

The relationship between the genus *Albaillella* Deflandre and the ceratoikiscid Radiolaria

ABSTRACT

Study of uppermost Viséan and Namurian species of *Albaillella* Deflandre and Namurian species of *Ceratoikiscum* Deflandre confirms an earlier suggestion that the two genera are closely related. The argument rests upon similarities between the fundamental skeletal geometries of the two taxa and most importantly upon the constant angular relationship between diagonal structures and the single straight rod of the skeletal frame which is common to both genera. Consequently, both *Ceratoikiscum* and *Holoeciscus* Foreman are assigned to the suborder Albaillellaria, which must now be regarded as ranging from Silurian to Namurian rather than as being confined to the Carboniferous.

INTRODUCTION

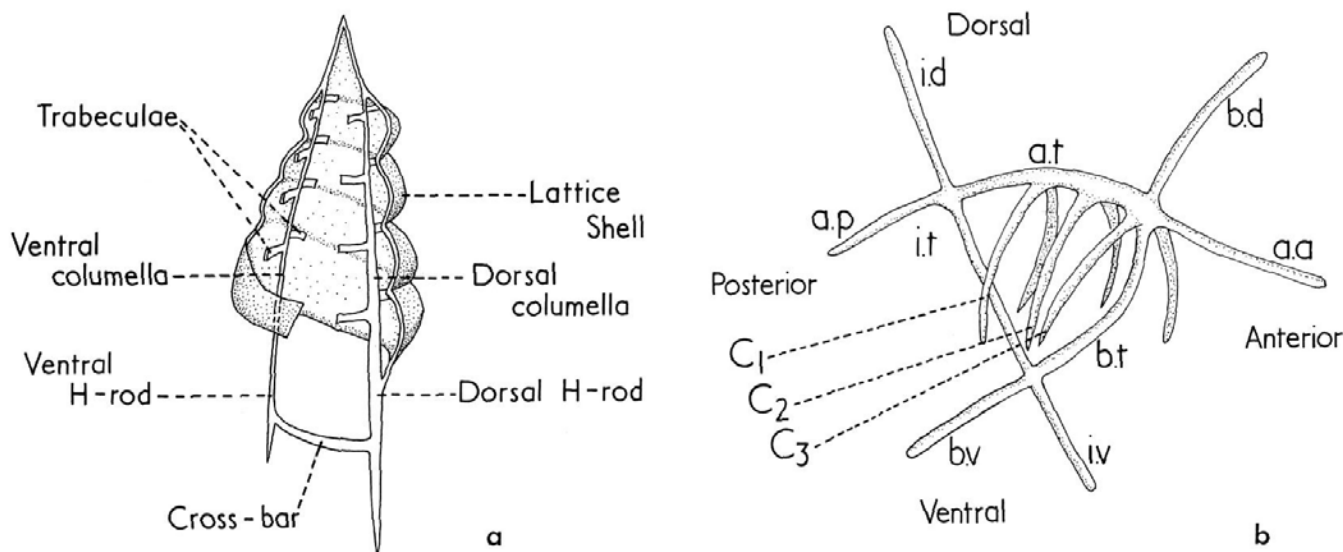
During the last fifteen years, knowledge of the Palaeozoic Radiolaria has increased considerably. Apart from the Palaeozoic members of the suborder Spumellaria, largely classifiable in the family Entactiniidae Riedel (1967), at least eight exclusively Palaeozoic genera are well established.

Albaillella, the first of these genera to be described (Deflandre, 1952), was taken by Deflandre (1953a) as the type form of an entirely new order of Radiolaria – the Albaillellidea, a group characterized by the very marked bilateral symmetry of frame and lattice shell. The group was demoted to a suborder by Holdsworth (1966a). Currently, only two families are recognized within the suborder, the Albaillellidae and the Lapidopiscidae (Deflandre, 1958), each represented by only a single genus, *Albaillella* and *Lapidopiscum* respectively.

As far as is known, these two genera are confined to the Carboniferous. *Albaillella* ranges upwards at least to the Kinderscoutian Stage (R1) of the Namurian Series (Holdsworth, 1966a) but *Lapidopiscum* is apparently absent in the Namurian and is as yet known only from Deflandre's Viséan type material. A much longer ranging group of Palaeozoic non-spumellarians is that exemplified by the genus *Ceratoikiscum* Deflandre, 1953, and here referred to as the "ceratoikiscids". This group, now considered to constitute the family Ceratoikiscidae Holdsworth, 1969, contains the genera *Ceratoikiscum*, *Holoeciscus* Foreman, 1963, and an as yet undescribed genus known from the high Viséan (Zone P2b) and Namurian. *Ceratoikiscum* has a known range from Silurian to Namurian (Holdsworth, 1969), while *Holoeciscus* is represented by only a single species known from the Devonian.

Like the Albaillellaria, the ceratoikiscids have a markedly bilaterally symmetrical organization, but they differ from *Albaillella* in possessing a closed skeletal frame (see text-figure 1a–b). At present the taxonomic position of the three ceratoikiscid genera is in doubt. Foreman (1963), on the basis of her work with upper Devonian species of *Ceratoikiscum* and *Holoeciscus*, and comparison with the four then-known species of *Albaillella*, tentatively suggested homologous relationships between the ceratoikiscids and *Albaillella*.

Since 1964 the writer has studied *Albaillella* and ceratoikiscids excellently preserved in Namurian concretionary limestones (see Holdsworth 1964, 1966a, 1966b), and the homologies of ceratoikiscids and *Albaillella* can now be discussed in somewhat greater detail. The purpose



TEXT-FIGURE 1

a, anatomical nomenclature of Namurian *Albaillella*; b, anatomical notation of the *Ceratoikiscum* frame. For full explanation, see Holdsworth (1969).

of the present paper is to show the probability of important homologies between the closed ceratoikiscid frame and the open frame of *Albaillella*. The ceratoikiscid Radiolaria should thus be considered a family of the *Albaillellaria*, this suborder now being found to range from at least Silurian to Namurian, rather than being confined to the Carboniferous, and to contain five of the eight well-established Palaeozoic non-spumellarian genera.

ANATOMICAL NOMENCLATURE

The fundamental anatomy of *Albaillella*, as observed in Namurian specimens, was described by Holdsworth (1966a), and the nomenclature is summarized in text-figure 1a. Foreman (1963) gave the first clear account of the *Ceratoikiscum* organization, and her nomenclature, somewhat elaborated by Holdsworth (1969), is summarized in text-figure 1b.

THE RELATIONSHIPS BETWEEN CERATOIKISCUM AND ALBAILLELLA

The material discussed in this section is known to the writer from personal observation and ranges in horizon from Zone P2b of the Viséan to Zone R1a of the Namurian. Figured specimens (plate 1, figures 5 and 7) are deposited at the University of Keele in the Department of Geology's collection of Palaeozoic Radiolaria. The initial part of the argument is based upon this material and may be set forth in eight steps:

1) The clearest similarity between *Albaillella* and *Ceratoikiscum* is the common possession of three

fundamental skeletal rods, a point first made by Foreman (1963, p. 286) (see plate 1, figure 1).

2) Therefore, the problem in relating the two genera is to clothe any two rods of *Ceratoikiscum* with the conical lattice shell of *Albaillella*, the third rod representing the crossbar of the external H-frame. There are thus three possible cases (see plate 1, figure 2).

3) In considering the relative merits of the three cases, certain properties of the *Ceratoikiscum* frame are important:

a) Only the a-rod bears paired spines (caveal ribs), although in *Holoeciscus* a few paired spines originate from the b-rod, and these paired spines are confined to the portion of the rod forming one side of the central triangle (a.t).

b) In spite of all other modifications in *Ceratoikiscum* and the other known ceratoikiscids, the intersector rod (i) is almost invariably straight and is always straighter than any other rod.

c) In *Ceratoikiscum tricancellatum* Holdsworth, 1969, b.v is demonstrably capable of being offset from b.t along i.t (see plate 1, figure 3).

4) Furthermore, in *Ceratoikiscum tricancellatum* the curvature of a.t and b.t is such as to constitute an almost continuous arc against i, with b.v offset and a.a and a.p suppressed (see plate 1, figure 4).

5) The anteroventral aspect of *Ceratoikiscum tricancellatum* bears a striking similarity in arrangement to the

H-frame of *Albaillella* aff. *pennata* Holdsworth, 1966 (see plate 1, figure 5). The most important feature is the continuous curvature of one H-rod with the crossbar, the crossbar having a relatively abrupt junction with the other H-rod, which is straight. This feature is seen not only in *A. aff. pennata* (plate 1, figures 5, 7b) but also in *Albaillella pennata* Holdsworth, 1966 (plate 1, figure 7a), and in *Albaillella*, n. sp. (plate 1, figure 7c). In all of these species the internal columellae are usually quite straight, but in a few specimens one columella is slightly bowed, and invariably it is the bowed columella which is continuous with the H-rod showing continuous curvature with the crossbar.

6) Thus *Albaillella* aff. *pennata* might be considered to correspond with case 3 (see plate 1, figure 2), and the skeletal rods can be given a tentative ceratohiscid notation (see plate 1, figure 5b).

As the great majority of paired spines (caveal ribs) in the ceratohiscids are borne on a.t, and as the Viséan P2b and Namurian *Albaillellas* have well-developed paired trabeculae on both columellae, then, if Foreman's (1963, p. 286) suggestion of homology between caveal ribs and trabeculae is correct, the trabeculae of only one columella are likely to be strictly homologous with caveal ribs. In fact, in the Viséan P2b and Namurian *Albaillellas* it could be argued that no trabeculae homologize with caveal ribs, for a) trabeculae of both columellae are identical, which would be unlikely if they had different origins, and b) trabeculae of a pair are commonly offset, a feature never convincingly evident with respect to caveal ribs in *Ceratohiscum* (see plate 1, figure 6).

7) Nevertheless, if the essential thesis is correct, it seems likely that one H-rod or columella, the a-rod homologue, should bear true homologues of caveal ribs. In *Albaillella* aff. *pennata*, if case 3 holds, they should be found between ?b.d and the shell aperture (see plate 1, figure 5b). In fact, in the majority of well-preserved specimens, one to three pairs of spines, unduplicated on the opposite H-rod, may be found in this position (see plate 1, figures 5b, 7b). In *A. aff. pennata* these unduplicated spines are sometimes not offset, but the point is of little significance as in many specimens trabeculae of the columellae are only weakly offset. In *Albaillella*, n. sp., one to three pairs of unduplicated spines may be found in analogous position (plate 1, figure 7c), but in this species, in which trabeculae are always strongly offset, the unduplicated spines are offset also. Even so, it is tempting to consider these external, unduplicated and apparently "functionless trabeculae" as true caveal rib homologues.

8) In *Albaillella* aff. *pennata* and *Albaillella*, n. sp., no consistent difference in thickness exists between the two columellae or H-rods, and it is thus impossible to directly determine whether the H-rod now identified on two counts as a.t is dorsal (strong) or ventral (weak). In *A. pennata*, in which differential strength of H-rods and columellae is marked, the H-frame is seldom well preserved, but it is the weaker (ventral) H-rod which shows continuous curvature with the crossbar (plate 1, figure 7a) and which may therefore be identified as a.t (see 5) and 6) above). When the criterion of shell obliquity is used to detect the a-rod homologue in *Albaillella* species described by Deflandre (1952) (see 13) below), it is again apparent that the ventral (weaker) H-rod has the characteristics of a.t. Thus the general rule may be formulated that in *Albaillella* the ventral H-rod, the a-rod homologue, shows one or more of the following properties: 1) It is the weaker rod, 2) it is the rod which shows the more continuous curvature with the crossbar, 3) it is the rod which bears unduplicated spine pairs.

THE RELATIONSHIPS BETWEEN *HOLOECISCUS*, THE VISÉAN *ALBAILLELLAS* OF DEFLANDRE, AND THE P2b-NAMURIAN *ALBAILLELLAS*

Though not seen by the writer, *Holoeciscus* has been fully described by Foreman (1963), and the structure is well established. Some doubt still remains regarding the details of Deflandre's (1952) *Albaillella* species, and their precise horizons in the Viséan are uncertain. The argument for the relationships between *Holoeciscus*, Deflandre's *Albaillellas* and the P2b-Namurian *Albaillellas* is set forth in seven further steps.

9) It has been argued that in the Viséan P2b and Namurian *Albaillellas* the caveal rib homologues exist outside the lattice shell, and that the ventral H-rod is a.t, the dorsal H-rod i.t and the crossbar b.t. By implication, the internal columellae are modified homologues of the extratriangular rod portions a.p and i.d (see plate 1, figure 8).

10) Thus the lattice shell of the Viséan P2b and Namurian *Albaillellas* is not homologous with the shell of *Holoeciscus*, which undoubtedly contains true caveal ribs (see plate 1, figure 9).

11) This finding is significantly at variance with Foreman's (1963) observation of: "... the similarity between the solid-walled chamber of *Albaillella* (with its diagonal structures) and that of *Holoeciscus* ..." (p. 286). The Viséan P2b and Namurian species of *Albaillella* known to the writer do not possess the strong oblique banding of Deflandre's species (Holdsworth, 1966a, p. 322). The contrast is expressed in plate 1, figure 10.

Whereas in Deflandre's *Albaillella paradoxa* oblique bands cut the shell aperture, in *A. pennata* the aperture is in a single relatively weakly oblique segment.

12) To appreciate the significance of this oblique banding in *Albaillella paradoxa*, further reference is necessary to *Ceratoikiscum*. In this genus, as Foreman was the first to recognize, the caveal ribs "... curve towards the junction of the b-spine and intersector" (Foreman, 1963, p. 286). In three known species the most posterior caveal rib pair (C1) have their distal ends rejoined to the frame at or very close to b.v (see plate 1, figure 3). In *Holoeciscus* the ribs are also clearly directed towards the junction of b and i (see plate 1, figure 9).

13) Thus, if the oblique banding, reflected by apertural spines, of Deflandre's *Albaillellas* is related to caveal rib organization (as the similar structures of *Holoeciscus* undoubtedly are), then the bands should be directed to the junction b-/i, i.e., towards the intersector homologue. Deflandre wrote of *Albaillella paradoxa*: "... its aperture bears oblique spines, always directed towards the stronger branch of the skeleton". The "stronger branch" is the dorsal columella plus dorsal H-rod, and from an independent line of argument it has been shown that in the Viséan P2b and Namurian *Albaillellas* the dorsal columella plus H-rod is the intersector homologue (see plate 1, figure 8). It is also significant that in the Viséan P2b and Namurian *Albaillellas* the unduplicated spine pairs of the ventral H-rod, the suggested caveal rib homologues (see section 7) above), are invariably directed to the junction between crossbar and dorsal H-rod, i.e., towards the independently inferred b-/i homologue (see plate 1, figure 5).

14) With the essential unity of *Holoeciscus* and *Albaillella paradoxa* established, it becomes apparent that the *A. paradoxa* type of frame can be derived from the *Holoeciscus* type by breaking the closed *Holoeciscus* frame at junction a-/i and rotating the a- and b-rods towards i.v, b.t becoming relatively shortened but the caveal ribs continuing to be directed towards b-/i (see plate 1, figure 11).

15) Thus Deflandre's Viséan *Albaillellas*, characterized by *A. paradoxa*, might be considered as "primitive" forms in which, as in the Devonian *Holoeciscus*, caveal ribs are retained in the shell. In the Viséan P2b and Namurian forms the aperture of the shell has migrated towards i.d and a.p, so that the caveal rib homologues remain exterior (see plate 1, figure 12).

However, this view probably overemphasizes the differences between the *Albaillella paradoxa* and *A.*

pennata types of structure. Though the Viséan P2b and Namurian *Albaillellas* do not have oblique bands cutting the aperture periphery, nevertheless the segments do show an oblique arrangement. Any one segment invariably declines from ventral columella to dorsal columella in the direction of the aperture. The obliquity is thus in the same sense as that of Deflandre's species and most probably has a common origin.

ORIGIN OF COLUMELLAE AND TRABECULAE

In the Viséan P2b and Namurian forms the trabeculae of both columellae contact the lattice shell at the constrictions between segments, and opposing pairs are thus oblique in the sense of the segments themselves. In considering the homologies of trabeculae, the question arises as to whether the disposition of the trabeculae determines the obliquity of segments, thereby implying that the trabeculae of the ventral columella are, in spite of arguments to the contrary (see section 6) above), caveal rib homologues, or whether the trabeculae, independently acquired, merely follow an oblique shell "grain" which *Albaillella* possesses by virtue of its ceratoikiscid ancestry.

From consideration of Deflandre's possibly "primitive" species, the latter view may be slightly the more attractive. Though the internal structure of these forms is still not wholly clear, it is significant that in some specimens, apparently the majority, only the dorsal columella, the intersector homologue, bears trabeculae. Yet the oblique banding, so reminiscent of *Holoeciscus*, is well developed, even though the a-rod homologue, the ventral columella, is short and bare of trabeculae.

Thus, one acceptable view is that in the *Albaillella paradoxa* type the ventral columella is the a.t homologue, which often provides direct support for a shell in which caveal ribs are represented either by the junctions between strongly oblique bands or by the apertural spines in which bands terminate. At the same time, the i.t homologue, the dorsal columella, develops new structures, trabeculae, to support the shell. In the Viséan P2b and Namurian *Albaillellas*, the a-homologue, the ventral columella, never directly supports the shell but has developed trabeculae identical with those of the i-homologue. Possibly this reflects the progressive exclusion of a.t from the shell interior, the internal ventral columella with trabeculae being more closely comparable with a.p, and a.t being represented by the ventral H-rod with its unduplicated spine pairs. Associated with this exclusion of the caveal-rib-bearing a.t from the shell is a reduction in shell obliquity.

A simple rationale for this hypothetical "progressive" trend in *Albaillella* structural organization may be found

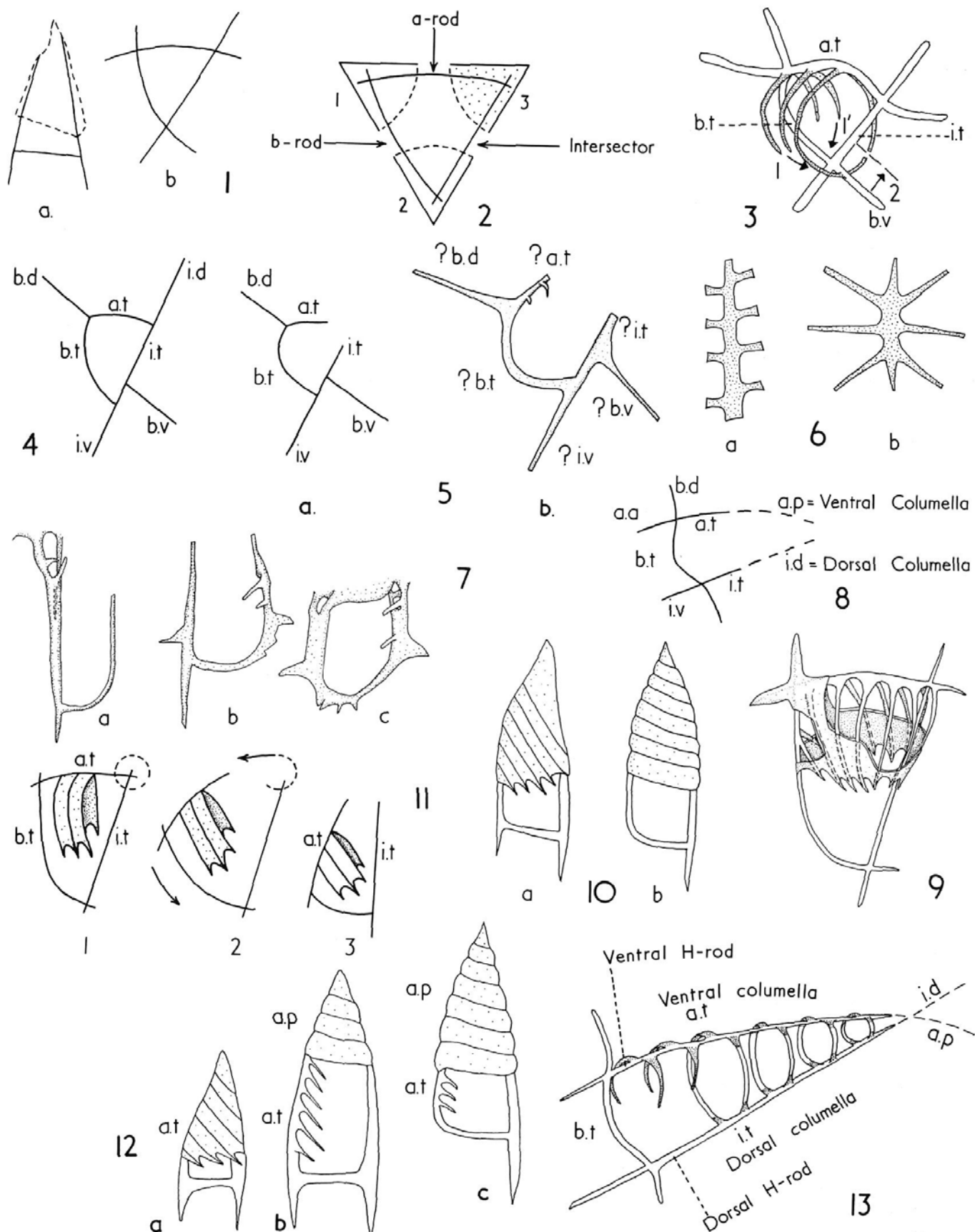
in the basic geometry of the *Ceratoikiscum* frame. As the triangle is approximately equilateral, and as only a.t bears caveal ribs, a conical cover to the triangular frame can, in theory, be supported by caveal ribs only along a distance equal to $a.t = b.t = i.t$. In developing an acute cone, while still retaining the bilaterally symmetrical frame, support is required along a proportionately longer distance in the a and i directions; and, once independent structures, the trabeculae, have been developed for this purpose on the theoretically indefinitely extendable a.p and i.d homologues, it seems logical that caveal ribs, even though modified for support, would become redundant. Thus the offset but unduplicated spine pairs in the Viséan P2b and Namurian forms are probably to be viewed not as rudimentary primitive caveal ribs but as redundant ribs secondarily modified by offsetting to increase their effectiveness as supporting structures.

While retaining the apparently sound conclusions regarding the identities of a-rod, b-rod and intersector homologues in *Albaillella*, a somewhat simpler hypothesis of columella origin may be arrived at by supposing a) that the ventral trabeculae are the proximal ends of true caveal ribs and not significantly different from the external, unduplicated spine pairs, and b) that the proportions of the ceratoikiscid triangle are capable of gross modification.

Some support for this latter supposition is found in *Holoeciscus*, where a.t is considerably shorter than either b.t or i.t. Foreman (1963) also noted that in this genus some of the caveal ribs become attached at their distal ends to i.t. the ribs most likely to do this being presumably those borne on the posterior portion of a.t. In plate 1, figure 13, the structural organization of the Viséan P2b and Namurian *Albaillellas* has been

PLATE 1

- 1 Comparison of basic frames; a, *Albaillella*; b, *Ceratoikiscum*.
- 2 The three possible relationships between the conical shell of *Albaillella* and the triangular frame of *Ceratoikiscum*.
- 3 Important features of the *Ceratoikiscum* structural organization. Arrows 1, 1' indicate the direction in which caveal ribs (stippled) point. Arrow 2 indicates the direction in which b.v is sometimes offset from b.t.
- 4 Diagram of the frame of *Ceratoikiscum tricancellatum* Holdsworth.
- 5 Comparison of anteroventral aspects; a, frame of *Ceratoikiscum tricancellatum* Holdsworth; b, H-frame of *Albaillella* aff. *pennata* Holdsworth (D.057).
- 6 a, arrangement of trabeculae on columella of *Albaillella pennata* Holdsworth; b, contrasting arrangement of caveal ribs on a.t of *Ceratoikiscum tricancellatum* Holdsworth.
- 7 H-frames of species of *Albaillella*, illustrating the common tendency for the crossbar to show continuous curvature with one H-rod (ventral), the other H-rod (dorsal) being more or less independent of this curvature. Specimens illustrated in b and c also show pairs of spines borne on the ventral H-rod and not duplicated on the dorsal H-rod. In both cases two such pairs are present, but only one spine of each pair is visible. a, *Albaillella pennata* Holdsworth (D.138); b, *A. aff. pennata* (D.060); c, *Albaillella*, n. sp. (D.148).
- 8 An interpretation of the *Albaillella* structure in terms of the ceratoikiscid organization scheme.
- 9 Cut-away diagram of *Holoeciscus* showing the relationship of the caveal ribs to the shell.
- 10 Comparison between shell forms; a, *Albaillella paradoxa* Deflandre type of shell; b, *Albaillella pennata* Holdsworth type of shell.
- 11 Conceptual derivation of *Albaillella* structure - 3 - from *Holoeciscus* - 1.
- 12 Possible relationship between a, *Albaillella paradoxa* Deflandre type of structure and c, *Albaillella pennata* Holdsworth type of structure.
- 13 An alternative interpretation of the *Albaillella* structure in terms of the ceratoikiscid organization scheme (compare with text-figure 9). The ventral and dorsal trabeculae (stippled) are viewed respectively as the proximal and fused distal ends of offset caveal ribs.



achieved by "stretching" a.t and i.t posteriorly, offsetting the origins of caveal ribs on a.t, and linking the distal ends of the more posterior ribs to i.t. The trabeculae of the dorsal columella are here interpreted as homologues of the distal ends of caveal ribs. The non-duplication of spine pairs on the ventral H-rod may now be explained, not by postulating that these are the only true caveal ribs (see section 7) above), but by supposing that they are caveal ribs which have failed to grow completely across the widest part of the stretched triangle to attain distal fusion with i.t.

This theory adequately explains the features of the Viséan P2b and Namurian *Albaillellas*, and homologues of the main portions of the distally fused ribs may perhaps be found in the slight lattice shell thickening along the apical sides of constrictions observed in *Albaillella pennata* (Holdsworth, 1966a, p. 324). The applicability to Deflandre's species is not completely clear. The serrated apertural periphery of the *A. paradoxa* type may be viewed as due to the inclusion of the anterior ribs, unfused distally, within the lattice shell. If, however, the dorsal trabeculae of this type are strictly comparable with those of the Viséan P2b and Namurian forms, they should show some close coincidence in position with the rib-governed diagonal structures of the shell (see section 13) above). It is unclear from the published description whether or not this is so.

CONCLUSIONS

In spite of some remaining doubt regarding the precise homology of trabeculae and the extent to which a.t is incorporated in the ventral columella, an explanation of *Albaillella* in terms of the basic ceratoikiscid organization rests convincingly, in the writer's opinion, on the following points:

- 1) The common possession of a three-rod, essentially triangular, skeletal frame.
- 2) The superficial resemblance between the shells of *Holoeciscus* and *Albaillella paradoxa*.
- 3) The common possession of a single strong notably straight rod, the intersector in the ceratoikiscids, the dorsal columella-H-rod in *Albaillella*.
- 4) The common tendency for the remaining two skeletal rods to show mutual curvature, the a- and b-rods in ceratoikiscids, the ventral columella-H-rod and cross-bar in *Albaillella*.
- 5) The comparability of the ventral columella-H-rod of *Albaillella* with the a-rod of ceratoikiscids, assuming the dorsal columella to be the intersector homologue, on the grounds that:

a) Only the ventral H-rod of Viséan P2b and Namurian forms bears unduplicated spine pairs explicable either as the only true caveal rib homologues or as anterior caveal ribs which, as in *Holoeciscus*, do not fuse distally with the intersector.

b) There is a tendency for unduplicated spines and all diagonal structures of *Albaillella* to decline from the ventral columella towards the junction between cross-bar and dorsal H-rod, this point being the homologue of the b-rod/intersector junction and the point to which, in the ceratoikiscids, caveal ribs are directed.

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