

## Workshop: “Biology of Ampullariidae”

### Minireview

## Old species and new concepts in the taxonomy of *Pomacea* (Gastropoda: Ampullariidae)

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**ABSTRACT:** The taxonomic history of the South American genus *Pomacea* Perry, 1810, and some shifts of systematic concepts during recent decades are briefly reviewed. Too many pre-evolutionist, shell-defined species created a gibberish, the only acceptable solution of which being perhaps a conventional, somewhat authoritarian decision based on expertise. The addition of other sources of morphological, biochemical, ecological or genetic information should not solve the problem if it is not accompanied by a sound reappraisal of the species concepts. Since the assumptions of each concept differ, any correspondence between them is irrelevant, and may drive to incompatible results. The shell variability of *Pomacea canaliculata* was acknowledged for most authors throughout more than a century. A recent insight into its life-history traits demonstrated they are as variable as the morphology. These findings stress the need of determining the ecological identity of any pest apple-snail population at a local scale, because its invading ability may be not exactly correlated to its taxonomical identity. Probably, all the *canaliculata*-like apple snails constitute a single, very variable “species” in most senses, even though different subsets may be recognized under other incommensurable concepts.

Pain (1960) said that the taxonomy of the Amazonian Ampullariidae was “in a state of hopeless confusion”, an assertion that was also valid for the whole diversity of South American apple snails. Forty years later, the situation has been made simpler for some species groups within the genus *Pomacea* Perry, 1810, but it is very disappointing for other subsets.

Meanwhile many things have changed. There was a dramatic shift in the aims and methods of systematics, which has evolved from a discipline concerned with clas-

sifications towards a discipline mainly dealing with the reconstruction of the evolutionary history of life (O’Hara, 1993). It is now desirable that taxonomic characters are not used for defining classes of organisms but for reconstructing historical hypotheses (De Queiroz and Donoghue, 1988). The analogy of systematics to classification is in fact a relict of the pre-evolutionary period, when diversity was viewed ahistorically (O’Hara, 1994). Indeed, the contradictions between taxonomy and biological nomenclature, that were already described and discussed some 30 years ago (Whitehead, 1972), are now so flagrant that a new non-essentialistic approach to nomenclature is coming into due development (De Queiroz and Gauthier, 1993) so that the abandon of the Linnean structures in nomenclature is foreseeable.

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Simultaneously, an impressive insight was gotten into the epistemological problems affecting the species concept and its underlying speciation mechanisms (Luckow, 1995). At present, biologists are not really sure of what sort of things species are and how to discover such entities in nature (Sluys and Hazevoet, 1999). This is not a question of definitions but a true conceptual problem (Blackman, 1995), and application of different species concepts may drive to incompatible results. So, this review of the taxonomy of *Pomacea* contains many general considerations that, of course, apply to other zoological groups.

Essentialistic criteria<sup>1</sup> were mostly applied up to now in the taxonomy of *Pomacea*, with a predominance of informal shell comparisons. Almost all is still to be done to construct meaningful hypotheses about their phylogeny. Since taxonomic problems have no single solutions, theoretical explicitness and testable hypotheses are needed to produce significant advances and to improve the conditions of discussion.

The awareness on this “new” approach is fundamental for a meaningful consideration of internal morphology, interbreeding experiments, chromosome analysis, immunological tests, DNA studies or any other data source. It is not the source of information but the kind of tests performed on these data what may answer sound specific questions.

### Higher level taxonomy and nomenclature

An intricate series of nomenclatural misunderstandings accompanied the taxonomical history of the Ampullariidae, but their position among the mesogastropod prosobranchs (order Caenogastropoda), as sister group of the Viviparidae (Berthold, 1989), is not controversial.

Berthold (1991) tried to analyze the phylogenetic relationships within the family in a cladistic context and, even though his attempt merits several methodological criticisms (Bieler, 1993), it was a major step on a road going out the stasis of previous approaches. The monophyly of the family is now supported by 29 synapomorphies.

After an application by Cowie (1997), the International Commission on Zoological Nomenclature (ICZN, 1999a) finally sanctioned the validity of the family name Ampullariidae Gray, 1824 (instead of Pilidae Preston,

1915), a merely formalistic but convenient progress. At the same time, the genus name *Pomacea* Perry, 1810 was definitively validated.

*Pomacea* belongs to the subset of South American longisiphonate genera (Michelson, 1961), which is now recognized as a monophyletic group. Berthold (1991) called it Neopomata (with no formal nomenclatural bearing), based on six synapomorphies. This group outlived Bieler's (1993) re-analysis.

Three subgenera are generally recognized within *Pomacea*: *Pomacea* (*Pomacea*) Perry, 1810, *P. (Effusa)* Joussemae, 1889, and *P. (Limnopomus)* Dall, 1904. Berthold (1991) dropped the latter in the synonymy of *P. (Pomacea)*. The sister-group relationship of *Effusa* and *Marisa* Gray, 1824 seems a well-supported hypothesis in the final consensus tree by Bieler (1993).

### The conchological morphospecies

At present some 50 nominal species of *Pomacea* are known from South America, after discounting many old shell-defined names that conchologists, based on subjective judgments and comparisons, sank into the synonymy of other species whose descriptions and illustrations were not necessarily more adequate. The limits among species are exclusively based on personal opinions that are seldom transmissible: the species is in the eye of the expert.

When Alderson (1925) published the latest worldwide monograph on the family, explicitly recognized that the identification of many apple-snail shells is a mere matter of opinion and recommended to try gaining skills for recognizing minimum “subtleties of line, which can hardly be expressed in a figure, and not at all in a description”. Contrasting shells and figures was the main way to apprehend the essence of the apple snail species. A special kind of artistic sensitivity that Reeve (1856) called “iconographical acumen” was deemed to be critical for a correct taxonomical study.

Pre-Darwinian authors working in cabinets tended to split species, sometimes with a frustrating ignorance of environmental and even geographical information (e.g. Reeve, 1856), while naturalists that walked the ground, either creationists (e.g. d'Orbigny, 1835-1846) or evolutionists (e.g. Strobel, 1876), with a better sense of natural variability, generally were more cautious in incorporating new names, and often used terms as “varietates” or “mutationes”.

Mostly after the invasion of rice fields in South-east Asia by *Pomacea canaliculata* and allied forms, the interest to clarify the identity of the invaders came

<sup>1</sup> For a philosophical discussion on the meaning of “essentialism” in this context, see De Queiroz (1994).

across a great attention. The newcomers clearly fit in the “*canaliculata* group”, i.e., a set of shell-defined species that show a noteworthy uniformity both in their external and internal morphology, within the subgenus *Pomacea* (*Pomacea*). This species group thrives from Colombia to Argentina, and is formed by some ten nominal species; the most frequently cited ones being *P. canaliculata* (Lamarck, 1822)<sup>2</sup>, *P. insularum* (d’Orbigny, 1835), *P. lineata* (Spix in Wagner, 1827), *P. dolioides* (Reeve, 1856), *P. haustum* (Reeve, 1856), and *P. gigas* (Spix ex Wagner, 1827) (= *P. maculata* Perry, 1810, type species of the genus). Almost all possible combinations were intended in the synonymy of these names throughout the last century, as commented by Cazzaniga (1987).

Based on his field experience, d’Orbigny (1840)<sup>3</sup> described at length the variations of *P. canaliculata* and, to justify the inclusion of *gigas* and *lineata* in its synonymy, he said that “taking into account the extreme forms, one could easily multiply the number of species up to infinite; but the always identical animal, the sameness of the egg color, gave us the certainty that, as different as they are, all these varieties are no more than modifications of a single species. Only in each one of the innumerable small lakes of the Corrientes province [Argentina], the species change the form of the shell to such an extent that one has the certitude of finding an entirely different form after walking a hundred steps” (original in French).

Strobel (1876) demonstrated that he was able to recognize the conchological species, but extensively argued for the variability of *P. canaliculata*, including *australis*, *insularum*, *gigas* and *P. orbignyana* (Philippi, 1851) as varieties: “this species fairly varies in its dimensions, form, and color. [...] It happens that in certain localities almost all the individuals are distinguishable by shells that show a complex set of characters, while in other localities they show a different or opposite set of characters. And in such extreme forms one might believe that they are different species. But among these [shells] one finds, either in the same place or in intermediate sites, a number of transitional forms; this is why the extreme, and almost constant forms in a given locality should be considered, at most, as varieties of the same species, and not as different species” (original in Italian).

Nevertheless, many other authors insisted upon

distinguishing the old forms and, as late as 1949, Pain added another conchological species from the La Plata river at Buenos Aires, *Pomacea vickeryi*, intermediate between *P. australis* (= *P. canaliculata*) and *P. insularum*. Typical *P. insularum* from the Paraná river delta are readily recognizable, but many intermediate or doubtful shells are found eastwards, in the area of La Plata city. Hylton-Scott (1957) placed *P. vickeryi* as a synonym of *P. insularum*.

The limits of variation of any species on shell morphology grounds are defined subjectively. *P. canaliculata* shows very different sizes depending on habitat, from gigantic shells 10 cm high in some lakes and swamps in northern Argentina, to animals less than 4 cm high in temporary roadside pools. Thickness varies from rough shells, with striated or martelée sculpture, up to a smooth surface, or even snails with a paper-like, almost transparent shell in the big *Pomacea canaliculata chaquensis* Hylton-Scott, 1948, which Cazzaniga (1987) refused as a valid subspecies. The spire varies from produced to fully immersed, with a consequently more and more channeled suture. Allometric changes of form were also described (Estebenet, 1998), so that young snails may give the impression of being different to adults. Other *Pomacea* “species” lie within or nearly beyond this variation, but some authors still persist in keeping specific names for them.

The form and proportions of the aperture may prove useless, or at least doubtful, for specific discrimination if sexual dimorphism is ignored (Cazzaniga, 1990; Estebenet, 1998). For example, to differentiate his Brazilian species *Pomacea haustum* from the Argentinian *P. insularum*, Reeve (1856) only commented: “Its chief points of difference consist in being less distinctly umbilicated, and in having a much larger and more expanded aperture”. These conditions are not taxonomically decisive. Alderson (1925) already discussed the variability of the umbilicus, “so that we cannot regard the presence or absence of the umbilicus [...] as proof positive of specific distinction”. At least in *Pomacea canaliculata* and *Marisa cornuarietis* (L.), the aperture and operculum show sexual dimorphism, male shells having more expanded ones (Cazzaniga, 1990; Demian and Ibrahim, 1972), and therefore, a study of these aspects should be made on Brazilian material to re-assess the conchological differentiation of *P. haustum*, whose figure in Reeve (1856) looks like a male *P. insularum*.

Shell variations affecting size and thickness among populations of *P. canaliculata* from southern Buenos Aires Province (Argentina) are mainly ecophenotypical, and not genetically determined, as Martín and Estebenet

<sup>2</sup> The conservation of this specific name by skipping the fact that it was pre-occupied by another snail species was the subject of a well-founded application by Cowie *et al.* (2001).

<sup>3</sup> For the correct dates of publication of the different chapters of d’Orbigny’s Voyage, see Parodiz (1957).

(2002) demonstrated experimentally. Such a result, should have an influence on taxonomy.

Since isolated shells were the only material available for many original specific descriptions, with no reference to their natural variability, it is probable that we can find a name (or more than a name) for every local population in which some individuals have a given aspect: "Among these Protean shells one rarely finds an absolutely typical specimen [...] Of specimens that are exactly 'according to the book', we shall, perhaps, on an average, find one in twenty" (Alderson, 1925).

The fact of having the same variability range and the rarity of "typical" specimens should lead to acknowledge the weakness of the argument for specific discrimination, but instead these circumstances are often mentioned as a sign of the difficulty for revealing the true essence of each species. The name is before the facts. The cart is before the horse.

Taxonomists able to manage "subtleties of line" and to find a Latin name for every material, tended to deplore the negligence or insensitivity of the authors that prefer lumping hypotheses. For example, Martens (1857) decided to include under *P. canaliculata* the following synonyms: *gigas*, *haustrum*, *insularum*, *immersa*, from Guyana to La Plata; and later he also added *dolioides* and *orbignyana* to the list (Martens, 1868). Though recognizing him as an excellent conchologist, Alderson (1925) lamented these decisions by opining that Martens did not seem to have a special talent to evaluate drawings: "This is somewhat strange, considering that he not only came of an artistic family but was also possessed of considerable skill as a draughtsman". This is clearly an *ad hominem* argument, absolutely out of reason and respect. As most present-day conchologists acknowledge (or should acknowledge), people who do not accept some shell divergences as indicative of specific differences are not necessarily negligent or poorly trained.

It is almost a truth of thumb that any character that cannot be expressed in a description or cannot be managed mathematically probably is not a character at all. To define any acceptable shell difference, the intra- and interpopulational variability must be studied at local and regional scales, preferably through multivariate statistical methods. This kind of studies is inexistent for species in the *Pomacea canaliculata* group. Only Gutiérrez *et al.* (1994) tried to differentiate two non-sympatric forms from Cuba (probably *Pomacea paludosa* and *P. poeyana*) by Principal Component Analysis.

## Type localities

To interpret shell-defined species, especially those briefly described more than a century ago, it is very useful to collect live animals in the type locality, provided this one is identifiable. Quite often, type localities are not specific enough to know where the original shells exactly came from. For example, localities as "Rio Parana, South America" (some 4000 km), or "Brazil" are obviously uninformative references that include very different biogeographical regions. Still worse is the condition of the "homeless" species, whose original localities were either unknown or certainly erroneous. In Reeve (1856) for example, more than 40 out of the 135 figured species have a question mark as the only reference to place of origin.

*Pomacea canaliculata* and *Pomacea dolioides* are good examples of misleading distributions. Reeve (1856) gave "Bombay" as the type locality of *P. dolioides*, and most authors repeated this mistake up to the beginnings of the 20<sup>th</sup> century. Sowerby (1909) suggested La Plata (Argentina) as the probable origin of this shell. Pain (1950) did not recognize it in his collections from the area of La Plata, but cited *P. dolioides* from Guyana. Geijskes and Pain (1957) said that the shells from Surinam that Vernhout (1914) identified as *P. canaliculata* "appeared to be an extreme form of *P. dolioides* with a deeply channeled suture".

Pain (1946) tried to ascertain the original locality of *P. canaliculata*, because the one given by Lamarck ("rivières de la Guadeloupe") seemed erroneous. Only species in the subgenus *Pomacea (Effusa)* live in the Caribbean island of Guadeloupe (Pain, 1949; Pointier, 1974), and no evidence was given for a local extinction of *P. canaliculata* in the island. D'Orbigny (1840) mentioned that typical specimens of *P. canaliculata* are found in Corrientes (Argentina). Pain (1949) said that typical *P. canaliculata* are collected in the Paraná river, near Rosario (Argentina), and Hylton-Scott (1957) pointed out that there is a lagoon called Guadalupe in that area.

These conjectures do not warrant where the true original locality was. The only concrete conclusion is that both *P. canaliculata* and *P. dolioides*, whichever their relationships are, live in South America, either in Argentina, or in Guyana, or both.

Anyway, even in species for which a type locality was clearly defined, collecting there is useful only if one can trust that the place has not suffered much alteration since the original description. Eutrophication,

pollution, changes in water acidity, or other degrading processes could have occurred and, under such ecological pressures, microevolutive or ecophenotypic mechanisms are quick enough to adaptively modify shell morphology in *Pomacea*, so that the same species appears now under a different aspect. This fact may be undistinguishable from true replacements of species, a process that is favored by, e.g., construction of waterways and dams, or species transport by human activities.

### The game ends when the game master decides it

When facing such a state of taxonomic uncertainty, it is a common procedure that identifications be confirmed by the expert eye of some authority able to compare and discriminate shell differences. His/her opinion is the only way to come to some relative certitude.

One day, the game master decides that it was enough and reduces the trouble to a smaller number of names, as Pain (1964) did with the so-called *Pomacea flagellata* group. He reduced this “complex” to a single species, with four subspecies, which had received some 30 specific names and several variety names along near one century and a half.

Dr. Pain was an extraordinaire expert, the last old-style conchologist, who studied worldwide ampullariid shells for more than three decades, at the end of which he reached the conviction that a *lumper* attitude was more realistic, at least for the Central America *Pomacea*. Did Pain expose either molecular, or ultrastructural, or anatomical, or even statistical information on shells before dropping all these names into a synonymy? Of course, he didn't. He simply announced, from the heights of his incomparably large experience, his intention of removing some of the “dead wood” (sic) by offering an eye-made synonymy.

Malacologists peacefully accepted this authoritarian procedure, which lessened the frustration deriving from a weak and very complex taxonomic gibberish, making free the way for new research.

This kind of conventional, “non-scientific” solutions disgusts people that are not aware that the essentialistic concepts of species are also non-scientific. The rationale is that if the authority of an expert is accepted, and sought, when he/she feels able to discriminate sets of shells, then it also has to be accepted when the same expert admits he/she is no longer able to believe in such an amount of species.

Pain's decision arrived at a time when most biologists already acknowledged that species are variable and sensitive to environmental patchiness, and that morpho-

logical differences have to be established through unambiguous methods.

Later, Naranjo-García and García-Cubas (1986) showed the distribution of *P. flagellata* in Mexico and Central America, and said they could not find any shell or radular differences that justify even the four subspecific taxa rescued by Pain (1964). Rangel-Ruíz (1988) also doubted of the validity of these subspecific names.

A similar agreement occurred with the subgenus *Pomacea (Effusa)*. Old monographs contained many species relative to *Pomacea glauca* (L.). Sowerby (1909), by his own authority, cited nine of them as varieties of *P. glauca*. Alderson (1925) raised them to the specific level again. Baker (1930) said *P. glauca* “is easily the most variable species that I have ever studied”, and divided it in nine varieties (not ever geographic subspecies), which were not the same as those in Sowerby (1909) and did not cover all the known variability (Arias, 1952). Pain (1950) cited *P. glauca* from Guyana as including only four varieties. Pointier (1973, 1974) showed the great, almost continuous variability of *P. glauca* in Guadeloupe and, from that time onwards, the literature only mentions *P. glauca*, disregarding the variety concept (McKillop and Harrison, 1980; Starmühlner, 1984, 1988). There are better ways to document the variability than multiplying Latin names.

*Pomacea flagellata* and *P. glauca* extend over a much more limited geographical range than the *P. canaliculata* group, the two former being exclusively limited to tropical areas, whereas the latter also reaches temperate and semiarid regions (Cazzaniga, 1987), with a consequent shift in food availability, reproductive strategy, seasonal activity, etc. (Estebenet and Martín, in this issue of BIOCELL). The variety of habitats and ecological conditions being much broader, it is reasonable to expect that shells of *P. canaliculata* show a greater morphological diversity too.

### The contribution of internal anatomy

The anatomy of species in *Pomacea* was not used for taxonomical discrimination before the 1950s. The existing anatomical literature generally refers to single shell-identified species in a context that does not allow true comparative procedures. *Pomacea falconensis* Pain and Arias (1958), from Venezuela, seems to be the only species whose original description included both a shell description and an anatomical study of the soft parts.

Souza-Lopes (1955, 1956a, b) illustrated the anatomy of some species from Brazil, with shell identification by Dr. Pain in London. Special reference was

made to the male genital system, which is deemed to be the only source of taxonomically useful characters. However, these papers are not strictly comparative because they almost lack a discussion, so that the differences among species are not always self-evident.

Pain (1952) had considered that *P. dolioides* was a synonym of *P. lineata*, but later accepted them as different species by saying: "Examination of the soft anatomy of a specimen of *P. dolioides* (Rve.) from Recife in Pernambuco, Brazil, by H. de Souza-Lopes (Instituto Oswaldo Cruz) has shown that it differs considerably from that of typical specimens of *P. lineata* (Spix) from Brazil (Atlantic drainage)" (Geijskes and Pain, 1957). To the best of my knowledge, the anatomical study on *P. dolioides* was never published, and therefore these differences cannot be assessed.

Hylton-Scott (1957) did not account for anatomical differential traits between *P. canaliculata* and *P. insularum*. Along her excellent description, most organs are referred to as being homogeneous among species of the same genus. She drew the radular teeth of various species, but not of *P. canaliculata*. The penial complex is well illustrated for *P. insularum*, while the feminine sexual organs are illustrated for *P. canaliculata* only. Since she failed to define anatomical gaps, Hylton-Scott (1957) elaborated new, very detailed specific diagnoses with shell features only, and avowed for a biological characterization of the two species, that live in different habitats: *insularum* in rivers; *canaliculata* in still waters.<sup>4</sup>

Mesquita *et al.* (1991) also concluded that the anatomy of the masculine organs is not conclusive for discriminating *P. canaliculata* and *P. insularum*: "It seems that such characters are of generic rather than specific value. In the penial sheath there are some differences affecting the position of the glands, roughs (folds) and volume of the organ. Nevertheless, the appreciation of these differences is not easy, and they are not used for identification, since they are variations in form and proportions of difficult measurement" (original in Portuguese).

Moretto and Nahabedian (1989) described some slight radular differences between *P. canaliculata* and *P. insularum*, affecting the silhouette, concavity and strength of some cusps and processes of the teeth. They are not clear-cut, but a question of grade. Pain (1972) had already denied the utility of such radular variations

as arguments for separating species within the Ampullariidae.

Andrews (1964) studied the anatomy of the reproductive system of *P. canaliculata* magisterially, though not in a comparative context to other South American species. Thiengo (1987) and Thiengo *et al.* (1993) re-described the anatomy of *Pomacea lineata* and *P. canaliculata* from Brazil and Argentina respectively. Cazzaniga (1987) also illustrated the penial complex of *P. canaliculata* from northwestern Argentina.

The coincidences and divergences among these descriptions are not easily solvable in the absence of clear correlations between external and internal morphology. People who remain most confident on conchology may interpret the existence of anatomical differences among animals that are under a same Latin name as an evidence that the anatomist misidentified the species under study. When no anatomical differences are found among animals with different shell morphology, disbelief may be poured over the anatomist's talent. Even though an absolute respect and due courtesy prevails among authors, the use of internal anatomy does not prevent the basic problem that defining species through morphological discontinuities, in a pre-hennigian way, is an ahistorical approach depending on personal feelings.

Once again, the intra- and interpopulational variability of the internal organs is to be analyzed before concluding about the taxonomical consequences of similarities and dissimilarities. It is a merit of Souza-Lopes (1956b) having tried to show this kind of variability for his material of *P. canaliculata* from Brazil.

### Non-morphological characters

Characters other than morphological were explored only recently, and they were not used for extensive taxonomic studies in *Pomacea*.

The information on cytogenetics is scarce. Diupotex Chong (1994) studied the karyotype of *Pomacea flagellata* from Mexico ( $2n = 26$ ), which was later compared to *P. patula catamacensis*, which has the same chromosome number and morphology (Diupotex Chong *et al.*, 1997).

Kawano *et al.* (1990) studied the karyotype of a *Pomacea* in the "*canaliculata* group" from São Paulo, Brazil (maybe *P. lineata*) ( $2n = 28$ ). Mercado-Laczko and Lopretto (1998) found the same chromosomal number and morphology in *P. canaliculata* from Buenos Aires (Argentina). Von Brandt *et al.* (1990) also studied the chromosomes of *P. canaliculata* introduced into

<sup>4</sup> A discussion on the habitats of *P. canaliculata* in southern Buenos Aires province, and factors affecting its distribution was recently published (Martín *et al.*, 2001).

Japan. The comparative basis is very limited and did not produce remarkable differences within the *P. canaliculata* group.

Keawjam and Upatham (1990) tried to combine conchology, anatomy and molecular genetics to differentiate three forms of *Pomacea* introduced into Thailand, which they called *Pomacea canaliculata*, *P. insularis*,<sup>5</sup> and *Pomacea sp.* Their results show that animals with different shell characteristics may give similar genetic patterns, while individuals that have almost identical shells differ genetically. The anatomical differences among the three shell-defined units are mostly restricted to a judgment of the size and relative position of the seminal vesicle.

The assignment of specific names by Keawjam and Upatham (1990) seems rather arbitrary, since their shell descriptions are not coincident with (and even are opposite to) the literature. No South American study was cited for comparison. What they called both *P. canaliculata* and *P. insularum* seem to fit better to *P. insularum* in the descriptions by d'Orbigny (1840) and Hylton-Scott (1957), while Thai *Pomacea sp.*, with a not-so-thick, banded shell, and thin operculum rim seems more similar to the *P. canaliculata* studied by Bachmann (1960) and Thiengo *et al.* (1993).

Anyway, that paper opened a new source of useful information, even though it was not analyzed phylogenetically.

Yusa and Hirayae (1998) recently developed a protocol for amplification of DNA fragments of fresh and alcohol-preserved *P. canaliculata* from Japan. They found a high variation among populations and among individuals of the same population. The limits of the specific variability are now to be explored.

### The biological and recognition concepts of species

Since its formulation by Dobzhansky and Mayr in the 1940s, the "biological concept" of (genetically isolated) species has been one of the most popular views among zoologists. Under such a model, the main grouping criterion is a judgment on the actual or potential ability to exchange genes by individuals from different populations, irrespective of their morphological simi-

tude or difference. Paterson (1985) transformed it to a "recognition concept", where the internal cohesion of the species and the development of recognition-of-mate mechanisms are emphasized over the mere reproductive (genetic) isolation.

The antecedents on interbreeding experiments in the *canaliculata* group almost reduce to Bachmann (1960), who failed to observe copulas among individuals of *P. canaliculata* and *P. insularum*; only a few couples tried to mate, with no record of oviposition. Therefore, he refused his original hypothesis that they were two conspecific ecological races, and tried to re-characterize them as valid species. He pointed out the flexibility of the operculum, the general activity of the individuals, and the egg color as specifically distinctive. However, Souza-Lopes (1956b) had described that the egg color is also variable depending on the place and it changes in successive generations if reared in the laboratory.

The size of the eggs was also mentioned as a differential trait, but Estebenet and Cazzaniga (1993) showed that *P. canaliculata* has an intrapopulational variation of the egg size (even among egg masses deposited by a single female) that surmounts the alleged specific difference. Bachmann also stated a distinction affecting the growth pattern and length of the life cycle, but Estebenet and Cazzaniga (1992) demonstrated experimentally that apple snail growth, lifespan and reproductive strategy are also variable (see also Estebenet and Martín in this issue of BIOCELL), and probably unspecific.

In Japan, apple snails inhabiting rice fields near Kumamoto (Kyushu) are smaller than snails coming from lotus fields, and they seem to reach maturity at a different size (T. Wada, pers. comm.). Therefore, during a sojourn at the Kyushu National Agricultural Experiment Station (Nishigoshi, Japan), I made some crossing trials among apple snails collected in both habitats, in 40 small aquaria where couples of the same and mixed origin were maintained during July 1999. Mating was observed in almost all the aquaria, irrespective of the origin of the snails (unpubl. data).

Such an experiment does not give a clear-cut taxonomic answer, because these populations may pertain to the same species, to incipient species or to not-so-different species that readily hybridize. The acquisition of a recognition-of-mate mechanism is a prerequisite, and not a consequence, of speciation.

Genetic studies should be necessary to evaluate the frequency of syngamy, but the important thing here is that, in spite of their different shell morphology, the individuals coming from different crops shared the same recognition-of-mate mechanism, i.e., they recognized

<sup>5</sup> Some authors erroneously used the specific name *insularis* in replacement of *insularum*. However, the latter must not be changed anyway, because *insularum* is a declined form of the Latin noun *insula* (plural genitive case, meaning "of the islands"), and therefore is invariable as scientific name (articles 11.9.1.3 [example: *thermopilarum*], 31.2.1 and 34.2.1: ICZN, 1999b). I consider *insularis* as a mistake, not intended for an emendation in the terms of article 33.2 of the Code, and then it is unavailable (article 33.3).

each other as potential mating partners. Under this concept, the isolation of gene pools is no longer a necessary condition for defining species (Ferguson, 1992; Hulley and Hill, 1992).

### Then, how many species of *Pomacea* are there?

Describing a species always means to advance a hypothesis of some sort. By the terms “new species” an author wishes to say that he/she is defining either a morpho-physiologically unique set of living beings (i.e., they share a different Aristotelian essence: a non testable hypothesis; Hull, 1965, 1966); or a class of organisms that are genetically isolated from other similar groups (a seldom testable, if not untestable, hypothesis; Paterson, 1981; Sluys, 1991); or a natural set of organisms that developed a specific mechanism of mate recognition (Paterson, 1985); or that he/she discovered an individual pattern of ancestry and descent (Cracraft, 1987), or any other thing among the 29 concepts and views of species that were compiled by Zink (1997).

It is obvious that, to be sure on what we are talking about, we should know what the author’s purpose was when he/she published a new name. Should this not be the case then it is unfruitful to try to test such a “species” under a different species concept. These concepts stand on different and conflicting sets of assumptions, which may or may not agree in the resultant circumscription of a species. Since the assumptions of each concept differ, any correspondence between them is irrelevant (Luckow, 1995) and, in scientific research, one usually considers only the hypotheses that are relevant to one’s own theoretical network. It is quite unwise to expect that conchological species described under a pre-evolutionary paradigm coincide with, for example, biochemical, ecological or phylogenetic concepts that were conceptualized more than two centuries later.

The “legal” existence of a species, that is the record of a name under certain regulations, has very little bearing on the scientific need of recognizing ontologically convincing natural entities.

Grouping organisms in classes by diagnostic criteria or unique combinations of characters (even though they include morphological and non-morphological features) actually correspond to different biological, ecological or phylogenetic realities (Sluys, 1991; Baum and Donoghue, 1995).

Sluys and Hazevoet (1999) argue for pluralism to solve the “species problem”, because there is no single preferred way in which living organisms can be grouped into species, the choice of concepts being governed by

one’s research interest. Pluralism does not mean that the term ‘species’ has no precise meaning or should be used in an equivocal way in scientific discourse. Instead, the sense and context of the term have to be specified and, if necessary, the different species-level units will be referred to by different terms.

This problem is perhaps comparable to what happened with the “ecological stability problem” in the 1970s, when eight different community properties were identified under the term (constancy, inertia, resilience, elasticity, etc.). On the one hand, “stability” remains as a colloquial term that need to be qualified for any meaningful discussion, and on the other hand, a shift in the theory of ecological succession gave non-equilibrium concepts, i.e., those that refer to not competition-structured communities (Putman, 1994), that at present deserve much consideration, because they proved to be strong and sound for practical purposes, such as biodiversity conservation and resource management. Probably, in the “species problem” it is also time to accept that the different concepts involved are not necessarily rival, but incommensurable (Chalmers, 1988).

O’Hara (1993) stated that the outcome of the species problem perhaps will not get a solution, but a dissolution, i.e., we have not to solve it but to get over it. Both this possibility and the pluralistic solution raised by Sluys and Hazevoet (1999) suggest that the long-lasting problem of “how many species of *Pomacea* are there?” is a candidate to lose its scientific interest.

The possibility that the entire *Pomacea canaliculata* complex may be reduced to as few as three species –*P. canaliculata*, *P. gigas* and *P. lineata* (including *P. dolioides*)– as suggested by Cowie (MS), is an appealing hypothesis to work on, though the basis for such a number was not itemized yet. His hypothesis relies again on an extensive comparison of shells during his field and museum experience.

A taxonomic re-evaluation of *Pomacea* is deemed to contribute for developing more effective control measures of the apple-snail pest in Asia, by focusing their specific ecological features (Cowie, MS). I’m not so confident on that point, because members of the same taxonomic species may show as much ecological plasticity as they have in their morphology (Estebenet and Martín, in this issue of BIOCELL; Martín and Estebenet, 2002). The ecological identity of the pest populations is to be determined locally, their invading ability being not exactly correlated to their taxonomical identity. Probably, any *canaliculata*-like apple snails are able either to become a pest, or to vary their tolerance limits, or to adapt their life cycle traits, depending more on

external conditions and field management, than on their specific taxonomical position.

Not always organisms in nature are easy to be grouped into species, this being itself an evidence for the process of evolution (O'Hara, 1994). At present I am inclined to think that all the *canaliculata*-like apple snails constitute a single, very variable "species" in most senses, even though different subsets may be recognized under other incommensurable concepts. The convenience and criteria for recognizing such subsets depend on the explicit purposes of each research program.

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