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EVIDENCE FOR THE OCCURRENCE OF A "SKINNY" OR "MINUTE STAGE" IN THE ONTOGENETICAL DEVELOPMENT OF MIOCENE *VAGINELLA* (GASTROPODA, EUTHECOSOMATA) FROM THE NORTH SEA AND AQUITAINE BASINS

by

A. W. Janssen
Rijksmuseum van Geologie en Mineralogie, Leiden

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Well-preserved material of *Vaginella austriaca* Kittl, 1886 from the Middle Miocene of Winterswijk-Miste (The Netherlands) and *Vaginella depressa* Daudin, 1800 from the Burdigalian of Martillac (Aquitaine Basin, France) demonstrates that juvenile specimens of both species have a very flexible shell with an elliptical cross-section. In adult specimens the shell is more solid with an almost circular cross-section. Full-grown shells have lateral wrinkles at the base of the post-embryonic shell.

It is supposed that the transformation from a shell with an elliptical cross-section to an almost circular shell is caused by quickly developing soft parts executing a pressure power on the ventral and dorsal shell-walls. Tensions in the quite flexible shell material lead to the origin of wrinkles during deformation of the shell.

This mechanism strongly points to the occurrence of a "skinny" or "minute stage" in the ontogenetical development of *Vaginella*.

A. W. Janssen, Rijksmuseum van Geologie en Mineralogie, Hooglandse Kerkgracht 17, 2312 HS Leiden, The Netherlands.

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> *"Die Pteropoden sind überall zu unbedeutend."*
> H. G. Bronn: Italiens Tertiär-Gebilde
> (1831, p. 173).

SAMENVATTING

Aanwijzingen voor het bestaan van een "skinny" of "minute stage" in de ontogenetische ontwikkeling van het miocene geslacht *Vaginella* (Gastropoda, Euthecosomata) in het Noordzeebekken en het Bekken van Aquitaine.

In het veelal fraai geconserveerde pteropodenmateriaal van Winterswijk-Miste, dat afkomstig is uit het inwendige van grotere gastropoden (uitgeklopt sediment), werd o.a. een zeer fragiele, breed driekantige, tamelijk platte vorm aangetroffen, waarvan aanvankelijk werd aangenomen dat het om een nog niet beschreven *Clio*-soort ging. Nader onderzoek van dit materiaal toonde echter een grote overeenstemming aan met het oudste schelpgedeelte van de soort *Vaginella austriaca* Kittl, die een identieke vorm en orientatie van de embryonale schelp vertoont. Aangenomen moet worden dat de *Clio*-achtige schelpjes de juveniele vormen zijn van *V. austriaca*. Omdat echter volwassen exemplaren van deze laatste soort een schelp hebben met bijna cirkelronde dwarsdoorsnede moeten de juveniele exemplaren in de loop van hun ontwikkeling een schelpdeformatie hebben ondergaan.

In de zomer van dit jaar werden in afzettingen van Burdigalien-ouderdom te Martillac ("Pas-de-Barreau") in het Franse Aquitaine Bekken prachtig bewaarde exemplaren gevonden van de soort *Vaginella depressa* Daudin, ook in uitgeklopt sediment. In dit materiaal werden voor het eerst exemplaren van deze soort aangetroffen die nog in het bezit zijn van de embryonale schelp. Ook werden juveniele exemplaren gevonden die een grote gelijkenis vertonen met de jonge schelpjes van *V. austriaca* uit Miste: een zeer breekbare, nog flexibele, breed driehoekige vorm met elliptische dwarsdoorsnede.

Om een schelpje met elliptische dwarsdoorsnede te vervormen tot bijna cirkelrond is een drukkracht nodig tussen de ventrale en dorsale schelpwand. Aangenomen wordt dat deze kracht werd uitgeoefend door zich snel ontwikkelende weke delen van het dier. Door de vervorming van de schelp ontstaan spanningen in de schelpwand, die resulteren in de aanwezigheid van kleine rimpels ter weerszijden van de basis bij volwassen exemplaren, een verschijnsel dat zowel bij *V. austriaca* als bij *V. depressa* aanwezig is.

Een dergelijk mechanisme vertoont grote overeenkomst met de door Van der Spoel (1967) uitvoerig beschreven "skinny" en/of "minute stage" tijdens de ontogenetische ontwikkeling van verscheidene recente pteropodensoorten.

INTRODUCTION

Vaginella is an extinct genus belonging to the family Cavoliniidae, a group of bilaterally symmetric gastropods with a pelagic way of life. Together with the sinistrally ("ultra dextrally") coiled Spiratellidae (= Limacinidae) they form the suborder Euthecosomata. All representatives of this suborder are shell-bearing species, contrary to the closely related Pseudothecosomata, in which only a small group of species has sinistrally coiled calcareous shells (e.g. genus *Peraclis*), that usually may be distinguished from the Spiratellidae by the presence of a distinct anterior rostrum and a reticulated surface ornamentation. In Spiratellidae such a rostrum is always absent and the outer surface of the shell is either smooth or very faintly striated.

Euthecosomata and Pseudothecosomata form the order Thecosomata. Together with another order, the Gymnosomata, Thecosomata are generally indicated as Pteropoda, after the very specialized morphology of the wing-shaped foot, enabling active vertical motion of these planktonic organisms. Such vertical movements apparently are highly important for the animals, as several recent species are found at greater water depths during day times, whereas they are present near the surface over night.

In the fossil record Euthecosomata are known from the Early Eocene (one species already from the latest Paleocene; Janssen & King, in press). In the recent fauna some thirty species of Euthecosomata are recognized (data from Van der Spoel, 1967), nine of which belong to the Spiratellidae, the others to the Cavoliniidae. On a world-wide scale the numbers of species known now are about as follows (data on fossil species mainly from Bernasconi & Robba, 1982):

Quaternary	30 species (incl. Recent)
Oligocene	20 species
Early Miocene	40 species
Middle Miocene	65 species
Late Miocene	15 species
Pliocene	15 species
Eocene	30 species

These numbers may be subject to some changes, as it is difficult to decide whether or not several fossil forms really belong to the Euthecosomata (e.g. the genera *Euchilotheca* and *Thecopsella*, the species *Creseis fuchsi* Kittl and others).

Fossil pteropods are to a high degree a neglected group of organisms. They have very fragile, thin-walled aragonitic shells not very suitable to be fossilized and very quickly dissoluted by decalcification, so in many cases the material has to be studied on internal or external casts. Furthermore their fragility requires special techniques of sampling and sample treatment. For all these reasons it may be expected that, apart from some restricted areas, the fossil record of the pteropods is not yet well-known and the number of species may be increased considerably by tenacious research.

Especially because of their planktonic way of life pteropods seem to be a very promising group of fossils in the field of biostratigraphy with encouraging possibilities, both on a local scale or interregional.

THE "REMARKABLE DEVELOPMENTAL STAGES" OF CAVOLINIIDAE

Van der Spoel (1967), in his important thesis on the Recent Euthecosomata, extensively described some quite peculiar developmental stages during the ontogeny of cavoliniid species. He distinguished between "normal" development and development including so-called "skinny", "minute" and "aberrant stages".

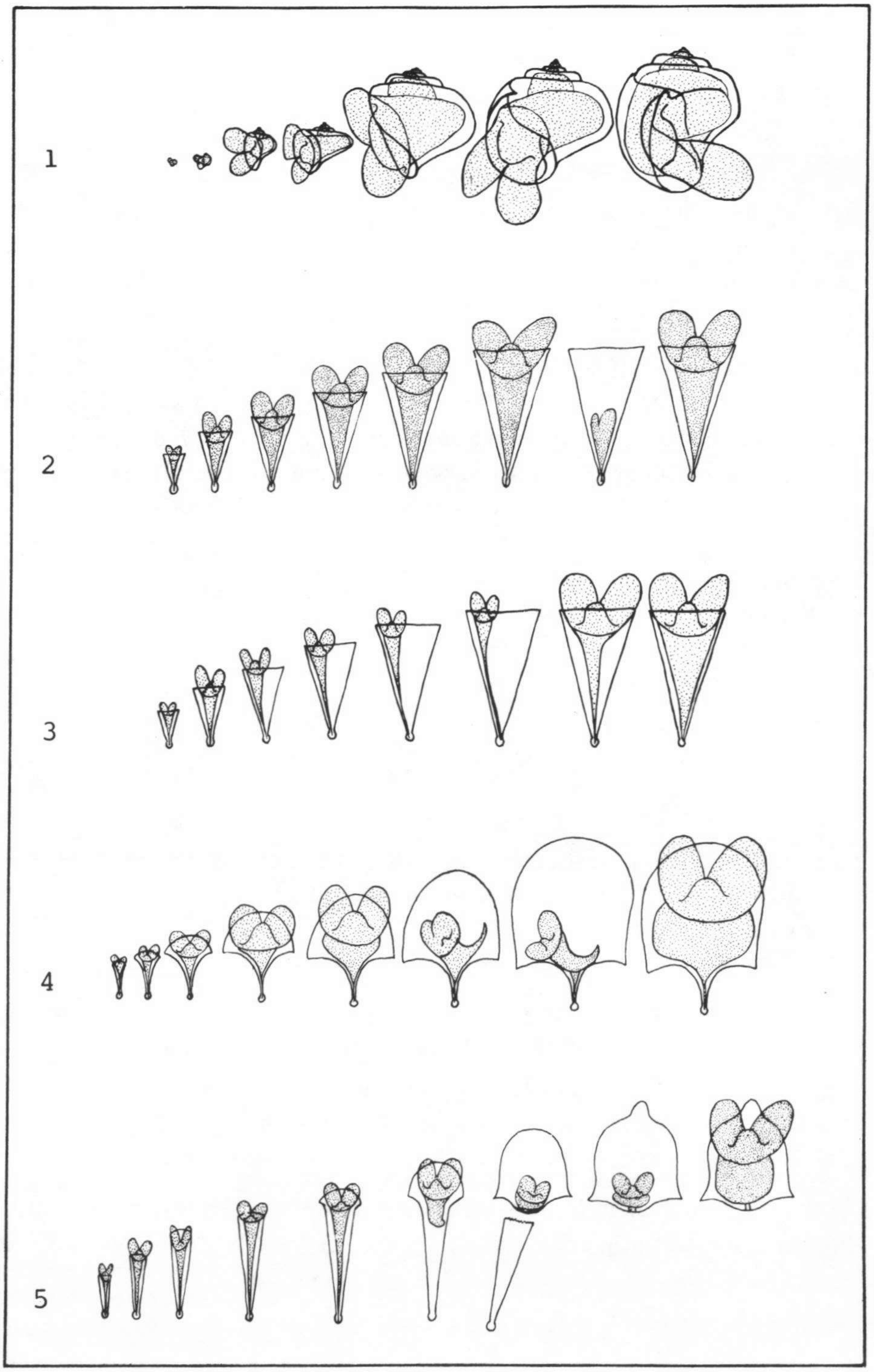


Fig. 1-5. Developmental stages in Euthecosomata.

1. Normal development in *Spiratella helicoides* (Jeffreys).
2. Development with aberrant stage in *Clio pyramidata* Linné.
3. Development with skinny stage in *Clio pyramidata* Linné.
4. Development with minute stage in *Cavolinia globulosa* (Gray).
5. Development with skinny stage and shell transformation in *Diacria quadridentata* (De Blainville).

All figures after van der Spoel (1967, p. 375).

In a "normal" development, occurring in all Spiratellidae and some Cavoliniidae, shell-size and body-size increase equally during ontogeny. This is also the case in species with an "aberrant stage" (only known from *Clio pyramidata* Linné), but after shell and animal have reached full-size a reduction of the soft parts occurs, resulting in the presence of a very small body in an adult shell (text-figures 1-2).

In a development including a "skinny stage" shell and animal start to grow to the same degree. Later on, however, the soft parts grow out to an extremely long and slender body, whereas the shell continues normal growth. Only after shell-growth is completed the soft parts start growing again and reach normal size and ratios. Skinny stages are known to occur in the genera *Creseis, Styliola, Hyalocylis, Clio, Cuvierina* and in one species of *Cavolinia* (compare text-figure 3).

Ontogenetic growth through a "minute stage" (text-figure 4) resembles the skinny stage, but here the soft parts remain strongly reduced in size (not elongated) during a normal continuation of shell-growth towards adult form. Some species with a minute stage in their ontogeny, e.g. *Cuvierina columnella* (Rang) and *Diacria quadridentata* (De Blainville), withdraw their soft parts from the embryonic shell during this stage and re-attach their columellar muscle at a higher position on the shell-wall, subsequently the juvenile shell (protoconch I and II) is thrown off when the soft parts start growing again (text-figure 5). *Cuvierina*, by the way, is a genus in which both minute and skinny stages occur (text-figure 6).

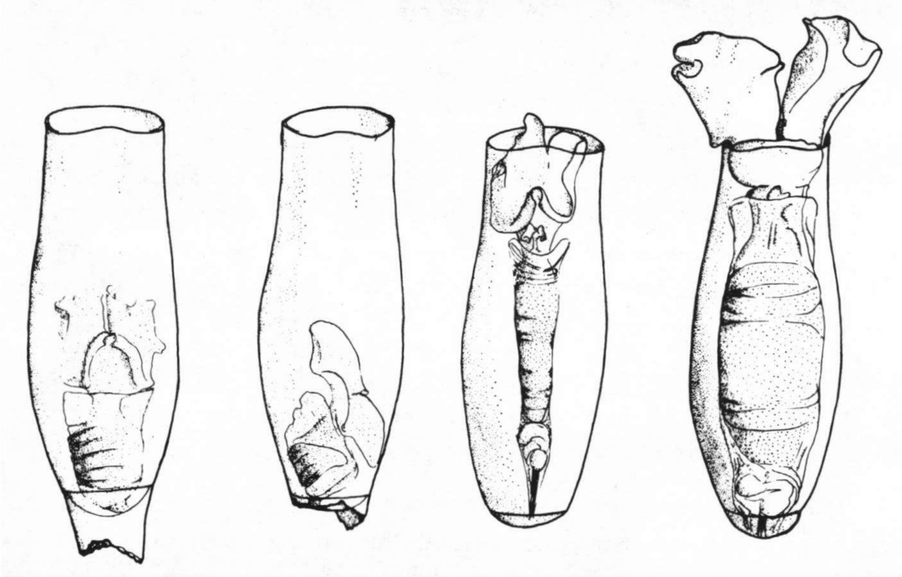


Fig. 6. Development with minute stage and skinny stage in *Cuvierina columnella* (Rang). After van der Spoel (1967, p. 331).

SHELL GROWTH DURING THE SKINNY AND MINUTE STAGES

An important question, of course, is how the animals in skinny or minute stage achieve a regularly continuing shell-growth, while their body is in a reduced stage and only in close contact with the shell-wall near the base of the shell. An animal in skinny stage should be able to reach the apertural margin of its shell, but as its diameter is considerably smaller than that of the shell it seems impossible that there could have been an overall contact between shell and body, which would have been necessary for a regular growth. Neither does it seem possible that the skinny animal succeeds in obtaining a regular shell growth by turning around in its shell. For animals in minute stage it seems even more impossible to reach the shell's margin, as their body is reduced to the basal part of the shell.

To solve the question of how shell growth takes place during skinny and minute stages van der Spoel evolved the following hypothesis. In Cavoliniidae the calcareous shell material is deposited on a non-mineralized conchiolin matrix, so the question of how shell growth takes place can be reduced to the growth of this matrix. This may take place in the basal part of the shell, after which the matrix shifts in an upward direction to beyond the solid shell parts. Calcareous matter may than precipitate onto the conchiolin matrix by some "physicochemical" process, according to the laws of crystallization.

Van der Spoel's theory, however, is very unlikely. For a juvenile pteropod in minute stage it seems possible that the ectoderm tissue covering the entire body is able to produce a conchiolin sheet at the inner side of the shell at those places where the body is in close contact with the shell-wall. Let us also imagine that this conchiolin sheet is capable to move in an upward direction. It is obvious, that by the increasing diameter of the shell very soon this matrix would loose contact with the inner shell-wall. Initially there may be some elasticity in the matrix matter but soon the necessity would arise to add more conchiolin to cover the increasing surface. And just that is impossible, because the animal can't reach the place where this has to be done. Therefore a continuing growth of the matrix to beyond the shell margin seems to be out of the question.

Furthermore, what physicochemical processes are capable of depositing calcareous matter on the outside of a matrix without the intervention of living tissue and still build a shell with characteristics that are determined by genetic laws? Most details of the adult shell must have been present in the matrix and therefore originate from the lower internal part of the shell, e.g. surface sculpture. In *Cuvierina*, for example, shell sculpture is only present on the external shell surface, not on the inside. So, if calcareous matter is deposited physicochemically on the conchiolin matrix it can only take its form and other details from the matrix on its inside, which apparently is unsculptured in *Cuvierina*.

Similar, but still more complicated considerations arise in the case of pteropods in skinny stage, where the animal even in its lowest parts does not cover the entire inner shell surface. Deposition of an upward shifting conchiolin matrix in "skinnies" is still more improbable.

Finally the resemblance between the macro-structure of the shell (with growth-lines, sculpture and all other details) in pteropods is so identical to that in other molluscs that it seems highly unlikely that pteropod shells do not originate through the same mechanism, i.e. the mantle tissue.

Biomineralization in pteropod shells was extensively studied for the species *Cuvierina columnella* by Bé, MacClintock & Currie (1972). They describe a unique aragonite micro-structure for this species, also recognized in other pteropods, consisting of an inner shell layer built up from dextrally coiled helical aragonite rods (diametre of the helices to about 28 μm). This helical micro-structure is unknown from any other mollusc group, which by the way lead these authors to the conclusion that pteropods are evolutionary neomorphs derived from non-shelled opisthobranch ancestors. Their relationship with the Pyramidellidae seems to be much less close than supposed up to then, as this latter gastropod family has shells of normal cross-lamellar structure.

Bé et al. (1972, p. 58) also deny the "matrix" theory of van der Spoel: "It seems likely to us that the mantle was extended to the shell margin during the 'minute' stage and that shell deposition was continuous from the 'juvenile' through the 'minute' stage. The mantle even may have been attached at the apertural area during the final time of 'juvenile' and phase-one growth. Bonnevie and Spoel doubt that any part of the 'minute' stage is capable of extending itself to the aperture of the shell. This is probably true for the main body, but it seems reasonable that the mantle of *living* pteropods could easily have extended to the aperture. In other molluscs the mantle is an extremely extendible organ in live animals. In preserved specimens soft, thin mantle tissues contract greatly. The only way to check mantle activities is to study living pteropods. With subsequent phase-two growth of the shell the animal passes from the 'minute' through the 'skinny' to the final 'adult' stage. It seems likely that in all these stages the mantle, in live animals, is fully extended over the whole inner surface of the shell."

Their supposition that the mantle tissue of the living animal covered the entire inside of the shell seems to be very acceptable as discussed above and the only real explanation for a continued shell-growth during minute and skinny stages.

Still, it appears to be a somewhat blunt and embarrassing supposition that van der Spoel's "matrix theory" was entirely the result of studying material preserved in alcohol or formaline in which the mantle tissue was strongly contracted. But indeed: the only way to check this is to study living pteropods. I have to leave this subject to the biologists.

SHELL TRANSFORMATION IN MIOCENE *VAGINELLA AUSTRIACA*

The very rich mollusc fauna of Winterswijk-Miste (Janssen, 1984c) yielded material of the cavoliniid pteropod species *Vaginella austriaca* Kittl, 1886 in large numbers, among which specimens in a magnificent state of preservation. Many full-grown shells are available (RGM-collection) with completely preserved embryonic shells. Most of this latter material, and also several other pteropod species (Janssen, 1984c, p. 381-384, pl. 20), were collected in sediment from the inside of larger gastropod shells. This apparently is a very sheltered environment, giving protection against both mechanical and chemical damages.

Among the pteropod material from Miste there were a few specimens of an extremely fragile, broadly triangular and flat form with an elliptical cross-section (text-figure 8) that initially was supposed to represent an undescribed *Clio*-species (Janssen & King, in press). Further study of this material, however, revealed that its embryonic shell is identical to that of *V. austriaca*, showing the same forward deflection with respect to the younger shell-parts as in that species. The post-embryonic shell has lateral carinae, but otherwise it differs strongly from *austriaca*. It is more compressed dorso-ventrally, with a much wider apical angle in front view and a smaller apical angle in a lateral view (text-figures 7-8). Lateral wrinkles, always present in the basal shell parts of *V. austriaca*, are absent in the *Clio*-like form. A further difference is found in the extremely thin, still quite flexible shell-wall, which is thicker and more solid in *V. austriaca*.

The conclusion is inevitable that the flexible shell is the juvenile form of *Vaginella austriaca*, as is convincingly demonstrated by the complete identity of the protoconchs. This leads us to some remarkable conclusions on the shell-growth of these creatures. The main question seems to be: how achieves the animal a transformation of a flat and triangular shell into an elongate shell with an almost circular cross-section? Supposing that the shell in the living animal was still more flexible than it is now as a fossil, there are two hypothetical possibilities (see text-figure 7):

A. Starting from a flexible shell with an elliptical cross-section and triangular form a shell with an almost circular cross-section and an elongate form may be obtained by a tractive power between the two extreme sides of the shell, or
B. the same may be achieved by a pressure force between the dorsal and ventral shell-walls.

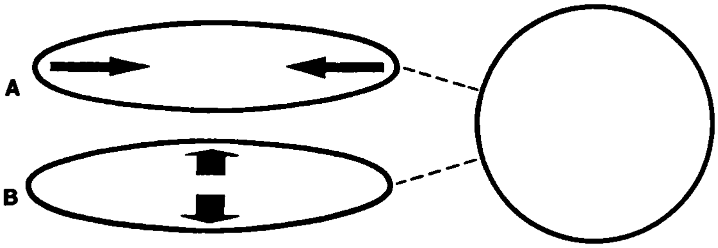


Fig. 7. (explanation see text).

A tractive power supposes the presence of a contractive muscle, but the only muscle of this kind that may be expected in pteropods is the columellar muscle, which in cavoliniids is attached to the shell-wall at one place only and serves to withdraw the soft parts into the shell.

A pushing power as illustrated in text-figure 7B cannot be executed by a muscle. It seems however fairly well possible that quickly developing soft parts are capable of such a pressure against both walls of the shell. Such a pressure could also account for the existence of the wrinkles present at both sides of the basal full-grown *Vaginella* shell. Apparently the power forcing the shell to fit its growing contents resulted in these wrinkles, leading to a decrease of tensions in the shell material. After this deformation has taken place the newly obtained shell form is consolidated by a renewed deposition of calcareous matter on the internal shell-wall, giving the shell more solidity (compare also text-figure 7 in Bé et al., 1972).

This second idea strongly points to the existence of a minute and/or skinny stage during the ontogeny of *Vaginella*. Obviously the juvenile pteropod shell developed gradually and regularly towards a certain'size, apparently without any pressure forces at the dorsal and ventral shell-walls (minute or skinny stage) and then suddenly the soft parts start growing at an accelerated speed, executing a pressure force on both ventral and dorsal shell-wall, resulting in a deformation of the shell (growth towards adult form). The resemblance with the developmental stages described for recent pteropods is very obvious.

Whether or not *Vaginella* retracted its soft parts, including the columellar muscle, from the oldest shell-parts is difficult to decide. Though many specimens found at Miste still possesses their embryonic shells this shell-part is extremely fragile and very easily broken off. No shells are known, however, in which the opening originating by a disconnection of the protoconch is closed secondarily by a calcareous septum, as e.g. in *Cuvierina* or *Diacria*.

VAGINELLA DEPRESSA

In the species *Vaginella depressa* Daudin, 1800, so commonly present in the Early Miocene deposits of the Aquitaine Basin in SW France, specimens still possessing their embryonic shell have never been mentioned in literature. Usually the base of the shell is described as "simply pointed"

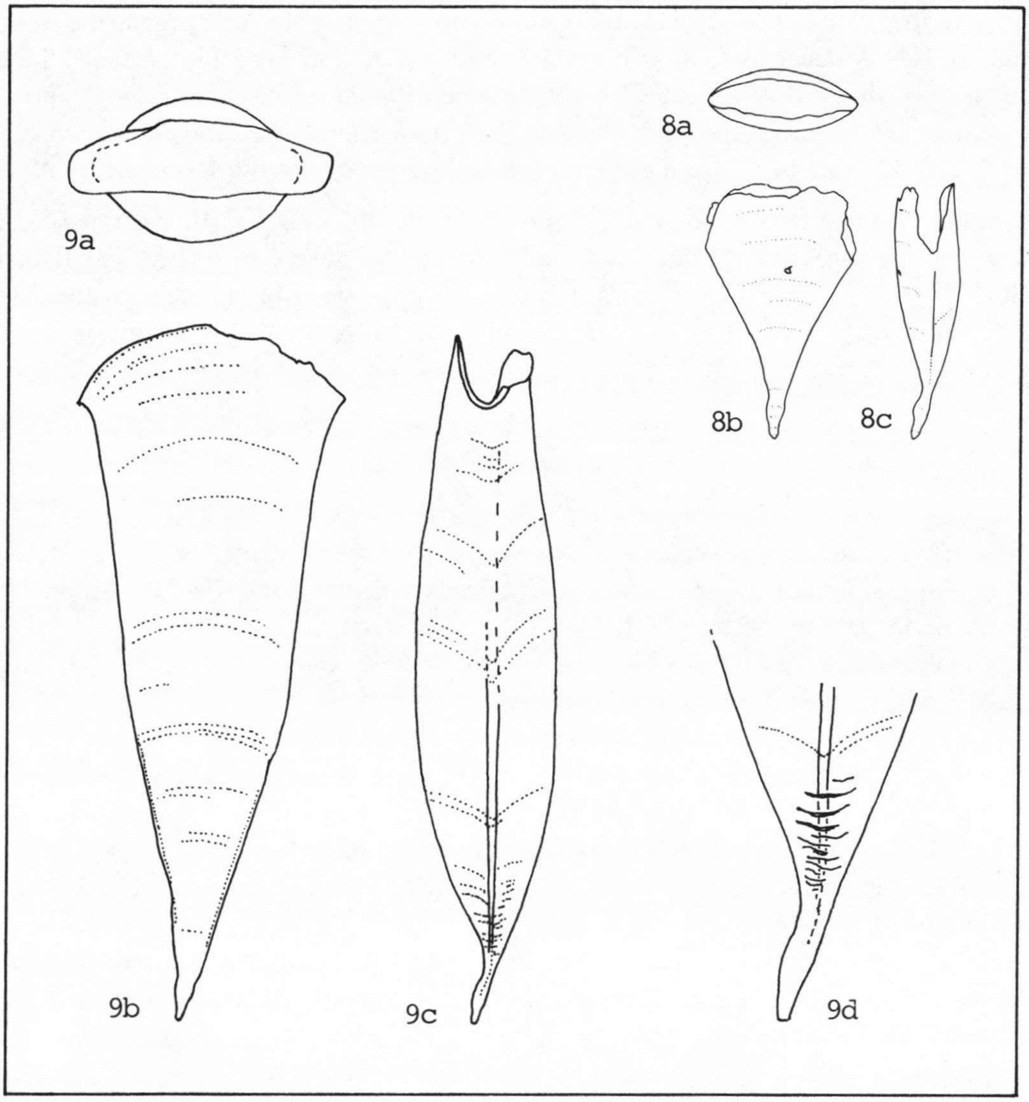


Fig. 8-9. *Vaginella austriaca* (Kittl).
8. Juvenile specimen, RGM 225 675.
9. Adult specimen, RGM 225 672.
a: apertural, b: ventral, c: left lateral; d: left lateral base of adult shell.
Magnifications: 9d x 25, all other figures x 12.

Winterswijk-Miste, temporary exposure. Miocene, Hemmoorian, Aalten Member, Miste Bed.

or words of the same tenor (Kittl, 1886; Čtyroký, Papp & Steininger, 1968; see also Janssen, 1984a). I studied hundreds of shells of *V. depressa*, but all shells demonstrate very convincingly a minute opening at their extreme base, indicating that a protoconch was thrown or broken off.

In the summer of 1984, however, I collected abundant material of *V. depressa* at a locality in the municipality of Martillac (department of Gironde), called Pas-de-Barreau, in a deposit of "Burdigalien moyen" age (Janssen, 1984b). Again from the sediment preserved in larger gastropod shells some magnificently preserved *depressa*'s were obtained, including juveniles and specimens still having their protoconchs (text-figures 10-13). The morphology of the protoconchs is entirely comparable to *V. austriaca*, including the presence of a double constriction. Usually however the protoconch in *V. depressa* demonstrates a lesser forward declination. In some cases the protoconch's axis even coincides with that of the adult shell, so that there is no declination at all (text-figure 13c). In such shells it is difficult to determine the ventral and dorsal side of the specimen.

The juvenile shells from Pas-de-Barreau resemble closely those of *V. austriaca* as described above. Here too the juveniles are flat and broadly triangular, devoid of wrinkles at their base and very flexible. In this material also some intermediate forms were found (text-figures 11-12) that completely acknowledge the fact that they really represent ontogenetical stages of one and the same species.

CONCLUSIONS

A study of well-preserved specimens of the pteropod species *Vaginella depressa* Daudin, 1800 (Burdigalian, Aquitaine Basin, France) and *V. austriaca* Kittl, 1886 (Hemmoorian, North Sea Basin, The Netherlands) demonstrated, that

1. Juvenile specimens of both species have a very flexible, thin-walled shell of a flat, broadly triangular form, with an elliptical cross-section.
2. Adult specimens have a more solid, slender shell with an almost circular cross-section. Furthermore the basal lateral parts of adult specimens possess wrinkles that are absent in juveniles.
3. During the ontogenetical development of both species apparently a pressure force against the dorsal and ventral shell-walls caused a deformation of the shell.
4. As a result of the deformation both sides of the shell's base are wrinkled to reduce tensions in the shell material.
5. The pressure force causing the deformation of the shell is thought to be carried out by quickly developing soft parts of the animal after a period of reduced body growth during which the flat and triangular juvenile shell was build.
6. This mechanism strongly indicates the occurrence of a minute and/or skinny stage during the ontogenetical development of *Vaginella*-shells, as described for recent pteropod species by van der Spoel (1967).
7. The protoconch of *Vaginella depressa*, hitherto not described in literature, strongly resembles that of *V. austriaca*. Usually this protoconch shows a minor forward declination with respect to the younger shell parts but sometimes the protoconch's axis coincides with that of the adult shell.

Fig. 10-13. *Vaginella depressa* Daudin.

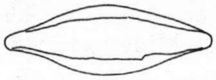
10-12. Successive growth stadia of juvenile shell, RGM 227 565-7.

13. Adult shell, RGM 227 568.

a: apertural, b: ventral, c: left lateral, d: left lateral base of adult shell.

Magnifications: 13d x 25, all other figures x 12.

Martillac, "Pas-de-Barreau" (Gironde, France). Miocene, Burdigalian, Falun de Léognan.



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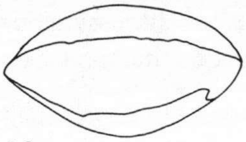

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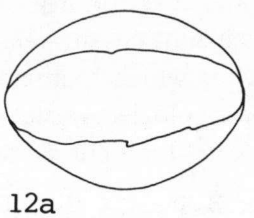

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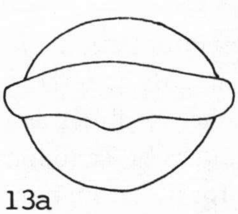

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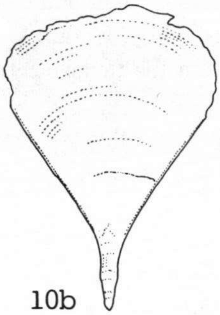

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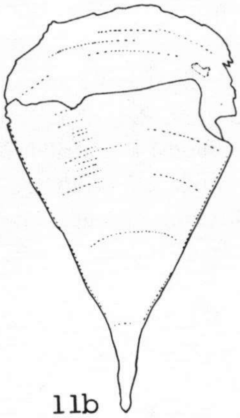

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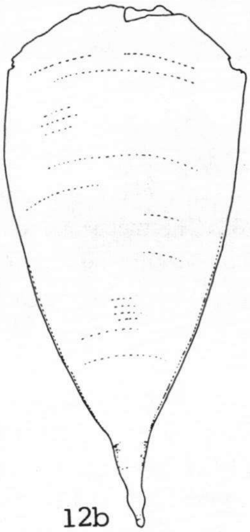

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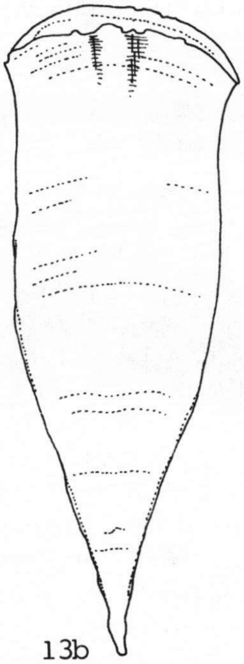

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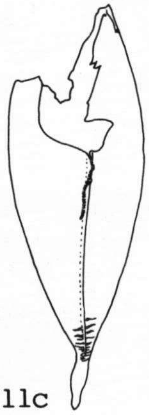

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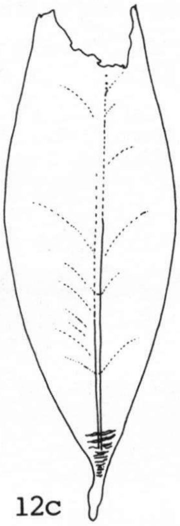

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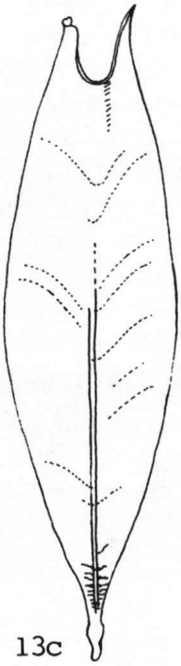

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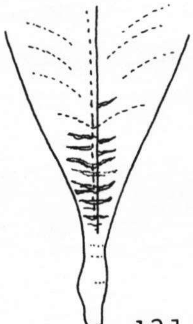

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