Native and introduced *Ampullaridae* in North America: History, status, and ecology

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June 13, 2006. Ongoing collaborative genetic analysis conducted at University of Hawaii by R.H. Cowie and K.A. Hayes and at Florida International University by T.M. Collins and T.A. Rawlings has provided insights into the identification of various *Pomacea* populations in the continental U.S. that were not available when this chapter was first drafted. R.H. Cowie (pers. comm.) and T.M. Collins (pers. comm.) recently reported their studies have shown that *Pomacea* with channeled shells introduced into California and Arizona are *P. canaliculata* and those populations examined from Texas and elsewhere in the mainland U.S. are actually *P. insularum*, except for the *P. haustrum* populations in Florida that produce green eggs. Further, the species typically seen in the aquarium trade and introduced into Florida that has long been considered to be *P. bridgesii* is actually *P. diffusa.*

Abstract

The family Ampullariidae included only a single species native in the United States (US), *Pomacea paludosa*, which was confined to peninsular Florida. However, other exotic species have been introduced into North American waters including *P. bridgesii, P. harustrum,* one or more species of the *P. canaliculata* complex (but without genetic confirmation of true *P. canaliculata* in North American to date), and *Marisa cornuarietis*. Additionally, *P. Paludosa* has been introduced at sites outside its native range, and shells of Central American *P. flagellata* have been documented in flotsam on southern Texas beaches. Established populations of *P. bridgesii* and *P. haustrum* are believed to be restricted to Florida, and *P. paludosa* is established in Georgia and

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Alabama. *Marisa cornuarietis* maintains populations in Florida and at three sites in central Texas. Large *Pomacea* with channeled shells have established populations in Alabama, Arizona, California, Georgia, Florida, and Texas, with unsuccessful introductions in North Carolina and Manitoba. Despite widely scattered introductions, no significant agricultural damage has been reported from exotic ampullariids, and ecological impacts have been limited to date. Among these species, established populations of *P. canaliculata* complex snails are perhaps of greatest concern. Thus far, populations of *P. canaliculata* complex in the US have not been associated with agricultural areas where crops could be impacted, except for those in southeastern Texas. Populations in southeastern Texas occur in rice irrigation canals, as well as in natural waters in the area; they do enter area rice fields, but without significant damage to cultivated plants. Methods and timing of rice farming in Texas appears to preclude *Pomacea* damage to crops when plants are most vulnerable. Nonetheless, the potential ecological and agricultural impact of exotic *Pomacea* could escalate in the future and should not be underestimated.

Key words: Channeled applesnail, golden apple snail, *Pomacea canaliculata*, *Pomacea canaliculata* complex, Ampullariidae, Florida applesnail, *Pomacea paludosa*, titan applesnail, *Pomacea haustrum*, spiketop applesnail, *Pomacea bridgesii*, giant ramshorn, *Marisa cornuarietis*, mystery snail, mystery snail.

Introduction

For more than 25 years, certain species of Ampullariidae have been relocated by people far from their native ranges to locations around the world. American species of the genus *Pomacea* and *Marisa cornuarietis* have been most widely distributed (Cowie 1998, 2002). A few Asian *Pila* have also been introduced in foreign areas (Cowie 1998). Unfortunately, many such introductions have had extensive negative impacts on important agricultural crops (Cowie 1998) as well as on aquatic and wetland ecosystems (Horne et al. 1992; Carlsson et al. 2004a). In other instances, introduced *Pomacea* now serve as vectors for parasites that directly threaten humans (Cowie 2002).

Many reasons have been used to justify these relocations and introductions. However, culture of ampullariids as a human food item and use as aquarium species serve as the two primary motivations (Cowie 1998, 2002). Other reasons include controlling weeds (Seaman and Porterfield 1964; Blackburn et al. 1971; Okuma et al. 1994a, b) or other gastropods (Cazzaniga 1990; Pointier and Jourdane 2000), culture in water gardens, and use as classroom or research animals in educational settings. Some populations may have also been inadvertently introduced when aquatic macrophytes were transplanted. Limited numbers of *P. paludosa* have been offered for sale in Asian food markets in Texas. Furthermore, the Texas Parks and Wildlife Department (TPWD) has addressed inquiries about allowing commercial production of *Pomacea* for human consumption.

Throughout Southeast Asia, the Indo-Pacific, and Oceania, most populations of *Pomacea* species arose from misguided attempts to use cultured snails to create a local Asian escargot industry (Su Sin 2003). Species of the *P. canaliculata* complex with channeled shells were initially taken from Argentina to Taiwan in 1979 and were subsequently distributed to the Philippines and other locations in the Indo-Pacific and Southeast Asia (Acosta and Pullin 1991; Mochida 1991). They were found in Hawaii in 1989 (Lach and Cowie 1999). Snails that escaped or were released from these failed culture efforts have become world-class crop pests that now significantly reduce production of *Oryza sativa* (rice) and *Colocasia esculenta* (taro or elephantear).

In the continental United States (US) and Canada, however, nearly all introductions are related to releases and escapes from aquarium and pet trade sources (Britton 1991; Howells 2001a, b). Species involved have included exotic *P. bridgesii*, *P. "haustrum,"* one or more members of the *P. canaliculata* complex, and *M. cornuarietis*, as well as relocations of native *P. paludosa* to sites outside its native range in peninsular Florida. Although there appear to have been earlier releases, significant introductions in US waters began in the 1950s and 1960s.

Terminology

Among members of the Ampullariidae, both common and scientific names have been and continue to be a source of confusion. The family name Pilidae, which is a junior synonym of Ampullariidae, continues to appear in recent literature. Introductions at widely scattered locations around the world have further contributed to confusion. In North America, species in two genera, *Pomacea* and *Marisa*, have been the primary groups of interest. Application of DNA analysis to members of this family is modifying understanding of these snails even as this paragraph is being written.

Species of *Pomacea* were once placed in the genus *Ampullaria,* and this name continues to be used by some in the aquarium industry. Common and scientific names recommended by the American Fisheries Society for species in US waters (Turgeon et al. 1998) include *P. paludosa* (Florida applesnail), *P. bridgesii* (spiketop applesnail), *P. "haustrum"* (titan applesnail), *P. canaliculata* (channeled applesnail), and giant rams-horn snail (*Marisa cornuarietis*), with "applesnail" being one word. The name Mexican applesnail is used herein for *P. flagellata.*

Among these taxa, *P. canaliculata* identification has become particularly problematic. This is in part, because as many as 15 species with channeled shells may exist. Distinctions between species are not always clear, and introductions may have included multiple taxa. Genetic analysis has indicated that specimens tested from Texas and Florida (Hayes 2004; Hayes and Cowie, in press) are apparently not true *P. canaliculata,* as initially thought, but rather one of the other channeled species. Additionally, the taxonomic status of *P. "haustrum"* and *P. bridgesii* in US waters also needs confirmation and clarification. Most US *Pomacea* populations have not been examined genetically thus far, and their actual identities remain uncertain. At present, samples from the *P. canaliculata* group have been obtained for genetic analysis from 15 locations in Florida, Texas, and California, in addition to those from other species and locations outside the continental US, and are being studied by staff at Florida International University and the University of Hawaii (T.M. Collins, Florida International University, personal communication, June 2005).

True mysterysnails (*Viviparidae*) which were once more popular in the aquarium trade, have been largely replaced by *Pomacea*. However, the term "mystery snail" has been widely retained for smaller ampullariid species and individuals. Typically, pet trade sources apply the name "apple snail" only to larger species and individuals.

In the Indo-Pacific and Southeast Asia, *P. canaliculata* and one or more other channeled species are widely known as golden apple snail, as well as golden kuhol or golden snail. Because *Marisa* (Dillon 1998-1999) and members of several *Pomacea* species commonly occur in gold-colored, xanthic morphs, use of "golden apple snail" in North America can be confusing. Conversely, "channeled applesnail" is not widely recognized in the Indo-Pacific and Asia. Additionally, the acronym GAS is often used in Asia and the Indo-Pacific for golden apple snail. However, the US Department of Agriculture (USDA) and other groups in the US use GAS in reference to giant African snails (*Achatina fulica* and several other species). In the US, the acronym CAS is often used for channeled applesnail (now also known to include species other than *P. canaliculata*).

Collectively, these points have created confusion among scientists, aquarium hobbyists, agricultural interests, and the laity alike. Further, in areas where various ampullariid species have been legally prohibited, some individuals appear to have used this confusion to facilitate continued sale and distribution of various species.

Reasons for introductions into North American waters

Unlike most other introduction sites around the world, the presence of exotic ampullariids in US waters largely reflects use of several *Pomacea* species and *M. cornuarietis* in the ornamental aquarium trade rather than for human consumption or biocontrol purposes. In the early to mid-1900s, balanced aquarium philosophy included the use of freshwater gastropods in aquarium culture. So, aquarists sought snails for this purpose.

A few collection records of living *Pomacea* and their shells at sites in the US prior to the 1950s suggest that some species were sporadically imported for the pet trade earlier in the 1900s. However, much of the early aquarium hobby interest focused on mysterysnails, members of Viviparidae, from the US, Europe, and eastern Asia. These large, live-bearing snails typically did not consume aquarium plants. But, they were generally not particularly heat tolerant. As the use of electric heaters in home aquaria gained wide use to support cold-sensitive tropical fishes, hobbyist tanks became increasingly inhospitable to mysterysnails.

In the 1950s and 1960s, use of native *P. paludosa* and other imported, exotic ampullariids in the aquarium trade increased dramatically. In time, as *Pomacea* replaced viviparid gastropods, the name "mystery snail" was retained by tropical fish dealers, exacerbating the confusion associated with terminology. *P. paludosa* and species in the *P. canaliculata* complex aggressively consumed aquarium plants and often failed to eat algae. Thus, these snails soon fell out of favor. Ultimately, *P. bridgesii*, which does not feed on macrophytes but does eat algae, became the primary snail in the American aquarium industry. Further, because of its subtropical climate, Florida became important in the mid-1900s as both a port-of-entry and site of fish farm culture of tropical aquarium fishes, mollusks, and plants. As a result, many of the earliest introduction records of exotic ampullariids come from Florida waters.

More recently, however, the use of living plants in home aquaria has declined, being replaced largely by realistic-looking artificial plants and improved mechanical filtration. This shift in aquarium management methodology made use of plant-feeding ampullariids in ornamental fish tanks once again more acceptable to hobbyists. Not unexpectedly, reports of exotic ampullariid introductions in a number of US states increased in the last half of the 20th century, particularly since the mid-1980s.

M. cornuarietis has been distributed primarily, and subsequently introduced into local waters, through the aquarium trade, similar to *Pomacea* species. *M. cornuarietis* has also been stocked to control noxious growths of aquatic macrophytes (Seaman and Porterfield 1964, Blackburn et al. 1971, Cowie 2002). Fortunately, the high density needed to control macrophytes and its limited cold tolerance served to discourage introductions for this reason. Nonetheless, when reports of this species damaging aquatic macrophytes in springs in central Texas reached the news media in the early to mid-1980s, TPWD offices began to receive inquiries about the possibility of using giant rams-horns to address noxious macrophyte problems in private ponds. Additionally, prior to legal restriction of *P. canaliculata* in Texas, reports surfaced of at least two private landowners in southeastern Texas who had deliberately stocked *P. canaliculata* complex snails to eliminate excessive growths of aquatic plants.

P. canaliculata has been utilized in the Philippines (Joshi 2005a,b) and elsewhere (Okuma et al. 1994a, b) to consume weeds in rice fields. Although deliberate use for this purpose has not been documented in the continental US, some rice farmers in Texas have reportedly noted that *P. canaliculata* complex snails did feed upon weeds in their fields. Despite reports of weed control in agricultural fields, Lach et al. (2000) illustrated generalist consumption of several macrophytes and explicitly recommended against stocking *Pomacea* for this purpose. Current feeding experiments support this characterization relative to *P. canaliculata* complex snails in Texas (see Examples of Recent and Ongoing Research below).

M. cornuarietis has been used to control other aquatic gastropods that serve as vectors for harmful parasitic worms with some reported degree of success (Pointier and Jourdane 2000). Members of the *P. canaliculata* complex have also been known to consume other snail species (Cazzaniga 1990).

There has been little apparent interest in using ampullariids for human consumption in the mainland US. *P. paludosa* has been observed among frozen seafoods in Asian food markets in Houston (R.G. Howells, unpublished observation), but there has been no indication of any major demand or volume of sales. A recent proposal to allow culture of legally prohibited *P. canaliculata* in Texas for sale to Asian food markets in Houston was denied by TPWD based on the threats this species poses to aquatic ecosystems and agricultural crops, and on the historic failure of similar efforts in Asia. A population of *P. canaliculata* complex snails in Chambers County, Texas is also rumored to have originated from an unsuccessful importation for human consumption in the mid-1990s, but this has not been confirmed.

Ampullarid species documented in North America and current status

P. canaliculata complex (Channeled Applesnail Complex; Golden Apple Snail) (Fig. 1)

For the purposes of this chapter, *Pomacea* with channeled shells found in US and Canadian waters are considered *P. canaliculata* complex, except *P. "haustrum"* types in Florida. Though nearly all were initially considered to be true *P. canaliculata*, at least some are now known to be other channeled taxa whose taxonomic status has yet to be fully studied. It remains unclear how many US populations are actually true *P. canaliculata.* However, the shell shown in Figures 2-3 from Hillsborough County in 1996 seems more morphologically similar to *P. canaliculata* from Argentina (Figs. 4-5) and Hawaii (Figs. 6-7) than to other *Pomacea* with channeled shells from Texas (see below), further suggesting the presence of multiple species with channeled shells in North America. Furthermore, how closely related North American *P. canaliculata* complex snails are to true *P. canaliculata* remains to be fully defined.

Alabama. Specimens of the *P. canaliculata* complex were apparently introduced into a park pond in Mobile around 2003 along with *P. bridgesii*, apparently from a local pet store, and a small population has persisted into the present (D.N. Shelton, Alabama Malacological Research Center, Mobile, personal communication, February 2005). "Channeled" specimens from the Mobile population have not been examined genetically to date.

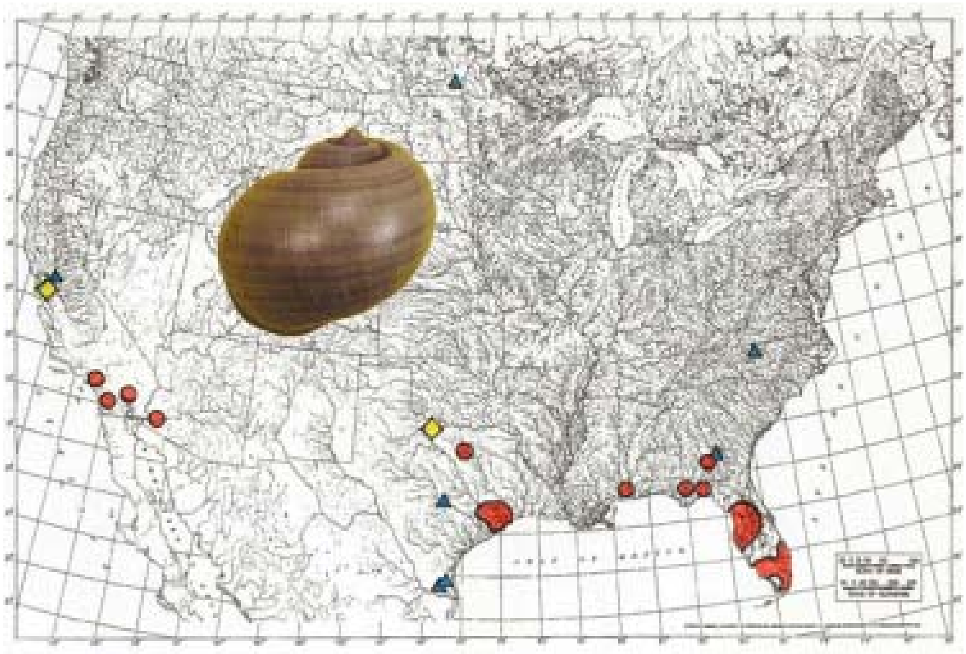


Fig. 1. Distribution records of *Pomacea canaliculata*-complex snails in North America. Red areas indicate living specimens or populations, blue represent collected shells or introductions of living specimens that did not become established, and yellow denotes populations that were found and destroyed. Genetic studies of snails with channeled shells are currently underway and more than a single species could be involved.

Fig. 2-3. *Pomacea "canaliculata"* collected in Hillsborough County, Florida, in 1996. This specimen shows affinities to true *P. canaliculata* from Argentina and Hawaii.

Fig. 4-5. *Pomacea canaliculata* from Argentina

Fig. 6-7. *Pomacea canaliculata* from Hawaii.

Arizona. Channeled *Pomacea* were reported to have been collected in the Colorado River at Yuma, Yuma County in early 2005 (Chuck Minckley, US Fish and Wildlife Service, Parker, Arizona, personal communication, January 2005). This population is still being evaluated and has yet to be examined genetically.

California. A population of channeled *Pomacea* was found in Lake Miramar, San Diego County in 1997 (Cerutti 1998, Hardy 2001). About that same time, another small population was discovered in an ornamental pond at the Norton Simon Museum in Pasadena, Los Angeles County (A.R. Hardy, California Department of Food and Agriculture, personal communication, June 2001) as well as in canals in Riverside County at Mecca near the Salton Sea (A.R. Hardy, personal communication, 2002). Samples for genetic analysis have been obtained from the Miramar and Mecca populations and are currently under study (T.M. Collins, Florida International University, personal communication, June 2005). A population found in Freemont, Alameda County in 1998 was eradicated by county personnel (A.R. Hardy, personal communication, 2002).

The population in an ornamental pond at the Norton Simon Museum in Pasadena was still present in May 2005 (John Sudolcan, operations director, Norton Simon Museum, personal communication, May 2005); however, daily egg mass removal by grounds staff has helped reduce the population size to levels that limit damage to macrophytes. Specimens for genetic analysis were collected by Brian Taylor (California Department of Food and Agriculture) and Matt Abbott (USDA) from populations in Lake Miramar and at Mecca in April 2005 (T.M. Collins, Florida International University, personal communication, June 2005).

Georgia (Figs. 8-9). In early 2005, two specimens with channeled shells were collected in the Alabaha River (Satilla River drainage), Pierce County: One living specimen was captured in a planted pine (*Pinus*) stand about 300 m from the river, and the second was a shell found along a small stream below an impoundment about 5 km from the first collection site (Brett Albanese, Georgia Department of Natural Resources, Social Circle, personal communication, March 2005). In July 2005, B. Albanse (personal communication) reported finding 30 egg clutches and three living adults within the original introduction site area.

Florida (Figs. 2-3). *Pomacea* with channeled shells, initially believed to be *P. canaliculata*, were first found in Palm Beach County in 1978 (Florida Museum of Natural History specimen). Other populations were later located in Collier (1996), Hillsborough (1996), and Pinellas counties in southern and central Florida. More recently, others have been found in Leon and Hamilton counties in northern Florida. Undated material in the Florida Museum of Natural History was collected in the Dade City area of Pasco County, and another sample was taken in Indian River County (2001). A distribution map produced by the Florida Department of Agriculture and Consumer Services in January 2005 indicated *P. canaliculata* complex snails reported from Broward, Collier, Dade, Hendry, Monroe and Palm Beach counties in southern Florida; Citrus, Hernando, Hillsborough, Lake, Manatee, Orange, Osceola, Pasco, Pinellas, Polk, Sarasota, Seminole, and Sumter counties in central Florida; and Hamilton and Leon counties in northern Florida. T.M. Collins, T.A. Rawlings, and P. Sharp (T.M. Collins, Florida International University; personal communication, June 2005) discovered a population near the Shark Valley entrance to Everglades National Park in May 2005. From January through June 2005, populations were confirmed present in 14 of the 21 counties listed above, with additional reports from Brevard, Duval, Highlands, St. Johns, and Volusia counties (Dana R.

Fig. 8-9. *Pomacea canaliculata*-complex specimens found in the Alabaha River drainage, Pierce County, Georgia, USA, in early 2005. Although not examined genetically to date, these specimens appear similar to species with channeled shells present in Texas that are not true *Pomacea canaliculata.*

Denson, Florida Department of Environmental Protection, Orlando, personal communication, July 2005). These introductions likely reflect release of unwanted aquarium specimens or escapees from area tropical fish farms. Specimens subjected to genetic analysis thus far have been shown not to be *P. canaliculata*, though most Florida populations have not been examined genetically.

North Carolina. Channeled *Pomacea* were found in Stoneville Reservoir, Rockingham County in 1992; however, the species did not become established at this location (Howells and Smith 2002).

Texas (Figs. 10-20). Fullington (1978) reported a shell of *P. paludosa* from Harlingen, Cameron County, lower Rio Grande Valley. Neck (1986) indicated that this specimen was actually *P. canaliculata* and reported a second "fresh dead" shell from Arroyo Colorado State Park, Cameron County, a few kilometers from the collection site of Fullington's specimen. Neck and Schultz (1992) later reported another shell from a dry creek bed in Austin, Travis County, also identified as *P. canaliculata.* These were likely random, unsuccessful releases of aquarium animals, and none of these sites has produced additional specimens since. Additionally, none of these were subjected to DNA analysis to confirm the reported species identifications.

The first confirmation of a breeding *Pomacea* population in Texas was that of Neck and Schultz (1992) at a pond in the Buffalo Bayou drainage in Hedwig (Sandalwood) Village, west central Houston, Harris County. This reproducing population was discovered in 1989 and overwintered into 1990. When the site was examined again in early 2001, living snails were still present (Howells 2001c). In July 2000, a population of *P. canaliculata* complex snails with channeled shells was discovered in a rice irrigation canal in Brazoria and Galveston counties between Houston and Galveston (Howells 2001a, b, c; Howells and Smith 2002). Ultimately, morphologically similar snails were found at sites throughout southern Harris, Waller, Fort Bend, Galveston, Brazoria, and Chambers counties in southeastern Texas (centrally located in the Texas rice-growing belt) (Howells 2001b, c; Howells and Smith 2002). Genetic analysis conducted on several snails from southeastern Texas in 2004 and early 2005 (R.H. Cowie, University of Hawaii, personal communication, January 2005) indicated that they were not true *P. canaliculata*, but were one of the other species in the *P. canaliculata* complex. However, most populations in Texas have not been examined genetically to date. In early 2005, populations were still present in all six of these counties.

An additional population of *P. canaliculata* complex snails located in Denton County, near Fort Worth, had been present for several years when first formally examined in early 2001 (Howells 2001c). A subsequent effort to locate specimens there produced only two empty shells. In spring, 2005, neither snails nor their eggs were found (D.K. Britton, University of Texas at Arlington; personal communication, May 2005). This population appears to have either failed to survive repeated northern Texas winters or to have declined dramatically. A population of *Pomacea* with channeled shells was found in a small, ornamental, backyard pond in Wichita Falls, Wichita County in 2001 and was destroyed (Howells and Smith 2002).

Thus far, all of the specimens taken in Texas waters have been typical, dark-colored wild types. None of the color variants seen in the aquarium and pet trade (Figs. 21-22) or found as feral populations elsewhere have been observed in Texas.

Manitoba. Three *Pomacea* that appeared to be *P. canaliculata* complex species were found in Winnipeg, Manitoba, Canada, in July 2002 (L.C. Graham, University of Manitoba; personal communication, May 2005). These snails were believed to have been an aquarium release. The largest measured about 35 mm. Although localized home garden damage was observed, the

Fig. 10-18. *Pomacea canaliculata*-complex specimens from locations in southeastern Texas. Genetic studies of snails from some of these sites indicate that they are not true *P. canaliculata.*

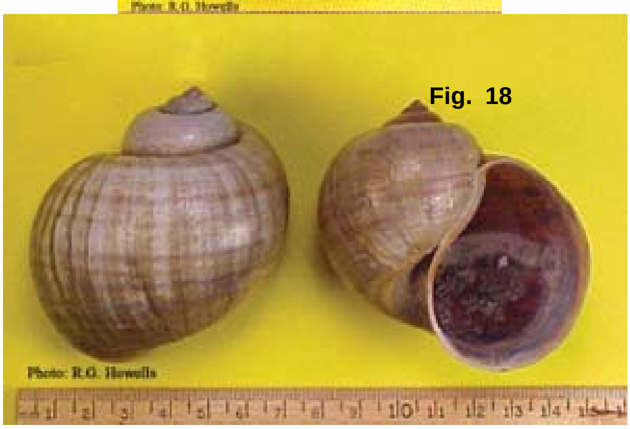


Fig. 19-20. *Pomacea canaliculata*-complex specimens taken in a pond in Bedford, Tarrant County, Texas, in the upper Trinity River drainage in 2001. Although this population reported persisted through several winters in northern Texas, no living specimens have been found at this site during the last two surveys (most recently in 2005).


Fig. 21-22. Gold-colored morphs of *Pomacea canaliculata*, and probably related species with channeled shells, are readily available in the pet and aquarium trade and occur in feral populations in some areas. However, all specimens encountered to date in Texas waters have been dark-colored wild-types.

far northern location of this release precluded overwinter survival and any associated ecological or agricultural threats. Nonetheless, there are hot springs in Canada in which a number of tropical fish species have been documented (Crossman 1984) and that could likely support certain Ampullariidae if introduced at those sites.

P. paludosa (Florida Applesnail) (Fig. 23)

Alabama. A population was reported in Gantt Lake, Conecuh River, Covington County in 1962 (Hubricht 1962). This population has persisted into the present, and this species has been discovered more recently in the Conecuh River below this impoundment (D.N . Shelton, Alabama Malacological Research Center, Mobile, Alabama, personal communication, February

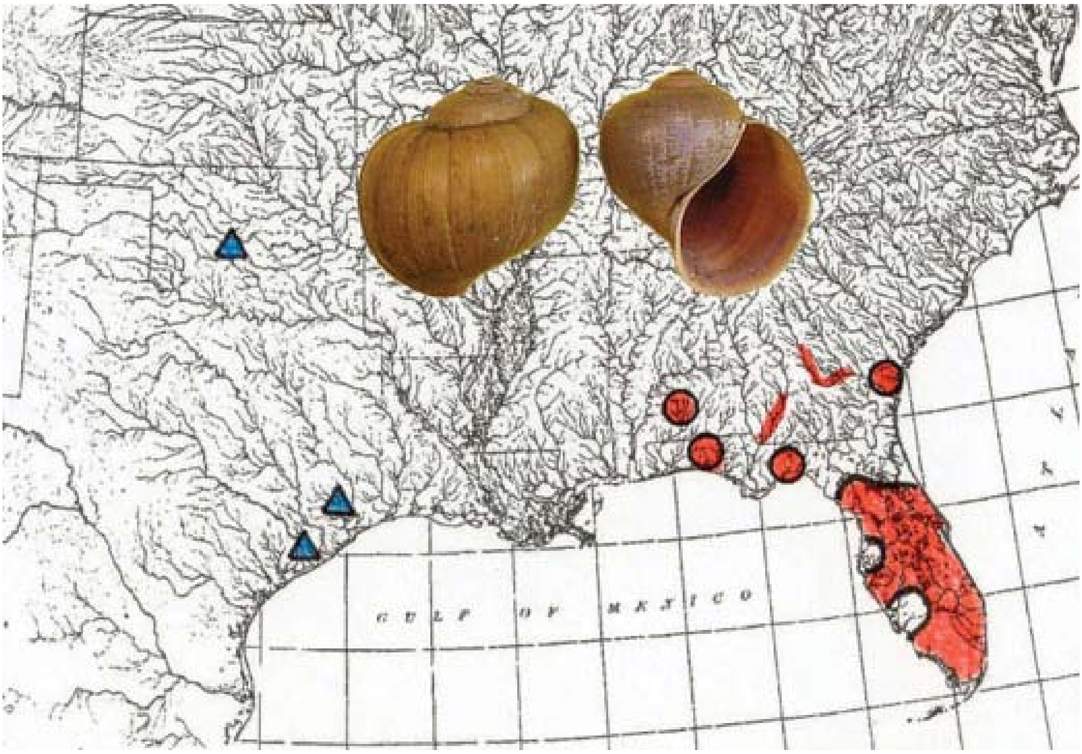


Figure 23. Distribution records of *Pomacea paludosa.* Red areas represent documented living individuals; locations in blue indicate either collections of shells (Texas) or sites with no recent records (Oklahoma).

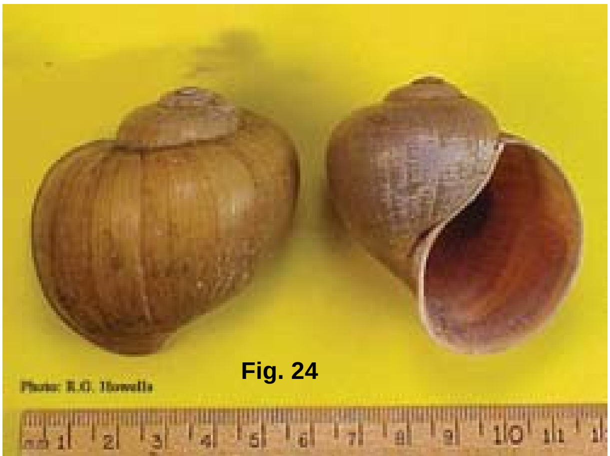
2005). Gantt Lake is a power plant reservoir that receives heated waters which may help this population to survive.

Florida (Figs. 24-27). Though native to the Florida peninsula (Thompson 1984), the northern range limit of this species in Florida is not entirely clear, having been confounded by apparent introductions at sites outside its native range. Limited cold tolerance (Strange 1998) has restricted its ability to invade or endure in northern waters. It reportedly occurs as far west as the Choctawhatchee River (Strange 1998). Feeding habits that include macrophytes limit its utility in the aquarium trade and subsequently its distribution through this vector.

Georgia. Thompson (1984) reported populations present in isolated springs in the Flint and Ocmulgee rivers. Additionally, the United States Geological Survey (USGS) database also documented this species in Hopeton, McIntosh County in 1974. No additional information on the status of these populations was obtained during preparation of this chapter.

Oklahoma. The USGS database includes a record of this species at the Bell Water Gardens, Oklahoma City, Oklahoma County in 1974. No additional references to this location in over 30 years since the first record were found during preparation of this paper.

Texas. Fullington (1978) reported shells found in Harris County (Houston area) and Matagorda County (Gulf of Mexico central coast). These specimens were actually shells collected years earlier. They likely represented releases of aquarium specimens that failed to survive, and no established populations have been confirmed before or since.



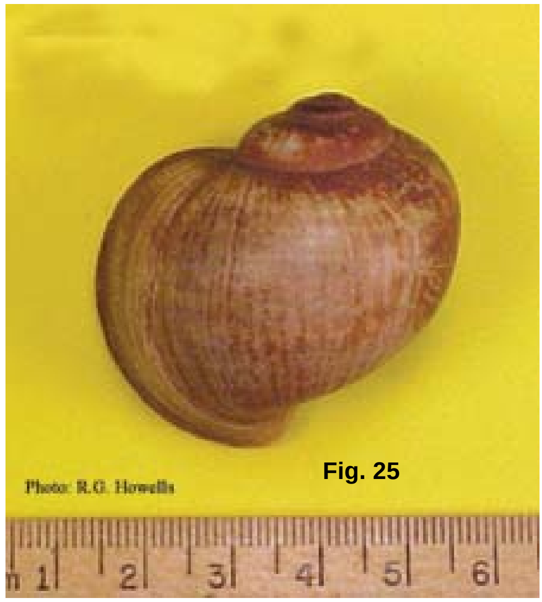


Fig. 24-26. *Pomacea paludosa* from Florida. This is the only native *Pomacea* in the U.S., but it has been introduced at sites outside its original range.

Fig. 27. *Pomacea paludosa* appears only occasionally in the pet and aquarium trade due to its propensity to consume aquarium plants.

P. "haustrum" (Titan Applesnail) (Fig. 28)

Florida (Figs. 29-30). South American *P. "haustrum"* was reported in Palm Beach County in 1989 (Winner 1991); however, the H.G. Lee collection contains an apparent *P. "haustrum"* from this location that was taken in September 1983 (Figs. 29-30). Material in the collection of the Florida Museum of Natural History was also gathered in Palm Beach County in

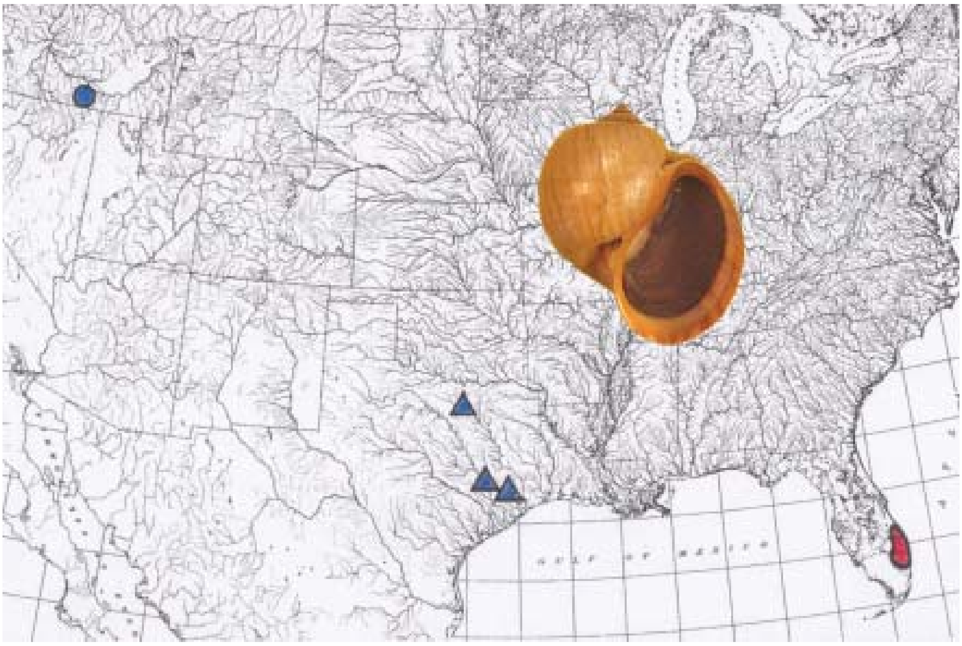


Fig. 28. Distribution of unidentified *Pomacea* species in Texas and Idaho and those assumed to be *P. "haustrum"* in Florida.

1989. Additionally, confirmation that the Florida population is actually this species is lacking (R.H. Cowie, University of Hawaii, personal communication, May 2005; T.M. Collins, Florida International University, personal communation, May 2005). This identification may have been based on green egg masses attributed to *P. haustrum* (Winner 1996), although other snails in this genus may lay green eggs as well. Additionally, both high- and low-spired forms have been found in Florida. Though initially thought to be related to and possibly synonymous with *P. canaliculata* (Thompson 1997, Turgeon et al. 1998), this assumption has been shown to be incorrect. DNA analysis by R.H. Cowie (presented in Joshi 2005a) and by T.M. Collins and T.A. Rawlings (T.M. Collins, Florida International University, Miami, Florida, personal communication, May 2005) indicated that the Florida *P. "haustrum"* appears to be genetically distant from other channeled *Pomacea* examined. This species probably reached US waters via the aquarium trade. It was reported still present in Palm Beach County in 2004 (Carole P. Marshall, personal communication, August 2004) and again in May 2005 (T.M. Collins and R.A. Rawlings, Florida International University, personal communication, June 2005).

P. bridgesii (Spiketop Applesnail) (Fig. 31)

There are two subspecies of this species: *P. bridgesii bridgesii* and *P. bridgesii diffusa*, with the possibility that "*diffusa*" may eventually be elevated to species level (R.H. Cowie, University of Hawaii, personal communication, May 2005). Some have suggested that the first of these is larger and less common, and the latter is the smaller and much more abundant form usually seen in the aquarium trade. For the purposes of this paper, the species "*bridgesii*" has been retained for both, but taxonomic views of these two forms may change in the future.

Fig. 29-30. Specimens presumed to be *Pomacea "haustrum"* from Florida. Populations in Palm Beach County, Florida, that lay green eggs have been considered to be this species, though positive confirmation is still lacking. Both high- and low-spire forms occur.

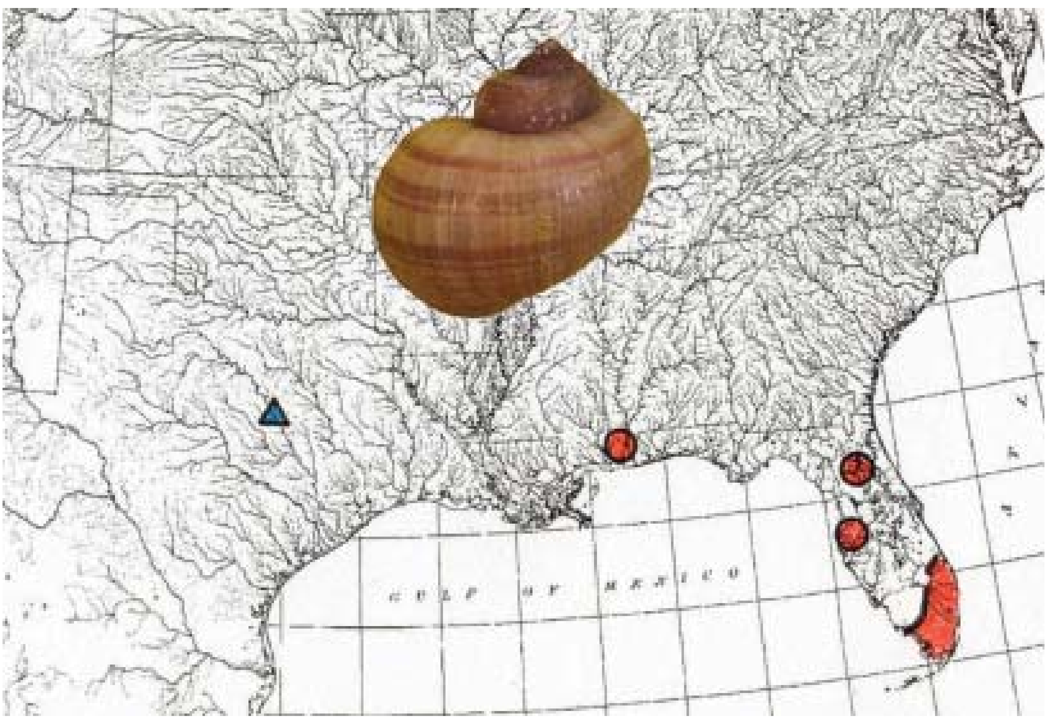


Fig. 31. Distribution records of *Pomacea bridgesii* in the U.S. Red areas represent living populations. The blue location in Texas indicates two specimens that were dead when collected and where no population is known to exist.

Alabama. D.N. Shelton (Alabama Malacological Research Center, Mobile, personal communication, February 2005) reported that this species had been introduced into a park pond in Mobile in approximately 2003 and had maintained a minimal population there since that time. Appearance at this site of this and one of the *P. canaliculata* complex species also close coincided with their availability in a local pet store.

Florida (Figs. 32-34). This popular aquarium species was first reported in Florida in the 1960s, but may have been present since the 1950s. It has been confirmed in Alachua (1981), Brevard (1971), Broward (1992), Dade (1973), Monroe, Palm Beach (1967), and Pinellas counties (Thompson 1984, Strange 1998). Florida populations almost certainly reached local waters through release from private aquaria or area tropical fish farms. This species appears to be well established in Florida waters.

Texas (Figs. 35-36). *P. bridgesii* was found in the Brazos River, Waco, McClennan County in January 2004 when two recently dead specimens were found during a low-water period and associated cold weather. Presumably these were aquarium specimens that been released

Fig. 32-34. *Pomacea bridgesii* from introduced populations in Florida.

earlier but failed to endure the cold winter temperatures. No population is currently known to exist in the state. Both of the specimens found in Texas were dark-colored wild types. None of the domestic color variants that are readily available in the aquarium and pet trade (Figs. 37-40) have been found in the field in Texas.

Pomacea sp. (Undefined Species)

Idaho. An unidentified *Pomacea* species was first reported in the outfall of geothermally heated spring waters from a tropical fish hatchery on Deep Creek, in the central Snake River drainage, Twin Falls County, in 1992 (Bowler and Frest 1992, Frest and Bowler 1992). It was included on a state list of gastropods in 2000 as well (Frest and Johannes 2000). Several color morphs were reported. No reports describing the current status of snails at this site were found during preparation of this chapter.

Texas. In 1989, Texas A&M University conducted predation experiments on an undefined species of *Pomacea* and on *Mylopharyngodon piceus* (black carp) (Collins 1996). The *M. piceus* from this work were ultimately delivered to a private fish farmer (Nico and Williams 1996), but the species of *Pomacea* involved, the eventual disposition of these snails, and the location of the research have not been reported. Texas A&M is located in the Brazos River drainage just upstream of some of the *P. canaliculata* complex populations now present in southeastern Texas. However, when TPWD field surveys were first launched in December 2000, no *Pomacea* were found at sites nearest the Brazos River and its tributaries nearest the university; they were detected only several kilometers to the east in the American Canal and Mustang Bayou, suggesting that presence at these sites may have been a separate introduction unrelated to the Texas A&M stock (Howells 2001b).

At about this same time (ca. 1990), a commercial water garden dealer in Brookshire, Waller County also obtained *Pomacea* of an undetermined species for culture at its facilities. When these macrophyte-feeding snails proved unacceptable for water garden culture, rearing ponds were drained and the snails destroyed. Bessies Bayou, which now supports a population of *P. canaliculata* complex, is only a few hundred meters from the now-closed water garden operation.

Fig. 35-36. *Pomacea bridgesii* specimens found in the Brazos River at Waco, McLennan County, Texas, in January 2004. These were collected during a low-water period and extremely cold temperatures. Both were dead when taken and no population is known to persist here.

Fig. 37-38. *Pomacea bridgesii* is the most-frequently sold snail in the aquarium trade, including dark-colored wild types (Fig. 37, left) and gold-colored individuals (Figs. 38, right).

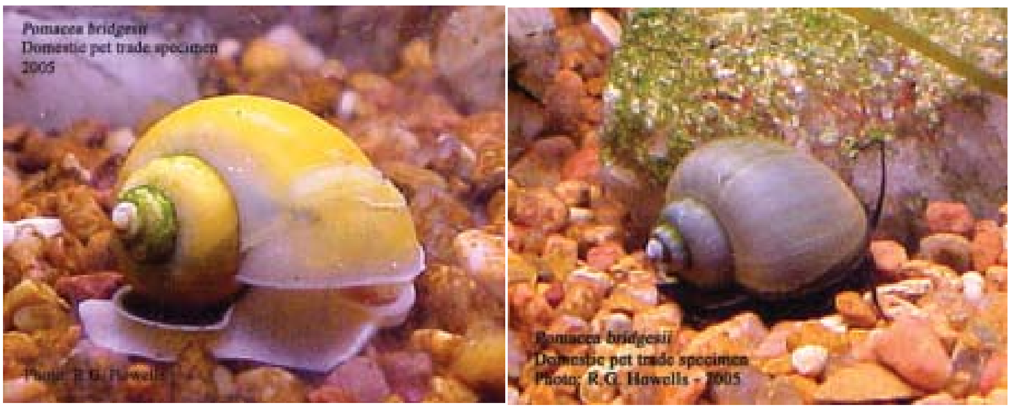


Fig. 39-40. *Pomacea bridgesii* probably occurs in more domestic color variants than any other *Pomacea.* Shell and body coloration can be different. Above left is a specimen with a gold-colored shell and albino body. Above right is an individual that has a translucent white shell and black body producing a blue-gray appearance.

A population of unidentified *Pomacea* once present at the Dallas Arboretum and Botanical Gardens, Dallas County, has not been observed there for at least 2 years and is apparently not longer extant (J.L. Turner, Dallas Arboretum and Botanical Gardens, personal communication, June 2005).

P. flagellata (Mexican Applesnail)

Texas. This Central American species has never been taken alive in Texas waters, but was listed by Andrews (1971) among Texas gastropods because its shells are "often washed up" on Texas beaches. Such shells apparently arise from specimens flushed from Mexican or other Central American rivers during storms.

M. cornuarietis (Giant Rams-Horn) (Fig. 41)

California. California Department of Fish and Game (2003) included this species on a list of macroinvertebrates documented in the state, but did not present details related to this record.

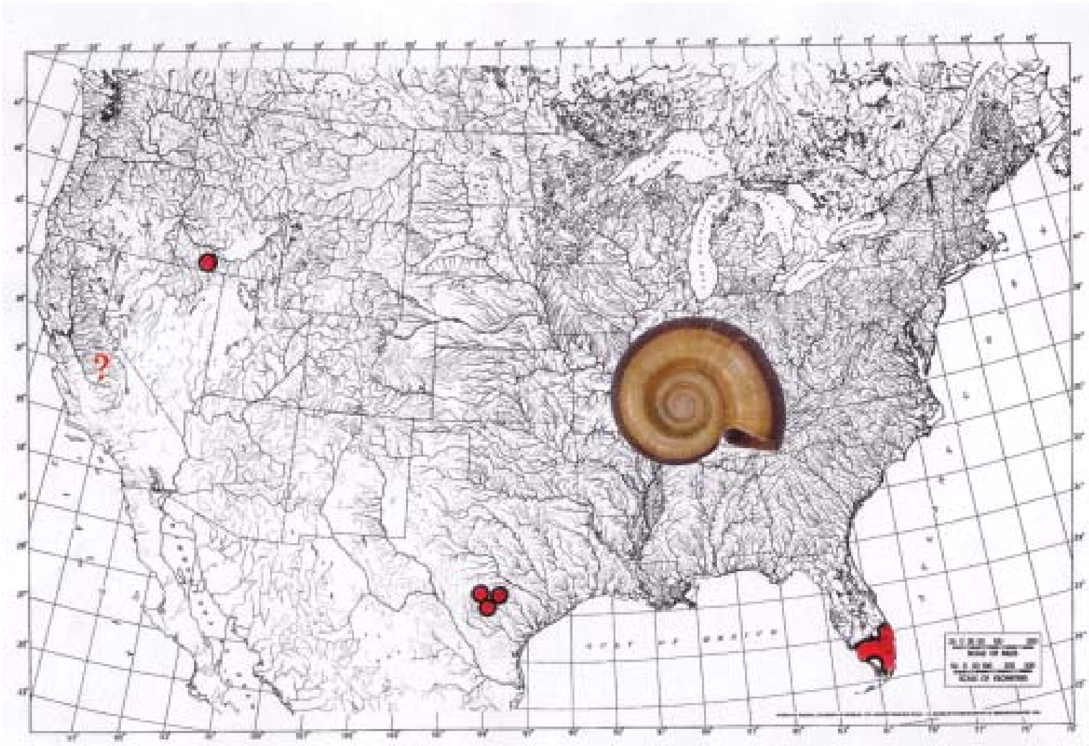


Fig. 41. Distribution records of *Marisa cornuarietis* in North America. Central Texas populations appear to be in a period of decline. Status of the introduction in Idaho has not been reported since 2000 and no details are available regarding this species in California.

Idaho. This species was first reported in the outfall of geothermally heated spring waters from a tropical fish hatchery on Deep Creek in the central Snake River drainage, Twin Falls County in 1992 (Bowler and Frest 1992, Frest and Bowler 1992). It was included on a state list of gastropods in 2000 as well (Frest and Johannes 2000), but there appear not to have been any subsequent reports of its status.

Florida. Just when this snail was relocated from its native waters in South America and southern Central America to Florida is uncertain. However, it was locally abundant when first discovered in 1957 near Coral Gables (Hunt 1958; Robins 1971). Introduction was almost certainly through the aquarium trade through release of unwanted specimens from private aquaria or escape from tropical fish farms in the area. It has been collected in Broward (1966), Dade (1966), Monroe, and Palm Beach (1989) counties in southern Florida (Thompson 1984) and more recently in Lee County (1971) (McCann et al. 1996). It is apparently still present in these counties.

Texas (Fig. 42-44). *Marisa* was first found in Texas in the headwaters of the San Marcos River, San Marcos (city), Hays County in 1981 (Neck 1984; Horne et al. 1992; Howells 2001c). It appeared in the headwaters of the Comal River, Comal County in 1984 (Horne et al. 1992) and in the headwaters of the San Antonio River, San Antonio, Bexar County in 2000 (Howells 2001c). All three sites are located in central Texas along the Balcones Fault. This species has limited tolerance to cold, so it has remained restricted to the cool but thermally stable

Fig. 42-44. *Marisa cornuarietis* occurs in a variety of banding patterns, or may be completely dark brown to black or light horn-colored. Additionally, domestic gold and albino color variants also occur.

headwaters, invading minimal distances downstream only in summer. Population levels in the Comal and San Marcos rivers have proved to be highly cyclic and appear to have been low for several years. Bio-West, Inc. (2004) reported that no living specimens were found in the San Marcos River in 2002 and 2003. Those in the upper San Antonio River have not been reported to have reached the density that occurred previously at the other two central Texas sites.

Impacts of North American introductions

Ecological and Agricultural Issues

P. canaliculata Group. Almost surprisingly, snails in this group established in mainland US waters are not known to have been associated with major negative ecological or agricultural damage. Although some populations examined genetically to date are not true *P. canaliculata* (known to cause extensive crop damage in some areas), populations in Texas (and apparently elsewhere in the continental US) are heavy macrophyte feeders and often grow significantly larger than *P. canaliculata.* Both ecological and agricultural damage might be expected from established populations of these snails. Lack of documentation of such impacts probably reflects several factors.

Except in southeastern Texas, populations in the continental US have not been established in agricultural areas, where they could easily have negative effects. Some such populations are in arid regions or urban settings, and others lack access to agricultural crops that they could harm. Further, when *P. canaliculata* and other members of the *P. canaliculata* complex were taken to Southeast Asia and the Indo-Pacific, founding populations that were released or escaped captivity following failed commercial production as escargot were probably quite large. In Texas (and probably elsewhere in North America as well), founding populations were likely quite small. Even when snails could access rice or other fields, the numbers at initial invasion may have been too limited to produce extensive damage. If populations build over time, threats to agriculture could increase.

Even in Texas, where members of the *P. canaliculata* complex have entered rice fields, no appreciable crop damage has been reported to date (June 2005). In some cases, a limited number of adults have entered crop lands and reproduced, but either pesticide applied to control insect pests killed these snails or water was drained away before young-of-the-year snails could grow large enough to damage developing rice plants. Furthermore, many Texas rice farmers do not flood fields at times that would facilitate the most damage from *Pomacea* so the snails have difficulty accessing rice plants when the seedlings are most vulnerable. Some growers in Texas do not flood their rice fields until the plants are 4-5 weeks old. Also, many Texas rice farmers alternate crops each year. Plowing and replanting a rice field with a terrestrial crop the year following rice production probably dramatically reduces the number of snails available to invade the next rice crop. Strange (1998) also indicated that nearly all Florida rice fields were also alternated with *Saccharum* spp. (sugar cane) or vegetables every other year as well. Some rice irrigation canals in Texas are also drained in winter to facilitate cold and desiccation kills, also reducing snail numbers.

When *P. canaliculata* complex snails reach high densities in natural aquatic ecosystems, the most direct negative impact is expected on macrophytes. Significant shifts in macrophyte community structure may follow selective consumption of favorable species. Decreased macrophyte diversity and production can initiate a chain of events throughout the entire ecosystem, including increased phytoplankton production, reduction in water clarity, and a general reduction in system diversity, with resulting impacts on fish and invertebrates.

Although there is some limited production of *Colocasia esculenta* as taro for human consumption and as elephantears for ornamental plantings, no significant damage from Ampullariidae has been reported thus far in North America. Often *Pomacea* are not present in growing areas or cannot readily reach farmed plants. In Texas, and probably many other locations, feral *C. esculenta* is considered a major invasive, exotic macrophyte that has been implicated in displacing native species. Little or no snail damage to these plants has been observed in southeastern Texas. However, some view *Pomacea* predation on feral *C. esculenta* somewhat favorably because of the ecological threat posed by the plant itself. Heavy consumption of exotic *Eichhornia crassipes* and *Alternanthera philoxeroides* by *P. canaliculata* complex snails has occurred at some sites in Texas and has also been viewed positively in some situations. Similarly, illegal production of *Ipomoea aquatica* (water spinach, ong choy, rau moung, kangkong) in southeastern Texas has included plants escaping greenhouses or being dumped in area fields. However, no feral *I. aquatica* plants have been documented in area canals and bayous. Interestingly, waters adjacent to production facilities have been invaded by the *P. canaliculata* group, and it is possible that one undesirable exotic species is preventing another from becoming established. More research into the interactions of these exotic snails with exotic plant species is needed to determine the community impact.

Cazzaniga (1990) documented predation by *P. canaliculata* on eggs, young, and adults of planorbid snails, but the predation rate was low (0.07 snails/day). Laboratory observations of the “channeled” *Pomacea* from Texas waters indicate that other snails are attacked and consumed only when macrophytes are absent and ampullariids are particularly hungry. Although introduced *Pomacea* populations might be expected to have negative impacts on native gastropods, under field conditions with abundant forage plants, direct predation on other snails may be relatively insignificant. Competitive interactions may be far more significant.

In the Philippines and adjacent areas, broken *Pomacea* shells have created injury risks to rice field workers (R.C. Joshi, Philippine Rice Research Institute, personal communication, March 2005). However, no such problems have been reported to date in US rice fields. Additionally, pesticides applied to control these snails outside North America have posed problems for agricultural workers and represent yet another source of chemicals in the environment (Su Sin 2003). The only pesticide used in US rice fields reported to date relative to *Pomacea* has been Lambda cyhalothrin (trade name Karate) to kill *Oebalus pugnax* (rice stink bug). Vast numbers of dead *Pomacea* were reported in some Texas rice fields following use of this chemical.

P. paludosa. Although present in Gantt Lake in Alabama for over 40 years, no significant impacts appear to have been reported. Other than possible minor introductions short distances outside its natural range in Florida and Georgia, this species has failed to become established at other sites in the continental US, and no impacts of failed introductions have been documented.

P. bridgesii. In Florida, Hale (1964) indicated that the endangered snail kite or Everglades kite (*Rostrhamus sociabilis*), which feeds almost exclusively on native *P. paludosa*, was unable to readily extract meat from shells of invading exotic *Pomacea* because of differences in shell curvature. Although this statement has been repeated by numerous subsequent authors, it is apparently incorrect. More recent observations find snail kites readily taking and consuming exotic *Pomacea* (Takekawa and Beissinger 1983; Jon Dodrill, Florida Fish and Wildlife Commission, personal communication, May 2005). This same bird also preys on other *Pomacea* species and on *Marisa* in South America (Snyder and Kale 1983), although the researchers did note kites having difficulty extracting meat from some snails due to their thick opercula. Nonetheless, there is a possibility that *P. bridgesii* and other exotic *Pomacea* may be displacing *P. paludosa* in Florida waters (Warren 1997). In Alabama, the *P. bridgesii* population apparently has a restricted distribution in a city park pond, contains a limited number of individuals, and has been present only for a short time, with no significant impact reported.

P. "haustrum." The population in Florida has been poorly studied. There is a preliminary indication that this species may be hybridizing with other *Pomacea* in Florida (T.M. Collins, Florida International University, personal communication, February 2005), but positive confirmation of introgression or a subsequent impact remains to be demonstrated.

M. cornuarietis. Although potential negative impacts on aquatic macrophytes were recognized not long after this species invaded Florida waters, subsequent reports of ecological impacts are largely lacking. In Texas, populations established in the headwaters of the Comal and San Marcos rivers began to attack native and exotic aquatic macrophytes and produced noticeable reduction in some beds (Horne et al. 1992). These Texas spring systems are important refuge sites for a number of endemic threatened and endangered species, so habitat destruction by this snail generated concern among resource managers. However, over time, it was found that *Marisa* experienced wide fluctuations in abundance. For several years, population levels have been very low at both sites, and major habitat damage is not occurring at present. The headwaters of the San Antonio River are channelized and heavily modified in urban areas of the city and in the San Antonio Zoological Gardens, where *Marisa* poses little threat to natural or agricultural areas. In Idaho, no reports of ecological damage were located during preparation of this chapter; however, possible interactions with native spring snails may deserve consideration.

Although *M. cornuarietis* will prey on other gastropods (Pointier and Jourdane 2000), laboratory observations of *M. cornuarietis* collected in Texas waters indicate that they attack and consume other snails only when macrophytes are absent and the ampullariids are especially hungry (R.G. Howells, unpublished observations). Under field conditions with abundant forage plants, direct predation on other snails may be relatively insignificant. Competition with native gastropods seems more likely to present negative impacts.

Pet and aquarium trade issues

Some species of Ampullariidae are legally prohibited by the USDA, TPWD, the California Department of Food and Agriculture, and probably other state agriculture or fish and game agencies. Despite these restrictions, including potential legal fines and even imprisonment, some *P. canaliculata* complex species continue to appear in the aquarium trade in Texas and elsewhere. Trade in larger adults appears to have been reduced, but dealers often cannot or will not distinguish between the small juveniles of relatively harmless *P. bridgesii* and harmful *P. canaliculata* complex species, especially with gold and other domestic color morphs. Use of different common and scientific names has also undoubtedly contributed to identification problems in the pet trade. Note, too, that while *P. bridgesii* can be useful in controlling algae in aquarium culture, snails that damage expensive aquarium plants appear to have an increased likelihood of being illegally released. Perhaps the most fair and functional approach to this problem would be to widely prohibit sale of all Ampullariidae except *P. bridgesii* larger than 20 mm. This would allow aquarists continued access to an algae-eating snail while precluding harmful and potentially harmful species, as well as small juveniles that could be more difficult to identify.

Medical concerns

Although *P. canaliculata* and other Ampullariidae can carry *Angiostrongylus cantonensis* (rat lungworm) (Halwart 1994), none of the *P. canaliculata* complex populations in the US have been reported as carriers thus far. However, two points need to be recognized. First, rats in New Orleans, Louisiana are known to host this parasite (Kliks and Palumbo 1992) and at least one case of human infection has occurred there (Campbell and Little 1988). Actively utilized highway and rail transport exists between areas with infected rats in Louisiana and *P. canaliculata* complex populations in Texas (and other states). Thus relocation of parasite-carrying rats is a real possibility. Second, although most biologists working with *Pomacea* in the US believe that local snail populations do not host the parasite, very few individual specimens or populations have actually been examined for the infection. Ampullariidae can also host a varied array of other parasites as well, but again, few US populations have ever been examined regarding associated parasites. Therefore, there is a necessity for a parasitological study of introduced *Pomacea* in the US *Marisa cornuarietis* apparently does not host *A. cantonensis* (Ferguson and Palmer 1958).

Examples of recent and ongoing research

Because Texas populations of *Pomacea* with channeled shells are closely associated with significant agricultural areas and important wetland habitats, an array of research and survey projects have been directed at these snails since mid-2000. The discovery in 2004 and 2005 that genetically tested individuals in Texas and Florida are likely not *P. canaliculata* further added to the significance of these studies with non-*canaliculata* snails.

Personnel from TPWD's Heart of the Hills Fisheries Science Center initiated field surveys in southeastern Texas in 2000 (Howells 2001b) (Fig. 45). More recently, staff and students from Stephen F. Austin State University (A.Y. Karatayev and L.E. Burlakova and graduate students

Fig. 45. Robert Howells examining one of the large *Pomacea* with channeled shells introduced into Texas waters. Texas Parks and Wildlife Department's Heart of the Hills Fisheries Science Center has been a major source of information and research on exotic fishes, shellfishes, and aquatic plants in the region for many years.

L. Cartwright, and D. Hollas, Nacogdoches, Texas), Southwestern University (R.L. Burks, Georgetown, Texas), and the University of Texas at Arlington (R.F. McMahon, Arlington, Texas) have launched a variety of inquiries regarding local *Pomacea* introductions. These academic efforts have received financial support from their institutions, USDA, the US Fish and Wildlife Service, and the Texas Commission for Environmental Quality Galveston Bay Estuary Program. Tissue samples from Texas snails have been submitted for genetic studies being conducted at the University of Hawaii, Florida International University, and the Philippine Rice Research Institute.

Genetic analysis at Florida International University (T.M. Collins and T.A. Rawlings, Miami, Florida) being used to examine both native and exotic *Pomacea*, as is additional genetic work at the University of Hawaii (R.H. Cowie and K.A. Hayes, Honolulu, Hawaii). Researchers at the University of West Florida (N.M. Corrao, P.C. Darby, and C.M. Pomory, Pensacola, Florida) have been examining declining populations of *P. paludosa,* and staff at the Florida Cooperative Agricultural Pest Survey (Gainesville, Florida) have focused attention on *P. canaliculata* complex populations in the state. Other research in Florida within the academic community and at state and federal agencies is being directed at native *P. paludosa.* Staff at Everglades National Park have also directed recent attention to exotic Ampullariidae in park waters. With the discovery of channeled *Pomacea* in Georgia, state personnel have initiated field monitoring and search-and-destroy efforts, with plans to investigate trapping, removal, and control methods (B. Albanese, personal communication, July 2005.).

Among the other states where Ampullariidae exist or have been reported, no significant current research appears to be ongoing in Alabama, California, or North Carolina.

Snail Densities

Burlakova, Karatayev, Hollas, and Cartwright (unpublished data, 2004-2005) found a maximum density of 36/m^2 and maximum live biomass of 2,890 g/m^2 of *P. canaliculata* complex snails in ponds in southeastern Texas. Snails in these ponds were limited to a narrow zone along the shoreline that was heavily covered with macrophytes (primarily *A. philoxeroides*). Central areas of these ponds were generally free of *Pomacea.* Mean densities within occupied areas of these ponds were 0.2-6.8/m^2 (Hollas et al. 2005). *Pomacea* densities were lower in lotic waters (streams and ditches) in southeastern Texas, varying from <0.01/m^2 to 2.4/m^2.

Feeding Habit Studies

In Texas, *Pomacea* sp. with channeled shells (listed at the time as *P. canaliculata*, but now known to be another channeled species) were reported by Howells (2002) to consume *Oryza sativa*, *Hydrilla verticillata*, *Cabomba caroliniana, Ceratophyllum demersum*, *Hygrophila polysperma*, *Limnophila sessiflora*, *Potamogeton illinoensis*, *Pistia stratiotes*, *Ceratopteris thalictroides*, *Typha minima*, *Sagittaria* sp., *Marsilea macropoda*, *Nymphaea mexicana*, *N. odorata*, *Iris pseudacorus*, *E. crassipes*, and *C. esculenta*, but were observed to reject aufwucks-periphyton. In companion trials with *P. bridgesii*, Howells (2002) found that *P. bridgesii* rejected these same macrophytes, but readily grazed aufwucks and periphyton from stones with such growths. Burlakova, Karatayev, Cartwright, and Hollas (unpublished data, 2004-2005) reported ongoing feeding trials indicating consumption of *Lacuta sativa* (used as a control), *E. crassipes*, *C. esculenta*, *Potamogeton* sp., *A. philoxeroides*, *Hymenocallis caroliniana, Sagittaria lancifolia, S. graminae*, *Panicum hemitomon*, *Scirpus californicus*, *S. maritimus*, *Canna glauca*, and *Ceratophyllum demersum* (Figs. 46-47), with snails feeding readily on most of these plants. Similarly, additional ongoing feeding trials reported by Burks (unpublished data, April 2005) found that juveniles preferred *Brassica*

Fig. 46-47. Dr. Lyubov Burlakova and students, Leah Cartwright and David Hollas, (left) and Dr. Alex Karatayev (right) at snail study facilities at Stephen F. Austin State University, Nacogdoches, Texas.

oleracea (cabbage) over *L. sativa* (lettuce), but consumed both, and adults also consumed *L. sativa* in addition to *Myriophyllum spicatum* (Fig. 48). Hatchlings of *P. canaliculata* complex specimens from Texas have been observed feeding on periphyton growing on the shells of large adults when housed in the same laboratory aquaria (R.L. Burks, unpublished observation). These feeding data from the channeled-type *Pomacea* present in Texas are particularly valuable when compared with feeding documented in known *P. canaliculata*, clearly a different species, elsewhere.

By comparison, *P. canaliculata* (presumably correctly identified) has been reported to consume *Azolla* spp. (Mochida 1991), *Chara* sp. (Mochida 1991), *Colocasia esculenta* (Mochida 1991), *C. monophyllus* (Mochida 1991), *E. crassipes* (Laup 1991), *I. aquatica* (Laup 1991, Cowie 1995), *Juncus decipiens* (Mochida 1991), *Lemna* sp. (Halwart 1994), *Nelumbo nucifera* (Laup 1991, Mochida 1991), *Oenanthe jacanica* (Mochida 1991), *Oryza sativa* (Laup 1991 and many others), *Scirpus californicus* (Cazzaniga and Estebenet 1992), *Trapa bicornis* (Adalla and Morallo-Rejesus 1989), *Vallisneria* sp. (Puchon 1977), *Vigna marina* (Lach et al. 2000), *Zannichellia palustris* (Estebenet 1995), *Myriophyllum elatinoides* (Estebenet 1995), *Rorippa nasturtium-aquaticum* (Estebenet 1995), *Potamogeton striatus* (Estebenet 1995), *I. aquatic* (Mochida 1991), *Vigna marina* (Lach et al. 2000), and *Zizania latifolia* (Mochida 1991), as well as up to 60 other species (Adalla and Morallo-Rejesus 1989, Baldia and Pantastico 1989). Interestingly, Estebenet (1995) reported selection against *Elodea canadensis*.

Size frequencies

As information about introduced *Pomacea canaliculata* complex snails in Texas was developed, it was suggested that these snails, and apparently others elsewhere in North America, may have larger average sizes than populations in Hawaii, the Philippines, and other Southeast Asian and Indo-Pacific sites. Sizes below for continental US populations follow Estebenet (1998), being measured in millimeters from the shell apex to the basal extreme of the aperture. Snails identified as *P. canaliculata* in Argentina, Hawaii, the Philippines, and Japan are presumed to have been correctly identified.

Among randomly selected *P. canaliculata* complex specimens collected in 2000 in southeastern Texas (R.G. Howells, unpublished data), mean shell size was 52.6 ± 6.2 mm SD (range 10-96 mm, N = 98), and specimens from the population in northern Texas near Fort Worth obtained in 2002 averaged 71.2 ± 6.2 mm SD (range 60-80 mm, N = 18). Burlakova and

Fig. 48. (left) Laboratory feeding trials at Southwestern University, Georgetown, Texas. Student Brandon Boland monitors test animals.

Karatayev (2005) and Burlakova, Karatayev, Hollas, and Cartwright (unpublished data, 2004-2005) also presented shell measurements for both living specimens and dead shells from stream and pond conditions for *P. canaliculata* complex specimens from southeastern Texas. Mean size of living snails in ponds was 63.5 ± 14.0 mm SD (range 7-81 mm, $N = 228$), and mean size of dead snails was 68.6 ± 13.1 mm SD (range 6-94 mm, $N = 234$). Both live and dead specimens from lotic habitats were significantly smaller (one-way ANOVA, $P < 0.001$), with mean size of living snails being 48.1 ± 13.3 mm SD (range 18-72 mm, $N = 68$) and of dead snails being 45.9 ± 11.8 mm SD (range 24-74 mm, $N = 54$).

Field samples of live snails and shells are inherently biased toward larger juveniles and adults, with small individuals being underrepresented in collections due to obscurity by muddy water and dense vegetation. In addition to size distribution data from Texas populations, Burks (unpublished data) and her students at Southwestern University are conducting laboratory growth studies on channeled *Pomacea* from southeastern Texas (Fig. 49).

In Argentina, Estebenet (1998) reported that size distribution among 363 *P. canaliculata* averaged 35.2 ± 15.6 mm SD (range 8.8-80.0 mm). Lach et al. (2000) presented size ranges for *P. canaliculata* collected in the field in Hawaii and found that few specimens at two collection sites exceeded 35 mm and very few were greater than 41 mm.

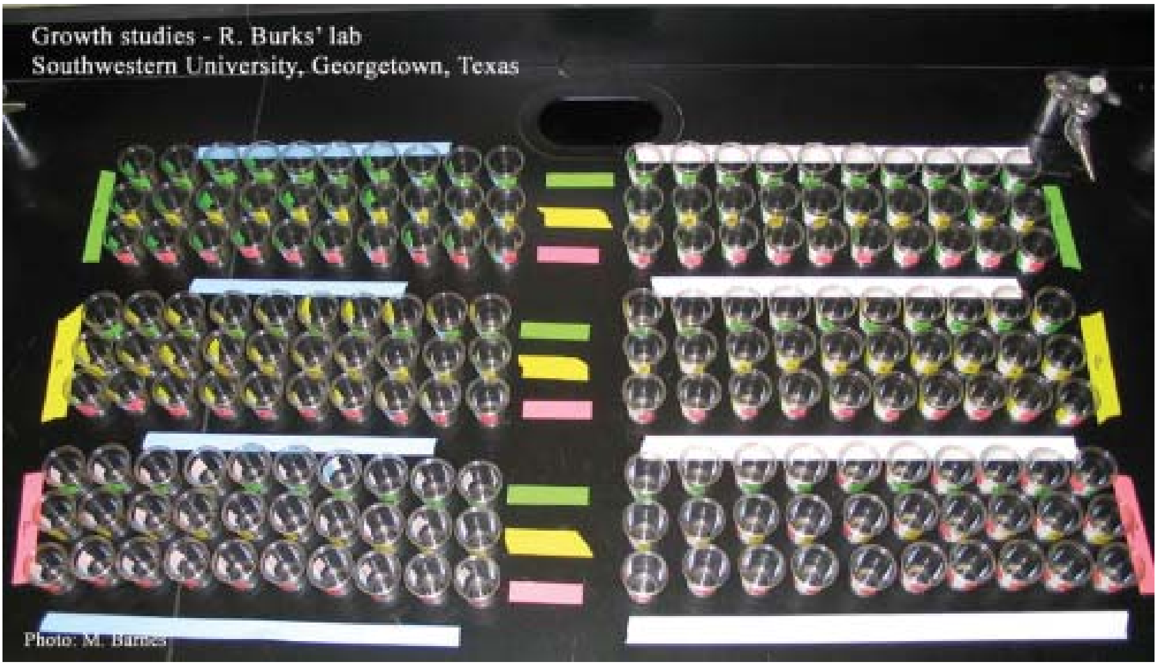


Fig. 49. (right) Laboratory growth rate studies at Southwestern University, Georgetown, Texas, monitoring development under different conditions.

Temperature Tolerance

Inability to tolerate extremely low temperatures has been reported for *Marisa cornuarietis* (Robins 1971, Thomas 1975), *Pomacea paludosa* (Freiburg and Hazelwood 1977), and *P. bridgesii* (Strange 1998), with an indication of limited ability to endure extremely cold temperatures for long periods. Intolerance of cold temperatures is likely a major factor in restricting introductions of these species in North America to thermally stable headwater springs, heated power plant reservoirs, or southern latitudes. No ongoing temperature tolerance work on these three species was discovered during preparation of this paper.

Members of the *P. canaliculata* complex, however, often have far greater tolerance for low temperatures. Oya et al. (1987) and Mochida (1991) reported that *P. canaliculata* could survive for 15-20 days at 0°C for 2 days at –3°C, and for 6 hours at –6°C. Furthermore, Oya et al. (1987) and Syobu et al. (2001) found that younger and smaller snails tolerated cold better than larger snails. Santos et al. (1987) reported *P. lineata* surviving for 1 hour at 5°C. Oya and Miyahara (1987) found that in December (winter in Japan), in fields that had been dewatered for more than 3 months, over 80% of buried *P. canaliculata* had survived, but also noted that survival was only 40% for those snails that had hidden under grass and had not burrowed.

In late December 2004, *P. canaliculata* complex populations in southeastern Texas experienced not only atypically cold temperatures, but several centimeters of snow as well. Air temperatures reached 5°C one night, -1°C one night, and were below 5°C for 7 days, with associated water temperatures as low as 6.2°C on 26 December 2004, measured in a pond at 0.5 m depth (Howells 2005; Burlakova, Karatayev, Hollas, and Cartwright, unpublished data). When a dewatered rice field was examined in April 2005, Burlakova, Karatayev, Hollas, and Cartwright (unpublished data) found piles of *Pomacea* shells 18-63 cm in height in drift areas, but also found that other snails had burrowed into the substrate to depths of 13-15 cm. Among 73 randomly collected snails found in these piles, 59 (81%) were closed, with the operculum in place, and 8 (14%) of those were still alive (Fig. 50). The density of snails in a plowed field was found to be $1.07 \pm 0.37/m^2$ SD (range $0.65\text{-}1.35/m^2$). No excavations were conducted to document the number of buried specimens or survivors among them. Snails were first found in this field in 2004 (C. Mowery, Mowery Farms, personal communication, 2005). Similarly, R.L. Burks (unpublished data) also found large numbers of shells, but few living individuals, in natural areas of nearby Armand Bayou, Galveston County, Texas in April 2005. Neck and Schultz (1992) reported another population in this same area that survived extremely cold weather during the winter of 1989-1990, but they did not report temperature data.

Salinity Tolerance

Because introductions of many Ampullariidae in North America have occurred in coastal states or in inland areas with saline waters, salinity tolerance of these exotic species can be an important element relating to their spread.

M. cornuarietis is reported to tolerate saline waters to at least 8.5 parts per thousand (ppt) or about 30% that of sea water (Hunt 1961; Robins 1971; Santos et al. 1987). Jordan and Deaton (1999) recorded 80% survival of *P. bridgesii* at 7 ppt salinity, but found 100% mortality at 14% ppt.

Fig. 50. *Pomacea canaliculata*-complex specimens found in a rice field in Harris County, Texas, in April 2005. Snails dug into the substrate in fall 2004 following rice harvest and after experiencing freezing temperatures in December 2004, at least 14% had survived.

Marfurt and Burks (2005) examined the survival of hatchling and adult *P. canaliculata* complex specimens from southeastern Texas in 24-hour exposure plunge tests at salinity values of 0–35 ppt. They found that both life stages survived 8 ppt for 24 hours, but none survived at 14, 20, or 35 ppt, which is consistent with reports for *P. bridgesii* (Jordan and Deaton 1999). Interestingly, they also found that adult specimens actually increased feeding at 8 ppt, while hatchling feeding did not differ between 0 and 8 ppt. Additional studies are in progress at Southwestern University and the University of Texas at Arlington.

Observations (A. Brinley and M. Kramer, Armand Bayou Nature Center, personal communication, June 2005) at Armand Bayou in southeastern Texas showed that no snails or egg masses were seen from 25 May to 16 June 2005 in areas where salinity reached 6 ppt. However, one egg mass and no snails were seen at another site where salinity ranged from 0 to 4 ppt, and 49 egg masses and > 20 snails were counted at a third location where salinity was < 1 ppt during this same time period.

Fujio et al. (1991) found different degrees of salinity tolerance among different "strains" of *P. canaliculata*, and Albrecht et al. (1996) reported that the species tolerated a broad range of salinity.

Baiting and Trapping

Efforts to control noxious ampullariid populations include an array of approaches. Baiting and trapping offer the potential of capturing unwanted snails without the extensive collateral damage to other organisms often experienced in more vigorous approaches. This can be particularly important in ecologically sensitive locations where lethal techniques are restricted. With this in mind, bait and trap studies were initiated in southeastern Texas in 2005 with its large *P. canaliculata* complex populations. Darby et al. (2001) had previously studied trapping of *P. paludosa*.

To confirm or refute anecdotal hypotheses, R.L. Burks (unpublished data., April 2005) initiated trapping tests in spring 2005 utilizing 20 traps (checked at 6 hours after initial deployment and then 10 hours after rebaiting) that had been baited with *Colocasia esculenta* (elephantear or taro), *Solanum melongena* (eggplant), *Citrullus lanatus* (watermelon), and newspaper, but captured only three snails in this preliminary study. Atypically cold, wet spring conditions may have confounded this trapping attempt, and other efforts are planned. Additional studies are also planned by Stephen F. Austin State University personnel. Additionally, Burks' laboratory recently discovered that the most effective way to collect *Pomacea* locally is to physically cut stands of *Colocasia esculenta* and search among the roots and culms, particularly those that have been submerged (Fig. 51). The presence of brightly colored and easily observed egg clutches also proved to be a good indicator of snail presence. However, egg clutches of *P. paludosa* were not necessarily a good indicator of snail abundance (Darby et al. 1997).

Reproductive Biology

Although many aspects of *P. canaliculata* reproductive biology have been reported, corresponding details relating to the *P. canaliculata* complex snails in the US (and elsewhere) are less clear. Understanding reproductive differences and similarities between species within this group could provide important clues for their control and management.

The reproductive season of *P. canaliculata* complex snails in southeastern Texas starts in March and ends in October-November, depending on seasonal temperature and precipitation

Fig. 51. R.K. Marfurt collecting *Pomacea* among *Colocasia* plants on Armand Bayou in southeastern Texas.

patterns. Egg deposition can be delayed several weeks during cold spring weather patterns (as seen in 2005; Burlakova, Karatayev, Cartwright, and Hollas, unpublished data; M. Kramer and A. Brinley, Armand Bayou Nature Center, personal communication, 2005). Conversely, exceptionally warm and sunny days in late winter and early spring may promote atypically early egg laying. In Texas, egg masses were found on a variety of objects including macrophytes, sticks, wooden pilings, stumps, occasionally even on the ground, and often on concrete structures like bridge walls and pillars.

Burlakova and Karatayev (unpublished data, 2004) found that egg mass densities ranged between 0.05 and 1.4/m^2 on hard structures selected by *P. canaliculata* complex snails in southeastern Texas (Fig. 52). Cartwright et al. (2005) found egg diameters in egg masses deposited by *P. canaliculata* complex snails in southeastern Texas to average 2.43 ± 0.13 mm SD (range 2.16-2.70 mm) (Fig. 53). Estebenet and Cazzaniga (1992) reported egg diameters for *P. canaliculata* in Argentina to range from 2.24 to 3.47 mm. Staff at Burks' laboratory also collected, weighed, and counted 48 egg clutches of *P. canaliculata* complex snails from southeastern Texas. Egg numbers ranged from 213 to 4607 (mean 1362±940, 1 SD), with weights from 2.28 to 20.46 g (mean 9.34±4.4 g SD). Shapes of these clutches varied depending upon the substrate, with more elongated clutches on *C. esculenta.* A current hatching study of 48 other egg clutches (averaging 1,000-1,500 eggs/clutch) suggests high hatching efficiency for this *P. canaliculata* complex species under laboratory conditions (Figs. 54-57).

Fig. 52-53. Egg masses from *Pomacea canaliculata*-complex snails in southeastern Texas.

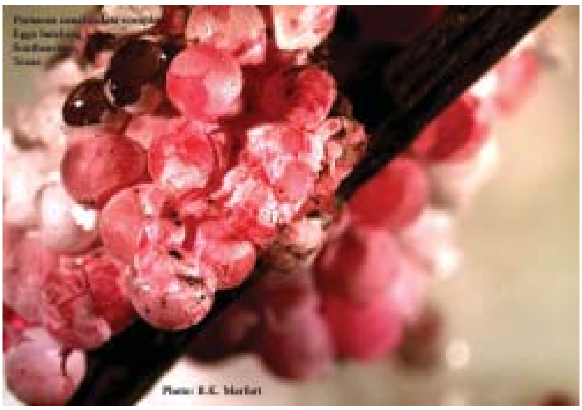


Fig. 54-55. Eggs of *Pomacea canaliculata*-complex from southeastern Texas hatching in the laboratory at Southwestern University, Georgetown, Texas.

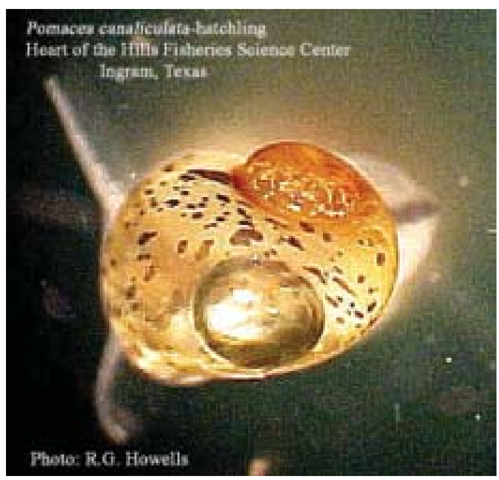


Fig. 56. (left) *Pomacea canaliculata*-hatchings from southeastern Texas at 1-day old in the laboratory at Southwestern University, Georgetown, Texas.

Fig. 57. (right). *Pomacea canaliculata*-hatchling at Heart of the Hills Fisheries Science Center, Ingram, Texas, with a shell length of about 1 mm.

Shifting Distribution

In Florida, new distribution maps for *P. canaliculata* complex indicate an apparent expansion of range in three major areas of the state, though most significantly in the central and southern regions (see USGS and Florida Cooperative Pest Survey Program maps on their respective internet sites). There seems to be less evidence that other ampullariids are expanding their ranges into new waters in Florida. Similarly, there has been little or no indication of ampullariid populations invading new waters in Alabama, California, or Idaho.

In Texas, lack of cold tolerance has, to large extent, prevented *Marisa* from expanding its range from protective headwater springs. Cold has likely been a major deterrent to *P. bridgesii* becoming established as well. The *P. canaliculata* complex snails that became established in southeastern Texas largely in the coastal plain region south of the city of Houston appear to be moving clockwise and counter clockwise around the east and west city borders into new waters to the north. Ongoing distributional studies have recently found these snails in Sims Bayou and Clear Creek in Brazoria and Harris counties and in other waters in southeastern Texas where they had not been previously reported (Burlakova, Karatayev, Hollas, and Cartwright, unpublished data, 2005).

To date, none of the *P. canaliculata* complex snails have become established in areas that support major sport fisheries and so have not yet impacted anglers. As these channeled snails move to waters north of Houston, they may reach several reservoirs important to anglers, where they could negatively impact important and valuable fisheries for species like *Micropterus salmoides* (largemouth bass). This fish is the most important freshwater gamefish in Texas and in much of the US, and millions of dollars and person-hours are directed at this fishery annually (Howells 2003). Furthermore, this fish is closely associated with macrophyte beds. If invading *P. canaliculata* complex snails reach important largemouth bass fishery waters, revenue losses could be significant.

Predators on Ampullariids

Although a number of predators have been linked to introduced ampullariids, a general lack of particularly effective predators is often a major reason for the success of members of this family when introduced outside their native ranges. Generally, at least some predatory species have been found to attack various ampullariids in introduced waters, but none appear to eliminate significant numbers of invading snails.

Yusa (2001) reported that *Solenopsis geminata* (an introduced exotic fire ant in Asia) attacked egg masses of *P. canaliculata* in the Philippines and Thailand. Although use of an exotic fire ant suggested to some a tantalizing possibility for snail control, ants appear not to have been particularly functional in this regard elsewhere. Indeed, *S. geminata* is native to Texas, and even within its native range, it has failed to show an ability to suppress invasive members of the *P. canaliculata* complex that have become established. Indeed, *S. wagneri* (generally given as *S. invicta*), called imported red fire ant in the US, has been observed attacking stranded *P. paludosa* during low-water periods (Stevens et al. 1999). This exotic fire ant has become more abundant and more aggressive than *S. geminata* in Texas but has also failed to control invasive *Pomacea* in the US. Despite observations of fire ant predation on snail eggs and adults, these insects should never be seriously considered as a *Pomacea* control option and should never be introduced for this reason. In the field in southeastern Texas, egg clutches of *P. canaliculata* complex are generally observed intact, with little or no indication of predation. However, in the laboratory, crayfish (Astacidae) have been observed to readily consume snail eggs (R.L. Burks, personal observation) and more experiments to quantify this predation threat are under way.

For reasons that are difficult to understand, a commercial water garden dealer in Texas obtained *Pomacea*, presumably *P. canaliculata* complex, for release into its water lily (*Nymphaea* spp.) rearing areas in the early 1990s. Apparently, when these macrophagous snails began to damage valuable aquatic plants in production ponds, efforts to eliminate the snails were initiated. When the ponds were drained, a glossy ibis (*Plegadis falcinellus*) flock reportedly consumed many of the stranded snails. Nonetheless, these birds, too, have failed to provide significant control under more natural conditions.

Anglers in southeastern Texas have reported to TPWD personnel that captured *Ictalurus furcatus* (blue catfish) have been found to have consumed large numbers of *Pomacea canaliculata* complex snails. However, no reduction in snail populations has been noted due to predation from this or other local catfish. While particularly large blue catfish are often mainly piscivorous, they are also opportunistic feeders that will take a variety of food items when available.

Lepomis microlophus (redear sunfish) juveniles and adults have been used by Burks (2005) and Marfurt and Burks (2005) in laboratory studies of predation on *P. canaliculata* complex from southeastern Texas. They found that both adults and juveniles of this mollusk-feeding fish took *Pomacea* and native gastropods equally and eliminated nearly all smaller *Pomacea* in the trials. Additionally, they found that this fish actually destroyed snails more effectively in the presence of aquatic vegetation (*Eichhornia crassipes*; see following comments on alarm responses). But *L. microlophus* has a relatively small mouth and cannot readily consume large, adult snails.

Alarm Responses and Reactions to Predators

Most ampullariids have not been the subjects of alarm responses or reactions to predators. However, alarm responses have been reported in *P. canaliculata* in Japan by Ichinose et al. (2003), who found that hatchlings would crawl out of the water when they were exposed to macerated remains of other snails.

Work by Marfurt and Burks (2005) similarly found that juvenile *P. canaliculata* complex specimens from southeastern Texas would also crawl from the water if no aquatic vegetation was available. In particular, they crawled from the water when exposed to benthic predators (crayfish, Astacidae). They also reacted to avoid predatory fish, but did not respond to adult *Pomacea* or the absence of a cue. This current work agrees with that of Carlsson et al. (2004b), who showed similar responses in juvenile snails and found that larger *P. canaliculata* specimens either dropped to the substrate when similarly stimulated or did not respond at all.

Restrictive legal regulations

USDA has long regulated importation and transport across state lines of land snails and slugs that are potential crop pests. However, with crop-threatening Ampullariidae in Florida and Hawaii, and later in other mainland areas in the continental US, agency concerns were expanded to include freshwater gastropods as well. USDA efforts in recent years have included a risk analysis of *P. canaliculata* (Smith and Fowler 2002) and creation of an action planning group to address developing issues with problematic Ampullariidae.

In Texas, *Marisa cornuarietis* was added to the TPWD list of harmful or potentially harmful fish, shellfish, and aquatic plants in 1990. This legally prohibits possession, culture, sale, and transport of this species (Howells 1999). *P. canaliculata* was added to this list in 2001. Unfortunately, efforts to expand the wording to prohibit all Ampullariidae except *P.*

bridgesii (a noncold-tolerant and nonmacrophyte-feeding species of minimal threat, but important to the aquarium trade) have still not been enacted into law in Texas.

In 2001, the Mississippi Bureau of Plant Industry moved to prohibit importation of any applesnail or materials on which they may occur from invaded states including California, Florida, Hawaii, North Carolina, and Texas (Smith and Fowler 2002). Nevada passed legislation providing for inspectors to devote additional time toward invasive exotic species, including *P. canaliculata.* The Florida Department of Agriculture and Consumer Services has authority to prohibit any plant-feeding snail it determines to be injurious. The California Department of Fish and Game has regulations prohibiting slugs and land snails; however, it also has the authority to join with the California Department of Food and Agriculture to similarly prohibit any potential pest species like *P. canaliculata.*

Summary

Exotic species pose a serious threat to native biodiversity, second only to habitat loss (Sala et al. 2000). When an introduction or invasion occurs, it is critical to respond to this threat during early establishment, when damage may be reduced or even reversed. Due to its voracious appetite and short maturation period, *P. canaliculata* and related channeled species now constitute significant agricultural and ecological pests. The Invasive Species Specialist Group (2004) included *P. canaliculata* among the worst 100 exotic species globally. Research that contributes to understanding genetic identity, defining ecological niches, clarifying interactions with other species, and expanding knowledge of basic species biology is critical to the formulation and implementation of action plans targeted at curbing the spread of and damage from ampullariid snails.

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