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GROWTH ALLOMETRY IN A BIVALVE *ANADARA DILUVII* (LAMARCK) FROM THE BADENIAN (MIOCENE) KORYTNICA CLAYS, POLAND

Abstract. — In *Anadara diluvii* from the Badenian (Miocene) Korytnica Clays, Poland, an allometry occurs in the growth of both the ligament and adductor muscles. In case of the ligament growth, the allometry was necessitated by duplivincular nature of the ligament itself and the endobyssate semi-infaunal mode of life. The low rate of juvenile adductor growth was extorted by some functional needs removed in the adults.

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, Poland (Radwański 1969). The paleoecology of their abundant fauna has recently been investigated by the present author (Hoffman 1977).

Anadara diluvii (Lamarck) was among the most common bivalve species in the Korytnica basin. It was a suspension feeder with large filibranch gills, a weak and sluggish burrower with low escape potential. It lived rather ubiquitously but occurred most commonly on shallow-water muddy flats.

The shell growth was entirely isometrical in the Korytnica population of *A. diluvii*. However, an apparent allometry (*sensu* Gould 1966, 1968) occurred in the growth of both the ligament and the adductor muscles. The aim of the present paper is just to analyse the functional significance of this allometry and its relation to the life habits.

This paper makes part of the doctoral thesis submitted to the University of Warsaw, supervised by Dr. Andrzej Radwański. Dr. Richard R. Alexander has kindly supplied the unpublished data on morphology and habitat of *Anadara trilineata*.

SHELL MORPHOLOGY

The statistical analyses clearly demonstrate that some shell parameters are strongly related to the ontogeny of *A. diluvii*, while others are independent of it (Table 1). Similar relationships between shell morphology and ontogeny were found by Saint-Martin (1975) in the Eocene *A. turonica*.

Table 1

Correlations of the length with other morphological characters of *Anadara diluvii* (Lamarck); the characters are defined as in Alexander (1974); sample size n = 75

Character	Correlation with length
height of shell	0.91
width of one valve	0.82
umbo eccentricity	0.11
ribs frequency	0.02
rib thickness	0.73
shell elongation	0.18

When analysing shell parameters related to the ontogenetic growth, the bivariate statistics has to be taken into account. The linearity of bivariate plots of the height and width versus the length of valve (fig. 1) indicates isometry of the shell growth in *A. diluvii*. Then, the shell length may be treated as an adequate measure of the overall size of the bivalve. The slopes of both regression lines are markedly lower than those determined by Saint-Martin (1975) for the Eocene *A. turonica*, and by Alexan-

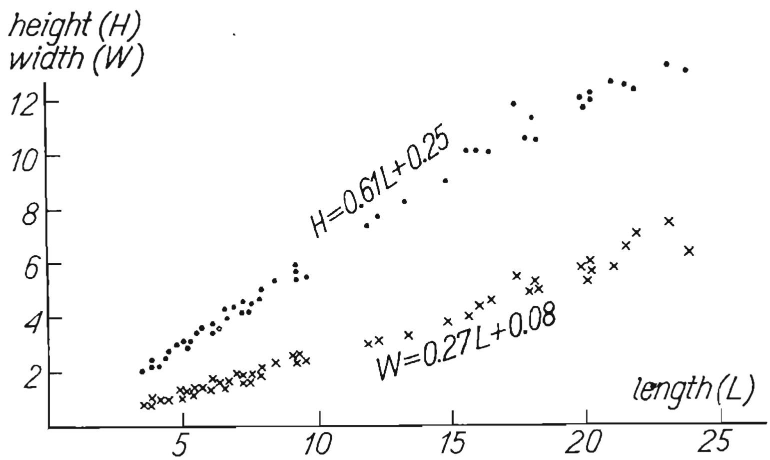

Fig. 1. Relative growth of the height and width with the length of shell in *Anadara diluvii* (Lamarck). Sample size n = 75; all dimensions are in millimeters.

der (unpublished data) for the Pliocene *A. trilineata*. This indicates a more elongate shape of *A. diluvii*. Indeed, its shell elongation is very high (Table 2), higher than in either *A. turonica*, or *A. trilineata*. It is comparable only to that regarded by Alexander (1974) as typical of true epibyssates. Nevertheless, one may claim that the ornamentation of valves is so distinct and heavy that the saturation of sea water with calcium carbonate

Table 2

Morphological characters of *Anadara diluvii* (Lamarck) independent of ontogenetic growth; sample size n = 75

Character	Mean value	Standard deviation
umbo eccentricity	0.36	0.04
ribs frequency	34	2
shell elongation	1.67	0.09

cannot have accounted for it. As the matter of fact, in shallow-burrowing bivalves, the ribs may help to stabilize the shell in more or less fluid substrates, and aid in burrowing process by acting as a support in the rocking motion of the shell. Hence, the semi-infaunal endobyssate mode of life can be postulated for the Korytnica population of *A. diluvii*.

This inference is also supported by the naticid to muricid prey ratio in the population, indicating that it made up the object of intergroup competition for food between the epifaunal and infaunal predatory boring gastropods (Hoffman *et al.* 1974).

LIGAMENT GROWTH

In common with most arcoids, *A. diluvii* has a duplivincular ligament. It is all but entirely external, the valves being articulated about an axis within its ventral margin. It grows by adding subsequent chevron sheets of lamellar and fibrous materials alternately beneath the umbones, while the ligamental area expands ventrally over the upper part of the hinge plate. The ligament opens the shell by exerting the moment about the hinge axis, opposite to the closing moment exerted by the adductors when they contract.

In general, ligament moment would maintain its relationship with the weight of shell that it must open without any allometry, since the tension exerted by the ligament increases at least as its cross-sectional area, and the moment arm increases as a linear dimension. Therefore, the allometry in growth of the ligamental area of *A. diluvii* (fig. 2*a*) appears to be necessitated by the very nature of duplivincular ligament itself, that is by its inefficiency resulting from the dorsal breakage (Thomas 1975, 1976). Despite this expansion of the ligamental area, the distance from the umbo to the median base of hinge plate increases approximately linearly with the size of shell (fig. 1*c*) because otherwise the size of mantle cavity would be reduced, the weight of shell would increase, and the center of gravity of the animal would move dorsally. Hence, the larger ligament cannot be accomodated by a ventral displacement of the hinge plate during ontogeny and the rate of the hinge-plate growth must decrease with size (fig. 2*b*). This decrease is markedly lower than it was described by Brower (1973) and Thomas (1975, 1976) in *Glycymeris*. In the latter bivalve, the height

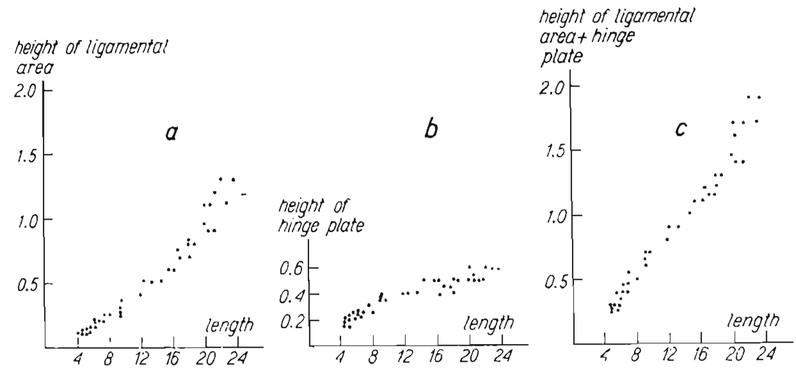

Fig. 2. Ontogenetic development of the ligament in *Anadara diluvii* (Lamarck). Sample size n = 39; all dimensions are in millimeters; *a* growth of the height of ligamental area; *b* growth of the height of hinge plate; *c* joint growth of the heights of ligamental area and hinge plate.

of the median part of hinge plate decreases absolutely at the adult stages. This difference in ligament growth may be related to respective differences in the weight of adult shell and in the mode of life.

The free-burrowing semi-infaunal arcoids like *Glycymeris* live mainly under high-turbulence conditions (Thomas 1975). They can be easily washed out by currents and need a very strong ligament moment to reburrow their thick and heavy, large shells. Indeed, bivalves with unfused margin lobes clap their valves together in order to loose the sediment before each pedal contraction sequence. Hence, they need very strong ligament moment to open the shell within the bottom sediment (Stanley 1972). Under such functional constraints, the strength of ligament is evidently more critical than the precise alignment of valves by hinge teeth which become reduced by the expanding ligament. On the other hand, *A. diluvii* seems better stabilized in its living position due to the endobyssate mode of life. Its much thinner, smaller shell does not require as strong ligament moment for reburrowing when disinterred, as the shell of *Glycymeris* does. Thomas (1976) demonstrated that in epibyssate

Arca noae the function of ligament is reduced to the point where it serves not so much to articulate the valves, as to hold them securely together along the dorsal margin. This is explained by the great dorso-ventral compression of this species which is adapted for permanent attachment.

When the arcoid cardinal plate is not to be displaced ventrally, the development of arcoid ligament is strongly dependent not only upon its own adaptive function but also upon the adaptive role of hinge teeth. In general, hinge teeth serve to prevent disarticulation of the closed valves by any shearing stress in the commissural plane, and to guide the gaping valves into perfect opposition when they close.

An epibyssate or semi-infaunal endobyssate mode of life requires perfect interlocking of the valves in order to resist extremely strong antero-posterior shearing stresses between the valves. The taxodont teeth of *Arca* or *Anadara*, mainly perpendicular to the hinge axis, seem well designed to perform this function. In contrast to *Glycymeris*, the disadvantages of a decrease in the interlocking ability of hinge teeth, which would follow an expansion of the ligamental area, apparently outweigh the possible need for a stronger ligament in these bivalves. One may conclude that the slightly allometrical ligament growth observed in the Korytnica population of *A. diluvii* was necessitated by the duplivincular nature of the ligament itself, and the endobyssate mode of bivalve life. *A. diluvii* worked out a compromise between the adaptive strategies of free-burrowing arcoids like *Glycymeris* and epibyssates like *Arca*, the former bivalve being designed to plough through the sediment in search of a new ground ("recovery strategy"), the latter to keep itself in the first place it had chosen ("stronghold strategy" of Thomas 1976).

ADDUCTOR-MUSCLES GROWTH

In general, closing moment exerted by adductor muscles about the hinge axis can be expected to increase in proportion to the weight of animal, which is required to maintain functional similarity (Gould 1971; Thomas 1975). As the matter of fact, the adductor-muscles growth is entirely isometrical (figs 3 and 4) in the Korytnica populations of *Pteromeris scalaris* (Sowerby) and *Venus multilamella marginalis* Eichwald. In *A. diluvii*, the closing moment of adductors grows allometrically with size and it keeps pace with the weight only at the adult stages of life (fig. 5c). A similar allometry is shown by the growth of the dimensions of adductor scars (fig. 5*a*—*b*).

Two explanations for this phenomenon are possible. Firstly, the adductors of *A. diluvii* might exhibit preparatory growth, being larger than necessary to perform their required function in the young animals (Bro-

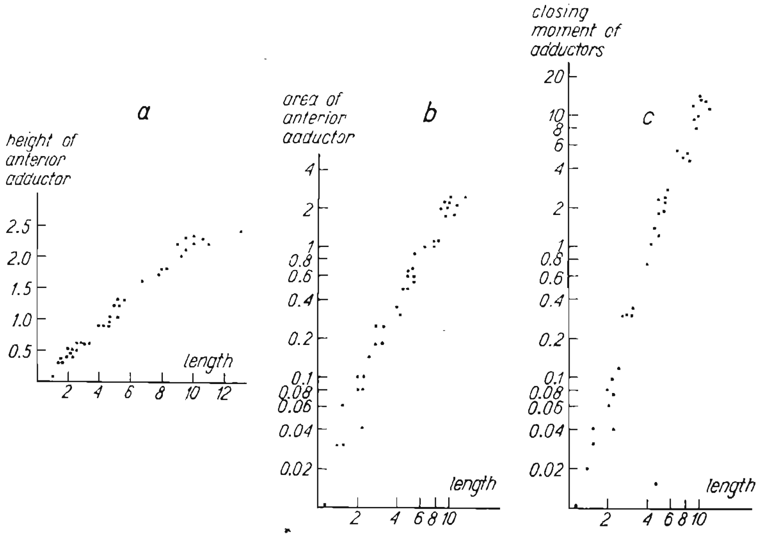

Fig. 3. Ontogenetic development of the adductor muscles in *Pteromeris scalaris* (Sowerby). Sample size n = 37; all dimensions are in millimeters; *a* growth of the height of anterior adductor scar; *b* growth of the area of anterior adductor scar; *c* growth of the closing moment exerted by both adductors.

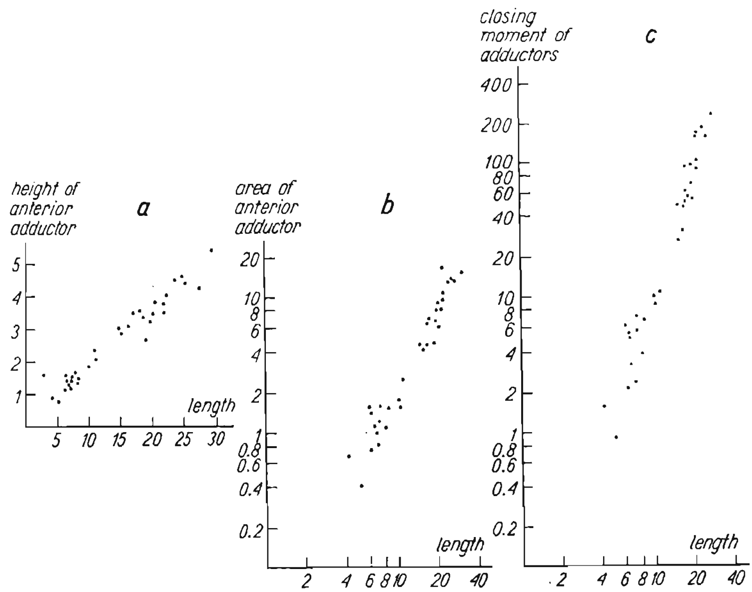

Fig. 4. Ontogenetic development of the adductor muscles in *Venus multilamella marginalis* Eichwald. Sample size n = 33; all dimensions are in millimeters: *a* growth of the height of anterior adductor scar; *b* growth of the area of anterior adductor scar; *c* growth of the closing moment exerted by both adductors.

wer 1973). Then, relatively large adductor scars of the juveniles can grow at significantly less than the rate needed to maintain isometry with respect to body weight; although at the later stages of life, this preparatory growth of the adductors appears insufficient to compensate the body growth and hence, allometry is required. Secondly, at the early stages of life, the low rate of growth of the adductors sizes might be extorted by some other functional needs removed or relaxed in the adults. Such a constraint might result e.g. from a necessity of maintaining relatively

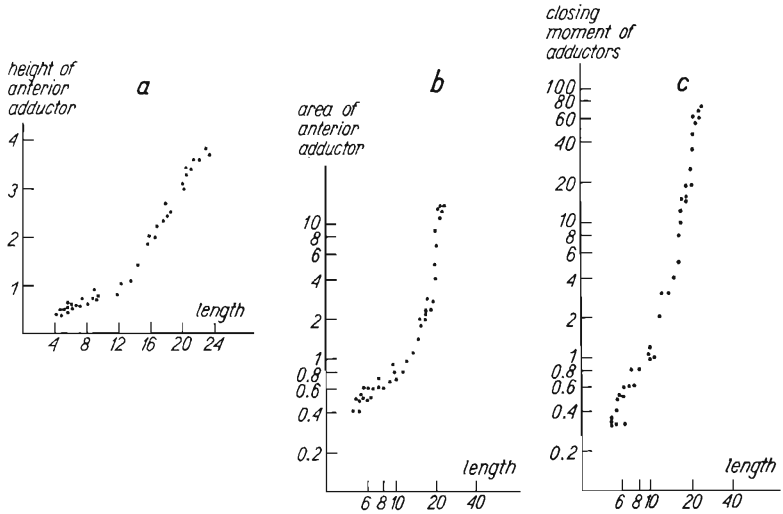

Fig. 5. Ontogenetic development of the adductor muscles in *Anadara diluvii* (Lamarck). Sample size n = 39; all dimensions are in millimeters; *a* growth of the height of anterior adductor scar; *b* growth of the area of anterior adductor scar; *c* growth of the closing moment exerted by both adductors.

large gills required by inefficient arcoid feeding (Lim 1966), while a possible rapid growth of the adductors would cause a significant decrease in the volume of mantle cavity.

Both these explanations can be indirectly tested by means of population-dynamics analysis. The former explanation is followed by the prediction of an approximate constancy of the ability to resist environmental stress during the ontogeny of *A. diluvii*. The latter one is followed by the prediction of a higher adaptedness of the adults than of the juveniles, which should be reflected by a decreasing mortality rate. As the matter of fact, relatively greater strength of the adductor muscles may result in *Anadara* in higher burrowing ability and higher resistance to predation by certain gastropods and starfish.

The present author (Hoffman 1976) demonstrated that the second prediction holds true. Hence, one may claim that in the Korytnica population of *A. diluvii* the low rate of early growth of the adductor muscles resulted from some unknown functional needs released in the adult life. One should, however, keep in mind that the mortality pattern could also depend upon other biotic and abiotic factors.

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ALLOMETRIA WZROSTU MAŁŻA *ANADARA DILUVII* (LAMARCK) Z MIOCEŃSKICH IŁÓW KORYTNICKICH

Streszczenie

W korytnickiej populacji *A. diluvii* wzrost muszli był izometryczny. Natomiast we wzroście więzadła i mięśni adduktorów zaznacza się wyraźna allometria. Ten allometryczny wzrost więzadła był wymuszony przez dupliwinkularny charakter więzadła i osiadły, na wpół infaunalny tryb życia tych małży. Stosunkowo małe tempo wzrostu adduktorów wymuszone było u osobników młodocianych przez jakieś niezidentyfikowane ograniczenia funkcjonalne, zanikające później u osobników dojrzałych.

АНТОНИ ХОФФМАН

АЛЛОМЕТРИЯ РОСТА ДВУСТВОРЧАТОГО *ANADARA DILUVII* (LAMARCK) КОРЫТНИЦКИХ МИОЦЕНОВЫХ ГЛИН

Резюме

В корытницкой популяции *A. diluvii* рост раковины имел изометрический характер. В то же время при росте лигамента и аддукторов видна значительна аллометрия. Этот аллометрический рост лигамента был обусловлен их дупливинкулярным характером и оседлым, полуинфаунальным образом жизни. Относительно медленный рост аддукторов был вызван у молодых представителей какими-то неизвестными функциональными ограничениями, исчезающими потом в зрелом возрасте.
