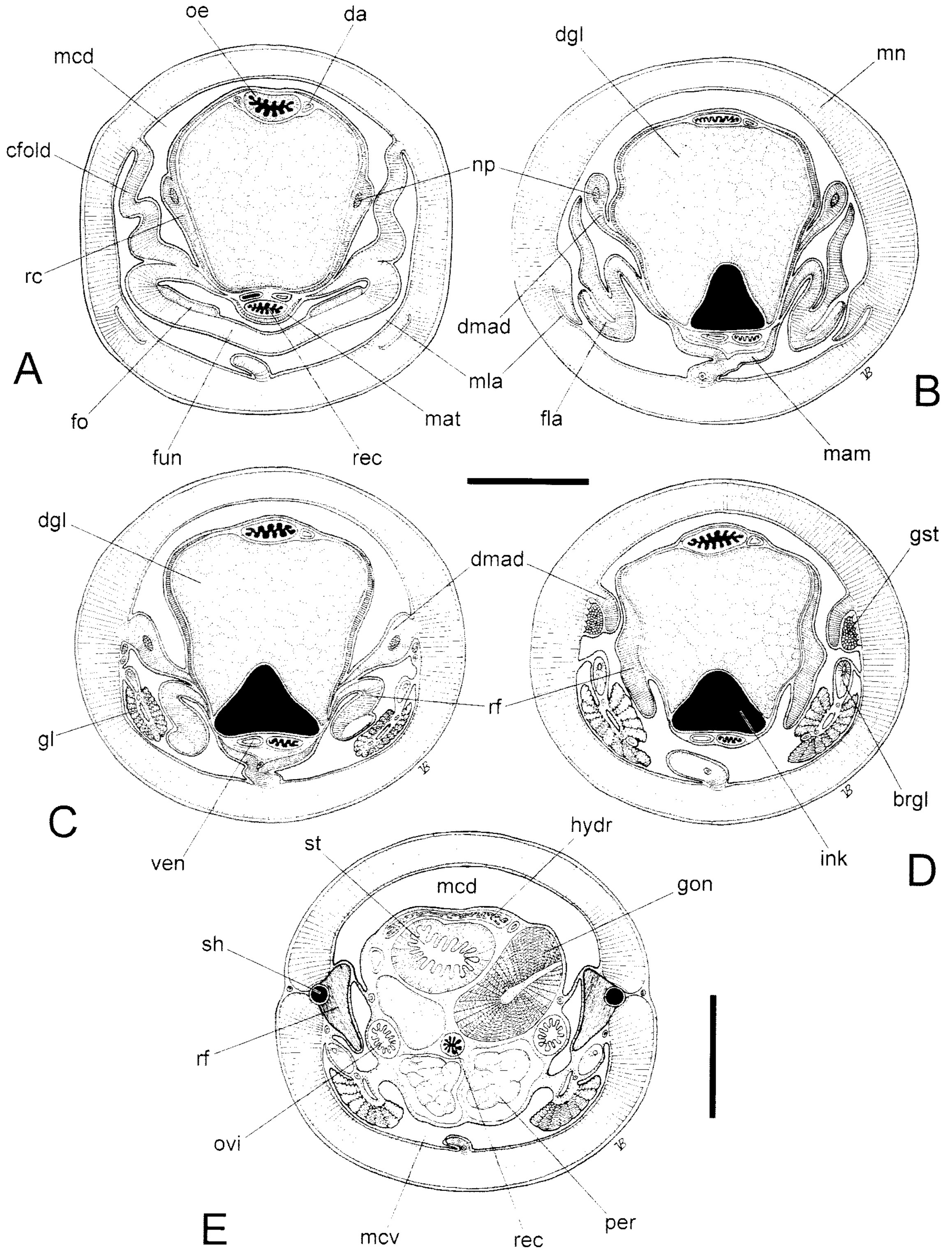


FIG. 37. Schematic cross-sections of the soft body of *Tremoctopus violaceus* (immature female: 57 mm ML). A. Section 1, at the level of the funnel. B. Section 2, behind the funnel. C. Section 3, at the level of anterior dorsal mantle adductors. D. Section 4, behind dorsal mantle adductors (level of the stellar ganglia). E. Section 5, at the level of attachment of the funnel retractors. Position of sections is indicated on Fig. 36. Scale bars = 1 cm.

РИС. 37. Срезы мягкого тела *Tremoctopus violaceus* (незрелая самка; 57 мм ДМ). A. Срез 1, на уровне воронки. B. Срез 2, позади воронки. C. Срез 3, на уровне передних дорсальных мантийных аддукторов. D. Срез 4, позади дорсальных мантийных аддукторов (на уровне звездчатых ганглиев). E. Срез 5, на уровне прикрепления ретракторов воронки. Положение срезов указано на Рис. 36. Масштаб = 1 см.

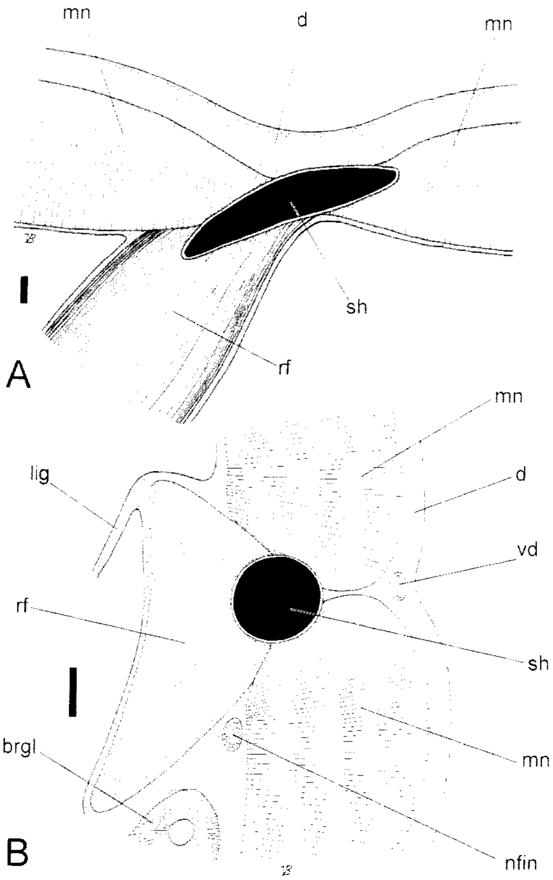


FIG. 38. Schematic sections showing attachment of muscles to the shell in *Tremoctopus violaceus*. A. Longitudinal section of the mantle along the left stylet. Anterior end is on the left: dorsal side is up. B. Transversal cross-section through the right stylet (enlarged fragment of Section 5: Figure 37E). Dorsal side is up: outer side is to the right. Scale bar = 1 mm.

РИС. 38. Крепление мышц к раковине *Tremoctopus violaceus*. А. Продольный срез мантии вдоль левого стилета. Передний конец слева: дорсальная сторона наверху. В. Поперечный срез через правый стилет (увеличенный фрагмент среза 5: Рис. 37E). Дорсальная сторона наверху: внешняя сторона справа. Масштаб = 1 мм.

This muscle extends along the mantle wall both anteriorly and posteriorly from the region of attachment to the visceral sac. Dorsally the adductor divides into two layers that diverge onto the sides of the visceral sac. The space between the diverging muscles is occupied by the rectum and vena cava. Anteriorly the adductor muscles extend into the funnel as a thin muscular layer covering the rectum, vena cava and the duct of the ink sac (Fig. 37A).

The funnel consists of single circular muscular layer; its ventral and lateral walls are fused together without boundaries (Fig. 37A). Collar folds originate from the dorsolateral walls of the funnel, pass along the sides of the visceral sac and attach to dorsolateral walls of the mantle. A funnel locking-apparatus in *Tremoctopus* is well developed and consists of cartilage-strengthened hook-like folds of the funnel corners and corresponding pockets in the ventral mantle wall (Fig. 37B).

Funnel retractors are wide, thick, muscular bands on the lateral sides of the visceral sac (Fig. 37D). They fuse with the visceral sac along the dorsomedial of their width, while the ventral quarter hangs freely inside the mantle cavity. At their sites of attachment to the stylets the funnel retractors are thick and triangular in cross-section (Figs. 37E; 38B). The wide medial side of each base projects into the mantle cavity, while the narrow outer apex attaches to the medial half of the stylet. The dorsal side of each retractor base connects to the visceral sac by a membrane (Fig. 37E). The gills attach to the mantle wall ventral to the attachment of the funnel retractors.

Attachment of the muscles to the stylets in *Tremoctopus* is unusual. Longitudinal preparation showed that each stylet is obliquely oriented in the animal body; its posterior part is embedded in the mantle muscle, while the anterior part projects into the funnel retractor (Fig. 38A). Compared to *Octopus*, the stylets are thick in relation to the mantle. The mantle muscles form a break over the stylets, that is clearly visible on both longitudinal and transversal sections (Fig. 38A,B).

COMMENTS. Straight stylets in *Tremoctopus* are not anchored in the mantle as effectively as stud-like stylets of benthic octopods. Instead, they are inserted in the mantle wall like obliquely knocked nails (Fig. 38A). The smooth surface of the stylets and the absence of the bend suggest that muscles attachment is weaker. This reduction is compensated, at least partly, by the special, well-developed funnel locking-apparatus, which eases the role of the funnel retractors in holding the funnel during jet-swimming. Obviously, *Tremoctopus* cannot swim, like *Alloposus*, with medusoid movement of its arm crown, as its interbrachial web is incomplete (absent between arms III and IV). Since jet propulsion is its only means of locomotion and it possesses a large, muscular mantle and well-developed stylets we assume that *Tremoctopus* is capable of relatively strong jet-swimming.

The hydrostatic organ that is reported for *Tremoctopus* for the first time represents an important adaptation for pelagic life and implies that the octopus can attain neutral or near-neutral buoyancy passively.

Ocythoidae Gray, 1849

Ocythoe tuberculata Rafinesque, 1814

HABITS AND HABITAT. Little is known about the life style and ecology of *Ocythoe tuberculata*. This pelagic octopod occurs in near-surface waters in subtropical to temperate regions of all oceans and

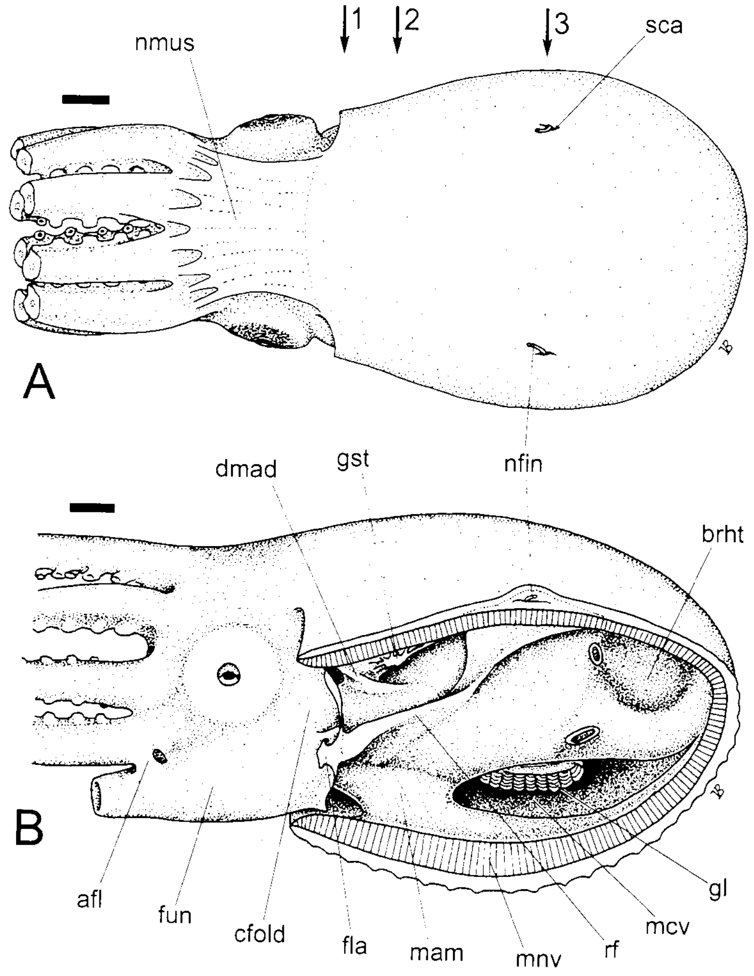


FIG. 39. General anatomy of *Ocythoe tuberculata*. A. Dorsal view after removal of the skin from the mantle and head (immature female: 96 mm ML). Bold arrows with numbers indicate the planes of corresponding cross-sections (shown in Fig. 41). B. Lateral view after removal of the mantle wall and gill from the left side (immature female; 103 mm ML). Scale bars = 1 cm.

РИС. 39. Строение *Ocythoe tuberculata*. А. Вид с дорсальной стороны после удаления кожных покровов с мантии и головы (незрелая самка: 96 мм ДМ). Стрелки с цифрами указывают положение соответствующих срезов (показаны на Рис. 41). В. Вид сбоку после удаления стенки мантии и жабры с левой стороны (незрелая самка; 103 мм ДМ). Масштаб = 1 см.

has often been caught by drift nets and pelagic trawls in upper 10 m of water at night [Roper, Sweeny, 1976; Mangold *et al.*, 1996b]. The daytime habitat is unknown. Females reach about 30 cm ML, while the adult males are dwarf, approximately one tenth the length of the females. The mantle is muscular and the octopod, presumably, is an excellent swimmer [Mangold *et al.*, 1996b]. Males and young females are often found residing inside the tests of salps [Nesis, 1982/1987]. Females have unusual hydrostatic organ, which is located in the middorsal region of the visceral mass [Packard, Wurtz: 1994].

EXTERNAL MORPHOLOGY OF FEMALES. The stylets are absent completely, and only muscular scars on the dorso-lateral sides of the mantle with the "fin" nerves penetrating them indicate the former position of the shell (Fig. 39). The mantle is ovoid, dense and muscular. The mantle length comprises about 25% TL; the mantle width is approximately 75% ML. Anterior dorsal margin of the mantle is fastened to the head by wide nuchal muscle. Arms are long (about 1.8 ML), ventral and dorsal arms are much longer than lateral arms. The web between arms is completely reduced. A pair of water pores is situated at the bases of ventral arms. Funnel is very long, projecting beyond the arms bases. Proximal of the funnel is fused with the head. Funnel locking-apparatus is very strong, formed by rigid cartilage-like corners of the funnel that coil outward like a spiral hooks and insert firmly into corresponding depressions in the mantle wall (Fig. 40B). The distal parts of the funnel corners are swollen where they reside inside the mantle ensu-

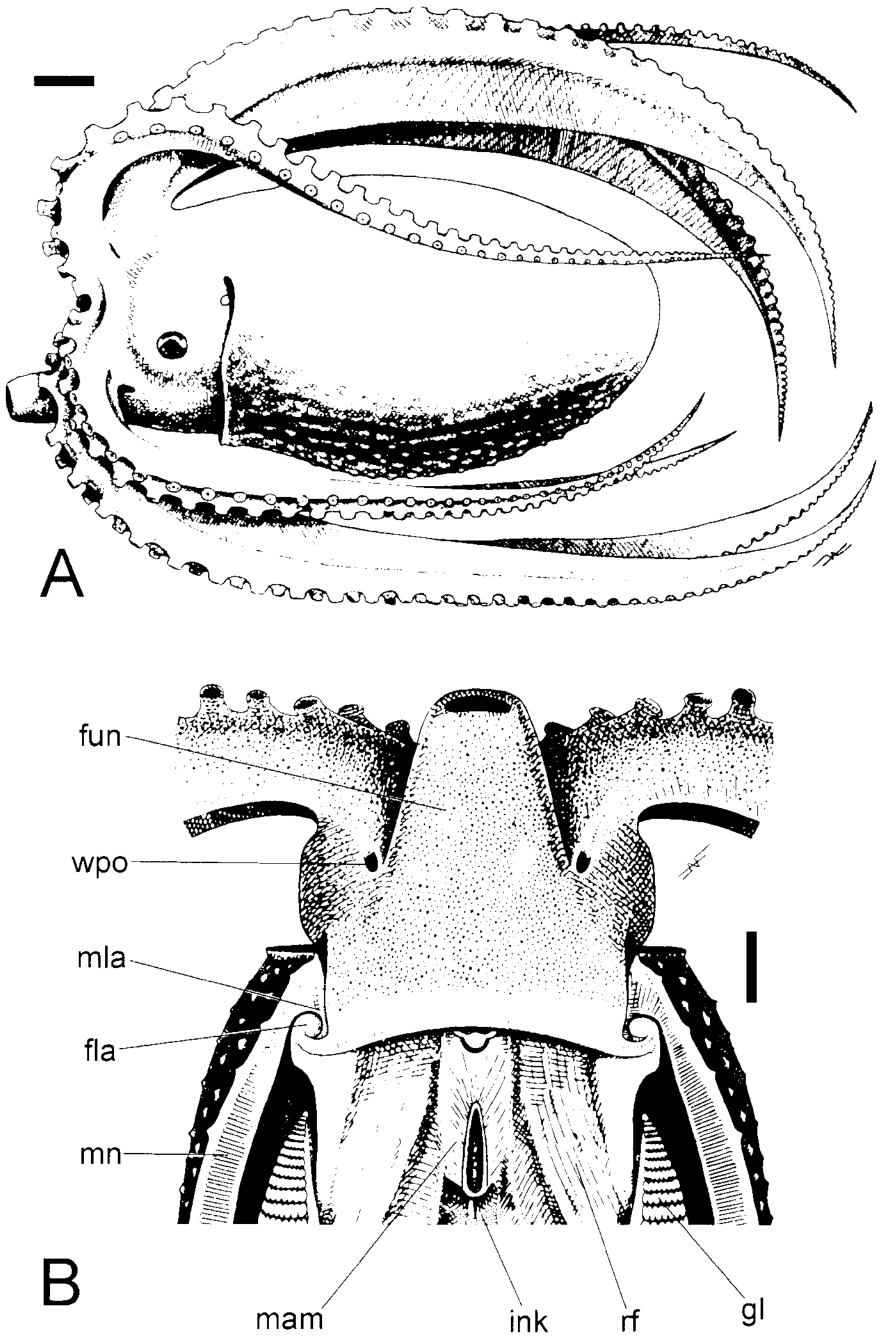


FIG. 40. *Ocythoe tuberculata*. A. General lateral view of an adult female. Note tubercles on ventral surface of the mantle. B. Ventral view of an adult female: ventral part of mantle removed to show the structure of mantle cavity and funnel locking-apparatus [from Naef, 1921/1923; modified]. Scale bars = 2 cm.

РИС. 40. *Ocythoe tuberculata*. А. Зрелая самка; вид сбоку. Вентральная сторона мантии покрыта сетчатой скульптурой. В. Зрелая самка; вид с вентральной стороны. Вентральная стенка мантии удалена; видно строение мантийно-вороночного замыкательного аппарата [из Naef, 1921/1923; с изменениями]. Масштаб = 2 см.

ring permanent, solid connection between the funnel and mantle. The mantle aperture is wide; its lateral margins are situated well above the level of eyes (Fig. 39B). The visceral sac is small. The anterodorsal mantle adductors have the shape of twisted, wide bands. The median mantle septum is wide and muscular. Its anterodorsal margin is well anterior to anteroventral mantle margin (Figs. 39B; 40B). Funnel retractors pass obliquely from the corners of the funnel alongside the visceral sac and attach to dorso-lateral walls of the mantle.

CROSS-SECTIONS. The mantle wall consists of the inner and outer muscular layers separated by a thin sheet of connective tissue (Fig. 41). The outer muscular layer is thicker than the inner one and the

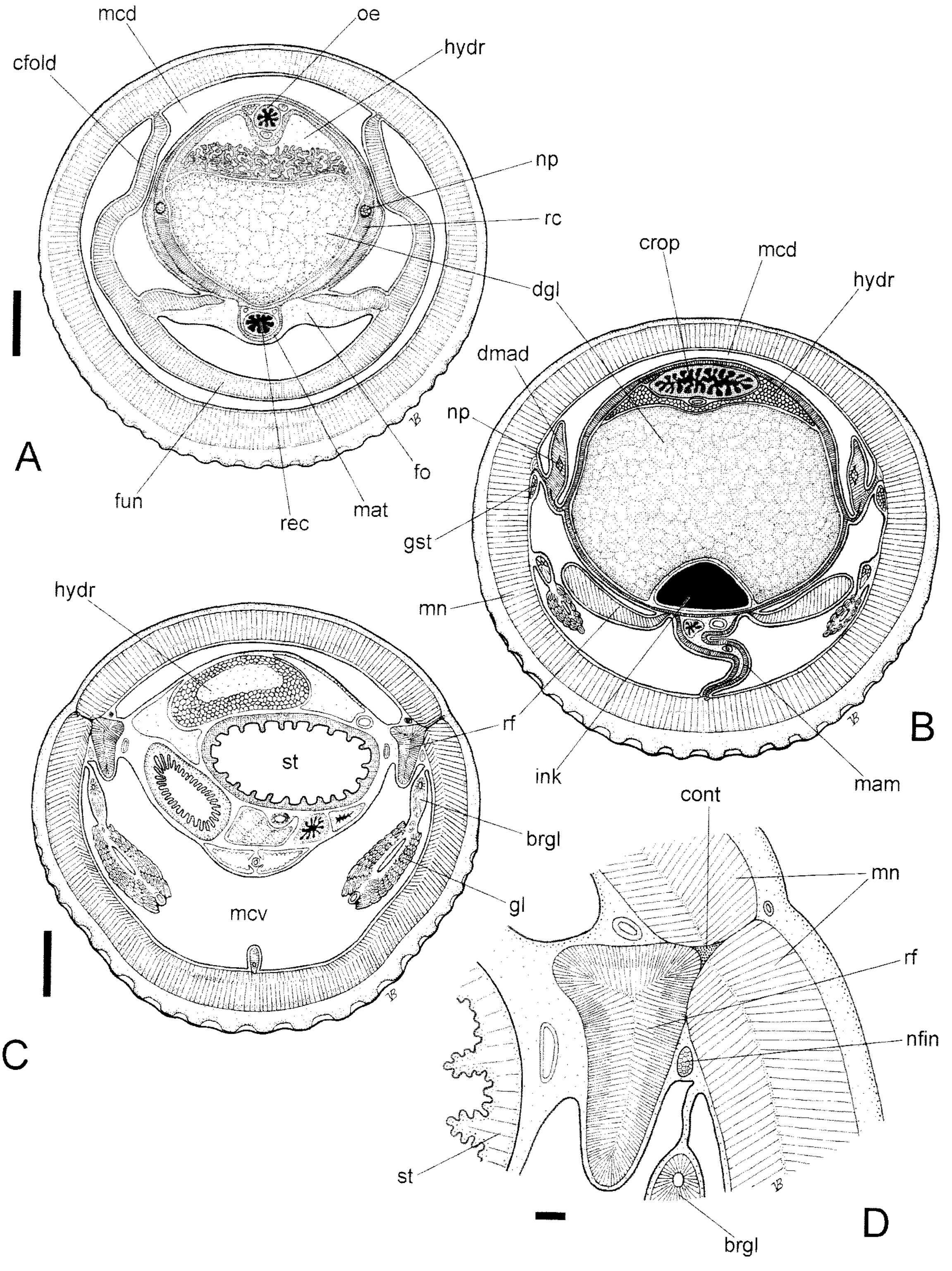


FIG. 41. Schematic cross-sections of the soft body of *Ocythoe tuberculata* (same specimen as in Fig. 39A). A. Section 1, at the level of the funnel. B. Section 2, at the level of anterior dorsal mantle adductors. C. Section 3, at the level of attachment of the funnel retractors. E. Enlarged fragment of Section 3, showing attachment of the funnel retractor to the mantle. Position of sections is indicated on Fig. 39. A-D: scale bars = 1 cm. E: scale bar = 1 mm.

РИС. 41. Срезы мягкого тела *Ocythoe tuberculata* (экземпляр тот же, что на Рис. 39А). А. Срез 1, на уровне воронки. В. Срез 2, на уровне передних дорсальных мантийных аддукторов. С. Срез 3, на уровне прикрепления ретракторов воронки. Е. Увеличенный фрагмент среза 3, показывающий прикрепление ретрактора воронки к мантии. Положение срезов показано на Рис. 39. А-D: масштаб = 1 см. Е: масштаб = 1 мм.

dorsal mantle wall is slightly thinner than the ventral and lateral walls. The dermis is thin and smooth on the dorsal side of the mantle, gradually becoming thicker and ridged toward the ventral side. The mantle cavity is large; its dorsal part is much smaller than the ventral one.

Visceral sac is relatively compact in anterior and posterior parts (Fig. 41A,C), swollen in the middle part (Fig. 41B). Digestive gland occupies most part of the visceral sac in its anterior and middle portions. Ink sac is large, triangular in cross-section, embedded into the digestive gland from ventral side. The hydrostatic organ is larger than in *Alloposus* and *Tremoctopus*, but similar in structure (Fig. 41A-C). It is an elongated thin-walled muscular sac situated in the middorsal region of the visceral sac, above the digestive gland. The interior of the hydrostatic organ in its anterior part is partly filled by branching membranes projecting inside from the ventral wall (Fig. 41A). The posterior part of the organ is occupied by loosely comb-like, membranous tissue not seen in the other two genera (Fig. 41B,C).

Head retractors are thin, wide and muscular. They form a muscular envelope of the visceral sac and spread from the head to the level of stellate ganglia. Near the base of the funnel the head retractors consist of two layers (inner and outer) with different orientation of their muscle fibers. The pallial nerves lie inside the inner layer of the head retractors, lateral to the visceral sac. Posterior to the collar folds, the outer head retractors branch outward from the visceral sac and form the anterodorsal adductors that attach to dorsolateral walls of the mantle (Fig. 41B). Anterodorsal adductors in *Ocythoe* are thick and muscular, with the pallial nerve passing in their middle part. Their unusual shape in Fig. 41B is a result of the section passing through the twisted mid-portion of the adductors. The stellate ganglia are situated posterolaterally to the attachment site of the anterodorsal adductors.

Ventral median mantle septum is thin and V-shaped in cross-section (Fig. 41B). It is formed by two very thin adductor muscles that diverge from the midline of the ventral mantle wall and attach to the ventral side of the visceral sac, in the region of the ink sac. The space between the ventral adductors contains the rectum, vena cava and the median pallial artery embedded in vacuolated connective tissue. The anterodorsal extension of the ventral adductor spreads into the funnel as a thin muscular layer covering the rectum and vena cava.

The funnel is very wide and semicircular in cross-section (Fig. 41A). It consists of two dorsal walls and wide, arc-like ventrolateral walls, the latter are fused with the collar folds into single muscular layers. The junctions of muscular fibers of different orientation mark the sites of attachment of the dorsal walls to the ventrolateral walls of the funnel. The collar folds are wide and muscular. They originate from the ventrolateral wall of the funnel and attach to the dorsal wall of the mantle, forming spacious collar pockets on both sides of the visceral sac.

The funnel retractors are thick, wide, muscular ribbons attached to the visceral sac along their medial margins (Fig. 41B). The usual position of stylets at the sites of attachment of the funnel retractors is occupied by dense cartilage, probably the remnant of the shell sac, which is wedged into the mantle wall on its inner side (Fig. 41C,D). A break in the mantle muscle occurs over the cartilage. The medial side of the cartilage together with the adjacent mantle wall form a shallow groove for attachment of the funnel retractors. At their attachment each retractor is irregularly triangular in cross-section, with a long, ventral apex projecting inside the mantle cavity, a short inner dorsal apex facing the visceral sac, and an outer dorsal apex inserting into the mantle wall. The gills fasten to the mantle wall ventral to the funnel retractors.

COMMENTS. Although there are no reports of *in situ* observations on the swimming mode of *Ocythoe*, the adult females are undoubtedly good jet-swimmers as indicated by the muscular mantle, the strong funnel locking-apparatus and the spacious ventral mantle cavity. On the other hand, the presence of well-developed hydrostatic organ or "swimbladder" in *Ocythoe* females indicate that this species apparently does not need to swim constantly to maintain position in the water.

There is an apparent contradiction between the absence of stylets and the ability for jet-swimming in *Ocythoe*. The loss of stylets means that the attachment of the funnel retractors to the mantle is weaker. The main function of the funnel retractors is to hold the funnel during jet propulsion. Apparently, the funnel retractors have partially relinquished their role in *Ocythoe* to the strong funnel locking-apparatus that prohibits movement between the mantle and the funnel. This is confirmed by the thin structure of the retractor muscles. A comparable situation is seen in some strong-jetting ommastrephids where the retractors are small and the funnel and mantle are permanently fused together. Otherwise reduction of stylets did not induce major morphological changes in *Ocythoe*. In general, this species retained the same octopodian Bauplan, though without the shell.

Argonautidae Tryon, 1879

Argonauta nodosa Solander, 1786

HABITS AND HABITAT. Argonauts, or paper nautiluses, are muscular epipelagic octopods inhabiting subtropical and tropical surface waters of all oceans, but only rarely encountered nearshore [Nesis,

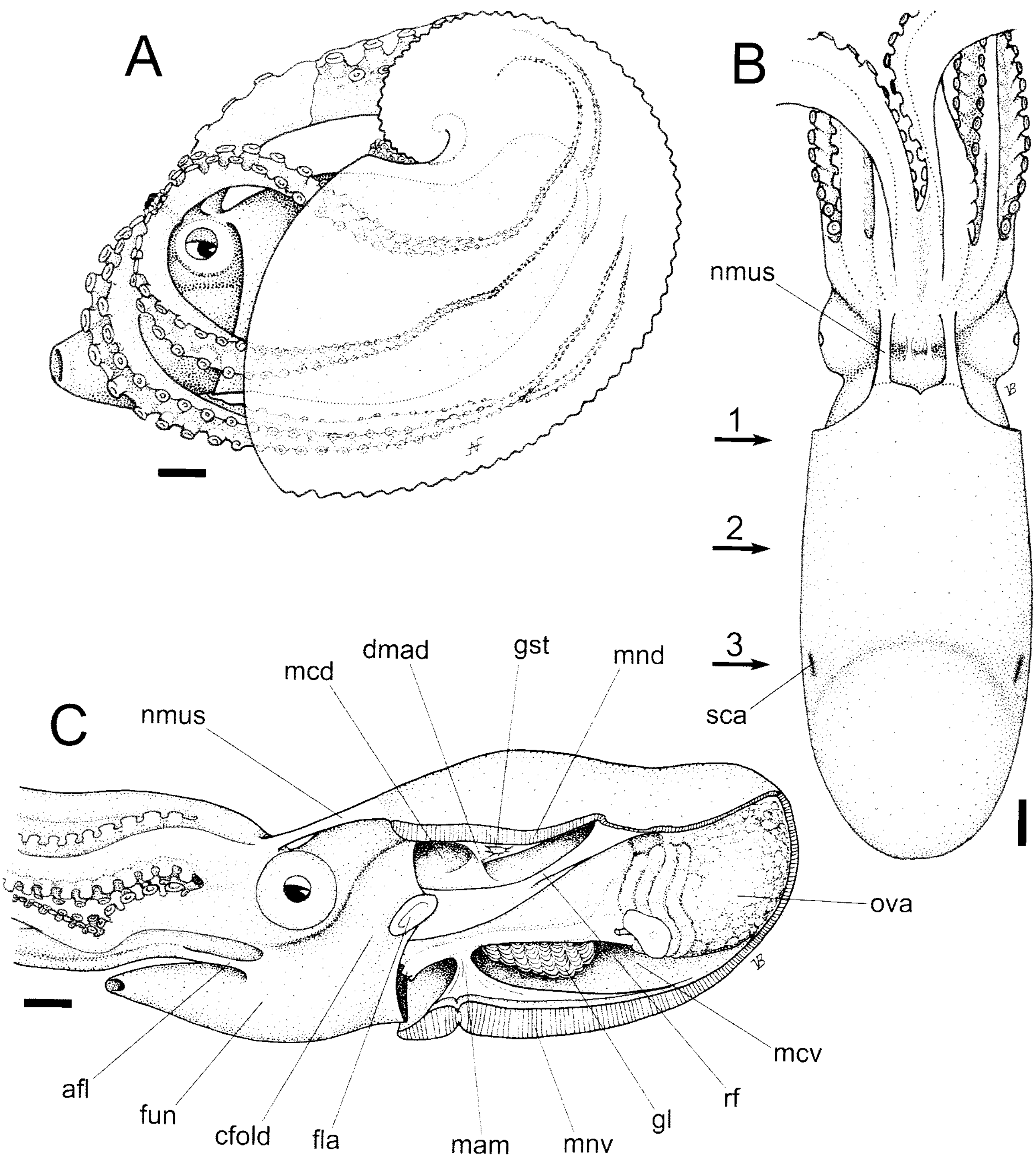


FIG. 42. General anatomy of *Argonauta*. A. Adult female of *Argonauta argo* in normal swimming position [from Naef. 1923]. B. Mature female of *A. nodosa* (108 mm ML): dorsal view. Bold arrows with numbers indicate the planes of cross-sections (shown in Fig. 43). C. Mature female (94 mm ML): lateral view after removal of the mantle wall and the gill from the left side. Scale bars = 1 cm.

РИС. 42. Строение *Argonauta*. А. Взрослая самка *Argonauta argo*. плывущая в естественной позе [из Naef. 1923]. В. Зрелая самка *A. nodosa* (108 мм ДМ): вид с дорсальной стороны. Стрелки с цифрами указывают положение соответствующих срезов (показаны на Рис. 43). С. Зрелая самка (94 мм ДМ): вид сбоку после удаления стенки мантии и жабры с левой стороны. Масштаб = 1 см.

1982/1987]. Females reach 10 cm ML and build the 'shell' up to 30 cm in length. Males are dwarf. approximately one tenth the size of females. and have been reported living within salps [Banas *et al.*. 1982]. Argonauts are poor swimmers. at least females.

EXTERNAL MORPHOLOGY OF FEMALES. The stylets are entirely lacking. A pair of breaks in the muscular tissue on the dorso-lateral sides in the posterior 1/3 of the mantle indicates the former position of the shell (Fig. 42). Although the true shell

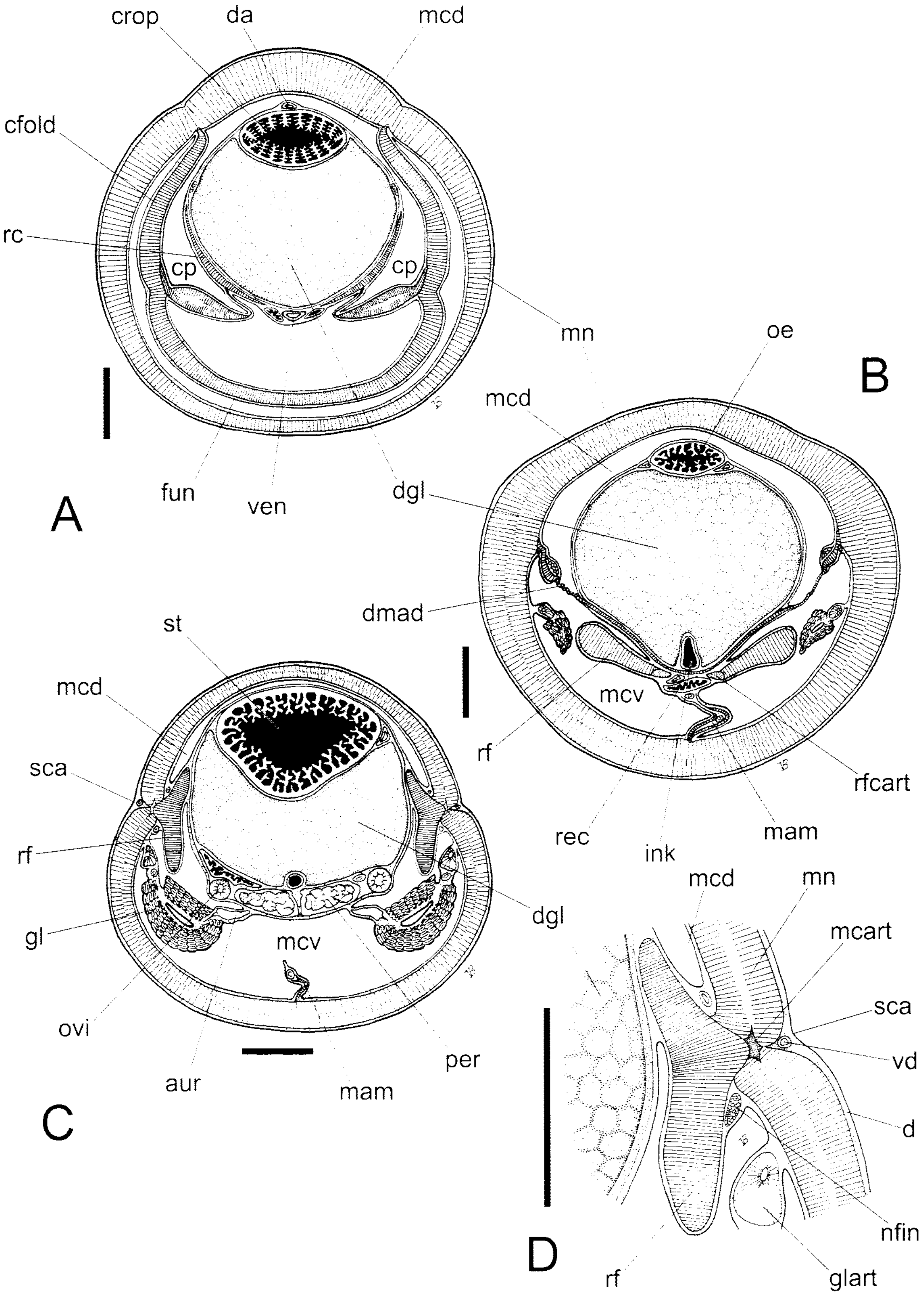


FIG. 43. Schematic cross-sections of *A. nodosa* (mature female: 108 mm ML). A. Section 1, at the level of the funnel. B. Section 2, at the level of dorsal mantle adductors. C. Section 3, at the level of attachment of the funnel retractors. D. Enlarged fragment of figure 'C' showing attachment of the funnel retractor to the mantle. Position of the sections is indicated on Fig. 42. Scale bars = 1 cm.

РИС. 43. Срезы *A. nodosa* (зрелая самка: 108 мм ДМ). А. Срез 1, на уровне воронки. В. Срез 2, на уровне передних дорсальных аддукторов. С. Срез 3, на уровне прикрепления ретракторов воронки. D. Увеличенный фрагмент вида 'С', показывающий прикрепление ретрактора воронки к мантии. Положение срезов показано на Рис. 42. Масштаб = 1 см.

is absent, females secrete a thin external calcareous shelter, often called the 'shell', in which they live and brood eggs [Nesis, 1982/1987]. This 'shell' is a planispiral, laterally compressed, boat-shaped structure with paper-thin, ribbed walls. The web between arms II- IV is distinct but shallow. Dorsal arms of females have large sail-like webs. The inner surface of the web is covered with glandular tissue and is responsible for secretion and shaping of the 'shell'. Typically the female sits in the 'shell' with the beak facing outward, its dorsal arms curved back with the web expanded over the 'shell' and all other arms inside the 'shell' holding onto it (Fig. 42A).

The mantle is muscular, smooth, elongated and ovoid. Posterior part of the mantle is curved dorsally, while its middle part forms distinct dorsal swelling giving the animal hampback appearance (Fig. 42A). The mantle length is ca. 27% TL; mantle width is about 47% ML. Anterior dorsal margin of the mantle has a shallow incision in the middle separating two anteriorly projecting lobes. Each lobe is connected with the head by a narrow and long nuchal muscle (Fig. 42B). The head is slightly narrower than the mantle. Water pores are absent.

Funnel is very broad and long, projecting well beyond the arm bases. Its distal half is free from the head for about of its length. Proximal part of the funnel is fused with the head and fastened to the bases of ventral arms by a pair of long, strip-like lateral funnel adductors (Fig. 42C). The funnel locking-apparatus is similar to that of squids: it consists of oval depressions on the funnel corners and corresponding cartilage-like knobs on the mantle. The mantle aperture is very wide; its lateral margins are situated well above the level of eyes. The anterodorsal mantle adductors are twisted long bands. Ventral median mantle septum is narrow. Anterior margin of the septum at its ventral attachment is at some distance from the anteroventral margin of the mantle. The mantle wall adjacent to the ventral adductor bears deep transversal groove, which looks as conspicuous constriction on longitudinal section (Fig. 42C).

CROSS-SECTIONS. The mantle wall is muscular; its inner and outer muscular layers are approximately equal in thickness and separated by a very thin layer of connective tissue. Where the anterodorsal adductors attach to the mantle, the mantle walls are slightly thicker than the dorsal and ventral walls (Fig. 43B). In posterior half of the mantle, its wall is thinner and approximately uniform in thickness around its circumference (Fig. 43C). The dermis is thin and smooth. The mantle cavity is large. Anteriorly the mantle cavity is somewhat larger dorsally than ventrally (Fig. 43A,B). Posteriorly this proportion is reversed (Fig. 43C). Anterior part of the visceral sac is almost entirely occupied by large digestive gland. The hydrostatic organ is absent.

Head retractors are very thin and narrow. They do not form a complete muscular envelope around the visceral sac, but run along its sides as a pair of thin muscular bands (Fig. 43A). Posteriorly they gradually become thinner and disappear by the level of stellate ganglia. Posterior to the collar folds, the external of the two head retractors separates and forms anterodorsal mantle adductors (Fig. 43B). The latter are long and very thin. They are oriented obliquely and pass from the ventrolateral sides of the visceral sac to the dorsolateral walls of the mantle. The pallial nerves are small and indistinct. Anteriorly they are situated on the inner sides of the head retractors. Posteriorly they pass through the anterodorsal adductors and into the stellate ganglia at the sites of attachment of the anterodorsal adductors to the mantle.

Median mantle septum is thin and weakly muscular (Fig. 43B). It is formed by two very thin adductor muscles, which originate on the midventral mantle wall, pass almost parallel to one another and attach to ventral side of the visceral sac. Space of the adductors is very small, containing solely the median pallial artery. The rectum, ink sac and vena cava are shifted toward the visceral sac. The median adductor muscles do not extend anteriorly into the funnel.

The funnel is semicircular in cross-section (Fig. 43A). Its ventrolateral walls are fused with the collar folds into thick muscular layers. Dorsal walls of the funnel are less muscular, than the ventral one. The parts of the dorsal walls close to the visceral sac are membranous. They attach to the ventrolateral sides of the visceral sac, in the region of the head retractors. The lateral parts are more muscular. They adhere to the ventrolateral wall of the funnel and disappear on its inner surface. The collar folds are thick and muscular. They originate from the ventrolateral wall of the funnel and attach to the dorsal wall of the mantle, forming spacious collar pockets on both sides of the visceral sac.

The funnel retractors are thick, muscular ribbons fused to the visceral sac along their inner margins (Fig. 43B). The funnel retractors are highly modified as compared with other octopods: anteriorly they attach to the visceral sac by thin connective-tissue membrane; posteriorly they attach through special supporting cartilages, oval in cross-section. Inner side of each supporting cartilage is embedded in the connective-tissue envelope of the visceral sac, while its outer side attaches to the funnel retractor. At the site of attachment to the mantle, each funnel retractor is triangular in cross-section, with the low outer apex inserted into the mantle, the long dorsal apex connected with the visceral sac, and the long, ventral apex hanging freely into the mantle cavity (Fig. 43C). Breaks in the mantle muscle at the sites of attachment of the funnel retractors mark the normal position of stylets. Each break is filled by cartilage, probably the remnant of the shell sac (Fig. 43D). The lateral sides of the cartilage attach to the mantle walls, while inner concave side of the cartilage together with the mantle wall, form a shallow concavity, in which the funnel retractors are inserted. Thus, the funnel retractors attach to the inner side of the cartilage the same way they attach to the stylets in other shell-bearing incirrates. The gills fasten to the mantle wall below the attachment of the funnel retractors.

COMMENTS. General morphological design of *Argonauta* shows many features of adaptation to epipelagic mode of life. This species does not have a hydrostatic organ like *Ocythoe*, *Tremoctopus* and *Alloposus*, but it is known to trap air in its 'shell' for buoyancy [Young, 1960]. Comparing with *Ocythoe*, muscular components in all adductors in *Argonauta* are much weaker indicating its less reliance on strong jet-swimming. The funnel retractors are connected with the visceral sac through thin connective-tissue membrane (anteriorly) and unusual cartilage (posteriorly) (Fig. 43A,B). Ventral median mantle adductor at the site of attachment to the visceral sac is thin and narrow (Fig. 43C) and does not extend very far (Fig. 43C). Anterodorsal mantle adductors are very weak as they consist partly of a thin membrane (Fig. 43B). Reduction of muscle tissue makes the animal body fragile and unable to produce rapid jet thrusts.

Reduction of stylets in *Argonauta*, similarly with *Ocythoe*, is compensated by the development of a strong funnel locking-apparatus of teuthid type and by unusual strengthening of the attachment of the funnel retractors to the visceral sac. As with *Ocythoe*, reduction of stylets in *Argonauta* did not induce any major morphological transformation.

Bolitaenidae Chun, 1911

Japetella diaphana Hoyle, 1885

HABITS AND HABITAT. *Japetella diaphana* is a meso-bathypelagic octopod inhabiting tropical and temperate zones of the world oceans [Nesis, 1982/87]. Adults occur at depths from 600 m to 1050 m and apparently do not perform diurnal migrations [Young, 1978]. This octopod grows up to 10 cm ML.

EXTERNAL MORPHOLOGY. The body is weakly muscled and jellylike (Fig. 44). Dermal integument is gelatinous and thick, especially on the dorsal side of the head between the eyes, where it forms hood-like cover. Eyes are relatively large (about 15% ML) and located at the dorsolateral sides of the head. The funnel is short, embedded dorsally in the head along nearly its entire length. A funnel locking-apparatus is absent. Arms are shorter than the mantle. The web is relatively deep, connecting all arms for about 2/3 of their length. The mantle is elongated-ovoid, comprising approximately 55% TL. The stylets are absent, and breaks in the mantle musculature are barely visible on the posterolateral mantle. Mantle aperture is wide, reaching laterally the level of eyes (Fig. 44B).

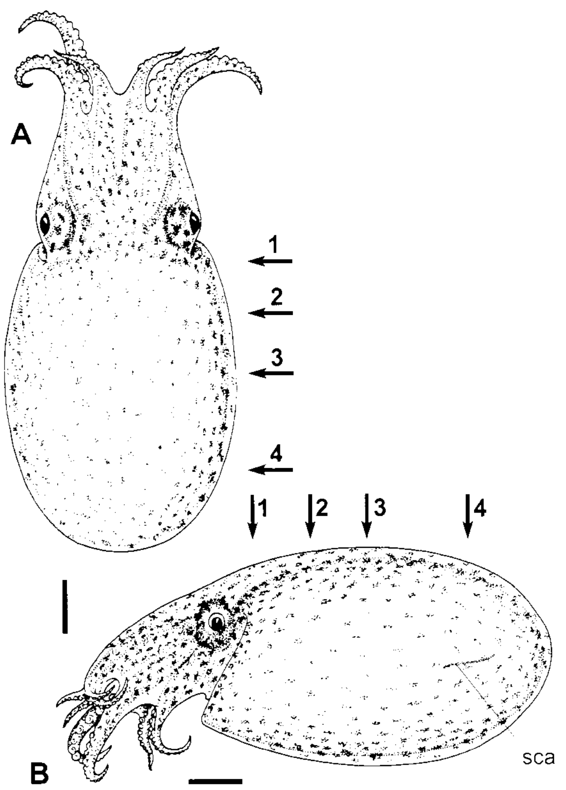


FIG. 44. General anatomy of *Japetella diaphana* (immature female: 57 mm ML). A. Dorsal view. B. Lateral view. Bold arrows with numbers indicate position of the cross-sections (shown in Fig. 45). Scale bars = 1 cm.

РИС. 44. Строение *Japetella diaphana* (незрелая самка: 57 мм ДМ). А. Вид с дорсальной стороны. В. Вид сбоку. Стрелки с цифрами указывают положение соответствующих срезов (показаны на Рис. 45). Масштаб = 1 см.

INTERNAL STRUCTURE. The walls of mantle and funnel are thick, but gelatinous and highly vacuolated. The mantle consists of two very thin layers of circular muscle separated by a thick gelatinous layer containing thin trabeculae of radial fibers (Fig. 45). Both ends of the trabeculae branch as they approach toward inner and outer surfaces of the walls of mantle and funnel. The dermal integument is thick. Mantle cavity is very large and almost reaches the posterior end of the mantle. Middle part of the visceral sac is occupied almost entirely by the digestive gland while the anterior part is filled by a gelatinous, watery core containing the esophagus,

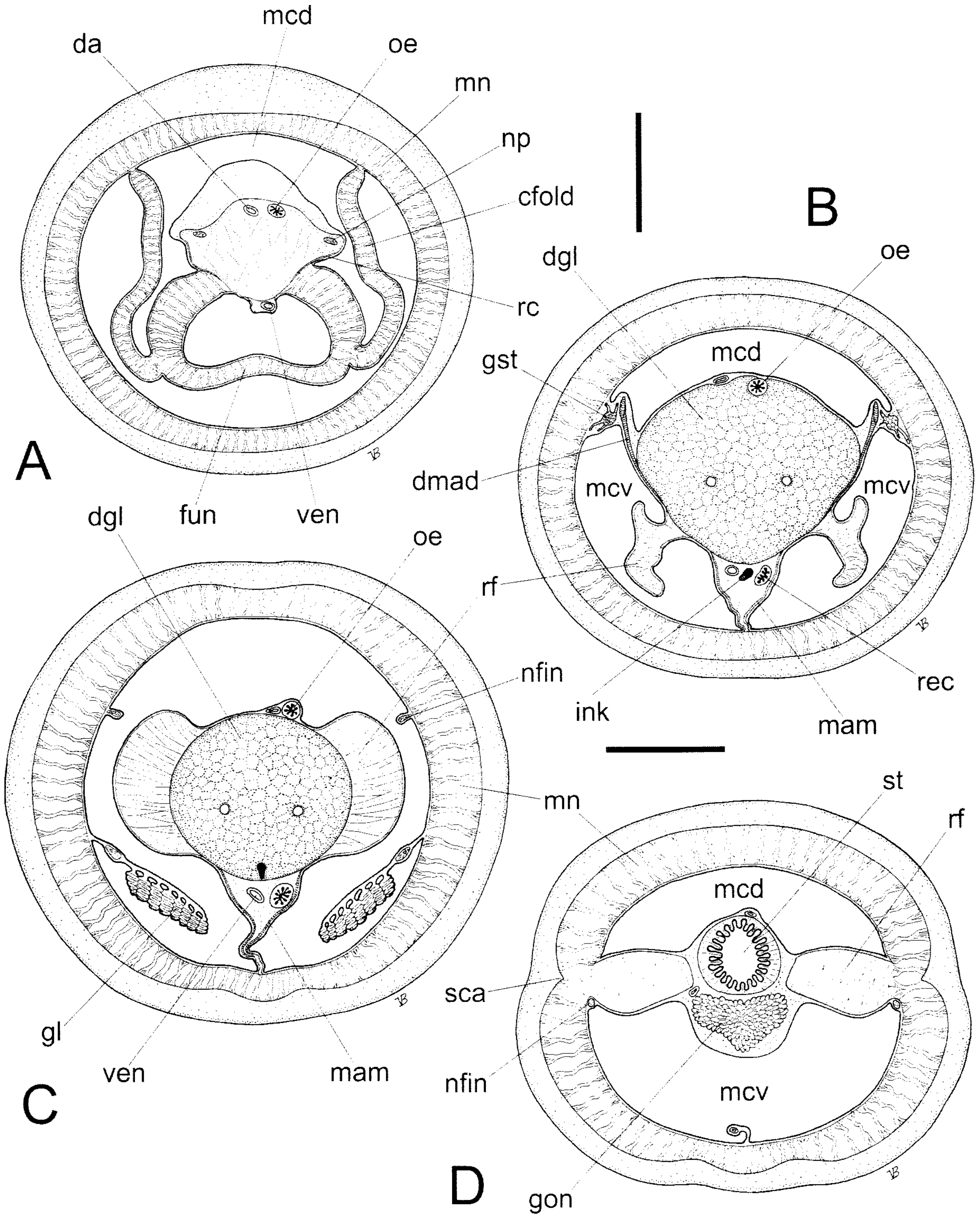


FIG. 45. Schematic cross-sections of *Japetella diaphana* (immature female: 57 mm ML). A. Section 1. at the level of the funnel. B. Section 2. at the level of dorsal mantle adductors. C. Section 3. between dorsal mantle adductors and funnel retractors. D. Section 4. at the level of attachment of the funnel retractors. Position of sections is indicated on Fig. 44. Scale bars = 1 cm.

РИС. 45. Срезы мягкого тела *Japetella diaphana* (незрелая самка: 57 мм ДМ). А. Срез 1. на уровне воронки. B. Срез 2. на уровне передних дорсальных мантийных аддукторов. C. Срез 3. между дорсальными мантийными аддукторами и ретракторами воронки. D. Срез 4. на уровне прикрепления ретракторов воронки. Положение срезов показано на Рис. 44. Масштаб = 1 см.

dorsal aorta and a pair of large pallial nerves (Fig. 45A). A hydrostatic organ is absent.

Head retractors are thin and barely visible in the cross-sections. They do not form complete envelope around the visceral sac but run as a pair of thin bands on its lateral sides (Fig. 45A). Behind collar folds the head retractors give origin to the anterodorsal mantle adductors (Fig. 45B). The latter are short. feebly muscular and extend between the dorsolateral sides of the visceral sac and the lateral walls of the mantle. The stellate ganglia lie on the mantle walls just ventral to the attachment sites of anterodorsal adductors.

The median mantle septum is relatively thick. but weakly muscular. It is formed by two thin adductor muscles that diverge from the middle line of the ventral mantle wall toward ventral side of the visceral sac (Fig. 45B.C). The rectum. vena cava and the ink sac are situated between and are embedded in gelatinous connective tissue.

The funnel is broad and its ventral and dorsolateral walls fuse into a single muscular layer (Fig. 45 A). The funnel walls attach to the ventrolateral sides of the visceral sac just ventral to the head retractors. The walls here are approximately twice as thick as the ventral wall of the funnel. Collar folds originate from lateral walls of the funnel. run alongside the visceral sac and attach to dorsal wall of the mantle. Muscular layers of the collar folds and funnel are fused and the boundaries between them are apparent only in the orientation of the radial muscles.

The funnel retractors in *Japetella* are unusual in shape. They are very wide, thick, long and broadly fused with the visceral sac along their entire length (Fig. 46C,D). Despite large size. the funnel retractors are weakly muscular, their nearly whole volume is occupied by gelatinous tissue with sparse. thin. radial muscle-fibers crossing into it. The cross-sections of the funnel retractors remind me of a pair of huge ballast tanks in a submarine (Fig. 45C). The gills are small and fragile: they fasten to the lateral mantle walls by thin ligaments.

Attachment of the funnel retractors to the mantle occurs unusually far posterior. in the posterior quarter of the mantle (Fig. 45B). At the site of attachment the funnel retractors extend horizontally, to the lateral sides of the visceral sac (Fig. 45D) and form an unusual horizontal partition of the mantle cavity. The funnel retractors are slightly thicker than the mantle muscle. The mantle muscles and funnel retractors are fused together without internal boundaries other than provided by the orientation of the radial muscles. Supporting cartilages are absent. The mantle does not have a break at the site of attachment, but its outer side bears distinct indentation indicating the normal position for a shell.

COMMENTS. Soft body anatomy of *Japetella* exhibits a number of features indicating that this species evolved mainly as passive deep-water floater. Its funnel fuses with the head along its entire length (Fig. 44B). Mantle musculature is greatly reduced and consists mainly of radial trabeculae (Fig. 45). The weak nature of virtually all musculature indicates reduction in animal activity. On the other hand. the presence of huge vacuoles in nearly all muscle tissue suggests that this gelatinous tissue is positively buoyant and acts as a floating device. The funnel retractors therefore, may truly be ballast tanks. Attachment of the funnel retractors to mantle is very weak. It is not supported either by shell or by connective tissue.

Reduction of stylets in *Japetella* did not induce any major transformation in its general morphological design. Despite some specialized characters, *Japetella* retained typical incirrate Bauplan. Unlike representatives of Argonautoidea clade. reduction of stylets in *Japetella* was not coupled with development of any functional substitutes (funnel locking-apparatus. mantle cartilages *etc.*). replacing the stylets. Such a reduction was apparently caused by general decline in animal activity. associated with pelagic life in the deep ocean.

Amphitretidae Hoyle, 1886

Amphitretus pelagicus Hoyle, 1885

HABITS AND HABITAT. Little is known about biology and ecology of *Amphitretus*. It is a rare meso-bathypelagic octopod inhabiting tropical and subtropical waters of the world oceans [Nesis, 1982/1987]. It has transparent, gelatinous and nearly colorless body and reaches up to 90 mm ML [Nesis. 1982/1987]. Young *Amphitretus* occur in upper mesopelagic depths during the day, judging by a few captures [Young et al., 1996]. There is no report on observations of this species from submersibles. but it has been observed in shipboard aquaria [Young *et al.*. 1998].

EXTERNAL MORPHOLOGY. Body is weakly muscular, jellylike, semitransparent and nearly colourless. The dermal integument forms a very thick, gelatinous cover over the body disguising its outline (Fig. 46). The stylets are absent, and the breaks in the mantle are not visible. The arms are long, about 1.5 ML and are connected by a deep transparent web for approximately 2/3 of their length. Anterior ventral walls of the mantle fuse with the funnel and head. As a result of this fusion, the mantle aperture is reduced to two small openings on the lateral sides of the head through which the water can be pumped inside the mantle cavity. The funnel is very long. tube-like and fused dorsally with the head for about of its length. The eyes are situated on dorsal side of

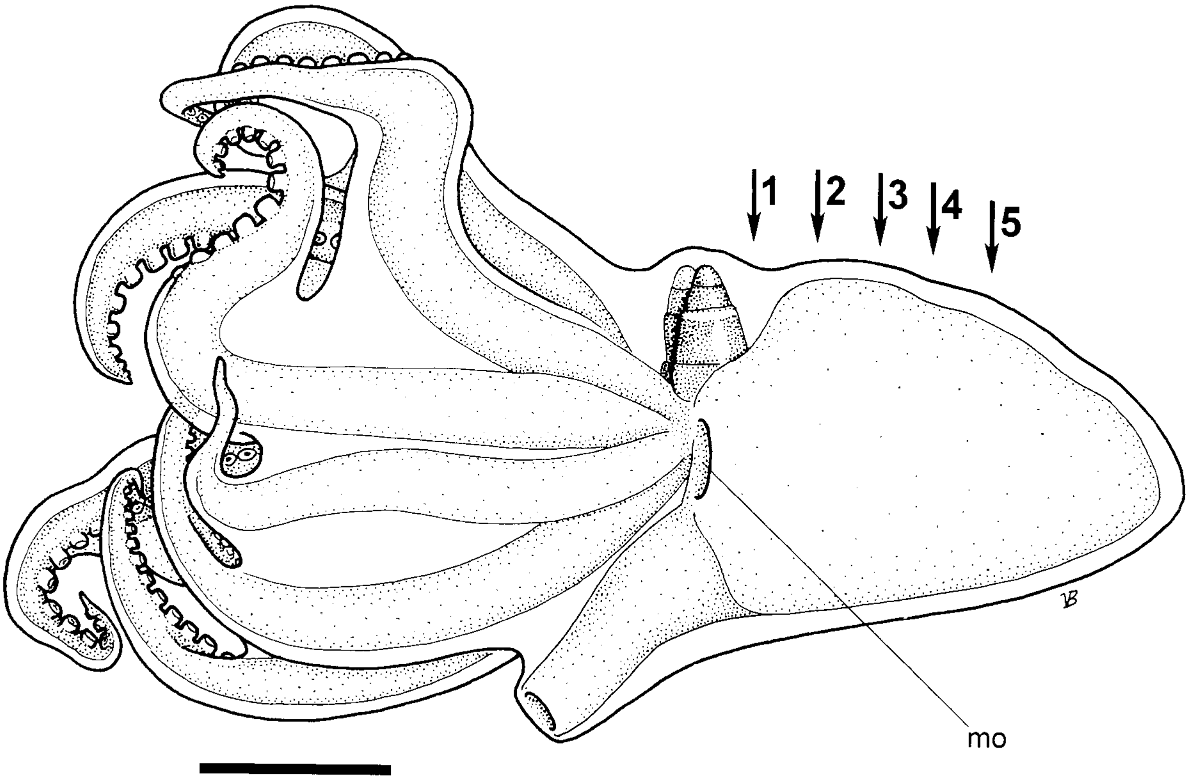


FIG. 46. Lateral view of *Amphitretus pelagicus* (immature male; 26 mm DML). Bold arrows with numbers indicate position of the cross-sections shown on Fig. 47. Scale bar = 1 cm.

РИС. 46. Вид сбоку *Amphitretus pelagicus* (незрелый самец; 26 мм ДМ). Стрелки с цифрами указывают положение соответствующих срезов, изображенных на Рис. 47. Масштаб = 1 см.

the head, their bases being in direct contact. They are unusual in shape and oriented dorsally.

CROSS-SECTIONS. A striking feature in *Amphitretus* anatomy is the presence of broad fusion between the anteroventral margins of the mantle, the collar folds and the lateral sides of the funnel (Fig. 47A) and between the posterolateral parts of the collar folds and the visceral sac (Fig. 47B). *Amphitretus* is the only incirrate octopod having such a fusion which is strikingly similar in position and structure with the collar fusion found in cirrates (e.g., *Grimpoteuthis*, Fig. 12A; *Cirroteuthis*, Fig. 17B,C) but differs in maintaining lateral openings to the mantle cavity. The fusion between the funnel and mantle has the effect of eliminating the mantle wall beneath the funnel, which forms a deep incision in the ventral mantle wall.

Funnel is wide but thin-walled. Its ventral and lateral walls are formed by single muscular layer that differs from the dorsal walls in the orientation of muscle fibers (Fig. 47A). The collar folds represent dorsolateral extensions of the dorsal walls of the funnel. They pass alongside the visceral sac and attach to the dorsal mantle wall forming spacious collar pockets on both sides of the visceral sac. The lateral sides of the funnel and adjacent parts of the collar folds are fused with the mantle. Posteriorly the collar folds fuse both with the mantle and with the visceral sac (Fig. 47B). Here the fusion between the collar and the visceral sac is very thick and consists of an outer thin muscular layer and a thick inner vacuolated, gelatinous core. The core is pierced by radial muscle-bundles running from the outer layer to the visceral sac (Fig. 47B).

The walls of mantle and funnel are thin, gelatinous and weakly muscular. The mantle bears a wide longitudinal groove on its dorsal side and a narrow groove on its ventral side defined by the mantle thickness in these areas (Fig. 47C-E). The mantle wall in the dorsal groove is approximately half as thick as the adjacent areas. The thickness of the dermal integument is roughly equal to or greater than that of the mantle. Mantle cavity is very large but the visceral sac is rather small. The digestive gland is elongated vertically, so it looks disproportionately large on cross-sections. The anterodorsal part of the visceral sac is fused with dorsal mantle wall (Fig. 47A). The stomach occupies

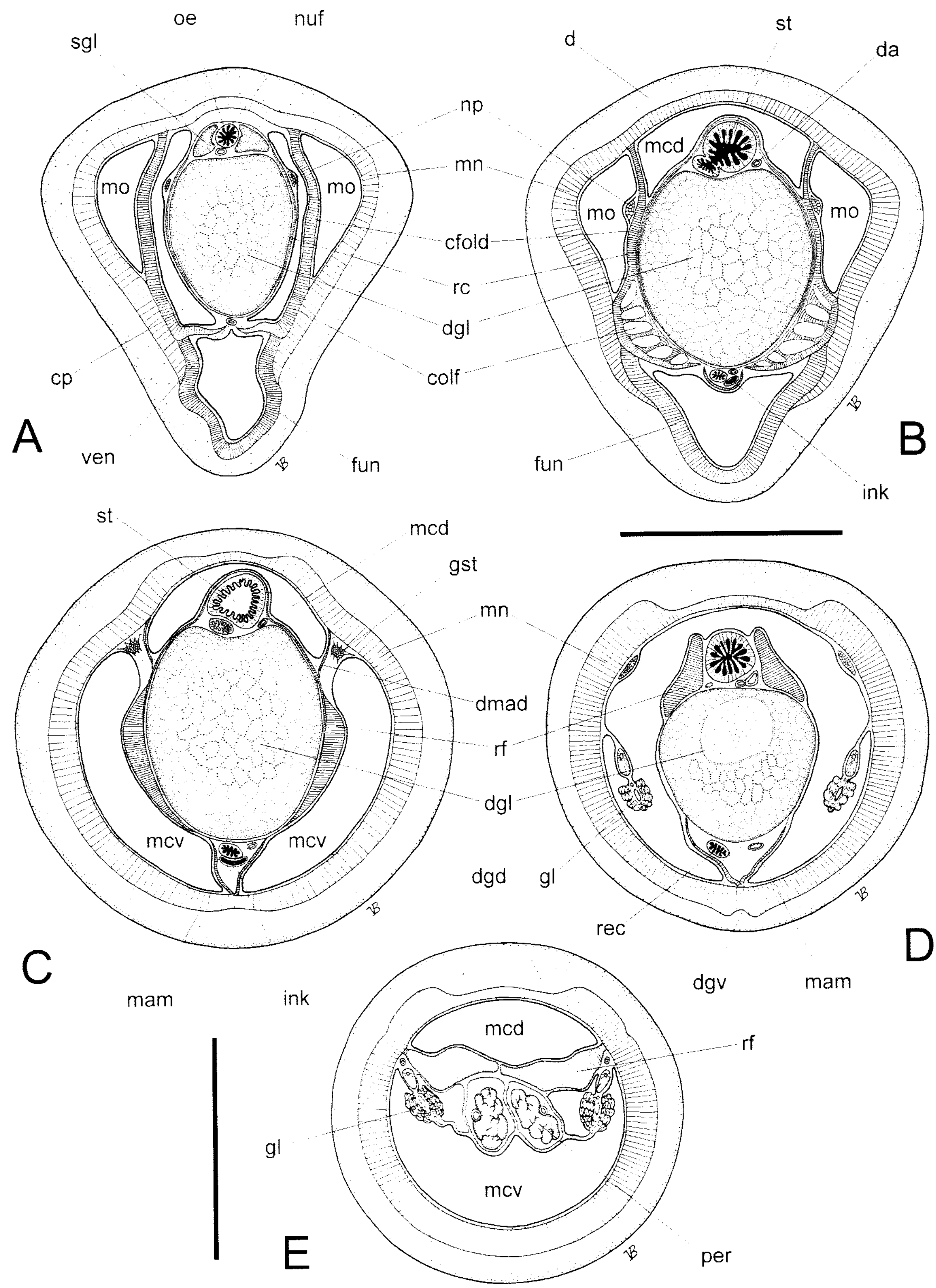


FIG. 47. Schematic cross-sections of *Amphitretus pelagicus* (immature male: 26 mm DML). A. Section 1, at the level of anterior margin of the mantle. B. Section 2, at the level of the posterior part of the funnel. C. Section 3, at the level of dorsal mantle adductors. D. Section 4, behind dorsal mantle adductors. E. Section 5, at the level of attachment of the funnel retractors. Position of sections is indicated on Fig. 46. Scale bars = 1 cm.

РИС. 47. Срезы мягкого тела *Amphitretus pelagicus* (незрелый самец; 26 мм ДМ). А. Срез 1, на уровне переднего края мантии. В. Срез 2, на уровне задней части воронки. С. Срез 3, на уровне передних дорсальных мантийных аддукторов. D. Срез 4, позади дорсальных мантийных аддукторов. Е. Срез 5, на уровне прикрепления ретракторов воронки. Положение срезов показано на Рис 46. Масштаб = 1 см.

a position on the dorsal side of digestive gland (Fig. 47B,C). A hydrostatic organ is absent.

The head retractors are very thin and barely visible in the cross-sections. They run along the lateral sides of the visceral sac as film-like muscular bands (Fig. 47B). Posterior to the funnel they branch outward forming anterodorsal adductors (Fig. 47C). The latter are thick but weakly muscular consisting mainly of gelatinous connective tissue. They extend obliquely between the visceral sac and the dorsolateral walls of the mantle. Anteriorly the small pallial nerves are situated on dorsolateral sides of the visceral sac. The nerves pass through the collar muscle and the anterodorsal adductors and enter the stellate ganglia. The latter occupy the typical position adjacent to the attachment sites of anterodorsal adductors to the mantle.

The median mantle septum is thick, broadly triangular in cross-section, and weakly muscular (Fig. 47C,D). It is formed by two very thin adductor muscles, that diverge from the mid-line of the ventral mantle wall toward ventral side of the visceral sac. Between the adductors are the ink sac, intestine and vena cava embedded in gelatinous connective tissue.

The funnel retractors occupy unusual positions: they originate from the dorsal walls of the funnel, pass along lateral sides of the visceral sac to its dorsal side where they merge together forming a single muscular layer over the visceral sac to their attachment sites on the mantle (Fig. 47E). The mantle wall exhibits no modifications where the retractors attach. Supporting cartilages are absent.

COMMENTS. General morphological design of *Amphitretus* shows a unique set of adaptations to planctonic life in deep ocean waters. Watery consistency of the body and the loss of heavy musculature apparently contributes greatly to buoyancy. However, the structure that provides some positive buoyancy is unknown. The mantle cavity is more complex in *Amphitretus* due to the fusion of the collar folds with the mantle and visceral sac and vertical orientation of the digestive gland (Fig. 47A,B). The latter is achieved by special muscles that actively maintain the digestive gland in vertical position in different postures of the animal [Young *et al.*, 1998]. Functional meaning of the fusion between the ventral mantle wall with the funnel and collar folds is unclear. It may help to optimize respiration flows at low energy costs and/or fix position of the funnel. Presumably the primary locomotion for *Amphitretus* is slow swimming with medusoid contraction of its deep umbrella.

Despite many specialized characters, *Amphitretus* retained typical incirrate plan of structure and, according to Nesis [2002] and Voight [1997], evolved apparently from benthic incirrate octopods, all of them having open mantle aperture. Fusion of the mantle and funnel means that there was no more need to anchor the funnel retractors in the mantle by stylets, and the latter became redundant and was lost. The role of the funnel retractors changed from support of the funnel to support for the visceral sac. This new role is the most obvious at the level of attachment of the funnel retractors to the mantle, where the funnel retractors fuse together making muscular 'roof' above the visceral sac (Fig. 47E). Like in other shell-lacking incirrate octopods, position of the former stylets in *Amphitretus* may be spotted by attachment of the funnel retractors. General morphological design of mantle complex in *Amphitretus* represents the most specialized state among the species described in the present study. The means by which the peculiar funnel mantle fusion occurs is described for the first time.

DISCUSSION

> *Look around and see all the jellyfish.*
> *You sayin' flotation is groovy, baby.*
> Jimi Hendrix, 'Power of soul'

Variation of the shell structure and shell-soft body relationship in Vampyropoda

In order to determine the evolution of the shell in octopodiforms, the species with the most primitive shells in each group will be selected and its pertinent characters listed.

Vampyromorphida

A single representative exists. The characteristics of the vampyromorph that are considered to be primitive and pertinent to this study are the following (Table 2):

1. The length of the gladius is about equal to the mantle length.

2. The gladius consists of three morphological parts (dorsal plate, conus and rostrum), is built of three shell layers (ostracum, hypostracum, and periostracum), and its dorsal plate (= proostracum) consists of five longitudinal elements: middle plate (rachis), a pair of lateral plates and a pair of wings. All elements of the proostracum are delimited by asymptotic borderlines. I call this combination of characters the 'teuthoid plan'.

3. The middle plate (rachis) is wide and tongue-shaped. It is the longest part of gladius proostracum. Lateral plates of proostracum are much narrower than the wings.

4. The growth of the gladius occurs by adding layers to each of the three shell layers. The middle layer (ostracum) grows by increments added from the anteroventral side and arranged in tile-like pat-

Table 2. Characteristic features of the shell and its relationship with the soft body in Vampyropoda.

Таблица 2. Характерные черты строения раковины и ее взаимоотношения с мягким телом у Vampyropoda.

Character	**Vampyromorphida**	**Cirrata**	**Incirrata**
Shell condition and structure:			
Presence of the inner shell	present	present	present or absent
Condition of the shell	longitudinal chitinous plate (gladius)	transversal cartilage-like U-shaped plate	a pair of cartilage-like rods (stylets)
Shell length	approx. equal to the ML	less than the ML	less than the ML
Shell structure	entire	entire	divided in the median part
Structural parts: proostracum, conus and rostrum	present	absent	absent
The shell layers (ostracum, hypostracum and periostracum)	all three shell layers are present	one shell layer is present (hypostracum?)	one shell layer is present (hypostracum?)
Shell growth pattern	tile-like pattern (ostracum and hypostracum) and concentric pattern (periostracum)	concentric pattern	concentric pattern
Position of shell in the body	superficial, terminal	superficial, subterminal	superficial, subterminal
Muscle attachment:			
Funnel retractors	attach to the wings	attach to anteroventral parts of the wings	attach from inside to anterior half of the stylets
Head retractors	attach to the lateral plates	attach from inside to anterior, dorsal and ventral margins of the wings	attach to the mantle
Upper margins of the collar folds	attach anteriorly to lateral sides of the nuchal cartilage	posteriorly to the shell sac and the visceral sac	attach to the mantle
Soft body morphology:			
Nuchal fusion between the mantle and the head	fused in young and adults	free in paralarvae	fused at all stages
Stellate ganglia	closely situated in paralarvae	widely separated in adults	widely separated
Dorsal mantle cavity	absent	present	present
Anterodorsal mantle adductors	absent	absent	present
Number of fins	two pairs	one pair	fins absent
Articulation of the fins	fin bases are separated from the shell sac by epithelial basal pockets	fin bases are fused with the shell sac. Basal pockets absent	—
Ventral median mantle adductor	absent	present	present
Funnel locking-apparatus	present, primitive	absent	absent in primitive forms

tern: each next increment is shifted anteriorly against the previous increment. As a result, the thickness of the ostracum gradually increases with growth, while the earlier regions of the ostracum lose contact with the shell epithelium and stop growing. Growth of the inner layer (hypostracum) occurs by adding of cartilaginous-like material to the ventral surface in the posterior half of the proostracum. The increments of the inner layer are slightly shifted forward against each other, and every newly secreted layer overlaps the anterior margin of the previous layer while posteriorly it gradually wedges in the region of the cone flags. Outer layer (periostracum) grows by concentric layers of conical shape that are laid down on the outer surface of the previous layer. Center of growth of all three layers (initial shell) is situated in the apical part of the conus [Bizikov, 1996].

5. The gladius occupies a superficial position: the mantle muscles attach to the ventral (inner) side of the gladius along its entire periphery, except for the anterior margin of free rachis.

6. The funnel retractors attach to the anterior margins of the wings.

7. The head retractors attach to anterior margins of the lateral plates.

8. The visceral sac is fused with the shell sac along its entire length. Dorsal mantle cavity and anterodorsal mantle adductors are absent.

9. The head originally is not fused with the mantle. In adults the head is fused; however, in paralarvae, anterior dorsal margin of the mantle is not fused with the head in the nuchal region [Young, Vecchione, 1999].

10. The shell sac is fused with the visceral sac throughout its length (i.e., a dorsal mantle cavity is absent).

11. The stellate ganglia are situated on both side of the gladius at the level of lateral plates and in adults are widely separated.

12. Two pairs of fins are present: a paralarval pair that is eventually resorbed and a juvenile/adult set that develops later and more anteriorly [Pickford, 1940; 1949]. Paralarval fins, which are considered the primitive fins, lie over the wings of the gladius and attach to the shell [Young, Vecchione, 1996]. The adult fins are separated from the shell sac by epithelial basal pockets.

13. Upper margins of collar folds attach to lateral sides of the nuchal cartilage and the shell sac anteriorly and to the visceral sac and the shell sac posteriorly.

COMMENTS. Pickford [1949] found that development of fins in *Vampyroteuthis* is unique among cephalopods. In this species early paralarvae (Pickford's "stage 1 larvae") have one pair of fins. Then the second pair of fins develops anteriorly of the first pair, and the number of fins reaches four ("stage 2"). As development proceeds, the first pair of fins gradually resorbs and finally disappears, while the second pair increases in size ("stages 3 and 4"). The first pair of fins is proved to be homologous to the fins of other cephalopods [Young, Vecchione, 1996]. Our data show that articulation of adult fins with the shell and mantle in *Vampyroteuthis* follows the same basic coleoid pattern described earlier in teuthids [Naef, 1921/1923: Fig. 66] and sepiids [Naef, 1921/1923; Fig. 290]. It is especially close to condition found in some oegopsid families, for example, Enoploteuthidae, where the gladius occupies superficial position and the fin bases rest on its dorsal side, separated from the shell sac by basal pockets [Naef, 1921/1923: Fig. 66a].

Apart from the fin structure, *Vampyroteuthis* paralarvae are very similar to adults in other respects. On the contrary, the hatchlings look very different, exhibiting a number of archaic features that disappear during later development. Young and Vecchione [1999] described recently hatched *Vampyroteuthis* (8 mm ML) that had large funnel, which was not embedded in the head, no fusion of the mantle and head, no thick gelatinous integument covering the body, short arms, no web between arms, thick filaments that were approximately equal to the arms in length and situated in one circle with the other arms, and the gladius with 'somewhat narrower median field' (Fig. 48). The gladius of *Vampyroteuthis* hatchlings deserves a special attention. In contrast to adults, it has narrow rachis (median plate), which has long anterior free part. The lateral plates and wings are short, weekly developed and fused with the cone flags forming posterior extension of the gladius. The rostrum seems to be very small. Position of wings in posterior half of the gladius means that the funnel retractors in hatchlings should be much longer than in adults. The structure of gladius in *Vampyroteuthis* hatchling is surprisingly similar to the gladii of some recent oegopsid squids.

Another remarkable feature of *Vampyroteuthis* is that its stellate ganglia are weakly developed and apparently shift their position during ontogeny. Position of stellate ganglia is different in teuthoids and octopodiforms. Being situated laterally of the shell in all coleoids [Naef, 1921/1923], the stellate ganglia in teuthoids are located extremely close to one another and are connected by an interstellate connective [Ivanov, Strelkov, 1949]. In octopods they are set widely apart and are not connected. In *Vampyroteuthis* the interstellate connective is absent, and the stellate ganglia apparently shift their position during ontogeny in accordance with ontogenetic widening of the gladius. In hatchlings they are apparently situated closer to each other, like in teuthoids, while in adults they are set widely apart, like in octopods (Fig. 2A).

Thus, ontogenetic data show that recent *Vampyroteuthis* apparently evolved from some ten-armed four-finned coleoids with free funnel and free anterodorsal mantle margin. In general, *Vampyroteuthis* exhibits basically the same pattern of gladius-soft body relationship as the one described earlier in some egopsid squids [Bizikov, 1996; Bizikov, Arkhipkin, 1997]. Obviously, it is very close to the ground coleoid pattern of shell-soft body relationship. In Oegopsida the muscle arrangement is the most close to *Vampyroteuthis* with retractors of the head and the funnel attaching correspondingly to the lateral plates and wings of the gladius, and the fins lying over the wings of the gladius and attaching to it through the epithelial basal pockets [Bizikov, 1996: Fig. 40]. In Myopsida the muscle arrangement is similar except for the fins that do not contact with the shell but lie over the mantle wall and attach to it through the basal pockets [Bizikov, 1996: Fig. 39]. Thysanoteuthids have unique pattern of muscle arrangement, with the head retractors at-

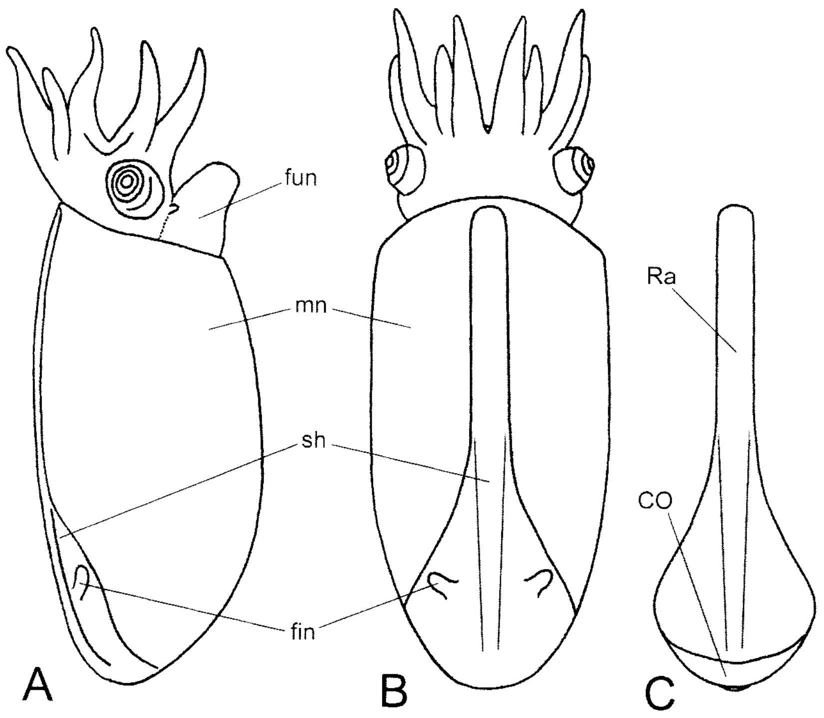


FIG. 48. Schematic drawings of *Vampyroteuthis infernalis* hatchling illustrating position and shape of its gladius [redrawn from Young, Vecchione, 1999]. A. Lateral view from right side. B. Dorsal view. C. Ventral view of the gladius.

РИС. 48. Внешний вид личинки *Vampyroteuthis infernalis* непосредственно после выклева, иллюстрирующий форму и положение гладиуса [из Young, Vecchione, 1999]. А. Вид с правой стороны. В. Вид с дорсальной стороны. С. Вид гладиуса с вентральной стороны.

taching to extremely wide anteriorly protruding 'wings' and long funnel retractors attaching to the 'cone fields' [Bizikov, 1966; Fig. 38]. The fins in Thisanoteuthidae attach to the mantle the same way as in Myopsida.

Cirrata

Of the genera examined, *Opisthoteuthis* appears to be the most primitive in respect to the shell as it is the only taxa that has the funnel retractors attached to the shell. The characteristics of the Cirrata that are considered to be primitive and pertinent to this study are the following (Table 2):

1. Gladius is thick cartilage-like U-shaped structure without asymptotic lines lying transversally on dorsal side of the mantle.

2. Gladius grows by concentric increments of cartilage-like substance. The center of growth (initial shell) is situated in the medial part of the gladius.

3. The gladius occupies superficial subterminal position. The mantle attaches to the gladius along its entire periphery, including anterior middle part.

4. The funnel retractors attach to anteroventral parts of the wings that sometimes may be extended into flexible 'horns'.

5. The head retractors attach from inside along periphery of the wings (dorsal, anterior and ventral margins of the wings).

6. A dorsal mantle cavity is present. It is a narrow slit between the visceral sac and the dorsal mantle wall that extends posteriorly between stellate ganglia almost to the level of the shell and connects laterally to the ventral mantle cavity. Anterodorsal mantle adductors are absent.

7. The stellate ganglia are set widely apart lying at the junction of the visceral sac and the lateral mantle walls.

8. The anterior dorsal mantle margin fused with the head.

9. The fins bases adhere tightly to the shell sac over flat outer surface of lateral wings of the gladius. Basal pockets are absent.

10. Upper margins of collar folds attach to the mantle.

COMMENTS. In recent Cirrata, primitive wide U-shaped gladii with relatively long and narrow lateral wings are found in *Opisthoteuthis*, *Grimpoteuthis*, *Cirroctopus*, *Luteuthis* and *Stauroteuthis* (Fig. 49). Among the genera listed, *Cirroctopus* deserved special attention as it includes the species with the gladii exhibiting transitional features between Cirrata and Incirrata. For example, *C. antarctica* (Ku-

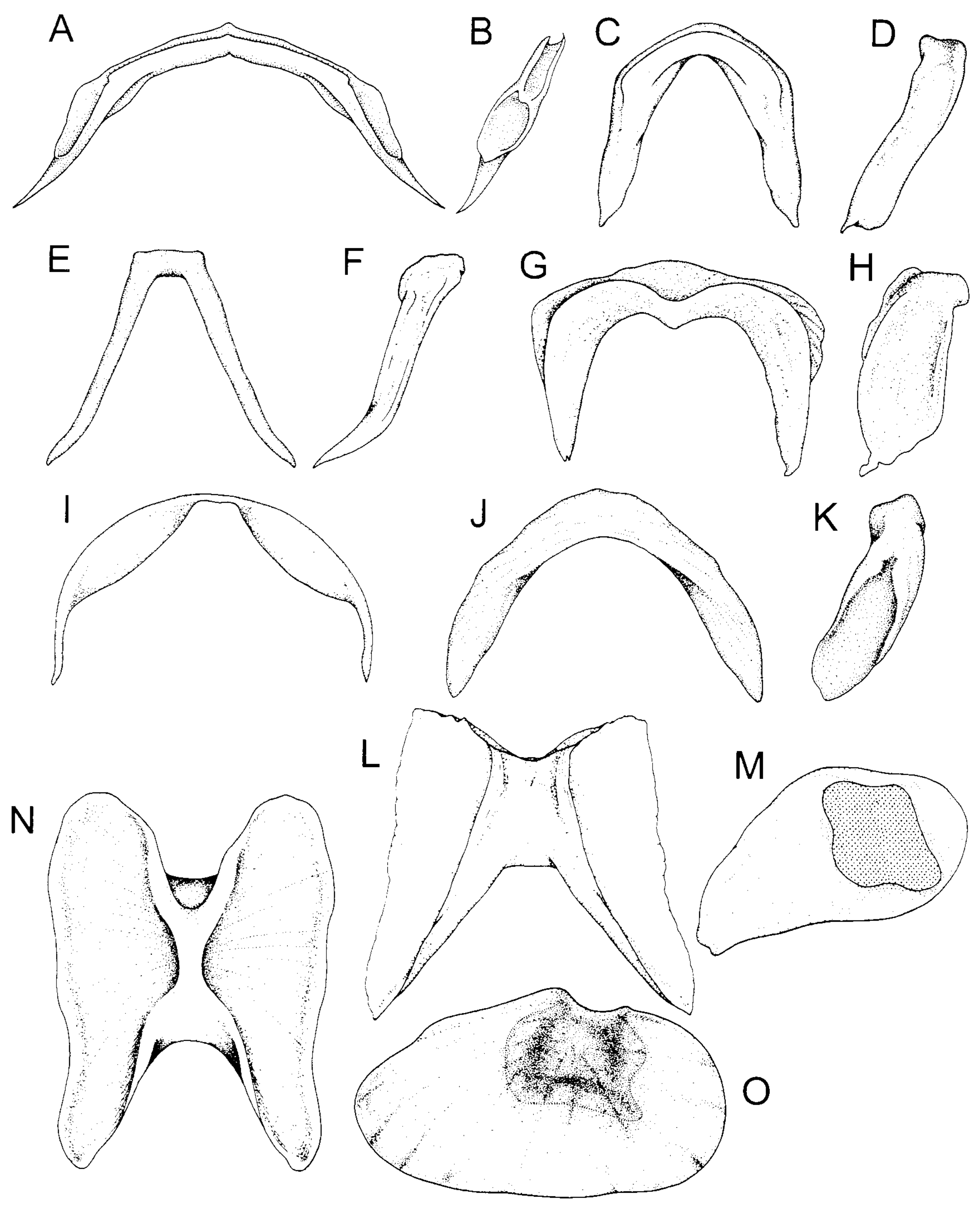


FIG. 49. Morphological variability of gladii in Cirrata (not in scale). A, B – *Opisthoteuthis californiana* Berry, 1949. C, D – *Grimpoteuthis umbellata* (Fischer, 1883). E, F — *Cirroctopus hochbergi* O'Shea, 1999. G, H – *Luteuthis shuishi* O'Shea et Lu, 2002. I – *Cirroctopus antarctica* Kubodera et Okutani, 1986. J, K – *Stauroteuthis syrtensis* Verrill, 1879; L, M — *Cirrothauma murrayi* Chun, 1911. N, O – *Cirroteuthis muelleri* Eschricht, 1838. A, C, E, G, I and J — anterior view (dorsal side is up). L, N – dorsal view (anterior end is down). B, D, F, H, K, M and O — lateral view (anterior end is on the left; dorsal side is up). [A-D, L and M – figures of the author; E-H – after Vecchione, Young, 2003b; I – after Kubodera, Okutani, 1986; J, K – after Collins, Henriques, 2000; L, M – after Aldred et al., 1983].

РИС. 49. Морфологическое разнообразие гладиусов цирратных осьминогов (масштаб не соблюден). A, B – *Opisthoteuthis californiana* Berry, 1949. C, D – *Grimpoteuthis umbellata* (Fischer, 1883). E, F — *Cirroctopus hochbergi* O'Shea, 1999. G, H – *Luteuthis shuishi* O'Shea et Lu, 2002. I – *Cirroctopus antarctica* Kubodera et Okutani, 1986. J, K – *Stauroteuthis syrtensis* Verrill, 1879; L, M — *Cirrothauma murrayi* Chun, 1911. N, O, – *Cirroteuthis muelleri* Eschricht, 1838. A, C, E, G, I и J – вид спереди (дорсальная сторона наверху). L, N – вид с дорсальной стороны (передняя сторона внизу). B, D, F, H, K, M and O – вид сбоку (передняя сторона слева; дорсальная сторона наверху). [A-D, L и M – рисунки автора; E-H – из Vecchione, Young, 2003b; I – из Kubodera, Okutani, 1986; J, K – из Collins, Henriques, 2000; L, M – из Aldred et al., 1983].

Table 2. Principal morphological characteristics of stylets in Incirrata (average values).

Таблица 2. Основные морфометрические характеристики стилетов Incirrata (средние значения).

	Enteroctopus	Benthoctopus	*Bathypolypus*	*Eledone*	*Alloposus*	*Tremoctopus*
Stylets length (in % of ML)	24	10	17	17	10	17
Distance between stylets (in % of ML)	50	43	52	80	54*	45*
Thickness of stylets (in % of stylet length)	6.6	16	14	7	46	18
Anterior shoulder length (in % of stylet length)	33	33	33	40	33	33
Angle between shoulders	140°	125°	112°	127°	135°	180°
Surface of angle	sculptured	smooth	sculptured	smooth	smooth	smooth
Consistency	stiff	soft	moderately soft	soft	gelatinous	moderately soft

Remarks: asterisk (*) marks position of stylets on lateral side of the mantle. In these cases distance between stylets is equal to the mantle width.

Примечание: (*) помечены стилеты, расположенные на боковых сторонах мантии. В этих случаях расстояние между ними соответствует ширине мантии.

bodera et Okutani, 1986) has the gladius with markedly weakened medial part and thickened sigmoidal lateral wings (Fig. 49 I). Such a shape of the gladius is unique among recent octopods, but it is strikingly similar to the gladius of fossil *Palaeocopus newboldi* (Woodward, 1896), the earliest incirrate octopod from the late Cretaceous (Fig. 55E,F). Another congeneric species, *C. hochbergi* O'Shea, 1999, has the gladius with long rod-like lateral wings, which diverge in a V-like pattern and are distinctly bent in their distal parts (Fig. 49E,F). The bend of the wings in *C. hochbergi* apparently marks the places of attachment of the funnel retractors and corresponds to characteristic bend in incirrate stylets. Gladii of *C. antarctica* and *C. hochbergi* illustrate how the transformation of cirrate gladius into incirrate stylets could happen in evolution.

Butterfly-like gladii of *Cirroteuthis* and *Cirrothauma* represent the most evolutionary advanced stage of the shell in Cirrata. Flared lateral wings providing support for the fins, become the most prominent element of the gladius. The saddle is very narrow and deep. The funnel retractors do not contact with the gladius, but attach to the mantle wall.

Incirrata

Of the genera examined, *Enteroctopus* appears to be the most primitive in respect to the shell as it is the genus with the most well-developed shell and associated muscles; the shells of all other genera appear to be derived via reduction. The characteristics of the Incirrata that are considered to be primitive and pertinent to this study are the following (Table 2):

1. The shell is reduced to a pair of stylets each with a shell sac. The stylets are thin cartilage-like rods with pointed ends lying on dorsolateral side of the mantle at sharp angle to longitudinal axis. Each stylet is bent in its anterior part into obtuse angle with the apex directed inside the mantle.
2. The stylets grow by concentric increments of cartilage-like substance with the center of growth (initial shell) for each stylet in its bend.
3. The stylets occupy subterminal position. The mantle attaches to the stylets along their entire periphery. Both anterior and posterior ends of each stylet are embedded inside the mantle wall, while the middle part occupies a superficial position.
4. The funnel retractors attach to the inner sides in the anterior half of the stylets. At the sites of attachment the stylets may be bent inward.
5. The head retractors are thick and muscular anteriorly, but become thinner posteriorly. At the level of stellate ganglia, the outer layers of the head retractors branch off the visceral sac forming the anterodorsal mantle adductors. Each adductor exhibits a twist of about 180°.
6. A dorsal mantle cavity extends from the nuchal region to the level of posterior margins of the stylets. Dorsal and ventral mantle cavities are broadly confluent on lateral sides of the visceral sac

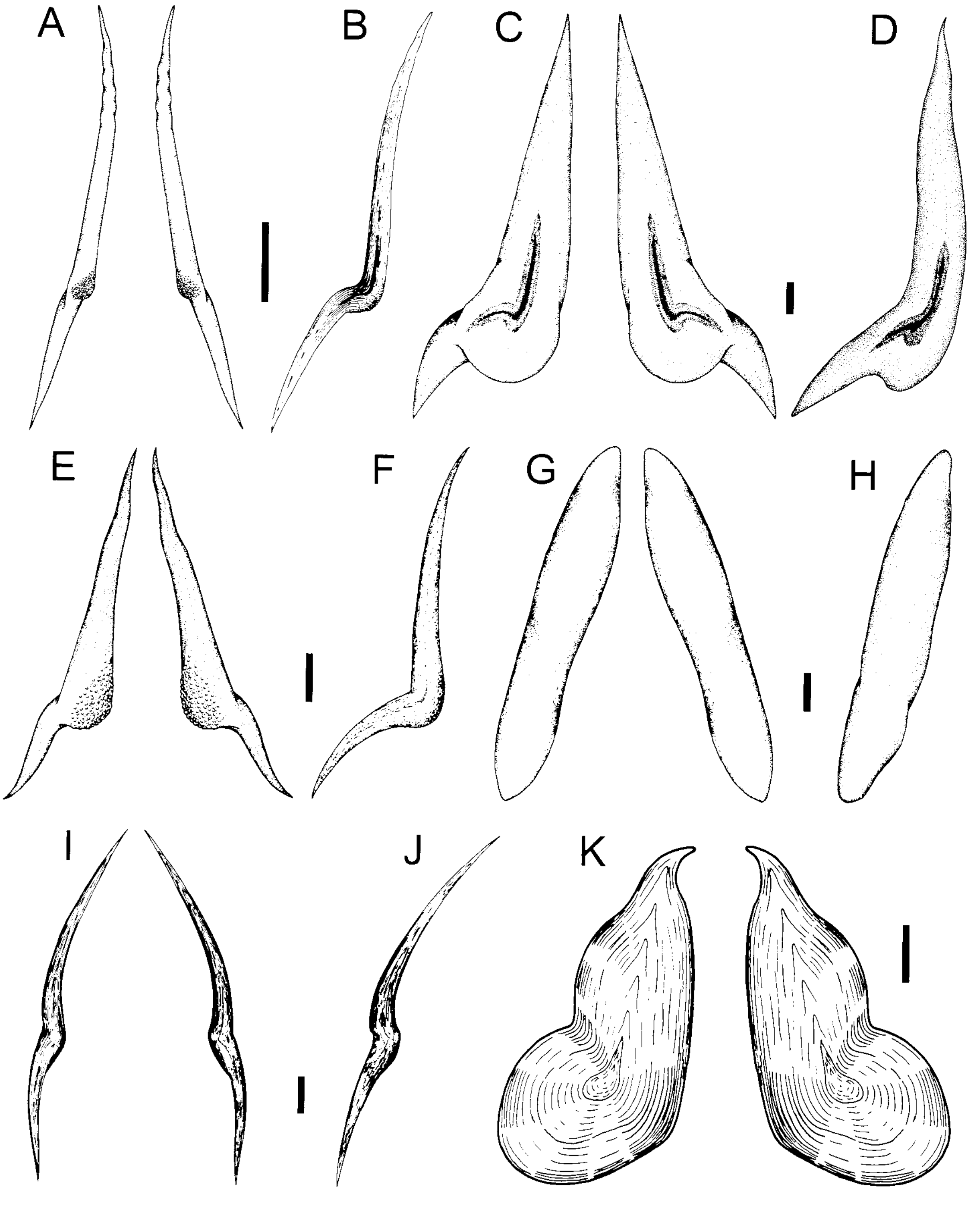


FIG. 50. Morphological variability of the shell remnants (stylets) in Incirrata. A, B – *Enteroctopus dofleini* (Wülker, 1910). C, D – *Benthoctopus sibiricus* Loyning, 1930. E, F – *Bathypolypus salebrosus* (Sasaki, 1920). G, H – *Tremoctopus violaceus* delle Chiaje, 1830. I,J – *Eledone messyae* Voss, 1964. K – *Alloposus mollis* Verril, 1880. A, C, E and G — ventral view of a pair of stylets (anterior end is down). I – dorsal view of a pair of stylets (anterior end in down). K – inner lateral view of a pair of stylets (ventral sides of both stylets face inside; anterior end is down). B,D,F, H and J – lateral view (anterior end is down; ventral side is on the right). A,B: scale bar = 1 cm. C — K: scale bar = 1 mm. All figures made by the author.

РИС. 50. Морфологическое разнообразие парных стилетов (рудиментов раковины) инцирратных осьминогов. A, B – *Enteroctopus dofleini* (Wülker, 1910). C, D – *Benthoctopus sibiricus* Loyning, 1930. E, F – *Bathypolypus salebrosus* (Sasaki, 1920). G, H – *Tremoctopus violaceus* delle Chiaje, 1830. I,J – *Eledone messyae* Voss, 1964. K – *Alloposus mollis* Verril, 1880. A, C, E и G – вид с вентральной стороны (передняя сторона внизу). I – вид с дорсальной стороны (передняя сторона внизу). K – вид пары стилетов сбоку (изнутри): вентральная сторона обоих стилетов обращена внутрь; передняя сторона внизу. B,D,F, H и J – вид сбоку (передняя сторона внизу; вентральная сторона справа). A,B: масштаб = 1 см. C — K: масштаб = 1 мм. Рисунки автора.

anteriorly and posteriorly to the anterodorsal adductors.

7. The stellate ganglia are set widely apart lying on the inner surface of the mantle just lateral to the attachment sites of the anterodorsal adductors.

8. The anterodorsal mantle margin is fused with the head.

9. The upper margins of the collar folds attach to the mantle.

10. The fins are absent.

COMMENTS. Relatively long, stiff, moderately thick and distinctly bent stylets of Octopodidae apparently represent the most primitive condition of incirrate type of shell. Such stylets could be evolved directly from primitive gladius of cirrate type through reduction of median transversal connection (saddle). In benthic shallow-water *Enteroctopus* the stylets are stiff, with well-developed sculptured bend (Fig. 50A,B). The stylets in *Enteroctopus* are the largest among Incirrata reaching up to 30 % ML (Table 3). In deep-sea octopodids the stylets decrease in size, become softer and sometimes smooth. In *Benthoctopus* they retain considerable thickness (ca. 16% of stylets length; Table 3: Fig. 50C,D) and well-developed bend, but lack sculpture and become soft. Stylets of *Bathypolypus* occupy intermediate position between well-developed stylets of *Enteroctopus* and reduced ones in *Benthoctopus* (Fig. 50E,F). The stylets in *Eledone* are very narrow (their greatest width is about 7% of their length), soft, smooth and almost straight (Fig. 50I,J).

Among pelagic octopods of Argonautoidea clade the stylets are found in two primitive families only: Alloposidae and Tremoctopodidae. In both cases they show signs of deep reduction. In *Alloposus* the stylets lost stiffness and became gelatinous, water-rich and inflated (Fig. 50K). As a result, width of the stylets in *Alloposus* reaches 46% of their length, the greatest value among Incirrata. In *Tremoctopus* the stylets are straight, moderately soft and smooth (Fig. 50G,H). Attachment of the funnel retractors shifted toward anterior end of the stylets, resulting in reduction of the bend. In *Ocythoe* and *Argonauta* the stylets disappear, leaving just small mantle cartilages in places of attachment of the funnel retractors. Pelagic octopods of Bolitaenoidea clade also lost the stylets. Remarkably, reduction of stylets in both pelagic clades (Argonautoidea and Bolitaenoidea) did not result in transformation of their muscular arrangement, which remained generally the same as in benthic Octopodidae.

Homologies of the shell among Vampyropoda

The only evidence available for determining the homologies of the shells among these taxa rests with the position of the fin and the sites of attachment of the mantle muscle and the head and funnel retractors to the shell sac (Fig. 51). Since the ancestral incirrates had fins as testified by the presence of fins in *Palaeoctopus newboldi* (Woodward 1896), we assume that recent fin-bearing cirrates have a shell that is closest to the ancestral octopod shell.

The paralarval fin in *Vampyroteuthis* lies over the wings of the gladius. We can assume, therefore, that the wings and the region of the shell (rachis) between them evolved into most of the cirrate shell as the cirrate fins occupy much of the dorsolateral surfaces in the cirrate wings. In *Vampyroteuthis* the mantle muscle attaches around the periphery of the shell (rachis, lateral plates, wings and conus) except for the anterior free end of the rachis (Fig. 51A). In the primitive cirrate the same situation occurs although without a gap to represent the free end of the rachis. Presumably, all of these regions contributed something to the cirrate shell. In *Vampyroteuthis* the head retractors attach to the lateral plates of the gladius and the funnel retractors attach to the anterior regions of the wings.

In cirrates the head retractors attach to the periphery of the wings and the funnel retractors attach to the anteroventral edges of the wing horns (Fig. 51B). This confirms the homology with the lateral plates and anterior wings of *Vampyroteuthis*, but since the muscle attachments to the cirrate shell do not maintain the same positional relationships, further refinement of areas of homology is not possible.

The evolution of the incirrate shell from the cirrate-type shell involved the loss of the saddle (presumably mostly rachis-homologue) and a general decrease in the size of the remaining parts. In the incirrate stylets, the funnel retractors attach to the bend and anterior shoulders of the stylets which, presumably, are the homologues of the horns in the cirrate gladius, while posterior shoulders, which are embedded in the mantle, represent the remnants of lateral wings (Fig. 51C).

The octopod shell may be mostly the homologue of the gladius hypostracum as the cirrate shell has thickness and consistency similar to the hypostracum in some teuthoids.

The process of shell transformation

Here we explore the stages in the transformation of the shell and the formation of the dorsal mantle cavity in Vampyropoda. The gladius in Cirrata apparently evolved through the reduction of the free rachis and conus and the loss of the rostrum. The anterior loss of the free rachis would expand dorsal space between the free mantle margin and the nuchal cartilage to form a nuchal cavity. Such a cavity presently exists in *Spirula* due to the loss of its proostracum and the expansion of the muscular

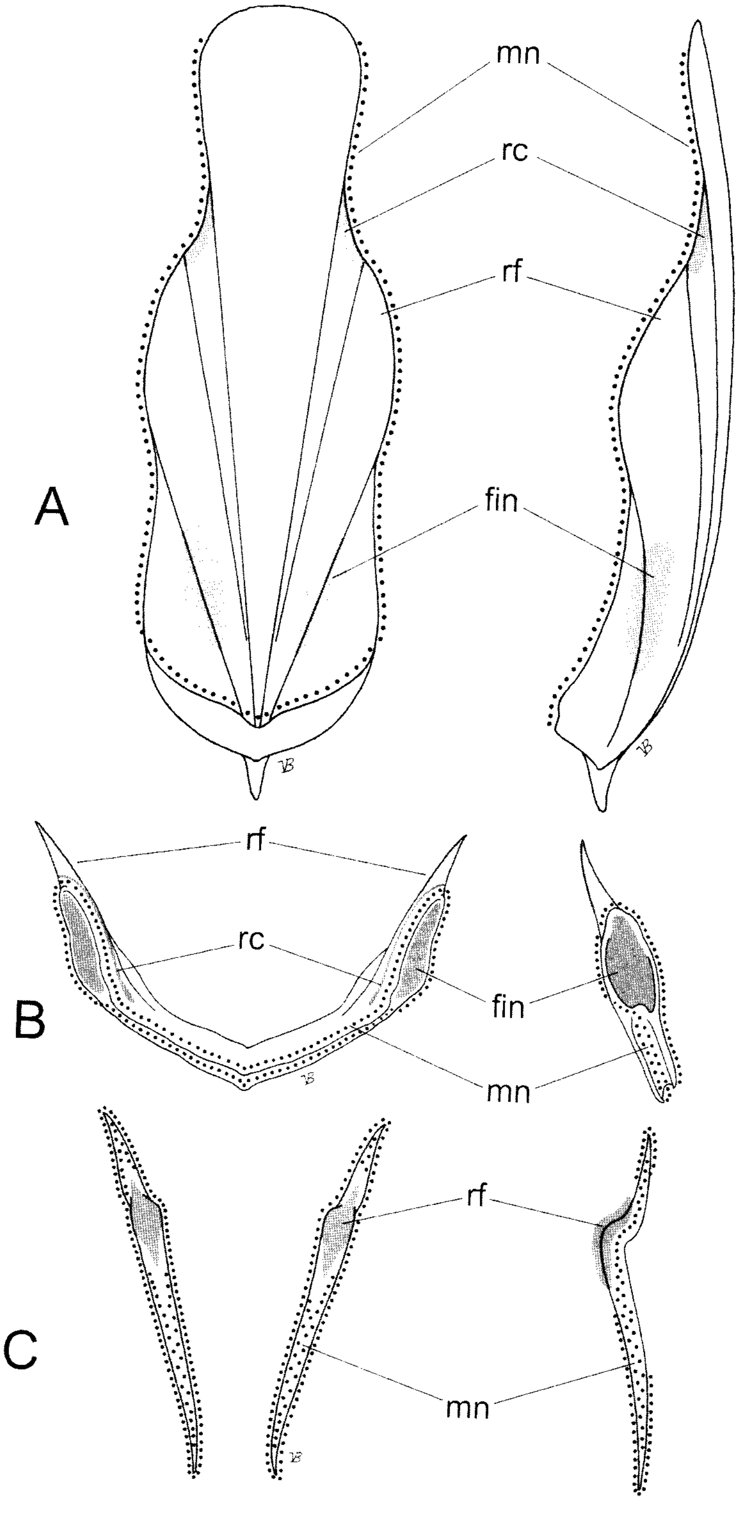


FIG. 51. Scheme illustrating attachment of main muscles to the shell in Vampyropoda. A. *Vampyroteuthis*. B. *Opisthoteuthis*. C. *Octopus*.

Left column: A,C – ventral view (anterior end is up): B – dorsal view (anterior end is up).

Right column: lateral view from the left side (dorsal side is on the right).

РИС. 51. Схема, иллюстрирующая прикрепление мышц к раковине Vampyropoda. A. *Vampyroteuthis*. B. *Opisthoteuthis*. C. *Octopus*.

Левая колонка: A,C – вид с вентральной стороны (передний конец наверху): B – вид с дорсальной стороны (передний конец наверху).

Правая колонка: вид сбоку с левой стороны (дорсальная сторона справа).

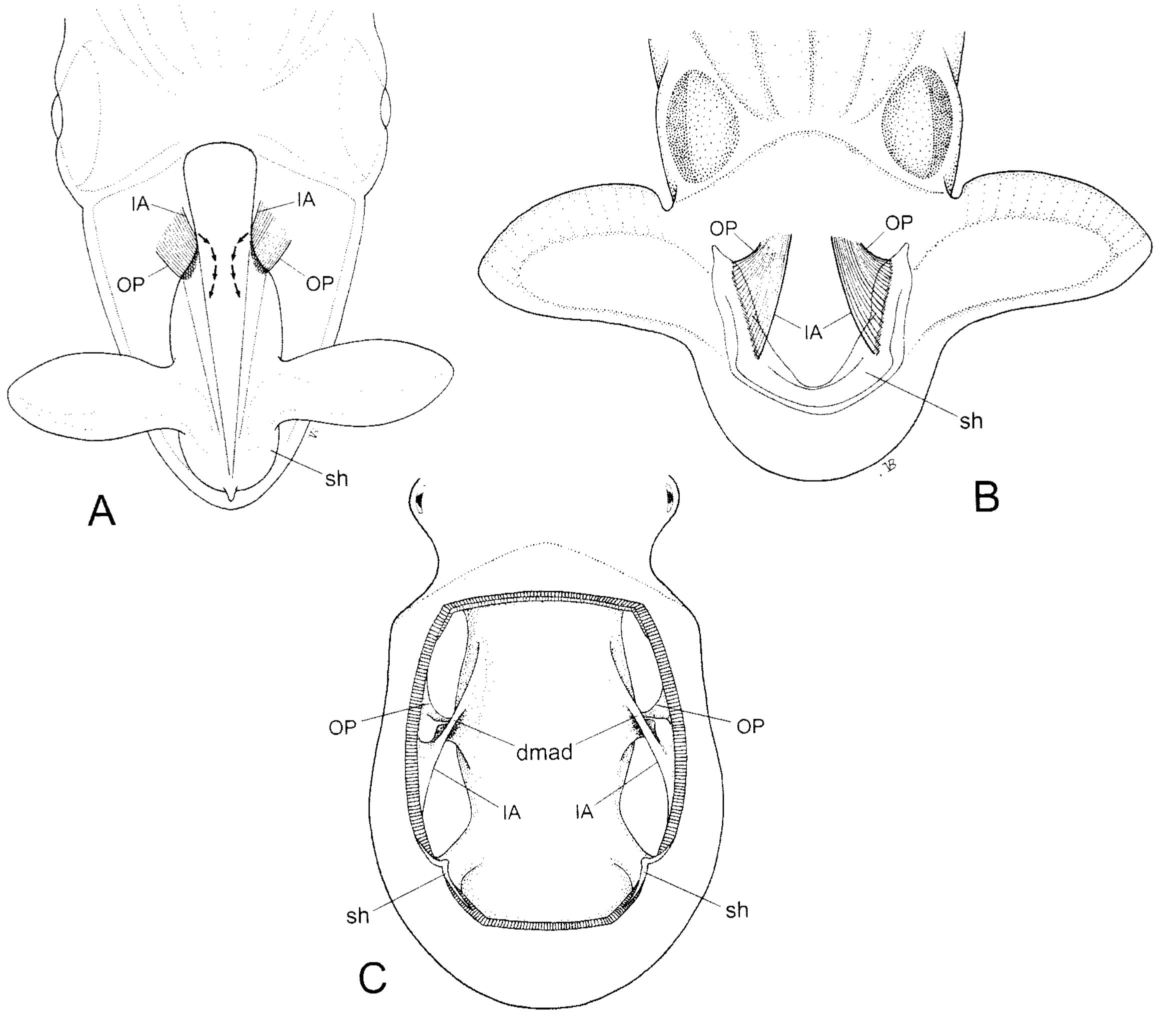


FIG. 52. Diagram showing attachment of the head retractors in different groups of Vampyropoda. A. *Vampyroteuthis*. Dorsal view (the mantle is shown transparent). Arrows indicate direction of hypothetical transposition of inner anterior margins of the head retractors during reduction of the middle plate of the gladius. B. *Grimpoteuthis*. Dorsal view (the mantle is shown transparent). C. *Octopus*. Dorsal view (the muscular mantle is cut off to show attachment of the visceral sac to the mantle). Abbreviations: IA, inner anterior margins of the head retractors; OP, outer posterior margins of the head retractors; sh – shell (gladius or stylets); dmad – anterior dorsal mantle adductors.

РИС. 52. Прикрепление ретракторов головы в различных группах Vampyropoda. А. *Vampyroteuthis*. Вид с дорсальной стороны (мантия изображена прозрачной). Стрелки указывают направление гипотетического смещения переднего края ретракторов головы при редукции медиальной пластинки гладиуса. В. *Grimpoteuthis*. Вид с дорсальной стороны (мантия изображена прозрачной). С. *Octopus*. Вид с дорсальной стороны (дорсальная стенка мантии удалена, чтобы показать крепление висцерального мешка). Условные обозначения: IA, внутренние передние края ретракторов головы; OP, внешние задние края ретракторов головы; sh – раковины (гладиус или стилеты); dmad – передние дорсальные мантийные аддукторы.

mantle dorsally to form an anterior muscular cylinder [Chun 1910-1915]. In octopods, fusion of the dorsal mantle margin and head would create the dorsal mantle cavity. Reduction of the conus resulted in the development of posterior mantle wall that forms the dome-shaped posterior apex of the body. This development resulted in U-shaped circular muscle fibers with ends attached to the cirrate shell.

Further clues to the transformation of the shell and the formation of the dorsal mantle cavity are found in the characteristic twisting of anterior dorsal adductors in Incirrata (Fig. 52). The inner margins of the head retractors in *Vampyroteuthis* attach to the gladius anteriorly to their outer margins (Fig. 52A). In Cirrata, reduction of the middle plate in the gladius caused transposition of the attachment sites of the head retractors to inner surface of lateral wings of V-shaped gladius (Fig. 52B). As a result, the attachment of the head retractors became inverted: their inner margins attach to the gladius posteriorly from the outer margins. Finally, in Incirrata head retractors formed the anterodorsal adductors, which attach to the mantle wall anterior to the shell remnants (Fig. 52C). But orientation of the attachment of these adductors remained as in the Cirrata: the inner margins of the adductors attached to the mantle wall far posteriorly from the outer margins giving the adductors nearly a 180° twist in a clockwise (left adductor) or counter — clockwise (right adductor) direction. It seems like the anterodorsal adductors in Incirrata, having lost connection with the shell, retained the former orientation as if they are still attached to the gladius of cirrate type.

Apparently at some stage of incirrate evolution expansion of dorsal mantle cavity resulted in formation of two dorsolateral epithelial septa passing from the stellate ganglia toward the sites of attachment of the funnel retractors. As the expansion continued, these septa were perforated, and dorsal and ventral parts of mantle cavity merged together in the branchial region isolating the anterodorsal adductors. According to Naef [1921/1923: p. 658], repetition of this process can still be traced during ontogenetic development of young *Octopus*.

Radical reduction of the gladius of teuthoid type into a U-shaped structure is not unique for Cirrata. Similar reduction of the gladius occurred in recent mesopelagic oegopsid squid *Bathothauma lyromma* Chun, 1906 (family Cranchiidae). In *Bathothauma* the rachis separated from the conus and reduced to a narrow and feeble needle-like rod embedded in anterior dorsal part of the mantle (Fig. 53). Ventral part of the conus lost completely and the dorso-lateral parts unfolded into U-shaped plate providing support for the fins on posterolateral sides of the mantle (Fig. 53C). At the first glance, the general morphological design of *Bathothauma* does not differ from that of Cirrata. However, the principal difference is a position of the stellate ganglia that are set close and connected to each other in *Bathothauma* and widely separated in Cirrata. The fact that all other representatives of family Cranchiidae have typical teuthoid gladii indicates that transformation of gladius into U-shaped transversal plate in *Bathothauma* apparently was a result of a single structural mutation rather than a gradual evolutionary trend.

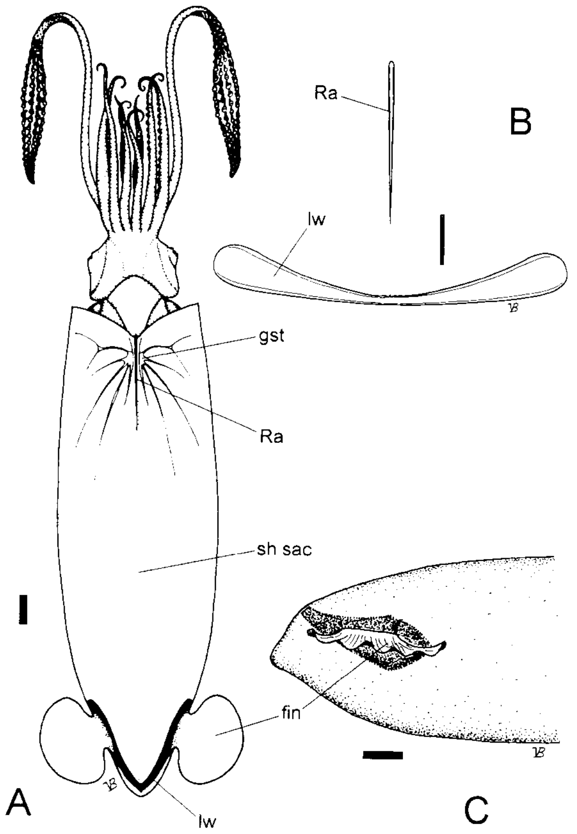


FIG. 53. Pelagic squid *Bathothauma lyroma* Chun, 1906 (adult female: 192 mm DML). A. Dorsal view. B. Dorsal view of the gladius showing its separation into two parts: anterior axial rod (rachis) and posterior transversal band (unfolded) representing the remnant of conus and conus fields). C. Posterior part of the mantle from the lateral side. Scale bar = 1 cm.

РИС. 53. Пелагический кальмар *Bathothauma lyroma* Chun, 1906 (взрослая самка: 192 мм ДМ). А. Вид с дорсальной стороны. В. Вид гладиуса с дорсальной стороны. Гладиус разделен на две части: переднюю осевую пластинку (рахис) и заднюю поперечную пластинку (развернута), представляющую собой рудимент конуса и его флагов). С. Вид задней части мантии сбоку. Масштаб = 1 см.

Palaeontological evidences

According to the opinion currently accepted by many paleontologists, extant Vampyromorphida and Octopoda origin from "Fossil Teuthids": a primitive group of Triassic — Cretaceous coleoids, which had gladii with partly decalcified five-partied proostracum [Berthold, Engeser, 1987; Engeser, Bandel, 1988; Doyle *et al.* 1994; Haas, 2002]. Remarkable diversity of the morphology of the gladii in "Fossil Teuthids" indicate a great variety of life styles (Fig. 54). Phylogenetical affinity of "Fossil Teuthids" to either Octobrachia or Decabrachia has been controversially discussed for many years. Some authors assigned some of these forms to ten-armed Teuthida on the basis of similarity of their gladii with those of recent squids and indistinct imprints interpreted as tentacles [Naef, 1921/1923; Jeletzky, 1966; Donovan, 1977; 1983; Vecchione *et al.* 1999]. Others assigned all "Fossil Teuthids" to ancient eight-armed Vampyromorphida on the basis of rare and indistinct imprints interpreted as the eight arms united by interbrachial web, uniserial sessile suckers without horny rings, two rows of cirri along lateral edges of the oral surface of the arms and two

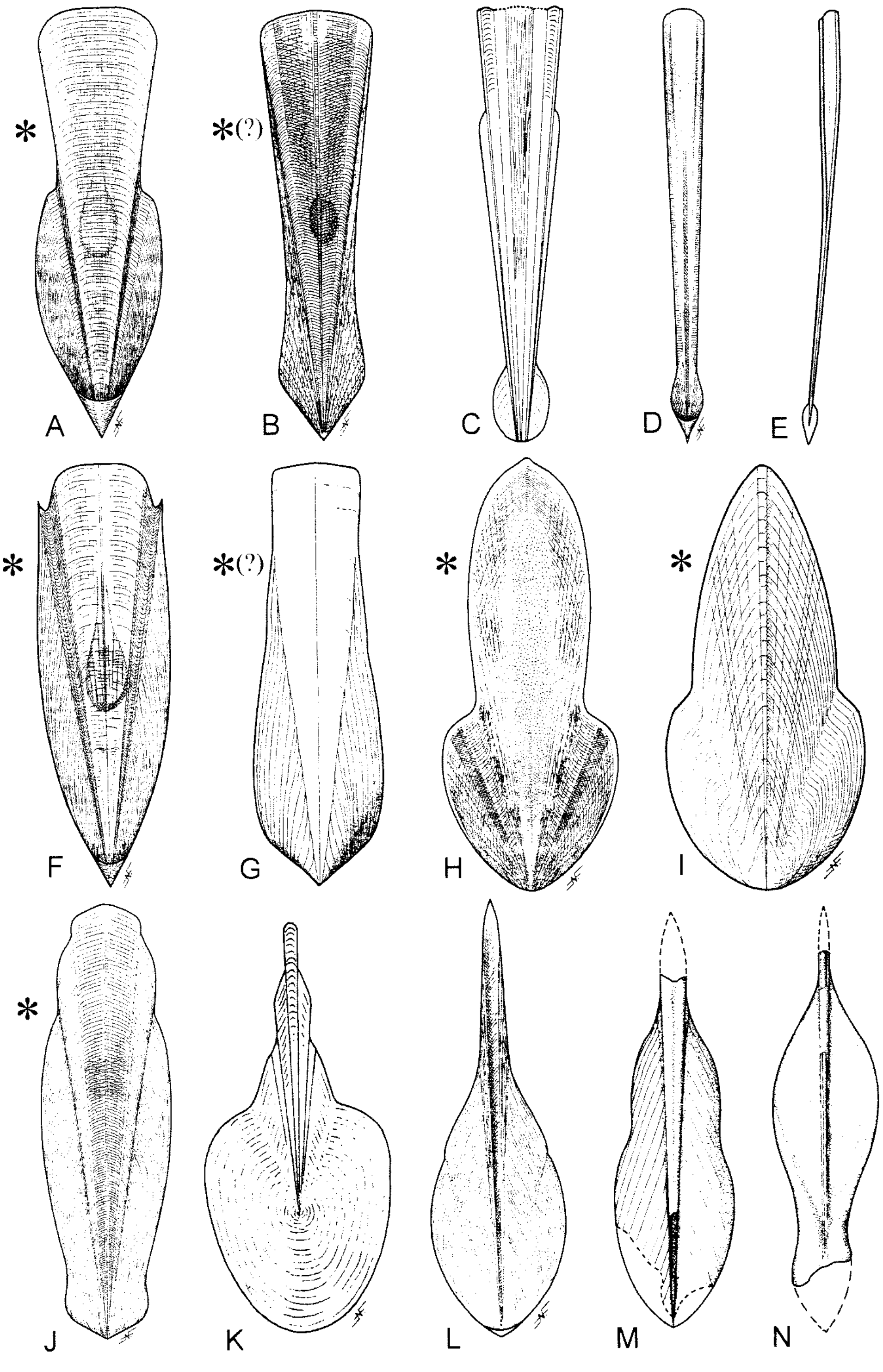


FIG. 54. Gladii of Jurassic and Cretaceous "Fossil Teuthids". A. *Geoteuthis simplex* (Voltz 1840) from late Jurassic (Tithonian). B. *Paraplesioteuthis sagittata* (Münster 1843) from late Jurassic (Tithonian). C. *Boreopeltis sagittata* (Naef. 1921) from late Jurassic (Tithonian). D. *Plesioteuthis prisca* (Rüppell 1829) from late Jurassic (Tithonian). E. *Maioteuthis morroensis* Reitner et Engeser. 1982 from early Cretaceous (Barremian). F. *Loligosepia aalensis* (Zieten. 1830) from early Jurassic (Toarcian). G. *Mastigophora brevipinnis* Owen. 1856 from middle Jurassic (Callovian). H. *Trachiteuthis hastiformes* (Rüppell. 1829) from early Jurassic (Toarcian). I. *Teudopsis subcostata* (Münster. 1843) from early Jurassic (Toarcian). J. *Leptoteuthis gigas* Meyer. 1834 from early Jurassic (Toarcian). K. *Celaeno conica* Münster 1842 from early Jurassic (Toarcian). L. *Palaeololigo oblonga* Wagner (1860) from early Jurassic (Toarcian). M. *Marekites vinarensis* (Fritsch. 1910) from early Cretaceous (Barremian). N. *Eoteuthoides caudata* (Fritsch. 1910) from early Cretaceous (Barremian). The gladii marked by asterisks represent possible ancestors of resent Vampyromorphida and Octopoda. The rest gladii belong to representatives of other coleoid lineages. A. B. D. F. H. I. J. K and L – after Naef. 1922: C – after Engeser. 1986: E – after Reither. Engeser. 1982: G – after Donovan. 1983: M. N – after Kostak. 2002.

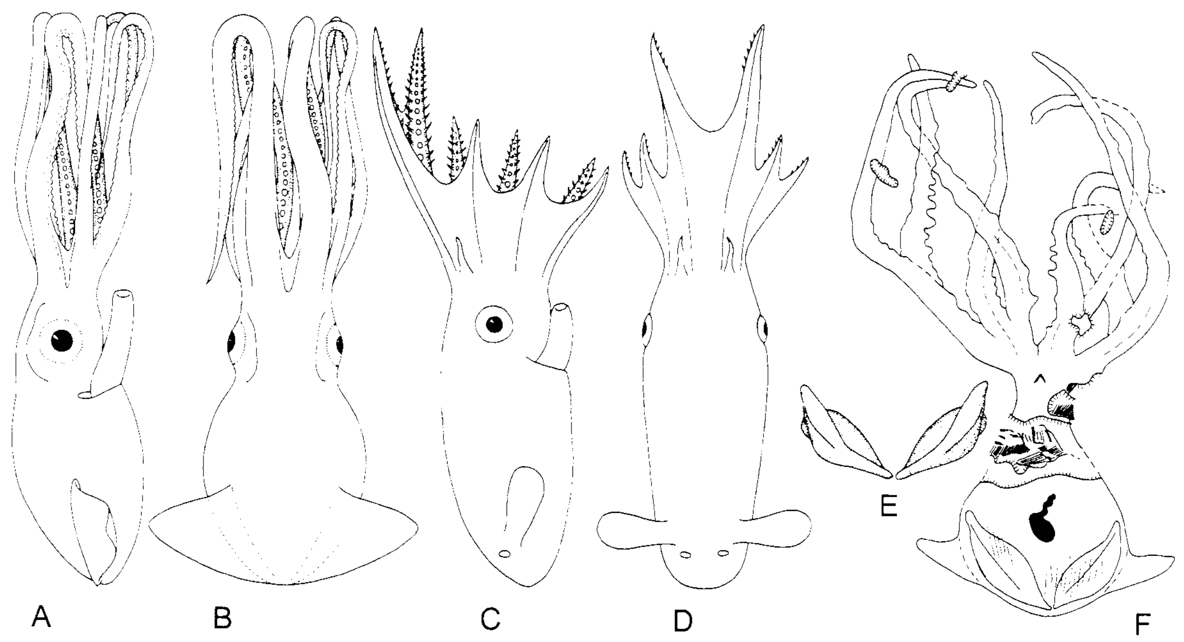


FIG. 55. Reconstructions of fossil octopods and vampyromorphs. A,B — *Proteroctopus ribeti* Fischer et Riou 1982 from middle Jurassic (Callovian). C,D — *Vampyronassa rhodanica* Fischer et Riou 2002 from middle Jurassic (Callovian). E,F — *Paleoctopus newboldi* (Woodward 1896) from late Cretaceous (Campanian). A, C – lateral view. B,D, F – dorsal view. E – shell remnants (stylets). A,B – after Fischer, Riou, 1982. C,D – after Fischer, Riou, 2002. E,F – after Haas, 2002.

РИС. 55. Реконструкции ископаемых осьминогов и вампироморф. A,B — *Proteroctopus ribeti* Fischer et Riou 1982 из средней Юры: Келловейский век. C,D — *Vampyronassa rhodanica* Fischer et Riou 2002 из средней Юры: Келловейский век. E,F — *Paleoctopus newboldi* (Woodward 1896) из позднего Мела: Кампанский век. A, C – вид сбоку. B,D, F – вид с дорсальной стороны. E – рудименты раковины (стилеты). A,B – из Fischer, Riou, 1982. C,D – из Fischer, Riou, 2002. E,F – из Haas, 2002.

pairs of fins [Bandel, Leich, 1986; Doyle *et al.* 1994; Donovan *et al.* 2003; Fuchs *et al.* 2003].

The present study of the shell-soft body relationship in recent vampire squid and octopods provide new data for phylogenetic comparison between extant and fossil coleoids. Reduction of the middle plate in the gladius of pre-octopods did not change position of the stellate ganglia that remained lying on lateral sides of the mantle posteriorly from the funnel folds. Wide separation of the stellate ganglia in all recent octopods represents conclusive evidence that this group evolved from some vampyromorph ancestors with wide middle plate of proostracum. The forms with narrow middle plate of proostracum like *Plesioteuthis*, *Celaeno*, *Palaeololigo*, *Eoteuthoies* and others could not possibly be ancestors of recent Octopoda, as all of them apparently had the stellate ganglia set close to each other. The forms with wide middle plate of proostracum (*Loligosepia*, *Trachiteuthis*, *Teudopsis*, *Leptoteuthis*, etc.) could possibly belong to octopodian evolutionary stem. Among these, the forms like *Teudopsis* Mьnster, 1842 (family Teudopseidae) from the early Jurassic (Toarcian), in my opinion, seems to be the most likely ancestors of recent Octopoda, as they had wide thick gladius with partly reduced medial plate (Fig. 54 I).

The fossil records of undoubted octopods and octopod-like vampyromorphs are extremely rare. Only three fossil octopod species, *Proteroctopus*

РИС. 54. Гладиусы юрских и меловых "ископаемых кальмаров". A. *Geoteuthis simplex* (Voltz 1840); поздняя Юра: Титонский век. B. *Paraplesioteuthis sagittata* (Münster 1843); поздняя Юра: Титонский век. C. *Boreopeltis sagittata* (Naef, 1921); поздняя Юра: Титонский век. D. *Plesioteuthis prisca* (Rüppell 1829) поздняя Юра: Титонский век. E. *Maioteuthis morroensis* Reitner et Engeser, 1982; ранний Мел: Барремский век. F. *Loligosepia aalensis* (Zieten, 1830); ранняя Юра: Тоарский век. G. *Mastigophora brevipinnis* Owen, 1856; средняя Юра: Келловейский век. H. *Trachiteuthis hastiformes* (Rüppell, 1829); ранняя Юра: Тоарский век. I. *Teudopsis subcostata* (Münster, 1843); ранняя Юра: Тоарский век. J. *Leptoteuthis gigas* Meyer, 1834; ранняя Юра: Тоарский век. K. *Celaeno conica* Münster 1842; ранняя Юра: Тоарский век. L. *Palaeololigo oblonga* Wagner (1860); ранняя Юра: Тоарский век. M. *Marekites vinarensis* (Fritsch, 1910); ранний Мел: Барремский век. N. *Eoteuthoides caudata* (Fritsch, 1910); ранний Мел: Барремский век. Гладиусы, отмеченные звездочкой, могут являться возможными предками современных Vampyromorphida and Octopoda. Остальные гладиусы принадлежат к иным эволюционным линиям. A, B, D, F, H, I, J, K и L – из Naef, 1922; C – из Engeser, 1986; E – из Reither, Engeser, 1982; G – из Donovan, 1983; M, N – из Kostak, 2002.

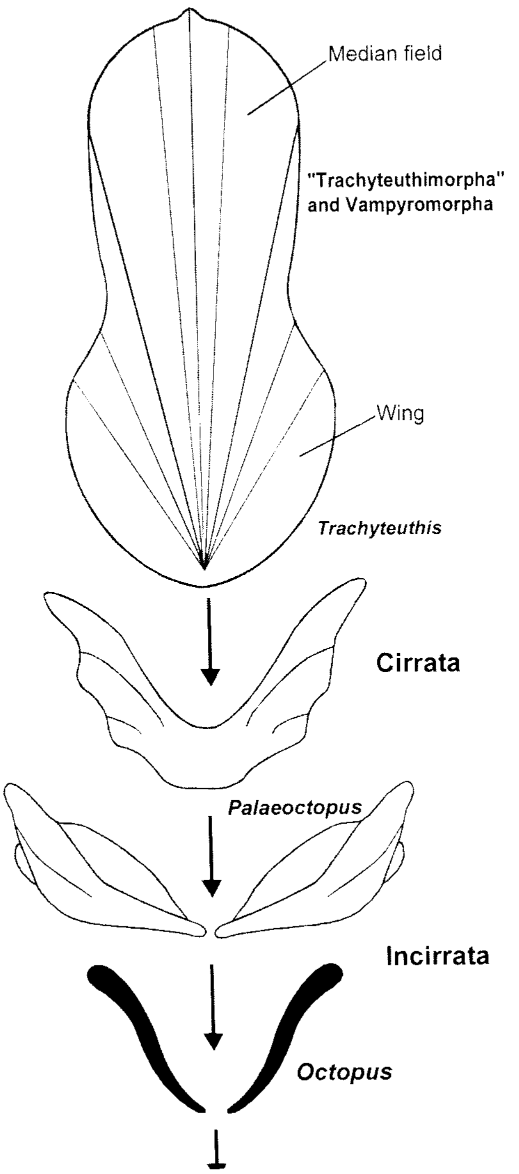


FIG. 56. Diagram showing the reduction of the gladius in Vampyropoda [after Haas, 2002].

РИС. 56. Схема, иллюстрирующая редукцию гладиуса у Vampyropoda [по Haas, 2002].

riberti Fischer et Riou, 1982, *Vampyronassa rhodanica* Fischer et Riou, 2002 and *Palaeoctopus newboldi* (Woodward, 1896), have been described (Fig. 55). The first two species are known from the Middle Jurassic (Callovian) of France [Fischer, Riou, 1982; 2002]; the latter was reported from the Late Cretaceous (Campanian) of Lebanon [Woodward, 1896; Naef, 1922]. All three forms were preserved by organic casts that reflect many important features of their soft body but conceal completely the structure of gladius. *Proteroctopus* had generally octopod-like habitus with short sac-shaped mantle fused with the head on dorsal side, well-developed triangular terminal fins, long free funnel and very long arms without interbrachial web (Fig. 55A,B). Each arm bore a single row of suckers without stalks and rings. According to Fischer and Riou [1982], the morphology of *Proteroctopus* denotes a necto-epipelagic mode of life. *Vampyronassa* exhibited characteristic vampyromorph features, including eight arms and two filaments (modified second pair of arms), deep interbrachial web, uniserial sucker with bordering cirri on each arm, elongated mantle that was fused with the head on dorsal side and two oar-like subterminal fins (Fig. 55C,D). Basing on general morphology, Fischer and Riou [2002] tentatively suggested that *Vampyronassa* was a mesopelagic animal. *Palaeoctopus newboldi* from the late Cretaceous of Lebanon is commonly considered to be the earliest representative of Incirrata [Engeser, 1988]. This animal had wide almost spherical mantle, fused with the small head on the dorsal side, very long arms with uniserial suckers, two small triangular fins and no interbrachial web (Fig. 55F). The most striking feature of *Palaeoctopus* is the structure of its gladius that was recently described by Haas [2002]. The gladius consisted of two sigmoidal—lanceolate conchyolin plates separated from each other in the middle (Fig. 55E). Separation of lateral halves in the gladius of *Palaeoctopus* clearly testifies its affinity to Incirrata. It presents conclusive evidence that divergence of octopod stem into Cirrata and Incirrata had already occurred by the late Cretaceous.

Evolution of the shell in Vampyropoda.

Basing mainly on paleontological data, Haas [2002] proposed the origin of the shell of recent octopods from the gladii of "Fossil Teuthids" (Trachyteutimorpha) through reduction of the median field of proostracum and conus (Fig. 56). He suggested that the step-wise reduction of the gladius in Octopodiform lineage was probably stipulated by increasing swimming activity. Sagittal interruption of the gladius in *Palaeoctopus*, according to Haas, has improved the capability of its muscular mantle for more vigorous inflation and deflation during swimming and breathing.

In my study the general scheme of evolution of the shell in Vampyropoda was made on the basis of broad comparison of the shell structure and shell-soft body relationship in recent vampire squid and octopods (Fig. 57). This scheme supports the conclusion of Haas [2002] on origin of Vampyropoda from 'Fossil Teuthids' with wide middle plate of proostracum and partly reduced conus. However, in my opinion, reduction of the gladius in Octopoda did not improve their swimming and breathing per-

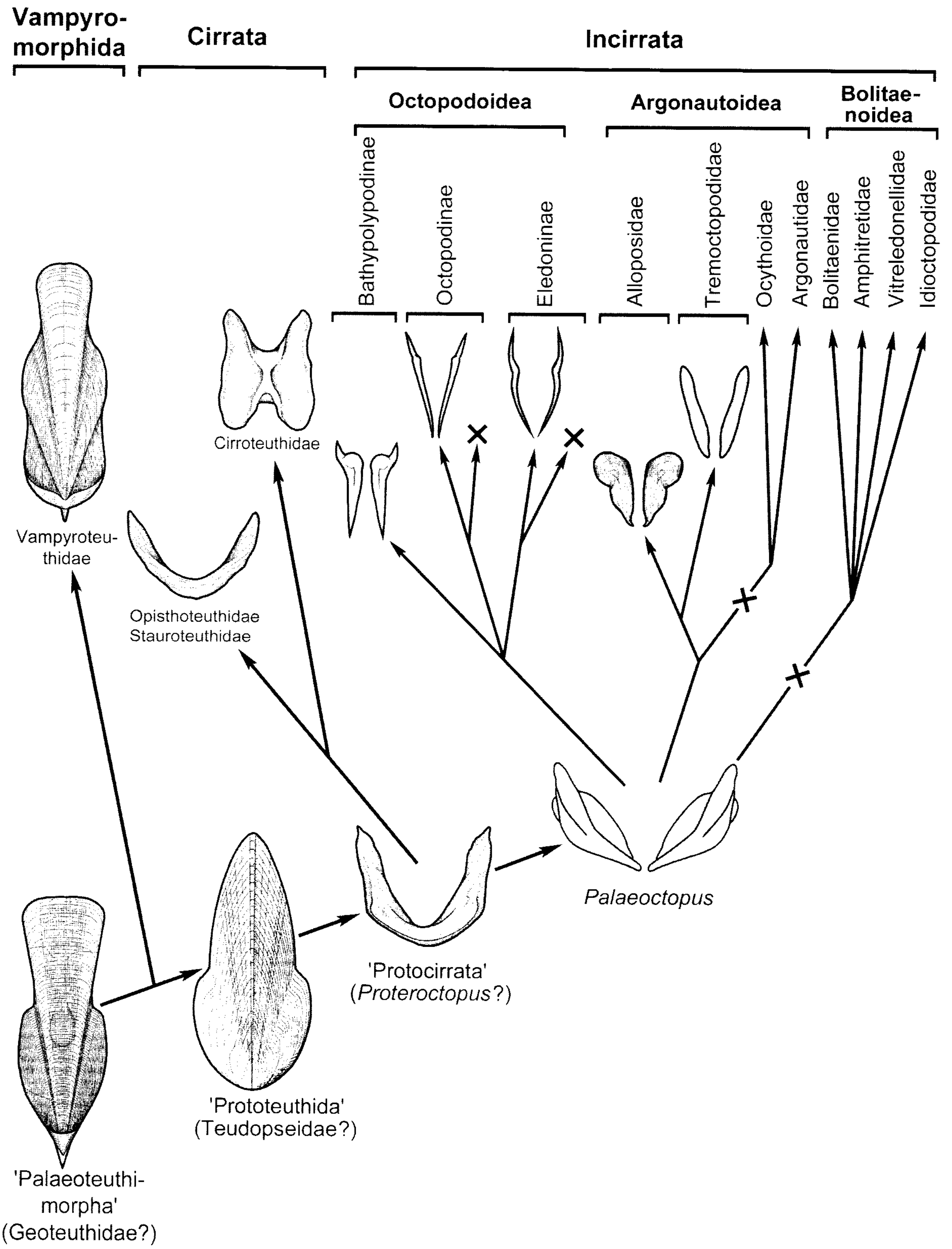


FIG. 57. Scheme illustrating possible ways of evolution of the shell in Vampyropoda. Symbol 'x' means complete reduction of the shell in corresponding phyletic line.

РИС. 57. Схема, иллюстрирующая возможные пути эволюции раковины у Vampyropoda. Символы 'x' означают полную редукцию раковины в соответствующих филетических ветвях.

formance and apparently was determined by other reasons.

Two crucial events took place in evolution of the shell in Octopodian lineage:

1. Reduction of the middle plate of proostracum and conus in the gladius of vampyroteuthoid type resulting in its transformation into the gladius of cirrate type;

2. Reduction of transversal connection (saddle) in gladius of cirrate type resulting in its transformation into paired stylets of Incirrata.

The first event was the most important as it predetermined the whole following evolution of octopods. It seems surprising, how typical teuthooid gladius of ancient vampyromorphs could transform into a bizarre U-shape gladius of cirrate type lacking distinctive structural elements. What were the possible causes of such transformation? What advantages got an animal having ridden of medial part of proostracum? To answer these questions let us consider the possible sequences of such reduction. Reduction of the medial part of proostracum meant that the mantle ceased to have fixed length, its anterior margin lost support, but the body plasticity enhanced. Such a transformation could happen (and be supported by natural selection) only in slow-swimming forms, in which dorsal anterior mantle margin had already been fused with the head, and the fins (not the mantle) were the main means of locomotion. Reduction of median plate of proostracum could not happen in a jet-swimming nektonic coleoid, because it transformed the animal from a jetting torpedo into soft sausage. Thus, it seems very likely that hypothetical ancestors of Octopoda swam slowly using the fins and had the mantle fused with the head on dorsal side. Apparently, these animals evolved toward pelagic (bentho-pelagic?) life form, and the presence of wide heavy gladius of vampyroteuthoid type became an obvious obstacle on this evolutionary pathway.

Gladii of "Fossil Teuthoids" were built by thick dense chitin that apparently had substantial negative buoyancy. Such gladii were adequate for active necto-benthic forms but were too heavy for pelagic forms. Lightening of the gladius could be achieved either through general reduction of the weight or through reduction of some morphological parts. Apparently both ways were explored in evolution. The first way (general lightening of the gladius) led to recent Vampyroteuthidae. The gladius in *Vampyroteuthis* decreased in thickness and its dense heavy modification of chitin was substituted by its loose water-rich modification with nearly neutral buoyancy. Lightening of the gladius in vampyromorphs resulted in decrease of its mechanical strength and corresponding decrease of its supporting function. The general plan of gladius structure was conserved and did not change considerably during subsequent evolution of this group. As a result, the gladius in recent *Vampyroteuthis* is strikingly similar to the gladii of some "Fossil Teuthids" from the Lower Jurassic. Despite its apparent fragility, the gladius of *Vampyroteuthis* has most of the muscular attachments found in decapodiforms. It provides support for fins that have become the main organ of locomotion in this animal and can propel it at surprisingly fast speeds. It also serves as a 'backbone' of the soft body but less as a rigid support than as a structure that provides support through its resistance to stretching. Another important function of vampire gladius is strengthening the attachment of the head and mantle. The rostrum underwent radical reduction in *Vampyroteuthis*. Its absence in some individuals suggests that it no longer has a function. Lightening of the gladius of the ancestral teuthoid plane together with other adaptations enabled vampyromorphs to evolve pelagic forms, as testified by a single living representative. However, this evolutionary line turned out to be a dead end. When the finfishes entered the seas in the Jurassic-Cretaceous, vampyromorphs apparently could not compete with them and survived only in bathy-pelagic refuge.

Another means of lightening the shell, its radical reduction, was realized in evolution of octopods. In course of this reduction, the medial part of proostracum (rachis and, probably, lateral plates), conus and rostrum were lost. The ostracum and periostracum were also reduced and the gladius transformed into the shell of cirrate type: a cartilage-like U-shaped structure, composed by concentric layers of hypostracum. As a result of such reduction the gladius lost the role of 'backbone' for the mantle musculature but retained its function of the fin support. Reduction of proostracum, apart from lightening the shell, greatly increased flexibility of the body, which was an important preadaptation for the settlement on the ocean floor. The habit to explore large objects with the arms was another preadaptation that predetermined an oral-end-down approach of "pre-octopod" to the bottom [Young *et al.*, 1998].

As testified by the fossil evidences (*Palaeoctopus*), the divergence of pre-octopod lineage into Cirrata and Incirrata occurred before the Late Cretaceous. Ancestors of cirrates continued to evolve mainly as bentho-pelagic forms relying on swimming with fins. The gladius in cirrates evolved mainly as the structure supporting the fins and connecting the mantle, fins and the visceral organs. Reduction of basal pockets in this lineage was probably stipulated by development of a new bird-like way of swimming with fins, that required stronger connection between fin bases and the gladius. Two evolutionary lineages may be traced within Cirrata. In one lineage the animals adapted to quasi-benthic life acquiring oral-end-down orientation and flat cake-like body (*Grimpoteuthis* and *Opisthoteuthis*). The gladius in this lineage remained wide and retained some primitive ancestral characters: the presence of lateral horns serving for attachment of the funnel retractors and the presence of dorsal groove on the saddle serving for attachment of the mantle. Another lineage of cirrates led to bentho-pelagic forms like *Cirroteuthis* and *Cirrothauma*. Evolution in this line was associated with swimming with fins, and the gladius evolved exclusively as the fins support. The lateral wings of the gladius came closer together and greatly expanded to provide effective support for increasing fins. Axial part of the gladius became very thick and rigid. Evolving in this way, the gladius transformed into perfect fin support. It allowed pelagic cirrates virtually to fly in the water by powerful fin stroke, like the birds fly in the air.

Ancestors of incirrates descended to the bottom in oral-end-down position and began to adapt to cryptic benthic life associated with crawling movement with the use of the arms. Apparently first incirrates were shallow-water forms with wide U-shaped gladius and well-developed oar-like fins. However, it seems that the life on the bottom was not easy in Cretaceous seas where the key positions were gradually taken by new evolving predators, the finfishes. For animals unprotected by the shell, adaptation to benthic environment required enhancement of the body flexibility to hide in every possible minute shelter on the bottom. The fins and supporting it rigid U-shaped gladius became an obstacle and had to be reduced. These reasons stipulated the second major event in evolution of the octopodian shell: reduction of the transversal fusion in U-shaped gladius and its separation into paired lateral rods, stylets.

The first known representative of incirrate lineage, *Palaeoctopus newboldi*, still exhibited some characteristic features of Cirrata: presence of fins, thick gladius and cirri on the arms [Haas, 2002]. However, the fins in *Palaeoctopus* showed distinct signs of reduction: they were relatively small and lacked solid support as the gladius had already separated in the middle. In course of evolution of incirrate octopods the fins reduced completely, and the gladius changed its function from the fin support to support for the funnel. The reduction of the shell in Incirrata appears to significantly affect their capability for jet-swimming. Reduction of entire shell prohibits octopods from fixing their mantle length and streamline shape during swimming. When inhaling, *Octopus* decreases its length by 12-14% [Zuev, 1965]. Thick ventral mantle adductor diminishes the volume of ventral mantle cavity considerably. Unique pattern of attachment of the visceral sac to the mantle by means of five adductor muscles found in octopods is much weaker than complete fusion of the visceral sac to the shell as found in vampyromorphs. However, this pattern ensured incredible mobility of the visceral sac inside the mantle cavity that was an important adaptation to the benthic way of life. Together with the absence of fins, it made octopod body virtually shapeless. It allowed the animals to hide in narrow cracks and slits in rocks and to squeeze oneself 'part by part' through chinks with the width just 1/10 of the animal mantle length [Akimushkin, 1963]. Reduction of the median connection in the gladius and deep reorganization of the body plan predetermined the evolution of Incirrata. On the one hand, it prohibited this group to evolve active nektonic life forms. On the other hand, it opened for ancient incirrates new possibilities to evolve benthic and later bentho-pelagic life forms and laid down the basis for contemporary biological success of this group.

Evolution of Incirrata was associated with progressive reduction of the shell until its complete loss in some lineages. Benthic shallow-water Octopodidae retained the most primitive stylets reaching sometimes up to 24% ML (*Enteroctopus*). Gradual reduction of the stylets in deep-water Octopodidae was apparently stipulated by the general decline of their activity. In *Benthoctopus*, *Bathypolypus*, *Eledone*, *Pareledone*, *Tetracheledone*, *Velodona* the stylets decreased in size and became softer while in *Eledonella* and *Graneledone* the shell has been lost completely [Voight, 1997]. Some muscular shallow-water Octopodidae (*Ameloctopus*, *Hapalochlaena*, etc.) have also lost the stylets [Voight, 1997]. Together with stylets, these forms apparently lost ability for jetting swimming as testified by decreased size of their mantle in relation to the arms.

At least two independent lineages of Incirrata re-invaded the pelagic realm: Bolitenoidea (Ctenoglossa) and Argonautoidea. In both lineages development of pelagic forms was accompanied by complete loss of the gladius. Bolitaenoidea represents a more specialized pelagic lineage than Argonautoidea. The stylets in this lineage are missing already in primitive forms (*Japetella*), while in the advanced form (*Amphitretus*) even the breaks in the mantle musculature marking location of the former shell have been lost. In Argonautoidea gradual reduction of the stylets can be traced in *Tremoctopus* and *Alloposus* until compete loss of the shell in *Ocythoe* and *Argonauta*. In this clade reduction of the shell was accompanied by development of strong funnel locking-apparatus of teuthid type that substituted the shell functionally.

Thus, the last event in evolution of the shell in

Vampyropoda, its complete loss, repeatedly and independently occurred in Incirrata. In benthic Octopodidae (*Ameloctopus*, *Hapalochlaena*) reduction of the stylets was caused by abandonment of the jet-swimming and development of crawling habit with the use of arms. In pelagic clades (Bolitaenoidea, Argonautoidea) the main causes of the complete loss of stylets were either the loss of ability for jet-swimming (*Alloposus*, *Amphitretus*) or development of strong funnel locking-apparatus/fusion between the funnel and the mantle (*Ocythoe*, *Tremoctopus*). Remarkably, loss of stylets in all pelagic octopods did not result in transformation of their muscular arrangement, which remained generally the same as in benthic Octopodidae.

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Раковина восьмируких головоногих моллюсков (Vampyropoda; Cephalopoda): морфология, функциональная роль и эволюция.

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РЕФЕРАТ. Исследована сравнительная морфология, микроструктура и функциональная роль внутреннего рудимента раковины у 14 видов современных восьмируких головоногих моллюсков (н/отр. Vampyropoda), в том числе у единственного современного представителя вампиров, Vampyroteuthis infernalis Chun, 1903; 3 видов плавниковых осьминогов (отр. Cirrata) и 10 видов бесплавниковых осьминогов (п/отр. Incirrata). Взаимоотношение между раковиной и мягким телом моллюсков исследовано по тотальным срезам, сделанным на различных уровнях. Показано, что раковина выполняет различную роль в разных группах восьмируких головоногих, и эволюция ее формы по-видимому была обусловлена эволюцией ее функции. У Vampyroteuthis (отр. Vampyromorphida), наиболее архаичного представителя Vampyropoda, раковина представляет собой типичный гладиус теутоидного плана строения и служит опорой мантии, плавникам, мускулам-ретракторам воронки и головы, а также висцеральному мешку. Необычный U-,V- или W-образный хрящеподобный гладиус плавниковых осьминогов (отр. Cirrata) представляет собой рудимент флагов конуса, крыльев и латеральных пластинок проостракума. Его главная функция — опора плавникам. У бесплавниковых осьминогов (отр. Incirrata) раковина редуцирована до пары хрящеподобных палочек, стилетов, главная функция которых — опора ретракторам воронки.

Каждая группа современных восьмируких головоногих: Vampyromorphida, Cirrata и Incirrata — характеризуется специфическим строением раковины и ее взаимоотношением с мягким телом. Расположение звездчатых ганглиев, широко расставленных на внутренней стороне дорсальной стенки мантии у всех современных Vampyropoda, свидетельствует о том, что осьминоги произошли от вампироподобных предков с широкой медиальной пластинкой гладиуса. В эволюции раковины восьмируких головоногих прослеживается два ключевых события: 1) редукция медиальной пластинки проостракума и конуса, в результате которой гладиус вампиротеутидного плана строения превратился в гладиус цирратного типа; 2) редукция поперечной перемычки (седла) в цирратном гладиусе, в результате которой он трансформировался в парные образования (стилеты) инцирратных осьминогов. У Incirrata эволюция раковины шла по пути ее редукции вплоть до полного исчезновения, которое шло параллельно в каждом из трех надсемейств: Octopodoidea, Bolitaenoidea и Argonautoidea. Во всех случаях окончательная редукция раковины была связана с потерей способности к реактивному плаванию и сопровождалась либо развитием своеобразного способа "хождения" на руках по дну (у донных Octopodoidea), либо приспособлением к пассивному парению в толще воды у представителей пелагических Bolitaenoidea и Argonautoidea. Полная утрата раковины у эволюционно продвинутых представителей Incirrata не повлекла за собой изменений их плана строения, который остался в целом таким же, как и у примитивных представителей этого отряда.