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Taxonomy of Anguispira (?) marmorensis (H. B. BAKER, 1932) with notes on the taxonomy of the genera Anguispira Morse and Discus FITZINGER (Gastropoda, Endodontidae)

Stanowisko systematyczne Anguispira (?) marmorensis (H. B. BAKER, 1932) i uwagi o taksonomii rodzajów Anguispira Morse i Discus FITZINGER (Gastropoda, Endodontidae)

Систематическое положение Anguispira (?) marmorensis (H. B. BAKER, 1932) и заметки о таксономии родов Anguispira Morse и Discus Fitzinger (Gastropoda, Endodontidae)

[19 text-figures and 1 table]

Anguispira (?) marmorensis (H. B. Baker, 1932)
Discus (Gonyodiscus) marmorensis H. B. Baker, 1932, Nautilus, 45: 84, pl. 5, figs. 1—3.

This species was described by Baker from the mountains of the Idaho Co., Idaho, USA (900 metres elevation, approx. 116°20' W long., 45°35' N lat.). The writer gave a thorough description and excellent drawings of the shell, but did not go into details of the inner morphology of that animal. He mentioned only that the penial retractor joins the columellar muscle. While studying the palearctic species of *Discus* Fitz. I have found some inaccuracies in the papers of H.B. Baker, and so I decided to check his data as to the species in question.

Material. USA, Idaho, Idaho Co., 2,7 miles up John Day Creek, near Lucille, elevation 2800 ft., April 22, 1960, M. L. Walton & A. Solem leg. 5 specimens in alcohol. This material was donated by Dr. Alan Solem (Chicago) to the Zoological Institute, Polish Academy of Science, Warsaw, and is kept there.

Shell. The diameter major varies from 6,7 to 8,1 mm, the height from 3,7 to 4,7 mm respectively, the number of whorls from $5\frac{1}{2}$ to 6. The drawings and description given by BAKER (1932) form a full and thorough picture of the

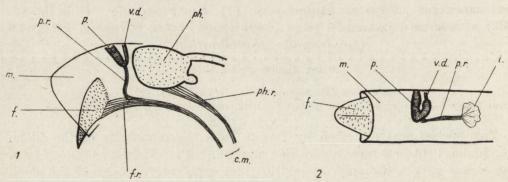


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shell morphology of this species. Yet I have to disagree with the opinion of BAKER: "It does resemble considerably, both in shell and soft parts, the palearctic D. perspectivus (MÜHLF.)...". In my opinion the shell bears only a slight resemblance to those of the European species of the subgenus Gonyodiscus FITZ. It is rather similar to the high shells of Discus (Discus) ruderatus pauper (GOULD). Substantial differences in the anatomy of these animals make me believe it to be just a convergency, which is a phenomenon frequently found in land snails.

It should be stressed that the shell of A. (?) marmorensis (H. B. BAKER) resembles closely that of Anguispira nimapuna H. B. BAKER. The shape of the shell, the aperture, the sculpture of the shell-surface and the geographical distribution (both species inhabit the mountainous regions of Idaho) suggest the possibility of closer relationship of these species. Anguispira (?) marmorensis (H. B. B.) differs from the other species of Anguispira Morse in being much smaller. On the other hand there are numerous examples of closely related snail-species differing greatly in size. The species most similar in its dimensions would be the little known Anguispira clarki Vanatta, 1924.

In spite of these similarities the shell of Anguispira (?) marmorensis (H.B.B.) is very characteristic and distinct in form and sculpture from the shells of all other Endodontidae.

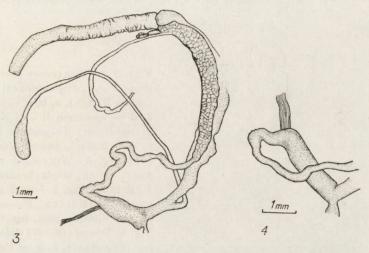


Figs. 1, 2. Diagrams showing the position of the penial retractor. Fig. 1. Anguispira (?) marmorensis (H. B. Baker), anterior part of the body, underside view. Fig. 2. Discus (Gonyodiscus) rotundatus (Müller), anterior part of the body, lateral view. C.m. — columellar muscle, f. — foot, f.r. — foot retractor, i. — ingrowth of the penial retractor into the diaphragm, m. — mantle, p. — penis, ph. — pharynx, ph.r. — pharyngeal retractor, p.r. — penial retractor, v.d. — vas deferens.

Genitalia. As it was stated by Baker, the penial retractor is connected with the foot retractor of the columellar muscle. This character is of a serious taxonomical value. Baker regarded it as a characteristic feature of the subgenus Gonyodiscus Fitz. Studies of Forcart (1957) and my own (Umiński, 1962) proved, however, that in no species of the subgenus Gonyodiscus Fitz. this sort of connection exists. The penial retractor joins instead the diaphragm at the left (outer) side of the body by means of a flabelliform ingrowth [Fig. 2].

Otherwise it is well known (PILSBRY, 1948) that in the genus Anguispira Morse the penial retractor joins the columellar muscle. This would strongly imply that the species in question belongs to the genus Anguispira Morse.

The penis is highly peculiar in form, different from that of the species both of the subgenera *Discus* s. str. and *Gonyodiscus* Fitz. Its shape diverges also markedly from that found in the other species of *Anguispira* Morse. The proximal part of penis (from genital atrium to the insertion of the penial retractor) is strongly thickened. The distal part, i. e. placed distally from the



Figs. 3, 4. Anguispira (?) marmorensis (H. B. Baker), USA, Idaho, Idaho Co., 1960, leg. M. L. Walton & A. Solem. Fig. 3. Genitalia, specimen No. 3. Fig. 4. Penis, specimen No. 2.

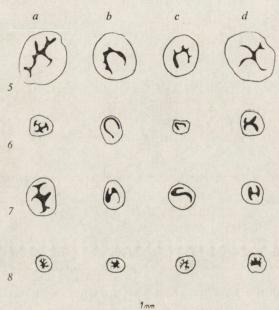
insertion of the penial retractor, is much thinner than the proximal part. It narrows gradually into the vas deferens without any marked boundary between them. This part could be called epiphallus. It resembles most that of Anguispira kochi (Pfeiffer) (Pilsbry, 1948, Fig. 304 E). In spite of the fact that in A. (?) marmorensis (H. B. B.) the transition between penis and epiphallus is continuous, while in A. kochi (Pfeiffer) these parts are separated by a distinct contraction the general similarity of these two species is evident.

Transverse sections of the penis show that its inner structure is fairly variable. Arrangement of the inner folds shows a high degree of individual variability. It is different in different parts of the penis and surely it does depend upon the degree of contraction of the animal. In this respect only *Discus* (*Discus*) ruderatus (FÉRUSSAC)² [Fig. 8] has a clearly distinct position. The characteristic arrangement of little, numerous folds with a comparatively big

¹ The terms "proximal" and "distal", in the case of the genital organs, are related to the genital orifice in the epidermis, taken as the base of orientation. The parts of the organs, situated nearer to the genital orifice are characterized as proximal, those situated more distantly as distal.

² See page 11.

lumen in the middle is entirely different both from that in the subgenus Gonyo discus FITZ. and in A. (?) marmorensis (H.B.B.). The two species of Gonyodiscus FITZ. exhibit a great similarity to one another and a visible resemblance to A. (?) marmorensis (H.B.B.). This is easily seen when Figs. 5 a and 7 a and the Figs. 5 b, c, d and 6 b, c, d are compared. These observations show that A. (?) marmorensis (H.B.B.) is probably much more closely related to the subgenus Gonyodiscus FITZ. than to Discus s. str. Curiously enough, I have not seen the arrangement of folds, considered by PILSBRY (1948) to be characteristic for Anguispira Morrow, in A. (?) marmorensis (H.B.B.), but I found



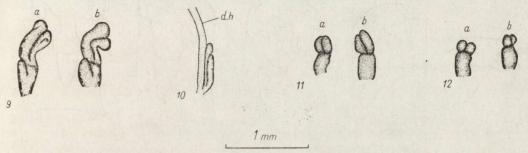
Figs. 5-8. Transverse sections of the penis. Fig. 5. Anguispira (?) marmorensis (H. B. BAKER), a, b, c — specimen No. 3, d — specimen No. 4. Fig. 6. Discus (Gonyodiscus) perspectivus (MÜHLFELD), a, c - Poland, Sudety Mts., Bardo Śl., 1956, leg. A. WIKTOR, b, d - Poland, distr. Sanok, Międzybrodzie, 1956, leg. A. Riedel. Fig. 7. Discus (Gonyodiscus) rotundatus (MÜLLER), Poland, Kazimierz on the Vistula, 1961, leg. C. DZIADOSZ. Fig. 8. Discus (Discus) ruderatus ruderatus (FÉRUSSAC), a, b — Poland, Tatra Mts., 1932, leg. A. Jankowski, c, d -Poland, distr. Grójec, Konary, 1919, leg. W. Roszkowski.

it, and very typical in D. (G.) rotundatus (MÜLL.) [Fig. 7 b, c]. I presume that in all the species of Anguispira Morse the variability of the inner structure of the penis is much greater than it was stated by Pilsbry (1948), and that it is much more like that of Discus Fitz. Unfortunately, the lack of alcohol material of Anguispira Morse prevents me from stating it decisively.

The prostata (the masculine part of the spermoviduct) is entirely unlike that of *Discus* s. str. It is built of folds, arranged similarly as in *Gonyodiscus* Fitz., but the folds are smaller and more numerous, and the general shape of the prostata is different. It is of the shape of a very elongated rectangle. In the general shape, as well as in the arrangement of folds the prostata of A. (?) marmorensis (H.B.B.) resembles clearly that of other species of Anguispira Morse.

Attention should be paid also to the vesicula seminalis (= talon, PILSBRY, 1948), one of the other structures of a taxonomical value. In the genus Discus FITZ. it consists of one proximal vesicle and two distal ones, opening into

it. In the subgenus Discus s. str. [Fig. 10] the distal vesicles are elongated, thin and tightly adhering to each other, while the basal vesicle is very small. All these structures become discernible only when mounted in canada balsam or Faure's medium. Hence probably the erroneous statement of PILSBRY (1948) that in Discus FITZ. "... the talon is simple, clubshaped....". In Gonyodiscus FITZ. [Figs. 11, 12] the basal vesicle is comparatively big, and the distal ones rather thick. The whole vesicula seminalis is covered by a thick layer of black pigmented fibrillae. In Anguispira (?) marmorensis (H.B.B.) [Fig. 9] the proportions of vesicula seminalis are similar to those of Gonyodiscus FITZ. In both groups the vesicula seminalis is similarly overlaid with the pigmented fibrillae. This would constitute a serious difference between A. (?) marmorensis (H.B.B.) and other species of Anguispira Morse, provided that the information of PILSBRY



Figs. 9-12. Vesicula seminalis. Fig. 9. Anguispira (?) marmorensis (H. B. Baker), a—specimen No. 3, b—specimen No. 4. Fig. 10. Discus (Discus) ruderatus ruderatus (Férussac), Poland, Tatra Mts., 1951, leg. A. Riedel. Fig. 11. Discus (Gonyodiscus) perspectivus (Mühlfeld), a—Poland, Sudety Mts., Bardo Śl., 1956, leg A. Wiktor, b—Poland, distr. Sanok, Międzybrodzie, 1956, leg. A.Riedel. Fig. 12. Discus (Gonyodiscus) rotundatus (Müller), Poland, Kazimierz on the Vistula, 1961, leg. C. Dziadosz. d. h.—ductus hermaphroditicus.

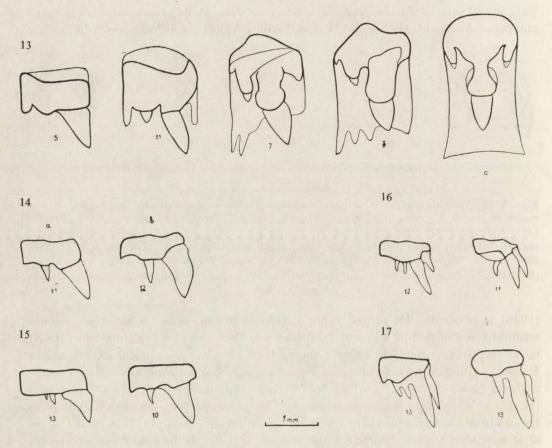
(1948) is accurate. He stated namely that in Anguispira Morse the vesicula seminalis is trifid, but did not mention, whether the observations were based on cross sections, canada balsam mounts, or simply on external examination. I know from my own experience that the external outlook of vesicula seminalis in these animals in often misleading. In the same A. (?) marmorensis (H.B.B.) the vesicula seminalis when examined externally looks as though it were tripartite or even five fold [Fig. 3]. It is only in the microscopic slide, that the real structure is visible. Moreover the furrows which can be found sometimes on the surface of the vesicles are filled with pigmented fibrillae. The presence of these furrows makes the interpretation of that structure very difficult, even in the case, when the organ is examined microscopically.

Besides, in A. (?) marmorensis (H.B.B.) the basal vesicle is elongated and the distal vesicles open not on the top of it but on one side, and approximately at half its length. With some reservations this structure could be described as tripartite also.

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Probably the vesicula seminalis of the species in question forms either a transition between the genus Anguispira Morse and the subgenus Gonyodiscus FITZ., or in the other species of Anguispira Morse it is of the same type as in A. (?) marmorensis (H.B.B.) and the different descriptions are due to different methods of examination.

Radula. Within the family *Endodontidae* the radula bears little taxonomical importance, since it displays only a small variability. While the differences in the form and number of the radula teeth between different species are barely noticeable the range of individual variation within one species is relati



Figs. 13-17. Radula. Fig. 13. Anguispira (?) marmorensis (H. B. Baker), specimen No. 4. Fig. 14. Discus (Discus) ruderatus ruderatus (Férussac), a — Poland, Tatra Mts., 1951, leg. A. Riedel, b — USSR, Armenia, distr. Stepanavan, Gerger, 1951, leg. N.N. Akramovski. Fig. 15. Discus (Discus) ruderatus pauper (Gould), South Kuril Is., Sikotan, 1948, leg. Strelkov. Fig. 16. Discus (Gonyodiscus) perspectivus (Mühlfeld), Poland, distr. Sanok, Wujskie, 1954, leg. A. Riedel. Fig. 17. Discus (Gonyodiscus) rotundatus (Müller), Poland, Szczecin, 1956, leg. A. Riedel, both teeth from the same specimen, from different rows. c — central tooth, numerals indicate the position of the tooth in the radula.

vely big. This refers to the shape of the teeth as well as to their number and the delimitation of lateral and marginal teeth. Usually no sharp boundary between the laterals and marginals can be drawn because there are several intermediate teeth of transitional character. This makes it difficult to give the exact number of lateral or marginal teeth. It is hard, therefore, to draw any definite conclusions as to the taxonomical position of A. (?) marmorensis (H.B.B.) on the basis of the radula. Nevertheless the comparison with the radulae of the genus Discus FITZ. gives interesting suggestions.

Table 1

Numbers of the radula teeth

Species	Lateral teeth	Marginal teeth	Total (lateral and marginal teeth)
Anguispira (?) marmorensis (H. B. Baker)	9	9 - 11	18 - 20
Discus (Discus) ruderatus ruderatus (Férussac)	8 - 9	9 - 10	17 - 19
Discus (Discus) ruderatus pauper (Gould)	7 - 8	8 - 10	15 - 17
Discus (Gonyodiscus) perspectivus (Megerle VON MÜHLFELD)	5 - 7	7 - 10	12 - 16
Discus (Gonyodiscus) rotundatus (Müller)	5 - 7	11 - 13	16 - 19

In D. (G.) rotundatus (MÜLLER) the lateral and marginal teeth can be discerned from each other easily, in D. (G.) perspectivus (MÜHLFELD) fairly easily. In the remaining species such a distinction is difficult to be made.

The radula teeth of A. (?) marmorensis (H.B.B.) are bigger than those of the species of the genus Discus Fitz. The number of teeth and the ratio between the number of laterals and marginals separate the species in question from those of the subgenus Gonyodiscus Fitz. [table 1]. It is the subgenus Discus s. str. which is much more similar in this respect.

The central and lateral teeth are the least variable, the differences between them being hardly visible and extremely difficult to define. On the other hand the marginal teeth display a wider range of variation [Figs. 13–17]. Here again a remarkable difference from *Gonyodiscus* FITZ. and a slight resemblance to *Discus* s. str. is to be noted. It should be stressed that all teeth of the radula of A. (?) marmorensis (H.B.B.) are very similar to those of Anguispira alternata (SAY) (PILSBRY, 1948, Fig. 304).

Generally speaking the radula of Anguispira (?) marmorensis (H.B.B.) gives the evidence that this species belongs to the genus Anguispira Morse and

proves its distinctness from the subgenus *Gonyodiscus* Fitz. It bears also some similarity to that in the subgenus *Discus* s. str., which is probably the result of a convergence.

Taxonomy. I was able to compare A. (?) marmorensis (H.B.B.) only with the species of the genus Discus FITZ. Because of the lack of alcohol material of the genus Anguispira Morse any comparison with the other species of that genus was based on the data from literature.

I presume, that, taking into account the anatomy of the genital organs and to some extent the shape of the shell, the species in question can not be included into the genus Discus FITZ. Similarities in the form of penis and vesicula seminalis suggest some relationship with the subgenus Gonyodiscus FITZ. On the other hand, the form of all the mentioned organs as well as of the radula, come nearest to that of the genus Anguispira Morse. A. (?) marmorensis (H.B.B.) takes a rather isolated position between the two genera involved. Of all the species of Anguispira Morse the Anguispira nimapuna H. B. Baker seems to be most closely related to A. (?) marmorensis (H.B.B.). Possibly Anguispira elarki Vanatta could be taken also into account.

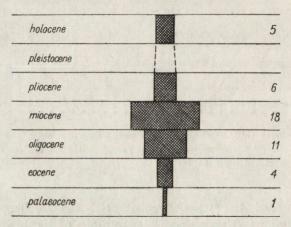


Fig. 18. Number of tertiary and recent forms of the genus Discus Fitzinger in the Palearctic realm. Based on the data of Wenz (1923).

The subfamily Endodontinae (= Discinae auct.) probably separated and evolved in the western hemisphere as it is indicated by a greater amount and variety of its representatives in the North and Central America and in the islands of Pacific. The Eurasian area was occupied by this subfamily later. During the Tertiary numerous species of Discus Fitz. lived in the Palearctic from palaeocene on, reaching maximum in miocene (see Wenz, 1923 and Fig. 18). The recent species should be regarded as a small remnant of the former number, especially as not all the extinct species are known at present.

Out of the recent forms the species of the subgenus Gonyodiscus Fitz. have much smaller distribution areas and their morphology is less variable, as it is

observed in relicts. In *Discus* (G.) perspectivus (MÜHLF.) the individual variability is smallest and its distribution area is also the smallest one. *Discus* (G.) rotundatus (MÜLL.) displays a wider range of variation and its distribution area is bigger.

The subgenus *Discus* s. str. inhabits a vast territory, covering the whole of the Holarctic. In this subgenus a great variability of form, both in the shell and in the anatomy can be observed. The various forms of *Discus* (*D.*) ruderatus pauper (Gould) (Umiński, 1962) or the numerous species and subspecies of *Discus* s. str. from North America may serve as a good example. Hence the conclusion that probably *Discus* s. str. is a young and evolving group. Its subspecies

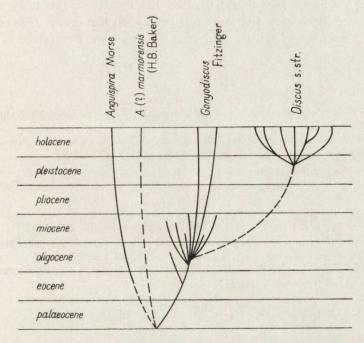


Fig. 19. A phylogenetic tree of the genera Anguispira Morse and Discus Fitzinger.

cies are to be regarded as species in statu nascendi. The subgenus Gonyodiscus FITZ. is a phylogenetic older group which has passed its maximum of development and is now on the decline. As the genus Anguispira Morse was reported from the lower eocene of North America (ZILCH, 1959) it is perhaps of the same age as the subgenus Gonyodiscus FITZ.

It seems that Anguispira (?) marmorensis (H.B.BAKER) is an old species, being either a descendant of the common ancestral stock of both genera Anguispira Morse and Discus Fitzinger or a descendant of forms, that stood very near to that common stock. After, or about the time of formation of A. (?) marmorensis (H.B.B.) this common stock was split in two. One of them evol-

ved into the genus Anguispira Morse while the other gave rise to the numerous species of the subgenus Gonyodiscus Fitz. (of which only two survived until recent times). Out of one of these extinct species the subgenus Discus s. str. must have evolved, occupying later the whole Holarctic and starting to differentiate rapidly.

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It can be concluded that the species in question should be included into the genus Anguispira Morse as Anguispira (?) marmorensis (H.B. Baker). It should be understood, however, that its taxonomical position within this genus is not yet clear and needs further studies. Most probably it is an old species, relating the genus Anguispira Morse with the genus Discus Fitzinger or, strictly speaking, with the subgenus Gonyodiscus Fitzinger.

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STRESZCZENIE

Autor stwierdza na podstawie badań anatomicznych, że gatunek opisywany pod nazwą Discus (Gonyodiscus) marmorensis H. B. Baker należy zaliczyć do rodzaju Anguispira Morse. Gatunek ten jest jednak spokrewniony z rodzajem Discus Fitzinger, podrodzajem Gonyodiscus Fitzinger. Należy sądzić, że Anguispira (?) marmorensis (H.B. Baker) jest gatunkiem starym, wywodzącym się od wspólnych przodków rodzajów Anguispira Morse i Discus Fitz. i stąd stanowi niejako ogniwo pośrednie między nimi. W rodzaju Discus Fitz. podrodzaj Gonyodiscus Fitz. jest grupą filogenetycznie starszą, dziś bardzo już nieliczną i morfologicznie stabilną, zaś podrodzaj Discus s. str. jest grupą młodą i rozwijającą się.

РЕЗЮМЕ

Автор устанавливает на основании анатомических исследований, что описанного под названием Discus (Gonyodiscus) marmorensis Н.В. Вакек моллюска следует зачислить к роду Anguispira Morse. Этот моллюск родственный однако с родом Discus Fitz., подродом Gonyodiscus Fitz. Следует полагать, что Anguispira (?) marmorensis (H.B.B.) является старым видом происходящим от общих предков родов Anguispira Morse и Discus Fitz. и отсюда составляет как будто промежуточное звено между ними. В роде Discus Fitz. подрод Gonyodiscus Fitz. это группа филогенетически более старая, сейчас уже очень немногочисленная и морфологически стабильная, а подрод Discus s. str. является молодой и развивающейся группой.

Note: In my previous paper (UMIŃSKI, 1962) Discus ruderatus HARTMANN, 1821 was erroneously regarded as the valid name. According to Opinion 335 of the International Comission on Zoological Nomenclature, issued 17th March, 1955 the name placed on the Official list of Specific Names in Zoology is Discus ruderatus Férussac 1821, Tabl. syst. Anim. Moll., p. 44.

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