

THE MORPHOLOGY OF *HYDROBIA TRUNCATA* (GASTROPODA:
HYDROBIIDAE): RELEVANCE TO SYSTEMATICS
OF *HYDROBIA*

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The genus *Hydrobia* is of considerable current interest to ecologists and systematists. Hydrobiids comprise one of the most important groups of deposit-feeding invertebrates to be found in estuaries and salt marshes of eastern North America and northern Europe. For example, an exceptionally high density of 42,000 individuals/m² may be attained in the mid-intertidal offshore bank of an estuary (Russell-Hunter and Russell-Hunter, 1962). Considerable attention has been given to how various hydrobiid species are deployed, use resources, interact when sympatric, and occupy different niches (Russell-Hunter and Russell-Hunter, 1962; Newell, 1965; Fenchel, 1975; Hylleberg, 1975; Fenchel, Kofoed, and Lappalainen, 1975; Fenchel and Kofoed, 1976; Levinton and Lopez, 1977; Lopez and Levinton, 1978; Wells, 1978).

While the species status within northern European *Hydrobia* has seemingly been clarified (Muus, 1967), this is not the case in North America. There is no systematic study comparing species of *Hydrobia* along the east coast of North America. *Hydrobia totteni* Morrison (1954) and *Hydrobia salsa* Pilsbry (1905) from New England have been characterized by salinity preferences, diameter of egg capsules, and diameter of eggs (Mazurkiewicz, 1972). The external topography, radula and male reproductive system of *Hydrobia totteni* have been studied (Davis, 1966). However, because *Hydrobia truncata* Vanatta (1924) has not been studied, because the detailed comparative anatomy of all organ systems of *H. salsa*, *H. totteni*, and *H. truncata* has not been presented, and because it is suspected that there is a complex of undescribed brackish-water hydrobiid species along the east coast of North America (Morrison, 1970), we cannot be sure which species has really been studied in current ecological literature.

The purposes of this paper are to present a detailed morphological study of *Hydrobia truncata* Vanatta to be used for comparison within and between populations of North American *Hydrobia*, and to show that three species of *Hydrobia* live in the same geographic area in New England. Detailed morphology is presented for four reasons: It has been shown that clarification of the systematic relationships among hydrobioid snails (*i.e.* those resembling hydrobiids in shell, penis, radula, and operculum) is dependent on morphological studies that include all organ systems, and that characters seen in the female reproductive system, entire male reproductive system, nervous system, and radular teeth have thus far best served to delineate taxa of hydrobioids (Davis, 1979). The Hydrobiidae of authors pre-1979 were a worldwide family consisting of about 100 genera and over 1000 species. However, it has been shown by detailed morphological studies that the Hydrobiidae *sensu lato* are polyphyletic (Davis, 1979). The large North American hydrobioid fauna of some 25 genera and 100 species, mainly of fresh

water (Thompson, 1968), is poorly understood. There are no detailed morphological studies on North American *Hydrobia* or other related brackish water hydrobioid snails. The relationships between North American and northern European *Hydrobia* are unclear (Muus, 1963; Davis, 1966).

Ecological data are given for specimens of *Hydrobia truncata* from Stone Harbor, New Jersey, to facilitate comparisons with other taxa. A conchological comparison is made between paratypes of *H. truncata*, *H. salsa*, and other taxa referred to *H. totteni* and *H. truncata*.

MATERIALS AND METHODS

Localities

Specimens of *Hydrobia truncata* were collected from a salt water marsh at the Wetlands Institute, Stone Harbor, Cape May Co., New Jersey, from May to August, 1977–1978. They came from a shallow high intertidal pool in the marsh near a channel that emptied into the inlet at Stone Harbor. Other pools were present in the marsh; they appeared isolated but were connected during extremely high tides (E. Hoagland, personal communication). Salinity at high tide was determined using an American Optic salinometer. Snails were collected with a hand sieve from the substrate and algae.

Field excursions were made to the type locality at marshes of the Little Choptank River, Towne Point, Delaware-Maryland Peninsula, Dorchester Co., Maryland. *H. truncata* was not found there.

Anatomy

Dissections were carried out on more than 100 individuals at magnifications of 25 \times and 50 \times using a WILD M-5 microscope. Established techniques were used (Davis and Carney, 1973; and Davis, 1979). Specimens were prepared for histology by fixation in Bouin's solution and were sectioned at 7 μ m and stained in hematoxylin and eosin. Shells were cleansed of periostracum and debris by soaking in Clorox (0.5% sodium hypochlorite). Radulae were obtained by dissecting out buccal masses and soaking them in Clorox to remove the soft tissue. After initial measurements and row counts, the radulae were permanently mounted in Euparal for study under high magnification, including oil immersion. Drawings of organs were prepared from sketches and checked against measurements for accuracy using the technique of Davis and Carney (1973).

Shells of the following populations were compared: *Hydrobia truncata* (holotype and paratypes, A.N.S.P. [Academy of Natural Sciences of Philadelphia] 132886); Stone Harbor, Cape May Co., New Jersey (A.N.S.P. 349361); Salt Pond, behind Falmouth Beach, Barnstable Co., Massachusetts, July, 1978, (A.N.S.P. 349374). *Hydrobia totteni*, Wild Harbor River, N. Falmouth, Buzzards Bay, Barnstable Co., Massachusetts, September, 1969 (A.N.S.P. 349375); Provincetown, Barnstable Co., Massachusetts, 1884 (A.N.S.P. 134452); Katama Bay, Martha's Vineyard, Dukes Co., Massachusetts, 1875 (A.N.S.P. 102648). The type of *H. totteni* has not been located and is presumed lost. *Hydrobia salsa* (holotype and paratypes, A.N.S.P. 90445) Cohasset, Norfolk Co., Massachusetts. Note that *Hydrobia minuta* (= *Turbo minuta* Totten, 1834) is a synonym of *H. totteni* (see Morrison, 1954).

TABLE I
 Comparison between shell parameters of populations of Hydrobia studied. \bar{X} , mean; s.d., standard deviation.

| Population | Parameters | | | | | | | | | |
|---|----------------------|------|--------------------------------------|------|--|------|------------------------------------|------|---------------------------------------|------|
| | Length last 3 whorls | | Shell width/ Length last 3 whorls | | Length body whorl/ Length last 3 whorls | | Length aperture/ Width aperture | | Length aperture/ Length last whorl | |
| | \bar{X} | s.d. | \bar{X} | s.d. | \bar{X} | s.d. | \bar{X} | s.d. | \bar{X} | s.d. |
| <i>H. tolleni</i> (N = 25) Provincetown | 2.56 | 0.28 | 0.61 | 0.02 | 0.74 | 0.03 | 1.47 | 0.09 | 0.47 | 0.03 |
| <i>H. tolleni</i> (N = 25) Martha's Vineyard | 2.52 | 0.18 | 0.63 | 0.02 | 0.75 | 0.02 | 1.51 | 0.11 | 0.78 | 0.02 |
| <i>H. tolleni</i> (?) (N = 4) Wild Harbor River (sample II-1-Grassle) | 2.56 | 0.28 | 0.56 | 0.01 | 0.75 | 0.03 | 1.52 | 0.06 | 0.47 | 0.03 |
| <i>H. salsa</i> (N = 5) paratypes | 3.18 | 0.10 | 0.64 | 0.01 | 0.76 | 0.02 | 1.48 | 0.06 | 0.49 | 0.04 |
| <i>H. irvincta</i> (N = 10) (Salt Pond, 7/78) | 3.32 | 0.22 | 0.60 | 0.02 | 0.68 | 0.03 | 1.44 | 0.08 | 0.43 | 0.02 |
| <i>H. irvincta</i> (N = 25) Stone Harbor | 2.81 | 0.20 | 0.58 | 0.03 | 0.69 | 0.02 | 1.48 | 0.08 | 0.44 | 0.02 |
| <i>H. irvincta</i> (N = 25) paratypes | 2.59 | 0.14 | 0.56 | 0.02 | 0.67 | 0.02 | 1.54 | 0.05 | 0.43 | 0.02 |

Shells were considered to house mature animals if the parietal callus was complete. Length of the body whorl, width of the fourth whorl (counting adapically from the aperture), width of the body whorl, and length and width of aperture were measured on mature specimens. Because the shells of many populations have eroded apices or are decollate, one cannot compare sizes of individuals by total shell length. Accordingly, length of the last three whorls and length of the body whorl were used as indices of size (Davis, 1969a). Populations were compared using length of body whorl/length of the last three whorls; they were compared by width of the fourth whorl/length of the last three whorls. Computer-mediated comparisons of length of body whorl per length of the last three whorls were made for six populations. The statistical analysis system was used with the General Linear Model procedure for linear regressions. Regressions were compared using the standard *t* test. Other ratios were also employed (Table I).

RESULTS

Ecology

H. truncata was found only in the one pool at Stone Harbor, New Jersey that received regular tidal flow. The salinity was 32‰. The pool had a hard-packed mud-silt bottom paved with live and dead specimens of *Gemma gemma* (Totten) (Bivalvia); the pool was anoxic at the bottom. Specimens of *H. truncata* were found on the few bare patches, on the *Gemma* shells, and on immersed algae (red and green). The snails apparently preferred the green algae to the red. The snails were moderately abundant, as a single scoop of a hand sieve yielded 25 to 75 individuals. *Ilyanassa obsoleta* (Say), young specimens of *Mytilus edulis* Linné, *Mya arenaria* Linné, and an occasional specimen of *Sayella fusca* (C. B. Adams) (pyramidellid) were other molluscs found in the pool.

At low tide the depth of the pool was reduced to 7 to 15 mm; some areas of bottom were uncovered, leaving temporarily unconnected pools scattered about. The snails appeared to bury themselves just beneath the surface at low tide. At no time during the seven visits to the marsh at low tide was the entire bottom of the pool exposed.

Anatomy

External features. The head-foot morphology and pigmentation patterns of *H. truncata* are very similar to those described for *H. totteni* (Davis, 1966). The snout (Fig. 1A) is 0.58 mm long and darkly pigmented along most of its length with the anterior end (0.05-mm strip) unpigmented. The buccal mass is readily seen through the snout. The snout tip, when viewed anteriorly, is seen to have yellow granules imbedded within it (see Davis, 1966, Fig. 4). The cylindrical tentacles measure 0.85 mm from the eye lobes and extend beyond the tip of the snout. The tentacle tips are rounded and fringed with long cilia. Occasionally, snails have tentacles either bent along their length or forked near the tips. There are 5 to 8 ciliated tufts (hypertrophied) along the outer basal margin of the left tentacle as in *H. totteni* (Davis, 1966) (Fig. 1A). A black pigment bar, about 0.14-mm long, is medially placed near the tentacle tips. As in many hydrobioids, there are dense concentrations of yellow granules about the eyes (Fig. 1A). The concentration of granules in *Hydrobia* does not reach the extent of concentration in the Pomatiopsidae, where the lunate patch of glands

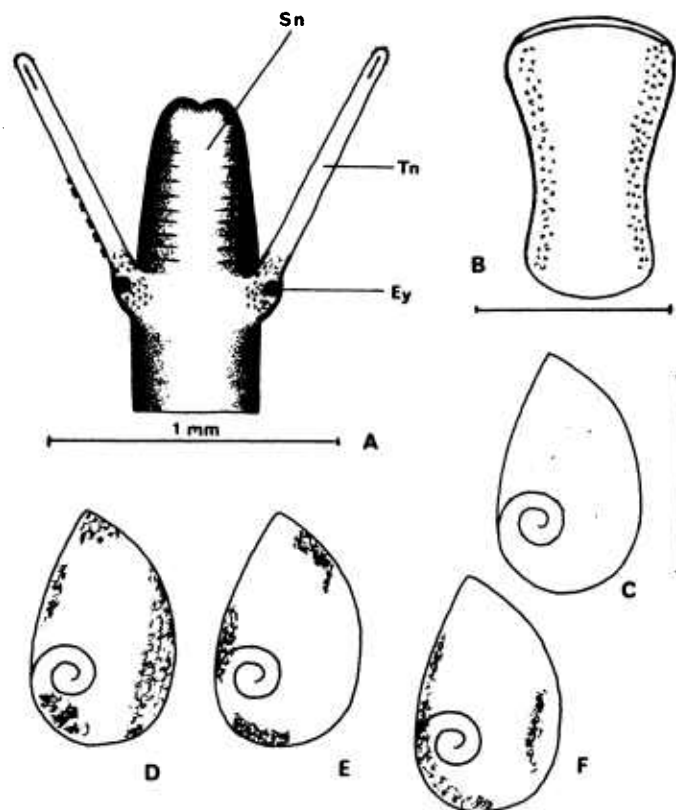


FIGURE 1. The head, foot, and operculum of Stone Harbor specimens of *Hydrobia truncata*. A: Dorsal view of the head; B: Ventral aspect of the foot showing anterior mucous slit; C: Operculum showing paucispiral condition. D-F: Variation in pigment pattern seen on the operculigerous lobe through the operculum.

is so dense that it has been called an "eyebrow." Similar granules are sparse within the tentacles. The eye lobes are only slight swellings compared to the bulging eye lobes of many pomatiopsid snails (Davis, 1967, 1979). Behind the snout the head and mantle cavity floor are peppered with white granules (Davis, 1966) except for a narrow strip along the center.

As in *H. totteni*, there is an unpigmented strip running obliquely along the side of the head-foot (Davis, 1966, Fig. 3). There is neither an omniphoric groove nor a pedal crease (contrast with *Pomatiopsis*, Davis, 1967). The foot (Fig. 1B), measures (with animal gliding) 1.4 mm by 0.88 mm, is elliptical in shape and is widest anteriorly. The sole is dotted along the sides with yellow granules. A narrow mucous slit is present along the anterior margin. The snails are agile and move rapidly by ciliary motion. Floating individuals are frequently found in the laboratory cultures.

A prominent yet small, highly ciliated pallial tubercle is seen emerging from the extreme right mantle edge at a point where the mantle folds dorsally to encircle the head (Fig. 2A, B). This fold in the mantle is directly opposite the path of the exhalent current along the neck of the animal, and corresponds to the most adapical end of the shell aperture when the snail emerges. This is the first

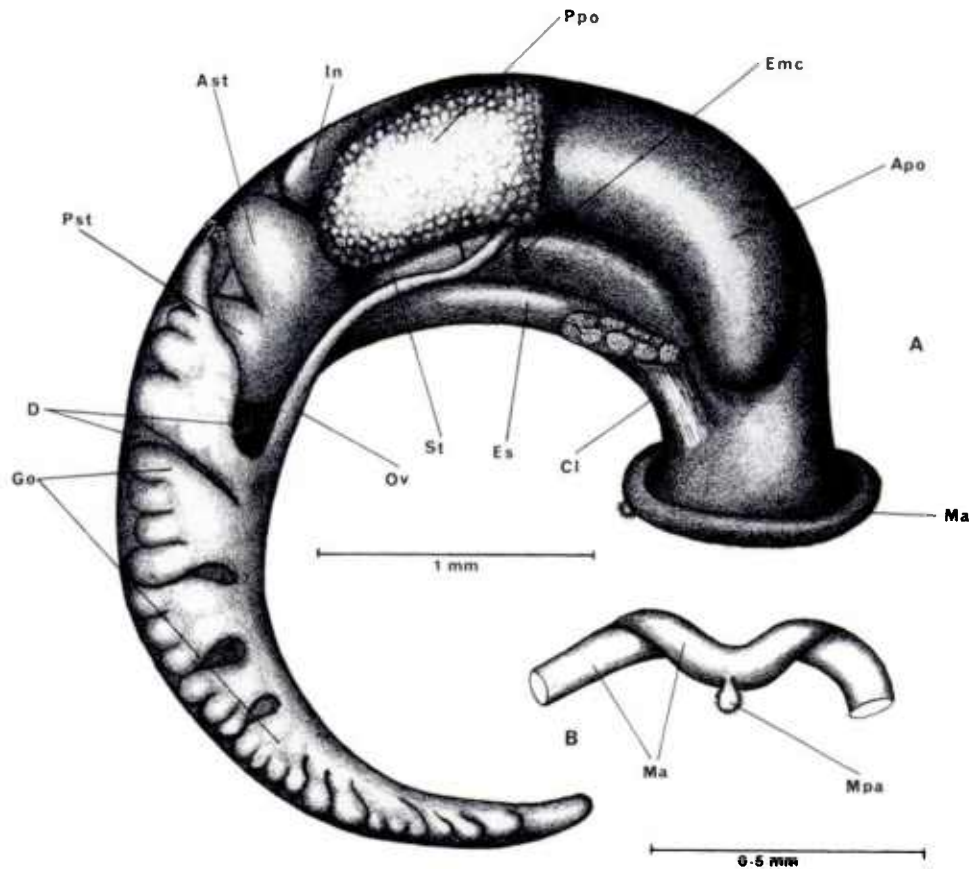


FIGURE 2. Female without head, showing organs as seen through the epithelium, but with kidney tissue removed to reveal the style sac (St), A; section of the mantle collar turned back to reveal the ciliated mantle papilla, B. Abbreviations are: Apo, anterior section of pallial oviduct (= capsule gland); Ast, anterior chamber of stomach; Cl, columellar muscle; D, digestive gland; Emc, posterior end of the mantle cavity; Es, esophagus; Go, gonad; In, intestine; Ma, mantle collar; Mpa, papilla of the mantle; Ov, oviduct; Ppo, posterior section of pallial oviduct (= albumen gland); Pst, posterior chamber of stomach; St, style sac.

description of such a tubercle in North American *Hydrobia*. *Hydrobia ulvae* of Europe has a much larger pallial tentacle, similarly located (Fretter and Graham, 1962, p. 581; personal observation; and Taylor, 1966), but no one has speculated as to its function. It may function as a sensory aid and/or assist in voiding excrement. It is found in both sexes. Body pigmentation consists of a dark dusting of melanin pigment on the dorsal surface with a much lighter dusting of pigment on parts of the ventral surface.

Operculum. The operculum (Fig. 1C) is corneous, thin and paucispiral with 2.5 to 2.75 rapidly expanding whorls. It is light brown in color. Its position on the operculigerous lobe is similar to that of *H. totteni* (Davis, 1966, Fig. 3). The pigmentation of the foot under the operculum varies from uniformly dark all around the perimeter to discrete patches along the perimeter (Fig. 1D-F). It does not differ much from that of *H. totteni* (Davis, 1966, Fig. 4).

TABLE II

Dimensions (mm) of non-neural organs and structures of Hydrobia truncata.

| Organ or structure | | No. | \bar{x} | s.d. | Range |
|---------------------------|-------|-----|-----------|-------|--------------|
| Body | (m) L | 5 | 5.34 | 0.134 | 5.16 - 5.52 |
| | (f) L | 7 | 6.26 | 0.446 | 5.80 - 7.06 |
| Gill number | (m) | 8 | 21.12 | 1.36 | 19-23 |
| | (f) | 6 | 23.3 | 2.25 | 19-25 |
| Osphradium (m) | L | 6 | 0.266 | 0.02 | 0.24 - 0.30 |
| | W | 6 | 0.083 | 0.008 | 0.08 - 0.1 |
| Gonad (m) | L | 7 | 2.990 | 0.226 | 2.68 - 3.22 |
| | W | 5 | 0.448 | 0.052 | 0.36 - 0.50 |
| | (f) L | 13 | 3.060 | 0.339 | 2.6 - 3.8 |
| | W | 10 | 0.628 | 0.042 | 0.56 - 0.68 |
| Prostate | L | 13 | 1.200 | 0.104 | 1.04 - 1.34 |
| | W | 13 | 0.417 | 0.056 | 0.26 - 0.48 |
| Penis | L | 9 | 1.530 | 0.210 | 1.27 - 1.94 |
| | W | 9 | 0.327 | 0.043 | 0.249- 0.388 |
| Pallial oviduct | L | 13 | 2.480 | 0.229 | 2.22 - 2.94 |
| | W | 11 | 0.589 | 0.056 | 0.50 - 0.70 |
| Bursa copulatrix | L | 14 | 0.366 | 0.046 | 0.3 - 0.42 |
| | W | 14 | 0.196 | 0.027 | 0.14 - 0.24 |
| Seminal receptacle (body) | L | 8 | 0.185 | 0.018 | 0.16 - 0.20 |
| | W | 8 | 0.121 | 0.008 | 0.11 - 0.14 |
| Seminal receptacle (duct) | L | 8 | 0.035 | 0.007 | 0.02 - 0.04 |
| | W | 8 | 0.048 | 0.010 | 0.04 - 0.06 |
| Digestive gland (f) | L | 7 | 2.760 | 0.337 | 2.3 - 3.3 |
| Buccal mass (m + f) | L | 14 | 0.704 | 0.118 | 0.56 - 0.98 |

Mantle Cavity. The organization of the mantle cavity and structure of the gills and osphradium are typically hydrobioid (see Davis, 1967; Davis, Kitikoon, and Temcharoen, 1976, for figures). Gill and osphradium statistics are given in Table II. The mantle cavity is about 1.7 mm long, all the length of which (except the anteriormost 0.18 mm) is occupied by the ctenidium. The osphradium is centered slightly less than half way back along the ctenidium.

Digestive System. The digestive system is typically hydrobioid. Two elongated salivary glands (length of 0.34 mm) open into the posterior dorsal buccal mass (Davis, 1969b, Fig. 32). As in other hydrobioids (Davis *et al.*, 1976), the salivary glands lie on top of the nerve ring and do not pass through the ring. The oesophagus enters the stomach between the two chambers (Figs. 2A, 4B). A single opening to the digestive gland is found. In both sexes the digestive gland extends to the tip of the snail and lies lateral to the gonad. No caecal appendix to the stomach (figured for *Pyrgula*, Radoman, 1955) was found in dissection or in section. Radoman (1973) has considered this structure to be a characteristic of the Hydrobiidae. The intestine exits anteroventrally from the style sac and bends back upon itself before running forward (Figs. 2A, 3A, 4B). Fecal pellets

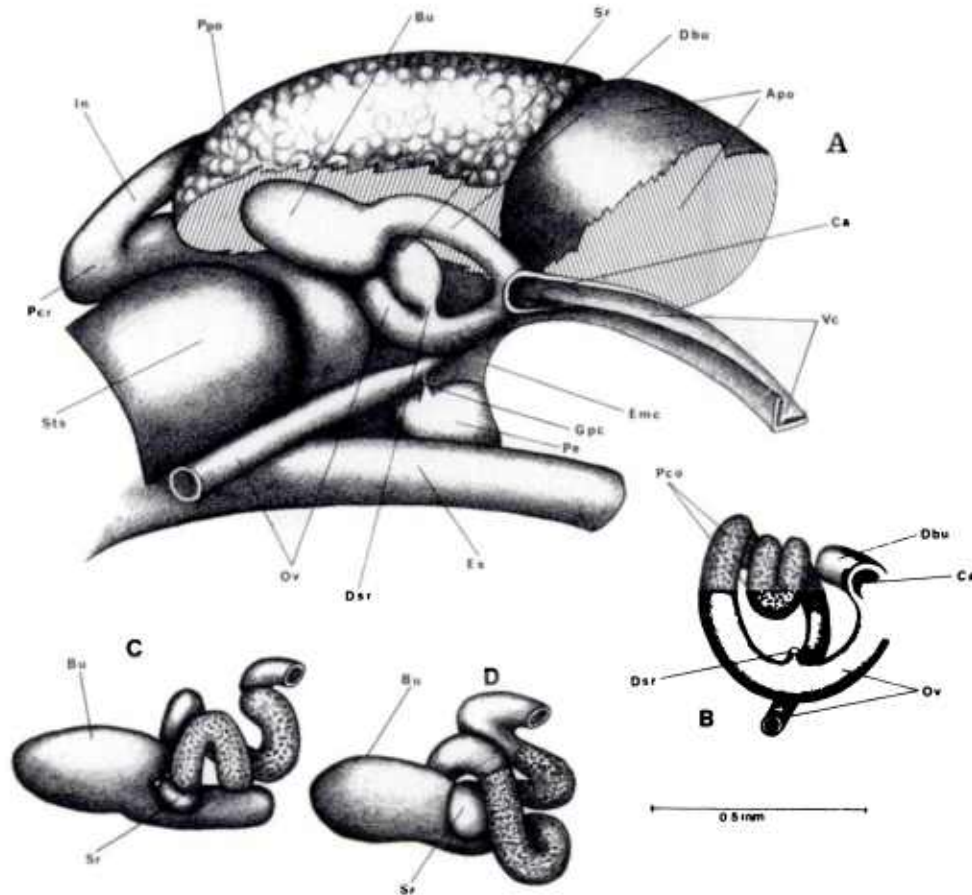


FIGURE 3. Female reproductive system. A: Same view as in Figure 2A, but restricted to the area immediately surrounding the bursa copulatrix complex. The epithelium and kidney tissue were removed. Much of the ventral section of the albumen gland (Ppo) was scraped away to reveal the bursa copulatrix (Bu) and seminal receptacle (Sr). Most of the capsule gland (Apo) was removed to reveal the interrelationship of the ciliated ventral channel (Vc) of the pallial oviduct, to the common aperture (Ca), to the duct of the bursa (Dbu), and the oviduct. The gonopericardial duct (Gpc) is clearly seen in this orientation, connecting the oviduct (Ov) to the pericardium (Pe). B: Same view as in Figure 2A, but with the bursa copulatrix and seminal receptacle removed to reveal the nature of the pigmented oviduct coils that are dorsal to the bursa in Figure 2A. C, D: The bursa copulatrix (Bu) seen in Figure 2A has been lifted and rotated to reveal how the seminal receptacle (Sr) tucks into the space caused by the juncture of the duct of the bursa and the projecting anterior end of the bursa. Abbreviations are: Apo, anterior pallial oviduct (= capsule gland); Bu, bursa copulatrix; Ca, common aperture of ventral channel, duct of the bursa, and oviduct; Dbu, duct of the bursa; Dsr, duct of the seminal receptacle; Emc, posterior end of the mantle cavity; Es, esophagus; Gpc, gonopericardial canal; In, intestine; Ov, oviduct; Pe, pericardium; Pco, pigmented coils of the oviduct; Pcr, pellet compressor; Ppo, posterior pallial oviduct (= albumen gland); Sr, seminal receptacle; Sts, style sac; Vc, ventral channel of the pallial oviduct.

are fusiform in shape and light brown in color, typical for hydrobioids (Taylor 1966).

The radula is typically taenioglossate. The tooth and cusp morphologies are as shown for *H. totteni* (Davis, 1966, Fig. 6). The central tooth has a single

basal cusp originating from a pronounced lateral angle as is typical for the Hydrobiidae (Davis, 1966, 1979). As in *H. totteni*, there is a pronounced basal process on the central tooth. Radular statistics based on 12 individuals with mean and standard deviation are as follows: length, 0.569 ± 0.05 mm; width, 0.117 ± 0.01 mm; width of base of central tooth, 0.032 ± 0.003 mm; number of rows of teeth, 41 ± 1.86 ; number of rows in formative stage, 2.92 ± 1.08 .

The various cusp arrangements on the four types of taenioglossate teeth are given with the percentage of radulae showing the formula at least once (in parentheses): central tooth; 3-1-3/1-1 (82), 4-1-4/1-1 (41), 4-1-3/1-1 (35), 3-1-2/1-1 (24), 5-1-4/1-1 (11); lateral tooth; 3-1-3 (86), 4-1-3 (79), 3-1-2 (43), 6-1-4 (7); inner marginal; 11 (77), 10 (53), 12 (47), 13 (18), 8 (12); outer marginal; 11 (88), 12 (62), 10 (56), 13 (25), 9 (25).

The formulae for the most common cusp arrangements in *Hydrobia truncata* are given with the percentage of radulae with this formula (in parentheses): central tooth, 3-1-3/1-1 (82); lateral tooth, 3-1-3 (86); inner marginal, 10-12 (94); outer marginal, 11-12 (100). The tooth morphologies, radula statistics and formulae vary little from those of *H. totteni* (Davis, 1966).

Female reproductive system. The female reproductive system is discussed in some detail because investigators of previous studies of North American hydrobiid anatomy have not discussed it (Davis, 1966) or have treated it incompletely (Thompson, 1974), and because this organ system has been useful in distinguishing clades within the hydrobioid grade of organization (Davis, 1968; Davis *et al.*, 1976; Davis, 1979).

The general organization of the female reproductive system is shown in Figures 2 and 3; organ measurements are presented in Table II. The ovary, which appears yellow-white in life, is long relative to body length (48.8%). There are usually 5 large anterior gonad branches and a variable number of small lobes posterior to them. The gonad is unusual in that the anterior-most gonadal lobe extends over the posterior stomach lobe, and the gonad always extends to the posterior tip of the digestive gland (Fig. 2A). Usually, hydrobioid ovaries occupy a fraction of the length of the digestive gland between the end of the stomach and the posterior tip of the snail (*e.g.*, *Pomatiopsis*, Davis, 1967). The gonadal lobes have a swollen appearance in mature females and oocytes are frequently seen.

The oviduct, ventrally viewed, passes over the oesophagus-stomach juncture and disappears beneath the pallial oviduct (Fig. 2A). The pallial oviduct (Ppo and Apo) is quite large, averaging 2.49 mm in length. The two sections of this organ, the glandular posterior albumen gland (Ppo) and the anterior capsule gland (Apo), are readily distinguishable when the living animal is lightly stained with neutral red. The capsule gland appears smooth and firm while the albumen gland has distinct glandular pustules and appears flimsy. The capsule gland is the longer of the two sections of the pallial oviduct. The bursa copulatrix is found to be imbedded in the mid to posterior ventral part of the albumen gland. The bursa is revealed by gently scraping away the ventral and ventro-lateral parts of the albumen gland (Fig. 3A). The posterior tip of the bursa copulatrix is located about 0.24 mm anterior to the posterior end of the pallial oviduct; the ventral bursa is free of the albumen gland, covered with kidney tissue, and presses against the ventral surface of the oviduct. A single tube, the duct of the bursa, extends from the anterior end of the bursa (Dbu, Fig. 3A).

The pear-shaped seminal receptacle (Sr) is found snugly fitted between the anterior end of the bursa and the duct of the bursa. The duct of the seminal receptacle (Dsr), very small and wider than long, joins the oviduct just before

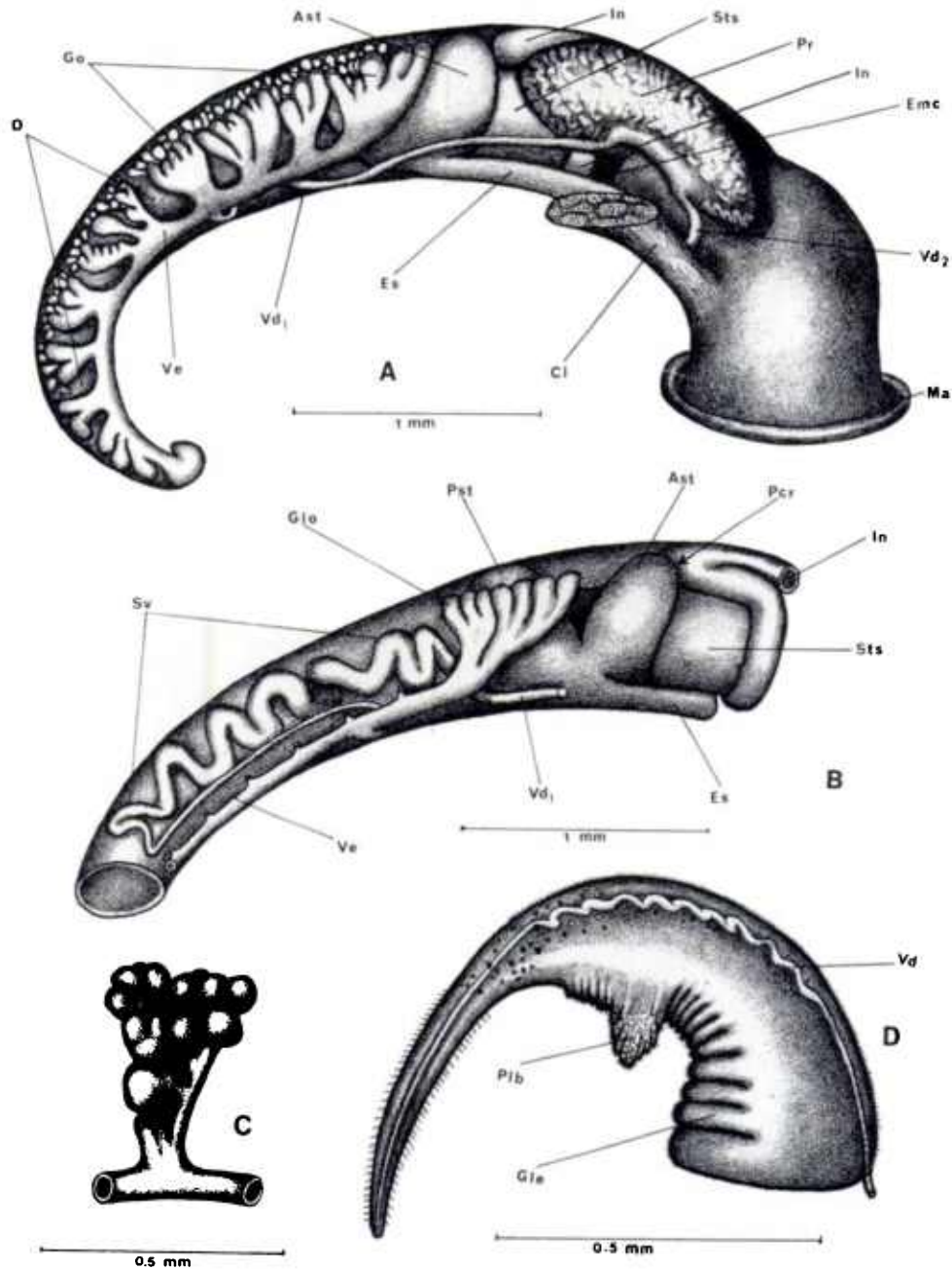


FIGURE 4. Male reproductive system. A: Male oriented as the female in Figure 2A. The kidney tissue was removed to reveal the style sac (Sts). B: Gonad with most gonadal lobes removed to reveal the position of the seminal vesicle (Sv). C: An enlarged view of one gonadal lobe with numerous sperm-producing pouches. D: The penis. Abbreviations are: Ast, anterior chamber of the stomach; Cl, columellar muscle; D, digestive gland; Emc, posterior end of the mantle cavity; Es, esophagus; Gle, glandular edge of the penis; Glo, gonadal lobe; Go, gonad; In, intestine; Ma, mantle collar; Pcr, pellet compressor; Pib, penial lobe; Pr, prostate; Pst, posterior chamber of the stomach; Sts, style sac; Sv, seminal vesicle; Vd, vas deferens; Vd₁, posterior vas deferens; Vd₂, anterior vas deferens; Ve, vas efferens.

the latter joins the duct of the bursa at a common opening (Ca) to the posterior end of the ciliated groove of the ventral channel (Vc). The ventral channel forms the ventral edge of the pallial oviduct with which it is in open communication. This V-shaped gutter has red-pink granules along its entire length. The morphological inter-relationships of the pallial oviduct, ventral channel, bursa and seminal receptacle characterize, in great part, the genus *Hydrobia*.

The bursa copulatrix-posterior pallial oviduct complex lies ventral to the style sac (Sts) of the stomach and the loop of the intestine circling the anterior end of the style sac. The common opening (Ca) to the ventral channel of the pallial oviduct is just posterior to the posterior end of the mantle cavity (Emc). The ratio of the length of the bursa copulatrix to the pallial oviduct is 0.15; the ratio of the length of the seminal receptacle to the length of the bursa is 0.51. The ratio of the length of the pallial oviduct to the length of the body is 0.40. The oviduct gives off a pronounced gonopericardial duct (Gpc) before reaching the pallial oviduct and diving down beneath the bursa complex. When the bursa is lifted, and rotated through 180° (Fig. 3B-D) the coiled nature of the oviduct dorsal to the bursa is readily discerned. The complex nature of this coiling is very constant within the species. A large segment of the coil is darkly pigmented (Fig. 3B-D), a condition seen in several European Hydrobiidae such as *H. acuta* and *H. ventrosa* (Radoman, 1977). *H. truncata* stores sperm within these coils, not within the seminal receptacle (as seen histologically). In some European hydrobioids, such as various species of *Pyrgula*, the seminal receptacle is a simple outpocketing from a section of the pigmented oviduct coil (Radoman, 1955, 1956). This outpocketing may represent a stage of seminal receptacle reduction leading to the condition of sperm storage in the coils as seen in *H. truncata*. The function of the seminal receptacle in *H. truncata* is not known.

Male reproductive system. Dimensions of organs are given in Table II. As in the female, the gonad is relatively long, 2.99 mm (56% of total body length). It extends anteriorly over the stomach, and posteriorly to the tip of the digestive gland. There are usually 6 to 8 distinct anterior gonad branches and a variable number of single-lobed posterior branches. The 3-dimensional branching pattern of the gonad (Fig. 4C) is similar to that of *Pomatiopsis* (Davis, 1967, plate 12). As in *Pomatiopsis* (Davis, 1967) and other pomatiopsids (Davis, 1979), the seminal vesicle branches off the vas efferens between $\frac{1}{2}$ and $\frac{3}{4}$ the way along the gonad (usually under the fourth branch), and coils behind the stomach (Fig. 4A, B). However, in *H. truncata* the vas deferens extends straight back 1 mm along the gonad and then doubles back upon itself to swell and coil (Fig. 4B). This is quite unlike the condition in *Pomatiopsis* where the coiling begins just anterior to where the vas deferens branches off the vas efferens (Davis, 1967, plate 12).

The prostate measures 1.2 mm long (22% of body length) and has the same glandular nature as in *Pomatiopsis* (Davis, 1967). The tubular collecting duct of the prostate is devoid of glands. The vas deferens enters the prostate about 0.25 mm from its posterior end, coincident with the end of the mantle cavity (Fig. 4A). The anterior vas deferens leaves the prostate 0.37 mm from its anterior tip. The positions of entrance and exit of the vas deferens from the prostate are somewhat intermediate between those of *Pomatiopsis* (Davis, 1967) and *H. totteni* (Davis, 1966). After extending down along the mantle wall to enter the head region, the vas deferens coils (more so than in Davis, 1966, Fig. 3) upwards to enter the penis.

The penis has one duct and a glandular lobe on the concave curvature (Fig. 4D). Its form is similar to that of *H. totteni* (Davis, 1966, Fig. 5), but it differs in

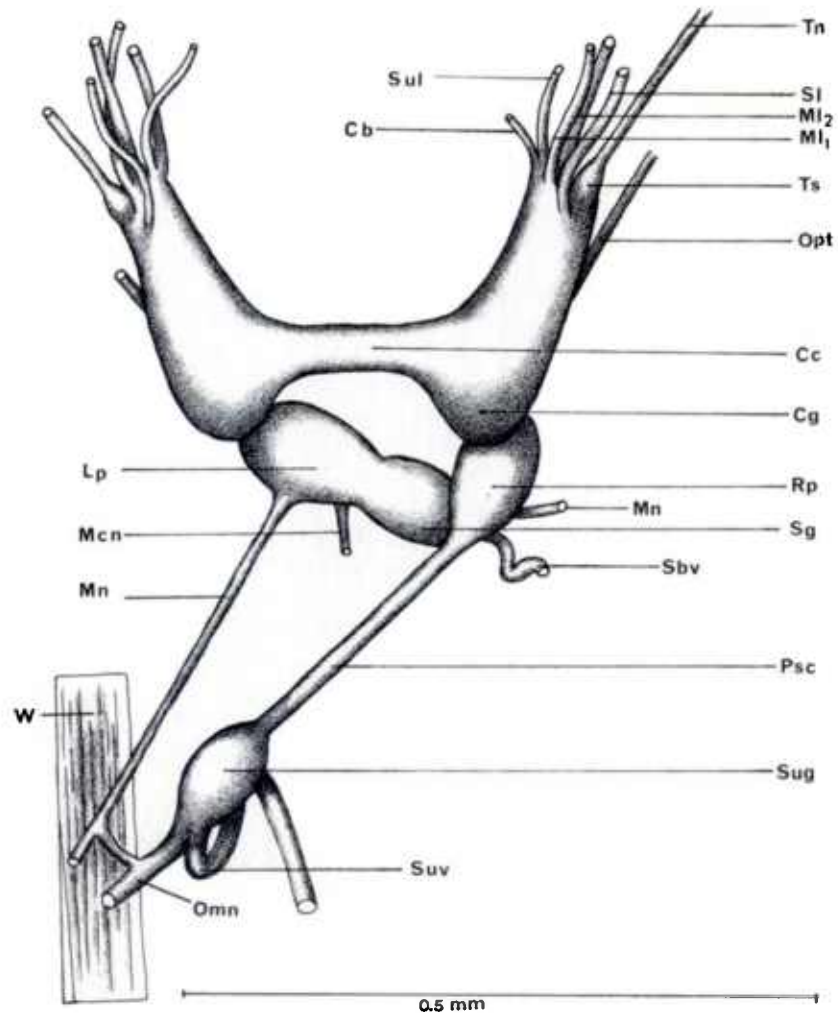


FIGURE 5. Dorsal nervous system. Abbreviations are: Cb, cerebro-buccal connective; Cc, cerebral commissure; Cg, cerebral ganglion; Lp, left pleural ganglion; Mcn, mid columellar nerve; Ml₁, median labial nerve 1; Ml₂, median labial nerve 2; Mn₁, mantle nerve 1; Mn₂, mantle nerve 3; Omn, osphradiomantle nerve; Opt, optic nerve; Psc, pleuro-supraoesophageal connective; Rp, right pleural ganglion; Sbv, subvisceral connective; Sg, suboesophageal ganglion; Sl, supralabial nerve; Sug, supraoesophageal ganglion; Sul, sublabial nerve; Suv, supraoesophageal connective; Tn, tentacular nerve; Ts, basal swelling of tentacular nerve; W, left cephalic wall.

several important respects. Penial folds line the entire concave surface of the verge from the lobe to the base of the verge, whereas in *H. totteni* the folds end far from the end of the base. The penial lobe is not a smooth, simple appendage as in *H. totteni* (Davis, 1966, Fig. 5); instead, it is more triangular and has glandular folds perpendicular to the verge. The glandular lobe seems to be further out along the penis from the base in *H. truncata* compared to its position in *H. totteni*. Comparing the ratio of the length of the verge from its base to the distal edge of the lobe to the length of the verge from its base to the end of the

glandular folds beyond the lobe, the ratio is 0.83 for *H. truncata* and 0.67 for *H. totteni*. The penial filament appears to be relatively longer and more attenuated than in *H. totteni*. The ciliation patterns of the verges of these two species are similar except that the entire concave surface of the verge of *H. truncata* is ciliated while that of *H. totteni* is unciliated beyond the filament. As in *H. totteni*, the vas deferens travels close to the convex surface of the verge and is frequently convoluted. There is no terminal papilla. The glands appear to be distributed over a wider area than those of *H. totteni* (contrast Fig. 4D with Fig. 5 of Davis, 1966). Two gland types, G_1 and G_2 (see Davis, 1969b) are found on the verge. G_1 glands, which appear as closely packed black dots, are found all over the verge, but particularly near the base of the penial filaments. G_2 glands, closely packed spheres, are usually clustered around the bends and folds of the vas deferens. As in *H. totteni*, the verge coils counter-clockwise in life.

Nervous system. The nervous system varies little from that described for other hydrobioids (Krull, 1935; Davis, 1967, 1968, 1969b; Davis and Carney, 1973, Davis *et al.*, 1976), except for degrees of concentration. Lengths of neural structures are given in Table III. The cerebral ganglia give off the same seven nerves as in all rissoaceans (Figs. 5, 6). The base of the tentacular nerve is somewhat swollen, but not as much as in "*Lithoglyphopsis*" *aperta* (Davis *et al.*, 1976). The cerebral commissure is quite elongated. The pleuro-supraoesophageal connective is relatively long as in other species of *Hydrobia* (see Krull, 1935, Davis *et al.*, 1976). The RPG ratio (see Davis *et al.*, 1976, for formula), an index of neural concentration, is 0.547, a value quite close to those of *H. ventrosa* and *H. ulvae* (Davis *et al.*, 1976). A dialyneury connecting the osphradio-mantle nerve and mantle nerve 1 is found (Fig. 5). This has been figured in other publications on hydrobioids (Davies, 1968b; Temcharoen, 1974, unpublished Ms. thesis, Thomas Jefferson University, Philadelphia, PA). As in *Pomatiopsis* (Davis, 1967), the mid-columellar nerve is variable in origin but usually it comes off the left pleural ganglion rather than the suboesophageal ganglion.

The cerebro-pedal complex (Fig. 6), is of the usual hydrobioid type. A minor lateral nerve (P_8) is frequently found on the pedal ganglion. The relative lengths of the propodial ganglia, the metapodial ganglia, and their connectives to the pedal ganglia are much more similar to those of *Pomatiopsis* (Davis, 1967) than in "*Lithoglyphopsis*" *aperta* (Davis *et al.*, 1976). As in other hydrobioids, the

TABLE III

Measurements (mm) of lengths of neural structures of *Hydrobia truncata*.

| Structure | No. | \bar{X} | s.d. | Range |
|------------------------------------|-----|-----------|-------|------------|
| Cerebral ganglion | 9 | 0.206 | 0.020 | 0.18 -0.24 |
| Cerebral commissure | 12 | 0.090 | 0.018 | 0.056-0.13 |
| Right pleural ganglion | 9 | 0.100 | 0.010 | 0.08 -0.12 |
| Left pleural ganglion | 8 | 0.104 | 0.007 | 0.10 -0.12 |
| Pleuro-supraoesophageal connective | 9 | 0.233 | 0.023 | 0.21 -0.26 |
| Supraoesophageal ganglion | 8 | 0.093 | 0.009 | 0.084-0.10 |
| Osphradial-mantle nerve | 6 | 0.058 | 0.016 | 0.04 -0.08 |
| Suboesophageal ganglion | 9 | 0.097 | 0.013 | 0.08 -0.12 |
| Pedal ganglion | 10 | 0.176 | 0.024 | 0.14 -0.22 |
| Pedal commissure | 13 | 0.040 | 0.013 | 0.036-0.06 |
| Buccal ganglion | 5 | 0.102 | 0.005 | 0.10 -0.11 |

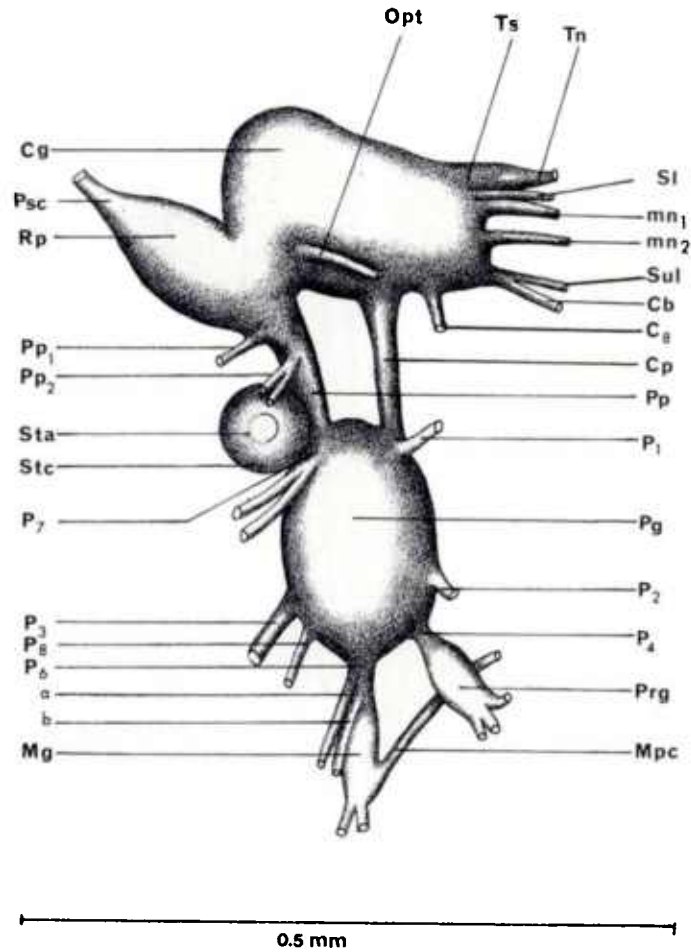


FIGURE 6. Lateral view (right) of Cerebropedal complex. Abbreviations are: a, nerve from metapodial connective; b, nerve from metapodial connective; Cb, cerebro-buccal connective; Cg, cerebral ganglion; Cp, cerebropedal connective; Cs, cerebro-tensor nerve; Mg, metapodial ganglion; Mn₁, media labial nerve 1; Mn₂, median labial nerve 2; Mpc, metapodial commissure; Opt, optic nerve; Pc, pedal commissure; Pg, pedal ganglion; P_p, pleuro-pedal connective; Prg, propodial ganglion; P₁, lateral retractor nerve; P_a, nerve to antero-ventral wall of the pedal haemocoel; P_s, major lateral nerve; P₄, propodial connective; P₆, meta-podial connective; P₇, dorso-lateral pedal nerve; P_m, minor lateral nerve of the pedal ganglion; Pp₁, lateral nerve 1; Pp₂, lateral nerve 2; Psc, pleuro-supraoesophageal connective; Rp, right pleural ganglion; SI, supralabial nerve; Sta, statolith; stc, statocyst; Sul, sublabial nerve; Tn, tentacular nerve; Ts, basal swelling of the tentacular nerve.

origin of the two nerves of the metapodial connective is variable. The connection between the two metapodial ganglia is seen as figured in *Oncomelania minima* (Bartsch) (Davis, 1969b). All the ganglia except the suboesophageal and supraoesophageal are pigmented.

Parasites. Loosely attached epibionts, similar in appearance to ciliated protozoans figured in Davis and Carney (1973), were found on the outside head-

TABLE IV

Analyses of nine shells from living specimens of *Hydrobia truncata* from Stone Harbor, N. J. (measurements in mm).

| Shell trait | Females | | Males | |
|----------------------|-----------|-------|-----------|-------|
| | \bar{X} | s.d. | \bar{X} | s.d. |
| Length | 3.11 | 0.105 | 2.81 | 0.087 |
| Width | 1.70 | 0.071 | 1.52 | 0.036 |
| Length of body whorl | 2.02 | 0.042 | 1.84 | 0.068 |
| Aperture length | 1.24 | 0.034 | 1.14 | 0.044 |
| Aperture width | 0.873 | 0.044 | 0.804 | 0.029 |

foot region of many individuals. Our dissection records show that an unidentified trematode parasitized 16% (33/206) of the Stone Harbor snails studied.

Shells. It may not be possible in every instance to distinguish among northeastern U. S. A. species of *Hydrobia* by examining shells under the dissecting microscope. They are all small (< 4.5 mm), ovate to ovate-conic, smooth, and brown to yellow brown. The umbilical area varies from closed to rimate, moderately open, or pronouncedly open. There is great intra- and interpopulation variability in size and shape. The following descriptions are a partial help for species identification.

Hydrobia truncata. Specimens of *Hydrobia truncata* from Stone Harbor (Fig. 7E-I) are sexually dimorphic (Table IV). Females were significantly larger than males. This could, in part, account for the separated clusters of individuals along the y axis in Figure 8.

The shell is more turreted than ovate-conic (contrast Figs. 7C and 7A) due to a low rate of whorl expansion (defined in Raup, 1966). By comparing the width of the fourth whorl (adapical from aperture)/length of the last three whorls, it is evident that the fourth whorl of *H. truncata* is proportionally larger than that of *H. salsa* or *H. totteni* (Figs. 7A, C; 8). The shell is decollate; the apical one to two whorls are not present on half grown to mature specimens. This decollation contrasts with the various stages of erosion of whorls seen in *H. totteni*. Decollation or erosion has not been seen in, or reported for *H. salsa*.

The whorls are very convex and the suture correspondingly deep. The length of the body whorl is less than that of *H. salsa* or *H. totteni* (Table I). The umbilicus is rimate (*i.e.* very small and slit-like). The length is variable depending on the population, ranging from 2.50 to 3.32 mm (length of last three whorls). Parasitized individuals may have a total length (rare cases with all whorls present; only at Stone Harbor) of 4 mm while unparasitized individuals are less than 3.5 mm in total length.

Hydrobia salsa. The shells are ovate-conic (Fig. 7B) and have a high rate of whorl expansion. The proportion of the fourth whorl compared to the length of the last three whorls is smaller than *H. truncata* (Fig. 8). The shell is entire with 5.0 to 5.5 whorls. The whorls are very convex and the sutures very deep. The length of the body whorl is greater than that of *H. truncata* and *H. totteni*. The umbilicus is very wide and pronounced. The shell length of the paratypes ranges from 3.0 to 3.2 mm (last three whorls); given all whorls the length may be 3.39 to 3.51 mm.

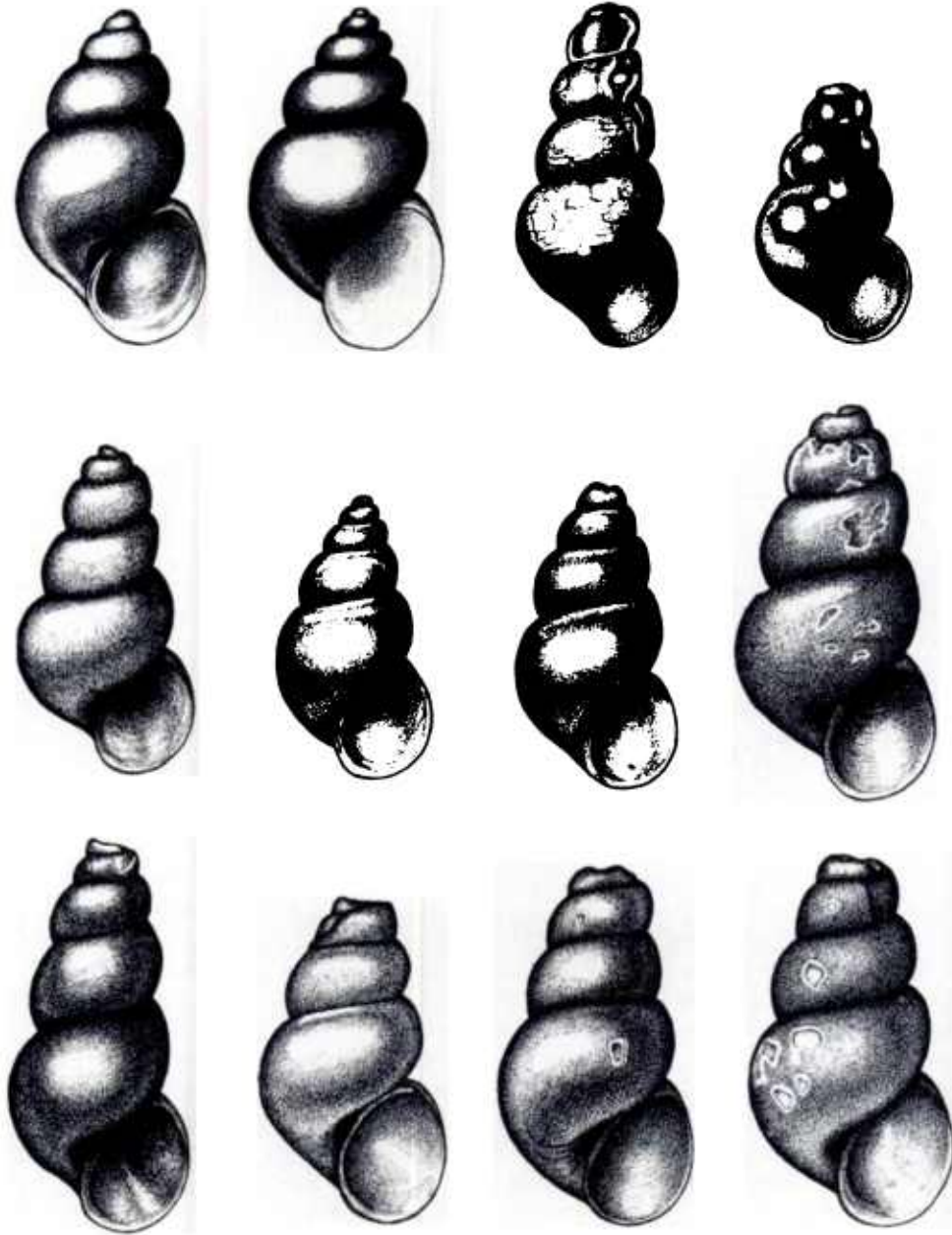


FIGURE 7. Left to right, top row to bottom, shells of *Hydrobia totteni* (A), *H. salsa* paratype (B), *H. truncata* paratypes (C, D), *H. truncata* from Stone Harbor (E-I), *H. truncata* from Salt Pond (J-L). The shell length of A is 3.2 mm; other shells are drawn to the same scale.

Hydrobia totteni. The shells vary from ovate to ovate-conic (Fig. 7A) and have a high rate of whorl expansion as discussed for *H. salsa* (Fig. 8). They vary from uneroded to severely eroded so that often only three whorls are seen; the degree of erosion varies with the population. When shells are entire, 5.0

whorls are seen. The convexity of whorls is greatly variable in a population, from slight to pronounced; sutures are correspondingly shallow to moderately deep. The length of the body whorl is greater than that seen in *H. truncata*, less than that seen in *H. salsa* (Fig. 9). The umbilical opening is rimate to moderately open. The shell length ranges from 2.52 to 3.07 mm, depending on the population; given all whorls, the length of the largest specimens ranges from 2.93 to 3.39 mm.

The shells of the seven populations are compared for five variables (Table I). Considering size alone (column 1), specimens of *H. truncata* from Salt Pond are the largest. However, as seen, absolute size varies considerably among populations of a species. Accordingly, the species cannot be simply identified on the basis of size. Specimens of *H. salsa* have the widest shell per size (column 2). Again, there is considerable variation among populations of a species. There is a clear difference between *H. truncata* (all populations), and *H. salsa* and *H. totteni* in length of body whorl per size (column 3). There is a difference between *H. truncata*, and *H. salsa* and *H. totteni* in length of aperture per size (last column). Considering the above descriptions and Table I, there is much more similarity between shells of *H. totteni* and *H. salsa* than between either of these and *H. truncata*. Further differences among populations and species are seen in Figures 8–10.

The ratio of length of body whorl is plotted against length of the last three whorls for shells of six populations (Figs. 9, 10). The regression for pooled data from the six populations was highly significant ($P = 0.0001$) yielding a formula of $y = 0.34$ to $0.58x$. Considering each population separately, the regression was

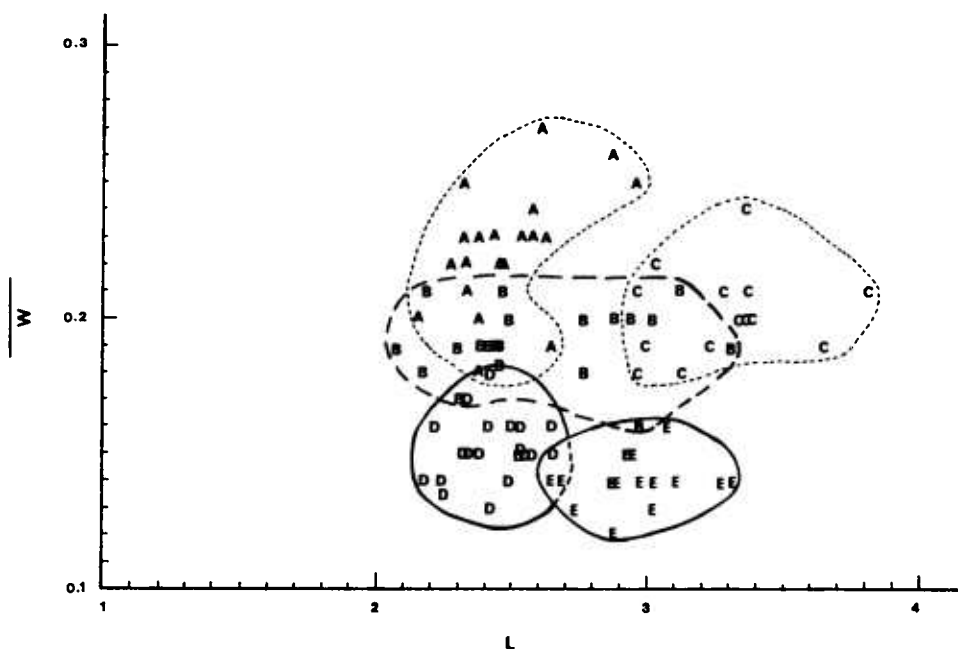


FIGURE 8. Analysis of shells from five populations involving the relationship of the width of the 4th whorl (adapical from the body whorl) divided by the length of the last three whorls (W) to the length of the last three whorls (L) in mm. A: *H. truncata*, paratypes; B: *H. truncata*, Stone Harbor; C: *H. truncata*, Salt Pond; D: *H. totteni*, Martha's Vineyard; E: *H. salsa* paratypes.

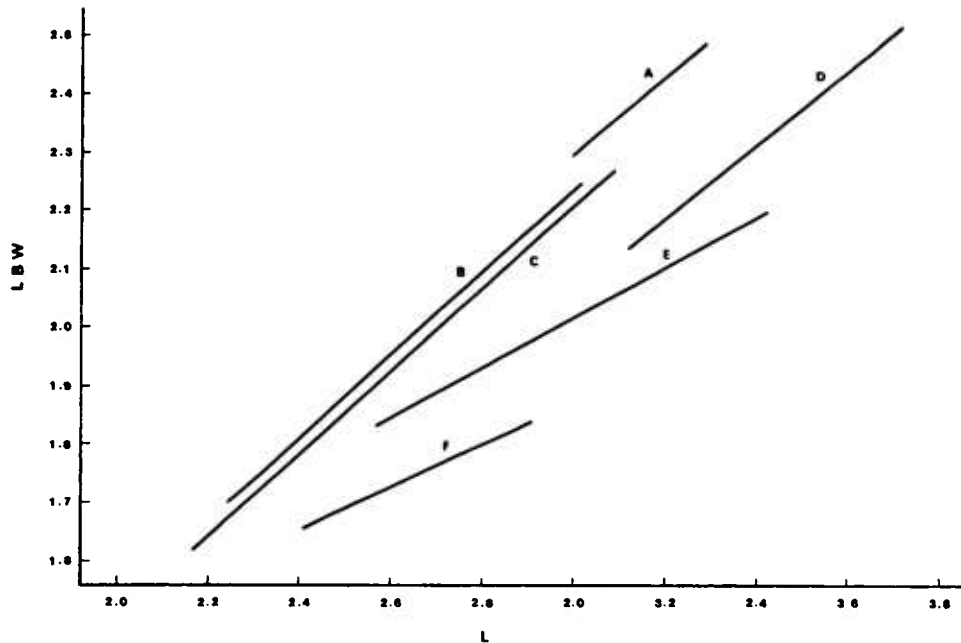


FIGURE 9. Computer plotted regressions of length of body whorl (LBW) on length of the last three whorls (L) (mm). A: *H. salsa*, paratypes; B: *H. totteni*, Martha's Vineyard; C: *H. totteni*, Provincetown; D: *H. truncata*, Salt Pond; E: *H. truncata*, Stone Harbor; F: *H. truncata*, paratypes; Towne Pt.

highly significant ($P = 0.0001$) for both populations of *H. totteni*, and *H. truncata* from Towne Point and Stone Harbor; significant ($P = 0.001$) for *H. truncata* from the Salt Pond; not significant for *H. salsa* ($P = 0.80$) (due to the scatter for only five data points). Each regression is shown in Figure 9.

Paratype specimens of *H. truncata* (Towne Point) and Stone Harbor specimens of *H. truncata* have a significantly greater slope than do the other populations (but not significantly different between themselves). Of the 15 possible cross comparisons for y intercept there were 5 significant differences ($P < 0.001$). These differences involved the two populations of *Hydrobia totteni* (Martha's Vineyard and Provincetown) compared with *H. truncata* from Stone Harbor and from Towne Point; there was a significant difference between the Salt Pond and Towne Point populations of *H. truncata*.

The scatter of data points for *H. salsa* coupled with observations on the rate of whorl increase and relative size of the fourth whorl (Fig. 8) indicated that *H. salsa* was not allometrically different from *H. totteni* but was larger than *H. totteni*. Accordingly, the data for *H. salsa* and the two populations of *H. totteni* were pooled and compared with the pool of data for these three populations considered to be *H. truncata*. The two regressions are significantly different (Fig. 10). The y intercepts and slopes are very significantly different ($P = 0.0001$).

H. salsa and *H. totteni* have a more rapid whorl expansion rate than do populations of *H. truncata* (Figs. 7, 8). The proportionally narrow fourth whorl more clearly separates *H. salsa* and *H. totteni* from *H. truncata* while again,

H. salsa is seen to be larger than *H. totteni* in overall size (Fig. 8). Distribution of data along the x axis indicates that the Stone Harbor and Cape Cod populations of *H. truncata* are quite similar except in size. The pattern of distribution of data along the y axis shows that some individuals of the Cape Cod population, and many individuals of the type population of *H. truncata* vary considerably in the width of the fourth whorl. Shells with the wider fourth whorls are rather cylindrical. As decollation beyond the fourth whorl of mature specimens is the rule, the trend in the data may indicate that in some specimens the larger fourth whorl reflects an advanced whorl stage in growth. This does not, however, account for the spread in data at a size of 2.35 mm.

DISCUSSION

This study presents the morphological groundplan of *Hydrobia truncata* as the starting point for future studies of *Hydrobia* world-wide. Three factors presented here have not been considered by previous students of *Hydrobia*, namely: the positional relationships of organs within the body relative to each other and to important topographical features such as the posterior end of the mantle cavity, the anterior end of the style sac, etc; the comparative size of different organs, for example, length of the bursa copulatrix to the length of the pallial oviduct; size and scaling such as discussed by Pilbeam and Gould (1974). These factors have been used with positive results in studies of the Pomatiopsidae (Davis and

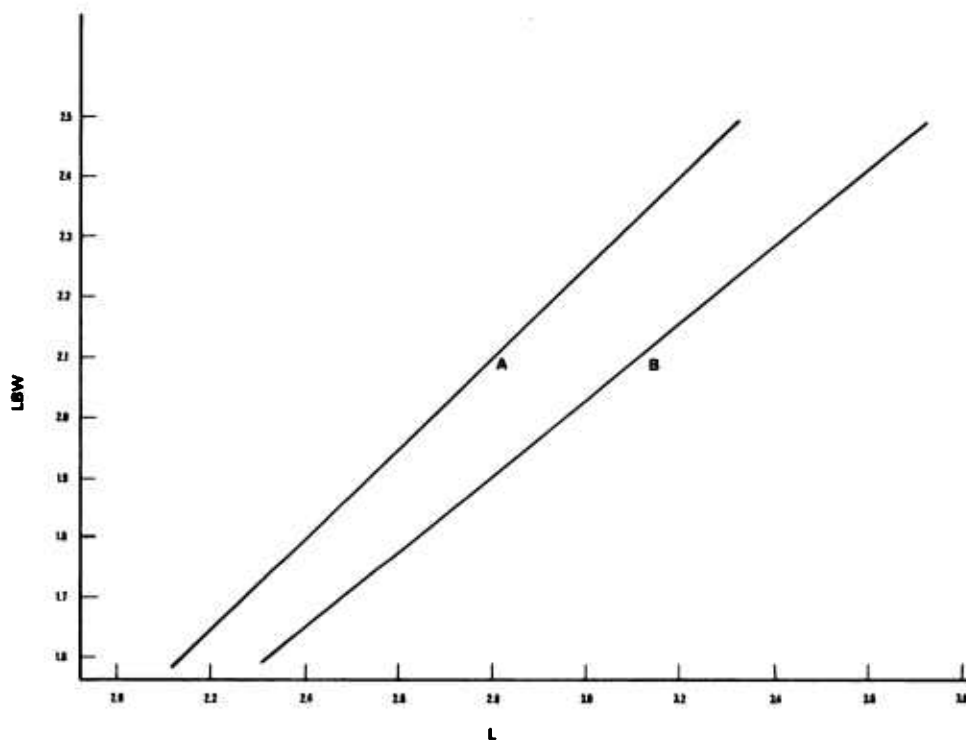


FIGURE 10. Computer plotted regressions of length of body whorl (LBW) on length of the last three whorls (L) (mm). A: *H. salsa* and the two populations of *H. totteni*; B: the three populations of *H. truncata*.

TABLE V

Eleven morphological differences between Hydrobia truncata and H. totteni.

| <i>H. truncata</i> | <i>H. totteni</i> |
|---|---|
| 1. Gill filament number 19-25 | 9-18 (depending on maturity) |
| 2. Pallial appendage projecting and prominent | Button-like and hidden inside mantle edge |
| 3. Penial appendage triangular and with folds | Appendage club-like, without folds |
| 4. Penial appendage near mid-penis: length of gland area in front of appendage to length of penis base to distal edge of appendage: 0.20-0.30 | Penial appendage near base of penis: ratio: 0.45-0.60 |
| 5. Glands widespread throughout penis | Glands concentrated near base of filament |
| 6. Prostate measures 1.2 × 0.42 mm | 0.67 × 0.24 mm |
| 7. Vas deferens leaves prostate 0.37 mm posterior to anterior end of prostate | Leaves anterior end of prostate |
| 8. Vas deferens greatly coiled before entering penis | Not coiled |
| 9. Length of body whorl/length of last three whorls: 0.74-0.75 | : 0.67-0.69 |
| 10. Shells decollate | Many eroded but not decollate |
| 11. Width of 4th whorl/length of last three whorls: 0.17-0.27 | : 0.12-0.17 |

Carney, 1973; Davis *et al.*, 1976; Davis, 1979). This study has also shown that *Hydrobia truncata* is found in localities where previously only *H. totteni* was thought to exist, namely from New Jersey to at least Massachusetts.

While the three populations of *Hydrobia totteni* differ little in shell length or in the regression analyses, there was considerable variability among populations of *H. truncata* both in shell length (Table I) and in the regressions of L1/L3 (Fig. 9). As one moves from Maryland to Massachusetts the size increases and the slope of the regression increases so that specimens of *H. truncata* from Massachusetts differ significantly from those from Maryland. The allometry of Massachusetts populations of *H. truncata* equals that of *H. totteni* only when specimens of *H. truncata* reach a size at maturity that is considerably larger than that of *H. totteni* (22% larger).

H. salsa is a larger species than *H. totteni* (about 19% larger) with a similar rate of whorl increase (Fig. 9) and probably the same allometry (Figs. 8-10). There are clearly two different classes of allometry considering the plots of L1/L3, one including *H. totteni* and *H. salsa*, the other *H. truncata*. Of particular interest is the change in shell size, and slope of L1/L3 in populations of *H. truncata* from south to north. We do not know why this occurs and the question remains: will other populations of *H. truncata* fit this pattern? It is likewise of interest that where the three species can be found in the same state (Massachusetts) the shell allometry regarding L1/L3 is the same for the three species. In Massachusetts, however, the species are separable on the basis of size, degree of umbilication, and rate of whorl increase.

Hydrobia truncata and *H. totteni* apparently differ by 11 character states (Table V), three of which are shell characters. However, we are far from

satisfied that all of these character state differences will be maintained when numerous populations from a given environment are studied. For example, while the position and shape of the penial lobe has been constant in the populations we studied, we are not convinced that interpopulation differences do not exist, and that conditions intermediate to those presented here will not be found. The specimens of *Hydrobia totteni* we examined from Wild Harbor River were sent to us unrelaxed and preserved. The penis type corresponded to that illustrated by Davis (1966). However, the penial lobes of some specimens were not pendulent, but rounded lappets. The shape was not triangular and the lobe did not have the folds described for *H. truncata*. The pallial appendage was not a large projecting tubercle as in *H. truncata*, but an insignificant button of tissue hidden within the edge of the mantle. This feature was previously overlooked (Davis, 1966). Further anatomical comparisons were not made because we have based our work on living, unrelaxed specimens, and because we had too few specimens to examine all variables. A thorough morphological study of living specimens of *H. totteni* is needed before more can be said about relationships between these species.

We see in the shells and penial anatomy of *H. truncata* and *H. totteni* a problem similar to one we see in Muus (1963) for *H. ventrosa*. He figured two

TABLE VI

Comparison among five species of *Hydrobia* using nine morphological characters. * Krull, 1935.

| Character and state | Taxa | | | | |
|--|--------------------|-------------------|--------------------|-----------------|--------------------|
| | <i>H. truncata</i> | <i>H. totteni</i> | <i>H. neglecta</i> | <i>H. ulvae</i> | <i>H. ventrosa</i> |
| 1. Pallial appendage | | | | | |
| Filament | — | — | ? | + | ? |
| Projecting tubercle | + | — | ? | — | ? |
| Hidden node | — | + | ? | — | ? |
| 2. Penis tip | | | | | |
| Long filament | + | + | — | — | + |
| Pointed, no filament | — | — | — | + | — |
| Blunt, no filament | — | — | + | — | — |
| 3. Penis with penial lobe | + | + | — | — | + |
| 4. Snout with anterior pigment bar | — | — | + | + | — |
| 5. Tentacles with pronounced terminal pigment streak | + | + | + | + | — |
| 6. Length of bursa/length of pallial oviduct | 0.15 | ? | ? | 0.07* | 0.20* |
| 7. Length of seminal receptacle/length of bursa | 0.51 | ? | ? | 0.75* | 0.55* |
| 8. Position of bursa | | | | | |
| Projecting posterior to albumen gland | — | ? | ? | + | + |
| Not projecting posterior to albumen gland | + | ? | ? | — | — |
| 9. Radula | | | | | |
| No. rows teeth | 37–45 | 31–43 | 38–45 | 42–52 | 38–44 |
| Length (mm) | 0.5–0.7 | 0.5–0.6 | 0.6–0.8 | 0.8–1.2 | 0.7–0.8 |

individuals: "A" with a conical shell similar to *H. truncata* had a shell of 7 whorls, the length of the body whorl was 2.2 mm, the length of the last three whorls was 3.6 mm, and the width of the fourth whorl (counting from the base) divided by the length of the last three whorls was 0.23; "B" was ovate conic like *H. totteni* and had corresponding data of 1.44, 2.64, and 0.16 mm. The "A" form groups with our salt pond population of *H. truncata* and the "B" form groups with the *H. totteni* population. The position of the penial lobe for "A" is similar to that of *H. truncata*; the position in "B" is similar to that in *H. totteni*. This poses several questions. Are the two types of individuals referred by Muus (1963) to *H. ventrosa* the same or different species? Is there variation in the position of the penial lobe in *H. ventrosa* and *H. totteni*? What accounts for the differences in shell types A and B if both really belong to the same species? The penial lobe illustrated by Muus resembles that of *H. totteni* illustrated by Davis (1966). Is that interpretation correct? Is the large form of *H. ventrosa* due to parasitism, as we see in larger specimens of *H. truncata*? If such extremes in shell shape and penial structure can be proved to exist in *H. ventrosa* does this indicate that *H. truncata* and *H. totteni* are the same species? Do *H. ventrosa* and *H. neglecta* have a pallial appendage?

Considering the limited data we do have, the three species of *Hydrobia* from eastern North America apparently are separate ecologically and morphologically. Confirmation rests with further studies of numerous populations.

Considering *H. salsa*, there are no soft-part morphological data. Shells are larger than those of *H. totteni*, much more ovate-conic than *H. truncata*. According to Mazurkiewicz (1972) *H. salsa* inhabits environments with 0.4 to 20‰ salinity; the lower level of salinity tolerance for adults is 0.2‰ and for veligers 1.0‰. Young emerged from capsules of 115–125 μm ; the egg diameter is 95 to 100 μm . *H. salsa* has free floating veligers. The question is, do populations studied by Mazurkiewicz correspond to the types?

Considering *H. totteni*, there are limited morphological data (Davis, 1966). Shells are smaller than those of *H. salsa* but of the same general shape. The shells are much less umbilicate than those of *H. salsa*. The species apparently lives in a wide range of salinities. Those reported from New England, U. S. A., lived in 32‰ or more (Mazurkiewicz, 1972). They are most dense on mid-intertidal sand flats of a Nova Scotia, Canada, estuarine marsh with salinities of 27.6 to 29‰ (Wells, 1978). Young emerged from egg capsules of 290 to 310 μm diameter. The diameter of the eggs was 150 to 160 μm . The lower limit of salinity tolerance was 5‰ for adults and 2‰ for emerging young (Mazurkiewicz, 1972).

We have considerable morphological data for *H. truncata*. The species apparently lives in high salinity (32‰) in high intertidal marsh pools. Snails from Stone Harbor brought into the laboratory and maintained in Petri dishes with substrate from their habitat laid eggs on shells and the bottom of the dish. The single egg capsules on the shells were 294 to 308 μm in diameter. A number of double egg capsules bound in a single membrane were observed on the bottom of the dishes. Crawling young emerged from the egg capsules. Salinity tolerances are not known.

We have much more morphological data for *H. ventrosa* than for *H. totteni* (Krull, 1935; Muus, 1963; Radoman, 1977; Bishop, 1976) yet we still do not know enough to enable an adequate comparison with *H. truncata*. The adults can easily tolerate salinities up to 35‰ but prefer quiet waters in estuaries where the salinities range from 5 to 24‰ (Muus, 1967). Bishop (1976) records salinity

range 6 to 29%. The egg capsule is 260 μm in diameter (Thorson, 1946) and thus smaller than that of *H. totteni*. The young hatch in the crawling state.

A limited comparison can be made between populations of *H. truncata* and *H. totteni* of eastern North America, and *H. neglecta* Muus, *H. ulvae* (Pennant) and *H. ventrosa* (Montagu) of northern Europe (Table VI). The North American species are clearly different from *H. ulvae* and *H. neglecta* in penis morphology and snout pigmentation. *H. ulvae* has a significantly larger radula than do other species. If data given by Krull (1935) are reproducible, and variation in length of the bursa copulatrix is small as in *H. truncata* (Table II), then *H. ulvae* has a relatively much smaller bursa than do *H. truncata* and *H. ventrosa*; the seminal receptacle of *H. ulvae* is relatively much larger in comparison to the bursa (Table VI).

Given the limited data available, *H. truncata* and *H. totteni* more closely resemble *H. ventrosa* than other species. Resemblance includes penis morphology, snout pigmentation, and radular length (Table VI). The similarity of *H. ventrosa* to *H. totteni* has been discussed previously (Muus, 1963; Davis, 1966). Bishop (1976) reexamined *H. ventrosa* and found that *H. ventrosa* and *H. totteni* did not differ in hypertrophy of cilia on the left tentacle, structure of radula (scanning electron microscopic studies showed Muus' drawings to be in error), or pigment streak on the tentacle (the streak is present in *H. ventrosa* to varying degrees in different populations).

A number of fundamental questions concerning morphology are unanswered for northern European *Hydrobia*. Do these species (*H. neglecta*, *H. ventrosa*) have a pallial filament or tubercle? How many gill filaments do they have? What is the exact morphology and position of the penial appendage? Are the oviduct coils pigmented? Is sperm stored in the seminal receptacle or in the coils of the oviduct? What is the length of the albumen gland relative to the length of the entire pallial oviduct? Does the gonad fill the digestive gland and overlap the stomach?

Considering the few morphological details of the female reproductive system of *H. ventrosa* given by Krull (1935) and Radoman (1977; material collected from Holland) it is not entirely clear what the situation is. There is apparent agreement that the length of the bursa copulatrix per length of the pallial oviduct is 0.20 and thus relatively larger compared with that of *H. truncata* (0.15). The length of the albumen gland compared to total pallial oviduct length is less in *H. truncata* (0.38–0.40 contrasted with 0.49 given by Radoman; not shown by Krull). The position of the bursa of *H. truncata* is anterior to the posterior end of the pallial oviduct; it is the same for *H. ventrosa* as portrayed by Radoman; it is posterior to the end of the pallial oviduct as shown by Krull. The shape of the penial lobe of *H. ventrosa* shown by Krull and Radoman is triangular, *i.e.* similar to that of *H. truncata*.

It is thus evident that a thorough quantitative morphological reevaluation of *H. ventrosa* is needed. It is hoped that future workers will provide measurements for major organs and for the length of the body, provide statistics for these measurements, illustrate organ systems relative to other body organs, provide statistics on shell parameters that include the length of body whorl, length of the last three whorls, L1/L3, and width of the fourth whorl per length of the last three whorls—in addition to others that might be made. The exact position of the penial appendage relative to the glandular fields of the penis is needed along with morphological details of the appendage.

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SUMMARY

1. Detailed morphological data for *H. truncata* are given as a standard for comparing species of *Hydrobia* worldwide, stressing the importance of quantitative data, scaling and allometry. The need for careful examination of all organ systems is stressed. Useful data for comparing species have been derived, in order of importance, from the female reproductive system, male reproductive system including details of penial filament, appendages, glands; radula, mantle-pallial structures, head pigment patterns, shell allometry.

2. Three populations of *Hydrobia truncata* from Maryland, New Jersey, and Massachusetts respectively were compared morphologically and ecologically with *H. totteni* and *H. salsa* of Massachusetts and *Hydrobia* from northern Europe. Three species of *Hydrobia* inhabit the same geographic region in Massachusetts.

3. *H. truncata* differs from *H. totteni* morphologically and ecologically. Shell size and allometry separate the species, as well as differences in eight anatomical character states. However, the complete anatomy of *H. totteni* has yet to be done.

4. *H. truncata* apparently increases in size and increases the length of body whorl relative to overall length from south to north. Allometry of Massachusetts *H. truncata* equals that of *H. totteni* when *H. truncata* exceeds *H. totteni* in size.

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