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THE BITHYNIIDAE (GASTROPODA: PROSOBRANCHIA) OF THAILAND:  
COMPARATIVE INTERNAL ANATOMY

Yaowaluk Prayoonhong Chitramvong<sup>1</sup>

**ABSTRACT** – Several species of Thai Bithyniidae are of medical importance because they serve as the first intermediate hosts of the human liver fluke in Thailand and other Southeast and East Asian countries. Some Thai bithyniid snails have not been implicated in disease transmission, although several may be considered as potential intermediate hosts. This study presents detailed descriptions of the internal anatomy and radulae of the nine species of Bithyniidae recognized in Thailand, emphasizing similarities as well as differences. Included in this study are the pallial organs (the heart, kidney, gill and osphradium), digestive system (the alimentary tract [the mouth, esophagus, stomach, intestine, and rectum (including fecal pellets) and anus] and accessory organs [buccal mass, with radula, and the salivary and digestive glands]) and the reproductive systems (testis, vas deferens, vas afferens, prostate gland, accessory gland, penis, flagellum, ovary, oviduct, bursa copulatrix, seminal receptacle and genital aperture). The well known European *Bithynia tentaculata* was used for comparison. The species and subspecies of Bithyniidae recognized for Thailand are *Bithynia funiculata*, *B. siamensis siamensis*, *B. siamensis goniomphalos*, *Gabbia erawanensis*, *G. pygmaea*, *G. wykoffi*, *Hydrobioides nassa*, *Wattebledia baschi*, *W. crosseana* and *W. siamensis*.

**Key words:** Bithyniidae, *Bithynia*, *Gabbia*, *Hydrobioides*, *Wattebledia*, morphology, pallial organs, digestive system, reproductive system, Thailand.

INTRODUCTION

Opisthorchiasis is a significant human disease in Thailand. The snail intermediate hosts mediating the disease are members of the prosobranch family Bithyniidae. Therefore, it is important that the biology and taxonomy of these medically important snails and their relatives are known with some precision. To that end, papers on the culture and maintenance of Thai bithyniid snails in the laboratory, and the snails' comparative external morphology have been prepared (Chitramvong, 1989; 1992). This current paper on comparative internal anatomy of Thai Bithyniidae is a continuation of those studies.

In spite of the medical importance of bithyniid snails, there are few publications on their anatomy. Itagaki (1965) studied aspects of the gross anatomy of the Japanese bithyniid *Parafossarulus manchouricus* (Bourguignat), and Chung (1984) studied mantle pigmentation and radulae of Korean *P. manchouricus*, *Gabbia misella* Gredler, and the European-American *Bithynia tentaculata* (Linnaeus), but as yet no detailed studies have been published on the anatomy of any other Asian bithyniid snail. Fretter & Graham (1962) compared the functional anatomy of the muscular, alimen-

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tary, vascular, excretory, nervous and reproductive systems of *B. tentaculata* with that of other prosobranch snails, but these authors did not describe *Bithynia's* anatomy in detail. Lilly (1953) presented some details on the male and female reproductive systems of *B. tentaculata*, but did not study other organ systems. Andrews (1968, 1971) studied the anatomy and histology of the nervous system of *B. tentaculata* with special reference to possible neurosecretory activity.

The purpose of this paper is to describe in detail the similarities and differences in the internal anatomy of the Thai Bithyniidae, and to compare the Thai species to the American-European *Bithynia tentaculata*, the species on which the genus *Bithynia* and the family Bithyniidae are based. This information will be used to assist others, e.g., taxonomists and parasitologists, in understanding the anatomy of the various species, and it will be used in my associated phylogenetic analyses.

#### Taxonomic Review

The family name Bithyniidae Gray 1857 is based on *Bithynia* Leach (in Abel) 1818. The type species of the genus *Bithynia* is Linnaeus' (1758) *Helix tentaculata*, a Eurasian species. The natural distribution of the Bithyniidae is throughout Europe, Asia, Africa and Australia (Thiele, 1929; Wenz, 1938-1944). *Bithynia tentaculata* was introduced long ago by humans to North America, and has subsequently spread widely on the northern part of the continent (Burch, 1982).

Bithyniid snails are clearly mesogastropods, but there has been no universal agreement as to their familial status or to their systematic relationships. Thiele (1929), Ankel (1936), Macan & Cooper (1949), Morrison (1949), Grossu (1956), Zhadin (1965) and Brandt (1980) ranked the bithyniids as a subfamily of the family Hydrobiidae, and this scheme has had rather wide acceptance. Baker (1928) and Berry (1943) referred *Bithynia* [as *Bulimus*] to the family Amnicolidae (which generally is considered a synonym of Hydrobiidae). Wenz (1938-1944) recognized the bithyniids as a family (as Bulimidae) placed between the Stenothyridae and the Iravadiidae in the Rissoacea [Rissooidea (= Truncatelloidea)]. Taylor (1966) also treated the bithyniids as a family, but indicated that they are not closely related to the Hydrobiidae or to other truncatelloids, and transferred the family to the Viviparoidea. Viviparoid characters of bithyniids are their size (adult shells are more than 10 mm long), calcareous concentric operculum, nuchal lobes of the head-foot, relatively long, flexible and acute tentacles, yellow and orange skin pigment granules, spirally constructed fecal pellets, use of the ctenidium in food gathering, pallial innervation of the penis, and dimorphic sperm (Taylor, 1966). Ponder (1988) pointed to sperm morphology, the type of osphradium and the advanced nervous system of bithyniids and concluded that they "are truncatelloidean and that any resemblance to the Ampullaroidae is due to convergence." Ponder & Warén (1988) placed the Bithyniidae between the Rissoidae and the Hydrobiidae.

The taxonomy currently in use within the family Bithyniidae is generally that of Thiele (1929) and Wenz (1938-1944), but the systematic status of many of the bithyniid taxa is still problematic. The systematics are based

mostly on shell characters alone (see Walker, 1918; Thiele, 1929; Ankel, 1936; Wenz, 1938-1944; Macan & Cooper, 1949; Mandahl-Barth, 1954; Grossu, 1956; Zhadin, 1965; Brown, 1980). However, a few systematic works have used additional characters. For example, Walker (1918) used characters of both shell and radula; Baker (1928) used characters of shell, radula, egg capsules, external morphology (head-foot and tentacles) and pigmentation of the soft parts; and Berry (1943) used characters of shell, radula and genital anatomy.

## MATERIALS AND METHODS

**Snail Localities.** The snails used in this study were as follows: *Bithynia siamensis goniomphalos* Morelet, *B. siamensis siamensis* Lea, *B. funiculata* Walker, *B. tentaculata* (Linnaeus), *Hydrobioides nassa* Theobald, *Wattebledia siamensis* Moellendorf, *W. crosseana* (Wattebled), *W. baschi* Brandt, *Gabbia erawanensis* Chitramvong & Upatham, *G. wykoffi* Brandt and *G. pygmaea* Preston. The guide used for snail identification was Brandt (1974). All of the mature snails were initially field-collected and all of the young snails studied were the first laboratory generation of the field-collected parents. Only one population was used to represent each snail species. Except for *B. tentaculata*, all snails were from Thailand. The locations of these populations were as follows: *B. siamensis goniomphalos*, Ban Nonggao, Yangtad District, Kalasin Province; *B. siamensis siamensis*, Thai Army Club, Rajavithi Road, Bangkok; *B. funiculata*, Ban Thaobunroeng, Hangdong District, Chiangmai Province; *B. tentaculata*, the southern part of Hamlin Lake, Michigan, U.S.A.; *H. nassa*, Ban Thaobunroeng, Hangdong District, Chiangmai Province; *W. siamensis*, Thai Army Club, Rajavithi Road, Bangkok; *W. crosseana*, Ban Noansomboon, Tumbon Thasala, Pooroea District, Loea Province; *W. baschi*, Panom District, Suratthani Province; *G. wykoffi*, Ban Thungchieng, Hangdong District, Chiangmai Province; *G. pygmaea*, Ban Tumtubtao, Fang District, Chiangmai Province; and *G. erawanensis*, Erawan Waterfall, Kanchanaburi Province.

Information on habitats, collecting methods and laboratory culture and maintenance are given in Chitramvong (1989, 1992).

**Internal Anatomy.** Five males and five females of each species were selected to study internal anatomy. The snails to be studied were prepared as described in Chitramvong (1992). The structures studied were the pallial organs (gill, osphradium, kidney and heart), digestive system (mouth, buccal mass, radula, esophagus, stomach, intestine [including the fecal pellets], anus, salivary glands and digestive glands) and reproductive systems (male system: testis, vas deferens, renal vas deferens, pallial vas deferens [including penial vas afferens], prostate gland, penis [including penial duct] and accessory gland or flagellum [including the duct of the accessory gland]; female system: ovary, oviduct, renal oviduct, pallial oviduct [including ventral channel], seminal receptacle, spermatheca or bursa copulatrix, muscular oviduct and female genital aperture).

Dissections were done at magnifications of x16 and x40 under a Wild Heerbrugg M3 stereoscopic binocular microscope with a Cole Parmer two-stalked fiberoptic dissecting light. Although all species were studied in detail, *Bithynia siamensis goniomphalos* was selected as the representative species for describing the various organs and systems, because in Southeast Asia this species is the most important intermediate host of *Opisthorchis viverrini*. For the rest of the bithyniid species and subspecies, only those parts that differed from *B. siamensis goniomphalos* are illustrated and described.

The sizes of the various organs and parts were measured at their mid regions from the camera lucida drawings using a map measurer (planimeter). The sizes of each

organ were checked by an ocular micrometer.

**Radula.** The entire buccal mass was extracted and submerged in hot 10% sodium hydroxide for 10 to 15 minutes to dissolve the tissues surrounding the radula. The radula was then washed in distilled water and attached to a SEM stub with double-stick tape. Care was taken to ensure that the cusp side of the teeth were turned upward. The SEM stub was placed in a dessicator for a week, then coated with a 100 Å thickness of gold. The specimens were examined with secondary electron imaging using 15 KV accelerating voltage (HITACHI S-430 Model E500). For each specimen, the teeth of 11 transverse rows in the middle part of the radula ribbon were photographed at magnifications from x200 to x500, and the central, the lateral and the marginal teeth of the mid transverse row were photographed at magnifications of x700 to x2000.

**Terminology.** Terms relating to the genital system are adapted from Baker (1928), Lilly (1953), Fretter & Graham (1962) and Itagaki (1965). Terminology for the morphology of the digestive system is after Graham (1939), Fretter & Graham (1962) and Burch (1982). Terminology for the pallial system follows Fretter & Graham (1962).

## RESULTS

### Pallial Organs

The pallial organs, *i.e.*, the organs of the mantle, consist of the heart, kidney, gill (ctenidium) and osphradium. Generally, no differences in shape or position were found in the pallial organs among any of the species studied. However, the gill size, the number of gill filaments, the position of the osphradium in relation to the gill, and the structure of the kidney tissue was in some species significantly different.

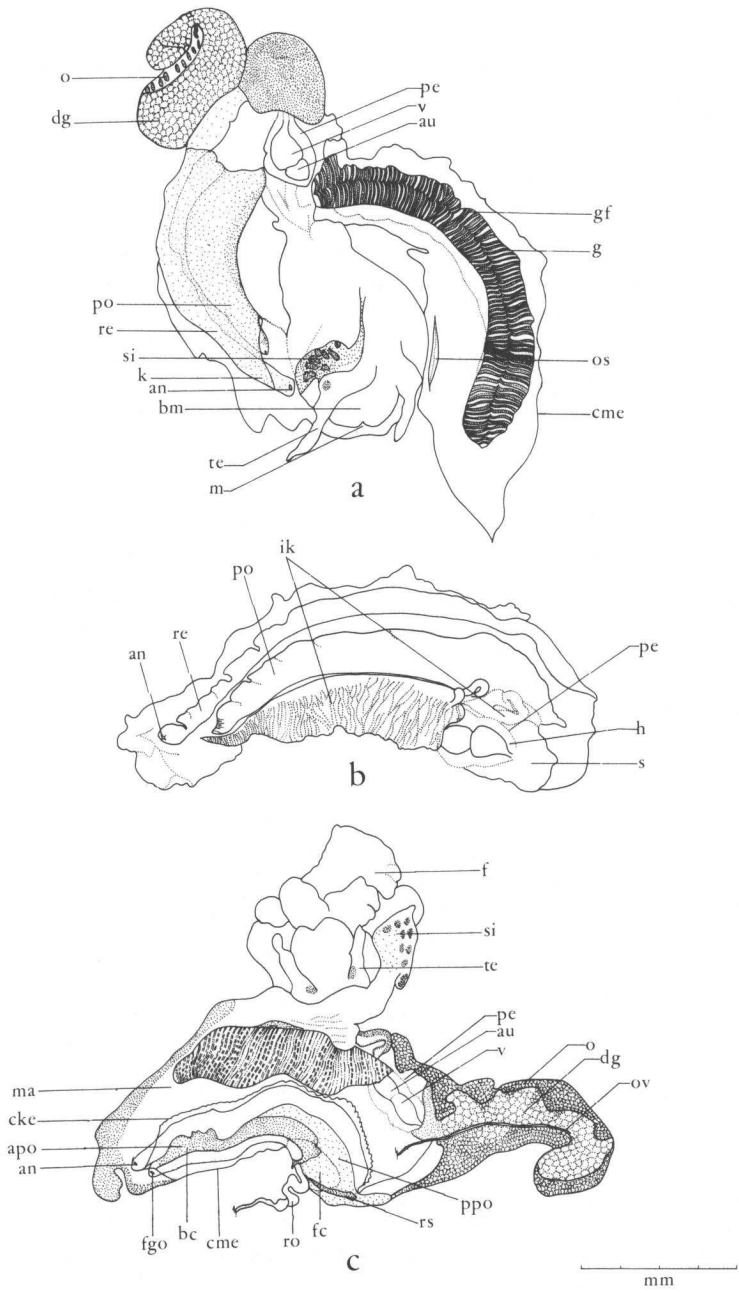
### Heart

The heart is at the posterior end of the mantle and lies between the posterior end of the kidney and the gill (Fig. 1). The auricle is adjacent to, and attaches to, the posterior end of the gill. The ventricle connects posteriorly to the auricle and lies adjacent to the posterior stomach. The left and right anterior corners of the pericardium attach to the gill and the kidney, respectively, and the posterior end of the pericardium attaches to the posterior end of the kidney and stomach. The pericardium is usually clear; the heart is light yellow in color.

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FIG. 1. (Facing page) Anatomy of *Bithynia siamensis goniomphalus*. a, The mid-dorsally cut mantle showing various organ systems of the female; b, the slit kidney of a female showing the inner kidney and the most obvious organs beneath the kidney; c, the female reproductive organs beneath the mantle roof after the kidney is removed. Abbreviations: an = anus; apo = anterior pallial oviduct; au = auricle; bc = bursa copulatrix; bm = buccal mass; cke = cut kidney edge; cme = cut mantle edge; dg = digestive gland; f = foot; fc = fertilization chamber; fgo = female genital opening; g = gill; gf = gill filament; h = heart; ik = inner kidney; k = kidney; m = mouth; ma = mantle; mo = muscular oviduct; o = ovary; os = osphradium; ov = oviduct; pe = pericardium; po = pallial oviduct; ppo = posterior pallial oviduct; re = rectum; ro = renal oviduct; rs = seminal receptacle; s = stomach; si = siphon; te = tentacle; v = ventricle. Scale line = 4 mm.





## Kidney

The kidney of all bithyniid snails is long and broad. Its posterior end curves past the posterior end of the stomach toward the gill and runs beneath the right side and posterior end of the heart. The kidney is located at the right side of the mantle wall and extends from the posterior end almost to the anterior end of the mantle (the anterior end of the kidney is a little behind the anterior margin of the mantle). In females, the kidney covers the whole length of the pallial oviduct (except the muscular oviduct) (Fig. 1a), and in males it covers the whole length of the prostate gland (Fig. 2c). The kidney also covers almost the entire length of the rectum, which is located in the mantle wall. Only a small area of the anterior end of the rectum is not covered by the kidney. The kidney is clear, its membrane somewhat opaque. The organs that are covered by the kidney (the prostate gland, pallial oviduct, seminal receptacle (of some species), renal oviduct and part of the rectum) can be seen through the translucent kidney. The outer part of the kidney is smooth, but the inner part is rather wavy, especially the posterior part (Figs. 1b, 2d). In larger snails, such as *Bithynia* and *Hydrobioides nassa*, the kidney membrane is thicker than it is in smaller species, such as *Wattebledia* spp., *Gabbia wykoffi*, *G. pygmaea* and *G. erawanensis*. The kidney membranes of the three *Gabbia* species are the thinnest of all.

The kidney aperture is on the right posteroventral side of the kidney near the pericardium (Fig. 2c). It can be seen clearly when the mantle is dissected from the left margin of the kidney, or it can be seen from the middle part of the kidney between the gill and the rectum. The renopericardial duct was not located.

## Gill

The gill is long, rather broad, more or less pointed at both ends, and it is usually clear (Fig. 1a). It is located along the left mantle margin, extending from the anterior margin almost to the posterior end of the mantle (Fig. 1a,b). Its posterior end connects with the auricle (Figs. 1a,c). The length of the gill of all bithyniid snails is shorter than the length of the rectum that lies in between the gill and part of the reproductive system (the pallial oviduct in the female and the prostate gland in the male) and the pallial oviduct that is on the right mantle margin. However, the gill is longer than the prostate gland in all of the snails studied. The average gill lengths of ten specimens (five males and five females) of each species, in mm, were as follows: *Bithynia siamensis goniomphalos*, 8.33; *B. siamensis siamensis*, 6.42; *B. funiculata*, 11.02; *B. tentaculata*, 8.62; *Hydrobioides nassa*, 7.32; *Wattebledia siamensis*, 3.85; *W. crosseana*, 6.35; *W. baschi*, 1.62; *Gabbia wykoffi*, 2.90; *G. pygmaea*, 1.15; and *G. erawanensis*, 1.85.

The gills are composed of gill filaments, which lie in transverse rows for the entire length of the gill (Figs. 1a, 3). The gill filament is a ridge-like structure, slightly curved in the middle. The average number of gill filaments in each of the bithyniid species were as follows: 122 in *B. siamensis goniom-*

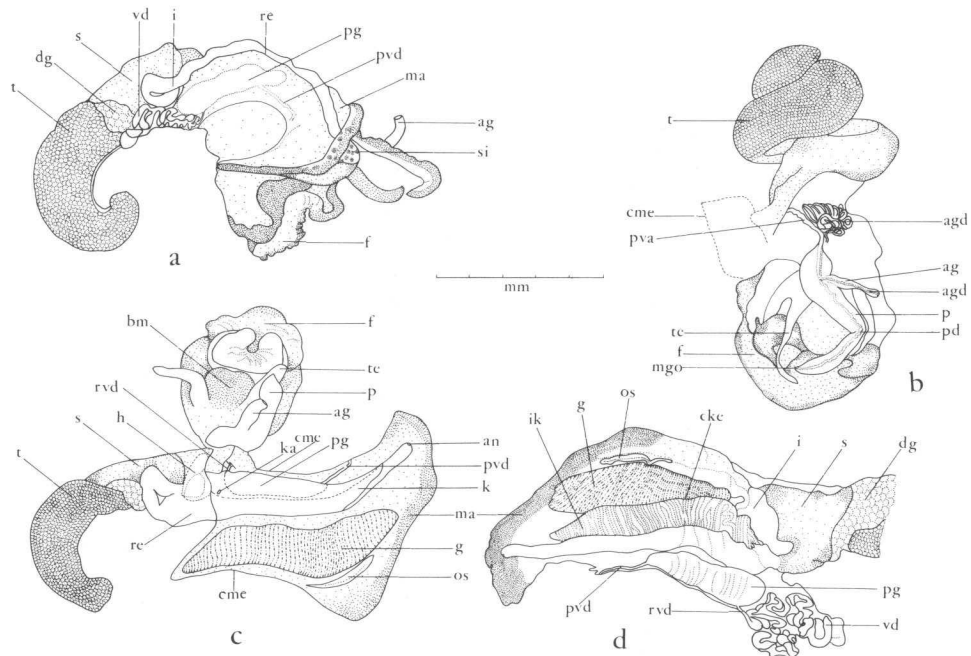


FIG. 2. Anatomy of *Bithynia siamensis goniomphalus*. **a**, The right side of a male showing the general appearance of the external soft parts; **b**, the dorsum of a male after the mantle has been removed; **c**, the internal organ systems of a male in the spire whorls and in the mantle cavity after the left and right mantle edges have been dissected; **d**, the parts of the male reproductive organs in the mantle cavity that can be seen after the kidney has been removed. Abbreviations: ag = accessory gland; agd = accessory gland duct; an = anus; bm = buccal mass; ckc = cut kidney canal; cme = cut mantle edge; dg = digestive gland; f = foot; g = gill; h = heart; i = intestine; ik = inner kidney; k = kidney; ka = kidney aperture; ma = mantle; mgo = male genital opening; os = osphradium; p = penis; pd = penial duct; pg = prostate gland; pva = penial vas afferens; pvd = pallial vas deferens; re = rectum; rvd = renal vas deferens; s = stomach; si = siphon; t = testis; tc = tentacle; vd = vas deferens. Scale line = 5 mm.

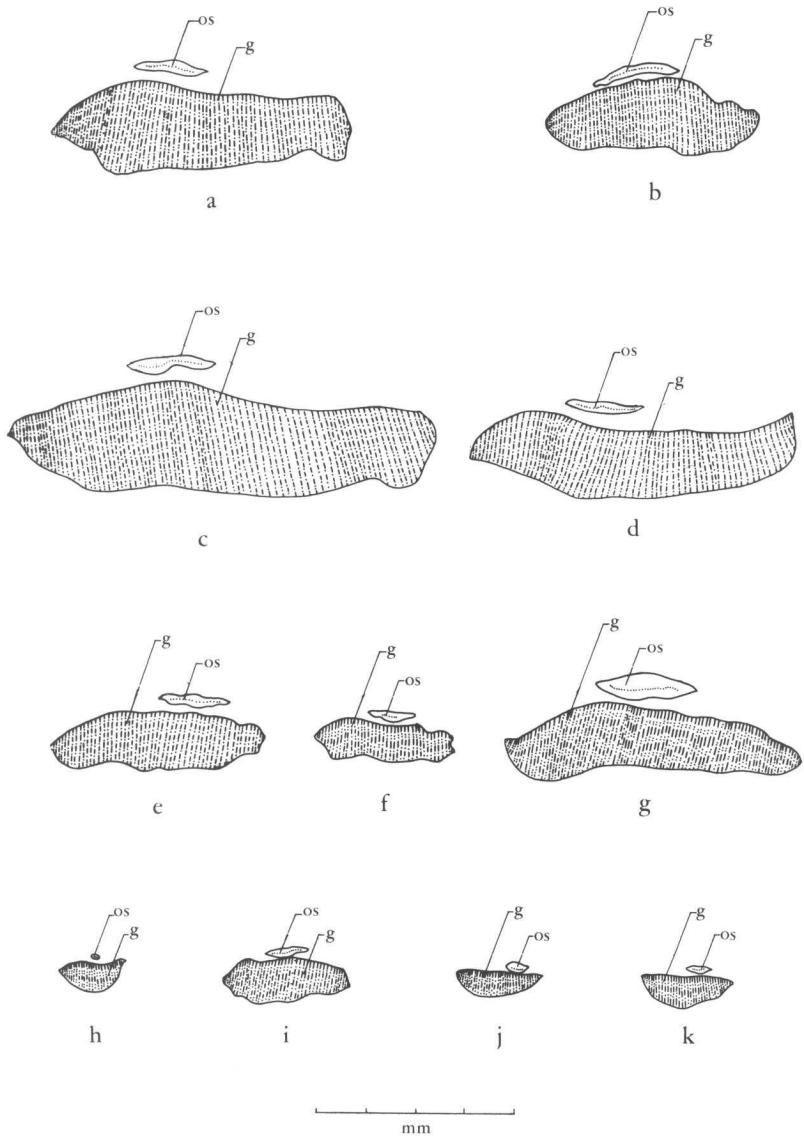


FIG. 3. Gills and osphradia of a, *Bithynia siamensis goniomphalos*; b, *B. siamensis siamensis*; c, *B. funiculata*; d, *B. tentaculata*; e, *Hydrobioides nassa*; f, *Wattebledia siamensis*; g, *W. crosseana*; h, *W. baschi*; i, *Gabbia wykoffi*; j, *G. pygmaea* and k, *G. erawanensis*. Abbreviations: g = gill; os = osphradium. Scale line = 4 mm.



*phalos*, 114 in *B. siamensis siamensis*, 126 in *B. funiculata*, 90 in *B. tentaculata*, 125 in *H. nassa*, 81 in *W. siamensis*, 92 in *W. crosseana*, 29 in *W. baschi*, 63 in *G. wykoffi*, 29 in *G. pygmaea* and 39 in *G. erawanensis*.

### Osphradium

The osphradium is light yellow in color. It is located at the left-most part of the anterior mantle and laterally it is next to the gill (Figs. 1a, 2c, 2d). Its position in relation to the gill is different in each species. The osphradium is located more toward the anterior of the gill in *Bithynia siamensis goniomphalos* (Fig. 3a), *B. siamensis siamensis* (Fig. 3b), *B. funiculata* (Fig. 3c), *B. tentaculata* (Fig. 3d) and *Wattebledia crosseana* (Fig. 3g), and in some specimens of *W. siamensis* and *W. baschi*. It is found in the middle of the gill in *Gabbia wykoffi* (Fig. 3i) and in most *W. siamensis* (Fig. 3f) and *W. baschi* (Fig. 3h). It is found more toward the posterior part of the gill in *Hydrobioides nassa* (Fig. 3e), *G. pygmaea* (Fig. 3j) and *G. erawanensis* (Fig. 3k).

The shape of the osphradia of each bithyniid species differs as follows: it is long and slender-fusiform in *Bithynia siamensis goniomphalos*, *B. siamensis siamensis*, *B. funiculata*, *B. tentaculata*, *Hydrobioides nassa*, *Wattebledia siamensis* and *W. crosseana*; it is broadly fusiform in *Gabbia wykoffi*, *G. pygmaea* and *G. erawanensis*; and it is oval in shape in *W. baschi*.

The average lengths in mm of the osphradia of the various species were as follows: *Bithynia siamensis goniomphalos*, 2.24; *B. siamensis siamensis*, 2.07; *B. funiculata*, 2.02; *B. tentaculata*, 1.48; *Hydrobioides nassa*, 1.23; *Wattebledia siamensis*, 1.12; *W. crosseana*, 1.95; *W. baschi*, 0.46; *Gabbia wykoffi*, 0.91; *G. pygmaea*, 0.26; and *G. erawanensis*, 0.90.

### Digestive System

The digestive system can be divided into (1) the alimentary tract and (2) the accessory organs. The alimentary tract consists of the mouth, esophagus, stomach, intestine and anus. The accessory organs are the buccal mass, radula, salivary glands and digestive glands.

The digestive systems of both males and females of all 10 bithyniid species are basically the same in regard to their shapes and the position of their organs. However, some differences were found, e.g., in the shapes of the radular teeth and the fecal pellets, in the position of the intestinal loops, and in the position of the opening of the esophagus into the anterior stomach.

#### Alimentary Tract

##### Mouth

In relaxed specimens of all of the bithyniid snails studied, the mouth is a narrow dorsoventral slit-like opening at the anterior end of the rostrum.

##### Esophagus

The esophagus of *Bithynia siamensis goniomphalos* is a tube passing over the dorsal surface of the buccal mass through the body whorl (Fig. 4a). It

runs along the left ventrolateral part of the stomach in the spire or upper whorls and joins the left posteroventral part of the stomach (Fig. 4f). The esophagus is light yellow and is covered with scattered melanin. Its average length was 7.70 mm.

The esophagus of *Bithynia siamensis siamensis* is similar to that of *B. siamensis goniomphalos*, but is more dense. The average length of the esophagus in this species was 5.43 mm. The esophagus of *B. funiculata* is basically the same, except that it is light reddish-brown in color. It is also covered with scattered melanin. Its average length was 7.06 mm. The esophagus of *Bithynia tentaculata* has the color and pigmentation of *B. siamensis siamensis*; its average length was 5.77 mm.

The esophagus of *Hydrobioides nassa* is similar to that of *Bithynia siamensis goniomphalos* in all aspects. Its average length was 7.48 mm.

The esophagus of *Wattebledia siamensis* joins the left lateral part of the anterior stomach (the entrance of the esophagus is at about the middle of the anterior stomach) (Fig. 5f). It is pale yellow, almost white, in color. Its average length was 2.64 mm. The esophagus of *W. crosseana* opens at the left ventral margin of the stomach and is a little anterior to the gastric shield, which lies in the right ventral part of the anterior stomach (Fig. 5g). The esophagus is without pigment. Its average length was 5.49 mm. The esophagus of *W. baschi* is basically the same as that of *Bithynia siamensis goniomphalos*. The way it joins the stomach is the same as in *W. siamensis* (Fig. 5h). The esophagus is colorless, and had an average length of 0.81 mm.

The esophagus of *Gabbia wykoffi*, *G. pygmaea* and *G. erawanensis* joins the left lateral part of the anterior part of the anterior stomach (Fig. 5i,j,k). The entrance of the esophagus of *G. wykoffi* is at the middle of the anterior stomach. The entrance of the esophagus of both *G. pygmaea* and *G. erawanensis* is at the posterior part of the anterior stomach. The esophagus of *G. wykoffi* is light yellow with scattered melanin when it is in the haemocoel and it is clear without melanin when it runs along the stomach. The esophagus of *G. pygmaea* is clear, except for the scattered melanin that covers it. The esophagus of *G. erawanensis* is whitish-yellow and is covered with scattered melanin. The average length of the esophagus in *G. wykoffi* was 3.40 mm, in *G. pygmaea* it was 1.62 mm, and in *G. erawanensis* it was 2.41 mm.

### Stomach

The stomach of *Bithynia siamensis goniomphalos* is a large crescent-shaped bag or sac (Fig. 4a) located in the whorl immediately preceding the body whorl. It is the organ in the spire or upper whorls that is next anteriorly to the gonad. The dorsal part of the stomach is light yellow in color with scattered calcium granules over the anterior stomach and with dense calcium granules over the posterior stomach. The ventral stomach is colorless and has fewer calcium granules than the dorsal stomach.

The stomach is divided into two portions, the anterior stomach, which is located toward the gonad, and the posterior stomach, which is next anteriorly to the anterior stomach toward the body whorl and ends behind the chambered heart. Note: The "anterior stomach" is the first part of the stomach, and the "posterior stomach" is the second (last) part (Fig. 4c).

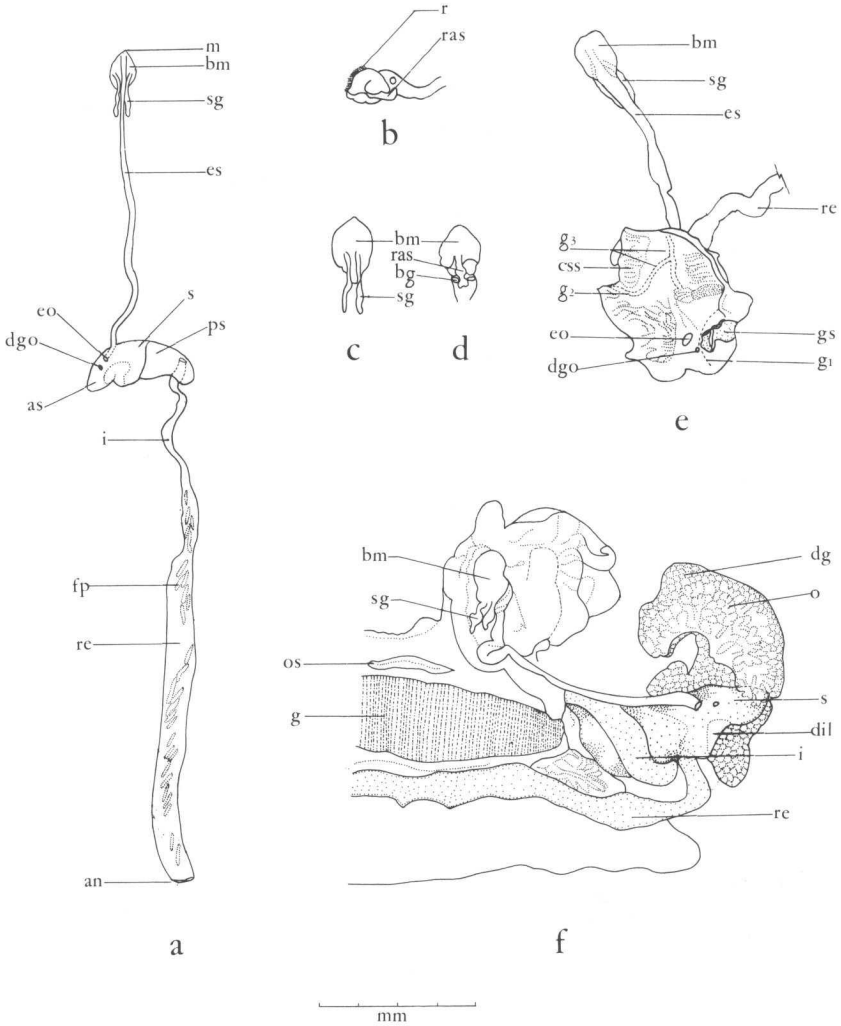


FIG. 4. The digestive system of *Bithynia siamensis goniomphalos*. a, Dorsal view of the entire digestive system; b, lateral view of the radula after the buccal mass is cut mid-dorsally; c, dorsal view of the buccal mass; d, ventral view of the buccal mass; e, dorsal dissection of the stomach to show the inner stomach; f, the natural position of the digestive system after the mantle and the mid dorsum of the body are dissected. Abbreviations: an = anus; as = anterior stomach; bg = buccal ganglion; bm = buccal mass; css = crystalline style sac; dg = digestive gland; dgo = digestive gland opening; dil = depression of the intestinal loop; eo = esophageal opening; es = esophagus; fp = fecal pellet; g = gill; g<sup>1</sup>, g<sup>2</sup>, g<sup>3</sup> = grooves 1, 2, 3, resp.; i = intestine; m = mouth; o = ovary; os = osphradium; ps = posterior stomach; r = radula; ras = radular sac; re = rectum; s = stomach; sg = salivary gland. Scale line = 4 mm.

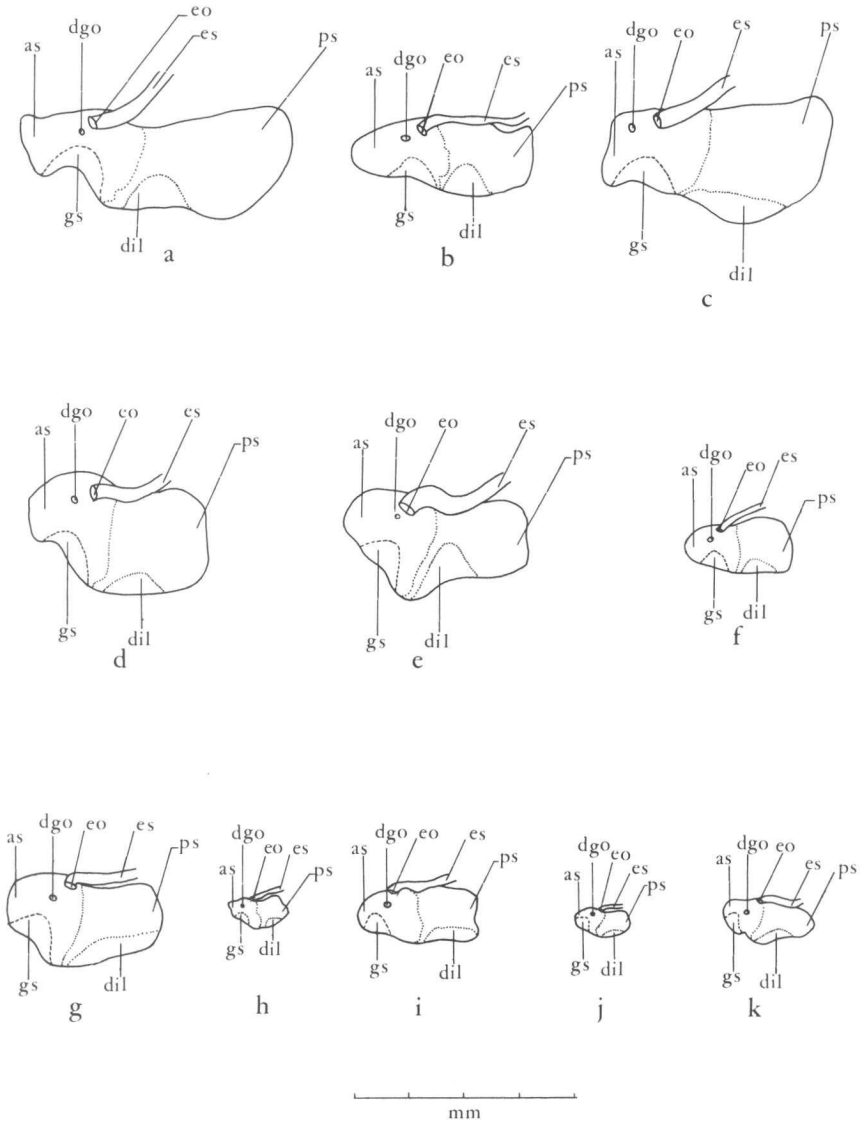


FIG. 5. Dorsal stomachs of a, *Bithynia siamensis goniomphalos*; b, *B. siamensis siamensis*; c, *B. funiculata*; d, *B. tentaculata*; e, *Hydrobioides nassa*; f, *Waitebledia siamensis*; g, *W. crosseana*; h, *W. baschi*; i, *Gabbia wykoffi*; j, *G. pygmaea* and k, *G. erawanensis*. Abbreviations: as = anterior stomach; dgo = digestive gland opening; dil = depression of the intestinal loop; eo = esophageal opening; es = esophagus; gs = gastric shield; ps = posterior stomach. Scale line = 4 mm.



However, due to the convoluted nature of the alimentary tract, the anterior stomach is actually posterior to the posterior stomach, and *vice versa* for the posterior stomach, in relation to the actual topography of the snail.

The anterior stomach contains the digestive gland opening, the entrance of the esophagus, and the gastric shield. The posterior stomach contains the style sac and the opening of the stomach into the beginning of the small intestine (Fig. 4a,e). The digestive gland opening and the entrance of the esophagus are at the posteroventral part of the anterior stomach (Fig. 5a). The opening of the digestive gland is a little posterior to the right of the entrance of the esophagus, which is more or less toward the left side of the anterior stomach. The gastric shield is on the right ventral side of the anterior stomach. It is cuticular and has an irregular shape, resembling a flat, uneven, oblong plate that has been bent spirally to form an incomplete tube. Therefore, it looks unevenly oblong (with the upper and lower edges) with a roof-like curve in the middle and slightly flexed off at both sides. The lower edge of the gastric shield points toward the posterior stomach. Only the lower edge of the gastric shield fits beneath the margin of the inner gastric shield. The gastric shield possesses a spine-like projection on its left margin. The gastric shield is shiny and colorless and the spine-like projection is dark brown in color.

The posterior stomach contains the elongate style sac. The style sac is next anteriorly to the gastric shield and it occupies the whole length of the right posterior stomach. It is found on both the dorsal and ventral walls of the right posterior stomach. The mid posterior part of the posterior stomach serves as the leading duct to the small intestine. This duct lies internally and anteriorly along the length of the posterior stomach toward the body whorl before it joins or opens into the small intestine at the left side of the anterior part of the posterior stomach (Fig. 4e).

The inner lining of the stomach has a much folded and corrugated appearance, especially in the anterior part. [According to Dazo (1965), in pleurocerid snails the folded appearance of the inner lining of the stomach is due to the gastric fold.] The inner lining of the stomach also has three main longitudinal grooves (observed from the dorsal side). The first groove ( $g_1$ ) curves around the left margin of the gastric shield, and leads to the point where the style sac bears against the gastric shield, then it continues toward the leading duct to the intestine. The second groove ( $g_2$ ) runs parallel to the first groove. The second groove originates between the opening of the digestive gland and the entrance of the esophagus, and it then runs anteriorly, passing the papilla, which is on the ventral wall of the stomach. According to Graham (1939), the papilla is the swollen end of a transverse ridge that delimits the style-sac and the intestine from the stomach. The third groove ( $g_3$ ) runs parallel to part of the posterior style sac and then goes to the leading duct (Fig. 4e).

The stomach of *B. siamensis siamensis* is light yellow in color. Very scattered melanin is at the anterior part of the ventral stomach, and a very dense melanin covers the posterior part of the ventral stomach and all of the dorsal stomach. Calcium granules cover the ventral stomach (except for the anterior part) and they cover the posterior part of the dorsal stomach. The

average length of the stomach was 4.79 mm. The stomach of *B. funicula* is mostly transparent, except for the anterior part of the ventral stomach, which is reddish-brown in color. Small, scattered melanin pigment granules are found over all of the dorsal and ventral stomach. Calcium granules also cover the stomach. The average length of the stomach was 4.76 mm. The stomach of *Bithynia tentaculata* is covered with melanin over all of the posterior part of the ventral stomach. Calcium granules also cover the stomach. The average length of the stomach was 4.00 mm.

The stomach of *Hydrobioides nassa* is light orange-yellow in color at the posterior part of the ventral stomach and it is light yellow at the anterior part of the ventral stomach. Melanin pigment covers the ventral stomach. The dorsal stomach is light yellow and is covered with scattered melanin. All of the stomach is sparsely covered with calcium granules. The average length of the stomach was 4.31 mm.

The stomach of *Wattebledia siamensis* is light yellow in color. The posterior stomach on both dorsal and ventral sides is covered with melanin and calcium granules, while the anterior part of the stomach has very few or no melanin and calcium granules. The average length of the stomach was 1.91 mm. The stomach of *W. crosseana* is light yellow in color. Dense melanin and scattered calcium granules are found along the margin of the dorsal stomach. Dense melanin is found over all of the posteroventral stomach and on the mid anteroventral stomach; calcium granules are scattered only at the posteroventral stomach. The average length of the stomach was 3.08 mm. The stomach of *W. baschi* is very light yellow in color. Scattered calcium granules are found mostly along the edge of the posterior dorsum of the stomach and scattered melanin is on the top of the scattered calcium granules. Scattered calcium granules cover the posterior ventral stomach and some areas of the anterior ventral stomach, and scattered melanin granules are on top of calcium granules. The average length of the stomach was 0.93 mm.

The stomach of *Gabbia wykoffi* is colorless, except in some small areas near the intestinal loop, which are light yellow in color. Scattered melanin granules are over all of the ventral and posterior dorsal stomach. Scattered calcium granules are found along the margin of the dorsal stomach. The average length of the stomach was 2.68 mm. The stomach of *G. pygmaea* is mostly light yellow in color, except at the anterior part of the anterior stomach, which is clear. Large scattered melanin granules cover the dorsal and ventral parts of the posterior stomach. Large and very scattered melanin granules are also on both sides at the anterior part of the anterior stomach. Calcium granules were not found. The average length of the stomach was 1.12 mm. The stomach of *G. erawanensis* is unpigmented, except for some areas that were light yellow in color (e.g., the middle part of the posterior stomach and the right posterior part of the anterior stomach). Large melanin granules cover the dorsal and ventral parts of the stomach, but the melanin pigment at the posterior stomach was a little denser than that at the anterior stomach. Very scattered calcium granules were found between the melanin granules. The average length of the stomach was 1.77 mm.

### Intestine

In *Bithynia siamensis goniomphalos*, the beginning of the intestine lies centrally along the posterior stomach and it goes to the side at the left ventral side of the anterior part of the posterior stomach (Fig. 2c). Then it goes across to the right anteroventral part of the posterior stomach, after which it runs backward along the laterodorsal part of the posterior portion of the posterior stomach and turns back anteriorly in a loop-like shape (Fig. 2d). It then runs anteriorly along the right side of the stomach and enters the right mantle. There is a depression of the intestinal loop at the right laterodorsal side of the posterior part of the posterior stomach. When the intestine enters the mantle, it abruptly enlarges. It is dorsoventrally flattened and lies longitudinally along the whole length of the right mantle. It is also located next to the left side of the reproductive organ (either the pallial oviduct [in the female] or the prostate gland [in the male]). It is mostly covered by the kidney, except at the very anterior part near the anus.

Part of the intestine that is found in the mantle wall is the rectum. The wall of the rectum is thin, transparent and is marked by many oblique transverse grooves.

The average lengths of the intestine and intestinal loop of *Bithynia siamensis goniomphalos* were, respectively, 1.65 and 2.27 mm.

The intestines of the other Thai bithyniid snails are similar to that of *Bithynia siamensis goniomphalos*, except that the position of the depression of the intestinal loop of some bithyniid species differs (Fig. 5). The average lengths in mm of the intestines of the various species were as follows: *B. siamensis siamensis*, 11.66; *B. funiculata*, 14.04; *B. tentaculata*, 13.43; *Hydrobioides nassa*, 12.27; *Wattebledia siamensis*, 2.15; *W. crosseana*, 10.73; *W. baschi*, 2.89; *Gabbia wykoffi*, 5.72; *G. pygmaea*, 1.88; and *G. erawanensis*, 3.90.

The depression of the intestinal loop of *Bithynia siamensis siamensis*, *B. tentaculata* and *Hydrobioides nassa* is at the posterior part of the posterior stomach (Fig. 5b,d,e), which is the same location as in *B. siamensis goniomphalos* (Fig. 5a). The intestinal loop in *B. funiculata*, *Wattebledia siamensis*, *W. baschi*, *Gabbia pygmaea* and *G. erawanensis* occupies almost the entire length of the right dorsolateral side of the posterior stomach (Fig. 5c,f,h,j,k). The intestinal loop of *W. crosseana* and *G. wykoffi* occupies the entire length of the dorsolateral side of the posterior stomach (Fig. 5g,i). Average lengths in mm of the intestinal loop in the various species were as follows: *Bithynia siamensis siamensis*, 1.66; *B. funiculata*, 1.73; *B. tentaculata*, 0.83; *Hydrobioides nassa*, 1.13; *Wattebledia siamensis*, 0.31; *W. crosseana*, 1.08; *W. baschi*, 0.06; *G. wykoffi*, 0.89; *G. pygmaea*, 0.15; and *G. erawanensis*, 0.69.

### Anus

In *Bithynia siamensis goniomphalos*, the anus is situated near the mantle collar and on the right side of the mantle cavity. It is terminal to the rectum, and lies transversely to it. The anus of the other ten bithyniid snails is basically similar to that of *B. siamensis goniomphalos*.

### Accessory Organs

**Buccal Mass.** In *Bithynia siamensis goniomphalos*, and in the other snails studied, the buccal mass is of considerable size. It is oval when viewed dorsally and elongate-ovate when viewed laterally (Fig. 4a-c). Its dorsal part is light brown in color and is surrounded by muscles. The ventral part of the buccal mass has odontophore cartilages, which are light orange in color. The lower part of the ventral buccal mass is cream colored. It contains a short radular sac in the middle, and has buccal ganglia on both sides of the posterior end of the radula sac (Fig. 4d). At its dorsal side, the buccal mass contains the radular ribbon. When the buccal mass is cut open dorsally, the radula, which lies over the dorsal surface of the buccal mass, is immediately seen (Fig. 4b).

**Radula.** The radula of *Bithynia siamensis goniomphalos* is found at the inner dorsal surface of the buccal mass. After the buccal mass is opened and observed in side view, the radula is seen at the upper front with the odontophore cartilages, which are located a little lower on both sides. With the radula sac, the radula occurs a little below the odontophore cartilages. The radula is S-shaped when viewed from the side. It is flexible (pliable), clear, and has a metallic appearance. The anterior radula, which lies toward the mouth, contains transverse rows of worn teeth. The central part of the radula ribbon contains transverse rows of more perfect teeth and the posterior part of the radula, which lies toward the esophagus, contains transverse rows of newly formed teeth. The teeth are formed only on the dorsal surface of the ribbon. There are seven teeth in each transverse row. The radula formula is 2:1:1:1:2 (marginals : lateral : central : lateral : marginals) (Fig. 6). The central teeth have two kinds of cusps, the anterior cusps, and the basal cusps on both right and left sides of the tooth base. Both kinds of cusps are numerous on each tooth. The lateral and marginal teeth are also multicuspid and, unlike the central teeth, lack basal denticles. The marginals consist of two slender teeth (an inner and an outer tooth) on each outer edge of the radula.

The radulae of the other bithyniid snails studied are basically the same as the radula of *Bithynia siamensis goniomphalos*, except as described below (also see Table 1).

**Central Tooth.** The anterior cusps of *Bithynia siamensis goniomphalos* are triangular with sharply pointed ends (Fig. 7a). The central tooth is bilaterally symmetrical, with a single central cusp (mesocone) and three (usually) or four smaller cusps (ectocones) becoming increasingly smaller distally on each side. The formula of the anterior cusps of *B. siamensis goniomphalos* is 3-1-3 (usually) or 4-1-4. The base of the mesocones is relatively moderate in width and is about twice as wide as that of the ectocones.

The basal denticles are pronounced and occur on a ridge near the lateral margins of the tooth. The more median denticles on each side are largest, with the other denticles becoming increasingly smaller distally. There are about six basal cusps on each side of the tooth, but the smaller most distal basal cusps (the fifth and sixth) are often fused into a bumpy ridge. Therefore, usually, three or four basal denticles occur on each side of the central tooth.



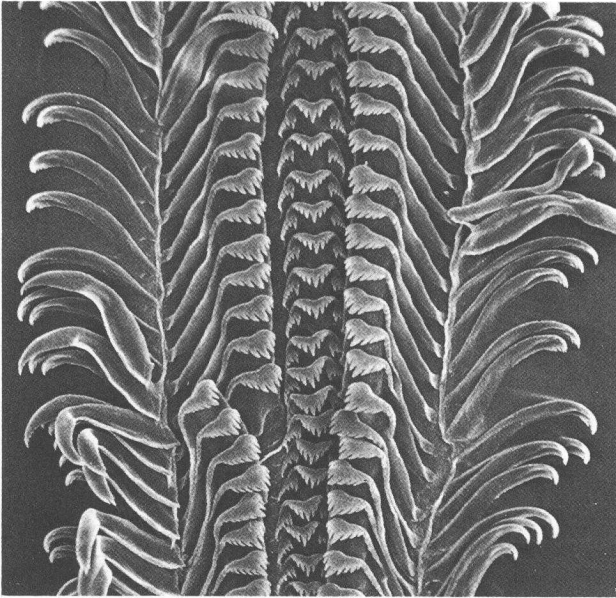


FIG. 6. Scanning electron micrograph of the radula of *Bithynia siamensis goniomphalos* showing the teeth of 19 transverse rows of teeth. Each transverse row is bilaterally symmetrical, with a central tooth in the middle. The central tooth also has basal denticles. The lateral teeth lie next to and on both sides of a central tooth. The inner marginal (sub-marginal) teeth are next to the left and right lateral teeth. The inner marginal teeth are comb-like. The marginal teeth are next to the left and right inner marginal teeth. The marginal teeth are the outermost teeth on the transverse row of the radula. The other bithyniid snails have the same arrangement of types of teeth in a transverse row. ca. x108.

The central teeth of *Bithynia siamensis siamensis* are similar to those of *B. siamensis goniomphalos*, but the mesocones of the anterior cusps have more sharply pointed ends (Fig. 7d). The bases of the mesocones are less than twice as wide as the bases of the ectocones (they are almost the same widths as the flanking cusps) and the bases of the mesocones are relatively narrower.

The shape, arrangement and formula of the basal cusps of *Bithynia siamensis siamensis* are similar to those of *B. siamensis goniomphalos*. However, the number of basal cusps is five instead of the six found in *B. siamensis goniomphalos*. Also, the smallest most distal basal cusps (the fifth) on each side are not as pronounced and have a greater tendency to form a bumpy ridge.

The central teeth of *Bithynia funiculata* are similar to those of *B. siamensis goniomphalos*, but the anterior cusp formula was sometimes 3-1-4 or 4-1-4 instead of 3-1-3, the usual formula (Fig. 8a). In addition, the base of the

TABLE 1. The number of cusps of various types of teeth in a transverse row of bithyniid radulae.

Species	Central			Lateral		Inner Marginal		Outer Marginal		
	anterior cusps	basal cusps	n*	cusps	n*	cusps	n*	cusps	n*	
<i>Bythinia siamensis</i>	3-1-3	3-3	1	4-1-3	2	15	2	7	1	
	<i>goniomphalos</i>	3-1-3	4-4	3	4-1-4	3	16	3	8	3
		4-1-4	4-4	1					11	1
<i>B. siamensis siamensis</i>	3-1-3	4-4	3	5-1-5	3	15	3	9	3	
	4-1-4	4-4	1	4-1-4	2	17	1	10	1	
	4-1-4	5-5	1			18	1	11	1	
<i>B. funiculata</i>	3-1-4	4-4	1	4-1-3	2	16	2	6	1	
	3-1-3	5-5	3	3-1-3	3	14	3	7	3	
	4-1-4	5-5	1					8	1	
<i>B. tentaculata</i>	4-1-4	3-3	1	5-1-5	1			11	1	
	4-1-4	4-4	3	4-1-4	4	16	5	13	4	
	5-1-5	4-4	1							
<i>Hydrobiooides nassa</i>	3-1-3	5-5	1	5-1-5	2	19	1	10	1	
	4-1-4	5-5	2	4-1-4	3	20	3	11	3	
	4-1-4	3-3	1			21	1	13	1	
	4-1-4	4-4	1							
<i>Wattebledia siamensis</i>	3-1-3	5-5	1	3-1-3	1	15	1	9	1	
	4-1-4	5-5	4	4-1-4	4	16	4	11	4	
<i>W. crosseana</i>	3-1-3	7-7	1	5-1-3	1	21	1	8	1	
	4-1-4	5-5	2	4-1-4	3	22	3	10	3	
	4-1-3	5-5	1	5-1-4	1	24	1	11	1	
<i>W. baschi</i>	4-1-4	4-4	1							
	7-1-8	1-1	1	5-1-3	1	26	1	26	1	
	7-1-7	1-1	3	4-1-3	4	28	4	25	4	
	8-1-8	1-1	1							
<i>Gabbia wykoffi</i>	3-1-3	3-3	3	4-1-3	4	20	4	13	4	
	3-1-3	2-2	1	5-1-4	1	24	1	15	1	
	4-1-4	4-4	1							
<i>G. pygmaea</i>	3-1-3	3-3	5	3-1-3	5	17	5	9	4	
<i>G. erawanensis</i>								11	1	
	5-1-5	3-3	2	3-1-3	4	23	3	16	3	
	4-1-4	3-3	1	4-1-3	1	25	2	18	2	
	5-1-5	6-6	1							
	8-1-8	3-3	1							

\*n = number of specimens.

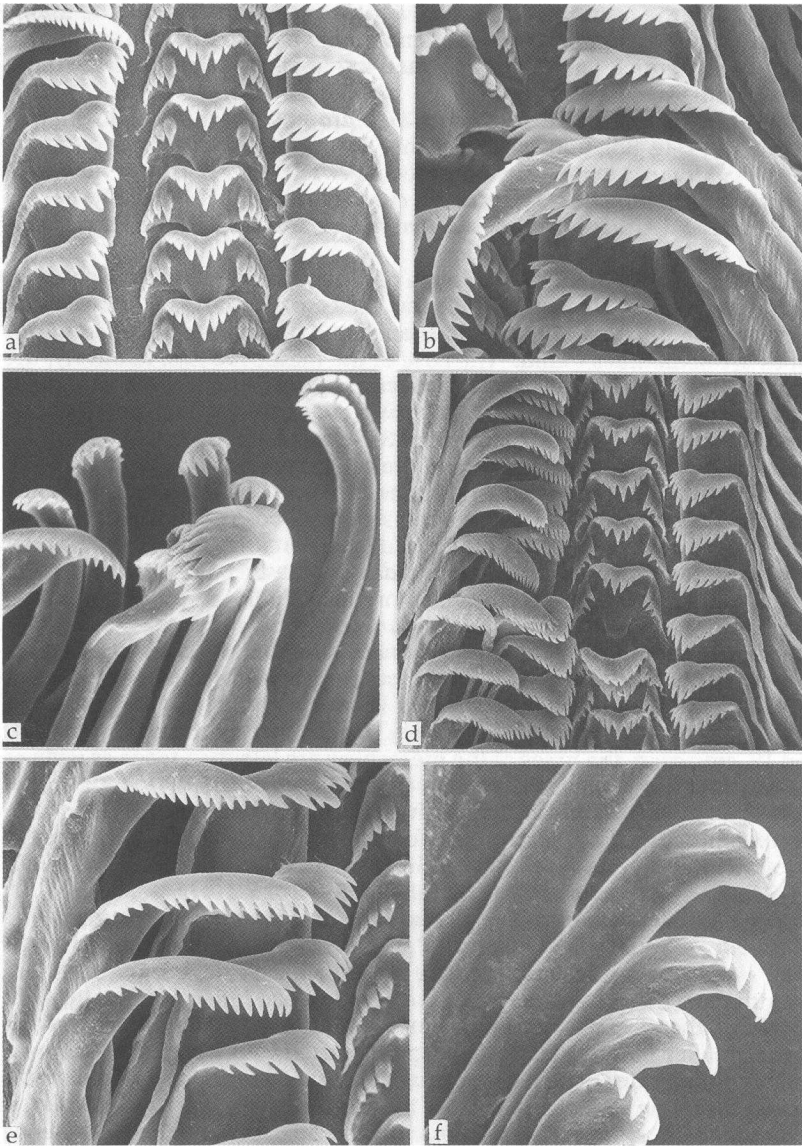


FIG. 7. Scanning electron micrographs of the radula of *Bithynia siamensis*. a-c, *B. siamensis goniomphalos*; d-f, *B. siamensis siamensis*. a, ca. x205; b,c, ca. x410; d, ca. x175; e, ca. x585; f, ca. x465.

mesocone of the central tooth is relatively wider than the base of the mesocone of *B. siamensis goniomphalos*, and, in the basal cusps, the sixth most distal basal denticles are usually formed into a bumpy ridge and the basal cusp formula is more often 5-5.

The central teeth of *Bithynia tentaculata* have broad, spade-shaped mesocones (Fig. 8d), and ectocones that are very similar to those of *B. siamensis goniomphalos*. The basal mesocone is relatively narrower than in *B. siamensis goniomphalos*. The anterior cusp formula is 4-1-4 (usually) or 5-1-5. The basal denticles of *Bithynia tentaculata* are similar in all aspects to those of *B. siamensis goniomphalos*.

The mesocones of the central teeth of *Hydrobioides nassa* have a variety of shapes (Fig. 9a), although, in general, they are like those of *Bithynia siamensis goniomphalos*. But, nipple-shaped and broad spade-shaped mesocones are sometimes found. The base of the mesocone has, relatively, the same width as found in *B. siamensis goniomphalos*, and is twice as wide as the base of the ectocones of *B. siamensis goniomphalos*. The anterior cusp formula is usually 4-1-4, but sometimes 3-1-3 was found.

The overall basal cusp formula of the central teeth is 6-6, but the fourth or fifth to sixth most distal basal denticles are sometimes fused into a bumpy ridge and usually the smallest most distal basal cusps (the sixth) are less pronounced and more like a bumpy ridge. Therefore, the most common basal cusp formula found in *Hydrobioides nassa* was 5-5. Additionally, the ridge bearing the basal denticles is more broadly flexed off of the lateral margins of the tooth than in *Bithynia siamensis goniomphalos*.

The central teeth of *Wattebledia siamensis* (Fig. 9c), *W. crosseana* (Fig. 9f) and *W. baschi* (Fig. 10c) show a similar outline of the shape of mesocones as in *Bithynia siamensis goniomphalos*. In *W. baschi*, the base of the mesocone is twice as wide as that of the ectocones. Unlike that found in *W. siamensis* and *W. crosseana*, the bases of the mesocones are less than twice as wide as the bases of the ectocones. Moreover, the bases of the mesocones of all three species of *Wattebledia* are relatively narrower than those of *B. siamensis goniomphalos*. The anterior cusp formulae of the *Wattebledia* species are as follows: 4-1-4 (usually) or 3-1-3 in *W. siamensis*; 4-1-4 (usually) or 3-1-3 or 4-1-3 in *W. crosseana*; and 7-1-7 (usually) or 8-1-8 or 7-1-8 in *W. baschi*.

The basal denticle formulae of *Wattebledia siamensis*, *W. crosseana* and *W. baschi* are usually 5-5, 5-5 and 7-7, respectively. The overall basal cusps of *W. siamensis* and *W. crosseana* are seven on each side, but the sixth and seventh most distal basal denticles are usually fused into a bumpy ridge. In *W. baschi*, the most proximal basal cusp is pronounced and usually the rest of the smaller most distal basal cusps are fused into a slightly bumpy or nearly smooth ridge. The ridge bearing the basal denticles of *W. siamensis* is usually near the lateral margins of the central tooth, as in *B. siamensis goniomphalos*. However, in *W. crosseana* the ridge bearing the basal denticles is slightly flexed off of the lateral margins of the central tooth (more often) in a straight fashion or the ridge bearing the basal denticles is near the lateral margins of the central tooth, like that sometimes found in *B. siamensis goniomphalos*. Further, the ridge bearing the basal denticles is generally more broadly flexed off of the lateral margins of the central tooth in a curved fashion in *W. baschi*.



FIG. 8. Scanning electron micrographs of the radula of a-c, *Bithynia funiculata*; d-f, *B. tentaculata*. a, x142; b, x620; c, x435; d, x310; e, f, x620.

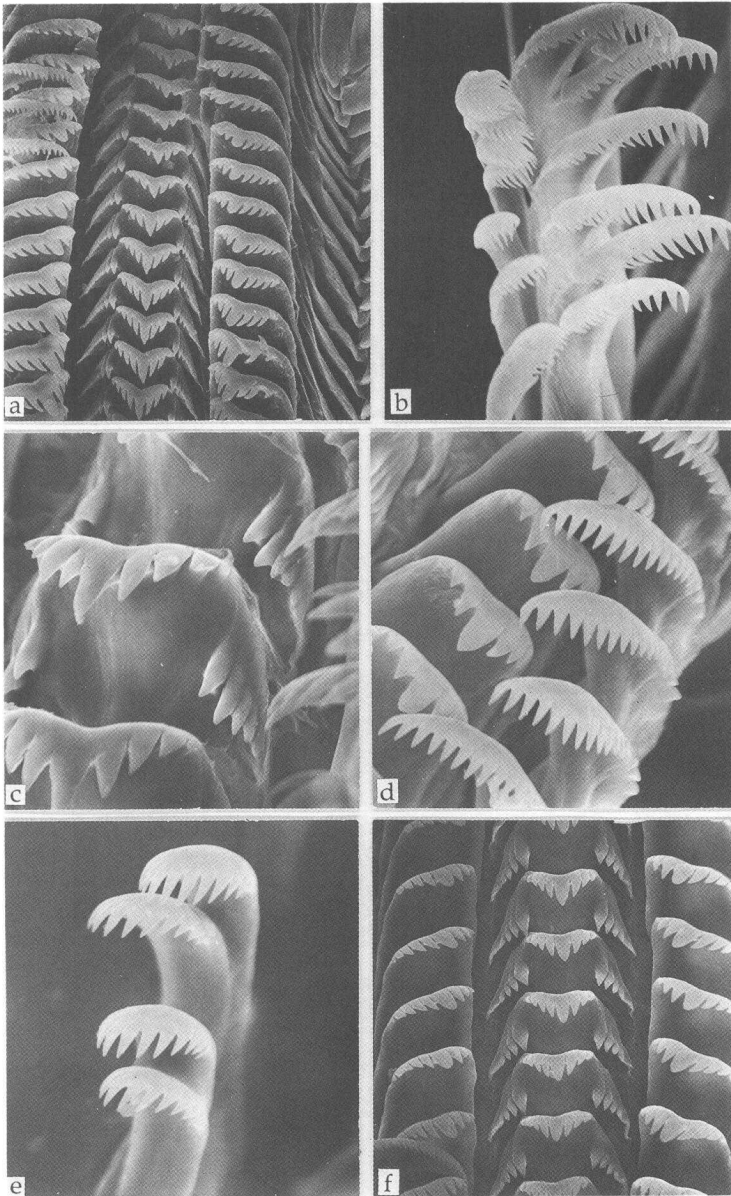


FIG. 9. Scanning electron micrographs of the radula of a-b, *Hydrobioides nassa*; c-e, *Wattebledia siamensis*; f, *W.rosseana*. a, ca. x185; b, ca. x620; c, d, e ca. x870; f, ca. x560.

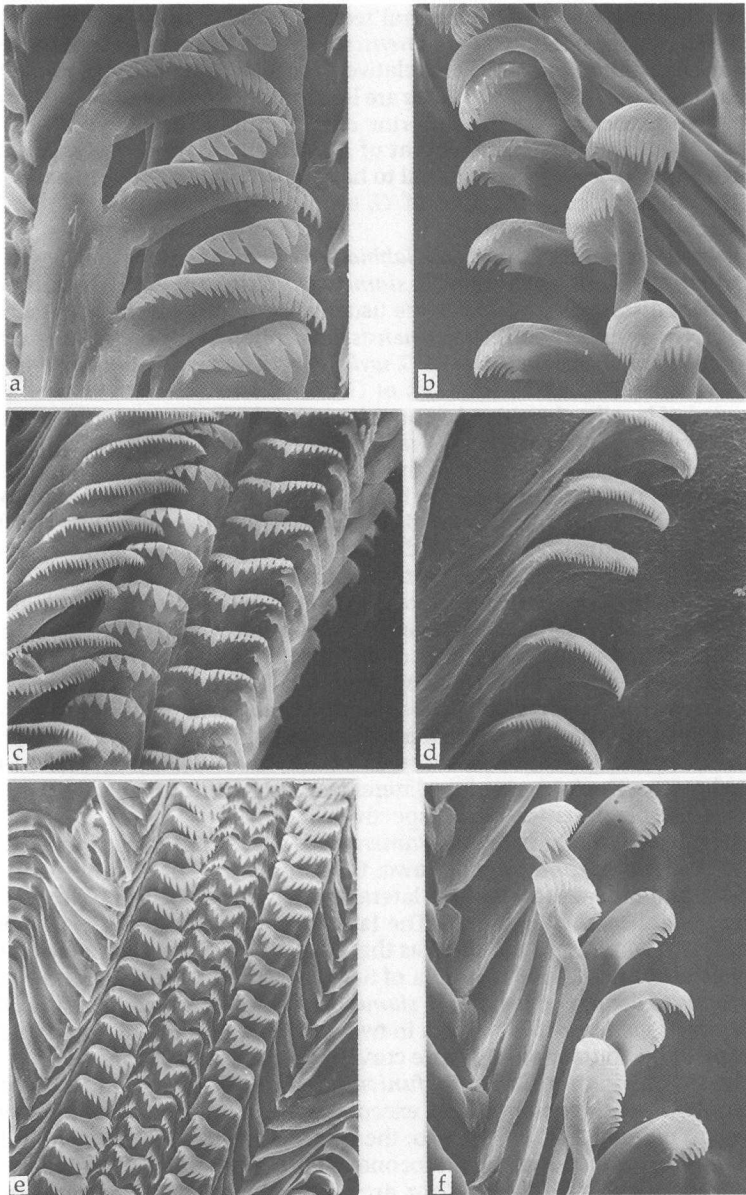


FIG. 10. Scanning electron micrographs of the radula of a-b, *Wattebledia crosseana*; c-d, *W. baschi*; e-f, *Gabbia wykoffi*. a, ca. x1170; b, ca. x700; c, ca. x760; d, ca. x880; e, ca. x290; f, ca. x700.



The anterior cusps of the central teeth of *Gabbia wykoffi* (Fig. 10e), *G. pygmaea* (Fig. 11a), and *G. erawanensis* (Fig. 11c) are similar to those of *B. siamensis goniomphalos*, but are relatively narrower (the bases of the mesocones of *G. wykoffi* and *G. pygmaea* are less than twice as wide as the base of their own ectocones). The anterior cusp formula of *G. wykoffi* and *G. pygmaea* is often the same as that of *B. siamensis goniomphalos*, even though some *G. wykoffi* were found to have an anterior cusp formula of 4-1-4. The anterior cusp formula of *G. erawanensis* is usually 5-1-5, but sometimes 4-1-4 or 8-1-8.

Overall, the basal denticles of *Gabbia wykoffi*, *G. pygmaea* and *G. erawanensis* are the same as those of *B. siamensis goniomphalos*. The fourth to sixth most distal basal denticles are usually fused into a bumpy ridge in *G. wykoffi*, *G. pygmaea* and *G. erawanensis*. Exceptionally, the third to sixth or the fifth to sixth basal denticles of *G. wykoffi* are fused into a bumpy ridge on both sides, and all basal denticles of *G. erawanensis* are sometimes pronounced. Usually, the ridge bearing the basal denticles is near the lateral margins of the central tooth in *G. wykoffi*, but in some specimens this ridge is sometimes slightly flexed off of the lateral margins of the central tooth. In *G. pygmaea*, the ridge bearing the basal denticles is commonly found to be more broadly and straightly flexed off of the lateral margins of the central tooth. Usually, the ridge bearing the basal denticles is more broadly flexed off of the lateral margins of the central tooth in a curved fashion.

**Lateral Teeth.** The lateral teeth of *Bithynia siamensis goniomphalos* have broad triangular-shaped mesocones with rounded ends and are flanked by four shorter and narrower ectocones and three or four (more often) shorter and narrower entocones (Fig. 7a,b). Both types of flanking cusps decrease progressively in size distally, have pointed ends, and are slightly curved toward the mesocone. Also, the mesocone of the first lateral tooth is slightly broader relatively (less than twice as broad) than the mesocone of the central tooth. The formula of the lateral teeth is 4-1-4 (usually) or 4-1-3 (ectocones-mesocone-entocones, respectively).

The lateral teeth of *Bithynia siamensis siamensis* differ from those of *B. siamensis goniomphalos* as follows: the cutting end of the mesocone is pointed, and the mesocone of the lateral tooth is about the same size as that of the central tooth (Fig. 7d,e). The lateral tooth formula of *B. siamensis siamensis* is sometimes the same as that of *B. siamensis goniomphalos*, but more often a lateral tooth formula of 5-1-5 was found. The ectocones and entocones of the lateral teeth of *B. siamensis siamensis* are similar to those of *B. siamensis goniomphalos*, except in two out of five specimens both types of flanking cusps were relatively more curved toward the mesocones.

The lateral teeth of *Bithynia funiculata* are usually similar to those of *Bithynia siamensis goniomphalos*, except that the cutting edges of the mesocones are pointed (Fig. 8a,c). Also, the mesocone was sometimes found to be about the same size as the mesocone of the central tooth. The ectocones and entocones of *B. funiculata* are similar to those of *B. siamensis goniomphalos*. The lateral tooth formula of *B. funiculata* is 3-1-3 (usually) or 4-1-3.

The lateral teeth of *Bithynia tentaculata* are similar to those of *B. siamensis goniomphalos*, but the mesocones of the lateral teeth are about the same

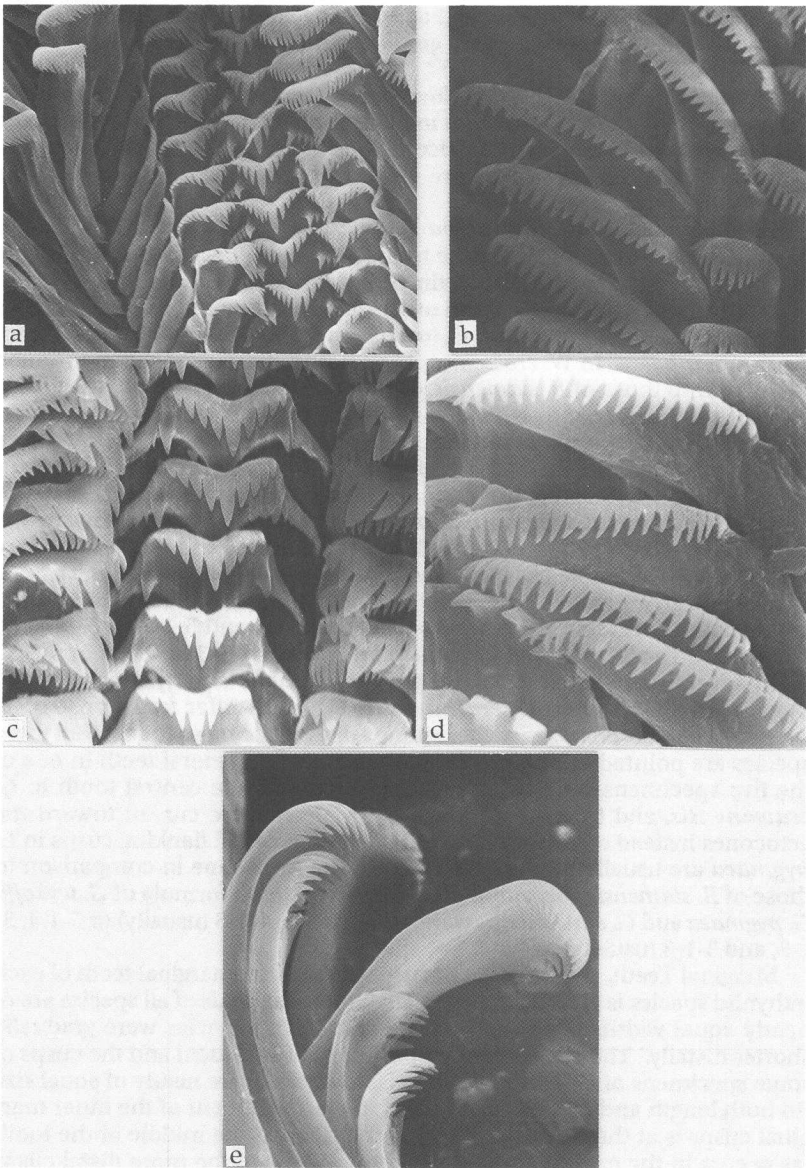


FIG. 11. Scanning electron micrographs of the radula of a-b, *Gabbia pygmaea*; c-e, *G. erawanensis*. a-b, x645; c, x775; d, x1290; e, x1032.

size as those of the central tooth (Fig. 8d). The lateral tooth formula is also the same as that of *B. siamensis goniomphalos*, but one specimen had a lateral tooth formula of 5-1-5.

The lateral teeth of *Hydrobioides nassa* are usually similar to those of *Bithynia siamensis goniomphalos* in all aspects (Fig. 9a). Occasionally, the mesocone of the lateral teeth is twice as wide as that of the central teeth. On both sides, the flanking cusps are curved toward their mesocones. The lateral tooth formula is 5-1-5.

The lateral teeth of *Wattebledia siamensis*, *W. crosseana* and *W. baschi* have pointed cutting edges, but the rounded cutting edges found in *Bithynia siamensis goniomphalos* are sometimes also found in *W. siamensis* (Fig. 9d). The mesocone of the lateral tooth of *W. siamensis* is about the same size as the mesocone of the central tooth (usually) or similar to those of *B. siamensis goniomphalos*. In *W. crosseana* (Fig. 9f), the characters just mentioned are similar to those of *B. siamensis goniomphalos*. In *W. baschi*, the mesocone of the lateral tooth is twice as wide as the mesocone of the central tooth (Fig. 10c). The shape of the ectocones and entocones of *W. crosseana* and *W. baschi* are similar to those of *B. siamensis goniomphalos*. The ectocones and the entocones of *W. siamensis* are usually similar in shape to those of *B. siamensis goniomphalos*, or they are more curved toward the mesocones. The lateral tooth formulae of *W. siamensis* and *W. crosseana* are the same as the formula usually found in *B. siamensis goniomphalos*, i.e., 4-1-4. However, in one specimen out of five examined of each species, the lateral tooth formulae were 3-1-3 (*W. siamensis*), and 5-1-3 or 5-1-4 (*W. crosseana*). The lateral tooth formula of *W. baschi* is 4-1-3 (usually) or 5-1-3.

In several respects, the lateral teeth of *Gabbia wykoffi* (Fig. 10e), *G. pygmaea* (Fig. 11a) and *G. erawanensis* (Fig. 11c) differ from those of *B. siamensis goniomphalos*, e.g., the cutting edges of the mesocones in all three species are pointed in outline, the mesocones of the lateral teeth in one of the five specimens were twice as wide as those of the central tooth in *G. erawanensis*, and the mesocones of *G. pygmaea* were curved toward the ectocones instead of being straight. Also, both types of flanking cusps in *G. pygmaea* are usually more curved toward the mesocone in comparison to those of *B. siamensis goniomphalos*. The lateral tooth formula of *G. wykoffi*, *G. pygmaea* and *G. erawanensis* were, respectively, 4-1-3 (usually) or 5-1-4, 3-1-3, and 3-1-3 (usually) or 4-1-3.

**Marginal Teeth.** The number of cusps of the inner marginal teeth of each bithyniid species is given in Table 1. The inner marginals of all species are of nearly equal width. The length of the cusps of all species were gradually shorter distally. The cusps of most specimens of *W. baschi* and the cusps of some specimens of *W. crosseana* and *G. erawanensis* are nearly of equal size (in both length and width). In addition, the arrangement of the inner marginal cusps is at the side of the tooth rather than at the middle of the tooth (as occurs in the central and lateral teeth). Some of the more distal cusps have a tendency to fuse in most specimens of *B. siamensis goniomphalos* (Fig. 7b), *B. funiculata* (Fig. 8c), some specimens of *B. siamensis siamensis* and *B. tentaculata*. In contrast, there seems to be less tendency for such a fusion in *B. siamensis siamensis* (Fig. 7e), *B. tentaculata* (Fig. 8e), *H. nassa* (Fig. 9b), *W. siamensis* (Fig. 9d), *W. crosseana* (Fig. 10a), *W. baschi* (Fig. 10c),

*G. wykoffi* (Fig. 10f), *G. pygmaea* (Fig. 11b), and *G. erawanensis* (Fig. 11d).

The outer marginal teeth are more slender than the inner marginals, and have fewer cusps. The number of cusps of the outer marginal teeth for each species are as follows: eight (usually), or seven or 11 in *Bithynia siamensis goniomphalos* (Fig. 7c); nine (usually) or 10 or 11 in *B. siamensis siamensis* (Fig. 7f); seven (usually) or six or eight in *B. funiculata* (Fig. 8b); 13 (usually) or 11 in *B. tentaculata* (Fig. 8f); 11 (usually) or 10 or 13 in *Hydrobioides nassa* (Fig. 9b); 11 (usually) or nine in *Wattebledia siamensis* (Fig. 9e); 10 (usually) or eight or 11 in *W. crosseana* (Fig. 10b); 25 (usually) or 26 in *W. baschi* (Fig. 10d); 13 (usually) or 15 in *G. wykoffi* (Fig. 10f); nine (usually) or 11 in *G. pygmaea* (Fig. 11b); and 16 (usually) or 18 in *G. erawanensis* (Fig. 11e).

The cusps of all species are rather pronounced. The arrangement of the cusps are more at the middle of the tooth than at the side, and they are also spread to the side symmetrically. The width of each cusp is about the same, but the length of some cusps is longest at the middle and then is gradually shorter distally on both sides of the tooth.

**Salivary Glands.** In the Bithyniidae, the salivary glands are a pair of light yellow, cylindrical, dorsoventrally flattened tubules, joining the left and right sides of the dorsal buccal mass near the posterior end. They are shorter than the buccal mass. The esophagus lies between them (Fig. 4a).

**Digestive Glands.** The digestive glands of all bithyniid snails are dark reddish-brown in color and contain numerous dark granules. The glands occupy most of the apical or spire whorls. There are two large lobes (dorsal and ventral) that cover most of the apical whorls (except part of the dorsal and ventral surfaces of the posterior part of the stomach). These glands consist of numerous branching tubules that vary in size. They are bound together by thin tissues. The way the testis and ovary are embedded in the digestive glands differs and can affect the sizes and shapes of the digestive glands. The testis wraps completely around the digestive gland; the ovary is embedded in the digestive gland only at its right and dorsal sides. The branching tubules of the digestive glands form the main duct. This digestive gland duct runs parallel to the oviduct from the apex to the left ventral side of the stomach and opens into the left ventral part of the stomach a little posterior to the right of the entrance of the esophagus (Fig. 4a, f). The positions of the opening of the digestive gland to the stomach of all bithyniid snail species are similar to those of *Bithynia siamensis goniomphalos* (Fig. 5).

#### Fecal Pellets

The shapes of fecal pellets of bithyniid snails differ depending on the species. The fecal pellets of *Bithynia siamensis goniomphalos* are long, slender and fusiform. They lie obliquely along the rectum and usually fill its whole length (Fig. 4a). When the snails defecate, the feces come out in pellets. Sometimes the pellets are attached in strings. The feces, after being expelled through the anus, pass through the siphon before leaving the snail.

The other Thai bithyniid snails have the same habits of defecation as *Bithynia siamensis goniomphalos*. The shape of the fecal pellets of *B. siamensis siamensis*, *B. funiculata* and *Hydrobioides nassa* is similar to those of

*B. siamensis goniomphalos*. The fecal pellets of *B. siamensis siamensis* and *B. funiculata* are, respectively, spiral, long, slender and fusiform-shaped, and long, stout and fusiform-shaped. The fecal pellets of *Wattebledia siamensis* are rather long, slender and cigar-shaped. Those of *W. crosseana* are similar to *W. siamensis*, but sometimes they are also spiral. The fecal pellets of *W. baschi* are cigar-shaped, and those of *Gabbia wykoffi*, *G. pygmaea* and *G. erawanensis* are oval.

## Reproductive System

### Male Reproductive System

In *Bithynia siamensis goniomphalos*, the testis is a glandular structure, bright orange in color. In mature individuals, it envelopes the digestive gland and occupies most of the upper whorls, including the apex (Fig. 2a-c). It ends in front of the anterior stomach (Fig. 2a). The average length of the testis was 5.98 mm<sup>2</sup>. The thick, muscular, coiled vas deferens runs anteriorly from the testis in a superficial position. It is located on the ventral side of the whorl and extends laterally to about 1/3 of the whorl on the right side (Fig. 12a). That part of the vas deferens that is located at the ventral part of the whorl is underneath the entire ventral part of the stomach, and that part of the vas deferens that is at the side of the whorl is covered by some of the right side of the posterior stomach of the snail. The average length of this duct was 30.25 mm. The vas deferens narrows and passes to the right posterior corner of the mantle cavity, and here merges into the ventral side of the tubular or glandular prostate gland, which is on the right side of the rectum and on the outer-most edge of the right mantle wall (Fig. 2c,d). The average length of the prostate gland was 4.31 mm. The prostate gland is separated from the mantle cavity by the forwardly projecting lobe of the kidney, covering its ventral part. The narrower vas deferens, which is covered by the lobe of the kidney, is referred to as the renal vas deferens (Fig. 2d). The average length of the renal vas deferens was 3.92 mm. The renal vas deferens runs anteriorly and, after emerging from beneath the lobe of kidney, runs along the right mantle wall transversely toward the right mantle margin and the right side of the body before going into the verge or penis. The narrow part of the vas deferens that runs along the mantle after the renal vas deferens has thinner walls than the renal vas deferens. This is the pallial vas deferens (Fig. 2a,d)<sup>3</sup>. After the pallial vas deferens, the vas deferens runs subepithelially along the right side of the body toward the base of the verge and

<sup>2</sup>In terms of measurements, it is worthwhile to know both lengths and widths of all male reproductive organs. However, there is some variation in male reproductive organ diameters, depending upon seasons (Lilly, 1953). For example, the prostate gland is most swollen during the breeding season. In such cases, the width of the male reproductive organs may not provide useful comparisons for taxonomic purposes. Therefore, in my studies I used only lengths of male reproductive organs.

<sup>3</sup>I refer to the duct that is located on the mantle as the "pallial vas deferens" and the duct that runs along the right side of the body of the snail the "penial vas afferens." But because of the short lengths of both ducts, I combined their lengths and called them the "pallial vas deferens" when I refer to male reproductive organ measurement. For the rest of the male reproductive organ names, I follow Lilly (1953).

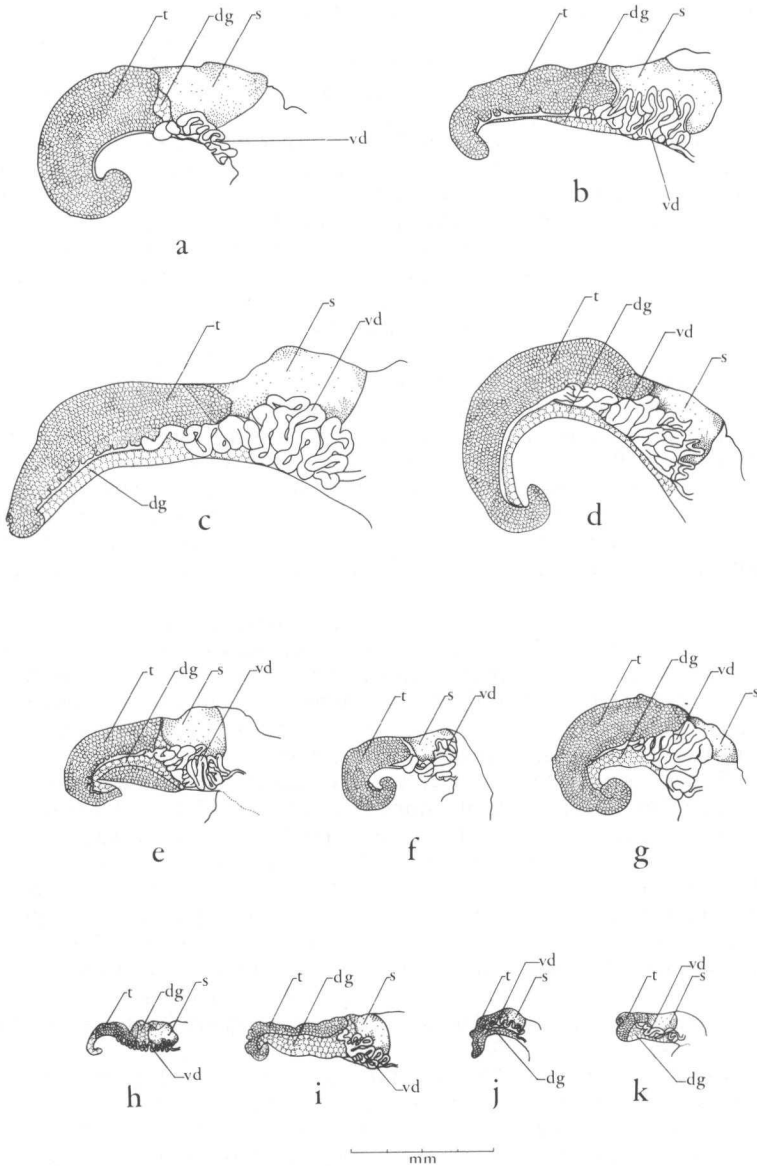


FIG. 12. Testis and vas deferens of a, *Bithynia siamensis goniomphalos*; b, *B. siamensis siamensis*; c, *B. funiculata*; d, *B. tentaculata*; e, *Hydrobioides nassa*; f, *Wattebledia siamensis*; g, *W. crosseana*; h, *W. baschi*; i, *Gabbia wykoffi*; j, *G. pygmaea* and k, *G. erawanensis*. Abbreviations: dg = digestive gland; s = stomach; t = testis; vd = vas deferens. Scale line = 4 mm.

becomes the penial duct inside the verge (Fig. 2b). This part of the vas deferens up to the verge is referred to as the penial vas afferens. The penial vas afferens is a very short duct, a little coiled, narrow and is as thin as the pallial vas deferens. The average length of the pallial vas deferens (including the length of the penial vas afferens) was 3.23 mm.

The penis extends from the back of the neck behind the right tentacle (Fig. 2b). The basal half of the verge is bifid and has a median finger-like flagellum, which is smaller than the verge (Fig. 2b). Inside the verge, the thick penial duct is a little coiled and runs from the base through the tip of the verge. It opens at the tip of the penis into the genital opening or genital aperture (Fig. 2b). The flagellum has an accessory prostate gland, which consists of a thin coiled tubule that curls to and fro on the broad base of the penis and extends into the haemocoel. The average lengths in mm of the various male reproductive organs were as follows: penis, 7.94; the relatively thick penial duct, 10.95; accessory gland, 1.41; and the relatively thin and coiled accessory gland duct, 27.27. In the natural position, when the penis is not in use, it curves to the left with a flagellum arising from the middle of its concave part. It looks somewhat plate-like, with the concave part as the inner side and the convex part as the outer side of the plate. During mating, the curved plate-like portion stretches out and becomes long, slender and tapered at the end, with the long, slender and finger-like flagellum at the middle of the left side of the penis. This position is also seen in well-relaxed specimens.

The male reproductive system of *Bithynia siamensis siamensis*, *B. funiculata*, *B. tentaculata*, *Hydrobioides nassa*, *Wattebledia siamensis*, *W. crosseana*, *W. baschi*, *Gabbia wykoffi*, *G. pygmaea* and *G. erawanensis* are similar to that of *B. siamensis goniomphalos*, except for the color and the position of the testis, the position of the vas deferens, and the length of some reproductive organs. These differences are described below.

In *Bithynia siamensis siamensis* (Fig. 12b), the testis is embedded in all of the apex, all of the right side, the dorsal side and 1/4 of the left dorsolateral position of the upper whorls. The average length of the testis was 5.98 mm. Its vas deferens is at the ventral side of the coil and beneath the ventral side of the stomach. However, a part of the vas deferens occupies half of the right ventrolateral side of the coil at the posterior part of the anterior stomach and part of the anterior part of the posterior stomach. The average lengths in mm of the various male reproductive organs are as follows: vas deferens, 22.36; renal vas deferens, 3.67; pallial vas deferens, 2.78; prostate gland, 4.09; penis, 5.33; penial duct, 8.20; accessory gland, 1.98; and the duct of the accessory gland, 29.98.

In *Bithynia funiculata* (Fig. 12c), the testis is embedded at the right and dorsal apex, the whole right and dorsal parts of the upper whorls and 1/4 of the left dorsolateral part of the upper whorls. The average length of the testis was 7.45 mm. It ends by overlapping the dorsal part of the anterior stomach. The position of the vas deferens is similar to that of *B. siamensis siamensis*. The average lengths in mm of the various male reproductive organs were as follows: vas deferens, 30.02; renal vas deferens, 4.79; pallial vas deferens, 3.51; prostate gland, 5.14; penis, 4.52; penial duct, 4.62; accessory gland, 1.87; and the duct of the accessory gland, 30.17.



In *Bithynia tentaculata* (Fig. 12d), the testis is pale orange in color and is embedded on the right and dorsal apex, and on all of the right, dorsal and half of the left dorsolateral part of the upper whorls. The testis ends by overlapping the dorsum of the anterior stomach. The average length of the testis was 6.64 mm. The coiled vas deferens adjacent to the testis runs across 2/3 of the right ventrolateral stomach. The vas deferens then runs underneath the ventral spire whorls before it enters the mantle. The average lengths in mm of the various male reproductive organs were as follows: vas deferens, 15.19; renal vas deferens, 3.48; pallial vas deferens, 4.35; prostate gland, 3.69; penis, 2.62; penial duct, 6.40; accessory gland, 0.89; and the duct of the accessory gland, 12.17.

In *Hydrobioides nassa* (Fig. 12e), the testis occupies most of the left side of the upper whorls. The average length of the testis was 4.67 mm. Also, its vas deferens is beneath only the ventral side of the stomach. The average lengths in mm of the various male reproductive organs were as follows: vas deferens, 21.57; renal vas deferens, 2.68; pallial vas deferens, 4.74; prostate gland, 3.90; penis, 5.19; penial duct, 10.93; accessory gland, 1.02; and the duct of the accessory gland, 68.50.

In *Wattebledia siamensis* (Fig. 12f), the testis is bright yellow in color. The testis is embedded in the right side of the apical whorl, in 2/3 of the right dorsolateral part, all of the dorsal part, and 1/3 of the left dorsolateral part of the other upper whorls. The average length of the testis was 3.26 mm. Its vas deferens is located at the ventral side of the whorl and underneath the ventral stomach. Also, a part of the vas deferens is on 2/3 of the right ventrolateral aspect of the whorl and on the right lateral side of the posterior stomach. The average lengths in mm of the various male reproductive organs were as follows: the vas deferens, 11.12; renal vas deferens, 1.51; pallial vas deferens, 2.11; prostate gland, 1.85; penis, 2.81; penial duct, 3.97; accessory gland, 0.56; and the duct of the accessory gland, 15.98.

In *Wattebledia crosseana* (Fig. 12g), the testis is bright yellow in color. The testis does not occupy all of the right dorsolateral part of the upper whorls, but only 3/4 of this space. The testis ends by a little overlap to the right side of the anterior stomach and adjacent to the left side of the anterior stomach. The average length of the testis was 5.63 mm. The position of the vas deferens of *W. crosseana* is similar to that of *Hydrobioides nassa*. The average lengths in mm of the various male reproductive organs were as follows: vas deferens, 16.38; renal vas deferens, 2.53; pallial vas deferens, 3.40; prostate gland, 2.94; penis, 3.15; penial duct, 3.45; accessory gland, 0.94; and the duct of the accessory gland, 20.17.

In *Wattebledia baschi* (Fig. 12h), the testis is yellow in color. The testis is not embedded in the apical whorl, but it occurs in all of the right side, the dorsal side, and half of the dorsolateral side of the other upper whorls. It ends in front of the stomach. The average length of the testis was 1.16 mm. Its vas deferens is beneath the ventral part of the anterior stomach and anterior of the posterior stomach. It then runs up along the right ventrolateral side at about 1/4 of the right ventrolateral part of the posterior stomach. The average lengths in mm of the various male reproductive organs were as follows: vas deferens, 5.73; renal vas deferens, 0.31; pallial vas deferens, 0.66; prostate gland, 1.08; penis, 1.66; penial duct, 2.21; accessory gland, 0.16; and



the duct of the accessory gland, 5.51.

In *Gabbia wykoffi* (Fig. 12i), the testis is embedded in all of the apical whorl, and in 1/2 of the right dorsolateral, all of the dorsal and almost all of the left dorsolateral parts of the other upper whorls. The average length of the testis was 2.74 mm. The vas deferens is located only underneath the ventral stomach. The average lengths in mm of the various male reproductive organs were as follows: vas deferens, 12.81; renal vas deferens, 1.26; pallial vas deferens, 1.07; prostate gland, 1.43; penis, 1.74; penial duct, 2.20; accessory gland, 0.30; and the duct of the accessory gland, 8.89.

In *Gabbia pygmaea* (Fig. 12j), the testis is embedded in all of the apical whorl, and all of the dorsal and half of the left and right dorsolateral parts of the other upper whorls. The average length of the testis was 0.63 mm. The vas deferens runs across only 1/2 of the right ventrolateral side of the stomach. The average lengths in mm of the various male reproductive organs were as follows: vas deferens, 4.08; renal vas deferens, 0.46; pallial vas deferens, 0.88; prostate gland, 0.63; penis, 1.69; penial duct, 2.23; accessory gland, 0.77; and the duct of the accessory gland, 5.28.

In *Gabbia erawanensis* (Fig. 12k), the testis is orange in color. The testis is embedded in all of the apical whorl, all of the dorsal, all of the right and half of the upper left parts of the other upper whorls. The average length of the testis was 2.15 mm. Its vas deferens is located only beneath the ventral part of the stomach, which also is in the ventral spire whorls. The average lengths in mm of the various male reproductive organs were as follows: vas deferens, 5.84; renal vas deferens, 0.77; pallial vas deferens, 0.64; prostate gland, 0.78; penis, 2.03; penial duct, 3.00; accessory gland, 0.53; and the duct of the accessory gland, 8.19.

#### Female Reproductive System

The ovary of *Bithynia siamensis goniomphalos* is bright orange in color. It is embedded in the digestive gland and is found mostly on the columellar side or the right side of the visceral mass (Figs. 1c, 4f). It spreads on the dorsal surface of the digestive glands that lie in the spire whorls. At the columellar side, the ovary starts (embedded in the digestive glands longitudinally from the posterior end of the apex) and it ends by overlapping longitudinally the posterior half of the anterior stomach (Fig. 13a). The average length of the ovary was 2.26 mm. Its shape is one of branching tubules or lobes with several sub-branching lobes. These lobes or tubules converge to join a single duct of about the same diameter as the lobes. This single duct lies superficially along the right ventrolateral aspect of the coil and continues anteriorly into the oviduct, which runs along the ventral side of the whorls anteriorly toward the right side of the mantle (Fig. 1c). The duct is narrow and very thin. Its average length was 3.73 mm. As the duct approaches the mantle, it gradually becomes thicker. The duct is very thick when it passes forwards toward the mantle, and on reaching the posterior end of the pallial oviduct (located in the right mantle wall) it runs underneath the pallial oviduct and inserts between this duct and the kidney. The duct coils transversely as it goes and then it turns backward and passes beneath the ventral pallial oviduct on its right side and enters the pallial

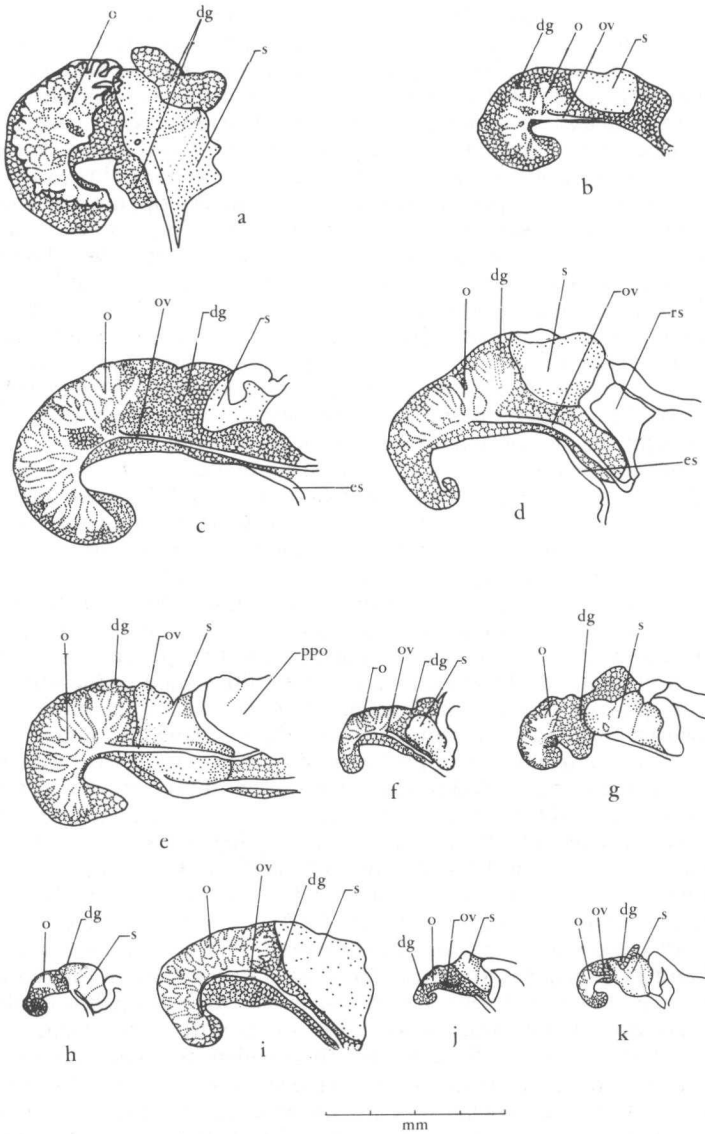


FIG. 13. Ovaries of a, *Bithynia siamensis goniomphalos*; b, *B. siamensis siamensis*; c, *B. funiculata*; d, *B. tentaculata*; e, *Hydrobioides nassa*; f, *Wattebledia siamensis*; g, *W. crosseana*; h, *W. baschi*; i, *Gabbia wykoffi*; j, *G. pygmaea* and k, *G. erawanensis*. Abbreviations: dg = digestive gland; es = esophagus; o = ovary; ov = oviduct; ppo = posterior pallial oviduct; rs = seminal receptacle; s = stomach. Scale line = 4 mm.

oviduct at the ventral side. The part of the thick oviduct that is coiled enters the mantle and runs between the kidney and the pallial oviduct until it enters the ventral channel of the pallial oviduct. This part of the oviduct is referred to as the renal oviduct (Fig. 1c). The renal oviduct is reddish-brown in color, and had an average length of 2.69 mm. The renal oviduct enters the pallial oviduct on its ventral side. The point of entry is in the posterior part of the posterior half of the pallial oviduct. Just before the point where the renal oviduct enters the pallial oviduct, it receives the opening of a thin-walled non-glandular sac, the seminal receptacle, which opens into the pallial oviduct via its thin duct (Fig. 1c). The seminal receptacle is long and slender, and is spade-shaped at the end (Figs. 1c, 14a). Sometimes the seminal receptacle has a small knob-like structure that branches off from the middle part of its left side. The color of the seminal receptacle ranges from bright yellow to bright orange, the latter being the usual color. The seminal receptacle is on the ventral pallial oviduct and is next posteriorly to the renal oviduct, which enters the pallial oviduct posteriorly at its right ventral margin. Its average length was 1.69 mm.

The most obvious reproductive organ in the mantle cavity is the pallial oviduct (Fig. 1). It is a long, broad, glandular structure, light yellow in color. It lies along the right wall of the mantle from the posterior end almost to the anterior mantle margin. It runs parallel to the rectum, which lies next to its left side and is covered ventrally almost its whole length, except for the anterior end next to the kidney, which is modified into a muscular structure, the muscular oviduct. After the animal is removed from its shell, the length of the pallial oviduct can be seen in dorsal view through the transparent mantle. Its length can be seen through the kidney membrane after the mantle margin is dissected and turned over. The average length of the pallial oviduct, measured from the ventral or inner part, was 8.74 mm.

There are two portions of the pallial oviduct, one anterior and the other posterior. The anterior pallial oviduct is thicker and is separated into two parts, one dorsal and the other ventral. The opening of the anterior pallial oviduct, which is dorsal to the spermathecal opening, leads into the muscular oviduct. The posterior pallial oviduct is much thinner and is not separated into two parts, except for the anterior part, which is above the point where the renal oviduct enters the pallial oviduct. A thin-walled sac, not completely separated from the pallial oviduct, lies ventral to the pallial oviduct and extends from the muscular oviduct to the front of the point of entry of the renal oviduct, which is located at the posterior pallial oviduct. There is no direct connection between this sac and the renal oviduct that enters the pallial oviduct. Because this thin-walled sac is not completely separated from the pallial oviduct, the whole sac can open into the ventral channel via the ventral pallial oviduct. This sac is called the spermatheca or bursa copulatrix (Fig. 1c). It is transparent, and had an average length of 7.56 mm. Next anteriorly to the anterior pallial oviduct and spermatheca is that part of the pallial oviduct that has its tissue modified into a muscular structure. It is a short, clear, non-glandular duct that is not covered by the kidney. It is referred to as the muscular oviduct (Fig. 1a). The muscular oviduct lies near the anterior mantle margin and its terminal region curves slightly towards the right mantle margin. The muscular oviduct leads to the

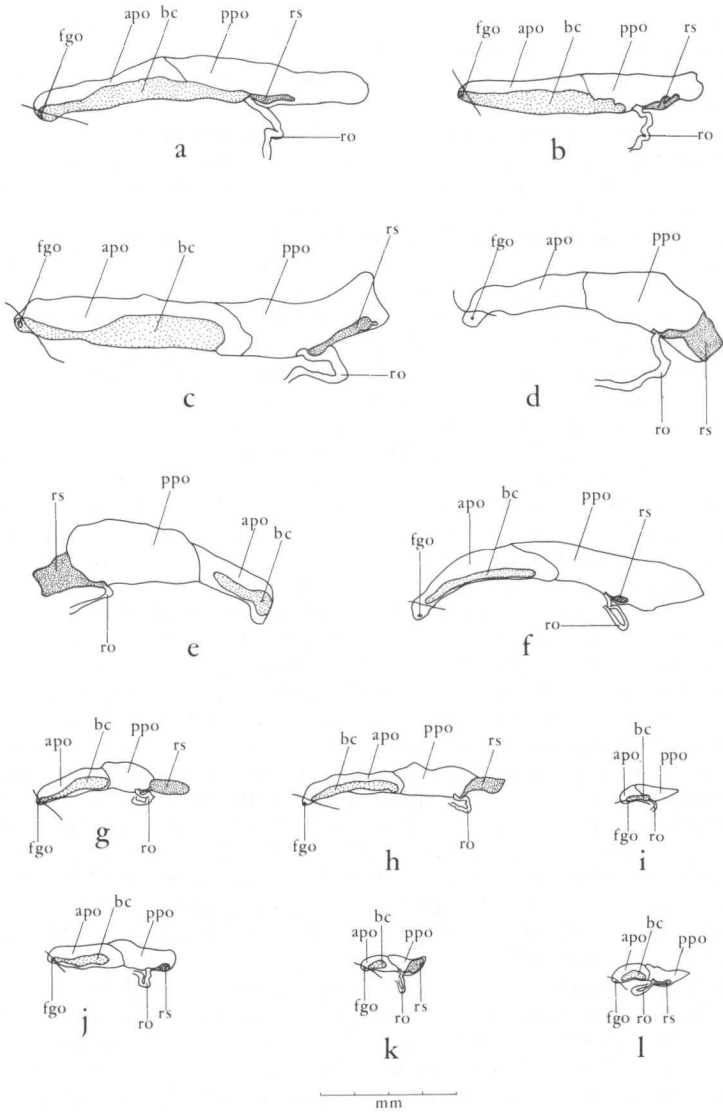


FIG. 14. Ventral views, except where indicated, of parts of female reproductive organs found in the mantle cavities of a, *Bithynia siamensis goniomphalos*; b, *B. siamensis siamensis*; c, *B. funiculata*; d, *B. tentaculata*; e, *B. tentaculata*, dorsal view; f, *Hydrobioides nassa*; g, *Wattebledia siamensis*; h, *W. crosseana*; i, *W. baschi*; j, *Gabbia wykoffi*; k, *G. pygmaea*; and l, *G. erawanensis*. Abbreviations: apo = anterior pallial oviduct; bc = bursa copulatrix; fgo = female genital opening; ppo = posterior pallial oviduct; ro = renal oviduct; rs = seminal receptacle. Scale line = 4 mm.

genital aperture (Fig. 1), which is subterminal and ventral to it. When observing live snails under the microscope with their head-feet extended, their genital apertures can be seen at the anterior margin of the mantle wall above the right side of the neck. When the animal contracts its head-foot, the genital opening is level with the base of the right tentacle.

The female reproductive system of *Bithynia siamensis siamensis* (Figs. 13b, 14b) differs from that of *B. siamensis goniomphalos* by the ovary occupying more than 2/3 of the anterior apical whorl. The ovary extends along the length of the upper whorls anteriorly and ends in front of the anterior stomach. Its color is yellow; its average length was 2.45 mm. The average length of the oviduct was 2.64 mm. The renal oviduct is white in color, and had an average length of 2.22 mm. The position of the renal oviduct at its point of entry into the pallial oviduct is more toward the anterior portion of the posterior pallial oviduct. The pallial oviduct is bright yellow in color and had an average length of 6.75 mm. The seminal receptacle is long, slender and has several branches at the end. It is bright yellow in color. Its average length was 1.74 mm. The average length of the spermatheca was 5.56 mm.

The female reproductive system of *Bithynia funiculata* (Figs. 13c, 14c) is basically similar to that of *B. siamensis goniomphalos*, but some differences were found. The ovary is bright orange in color and had an average length of 2.57 mm. The ovary runs from the apex (about 2/3 of the anterior apex) anteriorly along the coils of the spire whorls and ends in front of the stomach. The average lengths of the thin-walled oviduct and the renal oviduct were, respectively, 3.90 and 2.74 mm. The position of the point of entry of the renal oviduct into the pallial oviduct is similar to that in *B. siamensis siamensis*. The pallial oviduct is bright yellow; its length was 12.52 mm. The seminal receptacle is also bright yellow. It is located in the same position in *B. funiculata* as it is in *B. siamensis goniomphalos*. Its shape is long, slender, and rounded at the end. The average length of the seminal receptacle was 1.76 mm. The spermatheca forms a clear and thin-walled sac, and is completely separated from the pallial oviduct. The sac is on the ventral pallial oviduct when observed by turning the mantle over. The sac extends from the muscular oviduct almost to the anterior end of the anterior pallial oviduct. The opening of the spermatheca to the pallial oviduct is almost at the middle portion of the spermatheca. The average length of the bursa copulatrix was 5.22 mm.

The female reproductive system of *Bithynia tentaculata* (Figs. 13d, 14d,e) is similar to that of *B. siamensis goniomphalos*, except that the ovary is in the third and the fourth coils of the spire whorls and it ends by overlapping the posterior end of the anterior stomach. The ovary is pale yellow. Its average length was 1.61 mm. The oviduct is thin-walled; its average length was 2.89 mm. The point of entry of the renal oviduct to the pallial oviduct is at the posterior end of the posterior pallial oviduct. The average length of the renal oviduct was 3.19 mm. The pallial oviduct is yellow and had an average length of 8.11 mm. The seminal receptacle is a plate-like structure, irregularly shaped at the end. It is not on the pallial oviduct, but lies posteriorly next to the pallial oviduct and is on the right ventral margin of the mantle. It is yellow in color; its average length was 1.63 mm. The duct of the seminal receptacle runs transversely to join the renal oviduct before the renal

oviduct enters the pallial oviduct. The bursa copulatrix is completely separated from the pallial oviduct, but there is an opening into the anterior pallial oviduct near the anterior end of the bursa copulatrix. The position of the bursa copulatrix is different from that of *B. siamensis goniomphalos* in that it is on the dorsal part of the anterior pallial oviduct instead of lying beneath it. The average length of the bursa copulatrix was 1.80 mm. The opening of the bursa copulatrix to the pallial oviduct is a little behind the anterior end of the bursa copulatrix. The opening of the bursa copulatrix into the muscular oviduct is at about the same level as the genital aperture, and it is a little behind the genital aperture.

In *Hydrobioides nassa* (Figs. 13e, 14f), the ovary is bright yellow. Its average length was 1.79 mm. It is embedded in the digestive gland and starts from the posterior end of the second coil of the spire whorls. Then it runs anteriorly along the spire whorls (about the fourth coil of the spire whorls) and it ends in front of the stomach. The average lengths of the oviduct and the renal oviduct were, respectively, 3.00 and 1.77 mm. The position of the point of entry of the renal oviduct to the pallial oviduct is similar to that of *Bithynia siamensis siamensis*. The anterior pallial oviduct is light yellow in color and the posterior pallial oviduct is orange-yellow in color. The average length of the pallial oviduct was 8.94 mm. The seminal receptacle is light yellow in color. It is a knob-like structure and is not well developed. Its average length was 0.64 mm. The bursa copulatrix is completely separate from the pallial oviduct. The position of the opening of the bursa copulatrix into the pallial oviduct is similar to that of *B. tentaculata*. The opening of the bursa copulatrix to the muscular oviduct is at the anterior end of the bursa copulatrix. It is a little behind the genital aperture, and is at the same level as the genital aperture. The bursa copulatrix extends from the anterior end of the anterior pallial oviduct almost to the posterior end of the anterior pallial oviduct. The average length of the bursa copulatrix was 2.89 mm. The genital aperture is subterminal and is more usually located on the right lateroventral side of the muscular oviduct.

In *Wattebledia siamensis* (Figs. 13f, 14g), the ovary ranges in color from bright yellow to orange. It is found in the second and third whorls and it ends in front of the stomach. The average length of the ovary was 0.89 mm. The oviduct is bright yellow, and is pale or lighter at the anterior part (before the duct enters the mantle cavity). The average length of the oviduct was 1.62 mm. The renal oviduct is light yellow in color. Its average length was 1.59 mm. The position of the point of entry of the renal oviduct to the pallial oviduct is similar to that of *Bithynia tentaculata*. The anterior pallial oviduct is light yellow, while the posterior pallial oviduct is rather clear. The average length of the pallial oviduct was 4.01 mm. The seminal receptacle is a plate-like structure with a pointed end. Its position is similar to that of *B. tentaculata*. It is cream colored, or clear. Its average length was 1.30 mm. The bursa copulatrix is completely separated from the pallial oviduct. The position of the opening of the bursa copulatrix into the anterior pallial oviduct is similar to that of *B. tentaculata* and *Hydrobioides nassa*. However, the bursa copulatrix is on the ventral pallial oviduct and runs along the whole length of the anterior pallial oviduct. The opening of the bursa copulatrix to the muscular oviduct is similar to that of *H. nassa*. The average length of the

bursa copulatrix was 1.93 mm. The genital aperture is terminal and is on the right lateroventral part of the muscular oviduct.

In *Wattebledia crosseana* (Figs. 13g, 14h), the ovary is bright yellow in color. It is embedded in the digestive gland in the whorls of the anterior half of the apical whorl, and the second, third and fourth coils of the other upper whorls. It ends in front of the stomach. The average length of the ovary was 1.02 mm. The oviduct and the renal oviduct are colorless. Their average lengths were, respectively, 2.11 and 1.33 mm. The position of the point of entry of the renal oviduct to the pallial oviduct is similar to that of *W. siamensis* and *Bithynia tentaculata*. The anterior pallial oviduct is opaque white and the posterior pallial oviduct is clear. The average length of the pallial oviduct was 4.05 mm. The seminal receptacle is a plate-like structure with a rather pointed end. The position of the seminal receptacle is similar to that of *W. siamensis* and *B. tentaculata*. The seminal receptacle is colorless. Its average length was 1.38 mm. The bursa copulatrix is completely separated from the pallial oviduct. The position of its opening into the pallial oviduct is similar to that of *B. tentaculata*, *Hydrobiooides nassa* and *W. siamensis*. The opening of the bursa copulatrix into the muscular oviduct is similar to that of *H. nassa* and *W. siamensis*. The position of the bursa copulatrix on the ventral pallial oviduct is similar to that of *W. siamensis*. The bursa copulatrix is clear. Its average length was 1.90 mm. The genital aperture is terminal and is located on the ventral margin of the muscular oviduct.

In *Wattebledia baschi* (Figs. 13h, 14i), the ovary is light yellow in color. It has few lobes and a fan-like shape. The ovary is embedded in the digestive gland at the front of the third coil of the spire whorls. The ovary ends in front of the anterior stomach. The average length of the ovary was 0.07 mm. The oviduct is colorless. Its average length was 0.63 mm. The renal oviduct is opaque white. Its average length was 0.79 mm. The position of the point of entry of the renal oviduct into the pallial oviduct is at the anterior end of the posterior pallial oviduct. The pallial oviduct is light yellow in color. The average length of the pallial oviduct was 1.95 mm. A seminal receptacle was not located. It may be very rudimentary and therefore difficult to find, or it may not be formed. The bursa copulatrix is completely separated from the pallial oviduct. The opening of the bursa copulatrix to the muscular oviduct is similar to that of *Hydrobiooides nassa*, *W. siamensis* and *W. crosseana*. However, the opening of the bursa copulatrix into the pallial oviduct is almost at its posterior end. The bursa copulatrix lies on the ventral pallial oviduct and extends from the anterior end of the pallial oviduct to the anterior part of the posterior pallial oviduct, which is in front of the point of entry of the renal oviduct into the pallial oviduct. The average length of the bursa copulatrix was 0.42 mm. The genital aperture is terminal and is on the lateroventral side of the muscular oviduct (similar to that of *W. siamensis*).

In *Gabbia wykoffi* (Figs. 13i, 14j), the ovary is bright yellow in color. The ovary starts enveloping the digestive gland from the anterior 1/3 of the apical whorl, and it goes anteriorly along the second and third coils of the spire whorls, ending in front of the anterior stomach. The average length of the ovary was 0.91 mm. The part of the oviduct that runs next to the ovary is orange in color. However, as the oviduct goes anteriorly toward the mantle



cavity, its color changes to creamy-yellow. The average length of the oviduct was 1.46 mm. The renal oviduct is creamy-yellow in color. Its average length was 1.15 mm. The position of the point of entry of the renal oviduct into the pallial oviduct is similar to that of *Bithynia siamensis siamensis*, *B. funiculata* and *Hydrobioides nassa*. The anterior pallial oviduct is light yellow in color and the posterior pallial oviduct is creamy-yellow in color. The average length of the pallial oviduct was 3.35 mm. The seminal receptacle is colorless. It is a well-developed knob-like structure. The position of the seminal receptacle on the ventral pallial oviduct is similar to that of *B. siamensis goniomphalos*, *B. siamensis siamensis*, *B. funiculata* and *H. nassa*. The average length of the seminal receptacle was 0.78 mm. The bursa copulatrix is usually light yellow in color. Its average length was 1.26 mm. It is completely separated from the pallial oviduct. The position of the opening of the bursa copulatrix into the pallial oviduct is similar to that of *B. funiculata*. The opening of the bursa copulatrix into the muscular oviduct is similar to that found in *H. nassa* and the three species of *Wattebledia*. The position of the bursa copulatrix on the ventral pallial oviduct is similar to that of *H. nassa*. The genital aperture is subterminal and is more or less on the lateroventral side (similar to that of *W. siamensis* and *W. baschi*).

In *Gabbia pygmaea* (Figs. 13j, 14k), the ovary is yellow in color. The ovary has few lobes and it is fan-shaped. It is embedded longitudinally in the digestive gland. It extends from the anterior end of the second coil to the posterior end of the third coil of the spire whorls. The ovary ends in front of the stomach. The average length of the ovary was 0.30 mm. The average length of the oviduct was 0.77 mm. The posterior oviduct, which is connected to the ovary, is bright yellow in color. As it runs anteriorly toward the mantle cavity, it becomes opaque white. The renal oviduct is creamy-yellow in color. Its average length was 0.91 mm. The point of entry of the renal oviduct into the pallial oviduct is at the anterior end of the posterior pallial oviduct (similar to that of *Wattebledia baschi*). The pallial oviduct is generally opaque white. The average length of the pallial oviduct was 1.85 mm. The seminal receptacle is clear. It is long and broad, and has a rounded end. It is on the posterior part of the ventral pallial oviduct. It lies transversely along the width of the posterior pallial oviduct and is next posteriorly to the point of entry of the renal oviduct into the pallial oviduct. Its average length was 0.58 mm. The bursa copulatrix is usually creamy-yellow in color. Its average length was 0.41 mm. It is completely separated from the pallial oviduct. The position of the opening of the bursa copulatrix into the pallial oviduct is at its anterior end. The opening of the bursa copulatrix into the muscular oviduct is similar to that of *Hydrobioides nassa*, to the three species of *Wattebledia*, and to *G. wykoffi*. The position of the bursa copulatrix on the ventral pallial oviduct is similar to that of *H. nassa* and *G. wykoffi*. The muscular oviduct does not appear as strongly muscular as that of *B. siamensis goniomphalos*. The genital aperture is subterminal and is on the ventral side of the muscular oviduct.

In *Gabbia erawanensis* (Figs. 13k, 14l), the ovary is light yellow in color. The ovary starts enveloping the digestive gland at the second coil (it envelops almost all of the second coil) and extends to the posterior end of the third coil of the spire whorls, which is in front of the stomach. The average



length of the ovary was 0.15 mm. The part of the oviduct that is adjacent to the ovary is yellow in color, and as the duct goes anteriorly toward the mantle cavity the color of the duct becomes lighter, sometimes being white. The average length of the oviduct was 1.26 mm. The renal oviduct is either yellow or opaque white with very scattered melanin. The point of entry of the renal oviduct into the pallial oviduct is similar to that of *Wattebledia baschi* and *G. pygmaea*. The average length of the renal oviduct was 1.58 mm. The pallial oviduct is light yellow in color. The average length of the pallial oviduct was 1.98 mm. The seminal receptacle is a knob-like structure and is well developed. It is light yellow in color. It lies at the same position as that of *B. siamensis goniomphalos*. The average length of the seminal receptacle was 0.53 mm. The bursa copulatrix is completely separated from the pallial oviduct. The opening of the bursa copulatrix into the pallial oviduct is similar to that of *G. pygmaea*. The opening of the bursa copulatrix into the muscular oviduct is organized like that of *Hydrobioides nassa*, the three species of *Wattebledia*, and *G. wykoffi* and *G. pygmaea*. The position of the bursa copulatrix on the ventral pallial oviduct is similar to that of *H. nassa*, *G. wykoffi* and *G. pygmaea*. The bursa copulatrix is light yellow in color. Its average length was 0.68 mm. The muscular oviduct is not so strongly muscular as that of *B. siamensis goniomphalos*. The genital aperture is terminal and is on the lateroventral side of the muscular oviduct.

## DISCUSSION

### Pallial Organs

Differences in shapes or positions of the pallial organs between the species are rather minor. The differences are, in summary, (1) the position of the osphradium is more toward the anterior portion of the gill in *Bithynia siamensis goniomphalos*, *B. siamensis siamensis*, *B. funiculata*, *B. tentaculata* and *Watteblediarosseana*, while its position is in the middle of the gill in *Gabbia wykoffi*, *W. siamensis* and *W. baschi*, and the position of the osphradium is more toward the posterior part of the gill in *Hydrobioides nassa*, *G. pygmaea*, and *G. erawanensis*; (2) the shape of the osphradium is long and narrowly fusiform in *B. siamensis goniomphalos*, *B. siamensis siamensis*, *B. funiculata*, *B. tentaculata*, *H. nassa*, *W. siamensis*, *W.rosseana* and *W. baschi*, while a broadly fusiform osphradium is found in *G. wykoffi*, *G. pygmaea* and *G. erawanensis*, and an oval osphradium is found in *W. baschi*; (3) the number of gill filaments is different for each bithyniid species, except for *W. baschi* and *G. pygmaea*, both of which have the same number.

### Digestive System

The arrangement, position and shape of the stomach, intestine, anus, buccal mass, salivary gland and digestive gland of all the bithyniid snails I studied are similar. The interior stomach is difficult to observe and data on its characteristics were not obtained, including details of the crystalline style, which I did not find.

Differences in the digestive organs of bithyniid snails are: (1) the position of the opening of the esophagus into the stomach is at the left posteroventral part of the anterior stomach in *Bithynia siamensis goniomphalos*, *B. siamensis siamensis*, *B. funiculata*, *B. tentaculata* and *Hydrobioides nassa*; it is at the left lateral part of the anterior stomach in *Wattebledia siamensis*, *W. baschi*, *G. wykoffi*, *G. pygmaea* and *G. erawanensis*, and it is at the left ventral margin of the stomach in *W. crosseana*; (2) the intestinal loop is at the right laterodorsal side of the posterior part of the posterior stomach in *B. siamensis goniomphalos*, *B. siamensis siamensis*, *B. tentaculata* and *H. nassa*, the intestinal loop occupies almost the entire length of the right dorsolateral side of the posterior stomach in *B. funiculata*, *W. siamensis*, *W. baschi*, *G. pygmaea* and *G. erawanensis*, and it occupies the entire length of the dorso-lateral side of the posterior stomach in *W. crosseana* and *G. wykoffi*; and (3) the fecal pellets are usually long, slender and fusiform in *B. siamensis goniomphalos*, *B. siamensis siamensis*, *B. funiculata* and *H. nassa* [sometimes the shape of the fecal pellets of *B. siamensis siamensis* are spiral, long, slender and fusiform in shape, and the fecal pellets of *B. funiculata* are sometimes long, stout and fusiform-shaped], the fecal pellets of *W. siamensis* and *W. crosseana* are usually long, slender and cigar-shaped [sometimes spiral, long, slender, and cigar-shaped fecal pellets are found in *W. crosseana*], the fecal pellets of *W. baschi* are cigar-shaped, and the fecal pellets of *G. pygmaea*, *G. wykoffi* and *G. erawanensis* are oval in shape.

Arakawa (1962, 1963, 1965) and Taylor (1966) demonstrated a considerable variety of useful taxonomic characters in mollusk feces. Taylor (1966) reported that the fecal pellets of the bithyniids *Bithynia* and *Parafossarulus* are narrowly elongate, cigar-shaped, and spiral. In my observations, the shape of fecal pellets of *B. siamensis siamensis* and *W. crosseana* are sometimes found to have these characteristics. But, the fecal pellets of the three *Gabbia* species differ considerably from *Bithynia* s.s. and *Wattebledia*.

In the past, the radula is one of the structures that received much attention in the taxonomy of various groups of snails (e.g., see Stimpson, 1865; Baker, 1928; Thiele, 1929; Berry, 1943; Abbott, 1948; Taylor, 1966; Chung, 1984; Burch & Jeong, 1984; Hershler, 1985). The central tooth has often been emphasized for its taxonomic characters (e.g., see Radoman, 1955; Hadzisce, 1956; Taylor, 1966; Brandt, 1974). I observed shapes of all teeth and cusps of the radula, and the numbers of cusps as well. The bithyniid radular teeth vary in shape even in a single specimen, and particularly from one end of the radula to the other. Yet the shape and the number of cusps of each type of tooth can provide useful information, if the observations on the teeth are standardized. I arbitrarily chose to study the middle part of the ribbon because it was easy to locate, the teeth were fully formed there, and they were not badly worn.

The radula formula in a transverse row of the mesogastropod snails, including bithyniids, is 2:1:1:1:2. In my study, the following morphological differences in radular teeth were observed: (1) the cutting end of the mesocone of the anterior cusps of the central tooth is arrow-head shaped in all Thai bithyniid snails and spade shaped in *Bithynia tentaculata*; (2) the base of the mesocone of the anterior cusps of the central tooth is twice as wide as the bases of the ectocones in *B. siamensis goniomphalos*, *B. funiculata*, *B.*

*tentaculata*, *Hydrobioides nassa*, *Wattebledia baschi* and *Gabbia erawanensis*, while the base of the mesocone of the anterior cusps of the central tooth is less than twice as wide as the bases of the ectocones in *B. siamensis siamensis*, *W. siamensis*, *W. crosseana*, *G. wykoffi*, and *G. pygmaea*; (3) shapes of ridges bearing basal denticles are narrow in *B. siamensis goniomphalos*, *B. siamensis siamensis*, *B. funiculata*, *B. tentaculata*, *W. siamensis* and *G. wykoffi*, are very broadly flexed off in *H. nassa*, *W. baschi*, *G. pygmaea* and *G. erawanensis*, and are slightly flexed off in *W. crosseana*. The differing numbers of anterior cusps and basal cusps of the central, lateral, inner marginal and the outer marginal teeth of each species studied are shown in Table 1.

### Reproductive System

#### Male System

The male reproductive systems of each of the bithyniid snail species studied here are basically similar. However, in the males there are some differences in the position of the testis enveloping the digestive gland, the position of the vas deferens in the spire whorls, and in the size of various reproductive organs. Further, the testis of *Bithynia siamensis goniomphalos*, *B. siamensis siamensis*, *Hydrobioides nassa*, *Wattebledia siamensis*, *W. baschi*, *G. wykoffi*, *G. pygmaea* and *G. erawanensis* end at the front of the anterior stomach, while the testis of *B. funiculata*, *B. tentaculata* and *W. crosseana* overlap the stomach. The posterior part of the coiled vas deferens is ventral to the spire whorls and the anterior part of the coiled vas deferens is lateral to the spire whorls in *B. siamensis goniomphalos*, *B. siamensis siamensis*, *B. funiculata* and *W. siamensis*.

The renal vas deferens retains a connection with the pericardium in many prosobranchs (Fretter & Graham, 1962). Although it is presumably there, I did not find such a connection in any of the bithyniid snails I studied.

The color of most male reproductive organs is opaque white, except for the testis, which is yellow or orange, and the verge, which has melanin pigment. During the mating season, the testis has a brighter color and the vas deferens has a more silvery appearance than observed during the rest of the year (Lilly, 1953). The color of these latter two structures are ambiguous taxonomic characters. However, the pigmentation of the verge is more consistent.

#### Female System

Although the female reproductive organs of bithyniid snails are all basically similar, I noticed some differences in the position and shape of the ovary and the seminal receptacle, the position of the bursa copulatrix, the position of the entrance of the renal oviduct into the pallial oviduct, the position of the female opening, and the lengths of various female organs. The ovary of *Wattebledia baschi* and *Gabbia pygmaea* has only a few lobes, whereas it has many lobes in the other bithyniid snails. The ovary in *Bithynia siamensis goniomphalos* and *B. tentaculata* overlap the anterior stomach, while the

ovary in the other species is behind the anterior stomach. The bursa copulatrix of *B. siamensis goniomphalos* and *B. siamensis siamensis* is not completely separated from the pallial oviduct, but in the other species it is completely separated. The bursa copulatrix of *B. siamensis goniomphalos*, *B. siamensis siamensis* and *W. baschi* occupies all of the anterior pallial oviduct and part of the posterior pallial oviduct, while the bursa copulatrix of *B. funiculata*, *B. tentaculata*, *Hydrobioides nassa*, *Wattebledia siamensis*, *W. crosseana*, *G. pygmaea*, *G. wykoffi* and *G. erawanensis* is located only at the anterior stomach. The bursa copulatrix of *B. tentaculata* is dorsal to the pallial oviduct, but in all other Thai bithyniid snails it is ventral to the pallial oviducts. The shape of the seminal receptacle in *B. siamensis goniomphalos*, *B. siamensis siamensis* and *B. funiculata* is long and slender, in *B. tentaculata*, *W. siamensis* and *W. crosseana* it is plate-like, in *H. nassa*, *G. wykoffi* and *G. erawanensis* it is knob-like, and in *G. pygmaea* it is long and broad. I did not find the seminal receptacle of *W. baschi*. The seminal receptacle of *B. siamensis goniomphalos*, *B. siamensis siamensis*, *B. funiculata*, *H. nassa*, *G. wykoffi*, *G. pygmaea* and *G. erawanensis* is on the posterior part of the ventral pallial oviduct, while it lies next posteriorly to the pallial oviduct in *B. tentaculata*, *W. siamensis* and *W. crosseana*. The position of the entrance of the renal oviduct into the posterior pallial oviduct is close to the posterior portion in *B. siamensis goniomphalos*, close to the anterior portion in *B. siamensis siamensis*, *B. funiculata*, *H. nassa* and *G. wykoffi*, at the posterior end in *B. tentaculata*, *W. siamensis* and *W. crosseana*, and at the anterior end in *W. baschi*, *G. pygmaea* and *G. erawanensis*. The position of the genital aperture on the muscular oviduct is subterminal and ventral in *B. siamensis goniomphalos*, *B. siamensis siamensis*, *B. funiculata*, *B. tentaculata* and *G. pygmaea*, subterminal and lateroventral in *H. nassa* and *G. wykoffi*, terminal and lateroventral in *W. siamensis*, *W. baschi* and *G. erawanensis*, and terminal and ventral in *W. crosseana*.

Krull (1935) and Fretter & Graham (1962) described a gonopericardial duct leading from the renal oviduct and opening into the pericardial cavity in mesogastropods. In my dissections, I was not able to find such a connection.

It is interesting to note that the bursa copulatrix (spermatheca) is on top of the pallial oviduct in foreign bithyniid snails, and on the bottom of the pallial oviduct in Thai bithyniids. Also, in the species studied, only the bursa copulatrix of *Bithynia siamensis goniomphalos* and *B. siamensis siamensis* is not completely separated from the pallial oviduct. The presence, absence and shapes of the seminal receptacle, the positions of the genital aperture on the muscular oviducts, and the positions of the ovaries in the spire whorls may be the important steps in the evolution of genera in this family.

It is not known for certain about the place of fertilization in female bithyniid snails. Lilly (1953) pointed out that fertilization possibly may take place in the renal oviduct. I found that part of the posterior pallial oviduct that is located above the entrance of the renal oviduct into the pallial oviduct has a small chamber. Sometimes, the ova and the male secretion (e.g., the same secretion as found in the bursa copulatrix and seminal receptacle) are found in this chamber. It is possible that this part of the posterior pallial oviduct is modified to serve as the fertilization chamber. After mating, the sperm may

be collected in the bursa copulatrix. Then, the sperm may make their way to the seminal receptacle by passing the pallial oviduct at the opening to the bursa copulatrix. From the pallial oviduct, they may go past the renal oviduct to the opening of the seminal receptacle into the seminal receptacle and be stored there. Ripe ova from the ovary may go into the "fertilization chamber" via the oviduct and the renal oviduct, whereas oriented sperm from the seminal receptacle pass into the "fertilization chamber" via the duct of the seminal receptacle, which opens into the renal oviduct before the renal oviduct enters the pallial oviduct. Then, the fertilization takes place at the "fertilization chamber."

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A CHECKLIST AND OUTLINE OF CLASSIFICATION OF THE  
FRESHWATER SNAILS OF THE  
UNIVERSITY OF MICHIGAN BIOLOGICAL STATION AREA<sup>1</sup>

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This is the second in a three-part series of checklists of the Mollusca of the University of Michigan Biological Station (UMBS) area. The first checklist was on the land snails (Burch & Jung, 1987).

The UMBS is located in Cheboygan County on Douglas Lake, about 15 miles (24 km) south of the Straits of Mackinac in the center of the northern lower peninsula of Michigan. The area has a rich freshwater snail fauna. The objective of this publication is to give a brief description of the area, to present a list of the area's freshwater snails, and to place these mollusks in a modern frame of classification. For the purposes here, the UMBS area includes the counties of Emmet, Cheboygan and Presque Isle, an area of some 2,200 square miles. This area is bordered on the west by Lake Michigan, on the north and east by the Straits of Mackinac and Lake Huron, and on the south by Charlevoix, Otsego, Montmorency and Alpena counties. The list of freshwater gastropods presented here is based on collections made during the summers of 1985-1991, and on specimens collected previous to our study and now part of the collections of the Mollusk Division, Museum of Zoology, University of Michigan.

Forty-five species of freshwater snails have been found in the UMBS area. These species belong to 19 genera, which are placed in eight families. With further collecting, a few additional species perhaps will be added to the list in the future. On the other hand, further study may relegate to synonymy several of the currently used species names.

#### Physiography of the Area

The UMBS area is divided into three physiographic regions, the Lake-Border Plains, the Rolling Plains, and the Hill-Lands<sup>5</sup>. The northern-northeastern quarter of Emmet County, the northern two-thirds of Cheboygan County, and the northern/eastern half of Presque Isle County are in the Huron Lake-Border Plain physiographic region. The southeastern one-sixth of Cheboygan County and the southwestern half of Presque Isle County are in the Presque Isle Rolling Plain physiographic region. The southern three quarters of Emmet County and the southwestern one-sixth of Cheboygan County are in the Hill-Lands physiographic region.

The area varies from less than 600 feet to more than 1000 feet elevation above mean sea level. The lowest parts are the rather narrow shore areas of

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<sup>5</sup>Lawrence M. Sommers (Ed.), 1977, *Atlas of Michigan*, Michigan State University Press, East Lansing, Michigan. 242 pp.

lakes Michigan and Huron, and the contiguous shore areas of Crooked Lake-Crooked River, Burt Lake-Indian River, and Mullett Lake-Cheboygan River. The largest portion of the three counties is between 600 and 800 feet elevation, and lies adjacent to the lower shore areas. The southwestern quarter of Presque Isle County, the southern quarter of Cheboygan County, and various central and southern areas of Emmet County are between 800 and 1,000 feet elevation. Several small areas of central and southern Emmet County rise above 1,000 feet elevation.

The eastern and southern parts of Emmet County have the greatest surface relief in the area. The lowest relief is in the northeastern third of Cheboygan County and the northwestern tip and eastern half of Presque Isle County.

The bedrock of the area is Devonian in origin. The geological surface formations of the area have been greatly influenced by the past glaciation of the region. Along the Lake Huron shore of Cheboygan and Presque Isle counties, the surface formations are composed of sandy lake beds, probably partly of glacial deposition, and in places drifted by the wind into low ridges<sup>6</sup>. The northern shore area of Emmet County and the southern shore of Little Traverse Bay are composed of wind-drifted sand dunes. These sand dunes may be formed into rather sharp ridges.

Next inland from the shore in Cheboygan and Presque Isle counties are the clayey portions of the old lake beds, followed by either landlaid or waterlaid moraines. The moraines are the undulating glacial deposits formed at the border of the ice sheet. Landlaid moraines form the surface deposits of much of the western and southeastern parts of Emmet County, as well as much of the southern part of Cheboygan County and the western part of Presque Isle County. Also common in the southern half of Cheboygan County, in western and central Presque Isle County, and in the southern part of Emmet County are boulder clay plains, formed under the ice sheet. Intermixed among the latter two types of surface formations are areas of sandy old lake beds and clayey portions of old lake beds. These formations often contain swamps.

The eastern part of Presque Isle County is composed of areas of rock or thin drift. Boulder belts are frequent in the northern half of Cheboygan County, and the northwestern tip of Presque Isle County. Outwash plains occur in southern Cheboygan County along the Sturgeon River, including its West Branch, the Pigeon River, and Milligan and Stoney creeks, in Emmet County along Van Creek, and in Presque Isle County along the Little Ocqueoc River and the upper Ocqueoc River.

The soils in most of the UMBS area are predominantly spodosols, *i.e.*, they have accumulations of iron, aluminum and humus in the subsoil horizon. However, there are a few exceptions. Eastern Emmet and western Cheboygan counties have a contiguous north-south band of predominantly histosols, *i.e.*, they have developed from organic materials, and sections of northwestern and southcentral Presque Isle County have predominantly inceptisols, *i.e.*, they have weakly developed subsoil horizons.

<sup>6</sup>Frank Leverett, 1911, *Map of the surface formations of the Southern Peninsula of Michigan*, Geol. Surv. Mich., pl. 7, publ. 25.

The climax vegetation of the area consists mainly of Northern Hardwood, Pine, and Conifer Bog and Swamp communities.

### Fresh Waters of the Area

The most imposing hydrological features of the UMBS area are the two Great Lakes, lakes Huron and Michigan, by which the area is bounded on the east, north and west. These lakes are great expanses of fresh water, and provide a long, continuous shoreline. This shore is composed of boulders, stones, pebbles and sand, and is quite exposed to the elements of weather. During storms, the shore is pounded by large waves, providing generally unsatisfactory conditions for freshwater mollusks. Higher aquatic vegetation is virtually absent.

The largest river drainage in the UMBS area is that of the Cheboygan River. This drainage comprises the southeastern third of Emmet County, most of Cheboygan County, and the southwestern third of Presque Isle County. Many tributaries, all flowing generally northward, are included in the Cheboygan River system. The Cheboygan River empties into the upper end of Lake Huron at the city of Cheboygan.

Another relatively large watershed, that of the Thunder Bay River, reaches into the southern part of Presque Isle County. The rest of the streams in the three-county area are classified as short drainages flowing directly into Lake Huron or Lake Michigan.

Several significant lakes (*i.e.*, lakes listed among Michigan's ten largest) occur in the UMBS area. These are Burt and Mullett lakes in Cheboygan County, Black Lake, which is divided between Cheboygan and Presque Isle counties, and Grand and Long lakes in Presque Isle County. The southern part of Long Lake is in Alpena County.

### Habitats

The physiography of the North American continent is reflected in the differential makeup of the snail fauna. For example, much of the waters of southcentral and southeastern Canada and the northcentral and northeastern United States are dominated by lentic environments, and so there is a preponderance of pond and lake species. (In contrast, in the southern United States, most of the fresh waters were lotic in nature before the advent of man-made impoundments, so the aquatic habitats of that region were originally dominated by snails adapted to flowing-water environments.)

The UMBS area is liberally supplied with fresh waters. Living in these fresh waters is a significant fauna of aquatic snails, a molluscan fauna that ranks among the richest in the world. Although some snail species are widespread and common, other species are very restricted in their distributions, several species being known from only a single locality.

Freshwater snails have adapted to nearly all natural freshwater habitats, and a few species (*e.g.*, *Physa gyrina* (Say)) are tolerant enough to live successfully in all but the most heavily polluted waters. In general, however, freshwater snails do not tolerate much pollution, or chemical changes or physical disturbance of their habitats, and there has been a noticeable

general decline in the last several decades in the local distribution and abundance of many species of freshwater snails.

Aquatic snails have radiated into various kinds of freshwater habitats, with most species being restricted more or less to one or only several types of habitats. There are a few ubiquitous species, of course, but the restriction of species to specific types of habitats is the general rule. Habitats for freshwater snails in the UMBS area are as follows: benthic substrates in deep waters in large lakes, open shores of large and small lakes, quiet bays or ponds, marshes, mud-flats, in (as opposed to *on*) sand and mud in rivers and lakes, amphibious habitats, intermittent pools and streams, and large and small perennial streams.

### Freshwater Snails

The species of freshwater snails known to occur in Cheboygan, Emmet and Presque Isle counties are presented in the list below. This list is based almost entirely on our own collecting in the area and the specimens housed in the Museum of Zoology, University of Michigan. The species are arranged in their proper systematic order, together with their subclasses, orders, families, etc. Included are the authors of the taxa and dates the names were first published. Type species are placed in parentheses after each generic-group name.

#### Outline of Classification and List of Species

Subclass Prosobranchia Milne Edwards 1848

Order Mesogastropoda Thiele 1929

Superfamily Valvatoidea Gray 1840

Family Valvatidae Gray 1840

Genus *Valvata* Müller 1774<sup>7</sup> (*Valvata crista* Müller 1774)

*V. bicarinata* Lea 1841

*V. perdepressa* Walker 1906

*V. sincera* Say 1824

*V. tricarinata* (Say 1817)

Family Viviparidae Gray 1847

Genus *Campeloma* Rafinesque 1819 (*Campeloma crassula*  
Rafinesque 1819)

*C. decisum* (Say 1817)

Family Hydrobiidae Troschel 1857

Subfamily Amnicolinae Tryon 1862

Genus *Amnicola* Gould & Haldeman 1840

Subgenus *Amnicola s.str.* (*Paludina porata* Say 1821 = *Paludina*  
*limosa* Say 1817)

*A. limosus* (Say 1817)

Subgenus *Lyogyrus* Gill 1863 (*Valvata pupoidea* Gould 1841)

*A. (L.) walkeri* Pilsbry 1898

<sup>7</sup>The genera in each family and subfamily, and the species in each genus and subgenus, are listed in alphabetical order.

## Subfamily Emmericiinae Brusina 1870

Genus *Fontigens* Pilsbry 1933 (*Paludina nickliniana* Lea 1838)*F. nickliniana* (Lea 1838)

## Subfamily Nymphophilinae Taylor 1966

Genus *Pyrgulopsis* Call & Pilsbry 1886 (*Pyrgula nevadensis* Stearns 1883)*P. lustricus* (Pilsbry 1890)

## Family Pleuroceridae Fischer 1885

Genus *Elimia* H & A. Adams 1854 (*Melania autocarinata* Lea 1841=*Melania clavaeformis* Lea 1841 [synonym = *Goniobasis*])*E. livescens* (Menke 1830)Genus *Pleurocera* Rafinesque 1818 (*Pleurocera acuta* Rafinesque (in Blainville) 1824)*P. acuta* Rafinesque (in Blainville) 1824

## Subclass Pulmonata Cuvier 1817

Order Lymnophila Férussac 1812 [Basommatophora Keferstein 1864, in part]

Superfamily Lymnaeoidea Rafinesque 1815

## Family Lymnaeidae Rafinesque 1815

Genus *Bulimnea* Haldeman 1841 (*Lymnaeus megasomus* Say 1824)*B. megasoma* (Say 1824)Genus *Fossaria* Westerlund 1885Subgenus *Fossaria* s.str. (*Buccinum truncatum* Müller 1774)*F. exigua* Lea 1841*F. galbana* (Say 1825)*F. obrussa* (Say 1825)*F. parva* (Lea 1841)*F. peninsulae* (Walker 1908)Subgenus *Bakerilymnaea* Weyrauch 1964 (*Limnaea**cubensis* Pfeiffer 1839)*F. (B.) dalli* (F.C. Baker 1907)Genus *Lymnaea* Lamarck 1799 (*Helix stagnalis* Linnaeus 1758)*L. stagnalis appressa* Say 1821Genus *Stagnicola* Leach (in Jeffreys) 1830Subgenus *Stagnicola* s.str. (*Buccinum palustre* Müller 1774)*S. elodes* (Say 1821)*S. exilis* (Lea 1834)*S. emarginatus* (Say 1821)*S. petoskeyensis* (Walker 1908)Subgenus *Hinkleyia* F.C. Baker 1928 (*Lymnaeus caperatus* Say 1829)*S. (H.) caperatus* (Say 1829)

## Family Physidae Fitzinger 1833

Subfamily Aplexinae Starobogatov 1967

Genus *Aplexa* Fleming 1820 (*Bulla hypnorum* Linnaeus 1758)*A. elongata* (Say 1821)

Subfamily Physinae Fitzinger 1833

Genus *Physa* Draparnaud 1801 (*Bulla fontinalis* Linnaeus 1758)Subgenus *Physella* Haldeman 1833 (*Physa globosa* Haldeman 1841)*P. gyrina* (Say 1821)

- P. magnalacustris* (Walker 1901)  
*P. parkeri* (Currier (in DeCamp) 1881)  
*P. sayi* (Tappan 1838)  
 Subgenus *Costatella* Dall 1870 (*Physa costata* Newcomb 1801)  
*P. (C.) integra* (Haldeman 1841)  
*P. (C.) crassa* (Walker 1901)
- Family Planorbidae Rafinesque 1815  
 Subfamily Planorbinae Rafinesque 1815  
 Tribe Planorbini Rafinesque 1815  
 Genus *Gyraulus* 'Agassiz' Charpentier 1837  
 Subgenus *Gyraulus s.str.* (*Planorbis hispidus* Draparnaud 1805 =  
*Planorbis albus* Müller 1774)  
*G. deflectus* (Say 1824)  
 Subgenus *Armiger* Hartmann 1840 (*Planorbis cristatus*  
 Draparnaud 1805 = *Nautilus crista* Linnaeus 1758)  
*G. (A.) crista* (Linnaeus 1758)  
 Subgenus *Torquis* Dall 1905 (*Planorbis parvus* Say 1817)  
*G. (T.) circumstriatus* (Tryon 1866)  
*G. (T.) huronensis* Burch & Jung 1989  
*G. (T.) parvus* (Say 1817)
- Tribe Helisomini F.C. Baker 1928  
 Genus *Helisoma* Swainson (*Planorbis bicarinatus* Say  
 preoccupied = *Planorbis anceps* Menke 1830)  
*H. anceps* (Menke 1830)  
 Genus *Planorbella* Haldeman 1842  
 Subgenus *Planorbella s.str.* (*Planorbis campanulatus* Say 1821)  
*P. campanulata* (Say 1821)  
*P. smithi* (F.C. Baker 1912)  
 Subgenus *Pierosoma* Dall 1905 (*Planorbis trivolvis* Say 1817)  
*P. (P.) trivolvis* (Say 1817)  
 Genus *Planorbula* Haldeman 1840 (*Planorbis armigerus* Say 1821)  
*P. armigera* (Say 1821)  
 Genus *Promenetus* F. C. Baker 1935 (*Planorbis exacuouus* Say 1821)  
*P. exacuouus* (Say 1821)
- Family Ancyliidae Rafinesque 1815  
 Subfamily Ferrissiinae Walker 1917  
 Genus *Ferrissia* Walker 1903 (*Ancylus rivularis* Say 1817)  
*F. parallela* (Haldeman 1841)  
*F. rivularis* (Say 1817)
- Subfamily Laevapicinae Hannibal 1912  
 Genus *Laevapex* Walker 1903 (*Ancylus fuscus* C.B. Adam 1841)  
*L. fuscus* (C.B. Adams 1841)

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TWO NEW SPECIES OF MESOZOIC *DIPLODON* (BIVALVIA: HYRIIDAE: HYRIINAE) FROM URUGUAY

Sergio Martinez and Alfredo Figueiras<sup>1</sup>

ABSTRACT – Two new species of the genus *Diplodon*, *D. batoviensis* n. sp. and *D. dasilvai* n. sp. from the Lower Member of the Tacuarembó Formation, Uruguay, are described. There are some uncertainties about the age of the Tacuarembó Formation, the extreme limits proposed for the Lower Member being Late Triassic-Late Jurassic. The new species are the oldest freshwater bivalves from Uruguay and the oldest Hyriidae from the Rio de La Plata region.

Key Words: *Diplodon dasilvai*, *D. batoviensis*, Hyriidae, Tacuarembó Formation, Uruguay, Triassic-Jurassic.

INTRODUCTION

The fossil record of *Diplodon* from the Southern Hemisphere is very poor. Only two species have been described so far: *D. esperanzaensis* Camacho 1957, from the Jurassic of the Antarctic Peninsula, and *D. baqueroensis* Morton 1984, from the Cretaceous of Santa Cruz Province, Argentina.

On the other hand, in the South American Cenozoic there are at least 24 species recorded from the Paleocene to the Pleistocene (e.g., see Parodiz, 1968, 1969; Herbst & Camacho, 1970; Perea & Martinez, 1989).

Zoogeographical hypotheses about the origin and dispersion of the Hyriinae have been based principally on paleontological arguments (Parodiz, 1968; Parodiz & Bonetto, 1963; Herbst & Camacho, 1970), so the new findings have special importance as falsifiers of these hypotheses. This will be discussed in the last section of this paper.

In this article, two new species of *Diplodon* are described from sediments belonging to the Tacuarembó Formation, Uruguay. The geographic location of the outcrop is shown in Fig. 1. It should be stressed that these two species are the first bivalves found in this Formation, and they are the oldest freshwater bivalves from Uruguay.

Abbreviation: FCDP, Departamento de Paleontologia, Facultad de Ciencias, Montevideo, Uruguay.

STRATIGRAPHIC BACKGROUND

The Tacuarembó Formation develops in the Paraná Basin, outcropping mainly in the Tacuarembó and Rivera Departments in Uruguay (Fig. 1). Within it, two members are distinguished (Sprechmann *et al.*, 1981): (a) a Lower Member, in which subhorizontal stratification dominates, having abundant lentiform structures causing an alternation of different lithologies, predominantly sandstones (fine and medium), shales, siltstones, and mudstones; its deposition was in a fluviolacustrine environment; and (b) an

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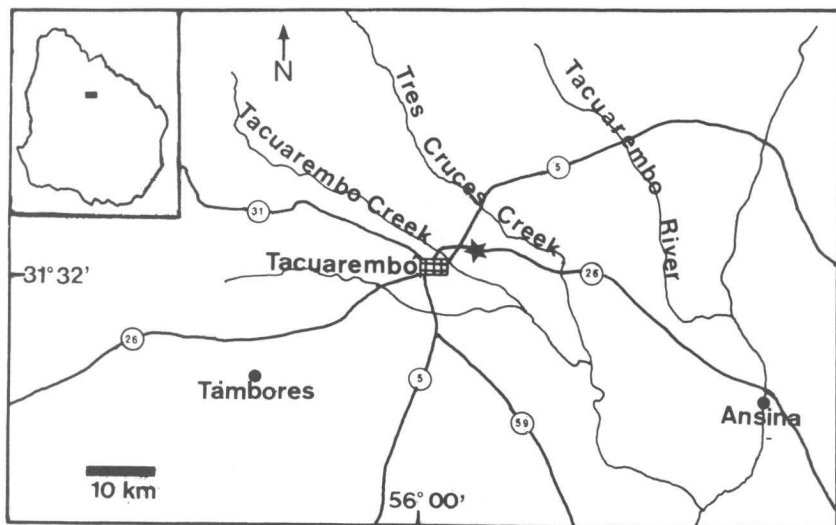


FIG. 1. Geographic location of the fossils. The star indicates the type locality.

Upper Member, which is characterized by the presence of sandstones produced by the fossilization of desert dunes.

The species described in this paper were found in the Lower Member of the Tacuarembó Formation, associated with viviparid gastropods in an horizon of fine sandstones (Fig. 2). The fossils were clearly accumulated by currents. Besides the type material, many fragmentary specimens were collected.

#### AGE

From the Lower Member of the Tacuarembó Formation, ostracods, fishes, and reptiles have been registered (Da Silva, 1990). These fossils are poorly preserved, which makes precise identification of lower taxa very difficult. Those adequately classified have a long stratigraphic range of occurrence. Therefore, none of the Lower Member fossils give clear evidence about the age of the Formation. Age estimations have traditionally been based on purely stratigraphic criteria.

Sprechmann *et al.* (1981) assigned to the Tacuarembó Formation an age interval from the Late Triassic or Early Jurassic to the Early Cretaceous. These authors state their relative uncertainty about the limits of the age, especially of the Lower Member. Mones & Figueiras (1981) believed that the Lower Member belongs to the Upper Jurassic and the Upper to the Lower Cretaceous. Herbst & Ferrando (1985) claimed that the Lower Member should be situated in the Upper Triassic and the Upper Member in the Lower or Middle Cretaceous.

The different opinions are more a matter of interpretation without a firm factual basis, and none of them have satisfied the present authors.

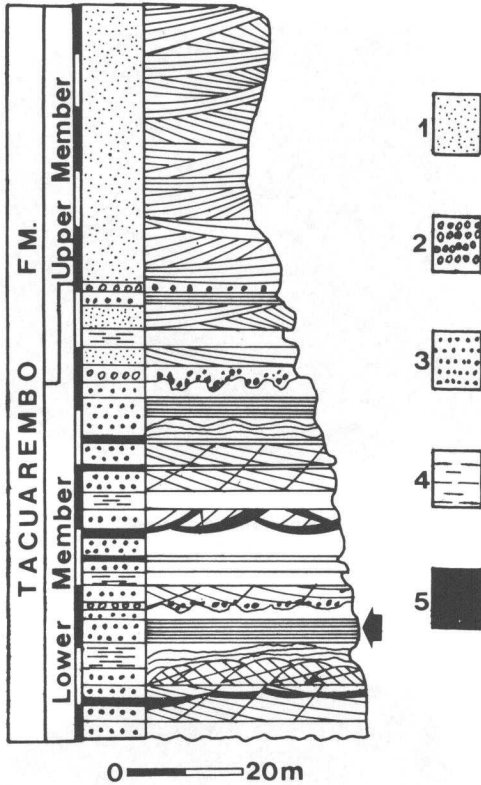
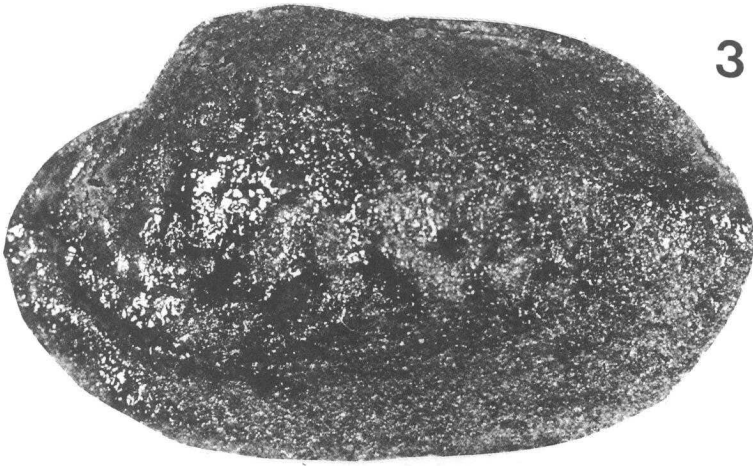


FIG. 2. Idealized stratigraphic column of the Tacuarembó Formation. The arrow indicates the horizon from which the fossils came. 1 = fine to medium sandstone, 2 = gravel, 3 = very fine and/or fine to medium sandstone, 4 = siltstone and mudstone, 5 = shale. (Modified from Sprechmann *et al.*, 1981.)

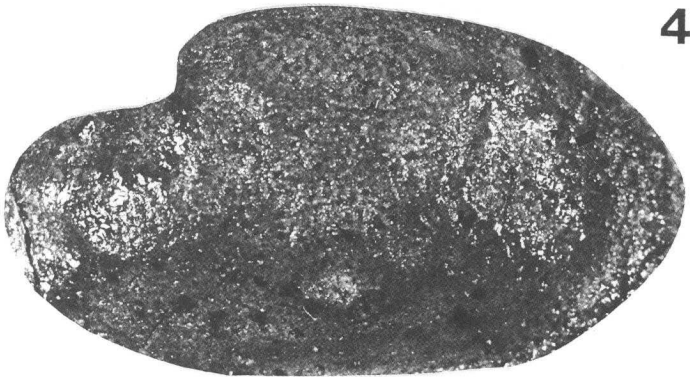
DESCRIPTIONS OF NEW SPECIES

*Diplodon dasilvai* n. sp.  
(Fig. 3)

Description. Shell moderately inflated. The umbo is prosogirous, rather prominent, situated in the anterior third. The dorsal margin is short in its anterior part, being inclined downwards; posteriorly it is straight, being truncated in its posterior portion. The posterior margin is very convex, almost acuminate. The ventral margin is smoothly convex. The anterior margin is very convex. From the umbo to the upper half of the posterior margin there is an angulation. This angulation, plus the straight dorsal margin, gives to the shell a "subalated" appearance. A pallial line is evident.



10 mm



10 mm

FIG. 3. *Diplodon dasilvai* n. sp., FCDP 2223, Holotype, left valve.

FIG. 4. *Diplodon batoviensis* n. sp., FCDP 2321, Holotype, left valve.

The muscle scars are not visible.

Holotype: FCDP 2223, an internal mold of a left valve; length: 34.5 mm; height: 20.0 mm.



Geographic locality: km 239.2 of Road 26, Tacuarembó Department, Uruguay.

Stratigraphic locality: Tacuarembó Formation, Lower Member, Upper Triassic?-Upper Jurassic?.

Etymology: in honor of Prof. Jorge S. Da Silva, collector of the majority of the known fossils of the Tacuarembó Formation.

Discussion. In spite of the absence of the hinge and the umbonal sculpture (the latter rarely present in fossils), we consider that the described characters are sufficient to include this and the next new species in the genus *Diplodon*. *Diplodon pehuenchensis* (Doello-Jurado, 1927) from the Paleocene of the Rio Negro Province, Argentina (Parodiz, 1969), is the species most similar to *D. dasilvai*, but *D. dasilvai* has the posterior umbonal angulation less pronounced, and it goes to the upper half of the posterior margin. In *D. pehuenchensis*, the posterior umbonal angulation goes to the lower half of the posterior margin, near the ventral margin. The umbo of *D. dasilvai* is more prominent, but the fact that the new species is represented only by internal molds (that accentuate umbonal height) may negate the value of this apparent distinction.

*Diplodon batoviensis* n. sp.  
(Fig. 4)

Description. Shell elongated. The umbo is prosogirous and is situated in the anterior third of the shell. The dorsal margin is rather convex in its posterior part. The anterodorsal margin is short and concave, forming a little notch. The posterior margin is curved; the ventral margin is slightly curved. The ligament area occupies slightly more than half of the posterior part of the dorsal margin.

Holotype: FCDP 2321, an internal mold of a left valve; length: 32.4 mm; height: 16.6 mm.

Paratypes: FCDP 2225, an internal mold of a left valve; length: 30.3 mm; height: 15.1 mm. FCDP 2322, an internal mold representing the two valves articulated in dorsal view.

Geographic locality: km 239.2 of the Road 26, Tacuarembó Department, Uruguay.

Stratigraphic locality: Tacuarembó Formation, Lower Member, Upper Triassic?-Upper Jurassic?.

Etymology: from Batovi, the name of the region where the outcrop is situated.

Discussion. *Diplodon batoviensis* is roughly similar to *D. colhuapensis* Ihering 1903, from the Paleocene of the Chubut Province (Argentina) (Parodiz, 1969), but this latter species is larger (51.5 x 30.0 mm according to Parodiz (1969), with different proportions ( $l/h$  *D. colhuapensis* = 1.7;  $l/h$  *D. batoviensis* = 1.9), and with the posterior margin less convex. The dorsal margin of *D. colhuapensis* is straighter in its posterior part, but since the new species is represented only by internal molds (that accentuate dorsal margin curvatures), this difference may not be significant.

*Diplodon batoviensis* is distinguished from *D. dasilvai* by the concavity anterior to the umbo, the more convex dorsal margin, and its greater size.

## BIOGEOGRAPHIC IMPLICATIONS

Parodiz (1969) proposed a Nearctic origin for the Hyriinae, with a migration to the south during the Late Cretaceous-Paleocene and later secondary migrations within South America. This author based his conclusions mainly on data from the fossil record when Mesozoic (Triassic) *Diplodon* were known only from North America.

The findings (Camacho, 1957; Morton, 1984) of *Diplodon esperanzaensis* in the Jurassic of the Antarctic Peninsula and *D. baqueroensis* in the Cretaceous of southern Argentina showed that the age of the migration must be situated earlier (although these authors did not claim it explicitly). The presence of *D. dasilvai* and *D. batoviensis* in at least Jurassic sediments in Uruguay confirms this idea.

Another hypothesis – based on the occurrence of *Diplodon esperanzaensis* – was postulated by Herbst & Camacho (1970), who suggested that the Hyriinae had their origin in the antarctic region, reaching the Rio de la Plata area in the late Tertiary. The finding of *Diplodon* in the Tacuarembó Formation of Uruguay shows that the Hyriinae reached this area much earlier. In respect to the antarctic origin of the subfamily, the Triassic *Diplodon* of North America (Parodiz, 1968), ignored by Herbst & Camacho (1970), invalidates this hypothesis.

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DISTRIBUTION AND ABUNDANCE OF *POTAMILUS CAPAX* AND  
OTHER FRESHWATER MUSSELS IN THE ST. FRANCIS  
RIVER SYSTEM, ARKANSAS AND MISSOURI, U.S.A.

Steven A. Ahlstedt<sup>1</sup> and John J. Jenkinson<sup>2</sup>

ABSTRACT – This survey of freshwater mussels in the St. Francis River and Floodway system, Arkansas and Missouri, was initiated primarily to document the occurrence and abundance of *Potamilus capax*, a federally-listed endangered species. The survey included qualitative sampling at 144 mainstem and tributary (ditch) sites in selected reaches totaling approximately 250 river miles and quantitative sampling at 11 of these sites.

Thirty-seven mussel species were found alive in the system. *Potamilus capax* was found in two areas: in adjacent reaches near the mouth of the river and in a variety of habitats near Marked Tree, Arkansas. Most specimens of the species were found in a mixture of sand, mud, and clay. Quantitative sampling yielded 0.02 *P. capax* per square meter in mainstem sites and 0.01 per square meter in ditch sites.

The survey extended the known distribution of *Potamilus capax* in the St. Francis system and demonstrated that the newly-discovered populations are at least as dense as those previously studied. Additional extensions of the species range in the drainage seem likely to occur when other tributaries are searched.

Key words: *Potamilus capax*, mussels, distribution, abundance, St. Francis River, Arkansas, Missouri.

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INTRODUCTION

In September 1986, the Memphis District, U.S. Army Corps of Engineers (USACE), contracted with the Tennessee Valley Authority (TVA) to conduct a freshwater mussel survey in selected five-mile reaches of the St. Francis River system. The objectives of this work were to (1) document the distribution of *Potamilus* [= *Proptera*] *capax*, commonly known as the fat pocketbook,

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within the survey area, and (2) describe the density and habitat of any live *P. capax* encountered. While *P. capax* was clearly the focus of this survey, distribution records of other freshwater mussel species also were to be collected.

Dennis (1985) summarized much of the existing information on the distribution, life history and ecology of *Potamilus capax*. Originally, the fat pocketbook occurred in larger streams throughout much of the Mississippi and Ohio River systems. Verified records exist from three areas: the upper Mississippi River (above St. Louis, Missouri), the Wabash River (Indiana), and the St. Francis River (Arkansas).

Collection records from recent years indicate *Potamilus capax* has been extirpated from much of its former range. This species is not known to persist in the Mississippi River north of Missouri or in any part of the Ohio River system, except possibly in the White River, Indiana. When Dennis compiled her review, the only known substantial population occurred in a short reach of the St. Francis River (Dennis, 1985). The reductions in range of *P. capax* previously had led the U.S. Fish and Wildlife Service to list the fat pocketbook as an endangered species (Anonymous, 1975).

The known distribution of *Potamilus capax* in the St. Francis River is derived from several recent reports. Gordon *et al.* (1980) prepared a checklist of Arkansas mollusk species by drainage and listed *P. capax* as occurring in the St. Francis River. Stansbery & Stein (1982) reported finding *P. capax* when their crew sampled the lower St. Francis River in 1978 as they investigated impacts from a chemical spill in Copperas Creek, a small tributary near Levesque, Cross County, Arkansas. In that report, Stansbery & Stein also included records of *P. capax* at Madison and Wittsburg in 1978 and downstream from the St. Francis Dam, near Marked Tree, in 1973.

A widespread search for rare or endangered mussels in the St. Francis, White and Cache rivers was conducted in 1978-1980 by Ecological Consultants, Inc., under contract to the USACE. In the report on that survey, Bates & Dennis (1983) indicated that *Potamilus capax* occurred only in an eight-mile reach of the St. Francis Floodway from Madison to Clark's Corner Cutoff (Floodway Miles 37-45). A more intensive search of St. Francis Floodway miles 26-69 and the lower ten miles of Straight Slough was conducted in 1984 by Ecosearch, Inc. In that study, Clarke (1985) found large numbers of live *P. capax* throughout the floodway reach and Straight Slough. In 1986, the Arkansas State Highway and Transportation Department conducted a mussel relocation project at Madison (Floodway Mile 37.6) to clear the vicinity of a proposed boat ramp (Harris, 1986). A total of 7,825 live freshwater mussels was removed from the project area, including 82 specimens of *P. capax*.

Considered together, these recent surveys indicate *Potamilus capax* is more widespread and more abundant in the St. Francis River system than was previously thought. This possibility prompted the USACE to design and fund an intensive survey.

#### PROJECT AREA

The St. Francis River is located in northeast Arkansas and southeast Missouri between Crowley's Ridge to the west and the Mississippi River to

the east. The river system has been substantially altered by local interests and the USACE in the process of protecting agricultural land. An elaborate system of ditches and levees has been constructed over the years to solve flooding problems in the extremely flat watershed. At present, the drainage system consists of two parts from Marked Tree (RM 155) to near the mouth (RM 10). The original river drains the eastern half of the watershed while the Oak Donnick-St. Francis Floodway drains the western half. The floodways and their tributaries are manmade water courses. River reaches both upstream and downstream from Marked Tree include unmodified areas and areas that have been dredged or straightened.

The scope of work prepared by the USACE called for sampling to be conducted in 53 identified reaches of the St. Francis River, St. Francis Floodway, tributaries, and ditches. Approximately 250 miles of stream and ditch habitat were included in the identified reaches ranging from the mouth of the river to Wappapello Dam in the headwaters. In essence, the survey involved all of the river mainstem from Wappapello Dam (RM 305) downstream to the Siphons Access near Marked Tree (RM 155), several ditches near Marked Tree, selected five-mile reaches between Marked Tree and Forrest City (RM 55), and the lowermost 25 miles of the St. Francis Floodway and River (Tables 1 and 2).

#### STUDY METHODS

Before the survey, access points were examined to locate boat launch and takeout points throughout the length of the reaches to be sampled. These access points were important because the survey was proposed to include four sites within each five-mile reach even though much of the watershed was not accessible by road.

Specific sampling sites were chosen in the field based upon the apparent quality of mussel habitat, uniform spacing of sites within the river reach, and accessibility by land or water. When available, 7.5-minute topographic maps were used for navigation and site location. When possible, an entire reach was floated in the process of selecting and examining collection sites.

When a sampling site was selected, the three- to five-man crew used appropriate methods to conduct a qualitative search for live and fresh-dead mussels. Methods typically employed included feeling along the substrate with hands or feet, raking, and collecting dead shells along the banks. Where necessary, snorkel or scuba equipment was used to perform an adequate search.

Collecting continued in all habitats at the site until the crew leader was satisfied that no additional species were being found. All mussel specimens encountered were sorted by species, identified by the crew leader, and counted. Records kept on the qualitative search included the site location, number of man-minutes of search time, collection techniques, and numbers of live, fresh-dead (shells with shiny nacre) and relict (dull nacre) specimens of each mussel species encountered. Live specimens were returned to suitable habitat at the site; fresh-dead and unusual relict shells were labeled and returned to the TVA Fisheries Laboratory in Norris, Tennessee.

Identification of virtually all specimens encountered during the survey was made by the leader of each field crew. These identifications were based upon considerable experience with all genera represented, augmented by specific study of species likely to occur in the St. Francis watershed. Species identification and synonymies were clarified during an examination of St. Francis material housed at the Ohio State University Museum of Zoology (OSUM). Specifically with regard to *Potamilus capax*, specimens encountered during the access survey were compared to verified material



TABLE 1. Location of Mainstem St. Francis River Mussel Collection Sites, September-October 1986.

Site	RM	Location	<i>P. capax</i>
1	2.0	St. Francis River upstream from confluence with Mississippi River, Phillips Co., Arkansas	0
2	3.0	St. Francis River upstream from confluence with Mississippi River, Phillips Co., Arkansas	0
3	4.0	St. Francis River upstream from confluence with Mississippi River, Phillips Co., Arkansas	1 live
4	5.0	St. Francis River two miles above Phillips Bayou, Lee Co., Arkansas	1 live
5	6.0	St. Francis River three miles above Phillips Bayou, Lee Co., Arkansas	0
6	7.0	St. Francis River four miles above Phillips Bayou, Lee Co., Arkansas	0
7	8.5	St. Francis River five and one-half miles above Phillips Bayou, Lee Co., Arkansas	0
8	10.0	St. Francis River downstream from mouth of the L'Anguille River, Lee Co., Arkansas	1 live
9	11.0	St. Francis River downstream from mouth of the L'Anguille River, Lee Co., Arkansas	1 fresh-dead
10	12.0	St. Francis Floodway downstream from Huxtable Dam, Lee Co., Arkansas	0
11	13.0	St. Francis Floodway downstream from Huxtable Dam, Lee Co., Arkansas	0
12	14.0	St. Francis Floodway at Greer Place, Lee Co., Arkansas	0
13	16.0	St. Francis Floodway above Greer Place, Lee Co., Arkansas	0
14	17.5	St. Francis Floodway upstream from mouth of L'Anguille River, Lee Co., Arkansas	0
15	19.0	St. Francis Floodway below Highway 79 bridge crossing, Lee Co., Arkansas	1 fresh-dead
16	21.0	St. Francis Floodway above Highway 79 bridge crossing, Lee Co., Arkansas	1 fresh-dead*
17	22.2	St. Francis Floodway above Highway 79 bridge crossing, Lee Co., Arkansas	0
18	23.8	St. Francis Floodway above Sandy Slough, Lee Co., Arkansas	1 live 1 fresh-dead
19	25.0	St. Francis Floodway above Cow Bayou, Lee Co., Arkansas	1 live
*	37.0	Highway 70 bridge at Madison, St. Francis Co., Arkansas (access survey only)	3 fresh-dead
20	55.3	One mile above Allen Bayou, St. Francis Co., Arkansas	0
21	57.2	Three miles above Allen Bayou, St. Francis Co., Arkansas	0
22	58.4	Filligrum Bend, St. Francis Co., Arkansas	0
23	59.4	Filligrum Bend, St. Francis Co., Arkansas	0
24	65.0	Highway 306 bridge crossing below Johnson Bend (Grassy Lake Cutoff), Cross Co., Arkansas	0
25	65.7	Above Highway 306 bridge crossing below Johnson Bend (Grassy Lake Cutoff), Cross Co., Arkansas	0
26	66.7	At Short Bend, Cross Co., Arkansas	0
27	67.4	At Short Bend, Cross Co., Arkansas	0
28	69.1	Below Elbow Slough, Cross Co., Arkansas	0
29	70.0	Above Elbow Slough, Cross Co., Arkansas	0
30	70.2	Above Elbow Slough, Cross Co., Arkansas	0
31	71.5	Below Parkin Slough, Cross Co., Arkansas	0
32	74.3	At Ash Bend, Cross Co., Arkansas	0
33	75.2	Above Ash Bend, Cross Co., Arkansas	0
34	80.4	Above Tyronza River, Cross Co., Arkansas	0

TABLE 1. (cont.)

Site	RM	Location	<i>P. capax</i>
35	81.5	Above Tyrnza River, Cross Co., Arkansas	0
36	83.5	At Love Place, Cross Co., Arkansas	0
37	84.3	Above Love Place, Cross Co., Arkansas	0
38	106.1	One mile below Turnbull Bar, Cross Co., Arkansas	0
39	106.6	One-half mile below Turnbull Bar, Cross Co., Arkansas	0
40	106.9	Turnbull Bar, Cross Co., Arkansas	0
41	107.2	Sugar Bar, Cross Co., Arkansas	0
42	107.4	Sugar Bar, Cross Co., Arkansas	0
43	107.9	Above Sugar Bar, Cross Co., Arkansas	0
44	108.5	Cow Island, Poinsett Co., Arkansas	0
45	109.8	Above Cow Island, Poinsett Co., Arkansas	0
46	110.2	Off Highway 75 below Steep Gut Bayou, Poinsett Co., Arkansas	0
47	111.5	Below Ditch 41 near Boat Run, Poinsett Co., Arkansas	0
48	111.8	Above Ditch 41, Poinsett Co., Arkansas	0
49	152.7	At island below Left Hand Chute of Little River above Marked Tree, Poinsett Co., Arkansas	4 live 12 fresh-dead*
50	153.0	At mouth of Left Hand Chute of Little River above Marked Tree, Poinsett Co., Arkansas	0
51	153.6	Mouth of Ditch 45 between Siphons Access and Marked Tree, Poinsett Co., Arkansas	0
52	154.5	One-half mile below Siphons Access above Marked Tree, Poinsett Co., Arkansas	0
53	155.0	Below Siphons Access above Marked Tree, Poinsett Co., Arkansas	1 live 34 fresh-dead*
54	155.1	Pool below Siphons Access above Marked Tree, Poinsett Co., Arkansas	2 live
55	157.0	Sunken Lands near Oak Donnicks Gage, Poinsett Co., Arkansas	0
56	159.1	Sunken Lands below Donnicks at Lead Fork, Poinsett Co., Arkansas	0
57	165.9	Sunken Lands two miles below Deep Landing, Craighead Co., Arkansas	0
58	167.0	Sunken Lands one-half mile above Deep Landing, Craighead Co., Arkansas	0
59	168.7	Sunken Lands one-half mile below new ditch connecting Ditch 60, Craighead Co., Arkansas	0
60	169.3	Sunken Lands above mouth of Cockle Burr Slough, Craighead Co., Arkansas	0
61	180.0	Sunken Lands at mouth of side ditch (Newton Island), Craighead Co., Arkansas	0
62	181.0	Sunken Lands west of Big Slough Ditch, Craighead Co., Arkansas	0
63	185.8	Sunken Lands at power line crossing south of Highway 412 bridge crossing, Greene and Craighead Co., Arkansas	0
64	186.2	Sunken Lands south of Highway 412 bridge crossing, Greene and Craighead Co., Arkansas	0
65	186.8	Sunken Lands at side channel near Arkansas and Missouri state lines, Greene Co., Arkansas, and Dunklin Co., Missouri	0
66	187.2	Sunken Lands in back channel south of Highway 412 bridge crossing, Greene Co., AR and Dunklin Co., Missouri	0
67	191.2	Sunken Lands upstream from Highway 412 bridge crossing at Riverside, Greene Co., AR and Dunklin Co., Missouri	0
68	192.0	Sunken Lands north of 412 bridge at Riverside, Greene Co., AR, and Dunklin Co., Missouri	0

TABLE 1. (cont.)

Site	RM	Location	<i>P. capax</i>
69	193.2	Sunken Lands near Hargrove, Greene Co., Arkansas, and Dunklin Co., Missouri	0
70	193.4	Sunken Lands in channel (Indian Hills Island) north of Hargrove, Greene Co., Arkansas, and Dunklin Co., Missouri	0
71	194.5	Sunken Lands at access north of Bertig, Greene Co., Arkansas, and Dunklin Co., Missouri	0
72	195.8	Sunken Lands at channel above Indian Hills Island, Greene Co., Arkansas, and Dunklin Co., Missouri	0
73	197.0	Sunken Lands at channel below Gum Island, Greene Co., Arkansas, and Dunklin Co., Missouri	0
74	199.0	Sunken Lands at Bone Camp Island, Green Co., Arkansas, and Dunklin Co., Missouri	0
75	200.4	Sunken Lands upstream from Bone Camp Island, Greene Co., Arkansas, and Dunklin Co., Missouri	0
76	203.0	Sunken Lands above Bone Camp Island, Greene Co., Arkansas, and Dunklin Co., Missouri	0
77	208.8	Sunken Lands at ditch downstream of Highways 84 and 90 bridge crossings, Clay Co., Arkansas, and Dunklin Co., Missouri	0
78	209.6	Sunken Lands at Highways 84 and 90 bridge crossings, Clay Co., Arkansas, and Dunklin Co., Missouri	0
79	211.2	Sunken Lands at side channel near former railroad bridge, Clay Co., Arkansas, and Dunklin Co., Missouri	0
80	214.5	Sunken Lands at channel southeast of Nimmons at Ten Mile Island, Clay Co., Arkansas, and Dunklin Co., Missouri	0
81	223.0	Sunken Lands at Highway 1 bridge crossing below Browns Ferry, Clay Co., Arkansas, and Dunklin Co., Missouri	0
82	224.5	Sunken Lands one and one-half miles above Highway 1 bridge crossing, Clay Co., Arkansas, and Dunklin Co., Missouri	0
83	226.0	Sunken Lands at Big Bend northeast of Piggott, Clay Co., Arkansas, and Dunklin Co., Missouri	0
84	228.0	Sunken Lands two miles below Highway 62 bridge crossing at St. Francis, Clay Co. Arkansas, and Dunklin Co., Missouri	0
85	229.2	Sunken Lands just below Highway 62 bridge crossing at St. Francis, Clay Co., Arkansas, and Dunklin Co, Missouri	0
86	229.3	Sunken Lands above Highway 62 bridge crossing at St. Francis, Clay Co., Arkansas, and Dunklin Co., Missouri	0
87	230.3	Below Chalk Bluff, Clay Co., Arkansas, and Dunklin Co., Missouri	0
88	231.8	Above Chalk Bluff, Clay Co., Arkansas, and Dunklin Co., Missouri	0
89	234.0	Wilhelmina cutoff at confluence of St. Francis River, Dunklin and Butler Counties, Missouri	0
90	245.0	Middle of Wilhelmina cutoff, Dunklin and Butler Counties, Missouri	0
91	253.0	At Dekyngs Gage Highway 53 bridge crossing, Dunklin and Butler Counties, Missouri	0
92	254.5	Above Highway 53 bridge crossing, Dunklin and Butler Counties, Missouri	0
93	255.0	Below power line west of Glennonville, Dunklin and Butler Counties, Missouri	0
94	258.0	West of Caligoa, Dunklin and Butler Counties, Missouri	0
95	261.0	West of Caligoa, Dunklin and Butler Counties, Missouri	0

TABLE 1. (cont.)

Site	RM	Location	<i>P. capax</i>
96	264.5	North of Caligoa, Dunklin, Butler, and Stoddard Counties, Missouri	0
97	266.5	Below ditch approximately one-half mile near Highway JJ, Butler and Stoddard Counties, Missouri	0
98	269.5	Highway U bridge crossing to Powe, Butler Co., Missouri	0
99	275.0	Above Dudley Main Ditch, Stoddard Co., Missouri	0
100	275.5	Above Dudley Main Ditch, Butler and Stoddard Counties, Missouri	0
101	284.0	Below old Highway 60 bridge crossing at Fisk, Butler and Stoddard Counties, Missouri	0
102	285.5	At old Highway 60 bridge crossing at Fisk, Butler and Stoddard Counties, Missouri	0
103	285.8	Above old Highway 60 bridge crossing above Fisk, Butler and Stoddard Counties, Missouri	0
104	286.0	Above new Highway 60 bridge crossing above Fisk, Butler and Stoddard Counties, Missouri	0
105	293.0	Above Owens Cemetery, Butler and Stoddard Counties, Missouri	0
106	297.8	Above Rombauer railroad bridge at Mud Creek, Butler and Stoddard Counties, Missouri	0
107	301.8	Above Peppermint Creek, Butler and Stoddard Counties, Missouri	0
108	302.5	At Duck Creek, Butler and Stoddard Counties, Missouri	0
109	303.1	Above Duck Creek, Wayne County, Missouri	0
110	303.8	Below Mingo Creek, Wayne County, Missouri	0
111	304.7	At Iron Bridge gaging station, Wayne County, Missouri	0
112	305.3	Half-mile below Wappapello Dam, Wayne County, Missouri	0
113	305.5	Three hundred yards below Wappapello Dam, Wayne County, Missouri	0

\**Potamilus capax* totals for these sites include some specimens found during the access survey.

TABLE 2. Location of all Ditch Sites Collected During the St. Francis River Mussel Survey, September-October 1986.

Site	Location	<i>P. capax</i>
1	Ditch 109 near Oak Donnck Floodway nine-tenths of a mile above its mouth to Cross County Ditch, Poinsett and Cross Counties, Arkansas	0
2	Ditch 109 near Oak Donnck Floodway (remnant portion of ditch), Poinsett and Cross Counties, Arkansas	0
3	Ditch 23 near Oak Donnck Floodway downstream to its confluence with Ditch 10 near Bay Village, Poinsett Co., Arkansas	1 fresh-dead
4	Ditch 23 near Oak Donnck Floodway above mouth of Ditch 10 approximately 300 yards, Poinsett Co., Arkansas	0
5	Ditch 23 near Oak Donnck Floodway downstream from Highway 373 bridge crossing south of Anderson Tully (Stewart), Poinsett Co., Arkansas	0
6	Ditch 23 near Oak Donnck Floodway upstream from Highway 373 bridge crossing south of Anderson Tully (Stewart), Poinsett Co., Arkansas	1 live 3 fresh-dead

TABLE 2. (cont.)

Site	Location	<i>P. capax</i>
7	Ditch 10 near Oak Donnicks Floodway upstream from its mouth to Ditch 23 near Anderson Tully (Stewart), Poinsett Co., Arkansas	2 live 2 fresh-dead
8	Ditch 10 near Oak Donnicks Floodway at Highway 373 bridge crossing to Anderson Tully (Stewart), Poinsett Co., Arkansas	3 live 2 fresh-dead
9	Ditch 10 above Oak Donnicks Floodway at Highway 14 bridge crossing to Lander, Poinsett Co., Arkansas	0
10	Ditch 10 above Oak Donnicks Floodway at Highway 214 bridge crossing to Promised Land Church, Poinsett Co., Arkansas	5 live
11	Ditch 10 above Oak Donnicks Floodway at Highway 69 bridge crossing to Trumann, Poinsett Co., Arkansas	0
12	Ditch 10 above Oak Donnicks Floodway upstream of Highway 69 bridge crossing to Trumann, Poinsett Co., Arkansas	1 live
13	Ditch 1 above Oak Donnicks Floodway at Highway 214 bridge crossing near Pleasant Hill Church, Poinsett Co., Arkansas	0
14	Upstream confluence of Ditches 60 and 61 (Oak Donnicks Floodway) just south of railroad bridge, Poinsett Co., Arkansas	1 fresh-dead
15	At channel flowing into mouths of Ditches 60 and 61 (Oak Donnicks Floodway) upstream from railroad bridge, Poinsett Co., Arkansas	2 live
16	Ditch 60 (Oak Donnicks Floodway) at small creek on left bank of ditch approximately two miles below Highway 63 bridge crossing west of Marked Tree, Poinsett Co., Arkansas	23 live 46 fresh-dead
17	Ditch 60 (Oak Donnicks Floodway) below floodway dam, Poinsett Co., Arkansas	1 fresh-dead
18	Ditch 60 (Oak Donnicks Floodway) below floodway dam, Poinsett Co., Arkansas	0
19	Ditch 60 (Oak Donnicks Floodway) in pool above floodway dam, Poinsett Co., Arkansas	0
20	At side channel connecting Ditches 60 and 61 (Oak Donnicks Floodway) in Sand Slough, Poinsett Co., Arkansas	0
21	Ditch 61 (Oak Donnicks Floodway) just above confluence with Ditch 60, Poinsett Co., Arkansas	0
22	Ditch 61 (Oak Donnicks Floodway) above Highway 63 bridge crossing west of Marked Tree, Poinsett Co., Arkansas	0
23	Unnumbered ditch above Oak Donnicks Floodway upstream from Siphons Access north of Marked Tree, Poinsett Co., Arkansas	1 live
24	Unnumbered ditch above Oak Donnicks Floodway approximately two and one-half mile above Siphons Access north of Marked Tree, Poinsett Co., Arkansas	1 live
25	Unnumbered ditch above Oak Donnicks Floodway approximately five miles above Siphons Access north of Marked Tree, Poinsett Co., Arkansas	0
26	Mouth of Iron Mines Creek at Siphons Access north of Marked Tree, Poinsett Co., Arkansas	6 live 6 fresh-dead*
27	Iron Mines Creek one mile above Siphons Access north of Marked Tree, Poinsett Co., Arkansas	4 live 3 fresh-dead*
28	Tulot Seep Ditch at bridge crossing to Payneway above Highway 63 bridge crossing near Harrisburg Corner, Poinsett Co., Arkansas	1 fresh-dead
29	Tulot Seep Ditch at confluence of Ditch 33 one mile east of Trumann, Poinsett Co., Arkansas	0
30	Tulot Seep Ditch at start of Highway 198 west of Stevens Landing, Poinsett Co., Arkansas	0
31	Tulot Seep Ditch at Highway 69 above Ditch 31, Craighead Co., Arkansas	0

\**P. capax* totals for these sites include some specimens found during the access survey.

in the McClung Museum (University of Tennessee) and OSUM. Shell and soft part characteristics of *P. capax* were discussed with several malacologists and knowledgeable field biologists to resolve any possible confusion.

Quantitative sampling was conducted only if live specimens of *Potamilus capax* were found during the qualitative search. Sampling consisted of carefully searching for mussels in ten-meter intervals along a cable laid across the width of the river or ditch. Typically two biologists would wade, snorkel, or use scuba equipment to check for mussels within one-half meter on each side of the cable. A full quantitative search included two transects at least 20 meters apart. In the lower St. Francis River, this procedure was modified to taking single transects 30 meters in length. These transects typically ran from the center of the river across the current toward one bank. Wherever the quantitative samples were taken, mussels found in each ten-meter interval were identified to species, counted, and recorded along with substrate composition and water depths.

All live and unbroken fresh-dead *Potamilus capax* specimens encountered during the access or float survey were measured using dial or vernier calipers. Measurements taken included maximum anterior-posterior length, maximum height from anterior of umbos to ventral margin, and maximum thickness across the two shells. These data were recorded to the nearest 0.1 mm.

## RESULTS

TVA crews conducted this survey between September 29 and October 24, 1986. Most of the survey was performed under exceptional field conditions. At the time, the southeastern United States was still suffering from a record drought and water levels in the St. Francis River system were usually at or near record lows. As the survey started, water temperatures were near 80°F but dropped to below 60°F before the field work was completed. Visibility in the water was described by area residents as being "unusually good" but was rarely more than 15 cm.

Sampling conditions near the mouth of the river were substantially worse than elsewhere in the system. Upstream flood water in the Mississippi River backed into the St. Francis, raising it six to eight meters. Flow was negligible, but selection and sampling of suitable mussel habitats were severely hampered by the high water.

TVA biologists searched for *Potamilus capax* and other freshwater mussels at 144 sites in the St. Francis River watershed: 113 sites in the mainstem and 31 sites in ditches or tributaries. Sites examined are identified in Tables 1 (mainstem locations) and 2 (ditch and tributary locations). These sites also are indicated on maps (Figs. 1-6).

In all, 14,606 live or fresh-dead mussels were encountered. These specimens represented 37 species, including *Potamilus capax*. Site-by-site records for these species are presented in Appendix A and are summarized in Table 3.

A total of 77 quantitative samples were taken at 17 sites (Tables 4 and 5). These ten-square-meter samples yielded 211 live mussels representing 17 species. The 19 mainstem samples produced 0.84 mussels per square meter while the 58 ditch and tributary samples produced 0.09 mussels per square meter.

Measurement data were taken from 146 live and unbroken fresh-dead

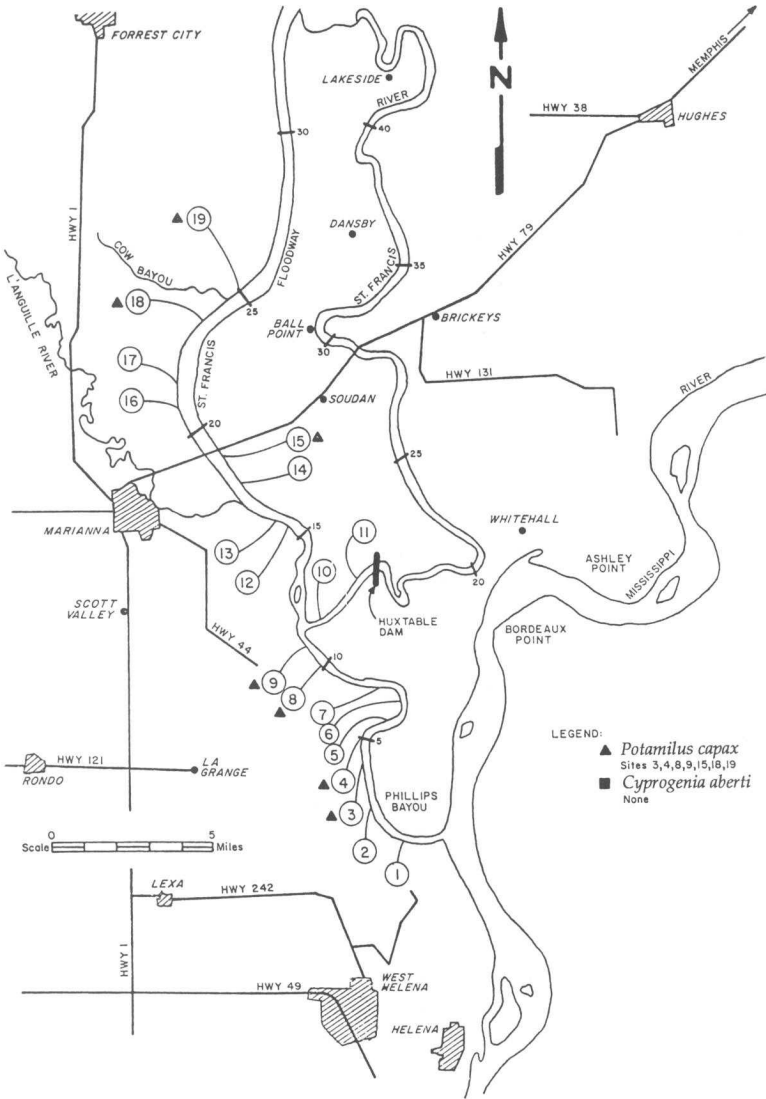


FIG. 1. Lower St. Francis River freshwater mussel collecting sites below Forest City, Arkansas.

*Potamilus capax* specimens encountered while locating access points and during the survey. Length, height and thickness data on each of these specimens are presented in Appendix B. The length data from each site are summarized by 10 millimeter intervals in Table 6.



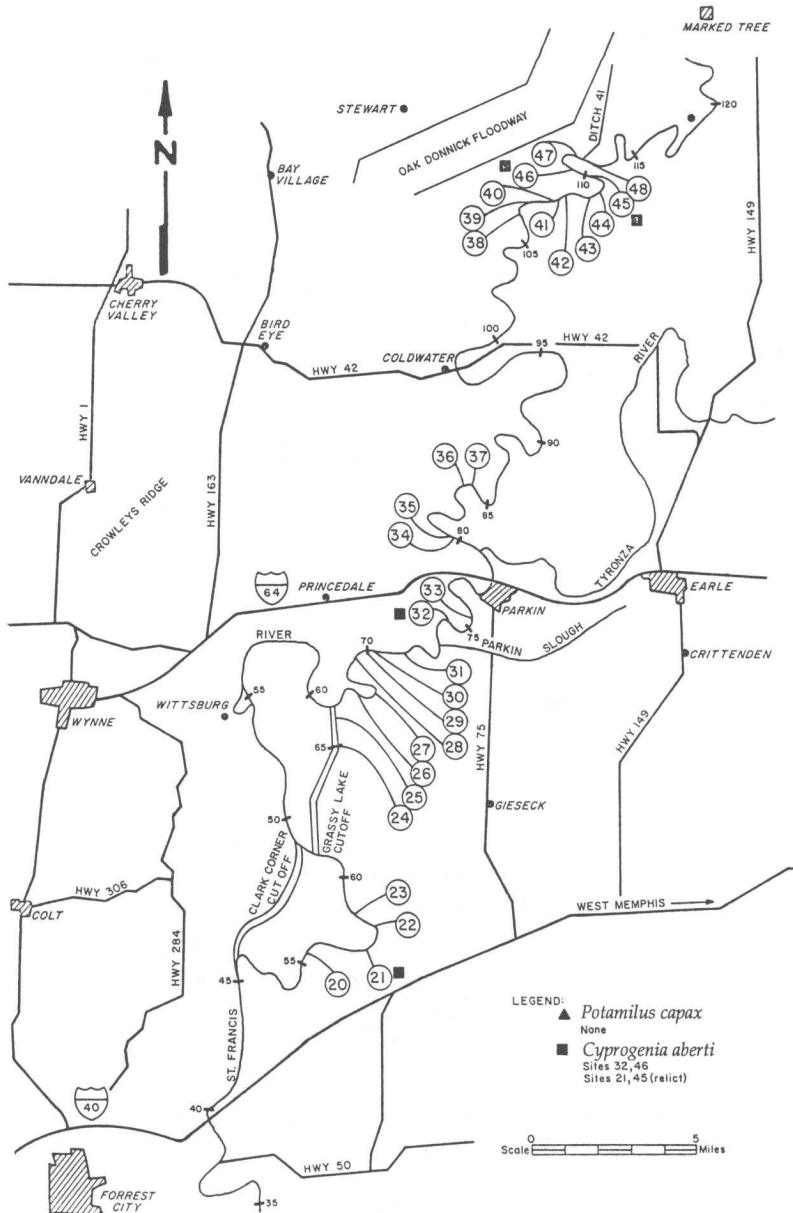


FIG. 2. Lower St. Francis River freshwater mussel collecting sites below Marked Tree, Arkansas.

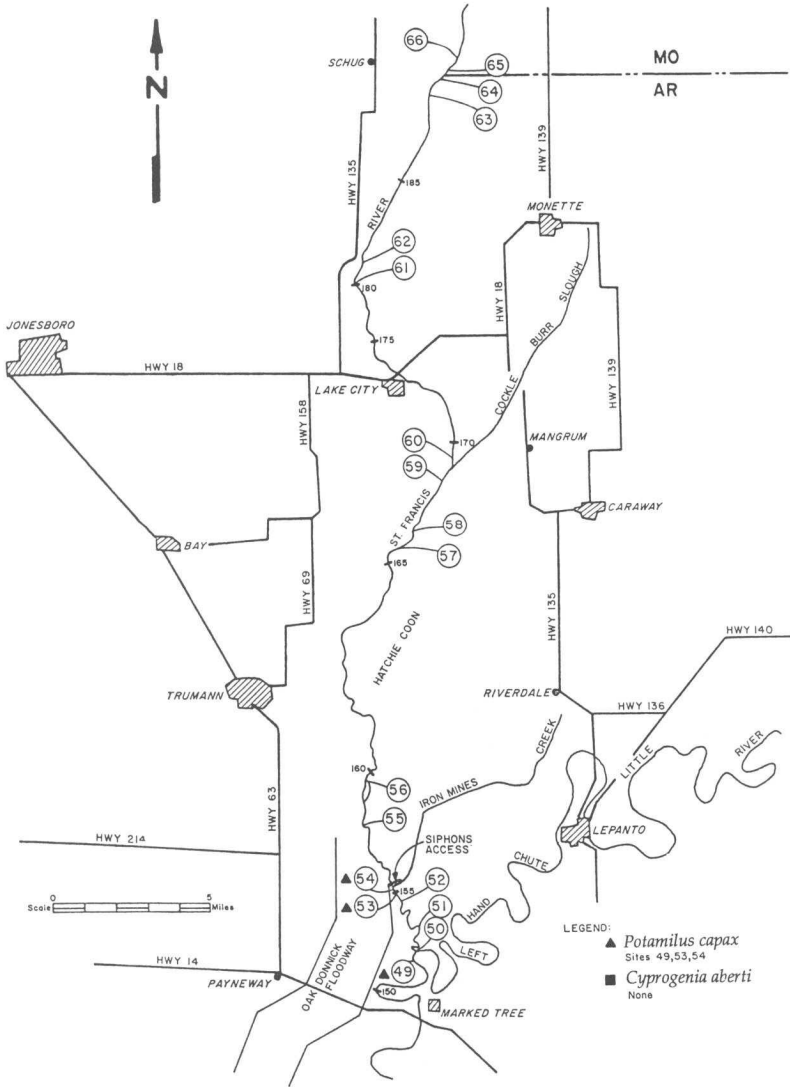


FIG. 3. Middle to lower St. Francis River freshwater mussel collecting sites below Paragould, Arkansas.

DISCUSSION

Mussel Distribution

The collection-by-collection results presented in Appendix A and summarized in Table 3 indicate the range and relative abundance of *Potamilus*

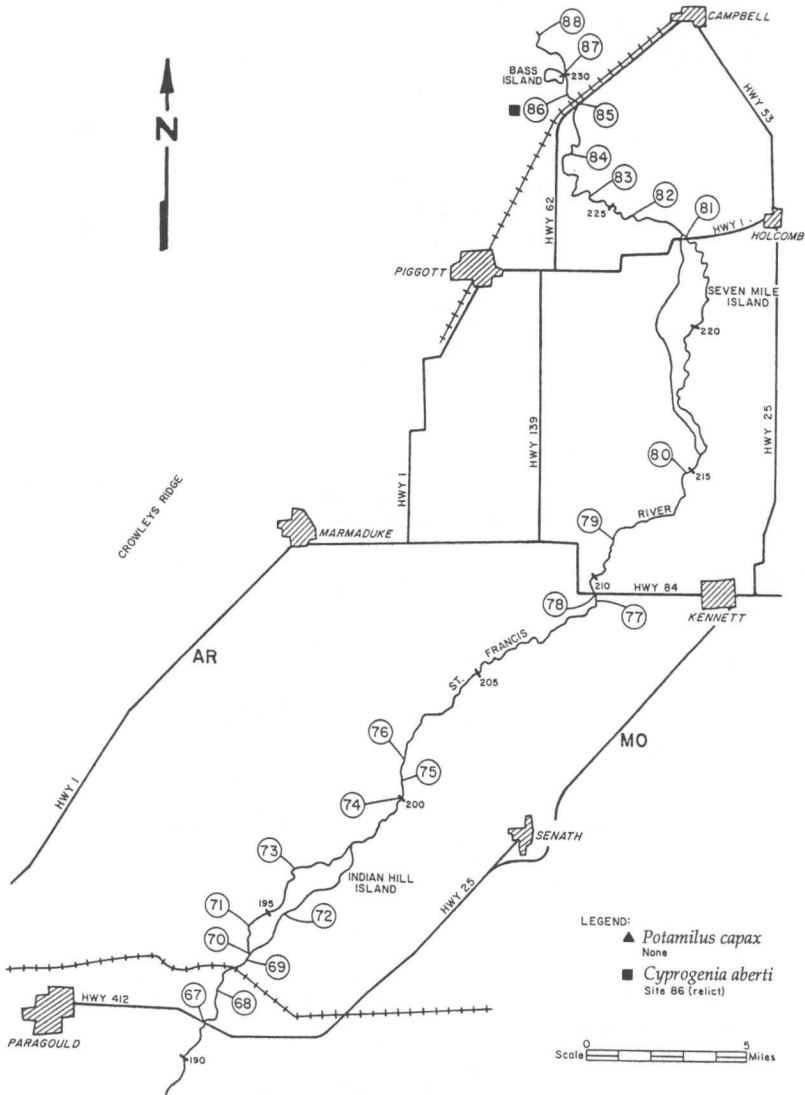


FIG. 4. Upper St. Francis River freshwater mussel collecting sites below Paragould, Arkansas.

*capax* and other mussel species encountered during this survey of the St. Francis River system. By themselves, these numbers do not provide a complete picture of mussel distribution patterns in the watershed. While the St. Francis River system downstream from Wappapello Dam flows exclusively on the Mississippi River floodplain deposits, mussel distribution appears to

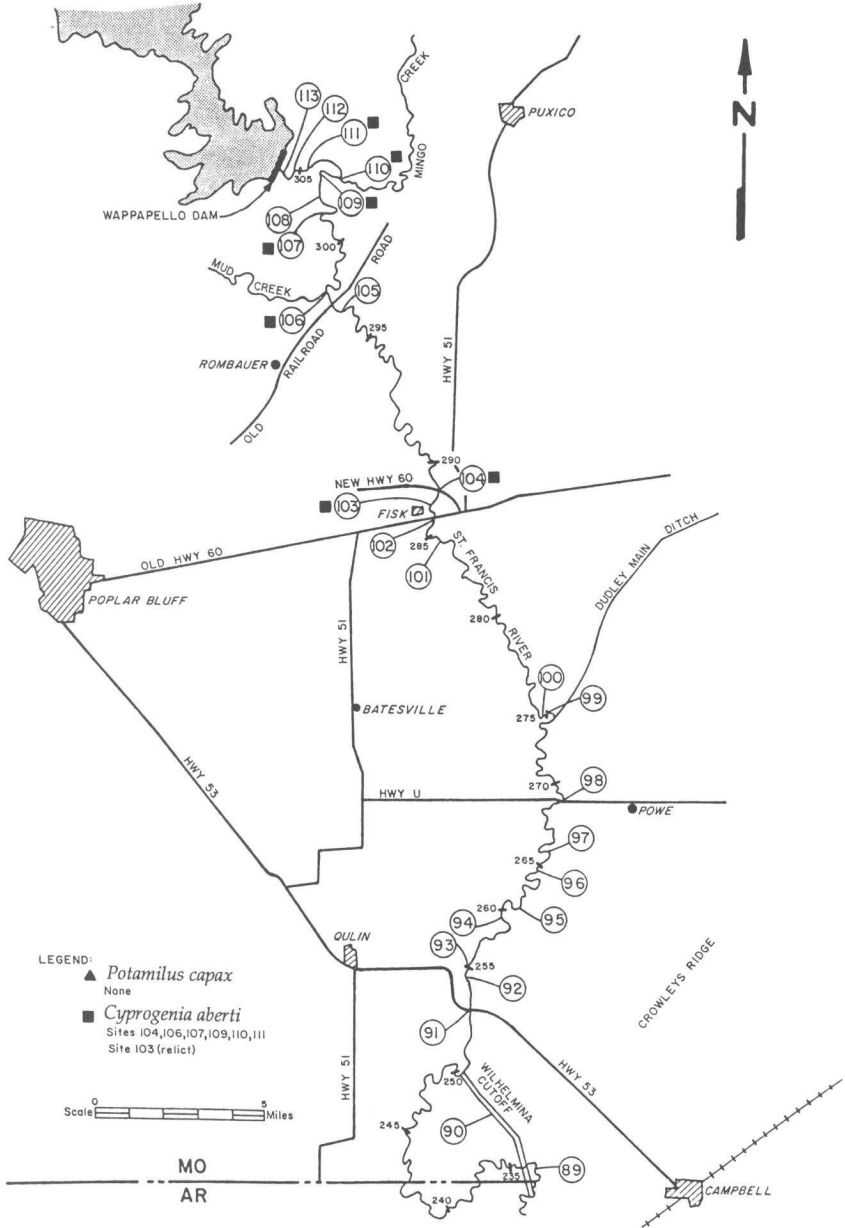


FIG. 5. Upper St. Francis River freshwater mussel collecting sites below Wappello Dam, Missouri.

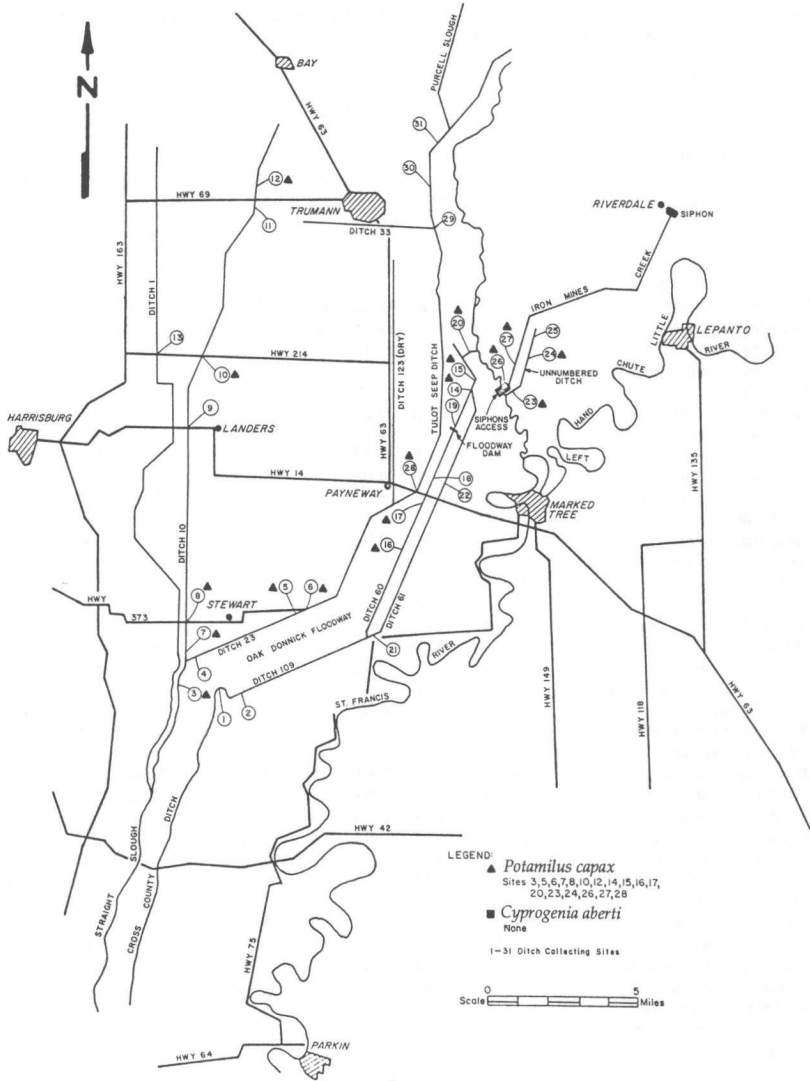


FIG. 6. St. Francis River ditch collecting sites near Marked Tree, Arkansas.

be closely associated with the specific habitat present at a site. In Table 3 St. Francis River stream reaches examined during this survey have been sorted into five geographic areas: (1) lower river and floodway, (2) lower river, (3) middle river, (4) upper river, and (5) ditches and tributaries. Habitat conditions, components of the mussel communities and unusual occurrences in each of these areas are discussed in the following paragraphs.

TABLE 3. Summary of live and fresh-dead freshwater mussel records, St. Francis River survey, September-October 1986.

Reaches (river miles)	River and floodway areas									
	2.0-25.0	%	55.3-155.1	%	157.0-229.3	%	230.3-275.5	%	284.0-305.5	%
No. sites	19		35		32		14		13	
Species										
<i>Actinonaias ligamentina</i>									153	10.86
<i>Ambleria plicata</i>	4	2.61	7150	64.47	188	19.34	8	6.25	531	37.69
<i>Anodonta grandis</i>	3	1.96	162	1.46	30	3.09			4	0.28
<i>Anodonta imbecillis</i>			18	0.16					3	0.21
<i>Anodonta suborbiculata</i>					5	0.51				
<i>Arcidens confragosus</i>			65	0.59	5	0.51			3	0.21
<i>Cyprogenia aberti</i>			10	0.09					17	1.21
<i>Fusconaia ebena</i>	1	0.65	40	0.36	1	0.10				
<i>Fusconaia flava</i>			60	0.54	25	2.57	1	0.78	56	3.97
<i>Lampsilis radiata hydiana</i>			4	0.04						
<i>Lamp. t. f. anodontoides</i>	2	1.31	112	1.01	65	6.69	15	11.72	4	0.28
<i>Lamp. teres f. teres</i>	1	0.65	6	0.05	7	0.72	9	7.03	13	0.92
<i>Lampsilis ovata</i>			82	0.74	21	2.16	2	1.56	11	0.78
<i>Lasmigona complanata</i>	2	1.31	29	0.26	40	4.12			11	0.78
<i>Leptodea fragilis</i>	22	14.38	488	4.40	146	15.02	50	39.06	96	6.81
<i>Ligumia recta</i>			3	0.03						
<i>Megaloniais nervosa</i>	4	2.61	467	4.21	11	1.13			1	0.07
<i>Obliquaria reflexa</i>	25	16.34	120	1.08	70	7.20	4	3.13	18	1.28
<i>Ellipsaria lineolata</i>			15	0.14						
<i>Plectomerus dombeyanus</i>			7	0.06	1	0.10			31	2.20
<i>Pleurobema rubrum</i>			76	0.69	1	0.10			1	0.07
<i>Pleurobema sintoxia</i>			184	1.66					18	1.28
<i>Potamilus capax</i>	8	5.23	25	0.23						
<i>Potamilus ohioensis</i>	26	16.99	167	1.51	36	3.70	20	15.63	7	0.50
<i>Potamilus purpuratus</i>	12	7.84	429	3.87	75	7.72	18	14.06	35	2.48
<i>Quadrula metanevra</i>			132	1.19	1	0.10			7	0.50
<i>Quadrula nodulata</i>	16	10.46	115	1.04	1	0.10				
<i>Quadrula pustulosa</i>	2	1.31	639	5.76	105	10.80			317	22.50
<i>Quadrula quadrula</i>	20	13.07	349	3.15	93	9.57	1	0.78	35	2.48
<i>Strophitus undulatus</i>									2	0.14
<i>Toxolasma texasensis</i>					3	0.31				
<i>Tritogonia verrucosa</i>	1	0.65	74	0.67	15	1.54			6	0.43
<i>Truncilla donaciformis</i>			7	0.06					25	1.77
<i>Truncilla truncata</i>	4	2.61	55	0.50	16	1.65			4	0.28
<i>Unio merus declivis</i>					11	1.13				
<i>Unio merus tetralasmus</i>										
<i>Villosa lienosa</i>										
Total specimens	153	100.00	11090	100.00	972	100.00	128	100.00	1409	100.00
Species included	17		30		25		10		26	

Lower River and Floodway. — The St. Francis Floodway joins the original river channel downstream from Huxtable Dam approximately 10 miles before the confluence with the Mississippi River near Helena, Arkansas (Fig. 1). Nineteen collecting sites were examined in this area: 11 sites in the lower St. Francis River (sites 1-11), and eight sites in the St. Francis Floodway (sites

TABLE 3. (cont.)

Species	Reaches No. sites	River totals 113	%	Ditch totals 31	%	Grand totals 144	%
<i>Actinonaias ligamentina</i>		153	1.11			153	1.05
<i>Amblema plicata</i>		7881	57.31	90	10.54	7971	54.57
<i>Anodonta grandis</i>		199	1.45	67	7.85	266	1.82
<i>Anodonta imbecillis</i>		21	0.15	14	1.64	35	0.24
<i>Anodonta suborbiculata</i>		5	0.04	18	2.11	23	0.16
<i>Arcidens confragosus</i>		73	0.53	11	1.29	84	0.58
<i>Cyprogenia aberti</i>		27	0.20			27	0.18
<i>Fusconaia ebena</i>		42	0.31			42	0.29
<i>Fusconaia flava</i>		142	1.03	4	0.47	146	1.00
<i>Lampsilis radiata hydiana</i>		4	0.03			4	0.03
<i>Lamp. t. f. anodontoides</i>		198	1.44	38	4.45	236	1.62
<i>Lamp. teres f. teres</i>		36	0.26			36	0.25
<i>Lampsilis ovata</i>		116	0.84	13	1.52	129	0.88
<i>Lasmigona complanata</i>		82	0.60	59	6.91	141	0.97
<i>Leptodea fragilis</i>		802	5.83	79	9.25	881	6.03
<i>Ligumia recta</i>		3	0.02			3	0.02
<i>Megalonaias nervosa</i>		483	3.51			483	3.31
<i>Obliquaria reflexa</i>		237	1.72	17	1.99	254	1.74
<i>Ellipsaria lineolata</i>		15	0.11			15	0.10
<i>Plectomerus dombeyanus</i>		39	0.28			39	0.27
<i>Pleurobema rubrum</i>		78	0.57			78	0.53
<i>Pleurobema sintoxia</i>		202	1.47	1	0.12	203	1.39
<i>Potamilus capax</i>		33	0.24	109	12.76	142	0.97
<i>Potamilus ohioensis</i>		256	1.86	66	7.73	322	2.20
<i>Potamilus purpuratus</i>		569	4.14	91	10.66	660	4.52
<i>Quadrula metanevra</i>		140	1.02			140	0.96
<i>Quadrula nodulata</i>		132	0.96	71	8.31	203	1.39
<i>Quadrula pustulosa</i>		1063	7.73	2	0.23	1065	7.29
<i>Quadrula quadrula</i>		498	3.62	84	9.84	582	3.98
<i>Strophitus undulatus</i>		2	0.01			2	0.01
<i>Toxolasma texasensis</i>		3	0.02	1	0.12	4	0.03
<i>Tritogonia verrucosa</i>		96	0.70			96	0.66
<i>Truncilla donaciformis</i>		32	0.23	1	0.12	33	0.23
<i>Truncilla truncata</i>		79	0.57	5	0.59	84	0.58
<i>Uniomerus declivis</i>		11	0.08			11	0.08
<i>Uniomerus tetralasmus</i>				10	1.17	10	0.07
<i>Villosa lienosa</i>				3	0.35	3	0.02
Total specimens		13752	100.00	854	100.00	14606	100.00
Species included		35		23		37	

12-19).

Habitat conditions at all sites examined in this area were relatively consistent. Substrate consisted of sand and mud overlain with flocculent silt.

A total of 17 mussel species was found in this area, including *Potamilus capax* (Table 3). Ten of the species were represented by five or fewer specimens. *Potamilus ohioensis* was the most abundant species, followed by *Obliquaria reflexa*, *Leptodea fragilis* and *Quadrula quadrula*. Eight specimens of *P. capax* were found. During their studies, Bates & Dennis (1983)



TABLE 4. Quantitative sampling results, mainstem sites, St. Francis River mussel survey, September-October 1986.

Species	Site River mile	3 4.0	4 5.0	8 10.0	18 23.8	19 25.0	49 152.7	Avg. sq. m	No. speci- mens
<i>Amblema plicata</i>							0.75	0.16	30
<i>Anodonta grandis</i>							0.02	0.01	1
<i>Arcidens confragosus</i>							0.02	0.01	1
<i>Fusconaia flava</i>							0.02	0.01	1
<i>Lamp. t. f. anodontoides</i>							0.02	0.01	1
<i>Lasmigona complanata</i>							0.05	0.01	2
<i>Leptodea fragilis</i>		0.03			0.03		1.12	0.25	47
<i>Megaloniaias nervosa</i>					0.07		0.38	0.09	17
<i>Obliquaria reflexa</i>			0.03	0.03			0.15	0.04	7
<i>Potamilus capax</i>							0.08	0.02	3
<i>Potamilus ohioensis</i>			0.07				0.25	0.06	12
<i>Potamilus purpuratus</i>		0.03	0.03		0.03		0.35	0.09	17
<i>Quadrula nodulata</i>							0.12	0.03	5
<i>Quadrula pustulosa</i>							0.12	0.03	5
<i>Quadrula quadrula</i>				0.03	0.03		0.15	0.04	8
<i>Tritogonia verrucosa</i>							0.08	0.02	3
Totals									
No./sq. m		0.07	0.13	0.03	0.17	0.00	3.70		
No. samples (10 sq. m)		3	3	3	3	3	4		
No. mussels found		2	4	1	5	0	148		160

found 16 mussel species in this area and Clarke (1985) found 12 species between St. Francis Floodway miles 25-35.

Few specimens of commercially important mussel species (*Amblema plicata* and *Megaloniaias nervosa*) were collected; however, discussions with local fishermen and the large number of cull piles observed during the access survey indicate a viable commercial mussel fishery exists in this area. The high water and poor sampling conditions during the sample period probably led us to underestimate the abundance and diversity of the fauna in this area.

Lower River. — Thirty-five sites were examined in the largely unmodified portion of the St. Francis River from Allen Bayou (RM 55.3, site 20) upstream to the Siphons Access near Marked Tree (RM 155.1, site 54). Twenty-nine of these sites were located in four widely spaced five- or ten-mile reaches of the river between RM 55 and RM 112 (Fig. 2). Included in this area are two sites (24 and 25) in Grassy Lake Cutoff, a manmade bypass of the original river channel. The other six sites were located between Marked Tree (RM 150) and the Siphons Access (Fig. 3).

River substrate in this area consisted of sloping, muddy banks and shifting sand across the width of the river channel. Gravel bars occurred only at four sites (21, 32, 35, and 45). The substrate in Grassy Lake Cutoff was similar to other parts of the area except that the banks were more vertical and there were wide expanses of packed sand in the channel.

TABLE 5. Quantitative sampling results, ditch and tributary sites, St. Francis River mussel survey, September-October, 1986.

Species	Site											Avg. per sq. m	Number of specimens
	D-6	D-7	D-8	D-10	D-12	D-15	D-16	D-23	D-24	D-26	D-27		
<i>Amblema plicata</i>	0.02									0.07		0.009	5
<i>Anodonta grandis</i>						0.03				0.03		0.005	3
<i>Anodonta suborbiculata</i>										0.03		0.003	2
<i>Lampsilis teres</i> f. <i>anodontooides</i>							0.02					0.002	1
<i>Lasmigona complanata</i>										0.07	0.04	0.010	6
<i>Leptodea fragilis</i>			0.02							0.03		0.007	4
<i>Obliquaria reflexa</i>									0.05			0.005	3
<i>Potamilus capax</i>		0.01	0.02				0.05			0.03		0.010	6
<i>Potamilus ohioensis</i>		0.01						0.02	0.02	0.02	0.02	0.009	5
<i>Potamilus purpuratus</i>	0.02									0.05		0.007	4
<i>Quadrula nodulata</i>				0.02		0.03						0.003	2
<i>Quadrula quadrula</i>	0.02	0.02	0.02	0.08					0.02	0.02		0.017	10
Totals													
No./sq. m	0.08	0.04	0.06	0.10	0.00	0.07	0.05	0.02	0.10	0.35	0.06	0.088	
No. samples (10 sq. m)	4	10	10	4	4	3	2	4	6	6	5	58	
No. mussels found	3	4	6	4	0	2	1	1	6	21	3		51

TABLE 6. Lengths of *Potamilus capax* specimens encountered alive or as fresh-dead shells in the St. Francis River watershed, September-October, 1986.

Sites	Mean	20	30	40	50	60	70	80	90	100	110	120	130	140	Totals
3	54.10				1										1
4	95.70								1						1
8	84.30							1							1
9	88.00							1							1
15	101.40									1					1
16	83.20							1							1
18	80.90						1	1							2
19	105.10									1					1
*	90.67						1		1	1					3
49	92.63	1			1		2	5	2	1	1	2		1	16
53	0.00			2	2	1		15	10	1	2	2			35
54	77.60				1				1						2
River site totals	90.12	1	0	2	5	1	4	24	15	5	3	4	0	1	65
D 6	108.20									1					1
D 7	110.15								1			1			2
D 8	84.70				1			1	1	1					4
D 10	95.00							1	3	1					5
D 12	112.40										1				1
D 14	83.60							1							1
D 15	32.80	1	1								1				2
D 16	0.00	1	11	16	13	3	1	1	2		1				49
D 23	123.40											1			1
D 24	123.00											1			1
D 26	85.39			1	1			1	3				1		7
D 27	64.83				1	4		1				1			7
Ditch site totals	64.47	2	12	17	16	7	1	6	10	3	2	4	1	0	81
Grand totals	75.89	3	12	19	21	8	5	30	25	8	5	8	1	1	146

\* Site visited only during access survey.

Thirty mussel species were found in this area (Table 3). The vast majority of individuals and species occurred in narrow bands where the shifting sand in the channel met the mud or clay of the banks. Few mussels were found in the relatively firm sand substrate in the river channel even though it appeared stable at several sites.

By far the most abundant species in this area was *Amblema plicata*. Common species included *Quadrula pustulosa*, *Leptodea fragilis*, *Megaloniaias nervosa* and *Potamilus purpuratus*. Uncommon species in this area were *Lampsilis hydiana*, *Ligumia recta* and *Truncilla donaciformis*. Only seven live specimens of *Plectomerus dombeyanus* were found in this area but large numbers of old dead (relict) specimens were observed at many sites. Some of these specimens may have died from previous low flow conditions; however, that explanation could not account for the vast numbers of dead *P. dombeyanus* found among live mussels of other species.

Thousands of mussels occurred at each of the four sites with a gravel bar. At two sites (RM 57.2, site 21, and RM 74.3, site 32), there appeared to be more mussels than rocks. These sites also yielded several species found very rarely elsewhere in the area. Mussel species found only at the gravel bars were *Cyprogenia aberti*, *Pleurobema rubrum*, *Pleurobema sintoxia* and *Quadrula metanevra*. Pleurocerid snails (*Pleurocera* sp.) were present only on the gravel bars at sites 21 and 32. These snails were not found at any other site during the entire survey.

In this area, *Potamilus capax* was found only in the reach between Marked Tree and the Siphons Access (RM 152.7-155.1, sites 49-54). Since river reaches between Marked Tree (RM 150) and RM 112 were not included in the survey, it is uncertain where *P. capax* drops out of the community.

As crews floated through the area, they encountered commercial mussel fishermen at several sites. These individuals were hand collecting ("hogging") and using compressed air equipment while diving to harvest *Amblema plicata*, *Megaloniaias nervosa* and *Potamilus purpuratus*. These observations and several cull piles indicate this portion of the river still supports a viable mussel fishery.

Middle River. — The 70-mile section of the St. Francis River between the Marked Tree Siphons (RM 157) and Highway 62 bridge (RM 229), known as the "Sunken Lands," is a braided series of channels, oxbows, sloughs and ditches (Figs. 3 and 4). In some places within this area, the river indicated on maps was dry and the water was flowing in other natural or manmade channels. Sampling occurred at 32 sites in this area, some in the identified river channel and some in other flowing-water channels within the various five-mile reaches.

Aquatic habitat in this area was surprisingly diverse. Typically, the stream banks were forested and extremely low, often with water standing around the trunks and roots of cypress or gum trees. Along the edges of what appeared to be well defined channels, there was a band of detritus and soft mud. This was followed by a complete transition through mud, muddy sand, loose sand, and hard packed sand out in the current. Often there were large pockets of firm mud with only a light cover of fine silt.

Twenty-five species were found in the Sunken Lands. Mussels were evenly distributed throughout this area although they were not particularly

abundant. The dominant species were *Amblema plicata*, *Leptodea fragilis*, *Quadrula pustulosa* and *Quadrula quadrula*. *Uniomerus declivis* and *Toxolasma texasensis* were only found in the Sunken Lands and both species came from only a few sites. *Potamilus capax* was not encountered alive upstream from the channel feeding ditches 60 and 61.

Upper River. — Between RM's 230 and 275, the St. Francis River has been straightened and dredged but between RM's 275 and 305 (Wappapello Dam) the river is largely unmodified. Fourteen sites were sampled in the upper dredged portion of the river (sites 87-100) and 13 sites (101-113) were sampled in the original channel below Wappapello Dam (Figs. 4 and 5).

Habitat in the dredged portion of the river consisted of steep vertical banks, large expanses of shifting sand, occasional mud flats, numerous snags, and drift. The unmodified portion had a narrow channel composed of stable sand, especially at sites closest to Wappapello Dam. This portion also included a few gravel bars. Stream banks were forested in the unmodified area and were covered with grasses and shrubs in the dredged area.

Ten mussel species were reported from the dredged area and 26 species were found in the unmodified area. *Potamilus capax* was not encountered. Of the species present in the dredged portion, *Leptodea fragilis* was the most abundant, followed by *Potamilus ohiensis*, *Potamilus purpuratus* and *Lampsilis teres* form *anodontoides*. Only 128 mussels were found scattered along the sides of mud flats or on sand bars at the 14 sites within this area.

In the less modified portion, large numbers of young mussels were encountered, especially at sites closest to the dam (RM 303.1-305.5, sites 109-113). The abundant species in this area were *Amblema plicata* and *Quadrula pustulosa*, followed by *Actinonaias ligamentina* and *Leptodea fragilis*. Seventeen specimens of *Cyprogenia aberti* were found; all at sites with large amounts of gravel substrate. *Actinonaias ligamentina* occurred at eight sites between RM's 284-305. This species was not found anywhere else during the survey.

Ditches and Tributaries. — Ten reaches included in this survey were manmade ditches or modified St. Francis River tributaries (Fig. 6). All of these water courses except the unnumbered ditch drain into Oak Donnick Floodway west and south of Marked Tree. The unnumbered ditch flows into the St. Francis River downstream from the Siphons Access.

A total of 31 sites were sampled in these ditches. In ditches with flowing water, the habitat consisted of vertical banks dropping off into sand- or clay-lined channels. Ditches with low or moderate current had substrates that were various mixtures of sand and mud. Ditches carrying high flows (like Ditch 60) had substrates that were often scoured to firm clay but also had large expanses of shifting sand. In ditches which appeared to be older than the others based on bankside vegetation (Iron Mines Creek and Tulot Seep Ditch), the substrate seemed to be more stable and included distinct patches of various mud and sand combinations.

Twenty-three mussel species were found at the ditch sites (Table 3). Live mussels were present in all ditches with flowing water at the time of the survey. The most abundant mussel species found in the ditches was *Potamilus capax*, followed by *Potamilus purpuratus*, *Amblema plicata*, *Quadrula quadrula* and *Leptodea fragilis*. Ten specimens of *Uniomerus*

*tetralasmus* and three specimens of *Villosa lienosa* were found only at sites in Ditches 1 and 10. In both locations, these species were collected in damp mud with no surface water present. Ditch 123 was not sampled because it was completely dry and overgrown.

### *Potamilus capax*

The focus of this survey, the fat pocketbook, was represented by 142 specimens (61 live and 81 fresh-dead) found at 24 collection sites during the float survey. These records form the basis for the following comments on species distribution, habitat, and population factors. Measurement data on several *Potamilus capax* specimens encountered during the access survey also are included in the population factors discussion.

Distribution. — As indicated in preceding sections and Appendix A, *Potamilus capax* was found at seven sites in the lower St. Francis Floodway and River, at three sites in the St. Francis River between Marked Tree and the Siphons Access, and at fourteen sites in the ditches. The fat pocketbook was not found at any sites in the original river channel between RM 55 and RM 110 or upstream from the southern tip of the Sunken Lands. In the Sunken Lands, *P. capax* was found alive in the feeder channel to Ditches 60 and 61 (sites D-14 and D-15), and a relict specimen was found in the ponded area (RM 157.0, site 55) approximately two RM's further upstream.

In general, *Potamilus capax* appears to inhabit manmade parts of this watershed and to be absent in the natural areas. Sites where Bates & Dennis (1983), Clarke (1985) and Harris (1986) found *P. capax* all fall into this pattern. Live specimens have been found throughout the length of the floodway all the way downstream to its mouth (and the downstream 11 miles of the river) and upstream as far as small ditches (like Tulot Seep Ditch), north of Marked Tree (Figs. 1, 3 and 6).

Exceptions to this pattern are the specimens which exist in the Sunken Lands and Iron Mines Creek just above the Siphons, and those in the original river channel and the unnumbered ditch just downstream from the Siphons Access (Fig. 6). The Sunken Lands are connected to the floodway system through Ditches 60 and 61 and the old river channel is fed from the Sunken Lands whenever the siphons are used.

This apparent distribution pattern of *Potamilus capax* was not shared with any other mussel species encountered during this survey. Other species were either found in both the floodway and river systems or were restricted to short reaches, often associated with atypical habitats.

Mussel communities in major portions of the St. Francis River system have yet to be examined. When this is done, the present distribution pattern of *Potamilus capax* might be altered. At present, however, the pattern suggests that the fat pocketbook gains access to new sites through the floodway system. This could occur because the fish host exists in the floodway but does not have sufficient access to the remaining parts of the original river channel. Other possible explanations for this distribution pattern could include the existence of several relict *P. capax* populations in various parts of the drainage, or as yet unidentified habitat preferences of *P. capax* or its fish host.

Habitat. — During the survey, TVA biologists were unable to predict the habitat in which *Potamilus capax* would be found. Overall, habitats which contained a mixture of sand, mud and clay (“sticky mud”) were most likely to yield a fat pocketbook.

Streambanks along *Potamilus capax* habitat ranged from low sloping banks with heavy canopy to those where the vegetation consisted only of a few scattered bushes and shrubs. Substrates where *P. capax* was found ranged from mud (ooze), to mixtures of sand, mud, and clay, to shifting sand. The largest concentration of *P. capax* occurred at a ditch site (D-16) with a sand, gravel, and mud mixture that appeared relatively stable, although the surrounding habitat consisted of shifting sand.

Abundance. — In qualitative searches (Table 3), *Potamilus capax* comprised 5% of the total number of mussels collected in the lower river and floodway area, 0.2% in the lower river area, and nearly 13% in the ditches. As discussed earlier, *P. capax* was not present in the Sunken Lands or the upper river. When all qualitative data are considered, the fat pocketbook comprised one percent of the total (142 of 14,606 specimens).

At sites where quantitative sampling was conducted, *Potamilus capax* average 0.02 per square meter in 19 river samples (Table 4), and 0.01 per square meter in 58 ditch samples (Table 5). During his study, Clarke (1985) found 226 live *P. capax* in 77,657 square meters of floodway and slough habitat, or 0.0029 *P. capax* per square meter. A more appropriate comparison with data from the present survey would be to say Clarke's 226 specimens came from 58,152 square meters of habitat in which *P. capax* was found alive, or 0.0039 specimens per square meter. Differences in field procedures may account for some of the order-of-magnitude difference between these abundance estimates; however, *P. capax* appears to have been at least as abundant where it was found during this survey as it was in the areas Clarke examined.

Population Structure. — As indicated in Results and Appendix B, 146 *Potamilus capax* specimens encountered during the access and float surveys were measured in three dimensions (length, height and thickness). Graphic inspection of the relationships between pairs of these measurements suggested very high correlations among all three. For simplicity, the following discussion deals only with length — the measurement which provided the greatest spread of the specimens.

Lengths of the *Potamilus capax* specimens ranged from 28.0 to 140.2 mm (Appendix B) and included some individuals in each ten millimeter interval between these extremes (Table 6). The interval totals in Table 6 include large numbers of specimens in the 80-90 and 90-100 mm ranges. There also are relatively large numbers of specimens in the 40-50 and 50-60 mm ranges, suggesting a bimodal distribution. Examination of Table 6 indicates that most of the 40-60 mm length specimens (29) came from site D-16, a small creek entering Ditch 60 downstream from Highway 63 bridge. At this site, a large number of small *P. capax* specimens were moving in the extremely shallow, clear water. Both the movement of these specimens and their high density in the remaining width of the creek made finding them easy. This combination of circumstances was not encountered at any other collection site.

With or without including specimens from site D-16, there appear to be fewer individuals in the lower length groups than expected. The low numbers of the shortest length intervals could be attributable to the typical inability of mussel sampling to locate small specimens. Low numbers in the 60-70 and 70-80 mm intervals may suggest environmental stress when those age classes were spawned. These low numbers also might suggest rapid growth at a particular life stage or previous time period.

In general, these measurement data suggest that a variety of size classes exist in *Potamilus capax* populations in the St. Francis River watershed. Larger and smaller individuals occur both in the mainstem and tributary watercourses.

For other mussel species and, perhaps with *Potamilus capax* populations in other rivers, this discussion of length data would be tied closely to age of the specimens as indicated by growth rests on the shells. In the St. Francis River, TVA biologists were unable to make consistent, reliable counts of growth rests on *P. capax* shells. Not uncommonly, one count of growth rests could be made on one side of a specimen and a substantially different count could be made on the other. *Potamilus capax* has an extremely smooth and uniform shell which, at least in the St. Francis River, is so difficult to age with reasonable certainty that we have chosen not to add what we feel would be mostly speculation about age and growth.

#### SUMMARY

This survey of the St. Francis River and Floodway system was conducted to document the occurrence and abundance of *Potamilus capax* and other mussel species throughout the reaches selected for study by the USACE. The sampling objective was to visit four sites in each five-mile reach. In actuality, the survey averaged between two and three sites per reach. This level of effort was sufficient to recognize distribution patterns for most of the species, including *P. capax*. For many of these species (but not *P. capax*), habitat present at specific sites appears to be more important than geographic locations within the watershed.

*Potamilus capax* was found to exist in two areas: in adjacent reaches near the mouth of the river, and in a variety of habitats from the southwest to the north of Marked Tree, Arkansas. When combined with the results from previous studies, *P. capax* appears to occur throughout the St. Francis-Oak Donnick floodway system and in small portions of the original river system that still have contact with the floodway. Additional survey work and identification of the fish host may be required to substantiate and explain this apparent pattern.

Habitats in which the fat pocketbook occurred ranged from pure shifting sand to flocculent mud. More specimens of the species were found in a mixture of sand, mud and clay ("sticky mud") than in any other type of substrate.

In terms of relative abundance, the 142 fat pocketbook specimens encountered alive or as fresh-dead shells during the survey constituted one percent of all 14,606 mussels examined. Where quantitative sampling was conducted, *Potamilus capax* averaged 0.02 per square meter in mainstem sites and 0.01 per square meter in ditch sites. These values are approximately one order of magnitude higher than estimates that can be calculated from prior data; however, differences in field procedure are likely to account for some of this disparity.

Length data were used to represent population structure largely because specimens could not be aged accurately. Measured lengths indicate all size classes are present in both mainstem and ditch locations. Few very small specimens were



encountered, a situation that is typical of most mussel surveys and thought to represent the difficulty in locating small shells. The fewer than expected number of shells in the 60-80 millimeter range might reflect missing length (age) classes or a period of rapid growth.

This survey has extended the known distribution of *Potamilus capax* in the St. Francis River system and indicated that the newly-discovered populations are at least as abundant as those previously studied. Additions to the range of this species in the watershed are likely as other ditches and tributaries are searched.

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In the field, during part of the survey we were joined by Alan Buchanan and Leroy Koch, both from the Missouri Department of Conservation. Their participation was appreciated and quite enjoyable. All of the other members of the field crews were TVA employees. These TVA biologists not only tolerated long hours, unexpected field conditions, and extended absences from their families but maintained a level of enthusiasm for the work that made the survey an enjoyable experience. Without their individual commitments, this project never would have been completed so successfully.

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APPENDIX A. Site records for mainstem and tributary collections, St. Francis watershed, Arkansas and Missouri, September-October 1986.

Species	Site > River mile >	River samples																											
		1 2.0	2 3.0	3 4.0	4 5.0	5 6.0	6 7.0	7 8.5	8 10.0	9 11.0	10 12.0	11 13.0	12 14.0	13 16.0	14 17.5	15 19.0	16 21.0	17 22.2	18 23.8	19 25.0	20 55.3	21 57.2	22 58.4	23 59.4	24 65.0	25 65.7			
<i>Actinonaias ligamentina</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	109	800	110	367	9	22			
<i>Amblema plicata</i>	-	2	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	1	1	5	2	-	1			
<i>Anodonta grandis</i>	-	-	-	1	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	2	-	2	-	-	1			
<i>Anodonta imbecillis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
<i>Anodonta suborbiculata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
<i>Arcidens confragosus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
<i>Cyprogenia aberti</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-			
<i>Fusconaia ebena</i>	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
<i>Fusconaia flava</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
<i>Lampsilis radiata hydiana</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	28	-	-	-	-	-			
<i>Lampsilis teres f. anodontoides</i>	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1			
<i>Lampsilis teres s.s.</i>	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	-	-	-	-	-			
<i>Lampsilis ovata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1			
<i>Lasmigona complanata</i>	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	26	-	-	-	-	1			
<i>Leptodea fragilis</i>	1	2	2	2	2	2	-	2	1	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	4			
<i>Ligumia recta</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-			
<i>Megaloniais nervosa</i>	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-			
<i>Obliquaria reflexa</i>	-	13	-	1	-	-	-	-	-	1	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1			
<i>Ellipsaria lineolata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
<i>Plectomerus dombeyanus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
<i>Pleurobema rubrum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
<i>Pleurobema sintoxia</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
<i>Potamilus capax</i>	-	-	1	1	-	-	-	1	1	-	-	-	-	-	1	-	-	-	-	-	13	-	-	-	-	-			
<i>Potamilus ohioensis</i>	-	-	1	5	-	-	-	7	3	1	3	-	-	-	-	-	-	-	-	-	19	-	-	-	-	-			
<i>Potamilus purpuratus</i>	1	-	1	1	-	-	1	6	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7			
<i>Quadrula metanevra</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
<i>Quadrula nodulata</i>	-	-	-	-	-	-	8	1	-	3	2	-	-	-	-	-	-	-	-	-	21	-	-	-	-	2			
<i>Quadrula pustulosa</i>	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	2	-	-	-	-	2			
<i>Quadrula quadrula</i>	-	8	-	1	1	-	-	3	-	2	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
<i>Strophitus undulatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
<i>Toxolasma texasensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
<i>Tritogonia verrucosa</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1			
<i>Truncilla donaciformis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-			
<i>Truncilla truncata</i>	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
<i>Unio merus declivis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Total	-	2	32	5	13	4	2	10	22	6	9	14	2	1	0	1	5	4	19	2	242	1259	233	493	74	44			

## APPENDIX A (cont.)

Species	Site >		River samples																											
	River mile >		26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50			
			66.7	67.4	68.1	70.0	70.2	71.5	74.3	75.2	80.4	81.5	83.5	84.3	106.1	106.6	106.9	107.2	107.4	107.9	108.5	109.8	110.2	111.5	111.8	152.7	153.0			
<i>Actinonaias ligamentina</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
<i>Amblema plicata</i>	198	250	300	750	329	213	81	252	350	269	275	77	326	168	149	72	90	80	50	320	1	295	672	36	122					
<i>Anodonta grandis</i>	5	3	5	7	1	5	1	3	-	4	3	2	5	1	5	4	-	4	6	-	-	2	14	16	12					
<i>Anodonta imbecillis</i>	1	1	1	-	-	-	-	-	-	1	-	-	4	-	-	-	-	-	-	1	2	1	1	-	-					
<i>Anodonta suborbiculata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>Arcidens confragosus</i>	1	3	-	-	2	3	3	2	-	7	13	7	1	-	-	-	-	-	-	1	-	2	3	2	1					
<i>Cyprogenia aberti</i>	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-					
<i>Fusconaia ebena</i>	-	-	6	1	-	2	5	1	2	1	-	2	-	-	-	-	-	-	-	1	-	2	-	-	-					
<i>Fusconaia flava</i>	-	-	2	-	-	10	-	4	4	-	7	-	-	-	-	1	-	-	8	3	9	4	1	-	-					
<i>Lampsilis radiata hydiana</i>	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-					
<i>Lampsilis teres f. anodontoides</i>	1	-	-	-	3	1	18	2	-	2	3	-	2	1	1	-	-	-	2	-	2	7	4	-	-					
<i>Lampsilis teres s.s.</i>	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
<i>Lampsilis ovata</i>	-	-	1	7	3	4	4	9	2	4	2	-	3	-	2	-	2	-	11	-	-	9	-	-	-					
<i>Lasmigona complanata</i>	-	2	-	4	-	-	-	-	1	-	-	-	-	-	1	-	1	1	-	-	-	1	1	5	1					
<i>Leptodea fragilis</i>	16	6	10	39	17	15	36	13	13	33	25	50	4	-	-	8	2	8	9	7	-	1	18	58	1					
<i>Ligumia recta</i>	-	-	-	2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
<i>Megalonaias nervosa</i>	26	9	24	19	18	23	17	9	17	7	12	34	3	-	-	-	-	-	14	-	2	11	15	11						
<i>Obliquaria reflexa</i>	-	-	2	3	-	-	11	3	1	15	2	12	-	-	-	-	-	-	-	2	35	1	5	8	-					
<i>Ellipsaria lineolata</i>	-	-	-	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	-	-	-					
<i>Plectomerus dombeyanus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	4	1	-					
<i>Pleurobema rubrum</i>	-	-	-	1	-	2	22	8	24	1	7	2	-	-	-	-	-	-	-	-	-	8	-	-	-					
<i>Pleurobema sintoxia</i>	-	-	1	2	-	-	-	1	-	-	-	-	-	1	-	-	1	-	-	-	12	-	-	-	-					
<i>Potamilus capax</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7				
<i>Potamilus ohioensis</i>	8	-	1	5	2	1	5	2	1	5	2	3	1	-	-	2	2	-	3	-	-	3	15	9						
<i>Potamilus purpuratus</i>	22	4	15	41	23	12	18	20	7	20	13	10	4	7	7	5	3	5	4	13	-	3	41	20	8					
<i>Quadrula metanevra</i>	-	-	-	-	-	-	76	-	1	-	-	3	-	-	-	2	-	-	-	28	11	1	2	-	-					
<i>Quadrula nodulata</i>	2	-	2	2	-	4	11	7	2	15	8	18	-	-	-	3	-	1	4	-	4	-	5	-						
<i>Quadrula pustulosa</i>	7	7	8	2	3	14	40	41	38	60	55	133	-	-	-	8	1	3	8	72	13	9	28	5	1					
<i>Quadrula quadrula</i>	-	-	7	-	4	7	29	4	22	29	53	44	-	-	-	4	-	-	1	6	8	1	7	6	6					
<i>Strophitus undulatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
<i>Toxolasma texasensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
<i>Tritogonia verrucosa</i>	-	-	3	2	2	2	13	-	1	1	10	-	-	-	-	2	-	1	-	3	1	5	5	5	3					
<i>Truncilla donaciformis</i>	1	-	-	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-					
<i>Truncilla truncata</i>	-	-	-	2	-	-	8	2	1	4	-	2	-	-	-	-	1	-	-	1	-	28	-	3	-					
<i>Unio merus declivis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
Total	291	285	388	888	409	309	422	380	485	483	474	416	356	177	165	113	99	105	83	507	117	342	835	208	175					

## APPENDIX A (cont.)

Species	River samples																									
	Site > River mile >	51 153.6	52 154.5	53 155.0	54 155.1	55 157.0	56 159.1	57 165.9	58 167.0	59 168.7	60 169.3	61 180.0	62 181.0	63 185.8	64 186.2	65 186.8	66 187.2	67 191.2	68 192.0	69 193.2	70 193.4	71 194.5	72 195.8	73 197.0	74 198.0	75 200.4
<i>Actinonaias ligamentina</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Amblema plicata</i>	6	-	2	-	11	47	1	26	32	7	-	-	-	-	2	2	30	11	-	3	2	-	4	1	-	-
<i>Anodonta grandis</i>	12	13	19	-	2	-	2	7	1	3	3	-	3	-	-	-	-	1	-	2	-	-	-	-	-	-
<i>Anodonta imbecillis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Anodonta suborbiculata</i>	-	-	-	-	3	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
<i>Arcidens confragosus</i>	5	2	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	1	-	-	-	1	-	-
<i>Cyprogenia aberti</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Fusconaia ebena</i>	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Fusconaia flava</i>	-	-	-	-	-	5	1	2	1	7	-	-	-	-	-	-	1	5	-	-	-	-	-	-	-	-
<i>Lampsilis radiata hydiana</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lampsilis teres f. anodontoides</i>	1	1	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
<i>Lampsilis teres s.s.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	-
<i>Lampsilis ovata</i>	-	-	-	-	-	-	6	1	-	-	-	-	1	-	-	-	2	5	-	1	-	-	-	-	-	-
<i>Lasmigona complanata</i>	2	1	2	-	3	4	-	8	3	13	1	-	-	-	-	-	1	1	2	-	-	-	-	-	-	-
<i>Leptodea fragilis</i>	1	7	-	-	1	1	3	2	1	3	3	3	3	2	-	1	2	8	5	12	3	6	9	22	3	-
<i>Ligumia recta</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Megalonaias nervosa</i>	-	-	-	-	4	2	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
<i>Obliquaria reflexa</i>	-	1	1	-	-	-	-	1	1	-	-	-	-	-	-	4	9	7	4	-	1	-	-	1	4	-
<i>Ellipsaria lineolata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Plectomerus dombeyanus</i>	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
<i>Pleurobema rubrum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pleurobema sintoxia</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Potamilus capax</i>	-	-	16	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Potamilus ohioensis</i>	7	32	42	-	2	-	-	-	-	-	-	-	1	-	-	-	1	3	-	-	-	-	1	1	1	-
<i>Potamilus purpuratus</i>	17	11	19	-	-	-	-	1	1	-	1	1	-	-	1	-	3	2	3	-	2	2	11	-	-	-
<i>Quadrula metanevra</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Quadrula nodulata</i>	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Quadrula pustulosa</i>	-	-	-	-	-	13	2	6	4	5	1	-	-	-	2	10	8	10	-	-	1	-	1	3	1	-
<i>Quadrula quadrula</i>	-	2	-	-	4	1	-	2	1	15	-	1	-	-	1	16	5	3	11	-	3	13	12	1	-	-
<i>Strophitus undulatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Toxolasma texasensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1	-	-
<i>Tritogonia verrucosa</i>	-	-	-	-	1	-	2	-	-	-	-	-	-	-	-	-	-	-	3	1	-	-	-	-	-	-
<i>Truncilla donaciformis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Truncilla truncata</i>	-	-	-	-	2	-	-	-	-	-	1	-	-	-	-	7	-	-	2	-	1	-	2	-	-	-
<i>Unioemerus declivis</i>	-	-	-	-	-	1	1	1	3	-	-	-	-	-	-	-	-	-	-	-	1	-	4	-	-	-
Total	51	71	109	2	33	76	18	60	48	54	10	5	7	0	11	47	72	48	36	9	20	27	61	14	1	

Species	River samples																									
	Site > River mile >	76 203.0	77 208.8	78 209.6	79 211.2	80 214.5	81 223.0	82 224.5	83 226.0	84 228.0	85 229.2	86 229.3	87 230.3	88 231.8	89 234.0	90 245.0	91 253.0	92 254.5	93 255.0	94 258.0	95 261.0	96 264.5	97 266.5	98 269.5	99 275.0	100 275.5
<i>Actinonaias ligamentina</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Amblema plicata</i>	-	-	1	4	3	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-
<i>Anodonta grandis</i>	-	-	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Anodonta imbecillis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Anodonta suborbiculata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Arcidens confragosus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cyprogenia aberti</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Fusconaia ebena</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Fusconaia flava</i>	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Lampsilis radiata hydiana</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lampsilis teres f. anodontoides</i>	1	-	2	7	24	9	-	3	6	3	8	5	-	3	-	4	-	-	-	-	-	-	2	-	-	1
<i>Lampsilis teres s.s.</i>	-	-	-	-	-	-	-	-	-	-	4	2	1	-	2	-	1	-	-	-	-	-	-	-	3	-
<i>Lampsilis ovata</i>	-	-	1	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-
<i>Lasmigona complanata</i>	-	-	1	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Leptodea fragilis</i>	3	3	2	22	5	2	1	2	3	5	8	4	-	15	1	2	1	-	1	-	3	3	3	9	8	-
<i>Ligumia recta</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Megaloniais nervosa</i>	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Obliquaria reflexa</i>	-	-	6	14	14	-	1	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	2	2	-
<i>Ellipsaria lineolata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Plectomerus dombeyanus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pleurobema rubrum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pleurobema sintoxia</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Potamilus capax</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Potamilus ohioensis</i>	-	-	-	-	6	3	-	5	5	7	5	-	6	1	2	-	2	-	-	-	1	-	2	1	-	-
<i>Potamilus purpuratus</i>	1	-	3	8	12	4	-	3	4	12	3	-	5	-	3	1	-	-	-	-	-	-	1	4	1	-
<i>Quadrula metanevra</i>	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Quadrula nodulata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Quadrula pustulosa</i>	-	1	5	2	29	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Quadrula quadrula</i>	-	-	-	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Strophitus undulatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Toxolasma texasensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Tritogonia verrucosa</i>	-	-	-	-	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Truncilla donaciformis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Truncilla truncata</i>	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Uniomereus declivis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total	5	4	24	65	114	18	2	5	18	18	42	19	1	29	4	11	3	2	1	0	4	5	7	27	15	-

## APPENDIX A (cont.)

Species	Site > River mile >	River samples													Total	No. sites
		101 284.0	102 285.5	103 285.8	104 286.0	105 293.0	106 297.8	107 301.8	108 302.5	109 303.1	110 303.8	111 304.7	112 305.3	113 305.5		
<i>Actinonaias ligamentina</i>		1	11	90	16	-	20	13	-	-	1	1	-	-	153	8
<i>Amblema plicata</i>		-	13	4	2	1	8	3	22	13	35	232	192	6	7881	66
<i>Anodonta grandis</i>		-	-	-	-	1	-	-	-	-	-	2	1	-	199	48
<i>Anodonta imbecillis</i>		-	-	-	1	1	-	-	-	-	-	-	-	1	21	15
<i>Anodonta suborbiculata</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	5	3
<i>Arcidens confragosus</i>		-	-	-	-	-	-	-	-	-	-	1	1	1	73	28
<i>Cyprogenia aberti</i>		-	-	-	1	-	3	5	-	1	3	4	-	-	27	9
<i>Fusconaia ebena</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	42	15
<i>Fusconaia flava</i>		-	3	5	1	-	10	6	-	-	-	30	-	1	142	29
<i>Lampsilis radiata hydiana</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	4	3
<i>Lampsilis teres f. anodontooides</i>		-	2	1	-	-	-	-	-	-	-	1	-	-	198	43
<i>Lampsilis teres s.s.</i>		5	1	-	1	1	1	-	-	-	-	-	3	1	36	20
<i>Lampsilis ovata</i>		2	-	1	-	-	1	2	-	1	3	-	1	-	116	36
<i>Lasmigona complanata</i>		-	1	-	-	-	1	-	-	-	2	3	3	1	82	36
<i>Leptodea fragilis</i>		18	12	2	1	-	10	5	5	2	10	7	23	1	802	97
<i>Ligumia recta</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	3	2
<i>Megalonaias nervosa</i>		-	-	1	-	-	-	-	-	-	-	-	-	-	483	29
<i>Obliquaria reflexa</i>		-	-	-	-	-	1	1	1	-	1	10	4	-	237	48
<i>Ellipsaria lineolata</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	15	4
<i>Plectomerus dombeyanus</i>		-	3	1	1	-	3	-	-	1	-	7	15	-	39	11
<i>Pleurobema rubrum</i>		-	-	-	-	-	1	-	-	-	-	-	-	-	78	12
<i>Pleurobema sintoxia</i>		-	-	8	3	-	7	-	-	-	-	-	-	-	202	10
<i>Potamilus capax</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	33	10
<i>Potamilus ohioensis</i>		-	2	-	-	-	-	-	1	-	3	1	-	-	256	56
<i>Potamilus purpuratus</i>		3	12	1	2	3	2	2	-	-	5	2	2	1	569	76
<i>Quadrula metanevra</i>		-	-	-	3	-	2	1	-	-	-	-	1	-	140	14
<i>Quadrula nodulata</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	132	27
<i>Quadrula pustulosa</i>		1	7	9	14	2	22	11	38	9	15	84	104	1	1063	62
<i>Quadrula quadrula</i>		-	7	4	-	-	-	-	-	-	3	3	17	1	498	53
<i>Strophitus undulatus</i>		-	-	-	-	-	-	-	-	-	1	-	1	-	2	2
<i>Toxolasma texasensis</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	3	3
<i>Tritogonia verrucosa</i>		-	-	-	-	-	4	1	-	-	1	-	-	-	96	29
<i>Truncilla donaciformis</i>		-	-	-	-	-	-	-	12	3	4	-	6	-	32	11
<i>Truncilla truncata</i>		-	-	-	-	-	-	-	-	-	1	1	2	-	79	24
<i>Unio merus declivis</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	11	6
Total		30	74	127	46	9	96	50	79	30	88	389	376	15	13752	

## APPENDIX A (cont.)

Species	Ditch samples																
	Site >	D-1	D-2	D-3	D-4	D-5	D-6	D-7	D-8	D-9	D-10	D-11	D-12	D-13	D-14	D-15	D-16
<i>Amblema plicata</i>	-	-	-	-	-	3	7	1	4	-	1	-	2	-	-	-	15
<i>Anodonta grandis</i>	4	-	-	1	-	7	1	-	1	-	1	-	4	-	2	-	-
<i>Anodonta imbecillis</i>	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	12
<i>Anodonta suborbiculata</i>	2	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
<i>Arcidens confragosus</i>	-	-	-	-	3	1	-	-	-	-	-	-	-	-	-	-	-
<i>Fusconaia flava</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lampsilis teres form anodontooides</i>	-	-	-	2	3	16	2	2	-	-	-	1	6	1	-	2	-
<i>Lampsilis ovata</i>	-	-	-	-	4	1	-	2	-	-	-	-	-	-	-	-	-
<i>Lasmigona complanata</i>	1	-	-	-	1	1	3	5	-	2	-	1	-	-	-	1	-
<i>Leptodea fragilis</i>	-	-	-	-	3	7	6	4	-	2	-	2	-	3	1	27	-
<i>Obliquaria reflexa</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
<i>Pleurobema sintoxia</i>	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Potamilus capax</i>	-	-	1	-	-	4	4	5	-	5	-	1	-	1	2	69	-
<i>Potamilus ohioensis</i>	-	-	1	-	1	-	3	9	-	-	-	1	-	2	-	17	-
<i>Potamilus purpuratus</i>	-	-	-	-	9	24	2	1	-	1	-	1	1	2	1	9	-
<i>Quadrula nodulata</i>	-	-	1	-	-	1	-	51	-	1	-	-	-	1	2	-	-
<i>Quadrula pustulosa</i>	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-
<i>Quadrula quadrula</i>	-	-	-	-	-	10	4	31	-	7	-	15	1	-	-	1	-
<i>Toxolasma texasensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
<i>Truncilla donaciformis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
<i>Truncilla truncata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
<i>Unio merus tetralasmus</i>	-	-	-	-	-	-	-	-	9	-	-	-	1	-	-	-	-
<i>Villosa lienosa</i>	-	-	-	-	-	-	-	-	1	-	-	-	2	-	-	-	-
Total	7	0	4	3	28	80	26	115	11	19	1	25	15	10	12	155	-

## APPENDIX A (cont.)

Species	Ditch samples																Total spec.	Total sites
	Site >	D-17	D-18	D-19	D-20	D-21	D-22	D-23	D-24	D-25	D-26	D-27	D-28	D-29	D-30	D-31		
<i>Amblema plicata</i>	3	1	-	3	-	-	-	7	5	5	5	19	1	2	6	90	18	
<i>Anodonta grandis</i>	-	-	-	2	-	-	4	2	-	2	5	4	9	8	10	67	17	
<i>Anodonta imbecillis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14	3	
<i>Anodonta suborbiculata</i>	-	-	-	5	-	-	1	-	-	7	1	-	-	-	-	18	6	
<i>Arcidens confragosus</i>	-	-	-	-	-	-	-	-	1	1	-	1	1	-	3	11	7	
<i>Fusconaia flava</i>	-	-	-	-	-	-	-	1	2	-	-	1	-	-	-	4	3	
<i>Lampsilis teres form anodontoides</i>	-	-	-	-	-	-	-	1	-	-	-	1	-	1	-	38	12	
<i>Lampsilis ovata</i>	-	-	-	-	-	-	-	1	-	-	-	1	1	3	-	13	7	
<i>Lasmigona complanata</i>	-	-	-	-	-	1	3	5	-	6	5	3	2	7	12	59	17	
<i>Leptodea fragilis</i>	-	1	1	1	-	4	1	3	4	4	-	3	-	-	2	79	19	
<i>Obliquaria reflexa</i>	-	-	10	-	-	-	-	5	1	-	-	-	-	-	-	17	4	
<i>Pleurobema sintoxia</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	
<i>Potamilus capax</i>	1	-	-	-	-	-	1	1	-	7	7	-	-	-	-	109	14	
<i>Potamilus ohioensis</i>	-	2	-	8	-	-	6	8	1	5	2	-	-	-	-	66	14	
<i>Potamilus purpuratus</i>	-	1	-	1	-	-	3	5	2	9	-	8	3	4	4	91	20	
<i>Quadrula nodulata</i>	-	-	-	-	-	-	-	-	-	1	13	-	-	-	-	71	8	
<i>Quadrula pustulosa</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	
<i>Quadrula quadrula</i>	-	-	-	-	-	-	-	3	2	4	1	2	2	1	-	84	14	
<i>Toxolasma texasensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	
<i>Truncilla donaciformis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	
<i>Truncilla truncata</i>	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	5	2	
<i>Unio merus tetralasmus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	2	
<i>Villosa lienosa</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	2	
Total	4	5	11	20	0	5	19	42	22	51	39	43	19	26	37	854		



APPENDIX B. Individual measurements of *Potamilus capax* specimens encountered during the access or float surveys of the St. Francis River system, September-October 1986.

Site no.	Locality	Length	Height	Thickness
<u>Mainstem</u>				
3	RM 4.0	54.1	43.7	35.4
4	RM 5.0	95.7	70.7	57.2
8	RM 10.0	84.3	63.5	49.9
9	RM 11.0	88.0	66.6	52.3
15	RM 19.0	101.4	76.9	62.8
16	RM 20.5	83.2	64.8	52.3
18	RM 23.8	79.6	62.0	53.4
		82.2	61.4	48.9
19	RM 25.0	105.1	82.2	63.4
*	RM 37.0	70.5	51.6	45.4
		96.2	67.7	51.8
		105.3	76.9	62.2
49	RM 152.7	21.9	15.5	11.9
		58.6	43.9	34.7
		77.8	58.8	44.0
		78.3	58.0	49.8
		86.1	62.4	54.7
		86.2	64.2	53.2
		86.3	62.5	51.3
		88.5	67.6	52.9
		89.8	64.6	54.6
		96.6	69.7	56.4
		96.9	72.9	60.3
		108.0	75.6	62.4
		113.2	80.9	67.7
		125.7	89.8	71.6
		128.3	90.6	71.5
		140.2	107.7	80.9
53	RM 155.0	46.0	28.4	22.9
		49.6	30.0	24.3
		52.4	31.5	23.6
		56.1	39.5	30.0
		69.8	49.7	38.6
		81.2	59.2	50.6
		82.5	60.5	49.5
		83.2	59.4	50.4
		83.3	61.4	49.9
		84.0	59.4	51.6
		84.3	60.4	49.7
		85.2	63.6	55.3
		86.4	64.9	49.5
		86.7	63.2	50.6
		87.4	60.9	51.3
		87.4	64.0	56.7
		87.9	63.9	50.8

APPENDIX B (cont.)

Site no.	Locality	Length	Height	Thickness
		89.4	61.0	51.9
		89.5	66.3	53.8
		89.7	65.4	52.0
		90.4	64.7	55.4
		90.8	65.4	52.7
		91.2	67.7	56.0
		91.5	70.8	58.2
		92.3	65.5	54.3
		92.4	69.4	59.3
		94.1	68.2	59.2
		94.3	69.5	60.5
		95.4	68.2	56.9
		99.8	72.4	59.3
		108.0	84.1	62.4
		113.1	78.6	62.7
		118.6	83.5	63.5
		125.0	86.1	69.8
		125.6	89.3	72.4
54	RM 155.1	55.7	43.1	35.6
		99.5	73.9	57.7
<u>Ditches</u>				
D-6	Ditch 23 near Oak Donnicks	108.2	79.1	62.4
D-7	Ditch 10 near Anderson Tully	99.9	76.3	56.2
		120.4	87.7	72.0
D-8	Ditch 10 at Rt 373 bridge	54.1	39.5	32.2
		84.9	67.6	54.0
		94.7	76.3	60.3
		105.1	79.1	59.3
D-10	Ditch 10 at Rt 214 bridge	85.3	59.3	50.0
		90.6	50.3	50.2
		90.8	70.8	60.4
		99.0	75.9	66.0
		109.3	77.3	66.1
D-12	Ditch 10 at Rt 69 bridge	112.4	77.3	62.4
D-14	Ditch 60 & 61 so. of railroad	83.6	61.3	55.8
D-15	Ditch 60 & 61 no. of railroad	28.6	21.2	15.4
		37.0	28.1	21.2
D-16	Ditch 60 at small creek	28.0	20.0	14.0
		30.0	21.0	15.0
		32.4	24.8	19.8
		33.1	26.9	20.5
		34.0	24.0	18.0
		34.0	25.0	18.0
		34.3	26.7	21.7
		36.0	26.0	19.0
		37.5	28.5	22.9
		37.7	28.0	20.9
		38.2	29.4	22.9

## APPENDIX B (cont.)

Site no.	Locality	Length	Height	Thickness
		39.6	30.7	24.0
		40.0	30.6	24.0
		40.2	30.4	24.9
		40.8	30.3	24.4
		40.8	30.9	24.2
		41.0	30.0	21.0
		41.0	30.0	22.0
		42.0	29.0	23.0
		42.1	32.8	24.8
		43.6	32.2	26.1
		44.0	34.8	28.1
		44.3	32.4	24.1
		45.0	32.0	26.0
		46.0	33.0	22.0
		47.0	33.0	26.0
		47.4	36.7	30.3
		49.1	36.3	31.5
		50.1	38.1	31.8
		51.0	36.0	29.0
		51.0	38.0	31.0
		52.0	38.0	30.0
		52.0	40.0	30.0
		52.7	40.5	32.7
		53.0	41.5	34.4
		53.5	40.5	33.3
		54.0	40.0	32.0
		55.0	39.0	32.0
		56.0	40.0	34.0
		56.0	40.0	32.0
		58.0	43.0	33.0
		61.0	43.0	38.0
		62.0	42.0	33.0
		69.7	51.9	42.8
		78.3	57.5	49.9
		87.2	67.2	54.9
		90.0	66.0	53.0
		96.4	70.5	57.5
		111.4	82.4	62.9
D-23	unnumbered above siphons	123.4	93.8	72.5
D-24	unnumbered 2.5 mi. above	123.0	90.2	70.4
D-26	mouth of Iron Mines Cr.	42.7	30.9	24.8
		58.8	44.9	44.6
		88.6	66.3	56.5
		90.0	69.2	57.7
		91.0	67.0	58.7
		95.8	73.2	61.0
		130.8	89.0	68.0
D-27	Iron Mines Cr. 1 mi. up	55.1	44.1	34.8
		61.3	43.5	36.9
		62.1	45.9	37.6

APPENDIX B (cont.)

Site no.	Locality	Length	Height	Thickness
		62.3	46.9	38.9
		69.4	51.7	41.8
		84.5	62.6	54.6
		120.3	89.9	68.5
	Grand means	75.3	55.2	44.8

\* Site visited only during access survey.



GLOSSARY FOR NORTH AMERICAN FRESHWATER MALACOLOGY.  
I. GASTROPODA

J. B. Burch<sup>1</sup>

Many technical terms are found in taxonomic monographs on North American freshwater snails. Without an extensive vocabulary in this specialized subject, any student dealing with freshwater snails is seriously disadvantaged. The glossary below is presented as an aid to freshwater malacology. Included in the glossary are various anatomical terms used in taxonomy, some geographical terms used in species distributions, and certain literary terms found in taxon descriptions. Included also are chemicals commonly used to prepare molluscan specimens for taxonomic study.

- Abaxial.** Directed away from the shell axis (*i.e.*, the central line or central column of a coiled gastropod shell) outward.
- Acroloxid.** A common-name adjective referring to a member of the family Acroloxidae.
- Acteophile.** A common name adjective referring to a member of the pulmonate snail order Acteophila.
- Acuminate.** Having a long, tapering point.
- Acute.** Sharp at the end.
- Acutiform.** Sharply pointed; shell narrow and terminating in a sharply pointed spire.
- Adventitious.** Occurring in an unusual place, as the brood pouch in thiarid snails.
- AFA.** See formalin-alcohol-acetic acid fixative.
- Afferent.** Refers to a blood vessel, siphon or nerve that takes a substance or impulse to the primary organ.
- Albumen gland.** A gland of the female reproductive system that supplies an envelope of nutritive material (albumen) to the egg immediately after the egg is fertilized. In most pulmonate snails, the albumen gland is embedded in the digestive gland just apical to the lung.
- AMNH.** Abbreviation, usually associated with museum specimen catalogue numbers, for the American Museum of Natural History.
- Amnicoline.** A common-name adjective referring to a member of the hydrobiid subfamily Amnicolinae.
- Ampullariid.** A common-name adjective referring to a member of the family Ampullariidae (= Piliidae).
- Ancylid.** A common name adjective referring to a member of the freshwater snail family Ancyliidae.
- Ancyliform.** Limpet-shaped; patelliform; shaped like an obtuse cone.
- Ancyline.** A common-name adjective referring to a member of the ancylid subfamily Ancyliinae.
- Angular, angulate.** Having an angle or having the tendency to form an

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- angle, in contrast to being round.
- Angulation.** Edge along which two surfaces in different planes meet at an angle.
- Annulated.** Marked with differently colored or sculptured rings.
- Annulation.** A ring of different color or form.
- ANSP.** Abbreviation, usually associated with museum specimen catalogue numbers, for the Academy of Natural Sciences of Philadelphia.
- Anterior.** At or towards the head.
- Anterior end of shell.** That part of the shell closest to the snail's head when the animal is active; generally that part of the shell farthest from the apex.
- Aperture.** The opening or "mouth" of a snail shell through which the head-foot protrudes when the snail is active.
- Apex.** The tip of a gastropod shell farthest from the aperture.
- Aphallate.** The condition of lacking a penis, where the possession of a penis would be the normal condition.
- Apical.** Situated at or close to, or referring to, the apex of a snail shell.
- Apical digitations.** In the physine Physidae, the posterior mantle collar digitations that extend onto the parietal wall at the posterior shell aperture. In very short-spined physid snails, the apical digitations extend noticeably close to the shell apex. Also called posterior digitate projections.
- Apical viscera.** The internal organs (*e.g.*, liver; upper parts of the reproductive, renal and digestive systems, etc.) outside the head-foot hemocoel.
- Aplexine.** A common-name adjective referring to a member of the physid subfamily Aplexinae.
- Apophysis** (*pl.* apophyses). A calcareous protuberance or elongate structure, such as that on the inner side of a neritid operculum. It normally consists of two pieces, a short and stout "peg," and a longer and narrower "rib."
- Attenuate.** Slender; elongated; long and slender.
- Auctorum** (abbr. *auct.*). Of authors.
- Auger-shaped.** Shaped like an auger, *i.e.*, with a flattened base terminating in a sharp, pointed twist.
- Auriculated.** Lobed; having a lobe (or ear-like appendage) on each side.
- Axial.** Parallel to the axis or columella of a snail's shell, *i.e.*, transverse to the direction of the shell's spiral coil.
- Axial sculpture.** Surface markings on a snail shell that are parallel to the axis and lip or peristome of the shell and at right angles to the direction of the whorls; transverse sculpture.
- Base** (*adj.* basal). The part of a snail's shell opposite the apex. When a shell is held with the apex directed upward, the base is the "bottom" part of the shell. In regard to the natural position of the shell as carried by the snail, in an elongate shell the "base" is the anterior end.
- Basommatophoran.** A common-name adjective referring to a member of the pulmonate snail order Basommatophora (= Acteophila + Lymnophila).
- Bellamyine.** A common-name adjective referring to a member of the viviparid subfamily Bellamyinae.
- Bicarinate.** Having two carinae or spiral ridges.

- Bicuspid.** Having two cusps (in reference to a radular tooth with two cusps, *i.e.*, cutting projections).
- Bifid.** Divided into halves by a linear sinus, with straight margins.
- Bilobed.** Consisting of two lobes.
- Binomial.** Being composed of two names, *i.e.*, the unique combination of two names given to each animal or plant species: a generic name combined with a specific or trivial name. See zoological nomenclature.
- Biramose.** Having two lateral branches.
- Bipectinate.** Having two margins furnished with outwardly projecting parallel filaments, like the teeth of a double-sided comb.
- Bithyniid.** A common-name adjective referring to a member of the family Bithyniidae.
- Body whorl.** The last complete whorl or volution of a spiral snail shell, measured from the outer lip back to a point immediately above the outer lip; ultimate whorl. The body whorl is normally the largest whorl of the shell and is called the body whorl because it encloses the greatest part of the snail's body.
- Boreal.** Referring to or located in northern regions; northern.
- Boss.** A protuberance; a prominence; a projecting knob or stud.
- Bouin's fluid** (Bouin's picro-formol). A general purpose fixing and preserving fluid consisting of 75 parts by volume of saturated aqueous picric acid, 25 parts formalin, and 5 parts glacial acetic acid.
- Branchia** (*pl.* branchiae). See gill.
- Breathing pore** (pulmonary opening; pneumostome). The opening through which air passes to and from the lung in pulmonate snails.
- Brood pouch.** A sac-like cavity in the body of a female snail in which eggs or embryos are placed and develop.
- Buccal.** Refers to the structures in the anterior part of the alimentary canal that are associated with and assist the radula and jaws, *i.e.*, the musculature, innervation and supporting cartilage.
- Bulbous.** Rounded, globular or pear-shaped; swollen like a bulb.
- Bulimoid.** Shaped like the genus *Bulimus* [*Megalobulimus*] or many members of the land snail family Bulimulidae, in which the body whorl is relatively large, ovate, moderately rounded and not shouldered, the shell aperture is oval, the spire is relatively small, with convex sides and moderately rounded whorls, and the apex is more or less blunt.
- Bursa copulatrix.** A sac-like diverticulum in the female reproductive system close to the gonopore, used to store sperm obtained during mating; also called spermatheca or seminal receptacle.
- Calcareous.** Formed of calcium carbonate (carbonate of lime).
- Callus** (*adj.* callous). A layer of calcareous material on a shell secreted by the snail's mantle.
- Campanulate.** Flared at the end; bell-shaped.
- Canaliculate.** Bearing a channel or groove.
- Cancellate.** Meshed with lines crossing each other (*e.g.*, spiral and transverse lines) forming a lattice-like appearance.
- Carina** (*pl.* carinae). A sharp spiral edge, ridge or "keel" on the outer shell surface.



- Carinate.** Having one or more sharp spiral edges, ridges or keels on the outer shell surface.
- Carrefour.** In the freshwater snail reproductive system, a complex of structures (a juncture of pathways) consisting [*e.g.*, in a lymnaeid snail] of the insemination pocket, oviducal caecum and oviducal labyrinth, and the distal end of the hermaphroditic and albumen gland ducts and the seminal gutter, and the proximal end of the prostate gland duct.
- Central tooth.** The median or rachidian tooth of a transverse row of radular teeth. It is flanked by lateral teeth.
- Channeled.** Bearing a channel or groove.
- Chink.** A narrow slit, cleft or crack at the columellar opening of a snail shell; often formed by the expanded or reflected columellar lip partially covering the narrow umbilicus.
- Chitin.** A hard, amorphous, nitrogenous polysaccharide that forms the base for the cuticle of arthropods and is of limited occurrence in other invertebrates, including mollusks.
- Chitinized.** To become hardened with a chitin-like substance.
- Chitinous.** Formed of or containing chitin, and often or generally brown in color.
- Chloreton** (chlorobutanol;  $C_4H_7Cl_3O$ ). An anesthetizing agent for mollusks and other invertebrates. One gram dissolves in 1 ml of ethanol. It is used as a 1% (by volume) aqueous solution.
- Circumboreal.** Distributed around the boreal regions of the globe; holarctic.
- Class.** A higher taxonomic category or group between the order and phylum in the hierarchy of animal classification. Each class contains one or more orders. The living mollusks are divided into seven classes, the Gastropoda (snails, slugs, limpets), Bivalvia or Pelecypoda (clams, mussels, oysters, scallops, etc.), Scaphopoda (tusk and tooth shells), Aplacophora (*e.g.*, solenogasters), Monoplacophora, Polyplacophora (chitons) and Cephalopoda (squid, cuttlefish, octopusses).
- Clavate.** Club-shaped; growing gradually thicker toward one end.
- Cleaver-like.** Shaped like a butcher's cleaver, *i.e.*, like a short, flat, broad cutting instrument.
- Cochliopine.** A common-name adjective referring to a member of the hydrobiid subfamily Cochliopinae.
- Coil.** A single loop of a circular, spiral turn; to follow a circular, spiral direction.
- Collabral.** Having the same shape as the labrum or outer lip of the shell under examination.
- Color bands.** Revolving spiral stripes of a darker hue or different color from the ground or background color that occur on some species of gastropod shells.
- Columella.** A small column; the internal column around which the whorls revolve; the axis of a spiral shell.
- Columellar digitations.** In the physine Physidae, the anterior mantle collar digitations that extend over the columellar portion of the shell aperture onto the anterior parietal wall of the body whorl; also called columellar-

parietal digitate projections.

**Columellar lip.** The apertural margin at the columellar region of a coiled gastropod shell.

**Compressed.** Refers to the spire of a gastropod shell that is relatively flattened, *i.e.*, is not elongated; depressed.

**Concave.** Curved or rounded inward.

**Concentric.** From the same center; having a central point or nucleus about which succeeding lines, each with a slightly larger circumference, encircle.

**Conchology.** The science dealing with molluscan shells, *i.e.*, the nature and formation of molluscan shells, and the practice of classifying mollusks by their shells; the science dealing with mollusks, especially in a narrow sense, relating mostly to their shells (as opposed to the study of mollusks as whole animals and as biological entities).

**Conical.** Shaped like a cone, *i.e.*, tapering evenly from a wide, circular base to a point.

**Constricted.** Narrowed; compressed; being divided into equal or unequal halves by a groove or depression.

**Continental Divide.** The highland which divides the North American continent into two very large drainage regions, one in which the streams flow generally eastward into the Gulf of Mexico, Atlantic Ocean, Hudson Bay and the Arctic Ocean, and the other in which the streams flow generally westward into the Great Basin, the Gulf of California, the Pacific Ocean and the Bering Sea.

**Contractile.** Capable of reducing length by shortening and thickening, *e.g.*, the tentacles of most acteophile and lymnophile (basommatophoran) snails.

**Convex.** Bulging or rounded outward.

**Corneous.** Resembling horn in color or consisting of a horn-like material.

**Corroded.** Dissolved away by abrasion or chemical action, or both.

**Costa** (*pl.* costae). A transverse rib or rounded ridge of substantial size on the surface of a shell.

**Costate.** Refers to a shell in which the surface is sculptured with heavy, regular transverse ridges or ribs.

**Couplet.** In a taxonomic identification key, two opposing sets of contrasting characters, from which a choice must be made in order to pass on to the next couplet. The object of the taxonomic key is to lead the observer to the correct taxonomic determination for the taxon in question.

**Crassate.** Gross; thick; coarse; neither thin nor fine.

**Crenulate, crenulated.** Notched on the edges.

**Crepidulaform.** Shaped like *Crepidula*, *i.e.*, limpet-like with a small, coiled apex.

**Crescentic.** Shaped like a crescent, or new moon.

**Crop.** A temporary storage area for ingested food formed by the widening of the posterior esophagus.

**Ctenidium** (*pl.* ctenidia). The characteristic respiratory appendage or gill of mollusks.

**Cusp.** The cutting blade or blades projecting from each tooth of the molluscan radula.

**Cylindrical.** Round and elongate with parallel sides; shaped like a cylin-

- der.
- Decollate.** Cut off, *i.e.*, as in the shell of some snails where the top several whorls or the spire break off or erode away.
- Deflected.** Bent downward from the natural plane of growth, as in the terminal part of the last whorl in some snail shells.
- Depauperate.** Condition in which an individual, colony or race exhibits the outward manifestation of disease, accident or malnutrition. See depauperization.
- Depauperization.** The outward manifestations of disease, accident or malnutrition, or a reaction to inimical environment. It affects individual mollusks fairly frequently, but also it sometimes involves whole colonies and races. Symptoms of depauperization are dwarfing, lack of nacreous material (in certain bivalves), loose coiling and simplification of shell characters (Goodrich, 1939, *The Nautilus*, 52(4): 124-128).
- Depressed.** Flattened dorso-ventrally or postero-anteriorly, as the spire of a snail shell.
- Depressed conic.** Designation for a snail shell with a spire angle of about  $100^\circ (\pm 5^\circ)$ ; widely conic.
- Dextral.** Coiled to the right. The direction of coil of a snail's shell can be determined by holding its apex up and its aperture toward the viewer. In such a position, if the aperture is on the right of the columella, the shell is dextral.
- Diameter.** The width of a shell at a right angle to the shell axis or columella. The "diameter" of a shell usually refers to its largest diameter, *i.e.*, as measured at the outer lip to the opposite side of the whorl.
- Dichotomous key.** A taxonomic identification guide that is composed of a series of couplets (statements), each of which opposes the other, giving the reader the choice between two sets of contrasting characters. By successively choosing between the two presented choices of each couplet, and thereby being brought to the next couplet, the reader is led eventually to a name that is the proper identification (if the correct choices were made along the way) for the taxon in question.
- Dichotomy.** A branching which results from the division of one part into two succeeding parts; repeated forking.
- Diffuse.** Widely spread, as certain types of pigment on a snail's body.
- Digitation.** A finger-shaped elongation or protuberance.
- Dilated.** Expanded; spread out; as the adult shell lip of some snail specimens or species.
- Dioecious.** Having separate sexes, *i.e.*, a species with the male sex in one individual and the female sex in another individual; gonochoristic.
- Discoidal.** Round and flat like a disc.
- Disk.** The flat ventral part, or sole, of the gastropod foot (as used in the older literature).
- Distal.** At a distance or more distant from the organ or part under consideration; located at a distance from the origin or point of attachment.
- Diverticulum.** A distally blind tube or sac branching off from a main canal or cavity.
- Dorsal.** The back; the upper side; in non-planate snails, the side opposite the shell aperture or the sole of the foot.

- Dorsoventral.** Refers to the direction or axis from dorsal to ventral; in a snail shell from the apex to the base.
- Early whorls.** The first whorls of a spiral snail shell; the first several whorls of the spire, beginning with the nuclear whorl.
- Eccentric.** Away from the center; positioned off-center, as the nucleus of the operculum of some species; excentric.
- Ecophenotype.** A non-hereditary form or phenotype produced by ecological or environmental conditions.
- Efferent.** Refers to a blood vessel, siphon or nerve that conducts a substance or impulse away from a source.
- Elevated.** Raised or lengthened, as the spire of a shell, in contrast to a species with a more depressed spire.
- Elliptical.** Having the form of an ellipse.
- Elongate.** Lengthened; extending length-wise; especially higher than wide.
- Elongately conic.** Designation for a snail shell with a spire angle of about  $30^\circ (\pm 5^\circ)$ .
- Emarginate.** Bluntly notched, as the shell lip margin; terminating in a notch.
- Embryonic shell.** The shell formed by the embryo; protoconch. The embryonic shell of many species has a different surface sculpture from the shell formed after hatching or settling.
- Emmericiine.** A common-name adjective referring to a member of the hydrobiid subfamily Emmericiinae.
- Encrustation.** See incrustation.
- Entire.** Refers to the lip or peritreme of a shell that forms a continuous circle or oval, *i.e.*, it is not broken by a space where it meets the parietal wall of the body whorl.
- Equidistant.** Equally spaced; having the same interval between objects or structures, as the spiral or transverse sculpture of a shell's surface.
- Esophagus.** The tube through which food passes from the buccal mass to the stomach.
- Evaginate.** To evert; to turn inside out.
- Evert.** To evaginate; to turn inside out.
- Excentric.** Away from the center; positioned off-center, as the nucleus of the operculum of some species; eccentric.
- Expanded.** Spread out; trumpet shaped; as the adult shell aperture of some snail species.
- Extralimital.** Refers to outside the geographical area under consideration.
- FAA.** See formalin-alcohol-acetic acid fixative.
- Family** (*adj.* familial). A taxonomic group of genera sharing certain basic features that set them off from other such groups of genera. (A few families contain only one genus.) The family is a level of classification between the genus and the order. Names of families end in *-idae*.
- Fathom.** A nautical unit of depth (or length). One fathom is equal to six feet or 1.83 meters.
- Fauna.** The animals occupying a given area.
- Ferrissiine.** A common-name adjective referring to a member of the ancylid subfamily Ferrissiinae.
- Filamentous.** Slender, thread-like; filiform.

**Filiform.** Long and slender; thread-like; filamentous.

**Fissure.** A narrow slit.

**Flagellum.** In some Hydrobiidae, *e.g.*, the genus *Amnicola*, a protuberance or lobe on the verge in addition to the penis proper; penial lobe. In *Amnicola*, the flagellum contains a duct from the penial or accessory gland.

**Flattened.** Deviating from being round, and approaching a flat surface. Commonly used to describe shell whorls that diverge from an evenly rounded contour.

**FMNH.** Abbreviation, usually associated with museum specimen catalogue numbers, for the Field Museum of Natural History, Chicago, Illinois.

**Fold.** A structure made by, or appearing to be made by, folding, *i.e.*, a bending of one part over itself; a spiral ridge on the columella.

**Foot.** The muscular ventral part of a snail's body functioning mainly in locomotion; the ventral surface of the foot is the sole.

**Form** (*abbr.* f.). A particular variation or aggregate of variations within a population. The terms "form" or "forms" have some utility in discussing interpopulational variations, but a "form" has no formal standing in our system of zoological nomenclature.

**Formalin.** A widely used zoological fixing and preserving fluid, prepared by mixing formaldehyde [ $\text{CH}_2\text{O}$ ] gas (about 37% by weight) with water. As commercial formalin, such a solution is regarded as 100%. A 10% formalin solution, for example, is 10 parts (by volume) of commercial formalin mixed with 90 parts water. A 10% formalin solution is commonly used as a fixative. A 4% or 5% solution is used for long term preservation. With shelled mollusks, the formalin must be neutralized to prevent dissolution of the calcium carbonate of the shell.

**Formalin-alcohol-acetic acid fixative** (FAA; AFA; Lavdowsky's fluid). A zoological fixative that penetrates and preserves tissues well. After fixation, the fluid is replaced with 65% to 70% ethanol for storage. FAA contains commercial [37% formaldehyde] formalin (10 parts by volume), 95% ethanol (50 parts), glacial acetic acid (2 parts) and distilled water (40 parts).

**Formaldehyde.** An organic chemical ( $\text{HCHO}$ ), the simplest aldehyde, used as a fixative and preservative for biological specimens; formol; methylene oxide.

**Fragile.** Delicate; easily broken.

**Funicular.** Funnel-shaped.

**Furrow.** A shallow groove.

**Fusiform.** Spindle-shaped, *i.e.*, with a relatively thick middle and tapered to a point at each end.

**Gastropod.** A snail; a member of the molluscan class Gastropoda.

**Geniculate.** Having a joint or bend.

**Genital pores.** The separate openings to the outside of the male and female reproductive systems in lymnophile snails; gonopores.

**Genitalis** (*pl.* genitalia). An organ of reproduction, especially the organ used in coitus.

**Genus** (*pl.* genera; *adj.* generic). A basic category of biological classification

above the species level that contains (usually) two or more related species that share certain features. A few genera are monotypic, *i.e.*, contain only one species.

**Gibbous.** Very convex or swollen; tumid.

**Gill** (branchia, *pl.* branchiae). The filamentous outgrowth, usually located within the mantle cavity, serving as the respiratory organ of aquatic mollusks. The basic structure of the molluscan gill ("ctenidium") is characteristic throughout the phylum.

**Gill filament.** One of the leaflets of the gill.

**Gizzard.** A muscular portion of the alimentary canal used to process food.

**Glassy.** Smooth and very glossy; polished; shiny.

**Globose.** Globular or spherical; approaching a globe or sphere in shape.

**Globosely conic.** Designation for a snail shell with a spire angle of about  $80^\circ (\pm 5^\circ)$ .

**Glossy.** Smooth and shining; highly polished.

**Gonochoristic.** Having separate sexes, *i.e.*, a species with the male sex in one individual and the female sex in another individual; gonochoristic; dioecious.

**Gonopore.** An opening of the reproductive system to the outside.

**Gradate.** Arranged in steps, as a spire with shouldered whorls.

**Greatest (or major) diameter.** The greatest diameter of a discoidal shell, as measured from the outermost edge of the outer lip directly across the shell to the opposite periphery of the body whorl (as opposed to minimum diameter, which is measured on the body whorl at the inner (parietal) lip to a point at the shell periphery directly opposite).

**Groove.** A narrow channel in the surface; furrow.

**Growth lines.** Minute lines on the outer shell surface indicating minor rest periods during growth. Not to be confused with the major "rest marks" (called "varices" on snail shells) caused by prolonged growth arrest (as during winter). There are many growth lines on any shell (but only one, several or no varices per whorl).

**Head-foot.** The combined head and foot organ of a snail. The foot (the snail's locomotory organ) anteriorly is in close proximity to and is generally not separated from the snail's head.

**Helicoid.** In the form of a low three-dimensional spiral; with a somewhat depressed spire and whorls that increase regularly in diameter.

**Hemocoel.** An expanded portion of the circulatory system that replaces the true coelom and surrounds various of the snail's internal organs. In gastropods, there are two main hemocoels, one in the head-foot and the other around the viscera.

**Hemocoelic viscera.** The internal organs (*e.g.*, the anterior parts of the digestive system, the terminal genitalia and the central nervous system) located in the hemocoel of the head-foot.

**Hemocyanin.** The copper-containing respiratory pigment in the hemolymph (blood) of most mollusks.

**Hemoglobin.** The iron-containing respiratory pigment in the hemolymph (blood) of most Planorbidae.

**Hemolymph.** The fluid in the tissues, vessels of the circulatory system and hemocoels of mollusks; blood.

- Hermaphroditic.** Having both sexes in the same individual; monoecious.
- High spired.** A shell in which the smaller whorls protrude above (or behind, in the natural position) the larger last or body whorl (in contrast to a discoidal shell, where the spire whorls are even with the body whorl, or are inverted below its margins).
- Hirsute.** Covered with hairs or hair-like processes.
- Holarctic realm.** The zoogeographic region that consists of the combined Palearctic and Nearctic realms.
- Holotype.** The single specimen on which a species is based, and being specifically designated as the "type" by the author, or, if not so designated, being the only specimen before the author when the species was originally described.
- Hyaline.** Glassy; glossy and translucent or nearly transparent.
- Hydrobiid.** A common name adjective referring to a member of the freshwater snail family Hydrobiidae.
- Hydrobiine.** A common-name adjective referring to a member of the hydrobiid subfamily Hydrobiinae.
- Imperforate.** Refers to a spiral gastropod shell that has no opening or external cavity at its base. In such a case, the inner sides of the coiled whorls are appressed, leaving no cavity, or, if they are not appressed and a cavity is formed, then in adult shells its opening is completely covered by a callus or the reflected columellar apertural lip.
- Impressed.** With a distinct groove or furrow, as the suture of some shells; lines below the surface, as the surface sculpture of some shells.
- Inflated.** Swollen; expanded; distended; tumid; in gastropods refers to shells or individual whorls that are bulbous or swollen in appearance.
- Incised.** Grooved; engraved.
- Incrustation (encrustation).** A deposit of material from the habitat, usually inorganic, on the surface of the shell.
- Inoperculate.** Without an operculum; in North American fresh waters, the pulmonate snails (subclass Pulmonata).
- In situ.** in place; in its original place; used in reference to an item or structure that is left or shown in its normal place, *i.e.*, not moved or removed.
- Invaginable.** Capable of withdrawing by being inverted, *e.g.*, the tentacles of geophile (stylommatophoran) snails. Freshwater snails cannot invert their tentacles.
- Inverted.** Turned inward; in a reversed position from normal.
- Keel.** A prominent ridge; a carina.
- Key.** [See "Dichotomous key."]
- Kidney.** The excretory organ; renal organ; nephridium (metanephridium). In a mollusk, the kidney is usually developed from the left urogenital duct and normally lies against the apical wall of the mantle cavity or lung.
- Labial palp.** One of the two velar lobes on either side of the mouth, especially seen in acteophile and lymnophile snails.
- Labium.** The inner or parietal or columellar lip; it extends on the parietal side of the body whorl from the posterior labrum to the basal lip.
- Labrum.** The outer (palatal) part of the mantle collar, or shell apertural lip, of a coiled gastropod, as opposed to the parietal mantle or umbilical lip and the basal (anterior) mantle or shell lip.

- Laevapecine.** A common-name adjective referring to a member of the ancyliid subfamily Laevapecinae.
- Lamella** (*pl.* lamellae). A calcareous plate, blade, "tooth" or scale-like structure.
- Lamellate** (lamellar, laminate). Formed in thin plates, composed of thin plates or covered with them.
- Lamina.** A thin leaf-like structure or tissue.
- Lancine.** A common-name adjective referring to a member of the lymnaeid subfamily Lancinae.
- Lateral teeth.** The teeth on each side of the central or rachidian tooth in a transverse row of radular teeth.
- Large** (in reference to shell size). A term used to refer to a snail shell that is more than 30 mm in length or diameter.
- Last whorl.** The terminal whorl on a snail shell, and on North American freshwater snails, it is the largest whorl; the body whorl.
- Lateral teeth.** The teeth on each side of the central or rachidian tooth in a transverse row of radular teeth.
- Lectotype.** One of the syntypes of a species that is later selected (usually by a different author) to serve as the "type."
- Length.** The longest dimension of an object. In snail shells, the length is measured along the shell's columellar axis, and is a term used mainly in regard to elongate shells.
- Limpet.** A snail with an uncoiled shell, shaped like a low, obtuse cone. In North America, a member of the family Ancyliidae or the family Acroloxidae. A few limpet-shaped species occur in the Lymnaeidae and the Planorbidae.
- Limpet-shaped.** Flattened, cup- or cap-shaped, or shaped like a very obtuse cone; ancyliiform.
- Lioplacine.** A common-name adjective referring to a member of the viviparid subfamily Lioplacinae.
- Lip.** Edge of the aperture of a shell; peristome; peritreme.
- Lira** (*pl.* lirae). A large ridge, specifically a spiral ridge, on the outer surface of a snail shell.
- Lirate.** Refers to a shell with lirae or spiral ridges on its external surface.
- Lithoglyphine.** A common-name adjective referring to a member of the hydrobiid subfamily Lithoglyphinae.
- Liver.** A name often used for the digestive or mid-gut gland in snails, so-called because of its appearance and its close proximity to the stomach and intestine. Since it does not function like a vertebrate liver, a more appropriate name is digestive gland.
- Longitudinal.** Refers to shell sculpturing that is at right angles to the spiral direction of the shell's coil; transverse.
- Lunate.** In the shape of a half-moon; crescent-shaped.
- Lung.** An internal, vascularized space used for respiration, formed from, or an extension of, the mantle cavity. All members of the large gastropod subclass Pulmonata possess a lung (pulmonary cavity).
- Lymnaeid.** A common name adjective referring to a member of the freshwater snail family Lymnaeidae.
- Lymnaeine.** A common-name adjective referring to a member of the lym-



naeid subfamily Lymnaeinae.

**Lymnophile.** A common-name adjective referring to a member of the pulmonate snail order Lymnophila. This group includes all of the freshwater pulmonate snails.

**Major diameter.** The widest diameter of a snail's shell as measured from the outer apertural lip to the outer edge of the body whorl opposite the aperture; greatest diameter. When only the single word "diameter" is used in giving a shell's measurement, it is always the major diameter. See diameter.

**Malacology.** The science dealing with mollusks, *i.e.*, members of the phylum Mollusca.

**Malleated.** Dented as if hit by a hammer.

**Mantle.** The skin covering the apical viscera of a mollusk. Also called pallium. It is an extension of the dorsal body wall as a fold (or, in bivalved mollusks, a pair of folds) that usually secretes a shell and encloses a mantle cavity, typically containing gills. The mantle normally lies next to and under the shell.

**Mantle collar.** The edge of the mantle, often thickened, that lies next to and under the apertural lip of a snail's shell; sometimes called peristomal collar.

**Mantle digitations.** In the physine Physidae, finger-like or triangular lobes of the mantle collar that extend onto the parietal wall of the shell when the snail is active. The anterior lobes are called columellar or collumellar-parietal digitations and the posterior lobes are called apical or posterior digitations.

**Mantle lobe.** In freshwater pulmonate snails, a flexible, flap-like structure under the mantle collar that can be rolled into a tube for breaking the water surface and admitting air into the lung; also called siphon and, loosely, "pneumostome."

**Mantle margin.** The edge of the mantle or pallium, the characteristic outer fold of integument covering the body of mollusks. In snails, the mantle margin is adjacent to the shell aperture.

**Marginal.** At or toward the outer edge, *e.g.*, the margins of the molluscan radula. The teeth at the radular margins, often having their own distinctive morphology, are called "marginal teeth."

**Matrix.** The ground substance of a structure, organ or tissue.

**MCZ.** Abbreviation, usually associated with museum specimen catalogue numbers, for the Museum of Comparative Zoology, Harvard University.

**Median cusp.** The middle cusp of a molluscan radular tooth, generally flanked by smaller lateral cusps.

**Median tooth.** The central or rachidian tooth of a transverse row of radular teeth. It is flanked by lateral teeth.

**Medium** (in relation to shell size). A term used to refer to a snail shell that is 10-30 mm in largest dimension (length or diameter).

**Melanin.** Black pigment.

**Menthol** [C<sub>10</sub>H<sub>20</sub>O]. An anesthetizing agent for mollusks, obtained from mint oils or prepared synthetically. It is used by floating a few crystals on the surface of the water containing the snails. Menthol is only slightly soluble in water.

- Micromelaniid.** A common-name adjective referring to a member of the family Micromelaniidae.
- Minimum (or minor) diameter.** The smallest diameter of a discoidal shell, measured on the body whorl at the inner (parietal) lip to a point at the shell periphery directly opposite (as opposed to the major diameter, which is measured from the outermost edge of the outer lip directly across the shell to the opposite periphery of the body whorl).
- Minute** (in relation to shell size). A term used to refer to a snail shell that is less than 3 mm in length (for an elongate shell) or width (for a depressed shell that is wider than high).
- Monoecious.** Having both sexes in the same individual; hermaphroditic.
- Monotypic.** A taxon (e.g., genus, family) consisting of only one species.
- Mottled.** Irregularly covered with spots or marks of different sizes and shapes; blotched.
- Mouth.** The anterior opening of the digestive tract; the aperture of a snail's shell.
- Mucin.** A glycoprotein that is the one of the main constituents of mucus.
- Mucus** (*adj.*, mucous). A viscous, lubricating fluid secreted by glands, consisting mainly of mucin and water.
- Multispiral.** Refers to an operculum in which there are numerous, very slowly increasing spirals, coils or whorls.
- Narrowly conic.** Designation for a snail shell with a spire angle of about  $20^\circ (\pm 5^\circ)$ .
- Narrowly subovately conic.** Designation for a snail shell with a spire angle of about  $40^\circ (\pm 5^\circ)$ .
- Neanic.** The adolescent, pre-adult stage, from hatching to the beginning of adulthood; nepionic.
- Nearctic realm.** The zoogeographic region that consists of all of North America (including Greenland) south to central Mexico.
- Neck.** The posterior termination of the head.
- Nembutal** (sodium pentobarbital;  $C_{11}H_{17}N_2NaO_3$ ). A narcotizing agent for mollusks and other animals, used in various aqueous concentrations, depending on the species being studied and the preferences of the researcher.
- Neoplanorbine.** A common-name adjective referring to a member of the planorbid subfamily Neoplanorbinae.
- Nephridial pore; nephridiopore; renal pore.** The opening of the renal system to the outside.
- Nephridium.** The tubular renal organ of mollusks and various other invertebrates; kidney.
- Nepionic.** Juvenile; post-embryonic and pre-adult; neanic.
- Neritid.** A common-name adjective referring to a member of the family Neritidae.
- Neritiform.** Shaped like *Nerita*, i.e., subglobose or hemispherical, with rapidly enlarging whorls, very reduced spire, and a heavily calloused and expanded parietal apertural margin.
- Nidamental gland.** A glandular structure in the female reproductive system that secretes covering material for eggs or egg masses.
- Nodule.** A small prominence or knob.

**Nomenclature.** [See "Zoological nomenclature."]

***Nomen dubium*** (pl. *nomina dubia*). A dubious name; one that cannot be applied with certainty to any known taxon.

***Nomen nudum*** (pl. *nomina nuda*). A newly introduced species name without sufficient description to justify its acceptance in the zoological literature.

***Nomen oblitum*** (pl. *nomina oblita*). A forgotten name. A name that has not been used as a senior synonym in the primary zoological literature for more than 50 years. Such a name lacks validity in zoological nomenclature.

**Nominal.** Existing in name only, e.g., a "species" named for a minor growth or ecological form of an already named species; any species name, without regard to the biological validity of the species.

**Non-planate.** Not flattened; having an everted spire; high spired, in contrast to the flattened or inverted spire of the shell of the discoidal (planate) Planorbidae.

**Nuchal.** An adjective referring to the neck region (hence sometimes meaning simply an anterior region).

**Nuclear whorl(s).** The first whorl(s) of a shell, formed by the embryo; embryonic whorl(s); protoconch. The nuclear whorls often have a surface sculpture differing from that of the rest of the shell.

**Nucleus.** The first-formed (earliest) part or beginning of a shell or operculum.

**Nymphophiline.** A common-name adjective referring to a member of the hydrobiid subfamily Nymphophilinae.

**Oblique.** Slanting, as some ridges that are not parallel to the concentric growth lines; greater or less than a right angle; neither parallel with nor perpendicular to.

**Obsolete.** Rudimental; poorly developed; obscure; indistinct; atrophied.

**Obtuse.** Blunt or rounded at the end, not acute or pointed.

**Opaque.** Not emitting or transmitting light; neither translucent nor transparent.

**Operculigerous lobe.** The lobe on the posterior dorsal surface of the foot of prosobranch snails that secretes and bears the operculum.

**Operculate.** A snail bearing an operculum to close the aperture when the snail has withdrawn into its shell; in North American fresh waters, a member of the subclass Prosobranchia.

**Operculum** (pl. *opercula*). A corneous or calcareous plate borne on the dorsal posterior foot of prosobranch snails that closes the aperture when the snail withdraws into its shell.

**Order** (*adj.* ordinal). A higher taxonomic category or group between the family and class in the hierarchy of animal classification. Each order contains a group of families related to one another by common morphological characteristics.

**Osphradium.** Chemical sense organ of freshwater snails.

**OSUM.** Abbreviation, usually associated with museum specimen catalogue numbers, for the Museum of Zoology, Ohio State University.

**Outer lip.** The outer or palatal edge of the shell aperture.

- Oval, ovate.** In the shape of the longitudinal section of a hen's egg, *i.e.*, oblong and curvilinear, with one end narrower than the other.
- Ovate-conic.** Oval in shape, and somewhat conically elongated.
- Ovatly conic.** Designation for a snail shell with a spire angle of about  $60^\circ (\pm 5^\circ)$ .
- Oviduct.** The tube through which the eggs travel from the ovary or ovotestis to reach the outside of the snail; uterine duct.
- Oviparous.** Laying eggs that develop and hatch externally. See also ovo-viviparous and viviparous.
- Ovotestis.** A gonad that produces both eggs (ova) and sperm within the same acinus, often, or usually, simultaneously. Such a gonad is a characteristic of all pulmonate snails, and differentiates them from nearly all prosobranchs.
- Ovoviviparous.** Condition in which young snails are formed within eggs inside the mother snail, but hatch after they are laid, *i.e.*, the eggs are laid with already well developed infant snails within the egg shell or membranes. Also commonly used simply for giving birth to live young. See viviparous and oviparous.
- Oxalic acid** [ $C_2H_2O_4$ ]. A poisonous, weak organic acid used for removing natural incrustations on the shells of mollusks. Oxalic acid is found in the cell sap of many plants, including *Oxalis*, from which it gets its name. Oxalic acid should be used with caution, because it is caustic and corrosive to skin and mucous membranes.
- Pagoda-like.** Shaped like a pagoda, *i.e.*, with a tapering, tower-like, storied, carinate shell spire.
- Palatal.** Pertaining to the outer lip or terminal part of the body whorl of a snail shell.
- Palaearctic realm.** The zoogeographic region that includes Europe, the Near East, Africa, Asia south to the Himalayas, and some islands (Iceland, Canary Islands, Cape Verde Islands, Japan).
- Pallium.** The skin covering the apical viscera of a mollusk. Also called mantle. It is an extension of the dorsal body wall as a fold (or, in bivalved mollusks, a pair of folds) that usually secretes a shell and encloses a mantle cavity, typically containing gills. The pallium normally lies next to and under the shell.
- Parallel.** Equidistant apart throughout the length, *e.g.*, the growth lines of most snails' shells; the growth lines may be curved, but throughout their length they are equidistantly apart.
- Paratype.** A specimen of the type series in addition to the holotype that was before the author at the time the species was described, where a "type" or holotype was designated.
- Parietal.** That part of the body whorl of a snail shell that is near and adjoins the columellar lip of the aperture; pertaining to the inner wall of the shell aperture.
- Parthenogenetic.** The condition whereby a female animal, for example, a female snail, can produce eggs that hatch and develop without being fertilized by sperm.
- Patelliform.** Limpet-shaped; ancyliiform; shaped like an obtuse cone.
- Paucispiral.** Refers to an operculum in which there are few rapidly enlarg-

ing spirals, coils or whorls.

**Peg.** The shorter and stouter part of the two pieces comprising the apophysis on the inner surface of the operculum of the Neritidae. The longer and narrower projection is called the "rib."

**Pellet compressor.** A muscular segment of the intestine that compresses fecal material.

**Penial lobe.** In some Hydrobiidae, *e.g.*, the genus *Ammicola*, a protuberance or lobe on the verge in addition to the penis proper; flagellum. In *Ammicola*, the penial lobe contains a duct from the penial or accessory gland.

**Penial retractor muscle.** One of the muscles that introverts the penis in a pulmonate snail following copulation.

**Penis.** The male copulatory organ. In pulmonate snails, it is an introvert, which is everted when functioning, but it is usually described and illustrated when introverted.

**Penis sheath.** A wall around the penis or penial complex that is distinct (and separated) from the muscular walls of the penis.

**Penultimate whorl.** The next to last complete whorl or volution of a spiral snail shell. The penultimate whorl immediately precedes the ultimate whorl.

**Perforate.** Refers to a spiral gastropod shell that has a very narrow perforation at its base, formed where the inner sides of the coiled whorls do not join.

**Periostracal rib, ridge or spine.** A projection, *e.g.*, a "rib," ridge or spine, on the shell surface composed of periostracal material rather than shell (calcareous) material.

**Periostracum** (*adj.* periostracal). The thin proteinaceous external layer covering most mollusk shells.

**Periphery.** The edges of a shell as seen in outline; the part of the whorls farthest from the shell's axis of coiling.

**Peristomal collar.** The edge of the mantle, often thickened, which lies next to and under the apertural lip of a snail's shell; mantle collar.

**Peristome.** Around the mouth. Conchologically, the edge of the aperture (peritreme) of a snail shell; anatomically, the area around the snail's mouth.

**Peritreme.** The peristome, apertural "lip" or apertural margin of a gastropod shell. (Does not include the parietal wall in shells without an entire (continuous) apertural margin.)

**Phallate.** In the form of, or shaped like, a phallus; the normal condition of possessing a penis (in contrast to aphally, where the penis that would ordinarily be present is absent).

**Physid.** A common name adjective referring to a member of the freshwater snail family Physidae.

**Physine.** A common-name adjective referring to a member of the physid subfamily Physinae.

**Physoid.** Shaped like the shell of a member of the family Physidae, *i.e.*, sinistral and with a raised spine.

**Pilid.** A common-name adjective referring to a member of the family

- Pilidae** (*syn.* Ampullariidae).
- Plait.** A fold or strong twist on the columella in some snail species, caused by the twisting of the columella.
- Planate.** Flattened; flattened on both sides, *i.e.*, without an everted spire; the form of the shell in the discoidal Planorbidae.
- Planispiral.** Coiled in one plane.
- Planorbid.** A common name adjective referring to a member of the freshwater snail family Planorbidae.
- Planorbine.** A common-name adjective referring to a member of the planorbid subfamily Planorbinae.
- Planorboid.** Shaped like a planorbid snail; planispiral; disk-shaped.
- Pleurocerid.** A common name adjective referring to a member of the freshwater snail family Pleuroceridae.
- Plica** (*pl.* plicae). A transverse or "vertical" ridge or "rib" on the outer shell surface.
- Plicate.** Bearing plicae, which are transverse or "vertical" ribs on a shell.
- Plicate-striate.** Refers to a shell having longitudinal (transverse) folds or ribs on its surface that are crossed by raised spiral lines.
- Pneumostome.** The opening from the outside into the respiratory cavity (pulmonary cavity; lung) of a pulmonate snail; breathing pore. The pneumostome usually has a sphincter muscle to close it.
- Pomatiopsid.** A common-name adjective referring to a member of the family Pomatiopsidae.
- Ponderous.** Very heavy; very thick.
- Posterior.** Towards the rear. In gastropod anatomy, posterior usually means toward the apical end of the viscera.
- Posterior end of shell.** The end of a snail's shell opposite to that in which its head normally points when the animal is active. In an elongate or high-spired shell, the posterior end is the apical end.
- Postintestine.** The distal part of the intestine; in snails, because of their torsion, it is the anterior-most part of the intestine.
- Preoccupied.** A term used in zoological nomenclature for the scientific name of a taxon that has been used earlier as the name of a different taxon.
- Preputium.** In the reproductive system of lymnophile snails, the most distal tubular part of the male intromittent complex, terminating at the male gonopore. It is a thin-walled, sac-like structure next distal from the penis/penis sheath. The preputium is everted during copulation.
- Prointestine.** The proximal part of the intestine, near the stomach; in snails, because of their torsion, it may be the posterior-most part of the intestine.
- Proboscis.** The anterior extension of the head on prosobranch snails that bears the mouth at its tip. Also called rostrum or snout.
- Prosobranch.** A common name adjective referring to a member of the gastropod subclass Prosobranchia. As a result of torsion, these snails have their gill (ctenidium) in front of the heart, as opposed to the opisthobranch gastropods (detorted) and other mollusks, which have their gills behind the heart.

- Prostate gland.** A gland of the male reproductive system that adds seminal fluid to the masses of passing sperm during mating.
- Protoconch.** The first whorl(s) of a shell, formed by the embryo; embryonic whorl(s). The protoconch often has surface sculpture differing from that of the rest of the shell (*i.e.*, the teleconch).
- Proximal.** Near the organ or part under consideration; nearest the origin or point of attachment.
- Pseudobranch.** A "false" or secondarily derived gill; a vascularized, fleshy outgrowth near the opening to the pulmonary cavity (pneumostome) of aquatic pulmonate snails which aids in respiration. Not a true ctenidium.
- Pseudodextral.** See Ultrasinistral.
- Pseudosinistral.** See Ultradextral.
- Pulmonate.** A common-name adjective referring to a member of the gastropod subclass Pulmonata. These snails have a lung as a respiratory organ rather than the gills that characterize the other two gastropod subclasses.
- Pyriform.** Pear-shaped, *i.e.*, large and round at one end and tapering at the other end.
- Quadrilateral.** Having four sides and four angles.
- Race.** A geographically or ecologically isolated group of individuals or populations that differ in one or more characters from other individuals or populations of the same species in other locations; a subspecies.
- Radiating.** Extending outward from a common center, as the "spiral" sculpture of an ancyliid shell.
- Radula** (*pl.* radulae). A rasp-like structure in the anterior end of the digestive tract of all mollusks except pelecypods that is used to scrape food off surfaces and into the mouth during feeding. The radula consists typically of a number of longitudinal and transverse rows of minute sharp "teeth," each with one or more cutting blades or "cusps."
- Rhipidoglossan radula.** A type of prosobranch radula with rows of numerous, narrow, hooked teeth radiating out like sections of a fan. This type of radula exhibits a large number of marginal teeth, and is characteristic of the non-limpet Archaeogastropoda and the Neritacea.
- Reflected.** Turned outward, *e.g.*, a portion of the apertural lip of some snails' shells.
- Rest mark.** A darker or thicker part of the shell characteristically formed during a rest period in growth.
- Reticulate.** Having lines crossing each other like a network; constructed like the meshes of a net.
- Revolving lines.** A term sometimes used for spiral striae; occasionally also called "spirals."
- Rhomboidal.** Having the shape of a rhomboid, *i.e.*, quadrilateral with opposite sides and angles equal, but neither equilateral nor equiangular.
- Rib.** A transverse elevation or ridge of significant size on the surface of a shell; costa. In regard to the operculum of the Neritidae, the rib is the longer and narrower part of the two pieces comprising the apophysis on the inner opercular surface.
- Riblet.** A small rib.
- Ridgelet.** A small transverse ridge on a snail shell.

- Rimate.** Refers to a coiled gastropod shell that has at its base a rather narrow "umbilical" opening that is partially closed by the expansion of the anterior columellar lip.
- Rissooid.** A common-name adjective referring to a member of the superfamily Rissooidea (*syn.* Truncatelloidea).
- Rostrum.** The anterior extension of the head on prosobranch snails that bears the mouth at its tip. Also called proboscis or snout.
- Rounded.** Having a more or less evenly curved contour, in contrast to being angular.
- Rudimentary.** Vestigial; not or barely functional in one species as contrasted to being developed in others.
- Sarcobellum.** In lymnophile snails, a fleshy ring around the outlet of the penis sheath, or an extension of the distal end of the penis sheath into the preputium.
- Scalar.** Pertaining to or like a flight of steps, *i.e.*, a shell with elevated spire formed of right-angular whorls.
- Scalariform.** Shell form, usually pathologically produced, in which the whorls are disjoined or tend to become so.
- Sclerotized.** Hardened.
- Sculpture.** The natural surface markings, other than those of color, usually found on snail shells, and often furnishing identifying marks for species recognition.
- Seminal receptacle.** A sac-like diverticulum in the female reproductive system at the head of the oviduct used to receive sperm obtained during mating; sometimes also used for the spermatheca or bursa copulatrix, which is a diverticulum near the female gonopore.
- Seminal vesicle.** A sac-like (or differently shaped) structure in the male reproductive system used to store sperm until they can be discharged during mating.
- Sensu lato** (abbr. *s.lat.* or *s.l.*). In the broad sense.
- Sensu stricto** (abbr. *s.str.* or *s.s.*). In the strict sense.
- Serrated.** Notched on the edge.
- Serpentine.** Resembling a serpent; moving in a winding fashion, turning one way and the other, like a serpent.
- Sexually dimorphic.** Males and females of the same species being morphologically different.
- Shallow.** Having little depth; hardly or little indented.
- Sheen.** Luster; gloss; brightness.
- Shell.** The hard outside protective covering of most mollusks, produced by the mantle and composed primarily of calcium carbonate crystals deposited in an organic matrix. In snails, the shell is usually coiled, and it provides characters for species identification and classification.
- Shell mouth.** The opening or aperture of a snail shell through which the head-foot protrudes when the snail is active.
- Shoulder.** A bend in the curvature of a snail shell at the periphery just below (anterior to) the suture, which resembles a human shoulder in shape.
- Shouldered.** Refers to the appearance (in outline) of the posterior outer peripheral part of a whorl that is sharply rounded in contrast to the more



- even curvature of the rest of the shell.
- Sic.* Thus (to indicate exact transcription).
- Sigmoid.** S-shaped; in the shape of the letter S; sinuous.
- Sinistral.** Coiled to the left. The direction of coil of a snail's shell can be determined by holding its apex up and its aperture toward the viewer. In such a position, if the aperture is on the left of the columella, the shell is sinistral.
- Sinuate, sinuous.** Having the edge alternately curving inward and outward; wavy or S-shaped.
- Sinus.** A recess, indentation or embayment.
- Siphon.** In freshwater pulmonate snails, a flexible, flap-like structure under the mantle collar that can be rolled into a tube for breaking the water surface and admitting air into the lung; also called mantle lobe and, loosely, "pneumostome." In freshwater prosobranch snails, the siphon is the modified and extended left-anterior edge of the mantle that facilitates water flow into the mantle cavity.
- Siphonal canal.** A tubular extension of the anterior aperture on some prosobranch snail shells that encloses the siphon. A siphonal canal is especially characteristic of the prosobranch order Neogastropoda.
- S.lat. or s.l.* See *sensu lato*.
- Slough.** A muddy, water-filled depression; a swamp or marsh.
- Small** (in reference to shell size). A term used to refer to a snail shell that is more than 3 mm in length (or diameter for a shell with a depressed spire), and less than 10 mm.
- Snail.** A member of the molluscan class Gastropoda. Gastropods all undergo torsion, *i.e.*, a developmental process during early embryology in which the viscera, mantle and mantle cavity are twisted 180° in relation to the head-foot. Most snails are characterized by possessing a spirally coiled external shell consisting largely of calcium carbonate and used for protection.
- Snout.** The anterior extension of the head on prosobranch snails that bears the mouth at its tip. Also called proboscis or rostrum.
- Sole.** The flat ventral part of a snail's foot (called the "disk" in older literature), on which the snail crawls during locomotion.
- Solid.** A term applied to snail shells that are thick and strong.
- Spade-shaped.** Shaped like a spade, *i.e.*, like a broad, flat blade tapering rapidly at one end.
- Spatulate.** Shaped like a spoon; having a broad, rounded apex and tapering to the opposite end.
- Species** (*pl.* species; *adj.* specific). A taxonomic group comprising the same "kinds" of closely related individuals potentially able to breed with one another, and unable to breed with other "kinds."
- Spermatheca.** An organ at the end of the apex of the vagina in the female genital system for storage of sperm received from the mating partner. Also called bursa copulatrix or seminal receptacle.
- Spermatophore.** A bundle or packet of sperm.
- Spindle-shaped.** Shaped like a spindle, *i.e.*, with a relatively thick middle and tapered to a point at both ends; fusiform.

**Spines.** Sharp, pointed projections extending outwardly from the surface of some snail shells.

**Spiral.** Winding, coiling or circling obliquely around a central axis, so as to resemble a spire; winding around a fixed point and continually receding from it; the form of the shell of most snails.

**Spiral sculpture.** Surface markings on a snail shell that follow the direction of the shell's spiral and pass continuously around the whorls more or less parallel to the suture.

**Spire.** The whorls of a snail shell, excepting the last or body whorl. The spire is measured as the distance (parallel to the columella) from the suture where the apertural lip meets the body whorl to the shell apex.

*S.str.* or *s.s.* See *sensu stricto*.

**Stomach.** The muscular enlargement of the alimentary tract between the esophagus (or crop) and the intestine; gizzard. The stomach (gizzard) lies in the apical viscera.

**Stria** (*pl. striae*). A slight superficial spiral groove or fine furrow on the outer shell surface, or a fine spiral threadlike line or streak. Commonly used also, in a less precise sense, for raised spiral threads on the shell surface.

**Striate.** Refers to a shell having fine, spiral, incised lines or striae on its surface. Also used, less precisely, for shells with spiral raised lines, or for shells covered with fine transverse lines.

**Stylet.** A chitinous or calcareous dagger-like tip on end the penis of some snails.

**Subcentral.** Not quite central; off-center.

**Subclass.** A higher taxonomic category or group between the class and order in the hierarchy of animal classification. Subclasses are used when it is necessary to divide a class into more than one group of orders. In the class Gastropoda (snails, slugs, limpets), the subclasses are the Prosobranchia (gill breathers, with the gills anterior to the heart), Opisthobranchia (generally gill breathers, with the gills, when present, posterior to the heart) and Pulmonata (lung breathers).

**Subfamily** (*adj. subfamilial*). A taxonomic category or group between the genus and family in the hierarchy of animal classification. Subfamilies are used when it is necessary to divide a family into more than one group of closely related genera. The subfamily is therefore a subordinate category to the family. Each subfamily contains one or more genera. Names of subfamilies end in *-inae*.

**Subgenus** (*pl. subgenera; adj. subgeneric*). A taxonomic category or group between the species and genus in the hierarchy of animal classification. Subgenera are used when it is necessary to divide a genus into more than one group of closely related species. The subgenus is therefore a subordinate category to the genus. Each subgenus contains one or more species.

**Subglobose.** Not exactly globular or spherical in shape, but approaching such a form.

**Subglobosely conic.** Designation for a snail shell with a spire angle of about  $70^\circ (\pm 5^\circ)$ .

**Subobsolete.** Hardly visible.

**Subovate.** Not exactly oval in shape, but approaching such a form.

- Subovately conic.** Designation for a snail shell with a spire angle of about  $50^\circ (\pm 5^\circ)$ .
- Subspecies** (*pl.* subspecies; *adj.* subspecific; *syn.* race, variety). One or more populations of a species that inhabit a distinct geographic area and that share morphological features setting them off from other populations of the species.
- Succiniform.** *Succinea*-like, *i.e.*, with a thin and fragile shell, which has a large oval aperture and body whorl and a small spire.
- Superfamily.** A taxonomic category or group between the family and order in the hierarchy of animal classification. Superfamilies are used when it is necessary to divide an order into more than one group of closely related families. Names of superfamilies end in *-oidea* (although it also has been common practice in malacology to use the ending *-acea*).
- Suture.** The external line on the shell where the surfaces of two adjacent whorls meet.
- Synonym.** A name for something that has another name; in zoological nomenclature, one of two or more names for the same taxon (species, genus, etc.). The earliest name is the "senior synonym" and has priority. The more recent name is a "junior synonym" and is rejected for nomenclatural purposes.
- Synonymy.** A list of synonyms. In taxonomy, a synonymy is a list of scientific names, in chronological order (with authors and dates, and generally with bibliographic references, including volume, page and figure numbers) that have been used (either correctly or as misidentifications) for a particular taxon.
- Syntype.** One of two or more specimens examined by the author of a species when the species was first described, where the author did not specifically select one of the specimens as the "type" or holotype. Syntype specimens of any particular species have equal nomenclatural rank.
- Taenioglossan radula.** A type of prosobranch radula characterized by having seven teeth in each transverse row: a central tooth flanked by two inwardly directed lateral teeth and two pairs of outwardly directed marginal teeth. This type of radula characterizes the order Mesogastropoda.
- Tail.** The posterior end of the foot in a land snail.
- Taxon** (*pl.* taxa). Any taxonomic group, *e.g.*, a subspecies, species, genus, family, order, etc.
- Taxonomic key.** A device, using "key characters," whose object is the identification of taxa (as simply as possible). This is accomplished by recognizing, separating and segregating key characters of the taxa under consideration and arranging the characters into sets of two (dichotomous) characters that give the reader a succession of alternative choices, leading eventually to a taxon (species, genus, family, etc.) name, which is the name of the object under consideration.
- Teleconch (teleoconch).** All of the whorls of a snail shell formed after the protoconch.
- Tentacle.** One of a pair of elongated, flexible organs on the head of snails used for feeling, or tasting or smelling, or for sensing light. Geophile snails have two pairs of tentacles, with an eye at the tip of each tentacle of the

- larger, upper pair. The freshwater snails have one pair of tentacles, with an eye at the base of each tentacle.
- Tessellate; tessellation; tesselloid.** Formed into or of squares (tessellae; tesserae); checkered.
- Thiarid.** A common-name adjective referring to a member of the family Thiariidae.
- Tongue-shaped.** Shaped like a tongue, *i.e.*, elongate and bluntly round at the end.
- Tooth** (*pl.* teeth). A hard, sharp, chitinous projection of the molluscan radula that tears away or punctures the food surface, or is modified for food capture. Also, a hard, calcareous nodule or projection in or around the aperture of the shell of some snail species (*e.g.*, *Planorbula armigera*) that functions to restrict entry into the shell by predators. Also called a barrier.
- Topotype.** A specimen of the nominal species collected at the type locality at a later time than the holotype, paratype(s), or syntypes were collected.
- Torsion.** In gastropods, the 180° twisting of the visceral mass in relation to the head-foot. Early gastropod embryos are untorted, then undergo torsion in later larval development. Torsion is the prime characteristic used in defining the molluscan class Gastropoda.
- Translucent.** Partially transparent; allowing diffused light to be transmitted.
- Transparent.** Clear; transmitting light without scattering, so that structures lying beyond are clearly visible.
- Transverse.** At right angles to the spiral direction of the whorls; parallel to the columella or axis of the shell; in the same direction (*i.e.*, parallel to) the growth lines of a snail shell.
- Transverse sculpture.** Surface markings on a snail shell that are parallel to the axis and lip of the shell and at right angles to the direction of coiling of the whorls; axial sculpture.
- Trapezoidal.** Having a quadrilateral shape, no two sides of which are parallel.
- Tricuspid.** Having three cusps (in reference to a radular tooth with three cusps, *i.e.*, cutting projections).
- Trifid.** Divided into three parts, or terminating in three elongated projections.
- Truncate, truncated.** Having the end cut off more or less squarely; terminating abruptly; ending in a transverse line.
- Truncatelloid.** A common-name adjective referring to a member of the superfamily Truncatelloidea (= Rissoidae).
- Tubercle.** A nodule or small eminence, such as a solid elevation occurring on the shell surface of some gastropods.
- Tuberculate.** Covered with tubercles or rounded knobs.
- Tumid.** Swollen or enlarged.
- Turbinate, turbiniform.** Shaped like a turban; refers to a shell in which the whorls decrease rapidly in diameter and taper broadly from a circular base to the apex.
- Turreted.** Shaped like a tower.
- Type species.** The one particular species on which a nominal genus or

subgenus is based, and is either the only species in the nominal genus or subgenus, or is specifically designated as the "type species" of the nominal genus or subgenus.

**Type specimen.** The specimen, nearly always housed in a museum (and usually in a large, well-known one), on which a species or subspecies name is based; holotype.

**Type locality.** The geographic locality at which a holotype or the syntypes were collected. In older literature, the type locality was often imprecise.

**Typhlosole.** A longitudinal invagination of the intestinal wall that functions to increase absorptive area.

**UF.** Abbreviation, usually associated with museum specimen catalogue numbers, for the Florida Museum of Natural History, University of Florida.

**Ultimate whorl.** The last complete whorl or volution of a spiral snail shell, measured from the outer lip back to a point immediately above the outer lip; body whorl. The ultimate whorl is normally the largest whorl of the shell.

**Ultradextral.** A descriptive term applied to a species that, because of the shape of its shell aperture or the inversion of its "spire" and relatively less inversion (or eversion) of its basal (or "umbilical") whorls, appears to be sinistral, but has a dextral body (*i.e.*, the distal openings of the digestive, renal, reproductive [and respiratory systems in pulmonate snails] are on the right side); pseudosinistral; hyperstrophic.

**Ultrasinistral.** A descriptive term applied to a species that, because of the shape of its shell aperture or the inversion of its "spire" and relatively less inversion (or eversion) of its basal (or "umbilical") whorls, appears to be dextral, but has a sinistral body (*i.e.*, the distal openings of the digestive, renal, reproductive [and respiratory systems in pulmonate snails] are on the left side); pseudodextral.

**Umbilical chink.** A very small, rimate, umbilical opening.

**Umbilical side of shell.** The side or end of the shell in which the umbilicus is located; the side of the shell opposite the apex.

**Umbilicate.** Refers to a spiral gastropod shell that has an opening or cavity at its base, and more specifically to one in which the opening is more than a very narrow perforation. This cavity is formed in those shells in which the inner sides of the coiled whorls do not join.

**Umbilicus.** An opening or cavity in the center of the columella or axis of the shell, formed in those shells in which the inner walls of the whorls at the central axis do not coalesce to form a solid center.

**UMMZ.** Abbreviation, usually associated with museum specimen catalogue numbers, for the University of Michigan Museum of Zoology.

**Unipectinate.** Having one margin furnished with outwardly projecting parallel filaments, like teeth of a comb.

**Univalve.** Consisting of one valve, as the shell of a gastropod (in contrast to the bivalved shell of a bivalve or pelecypod, or to the eight-valved shell of a Polyplacophoran).

**Ureter.** A tube conveying nitrogenous wastes from the renal organ (kidney) to the nephridiopore for discharge to the outside.

**USNM.** Abbreviation, usually associated with museum specimen catalog

numbers, for the National Museum of Natural History (formerly the United States National Museum), Smithsonian Institution.

**Uterine.** Pertaining to uterus, an enlarged portion of the oviduct in the female snail that serves for passage of eggs, or for the development of eggs or young.

**Vagina.** The copulatory sheath of the female system. It extends from the female genital pore to the spermathecal duct.

**Valve.** The single undivided shell of a gastropod, scaphopod and monoplacophoran mollusk, or one of the opposing halves of the divided shell of a pelecypod mollusk, or one of the eight dorsal plates of a polyplacophoran mollusk.

**Valvated.** A common name adjective referring to a member of the freshwater snail family Valvatidae.

**Varicose.** Having several or many varices.

**Varix** (*pl.* varices). A prominent transverse collabral mark on a snail shell that is the result of thickening of the outer lip by calcium deposition during a period when linear growth was halted (usually during the winter in temperate regions). A varix is usually discolored, making it particularly evident.

**Velum.** The fleshy lobe, or bilobed flap, on which the mouth is situated in lymnophile snails; a proximal inner collar around the opening into the preputium from the penis sheath.

**Ventral.** The lower side.

**Verge.** The non-introversible male copulatory organ of prosobranch snails, through or along which sperm are discharged during copulation. In some taxa, the verge is variously branched, with one or two branches containing a duct or ducts from accessory glands. In the latter type of verge, the penis is that branch (or papilla or filament) that contains the sperm duct.

**Viscera.** The internal organs, especially those of the apical viscera, *i.e.*, the internal organs (*e.g.*, liver; upper parts of the reproductive, renal and digestive systems, etc.) outside of the head-foot hemocoel.

**Viviparid.** A common name adjective referring to a member of the freshwater snail family Viviparidae.

**Viviparine.** A common-name adjective referring to a member of the viviparid subfamily Viviparinae.

**Viviparity.** The state or condition of giving birth to infant crawling snails, in contrast to laying eggs externally (oviparity), which subsequently hatch outside the mother's body. Viviparity includes ovoviviparity, where the eggs are laid with already well developed infant snails within the egg shell or membranes. See also ovoviviparous and oviparous.

**Viviparous.** See viviparity.

**Whirl.** See "whorl."

**Whorl** (spelled 'whirl' in early literature). One complete turn (through 360 degrees) or coil of a spiral gastropod shell.

**Widely conic.** Designation for a snail shell with a spire angle of about 100° ( $\pm 10^\circ$ ); depressed conic.

**Width.** The diameter of a snail's shell.

**Zebrated.** Shell surface marked with zebra-like alternating light and dark transverse bands.

**Zoological nomenclature.** The scientific names used to denote species of animals, and groups of species; the system of taxon names, intended to provide universality and stability, used in zoology. The nomenclatural system in use by zoologists employs the Linnean, or binomial system, whereby each animal species is given a unique combination of two names, a generic name combined with a specific or trivial name. The use of zoological taxon names is regulated by the periodically revised and published International Rules of Zoological Nomenclature. The latest (3rd) edition of the Rules was published in 1985, and can be obtained from the American Association for Zoological Nomenclature, c/o National Museum of Natural History, Washington, D.C. 20560.



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