# A PHYLOGENETIC STUDY OF THE TEREBRINAE (MOLLUSCA, CAENOGASTROPODA, TEREBRIDAE) BASED ON SPECIES FROM THE WESTERN ATLANTIC

Luiz Ricardo L. Simone

Museu de Zoologia da Universidade de Sao Paulo, Cx. Postal 42694,
04299-970 Sao Paulo, SP, Brazil. E-mail: lrsimone@usp.br

**Abstract.** *A phylogenetic study of the Terebrinae (Mollusca, Caenogastropoda, Terebridae) based on species from the [illegible]st Atlantic. J. Comp. Biol. 3(2):137-150.* Terebrin characters, including shell and foregut features and other structures are discussed. A phylogenetic analysis was performed, using as terminal taxa the best known species, mainly from the Western Atlantic - *Hastula cinerea* (Born); *H. hastata* (Gmelin); *Terebra gemmulata* Kiener; *T. crassircticula* Simone; *T. leptapsis* Simone; *T. brasiliensis* Smith; *T. spirosulcata* Simone & EM. Costa; *T. taurina* Lightfoot; *T. dislocata* (Say) (this latter species is redescribed). Considering this sample of the subfamily Terebrinae and literature data, a ground plan of the subfamily is proposed and its monophyly discussed. A set of 44 characters (55 states) were cladisticly analyzed (3 of shell, 7 of head-foot, 9 of pallial organs, 2 of kidney, 10 of foregut, 3 of remainder digestive system, 10 of genital system), from which a single most parsimonious tree was obtained: ((*H. cinerea* + *H. hastata*) + (*T. taurina* + ((*T. crassircticula* + *T. leptapsis*) + (*T. spirosulcata* + (*T. gemmulata* + *T. brasiliensis*))))) (length 74; CI 70; RI 57). Terebrinae, *Terebra* and *Hastula* are monophyletic. The terebrines are characterized, beyond the obvious shell characters, by the following apomorphies: reduction of the cephalic tentacles, anterior end of the ctenidial vein prominent (without gill filaments), rhynchodeal introvert, and anus situated very posteriorly in the pallial cavity. *Hastula* synapomorphies include enlarged foot and complexity of osphradium filaments. *Terebra* synapomorphies include the eye situated at the apex of the tentacles and a clear tendency for enlargement of the introvert, reduction of the proboscis and venom apparatus with their entire reduction in the last elements of the clade. The accessory proboscis structure is considered homoplastic in two clades of *Terebra*, but may be a terebrid synapomorphy, since it is present in some spcies of *Hastula*, so it could have been secondarily lost in several species.

*Keywords.* Mollusca; Gastropoda; Terebridae; Morphology; Phylogeny; Brazil; Western Atlantic.

## *Introduction*

The Terebridae is easily distinguished from the other two families of Conoidea by their elongated, multispiral shell. The superfamily Conoidea (= Toxoglossa) is characterized mainly by a modified foregut and the presence of a complex venom apparatus (Kantor, 1990). The classification and important characters of the shell, operculum and foregut are dealt with in an important paper by Taylor, Kantor & Sysoev (1993), who provide also a standardization of the anatomical terminology and a phylogenetic analysis.

The foregut characters of the Terebridae have been focused by several recent papers (Miller, 1971; Taylor & Miller, 1990; Taylor, 1990). A list of the recent species of the world is given by Bratcher & Cernohorsky (1987). The classification of the Terebridae evolved little since Bruguière (1789), who created the genus *Terebra* for the Linnaean species *Buccinum subulatum*. Forty-one terebrid genera and subgenera have been proposed (Wenz, 1938; Bratcher & Cernohorsky, 1987), but had little acceptance amongst malacologists, and now almost all species are included in *Terebra*. A synthesis of the present classification of the family is as follows (fossils not included): subfamily Pervicaciinae (about 25 species of the Indo-Pacific region), including *Pervicacea* redale, 1924 and *Diplomeriza* Dall, 1919 (= *Duplicar* Dall, 1908; not Rafinesque, 1833); subfamily Terebrinae (worldwide), including *Terebra* (over 200 species) and *Hastula* H. & A. Adams, 1853 (about 30 species).

The Brazilian terebrids were revised by Matthews *et al.* (1975). They were also considered in isolated papers (Marcus & Marcus, 1960; Bratcher & Cernohorsky, 1985; Auffenberg & Lee, 1988; Simone & Verissimo, 1995; Simone, 1999), some of them with anatomical data.

In a larger project on the interrelationship of several groups of Caenogastropoda, each family or superfamily has been investigated. The main objective of this project is to provide morphological data for a phylogenetic analysis.

The only phylogenetic study of the terebrids published to date is part of a larger analysis of the conoid (Taylor et al., 1993). The terebrids were represented in that study by seven species of Terebrinae and seven of Pervicaciinae. In the majority-rule (50%) consensus tree (Taylor *et al.*, 1993:154), 14 species are gathered in three terminal clades. The family itself has the following synapomorphies: (1) rhynchodeal introvert; (2) accessory proboscis structure; (3) terebriform shell; (4) absence of anal sinus in shell aperture and (5) more than nine teleoconch whorls.

The main goal of the present paper is to discuss a number of terebrine characters, both obtained in this study and available in the literature, including no only features from the shell and the foregut, but also from other organs and systems.

*Methods*

The data for the phylogenetic analysis come from a recent paper (Simone, 1999), which presents a detailed morphological study of eight Brazilian species. Another species is studied here. Information from other papers is also used, especially from *Hastula cinerea* (Marcus & Marcus, 1960) and on *Terebra crassireticula* (Simone & Verissimo, 1995).

The specimens of *Terebra dislocata* were dissected under stereomicroscope by standard techniques, immersed in water. For the extraction of the soft parts, the shells were decalcified or the shells were broken. Serial sections of the anterior regions were made by standard histological techniques and stained with Mallory's triple stain. Some structures were also cleared in creosote after dehydration in an ethanol series and stained in carmine. General anatomical terminology follows Marcus & Marcus (1960) except for the foregut, following Taylor *et al.* (1993).

The cladistic analysis was performed using the computer program "Tree Gardner 2.2" platform (Ramos, 1997) for the Hennig86 (Farris, 1988) program. Polarization followed Maddison *et al.* (1984).

In the figures the following abbreviations are used: **aa**, anterior aorta; **ac**, anterior extremity of ctenidial vein; ag, albumen gland; al, anal gland; an, anus; ap, anal papilla; au, auricle; bm, buccal mass; **bs**, blood sinus; ca, capsule gland aperture; cg, capsule gland; cm, columellar muscle; **cv**, ctenidial vein; dd, duct to digestive gland; dg, digestive gland; ep, esophageal pouch; **es**, esophagus; ey, eye; fs, foot sole; ft, foot; gi, gill; hg, hypobranchial gland; ia, rhynchodeal introvert distal aperture or rhynchostome; in, intestine; kd; dorsal lobe of kidney; **ki**, kidney; km, membrane between kidney and pallial cavity; **ks**, ventral septate lobe of kidney attached to intestine; **mb**, mantle border; ne, nephrostome; ng, nephridial gland; **nr**, nerve ring; op, operculum; os, osphradium; ov, oviduct; oy, ovary; pb, vestigial proboscis; pc, pericardium; pd, penis duct; **pe**, penis; pg, anterior furrow of pedal glands; ph, penis distal chamber; po, pallial oviduct; pp, penis papilla; ps, pallial spermoduct; re, rectum septum; ri, rhynchodeal introvert; rt, rectum; rw, rhynchodeal wall; sa, salivary gland aperture; sd, salivary duct; sg, salivary gland; **si**, siphon; st, stomach; te, cephalic tentacles; tg, tegument; **tp**, terminal pouch; **ts**, testis; **tw**, thick region of rhynchodeal wall; vd, visceral vas deferens; ve, ventricle.

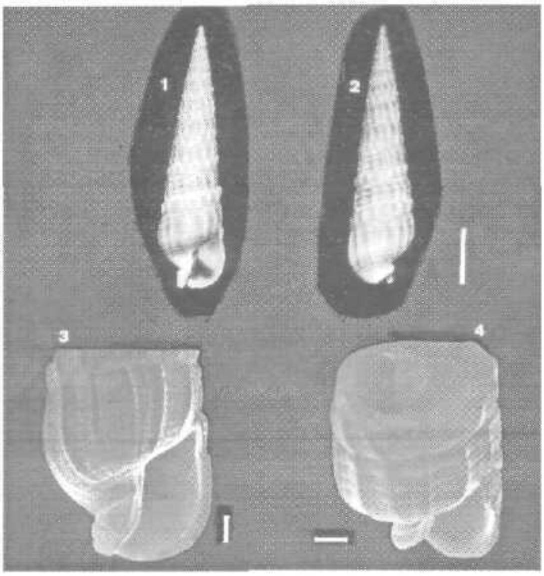
In this study, nine species of Terebrinae were studied in detail. They are referred to below. Studies considering the morphology of each species are cited.

***Hastula*** *cinerea* (Born, 1778): Marcus & Marcus (1960); Simone (1999).
***Hastula hastata*** (Gmelin, 1791): Simone (1999).
*Terebra* ***gemmulata*** Kiener, 1839: Simone (1999).
*Terebra* ***crassireticula*** Simone, 1999; Simone & Verissimo (1995: 460-466, figs 1-8).
*Terebra* ***leptapsis*** Simone, 1999.
***Terebra brasiliensis*** Smith, 1873: Simone (1999).
*Terebra* ***spirosulcata*** Simone & EM. Costa in Simone (1999).
*Terebra* ***taurina*** (Lightfoot, 1786): Simone (1999).
*Terebra dislocata* (Say, 1822): presently described.

As outgroups a set of caenogastropod species of different levels of relationship were taken, as *e.g.*, Cerithioidea, *Littorina flava*, Hydrobioidea (Simone & Moracchioli, 1994; Simone, 1995a), tonnids (Simone, 1995b) several muricoideans as *Buccinanops spp.* (Simone, 1996), *Thala crassa* (Simone, 1995c), *Austromitra sp.* (Turner & Simone, 1998); the turrid *Cochlespira spp.* (Simone, 1999) and the conid *Conus bertarollae* Costa & Simone, 1997 (as closer relatives). The outgroups, however, were not included in the matrix.

### *Terebra dislocata* (Say, 1822)
(Figs 1-18)

Synonymy: see Matthews *et al.*, 1975: 93-94; Bratcher & Cernohorsky, 1987: 159.
References: *Terebra dislocata;* Rios, 1985: 130



Figures 1 -4. *Ter dislocata* shell. 1. frontal view; 2. dorsal view; 3-4. SEM: 3. gment of two last whorls showing fold of columella; 4. detail of aperture, frontal view. Scales 1-2— 5 mm, 3-4 = 1 mm.

(fig. 586); 1994: 180 (fig. 835).
*Types:* See Brateher & Cernohorsky, 1987: 159.
*Type locality:* Key West, Florida, USA.

## Redescription

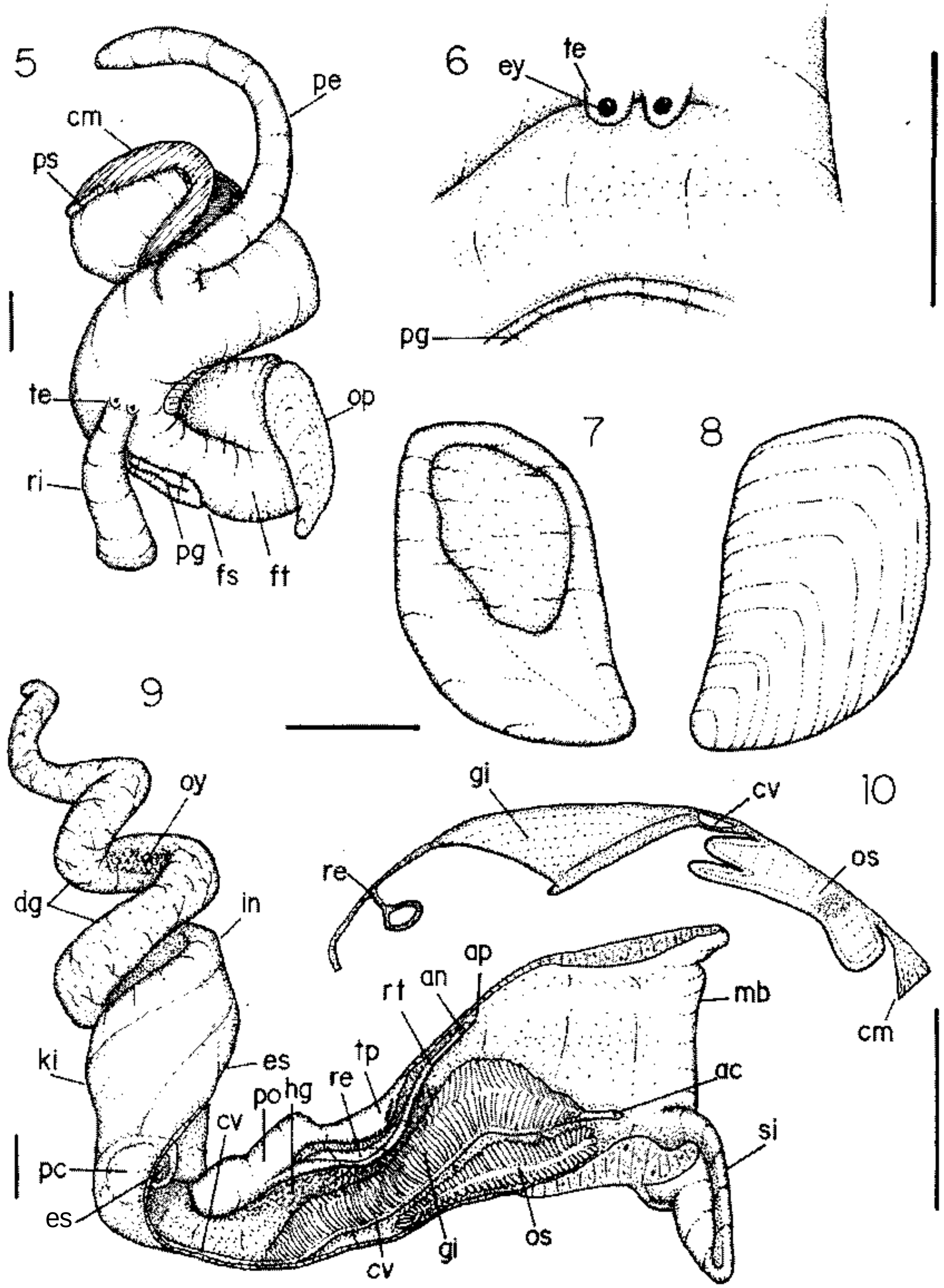
Shell (Figs 1-4). Shell description see Matthews *ct al.*, 1975:94 (Figs 17-19); Brateher & Cernohorsky, 1987:159 (Figs. 185a-c). Protoconch of one smooth, opaque whorl. Columclla with a median, low, spiral fold all along its length (Fig. 4), finishes in middle region of inner lip as a low tooth (Fig. 3).

Head-foot. Color homogeneous yellowish cream. Head inlaid (Figs. 5-6). Tentacles *very* short, dorso-ventrally flattened, rounded tip (Figs. 5, 6, 12). Eyes dark, spherical, situated near tentacles tip (Fig. 6). Basal, proximal introvert aperture somewhat broad, transverse, anterior and ventral to tentacles (Fig. 5). Foot occupying almost half a whorl, without divisions; sole without folded borders. Anterior furrow of pedal glands. Columellar muscle with about 1.5 whorls, somewhat thick (Fig. 5). Males with a slight long penis in central-right region posterior from head.

**Operculum**. Large, unguiculate, pale-brown, nucleus terminal (Figs. 7, 8). Occupying entire shell aperture (Fig. 5). Inner sear sub-quadrate, near superior and inner margins (Fig. 7).

Mantle organs. Mantle border simple, not pigmented. Siphon well developed, yellowish cream in color, with smooth borders (Fig. 9). Mantle cavity of about 2.5 whorls. Osphradium, elliptical, long, about half of gill length (Fig. 9); with several, uniform filaments on both sides of osphradial ganglion; right filaments larger (about twice) and more complex and numerous than left filaments; right filaments with bifid extremity, with ventral branch narrower the dorsal branch (Fig. 10). Osphradium anterior half broader than posterior, which tapers gradually; in posterior extremity only right filaments present (Fig. 9). Gill long, about 7/10 of pallial cavity length; anterior end somewhat far from mantle border, only with a short portion of ctenidial vein, in form of a very small septum, present; filaments begin gradually at some distance from anterior end (Fig. 9, ac); anterior half broader than posterior half. Each gill filament triangular, low, apex almost central, both margins almost straight (Fig. 10); gill posterior extremity far from pericardium, a long portion of cteniclial vein free from gill filaments (Figs. 9, 17). Ctenidial vein narrow and uniform all along its length, except for its broader anterior extremity. A slight narrow space between gill and rectum. Hypobranchial gland thin, located in posterior half of cavity, at left of rectum, whitish in color. Anal gland with some slender, irregular and somewhat longitudinal acina, immersed in right margin of hypobranchial gland, in anterior half of rectum, but far from anus (Figs. 17, 18), brown in color. Pallial gonoducts run along right margin of posterior half of pallial cavity, attached also to pailial floor (Figs. 17, 18). Rectum narrow, lying ventral to and to the left of pallial gonoducts; in females, in its middle region it separates from oviduct on margin of a pallial septum (Fig. 18: re). Anus far from anterior extremity of pallial oviduct in females; bears a small papilla. Anterior 1/3 of pallial right margin and posterior 1/3 of its left margin without inner structures (Fig. 9).

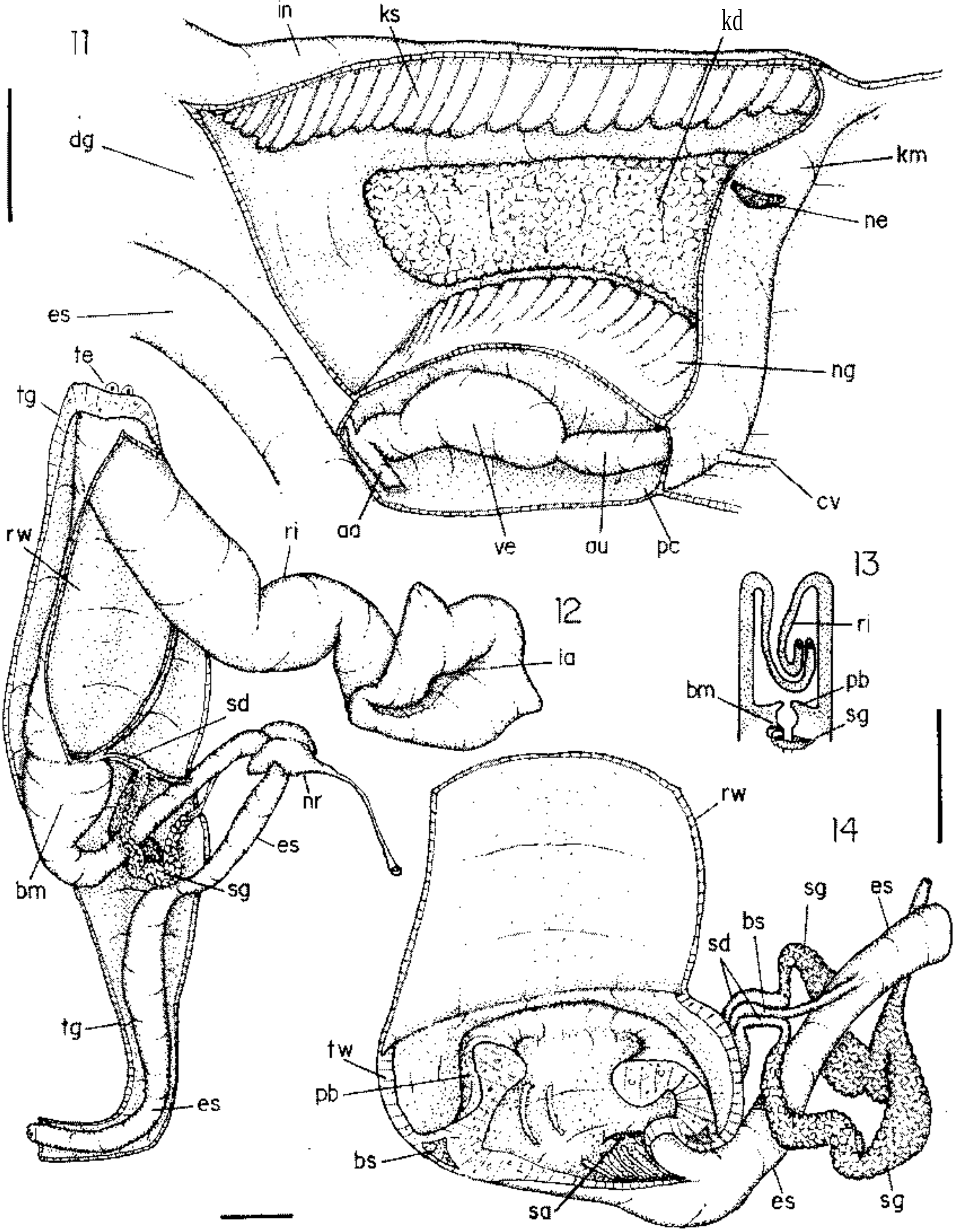
Circulatory and excretory systems (Fig. 11). Pericardium long (about half whorl) and slight narrow, in posterior-left extremity of pallial cavity Heart large, auricle anterior to ventricle. Kidney of almost one whorl, ample, flattened, located in right region of posterior limit of pallial cavity. Kidney with a large and ample inner chamber separating two whitish glandular lobes. Dorsal glandular lobe somewhat thin, slight homogeneous surface. Ventral-right lobe thick, edges attached to rectum, bearing several transverse, tall, uniform folds. Nephridial gland narrow, transversally folded, color pale cream,



**Figures 5-10.** ***Terebra dislicata*** **anatomy. 5. head-foot, frontal view, mantle fully removed, specimen preserved with part of the introvert exposed; 6. detail of head, just in region of tentacles, specimen with introvert retracted; 7. operculum, inner view; 8. operculum, outer view; 9. mantle cavity (ventral-inner view) and hole visceral mass of female; 10. pallial cavity, female, transversal section on middle level of osphradium. Scales: 1 mm.**

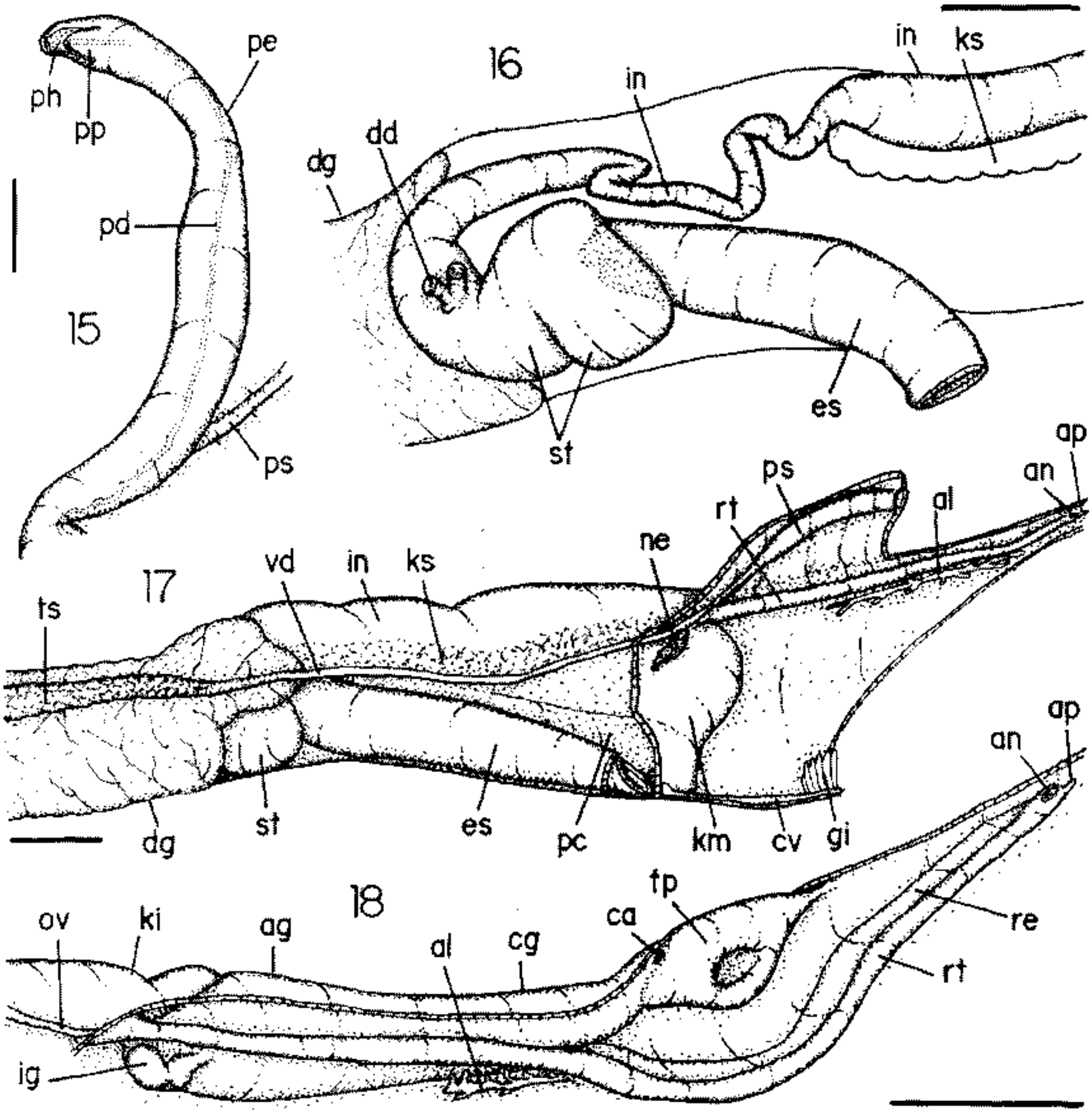
transverse slit in middle region of membrane between kidney and pallial cavity (Figs. 11, 17).

**Digestive system.** Rhynchodeal introvert very long, length about 1.5 times rhynchocoel length



**Figures 11-14.** ***Terebra dislocata*** **anatomy. 11. anterior region of visceral mass, ventral view, kidney chamber and pericardium opened longitudinally, posterior limit of pallial cavity also shown; 12. head and haemocoel, ventral view, foot removed, rhynchodeal wall (rw) opened longitudinally and the introvert partially uncoiled and deflected to outside, esophagus also partially deflected; 13. haemocoel and forefut schematic picture, dorsal view, following the model of current literature, not to scale nor proportions; 14. detail of posterior region of foregut with structures partially opened longitudinally, inner surfaces exposed. Scales: 1 mm.**

section triangular, edges dorsal margin of membrane between kidney and pericardial chambers (Fig. 11: ng). Nephrostome a (coiled in retracted condition), cylindrical (Figs. 5, 12), thick-muscular walls with two layers closely connected with each other; outer layer (in retracted



**Figures 15-18.** ***Terebra dislocata*** **anatomy. 15. penis and adjacent region of head in its base, dorsal view, apical structures seen if it was a transparent structure; 16. visceral mass, one whorl before its anterior limit, ventral view, digestive gland partially removed, remainder structures beyond digestive tubes not drawled; 17. last (anterior) whorl of visceral mass and posterior region of pallial cavity uncoiled, male, ventral view; 18. pallial oviduct and adjacent structures, ventral view. Scales: 1 mm.**

condition) of longitudinal fibers, inner layer of circular fibers; in anterior region a thin layer of superficial circular fibers present. Distal aperture of rhynchodeal introvert (rhynchostome) large, with a terminal muscular sphincter; a pair of angular, flattened, lateral expansions present (Fig. 12). Both layers of introvert walls do not glide over one another when it is protracted, but in this case the whole wall is evagined. Rhynchodeal wall very thin, transparent, covers inner surface of anterior half of haemocoel (Figs. 12, 14). Several small muscle fibers connect rhynchodeal walls with inner surface of haemocoel, more concentrated in anterior extremity; they also connect other foregut structures. Proboscis very small, reduced, present only as muscular ring around anterior surface of bucal mass (Fig. 14) Rhynchodeal wall region preceding proboscis suddenly becomes slightly thick muscular (Fig. 14: tw). Buccal mass semi-spherical. Pair of retractor muscles absent. Radular sac wanting. Salivary glands yellow, divided into two separated, long masses (Figs. 12, 14), located side-by-side in esophagus just posterior to buccal mass. Both salivary glands are connected to each *other* in *both* extremities and surround, as a ring, anterior esophagus (Figs. 13, 14); in their distal extremities a long ligament connects both glands with adjacent esophagus, just anterior to nerve ring; in proximal extremities both glands are connected by a long ligament bearing their ducts running on both its sides and a vessel running in center; they insert in left-anterior region of buccal mass, run a short distance attached to its outer surface towards posterior, afterwards both ducts open into buccal mass, close to each other, just on limit with esophagus (Fig. 14, sa). Venom gland and muscular bulb absent. Scheme of foregut structures shown in Figure 13. Inner surface of buccal mass almost smooth, only some longitudinal, low folds present (Fig. 14). Esophagus long and somewhat broad, runs almost straight towards anterior where it passes though nerve ring, twists and returns to posterior (Fig. 12); no developed inner glands; inner surface of esophagus entirely with many narrow, longitudinal folds, about 15 near stomach. Stomach broad, curved (Fig. 16), marked by a sudden increase of esophagus after a thin sphincter. Stomach located half whorl posterior to kidney, part immerse in digestive gland (anterior-left surface exposed) (Fig. 17). Duct to digestive gland single, located in middle, ventral region of stomach (Fig. 16). Stomach inner surface with longitudinal folds (similar to those of esophagus) in its anterior half, and almost smooth in its posterior half. Digestive gland of about three whorls posterior to stomach and about 1/4 whorl anterior and ventral to it (Figs. 9, 17), clear brown in color. Intestine gradually narrowing after stomach (Fig. 16), with thin walls, almost smooth inner surface; runs slightly coiled posterior to kidney. Rectum and anus described above.

**Genital system.** Male. Testis brown, short (about one whorl) and narrow (Fig. 17), running into the columellar side of visceral whorl posterior to kidney. Visceral vas deferens runs close to columella, very narrow, almost straight, edges left margin of kidney (Fig. 17). Seminal vesicle and prostate not differentiable. Pallial vas deferens narrow, runs along right margin of floor of pallial cavity, in its anterior region immersed in head tegument (Fig. 5). Penis long, little more than half a whorl (Fig. 5) and flattened; slight uniform width along its length (Fig. 15). Penis duct very narrow, slightly coiled at penis base, runs near left margin of penis (Fig. 15). Penis distal end with a deep concavity turned to right, aperture small; papilla rather large, in center of this concavity. Penis duct opens on papilla tip.

**Female.** Ovary similar in localization to testis, also narrow, with almost two whorls (Fig. 9). Visceral oviduct very narrow (Fig. 18), runs close columella edging left margin of kidney, inserts in pallial oviduct in its right posterior extremity; no gono-pericardial duct. Pallial oviduct broad and long (about half of pallial cavity length), no separated albumen and capsule glands, but a single, uniform, whitish, thick walled tube (Fig. 18), with a broad, flattened inner duct. Ingesting gland small, vesicle-like, located in left-posterior region of pallial oviduct; *receptaculum seminis* very short. Inner duct of Pallial oviduct narrows in its anterior region, opens in a small slit to the right of base of terminal pouch at tip of a small elevation (Fig. 18). Terminal pouch broad, outstanding, with a circular, shallow, blind-sac aperture; it occupies almost half of total length of pallial gonoduct (Figs. 9, 18). Rectum runs in ventral surface of pallial oviduct, near its anterior region runs away from it on a small septum (Fig. 18) as described above.

**Habitat.** From intertidal to 52 m deep. Sanely substrates.

**Measurements** (in mm). Museu de Zoologia da Universidade de Sao Paulo (MZSP) collection # 28792: 23.5 by 5.8 (figured specimen).

**Distribution.** From Maryland, USA to Ceará, Brazil. Also reported from Pacific coast, from California to West Panama (Bratcher & Cernohorsky, 1987).

**Material examined.** — UNITED STATES OF AMERICA; **Florida,** Sanibel Island, MZSP # 28792, 2 males, 3 females (Ross Gundersen col., 15/xi/1998, J. Leal leg.).

## *Character Discussion*

In the following discussion, the account of each character begins with an abbreviated descriptive sentence followed by plesiomorphic and derived condition(s); also included are the CI and RI (consistency and retention indices, respectively) values for the character under the most parsimonious hypothesis. When pertinent, a discussion of the character is given. The discussion excludes characters commented on by Taylor, Kantor & Sysoev (1993), except if there is any interesting comment. The data matrix for the characters is in Table I. The resulting cladogram is in Figure 19.

### Shell

**1. Form: 0= fusiform; 1= turriform; 2=**

Table I. Characters matrix for the analysis of the **Terebrinae**. See text for list of characters.

| character | | 1 | | 2 | | 3 | | 4 | |
|---|---|---|---|---|---|---|---|---|---|
| | 12345 | 67890 | 12345 | 67890 | 12345 | 67890 | 12345 | 67890 | 1234 |
| outgroup | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | 0000 |
| *H. cinerea* | 10111 | 11001 | 11001 | 00001 | 01110 | 01000 | 00101 | 00000 | 0000 |
| *H. hastata* | 10100 | 10001 | 21001 | 00001 | 01100 | 01000 | 00001 | 00100 | 1100 |
| *T. taurina* | 12000 | 10110 | 00001 | 011?1 | 01100 | 10000 | 11101 | 10011 | 0?00 |
| *T. crassireticula* | 10000 | 11100 | 00110 | 10011 | 11110 | 00010 | 00101 | 10010 | 011? |
| *T. leptapsis* | 10100 | 10100 | 00111 | 101?1 | 11110 | 10010 | 20101 | 10010 | 0??? |
| *T. spirosulcata* | 10000 | 11100 | 00121 | 01011 | 01210 | 00000 | 00011 | 12010 | 0000 |
| *T. brasiliensis* | 20000 | 10100 | 00111 | 01100 | 01211 | 22111 | ?0111 | 10000 | 0101 |
| *T. gemmulata* | 10000 | 11200 | 00021 | 01011 | 01211 | 23101 | ?1101 | 11010 | 0000 |
| *T. dislocata* | 11000 | 11100 | 00121 | 01011 | 01211 | 22101 | ?1101 | 12010 | 0100 |

**paedomorphic (CI=100 =100,** additive).

The elongated, turriform, multispiral shell of the terebrids is the long-known character of the family, as stated by Taylor *et l.* (1993). On the other hand, *T. brasiliensis* presents a form of the adult shell similar to other species when immature, *i.e.*, with proportionally few whorls and large protoconch. That this form may be "paedomorphic" (*i.e.*, young form) appears to be an adequate term to explain the condition in *T. brasiliensis*. This state is an autapomorphy.

2. **Columella:** 0= simple; 1= with a small fold; 2= with an outstanding fold **(CI=66 RI=0**; additive).

The normal form of the terebrid columella is simple, without any ornamentation. However *T. taurina* possesses a well-developed, outstanding fold running the entire middle region of the columella (Simone, 1999, fig. 25), clear until near its inner lip. A similar, but lower fold is found in *T. dislocata*. It is clear in the analysis of the present sample that this condition appeared at least twice in the evolution of the group. However, similar states are known in other terebrids, such as *T. variegata* Gray, 1834 (Bratcher & Cernohorsky, 1987: 13, fig. 5).

3. Number of **protoconch** whorls: 0= one whorl; 1= more than one whorl **(CI=50 RI=50)**.

Head-foot

4. Foot size: 0= about half whorl in length; 1= very large **(CI=100 RI=100)**.

5. **Operculum: 0=** large, occupying entire aperture; 1= reduced **(CI=100 RI=100)**.

6. **Tentacles: 0=** long (about half of foot length); 1= reduced **(CI=100 RI=100)**.

7. Tentacles relative position: **0=** far from each other; **1=** close to each other **(CI=25 RI=25)**.

Independently of the polarity of this character, a number of homoplastic origins must be assumed. ACCTRAN would result in five steps, while DELTRAN would result in four independent origins of the apomorphic condition, interpretation accepted here.

8. Eye position: 0= base of tentacle; **1=** tip of tentacle; 2= absent/reduced **(CI=100 RI=100,** non-additive).

It is interesting to observe the great variation in characters of the cephalic tentacle among the terebrids. There are repeated reductions in different terebrids, as well as displacement of the eye towards the tip (*Terebra*). Further studies on the ontogeny and of more species certainly will bring new insights to understand the character. Species of *Hastula* appear to have the eyes in their plesiomorphic condition located at the base of the tentacles, also present in *H. bacillus* (Deshayes, 1859) (cf. Taylor & Miller, 1990). The first state is synapomorphic for *Terebra*, the second a *T. gemmulata* autapomorphy.

9. A deep **columellar** furrow in soft parts, from foot to end of columellar muscle: **0=** absent; 1= present **(CI=100 RI=100)**.

A deep longitudinal furrow in the columellar region of head-foot structures is obviously caused by the tall columellar fold of the shell, present only in *T. taurina* (Fig. 126).

The distribution of muscular tissue appears to be greatly modified by the fold, mainly at the posterior end of the columellar muscle, which is bifurcated (Simone, 1999, fig. 124).

10. Anterior furrow of pedal glands: 0= present; 1= absent (**CI=100=100**).

Pedal glands are obviously present in all terebrids, but probably due to modifications on the foot (particularly its development) a clear anterior furrow is absent in both species of *Hastula.*

**Pallial** organs

11. Siphon border: 0= smooth; **1**= papillate; 2= pair of basal projections (**CI=100 RI=100,** non-additive).

Of the species examined, *H. cinerea* is the only one constantly exposed to intertidal waves. The papillae on the siphon border could be an adaptation to avoid sand pollution in the pallial cavity (Simone, 1999: fig. 47), maybe not necessary in deeper water species. Some of them are occasionally exposed in low tide, as *T. dislocata* (cf. Mollick, 1973). The pair of basal projections of the siphon border *of H. hastata* (Fig. 61) resembles, on the other hand, those found in the Volutidae (Muricoidea).

12. Osphradium filaments: 0= smooth; 1= scalloped (**CI=100 RI=100**).

13. Osphradium: 0= symmetrical (both sides similar); **1**= asymmetrical (fewer left than right filaments) (CI=50 **RI=75**).

The osphradium is always well developed in these predatory animals. In some species, it is even larger (in area) than the gill (*e.g.*, *T. crassireticula* and *T. leptapsis*). The change in filament shape seems to be synapomorphic for *Hastula.* Reduction of the left filaments, present in *T. crassireticula*, *T. leptapsis, T. brasiliensis*, *T. spirosiilcata* and *T. dislocata,* is normally observed in groups with size reduction, e. g., the Columbellidae (Muricoidea). From the above-cited species, only *T. spirosulcata* is not small. This most parcimonious explanation for the evolution of this character is as a synapomorphy of the group of *Terebra*, excluding *T. taurina*, with a secondary reduction in *T. gemmulata.*

14. **Osphradium** length: 0= 2/3 of gill length; 1= almost the same as gill length; 2= 1/2 of gill length (CI=66 **RI=80,** non-additive).

A first degree of reduction in osphradium length appears to be synapomorphic for *Terebra.* A further reduction seems to have occurred twice, in *T. spirosiilcata* and in *T. gemmulata* + *T. dislocate.*

15. Anterior end of **ctenidial** vein: 0= united with gill anterior end; 1= raised, septum-like, anterior to gill filaments on anterior end (CI=50 **RI=0**).

The presence of a small septum preceding the gill appears to be a modification of the ctenidial vein, but more detailed study is necessary. However, the absence of this character in the outgroups indicates that it could be a synapomorphy of the Terebrinae, probably with secondary loss in *T. crassireticula.*

16. Gill and osphradium filaments: 0= uniformly distributed; **1**= concentrated in their posterior region (CI=100 **RI=100**).

This feature gathers *T. crassireticula* and *T. leptapsis* in a monophyletic group within the genus.

17. Posterior region of ctenidial vein: 0= with gill filaments; **1**= free from gill filaments (CI=50 **RI=75**).

Normally in neogastropods, the posterior end of the gill is near the pericardium and the ctenidial vein connects with the auricle at a short distance behind the gill. In *Terebra,* however, a prolongation of this region of the ctenidial vein (free from gill filaments) is observed. This has most probably been lost in (*T. crassireticula* + *T. leptapsis).*

18. Anal gland: 0= present; 1= absent (CI=33 **RI=0**).

The long and digitiform glandular acina, of conspicuous purple color, are here called anal gland, following Marcus & Marcus (1960). Further research, however, is necessary to confirm its primary homology with the anal gland of the Muricidae. The terebrine anal gland appears to be a specialized region of the hypobranchial gland rather than a structure connected to the anus, from which it is separated in some species. Anyway, its absence in *T. crassireticula*, *T. leptapsis*, *T. brasiliensis* and *T. taurina* is regarded as apomorphic. It seems more reasonable to admit a single origin with three independent losses than three independent, identical acquisitions in groups of *Terebra.* Differently from the normal purple color observed in most species, the anal gland in *T. dislocata* is pale brown and longitudinal (and not with transversal acina).

19. Septum connecting rectum in mantle in females: 0= absent; 1= present (CI = 50 RI=66).

In *T. crassireticula*, *T. spirosulcata,* and *T. dislocata,* the anterior region of the rectum runs on the border of an enigmatic septum, instead of being directly connected to the mantle surface. This character is absent in males. Investigation in the immature females is also necessary It seems to be no alternative except admitting three independent acquisitions.

Kidney and heart

20. Type: 0= mostly solid; 1= comprising a broad chamber limited by two lobes, one lobe septate attached to rectum and the other flattened **dorso-ventrally** (CI=50 **RI=0**).

An almost solid kidney (without a large inner hollow chamber) is similar in outgroups and may be regarded as plesiomorphic, even though some doubts exist with respect to the kidney of other conoideans. Anyway, the kidney described in state 1 is regarded for the moment as a terebrine synapomorphy, but further analysis of other conoideans could change this concept. The plesiomorphic condition of the *T. brasiliensis* kidney may be another indication of paedomorphosis.

21. **Heart-pericardial** area: 0= about 1/4 of kidney area; 1= about 1/8 of kidney area (**CI=100 RI=100**).

Maybe due to the predatory habit and the necessity of extending the proboscis (and other organs, *e.g.*, the introvert) the heart in neogastropods is large in comparison to caenogastropods. This condition may help in hydrostatic pressure. However, in *T. crassireticula* and *T. leptapsis* the heart is not so large, an apomorphy within the genus.

Digestive system

22. Rhynchodeal wall: **0**= muscular; 1= membranous (**CI=100 RI=100**).

In the outgroup *Cochlespira* and some Crassispirinae (Kantor et *al.*, 1997), muscle fibers present in the rhynchodeal wall indicate some degree of contractile function. This state is not found among terebrids, of which the inner rhynchodeal wall is practically only a muscleless membrane. This condition is regarded as apomorphic. Several other conoideans, however, show this condition. The terebrid rhynchodeal wall still presents a thin layer of muscular fibers near the retractor muscles of the proboscis (Simone, 1999, fig. 135). Simone (1999) provided a more extensive discussion of proboscis and foregut structures and their probable evolution from structures present in other neogastropods.

Taylor *et al.* (1993) grouped the terebrids *Pervicacia* and *Duplicaria* on the basis of a septum dividing the anterior and posterior areas of the rhynchocoel. Nothing similar to this structure, however, was found in the Terebrinae, indicating that such a condition must be a synapomorphy of those two genera.

23. Rhynchodeal introvert: 0= absent; 1= present, short; 2= present, very long (**CI=100 RI=100,** additive).

The rhynchodeal introvert is a specialized tube of the anterior extremity of the foregut, inserted in the rhynchostome region of the rhynchodeal cavity. It may be entirely retracted within this cavity. It is absent in outgroups and appears to be a terebrine synapomorphy. The introvert is very long (*i.e.*, as long as, or longer than the remainder of the rhyiichocoel) in *T. brasiliensis, T. spirosulcata*, *T. gemmulata* and *T. dislocata.* In some species, such as *T. gemmulata* and *T. dislocata*, only the introvert is present, most of other foregut structures, including the proboscis and the venom apparatus, being missing. However, the large increase of the introvert is not necessarily accompanied by loss of the proboscis, as shown *T. spirosulcata.* Other comments on the introvert are found in Taylor *et al.* (1993:128), who interpret it as a terebrid synapomorphy.

24. Accessory salivary glands: 0= present; 1= absent (**CI=50 RI=50**).

A pair of very long and developed accessory glands is present in *H. hastata* and *T. taurina*. However, in *H. hastata* they are far from each other, each inserted on the opposite side of the proboscis base (close to the retractor muscle), while in *T. taurina* they are inserted close to each other in the buccal mass. The accessory salivary glands are considered more plesiomorphic in the family, but further studies are necessary to determine the primary homology with similar structures of the neogastropods. This seems to indicate that the loss within *Hastula* was independent from that of all *Terebra* except *T. taurina.*

**25. Proboscis: 0= normal; 1= reduced (CI=100 RI=100).**

The so-called normal proboscis is longer than half the rhynchodeum. In *T. brasiliensis, T. gemmulata* and *T. dislocata,* however, the proboscis is greatly reduced, becoming only a muscular ring preceding the esophagus, but, in these cases, the vestigial proboscis is distinct. In the tree published by Taylor *et al.* (1993, 153), the absence of a well-developed proboscis is a synapomorphy for a terebrid subgroup.

The supposition of close relationship between the intraembolic conoidean proboscis with the pleurembolic proboscis of its relatives (*e.g.*, Muricoidea and Cancellarioidea) was extensively discussed in Simone (1998, fig. 149). The conoidean proboscis appears to be homologous to the buccal mass part of the pleurembolic proboscis, and the rhynchodeal wall of the conoideans appears to be homologous to the remaining regions of the pleurembolic proboscis. The polyembolic proboscis, found in some conoideans such as *Terebra brasiliensis, T. gemmulata* and *T. dislocata* would represent, as noted Miller (1989) and Taylor er *al.* (1993), a great development of the introvert accompanied by reduction of the proboscis and other structures of the buccal mass.

**26. Retractor muscle of proboscis: 0= a pair; 1= several small pairs; 2= reduced (CI=66 RI=66; non-additive).**

As is normal for probosciferous prosobranchs, most terebrines possess a pair of strong retractor muscles at the base of the proboscis. But *T. crassireticula*, *T. leptapsis* and *T. taurina* possess several small pairs, distributed around the basal region of the proboscis, connecting it with adjacent region of inner surface of haemocoel. Some fibers of the retractor muscles also insert into the rhynchodeal wall and buccal mass. In *T. gemmulata, T. brasiliensis* and *T. dislocata*, the reduction of the retractor muscle is obviously a reflex of the reduction of the proboscis.

**27. Salivary glands: 0= amorphous; 1= two hemispherical masses; 2= modified in position; 3= lost (CI=75 RI=85, non-additive).**

In *Hastula,* the salivary glands are two small spheres connected to each other (as also noted by Marcus & Marcus 1-960, fig. 6). In most other species of the family the salivary glands are amorphous, surrounding the esophagus and the region near the nerve ring. This state is shared with outgroups and regarded as plesiomorphic. In the species with a reduction of the venom apparatus, the salivary glands are missing *(T. brasiliensis)* or strongly displaced *(T. gemmulata, T. dislocata).* In *T. dislocata,* the modified salivary gland may produce the poisonous secretion referred to by Bratcher & Cernohorsky (1987: 159).

**28. Radular sac: 0= present; 1= absent (CI=100 RI=100).**

The loss of the radular sac also usually follows the reduction of the proboscis and the loss of the venom apparatus in the species group composed by *T. brasiliensis, T. gemmulata* and *T. dislocata.*

**29. Accessory structure of proboscis: 0= absent; 1= present (CI=50 RI=50).**

The accessory structure of the proboscis is another enigmatic character of terebrids. It was considered synapomorphic for the family (shared with the sister-taxon Pervicaciinae) by Taylor *et al.* (1993: 129) and by Simone (1999). Only three terebrid species possess this structure in the present sample (*T. crassireticula*, *T. leptapsis*, *T. brasiliensis*). Considering that in several species of *Terebra* the accessory structure is always located in same side of rhynchodeal wall and present the same inner organization, and that it is present in a *Hastula* species (Taylor & Miller, 1990), Simone (1999) considered that the structure could have appeared in the ancestor of the terebrid and disappeared in several of its subgroups.

**30. Venom gland: 0= present; 1= absent (CI=100 RI=100).**

Taylor *et al.* (1993) also considered the absence of a venom gland apomorphic, but it was not used as a character in the terebrid branch of their tree. On the other hand, the altered histology of the anterior portion of the venom gland was used as a state uniting a subgroup of the terebrids (*Pervicacia* and *Duplicaria*). This state was not used herein because it is found only in *T. spirosulcata* (Simone, 1999, Figs. 138-139). It would be just another autapomorphy.

31. Venom gland position in relation to nerve ring: **0=** nerve ring on about its middle region; 1= on anterior third; 2= on posterior third (CI=66 **RI=0,** non-additive).

The displacement of the venom gland corresponds to independent autapomorphies in *T. taurina* and *T. leptapsis.*

32. Rectum: 0= attached to **pallial gonoduct;** 1= far from **pallial** gonoduct (CI=50 **RI=50).**

Most terebrids and outgroup species possess the female pallial gonoducts closely attached to the rectum, but in *T. gemmulata*, *T. taurina* and *T. dislocata* the rectum deflects in the middle or anterior region of the oviduct, somewhat away from it.

33. Anus location in the pallial cavity: **0=** anterior third; 1= in middle (CI=50 **RI=0).**

There is a tendency in the terebrids for the anus to be located posteriorly, far from the mantle border. There is a relatively long region at the right of the pallial cavity without any visible structure.

34. Anal papilla: 0= present; 1= absent (CI=50 **RI=50).**

The anal papilla is found in the outgroup *Cochlespira*, and its presence in most terebrids is regarded as plesiomorphic. This papilla appears to have been lost twice in *Terebra* (*T. brasiliensis* and *T. spirosulcata*).

Genital system

35. Gonad anterior end: 0= rounded; 1= tapering gradually (CI=100 **RI=100).**

The testis-seminal vesicle complex and the ovary of the terebrines taper gradually to the origin of the gonoduct. In other groups there is normally a sudden constriction separating both structures. However, this character is still obscure among other conoideans.

36. Narrow part of anterior visceral gonoduct (adjacent to kidney): 0= short; 1= long (about half whorl) **(CI=100 RI=100).**

This seems to be a synapomorphy of the genus *Terebra.*

37. Prostate location: **0=** pallial cavity; 1= visceral mass; **2=** absent as a differentiated organ (CI=50 **RI=33,** non-additive).

Usually the prostate gland is present in the pallial cavity. Two modifications occur in the family. In *T. gemmulata*, the prostate is located in the anterior region of visceral mass, by the side of (and compressing) the kidney (37a). In *T. spirosiilcata* and *T. dislocata*, it may be present, but distributed as a glandular tissue along the pallial spermoduct (37b), since there is not a morphologically differentiated prostate as in other species. Conditions 1 and 2 are non-additive and the 37b condition would have originated twice.

38. Penis muscular root; 0= inconspicuous; 1= very developed **(CI=100 RI=100).**

Some muscles of the penis base (root), protruding into the haemocoel, are sometimes clearly visible in several caenogastropods, but in *H. hastata* they are much more complex and enlarged, displacing the foregut structures to the left when fully developed.

39. Penis origin: 0= to right side of head; 1= near median line (CI=50 **RI=66).**

The polarization of the states of this character is based on the usual lateral (right) situation of the penis in outgroups. But *T. gemmulata*, *T. crassireticula*, *T. leptapsis*, *T. spirosiilcata, T. taurina* and *T. dislocata* present an almost central origin of the penis.

40. Tip of the penis with a papilla, within a terminal chamber: 0= present; **1=** absent **(CI=100 RI=100).**

41. Penis with deep chamber at tip: 0= absent; 1= present **(CI=100 RI=100).**

Although the closer outgroup *Cochlespira* has a more complex penis tip, it has a central papilla surrounded by a terminal chamber, which may indicate the plesiomorphic condition. In *T. taurina* and *H. hastata* this condition is modified. The former has probably lost any apical structures, with the penis duct opening at the penis tip in a simple fashion. *H. hastata*, on the other hand, developed a very deep chamber to the side of the papilla.

42. Ingesting gland: **0=** between albumen and capsule glands; **1=** posterior to albumen gland (CI=25 **RI=0).**

The ingesting gland is situated between the albumen and capsule glands of the pallial oviduct in most neogastropods. In *H. hastata,*

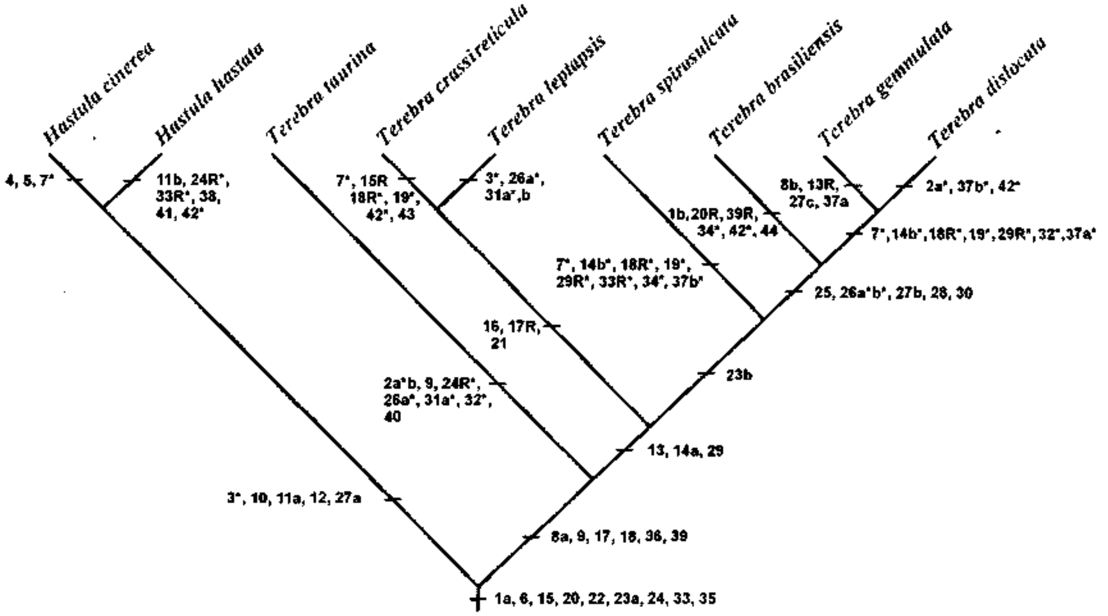


Figure 19. Single most parsimonious tree of the analyzed **Terebrinae (length,** 82; CI, 67; **RI,** 63), with synapomorphies shown (*, homoplasy; R, reversion).

*T. crassireticula*, *T. brasiliensis*, and *T. dislocata*, however, it is the more posterior structure of the pallial oviduct. They are considered independent apomorphies.

43. Terminal pouch: 0= present; 1= absent **(CI=100 RI=100).**
44. Terminal pouch aperture: 0= large; 1= anterior and narrow **(CI=100 RI=100).**

The terminal pouch with a large aperture of some terebrines is here regarded as plesiomorphic since it is found in several other conoidean species. It may be a synapomorphy of the superfamily or of one of its subgroups. *T. crassireticula* has probably lost this structure. *T. brasiliensis*, on the other hand, possesses an anterior, very narrow terminal pouch aperture, with a deep, blind sac duct. This condition resembles the bursa copulatrix of several Muricoidea and of *Conus bertarollae*, to which the terminal pouch may be homologue. If this is correct, the *T. brasiliensis* bursa-like terminal pouch could have assumed a condition similar to the plesiomorphy of the superfamily, another possible indication of paedomorphosis.

## *Discussion of* ***the cladogram***

The monophyly of the terebrines (Figure 19) is supported by eight synapomorphies (one of shell, two of foregut and five of other structures). *Hastula* and *Terebra* are monophyletic taxa, with five and four synapomorphies respectively. In the evolution of *Terebra*, there is an increase in the size of the introvert as a synapomorphy of the group *spirosulcata*$^+$ and a reduction of the venom apparatus, proboscis and associated structures, occurred at different levels in the evolution of the *Terebra*. The secondary loss of the accessory proboscis structure occurred convergently, but this structure is known in *Hastula* species not sampled in this study [*T. imitatrix* Auffenberg & Lee, 1988 and in *H. bacillus* (Deshayes) (cf. Taylor & Miller, 1990)]. As commented previously, if all accessory proboscis structures are homologous, there is a strong possibility that this structure is a terebrine synapomorphy, secondarily lost in some species of the group, as advocated by Taylor *et al.* (1993).

Taylor et *al.* (1993) proposed a cladogram in which *Hastula* is separated from (*Pervicacia* + *Duplicaria*) (both Pervicaciinae). The present paper considers species of both, *Hastula* and *Terebra*. What we need now is a more comprehensive analysis, including all the genera of the subfamily and clearly identifying synapomorphies at all levels in the evolution of the group.

## *Conclusions*

Three main conclusions may be drawn from the analysis made in this paper:

- the monophyly of the terebrines is presently supported by eight synapomorphies.
- the genera *Hastula* and *erebra* appear to form a monophyletic group within the subfamily, supported respectively by five and four known synapomorphies.
- several anatomical structures (beyond the shell and foregut ones) proved useful for comparative analysis from family to species levels, and for phylogenetic studies.

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