

ANATOMY, REPRODUCTIVE BIOLOGY AND SYSTEMATIC POSITION OF
FOSSARUS AMBIGUUS (LINNÉ) (FOSSARINAE: PLANAXIDAE;
PROSOBRANCHIA)

Richard S. Houbrick

Department of Invertebrate Zoology
National Museum of Natural History
Smithsonian Institution, Washington, D.C. 20560 U.S.A

ABSTRACT

The anatomy of *Fossarus ambiguus* (Linné, 1758), the type species of *Fossarus* Philippi, 1841, was examined for characters diagnostic of the family Fossaridae Troschel, 1861. This group was judged to be defined by several characters of non-familial significance. *Fossarus ambiguus* has dwarf males and is a probable protandric hermaphrodite; if so, this constitutes the only known example of this phenomenon among Cerithioidea. *Fossarus ambiguus* has a cephalic brood pouch of ectodermal origin from which embryos are released at the veliger stage. The brood pouch and many other anatomical characters of fossarids, especially those of the reproductive system, are shared with the family Planaxidae Gray, 1850. Within Planaxidae, fossarids comprise a subfamily, Fossarinae, defined by the following characters: 1) a turbinate shell with a large, umbilicate body whorl sculptured with strong spiral cords; 2) a heavily ciliated cephalic hood; 3) a wide ciliated strip on the dorsal surface of each tentacle; 4) a tightly organized nervous system with a very short supraesophageal connective; 5) dwarf males and possible protandry.

RESUMO

A anatomia de *Fossarus ambiguus* (Linné, 1758), a espécie tipo de *Fossarus* Philippi, 1841, foi examinada em busca de caracteres diagnosticantes da família Fossaridae Troschel, 1861. Julgava-se que este grupo era definido por caracteres de significado não familiar. *Fossarus ambiguus* possui machos anões e é provavelmente hermafrodita protândrico; assim sendo, este constitui o único exemplo deste fenômeno entre os Cerithioidea. *Fossarus ambiguus* possui uma bolsa incubadora cefálica de origem ectodérmica da qual os embriões são largados no estágio de velígeros. A bolsa incubadora e muitos outros caracteres anatómicos dos fossarídeos, especialmente os do aparelho reprodutor, são compartilhados com a família Planaxidae Gray, 1850. Dentro dos Planaxidae, os fossarídeos formam uma subfamília, Fossarinae, definida pelos seguintes caracteres: 1) concha turbinada com última volta grande, umbilicada, gravada com fortes cordões espirais; 2) capacet cefálico fortemente ciliado; 3) larga faixa ciliada na superfície dorsal de cada tentáculo; 4) sistema nervoso compactamente organizado, com o conectivo supraesofágico muito curto; 5) machos anões e possível protândria.

INTRODUCTION

The genus *Fossarus* Philippi, 1841, comprises a small group of poorly known, small-shelled species

of taenioglossate prosobranchs assigned to the family Fossaridae. The family was proposed by Troschel in 1861, on the basis of radular morphology, and has received little at-

tion since then. The sketchy history of the group has been summarized by Warén & Bouchet (1988: 75). Keen (1971: 453) remarked that fossarids had been long neglected by authors and noted that there was no single useful reference to the family. Fossarids do not comprise a large group and include several poorly known genera, some of uncertain affinities. Thiele (1929: 238) considered the Fossaridae to comprise the genera *Fossarus* Philippi, 1841; *Fossarella* Thiele, 1925; *Megalomphalus* Brusina, 1871; *Chilkaia* Preston, 1915; *Couthouyia* A. Adams, 1860; and with a query, *Pendroma* Dall, 1927, and *Conradia* A. Adams, 1860. The genera *Fossarella*, *Megalomphalus* and *Couthouyia* recently have been shown to belong to the Vanikoridae (Warén & Bouchet, 1988: 73, 94). *Fossarus* has been assigned to a number of superfamilies, and was originally considered a member of the Littorinidae (Littorinoidea) by Philippi (1841). This assignment was followed by Gray (1850), H. & A. Adams (1854: 319), Troschel (1861: 153), Tryon (1882: 245), and Fischer (1887: 711). The last author placed Fossaridae between Littorinidae and Solariidae (=Architectonicidae). More recently, authors have referred *Fossarus* to the superfamily Hippoicoidea (Thiele, 1929; Wenz, 1940; Taylor & Sohl, 1962; Boss, 1982). The Fossaridae was put in "stirps" Amaltheacea (=Hippoicoidea) after the aglossan gastropods and following the Pyramidellidae by Thiele (1929: 238). Wenz (1940: 879)

placed Fossaridae before Vanikoridae in the superfamily Hippoicoidea, between Pyramidelloidea and Calyptroidea. Ponder (1980) was the first to describe the cephalic brood pouch of *Fossarus* and to suggest a relationship with *Planaxis*. Although Boss (1987: 1004) assigned Fossaridae to Hippoicoidea, he noted Ponder's observation that the cephalic brood pouch of *Fossarus* is similar to that of members of the Planaxidae, and suggested a possible allocation to Cerithioidea. A Cerithioidean assignment has been advocated recently by Ponder & Warén (1988: 295), who cited the presence of open pallial gonoducts and apha-late males as further cerithioidean characters.

As seen above, systematic allocation of *Fossarus* has been diverse, conjectural, and largely without supporting evidence. As the internal anatomy of *Fossarus* and members of the component genera of fossarids has been unknown, the exact placement of the group among Caenogastropoda has been based only on shell characters and the poorly understood radula. The biology and anatomy of *Fossarus* species have, for the most part, never been described until recently, when Warén & Bouchet (1988: 77, figs. 3-4) presented a few notes about the ecology of *Fossarus ambiguus* from Corsica and illustrated some external anatomical features. Troschel (1861: 153-154, pl. 12, fig. 14) was the first to depict the radula of *Fossarus* species, but the figure is poor, and lacking in

details. Thiele (1925: 93, pl. 16, fig. 16) presented a better figure of the radula of *Fossarus ambiguus* (Linné), which shows more details of the tooth denticles, and compared the radula of *Fossarus* with those of a few other fossarid genera. Recently, Warén & Bouchet (1988) published the first SEM figures of the radula of *Fossarus ambiguus*. A short publication by Ponder (1980: 257) recorded the presence of a cephalic brood pouch in *Fossarus*, which was noted by Houbrick (1987: 38-39; 1988: 98) in his systematic survey of brood pouches among Cerithioidea.

It is obvious from the above history that a descriptive study of the anatomy of *Fossarus* is needed. Collection and study of large numbers of *Fossarus ambiguus* (Linné, 1758), the type-species of *Fossarus* Philippi by original designation (cited incorrectly as *Fossarus adansonii* Philippi, 1841), on the island of São Miguel, Azores plus examination of a few specimens of *Fossarus orbignyi* Fischer, 1864, from the Florida Keys, has resulted in the following description of the reproductive biology, ecology and anatomy of this poorly known prosobranch group.

MATERIALS AND METHODS

Living specimens of *Fossarus ambiguus* (Linné) were collected at Ponta da Pirâmide, São Miguel, Azores, where they were found in crevices of large boulders in a somewhat protected rocky, intertidal spit, which was exposed at low tide. Ad-

ditional specimens of *F. orbignyi* Fischer were collected under rocks at Big Pine Key, Florida, for comparison. Snails were kept alive in petri dishes filled with seawater and were relaxed in 7.5% MgCl₂ for study and dissection under a Wild M-8 dissecting microscope. Shells were cracked and animals removed for anatomical study and fixation for sectioning. Methylene blue solution was used to enhance examination of anatomical structures. Gametes and cellular structures were examined with a Leitz Laborlux D light microscope. Tissues were fixed in Bouin's Solution in seawater and 10% formalin and were embedded in paraffin, sectioned at 7 µm, and stained with Harris' hematoxylin and eosin for histological studies. Photomicrographs of sections were made with a Zeiss Photomicroscope III. Radulae, protoconchs and shell ultrastructure were examined with a Zeiss Nova-scans-30 scanning electron microscope. The term autpomorphic is used in reference to the characters set forth in *Cerithioidean Phylogeny* (Houbrick, 1988). All specimens of *Fossarus ambiguus* have been deposited as vouchers (USNM 859367).

DESCRIPTION

External anatomy. The shell of *Fossarus* (Fig. 1, A-D) is white and small, ranging up to 4 mm length, with a very short spire comprising four, strongly angulate whorls sculptured with spiral incised lines

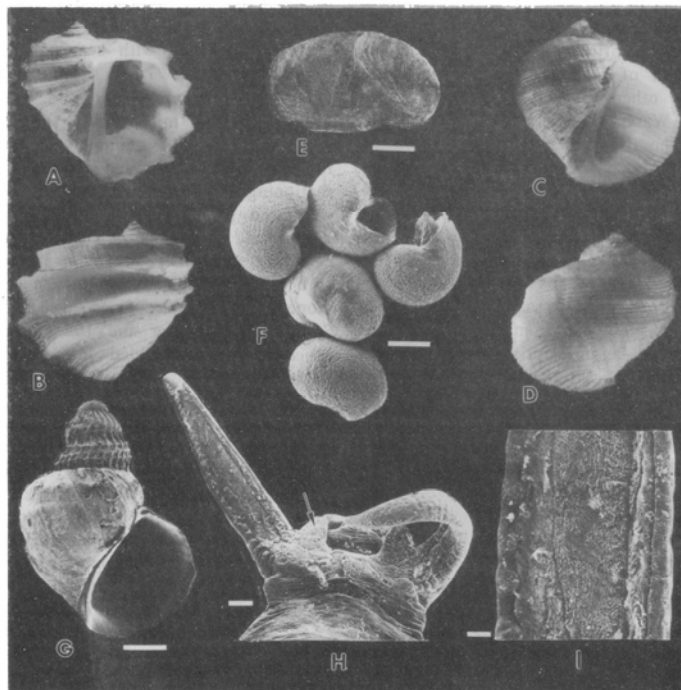


FIG. 1. *Fossarus ambiguus* (Linné), Ponta da Pirâmide, São Miguel, Azores, USNM 859367. A-B, apertural and dorsal views of strongly sculptured shell (3.2 mm length); C-D, apertural and dorsal views of weakly sculptured shell (3.6 mm length); E, operculum (bar = 0.6 mm); F, SEM of veliger stage embryonic shells removed from brood pouch prior to hatching (bar = 38 μ m); G, shell of male showing protoconch-2 reticulate sculpture (bar = 65 μ m); H, SEM of critical point dried head showing cephalic tentacles and heavily ciliated cephalic hood (arrow) (bar = 100 μ m); I, SEM of critical point dried dorsal portion of cephalic tentacle showing ciliated strip (bar = 20 μ m).

and 3-4 keel-like spiral cords. The body whorl is very large, umbilicate, and with a large, semicircular aperture with straight-sided columella and strongly crenulated outer lip. The protoconch is brown, and comprises three whorls; protoconch-1 is smooth, about one whorl; protoconch-2 comprises two strongly cancellate whorls and has a deep sinuigeral notch. The operculum (Fig. 1, E) is corneous, lenticular, has a terminal nucleus and tightly fits the shell aperture.

The animal is translucent white except for an opaque white spot on the "horns" between the cephalic tentacles. The animal comprises about 1.5-2 whorls and is loosely coiled in external aspect (Fig. 2, B-C), having a foot with a very broad sole (Fig. 2, A) and a large, lenticular operculum (Fig. 1, E). The sole of the foot is triangular, narrow anteriorly and with a thin, crescent-shaped, propodial mucus gland (Fig. 2, A, amg), which is not very deep. The mid- and posterior foot (sole) is longitudinally furrowed. Debris and mucus leaving the mantle cavity move down the right side of the foot and collect at the extreme posterior end of the foot before dislodgement. The head protrudes from the body on a long, somewhat narrow neck and is distinctive in having very long, broad cephalic tentacles, each with a lobe ("horn") at its inner base, forming a cephalic hood (Figs. 1, H; 2, B, C, D, cr). The cephalic hood is heavily ciliated (Fig. 1, H), but the exact function of this ciliated area

is unknown. The tentacles are directed laterally, at 45 degrees to the head and are moved up and down to alternately touch the substrate when the animal is crawling. Cephalic tentacles are concave-flat on their dorsal surfaces; but rounded and convex on their ventral sides (Fig. 1, H). Densely packed compound cilia on the dorsal surface of the tentacles (Figs. 1, I; 2, B, D, cts) produce a strong, posteriorly directed ciliary beat, leading toward the mantle cavity. A tiny black eye lies at the junction of each tentacle base and the neck. Beneath the heavily ciliated cephalic hood a short snout (Fig. 2, B-D, sn) with bilobed tip extends ventrally. In brooding females the neck beneath the snout and the back (dorsal surface of head) are swollen and distended due to the large cephalic brood pouch (Figs. 2, B, C, D; 4, A-B, bp) filled with embryos. The edge of the mantle is smooth, with a weakly scalloped, wavy edge. It is extremely short on its ventral side, nearly fused to the columellar muscle. The mantle is thick and strongly reflexed at the exhalant siphonal area (Fig. 2, B, exh). In the short visceral mass, the cream-colored gonad partially covers the darker digestive gland (Fig. 2, C, dg), and the tan kidney (Fig. 2, C, K) appears to comprise only one lobe.

Mantle cavity organs. The mantle cavity is broad, but not deep. The osphradium (Fig. 2, D, os), located in the anterior mantle cavity, comprises a simple ridge flanked on each

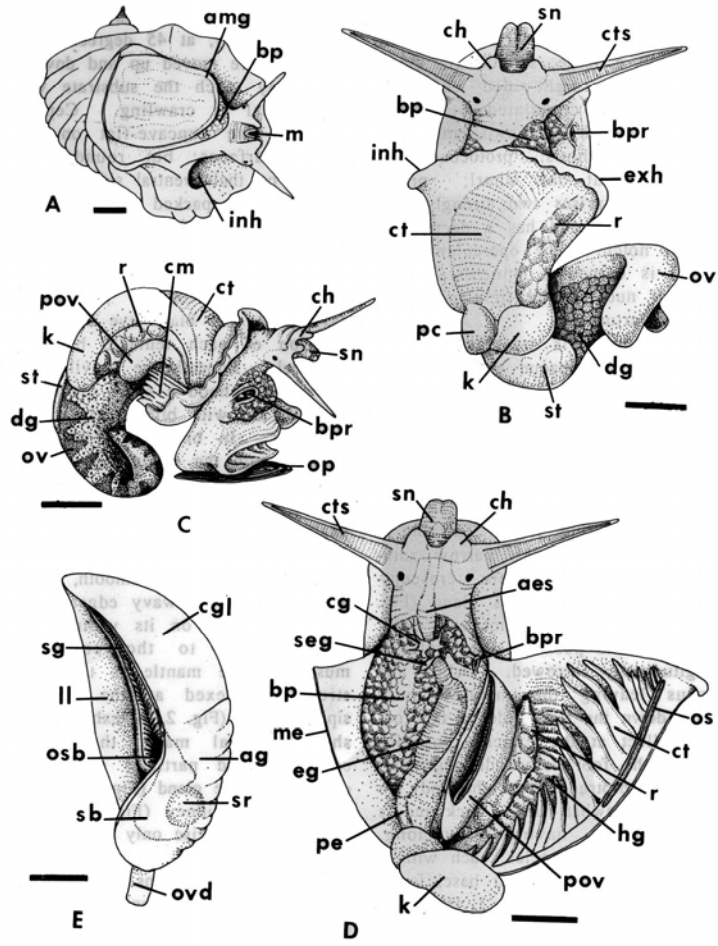


FIG. 2. Anatomy of *Fossarus ambiguus* (Linné). [Legends in following page]

side by a raised ciliated strip, and is a little less than one-half the ctenidial length. The ctenidium (Fig. 2, D, ct) is formed of 35-40 long finger-like lamellae with narrow bases. The hypobranchial gland (Fig. 2, D, hg) is well developed and comprised of heavy, transverse, glandular folds, visible through the mantle epithelium. The mantle cavity is relatively shallow, its posterior half partially overlain by the kidney. The rectum (Fig. 2, D, r) is a wide tube filled with large, oval-spherical, loosely-packed fecal pellets. The pallial gonoduct (Fig. 2, D, pov) is an open tube comprised of an inner, attached lateral lamina and an outer, free, medial lamina.

Reproductive system. Only the very smallest individuals (0.4-0.8 mm) are males; all others, including small snails, are functional females with ripe ovaries and brood pouches containing embryos. Gonads are the same white color in both sexes, but in females the large eggs may be seen through the ovarian epithelium. Very small males occur on the shells of females, as in *Crepidula* species, and suggest that *Fossarus* is a prot-

andric hermaphrodite. Squashes of living gonadal tissue from these very small snails revealed viable sperm, but only euspermatozoa were seen. These were of the general morphology typical of cerithioideans (Hcaly, 1988). Histological sections confirm that very small individuals are males. Males are aphyllate and the male pallial gonoduct is a simple open tube, with no glandular areas. The female pallial oviduct (Fig. 2, E) is open along most of its length, but the posterior part is closed over by the folded edge of the medial lamina. The anterior two-thirds of both laminae, including the oviductal groove, are composed of thin, non-glandular epithelium, and the lateral lamina (Fig. 2, E 11) is very thin along its entire length. The posterior portion of the oviductal groove of the medial lamina is highly glandular and probably comprises the albumen gland (Fig. 2, E, ag). A long sperm gutter (Fig. 2, E, sg) lies along the edge of the medial lamina and opens into a large bursa (Fig. 2, E, sb), which appears to be homologous with the spermatophore bursa of other cerithioideans. The bursa is located in the posterior part of the

FIG. 2. Anatomy of *Fossarus ambiguus* (Linné). A, animal emerging from shell showing sole of foot and mouth (bar = 0.25 mm); B, dorsal view of animal removed from shell (bar = 0.25 mm); C, right lateral view of animal showing brood pore opening in side of neck (bar = 0.35 mm); D, mantle cut open and folded to right exposing mantle cavity organs (bar = 0.25 mm); E, pallial oviduct (bar = 0.50 mm). aes, anterior esophagus; ag, albumen gland; amg, anterior pedal mucus gland; bp, brood pouch; bpr, brood pore; cg, cephalic ganglion; cgl, capsule gland; ch, cephalic hood; cm, columellar muscle; ct, ctenidium; cts, ciliated tentacular strip; dg, digestive gland; eg, esophageal gland; exh, exhalant siphon; hg, hypobranchial gland; inh, inhalant siphon; k, kidney; ll, lateral lamina; m, mouth; me, mantle edge; op, operculum; os, osphradium; osb, opening to spermatophore bursa; ov, ovary; ovd, coelomic oviduct; pc, pericardium; pe, posterior esophagus; pov, pallial oviduct; r, rectum; sb, spermatophore bursa; seg, supra-esophageal ganglion; sg, sperm gutter; sn, snout; sr, seminal receptacle; st, stomach.

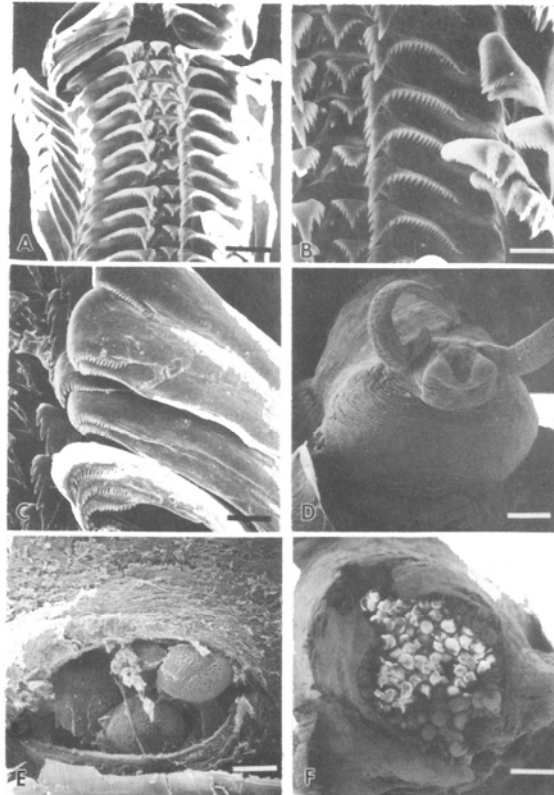


FIG. 3. Radular and brood pouch morphology. A, section of radula with marginal teeth spread back (bar = 21 μ m); B, detail of rachidian and lateral teeth (bar = 10 μ m); C, detail of marginal teeth (bar = 10 μ m); D, anterior view of critical point dried female showing neck swollen by enlarged cephalic brood pouch (bar = 0.25 mm); E, distended brood pore showing emerging veliger larvae (bar = 38 μ m); F, break in body wall behind head of critical point dried female showing many advanced larvae in cephalic brood pouch (bar = 0.22 mm).

medial lamina. In the medial lamina wall, adjacent to the bursa, is a circular seminal receptacle containing oriented sperm (Fig. 2, E, sr). A ciliated tract leads from the anterior of the pallial oviduct down the right side of the foot to the brood pore (Fig. 2, B, C, D; 4, A-B, D, bpr), a small slit in the side of the neck, close to the edge of the sole. The brood pore may gape when the cephalic brood pouch is filled with veliger stage larvae (Figs. 3, D-E; 4, C). The cephalic brood pouch may be regarded as an accessory extension of the pallial oviduct, but external to the mantle cavity. The cephalic brood pouch is a very large ectodermal invagination in the head-foot, and is finely ciliated internally. It extends from the muscular brood pore (Fig. 4, D, bpr) in the right side of the neck, under the head and buccal mass (Fig. 4, D, bm) and its cavity and up the left side of the head-foot (Fig. 4, E) to the dorsal posterior surface of the body (Figs. 2, B, D, bp; 4, F) where it occupies nearly all of the animal's body, exclusive of the columellar muscle (Fig. 3, F). The brood pouch becomes large, swollen and distended when filled (Figs. 3, D; 4, C), and may contain large numbers of embryos (up to 2,000), all of which appear to share the same stage of development and presumably belong to the same cohort. Most of the brood pouch lies just beneath the thin, nearly transparent epithelium of the neck and back (Fig. 4, E, F) through which may be seen the nerve ring (Figs. 2, D, cg; 4, A, bp) and

midsophageal gland (Figs. 2, D, eg; 4, F, es), which are displaced by it markedly to the right (Fig. 4, F, es, cg). Early developing eggs and embryos appear white, becoming orange as they approach the veliger stage due to the color of the aperture of the developing protoconch. Each embryo is surrounded by a thin transparent hyaline capsule (Fig. 4, E, arrow). When the veliger stage is attained, embryos are released from the brood pore by a strong muscular contraction of the head-foot, after which they shed their hyaline capsules and become active, free-swimming larvae. Larvae have full velar lobes and beating cilia. Newly hatched larval shells (protoconch-1) have a pitted surface (Fig. 1, F), but are unsculptured and have an orange columella and lip edge.

Alimentary system. A pair of lateral jaws lies at the tip of the mouth on the bifid snout. The very small radula (Fig. 3, A-C) is taenioglossate (2+1+1+1+2) and a little over one-third the shell length. The rachidian tooth (Fig. 3, B) is trapezoidal in overall shape, having a cutting edge forming a triangular, pointed cusp serrated with about 8-9 pointed denticles on each side; a flat basal plate is strengthened on each side by a lateral ridge bearing a denticle. The lateral tooth (Fig. 3, B) is rod-shaped with a very long lateral extension of the broad, flat basal plate. The cutting edge of the lateral tooth has about 12 very small pointed denticles on its outer side and a long

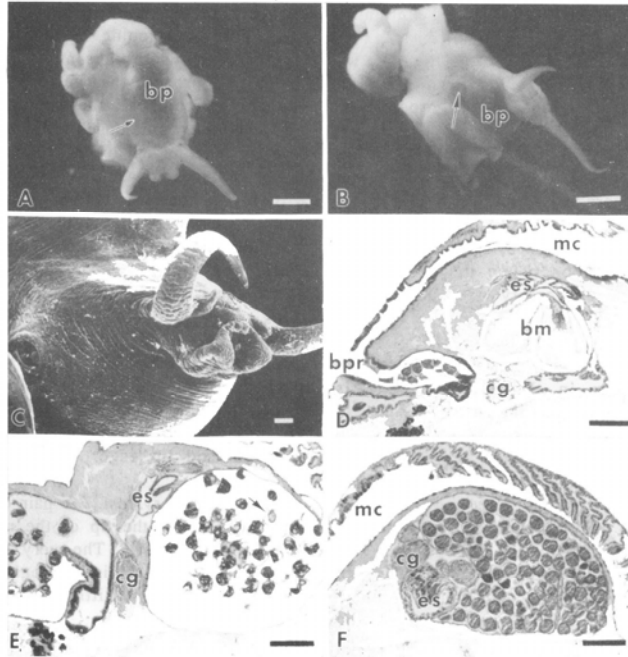


FIG. 4. Morphology of brood pouch. A, dorsal view of animal removed from shell showing embryos in brood pouch (bp) under thin neck epithelium and displacement of nerve ring (arrow) to right (bar = 0.25 mm); B, right lateral view of animal showing location of brood pore (arrow) on right side of neck and brood pouch (bp) under head (bar = 0.25 mm); C, right lateral view of critical point dried specimen showing brood pore on right side of neck and swollen neck due to filled brood pouch (bar = 100 μ m); D, frontal section of head-foot and mantle cavity (mc) showing brood pore (bpr) on right side of neck, and cerebral ganglion (cg) beneath esophagus (es) and buccal mass (bm) (bar = 0.17 mm); E, frontal section through head-foot showing location of brood pouch under head as it passes under nerve ring (cg) and dorsally to esophagus (es); note veliger-stage embryos in brood pouch, each within its own hyaline capsule (arrow) (bar = 0.17 mm); F, frontal section through mid-esophagus showing dorsal location of brood pouch filled with early embryos and displacement of cerebral ganglion (cg) and mid-esophagus (es) to right (bar = 0.17 mm).

pointed major cusp with 3-4 denticles on its inner side. The marginal teeth (Fig. 3, C) are long and spatulate having broad tips with fine serrations on their outer surfaces, a small pointed denticle and more fine serrations along the top edge of the tooth. The anterior esophagus (Figs. 2, D, aes; 4, D-E, es) has a typical dorsal food channel. The paired salivary glands are thin tubes that run through the nerve ring. The mid-esophagus enlarges behind the nerve ring to become a wide esophageal gland (Figs. 2, D, eg; 4, F, es) which has many internal transverse ridges. The stomach is large, about two-thirds the length of a whorl and when opened by a dorsal longitudinal cut is seen to have a style sac with prominent gastric shield, a large central ridge and a right sorting area. The wide esophageal opening is on the right side and there is a single duct to the digestive gland. The style sac appears to be separate from the intestine. The rectum (Fig. 2, D, r) in the pallial cavity is a wide, thick tube containing large ovoid fecal pellets.

Nervous system. The nervous system is epiathroid, and distinctive in that both esophageal ganglia (Fig. 2 D, seg) are very close to the cerebral (Fig. 2, D, cg) and pleural ganglia, and there is virtually no supra-esophageal connective. Each pedal ganglion has a prepedal swelling with a single distinct statolith in a statocyst attached to the ganglion. The cerebral-pedal connectives are

10 times as long as the short cerebral connectives. The connective between the pedal ganglia is a few times longer than the cerebral connectives. Three small nerves, the middle one being largest, emerge from each pedal ganglion and extend to the anterior foot terminating in a tiny ganglion which sends forth branches innervating the walls of the brood pouch. As mentioned earlier, the nerve ring is displaced markedly to the right (Fig. 4, A, arrow, F, cg) when the cephalic brood pouch is filled with embryos.

DISCUSSION

Ecology. In the Azores, *Fossarus ambiguus* lives intertidally in dark crevices of the undersides of large boulders and rocks along protected parts of the coast. It frequently occurs in groups or colonies, many individuals being crammed into one tiny crack or crevice. Warén & Bouchet (1988: 76) described a similar habitat in Calvi, Corsica, and suggested that *Fossarus* colonies may spend their entire lives in the same cavities, as these often lack exits large enough for the snails to emerge. All age classes are found together: one sample taken from a boulder hole in the Azores comprised 113 individuals.

There is considerable intraspecific variation in shell sculpture among a population, ranging from strongly sculptured phenotypes (Fig. 1, A-B) to very smooth individuals (Fig. 1, C-D). The very smallest

snails (0.4-0.8 mm) occur on the shells of large females and are all functional males (Fig. 1, G). Small to large individuals (0.9 - 5 mm) are functional females with brood pouches and embryos, and comprise most of the population. The large, elaborately sculptured protoconch-2, on the apex of large, adult shells (Fig. 1, G), indicates that hatched veliger larvae undergo a long-term planktotrophic stage prior to settlement. An identical protoconch has been illustrated for *Fossarus ambiguus* from Calvi, Corsica, by Warén & Bouchet (1988: 76, fig. 2).

The western Atlantic species, *Fossarus orbignyi* Fischer, is anatomically identical with *F. ambiguus* and is probably conspecific with it.

It is probable that *Fossarus* is a protandrous hermaphrodite, a reproductive strategy which fits well with their gregarious life style. However, the possibility that the small males may be permanent, mature male dwarfs should not be overlooked. This kind of habitat and life style are unusual among cerithioideans.

Systematics. Among cerithioideans, *Fossarus* shares with *Modulus* the distinction of having a turbinated shell, although the aperture is much wider and longer in *Fossarus*. Wide shell apertures and the presence of tiny males on the shells of larger females are also seen in hipponicids and calyptraeids, probably explaining why fossarids were previously included with these groups by most authors. Ponder (1980) and Boss

(1982: 1004) were the first to suggest that this relationship might be incorrect. The superfamily Hipponicoidea had been previously thought to embrace four families; the Hipponicidae, Vanikoridae, Caledoniellidae and Fossaridae (Boss, 1982: 1003). It is now apparent that *Fossarus* is significantly different in anatomical layout from all known hipponicid groups; consequently, it should be unequivocally excluded from Hipponicoidea. Ponder & Warén (1988: 295) recently transferred Fossaridae from Hipponicoidea to Cerithioidea, and suggested close relationship to the Planaxidae, on the basis of unpublished anatomical characters. It is clear from the detailed anatomical study of *Fossarus ambiguus* presented above that their action was correct and well-justified. The presence of open pallial gonoducts, aphallate males, and a brood pouch of ectodermal origin indicate an assignment to the superfamily Cerithioidea (see Houbrick, 1988). Among cerithioideans, *Fossarus* is the only known genus to exhibit possible protandrous hermaphroditism.

The placement and structure of the brood pouch of *Fossarus* is a feature shared in common with many other groups of cerithioideans (Houbrick, 1987: 38-39; 1988: 98). The brood pouch of *Fossarus* is nearly identical to that observed in members of the Planaxidae Gray, 1850 (Houbrick, 1987), such as *Planaxis* Lamarck, 1822, and in particular to members of the genus *Sup-*

planaxis Thiele, 1929. Release of larvae at the veliger stage and subsequent planktotrophic development are also common to the Planaxidae. The brood pouch of *Fossarus* also closely resembles that of *Tanganika rufifilosa* (E. A. Smith, 1880), of the freshwater Thiaridae (Moore, 1899: 160-161). Morphological similarities in brood pouch anatomy between the Planaxidae and Thiaridae have been noted previously (Houbrick, 1988), suggesting additional affinity with *Fossarus*. The layout of the sperm gutter, bursa and seminal receptacle in the pallial oviduct of *Fossarus* is very similar to the pattern observed in members of some other cerithioidean genera such as *Cerithium* Bruguière, 1789, and *Planaxis* Lamarck, 1822.

The data presented above indicate that *Fossarus* has close affinity to planaxids. The lenticular operculum, shape and movement of the cephalic tentacles, presence and layout of the brood pouch, tiny ganglia on the anterior nerve extensions of the pedal ganglia, larval ecology, paired denticles on the basal plate of the rachidian tooth, and the broad, spatulate, finely serrated tips of the marginal teeth are characters shared with members of the Planaxidae Gray, 1850, and suggest that fossarids comprise a subfamily, Fossarinae, within that family. The Fossarinae is diagnosed by three autapomorphic characters. These include: 1) a heavily ciliated cephalic hood; 2) a wide ciliated strip on the dorsal surface of each cephalic tentacle; 3)

dwarf males and possible protandry. The small turbinate shell with large body whorl and aperture, tightly organized ganglia comprising the nerve ring, and the very short supraesophageal connective, are also distinctive characters, although not unique to fossarids.

ACKNOWLEDGEMENTS

I thank Dr. António Frias Martins for the use of equipment and facilities and for logistic support in the field. This study was supported by a grant of the Portuguese University of the Azores and the Sociedade de Estudos Açorianos "Afonso Chaves". I am grateful to Julia Piraino, Smithsonian Marine Station at Link Port, who assisted with the critical point drying apparatus. The staff of the Smithsonian Scanning Electron Microscope Laboratory, National Museum of Natural History, assisted with the SEM micrographs. I thank Beth Fricano, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, for assistance with histology. Paula Mikkelsen, Harbor Branch Foundation, critically read the final draft of the manuscript. This is Smithsonian Marine Station contribution No. 231.

LITERATURE CITED

- ABBOTT, R. T., 1954. *American Seashells*, 40 plates, 541 pages, illustrated. New York.

- ADAMS, A., 1860. On Some New Genera and Species of Mollusca from Japan. *Annals and Magazine of Natural History*, series 3, 5: 299-303; 405-413.
- ADAMS, H. & A., 1853-1858. *The Genera of Recent Mollusca*, vol. 1: 484 pages. London
- BOSS, K. J., 1982. Mollusca. In: S. P. PARKER, (Ed.), *Synopsis and Classification of Living Organisms*, Vol. 1: 945-1166. McGraw-Hill, New York.
- BRUSINA, S., 1871. Saggio dalla Malacologia Adriatica. *Bollettino Malacologico Italiano*, 4: 5-9
- DALL, W. H., 1927. Diagnosis of Undescribed New Species of Mollusks in the Collection of the United States National Museum. *Proceedings of the United States National Museum*, 70(2668): 1-11.
- FISCHER, P., 1880-1887. *Manuel de Conchyliologie et de Paléontologie Conchyliologique ou Histoire Naturelle des Mollusques Vivantes et Fossiles*, 1369 pages, 23 plates. Paris.
- GRAY, M. E., 1850. *Figures of Molluscan Animals, Selected from Various Authors*. Vol. 4, Explanation of Plates and List of Genera, 124 pages. Longmans, London.
- HEALY, J. M., 1988. Sperm Morphology and its Systematic Importance in the Gastropoda. *Malacological Review*, 1988, Supplement, 4: 251-266.
- HOUBRICK, R. S., 1987. Anatomy, Reproductive Biology, and Phylogeny of the Planaxidae (Cerithiacea: Prosobranchia). *Smithsonian Contributions to Zoology*, No. 445: iii+57 pp., 27 figs.
- HOUBRICK, R. S., 1988. Cerithioid Phylogeny. *Malacological Review*, 1988, Supplement, 4: 88-128.
- KEEN, A. M., 1971. *Sea Shells of Tropical West America*, 2nd Ed, 1064 pp., 22 pls. Stanford.
- LAMARCK, J. P. B. A., 1822. *Histoire Naturelle des Animaux sans Vertèbres...* Vol. 7, 711 pp. Paris.
- LINNE, C., 1758. *Systema naturae sive regna tria naturae...* editio decima, reformata. Vol. 1 (Regnum Animale). Stockholm.
- MOORE, J. E. S., 1899. The Molluscs of the Great African Lakes. III. *Tanganyikia rufofilosa*, and the genus *Spekia*. *Quarterly Journal of Microscopical Science*, vol. 42: 155-185.
- PHILIPPI, R. A., 1841. Zoologische Bemerkungen. *Fossarus*, ein neues Genus der Kammkiemigen Mollusken. *Archiv für Naturgeschichte*, 7(1): 42-49, pl. 5.
- PONDER, W. F., 1980. Cephalic Brood Pouches in *Planaxis* and *Fossarus* (Fossaridae and Planaxidae, Cerithiacea, Gastropoda). *Journal of the Malacological Society of Australia*, 4 (4): 257-258.
- PONDER, W. F. and A. WARÉN, 1988. Classification of the Caenogastropoda and Heterostropha — a List of the Family Group Names and Higher Taxa. *Malacological Review*, 1988, Supplement, 4: 288-326.

- PRESTON, H. B., 1915. A Further Report on Mollusca from Lake Chilka on the East Coast of India. *Records of the Indian Museum*, part 3, 11 (15): 289-310.
- TAYLOR, D. W. and N. SOHL, 1962. An Outline of Gastropod Classification. *Malacologia*, 1: 7-32.
- THIELE, J., 1925. *Gastropoda der Deutschen Tiefsee-Expedition*, 2 Prosobranchia, 348 pp., 34 pls.
- THIELE, J., 1929. *Handbuch der Systematischen Weichtierkunde*. Part 1: 376 pp. Jena.
- TROSCHEL, F. H., 1856-1863. *Das Gebiss der Schnecken zur Begründung einer natürlichen Classification*, vol. 1: 661 pp., 32 pls. Berlin.
- TRYON, G. W., 1882. *Structural and Systematic Conchology*, 1: 453 pp., 140 pls.
- WARÉN, A. and P. BOUCHET, 1988. A new Species of Vanikoridae from the Western Mediterranean, with Remarks on the Northeast Atlantic Species of the Family. *Bollettino Malacologico*, 24 (5-8): 73-100.
- WENZ, W., 1938-1944. *Gastropoda*, Teil 1: Allgemeiner Teil und Prosobranchia. In: SCHINDEWOLF, (Ed.), *Handbuch der Paläozoologie*, 6: vi+1639 pp., illustrated. Be.lin.