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SHELL GROWTH IN *TURRITELLA BADENSIS* SACCO  
(GASTROPODA) FROM THE BADENIAN (MIOCENE)  
KORYTNICA CLAYS, POLAND

*Abstract.* — The lack of any significant allometry in growth of the aperture size and shape indicates that *Turritella badensis* probably increased its ciliary feeding activity in order to overcome the constraints of aperture size on the body volume. This contrasts with purely morphological responses observed in some other turritellids. The physiological response was extorted in *T. badensis* by the high level of morphological integration.

INTRODUCTION

The Korytnica Clays were deposited in a shallow and protected small bay of the Badenian (Miocene) sea transgressing onto the southern slopes of the Holy Cross Mts (Radwański 1969). The paleoecology of their abundant fauna has recently been investigated by the present author (Hoffman 1977).

*Turritella badensis* Sacco was among the most common gastropod species in the Korytnica basin. It was a largely sessile suspension feeder living infaunally or semi-infaunally on shallow-water muddy substrates.

The aim of the present paper is to analyse the shell form and function in *T. badensis*, and to see whether the essential regularity of shell has been associated with any significant integration of morphological characters in this species.

This paper makes part of a doctoral thesis submitted to the University of Warsaw, supervised by Dr. Andrzej Radwański.

SHELL GROWTH

The turritellid shell shape is largely determined by the interplay between the need for efficiency of a filtering process and the necessity of maintaining a relatively small aperture (Andrews 1974). The aperture

cannot be very large relative to the total shell volume because otherwise the protective function of the shell is defeated. On the other hand, the amount of water entering the mantle cavity and thereafter filtered by the cilia depends upon the area of abapical part of the aperture. Hence, the volume of a growing turrnellid shell expands as a cube, while the amount of nutrients available to the animal grows only as a square of a linear dimension.

In other words, the amount of water entering the mantle cavity will decrease in ontogeny relative to the body weight if there is no allometry in the aperture growth. Obviously, the turrnellids may also respond physiologically, that is may draw stronger and faster inhalant currents into the mantle cavity, and by this way increase the amount of nutrients available. Another strategy would be to develop a negative allometry between the body size and the aperture size. However, the growth of body length cannot be completely stopped and hence, the reduction in body-size growth can hardly be adequate to the constraints of aperture size. In the case of Paleocene *T. mortoni*, Andrews (1974) was able to demonstrate the use of strategy developing allometry in growth of the aperture shape. He showed that as the shell increases in size the abapical part of the shell becomes more convex and inflated thus, increasing the area of the inhalant portion of the aperture relative to other shell dimensions.

In the absence of ontogenetic strengthening the ciliary action or allometry in either aperture shape or size, still another adaptive strategy can be postulated. The aperture might start out larger than it needs to be to assure the adequate incurrent. A subsequent decrease in the amount of incoming nutrients during the ontogeny would reduce gradually the

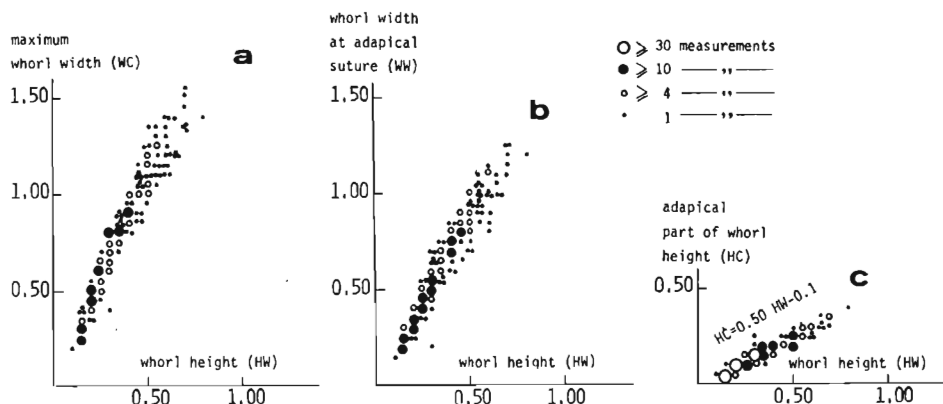


Fig. 1. Biometry of *Cerithiopsis tubercularis* (Montagu). Sample size  $n = 35$ ; all dimensions are in millimeters a—relative growth of the maximum width of whorl with the height of whorl; b—relative growth of the width of whorl as measured at the adapical suture, with the height of whorl; c—relative growth of the height of adapical part of whorl with the total height of whorl.

margin of safety but never drop below a critical value. Such a strategy of preparatory growth is fairly common among animals but it appears implausible in the turritellid aperture since it would be strongly counteracted by the selection for a small aperture, induced by the protective needs.

The biometry of the Korytnica population of *Cerithiopsis tubercularis*, a largely sessile, small-sized parasite on sponges (Fretter 1951), shows that even in very small gastropods the morphological effects of selection for a small aperture can be fairly significant. The bivariate analyses (fig. 1) demonstrate that there is a significant negative allometry in the relative growth of maximum whorl width and whorl height, whereas the other features of a whorl grow largely isometrically. This results in a negative allometry in the growth of aperture area. In other words, the ratio of the aperture area to the body volume declines with age just as it is required by the protective needs.

The biometrical analysis of the Korytnica population of *T. badensis* (figs 2 and 3) reveals that the ontogenetic growth of shell is largely

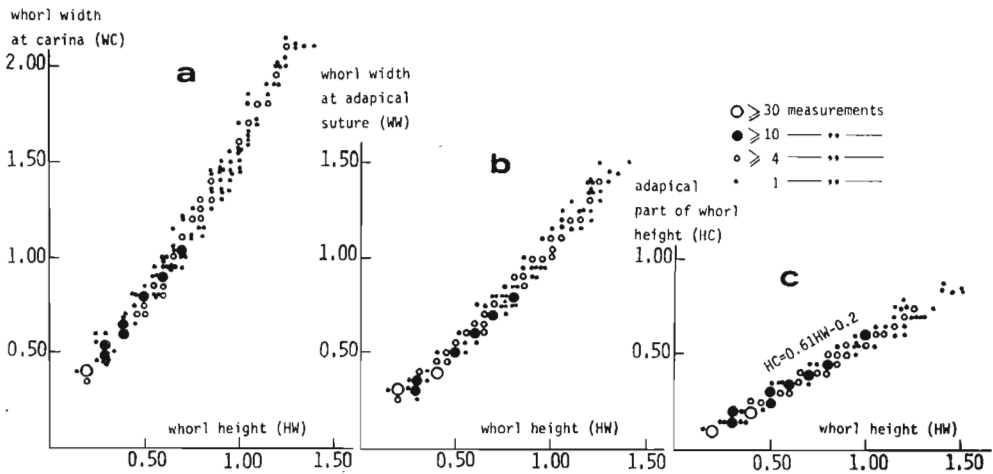


Fig. 2. Biometry of juvenile *Turritella badensis* Sacco. Sample size  $n = 37$ ; all dimensions are in millimeters *a*—relative growth of the width of whorl as measured at the middle carina, with the height of whorl; *b*—relative growth of the width of whorl as measured at the adapical suture, with the height of whorl; *c*—relative growth of the height of adapical part of whorl with the total height of whorl.

isometrical, 5 or 6 first whorls of the teleoconch forming an exception. Thus, generally, the rates of whorl translation and expansion are directly proportional. There is no change in the generating curve in ontogeny. In other words, the shape of whorl remains more or less constant during the ontogeny. Slightly allometric increase in the whorl width and hence, a change in the aperture size and shape relative to the whorl height at the juvenile stages of life (fig. 2*a-b*), is restricted to a few first whorls of the teleoconch, whereas in adult specimens the teleoconch consists of

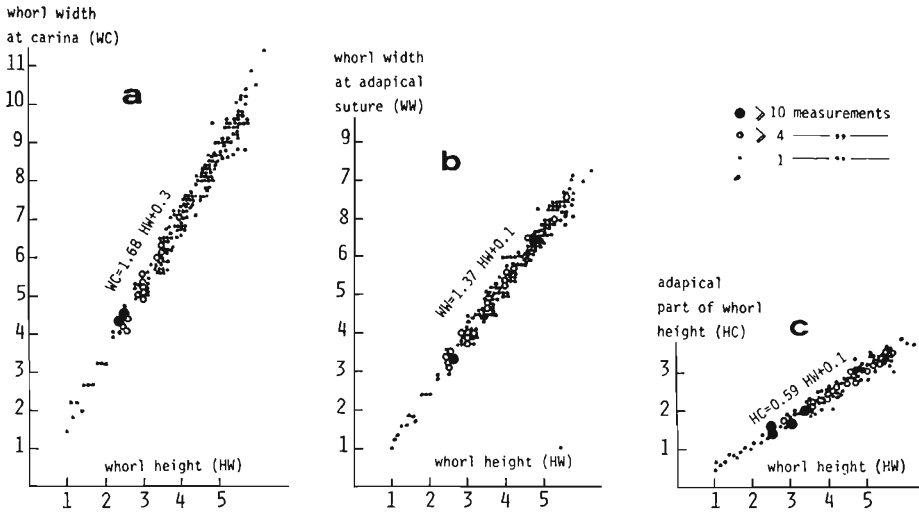


Fig. 3. Biometry of adult *Turritella badensis* Sacco. Sample size  $n = 45$ ; all dimensions are in millimeters *a*—relative growth of the width of whorl as measured at the middle carina, with the height of whorl; *b*—relative growth of the width of whorl as measured at the adapical suture, with the height of whorl; *c*—relative growth of the height of adapical part of whorl with the total height of whorl.

some 20 or even more whorls. This allometry cannot be regarded as adequate to the constraints of aperture size on the body volume.

Apical secretions in the shells and the broken off shell tips indicate clearly that the strategy of reducing body-size growth relative to the shell-size growth was used by the Korytnica population of *T. badensis*.

Nevertheless, one may claim that the essential regularity of the shell shape indicates the lack of any significant allometry in growth of the aperture size or shape and suggests that *T. badensis* strengthened its ciliary action in order to overcome the constraints of aperture size on the body volume.

The adaptive strategy chosen by the Korytnica population of *T. badensis* appears to have been essentially different from that developed by the Belvedere Beach (Paleocene, USA) population of *T. mortoni*; although both these strategies were intended to solve the problem of equilibrating in ontogeny the feeding-efficiency requirements and the protective function of the shell (Andrews 1974). The former population responded mainly physiologically, whereas the latter one responded by introducing allometrical growth, i.e. by changing the morphological relationships.

This supports the view of Gould (1968) who claimed that in general an adaptation is only one among a number of possible solutions, even within a single genus. Anyway, such a flexibility in response by changing either morphology, physiology, or both, is most likely when there is no strong interdependence in the whole of morphological and physiological features. Therefore, any flexibility cannot be expected in such animals as

the arcoid bivalves, because the unusually strong interrelationships among their ligament, hinge dentition and efficiency of the adductor muscles impose a fairly rigid framework to possible morphological changes, enabling only certain particular solutions (Brower 1973; Thomas 1975; Hoffman 1978).

#### MORPHOLOGICAL INTEGRATION

Gould (1968, 1969) and Eldredge (1968) demonstrated that all the four basic parameters of gastropod-shell form (shape of generating curve, rate of translation along the axis, rate in change of distance from the axis, and rate of expansion of the generating curve; Raup 1966) can vary independently in gastropod ontogeny and phylogeny thus, allowing a strategy involving morphological changes.

Indeed, Andrews (1974) showed that in *T. mortoni* particular features on different whorls are more integrated than different characters on particular whorls. In contrast, factor analysis of the relationships among morphological characters in the shell ontogeny in *T. badensis* reveals a significant integration of the morphological characters on each particular whorl.

In the Korytnica Clays, the turritellid shells are only rarely preserved complete, that is together with their tips. Hence, the juveniles and the adults of *T. badensis* were analysed separately. On each whorl of a specimen the following measurements were made: total whorl height from adapical to adapertural suture (HW), height of whorl from adapical suture to middle carina (HC), width of whorl at adapical suture (WW), and width of whorl at middle carina (WC). In the juveniles, the measurements were made on each of the first 8 whorls adapertural to and including the whorl where a normal ornamentation starts. In the adults, a method similar to that used by Sadlick and Nielsen (1963) was accepted: the measurements were made on each of the first 5 whorls adapertural to and including the whorl where a total height of 3 mm is attained. In both cases, the R-mode factor analysis of correspondences was performed by means of the method of Benzecri (1973).

In the juveniles (Table 1), the first factor axis clusters separately the measurements on the first 5 or 6 whorls from those on the later ones. It accounts for 25% of the total variability of the data matrix. Presumably, this factor reflects the allometry observed at the juvenile stages of life (fig. 2a-b). The second factor axis separates the heights and widths at each particular ontogenetic stage and thus, it represents mutual independence of the basic parameters of shell growth. It accounts for 16% of the total variability. The next 5 factor axes reflect highly complex correlations among different morphological characters, which cannot be unequivocally interpreted in biological terms. They account jointly for some

Table 1

R-mode factor analysis of the morphological characters of juvenile *Turritella badensis* Sacco; explanations of the symbols in the text; sample size  $n = 37$

Character	I axis	II axis	III axis	IV axis	V axis	VI axis	VII axis
OHW	24	-10	13	-17	19	-9	19
OWW	33	12	26	-12	16	-14	18
OHC	21	-4	19	-10	14	-12	16
OWC	23	5	26	-17	21	-13	11
1HW	34	9	29	13	6	-26	7
1WW	66	-3	3	14	18	60	-15
1HC	59	73	-26	-5	-27	24	82
1WC	29	-32	3	-11	6	-2	-13
2HW	29	-3	21	-4	1	-10	14
2WW	28	5	-14	4	0	4	6
2HC	19	36	8	-37	-12	9	1
2WC	17	-30	7	-9	0	-5	-6
3HW	24	3	1	-18	0	-8	1
3WW	29	4	-19	-12	25	10	-2
3HC	34	37	-61	-60	-10	-1	-17
4HW	25	-1	4	7	-5	-19	-7
4WW	18	2	8	-14	-5	2	11
4HC	57	31	2	14	-36	-9	-25
4WC	5	-34	4	3	-10	3	2
5HW	28	22	-20	40	0	-8	-1
5WW	26	-7	12	6	2	12	-4
5HC	26	13	23	17	-13	-12	-12
5WC	-2	-20	-2	-7	-17	-1	4
6HW	-11	-3	-7	4	4	-8	-7
6WW	9	-12	-24	-8	7	-6	-5
6HC	-32	26	7	-6	-18	12	0
6WC	-17	-13	-3	10	-19	4	9
7HW	-6	20	-20	25	19	-4	2
7WW	-22	-18	-13	-10	-2	-3	-1
7HC	-19	33	16	-6	-1	-13	-4
7WC	-39	-9	4	-1	2	3	-2
8HW	-22	18	6	0	12	-2	0
8WW	-29	4	-12	-1	0	1	6
8HC	-18	52	22	-7	-10	18	-18
8WC	-21	1	9	4	11	7	2
variability accounted for by the axis	25.1%	16.0%	8.4%	7.4%	5.6%	5.1%	4.3%

30% of the total variability. The quality of representation of the morphological characters by the first 7 factors is fairly good: in average, about 70%.

In the adults (Table 2), the first factor axis clusters separately the different measurements on each particular whorl and thus, it represents

Table 2

R-mode factor analysis of the morphological characters of adult *Turritella badensis* Sacco; explanations of the symbols in the text; sample size = 45

Character	I axis	II axis	III axis	IV axis	V axis	VI axis	VII axis
OHW	32	-2	6	-7	11	-2	7
OWW	30	-21	-11	-15	-4	-7	-16
OHC	33	12	4	6	13	4	-4
OWC	16	-15	1	0	4	0	-7
1HW	28	-2	9	0	4	-4	15
1WW	16	-13	-18	7	4	-1	-2
1HC	31	26	-8	4	-1	-10	-5
1WC	10	-7	2	11	7	3	1
2HW	25	1	4	-1	-2	-7	12
2WW	9	-4	-8	13	4	9	0
2HC	13	25	-8	17	-5	-18	0
2WC	0	-6	12	6	-2	9	3
3HW	9	8	8	-11	-6	5	6
3WW	-1	-8	-4	4	-12	12	3
3HC	6	37	13	-8	-11	3	-5
3WC	-9	-5	13	1	-2	-1	-2
4HW	7	7	8	-5	-6	-3	1
4WW	-10	-3	-2	-1	-10	0	0
4HC	-7	31	0	18	-4	4	-12
4WC	-18	-6	9	-1	0	-5	-2
5HW	0	14	-3	-16	14	12	-3
5WW	-20	6	-27	-4	-1	-1	7
5HC	-5	22	3	7	13	-3	2
5WC	-28	-5	4	0	10	-3	0
variability accounted for by the axis	31.2%	17.0%	12.1%	7.0%	6.1%	4.5%	3.8%

the morphological integration at each successive growth stage. It accounts for 31% of the total variability. The second factor axis separates the heights and widths on each particular whorl, and can be interpreted as reflecting mutual independence of the rates of whorl translation and expansion. It represents about 17% of the total variability. The third factor axis clusters separately the widths at the adapical suture from the widths at the middle carina, reflecting independence of the shape of generating curve. It accounts for about 12% of the total variability. The next 4 factors cannot be interpreted directly in biological terms. They represent jointly a little more than 20% of the total variability of the data matrix. The quality of representation of the measured features by the first 7 factors is good: in average, it significantly exceeds 75%.

In general, low size of the samples resulted in relatively low proportion of the total variability actually accounted for by the factors distinguished.

Nevertheless, the entire consistency of the results of both analyses with each other and with the bivariate analyses strongly supports the view that they can be regarded as biologically meaningful.

Then, one may conclude that in the Korytnica population of *T. badensis* the morphological integration of different characters on each particular whorl was more important than the relations among the same features on different whorls. In other words, the rates of whorl translation and expansion, and the shape of generating curve could not vary independently in ontogeny. The rate of changes in distance from the coiling axis did not influence the growth of *T. badensis* because the whorls were always tangent to the axis.

The high level of morphological integration may explain why *T. badensis* did not use any strategy involving morphological changes in shell ontogeny. Consequently, a physiological response became the only possible way to overcome the constraints of aperture size on suspension-feeding efficiency.

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WZROST MUSZLI ŚLIMAKA *TURRITELLA BADENSIS* SACCO  
Z MIOCENSKICH IŁÓW KORYTNICKICH

*Streszczenie*

O wielkości apertury decyduje u turritellidów konieczność zrównania wymogów efektywnego procesu filtracji (a więc — odżywiania) i skutecznej ochrony przed drapieżnikami. Różne gatunki turritellidów pokonują te ograniczenia dzięki alometrii wzrostu. Natomiast w korytnickiej populacji *T. badensis* wzrost apertury jest niemal izometryczny, co wskazuje, że ślimaki te nasilały z wiekiem aktywność aparatu filtracyjnego. Ta czysto fizjologiczna reakcja wymuszona była przez daleko idącą integrację morfologiczną muszli.

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АНТОНИ ХОФФМАН

РОСТ РАКОВИНЫ БРЮХОНОГИХ *TURRITELLA BADENSIS* SACCO  
ИЗ МИОЦЕНОВЫХ ГЛИН КОРЫТНИЦЫ (ПОЛЬША)

*Резюме*

У туррителлидов на величину апертур влияет необходимость уравновешивания требований эффективного процесса фильтрации (а значит и питания) и действительной защиты от хищников. Различные виды туррителлидов прео-

долевают эти ограничения при помощи аллометрии роста. Однако у корытницкой популяции *T. badensis* рост апертуры является почти изометрическими, что указывает на увеличение активности фильтрующего аппарата с возрастом организма. Эта сугубо физиологическая реакция была вызвана далеко идущей морфологической интеграцией раковины.