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DISTRIBUTION, REPRODUCTIVE ANATOMY, AND VARIATION OF *MONADENIA TROGLODYTES* HANNA AND SMITH (GASTROPODA: PULMONATA) WITH THE PROPOSAL OF A NEW SUBGENUS

By
Barry Roth

Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118

ABSTRACT: *Shastelix*, new subgenus of *Monadenia* (type-species, *M. troglodytes troglodytes*) is proposed, based principally on genital characters. The new subgenus is mostly confined to the Klamath Mountains of California and is parapatric with *Monadenia*, sensu stricto. *Monadenia troglodytes* is common in a limited area of Shasta County, associated with limestone terrane. Three subspecies are recognized based on morphometry and geography—*M. t. troglodytes* along the McCloud River arm of Shasta Lake; *M. t. wintu*, new subspecies, between the Pit River and Squaw Creek, with one disjunct, outlying population south of Shasta Lake; and *M. t. chaceana* (formerly ranked as a distinct species) near the confluence of the Shasta and Klamath rivers in Siskiyou County. Sympatric *Monadenia churchi* and *M. troglodytes* differ little in reproductive anatomy; elaborations of the female genitalia are probably not important in species recognition or reproductive isolation. A phylogenetic hypothesis and evolutionary scenario for the three subgenera of *Monadenia* are presented.

INTRODUCTION

The western North American helicacean snail genus *Monadenia* Pilsbry, 1895, includes conspicuous species that have long attracted the attention of malacologists. Its type-species, *Helix fidelis* Gray, 1834, was the first land mollusk described from the Pacific coast. It includes the most northern helicacean species—and some of the most northern large land snails—on the North American continent. *Monadenia* is one of the few temperate genera of snails with an elaborate color pattern (Comfort 1951), and *M. fidelis* is the only snail in the far west with a dramatic polymorphism of shell color and banding (Roth in press).

Pilsbry (1939) and Berry (1940a) divided *Monadenia* into two groups of species, based on reproductive anatomy and shell characters—*Monadenia*, sensu stricto, and *Corynadenia* Berry, 1940. The range of the genus extends from southern Alaska to central California, principally west of the Cascade Range but penetrating inland along major river valleys. One branch reaches south along the east side of the Sacramento Valley; the other follows the southern Klamath Mountains and Coast Ranges to the San Francisco Bay region (Figure 1). The subgenus *Corynadenia* exists as an apparently disjunct group of species on the west side of the Sierra Nevada. Roth (1975) showed that *Monadenia churchi* Hanna and Smith, 1933, which occupies a fairly wide range around the north end of the Sacramento Valley, and which Pilsbry (1939) and Berry (1940a) had grouped with the

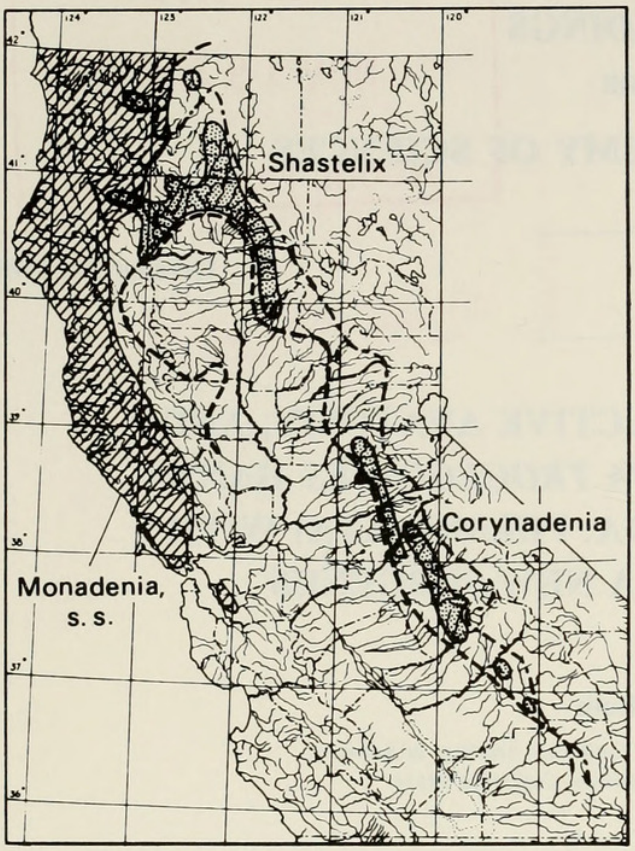


FIGURE 1. Distribution of the subgenera of *Monadenia* in California. Diagonal hachure, generalized range of *Monadenia*, sensu stricto; stippling, in Klamath Mountains region, *Shastelix*, in Sierra Nevada, *Corynadenia*. Dashed line represents 36 C mean maximum July isotherm; dot-dashed line, −4 C mean minimum January isotherm (thermal data after Elford 1970).

Sierran subgenus, combines anatomic and shell characters of *Monadenia*, s.s., and *Corynadenia*. A number of other species from northern California described by Berry (1940b) have not yet been dissected or assigned unequivocally to subgenus. Parapatry and possible sympatry of species have been demonstrated (Roth and Eng 1980; and herein), and it is clear that the zoogeography of *Monadenia* is more complex than earlier authors imagined.

Monadenia is ecologically diverse, comprising species of rock crevices and rockslides, others that inhabit deep leafmold, semi-arboreal forms, and snails that crawl out exposed on low plant cover. The relations between habit and habitat, on the one hand, and morphology and variation, on the other, are important for understanding the evolutionary history of the group. This paper is one of a projected series of studies aimed at elucidating those relationships.

Monadenia troglodytes Hanna and Smith, 1933, was described from fossil shells of presumed Pleistocene age collected in Samwel Cave, Shasta County, California (sec. 5, T. 35 N, R. 3 W, Mount Diablo Base and Meridian, USGS Bollibokka Mountain Quadrangle). Other shells of the species, likewise interpreted as Pleistocene, were reported from Potter Creek Cave (sec. 23, T. 34 N, R. 4 W, MDB&M, USGS Lamoine Quadrangle), Shasta County (Hanna and Smith 1933). Empty shells were later found by Stanford University speleologists a short distance outside Samwel Cave (Smith 1957), and in 1963 the species was discovered alive in the same general area (Walton 1970). Smith (1970) and Roth (1972a, 1972b) cited *M. troglodytes* as rare and of limited distribution.

In May 1973 the late Allyn G. Smith of the California Academy of Sciences found the species at a new locality, in limestone rockslides near Ellery Creek (SE¼ sec. 6, T. 35 N, R. 3 W, MDB&M, Bollibokka Mountain Quadrangle), west of the McCloud River arm of Shasta Lake (Fig. 2). He collected many empty shells in various states of preservation and one living specimen. Since then, additional collections, including a substantial amount of material secured independently by S. E. Hirschfeld, D. C. Rudolph, and R. L. Seib, indicate that the species is fairly common in a limited area in Shasta County and is strongly associated with limestone terrane.

Dissections of the reproductive system show that *M. troglodytes*, along with *M. churchi*, belongs to a new subgenus, which is named herein. Selected shell characters were measured to analyze shell variability. A new subspecies is described, distinguished from typical *M. troglodytes* by details of color, shell microsculpture, and morphometry. *Monadenia chaceana* Berry (1940b) is similar in general shell character but differs consistently in certain shell measurements and is regarded as a third subspecies. One other species of *Monadenia* occurs within the range of *M. troglodytes*, permitting a consideration of species criteria within the genus. An hypothesis of phylogenetic relationships within *Monadenia* is presented.

The use of a trinomial to designate the nominate subspecies—a convention sparingly observed in American land malacology, but one necessary to distinguish the subspecies from the species sensu lato—is here introduced for *Monadenia troglodytes troglodytes*.

FIGURE 2. Gilman Road crossing of Ellery Creek (Locality 26); typical *Monadenia troglodytes* habitat in brush-covered talus at foot of prominent limestone outcrop.

The following institutional abbreviations are employed:

AMNH—American Museum of Natural History
ANSP—Academy of Natural Sciences, Philadelphia
CAS—California Academy of Sciences, Department of Invertebrate Zoology
CASGTC—California Academy of Sciences, Geology Type Collection, Department of Geology
FMNH—Field Museum of Natural History
LACM—Los Angeles County Museum of Natural History
SSB—Private collection of S. Stillman Berry, Redlands, California
SUPTC—Stanford University Paleontological Type Collection, now in Department of Geology, California Academy of Sciences
UCMP—Museum of Paleontology, University of California, Berkeley
USNM—United States National Museum of Natural History

Monadenia Pilsbry

Monadenia PILSBRY, 1895:198.—PILSBRY 1939:31–35.

TYPE-SPECIES: *Helix fidelis* Gray, 1834, by original designation.

Shastelix, new subgenus

TYPE-SPECIES: *Monadenia troglodytes troglodytes* Hanna and Smith, 1933.

DIAGNOSIS.—*Monadenia* with large, globose atrium; mucus gland much longer than dart sac, its lower part adnate to atrium; penial retractor inserted near middle of epiphallus; flagellum (epiphallic caecum) substantially longer than penis plus epiphallus and borne in a series of helical coils. Penis sessile on atrium, not invaginated into it. Spermatophore helically coiled (?). Shell of moderate size for the genus, smooth or granulose, protoconch sculpture of minute, somewhat confluent granules, tending to align in diagonal series.

The genitalia of *Monadenia troglodytes* (Figs. 4–6) differ most obviously from those of species

TABLE 1. CHARACTER COMPLEXES IN THE SUBGENERA OF *Monadenia*.

Characters	*Monadenia*, s.s.	*Shastelix*	*Corynadenia*
Atrium large and globose (+), or small and narrow (−)	+	+	−
Mucus gland many times longer than (+), or about equal to (−), dart sac	+	+	−
Lower part of mucus gland adnate to (+), or free from (−), atrium	−	+	−
Dart sac 5 mm or less in length (+), or longer than 5 mm (−)	−	+	−
Flagellum ≥1.5 times length of (+), or about as long as (−), penis plus epiphallus	−	+	+
Flagellum (and spermatophore) helically coiled (+), or straight (−)	−	+	+
Basal chamber of penis invaginated into (+), or sessile on (−), atrium	+	−	+
Penial retractor inserted near middle (+), or on distal third (−), of epiphallus	−,+	+	+

of the nominate subgenus (*M. fidelis*, *M. infumata* (Gould, 1855), *M. setosa* Talmadge, 1952) in the long, helically coiled flagellum. The flagellum in *Monadenia*, sensu stricto, is thick and straight or simply curved and about as long as the penis plus epiphallus (Pilsbry 1939:figs. 15A, B, *M. fidelis*; Roth and Eng 1980:fig. 3, *M. setosa*; the genitalia of *M. infumata* are similar). The flagellum is the organ which secretes the spermatophore; the spermatophore of *M. fidelis* (Webb 1952:fig. 8A) is straight. In the Sierran *Monadenia* (*Corynadenia*) *hirsuta* Pilsbry, 1927, a species with helically coiled flagellum, the spermatophore is coiled like a corkscrew. It seems probable, therefore, that species of *Shastelix* also secrete coiled spermatophores.

Both *Shastelix* and *Monadenia*, s.s., have a large, globose atrium. (I follow Pilsbry [1939], Berry [1940a] and other authors in using the term "atrium" for the large, saccular elaboration of the lower genitalia upon which the penis, dart sac, and vagina insert and which when everted forms the copulatory pad or disk. This organ is mainly developed above the insertion of the penis and is homologous to the lower part of the vagina in other helicoid genera. In these other genera the term "atrium" is conventionally restricted to the common passage to the external genital pore below the insertion of the penis.) In *Shastelix* the lower ductlike portion of the mucus gland is adnate to the atrium, whereas in *Monadenia*, s.s., it runs along the surface of the atrium but is not fused to it. The dart sac in *Shastelix* is smaller than that in the nominate subgenus. In *Monadenia*, s.s., the basal part of the penis is invaginated into the wall of the atrium, which clasps it like a collar; in *Shastelix* the basal part of the penis is sessile on the atrium.

In the subgenus *Corynadenia* Berry, 1940a (type-species, *Helix hillebrandi* Newcomb, 1864; see Pilsbry 1939:fig. 15C), the atrium is smaller, narrow and elongate, and the mucus gland is shorter or very slightly longer than the dart sac. The flagellum is longer than the penis plus epiphallus and, at least in some species, helically coiled. The basal part of the penis is invaginated into the wall of the atrium, as in *Monadenia*, s.s.

Character complexes differentiating the three subgenera are summarized in Table 1.

Monadenia churchi also belongs to *Shastelix* and resembles *M. troglodytes* in genitalia (Fig. 8) and protoconch sculpture. It is probable that some undissected species from the Klamath Mountains (particularly *M. cristulata* Berry, 1940, and *M. marmarotis* Berry, 1940) will also prove to belong to *Shastelix*. The known range of the subgenus (Fig. 1) extends from Butte County on the south and east, around the north

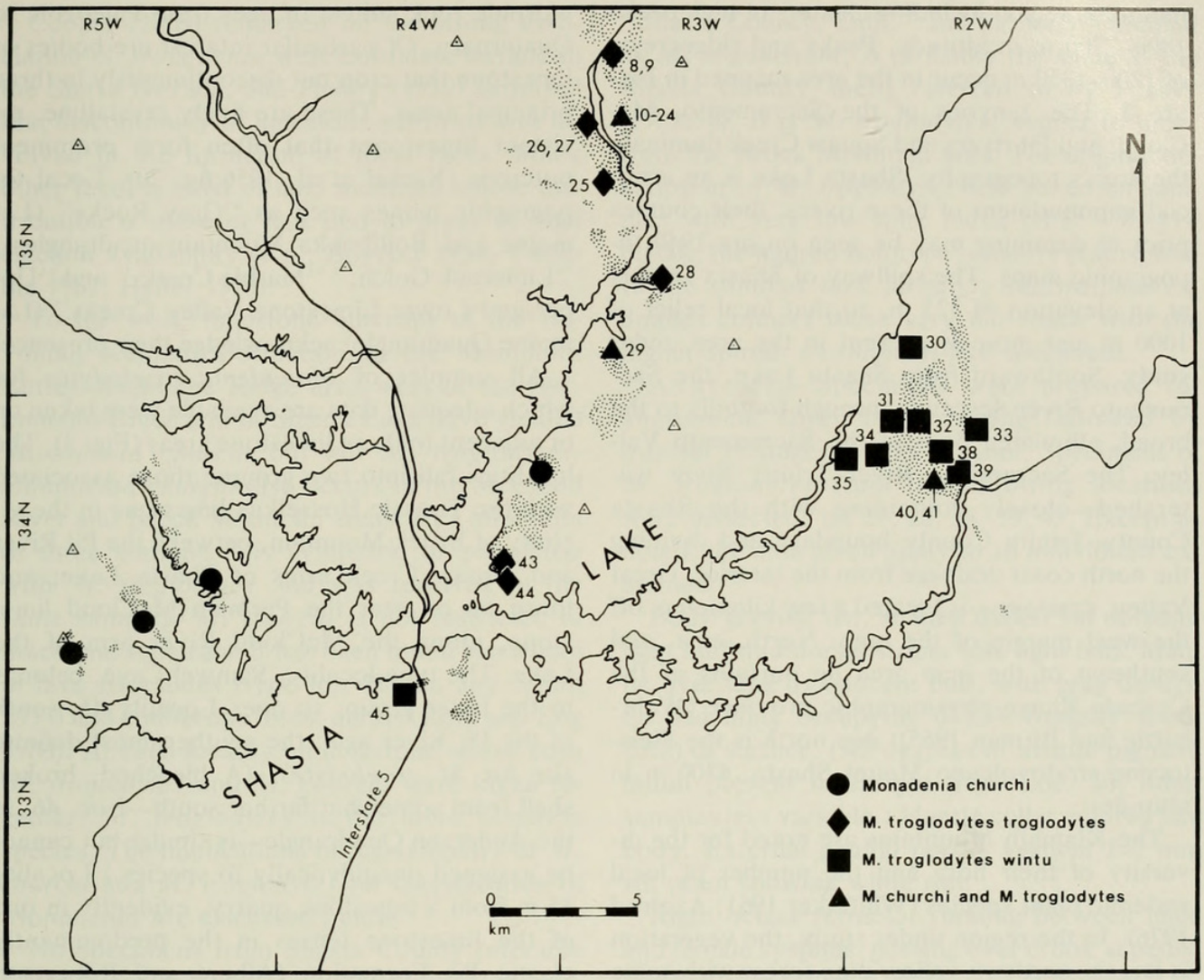


FIGURE 3. Distribution of *Monadenia* species in vicinity of Shasta Lake, Shasta County, Calif. Stippling indicates surface outcrops of limestone. Open triangles denote peaks of more than 1000 m elevation. Geology after: Diller (1906); Kinkel et al. (1956); Coogan (1960); Albers and Robertson (1961); Demirmen and Harbaugh (1965); Irwin and Galanis (1976).

end of the Sacramento Valley, to near Burnt Ranch, Trinity County, on the west, and the Shasta River–Klamath River confluence on the north. *Monadenia churchi* and *M. troglodytes* are sympatric in the vicinity of Shasta Lake. In the drainage of the Trinity River, *Shastelix* is parapatric with *Monadenia*, s.s. There *M. fidelis* and *M. setosa* tend to occur in riparian woodland close to streambeds, while *M. churchi* occurs on drier, more exposed slopes and in rockslides. Only the subgenus *Corynadenia* is known to occur in the Sierra Nevada.

The subgenus name is derived from the placename *Shasta*—lake, mountain, river, and county—plus the Greek *helix*, a spiral, hence a snail. Its gender is feminine.

DISTRIBUTION, ANATOMY, AND GEOGRAPHIC VARIATION OF *Monadenia troglodytes*

The material now available, summarized in the Appendix, makes it clear that *Monadenia troglodytes* is not only extant (Walton 1970) but occupies a considerable range in the vicinity of Shasta Lake (Fig. 3). At several of the localities, living individuals were found to be common.

The ranges of *M. t. troglodytes* and a second subspecies described herein lie within the "Eastern Klamath Belt," the easternmost of several concentric lithic belts that constitute the Klamath Mountains physiographic province of northwest California and southwest Oregon (Irwin 1972). The Klamath Mountains are a rugged

mountain region including clusters of high peaks 1800–2700 m in altitude. Peaks and ridgecrests of 1200–1350 m occur in the area mapped in Figure 3. The canyons of the Sacramento, McCloud, and Pit rivers and Squaw Creek dominate the area's topography. Shasta Lake is an artificial impoundment of these rivers; their courses prior to damming may be seen on pre-1940 topographic maps. The spillway of Shasta Dam is at an elevation of 325 m, so that local relief of 1000 m and more is present in the area under study. Southward from Shasta Lake, the Sacramento River descends through foothills to the broad, alluviated floor of the Sacramento Valley. The Sacramento River–Trinity River watershed—closely coinciding with the Shasta County–Trinity County boundary and dividing the north coast drainage from the interior, Great Valley, drainage—is located a few kilometers off the west margin of the map. North, east, and southeast of the map area lie portions of the Cascade Range physiographic province (Wahrhaftig and Birman 1965); due north is the Pleistocene stratovolcano Mount Shasta, 4300 m in altitude.

The Klamath Mountains are noted for the diversity of their flora and the number of local endemic plant species (Whittaker 1961; Axelrod 1976). In the region under study, the vegetation is largely northern yellow pine forest with some Sierran montane forest (Küchler 1977), particularly between the Pit and McCloud rivers. Lower elevations and exposed slopes are covered by a growth of scrub oak and chaparral. The land at higher elevations was originally densely timbered with coniferous forest, but in many areas logging, fires, and the effects of smelter smoke have removed the original timber, so that second-growth forest and brush are widespread. Manzanita (*Arctostaphylos*) is the dominant brush plant.

The normal annual precipitation is between 120 and 180 cm, more than 90 percent of it falling in the months October through April (Elford 1970; Major 1977). Mean monthly temperatures at Shasta Dam range from around 5 C in January to about 25 C in July (Major 1977). Daytime temperatures in excess of 40 C are not uncommon from June through September. Local microclimatic variation is considerable.

Geology of the region is complex, including intrusive and extrusive, sedimentary, and metamorphic rock suites, of ages from Paleozoic to Quaternary. Of particular interest are bodies of limestone that crop out discontinuously in three principal areas. These are finely crystalline, resistant limestones that often form prominent outcrops (Kinkel et al. 1956:fig. 20). Local topographic names such as "Gray Rocks" (Lamoine and Bollibokka Mountain quadrangles), "Limerock Gulch," "Marble Creek," and "Upper and Lower Limestone Valley Creeks" (Lamoine Quadrangle) acknowledge their presence.

All samples of *Monadenia troglodytes* for which adequate data are available were taken on or adjacent to these limestone areas (Fig. 3). The localities fall into two groups: those associated with the Triassic Hosselkus limestone in the vicinity of Brock Mountain, between the Pit River and Squaw Creek arms of Shasta Lake; and those on or near the Permian McCloud limestone, along the McCloud River arm of the Lake. The type-locality, Samwel Cave, belongs to the latter group; so does Locality 45, south of the Pit River arm, the southernmost definite site for *M. troglodytes*. (A bleached, broken shell from somewhat farther south—Loc. 46, in the Anderson Quadrangle—is similar but cannot be assigned unequivocally to species.) Locality 35 is from a limestone quarry, evidently in one of the limestone lenses in the predominantly clastic Pit Formation (Albers and Robertson 1961).

Limestones in the Shasta Lake region are discontinuous because of faulting and erosion. The McCloud and Brock Mountain locality groups are separated by approximately 10 km of nonlimestone terrane—chiefly volcanics, pyroclastics, and mudstones. Squaw Creek, its canyon, and a watershed of 830 m minimum elevation also stand between the two groups. Morphologic distinctions between the Brock Mountain and McCloud River herds, discussed below, indicate that a certain amount of genetic isolation exists as well. Localities yielding *M. troglodytes* range in elevation from about 330 to 760 m, so it does not seem likely that the altitude of the watershed alone constitutes an isolating factor. Exposure and seasonal lack of moisture on ridgetops may restrict the snails' mobility, but since some collections of *M. troglodytes* were made in zones of high insolation, with snails active in shaded spots even during July, limestone substrate seems a more likely limiting factor.

Cooper (1869) remarked on the strong association of *Monadenia* with carbonate terrane in the Sierra Nevada; and Pilsbry (1939) surmised that discontinuity of limestone substrata was involved in the formation of local races. Many other records exist of land mollusks whose distribution is more or less tied to areas of high calcium availability (e.g., Boycott 1934; Tweedie 1961; Heller 1975).

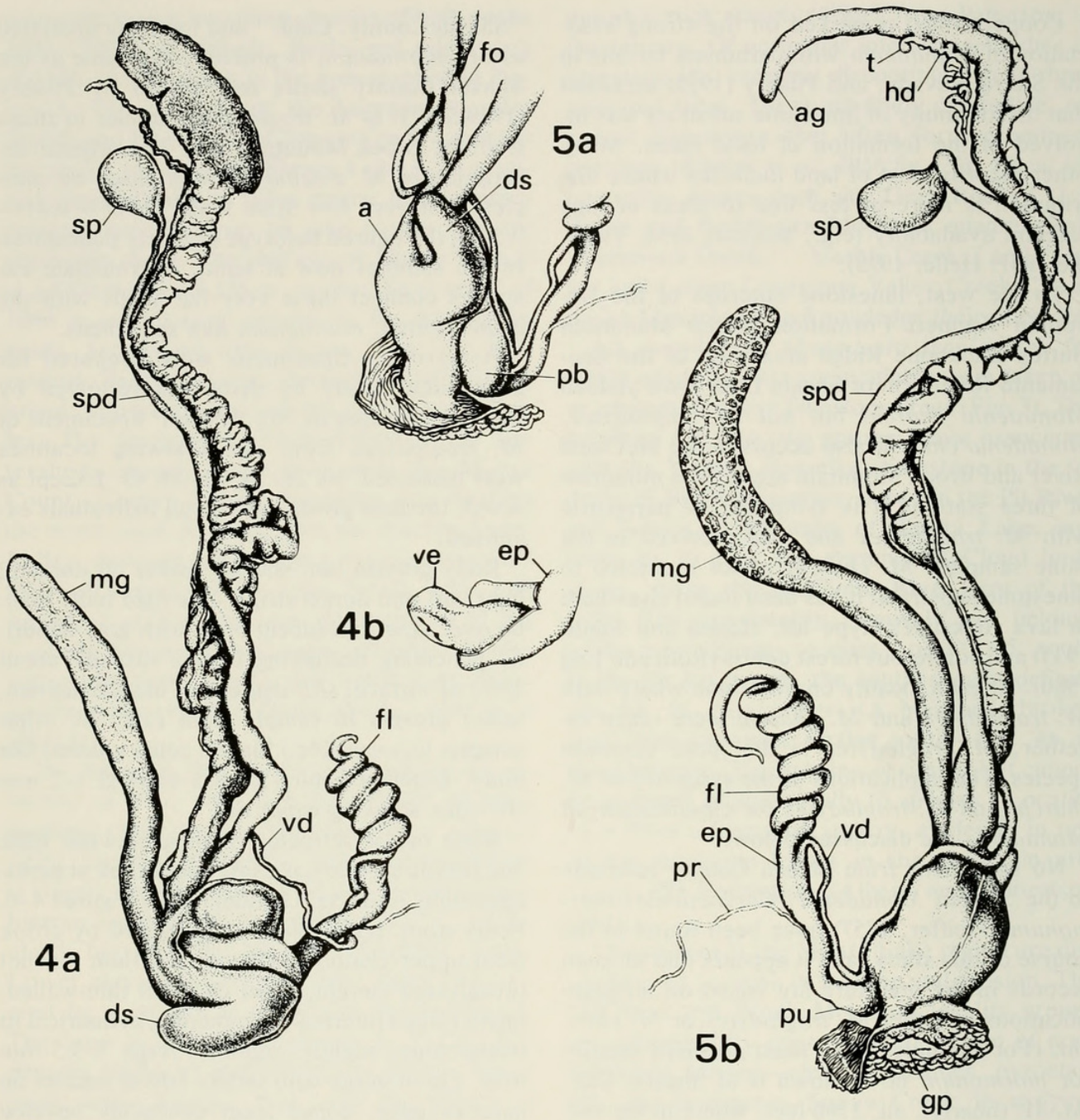
To the west, limestone outcrops of the Devonian Kennett Formation in the Mammoth Buttes–Backbone Ridge area west of the Sacramento River arm of Shasta Lake have yielded *Monadenia churchi* but not *M. troglodytes*. *Monadenia churchi* also occurs in the McCloud River and Brock Mountain areas. At a minimum of three stations it is sympatric or parapatric with *M. troglodytes* and was received in the same samples. *M. churchi* is not restricted to limestone substrata; it has been found elsewhere in lava rockslides (type lot; Hanna and Smith 1933) and coniferous forest debris (Roth and Eng 1980). At each locality on limestone where both *M. troglodytes* and *M. churchi* were taken together, *M. troglodytes* is the more common species. The implications of the sympatry of *M. churchi* and *M. troglodytes* for classification of *Monadenia* are discussed below.

No specimens from Shasta County referable to the Sierran *Monadenia* (*Corynadenia*) *mormonum* (Pfeiffer, 1857) have been found in the course of this study, and it appears that all such records in the literature are based on misidentifications of either *M. troglodytes* or *M. churchi*. (For example: "The most northern locality for *mormonum* now known is at Shasta, Cal., lat. 41° (nearly), alt. 1160 feet, where in the volcanic region Dr. Yates found a very few stunted specimens with but five and a half whorls and the bristle-granulations of the young very strongly developed" [Cooper 1879:285]. "In Shasta County, far north of the localities mentioned, a race of *mormonum* has been found in the Upper Sonoran Zone at and near the junction of the Pitt [*sic*] with the Sacramento river (Brewer, Gabb). They agree with the typical form in the absence or extreme faintness of spiral striae and in coloration; the shell is smaller and the spire generally higher. They are within the area of *M. churchi*" [Pilsbry 1939:56].) A lot collected in the nineteenth century, UCMP 2491, *ex* D. O. Mills collection no. 290, labeled "Shasta County, Calif." and formerly identified as *M. mormonum*, is probably the same as the Shasta County shells referred to by Pilsbry (1939:56). It is *M. troglodytes*, similar to those from the Brock Mountain area. The original description of *M. troglodytes* was based on samples with very low spire index (H/D = 0.411–0.500); the figured holotype is nearly planispiral. In the samples now at hand, intermediate examples connect these very flat shells with the higher-spired, *mormonum*-like specimens.

ANATOMY.—Specimens were prepared for anatomical study by drowning followed by transfer in stages to 70% ethanol. Specimens of *M. troglodytes* from the following localities were dissected: 10, 26, 28, 34, 39, 43. Except as noted, the data given apply to all individuals examined.

Body grayish tan, shaded darker on dorsum; light buff mid-dorsal stripe; sole light buff. Mantle over lung translucent buff, with gray dendritic pencilling occupying 0–35% (usually about 20%) of surface. (All degrees of mantle pigmentation present in sample from Loc. 10; other samples less variable.) Mantle collar colored like body. External genital pore a vertical 1–2 mm slit often showing white rim.

Right ocular retractor running between male and female systems, passing over crook at penis-epiphallus junction. Genitalia as in Figures 4–6. Penis stout, basal chamber separated by crook from upper chamber, adnate to atrium but not invaginated therein; upper chamber thin-walled, finely ridged internally, containing cylindrical to ovate-conic, slightly rugulose verge 3–3.5 mm long. Tip of verge with slitlike lateral meatus on anterior edge, dorsal facet concavely beveled (Fig. 4*b*). (End of verge of specimens from Loc. 43 blunt, as broad or broader than stalk, with flaplike expansion of tip opposite meatus.) Wall of upper penial chamber bearing a single large pilaster that fits against beveled facet of verge and extends into basal chamber. Epiphallus from ½ to ¾ as thick as penis at their junction. Penial retractor (originating on floor of lung) long, narrow, slightly expanded just before insertion on medial part of epiphallus. Flagellum (epiphallic caecum) longer than penis plus epiphallus, as thick as epiphallus, borne in 4 to 7 helical coils; distal end tapering to fine point. Vas deferens with 2–3 convolutions where it passes under atrium. Spermatheca (bursa cop-



FIGURES 4–5. Genitalia of *Monadenia troglodytes*. Figs. 4*a–b*. *M. t. troglodytes*; (*a*.) dorsal aspect, Loc. 28, atrium rotated 90° downward with respect to oviduct; (*b*.) detail of verge, Loc. 10. Figs. 5*a–b*. *M. t. wintu*, n. subsp., holotype CAS 018431, Loc. 34; (*a*.) dorsal aspect; (*b*.) ventral aspect. Abbreviations: *a*—atrium; *ag*—albumen gland; *ds*—dart sac; *ep*—epiphallus; *fl*—flagellum; *fo*—free oviduct; *gp*—external genital pore; *hd*—hermaphroditic duct; *mg*—mucus gland; *pb*—basal chamber of penis; *pr*—penial retractor muscle; *pu*—upper chamber of penis; *sp*—spermatheca; *spd*—duct of spermatheca; *t*—talon (fertilization pouch); *vd*—vas deferens; *ve*—verge.

ulatrix) globose; spermathecal duct long, straight, unbranched, capacious for lower three-fourths, narrower below spermatheca. Dart sac small to moderate-sized, sessile at convergence of two atrial crura which, when everted, form a copulatory pad or disk (Fig. 7); sac containing a 2-mm, tubular, calcareous dart. Mucus gland large, bent near middle, lower portion adnate to atrium and running along lower edge of superior atrial crus to insertion at base of dart sac.

Measurements of selected organs are given in Table 2. All show considerable variation. There appears to be no systematic difference between samples except that those from the Brock Mountain area tend to have more coils to the epiphallus.

TABLE 2. LENGTHS (in mm) OF SELECTED ORGANS OF *Monadenia troglodytes* AND *M. churchi* (range, with sample mean in parentheses).

	M. t. troglodytes		*M. t. wintu*		*M. churchi*	
Loc. (n)	10 (6)	43 (5)	34 (3)	45 (1)	Mammoth Butte (3)	29 (1)
Free portion of mucus gland	16.0–21.2 (18.82)	10.9–21.0 (17.12)	16.1–30.0 (21.0)	15.7	15.7–18.1 (16.77)	17.3
Dart sac	2.6–4.5 (3.18)	2.1–2.4 (2.33)	2.5–3.2 (2.87)	2.1	1.8–2.7 (2.23)	1.9
No. of coils of flagellum	3.5–5 (4.13)	3.5–5 (4)	5–7 (6)	5	3.5–4 (3.67)	6
Free (upper) chamber of penis	3.3–4.8 (3.55)	3.4–4.7 (3.84)	3.7–4.6 (4.23)	4.0	3.5–3.6 (3.6)	3.5
Epiphallus	5.6–8.7 (7.93)	5.7–8.6 (6.72)	8.4–8.9 (8.63)	8.1	5.2–6.5 (5.63)	6.6
Base of epiphallus to insertion of penial retractor	2.6–4.9 (4.07)	2.9–4.1 (3.5)	3.5–4.7 (4.03)	4.1	2.2–3.2 (2.7)	2.6

In their exserted state the atrial crura form a copulatory pad (Fig. 7). The female genital pore is located on the bottom of the pocket between the two crura. The male opening, through which the verge is exserted, is located near the middle of the forward edge of the anterior crus. The pore of the dart sac is at the convergence of the crura; further eversion of the dart apparatus was not observed.

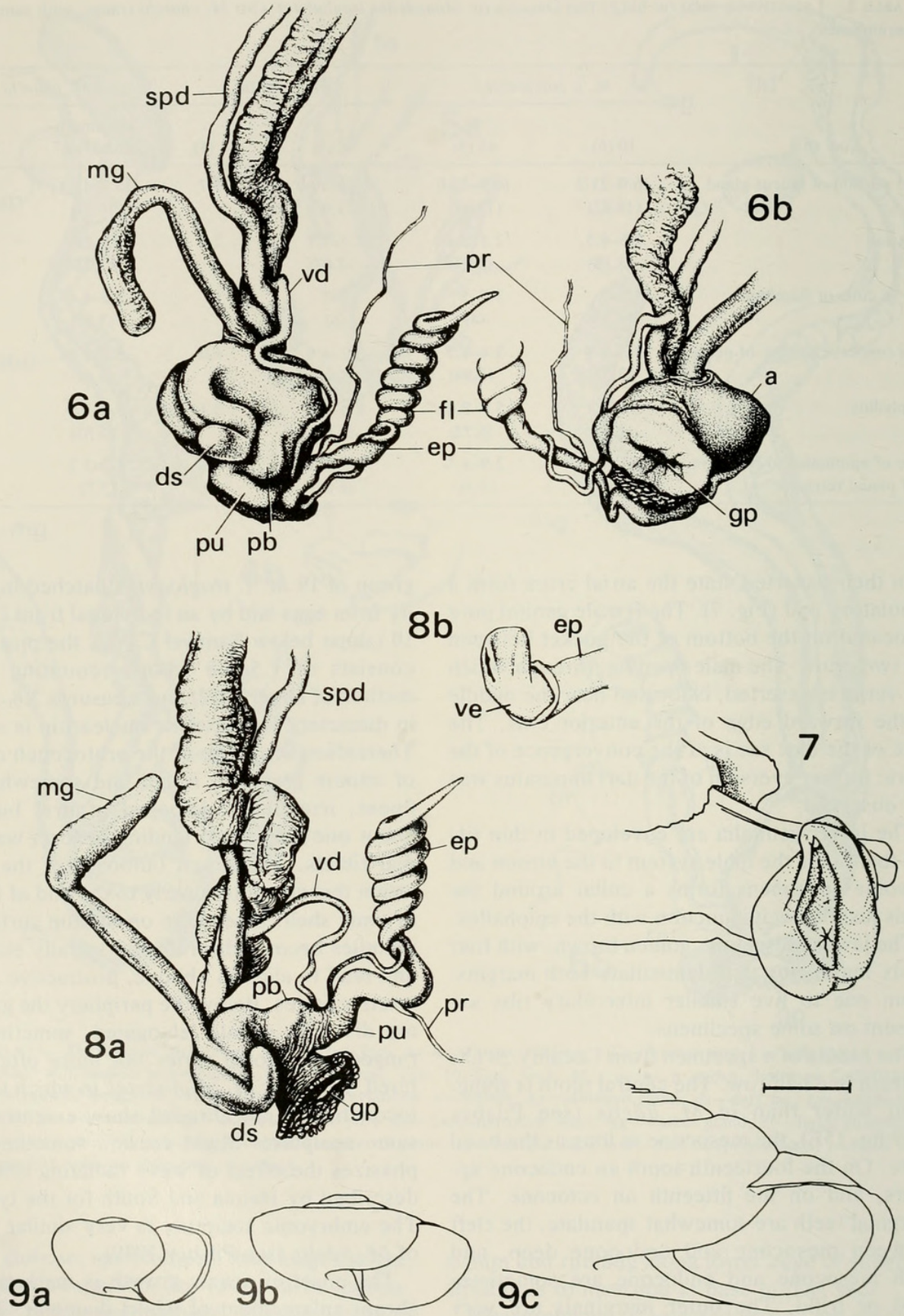
The lower genitalia are enveloped in thin tissue that binds the male system to the atrium and in some specimens forms a collar around the penis just below its junction with the epiphallus.

The jaw is crescentic, golden brown, with four to six major ribs that denticulate both margins. From one to five smaller intercalary ribs are present on some specimens.

The radula of a specimen from Locality 28 has 41 teeth in a half row. The central tooth is somewhat wider than in *M. fidelis* (see Pilsbry 1939:fig. 15E), the mesocone as long as the basal plate. On the fourteenth tooth an endocone appears, and on the fifteenth an ectocone. The marginal teeth are somewhat spatulate, the cleft between mesocone and endocone deep, and both mesocone and endocone are sometimes bifid or trifid. The outer marginals are very short.

SHELL CHARACTERS AND VARIATION.—Hanna and Smith (1933) described the protoconch of *Monadenia troglodytes* as consisting of 1½ whorls marked by wavy radiating riblets. In a group of 19 *M. t. troglodytes* hatched in captivity from eggs laid by an individual from Locality 10 (slope below Samwel Cave), the protoconch consists of 1.5–1.8 whorls (counting by the method of Diver 1932) and measures 2.8–3.5 mm in diameter. The extreme nuclear tip is smooth. Thereafter, sculpture of the protoconch consists of minute granules, round and somewhat confluent, irregularly disposed at first but after about one half whorl tending to form wavy, radial riblets. Those just outboard of the suture retain this character nearly to the end of the embryonic shell. Elsewhere on the top surface the granules become discrete and spirally elongated and tend to align in oblique, protractive and retractive series. Below the periphery the granules are discrete, spirally elongated, sometimes arranged in diagonal series but more often scattered. All other *M. troglodytes* in which the protoconchs are not abraded show essentially the same sculpture. Slight erosion sometimes emphasizes the effect of wavy radiating riblets, as described by Hanna and Smith for the type lot. The embryonic sculpture is very similar to that of *M. fidelis* (see Pilsbry 1939).

The onset of neanic growth is marked by an abrupt enlargement of whorl diameter. The intensity of surface granulation on early neanic whorls is less than that on the protoconch; the granules are sometimes obscure or localized in a few patches. Irregular, axial growth ridges are the dominant sculptural feature. Between these



FIGURES 6–9. Figs. 6*a–b*. Genitalia of *Monadenia troglodytes wintu*, n. subsp., Loc. 45; (*a*.) dorsal aspect; (*b*.) ventral aspect, atrium partially everted. Fig. 7. Copulatory pad of *M. t. wintu*. Figs. 8*a–b*. Genitalia of *Monadenia churchi*, Loc. 29. (*a*.) dorsal aspect; (*b*.) detail of verge. Figs. 9*a–c*. Ontogenetic shape change in *Monadenia troglodytes troglodytes*, Loc. 10. Scale line = 5 mm for Fig. 9*a*, 10 mm for Figs. 9*b*, 9*c*. Abbreviations as in Figs. 4–5.

ridges there is an extremely fine, wrinklelike, parallel lineolation, particularly evident on the base. Closely set, wavy, spiral striation appears on the base, usually by the end of the first postnuclear whorl. These striae are irregular in both strength and spacing.

Variably expressed, these elements—granulation, growth rugae, wrinkle-lineolation, and spiral striae—constitute the microsculpture of adult shells. When not pitted or breached by erosion, the periostracum is smooth and glossy; in adult shells it is often scratched and abraded on base and spire. Fine, wavy, spiral striation on the base is apparently standard but frequently removed by abrasion. On some shells, stronger, incised striae occur on the shoulder of the last whorl and may be prominent behind the lip.

After about the three-whorl stage, granulation is rare below the shoulder. It persists on the spire for a varying number of whorls, usually becoming sparser with ontogeny, the granules becoming lower, more elongate, and less clearly defined until, in some cases, they finally merge into the general undulation of the periostracal surface. In most instances, however, granulation stops at or near a growth rest, and when growth is resumed the granules are few, irregular, or absent.

The last granulose whorl varies from locality to locality (Fig. 10), and there is a half-whorl to two-whorl range in all samples large enough for consideration. The means of the last granulose whorl increase in populations from north to south along the McCloud River. (Far to the north, *M. t. chaceana* has a mean of 1.83 granulose whorls, seemingly continuing the cline.) Variation in the Brock Mountain herd is less obviously clinal: the westernmost samples, Localities 34 and 35, have few granulose whorls ($\bar{x}$ = 2.38 and 2.10, respectively); the few measurable shells from the more eastern localities 33, 38, 40, and 41 are in the 2.5–3.5 whorl range; and Locality 39, situated geographically amid the other eastern localities, has a predominance of shells pustulose at 4.5 whorls and beyond ($\bar{x}$ = 4.17). Locality 45, south of Shasta Lake, also has populations whose granulation persists onto the later whorls ($\bar{x}$ = 3.73). The difference in number of granulose whorls between the McCloud River and Brock Mountain locality groups is highly significant ($P < 0.001$).

In hatchlings, the protoconch is golden tan;

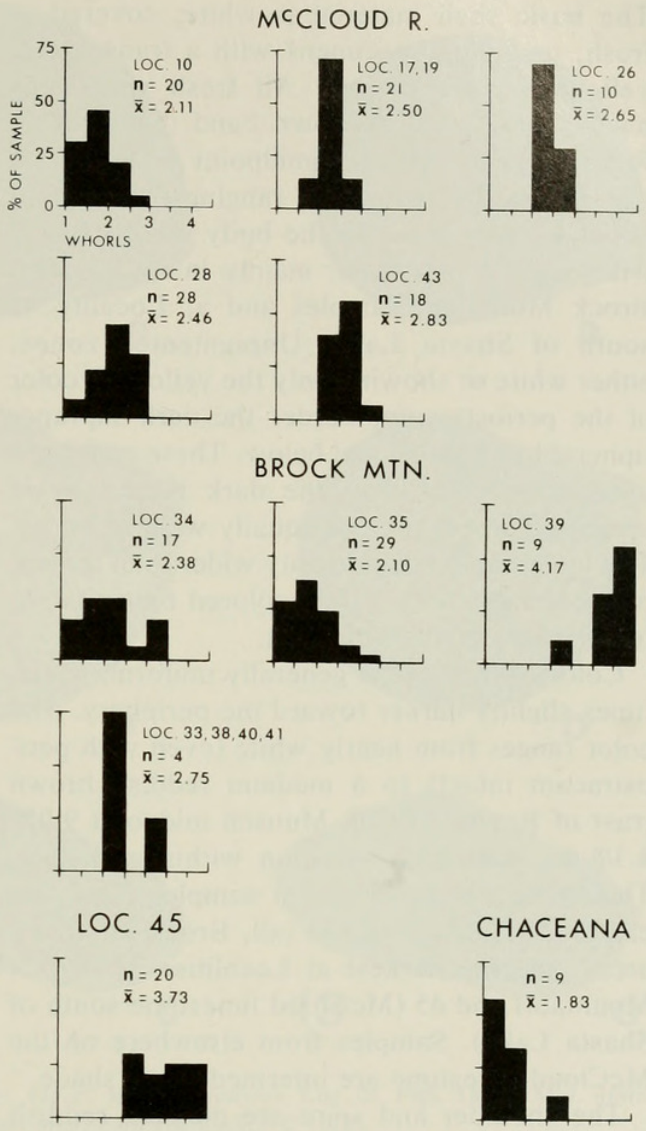


FIGURE 10. Histograms of last granulose whorl (to the nearest half whorl) in *Monadenia troglodytes* samples from along the McCloud River (*M. t. troglodytes*), Brock Mountain region and Loc. 45 south of Shasta Lake (*M. t. wintu*, n. subsp.), and Siskiyou County (*M. t. chaceana*).

some show a faint reddish-brown spiral band at the periphery of the last half whorl. From the first, the teleoconch shell material is lighter tan than the protoconch. Beginning with the first neanic whorl, narrow whitish zones border the reddish-brown band above and below, the lower zone seeming to appear earlier than the upper. Gradually the narrow band becomes darker and more prominent, partly by contrast with the increasing whitish opacity of the rest of the shell. The advancing suture partly or wholly obscures the band.

Color of adult *Monadenia troglodytes* is variable, although fairly uniform within a sample.

The basic shell material is white, covered in fresh, uneroded specimens with a transparent, yellowish periostracum. All fresh specimens have a dark reddish-brown band (chestnut of Rayner [1970]; Munsell midpoint 9.5R/2.3/3.8) just above the periphery, ranging from 0.5 to about 1.5 mm wide on the body whorl. Bands wider than 1 mm occur mainly in the eastern, Brock Mountain, samples and at Locality 45 south of Shasta Lake. Unpigmented zones, either white or showing only the yellowish color of the periostracum, border the dark supraperipheral band above and below. These zones are usually narrower than the dark band, but in some instances they are equally wide or wider. The lower zone is commonly wider than the upper; on shells with a light-colored base, its anterior edge may be indistinct.

Color of the base is generally uniform, sometimes slightly darker toward the periphery. The color ranges from nearly white (even with periostracum intact) to a medium reddish brown (rust of Rayner [1970]; Munsell midpoint 9.0R/4.3/8.0), with little variation within a sample. The lightest bases occur in samples from Localities 35, 38, 40, and 41 (all, Brock Mountain area); and the darkest at Localities 39 (Brock Mountain) and 45 (McCloud limestone south of Shasta Lake). Samples from elsewhere on the McCloud limestone are intermediate in shade.

The shoulder and spire are medium reddish brown, as dark as or darker than the base. They are never as dark as the supraperipheral band. The darkest spires occur in the Brock Mountain area and the lightest along the McCloud River. In both groups there is a tendency for the center of the shoulder to be lighter, producing a shadowy secondary banding that is most evident on the lighter shells of the McCloud River herd. The secondary banding is never as distinct as that in *Monadenia fidelis* (see Talmadge 1960; his "multibanded phase"). One other color effect is observable: some individuals have radial streaks of darker pigment on the shoulder. These streaks usually precede a growth rest and evidently represent concentrated pigment deposition at times when shell growth is slowing down. They are often followed by a whitish radial streak (as growth starts up again rapidly?). When combined with secondary banding, as in some McCloud River shells, the streaks produce a mottled effect.

It seems likely that the same shell pigment, in various dilutions, produces the supraperipheral band, base, and shoulder coloration.

The expanded lip of adult specimens is white.

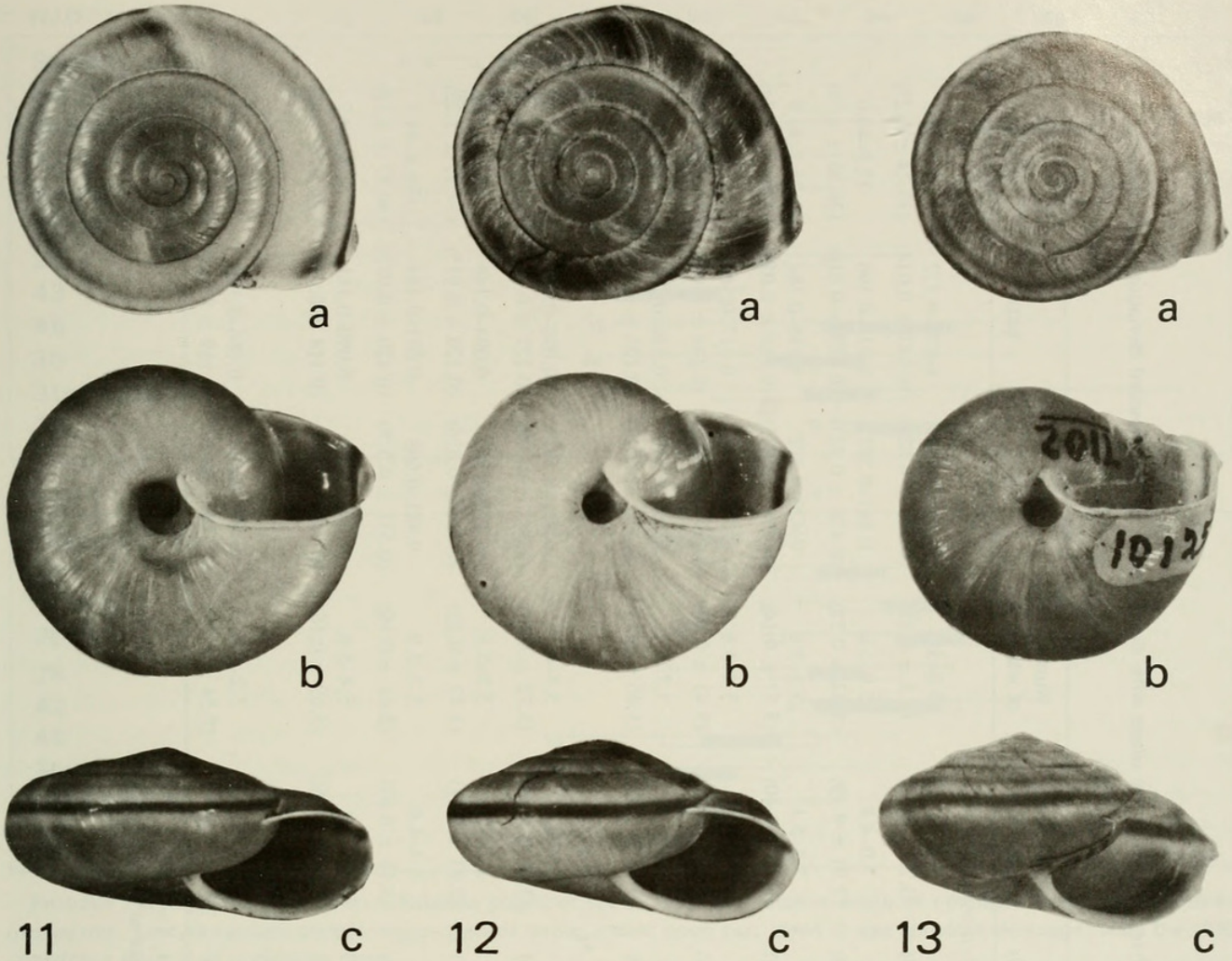
Color variation in *M. troglodytes* segregates geographically: populations in the Brock Mountain area have the darkest spires, both the darkest and the lightest bases, and the broadest bands near the periphery. Populations along the McCloud River have the lightest-colored shells and the greatest incidence of secondary banding and mottling.

In the course of ontogeny, the shell of *Monadenia troglodytes* undergoes several significant changes in shape. The protoconch—that portion of the shell which forms within the egg—is almost hemispherical, with nearly flat spire and deeply convex base. Gould (1969) suggested that mechanical limitations of space within the egg largely determine protoconch shape in the zonitid snail *Poecilozonites*, and in fact, the protoconch of *M. troglodytes* is shaped very much like that of *Poecilozonites bermudensis bermudensis* (Gould 1969:pl. 6, figs. 6, 7).

Post-embryonic juvenile shells are wide, flat- to low-spired, angulate at the shoulder, and tumid at the base. Again as in *Poecilozonites*, postembryonic growth begins with a marked increase in relative width. As growth proceeds, the whorl changes in cross section (Fig. 9) from crescentic and taller than broad, in the embryonic shell, to auriculate and broader than tall in the adult. Also with growth, the periphery, which is above the middle in juvenile shells, migrates downward until it is medial in adults and changes gradually from angulate to rounded.

Spire height increases allometrically with respect to shell diameter, producing a domed spire. Since from about the third whorl on, the height-diameter ratio of the shell remains practically constant, the allometry is due chiefly to the downward migration of the periphery.

In *Monadenia*, as in most other helicacean snails, growth is determinate. The shell enlarges up to a point, generally coincident with sexual maturity, when the lip is thickened and turned outward. Thereafter, no additional spiral growth takes place. In *M. troglodytes*, the greatest absolute height of aperture and often the greatest total shell height are achieved one-half to one-quarter whorl before the cessation of growth. For the last quarter turn, translation along the



FIGURES 11–13. Shells of *Monadenia troglodytes*, ×1.5. Figs. 11*a–c*. *M. t. troglodytes*, Loc. 26. Figs. 12*a–c*. *M. t. wintu*, n. subsp., holotype CAS 018431, Loc. 34. Figs. 13*a–c*. *M. t. chaceana*, paratype CASGTC 10125.

vertical axis is halted or reversed, and at the same time, the whorl is compressed apico-basally. The final 3–4 mm increment of growth strikes downward at about a 30° angle to the suture, bringing the peristome nearly into tangency with the face of the body whorl. Similar terminal growth occurs in many genera of helicacean snails, particularly those from xeric environments. It is presumably an adaptation to enhance the snails' mucous seal to the substratum, in order to retard water loss or exclude predators. The final half-whorl "leap" of growth is most strongly expressed in populations along the McCloud River north of Shasta Lake and contributes to their generally low height-diameter ratios compared to Brock Mountain populations.

As already noted above, *Monadenia troglodytes* undergoes a much greater range of variation in shape than was evident from the type lot alone. Data on basic shape measurements and indices—height (H), diameter (D), H/D ratio, number of whorls, umbilical width (U), and U/D ratio—are summarized in Table 3. Data from adult shells (those with reflected lip) only are included. Samples were collected without special procedures to insure randomness, but there is no reason to suspect bias with regard to any of the dimensions or ratios used here.

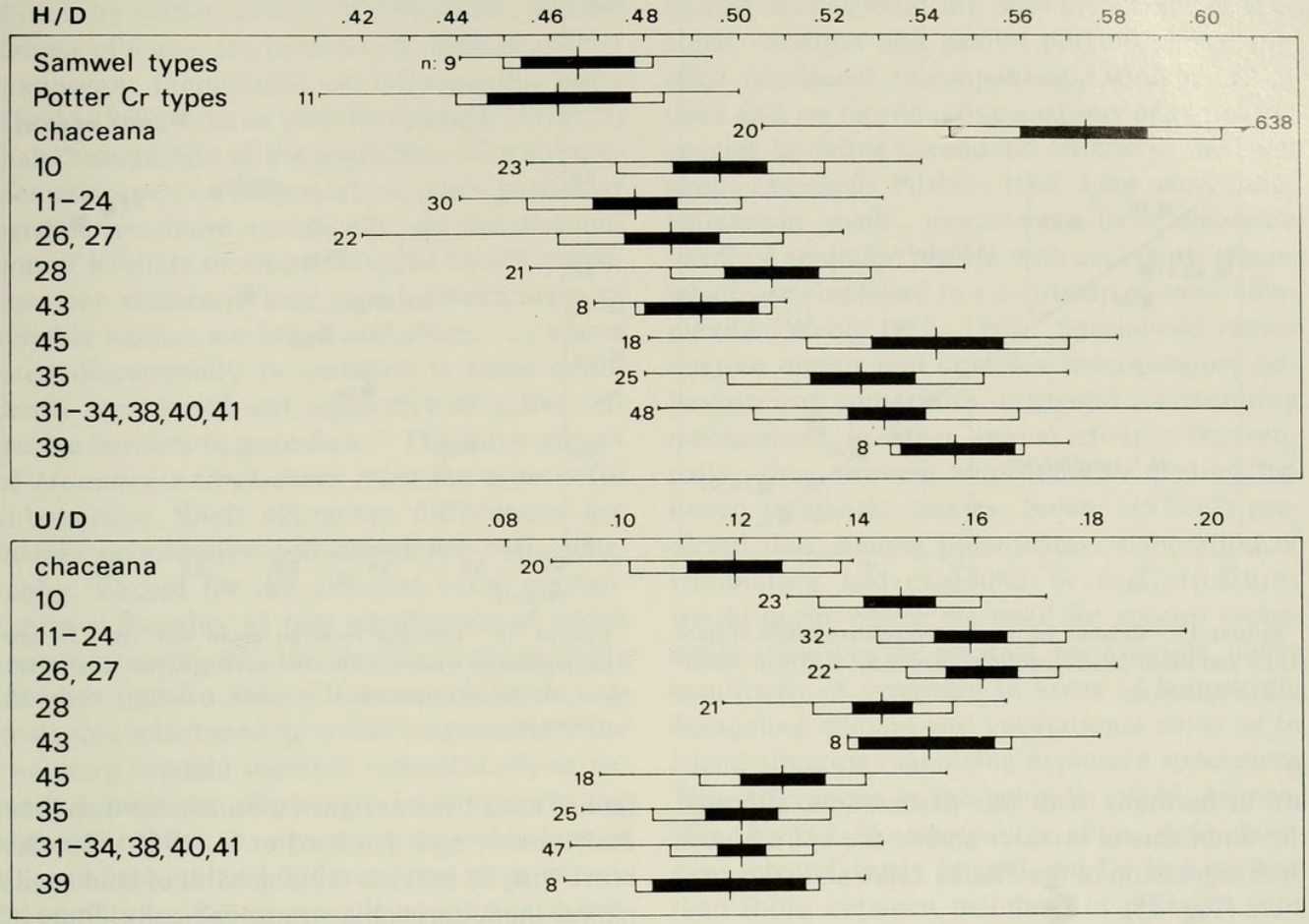
All shells were measured with a hand-held caliper with vernier scale. Height (H) was measured parallel to, and maximum diameter (D) perpendicular to, the axis of coiling of the shell. The expanded lip of adult shells was excluded from these dimensions. Umbilical width (U) is an inside caliper measurement taken parallel to

TABLE 3. SHELL DIMENSIONS (in mm) AND RATIOS IN *Monadenia troglodytes*. Statistics are range with sample mean ± one standard deviation in parentheses. Only adult shells included.

Locality	n	Height (H)	Diameter (D)	Umbilical width (U)	Number of whorls	H/D	U/D	H + D
				M. t. troglodytes				
Slope below Samwel Cave (10)	23	10.0–12.3 (11.01 ± 0.58)	20.9–24.5 (22.23 ± 0.84)	2.8–4.0 (3.27 ± 0.37)	5.0–5.5 (5.3 ± 0.15)	0.455–0.539 (0.496 ± 0.022)	0.128–0.172 (0.147 ± 0.014)	31.5–36.5 (33.24 ± 1.25)
Vicinity of Samwel Cave (11–24)	*	10.2–13.1 (11.75 ± 0.79)	21.9–27.2 (24.65 ± 1.14)	3.0–4.8 (3.91 ± 0.39)	5.0–6.0 (5.42 ± 0.21)	0.441–0.531 (0.478 ± 0.023)	0.135–0.196 (0.159 ± 0.016)	32.1–40.0 (36.36 ± 1.76)
Ellery Creek (26, 27)	22	11.5–14.0 (12.69 ± 0.77)	23.7–28.1 (26.13 ± 1.14)	3.5–5.1 (4.20 ± 0.40)	5.3–5.9 (5.57 ± 0.14)	0.420–0.522 (0.486 ± 0.023)	0.136–0.184 (0.161 ± 0.013)	35.2–41.9 (38.85 ± 1.74)
Dekkas Rock (28)	21	10.1–12.6 (11.62 ± 0.70)	20.6–25.0 (22.95 ± 1.38)	2.5–4.1 (3.32 ± 0.37)	5.2–5.8 (5.41 ± 0.19)	0.456–0.548 (0.507 ± 0.021)	0.117–0.164 (0.144 ± 0.012)	31.6–37.6 (34.57 ± 1.97)
Potter Creek (43)	8	11.3–12.6 (11.81 ± 0.47)	22.8–24.9 (24.04 ± 0.80)	3.2–4.5 (3.66 ± 0.40)	5.2–5.7 (5.46 ± 0.15)	0.469–0.510 (0.492 ± 0.014)	0.140–0.181 (0.125 ± 0.014)	34.3–37.3 (35.85 ± 1.17)
				M. t. wintu				
Calveris cement quarry (45)	18	12.0–15.5 (13.42 ± 1.00)	22.6–27.2 (24.78 ± 1.36)	2.4–3.7 (3.14 ± 0.34)	5.5–6.1 (5.72 ± 0.15)	0.481–0.581 (0.542 ± 0.028)	0.096–0.155 (0.127 ± 0.014)	34.6–42.2 (38.20 ± 2.17)
Above Squaw Creek (35)	25	11.2–14.9 (12.84 ± 0.88)	21.9–27.6 (24.53 ± 1.47)	2.2–3.6 (2.93 ± 0.42)	5.2–5.8 (5.47 ± 0.21)	0.480–0.570 (0.526 ± 0.026)	0.094–0.148 (0.120 ± 0.015)	33.9–42.5 (37.37 ± 2.22)
NE of Brock Mtn (31–34, 38, 40, 41)	**	12.0–16.4 (14.07 ± 1.00)	22.6–29.3 (26.47 ± 1.48)	2.3–4.0 (3.16 ± 0.41)	5.2–5.9 (5.61 ± 0.16)	0.483–0.608 (0.531 ± 0.028)	0.091–0.144 (0.120 ± 0.012)	36.4–44.7 (40.57 ± 2.23)
Above Brock Creek (39)	8	13.0–14.2 (13.60 ± 0.41)	23.6–25.6 (24.91 ± 0.76)	2.3–3.6 (2.94 ± 0.36)	5.4–5.9 (5.69 ± 0.16)	0.529–0.570 (0.546 ± 0.014)	0.090–0.141 (0.118 ± 0.015)	36.8–39.7 (38.51 ± 1.07)
				M. t. chaceana				
Hornbrook and Yreka Quadrangles (1, 4–7)	20	10.5–14.6 (13.34 ± 1.10)	18.0–26.0 (23.27 ± 1.99)	1.7–4.0 (2.77 ± 0.51)	5.2–5.8 (5.54 ± 0.19)	0.506–0.638 (0.574 ± 0.029)	0.088–0.139 (0.119 ± 0.018)	28.5–40.2 (36.61 ± 2.97)

* For H, H/D, H + D, n = 30; for D, U, U/D, n = 32; for number of whorls, n = 29.

** For H, n = 49; for D, H/D, H + D, n = 48; for U, U/D, n = 47; for number of whorls, n = 46.



FIGURES 14*a* (upper), 14*b* (lower). Relative height of spire (H/D) and relative width of umbilicus (U/D) in *Monadenia troglodytes*. Line designates sample range; vertical strike, mean; open bar, mean ± one standard deviation; solid bar, 95% confidence interval of population mean.

the maximum diameter and occasionally required breaking away a portion of the inner lip. Number of whorls was determined, with the use of a binocular microscope, by the method of Diver (1932) except that the final fraction of a whorl was estimated without pencil lines being drawn on the shell. The measurement is rounded to the nearest 0.1 whorl. Pilsbry (1939:xi, fig. B) evidently counted whorls by approximately the same method, although he usually expressed results to the nearest one-quarter or one-third of a whorl and sometimes quoted uncritically the figures of other authors.

The simple measurements of size (H, D, H + D) show that as a group the McCloud River herd averages smaller than the Brock Mountain herd, although there is extensive overlap of ranges in all categories. The smallest averages belong to the samples from Localities 10 (below Samwel Cave) and 28 (Dekkas Rock). Shells of large diameter (and large H + D) occur near Ellery Creek (Locs. 26, 27).

Relative height of spire (H/D) segregates geographically (Fig. 14*a*), with McCloud River shells significantly lower-spired than those from Brock Mountain. As in most other parameters, shells from Locality 45 segregate with the Brock Mountain herd. The U/D ratio, the relative width of the umbilicus, segregates along the same lines (Fig. 14*b*)—not surprisingly, since the two ratios, H/D and U/D, may be aspects of the same variable. A tapering tube of a given size and rate of expansion may be coiled steeply (high rate of translation along coiling axis and small distance of generating curve from axis: Raup 1966) or flatly (low rate of translation, large distance from axis). The first mode generates a high-spired shell with small umbilicus, the second a low-spired shell with wide umbilicus. A correlation coefficient of −0.951 for sample mean H/D and mean U/D further attests to the association between the two parameters in *M. troglodytes* in the Shasta Lake region. The high spire and small umbilicus of *M. t. chaceana*

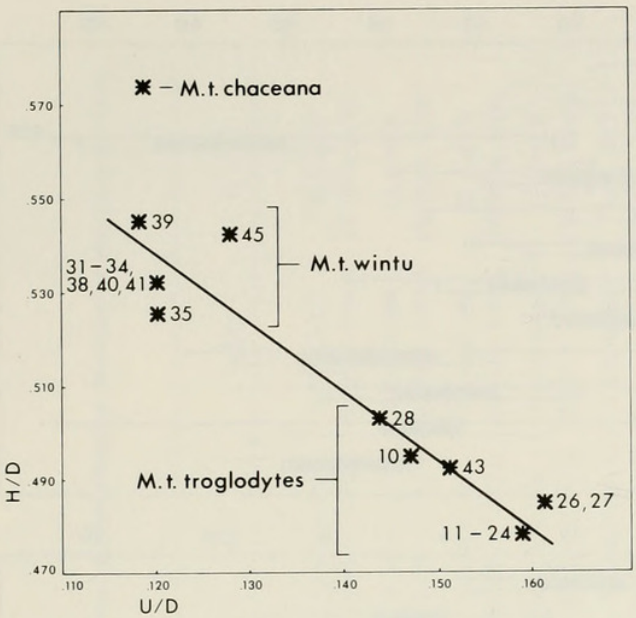


FIGURE 15. Relation between mean relative height of spire (H/D) and mean relative width of umbilicus (U/D) in *Monadenia troglodytes*.

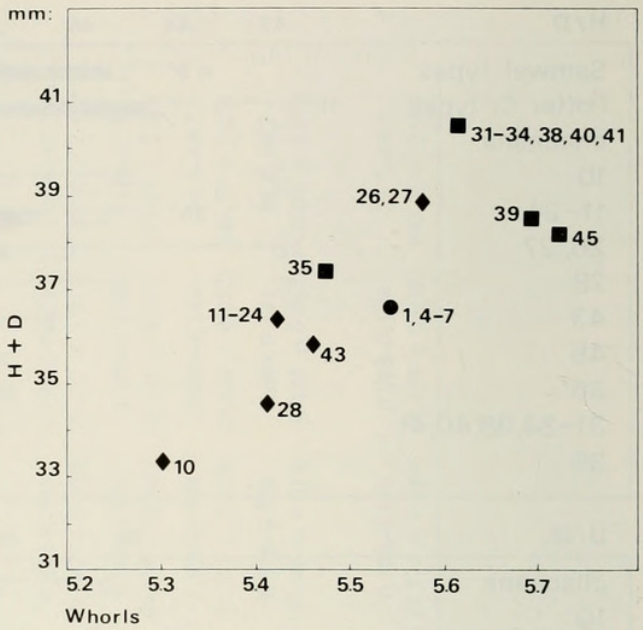


FIGURE 16. Relation between mean size (H + D) and mean number of whorls in *Monadenia troglodytes*. Diamonds, *M. t. troglodytes*; squares, *M. t. wintu*, n. subsp.; circle, *M. t. chaceana*.

are in harmony with this association, although the umbilicus is broader and/or the spire higher than regression of the Shasta Lake statistics predicts (Fig. 15).

Figure 16 plots the relationship between mean size (H + D) and whorl number. Although the scatter of individual (specimen) points overlaps extensively, again there is geographic segregation of means. Locality 45 sorts with the Brock Mountain herd, nearest to the pustulose shells from Locality 39. Mean size and mean whorl number correlate strongly in the McCloud River herd (r = 0.954); the more heterogeneous Brock Mountain herd displays no such tight correlation.

Based on the dimensions given by Hanna and Smith (1933), the type lot of *M. troglodytes* from Samwel Cave and their material from Potter Creek Cave are flatter (lower H/D) than any of the samples here studied. Both the mean diameter and mean H/D ratio of the type lot differ significantly from those of the nearest living sample, from Locality 10. It would be premature, however, to conclude that the difference represents evolutionary change. Hanna and Smith accepted a Pleistocene age for the cave specimens, first because they believed the species extinct and, second, because the shells had been associated with bone deposits. (The Samwel Cave and Potter Creek Cave vertebrate faunas have been assigned a Rancholabrean [late Pleistocene] age; Hibbard et al. 1965.) But the burrowing or crevice-seeking habit of land snails makes them unreliable stratigraphically. State of preservation is not very informative: in the several cave samples now at hand, there are shells in every gradation from slightly dusty to heavily encrusted with calcium carbonate, and there may be a more or less continual influx of shells drifting or washing into the caves. Independent evidence of age, such as radiometric dating, and collections with good stratigraphic control are needed before one can place the cave samples in a time framework.

SYSTEMATICS

TAXONOMIC CRITERIA IN *Monadenia*.—Individuals of *Monadenia troglodytes* in the Shasta Lake region group strongly into two geographic units based on shell color and texture, microsculpture, and morphometry. *Monadenia chaceana* constitutes a third such unit. Although its internal anatomy is not yet known, its shell characters are highly similar to *M. troglodytes*, and it is thus given coordinate rank with the latter two groups.

The subspecies category has been employed somewhat unevenly in terrestrial malacology. Early workers responded to the manifold variability of some tropical snail groups, for in-

stance, by naming dozens of subspecies, and the morass of names led in turn to a reaction against taxonomic recognition of infraspecific units (Gould 1969). I agree with Kavanaugh (1979:93) that "recognition of the usefulness of a subspecies concept . . . [depends] on one's particular perspective; more specifically, on the distribution of habitats or areas occupied by the organisms one studies. Where gaps between areas of suitable habitat are broad and clear, . . . correlated discontinuity in variation is more confidently recognized and suggestive of active, effective barriers to gene flow." The three groups of *Monadenia troglodytes* meet the criteria for subspecies. Shell character differences are mainly quantitative and correlated with geography. Except for the different verge configuration at Locality 43 (the significance of which remains unresolved), the identity of the genitalia between the two Shasta Lake region herds suggests that interbreeding would be possible if the two were brought together sympatrically in nature. Limestone substratum is apparently the required habitat, its absence a probable barrier to gene flow, at least under present environmental conditions. Rivers are at least short-term barriers, but over the long term may be important agents of dispersal. The population at Locality 45 may well have been established by riverborne waifs rafted down the Pit River—perhaps from the population of Locality 39, with which it groups morphologically (Figs. 10, 14–16). Clinal variation in granulation along the McCloud River arm suggests incomplete genetic isolation between those localities. Populations on the McCloud limestone, exclusive of Locality 45, constitute one unit; since it includes the type-locality, this unit is the nominate subspecies, *Monadenia* (*Shastelix*) *troglodytes troglodytes*. Populations between the Pit River and Squaw Creek arms of Shasta Lake, and the southern population at Locality 45, are named as a new subspecies below.

The sympatric or parapatric occurrence of *Monadenia churchi* and *M. troglodytes* at several localities in the Shasta Lake region should, theoretically, permit an estimate of the degree of morphologic difference that can be expected between species of the genus, and by analogy aid in ranking allopatric taxa. Reproductive structures are particularly suitable for such an analysis, because a major difference in genitalia (taking into account the possible effects of seasonal variation and genital polymorphism) implies functional incompatibility. Solem (1975) used data on reproductive anatomy of sympatric species to define taxonomic criteria in the snail genus *Oreohelix* Pilsbry, 1904. Like many other helicacean snails, monadenias have elaborate terminal genitalia, replete with accessory organs which are employed in a courtship of some complexity (Webb 1952, 1966). Specialized reproductive organs and complex precopulatory behavior are sometimes regarded as isolating mechanisms in other animal groups; theoretically, they prevent unproductive mating between sympatric species. Solem (1978:67) predicted that, among pulmonates, elaboration of stimulatory and glandular or dart structures would occur where the need for species recognition signs was the greatest, for example, under conditions of sympatry in areas of historically fluctuating climate and vegetational cover or in island situations involving explosive speciation. The differences in the genitalia of *M. churchi* (Fig. 8) and *M. troglodytes* (Figs. 4–6), however, are relatively limited and far less marked than those between members of different subgenera.

The values for organ lengths in *M. churchi* (Table 2) fall mostly within the range of variation of *M. troglodytes*. The dart sac averages smaller in *M. churchi*, but the size range overlaps that of *M. troglodytes*. Length of the mucus gland is highly variable in both species and may vary according to recency of copulation. *M. churchi* from Mammoth Butte, west of Shasta Lake, and others from the Trinity River drainage have a thin, cylindric verge with the end squared and compressed, the meatus transverse. The verge of a specimen from near Campbell Creek on the east side of the McCloud River arm (Loc. 29) is also squared at the tip but thicker, with lateral meatus and concave facet as in *M. troglodytes* (Fig. 8*b*). All specimens examined have a single large pilaster in the penial chamber. It appears, therefore, that reproductive anatomy in *Shastelix* is too variable and too weakly differentiated to offer reliable characters for diagnosis.

The two species are much more readily distinguished on shell characters: *M. churchi* has strong, pustulose microsculpture over the entire shell, even when adult; a dull periostracal surface; and uniform brown color on base and

spire. Quantitative differences, not always present but usually helpful in distinguishing the two species, include higher spire, stronger growth rugae, and more tightly coiled last whorl.

I have detected no systematic conchological differences between *M. troglodytes* found with *M. churchi* and those occurring alone. In each case the *M. troglodytes* shells retain the standard characters of their herd. On the other hand, *M. churchi* from within the range of *M. troglodytes* tend to be larger, shinier, more inflated, and less densely pustulose than specimens from elsewhere. Whether this apparent convergence with *M. troglodytes* goes beyond independent geographic variation will be examined in a later paper.

The finding that in reproductive anatomy *M. churchi* and *M. troglodytes* differ from each other chiefly in verge shape also implies that the elaborations of the female side of the genital system—dart sac, copulatory pad, etc.—may not be involved in species recognition during courtship or maintenance of reproductive isolation. According to the sexual selection model of Charnov (1979), hermaphroditic animals may copulate not so much to gain sperm to fertilize eggs as to give sperm away (to gain access to another's eggs). "There must often exist a conflict of interest between mating partners—as a recipient each should be inclined to accept sperm (not necessarily for fertilization of its own eggs) in order to give its sperm away" (Charnov 1979:2482). In order to pair with and fertilize a partner, a *Monadenia* may have to display its own *apparent* receptivity to the partner's sperm. Like any character that individuals use to choose sperm donors, the organs involved in such a display would be subject to exaggeration through time. Selective pressure toward species-specific differentiation of the organs would depend on (1) frequency of the opportunity for interspecific mating, based both on degree of sympatry and the effectiveness of other organ or behavior systems in maintaining isolation; and (2) relative fitness of resulting hybrids.

Monadenia (Shastelix) troglodytes troglodytes Hanna and Smith

(Figures 4*a–b*, 9*a–c*, 11*a–c*)

Monadenia troglodytes Hanna and Smith, 1933:84–85, pl. 5, figs. 6–8.—Pilsbry 1939:54, fig. 22(6–8).—Smith 1957:26; 1970:40.—Walton 1970:111.—Roth 1972a:7; 1972b:7; 1979:13.

Original Description.—"Shell light buff, medium size, widely umbilicate; spire greatly depressed; whorls 5½ with moderately deep suture; the last whorl slightly depressed near the aperture; outer margin expanded very little, the basal margin somewhat more so; one pale brown spiral band appears just above the periphery, which is bounded above and below by white bands that are slightly wider; surface without markings except growth lines; nucleus consisting of 1½ whorls marked by radiating wavy riblets. Diameter 24.2; altitude 10.8 mm" (Hanna and Smith 1933). This description was repeated by Pilsbry (1939).

Type Material.—**Holotype:** UCMP 32394 (shell): California: Shasta County: Samwel Cave (UCMP loc. 1008).

Paratype: CASGTC 5842 (shell); same locality as holotype.

Referred Material.—California: Shasta County: Bollibokka Mountain Quadrangle: Loc. 8 [2 specimens], 9 [5], 10 [32], 11 [6 in addition to holotype and paratype], 12 [2], 13 [2], 14 [2], 15 [2], 16 [1], 17 [4], 18 [2], 19 [31], 20 [2], 21 [6], 22 [1], 23 [2], 24 [9], 25 [2], 26 [30], 27 [5], 28 [38], 29 [3]. Lamoine Quadrangle: Loc. 42 [1], 43 [22], 44 [12], 47 [1], 48 [1]. Figure 3 maps these localities.

Discussion.—As described above in the section on geographic variation and graphically shown in Figures 14–16, *M. t. troglodytes* has the lowest-spired and most broadly umbilicate shells of any subspecies. The shells average smaller than those of the Brock Mountain herd (*M. t. wintu*, next described), but large shells occur near Ellery Creek. The lightest-colored shells and the greatest incidence of secondary banding and mottling occur in *M. t. troglodytes*. The nominate subspecies tends to have fewer coils to the epiphallus than *M. t. wintu*.

Monadenia (Shastelix) troglodytes wintu, new subspecies

(Figures 5*a–b*, 6*a–b*, 7, 12*a–c*)

Diagnosis.—*M. troglodytes* with moderately high spire (sample mean H/D = 0.526–0.546), shell solid, lustrous, shoulder reddish brown, strong white zones above and below brown supraperipheral band, base either nearly white, or reddish brown, as dark as shoulder. Granulation often persisting past third whorl.

Description.—Shell of moderate size for the genus, solid, moderately to distinctly thick, lustrous; spire convexly conic, moderately elevated; whorls 5.2–6.1 in adult, tightly coiled; body whorl slightly expanded over last ½ turn. Protoconch of 1.5–1.9 whorls, nuclear tip smooth,

followed by fine granulation tending to form wavy, radial riblets below suture; granules elsewhere spirally elongated, in diagonal series or irregularly scattered. Early neanic whorls less densely granulated, granulation becoming sparser with growth, usually persisting past the 2.5-whorl stage and often past the 3-whorl stage in at least some members of each sample. Body whorl sculptured with fine growth rugae and microscopic, wavy, parallel, spiral lineolation, most evident behind lip. Juvenile shells with base tumid, spire low, shoulder angulate; periphery becoming first obtusely angular and finally rounded with maturity. Base of adult shells rounded, umbilicus open, steep-walled, diameter 0.090–0.155 times major diameter of shell. Last 3–4 mm of body whorl striking downward at about 30° angle to suture. Aperture broadly auriculate, apico-basally compressed, oblique. Peristome slightly thickened, everted; inner lip covering 10–25% of umbilicus. Color of spire and shoulder medium reddish brown (rust of Rayner [1970]; Munsell midpoint 9.0R/4.3/8.0); dark reddish brown (chestnut of Rayner [1970], Munsell midpoint 9.5R/2.3/3.8) band just above periphery, 1–1.5 mm wide in adult, bordered above and below with white or light tan zones, upper zone either narrower or about as wide as brown band, lower zone usually as wide or somewhat wider; base whitish with light tan suffusion or (at some localities) reddish brown as dark as shoulder. Periostracum smooth, colorless or very light yellowish tan. Dimensions: holotype, height 12.8 mm, diameter 25.1 mm, diameter of umbilicus 3.0 mm, 5.6 whorls; largest paratype (Loc. 35), height 14.9 mm, diameter 27.6 mm, diameter of umbilicus 2.9 mm, 5.6 whorls. Dimensions of other referred material summarized in Table 3.

Body of animal dove gray to sooty black with a reddish or purplish cast, darker on dorsum; light mid-dorsal stripe; sole light buff with gray margin. Mantle over lung translucent buff with gray pencilling covering less than 10% of surface. Genitalia (Figs. 5, 6) as in typical subspecies.

Jaw as in *M. t. troglodytes*. Radula substantially as in *M. t. troglodytes*, with 42 teeth in a half row (Locs. 34, 45), an endocone developed on tooth 21 (Loc. 34) or 14 (Loc. 45), an ectocone on tooth 22 (Loc. 34) or 17 (Loc. 45). Bifid and trifid endocones occur sporadically.

TYPE MATERIAL.—**Holotype:** CAS 018431 (shell, radula, and soft parts); CALIFORNIA: Shasta County: NW¼ NE¼ sec. 8, T. 34 N, R. 2 W, USGS Bollibokka Mountain Quadrangle (15-minute Series [Topographic]; ed. 1957), cave between two limestone buttes at south end of Gray Rocks, above Pit River arm of Shasta Lake. S. E. Hirschfeld coll., Oct. 1975. [Loc. 34.]

Paratypes: CAS 018432, 018433 (shells and soft parts), same locality as holotype. CAS 018434, 16 shells, same locality as holotype. CAS 018435, 5 shells, Loc. 35. USNM, ANSP, AMNH, FMNH, LACM, one shell each, Loc. 35.

REFERRED MATERIAL.—CALIFORNIA: Shasta County: Bollibokka Mountain Quadrangle: Loc. 30 [2 specimens], 31 [19], 32 [8], 33 [1], 36 [3], 37 [5], 38 [7], 39 [13], 40 [14], 41 [20]. Project City Quadrangle: Loc. 45 [40]. Figure 3 maps these localities.

ETYMOLOGY.—The subspecies is named for the people native to the region where it is found, the Wintu tribe.

DISCUSSION.—The major features of variation within the subspecies and its morphological relationship to other subspecies are discussed above and graphically shown in Figures 14–16. In coloration and spire height, *M. t. wintu* and *M. t. chaceana* are more similar than either is to *M. t. troglodytes*, whereas in microsculpture and relation of whorl number to overall size, *M. t. chaceana* and *M. t. troglodytes* group more closely.

Monadenia (Shastelix) troglodytes chaceana Berry

(Figures 13*a–c*)

Monadenia chaceana BERRY, 1940b:9–11, figs 9, 10.—PILSBRY 1948:1092.—SMITH 1960:97.—ROTH 1972a:5; 1972b:6.

ORIGINAL DESCRIPTION.—"Shell of but moderate size, weight, and thickness; spire low-conic to moderately elevated; whorls 5½ to 6, subangulate and carinate above the middle during juvenility, subcarinate at adolescence, but becoming obtusely angular and finally quite well rounded at maturity; base tumid, the umbilicus open, steep-walled, permeable to apex, and contained on the average about 8.4 times (7.45 to 9.88 in those measured) in the major shell-diameter. Aperture somewhat descending above, oblique, rounded to round-ovate, slightly or not at all flattened below; peristome nearly simple above, elsewhere usually little thickened and but moderately everted, terminating below in a very moderate columellar flare which covers only the edge of the umbilicus.

"Embryonic shell swollen, of 1¾ to 2 whorls; the surface initially smooth, but almost at once breaking into a few, irregular axial waves suc-

ceeded by a close, fine, crowded granulation, which abruptly ceases with the first post-embryonic whorl, the often heavy but extremely variable growth-striae thenceforth becoming the dominant feature; a few indistinct, elongate, and commonly confluent papillae arranged in rather distant forward-descending series appear on the early turns, but gradually give way on the later whorls to a weak and not very regular spiral striation which may become quite indistinct on the base; general surface between the striae and growth-lines very finely *microscopically* wrinkled in a cloth-like pattern.

"Periostracum smooth and lustrous; deep brown, encircled by a conspicuous dark-brown band about 2 mm. wide just above the periphery, bordered by a much narrower yellowish band and yet narrower band of the same pale tone just above, while on the shoulder some shells show varying traces of yet another band of intermediate brownish tone, best seen in juvenals" (Berry 1940b).

TYPE MATERIAL.—**Holotype:** SSB 8678 (shell); CALIFORNIA: Siskiyou County: among rocks about halfway up a spur of Badger Mountain on west side of Shasta River Canyon not far above its mouth (Berry 1940b).

Paratypes: CASGTC 10125 (formerly A. G. Smith no. 7102; shell); SUPTC 6555 (shell); according to Berry (1940b), additional paratypes are in the Berry Collection, with others originally to be deposited in the USNM and the Emery P. Chace Collection.

DISTRIBUTION.—*Monadenia t. chaceana* is known only from the general vicinity of the type-locality, in the Hornbrook Quadrangle, Siskiyou County (Locs. 1–5), and from one site (Loc. 6) in the Yreka Quadrangle, Siskiyou County (see also Fig. 1). Locality 7, "near Yreka" is too generalized to assign to a quadrangle with confidence. Limestone areas west of Gazelle and southeast of Scott Valley need additional prospecting for *Monadenia*.

DISCUSSION.—In coloration, *M. t. chaceana* most closely resembles the darker samples of *M. t. wintu*. The base is as dark as the spire, although neither is as dark as the supraperipheral band. At Localities 5 and 7, along with the usual dark-spired individuals, a form is present with light shoulder and one narrow, medium-brown, secondary band about two-thirds the distance from the suture to the periphery.

The substance of the shell is thinner and more translucent than in the Shasta Lake region groups.

Monadenia troglodytes chaceana has the highest mean H/D ratio of any subspecies (Table 3, Fig. 14*a*), differing highly significantly from any sample of *M. t. troglodytes* or *M. t. wintu*. At equivalent diameters, adult *M. t. chaceana* average 0.49 whorl more than *M. t. wintu* from the Brock Mountain area.

Berry (1940b) compared his *M. chaceana* to *Monadenia mormonum cala* (Pilsbry, 1900) and *M. churchi*. He also intimated a possible relationship to *Monadenia fidelis minor* (Binney, 1885) and surmised that the type-locality of that subspecies might be the Mount Shasta region. The latter supposition was evidently based on a statement by Binney (1885; Binney and Bland 1869) that small *Monadenia fidelis* occur at Mount Shasta.

Binney (1885:121, fig. 91) proposed "*Aglaia fidelis* var. *minor*" without a diagnosis and his original figure is unlocalized, but elsewhere (1885:141, footnote; 493) he recorded it from The Dalles, Oregon, collected by Henry Hemphill. Henderson (1936) and Pilsbry (1939) accepted The Dalles as the type-locality. The California Academy of Sciences collection contains two probable syntypes of *A. f.* var. *minor*, CASGTC 6001–6002, formerly H. Hemphill Collection no. 8598 and labeled "Helix fidelis Gray,/ var. minor W. G. Binn/depressed near mormonum/Near The Dalles, Oregon/Types/HH" in Hemphill's handwriting. They are small *M. fidelis*, agreeing well with Pilsbry's (1939) diagnosis of *M. fidelis minor* and moderately well with Binney's original engraving. That figure shows a pale shoulder with a light-centered spiral band and an indication of strong radial growth striae on the early whorls—all characteristic of the Dalles form.

The Binney and Bland Collection of terrestrial mollusks, now at the American Museum of Natural History (Gratacap 1901), contains one specimen of *M. fidelis* labeled "H. fidelis/Mt. Shasta/ Cooper." An oval, gold-edged, adhesive label on the specimen states "Mt. Shasta/WHB JGC"; the shell was evidently collected by William H. Brewer and given to James G. Cooper, who passed it on to Binney. This specimen, AMNH 57788, is 25.8 mm in diameter, 16.1 mm high, with 6.0 whorls. The shoulder is unpigmented except for faint, discontinuous traces of a light-centered spiral band. It is not the specimen illustrated by Binney (1885).

To my knowledge, *M. fidelis* does not live at Mt. Shasta proper, the nearest localities being Beaver Creek near the Klamath River, Siskiyou County (subspecies *M. f. leonina* Berry, 1937), and near the shores of Klamath Lake, Oregon (unnamed subspecies cited by Pilsbry [1939:42, fig. 18e] as *M. f. minor*). The Binney specimen is similar to the latter but more narrowly umbilicate. Brewer probably collected this shell on his 1863 trip through the Klamath Mountains, rather than on his 1862 climb of Mount Shasta (Brewer 1930). Cooper (1869) mentioned receiving from Brewer *M. fidelis* collected at Crescent City, the western terminus of Brewer's Klamath route. I conclude (1) that the name *minor* applies to a race of small *Monadenia fidelis* (Gray) from around The Dalles, Oregon, and (2) that Berry was mistaken about the similarity of his *M. chaceana* to Binney's "Mount Shasta" material.

Phylogenetic Hypotheses Concerning *Monadenia*

Early statements about evolution within *Monadenia* tended to accord the widespread and conspicuous *M. fidelis* a central—and in some unspecified way archetypal—position, while the smaller, more remote and cryptic *M. hillebrandi*, *M. mormonum*, and similar forms were viewed as derivative (and possibly degenerate) offshoots (for example, see Cooper 1887; Stearns 1900). A questionable exception is that of Cooper (1873), who evidently attempted to adduce general principles for the direction of character-state transformation in west coast snail genera. One can readily speculate as to what extent an ethnocentric outlook colored such views. A second generation of malacologists studying *Monadenia* (chief among them Pilsbry, S. S. Berry, G D. Hanna, and Junius Henderson) concerned themselves more with description and less with interpretation of evolutionary relationships. But in their work too, a typological bias, with *M. fidelis* the "type" in more than a nomenclatural sense, may be detected. In a recently proposed alternative hypothesis (Roth 1979), the ancestral *Monadenia* was seen as a ground-dwelling, low-spired, and somewhat variable form, from which the exposed-crawling, partly diurnal, and semi-arboreal *M. fidelis* evolved: "Once emancipated from life in holes in the ground, the *fidelis* group achieved large size, relatively high spire, and an extensive range which now reaches farther north than any other American helicacean" (Roth 1979:13). Roth and Eng (1980) offered a conjectural, "narrative" (sensu Ball 1976) hypothesis for the origin of *Monadenia setosa* Talmadge. Such narrative explanations are not analytical and have little predictive power. To date, none of these competing models has specified the criteria for judging relationships, and none has been couched in testable propositions.

Table 4. Character Complexes in *Monadenia* (apomorphous states listed first).

1. Atrium small and narrow (large and globose).
2. Mucus gland about equal to (many times longer than) dart sac.
3. Lower part of mucus gland adnate to (free from) atrium.
4. Dart sac 5 mm or less in length (longer than 5 mm).
5. Flagellum about as long as (≥1.5 times length of) penis plus epiphallus.
6. Flagellum and spermatophore straight (helically coiled).
7. Basal chamber of penis sessile on (invaginated into) atrium.
8. Penial retractor inserted near middle (on distal third) of epiphallus.
9. Habit at least partly arboreal (ground-dwelling).
10. Granulose microsculpture present on teleoconch (limited to protoconch).
11. Shoulder band pigmentation monomorphic (polymorphic).

Phylogenetic systematics, the methodology of Willi Hennig (1966), seeks to analyze the probable direction of evolutionary character transformation in a particular group of organisms and, from this analysis, to reconstruct the evolutionary history of the group. An important virtue of this method is that it generates testable hypotheses about phylogenetic relations. (See Kavanaugh [1972] for an exposition of Hennig's approach to systematics and Gaffney [1979] for a useful bibliography of papers dealing with cladistic methodology.) In land malacology, Van Goethem (1977), Breure (1979), and Bishop (1979) have applied these principles to the land snail groups Urocyclinae, Bulimulidae, and American Camaenidae, respectively, and the same approach is implicit in the writings of a number of other malacologists.

Of 55 morphological and natural history characters studied, 11 (Table 4) were incorporated in a cladistic analysis. Characters excluded were those in which polarity of the transformations could not be interpreted, those that occur only

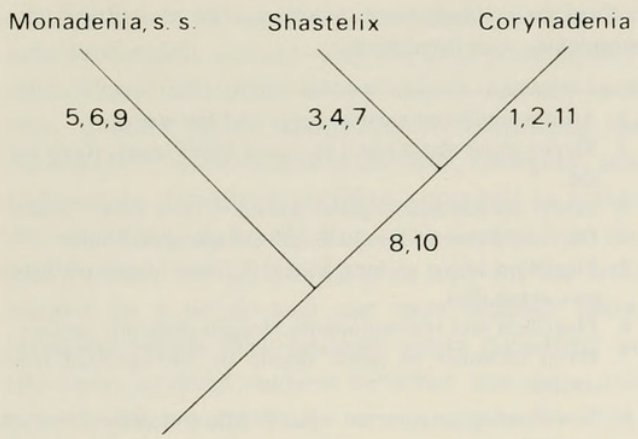


FIGURE 17. Suggested cladogram for the subgenera of *Monadenia*. Numbers refer to apomorphous states of character complexes listed in Table 4.

in states judged to be symplesiotypic for the genus, and those that are unique (as apomorphies) to one species and hence provide no information for grouping.

Figure 17 illustrates the relationship of character states in the three subgenera of *Monadenia*. It is well to emphasize that the hypothesis presented here is preliminary and undoubtedly will be modified as study of the genus progresses. This cladogram is based mainly on reproductive anatomy. In general, shell characters are much more labile, phenotypic responses to environment are common, and the number of conchologically polytypic species in *Monadenia* hampers the use of shell features in this kind of analysis. As Bishop (1979:275) noted, snail shells offer relatively few characters for analysis and are difficult to characterize objectively, "though both shape and texture may be most informative to the eye of an experienced worker in a manner which is hard to express in words." Moreover, shell characters are subject to numerous parallelisms and convergences, usually associated with habit and habitat (for example, the often-remarked similarity between the rock crevice-dwelling species, *Monadenia circumcarinata* (Stearns, 1879) and *Oreohelix elrodi* (Pilsbry, 1900)). A closer study is needed to discriminate analogous from homologous shell character states and extend the cladistic analysis to the species level.

Three character complexes, especially, illustrate the problems left unsolved by this analysis. The arboreal habit in *Monadenia*, s.s., is regarded as an apomorphy, but many of the associated apomorphic characteristics (potential for large size, high spire) are differentially expressed in the various subspecies of the polytypic *Monadenia fidelis*. Are these characters secondarily lost in such subspecies as the low-spired *M. f. scottiana* Berry and the small-shelled, unnamed race near Klamath Lake, or do these races preserve the plesiomorphous condition? Perhaps the arboreal habit and its associated character states are better viewed as expressions of a physiologically based eurytopy which permits life in the trees but also allows *M. fidelis* to inhabit low herbage near the coast (*M. f. pronotis* Berry) or rockpiles (Klamath Lake race). A specialized arboreal habit, such as the dependence of *M. setosa* on standing broadleaf deadwood for juvenile habitat (Roth and Eng 1980), is probably a second level of apomorphy, derived from a more generalized arboreal potentiality.

A transparent periostracum, through which shell banding is visible, is probably plesiomorphous for the genus. Banding, which is widespread in Helminthoglyptidae and other helicacean families, presumably evolved in the face of visual predation pressure (Roth, in preparation). An opaque periostracum that masks the banding (still present in the shell underneath) seems to be associated with cryptic habits and independently derived in *Monadenia*, s.s., and *Corynadenia*.

Carination of the margin of the adult shell is a paedomorphy (compare Gould 1969, *Poecilozonites*), independently derived in *Monadenia*, s.s., *Corynadenia*, and probably *Shastelix*. "Hypercarination" (carina set off by pinched grooves) is a further derived state among several deep rock-crevice-dwelling forms of the Sierra Nevada.

While a cladogram, such as that in Figure 17, is nothing more than a branching diagram depicting the nested pattern of synapomorphies among the taxa under study, a phylogeny is an explicit statement concerning the exact nature of the evolutionary relationship among the taxa (Eldredge 1979). A phylogenetic tree is "a diagram (not necessarily branching!) depicting the actual pattern of ancestry and descent among a series of taxa" (Eldredge 1979:168) and embodies assumptions and information not required in (and theoretically excluded from) the construction of a cladogram. With the further addition of

explanatory narrative, one can often devise a scenario to suggest how the phylogenetic relationship, and the pattern of synapomorphies in the underlying cladogram, came to be.

Strictly speaking, the construction of phylogenetic trees is limited to species; species, not genera or other higher taxa, give rise to other species. Therefore, when we speak of a dichotomy arising between subgenera (as herein), we are really maintaining that the dichotomy arose between two species which would be classed in the separate subgenera.

The suggested cladogram for the subgenera of *Monadenia* specifies three detected autapomorphies in the subgenus *Monadenia*, s.s., two synapomorphies shared by *Shastelix* and *Corynadenia*, and three autapomorphies each in *Corynadenia* and *Shastelix*. The effect of this distribution of apomorphies is to falsify all possible phylogenetic trees for the group except that which is isomorphous with the cladogram (see Platnick 1977:440–441, fig. 2). Consequently, the proposed phylogenetic history of *Monadenia* consists of (1) a dichotomy between *Monadenia*, s.s., and the common ancestor of *Corynadenia* and *Shastelix*, followed in time by (2) the dichotomy between *Corynadenia* and *Shastelix*.

THE SCENARIO.—In the John Day Formation (late Oligocene to early Miocene) of central Oregon, three fossil forms referred to *Monadenia* are present: *M. antecedens* (Stearns, 1900), large-shelled and so similar in general appearance to *M. fidelis* that it was formerly ranked as a subspecies of the latter; *M. dubiosa* (Stearns, 1902), said to be another *fidelis*-like form (Pilsbry 1939); and *M. marginicola* (Conrad, 1871), which Hanna (1920) believed to be related to "the *mormonum* group" (i.e., *Corynadenia*). No anatomical details are available, of course, and the shell microsculpture, if preserved, is not specified in the literature, but the distinction between large *fidelis*-type shells and smaller shells with the character of present-day ground-dwelling forms is consistent with the hypothesized early split between *Monadenia*, s.s., and the *Shastelix-Corynadenia* stock.

At the time of deposition of the John Day Formation (36.4–22 million years before present; Hammond 1979), the Cascade Arc had rotated from its earlier northwest-southeast orientation almost to its present north-south position, east of the presumably coastal Klamath Mountains–Coast Range block (Hammond 1979:figs. 8, 9). The John Day accumulated as clayey and tuffaceous sediments in an inland basin contemporaneously with formation of the volcanic and pyroclastic rocks of the middle Western Cascades Group. During this episode, Cascade volcanism was centered in randomly spaced stratovolcanoes and calderas; the string of high volcanic edifices that characterizes the modern Cascade Range had not yet developed. Contemporaneous floras from the Coast Range block to the west are similar in floristic composition and leaf physiognomy to the Bridge Creek Flora from the lower member of the John Day (Brown 1959; Wolfe and Hopkins 1967), indicating that the Cascade Range was not a significant climatic or vegetational barrier at this time.

The Bridge Creek Flora, associated with a radiometric date of 31.5 million years (Evernden and James 1964), represents a mixed mesophytic forest dominated by broad-leaved deciduous trees, in a temperate climate with ample summer rainfall (Chaney 1948; Brown 1959; Wolfe and Hopkins 1967). Its greatest similarities are with modern hardwood forests of eastern North America and eastern Asia (Chaney 1948; Whittaker 1961). Temperature parameters suitable for forests of this composiion are now lacking in the Pacific coast states except in isolated, small, interior valleys (Wolfe 1979).

The source of the John Day land mollusks is evidently the vertebrate-rich middle member, of early Arikareean (late Oligocene) age (Wood et al. 1941) and about 25 million years old (Berggren and Van Couvering 1974). Contemporaneous floras are also mixed mesophytic, possibly somewhat warmer than the Bridge Creek Flora. The diverse vertebrate remains likewise indicate a temperate and wet climate, quite unlike the semiarid interior of Oregon of the present. It seems plausible that such an environment could have supported greater intrageneric snail diversity than now seen in any forests of the west, much as the hardwood forests of the eastern United States now support a substantial diversity of snails in genera of the Polygyridae. Part of the early diversification of *Monadenia* forms probably involved habitat partitioning between ground-dwelling and arboreal species.

The subsequent vegetational and climatic his-

tory of western North America (greatly simplified) includes warming from late Oligocene to middle Miocene, followed by gradual, fluctuating cooling through the Pleistocene, and a shift from summer-wet to summer-dry climate. By the Pliocene the woody flora was depauperate, with extinctions most marked in broad-leaved lineages with paratropical and subtropical affinities (Wolfe 1979). Latitudinal and altitudinal zonation became pronounced in the later Tertiary, accompanied by a differentiation of forest types into several adaptive zones (Axelrod 1976:fig. 7). As the rising Cascade Range cast a more profound rain shadow on the interior, humid forests became confined to the windward, west slope of the Cascades and lands to the west—the modern range of *Monadenia*, s.s.

At this time (late Miocene–Pliocene), a substantial allopatry between the two existing stocks of *Monadenia* may have arisen, with the *Shastelix-Corynadenia* stock inhabiting the drier, interior regions, and *Monadenia*, s.s., perhaps exploiting a tendency toward eurytopy in humid environments. Equability of climate may also have been a factor. Parapatry like that which now occurs in the Klamath Mountains, where *M.* (*Monadenia*) *fidelis* and *M.* (*M.*) *setosa* inhabit riparian woodland while *M.* (*Shastelix*) *churchi* occupies drier, more exposed slopes and rockslides, may have been common where the environments interfingered. (In this connection, according to Whittaker [1961] and Axelrod [1976], the modern Klamath Mountains preserve a climate and vegetation more like that of the later Cenozoic than any other region in the west.) Some time in this interval *Monadenia* became extinct in central Oregon.

On a graph of mean annual temperature versus mean annual range of temperature (compare Wolfe 1979), only the thermal range of *Shastelix* overlaps that of present-day mixed mesophytic forest (Fig. 18). Because the John Day fossil occurrence represents only one datum, we do not know what the total Oligocene thermal range of *Monadenia* might have been; but certainly the large, *fidelis*-type snails of the typical subgenus have shifted away (toward the right—equable—side of the graph) from the thermal zone of mixed mesophytic forest. *Shastelix* has shifted less, if at all. The narrow overlap of thermal ranges of *Monadenia*, s.s., and *Shastelix* parallels their narrow geographic zone of parapatry and suggests progressive range/habitat differentiation along a climatic gradient. In contrast, the thermal range of *Corynadenia* overlaps those of both other subgenera extensively. It occupies a considerable range of mean annual temperatures, but a limited zone of mean annual temperature *ranges*. If *Corynadenia* differentiated from *Shastelix* along a climatic gradient, it was presumably not chiefly a gradient of mean temperature and equability.

The autapomorphies of *Corynadenia* can be interpreted as adaptations to the rockslide/rock-crevice habitat and prolonged summer drought. The range of *Corynadenia* receives the least precipitation of any zone inhabited by *Monadenia* (Elford 1970). Reduction or partial loss of the genital apparatus is associated with adaptation to xeric environments in other groups of Helminthoglyptidae (Gregg 1960; Bequaert and Miller 1973). Retention of granulose microsculpture on the teleoconch is evidently a paedomorphy, and is most strongly developed in species (*M. hillebrandi*, *M. circumcarinata*) with paedomorphic carination of the adult shell. Small size and low-spired, lenticular shape are other crevice-related characteristics that occur in some species and races of *Corynadenia*.

Additional evidence for the relationship of temperature and distribution in *Monadenia* is seen in the close correspondence between maximum summer and minimum winter isotherms and the range limits of *Shastelix* and *Corynadenia* (Fig. 1). The 36 C mean maximum July isotherm practically coincides with the "downhill" limit of the genus in the Klamath Mountains and Sierra Nevada, and the −4 C mean minimum January isotherm, more loosely, with the "uphill" limit. (At this scale, the isotherms are highly generalized and each stands for a range of related microhabitat temperatures.) The southern limit of *Corynadenia* occurs just north of where these two isotherms pinch together. Similarly, between the southern limit of *Shastelix* and the northern limit of *Corynadenia*, the July isotherm bulges eastward, almost but not quite intersecting the January isotherm. At this point, the 33 C mean maximum July isotherm, which most closely coincides with the very southern limit of *Shastelix*, is actually east ("uphill") of the −4 C January isotherm. If it persisted long enough, a thermal configuration like this could have produced vicariance within

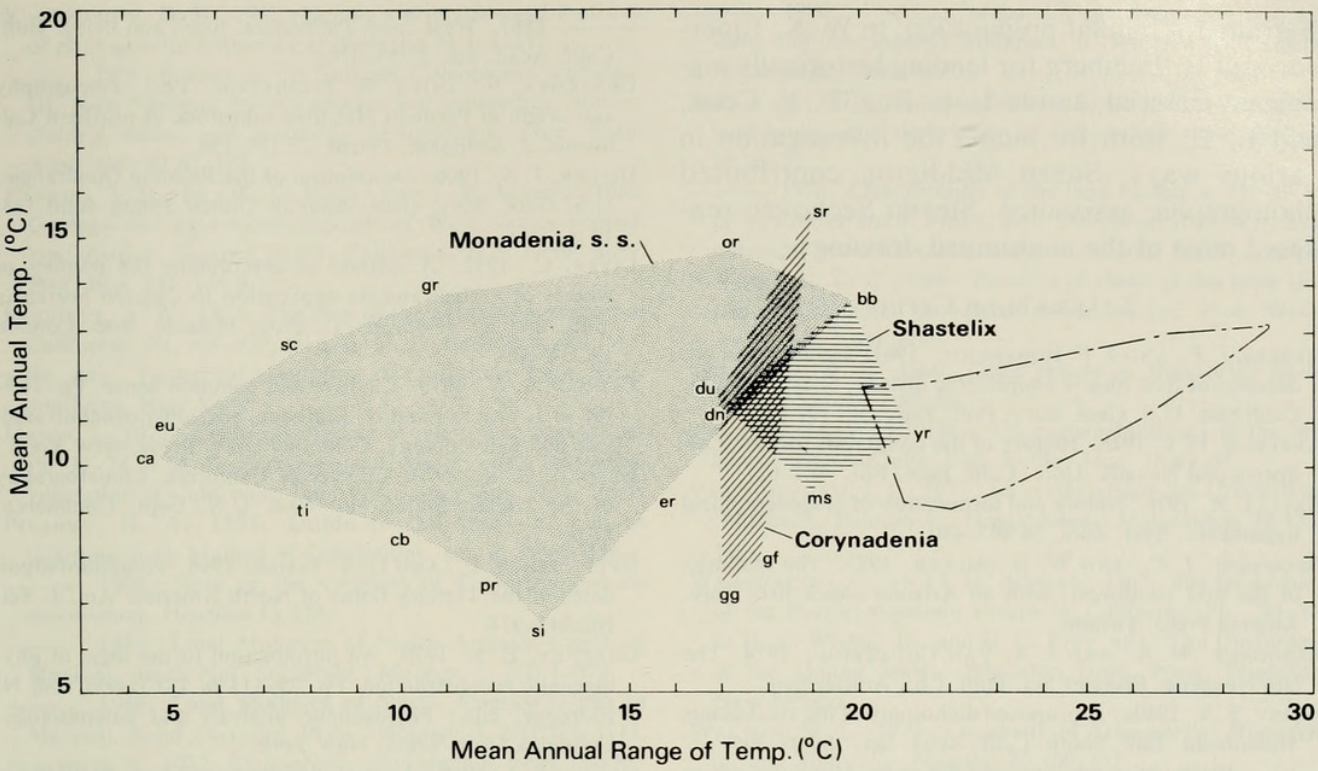


FIGURE 18. Graph of thermal ranges of the three subgenera of *Monadenia* in relation to temperature parameters. Stippling, *Monadenia*, sensu stricto; diagonal hachure, *Corynadenia*; horizontal hachure, *Shastelix*. Dot-dashed line encloses thermal range of present-day mixed mesophytic forest of eastern Asia (after Wolfe 1979). Abbreviations for stations defining the subgeneric polygons (in California unless otherwise indicated): *bb*, Big Bar; *ca*, Cape Blanco, Oreg.; *cb*, Clallam Bay 1 NNE, Wash.; *dn*, Dunsmuir; *du*, Dudley; *er*, Elwha Ranger Station, Wash.; *eu*, Eureka; *gf*, Giant Forest; *gg*, Grant Grove; *gr*, Graton 1 W; *ms*, Mount Shasta; *or*, Orleans; *pr*, Prince Rupert, Brit. Col.; *sc*, Scotia; *si*, Sitka, Alaska; *sr*, Sonora Ranger Station; *ti*, Tatoosh Island, Wash.; *yr*, Yreka. Thermal data from Elford (1970), Wolfe (1979).

the *Shastelix-Corynadenia* stock. The present configuration of the isotherms must be short-lived in geologic terms, particularly in the face of the great climatic fluctuations of the Pleistocene; while it may now enforce the geographic separation of *Shastelix* and *Corynadenia*, their initial cleavage undoubtedly took place earlier. Alone, or in combination with climatic factors, Miocene or later topographic developments could have fostered the vicariance. (Pliocene through Holocene volcanic rocks of the High Cascades Group overlap the edges of the northern Sierra Nevada and eastern Klamath Mountains, separating the metamorphic and plutonic rocks of these two provinces for a distance of about 80 km [Hammond 1979]. They were extruded initially as basaltic flows and later as andesitic, cone-building eruptions, filling a structural trough and lowland between the Klamath and Sierran blocks. For a calcicolous ancestral *Monadenia*, these volcanic rocks could have been a barrier leading to allopatric differentiation or interrupting a cline along which some differentiation had already proceeded.) Given the complexity of relations between land snails and their environment, it is unlikely that a single event can be pinpointed as the cause, but no details of phylogeny, distribution, or thermal relations contraindicate vicariance in the general geographic setting of the present.

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Appendix: Localities

Localities for material studied are listed below, grouped according to geographic area. The numbers assigned are for purposes of this study; samples are on deposit in the mollusk collection of the California Academy of Sciences. Map quadrangle names refer to the most recent edition of the U.S. Geological Survey 7.5- and 15-minute Series (Topographic). The number in brackets following the collection data is the total number of specimens examined from that locality; it does not always agree with sample size numbers cited in the text because not every character could be measured for every specimen and because many of the computations utilized adult shells or anatomies only. Distances are cited as received in the collectors' notes and have not been converted to the metric system.

California: *Siskiyou County:* Hornbrook Quadrangle

1 Along creek 1.5 mi sw of Hornbrook. G D. Hanna, Apr. 1928 [5].

2 SW¼ sec. 18, T. 46 N, R. 6 W, 1000 ft up Klamath River from mouth of Shasta River. D. E. Marsh, 1931 [2].

3 Among rocks about half-way up a spur of Badger Mountain on west side of Shasta River canyon not far above its mouth. E. P. Chace, 29 Sep. 1937 [3]. (Type-locality, *M. t. chaceana.*)

4 Shasta River near junction with Klamath River. E. P. Chace [3].

5 Sec. 25(?), T. 46 N, R. 7 W, banks of Shasta River, 2–3 mi from mouth, in shaded rockslides. A. G. Smith, 11 Sep. 1934 [5].

California: *Siskiyou County:* Yreka Quadrangle

6 Chastain's Quarry, west of Gazelle. E. P. and E. M. Chace, 28 Sep. 1937 [3].

7 [?] "Near Yreka." E. J. Elliott, autumn 1933 [5].

California: *Shasta County:* Bollibokka Mountain Quadrangle

8 Near McCloud River bridge, 30 mi ne of Redding. D. C. Rudolph, B. Martin, S. Winterath, 9 Apr. 1979 [2].

9 Sec. 32, T. 36 N, R. 3 W, west slope of Bollibokka Mountain, 0.75 mi e of bridge across McCloud River. J. W. Durham, E. C. Allison, 18 Apr. 1964 [5].

10 Sec. 5, T. 35 N, R. 3 W, slope below Samwel Cave, above McCloud River arm of Shasta Lake. R. L. Seib, 11 Mar. 1978 [32].

11 Sec. 5, T. 35 N, R. 3 W, Samwel Cave, ch. 1, sec. 2–5 (=UCMP loc. 1008). E. L. Furlong [8]. (Type-locality, *M. t. troglodytes.*)

12 Sec. 5, T. 35 N, R. 3 W, Samwel Cave, in gravel slope filling grotto at south end, ch. 2, sec. 4 (=UCMP loc. 1009). E. L. Furlong [2].

13 Sec. 5, T. 35 N, R. 3 W, Samwel Cave, with bone matter, 50 ft in from twilight zone. R. E. Graham, 5–6 Jan. 1957 [2].

14 Sec. 5, T. 35 N, R. 3 W, Samwel Cave, twilight zone floor. R. de Saussure, 10 May 1957 [2].

15 Sec. 5, T. 35 N, R. 3 W, Samwel Cave. R. de Saussure, 5 June 1957 [2].

16 Sec. 5, T. 35 N, R. 3 W, Samwel Cave, entrance to main cave. R. de Saussure, 5 June 1957 [1].

17 Sec. 5, T. 35 N, R. 3 W, Samwel Cave, surface, second exit. R. de Saussure, A. Dacey, 5 June 1957 [4].

18 Sec. 5, T. 35 N, R. 3 W, Samwel Cave. N. Slusser, 4–7 June 1957 [2].

19 Sec. 5, T. 35 N, R. 3 W, within 25 ft of entrance to Samwel Cave. R. E. Graham, 8 June 1958 [31].

20 Sec. 5, T. 35 N, R. 3 W, Samwel Cave, bone chamber pit containing bone and rubble matrix, 7 to 12 inches depth. R. E. Graham, 10–14 June 1958 [2].

21 Sec. 5, T. 35 N, R. 3 W, Samwel Cave. R. E. Graham, 27 Dec. 1958 [6].

22 Sec. 5, T. 35 N, R. 3 W, Samwel Cave. R. E. Graham, 18 June 1959 [1].

23 Sec. 5, T. 35 N, R. 3 W, Samwel Cave. R. E. Graham, 19 Dec. 1959 [2].

24 Sec. 5, T. 35 N, R. 3 W, Samwel Cave and vicinity. D. C. Rudolph, B. Martin, S. Winterath, 9 Apr. 1979 [9].

25 SE¼ sec. 7, T. 35 N, R. 3 W, limestone outcrop, summit of Hirz Mountain, 2 mi sw of Samwel Cave. R. E. Graham, June 1960 [2].

26 SE¼ sec. 6, T. 35 N, R. 3 W, Ellery Creek on Gilman Road, 15 mi ne of junction with Interstate Hwy. 5, limestone rock slides. A. G. Smith, 17 May 1973; B. Roth, Mar. 1980 [30].

27 SE¼ sec. 6, T. 35 N, R. 3 W, Ellery Creek, w side of McCloud River arm of Shasta Lake. R. L. Seib, 24 Mar. 1978 [5].

28 SW¼ sec. 21, T. 35 N, R. 3 W, Dekkas Rock at junction of Dekkas Creek with e side of McCloud River arm of Shasta Lake. R. L. Seib, 24 Mar. 1978 [38].

29 NW¼ NE¼ sec. 32, T. 35 N, R. 3 W, limestone outcrop 0.3 mi ssw of junction of Campbell Creek with e side of McCloud River arm of Shasta Lake. R. L. Seib, 24 Mar. 1978 [3].

30 Sec. 28, 29(?), T. 25 N, R. 2 W, Low Pass Creek. J. Gorman, 29 Jan. 1953 [2].

31 SE¼ NW¼ sec. 4, T. 34 N, R. 2 W, caves at headwaters of Brock Creek drainage. S. E. Hirschfeld, July 1975 [19].

32 SE¼ NW¼ sec. 4, T. 34 N, R. 2 W, shelter below and to left of Goblin Shelter, headwaters of Brock Creek drainage. S. E. Hirschfeld, July 1975 [8].

33 NE¼ SW¼ sec. 3, T. 34 N, R. 2 W, small cave in Hosselkus limestone in gray rocks on e side of eastern ne–sw-trending ridge. S. E. Hirschfeld, 3 Apr. 1970 [1].

34 NW¼ NE¼ sec. 8, T. 34 N, R. 2 W, cave between two limestone buttes at south end of Gray Rocks, above Pit River arm of Shasta Lake. S. E. Hirschfeld, Oct. 1975 [49]. (Type-locality, *M. t. wintu.*)

35 SW¼ NW¼ sec. 7, T. 34 N, R. 2 W, limestone quarry 1 mi n, ⅝ mi e of Brock Mountain Lookout, above Squaw Creek arm of Shasta Lake. R. L. Seib, 25 Mar. 1978 [39].

36 Squaw Creek. A. M. Strong, 1898 [3].

37 Squaw Creek. J. Gorman, 14–15 Mar. 1953 [5].

38 N ctr., SE¼ sec. 9, T. 34 N, R. 2 W, caves in Brock Creek limestone, above Pit River arm of Shasta Lake. S. E. Hirschfeld, July 1975 [7].

39 NW¼ SE¼ sec. 9, T. 34 N, R. 2 W, lower limestone across from Brock Spring, above Brock Creek, above Pit River arm of Shasta Lake. S. E. Hirschfeld, July 1975 [13].

40 NE¼ SW¼ sec. 9, T. 34 N, R. 2 W, "Monadenia Cave" and vicinity, above Pit River arm of Shasta Lake. S. E. Hirschfeld, July 1975 [14].

41 NE¼ SW¼ sec. 9, T. 34 N, R. 2 W, "Elk Antler Cave," above Pit River arm of Shasta Lake. S. E. Hirschfeld, July 1975 [20].

CALIFORNIA: *Shasta County:* Lamoine Quadrangle

42 SW¼ sec. 13, T. 34 N, R. 4 W, Shasta Lake Caverns. D. C. Rudolph, B. Martin, S. Winterath, 10 Apr. 1979 [1].

43 SE¼ SE¼ sec. 23, T. 34 N, R. 4 W, Potter Creek, along McCloud River arm of Shasta Lake. R. L. Seib, 11 Mar. 1978 [22].

44 Sec. 23, T. 34 N, R. 4 W, Potter Creek Cave, "past kitchen" (=UCMP loc. 1055) [12].

CALIFORNIA: *Shasta County:* Project City Quadrangle

45 SE¼ sec. 4, T. 33 N, R. 4 W, Calveris Cement Co. quarry above Interstate Hwy. 5 just south of Shasta Lake bridge, 2.5 mi NNE of Mountain Gate. R. L. Seib, 11 Mar. 1978 [40].

CALIFORNIA: *Shasta County:* Anderson Quadrangle

46 Clear Creek, on road between Redding and Beegum. G D. Hanna, Sep. 1952 [1].

CALIFORNIA: *Shasta County:* quadrangle uncertain

47 Crystal Shasta Cave. K. Howard, 1958(?) [1].

48 Chute Cave. R. de Saussure, Nov. 1957 [1].

49 "Shasta County, Calif.," *ex* D. O. Mills collection, UCMP [3].

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