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THOUGHTS ON *PLICATULA* LAMARCK (PECTINACEA : BIVALVIA)

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ABSTRACT

The pleurothetic bivalve genus *Plicatula* Lamarck is indifferently attached by its left or right valve; the attached valve is more convex than the other. Identification of the monomyarian muscle scar and the posterior projection of the shell are useful guides for determination of the anatomical left and right valves. Family Plicatulidae Watson apparently embrace *Plicatula* only (with its two subgenera *Plicatula* s.s. and *Darteplicatula* Freneix and Gorodiski).

INTRODUCTION

The present note stems from the scrutiny of the incongruity in the figures of *Plicatula* s.s. and *Darteplicatula* Freneix and Gorodiski (subgenera of *Plicatula* Lamarck) as reproduced by Cox and Hertlein (1969, p N377, figs. C98, 1 and 2 respectively). They have figured two examples each of *Plicatula* s.s. (p N378, figs. C98, 2a-b). Of these, figures C98, 1a and 1c of *Plicatula* s.s. have been mentioned as 'LV ext.' and 'RV int.' respectively, whereas the identical valves of *Darteplicatula* with matching convexity, obliquity, position of the adductor scar and basic surface sculpture have been labelled as 'RV ext.' and 'LV int.' respectively. Since plicatulids are monomyarian bivalves, the side bearing this adductor is unequivocally the posterior side, to which direction a greater shell prolongation can always be found. Judging by these parameters, the figures of *Plicatula* s.s. (fig. C98, 1a and 1c) are those of right and left valves and not the reverse as mentioned in the text by Cox and Hertlein (1969,p N378). Newell, in a personal communication (March 1983), had conceded that this 'error' had crept in due to clerical mistake in the editor's office of the Treatise (of Invertebrate Paleontology, Kansas, U.S.A.)!

A further search through the previous literature revealed that many considered the notion (attachment by right valve and its greater convexity in *Plicatula*) as empirical although quite a few observations by contemporary (late nineteenth, and early and middle twentieth centuries) workers are to the contrary. Apparently, no heed has been paid to these few reportings for the likely cause of their being infrequent. However, it would be more exacting *now* not to remain entwined with any particular opinion since none of these appear to be unfounded.

The present paper aims at examining both 'types' of the plicatulas and then to synthesize and harmonize the different views aired by the foremost students of the fossil bivalves in order to put forth a coherent argument to bridge the premises and conclusions.

ATTACHMENT-BY-RIGHT VALVE SYNDROME

Plicatula, the stem-genus of the family Plicatulidae Watson (1930), was earlier used to be placed under Spondylidae Gray, e.g., Arkell (1930), Cox (1925; 1929; 1935, p.5: though later, on pp 14 and 18, he did place it under Plicatulidae), both pleurothetic epifaunal bivalves. Watson (1930) separated *Plicatula* from Spondylidae chiefly on soft part anatomy. However, certain features such as the lack of a byssal sinus, nature of dentition, resilium, etc. are similar in the two groups. Palaeontological differences of significance is said to be the difference in ornamentation; spondylids usually have spines of various strengths over the radial elements. However, Mesozoic plicatulas from the Indian subcontinent do show spines (e.g., those figured by Cox, 1952) over the radials. Another external feature appears to be more useful for distinguishing between the two genera and that is the conspicuously developed cardinal area on the right valve of *Spondylus* (along with other members of the family), lacking altogether in *Plicatula* s.s. and its kindred.

The virtual parallelism between *Plicatula* and *Spondylus*, having their right valves attached to some hard objects, was emboldened by Watson (1930). Subseqently many authors, such as Cox (1952), Cox and Hertlein (1969), etc. reiterated that the right valve grows attached to some hard substrate. Newell and Boyd (1970, p 229), too, believe that the Plicantulidae are dextral (right valve lowermost and cemented). According to Stenzel (1971, p N1052), the Plicatulidae and Spondylidae 'living today' are cemented by their right valves. Cox, however, had cautioned elsewhere (1952, p 39) against putting *too much* weight for this notion. Contrary to this 'attachment-by-right valve' syndrome, it was Arkell (1930, p 90) who stated categorically that the plicatulas are 'not generally attached by their right valve like *Spondylus*'. Even Cox, who had later strongly advocated attachment of *Plicatula* by the right valve, had earlier recorded left valves with easily recognisable attachment area (1935,p 5, pl. 1, fig. 5) in *P. Pspinosa* (Schlotheim) from the 'Lias'

of Attock in Pakistan. At least one example from the Cretaceous rooks of Trichinopoly (S. India) can be cited (*P. instabilis* Stoliczka, 1871, figs. 11, pl. 34: Geological Survey of India Type No. 1351) exhibiting a convex left valve bearing an attachment mark!

That arguing in favour of the attachment by any particular valve is futile, is explicitly exemplified by the figures of *Plicatula* s.s and *Darteplicatula* reproduced by Cox and Hertlein (1969). There, the figure of *Darteplicatula*, a right valve, does not reveal any sign of an attachment area, not even at the umbonal pole (although the plaster casts of the two isolated right valve specimens of *Plicatula (Darteplicatula) polymorpha* (Bellardi) from the Eocene of S. Nigeria kindly sent by Mme. Suzanne Freneix from the collection of the Museum National d'Histoire Naturelle, Institut de Paléontologie, Paris, do show attachment areas on their umbonal regions), while that of *Plicatula* s.s. (figs. C98, 1a, p N377), also a right valve (explained above), does show a small attachment area truncating the corresponding region. *P. spinosa* from Pakistan reveal attachment mark on both the valves (Cox, 1935, pl. 1, figs. 4,5) as determined by their posterior projections (*vide infra*).

It may be, therefore, argued that *Plicatula* is an ambidextral (attachment indifferently by either valve) pleurothetic genus. Similar ambidextrality has also been observed in *Enantriostron* Bittner (Seilacher, 1954, p. 175; also see Cox, 1969. P N380), which has been considered (Cox, 1952, p 39) to be the likely ancestor of *Plicatula*!

THE RIDDLS OF THE VALVE CONVEXITY

The problem of cementation of a valve acrued to the riddle of valve convexity. Pleurothetic invertebrates have their saggital planes more or less parallel to the bottom surface which is the most suitable position for leading such a sedentary mode of life. The valve which is lowermost and attached is the most important one housing the viscera, etc. The large and only adductor muscle activates on the inner surface of this valve to which it is immutably fixed. The other valve merely serves as a lid protecting the soft parts of the animal. Obviously the attached (lower) valve has to be roomy, while it is necessary for the free (upper) valve to be smaller, thinner and preferably flat or concave, or only feebly convex, depending upon the substrate morphology and the rate of sedimentation, in order to be less burdensome and thus exerting only a minimum of gravity over the functioning ability of the muscles and ligaments. The function of the valves in pleurothetic stocks is, therefore, more like the dorsoventral arrangement in brachiopods, rather than the customary left-right placement in ordinary bivalvians.

It should be recalled that most of the juvenile bivalve shells possess a left valve more convex than the right one while others have practically equivalved shells. Larval shells with a more convex right valve are virtually unknown. Therefore, it appears that the question of a deeper, or in other words, more convex attached right valve has nothing to do with the anatomical left and right concept but is a function probably determined by genetic factors selected for the 'adaptive values' of the pleurothetic bivalves (Kauffman, 1969, p N155). This philosophy apparently did not dawn upon ardent workers like Arkell (1930, p 90) who claimed the left valve to be 'always' convex and the right valve flat or concave*, or Cox (1952), and others considering the reverse 'only' as empirical.

The fickeling reverie in upholding a rigid stance in deciding the left and right valves of *Plicatula* could be best exemplified by *P. spinosa* (Schlotheim) from the Attock district of Pakistan studied by Cox (1935, p 6), according to whom, *all* the Attock material at his disposal are 'fairly gibbose left valves'. Cox's contention of having only left valves in his Attock material, however, is not entirely true because, at least, his fig. 4 specimen (one of the two with the G.S.I. No. K 24/785) is an equally convex right valve as evidenced by its slight, but definite, posterior projection (*vide infra*). Subsequently, Cox (1952, p 40), followed by Cox and Hertlein (1969, p N 377), etc., projected an almost reverse picture, i.e. the right valve being more convex than the left. What ensues from the above analysis is that probably none of these opinions are unfounded!

ADAPTATION OF THE LARVAL *PLICATULA*

A larva with a more convex left valve would settle on its convex surface in contact with the substrate and would remain so as long as currents are absent or feeble and would get eventually cemented to the substrate. Stronger currents, soon after settling, would tend to topple them over their flat right valves for a stable position on the substrate before cementation starts (fig. 1). In the former case a more convex left valve can always be anticipated, as in many oysters and pectens. However, currents cannot be expected to be absent except in certain particular cases. That is why a greater number of instances show a cemented right valve which is more convex too (*vide supra*). Another likely factor capable of

*Roeder and Loriol also thought that plicatulas have their left valves more convex than the right ones and have accordingly re-assigned a few 'plicatulid forms' with more convex right valves to *Spondylus* (Arkell, 1930, p 91).

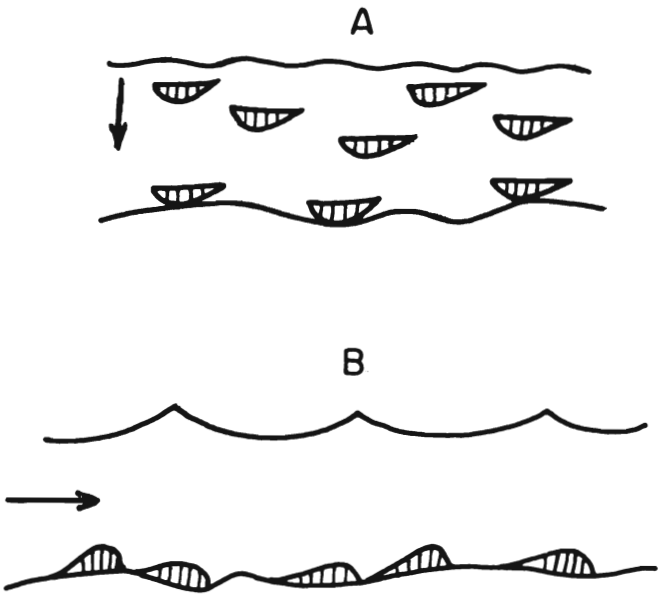

Fig. 1:A Lateral currents absent or feeble: larvae with the convex (left) valves to settle under gravity (shown by an arrow) to rest on the substrate.

After cementation this valve grows deeper (convex) than the other which is flat or concave or feebly convex according to the influx of sediments in the region of habitat (not to scale).

Fig. 1:B When currents are present (shown by an arrow): larvae to rest on their flatter (right) valves on the substrate to attain greater stability.

After comentation this lower (right) valve, initially flat, grows deeper (convex) than the other. The initially convex left valve will assume subsequently a flatter aspect; may produce a resupinate nature of the grown-up upper valve (not to scale).

producing a left-right controversy in *Plicatula* may be the tendency of a change in growth from 'backward' to 'forward', as observed in many members of Pectinacea. Such a 'change in growth' might have been induced by the characters of the substrate, or by a change in current direction and velocity restraining the growth in a certain direction, or reducing the food supply, or both, or an 'urge' to regain the larval conditions in respect to its (observed) attitude of having a more convex left valve, or an interplay of some or all of these situations. Changing to a 'pro-crescent' through 'infra-crescent' stages (Newell and Boyd, 1970, p 229) can be perceived vis-a-vis a greater secretion of shell material from the other margin of the mantle (for the likely reasons enumerated above), and as demand of the changed condition of a resultant shell-weight imbalance, a consequent shift in the position of the 'only' adductor to ease the strain experienced by the muscle system, or otherwise, would effectively alter the appearance of an immature or submature attached, convex right valve into a mature convex left one or vice-versa (fig. 2). The holotype of *P. weymouthiana* Damon, figured by Arkell (1930, pl. 6, fig. 5), is probably the best example of such a phenomenon.

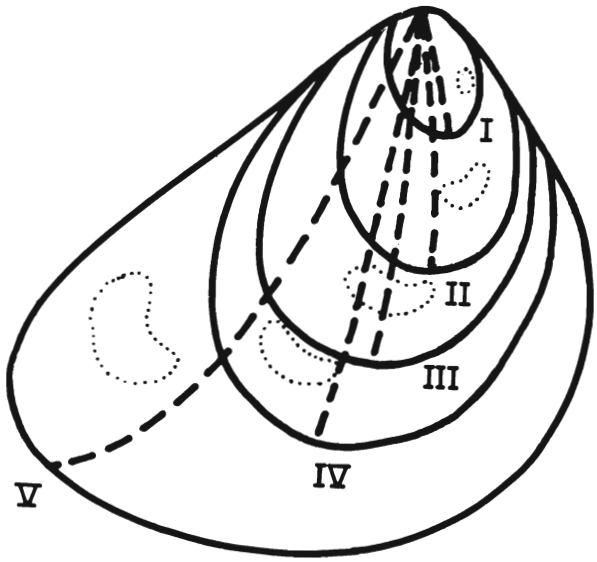

Fig. 2: Broken lines indicate the direction of principal growth-gradient. Circular or elliptical dotted curves indicate the likely position of the posterior adductor vis-a-vis the growth pattern. A hypothetical shell outline in bold lines showing retro-crescent (I,II), infra-crescent (III), and pro-crescent (IV,V) stages of growth with shifting positions of the posterior adductor muscle changing the antero-posterior phenomenon, and hence the left-right concept of the valves from nepionic to adult stages of growth (not to scale).

From the above deliberations, it is apparent that most of the plicatulas are attached by their right valves which are also the more convex of the two. However, opposite cases are not altogether lacking. Below, an attempt has been made to analyse the dual facts and to decide the factor(s) helpful in determining the left and right valves of *Plicatula*.

THE PROBABILITY

The arbitrary assumption of convexity or cementation of a particular valve has culminated into a state of confusion regarding the identification of left and right valves of *Plicatula*. The right valve examples of *Plicatula* s.s. and *P. (Darteplicatula)* reproduced by Cox and Hertlein (1969) are of similar convexity and obliquity but, while the former possesses a small but well marked attachment surface truncating its umbonal pole, that in the latter seems wanting (although the plaster casts of the two examples of *Darteplicatula* provided to the author by Freneix do show identifiable attachment marks over the umbonal tips of the specimens).

There are quite a few examples of *Plicatula* s.s. having their left valves more convex than their counterparts, e.g., *P. weymouthiana* Damon figured by Arkell

(1930). Some Indian examples of *P. peregrina* d'Orbigny, preserved in the G.S.I., Calcutta (Nos. K 40/656-665), too, feature this phenomenon. Besides, some Pakistani representatives of *P. spinosa* (Schlotheim) also have very convex left valves with attachment areas too (Cox, 1935, p 5).

As elaborated earlier, the identification of the anatomical left and right valves on the basis of valve convexity and/or cementation by any particular valve are not very sound criteria for the purpose. It would be more fruitful to depend on identification of the posterior side by finding out the only adductor muscle scar. In all cases where the interior is visible it is not difficult. It can also be verified that barring few acline (infracrescent) examples, majority of the *Plicatula* shells show a discernible projection towards the side quartering the monomyarian scar, and this feature can be advantageously used for a satisfactory identification of the two valves of plicatulas. Many authors have recognised the 'posterior projection' of the shell (Cox, 1935, p 18; Agrawal, 1956, p., 83; Tamura, 1959, p. 178) highlighting the utility of the feature.

OTHER SO-CALIED PLICATULIDS

Cox and Hertlein (1969, p N377) have grouped *Plicatula* (together with the subgenera *Plicatula* s.s., *Darteplicatula* and *Pseudoplacunopsis* Bittner), *Atreta* Etalloon *and Saintiopsis* Sacco under the family plicatulidae. Of these, *Pseudoplacunopsis, Atreta* and *Saintiopsis* are materially much different from *Plicatula* on account of the invariably flatter right and more convex left valves, besides having a weaker ornamentetion consisting of delicate, divaricating, wavy threads. *Atreta* is devoid of interlocking teeth (Stenzel, 1971, p N1052). *Pseudoplacunopsis* was referred to plicatulidae on Cox's advocacy not taking into account the features of the type species (*P. affixa* Bittner) which does reveal the interior, but on Late Triassic *"Anomia" fissistriata* Winkler having 'plicatuloid dentition', a right valve flatter than the left and ornamentation similar to that of *Placunopsis* Morris and Lycett" (Cox, 1952, p 45)! It can be recalled that there are some genera belonging to the family Anomiidae Rafinesque (Myra Keen, 1969, p N383) possessing "ridges (orura)", such as in *Placuna* Lightfoot, and the *Placunopsis*-type ornamentation is seen in many anomiid taxa. This author would, therefore, tentatively refer *fissistriata* to Anomiidae. *Saintiopsis*, with a flat right and convex left valve, which are thin shelled and smooth, sporting widely divergent crura, may also be safely transferred to the Anomiidae. *Pseudoplacunopsis* and *Atreta* are, apparently, nearer to *Gerlus* de Gregorio and *Placunopsis* (? Terquemiidae cox) and probably not closely related to the *Plicatula* stock *(sensu lato)*.

CONCLUSION

Plicatula is an ambidextral genus getting attached indifferently by its left or right valve according to the conditions at the time of settling of its larvae or even subsequently due to a change in the direction of the current (and food), substrate nature or the space available for its growth. Consequently, any of the two valves may be more convex than the other. The position of the lone adductor muscle is the dependable index for identification of the posterior side for determining the anatomical left and right valves of the genus. The posterior projection of the shell is an useful guide for such specimens which do not expose their interior.

Pseudoplacunopsis, Atreta and *Saintiopsis* are nearer to *Gerlus* and *Placunopsis* (? Terquemiidae) than to *Plicatula* s.s. and *Darteplicatula* (Plicatulidae).

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