

COMPARATIVE ANATOMY OF FOUR PRIMITIVE MURICACEAN GASTROPODS: IMPLICATIONS FOR TROPHONINE PHYLOGENY

M. G. HARASEWYCH
DEPARTMENT OF INVERTEBRATE ZOOLOGY
NATIONAL MUSEUM OF NATURAL HISTORY
SMITHSONIAN INSTITUTION
WASHINGTON, D.C. 20560, U.S.A.

ABSTRACT

The main features of the shell, head-foot, pallial complex, alimentary and reproductive systems of *Trophon geversianus* (Pallas), *Boreotrophon aculeatus* (Watson), *Paziella pazi* (Crosse), and *Nucella lamellosa* (Gmelin) are described, and phenetic and cladistic analyses based on subsets of these data presented. Similarities in shell morphology revealed by phenetic studies are interpreted as being due to convergence, and are indicative of similar habitats rather than of close phylogenetic relationships. Convergences are also noted in radular and stomach characters. Cladistic analyses of anatomical data support the following conclusions: 1) Thaididae are a primitive and ancient family of muricaceans forming a clade equal in taxonomic rank with Muricidae; 2) Within Muricidae, *P. pazi* more closely resembles the ancestral muricid phenotype than any trophonine; 3) Trophoninae comprise a comparatively recent monophyletic group with differences due to a subsequent austral adaptive radiation.

The Muricidae are considered to be the most primitive family within Neogastropoda according to most (Thiele, 1929; Wenz, 1941; Taylor and Sohl, 1962; Boss, 1982) but not all (Golikov and Starobogatov, 1975) recent classifications. Of the five subfamilies of Muricidae, the Trophoninae, proposed by Cossmann (1903) on the basis of shell and opercular characters to include a number of boreal and austral species, are the most poorly understood. The systematic status and affinities of the Trophoninae have been the subjects of varying interpretations. Ponder (1973) considered this group to be the most primitive subfamily of the Muricidae, while Vokes (1971) suggested that at least some trophonines are descended from an early muricine lineage. Cossmann (1903) and Bouvier (1888) both considered Trophoninae to be intermediate between Muricinae and Thaididae.

In the most recent systematic revision of the Muricidae, Radwin and D'Attilio (1976:13) consider the Trophoninae "a subfamilial category for the sake of convenience," and note (1976:2) that "within the Trophoninae, relationships and even species delimitations are so poorly understood, . . . , that we have attempted nothing beyond describing and illustrating the type species of the more plausible genera". These authors (1976) transferred several genera (eg. *Austrotrophon* Dall, 1902; *Zaccatrophon* Hertlein and Strong, 1951) from the Trophoninae to the Thaididae on the basis of radular characters, and appear to support the hypothesis that Trophoninae are polyphyletic, citing (Radwin

and D'Attilio, 1976:13) a personal communication from E. H. Vokes "it appears likely that the most northern trophons are derived from the *Paziella-Poirieria* line, and that the several austral forms that are unquestionably "trophonine" are probably derived from the Thaididae".

Thus, according to most published work, the Trophoninae are in a position to shed light on the systematics and the primitive morphology of the Muricacea. Taxonomic works on this group have been few, and these limited to studies of the morphologies of the shell, operculum and, in some cases, radulae (Strebel, 1904; Powell, 1951; Ponder, 1972; Houart, 1981).

What little is known of trophonine anatomy is limited to portions of the alimentary, reproductive and nervous systems of a handful of species (Bouvier, 1888; Eales, 1923; Taki, 1938; Smith, 1967; Houston, 1976). In contrast, the spawn and/or early development of over a dozen species have been studied (Jeffreys, 1867, Melvill and Standen, 1898; Strebel, 1904; Hedley, 1917; Lamy, 1928; Lebour, 1936; Thorson, 1940, 1946; Fioroni, 1966; Zaixso, 1973; Penchaszadeh, 1976; Picken, 1979).

The present study has as its objectives to present accounts of the anatomy and shell morphology of: 1) *Trophon geversianus* (Pallas, 1774), the type species of the type genus of Trophoninae, and an example of an intertidal austral species, 2) *Boreotrophon aculeatus* (Watson, 1882), an example of a bathyal "northern trophon", 3) *Paziella pazi* (Crosse, 1869) a primitive muricine from a line hypothesized

to be ancestral to Trophoninae, and 4) *Nucella lamellosa* (Gmelin, 1791) an intertidal boreal example of the Thaididae, and on the basis of these data, to investigate the phylogenetic relationships between these taxa using phenetic and cladistic techniques.

MATERIALS AND METHODS

The following preserved material was used in this study:

Trophon geversianus 3 ♂ and 2 ♀ Intertidal rocks, Puerto Basil Hall, Isla de los Estados, Tierra del Fuego, Argentina (54°45.45'S, 64°10.1'W) USARP-SOSC-R/V HERO (LACM 71-289) 2 ♂ and 1 ♀ Puerto Madryn, Argentina (USNM 841239) 2 ♀ Punta Arenas, Chile (ANSP A9442)

Boreotrophon aculeatus 7 ♂ and 4 ♀ COLUMBUS ISELIN sta. C1-161, Tongue of the Ocean, Bahamas (23°40'N, 77°06'W) in 1370 meters. (voucher specimens USNM 841240)

Paziella pazi 1 ♂ and 1 ♀ PILLSBURY sta. P-984, W. of Anguilla, Leeward Islands (18°26.4'N, 63°12.6'W) in 421–439 meters. (voucher specimen USNM 841241)

Nucella lamellosa 4 ♂ and 2 ♀ Intertidal rocks, Deception Pass, Fidalgo Island, Puget Sound, Washington (USNM 841242)

Dry material from the USNM collections was used to supplement shell measurement data.

Specimens for anatomical studies were immersed in 10% hydrochloric acid (HCl) until the shells dissolved. Soft parts were rinsed in distilled water and returned to 70% ethanol for dissection. Dry shells were cracked in a vise in order to examine internal surfaces. Scanning electron micrographs were taken using a Cambridge 100 SEM. Phenetic analyses were conducted using mean values of the 13 continuous variables listed in table 1. Characters include eight morphometric descriptors of generalized shell shape (Harasewych, 1982) and five morphometric and sculptural parameters. The CLUSTAN cluster analysis program (Wishart, 1978) was used to standardize the data so that each character had a mean of zero and a standard deviation of one, to produce a matrix of inter-taxa distances using squared Euclidian distance, and to generate phenograms using both unweighted pair-group arithmetic averaging (UP-GMA) and Ward's method (error sum of squares) clustering algorithms.

Cladistic analysis is based on 15 qualitative anatomical characters. Character polarizations are based on the criterion of outgroup comparison. Discussion of the choice of outgroups requires a review of the taxonomy of rachiglossan gastropods. The majority of the literature (as exemplified by Taylor and Sohl, 1962) divides the suborder Rachiglossa into three superfamilies: Muricacea, Buccinacea and Volutacea. Ponder (1973) includes all rachiglossan gastropods in one superfamily, the Muricacea, recognizing 17 families as "more-or-less equally distinct." The present paper uses the

Table 1. Shell characters used in phenetic analyses of relationships between muricacean taxa. Characters 1 through 8 describe geometry of the generalized shell form (Harasewych, 1982).

1. Shape of the generating curve of the body cavity (Sbc)
2. Shape of the generating curve of the siphonal canal (Ssc)
3. Relative siphonal length (Rsl)
4. Siphonal angle (beta)
5. Rate of whorl expansion (W)
6. Angle of the generating curve (theta)
7. Position of the generating curve relative to the axis (D)
8. Rate of whorl translation (T)
9. shell length (L)
10. shell width/shell length (W/L)
11. aperture length/shell length (AL/L)
12. Number of whorls of teleoconch (# whorls)
13. Number of varices/lamellae on the final whorl (# var)

earlier classification, recognizing Muricacea, Buccinacea and Volutacea as subgroups of Rachiglossa, although not strongly advocating superfamily status for each group. Muricacea is used in the sense of Radwin and D'Attilio (1971) with the exception that Columbariidae has been transferred to Volutacea (Harasewych, 1983). As it is unclear whether Buccinacea or Volutacea is more closely related to Muricacea, and as neither group has all the characters used in this study, both are used for outgroup comparison. The tendency toward parallelism in the evolution of the major organ systems within Rachiglossa has been well documented (Ponder, 1973). In several cases both primitive and presumably convergently derived characters are present in some outgroups. In such instances the character states of the most primitive members of the outgroups, as determined from existing taxonomic works, were considered to be primitive. The Wagner 78 program (Farris, 1970; Wiley, 1981) was used to generate a Wagner Tree of the 4 taxa. The Largest Clique Program, version 2.0 of Felsenstein was used to analyze compatibility of the anatomical characters. Results of these analyses are then compared with ecological data and with evidence from the fossil record, and a most parsimonious phylogenetic classification is proposed.

Some of the data used for character polarizations are based on unpublished observations and are identified by the writer's initials following such information.

The repositories of figured and examined specimens are indicated by the following abbreviations:

- ANSP Academy of Natural Sciences, Philadelphia
- BM(NH) British Museum (Natural History)
- LACM Los Angeles County Museum of Natural History
- MCZ Museum of Comparative Zoology
- USNM National Museum of Natural History, Smithsonian Institution

RESULTS

MORPHOLOGY

Trophon geversianus (Pallas, 1774)
(Figs. 1–3, 15, 19–25)

This is the type species of the genus *Trophon* Montfort, 1810 (as *Murex magellanicus* Gmelin, 1791) by original designation. The fate of the subfamilial name Trophoninae, therefore, is dependent on the systematic position of this species. *Trophon geversianus* is common intertidally and subtidally in the Magellanic region. Shell morphology is very variable, the numerous morphs having been amply figured by Strebel (1904), who also included and extensive synonymy.

Shell morphology: Shell large (to 90 mm), moderately thin, globosely fusiform (Figs. 1,2). Protoconch (Fig. 15) of 1¼ whorls, inflated, glassy, pitted. Transition to teleoconch abrupt, marked by appearance of spiral and axial sculpture. Teleoconch with up to 6 inflated whorls. Spire angle 58–91°. Axial sculpture of 16–21 lamellae per whorl. These may be flaring (Fig. 1) or smooth and barely perceptible (Fig. 2), especially in young or eroded specimens. Spiral sculpture of 12–20 cords on the last whorl and 4–6 on the penultimate whorl, with 0–1 fine threads between. Suture abutted, shoulder rounded to tabulate. Aperture broadly elliptical, deflected from coiling axis by 15–20°. Siphonal canal about ½ as long as the aperture, open, axial or only slightly deflected, in which case a pseudo-umbilicus is present. Inner lip smooth, appressed. Outer lip smooth, flaring. Shell color ranges from white to dark brown. Aperture reddish brown with a lighter marginal band. Fractured shells reveal smooth, topographically simple internal surfaces. Operculum (Fig. 3) broadly unguiculate, with nucleus terminal in juveniles and subterminal in larger specimens. Attachment area elliptical, internal surface thickened and unattached along abaxial and anterior margins. Anterior area abraded or broken in most specimens.

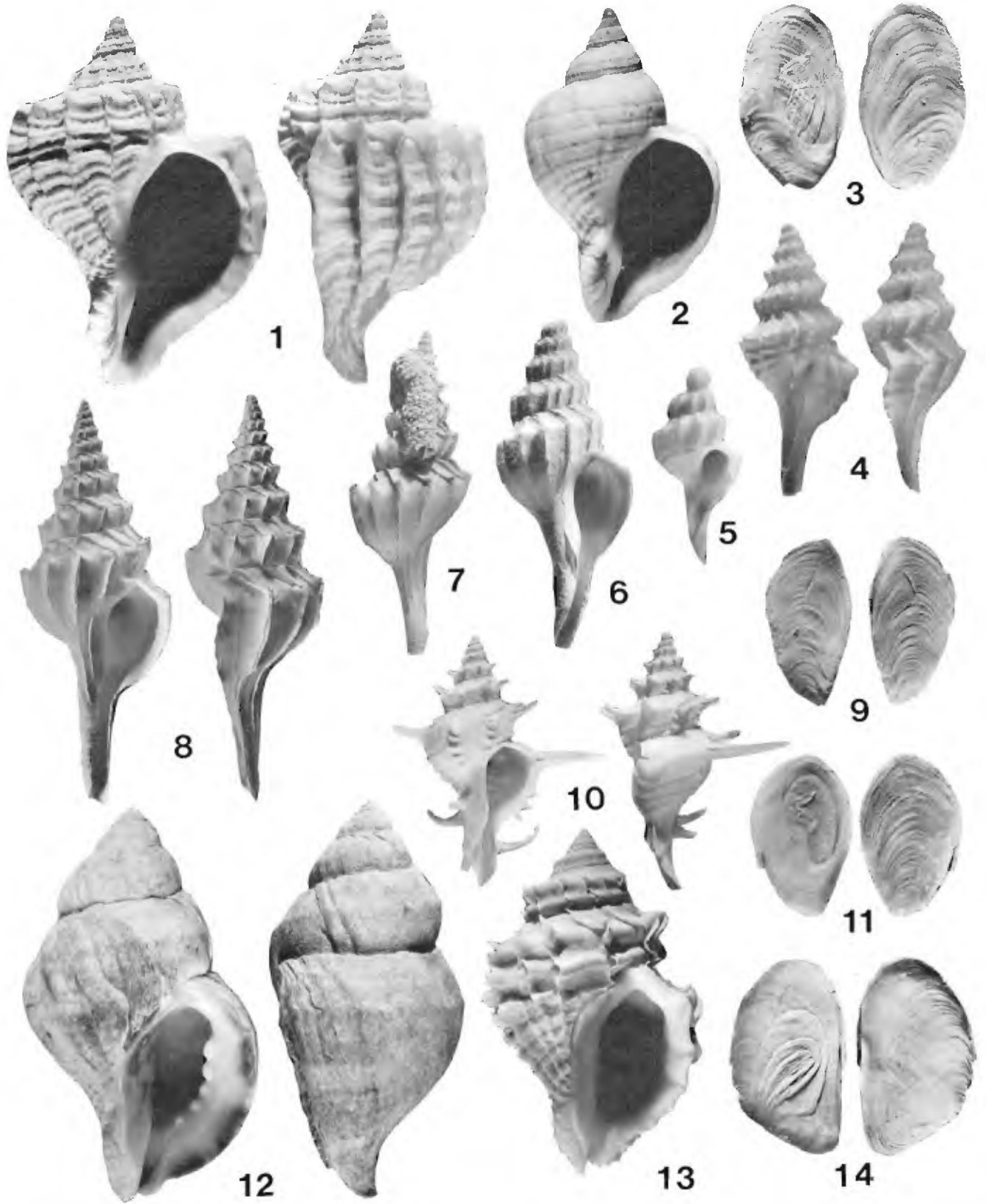
Animal—external features: The body consists of roughly 2½ whorls, of which the mantle cavity spans 2/3 whorl, the kidney 1/3 whorl and the digestive gland-gonad about 1¼ whorl. The columellar muscle is large and has a broad attachment area. Preserved animals are uniformly tan in color. The mantle edge is smooth, the siphon (Fig. 19,s) short. Tentacles are short and blunt, with large black eyes. The foot is broad and rectangular, with a glandular sole and a prominent propodial groove (Fig. 20,pg). An accessory boring organ (Fig. 20,abo) is situated medially, just behind the propodial groove.

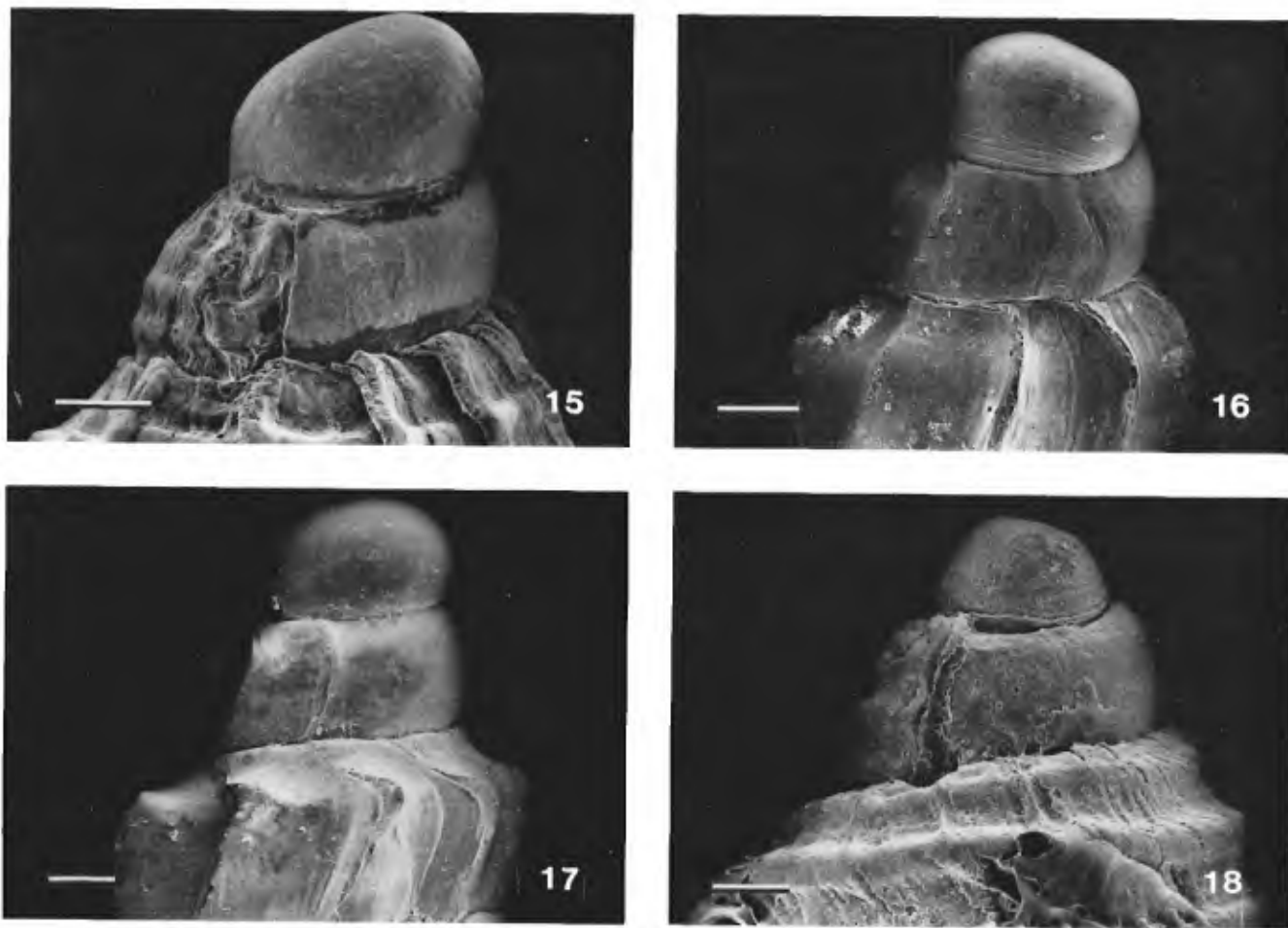
Pallial complex: The mantle cavity is broad and high, with pallial organs arranged as in other rachiglossans. The osphradium (Fig. 19,os) is short, wide (L/W = 2) and asymmetrical, with 40–45 broad leaflets above and 30–35 narrow leaflets below the thick osphradial ganglion. The adjacent ctenidium (Fig. 19,ct) is twice as wide and twice as long as the osphradium, and contains 200–240 triangular leaflets. To its right lies the thick, purplish hypobranchial gland (Fig. 19,hg), and to its right, the rectum (Fig. 19,r) and

genital ducts, which are enclosed in connective tissue and occupy a considerable volume, thereby raising the ceiling of the mantle cavity. A large pericardium (Fig. 19,pc) borders the left rear wall of the mantle cavity. The kidney (Fig. 19,k) with a large nephridial gland (Fig. 19,ng) that overlies much of the pericardium, empties into the mantle cavity through its right rear wall (Fig. 19,ko).

Alimentary system: The pleurembolic proboscis is short and broad, and when retracted, the buccal musculature projects beyond its posterior limits and abutts against the gland of Leiblein. From the mouth (Fig. 21,m) situated at the tip of the proboscis, a short oral tube leads to the buccal cavity. The radular ribbon (Fig. 21,rs) is long (0.4 shell length, $n = 5$), extending beyond the rear of the buccal mass and containing 228–243 rows of teeth ($n = 5$). The rachidian (Fig. 25) is broad, five-cusped, with the central and outer cusps strong and blunt, and the intermediate cusps shorter and partially fused to the inner edges of the outer cusps. Lateral teeth have a single scythe-shaped cusp emanating from a short basal area. There is a modified medial jaw or "sclerite" (Carriker, 1943) on the dorsal edge of the buccal cavity anterior to the esophageal opening. The esophagus runs posteriorly with ducts of the salivary glands adherent but not embedded. At the rear of the buccal mass are two pairs of salivary glands: the golded, tubular accessory salivary glands (Fig. 21,asg) are embedded in the normal salivary glands (Fig. 21,sg). Posterior to the conical valve of Leiblein (Fig. 21, vl) the esophagus passes through the nerve ring (Fig. 21,nr), widens and loops dorsally (Fig. 21,hl) along the left anterior portion of the gland of Leiblein (Fig. 21,gl). It is joined by a duct from this gland before constricting and running posteriorly along the floor of the cephalic sinus. The posterior esophagus passes under the kidney and ascends the left side of the digestive gland (Fig. 19,dg) where it joins the simple, tubular stomach (Figs. 19,24,sto). A mid-dorsal incision reveals that both ducts to the digestive gland are near the esophageal opening, and that the posterior mixing area is greatly reduced. The intestine runs anteriorly, expanding slightly along the pallial gonoduct to form the rectum (Figs. 19,24r) and detaching several millimeters before forming the anus (Fig. 21,a). No trace of an anal gland was found in any of the specimens examined.

Female reproductive system: A large, acinous ovary lines the columellar side of the digestive gland along its entire length. From it, a thin-walled oviduct leads to the rear of the mantle cavity without giving rise to a gonopericardial duct. The pallial gonoduct consists of an albumen gland (Fig. 22, ag) that joins the rear of the capsule gland (Fig. 22,cg), which, when viewed in transverse section, can be seen to consist of left and right lobes each with dorsal and ventral glandular areas similar to those of *Nucella lapillus* (Fretter, 1941). A blind, muscular bursa copulatrix (Fig. 22,bc) joins the duct that leads from the female opening to the capsule gland. The ventral pedal gland is situated along the midline of the foot, just behind the accessory boring organ. Egg capsules (Fig. 23) are stalked, have a medial hatching aperture and contain 5–37 ova (Zaixso, 1973).





Figs. 15–18. Scanning electron micrographs of protoconchs. 15, *Trophon geversianus*. Scale bar = 500 μm . 16, *Boreotrophon aculeatus*. Scale bar = 250 μm . 17, *Paziella pazi*. Scale bar = 250 μm . 18, *Nucella lamellosa*. Scale bar = 250 μm .



Figs. 1–3. *Trophon geversianus* (Pallas). 1, Intertidal rocks, Puerto Basil Hall, Isla de los Estado, Tierra del Fuego, Argentina (54°45.45'S, 64°10.1'W) USARP-SOSC-R/V HERO (LACM 71-289), Horizontal Width (HW) = 28.7 mm for apertural view, HW = 24.7 mm for lateral view. 2, Puerto Madryn, Argentina (USNM 841239) HW = 22.0 mm. 3, operculum of specimen in figure 2, HW = 7.2 mm.

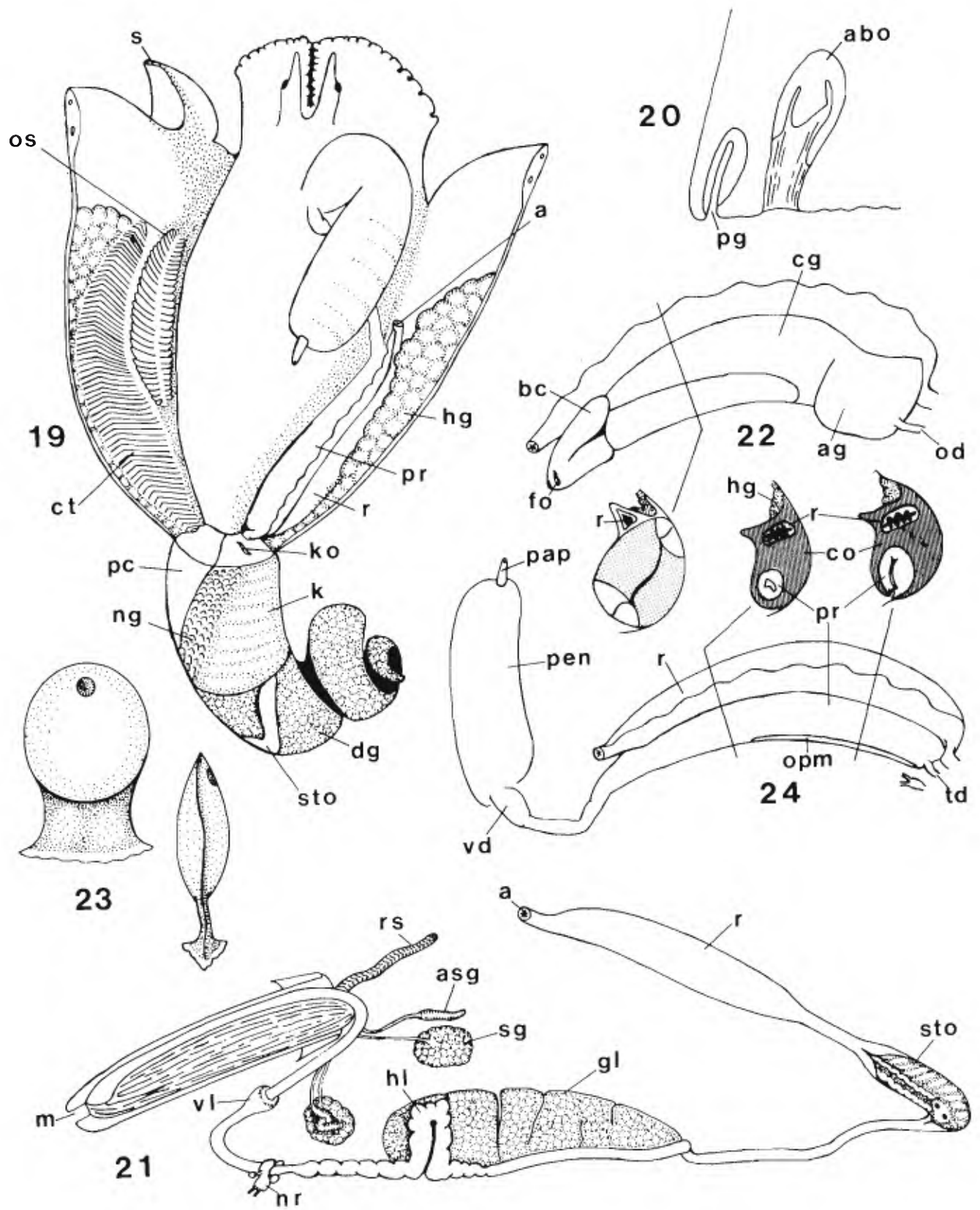
Figs. 4–5. Syntypes of *Trophon aculeatus* Watson. CHALLENGER sta. 122, off Pernambuco, Brazil. (9°5'S, 34°50'W) in 350 fathoms. [BM(NH) 1887.2.9.576-7] Fig. 4 HW = 5.0 mm for apertural view, HW = 4.25 mm for lateral view. Fig. 5 HW = 1.88 mm.

Fig. 6. Holotype of *Boreotrophon lacunellus* (Dall). BLAKE sta. 163, off Guadeloupe, in 769 fathoms. (MCZ 7312) HW = 14.7 mm.

Figs. 7–9. *Boreotrophon aculeatus* (Watson). COLUMBUS ISELIN sta. CI-161, Tongue of the Ocean, Bahamas (23°40'N, 77°06'W) in 1370 meters. (USNM 841240), Fig. 7 HW = 10.0 mm Fig. 8 HW = 12.0 mm for apertural view, 11.0 mm for lateral view 9, operculum of specimen in figure 8 HW = 3.0 mm.

Figs. 10–11. *Paziella pazi* (Crosse). PILLSBURY sta. P-984, W of Anguilla, Leeward Islands (18°26.4'N, 63°12.6'W) in 421–439 meters. (USNM 841241), Fig. 10 HW = 18.0 mm including spines for apertural view only, HW = 16.0 mm including spines for lateral view, Fig. 11 HW = 3.4 mm.

Figs. 12–14. *Nucella lamellosa* (Gmelin). 12, intertidal rocks, Deception Pass, Fidalgo Island, Puget Sound, Washington. (USNM, 841242) HW = 26.0 mm for apertural view, HW = 22.0 mm for lateral view. 13, Point Wells, Snohomish Co., Washington (48°40'N, 122°24'W) SCUBA in 12.0 meters. (USNM 655925) HW = 37.0 mm 14, operculum of specimen in figure 12 HW = 7.4 mm.



Male reproductive system: The ripe testis lines the col-umellar side of the visceral mass from its apex to just behind the kidney. It gives rise to a testicular duct (Fig. 24,td) that runs anteriorly, entering the mantle cavity just above the visceral ganglia and expanding to form the prostate gland (Fig. 24,pr). The prostate gland and rectum are joined by connective tissue (Fig. 24,co) to form a large cylindrical mass that runs half the length of the mantle cavity. The lumen of the prostate gland is in the form of a longitudinal slit, and communicates with the mantle cavity along the posterior $\frac{2}{3}$ of its length (Fig. 24,opm). Below the anus, the testicular duct constricts, becomes muscular, and descends to the floor of the mantle cavity (Fig. 24,vd) expanding slightly before reaching the base of the penis. The broad, dorsoventrally compressed penis (Fig. 24,pen) extends half the length of the mantle cavity and has a terminal papilla (Fig. 24,pap).

Boreotropon aculeatus (Watson, 1882)

(Figs. 4–9, 16, 26, 29–31)

This species was described on the basis of two very young specimens ($4\frac{3}{4}$ and $2\frac{1}{3}$ postnuclear whorls, Figs. 4,5) taken by the CHALLENGER Expedition in 640 meters off Pernambuco (now Recife), Brazil. Several years later, Dall (1889) proposed the taxon *Boreotropon aculeatus* Watson var.?) *lacunellus* based on a single large specimen (Fig. 6) from 1,406 meters off Guadeloupe. In his description, Dall stated "It is most closely related to *T. aculeatus* Watson, from deep water off Pernambuco, and I am disposed to consider them the same, . . .". Comparison of the type specimens of both nominal taxa with additional specimens, including juveniles referred to by Dall (1889) as "young specimens of what I suppose to be the same species," leaves little doubt that the taxon *B. lacunellus* Dall does not warrant even subspecific distinction from *B. aculeatus* (Watson).

This species inhabits sand and mud bottoms at depths ranging from 400 to 1,400 meters, and has been taken off North Carolina, the Bahamas, the Lesser Antilles and Brazil as well as in the Gulf of Mexico. The presence of polychaete tubes (Fig. 7) on several specimens indicates an epifaunal habitat.

Shell morphology: Shell small (to 40 mm), thin, narrowly fusiform (Figs. 4–8). Protoconch of $1\frac{1}{4}$ whorls, inflated, glassy, with 18–20 fine spiral threads on some (Fig. 16) but not all specimens. Transition to teleoconch distinct but not pronounced. Teleoconch with up to 10 sharply shouldered whorls. Spire angle $32\text{--}37^\circ$. Axial sculpture of 10–13 lamel-

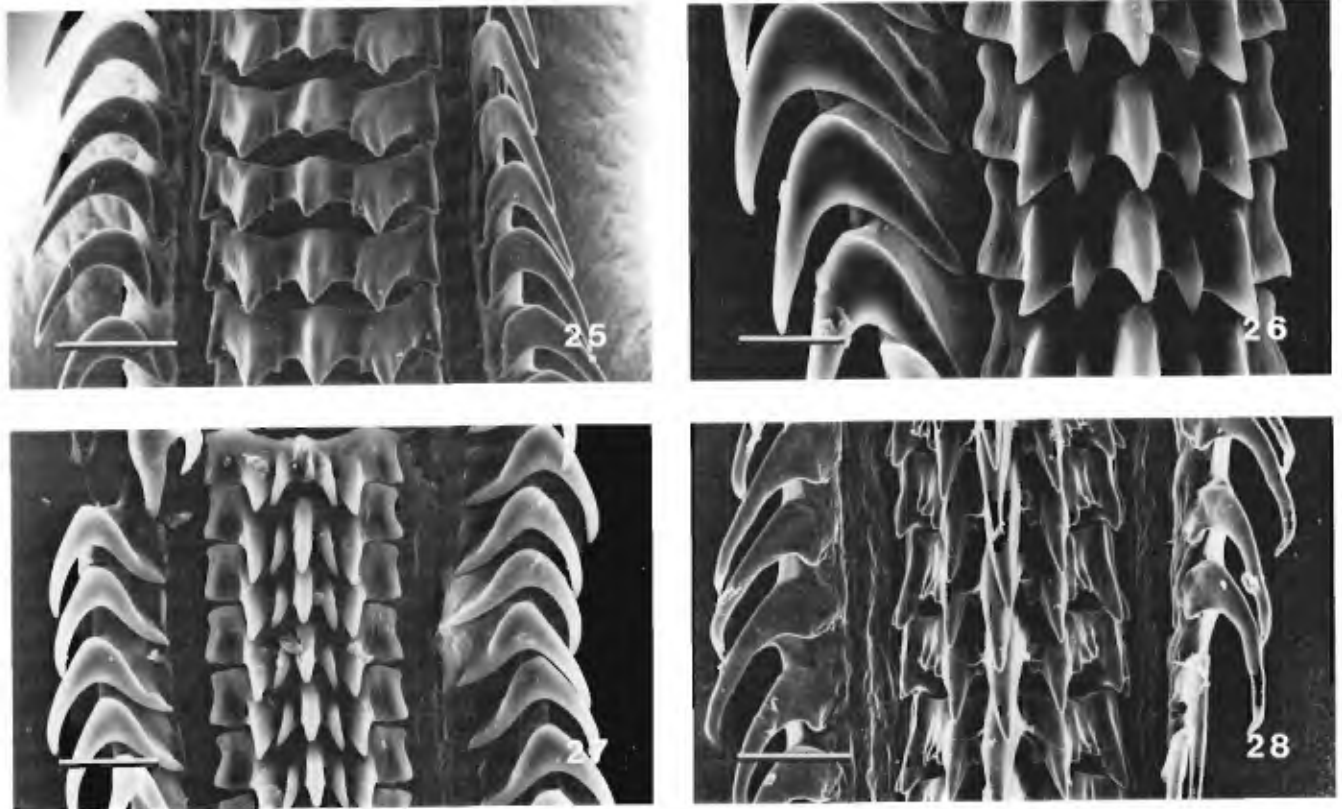
lae. Spiral sculpture generally absent, although young specimens may have 3–6 weak cords on the last whorl (Fig. 4). Suture adpressed. Aperture ovate, deflected from coiling axis by $10\text{--}15^\circ$. Siphonal canal slightly longer than aperture, open, axial. Inner lip smooth, appressed. Outer lip smooth, flaring. Shell and aperture color pure white. Internal surfaces are smooth and topographically simple. Operculum (Fig. 9) is narrowly unguiculate, terminally nucleate, with anterior and abaxial margins thickened. Nucleus often abraded or broken.

Animal—external features: The shell-less animal comprises 3 whorls, the mantle cavity overlying 1 whorl, the kidney occupying $\frac{1}{4}$ whorl and the digestive gland-gonad $1\frac{1}{2}$ whorls. Preserved animals were retracted $\frac{2}{3}$ whorl within the aperture, and were uniformly pale tan in color. The mantle edge is smooth, the siphon long, and tentacles short and broad. The foot is broad, short, squarish, with a deep propodial groove and a small medial accessory boring organ.

Pallial Complex: The mantle cavity is narrow, deep and low. The osphradium is very wide ($L/W = 2$) and extremely assymmetrical, with 52–57 broad leaflets above and 28–33 short leaflets below the osphradial ganglion. The ctenidium is slightly narrower than and over twice as long as the osphradium, and has 110–130 deeply hanging triangular leaflets. The hypobranchial gland is thick, purplish, transversely pleated. The rectum and genital ducts are surrounded by connective tissue, but are not nearly as large as in the preceding species. The pericardium is small, and is bordered on the right by a narrow nephridial gland and kidney.

Alimentary system: The proboscis is short, stout, pleurembolic. Large cartilages support the radular ribbon, which is 1.5 times as long as the buccal mass, but only 0.1 times the shell length. The radula (Fig. 26) consists of 109–138 rows of teeth ($n = 5$). Rachidia are broad and have wide, simple basal areas. The central and outer cusps are stout and heavily buttressed anteriorly, the intermediate cusps are shorter and sharper. Lateral teeth have a wide basal plate and a long scythe-shaped single cusp. A broad cartilaginous jaw is situated along the anterior dorsal edge of the buccal cavity. From the buccal mass, the esophagus runs posteriorly and expands into a wide valve of Leiblein (Fig. 29,vl). Ducts of the normal salivary glands become embedded in the esophagus just anterior to the valve of Leiblein, while ducts of the accessory salivary glands join ventral to the esophagus to form a single duct that runs anteriorly. The esophagus passes through the nerve ring (fig. 29,nr), runs posteriorly along the floor of the cephalic sinus, under the

Figs. 19–24. *Trophon geversianus*. **19**, male specimen removed from its shell, partially uncoiled, with the mantle cavity opened mid-dorsally to display its contents. **20**, sagittal section through the anterior portion of the foot. **21**, Diagrammatic representation of the alimentary system. **22**, the female pallial gonoduct, including a transverse section through the capsule gland and rectum. **23**, anterior and lateral views of an egg capsule. **24**, the male pallial gonoduct, including two transverse sections through the prostate gland and rectum. a, anus; abo, accessory boring organ; ag, albumen gland; asg, accessory salivary gland; bc, bursa copulatrix; cg, capsule gland; co, connective tissue; ct, ctenidium; dg, digestive gland; fo, female opening; gl, gland of Leiblein; hg, hypobranchial gland; k, kidney; ko, kidney opening; m, mouth; ng, nephridial gland; nr, nerve ring; od, oviduct; opm, pallial opening of prostate; os, osphradium; pap, papilla; pc, pericardium; pen, penis; pg, propodial groove; pr, prostate gland; r, rectum; rs, radular sac; s, siphon; sg, salivary gland; sto, stomach; td, testicular duct; vd, vas deferens; vl, valve of Leiblein.



Figs. 25–28. Scanning electron micrographs of radulae. **25**, *Trophon geversianus*. Scale bar = 100 μm . **26**, *Boreotrophon aculeatus*. Scale bar = 20 μm . **27**, *Paziella pazi*. Scale bar = 25 μm . **28**, *Nucella lamellosa*. Scale bar = 100 μm .

large dark brown gland of Leiblein (Fig. 29,gl), and is joined by a duct from this gland just behind its anterior edge. The anterior aorta (Fig. 29,aa), which paralleled the esophagus until this point now turns dorsally, ascends to the top of the gland of Leiblein, passing between adpressed folds of this highly convoluted gland, and descends along its left side before again running alongside the esophagus. The esophagus continues posteriorly to join the stomach, which differs from the preceding species in having a large posterior mixing area, but agrees in most respects with that of *Boreotrophon truncatus* (Ström, 1768) figured by Smith (1967, text-fig. 2, as *Trophon truncatus*). The intestine passes through the kidney and runs along the right wall of the mantle cavity before detaching and ending in an anus (Fig. 29,a). A large anal gland (Fig. 29,rg) runs dorsal to the rectum (Fig. 29,r) for half its length.

Female reproductive system: The ovary and upper oviduct do not differ from those of *T. geversianus*. The pallial oviduct, however, is proportionally narrower, and the crest along the rectum is reduced. The albumen gland (Fig. 30,ag) is narrower and more tubular, and its juncture with the capsule gland (Fig. 30,cg) is more constricted. The bursa copulatrix (Fig. 30,bc) consists of a simple, muscular tube the leads from the female opening (Fig. 30,fo) to the capsule gland

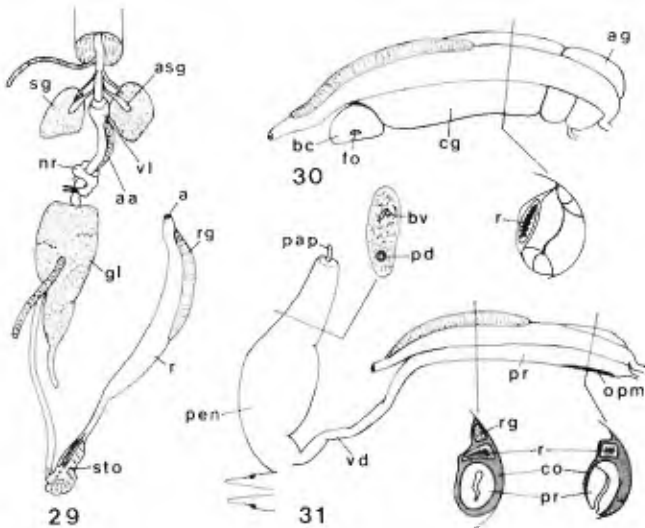
without giving rise to a diverticulum. The ventral pedal gland is simple and shallow. Morphology of the egg capsules is unknown.

Male reproductive system: As in *T. geversianus*, a simple, tubular testicular duct leads from the testis to the rear of the mantle cavity. The prostate gland (Fig. 31,pr) opens into the mantle cavity through a short ventral slit (Fig. 31,opm). It is joined to the rectum by connective tissue (Fig. 31,co), but without forming the voluminous mass that occurs in *T. geversianus*. The vas deferens (Fig. 31,vd) descends to the floor of the mantle cavity just below the anus, and continues anteriorly to the base of the penis, where it becomes expanded and very muscular. The penis (Fig. 31,pen) is broad and flattened, extends half the length of the mantle cavity, and has a pronounced terminal papilla (Fig. 31,pap).

Paziella pazi (Crosse, 1869)

(Figs. 10, 11, 17, 27, 32–34)

The genus *Paziella* dates back to the Upper Cretaceous, and is presently considered to be the oldest of muricine genera (Vokes, 1970). Similarities between *Paziella pazi*, the type species of the genus, and certain trophons have been noted by Dall (1889). More recently, Vokes (1971) has suggested that the Trophoninae, at least in part, are an



Figs. 29–31. *Boreotrophon aculeatus*. 29, diagrammatic representation of the alimentary system. 30, the female pallial gonoduct, including a transverse section through the capsule gland and rectum. 31, the male pallial gonoduct, including two transverse sections through the prostate gland and one through the penis. a, anus; aa, anterior aorta; ag, albumen gland; asg, accessory salivary gland; bc, bursa copulatrix; bv, blood vessel; cg, capsule gland; co, connective tissue; fo, female opening; gl, gland of Leiblein; nr, nerve ring; opm, pallial opening of the prostate; pap, papilla; pd, penial duct; pen, penis; pr, prostate gland; r, rectum; rg, anal gland; sg, salivary gland; sto, stomach; vd, vas deferens; vl, valve of Leiblein.

offshoot of the *Paziella*-*Poirieria* line. *Paziella* is represented in the Recent fauna by a very few species, these occurring in the deeper waters of the tropical western Atlantic and the Galapagos. As Radwin and D'Attilio (1976) have synonymized several distinct phenotypes under the name *P. pazi*, it may be well to state that the two specimens used in this study are representative of the taxon in the strictest sense. Little is known of the biology of this species other than it inhabits the upper continental slope off eastern Florida and the Caribbean Sea.

Shell morphology: Shell small (to 35 mm), thin, biconical (Fig. 10). Protoconch (Fig. 17) of $1\frac{1}{2}$ whorls, inflated, smooth. An outward flare of the lip and the first occurrence of axial growth striae mark the beginning of the teleoconch, which continues for up to 7 whorls. Spire angle $43\text{--}48^\circ$. Axial sculpture consists of 5–9 flaring varices per whorl, the number decreasing with increase in shell size. Each varix has a long open spine at the shoulder, and 1–2 shorter, recurved spines on the siphonal canal. Spiral sculpture comprised of 4–6 cords, each producing a short spine upon intersecting the varices. Suture impressed, shoulder rounded. Aperture ovate, deflected from the coiling axis by $10\text{--}15^\circ$. Siphonal canal open, dorsally deflected, equal in length to the aperture. Inner lip smooth, appressed along its entire length. Outer lip smooth, with only the spines flaring. Shell and aperture color white. Internal surfaces smooth and simple.

The operculum (Fig. 11) is corneous, sharply ovate, terminally nucleate.

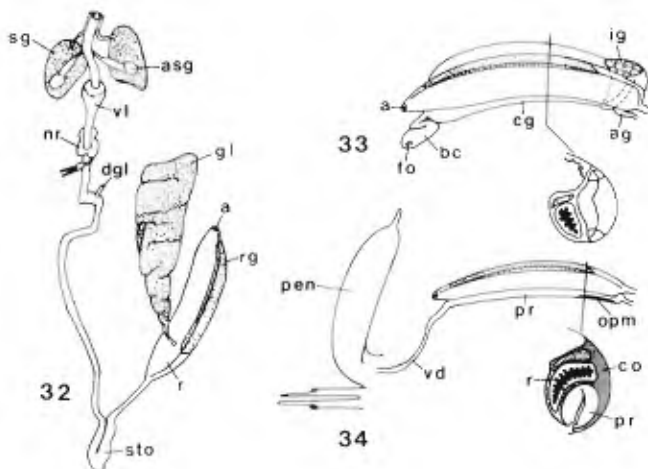
Animal—external features: The soft parts comprise $3\frac{1}{4}$ whorls, the digestive gland-gonad occupying $1\frac{3}{4}$ whorl, the kidney $\frac{1}{4}$ whorl and the mantle cavity spanning an entire whorl. Preserved animals are a light golden tan in color. The mantle edge is smooth, the tentacles very long and slender. The foot is squarish, with a deep, extremely glandular propodial groove and a small accessory boring organ.

Pallial complex: The mantle cavity is deep and narrow. The osphradium is long, narrow ($L/W = 4$), roughly symmetrical, with approximately 115 leaflets per side. The ctenidium is as wide as the osphradium and nearly twice as long, and has 180–200 deeply hanging triangular leaflets. The hypobranchial gland is slightly wider than the ctenidium and is nodular in appearance. The rectum and genital ducts are joined by connective tissue, and a simple, crested ridge can be discerned along the rectum. The pericardium is small, bordering the left rear corner of the mantle cavity. The adjacent kidney is large and has a pronounced nephridial gland.

Alimentary system: The alimentary system is similar to that of *B. aculeatus* in most regards. The radular ribbon (Fig. 27) is less than 0.1 times the shell length, and contains 168–172 rows of teeth ($n = 2$). The rachidian resembles that of *B. aculeatus*, but the cusps are less stout and are concentrated toward the center of the tooth. Lateral teeth resemble those of *B. aculeatus* but have proportionally longer cusps. The large, ovate valve of Leiblein (Fig. 32, vl) is bounded on either side by large, acinous salivary glands (Fig. 32, sg), the ducts from which are adherent to, but not embedded in the esophagus. Accessory salivary glands (Fig. 32, asg) are tubular, but each has a posterior “bladder” that is thin walled, non-glandular, and contains a clear, amber colored gel. The esophagus passes through the nerve ring (Fig. 32, nr) and under the gland of Leiblein (Fig. 32, gl). This gland consists of a highly folded glandular tube the empties into the esophagus via a duct (Fig. 32, dgl) anteriorly, and tapers posteriorly, ending in a clear ampulla. The esophagus continues posteriorly, paralleling the stomach (Fig. 32, sto) along its left side before entering it near its posterior limit. The intestine expands into a broad rectum (Fig. 32, r) when adjacent to the pallial gonoduct. An anal gland (Fig. 32, rg) runs along most of the length of the rectum. The anus (Fig. 32, a) is situated slightly anterior to the midlength of the mantle cavity.

Female reproductive system: The ovary and oviduct do not differ noticeably from those of the preceding species. The pallial oviduct contains an ingesting gland (Fig. 33, ig) that joins the albumen gland (Fig. 33, ag) near its juncture with the capsule gland (Fig. 33, cg). The bursa copulatrix (Fig. 33, bc) is muscular and triangular in outline. Dissection reveals it to be a simple S-shaped tube. Egg capsules and reproductive biology are unknown.

Male reproductive system: As in the preceding species, the testis lines the columellar side of the digestive gland, and the sperm travel via a simple, tubular testicular duct to the prostate gland (Fig. 34, pr). This gland extends along the posterior half of the mantle cavity, and communicates with it



Figs. 32–34. *Paziella pazi*. 32, diagrammatic representation of the alimentary system, with the gland of Leiblein displaced to the right. 33, the female pallial gonoduct, including a transverse section through the capsule gland, anal gland and rectum. 34, the male pallial gonoduct, including a transverse section through the prostate gland, anal gland and rectum. a, anus; ag, albumen gland; asg, accessory salivary gland; bc, bursa copulatrix; cg, capsule gland; co, connective tissue; dgl, duct of the gland of Leiblein; fo, female opening; gl, gland of Leiblein; ig, ingesting gland; nr, nerve ring; opm, pallial opening of the prostate; pen, penis; pr, prostate gland; r, rectum; rg, anal gland; sg, salivary gland; sto, stomach; vd, vas deferens, vl, valve of Leiblein.

along a short ventral slit (Fig. 34,opm). The prostate, together with the anus and anal gland, are surrounded by connective tissue (Fig. 34,co). The vas deferens (Fig. 34,vd) is not muscular as in the preceding species, and the penis (Fig. 34,pen) is broad and flat, tapering rapidly at its distal end without forming a papilla. The rapid taper may be an artifact of preservation.

Nucella lamellosa (Gmelin, 1791)

Figs. 12–14, 18, 28, 35–37)

This species was chosen for this study because of its superficial similarity to *T. geversianus*, both in shell morphology and in habitat. Shell morphology is extremely variable, and has been well documented by Kincaid (1957). Abbott (1974) provides a recent synonymy for this species. *Nucella lamellosa* is common intertidally and subtidally along the northwestern coast of North America.

Shell morphology: Shell large (to 82 mm), heavy, fusiform (Figs. 12–13). Protoconch (Fig. 18) of $1\frac{1}{2}$ whorls, globose, pitted. Transition to teleoconch marked by onset of spiral sculpture. Teleoconch with up to $6\frac{1}{2}$ inflated whorls. Spire angle $45\text{--}75^\circ$. Axial sculpture may be lacking in young or eroded specimens (Fig. 12), but more usually comprises 8–14 lamellae per whorl (Fig. 13). Spiral sculpture consists of 6–8 strong cords on the last whorl and 2 on the penultimate whorl. Suture appressed, shoulder rounded to tabulate. Aperture hemi-elliptical, deflected from the coiling axis by $20\text{--}25^\circ$. Siphonal canal about $\frac{1}{2}$ as long as the aperture,

open, axial or slightly deflected. Outer lip may be smooth and flaring or greatly thickened, with 5–7 denticles. Inner lip smooth, appressed along its entire length. Shell color ranges from pure white to orange and red, and may be solid or occur in spiral bands. Specimens with thin shells and prominent lamellae have smooth, topographically simple interiors, while heavy shelled individuals tend to have periodic internal thickening of the shell and pronounced apertural lirae every 120° . The operculum (Fig. 14) is thin, flexible, trapezoidal in outline and laterally nucleate.

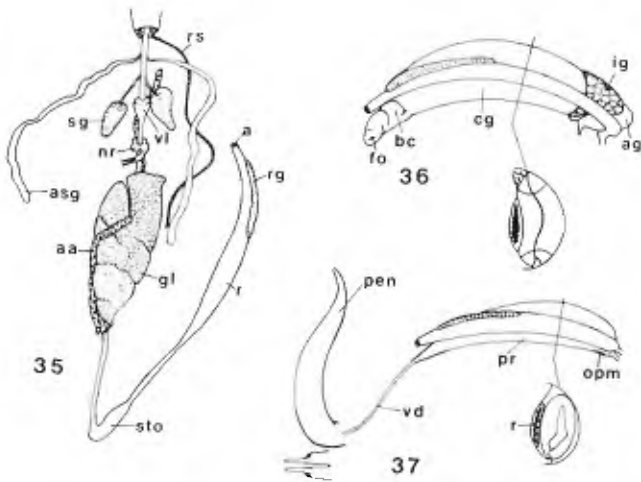
Animal—external features: The body consists of $2\frac{1}{2}$ whorls: the mantle cavity spanning $\frac{1}{2}$ whorl, the kidney $\frac{1}{4}$ whorl and the digestive gland-gonad $1\frac{1}{2}$ whorls. Preserved animals were retracted $\frac{1}{2}$ to $\frac{3}{4}$ whorl within the aperture and were uniformly light tan in color. The mantle edge is smooth, the siphon and tentacles are short. A large accessory boring organ is situated medially, just behind the deep propodial groove.

Pallial complex: The mantle cavity is short and broad. The osphradium is long, broad ($L/W = 2.5$) and roughly symmetrical, with 36–43 leaflets per side. The ctenidium is slightly wider than and twice as long as the osphradium and has about 200 leaflets. The hypobranchial gland, which produces a purplish secretion, is wider than the ctenidium and extends over the rectum and genital ducts. The rectum is adjacent to the genital ducts, but is not encapsulated with them by connective tissue. The pericardium, kidney and nephridial gland are similar to those of the preceding species.

Alimentary system: From the mouth, situated at the tip of a short, broad proboscis, an oral tube leads to the buccal cavity, which has the modified jaw in the usual position. The radular ribbon (Fig. 35,rs) is very long (0.4 shell length, $n = 5$) and contains 336–371 rows of teeth. The rachidia (Fig. 28) are broad, with the lateral posterior edges of the basal plate bifurcated, and with 3 long sharp cusps and 2 shorter cusps partially fused to the inner edges of the outer cusps. Lateral edges of the outer cusps have 3 serrate denticles. Lateral teeth each have a single, long, distally recurved cusp rising from a short basal area. Ducts of the normal salivary glands are embedded in the esophageal wall beneath the dorsal folds. Normal salivary glands (Fig. 35,sg) are reduced in size compared to the extremely large accessory salivary glands (Fig. 35,asg), which, when uncoiled, are half as long as the shell. Posterior to the valve of Leiblein (Fig. 35,vl) the esophagus passes through the nerve ring (Fig. 35,nr), is joined by a duct from the highly compacted gland of Leiblein (Fig. 35,gl), and proceeds to the tubular stomach (Fig. 35,sto). An anal gland (Fig. 35,rg) spans half the length of the rectum (Fig. 35,r).

Female reproductive system: The female reproductive system is similar to that of *P. pazi*, the major differences being that *N. lamellosa* has a larger ingesting gland (Fig. 36,ig) and a bursa copulatrix (Fig. 36,bc) with a blind muscular pouch. The ventral pedal gland is deep, being situated in the usual position.

Male reproductive system: The male reproductive system differs most notably from those of the preceding species



Figs. 35–37. *Nucella lamellosa*. **35**, diagrammatic representation of the alimentary system. **36**, the female pallial gonoduct, including a transverse section through the capsule gland and rectum. **37**, the male pallial gonoduct, including a transverse section through the prostate gland and rectum. a, anus; aa, anterior aorta; ag, albumen gland; asg, accessory salivary gland; bc, bursa copulatrix; cg, capsule gland; fo, female opening; gl, gland of Leiblein; ig, ingesting gland; nr, nerve ring; opm, pallial opening of the prostate; pen, penis; pr, prostate gland; r, rectum; rg, anal gland; rs, radular sac; sg, salivary gland; sto, stomach; vd, vas deferens; vl, valve of Leiblein.

having a convoluted testicular duct, a prostate gland with a large lumen, a thin, non-muscular vas deferens and a gradually tapering penis.

PHYLOGENY RECONSTRUCTION

Phenetics

Phenetic analyses of shell character data (Table 2) using UPGMA and Ward's method clustering produce the phenograms shown in figure 38. Both have the same topology, differ only in the morphological distance at which the final fusion is made, and, if interpreted as phylogenies, would support the hypothesis of a polyphyletic Trophoninae.

Cladistics

Character descriptions and analyses

Character 1. Cephalic tentacles:

- (a) short, broad
- (b) extremely long, narrow

Buccinaceans, volutaceans and non-muricine muricaceans possess short, broad tentacles. The increase in tentacle length observed in *Paziella pazi* also occurs in at least some other muricines (eg. *Murex acanthostephes* Watson, 1883, Abbott, 1972:157; *Chicoreus palmarosae* Lamarck, 1822, M. G. H.), and appears to be correlated with the presence of spines along the anterior portion of the shell. Elongated cephalic tentacles are considered to be a derived state.

Character 2. Osphradium:

- (a) symmetrical
- (b) dorsally expanded

Osphradia with an increased number of dorsally enlarged leaflets above the osphradial ganglion occur in *Trophon geversianus* and *Boreotrophon aculeatus* but not in other muricaceans studied nor in the Buccinacea or Volutacea, and are regarded as derived. This feature was not reported by Eales (1923) in her discussions of the anatomy of *Trophon shackletoni* Hedley, 1911 and *T. longstaffi* Smith, 1904, nor is it discernible in Taki's (1938) figure of the gross anatomy of *Boreotrophon alborostratus* Taki, 1938, but is very pronounced in *T. bahamondei* McLean and Andrade, 1982 (M.G.H.). The functional significance of this asymmetry is not known.

Character 3. Intermediate cusps of rachidia:

- (a) free
- (b) fused to outer cusps

Reduction in the number of cusps on the rachidian has been well documented in several rachiglossan lineages (Ponder, 1973). Although certainly convergent between these lineages, the possibility that it may be homologous within each lineage has yet to be investigated. One mechanism by which the number of cusps may be reduced is by fusion of cusps. This character state is provisionally considered to be derived.

Character 4. Major cusps of rachidia:

- (a) long, slender
- (b) short, broad

The more primitive members of Buccinacea and Volutacea have rachidia with numerous long, slender cusps of equal length. Reduction in the number of cusps and the shortening and buttressing of the remaining cusps are two trends that may be indicative of a shift from a raking to a gouging function of the rachidia. Both are considered to be derived traits.

Character 5. Lateral edges of rachidia:

- (a) smooth
- (b) denticulate

The presence of secondary denticles on the rachidian is uncommon in the Rachiglossa (Thiele, 1929), although less so in the Muricacea (Radwin and D'Attilio, 1976), where it appears to be restricted to the Thaididae, Ocenebridae and, to a lesser extent, the Muricopsinae. The presence of denticles is interpreted as a derived condition, although it may not be homologous in all of these groups.

Character 6. Postero-lateral edge of rachidian basal plate:

- (a) simple
- (b) with bifid edges

The bifid condition is prevalent throughout the Thaididae (Wu, 1965; Kool, personal communication) and also occurs, although not necessarily in homologous form, in the Ocenebrinae and Muricopsinae, but has not been reported outside the Muricacea. It may function as an interlocking mechanism for rachidia and/or lateral teeth. Its presence is considered a derived state.

Table 2. Measurements of shell characters presented in the format Mean/Standard Deviation. All linear measurements are in mm. The mean values constitute the data matrix for phenetic analysis.

Character	<i>T. geversianus</i> (n = 10)	<i>B. aculeatus</i> (n = 10)	<i>P. pazi</i> (n = 5)	<i>N. lamellosa</i> (n = 10)
1. Sbc	1.35/0.04	1.88/0.05	1.74/0.07	1.53/0.13
2. Ssc	2.23/0.14	6.41/0.51	5.24/0.31	2.44/0.23
3. Rsl	0.54/0.03	1.14/0.07	1.19/0.09	0.56/0.03
4. beta	2.5°/0.11°	14.7°/1.99°	9.5°/0.88°	-7.3°/0.91°
5. W	2.11/0.31	1.41/0.21	1.29/0.42	1.70/0.22
6. theta	22.8°/3.1°	25.2°/1.08°	20.6°/0.81°	18.3°/1.77°
7. D	0.127/0.01	0.216/0.03	0.175/0.02	0.089/0.01
8. T	3.56/0.15	5.82/0.21	5.02/0.18	4.53/0.21
9. L	52.6/15.1	30.1/4.8	30.9/8.8	54.7/13.2
10. W/L	0.62/0.05	0.31/0.02	0.41/0.01	0.51/0.03
11. AL/L	0.44/0.03	0.26/0.02	0.27/0.01	0.34/0.02
12. # whorls	5.2/0.8	8.6/0.4	6.6/1.2	5.6/0.4
13. # var	18.5/2.0	12.1/0.9	5.8/0.4	10.3/1.2

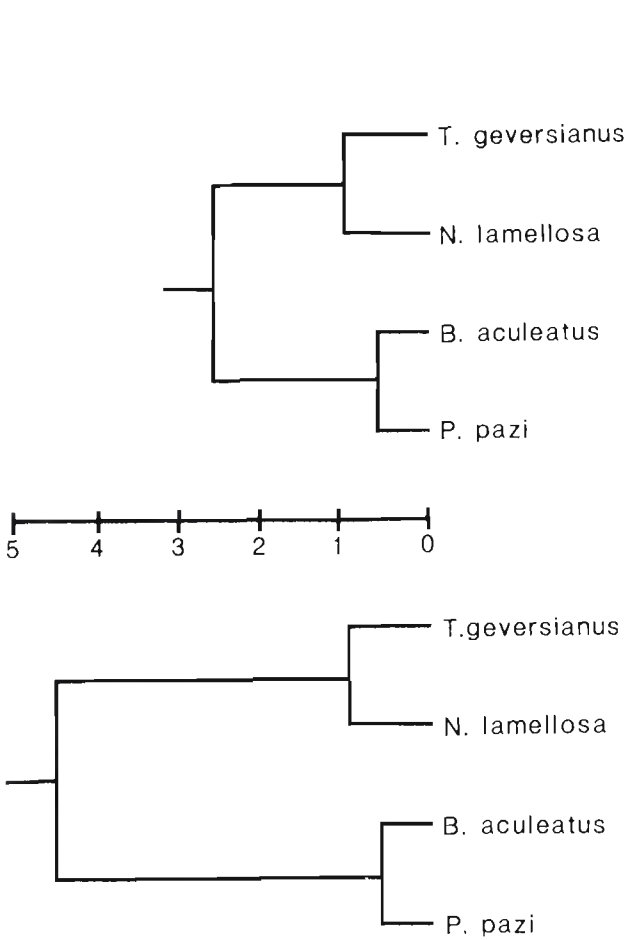


Fig. 38. Phenograms based on UPGMA (upper) and Ward's Method (lower) cluster analyses of morphological distance.

Character 7. Basal plates of lateral teeth:
 (a) with broad attachment area
 (b) with narrow attachment area

A decrease in the number of cusps on the lateral teeth has occurred independently in at least 8 rachiglossan lineages (Ponder, 1973). In the Muricacea, this has resulted in a monocusped condition, with a long cusp along the outer edge of the basal plate. This scythe-like configuration, here considered a synapomorphy uniting all Muricacea, is nevertheless primitive within the group and suggests a piercing, slicing function. Reduction and concentration of the attachment area would increase the flexibility of the tooth about the cusp axis, which would be more useful if the tooth were to assume a grappling function.

Character 8. Accessory salivary glands:
 (a) longer than and free of salivary glands
 (b) shorter than and embedded in salivary glands

The polarity of this transformation is based on the tendency within Rachiglossa toward loss of the accessory salivary gland. Total loss has occurred in all Buccinacea, in several volutacean families (Ponder, 1973) as well as in one muricacean family (Ward, 1965; Ponder, 1973) and several muricid genera (Wu, 1973; Carriker, 1981). Within the Volutidae, large free accessory salivary glands are found in the most primitive subfamily (Volutinae), becoming smaller and embedded in the salivary glands in the more advanced subfamilies (Zidoninae and Odontocymbiolinae) (Clench and Turner, 1964).

Character 9. mid-esophagus:
 (a) simple, tubular
 (b) greatly expanded, dorsally recurved

The mid-esophagus, which extends from the valve of Leiblein to the duct of the gland of Leiblein, is simple and tubular in most Buccinacea and Volutacea. Within Muricacea this area

exhibits varying degrees of expansion and elongation (Ponder, 1973). Ponder (1973) reported that the dorsal folds have been stripped from the mid-esophagus by the fusion of their apices in the trophonine *Xymene ambiguus* (Philippi, 1844).

In *Trophon geversianus* and *T. bahamondei* (M.G.H.), this section becomes greatly expanded and increases in length, forming a dorsal loop (Fig. 21,hl). It is considered likely that the "coiled caecum" reported in *T. shackletoni* and *T. longstaffi* (Eales, 1923) corresponds to this structure. The presence of this feature in austral species of *Trophon* is considered a derived feature.

Character 10. Stomach with:

- (a) broad posterior mixing area
- (b) reduced posterior mixing area

The widespread occurrence of broad posterior mixing areas or caeca in Muricacea (Graham, 1949; Wu, 1965; Smith, 1967; Ponder, 1973), Buccinacea (Brock, 1936; Smith, 1967; Ponder, 1973) and to a lesser extent in Volutacea (Ponder, 1973) is regarded as representing the primitive state. The tendency for the neogastropod stomach to become U-shaped and tubular has been discussed at length by several authors (Graham, 1949; Smith, 1967) and this condition is considered to be derived.

Character 11. Anal gland:

- (a) present
- (b) absent

The widespread if sporadic occurrence of an anal gland in muricacean, volutacean and certain toxoglossan families suggests that its presence may be regarded as a primitive state. Its loss in such diverse taxa as Buccinacea, Magilidae and Vasiniae is a derived condition convergent between but homologous within each taxon.

Chapter 12. Separate sperm ingesting gland:

- (a) present
- (b) absent

A separate sperm ingesting gland has been reported in some but not all members of the 3 superfamilies of Rachiglossa (Ponder, 1973). Houston (1976) reported this structure lacking in 2 trophonines and one ocenebrine but present in 7 other muricacean taxa. The loss of this gland is regarded as a derived state. Its function has likely been taken over by another portion of the pallial gonoduct.

Chapter 13. Position of the rectum relative to the prostate gland:

- (a) medial
- (b) dorso-lateral
- (c) dorsal, both enclosed in connective tissue

The rectum is medial to the female pallial gonoduct in all rachiglossans studied, and a similar arrangement in males is provisionally regarded as a primitive state. The migration of the rectum to a dorso-lateral and ultimately to a dorsal position is interpreted as representing progressively more derived conditions. The enclosure of both organs in connective tissue in Trophoninae may serve to increase the height of the mantle cavity.

Character 14. Vas deferens:

- (a) thin, tubular
- (b) thick, muscular

The thick, muscular condition of the vas deferens, found in *Trophon geversianus*, *T. bahamondei* (M.G.H.) and *Boreotrophon aculeatus*, is distinctive, and has not been reported in other rachiglossans. Presence of this modification is regarded as a derived trait.

Character 15. Penis tip with terminal papilla:

- (a) present
- (b) absent

Within the Muricacea, penial papillae have not been reported outside the Trophoninae (Wu, 1973; Houston, 1976), and their presence is regarded as a derived condition. Similar structures are found in Buccinacea, and can be attributed to convergence.

Cladistic analysis of the 15 anatomical and radular characters, comprising 31 character states, listed in Table 3 produced the cladogram in figure 39. The cladogram required 19 changes of character state, of which 3 (characters 3, 7, 10) occurred twice, and are interpreted as being convergent. Open circles, labelled A, B, and C, represent hypothetical ancestors, and correspond to the ancestral trophonine, muricid and muricacean respectively. Reconstructed phenotypes of these hypothetical ancestors are included in Table 3.

Character compatibility analysis of the anatomical data yielded 2 cliques of mutually compatible characters (Table 4). The largest, Clique I, is supported by 13 characters and is compatible with the cladogram in figure 39. The smaller, Clique II, is supported by 8 characters, and is compatible with the arrangement produced by the phenetic analyses. It should be noted, however, that 5 characters (1, 5, 6, 9, 11) are non-discriminating, and would support any phylogenetic arrangement of the 4 taxa.

DISCUSSION

Phenetic analyses of shell character data cluster *Trophon geversianus* with *Nucella lamellosa* and *Boreotrophon aculeatus* with *Paziella pazi*, raising the question, are these similarities indicative of phylogenetic relationships or of convergent responses to habitat. The relationship between shell morphology and habitat has been convincingly demonstrated by Davis (1979) in Pomatiopsidae, and similar convergence is known to occur in other gastropods (eg. Buccinacea, Ponder, 1973; shelled opisthobranchs, Gosliner, personal communication). If shell morphology is significantly influenced by habitat, one would expect species that are sympatric over part of their ranges to be more similar than species inhabiting similar habitats a hemisphere apart. Although considerably more data are required to seriously evaluate this hypothesis, the data from this study at least conform to its prediction.

The most parsimonious cladogram generated by the Wagner algorithm (Fig. 39) is congruent with the largest clique of mutually compatible characters. Further support for this phylogenetic arrangement is provided by the fossil record. The Thaididae, here considered the most primitive of the taxa studied, is also the oldest, dating back to the Albian stage of the Upper Cretaceous (Sohl, 1969; Taylor et al., 1983). *Paziella*, the oldest of the muricid genera, first appears in the Cenomanian stage (Vokes, 1970), while Trophoninae, the youngest and most specialized of the taxa under investigation, is first reported from the Eocene (Wenz, 1941).

The 3 characters (2 radular, 1 stomach) that are incongruent with this cladogram all have identical distributions. Changes in polarization of their transformation series do not improve their compatibility. Wu (1965a) considered the bifid edges of thaidid rachidian teeth to consist in part of laterally displaced outer cusps. Under this interpretation, the fused intermediate cusps of *Nucella lamellosa* would be denticles, and not homologous to the fused intermediate cusps of *Trophon geversianus*. In light of the numerous, well documented (Ponder, 1973) instances of convergence in rachiglossan radular morphology, it is likely that these presumed synapomorphies are, in fact, due to convergence. It also appears likely that changes in stomach morphology are not homologous.

Many of the characters that support the proposed phylogenetic arrangement pertain to the reproductive systems, which are "more conservative and useful in determining systematic arrangements" (Wu, 1973).

The morphologies of the egg capsules of 3 of the species in this study are unknown. Nevertheless, it should be noted that two different types of egg capsules occur in the Trophoninae. Most species studied have primitive, lenticular capsules (Bandel, 1976), but species of *Trophon* s.s. pro-

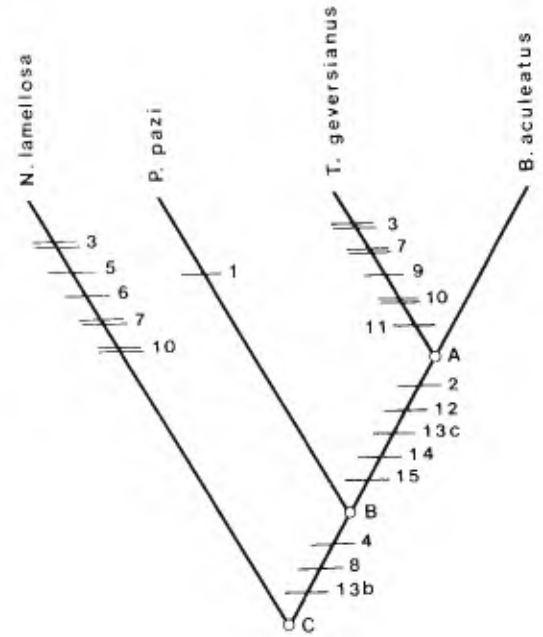


Fig. 39. Wagner reconstruction of phylogenetic relationships of muricacean taxa. Open circles represent hypothetical ancestors. Single slashes across tree branches signify transformation of the corresponding character from the primitive to the derived state. Double slashes indicate character transformations that occur more than once.

duce stalked capsules (Fig. 23) similar to those of Thaididae and Ocenebrinae.

Examination of figure 39 reveals that both deep-water species (*P. pazi* and *B. aculeatus*) differ little if at all from their

Table 3. Character state distributions of qualitative anatomical characters. A, B and C represent reconstructed phenotypes of hypothetical ancestors.

Character	<i>T. geversianus</i>	<i>B. aculeatus</i>	<i>P. pazi</i>	<i>N. lamellosa</i>	A	B	C
1.	a	a	b	a	a	a	a
2.	b	b	a	a	b	a	a
3.	b	a	a	b	a	a	a
4.	b	b	b	a	b	b	a
5.	a	a	a	b	a	a	a
6.	a	a	a	b	a	a	a
7.	b	a	a	b	a	a	a
8.	b	b	b	a	b	b	a
9.	b	a	a	a	a	a	a
10.	b	a	a	b	a	a	a
11.	b	a	a	a	a	a	a
12.	b	b	a	a	b	a	a
13.	c	c	b	a	c	b	a
14.	b	b	a	a	b	a	a
15.	b	b	a	a	b	a	a

Table 4. Memberships of cliques of mutually compatible characters.

Clique	Membership
I	1b,2b,4b,5b,6b,8b,9b,11b,12b,13b,13c,14b,15b
II	1b,3b,5b,6b,7b,9b,10b,11b

immediate ancestors, while the shallow-water species (*T. geversianus* and *N. lamellosa*) have each undergone transformations in several characters. These observations are in agreement with the onshore-innovation, offshore-archaic evolutionary model discussed by Jablonski et al. (1983).

The results of this study support the following reconstruction of muricacean phylogeny. The Thaididae are probably the most primitive and, together with the Rapanidae, the most ancient members of the superfamily, and should be accorded a status equal to that of the Muricidae. The family Muricidae is morphologically the most advanced of the muricacean families (the Magilidae, geologically slightly younger than the Muricidae, are here considered to be a specialized offshoot from either the thaidid or rapanid lines). Within Muricidae, *P. pazi* more closely resembles the ancestral muricid phenotype (Ancestor B) than any trophonine, and it is suggested that Muricinae is the most primitive of the muricid subfamilies. The Trophoninae comprise a comparatively recent monophyletic group characterized by unique specializations of the osphradium and reproductive organs.

Finally, it is noted that the characters upon which virtually all trophonine taxonomy is based (i.e.—shell and radular characters) are most subject to convergence, and are less reliable as systematic characters than has been previously realized. In light of this information, reassignments of trophonine genera to Thaididae based on radular characters should be reappraised.

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