A Revision of the North American Freshwater Snail Genus *Fontigens* (Prosobranchia: Hydrobiidae)

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and
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SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 509

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SMITHSONIAN INSTITUTION PRESS
Washington, D.C.
1990

ABSTRACT

Hershler, Robert, John R. Holsinger, and Leslie Hubricht. A Revision of the North American Freshwater Snail Genus *Fontigens* (Prosobranchia: Hydrobiidae). *Smithsonian Contributions to Zoology* number 509, 49 pages, 37 figures, 9 tables, 1990.—*Fontigens* Pilsbry, 1933, contains a few species widely and disjunctly distributed in the eastern and east-central United States. These species live in small-sized, perennial epigean and hypogean groundwater habitats (e.g., primarily springs and cave streams). *Fontigens* and the European *Emmericia* Brusina, 1870, are grouped in the probably monophyletic subfamily Emmericiinae Brusina. The distinguishing features of *Fontigens* are from protoconch sculpture, radula, penis, and pallial oviduct complex. Nine modern species (comprising three groups) are recognized: *F. aldrichi* (Call and Beecher); *F. antroecetes* (Hubricht); *F. bottimeri* (Walker), new combination; *F. morrisoni*, new species (from Upper James River basin of Virginia); *F. nickliniana* (Lea); *F. orolibas* Hubricht; *F. proserpina* (Hubricht); *F. tartarea* Hubricht; and *F. turritella* Hubricht. Four species occur exclusively in subterranean habitats, whereas four others are found in small surface springs and cave streams, and one is primarily found in surface waters. *Fontigens holsingeri* Hubricht is placed in synonomy with *F. tartarea* Hubricht, while *F. cryptica* Hubricht is considered a distinctive form of uncertain status that is possibly extinct. *Cincinnatia binneyana* Hannibal is probably not referable to *Fontigens* (contrary to previous opinion).

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging-in-Publication Data
Hershler, Robert
A revision of the North American freshwater snail genus Fontigens (Prosobranchia:Hydrobiidae) / Robert Hershler, John R. Holsinger, and Leslie Hubricht.
p. cm.—(Smithsonian Contributions to Zoology ; no. 509)
Includes bibliographical references (p.
1. Fontigens—North America—Classification. I. Holsinger, John R. II. Hubricht, Leslie. III. Title. IV. Series: Smithsonian Contributions to zoology ; no. 509.
QL1.S54 no. 509 [QL430.5.H9] 591 s—dc20 [594'.32] 90-10130

Contents

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Introduction

Fontigens Pilsbry, 1933, is a small group of hydrobiid snails distributed broadly within the Ozark Plateau/Central Lowland and Appalachian Mountains of the eastern United States. The genus is unusually diverse in terms of habitats occupied: all species recognized herein have been found in cave streams, and some also inhabit perennial surface waters, usually of small size and including springs and spring-fed streams as well as small lacustrine bodies.

As with many of the North American hydrobiids, *Fontigens* has a brief taxonomic history. This reflects paucity of study of these small snails: information on anatomy and geographic variation is particularly lacking, and taxonomic problems range from questionable assigment of species to the genus, to poorly defined species concepts based entirely on shell. Clessin (1878) erected the monotypic genus *Stimpsonia* (preoccupied) for *Paludina nickliniana* Lea, which Pilsbry (1933) later replaced with *Fontigens*. This widespread species is poorly known, although a few important morphological details were provided by Berry (1943). The only other snails described as *Fontigens* were four Appalachian species named by Hubricht between 1957 and 1976. Treatments of these were brief and anatomical information (limited to a short description of penis) was provided only for *F. turritella* Hubricht. In addition, four species were transferred to *Fontigens* between 1947 and 1978, none of which has received anatomical study.

We provide herein a revision of the genus based on a study of material from museums, the large personal collection of Leslie Hubricht, and newly collected material. Nine species are recognized, of which one is new. *Paludestrina bottimeri* Walker is transferred to *Fontigens* and *F. holsingeri* Hubricht is considered a subjective junior synonym of *F. tartarea* Hubricht. *Fontigens cryptica* Hubricht and *Cincinnatia binneyana* Hannibal (later assigned to *Fontigens)* are of uncertain status, and the latter almost certainly does not belong in *Fontigens*. Fossil taxa described as *Fontigens* from the Pliocene of Florida were not treated inasmuch as we concur with an earlier opinion (Thompson 1968:12) that these cannot be compared meaningfully with living forms. This study is not definitive for several reasons. More fieldwork will be necessary to verify whether *Fontigens* is actually absent from large regions in eastern North America. Additional study is needed to further clarify the taxonomy of small-sized species from the Appalachians of Virginia and West Virginia. A satisfactory phylogenetic analysis of the genus could not be done because of the small morphological data set; incorporation of electrophoretic or other genetic data will be necessary to meet this end.

RECOGNIZED SPECIES.—Genus *Fontigens* Pilsbry, 1933 (= *Stimpsonia* Clessin, 1878, non Girard, 1854) is comprised of the following species:

F. aldrichi (Call and Beecher, 1886)
F. antroecetes (Hubricht, 1940)
F. bottimeri (Walker, 1925), new combination
F. morrisoni Hershler et al., new species
F. nickliniana (Lea, 1838)
F. orolibas Hubricht, 1957
F. proserpina (Hubricht, 1940)
F. tartarea Hubricht, 1963
F. turritella Hubricht, 1976

MATERIALS AND METHODS.—Shell morphometric and other specimen-related methods were described by Hershler (1989a).

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Sections were cut at 4 μm and stained with hematoxylin and eosin. Penes were either temporarily mounted (unstained) in water or prepared as whole mounts after staining in hematoxylin, dehydration, and clearing. Descriptive statistics were generated using SYSTAT (Wilkinson, 1986). Species are treated in alphabetic order, with exception of the type species, which was studied in the most detail and is presented first. Morphological features characteristic of the genus are not repeated in the species descriptions. Dots on the distribution maps represent one or several (closely spaced) localities. Morphological and taxonomic work is that of Hershler, who prepared distribution maps and wrote the zoogeographic analysis together with Holsinger. All three authors participated in fieldwork.

ABBREVIATIONS.—Museum and collection acronyms referred to in the text are those of Leviton et al. (1985). "LH" refers to the personal collection of Leslie Hubricht. United States Postal Service abbreviations for state names used in the distributional data are as follows:

AL	Alabama
DC	District of Columbia
IL	Illinois
IN	Indiana
MD	Maryland
MI	Michigan
MO	Missouri
NY	New York
OH	Ohio
PA	Pennsylvania
VA	Virginia
WI	Wisconsin
WV	West Virginia

Definitions used for abbreviations on the figures and in the text are as follows:

Ag	albumen gland
Bu	bursa copulatrix
Cb	capsule gland
Dbu	duct of bursa copulatrix
Dl	distal penial lobe
Gp	glandular patch
Ml	median penial lobe
Ov	oviduct
Pf	penial filament
Pl	proximal penial lobe
Pn	penis
Ra	radula
Sg	salivary gland
Tg	tubular penial gland
Vc	ventral channel of capsule gland
Vd	vas deferens

ACKNOWLEDGMENTS.—Fieldwork of Hershler and Holsinger was supported (in part) by the Smithsonian Research Opportunities Fund. The National Park Service provided a permit to collect snails in Rock Creek Park, Washington, D.C. We also thank numerous private land owners for permission to collect snails on their property. Assistance in the field was provided by D. Figg, A. Gerberich, P. Greenhall, S. Kool, R. Mitchum, R. Phillips, E. Vale, and B. Yeaman. Staff of the Smithsonian Scanning Electron Microscopy Laboratory took and developed scanning electron micrographs, which were printed by V. Krantz of the Smithsonian Photographic Division. B. Fricano prepared histological sections and P. Greenhall digitized shells. We thank the following curators and institutions for access to collections: K.J. Boss (MCZ), J.B. Burch (UMMZ), G.M. Davis (ANSP), A. Solem (FMNH), and S.-K. Wu (UCM).

Family HYDROBIIDAE Troschel, 1857

Subfamily EMMERICIINAE Brusina, 1870

[= FONTIGENTINAE Taylor, 1966]

Genus *Fontigens* Pilsbry, 1933

Stimpsonia Clessin, 1878:151 [non Girard, 1854 (Enteropneusta); non Bate and Westwood, 1862 (Crustacea)]. [Type species: *Paludina nickliniana* Lea, 1838:92, by monotypy; Clessin, 1878:151.]

Fontigens Pilsbry, 1933:12 [replacement for above]. [Type species: *Paludina nickliniana*, by original designation; Pilsbry, 1933:12.]

DIAGNOSIS.—A North American group with small (<5.0 mm tall), ovate to turreted shell. Protoconch sculpture of spiral lines or striae, central tooth of radula with one or more pairs of basal cusps, penis with two or three accessory lobes containing glandular structures, and capsule gland with simple ventral channel. Differs from related *Emmericia* Brusina, 1870, principally by smaller size and presence of cusps on lateral and base of central radular teeth.

DESCRIPTION.—Shell clear-white, opaque to transparent. Whorls near flat to well-rounded, with indented sutures and frequently with slight adapical shoulders. Aperture ovate to near-circular, rounded below and usually angled above; apertural plane almost parallel to coiling axis. Umbilicus closed to open. Protoconch near-flat to slightly protruding. Teleoconch smooth or with spiral lines, collabral growth lines usually prominent. Periostracum thin-moderately thick, amber-brown. Operculum corneous, paucispiral, without ventral thickening or peg. Animal pigmentation variable, ranging from epigean specimens with black eyespots and dark covering of melanic pigment on most of head/foot and body to cavesnails with clear-white eyespots and no body pigment (apart from brown granules in digestive gland and scattered black-brown granules on portions of the visceral coil). Central radular tooth broadly trapezoidal with well-defined basal process; cusps dagger-like. Marginal teeth with numerous small cusps. Stomach without posterior caecal chamber; style sac shorter than remaining stomach. Pallial intestine usually without coils or undulations. Ctenidium fully formed, filling most of pallial cavity length; osphradium usually short relative to ctenidial length. Gonads simply lobate, usually positioned just posterior to stomach. Vas efferens absent; seminal vesicle exiting from near anterior tip of testis and consisting of a few coils totally beneath or partly anterior to anterior testis. Prostate gland

elongate, bean-shaped, with at least half of length pallial. Posterior vas deferens enters gland just posterior to end of pallial cavity; anterior vas exits from anterior tip of gland. Penis with narrow distal filament in which vas deferens courses without coiling. Invariably present is a distal or medial lobe containing a tubular, muscularized, clear gland of narrow diameter that coils in the lobe and discharges through the lobe tip via a muscular bulb. Gland protrudes into nuchal cavity where it coils and broadens dorsal to the oesophagus (and ends blindly). Also present is a distal lobe containing a similar gland with wide diameter that is largely or wholly contained within the penis and/or a small proximal lobe containing a short, bulbous, non-muscular, amber colored gland also contained within penis (both glands uncoiled and with simple terminal openings). Females oviparous. Pallial oviduct small; capsule gland usually longer and narrower than albumen gland. Capsule gland bipartite, with elongate, lobate, white posterior section and short, clear anterior section. Opening of capsule gland sub-terminal, simple. Bursa copulatrix large, sometimes overlapping (usually on right lateral side of) albumen gland. Muscular oviduct coil positioned (usually) against left side of bursa and serving as seminal receptacle. Duct from bursa joins oviduct; resulting duct enters albumen gland.

DISTRIBUTION AND HABITAT.—This genus is found widespread in eastern North America, but concentrated in three largely disjunct areas: (1) Great Lakes region, including drainage of lakes and Illinois River; (2) Mississippi River basin of eastern Missouri and western Illinois; (3) Appalachian Mountains and environs, including a few coastal plain drainages, as well as upper parts of Ohio and Tennessee River basins. The most common epigean habitat is springs and spring brooks, where snails are found (usually abundantly) on aquatic vegetation or stones in flowing, clear water. Cavesnails may occur from near entrances to very deep in a cave system; specimens are usually found on the undersides of small stones in riffle zones. Sympatry of congeners is rare among *Fontigens*. The only example confirmed in detail was at a small spring pond in Buffalo Marsh Run, Frederick Co., Virginia, where darkly pigmented *F. nickliniana* was common throughout the pool while pale *F. orolibas* was found (syntopic with the above) only in the small spring orifice area.

RELATIONSHIPS AND ZOOGEOGRAPHY.—*Fontigens* and *Emmericia* (from the eastern Adriatic coast of Italy and Yugoslavia) are sister groups sharing the following derived features: (1) trifid penis with two accessory lobes containing tubular glands (not seen in all *Fontigens*); (2) enlarged bursa copulatrix usually overlapped (on left lateral side) by the albumen gland[1]; (3) bursa duct not issuing from anterior tip of structure; (4) absence of seminal receptacle. Although a fossil record is not available, the recent distribution suggests that this is an old freshwater group dating back to the Mesozoic, prior to separation of Laurasia into North America and Eurasia. The oldest proposed name available for this group is Emmericiinae Brusina, 1870, to which Morrison (1949:14) allocated *Fontigens*. Taylor (1966:182), however, later assigned *Emmericia* to the Micromelaniidae Thiele based on the absence of basal cusps on their central radular teeth, and created the Fontigentinae for the North American genus. Diverse hydrobiids lack basal cusps on the central tooth and placement of these into a family-level group based on possession of this feature is undesireable. In the present case, the unusual radula of *Emmericia*, with massive, blunted, and cuspless central and lateral radular teeth probably reflects feeding specialization not particularly indicative of supra-generic systematic relationships and therefore we retain both *Emmericia* and *Fontigens* in the Emmericiinae.

The Amnicolinae Tryon (which has a similar distribution) is the only other hydrobiid group in which a tubular gland is present in the penis (extending into nuchal cavity). The gland is virtually identical in histology to that of *Fontigens* (albeit within a thinner muscular cover) and opens through a terminal muscular structure precisely as does the gland always found in the above. Amnicolids are distinguished from Emmericiinae by other important features (e.g., presence of spermathecal duct separate from pallial oviduct, presence of seminal receptacle; see Hershler and Thompson, 1988:90) and the continued recognition of these groups as separate subfamilies is appropriate. A broad-scale phylogenetic analysis will be necessary to determine whether these subfamilies are in fact closely related, and, if so, whether they collectively merit recognition as a family separate from the Hydrobiidae.

While phylogenetic relationships among *Fontigens* spp. cannot be adequately resolved on the basis of available information, three species groups are recognizable based on penial morphology: (1) *nickliniana* group, including species with two accessory lobes containing tubular glands (*F. aldrichi, F. nickliniana, F. turritella*); (2) *orolibas* group, including species with two accessory lobes containing tubular (distal lobe) and bulbous (proximal) glands (*F. morrisoni, F. orolibas, F. tartarea*); and (3) *bottimeri* group, including species with three accessory lobes containing tubular (two distal) and bulbous (proximal) glands (F. *antroecetes, F. bottimeri, F. proserpina*). The penial arrangement of *nickliniana* group is identical to that of *Emmericia*, and presumably represents the primitive condition from which the others were derived.

Of zoogeographic interest is the fact that all species of the *orolibas* group are restricted to the Appalachians, whereas the other two groups are represented by species in both the Ozarks and Appalachians. Moreover, one species—*F. nickliniana*—occurs in both the Great Lakes and Appalachian regions and has a much broader range than any other species in the genus. Also note that each species group contains at least one

[1]Radoman (1967:34; 1983:158) described the bursa copulatrix of *Emmericia* as being entirely inside the albumen gland, but it is clear from his illustrations (and from personal observations of senior author) that the bursa is actually lateral to the gland.

stygobiont species (i.e., obligatory to subterranean groundwater habitats), suggesting that subterranean groundwaters have been colonized independently by epigean ancestors on several occasions during the evolutionary history of the genus. The stygobionts include, *F. turritella* in the *nickliniana* group, *F. tartarea* in the *orolibas* group, and *F. antroecetes* and *F. proserpina* in the *bottimeri* group.

Each group also contains species that simultaneously inhabit both subterranean groundwaters in caves and surface springs. But other than for loss of body pigment and often eye pigment, these hypogean populations closely resemble the epigean ones morphologically, although they do not appear to be any less troglomorphic than the four stygobionts mentioned above. However, it should be stressed that future electrophoretic or other genetic studies may very well reveal differences between the pigmented spring populations and the unpigmented cave populations, especially in areas where these are spatially far apart. Moreover, genetic differences between populations isolated in different drainage basins also are likely. For example, *F. orolibas*, whose range is restricted to a part of the Appalachians (see Figure 27), is represented by populations of darkly pigmented individuals living in springs and spring runs in the Blue Ridge Mountains and by unpigmented snails living in caves in karst valleys to the west. In most instances, the cave populations not only are separated from the spring populations by great distances, but also occur in separate drainage systems (see Holsinger and Culver, 1988). Whether these hypogean populations reflect recent invasions and colonizations of caves by epigean animals that have migrated into subterranean streams via springs, or very old colonizations by animals that now are isolated genetically, but have not changed morphologically from those at the surface remains problematic. It is unfortunate that this important question cannot be resolved with the present data set.

Key to Species of *Fontigens*

1. Penis with two accessory lobes 2
   Penis with three accessory lobes 7
2. Proximal penial lobe containing tubular gland 3
   Proximal penial lobe containing bulbous gland 5
3. Shell large (to 6 mm tall), elongate-conic; penis massive, extending well beyond mantle edge . . . . . ***F. nickliniana***
   Shell smaller (to 3 mm), broadly conical or turriform; penis scarcely extending beyond mantle edge 4
4. Shell broadly conical; teleoconch smooth . . . . . ***F. aldrichi***
   Shell turriform; teleoconch with spiral striae . . . . . ***F. turritella***
5. Shell broadly conical (height usually less than one and a half times width) . . . . . ***F. morrisoni,*** new species
   Shell ovate- to elongate-conic 6
6. Shell ranging up to 4.0 mm tall; springs and caves in Virginia from Potomac River basin south to Upper Clinch River basin . . . . . ***F. orolibas***
   Shell up to 2.3 mm tall; caves in Ohio River basin of eastern West Virginia . . . . . ***F. tartarea***
7. Teleoconch with spiral striae . . . . . ***F. proserpina***
   Teleoconch smooth 8
8. Shell large (to 4.5 mm), elongate-conic; caves in Mississippi River basin of western Illinois . . . . . ***F. antroecetes***
   Shell moderate sized (to 3.0 mm), low conical; springs and caves in Potomac River basin of Maryland, Virginia, and District of Columbia . . . . . ***F. bottimeri,*** new combination

Fontigens nickliniana (Lea)

FIGURES 1-11; TABLE 1

Paludina Nickliniana Lea, 1838:92, pl. xxiii: fig. 109.
Amnicola nicliniana [sic].—Haldeman, 1845:21, pl. I: fig. 12.
Bythinella Nickliniana.—Stimpson, 1865:19, fig. 8.
Bythinella nicklinana.—Binney, 1865:68, figs. 133, 134.—Tryon, 1870:46.
Paludestrina nickliniana.—Baker, 1902:338, fig. 122; pl. XXVI: fig. 11.—Walker, 1918:138.
Stimpsonia nickliniana.—Baker, 1928:132, figs. 57-59; pl. VII: figs. 9-12.
Fontigens nickliniana.—Pilsbry, 1933:12; 1950:38, pl. 1: fig. 5.—Hubricht, 1976:88.—Burch and Tottenham, 1980:126, figs. 283, 319.
Hydrobia nickliniana.—Berry, 1943:44, fig. 7; map 7; pl. I: fig. 16, pl. IV: fig. 2, pl. VI: fig. 5.
Amnicola attenuata Haldeman, 1842:200 [figure in Haldeman, 1845, pl. 1: fig. 13 (labeled *A. elongata*)].

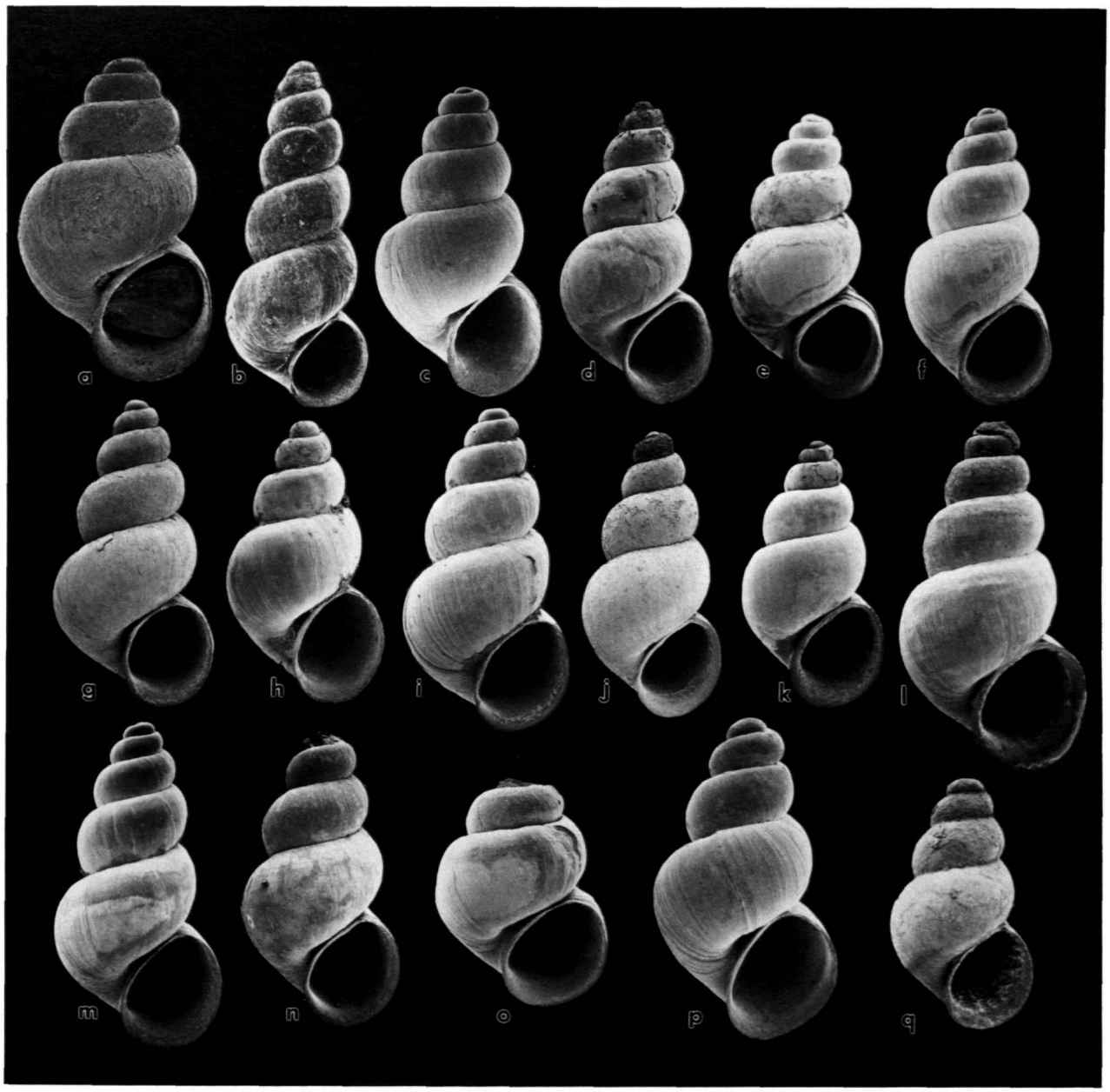

FIGURE 1.—*Fontigens nickliniana* (Lea): *a*, Hot Springs, Bath Co., VA, ANSP 316958 (paratype; shell height, 3.4 mm); *b*, Spring connected to Roanoke River, Montgomery Co., VA, ANSP 69472 (lectotype, *Amnicola attenuata* Haldeman; 6.4 mm); *c*, Warm Springs, Bath Co., VA, USNM 853157 (3.2 mm); *d*, 1.6 km N of Spruce Creek P.O., Huntingdon Co., PA, USNM 783938 (3.8 mm); *e*, Spring-fed brook near Williamsville, Erie Co., NY, USNM 791435 (3.6 mm); *f*, Button Lake, Kent Co., MI, USNM 590367 (3.9 mm); *g*, Stream 4.8 km ESE of Battle Creek, Calhoun Co., MI, USNM 622788 (3.9 mm); *h*, Old mill dam of Little Kankakee River, La Porte Co., IN, USNM 653447 (3.56 mm); *i*, Fulton Co., IL, USNM 28511 (4.1 mm); *j*, Spring in Buffalo Marsh Run, Frederick Co., VA, USNM 858043 (3.0 mm); *k*, Spring 3.7 km NW of Honaker, Russell Co., VA, LH 42102 (3.4 mm); *l*, Spring-fed tributary to Hogue Creek tributary, Frederick Co., VA, USNM 431715 (3.7 mm); *m*, Spring 1.1 km SE of Gap Mills, Monroe Co., WV, USNM 431746 (4.1 mm); *n*, Bakers Spring, Augusta Co., VA, USNM 522837 (3.7 mm); *o*, Bakers Spring, Augusta Co., VA, USNM 522836 (2.8 mm); *p*, Unthanks Cave, Lee Co., VA, USNM 858045 (2.6 mm); *q*, Tannehill Spring, Tuscaloosa Co., AL, LH 13488 (2.6 mm).

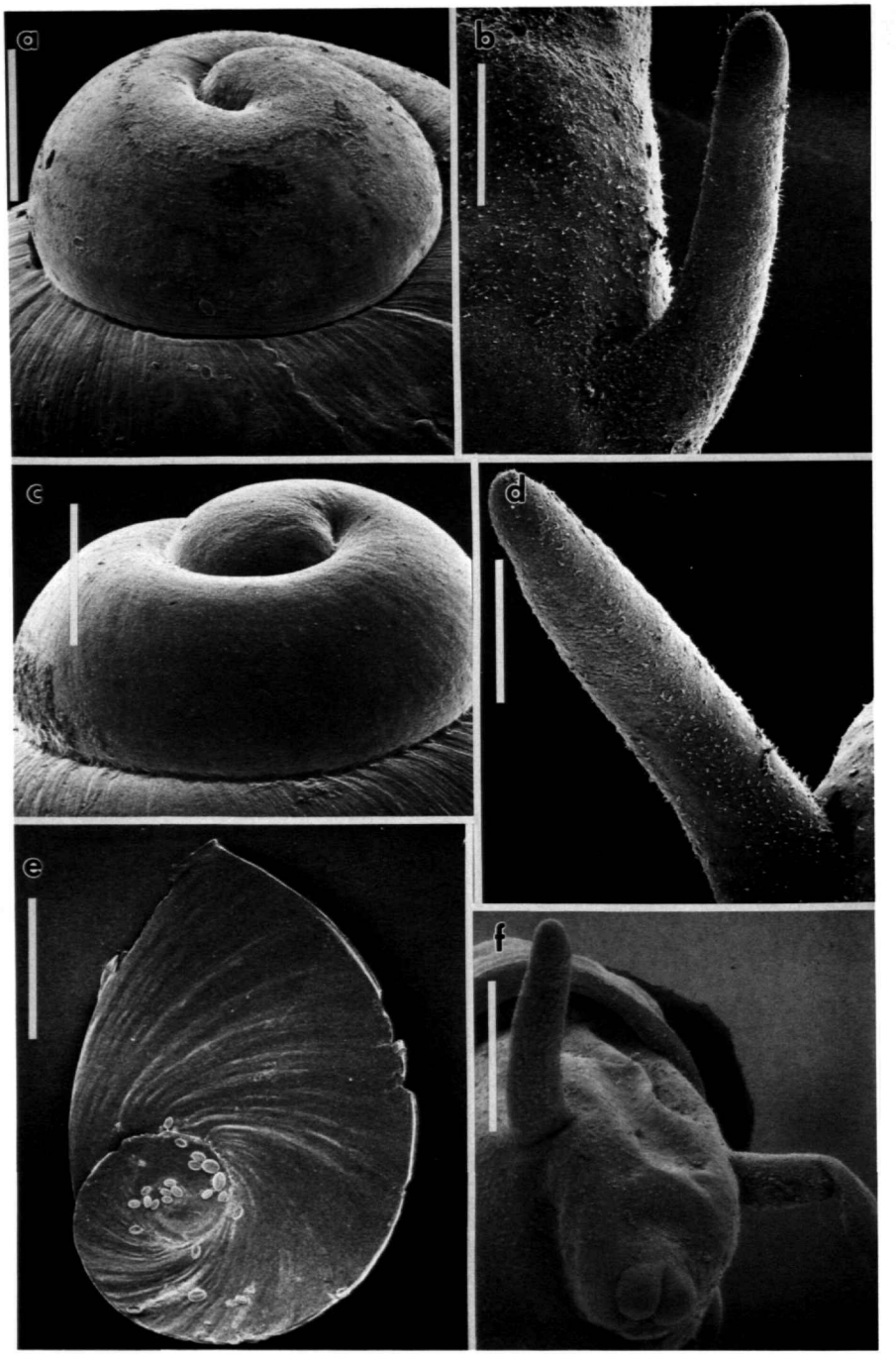

FIGURE 2.—Shell and external features of *F. nicklíniana: a,* protoconch, D.A. Huffmans Spring, Craig Co., VA, USNM 853153 (bar = 120 μm); *b,d,* Dorsal cephalic tentacles, Spring 1.6 km NE of Dickensonville, Russell Co., VA, LH 40771 (bars = 150, 176 μm, respectively); *c,* Protoconch, Warm Springs, Bath Co., VA, USNM 853157 (bar = 136 μm); *e,* View of dorsal operculum, Nolleys Spring, Montgomery Co., VA, USNM 858047 (bar = 1.2 mm); *f,* Head and cephalic tentacles, Spring 1.6 km NE of Dickensonville, Russell Co., VA, LH 40771 (bar = 0.43 μm).

TABLE 1.—Selected shell parameters for *Fontigens nickliniana* (Lea), expressed as $\bar{x}$ with SD in parentheses. Shell height (SH) and width (SW) are given in mm. NW = number of whorls, W = whorl expansion rate, D = distance of generating curve from coiling axis, T = translation rate, AS = aperture shape.

Locality	NW	SH	SW	W	D	T	AS
Spring, Albion, Calhoun Co., MI LH A8028 (n = 11)	5.00(0.11)	4.38(0.28)	2.24(0.14)	1.66(0.12)	0.62(0.03)	7.56(0.81)	1.26(0.07)
Button Lake, Kent Co., MI USNM 590367 (n = 9)	5.14(0.13)	4.14(0.10)	2.03(0.09)	1.55(0.12)	0.62(0.07)	8.01(0.91)	1.27(0.07)
Spring-fed brook, Williamsville, Erie Co., NY USNM 791435 (n = 15)	5.23(0.15)	4.51(0.72)	2.30(0.38)	1.51(0.21)	0.56(0.04)	7.16(1.00)	1.28(0.10)
Bellefonte, Centre Co., PA USNM 463115 (n = 10)	5.13(0.13)	4.15(0.21)	2.10(0.13)	1.54(0.11)	0.65(0.03)	8.75(1.34)	1.24(0.06)
Warm Springs, Bath Co., VA USNM 853157 (n = 12)	5.17(0.16)	3.46(0.20)	1.89(0.11)	1.50(0.08)	0.56(0.05)	7.14(0.74)	1.28(0.05)
J.W. Reynolds Spring, Giles Co., VA USNM 858044 (n = 10)	5.05(0.20)	3.77(0.17)	2.01(0.10)	1.51(0.16)	0.59(0.05)	7.36(1.29)	1.28(0.08)
Spring, 3.7 km NW of Honaker, Russell Co., VA LH 42102 (n = 10)	5.13(0.24)	3.83(0.39)	2.04(0.19)	1.60(0.15)	0.61(0.05)	6.65(1.29)	1.25(0.07)
Spring, Lantz Mills, Shenandoah Co., VA USNM 853149 (n = 13)	4.65(0.24)	3.59(0.22)	1.93(0.14)	1.50(0.16)	0.58(0.06)	7.34(0.96)	1.22(0.07)
Spring, 1.1 km SE of Gap Mills, Monroe Co., WV USNM 431746 (n = 15)	5.57(0.18)	4.76(0.20)	2.35(0.09)	1.42(0.17)	0.57(0.04)	7.11(0.80)	1.26(0.05)

Bythinella attenuata.—Stimpson, 1865:20.—Binney, 1865:68, fig. 132.—Tryon, 1870:46.
Paludestrina nickliniana var. *attenuata*.—Pilsbry, 1899:22.
Paludestrina nickliniana attenuata.—Walker, 1918:138.
Stimpsonia nickliniana attenuata.—Baker, 1928:136, pl. VII: figs. 13, 14.
Amnicola gracilis Gould in Anonymous, 1844:167 [nomen nudum].
Fontigens sp. (near *nickliniana*?).—Holsinger and Culver, 1988:22.
Fontigens sp.—Hershler, 1989b:99.

DIAGNOSIS.—A moderate- to large-sized species with elongate conic shell. Penis with two accessory lobes containing tubular glands. Most similar to *F. aldrichi*, but differing by more elongate shell.

DESCRIPTION.—Shell (Figure 1, Table 1) 2–6 mm tall, elongate conic, ovate-conic in rare instances (usually due to shell erosion); height/width, 160%–220%. Whorls, 4–8, well rounded, occasionally shouldered adapically. Spire outline convex. Aperture ovate, somewhat angled above. Inner lip moderately thickened, slightly-moderately reflected, slightly separated from or adnate to small portion of body whorl. Umbilicus usually slit-like, but varying from absent to open. Apex (Figure 2*a*,*c*) protruding slightly; protoconch (Figure 2*a*,*c*) striae faint but numerous. Periostracum often covered by deposits. Operculum shown in Figure 2*e*.

Epigean animals often near-uniformly covered with dark brown black epithelial melanic pigment. Pigment somewhat lighter on distal cepalic tentacles (Figures 3*a*, 4*a*), and absent from small circular areas around the eyespots and sole of foot. Dense yellow-white subepithelial granules clustered in small areas posterior to (and sometimes slightly overlapping) eyespots and scattered in proximal half of tentacles. Visceral coil darkly pigmented (surface of gonoducts sometimes lighter), particularly on dorsal surface. Penis often darkly pigmented on most of dorsal surface. Snails from caves thoroughly depigmented, including absence of pigment on eyespots (Figure 4*b*).

Snout squat, somewhat expanded distally. Tentacles elongate, circular in cross-section, gently tapering with rounded tips. Cilia short, and uniformly distributed on dorsal surfaces of tentacles (Figure 2*b*,*d*). Ventral tentacles with central zone of hypertrophied cilia (Figure 2*f*). Ciliary patches scattered throughout remaining portions of head/foot.

Radular formula (Figures 5, 6): (3-7)-1-(3-7)/1(2)-1(2), 2(3)-1-2(3), 18-27, 15-37. Lateral teeth with large, hoe-like central cusp. Inner marginal teeth often with enlarged cusp near lower end.

Ctenidial filaments, 20–30. Testis filling 1.0 whorl, partly overlapping posterior stomach. Penis (Figures 3*b*, 8*a*) large relative to head, extending well beyond mantle collar. Penial filament (Pf) usually of corkscrew appearance due to several twists along its length. Vas deferens (Vd) opening subterminally (Figure 8*b*). Penial filament generally short relative to distal lobe. Distal lobe variable in size, but usually longer than proximal lobe (Figure 7). Gland in distal lobe (Dl) variable in length (Figure 9*a*,*c*,*d*), but rarely extending into nuchal cavity. Distal tip of lobe fringed by dense cilia that surround tip of gland (Figure 8*c*). In section (Figure 10*c*,*d*) penial glands appear identical and consist of a thick muscular layer covering tall, densely packed glandular cells that discharge into a central lumen.

Ovary, <0.25 whorl. Capsule gland slightly longer than

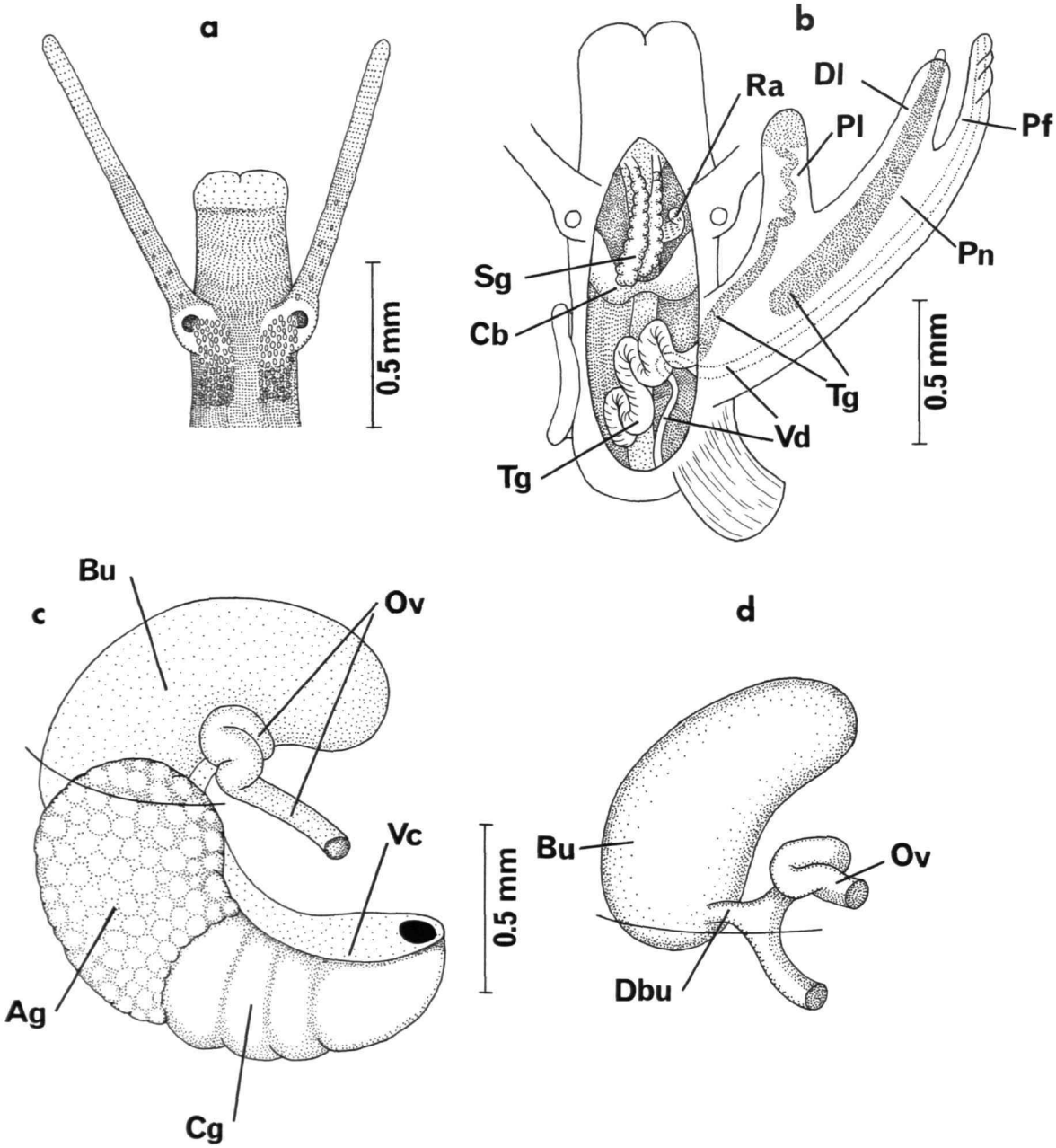

FIGURE 3.—Anatomy of *F. nicklíniana: a,* Dorsal aspect of head, showing dark pigmentation and dense cluster of granules around the eyespots, Spring at Natural Bridge, Rockbridge Co., VA, USNM 858065; *b,* Dorsal aspect of head of male, with head slit open to expose contents of nuchal cavity, Spring on Tanker Creek, Pittsylvania Co., VA, LH A8651; *c,* Left lateral aspect of pallial oviduct complex, Spring 12.3 km WNW of Dickensonville, Russell Co., VA, LH 40772; *d,* Left lateral aspect of bursa copulatrix and associated structures, from above lot.

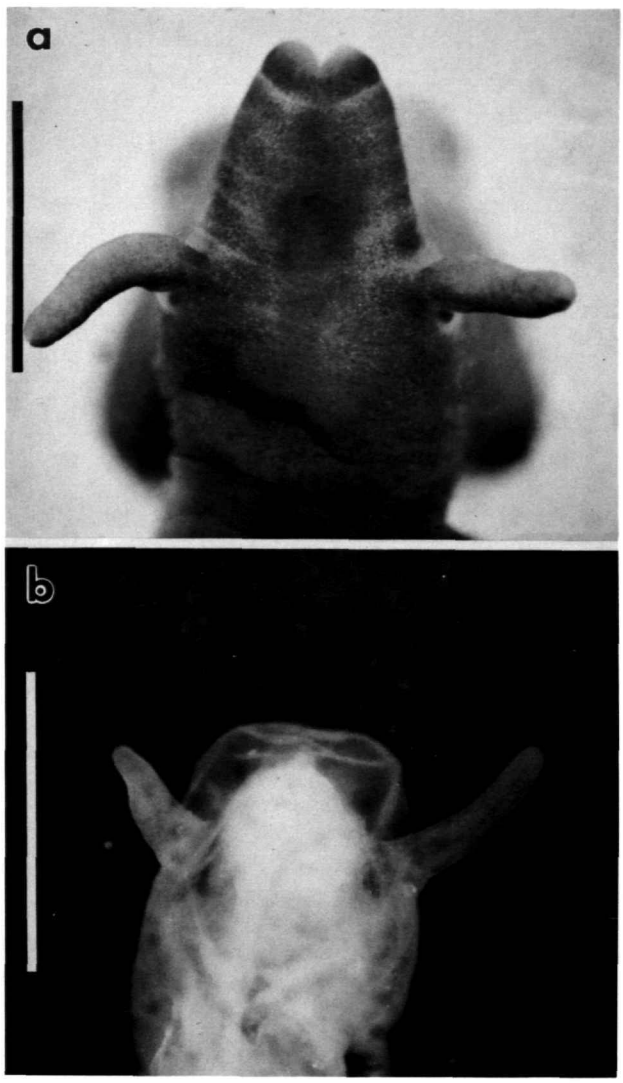

FIGURE 4.—Photographs of heads of relaxed, alcohol preserved *F. nicklíniana*, illustrating end points of pigment variation: *a*, Spring 1.6 km NE of Dickensonville, Russell Co., VA, LH 40771 (bar = 1.0 mm); *b*, Unthanks Cave, Lee Co., VA, USNM 858045 (bar = 1.0 mm).

albumen gland. Ventral channel (Vc) moderately wide (Figure 10*a*). Bursa copulatrix (Bu) massive, overlapping posterior two-thirds of albumen gland and extending well posterior to gland (Figures 3*c*, 10*b–d*). Oviduct coil small: note presence of oriented sperm within duct (Figure 10*c,d*). Surface of coil bulging and irregular. Duct from bursa short and issuing from anterior half of structure. Eggs laid singly; of simple hemispherical appearance and about 0.5 mm diameter.

TYPE LOCALITY.—A spring-fed stream at Hot Springs, Bath Co., Virginia (precise location unknown). Lectotype, ANSP 66110a (designated by Pilsbry in Baker 1964:174); paratypes, ANSP 316958, 368404, USNM 853156.

DISTRIBUTION AND HABITAT.—Widely distributed, including Great Lakes region (drainage of Lakes Michigan, Huron, and Ontario; Illinois River basin) and Appalachians (Hudson, Susquehanna, Potomac, Shenandoah, James, Roanoke, New, Holston, Clinch, Powell River basins), including a disjunct population as well in the southern end of the range in the Black Warrior River drainage of Alabama (Figure 11). Snails found in a variety of habitats, ranging from small lakes to springs and spring-fed streams to a few caves (in southwestern Virginia).

VARIATION.—Despite the broad and disjunct distribution of this snail, geographic variation is relatively minor, with even the northern lacustrine populations relatively undifferentiated. Two spring populations in the vicinity of Waynesboro, Augusta Co., Virginia, exhibited dimorphism in shell form, with both the typical form as well as enlarged, stout (and apically eroded) individuals being represented (Figure 1*n,o*). Further study will be necessary to document adequately the extent and significance of this variation.

REMARKS.—*Amnicola attenuata* Haldeman from the Roanoke River basin, Montgomery Co., Virginia, is merely an elongate form of *F. nickliniana*, as pointed out by Berry (1943:48). Although neither type, figure, nor description is available for *Amnicola gracilis* Gould, this almost certainly is a junior subjective synonym given that it was described from a known (in fact type) locality of *F. nickliniana* that lacked other hydrobiids.

MATERIAL EXAMINED.—ALABAMA. *Tuscaloosa County:* Tannehill Spring, 2.4 km S of Bucksville, LH 13488, UF 113412, uncat., UMMZ 55728.

ILLINOIS. *Cook County:* Calumet Lake, USNM 133206; Calumet, UF 78422; Chicago, ANSP 69177. *Fulton County:* USNM 28511.

INDIANA. *La Porte County:* Spring Brook Farm, 8 km E of Michigan City, ANSP 219084, FMNH 58682, MCZ 222018, UMMZ 69904, 119218, USNM 653448; Spring, Michigan City, UMMZ 119217; Old mill dam of Little Kankakee River, 8 km E of La Porte, FMNH 58683, MCZ 222019, UMMZ 119220, USNM 653447; Little Kankakee River, UMMZ 69903, 119213; Small ditch, Kankakee Twp., UMMZ 119219. *Lake County:* Berry Lake, UMMZ 119216, FMNH 145782. *St. Joseph County:* St. Joseph River, South Bend, MCZ 2223.

MICHIGAN. *Allegan County:* Small stream, 4.8 km E of Plainwell, USNM 622782. *Barry County:* Small creek, 14.4 km WSW of Oakland, UF 113413; Creek, 14.4 km WSW of Hastings, UF uncat. *Berrien County:* Stream running through Tamarack Bog, near Berrien Springs, USNM 853136. *Calhoun County:* Small brook, Battle Creek Biological Preserve, USNM 529565; Small stream, 4 km ESE of Battle Creek, LH A7905; Small stream, 4.8 km ESE of Battle Creek, LH A7791, USNM 622788; Spring, County Park, 6.4 km ESE of Battle Creek, LH A7908, USNM 622785; Seep, on bank of Brigham Lake, 4.8 km E of Battle Creek, LH A7861, USNM 622787; Spring,

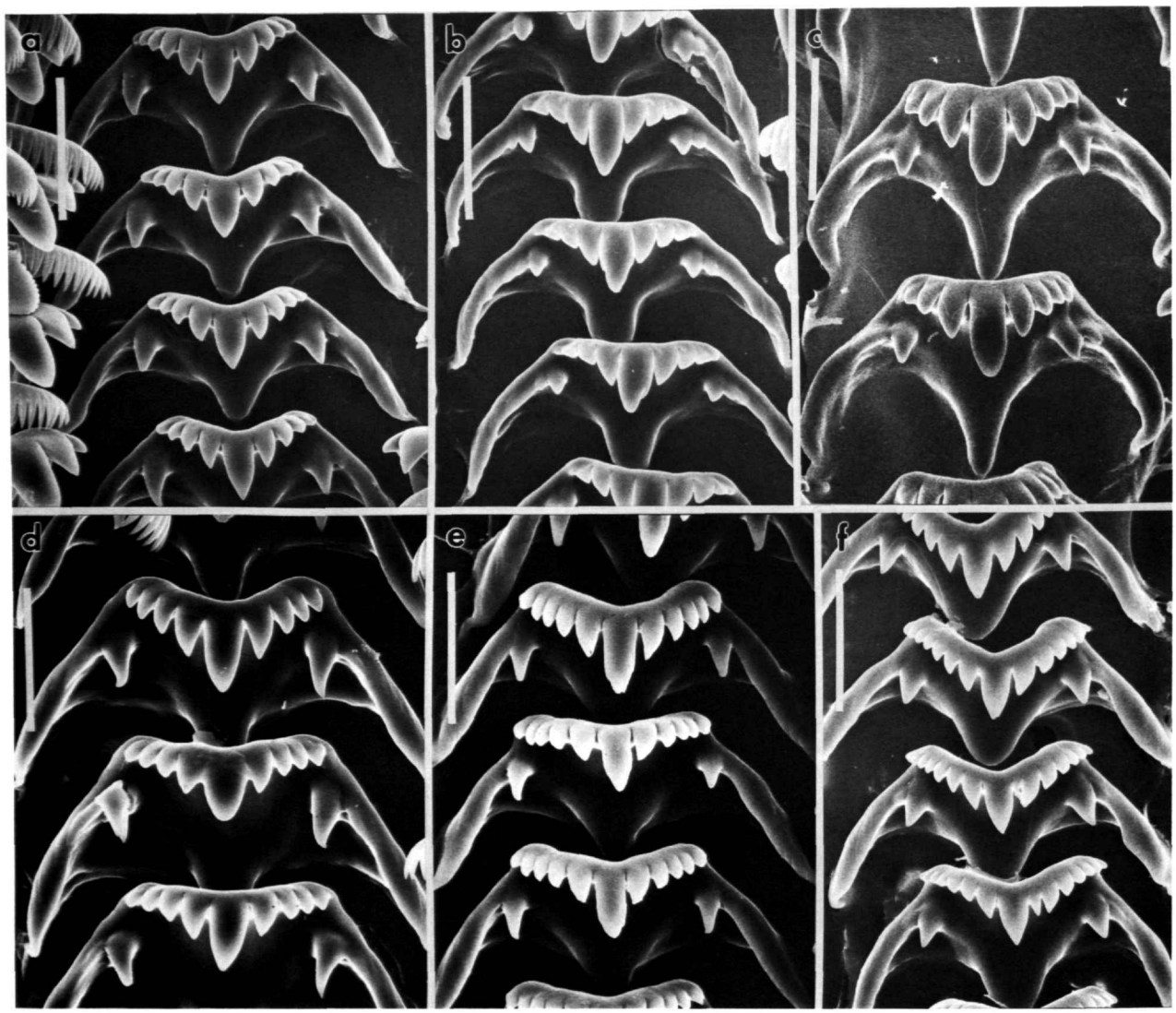

FIGURE 5.—Central radular teeth of *F. nicklíniana: a*, Warm Springs, Bath Co., VA, USNM 853157 (bar = 13.6 μm); *b*, Unthanks Cave, Lee Co., VA, USNM 858045 (bar = 15.0 μm); *c*, Nursery Spring, Augusta Co., VA, LH 46946 (bar = 17.6 μm); *d*, Creek 14.4 km WSW of Oakland, Barry Co., MI, UF 113413 (bar = 12.0 μm); *e*, Nursery Spring, Augusta Co., VA, LH 46946 (bar = 12.0 μm); *f*, Tannehill Spring, Tuscaloosa Co., AL, UF 113412 (bar = 12.0 μm).

Victory Park, Albion, LH A8028, FMNH 29058, USNM 622784. *Charlevoix County:* Charlevoix, UF 8281. *Emmet County:* Round Lake, Petoskey, ASNP 68453. *Huron County:* Rush Lake, UMMZ 119223. *Kalamazoo County:* Lincoln Creek, UMMZ 119229; Spring run, 0.8 km W of Millwoods, LH A8200, USNM 622786; Small stream, 3.2 km N of East Cooper, LH A8060, USNM 622783. *Kent County:* Eagle Mill, ANSP 68452, FMNH 87862, UMMZ 119224, USNM 133207; Grand Rapids, ANSP 68450, 70224, 70237, FMNH 32773, 58681, 87882, UMMZ 143641, USNM 519981; Spring-fed brook near Grand Rapids, UMMZ 63607; Small brook, Grand Rapids, FMNH 138078; Reeds Lake, Grand Rapids, UMMZ 143638; Button Lake, FMNH 87986, UMMZ 119226, 162925, UF 88637, 88639, USNM 590367; Spring, Button Lake, FMNH 137959; Perch Lake, UMMZ 143640; Byers Trout Pond, FMNH 114739, UF 14, 88510, UMMZ 119227, 143639; Byers Point, MCZ 281963. *Lake County:* Marl Lake, UMMZ 161825. *Montcalm County:* Marsh E of Mud Lake, UMMZ

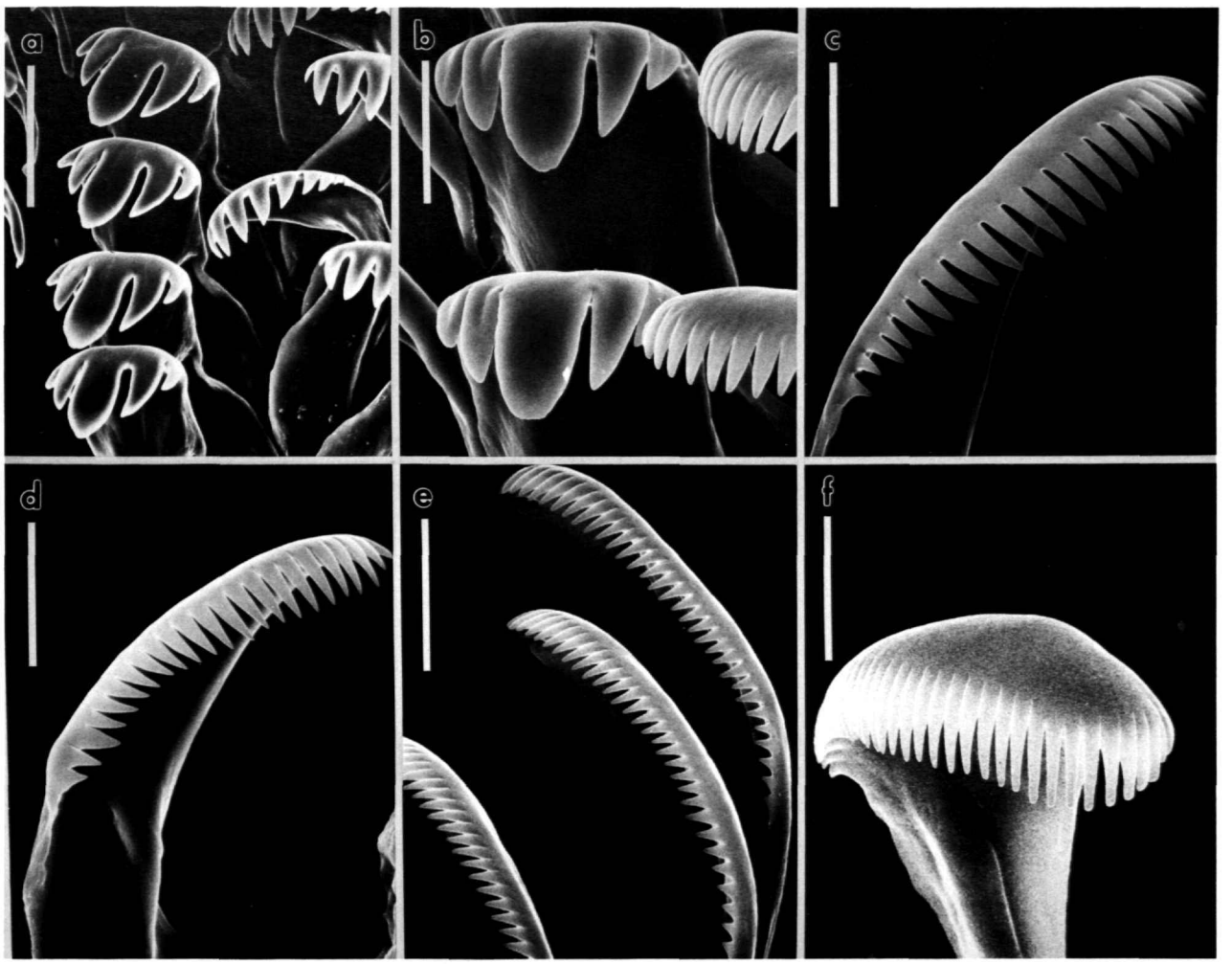

FIGURE 6.—Lateral and marginal radular teeth of *F. nickliniana: a,* Laterals and inner marginals, Nursery Spring, Augusta Co., VA, LH 46946 (bar = 27 μm); *b,* Laterals, Unthanks Cave, Lee Co., VA, USNM 858045 (bar = 8.6 μm); *c,* Inner marginal, Creek 14.4 km WSW of Oakland, Barry Co., MI, UF 113413 (bar = 7.5 μm); *d,* Inner marginal, Warm Springs, Bath Co., VA, USNM 853157 (bar = 7.5 μm); *e,* Outer marginals, Tannehill Spring, Tuscaloosa Co., AL, UF 113412 (bar = 5.0 μm); *f,* Outer marginal, Nursery Spring, Augusta Co., VA, LH 46946 (bar = 5.0 μm).

119228. *Newaygo County:* Brooks Lake, FMNH 138116. *Ottowa County:* Jamestown, UMMZ 143636. *St. Joseph County:* Klingers Lake, UMMZ 160688. *Van Buren County:* Spring run, below dam, 1.6 km N of Paw Paw, LH A8199, UMMZ 171788, USNM 622789; Campbells Creek near Kendall, UMMZ 37662.

NEW YORK. *Erie County:* Spring-fed brook in Williamsville, USNM 592511, 592512, 791435; Williamsville, UF 88534; Brook at Blocher Homes, FMNH 114688; Buffalo, UMMZ 119212. *Westchester County:* Marshes, Hastings-on-the-Hudson, FMNH 87987.

OHIO. *Washington County:* Marietta, FMNH 32771.

PENNSYLVANIA. *Berks County:* Moselem Springs, ANSP 160618. *Centre County:* Bellefonte, ANSP 92032, UMMZ 28906, USNM 463115; Spring-fed creek, Bellefonte, ANSP 122214, FMNH 32772. *Clinton County:* Fishing Creek, USNM 121387. *Cumberland County:* Near Carlisle, USNM 791432, 791479. *Franklin County:* Spring-fed tributary stream, 0.8 km SE of Waynesboro, USNM 522080. *Huntingdon County:* 1.6 km N of Spruce Creek P.O., USNM 783938.

VIRGINIA. *Alleghany County:* Large spring, Lowmoor, LH 43792; Spring at Lowmoor, USNM 853160; Spring along

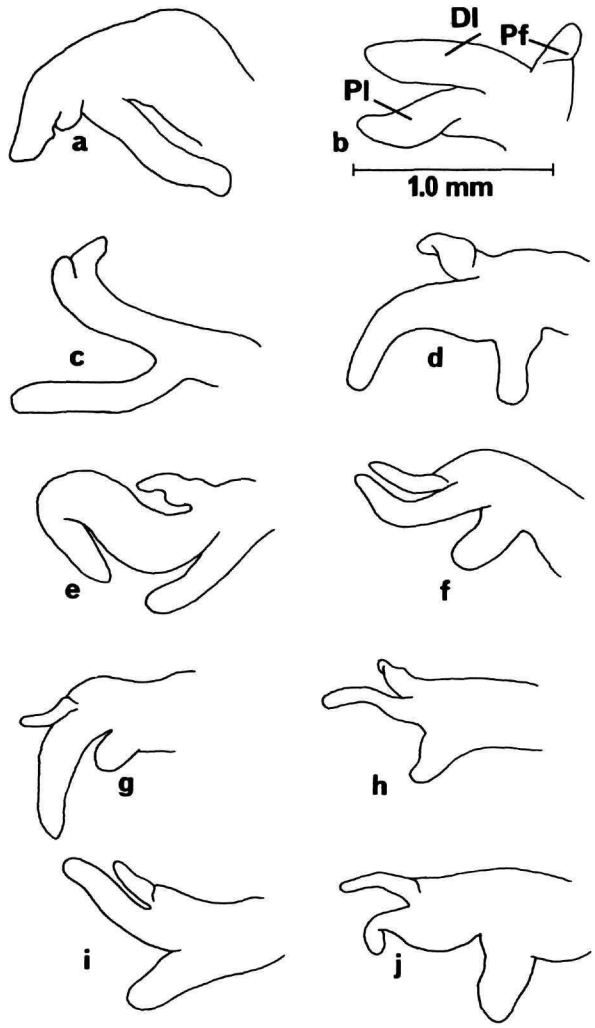

FIGURE 7.—Camera lucida outline drawings of penes of *F. nickliniana*: *a*, Spring 4.5 km SW of Claypool Hill, Tazewell Co., VA, LH 40770; *b*, Spring 1.6 km NE of Dickensonville, Russell Co., VA, LH 40771; *c*, Spring 3.7 km NW of Honaker, Russell Co., VA, LH 42102; *d*, Tannehill Spring, Tuscaloosa Co., AL, UF 113412; *e*, Spring, Sinking Creek, Craig Co., VA, LH 39854; *f*, Creek 14.4 km WSW of Oakland, Barry Co., MI, UF 113413; *g*, Spring, Lantz Mills, Shenandoah Co., VA, LH 43699; *h*, Unthanks Cave, Lee Co., VA, USNM 858045; *i*, Spring on Tanker Creek, Pittsylvania Co., VA, LH A8651.

Smiths Creek, 4 km N of Clifton Forge, USNM 853158, 853159. *Augusta County:* Staunton City Spring, on south bank of Middle River, 9.6 km NW of Staunton, USNM 473632–473634; Coiner Spring, 4.8 km S of Waynesboro, ANSP 189803, LH 12166; Coiner Spring, Waynesboro Waterworks, Well (#1), ~3.2 km SW of city, USNM 605558; Nursery Spring, 2.4 km W of Lyndhurst, LH 46946, 46947, USNM 758764, 758765; Bakers Spring, Waynesboro, USNM 522833–522840; Basic City, USNM 426849; Staunton (marl in cave)(subfossil), USNM 225867. *Bath County:* Warm Springs, USNM 853157, ANSP 27800 59471, 316957; Hot Springs, UMMZ 119209, 119206. *Craig County:* D.A. Huffmans Spring, on Route 42, USNM 853153; Wyrick Spring, Crockett, USNM 433503; Spring, 0.5 km NE of Huffman, LH 18783; Spring, Sinking Creek, LH 39854; Spring, 1.6 km SW of Sinking Creek, LH 18782. *Frederick County:* Spring-fed tributary of Hogue Creek, SW of US 50 bridge, 1.6 km E of Hayfield, USNM 431714, 431715, 853140; Blue Spring, near Marlboro, USNM 791452; Large spring, 4.2 km NW of Middletown, LH 43684; Ogdens Cave, drift on cave walls (smaller of 2 specimens may be *F. bottimeri*), USNM 431629; Spring in Buffalo Marsh Run, 4 km NW of Middletown, USNM 858043. *Giles County:* J.W. Reynolds Spring, 1.6 km N of Newport, USNM 858044. *Lee County:* Gallohan Cave (#1), 10.4 km SE of Rose Hill, LH 40408; Pool in Smiths Milk Cave, 11.2 km SW of Rose Hill, LH 44327; Spring, 1.0 km E of Jonesville, LH 44054; Spangler Cave, 5.6 km W of Jonesville, LH 40407; Unthanks Cave, 11 km SW of Jonesville, USNM 858045; Springs feeding Batie Creek, off HW 662, 3.2 km SW of Jonesville, USNM 858046. *Montgomery County:* Spring connected with Roanoke River, ANSP 69472 (lectotype, *Amnicola attenuata*), ANSP 368408; Nolleys Spring, 6.4 km S of Christiansburg, USNM 858047; Spring, 1.6 km W of Lafayette, LH 12486; Spring near Ingles Ferry, 3.2 km S of Radford, LH A8448; Stream drift, Elliston, USNM 853162; Spring in Elliston at intersection of US 460 and SR 745, USNM 858048; Cedar Springs, USNM 858049. *Page County:* Spring, 1.6 km S of Luray, LH 46948; Underground tributary to Hawksbill Creek, Luray, USNM 853137; Luray, ANSP 60323, USNM 347928, 360655, 526820, 853143; Head of spring tributary to Hawksbill Creek, Luray, USNM 853144–853148. *Pittsylvania County:* Spring on Tanker Creek, 8 km N of Sandy Level, LH A8651, USNM 791450, 791451. *Pulaski County:* Dublin Spring, Radford Arsenal property, USNM 791449; Spring, 1.1 km W of Snowville, LH 13075. *Rockbridge County:* McKees Spring, USNM 184348; Spring, 3.2 km NW of Lexington, USNM 858050; Spring at Natural Bridge, USNM 858065. *Rockingham County:* Spring, Lacey Spring, LH 43721; Lacey Spring, Lacey Spring P.O., LH 19070, USNM 431618, 431619; Poor Farm, Harrisonburg, USNM 853152; Massanetta Spring, near Harrisonburg, USNM 858051. *Russell County:* Brook opposite Fink, USNM 119214; Spring, 12.3 km WNW of Dickensonville, LH 40772; Spring, 3.7 km NW of Honaker, LH 42102; Spring, 1.6 km NE of Dickensonville, LH 40771; Will Humboldt Spring, Lebanon, USNM 433505. *Shenandoah County:* Spring, Lantz Mills, LH 43699, USNM 853149, 853150, 853151; Cedar Creek N of Strasburg, just above US 11 bridge, USNM 431702. *Smythe County:* Spring and headwaters of South Fork Holston River, Sugar Grove,

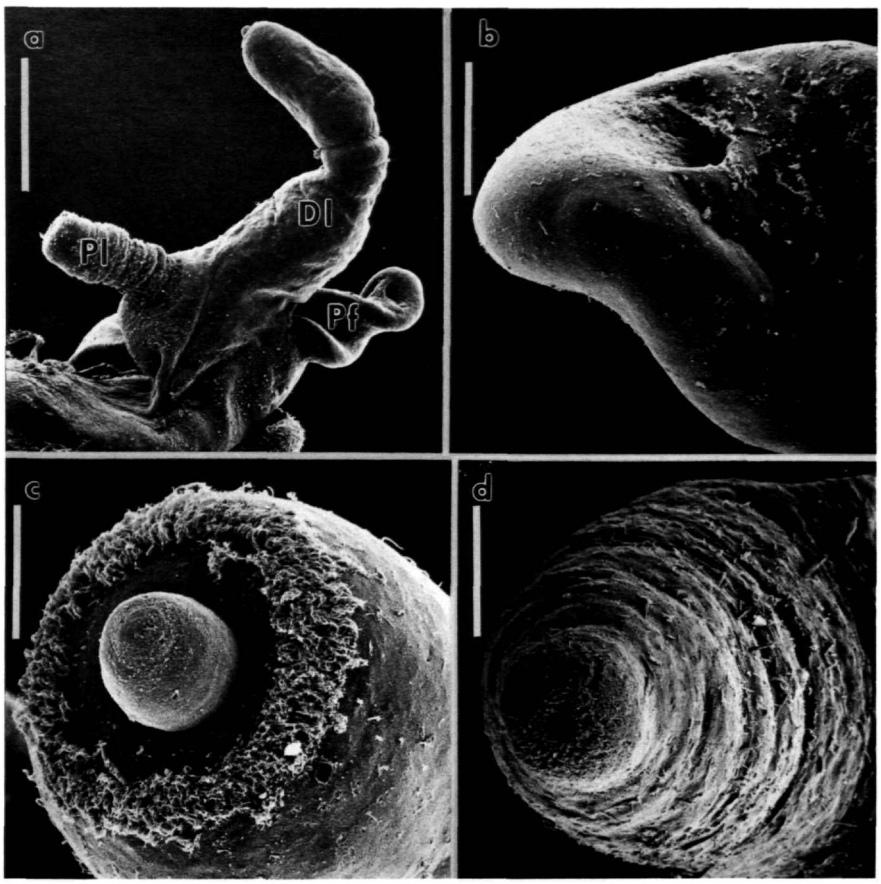

FIGURE 8.—Scanning electron micrographs of penes of *F. nicklinianа: a,* Distal tip of penial filament showing opening of vas deferens, Tannehill Spring, Tuscaloosa Co., AL, UF 113412 (bar = 0.33 mm); *b,* Distal tip of proximal penial lobe, from above lot (bar = 60 μm); *c,* Dorsal penis, lot as above (bar = 0.43 mm); *d,* Distal tip of median lobe, Spring 1.6 km NE of Dickensonville, Russell Co., VA, LH 40771 (bar = 86 μm).

USNM 608780; Cedar Spring, USNM 433504. *Tazewell County:* Spring, 4.5 km SW of Claypool Hill, LH 40770. *Washington County:* Spring, 3.2 km E of Wallace, UMMZ 162403; Davis Spring, 3.2 km NW of Meadowview, LH A9893; Spring, 5.1 km N of Lodi, LH 48074. *Wythe County:* Spring, 1.9 km N of Rural Retreat, LH A9007; Harkrader Spring, Grahams Forge, UMMZ 119208, USNM 433502.

WEST VIRGINIA. *Berkeley County:* Martinsburg, UMMZ 119211. *Jefferson County:* Shenandoah River drift, Bloomery, USNM 421168. *Monroe County:* Spring, 1.1 km SE of Gap Mills, USNM 431744–431746; Hunt Cave near Sinks Grove, LH 40410; Spring, 6.7 km W of Sinks Grove, LH 40717. *Pocahontas County:* Spring, Huntersville, LH A4943; Spring, 0.8 km NE of Mill Point, LH 47460.

WISCONSIN. *Door County:* Kangaroo Lake, FMNH 64021.

Fontigens aldrichi (Call and Beecher)

FIGURES 12–14; TABLE 2

Bythinella aldrichi Call and Beecher, 1886:190, fig. 4; pl. 7: figs. 11–14.
Paludestrina aldrichi.—Walker, 1918:137.
Amnicola a. aldrichi.—Hubricht, 1940:118, pl. 14: figs. A, D–H.—Burch and Tottenham, 1980:120, fig. 277.
Fontigens aldrichi.—Craig, 1975:2; 1977:82.—Peck and Lewis, 1978:44.—Gardner, 1986:8.
Amnicola a. antroecetes.—Hubricht, 1941:112.
Amnicola a. insolita Hubricht, 1940:119, pl. 14; figs. B, C.
Amnicola missouriensis Pilsbry, 1898:43. [New synonymy.]

DIAGNOSIS.—A moderate-sized species with broadly conical shell. Penis with two accessory lobes containing tubular glands.

DESCRIPTION.—Shell (Figure 12, Table 2) 1–3 mm tall, usually low trochoid, rarely elongate conic; height/width, 107%–163%. Whorls, 3.0–5.0, well rounded, sometimes with

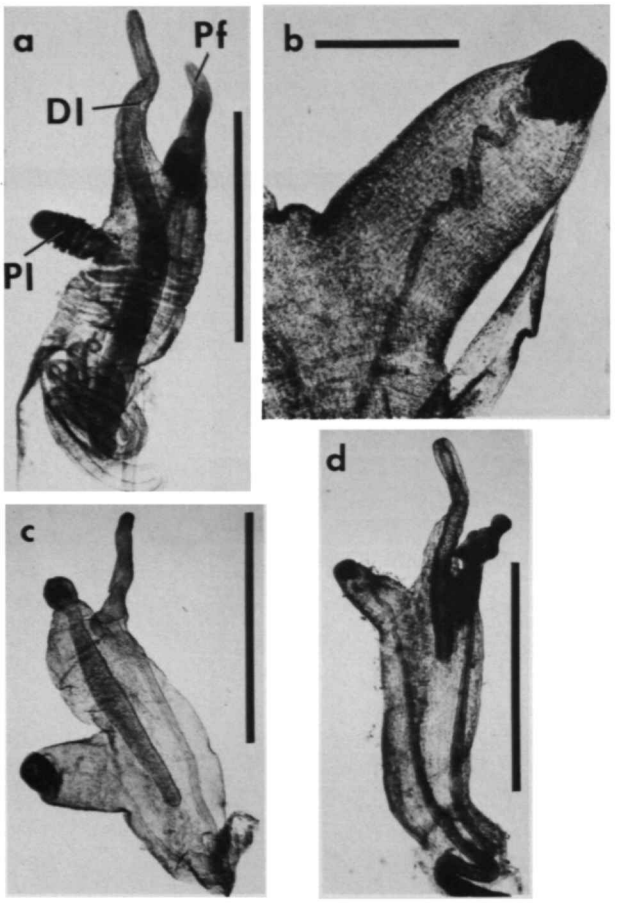

FIGURE 9.—Dorsal aspects of mounted penes of *F. nickliniana*: *a*, Spring 0.8 km NE of Mill Point, Pocahontas Co., WV, LH 47460 (bar = 1.0 mm); *b*, Close-up of proximal penial lobe showing coiled glandular duct entering terminal cup-like structure, Spring on Tanker Creek, Pittsylvania Co., VA, LH A8651 (bar = 0.25 mm); *c*, from above lot (bar = 1.0 mm); *d*, Unthanks Cave, Lee Co., VA, USNM 858045 (wet mount; bar = 1.0 mm).

pronounced adapical shoulders. Spire outline convex. Aperture ovate, somewhat angular above. Inner lip moderately thickened, usually well reflected, slightly separated from or adnate to portion of body whorl. Umbilicus slit-like to open. Apex almost flat (Figure 13*g*); protoconch with broadly and uniformly separated incised spiral lines.

Body pigmentation variable, ranging from nearly uniform jet black to absent (in cave forms), with various intermediate conditions represented. Pigment in penis (when present) concentrated in penial filament (Figure 13*h*).

Radular formula (Figure 13*a-f*): 6(7)-1-6(7)/1-1, (2-4)-1-4(5), 23-30, 23-27. Central cusp of lateral tooth slightly to moderately enlarged, hoe-like. Inner marginal often with enlarged cusp near lower end.

Ctenidial filaments, 10–20. Testis, 0.5 whorl. Seminal vesicle partly overlapping stomach. Penis (Figure 13*h*) small; penial filament short relative to lobes, rarely twisted. Ovary, <0.25 whorl. Capsule gland much longer than albumen gland. Ventral channel narrow. Bursa copulatrix very large, overlapping more than half of albumen gland. Duct issuing from near mid point of bursa. Oviduct coil small.

TYPE LOCALITY.—A spring-fed tributary to Black River, Reynolds Co., Missouri (precise location unknown). Lectotype (designated herein), ANSP 199452, (4.25 whorls; shell height, 2.59 mm; shell width, 1.0 mm); paralectotypes, ANSP 374556, USNM 74116, 525666, 526500.

DISTRIBUTION AND HABITAT.—Species widespread in Mississippi River basin of eastern Missouri (Figure 14), including drainages of Missouri, Gasconade, Meramec, St. Francis, Black, and Current Rivers. Disjunct populations to the northeast along Illinois River are known only from shell, and are of uncertain taxonomic status. Snails found in both small springs and caves.

REMARKS.—*Amnicola aldrichi insolita* Hubricht from Coldwater, Wayne Co., Missouri, and *Amnicola missouriensis* Pilsbry from Carter Co., Missouri, are small-sized variants of *F. aldrichi* not requiring formal taxonomic recognition.

MATERIAL EXAMINED.—ILLINOIS. *Fulton County:* Canton, UMMZ 69851, 120718. *La Salle County:* Utica, USNM 535723.

MISSOURI. *Butler County:* Keener Spring, Keener, LH A5278, UMMZ 138631, USNM 535868, 791460, 858019. *Carter County:* ANSP 27790 (lectotype, *Amnicola missouriensis*), ANSP 368400; Stream, 13.6 km SE of Van Buren, LH 48892; Drip-pool, in Cat Track Cave, 11.2 km NW of Van Buren, LH 48859; Midco Cave, 2.4 km N of Fremont, UCM 33753; Midco Spring, 12.8 km SW of Van Buren, UCM 33755. *Crawford County:* Onondaga (Cave) Spring, 8 km SE of Leasburg, LH A4659, UMMZ 138635, 162378, USNM 791461, 858020; Onondaga Cave (= Missouri Caverns), 8 km SE of Leasburg, LH A5068, UCM 33778, USNM 535865, 858021; Cathedral Cave, 8 km SE of Leasburg, LH A4477, USNM 858022; Round Spring Cavern Spring, USNM 791491; Jagged Canyon Cave, Meramec River bluff, 0.8 km N of mouth of Huzzak Creek, LH 43062; Greens Cave, 7.2 km SE of Sullivan, LH A5608; Greens Bluff Cave, 13.6 km NE of Bourbon, UCM 33757; Hamilton Cave, Meramec State Park, UCM 32979; Hamilton Spring, UCM 32985. *Dent County:* Montauk Springs, Montauk, ANSP 162934, 162935, 170244, FMNH 130279, LH A1456, UMMZ 58597, USNM 858064; Howes Spring, Howes Mill, LH A6853, UMMZ 162379; Bounds Branch Cave, 8 km SSW of Bunker, LH 48298. *Franklin County:* Camp Cave, 4.8 km ESE of Sullivan, LH 48843; Cooper Hollow Spring, 3.2 km S of Stanton, LH A6410; On rocks in spring, mouth of Cooper Hollow Spring Cave, 5.6 km E of Sullivan, LH 48839; Mushroom Cave, 4 km E of Sullivan, LH A6409; Spring, 3.2 km W of Lone Dell, LH A3062; Fishers Cave, Meramec State Park, UCM 32975; Bear Cave, Meramec State Park, 5.3 km E of Sullivan, UCM 32978,

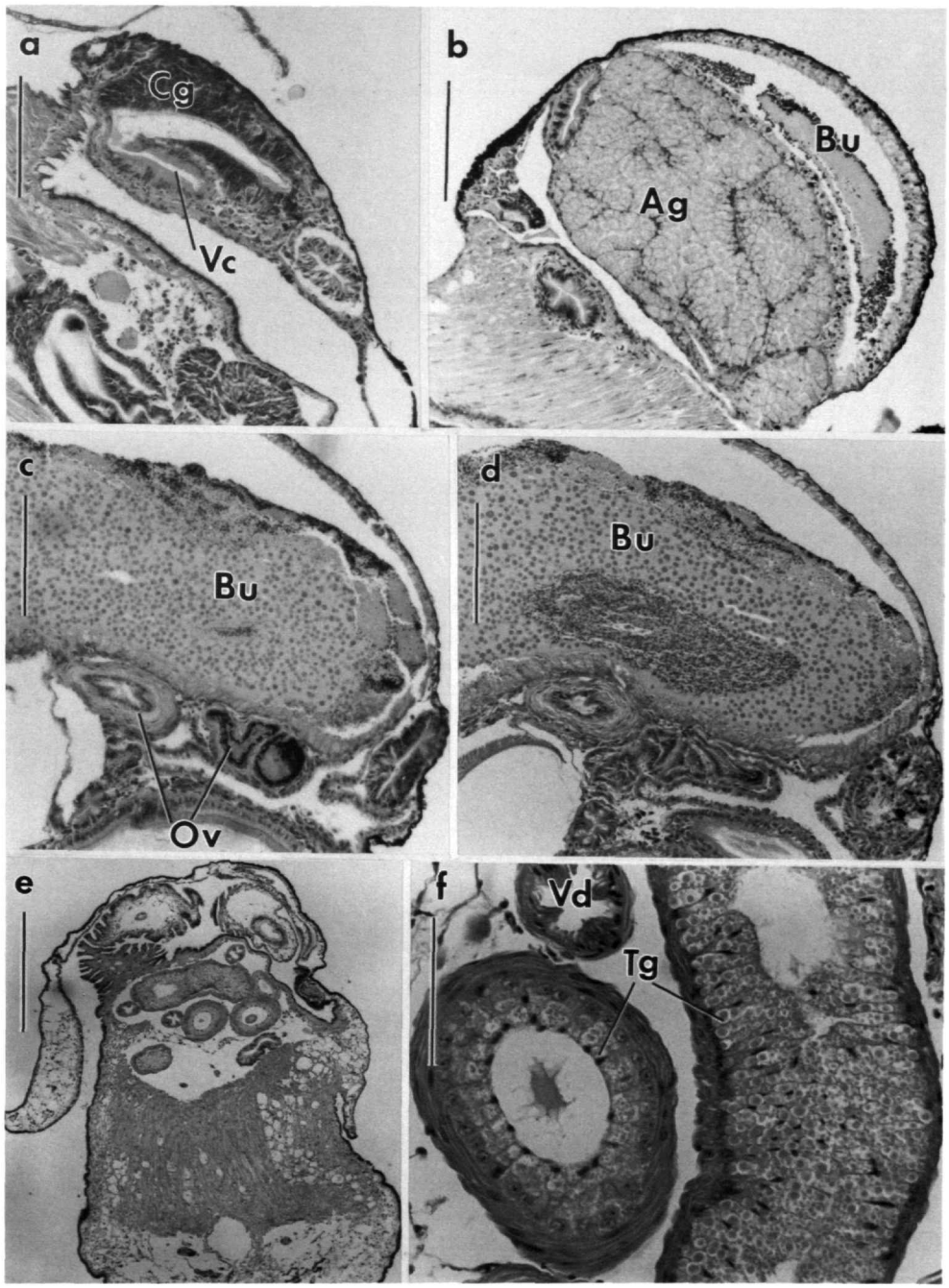

FIGURE 10.—Histological sections of reproductive morphology of *F. nicklíniana*, Nolleys Spring, Montgomery Co., VA, USNM 858047: *a*, Cross section through anterior capsule gland and intestine (bar = 0.2 mm); *b*, Cross section through albumen gland and bursa copulatrix (bar = 0.2 mm); *c,d*, Longitudinal sections through bursa copulatrix and coiled portion of oviduct (note presence of sperm within; bars = 0.2 mm); *e*, Cross section through head/foot (posterior to cephalic tentacles) showing (penial) glands in cepahlic haemocoel (bar = 0.5 mm); *f*, Cross section through penial glands (bar = 0.1 mm).

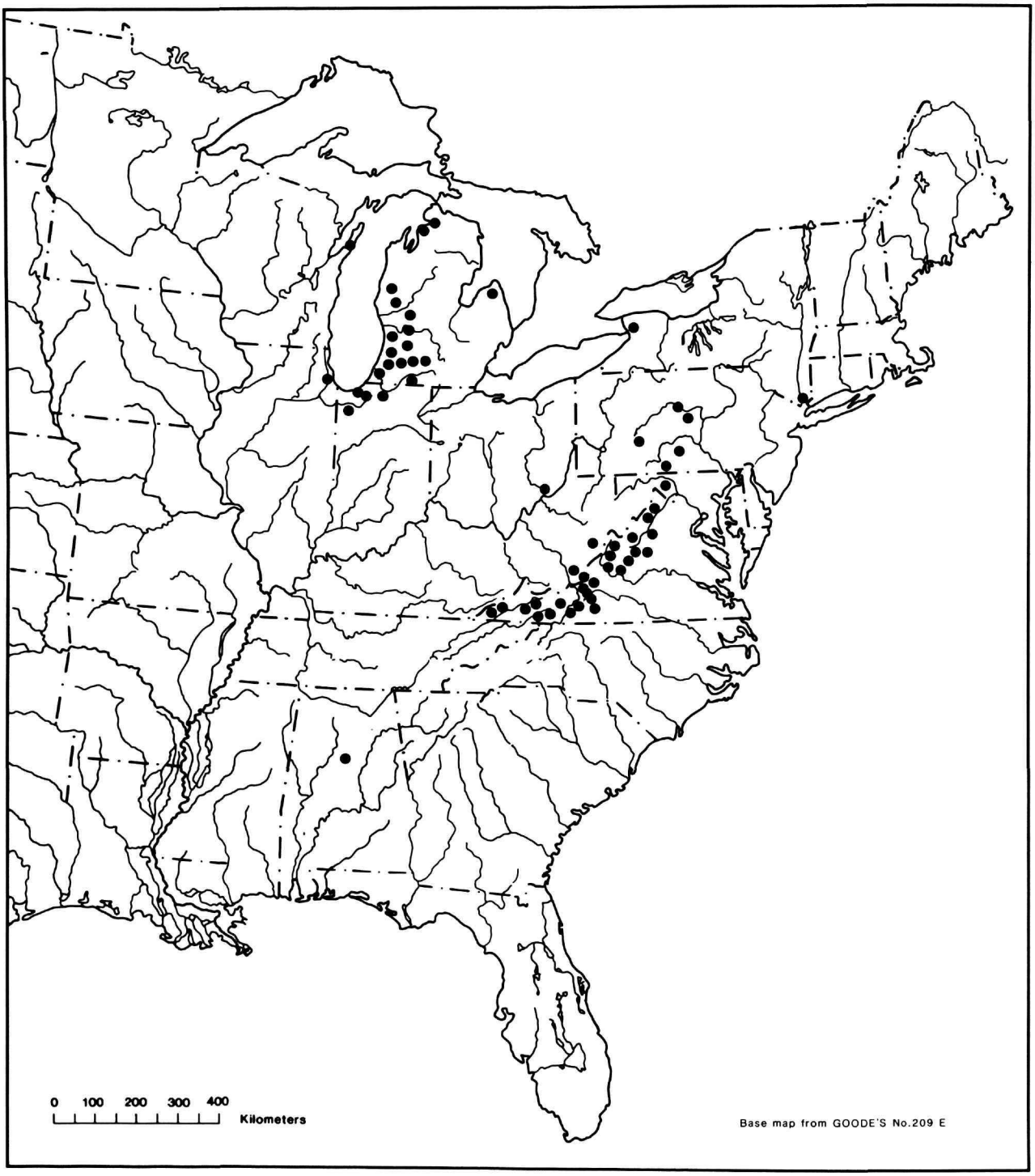

FIGURE 11.—Map showing distribution of *F. nickliniana*.

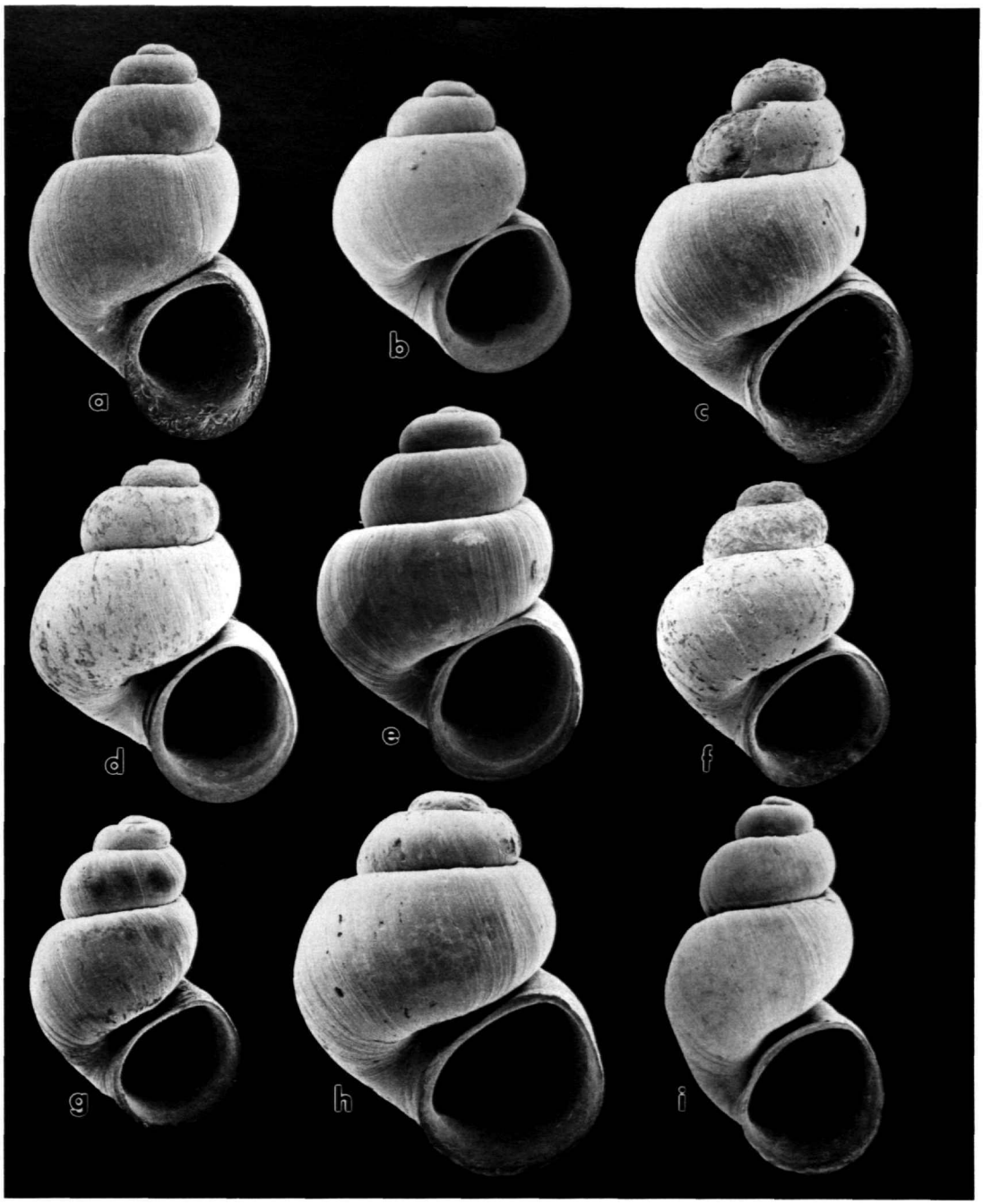

FIGURE 12.—*Fontigens aldrichi* (Call and Beecher): *a*, Spring, Ozark Mountains, Reynolds Co., MO, ANSP 374556 (paralectotype; shell height, 2.6 mm); *b*, Coldwater Spring, Wayne Co., MO, USNM 791472 (topotype, *A. aldrichi insolita* Hubricht; 1.9 mm); *c*, Montauk Springs, Dent Co., MO, ANSP 170244 (2.3 mm); *d*, Rockwood Spring, St. Louis Co., MO, USNM 858028 (2.2 mm); *e*, Meramec Caverns, Phelps Co., MO, USNM 858024 (1.5 mm); *f*, Keener Spring, Butler Co., MO, USNM 858019 (1.8 mm); *g*, Cave Hollow Spring, Shannon Co., MO, LH A702 (2.1 mm); *h*, Spring 0.6 km S of Koester, St. Francois Co., MO, LH A4715 (1.8 mm); *i*, Jam-up Cave, Shannon Co., MO, LH A5735 (2.5 mm).

TABLE 2.—Selected shell parameters for *Fontigens aldrichi* (Call and Beecher), expressed as $\bar{x}$ with SD in parentheses. Shell height (SH) and width (SW) are given in mm. NW = number of whorls, W = whorl expansion rate, D = distance of generating curve from coiling axis, T = translation rate, AS = aperture shape.

Locality	NW	SH	SW	W	D	T	AS
Spring, Ozark Mountains, Reynolds Co., MO USNM 525666 (paratypes) (n = 9)	4.06(0.11)	2.35(0.14)	1.53(0.11)	1.62(0.12)	0.61(0.07)	5.14(0.72)	1.21(0.05)
Keener Spring, Butler Co., MO USNM 858019 (n = 11)	3.30(0.10)	1.82(0.10)	1.51(0.05)	1.91(0.18)	0.55(0.04)	4.04(0.47)	1.03(0.06)
Cathedral Cave, Crawford Co., MO USNM 858022 (n = 10)	3.85(0.29)	1.42(0.07)	0.94(0.07)	1.71(0.19)	0.62(0.04)	5.03(0.76)	1.23(0.07)
Montauk Springs, Dent Co., MO USNM 858064 (n = 12)	4.04(0.14)	2.49(0.12)	1.70(0.11)	1.57(0.07)	0.59(0.05)	4.77(0.80)	1.17(0.05)
Spring, in Big Spring Hollow, Jefferson Co., MO LH A6386 (n = 9)	3.92(0.13)	2.20(0.21)	1.54(0.11)	1.68(0.11)	0.59(0.05)	4.87(0.64)	1.17(0.04)
Boulware Cave, Maries Co., MO LH A6336 (n = 7)	3.75(0.32)	1.45(0.09)	1.02(0.06)	1.53(0.08)	0.61(0.07)	4.50(0.47)	1.18(0.06)
Spring, 0.6 km S of Koester, St. Francois Co., MO LH A4715 (n = 9)	3.78(0.29)	2.16(0.22)	1.63(0.11)	2.02(0.36)	0.64(0.04)	4.36(0.67)	1.15(0.05)
Rockwood Spring, St. Louis Co., MO USNM 858028 (n = 8)	3.91(0.13)	2.04(0.14)	1.55(0.12)	1.62(0.08)	0.60(0.07)	3.97(0.71)	1.12(0.12)
Coldwater Spring, Wayne Co., MO USNM 858030 (n = 9)	3.39(0.13)	2.01(0.15)	1.72(0.11)	1.82(0.36)	0.56(0.05)	3.33(0.51)	1.08(0.08)

33784. *Iron County:* Cave Hollow Cave, 20 km NNE of Bunker, LH 48853; Bradshaw Cave Spring, 4 km N of Redmondville, LH A6267, UMMZ 162380; Kieth Spring, 2.4 km S of Enough, LH A6855, UMMZ 162381. *Jefferson County:* Spring (#18) on Antire Creek, 4 km SW of High Ridge, LH A6967, USNM 791459; Spring on bluff above Glaise Creek, 3.2 km W of Barnhart, ANSP 170243, LH A736, UMMZ 162382; Becker Spring, 0.8 km E of Seckman, ANSP 170241, LH A3677, UMMZ 162383; Spring on Antire Creek, 4.8 km S of Tyson, ANSP 161201, LH A69; Spring, in Big Spring Hollow, 4.8 km ENE of Valles Mines, LH A6386, UMMZ 162384; Spring on hillside, Moss Hollow, 4 km SW of Antonia, ANSP 170240, LH A3678; Spring (#16) along Antire Creek, 4 km SW of High Ridge, USNM 858023. *Maries County:* Boulware Cave, 19.2 km S of Vienna, LH A6336. *Oregon County:* Stream, mouth of Bluehole Cave, 14.4 km ENE of Alton, LH 48596; Spring above falls, Cook Hollow, 14.4 km N of Greer, LH 40427. *Osage County:* Dowlers Cave, 4.8 km W of Cooper Hill, LH A5799. *Phelps County:* Coon Cave (#3), 8 km S of Newburg, LH 48842; Hanley Cave, 9.6 km SW of Newburg, LH 47926; Meramec Spring, 8 km S of St. James, ANSP 344006, LH A4660, UMMZ 138635, USNM 160743, 162747, 535860, 535854, 791464, 858027; Meramec Caverns, Stanton, USNM 858024; Saltpeter Cave, 11.2 km N of Newburg, LH A5176, UMMZ 162397, 162398, USNM 858025. *Pulaski County:* Small spring, near Ash Cave, 4 km W of Jerome, LH A5636; Spring near Piquet Cave, 6.4 km SW of Dixon, LH A5699, UMMZ 162377, 162394; Piquet Cave (total darkness), 6.4 km SW of Dixon, LH A5702; Mouth of Piquet Cave, 6.4 km SW of Dixon, LH A5700, A5701; Piquet Cave, 5.6 km SW of Dixon, UCM 34132; Spring Cave, 8 km S of Crocker, LH A5670, UMMZ 162396; Tunnel Cave, 6.8 km SE of Crocker, UCM 34131. *Reynolds County:* Reeds Spring, 0.8 km E of Centerville, LH A5772, UMMZ 162385; Spring in Ozark Mountains, ANSP 175556, USNM 742942; Spring W of Well Cave, E of Black River, USNM 858026. *St. Francois County:* Spring near Iron Mountain, USNM 121326; Spring, 0.6 km S of Koester, LH A4715, UMMZ 162386; Shaver Cave, 2.4 km N of Bonne Terre, LH 6306; Falling Rock Spring Cave, 4.8 km NW of Leadwood, LH 48836; Spring, Koester, LH 16183. *Ste. Genevieve County:* Spring on Coldwater Creek, 0.5 km S of Nations Mill, LH A6385; Gilliam Cave, 8 km S of Ste. Genevieve, LH A6363, UMMZ 162398; Spring near Nations Mill, UMMZ 162387. *St. Louis County:* Rockwood Spring, USNM 858028; Spring on Hamilton Creek, 4.5 km NW of Glencoe Station, LH A2578, UMMZ 162389; Spring (#6), Antire Creek, 6.4 km E of Eureka, LH A1988, UMMZ 162388; Spring (#7), Antire Creek, 4.8 km S of Tyson, FMNH 138149, USNM 528055; Spring under bluff along roadside just W of HW 109, 8 km N of Eureka, USNM 701949; Spring on Glencoe Creek, 4.5 km NW of Glencoe Station, USNM 791458; Spring, 3.2 km S of Tyson, UMMZ 54628. *Shannon County:* Cavern Spring, 19.2 km N of Emminence, UMMZ 138632; Medlock Cave Spring, 3.2 km NW of Akers, LH A5719, UMMZ 162391; Welch Spring, 1.6 km N of Akers, LH A5716, UMMZ 162390; Middle opening (twilight), Jam-up Cave, 6.4 km NNW of Montier, LH A5735, UMMZ 162401; Spring, near Jacks Fork, N of Teresita, LH A5728; Stream,

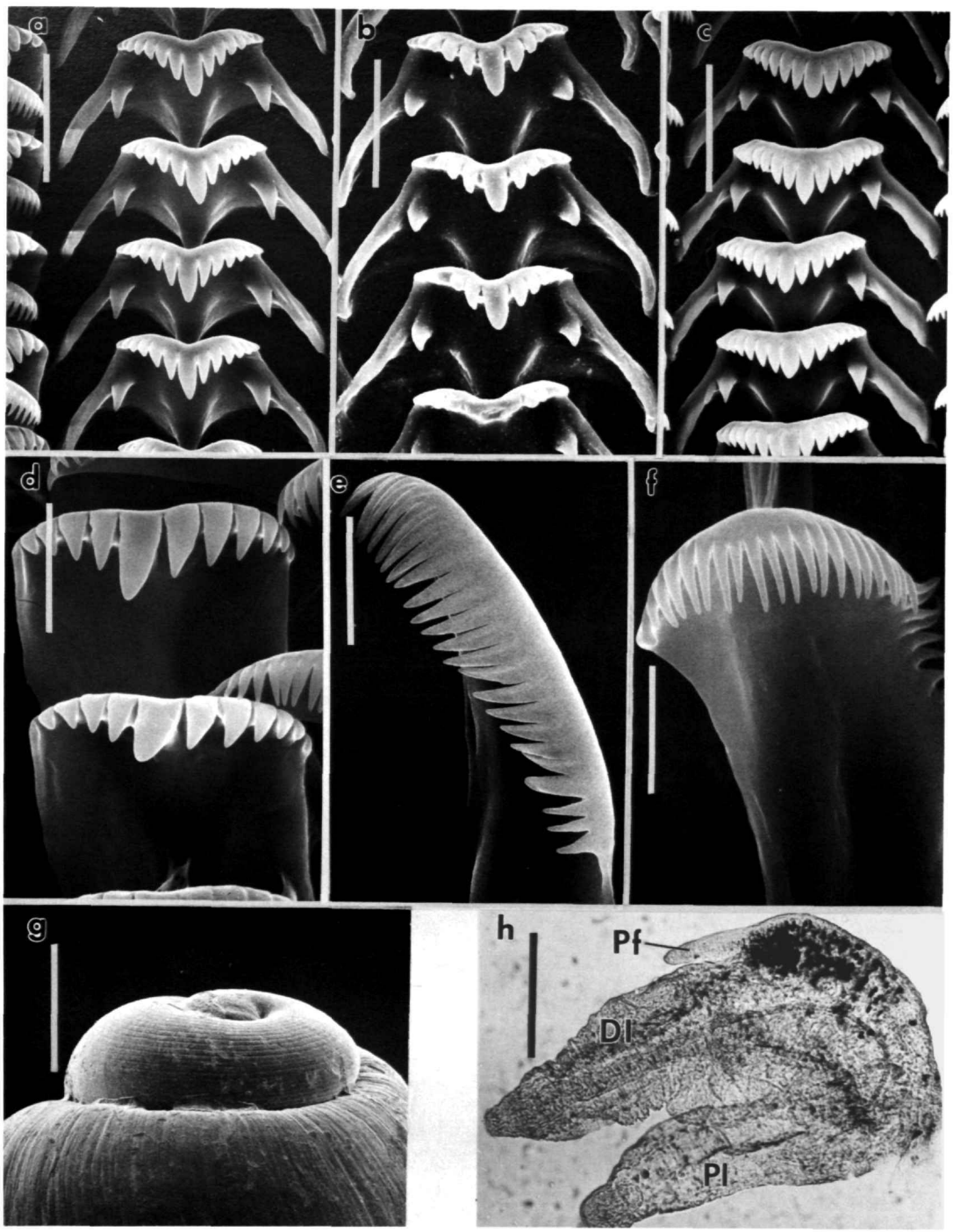

FIGURE 13.—Morphology of *F. aldrichi*: *a*, Central radular teeth, Spring W of Well Cave, Reynolds Co., MO, USNM 858026 (bar = 10.0 μm); *b*, Central radular teeth, Coldwater Spring, Coldwater, Wayne Co., MO, USNM 791472 (bar = 10.0 μm); *c*, Central radular teeth, Rockwood Spring, St. Louis Co., MO, USNM 858028 (bar = 12.0 μm); *d*, Lateral teeth, Onondaga Spring, Crawford Co., MO, USNM 858020 (bar = 7.6 μm); *e*, Inner marginal tooth, Spring on Antire Creek, Jefferson Co., MO, LH A6967 (bar = 5.0 μm); *f*, Outer marginal tooth, from above lot (bar = 3.0 μm); *g*, Protoconch, Spring, Ozark Mountains, Reynolds Co., MO, ANSP 374556 (Paralectotype; bar = 200 μm); *h*, Whole mount of penis (dorsal aspect), Rockwood Spring, St. Louis Co., MO, (bar = 0.5mm).

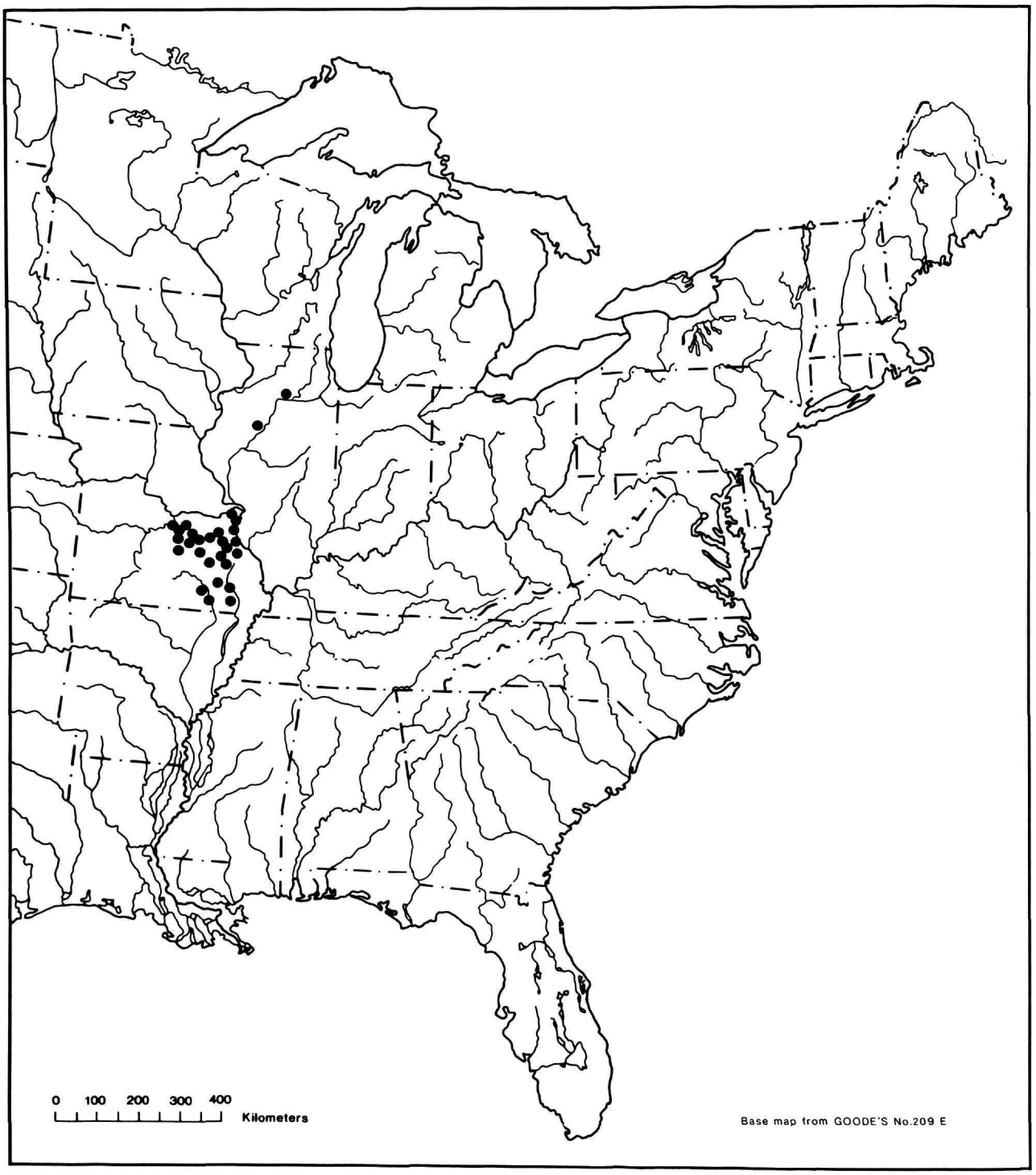

FIGURE 14.—Map showing distribution of *F. aldrichi*.

TABLE 3.—Selected shell parameters for *Fontigens antroecetes* (Hubricht), expressed as $\bar{x}$ with SD in parentheses. Shell height (SH) and width (SW) are given in mm. NW = number of whorls, W = whorl expansion rate, D = distance of generating curve from coiling axis, T = translation rate, AS = aperture shape.

Locality	NW	SH	SW	W	D	T	AS
Stemmlers Cave, St. Clair Co., IL LH A4295 (paratypes)(n = 9)	4.03(0.08)	2.73(0.12)	1.71(0.07)	1.56(0.26)	0.64(0.05)	5.54(0.10)	1.18(0.04)
Schindler Cave, Perry Co., MO LH A6376 (n = 11)	4.16(0.13)	3.35(0.20)	2.06(0.09)	1.45(0.22)	0.53(0.05)	5.61(0.50)	1.36(0.06)
Tom Moore Cave, Perry Co., MO LH 38751 (n = 6)	4.29(0.10)	2.85(0.24)	1.73(0.14)	1.47(0.09)	0.55(0.06)	6.60(1.76)	1.28(0.07)
Mystery Cave, Perry Co., MO LH 44319 (n = 10)	4.28(0.08)	3.10(0.10)	1.91(0.14)	1.58(0.17)	0.50(0.07)	6.01(1.10)	1.31(0.05)

Bunker Hill Cave, 9.6 km NW of Birch Tree, LH 48894; Blue Spring, 17.6 km E of Emminence, LH 48297; Entrance, Hollow Cave, 3.2 km SE of Akers, LH 48896; Powder Mill Spring, near Owls Bend, LH 38761; Twilight zone, Round Spring Cavern Spring, 19.2 km N of Emminence, LH A4668, USNM 535861; Cave Hollow Cave, near Ebb and Flow Spring, 9.6 km N of Montier, LH A5571; Cave Hollow Spring, 9.6 km N of Montier, ANSP 170242, LH A702, UMMZ 162392. *Texas County:* Pool, Bear Cave, 6 km N of Mountain View, LH 48862. *Washington County:* Mossy Spring Cave, Pea Ridge State Forest, USNM 858029; Greens Cave, 7.2 km SE of Sullivan, UMMZ 162399; Hamilton Cave, 8.8 km SE of Sullivan, LH A5610, A6878, UMMZ 162400; Camp Branch Cave, 28.8 km E of Steelville, LH 48296; Crystal Spring, Old Mines, LH A5810, UMMZ 162393. *Wayne County:* Coldwater Spring, Coldwater, ANSP 170760, 175556 (holotype, *Amnicola a. insolita*), 175557, LH A4418, USNM 791472, 858030.

Fontigens antroecetes (Hubricht)

FIGURES 15–17; TABLE 3

Amnicola aldrichi antroecetes Hubricht, 1940:120, pl. 14; figs. i, j, k; 1950:17.
Fontigens antroecetes.—Peck and Lewis, 1978:44.

DIAGNOSIS.—A moderate-sized species with elongate-conic shell. Penis with three accessory lobes containing tubular (two distal lobes) or bulbous (proximal lobe) glands.

DESCRIPTION.—Shell (Figure 15, Table 3) 2.5–4.5 mm tall; height/width, 140%–180%. Whorls, 4.0–4.5, moderately rounded, usually with moderate adapical shoulders. Spire outline slightly concave to moderately convex. Aperture broadly ovate, pyriform above. Aperture plane slightly tilted (adapical end advanced). Outer lip expanded (particularly below); inner lip moderately thickened and reflected, slightly separated from or adnate to small portion of body whorl. Umbilicus slit-like to open. Apex blunt (Figure 16*e*); protoconch sculptured with numerous incised spiral lines. Periostracum usually covered with blackened deposits.

Body unpigmented except for small black granules scattered on digestive gland, stomach, and gonoducts. Penial pigmentation concentrated in filament.

Radular formula (Figure 16*a–d*): 5(6)-1-5(6)/1-1, 3-1-3, 21, 22. Central cusp of lateral tooth slightly enlarged, hoe-like.

Ctenidial filaments, 25–30. Testis, 0.5 whorl. Penis (Figure 16*f*) fairly large relative to head, projecting beyond edge of mantle collar. Penial filament short. Distal lobe elongate, with pronounced bulge on inner edge; tubular gland extending almost to base of penis. Proximal lobe short, tapering. Ovary <0.25 whorl. Capsule gland only slightly longer than albumen gland. Ventral channel narrow. Bursa copulatrix large, overlapping most of albumen gland; duct from bursa issuing from near anterior end. Oviduct coil enlarged, with diameter sub-equal to width of bursa.

TYPE LOCALITY.—Stemmlers Cave, St. Clair Co., Illinois. Holotype, ANSP 175554; paratypes, ANSP 17555, 328058, LH A4295, USNM 53582, 858031.

DISTRIBUTION AND HABITAT.—Species known only from caves in Mississippi River basin of eastern Missouri and western Illinois (Kaskaskia River drainage)(Figure 17).

REMARKS.—Recognition of *F. antroecetes* as a full species separate from *F. aldrichi* is justified by its more elongate shell and penis with three (as opposed to two) accessory lobes.

MATERIAL EXAMINED.—MISSOURI. *Perry County:* Clump Cave, 4 km NE of Perryville, LH 44318; Berome Moore Cave, Perryville, LH 35127; Running Bull Cave, 6.4 km E of Perryville, LH 44316; Schindler Cave, 4.8 km ENE of Perryville, LH A6376, UMMZ 162396; Tom Moore Cave, 4.8 km N of Perryville, LH 38751; Mertz Cave, 6.4 km NE of Perryville, LH 44317; Mystery Cave, 8 km SE of Perryville, LH 44319. *St. Louis County:* Cliff Cave, LH A4432.

Fontigens bottimeri (Walker), new combination

FIGURES 18–20; TABLE 4

Paludestrina bottimeri Walker, 1925:8, pl. 1: fig. 5.
"Paludestrina" bottimeri.—Burch and Tottenham, 1980:130, fig. 318 [as Incertae Sedis].

DIAGNOSIS.—A small-sized species with low conical shell. Penis with three accessory lobes containing tubular (distal lobes) and bulbous (proximal lobe) glands; presence of a third

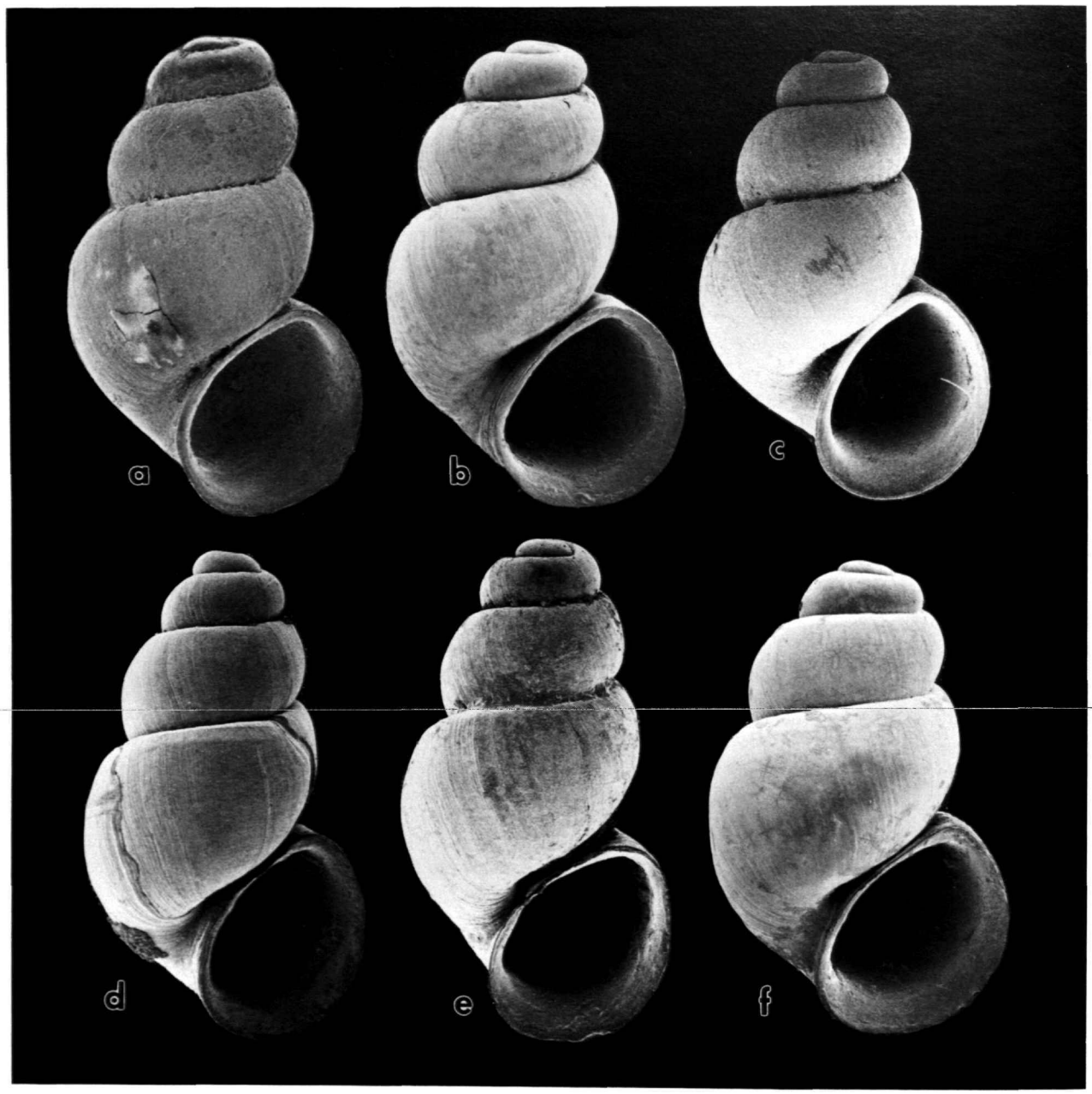

FIGURE 15.—*Fontigens antroecetes* (Hubricht): *a*, Stemmlers Cave, St. Clair Co., IL, ANSP 175554 (holotype; shell height, 2.9 mm); *b*, locality as above, LH A4295 (2.8 mm); *c*, Mystery Cave, Perry Co., MO, LH 44319 (2.7 mm); *d*, Tom Moore Cave, Perry Co., MO, LH 38751 (2.9 mm); *e*, Mertz Cave, Perry Co., MO, LH 44317 (3.0 mm); *f*, Schindler Cave, Perry Co., MO, LH A6376 (2.8 mm).

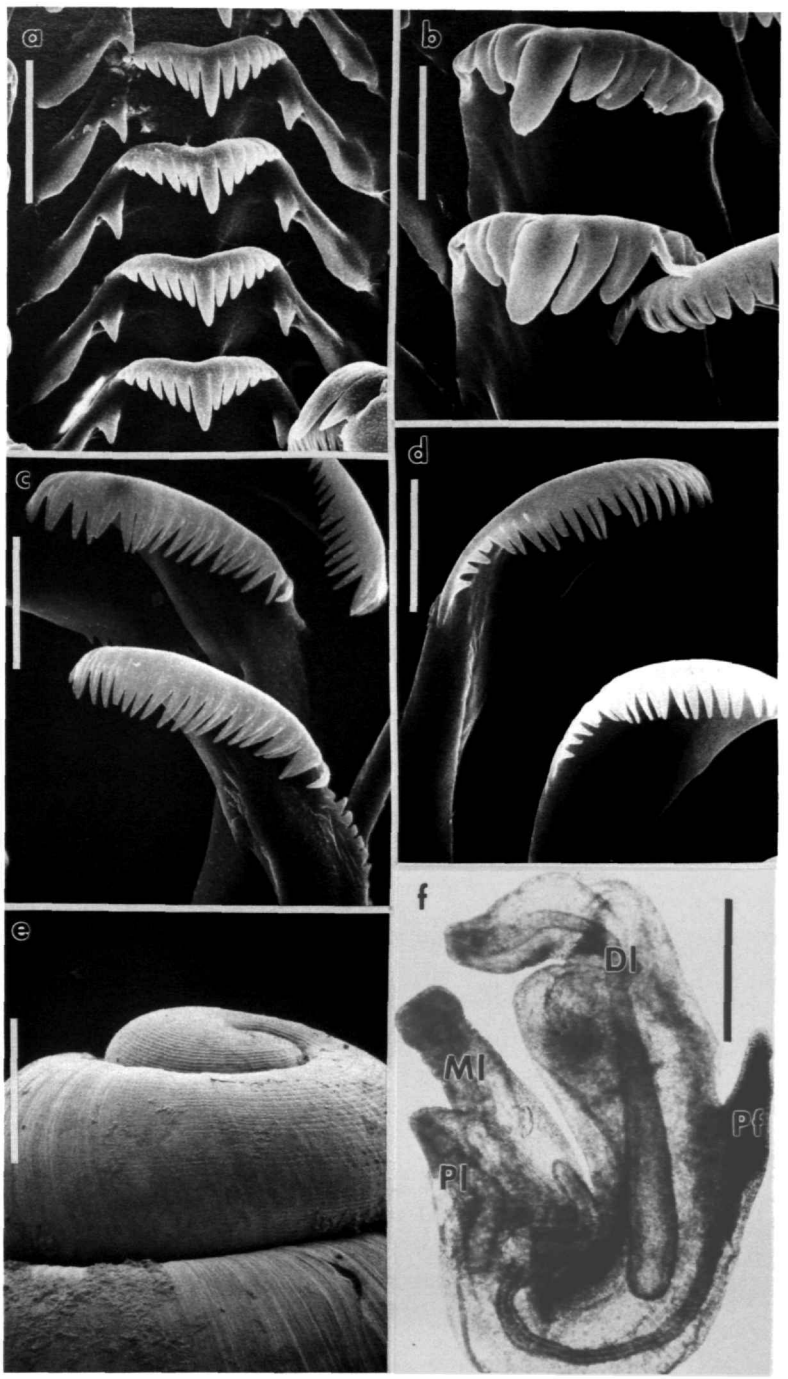

FIGURE 16.—Morphology of *F. antroecetes: a*, Central radular teeth, Stemmlers Cave, St. Clair Co., IL, LH A4295 (topotypes; bar = 12.0 μm); *b*, Lateral radular tooth, Tom Moore Cave, LH 38751 (bar = 6.0 μm); *c*, Inner marginal teeth, Stemmlers Cave (as above; bar = 8.6 μm); *d*, Outer marginal teeth, Tom Moore Cave (as above; bar = 5.0 μm); *e*, Protoconch, Stemmlers Cave (as above; bar = 200 μm); *f*, Whole mount of penis (dorsal aspect), Tom Moore Cave (as above; bar = 0.5 mm).

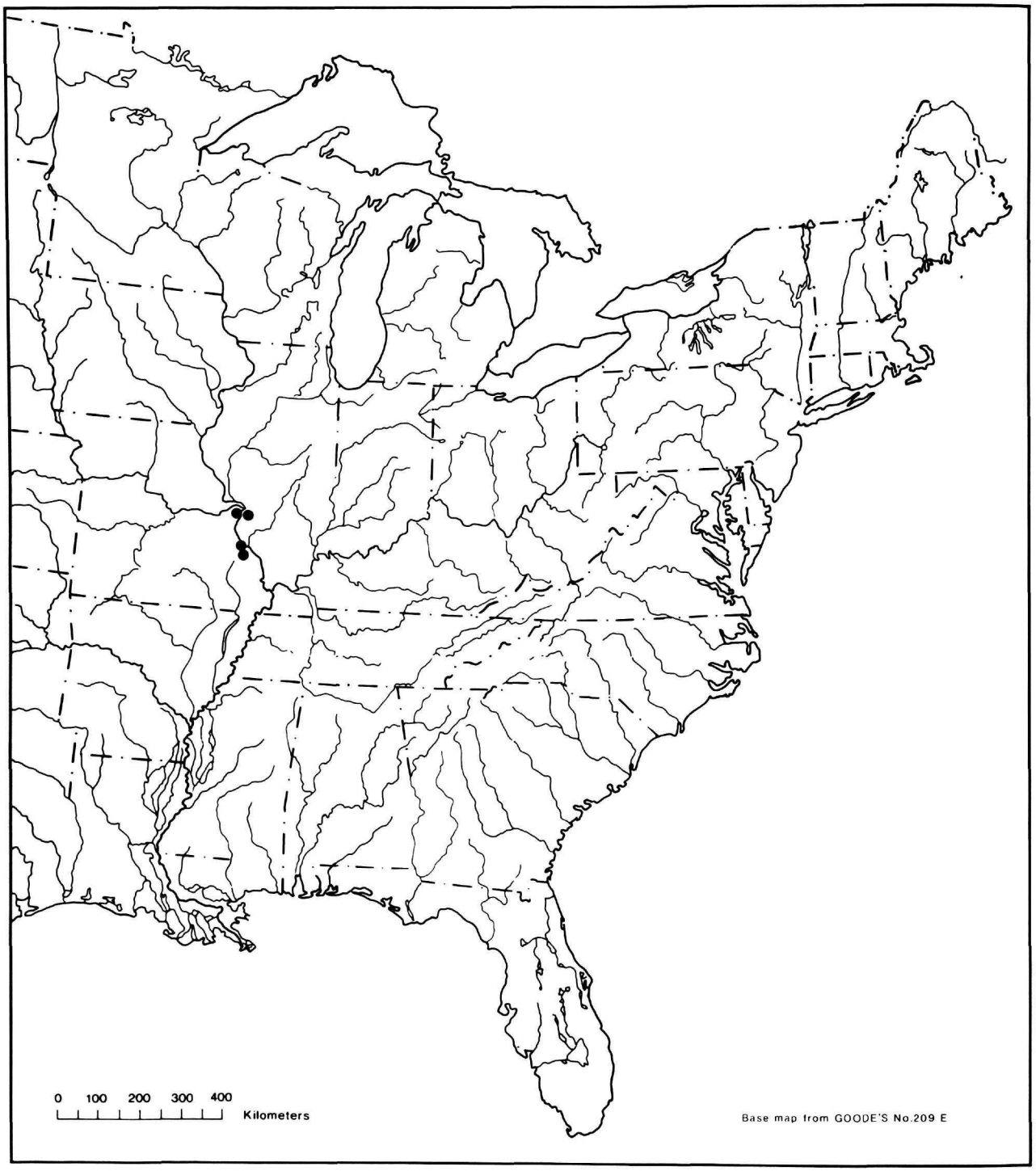

FIGURE 17.—Map showing distribution of *F. antroecetes*.

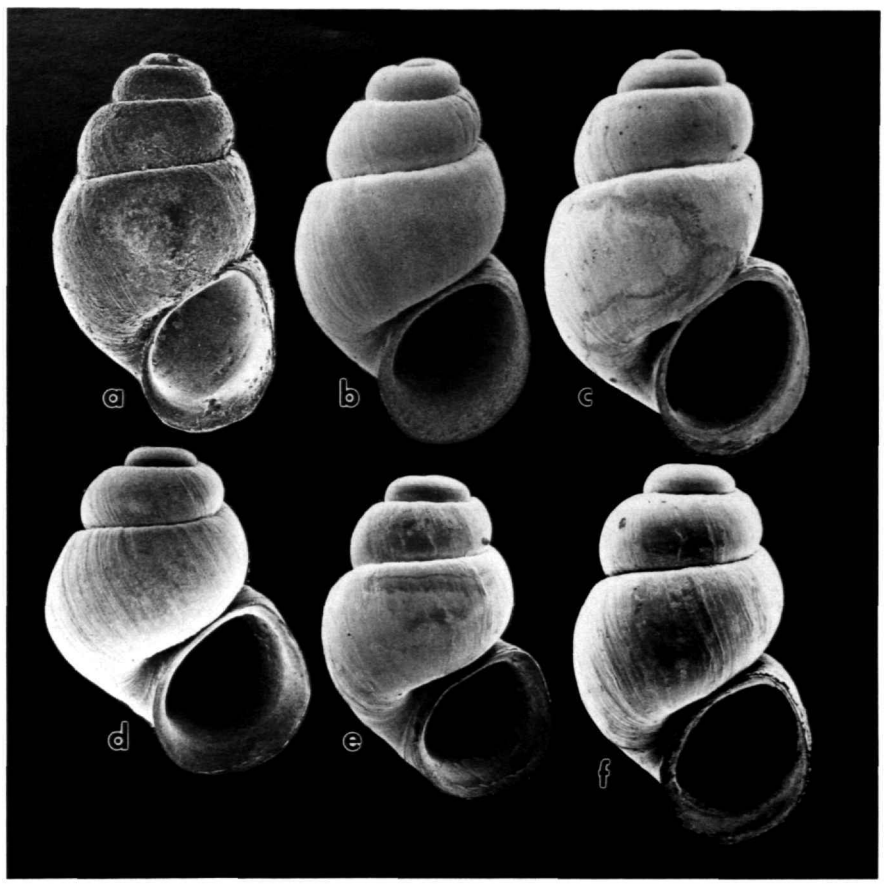

FIGURE 18.—*Fontigens bottimeri* (Walker): *a*, Glenn Echo, Montgomery Co., MD, UMMZ 118481 (holotype; shell height, 2.1 mm); *b*, Spring, Glenn Echo, USNM 858038 (topotype; 2.1 mm); *c*, Spring, Rock Creek Park, DC, USNM 858033 (2.0 mm); *d*, Ogdens Cave, Frederick Co., VA, USNM 431626 (1.4 mm); *e*, Spring 0.6 km S of Little Heiskell Quarry, Washington Co., MD, LH 32972 (1.6 mm); *f*, Springs, A.M. Powell Fish Hatchery, Washington Co., MD, USNM 858040 (1.9 mm).

lobe distinguishes snail from similar-shelled *F. orolibas*.

DESCRIPTION.—Shell (Figure 18, Table 4) of "stubby" appearance, 1.0-3.0 mm tall; height/width, 130%-180%. Whorls, 3.5-4.5, near flat to well rounded, with slightly to highly pronounced adapical shoulders. Spire slightly to highly convex. Aperture ovate, sometimes enlarged (Figure 18*c*), sometimes expanded below. Inner lip slightly thickened and reflected, adnate to or slightly separated from body whorl. Umbilicus slit-like to narrowly open. Apex (Figure 19*g*) slightly protruding; protoconch with well-spaced, shallowly incised lines.

Eyespots pigmented. Epigean representatives pale, with melanic pigment (light grey) found only on snout. Cavesnails unpigmented on body.

Radular formula (Figure 19*a-e*): 5(6)-1-5(6)/1-1, 3(4)-1-4(5), 27, 27. Central cusp of lateral tooth slightly enlarged, dagger like.

Ctenidial filaments, 15-20. Testis, 0.5 whorl. Penis (Figure 19*f,h*) small. Penial filament reduced, much shorter than distal lobe. Tubular gland in distal lobe extending to base of penis; small glandular patch (Gp) often present on outer edge of lobe near base. Median lobe about equal in length to distal lobe. Ovary, <0.25 whorl. Capsule gland considerably longer than albumen gland. Ventral channel narrow. Bursa copulatrix large (overlapping much of albumen gland), ovate, with duct exiting from anterior portion. Oviduct coil small.

TYPE LOCALITY.—Glenn Echo, Montgomery Co., Maryland (precise location unknown). The small spring on the Dawsons property in Glenn Echo may be the type locality as it closely conforms to the description provided by the collector Bottimer

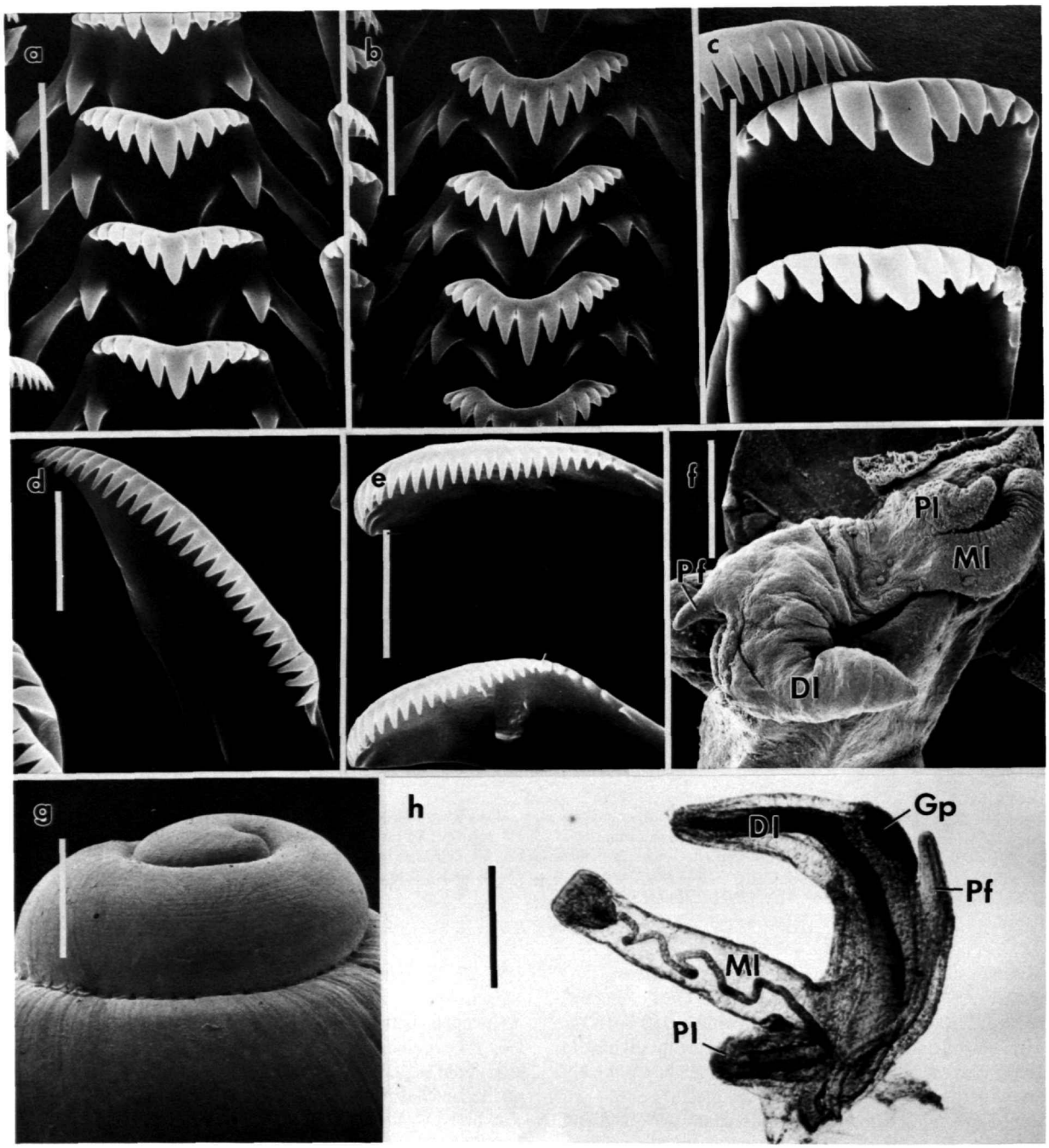

FIGURE 19.—Morphology of *F. bottimeri*: *a*, Central radular teeth, Spring, Glenn Echo, Montgomery Co., MD, USNM 858038 (topotype; bar = 6.0 μm); *b*, Central radular teeth, Ogdens Cave, Frederick Co., VA, USNM 858041 (bar = 6.0 μm); *c*, Lateral teeth, Spring, Glenn Echo (as above; bar = 3.8 μm); *d*, Inner marginal tooth, Spring, Glenn Echo (as above; bar = 4.3 μm); *e*, Outer marginal teeth, Spring, Glenn Echo (as above; bar = 3.8 μm); *f*, Dorsal aspect of critical point dried penis, Spring, Glenn Echo (as above; bar = 0.3 mm); *g*, Protoconch, Spring, Glenn Echo (as above; bar = 176 μm); *h*, Dorsal aspect of whole-mounted penis, Ogdens Cave (as above; bar = 0.25 mm).

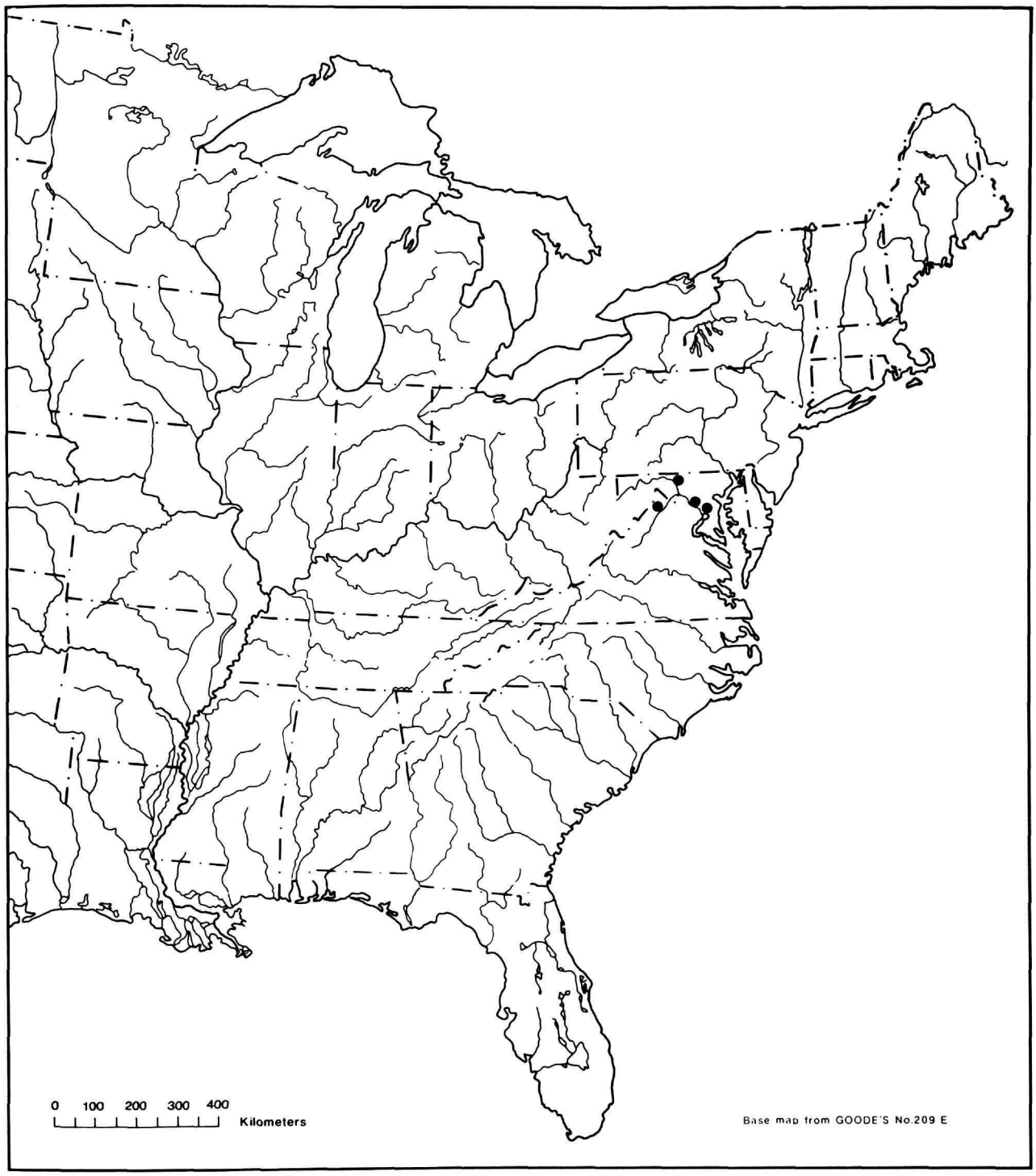

FIGURE 20.—Map showing distribution of *F. bottimeri*.

TABLE 4.—Selected shell parameters for *Fontigens bottimeri* (Walker), expressed as $\bar{x}$ with SD in parentheses. Shell height (SH) and width (SW) are given in mm. NW = number of whorls, W = whorl expansion rate, D = distance of generating curve from coiling axis, T = translation rate, AS = aperture shape.

Locality	NW	SH	SW	W	D	T	AS
Spring, Glenn Echo, Montgomery Co., MD USNM 858039 (n = 15)	4.23(0.15)	2.28(0.08)	1.42(0.08)	1.56(0.07)	0.65(0.05)	4.84(0.56)	1.25(0.06)
Ogden's Cave, Frederick Co., VA USNM 431626 (n = 10)	3.68(0.17)	1.56(0.06)	1.11(0.07)	1.81(0.13)	0.59(0.06)	5.52(1.26)	1.22(0.06)

(in letter to J.P.E. Morrison, dated 5/16/1966). Holotype, UMMZ 118481; paratypes, MCZ 82099.

DISTRIBUTION AND HABITAT.—Known from a few localities in Potomac River basin of District of Columbia and Maryland, and Shenandoah River basin of northwestern Virginia (Figure 20). Found in both caves and small springs; in latter, snails were common among leaf litter and other plant debris near spring sources.

MATERIAL EXAMINED.—DISTRICT OF COLUMBIA. Spring, Rock Creek Park, S of Military Road (near Nature Center), USNM 858032, 858033; Wetzels Spring, Glover Archbold Park, just N of Reservoir Road, Georgetown, USNM 858034–858036; Spring, Glover Archbold Park, 0.4 km S of Reservoir Road, Georgetown, USNM 858037.

MARYLAND. *Montgomery County:* Spring, Dawson residence, Goldsboro Road, Glenn Echo, USNM 858038, 858039. *Washington County:* Springs, A.M. Powell Fish Hatchery, 9.3 km SE of Hagerstown, USNM 858040; Under stone, large spring, 0.6 km S of Little Heiskell Quarry, LH 32972.

VIRGINIA. *Frederick County:* Ogdens Cave, 5.6 km WNW of Middletown, LH 43682, USNM 431625–431628, 853163–853165, 858041.

Fontigens morrisoni, new species

FIGURES 21–23; TABLE 5

Fontigens aldrichi.—Hubricht, 1976:87.—Holsinger and Culver, 1988:22. [In part.]

Fontigens orolibas(?).—Holsinger, 1982:98.

DIAGNOSIS.—A small-sized species with stout, ovate-conic shell. Penis with two accessory lobes containing tubular and bulbous glands.

DESCRIPTION.—Shell (Figure 21, Table 5) 1.5–2.5 mm tall; height/width, 125%–160%. Whorls, 3.25–4.0, well rounded, often with narrow adapical shoulders. Spire convex. Aperture broadly ovate, only moderately angled above. Inner lip slightly thickened and reflected, usually adnate to small portion of body whorl. Umbilicus usually open. Apex (Figure 22*c*) slightly depressed to slightly protruding; protoconch with numerous well incised striae.

Eyespots pigmented. Head/foot pale or covered with light, brown pigment. Dorsal surface of visceral coil brown-black, digestive gland especially darkened.

Radular formula (Figure 22*a,b,d-f*): 7-1-7/1-1, 2(3)-1-3(4), 20-22, 17-24. Central cusp of lateral tooth enlarged, hoe-like.

Ctenidial filaments, ~17; osphradium slightly elongate compared to that of other congeners. Testis, 1.0 whorl. Penis (Figure 22*g*) moderate-sized. Penial filament broad, distal portion with pronounced sub-terminal bulge. Proximal lobe short, stout. Ovary, 0.25 whorl. Capsule gland slightly longer than albumen gland. Ventral channel very broad (width almost that of capsule gland) along entire length. Bursa copulatrix gourd-shaped; narrow anterior portion overlapping half of albumen gland length. Duct of bursa originates from near mid-point of structure and extends over much of albumen gland. Oviduct coil enlarged.

ETYMOLOGY.—Named after the late Dr. J.P.E. Morrison of the National Museum of Natural History, who had a deep interest in *Fontigens* and whose extensive collection of these snails was invaluable to the present study.

TABLE 5.—Selected shell parameters for *Fontigens morrisoni* new species, expressed as $\bar{x}$ with SD in parentheses. Shell height (SH) and width (SW) are given in mm. NW = number of whorls, W = whorl expansion rate, D = distance of generating curve from coiling axis, T = translation rate, AS = aperture shape.

Locality	NW	SH	SW	W	D	T	AS
Spring-fed brook, SW of Mustoe, Highland Co., VA USNM 860467 (paratypes)(n = 8)	3.94(0.12)	2.20(0.13)	1.63(0.12)	1.78(0.14)	0.59(0.07)	5.04(1.42)	1.11(0.04))
Butler Cave, Bath Co., VA LH 38731 (n = 8)	3.84(0.13)	1.76(0.08)	1.24(0.05)	1.58(0.10)	0.59(0.05)	5.37(0.71)	1.22(0.07)
Spring, 2.1 km N of Mustoe, Highland Co., VA LH 40581 (n = 8)	3.84(0.13)	1.94(0.07)	1.46(0.05)	1.74(0.17)	0.58(0.05)	4.77(0.46)	1.15(0.05)

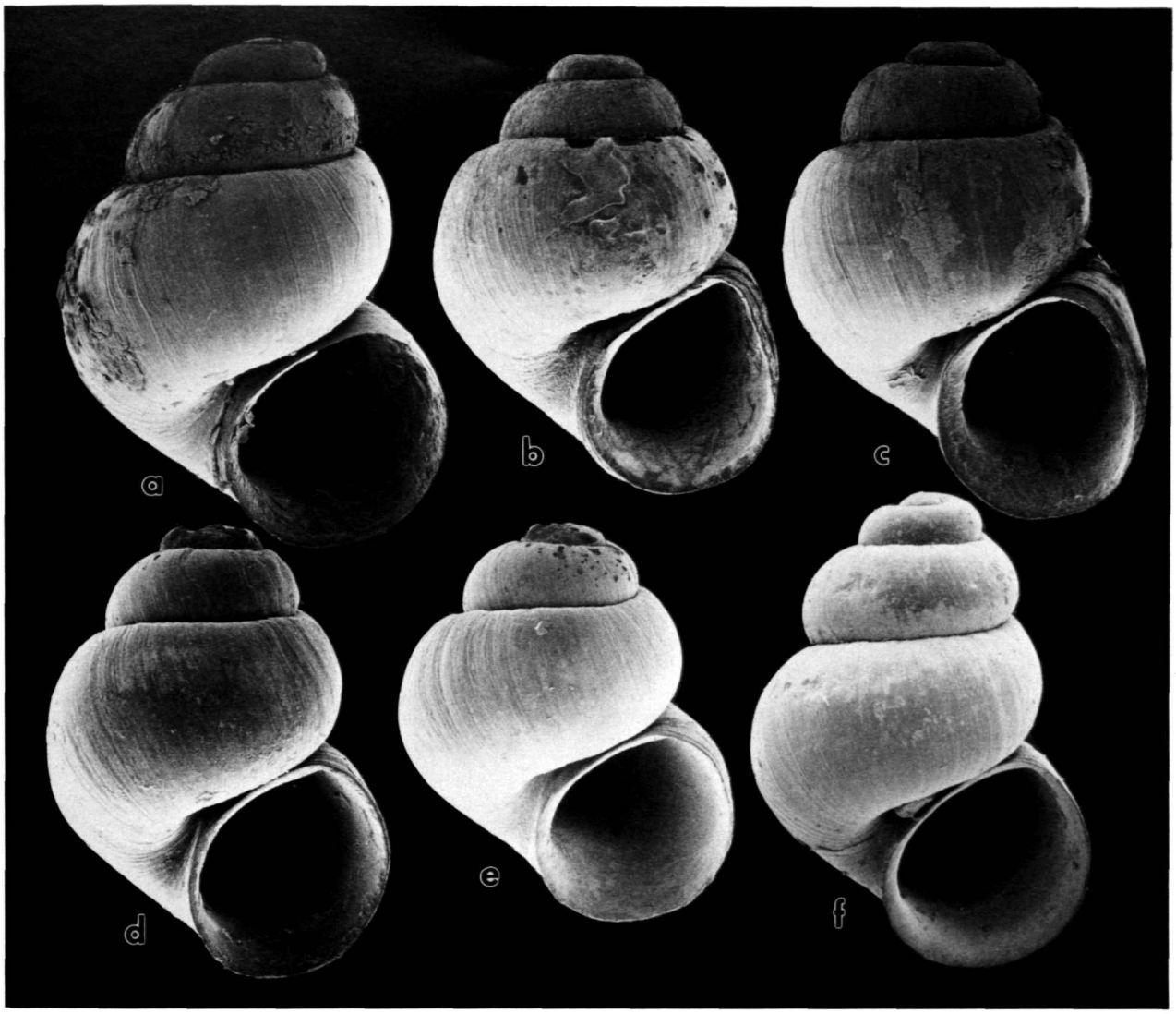

FIGURE 21.—*Fontigens morrisoni* Hershler et al., new species: *a*, Spring-fed brook SW of Mustoe, Highland Co., VA, USNM 860466 (holotype; shell height, 2.1 mm); *b,c*, locality as above, USNM 860467 (paratypes; 1.8, 2.0 mm, respectively); *d,e*, Spring 2.1 km N of Mustoe, Highland Co., VA, LH 40581 (1.9, 1.6 mm, respectively); *f*, Butler Cave, Bath Co., VA, LH 38731 (1.7 mm).

TYPE LOCALITY.—A small spring-fed brook SW of Mustoe (along HW 220), Highland Co., Virginia. Holotype, USNM 860466; paratypes, USNM 860467.

DISTRIBUTION AND HABITAT.—Known from two springs and two caves in Upper James River basin, Bath and Highland counties, Virginia (Figure 23).

MATERIAL EXAMINED.—VIRGINIA. *Bath County:* Blowing Cave, 1.7 km NW of Millboro Springs (LH coll.); Butler Cave, 1.6 km N of Burnsville, LH 38731. *Highland County:* Spring, 1.1 km SW of Mustoe, LH 40580; Spring, 2.1 km N of Mustoe, LH 40581.

Fontigens orolibas Hubricht

FIGURES 24-27; TABLE 6

Fontigens orolibas Hubricht, 1957:9 [fig. on p. 10]; 1976:87.—Burch and Tottenham, 1980:126, figs. 312, 313.—Holsinger and Culver, 1988:22.
Fontigens spp.—Holsinger and Culver, 1988:22, [in part].

DIAGNOSIS.—A moderate-sized species with ovate- to elongate conic shell. Penis with two accessory lobes containing tubular and bulbous glands.

DESCRIPTION.—Shell (Figure 24, Table 6) 1.5-4.0 mm tall; height/width, 150%-220%. Whorls, 3.5-5.5, slightly to well

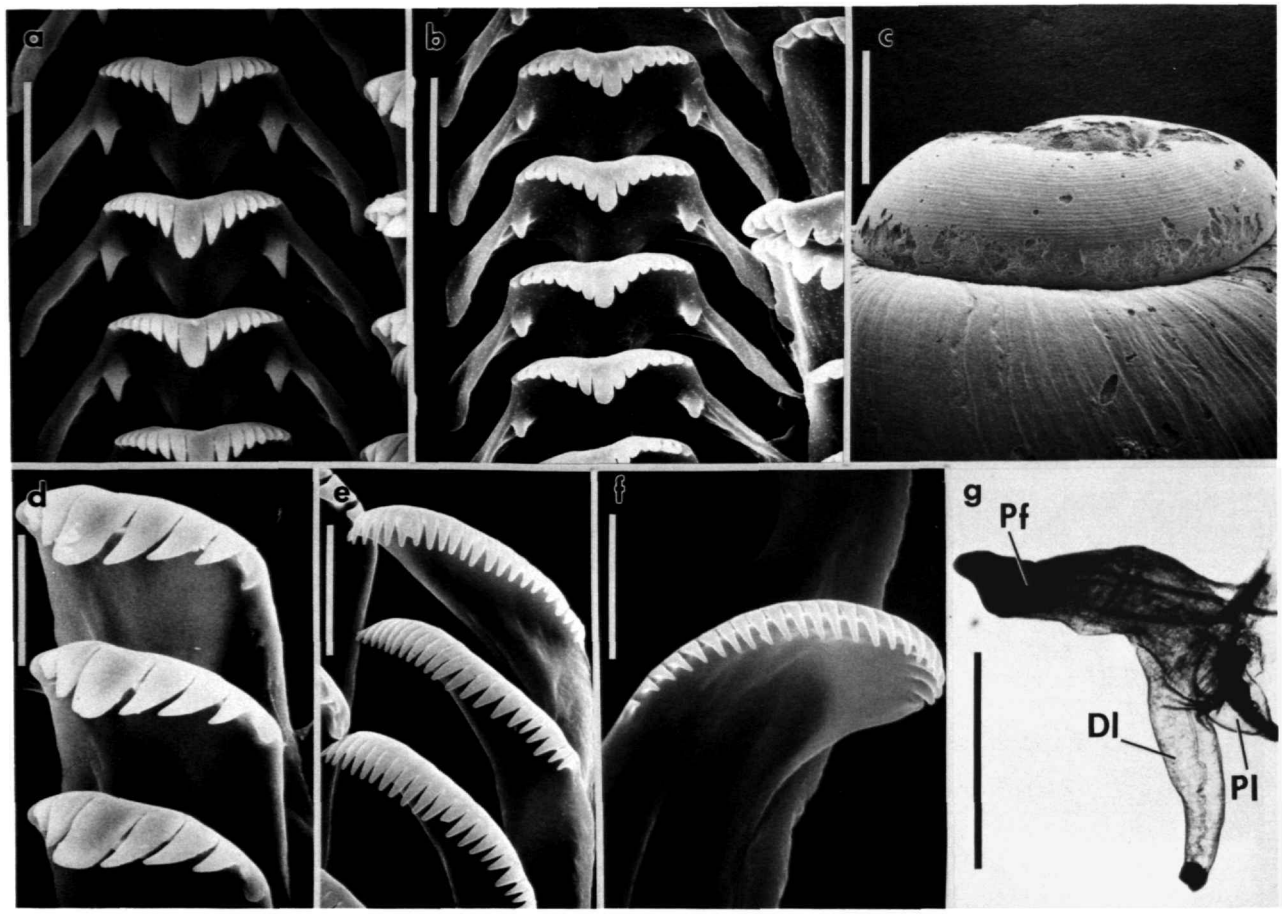

FIGURE 22.—Morphology of *F. morrisoni*: *a*, Central radular teeth, Spring-fed brook SW of Mustoe, Highland Co., VA, USNM 860467 (paratypes; bar = 10.0 μm); *b*, Central radular teeth, Butler Cave, LH 38731 (bar = 8.0 μm); *c*, Protoconch, Spring 2.1 km N of Mustoe, Highland Co., VA, LH 38731 (bar = 136 μm); *d*, Lateral teeth, Spring-fed brook SW of Mustoe (as above; bar = 7.5 μm); *e*, Inner marginal teeth, Spring-fed brook SW of Mustoe (as above; bar = 8.6 μm); *f*, Outer marginal tooth, Spring-fed brook SW of Mustoe (as above; bar = 4.3 μm); *g*, Dorsal aspect of wet mount of penis, Spring-fed brook SW of Mustoe (as above; bar = 1.0 mm).

rounded, adapical portions with narrow shoulders and occasional pronounced angulations. Spire slightly convex to slightly concave. Aperture broadly ovate, slightly angled above. Inner lip slightly to highly thickened, slightly reflected, adnate to or slightly separated from body whorl. Umbilicus slit-like to open. Apex (Figure 26*e*) depressed to slightly protruding; protoconch with numerous striae.

Eyespots either with or without dark pigment. Epigean individuals with grey-black pigment on tentacle bases, proximal snout, "neck," operculigerous lobe, edge of mantle collar, dorsal stomach, pericardium region, and digestive gland (lighter). Dark subepithelial pigment also in snout and penial filament. Cavesnails sometimes entirely without body pigment.

Radular formula (Figures 25, 26*a–d*): (5-7)-1-(5-7)/1(2)-1(2), 3-1-4, 21-25, 19-25. Central cusp of lateral tooth slightly enlarged, dagger-like.

Ctenidial filaments, ~17. Testis, 1.0 whorl. Penis (Figure 26*f*) moderate-sized. Penial filament broad and long; outer edge with sub-terminal constriction. Distal lobe elongate. Ovary, <0.25 whorl. Capsule gland slightly longer than albumen gland. Ventral channel narrow. Bursa copulatrix broad, moderate-sized, overlapping small portion of albumen gland; duct from bursa issuing from near anterior end. Oviduct coil small.

TYPE LOCALITY.—Spring, Hawksbill Shelter, Madison Co., Virginia. Holotype, USNM 618868; paratypes, USNM 618869, LH 12059.

DISTRIBUTION AND HABITAT.—*Fontigens orolibas* origi-

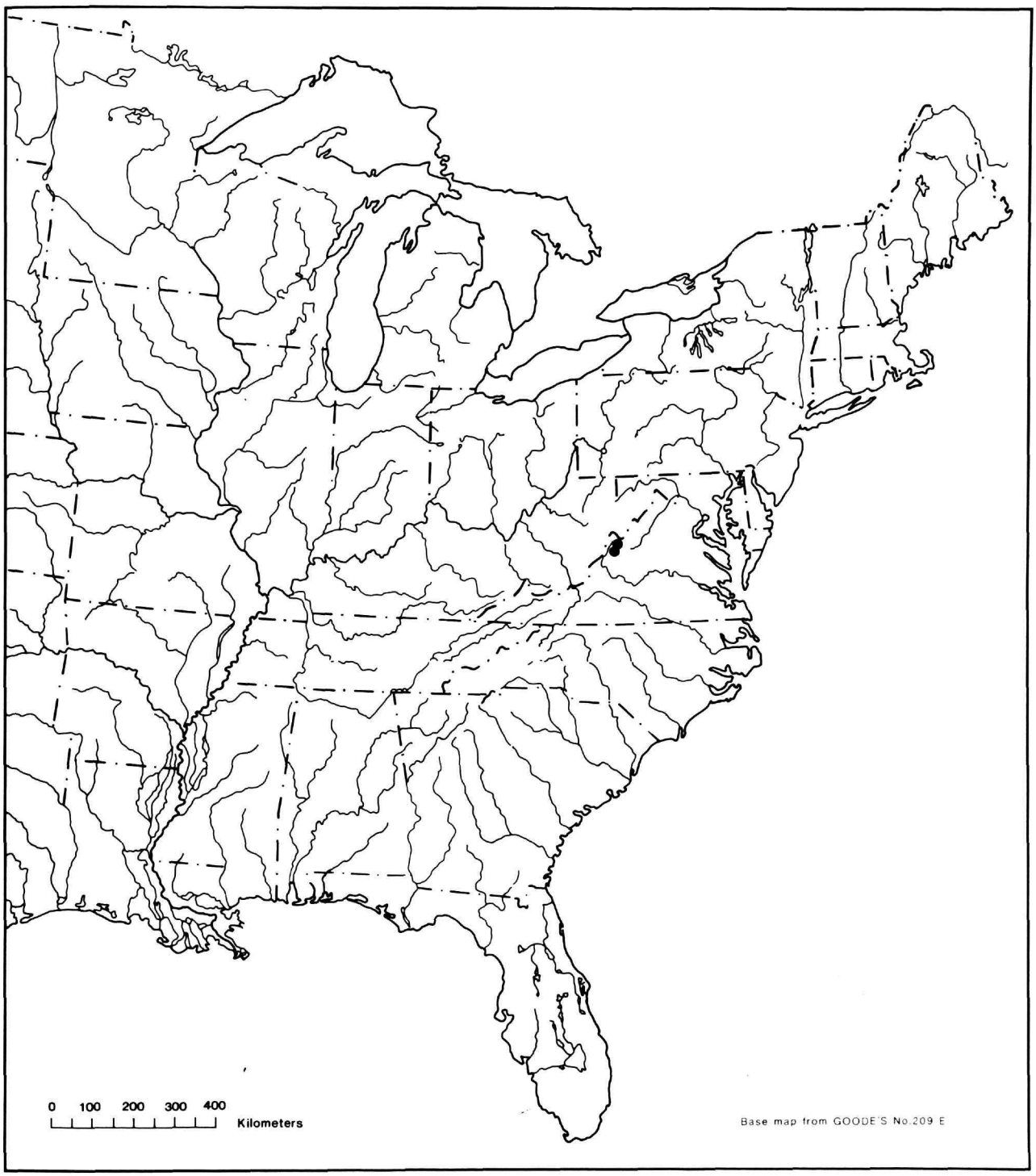

FIGURE 23.—Map showing distribution of *F. morrisoni*.

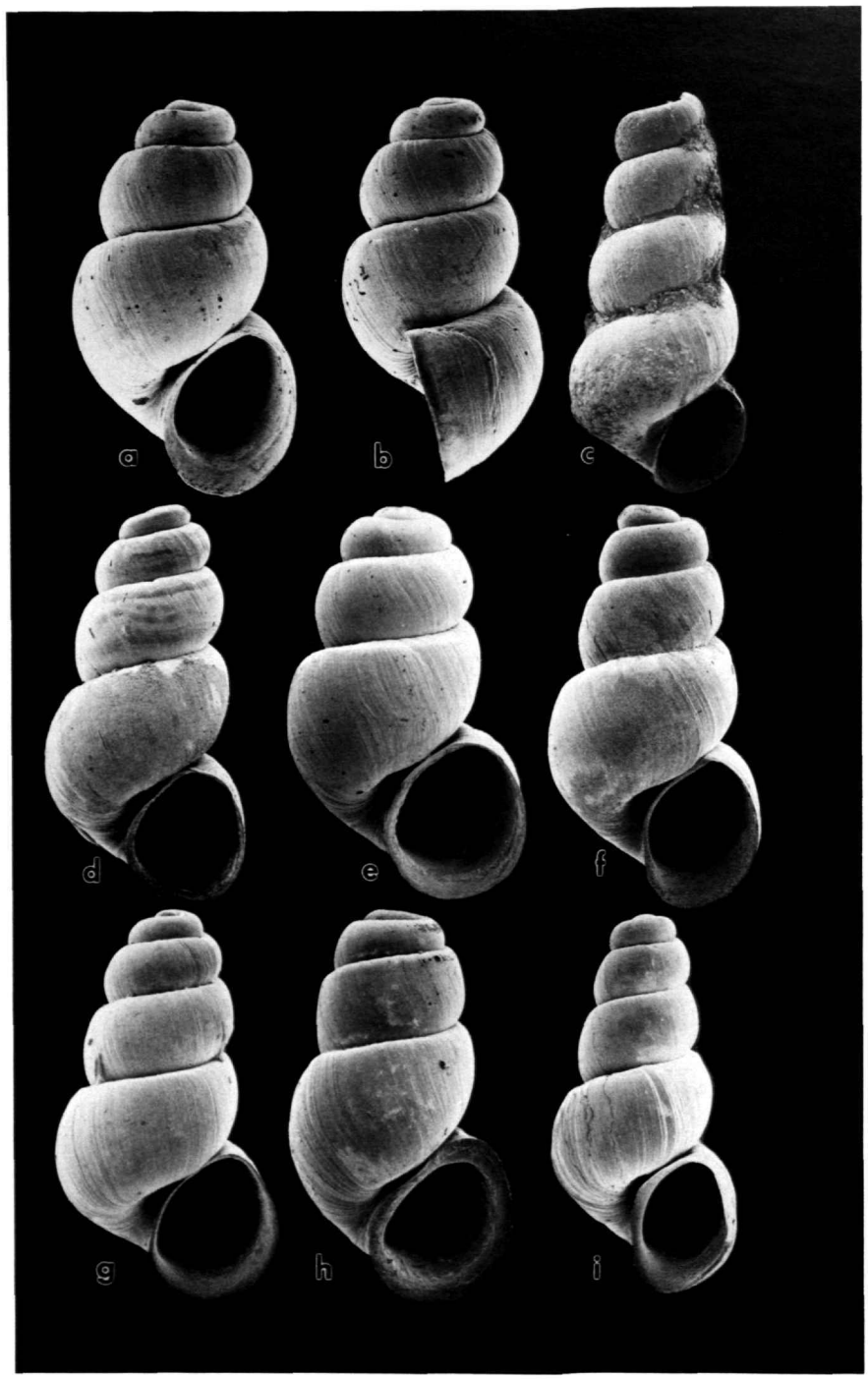

FIGURE 24.—*Fontigens orolibas* Hubricht: *a,b*, Spring, Hawksbill Shelter, Madison Co., VA, USNM 618869 (paratypes; both shells are 2.1 mm high); *c*, Needys Cave, Franklin Co., PA, USNM 522087 (2.8 mm); *d*, Spring, Blue Ridge Parkway, Augusta Co., VA, LH 12006 (2.4 mm); *e*, Spring, Buffalo Marsh Run, Frederick Co., VA, USNM 858052 (2.1 mm); *f*, Skyline Caverns, Warren Co., VA, USNM 858057 (1.9 mm); *g*, Witheros Cave, Bath Co., VA, USNM 853170 (1.9 mm); *h*, Tawneys Cave, Giles Co., VA, USNM 853175 (1.9 mm); *i*, Hugh Young Cave, Tazewell Co., VA, LH 40519 (2.6 mm).

TABLE 6.—Selected shell parameters for *Fontigens orolibas* Hubricht, expressed as $\bar{x}$ with SD in parentheses. Shell height (SH) and width (SW) are given in mm. NW = number of whorls, W = whorl expansion rate, D = distance of generating curve from coiling axis, T = translation rate, AS = aperture shape.

Locality	NW	SH	SW	W	D	T	AS
Spring, Hawksbill Shelter, Madison Co., VA LH 12059 (paratypes)(n = 10)	4.58(0.36)	2.53(0.15)	1.46(0.10)	1.27(0.08)	0.56(0.04)	5.57(0.85)	1.24(0.05)
Spring, Blue Ridge Parkway, Augusta Co., VA LH 12063 (n = 9)	5.03(0.08)	3.27(0.17)	1.69(0.08)	1.23(0.07)	0.50(0.08)	7.61(1.10)	1.39(0.13)
Witheros Cave, Bath Co., VA USNM 853171 (n = 13)	4.23(0.07)	1.63(0.10)	0.99(0.05)	1.39(0.08)	0.55(0.03)	5.41(0.78)	1.22(0.08)
Tawneys Cave, Giles Co., VA USNM 853175 (n = 10)	4.40(0.18)	2.07(0.12)	1.20(0.06)	1.44(0.35)	0.57(0.03)	6.04(0.80)	1.21(0.04)
Harveys Cave, Giles Co., VA USNM 522847 (n = 9)	4.22(0.23)	1.98(0.14)	1.14(0.10)	1.40(0.12)	0.65(0.08)	7.44(1.20)	1.23(0.08)
Spring, Indian Run Shelter, Rappahannock Co., VA LH 12012 (n = 12)	4.25(0.00)	2.45(0.10)	1.38(0.06)	1.35(0.09)	0.62(0.05)	6.22(0.74)	1.18(0.05)
Spring, Browntown Valley Overlook, Warren Co., VA USNM 858056 (n = 10)	5.03(0.08)	2.76(0.22)	1.42(0.09)	1.23(0.06)	0.62(0.08)	6.40(0.77)	1.26(0.10)

nally was described from springs above 610 m in Blue Ridge Mountains (Shenandoah, Rappahanock, and James River basins). Inclusion of cave populations assigned to the species by Hubricht (1976) and herein broadens range from the Potomac River basin in southern Pennsylvania southwest to the Clinch and Holston River basins in southwestern Virginia, including parts of both the New and Roanoke River basins (Figure 27).

REMARKS.—Some of the populations known only from dry shell are assigned to this species tentatively. Of particular concern are some of the northern populations, such as that in Needys Cave, which are difficult to distinguish from *F. bottimeri*, whose range abuts against that of *F. orolibas*. Additionally, two populations (Hugh Young, Perkins Caves) from the southern end of the range, which occur in the upper Tennessee River drainage, are distinctive in shell and could represent differentiated forms meriting formal taxonomic recognition.

MATERIAL EXAMINED.—PENNSYLVANIA. *Franklin County:* Needys Cave, Waynesboro, USNM 522087, 522846, 853173.

VIRGINIA. *Albermarle County:* Spring, Doyle River Cabin, Shenandoah National Park, LH 12062. *Augusta County:* Roadside spring, 0.5 km N of Milepost 8, Blue Ridge Parkway, LH 12064; Spring, 1.0 km N of Calf Mountain Overlook, Shenandoah National Park, LH 12008; Roadside spring, 0.5 km S of Milepost 6, Blue Ridge Parkway, LH 12063, USNM 618872; Spring in pasture at Milepost 6, Blue Ridge Parkway, LH 12006. *Bath County:* Witheros Cave, 4.0 km ENE of Millboro Springs, USNM 853169-853171. *Botetourt County:* Karls Pit (cave), ~8.8 km NW of Buchanan, USNM 858063. *Frederick County:* Spring in Buffalo Marsh Run, 4 km NW of Middletown, USNM 858052; Blue Spring, near Marlboro, USNM 791447. *Giles County:* Tawneys Cave, 3.2 km N of Newport, LH A8724, USNM 853154, 853155, 853174, 853175, 858059; Harveys Cave[2], on Sinking Creek upstream from junction of Rt. 112 and 42, USNM 522847; Smoke Hole Cave, Newport (Hubricht 1976:88); Starnes Cave, 5.6 km SSE of Narrows (Hubricht 1976:88). *Greene County:* Spring, Pinefield Shelter, Shenandoah National Park, LH 12010, USNM 858053; Spring, 0.5 km S of Milepost 62, Shenandoah National Park, LH 12817; Spring, Pocosin Cabin, Shenandoah National Park, ~14.4 km S of Big Meadows, LH 12165, USNM 858054. *Madison County:* Little Stony Man Spring, Shenandoah National Park, LH 12159; Spring, Bear Fence Mountain Shelter, Shenandoah National Park, LH 12148. *Page County:* Overflow from spring near summit of Stony Man Mountain, USNM 180855; Spring, Hawksbill Gap, Shenandoah National Park, LH 12056; Lewis Spring, Shenandoah National Park, LH 12149; Furnace Spring, Shenandoah National Park, LH 12747; David Spring, Big Meadow Camp Grounds, Shenandoah National Park, LH 12060; Spring, Skyland, Shenandoah National Park, LH 12058, 628870, USNM 522316; Spring, Elkwallow Gap Shelter, Shenandoah National Park, LH 12057, USNM 858060. *Rappahannock County:* Spring, Indian Run Shelter, Shenandoah National Park, LH 12012; Spring, below Little Hogback Overlook, Shenandoah National Park, LH 12160; Gravel Spring, Shenandoah National Park, LH 12014. *Rockingham County:* Roadside spring, 0.32 km N of Milepost 80, Shenandoah National Park, LH 12061, USNM 618868, 618871. *Shenandoah County:* George Hinkins Spring, Strasburg, USNM 433509, 853166; Cedar Creek, N of Strasburg, USNM 853176. *Tazewell County:* Hugh Young Cave, 5.6 km SW of Liberty Hill, LH 40519, USNM 858055. *Warren County:* Spring, near Browntown Valley Overlook, Shenan-

[2]Virginia Speleological Survey has no cave recorded by this name; it is probably Canoe Cave or a cave unknown to the Survey.

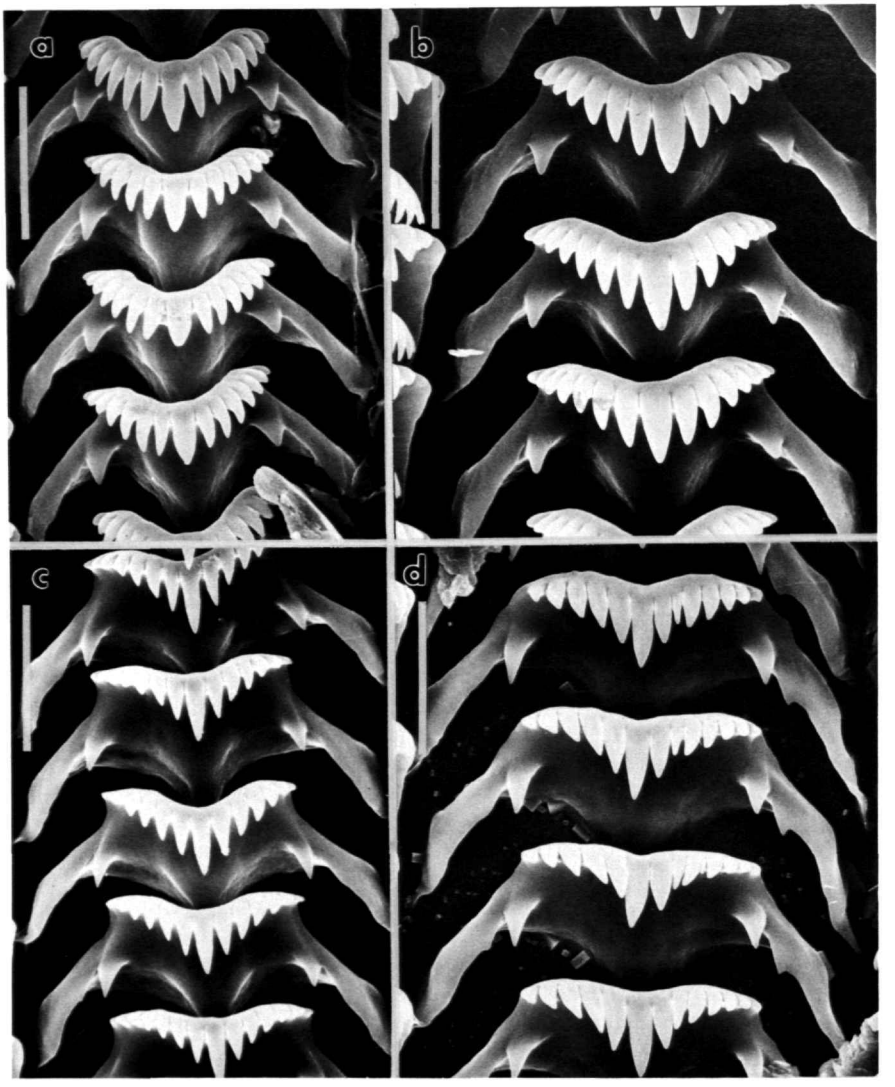

FIGURE 25.—Central radular teeth of *F. orolibas: a*, Spring near Browntown Valley Overlook, Warren Co., VA, USNM 858056 (bar = 7.5 μm); *b*, Skyline Caverns, Warren Co., VA, USNM 858057 (bar = 6.0 μm); *c*, Tawneys Cave, Giles Co., VA, USNM 853175 (bar = 7.5 μm); *d*, Hugh Young Cave, Tazewell Co., VA, LH 40519 (bar = 7.5 μm).

doah National Park, LH 12004, USNM 858056; Skyline Caverns, 3.2 km S of Front Royal, LH A4840, USNM 522318, 522848-522850, 522856, 852142, 858057. *Washington County:* Perkins Cave, 16 km NNE of Abingdon, UF 113411.

Fontigens proserpina (Hubricht)

FIGURES 28-30; TABLE 7

Amnicola proserpina Hubricht, 1940:121; 1942:105.—Burch and Tottenham, 1980:124.

Amnicola procerpina [sic].—Hubricht, 1941:112; 1950:17.

Fontigens proserpina.—Peck and Lewis, 1978:44.

DIAGNOSIS.—A moderate-sized species with elongate-conic shell; teleoconch with spiral striae. Penis with three accessory lobes containing tubular (distal lobes) and bulbous (proximal lobe) glands.

DESCRIPTION.—Shell (Figure 28, Table 7) 1.9-3.9 mm tall; height/width, 173%-224%. Whorls, 4.75-6.75, well rounded, with adapical shoulders. Spire slightly convex. Aperture broadly ovate to near-circular, slightly angled above. Inner lip slightly reflected and thickened, adnate to or slightly separated from body whorl. Outer lip sometimes expanded. Umbilicus

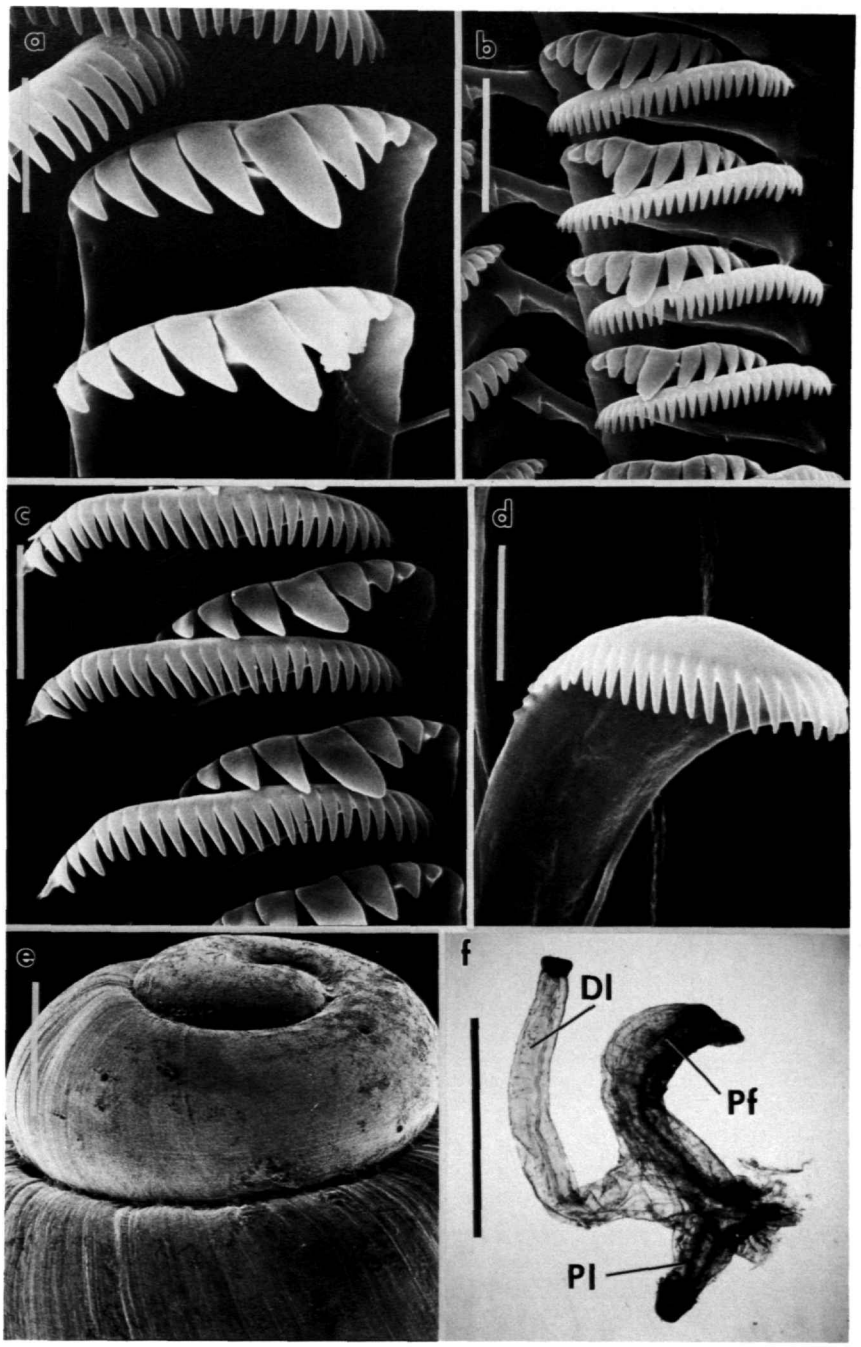

FIGURE 26.—Morphology of *F. orolibas: a,* Lateral radular teeth, Skyline Caverns, Warren Co., VA, USNM 858057 (bar = 3.0 μm); *b,* Lateral and inner marginal teeth, Spring near Browntown Valley Overlook, Warren Co., VA, USNM 858056 (bar = 7.5 μm); *c,* Lateral and inner marginal teeth, Skyline Caverns (as above; bar = 5.0 μm); *d,* Outer marginal tooth, Skyline Caverns (as above; bar = 2.7 μm); *e,* Protoconch, Spring, Hawksbill Shelter, Madison Co., VA, USNM 618869 (paratype; bar = 176 μm); *f,* Dorsal aspect of whole mount of penis, Hugh Young Cave, Tazewell Co., VA, LH 40519 (bar = 1.0 mm).

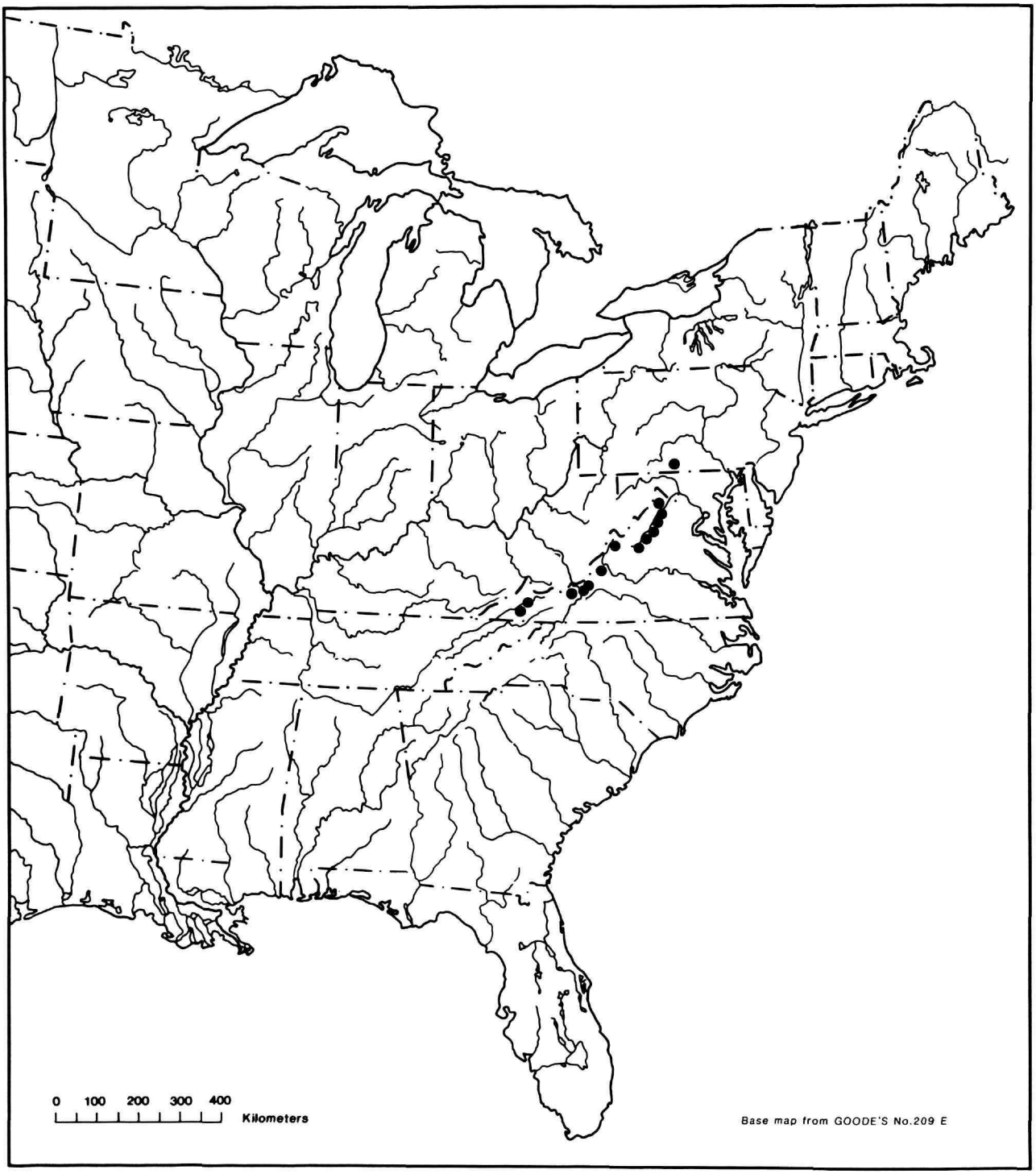

FIGURE 27.—Map showing distribution of *F. orolibas*.

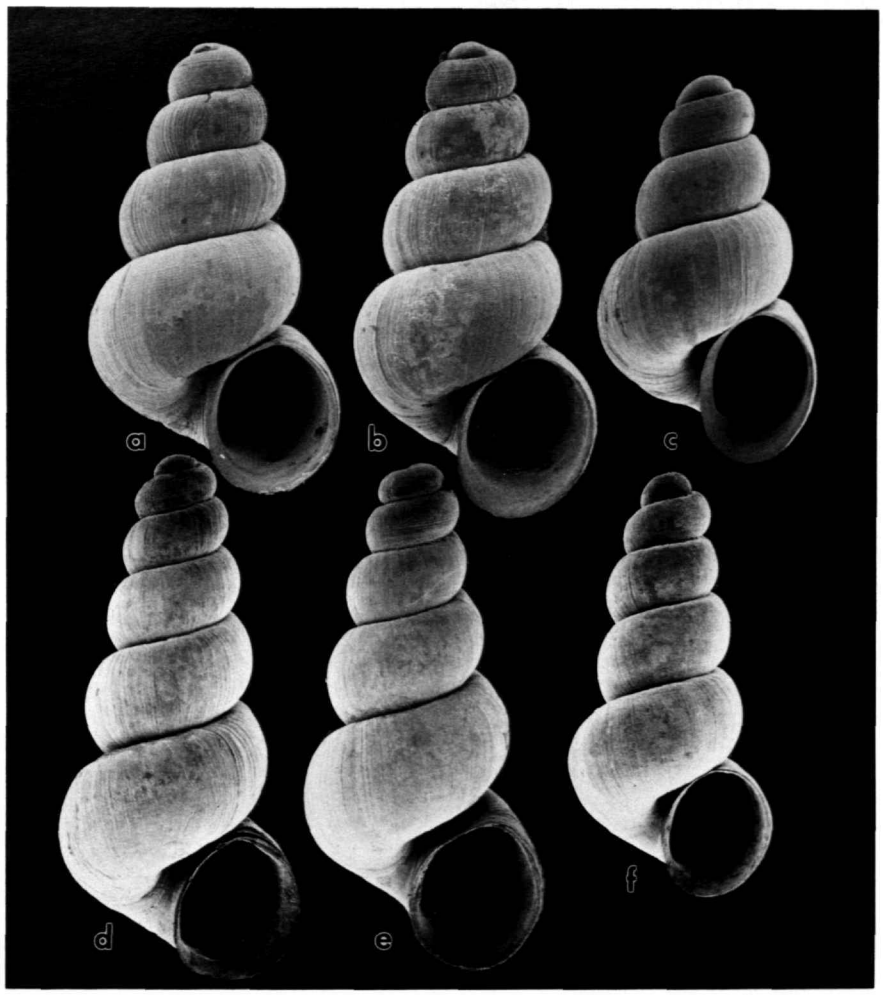

FIGURE 28.—*Fontigens proserpina* (Hubricht): *a,b*, Rices Cave, Jefferson Co., MO, LH A4676 (paratypes; shell height, 2.1, 2.2 mm, respectively); *c*, locality as above, USNM 535682 (paratype; 1.8 mm); *d,e*, Drain tile outlet, Osage Hills Golf Course, St. Louis Co., MO, LH A4405 (2.7, 2.6 mm, respectively); *f*, Saltpeter Cave, Ste. Genevieve Co., MO, LH A6343 (2.4 mm).

TABLE 7.—Selected shell parameters for *Fontigens proserpina* (Hubricht), expressed as $\bar{x}$ with SD in parentheses. Shell height (SH) and width (SW) are given in mm. NW = number of whorls, W = whorl expansion rate, D = distance of generating curve from coiling axis, T = translation rate, AS = aperture shape.

Locality	NW	SH	SW	W	D	T	AS
Rice's Cave, Jefferson Co., MO LH A4676 (n = 9)	4.92(0.13)	2.12(0.05)	1.13(0.06)	1.36(0.10)	0.57(0.04)	6.41(0.83)	1.24(0.11)
Drain tile outlet, Kirkwood, St. Louis Co., MO LH A4405 (n = 10)	6.03(0.30)	3.61(0.18)	1.64(0.08)	1.30(0.16)	0.52(0.05)	7.54(0.80)	1.22(0.06)

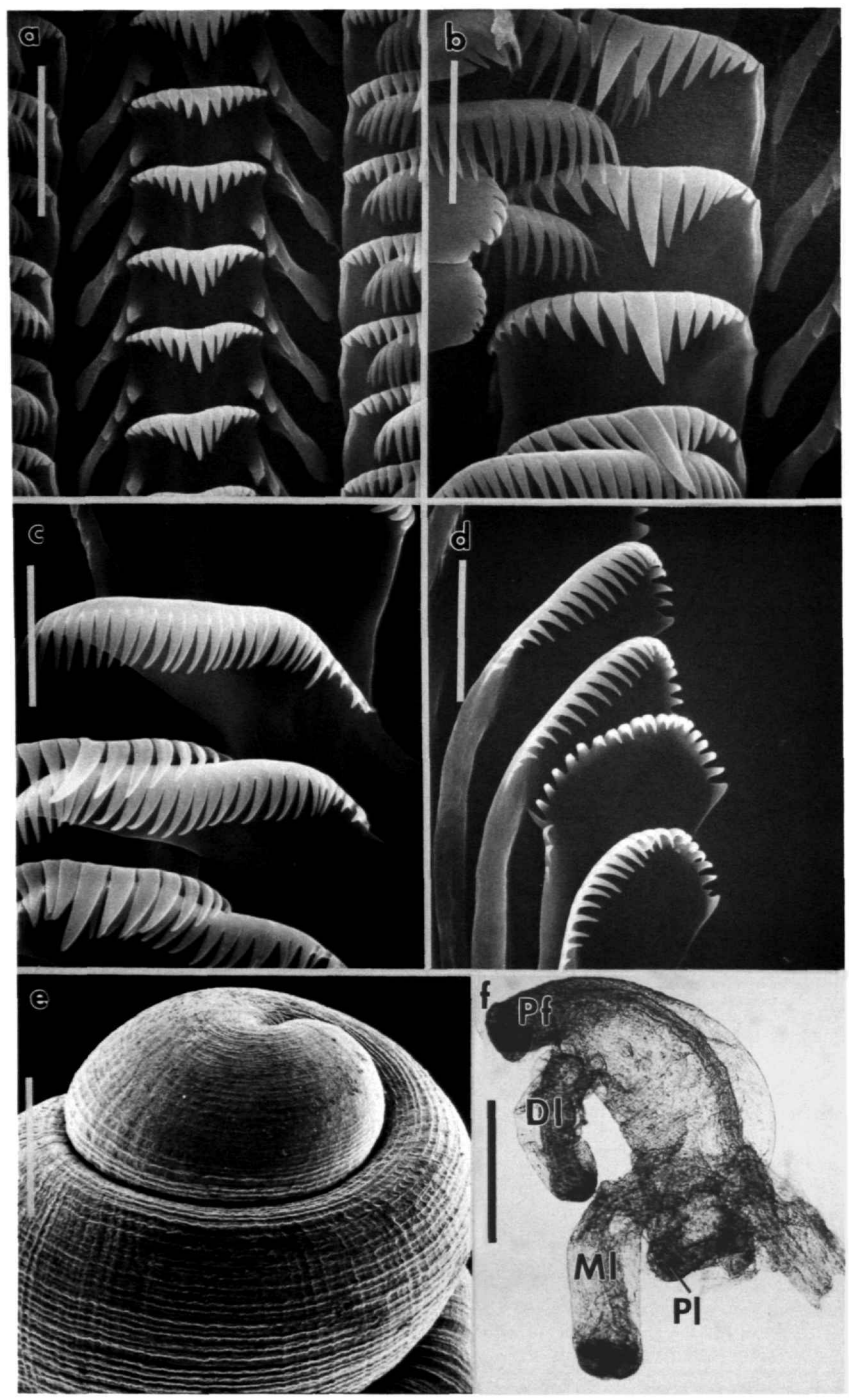

FIGURE 29.—Morphology of *F. proserpina*, Rices Cave, Jefferson Co., MO, USNM 858061 (topotypes): *a*, Central radular teeth (bar = 7.5 μm); *b*, Lateral teeth (bar = 5.0 μm); *c*, Lateral and inner marginal teeth (bar = 5.0 μm); *d*, Outer marginal teeth (bar = 6.0 μm); *e*, Protoconch (bar = 136 μm); *f*, Dorsal aspect of wet mount of penis (bar = 0.25 mm).

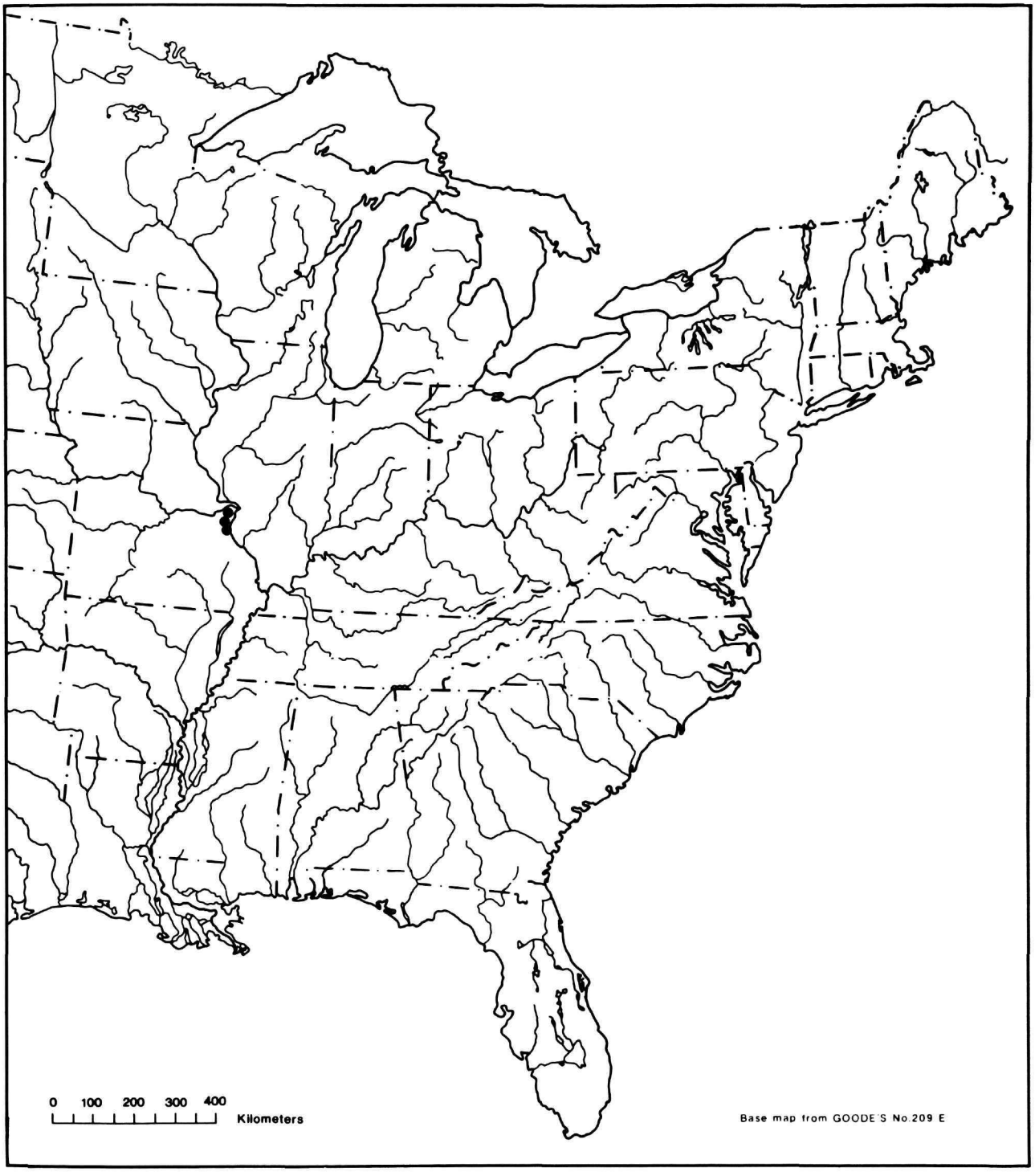

FIGURE 30.—Map showing distribution of *F. proserpina*.

slit-like to narrowly open. Apex (Figure 29*e*) protruding; numerous striae pronounced on protoconch. Striae usually present on entirety of shell, but sometimes reduced to absent on later whorls. Striae sometimes crossed by elevated growth lines, yielding cancellate appearance.

Animal unpigmented.

Radular formula (Figure 29*a–d*): 6(7)-1-6(7)/3-3, 6-1-8, 30, 19-22. Central and lateral teeth unusually multicuspate; lateral tooth with slightly enlarged, dagger-like central cusp.

Ctenidial filaments, ~17. Testis, <0.25 whorl. Penis (Figure 29*f*) moderate-sized. Penial filament short, with blunt distal end. Distal lobes slightly longer than filament; tubular gland in distal of these extending only to base of lobe. Ovary, <0.25 whorl. Capsule gland and albumen gland about equal in length. Ventral channel narrow. Bursa copulatrix about equal in length to and virtually non-overlapping albumen gland. Duct issuing from posterior end of bursa and extending lateral to small oviduct coil.

TYPE LOCALITY.—Rices Cave, Jefferson Co., Missouri. Holotype, ANSP 175558; paratypes, LH A4676, USNM 535682.

DISTRIBUTION AND HABITAT.—Recorded from two caves and a drain outlet in Mississippi River basin of southeastern Missouri (Figure 30). Probably restricted to subterranean habitats, inasmuch as specimens from the drain tile apparently were washed out of an underground habitat prior to collection.

MATERIAL EXAMINED.—MISSOURI. *Jefferson County:* Rices Cave, 4.8 km NE of Goldman, USNM 858061. *Ste. Genevieve County:* Saltpeter Cave, 4.8 km NW of Minnith, LH A6343. *St. Louis County:* Outlet of drain tile, Osage Hills Golf Course, Kirkwood, LH A4405, USNM 535853.

Fontigens tartarea Hubricht

FIGURES 31-34; TABLE 8

Fontigens tartarea Hubricht, 1963:140, pl. 8; figs. c, d; 1976:88.—Holsinger et al., 1976:15.—Burch and Tottenham, 1980:126, fig. 314.

Fontigens holsingeri Hubricht, 1976:86, fig. 1a.—Burch and Tottenham, 1980:126, fig. 311.—USDI, 1989:576. [New synonymy.]

Fontigens spp.—Holsinger et al., 1976:15 [in part].

DIAGNOSIS.—A small-sized species with ovate- to elongate-conic shell. Penis with two accessory lobes containing tubular and bulbous glands.

DESCRIPTION.—Shell (Figure 31, Table 8) 1.0–2.3 mm tall; height/width, 148%–211%. Whorls, 3.5–5.5, nearly straight to well rounded; extremely narrow adapical shoulders sometimes present. Spire variably convex. Aperture ovate, slightly angled above. Inner lip very slightly thickened and reflected, adnate to or slightly separated from body whorl. Umbilicus narrowly to broadly open. Apex (Figure 32*e*) slightly to moderately protruding; protoconch with pronounced striae.

Animal unpigmented.

Radular formula (Figure 32*a–d*): 6-1-6/1-1, 4-1-5, 21-22, 16-20. Central cusp of lateral tooth slightly enlarged, dagger-like. Pallial intestine sometimes with series of undulations or coils.

Ctenidial filaments, ~10. Testis filling half a whorl. Penis (Figure 32*f*) small relative to head. Penial filament and distal lobe elongate, near-equal in size. Tip of filament with subterminal bulges. Ovary filling less than a quarter whorl. Capsule and albumen glands near-equal in length (Figure 33). Capsule gland opening simple. Ventral channel broad. Bursa copulatrix small, overlapping small portion of (left lateral) albumen gland. Duct issuing from posterior end of bursa and extending along edge of bursa (dorsal to most of oviduct coil). Oviduct coil large and positioned along posterior half of bursa.

TYPE LOCALITY.—Organ Cave, Greenbrier Co., West Virginia. Holotype, FMNH 116917; paratypes, LH 43635, USNM 673529.

DISTRIBUTION AND HABITAT.—Found in caves in Ohio River drainage of eastern West Virginia, from the Monangahela River south to New River basin (Figure 34).

REMARKS.—Although diverse in shell form, the West Virginia cavesnails exhibit intergradation between the elongate conic, nearly flat-whorled, typical *Fontigens tartarea* and the broadly conical, round-whorled *F. holsingeri* s.l., and are uniform (where known) in penial morphology; thus the latter is considered a synonym.

MATERIAL EXAMINED.—WEST VIRGINIA. *Greenbrier County:* Organ Cave, near Organ Cave P.O., LH A4845, 38351, USNM 673528, 853168, 858058. *Monroe County:* Rock Camp Cave, 2.6 km S of Rock Camp, LH 40723; Indian Draft Cave,

TABLE 8.—Selected shell parameters for *Fontigens tartarea* Hubricht, expressed as $\bar{x}$ with SD in parentheses. Shell height (SH) and width (SW) are given in mm. NW = number of whorls, W = whorl expansion rate, D = distance of generating curve from coiling axis, T = translation rate, AS = aperture shape.

Locality	NW	SH	SW	W	D	T	AS
Organ Cave, Greenbrier Co., WV USNM 853168 (topotypes) (n = 9)	4.67(0.56)	1.91(0.12)	1.03(0.08)	1.36(0.17)	0.53(0.07)	6.09(1.31)	1.31(0.11)
Harman Cave, Randolph Co., WV LH 43635 (n = 5)	4.15(0.29)	1.55(0.16)	0.95(0.03)	1.40(0.06)	0.62(0.19)	5.31(0.77)	1.27(0.08)
Harpers Cave, Tucker Co., WV LH 42563 (n = 9)	4.53(0.23)	1.82(0.07)	1.06(0.04)	1.42(0.16)	0.54(0.06)	6.31(1.10)	1.25(0.05)

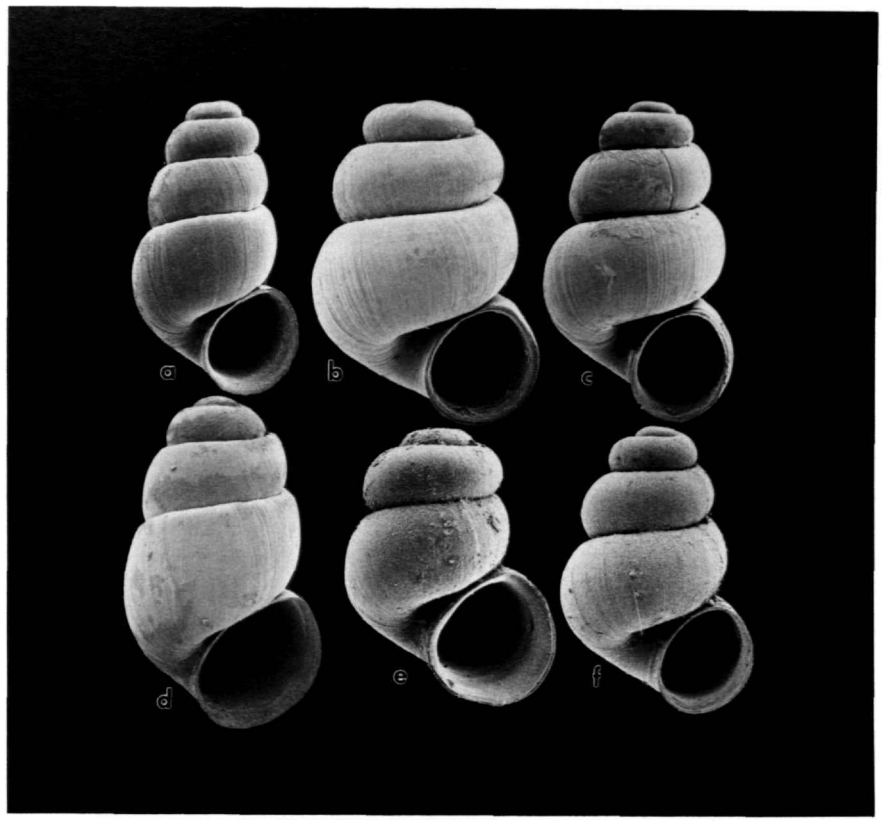

FIGURE 31.—*Fontigens tartarea* Hubricht: *a*, Organ Cave, Greenbrier Co., WV, USNM 853168 (topotype; shell height, 1.7 mm); *b*, Harman Cave, Randolph Co., WV, USNM 858042 (topotype, *Fontigens holsingeri* Hubricht; 1.6 mm); *c*, Bazzle Cave, Randolph Co., WV, LH 42561 (1.8 mm); *d*, Bowden Cave, Randolph Co., WV, LH 42562 (1.2 mm); *e*, Rock Camp Cave, Monroe Co., WV, LH 40723 (1.6 mm); *f*, Pidling Pit Cave, Pocahontas Co., WV, LH 36839 (1.4 mm).

a few km S of Wayside, LH 40411; McClung-Zenith Cave, Zenith (Hubricht 1976:88). *Pocahontas County:* Pidling Pit Cave, 16 km NNE of Marlington, LH 36839; Marthas Cave, 3 km SW of Hillsboro, LH 38730. *Randolph County:* Harman Cave, 0.8 km SW of Harman, FMNH 170893 (holotype, *F. holsingeri* Hubricht), LH 43635, USNM 858042; Bazzle Cave, 1.6 km SSE of Harman, LH 42561; Simmons-Mingo Cave, 2.4 km SW of Mingo, LH 42892; Bowden Cave, 11.2 km E of Elkins, LH 42562. *Tucker County:* Harpers Cave, 8 km SE of Hendricks, LH 42563.

Fontigens turritella Hubricht

FIGURES 35*a,b*, 36, 37; TABLE 9

Fontigens turritella Hubricht, 1976:87, fig. 1b.—Burch and Tottenham, 1980:126, fig. 310. —USDI, 1989:576.
Fontigens spp.—Holsinger et al., 1976:15 [in part].
Lartetia(?) sp.—Holsinger et al., 1976:15.

DIAGNOSIS.—A small-sized species with turreted shell; teleoconch with variably developed spiral striae. Penis with two accessory lobes containing tubular glands.

TABLE 9.—Selected shell parameters for *Fontigens turritella* Hubricht, expressed as $\bar{x}$ with SD in parentheses. Shell height (SH) and width (SW) are given in mm. NW = number of whorls, W = whorl expansion rate, D = distance of generating curve from coiling axis, T = translation rate, AS = aperture shape.

Locality	NW	SH	SW	W	D	T	AS
McClungs Cave, Greenbrier Co., WV LH 40694 (paratypes) (n = 5)	5.30(0.11)	1.84(0.07)	0.88(0.07)	1.23(0.11)	0.56(0.04)	6.23(0.95)	1.16(0.09)

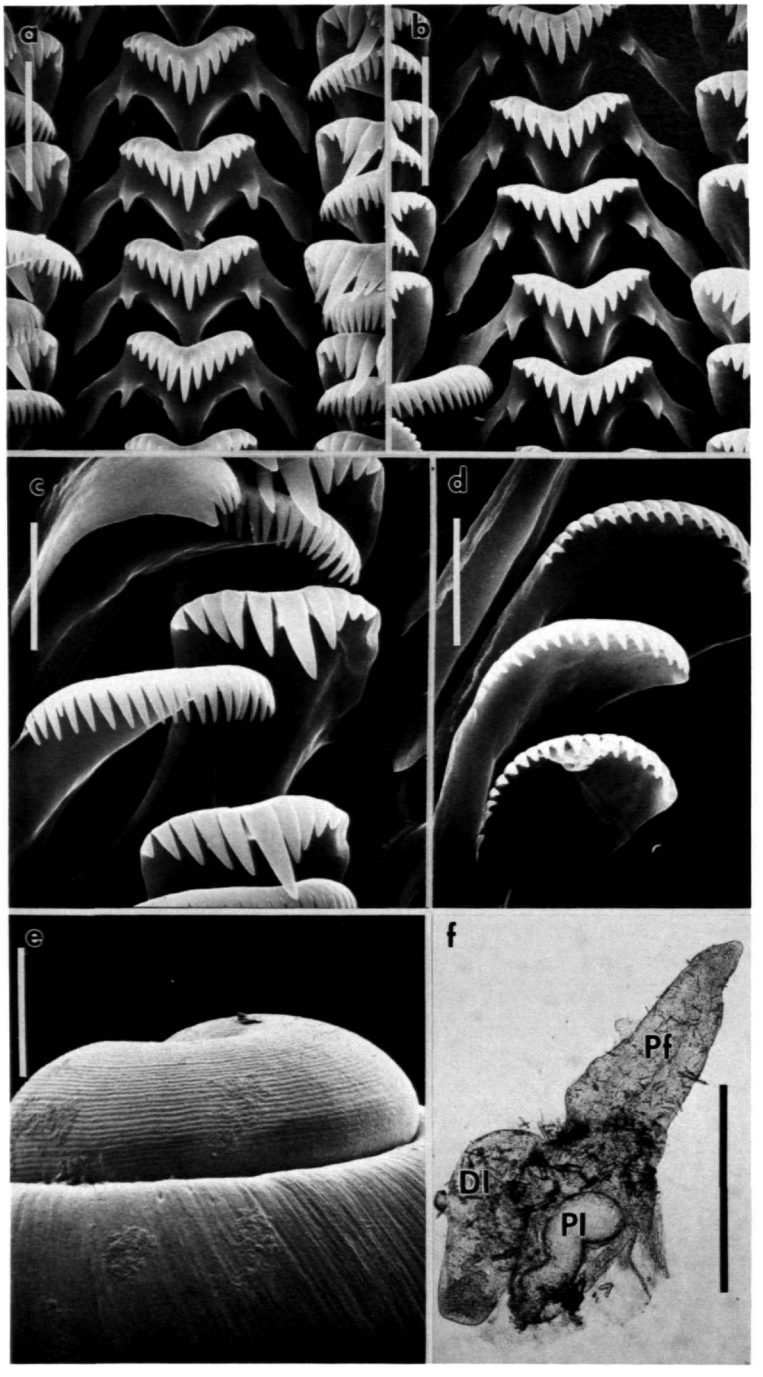

FIGURE 32.—Morphology of *F. tartarea: a,* Central radular teeth, Organ Cave, Greenbrier Co., WV, USNM 858058 (topotype; bar = 7.5 μm); *b,* Central radular teeth, Harman Cave, Randolph Co., WV, USNM 858042 (bar = 7.5 μm); *c,* Lateral and inner marginal teeth, Organ Cave (as above; bar = 5.0 μm); *d,* Outer marginal teeth, Harman Cave (as above; bar = 3.8 μm); *e,* Protoconch, Organ Cave (as above; bar = 100 μm); *f,* Dorsal aspect of wet mount of penis, locality as above, LH A4845 (bar = 1.0 mm).

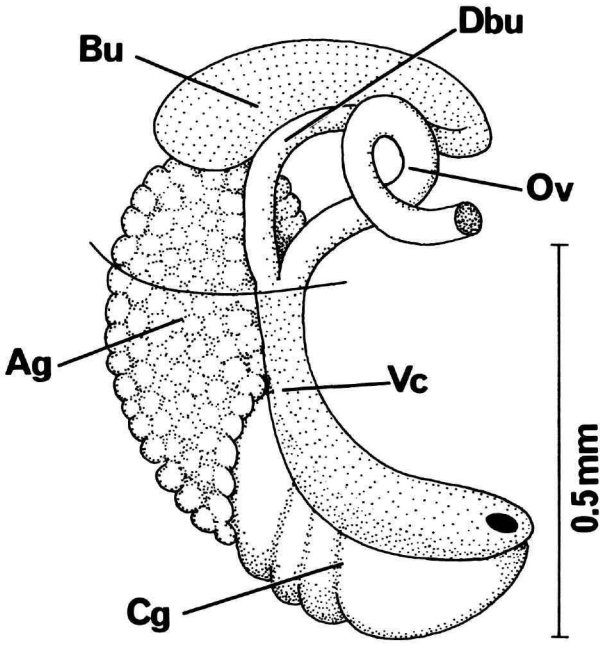

FIGURE 33.—Left lateral aspect of pallial oviduct complex of *F. tartarea*, Harman Cave, Randolph Co., WV, USNM 858042. Curved line indicates the posterior wall of the pallial cavity.

DESCRIPTION.—Shell (Figure 35*a,b*, Table 9) 1.7–2.0 mm tall; height/width, 194%–220%. Whorls, 5.25–5.50, moderately rounded, with adapical shoulders. Spire slightly convex. Aperture small, 27%–34% of shell height, broadly ovate to subcircular, only slightly more angled above than below. Inner lip very slightly thickened and reflected, adnate to or slightly separated from body whorl. Umbilicus narrowly open. Apex (Figure 36*e*) slightly protruding; protoconch striae broad, well-developed. Teleoconch striae well separated, moderate in number, usually strong even on body whorl.

Body and eyespots without melanic pigment.

Radular formula (Figure 36*a–d*): 7-1-7/1-1, 4(5)-1-5, 20-21, 17-19. Central cusp of lateral tooth slightly enlarged, dagger like.

Ctenidial filaments, 16–17. Testis filling a half whorl. Penis (Figure 36*f*) moderate-sized. Penial filament and distal lobe narrowly separated, short; tip of filament simple. Tubular glands in both lobes extending into nuchal cavity. Ovary filling less than a quarter whorl. Capsule and albumen glands near-equal in length. Ventral channel narrow. Bursa copulatrix ovate, largely posterior to albumen gland. Duct issuing from near anterior end of bursa. Oviduct coil large, pressed against posterior albumen gland (rather than bursa).

TYPE LOCALITY.—McClungs Cave, Greenbrier Co., West Virginia. Holotype, FMNH 170891; paratypes, LH 40694.

DISTRIBUTION AND HABITAT.—Recorded from type locality as well as nearby The Hole Cave, both in the Greenbrier River drainage (Figure 37).

MATERIAL EXAMINED.—WEST VIRGINIA. *Greenbrier County:* McClungs Cave, 3.2 km NE of Maxwelton, USNM 858066; The Hole Cave, 3.2 km E of Frankford (Hubricht 1976:87).

SPECIES OF QUESTIONABLE STATUS

Fontigens cryptica Hubricht (Figure 35*c*) was described from a collection taken from a small spring orifice along the Ohio River in southeast Indiana (Hubricht 1963:139). The senior author was unable to find the snail during two recent vists to the type locality (and nearby localities), nor was it taken during an extensive survey of subterranean habitats in the region (Lewis 1983). Although the shell probably is that of a *Fontigens*, we have not included the species in our study because alcohol-preserved material necessary to verify the above is not available. Another species commonly placed in the genus is *Cincinnatia binneyana* Hannibal (= *Paludina obtusa* Lea non Troschel) from Ohio, which was transferred to *Fontigens* by Morrison (1947). The anatomy of this species is unknown, but the shell (Figure 35*d*) more closely resembles that of *Probythinella lacustris* (F.C. Baker) than *Fontigens*. Note that Lea's type material was collected from "Ohio" and could represent drift from the shore of Lake Erie, where *P. lacustris* occurs in relatively shallow water.

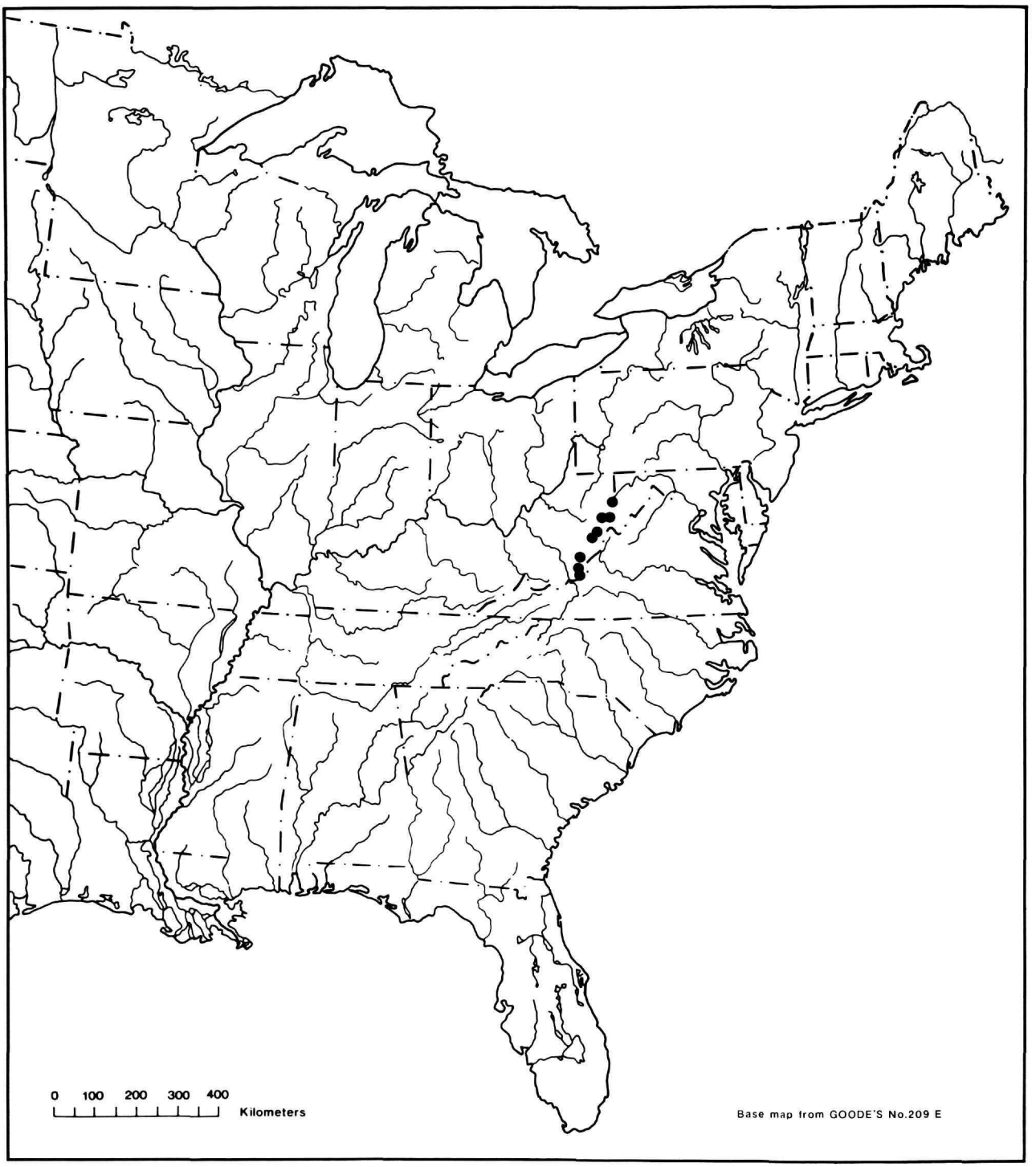

FIGURE 34.—Map showing distribution of *F. tartarea*.

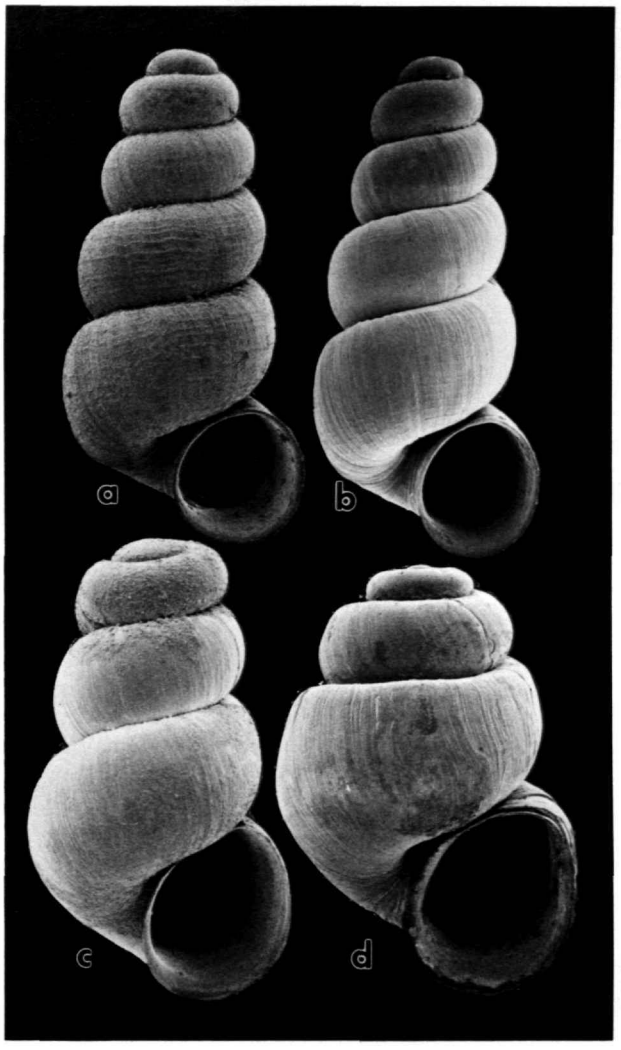

FIGURE 35.—*Fontigens* spp.: *a,b, F. turritella* Hubricht, McClungs Cave, Greenbrier Co., WV, LH 40694 (paratypes; both shells 1.7 mm high); *c, F. cryptica* Hubricht, Spring W of Bethlehem, Clark Co., IN, USNM 673533 (topotype; 1.6 mm); *d, Cincinnatia binneyana* Hannibal, OH, USNM 853167 (2.2 mm).

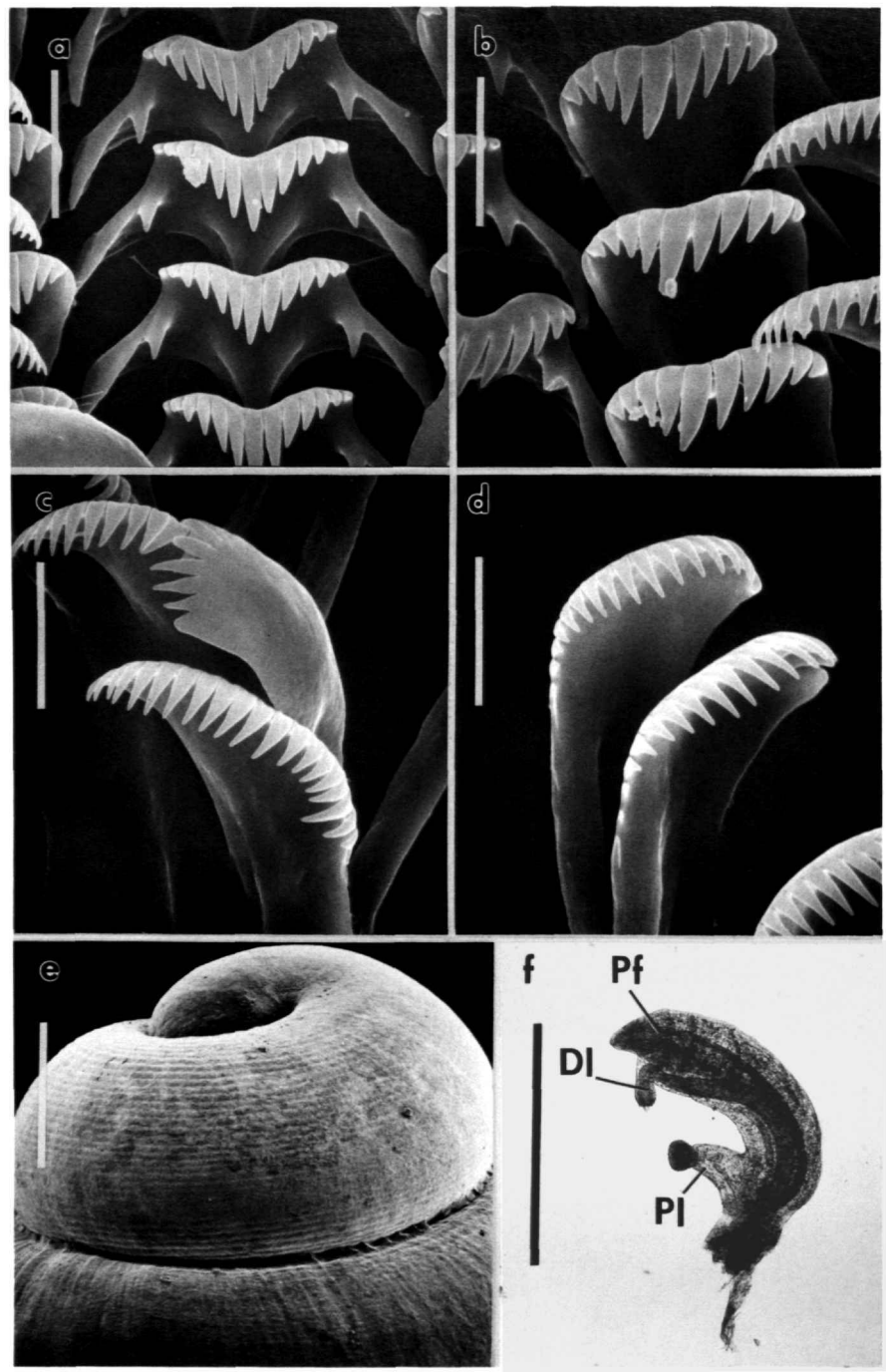

FIGURE 36.—Morphology of *F. turritella*: *a*, Central radular teeth, McClungs Cave, Greenbrier Co., WV, USNM 858066 (topotype; bar = 6.0 μm); *b*, Lateral teeth, from above lot (bar = 5.0 μm); *c*, Inner marginal teeth, from above lot (bar = 4.3 μm); *d*, Outer marginal teeth, from above lot (bar = 3.8 μm); *e*, Protoconch, from above locality, LH 40694 (paratype; bar = 100 μm); *f*, Dorsal aspect of wet mount of penis, from above lot (bar = 1.0 mm).

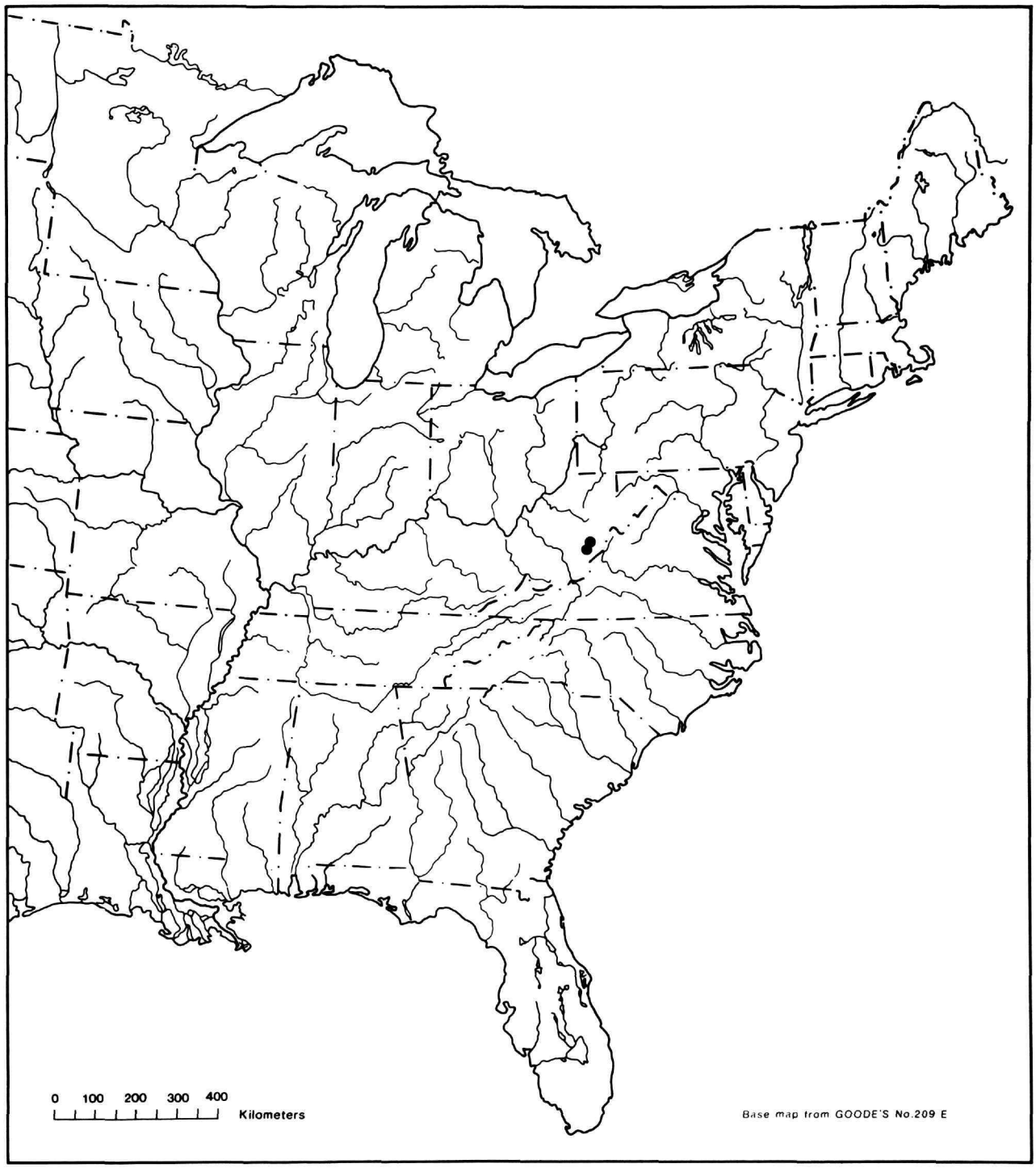

FIGURE 37.—Map showing distribution of *F. turritella*.

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