

Workshop: Biology of Ampullariidae

Fossil record of *Pomacea* (Caenogastropoda: Ampullariidae) in Argentina and its paleoenvironmental implications

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In many aspects *Pomacea canaliculata* (Lamarck, 1822) is the best known native snail from Argentina, a fact that has been enhanced since its establishment as a serious rice plague in Asian rice fields (Estebenet *et al.*, 2006). Notwithstanding, from a paleontological viewpoint, the knowledge of this species is far from being sound and integrated. The aims of our paper are to review the fossil record of *Pomacea* Perry, 1810 in Argentina, to analyze the preservation of its remains and their usefulness as paleoenvironmental indicators, and to highlight their contribution to the understanding of its present distribution.

Fossil record of *Pomacea*

Berthold (1991), mainly based on present distribution and fossil evidence, suggested Gondwanic roots for

the family Ampullariidae, with an origin on the African plate and further spread towards the South American and Indian plates. The fossil record of ampullariids or apple snails is quite incomplete (Boss and Parodiz, 1977), only fragmentary information existing on the origin and evolution of this group worldwide. Occasionally, rich and well preserved deposits have permitted detailed reconstructions of evolutionary history, for example, for lacustrine African ampullariids (van Damme and Pickford, 1995). In South America, however, the evolutionary history of this group as well as its origin and radiation are unknown. According to Boss and Parodiz (1977), the American fossil apple snails belong entirely to *Pomacea*, the oldest ones belonging to the gigantic *Pomacea prourceus* Boss and Parodiz, 1977 from the late Eocene of Peru (40 Ma). However, internal casts assigned to *Pomacea* have recently been recorded from early Eocene deposits (50 Ma) from the Gran Salitral Formation in Southwestern La Pampa Province (Argentina) (Melchor *et al.*, 2002). If confirmed, these casts constitute the southernmost fossil record of the family Ampullariidae worldwide.

Other Tertiary records of *Pomacea* in Argentina are from the Miocene (14-25 Ma) of Valles Calchaquíes (Salta) (Vilela and García, 1978, *vide* Morton, 1992)

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and from the Pliocene (1.8-5.3 Ma) of Paraná (Entre Ríos) (Ihering, 1907; Boss and Parodiz, 1977). However, the presence of *Pomacea* in the Miocene of Valles Calchaquies is doubtful since this genus was not reported in later reviews published for this area (Herbst *et al.*, 2000). Freshwater molluscan fossils, including the Ampullariidae, are completely absent from the Paleocene to Miocene in the Chaco-Pampean district (Parodiz, 1982). The most abundant fossils of *Pomacea*, usually identified as *P. canaliculata* or one of its many synonyms, are those belonging to Quaternary deposits (late Pleistocene and Holocene, 1 Ma-5 ka) from the lower Río de la Plata Basin (e.g. Camacho, 1966; Frenguelli, 1945, 1957; Lissa *et al.*, 1989; Dangavs and Blasi, 1992, 2002; Martínez and Rojas, 2004; Prieto *et al.*, 2004).

Preservation of *Pomacea* remains

The fossil evidence of *Pomacea* from the late Pleistocene and Holocene usually involves unaltered shells (e.g. Dangavs and Blasi, 1992; De Francesco and Prieto, 1999; Martínez and Rojas, 2004; Prieto *et al.*, 2004). Contrarily, the fossils from older deposits consist of moulds or casts (e.g., Ihering, 1907; Parodiz, 1969; Boss and Parodiz, 1977; Melchor *et al.*, 2002). Probably because of this fact and to the lack of very distinctive features in the shell of *Pomacea*, some old American fossils have been only tentatively identified in their original descriptions (for example, Ihering, 1907). On the other hand, some paleospecies of *Pomacea* have been subsequently considered to belong to other taxa by later authors; for example, *Pomacea bibliana* Marshall and Bowles, 1932 was re-identified as a prosobranch land snail by Parodiz (1969). Given the problems faced by neontologists when trying to define morphospecies in this group (Cazzaniga, 2002), the problems encountered by paleontologists dealing with *Pomacea* or *Pomacea*-like fossils are not surprising. Similar uncertainties have arisen with old fossils of African apple snails (van Damme and Pickford, 1995).

To our best knowledge there are no records of fossil evidences of *Pomacea* other than shells or their casts. The fossil evidence of gastropod opercula belongs only to those on which calcitic or aragonitic layers are deposited during operculum growth (Checa and Jiménez-Jiménez, 1998). Among the Ampullariidae, only the Old World genera *Pila* Röding, 1798 and *Turbinicola* Annandale and Prashad, 1921 show calcified opercula (Berthold, 1991), while in the rest it is not calcified and

it is often papiraceous. Even the often heavily calcified opercula of *Pila* are extremely rare in fossil shell deposits (van Damme and Pickford, 1995), so the lack of fossil evidence of this structure in *Pomacea* deposits from Argentina is not surprising. Similarly constructed and non-calcified opercula of Vivipariidae have fossilized only under exceptional conditions (van Damme and Pickford, 1999).

On the other hand, the lack of fossil evidence on the egg masses of *Pomacea* is noteworthy since they are several centimeters in length and are composed of hundreds of calcareous-shelled eggs (Estebenet and Cazzaniga, 1993; Perera and Walls, 1996). Calcareous eggshells of land snails, even those quite smaller than those of *Pomacea*, are common fossils in certain localities, although they were frequently mistaken for fossil cladocera or tetrapod eggs (Tompa, 1984; Pierce, 1993). The cleidoic egg masses of *P. canaliculata* are deposited on emergent substrates on waterbody margins, where water level fluctuations can submerge them or leave them on dry terrain. Permanent submersion of the egg masses leads to death of the embryos and unfastening of the eggs, although individual eggshells are not affected for at least two months (Pizani *et al.*, 2005), so they are presumably liable to both terrestrial and aquatic fossilization. The detection of fossil land snail eggshells mostly depends on the gentleness of the prospecting and preparation methods used (Pierce, 1993), though there are probably other reasons for the absence of *Pomacea* eggshells in the fossil record. Contrarily to the calci-

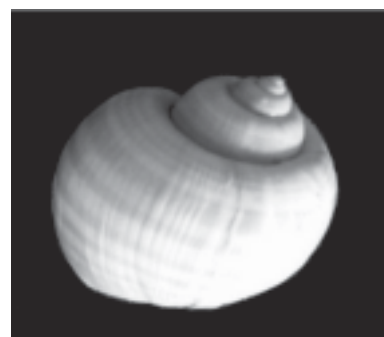


FIGURE 1: Fossil shell of *Pomacea canaliculata* from Luján River Holocene deposits (Puente de la Tropa site (34° 34' 40" S; 59° 08' 14' W), Buenos Aires Province, Argentina).

fied eggshells of land snails which are all of calcitic nature, those of *Pomacea* spp. are composed of vaterite (Watabe, 1983); since vaterite has the highest solubility among the different morphs of calcium carbonate, their different composition is probably related to a lower fossilization propensity.

Fossil shells of *P. canaliculata* from late Pleistocene and Holocene sediments are usually well preserved and little fragmented, showing evidence of the characteristic banding pattern (Fig. 1). However, they are less abundant in these deposits than other freshwater snails (*Heleobia* spp., *Chilina* spp., *Biomphalaria* spp., etc.) that today inhabit the same environments (Dangavs and Blasi, 1992; De Francesco and Prieto, 1999; Prieto *et al.*, 2004; pers. obs.). Considering the very much bigger size and thickness of *Pomacea* shells relative to that of the other genera of aquatic snails, this evidence suggests that their scarceness in the fossil record reflects a lower abundance in the past rather than a low fossilization propensity.

***Pomacea* as paleoenvironmental indicator**

To the present, fossil assemblages containing *Pomacea* have been seldom studied as paleoenvironmental indicators. *Pomacea canaliculata* has been considered a species characteristic of lentic waterbodies while the close *Pomacea insularum* (D'Orbigny, 1835) has been considered a lotic dweller (Hylton-Scott, 1958; Bachmann, 1960). This suggests a great potential for paleoenvironmental reconstruction, which has been applied somewhat loosely in a paleoecological context; for example, several authors have considered *P. canaliculata* as a species from swamps (Frenguelli, 1945; Zárate *et al.*, 1997). However, a study of its present distribution in Southern Pampas showed that though *P. canaliculata* prefers still or slow-running waters, it inhabits both lentic and lotic habitats, it being present in more than half of the plain streams in the Southern limit of its natural range, and that in fact it is more abundant in the latter (Martín *et al.*, 2001). The euryoicness of *P. canaliculata* has been acknowledged in a recent paper on the paleoecology of fossil molluscan faunas from Uruguay (Martínez and Rojas, 2004).

Although its mere presence is probably not a good indicator of habitat type, other features observed in present populations of *P. canaliculata* would help in paleoenvironmental reconstruction. For example, in both sexes the mean shell length of lentic populations is higher than that of lotic ones from Southern Pampas (Estebenet

et al., 2006); in addition, the mean shell shape of both sexes is also different between these waterbody types.

Recently, actualistic taphonomic studies have been initiated on *P. canaliculata* shells accumulated as consequence of the predatory activity of the snail kite *Rostrhamus sociabilis* (Vieillot, 1817), an odd raptor that preys almost exclusively on *Pomacea* snails (Beissinger *et al.*, 1994; Sykes, 1987). The aim of these studies is to differentiate predated shells from naturally accumulated deposits in the fossil record. Several modern deposits have been analyzed in shallow lakes from central Buenos Aires Province, recording those taphonomic attributes that can be studied in fossil deposits as well, such as the degree of breakage, size-frequency distribution and spatial orientation (De Francesco *et al.*, 2006). That study showed that nearly 63% of shells displayed a notch in the aperture, which is probably related to the action of the bird when extracting the flesh with the beak. Additionally, sizes preyed by snail kites ranged from 23 to 66 mm, probably because adult specimens are easier for them to see or are more profitable from an energetic viewpoint (Beissinger *et al.*, 1994; Sykes, 1987). These two characteristics appear as useful tools to infer the presence of snail kites in the past. Limpkins, *Aramus guarauna* (Linnaeus, 1766), are other birds that prey upon *Pomacea* spp. They select their prey on the basis of size and produce distinctive holes in the body whorl of the shell (Reed and Janzen, 1999) and therefore their attacks could also be detected in the fossil record. The application of actualistic criteria in Holocene *Pomacea* shells from Northeastern Buenos Aires province (Luján River), suggests the absence of predatory activity by snail kites and limpkins in the area (unpub. data), and therefore a recent southward expansion of these malacophagous birds, which now reach the Northern outcrops of Tandilia and Ventania Mountains during warm months. Fossil shell damage and repair scars have been used to reconstruct predation pressures driving conchological evolution in African lacustrine ampullariids (van Damme and Pickford, 1995).

The corroded apex and the growth marks present in the shells of *Lanistes heynderycxi* van Damme and Pickford, 1995 from the Miocene of Uganda have been considered as an indication of low calcium carbonate contents and seasonal drying of the paleoenvironment that it inhabited (van Damme and Pickford, 1995). These traits are very common in present populations of *P. canaliculata* (pers. obs.), although their value as paleoenvironmental indicators is not clear. For example, apex corrosion in a species of *Pomacea*, probably *P.*

lineata (Spix in Wagner, 1827), has been attributed to the activity of algae (Geus, 1968) and shell marks resulting from arrested growth can appear either during estivation or hibernation in the case of *P. canaliculata* (Estebenet and Martín, 2002).

Past and present distribution of *Pomacea*

Compared to more tropical ampullariids, *P. canaliculata* shows lower tolerance to high temperatures and higher tolerance to low and even freezing temperatures (Cowie, 2002). Although its distribution is basically tropical and subtropical, *P. canaliculata* is the ampullariid naturally ranging to southernmost latitudes and some populations have been detected in the Southern slope of Ventania and Tandilia Mountains in Buenos Aires Province (e.g. Cazzaniga, 1987a; Estebenet and Cazzaniga, 1998; Fig. 2). Berthold (1991) suggested that climate, specially the combination of the 10°C isotherm and the 600 mm isohyetal line, sets the limits of the distribution of ampullariids worldwide. However, the combination of paleontological and distributional data

suggest an alternative hypothesis on the factors actually limiting the southward distribution of *P. canaliculata* in this region.

Populations of *P. canaliculata* are common and widespread on the Northern slope of Ventania and Tandilia Mountains, being rare and quite isolated in the Southern one (Martín *et al.*, 2001; Fig. 2). Even discarding those deposited under estuarine conditions (e.g. Farinati and Zavala, 1995; De Francesco and Zárata, 1999; Espinosa *et al.*, 2003), late Pleistocene-Holocene deposits containing fossil freshwater snails are quite common on both slopes (e.g., Frenguelli, 1928; Kerlleñevich; 1989; Bonadonna *et al.*, 1995; Figini *et al.*, 1995). Nevertheless, *P. canaliculata* fossils are restricted almost entirely to the Salado and Río de la Plata Basins on the northern slope (Frenguelli, 1945, 1957; Camacho, 1966; Dangavs, 1988; Dangavs and Blasi, 1992, 2002; De Francesco and Prieto, 1999; Prieto *et al.*, 2004); the only record on the southern slope is that of Frenguelli (1921), who identified late Pleistocene shell fragments from Miramar town as belonging to *P. canaliculata*, although it was not recorded among later fossil snails there. Although date estimations vary, most

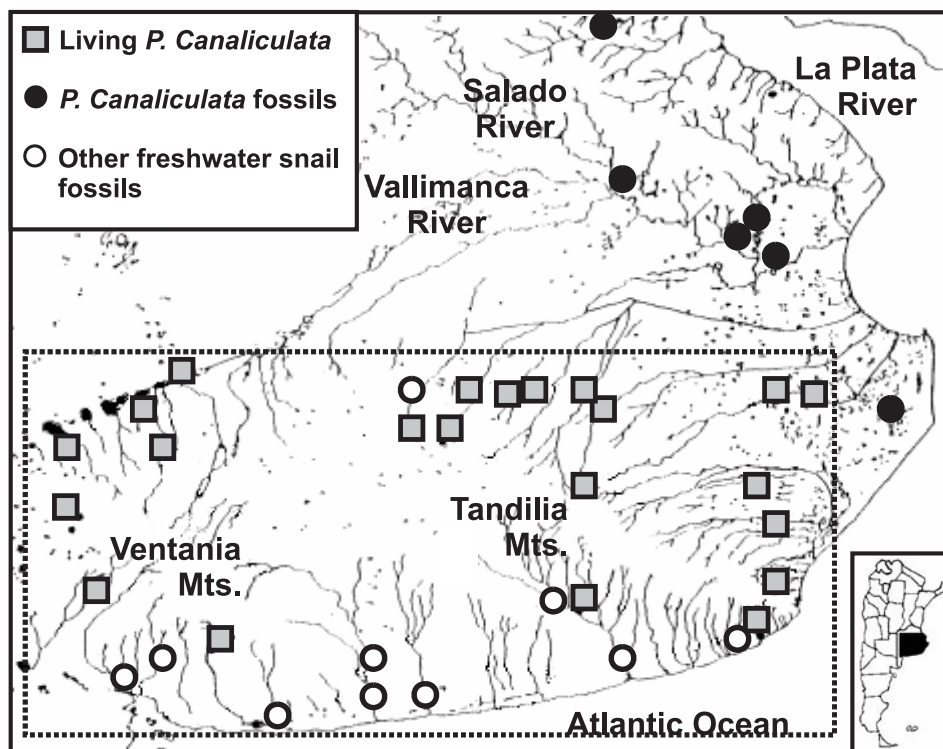


FIGURE 2: Map of the Buenos Aires province (inset: political map of Argentina). Dotted line indicates the zone surveyed for *Pomacea canaliculata* populations by Martín *et al.* (2001). Squares locate sites inhabited by *P. canaliculata*. Circles indicate Quaternary deposits of fossil freshwater snails with *P. canaliculata* (filled circles) and without it (empty circles).

authors agree that since the Last Glaciation Maximum (ca. 20 ka BP) a climatic warming event took place in this region (e.g. Clapperton, 1993; Iriondo and García, 1993). However, *P. canaliculata* never trespassed the Ventania and Tandilia Mountains, suggesting that this hydrological discontinuity has been the barrier impeding the southward spread of *P. canaliculata*. The lack of fossil evidence of *P. canaliculata* on the Southern slope also suggests that present populations found there are the result of anthropogenic dispersal, probably due to fish sowing or as fishing bait (Martín *et al.*, 2001).

Fossil record can also help to understand the distribution of *P. canaliculata* in the Cuyo region in Western Argentina. Contrarily to other regions of Argentina, the first collections from this arid region date from 1930 and a few new isolated localities have been reported since then (Cazzaniga, 1987a,b). Cazzaniga (1987a) discarded an anthropic origin of these populations, though Castellanos (1994) suggested a contemporary spread towards the West. Recently, Albrecht (1998) mentioned new localities from Mendoza Province in Southern Cuyo. Zarate *et al.*, (1997) registered the presence of *Ampullaria* (= *Pomacea*) in an archeological site (7.5 ka BP) in Mendoza Province, though the remains were probably misidentified (M. Zárte, com. pers.). Recent paleontological surveys on several mid-Holocene deposits (5-8 ka BP) in Mendoza Province revealed the presence of several species of freshwater snails that nowadays inhabit the zone, but *Pomacea* shells were entirely absent (Dieguez *et al.*, 2004a,b; pers. obs.), suggesting a recent colonization of this area.

Conclusions

The fossils of *Pomacea* from Pleistocene and Holocene sediments in Argentina suggest a more restricted distribution and lower relative abundance in the past than nowadays. This may be the result of a combination of different local environmental conditions with megascale hydrographic changes that facilitated a southward expansion of many aquatic mollusks (i.e. the formation of the Paraná-Paraguay-Uruguay-La Plata drainage system in the late Pleistocene (Parodiz, 1982)).

The steadily increasing body of information about present populations of *Pomacea canaliculata* would bring new clues for paleoenvironmental reconstruction through the analysis of their Quaternary fossil assemblages. Nevertheless, a more rigorous testing of the origin of fossil evidence through actualistic experiments or surveys is still necessary in most cases before they

can be applied to paleoenvironmental reconstruction. On the other hand, the contribution of the paleontological evidence on past distribution of *P. canaliculata* in the frame of the geomorphological evolution of the region, together with the still wanting contribution of molecular genetics, would contribute to a better understanding of its present distribution and its possible range expansion in recent times.

The taxonomy of *Pomacea* and other apple snails have long suffered the lack of an historical perspective (Cazzaniga, 2002), although Berthold (1991) and Bieler (1993) made the first attempts to reconstruct the evolutionary history of the Ampullariidae and to develop a natural grouping of genera. Although perhaps less evident, the understanding of many aspects of the biology and ecology of *Pomacea* would also benefit by the contribution of a chronological component provided by paleontological evidence.

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