

FUNCTIONAL MORPHOLOGY AND
ONTOGENETIC VARIATION IN THE
CALLOVIAN BRACHIOPOD *SEPTIRHYNCHIA*
FROM TUNISIA

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ABSTRACT. The brachiopod *Septirhynchia numidiensis* sp. nov. is described from the Callovian (Jurassic) of southern Tunisia. Studies of the internal characters and their development reveal that only the adult forms possess the cardinal process and ventral median septum regarded as diagnostic of the genus. Inferred functional morphology suggests that these adult features represent direct or indirect adaptations to living partially buried in sediment, and their gradual development reflects a progressive change from an epifaunal to a semi-infaunal mode of life during ontogeny. Reports in the literature of synchronous homeomorphs with other species of *Septirhynchia* seemingly refer to juvenile forms. The implications for brachiopod taxonomy of the observed ontogenetic variation in *Septirhynchia* are discussed. The possible affinities and origins of the genus are re-examined and it is proposed that the present monotypic family based on *Septirhynchia* should be lowered to the level of a subfamily, the Septirhynchiinae within the Rhynchonellidae. The known stratigraphical and geographical distribution of the genus is reviewed, showing an apparent restriction to the Callovian of the south Tethyan region.

THE Jurassic rhynchonellid brachiopod genus *Septirhynchia* (Muir-Wood 1935) has been considered sufficiently distinct from other Mesozoic forms to be placed in a separate family, the Septirhynchiidae (Muir-Wood and Cooper 1951). The presence of a ventral median septum and a cardinal process in the brachial valve, in conjunction with large size and pentameroid appearance, were features that suggested a possible complete separation from the mainstream of Mesozoic brachiopod evolution (e.g. Ager 1959, p. 327; Ager *et al.* 1972, p. 221).

Members of this genus have been reported from Callovian and Kimmeridgian sediments of East Africa, the Middle East, and North Africa. The internal structures of the group have been little studied, mainly because of limited material, so that previous knowledge of internal structures rested almost entirely on a few silicified specimens described by Muir-Wood and Cooper (1951). In that paper, however, the occurrence in the same sediments as *Septirhynchia* of forms externally similar but lacking one or both diagnostic internal structures was noted. Subsequently, Dubar (1967) and Rousselle (1970) have reported other forms apparently homeomorphic with *Septirhynchia* from the Jurassic of North Africa. The consequent uncertainty over the validity and constancy of the internal morphology of *Septirhynchia* has compounded the problem of relating this genus to other rhynchonellid groups.

In the course of fieldwork in southern Tunisia, one of us (C. D. W.) collected nearly 100 specimens of a new species of *Septirhynchia* from Callovian sediments. Detailed studies of the internal morphology of this species at different ontogenetic stages have revealed information on the characteristics, status, and probable affinities

of the genus. An interpretation of these internal and external features in terms of functional morphology has produced conclusions which have wider ranging implications for brachiopod taxonomy.

SYSTEMATIC PALAEOLOGY

Abbreviations. L, length; W, width; T, thickness (all measurements to the nearest mm). NVC, no. of ventral valve costae; NDC, no. of dorsal valve costae (as counted at commissure).

Family RHYNCHONELLIDAE Gray, 1848

Subfamily SEPTIRHYNCHINAE (Muir-Wood and Cooper, 1951; *nom. transl.* herein)

Genus SEPTIRHYNCHIA Muir-Wood, 1935

Septirhynchia numidiensis sp. nov.

Plate 36, figs. 1-14; text-figs. 1-4

Derivation of name. After Numidia, the ancient kingdom and Roman province of northern Africa.

Type locality. 60 m below the summit of Djebel Broumett marked by the 'Poste Optique', approximately 1.5 km north-west of Tatahouine, near Medenine, southern Tunisia.

Age and distribution. Confined to the lower portion of the Foum Tatahouine Limestone and Marls Formation (Busson 1967) in the area around Tatahouine. All material was collected from a single horizon, probably of early Callovian age (Busson 1967). The presence of *Erymnoceras* sp. some 20 m above this bed would tend to confirm this age.

Material. Approximately 100 specimens, some very fragmentary. Holotype and figured paratypes deposited at the Department of Palaeontology, British Museum (Natural History), London, catalogue numbers BB 76530-76539. Other paratypes will be housed in the Department of Geology, University College, Swansea, and Service géologique de Tunisie.

Diagnosis. *Septirhynchia* with subtriangular outline, adult size large for genus. Typically with a strong median sinus on the ventral valve. The number of costae on each valve decreases from 13 in the juvenile to 8 or 9 in the adult, the average being 10, of which 2-3 lie in the ventral sinus. The umbo of the ventral valve is sharply pointed and strongly incurved in the adult form.

Dimensions. The material may be divided conveniently into two groups, the smaller specimens, relatively much thinner, with width often greater than length, and the larger, more globose forms which have thickness

EXPLANATION OF PLATE 36

Septirhynchia numidiensis sp. nov., Callovian, Djebel Broumett (southern Tunisia). All specimens are oriented with the pedicle valve uppermost. All $\times 1$.

Figs. 1-5. Holotype BB 76530 (adult). 1, posterior view; 2, dorsal view; 3, lateral view; 4, anterior view; 5, ventral view.

Figs. 6, 10. Paratype BB 76534 (narrow adult). 6, posterior view; 10, lateral view.

Figs. 7, 8, 11. Paratype BB 76535 (small adult). 7, lateral view; 8, posterior view; 11, dorsal view.

Fig. 9. Anterior view of juvenile specimen BB 76539a.

Figs. 12-14. Paratype BB 76532 (juvenile). 12, dorsal view; 13, posterior view; 14, lateral view.



MANCENIDO and WALLEY, *Septirhynchia numidiensis*

as their greatest measurement with length being greater than width. There is, however, a continuous gradation between these two groups which are interpreted as being the juvenile and adult individuals respectively.

The following are typical values. Specimens BB 76532-76533 are the extremes of the size range collected.

Holotype	(BB 76530)	L = 45;	W = 44;	T = 45;	NVC = 11;	NDC = 10
Paratype	(BB 76531)	L = 49;	W = 41;	T = 46;	NVC = 10;	NDC = 9
"	(BB 76532)	L = 25;	W = 26;	T = 19;	NVC = 12;	NDC = 13
"	(BB 76533)	L = 57;	W = 62;	T = 58;	NVC = 9;	NDC = 8
"	(BB 76534)	L = 54;	W = 43;	T = 57;	NVC = 9;	NDC = 8
"	(BB 76535)	L = 36;	W = 41;	T = 31;	NVC = 10;	NDC = 9
"	(BB 76536)	L = 47;	W = 40*;	T = 42;	NVC = 12*;	NDC = 11
"	(BB 76537)	L = 34;	W = 34;	T = 26;	NVC = 13;	NDC = 14
"	(BB 76538)	L = 36;	W = 33;	T = 29;	NVC = 12;	NDC = 11
"	(BB 76539a)	L = 29;	W = 18*;	T = 21;	NVC = 10*;	NDC = 10*
"	(BB 76539b)	L = 50;	W = 46;	T = 49;	NVC = 10*;	NDC = 9*

* Approximate, due to crushing of specimen.

Variation in the number of ribs of the fifty-nine measurable specimens according to size classes (based on averaging length and width)

Number of ribs (ventral valve)								L + W
7	8	9	10	11	12	13	14	2
—	1	2	1	1	—	—	—	50-59
1	1	2	7	7	6	—	—	40-49
—	1	1	6	10	4	—	1	30-39
—	—	—	1	2	1	2	1	20-29

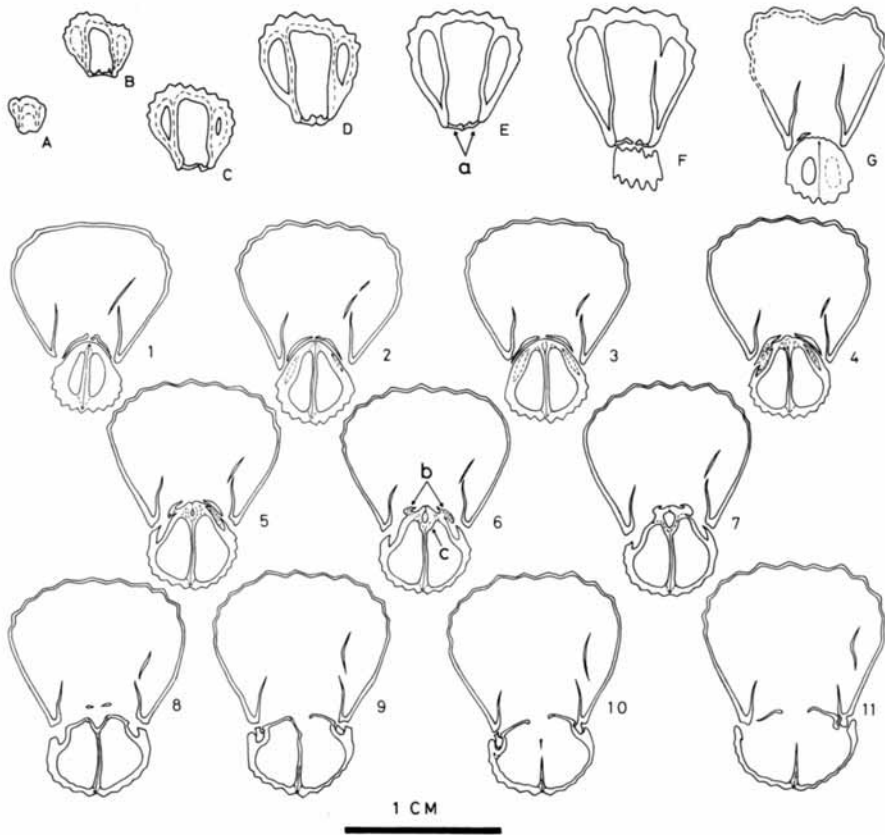
Description

Exterior. Strong differences are present in external morphology between adult and juvenile forms. There are, however, many transitional forms, and the shape of the juveniles can be recognized in the growth lines of the adults, suggesting a simple ontogenetic series.

In juveniles the valves are moderately convex, with width approximately equal to or greater than length. The ventral umbo is gently curved and the foramen faces dorsally. There is only a slight trace of a ventral sinus and the anterior commissure is a simple rectimarginate type with a zig-zag serial deflexion superimposed. Lateral commissure nearly straight with only the slightest dorsal projection of the posterior of the ventral valve. Juveniles have a maximum of thirteen or fourteen low, angular costae (as measured at the commissure) and the bare planareas of the valves are small and only slightly concave.

Adult forms tend to be gibbous, with both valves strongly incurved. In particular, the umbo of the ventral valve almost touches the dorsal valve in some adults and the minute foramen faces ventrally (Pl. 36, fig. 10). The ventral valve completely encloses the umbo of the incurved dorsal valve and the deltidial plates are concealed. The conspicuous ventral sinus originates some distance from the apex of the pedicle valve and deepens gradually towards the anterior commissure where it is marked by a simple uniplication combined with a zig-zag serial deflexion. The lateral commissure is deflected dorsally along its posterior portion by a dorsal protrusion of the ventral valve, which in fact projects some way inside the brachial valve forming a feature comparable to the 'squama and glotta structure' of uncinulid brachiopods discussed by Westbroek *et al.* (1975). The valves have from eight to ten coarse angular costae which may be up to 10 mm wide, the sinus generally containing two or three costae. The decrease in number of costae from juvenile to adult stage is due to the relative expansion of the planareas at the expense of the small lateral costae, in the same fashion as described by previous workers in other species of *Septirhynchia*. The planareas of both valves are smooth and deeply concave, giving the posterior part of the shell a characteristic 'hour-glass' outline in transverse section (text-fig. 2).

There is a good deal of variation in the morphology of the adult form and a few large specimens with a wide anterior commissure and less pronounced gibbosity are known.

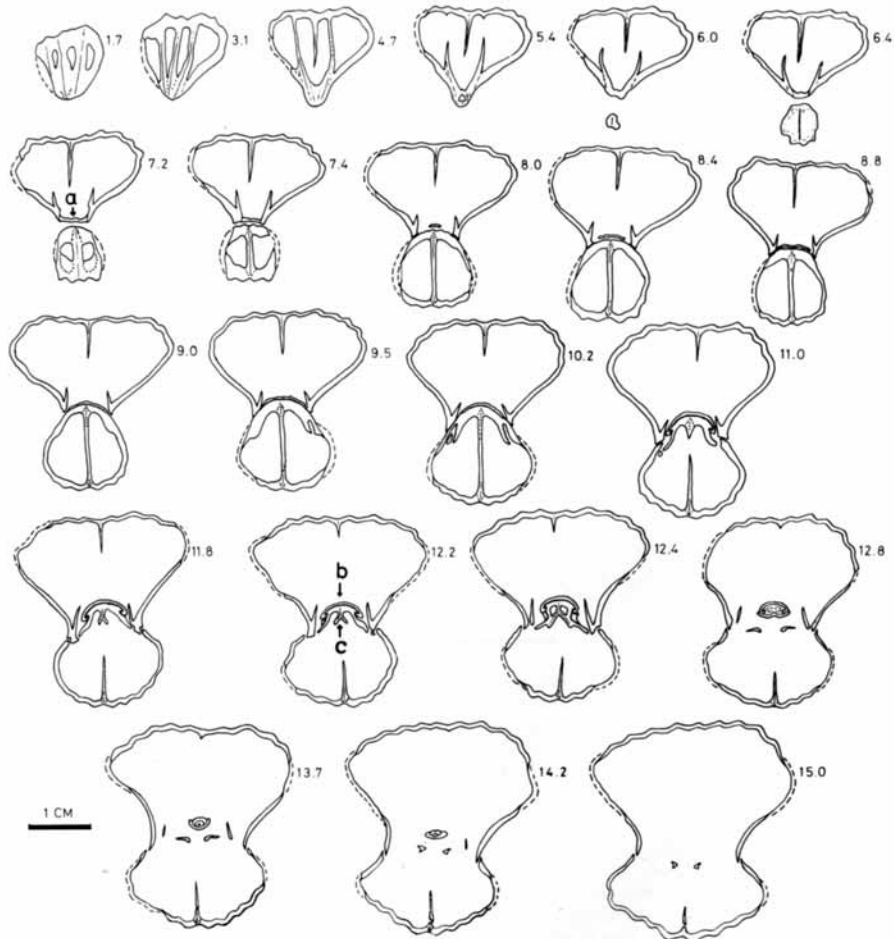


TEXT-FIG. 1. Enlarged transverse serial sections drawn from acetate peels of juvenile specimens of *Septirhynchia numidiensis*. A-G, individual crushed anteriorly; original length 29 mm; this sequence extends to 3.5 mm from the tip of the beak. 1-11, individual with a broken beak (so distance from ventral umbo not shown); original length of specimen approx. 25 mm; this sequence 1-11 covers an interval of 5 mm from the brachial umbo. Key a = deltidial plates, b = incipient cardinal process, c = normal septalium.

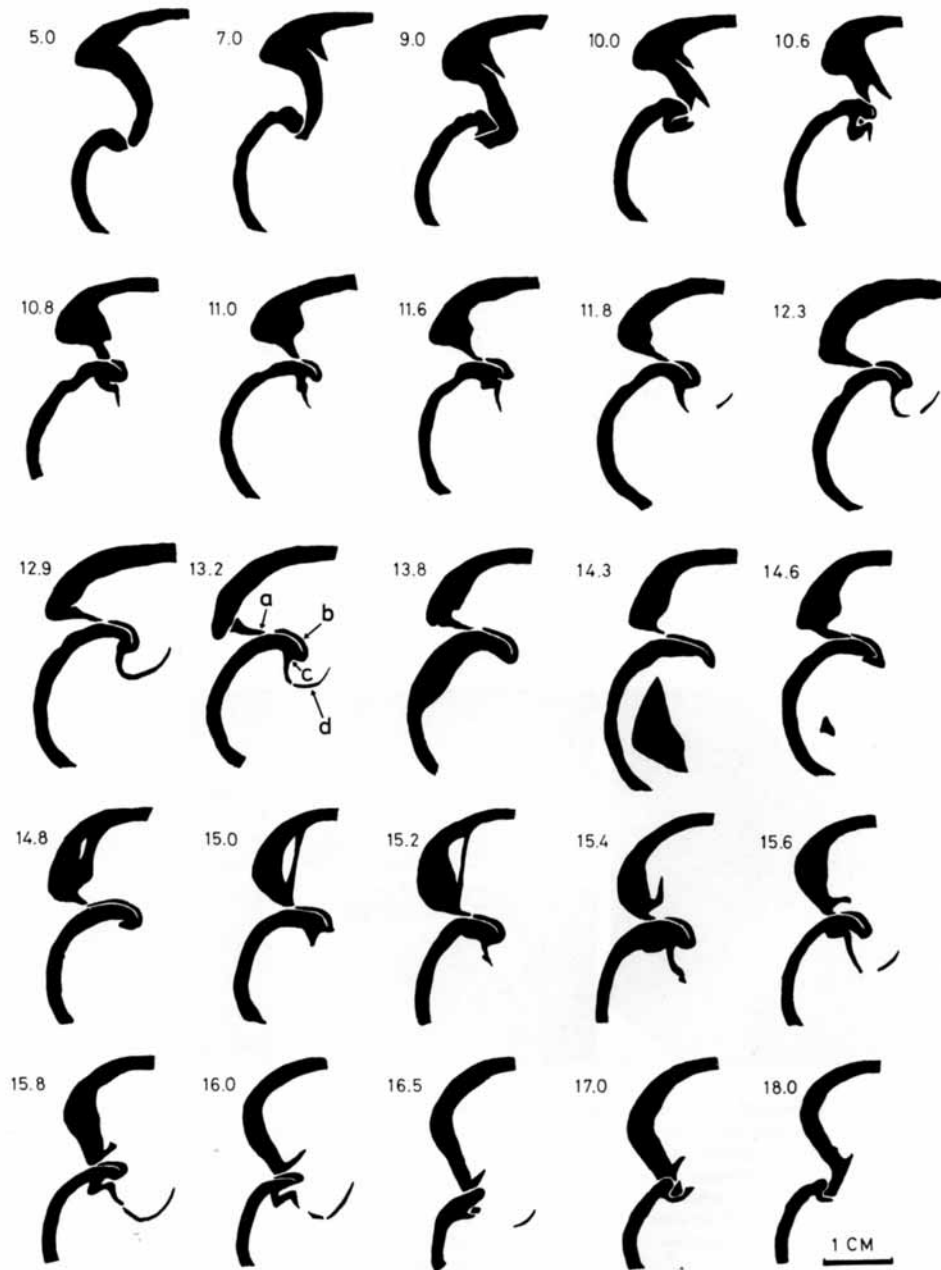
Interior. Remarkable differences have been observed between the internal structures of the sectioned juvenile and adult individuals, although the examination of a number of other specimens has revealed a continuous series of intermediate forms. Among the juveniles the smallest specimen examined was posteriorly broken but originally was probably only a little over 25 mm long. The internal structure of this type, as revealed by serial grinding, is shown in text-fig. 1 (1-11).

The delthyrial chamber is bounded by two dental lamellae which lie parallel to the plane of symmetry in section, diverging from each other anteriorly. The dental lamellae sharply decrease in height anteriorly and project straight into the dorsal valve forming massive, smooth teeth which are completely enclosed by the sockets of the dorsal valve. The deltidial plates are disjunct.

A ventral median septum is absent in this specimen. Careful sectioning of the umbonal region of a slightly larger (29 mm long) specimen (text-fig. 1A-G) and examination of other fragmentary forms has shown that there is no trace of a ventral septum in juveniles of this species. In a number of what might be termed younger adult forms the ventral septum is represented only by a low ridge. Unbroken weathered adult specimens (and also the silicified *S. pulchra* and *S. azaisi* figured by Muir-Wood and Cooper, 1951, pl. 1, fig. 8; pl. 2, figs. 2, 6) show that the ventral median septum disappears towards the umbo, confirming the absence of this feature in the juvenile.



TEXT-FIG. 2. Transverse serial sections drawn from acetate peels of an adult specimen of *Septirhynchia numidiensis*. Distance from ventral umbo given in mm. Length of specimen 39 mm. Key: a = fused deltidial plates, b = cardinal process, c = overturned septalium.

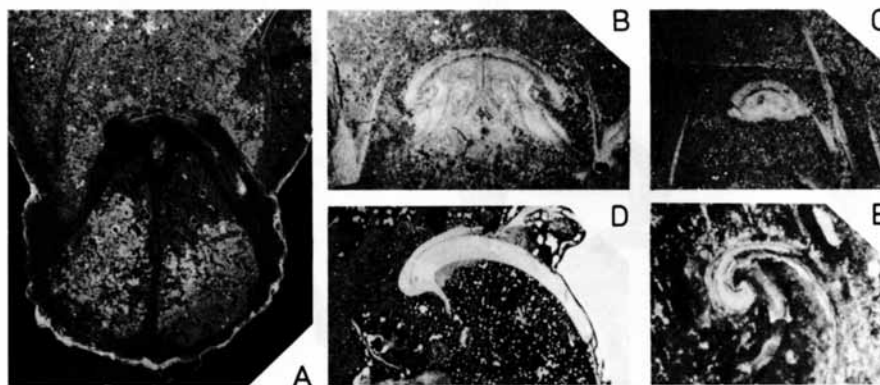


TEXT-FIG. 3. Longitudinal serial sections drawn from acetate peels of an adult specimen of *Septirhynchia numidiensis*. Measurements given are from lateral edge of specimen in mm. Length of specimen 38 mm. Key: *a* = fused deltidial plates, *b* = recurved cardinal process, *c* = overturned septalium, *d* = raduliform crus.

The brachial valve has a simple septalium [used here in the restricted sense of Childs (1969), which is equivalent to Pearson's (1977) 'muscle trough'] and delicate raduliform crura. The dorsal median septum is present in the very smallest forms examined. A pedicle collar has been observed in one or two juveniles.

Two adult forms have been transversely serial-sectioned, of which one is figured (text-fig. 2). A third adult has been sectioned longitudinally (text-fig. 3). All the sectioned forms and some fragmentary specimens show consistently similar internal features. The ventral valve contains a large blade-like median septum, up to 8 mm in depth in some specimens, which extends from near the valve apex towards the anterior where it ends suddenly, generally about midway along the valve. In specimens which have been developed out of the matrix the septum surface can be seen to be smooth and to lack any signs of muscle attachment areas. The dental lamellae are thin and decrease in height rapidly anteriorly, and project straight dorsally into the brachial valve where they form massive teeth. The sockets in the dorsal valve do not enclose the teeth antero-dorsally (text-fig. 2, 10.2-11.8). The deltidial plates are fused anteriorly to form a henidium and a small pedicle collar can sometimes be recognized.

The dorsal valve is so incurved that the septalial cavity faces dorsally. The umbo is covered and partially enveloped by a series of thin calcite sheets which form a complex structure on top of, and to some extent enfolding, the septalium. This is the so-called cardinal process of Muir-Wood and Cooper (1951) and can be clearly seen in text-fig. 3, 10.8-16.0. The main feature of this structure is the thin sheet extending back posteriorly over the brachial umbo (see also text-fig. 2). The simple raduliform crura, triangular in cross-section, are strongly curved towards the ventral valve and lack terminal processes. The high, thin, blade-like dorsal median septum ends abruptly in the anterior portion of the valve. In both adults and juveniles neither Buckman's calcination technique nor examination of natural internal casts has yielded any reliable evidence of muscle scars.



TEXT-FIG. 4. Selected set of acetate peels to illustrate details of internal structure. A-D, *Septirhynchia numidiensis* sp. nov. from the Callovian of Djebel Broumet (southern Tunisia); A, section of juvenile specimen showing typical septalium and incipient cardinal process (equivalent to section 6 of text-fig. 1), $\times 7.5$; B, posterior portion of cardinal process showing overturned septalium (equivalent to section 12.2 of text-fig. 2), $\times 4$; C, apex of brachial valve enveloped by skeletal material from the cardinal process (equivalent to intermediate condition between sections 12.8 and 13.7 of text-fig. 2), $\times 4$; D, enlarged portion of saggittal section of paratype BB 76536 (adult) showing nature of cardinal process and crura base (equivalent to sections 12.3-15.6 of text-fig. 3), $\times 3$; E, enlarged portion of transverse section across the umbo of a left valve of the Recent pholadacean bivalve *Barnea candida* (Linnaeus) from Swansea Bay (South Wales), showing the nature of the umbonal reflection for comparison, $\times 4$.

Taxonomic remarks. *Septirhynchia numidiensis* is distinguished from previously described species by its subtrigonal outline, the presence of a prominent ventral sinus, and the nine to twelve, wide, angular costae. Only two other species (each described from single specimens) are sufficiently similar to *S. numidiensis* to deserve more detailed comparison. *S. madashonensis* Muir-Wood (1935) is based on a fragmentary specimen with fifteen broad costae. No specimen of *S. numidiensis* of a similar size is either as spherical or possesses such a deep sinus. *S. pulchra* Muir-Wood and Cooper (1951) has the closest resemblance to the new species but has more costae (13), is less trigonal in outline, and seems to have a less well-defined sinus. The only specimen described appears, on the basis of internal and external evidence, to have attained an ontogenetic stage equivalent to much larger forms of *S. numidiensis*. The material described from other Tunisian localities by Dubar (1967) as *S. pulchra* more closely resembles the new species and might be conspecific. In addition the specimen figured by Stefanini (1932, pl. 4, fig. 9) as *Rhynchonella azaisi*, from what was then Italian Somaliland does not appear to belong to Cottreau's species but seems more closely related to either *S. numidiensis* or even *S. pulchra*.

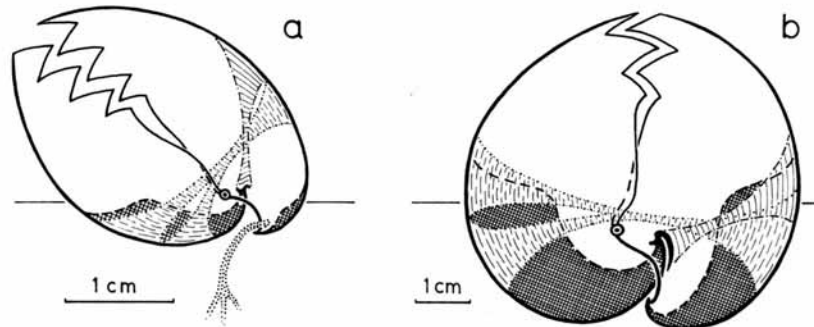
Palaeoecology and functional morphology

S. numidiensis occurs in a pale-grey micrite, in which it is locally abundant. There is little associated fauna other than rare, poorly preserved regular echinoids and nerineid gastropods. Some slight transportation seems to have taken place in that a number of the larger specimens are disarticulated and there is an absence of forms below 20 mm in length. A number of the larger specimens are found buried with their umbones downwards.

Almost all the adult specimens studied have their anterior commissures crushed. This, together with their strongly incurved gibbous profile and the tiny, obscured foramen implying extreme reduction (or loss) of a functional pedicle, suggests that these adult forms lived unattached, their umbones buried in soft sediment with the lateral commissure approximately vertical. In fact such an orientation is the only stable one which would have kept the gaping portion of the commissure clear of the muddy substrate. That specimens have actually been found in such a position would strongly support this hypothesis as it is most improbable that any transported shells would have come to rest in such an orientation.

Nearly all the features of the adult morphology can be interpreted as adaptations to this mode of life. The projection of the ventral planareas into the dorsal valve appears to have been a device to allow the gaping of the valves without mud seeping through the buried posterior portion of the commissure. Westbroek *et al.* (1975) proposed a similar function for an analogous structure in Devonian uncinulids. A consideration of how these overlapping commissural portions worked in *Septirhynchia* as the valves were opened reveals that this structure was a very efficient yet economic way of sealing the lateral commissure using the minimum of skeletal material (text-fig. 5). The anterior limits of this 'double sealing' of the shell may be assumed to mark the maximum permissible burial depth of the organism.

The fused deltidial plates (the henidium) of the adult appear to have served a similar purpose in preventing mud from entering over the enclosed dorsal umbo. This sealing of the umbonal part of the shell is so complete that when serial grinding it is easy



TEXT-FIG. 5. Idealized internal reconstruction of *S. numidiensis* at two ontogenetic stages: *a*, 'late' juvenile, and *b*, adult. These approximately correspond to the growth stages of the sectioned specimens shown in text-figs. 1 and 2. Both are oriented in the same way as in text-fig. 6, but the juvenile has been enlarged twice relative to the adult to facilitate comparison. The specimens are drawn as though the shell were transparent but with the septalium and cardinal process shown in sagittal section, and with crura and dental lamellae omitted for clarity. Key: cross-hatching = dorsal and ventral median septa; continuous lines = diductor muscles (contracted); broken lines = adductor muscles (relaxed). Circle marks hinge axis. Musculature and pedicle morphology necessarily somewhat speculative.

to overlook the abrupt passage from the henidium to the thin recurved sheet of the cardinal process (text-fig. 3, 11·8-15·6).

The gibbous shape of the adult and the strongly incurved pedicle beak would have allowed both umbones to lie at approximately the same level within the mud. This and the symmetrical balance of the approximately equal valves (when the commissure is vertical) would have given the animal a certain stability and helped prevent toppling over. The development of a fold and sulcus almost certainly aided the separation of the inhalant from the exhalant water currents (cf. Rudwick 1970). The associated ventral sinus would have helped to channel the exhalent currents away.

The juveniles of this species, lacking any of these features and with a less incurved beak and proportionately larger foramen, can be assumed to have had a functional pedicle by which they were attached to the substrate either by a stalk-like pedicle or else by a ramifying, byssus-like structure (cf. Rudwick 1961). The differences in external morphology between the juveniles and adults reflect these very different modes of life and for the most part the variation in internal structure can be similarly explained. These differences are summarized in text-fig. 6.

A comparison of text-fig. 5*a* and *b* suggests that the fractional volume of the organism occupied by skeleton was not constant but diminished throughout ontogeny, thus decreasing the bulk density of the animal. Thayer (1975, p. 182) has shown how this may be advantageous for organisms living on soft sediment and also (p. 186) that a certain degree of sinking would have provided a greater load bearing area for the adult shell. The increase in gibbosity of the valves during ontogeny appears to have been largely due to an allometric mode of growth, clearly evident in the gradual increase of the spiral angle of growth (cf. text-figs. 5-6 and Thompson 1942, fig. 352).

In the dorsal valve, such increasing curvature would have presented problems for the attachment of the diductor muscles in that the orientation of the septalium would have been shifted until it faced dorsally in a useless position. This problem was solved by the development of a thin enveloping calcite sheet which grew back over the umbo, keeping pace with the incurvature and forming the cardinal process (text-figs. 3; 4B, C, D; and 5). The calcite sheet also wrapped around the septalium forming an extremely strong, wide base for muscle attachment. In the mode-of-life model proposed, the pressure of mud against the posterior portion of the shell would have been such as to require powerful diductor muscles (and hence a wide, firm muscle platform). The approximate arrangement of these muscles, inferred from the relationships of the hinge mechanism (cf. Jaanusson and Neuhaus 1965; Rudwick 1970), are indicated in text-fig. 5.

The differences in dentition between the juveniles and adults are also significant. In the adult the dental sockets are open antero-dorsally, a feature that is only explicable if the anterior commissure was orientated upwards so that the teeth were held in by gravity. Disarticulation has not been noted in the juvenile specimens whilst disarticulated (but largely unbroken) adult valves are not uncommon.

This saving of skeletal material in the formation of the adult sockets, the thinness of the valves, and the minimal nature of the overlap of the lateral commissure suggest that skeletal economies were important in *S. numidiensis*. It is possible that this may have been due to the need to keep body weight as low as possible in order to prevent excessive sinking in the soft muddy substrate. In view of this it seems unlikely that the ventral median septum was non-functional, although the precise function it performed cannot be determined with certainty. It was most probably involved in strengthening the shell, although this is difficult to prove. A paradigmatic approach to interpreting this structure, in the fashion of Rudwick (1964, 1968), is difficult because any such structure must be a compromise between architectural optimization and biological constraints, with major uncertainties attached to both. It would seem likely, however, that the main stresses would have been vertical (due to shell weight) and perpendicular to the commissural plane (due to sediment pressure against the opening valves). A thin blade-like structure oriented in the plane of both stresses might have been the best compromise, especially in view of the apparent restrictions on building more massive skeletal features.

Evidence for such a function comes from the abrupt termination of the septum, coinciding with the level of the anterior end of the overlapping portion of the lateral commissure, a point indicative of the maximum tolerable depth of burial (see above). The absence of the septum in other, smaller Jurassic rhynchonellids which are heavily thickened and in the juveniles of the species under discussion, further suggests a function associated with one of the unusual features of *Septirhynchia*, such as its mode of life or large adult size. Whilst proving a strengthening function for the ventral septum is difficult, the fact remains that alternative functions that would have been of value to the adult *Septirhynchia* are difficult to imagine. It has been suggested to the authors that the lack of a ventral median septum in the juvenile might have been due to the need for a large pedicle capsule, which subsequently atrophied allowing the growth of a median septum to help support the body wall anteriorly.

There are other features which suggest possible behavioural adaptations to the semi-infaunal mode of life. It seems likely that *S. numidiensis* could have maintained a constant depth of burial during periods of sedimentation as the very process of opening the valves even slightly would have tended to lever the organism upwards in the sediment. In this case the loss of a functional pedicle would have been a distinct advantage in allowing free movement upwards.

The gregarious association of *S. numidiensis* would have been of advantage in breaking up slow water currents into more turbulent eddying flow, which would have been better for the feeding current system of the individuals.

A broadly similar mode of life has been invoked for a number of Palaeozoic groups. Ivanova *et al.* 1964 (re-figured in Ager 1967a) and Ziegler *et al.* (1966) have suggested on the basis of field evidence that a number of Silurian and Devonian pentameroid brachiopod species lived with their umbones downwards. Westbroek *et al.* (1975) made a similar suggestion for Devonian uncinulids, as did Grant (1971) for the Permian tetracamerid *Septacamera*. Many of these forms share common morphological features with *Septirhynchia*, probably representing convergence due to similar life habits.

THE GENUS SEPTIRHYNCHIA—A REAPPRAISAL

In this section an attempt is made to reinterpret all the available information on the genus *Septirhynchia* in the light of the results of the studies of *S. numidiensis*. Particular problems considered are those of the supposed homeomorphs, the generic characteristics, the origin of the cardinal process, and the taxonomic affinities of the genus.

The variation between juvenile and adult forms of *S. numidiensis* has been discussed above and is summarized in text-fig. 6. There is considerable evidence that such variation is also present in the other species of *Septirhynchia*. For instance, Dubar (1967) described a new species of rhynchonellid, *Rhynchonella pseudoazaisi* for a form which, except for its lack of a ventral median septum, seemed to him to have the appearance of being a juvenile of *S. azaisi* (Cottreau) with which it was found associated. The serial sections that he figured (p. 51, fig. 3) are very similar to those from the young specimens of *S. numidiensis* (text-fig. 1) with a septalium and a cardinal process in an early stage of formation. It would seem therefore that *R. pseudoazaisi* is best regarded as a juvenile form (and consequently a junior synonym) of *S. azaisi* (Cottreau).

Moreover, the small specimens that Dubar described as *R. cf. budulcaensis* on the grounds that they resembled the somewhat larger *S. ?budulcaensis* apart from the absence of a ventral median septum, are probably juveniles of the latter species.

In addition to these examples from Tunisia, a few other cases of alleged homeomorphy with *Septirhynchia* have to be considered before reassessing the nature and status of this genus.

Two specimens were mentioned briefly by Muir-Wood and Cooper (1951, p. 4) as lacking in the one case a ventral median septum, and in the other, both septum and cardinal process. Yet, from what is now known about the ontogeny of *Septirhynchia* and the limited information given about these specimens it would seem that they might well have been juveniles of *S. azaisi* with which they occurred.

By contrast, the specimens of Rousselle (1970) from the Oxfordian/Kimmeridgian of southern Algeria which she called ?*S. cf. budulcaensis* are almost certainly not members of this genus. Their outline, 'normal' rhynchonellid lateral commissure, large number of ribs, and only moderately large size distinguishes them from *Septirhynchia*. Internally there are only a few points of resemblance and the extensive secondary thickening is quite uncharacteristic of *Septirhynchia*. Very similar forms to this species have been collected from the Oxfordian of Morocco by Dr. A. E. Adams and on the basis of internal and external evidence are attributed to the genus *Somalirhynchia*. Also closely comparable are the specimens of *S. cf. africana* (Weir) from eastern Spain, serial sections of which are shown by Ager and Walley (1977, fig. 6). The 'ventral septum' found in one of Rousselle's specimens appears to be little more than a myophragm (euseptoidum) which probably has little generic significance (Cooper 1970, p. 223) and is also known in some species of *Somalirhynchia*. In addition, as discussed below, there is very little evidence for the much cited Kimmeridgian age of *S. ? budulcaensis*, and an early Callovian age is more likely. It would seem therefore that the only records of *Septirhynchia* lacking either the ventral median septum and/or cardinal process that can be accepted almost certainly refer to juveniles.

Hence, taking together this re-interpreted evidence with the known ontogeny of *S. numidiensis*, it seems unavoidable to draw the conclusion that both the ventral median septum and the cardinal process are developed rather late in the ontogeny throughout the genus, with a tentative suggestion that the process was formed slightly earlier than the septum (the fact that forms with a ventral median septum but without cardinal process have not been described may be considered significant).

The development of both features only in the adult forms of *Septirhynchia* involves the variation of internal structures through ontogeny to an extent previously unrecognized in this group, where the 'classical' viewpoint, currently epitomized by Cooper (1970, pp. 220ff.) confers great weight on the existence of reputedly stable internal features (such as cardinal process, septa, etc.) for supraspecific taxonomy.

Rudwick (1970, p. 32) perceptively pointed out that failure to recognize the change in external morphology undergone by a brachiopod during ontogeny 'may even result in an assignment of juvenile and adult individuals to different species or even different genera!' In the case of *Septirhynchia*, with its additional internal modifications, a traditional typological approach to taxonomy would have almost inevitably resulted in juveniles and adults being separated at family level.

This demonstrates the manifest inadequacy of a classification based on the mere presence or absence of a character at an adult stage. Far more desirable is the erection of taxa on the basis of both juvenile and adult morphology and the inclusion of this in the diagnosis. In the absence of juveniles some idea of ontogenetic variation can generally be obtained by a more interpretative approach to adult characters. The development of external features can frequently be traced by examination of the growth lines, and the origins of internal features can often be similarly inferred from details of shell structure (see Ager 1965a, pp. 212-213; Pearson 1977, p. 13). For example, despite the remarkable variation in *S. numidiensis*, there is in fact little about the external and internal morphology of the juvenile that cannot be deduced from the adult form.

Whether the degree of ontogenetic variation seen in *Septirhynchia* is peculiar to that genus or else is common in other brachiopods is unknown and can be ascertained only by much careful work. Such cases might be expected when adults and juveniles of a species are clearly adapted to markedly different modes of life.

Revised diagnosis of Septirhynchia (Muir-Wood, 1935)

On the basis of this new information it is necessary to alter greatly the original diagnosis of this genus, proposed by Muir-Wood (1935, p. 106), and only slightly modified in Muir-Wood and Cooper (1951, p. 2). Confirmation of this revision awaits the detailed study of the type species *S. azaisi*, the internal structure of which (especially the brachial valve) has never been properly investigated. However, it has been possible to examine a good photograph (kindly provided by Mme J. Drot) of the sagittally sectioned specimen which was rather curiously chosen as the lectotype of Cottreau's species by Muir-Wood. This clearly shows a cardinal process similar to *S. numidiensis* in that it is built up of a number of recurving sheets. The assumption throughout this emended diagnosis is therefore that, as discussed above, the ontogenetic variation observed in specimens of *S. numidiensis* is typical of the genus as a whole:

Adult size large, pentameroid in shape, dorsal fold low, median sinus of variable depth. Ventral umbo long and acute, greatly incurved in the adult, concealing minute foramen and deltidial plates which are disjunct in the juvenile but fused later in ontogeny. Dental lamellae strong, uniting with the base of the ventral median septum when present. Ventral septum occurs only in the adult when it may extend to up to two-thirds of the pedicle valve length; in the juvenile it is absent or represented by a low ridge. Dorsal median septum well developed throughout ontogeny. Septalium present in juvenile forms and overturned and concealed by the cardinal process in the adult. The cardinal process is formed by the partial envelopment of the dorsal umbo and septalium by recurved thin calcite sheets. Crura raduliform, simple, and uniformly curved. A pedicle collar may be present. Lateral planareas smooth, well developed, increasing in importance in the adult at the expense of lateral ribs. Posterior lateral commissure arched dorsally for a short distance where the dorsal valve overlaps the extension of the ventral valve. Shell typically ornamented by coarse unbranching costae which may vary greatly in number depending on species and ontogenetic stage.

Distribution of species of Septirhynchia

Partly for the sake of completeness and partly because of the interest in *Septirhynchia* as a typical faunal element of the Jurassic Ethiopian Province (e.g. see Ager 1967b, 1973; Hallam 1975) a brief review of the records of the component species and their stratigraphical and geographical distribution is given below (see also text-fig. 7).

S. azaisi (Cottreau) (1924, p. 581, pl. 17, figs. 1-4) was made the type species of the genus *Septirhynchia* by Muir-Wood (1935, p. 107, pl. 9, figs. 3, 4) who figured another specimen also from the Somalia/Ethiopia region and gave a short list of early synonyms. Muir-Wood and Cooper (1951, p. 4, pl. 1, figs. 6-10) and Jaboli (1959, p. 26, pl. 4, fig. 1) also described specimens of this species from the same area. Dubar (1967, p. 48, pl. 1, figs. 4, 7) described *S. azaisi* from southern Tunisia as well as *Rhynchonella pseudoazaisi* which we believe to be its juvenile form as discussed above. In the East African region the age of *S. azaisi* is not really known with precision but is generally given as Callovian. In Tunisia, the specimens of Dubar come from horizons of early to possibly mid Callovian age. *S. madashonensis* Muir-Wood (1935, p. 109, pl. 10, fig. 11) was described from a single incomplete specimen from the Callovian of eastern British Somaliland. Another single specimen has been identified by us from Tunisia, where it is found slightly below the *S. numidiensis* horizon and is therefore probably of early Callovian age (see also the list of unconfirmed records of *Septirhynchia* below). *S. mogharaensis* Muir-Wood (1935, p. 110) was based on the specimen figured by Douvillé and Cossmann (1926, p. 326, pl. 7, fig. 9) as *R. decorata* (Schlotheim) from the Callovian (possibly Bathonian) of Sinai.

S.? *budulcaensis* (Stefanini) (1932, p. 109, pl. 5, figs. 1, 2) was originally referred to *Rhynchonella* (*Stolmorhynchia?*), and included a form figured by Weir (1929, p. 36, pl. 4, fig. 5) as *Stolmorhynchia azaisi* (Cott.) var. from the 'Kimmeridgian' of Somalia, but Muir-Wood (1935, p. 106) transferred it to her new genus *Septirhynchia*. Possibly conspecific are *Rhynchonella inflata* Jaboli (1959, pp. 17-18, pl. 2, fig. 1) from approximately the same area, and *R. (Stolmorhynchia?) affii* Farag and Gatinaud (1962, p. 85, pls. 1-11, fig. 5) from the Callovian of Maghara, Sinai, which were both included by Dubar in the synonymy of the forms he described as *R. cf. budulcaensis* Dubar (1967, p. 52, pl. 1, figs. 8, 9). As discussed previously these were almost certainly juveniles of *Septirhynchia? budulcaensis*: we have identified further specimens of this species in material from approximately the same horizon and locality in southern Tunisia. Although frequently quoted as being a Kimmeridgian species, there is very little real evidence for this and the age of the Tunisian specimens is either earliest Callovian or latest Bathonian. *S. pulchra* Muir-Wood and Cooper (1951, p. 2, pl. 1, figs. 1-5, 11, 12, pl. 2, figs. 1-6) was described from a single silicified specimen from the Callovian of Ethiopia. Whether the specimens attributed to this species by Dubar (1967, p. 46, pl. 1, figs. 1, 2) belong here with *S. pulchra* or with *S. numidiensis* is not completely clear.

S. numidiensis is currently known with certainty only from the Lower or Middle Callovian sediments of southern Tunisia.

A survey of the literature and an examination of the brachiopod collection of the British Museum (Natural History) has provided a great deal of information on the geographical range of *Septirhynchia*.

We have examined a plaster cast of a single specimen identified by Doudet (1959, p. 36, pl. 4, fig. 2) as *Stolmorhynchia* sp. from the Callovian of Andranomantsy, northern Madagascar (kindly provided by Dr. J. H. Delance). It has external features very similar to *Septirhynchia madashonensis* Muir-Wood but unfortunately information on internal structures is lacking.

Specimens from the Callovian Muddo Erri Limestone of north-east Kenya (Muddo River locality) include forms identified as *S. azaisi* by Muir-Wood (MS.) and others attributable to *S. madashonensis* and *S.?* *cf. budulcaensis*.

A number of poorly preserved specimens from Djebel Hagab on the Oman Peninsula are definitely *Septirhynchia* but cannot be satisfactorily identified below generic level. This suggests that the unfigured record of *S. azaisi* from the Middle-Upper Jurassic Surmeh Formation, at Surmeh, in Iran by James and Wynd (1965, p. 2198) may be genuine but so far this has not been confirmed.

Similarly, two references to *S. azaisi* are made in the *Lexique Stratigraphique* for Lebanon and Syria (Dubertret 1963). In both cases the ages are imprecisely known but possibly Callovian. In one case (p. 75) Dubertret records '*Rhynchonella azaisi* Stef. (non Cott.)' from northern Lebanon and in another (p. 77) *R. azaisi* (Cott.) is reported from Djebel Ansariyeh, north-western Syria. Furthermore, there are a few fragmentary specimens from the latter area in the British Museum which can be confidently assigned to *Septirhynchia*.

Museum material from the Callovian strata of the Zerka River area of western Jordan contains a single specimen which is very similar in morphology to *S.?* *budulcaensis*.

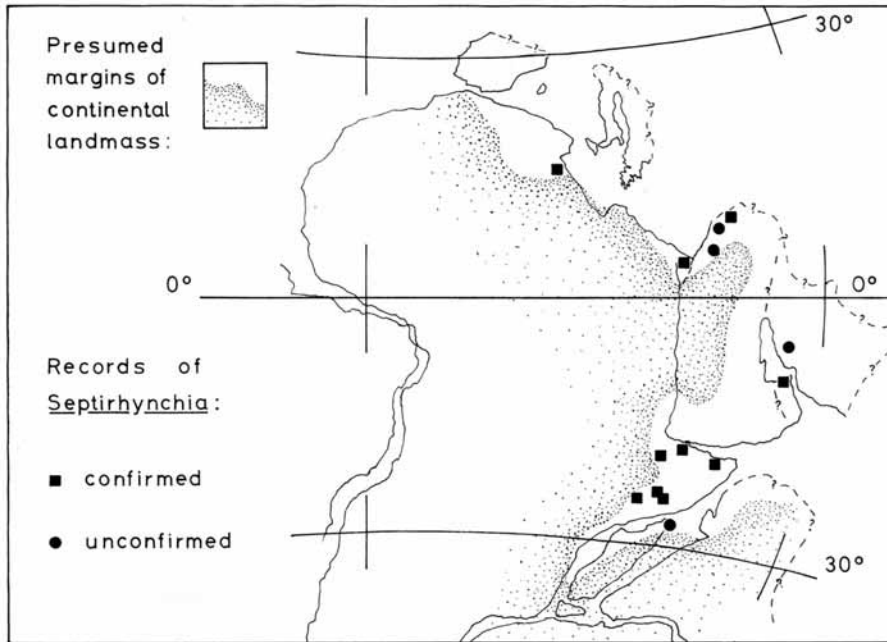
Other forms which resemble *S.?* *cf. budulcaensis* have been described and illustrated, under a so far unpublished (and hence unavailable) generic and specific name, from the Middle-Upper Dhurma Formation (Bathonian-Callovian) of Djebel Tuwaiq, central Saudi Arabia, by Nazer (1970, p. 40, pl. 3, figs. 2-5, pl. 4, fig. 1).

Other very large Callovian rhynchonellids in the British Museum from Hadramaut and Kutch (India) have also been examined but they appear to have only the most superficial similarities to *Septirhynchia*. A decision on the affinities of such forms must await further work on these poorly known faunas.

The geographical distribution of *Septirhynchia* is illustrated in text-fig. 7. The distribution around the palaeoequator is particularly noteworthy. Summarizing the stratigraphical distribution, *Septirhynchia* appears to be confined to Lower and Middle Callovian sediments, with the possibility of some species being late Bathonian in age.

There is unfortunately little stratigraphical data on the provenance of the earliest *Septirhynchia* faunas. Despite the genus being commonly considered a typical faunal representative of the Ethiopian province, there is in fact no unequivocal evidence that *Septirhynchia* originated in the East African area.

There is a little more evidence for the stratigraphical distribution of the species within the genus, if the sequence in Tunisia is representative. Dubar (1967) found *S.?* *budulcaensis* as the earliest form, well below strata containing *S. azaisi* and *S. 'pulchra'*. Work by one of us (C. D. W.) has in part confirmed this, having found *S.?* *budulcaensis* at the same level as Dubar (late Bathonian-early Callovian), and some distance



TEXT-FIG. 7. Geographical distribution of *Septirhynchia*. Map based on the Callovian palaeocontinental reconstructions of Smith and Briden (1977, p. 66) using an equal-area projection. Approximate position of shoreline derived from various sources.

above this, a horizon with *S. madashonensis* a few metres below the horizon with *S. numidiensis* (to which Dubar's *S. pulchra* may belong). *S. numidiensis* appears to be the youngest species, at least in Tunisia. Whether this sequence has any more than local significance is not known.

Ancestry and higher taxonomy of Septirhynchia

The results of the studies of *S. numidiensis* have cast new light on the possible ancestry and taxonomic position of the genus *Septirhynchia*. In particular the emphasis placed on the presence of the cardinal process needs to be re-examined.

The cardinal process of *Septirhynchia* seems to differ fundamentally from all other brachiopod cardinal processes so far described. No structure comparable in mode of formation to this recurving and growing back of skeletal sheets over the brachial umbo is known to us amongst the brachiopods. There is a very close analogue in Recent pholadacean bivalves where, in such species as *Barnea candida* (Linnaeus) (the white piddock), the anterior adductor muscle has migrated from just inside the valve over the umbo. This process results in the muscles, with an associated skeletal accessory plate, becoming attached to the so-called umbonal reflection, thus overlying what was originally the external surface of the umbo (see text-fig. 4D, E).

The cardinal process of *Septirhynchia* is well seen in the single silicified specimen of

S. pulchra figured by Muir-Wood and Cooper (1951, pl. 1, figs. 11, 12, pl. 2, figs. 3-6) showing many of the features described in *S. numidiensis*. Although Muir-Wood and Cooper noted that a septalium was present and 'partially concealed by the incurvature of the umbo' (p. 3) no attempt was made to explain the presence of two structures for the same function.

The uniqueness, and yet at the same time, the fundamental simplicity of the cardinal process in *Septirhynchia*, coupled with the presence of a septalium in the juvenile, suggests that it has developed secondarily. There is no evidence for this feature having been inherited from a Palaeozoic ancestor. It will be very interesting to see if similar cardinal processes, probably also associated with enclosed, highly incurved brachial umbones can be found in other rhynchonellid groups.

Some answers to the questions surrounding the ancestry and affinities of *Septirhynchia* can now be proposed in view of our new knowledge of the genus. In particular it would seem that if the characteristic adult features of the genus are directly or indirectly adaptations for a certain mode of life and they are absent in the youngest forms, then it can be assumed that even an immediate ancestor need not have possessed these features. In such a case a suitable ancestral stock would have probably been characterized by a sharp beak, a septalium, raduliform crura, and a dorsal septum, all features that are common in the subfamily Tetrarhynchiinae of the Rhynchonellidae.

The most immediately obvious candidate for such an ancestral form amongst the Bathonian Tetrarhynchiinae is *Isjuminella decorata* (Schlotheim). This large, coarsely costate form, known from France and Portugal, has recently been reviewed by Alméras (1966) and Drot and Fischer (1966) and has a number of features in common with *Septirhynchia*. Externally it is a fairly globose form, with strongly incurved umbones, a tiny foramen, and well-developed planareas. It is also extremely variable (Drot and Fischer 1966, figs. 10-21) with some forms looking very much like *Septirhynchia* (in many early records, species of *Septirhynchia* were either compared with or identified as *Rhynchonella decorata* Schlotheim). Internally *Isjuminella* has a simple septalium but no cardinal process, raduliform crura, and shows no ventral septum, but is extremely thickened instead. The evidence necessary to decide whether these similarities are due to a very close phylogenetic relationship or merely to convergent evolution is not at present available. However, when attention is turned from obviously similar forms to what little is known about trends within the genus *Septirhynchia* other possibilities suggest themselves.

As discussed above, the earliest known species of *Septirhynchia*, at least in Tunisia, is *S. budulcaensis*. This is a form which looks far more like a 'normal' rhynchonellid than any of the other species of the genus, having a smaller size, more numerous, much finer costae (26-28), and few pentameroid characters. If *Septirhynchia* did develop from a *S. budulcaensis*-type form then it is easy to imagine the derivation of the remaining species through a tendency towards larger size accompanied by decreasing numbers of costae. Such a trend is also seen in ontogeny (see above, and text-fig. 6).

Curiously enough it would seem that in the Tunisian sedimentary column the vertical disposition of the species agrees broadly with this trend, with *S. numidiensis* (with eight to ten costae in the adult) being the youngest species known, and the more costate *S. madashonensis*, *S. pulchra*, and *S. azaisi* being found immediately below.

In view of the fact that the Tunisian sequences are the only ones that have been examined in detail it would be premature to draw any wider conclusions from what may be a purely local phenomenon.

If *S.?* *budulcaensis* is the species closest to the immediate ancestors of the genus *Septirhynchia* then it follows that such forms may have been so morphologically unremarkable that it is difficult to know how they might be recognized. However, at a broader level, it can be reasonably assumed that such forms would probably have sprung from that plexus of the Tetrarhynchiinae which gave rise to such genera as *Kutchirhynchia*, *Burmirhynchia*, *Daghanirhynchia*, and *Somalirhynchia* (see Ager *et al.* 1972, pp. 95 ff., fig. 6).

Were the evidence of *S.?* *budulcaensis* ignored and origins from something like a shared immediate ancestor with *Isjuminella* proposed, the roots of the genus *Septirhynchia* would still lie in the mid (or early) Jurassic Tetrarhynchiinae. For the purposes of taxonomic classification, despite the affinities with the Tetrarhynchiinae, it cannot be denied that there are major differences. The presence of a cardinal process and ventral median septum represent structural innovations apparently without parallel in the history of that subfamily.

It is here proposed, therefore, that *Septirhynchia* is more appropriately classified in a subfamily (the Septirhynchiinae) rather than in a family of its own, as originally envisaged by Muir-Wood and Cooper (1951, p. 5). This subfamily (being monotypic and apparently restricted stratigraphically to a single stage or so) is to be regarded as a minor taxon by comparison with the other established subfamilies of the Rhynchonellidae to which it is assigned. If allowance is made for ontogenetic variation, the diagnosis given by Muir-Wood and Cooper (1951, p. 5) and in the *Treatise* (Ager 1965b, p. H619) for the family is satisfactory for the subfamily. This proposal does not preclude the possibility that future research may reduce even further the taxonomic category to which *Septirhynchia* is assigned.

In summary the genus *Septirhynchia* presents something of an enigma, a highly specialized form with a number of anomalous and apparently aberrant features, yet seemingly very closely related to ordinary rhynchonellids. The problem is further deepened by the striking contrast between the extensive geographical success of the group and its brief stratigraphical range. Can these curious features be combined into any sort of satisfactory picture?

A tentative solution can be proposed if it is remembered that in the Silurian and Devonian many brachiopods lived semi-infaunally in soft muds, but gradually the bivalves, better adapted to such a substrate, came increasingly to dominate this environment in post-Palaeozoic times (Stanley 1968). It would seem that in *Septirhynchia* the brachiopods, however briefly, regained this niche.

What appears to have happened is that in Bathonian-early Callovian times a widespread marine transgression created large areas of shallow marine carbonate mud across the southern portion of the Tethys. With what was probably the minimum of competition, *Septirhynchia* seems to have evolved rapidly to fill the niche, in the process developing again many features possessed by the Palaeozoic occupants of this habitat. The apparently abrupt demise of this genus was probably due to the loss of these environments by regression and also to increasing competition from the more tolerant and flexible bivalves.

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