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PLEISTOCENE MOLLUSCA FROM THE SHELTON MASTODON SITE, OAKLAND COUNTY, MICHIGAN, U.S.A.

Steven J. Thurlow[1] and Jeheskel Shoshani[2]

ABSTRACT – Shells of freshwater Mollusca of 15 genera have been collected in Oakland County, Michigan, from July, 1983, to August, 1987, at a mastodon excavation site bearing wood and bone samples radiocarbon dated 12,320 ± 110 to 10,020 ± 80 years before present. All 15 molluscan genera are common in Michigan today. The habitats of the 11 genera of snails and four genera of clams range from swiftly running water to lakes and temporary ponds. The Pleistocene Mollusca of the site show greater diversity than do the Holocene specimens.

Key words: freshwater mollusks, Pleistocene, mastodon.

INTRODUCTION

The Shelton Mastodon Site (SMS) is located 1.6 km east of the intersection of Sashabaw and Seymour Lake Roads in Brandon Township, Oakland County (SE 1/4, SE 1/4, Section 26), Michigan, U.S.A. (Fig. 1). In 1977 the dredging of a pond produced a dump pile containing the mastodon tusk and cranium fragments that first raised interest in the site. The pond was dug along a natural creek that flows to the northeast emptying into Oakland County's "Paint Creek Drain." The creek drains a low marshy ground bounded by glacial moraines. Very few trees are present on the site today, with the ground cover consisting largely of reed canary grass (*Phalaris canariensis* Linnaeus), wild oats (*Avena fatua* Linnaeus) and various members of the family Compositae. The topsoil is made up of Houghton and Adrian mucks and/or Oshtemo-Boyer loamy sands (U. S. Dept. of Agriculture, 1982).

Excavated material includes vertebrates (fish, amphibians, birds, and mammals), invertebrates (mollusks presented here, and insects), diatoms, and terrestrial vegetation (water-logged logs and tree stumps with root systems, numerous conifer cones, needles, and pollen samples), and soil samples. Most noticeable among the mammal remains are the bones and teeth of the American mastodon (*Mammut americanum* Kerr, family Mammutidae, order Proboscidea) and Scott's moose (*Cervalces scotti*, family Cervidae, order Artiodactyla). Samples of wood material associated with *M. americanum* were radiocarbon dated with dates ranging from

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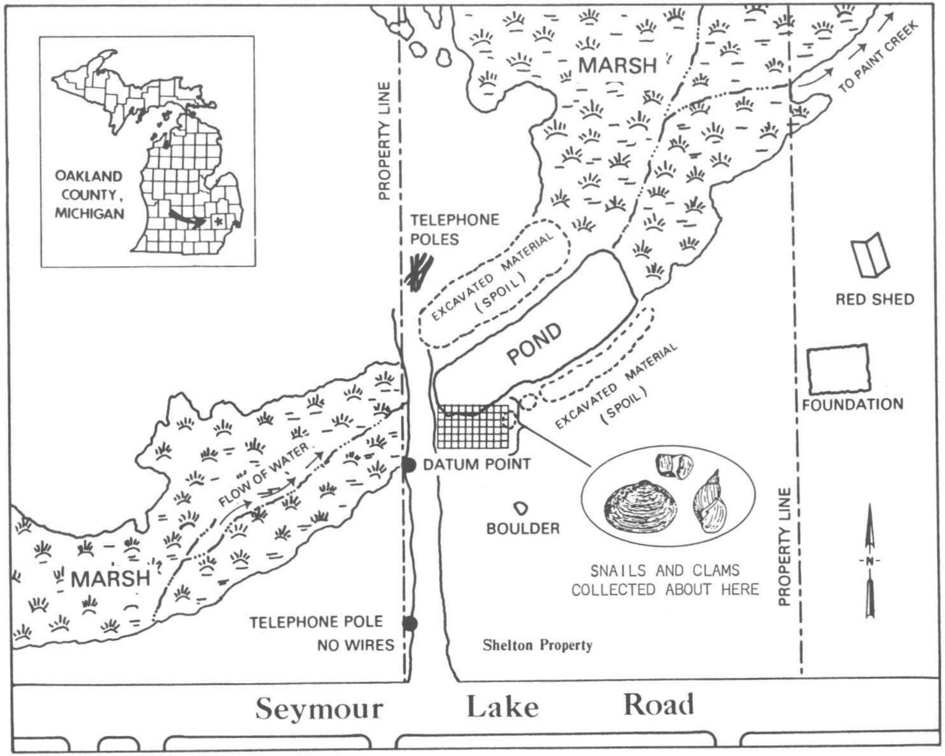

FIG. 1. Map of the Shelton Mastodon Site (Brandon Township, Oakland County, Michigan) showing location of mollusk collections (artwork by J. S. Grimes).

12,320 ± 110 to 11,770 ± 110 years before present (ybp). Likewise, wood associated with the *Cervalces scotti* material was radiocarbon dated at 10,970 ± 130 ybp. The invertebrate material includes shells of freshwater Mollusca of the classes Gastropoda, orders Mesogastropoda and Limnophila, and Pelecypoda, orders Unionoida and Veneroida. Preliminary identification of gastropods following keys by Burch (1982) and of pelecypods with the aid of the key by Pennak (1989) were confirmed or corrected by J.B. Burch, Walter R. Hoeh, and Younghun Jung of the Museum of Zoology, University of Michigan. Voucher specimens have been deposited in the Museum of Zoology, University of Michigan, and the remander of the specimens are deposited in the Cranbrook Institute of Science, Bloomfield Hills, Michigan. The information presented in this report, along with the results of the fauna and flora described elsewhere, has been combined in an attempt to reconstruct the Pleistocene paleoecology of the SMS (Shoshani *et al.*, 1989).

MATERIALS AND METHODS

The standard excavation technique of marking off quadrants and removing soil layer by layer was used (Joukowsky, 1980; Kummel & Raup, 1965). After obvious bones, shells, conifer cones, and other specimens were removed by hand, the remaining soils were passed through 5 mm and 1 mm screens either by hand or with the aid of water pumped from the pond. Because very small shells were missed by this method, some soil samples were placed in water so that the smaller specimens could be picked out. These sampling techniques varied between samples, so that some samples showed disproportionately large numbers of the larger shells.

RESULTS

Table 1 summarizes collection statistics by sample, site location and species, and Table 2 summarizes ecological preferences known for these species in Recent times. Fig. 2 represents a cross-section of the excavation site at sample square U9, where snail and clam shells were found, and Fig. 1 is a map of the SMS.

LIST OF SPECIES AND HABITATS

Class Gastropoda
Subclass Prosobranchia
Family VALVATIDAE

Valvata sincera Say. Large and small lakes, permanent ponds, and large and small rivers (Clarke, 1973).

Valvata tricarinata (Say). Large and small lakes, permanent ponds, and

TABLE 1. Collection statistics of Shelton Mastodon Site mollusks.

Sample	Quadrant	Date	Vs	Vt	Ml	Al	Fg	Ls	Se	Pi	Pg	Ps	Gp	Gc	Ha	Pc	Fp	Ag	Ss	Pm	Pn	Ms	T
I7/83	W end pond	7 Jul 83	-	-	-	-	-	-	-	-	-	-	-	-	7	3	-	-	-	-	-	-	10
I8/124	d1	9 Jul 83	-	-	-	-	-	-	-	-	-	-	-	-	4	1	-	-	-	-	-	-	5
I9/126	D3	9 Jul 83	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	2
I11/164	B3	12 Jul 83	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
I12/170	D4	12 Jul 83	-	4	1	1	-	-	-	-	-	-	12	-	-	-	1	-	-	1	-	-	20
I13/172	D4	12 Jul 83	-	-	-	-	-	-	-	-	-	-	-	-	2	8	-	-	-	-	-	-	10
I14/181	B4	13 Jul 83	-	-	-	-	-	-	-	-	-	-	-	-	17	17	-	-	8	-	-	-	42
I15/184	D4	13 Jul 83	-	-	-	-	-	-	-	-	-	-	-	-	13	6	1	-	1	-	-	-	21
I18/209	E4	17 Jul 83	-	-	-	-	-	-	-	1	-	-	-	-	2	5	-	-	-	-	-	-	8
I21/286	C3/C4	26 Jul 83	1	4	-	-	-	-	-	-	-	-	-	-	23	1	-	-	-	-	-	-	31
I22/374	W end pond	11 Jul 84	-	-	-	-	-	-	-	-	-	-	-	-	8	1	-	-	-	-	-	-	9
I31/501	E3	10 Jul 84	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
I32/502	bb5	21 Jul 85	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	3	2	-	-	7
I41/751	CC3	4 Aug 86	6	29	11	-	6	-	-	-	-	-	30	1	5	-	-	-	-	8	1	-	94
I42/752	B4	8 Aug 86	-	-	-	1	-	-	-	-	2	-	2	-	5	-	-	-	1	1	-	-	12
I44/754	Q11	18 Aug 86	4	82	113	1	11	-	6	-	-	-	61	-	40	6	1	-	3	4	-	1	333
I45/755	A4	12 Aug 86	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1
I48/758	R,S,T tr.	18 Aug 86	-	4	13	-	1	-	-	-	-	-	8	-	23	1	-	-	2	7	-	-	60
I51/951	C-E/3-5	25 Jul 87	3	6	-	-	-	-	2	1	-	-	7	-	127	24	-	-	3	4	-	-	175
I52/952	U10	29 Jul 87	1	3	3	-	2	1	-	-	1	1	8	-	32	1	1	-	-	-	-	-	54
I53/953	U9	1 Aug 87	2	13	8	-	3	-	-	-	-	-	6	-	21	-	-	-	-	12	-	-	65
I54/954	V35	18 Aug 87	3	2	3	-	5	-	-	-	-	-	6	-	7	2	-	-	-	4	-	-	32
I57/957	N of pond	15 Aug 87	-	-	-	-	1	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	4
	TOTALS		20	147	152	3	29	1	9	4	3	1	141	1	340	76	4	1	20	43	1	1	997

KEY: Vs = *Valvata sincera*, Vt = *V. sincera*, Ml = *Marstonia lustrica*, Al = *Amnicola limosa*, Fg = *Fossaria galbana*, Ls = *Lymnaea stagnalis appressa*, Se = *Stagnicola elodes*, Pi = *Physella integra*, Pg = *P. gyrina gyrina*, Ps = *P. g. sayi*, Gp = *Gyraulus parvus*, Gc = *Gyraulus (Armiger) crista*, Ha = *Helisoma anceps*, Pc = *Planorbella campanulata*, Fp = *Ferrissia parallelus*, Ag = *Anodonta grandis*, Ss = *Sphaerium simile*, Pm = *Pisidium compressum*, Pn = *P. nitidum*, Ms = *Musculium securis*, T = total. Number of valves collected are listed for pelecypods.

TABLE 2. Habitats of the SMS mollusks (Clarke, 1973; Baker, 1928; Burch, 1975, Strayer, 1987)

	Lotic			Lentic					Substrate	Aquatic vegetation
	L	S	P	L	M	S	l	s		
Valvata sincera	X	X	X	X	X			X	mud, rocks	present
Valvata tricarinata	X	X	X	X	X	X	X		all types	nearly always present
Marstonia lustrica	X	X				rivers			stones, sand, mud	moderate to thick
Amnicola limosa	X	X		X	X	X	X	X	all types	sparse to thick
Fossaria galbana	X	X	X	X						medium to thick
Lymnaea stagnalis appressa	X	X	p	X	X	X	X	X	all types	present
Stagnicola elodes	X	X	p,v	X	X	X	X	X	all types	usually present
Physella integra	X					rivers			all types	
Physella gyrina gyrina	X	X	p,v	X	X	X	X	X	mostly mud	nearly always present
Physella gyrina sayi	X	X	p,v	X	X	X	X	X	mostly mud	nearly always present
Gyraulus parvus	X	X	p,v	X	X	X	X	X	mostly mud	nearly always on vege.
Gyraulus (Armiger) crista			e						mud	thick
Helisoma anceps	X	X	p	X	X	X		X	all types	always present
Planorbella campanulata	X	X	p	X	X	X	X		all types	sparse to abundant
Ferrissia parallelus	X	X	X	X				X	mud, sand, clay	sparse to thick
Anodonta grandis	X	X	X	X	X	X			all types	sparse to dense
Sphaerium simile	X	X	p	X	X	X	X	X	mud, sand, etc.	always present
Pisidium compressum	X	X	p	X	X	X	X	X	mostly mud, sand	absent to variable
Pisidium nitidum	X	X	p	X	X	X	X		usually mud	absent to thick
Musculium securis	X	X	p	X	X	X	X		usually mud	thick

Only those habitats indicated in the above literature are listed.

Key to lotic habitats: L = large lakes, S = small lakes, P = ponds, p = permanent ponds, v = vernal ponds, e = eutrophic ponds.

Key to lentic habitats: L = large rivers (>100 feet in width), M = medium rivers (50-100 feet in width), S = small rivers (25-50 feet in width), l = large streams (10-25 feet in width), s = small streams (<10 feet in width).

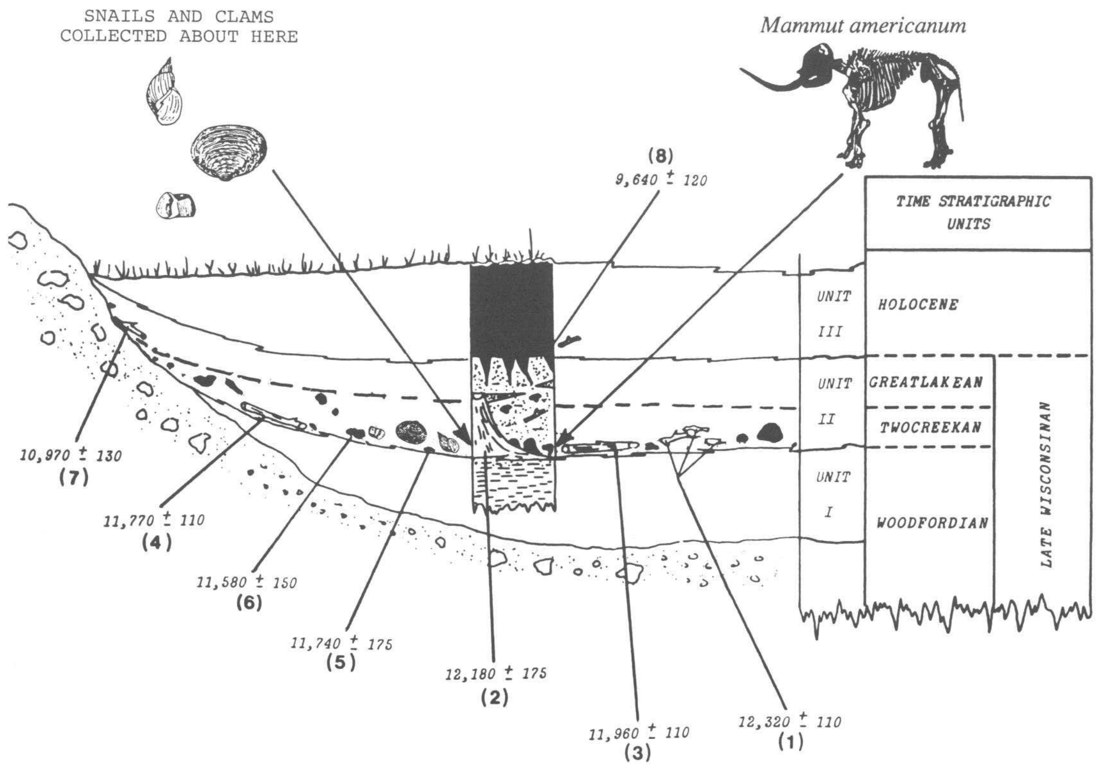

FIG. 2. A generalized cross section of the Shelton Mastodon Site, showing stratigraphy and locations of mollusk and mastodon specimen collections. Radiocarbon dates, in years before present, are numbered 1 through 8 in desending order from the least to most recent (artwork by J. M. Zawiskie).

large and small rivers (Clarke, 1973).

Family HYDROBIIDAE

Amnicola limosa (Say). All unpolluted aquatic habitats where macroscopic aquatic vegetation grows (Clarke, 1973).

Marstonia lustrica (Pilsbry). Eutrophic lakes or eutrophic areas of mesotrophic lakes, with vegetation and sand or mud bottoms (Clarke, 1973), wide variety of habitats, including lakes, ponds, marshes, rivers and streams (Thompson, 1977).

Subclass Pulmonata
Family LYMNAEIDAE

Fossaria galbana (Say). Found in cold, highly oxygenated medium to large lakes or large rivers with abundant vegetation (Clarke, 1973).

Lymnaea stagnalis appressa Say. Any permanent bodies of water which support substantial vegetation (Clarke, 1973)

Stagnicola elodes (Say). Many types of quiet waters (perennial and vernal) with abundant vegetation (Burch & Jung, 1987)

Family PHYSIDAE

Physella integra (Haldeman). Prefers moving water but is often found in standing waters (Te, 1975; Clarke, 1979).

Physella gyrina gyrina (Say). Occurs in almost all perennial-water habitats and in temporarily flooded pools and swamps (Clarke, 1981).

Physella gyrina sayi (Tappan). Found in various lakes, on bottoms of mud, sand, gravel, rock and boulder (Baker, 1928).

Family PLANORBIDAE

Gyraulus parvus (Say). Standing waters of varying productivities and brooks, streams, and rivers. "...one of the most eurytopic and widespread freshwater snails in North America" (Strayer, 1987).

Gyraulus (*Armiger*) *crista* (Linnaeus). Reported from eutrophic ponds and a slow-moving creek (Clarke, 1973) and from a shallow brook (Baker, 1928).

Helisoma anceps (Menke). Lakes, ponds, rivers, and streams (Clarke, 1981).

Planorbella campanulata (Say). Lakes and ponds of all sizes, and in rivers (only slow moving or backwater portions) (Clarke, 1981).

Family ANCYLIDAE

Ferrissia parallelus (Haldeman). Mesotrophic and eutrophic standing waters (Clarke, 1979).

Class Pelecypoda
Order Unionoida
Family UNIONIDAE

c.f. *Anodonta grandis* (Say). Medium to large-sized lakes and rivers with bottoms of all types, with vegetation ranging from thick to absent (Clarke, 1973).

Order Vereroida
Family SPHAERIIDAE

Sphaerium simile (Say). Large to small lakes, permanent ponds, and large rivers to small streams, all with submerged vegetaion Current in the lotic sites is generally slow to moderate (Clarke, 1973).

Pisidium compressum Prime. Large to small lakes, permanent ponds, and large rivers to small streams. Vegetation present in varying amounts (Clarke, 1973).

Pisidium nitidum Jenyns. Large to small lakes, permanent ponds, and large rivers to small streams, nearly always with submerged vegetation. (Clarke, 1973).

Musculium securis (Prime). Large to small lakes, permanent ponds, and slow-moving rivers and streams, vegetation thick to moderate (Clarke, 1973).

CONCLUSION

The presence and abundance of mollusks typical of standing and slow-moving waters corroborates the hypothesis proposed by Shoshani *et al.* (1989) that a small nutrient-rich, oxygenated lake, supporting a diverse molluscan fauna and diatom flora was progressively infilled by clastic sediment over a 2,000 year period (12,320 ± 110 to 10,020 ± 110 ybp). Some expansion and contraction took place during which the deposition of vertebrate material occurred (Shoshani *et al.*, 1989).

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TERRESTRIAL AND FRESHWATER MOLLUSCS OF A HEAVILY-IMPACTED URBAN SITE ON THE UNIVERSITY OF WASHINGTON CAMPUS, SEATTLE, WASHINGTON, U.S.A.

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ABSTRACT – The freshwater and terrestrial molluscan fauna of a disturbed site on the campus of the University of Washington in Seattle, King County, Washington, U.S.A., was sampled. The fauna was dominated by exotic species that are native to Europe. The degree of dominance of the fauna by the exotic species component may be related to the degree of disturbance and subsequent recovery of the major habitat types. The relative proportion of native and introduced species may provide an index to the degree of anthropogenic habitat alteration and habitat regeneration.

Key words: freshwater molluscs, terrestrial gastropods, habitat disturbance, exotic species, native species, Washington, U.S.A.

INTRODUCTION

Native non-marine molluscan faunas have been greatly impacted by a variety of human activities. Impacted sites may support a varied fauna that is likely to be dominated by non-native species. The present survey was conducted during a visit to the campus of the University of Washington in Seattle, King County, Washington. Although an intact native molluscan fauna would not be expected to have survived the habitat alterations to this area, the relative proportion of native and introduced species may provide an index to the degree of anthropogenic habitat alteration and habitat regeneration.

STUDY SITE AND METHODS

The study site is located on the campus of the University of Washington between 23rd Avenue south and the shores of Union Bay, a small embayment off Lake Washington. Margins of the lake were sampled by examining plants, anthropogenic structures, and the lake bottom. Terrestrial habitats were sampled by systematic pedestrian surveys of microsites that appeared likely to conserve available moisture. Few woody plants existed in the area except along the lake shore where shrubs and small trees grew alongside a mixed grass/forb community. The terrestrial habitat is effectively a rather xeric site due to the removal of native vegetation and continued disturbance, although the general region experiences heavy precipitation and low evaporation. Only limited numbers of boards and debris that could supply cover are available at this site. This site was sampled on 9 August 1983.

Twelve sampling sites were identified in the field. Four sites were located along the shallow margin of Union Bay: site 1 – benthic substrate within one meter of the shoreline;

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site 2 – milled boards floating in quiet water near docks; site 3 – submerged portions of vertical dock supports; and site 4 – submerged portions of isolated rush stems. An additional three sites were located in a rush marsh that was relatively homogeneous except for the density of rush stems and the relative percentage of vertical, slanting, and horizontal rush stems; site 5 – subaqueous portions of the rush stems; site 6 – subaerial portions of vertical rush stems; and site 7 – subaerial portions of non-vertical rush stems. A total of five collection sites were located in the terrestrial portion of the study site: site 8 – downed wood close to the shoreline; site 9 – underneath a piece of corrugated cardboard; site 10 – isolated piece of milled lumber; site 11 – a second isolated piece of milled lumber; and site 12 – a third isolated piece of milled lumber.

Voucher specimens are in the Houston Museum of Natural Science, Houston, Texas, U.S.A.

RESULTS

Ten species of molluscs (one bivalve, three freshwater gastropods, and six terrestrial gastropods) were collected during this survey (Table 1). Observations on the various species are presented below.

TABLE 1. Occurrence of freshwater and terrestrial molluscs at study site of the University of Washington campus, Seattle, King County, Washington, U.S.A.

Species	Habitat Type											
	Union Bay				Reed Marsh			Terrestrial				
Sample Site	1	2	3	4	5	6	7	8	9	10	11	12
Sphaerium securis	1											
Pseudosuccinea columella			8									
Stagnicola elodes			5	2	4							
Physella gyrina		4	9	5	3	2						
Cochliocopa lubrica								31		7		3
Oxyloma nuttaliana chasmodes						5	21					
Arion subfuscus											1	
Limax maximus									1			
Deroceras reticulatum									3	2		2
Oxychilus alliarus								13		4	1	1

Sphaerium securis (Prime 1851), a fingernail clam, was represented in the samples by a single small living specimen (4.2 mm shell length) recovered from a bottom sample.

Pseudosuccinea columella (Say 1817) was found on boards of old boathouse supports. The diagnostic cross-striations are very finely sculptured but unmistakable; the shell color is dark brown. This freshwater gastropod is introduced from eastern North America and appears be previously unreported from Washington State (see Henderson, 1929; 1936; Branson, 1977). Other introduced populations of *P. columella* in the western United States have been reported (*e.g.*, Russell, 1971), and this species has been transported around the world as a result of human activities (Malek & Cogswell, 1980).

Stagnicola elodes (Say 1821) is another freshwater gastropod that was found on the same boards as the previous species, as well as on submerged portions of stems of rushes. The largest specimen collected from this site measured 18.35 mm in shell height.

Physella gyrina (Say 1821) is a widespread freshwater gastropod that was common on submerged boards and stems of rushes. A few specimens were observed on the lower portions of aerially exposed stems. The largest specimen collected was 13.8 mm in shell height.

Cochlicopa lubrica (Müller 1774) is a terrestrial gastropod that was abundant under wood lying on the ground near the lake shore. Snails were found above the water level, but the preferred microhabitat seems to be a very mesic location for terrestrial gastropods as the underlying soil was saturated with water.

Oxyloma nuttaliana chasmodes Pilsbry 1948 is a terrestrial gastropod typically found along margins of wetland habitats. At the Union Bay site this snail was found on rushes at and slightly above the water level. Individuals were particularly common on slanting and horizontal rush stalks, whereas only a few were found on vertical stalks. Shell and soft-part anatomies of members of this population have been described by Franzen (1985).

Arion subfuscus (Draparnaud 1805) is a terrestrial slug native to northwestern Europe. At this Seattle site *A. subfuscus* was represented by a single specimen that was found underneath a board in a limited area of mesic microhabitat that was spatially isolated from other suitably mesic areas.

Limax maximus Linnaeus 1758 is a slug native to southern and western Europe. The single specimen observed in this study site was found underneath a piece of cardboard in an area of slightly lower elevation that functions as a very shallow intermittent watercourse. The length of this single specimen when crawling was 107.5 mm.

Deroceras reticulatum (Müller 1774) is a small slug native to Europe. Collections at this site contained one grayish and six whitish individuals. The largest specimen measured 38 mm in length. Several specimens were found with *Limax maximus.*

Oxychilus alliarus (J.S. Miller 1822) is a shelled terrestrial gastropod that is native to western Europe. It was found in the very same mesic microhabitats as *Cochlicopa lubrica. Oxychilus alliarus* was very common in these areas.

DISCUSSION

The terrestrial gastropod fauna of this site on the campus of the University of Washington in Seattle is dominated by introduced species. Such an occurrence is common in heavily impacted urban sites. The only native terrestrial gastropod recovered at this site was *Oxyloma nuttaliana chasmodes,* which is an amphibious species found in the wetland ecotone along the shores of protected inlets of Union Bay. The freshwater fauna consists of one native fingernail clam species and three gastropod species (one introduced into the region and two native to the area).

Most of the terrestrial species are native to Eurasia, although the Holarctic *Cochlicopa lubrica* is also native along the northern margins of North America. Most of the species recovered at this site, especially the exotic slugs, also occur in impacted sites in the northeastern United States (Chichester & Getz, 1973) where precipitation/evaporation ratios are favorable. The urban fauna is very similar to the fauna reported from a residential area in Lynnwood, a suburb of Seattle. Roth & Pearce (1984) reported the same five truly terrestrial species that were found in this study. However, the Lynnwood site also supported populations of *Vitrea contracta* (Westerlund 1871) and *Arion rufus* (Linnaeus 1758). The amphibious snail, *Oxyloma nuttaliana chasmodes* was (quite naturally) not found in the Lynnwood survey.

None of the many native snail species collected in less disturbed sites in rural areas south of Seattle (Kozloff, 1976: 80-92, 203-204; Neck, unpublished) were collected at this urban site. No specimens representing the genera *Allogona, Vespericola, Monadenia, Haplotrema, Prophysaon, Ariolimax,* etc. were recovered at this site. Even the non-native slugs, *Arion ater* (Linnaeus 1758) and *Arion rufus,* which are extremely abundant in urban sites in the Pacific Northwest, were not collected at this site. Note that *Arion rufus* was seen around campus buildings during a cool rain on 11 August 1983, a time during which the disturbed study site was not sampled. These two slug taxa could occur at this site in very low densities with surface activity occurring only during very wet periods. However, the highly disturbed nature of this site and the absence of several mesic habitat indicator species suggest that these slug species do not exist in this study area. The interior campus areas and typical residential areas, *e.g.,* the Lynnwood site reported by Roth & Pearce (1984), provide much more protected microhabitats for these slugs than are present in the current study site. *Vitrea contracta* is a Eurasian species that has been reported only rarely from North America (Roth, 1977; Roth & Pearce, 1984). The absence of *Vitrea contracta* from this campus site also reflects the absence of litter accumulations, a microhabitat favored by this species (Roth, 1977).

The degree of alteration exhibited by each of the major habitat types – aquatic, transitional, and terrestrial – is reflected in the zoogeographic composition of the molluscan fauna. The aquatic system represented by Union Bay is relatively natural, having largely recovered from the highly polluted condition of Lake Washington in the past. Anthropogenic structures, *i.e.*, dock supports and loose, floating boards, have added to the three-dimensional structure of the habitat and have increased the substrate area available to freshwater gastropods. Most of the aquatic species recovered during this study are native to this area; one introduced species, *Pseudosuccinea columella,* was rather common.

All of the truly terrestrial species collected at this site are exotic to this locality. The lack of native species is a reflection of the heavily-disturbed and altered nature of this habitat. Only species that can survive under isolated boards that conserve moisture as well as forms that readily burrow, *e.g.*, the various species of slugs, can maintain viable populations in this area. Native woodland gastropods that are typically found in protective leaf litter and under downed logs are not present, probably because of the absence of these two microhabitat factors and the highly exposed nature of this terrestrial site.

The least disturbed habitat is the transitional lake shore where the native *Oxyloma nuttaliana chasmodes* was observed to be abundant. The native freshwater gastropod, *Physella gyrina,* also occurs in the lowermost portion of subaerially exposed portions of rush stems that dominated the vegetation of this transitional zone.

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THE FRESHWATER MUSSEL AND SNAIL SPECIES OF THE TALLAPOOSA RIVER DRAINAGE, ALABAMA, U.S.A.

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ABSTRACT – Although the river systems of Alabama support some of the most diverse and endangered assemblages of mussel and aquatic snail species in the world, the mussel and snail faunas of the Tallapoosa River drainage have never been fully documented. To increase the available knowledge of these faunas we conducted a survey of 39 tributaries, two reservoir sites, and four main channel sections, collecting 21 mussel species and 11 snail species. Most unionid mussel species were found in the main river channel, reservoirs, and large tributaries. The introduced Asiatic clam, *Corbicula fluminea,* was the most widely distributed bivalve in the drainage, and we collected shells of the federally threatened mussel, *Lampsilis altilis,* from the main river channel in Cleburne, Co., Alabama, U.S.A. We collected two species of unionid mussel not previously reported from the drainage, *Fusconaia ebena* and *Truncilia donaciformis,* while 12 species found in earlier collections were not collected in this survey (likely because we did not survey areas that were intensively sampled in previous studies). The endemic pleurocerid snail, *Elimia flava,* was the most widely distributed gastropod in the Tallapoosa River drainage, collected from 24 tributary sites and the main river channel. Three species of *Physella* and *Pseudosuccinea columella* were common in tributaries. Six other gastropod species were collected only rarely and we were unable to determine the extent of their distribution from these collections.

Key words: freshwater, mussels, Unionidae, *Corbicula fluminea,* snails, Tallapoosa River drainage, Alabama.

INTRODUCTION

North America supports a great diversity of freshwater mussels and snails, with an estimated 500 snail species and 297 mussel species (Pennak, 1989; Williams & Neves, 1995). The river drainages of Alabama harbor the greatest diversity on the continent with at least 175 species of freshwater mussels (Williams & Neves, 1995) and 147 species of freshwater snails (Lydeard & Mayden, 1995) having been collected in the state. The Tombigbee River drainage, flowing from Mississippi east into Alabama, historically supported 46 species of mussels (van der Schalie, 1981). The next basin to the east, the Black Warrior, supported 48 species of freshwater mussels (Williams *et al.*, 1992a). Forty-eight mussel species and 24 snail species have been collected in the Cahaba River, a drainage-adjacent to the Black Warrior (van der Schalie, 1981; Bogan & Pierson, 1993a). The Coosa River once supported 65 species of freshwater mussels (Hurd,

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1974) and 78 snails (Bogan & Pierson, 1993b).

Although large numbers of species have been collected historically in Alabama drainages, the aquatic diversity in the Southeastern United States is rapidly declining. At least 31 species of freshwater snails and 11 species of freshwater mussels are considered to have been extirpated from Alabama waters. Many biologists agree that an additional 64 species of snails and 73 species of mussels should be considered endangered or threatened (Lydeard & Mayden, 1995). Of the 118 species of freshwater snails in the Mobile River Basin, 104 are listed on the Federal Register as candidates for the Federal Endangered Species list (Bogan *et al.*, 1995). As many as 122 of the 175 species of freshwater mussels found in Alabama may be imperiled (Williams & Neves, 1995).

Large gaps in our knowledge of the geographic distribution and habitat requirements of much of this imperiled fauna hinder both status assessments and conservation efforts. For example, the molluscan fauna of the Tallapoosa River has never been fully documented (Hurd, 1971). Previous survey work has been limited to the southern portion of the drainage. A survey of Chewacla and Saugahatchee creeks, within Elmore, Lee, and Macon counties, yielded seven species of snails and 16 species of mussels (Tables 1 and 2). The mussel list was expanded to 26 species through a subsequent survey of these and six other creeks in Elmore, Lee, Macon, and Russell counties (Table 1). Our first objective in this study was to survey waters throughout the Tallapoosa River drainage in Alabama to develop a comprehensive list of mussel and snail species. Our second objective was to compare the distributions of these organisms with physical and chemical habitat characteristics of the tributaries. Previous work has yielded conflicting results relative to the primary factors influencing the distribution of mussels and snails. Many authors have discussed the importance of water chemistry characteristics, such as total hardness, pH, and calcium concentration, to the distribution of mollusks (Boycott, 1936; Macan, 1950; Aho, 1966; Dussart, 1976; Økland, 1983; Pip, 1983). However, physical habitat characteristics, such as depth and substrate composition, have also been considered important to molluscan distribution (Harman, 1972; Salmon & Green, 1983; Lewis & Riebel, 1984; Way *et al.*, 1989; Forbes & Lopez, 1990; Thompson & Hershler, 1991). Lodge *et al.* (1987) suggested that water chemistry determines the distribution of freshwater snails among biogeographic regions, and that a hierarchy of factors (habitat availability, disturbance, predation, and competition) influences their distribution within and among water bodies.

We expected the distribution of mollusks within the Tallapoosa River drainage to be related to a combination of both chemical and physical

TABLE 1. Freshwater bivalve species collected in current and historical surveys of the Tallapoosa River drainage within Alabama.

Species	Current Survey	McGregor (1993)	Pierson (1991)	Jenkinson (1973)	Hurd (1971)	Museum Records[a]
Amblema atrocostata						x
Anodonta grandis[b]	x	x	x	x		
Anodontoides radiatus						x
Corbicula fluminea	x	x	x			
Elliptio arca	x		x			
Elliptio arctata[c]	x	x		x	x	
Elliptio crassidens	x	x	x	x		x
Fusconaia cerina[d]	x	x	x	x	x	x
Fusconaia ebena	x					
Lampsilis altilis[e]	x	x	x	x	x	x
Lampsilis ornata[f]	x	x	x	x	x	x
Lampsilis straminea claibornensis	x	x	x	x	x	x
Lampsilis teres[g]	x	x	x	x	x	x
Lasmigona complanata alabamensis			x			
Leptodea fragilis	x	x	x	x	x	x
Megalonaias nervosa						x
Obliquaria reflexa	x	x	x			
Pleurobema decisum		x	x	x		
Pleurobema perovatum			x	x		
Potamilus purpuratus[h]		x	x	x	x	x
Quadrula apiculata	x	x	x			
Quadrula asperata[i]	x	x	x	x	x	
Quadrula archeri						x
Quadrula rumphiana			x			x
Strophitus connasaugaensis						x
Strophitus subvexus		x	x	x		x
Toxolasma parvus[j]				x	x	x
Tritogonia verrucosa	x	x	x	x	x	x
Truncilla donaciformis	x					
Uniomerous tetralasmus[k]		x		x	x	
Utterbackia imbecillis[l]	x	x	x	x	x	x
Villosa lienosa[m]	x	x	x	x	x	x
Villosa vibex[n]	x	x	x	x	x	x

a: Museum records were provided by Dr. James D. Williams. For further details please see Appendix 4 of Johnson (1997).
b: McGregor (1993) = *Pyganodon grandis;* Pierson (1991) = *Pyganodon grandis;* Jenkinson (1973) = *Anodonta cataracta*
c: Jenkinson (1973) = *Elliptio icterina;* Hurd (1971) = *Elliptio complanata*
d: Jenkinson (1973) = *Fusconaia rubida;* Hurd (1971) = *Fusconaia flava*
e: Jenkinson (1973) = *Lampsilis clarkiana;* Hurd (1971) = *Actinonais carinata*
f: Jenkinson (1973) = *Lampsilis excavatus;* Hurd (1971) = *Lampsilis ovata*
g: Jenkinson (1973) = *Lampsilis anodontoides;* Hurd (1971) = *Lampsilis anodontoides*
h: Hurd (1971) = *Proptera alata*
i: Hurd (1971) = *Quadrula pustulosa;* Hurd (1971) = *Carunculina moesta*
j: Hurd (1971) = *Carunculina moesta*
k: Hurd (1971) = *Elliptio buckleyi*
l: McGregor (1993) = *Pyganodon imbecillis;* Hurd (1971) = *Anodonta imbecillis*
m: Hurd (1971) = *Villosa vanuxemi*
n: Hurd (1971) = *Villosa iris*

TABLE 2. Freshwater gastropod species collected in current and historical surveys of the Tallapoosa River drainage within Alabama.

Species	Current Survey	Hurd (1971)	Museum Record
Amnicola sp.	x		
Campeloma coarctatum[a]	x	x	x
Campeloma geniculum			x
Elimia flava[b]	x	x	
Fossaria humilis			x
Fossaria modicella	x		x
Helisoma anceps[c]			
Micromenetus dilatatus			
Physella cubensis[d]		x	x
Physella gyrina albofilata[d]		x	x
Physella heterostropha pomila[d]	x	x	
Pseudosuccinea columella[d]	x	x	
Somatogyrus sp.[e]	x		x

a: Hurd (1971) = *Campeloma decisum;* UFMNE = *Campeloma decisum*
b: Hurd (1971) = *Goniobasis symmetrica, G. difficilis, G. gerhardti, G. gracilis*
c: Hurd (1971) record of *Helisoma* trivolvis may be *Planorbella trivolvis* or *Helisoma anceps*
d: Hurd (1971) = *Physa pomila*
e: UFMNH record of *Somatogyrus hinkleyi* and *S. pilsbryanus*

factors. The geology of the Tallapoosa River drainage differs relative to adjacent drainages (*e.g.*, the Coosa River drainage), and may supply too little calcium for development of a rich molluscan fauna (van der Schalie, 1981). As such, we expected to find few species inhabiting the tributaries of the Tallapoosa. Low-calcium levels, in combination with low alkalinity, may reduce stream buffering capacity resulting in fluctuations in pH. Under such conditions, pH levels might fall below tolerance thresholds of some molluscan species, further limiting their distributions within the drainage (see Aho, 1966). Relative to physical factors, we expected substrate composition to differ between the Piedmont and Coastal Plain provinces, affecting the distribution of mussel and snail species.

STUDY AREA

From its headwaters in northeast Georgia, the Tallapoosa River flows south-southwest through Alabama until it joins the Coosa to form the Alabama River. In this study, we surveyed the Tallapoosa River drainage within Alabama only. All references to the Tallapoosa River drainage are to waters flowing within the state of Alabama. The river basin drains the Alabama counties of Bullock, Chambers, Clay, Cleburne, Coosa, Elmore, Lee, Macon, Montgomery, Randolph, Russell and Tallapoosa.

Four dams operated by the Alabama Power Company for hydroelectric generation, flood control, and recreation, impound portions of the main channel Tallapoosa River (Fig. 1). Alabama's first hydroelectric plant was built on the Tallapoosa River near Tallassee, Alabama and began operation in 1912. In 1928, Yates Dam was constructed on the same site, impounding 809 hectares between Elmore and Tallapoosa counties. Thurlow Dam, 4.8 kilometers down river from Yates Dam, was completed in 1930 and impounds 232 hectares. Martin Dam, located near Dadeville, Alabama, was completed in 1923 and impounds 16,188 hectares (the largest reservoir on the Tallapoosa River). Finally, Harris Dam, completed in 1982, forms the northernmost impoundment on the Tallapoosa River, impounding a surface area of 4,314 hectares.

The Tallapoosa River Basin lies within two physiographic provinces: the Piedmont and Coastal Plain (Alabama Water Improvement Commission, 1976b). Cleburne, Clay, Randolph, Tallapoosa, Chambers, northern Elmore and northern Lee counties lie within the Piedmont province. This province is characterized by metamorphosed sedimentary and igneous rock, mostly schists and gneisses. Macon, Montgomery, and Bullock counties are in the Coastal Plain, which exhibits different geology, the main soil constituents being sand, clay, and gravel over shale and limestone. A distinctive portion of the Coastal Plain province, the Black Belt, is underlain by chalk. Within the Tallapoosa River drainage, the Black Belt cuts through eastern Montgomery County, southern Macon County, and northern Bullock County (Alabama Water Improvement Commission, 1976b). The Fall Line is formed at the boundary between the Piedmont and Coastal Plain provinces in the vicinity of Thurlow Dam. A substantial change in elevation creates waterfalls and rapids (Mulholland & Lenat, 1992) and also marks the northern limit of marine incursion during the Cretaceous period (Isphording & Fitzpatrick, 1992).

METHODS

We used United States Geological Survey 7.5-minute topographic maps of the Tallapoosa River drainage to locate bridge crossings that could serve as sample sites. A total of 150 sites were identified and visited during July and August 1994, and 35 sites were selected to be used in this study (Fig. 1). Site rejection was based on lack of access, evidence of dumping, heavy siltation, depth greater than 2 meters below the bridge, obvious channel modification (*e.g.*, rip-rap, channelization), and lack of visible current. The formal survey for mussels and snails was conducted during June through August 1995. Water chemistry data were collected at each tributary site during the formal survey and once at each site in

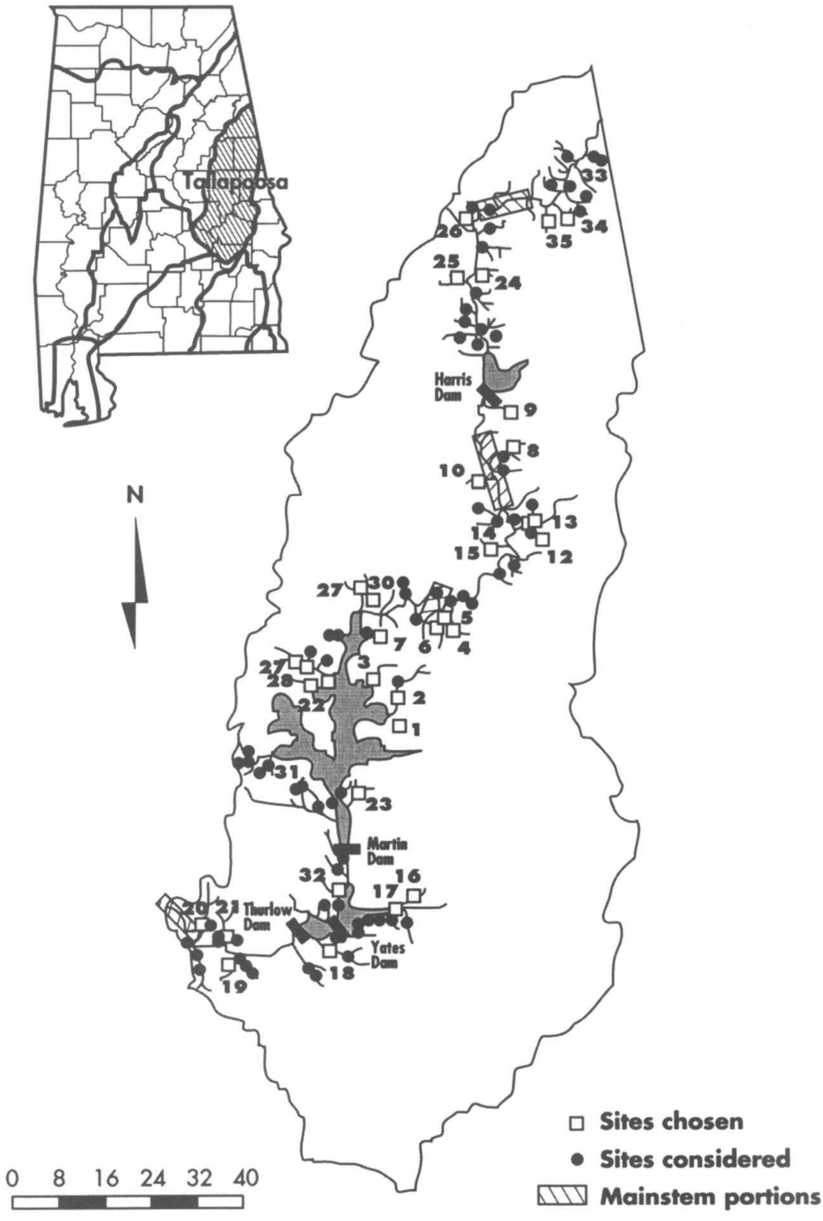

FIG. 1. The Tallapoosa River drainage in Alabama. For specific locations of numbered sites see Johnson (1997).

December 1995, March 1996, and June 1996. Two reservoir sites and four sections of the main river channel were surveyed for bivalves. The beach front at Wind Creek State Resort Park on Martin Reservoir was surveyed on 30 January 1995 and the shoreline surrounding the Alabama Game and Fish public boat ramp on Harris Reservoir was surveyed on 11 January 1996. The main river channel was surveyed from Malone, Alabama to Wadley, Alabama in Randolph County on 11 September 1995, from Cleburne County Road 46 bridge and Cleburne County Road 84 bridge on 12 September 1995, and from Fort Toulouse, Alabama to the US Highway 231 bridge in Montgomery, Alabama on 20 September 1995. Eight additional sites in the Horseshoe Bend National Military Park were surveyed during August 1996.

ABIOTIC DATA COLLECTION

We measured conductivity and water temperature at each site using a YSI Salinity-Conductivity-Temperature meter Model 33. Alkalinity, total hardness, calcium hardness, pH, nitrate, and phosphate levels were measured once every three months at each site using Lamott water testing kits. All water chemistry samples were collected before we surveyed for organisms.

Visual estimates of substrate composition, average stream width, and average depth were recorded once at each site between August 1994 and December 1994. Between June 1995 and August 1995, a riffle and a pool unit in both upstream and downstream reaches were used in determining substrate composition and measuring width and depth. A transect across each unit was established, the width of the stream was measured at this transect and depth was measured at five equally-spaced distances across the transect. To assess substrate composition, we crossed the transect heel-to-toe and the substrate particle at the toe was measured across its longest cross-section (Wolman, 1954; Leopold, 1970; Potyondy & Hardy, 1994). We measured 25 particles from each unit, and a total of 100 particles measured for each stream. We determined stream order by the Horton-Strahler method (Strahler, 1957) and link magnitude from the 7.5-minute topographic maps, where link magnitude is an alternative measure of stream size defined as the number of first-order streams that join to form the stream reach under consideration (Osborne & Wiley, 1992).

BIOTIC DATA COLLECTION

Each tributary site was surveyed once between August 1994 and December 1994 (100 meters downstream and upstream of the bridge crossing) and once between June 1995 and August 1995 (200 meters in both directions). We scanned the substrate for snails and mussels using a viewing apparatus consisting of a plastic waste basket fitted with a Plexiglas© bottom. Substrate was sifted by hand or with a 5 mm mesh dip net for mussels and snails. Sand bars were searched for shell material, and rootwads, leaf packs, woody debris, and stones were examined for live snails. Within main channel and reservoir sites, the shoreline, gravel bars, and animal middens were searched for shell material, and shallow portions were surveyed via snorkeling and wading. Specimens collected were preserved in 95% ethanol. Identifications of bivalves were confirmed by Dr. Paul Hartfield (U.S. Fish and Wildlife Service, Jackson, Mississippi) and gastropod identifications were confirmed by Dr. Fred Thompson (Curator of Malacology, Florida Museum of Natural History, Gainesville, Florida). All specimens were deposited in the Florida Museum of Natural History.

DATA ANALYSIS

Two-way analysis-of-variance was used to assess the influence of individual chemical parameters and seasonal effects on the presence or absence of individual species as well as all bivalves as a group and all gastropods as a group. We compared the values of a chemical parameter across the four seasons (one class variable) and between sites where the species or group was present versus sites where the species or group was absent (*i.e.*, presence/absence of species i or group i was the second class variable). As such, the variable that was analyzed was the value of the chemical parameter itself, which was tested for differences across seasons and between sites with versus without species i. The interaction term described the degree to which differences between sites with versus sites without species i varied across seasons. All chemical data, except pH, were log-transformed to adjust for non-normality. Data from a single site on each tributary were used in the analysis to ensure spatial independence of replicate observations. Of the non-independent sites within a single tributary (sites 4 and 5; sites 12, 13, and 14; sites 16 and 17; and sites 27 and 28), the one with the most complete data set for each site were chosen for inclusion in the analysis. Several data sets were incomplete because data could not be collected from particular sites on a particular date due to equipment malfunction, or bank erosion. Because we were unable to collect abiotic data on sites 11 (>3 cm of manure over substrate), 19 (consistently flooded), 31 (dry stream bed), and 33 (poultry refuse dumped in stream) they were not included in any statistical analysis. Presence of a particular species at two or more sites was necessary for inclusion in the ANOVA. As a result, only four species of bivalves (*Corbicula fluminea* (Muller 1744), *Elliptio arca* (Conrad 1834), *Villosa lienosa* (Conrad 1834), and *Villosa vibex* (Conrad 1834)) and six species of gastropods (*Elimia flava* (I. Lea 1862), *Pseudosuccinea columella* (Say 1817), *Helisoma anceps* (Menke 1830), *Physella cubensis* (Pfeiffer 1839), *Physella gyrina albofilata* (Sampson 1892), and *Physella heterostropha pomila* (Conrad 1834)) were used in the analysis.

We used the Student's t-test to determine whether physical habitat factors differed between sites with versus sites without a particular species. These data also were log-transformed to adjust for non-normality. Sites and species used in the analysis of physical characteristics were the same as those used in the analysis of chemical factors.

RESULTS

Twenty unionid mussel species and one species of corbiculid clam, *Corbicula fluminea,* were collected within the Tallapoosa River drainage during this survey (Table 1). This, combined with an additional 12 species that have been documented historically (Table 1) yields a total of 33 bivalve species. Two species that we collected, *Fusconaia ebena* (I. Lea 1831), and *Truncilla donaciformis* (I. Lea 1828), had never been documented previously in this drainage. In addition, several species found in earlier collections were not collected in this survey. Perhaps this is due to the fact that we did not survey areas that had been intensively sampled in previous studies (*i.e.,* tributaries in Tuskegee National Forest and Lee County).

Eleven species of freshwater gastropods were collected during this survey (Table 2). A previous survey (Hurd, 1971) produced only one additional species, *Helisoma trivolvis,* bringing the total gastropod species list to 12 (Table 2). By current taxonomy, this species is known as *Planorbella trivolvis* (Say 1817) although it may represent a historical misidentification of *Helisoma anceps,* which we did collect. Due to the wide dispersion of collected material and the general uncertainty concerning gastropod taxonomy, we are unable distinguish whether specimens collected in this survey represent previously undocumented locations for these gastropod species.

We did not find any bivalves in 14 of the tributary sites (3, 4, 5, 6, 8, 15, 20, 21, 22, 24, 30, 31, 32, and 35) or in the tributaries within Horseshoe Bend National Military Park. The introduced asiatic clam, *Corbicula fluminea,* was the only bivalve present at nine other sites (1, 2, 12, 13, 16, 23, 29, 33, and 34) and was the most widely distributed of all bivalves encountered, occurring at a total of 18 sites. Unionid mussels and *C.*

fluminea were collected at nine tributary sites (9, 14, 17, 18, 19, 25, 26, 27, 28) as well as in the main river channel.

In addition to *Corbicula fluminea,* three species of unionid mussels, *Elliptio arctata* (Conrad 1834), *Fusconaia cerina* (Conrad 1838) and *Lampsilis altilis,* were collected in the main river channel in Cleburne County, Alabama. Only *C. fluminea* was collected in the main channel between Malone, Alabama and Wadley, Alabama. Two species, *C. fluminea* and *Villosa vibex,* were collected in the main river channel within the boundaries of Horseshoe Bend National Military Park. Finally, 15 species were collected in the main channel of the river below the US 231 bridge in Montgomery, Alabama to Fort Toulouse, Alabama: *C. fluminea, Fusconaia ebena, Truncilla donaciformis, Obliquaria reflexa* (Rafinesque 1820), *Quadrula apiculata* (Say 1829), *Quadrula asperata* (I. Lea 1861), *Lampsilis teres* (Rafinesque 1820), *Lampsilis ornata* (Conrad 1835), *Tritogonia verrucosa* (Rafinesque 1820), *Elliptio crassidens* (Lamarck 1819), *Potamilus purpuratus* (Lamark 1819), *Leptodea fragilis* (Rafinesque 1820), *Lampsilis straminea claibornensis* (I. Lea 1838), *Villosa lienosa, Villosa vibex.*

We did not find gastropods in nine tributary sites (1, 15, 20, 21, 24, 29, 31, 32, and 33) or in the tributaries of Horseshoe Bend National Military Park. *Physella* sp. was the only gastropod found at site 10. *Elimia flava* was the only gastropod collected in ten tributary sites (3, 6, 8, 13, 14, 22, 23, 25, 30, and 34). Fourteen other sites each produced two or more gastropod species including *E. flava* (2, 4, 5, 7, 9, 12, 16, 17, 18, 19, 26, 27, 28, and 35). *E. flava* and *Physella gyrina albofilata* were the two most widely distributed gastropods, co-occurring at ten sites (2, 5, 7, 9, 12, 16,17, 18, 27, and 35). *E. flava* was observed within all main river channel sections surveyed and *P. gyrina albofilata* was collected from a gravel bar in the main river channel section below the US 231 bridge in Montgomery, Alabama downstream to Fort Toulouse, Alabama. Other species appear limited to specific microhabitats requiring more intensive survey to assess their true distributions.

The average number of gastropod species in first- and second-order tributaries were 1.25 ($n = 4$) and 1.36 ($n = 11$), respectively. The average number of gastropod species in third-order streams increased to 1.6 ($n = 10$), whereas fourth-order streams produced the highest average number of species at 4.6 ($n = 3$). We collected only two gastropod species from the fifth-order stream we surveyed.

The presence of the bivalves was significantly associated with several chemical and physical parameters. When we examined the relationship between our measured chemical and physical parmeters and the distributions of all bivalve species combined, we found bivalves were present at sites with higher pH ($F_{7.93}$ = 6.56, p = 0.001), higher total hardness ($F_{7.93}$ = 5.45, p = 0.02), and higher conductivity ($F_{6.63}$ = 5.94, p = 0.02) than was found at sites without bivalves. However, the F values for all bivalves combined are identical to those for *Corbicula fluminea,* indicating that these results are driven primarily by the distribution of *C. fluminea.* When considered individually, no other bivalve species distribution was significantly associated with any chemical parameter. Similarly, the presence of bivalves as a group was significantly associated with greater pool depth ($t_{1.23}$ = 3.97, p = 0.0006), higher stream order ($t_{1.23}$ = -3.01, p = 0.006), and higher link magnitude ($t_{1.23}$ = -2.4l, p = 0.02). When considered individually, the presence of *C. fluminea* was significantly associated with these physical parameters and the t values were identical to those for bivalves as a group. However, the presence of *Villosa lienosa* was also significantly associated with pool depth ($t_{1.23}$ = -2.39, p = 0.03). The presence of gastropods was also significantly associated with several chemical and physical habitat parameters. When we considered all gastropod species combined, they were present at sites with higher pH ($F_{7.93}$ = 12.19, p = 0.0007), higher alkalinity ($F_{7.93}$ = 16.88, p = 0.0001), and higher conductivity ($F_{7.62}$ = 8.92, p = 0.004) than at sites without gastropods. Just as the group results for bivalves were driven by the presence of *Corbicula fluminea,* the gastropod results were driven by *Elimia flava.* However, the presence of *Pseudosuccinea columella* was also associated with higher conductivity ($F_{7.62}$ = 6.26, p = 0.02), and the presence of *Physella gyrina albofilata* was significantly associated with every chemical parameter measured. No physical habitat parameters were significantly associated with gastropods as a group. When considered individually, the presence of *Physella gyrina albofilata* was significantly associated with smaller-pool substrates ($t_{1.23}$ = 2.13, p = 0.04) and the presence of *Physella heterostropha pomila* was significantly associatedwith deeper pools ($t_{1.23}$ = -1.66, p = 0.11) and high stream order ($t_{1.23}$ = -2,17, p = 0.04).

DISCUSSION

Prior to this survey, knowledge of the mussels and snails of the Tallapoosa River was extremely limited, with no previous work specifically addressing chemical and physical habitat characteristics of the streams these organisms occupy within the drainage. Van der Schalie (1981) suggested that geologic formations in the basin may supply too little calcium for the development of the rich molluscan fauna found in other drainages of Alabama. As such, it was widely believed that only a depauperate fauna existed in this drainage. When compared to the adjacent Coosa River drainage, the richness of molluscan species in the

Tallapoosa River drainage could appropriately be described as depauperate. The Coosa River drainage historically supported more than 78 species of gastropods and 65 species of bivalves, whereas the Tallapoosa River drainage is known to support only 12 gastropods and 32 bivalves. Although the disparity in these species numbers certainly reflects, in part, the amount of survey work that has been conducted in each drainage, we believe that the fundamental basis for this disparity is a matter of basin geology. For example, Choccolocco Creek (in the Coosa River drainage) has higher conductivity, alkalinity, and hardness than Tallapoosa River tributaries (Alabama Water Improvement Commission 1976a, 1976b). The Coosa River drainage flows through four geological provinces: the Sand Mountain (sedimentary sandstone and shales), the Southern Appalachian Ridge and Valley (sandstone and shale ridges with shale and limestone valleys), the Southern Piedmont (metamorphic schists and gneiss) and the Coastal Plain (sands, clays and gravels), while the Tallapoosa River drainage flows through only two provinces, the Piedmont and Coastal Plain (Alabama Water Improvement Commission 1976a, 1976b). The limestone deposits of the Coosa River drainage likely supply higher levels of calcium and carbonate, principal components of the molluscan shell, whereas the geology of the Tallapoosa River drainage does not provide the same levels of these nutrients.

Several authors have suggested that water chemistry characteristics such as calcium concentration, hardness and pH influence the distribution, density and richness of molluscan faunas. (Boycott, 1936; Macan, 1950; Dussart, 1976; Økland, 1983). Although the total range of values for each chemical parameter in the tributaries we surveyed was limited and may not exceed any tolerance thresholds of these species, we did find significant associations for the presence of *Elimia flava* and *Corbicula fluminea,* the two most common species collected in this survey. In addition, the presence of *Physella gyrina albofilata* was significantly associated with every chemical parameter measured. These significant associations support our expectations of the importance of chemical characteristics to the distribution of mussels and snails, at least for these widely-distributed taxa.

Geology and water chemistry appear to influence molluscan distribution in the Tallapoosa River drainage and although our statistical tests yielded few significant associations, the physical character of the drainage also may play an important part. Physical parameters, especially stream order, may be more important than our tests indicate because our analysis was based on habitat data from tributaries only; chemical and physical characteristics of the main channel were not assessed. In the

River Continuum Concept, Vannote *et al.* (1981) suggested that the relative dominance of invertebrate functional groups should change with increasing stream order in a predictable manner as a reflection of the type of food resources available. Relative dominance by grazers (such as snails) is predicted to be associated with small (orders 1-3) to medium-sized streams (orders 4-6) and increased primary production (Vannote *et al.*, 1981). Likewise, relative dominance of collectors (such as mussels) is predicted to be associated with medium (orders 4-6) to large-sized streams (orders 6-12) and the availability of particulate organic matter (Vannote *et al.*, 1981). In our survey, snails were absent from the smallest streams that we surveyed, the tributaries within Horseshoe Bend National Military Park, and the number of species increased with stream order to a maximum of eight species in one fourth-order stream. As predicted by the River Continuum Concept, bivalves in the Tallapoosa River drainage were generally found in large tributaries and in the main river channel. Tributaries containing *Corbicula fluminea* were of higher stream order and higher link magnitude than tributaries where they were not present. Unionid shell material was found at nine tributary sites. With the exception of two sites, all were higher order streams (range: 3-5, total range 1-5) with high link magnitude (range: 15-191, total range: 1-191). Thirteen of 20 unionid species collected were found only in the main river channel.

We found an unexpected pattern in the distribution of unionid mussels within the main river channel: three species were collected above Harris dam, one species was collected below Harris dam, and 14 species were collected below Thurlow dam. Williams *et al.* (1992a, 1992b) suggested that anthropogenic disturbances, such as the impoundment of a river, can eliminate unionid mussel habitat by altering existing flow regimes and preventing or decreasing interactions of mussels and their fish hosts. This may explain the low species diversity of unionid mussels in the main river channel below Harris dam. The high diversity below Thurlow dam may result from its unimpeded downstream connections with the Coosa and Alabama Rivers.

Our primary goal in this study was to generally increase the available knowledge of the mussels and snails of the Tallapoosa River drainage. Although we found few significant associations between physical and chemical characteristics of the tributaries and the distribution of these organisms, some patterns were evident. Higher pH, alklinity, hardness and conductivity were significantly associated with the presence of molluscan species within the Tallapoosa River drainage. In addition, molluscan species richness appeared to increase with stream order, as predicted by the River Continuum Concept (Vannote *et al.*, 1981). The average number of snail species increased with stream order up to fifth-order streams, and most unionid mussel species were collected in the main channel of the Tallapoosa River and large tributaries. The absence of unionid species from the river channel below Harris Reservoir and Dam may reflect impacts from alteration of the natural flow regime of the river.

This study also has implications in the assessment of the conservation status of several species found in the Tallapoosa River drainage. Two mussel species, *Pleurobema decisum* and *P. perovatum*, are currently listed as Federally endangered (Department of the Interior, 1993). Although *P. decisum* was not collected in the current survey, it was collected from tributaries in the southern portion of the drainage as recently as 1993 (McGregor, 1993). The most recent collection of *P. perovatum* was made in 1991 (Pierson, 1991), also from southern tributaries. Fortunately, many of the tributaries from which these collections were made flow through the Tuskegee National Forest (McGregor, 1993) and forestry resource management within this area should offer some protection for these endangered species. A third mussel species, *Lampsilis altilis*, is listed as Federally threatened (Department of the Interior, 1993). Like the *Pleurobema* species, *L. altilis* historically was collected from tributaries in the southern portion of the drainage. In this survey, it was also collected from the main river channel in the northern portion of the drainage. In order to protect this species, we recommend further investigation of populations of *L. altilis* in the main channel of the Tallapoosa River.

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EFFECT OF THERMAL DISCHARGES FROM A POWER PLANT ON THE FRESHWATER SNAIL FAUNA IN THREE POLISH LAKES

Malgorzata Strzelec[1]

ABSTRACT – This paper reports the results of a study on the modifications of the freshwater snail fauna in three lakes of central Poland after 40 years of the use of their water in the cooling systems of the power plants "Patnów" and "Konin." In this time period, there has been a progressive reduction in the number of species of native snails and a simultaneous increase in abundance of the introduced thermophilic species *Potamopyrgus antipodarum* (Grey) from New Zealand and *Physella acuta* (Draparnaud) from southern Europe. The transformation of the snail fauna probably is caused by the shift in freshwater vegetation of the lakes and the resulting impoverishment of periphyton, which is the main food for the majority of native snails.

Key words: freshwater snails, thermal discharges, heated lakes, central Poland.

INTRODUCTION

Together with the industrialisation of central Poland, which took place in the second half of the 20th century, the natural freshwater habitats were exploited, *e.g.*, using the waters of rivers and lakes for cooling systems of electric power plants. The water in such plants flows in closed systems: taken out from one site of a river or lake to be discharged in another place after being heated in an industrial installation. Some authors have called the heated discharges into water bodies "thermal pollution." The influence of such pollution on biocenotic patterns has been a matter of interest for many hydrobiologists for more than 30 years. Most past studies have dealt with river habitats rather than reservoirs, because rivers are more often the source of water for cooling purposes in industry.

Studies in which the malacocenoses were analysed in relation to thermal pollution of their habitats are very rare. The most comprehensive one is the publication of Berger & Dziêczkowski (1977) discussing the malacofauna of the heated Konin lakes after 20 years of power plant activity, activity which greatly affected the ecological conditions of the lakes. These authors observed the tendency for extirpation of some species of freshwater molluscs and the considerable expansion of several other species.

My investigations were carried out after another 20 years (during

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the period 1990-1992) in three Konin lakes immediately affected by the discharge of heated water. My study shows that further fundamental changes have taken place with the freshwater snail fauna in these three lakes.

The aim of the present study is to explain the role of some environmental factors in faunistic changes, and in particular the effect of high temperatures and the impact of some introduced foreign species (which have colonised the habitats studied in the last several decades) on the native snail fauna.

MATERIAL AND METHODS

In the littoral zone of the three lakes studied, 5523 living specimens were collected. The snails were gathered by hand from plants, the lakes' bottoms, and submerged objects, including stones, in the water. The samples of silt and plant debris were sieved through a 0.6 mm mesh screen. Because of the qualitative method of collecting material, the proportional abundance of particular species, and not their numbers, is comparable with the data given by Berger & Dziêczkowski (1977) for the period 1970-1971, which also were based on qualitative collections.

The taxonomical similarity of snail communities was calculated according to the formula:

$$S = \frac{w}{a + b - w}$$

where **S** is the similarity index, **w** is the number of species in common in both communities, **a** is the number of species in community A, and **b** is the number of species in community B.

In the water analysis, the chemical methods used were those most convenient.

In this study, I applied the systematics and nomenclature system of Glöer & Meyer-Brook (1994).

STUDY AREA

The Konin lakes are situated in central Poland in the eastern part of the Wielkopolska Lake District, about 10-20 km from the town of Konin (Fig. 1).

All of the lakes are of medium size and are rather shallow. The morphological characteristics of the three lakes studied and the chemistry of their water are shown in Table 1. These lakes belong of the beta-mesosaprobic type, and they are eutrophic. Beside thermal pollution, these lakes are polluted with industrial wastes from several factories and with communal wastes from neighbouring villages. The most polluted are Goslawickie and Patnowskie lakes.

The changes in mean monthly water temperatures in the three particular lakes is shown on Fig. 2. As can be seen, the lakes absorb large discharges of heated water from the power plant. None of the lakes studied freeze in winter.

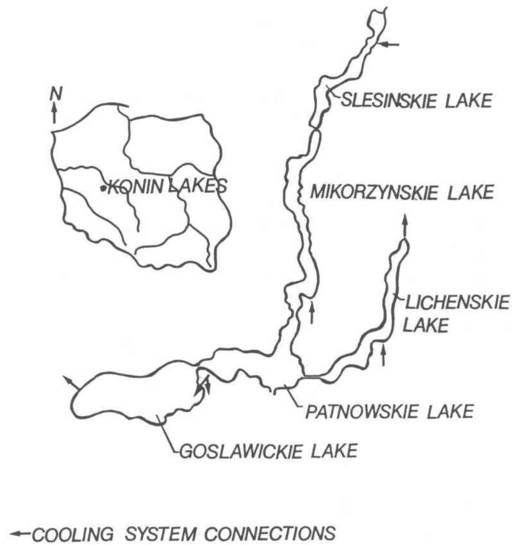

FIG. 1. The study area and its localisation in Poland.

Goslawickie Lake, the largest of the Konin lakes, is also the shallowest. The Patnów power plant is situated on Goslawickie Lake's northern bank. The water going into the power plant comes from the western part of the lake and is discharged, after heating, near the eastern bank. The bottom of Goslawickie Lake is covered by calcarious sediments.

Patnowskie Lake is classified as a shallow lake, but its depth is twice that of Goslawickie Lake. Characteristic of Patnowskie Lake is its strong wave action, which is stronger than in the other lakes. The bottom is mainly sandy, but in some places it is covered with pale silt. The bottom of the southern coast is peaty. The effects of the increase of water temperature in Patnowskie Lake are of less significance than in the other lakes.

Lichenskie Lake is extremely disturbed by the rise of water temperature. The bottom is almost entirely sandy; in only a few places is it covered with a pale organic mud. The vegetation, almost fully destroyed in previous years, regenerated in the 1990s to a very small degree.

SHIFTS IN VEGETATION

Before the heating of their waters, the vegetation of the lakes studied here was typical for central European natural lakes, *i.e.*, eutrophi-

TABLE 1. Morphology of the Konin lakes studied and some data about chemistry of their water in 1991.

Lake Characteristics	Goslawickie Lake	Patnowskie Lake	Lichenskie Lake
Area in ha	454.5	307.4	153.6
Maximal depth in m^3	3.0	5.4	13.3
Volume in $10^3\,m^3$	4865	8143	7471
Total hardness dH°	43.3	43	42.4
Alkalinity in $mval/dm^3$	2.12	2.24	2.12
Ca^{2+} content in mg/dm^3	90.3	50.2	97.3
Mg^{2+} content in mg/dm^3	133.4	159.6	125.0
Fe in mg/dm^3	2.0	0.8	2.0
Cl^- in mg/dm^3	101.9	110.8	112.3
pH	7.9-8.6	8.3-8.6	7.7-8.4

cation occurred to a considerable degree. In that period the algal blooms were often observed. After the rise of water temperature, the abundance of macrophytes, particularly of some submerged plants, has increased, whereas some other species were simultaneously reduced. Beds of *Potamogeton perfoliatus* Linnaeus and *Potamogeton lucens* Linnaeus became very abundant during this period, while *Potamogeton filiformis* Pers. was greatly reduced.

The excessive development of submerged vegetation caused considerable perturbations in the activity of cooling systems of power

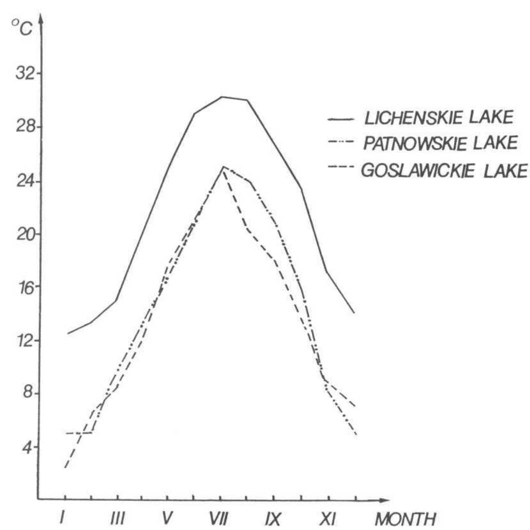

FIG. 2. Course of mean monthly temperatures of the water of the three lakes.

plants. To diminish the unwanted processes, the herbivorous fishes (mainly *Ctenopharynodon idella* Val., the white amur) were introduced successively in 1966-1968. The immediate consequence was an almost complete wasting of submerged plants in Lichenskie and Goslawickie lakes (Biesiadka & Sywula 1977). In Lichenskie Lake, a considerable reduction of reeds was observed at the same time.

The reduction in number of fish which occurred during 1970-1971 caused the gradual regeneration of macrophytes. At the same period the sudden expansion of *Najas marina* Linnaeus was observed in Goslawickie and Patnowskie lakes.

In Goslawickie Lake before heating, the reed beds (mainly *Typha latifolia* Linnaeus, *Schoenoplectus lacustris* (Linnaeus) Palla and *Phragmites communis* Trin.) formed the largest plant associations. Nymphaeids occurred abundantly also. Submerged vegetation covered almost the whole bottom, forming dense conglomerations by the banks. After heating, the increase in *Potamogeton lucens* Linnaeus was especially observed.

The fish activity resulted in elimination of most submerged plants, or those with floating leaves and, to a lesser degree, the reeds. After the decrease in number of fish, an increase in abundance of submerged macrophytes was observed, whereas the rush belt was still scanty. *Najas marina* dominated the vegetation of Goslawickie Lake, forcing the other plant species out.

In the 1990s, the vegetation was rather luxuriant, but consisted of a small number of species, with *Najas marina, Phragmites communis* and *Potamogeton lucens* being dominant.

Patnowskie Lake, affected by the hot water discharges to a lesser degree after the elimination of fish, quickly regenerated vegetation, of which as early as the 1970s the submerged plants became very abundant, with *Potamogeton perfoliatus, Potamogeton lucens* and *Potamogeton filiformis* becoming dominant. A broad belt of *Nymphaea alba* Linnaeus occurred along the northern bank, and along the whole water's edge dense thickets of *Phragmites communis* occurred. After 1971, a rapid expansion of *Najas marina* was observed.

The vegetation of Lichenskie Lake was almost totally destroyed by fish. Of the three lakes studied, the impoverishment in number of plant species was the greatest in Lichenskie Lake. In the 1970s, only small clumps of *Potamogeton perfoliatus* survived in the southern part of this lake, and only single *Phragmites communis* clusters survived in some places in the littoral zone. In the 1990s, a weak regeneration of plants was observed. In total vegetation, the participation of *Najas marina* in the community was smaller than in other lakes.

In Table 2, all vascular plant species found in the three lakes during the period 1990-1991 are listed.

RESULTS

In the period following the rise of water temperature in the Konin lakes, the freshwater snail fauna has changed considerably. The changes included two main trends: progressive impoverishment in number of species, and the total reconstruction of the dominance patterns in particular snail communities. Immediately after the first discharge of heated water from the power plants to the lakes, a visible impoverishment of the snail fauna occurred. In comparison with tanatocenoses (heaps of empty shells accumulated mainly near the lake banks [and dated from before 1970]), various snail species disappeared from the fauna of the lakes. From the fauna of Goslawickie Lake, three species disappeared: *Lymnaea corvus, Anisus spirorbis* and *Gyraulus acronicus;* from Patnowskie lake, six species disappeared: *L. stagnalis, Planorbarius corneus, Planorbis carinatus, A. spirorbis, G. albus* and *G. acronicus;* and from Lichenskie lake, *Planorbarius corneus* disappeared. Some of the species came back in succeeding years. Percentages of particular species in tanatocenoses are rough estimates, of course, because of various persistence of different shells. In the 1970s, the snail fauna contained 21 species in each lake (Berger & Dziêczkowski, 1977) and the faunistic similarity between the lakes was rather high. The similarity index amounts to 0.68 for Goslawickie and Patnowskie, 0.68 for Goslawickie and Lichenskie, and 0.75 for Patnowskie and Lichenskie

TABLE 2. Vascular vegetation of studied lakes in 1990-1992.

Plant species	Lake: Goslawickie	Lake: Patnowskie	Lake: Lichenskie
Potamogeton natans Linnaeus	+	+++	+
Potamogeton lucens Linnaeus	+++	+	–
Najas marina Linnaeus	+++	+++	+
Schoenoplectus lacustris (Linnaeus) Palla	–	++	–
Phragmites communis Trin.	+++	+++	++
Glyceria aquatica (Linnaeus) Wahlb.	++	++	–
Lemna trisulca Linnaeus	–	+	–
Typha latifolia Linnaeus	+++	+	–
Nuphar luteum (Linnaeus) Sm.	–	+	–
Ceratophyllum demersum Linnaeus	+	+	+
Myriophyllum spicatum Linnaeus	+	+	+

lakes.

After another 20 years, a significant decrease in number of species in all lakes occurred, but its measure in individual lakes differed. The loss in Goslawickie Lake amounted to 19 species, but with the simultaneous appearance of three new species. The net result in this lake is that the snail fauna decreased to only five species. From among the snail fauna of Patnowskie Lake, nine species have disappeared and two new species have been found, but only one individual of each. Lichenskie Lake lost 16 snail species, and two new species appeared. One of these newcomers, *Physella acuta,* has recently become the most abundant species in this lake.

All data about the contribution of particular species to the fauna in the tanatocenose and in both study periods are compiled in Table 3.

The similarity index for communities of different periods in the same lake indicate their total reconstruction during 20 years. The similarity index for communities of Goslawickie Lake was 0.14; for Patowskie Lake it was 0.24; and for Lichenskie Lake it was 0.03. Thus, the three lakes now have completely different communities.

In the 1990s, the similarity index for each pair of lakes was: Goslawickie-Patnowskie, 0.27; Goslawickie-Lichenskie, 0.71 and Patnowskie-Lichenskie, 0.40. Community evolution went in the same direction only in Goslawickie and Lichenskie lakes. Patnowskie Lake, probably because of the smaller amount of warm-water inflow, showed smaller changes in the snail fauna and apparently took a distinctly different course of community evolution.

Data compiled in Table 4 show that in the study period the dominance patterns changed in all three lakes. In the tanatocenose of Goslawickie Lake, *Gyraulus acronicus* and *Valvata piscinalis* dominated, but they disappeared almost completely in later periods. In the 1970s, the dominance of species characteristic of eutrophic pond environments began. In the 1990s, an additional effect was exerted by the appearance of the introduced New Zealand species, *Potamopyrgus antipodarum,* which, as shown in previous studies (Strzelec, 1992; Strzelec & Serafinski, 1996) is the cause of significant impoverishment in the snail fauna of water bodies which it has colonised.

In the tanatocenose of Patnowskie lake, the dominant snail species were *Valvata piscinalis* and *Bithynia tentaculata. Valvata piscinalis* also was dominant in the community in the 1970s, but it disappeared prior to the 1990s. The participation of *Bithynia tentaculata* in the community in later years was insignificant. *Potamopyrgus antipodarum* occurred

TABLE 3. Percentage of particular species in materials collected.

Species	Goslawickie Lake			Patnowskie Lake			Lichenskie Lake		
	Tanato-cenose	1971–1972	1991–1992	Tanato-cenose	1971–1972	1991–1992	Tanato-cenose	1971–1972	1991–1992
Valvata cristata (Müller)	0.72	2.89	–	1.98	7.81	0.03	6.63	7.48	–
Valvata piscinalis (Müller)	42.30	0.51	–	63.00	11.58	–	35.70	0.44	–
Potamopyrgus antipodarum (Gray)	–	–	23.78	10.80	30.40	70.66	0.51	0.33	3.44
Marstoniopsis scholtzi (Schmidt)	–	–	–	0.09	0.67	–	–	–	–
Bithynia tentaculata (Linnaeus)	1.80	4.59	–	17.55	2.57	1.73	16.32	0.77	0.75
Bithynia leachi (Shepp.)	0.18	2.55	–	0.27	1.23	–	2.04	2.75	–
Physa fontinalis (Linnaeus)	0.18	5.27	–	–	0.11	–	–	3.41	–
Physella acuta (Drap.)	–	–	3.88	–	–	–	–	–	80.27
Lymnaea stagnalis (Linnaeus)	0.18	0.51	–	0.18	–	–	–	–	–
Lymnaea corvus (Gmel.)	0.18	–	0.08	–	0.22	6.72	–	0.11	2.39
Lymnaea palustris (Müller)	0.18	12.07	–	0.09	1.90	0.99	3.57	3.63	3.29
Radix auricularia (Linnaeus)	–	8.67	–	0.27	0.22	–	–	0.55	–
Radix peregra (Müller)	1.26	23.29	41.62	0.63	1.56	5.38	2.04	8.69	2.39
Planorbarius corneus (Linnaeus)	1.36	0.17	30.64	0.27	–	0.03	0.51	–	7.47
Planorbis planorbis (Linnaeus)	1.62	15.47	–	0.18	3.57	12.38	1.02	23.32	–
Planorbis carinatus (Müller)	1.26	3.57	–	1.08	–	–	–	–	–

TABLE 3. (cont.)

Species	Goslawickie Lake			Patnowskie Lake			Lichenskie Lake		
	Tanato-cenose	1971–1972	1991–1992	Tanato-cenose	1971–1972	1991–1992	Tanato-cenose	1971–1972	1991–1992
Anisus spirorbis (Linnaeus)	0.18	–	–	0.09	–	–	–	3.08	–
Anisus vortex (Linnaeus)	2.34	2.89	–	0.09	6.25	0.71	2.55	4.29	–
Anisus vorticulus (Troschel)	0.18	0.51	–	–	0.33	–	–	0.11	–
Bathyompholus contortus (Linnaeus)	0.54	4.25	–	0.90	4.80	1.02	9.18	18.04	–
Gyrauls riparius – (Westerl.)	–	–	–	–	–	0.51	1.32	–	
Gyraulus albus (Müller)	0.72	2.89	–	7.92	–	0.03	1.53	0.44	–
Gyraulus leavis (Alder)	–	–	–	0.09	0.11	–	–	–	–
Gyraulus acronicus (Fer.)	45.18	–	–	1.80	–	–	–	–	–
Gyraulus crista (Linnaeus)	0.54	0.17	–	1.08	8.37	–	–	0.44	–
Hippeutis complanatus (Linnaeus)	–	0.34	–	1.71	10.82	0.08	1.02	0.11	–
Segmentina nitida (Müller)	0.54	1.87	–	0.09	5.47	0.19	2.55	18.81	–
Menetus dilatatus (Gould)	–	3.74	–	0.45	0.56	0.05	12.24	3.52	–
Acroloxus lacustris (Linnaeus)	0.18	0.17	–	4.50	1.56	–	0.51	–	–
Number of specimens	559	587	1211	1279	896	3643	194	924	669
Species number	21	21	5	24	21	14	17	21	7

TABLE 4. Domination patterns (in %) in different periods.

Lake	Periods		
	Tanatocenose	1971 - 1972	1991 - 1992
Goslawickie	*G. acronicus* 45.18 *V. piscinalis* 42.30	*R. peregra* 23.29 *P. planorbis* 15.47 *L. palustris* 12.07	*R. peregra* 41.46 *P. corneus* 30.64 *P. antipodarum* 23.78
Patnowskie	*V. piscinalis* 63.00 *B.tentaculata* 17.55 *P. antipodarum* 10.80	*P. antipodarum* 30.40 *V. piscinalis* 11.58 *H. complanatus* 10.82	*P. antipodarum* 70.66 *P. planorbis* 12.38
Lichenskie	*V. piscinalis* 35.70 *B. tentaculata* 16.32 *M. dilatatus* 12.24	*P. planorbis* 23.32 *S. nitida* 18. 81 *B. contortus* 18.04	*P. acuta* 80.27

abundantly in the tanatocenose and was dominant in the 1970s, as it was in the 1990s. In latter years, it has constituted more than 70% of the individuals in the snail community.

The rapid increase in the number of *Planorbis planorbis,* which was 0.16% in the tanatocenose, increased to 12.38% of the snail community in the 1990s, and is interesting. This increase of *P. planorbis* is probably due to eutrophication and the increase in the area of the muddy bottom. An enigmatic event is the very great abundance of *Hippeutis complanata* in the community in the 1970s and its complete disappearance in the 1990s. It would seem that this species, which prefers habitats with rich aquatic vegetation and a muddy bottom, would have better conditions for life in the 1990s than formerly. It may be that *H. complanata* was eliminated as a result of the rapid increase of *Potamopyrgus antipodarum.*

Dominant in the tanocenose of Lichenskie lake were the prosobranchs *Valvata piscinalis* and *Bithynia tentaculata,* which have almost completely disappeared in later years. In the 1970s, the transformation from a lake to a pond snail community took place. The colonisation of this habitat in the 1970s by the thermophilous pulmonate *Physella acuta* resulted in the expulsion of the previous snail community. In the 1990s, the newcomer was the only abundant species there. It is interesting that in later years only those species survived that are known to be very resistant to unfavourable environmental conditions. Unexplained is the extinction of the thermophilous *Menetus dilatatus,* which in the 1970s was a fairly abundant species.

CONCLUDING REMARKS

During two 20-year periods after the incorporation of Goslawickie, Patnowskie and Lichenskie lakes into the cooling systems of the power plants "Konin" and "Patnów," a progressive impoverishment of the freshwater snail fauna was observed. This impoverishment may be related to the rise of the water temperature in the lakes and its consequences. The strongest decrease in number of species occurred in Lichenskie Lake, which was the most devastated of the three lakes by thermal pollution. In this lake, the appearance in the 1990s of numerous populations of the thermophilous *Physella acuta* happened at the same time as the total extinction of snail species that previously were dominant in the community. A causal link between these events is possible, but needs further study.

In Patnowskie Lake, the great increase of the *Potamopyrgus antipodarum* population has dominated the freshwater snail community, although the rather good environmental conditions in this lake enabled the survival of other species. However, only two ubiquitous and resistant-to-pollution species (*Radix peregra* and *Planorbis planorbis*) recently formed stable populations, whereas the remaining species occur in very small numbers.

Thus, one may conclude that the changes in the freshwater snail fauna in thermally polluted lakes have various direct or indirect causes. The changes in abundance and diversity of aquatic vegetation may affect the amount and variety of periphyton, which will result in decrease of the food supply for most pulmonate snails. And, in fact, the earliest eliminated species, except the ecologically most tolerant ones, are mainly planorbids and lymnaeids, which feed on periphyton.

It is interesting that as a result of the temperature rise of water in Goslawickie Lake, the typical lake snail community was transformed into a pond community, with *Radix peregra* and *Planorbarius corneus* being the dominant species.

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CORBICULA FLUMINEA IN CUBA

Gloria Perera[1], Lorenzo Diéguez[2] and Mary Yong[1]

Since 1985 a bivalve species from the bivalve family Corbiculidae has appeared repeatedly in the surveys conducted by the Laboratory of Malacology of the Instituto Pedro Kourí, Cuba. These surveys began in 1979 and were performed periodically in order to learn about the distribution and abundance of the different freshwater snails present on the Island. As a result, several new representatives of our molluscan fauna were reported as were *Biomphalaria schrammi* (Crosse) (Yong *et al.*, 1984), *Planorbella duryi* (Wetherby) (Perera *et al.*, 1984), *Biomphalaria peregrina* (Orbigny) (Yong *et al.*, 1989), *Melanoides tuberculata* (Müller) (Perera *et al.*, 1987) and *Biomphalaria orbignyi* (Paraense) (Yong & Perera, 1989).

The unidentified corbiculid clam was sent to Dr. Raymond Pearl at the Houston Museum of Natural Sciences, who kindly identified the bivalve as *Corbicula fluminea* (Müller 1774).

This introduced Asiatic clam is now becoming a dominant species in some areas and attains great densities – mainly in lakes, although it has been found in a wide variety of waterbodies with different ecological conditions that include lagoons, rivers and creeks. The central provinces of Cuba (Villa Clara, Cienfuegos, Sancti Spiritus and Camagüey) seem to be those that have the best conditions for the establishment of *Corbicula fluminea* populations. Some ecological research is being carried out on this bivalve and preliminary results point to a different behaviour as that found in other countries (Diéguez *et al.*, 1993).

The genus *Corbicula* has native species on every continent except those of the Western Hemisphere (North and South America). Yet, even in North America, fossils of the genus have been found, although during the Quaternary corbiculids have been absent from the continent (Britton & Morton, 1982). The modern *Corbicula fluminea* was introduced to the North American west coast sometime prior to 1938, and was first reported by John Q. Burch (1944). Since then, the species has spread across the southern United States and into Mexico (Britton & Morton, 1982), and north in the central states to as far as southern Michigan (White *et al.*, 1984; French & Schloesser, 1991; Janech & Hunter, 1995). Now *C. fluminea* has spread into the Caribbean area, as evidenced by our finding it in Cuba.

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NEW TAXA OF *DIPLOMMATINA* FROM THAILAND (PROSOBRANCHIA: DIPLOMMATINIDAE)

Somsak Panha[1], Budsabong Kanchanasaka[2] and John B. Burch[3]

ABSTRACT – Four new taxa of *Diplommatina* are described from Thailand. *Diplommatina crispata khaochamaoensis* n. ssp., *D. nimanandhi* n. sp., *D. ljirasaki* n. sp., and *D. pongrati* n. sp. were collected from limestone areas at Khaochamao National Park, Chantaburi Province; Banpangkam Cave, Maehongson Province; Khaopoo Khaoya National Park, Pattalung Province; and Tamkuha, Surathani Province, respectively. *Diplommatina crispata khaochamaoensis* has a fusiform, dextral shell, with about 6 3/4 whorls; the penultmate whorl is the largest and has a distinct prominent spiral crest at the middle of the whorl, and prominent radial ribs; spiral striae distinct; columellaris well developed and directed downwards; shell length about 2.7 mm. *Diplommatina nimanandhi* has a conical, dextral, shell with 6 3/4 whorls; the penultimate whorl is slightly larger than the last whorl; the radial ribs of the antepenultimate whorl, the penultimate whorl and the last whorl are elongated semi-tubular projections ("spines"); shell length about 2.8 mm. *Diplommatina jirasaki* has an elongate-conical, acuminate, turreted, sinistral, shell with 7 1/2 angular whorls; the radial ribs from the third whorl to the last whorl are raised medially, becoming on the last several whorls semi-tubular projections; the radial ribs are very widely spaced; shell length about 2.4 mm. *Diplommatina pongrati* has an elongate and narrow, turreted, sinistral shell with 7 1/2 whorls; the last whorl is noticably smaller than the penultimate whorl; the ribs are low and widely spaced; the columellaris is bluntly rounded and not directed downward; shell length about 2.4 mm.

Key words: *Diplommatina angulifera umpangensis*, *D. crispata khaochamaoensis*, *D. jirasaki*, *D. nimanandhi*, *D. pongrati*, Prosobranchia, Diplommatinidae, Thailand.

INTRODUCTION

The cyclophoroidean genus *Diplommatina* is a very large one, with well over 300 described species (*e.g.*, see Laidlaw, 1949; Vermeulen, 1993). Shells of the species are ovate to acuminate, and are very small to minute, yet they are highly sculptured, usually with transverse ribs, and commonly with spiral striae. The species are found in southern, southeastern and eastern Asia.

Ten species of *Diplommatina* have been reported previously from Thailand (Panha, 1996, 1997; Panha & Burch, 1997). Numerous other species have been been described from neighboring Myanmar [Burma] in the

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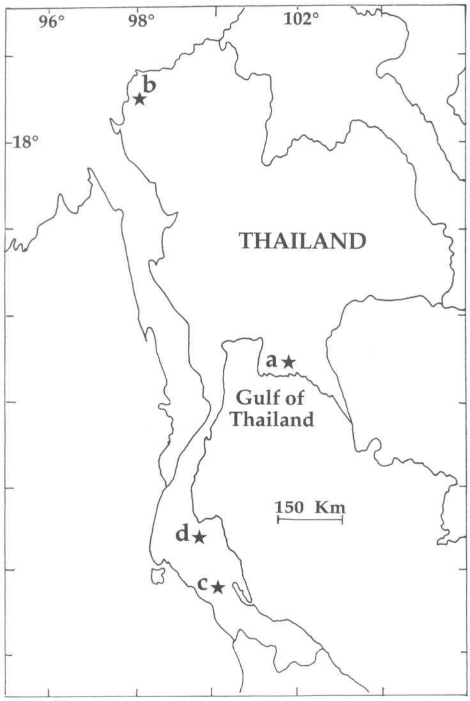

FIG 1. Map showing locations (stars) of type localities. **a**, Khaochamao National Park; **b**, Banpangcam Cave; **c**, Khaopoo Khaoya National Park; **d**, Tamkuha.

publications of W.T. Blanford, H.H. Godwin-Austen, G. Neville, F. Stoliczka, and W. Theobald; from Indochina by A. Bavay, P. Dautzenberg, and H. Fischer; and from peninsular Malaysia by W.S.S. van Benthem Jutting, H. Crosse, H.H. Godwin-Austen, F.F. Laidlaw, O.F. von Möllendorff, and J.R. le B. Tomlin. The present paper adds to our knowledge of *Diplommatina* in Thailand.

Diplommatina crispata khaochamaoensis n. ssp.

(Fig. 2)

Description of holotype. Shell fusiform, dextral, with 6 3/4 whorls, the penultimate whorl widest the last whorl and the whorl before the penultimate whorl are almost the same diameter. The periphery of the first several whorls is rounded, but beginning with the third whorl the periphery becomes increasingly angular. The sides of the spire are concave. Tuba 1/3 whorl. Slightly sinuous radial ribs begin to appear at the second whorl and gradually become more distinct, becoming very dis-

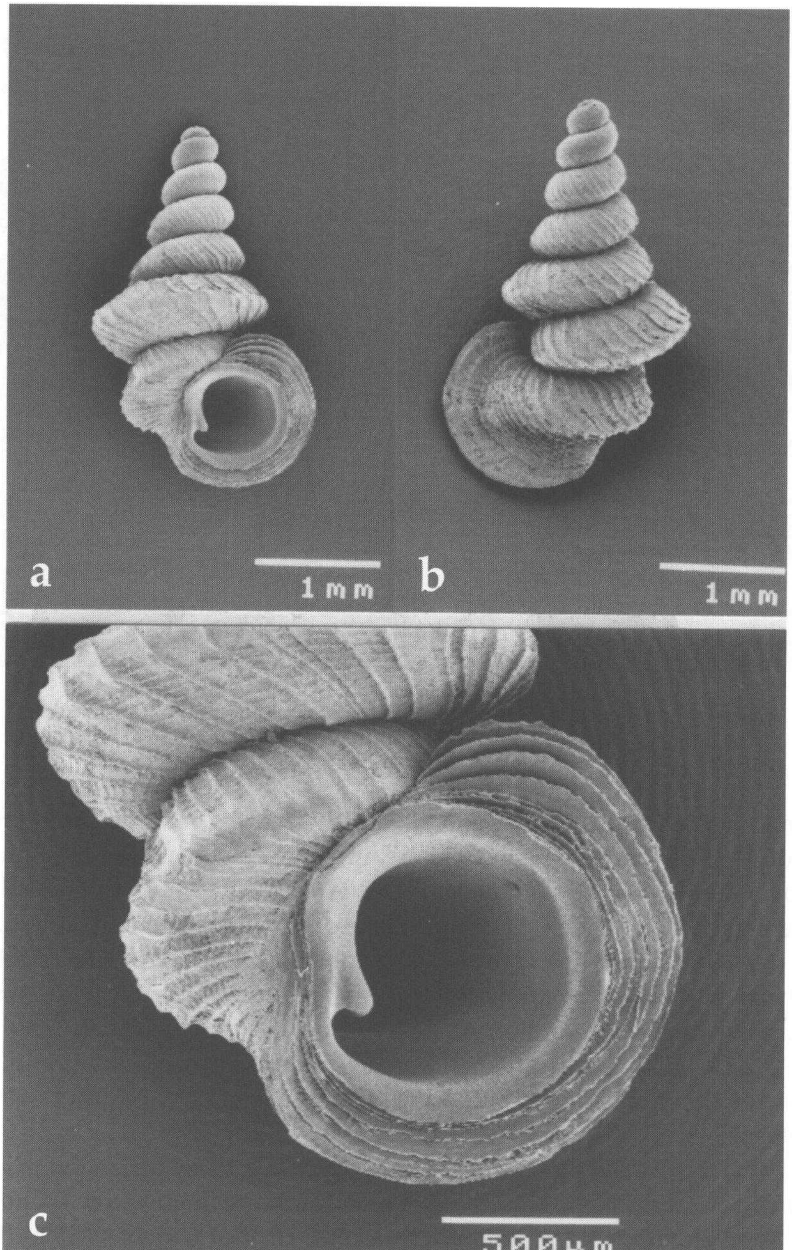

FIG. 2. *Diplommatina crispata khaochamaoensis* n. sp. **a**, **b**, Holotype, X ca. 7.3; **c**, aperture, X ca. 48. [Fig. 2 is continued on the next page.]

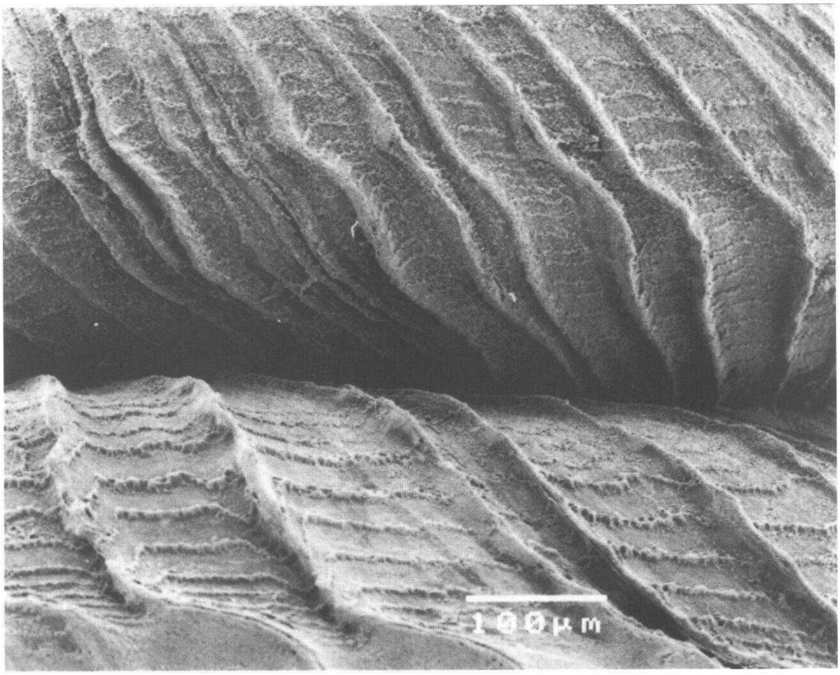

FIG. 2 [continued]. *Diplommatina crispata khaochamaoensis* n. sp. **d**, Dorsal side of penultimate whorl (upper part of picture) and last whorl (lower part of picture), X ca. 187.

tinct on the penultimate and last whorls. The ribs are a bit more produced at the angular part of the whorl. Close-set, raised spiral striae cover the whorls. The umbilicus is closed. The aperture is rounded; the peristome, in side view, is straight. The columellaris [columellar tooth] is distinct, directed downwards. The peristome is expanded, and double. Shell length 2.7 mm; shell width 1.4 mm; aperture length 0.6 mm. Comparative dimensions of the holotype and paratypes are given in Table 1.

Type locality. Thailand, Khaochamao National Park, Chantaburi Province at 12°53′19″ N, 101°49′7″ E, 540 meters elevation (CUIZM, Di 034) 1997; Fig 1a.

Etymology. The subspecific epithet *khaochamaoensis* is from the name of Khaochamao National Park, where the snail specimens were found.

Type materials. The holotype (CUIZM, Di 034) is deposited in the Chulalongkorn University Zoological Museum together with four shell paratypes (CUIZM, Di 035); other shell paratypes (CUIZM, Di 036), four shells, have been deposited in University of Michigan Museum of Zoology (UMMZ) Ann Arbor. Legacy S. Panha.

Habitat and geographical distribution. *Diplommatina crispata khaochamaoensis* is known at present only from Khaochamao National Park, Chantaburi Province. The snails live on limestone mountain walls with vegetation in the vicinity. Other snail species found in its habitat were *Amphidromus atricallosus* (Gould 1843) and *Chloritis* (*Trichochloritis*) *diplochone* Möllendorff 1898. *Diplommatina c. khaochamaoensis* was found at elevations between 160 and 540 meters.

Diagnosis. Shell fusiform, dextral, with about 6 3/4 whorls; the penultimate whorl largest with distinct prominent spiral crest at the middle of the whorl, and prominent radial ribs; spiral striae distinct; columellaris well developed and directed downwards; shell length about 2.6 mm.

Remarks. The size of the shell, the angular whorls, the enlarged penultimate whorl and the smaller last whorl, the relative prominence of the ribs, the rounded aperture and character of the columellaris of *Diplommatina crispata khaochamaoensis* n. ssp. are very similar to *D. crispata* Stoliczka 1871 described from Damotha, near Moulmein, Myanmar [Burma] (cf. Godwin-Austen, 1889, pl. 49, fig. 4). The spire of *D. c. khaochamaoensis* is relatively narrower and has one more whorl than *D. crispata. Diplommatina umpangensis* Panha 1998 (Fig. 3) is also very similar to *D. crispata,* but its spire, too, is relatively narrower and has one more whorl, and the last whorl is relatively wider and the shell is smaller.

TABLE 1. Holotype and paratype dimensions of *Diplommatina crispata khaochamaoensis* n. ssp.

Type	Dimensions (in mm)		
	Height	Width	Aperture length
Holotype	2.7	1.4	0.6
Paratypes			
1	2.7	1.4	0.6
2	2.6	1.4	0.6
3	2.6	1.4	0.6
4	2.6	1.4	0.6

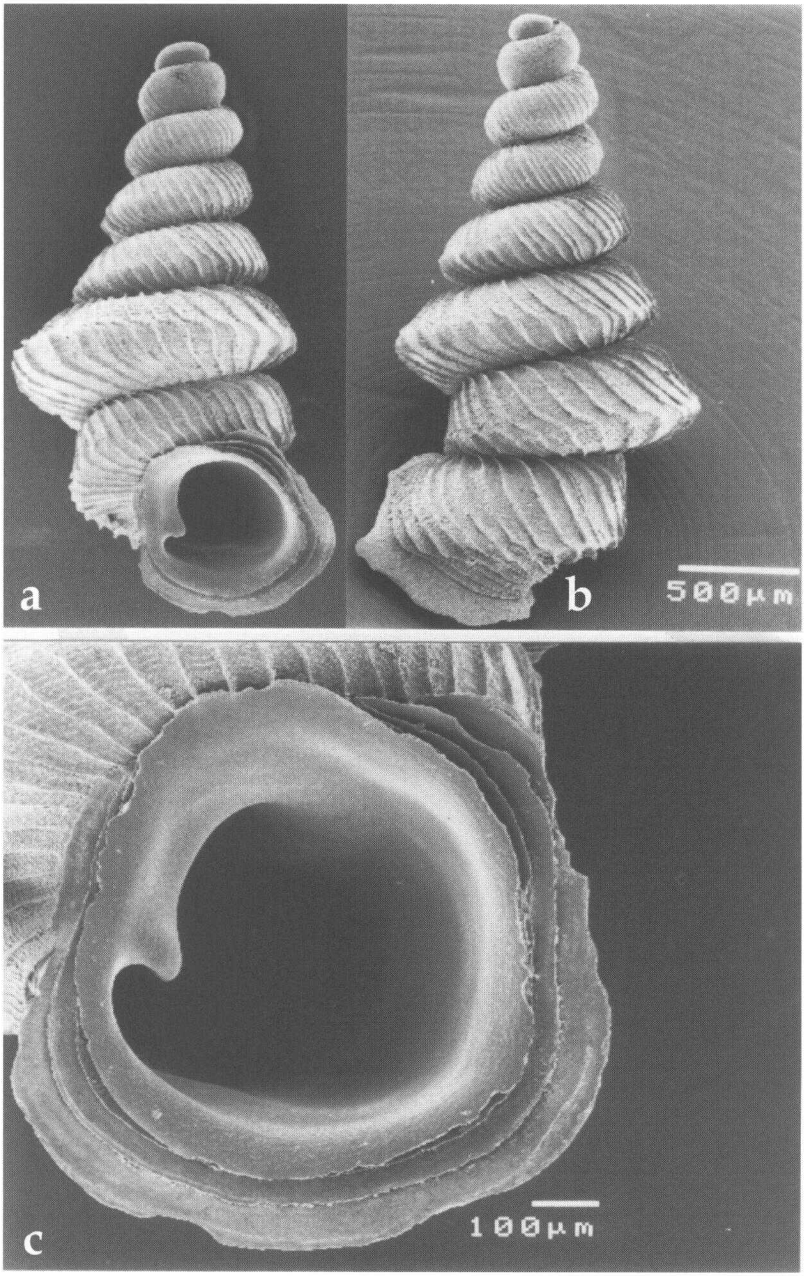

FIG. 3. *Diplommatina angulifera umpangensis* Panha 1998, **a**, **b**, Apertural and dorsal views of shell, X ca. 32; **c**, aperture, X ca. 45. [Fig. 3 is continued on the next page.]

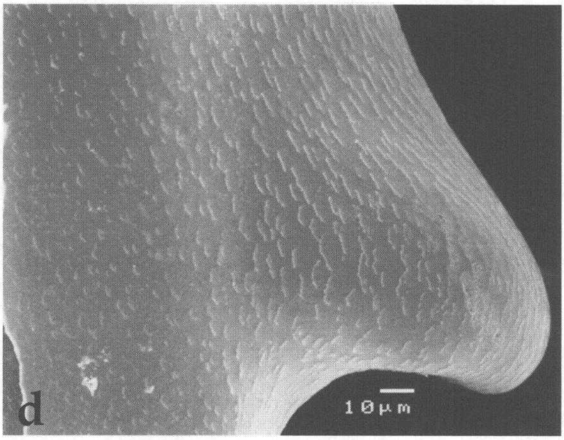

FIG. 3 [continued]. *Diplommatina angulifera umpangensis* Panha 1998. **d**, Surface of columellaris, X ca. 630.

[*Diplommatina umpangensis* is also especially similar to *D. angulifera* Bavay & Dautzenberg 1912 from Ban-Lao, Indochina (Bavay & Dautzenberg, 1912). At present, it may be best to consider *D. umpangensis* a subspecies of the larger *D. angulifera*.]

Other species of *Diplommatina* have elongate shells with the penultimate whorl larger that the last whorl, and their shells have similar ribbing (*e.g.*, *D. lucifuga* Benthem Jutting 1958 and *D. torquilla* Benthem Jutting 1958, to name only two), but their whorls are not angled as they are in the *D. crispata* and *D. angulifera* groups.

The shell of *Diplommatina suratensis* Panha & Burch 1998 is very similar to *D. crispata khaochamaoensis*, but the spire of *D. suratensis* is broader and straight-sided, and the shell is sinistral.

Diplommatina nimanandhi n. sp.
(Fig. 4)

Description of holotype. Shell conical, dextral, with 6 3/4 whorls, whorls convex. Suture deeply impressed. Tuba 1/4 whorls. The penultimate whorl is slightly larger than the last whorl. Radial ribs begin to distinctly appear on the second whorl, and with the latter whorls they become more prominent and more widely spaced. The whorls are covered with close-set, raised spiral striae. The umbilicus is closed. The aperture is rounded. The peristome is double, expanded, with a small columellaris, which is not directed basally. Beginning on the whorl just

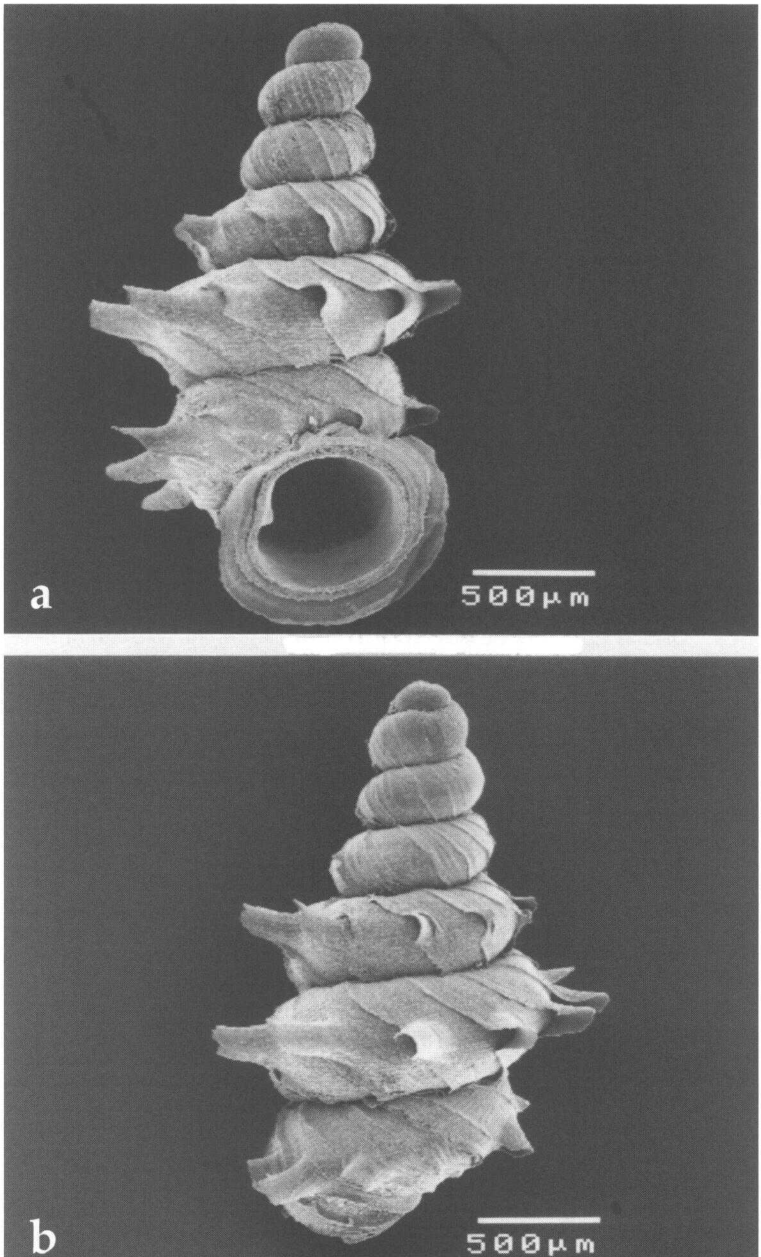

FIG. 4. *Diplommatina nimanandhi* n. sp. **a**, **b**, Holotype, X ca. 32 [Fig. 4 is continued on the next page].

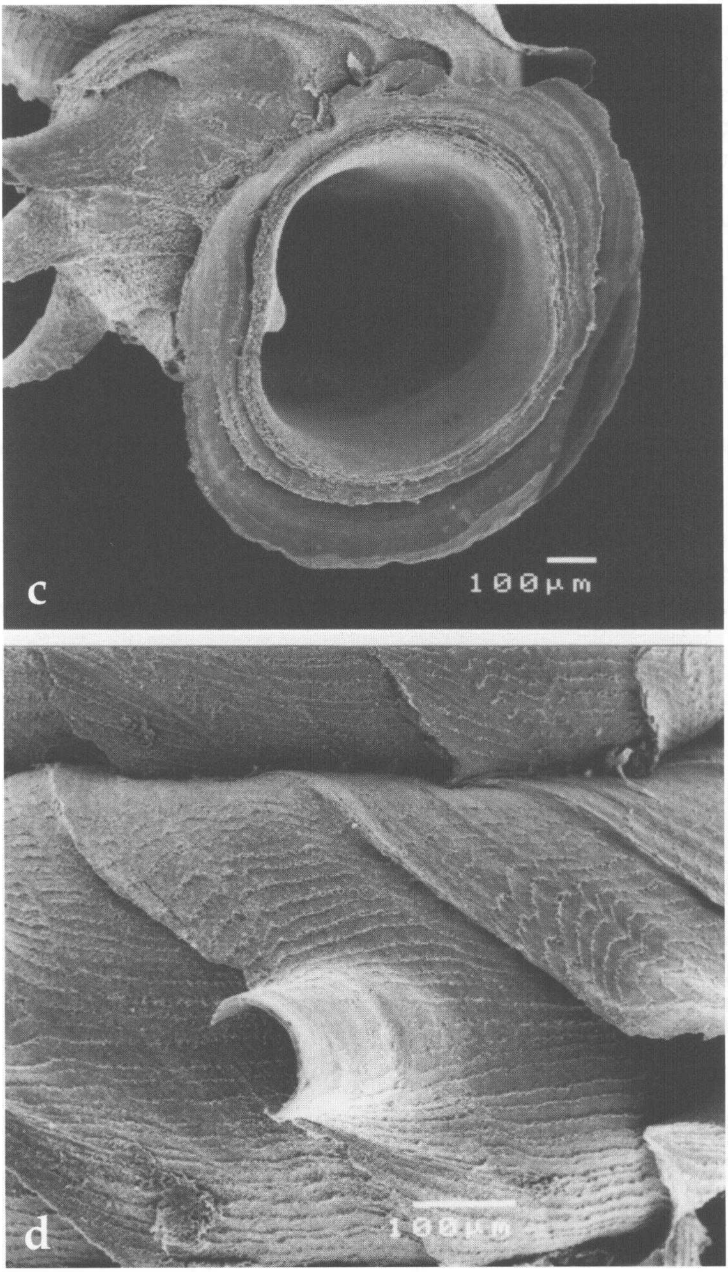

FIG. 4 [continued]. *Diplommatina nimanandhi* n. sp. **c**, Shell aperture and peristome, X ca. 67; **d**, Surface of penultimate whorl, X ca. 140.

prior to the penultimate whorl (*i.e.*, the antepenultimate whorl), and becoming more prominent thereafter, are tubular peripheral projections. These projections are medial protuberances of the individual ribs. Shell length 2.8 mm; shell width 0.9 mm; length of aperture 1.1 mm; width of aperture 1.1 mm. The comparative dimensions of the holotype and paratypes are shown in Table 2.

Type locality. Thailand, Banpangcam Cave, Maehongson Province at 19°40'39" N, 98°12'28" E, 860 meters elevation (CUIZM, Di 037), 1997; Fig 1b.

Etymology. The specific epithet *nimanandhi* is from the name of Mr. Amonrapan Nimanandh, the Vice Governor of Maehongson Province, who generously supported our study in the Maehongson limestone areas.

Type materials. The holotype (CUIZM, Di 037) is deposited in the Chulalongkorn University Zoological Museum together with 14 paratype specimens (CUIZM, Di 038); another six paratype specimens (CUIZM, Di 039) are stored in the Museum of Zoology, University of Michigan (UMMZ), Ann Arbor. Legacy S. Panha.

Habitat and geographical distribution. *Diplommatina nimanandhi* is

TABLE 2. Holotype and paratype dimensions of *Diplommatina nimanandhi* n. sp.

Type	Dimensions (in mm)		
	Height	Width	Aperture length
Holotype	2.8	0.9	1.1
Paratypes			
1	2.9	0.9	1.1
2	2.9	0.9	1.1
3	2.9	0.9	1.0
4	2.9	0.9	1.0
5	2.9	0.9	1.0
6	2.9	0.9	1.0
7	2.8	0.8	1.0
8	2.8	0.8	0.9
9	2.7	0.8	0.9
10	2.7	0.8	0.9
11	2.7	0.8	0.8
12	2.7	0.8	0.8
13	2.7	0.8	0.8
14	2.7	0.8	0.8

known only from Banpangcam Cave, Maehongson Province. The snails live on limestone walls with bluegreen algae. Subulinid snails were also found in the same habitat. *Diplommatina nimanandhi* was found at elevations between 800 and 860 meters.

Diagnosis. Shell conical, dextral, with 6 3/4 whorls; the penultimate whorl is slightly larger than the last whorl; the radial ribs of the antepenultimate whorl, the penultimate whorl and the last whorl are elongated semi-tubular projections ("spines").

Remarks. *Diplommatina nimanandhi* is similar to *D. pagodula* Bavay & Dautzenberg 1909 from Ban-Lao, Indochina, the latter named for its pagoda-like appearance. *Diplommatina pagodula* is considerably larger than *D. nimanandhi* (see Bavay & Dautzenberg 1909, pl. 11, fig. 12). *Diplommatina pagodula* has two more whorls than *D. nimanandhi,* and its columellaris is more on the parietal area of the peristome than it is in *D. nimanandhi.*

We have not been able to compare the shell of *Diplommatina nimanandhi* with that of *D. spinosa* Godwin-Austen 1889. A shell very similar to *D. nimanandhi* is shown in Hanley & Theobald (1876, pl. 141, fig. 6) and erroneously stated to be *D. crispata* Stoliczka (cf., Godwin-Austen's 1889 figure of Stoliczka's *D. crispata*). *Diplommatina prakayangensis* Panha 1998, in comparison to *D. nimanandhi,* has more extreme development of the spines, and is sinistral.

Several species of *Diplommatina* on the island of Borneo (see Vermeulen, 1983) have spinose shells, showing that shells with this character extend across the Karimata Straits.

Diplommatina jirasaki n. sp.

(Fig. 5)

Description of holotype. Shell elongate and narrow, conical, turreted, sinistral, with 7 1/2 angular whorls that increase regularly in size until the penultimate whorl, which is the largest whorl. The last whorl is smaller than the penultimate whorl. Sutures deep; tuba 1/2 whorl. Radial ribs begin appearing on the second whorl. Starting on the third whorl the radial ribs begin to be tubular projections. These continue on to the last whorl. Spiral striation present. The umbilicus is closed. The aperture is rounded. The peristome is double, expanded, with only a subobsolete columellaris. Shell length 2.5 mm; shell width 0.8 mm; length of aperture 0.6 mm; width of aperture 0.7 mm. The comparative dimensions of the holotype and paratypes are shown in Table 3.

Type locality. Thailand, Khaopoo Khaoya National Park, Pattalung

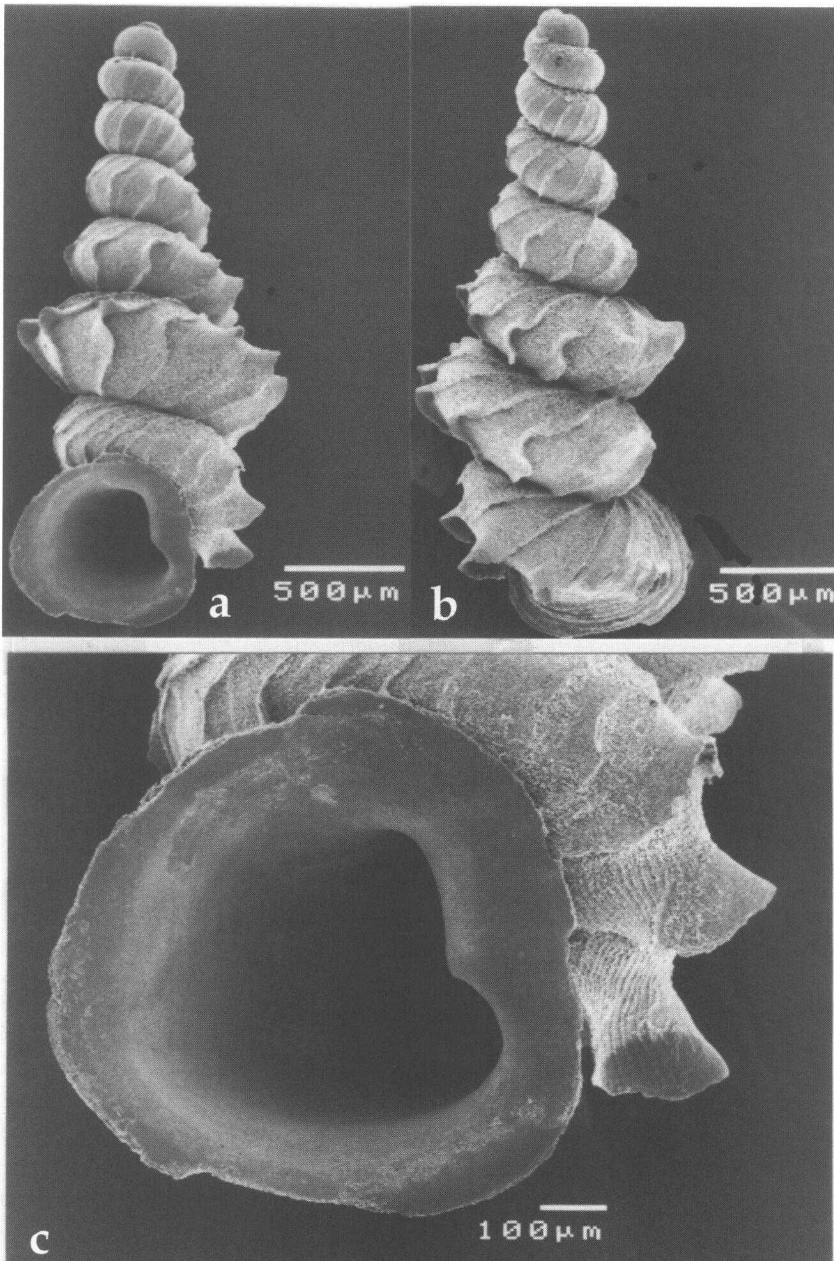

FIG. 5. *Diplommatina jirasaki* n. sp. **a**, **b**, Holotype, X ca. 32; **c**, apertural view, X ca. 91. [Fig. 5 is continued on the next page].

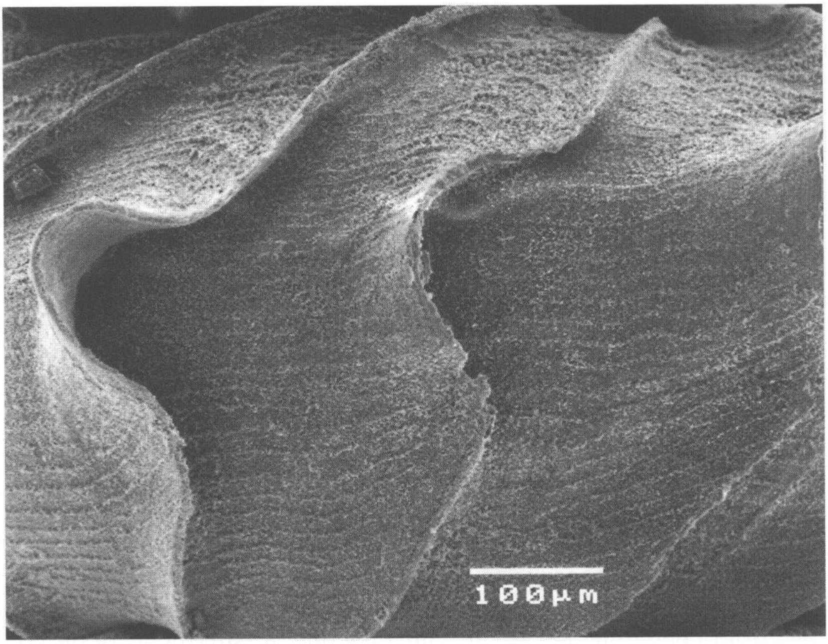

FIG. 5 [continued]. *Diplommatina jirasaki* n. sp. **d**, Surface of penultimate whorl, X ca. 180.

TABLE 3. Holotype and paratype dimensions of *Diplommatina jirasaki* n. sp.

Type	Dimensions (in mm)		
	Height	Width	Aperture length
Holotype	2.5	0.8	0.6
Paratypes			
1	2.2	0.7	0.5
2	2.2	0.7	0.5
3	2.2	0.7	0.5
4	2.0	0.6	0.4
5	2.0	0.6	0.4
6	2.0	0.6	0.4

Province at 7°39′38″ N, 100°2′30″ E, 220 meters elevation (CUIZM, Di 040), 1997; Fig 1c.

Etymology. The subspecific epithet *jirasaki* is from the name of Mr.

Jirasak Sujarit, who collected the snails.

Type materials. The holotype (CUIZM, Di 040) is deposited in the Chulalongkorn University Zoological Museum together with six paratype shells (CUIZM, Di 041). Another four paratypes (CUIZM, Di 042) are stored in the Museum of Zoology, University of Michigan (UMMZ), Ann Arbor. Collector: J. Sujarit.

Habitat and geographical distribution. *Diplommatina jirasaki* is known only from Pattalung Province. The snails live on limestone mountain walls. *Gyliotrachela khaochongensis* Panha 1998 and *Diplommatina naiyanetri* Panha 1998 were also found at the same habitat. *Diplommatina jirasaki* was found at elevations between 140 and 220 meters.

Diagnosis. Shell elongate-conical, acuminate, turreted, sinistral, with 7 1/2 angular whorls. The radial ribs from the third whorl to the last whorl are raised medially, becoming semi-tubular projections on the last several whorls. The radial ribs are widely placed; the penultimate whorl has only seven radial ribs showing in apertural view, and the antepenultimate whorl has only five showing. The columellaris is subobsolete.

Remarks. Our specimens of *Diplommatina jirasaki* from Khaopoo Khaoya National Park are closest in appearance to *D. lenggongensis* Tomlin 1941 from Lenggong, Perak. Tomlin gave the measurements of his species as length (height) 3.25 mm, maximum diameter 1.60 mm. The shell figured by Laidlaw as *D. lenggongensis* is about 2.8 mm in length. Both authors figured specimens very similar to *D. jirasaki,* from Khaopoo Khaoya National Park, but differing in having more numerous and more closely spaced radial ribs, and having differences in development of the columellaris. *Diplommatina jirasaki* has seven radial ribs showing in apertural view of the penultimate whorl, and five showing on the antepenultimate whorl. *Diplommatina lenggongensis* has nine and seven radial ribs showing on the penultimate and antepenultimate whorls, respectively (as ahown by both Tomlin and Laidlaw). The columellaris in *D. jirasaki* is very poorly developed, compared to that of *D. lenggongensis.* Tomlin refers to it as a "tubercle."

The shells of *Diplommatina superba* Godwin-Austen & Neville (Godwin-Austen & Neville, 1879) and *D. s. brevior* Laidlaw (Laidlaw, 1949) are both less elongate, wider, and have more numerous and close-set radial ribs than *D. jirasaki.*

The shell of *Diplommatina naiyanetri* Panha 1998 from Khaochong Wildlife sanctuary is sinistral and has a similar acuminate shape, but the ribs are closer together and lack the well developed median flange-like processes. Also, in *D. naiyanetri,* the columellaris is well developed. *Diplommatina diminuta* Möllendorff 1891 from Bukit Pondong, Malakka

(Perak), is similar to *D. naiyanetri*, but the ribs are even closer together.

Diplommatina pongrati n. sp.

(Fig. 6)

Description of holotype. Shell elongate and narrow, turreted, sinistral, with 7 1/2 angular whorls that increase regularly in size until the penultimate whorl, which is the largest whorl. The last whorl is smaller than the penultimate whorl. Tuba 1/2 whorl. Radial ribs become distinct on the second whorl. The ribs are relatively far apart on all of the whorls. The radial ribs have no well developed flanges or tubular projections. Spiral striation present. The umbilicus is closed. The aperture is rounded. The peristome is double, expanded. The collumellaris is rather bluntly rounded, and inset a bit from the edge of the peristome. Shell length 2.5 mm; shell width 0.8 mm. Length of aperture 0.6 mm; width of aperture 0.6 mm. Comparative dimensions of the holotype and paratypes are given in Table 4.

Type locality. Thailand, Tamkuha, Surathani Province at 8°4′30″ N, 98°50′33″ E, collected from soil samples (CUIZM, Di 043), 1997; Fig 1d.

Etymology. The specific epithet *pongrati* is from the name of Mr. Pongrat Dumrongrojwatana, who collected the snails.

Type materials. The holotype (CUIZM, Di 043) is deposited in the Chulalongkorn University Zoological Museum together with four paratype shells (CUIZM, Di 044). Another three paratypes (CUIZM, Di 045) are stored in the Museum of Zoology, University of Michigan (UMMZ), Ann Arbor. Collector: Pongrat Dumrongrojwatana.

Habitat and geographical distribution. *Diplommatina pongrati* is known only from Surathani Province. All shells were collected from soil samples. *Macrochlamys asamurai* Panha 1997 was also found at the same habitat.

Diagnosis. Shell elongate and narrow, turreted, sinistral, with 7 1/2 whorls. The last whorl is noticably smaller than the penultimate whorl. The ribs are low and widely spaced. The columellaris is bluntly rounded and not directed downward.

Remarks. *Diplommatina naiyanetri* Panha 1998 from Khaochong Wildlife Sanctuary is very similar to *D. pongrati*, but in the latter the peristome is broader, the columellaris is better developed, and it points basally.

Sinistral species from peninsular Malaysia that have similar shells to *Diplommatina pongrati* are *D. diminuta* Möllendorff 1891, *D. attenuata* Laidlaw 1949, *D. parabates* Laidlaw 1949, and, to some extent, *D. acme* Laidlaw 1949. *Diplommatina parabates* from Lenggong, Perak, is most similar – in attenuate shell, looseness of shell coiling, nature of the ribs,

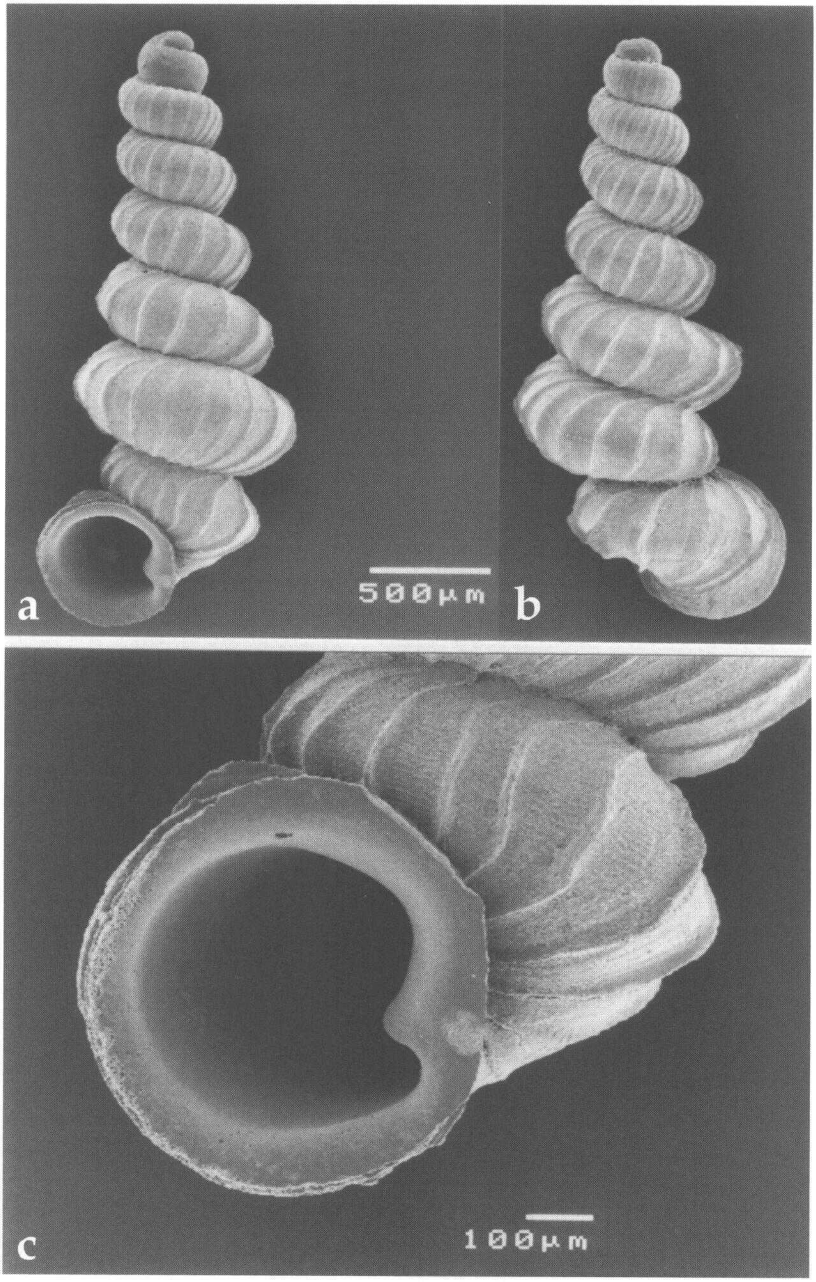

FIG. 6. *Diplommatina pongrati* n. sp. **a**, **b**. Holotype, X ca. 32; **c**, apertural view, X ca. 90. [Fig. 6 is continued on the next page.]

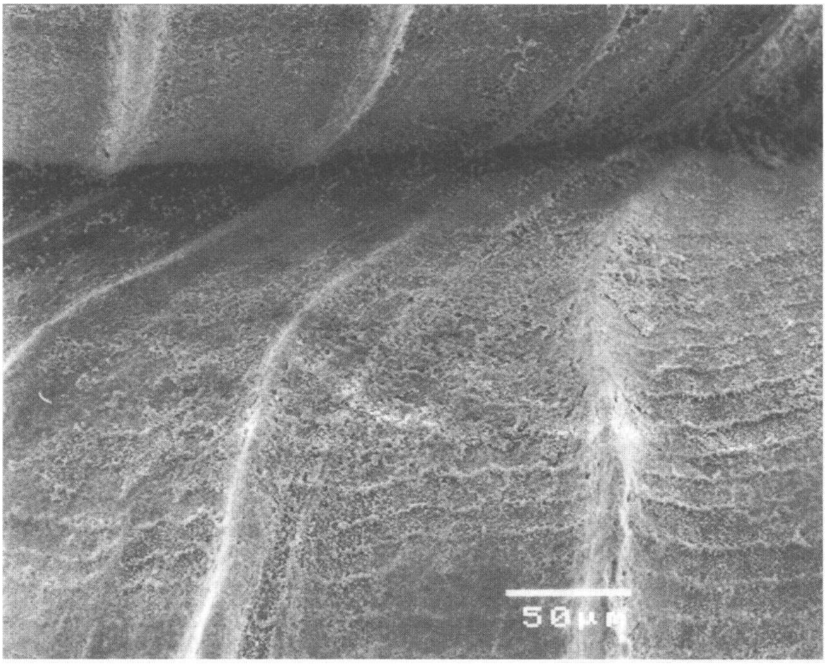

FIG. 6 [continued]. *Diplommatina pongrati* n. sp. **d**, Surface of penultimate whorl, X ca. 323.

TABLE 4. Holotype and paratype dimensions of *Diplommatina pongrati* n. sp.

Type	Dimensions (in mm)		
	Height	Width	Aperture length
Holotype	2.5	0.8	0.6
Paratypes			
1	2.4	0.8	0.6
2	2.4	0.8	0.6
3	2.4	0.8	0.6
4	2.3	0.8	0.6

and characteristics of the columellaris. However, in *D. parabates* the ribs are closer together and more numerous, and the last whorl is relatively larger. In *D. attenuata* from Gua Bama, Pahang, the shape of the aperture, and the aperture's relation to the last and penultimate whorls is different, and the penultimate whorl has better developed ribs. Also, the ribs on the whorls preceding the penultimate whorl are closer together and more numerous in *D. attenuata* than in *D. pongrati.* The shell of *D. diminuta* from Perak has a broader spire, the whorls are rounder, the ribs are more numerous and closer together, and the last whorl is scarcely smaller than the penultimate whorl. The shell of *D. acme* from Kaki Bukit, Perlis, is less attenuate than that of *D. pongrati,* and the ribs are more numerous and close-set.

ACKNOWLEDGMENTS

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THE LAND SNAIL GENUS *CARYCHIUM* (PULMONATA: CARYCHIIDAE) IN THAILAND

John B. Burch[1] and Somsak Panha[2]

ABSTRACT – *Carychium thailandicum* n. sp. is described from limestone mountains, Doichiang Dao Wildlife Sanctuary, Chiang Mai Province, Thailand. Its shell is carychiiform, minute, elongate, transparent, and has a thickened, expanded lip and a columellar lamella. The shell is imperforate and rimate, and there is a depression externally on the shell behind the peristome. On the inner side of the shell aperture at the corresponding position to the external depression is the palatal tooth, which is directly opposite the parietal tooth. The last whorl has evenly spaced, but not prominent, transverse striae. The shell lacks spiral sculpture. The adult peristome is thickened, expanded, and has a reflected outer marginal flange. The terminal end of the columella appears truncate, the truncated appearance due to a low, entering columellar lamella.

Key Words: *Carychium thailandicum*, Pulmonata, Carychiidae, Thailand.

INTRODUCTION

The minute pulmonate terrestrial snail genus *Carychium* O.F. Müller 1774 has a very wide distribution, occurring in North and Middle America (including the West Indies), Europe, and South, Southeast and East Asia. In Southeast Asia, it has been found in Indonesia, Malaysia and the Philippines). As fossils, *Carychium* is known from the Upper Jurassic, from Europe, Asia, the West Indies, and North America (*e.g.*, see Zilch, 1959). Until the present report, no species of the genus, Recent or fossil, had been found in Thailand. During a field survey of land mollusks in northern Thailand in May 1997, an apparently undescribed species of *Carychium* was found on decaying pieces of wood and leaves in the limestone mountains of Doichiang Dao Wildlife Sanctuary, Chaing Mai Province, Thailand. This new species of *Carychium* is described below.

Carychium thailandicum n. sp.
(Fig. 1)

Description of holotype. Shell minute, elongate, translucent or transparent, moderately glossy, with a thickened, expanded lip and a columellar lamella; shell length 1.7 mm, width 0.5 mm, length of aperture 0.5 mm;

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length of aperture, including the peristome, is 1/3 the shell length; when wet, the shell is completely transparent, as are dry fresh shells; on the outside of the shell, just behind the lip is a depression; on the inner side of the shell aperture at the corresponding position to the depression is the palatal tooth; the palatal tooth is directly across from (opposite to) the parietal tooth; shell with 4 3/4 moderately convex whorls; last whorl with evenly spaced transverse striae; shell without spiral sculpture; adult lip thickened, expanded, and with a reflected outer marginal flange; the terminal end of the columella is truncate in appearance; shell imperforate and rimate (*i.e.*, with columellar lip partly reflected back over the umbilical area). The comparative shell dimensions of 11 shells of the type lot are shown in Table 1. (An additional paratype shell, in Ann Arbor, with 5.0 whorls, is 1.55 mm in length and 0.66 mm in width; the embryonic shell, which is smooth, has ca. 1 3/8 whorls).

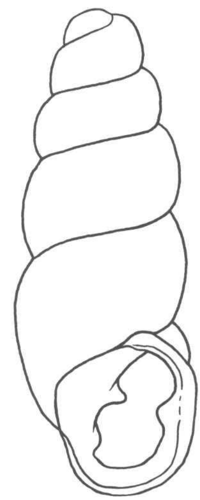

FIG. 1. Apertural view of shell of *Carychium thailandicum* n. sp.

Type locality. Kewlom base, Doichiang Dao Wildlife Sanctuary, Chiang Mai Province at 19°8′16″ N, 98°11′37″ E, 1950 meters elevation (CUIZM, Cr 001), Thailand, 1997.

Etymology. The specific epithet *thailandica* is from of the name of the country Thailand, the place we collected the new species.

Type material. The holotype (CUIZM, Cr 001) is deposited in the Chulalongkorn University Zoological Museum together with 27 paratype shells (CUIZM, Cr 002). Other paratype shells are in the Field Museum of Natural History (FMNH), Chicago (11 shells) and in the University of Michigan Museum of Zoology (UMMZ), Ann Arbor (25 shells). Legacy S. Panha and J. B. Burch.

Habitat and geographical distribution. *Carychium thailandicum* is known so far only from Doichiang Dao, Chiang Mai Province, northern Thailand. All shells were collected from decaying leaves and wood on a damp limestone hill.

Diagnosis. Shell carychiiform, minute (1.5-1.9 mm in length), elongate, transparent, with a thickened, expanded lip and a columellar lamella; shell imperforate and rimate; there is a depression externally on the shell behind the lip; on the inner side of the shell aperture at the corresponding

TABLE 1. Shell dimensions (in mm) of the holotype and paratypes of *Carychium thailandicum* n. sp.

Type	Length	Width	Length of aperture
Holotype	1.7	0.6	0.5
Paratypes			
1	1.9	0.6	0.5
2	1.8	0.6	0.5
3	1.8	0.6	0.5
4	1.8	0.6	0.5
5	1.7	0.6	0.5
6	1.7	0.6	0.5
7	1.7	0.6	0.5
8	1.7	0.6	0.5
9	1.7	0.6	0.5
10	1.7	0.6	0.5

position to the depression is the palatal tooth, which is directly across from (opposite to) the parietal tooth; last whorl with evenly spaced, but not prominent, transverse striae; shell without spiral sculpture; adult lip thickened, expanded, and with a reflected outer marginal flange; the terminal end of the columella is truncate, the truncated appearance due to a low, entering columellar lamella ("tooth").

Remarks. *Carychium thailandicum* seems to be closest in shell characters to *C. indicum* Benson 1849, as described from Simla and Landour, western sub-Himalayan Mountains (see Benson, 1849; Saussaye, 1850; Pfeiffer, 1857). However, on examining shell specimens of *C. indicum* from Simla (UMMZ 116245), that species is not as narrow and has a more tapering spire, the peristome is not entire (or only weakly so) in the parietal region, and the palatal tooth is not as prominent.

We have not been able to compare our Doichiang Dao specimens to the lowland *Carychium boysianum* Benson 1864 from the banks of the Juma [Yamuna] River at the "Táj, near Agra," India. Benson (1864, p. 210) says that *C. boysianum* "... is closely allied to the Himalayan species *C. Indicum*, B., but it is distinguished by its more elongated cylindrical and less rapidly attenuate form, and its flatter whorls, also by the narrower and more acute aperture, the right lip being straighter and less convex, and by the expanded parietal callus." Shell measurements given for *C. boysianum* are: length 2 mm, width scarcely 2/3 mm.

Möllendorff (1897) described *Carychium javanum* from Java, Indonesia, as follows: shell rimate, subcylindrical-oblong, small, transparent, hyaline-white, finely striate. Spire subcylindrical, apically obtuse. Whorls six, moderately convex. Aperture strongly oblique, oval, moderately excised, peristome moderately expanded, continuous, broadly appressed above; external margin subsinuous, subcalloused. Columellar lamella well developed, subhorizontal. Size: length 2.2 mm, width scarcely 1 mm. Compared to *C. thailandicum,* the shell of *C. javanum* is larger, more acuminate, not as glossy or translucent, strongly striate, the parietal tooth is longer and narrower, and the palatal tooth is less developed.

Benthem-Jutting (1959) compared Möllendorff's (1897) *Carychium javanum* [*sensu stricto*] with her Sumatran *C. javanum elatum* as follows, "The new subspecies differs from the Javanese *Carychium javanum javanum* Moellendorff in being higher, especially in the top whorls. All characteristics of the Javanese form are more developed: the striation is stronger, the peristome is broader and more calcified, the parietal tooth is stronger, and there occurs a weak infrapalatal tooth. This infrapalatal tooth lies somewhat deeper in the throat than the palatal tooth." Shell size of the holotype: length 2.5 mm, width 1.0 mm. Paratypes range from 2.6 to 2.2 mm in length.

The shell of *Carychium javanum elatum* is considerably larger than that of *C. thailandicum,* and *C. j. elatum* has a more tapered spire (body whorl to apex) and therefore less cylindrical shell, and in the shell aperture there is an infrapalatal tooth, a weaker palatal tooth, and the anterior end of the columella is not truncate. Also, the palatal tooth of *C. j. elatum* would seem to be less basally situated than it is in *C. thailandicum.*

Fulton (1899) described *Carychium balianum* from Bali Island as follows: "Shell elongate, rimate, smooth, glassy, semi-transparent; whorls 5 1/2, convex, regularly increasing; aperture oval, somewhat oblique; peristome thin, slightly expanded, continued over the parietal wall; a fold on upper part of columella. Diam. maj. 0.75, alt. 1.75 mm. ... I am indebted to Dr. von Möllendorff for a comparison of this species. He writes: 'Differs from *C. Javanum,* Mölldff., from Java, in being of a more slender form, smaller, and with a narrow aperture.'"

The shell of *Carychium thailandicum* differs from *C. balianum,* as figured by Fulton (1899, pl. 11, fig. 11), by having a more quadrate aperture, a palatal plica, a truncate columella, and a more cylindrical spire.

Chen (1992) described *Carychium tianmushanense* from Shanyuan Temple, Tianmushan Mountain (30°25' N, 119° 50' E), Zhejiang Province, China, as follows: "height [holotype] 1.74 mm, diameter 0.75 mm; Aperture height 0.55 mm, diameter 0.58 mm." ... "Shell very small, thin long-conoidal, semitransparent. Whorls 5-5 1/2, moderately convex with high spiral part, shells light yellow or light white-yellow in colour, with lustre, spire suture and growth line. Nearly lusterless except the second, but the protoconch ovate without lustre. Umbilicus without. Apex blunt, suture deeply. Aperture circular, thick, with two lops, and very expanded and reflexed with 3 papillary teeth; 1 outer lip tooth, 1 inner lip tooth, 1 axial lip tooth flaky-form in shape." Chen compared *C. tianmushanense* with *C. sibiricum* (Westerlund 1897), differing from the latter by its number of whorls, larger size, and "having 3 papillary teeth."

The shell of *Carychium tianmushanense* differs from that of *C. thailandicum* by being wider, having unevenly spiraled whorls (if drawn correctly in the original description), having sharper palatal plica and columellar lamella, a wider, more expanded apertural lip, and being yellow or yellowish in color.

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CONTRASTING OBJECTIVES IN ENVIRONMENTAL MEDIATION, RECONNAISSANCE BIOLOGY, AND ENDANGERED SPECIES PROTECTION — A CASE STUDY IN THE KANAB AMBERSNAIL, *OXYLOMA HAYDENI KANABENSIS* PILSBRY 1948 (GASTROPODA: STYLOMMATOPHORA: SUCCINEIDAE)

Earle E. Spamer[1] and Arthur E. Bogan[2]

ABSTRACT

Oxyloma haydeni kanabensis Pilsbry 1948 (Gastropoda: Stylommatophora: Succineidae), the Kanab ambersnail, is listed as Endangered by the U.S. Fish and Wildlife Service. It lives in two known populations 92 km apart; one near Kanab, Utah, the other at Vasey's Paradise, alongside the Colorado River in Grand Canyon National Park, Arizona. The Utah population is adversely affected by modified land use; the Arizona population is in a wilderness setting but is potentially threatened by significant outflows from the hydroelectric powerplant at Glen Canyon Dam, now operating under the provisions of an Environmental Impact Statement (EIS). Although it is a protected organism, the remedial provisions of the EIS, intended to moderate the adverse effects that hydropower production has had on the Colorado River through the Grand Canyon, will have some negative effects on the Grand Canyon's ambersnail population. As a consequence, the ecology and distribution of *O. h. kanabensis* have become focuses of attention of administrative agencies, conservational organizations, reconnaissance biologists, ecologists, and systematists alike. The identification of *O. h. kanabensis* is confused by the similarity of its shell to other succineid gastropods as well as to at least one lymnaeid gastropod (Lymnaeidae); anatomical dissection is the only reliable means of identification. However, protected-animal identifications are usually restricted to non-invasive methods conducted in the field. As a case study for similar conundrums in field biology, the morphological criteria for the identification of *O. h. kanabensis* are reconsidered for the purposes of field censuses and range determinations. Accordingly, the entire suite of type specimens of *O. h. kanabensis* is described and illustrated here for the first time, accompanied by a systematic and taxonomic review. A simple, reliable morphometric means of distinguishing *O. h. kanabensis* from two non-*Oxyloma* species of Succineidae also occurring in the region is introduced here for field use.

Key words: *Oxyloma haydeni kanabensis*, Succineidae, Arizona, Utah, Grand Canyon National Park, Colorado River.

INTRODUCTION

On 17 April 1992, the U.S. Fish and Wildlife Service added *Oxyloma haydeni kanabensis* Pilsbry 1948, the Kanab ambersnail, to its list of endan-

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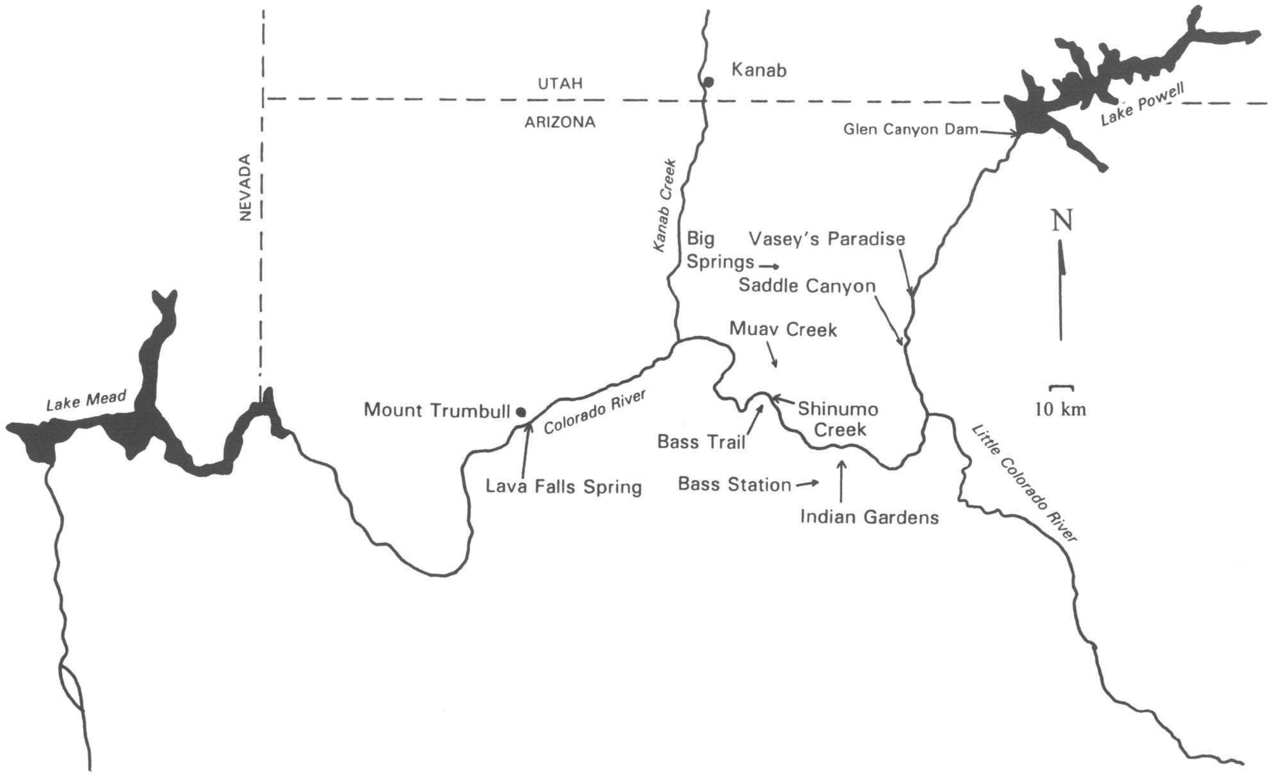

FIG. 1. Map of the Grand Canyon region showing mollusk localities cited in this paper.

gered wildlife (England, 1992; Blanchard, 1992). This succineid gastropod is thus far known only from two localities, 92 km apart; one on privately owned land near Kanab, Kane County, Utah (the type locality), the other at Vasey's Paradise, in Grand Canyon National Park, northern Arizona (Fig. 1). Until recently, Utah hosted two populations 2.1 km apart; one has been extirpated and the other is affected by changes in land use (U.S. Fish and Wildlife Service, 1994; J.L. England, personal communication, 1995). The Arizona population is in a national park, a legislatively protected area that is virtually pristine. Despite such protection, however, it may be exposed to human impacts. This population has been one of many subjects of ongoing research into environmental changes caused by hydroelectric power production at Glen Canyon Dam, 76 km upstream from Vasey's Paradise. A Final Environmental Impact Statement was recently completed pertaining to the operation of the powerplant; it includes *O. h. kanabensis* in its recommendations (U.S. Bureau of Reclamation, 1995).

Oxyloma h. kanabensis is the focus of Federal, State, and Native American efforts to investigate its distribution and habitat needs, to conserve it, and to promote its recovery so that it can be removed from the list of endangered wildlife (England, 1994; Terrell, 1994).

As a consequence of their habitats alongside running water, *Oxyloma h. kanabensis* populations are exposed to both naturally and artificially occurring flood events. Artificial events caused by humans include the effects of land use that raise separate issues of habitat protection and the limitations of legal safeguards over the owners of private land. Of far greater complexity, though, are issues related to artificial flood events inside a national park caused by the production elsewhere of electrical power that is distributed throughout the western United States. Scientific studies of the mollusk and its habitat are ongoing, including detailed field investigations at the Grand Canyon locality. These studies will greatly improve our understanding of the ecology and life habits of this snail, and they will provide a clearer picture of its ability to respond to rapid, temporary changes to its riparian environment.

This paper provides reconnaissance biologists with the basic information necessary to understand the presently known range, needs, and systematic placement of *Oxyloma h. kanabensis*. In addition, we introduce a simple, reliable morphometric means of distinguishing *O. h. kanabensis* from two non-*Oxyloma* species of Succineidae that also occur in the region. Together with new data derived from ongoing studies of this mollusk, field surveys should be able to better identify prospective localities that may host ambersnail populations.

SPECIES CONSERVATION VS. ENVIRONMENTAL MEDIATION

A Congressional mandate to draw up an Environmental Impact Statement (EIS) for the Glen Canyon Dam (GCD) powerplant has produced copious documentation of the effects of power production on the biotic, geomorphic, hydrologic, cultural, and recreational resources of the Colorado River corridor through the Grand Canyon (for summaries see Committee to Review the Glen Canyon Environmental Studies, 1991, 1994, 1996; and see extensive citations in Spamer, 1990, 1993). The dam was completed in 1963, but environmental studies in the Colorado River corridor prior to the 1970s are lacking.

The Final GCD-EIS (U.S. Bureau of Reclamation, 1995) outlines measures of environmental mediation that will necessarily affect the *Oxyloma h. kanabensis* habitat in the Grand Canyon. It calls for episodic high water flows that will redistribute bedload sediment to the beaches, recreating a normal effect of the pre-dam river environment. A consequence of these flows will be the inundation of the riverbanks to a level not normally reached since the dam was completed. After 1963, virtually all river-borne sediments from the upper Colorado River basin have settled in Lake Powell, the impoundment behind the dam. The artificially fluctuating flows of clear water from the dam have caused net erosion in the Colorado River corridor through the Grand Canyon, dramatically altering the riparian biotic community (Carothers & Brown, 1991).

The precise impacts that the EIS-mandated flows will have on *Oxyloma h. kanabensis* are as yet unclear, and intensive monitoring of the snail and its habitat continue after the high flow of March 1996. Ecological information about *O. h. kanabensis* is sparse and widely dispersed in published literature and in governmental and commissioned survey reports. Even so, nothing more than the original description (Pilsbry, 1948) is available prior to ca. 1990, and there have been no updated systematic studies of the species or subspecies. Reconnaissance biologists have expressed concerns that *O. h. kanabensis* can be confused with similar succineid snails, such as *Catinella* and *Succinea*. (We, too, had even been confused by a conchologically similar mollusk of another taxonomic family, as we explain herein.)

Constraints of budgets and staffing in the agencies that are charged with the mediation of environmental standards largely preclude the thorough anatomical studies that systematic biologists would use to identify individuals. As an endangered animal, too, the snail cannot now legally be collected without permit, so identifications of it must be made by methods that do not adversely impact the animals. These apparent conflicts create obstacles to the biologists who perform the field censuses and surveys, to the systematic biologists who need to study the bodies of the animals, and to the environmental biologists who seek to study the ecological aspects of the living animal.

Aside from the recent studies conducted on the Grand Canyon population, virtually nothing has been published about *Oxyloma h. kanabensis* since H.A. Pilsbry named it in 1948. This is a problem to field biologists who perform censuses of organisms within specific political boundaries. Reliable identifications have to be made, but the available literature is mostly anatomy-based and lacks unambiguous comparisons to conchologically similar species. The means of identification are still very much in the realm of systematists, but today field biologists and ecologists find the need to identify with some degree of reliability whole suites of organisms about which they may not be very familiar.

Oxyloma h. kanabensis is being sought elsewhere in the area. At these localities it can be identified reliably, but at newly found localities there is some potential to confuse it with other succineid gastropods (and perhaps other conchologically similar snails). So there is a need to derive a means by which this endangered animal can be distinguished from the others with some degree of certainty based on non-invasive techniques that can be used in the field. By examining the type material as well as recent collections, we present here a review of *O. h. kanabensis,* with special attention to the criteria by which biological census programs can identify it. The methods address anatomy, but non-invasive field observations are stressed. This paper provides the basic starting data necessary to work with this endangered mollusk.

GEOGRAPHIC DISTRIBUTION

The genus *Oxyloma* is widespread in the northern hemisphere and is known from some occurrences in the southern hemisphere. Pilsbry (1948: 775) specified: "Northern continents and South Africa; southern and insular limits elsewhere not known."

Oxyloma haydeni (Binney 1858) was reported by Pilsbry (1948: 797) to occur at the type locality, Nebraska, "between the rivers Loup Fork and L'Eau qui Court," as well as at the "Red River of the North and at Fort Resolution, Great Slave Lake," Canada (Pilsbry, quoting Binney's (1858) record of *O. haydeni* var. *minor*). The Department of Malacology in the Academy of Natural Sciences of Philadelphia (ANSP) holds dry shell material identified as this species from Nebraska, Utah, Wyoming, North Dakota, Montana, Idaho, Washington, and "Washington Territory" (Washington/Oregon). The nominate species has also recently been identified in the Grand Canyon. S.-K. Wu has identified specimens discovered at Indian Gardens, along the Bright Angel Trail (Stevens *et al.*, 1995a, b; 1997). This locality is 52 km southwest of Vasey's Paradise, also in Grand Canyon National Park, and 115 km south-southeast of Kanab, Utah, where live the nearest known populations of *O. h. kanabensis* (see below). Conchologically, the Indian Gardens *Oxyloma* more resembles *O. h. haydeni* than it does *O. h. kanabensis;* however, anatomical data have not yet been made available.

Oxyloma h. kanabensis is known thus far only from two localities (Fig. 1). The type locality north of Kanab, Kane County, Utah, was first collected in 1909 (Pilsbry & Ferriss, 1911, as *Succinea hawkinsi* Baird; Pilsbry, 1948), and subsequent known collections were made in 1953 and 1990. In 1990 the locality hosted two populations 2.1 km apart. The second known locality, Vasey's Paradise, Coconino County, Arizona, was first collected in 1991 (Spamer & Bogan, 1993a,b). Vasey's Paradise is on the west bank of the Colorado River at Mile 31.8 (Km 51.2), measured by convention downstream from Lees Ferry, Arizona, in the Marble Canyon section of Grand Canyon National Park (see Stevens, 1996).

Utah

Oxyloma h. kanabensis was first collected in 1909 near Kanab Creek north of Kanab, Kane County, Utah. At the time, Kanab's principal industries were stock-raising and farming; its population in 1900 was 710 (Heilprin & Heilprin, 1906: 927). Specimens were collected during a malacological reconnaissance by James H. Ferriss, which were sent to Henry A. Pilsbry, Curator of Malacology at the Academy of Natural Sciences of Philadelphia (ANSP). The time of year during which the reconnaissance was made is not recorded, but intuitively it was during the field season, between late spring and early fall. Ferriss had identified the specimens as *Succinea hawkinsi* Baird 1863, by which identification they were published by Ferriss (1910: 109) and by Pilsbry & Ferriss (1911: 192), and as which they remained in the ANSP collections until Pilsbry (1948) made the redetermination as the new subspecies, *O. h. kanabensis.* Kerns (1993) reported fossil specimens of *Oxyloma* in 9,200-yr-old sediments in Grand Gulch, southeastern Utah, just northeast of the area addressed by the present paper. A report of

O. h. kanabensis in a fossil deposit at Provo, Utah County, northern Utah (Baily & Baily, 1952: 91), is without any remark, illustration, or subsequent discussion of it, so we treat the record as suspect. Extralimitally, Harris & Hubricht (1982: 1609) recorded "*Oxyloma kanabensis* Pilsbry" at localities in southern Alberta, Canada, but discussed neither systematics nor the method of identification; the records are presently uncorroborated.

Ferriss had identified the Kanab Creek locality as "The Greens, 6 m[iles] above Kanab on Kanab Wash" (Ferriss label, ANSP), which is the locality published by Pilsbry & Ferriss (1911). The last four lines and Ferriss's signature, cut from a letter to Pilsbry, accompany the type material at ANSP; they provide the only other known data about the locality: "The *Succinea* were found on a wet ledge among the moss and moccasin (cypripedium) flowers: have about 100. Yours hastily Jas H Ferriss." The name, "The Greens," does not appear in contemporary or modern gazetteers, nor is it recognized by local residents today. Ferriss (1910: 109) alluded to "lakes in the mouth of caves along the Kanab Wash north of [Fredonia, Arizona, and Kanab]," where he found "*S. hawkinsi,*" but he provided no further information.

One of the two populations of recent record lives in Three Lakes Canyon, a tributary to Kanab Creek ca. 10 km northwest of Kanab; the other population, just recently extirpated, lived in a marsh by a cliff along Kanab Creek (England, 1992; U.S. Fish and Wildlife Service, 1994; J. L. England, verbal communication, 1995). ANSP 345170, a lot containing just two bleached white shells (thus dead collected) obtained by M.L. Walton on 27 October 1953 were taken from "5 1/2 up Kanab Wash from Kanab, Kane Co."; this is the only known collection of this snail between Ferriss' 1909 collections and those made during reconnaissance surveys ca. 1990.

Kanab Creek is a principal drainage in this part of Utah, together with Johnson Wash which parallels it 15 km to the east. This area has experienced much geomorphic change since the late 1800s due to modified land use patterns. Kanab Creek has a history of large-scale floods, some of which had lasting influence on the floodplain near Kanab. Although the precise localities that have hosted *Oxyloma h. kanabensis* are not specifically studied, the investigations of hydrologic and geomorphic events along Kanab Creek by Webb *et al.* (1991) bear some application to studies of the ambersnail habitat. Webb *et al.* (1991, figs. 1-8A, B) published photographs taken of Kanab Creek and the mouth of Three Lakes Canyon in 1939 and 1984. They showed that between these two times there had been aggradation of the flood plain, channelization, and vegetational colonization, which may have been due to the presence of a water-supply dam 4 km downstream.

In the early 1990s, surveys of the malacofauna of the State of Utah established that the Utah populations were in peril (England, 1992). The Three Lakes Canyon population of up to 100,000 individuals was largely destroyed by earth moving equipment late in 1990 (Clarke & Lunceford, 1991; U.S. Fish and Wildlife Service, 1991). In late 1994, the Three Lakes area experienced a flash flood. Although the area has not yet been fully appraised, the ambersnail population seems to still be relatively viable (J.L. England, personal communication, 1995).

The smaller population along Kanab Creek, numbering more than 300 individuals in the early 1980s (England, 1994: ii), was restricted to "a long narrow marsh measuring about 46 m (150 feet) long and 15 cm (6 inches) wide in 1990" (England, 1992: 13658). The marsh was partially dewatered by a ditch and drainpipe installed for livestock watering. This population has since been extirpated (U.S. Fish and Wildlife Service, 1994; J.L. England, personal communication, 1995).

Arizona

The genus *Oxyloma* was not known to be alive in Arizona until it was discovered during a 1991 survey of the Colorado River corridor through the Grand Canyon, conducted by Spamer as a part of the Glen Canyon Environmental Studies (GCES) (Spamer & Bogan, 1991, 1993a, b). Before *O. h. kanabensis* was discovered at Vasey's Paradise, shells of *Oxyloma* had previously been reported from Arizona only in fossil deposits in the southern part of the state (Bequaert & Miller, 1973; Mead, 1991).

The GCES program was a consortium of Federal, State, and Native American agencies, placed under the administrative purview of the U.S. Bureau of Reclamation. At the conclusion of the EIS studies, GCES programs were continued by a newly established consortium, the Grand Canyon Monitoring and Research Center. The GCES surveys established baseline data for biological, geomorphic, and hydrologic parameters of the Colorado River corridor downstream from Glen Canyon Dam (GCD). These data contributed to the Final EIS pertaining to the operation of the GCD hydroelectric powerplant. Since 1963, when the dam became operational, artificial fluctuations of relatively sediment-free water released from the dam have significantly altered the riparian community and physical characteristics of the river through most of the Grand Canyon (Carothers & Brown, 1991; Committee to Review the Glen Canyon Environmental Studies, 1991, 1994, 1996).

FIG. 2. Vasey's Paradise, Grand Canyon National Park, Arizona. The perennial springs issue from the Redwall Limestone. This view looks down from the opposite wall of the canyon, showing most of the locality. The Colorado River is seen at the bottom of the photo. River flow is to the left; part of a small rapid is seen to the right, and to the left is seen part of the return eddy at the foot of the rapid. Vegetation completely covers the canyon wall except where scoured by periodic spring floods. The vegetation-free area above the Colorado represents the approximate range of post-dam fluctuations. (Photograph September 1994, courtesy of L.E. Stevens, U.S. Bureau of Reclamation, GCES.)

Vasey's Paradise (Fig. 2) is the more exhaustively studied locality hosting *Oxyloma h. kanabensis* because of its role in the GCES program and the development of the GCD EIS. It is a small locality on the right bank of the Colorado River (descending), immediately below the mouth of a usually dry tributary, South Canyon. The vegetated area is in association with three cool-water spring outlets in the Redwall Limestone; the outlets are at altitude 925 m. Water cascades in several runs ca. 100 m to the Colorado River over the nearly vertical canyon wall, passing over several ledges on which there are pools. The largest pool, called the "main pool," measures approximately 3 x 5 x <1 m. The vegetational community is unique in the Grand Canyon. Primary vegetation types are poison ivy *(Toxicodendron ryderbergii)*, redbud trees *(Cercis occidentalis)*, and coyote willow *(Salix exiqua)*; secondary types are watercress *(Nasturtium officinale)*, crimson monkey flower *(Mimulus cardinalis)*, and maidenhair ferns *(Adiantum capillus-veneris)* (U.S. Fish and Wildlife Service, 1994; Stevens, 1996; Stevens *et al.*, 1995a, b, 1997). The floral community is rooted in rockfall debris derived from the canyon walls and from debris washed from South Canyon during flash floods. Vegetation is dense throughout most of the locality, except along the cascades and the fluctuating zone of the Colorado River.

The discovery of *Oxyloma h. kanabensis* at Vasey's Paradise was made from collections taken during a survey by Spamer on 25 July 1991. Early collections of *O. h. kanabensis* here were restricted mostly to the areas accessible along the stream runs (Spamer & Bogan, 1991; Blinn *et al.*, 1992), although subsequent studies have revealed a truer distribution of dense subpopulations in the surrounding littoral habitats, with estimates of up to 104,000 individuals in September 1995 (U.S. Fish and Wildlife Service, 1994; Stevens *et al.*, 1995a, b, 1997). The biotic community at Vasey's Paradise is affected by intermittent weather-related phenomena. L. Stevens (personal communication cited by Bills, 1993) reported that in April 1992 a waterfall over the rim of the canyon, slightly downriver of the main spring source, created a major flash flood at Vasey's Paradise. Bills' (1993) report stated, "Judging by the lack of vegetation and heavy silt content in the main pool, it appears that much of the run-off passed through the main pool. Evidence of scouring and scraping still exist on the rim wall." The lower part of Vasey's Paradise is inundated by regular (usually daily) rises of the Colorado River as a result of water flow from the Glen Canyon Dam powerplant. The maximum turbine capacity is 32,500 cubic feet per second (cfs) (910 m^3/s), and controlled releases not using the spillways can approach 49,000 cfs

(1,372 m^3/s). Rarely anymore is the maximum turbine capacity reached. Since 1963, six periods of flow exceeded 45,000 cfs (1,275 m^3/s), in 1965, 1980, and during 1983-1986 (Stevens *et al.*, 1995b, 1997). In 1983, extraordinary flood flows in the Colorado River drainage above Glen Canyon Dam filled Lake Powell. An emergency drawdown of the lake resulted in the maximum controlled release of 92,000 cfs (2,576 m^3/s) through the GCD powerplant, diversion tunnels, and spillways; very high releases were also seen in 1984. None of these flows inundated the whole of Vasey's Paradise, although a century earlier an ungaged flood flow in 1884, estimated at 300,000 cfs (8,400 m^3/s), must have drowned the site. Pre-dam seasonal floods of 100,000 cfs (2,800 m^3/s) were not unusual, which certainly had impacts on the site. In the post-dam regime, however, it is deemed that normal operations of the powerplant will have minimum impact on *O. h. kanabensis* (U.S. Bureau of Reclamation, 1995); maximum normal powerplant releases will be 20,000 cfs (560 m^3/s). How long the *O. h. kanabensis* population has lived at Vasey's Paradise is unknown. How the superflood of 1884 may have affected the fauna living at Vasey's Paradise is conjecture. There is circumstantial evidence that the ambersnail was seen during a cursory biotic survey in 1976, when it may have been misidentified as *Lymnaea* sp. (Cole & Kubly, 1976; Spamer & Bogan, 1993a, b). Although the high flows of 1983 and 1984 top recent records, they did not completely inundate the site; they did reach natural (pre-dam) springtime flows in the range of 100,000 cfs. The artificial low flows now experienced have changed the vegetational community at Vasey's Paradise (Stevens *et al.*, 1995b, 1997), but just how this has affected the ambersnail population therein is uncertain, other than to permit a wider distribution of the vegetation it prefers.

From the 1991 reconnaissance, 83 specimens were identified as *Oxyloma h. kanabensis* (Spamer & Bogan, 1991). The pioneering nature of the survey directed much time to prospecting all potential molluscan habitats. Many more specimens could have been collected but were not because of the broad qualitative and geographic objectives of the survey.

Subsequent visits to Vasey's Paradise by various investigators have yielded various results. Bills (1993) reported that on 5 May 1993, 14 ambersnail individuals were seen above a level 20 m above the Colorado River. "Individuals were located exclusively in areas of thick, wet stems of dead and decaying monkey flower." Since no individuals were seen in the fluctuating zone produced by Glen Canyon Dam powerplant, it has been assumed that high-volume outflows

FIG. 3. Vasey's Paradise during a tributary flood as seen from the Colorado River. The habitats alongside the stream runs are flushed by cascading water. (Photograph by Spamer, May 1993.)

from the dam could have an impact on the ambersnails and their habitat.

On 23 May 1993, Spamer visited the site while the Vasey's Paradise springs were in flood (Fig. 3). Access to the lower part of the locality was prohibited by the rushing cascades, and no mollusks were seen in the vegetation close to river level.

A site visit by Spamer on 27 May 1994 revealed that the Vasey's Paradise springs had recently experienced flood flows; vegetation alongside the stream runs was flattened, although still alive. All specimens of *Physella* sp. (Physidae), an aquatic snail usually occurring in great abundance here (Spamer & Bogan, 1993a), were absent, testifying to the intensity of the flood. L. Stevens (personal communication, 1994) had been on the site about 24 hours before. He reported seeing many specimens of *Oxyloma h. kanabensis,* but did not mention any evidence of a flood. On the other hand, Spamer found just one ambersnail during an hour of prospecting, in an unexpected location. It was found under an overhanging rock ledge about 2 m above river level, on damp moss in deep shade. The individual was very large and colored dark gray. On handling, it was unresponsive at first, but it began to move on the hand after a couple of minutes, perhaps in response to warming.

The circumstances of snail distributions following a tributary flooding event provide evidence that during some hydrologic events *Oxyloma h. kanabensis* can find small-scale refugia within the Vasey's Paradise habitat. However, the nature of tributary flooding is quite different from the inundating flows of rising Colorado River levels. Until more ecological studies of this snail have been made at this site, no direct comparison can be made of its response to different types of flooding events.

Spiller (1994) reported that a site visit in September, 1994, located "a large number" of ambersnails between the 20,000 cfs (560 m^3/s) and 45,000 cfs (1,260 m^3/s) flow levels. Based on estimated population densities, it was estimated that >1,000 individuals would be impacted by river flows in this range.

ENVIRONMENTAL MEDIATION AT KNOWN LOCALITIES

The type locality in Kanab, Utah, is privately owned. The landowners have indicated a willingness to conserve the ambersnail on their property (England, 1992), and some consideration has been taken of the possibility of the sale of the property to the Federal government (J.L. England, personal communication, 1995). However, continuing land-use practices resulted in the extirpation of the smaller population near Kanab Creek, and the reduction of the larger population at Three Springs Canyon (England, 1994). There is the possibility that the property may be commercially developed (England, personal communication, 1995). At this time, the future of *Oxyloma h. kanabensis* at its type locality is uncertain.

At Vasey's Paradise in Grand Canyon National Park, *Oxyloma h. kanabensis* is accorded protection by endangered-wildlife legislation as well as by various legislative measures associated with the national park. Impacts due to visitation by river travelers have not been quantified, although the steep walls, slippery ledges, and dense stands of poison ivy are deterrents to invasion. This matter is being monitored, and river travelers are educated in the need to avoid unnecessary trespass; no changes have yet been made by the National Park Service regarding site visitation. The operation of the Glen Canyon Dam hydropower plant will be moderated by the Final EIS (U.S. Bureau of Reclamation, 1995). However, the modified plans include periodic controlled high flows from the dam, whose purpose it is to redistribute accumulated river-bottom sediment to the eroding streamside beaches and riparian habitats. High flows will flood parts of Vasey's Paradise. Some flows higher than 20,000 cfs (560 m^3/s), and certainly all flows higher than 40,000 cfs (1,120 m^3/s), will have an impact on the ambersnail population (U.S. Fish and Wildlife Service, 1994). The first experimental flow, in March 1996, was accompanied by on-site monitoring and periodic monitoring continues (Stevens *et al.*, 1995a; Moody, 1996; GCES staff, personal communications). Preliminary results show that the flood did not seriously impact the population, but formal reports are pending. The most recently available comprehensive report is the 1995 Final Report (Stevens *et al.*, 1997).

POTENTIAL LOCALITIES

It is difficult to predict where terrestrial mollusks will be found. Similar habitats may be barren, and species which are colonial may be easily missed. *Oxyloma h. kanabensis* seems to require very specific physical and biological conditions. Bills (1993) had made a cursory examination of a habitat hosting few monkey flowers, in the shaded, vegetated portion of perennially wet Saddle Canyon (Colorado River Mile 47.0; Km 75.6). Although "Unidentified slugs, snails, and caddisflies were seen," no *Oxyloma* were seen. The 1991 mollusk survey (Spamer & Bogan, 1993a, b) investigated 43 sites, 15 of which were malacologically productive; a total of approximately 24.8 hours was spent searching (Spamer & Bogan, 1991). Since then, 17 additional sites have been examined by Spamer or by other investigators, 14 of which were productive; none yielded *Oxyloma.*

Potential habitats in this region of plateaus and canyons are likely few and far between. Springs (thus also perennially wet streams) are few, and access to many of them is laborious and time-consuming. A marshy wetland environment must be associated with the water source. It is apparent from the occurrences at Vasey's Paradise and along Kanab Creek (the artificially extirpated population in particular) that even small suitable areas can host this animal. The investigation of potential habitats in the Grand Canyon especially is encumbered by the logistical difficulties of travel in the Canyon, as well as by the administrative restrictions placed on river and backcountry travel. Federal, State, and Native American lands in the region all have special administrative controls on land use.

ECOLOGY

The ecology of *Oxyloma h. kanabensis* is being very closely studied at Vasey's Paradise. This work is a part of the surveys being made of the biotic and geomorphic impacts of modified river flows caused by the Glen Canyon Dam hydropower plant. Already many significant findings have been made (Stevens *et al.*, 1995a, b; personal communications with GCES biologists). However, since much specialized data are continually being accumulated and revised by various field and systematic workers *(e.g.*, Stevens *et al.*, 1995a, b; 1997), it is not prudent to repeat here anything more than basic information that is likely to be applicable to widely dispersed localities.

In both localities so far known to host *Oxyloma h. kanabensis,* the mode of occurrence is in perennially wet, marshy areas that afford suitable cover and vegetation. The animal appears to be restricted to such conditions where they occur at the bases of sandstone or limestone cliffs in which there are seeps and springs. It is found only on the surface of perennially wet soils, on wet rock alongside shallow standing water, or on the lower portions of plant stalks. It seems to inhabit the general conditions under which cat-tails *(Typha domingensis)* grow, although individuals will be found mostly on stems of the crimson monkey flower, *Mimulus cardinalis,* and watercress, *Nasturtium officinale* (U.S. Fish and Wildlife Service, 1994; Stevens *et al.*, 1995a, b, 1997). Between the two, its preference is for *Nasturtium;* this selection becomes much more pronounced during and after the peak reproductive season in mid- to late-summer (Stevens *et al.*, 1995a, b; 1997). This mollusk is dormant during the winter.

Aside from records of this snail just within the mouths of vole burrows at the type locality (Clarke & Lunceford, 1991), it does not seek the shelter of fallen plants and logs, nor of detritus or talus. From the perspective of its microhabitat, *Oxyloma h. kanabensis* lives exposed; apparently, the criterion of hiding-cover is of less importance than is that of temperature regulation. When it is found in direct sunlight, it is usually very near open and covered shade and is always within a zone of raised humidity and cooler temperatures influenced by nearby running water. In response to hydrologic events, the animal will migrate or seek shelter, including that of overhanging ledges where if temperatures are too cool it becomes less responsive to stimuli.

The reproductive behavior of *Oxyloma h. kanabensis* is unknown, although reproduction seems to peak in mid- to late-summer (Stevens *et al.*, 1995a, b; 1997). Population densities increase dramatically during the summer months. England (1994: 5) has summarized: "Great diversity in the size of individuals within its population early in the active growing season indicate that reproduction probably occurs throughout all warm, wet periods of the year and that the Kanab ambersnail overwinters as juveniles, sub-adults, and adults (Clarke, 1991) [*i.e.*, Clarke & Lunceford, 1991]. It is probable that the Kanab ambersnail has a life span of about 12 to 15 months (Clarke, 1991)." Studies at Vasey's Paradise are refining this information (Stevens *et al.*, 1995a, b; 1997).

The food needs of *Oxyloma h. kanabensis* are unknown. Clearly, by its mode of occurrence, it feeds upon microorganisms that live in a wet, organically enriched substrate. The preference for moist dead and decaying monkey flowers and watercress would seem to indicate the presence of favored microfloras (*e.g.*, diatoms or fungi) specialized to the decayed stems of these vascular plants.

Ecological surveys of the Vasey's Paradise population of *O. h. kanabensis* continue. From surveys to date (Stevens *et al.*, 1997), it appears that potential predators of the ambersnail include toads and treefrogs, several species of birds, and, when individuals are washed into pools at the Colorado River, rainbow trout (a non-indigenous fish in the Grand Canyon). More lately, there have been reports of predation by mice (personal communications from Arizona Game and Fish biologists), but the mammalian fauna of the locality remains undocumented (Stevens *et al.*, 1997). Some living ambersnails also have been collected because they were parasitized by the platyhelminth trematode *Leucochloridium cyanocittae* (Trematoda) (P. Lewis, personal communication cited by

Stevens *et al.*, 1997: 22); this relationship is still being investigated.

SYSTEMATIC DESCRIPTIONS

No systematic work has been done on *Oxyloma h. kanabensis* since Pilsbry's (1948) original description of it. Some workers are of the opinion that *O. h. kanabensis* should be elevated to species rank, but thus far no data have been published for this purpose (S.-K. Wu, personal communications). Accordingly, we retain its subspecific rank pending proper systematic studies. Its identification is dependent on the original systematic descriptions of the genus and species, but this information is widely scattered and not often immediately available to reconnaissance biologists. We provide here the brief original descriptions (and translations) for the genus *Oxyloma*, the species *O. haydeni*, and the subspecies *O. h. kanabensis.*

Oxyloma Westerlund 1885

Succinea (Oxyloma) Westerlund (1885: 1-2, 7-8)

Original Description. The taxon *Oxyloma* was originally named as a subgenus of *Succinea* Draparnaud 1801, including in it four species. The type species is *S. dunkeri* "Zelebar" Pfeiffer 1855, by subsequent designation by Westerlund (1902: 116).

> "*Oxyloma.* Kiefer hornig, mehr breit als lang, mattbraun, ohne Strahlenbündel u. ohne Zähnchen *(S. hungarica);* Geh. länglich, mässig glänzend, meistens dünn aber festschalig; Umg. s. schnell zunchnend; Münd. länglich; an der Spindel verläuft eine scharfe, weisse, oben eindringende u. hervorragende Falte." (Westerlund 1885: 1-2).
>
> [*Oxyloma.* Jaw horny, wider than long, matt brown, without bundle of rays and without denticles *(S. hungarica);* shell oblong, moderately shiny, generally thin but solid; coiling very rapidly expanding; aperture elongate; on the columella runs a sharp, white, dorsally impressed and prominent fold.]

The reference to *"S. hungarica"* is to *Succinea hungarica* Hazay 1881 (= *Oxyloma (Oxyloma) dunkeri* (Pfeiffer 1855); see Grossu, 1987).

Pilsbry's Redescription. Pilsbry segregated the genus *Oxyloma* into two groups, including *"Oxyloma effusa* Group (Section *Neoxyloma* Pilsbry)" [*O. effusa* ("Shuttleworth" Pfeiffer 1853)], about which he commented only, "This is the North American section of the genus. Although it is rather weakly differentiated from typical *Oxyloma,* the difference seems worth notice in view of the geographic segregation" (Pilsbry, 1948: 777).

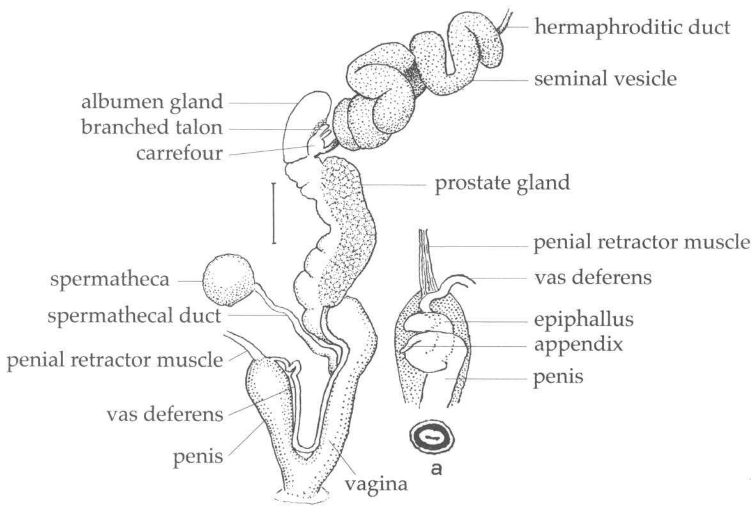

FIG. 4. Pilsbry's (1948, fig. 419A) original illustration of the internal anatomy of *Oxyloma haydeni kanabensis;* "a" indicates penis. Pilsbry did not annotate his figure; our annotations are added. Scale bar = 1 mm.

"The shell is very thin, with the whorls somewhat flattened above the periphery and the spire usually short. The penis terminates in a small appendix and an epiphallus. The thin sheath of the penis encloses also the sinuous or closely convoluted epiphallus. The jaw has a single median projection or rarely none. Marginal teeth of the radula numerous, with very narrow, long, tapering basal plates." (Pilsbry, 1948: 775).

Oxyloma haydeni (Binney 1858) (Figs. 7A, B)

Succinea haydeni Binney 1858: 114
Succinea haydeni var. *minor* Binney 1858: 115

Original Description. For a translation of this text, see Pilsbry's amended description (below).

"Succinea haydeni. Testa elongata-ovalis, tenuis, pellucida, succinea; spira parva, acuta; anfr. 3 convexi, ultimus rugis levibus incrementalibus et sulcis crassis spiralibus, interruptis, inequaliter notatus; sutura mediocris; colemella callo levi induta, apicem interiorem a basi testae mostrans; apertura obliqua, ovalis, 5-7 long. testae aequans, ad basin expansior. Long. 21; diam. 9 mill."

Pilsbry's Redescription. For his redescription of this species, Pilsbry (1948: 797) quoted Binney's (1858: 115) English description of *Succinea haydeni* var. *minor,* with slight changes. Pilsbry cited the measurements given by Binney for *S. haydeni.*

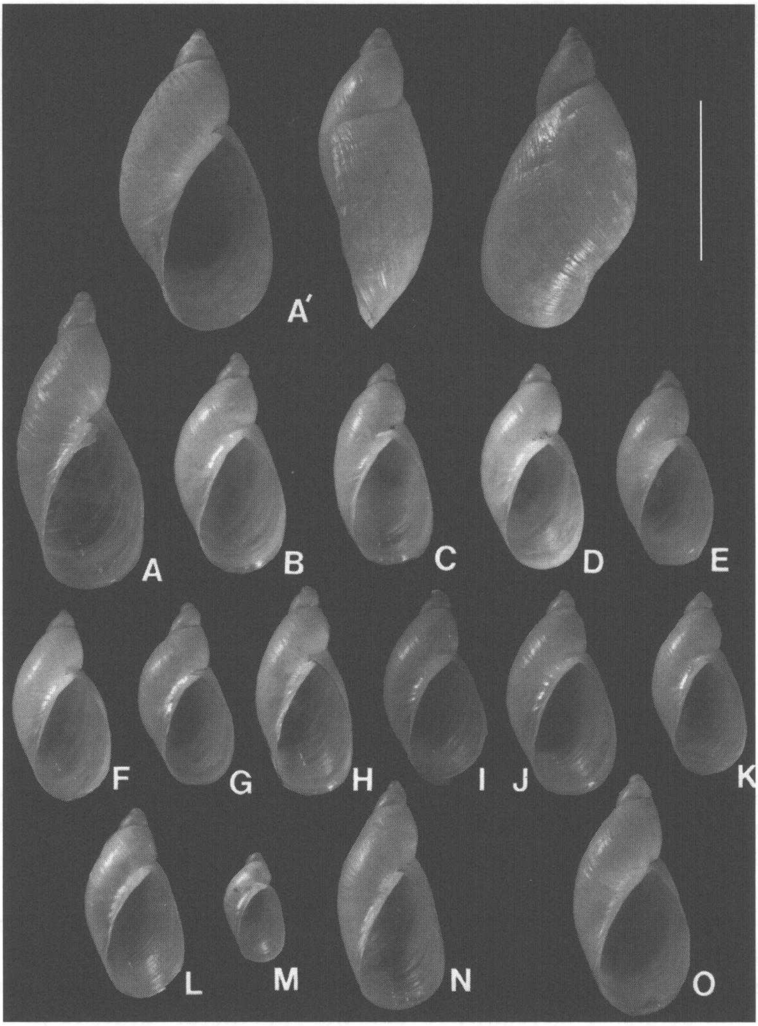

FIG. 5. Type specimens of *Oxyloma haydeni kanabensis* Pilsbry, from "The Greens," north of Kanab, Kane County, Utah, collected by J. H. Ferriss, 1909. **A′**, Holotype (ANSP 103166). **A-O**, Paratypes a-o (as marked in lot ANSP 391101). Scale bar = 1 cm.

"Shell elongate-oval, thin, shining, amber-colored; spire short, acute; whorls 3, convex, the last marked with wrinkles of growth and irregular, heavy, spiral furrows; suture moderate; columella covered lightly with callus, and allowing all the interior whorls to be seen from below to the apex; aperture oblique, oval, five-sevenths the length of the shell, the lower portion of its

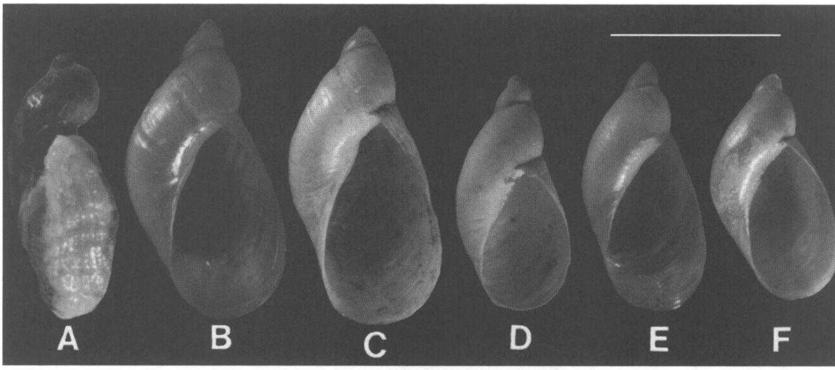

FIG. 6. Specimens of *Oxyloma haydeni kanabensis* from Vasey's Paradise, Grand Canyon National Park, Arizona, collected by E.E. Spamer, 25 July 1991. **A**, alcohol-preserved body removed from shell (shell shown in **B**) (ANSP A16171). **C**, **D**, ANSP 391069. **E**, ANSP 391083. **F**, ANSP 391094. Scale bar = 1 cm.

margin considerably expanded. Length, 21 mm.; diameter, 9 mm.

"Its aperture is nearer that of *S. ovalis* Gould [1841], not Say [1817], but the peristome is much more flexuose, and the upper third of the shell becomes gradually attenuated, so as to give a sharp-pointed appearance, though the spire itself is short. The revolving lines are sometimes continuous over the whole body-whorl, but generally interrupted, or confined to the interstices of the incremental striae or wrinkles. It shares this peculiarity with *S. concordialis* Gould [1848], and *S. lineata* [Binney 1857]."

Succinea ovalis Gould 1841 = *Oxyloma decampi gouldi* Pilsbry 1948, *nom. nov., pro S. ovalis* Say 1817 (= *Novisuccinea ovalis* (Say)). Pilsbry (1948: 810, 819) indicated that *S. lineata* Binney 1857, is neither *S. ovalis* var. *lineata* De Kay 1844, nor *S. lineata* of Binney (1885).

We note significantly that the original and revised descriptions omit anatomical characters of the body of *Oxyloma haydeni*, whereas the description of *O. h. kanabensis* (see below) is based partly on anatomical characters. This readily reveals the ephemeral nature of the systematic knowledge of *Oxyloma*, at least in western America, and the great need for renewed and modernized systematic work.

Oxyloma haydeni kanabensis Pilsbry 1948 (Figs. 4, 5, 6, 7K)

Succinea hawkinsi, Ferriss (1910: 109), Pilsbry & Ferriss (1911: 192)
Oxyloma haydeni kanabensis Pilsbry (1948: 797-798, figs. 419A (p. 784), 428), IUCN Conservation Monitoring Centre (1988: 91), Clarke & Lunceford (1991: 23-36, fig. 2 [from Pilsbry (1948)]), Moseley (1992: 1461-1462),

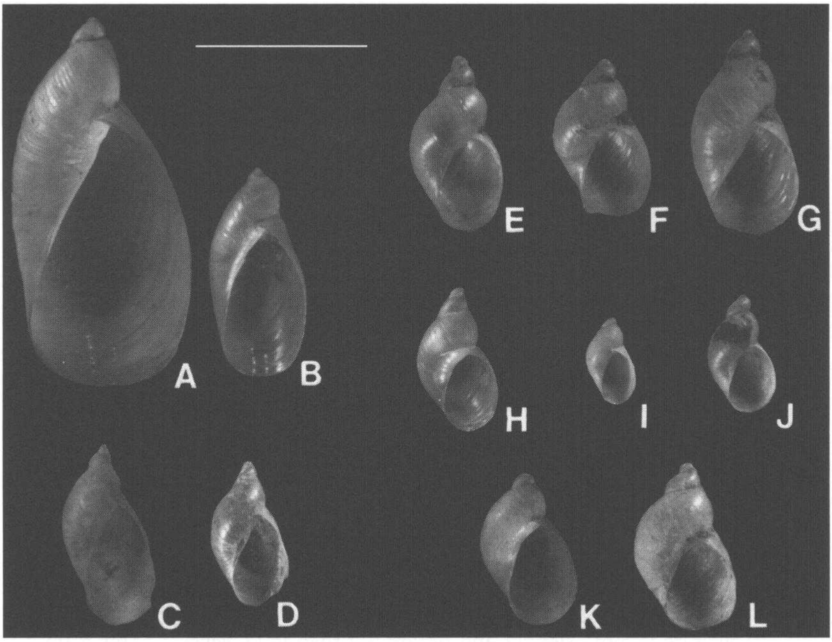

FIG. 7. **A**, **B**, *Oxyloma haydeni haydeni* from Nebraska (A.D. Brown Collection, ANSP). **A**, ANSP 3711; **B**, ANSP 10023 (a shell very similar to *O. h. kanabensis). ***C**, **D**, *Pseudosuccinea columella* (Say 1817) (Lymnaeidae). **C**, Paralectotype, from "Saunders Lake" (ANSP 330011); **D**, specimen introduced to a reservoir at Boyce Thompson Southwest Arboretum, Superior, Arizona, collected 1937 (ANSP 170435). **E-J**, **L**, *Catinella avara* (Say 1824), all from the Grand Canyon. **E**, **F**, confluence of Thunder River and Tapeats Creek (ANSP 391096); **G**, Saddle Canyon (fossil, ANSP 391070); **H**, **I**, Vasey's Paradise (ANSP 391095, 391098, respectively); **J**, Lava Falls (ANSP 391068); **L**, Saddle Canyon (Recent, ANSP 391085). **K**, small specimen of *O. h. kanabensis* from Vasey's Paradise, illustrated here to compare to *C. avara*. Scale bar = 1 cm.

Blinn *et al.* (1992: 19, 21, 22), Spamer & Bogan (1993a: 36, 37, 47, 52, 55-56, 1993b:295, 296), Clarke & Hovingh (1994: 101, 134-136, text-fig. 1 [from Pilsbry (1948)]), U.S. Fish and Wildlife Service (1994: 17-18, 24-25), Stevens *et al.* (1995a, b, 1997)

Oxyloma kanabensis, Harris & Hubricht (1982: 1609), Turgeon *et al.* (1988: 133), Mann & Plummer (1995: 110)

Oxyloma kanabense, Groombridge (1993: 138)

[?] *Lymnaea* sp., Cole & Kubly (1976: 83)

Types. Holotype ANSP 103166, 15 paratypes ANSP 391101; six alcohol-preserved specimens, not located (Spamer & Bogan, 1993a).

Taxonomy. The listings of *Oxyloma kanabensis* by Harris & Hubricht

(1982), Turgeon *et al.* (1988), and Mann & Plummer (1995), and *O. kanabense* by Groombridge (1993), were unexplained and were not based on any systematic criteria. Until the criteria are derived by which this taxon can be shown to be a separate species, it should continue to be called by its original name.

Original Description. [For anatomical details refer to Fig. 4 in the present paper.]

"The shell is pale ochraceous-buff with salmon color spire, or in smaller specimens these tints are diluted; glossy, with irregular wrinkles of growth. The spire is drawn out, of oblique, convex whorls, the last whorl flattened in the upper part, convex below. The aperture is ovate, shorter than in *Oxyloma haydeni* or *sillimani* [(Bland 1865)], the basal margin slightly retracted, not deeply curved. Columella thin, curving into the parietal margin. Parietal callus very thin.

"Length 19 mm., diameter 9.3 mm., length aperture 12.3 mm.; 3 1/2 whorls. Type.

"Length 14.3 mm., diameter 6.9 mm.; 3 3/4 whorls.

"Length 15 mm., diameter 7.3 mm.; 3 1/4 whorls.

"Utah: 'The Greens,' 6 miles above Kanab, on Kanab Wash, on a wet ledge among moss and cypripediums (J. H. Ferriss, 1909) [date of collection]. Type and paratypes 103166 A.N.S.P.

"The spire is more slender and drawn out than in *O. haydeni.* This form was referred to *S. hawkinsi,* with some doubt, at the time it was found, but according to the original account and figures, that species has 4 whorls, and a more slender body-whorl. This is one of those forms to be considered when the *haydeni, hawkinsi, sillimani* group can be revised.

"The genitalia show some resemblance to *O. nuttalliana* [(Lea 1841)], but this species differs by the short penis, more coiled epiphallus, the twinned seminal vesicles and (in the specimen dissected) the massive hermaphrodite duct.

"Mantle over the lung not pigmented. Genitalia, Fig. 419 A. The hermaphrodite duct is very large and swollen in specimens examined, and with the talon, is covered with a thin light gray membrane. The prostate gland is long. Penis short, somewhat swollen above, where it is abruptly bent, gives off a small, tapering appendix and the epiphallus, which make about one spiral turn (Fig. 419 a). The vagina is nearly as long as the penis." (Pilsbry, 1948:797-798.)

TYPE SPECIMENS

The type series is the standard against which other collections are compared; it neither represents total ranges in morphometric size, nor of total range in variability of other characters. Pilsbry's (1948) original description of *Oxyloma h. kanabensis* was generalized on the entire series of type shells and at least one body. There are today 16 shells (holotype and 15 paratypes) in the type series. The entry written by Pilsbry in the ANSP Department of Malacology catalogue indicates that there also were six alcohol-preserved specimens; these are now missing. There is no indication whether the alcohol-preserved specimens included shells, or if they were bodies removed from the type series of dry shells. There also is no indication whether the anatomical drawing included in Pilsbry's original description of the subspecies was based on the holotype or one of the paratypes. Ferriss's letter to Pilsbry (see above) alluded to having around 100 specimens, but only the shells and bodies sent to Pilsbry constitute type material. Pilsbry listed measurements for only three shells, including the holotype. In Table 1 we present for the first time measurements of the entire series of type shells. The 15 paratype specimens are arbitrarily marked a-o in the ANSP collection. Fig. 4 reproduces Pilsbry's illustration of a type body, which we have fully annotated.

The type series appears to represent specimens that had been live-collected. Each shell is amber-colored and translucent; among them there is little variation in coloring. The shell with the largest total height (H), largest diameter (D), and largest apertural opening (height, h, and width, w) was chosen as the holotype by Pilsbry (1948). Although this shell is still the tallest in the collections we have seen, and also the one with the largest apertural opening, one specimen from Vasey's Paradise, while shorter (16.4 mm), has the greatest diameter of the shells we have seen (10.0 mm). Within the type series, only one shell appears to be an immature specimen (paratype m); it is the smallest of the shells in the collections we have seen, thus reflecting a collecting bias that so far has excluded juvenile specimens. The number of whorls in the mature specimens in the type series ranges from 3 to 3 3/4; the immature specimen has 2 1/4.

There is considerable morphometric variation among the shells in the type series. Excluding the immature paratype m, the ranges are: H = 11.4-19.0 mm, D = 5.8-9.2 mm, h = 6.6-12.2 mm, w = 4.2-7.0 mm. The dimensions of paratype m are H = 6.9 mm, D = 3.9 mm, h = 4.2 mm, w = 2.6 mm. As a comparison, from among the measured specimens from Vasey's Paradise the ranges are: H = 9.0-16.4 mm, D = 5.5-10.0 mm, h = 5.8-11.0 mm, w = 3.4-7.0 mm.

The type series is not preferentially larger in any dimension. But there seems to have been a collecting bias for the largest specimens, as expressed by the specimens that Ferriss had sent to Pilsbry in 1909. The Vasey's Paradise collections extend the useful range of measurements into the smaller end of the range for mature and sub-adult specimens. The numbers also show that no one unit of measurement can be used as a reliable index by which to distinguish *Oxyloma h. kanabensis* from other succineids.

Shell sculpture in the form of growth lines is noticeable even without magnification, although it does not seem to be as pronounced as it is in some other succineids. The holotype, however, is distinct among the others by also exhibiting two grooves parallel to and near to the whorl suture, especially noticeable on the final whorl. These grooves appear to be a pathological condition because they appear after a pronounced break in the growth lines in the second whorl (see Fig. 5A').

NON-INVASIVE FIELD IDENTIFICATION

Collections of *Oxyloma h. kanabensis* may be made only by permit from the U.S. Fish and Wildlife Service and other agencies which may have similar protective measures and land-use protocols. Agencies and survey parties who engage in environmental surveys to take censuses of biological resources will generally have to make their determinations through non-invasive identifications in the field. This will introduce some uncertainty to the determinations, but we feel that there are sufficient criteria, excluding internal anatomy, to make preliminary identifications of *O. h. kanabensis* so long as additional succineid snail species are not introduced to the localities. The problem will be renewed at localities that have not before been prospected. Succineids other than *Oxyloma* previously identified from the region are, however, sufficiently distinct to allow at least mature individuals of *Oxyloma* to be identified.

The criteria we present here are solely to distinguish *Oxyloma* from other succineids at least in the Grand Canyon region; the criteria may not apply outside this area, and they will not apply to the identification of succineids on a larger taxonomic scale. We must reiterate Wu's (1993: 91) comment and pertinent citations:

> "Taxonomic placement of succineid snails based on shell characters alone is almost impossible, because in this family (and differing from most molluscan taxa) shell characters are not diagnostic. Currently, features of the shell, radula, reproductive tract, chromosomes and electrophoretic data are being used to define species (*e.g.*, Burch *et al.*, 1966; Patterson, 1971; Hoagland & Davis, 1987)."

At Vasey's Paradise, *Oxyloma h. kanabensis* may have been identified in an early Colorado River survey (Cole & Kubly, 1976:83) as *Lymnaea* sp. (Lymnaeidae, a family of aquatic gastropods). Their determination is reasonable since lymnaeid and succineid shells can be similar, and that the snail identified as a lymnaeid by Cole & Kubly was in fact not aquatic but "amphibious" (D. Kubly, personal communication cited by Bills, 1993). When we were sorting the specimens from the 1991 Colorado River survey (Spamer & Bogan, 1991, 1993a,b), those of *O. h. kanabensis* were problematical, in that they appeared to be something unrecorded from the Grand Canyon region. The lesson we learned is an instructive one for field biologists working on a regional census of organisms.

Since *Oxyloma* had been unknown from Arizona, we at first overlooked that genus, and, based on shell characters alone, tentatively identified it as *Pseudosuccinea columella* (Say 1817) (Lymnaeidae), a widely introduced species, which we thought could have been accidentally brought to the locality in fresh food carried by river runners. *Pseudosuccinea columella* has a remarkably varied shell form, sometimes appearing like *Oxyloma* (compare Baker, 1911, pl. 23, figs. 8-20, pl. 24, figs. 1-4). Even the shell of one of the type specimens of *P. columella* (paralectotype ANSP 330011, Fig. 7C) also is remarkably like *Oxyloma. P. columella* is endemic to the southeastern United States and is a Recent native to a large part of North and Central America and south to Paraguay (Baker, 1911; Bequaert & Miller, 1973). We had overlooked the fact that the shell sculpture of *P. columella* is a herringbone or reticulate pattern, different from the subparallel growth lines seen in *Oxyloma.* To have expected to find *P. columella* introduced to an Arizona locality is not without precedent. This species has been reported to have been introduced to a nursery pond in Tucson, Arizona (Bequaert & Miller, 1973: 200-201), and the ANSP collections contain a lot (ANSP 170435, Fig. 7D) that was taken from a reservoir at the Boyce Thompson Southwest Arboretum at Superior, Arizona; both localities are in the southern part of the state, 400-500 km from the two known localities of *O. h. kanabensis.*

Our anatomical examination of the body of the Vasey's Paradise enigmatic snail established that it was not *Pseudosuccinea,* but in fact *Oxyloma,* with affinities to *O. haydeni.* Specimens were sent to S.-K. Wu (University of Colorado Museum), who established that it was *O. h. kanabensis* (see Spamer & Bogan, 1993a, b). Based on its discovery at Vasey's Paradise, it was included in the U.S. Fish and Wildlife Service rulings that declared the animal Endangered (England, 1992; Blanchard, 1992).

Oxyloma h. kanabensis can be compared to species of *Catinella* and *Succinea.* The known regional record of succineid species is reasonably well established, even if somewhat confused by synonymous species and misidentifications. The associated malacofauna of the Utah locality has not been determined (J.L. England, personal communications), although Pilsbry & Ferriss (1911) recorded specimens from "The Greens" which they identified as *Succinea retusa* Lea *(Oxyloma retusa* (Lea 1834), now apparently a misidentification of *O. h. kanabensis), Physa gyrina* Say 1821 (Physidae) (perhaps a misidentification of *Physella virgata* (Gould 1855), cf. Bequaert & Miller, 1973:202), and *Pisidium* sp. (Bivalvia: Sphaeriidae). Revised records are available for the malacofauna of the Grand Canyon region generally (Spamer & Bogan, 1993a, b). Potentially, the only succineids from this region that might be confused with smaller individuals of *O. h. kanabensis* are *Catinella avara* (Say, 1824) and *Succinea grosvenorii* Lea 1864. The taxonomic distinction of species of *Catinella* and of *Succinea* is problematical, for which reason Spamer & Bogan (1993a, b), following preliminary identifications by S.-K. Wu, conservatively identified only *C. avara* among non-*Oxyloma* succineids in the Grand Canyon, until such time that proper anatomical examinations can be made. Since then, Wu has identified *C. avara, C. vermeta* (Say 1829), and *Catinella* sp. among species at Vasey's Paradise (Stevens *et al.,* 1995a, b; 1997).

Shell

Mature specimens of *Oxyloma h. kanabensis* are 14-19 mm in shell height. The shell is often translucent, usually amber-colored, sometimes pale, but also sometimes various shades of gray. It usually has a lustrous shine, part of which is characteristic of the shell material, but part of which is likely due to the wetness of the environment in which the animal lives. Growth lines in the shell are seen as finely, but slightly irregularly spaced, ribs parallel to the lip of the aperture. In living animals, the dark body and its mottled mantle markings can be seen through the translucent shell, which darkens the apparent color of the shell. Dead shells become chalky, opaque white, sometimes with a slight shine; usually they are nicked, scarred, or broken if they have been exposed for any length of time. The shell has a spire that accentuates the elongate appearance of the shell. The shell of a mature individual has from three to four whorls; the length of the aperture is more than half of the total length of the shell.

Immature specimens, which have been less-commonly examined, lack the large, ovate aperture that is the immediate visual indicator of this taxon. The length of the aperture is about half the total length of the shell, which makes it more closely resemble the shells of *Catinella* and *Succinea.* More mature specimens of *Oxyloma h. kanabensis* also develop the characteristically tall spire. There are no characteristics of shell sculpture or the appearance of the nuclear whorl that consistently and unambiguously segregate *O. h. kanabensis* from *C. avara* and *S. grosvenorii.*

We have discovered a consistently reliable conchological characteristic that segregates *Oxyloma h. kanabensis* from similar shells of *Catinella* and *Succinea.* Measurements have been made of 111 shells of *O. h. kanabensis, C. avara,* and *Succinea grosvenorii,* all from the Grand Canyon region (Table 1). (Take note that what we have identified as *C. avara* could represent two or more species of *Catinella,* since S.-K. Wu has identified additional species in collections made at Vasey's Paradise [Stevens *et al.,* 1995a,b; 1997]. Nonetheless, this does not affect the conclusions we reach here.) We restricted our measurements to those that can be made easily and quickly under field conditions, without significant physical impact on the animals: number of whorls, total shell height (H), maximum shell diameter (D), maximum aperture height (h), and maximum aperture width (w).

Figs. 8A-D illustrate the relationships between H, D, h and w in

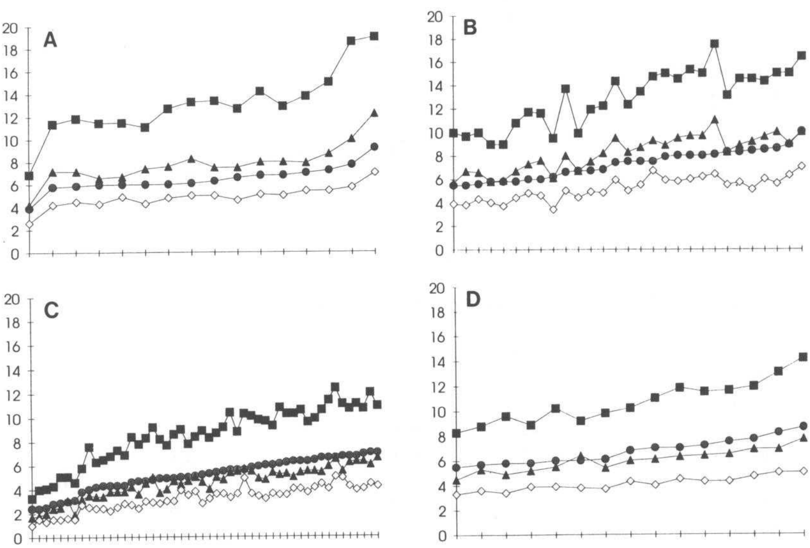

FIG. 8. Plots of measured morphometric variables of shells studied in this paper (Table 1). Each graph is plotted as a function of increasing shell diameter; vertical scale is marked in mm. For each plot shell variables are: total shell height (■), maximum shell diameter (●), maximum aperture height (▲), and maximum aperture width (◇) **A,** *Oxyloma haydeni kanabensis,* type series. **B,** *O. h. kanabensis,* specimens from Vasey's Paradise. **C,** *Catinella avara* (Say). **D,** *Succinea grosvenorii* Lea.

TABLE 1. Measurements and statistical summary of shells of *Oxyloma haydeni kanabensis*, *Catinella avara* and *Succinea grosvenorii* used in this study. H = total height of shell, D = maximum diameter of shell, h = maximum height of aperture, w = maximum width of aperture.

ANSP Catalog No.	H	D	h	w	whorls
Oxyloma haydeni kanabensis (type series, Kanab, Utah; holotype ANSP 103166; paratypes ANSP 391101)					
Holotype*	19.0	9.2	12.2	7.0	3.5
Paratype a	18.6	7.7	10.0	5.7	3.5
Paratype b	13.8	7.0	7.9	5.4	3.25
Paratype c	12.7	6.0	7.6	4.8	3.25
Paratype d	13.4	6.3	7.5	5.0	3.0
Paratype e	11.4	5.8	7.2	4.2	3.0
Paratype f	11.1	6.0	7.4	4.3	3.25
Paratype g	11.5	6.0	6.7	4.9	3.0
Paratype h	13.3	6.1	8.3	5.0	3.25
Paratype i	12.7	6.6	7.5	4.6	3.25
Paratype j	12.9	6.8	8.0	5.0	3.25
Paratype k	11.5	6.0	6.6	4.3	3.0
Paratype l	11.9	5.9	7.2	4.5	3.0
Paratype m	6.9	3.9	4.2	2.6	2.25
Paratype n*	14.2	6.8	8.0	5.1	3.75
Paratype o*	15.0	7.2	8.7	5.4	3.5
Mean	13.12	6.46	7.81	4.86	3.19
Std. Dev.	2.86	1.11	1.67	0.91	0.34
Var.	8.18	1.23	2.80	0.82	0.11
*specimens measured by Pilsbry (1948)					
Oxyloma haydeni kanabensis (Vasey's Paradise, Grand Canyon National Park)					
391067	9.0	5.8	5.9	3.7	2.75
391067	9.5	6.2	6.1	3.4	2.75
391067	14.4	8.0	8.4	5.3	3.25
391067	14.5	8.3	8.9	5.7	3.0
391067	14.5	8.4	9.2	5.1	3.0
391067	15.0	7.9	8.9	5.9	3.0
391067	15.0	8.6	10.0	5.6	3.0
391067	16.4	10.0	10.0	7.0	3.25
391069	9.9	6.7	6.7	4.4	2.75
391069	10.0	5.5	5.7	3.9	3.0
391069	10.0	5.6	6.6	4.3	3.0
391069	10.8	5.8	6.7	4.4	2.75
391069	11.7	6.0	7.3	4.8	2.75
391069	12.2	6.8	8.2	4.8	2.75
391069	13.4	7.5	8.7	5.5	3.0
391069	17.5	8.1	11.0	6.4	3.0

TABLE 1 (cont.).

ANSP Catalog No.	H	D	h	w	whorls
391083	9.7	5.5	6.7	3.8	3.0
391083	11.6	6.0	7.6	4.6	3.0
391083	11.9	6.7	7.5	4.9	3.0
391083	12.3	7.5	8.3	5.0	3.0
391083	13.1	8.3	8.3	5.5	2.75
391083	13.7	6.6	8.0	5.0	3.25
391083	14.3	7.4	9.5	5.9	3.0
391083	14.3	8.5	9.6	6.0	3.25
391083	14.5	8.0	9.5	5.8	3.25
391083	15.0	8.0	9.7	6.2	3.25
391083	15.0	8.9	9.0	6.3	3.25
391083	15.3	8.0	9.7	6.0	3.25
391093	9.0	5.8	5.8	4.0	2.75
391094	14.7	7.5	9.3	6.7	3.25
Mean	12.94	7.26	8.23	5.20	3.01
Std. Dev.	2.36	1.19	1.45	0.94	0.19
Var.	5.59	1.43	2.10	0.89	0.04
Catinella avara (Vasey's Paradise, Grand Canyon National Park)					
A16172	7.3	4.3	3.8	2.5	3.5
A16172	10.1	5.8	5.5	3.6	3.5
391095	8.3	4.7	4.5	3.0	3.75
391098	3.3	2.4	1.7	1.0	2.25
391098	5.1	3.0	3.1	1.6	2.25
Mean	6.82	4.04	3.72	2.34	3.05
Std. Dev.	2.67	1.36	1.44	1.05	0.74
Var.	7.13	1.84	2.06	1.10	0.54
Catinella avara (Saddle Canyon, Grand Canyon National Park)					
A16173	7.6	4.0	3.5	2.5	2.75
391070*	10.7	6.9	6.3	4.0	3.75
391070*	12.4	6.6	6.5	5.0	3.25
391085	7.8	5.0	4.7	3.5	3.25
391085	9.6	6.3	5.5	3.7	3.5
391085	9.9	6.4	5.5	4.1	3.25
391085	10.7	6.7	6.2	4.2	3.5
391086*	9.2	5.5	4.8	3.6	3.25
391086*	12.0	7.0	6.0	4.4	3.25
Mean	9.99	6.04	5.44	3.89	3.31
Std. Dev.	1.66	1.01	0.97	0.69	0.27
Var.	2.77	1.02	0.94	0.48	0.07

*fossil

TABLE 1 (cont.).

ANSP Catalog No.	H	D	h	w	whorls
Catinella avara (Thunder River, Grand Canyon National Park)					
391087	4.6	3.1	1.9	1.5	3.0
391087	6.3	4.2	3.4	2.4	3.0
391087	6.5	4.3	3.4	2.4	3.0
391087	8.3	5.3	4.0	3.2	3.5
391087	9.3	6.0	5.4	3.6	3.25
391087	9.8	5.9	4.9	3.4	3.75
391087	10.3	6.2	5.3	3.5	3.75
391087	10.3	6.3	5.0	4.0	3.75
391087	10.6	6.3	5.4	4.0	3.5
391087	10.6	6.6	5.4	4.4	3.5
391087	10.9	7.0	6.6	4.2	4.0
Mean	8.86	5.56	4.61	3.33	3.45
Std. Dev.	2.14	1.20	1.31	0.89	0.35
Var.	4.60	1.45	1.72	0.80	0.12
Catinella avara (Lava Falls Spring, Grand Canyon National Park)					
391068	5.8	3.8	3.2	2.7	2.5
391068	6.9	4.3	3.8	2.8	2.75
391068	8.4	5.1	5.0	3.8	2.75
Mean	7.03	4.40	4.00	3.10	2.67
Std. Dev.	1.30	0.66	0.92	0.61	0.14
Var.	1.70	0.43	0.84	0.37	0.02
Catinella avara (Muav Creek, Grand Canyon National Park)					
103307	7.7	4.9	4.0	3.0	3.0
103307	8.2	4.9	3.7	2.8	3.5
103307	8.7	5.4	5.0	3.6	3.25
Mean	8.20	5.07	4.23	3.13	3.25
Std. Dev.	0.50	0.29	0.68	0.41	0.25
Var.	0.25	0.08	0.46	0.17	0.06
Catinella avara (Shinumo Creek, Grand Canyon National Park)					
94070	4.0	2.4	1.8	1.5	3.0
94070	4.1	2.5	2.0	1.3	3.0
94070	4.3	2.8	2.4	1.5	2.25
94070	5.1	2.9	2.5	1.5	3.25
94070	8.4	4.6	4.2	2.7	3.5
94070	8.6	4.9	4.7	3.0	3.5
94070	8.9	5.2	4.6	2.8	3.25
94070	9.0	5.0	4.4	3.9	3.5

TABLE 1 (cont.).

ANSP Catalog No.	H	D	h	w	whorls
94070	9.7	6.0	4.8	3.2	3.5
Mean	6.90	4.03	3.49	2.38	3.19
Std. Dev.	2.44	1.37	1.27	0.94	0.41
Var.	5.96	1.88	1.62	0.89	0.17
Catinella avara (South Rim at Bass Station, Coconino Plateau, Kaibab National Forest)					
94066	10.3	5.6	5.7	4.9	3.5
Catinella avara (South Rim west of Bass Trail, Grand Canyon National Park)					
94067	6.8	4.3	3.8	2.2	3.0
94067	7.8	4.7	3.6	2.4	3.25
94067	8.8	5.6	5.5	3.6	3.25
94067	9.2	4.8	5.0	2.9	3.25
94067	10.4	5.6	5.4	3.3	3.5
94067	10.8	6.1	5.2	3.5	3.5
94067	11.1	6.7	5.5	4.9	3.5
94067	11.1	6.7	6.3	3.9	3.5
94067	11.4	6.6	5.9	4.0	3.5
Mean	9.71	5.68	5.13	3.41	3.36
Std. Dev.	1.64	0.92	0.90	0.84	0.18
Var.	2.70	0.84	0.80	0.70	0.03
Succinea grosvenorii (Mount Trumbull, Grand Canyon National Park)					
103311	9.2	6.0	6.4	3.8	3.5
103311	9.6	5.8	4.9	3.4	3.25
103311	9.8	6.1	5.4	3.7	3.25
103311	10.2	6.0	5.5	3.9	3.25
103311	10.2	6.8	6.0	4.3	3.5
103311	11.5	7.2	6.4	4.3	3.75
103311	11.8	7.0	6.3	4.5	3.5
103311	11.9	7.7	6.9	4.7	3.5
103311	14.1	8.6	7.7	5.0	3.75
Mean	10.92	6.80	6.17	4.18	3.47
Std. Dev.	1.55	0.94	0.84	0.52	0.20
Var.	2.40	0.88	0.71	0.27	0.04
Succinea grosvenorii (Big Springs, Kaibab Plateau, Kaibab National Forest)					
103163	8.3	5.5	4.5	3.3	3.25
103163	8.8	5.7	5.3	3.6	3.25
103163	8.9	5.8	5.2	3.9	3.0

TABLE 1 (cont.).

ANSP Catalog No.	H	D	h	w	whorls
103163	11.0	7.0	6.1	4.0	3.75
103163	11.6	7.5	6.5	4.3	3.75
103163	13.0	8.2	6.9	5.0	3.75
Mean	10.27	6.62	5.75	4.02	3.45
Std. Dev.	1.88	1.11	0.90	0.59	0.33
Var.	3.53	1.24	0.82	0.35	0.11

the type series of 16 *Oxyloma h. kanabensis* specimens, 30 specimens of *O. h. kanabensis* from Vasey's Paradise, 50 specimens of *Catinella avara* from several localities in and near the Grand Canyon, and 15 specimens of *Succinea grosvenorii* from two localities near the Grand Canyon. Our comparisons include shells of *S. grosvenorii* because they are conchologically similar to species of *Catinella* and immature *Oxyloma*, and because the species has been identified at localities near the Grand Canyon (although *Succinea* has not yet been identified in collections made inside the canyon). Conchologically determined identifications in the field may confuse these species with young *Oxyloma*. Including the number of whorls in any plot produced no meaningful data, even between smaller shells of *O. h. kanabensis* and non-*Oxyloma* species. But there is a consistent separation of *Oxyloma* and non-*Oxyloma* individuals when the shell diameter and the aperture height are plotted.

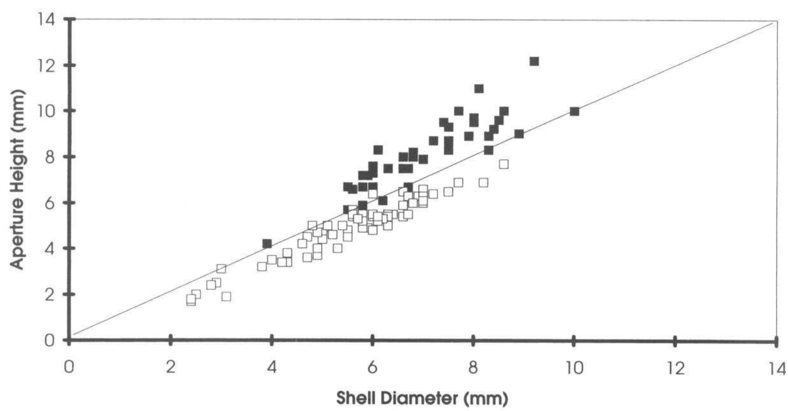

FIG. 9. Plot of maximum shell diameter (D) versus maximum aperture height (h). ■= *Oxyloma haydeni kanabensis* (type series + specimens from Vasey's Paradise). ❑ = *Catinella avara* + *Succinea grosvenorii* (specimens from the Grand Canyon and vicinity). Localities and measurements are itemized in Table 1.

In Figs. 8A-D, data are plotted as a function of increasing values of D. No specific morphometric variable segregates *Oxyloma h. kanabensis* from *Catinella* or *Succinea,* with one noticeable exception: in *O. h. kanabensis* h > D, while in *C. avara* and *S. grosvenorii* h < D. Fig. 9 plots h and D for all 111 measured shells, illustrating this striking conchological relationship. Thus we believe that h and D are very reliable indicators with which to distinguish *Oxyloma* from non-*Oxyloma* specimens in the field, at least within the approximate range of the endangered *O. h. kanabensis.* We point out further that if the identification of *O. h. haydeni* in the Grand Canyon is correct, its aperture is even more greatly enlarged, and the corresponding measurements will plot even more greatly apart than those we provide here for *O. h. kanabensis.*

Among small shells of *Oxyloma h. kanabensis* it appears that the measurements of h and D may plot very closely together (see for example the data point near 4 mm/4 mm in Fig. 9, which is the shell of paratype m, an immature individual). The data for a few of the mature individuals of *O. h. kanabensis* also show nearly equal values for these two measurements. The fact that in some shells of *Catinella avara* and *Succinea grosvenorii* h and D also plot nearly equally places uncertainty on the identification of species based on the measurements of individual shells. However, measuring more individuals will reveal a trend; from it can be determined whether one species or another dominates the community. Thus, the presence or absence of *O. h. kanabensis* at a locality can be documented with a satisfactory degree of certainty. Absolute specific identifications of individuals, however, should rely upon anatomical characters.

No collections are yet available that include juvenile specimens of *Oxyloma h. kanabensis.* It is apparent that some of the small *O. h. kanabensis* shells very closely resemble the shells of smaller mature individuals of non-*Oxyloma* species. Thus we are unable to predict yet whether the shell diameter-aperture height relationship will be distinct for specimens younger than sub-adult.

External Body Anatomy

The eyes of *Oxyloma h. kanabensis* can be seen as dark spots on the end of two long stalks; the smaller protuberance at the base of each eye-stalk is a tentacle. The stalks are quite noticeable, and they are slender with respect to the size of the head. The foot is lighter in color than the body; it exhibits several muscular bands perpendicular to the long axis, and shows about ten less well developed ribs that run parallel to the long axis (Fig. 6A). The overall head-foot is not disproportionately large compared to the shell, and the animal can retract almost fully into the shell.

The genital aperture, on the right side of the head just behind the stalk, is a reliable character to distinguish *Oxyloma* from *Succinea* when it is visible (see Burch, 1962: 67-68). The aperture is more inflated in *Oxyloma;* in *Succinea* it is like a slit. However, under field conditions the retraction of the animal into its shell upon disturbance could hamper the consistent observation of this character.

INVASIVE IDENTIFICATION

Internal body anatomy can be examined only with collected, relaxed sacrificed specimens. Genera and species of the family Succineidae are most reliably identified based on these characters, particularly the genitalia and radulae (*e.g.*, Pilsbry, 1948: 771-775).

When internal anatomical examinations of *Oxyloma h. kanabensis* are possible, only Pilsbry's (1948) original description of the subspecies thus far provides information about this animal. It was the criteria of penis and hermaphroditic duct sizes upon which Pilsbry distinguished *O. h. kanabensis* from *O. h. haydeni,* but he did not discuss the internal anatomy of *O. h. haydeni,* thus it is unclear what all the distinctions may be between these two taxa. Pilsbry's (1948: 784, fig. 419A) anatomical diagram of *O. h. kanabensis* clearly distinguishes the various anatomical characters, but he labelled only the penis. We provide here (Fig. 4) a fully annotated version of Pilsbry's figure, which can be used in conjunction with Pilsbry's (1948: 797-798) original description (see also above).

SUMMARY

At localities where *Oxyloma haydeni kanabensis* has already been discovered, adults and sub-adults can be easily distinguished from non-*Oxyloma* species. The determination can be made simply by visual inspection; the shell size and aperture shape are distinctive. At localities suspected to support *O. h. kanabensis,* or if there is some question as to whether a given specimen belongs to this taxon, measurements of the maximum shell diameter and maximum aperture height will segregate *O. h. kanabensis* (and presumably also *O. h. haydeni*) from conchologically similar species of *Catinella* and *Succinea.* For smaller, sub-adult specimens of *O. h. kanabensis,* the measurement of

these characters for several specimens, while not necessarily conclusive for an individual, should reveal whether the mollusk population at the locality is dominated by *O. h. kanabensis* or a non-*Oxyloma* species. Whether these relationships also reliably distinguish juvenile *O. h. kanabensis* from small mature individuals of *Catinella* or *Succinea* is presently not known.

When more studies improve our understanding of the ecological requirements of *Oxyloma h. kanabensis*, better predictive measures may be derived to locate this animal at other places in the southwestern United States. As a Federally listed Endangered animal, it can be safeguarded from extraordinarily negative artificial impacts. At the same time, if it can be demonstrated to have viable, safeguarded populations in a wider geographic range than that now known, it could be removed from the listing.

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