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The shell and its shape in Cavoliniidae (Pteropoda, Gastropoda)

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ABSTRACT

The shape of the shell in Cavoliniidae is studied in relation with the floating capacity of the specimens. A formula for this capacity (F) is given. The value for F proved to be higher in more specialized species and dependent on environmental conditions.

The theocosomatous Cavoliniidae can be subdivided into the following subfamilies: Clionae, Cuvierininae and Cavoliniinae. These subfamilies are characterized by the shell-shape; in Clionae it is pyramid-shaped, in Cuvierininae bottle-shaped and in Cavoliniinae it is more or less rounded. The shell is constantly present in Clionae; in Cuvierininae and most Cavoliniinae the caudal part is lost when the animal is mature (Van der Spoel, 1967).

When considering the shell as a floating object it is possible to determine its most favourable shape, and the effect of evolutional influences on it. In fig. 1 the shell of *Cavolinia inflexa* (Lesueur, 1813) forma *labiata* (Orbigny, 1836) is given with indications as to how the measurements used below were taken.

Enlargement of the lateral spines and the dorsal shell lip makes the floating surface of the shell larger, and the broader the shell the greater its floating stability. The floating capacity is, therefore, dependent on the sum of these $(D + 2S + B)$. The caudal spine and the whole shell section below the level of the lateral spines (P) is very heavy in relation to the anterior part (A) as the thickest shell elements with the smallest lumina are found caudally to the lateral spines. Consequently, the smaller these parts are in relation to the anterior part the better it is for floating, and, therefore, the floating capacity (F′) is larger when $(D + 2S + B) \times A/P$ is greater. The nearer the heaviest part of the shell is to its geometrical centre the more stable the floating shell

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will be. The enlargement of the value for M is thus influencing F′ in a negative may. The floating capacity can now be expressed as:

$$F' = \frac{(D + 2S + B) \,.\, A}{M.P.}.$$

A cavoliniid shell is, however, not only floating but also propelled by the action of the wing-shaped foot of the inhabitant animal. In planktonic animals it is an overall phenomenon, that when the locomotory organs are spread over greater parts of the body the shape of the body is long-drawn, as e.g. in *Sagitta, Euphausia,* most fishes, *Tomopterus* and *Planktonemertis.* Locomotion in all these animals is effected by a wave or eel-like movement. When the locomotory organs are localized to a smaller part of the body as in ostracodes, *Noctiluca milliaris,* most cephalopods, *Distephanus* and *Cavolinia,* the shape of the animals is more rounded, so as to be better navigable. Mobility is thus better in Cavoliniidae when the thickness (T) in relation to the length (L) is greater. In species with the locomotory organs in a smaller area of their body the floating and swimming capacity (F) is better when

$$F = \frac{(D + 2S + B) \,.\, A \,.\, T}{L \,.\, M \,.\, P} \text{ is greater.}$$

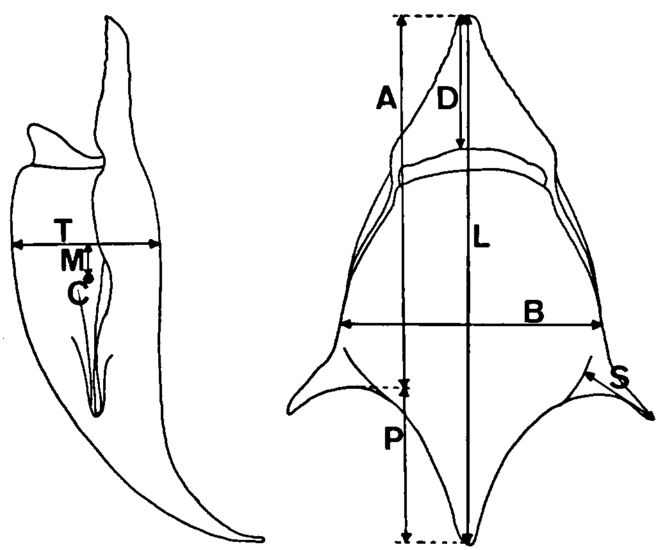

FIG. 1. Shell of *Cavolinia inflexa* forma *labiata* from the left and ventral side. A, shell part anterior to lateral spine; B, shell width; C, geometrical centre; D, length of dorsal shell lip; L, shell length; M, distance between C and greatest thickness of the shell; P, shell part posterior to lateral spines; S, length of the lateral spines; T, thickness of shell body.

To give an impression of the adaptation to floating in Cavoliniidae a graph is given of the rough values for log. F, calculated for several cavoliniid species, log. F being used instead of F to compress the graph which otherwise should have runned from 0.000001 to 500.0.

The graph in fig. 2 is divided into three blocks: block I contains the species of the subfamily Clionae, block II the Cuvierininae and those species of Cavoliniinae which likewise throw off an important part of the caudal shell, block III contains the remaining Cavoliniinae which throw off no — or only a small — part of the shell when adult. In block I a regular increase of log. F is seen. Exceptional species are 13, 14 and 15 which show a very low F value. These three are the only bathypelagic species in block I and it is commonly known that floating in deep-sea animals is less perfect than in epiplanktonic species, which is in agreement with the low F value. In bathypelagic species the shell is also generally thicker, as in the limaciniid *Limacina helicoides*, but the weight of the shells is not considered in this study. The numbers 7—12 concern formae of *Clio pyramidata*; 12 standing for *lanceolata* from the tropics, 11 for *convexa* from the subtropics,, 10 for *excisa* from subantarctic waters, 9 for *antarctica* from subantarctic waters and 8 and 7 for *sulcata* and *pyramidata* from the antarctic and boreal waters, respectively. In this species it is clearly shown that F is dependent indirectly on the latitude at which the animals live and directly on the water temperature and viscosity of the environment. The discontinuity between species 4 and 5, consequently between the genera *Creseis* and *Styliola*, shows that evolution did not transform the shell of *Creseis* into that of *Styliola* as the adaptation of the F value is lower in the latter than in the higher forms of *Creseis*. The great discontinuity between the species of block I and block II proves that the Cuvierininae and Cavoliniinae did not immediately descend from the Clionae (Van der Spoel, 1967). The species plotted in block II throw off their caudal spine when the animal is adult, so the F value of one and the same animal changes during life and consequently the value of log. F is indicated by larger black dots. Log. F for a specimen of *Diacria trispinosa* forma *trispinosa* with its caudal spine still present is —0.03 while it is +0.80 when the spine is broken off, which proves that the loss of the caudal parts is an adaptation in this plankton animal, enlarging the floating capacity. Comparing block II and III it is clear that the floating capacity of *Diacria* specimens with caudal spines is lower than the average capacity in the genus *Cavolinia*, the loss of the caudal spine, however, effects an enlargement of F to the level which is also found in *Cavolinia*. The effects of the loss in *Cavolinia* species are not plotted in the graph as it is of minor importance. In block III the graph can be splitted once more into three parts, the first three plots, belonging to the formae of *Cav. gibbosa*, the plots in the middle and those at the end concerning *Cav. longirostris* and *Cav. tridentata*. The values of log. F in *Cav. gibbosa* are rather low but the adaptation of F proceeds in the different formae. In the middle group *Cav. inflexa* forma *inflexa* (25) takes an exceptionally low place, but considering the general shape of the shell of this species it resembles more that of *Clio* than that of *Cavolinia* and in the past it has been sometimes incorrectly

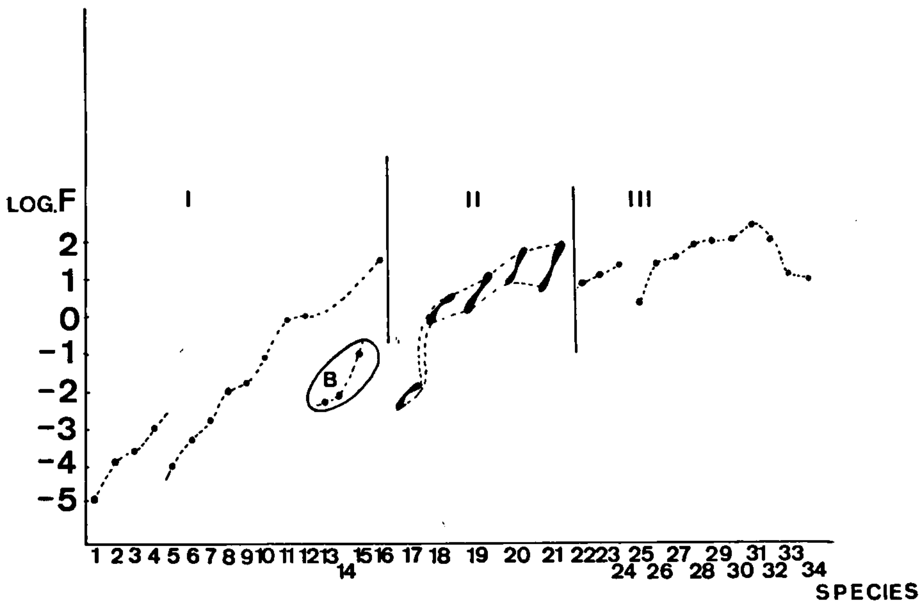

FIG. 2. Log. F value (vertical axis) of 34 species and formae of Cavoliniidae (horizontal axis).

1, *Creseis acicula acicula*
2, „ „ *clava*
3, „ *virgula virgula*
4, „ „ *conica*
5, *Styliola subula*
6, *Hyalocylis striata*
7, *Clio pyramidata pyramidata*
8, „ „ *sulcata*
9, „ „ *antarctica*
10, „ „ *excisa*
11, „ „ *convexa*
12, „ „ *lanceolata*
13, „ *polita*
14, „ *recurva*
15, „ *chaptalii*
16, „ *cuspidata*
17, *Cuvierina columnella columnella*
18, *Diacria trispinosa trispinosa*
19, „ „ *major*
20, „ *quadridentata orbignyi*
21, „ „ *quadridentata*
22, *Cavolinia gibbosa flava*
23, „ „ *plana*
24, „ „ *gibbosa*
25, „ *inflexa inflexa*
26, „ „ *imitans*
27, „ „ *labiata*
28, „ *uncinata*
29, „ *globulosa*
30, „ *longirostris angulosa*
31, „ „ *longirostris*
32, „ *tridentata tridentata*
33, „ „ *platea*
34, „ „ *kraussi*

B, bathypelagic species of the genus *Clio.*

referred to *Clio*. This species may be considered the most primitive one in the genus. The highest log. F value is found for *Cav. longirostris* (31), the most specialized species, which is highly specialized in its sexual gland and throws off the embryonic shell when still very young. The low values shown by *Cav. tridentata* are explained by the fact that in this species, like in *Cav. inflexa*, the caudal shell parts are never thrown off. In older specimens F is always higher than in younger animals of the same species; the graph (fig. 2) is consequently based on adult animals only, those with caudal spine being also adults which did not yet loose it.

Summarizing, it is clear that log. F is an indication for the stage of specialization of the species, and consequently for the course of evolution. The log. F value is furthermore dependent on the environment of the species: deep-sea species have a lower F value than epiplanktonic species and tropical species have a higher value than cold-water species. Log. F also indicates the effect and adaptive nature of the loss of the caudal spine.

Literature

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