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Mollusca Gastropoda : Systematic position and revision of *Haloceras* Dall, 1889 (Caenogastropoda, Haloceratidae fam. nov.)

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ABSTRACT

Haloceras, until now included in the Trichotropidae, is made the type of a new family, Haloceratidae, considered related to but more primitive than the Tonnoidea and the Echinospirida, on the basis of new anatomical information. The main difference from existing tonnoidean families is a more primitive nervous system and the absence of complex salivary glands. The new family shows similarities to the Trichotropidae, a family which should be included in the Echinospirida. *Micropiliscus* Dall, 1927, until now included in the Trochidae, is synonymized with *Haloceras*, and the new genus *Zygoceras* is introduced. Seventeen named species (ten new) and three left unnamed are here included in the family. All species live on the outer part of the continental shelf and the slope, down to about 3500 m depth. Species of Haloceratidae are known from the mid and low latitudes of the Atlantic, Indian, East and West Pacific oceans. All but one species have planktotrophic larval development and one species is known from both the Atlantic and the Indian Oceans.

RESUME

Position systématique et révision du genre *Haloceras* Dall, 1889 (Caenogastropoda, Haloceratidae fam. nov.).

Le genre *Haloceras* était jusqu'ici classé dans les Trichotropidae. Sur la base de nouveaux caractères anatomiques,une famille nouvelle Haloceratidae est créée. Elle est considérée proche de, mais plus primitive que les Tonnoidea et les Echinospirida. Les différences principales qui séparent les Haloceratidae de la lignée tonnoïde sont un système nerveux plus primitif et l'absence de glandes salivaires complexes. Cette nouvelle famille présente des ressemblances avec les Trichotropidae, qui doivent d'ailleurs être classés dans les Echinospirida. Le genre *Micropiliscus* Dall, 1927, jusqu'ici classé dans les Trochidae, est placé en synonymie d'*Haloceras*, et le nouveau genre *Zygoceras* est décrit. La famille comprend dix-sept espèces nommées (dont 10 nouvelles) et trois laissées sans nom; toutes vivent sur les parties profondes du plateau continental et sur la pente, jusqu'à 3500 m environ, aux latitudes basses et moyennes dans les océans Atlantique, Indien, Ouest et Est Pacifique. Toutes les espèces, sauf une, ont un développement larvaire planctotrophe et une espèce est connue à la fois de l'océan Atlantique et de l'océan Indien.

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INTRODUCTION

HISTORICAL BACKGROUND

Based on shell and opercular features, DALL (1889) introduced the name *Haloceras* for the NW Atlantic deep-sea gastropod *Cithna cingulata* Verrill, 1884. He considered *Haloceras* a subgenus of *Separatista* Gray, 1847 (then placed in the Adeorbidae, now, in our view correctly, placed in the Trichotropidae). THIELE (1929: 243) and WENZ (1940: 890) classified *Haloceras* as a subgenus of *Torellia* Jeffreys, 1867 in the family Trichotropidae (= Capulidae).

DALL (1927) described *Micropiliscus*, as a subgenus of the trochid genus *Solariella* Wood, 1842, differing from the typical species by having a brownish larval shell. *Micropiliscus* has since been retained in the Archaeogastropoda as a subgenus of *Solariella* by the few authors that have mentioned or listed it (THIELE, 1929: 48; WENZ, 1938: 275; QUINN, 1979: 43).

During the last 10 years we have been aware that there exist several species similar to *Haloceras*, and we have been accumulating material of them and searching museum collections we have visited. The present paper is based on all the 103 specimens and shells that, to our knowledge, have been taken by oceanographic expeditions worldwide in 120 years. The absence of fossil record should probably be interpreted as a reflection of the rarity of the family. It is remarkable to note that, whereas the first haloceratid specimen was collected in 1870 (although described in 1883), 64 % of the specimens now available have been taken in just the last 20 years. No haloceratid was taken during the "*Challenger*", "*Valdivia*" or "*Siboga*" expeditions, and half of the species had not been collected 10 years ago. Two regions, the South-West Pacific with 8 species and the North Atlantic with 6 species, now contain together 82% of the species of the family, but this simply represents a collecting effort artefact. We believe that future exploration of tropical deep waters will greatly increase the number of species in the family.

THE GENUS *CITHNA* A. ADAMS, 1863

The genus *Cithna* A. Adams, 1863 has frequently been used for strange, globular or discoid gastropods, among them *Haloceras*. Presently (THIELE, 1929: 64; WENZ, 1938: 336) *Cithna* is classified among the archaeogastropods. We figure (Figs 44-45) a syntype from USNM, to show the planktotrophic larval shell which directly excludes *Cithna* from the Archaeogastropoda. The soft parts are not known, but a position in the vicinity of *Scrupus* Finlay, 1924 (position in Rissooidea presently unknown, see PONDER, 1985), seems very likely, judging from shell morphology.

Abbreviations used in text:

sh(s) — (empty) shell(s);
spm(s) — (live taken) specimen(s);
AMS — The Australian Museum, Department of Invertebrate Zoology, Sydney;
BMNH — British Museum of Natural History, Mollusca Section, London;
LACM — Los Angeles County Museum of Natural History, Los Angeles;
MNHN — Muséum national d'Histoire naturelle, Paris;
MOM — Musée océanographique, Monaco;
NMNZ — National Museum of New Zealand, Wellington;
NSMT — National Science Museum, Tokyo;
RMNH — Rijksmuseum van Natuurlijke Historie, Leiden;
USFC — United States Fisheries Commission;
USNM — U.S. National Museum of Natural History, Division of Mollusks, Washington D.C.;
ZMC — Zoologisk Museum, Köbenhavn.

MATERIAL AND METHODS

Most species are known from empty shells, sometimes with partly decayed and dried soft parts. These were used for radular preparation after rehydration. The alcohol preserved specimens turned out to be a problem since the soft parts could not be extracted without damaging the shells, which was too great a drawback when often only one or two shells were known of the species. Therefore they were dried and the soft parts loosened from the columella by gently pushing them backwards, into the shell. After that they were rehydrated in buffered formalin and extracted. They could then be used for examination of external morphology and some rough dissections, including preparation of the radula.

The anatomical descriptions are thus mainly based on dried and rehydrated specimens of:

Haloceras carinata (RMNH)

Haloceras cingulata (USNM 52077)

Haloceras galerita (holotype). A partly damaged head-foot was serially sectioned in the same way as *Z. tropidophora*. It contained none of the organs behind the cephalopedal haemocoel.

Haloceras japonica (LACM 67-167.2)

Haloceras tricarinata ("*Discovery*" stn 10141)

Zygoceras tropidophora (paratype). The specimen was decalcified, serially sectioned at 5 µm and stained with Ehrlich's haematoxylin - eosin. One specimen was dried to allow safe removal of the body from the shell after rehydration and used for radular preparation.

ANATOMY

EXTERNAL MORPHOLOGY

Figs 1-2

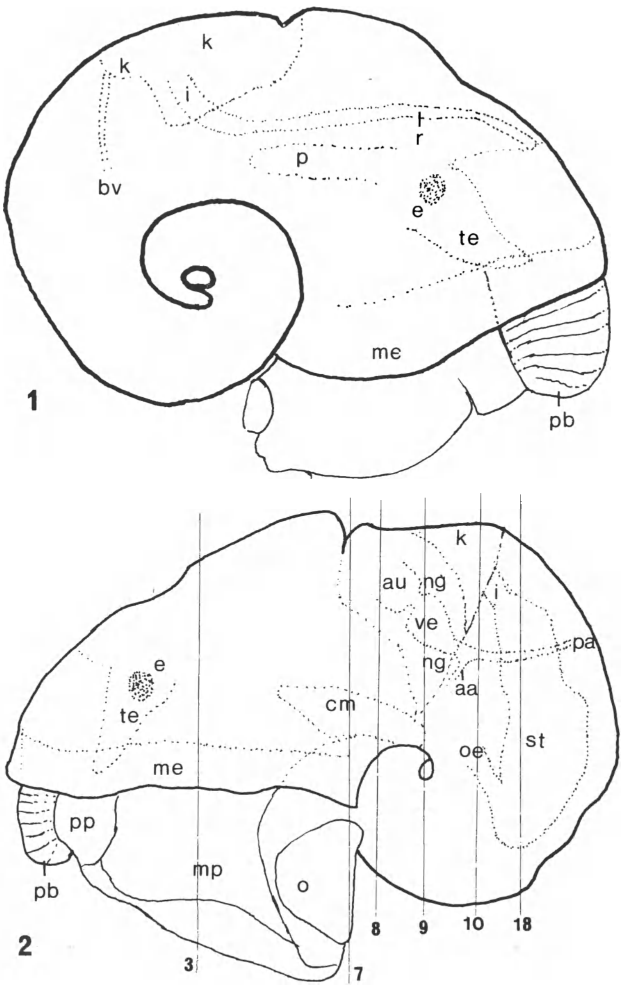
The general colour of the soft parts in alcohol is whitish-yellowish transparent, with a more opaque osphradium and occasionally (*Z. tropidophora*) a brownish-violet intestine and stomach.

The body consists of about 1.7 whorls in *Z. tropidophora*, of which the voluminous head-foot and pallial complex occupy 0.25-0.30 whorls. The rather shallow pallial cavity reaches back about 0.25 whorls and its most posterior part forms a blunt wedge-shaped space between the pericardium and cephalo-pedal haemocoel.

The columellar muscle (Fig. 2) is solid and broad but very short.

The head-foot is large, occupies about 0.25 whorls (slightly more in the tall-spired species) and the pallial skirt covers most of this when the soft parts are retracted. Many of the internal organs can be seen by transparency (Figs 1-2). In *H. tricarinata* the posterior part of the foot is quite suckershaped, in other species less so but to some extent it is divided in a more solid, rounded, posterior part and an anterior, thinner, strongly folded, and probably very motile part. The latter has been strongly contorted in all specimens but its anterior dorsal side carries a large and fleshy propodium, well aligned with the anterior edge of the foot. The lower part of the side of the foot is distinctly demarcated from the upper parts, by a more or less distinct horizontal furrow (Fig. 3) and by having a rougher surface. *H. tricarinata* and *Z. tropidophora* have a large posterior pedal gland opening in the posterior part of the foot. This could not be discerned in the other species, but neither could its absence be ascertained. On the rear, dorsal part of the foot, there is a thick but fragile, yellowish operculum. In species with a depressed or disc-shape shell the operculum (Figs 28, 31-34) is fan-shaped with the initial coils situated apically, but they are usually worn off in large specimens, so only the latest formed section of the fan remains. In more tall-spired species the operculum is more ovate and spirally coiled. If the nucleus is left, there is a distinctly set off part, which is thinner, smoother and multispiral, and which corresponds to the larval operculum.

The head is about as broad as the foot and equipped with tentacles which in one specimen of *Zygoceras tropidophora* are tapering, long and



FIGS. 1-2. — *Zygoceras tropidophora*, external view of soft parts. **1.** right side. — **2.** Left side. Fine vertical lines indicate position of cross sections with corresponding Fig. number.

aa — anterior aorta; *au* — auricle; *bv* — blood vessel; *cm* — columellar muscle; *e* — eye; *i* — intestine; *k* — renal organ; *me* — mantle edge; *mp* — mesopodium; *ng* — renal gland; *o* — operculum; *oe* — oesophagus; *p* — penis; *pa* — posterior aorta; *pb* — proboscis; *pp* — propodium; *r* — rectum; *st* — stomach; *te* — tentacle; *ve* — ventricle.

slender; in the other species, strongly wrinkled, short and conical, and evidently strongly contracted. All species have large eyes situated dorso-laterally on, and of a diameter corresponding to about 2/5 of, the tentacle base. The tentacles are connected by a thin skin-fold, covering the proboscis. The dorsal body-wall is quite thick and muscular.

Presumably no species have a snout. This could, however, not be verified in some specimens, because the proboscis has been more or less everted in all specimens examined and in some specimens which were badly preserved and dried it could not be seen if there was a tip of a proboscis or a snout.

The pleurembolic proboscis, often partly everted, is quite solid and muscular, in *Z. tropidophora* 5 mm long and 2.5 mm diameter, but can unquestionably be extended much more since the wall of the proboscis sheath is about 1 mm thick. The buccal mass is fairly small, 0.8 mm long and 0.6 mm diameter. There is a pair of solid, slender jaws (Figs 4, *j*; 29, 30).

All specimens examined had a simple, flattened, finger-shaped penis attached slightly behind and below the right tentacle (Fig. 1). In *H. japonica, H. galerita* and *H. cingulata,* the penis also had an anteriorly directed simple fold-like process. Such a flap was missing in *Z. tropidophora* and *H. carinata.* It was not possible to distinguish an external sperm groove, but it can be seen in sections of the two sectioned species.

Some species (*H. cingulata, Z. tropidophora*) have an external skinfold on the inner and distal part of the pallial oviduct, but its morphology could not be studied in detail.

One specimen of *Haloceras carinata* had a large egg-mass in the pallial cavity (Figs 64-65), measuring 0.9 x 0.9 x 1.6 mm and consisting of about 200 developing, shell-less embryos of a diameter of about 0.16 mm. Due to the dried state of the specimen it was not even possible to verify the presence of an oviduct, but a penis was present.

One specimen, *Haloceras japonica*, proved to be ovoviviparous and had 9 large embryos (Fig. 64) in the partly ruptured (from drying ?) oviduct. These embryos were lying in the duct behind the pallial cavity, along almost one whorl of the visceral mass. This specimen also had a penis of normal appearance and position for the genus.

The pallial cavity is wide and spacious (Fig. 3). The anterior edge of the pallial skirt has a simple, thick and muscular, well defined zone with no papillae or appendices. At the left corner this zone is broader and thicker, and may function as a siphon.

The gill occupies a narrow zone, from the thickened edge of the pallial skirt backwards to the bottom of the cavity and consists of about 25 flattened, fingershaped leaflets, in *Z. tropido-*

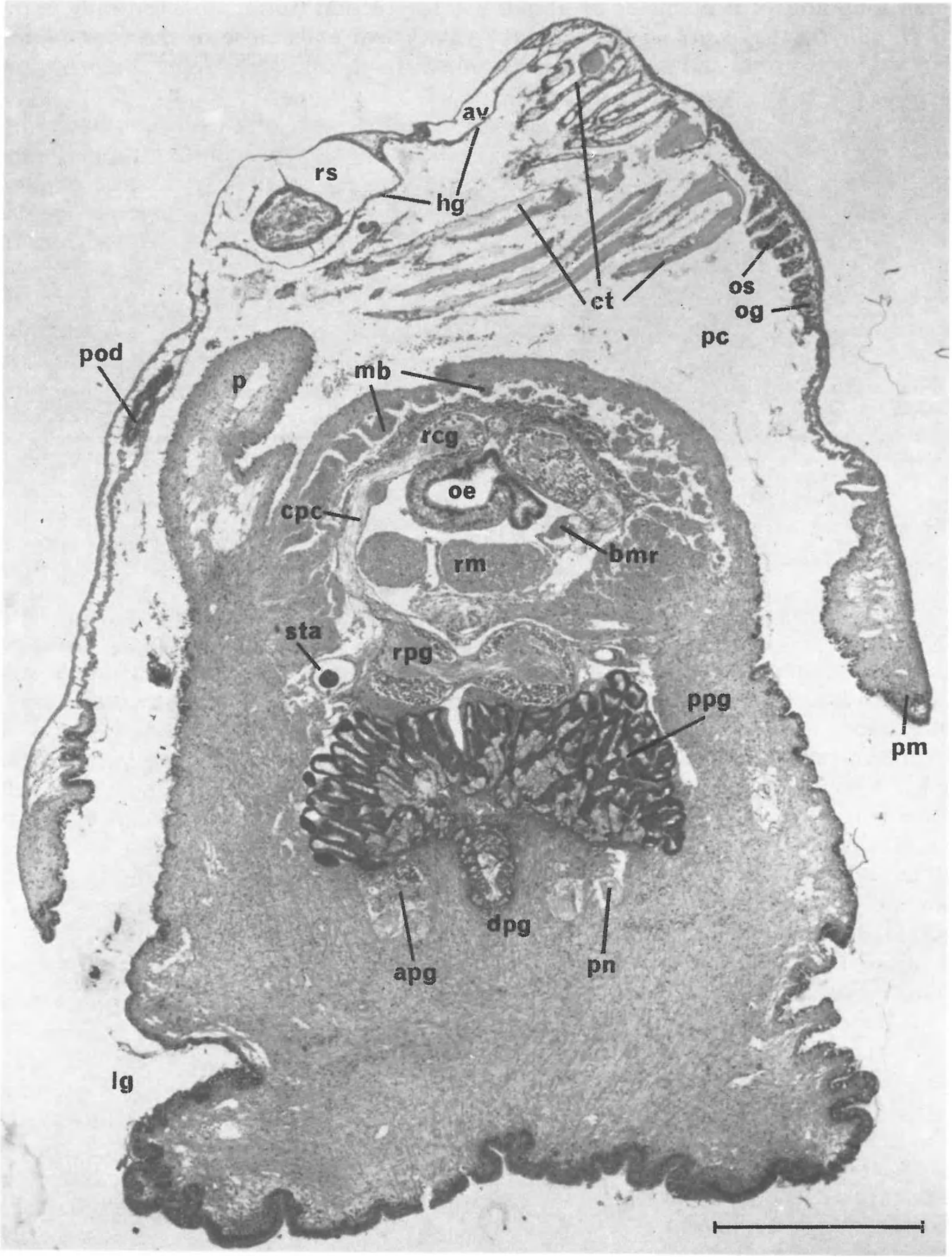


FIG. 3. — *Zygoceras tropidophora*, cross section of body behind tentacles.

apg — accessory pedal ganglion; *av* — afferent branchial vessel (from rectal sinus); *bmr* — buccal mass retractor; *cpc* — cerebro-pedal connective; *ct* — ctenidium; *dpg* — duct of posterior pedal gland; *hg* — hypobranchial gland; *lg* — lateral groove; *mb* — muscle bundles from proboscis sheath; *oe* — oesophagus; *og* — osphradial ganglion; *os* — osphradium; *p* — penis; *pm* — pallial margin; *pn* — (outer) pedal nerve; *pod* — pallial oviduct; *ppg* — posterior pedal gland; *rcg* — right cerebral ganglion; *rm* — retractor muscle of proboscis; *rpg* — right pedal ganglion; *rs* — rectal sinus; *sta* — statocyst. Scale line 1 mm.

phora 1.1 mm long and of a diameter of about 0.1 mm. In *H. galerita* they were 45 in number, 0.5 mm long, 0.07 mm broad and 0.03 mm thick. In the posterior part of the cavity the gill is fairly central, anteriorly it bends slightly over to the left.

The osphradium is partly bipectinate and it is situated along the anterior 3/5 of the gill. It consists of 15-30 leaflets (in *Zygoceras tropidophora* 0.5 mm long and 0.12 mm broad) facing the gill and half that number of smaller leaflets along facing to the left. In *H. tricarinata* only the outer half was bipectinate, in *Z. topidophora* the inner half bipectinate and in *H. cingulata* it was probably monopectinate.

The rectum runs almost centrally in the pallial cavity and ends close to the edge of the pallial skirt. Its most distal part is free from the pallial roof.

The specimen of *H. carinata* had white faecal pellets in rectum and a foraminiferan in the stomach. A specimen of *Z. tropidophora* had a few small faecal pellets in rectum, consisting of unidentified organic material and free from mineral particles.

The hypobranchial gland is very thin and inconspicuous. It covers the inner side of the rectal sinus and a part of the pallial skirt in the central part of the pallial cavity, but can only be discerned in histological sections.

INTERNAL ANATOMY

Figs 3-27

Head-foot

The tentacles, the sides and the back of the head-foot are covered by a thin epithelium, on the sides of the foot with numerous large mucus producing cells mixed with the epithelial cells. Mucous cells are common also on the penis. The hypobranchial (Figs 3, 5, *hg*) gland consists of a single layer of secreting cells, which covers the left side of the rectal sinus and the pallial roof leftwards to the gill, from just in front of the rectum back to the kidney.

The sole of the foot has a dense layer, one cell thick, of mucous cells directly under the epithelium. The posterior pedal gland (Fig. 3, *ppg*) is large and voluminous, anteriorly bilobed and abutting the pedal ganglia. Less than half-way to its opening the two lobes unite and form a common duct (Fig. 3, *dpg*) which opens posteriorly and centrally via a wide pore. The anterior pedal gland (Fig. 6, *ang*) fills a large cavity between the pro- and mesopodium, invades them both, and extends back to the pedal ganglia where it abuts the posterior pedal gland. It has a wide opening between the pro- and mesopodium.

Alimentary canal

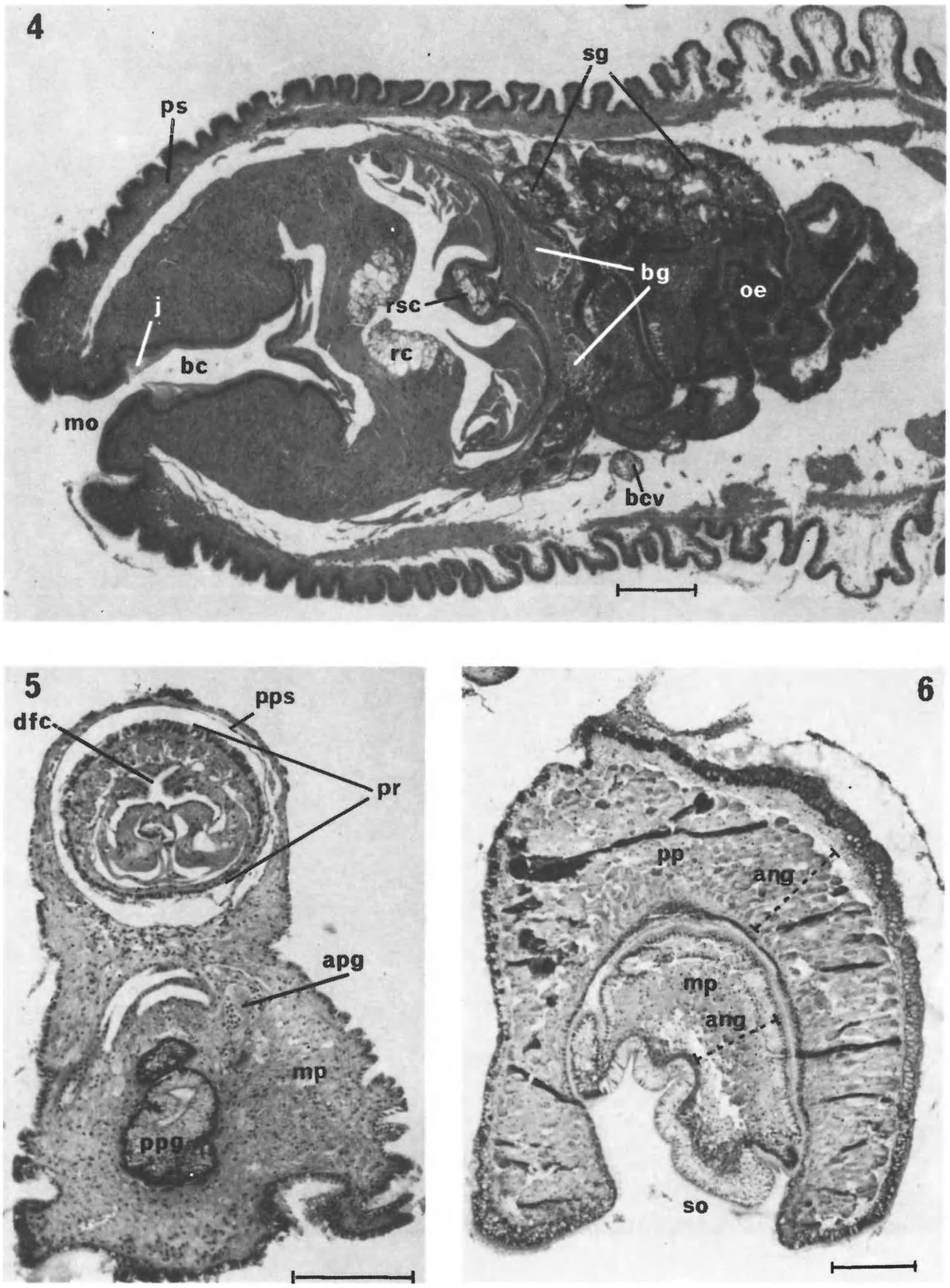
Figs 4, 11-22

The alimentary system consists of a pleurembolic proboscis, a buccal mass with taenioglossate radula, an anterior oesophagus with lateral pouches, a long midoesophagus, a comparatively short posterior oesophagus, a simple stomach, a short intestine and a long rectum.

The anterior part of the proboscis sheath is solid and muscular and can be retracted so the true mouth is situated immediately behind the tentacles and the posterior end of the muscular section abuts the cerebral ganglia. It is manipulated by two major ventral muscle bundles (Fig. 3, *rm*) which connect it to the columellar muscle, and numerous smaller muscles (Fig. 3, *mb*), which in *Z. tropidophora* end in the walls of the cephalopedal haemocoel. In *H. galerita* they fuse with the two ventral muscle bundles. The rear part of the sheath is extremely thin-walled (Fig. 5, *pps*) and when the proboscis is retracted, it leads from the rearmost, thick-walled section forwards to the level of the tentacles.

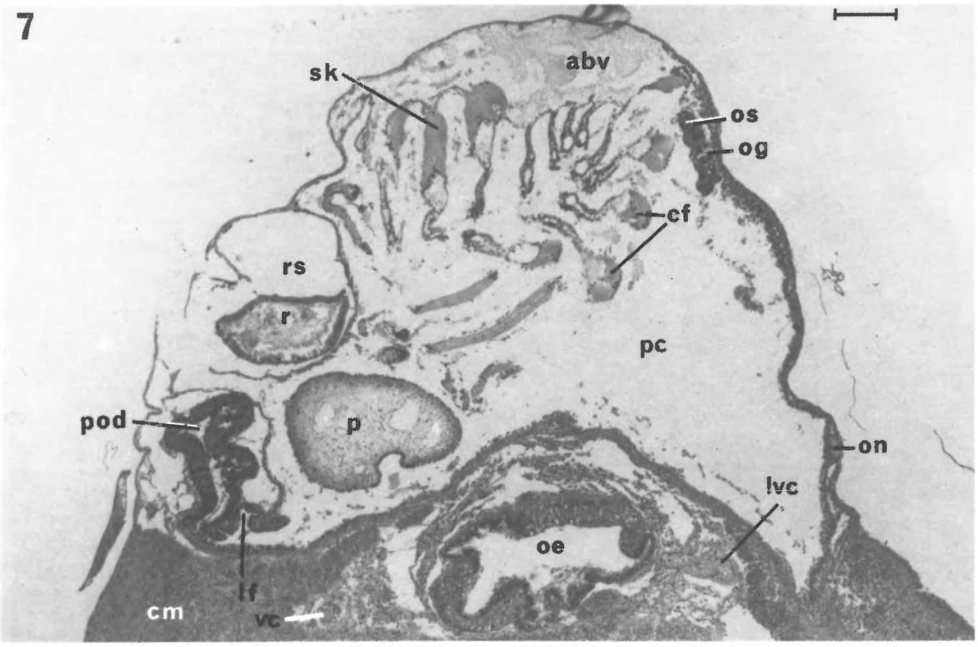
The mouth is situated terminally at the tip of the proboscis (Fig. 4, *mo*). The sides of the oral cavity are equipped with a pair of prismatic, semicircular jaws (Figs 4, *j*; 29-30) and the buccal cavity is largely lined with cuticle. The salivary ducts open shortly behind the jaws dorsolaterally via a small pore. Their ducts meander backwards; in *H. galerita* all the way through the nerve-ring, in *Z. tropidophora* they stop halfway. The salivary glands each consist of a single thick-walled coiled tube (Fig. 4, *sg*).

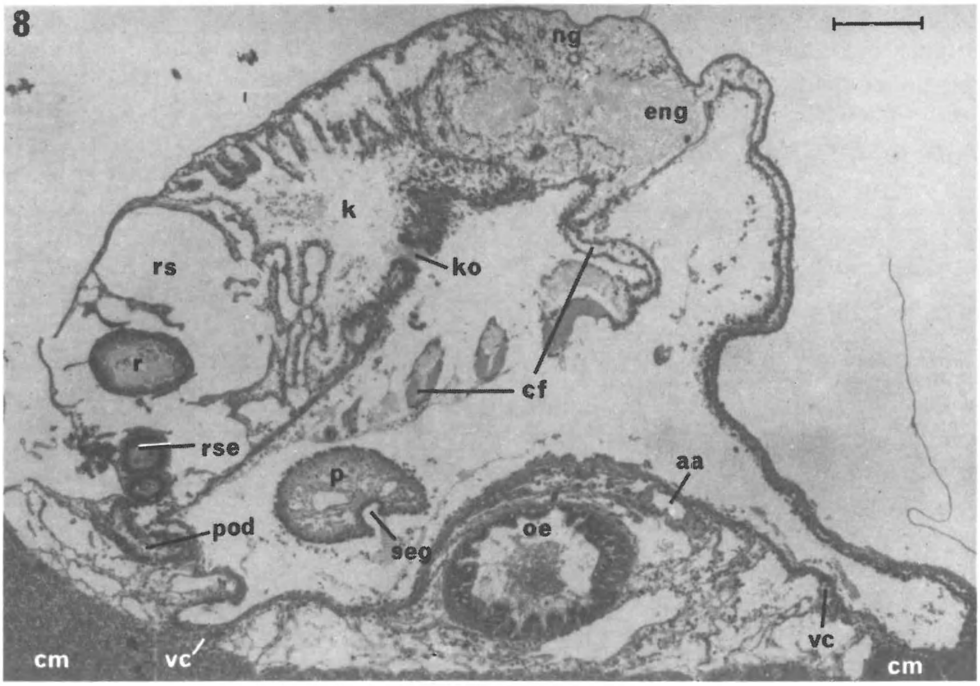
In *Z. tropidophora* the radular sac exits poste-



FIGS. 4-6. — **4.** *Zygoceras tropidophora*, horizontal section through anterior part of proboscis. — **5.** *H. galerita*, cross-section through head-foot between tentacles and penis. — **6.** *H. tropidophora*, horizontal section through pro- and mesopodium.

ang — anterior pedal gland; *apg* — acessory pedal ganglion; *bc* — buccal cavity; *bcv* — buccal connective; *bg* — buccal ganglia; *dfc* — dorsal food channel; *j* — jaw; *mo* — mouth; *mp* — mesopodium; *oe* — oesophagus; *pp* — propodium; *ppg* — posterior pedal gland; *pps* — posterior part of proboscis sheath; *pr* — proboscis; *ps* — proboscis sheath; *rc* — radular cartilage; *rsc* — radular sac; *sg* — salivary glands; *so* — sole of mesopodium. Scale line 0.25 mm.





FIGS. 7-10. — *Haloceras tropidophora*, cross section of pallial cavity and viseral mass. Position of sections indicated in Fig. 2. — **7.** Middle part of pallial cavity. — **8.** Anterior part of kidney. — **9.** Most posterior part of pallial cavity. — **10.** Visceral hump, anterior to stomach.

aa — anterior aorta; *abv* — afferent branchial vein; *arv* — afferent renal vein; *au* — auricle; *cf* — ctenidial filament; *cm* columellar muscle; *cph* — cephalo-pedal haemocoel; *dg* — digestive gland; *eng* — efferent cavity, collecting blood from renal gland and ctenidium; *i* — intestine; *is* — intestinal sinus; *k* — renal organ; *ko* — renal opening; *lvc*

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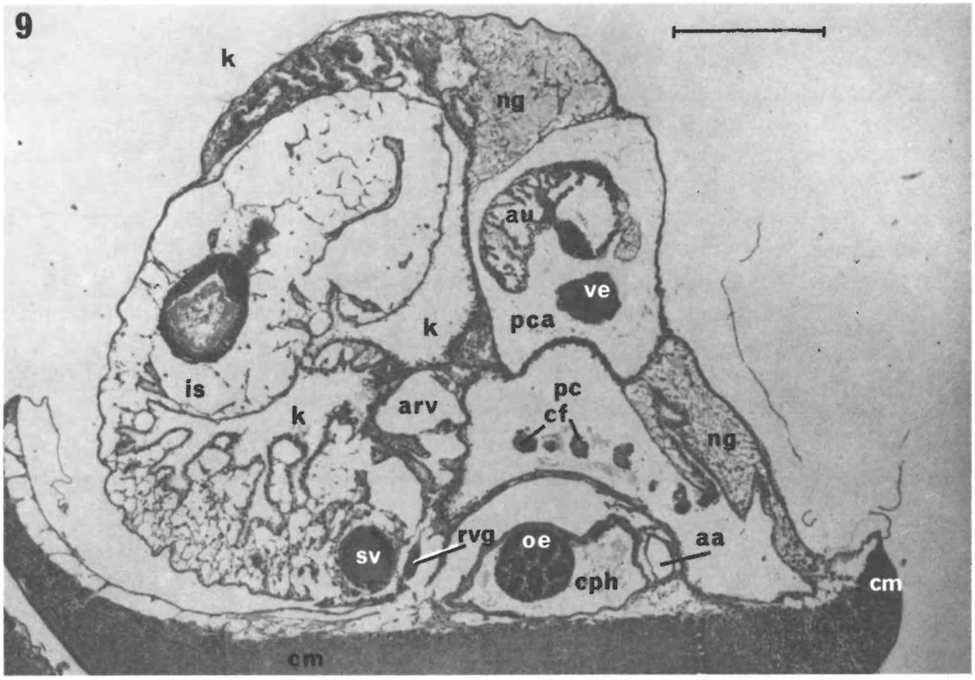

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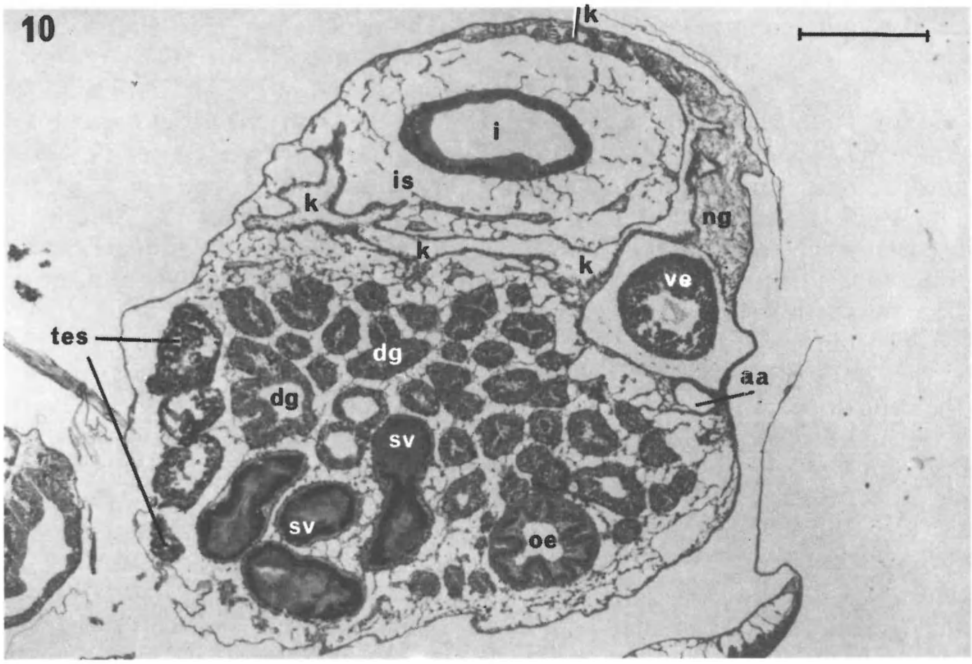


— left visceral connective; *lf* — lateral groove on free lobe of pallial oviduct; *ng* — renal gland; *oe* — oesophagus; *og* — osphradial ganglion; *on* — osphradial nerve; *os* — osphradium; *pc* — pallial cavity; *pca* — pericardium; *p* — penis; *pod* — pallial oviduct; *r* — rectum; *rs* — rectal sinus; *rse* — receptaculum seminis; *rvg* — right visceral ganglion; *seg* — seminal groove; *sk* — skeletal rod; *sv* — seminal vesicle; *tes* — testicle; *vc* — visceral connective; *ve* — ventricle. Scale lines 7-8, 0.25 mm, 9-10, 0.5 mm.

riorly and makes a sharp turn ventrally, then dorsally, so it ends ventrally to the anterior oesophagus, immediately behind the buccal mass. In *H. galerita* it exits posteriorly and parallels the anterior oesophagus (Figs 16-17, *rsc*) for a short distance before it ends just in front of the buccal ganglia, which are situated unusually far back in this species. The radular cartilages are well developed.

The oesophagus starts with a dorsal food channel (Fig. 16, *dfc*), which as soon as the ventral floor has been formed, widens to form a pair of shallow and thin lateral pouches over the posterior part of the buccal mass. These disappear behind the buccal mass. In *H. galerita* the dorsal food channel continues dorsally, ciliated and glandular, while the ventral floor of the oesophagus is lined by a cuticle (Fig. 17). The dorsal folds become broader and are strongly ciliated and the oesophagus gets a roughly I-shaped cross section, all the way back to the nerve ring, where the oesophagus widens and the walls become more uniform all around. Here the oesophagus is also quite compressed and folded so it was not possible to discern the torsion. In *Z. tropidophora* the ventral part of the anterior oesophagus is not lined by a cuticle, but the whole circumference, except the dorsal food channel is lined by mucus producing epithelium (Fig. 11). This thick-walled, ventral part then splits in two parts connected by a thin wall. At the same time the dorsal food channel has rotated to become ventral (Fig. 13, *dfc*) giving rise to an I-shaped portion (Fig. 13).

The posterior oesophagus (Fig. 14) begins at the end of the cephalopedal haemocoel and has folded walls. It opens ventrally and slightly in front of the posterior end of the stomach, jointly with two openings from the digestive gland. It could not be ascertained if these openings correspond to an anterior and posterior lobe of the digestive gland.

The stomach (Fig. 2, *st*; 18) is situated close to the left side of the body, just behind the pericardium. It is simple and sausage-shaped, tapering towards the anterior end where it goes over into the intestine via the style-sac without any abrupt change. It is almost three times as long as broad. There seems to be no crystalline style.

To the right of and posteriorly to the oesophageal opening there is a prominent gastric shield and a large cuticularized area where food is accumulated. In the ventral, posterior part of the stomach run two low and broad typhlosoles which continue some distance into the style sac (Fig. 20, *t1, t2*).

The intestine leaves the anteriorly and dorsally situated posterior part of the stomach, turns to the right under the left-most and posterior extension of the kidney (Fig. 10, *i*), in a very spacious haemocoel (Fig. 10, *is*), then it enters the pallial skirt and turns to the left, so the anus is more centrally situated than the proximal parts of the rectum (Fig. 7). There was no great histological difference between the proximal and more distal parts (rectum) (Figs 21-22).

Vascular system

Figs 7-10

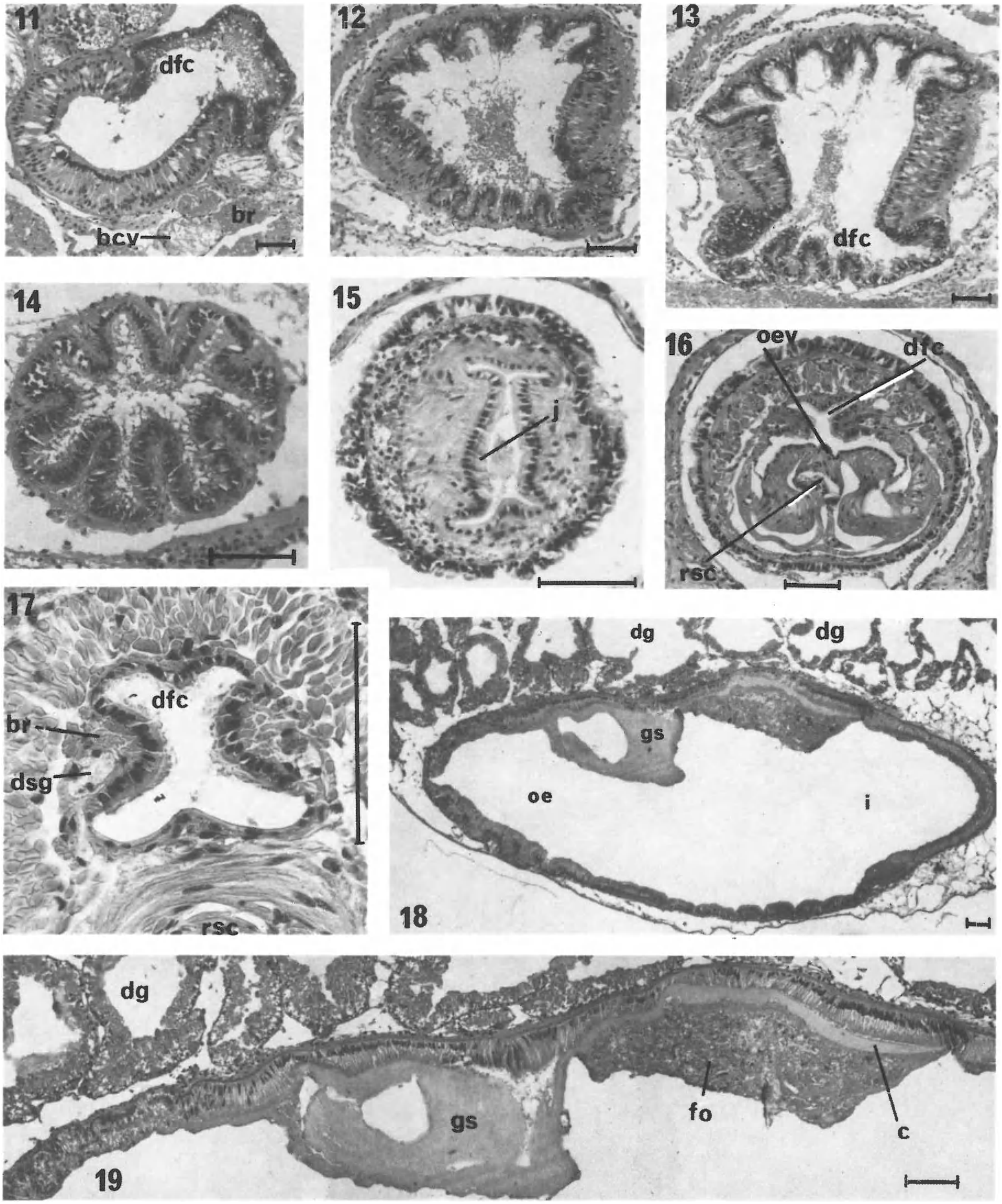
All organs are lying in a system of very spacious venous sinuses which are filled by a sponge-like system of interconnected cells, giving the tissues a very porous appearance.

The pericardium (Fig. 9, *pca*) is situated with its anterior end above the posterior part of the pallial cavity, with the auricle in front of and above the ventricle. In cross-section it is roughly triangular with one corner drawn out towards the center of the whorl. The renopericardial duct leaves this corner at the anterior part of the ventricle. There is no gonopericardial duct.

We assume that blood from the cephalopedal haemocoel collects in a system of large anastomosing venous cavities (Figs 9, 23, *arv*) which communicate with the visceral and intestinal haemocoels and the kidney. There is also a somewhat separate dorsal vein (Fig. 23, *kv*) which starts from spaces in the intestinal haemocoel and the venous cavities and connects with the kidney folds and the renal gland (Fig. 23, *ng*).

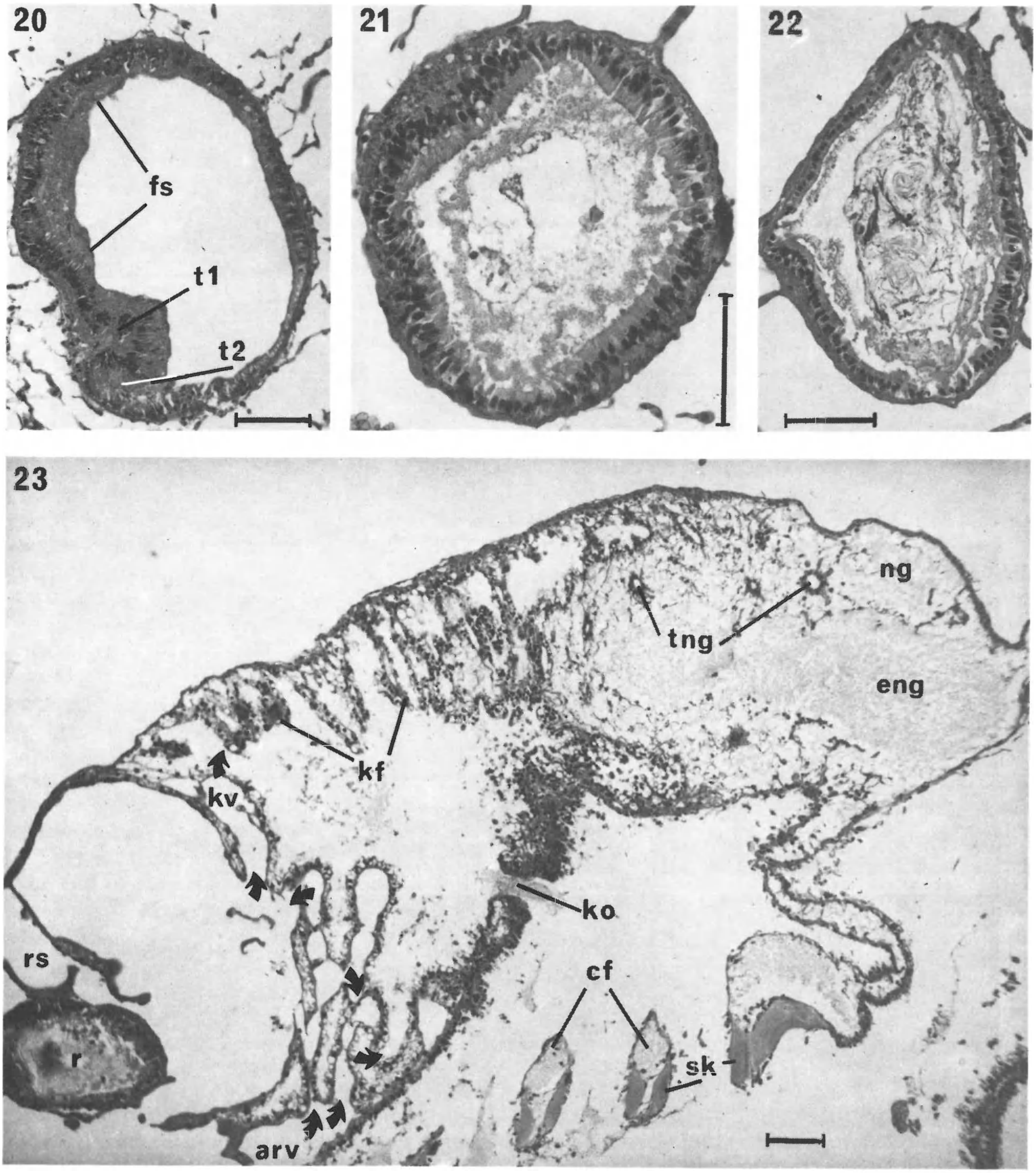
The efferent branchial vein and the efferent renal gland vein (Fig 23, *eng*) join anteriorly to the pericardium and carry the blood to the auricle.

The aorta leaves the ventricle posteriorly and splits directly into one anterior and one posterior branch. The posterior aorta is very thin-walled and continues superficially backwards, sending off smaller vessels which supply the visceral hump with blood. It was followed backwards past the stomach. The anterior branch of the aorta (Figs 8-10, *aa*) turns forwards, passes



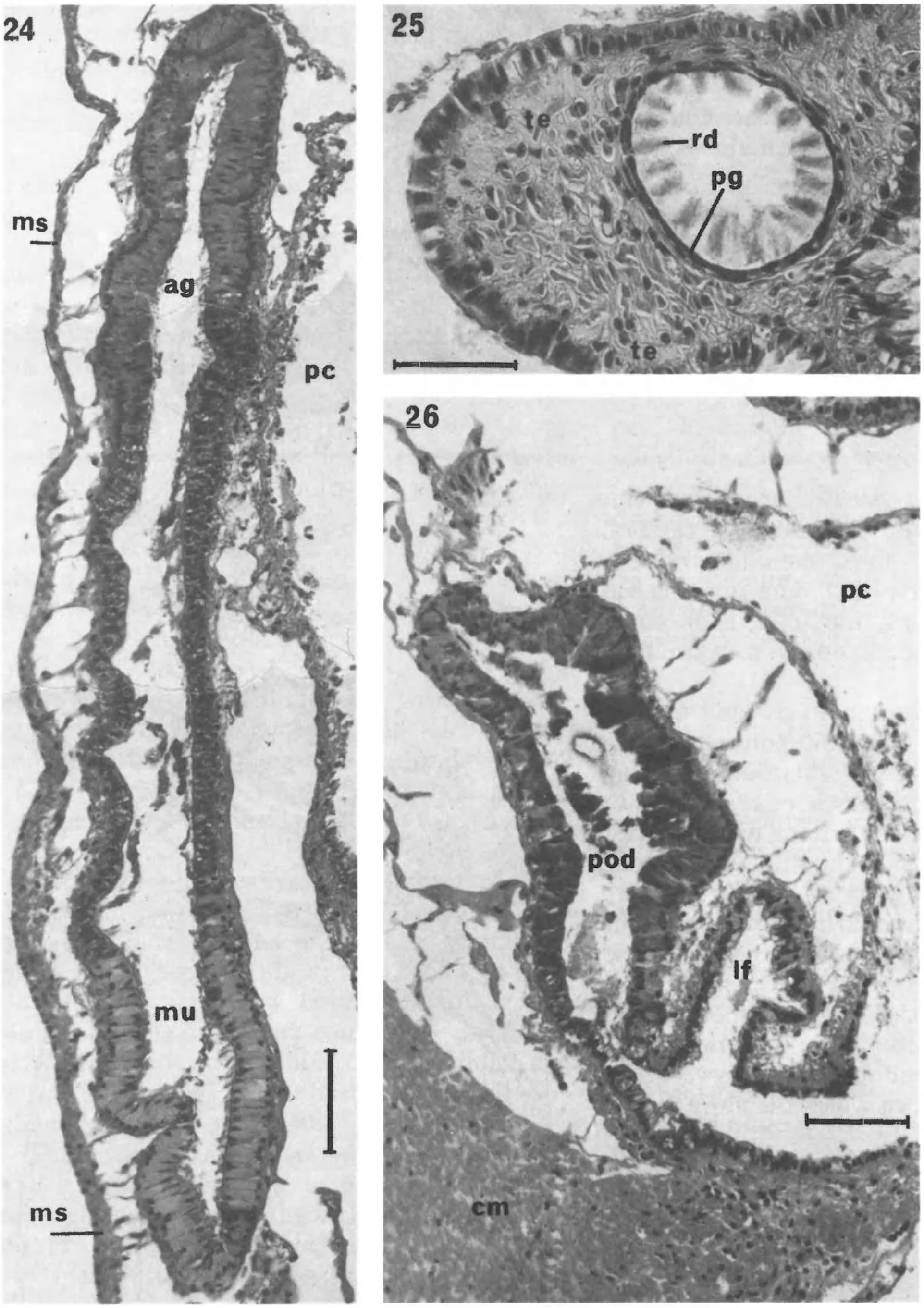
FIGS. 11-19. — Anterior alimentary canal and stomach of *Z. tropidophora* (11-14, 18, 19) and *H. galerita* (15-17). — **11.** Anterior oesophagus with dorsal food channel. — **12-13.** Midoesophagus, after the rotation of dorsal food channel. — **14.** Posterior oesophagus. — **15.** Proboscis tip with oral tube and left jaw. — **16.** Proboscis and buccal mass, retracted into head-foot. — **17.** Anterior oesophagus between buccal ganglia and buccal mass. — **18.** Stomach, longitudinal section at close to right angle to oesophagus and intestine. — **19.** Detail of gastric shield.

bcv — buccal connective; *br* — buccal mass retractor; *c* — cuticle lining; *dfc* — dorsal food channel; *dg* — digestive gland; *dsg* — duct of salivary gland; *fo* — food; *gs* — gastric shield; *i* — position of exit of intestine from style sac; *j* — jaw; *oe* — position of entrance of oesophagus; *oev* — oesophageal valve; *rsc* — radular sac. Scale lines 0.1 mm.



FIGS. 20-23. *Zygoceras tropidophora*, posterior alimentary canal and kidney. — **20.** Intestine shortly after stomach. — **21.** Intestine more distally. — **22.** Rectum. — **23.** Pallial skirt with anterior part of kidney.

cf — ctenidial filament; *eng* — efferent cavity, collecting blood from renal gland and gill, leading to auricle; *fs* — food string; *kf* — renal folds; *ko* — renal pore; *kv* — vessel connecting kidney folds and rectal sinus; *ng* — renal gland; *r* — rectum; *rs* — rectal sinus; *sk* — skeletal rods in gill filament; *t1, t2* — typhlosoles; *tng* — tubules of renal gland. Scale lines 0.1 mm.



FIGS. 24-26. — **24.** *Z. tropidophora*, Distal, closed part of pallial oviduct. — **25.** *Haloceras galerita*, cephalic tentacle with eye. — **26.** *Z. tropidophora*, open part of pallial ociduct and sperm grove.
ag — albumen gland; *cm* — columellar muscle; *lf* — lateral fold; *ms* — pallial skirt; *mu* -mucus producing epithelium; *pc* — pallial cavity; *pg* — pigment layer; *pod* — pallial oviduct; *rd* — rods of retina; *te* — cephalic tentacle. Scale lines 24, 26, 100 µm, 25, 50 µm.

through the anterior left corner of the renal gland and enters the cephalopedal haemocoel to the left of the oesophagus. It then follows the oesophagus forwards, turns to the right to a position dorsally to the oesophagus and splits in several smaller vessels shortly behind the supraoesophageal ganglion.

Excretory organs

Figs 2, 8-10, 23

The renal organ extends back to just past the ventricle; rightwards it extends dorsally and ventrally to the intestine; anteriorly it invades the pallial roof (Fig. 8, *k*). One lobe of the renal gland protrudes in front of the pericardium, surrounds the efferent branchial and renal vessels, and the anterior aorta and extends down to the columellar muscle (Figs 8-10, *ng*).

The renal pore (Fig. 23, *ko*) is situated dorsally in the pallial roof just in front of the pericardium.

Dorsally the right half of the renal organ is occupied by renal folds; the left half consists of the renal gland, penetrated by several narrow, blindly ending ducts from the cavity of the kidney (Fig. 23, *tng*).

Nervous system

Fig. 27

The nervous system is partly concentrated with the pleural ganglia being fused with the cerebral ones and short and thick commissures and connectives in the nerve-ring. The oesophageal ganglia have rather long, but solid, connectives and the visceral and buccal connectives are long and very thin.

The pedal ganglia are about as long as high and somewhat wider. They are connected by a very short commissure. At their anterior and ventral ends two large nerves emerge close to each other, an anterior one leading to an anterior accessory pedal ganglion and a ventral one leading to a posterior accessory ganglion. Both these pairs of ganglia are partly embedded in the posterior pedal gland. Each pedal ganglion also sends out at two large nerves laterally. The anterior accessory pedal ganglia innervate the anterior parts of the foot. The posterior accessory ganglia each send out two nerve stems backwards in the foot, of which the more central

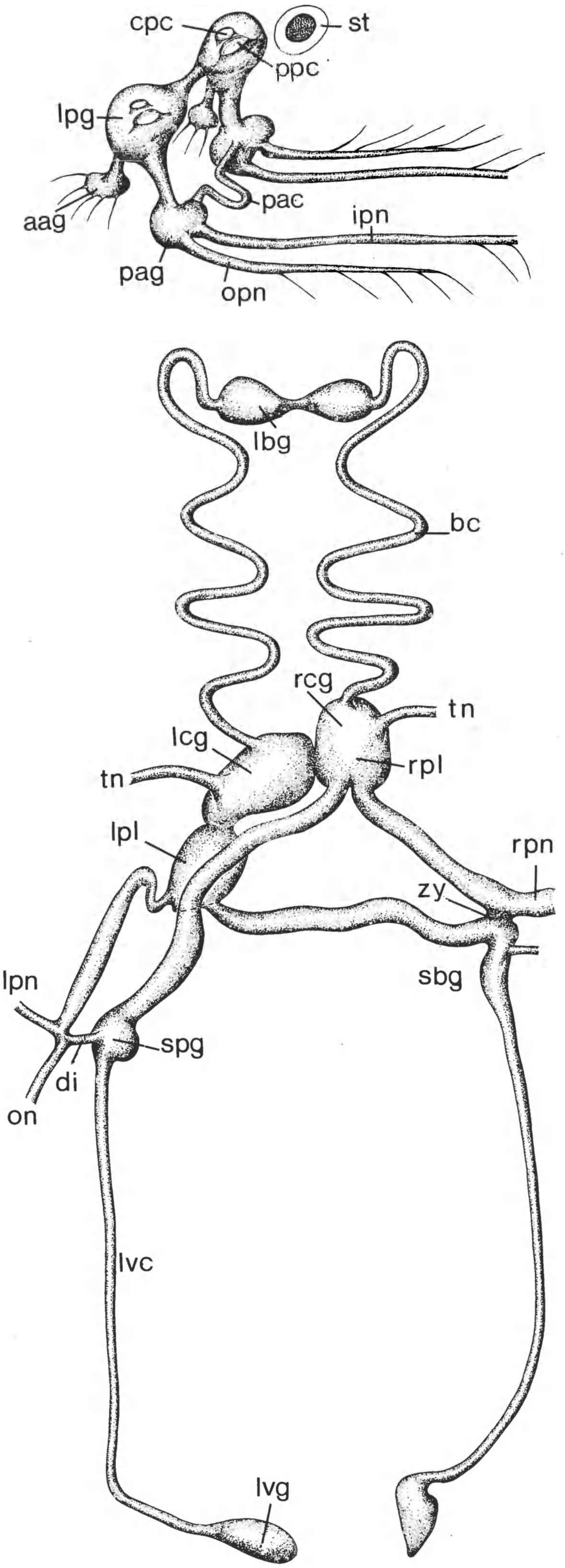


Fig. 27. — *Zygoceras tropidophora*, nervous system. Pedal ganglia separated from cerebral ones; only right statocyst drawn.

aag — anterior accessory pedal ganglion; *bcv* — buccal connective; *ca* — commissure between posterior accesory pedal ganglia; *di* — dialyneury; *ipn* — inner pedal nerve; *lbg* — left buccal ganglion; *lcg* — left cerebral ganglion; *lpg* — left pedal ganglion; *lpn* — lateral pedal nerve; *lpn* — left pallial nerve; *lvg* — left visceral ganglion; *opn* — outer pedal nerve; *pac* — commissure between posterior accessory pedal ganglia; *pag* — posterior accessory pedal ganglion; *plg* — pleural ganglion; *rpn* — right pallial nerve; *rvg* — right visceral ganglion; *sbg* — subeosophageal ganglion; *spg* — supraoesophageal ganglion; *stc* — statocyst; *tn* — tentacle nerve; *zy* — zygoneury.

nerve innervates the rear part of the foot, the more lateral one the middle part and sides of the foot. No connections between the stems were found. There is also a large nerve from each posterior accessory ganglion which follows the duct of the posterior pedal gland backwards for a short distance and then connect dorsally to the duct.

The cerebral ganglia are lying abutting each other, connected by a thin commissure. The right ganglion is completely fused with the right pleural ganglion. The tentacle nerve exits dorsolaterally at the anterior 1/4 and the nerve is simple. The buccal connective, together with several other nerves to the proboscis, leaves anteriorly. Posteriorly the right cerebro-pleural ganglion is drawn out into the pleural-supraoesophageal connective and a pallial nerve forming a zygoneury with the suboesophageal ganglion. The left cerebral ganglion is separated from the pleural ganglion by a shallow constriction. The left pleural ganglion sends out the pleural-suboesophageal connective and a pallial nerve which forms a dialyneury with the osphradial nerve. The cerebro- and pleuro-pedal connectives are of a length corresponding to 2/3 of the width of the combined cerebral ganglia and the pleural connective is about twice as thick as the cerebral one.

The suboesophageal ganglion is situated some distance behind the nerve ring in the right corner of the cephalopedal haemocoel, the supraoesophageal ganglion slightly further back and more dorsally. It sends out a large osphradial nerve, which after the dialyneury continues in the pallial skirt, anteriorly, till it joins the osphradial axis which is occupied by the large osphradial ganglion throughout its length.

The visceral connectives are long and slender and it was not possible to find the connection between the two visceral ganglia of which the left one lies in the cephalopedal vein, the right one in the space where the cephalopedal and visceral veins join.

In *Z. tropidophora* the buccal ganglia are situated on the posterior part of the buccal mass and joined by a commissure of about the same length as the diameter of the ganglia. In *H. galerita* the buccal ganglia are situated further back, behind the radular sac, closely appressed to each other and to the anterior oesophagus.

The innervation of the penis could not be worked out in detail, but it may be of both cerebral and pedal origin.

Sense organs

A pair of statocysts is present, lying posterolaterally to the pedal ganglia in *Z. tropidophora* (Fig. 3, *sta*), posteriorly in *H. galerita*. They have a single statolith.

The eyes (Fig. 25) are unusually large, equipped with a lens and a well developed retina. They are innervated by a branch of the tentacle nerve.

The osphradium (Figs 3, 7, *os*) is well developed, bipectinate with more leaflets along the inner side than on the outer side (see external morphology). The axis is filled by the large osphradial ganglion (Fig. 7, *og*). Due to poor preservation no detailed observations were made on the structure of the leaflets except that they are constricted basally and strongly ciliated above the constriction.

Reproductive organs

Figs 3, 7-10, 24, 26

In the sectioned specimen of *Z. tropidophora* the pallial oviduct is probably not fully formed, but it possesses also a complete set of male organs. These form the basis for the description.

The male organs consist of testis, a long and winding sperm duct opening in the posterior part of the oviduct; possibly a gutter along the free lobe of the oviduct; and a penis with a sperm gutter.

The testis (Fig. 10, *tes*) is situated along the right and more posteriorly also the dorsal side of the visceral mass. It consists of numerous tubules which anteriorly and ventrally unite to form a common sperm duct, which also functions as a seminal vesicle. Beside eu- and paraspermatozoa, there are also scattered eggs in early developmental stages in the gonad.

The sperm duct starts with a few coils (Figs 9-10, *sv*), then it passes straight forwards. Most of it contains a dense mass of euspermatozoa oriented with the heads towards the epithelium of the duct and a mass of slender paraspermatozoa in the center of the duct. The most distal tenth of the duct contains mainly paraspermatozoa (Fig. 9, *sv*). The sperm duct opens in the very proximal part of the pallial oviduct, close to the openings of the receptaculum seminis. No obvious connection to the sperm gutter on the penis (Fig. 8, *seg*) was found, unless a ciliated furrow along the ventral part of the free lobe of the pallial oviduct has such a function.

The female system consists of an open, glandular pallial oviduct with six seminal receptacles (Fig. 8, *rse*) opening via separate ducts to the very proximal part of the oviduct (Fig. 8, *pod*). The latter is presumably not fully formed.

The pallial oviduct is open (Figs 7, 26), except its most distal and proximal parts (Fig. 3, 24, 8, *pod*) which form wedge-shaped caeca in the pallial skirt. The posterior caecum is continued by a short blindly ending duct, to which the seminal receptacles open, via individual ducts. Anteriorly to these opens vas deferens. Along the broad edge of the free lobe of the oviduct runs a strongly ciliated gutter (Figs 7, 26, *lf*) which starts at the very first part of the ventral slit and continues anteriorly to shortly after where the oviduct closes anteriorly. There the free lobe of the gutter continues and transforms into a short (tongue-like?) skinfold.

The proximal 1/3 of the oviduct is lined by a low epithelium of several types of gland cells. After this part a tall (40-50 µm) dark greyish violet staining epithelium appears in the dorsal part of the oviduct. This epithelium which is interpreted as an albumen gland (Fig. 24, *ag*) then spreads ventrally so it covers most of the inside, except a narrow zone at the level of the slit. The low epithelium spreads again, at the beginning of the anterior caecum (Fig. 24), where it covers the mid 1/3 of the height of the caecum. The lower 1/3 is covered by tall (40-50 µm) mucus producing epithelium (Fig. 24, *mu*), which is continuous with the much lower but otherwise identical epithelium of the corner of the pallial cavity around the anterior part of the slit of the oviduct.

DISCUSSION

The capulids and trichotropids are presently (BOSS, 1982; PONDER & WARÉN, 1988 [as Capulidae]) placed in the Calyptraeoidea, but there is evidence from sperm morphology (J. HEALY, pers. comm.) that they actually are most closely related to the Tonnoidea, a view we share. This is also supported by further facts mentioned in « Relationships ».

Furthermore, in the forthcoming discussion we fully accept the view of PONDER & WARÉN (1988) that the Capulidae and Trichotropidae are synonyms and use the name Capulidae to include also the trichotropids.

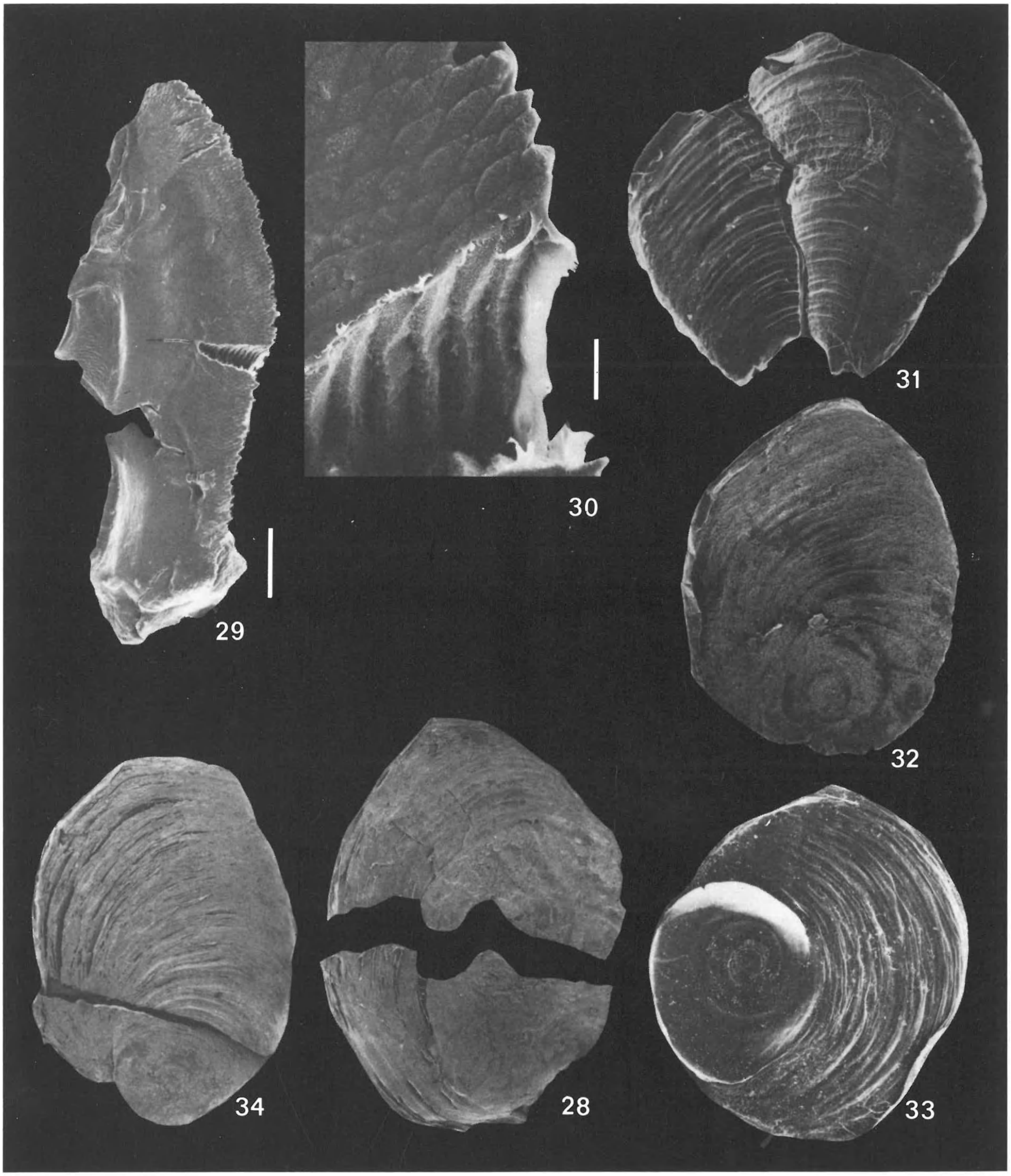
Scarcity of material and validity of results

The anatomical description is severely hampered by the fact that very little material has been available, and most of the information is derived from a single specimen of *Z. tropidophora*. Serial sections of the head-foot of *H. galerita* showed some differences in the structure of the oesophagus and minor differences in the shape of the ganglia of the central nervous system. The external morphology is, however, quite similar as far as could be observed from rehydrated bodies. There were differences in the shape of the penis and the foot, but not very great and the latter can to some extent be due to differences in fixation and a result of the drying and rehydration. There seem, however, to be present two types of penes; with or without an anterior lobe.

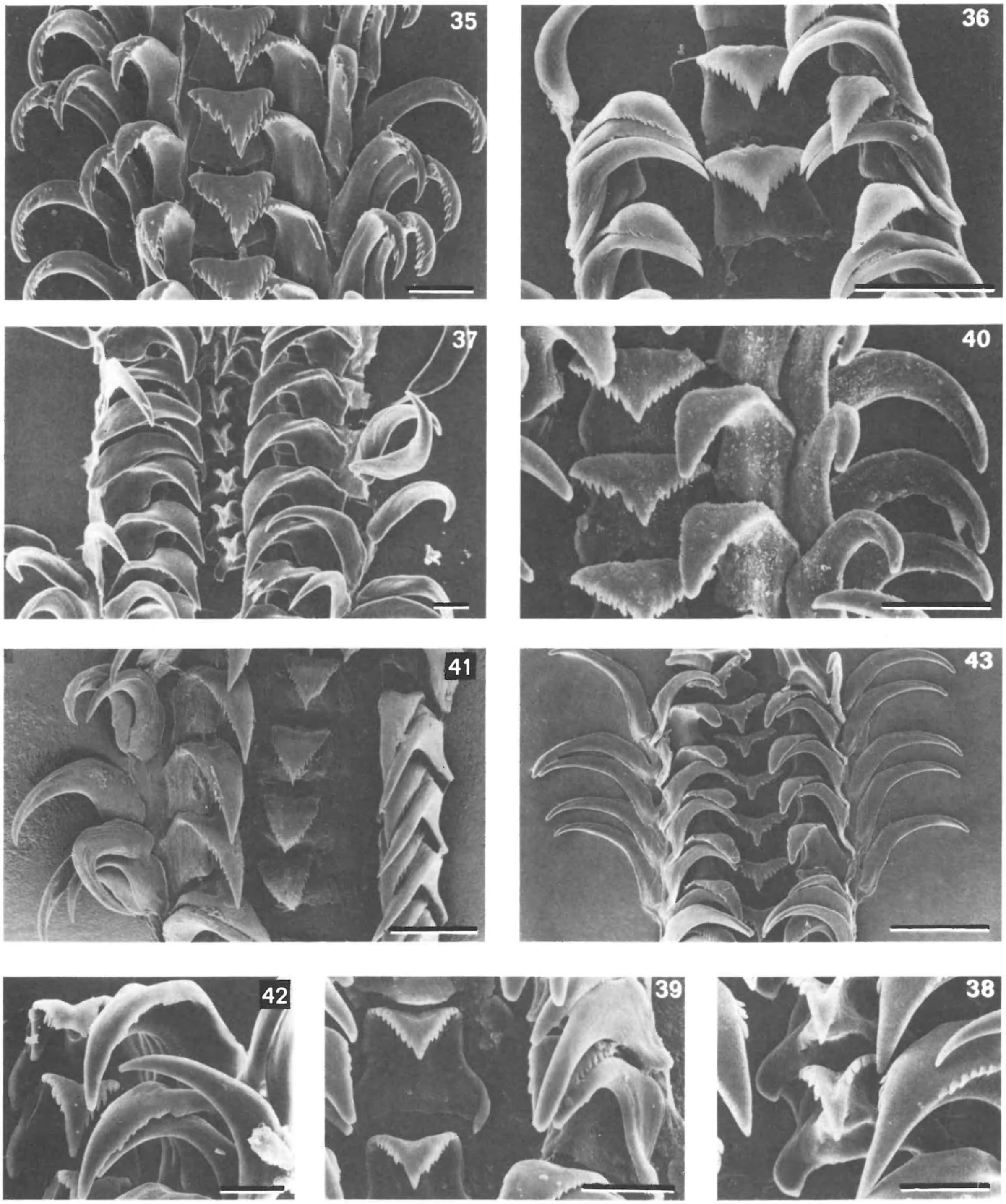
Larval shell

The morphology of the larval shell, with distinct protoconch I and II present in almost all species (not in *H. japonica*) indicates that they have planktotrophic development. This is further confirmed by the egg-capsule of *H. carinata* with embryos of a size of 0.16 mm, which corresponds well with the size of protoconch I in that species.

The larval shell is quite similar to some species of Capulidae, see Figs 48-49. A few capulids are known to have so-called echinospira larvae (*Capulus*: FRETTER & GRAHAM, 1962; *Trichosirius*: PILKINGTON, 1974, 1976). We have examined protoconchs of several species known to have echinospira larvae, from all families where this type of larval development is known and found that they conchologically are characterized by



FIGS. 28-34. — Jaws and opercula of Haloceratidae. — **28-30,** *Zygoceras tropidophora.* — 28, operculum, height 4.6 mm. — 29-30, jaw, scale lines 0.1 and 0.01 mm. — **31,** *Haloceras cingulata*, operculum, height 1.9 mm. — **32,** *H. phaeocephala*, operculum, height 1.13 mm. — **33,** *H. carinata*, operculum, height 0.8 mm. — **34,** *H. japonica*, operculum, height 1.84 mm.



FIGS. 35-43. — Radulae of Haloceratidae. — **35,** *Zygoceras tropidophora*, paratype. — **36,** *Haloceras carinata*, CANCAP stn 2.155. — **37-38,** *H. tricarinata*, BENTHEDI stn 87. — **39,** *H. tricarinata*, " *Discovery* " stn 10141. — **40,** *H. japonica*, off Oregon. — **41,** *H. cingulata*, USNM 52077. — **42,** *H. cingulata*, USNM 94898. — **43,** *H. phaeocephala*, paratype. Scale lines 25 µm (36, 39, 40, 42) and 50 µm (35, 37, 38, 41, 43).

the absence of a sharp distinction of protoconch I and II. Judging from the presence of such a distinct demarcation in the species of *Haloceras*, we believe that the similarity to some capulids cannot be used to infer that *Haloceras* has such echinospira larvae.

Teleoconch

The more or less planispiral teleoconch, with a large, irregularly shaped aperture and rapidly increasing diameter of the whorls hints towards a sedentary life probably on rocky bottoms or on some other solid substrate.

Anatomical details

The shape of the front part of the foot was always too distorted, to be used for comparisons between the species. It does, however, imply a sedentary mode of life. The division of the foot into a rear part that contracts to a solid lump and an anterior extensile part which contracts more folded can be seen in many trichotropids (GRAHAM, 1954; YONGE, 1962; WARÉN unpubl.) and is especially obvious in *Capulus*. YONGE (1962) described the behaviour of *Trichotropis cancellata*, which has a morphologically similar foot. Specimens of that species sit attached by the rear part of the foot, filtering sea-water with the gill. When crawling the anterior part of the foot can be extended far ahead. In *Haloceras* the anterior part of the foot is evidently not used as in *Capulus*, for holding and protecting the egg mass (THORSON 1965), since an egg mass with developing embryos was found in the pallial cavity of one specimen, which possessed this kind of foot.

The anterior pedal gland, the glandular layer on the propodium and on the front part of the mesopodium are unusually thick and certainly have some functional importance in connection with a sedentary life.

The very strongly contracted proboscis sheath, the folded oesophagus, the long, coiled and folded buccal and pedal connectives as well as the length of other nerves emerging from the cerebral ganglia, indicate that the proboscis can be extended considerably and that probably the cerebral ganglia move forwards during that process.

It is not certain how the pallial parts of the gonoduct function. It is obvious that (the own) sperm is transported to the initial part of the pallial oviduct by the vas deferens which also functions as a seminal vesicle. But after that there exist two possible ways: Either the sperm continue forwards in the pallial oviduct, or it leaves the pallial oviduct and uses the gutter along the edge of the free lobe of the oviduct. This gutter ends on a skin-fold on the outside of the lobe, at the same level as the penis. The skin-fold could then have a function to transfer the sperm to the penis since there seems to be no sperm gutter across the neck. This explanation, however, is not likely because the sperm gutter of the oviduct must be used for transport of sperm from another male at copulation, unless sperm can be transported both ways.

The absence of a bursa copulatrix can hardly be explained by the fact that the specimen is not a mature female, because, from a fertilization point of view, it actually is mature since the seminal receptacles were full of sperm.

Biology

Very little identifiable stomach and rectal contents were found. A foraminiferan was found in a single specimen of *Haloceras carinata*. Several other species had some unidentifiable organic material, but there were no remains of planktonic organisms or mineral particles. This excludes filter feeding or grazing the detritus cover of the bottom, since every such gastropod we have examined, invariably has the stomach and intestine filled with at least partly identifiable matter. Such a feeding is also unlikely in species with a well developed proboscis.

An active and predatory way of life is, however, unlikely because of the morphology of the foot, which suggests that this animal is adapted for a sedentary life.

The presence of unusually large eyes in a gastropod group almost exclusively living in the deep sea is somewhat surprising, but the eyes are not necessarily used during the benthic life. They may be a reminiscence from the planktonic life of the larva. BOUCHET & WARÉN (1986) found that almost no deep-sea eulimids with lecithotrophic development have eyes, while species with planktotrophic larvae usually have eyes. In some species, however, the eyes are lost soon after settlement.

The presence of a penis in every specimen, also those with unquestionably female features (egg mass in pallial cavity, developing embryos in oviduct) indicates that the species are either simultaneous or protandric hermaphrodites. The latter is supported by the histology of the testis of *Z. tropidophora*, which was almost exclusively male, but with some immature eggs present. Hermaphroditism is mainly known from prosobranchs with a sedentary or not very active mode of life.

A consequence of the specimen of *Z. tropidophora* being in the process of sex change is that it may be far from full grown, since most protandrous hermaphroditic prosobranchs change sex around or below half maximum size (e.g. *Trichotropis*: YONGE, 1962; *Eulima*: WARÉN, 1984; *Capulus*: THORSON, 1965 and own observations).

Another remarkable feature in the biology of the species of Haloceratidae is their apparent rarity. We know a total of 20 species from 103 specimens and shells. Only seven species are known from more than five specimens, although several occur in comparatively well investigated areas. Despite this rarity it is obvious that when one species is present, there is an unexpectedly high probability to find at least one more species:

H. tricarinata, laxa, cingulata and *carinata* were all found at SEAMOUNT stn CP 30, SW of Portugal in 2000m;

Haloceras japonica and *millestriata* were described from the same dredge haul off S Japan, 1300 m;

H. laxa and *carinata* at " *Porcupine* " Expedition 1870 stn 16, off Portugal in 1900 m;

H. aff. *laxa* and *H. cingulata* at " *Thalassa* " stn Z435 in the northern part of the Bay of Biscay in 1000m;

H. spinosa, *phaeocephala* and *Haloceras* sp. 1 at " *Kapala* " stn 80-20-10, off New South Wales in 1100 m;

H. biocalae and a damaged undetermined species at BIOCAL stn DW 48, off southern New Caledonia in 800 m;

H. cingulata and *H.* aff. *laxa* at BIOGAS stn CP 37, Bay of Biscay in 2200 m.

Considering that this material comes from more than 2000 dredge hauls in the depth range 400-4000m, it is obvious that the catches were not randomly distributed, but we do not know any uniting factor, except that these stations are sometimes unusually rich also in other gastropods.

To summarize the biological features of the two genera, we get a group of not very active deep-sea gastropods usually with planktotrophic development, and some unknown, very special requirements on the biotope. The species are probaly predators.

Relationships

The anatomical and biological features outlined above and in the description clearly indicate that *Haloceras* and *Zygoceras* belong to the Caenogastropoda, more precisely the Neotaenioglossa:

— Taenioglossate radula; not taenioglossate in Neogastropoda.

— A simple oesophagus; with a valve of Leiblein or similar structures in Neogastropoda.

— Both zygo- and dialyneury; none of these in Archaeotaenioglossa.

— Protandrous hermaphoditism present; very rare in Neogastropoda.

There is, however, no neotaenioglossate family in which *Haloceras* and *Zygoceras* can be included.

Several features point in different directions:

The larval shell of the species with assumed planktotrophic development shows the greatest similarity to the genus *Benthonella* (Rissoidae, Figs 46-47: *B. tenella* (Jeffreys, 1867); see also PONDER, 1985; BOUCHET, 1976). The distinct coloration, size, and sculpture of protoconch I and II are quite similar. Also certain capulids, for example *Trichotropis crassicostata* Melvill, 1912, have a similar larval shell, but it is smaller and more planispiral (Figs 48-49).

The teleoconch does not resemble any other group in a way that makes it possible to include it there, although there is some resemblance to the Capulidae, in that the shell is slightly irregularly shaped, paucispiral with rapidly increasing diameter, often has an irregular, rough sculpture and has a well developed periostracum. These features may, however, be convergences caused by a sedentary life.

The foot resembles that of many Tonnoidea

TABLE 1. — Comparison of *Haloceras*, Capulidae and Tonnoidea.

CHARACTER	LAUBIERINIDAE *	CAPULIDAE	*Haloceras*
Foot with lateral furrow	yes	yes	yes
Posterior pedal gland	?	poorly developed	present
Hypobranchial gland	thin	thick	thin
Anterior alimentary canal	pleurembolic proboscis	very short pleurembolic proboscis [1]	pleurembolic proboscis
Lower lip	unmodified	pseudoproboscis	unmodified
Jaws	present	absent	present
Salivary ducts	long and slender	short	long and slender
Salivary ducts pass nerve ring	yes	no	yes and no
Accessory salivary glands	present	absent	absent
Oesophageal gland	present	absent	absent
Digestive gland openings	*distant from each other	distant fom each other	close together
Crystalline style	*absent	present	absent ?
Osphradium	monopectinate/bipectinate *	monopectinate	bipectinate
Suboesophageal ganglion	with dialyneury	with or without dialyneury	with dialyneury
Supraoesophageal ganglion	?, with zygoneury *	with zygoneury	with zygoneury
Pedal ganglia	no accessory ganglia, no cross connective	with accessory ganglia, no cross connective	with accessory ganglia, with cross connective
Larval type	normal veligers	echinospira	normal veligers
Protoconch I distinct from II	yes	no	yes
Sperm duct on head-foot	*open or closed	open	not present ?
Seminal receptacle	*posterior, one or many	posterior, one	posterior, many
Bursa copulatrix	*anterior	absent	absent
Pallial oviduct	closed	open	open
Sperm gutter on pallial oviduct	? no	no	yes
Gonopericardial duct	unknown	no	no
Mode of feeding	*predatory	filterfeeders	predatory ?

An asterisk (*) indicates that the character is not known in the Laubierinidae and is extrapolated from other tonnoidean families. Anatomical details from Bouvier (1889), Dell & Ponder (1964), Lacaze-Duthiers (1872, 1901), Warén & Bouchet (1990), Yonge (1962).

[1] *Capulus ungaricus* as well as other capulids do have a very short pleurembolic proboscis, as can be seen from the skin fold between the tentacles. The pseudoproboscis actually is a drawn out part of the proboscis sheath (unpublished).

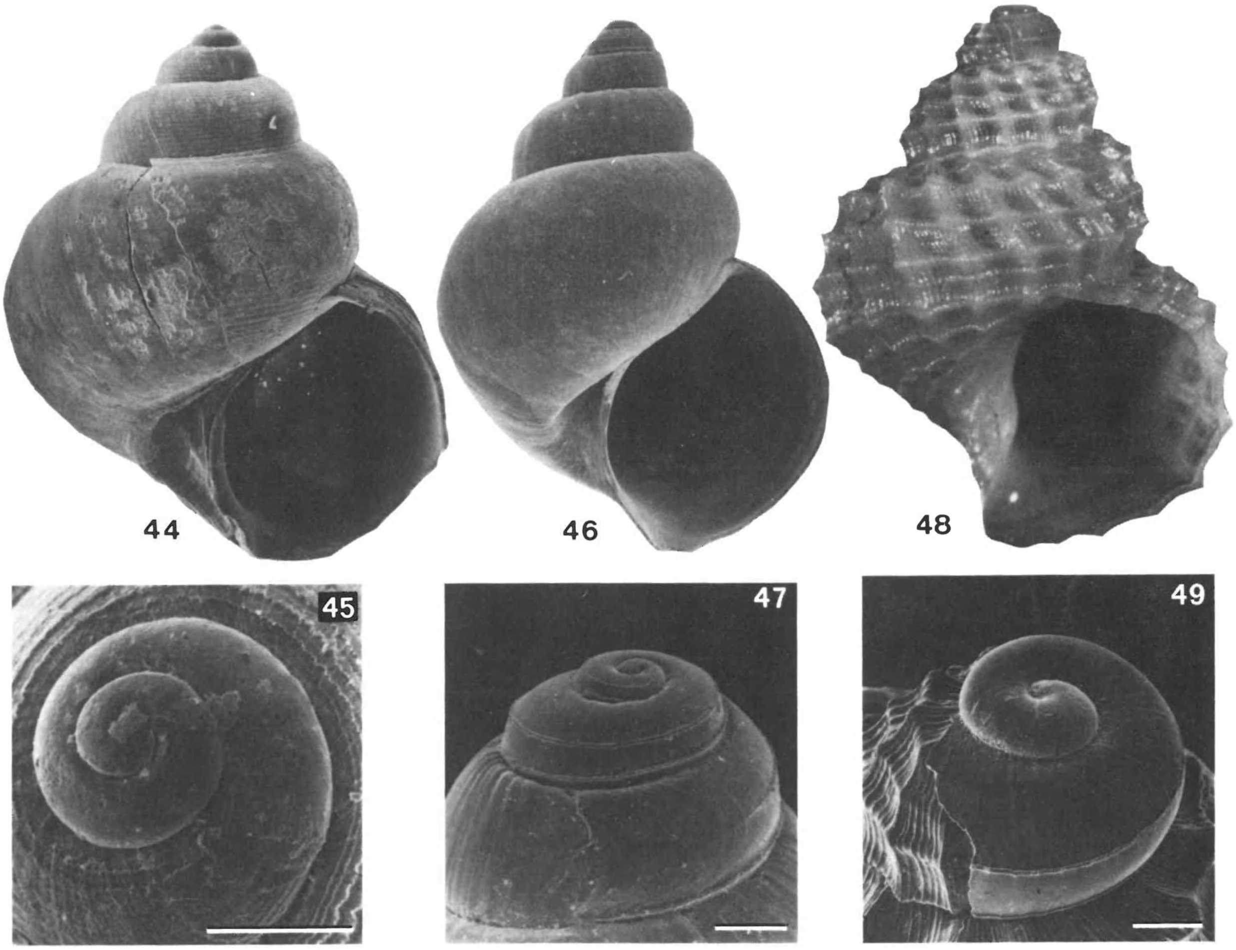
and the Capulidae in having a demarcated, rough zone along and above the edge of the sole. This is a rare character among gastropods and has rarely been noticed, but we have seen it in Aporrhaidae and Warén & Ponder (in press) reported it in the Loxonematoidea.

The foot also resembles many capulids (especially *Capulus*), all calyptraeids and some vanikorids in being divided into two functionally different parts. This is probably also functionally evolved since it also occurs in Amathinidae (Pyramidelloidea; Ponder, 1987), a totally unrelated group.

The operculum shows clear similarities to all capulids (Warén unpublished) and many tonnoids (Warén & Bouchet, 1990) in having the larval operculum remaining and clearly set off from the postlarval part when young and then losing the old part by some kind of erosion.

The alimentary system is very similar to that of the Laubierinidae and some other of the less modified Tonnoidea (see Warén & Bouchet, 1990), but differs in not having the complex and large salivary glands present in all tonnoids (except the Ficidae). Neither does it have a well developed oesophagal gland.

The radula is quite similar to that of many of the advanced mesogastropods, except some of



FIGS. 44-49. — *Cithna, Benthonella, Trichotropis.* — **44-45,** *Cithna globosa*, syntype USNM 186381, height 2.8 mm. — **46-47,** *Benthonella tenella*, BIOMEDE 2 stn 6, 39°40'N, 04°57'E, 2610 m, height 4.4 mm. — **48-49,** *Trichotropis crassicostata*, " *Marion-Dufresne* " cruise 32, stn DC10, 21°13'S, 55°52'E, 930-980 m, height 5.6 mm. Scale lines 200 µm.

the more modified groups (e.g. *Lamellaria*, *Cypraea*, *Pedicularia*, etc.), but it is especially similar to that of the two recently described tonnoidean groups Laubierinidae and Pisanianurinae (Ranellidae) (see WARÉN & BOUCHET, 1990).

The anatomy and ontogeny of the reproductive system is very similar to the Capulidae. Direct comparison with sectioned specimens of *Capulus hungaricus*, in the sexual phase when oocyte production just has started showed a similar construction of the oviduct, except that *Capulus* has only a single seminal receptacle, a less developed ciliated furrow and a shorter ventral slit of the oviduct.

On account of these characters we feel confident that a position in the vicinity of the Tonnoidea and the Capulidae is quite a realistic assumption, and we have tabulated a number of characters for the least modified tonnoidean family and the Capulidae in Table 1.

The larval development of the Capulidae, via an echinospira larva is a character shared with the Lamellariidae, Velutinidae, Triviidae and Eratoidae (we do not consider the status of these taxa, and the larva of Pseudosacculidae is not known). Whether it is a homologous character and its significance for these taxa being monophyletic was discussed by FRETTER & GRAHAM (1962:627). They concluded that this was the case, based on Graham's (1954) comparative study of *Capulus*, *Trichotropis* and *Calyptraea*, but maintained that *Capulus* is more closely related to Calyptraeoidea than to Lamellarioidea. Since then Pilkington (1974, 1976) has shown that also species of the old family Trichotropidae have echinospira larvae, which supports Fretter & Graham's ideas about Trichotropidae as an ancestral group of the species possessing echinospira larvae, the « Echinospiracea » (modified to « Echinospirida » by Golikov & Starobogatov, 1975). This finding also contributed to Ponder & Warén's (1988) view that the Trichotropidae and Capulidae should be considered one family.

To our ideas about the Capulidae not being related to the Calyptraeoidea, but to the groups possessing an echinospira-larva should be added the fact that all taxa within the Calyptraeoidea have a normal snout, while the Capulidae as well as the Lamellarioidea have a proboscis (not to be confused with the so-called pseudo-proboscis of the Capulidae, which is an additional process from the proboscis sheath).

If the echinospira larvae of the groups are homologous (as we believe) this certainly substantiates the use of that type of larvae for classification and makes it practical to maintain them as a group, without mixing them with species without that kind of larval development (unless it is lecithotrophic).

We thus get a situation with a caenogastropod lineage which splits into the Tonnoidea and the Echinospirida (disregarding Hennigian principles about ranks). The Laubierinidae and the Capulidae respectively are the most primitive members of these two branches. The problem then is: Where do *Haloceras-Zygoceras* join the « Y »?

There are actually no characters of the Echinospirida and Tonnoidea which are more primitive than in *Haloceras-Zygoceras*, but there are characters in *Haloceras* and *Zygoceras* which are more primitive, e.g. the closely placed openings of the digestive glands and the accessory pedal ganglia with a cross connection. The normal veliger larva is more primitive than the echinospira larva (unless one assumes the normal veliger to be secondary). This should support a position either on the basal limb of the « Y » or on the branch leading to the Tonnoidea, or on the branch leading to the Echinospirida, before the development of the echinospira larva took place. The anatomical information available is, however, hardly detailed enough to allow a clear answer to where to place the two genera.

Whatever the relationships may be, *Haloceras* and *Zygoceras* do not fit in any of the families mentioned, why we suggest a new family for them. We consider it related to but more primitive than the superfamily Tonnoidea and the suborder Echinospirida.

Family HALOCERATIDAE fam. nov.

Diagnosis. — Shell disc-shaped to fairly tall-spired, with 1.5-3 teleoconch whorls covered by a well developed, often fringed periostracum. Sculpture usually spiral ribs and sinuous growth-lines. Aperture rounded to depressed, without siphonal canal. Umbilicus usually broad and deep, occasionally closed. Protoconch I with numerous small short raised ridges, often encircling small round surfaces and usually aggregated to form 4-7 spiral ribs which are more well defined towards periphery. Sometimes micro-ridges are confined to spiral ribs and leave rest of shell smooth. Protoconch II with 1-3 whorls, 2-3 spiral keels close to periphery, sometimes also with pustules and other sculpture on last whorl.

Soft parts with bipectinate osphradium, pleurembolic proboscis, simple salivary glands with ducts which may or may not pass nerve-ring, fairly concentrated nervous system with dialyneury between supra- and cerebral, zygoneury between suboesophageal and cerebral ganglia. Two pairs of accessory pedal ganglia, posterior pair with commissure. Foot with anterior and posterior pedal glands and lateral furrow above edge of sole. Protandrous or simultaneous hermaphrodites.

SYSTEMATIC ACCOUNT

Genus ***HALOCERAS*** Dall, 1889

Separatista (Haloceras) Dall, 1889: 277. Type species: *Cithna cingulata* Verrill, 1884, by monotypy.
Solariella (Micropiliscus) Dall, 1927:130. (New synonym). Type species: *S.(M.) constricta* Dall, 1927, by original designation.

REVISED DIAGNOSIS. — Haloceratids with (in species with planktotrophic development) multispiral brown globular protoconch. Protoconch I with 4-8 spiral cords on a background of numerous anastomosing riblets and pustules. Protoconch II with 3 spiral keels, of which two remain uncovered above suture by successive whorl. Teleoconch trochiform to lenticular, umbilicus narrow to wide, whorls with 1 or 2 strong spiral keels. Soft parts with the characters of the family.

REMARKS. — The history of the name has been summarized in the introduction. For a comparison with *Zygoceras*, see that name.

Haloceras acrocomata sp. nov.

Figs 88, 93-94

TYPE MATERIAL. — Holotype in AMS C146278.

TYPE LOCALITY. — "*Kimbla*" 1977, stn 3, 23°33.7'S, 152°37'E, 348-339 m, E of Lady Musgrave Id, Queensland, Australia.

MATERIAL EXAMINED. — **Australia**. "*Kimbla*" 1977, stn 3, E of Lady Musgrave Island, Queensland, 23°33.7'S, 152°37'E, 348-339 m: holotype (AMS C146278). — Stn 22, off NW Island, Queensland, 23°15'S, 152°24'E, 284 m: 1 sh. (AMS C150187). — 1984, stn 15, E of Lady Musgrave Island, Queensland, 23°52'N, 152°42'E, 296 m: 1 sh., 1 juv. sh. (AMS C147272).

DESCRIPTION. — *Shell* small, thin, solid, consisting of 2 protoconch and 1.75 teleoconch whorls. Protoconch rather flat, almost planispirally coiled. Protoconch I, diameter 240 µm, sculptured by 6 strong spiral cords, continuous from nucleus to protoconch II, except for a small area near transition between protoconch I and II, which is occupied by granules. Protoconch II with 1.4 whorls, sculptured by two strong keels, a third keel hidden at suture, visible only in young postlarvae. Between keels, on later part of protoconch II small granules; rest of larval shell smooth or with occasional traces of periostracal spirals. Protoconch/teleoconch transition sharp. Teleoconch whorls turreted, broadly conical, with two strong keels giving whorls a very angular profile; no other spiral sculpture. Discrete axial sculpture made stronger by periostracal lamellae, best visible at periphery, where forming projecting scales between keels. Umbilicus broad, encircled by one strong thread. Aperture broadly quadrangular; lip sharp, thin, only very slightly reflected on columellar side. Colour of shell very light amber white, with 2 carinae and umbilical thread distinctly darker; protoconch light brown.

Dimensions: Height 2.07 mm, breadth 3.06 mm; aperture height 1.14 mm, breadth 1.26 mm.

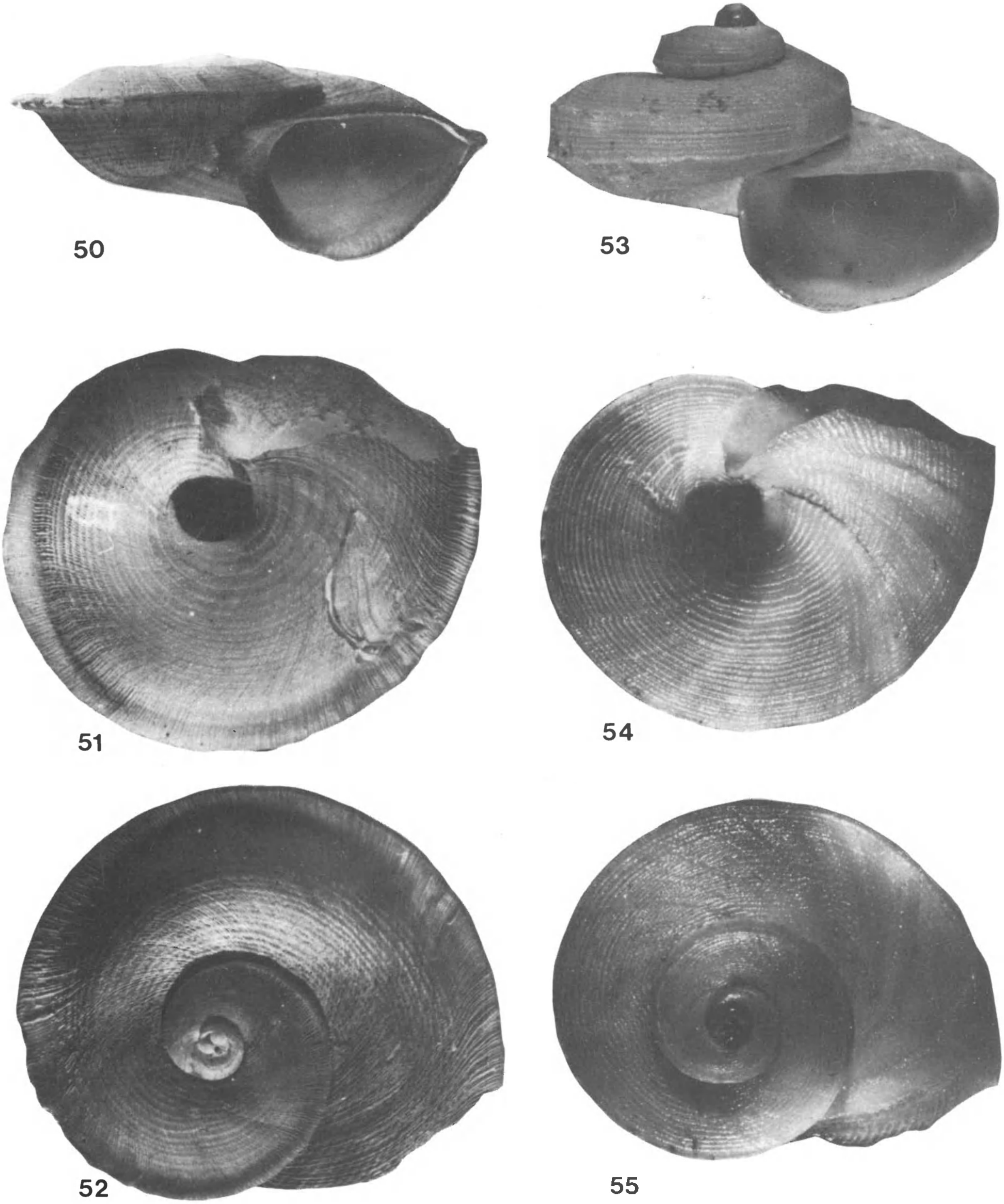
Larval shell measurements:

	diameter (µm)	no. whorls (prot. II)
holotype	940	1.4
AMS 147279	1000	1.6
AMS 142679	980	1.45
AMS 150187	960	1.5

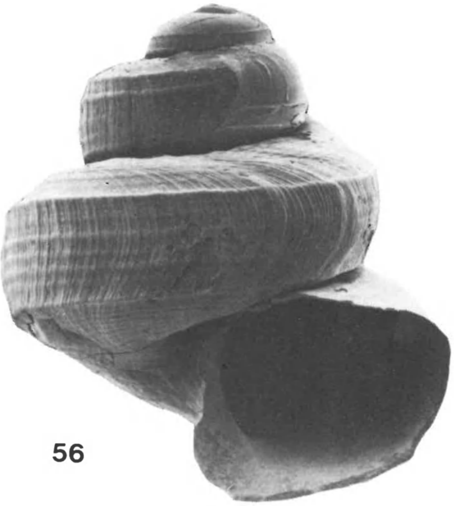
REMARKS. — One shell (AMS 150187) has a proportionally higher spire and narrower umbilicus (the two characters are linked), but otherwise identical protoconch and general morphology.

The two strong keels on the teleoconch of *H. acrocomata* make it resemble *H. exquisita* and *H. cingulata*. It differs from *H. exquisita* by its low-spired protoconch with fewer whorls, by teleoconch whorls which increase more rapidly in diameter, and its broader umbilicus. *H. cingulata* reaches a much larger size at the same number of postlarval whorls, and has a narrower umbilicus.

ETYMOLOGY. — From the Greek *akros*, at the top, and *comatas*, hairy; to remind of the hairy periostracum of the protoconch.



FIGS. 50-55. — Genus *Haloceras*. — **50-52,** *H. tricarinata*, BENTHEDI stn 87, diameter 14.0mm. — **53-55,** *H. cingulata*, BIOGAS stn CP37, diameter 13.8mm.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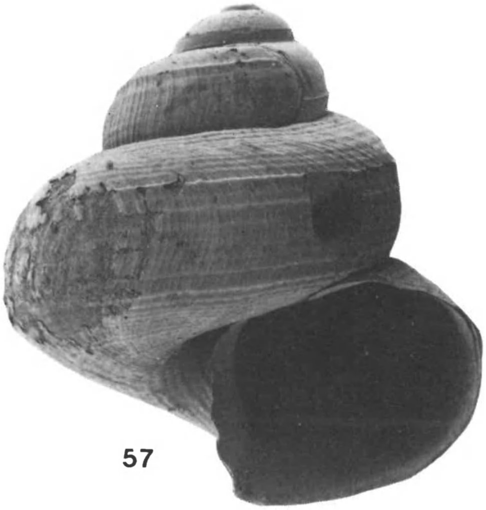
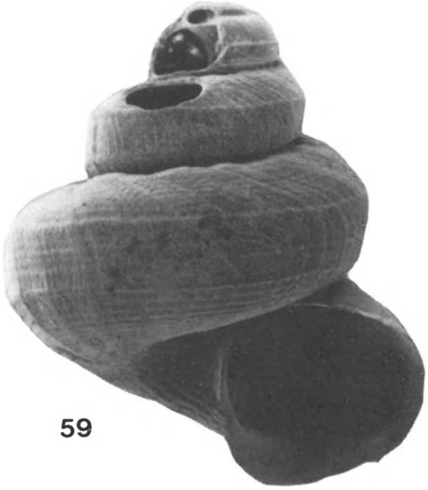

57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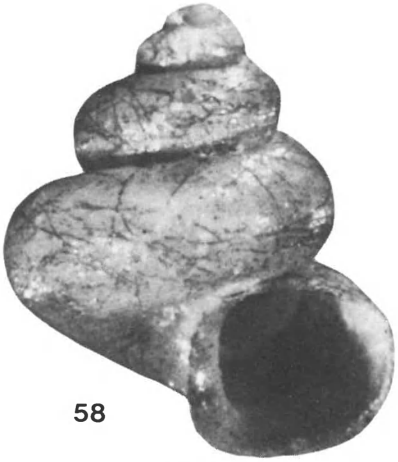
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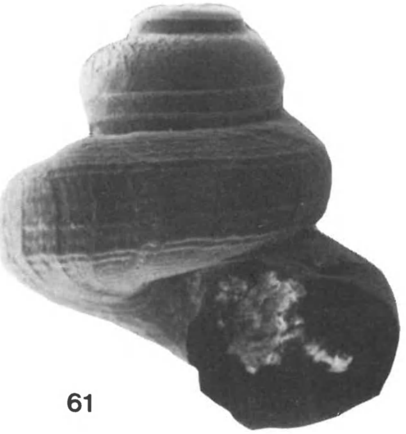
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FIGS. 56-61. — Genus *Haloceras*. — **56,** *H. mediocostata*, MONACO stn 703, height 3.2mm. — **57,** *H. mediocostata*, lectotype, height 3.5mm. — **58,** *H. carinata*, holotype of *Solariella constricta*, height 3.3mm. — **59-60,** *H. carinata*, BALGIM stn CP92, height 2.65mm, diameter 2.35mm. — **61,** *H. carinata*, CANCAP stn 2.155, height 1.6mm.

Haloceras carinata (Jeffreys, 1883)

Figs 33, 36, 58-61, 105-108

Cithna carinata Jeffreys, 1883: 111, pl. 20, fig. 9.
Solariella (Micropiliscus) constricta Dall, 1927: 130. (New synonym).
Solariella (Micropiliscus) constricta- QUINN 1979:43, figs 67, 68.

TYPE MATERIAL. — *C. carinata*: Holotype BMNH 1885.11.5.1623; *S. constricta*: 11 syntypes, USNM 108414a,b.

TYPE LOCALITIES. — *C. carinata*: " *Porcupine* " 1870, stn 16, 39°55'N, 09°56'W, 1810m, off Portugal; *S. constricta*: " *Albatross* " stn 2415, 30°44'N, 79°26'W, 805m, off Florida.

MATERIAL EXAMINED. — **Eastern Atlantic**. " *Porcupine* ", stn 16, off Portugal, 39°55'N, 09°56'W, 1810 m: 1 sh., holotype.
SEAMOUNT, stn CP30, Gorringe Bank, 36°44'N, 11°23'W, 1940-2075m: 1 sh., 2 frgms (MNHN). — Stn DW116, Galicia Bank, 42°52'N, 11°51'W, 985-1000m: 3 shs (SMNH).
BALGIM, stn CP92, Ibero-Moroccan Gulf, 34°24.3'N, 07°30.3'W, 1182m: 1 sh. (MNHN).
INCAL, stn DS3, W of the British Isles, 57°27'N, 11°03'W, 609-619m: 1 larva (lost).
CANCAP, stn 2.067, Canary Islands, 27°58'N, 14°12'W, 1820m: 1 sh. (RMNH). — Stn 2.155, Canary Islands, 27°35'N, 17°59'W, 700m: 1 spm., 3 shs (RMNH).
Western Atlantic (Florida). " *Albatross* ", stn 2415, 30°44'N, 79°26'W, 805 m, 11 shs (syntypes of *S. constricta* Dall, 1927).

DESCRIPTION. — *Shell* small, solid, conical, with 2.5 protoconch and up to 2.75 teleoconch whorls. Protoconch globular, multispiral. Protoconch I diameter 200 µm, with sculpture of star-shaped little knobs forming a reticulation, and 5 spiral cords formed by coalescing such knobs. Protoconch II with two spiral keels well visible above suture, third keel hidden by subsequent whorl. Sculpture of granules appear in subsutural zone after first whorl of protoconch II, then gradually expends over most of protoconch surface. 3-6 prosocline axial lamellae, situated on last part of protoconch II, just behind peristome. Protoconch lip expanded. Protoconch/teleoconch discontinuity very abrupt. Teleoconch trochoid with regularly convex whorls and very deep suture. Sculpture consisting mainly of spiral cords, two of which are sometimes stronger, forming weak spiral keels. About 25 spiral cords on penultimate whorl of large specimens. Base and umbilicus sculptured by similar cords. Border of umbilicus not marked by cord. Spiral cords cross much weaker incremental lines. Above shoulder intersection of spiral cords and incremental lines produces a kind of malleated surface, more distinct after coating for SEM. Base convex, umbilicus open and broad. Aperture rounded, peristome almost continuous. Outer lip thin, sharp, slightly reflected over umbilicus. Colour of protoconch brown, teleoconch dirty white.

Dimensions of shells: USNM 108414, height 3.24 mm, breadth 3.0 mm; aperture height 1.20 mm, breadth 1.45 mm. BALGIM stn CP92, height 2.62 mm, breadth 2.28 mm; aperture height 1.0 mm, breadth 1.10 mm .

Larval shell measurements:

	diameter (µm)	no. whorls (prot. II)
holotype *carinata*	840	1.8
USNM 108414	710	1.9
USNM 108414	720	1.8
USNM 108414	700	1.7
USNM 108414	770	1.9
USNM 108414	740	1.8
CANCAP 2.067	980	1.75
CANCAP 2.155	840	1.9
CANCAP 2.155	730	1.7
CANCAP 2.155	840	1.75
CANCAP 2.155	890	1.8
BALGIM CP 92	840	1.9
SEAMOUNT CP 30	920	1.9
SEAMOUNT DW 116	840	1.8
SEAMOUNT DW 116	900	1.9
SEAMOUNT DW 116	900	1.75

REMARKS. — WARÉN (1980: 20), misled by the similarities in the protoconch, commented that the holotype of *C. carinata* is: « A monstrosity of *Benthonella tenella* (Jeffreys) ».

QUINN (1979) listed as *Solariella constricta* (= *carinata*) three other lots which here are described as *Haloceras trichotropoides*. Indeed, the two species have rather similar teleoconchs, although *H. trichotropoides* can be recognized by its coarser sculpture, with fewer and stronger spiral cords. They can also be separated by *H. trichotropoides* having a flatter larval shell with fewer whorls.

H. carinata also resembles *H. mediocostata*. That species has a larger protoconch (diameter 1220 µm vs. 700-920 µm in *carinata*), and a broader teleoconch sculptured by stronger spiral keels.

Haloceras cingulata (Verrill, 1884)

Figs 31, 41-42, 53-55, 113-115

Cithna cingulata Verrill, 1884: 184, pl. 32, fig. 7.

TYPE MATERIAL. — Holotype USNM 38101.

TYPE LOCALITY. — "*Albatross*" stn 2076, 41°13′N, 66°01′W, 1658m, Georges Bank, S of Nova Scotia.

MATERIAL EXAMINED. — **Western Atlantic.** "*Albatross*", stn 2043, S of Nova Scotia, 39°49′N, 68°29′W, 2685 m: 1 spm., paratype (USNM 38104). — Stn 2076, Georges Bank, S of Nova Scotia, 41°13′N, 66°01′W, 1658 m: 1 sh., holotype (USNM 38101). — Stn 2084, S of Nova Scotia, 40°17′N, 67°05′W, 2361m, 1 sh., paratype (USNM 38105). — Stn 2571, S of Nova Scotia, 40°09′N, 67°09′W, 2480m: 1 spm. (USNM 52077). — Stn 2733, off North Carolina, 37°26′N, 73°43′W, 1728m: 1 spm. (USNM 94898).

Eastern Atlantic. BIOGAS, stn CP 37, Bay of Biscay, 47°34′N, 08°40′W, 2175 m: 1 spm. (MNHN).

"*Thalassa*", Stn Z 435, Bay of Biscay, 48°40′N, 09°56′W, 1050 m: 1 sh. (MNHN).

SEAMOUNT, stn CP30, Gorringe Bank, 36°44′N, 11°23′W, 1940-2075m: 7 juv. and frgms (MNHN).

DISTRIBUTION. — The temperate North Atlantic, between 36° and 49°N, in 1050-2685m (bathyal); amphiatlantic.

DESCRIPTION. — *Shell* large, solid, depressed, consisting of 2.5 protoconch and up to 2.6 teleoconch whorls. Protoconch globular, multispiral. Protoconch I diameter 250 µm, sculpture not very well preserved on available specimens, but reticulation of anastomosing star-shaped knobs present beside a few (3-5 ?) spiral cords. Protoconch II with two spiral keels apparent above suture, third keel concealed by subsequent whorl. Last half protoconch II whorl with discrete sculpture of tubercles in subsutural zone. Protoconch/teleoconch transition very sharp. Teleoconch with strongly keeled whorls, almost rectangular in cross-section, adhering to preceding whorl just below abapical keel, and concealing suture in deep furrow. Sculpture consisting of spiral cords and incremental lines. 25 spiral cords between suture and first keel on adapical part of body whorl; 6 between keels; and about 30 on base, also in umbilicus. In addition to incremental lines, also a few coarse, strongly prosocline ribs on shoulder of terminal part of body-whorl. Umbilicus very broad. Aperture rectangular, peristome almost continuous; outer lip sharp, simple. Parietal wall convex, strongly reflected towards umbilicus. Colour of protoconch brown, teleoconch dirty white.

Dimensions of a fully grown shell: Height 8.1 mm, diameter 13.2 mm; aperture height 4.3 mm, breadth 7.7 mm.

Larval shell measurements:

	diameter (µm)	no. whorls (prot. II)
USNM 52077	1380	2.2
SEAMOUNT CP 30	1510	2.2
SEAMOUNT CP 30	1490	2.25
SEAMOUNT CP 30	1660	2.3
SEAMOUNT CP 30	1580	2.1
BIOGAS CP 37	1340	?
"*Thalassa*" Z435	1300	2.1

REMARKS. — There is no species easily confused with *H. cingulata*. The two strong spiral keels appear early on the teleoconch, making identification of very young specimens possible. At comparable size only *Zygoceras biocalae* bears some resemblance but lacks almost completely a spiral sculpture and has a much smaller umbilicus.

Haloceras exquisita sp. nov.

Figs 83, 89-90

TYPE MATERIAL. — Holotype in MNHN.

TYPE LOCALITY. — BIOCAL, stn DW66, 24°55′S, 168°22′E, 505-515m, S of New Caledonia.

MATERIAL EXAMINED. — **New Caledonia.** BIOCAL, stn DW 66, 24°55′S, 168°22′E, 505-515 m: holotype (MNHN).

DESCRIPTION. — *Shell* small, thin, fragile, consisting of 2.5 protoconch and 1.5 teleoconch whorls. Larval shell globular, multispiral. Protoconch I diameter 215 µm, sculptured with rather irregularly disposed knobs in nucleus, later arranged in spiral lines. Protoconch II with 2.1 whorls, diameter 870 µm; first whorl sculptured by one strong spiral keel and one row of subsutural granules; later a second spiral keel, previously hidden by suture, and a sculpture of small knobs and granules appears, between keels. Surface of last half whorl of protoconch II completely covered by such granules and knobs. Teleoconch whorls turreted, with two very strong keels at periphery giving a very angular profile to whorls. No other spiral sculpture except for a discrete thread bordering umbilicus. Upper part of whorls with sculpture of prosocline axial ribs extending from suture to adapical keel, forming spiny intersections with keel. Axial ribs obsolete between keels. Base smooth. Umbilicus narrow. Aperture quadrangular, outer lip thin, sharp, a little reflected over umbilicus. Colour of protoconch brown, teleoconch white.

Dimensions: Height 1.80 mm, breadth 1.75 mm; aperture height 0.72 mm, breadth 0.77 mm.

Remarks. — *Haloceras exquisita* has a very distinctive protoconch and teleoconch morphology which should facilitate identification. The protoconch is smaller, at a similar number of whorls, than in any other haloceratid. The general morphology and sculpture of the teleoconch whorls resemble *H. acrocomata*, but the whorls are not as depressed as in *H. acrocomata*.

Etymology. — From the latin *exquisitus*, fine.

Haloceras galerita sp. nov.

Figs 66, 100-102

Type material. — Holotype AMS C150227.

Type locality. — "*Kapala*", stn K80.20.20, 33°35-37'S, 152°05'E, 1143-1106m, off Sydney, New South Wales.

Material examined. — **Australia.** "*Kapala*", stn K 80.20.20., off Sydney, 33°35'S, 152°05'E, 1143-1106 m: holotype (AMS C150227).

Description. — *Shell* small, solid, trochoid, consisting of 2.5 protoconch and 1.9 teleoconch whorls. Protoconch I diameter 200 µm, sculpture not very distinct but seemingly consisting of coarse spiral cords. Protoconch II with 2 spiral keels visible above suture, and a subsutural row of granules. Also a few distinct incremental ribs just before larval peristome; rest of protoconch smooth. Teleoconch whorls convex with rather deep suture. Sculpture of spiral cords and strong incremental, almost lamellar, lines. Two spiral cords form keels; abapical one, sharp and clearly defining basal surface. About 8 spiral cords above shoulder of body whorl, 6 at periphery between keels, and about 18 on basal area, extending into umbilical region. Incremental lines strongly curved, with most retracted point on adapical keel. Umbilicus narrow. Aperture ovoid, broader than high. Outer lip thin, simple, a little reflected over umbilicus. Colour of protoconch brown, teleoconch white.

Dimensions: Height 2.6 mm, breadth 2.8 mm; aperture height 1.2 mm, breadth 1.5 mm.

Larval shell measurements:

diameter (µm)	no.whorls (prot.II)
1080	2.0

Remarks. — *Haloceras galerita* resembles *H. mediocostata*, but it has a stronger, coarser spiral sculpture, with better defined spiral keels, the umbilicus is even more narrow and the diameter of the whorls increases less rapidly than in *mediocostata*.

Etymology. — From the Latin *galerum*, a hat or helmet; to remind of the large and conspicuous protoconch.

Haloceras heliptyx sp. nov.

(Figs 63, 103)

Type material. — Holotype in MNHN.

Type locality. — Biogeocal, stn DW289, 20°36'S, 167°00'E, 830-840 m, Loyalty Basin, E of New Caledonia.

Material examined. — **Loyalty Basin (E of New Caledonia).** Biogeocal, stn DW 289, 20°36'S, 167°00'E, 830-840 m: holotype (MNHN).

Description. — *Shell* small, solid, trochoid consisting of 2.75 teleoconch, and unknown number of protoconch whorls (apex broken). Protoconch probably globular; little more than last whorl remaining, diameter 770 µm. Protoconch II sculptured with two strong spiral keels, one at periphery, one just above suture; zone between two keels with numerous small pustules. Flexuous axial riblets above peripheral keel on last part of protoconch II. Teleoconch whorls very convex, with slightly channelled suture. Spiral sculpture stronger than axial sculpture, consisting of three strong keels and much weaker spiral cords. Abapical spiral keel hidden at suture on spire, apparent only on body whorl. 6 much finer cords on shoulder of whorls, one between keels, and 10 on basal area. Axial sculpture consisting of strongly prosocline cords, not extending to basal area and forming little nodules at intersections with spiral keels. Also numerous second order incremental ridges, extending over base. Umbilicus open, smooth inside. Aperture ovate, outer lip rather regularly convex, columellar region slightly reflected over umbilicus. Colour of protoconch brown, teleoconch white.

Dimensions: Height 3.1 mm, breadth 2.9 mm; aperture height 1.0 mm, breadth 1.25 mm.

REMARKS. — *H. heliptyx* resembles *H. galerita*, but differs by having stronger axial sculpture and fewer and stronger spiral cords. The umbilicus of *H. galerita* is almost closed and its protoconch II has a bigger diameter, 1080 µm. There is also a general resemblance to *H. japonica*, which has a thinner shell with thick periostracum and rounded aperture, and differs in its brooding reproductive biology.

ETYMOLOGY. — From the Greek *helix*, spiral, and *ptyx*, a fold; to remind of the strong spiral keels of the shell.

Haloceras japonica Okutani, 1964

Figs 34, 40, 62, 64-65

Halocerus japonicus Okutani, 1964: 397, pl. 6, fig. 8.

TYPE MATERIAL. — Holotype and 1 paratype in Tokyo University Museum, RM 8824.

TYPE LOCALITY. — 34°10'N, 140°05.5'E, 1230-1350m, 26 miles off Miyake Island, Japan.

MATERIAL EXAMINED. — **Japan**. 26 miles off Miyake Island, 34°10'N, 140°05.5'E, 1230-1350 m: holotype, 1 paratype (Tokyo Univ. Mus. RM 8824).
Eastern Pacific (Oregon). " *Yaquina* ", stn OTB-188, 45°50'N, 125°14'W, 1580 m: 1 spm. (LACM 67-167.2).

DESCRIPTION. — Teleoconch high, trochoid, consisting of more than 2.5 whorls (corroded) with thick, strongly adhering periostracum. Whorls convex, suture moderately deep. Sculpture consisting of spiral cords, of which two form keels at periphery, no spiral cords above shoulder, 2 between keels and 5 on base. Axial sculpture of periostracal lamellae. Umbilicus broad, encircled by a broad but indistinct cord. Aperture rounded, forming a slight angle at base of columellar pillar. Outer lip thin, sharp. Colour of shell chalky white, periostracum dark greenish brown.

Dimensions of holotype: height 5.95 mm, breadth 5.05 mm; diameter of the aperture 2.25 mm.

REMARKS. — Neither of the two known shells have a well preserved protoconch. The dried body of the specimen from off Oregon was found to contain 9 brooded embryos (Fig. 64). The shells of some of these embryos were extracted (Fig. 65). They are white, 1030-1050 µm in diameter, with a sculpture of coarse granules extending half a whorl further than on protoconch I of other haloceratids. The assignment of the species to *Haloceras* rather than *Zygoceras* is based on the general resemblance in the shape of the teleoconch compared with other species of *Haloceras*, primarily *H. galerita* and *H. heliptyx*.

Haloceras laxa (Jeffreys, 1885)

Figs 74-75, 116-118

Seguenzia laxa Jeffreys, 1885: 44, pl.5, figs 4-4a.

TYPE MATERIAL. — Holotype BMNH 1885.11.5.2586.

TYPE LOCALITY. — " *Porcupine* " 1870, stn 16, 39°55'N, 09°56'W, 1810m, off Portugal.

MATERIAL EXAMINED. — **Eastern Atlantic.** " *Porcupine* ", 1870, stn 16, off Portugal, 39°55'N, 09°56'W, 1810 m: holotype (BMNH 1885. 11.5.2586).
MONACO, stn 624, Azores, 38°59'N, 28°18'W, 2102m, 1 sh. (MOM).
" *Sarsia* ", stn 7614, Bay of Biscay, 43°43'N, 03°38'W, 1100m: 1 sh. (BMNH).
SEAMOUNT, stn CP 30, Gorringe Bank, 36°44'N, 11°23'W, 1940-2075 m: 7 shs (MNHN).
Three additional shells are tentatively identified as *Haloceras* aff. *laxa*:
" *Thalassa* " stn Y 378, off NW Spain, 41°34'N, 09°16'W, 1000m: 1 sh. (MNHN). — Stn Z 435, Bay of

Biscay, 48°40'N, 09°56'W, 1050m: 1 sh. (MNHN).
Biogas, stn CP 37, 47°34'N, 08°39'W, 2175m: 1 sh (MNHN).

Description. — *Shell* small, solid, discoid, consisting of 2.3 protoconch whorls and up to 1.4 teleoconch whorls. Protoconch globular, multispiral. Protoconch I diameter 220 µm, sculptured by combination of anastomosing star-shaped knobs and spiral cords. Protoconch II smooth, except two strong spiral keels and one subsutural row of granules. Protoconch/teleoconch transition abrupt. Teleoconch whorls convex, first rather regularly rounded in young postlarva, then cross-section of whorl becomes more and more depressed, ending up in a horizontally ovoid cross-section of body-whorl, with very deep suture. Sculpture consisting of strong spiral cords and incremental lines. Cords strongest at periphery and weaker or obsolete on shoulder and base. Incremental lines very regular and closely set, giving shell a shining appearance, especially on shoulder. Umbilicus wide, not encircled by cord. Aperture horizontally ovoid, peristome continuous, only slightly adhering to penultimate whorl. Inner lip strongly reflected over umbilicus. Colour of protoconch I brown, protoconch II much paler except at protoconch-/teleoconch transition, teleoconch white.

Dimensions of largest shell: Height 2.1 mm, diameter 3.4 mm; aperture height 0.9 mm, breadth 1.9 mm.

Larval shell measurements:

	diameter (µm)	no.whorls (prot.II)
Seamount CP 30	1130	1.8
Seamount CP 30	1150	1.8
Seamount CP 30	1100	1.75
Seamount CP 30	1100	1.75
Seamount CP 30	1140	1.75
Seamount CP 30	1140	1.8
Monaco 624	1200	?
" *Sarsia* " 7614	980	1.7
aff. *laxa*		
" *Thalassa* " Y378	1030	1.75
" *Thalassa* " Z435	1060	1.85
Biogas CP 37	1100	1.8

Remarks. — The holotype of *S. laxa* is 4.2mm high, it is badly broken and worn which makes identification of the name very difficult. Although the identification at family level is beyond doubt, there are no specimens collected in the NE Atlantic that match this fragment precisely. It could be a fragment of a very large *H. carinata* (but there is no specimen of *H. carinata* higher than 3.3 mm known), or it could be a fragment of the species we have used the name for (but it has less depressed whorls than our shells of that size). It is probable that when more NE Atlantic specimens become available, it will be possible to match this fragment more accurately, but it is incredible that Jeffreys based a new species on this worn fragment.

H. laxa can be identified from other species by the absence of well defined keels at the periphery of teleoconch whorls, its depressed whorls, and small adult size. *H. cingulata* is similarly depressed, but has strongly keeled whorls and a much larger adult size. *H. carinata* also lacks well defined spiral keels but it has a higher spire and considerably smaller protoconch. *H. rugosa*, from the SE Pacific, has an almost closed umbilicus and a distinctive sculpture on the adapical part of teleoconch whorls.

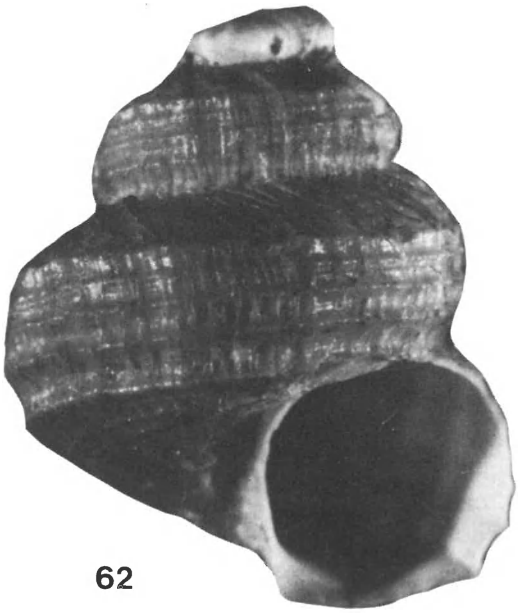
The shells referred to as *H.* aff. *laxa* differ in having a stronger spiral sculpture, and more regularly rounded, not depressed whorls. The protoconch sculpture and measurements are however indistinguishable from those in typical *laxa*. Two of these shells originate from the northern part of the Bay of Biscay, while the more depressed specimens are from further south. They may represent variation or belong to a distinct species.

Haloceras sp. 1

Figs 68-69, 70-71, 104

Material examined. — **New Caledonia.** Biocal, stn DW 70, 23°25'S, 167°53'E, 965 m: 2 shs (MNHN).
Australia. " *Kapala* " stn 80-20-10, off Sydney, 33°36'S, 152°05'E, 1105-1143m: 3 shs (AMS C157269).

Description. — *Shell* trochoid, with a low spire. Protoconch I, diameter 230 µm, not perfectly preserved but with reticulation of anastomosing knobs and spiral cords. Protoconch II with 2 visible spiral keels, one well visible and one at or just above suture. Subsutural zone granulated. Teleoconch with up to 1.9 convex,



FIGS. 62-63. — Genus *Haloceras*. — **62,** *H. japonica*, holotype, height 5.97mm. — **63,** *H. heliptyx*, holotype, height 3.1mm.

regularly rounded whorls, sculptured with spiral cords and incremental lines. Two spiral cords form indistinct keels at periphery. Umbilicus is open.

Dimensions of largest shell: Height 2.7 mm, breadth 3.1 mm.

Larval shell measurements:

	diameter (µm)	no.whorls (prot.II)
BIOCAL DW 70	1020	1.9
BIOCAL DW 70	1080	1.9
AMS 157269	900	1.75
AMS 157269	920	1.95
AMS 157269	900	2.0

REMARKS. — These shells are somewhat intermediate between *H. carinata* and *laxa*. They have a higher spire and a stronger spiral sculpture than *H. laxa*, and a lower spire and bigger protoconch than *H. carinata*. There is no doubt however that *Haloceras laxa* and *H. carinata* are two distinct species in the North Atlantic.

In fact these shells strongly resemble the NE Atlantic shells we have called *Haloceras* aff. *laxa* above, and may be conspecific with them. We would probably have treated them as a single species if they had originated from the same ocean. Considering the vast distances (more than 20,000 km) separating the locations, we judge the material insufficient to conclude if one, somewhat variable, or several, closely related species are involved.

Haloceras mediocostata
(Dautzenberg & Fischer, 1896)

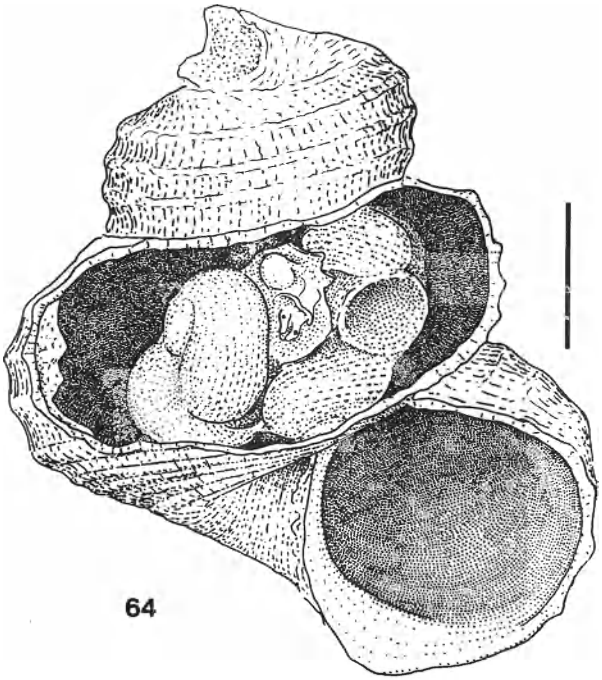
Figs 56-57, 97-99

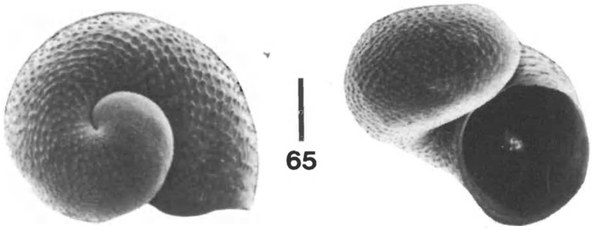
Cithna carinata var. *mediocostata* Dautzenberg & Fischer, 1896: 449.
Cithna jeffreysi var. *mediocostata* Dautzenberg & Fischer, 1897: 159.
Cithna carinata var. *mediocostata* — DAUTZENBERG 1927: 118.

TYPE MATERIAL. — Lectotype, here designated, one shell marked by DAUTZENBERG « type » in MOM (Fig. 57); paralectotype from the same station in MNHN.

TYPE LOCALITY. — MONACO, stn 553, 37°43'N, 25°05'W, 1385m, Azores.

MATERIAL EXAMINED. — **Eastern Atlantic.** MONACO, stn 553, Azores, 37°43'N, 25°05'W, 1385 m: Lectotype (MOM); 1 paralectotype (MNHN). — Stn 578, 38°26'N, 26°31'W, 1165m: 1 sh. — Stn 703, 39°21'N, 31°06'W, 1360m: 2 shs.





FIGS. 64-65. — *Haloceras japonica*, off Oregon. — **64,** Specimen with partly broken body whorl showing the embryos brooded in the oviduct; scale line 1 mm. — **65,** Larval shell of the embryos; scale line 0.25 mm.

DAUTZENBERG (1927) also listed material from stn 203, 683, 698 and 719. We have examined this material in MOM: the shell from stn 683 belongs to an undescribed species of *Zygoceras* (see p. 159); others are unrecognizable fragments, or have been destroyed by acidic glass tubes.

DESCRIPTION. — *Shell* small, thin, fragile, trochoid, consisting of 2.5 protoconch and up to 2.3 teleoconch whorls. Protoconch globular, multispiral. Protoconch I, diameter 200 µm, with a sculpture of spiral cords. Protoconch II with two spiral keels (one at or just above suture) and a subsutural row of granules. In last part of protoconch II, just before larval peristome, a few strong incremental ribs; rest of protoconch smooth. Teleoconch whorls regularly convex, suture slightly channeled but otherwise only moderately deep. Sculpture of spiral cords and incremental lines. Two stronger cords form spiral keels at periphery; about 8 spiral cords on shoulder of body whorl, 3 at periphery between keels; 12 on base, extending to umbilical region. Umbilicus rather narrow, not encircled by cord. Aperture rounded; outer lip thin, simple, inner lip a little reflected over umbilicus. Colour of shell white, protoconch brown.

Dimensions of a complete shell: Height 2.5 mm, breadth 2.6 mm; aperture height 1.2 mm, breadth 1.3 mm.

Larval shell measurements:

	diameter (µm)	no.whorls (prot.II)
MONACO 553	1220	2.1
MONACO 553	1240	2.1
MONACO 578	1200	2.0
MONACO 703	1300	2.1
MONACO 703	1240	2.0

REMARKS. — The assignment of this species to *Cithna jeffreysi* [= *Benthonella tenella* (Jeffreys, 1869); Rissoidae] by DAUTZENBERG & FISCHER, 1897 was due to a printer's mistake (DAUTZENBERG, 1927).

H. mediocostata bears some resemblance to the keeled specimens of *H. carinata* (which lives in the same part of the North Atlantic), but can be separated by the size of the protoconch: diameter 700-920 µm (mean 817 µm) in *H. carinata*, vs. 1200-1300 µm (mean 1240 µm) in *H. mediocostata*; *H. carinata* also has a higher spire.

Haloceras millestriata (Okutani, 1964)

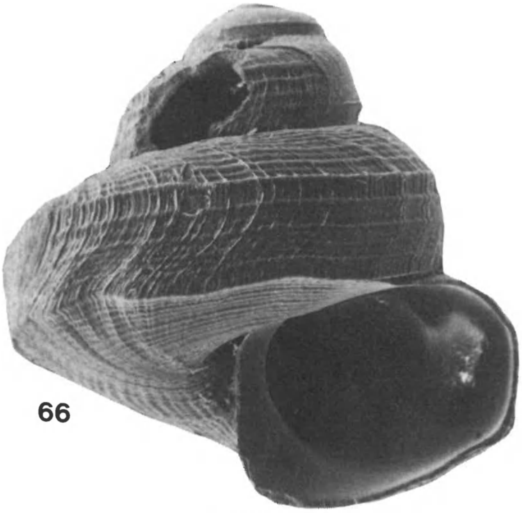
Fig. 67

Torellia millestriata Okutani, 1964: 397, pl. 6, fig. 4.

TYPE MATERIAL. — Holotype in Tokyo University Museum, RM 8822.

TYPE LOCALITY. — 34°10'N, 140°05.5'E, 1230-1350m, 26 miles off Miyake Island, Japan.

MATERIAL EXAMINED. — **Japan.** 26 miles off Miyake Island, 34°10'N, 140°05.5'E, 1230-1350 m: holotype (Tokyo Univ. Mus., RM 8822).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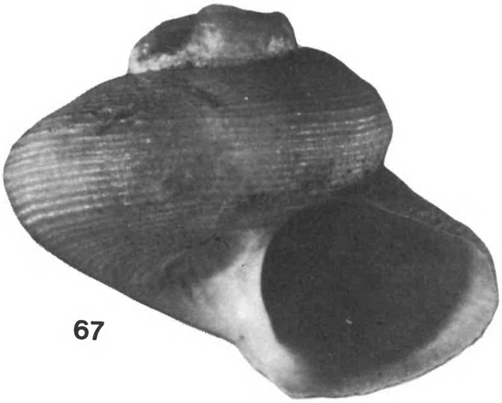
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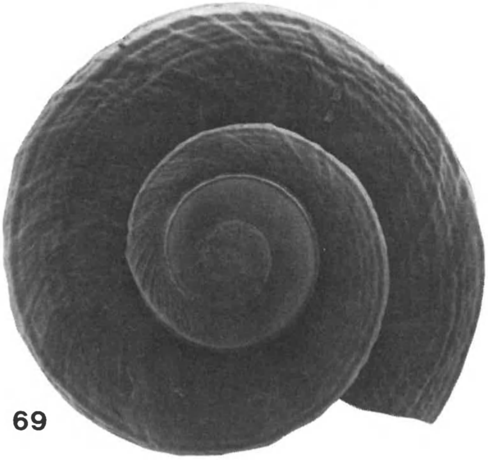
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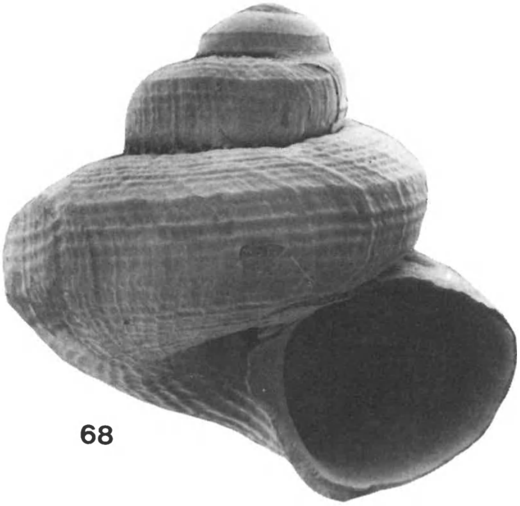
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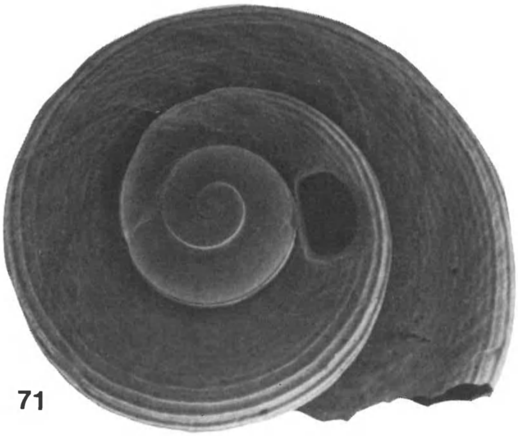
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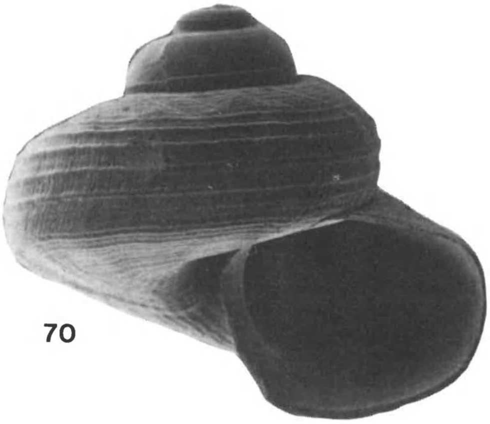
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FIGS. 66-71. — Genus *Haloceras*. — **66,** *H. galerita*, holotype, height 2.6mm. — **67,** *H. millestriata*, holotype, height 3.3mm. — **68-69,** *Haloceras* sp.1, AMS C 157269, diameter 2.35mm, height 2.65mm. — **70-71,** *Haloceras* sp.1, BIOCAL stn DW70, diameter 2.9mm, height 2.5mm.

REMARKS. — The holotype and only known shell of *H. millestriata* has no larval shell. Our generic assignment is based on the general morphology of the teleoconch. The whorls are depressed and the spiral sculpture forms two indistinct keels at the periphery. *Haloceras millestriata* ressembles a little *H. laxa* and *H. rugosa*, which both have a low spire, and regularly rounded whorls. It is however easily recognizable by its even sculpture of strong spiral lines, and moderately open umbilicus.

Haloceras phaeocephala sp. nov.

Figs 32, 43, 81-82, 95-96

TYPE MATERIAL. — Holotype and 2 paratypes (1 live taken) AMS C146202.

TYPE LOCALITY. — " *Kapala* " 1980, 33°36'S, 152°05'E, 1143-1106m, off Sydney, New South Wales, Australia.

MATERIAL EXAMINED. — **Australia.** " *Kapala* " 1980, off Sydney, 33°36'S, 152°03'E, 1143-1106 m: holotype, 2 paratypes (AMS C146202). — Off Sydney, 33°38'S, 152°03'E, 924-896m: 1 sh. (AMS C150189). — Off Wollongong, New South Wales, 34°26'S, 151°27'E, 1200m: 2 shs (AMS C150188). — NE of Batemans Bay, New South Wales, 35°30'S, 150°52'E, 960-969m: 1 spm. (AMS C150190).

DESCRIPTION. — *Shell* small, solid, depressed rissoiform, consisting of 2.3 protoconch and 2 teleoconch whorls with thick adhering periostracum. Protoconch I, diameter 230 µm, nucleus with thin spiral threads which soon stop, leaving rest of protoconch I smooth, except for 4 spiral threads above suture. First whorl of protoconch II sculptured by continuation of spiral threads from protoconch I. Later sculpture of irregular, raised scratches and spirally elongated knobs develops and completely covers last protoconch whorl. Protoconch/teleoconch discontinuity very sharp. Teleoconch whorls convex, shouldered, with moderately deep suture. Sculpture consists of strong, broad axial ribs, thin incremental lamellae and spiral cords. 11 axial ribs on first teleoconch whorl, and 15 on body whorl of holotype. 5 strong spiral cords at periphery of which adapical one forming a slightly spiny shoulder at intersections with axial ribs. 2, later on body-whorl 3, fainter spiral cords on shoulder, 8 on base, of which one demarcates umbilicus. Umbilical chink narrow. Outer lip thin, simple, with most projecting point at lower third; inner lip slightly reflected and forming narrow callus over umbilicus, a little protracted at base. Colour of larval shell reddish brown, teleoconch with yellowish white periostracum.

Dimensions: Height 3.33 mm, breadth 3.06 mm; aperture height 1.74 mm, breadth 1.50 mm.

Larval shell measurements:

	diameter (µm)	no.whorls (prot.II)
AMS 146202 (holotype)	1060	2.0
AMS 146202	940	1.8
AMS 146202	1000	1.9
AMS 150188	1000	1.9
AMS 150189	910	1.8
AMS 150190	890	1.8

REMARKS. — There is variation in the strength of the sculpture. One of the shells (AMS 150189) is almost devoid of axial ribs, but transitional specimens are present, although sculptured specimens appear to be more frequent. The sculpture, size and number of whorls of the protoconch are the same in strongly and weakly sculptured shells and they are undoubtedly conspecific.

The protoconch of *H. phaeocephala* differs from that of congeners in having a protoconch I with spiral threads on a smooth background, a character of *Zygoceras*. Protoconch II however is characteristic for the genus.

Recognition of this distinctive little haloceratid should be easy since it is the only representative of the family with a strongly sculptured, rissoiform shell.

ETYMOLOGY. — From the Greek *phaios*, brown, and *kephale*, head; to remind of the brown coloured protoconch.

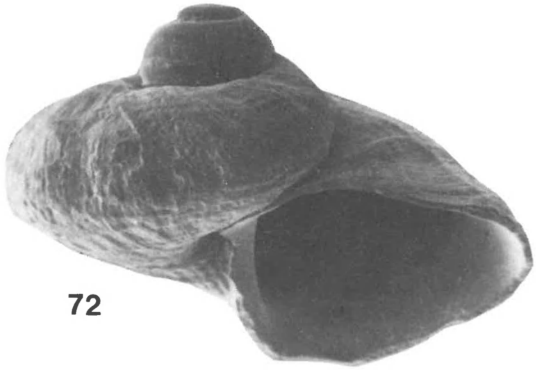
Haloceras rugosa sp. nov.

Figs 72-73, 91-92

TYPE MATERIAL. — Holotype LACM 2279.

TYPE LOCALITY. — Allan Hancock Foundation, stn 482, 01°09'S, 90°36'W, 455m, Galapagos Islands.

MATERIAL EXAMINED. — **Galapagos Islands.** ALLAN HANCOCK FOUNDATION, stn 482, 01°09'S, 90°36'W, 455 m: holotype (LACM 2279).



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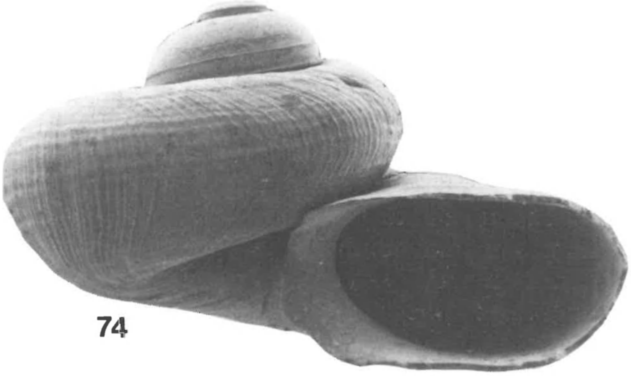

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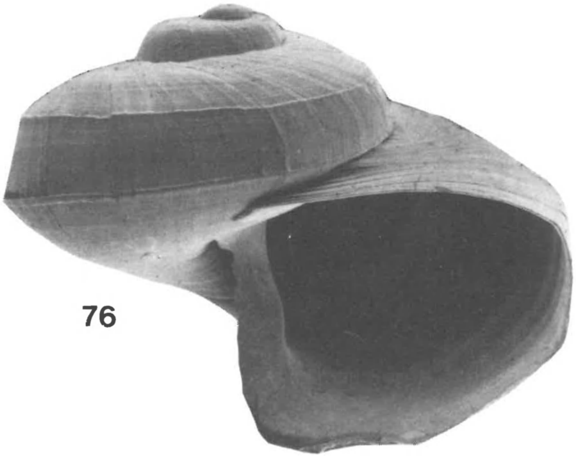

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FIGS. 72-77. — Genera *Haloceras* and *Zygoceras*. — **72-73,** *Haloceras rugosa*, holotype, height 2.95mm, diameter 3.65mm. — **74-75,** *H. laxa*, SEAMOUNT stn CP30, height 2.1mm, diameter 3.4mm. — **76-77,** *Zygoceras biocalae*, holotype, height 7.0mm, diameter 9.6mm.

DESCRIPTION. — *Shell* solid, globular, consisting of 2.5 protoconch and 1.25 teleoconch whorls. Protoconch I, diameter 200 µm, with about 10 irregular spirals, interconnected by a net of anastomosing short trabecles. Protoconch II with two spiral keels; one well exposed, one partly hidden at suture; rest of protoconch smooth except for one row of subsutural granules. Teleoconch whorls regularly convex, with deep suture. Umbilicus open, narrow. Sculpture above periphery of diverging, strongly opisthocline radiating ribs which intersect rather coarse, prosocline incremental ribs and produce irregular hammered appearance. 5-6 regular spiral cords at and below periphery; another group of similar spiral cords, more crowded towards basal and umbilical region. Incremental sculpture weak and indistinct. Aperture simple, outer lip sharp, thin, inner lip slightly reflected over umbilicus. Protoconch brown, teleoconch white.

Dimensions of shell: Height 2.95 mm, diameter 3.65 mm; aperture height 1.80 mm, breadth 1.95 mm.

Larval shell measurements:

diameter (µm)	no.whorls (prot.II)
1100	2.1

REMARKS. — *H. rugosa* is characterized by the malleated appearence of the surface of the adapical part of its whorls, with the strongly opisthocline ribs that cross prosocline incremental ribs. This character, in combination with the small umbilicus and regularly rounded, unkeeled whorl facilitates the identification.

ETYMOLOGY. — From the Latin *rugosus*, schriveled, wrinkled; to remind of the teleoconch sculpture.

Haloceras spinosa sp. nov.

Figs 80, 109-110

TYPE MATERIAL. — Holotype AMS C157270.

TYPE LOCALITY. — " *Kapala* ", stn K80.20.10, 33°36'S, 152°03'E, 1106-1143m, off Sydney, New South Wales, Australia.

MATERIAL EXAMINED. — **Australia.** " *Kapala* ", stn K 79.20.14, off Broken Bay, New South Wales, 33°38'S, 152°06'E, 1033 m: 1 sh. (AMS C146529). — Stn K 80.20.10, off Sydney, 33°36'S, 152°03'E, 1106-1143 m: holotype (AMS C157270).

Loyalty Basin (E New Caledonia). BIOGEOCAL, stn CP 232, 21°34'S, 166°27'E, 760-790 m: 2 shs (MNHN).

DESCRIPTION. — *Shell* small, solid, broadly rissoiform, consisting of 1.7 protoconch and 2.7 teleoconch whorls, with thin, transparent, adhering periostracum. Protoconch I, diameter 290 µm, sculptured with about 10 rather fine spiral threads. Shell corroded at transition protoconch I/II. Protoconch II smooth and shiny except for narrow subsutural zone of granules, and two strong spiral keels at periphery. Protoconch / teleoconch transition abrupt, with peristome of protoconch slightly flaring. Teleoconch whorls convex with rather deep channelled suture. Sculpture consisting of strong spiral cords and weaker, lamellar axial ribs, forming small raised spines when they intersect. 4 spiral cords on first whorl, secondary spirals appear on body whorl between adapical cords; also one cord encircling slightly convex base, 4 other cords on base and 2 more indistinct ones in umbilicus. Channeled appearance of suture results from it being lined by two adjacent raised spiral cords. 19 prosocline axial ribs on first teleoconch whorl, 32 on body whorl. Between these, fine incremental lines. Umbilicus open, small. Aperture slightly depressed; outer lip sharp, simple; inner lip slightly reflected over umbilicus. Colour of larval shell brown, teleoconch white.

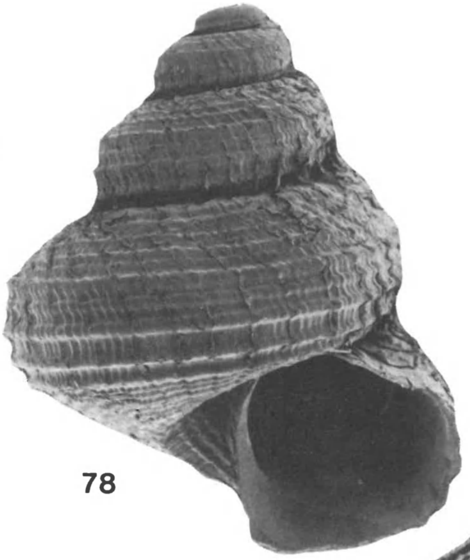
Dimensions: Height 3.28 mm, breadth 2.88 mm; aperture height 1.12 mm, breadth 1.32 mm.

Larval shell measurements:

	diameter (µm)	no.whorls (prot.II)
holotype	720	1.2
BIOGEOCAL CP 232	675	1.3
BIOGEOCAL CP 232	690	1.3

REMARKS. — *H. spinosa* is immediately separated from other haloceratids by the spiny general appearance.

ETYMOLOGY. — From the Latin *spinosus*, thorny; to remind of the teleoconch sculpture.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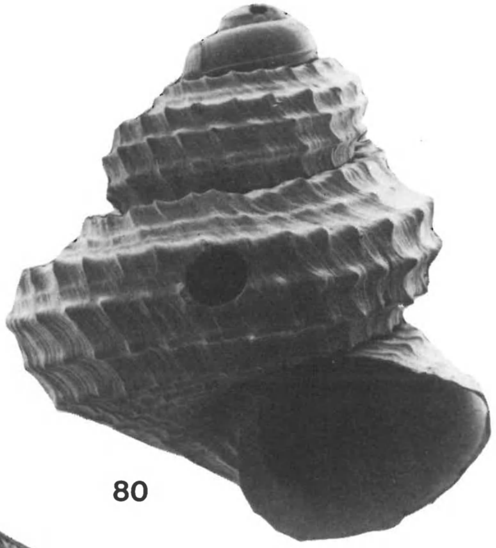
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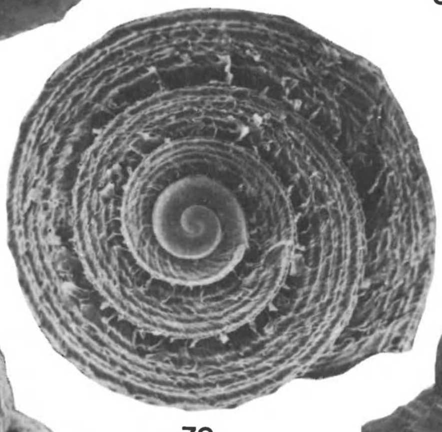
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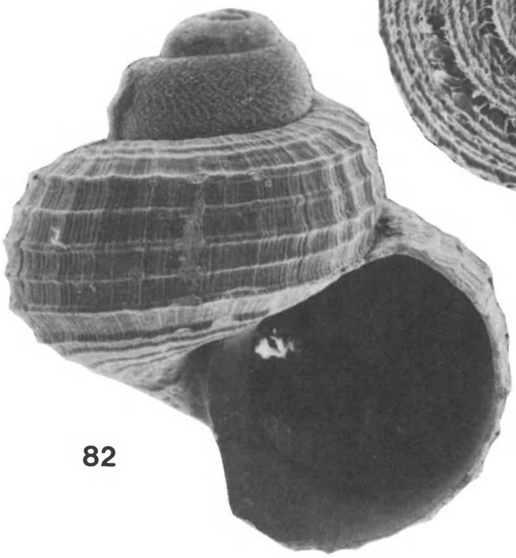
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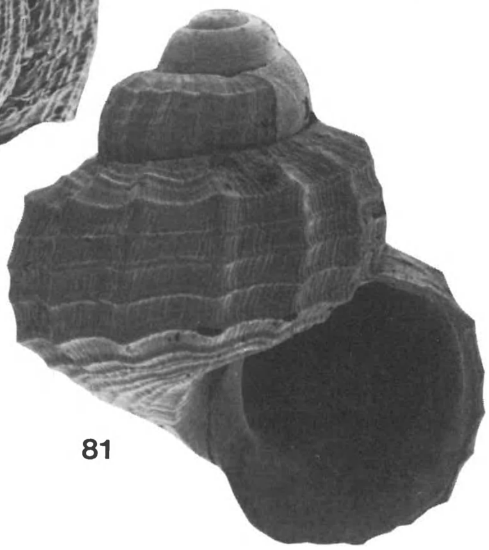
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FIGS. 78-82. — Genus *Haloceras*. — **78-79,** *H. trichotropoides*, holotype, height 3.57 mm, diameter 3.06mm. — **80,** *H. spinosa*, holotype, height 3.28mm. — **81,** *H. phaeocephala*, holotype, height 3.33 mm. — **82,** *H. phaeocephala*, AMS C 150189, height 2.50mm.

Haloceras tricarinata (Jeffreys, 1885)

Figs 37-39, 50-52, 119-120

Seguenzia tricarinata Jeffreys, 1885: 43, pl.5, fig.2.
Seguenzia tricarinata- Quinn 1983: 744.

Type material. — Holotype BMNH 1885.11.5.2589.

Type locality. — " *Porcupine* " 1870, stn 17a, 39°39'N, 09°39'W, 1347m, W of Portugal.

Material examined. — **Eastern Atlantic.** " Porcupine " 1870, stn 17a, W of Portugal, 39°39'N, 09°39'W, 1347 m: holotype (BMNH 1885.11.5.2589).

" *Discovery* ", stn 10141, 24°34'N, 19°41'W, 3460-3470 m: 1 spm and 1 larva (BMNH).

Seamount, stn CP30, Gorringe Bank, 36°44'N, 11°23'W, 1940-2075m: 1 young sh (MNHN).

Biacores, stn 126, Azores, 39°19'N, 33°47'W, 3360m: 1 larva (MNHN).

Biogas, stn DS 62, 47°33'N, 08°40'W, 2175m: 1 larva (MNHN).

Mozambique Channel. Benthedi, stn 87, SE Glorieuses Islands, 11°44'S, 47°35'E, 3716 m: 2 shs (MNHN).

South Africa. " *Galathea* ", stn 192, off Durban, 32°00'S, 32°41'E, 3430 m: 1 sh (ZMC).

Distribution. — Eastern Atlantic Ocean and SW Indian Ocean, between 40°N and 32°S, in 1940-3716m (abyssal).

Description (of a shell from Mozambique channel). — *Shell* large, solid, depressed, consisting of a globular larval shell with 3 whorls, and 1.75 planispirally coiled teleoconch whorls. Even on best preserved benthic specimen protoconch I and initial part of protoconch II corroded. Protoconch II with one strong, raised spiral thread well above suture, a second similar one, hidden by subsequent whorl, apparent only on terminal part of protoconch. In addition to raised spirals, also weaker periostracal spiral threads present on body-whorl of protoconch, 4 such spirals between adapical suture and raised keel, 4 between raised keel and abapical suture. Protoconch/teleoconch transition very sharp. Teleoconch with strongly keeled whorls, giving shell a lenticular appearance. Whorls convex above and below keel. Body-whorl adhering to penultimate whorl just below keel, thus concealing suture in a channel. Umbilicus broad and deep, continuous with larval umbilicus. Sculpture consists of spiral cords and thin, raised, periostracal incremental lamellae. About 15 spiral cords above periphery on early teleoconch, about 20 on later parts. Base of shell and umbilical region with about 25 such spiral cords. Outer lip thin, simple, angular at periphery; inner lip sharp, simple, slightly reflected over umbilicus. Shell chalky white with strong yellowish brown periostracum.

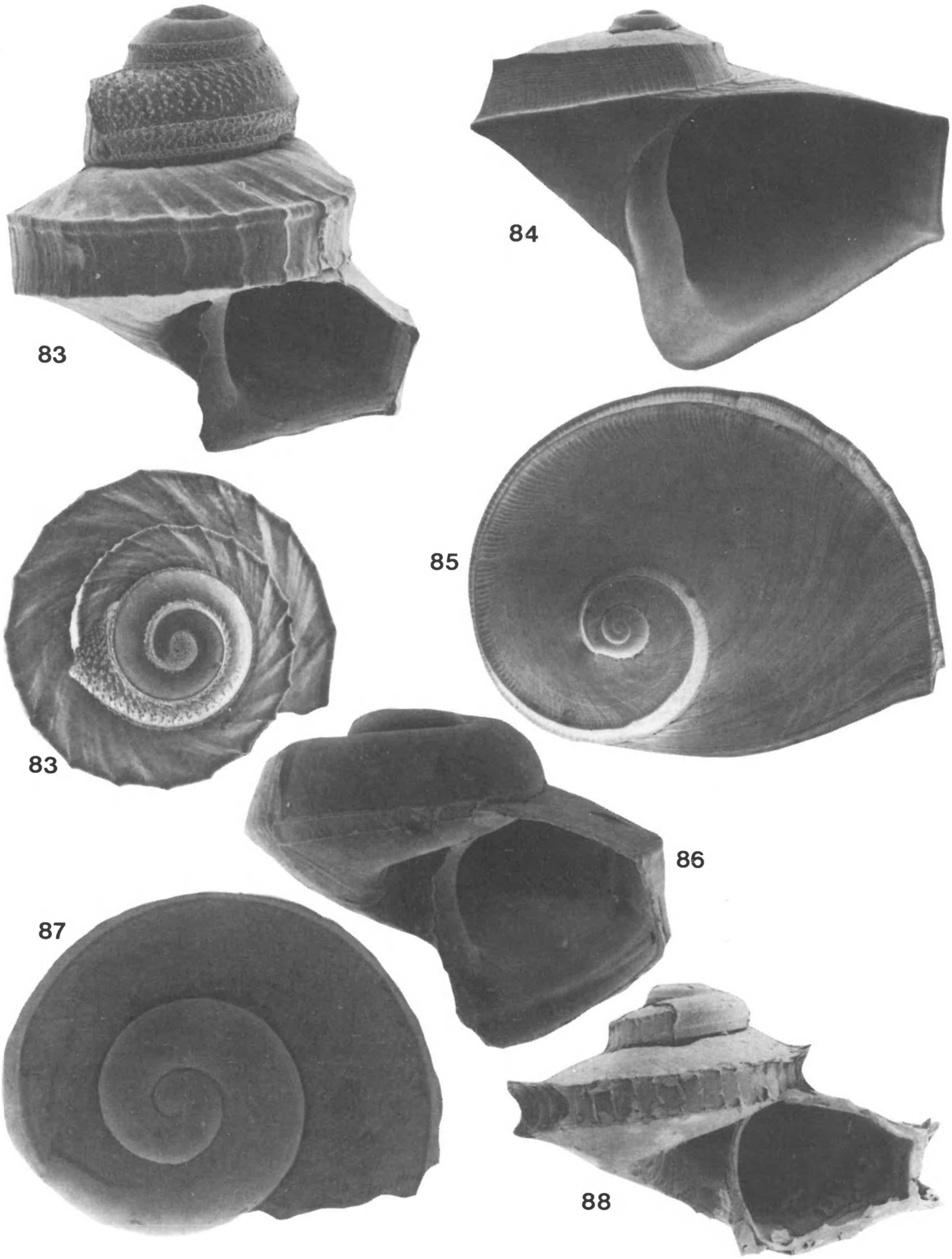
Dimensions of shell: Height 6.5 mm, max. diameter 14.1 mm; aperture height 4.8 mm, breadth 7.0 mm.

Larval shell measurements:

	diameter (µm)	no. whorls (prot.II)
Benthedi 87	1800	?
Benthedi 87	1920	?
" *Galathea* " 192	2300	2.3
" *Discovery* " 10141	1500	?
Seamount CP 30	2100	2.6
Unmetamorphosed larvae:		
holotype	2080	2.2
Biacores 126	2110	2.4
Biogas DS 62	1810	2.5
" *Discovery* " 10141	1750	2.5

Remarks. — Quinn (1983: 744) recognized that the holotype of *Seguenzia tricarinata* is a larval shell. Only a single species of Haloceratidae has a protoconch of this size (see measurements above and p. 159), which enables identification of *S. tricarinata*. This larval shell is superficially similar to certain nassarid larval shells and was erroneously regarded as such by Quinn (1983: 744). Nassarid larval shells have a broad and shallow sinusigera notch above the peripheral keel. The name *tricarinata* was based on the three strong keels present on the larval shell. Of these only the adapical keel remains well visible on the apex of the postlarva, the median keel is usually hidden just above or just below the suture, and the basal (abapical) keel is totally covered by the first teleoconch whorl.

Haloceras tricarinata can be identified, both as a larva and as a benthic snail, by its large protoconch. If this is destroyed, the lens-shaped, strongly keeled teleoconch, resembling certain land snails of the genus *Iberus* is characteristic. Among other species of Haloceratidae, it is only the larval shell of *H. cingulata* which approaches



FIGS. 83-88. — Genera *Haloceras* and *Zygoceras*. — **83,** *Haloceras exquisita*, holotype, height 1.8mm, diameter 1.75mm. — **84-85,** *Zygoceras tropidophora*, holotype, height 8.7mm, diameter 11.9mm. — **86-87,** *Zygoceras* sp., MONACO stn 683, height 1.25mm, diameter 1.7mm. — **88,** *H. acrocomata*, holotype, height 2.07mm.

the size of that of *H. tricarinata* (range 1300-1660 vs. 1500-2300 µm). The specific name is most unfortunate in view of the general appearance of the adult shell.

The specimen from off NW Africa (" *Discovery* ", stn 10141) is still more lenticular (height 3.6 mm, diameter 10.1 mm; aperture height 3.0 mm, breadth 6.2 mm), with a weaker spiral sculpture, and the diameter of the larval shell is significantly smaller than in the 3 Indian Ocean snails; it may represent another species, although the large sized larvae from the SW Indian Ocean and the NE Atlantic appear to be conspecific.

Haloceras sp. 2

not figured

MATERIAL EXAMINED. — **Australia.** " *Kimbla* " 1984, stn 17, NE of Sandy Cape, Queensland, 1330-1380m, 1 sh (AMS C146279).

DESCRIPTION. — *Shell* small, solid, lenticular, consisting of about 3 protoconch and slightly more than one teleoconch whorl. Larval shell globular, multispiral. Apical part partly corroded, only sutures left, so size and sculpture of protoconch I cannot be determined. Protoconch II smooth, except for two spiral keels. Teleoconch whorl depressed, with one sharp keel at periphery; parts of whorl above and below keel regularly convex. Body whorl is adhering to penultimate whorl just below keel, giving suture very deep appearance. Sculpture consisting of strong spiral cords and much finer, rather indistinct incremental lines. About 20 spiral cords above keel, same number on base, extending into umbilicus. Umbilicus very broad, not encircled by a cord. Aperture ovoid, much broader than high, angular at periphery. Outer lip sharp, thin, inner lip slightly reflected over umbilicus.

Dimensions: Height 2.7 mm, breadth 5.05 mm; aperture height 1.8 mm, breadth 2.70 mm.

Larval shell measurements:

diameter (µm)	no.whorls (prot.II)
1580	ca. 2.3

REMARKS. — *Haloceras* sp. 2 is very similar to *H. tricarinata* in having a single sharp peripheral keel. In typical *H. tricarinata* however, the whorls are increasing more rapidly in diameter: at a little more than 1 teleoconch whorl, their diameter is already 7.2-8.5 mm, vs. only 5mm in *Haloceras* sp. 2. Also, in *H. tricarinata*, the peripheral keel is still sharper and more prominent. However, the larval shell characteristics fall within the range of variation observed for typical *tricarinata*. Only further material may solve the identity of this single shell.

Haloceras trichotropoides sp. nov.

Figs 78-79, 111-112

TYPE MATERIAL. — Holotype and one paratype, both live taken, USNM 450423 and 859418.

TYPE LOCALITY. — " *Aeolis* ", stn 326, 136m, off Sand Key, Florida.

MATERIAL EXAMINED. **Western Atlantic (Florida).** " *Aeolis* ", stn 326, off Sand Key, 136 m: holotype (USNM 450423); 1 paratype (USNM 859418). — Stn 338, off Sand Key, 156 m: 1 sh (USNM 450526). — Stn 344, off Key West, 183m, 1 sh (USNM 450536). — Stn 369, off Ajax Reef, 146-182m, 1 sh (USNM 450971). — Stn 370, off Ajax Reef, 128-165m, 2 shs (USNM 450572). — Stn unknown: 1 sh (USNM 878134).

DESCRIPTION. — *Shell* small, solid, conical, trochiform, consisting of 1.5 protoconch and 3 teleoconch whorls. Protoconch depressed, almost planispirally coiled. Protoconch I diameter 280 µm, with about 12 regular spiral cords. Protoconch II with two strong spiral keels, otherwise smooth: A third more basal keel, hidden by first teleoconch whorl, is visible on a juvenile with less than one postlarval whorl. Teleoconch with regularly convex whorls, a deep suture, and thick adherent periostracum. Sculpture consists of spiral cords and axial periostracal lamellae. 5 spiral cords at periphery slightly stronger than 5 above shoulder and 7 on base, of which one encircles umbilicus and two are situated in umbilicus. Periostracal lamellae strongest on adapical part of whorl, where forming scale-like projections adhering to preceding whorl. Umbilicus rather broad, open. Aperture rounded; outer lip sharp, thin; inner lip not reflected over umbilicus, with shallow siphonal depression. Colour of protoconch brown, teleoconch light amber brown.

Dimensions: Height 3.57 mm, breadth 3.06 mm; aperture height 1.40 mm, breadth 1.38 mm.

Larval shell measurements:

	diameter (µm)	no.whorls (prot.II)
USNM 450572	670	1.05
USNM 450572	670	1.05
USNM 450526	700	1.0
USNM 450536	660	1.05
USNM 450971	610	1.0
USNM 438412	650	1.05
USNM 450423	650	1.05
USNM 450423	650	1.05

REMARKS. — *H. trichotropoides* has the smallest protoconch of all known haloceratids, with only a single, almost planispiral whorl in protoconch II. It resembles a little *H. carinata*, which is partly sympatric with it in the West Atlantic, but that species has less coarse teleoconch sculpture, and a globular protoconch consisting of 1.7-1.9 whorls in protoconch II.

ETYMOLOGY. — From the genus name *Trichotropis* and the suffix *-oides*, having the form of; meaning that it ressembles that genus.

Genus *ZYGOCERAS* nov.

TYPE SPECIES. — *Zygoceras tropidophora* sp. nov.

DIAGNOSIS. — Haloceratidae with (in species with planktotrophic development) light yellowish multispiral protoconch. Protoconch I smooth except for 4-6 thin spiral cords placed near periphery. Protoconch II with two strong spiral keels of which one is hidden below suture by successive whorl. Teleoconch depressed with strongly angular whorls, narrow to closed umbilicus, and aperture with a swelling at base of columellar pillar. Soft parts with characters of the family.

REMARKS. — *Zygoceras* differs from *Haloceras* by the general shape and sculpture of the protoconch. The protoconch is low spired and light yellowish in *Zygoceras*, high spired and brown in *Haloceras*. Protoconch I has only 4-6 thin spiral cords on a smooth background in *Zygoceras*, vs. anastomosing riblets and pustules in *Haloceras*. In *Zygoceras* protoconch II has two spiral keels, of which one only is left apparent above suture by successive whorl; in *Haloceras* there are three spiral keels, with two left apparent above suture. The columellar swelling of the teleoconch appears to be absent in *Haloceras*, also in the two larger species of comparable size (*cingulata, tricarinata*).

Although we have emphasized here the characters of the protoconch of species with planktotrophic development, we fully expect that species with non-planktotrophic development, and therefore paucispiral protoconch, may occur in both genera.

ETYMOLOGY. — From the Greek, *zygos*, a pair, and the suffix *-ceras*, as in *Haloceras*; to mean that the new genus forms a pair with *Haloceras*, and also to remind the two strong spiral keels.

Zygoceras biocalae sp. nov.

Figs 76-77, 123-124

TYPE MATERIAL. — Holotype in MNHN.

TYPE LOCALITY. — BIOCAL, stn DW48, 23°00'S, 167°29'E, 775 m, off S New Caledonia.

MATERIAL EXAMINED. — **New Caledonia.** BIOCAL, stn DW 48, 23°00'S, 167°29'E, 775 m: holotype (MNHN).

DESCRIPTION. — *Shell* large, thin, solid, globular, with low spire of 1.75 protoconch and 2.3 teleoconch whorls. Larval shell depressed dome-shaped. Sculpture and limits of protoconch I not visible on only shell available. Protoconch II with approximately 1.25 whorls, diameter 1000 µm. One spiral keel just above suture, a second one hidden at suture. Except for these keels, protoconch smooth. Protoconch/teleoconch transition less distinct than in other haloceratids. Teleoconch whorls convex; after first, regularly convex whorl, two spiral keels, becoming stronger on body whorl. In addition to keels, subtle, illdefined, spiral threads and strong, prosocline and oblique, incremental ribs. Very narrow umbilical chink, almost closed by reflected inner lip. Aperture wide, rather rounded despite spiral keels. Outer lip thin, columellar pillar straight. Teleoconch white.

Dimensions: Height 7.0 mm, breadth 9.6 mm; aperture height 4.5 mm, breadth 5.1 mm.

REMARKS. — *Zygoceras biocalae* is a very distinctive species, that is best identified by its bicarinated teleoconch whorls of rapidly increasing diameter, and by its almost closed umbilicus. *Haloceras cingulata* has a broad open umbilicus, and a sculpture of strong spiral cords; *H. exquisita* and *H. acrocomata* have thin, strong axial lamellae in addition to two very sharp keels at the periphery. It resembles *Z. tropidophora* in having a depressed protoconch with the keel almost hidden by the next whorl, and in that protoconch I lacks the complex sculpture of anastomosing ridges and granules.

ETYMOLOGY. — From the cruise name BIOCAL, a contraction for BIOlogie and CALédonie, during which the material was collected in 1985.

Zygoceras tropidophora sp. nov.

Figs 28-30, 35, 84-85, 121-122

TYPE MATERIAL. — Holotype in MNHN; one paratype dissolved for anatomical investigation.

TYPE LOCALITY. — MUSORSTOM 6, stn 438, 20°23'S, 166°20'E, 780m, Loyalty ridge, E of New Caledonia.

MATERIAL EXAMINED. — **Loyalty Islands (E of New Caledonia).** MUSORSTOM 6, stn 438, 20°23'S, 166°20'E, 780 m: holotype, 1 paratype (MNHN).

Kermadec Islands. " *Akademik Nesmeyanov* ", off Curtis Island, 30°28'S, 178°37'W, 1000 m: 1 sh (NMNZ MF49882).

DESCRIPTION. — *Shell* large, solid, depressed, consisting of 2 protoconch and 1.75 teleoconch whorls. Protoconch with very low spire. Protoconch I, diameter 300 µm, sculptured by a few spiral lines. Protoconch II, diameter 1400 µm, consisting of 1.6 whorls, smooth with sharp spiny keel at periphery, just above suture; projecting spines calcareous, not periostracal. Teleoconch whorls very angular, of rapidly increasing diameter. Body-whorl very large. 2 strong keels at periphery give the whorl a roughly square cross-section. Shoulder and base moderately convex. Beside 2 keels, sculpture consists of thin weak spiral cords and incremental ridges; ridges stronger at periphery and fading on shoulder and base. Between peripheral keels, spiral and axial sculpture of equal strength; intersections forming fine sharp decussation. No umbilicus. Aperture strongly angular, with basal part considerably drawn out, slightly flaring. Outer lip thin, sharp. Inner lip indistinct. Columellar pillar strong, excavated at mid aperture height, slightly twisted below. Colour of protoconch light yellowish brown, teleoconch white.

Dimensions: Height 8.7 mm, breadth 11.9 mm; aperture height 7.1 mm, breadth 6.8 mm.

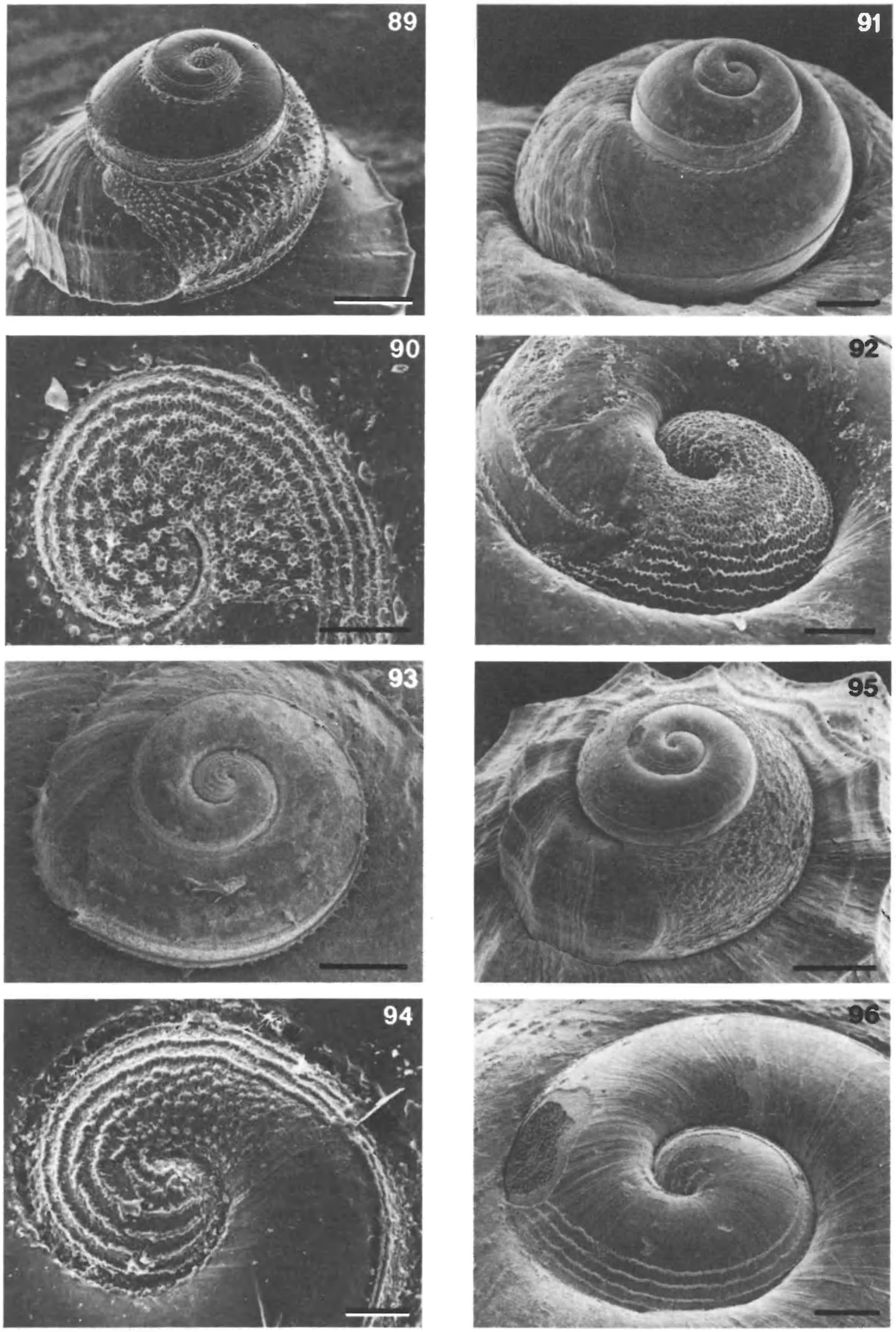
Larval shell measurements:

	diameter (µm)	no. whorls (prot.II)
holotype	1400	1.6
NMNZ 49882	1450	1.8

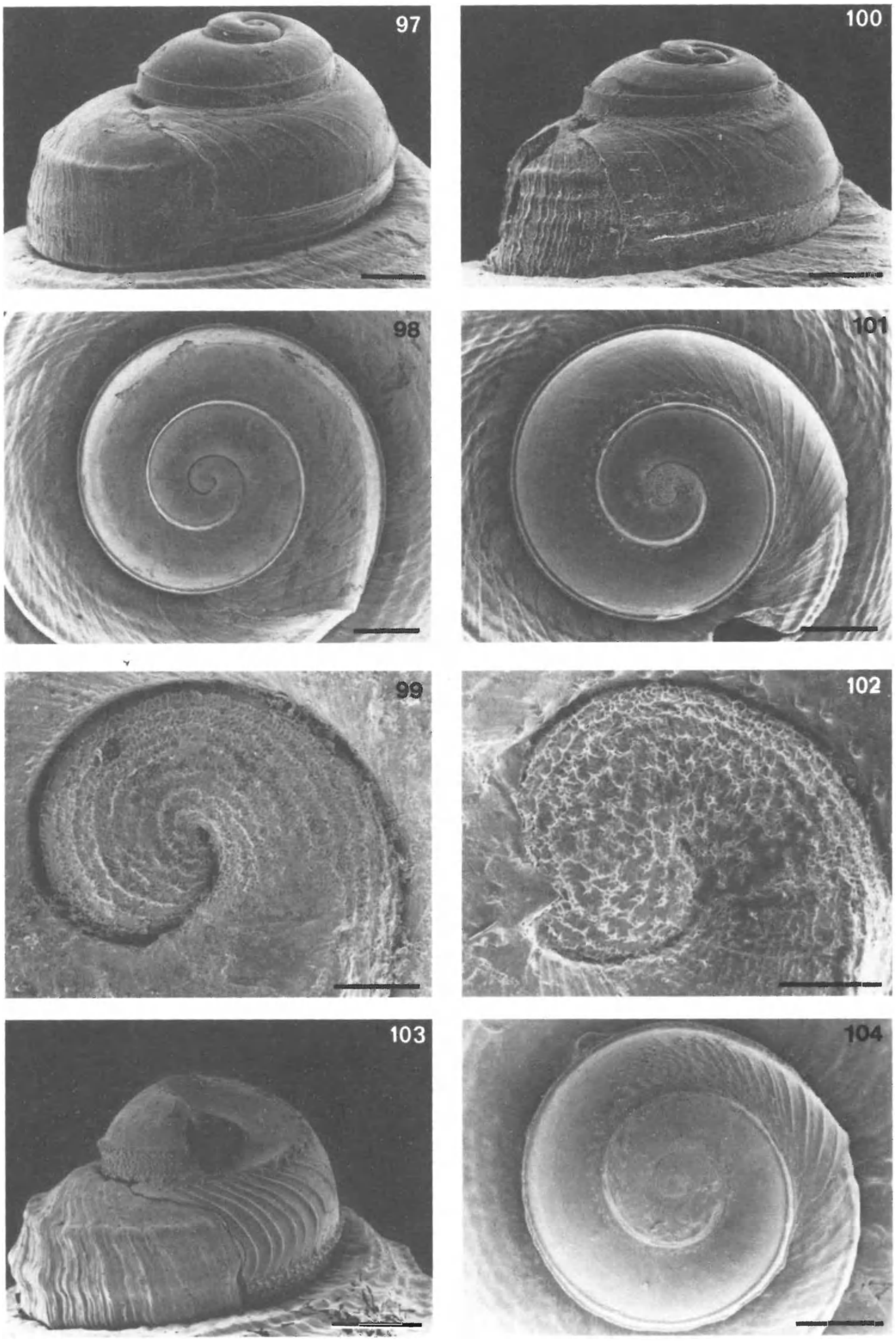
REMARKS. — *Zygoceras tropidophora* can hardly be confused with any other species of Haloceratidae. *Halocears cingulata* differs by having much more depressed whorls and aperture, weaker peripheral keels, and a broad open umbilicus. *Z. biocalae* has a similar low protoconch, but with fewer whorls and without projecting spines on the spiral keel. Furthermore it has a small but distinct umbilicus, weaker spiral sculpture and a more rounded aperture.

The protoconch of *Z. tropidophora* stands out among all gastropod larval shells we have examined in having a keel of solid calcified projecting spines (not periostracal bristles as is found in a number of Tonnoidea). In that respect it resembles a miniature *Cochliolepis gruveli* from West Africa (see ADAM & KNUDSEN 1969: fig.33).

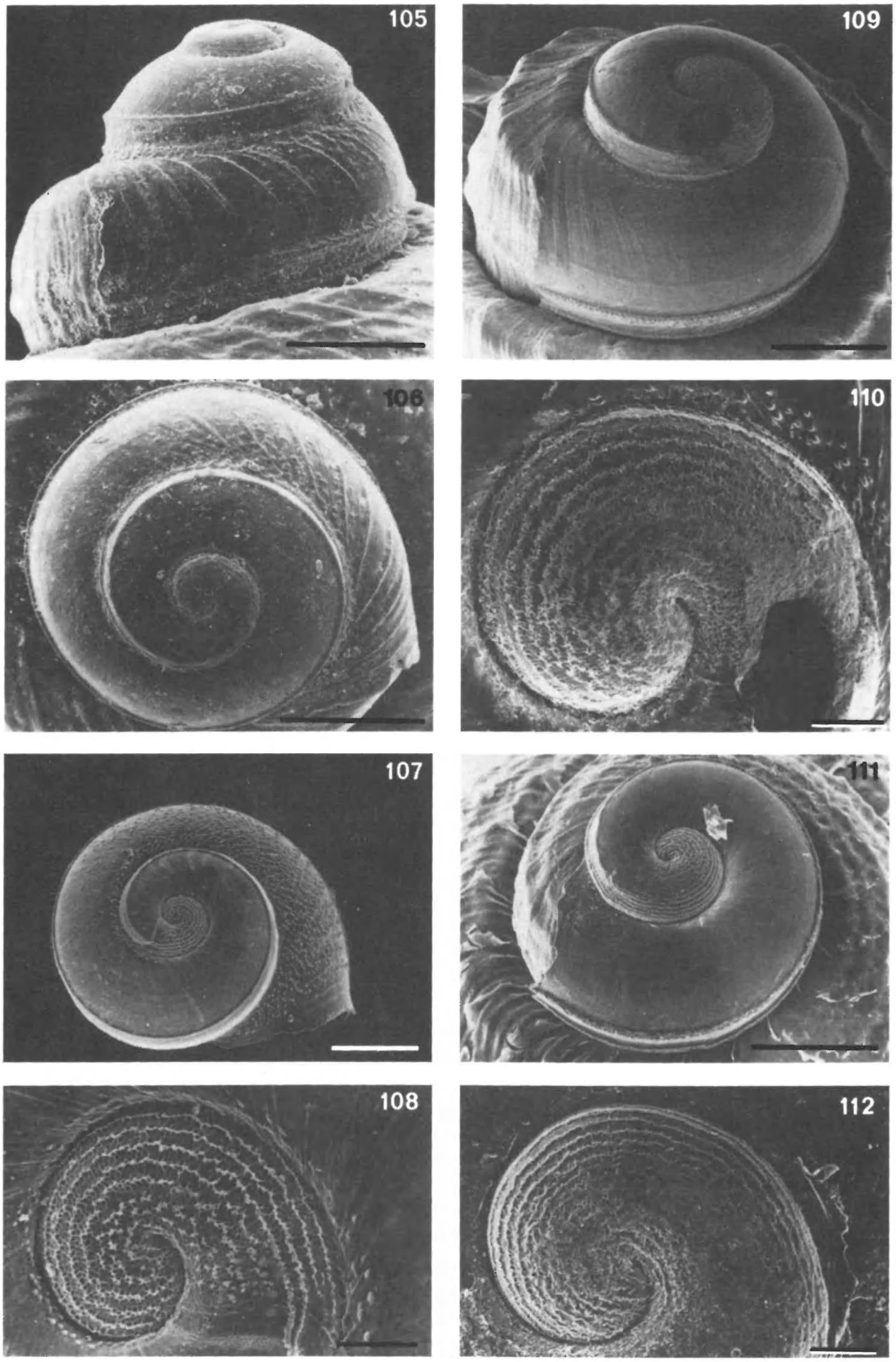
ETYMOLOGY. — From the Greek *tropis*, keel, and *phoreus*, carrier; to remind of the teleoconch sculpture. *Tropidophora* is also a genus of land snails from Madagascar, which has a superficial ressemblance with *Zygoceras*.



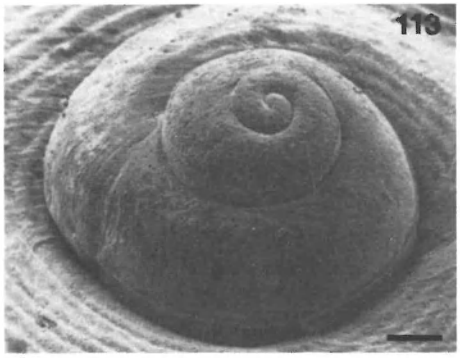
FIGS. 89-96. — Protoconchs of *Haloceras*. — **89-90,** *H. exquisita*, holotype. — **91-92,** *H. rugosa*, holotype. — **93,** *H. acrocomata*, holotype. — **94,** *H. acrocomata*, AMS C 147279. — **95-96,** *H. phaeocephala*, paratype. Scale lines 250 µm (89, 91, 93, 95) and 50 µm (90, 92, 94, 96).



FIGS. 97-104. — Protoconchs of *Haloceras*. — **97-99,** *H. mediocostata*, lectotype. — **100-102,** *H. galerita*, holotype. — **103,** *H. heliptyx*, holotype. — **104,** *Haloceras* sp.1, AMS C 157269. Scale lines 250 µm (97-98, 100-101, 103-104) and 50 µm (99, 102).



Figs. 105-112. — Protoconchs of *Haloceras*. — **105-106,** *H. carinata*, syntype of *Solariella constricta*. — **107-108,** *H. carinata*, unmetamorphosed larva, INCAL stn DS3. — **109-110,** *H. spinosa*, holotype. — **111-112,** *H. trichotropoides*, USNM 450526. Scale lines 250 µm (105-107, 109, 111) and 50 µm (108, 110, 112).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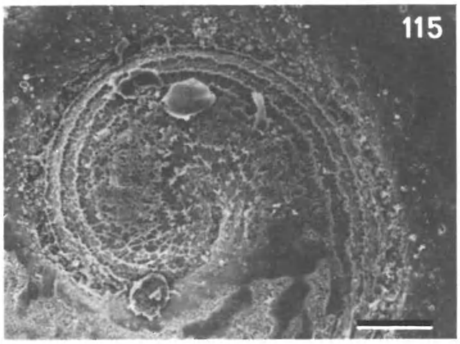
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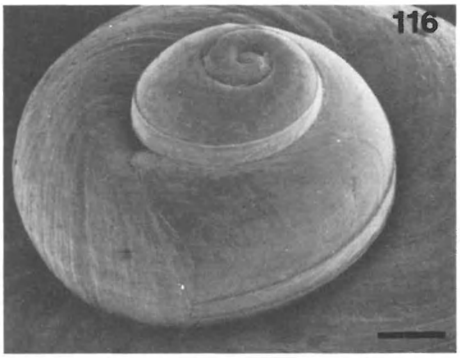
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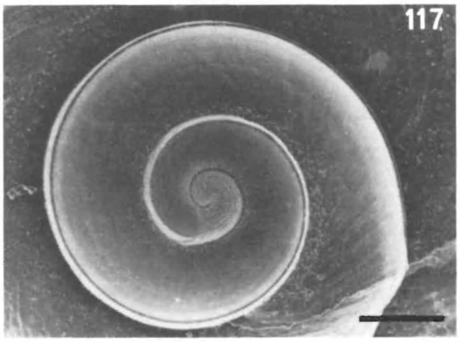
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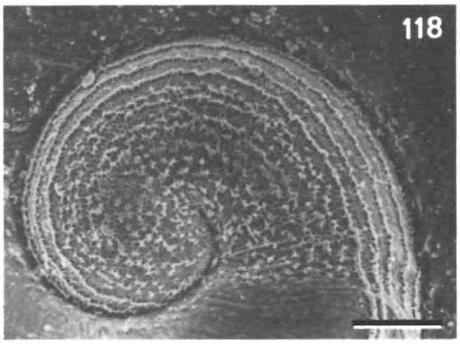
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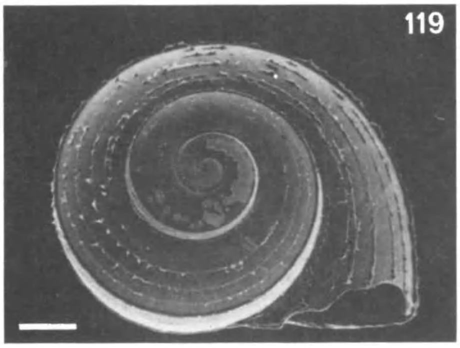
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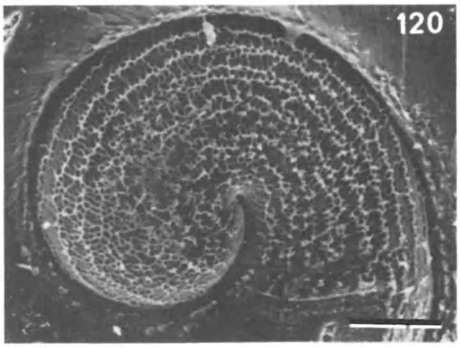
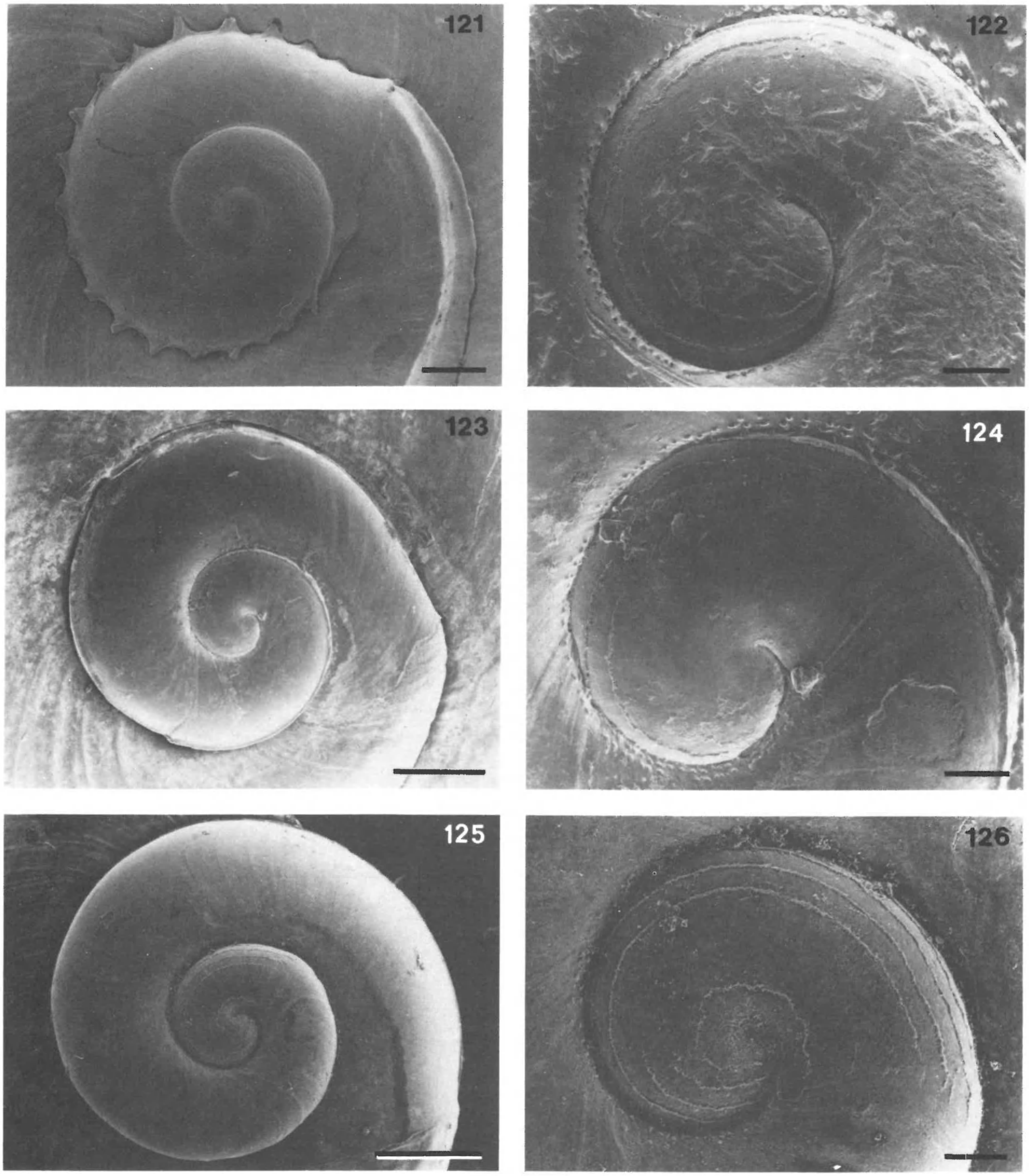

120

FIGS. 113-120. — Protoconchs of *Haloceras*. — **113,** *H. cingulata*, " *Thalassa* " stn Z435. — **114-115,** *H. cingulata*, SEAMOUNT stn CP30. — **116-118,** *H. laxa*, SEAMOUNT stn CP30. — **119-120,** *H. tricarinata*, " *Discovery* " stn 10141. Scale lines 250 µm (113-114, 116-117, 119) and 50 µm (115, 118, 120).



FIGS. 121-126. — Protoconchs of *Zygoceras*. — **121-122,** *Z. tropidophora*, holotype. — **123-124,** *Z. biocalae*, holotype. — **125-126,** *Zygoceras* sp., MONACO stn 683. Scale lines 250 µm (121, 123, 125) and 50 µm (122, 124, 126).

Zygoceras sp.

Figs 86-87, 125-126

Material examined. — **Eastern Atlantic.** Monaco, stn 683, Azores, 38°20'N, 28°05'W, 1550 m: 1 young sh (MOM).

Remarks. — A very characteristic juvenile with 0.6 postlarval whorl, which cannot be identified with any of the described species. Protoconch I, diameter 350 µm, has a sculpture of spiral cords on the nucleus and the abapical, coiled part, leaving a smooth adapical zone. Protoconch II, diameter 980 µm, is low-spired and has 1.25 whorls with only 2 keels instead of 3 as in *Haloceras*. One keel is visible above the suture, a second one concealed by the suture. The teleoconch has two strong keels at periphery.

IDENTIFICATION: SUMMARY OF LARVAL SHELL CHARACTERISTICS

The multispiral protoconch of the Haloceratidae offers very good characters for identification of the species. To facilitate comparisons, we have compiled the characteristics of all species below, arranged from the smallest to the largest larval shell.

Table 2. — Larval shell characteristics of Haloceratidae

	diameter(µm)		no.whorls prot.II		n
	range	mean	range	mean	
trichotropoides	610-700	657	1.0-1.05	1.04	8
spinosa	675-720	695	1.2-1.3	1.27	3
heliptyx	770	770	?		1
carinata	700-920	817	1.7-1.9	1.82	16
exquisita	870	870	2.1	2.1	1
phaeocephala	890-1060	967	1.8-2.0	1.87	6
acrocomata	940-1000	970	1.4-1.6	1.49	4
biocalae	1000	1000	1.25	1.25	1
galerita	1080	1080	2.1	2.1	1
laxa	980-1200	1118	1.7-1.8	1.76	8
rugosa	1100	1100	2.1	2.1	1
mediocostata	1200-1300	1240	2.0-2.1	2.06	5
tropidophora	1400-1450	1425	1.6-1.8	1.7	2
cingulata	1300-1660	1466	2.1-2.3	2.19	7
tricarinata	1500-2300	1930	2.2-2.6	2.42	9

Not entered in table: *japonica*, *millestriata*.

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