

# A Review of Morphological Characters of Hydrobioid Snails

ROBERT HERSHLER  
and  
WINSTON F. PONDER

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## ABSTRACT

Hershler, Robert, and Winston F. Ponder. A Review of Morphological Characters of Hydrobioid Snails. *Smithsonian Contributions to Zoology*, number 600, 55 pages, 21 figures, 1998.—We provide herein a description of morphological characters of aquatic gastropods of the family Hydrobiidae and of several other families of Rissooidea that resemble these snails in general features. The hydrobiid gastropods comprise the largest group of freshwater mollusks, with more than 1,000 species and more than 400 Recent and fossil genera. This compilation is a prelude to the first rigorous phylogenetic analysis of the higher taxa of this cosmopolitan, yet poorly understood, group, for which at least 70 family-group taxa have been proposed. It also was prepared to fulfill a need for standardization of terminology and interpretation of characters used in taxonomic descriptions of these small, often morphologically simple, snails. Given that taxonomic study of these animals has long been hampered by reliance on a limited number of morphological features, all aspects of the shell and the soft-part anatomy are reviewed as part of this treatment, and we attempt to be maximally inclusive in listing characters. Emphasis is placed on characters considered potentially useful in recognizing and defining hydrobiid clades, although features having utility for species-rank descriptions are summarized in an appendix. For 202 characters, sufficient information was available to delineate states and tentatively identify plesiomorphic conditions (based on outgroup comparisons). Features utilized are from the shell (29 characters), operculum (13), external features (32), pallial cavity (10), digestive system (29), life history (6), female reproductive system (52), and male reproductive system (31). Discussion of many characters is augmented by schematic diagrams and in almost all cases by reference to taxa and published figures illustrating given states. Many characters are extensively annotated, and in some cases new concepts of homology and/or division of characters are proposed.

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## Dedication

To George M. Davis, who has spearheaded modern study of hydrobioid systematics and inspired many students of the group, including ourselves.

# A Review of Morphological Characters of Hydrobioid Snails

*Robert Hershler  
and Winston F. Ponder*

## Introduction

The incorporation of cladistic methodology into systematic and evolutionary studies of Mollusca has been a slow process compared to that involving other large groups, such as insects and vertebrates. This may be due in part to the far greater number of active students of those groups, but it also reflects the traditional approach of many practicing malacologists, the perception that mollusks generally are unsuited for cladistic analysis owing to paucity of characters and extensive homoplasy (Gosliner and Ghiselin, 1984; Gosliner, 1985; Hershler and Thompson, 1992), and the reality that much emphasis still must be focused on describing these poorly known animals. The soft bodies of mollusks and their "plastic" shells lends to an interpretation (albeit largely untested) that morphological convergence is the rule and identification of unique synapomorphy is the exception in this group. Anatomical characters can, however, be usefully employed in cladistic analyses of gastropods if recognized states are truly homologous and are as finely discriminated as possible (Ponder and Lindberg, 1997). Much putative homoplasy is undoubtedly the result of inadequate character definition. Relatively sophisticated studies, employing ontogenetic, histochemical, ultrastructural, and molecular methodologies, will be required in some cases to confidently determine homology, but these methods are time consuming (therefore expensive) and are often impossible to apply to existing museum material. More precise examination

of anatomical structures, however, particularly study of histological details, can considerably improve character definition and can be applied to well-fixed museum material.

Among the mollusks, the small-sized aquatic snails of the family Hydrobiidae are especially promising candidates for evolutionary studies because they are extremely diverse (the family contains more than 1,000 Recent species (Boss, 1971) and over 400 Recent and fossil genera (Kabat and Hershler, 1993)), are an old group (which has been diversifying since the late Paleozoic; Solem and Yochelson, 1979), exhibit considerable morphological variation (e.g., Hershler and Thompson, 1992), and have distributional, ecological, and life history attributes that render them ideal for inquiries ranging from biogeography on the global scale (Taylor, 1988) to local investigations of speciation (e.g., Ponder et al., 1994). The currently chaotic state of hydrobiid taxonomy at virtually all ranks (Kabat and Hershler, 1993) provides an additional reason for preparing a rigorous phylogenetic framework for the family. This paper is intended as a forerunner to such an analysis.

Ponder's (1988b) analysis of rissooidean (the superfamily to which the hydrobiids belong) phylogeny detailed relationships between hydrobiids and related family groups. The related family Pomatiopsidae has been subject to a series of phylogenetic analyses by Davis and collaborators, initially based on set theory or generated by hand (e.g., Davis and Greer, 1980; Davis et al., 1983; Davis and Silva, 1984) but later derived using parsimony algorithms (Davis et al., 1984; Davis, 1992; Davis, Chen, Zeng, et al., 1994). There have been few such studies of hydrobiids, and of these the only analyses using parsimony are by Ponder and Clark (1990), Altaba (1993), Ponder et al. (1993), Hershler (1994, 1996), Falniowski and Szarowska (1995), and Hershler and Frest (1996), all of which dealt with only a few genera. This nevertheless represents more attention than most gastropod families have received. The higher classification of the Hydrobiidae has not been addressed within a rigorous phylogenetic framework, and the relationships between hydrobiid faunas of the world's continents have not been established.

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Given that hydrobiids are small animals and offer a relatively limited suite of characters, it is important that the information provided in taxonomic descriptions be maximized and, to the greatest extent feasible, standardized. In this way workers can maximally benefit from and efficiently use the literature, facilitating study of the phylogeny of these organisms. The need for standardization is particularly important because workers often have applied different terminology and interpretation to important characters (particularly those from the female reproductive system), thus making it difficult to compare structures, especially if not well illustrated, in published literature.

The value and need of a list of "standardized" characters was discussed and highlighted during an international workshop on hydrobiid systematics convened during the 10th Congress of *Unitas Malacologica* held in 1989. To attempt to meet this need we have compiled and described, for the first time, the morphological characters (and their states) that are useful in recognizing and defining hydrobiid taxa, especially taxa above the species rank. This compilation will be used as the basis for a cladistic analysis of major clades of hydrobiids now being prepared by the authors. Characters that typically vary within a genus, such as measurements or counts, have less utility in broad-scale phylogenetic inquiries, and, in general, we do not include them in our main compilation; however, because these features are useful either in separating taxa at the species rank or in demonstrating intrageneric relationships, they are summarized in the Appendix.

#### METHODS

Morphological study of hydrobiids is challenging owing to the small size of these animals. It optimally requires a multifaceted approach combining study of live animals, study of shells and gross dissection using light microscopy, study of selected features using the scanning electron microscope (SEM) (ideally preceded by critical-point drying of soft tissues), and histological study using serial sections. We recognize that optimal-quality material (i.e., living, or well-fixed and relaxed specimens) is not available for many taxa, but we nevertheless think it important to be as comprehensive as possible in our listing of morphological characters, given the limitations expressed above.

Characters are from the published literature, including cladistic analyses pertaining to hydrobiids and related families and other papers extensively detailing morphological characters (e.g., Taylor, 1966; Davis and Greer, 1980; Davis et al., 1983; Radoman, 1983; Davis et al., 1984; Davis and McKee, 1989; Ponder and Clark, 1990; Bodon and Giusti, 1991; Boeters and Meier-Brook, 1991; Bernasconi, 1992; Davis, 1992; Davis et al., 1992; Davis, Chen, Zeng, et al., 1994; Ponder et al., 1993; Hershler, 1994; Hershler and Frest, 1996), as well as from our unpublished observations and those shared by colleagues (see "Acknowledgments"). Characters pertain to

the Hydrobiidae and several closely related families (cf. Ponder, 1988b, fig. 4), including the Pomatiopsidae, Stenothyridae, Irvadiidae, and Assimineidae. This broad range of taxa was used because distinction between the Hydrobiidae and several other family groups of rissooideans, especially the Pomatiopsidae (e.g., Davis et al., 1985), is uncertain. This is evidenced by frequent use of the informal term "hydrobioid" in the literature to refer to members of the superfamily resembling hydrobiids in general features (fide Davis, 1979:7). (Note that this term was used by Davis in an informal sense and is not to be confused with the superfamily Hydrobioidea proposed by Nordsieck, 1972.)

Characters are excluded from the main compilation if they (a) are uniform among hydrobiids and related families or vary only in minor detail (e.g., graded size differences); (b) exhibit large specific variability within hydrobiid genera (e.g., number of ctenidial filaments); (c) are logically correlated, either with other (listed) characters or with body size (e.g., length of pallial cavity); or (d) are autapomorphies of single species (e.g., the scalloped pallial edge in *Mexithauma quadripaludium*), unless it was thought that these features might eventually turn out to be of wider occurrence. To assist workers in interpreting homology and assessing character states of hydrobiid outgroups, however, some characters that are absent or invariant in the Hydrobiidae but that are found in the above families are included.

The characters listed are clearly preliminary because few hydrobioids have been carefully studied beyond a limited description of the shell, perhaps together with the operculum, penis, and (sometimes) radula. Consequently, we anticipate that many additional characters and states will be discovered. Ultrastructural studies of hydrobioid morphology are almost entirely lacking and may prove to be an especially fruitful area of investigation. Many of the characters listed are poorly understood, as their states were determined using far from perfect criteria, but these may be further resolved following more detailed investigations.

Characters are grouped into sections, comprising the main aspects of morphology (e.g., shell, operculum, pallial cavity, etc.), which are arranged as in standard taxonomic descriptions. Subsets of these in turn are provided where multiple characters represent a character complex. Where feasible, character states are listed and numbered so that they can be conveniently referred to. For each character, the presumed plesiomorphic state (based on outgroup comparison) is listed first (state "0"), again to facilitate phylogenetic inquiries. (Note that the presumed plesiomorphic states have not been tested within the framework of a phylogenetic analysis and thus should be considered preliminary.) Both the Hydrobiidae and closely similar Pomatiopsidae were treated as the ingroup. Other rissooidean families were used as outgroups, such as the Assimineidae, Elachisinidae, Hydrococcidae, Irvadiidae, Stenothyridae, Truncatellidae, Vitrinellidae, and, occasionally, the Falscingulidae and Rissoidae. Schematic diagrams are



provided to illustrate many of the characters, and, in most cases, reference also is made to taxa (and published figures) exhibiting given states, although it was not our intention to exhaustively map distribution of characters (and their states) within the family.

The break-down of characters and their states reflects our opinions regarding homology and the range of variation within hydrobiids and related families. For continuous characters (e.g., those referring to size of one structure relative to another), states represent end-points (based on our knowledge of variation) and easily scored midrange values. Many characters are annotated (prior to listing of states), especially in cases where we propose new concepts regarding homology and/or division of characters.

We have not necessarily included a state where characters are inapplicable. For example, if a presumed derived structure is absent in some taxa, absence of that character is assumed to be plesiomorphic (state "0"), but for any characters resulting from further description of that structure (beyond presence or absence), the missing state is treated as inapplicable (and scored "?") to avoid undue weighting of that character in phylogenetic analysis.

Although some or many of the characters treated herein may be subject to homoplasy (e.g., shell form, Davis, 1979), such has not yet been tested inasmuch as a robust phylogeny is not available for these snails. Thus, we generally refrain from offering comments regarding homoplasy so as to avoid an a priori bias in selection of characters. Although the evolution of hydrobiid snails is poorly understood and the higher classification of the group remains unstable, we nevertheless refer throughout the text to a few commonly used (albeit not demonstrably monophyletic) subfamilies: Amnicolinae (sensu Hershler and Thompson, 1988), Cochliopinae (Hershler and Thompson, 1992), Lithoglyphinae (Thompson, 1984), Nymphophilinae (Thompson, 1979), and Tateinae (Ponder and Clark, 1990). We similarly refer to the two pomatiopsid subfamilies (Pomatiopsinae, Triculinae; Davis, 1979, and subsequent papers).

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## Description of Characters

### SHELL

Hydrobioids generally are small-sized (1.5–6.0 mm shell length), with smooth, medium-thick, convex-whorled, ovate-conic shells having small, variably sculptured protoconchs; a medium number of teleoconch whorls (4–6); and simple, medium-sized apertures. The calcareous shell is usually white (but sometimes varies owing to shell thickness differences), with the color usually imparted by the thin periostracum (which sometimes is colorless). Taxa from large inland habitats (i.e., rivers or lakes) may range up to 12 mm in shell height (*Benedictia* is exceptional in reaching up to 50 mm), whereas many subterranean forms are minute (~1.0 mm). Shell form varies widely within the group, from planispiral to turritiform. Hydrobioids typically have overlapping whorls. In many species the body whorl is somewhat separated behind the aperture, although in a few taxa the entire shell is uncoiled (Rex and Boss, 1976), which may result in a corkscrew-like condition (e.g., *Baicalia stiedae*, Rex and Boss, 1976, fig. 1d; *Heleobia mirum*, Hershler and Thompson, 1992, fig. 28g) or a horn-like shape (e.g., *Phreatoceras taylori*, Hershler and Longley, 1986b, fig. 4A,B). Shell growth is generally near isometric, although domed shells (i.e., those having a convex-spire outline) are typical of many species. Whorl expansion rate (fide Raup, 1966) generally is isometric, without the reduction near the end of growth typical of related *Stenothyra*. Teleoconch sculpture, when present, includes a variety of spiral and/or collabral permutations. Umbilical development varies greatly and is often related to shell shape. The number of teleoconch whorls is correlated, at least in part, to shell shape and size; for instance, globose-planispiral forms often have few whorls, whereas highly elongate, turritiform taxa may have many whorls. Falniowski (1989a, 1989b, 1990) and Falniowski and Szarowska (1995) described a number of shell-structure characters that appear to have potential systematic value.

### Protoconch

Only those hydrobioids having a protoconch consisting of protoconch I and II have a planktotrophic larva. We treat the protoconch for all nonplanktotrophic taxa as a single entity and regard it as homologous with protoconch I of planktotrophic animals. The following characters refer to the whole protoconch of nonplanktotrophic taxa or only to protoconch I for planktotrophic taxa. A planktotrophic larva is probably plesiomorphic, with direct development presumably having developed independently in different groups.

**PROTOCONCH I SCULPTURE.**—Hydrobioids have many types of protoconch microsculpture, some of which are described by Falniowski (1989a, 1989b, 1990), Falniowski and Szarowska (1995), and Ponder et al. (1993). A smooth protoconch produced by a planktotrophic larva (by outgroup comparison with Iravadiidae and Vitrinellidae) is probably plesiomorphic

for the "hydrobioid" clade. Most of the sculptural types grade into one another, and more than one type can be found on a given protoconch. Whether or not a particular sculpture is treated as surface depressions, raised ridges, or irregular wrinkles, for example, is often a matter of degree. Reticulate threads such as those seen in protoconch I of *Tatea* species (Ponder et al., 1991, fig. 3) apparently have broadened in other taxa to form raised areas separating shallow, dimple-like punctae. In the latter example, the feature focused on becomes the area surrounded by the raised elements (the dimple) rather than the separating elements themselves (the raised areas). Several sculptural types can be found in a single genus (e.g., *Beddomeia*, Ponder et al., 1993) or even within a small group of closely related species (e.g., the few species placed in *Trochidrobina*, Ponder et al., 1989, fig. 34; taxa closely allied to "*Beddomeia paludinella*," Ponder et al., 1993, fig. 33).

Subsurface features may be important but have not been properly investigated. Honeycomb-like textures have been described beneath dimples or pustules in a few taxa (e.g., "*Potamopyrgus*" *oscitans* and *Hemistomia beaumonti*, Ponder, 1982a, figs. 64, 95, respectively; *Bythinella micherdzinskii*, Falniowski, 1989a, pl. 9: figs. 31, 32), and it is possible that integration of these structures with surface features may help to better define protoconch characters.

Our division of protoconch microsculptural types is based on traditional descriptors of sculpture and in its present form may be inappropriate for cladistic analysis. This aspect of shell morphology needs more refinement and better definition (e.g., studies such as those of Falniowski, 1989a, 1989b, 1990; Falniowski and Szarowska, 1995).

The following is a list of terms used herein to describe sculptural features.

pit	shallow depression approximately circular or oval in shape and with concave sides
punctum	small pit
pore	surface depression with perpendicular sides
groove	excavated furrow, narrow, straight
granule	raised, small, spot-like
pustule	raised, blister-like (a large granule)
thread	slightly raised, very narrow, straight or nearly so
wrinkle	raised, narrow, irregular
ridge	raised, prominent, base a little wider than top in section, straight or nearly so
lamella	markedly raised, narrow, with base about equal to top in section, straight or nearly so
fold	markedly raised with base much wider than top in section, straight or nearly so

**Surface Depressions:** Various types of surface pitting occur and are probably not all homologous. A series of small pits is found in several North American phreatic genera (e.g., *Holsingeria unthinksensis*, Hershler, 1989b, fig. 3; *Antrorbis breweri*, Hershler and Thompson, 1990, fig. 3a-c) and is the common state in most Australasian taxa (e.g., *Potamopyrgus*

*antipodarum*, Fish and Fish, 1981, fig. 4B; *Fluviopupa* and *Hemistomia*, Ponder, 1982a; *Pseudotricula eberhardi*, Ponder, 1992, pl. 1C,D) and many others (e.g., *Hydrobia neglecta*, Fish and Fish, 1981, fig. 3C). Steep-sided pores occur in several species of *Bythinella* (Falniowski, 1990, figs. 113-119). States: absent (0); pits or punctae (1); pores (2).

**Spirals:** Spirally arranged sculptural elements are found in various hydrobiids and pomatiopsids and are probably not all homologous, although most have likely been derived in a similar way from originally reticulate elements. Spiral threads occur in many lithoglyphines (Thompson, 1984, figs. 40-42) and cochliopines (e.g., *Spurwinkia salsa*, Davis and McKee, 1989, fig. 5F; *Balconorbis uvaldensis*, Hershler and Thompson, 1992, fig. 16c). In other cases spiral elements constitute distinct riblets (e.g., *Fonscochlea zeidleri* and *Trochidrobina punicea*, Ponder et al., 1989, figs. 9d, 34a,b, respectively). Spiral grooves result when the raised spiral elements are broader than the spaces between and occur in some species of *Fontigens* (Hershler et al., 1990, figs. 13g, 16e, 32e; also in *Lyogyrus granum*, Thompson and Hershler, 1991, fig. 39), whereas others in that genus have the grooves about equal to, or broader than, the raised areas (e.g., *F. proserpina*, Hershler et al., 1990, fig. 29e). *Tryonia protea* has an apparently autapomorphic condition in which the otherwise smooth protoconch is lined with spiral series of short, slit-like, collabral depressions (Hershler, 1989a, fig. 53b,c). In some taxa the predominant protoconch microsculpture is wrinkles or pustules traversed by spiral grooves (e.g., *Antroselates spiralis*, Hershler and Thompson, 1992, fig. 10c) or threads (e.g., *Hydrobia neglecta*, Fish and Fish, 1981, fig. 3D; *Graziana pupula*, Haase, 1994, fig. 3D). The fusion of spirally arranged pustules (as in *Antrorbis breweri*, Hershler and Thompson, 1990, fig. 3) also could result in a state similar to that seen in *Fontigens*. States: absent (0); spiral threads (1); spiral grooves (2).

**Axials:** The main types of axial sculpture are narrow, sharp threads (e.g., *Cochliopina riograndensis*, Hershler and Thompson, 1992, fig. 22e; *Mexipyrgus carranzae*, Hershler and Thompson, 1992, fig. 47c) and blunt wrinkles or ridges (e.g., *Beddomeia paludinella paludinella*, Ponder et al., 1993, fig. 33B). States: absent (0); axial threads (1); axial wrinkles or ridges (2).

**Wrinkles:** A wrinkled protoconch was used by Thompson (1979) as a diagnostic feature for the subfamily Nymphophilinae (e.g., *Nymphophilus minckleyi*, Thompson, 1979, figs. 4-7; various other genera, Thompson, 1977, fig. 4). The condition is now known to be more widespread and is probably a composite of different states. A reticulate or irregular wrinkled pattern occurs in *Hydrobia ventrosa* (Fish and Fish, 1981, fig. 2B,C), and different forms occur among nymphophilines. A dense pattern with tall elements is seen in *Goceea ohridana* (Hadzisce et al., 1976, figs. 2-4) as well as in the cochliopines *Paludiscula caramba* (Hershler, 1985, fig. 20A) and *Texapyrgus longleyi* (Hershler and Thompson, 1992, fig. 69c). Some triculines (e.g., *Neotricula minutoides*, Davis et al., 1992, fig. 103D,E) also have this feature. A more regular arrangement

of the wrinkles results in spirally or axially oriented sculpture, and pustules or punctae also may be derived from a wrinkled state. An intermediate condition of partially axial wrinkles occurs in *Coahuilix hubbsi* (Hershler, 1985, fig. 16A), whereas largely fused and mainly spirally arranged elements occur in *Onobops jacksoni* (Davis and McKee, 1989, fig. 5E,G). States: absent (0); irregularly wrinkled (1).

**Pustules:** Raised pustules are known for a few taxa and typically are arranged in spiral rows (*Ascorhis* species, Ponder and Clark, 1988, fig. 3; *Holsingeria unthinksensis*, Hershler, 1989b, fig. 3; *Antrorbis breweri*, Hershler and Thompson, 1990, fig. 3). Hollow blisters occur in "*Potamopyrgus*" *oscitans* (Ponder, 1982a, figs. 63, 64). States: absent (0); present, in spiral rows (1); hollow blisters (2).

**Distribution of Sculpture:** Sculpture may be uniform over the protoconch or may change markedly as this portion of the shell grows. For example, the Australasian genera related to *Potamopyrgus* and *Hemistomia* typically have uniform, shallow pitting over the entire surface of the protoconch (e.g., "*Potamopyrgus*" *oscitans*, Ponder, 1982a, fig. 62), whereas in other taxa (e.g., *Cochliopina milleri*, Hershler, 1985, fig. 24A; *Pyrgulopsis* species, Hershler, 1994, fig. 1) this type of sculpture markedly weakens, disappears, or is modified on the last half whorl. A few taxa have the protoconch sculpture more strongly developed over the last half whorl than at the apex (e.g., some species of *Phrantela*, Ponder et al., 1993, fig. 84B,D). States: uniform (0); stronger at apex (1); stronger on last half whorl than at apex (2).

**PROTOCONCH II SCULPTURE.**—As above, this portion of the protoconch is usually smooth (e.g., in outgroup taxa such as the Iravadiidae, Ponder, 1984, fig. 10B,J) or spirally sculptured (e.g., *Hydrobia ulvae*, Bandel, 1975, fig. 13; Fish and Fish, 1977, pl. 1a; *Cyclostremiculus beauui* (Vitrinellidae), Bieler and Mikkelsen, 1988, figs. 9–11; *Tatea* species, Ponder et al., 1991, fig. 3). Other possibilities include axial, both spiral and axial, or irregular sculpturing. The sculpture (when present) is usually composed of raised elements. These can be broken down into separate characters as above, but given that the protoconch II has been illustrated for only a few hydrobiids (and probably is present in only a small number of taxa), we choose not to do so herein. States: smooth (0); spiral (1) (other states can be added as examples are found).

#### *Teleoconch*

**GROSS MORPHOLOGY.**—**Shape:** Shell shape is often used as the primary means of characterizing species and genera, and it is occasionally used to diagnose higher taxa (i.e., planispiral Horatiini, Taylor, 1966). Typically, hydrobioid shell shapes are divided as follows: planispiral (Figure 1a) (e.g., *Coahuilix hubbsi*, Taylor, 1966, figs. 8–13); depressed trochiform or valvatiform (Figure 1b) (e.g., *Bracenicula spiridoni*, Radoman, 1983, pl. 4: fig. 58); trochiform (Figure 1c) (e.g., *Cochliopa joseana*, Hershler and Thompson, 1992, fig. 20a); neritiform (Figure 1d) (shaped like the marine genus *Nerita*; e.g.,

*Lepyrium showalteri*, Thompson, 1984, figs. 59, 60); ovate-conic (Figure 1e) (e.g., *Fonscochlea zeidleri*, Ponder et al., 1989, fig. 14a,c); conic (Figure 1f) (e.g., *Heleobia andicola andicola*, Hershler and Thompson, 1992, fig. 28a); and elongate-conic or turriform (Figure 1g) (e.g., *Tryonia variegata*, Hershler and Sada, 1987, fig. 45c–h). States: ovate-conic, with spire (see Cox, 1955, fig. 1) slightly longer than shell width (0); planispiral (1); depressed trochiform or valvatiform, with a slightly raised spire (2); trochiform, shell length and width approximately equal (3); neritiform, with an enlarged body whorl, low spire, and D-shaped aperture (4); conic, with spire up to about twice shell width, shell outline conical (5); elongate-conic or turriform, with spire markedly longer than shell width (6).

**Decollation:** Decollation is not known for any hydrobiid, but it is included herein owing to its occurrence in the pomatiopsids *Cecina* (e.g., *C. manchurica*, Davis, 1979, fig. 7c) and *Coxiella* (e.g., Macpherson, 1957, figs. 1–3) and in the outgroup Truncatellidae (e.g., Clench and Turner, 1948, pls. 23, 25), although individual species living in acidic water may typically have an eroded apex. States: apex entire (0); shell decollate (1).

**Whorl Translation:** Raup (1966) defined translation as the rate of movement of the generating curve (in practice, the shell aperture) along the coiling axis relative to the movement of the curve perpendicular to the coiling axis. This is logically related to the elongation of the shell. Allometric change of whorl translation rate has important consequences for shell shape (Raup, 1966; Vermeij, 1980). Whereas isometric translation yields a straight shell outline, a gradual increase in translation produces a convex shell outline as exemplified by *Bythinella* (e.g., *B. schmidtii*, Giusti and Pezzoli, 1978, figs. 11–15) and similar forms (e.g., *Istriana mirnae*, Velkovrh, 1971, fig. 1). An abrupt increase in translation near the end of growth produces a "tighter last whorl" (e.g., *Probythinella louisianae*, Morrison, 1965, fig. 1; *Stenothyra* species (Stenothyridae), Hoagland and Davis, 1979, figs. 1–56; *Floridiscrobs dysbatus*, Ponder, 1985a, fig. 148D). A gradual decline in translation, producing a concave or flared whorl outline, is not seen in the Hydrobiidae. States: shell outline straight (0); shell outline convex (1).

**Whorl Outline:** The plesiomorphic state is a flat whorl outline. Shouldered whorls are often associated with a spiral keel (e.g., *Pyrgulopsis nevadensis*, Hershler 1994, fig. 22a) but not in all cases (e.g., *Tryonia clathrata*, Hershler and Thompson, 1987, figs. 1, 2). States: flat (0); convex (1); shouldered (2).

**Color:** Shell (not periostracal) color in hydrobioids is rarely present, although in a few taxa the shell is reddish or brown (e.g., *Fluminicola fuscus*, Hershler and Frest, 1996). States: absent (0); present (1).

**Aperture (peristome):** In most hydrobioids the aperture is complete, whereas in some species of *Pyrgulopsis* the peristome is incomplete (or is represented by a thin glaze)

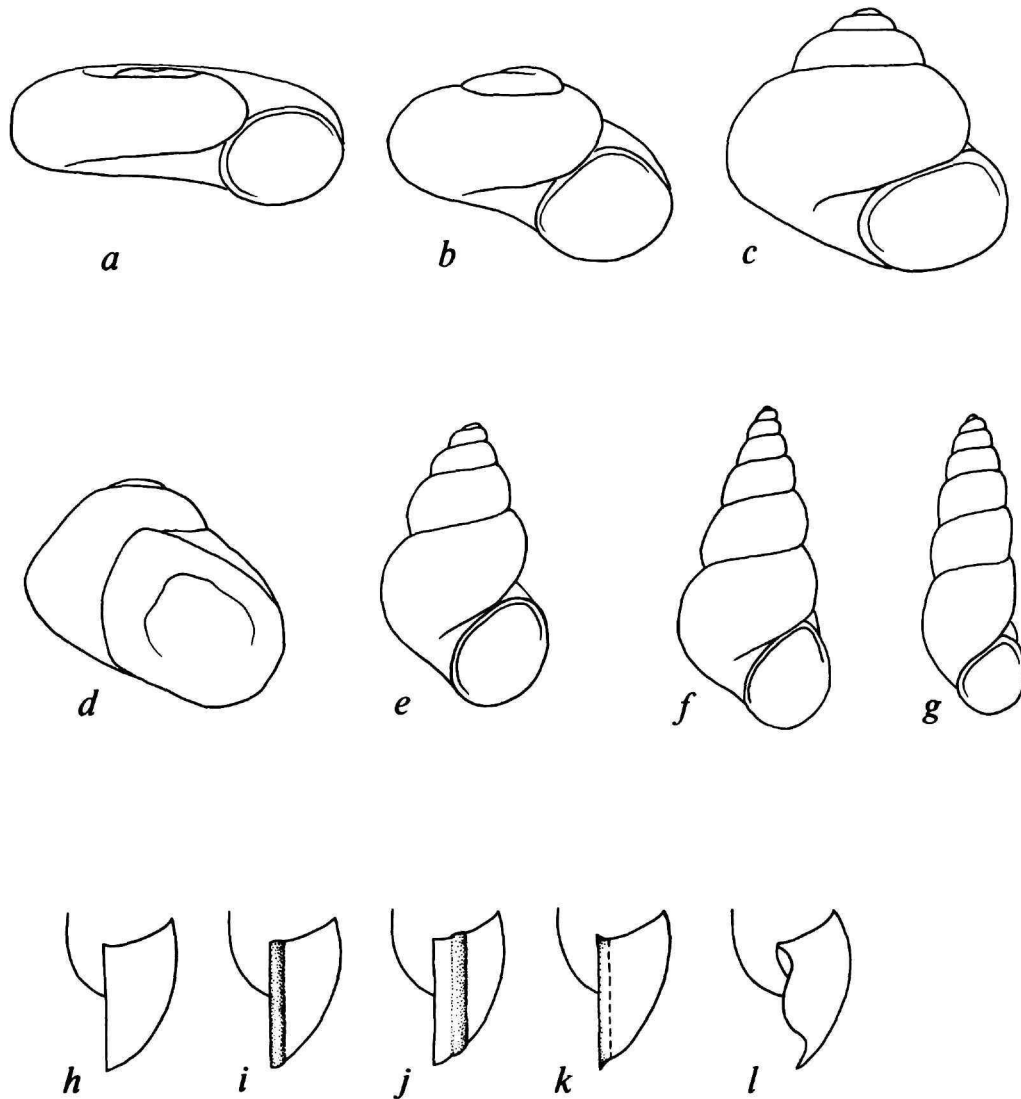


FIGURE 1.—Shell form (a-g) and condition of outer lip of shell (h-l): a, planispiral; b, depressed trochiform or valvatiform; c, trochiform; d, neritiform; e, ovate-conic; f, conic; g, elongate-conic or turritiform; h, simple outer lip; i, outer lip with varix (stippled); j, with varix behind outer lip; k, fluted outer lip; l, sinuate (both adapically and abapically) outer lip.

across the parietal wall (e.g., *P. agarhecta*, Thompson, 1977, fig. 3B). States: complete (0); incomplete or thin glaze (1).

**TELEOCONCH SCULPTURE.**—*Surface Depressions:* Pores on the teleoconch (e.g., *Moitessieria* species, Bodon and Giusti, 1991, fig. 3) are rarely seen in hydrobioids. States: absent (0); present (1).

*Spiral:* Variations include spiral threads (e.g., *Tryonia salina*, Hershler, 1989a, fig. 61a,b; *Stygopyrgus bartonensis*, Hershler and Thompson, 1992, fig. 63a), ridges (e.g., *Ginaia munda*, Radoman, 1983, fig. 86a,b; *Cochliopina milleri*,

Hershler, 1985, fig. 23), ribs (e.g., *Mexithauma quadripaludium*, Hershler, 1985, fig. 27), or one (e.g., *Posticobia brazieri*, Ponder, 1981, fig. 7; *Nymphophilus minckleyi*, Hershler, 1985, fig. 4; several species of *Pyrgulopsis*, Hershler, 1994, figs. 22a, 30e) or more prominent keels (e.g., two in *Pyrgula* species, Radoman, 1955, pl. 2: figs. 1-13; *Heleobia carinifera*, Hershler and Thompson, 1992, fig. 28e). States: absent (0); threads (1); ridges or ribs (2); keel(s) (3).

*Axial (collabral):* Strong axial ribs are rare in hydrobiids (but see *Tryonia clathrata*, Hershler and Thompson, 1987,

figs. 1, 2) but are more common in pomatiopsids (e.g., *Oncomelania hupensis*, *Hubendickia siamensis*, *Pachydrobia variabilis*, Davis, 1979, fig. 7a,i,r). Lamelliform structures are found in *Paludiscala caramba* (Hershler and Thompson, 1992, fig. 55a), *Phreatodrobia* species (Hershler and Longley, 1986a, fig. 4U; Hershler and Longley, 1987, fig. 4), and *Ohrigocea* species (Hadzisce, 1956, figs. 20, 23). Noncollabral axial ribs are unknown in hydrobioids. A collabral apertural varix is treated as a separate character below. States: growth lines only (0); rounded ribs (1); lamelliform ribs (2).

**Spines:** Well-developed spines are seen in a few pomatiopsids (e.g., *Karelania davisii*, Davis, 1979, fig. 7k). States: absent (0); present (1).

**Granular or Pustulose Sculpture:** This sculpture type is rarely found in hydrobioids (e.g., *Stiobia nana*, Thompson and McCaleb, 1978, fig. 1; *Hydrobia ventrosa*, Fish and Fish, 1981, fig. 2D; *Phreatodrobia conica*, Hershler and Longley, 1986a, fig. 5O). States: absent (0); present (1).

**OUTER PERISTOME.—Condition of Outer Lip Relative to Remainder of Apertural Plane:** The outer lip may be simple (Figure 1h), reflected or fluted either along its entire length (Figure 1k) (e.g., *Phreatodrobia imitata*, Hershler and Longley, 1986a, fig. 6A,B) or in part (e.g., *Phreatodrobia* species, Hershler and Longley, 1986a, figs. 4B, 5E), or thickened to form a (external collabral) varix either on the outside of the lip (Figure 1i) (e.g., many rissoids, iravadiids, and vitrinellids; several species of *Potamolithus*, Pilsbry, 1911, pl. 38) or behind the outer lip (Figure 1j) (e.g., *Probythinella louisianae* Morrison, 1965, fig. 1; *Heleobops torquatus*, Hershler and Thompson, 1992, fig. 33c,d). States: simple (0); fluted (1); with varix at edge of outer lip (2); with varix behind outer lip (3).

**Shape of Adapical and Abapical Portions of Outer Lip:** In lateral profile the outer lip may be straight (Figure 1h–k) or may be sinuate either adapically (e.g., *Potamolithus filiponei*, Pilsbry, 1911, pl. 41A: fig. 8; *Mexipyrgus carranzae*, Taylor, 1966, pl. 18), abapically (e.g., *Ammicola retromargo*, Thompson, 1968, fig. 68B), or both adapically and abapically (Figure 1l) (*Potamolithus binsinuatus obsoletus*, Pilsbry, 1911, pl. 41: fig. 6a; *Lyhnia sublitoralis*, Radoman, 1983, fig. 64). States: simple (0); adapically sinuated (1); abapically sinuated (2); both adapically and abapically sinuated (3).

**Inclination of Outer Lip Relative to Coiling Axis:** See Cox (1955, fig. 3) for a schematic illustration of the states that we recognize. States: orthocline (0); prosocline (1); opisthocline (2).

**Denticles within Aperture:** This feature has not been recorded for hydrobiids with the exception of some species of New Caledonian *Hemistomia* that have denticles deep inside the aperture about one-third to one-half whorl behind the outer lip (Haase and Bouchet, in press). States: absent (0); present (1).

**INNER PERISTOME.—Thickness of Peristome along Inner Wall (as compared to inner lip):** States: not thickened within

(0); slightly thickened within (1); significantly thickened within (2).

**Columellar Ornament:** Restricted to a few Australasian hydrobiids (e.g., *Hemistomia flexicolumella*, Ponder, 1982a, fig. 87; also see Ponder et al., 1993) and some pomatiopsids (e.g., Davis, 1979, figs. 21A, 22B,E,F; Davis, Guo, Hoagland, Chen, et al., 1986, fig. 74; Davis and Kang, 1990, fig. 2). States: absent (0); a low fold (1); a distinct tooth (2).

**Columellar Shelf:** A wide shelf is seen in *Lepyrium showalteri* (Thompson, 1984, fig. 59), *Lithoglyphus* (Radoman, 1983, pl. 11: figs. 195–197), and some triculines (e.g., *Lacunopsis harmandi*, Davis, 1979, fig. 21d). An intermediate-width shelf is exemplified by *Beddomeia paludinella* (Ponder et al., 1993, fig. 35A,C). States: absent or very narrow (0); intermediate (1); wide (2).

**UMBILICUS.—Size:** Umbilical size is closely related, but not identical, to the width/length ratio of the shell. In a few taxa the umbilicus is completely or partially covered by the columellar shelf at terminal growth, but these taxa should be treated as having an umbilicus, which can be readily observed in juveniles. States: absent (0); narrow relative to width of last shell whorl (1); wide (2).

**Excavation:** In some taxa (e.g., several *Potamolithus* species, Pilsbry, 1911, pl. 38: fig. 1, pl. 40: fig. 2; several *Fluminicola* species, Hershler and Frest, 1996, figs. 4, 13) the umbilical region is distinctly excavated (or furrowed) and is bordered by a prominent columellar ridge. States: absent (0); present (1).

**PERIOSTRACUM.—Surface:** Prominent projections are seemingly restricted to *Potamopyrgus* (e.g., *P. antipodarum*, Winterbourn, 1970, fig. 3), several New World cochliopines (e.g., *Mexithauma quadripaludium*, Hershler, 1985, fig. 27; *Pyrgophorus* sp., Hershler and Thompson, 1992, fig. 59a,b), and *Stenothyra* (e.g., *S. ornata*, Annandale and Prashad, 1921, pl. 16: figs. 1, 2). States: smooth (0); frilled or spinose (1).

**Color Bands:** Color bands are documented for various species of *Potamolithus* (Pilsbry, 1911, pls. 39–41) and a few cochliopines (e.g., *Cochliopina milleri*, Taylor, 1966, pl. 13: figs. 12, 13; *Mexipyrgus carranzae*, Hershler, 1985, fig. 37). States: absent (0); present (1).

**SHELL STRUCTURE.—Falniowski (1989a, 1989b, 1990) described shell-structure characters that, although poorly known (except for the European taxa that he studied), appear to have utility in distinguishing among hydrobiid clades (Falniowski and Szarowska, 1995). These describe the number of shell layers, presence of a so-called “pallisade layer” and how this is demarcated from other layers, composition of the inner layer (i.e., of cylindrical, lamellar, or fibre-like elements, etc.), details of the layer below the periostracum, presence or absence and structure of a so-called “spongy endostracum,” presence or absence of cavities in the outermost and innermost layers, and other features. Note that these features were not described using the standard terminology of Carter and Clark (1985) and Carter (1990).**

## OPERCULUM

**GROSS MORPHOLOGY.**—The operculum is attached to the dorsal surface of the foot, slightly posterior to the midpoint, with its long axis perpendicular to the long axis of the foot. The operculum almost always is composed of a “horny” or conchiolin substance and usually is of medium thickness, near flat, pale amber, ovate, paucispiral (i.e., of few whorls), with slightly eccentric nucleus, and without horny or calcareous thickenings on either surface. Operculum color is probably at least in part correlated with its thickness, thicker opercula being darker. The shape of the muscle attachment scar also may prove to be useful but requires further study. The putative assimineid *Septariellina congolensis* was reported to lack an operculum (Bequaert and Clench, 1941:5), which is an apparently autapomorphic condition but one requiring verification.

**Thickness:** The operculum is usually thin, transparent, and pliable, although in a few taxa (e.g., *Fonscochlea zeidlereri*) it is thick, opaque, and brittle. States: thin, pliable (0); thick, brittle (1).

**Overall Shape:** Opercular shape is logically correlated with the shape of the shell aperture. We recognize two apomorphic states: circular (Figure 2*b,c*) (e.g., *Hauffenia kerschneri*, Haase, 1993, fig. 2A) and elongate-ellipsoidal (Figure 2*d*) (e.g., *Neotricula aperta*, Davis et al., 1976, fig. 6A; *Tryonia clathrata*, Hershler and Thompson, 1992, fig. 71c). The position of the opercular nucleus (central, subcentral, submarginal; see Figure 2*a-e*) is strongly correlated with opercular shape, so it is not treated as a separate character. States: ovate (nucleus central or subcentral) (0); elongate-ellipsoid (nucleus submarginal) (1); circular (nucleus central) (2).

**Inner-Edge Shape:** The operculum comprises an inner, or columellar, edge (which is anterior when the animal is extended), an outer edge, and right and left sides (see Ponder, 1965:49, fig. 2). The inner edge may be straight (e.g., *Neotricula aperta*, Davis et al., 1976, fig. 6A; *Tricula gredleri*, Davis et al., 1992, fig. 127), convex (e.g., *Hydrobia truncata*, Davis, Forbes, et al., 1988, fig. 9), or concave (e.g., *Erhaia chinensis* and *Tricula maxidens*, Davis et al., 1992, figs. 17F,G, 138E, respectively). States: convex (0); concave (1); straight (2).

**Growth Pattern:** Whereas in most hydrobioids the operculum grows in a spiral fashion (Figure 2*a-d*), in bithyniids the material is added to the operculum in a concentric manner (Figure 2*e*) (e.g., *Sierraia leonensis*, Brown, 1988, fig. 8A,B). States: spiral (0); concentric (1).

**Coiling:** Whereas most hydrobioid opercula are paucispiral (Figure 2*a,b,d*), a multispiral condition occurs in various taxa (Figure 2*c*) (e.g., *Nymphophilus minckleyi*, Hershler, 1985, fig. 5B). This character is correlated with operculum shape but does not have an identical distribution because some circular opercula have few whorls (e.g., *Hauffenia wagneri*, Bole, 1970, pl. 2B; fig. 5; *Arganiella pescei*, Giusti and Pezzoli,

1981, fig. 2E) and others have many whorls (e.g., *Hauffenia michleri*, Bole, 1967, pl. 1: fig. 3). The occurrence of a multispiral condition also is partly correlated with shell size. States: fewer than four whorls (0); four or more whorls (1).

**Cross-Sectional Shape:** Most hydrobioids have a flat operculum, but in several taxa it is convex (relative to the outer surface), with extreme examples provided by *Heleobia ortonii* (Hershler and Thompson, 1992, fig. 29g-i) and *Goceia ohridana* (Radoman, 1983, fig. 42A). States: coiled in one plane (flat) (0); weakly to moderately convex (1); dish-shaped in cross section (2); V-shaped in cross section (3).

**White Material:** Presence of white (in some cases possibly calcareous) material is largely restricted to Australasian taxa, although other snails may have white smears on the operculum (possibly correlated with large body size?). Ponder et al. (1991:452) found no spectrographic evidence of calcium in the white opercular pegs of *Tatea*. The operculum is partly calcified in several of the outgroups (Assimineidae, Bithyniidae, Stenothyridae, Truncatellidae). Well-developed white opercular pegs probably represent a synapomorphy for a group of Australasian genera, whereas only bithyniids have a largely or entirely calcareous operculum. In some of the Australasian taxa, the white pegs are reduced, and in some the white material is lacking (e.g., some of the taxa from Lord Howe Island; Ponder, 1982a). These pegs cannot be considered homologous with horny pegs seen in other taxa (see below). States: absent (0); white smear or pegs on inner side (1); white streaks or smear on outer edge (2).

**INNER SURFACE.—Muscle Attachment Area Thickening:** Thickened scar margins (e.g., *Wuconchona niuzhuangensis*, Davis and Kang, 1990, fig. 4D-F; *Pyrgulopsis* species, Hershler, 1994, figs. 7c, 10i) are found in diverse taxa and may be homoplasious. States: muscle attachment area edges undifferentiated (0); muscle attachment area edges thickened (1).

**Muscle Attachment Area Peg(s):** The muscle attachment area is raised into one or more pegs in many Australasian taxa related to *Tatea* and *Hemistomia* (e.g., *H. whiteleggei*, Ponder, 1982a, fig. 74; *Fonscochlea* species, Ponder et al., 1989, fig. 8; *Tatea* species, Ponder et al., 1991, fig. 5), a few European taxa (e.g., *Istriana mirnae*, Bodon and Giovannelli, 1992, fig. 5; *Palacanthihiopsis verrierii*, Bernasconi, 1988, fig. 2b), and several North American genera (e.g., *Phreatodrobia coronae*, Hershler and Longley, 1987, fig. 14; *Holsingeria unthakensis*, Hershler, 1989b, fig. 4b-e). States: without pegs (0); one or more pegs present (1).

**Nuclear Thickening and Peg:** A nuclear thickening (e.g., *Heleobia umbilicata*, Hershler and Thompson, 1992, fig. 29e) or a peg arising from the nuclear area (e.g., *Hemistomia gentilsiana*, Solem, 1961, fig. 8d; *Catapyrgus spelaeus*, Climo, 1974, fig. 13A; *Hauffenia tovunica*, Radoman, 1983, fig. 67) are rare among hydrobioid snails. In some vitrinellids the nuclear area is raised into a small, rounded “pimple” (e.g., *Cyclostremiscus beaultii*, Bieler and Mikkelsen, 1988, figs. 36,

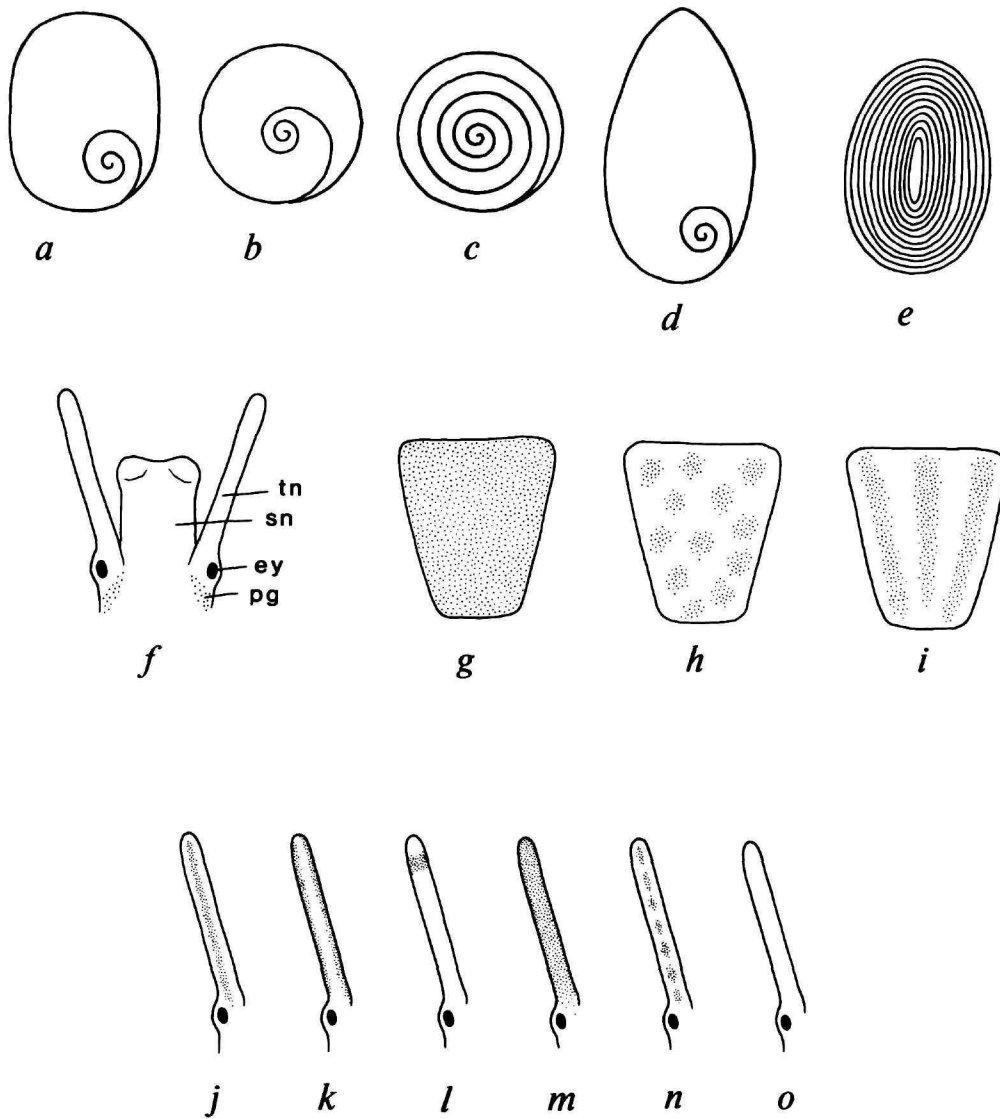


FIGURE 2.—Operculum shape, coiling, and position of nucleus (a-e); dorsal aspect of head (f); pallial roof pigmentation (g-i); and tentacle pigmentation (j-o): a, operculum ovate, spiral, paucispiral, nucleus submarginal; b, operculum circular, spiral, paucispiral, nucleus central; c, operculum circular, spiral, multispiral, nucleus central; d, operculum elongate-ellipsoidal, spiral, paucispiral, nucleus submarginal; e, operculum ovate, concentric, nucleus central; g, uniform pallial roof pigmentation; h, mottled pallial roof; i, pallial roof with longitudinal streaks; j, tentacle with medial longitudinal streak; k, tentacle with lateral longitudinal streaks; l, tentacle with distal, transverse band; m, tentacle uniformly pigmented; n, tentacle spotted; o, tentacle unpigmented. (ey = eyespot, pg = pigment cells, sn = snout, tn = cephalic tentacle.)

37). States: nucleus simple (0); nucleus area thickened (2); nucleus area raised into peg (3).

**Rim Close to Outer Edge:** A low ridge close to the outer edge occurs in *Hydrobia truncata* (Davis and McKee, 1989, fig. 3C) and several North American genera (e.g., *Pyrgulopsis*

*olivacea*, Hershler, 1994, fig. 29I). States: absent (0); present (1).

**OUTER SURFACE.—Growth Lines:** Most taxa have indistinct to distinct, simple, axial growth lines on the outer surface of the operculum, but in *Phrantela umbilicata* (Ponder et al.,

1993, fig. 29F) the growth lines are raised into sharp riblets. Other states similar to this, or even involving spirals, will probably be discovered. States: not raised (0); raised (1).

**Frill:** Although in most hydrobiids the outer surface of the operculum is entirely smooth, occasionally the edges of the opercular coils are loosened or slightly elevated above the general surface, with a frill being produced by the upturning of the edge of the whorl. In *Gocea ohridana* (Radoman, 1983, fig. 42A) and some species of *Heleobia* (Hershler and Thompson, 1992, fig. 29c,i), the frill forms a heavy ridge, but in *Heterocyclus* it is thin (Ponder, unpublished data). States: absent (0); weakly developed (1); strongly developed (2); forming a solid ridge (3).

#### HEAD-FOOT

Hydrobiids have a well-developed head-foot region, featuring a large, usually broad foot; prominent snout with obvious distal lips; and two typically elongate, narrow cephalic tentacles arising from the sides of the head and bearing small, dark eyespots near their bases (Figure 2f). Surfaces of the head-foot are variably ciliated, with ciliary patterns on the cephalic tentacles offering particular promise as potential synapomorphies. The foot is usually thin and contains an anterior mucus gland that discharges through a transverse, anterior slit. Many characters of the head-foot can be accurately scored only in living material because preserved specimens, even if well-relaxed, are significantly distorted (retracted, bloated, etc.). Shape of the distal edge of the tentacles and cross-sectional tentacle shape may be of systematic value (fide Taylor, 1966:168), but these features have been noted for only a few taxa; hence, we have not used them as characters. Similarly, ciliary fields are typically present on the right side of the neck, and ciliation patterns there and on the snout vary and may provide additional useful characters.

**PIGMENTATION.**—Dark melanic pigment is found on the head, cephalic tentacles, foot, pallial roof, and visceral coil (especially dorsal and anterior surfaces) of many epigeal hydrobiids. Subepithelial pigment (often yellow) also may be present, especially on the head-foot. The first two characters are not of the head-foot but are dealt with herein for convenience. Note that body pigmentation fades in preserved material and should be studied in living animals when possible.

**Melanic Pigment on Pallial Roof:** Pigment may be uniform (Figure 2g) or may be expressed as longitudinal streaks (Figure 2i) (e.g., *Pyrgulopsis lustrica*, Hershler, 1994, fig. 2e); mottling (Figure 2h) (e.g., *Oncomelania hupensis lindoensis*, Davis and Carney, 1973, fig. 8); or a few, large blotches (e.g., *Notogillia sathon*, Thompson, 1969, fig. 5A; *Neotricula aperta*, Davis et al., 1976, fig. 4). Absence of pigment in or on the pallial roof is a feature of most subterranean hydrobiids. States: uniformly pigmented (0); mottled (1); longitudinal streaks (2); large blotches (3); unpigmented (4).

**Yellow Pigment on Pallial Roof:** Taylor (1966:169) stated that only lithoglyphines have yellow pigment granules on the pallial roof and visceral coil. Yellow pigment cells were later recorded in the pallial roof of *Hydrobia ulvae* by Fish (1979). States: absent (0); present (1).

**Tentacle Pigmentation:** Tentacles may be unpigmented (Figure 2o); uniformly dark (Figure 2m) (e.g., *Pyrgulopsis chupaderae*, Taylor, 1987, fig. 11b); pale, with spots (Figure 2n) (e.g., *Nozeba topaziaca* (Iravadiidae), Ponder, 1984, fig. 11); have one dark, central, longitudinal stripe (or two lateral stripes) that may be elongate (Figure 2j,k) (e.g., *Notogillia sathon*, Thompson, 1969, fig. 5A; *Mexithauma quadri-paludium*, Hershler, 1985, fig. 29A) or distally restricted (e.g., *Clenchiella victoriae*, Abbott, 1948a, pl. 5: fig. 1; *Hydrobia truncata*, Davis, McKee, et al., 1989, fig. 2); or have a transverse band (distally) (Figure 2l), which is found in mainly estuarine taxa (e.g., *Littoridinops* species, Thompson, 1968, fig. 25E-G; *Ascorhis tasmanica*, Ponder and Clark, 1988, fig. 2; *Tatea huonensis*, Ponder et al., 1991, fig. 7). One or more distal transverse bands also are found in members of the Iravadiidae (Ponder, 1984, fig. 1) and some Stenothyridae (e.g., *Stenothyra divalis*, Davis, Guo, Hoagland, Zheng, et al., 1986, fig. 4). States: unpigmented (0); longitudinal stripe(s) (1); distal, transverse band (2); spots (3); uniformly dark (4).

**Pigmentation Behind Eyes:** Nonmelanic pigment cells are often concentrated behind the eyes as "eyebrows," especially in the Pomatiopsinae (Figure 3c) (e.g., *Pomatiopsis lapidaria*, Davis, 1967, fig. 1g; *Oncomelania hupensis lindoensis*, Davis and Carney, 1973, fig. 10A). In other taxa, pigment cells are absent in this region (Figure 3a) or are scattered (Figure 3b) (e.g., *Tricula bollingi*, Davis, 1968, fig. 12; *Heleobops carrikeri*, Davis and McKee, 1989, fig. 9A). Conditions in outgroup taxa vary, and the presumed plesiomorphic state is conjectural. States: absent (0); indistinct (1); distinct (2).

#### Cephalic Tentacles

**GROSS MORPHOLOGY.—Eyes:** Epigeal hydrobiids have well-developed black eyes at the bases of the tentacles, whereas many subterranean taxa lack eyes. Given that eyeless taxa are scattered both geographically and among the various hydrobioid groups (Bole and Velkovrh, 1986), it is probable that invasion of subterranean habitats has occurred iteratively during the evolution of these snails (as for other such groups; Barr and Holsinger, 1985), and loss or reduction of eye (and other body) pigmentation is homoplastic. States: present (0); absent (1).

**Length:** We are not aware of any hydrobiids having tentacles that are much shorter than the snout, whereas some related groups (Assimineidae, Truncatellidae, some Pomatiopsinae) are distinguished by this feature. Marked asymmetry in tentacle length has been reported for one species (fide Taylor, 1966:170), but this requires verification. We recognize the following conditions for this continuous character: long



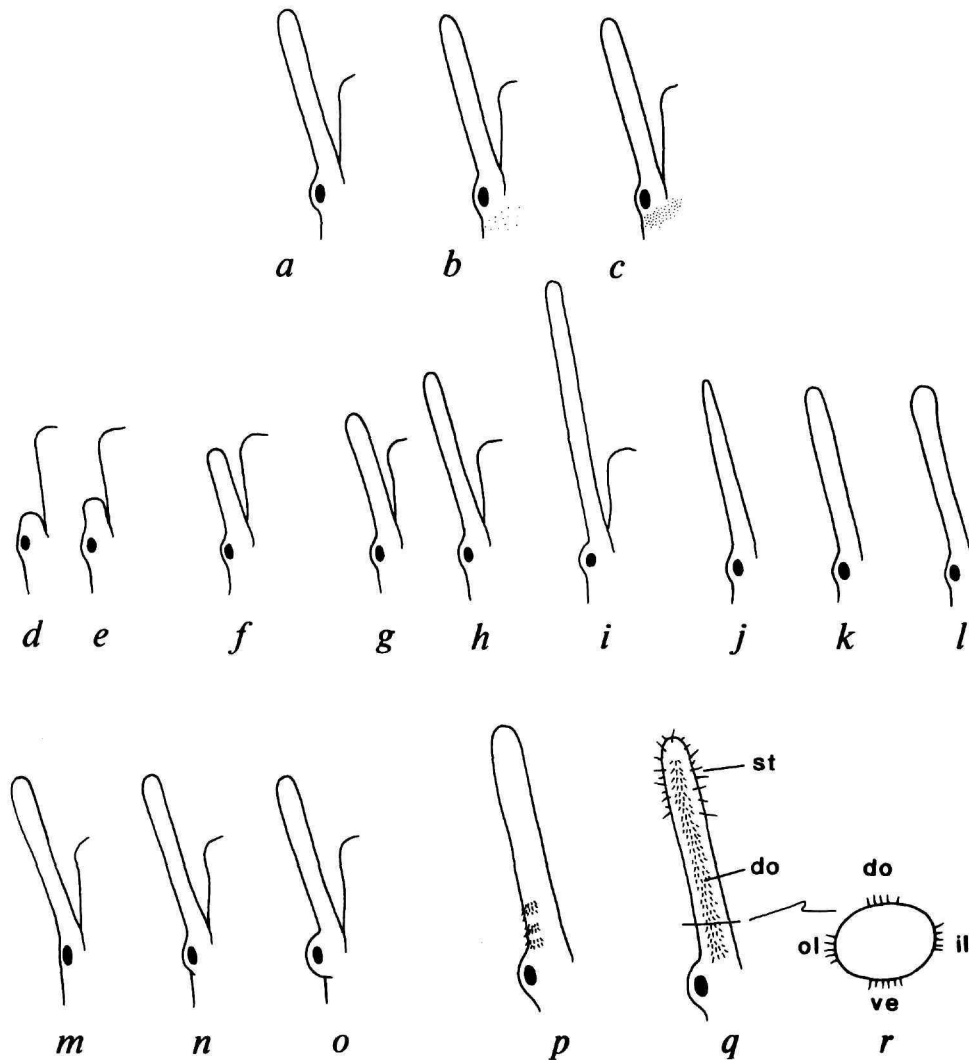


FIGURE 3.—Pigment behind eyes (*a-c*), tentacle length (*d-i*), tentacle shape (*j-l*), eyelobe development (*m-o*), and tentacle ciliation (*p-r*): *a*, tentacle unpigmented behind eye; *b*, tentacle with scattered pigment cells behind eye; *c*, pigment behind eye concentrated as eyebrow; *d,e*, tentacle about as long as wide; *f*, tentacle about five times as long as wide; *g*, tentacle about eight times as long as wide; *h*, tentacle about 10 times as long as wide; *i*, tentacle about 15 times as long as wide; *j*, overall shape of tentacle tapering, distal end nonexpanded; *k*, overall shape of tentacle parallel-sided, distal end nonexpanded; *l*, overall shape of tentacle parallel-sided, distal end expanded; *m*, eyelobe absent; *n*, eyelobe weakly developed; *o*, eyelobe well developed; *p*, transverse ciliation at base of tentacle; *q*, middorsal longitudinal ciliation and distal stationary cilia; *r*, transverse section of tentacle showing disposition of longitudinal bands. (do = dorsal ciliated tract; il = tract along inner (or anterior) edge; ol = tract along outer (or posterior) edge; st = stationary cilia; ve = ventral tract.)

(Figure 3*i*) (e.g., *Mexithauma quadripaludium*, Hershler, 1985, fig. 29A; *Ascorhis tasmanica*, Ponder and Clark, 1988, fig. 2; *Tatea huonensis*, Ponder et al., 1991, fig. 7), medium (Figure 3*g,h*) (e.g., *Hydrobia truncata*, Davis, 1966, fig. 2; *Truncatella kiusiuensis* (Truncatellidae), Kosuge, 1966, fig.

15; *Mexipyrgus carranzae*, Hershler, 1985, fig. 40A; *Fonscochlea* species, Ponder et al., 1989, fig. 11), short (Figure 3*f*) (e.g., *Pomatiopsis lapidaria*, Davis, 1967, fig. 1), and very short or stubby (Figure 3*d,e*) (e.g., *Blanfordia japonica*, *Cecina manchurica*, Davis, 1979, fig. 6). States: tentacles about as long

as wide (0); tentacles about three to five times as long as wide (1); tentacles about six to 10 times as long as wide (2); tentacles more than 10 times as long as wide (3).

**Overall Shape:** Cephalic tentacles may be tapered (Figure 3j) (e.g., *Hydrobia truncata*, Davis, 1966, fig. 2; Davis, Forbes, et al., 1988, fig. 8; *Potamolithus ribeirensis*, Davis and Silva, 1984, fig. 11A) or parallel-sided (Figure 3k) (e.g., *Duranguonella coahuilae*, Hershler, 1985, fig. 35A; *Tryonia gilae*, Taylor, 1987, fig. 17d). States: tapered (0); parallel-sided (1).

**Shape of Distal End:** The distal ends of the tentacles usually are rounded and are not otherwise differentiated from the proximal portions (Figure 3k). In a few taxa the tentacles are distally expanded (Figure 3l) (e.g., *Ascorhis tasmanica*, Ponder and Clark, 1988, fig. 2). States: nonexpanded (0); expanded (1).

**Eyelobes:** The outer sides of the tentacle bases are slightly swollen (constituting eyelobes) in most hydrobiids (Figure 3n) (e.g., species of *Fonscochlea* and *Trochidrobina*, Ponder et al., 1989, figs. 11, 24) but especially so in the Pomatiopsinae (Figure 3o) (e.g., *Pomatiopsis lapidaria*, Davis, 1967, fig. 1). Eyelobes are absent (Figure 3m) in relatively few hydrobiids (e.g., *Phreatodrobina nugax*, Hershler and Longley, 1986a, fig. 11). Additional subtle differences in eyelobe shape may characterize some hydrobiid clades (e.g., reduced eyelobe in the Lithoglyphinae, Taylor, 1966:168), but these have not been illustrated in the literature. States: absent or weakly developed (0); well developed (1).

**TENTACLE CILIATION.**—This feature (Figure 3p-r), best evaluated by SEM study of well-fixed material, has been investigated in very few hydrobioid snails. Distinctive ciliary patterns occur in other rissooideans (e.g., vitrinellids, Bieler and Mikkelsen, 1988, figs. 18, 20; Ponder, 1994, pl. 3A,B, pl. 5). Longer, isolated (stationary and compound) cilia on the tentacles (Figure 3q, st) have been described for a few taxa (e.g., *Hydrobia truncata*, Davis, 1966, fig. 2), but these have not been documented by SEM to date, with the exception of *Clenchiella* (which has stationary, compound cilia, Ponder, unpublished data).

**Longitudinal Dorsal Ciliation:** A few elongate, dorsal ciliated tracts (Figure 3q, do) are present in many hydrobiids (e.g., *Amnicola limosa*, Hershler and Thompson, 1988, fig. 3a-c; *Heleobops carrikeri*, Davis and McKee, 1989, fig. 10; *Tatea huonensis*, Ponder et al., 1991, fig. 8A,B; *Aphaostracon chalarogyrus*, Hershler and Thompson, 1992, fig. 1c; *Beddomeia krybetes*, Ponder et al., 1993, fig. 9B; *Pyrgulopsis* species, Hershler, 1994, fig. 3b-f). In *Nymphophilus minckleyi* the tracts are very short and numerous (Hershler, unpublished data). In some taxa (e.g., *Caldicochlea harrisi*, Ponder et al., 1996, fig. 8B) the tracts lie within a pronounced groove. States: one to a few well-developed tracts present (0); tracts absent (1); numerous tracts present (2).

**Longitudinal Ventral Ciliation:** A few elongate, ventral ciliated tracts (e.g., *Ascorhis tasmanica*, Ponder and Clark, 1988, fig. 10B; *Tatea huonensis*, Ponder et al., 1991, fig. 8C;

*Beddomeia bellii*, Ponder et al., 1993, fig. 10D) probably occur much more widely than has been indicated in the literature, but they are rarely figured or noted. As above, *Nymphophilus minckleyi* has numerous, very short ventral tracts. States: one to a few well-developed tracts present (0); tracts absent (1); numerous tracts present (2).

**Lateral Ciliation (anterior edge):** A ciliated tract along the anterior (inner, or leading) edge (Figure 3r) is found in many taxa (e.g., *Ascorhis tasmanica*, Ponder and Clark, 1988, fig. 10; *Heleobops carrikeri*, Davis and McKee, 1989, fig. 10B,C,D,F; *Pyrgulopsis californiensis*, Hershler, 1994, fig. 3d). States: tract absent (0); tract present (1).

**Lateral Ciliation (posterior edge):** A ciliated tract is found along the posterior (outer, or trailing) edge (Figure 3r) in some taxa (e.g., *Amnicola limosa*, Hershler and Thompson, 1988, fig. 3a-c; *Ascorhis tasmanica*, Ponder and Clark, 1988, fig. 10). States: tract absent (0); tract present (1).

**Transverse Ciliation:** Transverse or oblique ciliary ridges are found mainly on the left tentacle (Figure 3p) but are sometimes developed on the right tentacle as well. This character appears to be correlated with a brackish-water or estuarine habitat (e.g., *Ascorhis tasmanica*, Ponder and Clark, 1988, fig. 10C,D; *Heleobops carrikeri*, Davis and McKee, 1989, fig. 10A-D,F; *Spurwinkia salsa* and *Littoridinops tenuipes*, Hershler and Thompson, 1992, fig. 1a, 1d, respectively). We treat the presence of ciliary ridges on either tentacle as a single character. States: absent (0); present (1).

### Snout

**GROSS MORPHOLOGY.**—**Shape:** Snout appearance varies considerably, depending on feeding activity and other factors (e.g., *Pomatiopsis lapidaria*, Davis, 1967, pl. 1; *Tatea huonensis*, Ponder et al., 1991, fig. 7A,B). This character, and that described next, must be scored in living material, preferably when animals are in the nonfeeding (i.e., resting) state. A narrow snout is typical of many cochliopines (Figure 4b) (e.g., *Texadina barretti*, Andrews, 1977:82, fig. B; *Mexipyrgus carranzae*, Hershler, 1985, fig. 40A), whereas some other hydrobiids have a wide snout (Figure 4a) (e.g., *Potamolithus ribeirensis*, Davis and Silva, 1984, fig. 11A). States: about as wide as long (0); longer than wide (1).

**Shape of Distal End:** In some taxa the snout is uniformly shaped (Figure 4a,c,d), being either a simple square (e.g., *Potamolithus ribeirensis*, Davis and Silva, 1984, fig. 11A) or a rectangle (e.g., *Texadina barretti*, Andrews, 1977, p. 82, fig. B; *Ascorhis tasmanica*, Ponder and Clark, 1988, fig. 11), whereas in others it is distally tapered (Figure 4b,e) (e.g., *Mexithauma quadripaludium*, Hershler, 1985, fig. 29A; *Fonscochlea zeidlereri*, Ponder et al., 1989, fig. 11a,c). States: nontapered (0); tapered (1).

**Distal Lobation:** The degree of distal-snout lobation is rarely described or illustrated in the literature; however, based upon the few studies utilizing live material, we recognize the

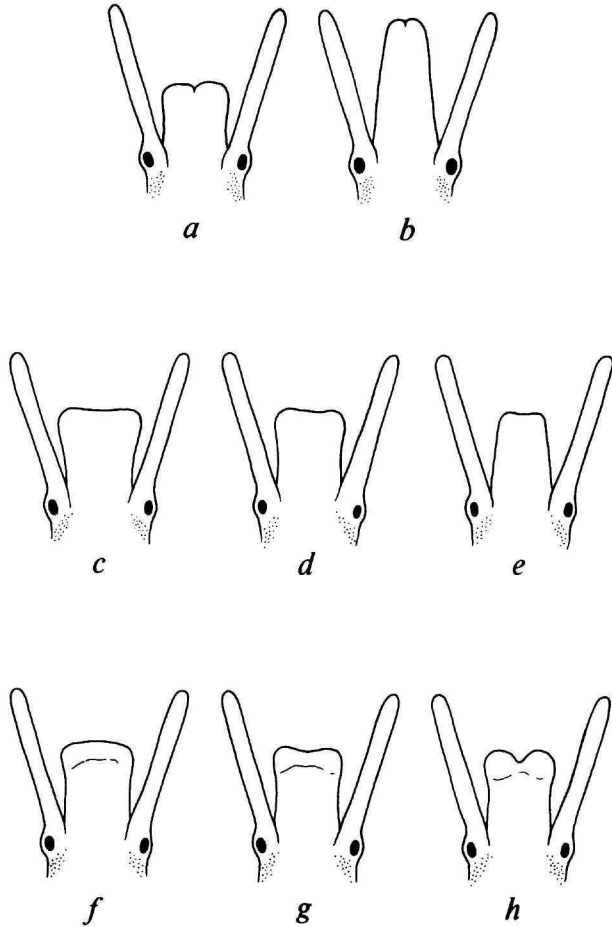


FIGURE 4.—Overall snout shape (*a,b*), shape of distal end of snout (*c-e*), and distal lobation of snout (*f-h*): *a*, snout about as long as wide; *b*, snout longer than wide; *c,d*, snout approximately parallel-sided; *e*, snout tapering; *f*, snout without distal lobation; *g*, snout with medium distal lobation; *h*, snout with strong distal lobation.

following conditions: lobation weak or absent (Figure 4*f*) (e.g., *Stenothyra austini austini* (Stenothyridae), Abbott, 1951, fig. 5*b*; *Iravadia mahimensis* (Iravadiidae), Ponder, 1984, fig. 1*C*), lobation medium (Figure 4*g*) (e.g., *Heleobia australis nana*, Marcus and Marcus, 1963, fig. 38; *Hydrobia truncata*, Davis, 1966, fig. 2; *Tricola bollingi*, Davis, 1968, fig. 12), and lobation strong (Figure 4*h*) (e.g., *Pomatiopsis lapidaria*, Davis, 1967, pl. 1: fig. 1; *Trochidrobia punicea*, Ponder et al., 1989, fig. 24*h*; *Botryphallus epidauricus*, Ponder, 1990, fig. 8*A*). States: weak or absent (0); medium (1); strong (2).

**Snout Pouches:** In female *Ascorhis tasmanica* the snout has prominent lateral pouches that hold sand grains used to coat egg capsules (Ponder and Clark, 1988, fig. 11*A*). States: absent (0); present (1).

**Distal Papillae:** The distal lobes of the snout of *Caldicochlea* have ciliated papillae (Ponder et al., 1996, fig. 9*D*), whereas those of other hydrobioids examined, as far as is known, are simple. States: absent (0); present (1).

**Dorsal Ciliated Groove Behind Lips:** A deep groove containing well-developed cilia is found in some members of the *Beddomeia* group (Ponder et al., 1993, figs. 10*E*, 11*C*) and in several other Australian taxa (Ponder, unpublished data), and it may prove to be more widely distributed. States: absent (0); present (1).

### Neck

**GROSS MORPHOLOGY.—Ciliated Strip/Omniphoric Groove** (right side of neck): Most (all?) aquatic species possess a ciliated strip that emerges from the pallial cavity; however, a well-defined omniphoric groove is not found in hydrobiids but is diagnostic of the Pomatiopsinae (e.g., *Pomatiopsis lapidaria*, Davis, 1967, figs. 2, 5) and Assimineidae (e.g., *Assimineia nitida guamensis*, Abbott, 1949, fig. 9*b*; *Assimineia infima*, Hershler, 1987, fig. 5*A,C*) and presumably is associated with the amphibious habitat of these taxa (Ponder, 1988*b*). This condition is transitory in some triculines, depending on the snail's movements (Davis, 1968). States: ciliated strip only (0); well-defined omniphoric groove (1).

**Nuchal Lobe** (females): A nuchal lobe has been recorded only in *Potamolithus ribeirensis* (Davis and Silva, 1984; fig. 6; but see Simone and Moracchioli, 1994:457). This structure, although possibly representing a rudimentary penis, also may be a secretory organ analogous to the head wart seen in some stylommatophorans (Taki, 1935; Takeda, 1982). A "true" rudimentary penis ("imposex," fide Smith, 1971) has been recorded in *Hydrobia ulvae* (Krull, 1935; Rothschild, 1938) and *Jardinella canarvonensis* (Ponder and Clark, 1990, fig. 29*C-F*). States: absent (0); present (1).

**Neck Lobe:** A neck lobe is present on the right side in *Bithynia* (e.g., *B. tentaculata*, Fretter and Graham, 1962, fig. 55) and functions as an exhalent siphon, but it has not been recorded in hydrobioid snails. States: absent (0); present (1).

### Foot

**GROSS MORPHOLOGY.—Overall Shape:** The foot may be short (Figure 5*d*) (e.g., *Hydrobia truncata*, Davis, 1966, fig. 4*A,C*), intermediate (Figure 5*b,c*) (e.g., *Oncomelania quad-rasi*, Abbott, 1945, pl. 3: fig. 2; *Assimineia habeii habeii* (Assimineidae), Abbott, 1958, pl. 16: fig. 3; *Ascorhis tasmanica*, Ponder and Clark, 1988, fig. 2), or elongate (Figure 5*a*) (e.g., *Botryphallus epidauricus*, Ponder, 1990, fig. 8*B*), although the majority of hydrobioids appear to have one of the first two conditions. Foot shape is plastic in living snails, and variation is rarely illustrated (an exception being *Pomatiopsis lapidaria*, Davis, 1967, figs. 3, 4, 6–9). States: elongate, about

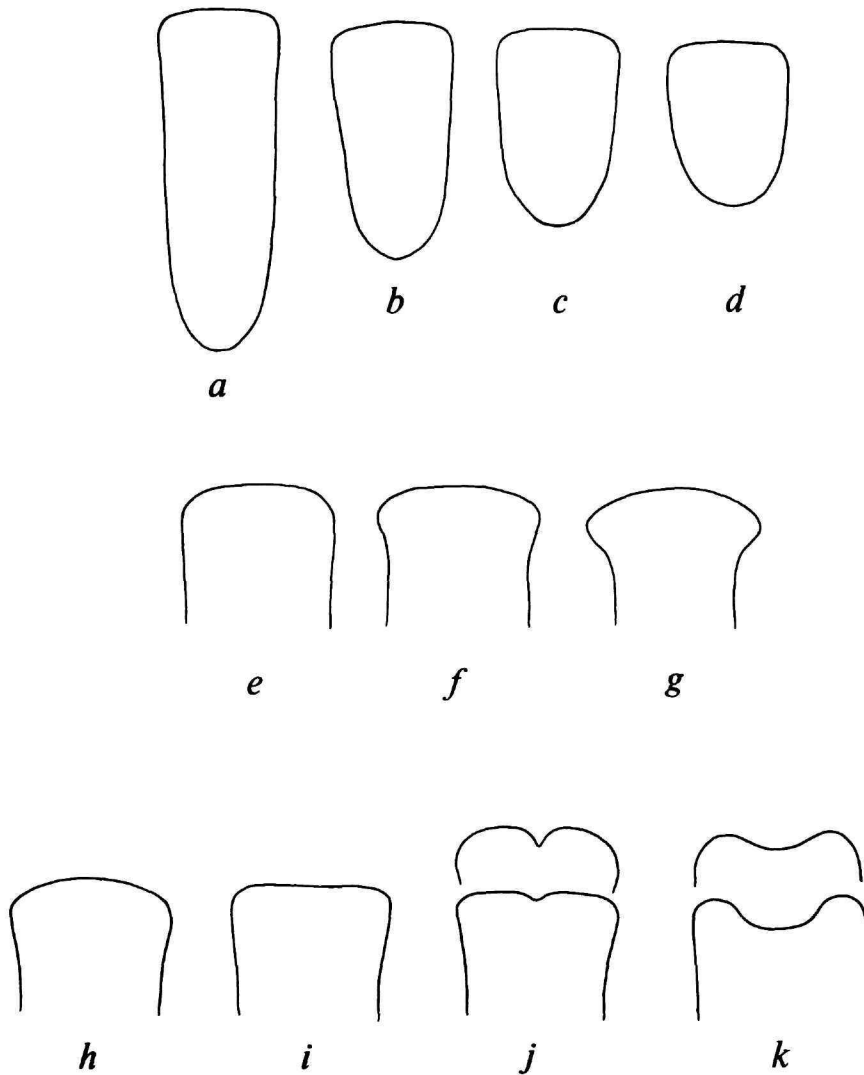


FIGURE 5.—Foot shape (a–d), anterior lateral wings of foot (e–g), and shape of anterior edge of foot (h–k): a, foot elongate; b, c, foot intermediate; d, foot short; e, lateral wings absent; f, lateral wings weakly developed; g, lateral wings well developed; h, anterior edge convex; i, anterior edge straight; j, anterior edge indented; k, anterior edge concave.

three times as long as wide (0); intermediate, about twice as long as wide (1); short, up to one and one-half times longer than wide (2).

**Lateral Wings:** The anterior end of the foot is either simple (Figure 5e) (e.g., *Oncomelania quadrasi*, Abbott, 1945, pl. 3: fig. 2; *Assimineea habeii* (Assimineidae), Abbott, 1958, pl. 16: fig. 3; *Voorwindia umbilicata* (Rissoiidae), Ponder, 1985a, fig. 45A; *Botryphallus epidauricus*, Ponder, 1990, fig. 8B) or expanded laterally into blunt wings or processes, which may be weakly (Figure 5f) (e.g., various Iravadiidae, Ponder, 1984,

fig. 1) or strongly (Figure 5g) (e.g., *Stenothyra austini austini*, Abbott, 1951, fig. 5b; *Spurwinkia salsa*, Davis et al., 1982, fig. 5A) developed. This character has rarely been treated in the literature. States: weakly developed (0); absent (1); strongly developed (2).

**Shape of Anterior Edge:** The anterior edge of the foot varies from convex (Figure 5h) to straight (Figure 5i) in most hydrobioids (e.g., *Pomatiopsis lapidaria*, Davis, 1967, pl. 1: figs. 3, 4, 6–9; *Ascorhis tasmanica*, Ponder and Clark, 1988, fig. 2; *Botryphallus epidauricus*, Ponder, 1990, fig. 8B; *Tatea*

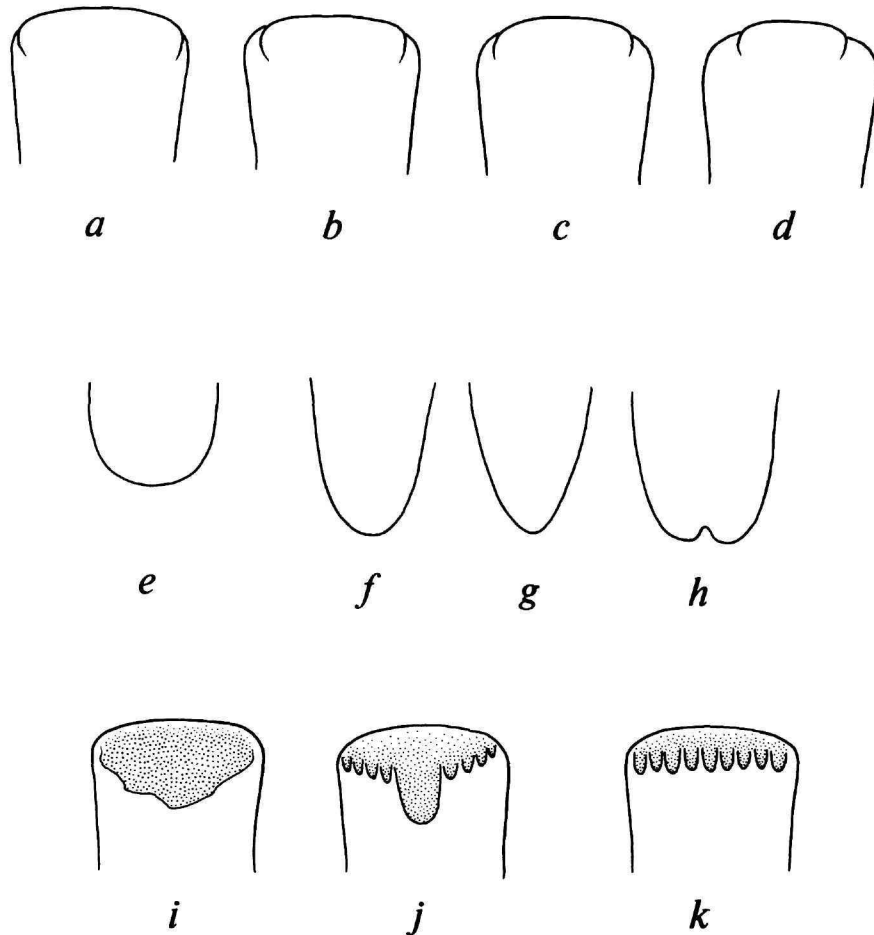


FIGURE 6.—Foot propodium (a–d), shape of posterior end of foot (e–h), and condition of anterior mucus gland (i–k): a, propodium completely overlapping anterior edge; b, c, propodium slightly narrower than anterior edge; d, propodium considerably narrower than anterior edge; e, posterior edge of foot rounded; f, g, posterior edge of foot tapering; h, posterior edge of foot indented; i, single mass (stippled); j, multiple glands, median gland enlarged; k, multiple, equal-sized glands.

*huonensis*, Ponder et al., 1991, fig. 7). An anteriorly indented (Figure 5j) (e.g., *Clenchiella victoriae*, Abbott, 1948a, pl. 5: fig. 3) or concave margin (Figure 5k) has been illustrated for several hydrobiids (e.g., *Hydrobia ulvae*, Fretter and Graham, 1962, fig. 307A; *Littoridinops monroensis*, Thompson, 1968, fig. 25E; *Notogillia wetherbyi*, Thompson, 1968, fig. 26A; *Spurwinkia salsa*, Davis et al., 1982, fig. 5A; *Rachipteron philopelum* (familial placement uncertain), Thompson, 1964, fig. 1B). An indented foot also occurs in iravadiids (Ponder, 1984, fig. 1), *Stenothyra miliacea* (Annandale and Prasad, 1921, fig. 3), elachisinids (Ponder, 1985b, fig. 1), and some vitrinellids (e.g., *Circulus mortoni*, Ponder, 1994, fig. 6). States: convex to straight (0); concave (1); indented (2).

**Propodium:** The propodium may be defined as the anterior portion of the foot overlapping the anterior mucus gland (depicted for *Cingula semicostata* (Rissoidea) and *Trivia* sp. (Triviidae), Fretter and Graham, 1962, figs. 67, 68, respectively). The propodium of hydrobiids (Figure 6a) is usually indistinct from the rest of the foot; hence, it has rarely been illustrated in the literature. Among related groups, however, the propodium may be either slightly (Figure 6b,c) (e.g., *Onoba semicostata*, Ponder, 1985a, fig. 33B) or considerably (Figure 6d) (e.g., *Parashiela ambulata*, Ponder, 1985a, fig. 29C) narrower than the anterior edge. States: completely overlapping anterior edge (0); slightly narrower than anterior edge (1); considerably narrower than anterior edge (2).

**Shape of Posterior End:** All hydrobioids have a foot with a rounded posterior end (Figure 6e) (e.g., *Jardinella thaanumi*, Ponder, 1991, fig. 4A), but some iravadiids (Ponder, 1984, fig. 1; Ponder, 1994, fig. 7), vitrinellids (Ponder, 1994, figs. 1, 6), and elachisinids (Ponder, 1985b, fig. 1) have a posteriorly indented foot (Figure 6h). A posteriorly tapering foot (Figure 6f,g) is seen in *Rachipteron philopelum* (familial placement uncertain) (Thompson, 1964, fig. 1B) and in many outgroup taxa, including *Stenothyra miliacea* (Annandale and Prashad, 1921, fig. 3). States: bluntly rounded (0); tapering (1); indented (2).

**Suprapedal Fold:** The suprapedal fold is a longitudinal fold separating the foot from the neck region. It is seen not seen in hydrobioids, but it is diagnostic of many Pomatiopsinae (Davis, 1979) (e.g., *Pomatiopsis lapidaria*, Davis, 1967, pl. 1: figs. 2, 3). States: absent (0); present (1).

**Pedal Crease:** A pedal crease has been observed in some Pomatiopsinae (e.g., *Pomatiopsis lapidaria*, Davis, 1967, pl. 1: figs. 2, 3; Davis, 1979, fig. 6A) but not in the related Triculinae (Davis, 1979). It comprises a line along which the sides of the foot crease during retraction. Its distribution in most groups is unknown. States: absent (0); present (1).

**Anterior Mucous Gland(s):** The anterior mucous gland opens beneath the propodium (anterior section of the foot) in most gastropods. In many rissoidaeans it opens as a single duct from one large, simple-lobed gland deeply embedded in the foot (Figure 6i), whereas in hydrobioids multiple glands open as a series of small tubules along the anterior edge of the foot (Figure 6k) (e.g., *Lithoglyphopsis modesta*, Davis et al., 1992, fig. 6), although one of these tubules may be larger than the others (Figure j) (e.g., *Neotricula aperta*, Davis et al., 1976, fig. 6B). This character has been adequately described or illustrated for very few taxa. States: single gland, located deep in foot (0); multiple anterior glands, median gland enlarged (1); multiple, anterior, equal-sized glands (2).

**Metapodial Tentacle:** A tentacle associated with the posterior end of the foot is present in some outgroup taxa (e.g., stenothyrids, some iravadiids, vitrinellids) and may be single (e.g., *Iravadia mahimensis* (Iravadiidae), Ponder, 1984, fig. 1c), paired (e.g., *Lantauia taylora* (Iravadiidae), Ponder, 1994, fig. 7), or multiple (e.g., *Alvania* (*Alvania*) *lineata* (Rissoidae), Ponder, 1985a, fig. 21C). Hydrobioids apparently lack a metapodial tentacle, with the possible exception of *Dabriana bosniaca* (Radoman, 1974, figs. 1, 3A; Radoman, 1983:168), although based on published illustrations, this large, centrally positioned "caudal tentacle" could alternatively be interpreted simply as a posteriorly tapering foot. The position of these tentacles varies among other rissoidaeans (especially the Rissoidae; Ponder, 1985a), and they may be found along either the posterior edge of the foot, dorsal posterior foot between the opercular lobe and posterior edge, or beneath the opercular lobe. States: absent (0); single tentacle present (1); paired tentacles present (2).

## PALLIAL CAVITY

The pallial cavity of hydrobiids usually contains a well-developed ctenidium (gill) that fills much of the length of the cavity; a shorter osphradium, positioned just ventral to the base of the ctenidium; and a hypobranchial gland that may cover portions of the pallial gonoduct, rectum, and pallial roof. Anterior portions of the kidney, pericardium, and gonoduct (or gonadal duct) usually also extend into the pallial cavity (the female gonoduct always does). The rectum courses along most of the length of the cavity, terminating in the anus, which is typically near the pallial edge. Anterior glandular pads to the left and right of the ctenidium have been recorded in some species of *Jardinella* (Ponder and Clark, 1990, fig. 4B). The mantle edge is smooth in most hydrobioids, although *Mexithauma quadripaludium* has a scalloped edge corresponding to the spiral lirae on the shell (Hershler, 1985, fig. 31A).

**POSTERIOR PALLIAL TENTACLE.**—Posterior pallial tentacles are rare in hydrobiids, occurring in *Hydrobia* (e.g., *H. truncata*, Davis, McKee, et al., 1989, fig. 5) and in some species of two Australasian genera, *Phrantela* and *Beddomeia* (Ponder et al., 1993). A pallial tentacle also was reported (but not illustrated) for *Mercuria confusa* by Boeters (1971:179). Double posterior tentacles are found in some of the outgroups, including the Vitrinellidae. Anterior pallial tentacles are known in Rissoidae, Vitrinellidae, and Elachisinidae (Ponder, 1988b). Davis, Forbes, et al. (1988, fig. 12) and Davis, McKee, et al. (1989, fig. 5) described in *Hydrobia truncata* a "sensory mass" along the inner surface of the mantle edge, which may be homologous with the posterior tentacle described above. States: present (0); absent (1).

## Ctenidium

**GROSS MORPHOLOGY.**—Shortening of the ctenidium relative to the pallial cavity can occur by migration from the anterior edge and also by elongation of the efferent ctenidial vessel (e.g., some members of the *Beddomeia* group, Ponder et al., 1993; *Pseudotricula eberhardi*, Ponder, 1992, fig. 1B). We have separated these as two characters.

**Anterior Reduction of Ctenidium:** States: ctenidium occupies nearly entire length of pallial cavity (0); ctenidium occupies posterior 66% or less of pallial-cavity length (1); ctenidium absent (?).

**Posterior Elongation of Efferent Vessel:** States: ctenidium occupies nearly entire length of pallial cavity (Figure 7a) (0); ctenidium occupies anterior 66% or less of pallial-cavity length (Figure 7b) (1); ctenidium absent (?).

**Filament Shape and Development:** Well-developed, broad, triangular filaments are found in many hydrobioid taxa (e.g., *Lepyrium showalteri*, Thompson, 1984, fig. 8; *Beddomeia paludinella paludinella*, Ponder et al., 1993, fig. 1; also see Davis et al., 1992, fig. 4). Reduced filaments occur in some hydrobiids as well as in other rissoidaeans (e.g., some caecids

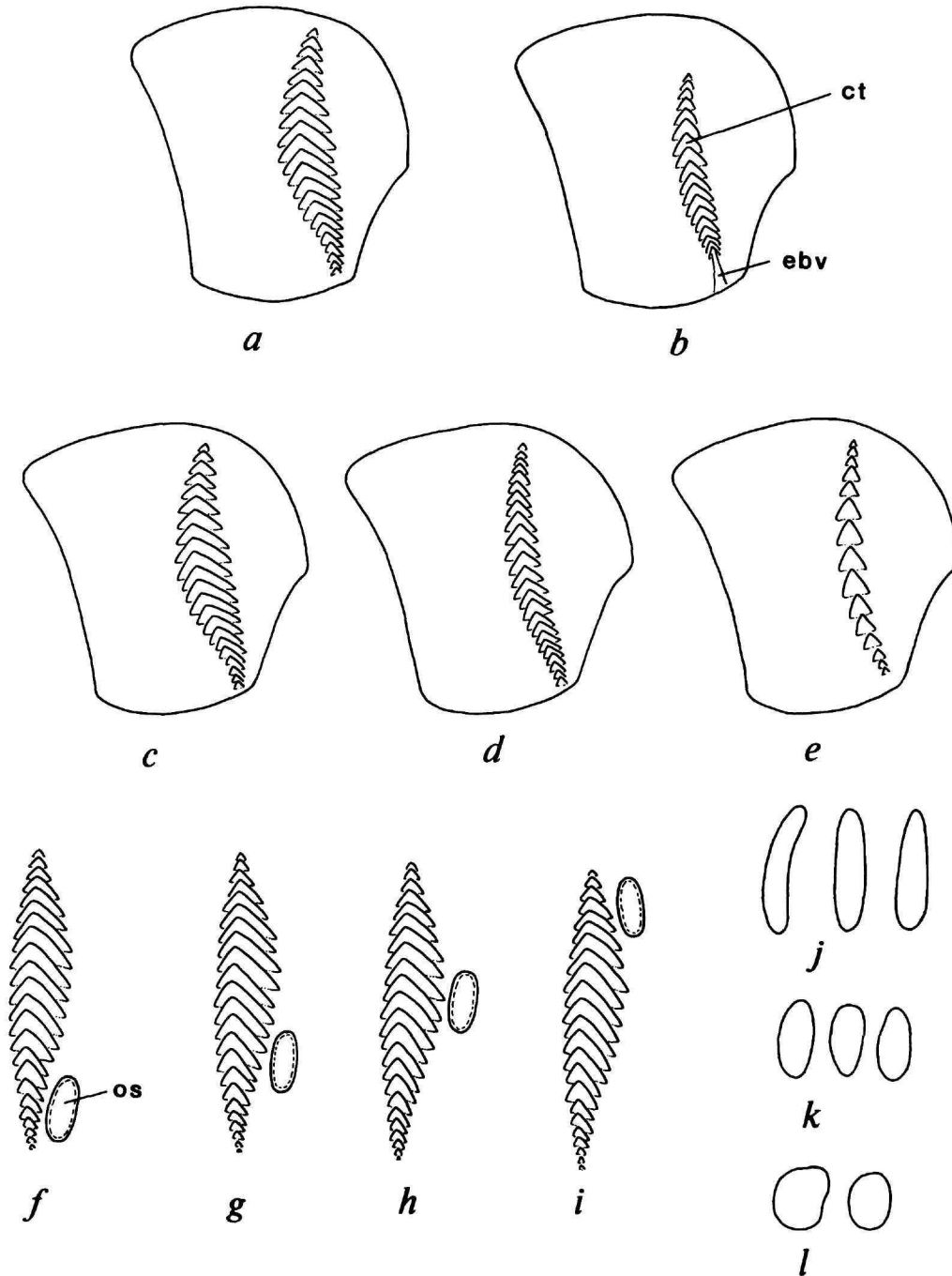


FIGURE 7.—Extent of ctenidium within pallial cavity (*a,b*), shape of ctenidial filaments (*c-e*), position of osphradium relative to ctenidium (*f-i*), and osphradium shape (*j-l*): *a*, ctenidium occupies nearly entire length of cavity; *b*, ctenidium occupies 66% or less of cavity length; *c*, ctenidial filaments broader than high; *d*, ctenidial filaments as broad as high; *e*, ctenidial filaments taller than broad; *f*, osphradium opposite posterior part of ctenidium; *g,h*, osphradium opposite approximate middle of ctenidium; *i*, osphradium opposite anterior part of ctenidium; *j*, osphradium elongate; *k*, osphradium of intermediate width; *l*, osphradium broadly ovate. (ct = ctenidial filament, ebv = efferent branchial vessel, os = osphradium.)

and rissoids) and may be shortened either in width (e.g., *Hauffenia wienerwaldensis*, Haase, 1992, fig. 5) or in height (e.g., *Oncomelania hupensis nosophora*, Davis and Carney, 1973, fig. 11A). Extreme reduction to a rudimentary or stubby condition (e.g., *Phreatodrobia micra*, Hershler and Longley, 1986a, fig. 13B; *Nannocochlea monticola*, Ponder et al., 1993, fig. 2C; *Erhaia jianouensis*, Davis and Kang, 1995, fig. 4) or loss of the ctenidium seems to be correlated with minute body size. The shape of the filaments should be determined from the middle part of the ctenidium. States: bases wider than height of filaments (Figure 7c) (0); filaments as broad as high (Figure 7d) (1); bases narrower than height of filaments (Figure 7e) (2); filaments stubby (3); filaments absent (?).

### Osphradium

**GROSS MORPHOLOGY.**—*Size:* Size is determined by the length of the osphradium relative to the length of the pallial cavity. Osphradia may be long (e.g., *Potamolithus ribeirensis*, Davis and Silva, 1984, fig. 6), medium (e.g., *Neotricula aperta*, Davis et al., 1976, fig. 7), or short (e.g., *Antillobia margalefi*, Altaba, 1993, fig. 5). A long, narrow osphradium is pleiomorphic by outgroup comparison with lower caenogastropods. States: more than 66% of ctenidium length (0); 50%–66% of ctenidium length (1); less than 50% of ctenidium length (2).

*Position Relative to Ctenidium:* The osphradium may be anterior (Figure 7i) (e.g., *Neotricula aperta*, Davis et al., 1976, fig. 7); posterior (Figure 7f) (e.g., *Fonscochlea*, Ponder et al., 1989, fig. 4F; *Jardinella edgbastonensis*, Ponder and Clark, 1990, fig. 4B); or it may occupy an intermediate position, at or slightly anterior (Figure 7h) or posterior (Figure 7g) to the middle of the ctenidium (e.g., *Jardinella carnarvinensis*, Ponder and Clark, 1990, fig. 4A). States: opposite posterior part of ctenidium (0); opposite middle of ctenidium (1); opposite anterior part of ctenidium (2); ctenidium absent (?).

*Overall Shape:* The osphradium may be much narrower than wide (Figure 7j) (e.g., *Potamolithus ribeirensis*, Davis and Silva, 1984, fig. 6; *Lithoglyphopsis modesta*, Davis et al., 1992, fig. 117), intermediate (Figure 7k) (e.g., *Gammatricula chinensis*, Davis et al., 1990, fig. 4B; *Potamolithus karsticus*, Simone and Moracchioli, 1994, fig. 5B), or broadly ovate (Figure 7l) (e.g., *Lithabitella chilodia*, Bole, 1971, fig. 1A; *Helebops carrikeri*, Davis and McKee, 1989, fig. 12A). States: more than three times longer than broad (0); two to three times longer than broad (1); less than twice as long as broad (2).

*Shape of Anterior End:* In most hydrobioids the anterior end of the osphradium is parallel to the ctenidial axis, but in a few taxa it is hooked (e.g., *Neotricula aperta*, Davis et al., 1976, fig. 7; *Beddomeia paludinella paludinella*, Ponder et al., 1993, fig. 1). States: simple (0); hooked (1).

### Hypobranchial Gland

**HISTOLOGY AND GROSS MORPHOLOGY.**—The histology of the hypobranchial gland has only been described in *Bythinella dunkeri* (Bregenzer, 1916) and *Lithoglyphus naticoides* (Krause, 1949). Even occurrence of the hypobranchial gland throughout the group is poorly known, partly because this structure can be missed in cursory gross dissection.

*Development:* We tentatively recognize three conditions for the development of the hypobranchial gland. States: thick (0); “normal” development (1); poorly developed or absent (2).

*Surface Appearance:* Although typically smooth in hydrobioids, a transversely ridged hypobranchial gland was described for *Beddomeia paludinella* (Ponder et al., 1993, fig. 1). States: smooth (0); ridged (1); gland absent (?).

### DIGESTIVE SYSTEM

The hydrobioid digestive system is typical of style-bearing neotaenioglossans. The mouth opens to a short oral area containing a pair of dorsolateral chitinous jaws composed of small, simple rodlets, immediately behind which is a well-developed buccal mass (situated within the snout). A pair of simple, unbranched, tubular salivary glands open anterodorsally to the buccal cavity and (almost always) pass posteriorly over the nerve ring, rarely stopping short of the ring, but never passing through it in hydrobioids (within the Rissosoidea the only known example of this is in some individuals of a vitrinellid; Bieler and Mikkelsen, 1988). The histology of the salivary glands is poorly known, although details may prove to be useful characters. Although variation in length is documented in the literature (e.g., *Tomichia* species, Davis, 1981, fig. 16), there is little or no information for most taxa. The radula is taenioglossate, and the radular sac extends behind the buccal mass. The oesophagus is narrow and lacks an oesophageal gland. The stomach contains a crystalline style in the anterior style sac, posterior sorting areas, typhlosoles, a cuticular gastric shield, and (sometimes) a posterior caecum. The large, lobate digestive gland typically opens through a single (rarely two) duct into the posterior stomach. The narrow intestine exits from and coils around the anterior edge of the style sac. The rectum courses along the right pallial wall, sometimes bending or looping. Fecal pellets are small and ovoid throughout the group, the one exception being *Bithynia*, which has spirally grooved pellets (Schäfer, 1953, fig. 3; Taylor, 1966:170–171). (Note that the spiral condition has not been recorded for other bithyniids; e.g., *Parafossarulus manhouricus*, Itagaki, 1965; Arakawa, 1972.)

### Radula

**GROSS MORPHOLOGY.**—Hydrobioids have a taenioglossate radula (i.e., seven teeth per row) comprising numerous rows of cusped teeth, each of which includes a typically squarish or



trapezoidal central tooth flanked on each side by lateral, inner marginal, and outer marginal teeth. Teeth near the anterior end of the radula are often worn or broken, whereas the proximal portion of the ribbon has several to many rows of poorly differentiated or incompletely formed teeth. To observe some characters, teeth must be isolated because overlapping teeth obscure details when whole mounts are photographed.

**Size of Radular Ribbon:** The size of the radula relative to body size varies among hydrobiids (Hershler, 1996) and may be evaluated relative to maximum shell dimension (length or width), an approximation of shell volume, or length of snout. States: medium, ribbon length 20%–35% maximum shell dimension (0); small, <15% maximum shell dimension (1); large, >40% maximum shell dimension (2).

**Shape of Radular Ribbon:** This character has rarely been used but may be informative. We divide this continuous character into three arbitrary states expressed in terms of the sac length relative to width. States: more than nine times longer than wide (0); three to nine times longer than wide (1); less than three times longer than wide (2).

**Relation of Radular Ribbon to Buccal Mass:** In most hydrobioids the radular ribbon protrudes or coils beneath the buccal mass, whereas in some pomatiopsids (e.g., *Erhaia* species, Davis et al., 1992, figs. 19A, 33) it loops onto the dorsal side of the buccal mass (above the nerve ring). States: positioned entirely beneath the buccal mass (0); looping onto dorsal side of buccal mass (1).

**Shape of Radular Sac Behind Buccal Mass:** In most hydrobioids the radular sac forms a U-shaped loop behind the buccal mass, whereas in *Taylorconcha serpenticola* (Hershler et al., 1994:235) it forms several coils. States: U-shaped loop (0); two or more coils (1).

**CENTRAL RADULAR TEETH.**—Each central tooth (Figure 8a) has a square or rectangular tooth face (tf), a row of cusps along the upper, cutting edge (ce), a basal tongue (bt) below, and, on each side, the lateral margin (lm) is usually thickened. The central teeth usually bear one or more pairs of basal cusps (bc1, bc2), located on either the tooth face or the lateral margins.

**Shape:** Trapezoidal central teeth (Figure 8c) are typical of hydrobioids (e.g., *Mesobia pristina*, Hershler and Thompson, 1992, fig. 45d), although square teeth (Figure 8d) are seen in several taxa (e.g., *Emmericia patula*, Radoman, 1967, fig. 5; *Phreatodrobia conica*, Hershler and Longley, 1986a, fig. 16F). Triangular (Figure 8e) (e.g., *Hydrorissoia elegans*, Davis, 1979, fig. 4V) and rectangular (Figure 8f) (e.g., *Pachydrobia variabilis*, Davis, 1979, fig. 4M) teeth are seen in some pomatiopsids and truncatellids (e.g., *Truncatella kiusiuensis*, Kosuge, 1966, figs. 5, 6). States: trapezoidal (0); square (1); triangular (2); broadly rectangular (3).

**Excavation of Base** (extension of lateral margins): Adjacent to the lateral margins the base (Figure 8a, ba) is usually deeply (e.g., *Erhaia kunmingensis*, Davis et al., 1985, fig. 16C–E; *Antrobia culveri*, Hershler and Thompson, 1992,

fig. 8d) to shallowly (e.g., *Birgella subglobosa*, Thompson, 1984, fig. 76) excavated. This gives the appearance that the lateral margins are longer (Figure 8b) or shorter (Figure 8a) relative to the base of the tooth. In the pomatiopsid *Akiyoshia chinensis*, the central-teeth bases have circular impressions (“sockets”) slightly dorsal to the excavated bases (Davis et al., 1992, fig. 15B,C,E), and this may merit recognition as a separate character. States: excavation less than 25% of tooth height to absent (0); excavation 25%–50% of tooth height (Figure 8a) (1); excavation more than 50% of tooth height (Figure 8b) (2).

**Basal-Tongue Length:** The basal tongue (Figure 8a, bt) lies between the lateral excavations of the base and is usually about as long as the lateral margins (Figure 8i). In rare cases it extends beyond the lower limits of the lateral margins (Figure 8a) (e.g., *Jullienia acuta*, Davis, 1979, fig. 4FF) or is shorter than the margins (Figure 8h) (e.g., *Pachydrobia variabilis*, Davis, 1979, fig. 4M). States: absent (Figure 8g) (0); shorter than lateral margins (1); about equal to lateral margins (2); extends beyond lateral margins (3).

**Basal-Tongue Shape:** Basal-tongue (Figure 8a, bt) shape is related to the shape of the tooth. This structure may vary within a species (e.g., *Oncomelania hupensis formosana*, Davis, 1967, pl. 29), although this has not yet been demonstrated using SEM. We recognize the following states: narrowly V-shaped (Figure 8j) (e.g., *Fontigens nickliniana*, Hershler et al., 1990, fig. 5; *Texapyrgus longleyi*, Hershler and Thompson, 1992, fig. 69d; *Phrantela* species, Ponder et al., 1993, fig. 85A,B,E,F), broadly V-shaped (Figure 8k) (e.g., *Ascorhis* species, Ponder and Clark, 1988, fig. 4), U-shaped to square (Figure 8l,m) (e.g., *Hubendickia gochenouri*, Davis, 1979, fig. 4O; *Tricula montana*, Davis, Rao, and Hoagland, 1986, fig. 9C; *Jardinella coreena*, Ponder and Clark, 1990, fig. 15C), and slightly convex (Figure 8n) (e.g., *Pachydrobia variabilis*, Davis, 1979, fig. 4M; *Tomichia* species, Davis, 1981, fig. 10). States: narrowly V-shaped (0); broadly V-shaped (1); U-shaped to square, end convex to straight, with approximately parallel sides (2); slightly convex (3).

**Position of Basal Cusps:** This character is correlated with tooth shape, number of basal cusps, and development of the lateral margins. In most hydrobioids the basal cusps arise from the lateral margins (Figure 8a, bc1). In some of these taxa, the bases of the cusps are strongly angled relative to the dorsal edge of the tooth (e.g., *Antrosetates spiralis*, Hershler and Hubricht, 1988, fig. 4a). In other taxa the basal cusps arise from the outer side of the face of the tooth (Figure 8a, bc2) (e.g., *Potamolithus ribeirensis*, Davis and Silva, 1984, fig. 14B; *Jardinella* species, Ponder and Clark, 1990; *Tatea* species, Ponder et al., 1991, fig. 6), and their bases are parallel to the dorsal edge of the tooth. In the Pomatiopsidae the inner basal cusps arise from the inner to the outer tooth face (e.g., *Jullienia* species, Davis, 1979, fig. 4J,FF), whereas the outer cusps arise from the lateral margin as in hydrobiids. States: all cusps arise from lateral margins (0);

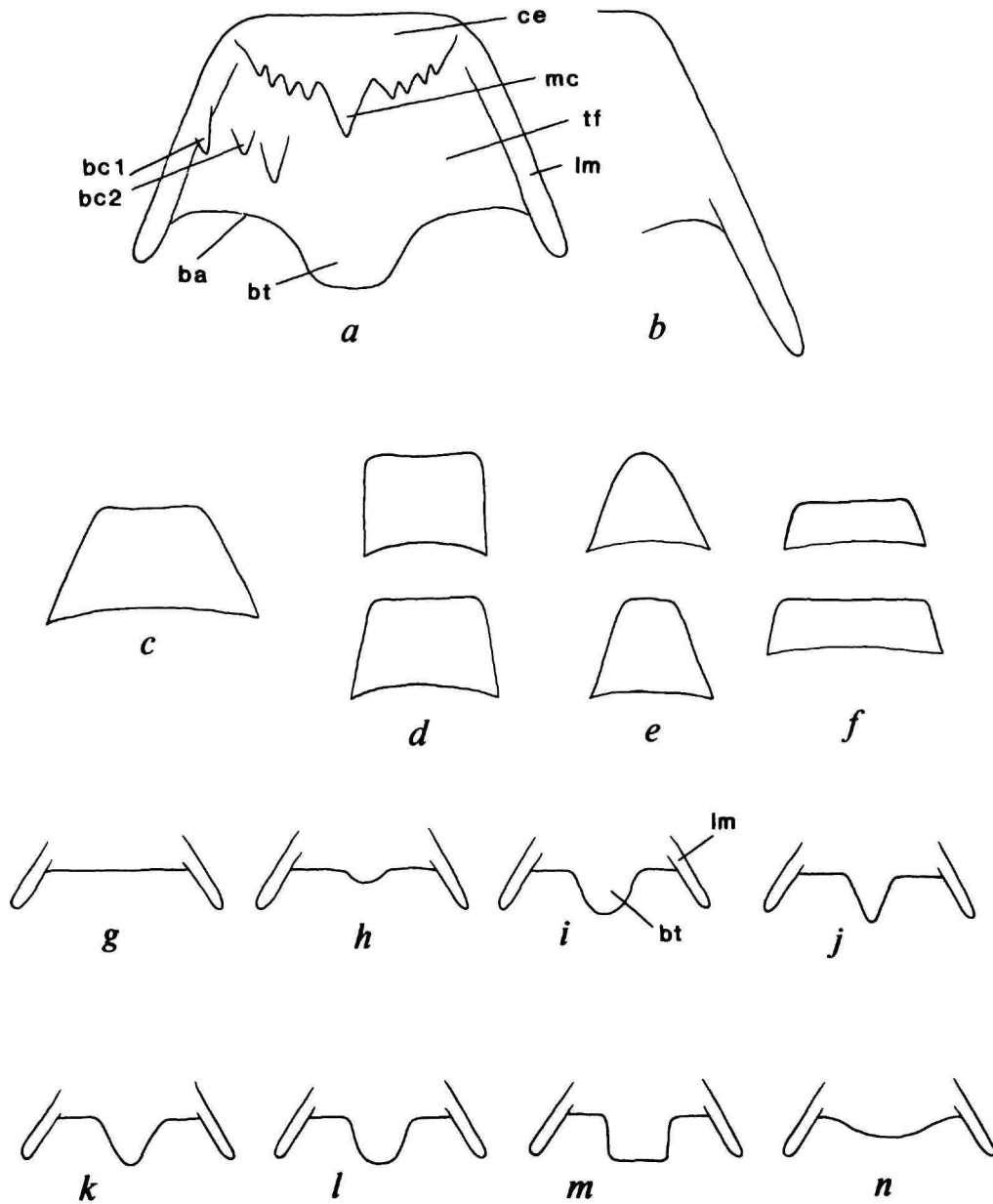


FIGURE 8.—General aspect of central radular tooth (*a*), elongate lateral margin of central tooth (*b*), shape of central radular tooth (*c-f*), length of basal tongue of central radular tooth (*g-i*), and shape of basal tongue of central radular tooth (*j-n*): *c*, trapezoidal central tooth; *d*, square central teeth; *e*, triangular central teeth; *f*, rectangular central teeth; *g*, basal tongue absent; *h*, basal tongue very short; *i*, basal tongue about equal to lateral margin; *j*, basal tongue narrowly V-shaped; *k*, basal tongue broadly V-shaped; *l*, basal tongue U-shaped; *m*, basal tongue square; *n*, basal tongue slightly convex. (*ba* = base of tooth, *bc1* = basal cusp on lateral margin, *bc2* = basal cusp on face of tooth, *bt* = basal tongue, *ce* = cutting edge, *lm* = lateral margin, *mc* = median cusp, *tf* = tooth face.)

one or more cusps arise from tooth face (1); cusps absent (?).

*Number of Pairs of Basal Cusps:* The majority of hydrobioids and outgroup taxa have one pair of basal cusps,

whereas some hydrobiids and most pomatiopsids have two or more. Several lithoglyphine (e.g., *Lepyrium showalteri*, *Clappia umbilicata*, Thompson, 1984, figs. 16, 20, respectively) and

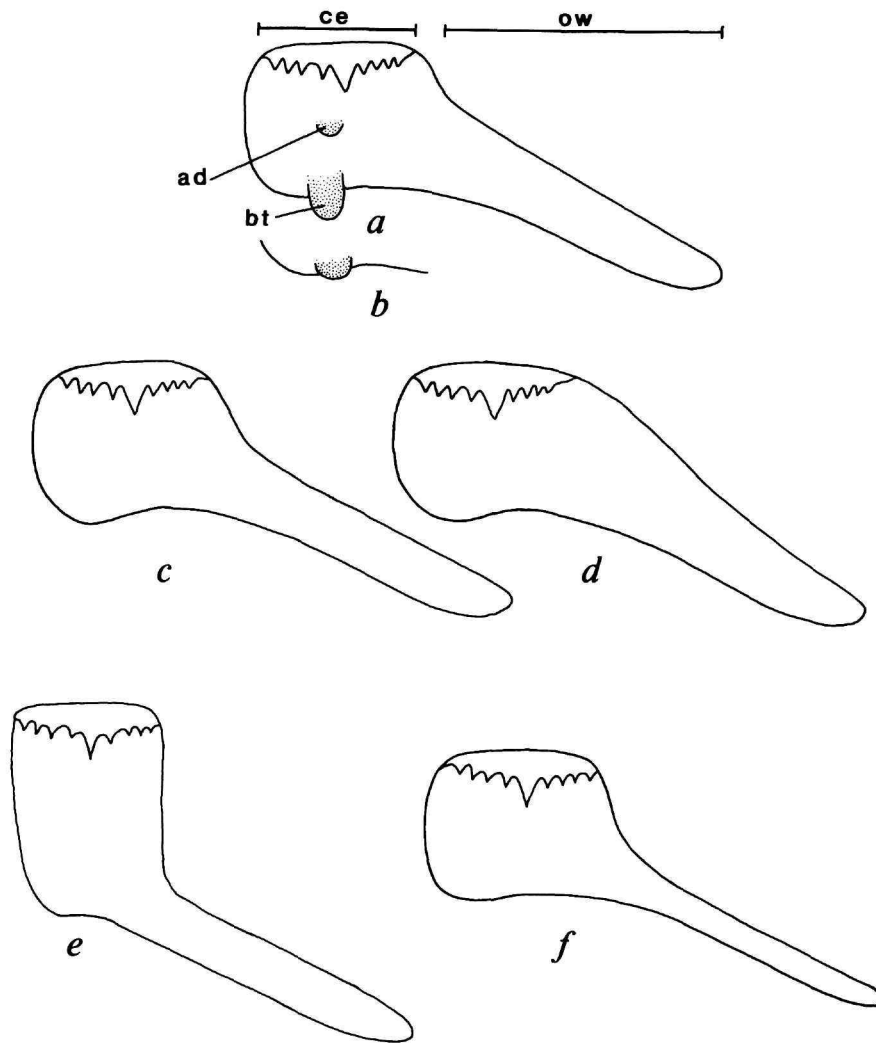


FIGURE 9.—General aspect of lateral radular tooth (a), base of lateral radular tooth, showing weakly developed basal tongue (b), and shape of lateral radular tooth (c,d); shape of face and outer wing of lateral tooth (e,f): c, outer margin of lateral tooth with concave bend; d, outer margin straight; e, face of lateral tooth rectangular; f, face of lateral tooth square, outer wing narrow. (ad = accessory denticle; bt = basal tongue; ce = cutting edge; ow = outer wing.)

Australasian (e.g., *Potamopyrgus subterraneus*, Climo, 1974, fig. 15A; *Tatea* species, Ponder et al., 1991, fig. 6) genera have numerous cusps, although a few taxa lack basal cusps (e.g., *Pyrgula annulata*, *Emmericia patula*, Radoman, 1983, figs. 72, 93, respectively; *Phreatodrobia conica*, Hershler and Longley, 1986a, fig. 16D). Basal cusps also are absent in some assimineids (e.g., some species of *Assiminea*, Abbott, 1958:221; *Austroassiminea lethae*, Solem et al., 1982, fig. 5) and bithyniids (e.g., *Soapitia dageti*, Binder, 1961, fig. 3; *Sierraia leonensis*, Brown, 1988, fig. 12B). States: one pair (0); two pairs (1); three or more pairs (2); basal cusps absent (3).

*Relative Sizes of Basal Cusps:* The inner cusp is largest in

most hydrobioids having multiple basal cusps (and in all pomatiopsids), whereas all cusps are approximately equal-sized in a few taxa (e.g., *Lepyrium showalteri*, Thompson, 1984, fig. 16; *Antroselates spiralis*, Hershler and Thompson, 1992, fig. 10d). States: outer cusp larger (0); all cusps equal-sized (1); one or no cusps (?).

**LATERAL RADULAR TEETH.**—Each lateral tooth (Figure 9a) consists of a squarish face that bears a cusped cutting edge (ce) above, a basal tongue below (Figure 9a, bt), and an (usually long) outer wing (ow). One or two “accessory plates” lying alongside the lateral tooth have been described for various assimineids (e.g., Thiele, 1927, figs. 2, 6, 7, 9–11; *Assiminea*

species, Abbott, 1958, pl. 17: fig. 4, pl. 20: fig. 7; *Omphalotropis nebulosa*, Turner and Clench, 1972, pl. 2F; *Assimineae* species, Pace, 1973, pl. 10), which Abbott (1958) suggested are the (separated) remnants of the lateral wing of the tooth. Published scanning electron micrographs of several assimineid species do not reveal a separate plate (e.g., *Austroassimineae lethae*, Solem et al., 1982, figs. 4, 6; *Assimineae* cf. *succinea*, Bandel, 1984, pl. 1: figs. 7, 8; *Assimineae infima*, Hershler, 1987, fig. 8E; *Cavernacmella kuzuuensis*, Fukuda and Mitoki, 1995, fig. 18), and this feature requires confirmation.

**Overall Shape:** We define the outer margin of a lateral tooth as that part of the upper edge of the tooth that is immediately lateral to the cutting edge. In most hydrobiids the outer margin is distinctly bent or flexed so that the cutting edge appears to be raised on a short "neck" (Figure 9c) (e.g., *Clappia umbilicata*, Thompson, 1984, fig. 21; *Beddomeia launcestonensis*, Ponder et al., 1993, fig. 16B), whereas in most outgroups (e.g., *Assimineae infima*, Hershler, 1987, fig. 8E) the outer margin is straight, or nearly so (Figure 9d). In most pomatiopsids the outer margin also is straight or nearly so (e.g., *Kunmingia kunmingensis*, Davis et al., 1984, fig. 12A; *Wuconchona niuzhuangensis*, Davis and Kang, 1990, fig. 12H) but not in *Erhaia kunmingensis* (Davis et al., 1985, fig. 16B), which has the hydrobiid condition. States: outer margin straight or nearly so (0); outer margin with distinct concave bend (0).

**Shape of Face:** In most hydrobioids (and outgroups) the face of the lateral tooth is taller than wide (Figure 9e) (e.g., *Lepyrium showalteri*, Thompson, 1984, fig. 17; *Assimineae infima* (Assimineidae), Hershler, 1987, fig. 8D,E; *Pseudobythinella shimenensis*, Davis et al., 1992, fig. 35A,B; *Beddomeia zeehanensis*, Ponder et al. 1993, fig. 44C,D; *Pyrgulopsis ventricosa*, Hershler, 1995, fig. 24E), although in a few taxa the face is square (Figure 9f) (e.g., *Truncatella kiusiuensis* (Truncatellidae), Kosuge, 1966, fig. 7; *Littoridinops monroensis*, Thompson, 1968, fig. 34B; *Baicalia carinata*, Radoman, 1983, fig. 110A; *Fluminicola virens*, Hershler and Frest, 1996, fig. 17H). States: taller than wide (0); square (1).

**Basal Projection:** Most hydrobioids have a bulbous projection or process (Figure 9a,b, bt) below the cutting edge near the ventral margin (e.g., *Spurwinkia salsa*, Davis et al., 1982, fig. 9E,F; *Potamolithus ribeirensis*, Davis and Silva, 1984, fig. 14C,D; *Beddomeia launcestonensis*, Ponder et al., 1993, fig. 16B), but this is absent in at least some pomatiopsids (e.g., *Pomatiopsis lapidaria* and *Oncomelania hupensis formosana*, Davis, 1967, pls. 19, 29, respectively; *Tomichia* species, Davis, 1981, figs. 9C, 10E). States: absent (0); present (1).

**Accessory Denticle:** A small accessory denticle is found on the face of the lateral tooth in some rissoids (e.g., *Alvania* (*Punctulum*) *wyvillethomsoni*, Ponder, 1985a, fig. 97B; *Benthonella tenella*, Ponder, 1985a, fig. 119E; *Rissoina* (*Ailinzebina*) *elegantissima*, Sleurs, 1993, fig. 42A) and in *Hydrococcus brazieri* (Ponder, 1982b, fig. 10) but has not been recorded in any hydrobioids. States: absent (0); present (1).

**Relative Length of Cutting Edge to Outer Wing:** This

character compares the length of the cutting edge with the length of the lateral wing. In taxa lacking a neck, the lateral wing is less well defined but is treated as commencing at the basal thickening (e.g., in *Tomichia natalensis*, Davis, 1981, fig. 9C, the cutting edge is a little shorter than the lateral wing). The cutting edge and lateral wing may be about equal (e.g., *Nymphophilus minckleyi*, Hershler, 1985, fig. 6B), or the lateral wing may be much longer (e.g., *Ascorhis* species, Ponder and Clark, 1988, fig. 4; *Beddomeia acheronensis*, Ponder et al., 1993, fig. 27E). States: cutting edge much shorter (0); cutting edge slightly shorter to about equal in length (1).

**Width of Outer Wing:** In most hydrobioids the width of the outer wing (as measured at about midlength) is at least 50% of the width of the tooth face (Figure 9a) (e.g., *Jardinella* species, Ponder and Clark, 1990, fig. 15B,F; *Cincinnatia integra*, Hershler and Thompson, 1996, fig. 4C; *Fluminicola* species, Hershler and Frest, 1996, figs. 8B,E,H,K, 17B,E,H), whereas in some taxa the outer wing is very narrow (Figure 9f) (e.g., *Trochidrobia punicea*, Ponder et al., 1989, fig. 35b; *Probythinella emarginata*, Hershler, 1996, fig. 3C). States: 50% or more of tooth-face width (0); less than 50% of tooth-face width (1).

**MARGINAL RADULAR TEETH.**—The marginal teeth (Figure 10a) are long, slightly curved, and lack basal cusps. The shape of the stem of the inner and outer marginal teeth is usually neglected as a character and is rarely well illustrated. These teeth sometimes bear very thin lateral wings on one or both sides (Figure 10a, lw) (e.g., *Pomatiopsis lapidaria*, Abbott, 1948b, pl. 3: fig. 8; *Potamolithus ribeirensis*, Davis and Silva, 1984, fig. 14E; *Beddomeia fromensis*, Ponder et al., 1993, fig. 26c; *Pyrgulopsis diablensis*, Hershler, 1995, fig. 2F), the presence and shape of which may prove to be useful characters, but at present their occurrence within the hydrobiids is poorly known.

**Cusp Size, Inner Marginal Teeth:** In most taxa, the cusps on the inner and outer marginal teeth are about equal in size (e.g., *Tomichia* species, Davis, 1981, figs. 9, 10; *Potamolithus ribeirensis*, Davis and Silva, 1984, fig. 14A; *Beddomeia* species, Ponder et al., 1993, fig. 27), whereas in some taxa the cusps on the inner marginal teeth are markedly larger (e.g., *Assimineae infima* (Assimineidae), Hershler, 1987, fig. 8F; *Helebops carrikeri*, Davis and McKee, 1989, fig. 24H; *Tatea* species, Ponder et al., 1991, fig. 6). We do not know of any examples among the hydrobioids in which the cusps on the inner marginal teeth are smaller than those on the outer marginal teeth, but this is a potential additional state. States: cusps larger than those of outer marginal teeth (0); cusps about as large as those of outer marginal teeth (1).

**Cusp Position, Inner Marginal Teeth:** The inner marginal teeth usually have the cusps at the anterior end of the tooth, typically with a short cutting edge on the outer edge at the upper end. The cutting edge is restricted to a short zone at the uppermost end in some taxa (e.g., *Tomichia* species, Davis, 1981, fig. 9A,C,E), but others have a longer cutting edge extending up to about one-third of the vertical length of the

tooth (e.g., *Erhaia kunmingensis*, Davis et al., 1985, fig. 16A; *Helebops carrikeri*, Davis and McKee, 1989, fig. 22F; *Tatea* species, Ponder et al., 1991, fig. 6; *Beddomeia* species, Ponder

et al., 1993, fig. 16A,F,G). We know of no hydrobioids that have the cusps extending around both sides of the tooth or cusps restricted to the inner side, although these are possible

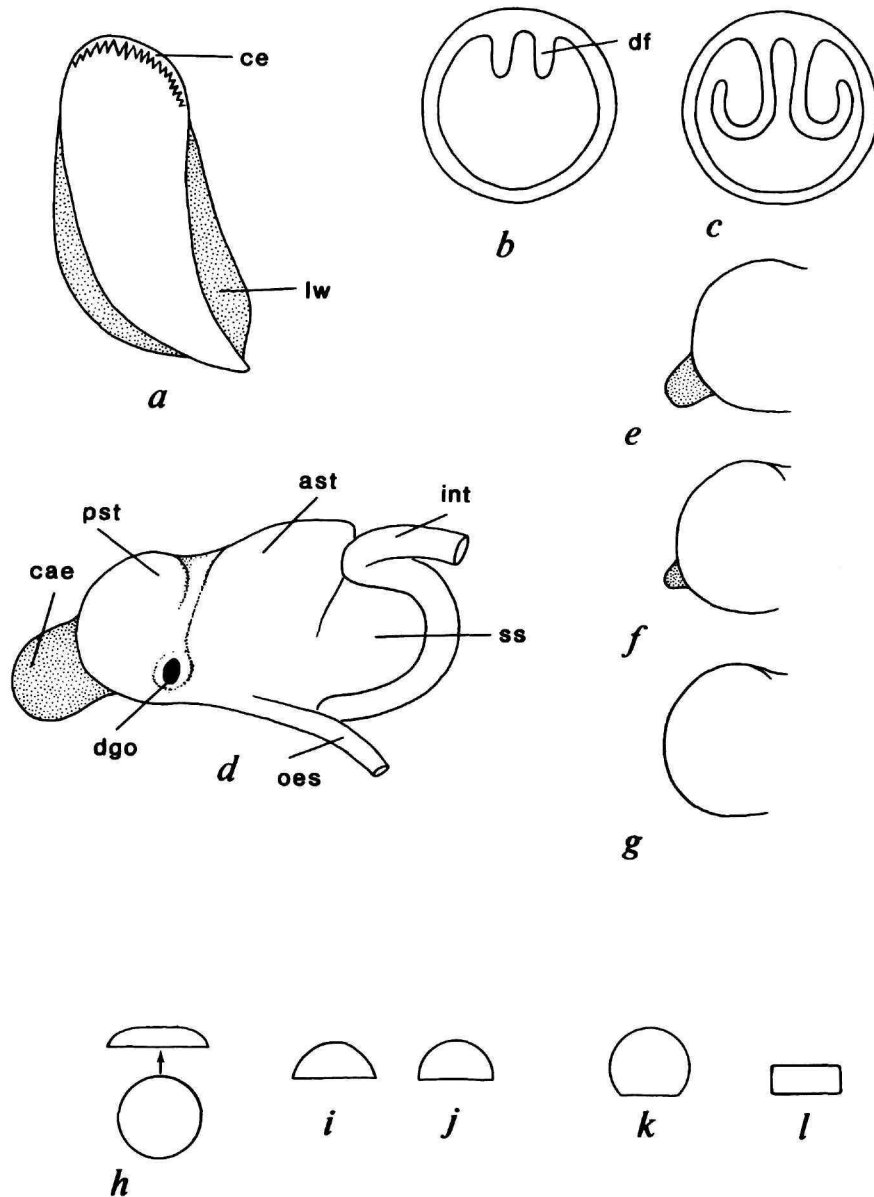


FIGURE 10.—Marginal radular tooth, showing lateral wings (a); dorsal folds of mid-oesophagus (b,c); general aspect of stomach, showing large posterior caecum (d); variation in size of posterior caecum (e-g); and egg capsule shape (h-l): b: dorsal folds of mid-oesophagus straight; c, dorsal folds recurved; e, f, posterior caecum of stomach small; g, posterior caecum absent; h, i, lenticular egg capsules; j, hemispherical egg capsule; k, subspherical egg capsule; l, pillbox-shaped egg capsule. Note that h shows both the dorsal view (lower view) and side view (upper view) of the egg capsule, whereas all others show only the side view. (ast = anterior stomach chamber, cae = posterior caecum, ce = cutting edge, df = dorsal fold of oesophagus, dgo = opening from stomach to digestive gland, int = intestine, lw = lateral wing, oes = oesophagus, pst = posterior stomach chamber, ss = style sac.)

additional states. States: cutting edge extends more than 25% down tooth length on outer side (0); cutting edge extends less than 25% down tooth length on outer side (1).

**Cusp Position, Outer Marginal Teeth:** The cusps of the outer marginal teeth are similar to those of the inner marginal teeth in that they are on the anterior end of the tooth, but the short cutting edge is known only from the inner (not outer) face at the upper end. The cutting edge is restricted to the distal end of the tooth in some taxa (e.g., *Tomichia* species, Davis, 1981, fig. 10A,C,E,G; *Heleobops carrikeri*, Davis and McKee, 1989, fig. 23E,F), but in others it is longer, extending up to about one-third of the vertical length of the tooth (e.g., *Potamolithus ribeirensis*, Davis and Silva, 1984, fig. 14E,F; *Cincinnatia winkleyi*, Davis and Mazurkiewicz, 1985, fig. 16H; *Erhaia kunmingensis*, Davis et al., 1985, fig. 17D,F; *Tatea* species, Ponder et al., 1991, fig. 6; *Beddomeia* species, Ponder et al., 1993, fig. 44A,C). States: cutting edge extends more than 25% down tooth length on inner side (0); cutting edge extends less than 25% down tooth length on inner side (1).

**Cusp Distribution, Outer Marginal Teeth:** In hydrobiids the cusps on the outer marginal teeth are uniformly distributed along the cutting edge, whereas in some assimineids groups of cusps are borne on separate, elongate stalks arising from near the base of the tooth (e.g., *Electrina succinea*, *Omphalotropis dubia*, *Rapanella andersoni*, Kondo, 1944, figs. 2, 3, 4, respectively; "*Assimania*" *aurifera*, Brown, 1980, fig. 11b,c; Hershler, unpublished data), a feature that has been used to diagnose the subfamily Omphalotropidinae (Abbott, 1949). States: cusps uniformly distributed (0); cusps arranged into distinct groups (1).

#### Digestive System Apart from Radula

**OESOPHAGUS.—Dorsal Folds of Mid-oesophagus:** In some hydrobioids the dorsal folds are straight (Figure 10b) and are short to long (sometimes extending to the floor of the oesophagus; e.g., *Bythinella dunkeri*, Bregenzer, 1916, fig. O). In other taxa the distal edges of the folds are recurved dorsally (Figure 10c) (e.g., various iravadiids, Ponder, 1984, fig. 2; *Pyrgulopsis bruneauensis*, Hershler, 1990, fig. 3d). States: simple (0); recurved (1).

**STOMACH.—**The relative sizes of the stomach proper and style sac (Figure 10d) are nearly uniform among hydrobioids thus far studied. Other than general external appearance, features of the stomach are poorly known, and details, such as the opening of the style sac to the intestine, have not been established for most taxa. The internal anatomy of the stomach has been examined in detail for only a few taxa: *Hydrobia ventrosa* and *Hydrobia ulvae* (Graham, 1939:85–87, not figured); *Pomatiopsis lapidaria* (Dundee, 1957, pl. 7: fig. 4); *Heleobia australis nana* (Marcus and Marcus, 1963, fig. 45); *Hydrobia truncata* and *Spurwinkia salsa* (Davis et al., 1982, figs. 6–8); *Ascorhis tasmanica* (Ponder and Clark, 1988, fig. 12); *Trochidrobia punicea* and *Fonscochlea accepta* (Ponder et al., 1989, fig. 44a, 44b, respectively); and *Antillobia*

*margalefi* (Altaba, 1993, fig. 7). In addition to those listed below, possible characters include disposition of the typhlosoles, detailed arrangement and strength of the cuticular ridges (incorrectly referred to as "sorting areas" by Davis et al., 1982, fig. 6), size of the gastric shield (fide Altaba, 1993:86), and connection between the intestine and the style sac.

**Relative Size of Anterior and Posterior Chambers:** The anterior and posterior chambers of the stomach are typically about the same size (e.g., *Potamolithus ribeirensis*, Davis and Silva, 1984, fig. 9; *Cincinnatia winkleyi*, Davis and Mazurkiewicz, 1985, fig. 17) or are slightly different (e.g., *Kunmingia kunmingensis*, Davis et al., 1984, fig. 6B; *Antillobia margalefi*, Altaba, 1993, fig. 7), but sometimes the posterior chamber is much smaller (e.g., *Ascorhis tasmanica*, Ponder and Clark, 1988, fig. 12B; *Tatea huonensis*, Ponder et al., 1991, fig. 24). States: chambers equal or subequal (0); posterior chamber much smaller (1).

**Shape of Dorsal Edge of Posterior Stomach Chamber:** In hydrobioids the posterior chamber is usually rounded or flat dorsally, although in *Caldicochlea* (Ponder et al., 1996, fig. 11) it is markedly pointed and elevated. States: simply rounded or flat (0); pointed (1).

**Number of Digestive-Gland Openings:** Two openings is considered to be the plesiomorphic state (e.g., *Stenothyra hunanensis*, Davis, Chen, et al., 1988, fig. 12), but this condition is known in only a few hydrobioids (e.g., *Spurwinkia salsa*, Davis et al., 1982, fig. 8; *Antillobia margalefi*, Altaba, 1993, fig. 7). The apparent paucity of records of this condition may reflect the fact that this character is easily overlooked in cursory gross dissection. The number of lobes of the digestive gland is obviously correlated with this character, although a single duct and an anterior (plus posterior) lobe of the digestive gland, possibly representing the anterior digestive gland opening, was reported for *Heleobops carrikeri* (Davis and McKee, 1989, fig. 18), and, again, this may be a character with a wider distribution than is currently recognized. A minute anterior lobe, absent in some individuals, was reported for *Hauffenia wienerwaldensis* (Haase, 1992, fig. 7). States: two openings (0); one opening (1).

**Posterior Caecum:** Although the gastric caecum is easily discerned in cases where it is somewhat small relative to the stomach, it may be overlooked when it is very small or even when it is large, in which case it may be confused with the posterior edge of the stomach. Dissection and histological study of thin sections (the caecum typically is lined with ciliated epithelium) of the stomach are recommended to confidently ascertain the presence or absence of a caecum. The caecum may be large (Figure 10d) (e.g., *Tatea huonensis*, Ponder et al., 1991, fig. 24), small (Figure 10e,f) (e.g., *Beddomeia launcestonensis*, Ponder et al., 1993, fig. 5), or absent (Figure 10g) (e.g., *Ascorhis tasmanica*, Ponder and Clark, 1988, fig. 12). States: large (0); small (1); absent (2).

**Shield Caecum:** This structure has been recorded only in the European hydrobiid *Graziana lacheineri* (Haase, 1994, fig. 7). It is positioned at the proximal end of the stomach,

protrudes between the lobes of the digestive gland, and its inner surface is covered by the cuticle of the gastric shield (Haase, 1994:229). Davis and Mazurkiewicz (1985, fig. 17) described a "mid-stomach" ridge in *Cincinnatia winkleyi* that may possibly be a homologue (in a reduced form) of this character. States: absent (0); present (1).

INTESTINE.—*Coiling*: Coiling of the intestine on the dorsal side of the style sac is known for few hydrobioids (e.g., *Phreatodrobia rotunda*, Hershler and Longley, 1986a, fig. 18B), and it appears to be correlated with minute size and/or with living in caves or phreatic environments. States: simple coil around style sac (0); coiled around style sac with additional coil on dorsal side of sac (1).

RECTUM.—*Shape Within Pallial Cavity*: Coiled or looped intestines are uncommon in hydrobioids and, as above, appear to be correlated with minute size and/or with living in caves or phreatic environments. Various states are listed and illustrated by Ponder et al. (1993, fig. 4). The simplest derived state is a U-shaped loop (e.g., *Balconorbis uvaldensis*, Hershler and Longley, 1986a, fig. 13H; *Phrantela umbilicata*, Ponder et al., 1993, fig. 92A). A more complex configuration, involving an S-shaped coil, has occurred in more than one way. In some taxa the coiling is initiated by the posterior part of the intestine swinging to the left across the mantle roof (e.g., *Phreatodrobia* species, Hershler and Longley, 1986a, fig. 13B–F), and in others the intestine bends to the right (e.g., *Pseudotricula eberhardi*, Ponder, 1992, fig. 1B) so that the resulting S-shaped coils are mirror images of each other. In both S-shaped states the loops may vary from open to tight coils, and even double coils occur in some *Phreatodrobia* species (Hershler and Longley, 1986a, fig. 13B–F). States: straight or with weak bend (0); with U-shaped bend (1); with S-shaped bend initiated to left (2); with S-shaped bend initiated to right (3).

#### LIFE HISTORY

Available data indicate that most hydrobioids have direct development, and only a few estuarine or brackish-water taxa have a pelagic larval stage (of short duration); however, very few hydrobioids have been reared to confirm their developmental modes. Most hydrobioids are oviparous, with females depositing small egg capsules, either singly or (rarely) in strings, on the substrate. A small number of hydrobioids are ovoviviparous, in which females brood shelled young in the pallial gonoduct.

Chromosome morphology and number have been little investigated in hydrobioids and allied taxa, although available studies (Butot and Kiauta, 1966; Kiauta and Butot, 1967; Kitikoon, 1982) revealed significant differences in karyotype among the few taxa studied and suggest that additional work would be fruitful.

EGG CAPSULES.—Most hydrobioids probably produce egg capsules, typically containing a single egg, but there are data for only a few species. Ovoviviparous species (e.g., *Pota-*

*mopyrgus antipodarum*, Fretter and Graham, 1962, fig. 309) have separate capsules in their brood chamber.

*Deposition*: Egg capsules often are deposited singly, although *Hydrobia ulvae* produces gelatinous egg masses containing up to 40 capsules (Fretter and Graham, 1962, fig. 204A, 1978:124). A string of linked capsules is found in many cochliopines (e.g., *Spurwinkia salsa*, Davis et al., 1982, fig. 10A; *Littoridina crosseana* and *Zetekina* sp., Hershler and Thompson, 1992, figs. 3b, 74a). Davis et al. (1982:161, fig. 10A) described these capsules as being linked by chalazae, but it is not clear whether these connecting elements are homologous with those described for various other gastropods (for compilation see Robertson, 1985). Bithyniids form a cluster of capsules (e.g., *Bithynia tentaculata*, Fretter and Graham, 1962, fig. 207; various species, Chung, 1984, figs. 35–38), which we treat as a separate state. States: single (0); multiple, arranged in a connected row (1); multiple, forming more than one row or a cluster (2).

*Shape*: Hydrobioid egg capsules are typically hemispherical to spherical (Figure 10j,k) (e.g., *Gillia altilis*, Baker, 1918, pl. 2: figs. 1–3; *Oncomelania quadrasi*, Abbott, 1946, pl. 9: fig. 1; *Ammicola limosa*, Davis, 1961, fig. 1; *Hydrobia ulvae*, Fretter and Graham, 1962, fig. 204A; *Heleobops carrikeri* Davis and McKee, 1989, fig. 5A; *Tatea* sp., Ponder et al., 1991, fig. 25; *Beddomeia* species, Ponder et al., 1993, fig. 69C–F) but also can be lenticular (Figure 10h,i) (e.g., *Rissoa parva*, Fretter and Graham, 1962, fig. 204D) or pillbox-shaped (Figure 10l) (e.g., *Beddomeia salmonis*, Ponder et al., 1993, fig. 69A,B). States: lenticular (0); hemispherical to spherical (1); pillbox-shaped (2); spherical (brooded) (3).

*Dorsal Keel*: The egg capsules of amnicolines have a prominent dorsal keel (e.g., *Ammicola limosa*, Baker, 1928, fig. 43B; *Marstoniopsis scholtzi*, Fretter and Graham, 1978, fig. 120), whereas those of other hydrobioids have a simple dorsal surface. States: absent (0); present (1).

*Composition*: Egg capsules may either be covered with sand grains (e.g., *Oncomelania quadrasi*, Abbott, 1946, pl. 9: fig. 1; *Hydrobia ulvae*, Fretter and Graham, 1962, fig. 204A; *Ascorhis tasmanica*, Ponder and Clark, 1988, fig. 5; *Tatea* sp., Ponder et al., 1991, fig. 25; *Beddomeia* and allied genera, Ponder et al., 1993, figs. 46, 69) or be simple and horny (e.g., *Heleobops carrikeri*, Davis and McKee, 1989, fig. 10A; *Fluvidona* species and *Posticobia* species, Ponder, unpublished data). States: simple (0); covered with sand grains (1).

OVOVIVIPARITY (brooding).—Among the group of rissooidean families of concern, only hydrobiids are known to brood, and this occurs only in some cochliopines, *Paxillostium nanum* (Gardner, 1970:183; Ponder, unpublished data), and *Potamopyrgus*. In all three groups the pallial oviduct is used as the brood chamber. Some taxa brood many small embryos (e.g., *Potamopyrgus antipodarum*, Fretter and Graham, 1962, fig. 309; *Cochliopina riograndensis*, Hershler and Thompson, 1992, fig. 23a), whereas others brood a few large embryos (e.g., *Durangonella coahuilae*, Hershler and Thompson, 1992, fig.

25a). States: females oviparous (0); females ovoviviparous (1).

SEXUAL MODE.—Parthenogenesis has been documented and thoroughly studied for only one hydrobiid (*Potamopyrgus antipodarum*; see references in Ponder, 1988a), although it also has been reported for some European *Heleobia* (Giusti and Pezzoli, 1984; Giusti and Manganelli, 1992). States: dioecious (0); parthenogenetic (1).

#### FEMALE REPRODUCTIVE SYSTEM

The female reproductive system provides an important suite of characters that, because of its complexity, has been used extensively to partly or wholly define higher taxa in the Pomatiopsidae (Davis, 1979, and many subsequent papers) and within what we regard as the Hydrobiidae (e.g., Radoman,

1983). Various interpretations have been offered for some of these structures, and in an effort to clarify the situation, we have broken up some functional analogues into several assumed homologous characters.

#### Genitalia

OVARY.—*Posterior Extent*: The ovary lies dorsal to the digestive gland in most hydrobioids. Typically the ovary occupies more than 66% of the visceral coil behind the stomach (e.g., *Spurwinkia salsa*, Davis et al., 1982, fig. 10A), but it sometimes occupies 50% or less (e.g., *Pyrgulopsis manantiali*, Hershler, 1985, fig. 14A). A few of the ovoviviparous cochliopines have extremely small (reduced?) ovaries (e.g., *Durangonella coahuilae* and *Mexithauma quadripaludium*,

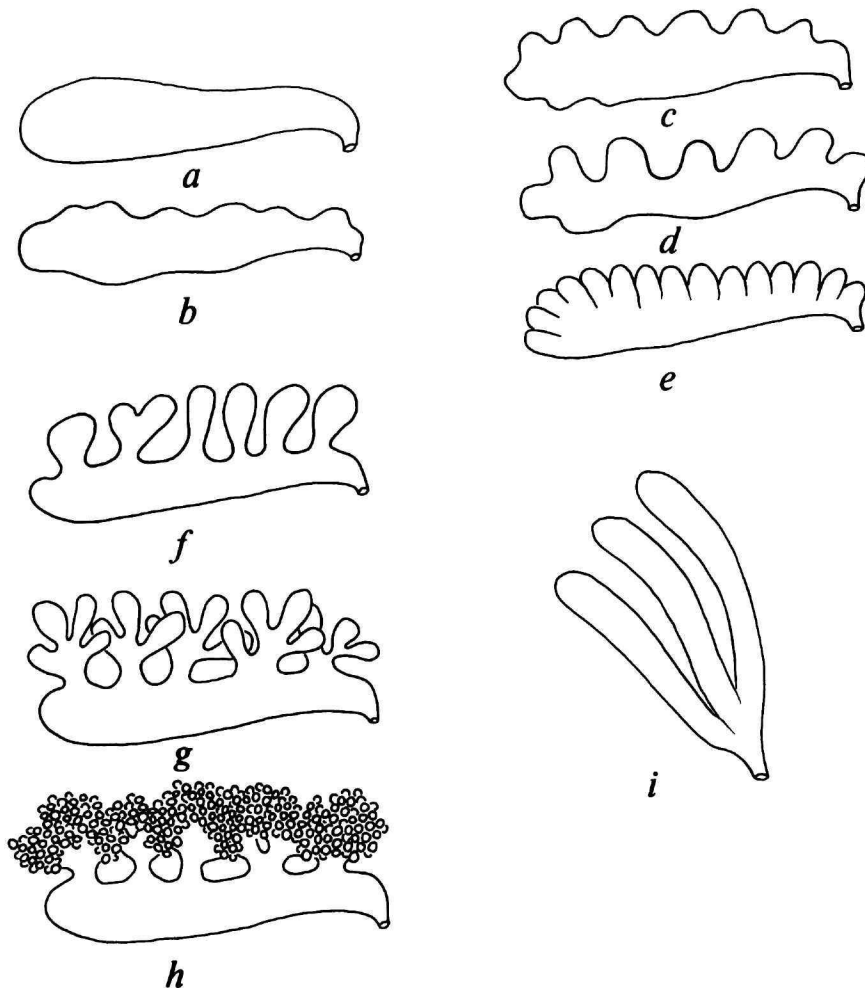


FIGURE 11.—Gonad structure: a,b, simple sac or weakly lobate; c-f, simple, stalked lobes; g,h, compound lobes; i, large, longitudinal lobes.



Hershler, 1985, figs. 30A, 36A, respectively). States: occupies more than 66% of visceral coil behind stomach (0); occupies about 50%–25% of visceral coil behind stomach (1); occupies less than 25% of visceral coil behind stomach (2).

*Anterior Extent:* The ovary overlaps the stomach in some taxa (e.g., *Spurwinkia salsa*, Davis et al., 1982, fig. 10A), but it is entirely behind the stomach in others (e.g., *Erhaia kunmingensis*, Davis et al., 1985, fig. 15C; *Paludiscala caramba*, Hershler, 1985, fig. 22A). States: overlaps stomach (0); does not overlap stomach (1).

*Structure:* Davis (1979) recognized several types of ovary branching patterns in pomatiopsids, and we have slightly modified his arrangement below. A simple tubular sac (Figure 11a) (e.g., *Durangonella coahuilae*, Hershler, 1985, fig. 36A), a lobulate tube (e.g., *Kunmingia kunmingensis*, Davis et al., 1984, fig. 7), and a simple globular sac (e.g., *Gammatricula chinensis*, Davis et al., 1990, fig. 6) are considered to be the same state as variation among them can occur even within a species (e.g., *Erhaia daliensis*, Davis et al., 1985, fig. 5C). Simple, stalked lobes (Figure 11c–f) (e.g., *Antillobia margalefi*, Altaba, 1993, fig. 4), compound lobes (Figure 11g,h) (e.g., *Potamolithus ribeirensis*, Davis and Silva, 1984, fig. 7; *Potamolithus* species, Simone and Moracchioli, 1994, fig. 8), and large, longitudinal lobes (Figure 11i) (e.g., *Hubendickia siamensis*, Davis, 1979, fig. 11A) are other states that we recognize. States: simple, tubular or globular mass, sometimes weakly lobulate (Figure 11b) (0); simple, stalked lobes (1); compound lobes (several lobes with common stem) (2); large, longitudinal lobes (3).

**PERICARDIAL DUCTS.**—*Gonopericardial Duct:* A gonopericardial duct (Figure 12a, gpd) has been recorded in many hydrobioid taxa based on the results of dissection. When investigated in sections, however, it is often difficult to verify the existence of a duct or, more particularly, an open duct. It seems that in many taxa a strand of tissue, perhaps representing a vestigial duct, is present that may be mistaken for an open duct in dissection. A systematic investigation is needed to verify the ontogeny and distribution of this character. Given these difficulties, we treat these two conditions (strand and narrow duct) as a single state. In some pomatiopsids (e.g., *Lacunopsis harmandi*, Davis, 1979, fig. 17; *Fenouilia kreitneri*, Davis et al., 1983, fig. 6A) the gonopericardial canal is well developed and is used for the transport of sperm. States: narrow or vestigial (0); used for sperm transport (1).

*Renopericardial Duct:* A renopericardial duct presumably is present in all taxa (well developed in *Truncatella* (Truncatellidae); e.g., *T. subcylindrica*, Fretter and Graham, 1962, fig. 314), although it has rarely been recorded. In some taxa having renal copulation, the renopericardial duct is used to transport sperm to the pericardium (e.g., *Lacunopsis harmandi*, Davis, 1979, fig. 17). States: not involved in sperm transport (0); involved in sperm transport (1).

**COILED OVIDUCT.**—The coiled (or renal) oviduct (Figure 12a, cov) is readily distinguished from the upper oviduct (uov)

by an abrupt thickening of the oviduct walls, reflecting a change from pavement epithelium to cuboidal or columnar cells. The gonopericardial duct (gpd), if present, opens to the proximal end of this part of the oviduct, which is embedded in the renal organ, appearing to be contained within it. Thus the coiled oviduct externally is covered with renal epithelium but also may be invested with muscle fibres, surrounded by connective tissue, and have pigment. The shape of the coiled oviduct has been used as an important character in species-rank diagnoses (Ponder et al., 1993; Hershler, 1994), but Ponder et al. (1994) showed that there can be considerable variation in coiling patterns within genetically defined species of *Fluvidona*. Within single populations these patterns may be uniform or, especially when complex coiling is found, may vary considerably. The histology of the renal oviduct has been described for several species of *Heleobia* (Marcus and Marcus, 1963; Chukhchin, 1976) and for *Hydrobia ventrosa* (Robson, 1922). It usually consists of a columnar ciliated epithelium, with the cells containing conspicuously granular cytoplasm. Whereas in hydrobiids the coiling patterns of the renal oviduct are relatively simple and are generally not used as a character defining higher groups, this structure is given considerable weight in the Pomatiopsidae (Davis, 1979, and subsequent papers), where the renal oviduct forms complex relationships with other parts of the female system (see below). There is sometimes a layer of muscles in the outer wall of the coiled oviduct (e.g., *Fonscochlea accepta* and *Trochidrobia punicea*, Ponder et al., 1989:77, 82, respectively), and with wider investigation, this feature may prove to be a useful character.

*Connective Tissue on External Surface:* The coiled oviduct of most Hydrobiidae and Pomatiopsidae does not have associated connective tissue, but some connective tissue is present in some species of *Phrantela* (Ponder et al., 1993), and the coiled oviduct is tightly bound in connective tissue in most species of *Beddomeia* (e.g., *B. launcestonensis*, Ponder et al., 1993, fig. 18A,B). States: absent (0); present in small quantity (1); present and tightly binding the coiled oviduct (2).

*Pigmentation:* *Hydrobia* (e.g., *H. truncata*, Hershler and Davis, 1980, fig. 3B–D) and a few related genera (e.g., *Corrosella falkneri*, Boeters, 1970, figs. 6–8; *Pseudamnicola lucensis*, Boeters, 1971, fig. 4; *Adriohydrobia gagatinella*, Radoman, 1977, fig. 4A) and several species of *Pyrgulopsis* (*P. gibba*, Hershler, 1995, fig. 12A; Hershler, unpublished data) have a pigmented coiled oviduct, the pigment being present within the thickened, glandular epithelium (Haase and Bouchet, in press). States: absent (0); present (1).

*Overall Coiling Pattern:* In many hydrobioids the coiled oviduct forms a simple loop (Figure 12b) (e.g., *Heleobia andicola andicola*, Hershler and Thompson, 1992, fig. 31; *Phrantela* species, Ponder et al., 1993, figs. 87A,D, 92B, 96A), but in other taxa several loops are present (Figure 12c,d) (e.g., *Hydrobia truncata*, Hershler and Davis, 1980, fig. 3B–D; *Beddomeia* species, Ponder et al., 1993, figs. 18A,B, 20A,D;

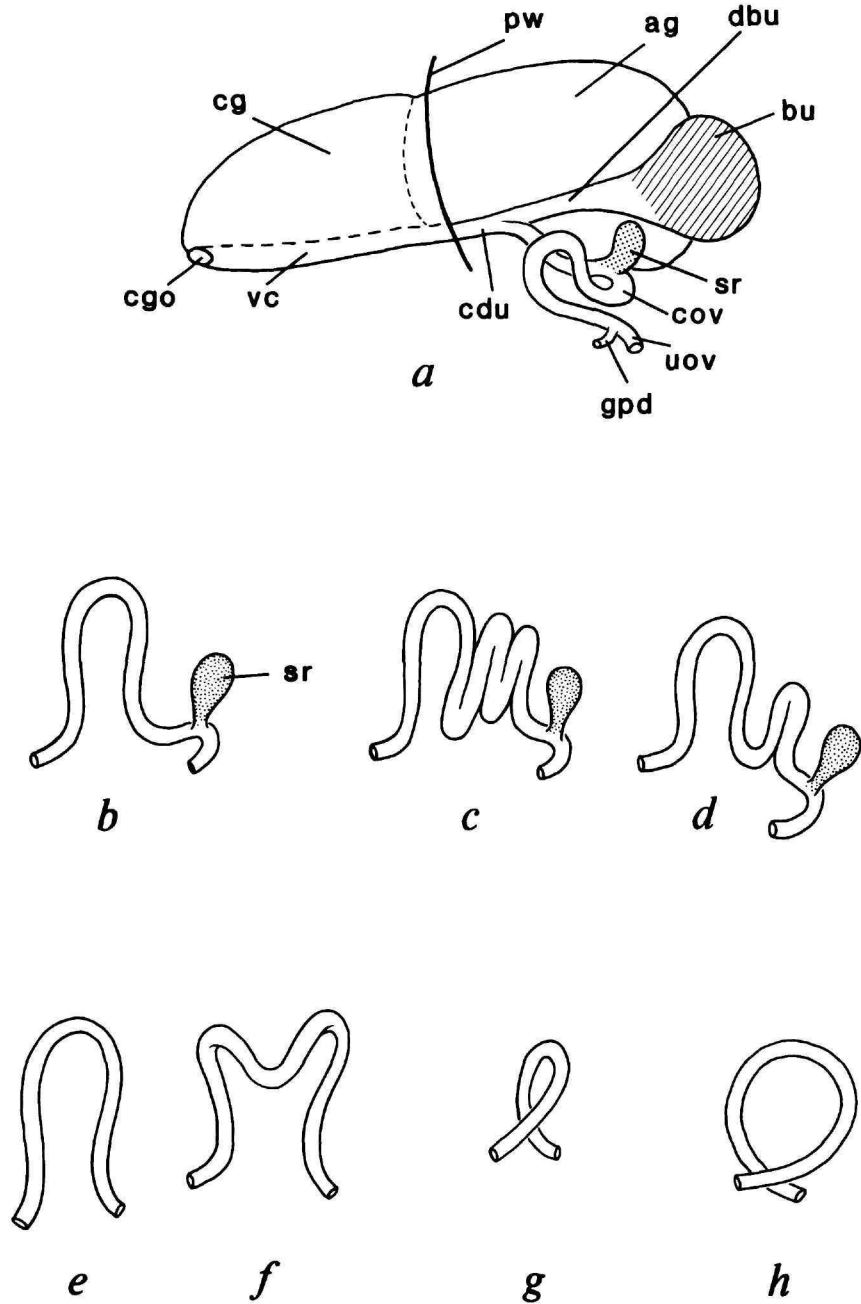


FIGURE 12.—General aspect of distal female genitalia, viewed from left side (*a*); overall pattern of coiled oviduct (*b-d*); shape of initial or primary bend of coiled oviduct (*e-h*): *b*, coiled oviduct with single bend or loop; *c, d*, coiled oviduct with two or more bends or loops; *e, f*, U-shaped initial loop; *g*, tight circle; *h*, open circle. (ag = albumen gland, bu = bursa copulatrix, cdu = common oviduct, cg = capsule gland, cgo = capsule gland opening, cov = coiled oviduct, dbu = bursal duct, gpd = gonopericardial duct, pw = pallial wall, sr = seminal receptacle, uov = upper oviduct, vc = ventral channel of capsule gland.)

*Pyrgulopsis brandi*, Hershler, 1994, fig. 4e), although these conditions are perhaps not all homologous. A few triculinaes have no loop (e.g., *Neotricula aperta*, Davis et al., 1976, fig. 8A; *Halewisia expansa*, Davis, 1979, fig. 13A). States: single bend or loop (0); two or more bends or loops (1); no loop (2).

**Initial or Primary Bend:** Most hydrobioids have a U-shaped loop (Figure 12e,f) (see examples for state "0" of previous character, together with *Pomatiopsis lapidaria*, Davis, 1967, pl. 8) or a variation of this in which a tight, circular loop is formed (Figure 12g) (e.g., some *Tomichia* species, Davis, 1981, fig. 19B; several cochliopine species, Hershler and Thompson, 1992, figs. 21a, 60a; *Pyrgulopsis* species, Hershler, 1994, figs. 4b,d, 5b,d). These two types of loops grade into one another and can vary within genera or even species, so we regard them as the same state. In some Triculinae the renal oviduct forms an open, circular loop (Figure 12h) (e.g., Davis, 1979, figs. 11A, 12C, 15C,D), whereas in others there is a tight loop with the bursa outside it as in hydrobiids (e.g., *Kunmingia kunmingensis*, Davis et al., 1984, fig. 8; see also fig. 21 for a summary of this character in the Triculinae). States: simple, U-shaped bend (0); open, circular loop (1); no loop (?).

**Extent of Posterior Loop:** In most hydrobioids the coiled oviduct is short relative to the albumen gland and bursa (e.g., *Hydrobia* species, Falniowski, 1987, fig. 7; *Tatea huonensis*, Ponder et al., 1991, fig. 10; many cochliopines, Hershler and Thompson, 1992; figs. 11a, 15, 21a, 23a; *Pyrgulopsis* species, Hershler, 1994, figs. 4a–d, 5). Some Australasian taxa related to *Beddomeia* (Ponder et al., 1993, figs. 20A,D, 38A, 43, 96A) and some European forms (e.g., *Pseudamnicola lucensis*, Boeters, 1971, fig. 4) have a long posterior loop (separate from the initial bend) of the coiled oviduct, sometimes resulting in a highly posterior position of the seminal receptacle. States: short (0); long (1).

**Posterior-Loop Position Relative to Albumen Gland:** In most hydrobioids the posterior loop lies against the left side of the albumen gland. In the South American *Andesipyrgus sketi*, the coiled oviduct loops around to the right side of the albumen gland (Hershler and Velkovrh, 1993, fig. 4a). States: on left side (0); on right side (1).

**Bursal-Duct Entry to Coiled Oviduct:** In hydrobioids the bursal duct opens to the distal end of the coiled section of the oviduct at different points relative to the posterior pallial wall. This character is inapplicable in taxa lacking a ventral channel. (Distal to the point where the oviduct and bursal duct join, we refer to the oviduct as the "common oviduct"; Figure 12a, cdu.) The duct may open slightly in front of the posterior pallial wall (e.g., *Cincinnati winkleyi*, Davis and Mazurkiewicz, 1985, fig. 9A), well in front of the posterior pallial wall (e.g., *Beddomeia kershawi*, Ponder et al., 1993, fig. 20A), at the posterior pallial wall (e.g., *Nymphophilus minckleyi*, Hershler, 1985, fig. 7B), slightly behind the posterior pallial wall (e.g., *Potamolithus ribeirensis*, Davis and Silva, 1984, fig. 8A; *Lepyrium showal-*

*teri*, Thompson, 1984, fig. 11; *Pyrgulopsis archimedis*, Hershler, 1994, fig. 4a), or well behind the posterior pallial wall (e.g., *Jardinella eulo*, Ponder and Clark, 1990, fig. 34F). These states are correlated in some cases with the extent of the albumen gland in the pallial roof. States: at posterior pallial wall (0); slightly behind posterior pallial wall (1); slightly in front of posterior pallial wall (2); well in front of posterior pallial wall (3); well behind posterior pallial wall (4); inapplicable (?).

**Opening Point of Oviduct to Oviduct Glands:** The opening point of the oviduct (e.g., the egg-conducting tube) into the oviduct glands varies considerably between taxa and may be an important character in distinguishing major clades. In most hydrobioids the oviduct opens at the junction of the albumen and capsule glands (e.g., *Hydrobia truncata*, Hershler and Davis, 1980, fig. 3A; *Amnicola limosa*, Hershler and Thompson, 1988, fig. 8a,b; *Beddomeia* species, Ponder et al., 1993). In one putative cochliopine, *Andesipyrgus sketi* (Hershler and Velkovrh, 1993, fig. 4a), the oviduct opens at the junction of the albumen and capsule glands, but in all other members of the subfamily it opens to the posterior end of the (recurved) albumen gland (see examples in Hershler and Thompson, 1992), with the exception of *Emmericiella novimundi* (Hershler and Thompson, 1992, fig. 27), in which the oviduct is shown as opening to the middle of the gland. In the latter taxon, however, it is possible that the recurved part of the albumen gland has fused with the rest of the gland. In pomatiopsids the oviduct enters either the posterior end (or close to it) (e.g., *Pomatiopsis lapidaria*, Davis, 1967, pl. 7: fig. 1; *Neotricula aperta*, Davis et al., 1976, fig. 8A; *Robertiella kaporensis*, Davis and Greer, 1980, fig. 6A) or the middle of the albumen gland (e.g., *Hydrorissia elegans*, Davis, 1979, fig. 12C; *Tomichia ventricosa*, Davis, 1981, fig. 18; *Tricula montana*, Davis, Rao, and Hoagland, 1986, fig. 5). States: at junction of albumen gland and capsule gland (0); at middle part of albumen gland (1); at posterior end of albumen gland (including posterior end curved anteriorly) (2).

**SPERM DUCT.**—The sperm duct (fide Davis, 1967:36) appears to be functionally analogous but possibly nonhomologous in different clades. It is found in those taxa with a sperm tube (pomatiopsids, amnicolines, cochliopines) and provides a means for sperm to enter the posterior oviduct for storage and, ultimately, fertilization. We recognize the following types, which we treat as separate characters.

**Type A Sperm Duct:** This duct (Figure 13a, sdu) is located behind the duct to the albumen gland and is assumed to have been split off in a posterior direction from the bursal duct (e.g., *Pomatiopsis lapidaria*, *Oncomelania hupensis formosana*, Davis, 1967, pls. 8, 23, respectively). The very short sperm duct of amnicolines (e.g., *Amnicola limosa*, Hershler and Thompson, 1988, fig. 8b) also may be referable to this type. States: absent (0); present (1); inapplicable (?).

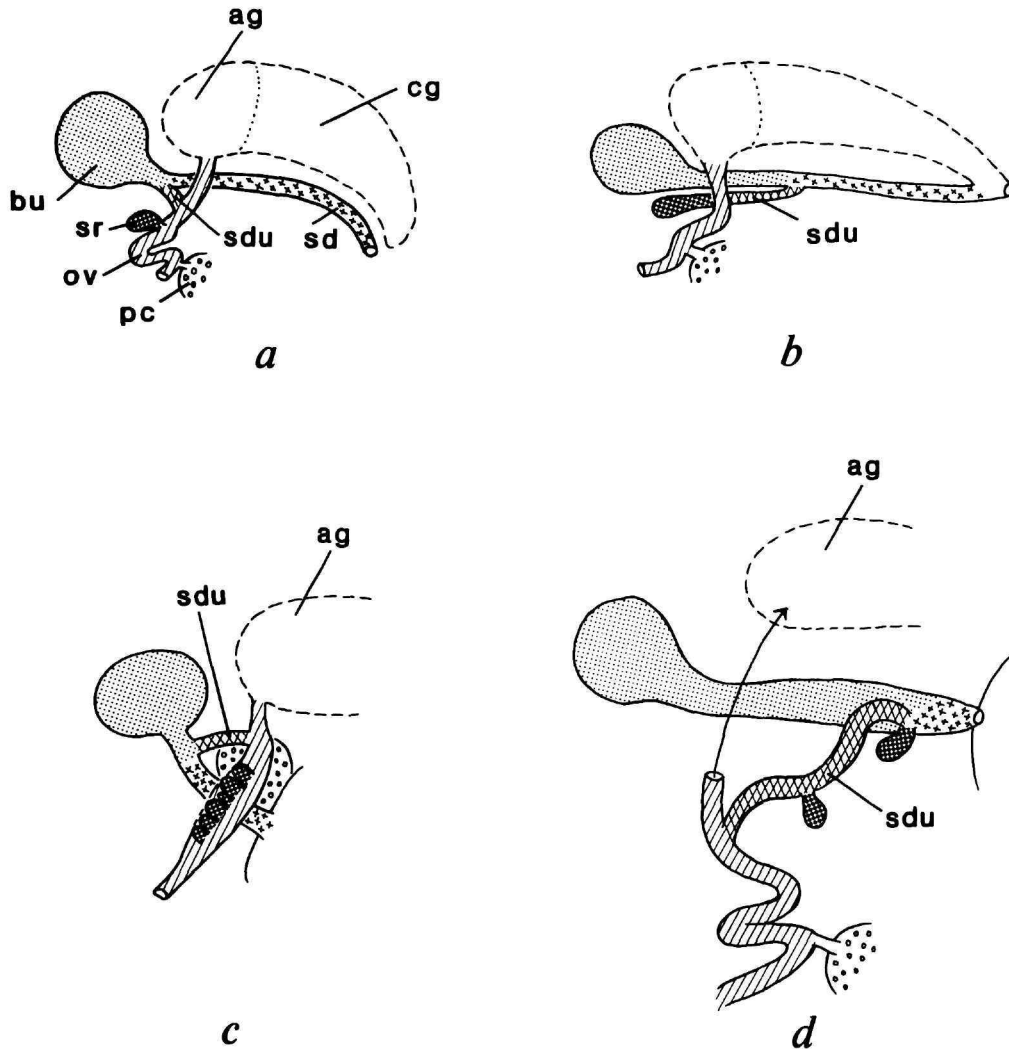


FIGURE 13.—Distal female genitalia (viewed from right side) showing four types of sperm ducts (sdu): a, type A (*Pomatiopsis lapidaria*); b, type B (*Spurwinkia salsa*); c, type C (*Gammatricula chinensis*); d, type D (*Stenothyra hunanensis*). (ag = albumen gland, bu = bursa copulatrix, cg = capsule gland, ov = oviduct, pc = pericardium, sd = spermathecal duct, sdu = sperm duct, sr = seminal receptacle.)

**Type B Sperm Duct:** This duct (Figure 13b, sdu) is located in front of the duct to the albumen gland and is assumed to have been split off in an anterior direction from the bursal duct (sometimes appearing to be a continuation of the seminal receptacle duct). The posterior bursal duct remains intact (e.g., *Spurwinkia salsa*, Davis et al., 1982, fig. 12). The type B sperm duct is sometimes coiled (e.g., *Mexipyrgus carranzae*, Hershler, 1985, figs. 42, 43). States: absent (0); present (1); inapplicable (?).

**Type C Sperm Duct:** This duct (Figure 13c, sdu) is located behind the duct to the albumen gland and may be a combination

of gonopericardial duct and bursal duct (e.g., *Neotricula aperta*, Davis, Rao, and Hoagland, 1986, fig. 7A; *Gammatricula chinensis*, Davis et al., 1990, fig. 7). States: absent (0); present (1); inapplicable (?).

**Type D Sperm Duct:** This duct (Figure 13d, sdu) is located in front of the duct to the albumen gland and is assumed to have been split off in an anterior direction from the bursal duct. It appears also to include part of the coiled oviduct containing the seminal receptacle(s) (e.g., *Stenothyra hunanensis* (Stenothyridae), Davis, Chen, et al., 1988, fig. 6). States: absent (0); present (1); inapplicable (?).

### Sperm Storage

Various sites for sperm storage have evolved independently in hydrobioid snails. We recognize two main types, containing either oriented sperm or unoriented sperm. The former is generally referred to as the seminal receptacle(s) and the latter as the bursa copulatrix.

#### Sites with Oriented Sperm

Among hydrobioid snails, various structures may contain oriented sperm. In addition to those listed below, each of the four types of sperm duct also can store oriented sperm, either within the duct or in a pouch opening to the duct.

**STRUCTURES APART FROM TRUE SEMINAL RECEPTACLE.—**  
**Coiled Oviduct:** In some hydrobioids sperm are stored in the coiled oviduct, sometimes in addition to being present in a seminal receptacle, and sometimes in the absence of a seminal receptacle (e.g., *Fontigens nickliniana*, Hershler et al., 1990, fig. 10c). Hershler and Davis (1980:205) stated that in *Hydrobia truncata*, oriented sperm are stored within the oviduct coils, but the seminal receptacle did not contain sperm, although the latter requires verification. States: sperm absent (0); sperm present (1).

**Albumen Gland:** Oriented sperm are stored in the albumen gland or in a pouch off the albumen gland in several cochliopines (e.g., *Coahuilix hubbsi* and *Paludiscala caramba*, Hershler, 1985, figs. 17A, 22C, respectively). States: sperm absent (0); sperm present (1).

**Bursal Duct:** Oriented sperm are stored in the bursal duct or in a pouch arising from or within this duct in the pomatiopsid *Robertsia kaporensis* (Davis and Greer, 1980, figs. 6E, 7). States: sperm absent (0); sperm present (1).

**TRUE SEMINAL RECEPTACLE.—**We define the seminal receptacle (found in most hydrobiids and pomatiopsids) as a sperm sac originating from the renal oviduct (see Ponder and Lindberg, 1997), containing oriented sperm and lined with a thin epithelium. A seminal receptacle is found in most hydrobioids but is occasionally absent (e.g., *Fontigens nickliniana*, Hershler et al., 1990, fig. 3c,d). The shape, position, size, and length of its duct are treated below as separate characters. States: present (0); absent (1).

**Shape:** The shape of the seminal receptacle may vary within a species depending on the amount of sperm it contains and also may vary considerably among congeners (e.g., *Pyrgulopsis*, Hershler, 1994, figs. 4, 5). The presence of sperm is easily discerned in dissection by the silvery sheen of the pouch, which may be elongate (Figure 14a,b) (e.g., *Pachydrobia bavayi*, Davis, 1979, fig. 14A; *Phrantela* species, Ponder et al., 1993) or pyriform (Figure 14c) to globular (Figure 14d,e) (e.g., *Beddomeia* species, Ponder et al., 1993). States: elongate (0); pyriform to globular (1).

**Number:** A single true seminal receptacle is found in the great majority of hydrobioids, but a few taxa (e.g., *Sadleriana schmidti*, Bole, 1972, pl. 4: figs. 2, 3; *Pauluccia minima*, Giusti

and Pezzoli, 1980, fig. 22C; *Anagastina vidrovini*, Radoman, 1983, fig. 21; *Dalmanella fluviatilis*, Radoman, 1983, fig. 22; *Orientalina callosa*, Bodon et al., 1992, fig. 17) have two pouches arising from the coiled oviduct, and *Baicalia* has numerous small pouches (Radoman, 1983, figs. 111A-C, 112A,B). In most cases where multiple seminal receptacles are present, all of the pouches open to the posterior arm of the oviduct coil; however, in *Probythinella* one of the two pouches opens to the oviduct distal to the coil (Hershler, 1996, fig. 5A,B), perhaps providing an additional character. States: one (0); two (1); more than two (2); none (3).

**Position Relative to Bursa Copulatrix:** This refers to the position of the seminal receptacle relative to the bursa copulatrix, prior to the oviduct being uncoiled. As with the character above, considerable variation can occur within a genus (e.g., *Beddomeia*, Ponder et al., 1993, fig. 7a; *Pyrgulopsis*, Hershler, 1994, figs. 4, 5). The seminal receptacle is entirely posterior to the bursa in *Pyrgulopsis manantiali* (Hershler, 1985, fig. 14B). States: all or mostly anterior to bursa (Figure 14f,g) (0); lying against bursa (Figure 14h-k) (1); behind bursa (Figure 14l) (2).

**Duct:** The duct of the seminal receptacle is usually short in hydrobioids (Figure 14n,o) (rarely exceeding the length of the receptacle), although in a few taxa, such as *Nurekia triculi-formis* (Izzatullaev et al., 1985, pl. 1: figs. 8, 9) and *Mesobia pristina* (Hershler and Thompson, 1992, fig. 46b), the duct is very long (Figure 14p). Many pomatiopsids, however, have elongate ducts that form broad loops along with the coiled oviduct (e.g., *Hydrorissioia elegans*, Davis, 1979, fig. 12C; *Pachydrobiella brevis*, Davis, 1979, fig. 15C,D). States: no distinct duct (Figure 14m) (0); distinct duct shorter than seminal receptacle (1); duct much longer than seminal receptacle (2).

#### Sites with Unoriented Sperm

**POSTERIOR BURSA COPULATRIX.—**The bursa copulatrix is located mainly or entirely behind the posterior pallial wall and is connected by its duct to the oviduct. The bursa contains a mass of unoriented sperm and yolk granules and is lined with a columnar epithelium. Anterior to the junction of the oviduct and bursal duct, the common oviduct extends forward to become the ventral channel of the capsule gland (in most hydrobiids) or to connect with the sperm tube (amnicolines, cochliopines, pomatiopsids). The posterior bursa copulatrix is absent in a number of hydrobioid taxa (e.g., *Pauluccia minima*, Giusti and Pezzoli, 1980, fig. 22c; *Islamia pusilla*, Giusti et al., 1982, fig. 2.1; *Balconorbis uvaldensis*, Hershler and Thompson, 1992, fig. 17a).

**Position Relative to Albumen Gland (1):** The bursa is usually located on the left side of the posterior end of the albumen gland in hydrobiids. A posteroventral position is typical of most pomatiopsines (e.g., *Pomatiopsis lapidaria*, Davis, 1967, pl. 7: fig. 1; *Tomichia ventricosa*, Davis, 1981, fig. 18) and some hydrobiids (e.g., *Potamolithus* species,

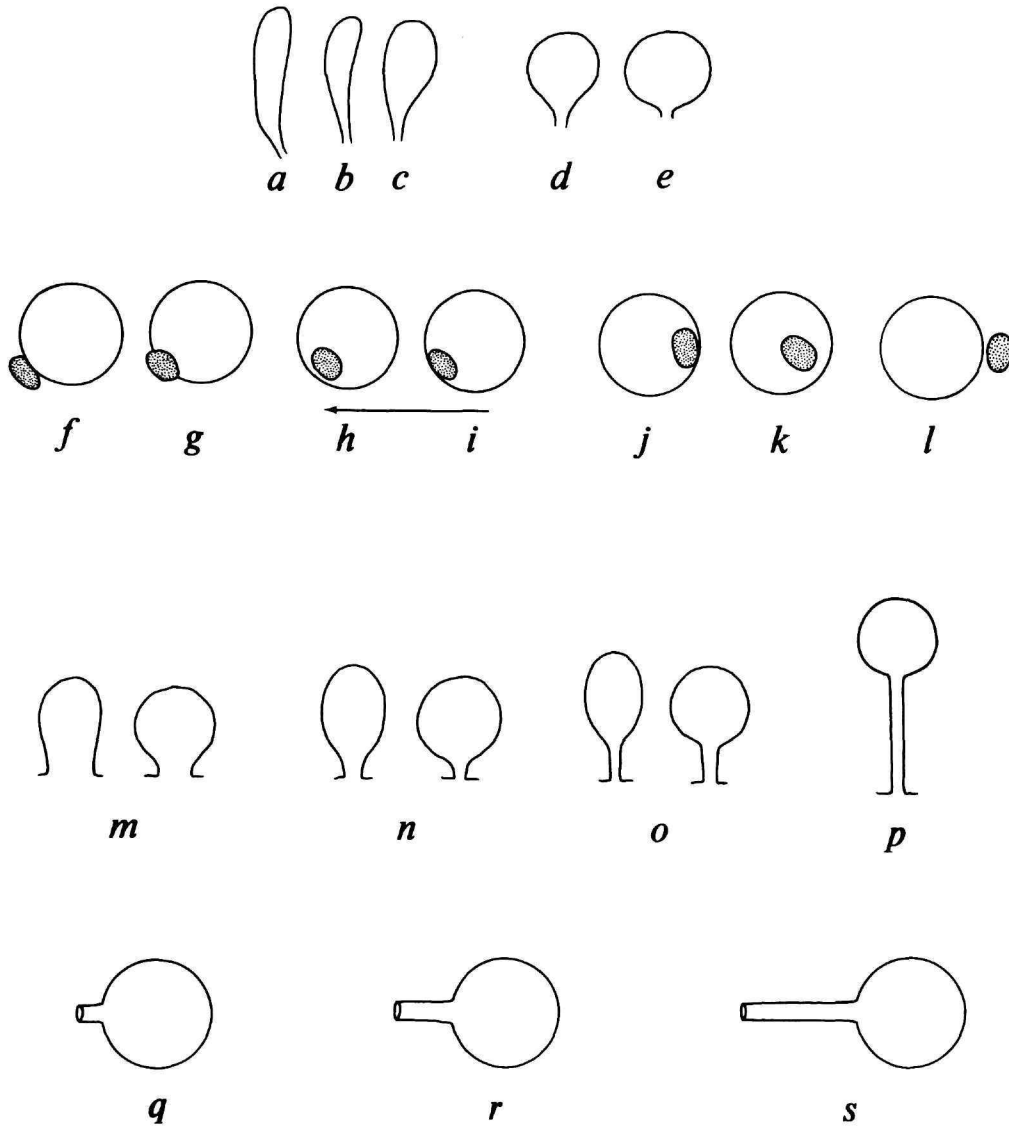


FIGURE 14.—Shape of seminal receptacle (a–e); position of seminal receptacle (stippled) relative to bursa copulatrix (f–l), viewed from left side, arrow points anteriorly; length of seminal receptacle duct (m–p); length of bursal duct (q–s): a, b, elongate seminal receptacle; c, pyriform seminal receptacle; d, e, globular seminal receptacle; f, g, seminal receptacle entirely or mostly anterior to bursa; h–k, seminal receptacle lying against bursa; l, seminal receptacle posterior to bursa; m, seminal receptacle without duct; n, o, seminal receptacle duct short; p, seminal receptacle duct long; q, bursal duct short; r, bursal duct medium length; s, bursal duct long.

Simone and Moracchioli, 1994, fig. 9). In triculines the bursa abuts the posterior end of the albumen gland, and if it overlaps, it does so on the right side (e.g., *Neotricula aperta*, sometimes overlapping the right side, Davis et al., 1976, figs. 8A,C; *Gammatricula chinensis*, distinctly overlapping the right side, Davis et al., 1990, fig. 6; *Neotricula jinghongensis*, entirely on the right side, Davis, Guo, Hoagland, Chen, Zheng, et al., 1986,

fig. 14). States: on left side (0); on right side (1); ventral (2); entirely behind (3).

*Position Relative to Albumen Gland* (2): The bursa usually lies against the albumen gland in hydrobioids, but in some taxa it may sit in a depression in the gland (e.g., *Cincinnatia integra*, Hershler and Thompson, 1996, fig. 5A) or lie deeply embedded within it (i.e., completely covered by the gland; e.g., *Stiobia*

*nana*, Thompson and McCaleb, 1978, fig. 4B). States: superficial (0); in depression (1); entirely embedded (2).

**Orientation Relative to Albumen Gland:** Bursal shape and orientation could be treated as a single character complex, although we list them separately (the former is treated in the Appendix). The long axis of the bursa may be transverse (or vertical) relative to the albumen gland (e.g., *Kerkia kusceri*, Radoman, 1983, fig. 58B; *Birgella subglobosa*, Thompson, 1984, fig. 83; *Nymphophilus minckleyi*, Hershler, 1985, fig. 7B; *Hydrobia truncata*, Davis, Forbes, et al., 1988, fig. 15A), longitudinal, which is typical of many pomatiopsids (e.g., *Neotricula aperta*, Davis et al., 1976, fig. 8D; *Halewisia expansa*, Davis, 1979, fig. 13A) and some hydrobiids (e.g., *Phrantela marginata* and *Victodrobia elongata*, Ponder et al., 1993, figs. 87A,B, 113B, respectively), or oblique (*Tatea huonensis*, Ponder et al., 1991, fig. 10). We regard bursae of a more or less globular shape (i.e., long axis not discernable) (e.g., *Pachydrobiella brevis*, Davis, 1979, fig. 15D; *Neotricula cristella*, Davis et al., 1992, fig. 65; *Beddomeia* species, Ponder et al., 1993, fig. 7F,G; *Fluminicola virens*, Hershler and Frest, 1996, fig. 18C) to be a separate state. States: transverse (0); longitudinal (1); anterior oblique (2); posterior oblique (3); bursa globular (4).

**Position Relative to Seminal Receptacle and Its Duct:** The bursa is normally positioned on the outside of the seminal receptacle and its duct, but in various triculines (e.g., *Pachydrobia brevis*, Davis, 1979, fig. 15D) it is encircled by the seminal receptacle duct. This character is correlated with the length of the seminal receptacle duct. States: bursa on outside of seminal receptacle duct (0); bursa encircled by seminal receptacle duct (1).

**BURSAL DUCT(S).—Origin:** Although the bursal duct may originate from any point around the circumference of the bursa, we recognize the following conditions (also see Ponder et al., 1993, fig. 7F–L): anterodorsal (e.g., *Pseudamnicola lucensis*, Radoman, 1978, fig. 8; *Ventrosia stagnorum*, Radoman, 1983, fig. 8B; *Micropyrgula stankovici*, Radoman, 1983, fig. 88A); anteroventral (e.g., *Hemistomia* species, Ponder, 1982a, figs. 107–112; *Cavernisa zaschevi*, Radoman, 1983, fig. 60; *Fontigens nickliniana*, Hershler et al., 1990, fig. 3d; *Tatea huonensis*, Ponder et al., 1991, fig. 10); anterior (e.g., *Turcorientalina anatolica*, Radoman, 1983, fig. 49; *Pontobelgrandiella nitida*, Radoman, 1983, fig. 59B; *Antroselates spiralis*, Hershler and Thompson, 1992, fig. 11b; *Pyrgulopsis* species, Hershler, 1994, fig. 5b,f); posterodorsal (e.g., *Tomic-hia natalensis*, Davis, 1981, fig. 20A); posteroventral (e.g., *Paladilhiopsis grobbeni*, Radoman, 1983, fig. 56C; *Texadina sphinctosoma*, Hershler and Thompson, 1992, fig. 68a; “*Phrantela*” *singularis*, Ponder et al., 1993, fig. 102D); and posterior (e.g., *Fontigens tartarea*, Hershler et al., 1990, fig. 33; *Victodrobia elongata*, Ponder et al., 1993, fig. 113B). We recognize that division of states is complicated somewhat by both the shape and position of the bursa (e.g., difficulty of distinguishing between anteroventral and anterodorsal origin

when the bursa is narrow and horizontal). States: anteroventral (0); anterodorsal (1); anterior (2); posterodorsal (3); posteroventral (4).

**Number:** Most hydrobioids so far investigated have a single duct connecting the bursa copulatrix to the oviduct. In several nymphophiline taxa, however, the bursa has both a “normal” anterior duct connecting to the oviduct at the junction of the albumen and capsule glands and a slender, posterior duct that opens to the oviduct slightly proximal to the above (e.g., *Cincinnatiata integra*, Hershler and Thompson, 1996, fig. 5A,B; Hershler, unpublished data). States: one duct (0); two ducts (1).

**Position:** As with the bursa copulatrix, the bursal duct of hydrobioids usually lies against the albumen gland, but in some taxa it may be shallowly (e.g., *Pyrgulopsis ogorhaphe*, Thompson, 1977, fig. 10A) or deeply embedded (e.g., *Gillia altilis*, *Fluminicola* sp., *Birgella subglobosa*, Thompson, 1984, figs. 48, 53, 83, respectively). This character may be partly correlated with that describing similar relationships between the bursa and albumen gland (see “Position Relative to Albumen Gland (2),” above). States: superficial (0); partly embedded (1); entirely embedded (2).

**Opening:** The bursal duct opens to one of the following: coiled oviduct (most hydrobioids except cochliopines, amnicolines, and some pomatiopsids, e.g., *Tricula*, Davis, Rao, and Hoagland, 1986, fig. 7B), spermathecal duct derived from ventral channel (cochliopines, amnicolines, some pomatiopsids), or “spermathecal duct” (we have called this the cordiseminal duct (see “Pallial Genital Openings(s),” below)) derived from a gonopericardial duct (some triculines). States: bursal duct opens to coiled oviduct (0); bursal duct opens to spermathecal duct (derived from ventral channel) (1); bursal duct opens to the cordiseminal duct (2).

**Length:** The bursal duct may be extremely short or virtually absent (Figure 14q) (e.g., *Fontigens nickliniana*, Hershler et al., 1990, fig. 3d; *Mexipyrgus carranzae*, Hershler and Thompson, 1992, fig. 48b; many pomatiopsids), intermediate in length (Figure 14r) (e.g., *Potamolithus ribeirensis*, Davis and Silva, 1984, fig. 10A), or elongate (Figure 14s) (e.g., *Adrioinsulana conovula*, Radoman, 1978, fig. 7; *Mesobia pristina*, Hershler and Thompson, 1992, fig. 46b). States: about 50%–100% of bursa length (0); less than 50% of bursa length (1); longer than bursa (2).

**Opening of Sperm Duct:** In most hydrobioids only the bursal duct(s) issues from the bursa, but in a few pomatiopsids (e.g., *Halewisia expansa*, Davis, 1979, fig. 13A) both the sperm duct and the bursal duct open separately to the bursa. Other pomatiopsids have a possibly intermediate state in which the sperm duct (type A) opens to the bursal duct close to the bursa (e.g., *Pomatiopsis lapidaria*, Davis, 1979, fig. 9; but note that the bursal duct and sperm duct open separately to the bursa in *P. cincinnatiensis*, Davis, 1979, fig. 9; *Neotricula*, Davis, Rao, and Hoagland, 1986, fig. 7A). States: bursal duct only (0); sperm duct and bursal duct (1).

**ANTERIOR SPERM SAC.**—The nonglandular end of the ventral channel is, in many taxa, expanded into a vestibule that is associated with the female genital opening. This is used as an anterior sperm pouch in some of the outgroups (Iravadiidae, Ponder, 1984) and in *Botryphallus epidauricus* (Ponder, 1990, fig. 8E), but it has not been recorded in other hydrobioids. This sperm sac may be positioned near the anterior end of the capsule gland and have a posterior duct to the gland (e.g., *Botryphallus epidauricus*, Ponder, 1990, fig. 8E), or it may lie alongside the posterior end of the gland and have either an anterior duct or a separate pallial opening (e.g., various iravadiids, Ponder, 1984). Ponder (1988b) suggested that this sac has been independently derived from the ventral channel in different groups. States: absent, ventral channel simple or with small vestibule (0); present, at anterior end of capsule gland, with posterior duct (1); present, at posterior end of capsule gland, with anterior duct (2); present, at posterior end of capsule gland, with separate pallial opening (3).

#### Sites with Sperm of Unknown Orientation

**SPERM STORAGE IN SPERM TUBE.**—An anterior pallial pouch (off the sperm tube) occurs in the cochliopine *Stygopyrgus bartonensis* (Hershler and Longley, 1986a, fig. 25A). This structure may be analogous to an anterior bursa copulatrix (Ponder, 1990:307). States: absent (0); present (1).

#### Oviduct Glands

The oviduct glands lie along the right side of the pallial cavity and bulge posteriorly into the kidney. They consist of two usually distinct glands, the posterior albumen gland and an anterior capsule gland.

**HISTOLOGY.**—Ponder (1988b) showed that, within the Rissoidae, the oviduct glands of some groups (e.g., *Caecum corneum*, Marcus and Marcus, 1963, fig. 75; *Botryphallus epidauricus*, Ponder, 1990, fig. 8D; also rissoids, barleoids) have a simple lining of tall columnar cells, whereas others (including hydrobiids) have a complexly folded glandular epithelium (e.g., *Hydrobia ventrosa*, Robson, 1922, fig. 10; *Bithynia tentaculata*, Lilly, 1953, fig. 5; *Oncomelania hupensis nosophora*, Roth and Wagner, 1957, pl. 5: figs. 34–37). States: simple (0); complex (1).

**ALBUMEN GLAND.**—The albumen gland lies posterior to the capsule gland and is entirely or partly visceral.

**Extension into Pallial Roof:** The albumen gland may end at or near the posterior end of the pallial cavity (e.g., *Fonsocochlea zeidleri*, Ponder et al., 1989, fig. 47; *Probythinella emarginata*, Hershler, 1996, fig. 5A) or may have a small (e.g., *Pyrgulopsis greggi*, Hershler, 1995, fig. 16A; *Cincinnati integra*, Hershler, 1996, fig. 5A) or large (e.g., *Pseudotricula eberhardi*, Ponder, 1992, fig. 3A; *Victodrobia elongata*, Ponder et al., 1993, fig. 113B) fraction of its length extending into the pallial cavity. Extension of the gland into the pallial roof may

vary considerably within genera (e.g., *Beddomeia* and related genera, Ponder et al., 1993; *Pyrgulopsis*, Hershler, 1994, figs. 4, 5). States: albumen gland abuts posterior wall of pallial cavity (0); less than 33% of albumen gland extends into pallial cavity (1); 33% or more of albumen gland extends into pallial cavity (2).

**Atrophy:** The albumen gland is well developed in most hydrobioids (i.e., subequal to the capsule gland in size), but it is extremely reduced (in length and width) in several of the ovoviviparous cochliopinids (e.g., *Durangonella coahuilae*, *Mexipyrgus carranzae*, Hershler, 1985, figs. 36A, 42A,B, respectively). States: albumen gland subequal to capsule gland (0); albumen gland very reduced relative to capsule gland (1).

**Shape:** The albumen gland is typically a simple, slightly curved structure in hydrobioids, but a U-shape condition occurs in some cochliopines (e.g., *Mexithauma quadripaludium*, Hershler, 1985, fig. 30A) and possibly in some pomatiopsids (e.g., *Pachydrobiella brevis*, Davis, 1979, fig. 15E). In extreme cases (several ovoviviparous cochliopine genera) the gland is developed into a complex series of coils (e.g., *Mexipyrgus carranzae*, Hershler, 1985, figs. 42, 43). States: simple (0); U-shaped (1); complexly coiled (2).

**CAPSULE GLAND.**—The capsule gland lies immediately anterior to the albumen gland, within the pallial cavity.

**Shape:** As with the albumen gland, the capsule gland typically is simple in shape. In several ovoviviparous cochliopines, however, the anterior portion of the gland is muscular and strongly reflexed (e.g., *Cochliopina milleri*, Hershler, 1985, fig. 26E; *Mexithauma quadripaludium*, Hershler, 1985, fig. 30C). States: simple (0); U-shaped (1).

**Glandular Zones:** Whereas the capsule gland appears as a single homogeneous unit in many hydrobioids, distinct glandular zones are present in many taxa (e.g., *Fluviopupa* species, Ponder, 1982a, figs. 49, 53, 54, 56; *Pyrgulopsis* species, Hershler, 1994, figs. 4, 5). The histochemistry of these different areas has not been investigated, but in histological preparations using trichrome stains, they sometimes stain differently in separate clades. This suggests a useful area for future investigation and a character that can ultimately be considerably refined. States: capsule gland homogeneous (0); two or more glandular zones present (1).

**Ventral Wall:** In most hydrobioids the female genital duct closes over during early ontogeny (Johansson, 1948). The few taxa with an open genital duct may not, however, necessarily be plesiomorphic as this condition may reflect paedomorphosis. Most hydrobioids have a ventral channel, but in those taxa with a spermathecal duct, the ventral wall of the capsule gland may be thin (e.g., *Amnicola limosa*, Hershler and Thompson, 1988, fig. 8d), glandular (e.g., *Pomatiopsis lapidaria*, *Oncomelania hupensis formosana*, Davis, 1967, pl. 9: fig. 5, pl. 23: fig. 1, respectively), or, in the case of the cochliopine *Subcochliopa trochus* (Hershler and Thompson, 1992, fig. 3a), folded so as to comprise a false ventral channel. States: open (0); with ventral channel (no spermathecal duct) (1); simple, thin-walled (with



spermathecal duct) (2); glandular (with spermathecal duct) (3); comprising a false ventral channel (with spermathecal duct) (4).

**Longitudinal Folds in Ventral Channel:** The longitudinal folds (i.e., "bolsters," fide Davis and Silva, 1984:84–85) are located on the left side of the ventral channel. These are well developed in some taxa but not in others. The distribution of this character within the Risssooidea has been described by Ponder (1988b, fig. 3), but it is insufficiently described within hydrobioids to permit recognition of states at present.

**Relationship between Capsule Gland and Ventral Channel:** The ventral channel overlaps the left side of the capsule gland to a varying degree among hydrobioids and, although representing a continuous character, may be useful in distinguishing among groups. States: ventral channel below capsule gland (0); ventral channel slightly overlapping capsule gland (1); ventral channel markedly overlapping capsule gland (2).

#### *Point of Entry of Sperm*

Copulation in hydrobioids is usually via an anterior opening to the glandular oviduct. This is not necessarily the plesiomorphic state, however, as several outgroups (iravadiids and vitrinellids) often have a posterior opening and a pallial bursa copulatrix, which first receives the sperm. In hydrobioids the ventral channel may be traversed at least in part by the penis, but it is more likely that the penis only enters the anteriormost section (i.e., vestibule). The sperm are probably carried to the posterior bursa copulatrix by cilia in the sperm duct of the ventral channel. In cochliopines and pomatiopsids there is a separate sperm duct ("spermathecal duct," fide Davis, 1967:38) that opens to either the anterior (Pomatiopsinae and various Cochliopinae) or posterior (Triculinae and various Cochliopinae) pallial cavity. Ponder (1988b) hypothesized that the sperm ducts seen in these taxa are homologues of the ventral channel that have been stripped from the glandular pallial oviduct. This hypothesis is supported by the fact that in some pomatiopsines (e.g., *Idiopyrgus souleyetianus*, Malek, 1983, fig. 1A) and cochliopines (e.g., *Spurwinkia salsa*, Davis et al., 1982, fig. 11A,B), the anterior end of the otherwise separate duct opens to the equivalent of the vestibular region of the capsule gland. Other entry points of sperm are via the pericardium (various pomatiopsids, e.g., *Kunmingia kunmingensis*, Davis et al., 1984, figs. 8, 9) and the renal opening (e.g., *Lacunopsis harmandi*, Davis, 1979, fig. 17). (See Ponder (1988b) for a discussion of the evolution of renal copulation.) These states are, however, not homologous, and we do not treat the point of entry of sperm as a character.

#### *Pallial Genital Opening(s)*

**CAPSULE-GLAND OPENING.**—The capsule-gland opening varies in position and shape, which we treat separately.

**Position:** The opening of the capsule gland (cgo) is usually terminal (Figure 15a) or subterminal (Figure 15b) in hydro-

bioids, but it is at about the middle of the capsule gland in some taxa (Figure 15c) (e.g., *Tatea huonensis*, Ponder et al., 1991, fig. 10). In some vitrinellids it is at the posterior end of the capsule gland (Figure 15d) (e.g., *Sigaretornus plana*, Ponder, 1994, fig. 4A). States: terminal to subterminal (1); at about middle of capsule gland (2); at posterior end of capsule gland (3).

**Shape:** Among hydrobioids, a ventrally open capsule gland has been reported only for *Ascorhis tasmanica* (Ponder and Clark, 1988, fig. 13A,D), but a long, slit-like opening occupies most of the ventral part of the capsule gland in *Ginaia munda* (Radoman, 1983, fig. 86A,B) and *Phrantela angulifera* (Ponder et al., 1993, fig. 96A). States: open along all or most of gland (0); open 25%–50% of gland length (1); short slit or pore (2).

**Muscularization:** In most hydrobioids the capsule gland opening is simple; however, in some taxa it forms a raised, muscular papilla (e.g., *Jardinella colmani*, Ponder and Clark, 1990, fig. 20C; *Aphaostracon rhadinus*, Hershler and Thompson, 1992, fig. 13a). States: simple (0); papilla-like (1).

**OTHER FEATURES.—Spermathecal Duct:** This structure is found in pomatiopsines, amnicolines, and cochliopines. We herein redefine the spermathecal duct (Davis, 1967) in hydrobioids as a sperm duct derived from the ventral channel or its homologue. In *Oncomelania hupensis*, the spermathecal duct is reported to arise as a bud from the bursa copulatrix (Davis et al., 1976:277), but the ontogeny of the ventral channel and common oviduct in hydrobiids is unknown except for the observations by Johansson (1948) on *Hydrobia*, in which the pallial oviduct commences as an open gutter. States: absent (0); common opening with capsule gland in anterior pallial cavity (1); opens separately to anterior pallial cavity (2); opens separately about halfway along capsule gland (3); opens separately to posterior pallial cavity (4).

**Cordiseminal Duct:** We introduce this new term (derived from the Latin *cordis*, heart, and *semen, seminis*, seed, sperm) for the sperm duct (which also has previously been referred to as a spermathecal duct) derived from the gonopericardial canal. This type of duct is found in triculines (see Davis, 1979, and subsequent papers). States: absent (0); opens from posterior coiled oviduct, posterior to seminal receptacle (1); opens from bursal duct (2).

**Relationship of Cordiseminal Duct to Pericardium:** The relationship between the cordiseminal duct and the pericardium varies, as does the manner in which the duct receives sperm. In some taxa the cordiseminal duct (csd) opens to the pericardium, which in turn receives sperm via the renal opening (Figure 15e) (e.g., *Lacunopsis harmandi*, Davis, 1979, fig. 17). In others it opens to the pericardium, which in turn has a separate pallial opening (Figure 15f) (e.g., *Kunmingia kunmingensis*, Davis et al., 1984, fig. 8; *Tricula*, Davis, Rao, and Hoagland, 1986, fig. 7B), and in some other taxa the duct is partially or completely separated from the pericardium and opens to the pallial cavity as a separate (albeit closely associated), short tube (Figure 15g)

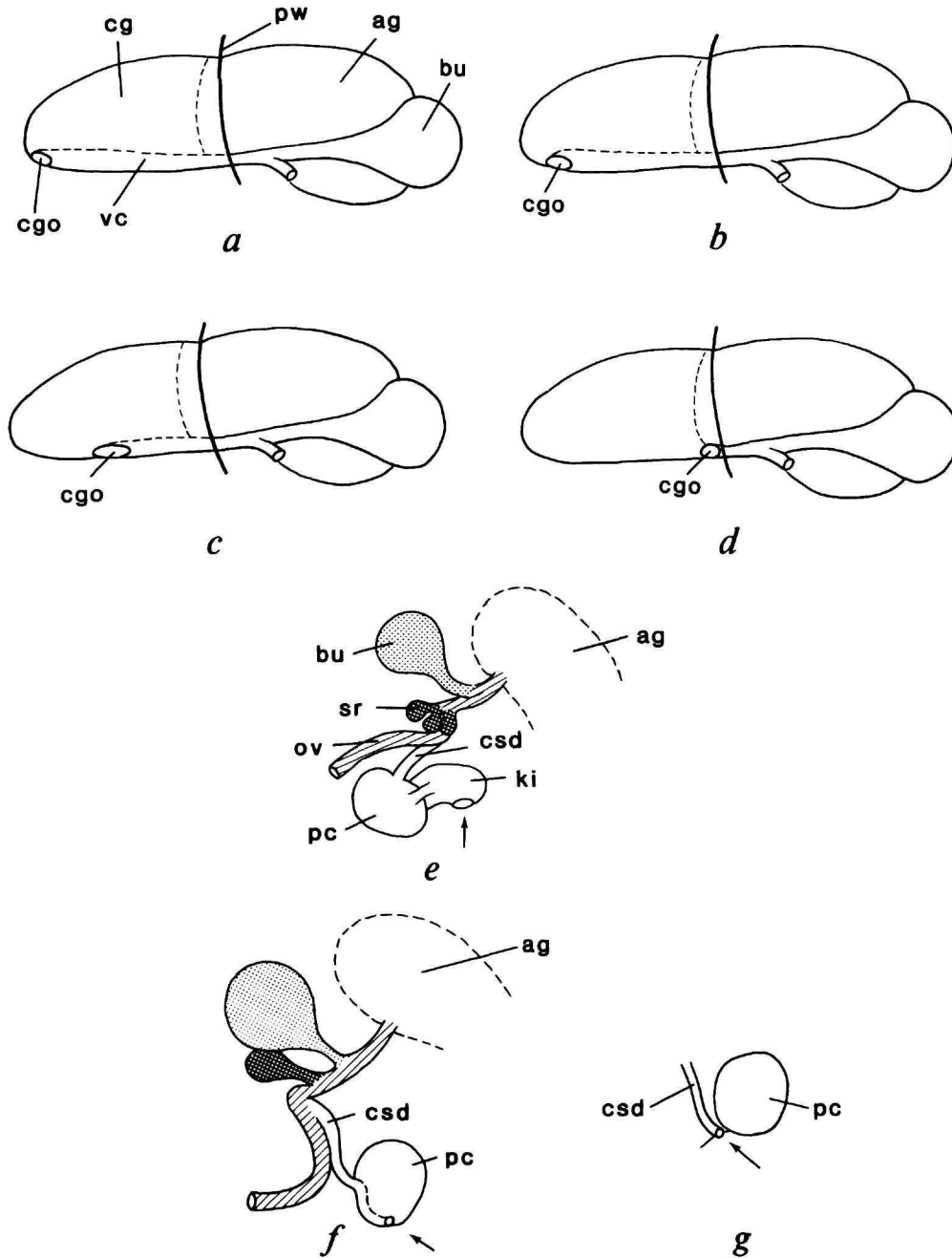


FIGURE 15.—Position of capsule-gland opening (*a-d*, viewed from left side); distal female genitalia (viewed from right side), showing pathway of sperm to female cordiseminal duct (*e-g*): *a*, capsule-gland opening terminal; *b*, capsule-gland opening subterminal; *c*, capsule-gland opening at middle of gland; *d*, capsule-gland opening at posterior end of gland; *e*, sperm enters cordiseminal duct through renal opening (arrow), which opens to pericardium (*Lacunopsis harmandi*); *f*, sperm enters cordiseminal duct through opening of pericardium (arrow) to pallial cavity (*Fenouilia kreitneri*); *g*, sperm enters cordiseminal duct through separate pallial opening (arrow) (*Kunmingia kunmingensis*). (ag = albumen gland, bu = bursa copulatrix, cg = capsule gland, cgo = capsule-gland opening, csd = cordiseminal duct, ki = kidney, ov = oviduct, pc = pericardium, pw = posterior wall of pallial cavity, sr = seminal receptacle, vc = ventral channel of capsule gland.)

(e.g., *Robertsia kaporensis*, Davis and Greer, 1980, fig. 7A; *Neotricula*, Davis, Rao, and Hoagland, 1986, fig. 7A). States: absent (0); opens to pericardium, sperm received through kidney (1); opens to pericardium, which has a separate, pericardial opening (2); fused (but external) to or separated from pericardium, with separate opening (3).

*Pericardial Bursa:* A pallial sperm storage area associated with the pericardium has been described for two species of *Tricula* (e.g., *T. gregoriana*, Davis, Guo, Hoagland, Chen, et al., 1986, fig. 39B). States: absent (0); present (1).

## MALE REPRODUCTIVE SYSTEM

### *Genitalia Apart from Penis*

**TESTIS.**—The testis is similar to the ovary in position and extent but usually extends farther back toward the tip of the visceral coil. Spermiogenesis and the ultrastructure of mature sperm have not been well studied in hydrobioids (but see Giusti and Mazzini, 1973; Healy, 1983, for studies of several outgroups) and are not used herein, but they may prove useful at least in helping resolve relationships among major groups.

*Extent:* The testis usually occupies more than 66% of the visceral coil behind the stomach (e.g., *Kunmingia kunmingensis*, Davis et al., 1984, fig. 5; *Somatogyrus rheophilus*, Thompson, 1984, fig. 43; *Heleobia davisi*, Silva and Thomé, 1985, fig. 7), but in some taxa it occupies about 50% or less of the visceral coil behind the stomach (e.g., *Halewisia expansa*, Davis, 1979, fig. 13C). States: occupies more than 66% of visceral coil (0); occupies less than 66% of visceral coil (1).

*Anterior Extension:* The testis typically overlaps the posterior chamber of the stomach, but in some taxa (e.g., *Spurwinkia salsa*, Davis et al., 1982, fig. 14A; *Potamolithus ribeirensis*, Simone and Moracchioli, 1994, fig. 10a) it overlaps the anterior and posterior chambers of the stomach, and in others (e.g., *Halewisia expansa*, Davis, 1979, fig. 13C) it lies behind the stomach. States: overlaps posterior chamber of stomach (0); overlaps anterior and posterior chambers of stomach (1); does not overlap stomach (2).

*Structure:* Davis (1979, fig. 19) provided figures of the states seen in pomatiopsids. The common state in hydrobioids is simple, vertical, digitate lobes (e.g., *Heleobia davisi*, Silva and Thomé, 1985, fig. 10; *Heleobops carrikeri*, Davis and McKee, 1989, fig. 17; *Potamolithus* species, Simone and Moracchioli, 1994, fig. 10). Other conditions include a simple sac (e.g., *Hubendickia* sp., Davis, Guo, et al., 1989, fig. 4) and simple, vertical lobes (e.g., *Phreatodrobia nugax*, Hershler and Longley, 1986a, fig. 19D). Some pomatiopsids have a few large, longitudinal lobes that may terminate simply (e.g., *Hubendickia siamensis*, Davis, 1979, fig. 11B) or have complexly branched ends (e.g., *Hydrorissia elegans*, Davis, 1979, fig. 12A), whereas others have large, complex, grape-like compound lobes (e.g., *Pomatiopsis lapidaria*, Davis, 1967, pl. 12; *Pachydrobia zilchi*, Davis, 1979, fig. 14B). Although the ovary and testis often have the same structure in a given

species, in other cases they are completely different (e.g., *Karelainia davisi*, Davis, 1979, fig. 11C,D; *Mexithauma quadripaludium*, Hershler, 1985, figs. 30A, 31A; *Erhaia wantanensis*, Davis and Kang, 1995, figs. 16, 18). States: simple sac (0); simple, vertical lobes (1); vertical compound lobes (2); longitudinal lobes that terminate simply (3); longitudinal lobes with terminal compound elements (4).

*Vas Efferens:* The portion of the genital duct to which the lobes of the testis discharge is referred to as the vas efferens. Davis and Greer (1980, table 13) distinguished two character states for this structure: narrow (most taxa) and broad (e.g., *Robertsia kaporensis*, Davis and Greer, 1980, fig. 9A). Davis et al. (1984, table 12) scored a vas efferens as absent in taxa in which the testis consisted of large, longitudinal lobes (e.g., *Hubendickia pellucida*, Davis, 1979, fig. 12D). States: narrow (0); wide (1); absent (2).

*Origin of Vas Deferens from Testis:* The vas deferens may exit from the testis at the anterior end (e.g., *Pachydrobiella brevis*, Davis 1979, fig. 15A; *Heleobops carrikeri*, Davis and McKee, 1989, fig. 17) or, more commonly, from well behind the anterior end to near the middle part of the testis (e.g., *Cecina manchurica*, Kosuge, 1969, fig. 29; *Hydrobia truncata*, Hershler and Davis, 1980, fig. 4A,B; *Potamolithus ribeirensis*, Davis and Silva, 1984, fig. 13; *Delavaya dianchiensis*, Davis, Guo, Hoagland, Chen, et al., 1986, fig. 5A). States: from anterior end (0); from middle region (1).

**SEMINAL VESICLE.**—The posterior vas deferens forms a convoluted seminal vesicle (for sperm storage) that usually commences beneath the testis and extends over the posterior and middle part of the stomach. The seminal vesicle may lie predominantly beneath the testis or on the stomach, but this feature varies considerably within taxa.

*Course of Duct:* In most hydrobioids the vas deferens begins coiling immediately after it emerges from the testis (as the seminal vesicle) and arches posteriorly before turning anteriorly (e.g., *Hydrobia truncata*, Hershler and Davis, 1980, fig. 4A,B; *Potamolithus ribeirensis*, Davis and Silva, 1984, fig. 13B; *Heleobops carrikeri*, Davis and McKee, 1989, fig. 18A). In other taxa the vas deferens again begins coiling immediately after leaving the testis, but it passes anteriorly without a posterior bend (e.g., *Karelainia davisi*, Davis, 1979, fig. 11D; *Pachydrobia bavayi*, Davis, 1979, fig. 14B; *Potamolithus* species, Simone and Moracchioli, 1994, fig. 10). Finally, in some pomatiopsids the vas deferens leaves the testis and extends anteriorly as a straight duct before turning posteriorly and coiling as the seminal vesicle (e.g., *Hydrorissia elegans*, Davis, 1979, fig. 12A; *Paraprososthenia levayi*, Davis, 1979, fig. 13D). States: coils immediately as it emerges from testis and passes anteriorly (0); coils immediately and arches posteriorly before turning anteriorly (1); extends anteriorly as straight duct before turning posteriorly and initiating coiling (2).

**PROSTATE GLAND.**—The prostate gland in all hydrobioids is at least partly pallial, lying against the right pallial wall,

although in most taxa it projects posteriorly and displaces the kidney, often for about one-half its length. The pallial extent of the gland is highly variable and hence is not treated as a

character. The plesiomorphic condition of the prostate gland is assumed to be pallial and ventrally open (Ponder, 1988b). The complex histology referred to in the oviduct glands also applies

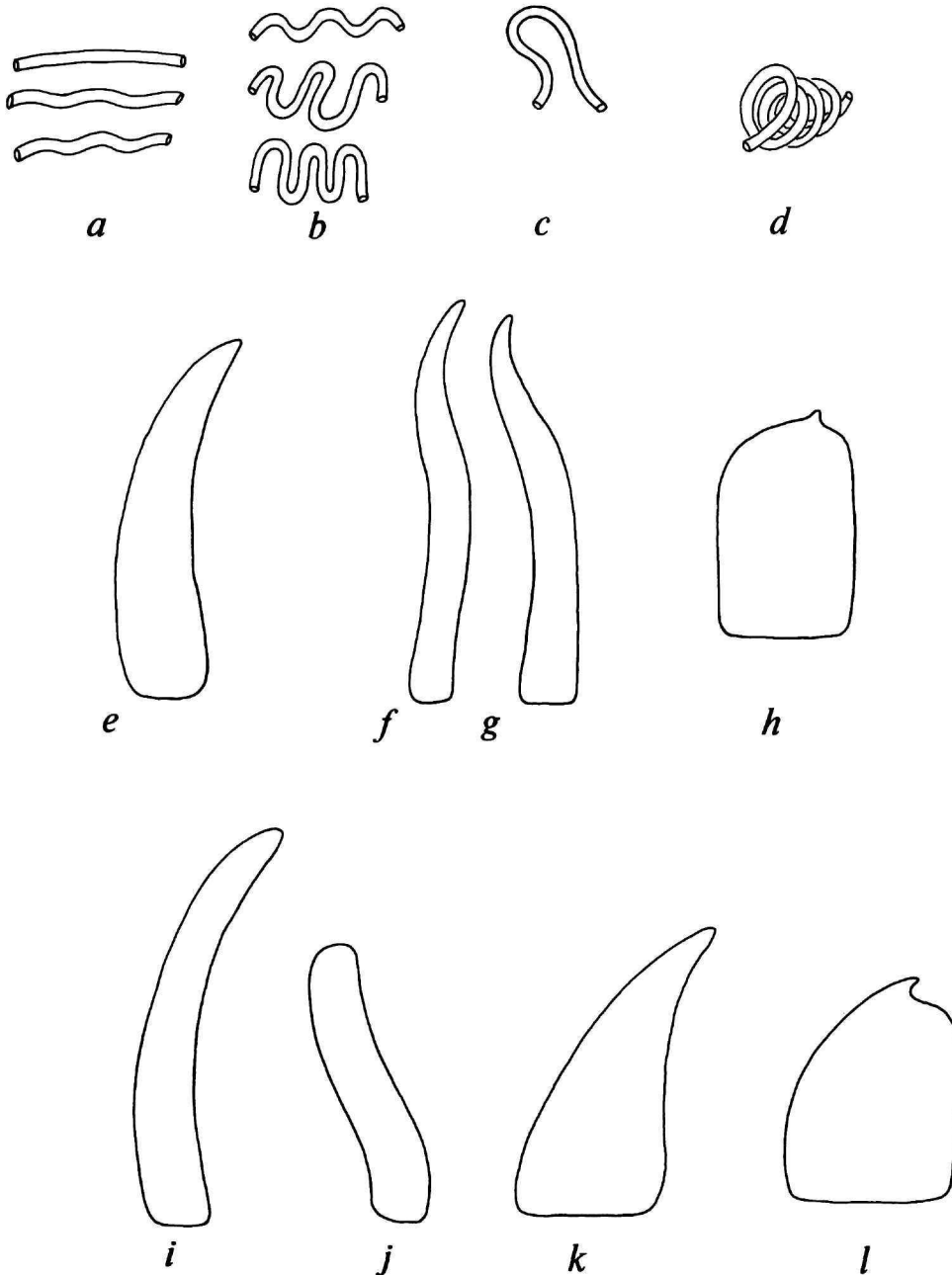


FIGURE 16.—Coiling patterns (applicable to vas deferens, seminal vesicle, and penial duct) (a-d) and shape of penis (e-l): a, duct straight to weakly undulating; b, duct strongly undulating; c, duct comprising a single loop; d, duct complexly coiled; e-g, penis gradually tapering; h, penis rectangular; i, j, penis strap-like; k, l, penis broadly triangular.

to the prostate gland and is concordant in males and females of all taxa so far examined (Ponder, 1988b); consequently, we do not treat this as a separate character.

**Ventral Surface:** Most hydrobioids have a closed prostate gland, but in *Ascorhis tasmanica* (Ponder and Clark, 1988:683) the gland has a ventral slit in the posterior one-half to two-thirds of the pallial section. Species of *Phrantela* have a thin ventral wall, and some (e.g., *P. richardsoni*, Ponder et al., 1993:683) are open ventrally. In *Phrantela marginata* and some related taxa (Ponder et al., 1993), the prostate gland has a short posterior opening. States: entirely open (0); with short posterior slit (1); closed (2).

**Exit of Pallial Vas Deferens:** The pallial vas deferens (i.e., that portion of the vas deferens in the pallial cavity) may exit from the anterior end (e.g., *Istriana mirnae*, Velkovrh, 1971, fig. 3H; *Pachydrobiella brevis*, Davis, 1979, fig. 15A; *Phrantela conica*, Ponder et al., 1993, fig. 86A) of the prostate gland or from various positions along its ventral surface. In the most common and probably most apomorphic state it exits from the posterior-most part of the pallial section (e.g., *Hydrobia truncata*, Davis, McKee, et al., 1989, fig. 8). States: from or slightly behind the anterior end of the prostate gland (0); from middle region (1); from posterior end of pallial portion (2).

**Shape:** Elongate prostate glands are found in a few hydrobiids (e.g., *Phrantela conica*, Ponder et al., 1993, fig. 86A; but those of closely allied species are shorter (Ponder et al., 1993, fig. 86D)) and most pomatiopsids (e.g., *Hydrorissosa elegans*, Davis, 1979, fig. 12A; *Pachydrobia* species, Davis, 1979, fig. 14B,D). Most hydrobioids have an oval to globular prostate (e.g., *Spurwinkia salsa*, Davis et al., 1982, fig. 14A; *Hydrobia truncata*, Davis, McKee, et al., 1989, fig. 8). States: pyriform to elongate (0); oval, bean-shaped, or globular (1).

**PALLIAL VAS DEFERENS.—Relationship to Epithelium:** The pallial vas deferens extends along the right side of the pallial roof and then onto the neck, in which it continues as the visceral (or proximal) vas deferens. It is usually a narrow, ciliated tube with no or few muscle fibres in its wall and lies just below the epithelium, typically forming a low ridge, but sometimes comprising a distinct lump (e.g., *Nymphophilus minckleyi*, Taylor, 1966:201–202). In some taxa it becomes more deeply embedded in the neck and/or penis and may become markedly muscular, forming an “ejaculatory duct” (fide Davis, 1979:68–69; *Pomatiopsis lapidaria*, Davis, 1967, pl. 11: fig. 5), whereas in others it is very superficial and is bound to the floor by connective tissue covered with a very thin epithelium, so that it almost appears to be loose or partly loose. States: largely or entirely superficial (0); deeply embedded (1).

**Musculature:** States: invested with few or no muscle fibers (0); muscular (1).

**Coiling:** The pallial vas deferens may be straight (Figure 16a), undulating or weakly coiled (Figure 16b) (e.g., *Heleobops carrikeri*, Davis and McKee, 1989, fig. 17; *Guoia viridulus*, Davis et al., 1992, fig. 51), strongly reflexed into a

single loop (Figure 16c) (e.g., *Cincinnatia integra*, Hershler and Thompson, 1996, fig. 6D), or a complexly coiled mass (Figure 16d) (e.g., *Omphalotropis nebulosa*, Turner and Clench, 1972, pl. 2D; some species of *Jardinella*, Ponder and Clark, 1990, fig. 4E). In the cochliopine *Lithococcus multicarinatus*, the duct is coiled in the pallial roof within a narrow tube (Hershler and Thompson, 1992, fig. 37b), which is apparently autapomorphic for that taxon. States: straight or very slightly undulating (0); undulating or weakly coiled (1); single loop (2); complexly coiled (3).

### Penis

The penis is usually attached to the neck behind the right eye, but in some taxa it is more centrally placed, although this difference is rarely clear-cut. Thus, we do not use point of attachment as a character.

**GROSS MORPHOLOGY.—Overall Shape:** We recognize two basic penial shapes (ignoring any lobes or glands and unusual differentiation of the distal end), parallel-sided and tapering, and these have each been divided into short and long conditions. Thus the penis may be gradually tapering (Figure 16e–g) (e.g., various pomatiopsids, Davis, 1979, fig. 10; *Hydrobia truncata*, Hershler and Davis, 1980, fig. 4D; *Antroselates spiralis*, Hershler and Thompson, 1992, fig. 11c; *Emmerciella novimundi*, Hershler and Thompson, 1992, fig. 27b; *Phrantela marginala*, Ponder et al., 1993, fig. 86C), broadly triangular (Figure 16k,l) (e.g., various lithoglyphines such as *Gillia altilis*, Thompson, 1984, fig. 51), rectangular (Figure 16h) (e.g., *Pyrgulopsis* species, Hershler, 1994, figs. 43–53), or strap-like (Figure 16i,j) (e.g., *Fluviopupa* species, Ponder, 1982a, figs. 36–46). States: gradually tapering (0); broadly triangular (1); rectangular (3); strap-like (3).

**Differentiation of Basal and Distal Portions:** The distal part of the penis may be distinct from the basal part (e.g., *Hydrobia truncata*, Hershler and Davis, 1980, fig. 4D; *Tatea* species, Ponder et al., 1991, fig. 9, and many related Australasian genera; several cochliopines, including *Aroa-pyrgus guatemalensis* and *Mexithauma quadripaludium*, Hershler and Thompson, 1992, fig. 4c, 4d, respectively). The demarcation is often because the base is folded, and in some taxa expanded, whereas the terminal part is smooth. In other taxa the distal and basal portions are not differentiated (e.g., various pomatiopsines, Davis, 1979, fig. 10; *Antrobia culveri*, Hershler and Thompson, 1992, fig. 4a). States: well demarcated from proximal portion (0); indistinct from proximal portion (1).

**Shape of Distal End:** This refers to the distal end of the penis (i.e., the tip), excluding the papilla, distal lobes (Figure 17j,k), and any glands (if present). The distal end may be tapered (Figure 17d,e) (e.g., *Hydrobia truncata*, Davis, Forbes, et al., 1988, fig. 18), blunt (Figure 17a–c,f,g,j,k) (e.g., *Durangonella coahuilae*, Hershler, 1985, fig. 35D; *Phrantela conica*, Ponder et al., 1993, fig. 78D), cup-shaped (Figure 17h) (e.g., *Tryonia* species, Hershler and Landye, 1988, fig. 46),

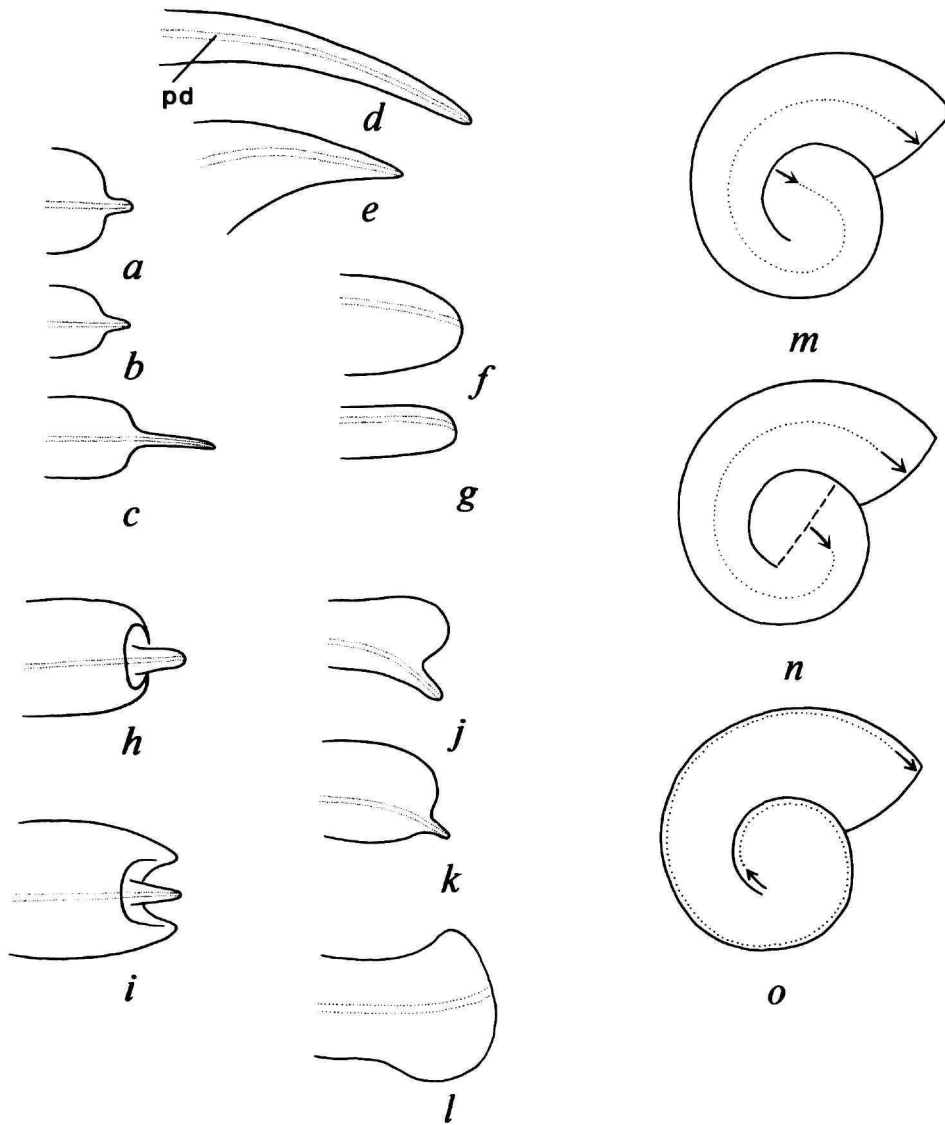


FIGURE 17.—Shape of distal end of penis (a–l) and alternative methods of counting protoconch whorls (m–o): a–c, j, k, distal end of penis blunt, with papilla; d, e, distal end tapered; f, g, distal end blunt, without papilla; h, distal end cup-shaped, with papilla; i, distal end cup-shaped, with ears and papilla; l, distal end expanded, without papilla; m, whorl count begins at initial edge or tip of apical whorl (method preferred by us), thus shell has 1.25 whorls; n, count begins at middle of “nucleus” (fide Verduin, 1982, fig. 4), resulting in a count of 1.2 whorls; o, count begins at initial suture (fide Solem, 1976, fig. 5; Burch, 1982, fig. 775), yielding a total of 1.5 whorls.

cup-shaped with “ears” (Figure 17i) (e.g., *Potamolithus ribeirensis*, Davis and Silva, 1984, fig. 12), or expanded (Figure 17l) (e.g., *Fluviopupa gracilis gracilis*, Ponder, 1982a, fig. 45). A twisted (“cork-screw”) penis form is seen in *Fontigens nickliniana* (Hershler et al., 1990, fig. 8a), but this is an autapomorphy and thus is not treated as a separate state.

States: tapered (0); blunt (1); expanded (2); cup-shaped (3); cup-shaped with ears (4).

**Distal Papilla:** In hydrobioids the penial duct may open flush with the distal end of the penis (Figure 17d–g, l) or may emerge as a small papilla (Figure 17a–c, h–k), which is noneversible in some taxa (e.g., *Neotricula aperta*, Davis et al.,

1976, fig. 10E–H; *Littoridina orcutti*, Hershler and Thompson, 1992, fig. 6b; *Emmericiella novimundi*, Hershler and Thompson, 1992, fig. 27b; *Beddomeia topsiae*, Ponder et al., 1993, fig. 67D) and eversible in others (e.g., *Oncomelania hupensis lindoensis*, Davis and Carney, 1973, fig. 15C). The position of the papilla varies (terminal or subterminal) and may serve as an additional character upon more detailed study. States: absent (0); present, noneversible (1); present, eversible (2).

**Corneous Stylet:** In a few taxa the penial duct opens through a corneous terminal stylet (e.g., *Rachipteron philopolum* (familial placement uncertain), Thompson, 1964, fig. 1D; the pomatiopsid *Robertsia kaporensis*, Davis and Greer, 1980, fig. 9B,C; *Hauffenia wienerwaldensis*, Haase, 1992, figs. 10, 11; *Lobaunia danubialis*, Haase, 1993, fig. 15). As with the last character, position of the stylet may vary somewhat among taxa (Haase, 1992). States: absent (0); present (1).

**Nonglandular Processes or Lobes (outer edge):** These may be distal (e.g., *Fluviopupa* species, Ponder, 1982a, figs. 37–46) or medial (e.g., *Jardinella* species, Ponder and Clark, 1990, fig. 10B,C; *Selmistonia beroni*, Bernasconi, 1995, fig. 4; some species of *Hemistomia*, Haase and Bouchet, in press; *Fluvidona* species, Ponder, unpublished data). States: absent (0); distal (1); medial (2).

**Nonglandular Processes or Lobes (inner edge):** These may be distal (e.g., several species of *Heleobops*, Hershler and Thompson, 1992, fig. 35a,b) or medial (e.g., *Hydrobia truncata*, Hershler and Davis, 1980, fig. 4D; a few species of *Beddomeia*, Ponder et al., 1993, figs. 10F, 67; several species of *Belgrandiella* and *Graziana*, Haase, 1994, fig. 6). States: absent (0); distal (1); medial (2).

**Distal Ciliation:** In some cochliopines, the penis is densely ciliated distally (e.g., *Heleobia australis nana*, Marcus and Marcus, 1965, pl. 10: fig. 42; *Tryonia gilae*, Hershler and Landye, 1988, fig. 45a,b), whereas in most other hydrobioids the distal end is weakly ciliated or without cilia. This character is not well known because few penes have been illustrated using SEM. Although we use only two states, it is likely that more will be added following the examination of additional taxa. States: weak or absent (0); prominent (1).

**PENIAL GLANDS APART FROM TUBULAR GLANDS.**—A wide variety of penial glands has been reported for hydrobioids, and our division of these into homologous subsets is preliminary; thus, their assumed homology requires testing. Most of the types of glands reported for European taxa, for instance, cannot be treated herein owing to the lack of detail in published illustrations. There is a great need for studies of fine structure of these glands, such as that done for the mammiform penial glands of *Littorina* (Buckland-Nicks and Worthen, 1992).

**Apocrine Glands:** These spherical glands are found in some cochliopines and possibly in other hydrobioid groups (e.g., *Alzoniella finalina*, Giusti and Bodon, 1984, fig. 2A–F). Discoidal, apocrine-like glands also are described for several pomatiopsines (e.g., several *Fukuia* species, Abbott and

Hunter, 1949, figs. 4, 5). The histology of these glands was described for *Heleobia* species (Hubendick, 1955, fig. 88; Marcus and Marcus, 1963, fig. 47; Chukhchin, 1976, fig. 7c), *Heleobops docima* (Thompson, 1968, fig. 38E), and *Texadina sphinctosoma* (Hershler and Thompson, 1992, fig. 5c,d). Apocrine glands may be superficial within the body of the penis (e.g., *Heleobops docimus*, Thompson, 1968, fig. 38A–C) or borne on short stalks (e.g., *Texadina sphinctosoma*, Hershler and Thompson, 1992, fig. 5a,b). Species attributed to *Heleobops* by Hershler and Thompson (1992) have both types. The position (outer or inner edge, distal or proximal) and number (single or multiple) of apocrine glands is useful in distinguishing between species and closely related genera. States: absent (0); present (1).

**Glandular Papillae:** These narrow glands are found in several cochliopines (Hershler and Thompson, 1992, figs. 13c, 37b, 60c), *Botryphallus epidauricus* (Ponder, 1990, fig. 8C), and possibly in other groups (e.g., *Pseudavenionia pedemontana*, Bodon and Giusti, 1982, fig. 2.1–2.3,2.6,2.7). The histology of these glands was described for *Littoridinops monroensis* (Thompson, 1968, fig. 38D) and for *Littoridina crosseana* and *Lithococcus multicarinatus* (Hershler and Thompson, 1992, figs. 6d, 7c,d, respectively). The position, number, and arrangement of these glands (e.g., whether or not they are grouped on lobes) is useful in distinguishing between species and closely related genera. States: absent (0); present (1).

**Glandular Fields (“ridges”):** These small glands may be single or arranged in linear series and are found in North American taxa assigned to the subfamily Nymphophilinae (e.g., various genera, Thompson, 1968, figs. 42–47) and possibly in some European taxa (e.g., *Lithhabitella elliptica*, Boeters, 1974, figs. 6, 7; *Islamia* species, Giusti et al., 1982, figs. 2–5; *Avenionia brevis*, Boeters and Winter, 1983, figs. 2–9; *Mercuria tachoensis*, Boeters, 1988, figs. 112, 113). Their histology has not been studied. Glandular fields are sometimes borne on raised swellings and may be found at various locations on both the dorsal and ventral penial surfaces. Terminology describing these glands was provided by Thompson (1968), Davis and Mazurkiewicz (1985), and Taylor (1987). The number and position of glandular fields varies widely within the Nymphophilinae and even within single genera (e.g., *Pyrgulopsis*, Hershler, 1994, figs. 43–53). States: absent (0); present (1).

**Brown Glands:** These low, ovoid, brown-colored glands lie on the outer edge of the penis and are found in one small subclade of *Beddomeia* (Ponder et al., 1993, fig. 67). Their histology has not been investigated. States: absent (0); present (1).

**Mushroom Gland:** The cochliopine *Lithococcus multicarinatus* (Hershler and Thompson, 1992, fig. 7) has a mushroom-shaped unit (in addition to glandular papillae) that is composed of a narrow stalk having a large, strongly ciliated, discoidal, glandular terminus. A few details of their histology were

provided by Hershler and Thompson (1992:15–16). States: absent (0); present (1).

**TUBULAR PENIAL GLAND(S).**—Tubular gland(s) are found in bithyniids and a few groups of hydrobioids. The histology of these glands was described for *Bythinella dunkeri* (Bregenzner, 1916), *Amnicola limosa* (Hershler and Thompson, 1988, fig. 7), and *Fontigens nickliniana* (Hershler et al., 1990, fig. 10e, f). These glands either terminate simply or through a muscular terminus. In *Ascorhis tasmanica* (Ponder and Clark, 1988, fig. 15) a single gland is present, which is contained entirely within the penis. In amnicolines a single gland is present, which extends into the cephalic haemocoel (e.g., *Amnicola dalli johnsoni*, Thompson, 1968, fig. 37D; *Bythinella schmidti*, Radoman, 1983, fig. 105A; *Amnicola limosa*, Hershler and Thompson, 1988, figs. 4d, 7). In *Emmericia* and some species of *Fontigens*, two glands are present, one contained entirely within the penis and one extending into the haemocoel (*E. patula*, Radoman, 1983, fig. 94D; *F. nickliniana*, Hershler et al., 1990, fig. 3b), whereas in other *Fontigens* species, three glands are present, one of which extends into the haemocoel (Hershler et al., 1990, figs. 16f, 19h).

**Number of Tubular Glands:** States: none (0); one (1); two or more (2).

**Position of Tubular Glands:** States: absent (0); in penis only (1); in penis and haemocoel (2).

**PENIAL DUCT.**—In many hydrobioids and pomatiopsids the penial duct (viewed when the penis is in the resting position) is straight to slightly undulating (e.g., various triculines, Davis, 1979, fig. 10), whereas in others the duct is strongly undulating to coiled (e.g., *Fluviopupa* species, Ponder, 1982a, figs. 37, 117; *Beddomeia* species, Ponder et al., 1993, fig. 67). This coiling can differ in the base and distal portion of the penis (e.g., *Neotricula lili*, Davis et al., 1992, fig. 100); hence, these are treated as separate characters.

**Coiling in Base:** States: straight to weakly undulating (0); coiled or strongly undulating (1).

**Coiling in Distal Penis:** States: straight to weakly undulating (0); coiled or strongly undulating (1).

**Position:** In many hydrobioids the penial duct is near centrally positioned, whereas in others (e.g., *Nymphophilus minckleyi*, Taylor, 1966, fig. 21) it is near the outer edge of the penis, at least in the broad, basal portion. States: near center (0); near outer edge (1).

**Ejaculatory Duct:** The penial duct is thickened, muscular, and reflexed or coiled in a few hydrobioids (e.g., *Potamolithus ribeirensis*, Davis and Silva, 1984, fig. 12A) and many pomatiopsids (e.g., *Pomatiopsis lapidaria*, Davis, 1967, fig. 5; *Hydrorissoa elegans*, Davis, 1979, fig. 12A). In some taxa the ejaculatory duct lies entirely within the base of the penis, and in others it is partly (e.g., *Tricula ludongbini*, Davis, Guo, Hoagland, Chen, et al., 1986, fig. 55D) or entirely (e.g., *Tricula gregoriana*, Davis, Guo, Hoagland, Chen, et al., 1986, fig. 38) in the head behind the penis. States: absent, i.e., penial duct narrow throughout (0); present, in base of penis (1); present, in head and behind penis (2).

#### NERVOUS SYSTEM

The nervous system appears fairly uniform in hydrobioids, and consequently we do not describe any characters. There have been few detailed studies of this aspect of morphology (but see Davis, 1967, and subsequent papers on *Oncomelania* for an important exception), however, and additional investigations will undoubtedly yield useful information. The concentration of the nervous system (often described using the “RPG ratio,” fide Davis et al., 1976) does vary somewhat among hydrobioids, as summarized by Davis and Mazurkiewicz (1985:45) (also see Appendix).

#### OTHER ANATOMICAL FEATURES

The density of connective tissue in body spaces (i.e., with much connective tissue, with very little or no connective tissue may) and the presence or absence of pigment in such tissue (e.g., *Bythiospeum* cf. *geyeri*, Haase, 1995, fig. 9) may serve as valuable characters, but these features have not been documented for most taxa.



# Appendix

## Characters Used to Distinguish Species of Hydrobioid Snails

### External Characters

**SHELL.**—See discussion of the shell in the main body of the paper. Shell measurements are particularly important because they are readily accessible and exhibit less variance than most soft-part measurements (Dillon, 1984; Hershler and Landye, 1988), which also are prone to variation owing to state of contraction (Dillon, 1984; Emberton, 1989). Diagrammatic summaries of measurements were given by Hershler and Sada (1987, fig. 7), Hershler and Landye (1988, fig. 2a), and Ponder et al. (1989, fig. 4A–C).

**Protoconch:** The diameter, number of whorls (see Figure 17*m–o* for explanation), and shape (flat-topped, dome-shaped, conical, etc.) can be scored. Major elements of protoconch sculpture are used as characters in the main body of the paper, but more detailed descriptions also are useful.

**Teleoconch:** Shell length and width, aperture length and width, last (body) whorl length, diameter of individual whorls, and width of umbilicus can be measured. These measurements are usually made perpendicular to, or coincidental with, the axis of coiling (e.g., Cox, 1960, fig. 80; Ponder et al., 1989, fig. 4A). Ratios between many of these measurements also are routinely used. Shape parameters (e.g., whorl expansion rate, translation rate, distance of generating curve from coiling axis, shape of generating curve; Raup, 1966) provide additional description of shell shape (e.g., Hershler and Sada, 1987). Parameters relating to alternative shell coiling models also are available (e.g., Illert, 1983, 1987, 1989; Ackerly, 1989; Schindel, 1990; Morita, 1991a, 1991b; Stone, 1995). The convexity ratio (Ponder et al., 1989, fig. 4B), which estimates the curvature of a particular whorl, and counts of the number of whorls and numbers of sculptural elements also can be determined.

Shell characters listed in the main body of the text relating to whorl and spire shape and sculpture also apply here. Periostracum color, ornament, and thickness also can be used.

**HEAD-FOOT.**—Measurements of cephalic tentacles, snout, and even the foot and columellar muscle may be obtained, but because of their extreme plasticity and the difficulty of obtaining accurate measurements in living material, their use is not recommended. The shape of the snout and the relative length of the cephalic tentacles are used in the main body of the paper as characters, but even these can be accurately judged only from living material.

**PIGMENTATION.**—Pattern, color, and intensity on the head and tentacles, foot, mantle roof, visceral coil, and other structures can be scored. This information can be lost in

preservative, so freshly fixed (or, ideally, living) material must be used.

**CILIATION.**—Details are usually only accessible using well-fixed, critical-point dried preparations examined with SEM. Observations on living material and/or Bouin's-fixed material, however, can reveal the major ciliation patterns.

**OPERCULUM.**—Length, width, distance of the nucleus from the edge, length of the pegs, and length of the white smear (see Ponder et al., 1989, fig. 4D,E), as well as the number of whorls and pegs and the color (e.g., pale to light amber, red), can be scored.

### Anatomical Characters

Measurements of organs and structures minimally distorted in living or preserved animals may be useful. Curved or coiled structures (e.g., the visceral coil) are difficult to measure accurately because of the need to measure around curves (see diagrammatic summary of this provided by Davis and Carney, 1973, fig. 4) and the necessity of having to straighten (and hence distort) the animal to some extent.

**PALLIAL CAVITY.**—The length and width of the entire pallial cavity can be measured but must be treated with caution as the anterior edge of the mantle can vary, depending on the state of relaxation.

**Ctenidium:** The length of the entire gill (often difficult to measure because of contraction and curvature) and the width and length (height) of the individual filaments (taken in the middle section) can often be measured (the latter is especially unreliable owing to contraction of these delicate structures). In addition, the relationship between the posterior end of the ctenidium and the pericardium (Figure 18*a–d*) can be ascertained. The number and shape of filaments (ideally standardized at the middle section of the ctenidium) and the position of the filament apex are additional data that can be readily obtained.

**Osphradium:** The color, length, width, and the distance from the anterior or posterior end of ctenidium, as well as the overall shape of the osphradium (e.g., broadly oval, elongately oval, etc., straight, curved), are readily observed.

**Other Pallial Structures:** Owing to its rather diffuse nature, the hypobranchial gland is not usually amenable to measurement, although we have used its thickness and surface-ridge condition as characters (see "Hypobranchial Gland" in main body of paper). The general extent of the hypobranchial gland and the extent to which it covers the

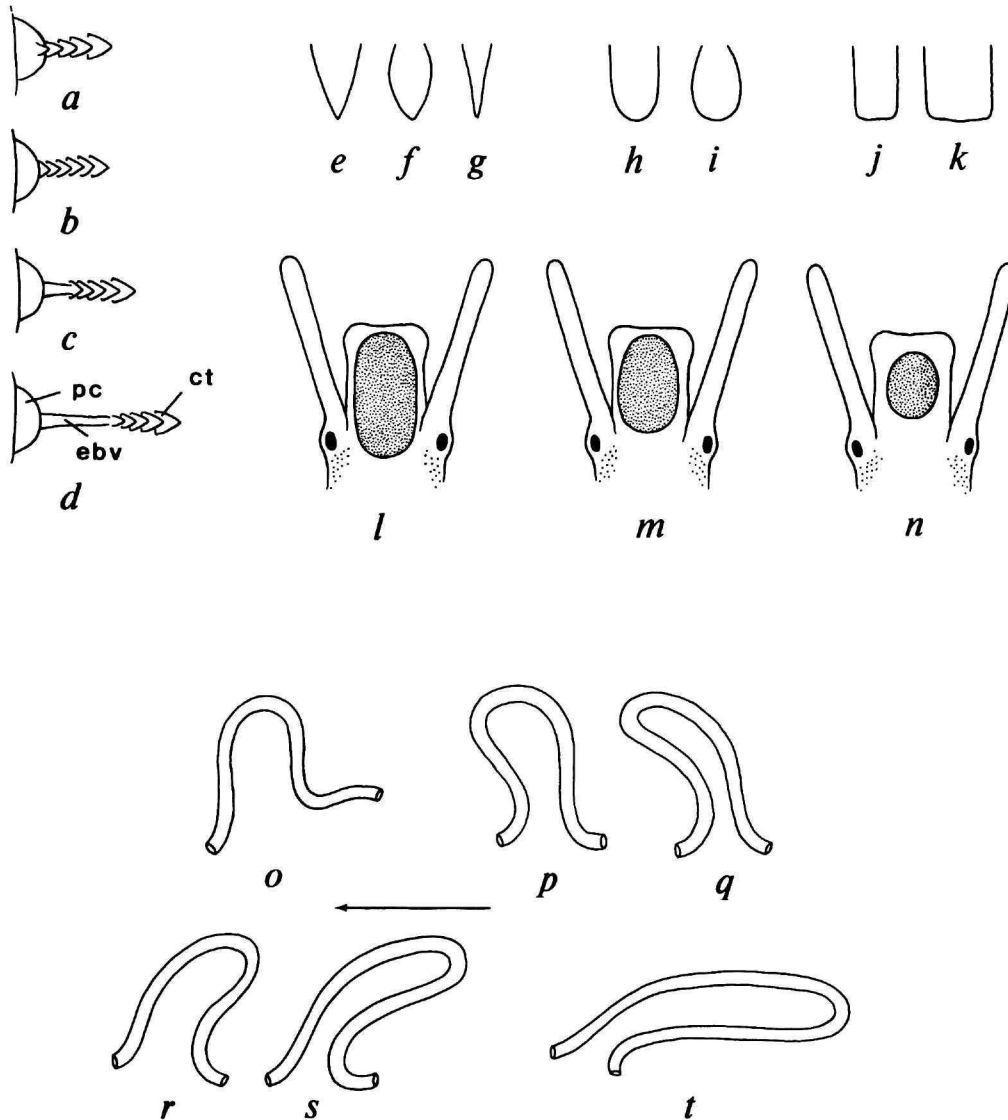


FIGURE 18.—Relationship between posterior end of ctenidium and pericardium (*a-d*), shape of distal end of median cusps (central and lateral radular teeth) (*e-k*), length of buccal mass (stippled) relative to snout (*l-n*), and orientation of initial or primary loop of renal oviduct (*o-t*) (arrow points anteriorly): *a*, ctenidial filaments overlap pericardium; *b*, ctenidium abuts pericardium; *c*, ctenidium connected to pericardium by short, efferent branchial vessel; *d*, ctenidium connected to pericardium by long, efferent branchial vessel; *e-g*, median cusp pointed; *h,i*, median cusp rounded; *j,k*, median cusp truncate; *l*, large buccal mass; *m*, medium-sized buccal mass; *n*, small buccal mass; *o*, vertical loop; *p,q*, anteriorly oblique loop; *r,s*, posteriorly oblique loop; *t*, horizontal loop. (ct = ctenidium, ebv = efferent branchial vessel, pc = pericardium.)

rectum, pallial genital duct, and pallial roof may help to distinguish species-group taxa. Other pallial or partly pallial structures (pallial gonoducts, penis, kidney, pericardium) are briefly discussed below.

**ALIMENTARY CANAL.**—Characters of the alimentary canal used in species rank taxonomy of hydrobiids are generally

restricted to the radula, external features of the stomach, and the shape of the rectum.

**Radula:** The radula, like the shell and operculum, is readily accessible from poorly fixed or even dried specimens that contain the soft parts. Characters include the length and width of the radular ribbon and the number of tooth rows in the entire

ribbon, including the number of rows in the "formative" stage. Other radular characters include the number of cusps on the cutting edges of the central, lateral, and marginal teeth; the number of basal cusps of the central teeth; the shape of the median cusps (central and lateral teeth) (Figure 18e-k); the relative lengths of median and lateral cusps on the central and lateral teeth; the shape and length of the basal tongue of the central and lateral teeth; the length of the cutting edge of the lateral teeth relative to the lateral wing; the length of the cutting edge of the marginal teeth relative to overall length (see radula characters in the main body of the paper); and the shape of the stem of both the inner and outer marginal teeth and the development of the lateral wings on those teeth.

*Jaws:* Jaw characters are rarely mentioned in descriptions but may provide useful data upon further comparative investigation.

*Buccal Mass:* The length and width of the buccal mass and the length of the radular sac behind the buccal mass can be measured, as can the length of the buccal mass relative to the snout length and the length (Figure 18l-n) and thickness of the salivary glands. The oesophagus is rather uniform and has not been used in species rank descriptions.

*Stomach (external):* Measurements or comparisons of the length and height (width) of the stomach, the length and height of anterior and posterior chambers and the style sac, and the length and width of the caecum can be made. The shape of the anterior and posterior chambers, the relative length of the style sac and stomach proper, and the shape of the caecum also are useful. Pigment on parts of the stomach can be species specific. Internal stomach characters have not been used to separate species and are rather difficult to ascertain, but their study may prove rewarding, especially if based on living material.

*Intestine and Rectum:* The coiling patterns for the rectum (and rarely the intestine, e.g., *Phreatodrobia* species, Hershler and Longley, 1986a) are sometimes useful. The pattern of packing of fecal pellets into the rectum can vary between taxa as, for instance, some have a wide rectum in which the pellets are usually packed sideways (see Ponder et al., 1993, fig. 4) rather than the more usual longitudinal packing.

*Anus:* The distance from the mantle edge and the distal end of the pallial glandular gonoduct can be measured, and the shape (e.g., simple or with papilla, e.g. *Antillobia margalefi*, Altaba, 1993, fig. 5) also may vary.

### Reproductive Systems

**FEMALE.—Ovary:** Ovary length and/or the number of whorls the ovary occupies can be scored. Subtle variation in the form of the ovary may be used to separate taxa, but we note that differences in reproductive maturity of individuals can significantly affect the appearance of the ovary. The point of departure of the upper oviduct from the ovary also may be a useful character but is rarely used.

*Renal Oviduct:* The length and width of the renal oviduct can be measured, but the former measurement is difficult

because of the typically looped or coiled shape. Comparisons of looping patterns and the orientation of the primary loop (e.g., vertical, oblique, horizontal, Figure 18o-t) can be used to separate taxa.

*Seminal Receptacle:* The length and width of the seminal receptacle and the length of the seminal-receptacle duct, as well as the shape of the seminal receptacle (used above as a character) and the shape of the anterior end (see Ponder et al., 1994:678), may be informative. The position of the opening of the seminal receptacle (distance from the bursal duct) and the size (Figure 19d-f) and location of the seminal receptacle relative to the bursa copulatrix also are important characters.

*Bursa Copulatrix:* Measurements of the length and width of the bursa copulatrix, as well as the length and width of the bursal duct (Figure 19a-c), can be taken. The shape of the bursa can be scored (Figure 19g-l). The size of the bursal duct relative to the oviduct glands also can be noted. The overall shape and the point of entry of the bursal duct to the bursa, the shape (bends, swellings, etc.) of the bursal duct, the point of entry of the bursal duct to the oviduct (see Ponder et al., 1994, fig. 48), and the size (Figure 19m-o) and position (Figure 19p-r) of the bursa copulatrix relative to the albumen gland also can be useful.

*Albumen Gland:* The length, height, and width (thickness) of the albumen gland can be measured, and its thickness and shape, both in longitudinal outline and transverse section, can be expressed as states or described comparatively. The position of the albumen gland relative to the posterior pallial wall and the relative length of this gland to the bursa and capsule gland also are useful. Additional characters include the point of opening of the oviduct to the albumen gland and the position of the oviduct opening relative to the length of the gland and relative to the ventral or lateral surface of the gland. Overlap of the albumen gland by the rectum and whether the contact with the rectum forms a channel along the gland are additional characters.

*Capsule Gland:* Measurements of this gland and the shape descriptors are the same as for the albumen gland. The lengths of the pallial opening, the details of individual glandular zones (including number, distribution, and color), and the vestibule are additional characters. The position of the genital opening relative to the anterior end of the capsule gland is an important character. The overlap by the rectum is as for the albumen gland. The width of the ventral channel can be measured or scored as can the size and development of the anterior vestibule (if present). The length and width of the spermathecal duct (if present) also can be scored or measured.

**MALE.—Testis:** As for the ovary. The point of departure of the vas deferens from the testis should be noted.

*Seminal Vesicle:* The number of whorls it occupies, its coiling pattern, the extent under the testis, and its development over the stomach are all characters that can assist in distinguishing taxa.

*Prostate Gland:* The length, height, and width (thickness) of the prostate gland and the length of its pallial portion can be

measured, and its overall shape, cross-sectional shape (Figure 20a-g), and the shape of the lumen (Figure 20h-k) can be scored or described. The openings to the pallial cavity, the thickness of the ventral wall, the point of departure of the pallial vas deferens, and the degree of overlap by the rectum are additional characters.

*Pallial Vas Deferens:* Useful information includes coiling patterns, relationship to the neck and the pallial roof, and the degree (if any) of muscle development.

*Penis:* Length and width of the penis (when at "rest") can be measured, and its size relative to the head (Figure 20l-n) and its position of attachment to the head (Figure 20o) can be

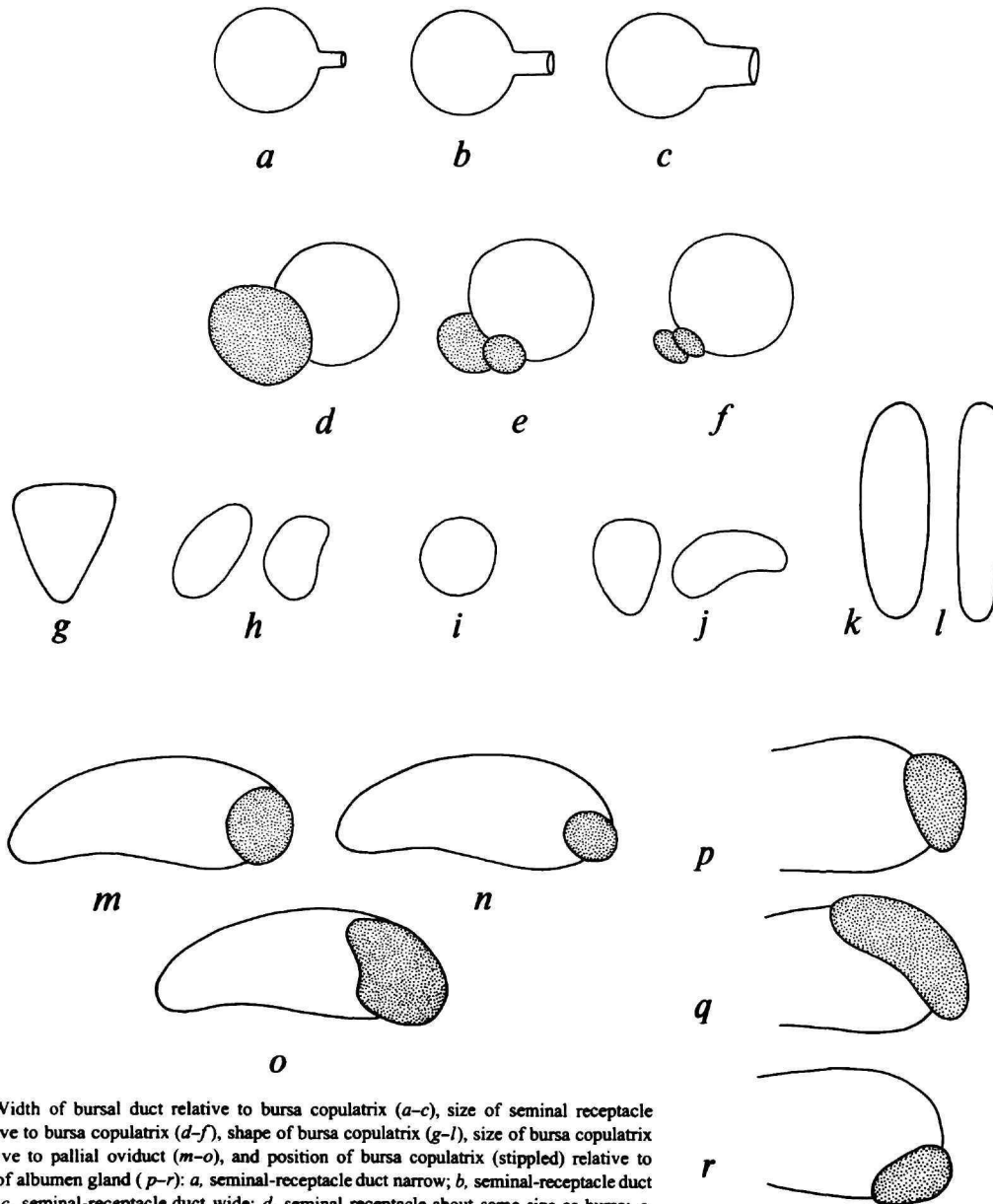


FIGURE 19.—Width of bursal duct relative to bursa copulatrix (a-c), size of seminal receptacle (stippled) relative to bursa copulatrix (d-f), shape of bursa copulatrix (g-l), size of bursa copulatrix (stippled) relative to pallial oviduct (m-o), and position of bursa copulatrix (stippled) relative to posterior edge of albumen gland (p-r): a, seminal-receptacle duct narrow; b, seminal-receptacle duct medium wide; c, seminal-receptacle duct wide; d, seminal receptacle about same size as bursa; e, seminal receptacle smaller than bursa; f, seminal receptacle much smaller than bursa; g, triangular bursa; h, ovoid bursa; i, globular bursa; j, pyriform bursa; k, l, elongate or cylindrical bursa; m, medium-sized bursa; n, small bursa; o, large bursa; p, posteriorly positioned bursa; q, dorsoposteriorly positioned bursa; r, posteroventrally positioned bursa.

scored or described. The distance to the anterior edge of the penial base from the eyes can be measured. The shape of the

basal (Figure 20*p-v*), middle, and terminal portions of the penis can be scored or described. The position, thickness, and

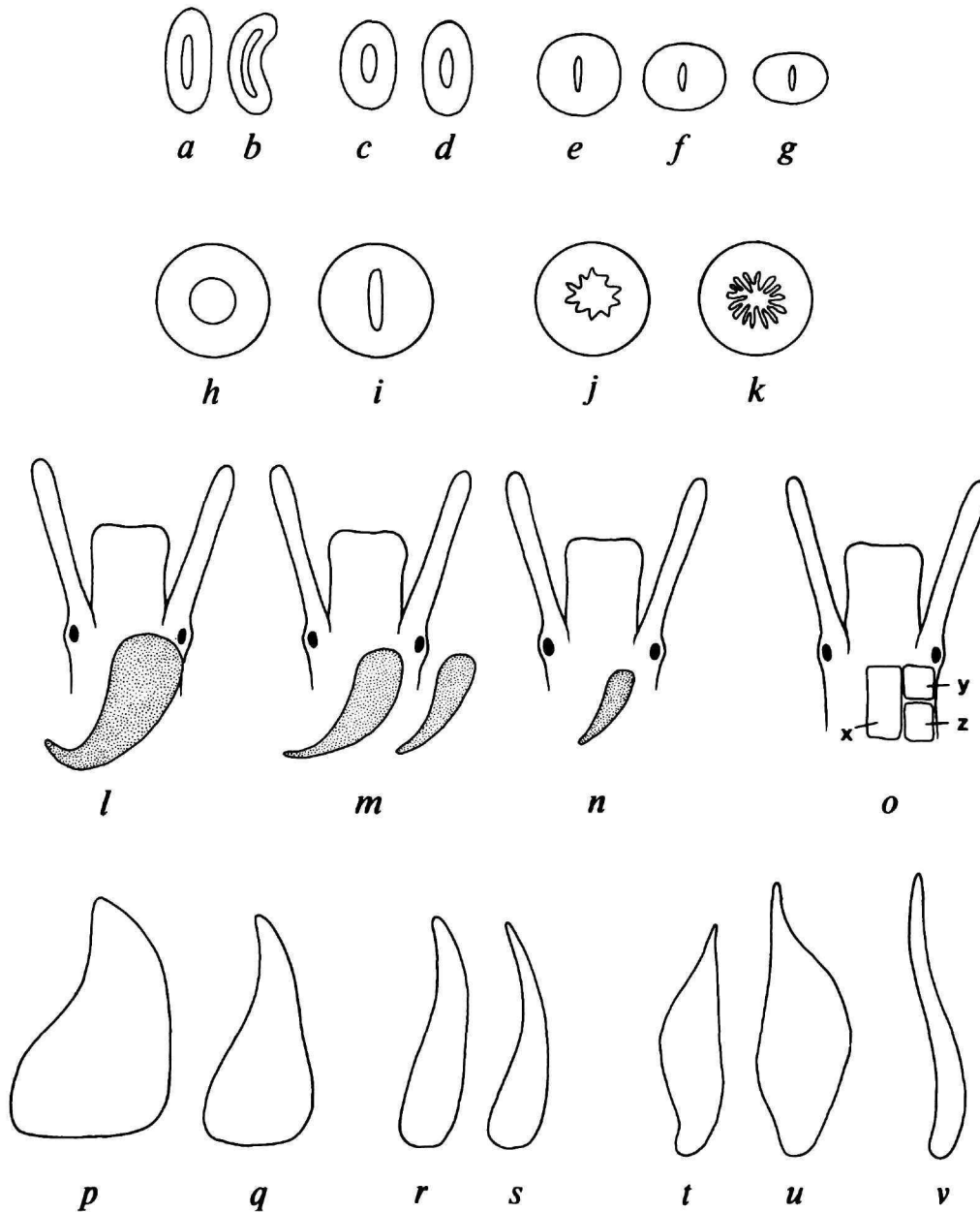


FIGURE 20.—Shape of prostate gland in transverse section (*a-g*), shape of prostate lumen in transverse section (*h-k*), variation in penis (stippled) size relative to head (*l-n*), attachment of base of penis to head (*o*), and width of basal portion of penis (*p-v*): *a, b*, prostate gland narrow in section; *c, d*, prostate gland ovate in section; *e-g*, prostate gland circular to broadly ovate in section; *h*, prostate lumen simple, circular; *i*, prostate lumen simple, slit-like; *j, k*, prostate lumen complex; *l*, large penis; *m*, medium-sized penis; *n*, small penis; *o*, attachment area central (*x*), attachment area close to right eye (*y*), attachment area well behind right eye (*z*); *p, q*, base of penis expanded; *r, s*, base of penis of intermediate width; *t-v*, base of penis narrow.

disposition (straight, undulating, coiled) of the penial duct and the position of the penial opening (terminal or subterminal) are important characters, and the amount of muscle invested in the penial duct should be noted (although sections may be needed). The number, shape, size, type, distribution, and color of penial glands (see penial-gland discussion and characters in main body of text), if present, also should be described. If present, the terminal filament should be described and the stylet shape and composition noted.

#### Renopericardial System

**RENAL ORGAN (Kidney).**—The length and width of the renal gland (this relatively large structure is easily measured) and the length of the kidney in the pallial roof can be measured, and/or the extent of the renal gland and its shape and orientation (Figure 21) (Ponder et al., 1993, fig. 3) can be scored or described. The overall extent of the kidney, although more difficult to ascertain, is potentially a useful character. The development of the renal sphincter (a well-developed sphincter usually appears as a white rim around the renal opening) also can be noted.

**PERICARDIUM.**—The extent in the pallial roof can be scored or measured. The size relative to the size of the kidney may be a useful character but has not been evaluated.

#### Nervous System

Lengths and widths of the circumoesophageal ganglia and lengths of the connectives can be measured, scored, or described. The "RPG" ratio (Davis et al., 1976; length of right pleural-supraoesophageal commissure/lengths of right pleural ganglion, supraoesophageal ganglion, and commissure) provides a useful comparative measure of the concentration of the nervous system. The general disposition of the ganglia (including the accessory pedal ganglia), principal nerves, and connectives are potentially useful characters but have rarely been used except in documenting gross differences. Ganglia pigmentation (if present) should be noted.

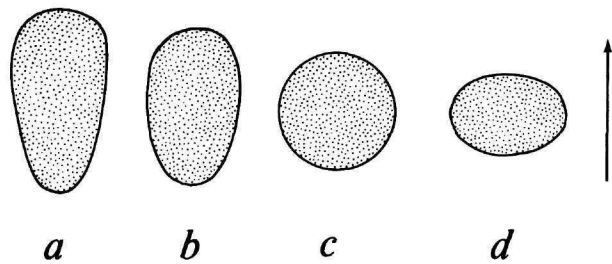


FIGURE 21.—Shape and orientation of renal gland (arrow points anteriorly): *a, b*, longitudinal; *c*, circular; *d*, horizontal.

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