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On the origin of *Cochlopupa* (= *Cylindrus* auct.) *obtusa* (Gastropoda, Pulmonata, Helicidae)

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ABSTRACT. Land snail *Cochlopupa obtusa* (Draparnaud, 1805) is an endemic of Eastern Alps. The mollusk has very unusual for helicids pupilloid shell, but its reproductive tract is quite typical for the subfamily Ariantinae (Helicidae). Neither this species nor any similar forms are totally absent in fossil deposits (the earliest records of *C. obtusa* conventionally dated by the “pre-Pleistocene”). According to suggested hypothesis, this species is very young and was formed within the existing area at the end of Würm glaciation due to mutation of some representative of Ariantinae.

Introduction

In Eastern Alps, on the territory of Austria, lives a very peculiar species of the Helicidae family – *Cochlopupa obtusa* (Draparnaud, 1805) (Fig. 1A). Externally this species is so drastically differs from all other Helicidae, that it has been separated in independent genus constituting a separate monotypic tribe Cylindruini [Schileyko, 2006]. At the same time, anatomical features clearly indicate that this species undoubtedly belongs to the Helicidae family [Martens, 1895; Sturany, Wagner, 1914; Schileyko, 1996] (Fig. 1B). This species is so strange that Adensamer [1937: 100] conventionally called the species “living fossil” (“lebendes Fossil”), although he himself understood that this term in the given case is not correct.

The peculiarity of *Cochlopupa obtusa* area is that the snails live at altitudes of 1600-2500 m above sea level and is presented by 150 fully isolated colonies (or groups of colonies) [Bisenberger et al., 1999; Klemm, 1961, 1974] (Fig. 2). Backhuys [1969] names such a phenomenon “elevation effect”. It is essential, that the animals conduct a secretive mode of life (they inhabit limestone rock slides) and have very limited individual activity.

The purpose of this publication is the analysis of the facts concerning the possible ways and time of origin of this peculiar species.

On the generic name

The generic name *Cylindrus* Fitzinger, 1833 (type species *Pupa obtusa* Draparnaud, 1805 by monotypy) is widely-used for the species of Helicidae during many tens of years. Unfortunately, this name is invalid because it is junior homonym of *Cylindrus* Batsch, 1789 (Gastropoda, Conidae) (type species *Conus textile* Linnaeus, 1758, by subsequent designation Dubois and Bour, 2010).

At the same time the generic name *Cylindrus* Fitzinger is a junior objective synonym of *Cochlopupa* Jan, 1830 with type species *Pupa obtusa* Draparnaud, 1805 (by monotypy). Thus, the correct binomen for the representative of Helicidae in accordance with the rules of the ICZN must be *Cochlopupa obtusa* (Draparnaud, 1805).

Some years ago I have written that I directed a petition to the International Commission on Zoological Nomenclature where I ask to conserve the name by Fitzinger [Schileyko, 2006: 1786]. In fact, at that time I did not send the petition (for reasons not related to the case), but it is now evident that the petition is not necessary.

So, formally the position of the genus and species is follow:

Fam. Helicidae Rafinesque, 1815

Subfam. Ariantinae Mörch, 1864

Genus *Cochlopupa* Jan, 1830

Jan, 1830: 5 (*Pupa* subgen.);
Cylindrus Fitzinger, 1833: 107, type species – *Pupa obtusa* Draparnaud, 1805, by monotypy; nom. praeocc., non Batsch, 1789 (Gastropoda, Conidae).

Type species – *Pupa obtusa* Draparnaud, 1805, by monotypy.

Discussion: facts and interpretations

To understand the reasons of appearance of such an unusual shell of *Cochlopupa obtusa* and the formation of such a peculiar area, we must answer four somewhat interrelated questions: 1. How could be formed such a peculiar area? 2. Where the species has originated? 3. Who could be an ancestor of this species? 4. When the species could appear (i.e. geological age of the species)?

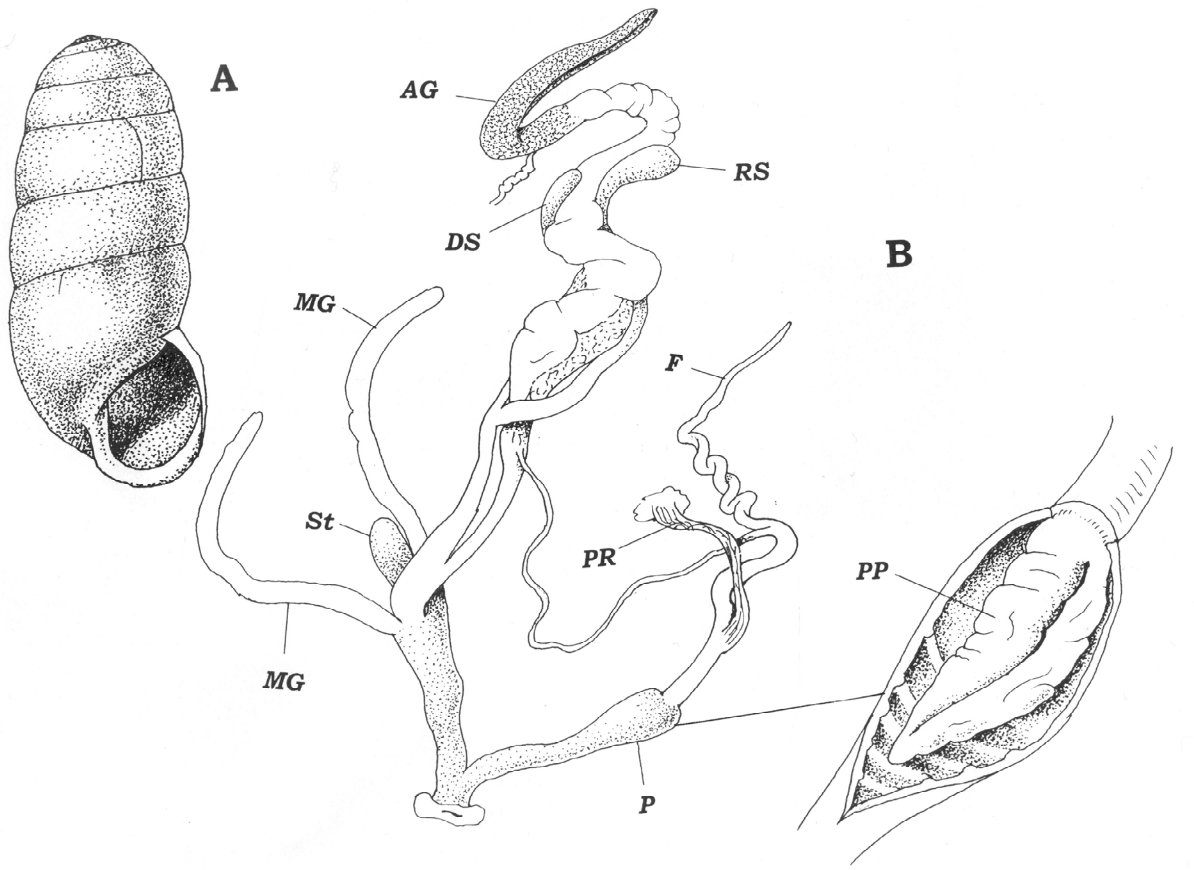

FIG. 1. *Cochlopupa obtusa* from Sengsengebirge, Hocher Nock, Haltersitz, 30 July, 2009. A – shell. B – reproductive tract and open penis. *AG* – albumen gland; *DS* – diverticle of spermathecal stalk; *F* – flagellum; *MG* – mucus gland; *P* – penis; *PP* – papilla of penis; *PR* – penial retractor; *RS* – reservoir of spermatheca; *St* – stylophore.

РИС. 1. *Cochlopupa obtusa* из Зенгзенгебирге, Хохер Нок, Хальтерзитц, 30 июля 2009. А – раковина. В – репродуктивный тракт и вскрытый пенис. *AG* – белковая железа; *DS* – дивертикул протока семеприемника; *F* – флагеллум (бич); *MG* – слизистая железа; *P* – пенис; *PP* – папилла пениса; *PR* – ретрактор пениса; *RS* – резервуар семеприемника; *St* – стилофор.

1. Way of formation of the *Cochlopupa* area

To answer the first question (taking into account the characteristics of the area), it is appropriate to search among external factors, primarily the geological history of the Eastern Alps, (in particular, the history of climate and glaciations), and the presence of suitable (calcified) soil.

Since the Oligocene, Mediterranean geosynclinal area has undergone intensive folding (Alpine orogeny). Actually the Alps as a mountain system emerged in the upper Miocene, i.e. about 10 million years ago [Popov et al., 2009], but what is known about malacofauna of the Eastern Alps before the glacial time, does not contribute to understanding the history of the species and its area. As said above, there are serious reasons to believe that the formation of the *Cochlopupa* area is connected, in particular, with glaciations.

In total, during the Holocene 4 glacial periods took place in the Eastern Alps [Penck, Brückner, 1909], but the fate of *Cochlopupa obtusa* is reasonably traced only after the very last and the most powerful glaciation (Würm), which ended, on geological scale, quite recently – just 10-12 thousand years ago.

The analyses of microfossilized plant pollens found in geological deposits, has chronicled the dramatic changes in the European environment during the Würm glaciation. During the height of this glaciation, *ca* 24,000-10,000 years ago, significant part of the territory of Austrian Alps (except for the easternmost parts) was covered with thick **ice fields** [van Husen, 1987] (Fig. 2). Thus, all Recent malacofauna of Eastern Alps arose due to invasion from adjacent territories or from some refugia within last 10-12 thousand years [Ložek, 1982], since, I am repeating, at the time of Würmian glaciation most of surface of Eastern Alps (except for easternmost parts) has been covered with ice shield. Herbert Ant [1969: 249] writes that "Keineswegs ist aber die Annahme berechtight, dass es im Sinne einer Tabula-rasa-Theorie zur völligen Auslöschung gekom-

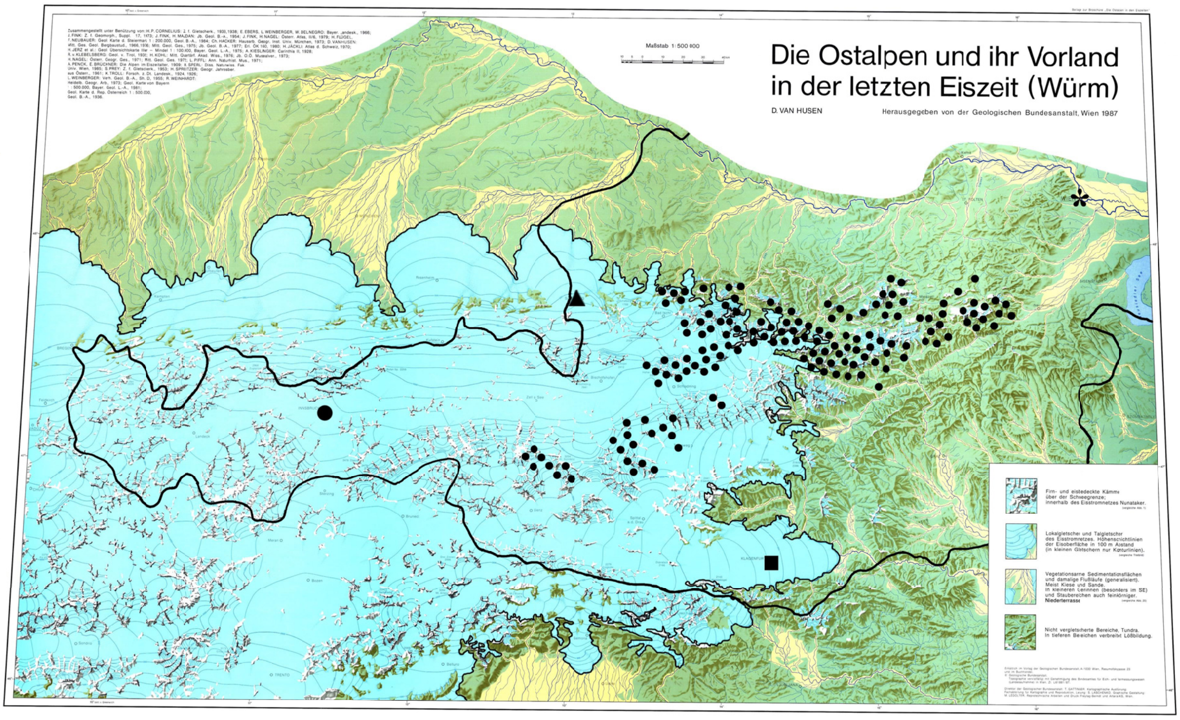

FIG. 2. Localities of *Cochlopupa obtusa* [after Klemm, 1973] superimposed on the map of Würm glaciation in Eastern Alps [after van Husen, 1987]. *Asterisk* – Vienna. *Square* – Klagenfurt. *Circle* – Innsbruck. *Triangle* – Salzburg. Thick line indicates the border of Austria.

РИС. 2. Места находок *Cochlopupa obtusa* [из: Klemm, 1973], наложенные на карту Вюрмского оледенения в Восточных Альпах [по: van Husen, 1987]. *Звёздочка* – Вена. *Квадрат* – Клагенфурт. *Кружок* – Инсбрук. *Треугольник* – Зальцбург. Толстая линия обозначает границу Австрии.

men ist" ("by no means is reasonable to assume that in terms of *tabula rasa* theory it [fauna] has come to the complete obliteration"); nevertheless we must accept the fact that the elements of malacofauna are preserved only at the margins of the ice fields, and among these elements *Cochlopupa obtusa* has never been found.

Thus, I see two possibilities to explain the presence of the species in the Eastern Alps and peculiarities of its range: either snails migrated from somewhere, or the species appeared here. Since nothing like *Cochlopupa* in Europe is absent and apparently never was, I am inclined to assume that the second way is the only possible one, and *Cochlopupa obtusa* originated *in situ*.

Based on the above, I propose a hypothesis that, in my opinion, could explain the formation of such a kind of area.

At the end of the Würm glaciation, 10-12 thousand years ago, when glaciers began to melt rapidly, the climate of the East-Alpine region was still cool, and this cold-loving species has been widespread over the discussed territory. During subsequent warming of climate the populations lived in the valleys of the Eastern Alps, got in adverse conditions and become extinct; with further warming of climate the lace of *Cochlopupa* area is gradually becoming increasingly sparse due to the extinction of populations which inhabited the lower parts of slopes, i.e., figuratively speaking, the snails were raised following the snow line, and the area eventually acquired the modern appearance. I would like to remind and underline once more, that, judging from actual situation, ancestors of *Cochlopupa obtusa*, whoever they were, lived in rather cold places.

Taking into consideration mode of life of *Cochlopupa* (secretive, little active), random dispersal ways, such as passive migrations of snails from one isolated mountain to another by wind, birds, large flying insects, etc., could theoretically occur, but the likelihood of such events is extremely low. Moreover, such events, considering the number of colonies of *Cochlopupa obtusa*, must have been repeated often enough (at least 149 times); this circumstance additionally lowers the probability of passive dispersal of the snails.

Finally, we must also bear in mind that these snails live almost everywhere (at these altitudes) where there is limestone. This may indicate either a high dispersal capacity of the species or that its initial distribution was much less sparse (almost unbroken). Taking into account the above, I am definitely inclined to the second supposition. Otherwise, it turns out that as soon as somewhere appears a patch with carbonate soil (at suitable altitudes), almost immediately in this place appears *Cochlopupa*. In this case we must assume that the species is very mobile, which contradicts the known facts.

2. **Place of *Cochlopupa* origin**

The fact that *Cochlopupa* has very restricted and compact area could be considered as an additional argument in favor of my hypothesis – it has formed *in situ* and has not migrate from any other region.

3. **Problem of the *Cochlopupa* ancestor**

The third question (i.e. who was the ancestor of *Cochlopupa*) is the competence of systematics, although I can say at once that a definite answer is now impossible to give, and the fossil material is unknown. We can only postulate, that this ancestor was a member of the subfamily Ariantinae (Helicidae), which is, quite possibly, still exists at the present time, but the shell of *Cochlopupa obtusa* is so strikingly different from the shells of all known species of Helicidae that without knowing anatomy the species can not be attributed to this family (the species was originally described by Draparnaud under the generic name *Pupa*).

C. Boettger [1949] was the first, who suggested mutagenic origin of *Cochlopupa obtusa*. To confirm that such a mutation is possible, Boettger refers to the findings of cylindrical shells of planorbid *Anisus leucostomus* (Millet, 1813) among normal flat shells. Boettger believed that the ancestor of *Cochlopupa* was some species of *Helicigona*, moreover, a particular species – *Helicigona cingulatum* (Studer, 1820). I think that Boettger was right, and *C. obtusa* originated during just a few generations as a result of genetic mutation. I am not sure that exactly *Helicigona cingulata* was the ancestor of *Cochlopupa*, but I fully support the Boettger's hypothesis on origin of *C. obtusa* by mutation. Counterarguments by Adensamer [1962] do not seem to me convincing. It is difficult to imagine the appearance of such a peculiar shell in a gradual, evolutionary way during such a short time (just several thousand years).

For comparison, it is worth recalling that in the Miocene (about 15 million years ago) the fauna of the Northern Caucasus contained many species of mollusks that live there to this day [Steklov, 1966].

I would suppose, it was some genetic failure in the gene of the ancestral species, controlling the peculiarity of shell coiling in the embryogenesis.

In general, the origin of new taxa among pulmonate snails as a result of mutations is not so rare phenomenon: the most glaring example – mutations in the direction of whorls coiling. Thus, the Central Asian species *Fruticicola sinistrorsa* Tzvetkov, 1938 (Bradybaenidae) with sinistral shell originated undoubtedly from dextral *Fruticicola lantzi* (Lindholm, 1927); several species of left-coiled Enidae have right-coiled analogues. A large family Clausiliidae consists predominantly of sinistral species. It is necessary to note in this connection that the intermediate forms between sinistral and dextral shells can not exist, and if the mutation on this character is viable, it could create a new species, which begins to evolve independently from ancestral species.

Of course, these examples can not be compared with the case of *Cochlopupa*, they show only that a single mutation can lead to the formation of a new species.

The theoretical possibility of instantaneous appearance of a new species by mutations (without speaking about chirality) is currently being seriously questioned. In particular, Mayr [1963] gives the detailed lists of reasons why such a path of appearance of new species is highly unlikely. Drs Elizabeth Haring and Helmut Sattmann (pers. com.) believe that, if adopt my hypothesis, I have to assume (1) the presence of strong selective advantages to explain why this new variant would has spread so fast; I must also (2) postulate that along with the morphological transformations this new variant automatically became reproductively isolated from "mother species"; this would mean that already the F1 is produced due to self-fertilization. At last, in this case I have to admit (3) that the new variant must immediately find another ecological niche or, if the same niche used by "mother species", compete with and on the long run to replace the original form.

These are serious objections and I will try to answer them.

(1). A species needs the selective advantages when strong competition exists. But competition arises if there is a subject for competition, i.e. some limiting factor (space, food, sexual partner etc.). There are many examples when closely related species live together. Moreover, the fact of coexistence (under the same stone, in the same rock-slide etc.) of two related species often serves as one of important criteria for their specific independence.

(2). *Cochlopupa* (if we adopt my hypothesis) is reproductively isolated from any other helicids because of purely mechanical reasons. As concerns the mode of reproduction (of course, a single specimen can reproduce only by self-fertilization or parthenogenesis), then theoretically it is possible that a mutation could appear in more than one individual in one clutch. So, Clauss [1965] found near Quedlinburg 4 sinistral shells of *Chondrula tridens* (Müller,

1774) (1 shell found in 1960, 3 in 1961 and 1962 years). However, it is unknown, whether these 4 individuals appeared independently, or they are descendants of one sinistral individual that emerged as a result of self-fertilization.

(3). Problem of ecological niche is connected with (1), and competition for it not always inevitable.

I admit that the starting point for the process of mutation *might be* an alpine form of, for example, *Arianta arbustorum* (Linnaeus, 1758). Note in passing that the genus *Arianta* is known from the Upper Miocene (Sarmat) of Europe (about 10 million years ago) [Zilch, 1960], i.e. history of the genus has at least 10 million years.

By the way, the total absence of *Cochlopupa obtusa* in the real fossil deposits may be indirect evidence in favor of my hypothesis – the geological history of the species is too short and *Cochlopupa* is unknown in the sediments not because it was not found, but because it is absent there. Many centuries ago Chinese philosopher Confucius said that it is difficult to find a black cat in a dark room, especially when there is none there – this is, in my opinion, exactly the same case.

It is necessary to mention that Frank [2006] indicates 14 sites with "fossil" *Cochlopupa*, but the most ancient findings she dates by "prepleistocene" age. Even if the age of *Cochlopupa* is "prepleistocene", it does not change the situation fundamentally, just age of *Cochlopupa* shifted to some of the previous interglacials. In this case, the species could persist in refugia (although no clear data from refugia), although I doubt it: what is refugium? – It is a place where one can survive an unfavorable period. But in order to exist there for a long time, it is necessary that this refugium has acceptable conditions for feeding and reproduction during many generations. It is hard to imagine such a place among or very close to the eternal ice. Adensamer [1939] writes that the *Cochlopupa* area is a relic. The relevant question – a relic of what epoch?

It should be added that some other recent species of molluscs in the Eastern Alps (*Cochlicopa lubrica*, *Vitrina pellucida*, *Trochulus oreinos* and some others) have been found in a fossil state [Frank, 2006], although, in fact they are found sooner in subfossil state – in the Quarternary sediments. At the same time it should be taken into consideration, that we do not know the rate of destruction of the *Cochlopupa* shells, and it is often impossible, without using of special methods of analysis, to establish the real age of an empty shell – five years, a few tens or hundreds of years. In this regard, it is essential that *C. obtusa* lives on the black, heavily calcified soils, which contribute to the long preservation of shells after death of the animal.

4. Age of *Cochlopupa*

The most objectionable and controversial question – when *Cochlopupa obtusa* has originated, i.e. age of the species.

Dr. Elisabeth Haring and co-workers came to the conclusion that age of *Cochlopupa* is much more than 10.000 (pers. com.). This estimation is based on the calculation of genetic distance ("molecular clock") between *Cochlopupa obtusa* and *Arianta arbustorum* which from the genetic point of view is the closest relative to *Cochlopupa*. It looks serious objection, but the method of molecular clock has some definite restrictions (as any other method), since it based on the assumption that the frequency of mutations in the given gene is more or less constant, so, the rate of evolution is constant as well. But actually it is not always true.

Criticism of the method of molecular clock is presented, in particular, by Cranston and Rannala [2005], which attempted to eliminate the contradictions between the paleontological data and the data obtained by the method of molecular clock. Unfortunately, in the case of *Cochlopupa*, we can use only the criterion of the molecular clock and cannot use paleontological data ("calibration procedure"). But this criterion in the absence of fossil material indicates just a genetic distance between *Cochlopupa* and *Arianta*, but speaks nothing about the absolute time passing since the moment of divergence. At the same time "… divergence time estimated from molecular data are often *far more ancient* [selected by me – A. Sch.] than those predicted from the paleontological record" [Hedges a. Kumar, 2003, cit. after Cranston a. Rannala, 2005: 461], and further: "This discrepancy can be uncomfortably large, sometimes hundreds of million of years" (loc. cit.). Not being a geneticist, I can not judge the specific mechanisms of mutations and their fixing in subsequent generations, but I do not see any other explanation of full absence *Cochlopupa* in the fossil state.

Summing up, I would say that the molecular clock is good when there is no real clock. The role of "real clock" in the given case could be played by the fossil material, but we do not have it.

If *Cochlopupa* has old life history, it all the more should be found in ancient deposits. The longer history of a species, the more chances to find it among fossils, and the more chances to discover some intermediate forms. I would like to underline once more, that either *Cochlopupa obtusa* or any similar shells have never been found in fossil state.

Thus, there is only one principal contradiction in the evaluation of the age of *Cochlopupa* between the proposed hypothesis and the genetic data: set of arguments listed here indicates that age of *Cochlop-*

upa does not exceed 12 thousands of years, whereas the method of molecular clock shows much greater age (see above). I am incline to think, that the reason for this contradiction is rooted in the fact that the method of molecular clock has some limitations, since the assumption of the ancient age is not consistent with the facts presented above.

Another controversial aspect - it is not clear, what means “ancient” – hundreds of thousands, millions or tens of millions of years.

There is one more indirect argument in favor of the hypothesis of recent, mutagenic, i.e., virtually instantaneous, origin of *Cochlopupa obtusa*: in three the easternmost populations (or groups of populations) the phenomenon of anatomical polymorphism has been established [Schileyko, 1996; Schileyko et al., 1997]. The polymorphism is that, the one or both of the mucous glands in different individuals more or less reduced. This might reflect the genetic instability that is often characteristic for historically young species and we can observe very high variability in the phylogenetically young groups (some South American Bulimulidae, especially Galapagos *Naesiotus*; Central Asian Enidae and Bradybaenidae; Northeast-Mediterranean clausiliids *Albinaria*; xerophilic Mediterranean Hygromiidae etc.).

5. **Phenomenon of *Cochlopupa***

For completeness, let us see whether there are other examples of the occurrence of high-spired shells in the groups of Stylommatophora with helicoid shells of about same size as *Cochlopupa*. Indeed, in the family Camaenidae in Southeast Asia there are two small genera: *Giardia* (2-3 sp. in Thailand and Vietnam), and *Pseudopartula* (2-3 sp. in Indonesia) with bullet-shaped shell, but in the fossil state they are not known. Family Bradybaenidae includes a group of genera (*Pseudobuliminus*, 6-7 sp.; *Rudens*, 1 sp.; *Secusana*, 1-3 sp.; *Stenogyropsis*, 1 sp.; *Buliminidius*, 3-4 sp.) whose shells vary from high-turbinate or low-conical to high-conical or even tower-shaped. All of them live in China (incl. Taiwan), and none of them is known in fossil state. However, in these cases there is no compelling evidence to suggest mutagenic origin, since among these taxa we find intermediate forms – from low-conical to very high-conical.

Thus, the case of *Cochlopupa obtusa* looks like a somewhat unique phenomenon.

I would like to emphasize once more that some points of this text are polemical or speculative, and I will be grateful for any criticism.

Conclusion

1. During post-Würmian warming of climate the populations of cold-loving species *Cochlopupa obtusa* which lived in the valleys of the Alps, got in adverse conditions and become extinct; with further warming of climate, the lace of *Cochlopupa* area was gradually becoming more and more sparse because of the extinction of populations which inhabited the lower parts of slopes. As a result the area of *Cochlopupa* has got a modern appearance.
2. *Cochlopupa obtusa* or its hypothetical ancestor did not migrate from adjacent regions but originated on the territory of Eastern Alps, where it lives now.
3. Origin of *Cochlopupa* is a result of genetical mutation of some representative of Ariantinae, most probably (but not necessary), *Arianta arbustorum*.
4. *Cochlopupa obtusa* appeared at the end of Würmian glaciation, i.e. about 10-12 thousand years ago.

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О происхождении *Cochlopupa* (= *Cylindrus* auct.) *obtusa* (Gastropoda, Pulmonata, Helicidae)

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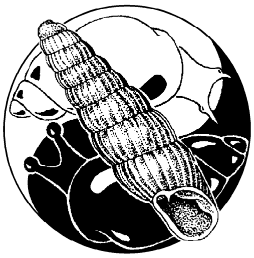
РЕФЕРАТ. Наземный моллюск *Cochlopupa obtusa* (Draparnaud, 1805) – эндемик восточных Альп, имеющий весьма своеобразную раковину и типичное для Ariantinae (Helicidae) строение репродуктивного тракта. Ни сам этот вид, ни какие бы то ни было похожие формы в ископаемом состоянии не обнаружены (наиболее ранние находки *C. obtusa* условно датируются «пре-плейстоценом»). Неизвестны также и формы, которые могли бы заполнить «зияние» между пупиллоидной раковиной *C. obtusa* и шаровидными или уплощенными раковинами, свойственными членам семейства Helicidae в целом и подсемейства Ariantinae в частности. В соответствии с предложенной гипотезой, *C. obtusa* сформировался на территории современного ареала в конце вюрмского оледенения (10-12 тысяч лет тому назад) путём мутаций какого-то представителя Ariantinae.



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