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REDESCRIPTION OF *IDIOSEPIUS PYGMAEUS* STEENSTRUP, 1881 (CEPHALOPODA:IDIOSEPIIDAE), WITH MENTION OF ADDITIONAL MORPHOLOGICAL CHARACTERS

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ABSTRACT

Idiosepius pygmaeus Steenstrup, 1881 is redescribed and illustrated. Mantle up to 20.5 mm. Fins terminal, small and kidney-shaped. Mantle free from head along the margin, but mid-dorsally completely fused with funnel complex. Cartilagenous locking device with simple longitudinal grooves on funnel; oval ridges on mantle. Nuchal cartilage absent, but we interpret an oval depression in the central neck region as a rudimentary nuchal cartilage. Left and right 4th arms of males hectocotylized, normally with 1-3 uniserial suckers, but up to 4 suckers in this material. Suckers in 2 rows on sessile arms and 2-4 rows on tentacular club. Membranous gladius covers the posterior 2/3 of the dorsum. Eyes with opaque, wrinkled secondary cornea in preserved specimens; anterior pores present. Olfactory crests prominent. Oviducts developed on both sides but functional on the left side only. Penis developed on left side only. We suggest that the genus *Idiosepius* is more closely related to *Teuthida* than to *Sepiina*.*I. pygmaeus* from mangroves on Phuket, Thailand is a new record for the Andaman Sea.

INTRODUCTION

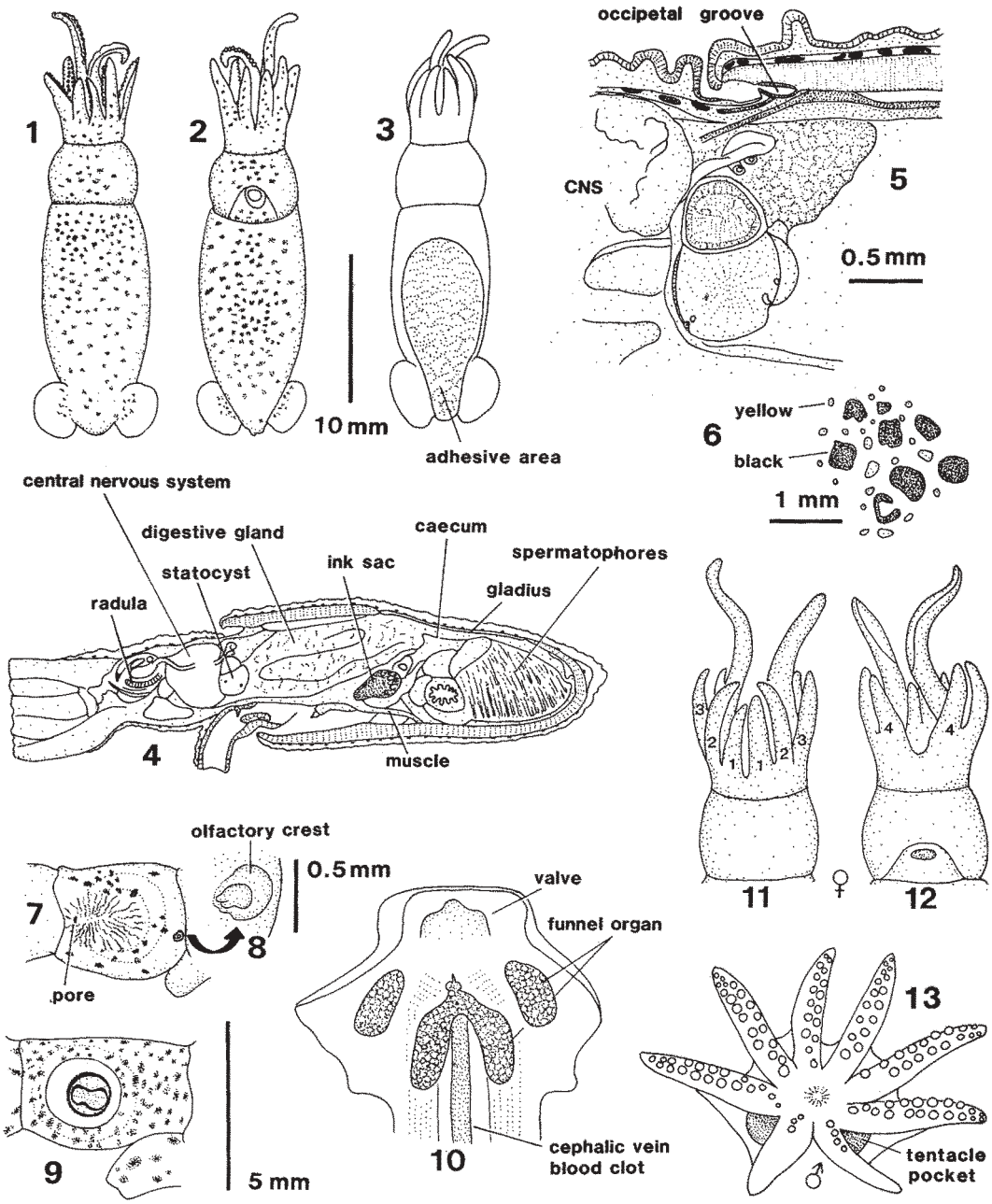
When Steenstrup (1881; English translation 1962) described *Idiosepius pygmaeus*, he found that it differed in so many essential points from the known genera that he had to erect a new genus to accomodate the species. According to Steenstrup (1881) *I. pygmaeus* was a myopsid with the 4th arm pair hectocotylized in males and with the normal appearance of a *Loligo* or *Loliolus*, having the small fins located posteriorly. On the other hand it had short arms like in sepiids and a similar locking apparatus on the mantle and funnel. Steenstrup (1881) found that *I. pygmaeus* lacked a dorsal gladius. There was, however, an inner dorsal arch-shaped sinew or hoop, which supported the viscera.

He had observed the peculiar sinew after cutting through the thin portion of the dorsal mantle. He found 2 firm strings, starting below the funnel collar, and diverging more and more posteriorly. He illustrated this so-called sinew in dorsal and lateral views (The present paper Figs. 50; 21' & 21").

Our material of *Idiosepius pygmaeus* agreed well with the general morphology of the species as shown by Steenstrup (1881; Figs. 10-33). However, when we made a cut as described by Steenstrup (1962, p. 93), we failed to see anything resembling an arch-shaped sinew, and we found that the species possesed a thin, although very clear gladius. These findings made us re-examine *Idiosepius pygmaeus* in an attempt to discover what Steenstrup (1881) might have seen and interpreted as a sinew. This unusual supporting structure was the reason for naming the genus *Idiosepius*.

Family IDIOSEPIIDAE

According to Nesis (1987) the genus *Idiosepius* comprises 6 valid species: *I. pygmaeus* Steenstrup, 1881 from the South China Sea, *I. paradoxus* (Ortmann, 1888) from Japan, *I. picteti* (Joubin, 1894) from Amboina, Indonesia, *I. notoides* Berry, 1921 from South Australia,



Figs. 1-13: *Idiosepius pygmaeus*. **1-2** female, dorsal & ventral views. **3** dorsal adhesive area. **4** longitudinal section of male. **5** section of statocyst area (*cf.* Fig. **4**). **6** pattern and colours of mantle chromatophores. **7** head of preserved male, lateral view. **8** enlarged olfactory crest (*cf.* Fig. **7**). **9** head of live male, lateral view. **10** dissected funnel showing valve, funnel organ and cephalic vein, ventral view. **11-12** anterior body, female, showing left and right arms 1-4. **13** arms of male, terminal view. Scales; Figs. **1-3, 11, 12**: 10 mm. Figs. **4, 7, 9, 10, 13**: 5 mm. Fig. **6**: 1 mm. Figs. **5, 8**: 0.5 mm.

I. biserialis Voss, 1962 from South Africa, and *I. macrocheir* Voss, 1962 from South Africa.

Grimpe (1931) divided *I. pygmaeus* into 3 subspecies with *I. pygmaeus hebereri* in the southern Pacific Ocean, *I. pygmaeus pygmaeus* in the central Indian Ocean, and *I. pygmaeus paradoxus* in the northern part of the Pacific Ocean. These subspecies have not been accepted by cephalopod researchers (Voss, 1963; Nesis, 1987).

Idiosepius pygmaeus Steenstrup, 1881 Figs. 1-49

Idiosepius pygmaeus Steenstrup, 1881, p. 219; Berry, 1921, p. 357; 1932, p. 46; Grimpe, 1931, p. 165-174; Voss, 1963, p. 63-67; Nesis, 1987, p. 137-141.

MATERIAL EXAMINED: PMBC 7268, 26 males and 5 females, Klong Mudong, surface water of mangrove channel at Ao Chalong, Phuket Island, 10.7.1988 and 18.7.1990. Hand netting, coll. S. Chantrapornsyl, A. Nateewathana and J. Hylleberg.

DESCRIPTION:

MANTLE: elongate, tapering and rounded at posterior end. Ventrally 0.4-0.6 mm thick; middorsally 0.1 mm in females (Fig. 24); thinner in the smaller males (Figs. 4,5). The dorsal margin straight (Fig. 1); ventral margin slightly excavated (Fig. 2). The posterior 3/4 of the dorsal mantle surface carries a prominent, rugose area which is strongly adhesive in live animals due to mucous secretion. The area is easy to detect in live animals by probing with a stick but not always easy to see in preserved animals (Figs. 1, 3). The ADHESIVE AREA is utilized by the squid to attach to objects in the water, e.g. prop roots and drifting leaves. The mantle is free around the neck but united to the funnel complex by complete fusion about 1 mm from the dorsal edge of the mantle (Fig. 4).

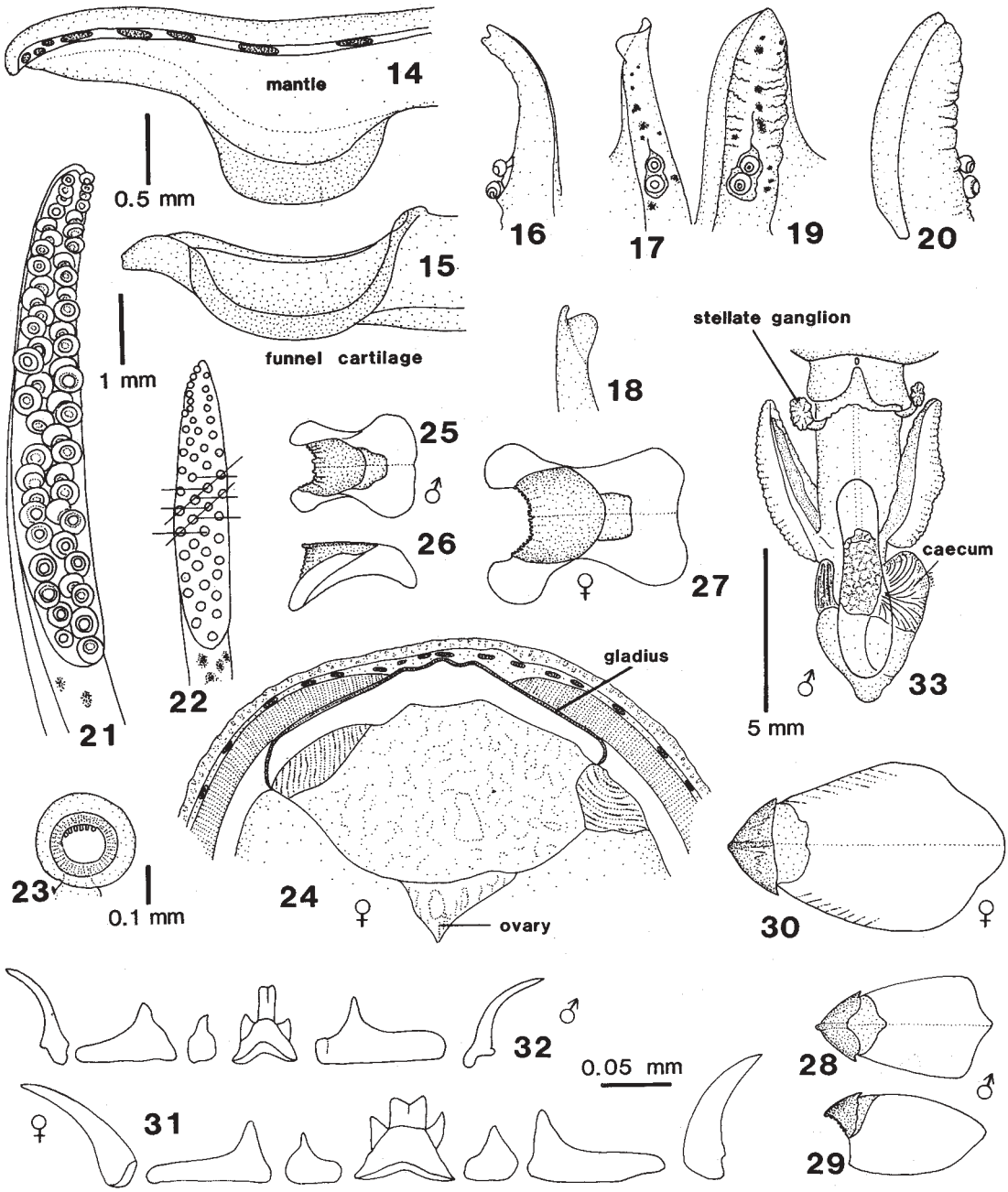
On the inner surface of the free part of the mantle is a small, narrow MUSCULAR "SCAR" located middorsally above a corresponding oval depression on the neck termed occipetal grove on Fig. 5. We interpret this structure as a rudimentary nuchal funnel cartilage.

In the posterior half of the mantle cavity, behind the gills, a VENTRAL MUSCLE connects the mantle to the body (Figs. 4, 34). A vertical muscular septum connects the mantle and body and divides the mantle cavity into right and left halves from above the ventral muscle to the posterior end of the body.

A pair of STELLATE GANGLIA are easily detached from the mantle in preserved specimens, and seen as a rounded discs together with the mantle connectives on either side of the dorsal median line after removal of the mantle (Fig. 33). Purple-brown and yellow CHROMATOPHORES cover the body (Fig. 6). The animals adapt a pale or black coloration according to their state of exitement. When, disturbed the body turns black and the squid ejects a coherent cloud of ink.

FINS: small, separate and attached to the base of the body at an angle (Figs. 1-3). Fins are kidney-shaped, distally free, projecting slightly beyond the posterior body. The muscular base carries many chromatophores; the outer fin is hyaline and very thin (Fig. 1); margin undulating in preserved specimens (not shown).

HEAD: small and compact, the width less than that of the mantle (Figs. 1-3); it extends below the mantle in preserved specimens and dorsally the neck carries an oblong oval depression interpreted as part of a rudimentary nuchal locking apparatus (Figs. 5, 37). The eyes are hardly visible in preserved specimens on account of wrinkled, opaque secondary cornea (Fig. 7). In live animals the eyes are silvery; the iris contractable to an oblong slit (Fig. 9) or completely



Figs. 14-33. *Idiosepius pygmaeus*. **14** mantle cartilage, longitudinal section, female. **15** funnel cartilage, longitudinal section, female. **16-18** hectocotylized left arm, lateral, oral and dorsal views. **19-20** hectocotylized right arm, oral and lateral views. **21** club of male. **22** club of male showing 2 horizontal and 4 oblique transverse rows of suckers, semischematic. **23** sucker from base of male club. **24** transverse section of female showing thin dorsal part of mantle and position of gladius. **25-27** upper mandible, male and female. **28-30** lower mandible, male and female. **31-32** teeth of radula, male and female. **33** male body, mantle removed, dorsal view. Scales; Fig. **33**: 5 mm. Figs. **14, 15, 21, 25-30**: 1 mm. Figs. **16-20, 22, 24**: 0-5 mm. Fig. **23**: 0.1 mm. Figs. **31, 32**: 0.05 mm.

closed in bright light. Eyes with minute anterior pores (Fig. 7). Small OLFACTORY CRESTS (Figs. 7, 8) posterior to the eyes; they are located under the mantle in preserved specimens but exposed in live animals.

FUNNEL: tapered tube with downwards pointing aperture, flap-like funnel valve, comparatively larger in the female (Fig. 10). Funnel organ complete: dorsal member inverted V-shaped with anterior papilla, 2 rounded-square ventrolateral pads. (Figs. 4, 10).

LOCKING APPARATUS: oval auriculate grooves on each side of the funnel (Figs. 10, 38). Oval tubercles on the inner surface of the mantle (Figs. 10, 37).

Rudimentary adductor muscles connect the dorsal side of the funnel with the lower side of the head. A pair of strong postero-lateral adductor muscles connect the funnel from the funnel cartilages to the sac of the rudimentary gladius (Figs. 37, 39, 50 labelled x).

ARMS: short and stout with blunt tips in the order 3,2,4,1 (Figs. 11, 12) but the arms do not differ much in length in both sexes. Keels absent. The web is very low except between III and IV which partly encloses the tentacles (Fig. 13). The suckers are biserial, almost spherical, and of equal size; diameter 0.21-0.30 mm (on male arm IV). There are 15-19 suckers on arm 1-3 in males and 21-31 in females on arm I-III; highest number are on arm III. Arm IV with 25 suckers in females. Arms IV markedly hectocotylized in males. Both arms are devoid of suckers except at the base where 1-4 suckers are found uniserially in various combinations (4-3, 3-3, 3-2, 3-1, 2-2, 2-1, 1-1) (Figs. 13, 16-20). The right arm is stout, somewhat triangular, rugose on oral surface, laterally with prominent membrane (Figs. 19, 20). The left arm is slender, nearly round, equal in length to the right one, tip flattened with prominent lateral flap, weak lateral membrane (Figs. 16-18).

TENTACLES: sheated in triangular pockets between the 3rd and 4th arms; the tentacles can only partly be withdrawn into pockets; 49-57 suckers in males, and 71-83 suckers arranged in 4 oblique rows in females. Live males carry 2 rows of suckers on tentacles (live females not observed). After preservation in formalin the rows may appear in 2 rows (Fig. 21) or be crowed into 3 or 4 oblique rows (Fig. 22).

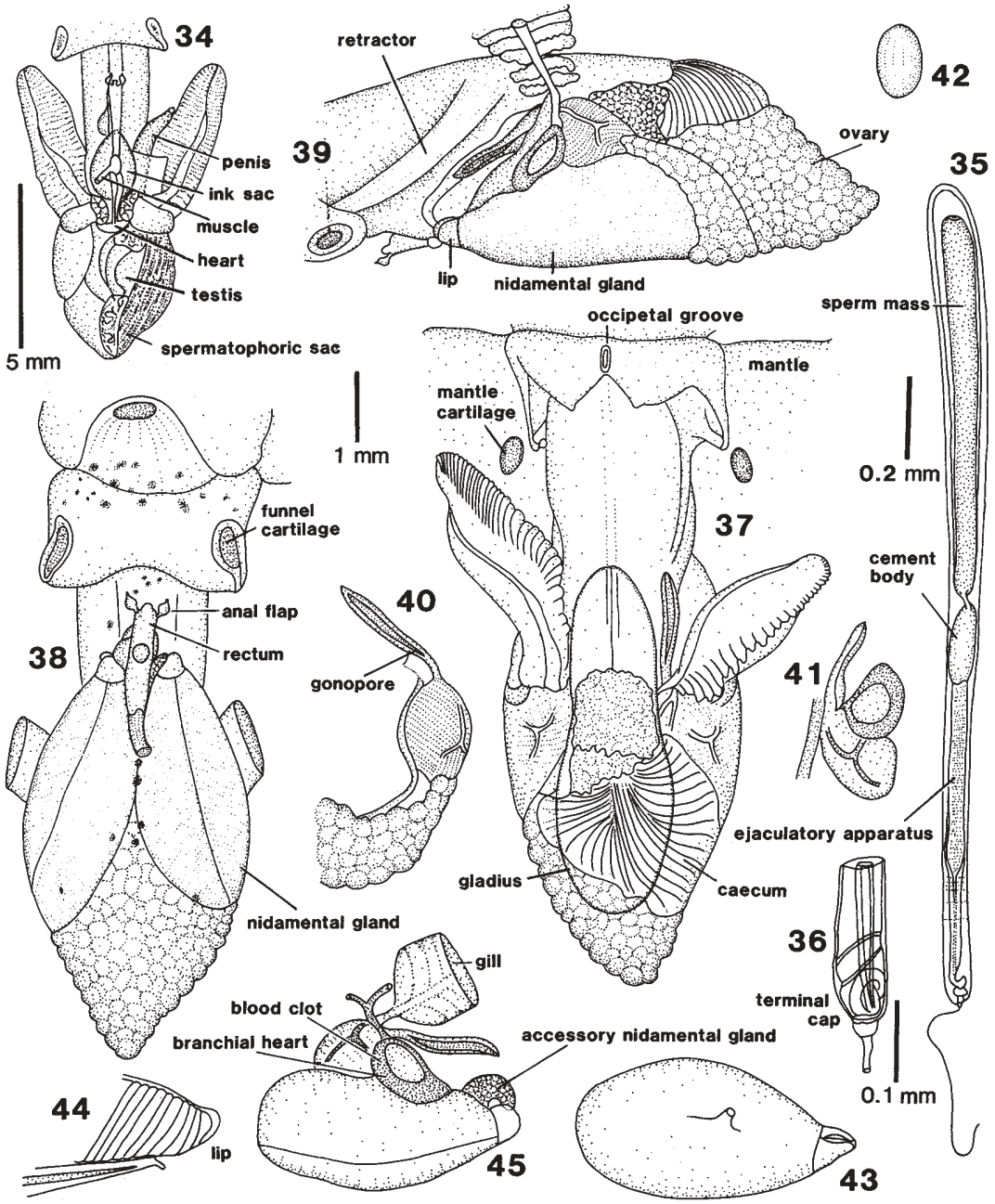
Suckers are largest on proximal part of club, decreasing in size towards the distal end. At 50 times magnification, the ring appears smooth on most suckers but suckers on tentacles may carry 6 irregular teeth (Fig. 23).

GLADIUS: slipper-shaped, very thin chitinous membrane without well developed rachis (Figs. 4, 24). The gladius is best observed in cross sections of the body (Fig. 24). Middorsally it is close to the connective tissue containing the melanophores (Fig. 24), continuing under the muscular layer of the mantle, and attached along the margin of the viscera (Fig. 24). The gladius is brittle in preserved specimens, and attempts to dissect it out were unsuccessful.

BUCCAL MEMBRANE: smooth without suckers (Fig. 13). Numerous spermatophores were found deposited on the membrane of one female.

BEAK: similar in both sexes. The upper mandible short, small black horny rostral hood with crenated edge (Figs. 25, 26, 27), thin hyaline rostral lamella and insertion plate. The lower mandible with small black rostrum, crenated edge, and large, thin, hyaline insertion plate (Figs. 28, 29, 30).

RADULA: typical rachidian with 7 rows in females. Prominent median teeth which carry a strong central tooth (with a tendency to split in the median line) and 2 lateral teeth (Fig. 31). Inner marginal row of small, pointed teeth; outer marginals broad and pointed. Lateral rows with slender hook-like teeth. Lateral rows without marginal plates (Fig. 31). Two males were studied. They both had a reduced rachidian radula with one row of inner marginals absent. Otherwise, as in females (Fig. 32).



Figs. 34-45. *Idiosepius pygmaeus*. **34** male body, mantle removed, ventral view. **35** spermatohore. **36** enlarged terminal cap (*cf.* Fig. **35**). **37** female body, mantle removed, dorsal view. **38** female body, mantle removed, ventral view. **39** female body, mantle removed, lateral view. **40** oviduct, gland and gonopore, left side. **41** non-functional gonopore, gland and branchial heart, right side. **42** egg, dissected from ovary. **43** nidamental gland, showing blood vessel, removed from the left side (*cf.* Fig. **38**). **44** longitudinal section of nidamental gland showing lips and vein, left side. **45** nidamental gland, removed from the right side. Scales; Figs. **34, 37-41, 43, 45**: 5 mm. Figs **42-43**: 1 mm. Fig. **36**: 0.1 mm.

REPRODUCTIVE SYSTEM: Male. Spermatophoric organ tightly packed with testis, glands and prostate (Fig. 34) and surrounded with a cover forming the genital sac occupying the posterior half of the male body. The exact number of glands and their connections was not studied. All males contained many spermatophores in the voluminous spermatophoric sac (Fig. 33) which on the left hand side (Fig. 34) turned into a fairly short, cylindrical penis not reaching the edge of the funnel.

SPERMATOPHORES: measured about 2.1 mm in length and 0.13 mm in width (Fig. 35). The granular sperm mass occupied half of the length of the spermatophore. The cement body, supporting cylinder, and ejaculatory apparatus constituted the other half (Fig. 35). Ejaculatory apparatus coiled, terminated with a long filament (Fig. 36).

FEMALE REPRODUCTIVE SYSTEM: Large ovary occupy posterior part of body (Figs. 37-39). Both oviducts present (Figs. 40, 41) but only the left one is functional (Fig. 40). Oviduct packed with oval eggs, about 1 mm long (Fig. 42). Oviducal glands egg-shaped, joined with oviduct at one end and projecting as a slender lip at the other end (Fig. 40). Large nidamental glands dominate the ventral body (Figs. 38, 39). The glands are elongated oval with short lips at anterior ends (Figs. 43, 44). The small accessory nidamental glands do not project anterior to the nidamental glands (Fig. 45).

INK SAC: pyriform, compact organ with silvery outer coating. In females: hidden under the nidamental glands (Fig. 38); in males: exposed on the dorsal side of the intestine in front of the branchial hearts (Figs. 4 ,34). The reservoir filled with dark brown ink; the duct as long as the ink sac (Figs. 4, 48).

DIGESTIVE SYSTEM: The oesophagus connects the buccal complex (Fig. 4) with the stomach, passing anteriorly through the brain (Fig. 46), continuing through the large midgut hepato-pancreatic gland (Fig. 47). The small stomach is hidden within the visceral mass while the prominent spiral part of the caecum dominates the posterior surface of the body (Figs. 33, 37). The intestine continues from the stomach to the ventral surface of the hepato-pancreatic gland, and terminates with the anus provided with 2 lanceolate flaps (Fig. 48).

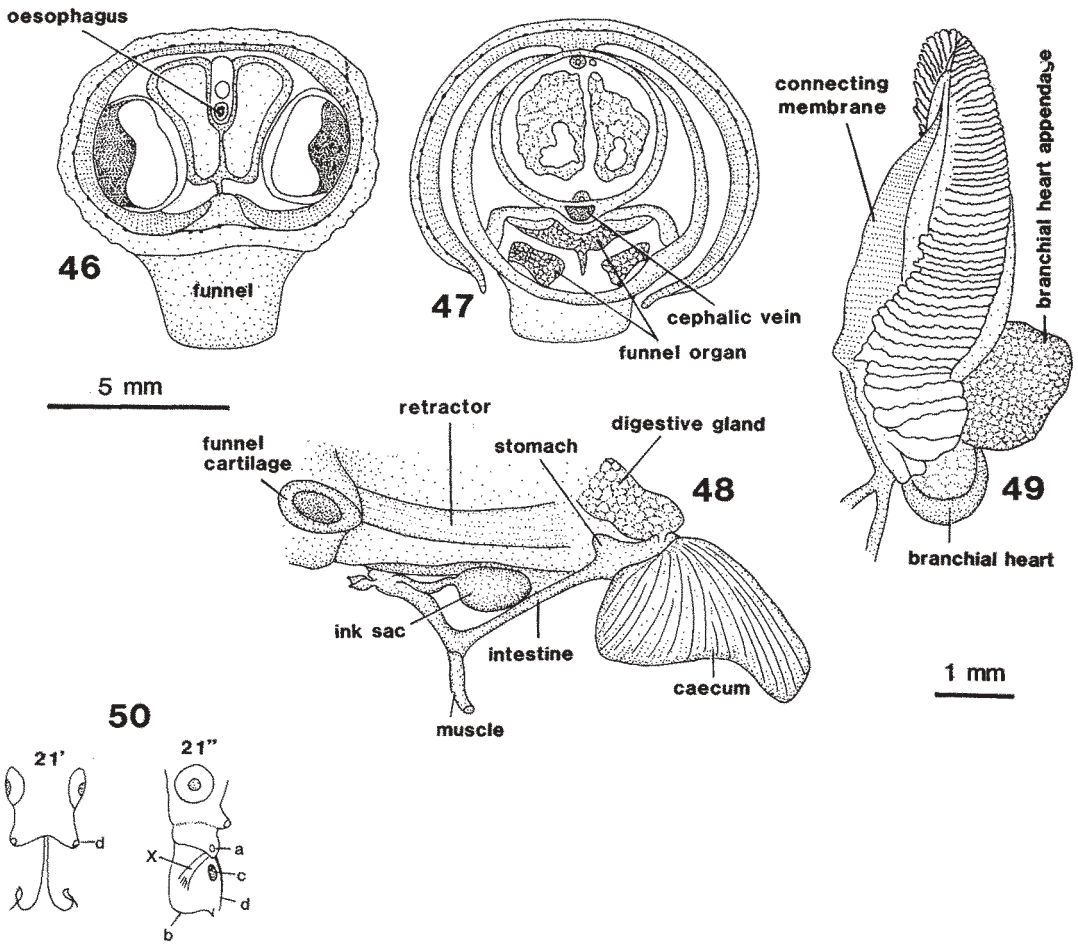
INNER CARTILAGENOUS SKELETON: located posterior to the eyes behind the central nervous system (CNS) transition between head and body. It is a rounded capsule with 3 sections: one dorsal part housing the brain and 2 ventro-lateral statocysts (Figs. 4, 5).

STATOCYSTS: with well developed maculae. Details in maculae, cristae and anticristae were not studied. Calcified statoliths not present (Fig. 5).

CIRCULATORY SYSTEM: Blood of living animals colourless. In preserved specimens the blood coagulates into a hard and brittle substance of brownish-green hue. Clot of blood is particularly prominent in veins: the cephalic vein, vena cava, in the branchial hearts, and in gills.

The spacious pericardial coelom contains the heart, branchial hearts (Fig. 45), branchial glands and renal sacs. The branchial hearts are muscular and provided with white, rounded glands. GILLS attached to the inner mantle wall by mesenterium. The free side of each demibranch has about 45 plicate filaments in females (Fig. 49) and about 30 filaments in males.

REMARK: On the basis of dissections of fresh and preserved specimens, we suggest that the structure Steenstrup (1881) referred to as sinew in the diaphragm (Fig. 50; 21"d) most likely is the cephalic vein containing coagulated blood (see Fig. 10). Similarly, the structure Steenstrup called inner sinus rod is part of the vascular system (Fig. 50; 21) and Fig. 50; 21" shows the same structure seen from the right side. It is erroneously labelled b. One possibility would be that Steenstrup saw coagulated blood in the



Figs. 46-50. *Idiosepius pygmaeus*. **46** transverse section in front of the funnel, posterior view, female. **47** transverse section behind the funnel, anterior, female. **48** part of the digestive system, dissection of the left side, female. **49** gill, branchial heart and branchial heart appendage dissected from right side of female.

50 copy of Fig. 21', 22", Steenstrup (1881). The original legend reads: " The inner sinus rod of *Idiosepius*, seen from the dorsal side, 21', and from the right side 21". a= funnel grooves, b= right retractor infundibuli, c= lens-shaped ink sac, d= sinew in the diaphram."

The correct legend should read: 21': d = **funnel groove**, also termed funnel cartilage in the present text. - 21": a = funnel groove, b = **inner sinew rod**, c = lens-shaped ink sac, d = sinew in the diaphragm. Furthermore, to 21" we have added the letter x = **right retractor infundibuli**. Scale; Figs. **46-48**: 5 mm., Fig. **49**: 1 mm. Fig. **50**: not to scale.

Table 1. MEASUREMENTS AND INDICES of 20 males and 5 females:
Means, Standard Deviations, and Ranges of Selected measurements and Indices (in percent) of *Idiosepius pygmaeus* Steenstrup, 1881. Indices abbreviated according to Ropes and Voss (1983).

Measure/ Index	MALES n	Mean	S.D. (n-1)	Range	FEMALES n	Mean	S.D. (n-1)	Range
TL (mm)	20	21.2	3.0	12.0-24.6	5	31.1	1.9	29.6-34.0
ML (mm)	20	11.7	1.0	9.0-13.5	5	17.5	1.9	16.0-20.5
MWI	20	46.1	4.1	39.1-55.6	5	48.1	3.7	43.7-52.9
FLI	20	27.1	5.6	17.4-36.4	5	24.5	3.8	18.7-25.0
FWI	20	49.1	4.4	42.5-58.3	5	49.2	7.2	40.6-58.8
HWI	20	42.1	3.0	38.2-50.0	5	35.9	1.8	33.3-37.5
HLT	20	40.8	5.5	25.6-50.0	5	31.9	7.5	24.4-44.1
$AL_{I}I$	20	26.9	3.2	22.7-35.6	1	-	-	21.9
$AL_{II}I$	20	31.6	3.8	26.4-36.7	1	-	-	26.8
$AL_{III}I$	20	33.1	4.0	26.4-42.2	1	-	-	26.8
$AL_{IV}I$	-	-	-	-	1	-	-	21.9
HcAI-L	20	22.5	3.5	16.4-31.1	-	-	-	-
HcAI-R	20	21.1	3.4	17.0-29.2	-	-	-	-
HcLI-L	20	73.8	7.4	63.3-90.0	-	-	-	-
HcLI-R	20	72.4	8.2	54.5-85.7	-	-	-	-
$ASC_{I}L$	20	18.0	2.0	15.0-24.0	2	-	-	24.0-25.0
$ASC_{I}R$	20	17.0	2.0	14.0-21.0	2	-	-	21.0-26.0
$ASC_{II}L$	20	21.0	3.0	15.0-26.0	2	-	-	28.0-31.0
$ASC_{II}R$	20	21.0	2.0	17.0-27.0	2	-	-	30.0-31.0
$ASC_{III}L$	20	21.0	2.0	18.0-24.0	2	-	-	25.0-29.0
$ASC_{III}R$	20	22.0	2.0	18.0-25.0	2	-	-	28.0-31.0
$ASC_{IV}L$	20	3.0	1.0	4.0-2.0	2	-	-	19.0-25.0
$ASC_{IV}R$	20	2.0	-	4.0-1.0	2	-	-	22.0-25.0
ClLI	20	26.2	5.3	16.4-37.8	5	32.4	5.7	27.3-41.2
EDI	20	23.2	2.7	17.4-27.3	-	-	-	-
LnDI	20	8.7	1.2	5.6-11.3	-	-	-	-

dorsal vessel which accompany the oesophagus. This is slightly visible through the skin of the digestive gland. However, one problem with this interpretation is, that the vessel does not continue as shown by Steenstrup (Fig. 50; 21') but descends into the visceral mass at the level of the branchial bases. It seems more likely that he observed the strong branchial veins, since he mentions two firms strings. But then the continuation anterior to the edge of the funnel is difficult to explain. Clot in the branchial hearts, could account for the peculiar termination of the diverging, arch-shaped sinew shown by Steenstrup (Fig. 50; 21'). The Fig. 50; 21' & 21" are also confusing in other respects. The structure labelled d in 21' should read a = funnel grooves. The structure labelled b in 21" is not the right retractor infundibuli, which is not la-

belled in 21"; we have added the letter x to the Figure. The x shows the right retractor infundibuli while b should read inner sinew rod.

Steenstrup (1881) compared this inner sinew rod to the inner ring around the margins of the spongy substratum (loculomenta) found in *Sepia brevimana* Steenstrup. However, in view of the absence of such a ring, and the presence of a thin, but distinct gladius, and an oval muscular "scar" in the position of a nuchal funnel locking cartilage, we suggest that the genus *Idiosepius* is more closely related to Teuthida than to Sepiina.

Voss (1953) described *Pickfordiateuthis pulchella,* a myopsid squid which he placed in the family Pickfordiateuthidae. This squid resembles *Idiosepius* in several respects, especially in the external morphology, but *P. pulchella* has nuchal locking apparatus present and a feather-like gladius with a broad fane. *P. pulchella* is placed in the order Teuthida, suborder Myopsida by Nesis (1987). At present we are unable to enter into a discussion concerning the systematics of myopsis squids. We believe that studies of ontogenesis are necessary in order to solve the question of relationships between Idiosepiidae, Pickfordiateuthidae, and Loliginidae. Berry (1932) remarked that much still remained to be worked out concerning the exact natural position are relationships of the genus *Idiosepius*. According to Berry (1932) its position is rather isolated on basis of statocyst structure; the adult organ remaining in a somewhat primitive condition. In view of the rudimentary gladius, and possibly rudimentary nuchal locking apparatus, we suggest that the relationships of myopsid squids should be reconsidered by systematists.

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