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A PROVISIONAL RADIOLARIA BIOSTRATIGRAPHY,
LATE DEVONIAN THROUGH LATE PERMIAN

By

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INTRODUCTION

This report provides a preliminary outline of a scheme for dating Late Devonian through Late Permian rock samples that contain reasonably well-preserved radiolarian faunas. The scheme is of most value in providing relative ages of samples from bedded chert terranes where few or no other means of age estimation are available. Provisional estimates of relative age are provided for a number of chert samples collected by U.S. Geological Survey and other field workers from Cordilleran formations (column A of chart).

Such dating is achieved by allocating a chert fauna to one of nine major, time-successive assemblages herein defined (column D of chart). The position and range of each assemblage in terms of standard stages or series is estimated (column F of chart). The earlier six assemblages appear to belong to Frasnian through Osagean; the latter three range from probable Chesterian through Guadalupian. The natures of Meramecian, and Ochoan through Spathian, Radiolaria associations are still uncertain, but faunal changes which are inferred to have occurred during Meramec deposition and prior to or during deposition of the Ochoan and Anisian are shown (column C of chart). Samples believed to be of such ages are indicated (columns A and E of chart).

The scheme is provisional and considerable uncertainties remain regarding the precise geologic time ranges of individual assemblages. Each assemblage contains the product of a single, index faunal-change "event" (columns B and C of chart; see below). However, in some cases, column C of chart indicates that several events appear to have been coincident with that which gave rise to the assemblage index taxon. In part this "clustering" of events almost certainly reflects an explosive rate of change of radiolarian faunas during latest Devonian and earliest Mississippian time. But elsewhere in the column clustering of events may reflect no more than the present inadequate sampling of the total time-rock record.

PRESENTATION

(1). The Events Chart (Column C)

The basic data regarding the apparent nature and relative ages of individual faunal events in Frasnian through Anisian radiolarian populations is summarized in column C of chart. This data derives in part from studies of Paleozoic Radiolaria prior to 1976 (see Holdsworth, 1977, for summary), in part from a few important studies published subsequent to the preparation of Holdsworth (1977) and in very large part from unpublished studies of faunas separated from North American cherts by the HF washing technique (Pessagno and Newport, 1971; Holdsworth and others, 1978) since 1976.

The conventions used in presenting this body of data in the form of an "events chart" are very similar to those now routinely used in presenting summaries of data on Mesozoic and Cenozoic faunas. It is stressed, however, that the quality of data is much poorer for Paleozoic events than for younger events. The "morphotypic base" or first appearance of a distinctive morphotype or morphotype group of unknown evolutionary origin is indicated by "m.b". The last (top) appearance of any morphotype or morphotype group is indicated by "m.t". Where grounds exist for believing that a particular morphotype or morphotype group originated by evolutionary change in an identifiable "ancestor" morphotype or morphotype group, ancestor(s) and descendant(s) are indicated "... ...". (In the present chart the arrow symbol does not imply critical change in frequency of ancestor and descendant as it has been used in some cases by previous authors.)

Evolutionary events of this last type are of the greatest biostratigraphic significance, for if correctly identified they must be time-successive and the evidence of their occurrence is likely to be relatively little perturbed by paleoecologic factors. A potential strength of the scheme set out in the chart is that eight of the nine biostratigraphic assemblages are defined in terms of index events of this type.

(2). Assignment of assemblages to stage/series
(column F) and reference faunas (columns E, G)

The greatest difficulty attends the independent geologic dating of successive segments of the Late Devonian through Permian Radiolaria record. Radiolarian rocks of this time span often contain few other fossil groups and frequently none of biostratigraphic utility. Conodonts, infrequently found in chert residues, provide the mainstay of our calibration. Conodonts are, however, prone to lengthy reworking in all environments and apparently are subject sometimes to morphologic modification in the deeper water bedded chert environment. Key reference faunas with conodonts (or other biostratigraphically significant content or context) which are relied upon for calibration of assemblages with the Geologic Rock-Time and Time scales are indicated by unbracketed numbers in column E of chart and European Carboniferous samples in column G.

Some radiolarian datum levels dated only by coexisting conodonts may in some cases have been assigned too great an age. For two samples, ages based on conodonts were rejected as there appeared great conflict between present understanding of the Radiolaria succession and the apparent "conodont age." In these cases reworking is postulated. Bracketed numbers in columns E and F indicate these samples and others of questionable value for calibration purposes.

(3). Paleontology

Advances in biostratigraphic understanding of the later Paleozoic Radiolaria has far outstripped publication of new data since 1977. Nevertheless, the great majority of taxa utilized in the scheme are named species, genera and families which will be familiar to the specialist. Important new, unpublished taxa are indicated "...." in column C of chart and briefly described in Notes on Paleontology and Evolution (below). Where Paleozoic species are thought to be allotted to inappropriate genera, but for which new names have not yet been proposed, the currently used genus is indicated '....'.

THE EVENTS CHART AND ASSEMBLAGES

Below are provided definitions and brief discussions of assemblages and Radiolaria associations not yet allotted an assemblage. Critical reference faunas used or rejected in age assignment of assemblages are detailed, the numbers allocated to faunas in the text being those used in columns E and G of chart. Roman numerals in the text refer to notes in the paleontology-evolution section.

Note that the earliest group of four events shown in the chart are only known to postdate the Wenlockian and predate the base of the Frasnian.

(A). Pre-Holoeciscus Assemblage, Late Devonian part

Distinguishable from Holoeciscus-1 Assemblage by absence of Holoeciscus Foreman in ceratoikisciid populations and by absence of Cyrtentactinia Foreman and all Pylentonemidae.

1, 2: Faunas with lower Polygnathus asymmetricus Zone conodonts cited in Holdsworth (1977). 3: Fauna from Frasnian portion of Egindinskaya Series, Urals (Nazarov, 1975).

Faunas of Assemblage with many entactiniid spumellarian species groups also known from Holoeciscus-1 Assemblage (cf. Foreman, 1963). Ceratoikisciid population also dominated by species groups common to Holoeciscus-1--Ceratoikiscum spinosiarcuatum Foreman Group (i), Ceratoikiscum bujugum Foreman Group (ii), and Ceratoikiscum planestellare Foreman Group.

No basal datum event is yet available to demark the Frasnian faunas of this assemblage from faunas of pre-Frasnian, Devonian age. Faunas of Wenlockian age are, however, clearly distinct from the Frasnian faunas cited here (see Holdsworth, 1977).

(B). Holoeciscus-1 Assemblage

The concept of this assemblage derives from 4: faunas described by Foreman (1963) from the lower portion of the Ohio Shale, apparently of earliest Famennian, upper Palmatolepis crepida Zone age (Winder, 1966). Faunas of assemblage postdate the index event of the evolution of the earliest known Holoeciscus - Holoeciscus auceps Foreman - from an unknown ceratoikisciid, probably Ceratoikiscum ancestor (iii). They predate the first appearance of Holoeciscus sp. nov. (iv) and the possible extinction of H. auceps, and also the first appearance of Popofskyellum Deflandre, viewed as the evolutionary descendant of the monospecific Cyrtentactinia Foreman s.s. (v).

(C). Holoeciscus-2 Assemblage

Type faunas of Assemblage are from upper basalt-free red cherts of Chulitna ophiolite, Alaska Range (Jones and others, in press). These faunas postdate the index first appearance of Holoeciscus sp. nov. (iv), the apparent extinction of H. auceps and the transition Cyrtentactinia -- Popofskyellum (v). Archocyrtium Deflandre, first known in the Wenlockian, makes a reappearance after apparent absence from the Frasnian pre-Holoeciscus and Holoeciscus-1 assemblages. Assemblage is distinguished from Holoeciscus-3 assemblage by absence of Pylentonema Deflandre and much greater abundance of Holoeciscus.

No fauna of assemblage is reliably dated by independent means, but the type faunas are of critical importance. Their excellent preservation and apparently truly oceanic provenance allows a reliable glimpse to be obtained of generic diversity achieved during the peak period of Holoeciscus abundance.

(D). Holoeciscus-3 Assemblage

Type fauna - 5 - is from Woodruff Formation (R. K. Hose, collector) some one-third of a mile northwest from localities 42 and 43 of Smith and Ketner (1975) which yielded Platyclymenia. Occurrence of the goniatites suggests but does not convincingly prove that 5 is of mid-Famennian age. Recent redating of the Webb Formation as Osagean (R. K. Hose, written commun., 1979) raises the possibilities of Kinderhookian levels within the Woodruff.

Assemblage distinguished from Holoeciscus-2 by presence of Pylentonema sp. nov. 1 (vi) with inner lattice, very probably derived from Formaniella cibdelosphaera (Foreman) or a derivative therefrom (vi-vii). Faunas of assemblage distinguished from those of Albaillella-1 Assemblage by absence of all albaillellids and all septactine Pylentonemidae other than Pylentonema.

(E). Albaillella-1 Assemblage

Index event is the first appearance of the primitive Albaillella sp. nov. (viii), which appears to be the evolutionary derivative of Holoeciscus (ix). The latter genus is not definitely known from any fauna of the assemblage. Apparently simultaneous with the first known appearance of Albaillella are the cryptophyletic first appearances of the septactine pylentonemids Cyrtisphaeractenium Deflandre, Cyrtisphaeronemium Deflandre, and Pararchocyrtium Deflandre - all genera of the remarkably rich pylentonemid faunas previously recognized in the early Carboniferous of France and Turkey (see Holdsworth, 1977, for discussion) being now present. Faunas of the assemblage are distinguished from those of the Albaillella-2 Assemblage by the absence of Albaillella paradoxa Deflandre Group (xiii). The distinctive Ceratoikiscus avimexpectans Deflandre (x) first appears in this Assemblage.

Type fauna is from allochthonous, Woodruff-like cherty siltstone of Fish Creek Range, Nevada (R. K. Hose locality 79-30). This locality is not independently dated. Poorly preserved faunas (6) of the "Lower" Ford Lake Shale, Alaska, at Alaska Museum locality A854 (see Holdsworth and others, 1978) contain the distinctive spiral-spine spheroids (xi) of Albaillella-1 and occur within 30 feet of an overlying Albaillella-2 level and 6 feet below the first known level with the lowest Kinderhookian conodont Siphonodella sulcata.

The Albaillella-1 Assemblage thus appears to be immediately pre-Kinderhookian and/or basal Kinderhookian (but see below).

(F). Albaillella-2 Assemblage

Faunas of Assemblage postdate the index first appearance of A. paradoxa Group (xiii), very probably the descendant of Albaillella sp. nov. (xii). Type fauna - 10 - from phosphatic nodule, Baltalimani Formation, Turkey (Holdsworth, 1973) also contains Albaillella undulata Deflandre and Albaillella cornuta Deflandre.

10: Underlies limestone level with latest Tournaisian Foraminifera;
11: Cabrieres district, Montagne Noire, France; lydite unit with early Visean goniatites; 8: Fish Creek Range, Nevada, R. K. Hose locality 78-115; cherty shale in probable mid-Osagean shale-limestone unit; 9: Fish Creek Range, R. K. Hose localities 78-40 and 78-75; cherty shale ca 300 ft above limestones with mid-Osagean algae and Foraminifera.

(7): Ford Lake Shale, Alaska Museum locality A854; chert levels under- and overlain by basal Kinderhookian conodonts of Siphonodella sulcata and Siphonodella sandbergi-Siphonodella duplicata Zones.

Faunas of (7) appear to indicate that this assemblage existed at least from earliest Kinderhookian, but Late Devonian conodonts are reworked in the section and so may be the Kinderhook elements. If so, Albaillella-1 may well be Kinderhookian and Albaillella-2 entirely post-Kinderhookian.

(G). Uncertain-Radiolaria associations of apparent Meramecian age

Presently, all faunas with A. paradoxa Group are considered to belong to the Albaillella-2 assemblage. The well-known association of A. paradoxa with Cyrtisphaeractenium is firmly dated in Europe as being at least as young as basal Visean - 11 - and in America at least as young as mid-Osagean - 8, 9.

At locality A854 in the Ford Lake Shale of Alaska, the extinction levels of both Cyrtisphaeractenium and Cyrtisphaeronemium apparently lie below level C.8 in the "Lower" Ford Lake Shale, and occur within the range of A. paradoxa Group. C.8 contains the earliest Pylentonema sp. nov. 2 (xv) and Pylentonemid gen nov. (xvi). Independently undated samples with A. paradoxa Group but lacking Cyrtisphaeractenium and Cyrtisphaeronemium are also known from the Tobin Range and Edna Mountains, Nevada (column A of chart), and it appears that these "late" Albaillella-2 faunas are at least as young as late Osagean and very probably of Meramecian age.

Independently undated faunas from Brooks Range, Alaska, lack A. paradoxa Group but contain A. undulata Group (xiv) in association with lanceolate, well-segmented Albaillella spp. of "advanced" type (xviii). One fauna - (12) - of this association type, Cache Creek Group, British Columbia (Whetten 77-5E), contained a conodont assemblage of apparent late Kinderhookian age. The nature of the Radiolaria assemblage is so different, however, from faunas of Early Mississippian age dated by Foraminifera and ammonoids (see above) that the apparent date is rejected in this synthesis.

The Sycamore Limestone, Oklahoma - (13) - lacks all Pylentonemidae, all early tubular Albaillellas including A. paradoxa and A. undulata Groups and contains the apparently "advanced" Albaillella cartalla Ormiston and Lane (Ormiston and Lane, 1976). Several other features of this Radiolaria fauna also suggest a level younger than that of earliest Osagean which is indicated by co-existing conodonts. The radiolarian beds of the lower Sycamore are here considered to be of later Meramecian age, probably not significantly older than the "latest Meramec or early Chester" conodonts reported as occurring some 182 ft above the base of the formation (Ormiston and Lane, 1976, p. 164).

(H). Albaillella-3 Assemblage

Index event is first appearance of Albaillella pennata Holdsworth Group (xxii), possibly derived from poorly known supposedly Meramecian lanceolate or winged segmented forms, possibly from A. cartalla. Faunas of assemblage predate the evolutionary first appearance of "Pseudoalbaillella spp." (xxiv). Type collection is from Reticloceras circumplicatile s.s. goniatite band, Dove Shale, Derbyshire, England (Holdsworth, 1966).

14: Concretion with latest Viséan, (Zone P2b), goniatites, County Clare, Ireland; 15: Concretion, Hombergian (E1), Fayetteville Shale, Arkansas (Nigrini and Nitecki, 1968); 16-18: Concretions with E2-R1 goniatites, Dove and Edale Shales, Derbyshire, England; (19): Concretion from basal R2, Reticloceras gracile goniatite band, North Staffordshire, England. The Radiolaria fauna is poorly diversified and does not convincingly prove the absence of "Pseudoalbaillella".

18A: Cherts, Mystic area, Alaska, which contain Albaillella pennata s.s. and are thus unlikely to predate Namurian H2-R1. Lack Spongodiscaceid gen. nov. (tetrahedral) (xxiii) though containing Spongotripus (xix). The morphotypic base of Spongodiscaceid gen. nov. (tetrahedral) appears, therefore, to be post at least H2.

The P2b Irish concretions (14) contain the youngest examples of 'Ceratoikiscum' omicron Ormiston and Lane Group (xx) and the earliest "Parahagiastriids" (xxi). Paronaella impella Group (xvii), 'Spongotripus' and Spongodiscaceid gen. nov. (tetrahedral) (xxiii) are all to be expected in faunas of this assemblage. They are known, however, only from bedded chert faunas, occurring neither in the black shale goniatite bands of England and Ireland, cited above, or in the single Fayetteville fauna. These forms appear to have been excluded from the relatively shallow, enclosed, black shale seas. Independently undated faunas from the Toyabe Range, Nevada, and Mystic area of Alaska, in at least one case with Albaillella pennata s.s., contain the youngest known Pylentonemidae, including Pylentonemid gen. nov. As previously suggested (Holdsworth, 1973, 1977) it appears that this group also was excluded by environmental factors from the Namurian black shale environments and also apparently from the intracontinent environment of the Sycamore Limestone, Arbuckle Mountains, Oklahoma (see above).

(I). "Pseudoalbaillella" Assemblage

Index event is the first appearance of "Pseudoalbaillella" spp. (xxiv), most probably the evolutionary derivatives of A. pennata Group and quite possibly of Albaillella pennata s.s. or its direct Albaillella descendant (xxv). Complex Paronaella s.l. spp. (xxvi) first appears in the Assemblage and "Parafollicucullus" spp. (xxviii) and mamillate spheroids (xxx) first appear in Leonardian faunas of Assemblage.

20: Chert of Kagvik sequence, Brooks Range, Alaska; Mayfield collection 78Md-75E. This sample has a "Pseudoalbaillella" population gradational with A. pennata and contains a conodont of the Idiognathoides noduliferous Group. This conodont group ranges in Britain from Namurian, H2 to Namurian, G1 (early to early-late Morrowan). As "Pseudoalbaillella" is absent in Britain at least to early Kinderscoutian, R1 (see above) 78Md-75E can be no older than Marsdenian, R2, or younger than Yeadonian, G1 - presuming no conodont reworking. (21): Cherts of Havallah Sequence, Nevada, with "Pseudoalbaillella"; both samples lack 'Spongotripus' and Spongodiscaceid gen. nov. (tetrahedral) and must postdate the extinctions of these forms: 77-J-16 with Idiognathoides macer could be at least as young as G2, latest Morrowan, but 77-J-24 with Idiognathoides noduliferous Group can apparently be no younger than G1. This suggests a very short range indeed - H2-G1 at most - for the tetrahedral spongodiscaceid. So short a range seems inherently improbable in view of the relatively large number of samples known to contain this form. Pending confirmation, therefore, m.t. Spongodiscaceid gen. nov. (tetrahedral) is considered to be of unknown position within the mid-Late Pennsylvanian, predating the first appearance of "Pseudoalbaillella U-forma" (xxvii).

The "Pseudoalbaillella" transition may, in fact, be post-Morrowan.

22: Concretions with Eoasianites (Glaphyrites) rionegrensis Closs, Uruguay, of supposed but not certain Middle Pennsylvanian age appear to lack "Pseudoalbaillella" in their Albaillella populations. This suggests that the first appearance of "Pseudoalbaillella" should be taken to postdate some part of the Middle Pennsylvanian but predate 23: late Desmoinesian concretions with "Pseudoalbaillella", Kansas (Nodine-Zeller, Holdsworth, and Berenson, in press).

Early Permian faunas of this assemblage appear distinctive and are relatively convincingly dated. 24: Chert, Alaska, 77AFr-3189; 25: Chert, Washington State, 77-55B; 26: Chert block in melange with Leonardian conodonts, Cache Creek, B.C.; 27: Chert, 77-J-19, Havallah Sequence, Nevada, with probable Leonardian Neogondolella.

(J). Follicucullus Assemblage

Index event is the first appearance of Follicucullus Babstock and Ormiston, apparently the evolutionary derivative of an unrecognized but probably generalized form of "Pseudoalbaillella" (xxix, but see also xxviii). Type fauna is 29: Lamar Limestone, Texas, Late Guadalupian (Ormiston and Babstock, 1979).

28: Chert, Klamath Mountains, Irwin-22-77, with Wordian conodonts.

(K). Uncertain associations of post-Guadalupian and possibly post-Guadalupian age

(30): Poor fauna from chert, overlying Leonardian Limestone and underlying Triassic sandstone; 78-JSE-3. Contains no familiar elements of "Pseudoalbaillella" or Follicucullus Assemblages and no recognizable Triassic elements. Contains "Helioasters" (xxxi), presently unique to this sample. 31: Chert, 78Md-293. Contains conodonts of Spathian-Anisian age. Radiolaria assemblage poorly preserved and of low diversity, with simple multicyrtoids (xxxii) of Mesozoic type, lacking many characteristic forms of the Late Triassic.

Notes on Paleontology and evolution

by

Brian K. Holdsworth

Notes on new taxa and evolutionary events are numbered in order of appearance from base of events chart.

- (i) Ceratoikiscum spinosiarcuatum Group: Ceratoikiscum spinosiarcuatum Foreman s.s. provides the type for a rather variable group of morphotypes in which three to five caecal ribs, often more elaborately vaned than in the type form, are confined to a.t., the posteriormost rib pair (C_1) distally joining the frame. In C. spinosiarcuatum s.s. rejunction is with b.v., but the early Frasnian Canol Shale fauna contains morphotypes possessing b.v. but having C_1 rejunction either with the postero-ventral patagium or with a new, discrete rod--"focus rod"--developed from the patagium. This rod is clearly the so-called "offset b.v." of Ceratoikiscum trican-cellatum Holdsworth of the Albaillella-3 Assemblage and demonstrates the close phyletic connection between these Ceratoikiscum spp. of widely different age. The extreme scarcity of the C. spinosiarcuatum Group in good Albaillella-1 and -2 faunas is thus puzzling.
- (ii) Ceratoikiscum bujugum Group: The form in the Pre-Holoeciscus, Canol Shale fauna, seems to differ from the Holoeciscus-1 type in possessing a second, posterior pair of delicate ribs.

- (iii) Holoeciscus appears to have arisen from a Ceratoikiscum with caveal ribs developed on both a.t. and the dorsal half of b.t. Change involved an equal degree of lengthening of b.t. and i.t. relative to a.t., and the development of lamellar shell between caveal ribs (Foreman, 1963; Holdsworth, 1969).
- (iv) Holoeciscus sp. nov. Differs from H. auceps in possessing spinose instead of spongy H-frame and having dorsal-most caveal rib pair of b.t. developed beyond shell periphery as upwardly curving spines.
- (v) The appearance of simple, unsegmented Popofskyellum spp. apparently immediately succeeding the extinction of Cyrtentactinia tends to support the earlier inference of evolutionary relationship (see Holdsworth, 1973).
- (vi) Pylentonema sp. nov. 1. A smaller form than Pylentonema antiqua Deflandre, with relatively longer spines and strong inner lattice.

- (vii) As far as can be determined Pylentonema sp. nov. 1 lacks the pylome net of Formaniella cibdelosphaera and may well have originated from this species by loss of net and acquisition of inner lattice. The very close relationship between Formaniella cibdelosphaera and Pylentonema spp. is demonstrated by the very rare Formaniella helenae Deflandre of a French Albaillella-2 fauna, a species which combines the pylome net of Formaniella with the internal lattice frequent in Pylentonema spp.
- (viii) Albaillella sp. nov. Distinguished from all named Albaillellas by small, rather triangular unsegmented shell with single strong, spinose projections from both dorsal and ventral sides; H-frame spongy with well-developed external ribs dorsally.

- (ix) Albaillella sp. nov. apparently arose from an unrecognized Holoeciscus sp. in which the triangle-forming portion of the intersector rod (i.t.) lengthened dorsally. The perpendicular contact of a.t. with i was thus changed to an oblique contact, giving a triangular rather than quadrangular shell in which b.t. and a.t. remain discernible as discrete arcs. The fundamental b.t./a.t. contact is marked by the dorsal spine of Albaillella sp. nov., the homologue of the Holoeciscus a.t./i.t. contact being marked by the ventral spine. The transformation is thus similar to that which gave rise to Lapidopiscum Deflandre, except that in this case the ancestor was a Ceratoikiscum (probably of Ceratoikiscum spinosiarcuratum Foreman Group) in which there had been no prior relative lengthening of b.t. as in Holoeciscus and in which caveal ribs had been lost from b.t. (see also Holdsworth, 1966).
- (x) Ceratoikiscum avimexpectans Group. Inter-fauna variation in strength of extratriangular spines and tightness of packing of the numerous caveal ribs is evident. The very probable ancestor of this species group is known in the pre-Holoeciscus Canol Shale fauna, but Holoeciscus-1 through 3 examples are unknown.

- (xi) Spiral-spine spheroids. Probable latticed entactiniids usually with 6 but sometimes 4 remarkably bladed, corkscrew spines superficially similar to those of Triassic genera.
- (xii) A. paradoxa retains the totally unsegmented shell of Albaillella sp. nov., the parallel rods of H-frame, and strong external ribs. Spongy tissue of H-frame and shell spines are lost and the original point of a.t./b.t. junction loses identity by smoothing of a.t. and b.t. into single curved rod.
- (xiii) Albaillella paradoxa Group. Used for all forms with the slender, sword-sheath form of shell of A. paradoxa s.s. Probable earliest forms are thinner shelled and more delicate and inferred latest forms smaller than type.
- (xiv) Albaillella undulata Group. Used for all narrowly conical, unwinged forms with multiple undulose segmentation. Inferred late examples are small.
- (xv) Pylentonema sp. nov. 2. Larger and with consistently relatively shorter spines than P. antiqua s.s.; probably the descendant of this form.
- (xvi) Pylentonemid gen. nov. Shell essentially spherical, pores pustulate, podome at junction with lattice markedly constricted and podome skirt strongly flared with needlelike terminations of the three feet. Four other main spines weakly developed from lattice. At least one group of small forms in late Albaillella-2 and immediately younger faunas may well derive from Pylentonemid gen. nov.

- (xvii) Paronaella impella Group. Used for all simple Paronaella s.l. morphotypes with parallel-sided arms or arms of elongate club form.
- (xviii) All present evidence suggests that the flattened rather than tubular shell-form in Albaillella, with marked oblique shell segmentation, is a relatively late acquisition and not inherited from the Albaillella ancestor.
- (xix) 'Spongotripus'. Used for forms comparable with 'Spongotripus' ruetae Ormiston and Lane.
- (xx) 'Ceratoikiscum' omicron Ormiston and Lane Group. Used for ceratoikiscids with single strong rib pair and modification of fundamental triangle to a ring. If omicron possesses, as is likely, the structure of undescribed latest Visean species it cannot usefully be included in Ceratoikiscum.
- (xxi) "Parahagiastriids". A diverse, undescribed group, in which three or more usually very narrow arms (rays) originate from a small perforate or imperforate central sphere, the arms being usually constructed of longitudinal straight or serpentine rods linked by numerous cross struts. In the distinctive "trumpet form" of late Pseudoalbaillella assemblage faunas the arms expand rapidly into an abruptly truncated cone.

- (xxii) Albaillella pennata Group. Populations in different faunas show variation in strength and spinosity of H-frame and development of wings. In type R1a(i) form, also present in H2a, the H-frame is extremely weak.
- (xxiii) "Spongodiscaceid gen. nov. (tetrahedral)". Solid, large, spongy lattice produced into four solid, spongy conical, spine-terminated arms, each with central thread. Probably closely related to P. impella Group and 'Spongotripus'.
- (xxiv) "Pseudoalbaillella". Conical to bilaterally flattened, winged, imperforate shells of unknown internal structure, sometimes superficially similar to late forms of Albaillella, but distinguished therefrom by pronounced, median, swollen "pseudothorax" bearing wings in plane of bilateral symmetry. Apical cone and "pseudoabdomen" often with subsidiary external segmentation. Differs from Follicucullus Ormiston and Lane in possession of winged pseudothorax.

- (xxv) Though it is not known whether "Pseudoalbaillella" ever possessed an external H-frame, early forms show a remarkable similarity in shell form to the late Albaillella pennata which provides a wholly logical ancestor. The locus of pseudothorax development is apparently a girdle which contains the original sites of the a.t./b.t. and a.t./i.t. junctions in the Holoeciscus ancestor of Albaillella (see vii, above). It is unlikely that "Pseudoalbaillella" possessed an H-frame, for in A. pennata Group reduction in strength of this structure proceeded rapidly in Namurian time and it is extremely weak in A. pennata s.s. of the Kinderscoutian (R1).
- (xxvi) "Complex Paronaella s.l. spp." Three armed forms with triangular or abruptly clubbed terminations to arms, the terminations frequently joined one with the other.
- (xxvii) "Pseudoalbaillella U-forma". Pseudoalbaillella with narrowly tapering shell, totally lacking secondary segmentation, strongly constricted below very small, subspherical pseudothorax and with rapidly flaring distal pseudoabdomen strongly reflexed to form tight U-bend with proximal portion.

- (xxviii) "Parafollicucullus". Distinguished from "Pseudoalbaillella" by additional, ringlike, inflated major segment interposed in constriction between "pseudothorax" and "pseudoabdomen." Murchey (oral commun., 1979) notes the possibility of phyletic relationship between "Parafollicucullus" and "Pseudoalbaillella U-forma", and it may be that these forms belong to a short-lived (Leonardian-early Wordian) lineage separable from the main Pseudoalbaillella -- Follicucullus progression. Alternatively, Parafollicucullus may be seen as the immediate ancestor of Follicucullus, implying that the pseudothorax was lost in the transition and that the median, bilobate segment of Follicucullus is homologous with the non-bilobate Parafollicucullus abdomen.
- (xxix) The "Pseudoalbaillella" ancestry of Follicucullus is strongly supported both by the fundamental similarities of the tri-segmented shells and the development in some later "Pseudoalbaillellas" of the bilobed pseudothorax seen in Follicucullus. The internal rods demonstrated in the apical cone of Follicucullus are apparently vestigial columellae inherited from the Albaillella ancestor.
- (xxx) "Mammilate spheroids". Superficially similar to Praeconocaryomma Rust, but not sufficiently well preserved for close comparison.
- (xxxi) "Helioasters". Never satisfactorily seen, but apparently forms with thinly discoidal lattice, the disc margin ornamented with numerous spines.

(xxxii) "Simple multicyrtoids". Small, parallel-sided, multicyrtoid tests, lacking clearly differentiated cephalis, thorax or abdomen, with single pore girdle per post-cephalic segment.

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Table 1. Location of samples shown on plate 2.

Locality	USGS MR Number	Collector	Quadrangle
ALASKA-CHULITNA			
78-JCh-12	0077	Jones	Healy A-6
78-JCh-15	0078	Jones	Healy A-6
76-J-1	0072	Jones	Healy A-6
76-J-13	0074	Jones	Healy A-6
76-J-26	0082	Jones	Healy A-6
76-J-19	0080	Jones	Healy A-6
76-J-20	0081	Jones	Healy A-6
76-AWn-164	0070	Jones	Healy A-6
76-AWn-162	0069	Jones	Healy A-6
76-J-9	0073	Jones	Healy A-6
ALASKA-WRANGELLIA			
79-JMH-11	0784	Jones	Mt. Hayes A-1
79-JMH-6	0780	Jones	Mt. Hayes A-1
78-JCh-30	0435	Jones	Healy A-1
79-JH-3	0820	Jones	Healy A-1
79-JH-1	0818	Jones	Healy A-1
79-JH-2	0819	Jones	Healy A-1
ALASKA-McKINLEY			
79-ARh-10B	0834	Richter	Talkeetna A-6
79-ARh-10D	0836	Richter	Talkeetna A-6
ALASKA-KANDIK BASIN FORD LAKE SHALE			
C-8	Holdsworth Collection	Holdsworth	Yukon River, Ford Lake Shale, Eagle D-1
C-7	Holdsworth Collection	Holdsworth	Yukon River, Ford Lake Shale, Eagle D-1
C-6	Holdsworth Collection	Holdsworth	Yukon River, Ford Lake Shale, Eagle D-1
A-854	Holdsworth Collection	Holdsworth	Yukon River, Ford Lake Shale, Eagle D-1
C-5	Holdsworth Collection	Holdsworth	Yukon River, Ford Lake Shale, Eagle D-1
C-4	Holdsworth Collection	Holdsworth	Yukon River, Ford Lake Shale, Eagle D-1
C-3	Holdsworth Collection	Holdsworth	Yukon River, Ford Lake Shale, Eagle D-1
C-2	Holdsworth Collection	Holdsworth	Yukon River, Ford Lake Shale, Eagle D-1
BC-75-127	Holdsworth Collection	Holdsworth	Yukon River, Ford Lake Shale, Eagle D-1
Basal Nodules			

Locality	USGS MR Number	Collector	Quadrangle
ALASKA-INNOKO			
68a-VABM-Moose	0954	Chapman	Tanana
71-Ch-89	0955	Chapman	Tanana
77-APa-8	0096	Patton	Medfra
77-APa-6c	0956	Patton	Medfra
77-APa-7c	0957	Patton	Medfra
77-Ch-17	0055	Chapman	Ruby
75-APa-120	0095	Patton	Medfra
77-APa-183A	0109	Patton	Medfra
77-APa-73	0100	Patton	Medfra
75-APa-118	0093	Patton	Medfra
77-APa-75	0101	Patton	Medfra
77-APa-75B	0101B	Patton	Medfra
77-Ch-18	0056	Chapman	Ruby
77-Ch-16	0054	Chapman	Ruby
ALASKA-70-MILE			
77-AFr-3189	0349	Foster/Keith	Big Delta D-1
ALASKA-MYSTIC			
79-JT-1	0762	Jones	Talkeetna A-6
79-JT-15	0774	Jones	Talkeetna A-6
79-JT-16	0075	Jones	Talkeetna A-6
79-JT-13	0772	Jones	Talkeetna A-6
79-JT-2	0763	Jones	Talkeetna A-6
79-JT-3	0764	Jones	Talkeetna A-6
79-JT-12	0771	Jones	Talkeetna A-6
79-JT-14	0773	Jones	Talkeetna A-6
79-JT-15	0774	Jones	Talkeetna A-6
79-JT-4	0765	Jones	Talkeetna A-6
79-JT-5	0766	Jones	Talkeetna A-6
79-JT-6	0767	Jones	Talkeetna A-6
79-JT-7	0776	Jones	Talkeetna A-6
79-JT-8, 8a	0769, 0768	Jones	Talkeetna A-6
79-JT-18	0777	Jones	Talkeetna A-6
ALASKA-BROOKS RANGE			
78-ACn-892	0804	Churkin	Chandler Lake
78-Md-37	0798	Mayfield	Misheguk Mountain
78-Ek-55B	0386	Ellersieck	Misheguk Mountain
78-Ek-19c	0816	Ellersieck	Misheguk Mountain
78-Ek-62	0817	Ellersieck	Misheguk Mountain
75-ATr-50.5	0809	Tailleur	Killik River
78-ACn-714	0805	Churkin	Misheguk Mountain
78-ACn-713	0806	Churkin	Misheguk Mountain
78-ACn-732	0807	Churkin	Misheguk Mountain

Locality	USGS MR Number	Collector	Quadrangle
ALASKA-BROOKS Range--cont.			
78-ACn-644	0808	Churkin	Misheguk Mountain
77-ACn-723	0022	Churkin	Misheguk Mountain
77-ACn-725	0023	Churkin	Misheguk Mountain
77-ACn-1012	0025	Churkin	Howard Pass
78-Md-95D	0042	Mayfield	Misheguk Mountain
77-Md-14D	0039	Mayfield	Misheguk Mountain
77-Md-85B	0045	Mayfield	Misheguk Mountain
78-AVy-282	0416	Vickery	Misheguk Mountain
78-ATr-58B	0810	Tailleur	Misheguk Mountain
77-ACn-1172	0027	Churkin	Howard Pass
78-ACn-721	0812	Churkin	Misheguk Mountain
78-Md-75E	0813	Mayfield	Misheguk Mountain
75-ATr-50.2.1	0811	Tailleur	Killik River
78-Md-29E	0367	Mayfield	Misheguk Mountain
60-ABe-588	0002	Brosge	Arctic
77-ACn-371	0012	Churkin	Misheguk Mountain
77-ACn-373	0013	Churkin	Misheguk Mountain
78-ACn-203	0814	Churkin	Howard Pass
78-ACn-894	0815	Churkin	Chandler Lake
78-Md-80C	0372	Mayfield	Misheguk Mountain
78-Md-80D	0373	Mayfield	Misheguk Mountain
77-Md-84	0044	Mayfield	Misheguk Mountain
77-Md-82X	0374	Mayfield	Misheguk Mountain
78-ACn-204	0960	Churkin	Howard Pass
78-ACn-1122	0802	Churkin	Howard Pass
60-ABe-591D	0004	Brosge	Arctic
78-Md-101C	0800	Mayfield	Misheguk Mountain
78-Md-81C	0801	Mayfield	Misheguk Mountain
78-Ek-50e.2	0380	Ellersieck	Misheguk Mountain
60-ARr-663	0112	Reiser	Christian
60-ABe-589	0003	Brosge	Arctic
77-AHe-56	0035	Churkin	Howard Pass
MP-41	0953	Payne	Arctic
78-ACn-201	0803	Churkin	Howard Pass

BRITISH COLUMBIA-CACHE CREEK

Trav-059	0245	Travers	Cache Creek
MV-76-4A	0237	Monger	O'Donnel River
78-BKH-1Db	Holdsworth Collection	Holdsworth	Cache Creek

Locality	USGS MR Number	Collector	Quadrangle
WASHINGTON-SAN JUAN ISLANDS & NORTH CASCADES			
Wh-77-55H	0136H	Whetten	Roche Harbor 7½'
Wh;78;34	0499	Whetten	Roche Harbor 7½'
Wh-77-55F	0136F	Whetten	Roche Harbor 7½'
Wh-77-55B	0136B	Whetten	Roche Harbor 7½'
Wh-5E	0120E	Whetten	Arlington East 7½'
NEVADA-HAVALLAH SEQUENCE			
77-JNev-12	0196	Jones	Antler Peak 2°
77-JNev-19	0203	Jones	China Mountain 2°
77-JNev-24	0208	Jones	China Mountain 2°
77-JNev-16	0200	Jones	China Mountain 2°
78-Sp-100	0555	Speed	Mt. Tobin
SNy-77-P1	0615	Snyder	Leach Hot Springs 15'
SNy-77-T16	0624	Snyder	Leach Hot Springs 15'
SNy-77-P3	0617	Snyder	China Mountain 7½'
SNy-77-P2	0616	Snyder	China Mountain 7½'
SNy-77-F8	0613	Snyder	Mount Moses
SNy-77-EM5	0611	Snyder	Edna Mountain 15'
SNy-77-T27	0625	Snyder	Buffalo Springs 15'
NEVADA-TOIYABE RANGE (PABLO)			
Spd-106A	0607	Speed	Tonopah Ranger Dist. D-5
Spd-Pablo 290	0608	Speed	Tonopah Ranger Dist. D-5
77-FP-31F	0742	Poole	Pablo Canyon 7½'
NEVADA-QUINN RIVER			
79-JNev-3	0686	Jones	Quinn River Crossing 15'
79-JNev-4	0688	Jones	Quinn River Crossing 15'
79-JNev-5	0689	Jones	Quinn River Crossing 15'
79-JNev-6	0690	Jones	Quinn River Crossing 15'
NEVADA-MINA			
78-JNev-9	0693	Jones	Camp Douglas 7½'
79-Sp-S-10	0848	Speed	Walker Lake 2°
79-Sp-S-8	0847	Speed	Walker Lake 2°
OREGON			
WR-9A	0958	Blome	Supplee area
GC-4A	0959	Blome	Supplee area