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THE VELIGER

Redescription of *Assiminea infima* Berry, 1947, from Death Valley, California

by

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Abstract. A morphological description, including aspects of the shell and soft-part anatomy, is provided for *Assiminea infima* Berry, 1947, from Death Valley, California. Habitat descriptions are given for Badwater Spring, the type locality, as well as for three new localitites for the species. *Assiminea infima* typically occurs either under a salt-crust roof fringing the water's edge or on moistened riparian vegetation. Snails are often found fully submerged, and only occur in the vicinity of spring sources. A review of morphological data suggests that *A. infima* may be closely related to *A. californica* (Tryon, 1865), a Pacific coastal species.

INTRODUCTION

THE GENUS *Assiminea* Fleming, 1828 (Prosobranchia: Rissoacea), comprises 50–60 nominal species, with most restricted to tropical or subtropical regions. Members of the genus are amphibious, living in moistened areas near the edge of marine or permanent nonmarine water bodies (ABBOTT, 1958). The group presents an interesting ecological radiation of probable marine ancestry (ABBOTT, 1958; FRETTER & GRAHAM, 1962); yet the lack of a modern systematic analysis of the genus (few species have received anatomical study) precludes a meaningful analysis of the radiation.

Assiminea is represented in North America by several coastal species, one of which, *A. californica* (Tryon, 1865), has received detailed morphological study (FOWLER, 1977, 1980). In addition, there is an inland deployment of *Assiminea* among spring-fed habitats in the arid southwest U.S. (BERRY, 1947; MORRISON, 1956; TAYLOR, 1966, 1983; LANDYE, 1973; FULLINGTON, 1978). The inland fauna has received scant attention, with systematic study restricted to the brief description of *A. infima* Berry, 1947, from Badwater Spring in Death Valley.

It has long been known that additional *Assiminea* populations occur in the Death Valley region (MORRISON, 1956; LANDYE, 1973). As part of a recent survey of rissoacean snails in the Death Valley region (HERSHLER, 1985), the author collected *A. infima* from Badwater Spring and three other localities in Death Valley (Figure 1). Based on study of this material, a morphological redescription of *A. infima* is provided herein that includes details of shell morphology as well as anatomy. Detailed habitat descriptions are provided as is a morphological comparison between *A. infima* and *A. californica*.

MATERIALS AND METHODS

Assiminea infima was collected by hand at the four Death Valley localities during February and November 1985. These collections are now housed in the National Museum of Natural History (USNM catalogue numbers are given below). Snails from Badwater Spring were used for study of internal anatomy. Shell measurements and dissections were done at 50× using a Wild M-5 dissecting microscope equipped with an ocular micrometer. Shells, opercula, radulae, and critically point dried whole specimens were photographed using a Hitachi S-570 scanning electron microscope.

TAXONOMY

Family ASSIMINEIDAE

Genus *Assiminea* Fleming, 1828

Type species (by original designation): *Assiminea grayana* Fleming, 1828.

Assiminea infima Berry, 1947

(Figures 1–12)

Material examined: California, Inyo County: Badwater Spring, Bennetts Well quadrangle (1952), 1:62,500, T.

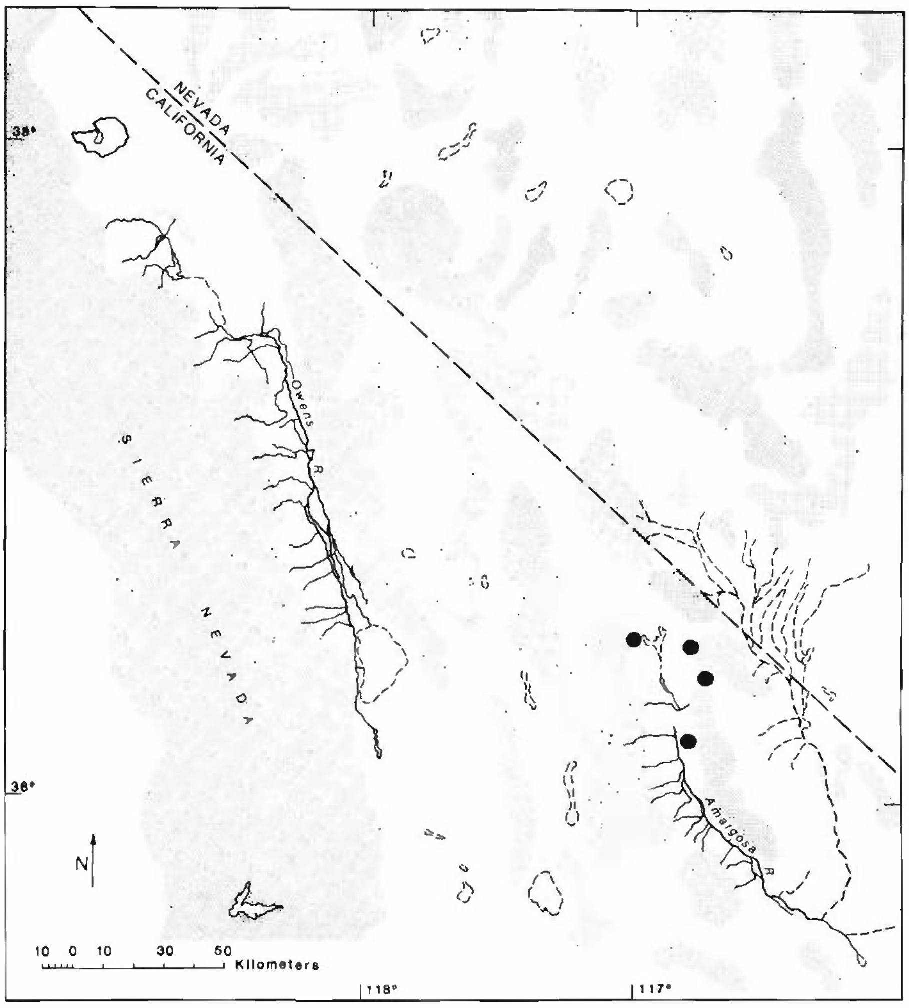


Figure 1

Map of the Death Valley drainage system, showing localities for *Assiminea infima*. The localities are (from north to south) Cottonball Marsh (west side of Death Valley), Nevares Springs (east side), Travertine Springs, and Badwater Spring. Stippled areas indicate the location of mountain ranges.

20S, R. 20E, 1.7 km SW of NE corner of quadrangle, USNM 591286 (paratypes), USNM 859018–859020 (all from North pool); Travertine Springs, Furnace Creek (1952), T. 27W, R. 1E, ¼NW ¼NW, Section 25, USNM 859021, USNM 859022; Nevares Springs, Chloride Cliff (1952), T. 28N, R. 1E, ¼NE ¼SW, Section 36, USNM 859023–859025; Salt Springs (feeding Cottonball Marsh), Chloride Cliff (1952), T. 17S, R. 45E, 0.7 km NE of SW corner of quadrangle, USNM 859026; Cottonball Marsh, Chloride Cliff (1951), T. 27S, R. 45E, 2.3 km NE of SW corner of quadrangle, USNM 859027, USNM 859028.

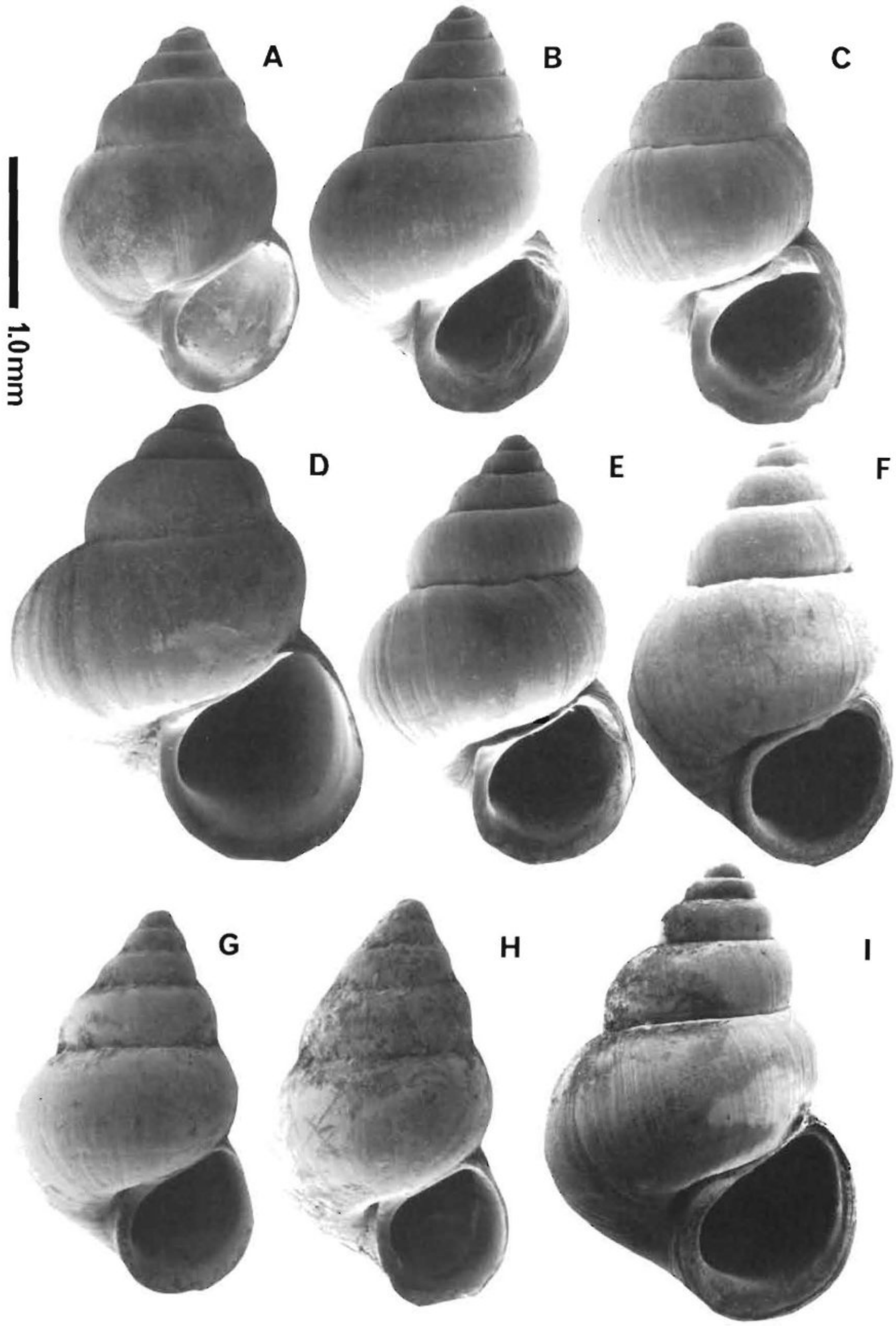
Diagnosis

A small-sized (shell height, 2.5–3.5 mm) species, distinguished from North American coastal *Assiminea* by its

Table 1

Summary of shell parameters for 14 mature adults from Badwater Spring.

Parameter	Mean	SD	Range
Shell height (mm)	2.81	0.22	2.62–3.25
Shell width (mm)	1.95	0.19	1.74–2.48
Aperture height (mm)	1.28	0.12	1.11–1.52
Aperture width (mm)	1.12	0.11	0.99–1.45
Body whorl height (mm)	2.02	0.16	1.74–2.41
Body whorl width (mm)	1.73	0.16	1.52–2.17
Number of whorls	4.73	0.17	4.5–5.0


A
B
C
1.0mm
D
E
F
G
H
I

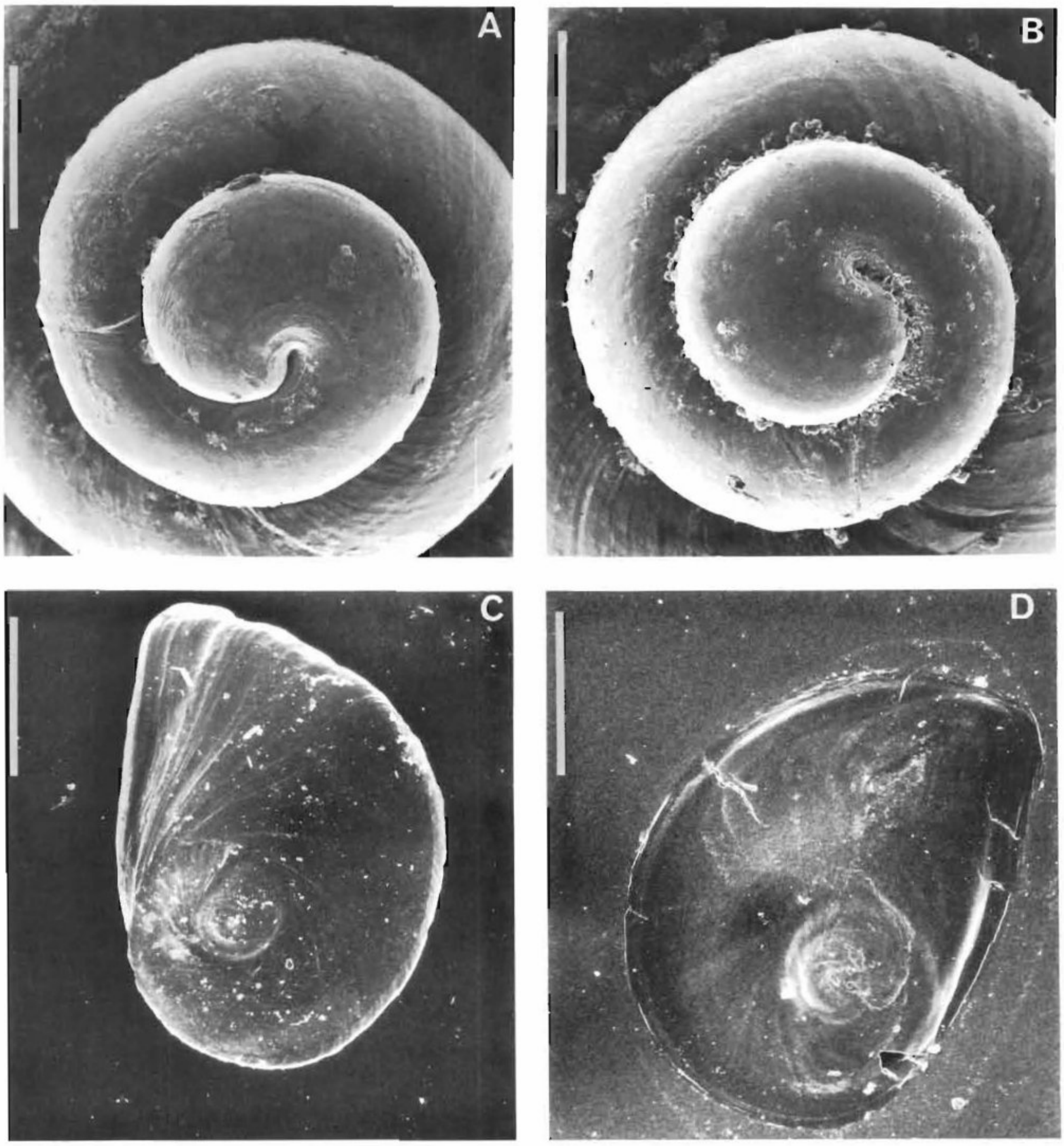


Figure 3

Photographs (SEM) of the protoconch (A, B; scale = 150 μm) and operculum (C, dorsal aspect; D, ventral; scale = 330 μm) of *Assiminea infima*.

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Figure 2

Photographs (SEM) of *Assiminea infima* from Badwater Spring (A–F), Travertine Springs (G), Nevares Springs (H), and Cottonball Marsh (I).

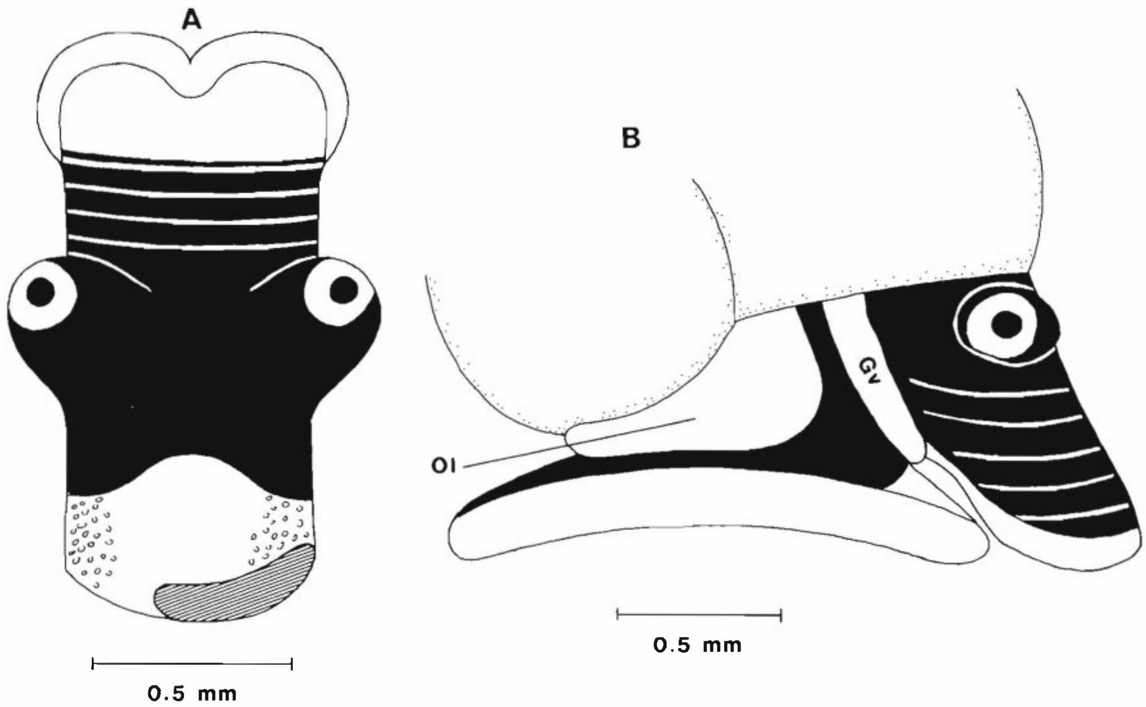

Figure 4

Head (A) and right lateral view of head-foot (B) of crawling, submerged *Assiminea infima*. Darkly pigmented regions are shaded black. The small circles posterior to the tentacles represent glandular clusters. Gv, ciliated groove; Ol, operculigerous lobe.

broadly conical shell with moderate to highly convex whorls (Figure 2). Other distinguishing features include the presence of a single, enlarged ctenidial filament anterior to the more typical, stubby filaments (Figure 6A), a thickened pallial swelling anterior to the rectum (Figure 6A), and the looping condition of the anterior vas deferens (Figure 11B).

Description

Shell: Measurements of shell parameters for 14 specimens from Badwater Spring (the only locality from which a large sample was obtained) (Figure 2) are summarized in Table 1. Adult shells have 4.0–5.0 whorls and shell height varies from 2.5 mm (Nevares Springs) to 3.5 mm (Cottonball Marsh). Females are typically slightly larger than males. Shells are fairly thin and translucent, with only a slight thickening at the aperture. Shell color is very light to dark amber. Shells from Badwater Spring and Cottonball Marsh are relatively wider with more convex whorls than those from Travertine and Nevares springs (Figure 2). The aperture is longer than wide, rounded below, and angled above. The inner lip is fully formed only in the largest specimens, and in these it often forms a broadened callus (Figure 2). Separation of the inner lip from the body whorl is rare. The umbilicus is often restricted due to peristome overlap and appears chinklike. The protoconch, with 1.25 whorls, is smooth or with a few faint spiral lines (Figures 3A, B). Teleoconch sculpture consists of strong collabral growth lines. The paucispiral operculum (Figures 3C, D) is thin, amber-colored, and without unusual features.

Head-foot: The broadly bilobed snout (Figures 4, 5A) is dorsoventrally flattened, longer than wide, and creased along most of its length. The distal end of the snout flares outward to form broad, fleshy oral lappets. The tentacles are short, thickened, rounded at the tips, and without cilia.

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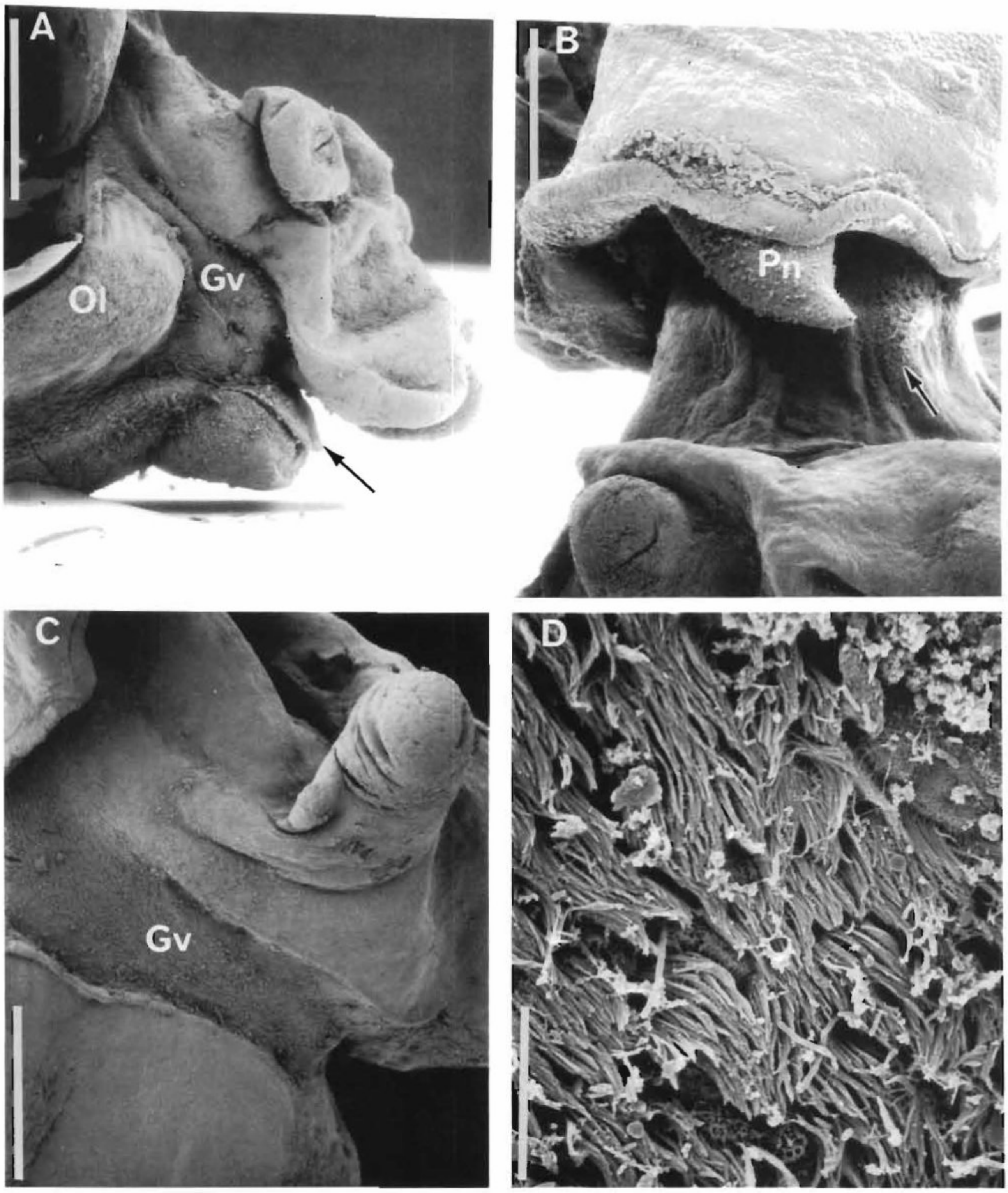
Figure 5

Photographs (SEM) of critical point dried specimens of *Assiminea infima*. A. Right lateral aspect of head-foot (specimen partly collapsed), with the arrow indicating the dorsoanterior flap of the foot (scale = 380 μm). Note



the stubby tentacles and bulging operculigerous lobe. B. Dorsal aspect of the neck, showing (arrow) the anterior portion of the ciliated patch on the pallial cavity floor (scale = 250 μm). C. Right lateral aspect of the head-foot, showing the typically wide ciliated groove (scale = 250 μm). D. Close-up of the ciliation in the groove (scale = 12 μm). Gv, ciliated groove; Ol, operculigerous lobe; Pn, penis.

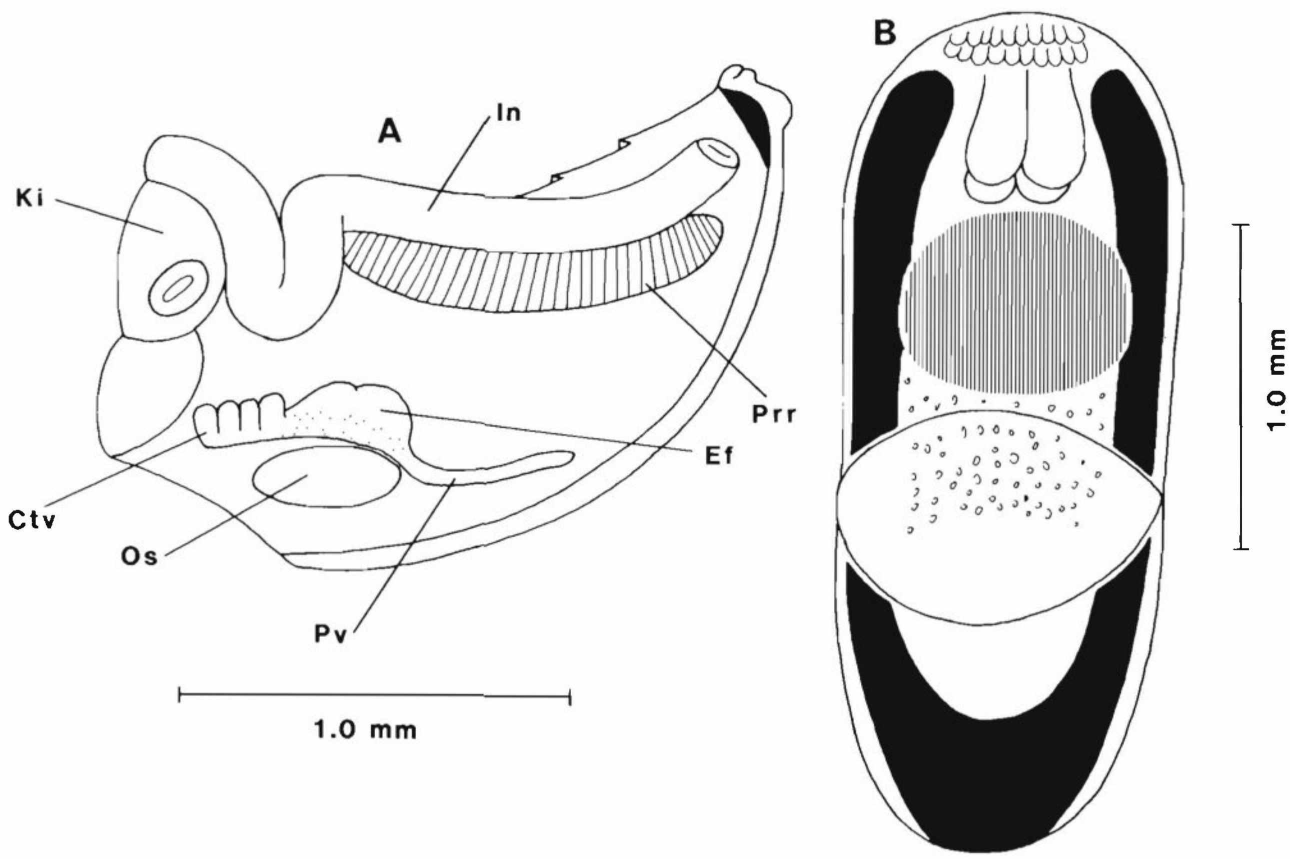
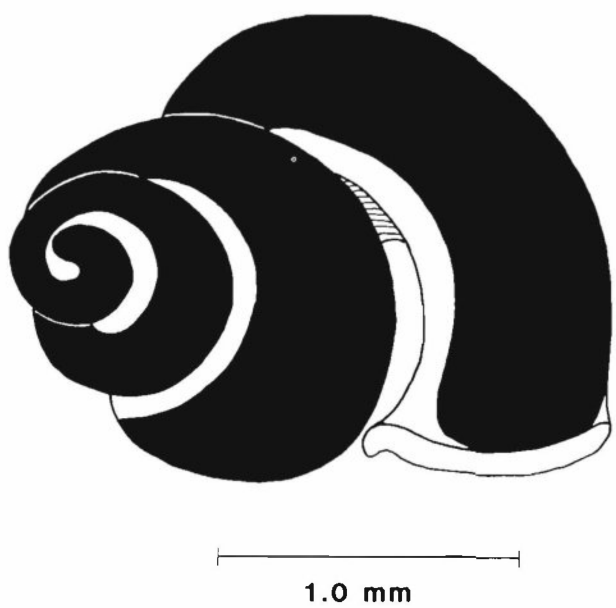


Figure 6

Pallial cavity and foot of *Assiminea infima*. A. Roof of the pallial cavity. Note the pigmented swelling anterior to the rectum. B. Dorsal aspect of the foot, showing the darkly pigmented region (black) and attachment area (lined screen) of the body. The pedal glands (at anterior end of foot), operculum, and glandular clusters (small circles) are also indicated. Ctv, ctenidial vestige; Ef, enlarged "filament"; In, intestine; Ki, kidney; Os, osphradium; Prr, ridged pallial roof; Pv, pallial vein.



The eyespots are near the distal ends of the tentacles (Figure 4A). A ciliated groove (Figures 4B, 5-Gv) extends along each side of the head-foot, originating where the snout joins the anterior foot and ending on the side of the "neck" (Figure 5B). The right lateral (or omniphoric) groove, along which fecal pellets frequently pass, is much wider than the left groove. The grooves are well inset and surrounded by angular, unciliated ridges. The operculigerous lobe (Figure 4-Ol) is quite swollen and fleshy, bulging outward from the surrounding portion of the head-foot (Figure 5A). The broad, thickened foot is rounded anteriorly and posteriorly (Figures 4, 5A). The center of the anterior pedal crease (Figure 5A) has a large pore through which pedal glands discharge. No suprapedal fold

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Figure 7

Dorso-right lateral aspect of body (minus head) of *Assiminea infima*. Darkly pigmented areas are shaded black.

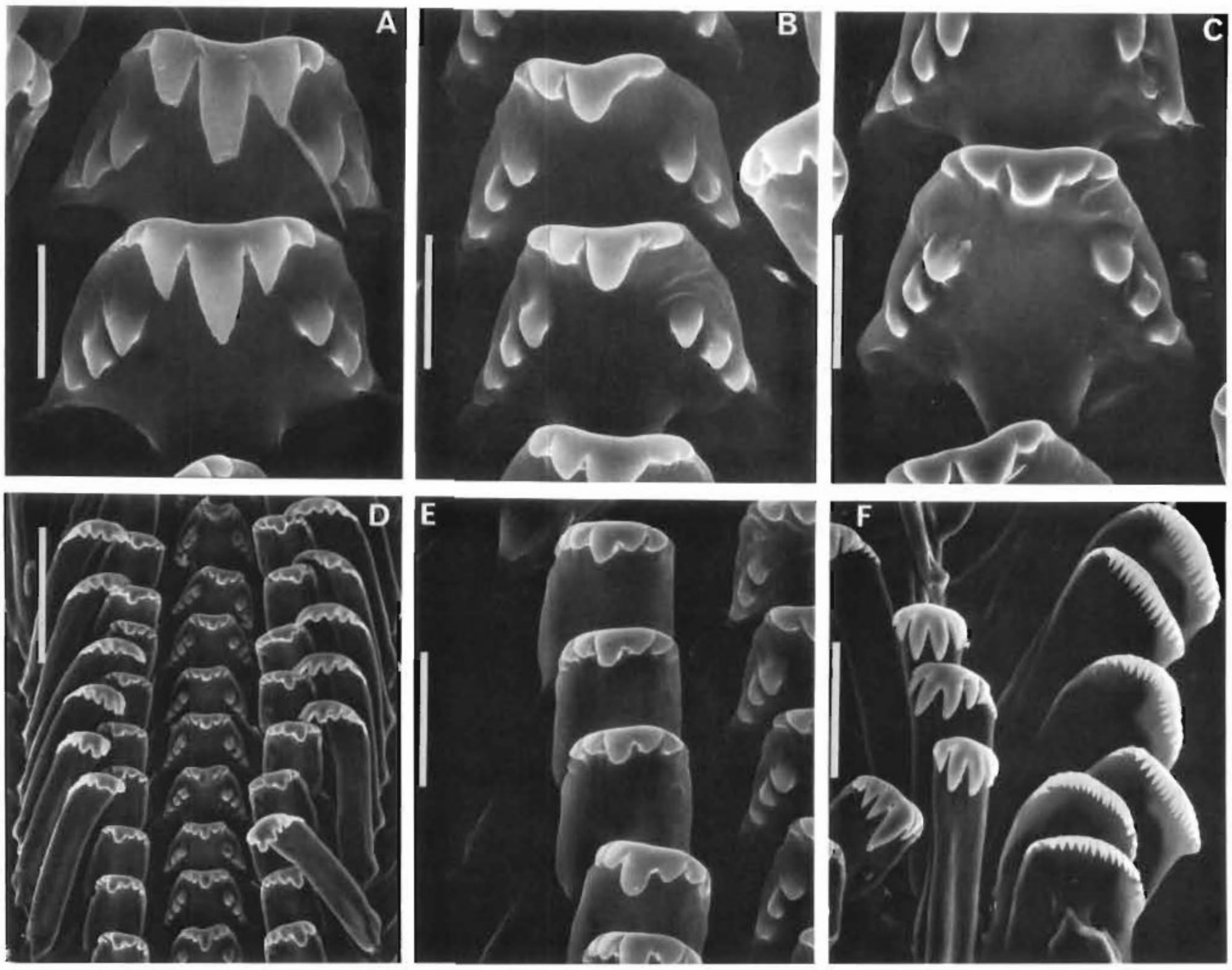

Figure 8

Photographs (SEM) of the radula of *Assiminea infima*. A–C. Centrals (scales = 8.6 μm, 10.0 μm, 8.6 μm). D. Section of radular ribbon (scale = 38 μm). E. Laterals (scale = 15 μm). F. Inner (to left) and outer (right) marginals (scale = 23.1 μm).

(*sensu* DAVIS, 1967) is evident, although the pedal crease extends slightly back along the foot (Figure 5A). A small dorsal flap is offset from the remainder of the foot by this crease and a shallow trough (Figures 4B, 5A). The pedal glands (Figure 6B) include both a large number of gray, small-sized glands as well as two pairs (one dorsal to the other) of much larger, white glands. The sole of the foot is densely ciliated.

The snails are active, especially when submerged. It is not known whether the snails tolerate prolonged submersion. Progression is steplike with the anterior quarter of the foot (the portion encompassing the dorsal anterior flap) lifting off the substratum, stretching and then adhering, with the posterior of the foot then following.

Pigmentation: For the Badwater Spring population, dark melanic pigment covers much of the head (posterior to the oral lappets), although circular unpigmented areas surround the eyespots (Figure 4). Occasionally the oral lappets are also pigmented. The deep creases in the snout are also unpigmented or have only a light dusting of melanin. White granules are clustered behind the tentacles. Most of the side of the head-foot is darkly pigmented, although pigment is absent from the ciliated grooves and sides of the foot (Figure 4B). The operculigerous lobe, which contains glandular clusters, is unpigmented or has a gray-colored appearance. The entirety of the dorsal body surface is darkly pigmented (Figure 7). A similar pigmentation pattern for the head-foot and body occurs in snails from Cottonball Marsh, whereas specimens from Travertine and Nevares springs generally lack pigment in the head-foot and have dorsal melanic body pigment only on the gonad.

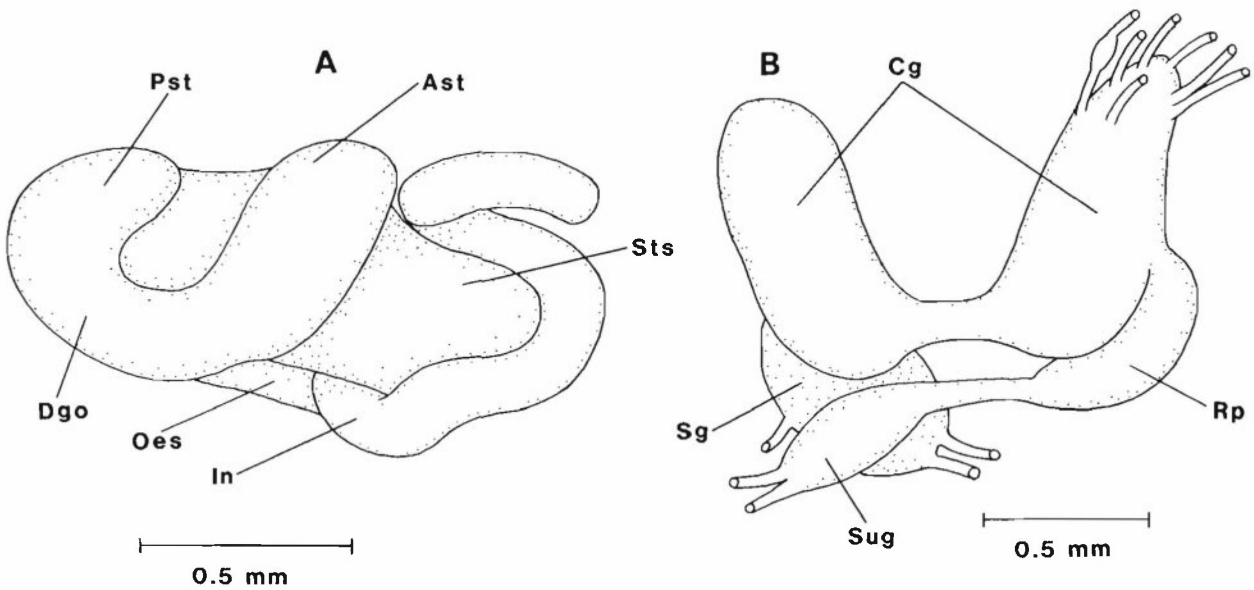

Figure 9

Stomach (A) and dorsal nervous system (B) of *Assiminea infima*. The positions of nerves are only indicated on the right cerebral glanglion. Note the enlarged ganglion (Sg) representing the fusion of the left pleural and suboesophageal ganglia. Ast, anterior stomach chamber; Cg, cerebral ganglion; Dgo, opening of the digestive gland into the stomach; In, intestine; Oes, oesophagus; Pst, posterior stomach chamber; Rp, right pleural ganglion; Sg, fused left pleural and suboesophageal ganglia; Sts, style sac; Sug, supraoesophageal ganglion.

Pallial cavity: The pallial cavity roof is shown in Figure 6A. The reduced ctenidium (Ctv) has three or four small, stubby filaments as well as a single broad, elongate "filament" (Ef) (anterior to the above), all of which are generously ciliated. It was not determined whether the latter has skeletal rods, which would indicate homology with true ctenidial filaments. The pallial vein (Pv) extends anterior to the filaments and ends near the mantle collar. The large osphradium (Os) is centered along the length of the ctenidial axis-pallial vein. The intestine (In) has a tight, U-shaped loop just anterior to the posterior end of the pallial cavity. Anterior to the loop, the intestine is fringed to the left (beneath in Figure 6A) by a well-delineated narrow, ridged area of the pallial roof (Prr), which is probably a hypobranchial gland. This region was seen (in section) to consist of tall, gobletlike cells. The mantle collar is smooth, except at the extreme right (above in Figure 6A), where a bulging swollen area (pigmented in the Badwater Spring population) occurs. The left side of the pallial cavity floor has dense, elongate cilia (Figure 5B) that are not continuous with the ciliary tract in the left lateral groove of the head-foot.

Digestive system: The radula is shown in Figure 8. The typical radular formula is as follows: central, 2-1-2/3-3; lateral, 2(3)-1-3; inner marginal, 9-10; outer marginal, 15-17. The width of the central tooth is about 2.19 μm. Cusp wear was apparent in all radulae examined, with cusps blunted or broken on the anterior portion of the ribbon. The basal process is well developed on the central tooth (Figure 8C). Note that the inner and outer marginals are quite dissimilar in tooth and cusp morphology (Figure 8F). The stomach and style sac are roughly equal

Table 2

Six morphological differences between *Assiminea infima* and *A. californica* (data from FOWLER, 1977).

Assiminea infima	*Assiminea californica*
1. Shell broadly conical, with moderate-highly convex whorls	More elongate-conic, whorls only slightly convex
2. Ctenidium with series of small, stubby filaments as well as a single, enlarged filament	Enlarged filament absent
3. Mantle collar with thickened swelling by the anus	Mantle collar smooth
4. Hypobranchial gland restricted to narrow region along left side of intestine	Gland covers most of pallial roof
5. Anterior vas deferens coils on right side of prostate	Anterior vas deferens without coils
6. Albumen and capsule glands nearly equal in length	Albumen gland relatively small

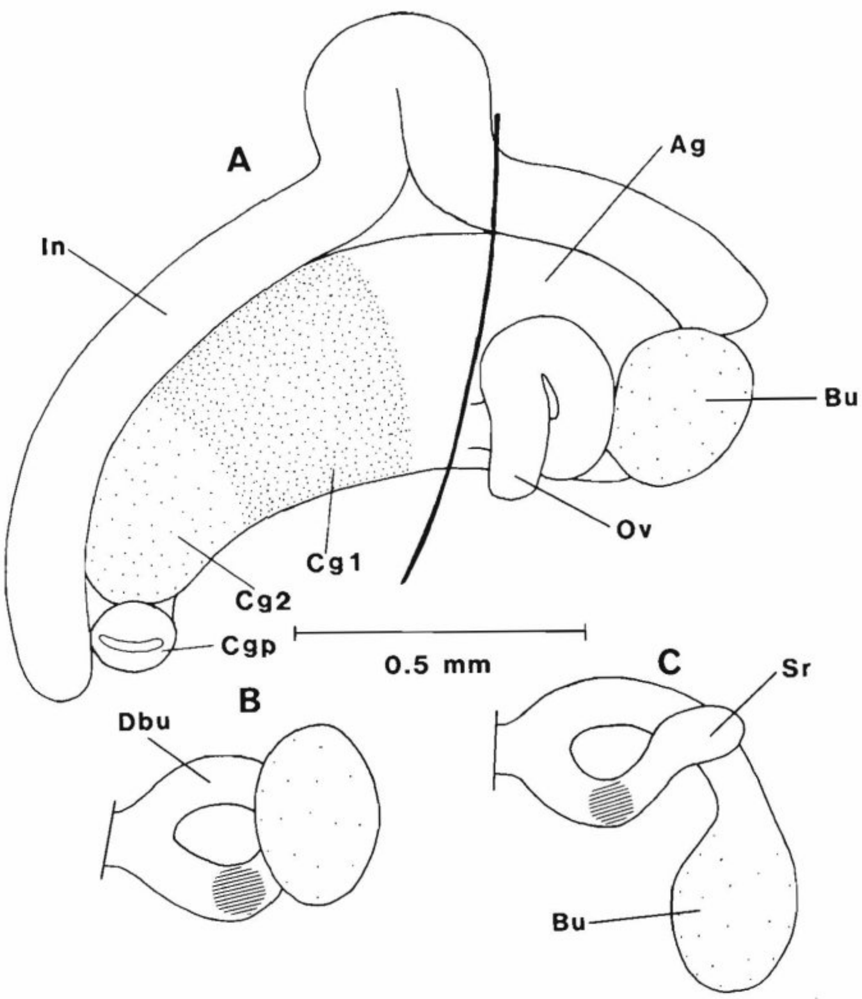

Figure 10

Right lateral aspect of pallial oviduct (A) and bursa copulatrix complex (B, C) of *Assiminea infima*. The oviduct coil was removed in B and C. Note the tripartite capsule gland. The thickened curving line in A (crossing the pallial oviduct) indicates the posterior end of the pallial cavity. The screened (lined) region in B and C indicates the junction with oviduct. In C, the bursa has been rotated to the left (toward the reader) to reveal the seminal receptacle. Ag, albumen gland; Bu, bursa copulatrix; Cgp, muscularized, anterior capsule gland section; Cg1, posterior capsule gland section; Cg2, middle capsule gland section; Dbu, duct of bursa; In, intestine; Ov, oviduct; Sr, seminal receptacle.

in length (Figure 9A). The posterior end of the stomach is well rounded and without a caecal chamber.

Nervous system: Study was restricted to the dorsal ganglion complex (Figure 9B). The cerebral ganglia (Cg) are connected by a short commissure. The right pleural (Rp) and supraoesophageal (Sug) ganglia are similarly connected by a short commissure; the RPG ratio (see Davis *et al.*, 1976) is 0.19. The left pleural ganglion and suboesophageal ganglion are fused, forming a single large ganglion (Sg).

Female reproductive system: The simple, lobate, white ovary occupies a single whorl posterior to the stomach. The pallial oviduct (Figure 10A) consists of the clear albumen gland (Ag) and three distinct capsule gland regions: a large, white-colored posterior section (Cg1), a smaller, clear, middle section (Cg2), and an anterior, muscular, papilla-like section (Cgp) with a slitlike terminal opening. The proximal end of the papilla is coiled onto the right side of the clear capsule-gland section into which it opens. The large bursa copulatrix (Bu) is positioned at the posterior end of the albumen gland (left side), while

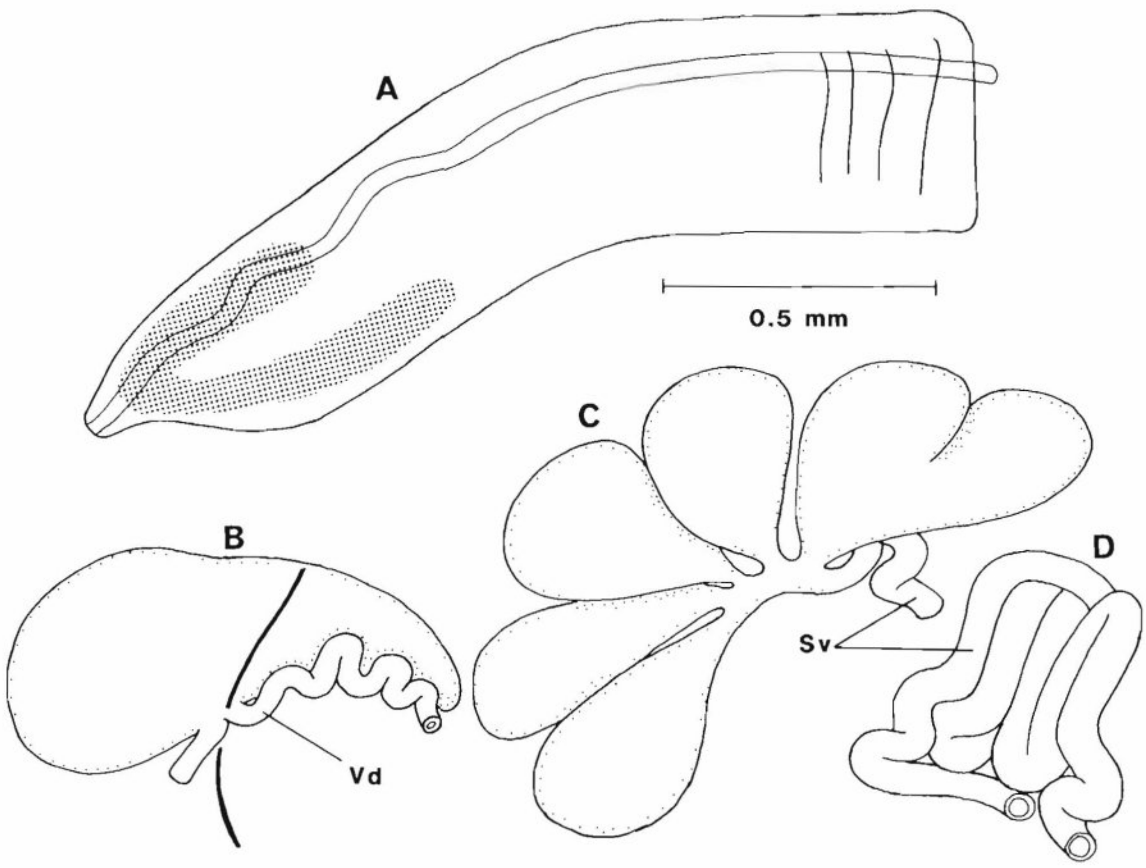

Figure 11

Male reproductive system of *Assiminea infima*. A. Dorsal aspect of penis. The stippled area indicates the densely glandular region. B. Right lateral aspect of prostate. The thickened curving line crossing the prostate indicates the end of the pallial cavity. C. Right lateral aspect of the testis, with the entirety of the seminal vesicle portrayed to the right. Sv, seminal vesicle; Vd, vas deferens.

the seminal receptacle (Sr) is pressed against the right side of the bursa (not visible in Figure 10A, but see Figure 10C). The oviduct (Ov) loops once on the left side of the albumen gland before receiving the duct of the seminal receptacle (Figures 10B, C). The oviduct and elongate bursal duct (Dbu) then join before entering the anterior end of the albumen gland (Figure 10C). Sperm enter the bursa via the pallial oviduct.

Male reproductive system: The testis, consisting of a few large lobes posterior to the stomach, is shown in Figure 11C. The seminal vesicle (Sv) consists of a small number of tall loops that are largely hidden by the testis. The prostate (Figure 11B) is elongate and enlarged, with half its length pallial. The anterior vas deferens (Vd, Figure 11B) exits near the mid-point of the prostate and continues as a loosely coiled, non-muscular tube before entering the "neck." The vas deferens also occasionally coils in the base of the penis. The penis (Figure 11A), which coils counterclockwise on the "neck," is relatively large, simple, and bladelike, with a narrow tip. The penis tip has a terminal, eversible papilla. Small annulations (not shown in Figure 11A) extend along much of the inner curvature. The well-defined, dense cluster of glands (stippled area) occurs in the anterior one-third of the penis. The gray glandular clusters consist of groups of both large and quite small spherical bodies. The epithelia of the penis are glandular and unciliated throughout.

Habitat

Badwater: Small seeps at Badwater discharge into two shallow (less than 5 cm) pools, 70 m apart (Figures 12, 13A), occupying an estimated 2023 m^2 (Hunt *et al.*, 1966). The salt-crust-covered sump that Badwater occupies is moist throughout, with the water table lying at or just beneath ground level. Spring sources are particularly no-

Figure 12

Aerial photograph of Badwater, showing the two large, permanent pools (top of photo, south pool; bottom, north). The width of the highway is about 7 m. Note the two whitened outflow channels from the south pool and the pickleweed bushes fringing the northeast portions of the pools. Photograph by P. Rowlands (Jan. 1986).

ticeable at the northeastern corner of the south pool (Figure 13B). During most of the year Badwater has no outflow. HUNT *et al.* (1966) estimated total discharge as 0.63 L/sec; water temperature at one of the spring sources was 17.0°C. Badwater is virtually saline, with total dissolved solids averaging about 23,000 ppm (HUNT *et al.*, 1966). Aquatic vegetation consists of dense stands of ditch-grass (*Ruppia* sp.), which are most common in the north pool. Pickleweed (*Allensolfia occidentalis*) fringes parts of both pools. The perimeter of the north pool is largely fringed by a salt-crust roof overhanging (sometimes just touching) the water's edge by 5–10 cm (Figure 13C). The south pool perimeter has been trampled down over the years by tourist activity and a salt-crust roof is currently restricted to the southeastern portion of the pool and seep inflows to the pool. *Assiminea infima* is most common on the undersides of the salt-crust roof (Figure 13D), where the snails are moistened and sometimes submerged. Snails were removed and counted from a few measured pieces of salt crust fringing the north pool (23 February 1985), yielding densities ranging up to 6748/m^2. Snails also occur under emergent offshore salt-crust pieces, on submerged drift-grass, and on moistened pickleweed roots in shaded situations. As much as 70–80% of the total Badwater population dwells in the north pool, with the density highest on the northern side of the pool where algal growth is low

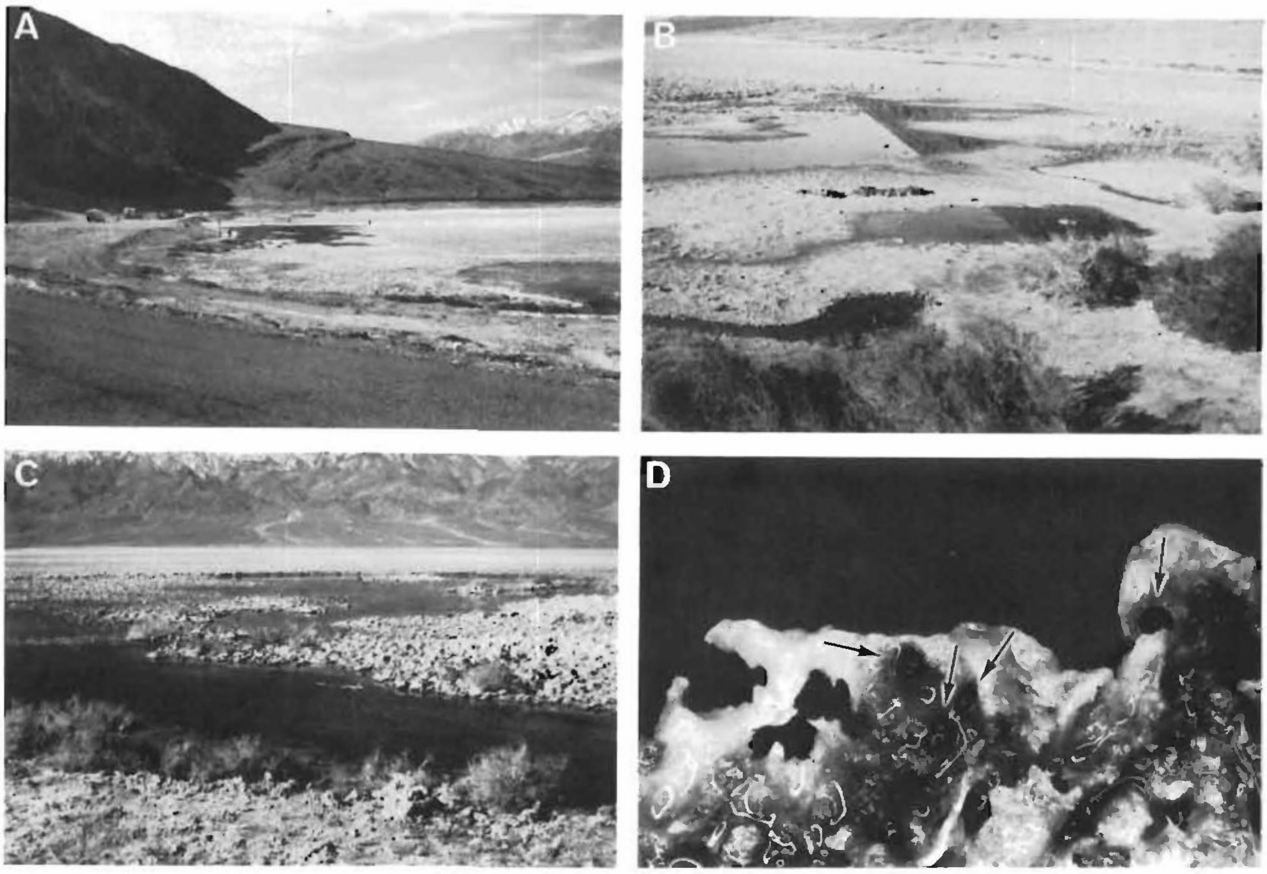

Figure 13

Badwater Spring. A. North (right) and south (left) pools (16 Feb. 1985). B. Seeps (3 cm across) feeding the south pool (23 Feb. 1985). C. North pool, with fringing salt crust and occasional pickleweed (16 Feb. 1985). D. Underside of salt-crust roof at north pool (piece measuring about 13 cm across), showing *Assiminea infima* (indicated by arrows). Photograph (Jan. 1986) by P. Rowlands.

and spring inflow probably occurs. Additional details of *A. infima* ecology at Badwater can be found in BERRY (1947) and TAYLOR (1981).

Travertine Springs: Travertine Springs emerge from low travertine mounds as a series of thermal (30–32°C) rheocrenes draining into Furnace Creek Wash. The springs are fairly small, with outflows typically 0.5 m across and 1–5 cm deep. The spring water is much softer than that at Badwater, with total dissolved solids of 640 ppm (HUNT *et. al.*, 1966). Dense sedge growth fringes the outflows (Figure 14B), shading much of their length. One of the larger springheads has been partly capped and the lower reaches of the streams now collect into diversion works. *Assiminea infima* is uncommon at Travertine Springs, with occasional individuals found in moistened masses of living and dead sedges along the stream outflows. This habitat is quite limited at Travertine Springs as the extent of sloping banks, which provide a moistened riparian environment, is minimal.

Nevares Springs: Nevares Springs emerge from a large travertine mound as thermal (30–35°C) rheocrenes, coalescing to form a single stream flowing along a wash (Figure 14C). The shallow (less than 6 cm) spring outflows occupy either narrow (about 0.5 m) incised channels or fan out as broad (3 m) streams. Riparian sedges are common along the streams on the mound, but are absent from the well-scoured wash. The largest spring has been capped, and at least one springhead was dug out in the past in an effort to increase discharge. *Assiminea infima* is moderately common in dense, moistened riparian vegetation lining the sides of upper spring outflows; no specimens were found along the stream in the wash.

Cottonball Marsh: Cottonball Marsh occupies a large (about 2.56 km^2) area on the west side of Death Valley. Salt Springs emerge west of the marsh and flow into large pools, which drain into the marsh farther out on the salt pan. Additional springs emerge on the salt pan in the middle of Cottonball Marsh (Figure 14A). HUNT *et al.*

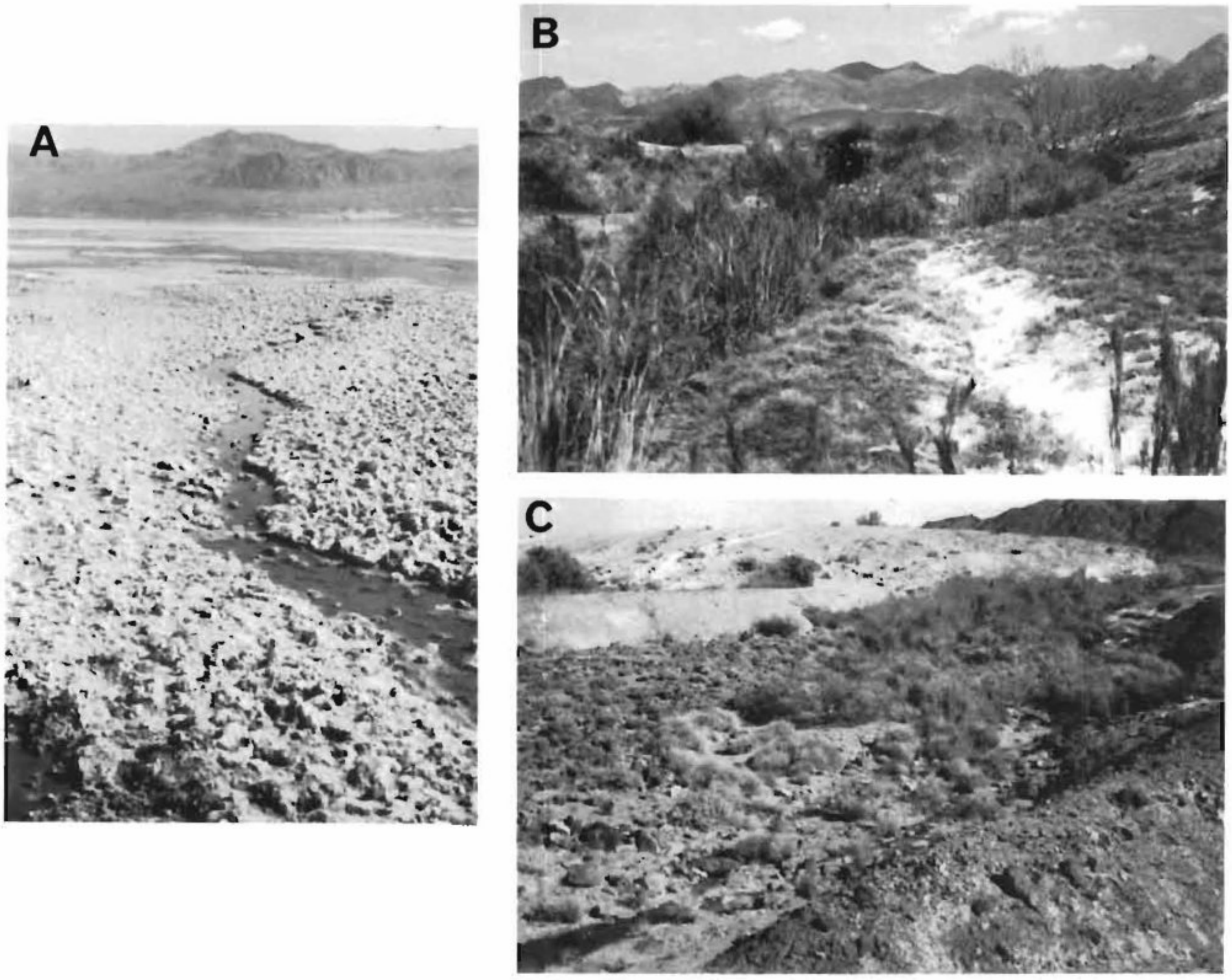

Figure 14

Assiminea infima localities. A. Spring brook (0.5 m across) flowing eastward (away from viewer) in Cottonball Marsh (22 Feb. 1985). B. Outflow of Travertine Springs, with dense riparian cover (2 Feb. 1985). C. Nevares Springs (1 Feb. 1985). Springs emerge on large travertine mound in background.

(1966) estimated the total discharge of the marsh to be 44 L/sec. Spring inflows to the marsh are thermal (31°C) and the marsh is saline, with total dissolved solids ranging from 14,000 to 160,000 ppm (Hunt *et al.*, 1966; LaBounty & Deacon, 1972). Water depth varies from less than 1 cm to nearly 1 m in the deep pools. As at Badwater, a salt crust covers much of the marsh and forms a fringing roof at the water's edge in many places. Saltgrass (*Distichlis* sp.) and pickleweed are common only at Salt Springs; the remainder of the marsh is almost entirely devoid of vegetation. Cottonball Marsh is in a remote portion of Death Valley rarely visited by people and remains in pristine condition. At Salt Springs *Assiminea infima* is common on the bases of moistened riparian vegetation and on the undersides of the salt-crust roof. Snails were not found between Salt Springs and the point where additional springs emerge, about 1.6 km out onto the salt pan. At those latter springs, *A. infima* is very common under the salt-crust roof (moistened or submerged) fringing stream outflows, especially on algal-covered salt-crust pieces.

DISCUSSION

Fowler's (1977, 1980) detailed study of *Assiminea californica* provides sufficient data for a morphological comparison with *A. infima*. Such a comparison is of interest as *A. californica*, found in the upper intertidal along the Pacific coast from Puget Sound to the Gulf of California (Taylor, 1981), is the geographically closest coastal representative of the genus to Death Valley, located 280 km inland. The two species can be placed in ABBOTT's (1958) *A. nitida* complex, a worldwide group of small, translucent- and brown-shelled taxa. The two taxa are further united by joint possession of an unusual character-state, fusion of the left pleural and suboesophageal ganglia. Such a character-state is neither seen in Atlantic coast *A. succinea* Pfeiffer, 1840 (MARCUS & MARCUS, 1965:figure 34) nor is its presence mentioned in discussions of the nervous system of *Assiminea* found in ABBOTT (1958:223) and FRETTER & GRAHAM (1962:313). A number of morphological differences do separate these two species (Table 2), the most significant of which involve the pallial-cavity complex. The hypobranchial gland of *A. infima* is quite reduced in areal extent relative to that of *A. californica*, whereas the latter lacks the pallial swelling near the anus (FOWLER, 1977; Hershler, personal observation). Despite these differences it appears likely that the two species are closely related.

The systematics of *Assiminea* in the Death Valley region is by no means resolved in this paper. Snails from additional localities in Death Valley and nearby areas do differ from *A. infima* somewhat in terms of size and shell features. The rarity of *Assiminea* at most of these localities has thus far precluded the collection of samples large enough to allow the detailed morphometric study necessary to resolve the systematic status of these populations.

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