Cretaceous Bryozoa from the Campanian and Maastrichtian of the Atlantic and Gulf Coastal Plains, United States

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The Late Cretaceous bryozoan fauna of North America has been severely neglected in the past. In this preliminary study based on museum material and a limited amount of fieldwork, we describe a total of 128 Campanian-Maastrichtian bryozoan species from Delaware, New Jersey, North Carolina, South Carolina, Tennessee, Georgia, Alabama, Mississippi, Louisiana and Arkansas. Eighty-two of these species are new, as are five (*Basslerinella*, *Pseudoallantopora*, *Kristerina*, *Turnerella* and *Peedeesella*) of the 77 genera.

One new family, *Peedeesellidae*, is proposed. Cheilostomes, with 94 species (73 per cent of the total), outnumber cyclostomes, with 34 species (27 percent), a pattern matching that seen elsewhere in the world in coeval deposits. There appear to be very few species (4) in common with the better known bryozoan faunas of the same age from Europe. Although both local and regional diversities are moderately high, most of the Atlantic and Gulf Coastal Plain bryozoans are encrusters; erect species are uncommon and are never present in sufficient density to form bryozoan limestones, in contrast to some Maastrichtian deposits from other regions.

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Introduction

Bryozoans are colonial invertebrates with a rich Ordovician to Holocene fossil record. Fossil bryozoans are most often found in sedimentary rocks formed in well-oxygenated shelf environments provisioned with firm or hard substrates, including sequences where clastic sediments and carbonate sedimentary rocks are intermixed. Just such conditions prevailed over the coastal plains of the eastern U.S.A. for much of the Late Cretaceous. However, so infrequently are Upper Cretaceous bryozoans from the eastern states of the U.S.A. mentioned in the literature that it would be easy to be misled into believing
that they are rare and of low diversity. This situation contrasts strikingly with coeval deposits in Europe where the high abundance and diversity of bryozoans is well-known, and where they are sometimes present in rock-forming quantities, for example in the Tuff-Chalk of Maastricht in The Netherlands (Felder & Bosch, 2000) and the contemporaneous Maastrichtian bryozoan mounds of Denmark (Larsen & Håkansson, 2000).

Knowledge of the fossil record of Cretaceous bryozoans is overwhelmingly dependent on European occurrences, even though diverse Cretaceous bryozoan faunas do occur in other parts of the world (e.g., South Africa – Brood, 1977; India - Guha & Nathan, 1996). Perceived evolutionary patterns during this important phase of evolutionary radiation are consequently dominated by European data. Our purpose here is to describe the diverse, yet hitherto largely neglected, latest Cretaceous bryozoan faunas from the Atlantic and Gulf Coastal Plains. The region of study extends from New Jersey in the northeast to Alabama in the south and Arkansas in the west.

Only two major works have ever been published on bryozoans from the Campanian-Maastrichtian deposits of this region. Canu & Bassler (1926) described 22 species of bryozoans from the Maastrichtian sequence of Coon Creek in Tennessee, a fauna briefly revised by McKinney & Taylor (in press). Shaw (1967) described the cheilostome bryozoans from the Upper Cretaceous of Arkansas. In addition, a handful of other papers have described, figured or mentioned Upper Cretaceous bryozoans from this broad geographical region (Butler & Cheetham, 1958; Frey & Larwood, 1971; Voigt, 1971; Turner, 1975, 1979; Cuffey, 1994; Taylor & Cuffey, 1996; Taylor & McKinney, 2000, 2002).

Reasons for the paucity of previous research on these bryozoan faunas are several-fold, but perhaps the most obvious is that most of the species present are encrusting forms (Plate 1) which are much less conspicuous to geologists than are the erect bryozoans that occur so commonly in the Upper Cretaceous of Europe, as well as in various Palaeozoic formations of North America. Although often small and inconspicuous, encrusters typically account for a greater diversity in post-Palaeozoic bryozoan faunas than do erect species (e.g., Cheetham et al., 1999).

This paper represents only a first attempt to describe the bryozoan fauna of a vast region. We have revised all of the bryozoan taxa (excluding ctenostome borings) established in the few previous publications mentioned above, as well as describing the bryozoans from new collections made available to us by other collectors or obtained during our own limited fieldwork. Our results should therefore be regarded as provisional - many additional species undoubtedly remain to be discovered and details of the geographical and stratigraphical distributions of species will need to be refined by future researchers. We know, for example, that there is much as yet unstudied material in the field collections of N.F. Sohl that are now in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Wherever possible we have made comparisons with contemporaneous bryozoan species from Europe (and elsewhere). However, the enormously rich European bryozoan biota is still inadequately described and illustrated, in spite of the efforts of, in particular, the late Professor Ehrhard Voigt. We have avoided applying the names used for poorly described European species to North American species. While revision of the myriad of European species created in the 19th century by such authors as d’Orbigny, Reuss, Pergens and von Hagenow, and subsequently in the early 20th century by Gregory, Lang and Levinsen, may eventually show that some of our new species are junior
synonyms, our conservative approach should minimize the pitfalls of spurious stratigraphical correlation and palaeobiogeography based on doubtful identifications.

**Geological setting**

Bryozoans occur in each of the eastern North American regions of Campanian to Maastrichtian outcrops in the Coastal Plain from its seaward termination in New Jersey to Arkansas, at the flexure from the western Cretaceous belts northward into the Mississippi Embayment (Fig. 1). The bryozoan-bearing units encompass a broad diversity of lithologies, generally siliciclastic and glauconitic sands along the Atlantic Coast and along the eastern margin of the Mississippi Embayment, where rivers draining the Appalachian Mountains were delivering abundant siliciclastic sediments. Farther away from such direct Appalachian influence, such as across the southern terminus of the mountains in Mississippi and Alabama and farther away in Arkansas, marls and chalks predominate.

**New Jersey and Delaware** – Bryozoans have been noticed for decades in two units in the central Atlantic states, the Mount Laurel Formation and the Navesink Formation (e.g., Richards & Shapiro, 1963; Owens et al., 1970), and cribromorph bryozoans have been described from the Navesink Formation in New Jersey (Turner, 1975, 1979). Directly underlying the Navesink Formation (Fig. 2), the Mount Laurel Formation consists predominantly of a massive, moderately well-sorted, glauconitic, feldspar-rich quartz sand, with local regions of interbedded sands and clays and a ubiquitous pebbly quartz sand at the top of the unit (Owens & Sohl, 1969; Owens et al., 1970; Olsson et al., 1988). It outcrops at the surface in both Delaware and New Jersey.

The overlying Navesink Formation consists of a massive, unconsolidated, clay- and silt-rich, medium- to coarse-grained, moderately to very poorly sorted, burrow-mottled glauconitic sand, although some quartz sand, apparently reworked from the underlying Mount Laurel Formation, occurs in the base of the unit (Owens & Sohl, 1969; Owens et al., 1970; Olsson et al., 1988). The Navesink Formation outcrops in New Jersey and continues into the subsurface in Delaware.

A wide diversity of macroscopic invertebrates, microfossils and some vertebrate remains occur in both the Mount Laurel and Navesink formations. In both units ostreid bivalves are the most conspicuous and generally most abundant macrofossils, although gastropod (mouldic) and cephalopod remains are also common. Age assignments of both units have varied through time. By the late 1980s, it was generally agreed that the Mount Laurel Formation was basal Maastrichtian and the Navesink Formation somewhat younger, based on foraminiferal zonation (e.g., Zullo, 1987; Olsson et al., 1988). However, more recent studies of ammonites (Kennedy & Cobban, 1994, 1997) have suggested an upper Campanian assignment for the Mount Laurel Formation, while determination of calcareous nanofossils from cores in both New Jersey and Delaware assign the Mount Laurel Formation to the Campanian calcareous nanofossil zones CC22-CC23 (75-72 Ma) and the Navesink Formation to the Maastrichtian calcareous nanofossil zone CC25b-CC26 (68-65 Ma), indicating an approximately 4 million year hiatus between the two units in Delaware (Sugarman et al., 1995; Benson & Spoljaric, 1996; Miller et al., 2003, 2004).
North Carolina and South Carolina – The presence of Upper Cretaceous bryozoans has been noted in the Carolinas, predominantly in the basal Peedee Formation (Maastrichtian), but also, less commonly, in the upper Campanian Black Creek Group (e.g., Sohl & Christopher, 1983). The uppermost unit of the Black Creek Group, the Donoho Creek Formation, consists of diverse, laterally interdigitated facies ranging from poorly sorted medium- to very coarse-grained siliciclastic sand, interbedded clay and fine-grained sand, and argillaceous fine sand (Owens & Sohl, 1989).

The Peedee Formation (Fig. 3) disconformably overlies the Donoho Creek Formation, and has a thin (50 mm or less) basal accumulation of abraded bone and shell, bored phosphate pebbles, and clasts reworked from the underlying Donoho Creek Formation, in a matrix of poorly sorted, coarse-grained sand (Sohl & Christopher, 1983). Most of the Peedee consists of grey, homogeneous, burrowed, calcareous, glauconitic, muddy fine- to very fine-grained siliciclastic sands (Swift et al., 1969; Sohl & Christopher, 1983; Gohn, 1988; Harris et al., 1986). In the vicinity of the Cape Fear Arch, in southeastern North Carolina, the top of the Peedee Formation consists of two siliciclastic units. The Rocky Point Member consists of dark grey quartz sand to quartzose carbonates varying basally from biomicrites through biosparites to uppermost biomicrudites (Gohn, 1988; Harris et al., 1986), and is overlain in New Hanover County and the coastal parts of Pender County by the Island Creek Member, an easterly thickening bioturbated dolomitic quartz wacke to sandy dolomite (Dockal et al., 1998).

The Donoho Creek Formation contains Exogyra cancellata, so has been considered by some to be basal Maastrichtian (e.g., Owens & Sohl, 1989). However, ammonites and calcareous nanofossils in the E. cancellata Zone of Delaware and New Jersey indicate that it is upper Campanian (see above), and Christopher & Prowell (2002) have placed it in calcareous nanoplankton zones CC22 and CC23a. The Peedee Formation in South Carolina has been placed in the upper lower Maastrichtian and upper Maastrichtian calcareous nanoplankton zones CC25a through CC26, so that the unconformity separating the Donoho Creek and Peedee Formations is approximately equal in duration to that separating the Mount Laurel and Navesink Formations of Delaware and New Jersey. The Island Creek Member in North Carolina yields calcareous nanofossil assemblages characteristic of zones CC25-26 (Dockal et al., 1998).

Central Georgia through western Tennessee – In the arcuate outcrop of Campanian through Maastrichtian rocks from central Georgia through Alabama and Mississippi to southwestern Tennessee (Fig. 1), bryozoans have been noted previously in the Prairie Bluff Chalk (Bryan & Jones, 1989; Bryan, 1992) and at the top of the Ripley Formation (Bryan, 1992). A diverse fauna of both cheilostome and cyclostome bryozoans has been described from the Coon Creek Formation (Canu & Bassler, 1926). In addition to bryozoans from these units, we have a limited amount of material from the Bluffport Marl Member of the Demopolis Chalk and from the Cusseta Sand.

The extended Upper Cretaceous outcrop belt from Georgia to southwestern Tennessee curves from the southeastern side of the Appalachian Mountains, across the structural grain of the Appalachians at their southern end, to the northwestern side of the mountains. During Late Cretaceous time, rivers draining the flanks of the mountains delivered siliciclastic sediments preferentially to the southeastern and northwestern ends of the arcuate belt, while carbonates and carbonate-rich, fine-grained siliciclastics
Fig. 1. Map of the eastern United States with Campanian and Maastrichtian outcrops indicated in black. The four regions are southern Arkansas (southwestern margin of map), a long arcuate belt from western Kentucky to central Georgia (southcentral portion of the map), a broad belt of exposure across the Cape Fear Arch centred on the North Carolina-South Carolina coastal region (southeastern portion of the map), and a narrow linear belt from Maryland to New Jersey (northeastern corner of the map).

Fig. 2. Campanian and Maastrichtian stratigraphic units exposed in Maryland through New Jersey. Modified from Carter & Rossbach (1984, chart).
Fig. 3. Campanian and Maastrichtian stratigraphic units exposed in North and South Carolina. Modified from Carter & Rossbach (1984, chart).

Fig. 4. Campanian and Maastrichtian stratigraphic units exposed along the Gulf Coast to the southeastern border of the Mississippi Embayment. Substantially modified from Carter & Rossbach (1984, chart).

Fig. 5. Campanian and Maastrichtian stratigraphic units of southwestern Arkansas. Compiled using information in Shaw (1967) and Bottjer (1986), with age determinations modified by more recent data on ammonite faunas.
accumulated in western Alabama and Mississippi (Fig. 4). In general, bryozoans are most common in the marls and other mixed carbonate-siliciclastic units.

The Demopolis Chalk is light-coloured throughout, consisting of a lower thin-bedded marly chalk, a median relatively pure massive chalk, and an upper unit of mixed chalky marl, very clayey chalk and calcareous clay (Copeland, 1968). The upper unit constitutes the Bluffport Marl Member; the lower units are not named. The Bluffport Marl grades upward in Alabama into the western portion of the Ripley Formation, and in Mississippi and Tennessee into the Coon Creek Formation.

The Cusseta Sand is an eastward stratigraphic equivalent of the lower Demopolis Chalk, and outcrops in eastern Alabama and western Georgia. It consists largely of siliciclastic sand locally replaced by glauconitic siltstone or interlaminated with silty clay (Skotnicki & King, 1989b). The Cusseta Sand is overlain by the Ripley Formation.

In eastern Alabama the Ripley Formation consists of diverse facies that in general succeed one another from north to south: carbonaceous, micaceous silty claystones, siltstones, and fine-grained planar-laminated sand; medium- to coarse-grained micaceous quartz sand with planar and trough cross-stratification; argillaceous, micaceous, glauconitic fine- to medium-grained sand; and micaceous, glauconitic, slightly sandy to silty calcareous clay and clayey marl (Skotnicki & King, 1989a). In western Alabama the Ripley Formation consists of light-coloured sand, sandy calcareous clay and thin indurated beds of fossiliferous sandstone, with a slightly sandy chalky clay at the base that interfingers with the Bluffport Marl (Copeland, 1968). Farther west and north, the Ripley Formation is replaced by the Coon Creek Formation, which consists of well-sorted, fine-grained, glauconitic marine sand and clay, the lower portion being calcareous and transitional into the underlying Demopolis Chalk (Russell, 1975). Large, flattened concretions occur locally in the upper interbedded sands and clay, and contain very abundant benthic marine carbonate fossils (Russell, 1975).

The Prairie Bluff Chalk overlies the Ripley Formation in central Alabama into Mississippi, although whether conformably (Mancini et al., 1996) or unconformably (King, 1994) is not agreed. The Prairie Bluff Chalk consists of massive, compact, white chalk with varying amounts of sand and with abundant molluscan fossils (Copeland, 1968).

Placement of the Campanian-Maastrichtian boundary has fluctuated somewhat in Georgia to southwestern Tennessee, in part because of the evolution of the placement of the *Exogyra cancellata* Zone, as noted above for the Carolinas, and for Delaware and New Jersey. Mancini et al. (1996) published calcareous nanoplankton zones for the Upper Cretaceous of the region. They determined that the Bluffport Marl Member of the Demopolis Chalk is Lower Maastrichtian (CC23) in Alabama, uppermost Campanian (upper CC22) to lowermost Maastrichtian (lower CC23) in Mississippi, and that the Demopolis Chalk is entirely Upper Campanian (CC21 and CC22) in Tennessee. The Cusseta Sand is laterally equivalent to the lower Demopolis Chalk and is therefore Upper Campanian. The lower Ripley Formation is Lower Maastrichtian (CC23), the upper Ripley Formation is Upper Maastrichtian (CC25), and the Coon Creek Formation is equivalent to the lower Ripley Formation and the Maastrichtian part of the Bluffport Marl. Lower Maastrichtian placement of the Coon Creek Formation is also indicated by its ammonite fauna (Cobban & Kennedy, 1994). Mancini et al. (1996) determined that the Prairie Bluff Chalk is Upper Maastrichtian (CC25), although Cobban & Kennedy (1995) suggested that the basal part of the Prairie Bluff Chalk in westernmost Alabama and in
Mississippi belongs within a substantially lower ammonite zone than does the thicker overlying portion that occurs within the highest Gulf Coast ammonite zone.

Arkansas – Upper Cretaceous cheilostome bryozoans from Arkansas were described by Shaw (1967) who collected from the Brownstown, Ozan, Saratoga and Nacatoch formations (Fig. 5). The Brownstown Formation appears to be Santonian (Micraster coranguinum zone equivalent) and bryozoans from it are not included in the present study, unless the species are also recorded in younger deposits. An examination of Shaw’s type specimens revealed the presence of common cyclostome bryozoans in addition to the cheilostomes that he described.

The Ozan Formation has a basal glauconitic, coarse-grained sand that is rich in shark teeth, phosphatic nodules and shell fragments, locally yielding bryozoans (Shaw, 1967). The basal glauconitic sand underlies a sequence about ten times as thick, composed of grey, calcareous, sandy clay.

The Saratoga Formation also includes a thin basal glauconitic facies (wackestone) yielding phosphatic nodules and abundant oyster shells (Bottjer, 1986). This is the facies within the formation in which bryozoans are most abundant (Shaw, 1967). The basal facies is succeeded by a much thicker sequence of quartz–rich sandy chalk (wackestone) that becomes more sandy toward the northwest and toward the top, where it becomes a marly chalk.

The Nacatoch Formation consists predominantly of grey to green, fine-grained, cross-bedded sand, the green colour corresponding with increased proportion of glauconite (Shaw, 1967). Fairly thick basal facies and matching, but thinner, uppermost facies of interbedded clay and sandy calcareous clay are also present. Bryozoans occur locally in the basal calcareous portion of the Nacatoch Formation.

Age determination of the Upper Cretaceous strata of southwestern Arkansas has varied through time. At the time the cheilostome fauna from the area was initially described, the Saratoga Formation was considered to span the Campanian-Maastrichtian boundary and to be largely Maastrichtian (Shaw, 1967). Papers published on ammonite faunas and ostracodes have yielded more precision. The base of the Annona Formation is uppermost middle Campanian to lowermost upper Campanian based on ammonites (Kennedy & Cobban, 1993a), suggesting that the Ozan Formation is early to middle Campanian. Similarly, the Saratoga Chalk has been determined to be latest Campanian (Kennedy & Cobban, 1993b). Ostracodes and planktonic foraminiferans indicate that the Aradelphia Formation is late Maastrichtian, placing the Nacatoch Formation most likely in the early Maastrichtian (Pitakpaivan & Hazel, 1994).

**Palaeoenvironments**

New Jersey and Delaware – Both Cretaceous bryozoan-bearing units in New Jersey and Delaware are interpreted to be shelf deposits. The Mount Laurel Formation is regarded as an inner-shelf mass of cross-bedded sand and adjacent interfingerling clays deposited in a shallow, subsurface sandbank (Owens & Sohl, 1969; Olsson et al., 1988), with transition to shoreface deposits to the northwest (Martino & Curran, 1990). The sequence is interpreted as shallowing-upward, with foraminiferans indicating mid- to
outer-shelf environments in the lower parts of the formation (Olsson et al., 1988), and a ubiquitous, pebbly, coarse-grained sand at its top, immediately underlying the unconformable contact with the Navesink Formation.

Poor sorting of sediments in the Navesink Formation indicates normally quiet-water conditions and the in situ generation of glauconite sand indicates a mid-shelf (Olsson et al., 1988) to outer shelf (Owens & Sohl, 1969) environment. The presence of quartz sand at the base, reworked from the underlying Mount Laurel Formation, changing to a relatively uniform sequence of muddy glauconite sand through most of the unit, suggests that the Navesink is a transgressive, deepening-upward succession.

North Carolina and South Carolina – The mixed, siliciclastic-rich Black Creek Group consists of a stacked sequence of unconformity-bounded units, the uppermost of which is the Donoho Creek Formation. The Donoho Creek, in common with the other sequences in the Black Creek Group, ranges from western deltaic through prodelta to more easterly shelf deposits (Gohn, 1988; Owens & Sohl, 1989).

The bioturbated, relatively uniform, fine-grained sediments that constitute most of the Peedee Formation are considered to be shelf, generally outer-shelf, deposits (Swift et al., 1969; Sohl & Christopher, 1983; Gohn, 1988) due to the lithology and the occurrence of mid- to outer-shelf foraminiferaans (Harris et al., 1986). The Rocky Point Member of the Peedee Formation is interpreted as a shallow-water deposit, due to the presence of relatively coarse-grained quartz sand within it, and is regarded as a nearshore capeshoal complex centred on the Cape Fear Uplift (Gohn, 1988). Harris et al. (1996) interpreted it as a shallowing-upward sequence based on the succession of carbonate facies and its termination in the Cretaceous-Tertiary unconformity.

Central Georgia to western Tennessee – All the facies in which Campanian and Maastrichtian bryozoans occur in the Georgia through western Tennessee outcrop belt are interpreted to be shallow marine, nowhere deeper than 40-50 m (Mancini et al., 1998). Most are inner- to mid-shelf deposits that varied in the amount of siliciclastic sediment input (Copeland, 1968; Skotnicki & King, 1989a).

The purer chalk facies of the Demopolis suggests outer-shelf environments (Bottjer, 1986). However, the bryozoan-bearing, interbedded variably sandy and silty beds of the Bluffport Marl Member are interpreted to have a mid-shelf origin (Puckett, 1992). The highly bioturbated, glauconitic, fine-grained marine deposits of the Cusseta Sand occur in association with planar to trough cross-stratified sands indicative of barrier-island shoreface and tidal-inlet environments, so are inferred to be inner-shelf deposits (Skotnicki & King, 1989b).

The low-diversity fauna that encrusts a rockground and associated cobbles at the top of the Ripley Formation in central Alabama appears to have developed on a rocky shore (Bryan, 1992). Other bryozoan-bearing beds within the Ripley Formation are interpreted as inner-shelf mixtures of siliciclastic and calcareous sediments, and represent the most offshore deposits of the generally back-barrier to lower shore-face sediments that make up the bulk of the Ripley Formation (Skotnicki & King, 1989a; Puckett, 1992). The upward transition in Mississippi and Tennessee from the mid-shelf Bluffport Marl into the increasingly siliciclastic-dominated Coon Creek Formation suggests that it, too, accumulated on the inner shelf.
The Prairie Bluff Chalk has been interpreted as middle- to outer-shelf based on its intermixture of chalk and coarse-grained siliciclastic sand, and absence of fine-grained siliciclastics (Puckett, 1992). The absence of fine-grained, but presence of coarser-grained siliciclastics indicates by-passing or winnowing of the former and suggests that the Prairie Bluff Chalk accumulated above normal wave base.

Arkansas – All the Campanian-Maastrichtian strata in which bryozoans have been found are open-shelf marine, containing abundant coccoliths, and, interestingly, bryozoans appear to be concentrated in the basal, glauconitic, epibenthic oyster-rich and commonly phosphate pebble-rich beds of each of the formations. Shaw (1967) interpreted the Ozan Formation to be a near-shore (inner-shelf) accumulation, based on bivalve biostromes within it. However, by analogy with similar patterns of basal glauconite- and phosphate-rich beds succeeded by less glauconitic, relatively finer-grained deposits in both the Annona and Saratoga formations, it may be better interpreted as a mid-shelf accumulation during a period of low sedimentation rate and deepening water as Bottjer (1986) inferred for the two younger units. The bryozoan-bearing calcareous clay of the basal Nacatoch Formation, superseded by cross-bedded fine-grained sand, probably represents inner-shelf deposits (Shaw, 1967) offshore of a prograding submarine siliciclastic bar.

Material and methods

Existing material in museum and other collections as well as specimens newly collected in the field have been utilized for this study. Repository abbreviations for material held or deposited in museum collections are as follows: NHM, Natural History Museum, London; LSUMG-I, Louisiana State University Museum of Geoscience Invertebrate Paleontology Collection; USNM, National Museum of Natural History, Smithsonian Institution (formerly United States National Museum), Washington, D.C.; ANSM, Academy of Natural Sciences Museum, Philadelphia; RU, Rutgers University, New Jersey; MNHN, Muséum National d’Histoire Naturelle, Paris; NNM, Nationaal Natuurhistorisch Museum, Leiden; VCSM, Voigt Collection, Senckenberg Museum, Frankfurt.

Bryozoans were collected in the field using a mixture of surface picking and bulk sediment sampling. The majority of species present are encrusters that are best obtained by collecting hard substrates, particularly mollusc shells, to which they are cemented. Some of the larger erect species are readily visible in the field, weathering out of the rock and becoming concentrated on rain-washed scree slopes. Small erect branches, plus encrusters detached from their original substrates, were recovered by sieving bulk sediment samples. However, in most cases such samples proved to be barren.

Cleaning methods varied according to the robustness of bryozoan preservation and the degree of matrix lithification. Bryozoans from some uncemented clays, notably the Ripley Formation of Coon Creek, Tennessee, are frail and were subjected to brief ultrasonic cleaning only; in some instances even this is too extreme. At the other end of the spectrum, robust bryozoans in lithified or semi-lithified chalks required more vigorous cleaning, including scrubbing under running water with a soft toothbrush. Partial removal of particularly stubborn chalk from colony surfaces was accomplished by repeated
soaking in sodium sulphate decahydrate solution, freezing and thawing, as described by Surlyk (1972).

Bryozoans were sorted and preliminary identifications made with the aid of binocular microscopes, utilizing a mounted needle to remove matrix that obscured surface details. The best-preserved specimens were selected for scanning electron microscopy (SEM). Four SEMs were employed during the course of this study; an ISI ABT-55 and a LEO 1455VP at the NHM, and a Hitachi S570 and Philips Quanta 200 FEI in the Department of Biology, Appalachian State University. The ISI, LEO and Philips SEMs were all equipped with low-vacuum chambers that permitted study of uncoated specimens under low vacuum conditions, with images generated using back-scattered electrons. The Hitachi S570 is a conventional high vacuum SEM that imaged coated specimens using secondary electrons. Differences in tonal qualities between the micrographs obtained from the four microscopes are due not only to back-scattered vs secondary imaging (see Taylor, 1986), but also to the type of back-scattered electron detector employed on the microscopes with low-vacuum chambers. These variations must be borne in mind when comparing images produced by different microscopes. In particular, the apparent convexity of frontal shields and prominence of topographic highs may vary according to the microscope. Wherever possible we have organized micrographs taken with the four microscopes into separate figure blocks. Images were initially captured photographically, but later acquired digitally. Photographs used for the figures were converted into digital files by electronically scanning the negatives.

Examples of the erect bryozoan species were thin sectioned. After resin impregnation, standardly oriented sections (longitudinal, transverse and tangentially) were cut to a thickness of 10-20 μm to allow observation of skeletal microstructure as well as larger-scale internal features.

Measurements and counts – Except where noted, measurements were made within the astogenetic zone of repetition of colonies. Most zooidal measurements were made from digital images using National Institute of Health software. A smaller proportion were made optically using a Wild M8 stereomicroscope with an ocular micrometer. Optical measurements were made to a precision of 10-15 μm. Each measurement or count is given in the text as mean plus or minus standard deviation, observed range, and – enclosed in parentheses – number of specimens used and total number of measurements or counts made. Except where noted, measurements are given in microns.

Measurements on cheilostomes, in μm, are identified by the following acronyms and abbreviations:

- **AL** Avicularium length
- **AoL** Avicularium opesia length
- **AoW** Avicularium opesia width
- **AW** Avicularium width
- **BRW** Branch width
- **Dis** Distance between midpoints of adjacent orifices
- **KL** Kenozooid length
- **KW** Kenozooid width
- **OL** Orifice length
- **OW** Orifice width
OOW  Ovicell orifice width (where different from normal orifice width)
OpL  Opesia length
OpW  Opesia width
OvL  Ovicell length
OvW  Ovicell width
RL  Rostrum length (avicularia)
RW  Rostrum width (avicularia)
VO  Diameter of opening in ‘vibraculum base’
VD  ‘Vibraculum base’ diameter
ZL  Autozooid length as seen on colony surface
ZW  Autozooid width as seen on colony surface

Measurements on cyclostomes, in μm, are identified by some of the same indications as for cheilostomes, but may also include the following acronyms and abbreviations:

AD  Diameter of equidimensional apertures
ADmn Minimum diameter of apertures
ADmx Maximum diameter of apertures
AS  Distance between midpoints of adjacent apertures
ASW Distance between midpoints of adjacent apertures within a row or fascicle
BCL Brood chamber length
BCW Brood chamber width
BrD Branch diameter or width
FD  Fascicle diameter
FS  Distance between centres of successive fascicles
FWL  Frontal wall length of single zooid
FWW Maximum frontal wall width of single zooid
Gap Distance between edges of adjacent fascicles
GL  Gonozooid length including proximal portion and brood chamber
KAD Kenozooid aperture diameter
KL  Kenozooid length
KW  Kenozooid width
NAD Nanozoid aperture diameter
NWL Nanozoid frontal wall length
NWW Nanozoid frontal wall width
MaD Diameter of maculae
OD  Ooeciopore diameter

Magnifications given for plates are based on scale bars in scanning electron microscope micrographs. Note that these commonly are imprecise, varying up to at least 10% from the true magnification.

Localities

Alabama
AL1. Ripley Formation (lower Maastrichtian); specimens collected as float from 3 m-thick exposure of brownish-grey, micaceous quartz wacke. Largely overgrown bank on
north side of Gammage Road, 6.2 km north of its intersection with US Highway 431 at the northern edge of Eufaula, Barbour County. 32°3.0′N, 85°10.1′W, Howe 7.5′ Quadrangle. Collected by F.K. McKinney and P.D. Taylor.

**AL2.** Ripley Formation (lower Maastrichtian); roadcut on US Highway 29, 2.7 km north of Bullock County Road 8, north of Perote, Bullock County. 31°57.8′N, 85°42.7′W, Perote 7.5′ Quadrangle. Collected by S.W. Henderson.

**AL3.** Uppermost Ripley Formation (upper Maastrichtian) and lower Prairie Bluff Chalk (upper Maastrichtian); specimens collected in situ from basal 500 mm of Prairie Bluff Chalk, consisting of sandstone cobbles derived from rockground at top of Ripley Formation and from siliciclastic-rich chalk matrix surrounding the cobbles. Stripped surface west of pond on west side of Alabama Highway 263, approximately 0.5 km south of intersection with Alabama Highway 21, Braggs, Lowndes County. 32°2.9′N, 86°48.4′W, Braggs 7.5′ Quadrangle. (Mosasaur locality (A) of Bryan, 1992). Collected by F.K. McKinney and P.D. Taylor.

**AL4.** Prairie Bluff Chalk (upper Maastrichtian); specimens collected as float and in situ from lower 2 m of several metres-high roadcut in light grey chalk. West side of Alabama Highway 263, approximately 1.7-2.0 km south of intersection with Alabama Highway 21, Lowndes County. 32°2.4′N, 86°47.6′W, Braggs 7.5′ Quadrangle. Collected by F.K. McKinney and P.D. Taylor.

**AL5.** Ripley Formation (upper Maastrichtian), Prairie Bluff Chalk (upper Maastrichtian), and Clayton Formation (Danian); specimens collected from 4 m-thick uppermost mollusc-rich calcareous quartz wacke of Ripley Formation and 2 m-thick exposure of mollusc-rich calcareous clay of the Prairie Bluff Chalk. Roadcut on south side of Alabama Highway 28, 2.2 km west of its intersection with Marengo County Road 21 at Jefferson, Marengo County. 32°23.1′N, 87°53.4′W, Jefferson 7.5′ Quadrangle. Collected by F.K. McKinney and P.D. Taylor.

**AL6.** Prairie Bluff Chalk (upper Maastrichtian); specimens collected in situ and as float from mollusc-rich chalk exposed in 1 m-high cut approximately 100 m long and stripped surface approximately 10 m wide cutting diagonally across approximately 2 m thickness above the cut. Just north of Lake Ridge Apartments on east side of Jaycee Park Road, Livingston, Sumter County. 32°35.4′N, 88°11.4′W, Livingston 7.5′ Quadrangle. Collected by F.K. McKinney and P.D. Taylor.

**AL7.** Prairie Bluff Chalk (upper Maastrichtian); specimens collected in situ and as float from mollusc-rich chalk exposed in 2 m-high cut approximately 20 m long on west side of Jaycee Park Road, Livingston, Sumter County. 32°35.3′N, 88°11.4′W, Livingston 7.5′ Quadrangle. Collected by F.K. McKinney and P.D. Taylor.

**AL8.** Prairie Bluff Chalk (upper Maastrichtian); specimens collected as float from stripped surface cutting at low angle across bedding of mollusc-rich calcareous clay. Service area on northeast corner of intersection of Interstate Highway 20/59 and Alabama Highway 28, Sumter County. 32°37.5′N, 88°12.4′W, Livingston 7.5′ Quadrangle. Collected by F.K. McKinney and P.D. Taylor.

**AL9.** Prairie Bluff Chalk (upper Maastrichtian); specimens collected in situ and as float from about 3 m high exposure of brownish grey marl. Low roadcut on east side of Alabama Highway 17, about 2.3 km north of intersection with Sumter County Road 24 in Emelle, Sumter County. 32°44.9′N, 88°18.8′W, Emelle 7.5′ Quadrangle. Collected by F.K. McKinney and P.D. Taylor.
AL10. Bluffport Marl Member of Demopolis Chalk (Lower Maastrichtian); specimens collected in situ and as float from approximately 3 m-high exposure of argillaceous limestone. Low roadcut on west side of Alabama Highway 21, about 3 km south of intersection with US Highway 11 in Epes, Sumter County. 32°39.9'N, 88°7.4'W, Epes 7.5' Quadrangle. Collected by F.K. McKinney and P.D. Taylor.

Arkansas (N.G. Shaw collection)

AR1. Saratoga Chalk, given by Shaw (1967) as upper Campanian Belemnitella mucronata Zone to lower Maastrichtian Belemnella lanceolata Zone; more recently assigned entirely to the uppermost Maastrichtian Nostoceras (N.) hyatti Zone by Kennedy & Cobban (1993b). Nacatoch Formation (lower Maastrichtian, Belemnella lanceolata Zone). High Bluff, 2.5 km north of Arkadelphia, west bank of the Ouachita River, Clark County. 34°8.4'N, 93°3.2'W, Caddo Valley 7.5' Quadrangle (Shaw, 1967, locality AC-1).

AR2. Saratoga Chalk (cf. AR1). Roadcut on Arkansas Highway 355, north edge of Saratoga, Howard County. 33°45.2'N, 93°54.2'W, Mineral Springs South 7.5' Quadrangle (Shaw, 1967, locality AH-1).

AR3. Upper Ozan Formation (lower Campanian, Marsupites testudinarium Zone) and lower Annona Formation (Campanian, Offaster pilula Zone). Riverbank escarpment at White Cliffs Station on Little River, Sevier County. 33°46.0'N, 94°3.6'W, Ben Lomond 7.5' Quadrangle (Shaw, 1967, locality AS-5).

AR4. Saratoga Chalk – Marlbrook Formation (both Campanian) contact; roadcut, approximately 1.6 km southwest of Saratoga, Hempstead County. 33°44.1'N, 93°54.8'W, Red Bluff 7.5' Quadrangle (Shaw, 1967, locality AHe-1).

Delaware

DE1. Mount Laurel Formation (upper Campanian); spoil area, north side of Chesapeake & Delaware Canal at Reedy Point, New Castle County. 39°33.8'N, 75°34.4'W, Delaware City 7.5' Quadrangle. Collected by K. Zipf.

Georgia

GA1. Ripley Formation (Maastrichtian); specimens collected in situ (most in densely packed lenses up to 200 mm thick and up to 2-3 m length in outcrop) from 1 m of bivalve-rich sandy marl about mid-way up 14 m sequence that is dominantly medium-grained quartz wacke. Roadcut on south side of Georgia Highway 39, about 0.3 km south of Bustahatchee Creek, near Florence, Quitman County. 31°58.4'N, 85°3.1'W, Georgetown 7.5’ Quadrangle. Collected by F.K. McKinney and P.D. Taylor.

GA2. Cusseta Sand (upper Campanian); roadcut on east side of US Highway 27/280, 9.7 km north of Lumpkin, Stewart County. 32°8.5'N, 84°49.6’W, Louvale 7.5’ Quadrangle. S.H. Henderson Collection.

Louisiana

LA1. Saratoga Chalk equivalent (Upper Campanian if coeval with Saratoga Chalk); exposure atop Rayburns dome, Bienville Parish. 32°15.3'N, 92°55.6’W, Bienville 7.5’ Quadrangle (Butler & Cheetham, 1958).
Mississippi

**MS1.** Demopolis Chalk (Campanian); specimens collected as float on stripped surface parallel with bedding in argillaceous marl containing abundant inoceramid bivalves. Above embankment on east side of US Highway 45 Bypass, just north of entrance road to Noxubee County vocational institute, 0.5 km north of intersection of US Highway 45 Bypass and Mississippi Highway 14, Noxubee County. 33°6.6' N, 88°32.7' W, Macon 7.5' Quadrangle. Collected by F.K. McKinney and P.D. Taylor.

**MS2.** Demopolis Chalk (Campanian), Macon, Noxubee County. Collected by E. Voigt, 1967.

**MS3.** Ripley Formation (Maastrichtian), Oktibbeha County. NHM material received in exchange with Mississippi State College, 1936.

New Jersey

**NJ1.** Navesink Formation (lower Maastrichtian); specimens collected *in situ* from lower 2 m of 6 m-thick burrow-mottled, greenish-grey, argillaceous, medium-grained glauconitic wacke. South bank of Poricy Creek, 50-100 m east of Middletown-Lincroft Road (County Road 50), 0.4 km south of Oak Hill Road, 5 km north of intersection of County Road 50 with New Jersey Highway 520 in Lincroft, Monmouth County. 40°22.1’N, 74°7.0’W, Long Branch 7.5’ Quadrangle. Collected by R. Turner and F.K. McKinney.

**NJ2.** Mount Laurel Formation (upper Campanian) and Navesink Formation (lower Maastrichtian); specimens collected *in situ* and as float from basal Navesink Formation: 15-m thick burrow-mottled, greenish-grey, argillaceous, medium-grained glauconitic wacke. Both banks along Big Brook, 50-150 m east of Boundary Road, approximately 1.7 km south of New Jersey Highway 520, east of Marlboro, Monmouth County. 40°19.2’N, 74°13.3’W, Marlboro 7.5’ Quadrangle. Collected by R. Turner and F.K. McKinney.

North Carolina

**NC1.** Rocky Point Member of Peedee Formation (upper Maastrichtian); individual boulders of coarse-grained calcareous quartz arenite. Boulders exposed at lowest tides on west bank of Northeast Cape Fear River, about 0.3 km east of North Carolina Highway 53 bridge, near Burgaw, Pender County. 34°35.6’N, 77°52.4’W, Stag Park 7.5’ Quadrangle. Collected by F.K. McKinney.

**NC2.** Rocky Point Member of Peedee Formation (upper Maastrichtian); specimens collected from spoil pile of dark grey, un lithified, medium-grained quartz sand with common *Flemingostrea*, all bryozoans encrusting this oyster. Martin Marietta Ideal Quarry, entrance on north side of North Carolina Highway 1002 approximately 3.2 km east of its intersection with US Highway 117, New Hanover County. 34°22.5’N, 77°51.7’W, Scotts Hill 7.5’ Quadrangle. Collected by F.K. McKinney and P.D. Taylor.

**NC3.** Rocky Point Member of Peedee Formation (upper Maastrichtian); specimens collected from spoil pile of weathered, dark grey, un lithified, medium-grained quartz sand. Martin Marietta Rocky Point Quarry, Rocky Point, Pender County. 34°25.5’N, 77°51.6’W, Moretown 7.5’ Quadrangle. Collected by F.K. McKinney and P.D. Taylor.

**NC4.** USGS Sohl locality 32192. Peedee Formation (Maastrichtian). 25-150 mm-thick muddy sand with abundant shells and shell fragments, overlying fine-grained sand of undetermined thickness. Bluff on right bank of Neuse River, Lenoir County, at 34.6 miles above New Bern. 35°20.0’N, 77°26.5’W, Ayden 7.5’ Quadrangle. Collected by N.F. Sohl.
NC5. USGS Sohl Collection 28929, accession 34958; Upper Cretaceous; 332-380 feet depth, well at Wilmington Waterworks, Wilmington, New Hanover County. Collected by N.F. Sohl.

NC6. USGS Sohl locality 31810, Peedee Formation (Maastrichtian); lower part of upper massive dark sand; right bank of Cape Fear River at Mitchells Landing, 30.4 miles above Wilmington, Acme Quadrangle, Brunswick County, North Carolina. 34°21.4′N, 78°12.6′W, Acme 7.5′ Quadrangle. Collected by N.F. Sohl.

NC7. USGS Sohl Collection 31808, Mitchells Landing, Cape Fear River, Brunswick County. 34°21.4′N, 78°12.6′W, Acme 7.5′ Quadrangle. Collected by N.F. Sohl.

NC8. USGS Sohl locality 32193, Maastrichtian, Peedee Formation, variably indurated sandstone 1.4 m above base of section; bluff on right bank of Neuse River, 34.6 miles above New Bern. 35°20.0′N, 77°26.5′W, Ayden 7.5′ Quadrangle. Collected by N.F. Sohl.

NC9. USGS Sohl locality 33098, Maastrichtian, presumably Peedee Formation; right bank of Cape Fear River at Niels Eddy Landing. Collected by N.F. Sohl.

Oklahoma (N.G. Shaw Collection)

OK1. Brownstown (Santonian) and Ozan (lower Campanian) Formations. Roadcut along US Highway 21, 1.9 km west of Oklahoma-Arkansas line, McCurtain County (Shaw, 197, locality O-1). 33°44.2′N, 94°30.2′W, Tom 7.5′ Quadrangle.

South Carolina

SC1. Donoho Creek Formation (upper Campanian) and Peedee Formation (lower Maastrichtian); specimens collected in situ from basal 3.5 m of Peedee Formation: fine- to medium-grained quartz wacke, lower 2 m burrow-mottled, overlain by 300 mm thickness with Skolithus; most bryozoans in upper 1.2 m which is variably lithified and boulder-producing. West bank of Pee Dee river at Burches Ferry, east end of Mill Branch Road, east of Mill Branch on South Carolina Highway 57, Florence County. 34°3.9′N, 79°31.7′W, Pamplico North 7.5′ Quadrangle. Collected by F.K. McKinney.

Tennessee

TN1. Ripley Formation, Coon Creek Member (lower Maastrichtian); bryozoans collected from the upper interbedded sand and clay. Along southeastern bank of Coon Creek, McNairy County. 35°19.86′N, 85°25.70′W to 35°20.09′N, 88°25.48′W, Leapwood 7.5′ Quadrangle. Collected by U. S. Geological Survey geologists, E. Voigt and S. Tracey.

Systematic palaeontology

This faunal study is not intended as a monographic revision of any particular higher taxa of bryozoans, nor a reclassification. Nevertheless, we have taken the opportunity to make remarks about the genera to which the described species have been referred. These comments include generic ranges which, given the almost invariable lack of recently-published taxonomic monographs, in most cases should be treated as best estimates – they are not based on exhaustive literature searches or detailed evaluation of the sometimes numerous species that have been assigned to the respective genera. Descriptions of cyclostome and cribrimorph cheilostome species were primarily written by FKM, non-cribrimorph cheilostomes by PDT.
Order Cyclostomata Busk, 1852
Suborder Tubuliporina Milne Edwards, 1838
Family Stomatoporidae Pergens & Meunier, 1886
Voigtopora Bassler, 1952

Type species – Alecto calypso d’Orbigny, 1850, Senonian, France; by original designation.

Remarks – Bassler (1952, p. 381) originally characterized Voigtopora as differing from Stomatopora by having autozooids that “are broad, elliptical, slightly constricted at their base, and marked by parallel transverse lines.” Illies (1976) re-examined the type specimen of V. calypso, noting that the species differs from typical ‘Stomatopora’ in having symmetrical zooids with a long initial portion covered medially by the next-proximal autozooid, and by the presence of both dichotomous and lateral budding (see also Pitt & Taylor, 1990), while Taylor (2002) included in the genus some species that lack dichotomous branching and added branches only by lateral budding.

Range – Upper Hauterivian (Jablonski et al., 1997) - Recent? (an extant Voigtopora-like genus, Jullienipora, was recently described by Reverter Gil & Fernández-Pulpeiro, 2005).

Voigtopora maconensis sp. nov.
Pl. 2.

Material – Holotype: NHM BZ 5107(1), Campanian, Demopolis Chalk, near Macon, Noxubee County, Mississippi (locality MS1). Paratypes: NHM BZ 5108-5110, BZ 5155(2); NNM RGM 507 023-507 025, details as for holotype.

Etymology – The species is named after its discovery near Macon, Mississippi.

Description – Colony encrusting, uniserial, branches originating solely by lateral budding at near 90°, branch internodes up to at least 17 autozooids long. Ancestrula approximately 500 μm in length, including approximately 300 μm diameter protoecium and short tubular extension, giving rise to a distal autozooid and two distolateral autozooids diverging proximally at about 60° to axis of ancestrula (Pl. 2, fig. 1d). Zone of astogenetic change includes the ancestrula and first three generations of increasingly larger budded autozooids, beyond which size of autozooids is variable, but does not on average increase.

Autozooids in the zone of astogenetic repetition large, elongate and gently widened distally to their maximum width proximal to the distally placed, generally short, narrow peristome that terminates in a circular aperture. Branches very slender relative to length of the autozooids. Autozooidal walls contain abundant circular pseudopores and are faintly wrinkled transversely (Pl. 2, fig. 1c).

Measurements (excluding zone of astogenetic change) – AS 1348±163, 988-1684 (6, 94); BRW 434±37, 326-532 (6, 91); AD 114±13, 85-247 (6, 81).
Remarks – *Voigtopora maconensis* resembles *V. dixoni* (Vine, 1893; holotype illustrated by Gregory, 1899, pl. 1, fig. 5), as described and illustrated by Taylor (2002), in having exclusively lateral budding of new branches, but differs in having three rather than two autozooids budded from the ancestrula, longer autozooids, narrower branch width and smaller apertures. Ancestrulae are preserved in the holotype (NHM BZ 5107(1)) and one paratype (NNM RGM 507 025).

*Voigtopora thurni* sp. nov.

Pl. 3.

Material – Holotype: NHM BZ 5111(1a), Maastrichtian, Prairie Bluff Chalk, Livingston, Alabama (locality AL6). Paratypes: NHM BZ 5111(1b), BZ 5111(1c), BZ 4803(4), BZ 4805(1), BZ 4805(2), NNM RGM 507 026-507 027, details as for holotype. NNM RGM 507 028-507 029, Maastrichtian, Jefferson, Marengo County, Alabama (locality AL5). Other material: BZ 4795(2), details as for holotype; LSUGM-I 8244/8248, 8272, Campanian, Upper Ozan Formation, White Cliffs Station, Sevier County, Arkansas (locality AR3). LSUGM-I 8258, Campanian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2). Other material: ANSM 80776-80778, Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1). RU 5601, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

Etymology – Named in honour of Richard Thurn, Professor of Geology at the University of West Alabama, who discovered one of the most prolific bryozoan sites in the Prairie Bluff Chalk of Alabama.

Description – Colony encrusting, uniserial, branches originating most commonly by approximately 90° bifurcations, secondarily by lateral budding also at approximately 90°, branch internodes up to at least six autozooids long. Ancestrula of variable length up to approximately 600 μm, including approximately 200 μm diameter protoecium, and giving rise to a single distal autozooid, to paired distal autozooids that diverge at approximately 180°, or to a distal and a distolateral autozooid that diverge at approximately 180° (Pl. 3, fig. 4). Astogenetic zone of change appears to be limited to the ancestrula and first asexually budded autozooids, beyond which size of autozooids is variable, but does not on average increase.

Autozooids in the zone of astogenetic repetition are of intermediate length, relatively broad, and taper both proximally and distally from their point of maximum width, which is about midway between the autozooidal aperture and that of the next-proximal autozooid. Peristomes rise near-perpendicularly to the substrate, may be up to about 300 μm long and terminate in a circular or occasionally slightly oval aperture. Autozooidal walls contain abundant small, circular pseudopores (Pl. 3, fig. 3b); transverse wrinkling may or may not be present.

Measurements – AS 614±123, 374-919 (9, 97); BRW 325±51, 207-481 (9, 90); AD 95±15, 58-134 (9, 85).
Remarks – Voigtopora thurni resembles V. calypso (d’Orbigny, 1850) (see Illies, 1976; Pitt & Taylor, 1990) in having both dichotomous and lateral branching, but differs in having smaller autozooids that are relatively more slender and have proportionally larger apertures. It differs from V. maconensis sp. nov. in having dichotomous (Pl. 3, fig. 1a) as well as lateral branching, in the much smaller dimensions of the autozooids and in having a more abrupt primary zone of astogenetic change.

Specimens of Voigtopora from the Campanian of Arkansas are included tentatively in V. thurni based on similar autozooids and early colony astogeny. However, only lateral budding was noted by us on the few small colonies available on the same small shell fragments as Shaw’s (1967) cheilostome type specimens. More specimens from Arkansas need to be examined to establish more fully the relationship between Alabama V. thurni and material from Arkansas that is tentatively assigned to this species.

Colonies encrust diverse ostreid shells and, in the Mount Laurel Formation, small pebbles of siltstone, sandstone and phosphate.

Family Oncousoeciidae Canu, 1918

Oncousoecia Canu, 1918

Type species – Tubulipora lobulata Hincks, 1880 (= Alecto dilatans Johnston, 1847; see Hastings, 1963), Recent, Britain; by original designation.

Range – Sinemurian(?), Aalenian to Recent. An unpublished record of probable Oncousoecia occurs in the Sinemurian (Blue Lias) of south Wales.

Oncousoecia? nonomologabili sp. nov.

Pl. 4.

Material – Holotype: RU 5600, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2). Paratypes: RU 5400, 5602, 5608, same details as holotype.

Etymology – Italian, non omologabili, meaning resistant to classification.

Description – Colony encrusting, multiserial, narrowly to broadly lobate, commonly with fine-scale concentric rugae parallel with the growing margin. Protoecial diameter approximately 200 μm; elongate adnate ancestrula and 3-4 generations of autozooids with increasing length and increasing apertural diameters constitute primary zone of astogenetic change.

Autozooids in zone of astogenetic repetition elongate, robust, terminating in isolated, short, cylindrical peristomes that are either perpendicular to the colony surface or gently inclined distally, some closed by a terminal diaphragm. Peristomes approximately quincuncially arranged, but variably spaced, resulting in locally relatively dense clusters (Pl. 4, fig. 1d). Frontal wall essentially fl at and perforated by approximately 10 μm-diameter circular to transversely oval pseudopores spaced approximately 40 μm from centre to centre (Pl. 4, fig. 1e).

Gonozooids not seen.
Measurements – FWL 746±225, 870-1222 (3, 27); FWW 156±20, 118-190 (3, 27); AD 107±12, 80-129 (3, 30); AS 356±94, 226-592 (3, 30).

Remarks – This species is consistent with many characters of *Oncousoecia*, including the encrusting lobed to fan-like growth, the quincuncial arrangement of short autozooidal peristomes and a similar primary zone of astogenetic change to that illustrated by Hayward & Ryland (1985b) for *O. dilatans* (Johnston), the type species. However, it cannot confidently be assigned to *Oncousoecia* at present because we lack information on the gonozooid.

All encrusting Campanian through Danian tubuliporines described by Brood (1972) from Scandinavia, as well as Aptian species of *Oncousoecia* from the Faringdon Sponge Gravels of England (Pitt & Taylor, 1990), have much smaller autozooidal apertures than the species described here. Colony form, autozooid size and quincuncial autozooid arrangement are similar to *Diastopora cholaensis* Guha & Nathan, 1996, from the Maastrichtian of southern India, differing in that *D. cholaensis* has moderate to long autozooidal peristomes where it is encrusting. Another Indian Maastrichtian species, *D. tewarii* Guha & Nathan, 1996, differs in having larger, more distantly spaced autozooidal apertures.

**Microeciella** Taylor & Sequeiros, 1982

*Type species* – *Microeciella beliensis* Taylor & Sequeiros, 1982, Toarcian of Spain; by original designation.

*Remarks* – This genus, named for two Jurassic species by Taylor & Sequeiros (1982), is characterised by having a small gonozooid with a longitudinally ovoidal outline. Subsequently, Hayward & Ryland (1985a) introduced *Eurystrotos*, based on a Recent type species, which has a somewhat more terminal ooeciopore than *Microeciella*. However, this is largely a matter of degree and Taylor & Wilson (1999) argued that the two genera may not be distinct, preferring to use *Microeciella* for the reception of two species from the Jurassic of the western U.S.A.

*Range* – Pliensbachian – Recent.

**Microeciella livingstoni** sp. nov.

Pl. 5.

*Material* – Holotype: NHM BZ 4796(7), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). Paratypes: NNM RGM 507 030(a, b), details as for holotype.

*Etymology* – Named for Livingston, Alabama, the type locality.

*Description* – Colonies thin, unilaminar, completely adnate; perimeter marked by narrow budding zone composed of 1-2 generations of autozooids, projecting flange of basal lamina lacking. Colonies essentially circular when small; larger colonies with less...
regular outlines and shape, commonly with subcolonies derived from pseudoancestrulae. Fine-scaled concentric rugae prominent on fixed-walled upper surface (Pl. 5, fig. 2a). Protoecium circular, about 125 μm in diameter, ancestrula short and distal portion very narrow, giving rise immediately to full-sized autozooids.

Autozooids small, arranged in well-developed quincuncial pattern. Peristomes short, isolated, never connate; inclined to nearly perpendicular to general colony surface. Frontal wall about four times longer than wide, gently convex transversely; zooidal boundaries clear; pseudopores approximately 4 μm in diameter, circular or slightly elongate parallel with growth direction.

Gonozooids small, developed even in colonies with few autozooidal generations; brood chambers conspicuously inflated, approximately equidimensional, not extending laterally beyond peristomial bases of two neighbouring autozooids; oociopore located on distal edge of brood chamber, circular, smaller than autozooidal apertures, with thickened rim, but no prominent ooeiciostome (Pl. 5, fig. 2b).

**Measurements** – FWL 308±35, 257-399 (6, 57); FWW 90±12, 69-116, (6, 56); AD 43±5, 30-53 (6, 56); BCL 291±28, 269-331 (3, 4); BCW 346±17, 324-365 (3, 4); OD 35±5, 29-39 (3, 3); PD 123±16, 104-135 (3, 3); AAD 31±6, 24-36 (3, 3).

**Remarks** – Species of *Microeciella* tend to be rather similar in skeletal morphology, all having small autozooids and ovate gonozooids. This makes their discrimination difficult, a task rendered even harder by the knowledge that an unknown number of species first described as *Berenicea* require reassignment to *Microeciella*. One such species may be *Berenicea acanthina* Gregory, 1899, from the British Chalk, which has more prominent peristomes than *M. livingstoni*. Jurassic species of *Microeciella* have larger zooids (*M. duofluvina* (Cuffey & Ehleiter, 1984), *M. reflexa* Taylor & Sequeiros, 1982), or proportionally smaller (*M. pollostos* Taylor & Wilson, 1999) or more subterminal oociopores (*M. beliensis* Taylor & Sequeiros, 1982).

The co-occurring *Hyporosopora praecox* sp. nov. has similar-sized colonies, autozooids and colony surface texture, but *M. livingstoni* differs in having more-equidimensional brood chambers without lateral lobes and subcolonies developed from pseudoancestrulae.

**Family Multisparsidae** Bassler, 1935

*Idmonea* Lamouroux, 1821

**Type species** – *Idmonea triquetra* Lamouroux, 1821, Bathonian, Normandy, France; by monotypy.

**Remarks** – This genus has a long history of misinterpretation. The Jurassic type species has predominantly encrusting colonies with ribbon-like, bifurcating branches that are subtriangular in cross-section and bear simple, longitudinally elongate gonozooids. The cross-sectional shape of the branches led to the name *Idmonea* being applied to numerous unrelated erect species, ranging to the present-day, with subtriangular branches and more complex gonozooids. These erect forms are now mostly referred to either *Idmidronea* or *Exidmonea* (e.g., Ostrovsky & Taylor, 1996). Erect branches are occasionally
produced in colonies of the type species, but these are compressed and ovoidal in cross-section.

Range – Aalenian to Maastrichtian?

Idmonea sp.
Pl. 6.

Material – RU 5500, 5631, Maastrichtian, Navesink Formation, New Jersey 1 and/or 2.

Description – Colony adnate, pluriserial, branches about 800-900 μm wide with sub-triangular cross sections and rounded tips; branches composed of up to at least six rows of autozooids. Ancestrula short, distal tube laterally curved (protoecium not seen), primary zone of astogenetic change comprising approximately four generations of similar autozooids and marginal selvedge, with increasing number of autozooids per generation.

Autozooids grading from relatively small and planar marginally to larger and slightly convex medially, about 1.8 times longer than wide; apertures circular, surrounded by low narrow peristome, increasing in size toward branch midline; pseudopores circular, about 8 μm diameter.

Kenozooids a single row on each flank making a narrow selvedge (Pl. 6, fig. 2c); planar to slightly concave transversely.

Gonozooids not observed.

Measurements – ZL 261±24, 219-316 (1, 12); ZW 140±22, 119-164 (1, 12); AD (marginal) 62±5, 57-71 (1, 7); AD (intermediate) 70±8, 55-80 (1, 8); AD (axial) 79±10, 63-99 (1, 8).

Remarks – We have seen only two small colony fragments of this species, one consisting only of the primary zone of astogenetic change and the other a short, non-fertile, exposed section at the distal end of a branch. These provide insufficient information for species determination.

Family Entalophoridae Reuss, 1869

Mecynoezia Canu, 1918

Type species – Entalophora proboscidea Milne-Edwards, 1838, Recent, Mediterranean; by original designation.

Remarks – Several cyclostome genera are characterized by erect, unjointed colonies of radially symmetrical branches composed of autozooids with exterior frontal walls and prominent isolated peristomes. These are often identified formally, or informally, as Entalophora Lamouroux, 1821. As shown by Walter (1970), true Entalophora has a narrow central lumen along the branch axis and possesses subtriangular gonozooids. Another genus, Mecynoezia, is characterised by the lack of this axial lumen and has an elongate or subglobular gonozooid with a small terminal ooeciopore. In these two
genera, along with other entalopherid genera with autozooidal apertures in annual bands or spirals (Voigt & Flor, 1970; see Spiropora below), autozooids bud at or near the branch axis. However, new autozooids are budded along the branch perimeter in the new species described below and in some previously illustrated entalopherids, such as Entalophora lineata Beissel (Stoliczka, 1873, pl. 3, fig. 10a; considered a junior synonym of Mecynoeia benedeniana (von Hagenow) by Guha & Nathan, 1996) and Entalophora icaunensis d’Orbigny (Canu & Bassler, 1928, fig.17A; reassigned to Mecynoeia by Canu & Bassler). The taxonomic significance of this perimetrical budding has yet to be evaluated and the new species described below, in which gonozooids are unknown, is questionably assigned to Mecynoeia for the time being.

Range – Aalenian – Recent.

Mecynoeia? exterogemma sp. nov.

Material – Holotype: USNM 526199, Maastrichtian, Peedee Formation, Neuse River, North Carolina (locality NC4). Paratypes: USNM 526200-526205, 528943 (20 specimens), details as for holotype. NHM BZ 4827-4831, Maastrichtian, Ripley Formation, Florence, Quitman County, Georgia (locality GA1).

Etymology – L., exterus, for exterior and L., gemma, bud, in reference to origin of autozooids around the perimeter of erect branches.

Description – Colony of oligoserial bifurcating branches, encrusting branches giving rise to erect branches. Encrusting branches (Pl. 7, fig. 8) with low convex cross-section appearing uniserial due to near-midline alignment of autozooidal apertures or peristomial bases, but with proximal portions of at least one autozooid passing to each side of the median aperture. Erect branches narrow and radially symmetrical. Ancestrula and primary zone of astogenetic change not seen.

Autozooids in zone of astogenetic repetition robust; extremely long frontal wall of inconstant width and slightly sinusoidal where passing by peristomial bases of other autozooids; surfaces flat to slightly convex transversely, separated by thread-like narrow groove (Pl. 7, fig. 7); terminating in circular peristome orientated perpendicular to encrusting branch surface and tilted distally at less than 90° to erect branch surface (Pl. 7, fig. 6), commonly broken or eroded to branch surface; broken peristomes occasionally sealed at branch surface by terminal diaphragms. Peristomes irregularly positioned, not in distinct rows in erect branches, closer around than along branches. Autozooids budded around erect branch circumference by intercalation between pre-existing autozooids, older autozooids occupying full radius from branch axis to branch surface. Frontal exterior walls and peristomes of autozooids perforated by circular to elongate elliptical pseudopores approximately 12-13 μm in diameter. Interzooidal pores present, but non-terminal diaphragms and other intrazooidal structures apparently lacking.

Gonozooids not seen.

Measurements (erect branches) – BRW 642±148, 478-1126 (12, 19); FWL >3338±51,
Family Tubuliporidae Johnston, 1838

Platonea Canu & Bassler, 1920

Type species – Reptotubigera phillipsae Harmer, 1915, Recent, Loyalty Islands, Australia; by original designation.

Remarks – The type species of Platonea is characterized by encrusting lobate growth, ovicells that ramify between several uniserial fascicles of autozooidal peristomes, a transversely elongate ooeciostome located near the axial end of a peristomial fascicle, and short ‘closed’ polygonal polymorphs covering the basal lamina that extends laterally to either side of a lobe of the colony (Harmer, 1915). All but the last of these characteristics of the type species were thought by Canu & Bassler (1920) to characterize Platonea and marginal kenozooids are neither mentioned nor figured in the two Paleogene species of this genus that Canu & Bassler erected. Although some authors have rejected Platonea as a distinct genus (Borg, 1944; Brood, 1972), Osburn (1953) and Harmelin (1976) argued that the gonozooid is sufficiently distinctive to characterize the genus, and they added species that are either erect or semi-erect.

Range – Campanian? to Recent.

Platonea adnata sp. nov.

Pl. 8.

Material – Holotype: NHM BZ 4189(1a), Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2). Paratypes: NHM BZ 4189(1b-d), additional colonies on same shell as holotype, NHM BZ 4175(4a-g), BZ 4188(1), details as for holotype.

Etymology – L., adnatus, for joined to or united with, in reference to the broad bands of kenozooids that laterally extend the base of adherence to the substrate.

Description – Colony encrusting, multilobate with elongate dichotomously branched lobes about 1.5-2.0 mm wide across the band of autozooids. Colonies closely appressed to the substrate; no elevated margins seen. Protoecium low discoidal, 165-196 μm in diameter, giving rise to laterally directed, initially adnate tubular portion of ancestrula (Pl. 8, fig. 3); two asexually budded autozooids originating on basal side of ancestrula very close to protoecium; subsequent generations of autozooids also budded basally with increasing number of autozooids per generation until full branch width of approximately ten autozooids per generation.

Autozooids in closely spaced transverse rows most commonly extending across entire lobe; long peristomes in uniserial connate rows, but divided into two portions because each peristome, along with its lateral neighbours, tilts toward the adjacent margin, leaving a median V-shaped gap in the row. Each fascicle consists typically of
5-7 autozooidal peristomes (Pl. 8, fig. 1c), each with a roughly quadrate cross section, some with convex-outward proximal and distal sides. Frontal exterior walls of autozooids perforated by circular pseudopores (Pl. 8, fig. 2).

Gonozooids gently inflated, densely perforated by pseudopores, extending across entire lobe, occupying entire colony surface area between as many as four rows of autozooids. Ooeiciopore transversely elongate, about 30 μm by 80 μm, placed about midway along length of brood chamber (Pl. 8, fig. 1d), adjacent to distal surface of connate row of peristomes, located by first to third peristome from lobe axis and situated either to right or left of axis.

Kenozooids forming narrow to broad selvage (up to over 1 mm wide) to lobate branches (Pl. 8, fig. 1a), short, polygonal, thin-walled.

**Measurements** – Holotype: ADmx 104±10, 90-120 (1, 10); ADmn 71±6, 60-75 (1, 10); FS 294±18, 255-315 (1, 10); BCL 1395±349, 990-1800 (1, 5); BCW 1152±68, 1080-1215 (1, 5).

**Remarks** – *Platonea adnata* differs from *P. subtrigonalis* Guha & Nathan, 1996, from the Maastrichtian or possibly Campanian of India, in having well developed bands of kenozooids along branch margins, more elongate branches and brood chambers located anywhere along the branch length rather than confined to branch bifurcations.

**Platonea catenula** sp. nov.  
**Pl. 9.**

**Material** – Holotype: NHM BZ 5099(2a), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). Paratypes: NHM BZ 5099(2b), NHM BZ 5099(2c), NHM BZ 5099(2d), NHM BZ 5099(2e), NNM RGM 507 031, details as for holotype. BZ 4436, BZ 5114(1), Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5). NNM RGM 507 056(2), Maastrichtian, Prairie Bluff Chalk, Braggs, Lowndes County, Alabama (locality AL3). ANSM 80361, Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1). RU 5602, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

**Etymology** – L., *catenula*, diminutive for chain, in reference to the appearance of branches that pinch and swell.

**Description** – Colonies encrusting with strap-like branches of almost semicircular cross section (Pl. 9, fig. 1a), typically about 1 mm wide, but less than 300 μm at origin of lateral branches and up to about 1.5 mm wide; branches locally cateniform due to irregular swelling and contraction; new branches arising adventitiously. Colonies closely adpressed to the substrate; no elevated margins seen. Protoecium hemispherical, giving rise to laterally directed, initially adnate tubular portion of ancestrula; two asexually budded autozooids originating on basal side of ancestrula very close to protoecium; subsequent generations of autozooids also budded basally with increasing number of autozooids per generation until approximately five autozooids per generation.

Autozooidal apertures circular, most commonly in moderately to poorly organized
transverse rows of 2-5 extending across entire lobe; peristomes short to moderate in length, isolated. Apertural diameter largest in middle of branch, progressively smaller toward branch margins. Frontal exterior walls of autozooids perforated by abundant circular pseudopores.

Gonozooids gently inflated, densely perforated by pseudopores, roughly equidimensional, occupying about two-thirds to three-quarters branch width, not perforated by autozooidal apertures, and interrupting normal placement of autozooidal apertures. Oocciopore distal, subcircular (Pl. 9, fig. 1c), slightly larger than half the diameter of autozooidal apertures, ooeistome very short.

Kenozooids forming marginal selvage proximal to growing tips of branches (Pl. 9, fig. 1d); short, polygonal, thin-walled, sealed terminally by exterior-walled diaphragms.

Measurements – FWL 311±54, 224-463 (6, 60); FWW 163±18, 131-222 (6, 60); AD 79±10, 62-107 (6, 60); AS 226±53, 141-358 (6, 60); BRW 975±203, 644-1418 (6, 13); BCL 682±39, 639-730 (1, 4); BCW 732±128, 578-879 (1, 4); OD 48±4, 45-52 (1, 3).

Remarks – This species differs from P. subtrigonalis Guha & Nathan, 1996, and from P. adnata sp. nov. in having well-developed bands of closed kenozooids along branch margins, adventitious branching, poorly organized transverse rows of isolated autozooidal apertures and gonozooids located along the branch length rather than confined to branch bifurcations. It differs from P. mississippiensis sp. nov. in having broader and more highly inflated branches, well-developed lateral bands of kenozooids and more poorly organized transverse rows of autozooidal apertures. The Indian species P. subtrigonalis Guha & Nathan, 1996, differs in the same characters, except perhaps for the degree of development of kenozooids.

Platonea mississippiensis sp. nov.

Pl. 10.

Material – Holotype: NHM BZ 5107(2a), larger colony encrusting same inoceramid as holotype of Voigtopora maconensis sp. nov., Campanian, Demopolis Chalk, near Macon, Noxubee County, Mississippi (locality MS1). Paratype: NHM BZ 5107(2b), smaller colony on the same inoceramid shell.

Etymology – Named after the State of Mississippi, in which the species was discovered.

Description – Colonies encrusting, thin strap-like branches, typically about 500 μm wide, but less that 200 μm at origin of lateral branches and up to about 1 mm wide where gonozooids are present; new branches arise adventitiously (Pl. 10, fig. 1a). Colonies closely adpressed to the substrate; no elevated margins seen. Ancestrula and primary zone of astogenetic change not observed.

Autozooids most commonly in transverse rows extending across entire lobe, but locally autozooid origins may be disordered in narrow parts of branches; peristomes short, isolated in proximal and narrow parts of branches, but in uniserial connate fascicles where branches are wider, divided into two portions because each peristome, along
with its lateral neighbours, tilts toward the adjacent margin, leaving a median V-shaped gap in the row. Each fascicle consisting typically of 3-5 autozooidal peristomes, each with rounded to roughly quadrate cross section. Frontal exterior walls of autozooids perforated by abundant circular pseudopores.

Gonozooids (Pl. 10, fig. 1d) gently inflated, roughly equidimensional, occupying entire colony surface area between two successive rows of autozooids. Ooeiostome distal, but size and shape of ooeiopore unknown.

Kenozooids in single row at branch margin forming a narrow selvage, short, polygonal and thin-walled.

Measurements – FWL 404±59, 324-511 (2, 20); FWW 116±17, 84-143 (2, 17); AD 72±10, 50-89 (2, 14); BCL 474±18, 450-493 (2, 4); BCW 420±45, 368-474 (2, 4); Gap 228±29, 192-273 (2, 11); GL 816±37 (1, 2).

Remarks – This new species differs from \( P. \) adnata sp. nov. in having narrower branches with adventitious rather than dichotomous branching, poorly developed lateral bands of kenozooids and a less elongate brood chamber. It differs from \( P. \) sub-trigonalis Guha & Nathan, 1996, in the same characters, except perhaps in the degree of development of kenozooids. Available colonies encrust an inoceramid shell fragment.

Idmidronea Canu, 1920

Type species – Idmonea maxillaris Lonsdale, 1845, Eocene, South Carolina; by original designation.

Remarks – There are approximately twenty idmidroneiform genera of erect cyclostomes characterized by subtriangular branch cross sections, autozooids originating along or near one side of the branch and apertures opening on the other two sides that constitute the branch frontal (Taylor & Voigt, 1992; Ostrovsky & Taylor, 1996; Viskova, 2004). In some of these genera the branch reverse is a simple exterior wall whereas in others it is formed of a primary layer or overgrowth of kenozooids which may be fixed- or free-walled. Viskova (2004) recently introduced a new terminology for the various types of kenozooids found in these cyclostomes, recognizing eight different kinds: reptozooecia, stenozooecia, angulizooecia, dactylethrae, nematozooecia, tergozooecia, firmatozooecia and cryptozooecia.

Provisionally, the most appropriate genus for reception of the new species described below is Idmidronea which is distinguished from the closely similar Exidmorea by the presence of kenozooidal overgrowths on branch reverse sides. Pleuronea Canu & Bassler, 1920, also has kenozooids on the reverse sides of the branches, but in this genus, as generally interpreted (Hinds, 1975), the kenozooids bud at distal growing tips simultaneously with autozooids on branch frontals rather than developing subsequently as an overgrowth. Therefore, all branches of Pleuronea have kenozooids whereas these polymorphs are lacking in the most distal branches of Idmidronea colonies.

Range – Maastrichtian-Recent.
**Idmidronea traceyi** sp. nov.

Pl. 11.

In press *Idmidronea* sp. nov.; McKinney & Taylor.

**Material** – Holotype: NHM BZ 5115, Maastrichtian, Ripley Formation, Coon Creek Member, above *Corbula* bed upstream from Field Center, Coon Creek, Tennessee (locality TN1). Paratypes: NHM BZ 5116-9, NNM RGM 507 033 (4 pieces), details as for holotype; ANSM 80362, Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1).

**Etymology** – Named in honour of Steve Tracey, who collected and donated most of the types.

**Description** – Colony erect, unilaminate, consisting of bifurcating branches 0.5-1.0 mm width, forming planar branch systems originating as single erect branch arising from small, circular encrusting base. Branch cross section subrounded triangular, obverse surface consisting of two facets joined at median keel; branch anastomoses occasionally present (Pl. 11, fig. 1a). Ancestrula not seen.

Autozooids terminate in transverse uniserial fascicles of 3-4 contiguous peristomes, each fascicle restricted to one side of obverse surface, but generally aligned with a fascicle on the opposite facet of the frontal surface. Autozooidal apertures diminish in diameter from obverse branch centre. Frontal walls of autozooids are exterior-(fixed-)walled, perforated by circular, 3-4 μm diameter pseudopores. Autozooids budded in thin-walled endoozone close to branch reverse side. Large interzooidal pores present, but diaphragms and other intrazooidal structures not seen.

Gonozooids lateral (Pl. 11, fig. 3a), occupying space between two autozooidal fascicles on one facet of obverse surface, roofed by densely porous exterior wall. Ooeciopore located near lateral end of the distal of the two fascicles. Ooeciostome short, continuing inwardly about 50 μm as a tube within the brood chamber, inner terminus flared and fluted (Pl. 11, fig. 3b).

Kenozooids cover reverse side of older branches, including colony base (Pl. 11, fig. 4), and may result in substantial thickening and rounding of reverse surface; distally orientated, interior-(free-)walled; commonly closed by thin skeletal plate. Kenozooids absent on obverse surface except along margins in thickest branches seen and near colony base.

**Measurements** – FWL 354±52, 270-474 (4, 32); FWW 104±19, 66-142 (5, 52); AD 79±12, 47-110 (7, 92); FS 475±49, 403-590 (5, 37); BCL 750 (1, 1); BCW 551 (1, 1); OD 78 (1, 1); BRW 779±170, 523-1136 (10, 20); KW 55±8, 38-70 (2, 20).

**Remarks** – *Idmidronea traceyi* differs from *I. globulosa* Brood, 1972 (Danian, Scandinavia), in having 3-4 peristomes per fascicle instead of 4-6, smaller autozooidal dimensions and smaller brood chambers that are placed laterally rather than between fascicles; from *I. suecica* Brood, 1972 (Campanian, Sweden), in fewer peristomes per fascicle and nearly equidimensional rather than elongated brood chambers; and from *I. orbissa*...
Guha & Nathan, 1996 (Maastrichtian, India), in having fewer peristomes per fascicle, smaller autozooidal apertures and smaller brood chambers placed laterally rather than frontally.

**Family Spiroporidae Voigt, 1968**

*Spiropora* Lamouroux, 1821

*Type species* – *Spiropora elegans* Lamouroux, 1821, Bathonian, France; by subsequent designation.

*Remarks* – *Spiropora* is one of several Mesozoic and early Cenozoic genera characterized by erect colonies of cylindrical, bifurcated branches consisting of autozoecia with elongate fixed frontal walls that are arranged most commonly in annular groups that completely encircle the branch. The genera are differentiated by distinctly different gonozooids and apparently belong to several different tubuliporine families (Voigt, 1968; Voigt & Flor, 1970). They have such similar features that it is essentially impossible to determine generic assignment in the absence of information on the brood chambers.

*Range* – Aalenian – Thanetian.

**cf. Spiropora verticillata** (Goldfuss, 1826)

Pl. 12.

cf. 1826 *Ceriopora verticillata* sp. nov.; Goldfuss, p. 24, pl. 11, fig. 1.
cf. 1865 *Spiropora verticillata* (Goldfuss); Beissel, p. 70, pl. 8, figs. 91-93.
cf. 1970 *Spiropora verticillata* (Goldfuss); Voigt & Flor, p. 44, pl. 8, figs. 6-19, pl. 9, figs. 1-15, pl. 10, figs. 1-11, pl. 11, figs. 1-19, pl. 14, figs. 7-8 (includes list of 31 accepted and 12 rejected literature citations).

*Material* – NHM BZ 5120, NNM RGM 507 034-507 035, Maastrichtian, Navesink Formation, Poricy Brook, Linford, Monmouth County, New Jersey (locality NJ1). RU 5622, 5623, 5624, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 and/or NJ2). ANSM 80363, Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1).

*Description* – Colony erect, with cylindrical, dichotomously dividing branches, about 1 mm in diameter, arising at several points from encrusting base. Encrusting base of colonies consisting of free-walled budding zone 2-4 zooids thick, most becoming kenozooids though locally the axes of a group of basal zooids turn away from the substrate and become the initial autozooids of an erect branch (Pl. 12, fig. 3).

Autozooids typically originating in groups along branch axis, gradually diverging to colony surface in regularly spaced annular bands encircling branches (Pl. 12, figs. 1a, 2), although some bands incompletely encircle the branch with a few isolated autozooidal apertures placed above or below the incomplete circle and a few bands form incomplete helices. Typically 12-16 autozooidal peristomes per complete band. Frontal wall of autozooid exterior-walled, gently curved transversely, perforated by abundant
pseudopores 8 μm in diameter, separated from laterally adjacent autozooids by narrow groove; peristomes, if present originally, abraded or otherwise lost in all specimens. Gonozooids not seen.

Kenozooids occurring only in encrusting base, of unknown length, but with zooidal axis parallel to substrate, sealed by fixed-walled terminal diaphragms that collectively form continuous fixed-walled surface of encrusting base except along peripheral budding zone.

Measurements – FWL 833±99, 637-1010 (4, 24); FWW 204±30, 136-281 (6, 46); AD 134±17, 107-168 (5, 39); FS 1049±101, 867-1213 (4, 18); BRW 1010±190, 668-1355 (6, 18).

Remarks – Flor (1968) and Voigt & Flor (1970), in extensive studies of Spiropora and its homeomorphs, defined Spiropora verticillata rather broadly, encompassing Santonian to Thanetian specimens from numerous localities across Europe. The specimens described here from the Mount Laurel and Navesink formations are the same approximate age as the holotype of S. verticillata; spacing of annular fascicles and branch widths fall between those reported by Flor (1968) for specimens from offshore localities (greater spacing between fascicles, generally narrower branches) and specimens from onshore localities (shorter spacing between fascicles, broader branches); and aperture sizes are within the range reported by Voigt & Flor (1970). In contrast, specimens described here differ from other Maastrichtian species (e.g., S. irregularis Brood, 1977, and S. spiralis Guha & Nathan, 1996) in one or more measured features, the number of peristomes per fascicle or in having annular vs spiral bands of apertures. However, we cannot confidently assign the specimens from the Mount Laurel and Navesink Formations to the genus Spiropora or to the species S. verticillata because none of them have gonozooids.

Family Plagioeciidae Canu, 1918

Plagioecia Canu, 1918

Type species – Tubulipora patina Lamarck, 1816, Recent, Europe; by original designation.

Remarks – This is one of several genera of tubuliporine cyclostomes with species formerly accommodated in the genus Berenicea. However, Berenicea is an unrecognizable genus and its constituent species are now distributed between genera defined by the morphology of the gonozooids (see Taylor & Sequeiros, 1982). In the case of Plagioecia, the gonozooid is transversely elongate and its roof is supported by autozooids that pass through the brood chamber.

Several of the species described here have a prominent median ridge along the frontal wall of the autozooids, culminating at the proximal margin of the aperture. At least three Cretaceous species of Plagioecia have similar autozooidal keels, including P. carinata (Levinsen, 1925), an undescribed Santonian specimen of Plagioecia in the NHM collections and P. carinata sp. nov. It is possible that a full revision of this genus, beyond the scope of the current paper, will justify the naming of a new genus for these keeled species.
Range – Oxfordian – Recent.

**Plagioecia cristata** sp. nov.

Pl. 13.

Material – Holotype: NHM BZ 5121(a), Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5). Paratypes: NHM BZ 5122, NNM RGM 507 036, Maastrichtian, Prairie Bluff Chalk, Jefferson, Marengo County, Alabama (locality AL5); BZ 4791(4), BZ 4806, BZ 5035(3), BZ 5099(4), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). NHM BZ 5217, Maastrichtian, Prairie Bluff Chalk, Emelle, Sumter County, Alabama (locality AL9). NHM BZ 5226(1), Maastrichtian, Prairie Bluff Chalk, Braggs, Lowndes County, Alabama (locality AL3). NHM BZ 5104(2a), BZ5104(2b), BZ 5123(1), Maastrichtian, Rocky Point Member, PeeDee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2). Other material: NHM BZ 5035(3), Maastrichtian, Prairie Bluff Chalk, Lake Ridge Apartments, Livingston, Sumter County, Alabama (locality AL6). RU 5500, 5618, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 and/or NJ2).

Etymology – L., *crista*, crest or ridge, in reference to the median keel along the frontal wall of autozooecia.

Description – Colony multiserial, thin, completely adnate; perimeter marked by narrow budding zone composed of one to two generations of autozooids, with broad projecting flange of basal lamina in well-preserved material. Colonies typically discoidal when small, but larger colonies have highly irregular outlines, partly due to extensive development of subcolonies on colony periphery (Pl. 13, fig. 3a); subcolonies originating from single autozooid (pseudoancestrula) or a few contiguous autozooids in peripheral budding zone, then developing as radially spreading unit (Pl. 13, fig. 3b), partially overlapping parent subcolony. Colonies primarily unilaminar except where plurilaminar due to colony overlap or self-overgrowth in complex microenvironments. Fine-scaled concentric rugae variably present on fixed-walled upper surface of some colonies, but usually absent. Protoecium approximately circular, about 150 μm in diameter, ancestrula overall long and slender, giving rise to astogenetic zone of change extending through 5-6 generations in which autozooidal diameter gradually increases.

Autozooids arranged in well-developed quincuncial pattern, autozooidal peristomes isolated, never connate, inclined away from centre of colony, length short to about three times diameter; most autozooids marked by prominent median keel (Pl. 13, fig. 1c) along frontal wall and in peristomes in well-preserved specimens, although apertures remain essentially circular. Frontal walls about 3-4 times longer than wide, convex at proximal end, then with a planar facet on each side sloping down from median keel; autozooidal boundaries generally distinct; pseudopores conspicuous, longitudinally oval, about 10 μm wide by 15 μm long.

Gonozooids commonly developed, with conspicuously inflated brood chambers (Pl. 13, fig. 2), 1.5-2.0 times wider than long, oval to semicircular with linear distal edge and incorporating peristomial bases of neighbouring autozooids, some autozooids passing through brood chamber and joined to perimeter of chamber by vertical internal
walls; frontal wall of brood chamber marked by sutures between adjacent perforating autozooidal peristomes, suggesting centrifugal skeletal growth from individual peristomes; oeociopore located on distal edge of brood chamber, circular, approximately 40 μm in diameter, elevated on short cylindrical oeociostome.

Measurements – FWL 372±56, 262-501 (5, 50); FWW 151±25, 98-204 (5, 50); AD 62±9, 45-89 (9, 90); AS 256±55, 159-416 (9, 90); BCL 531±110, 393-747 (2, 7); BCW 1047±326, 758-1629 (2, 7).

Remarks – The median keel in *Plagioecia cristata* is similar to that of the Danian species *P. carinata* (Levinsen, 1925), from which it differs in lacking lateral ridges along autozooidal borders. Also, Brood (1972) indicated slightly larger apertural diameters for *P. carinata* than those of *P. cristata* and illustrated (1972, pl. 18, fig. 2) an equidimensional, circular brood chamber for a specimen that he assigned to the former species.

*Plagioecia koinos* sp. nov.

Pl. 14.

Material – Holotype: NHM BZ 4803(1), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). Paratypes: NHM BZ 5099(3), NNM RGM 507 032, 507 042, details as for holotype. RU 5400, 5603, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 and/or NJ2).

Etymology – Gr., *koinos*, common, in reference both to the frequency with which this species is encountered in the Prairie Bluff Chalk and to the similarity of its characters to the norm for species of *Plagioecia*.

Description – Colony thin, non-maculate, multiserial, completely adnate, unilaminar except for uncommon local areas of self-overgrowth in complex microenvironments; discoidal when small, but larger colonies with highly irregular outlines usually due to substrate irregularities or obstructions, distinct subcolonies apparently not developed, but lobes occasionally present (Pl. 14, fig. 2b); perimeter marked by narrow budding zone composed of one to two generations of autozooids (Pl. 14, fig. 2c), with broad (up to 1 mm wide) projecting flange of basal lamina in well preserved material. Protoecium not seen in identifiable colonies, covered by recurved autozooids in primary zone of astogenetic change, which comprises ancestrula and about four generations of autozooids in which autozooidal length and apertural diameter increase.

Autozooids large, arranged in well-developed quincuncial pattern (Pl. 14, fig. 2a). Autozooidal frontal length about 4-5 times greater than width, gently convex transversely; boundaries variably clear; pseudopores in frontal wall small, circular; peristomes locally long on well preserved material, isolated, never connate, only slightly inclined away from centre of colony; broken bases of peristomes sealed by terminal diaphragms, commonly within three to four generations proximal of colony-margin budding zone.

Gonozooids commonly developed, large, with conspicuously inflated brood chambers (Pl. 14, fig. 1c), about 1.5 times wider than long, essentially oval although distal or
proximal wall may be somewhat straighter than the other, and incorporating peristomial bases of several neighbouring autozooids; ooeciopore located within distal half of brood chamber, but not on distal edge, circular, smaller than autozooidal apertures, with thickened rim, but no prominent ooeciostome.

**Measurements** – FWL 645±108, 463-865 (4, 40); FWW 157±16, 125-200 (4, 40); AD 76±9, 56-100 (4, 40); AS 329±35, 261-423 (4, 40); BCL 693±72, 642-744 (2, 2); BCW 1492±49, 1457-1526 (2, 2).

**Remarks** – _Plagioecia koinos_ differs from _P. madrasensis_ Guha & Nathan, 1996, and _P. rajani_ Guha & Nathan, 1996, in having smaller, much more widely spaced apertures, and from the former in having the ooeciopore placed medially rather than apparently laterally on the brood chamber.

**Plagioecia maculata sp. nov.**

Pl. 15.

1926 _Berenicea papillosa_ Reuss; Canu & Bassler, p. 38, pl. 7, fig. 8.
In press _Plagioecia sp. nov._; McKinney & Taylor, pl. 4B.

**Material** – Holotype: NHM BZ 5124(1a), Maastrichtian, PeeDee Formation, Rocky Point Member, Ideal Quarry, New Hanover County, North Carolina (locality NC2). Paratypes: NHM BZ 5124(1b), BZ 5124(1c), BZ 4175 (several colonies), BZ 4185(1), BZ 5104(3a), BZ 5104(3b), details as for holotype. Other material: USNM 69970, Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TE1); figured by Canu & Bassler, 1926, pl. 7, fig. 8 as _Berenicea papillosa_ Reuss.

**Etymology** – L., _macula_, spot, in reference to the irregularly distributed areas from which autozooids radiate and in which no autozooidal apertures are located.

**Description** – Colony thin, unilaminar, completely adnate; perimeter marked by narrow budding zone composed of 1-2 generations of autozooids (Pl. 15, fig. 2b), with projecting flange of basal lamina. Colonies discoidal (Pl. 15, fig. 2a) to lobate, the latter commonly with local marginal regions of autozooidal divergence where maculae are partially formed (Pl. 15, fig. 1a). Protoecium hemispherical (Pl. 15, fig. 3), about 150 μm in diameter, initiating adnate, distally expanding tube so that total ancestrula length is 2-3 times protoecium diameter. Primary zone of astogenetic change comprising ancestrula, and about four generations of autozooids in which autozooidal length and apertural diameter increase.

Autozooids relatively large, arranged in well-developed, quincuncial pattern in intermacular areas. Preserved portions of autozooidal peristomes isolated, seldom connate, short except in well preserved colonies; moderately inclined to vertical with respect to surface of colony. Except in centres of maculae, frontal recumbent length of autozooids about 2-3 times longer than wide, gently to pronouncedly convex transversely; autozooidal boundaries well marked; pseudopores circular, about 5 μm diameter.
Gonozooids with conspicuously inflated brood chambers (Pl. 15, fig. 2c), nearly 1.5 times wider than long, oval to crescentic, and incorporating peristomial bases of several neighbouring autozooids; ooeciopore located near, but not on, distal edge of brood chamber, circular, smaller than autozooidal apertures, in well-preserved colonies on long, recurved ooeciostome.

**Measurements** – FWL 417±54, 304-537 (4, 40); FWW 181±29, 117-233 (4, 40); AD 72±11, 48-93 (8, 80); AS 265±47, 161-390 (8, 80); BCL 1077±166, 810-1258 (5, 14); BCW 1562±365, 1170-2378 (5, 15); OD 54±12, 39-71 (4, 8).

**Remarks** – Although most species of *Plagioecia* have more transversely elongate brood chambers with the ooeciopores along the distal edge, others such as *P. sarniensis* (Norman, 1864) (see Harmelin, 1976, pl. 9, fig. 3, pl. 20, figs 7, 8) have brood chamber shapes and ooeciopore locations much like that of *P. maculata*. *Plagioecia maculata* differs from *P. cristata* in lacking the median keel on the autozooids, in the shape of the brood chamber, and in the position of the ooeciopore.

**Plagioecia amplimaculata** sp. nov.

Pl. 16, fig. 1.

**Material** – Holotype: ANSM 80364, Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1).

**Etymology** – L., *amplus*, large, and L., *macula*, spot, in reference to the large autozooidal apertures, and the irregularly distributed areas from which autozooids radiate and in which no autozooidal apertures are located.

**Description** – Colony thin, unilaminar, maculate (Pl. 16, fig. 1b); perimeter marked by narrow budding zone composed of one to two generations of autozooids, with projecting flange of basal lamina, locally thickened into regions of frontally-facing, free-walled zooids suggesting incipient erect growth (Pl. 16, fig. 1c). Holotype colony irregular in outline, intergrown with other epibionts on *Belemnitella* guard. Ancestrula and primary zone of astogenetic change not preserved.

Autozooids large, closely spaced, in irregular quincuncial pattern in intermacular areas. Preserved portions of autozooidal peristomes isolated, short, many capped by a terminal diaphragm, especially in maculae; moderately inclined to vertical with respect to surface of colony. Except in maculae, frontal recumbent length of autozooids less than two times longer than wide, gently to pronouncedly convex transversely, variably rugose with indications of episodic growth and repair; autozooidal boundaries indistinct. Pseudopores small, subcircular.

Gonozooid with conspicuously inflated, but deroofed, triangular brood chamber in holotype, slightly wider than long, incorporating peristomial bases of several neighbouring autozooids; ooeciopore not located on distal edge of brood chamber, but apparently within the area where the brood chamber roof has broken away.

**Measurements** – FWL 418±67, 325-521 (1, 10); FWW 229±21, 196-257 (1, 10); AD
Remarks – Although most species of *Plagioecia* have more transversely elongate brood chambers and have the ooeciopores along the distal edge, others, such as *P. dorsalis* (Waters, 1879) (see Harmelin, 1976, pl. 9, fig. 4), have brood chamber shapes and location of the ooeciopore much like that of *P. amplimaculata*. *Plagioecia amplimaculata* differs from *P. maculata* in its distinctly larger, relatively more closely spaced autozooidal apertures and greater frontal wall width. Localized thickening of the growing edge (Pl. 16, fig. 1c) may be a prelude to erect growth, in which case the generic assignment of the species should be reconsidered.

*Plagioecia kryptos* sp. nov.

Pl. 17.

**Material** – Holotype: NHM BZ 5214, Maastrichtian, Prairie Bluff Chalk, Emelle, Sumter County, Alabama (locality AL9). Paratypes: NHM BZ 5215, NNM RGM 507 062, same details as holotype.

**Etymology** – Gr., *crypto*, hidden, in reference to the similar dimensions of this species with those of *Plagioecia cristata* sp. nov. and its superficial similarity to small colonies of *P. koinos* sp. nov.

**Description** – Colony multiserial, thin, completely adnate except on rugged surfaces; perimeter marked by steep budding zone composed of two to three generations of autozooids, with no evidence of broad projecting flange of basal lamina. Colonies typically discoidal when small, but larger colonies with highly irregular outlines, partly due to extensive development of subcolonies on colony periphery (Pl. 17, fig. 1a); subcolonies originating from single autozooid (pseudoancestrula) or a few contiguous autozooids by eruptive budding, then developing as radially spreading unit across parent subcolony. Colonies primarily unilaminar except where locally plurilaminar due to peripheral subcolonies. Ancestrula and early colony astogeny not seen.

Autozooids arranged in well-developed quincuncial pattern, autozooidal peristomes isolated, circular to subcircular, seldom connate, inclined away from centre of colony, elongate where well preserved. Frontal walls about two times longer than wide, slightly inflated proximally and more so distally, where a keel may be developed (Pl. 17, fig. 1b); autozooidal boundaries slightly grooved.

Gonozooid conspicuously inflated (Pl. 17, fig. 1c), transversely oval with width about twice length, oval to semicircular, median indentation in distal edge perhaps associated with ooeciopore (not seen), incorporating bases of peristomes of a few neighbouring autozooids; ooeciopore not recognized.

**Measurements** – FWL 306±30, 248-360 (3, 30); FWW 144±25, 113-232 (3, 30); AD 78±12, 60-106 (3, 30); AS 237±37, 169-305 (3, 30); BCL 624 (1); BCW 940 (1).

**Remarks** – *Plagioecia kryptos* differs from *P. madrasensis* Guha & Nathan, 1996, and *P. rajani* Guha & Nathan, 1996, in having much smaller apertures. It differs from *P. cristata*...

sp. nov. in having somewhat larger apertures; from *P. koinos* sp. nov. in having smaller, more closely spaced apertures and relatively shorter frontal walls of autozooids; and from *P. maculata* sp. nov. in having smaller autozooids, smaller brood chambers and in apparently lacking maculae.

**Plagioecia? sp.**

Pl. 16, fig. 2.

*Material* – ANSM 80363 (on same shell as cf. *Spiropora verticillata*), Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1).

*Description* – Colony encrusting, sinuous, comprising transversely dividing oligo-serial to multiserial lobes up to ten rows of autozooids wide (Pl. 16, fig. 2a); flat to very gently convex in cross section; greatest width generally corresponding with occurrence of gonozooids. Ancestrula and primary zone of astogenetic change not seen.

Autozooids elongate, small, frontal wall about three times longer than wide, terminating in low, oblique peristomes of unknown length that diverge from lobe midline; regularly, quincuncially arranged; surface texture and pseudopores obscured by coarse preservation.

Gonozooid (Pl. 16, fig. 2b) with gently inflated brood chamber about half as long as wide, incorporating peristomes of several autozooids; ooeciostome(?) located at distal margin, adjacent to and about half the diameter of adjacent autozooidal peristome.

*Measurements* – FWL 376±36, 334-438 (1, 10); FWW 128±15, 98-152 (1, 10); AD 63±9, 47-80 (1, 10); AS 279±42, 222-345 (1, 10); BCL 564±146, 460-667 (1, 2); BCW 1124±57, 1083-1164 (1, 2).

*Remarks* – The lobate growth habit of this species differs from that usually found in *Plagioecia*, but the transversely elongate brood chamber, apparently encompassing peristomes of autozooids, appears typical of *Plagioecia*.

**Mesonopora Canu & Bassler, 1929a**

*Type species* – *Mesonopora typica* Canu & Bassler, 1929a (= *Berenicea concatenata* Reuss, 1867, fide Walter, 1970), Bathonian, Normandy; by original designation.

*Remarks* – This genus is characterised (Taylor & Sequeiros, 1982) by having broad gonozooids indented marginally by autozooidal peristomes, but, unlike *Plagioecia*, not perforated by an appreciable number of autozooids (cf. Walter, 1989a, who included some such species in his concept of the genus).

*Range* – Aalenian – Maastrichtian? Note that the upper range of this genus is very uncertain as re-evaluation of the myriad of *‘Berenicea’* species in the Cenozoic has yet to be attempted.
Mesonopora patane sp. nov.
Pl. 18.


Etymology – Gr., patane, flat dish, in reference to the appearance of typical flat, circular colonies.

Description – Colonies unilaminar, small, thick, completely adnate; perimeter marked by steeply inclined budding zone composed of 3-4 generations of autozooids (Pl. 18, figs 1c, 3); projecting flange of basal lamina narrow or absent; typically discoidal, but may be irregular in outline. Protoecium not seen and ancestrula inconspicuous within primary zone of astogenetic change, which is characterized by an increase in zooidal width within first few generations of budded autozooids.

Autozooids arranged in variably well-developed quincuncial pattern; peristomes isolated, never connate, inclined away from centre of colony. Apertures and peristomes essentially circular. Frontal walls gently convex with fine-scaled concentric rugae, autozooidal boundaries not prominent.

Gonozooids with conspicuously inflated brood chambers (Pl. 18, figs. 1b, 2), 2-3 times wider than long, with straight or slightly concave transverse axis, partially surrounding peristomial bases of neighbouring autozooids; ooeciopore located on distal edge of brood chamber, circular, smaller than autozooidal apertures, apparently not elevated on extended ooeciostome.

Measurements – FWL 341±43, 260-423 (3, 30); FWW 133±17, 94-165 (3, 30); AD 74±9, 58-93 (3, 30).

Remarks – This species resembles NHM specimens figured by Gregory (1899, pl. 5, fig. 5, pl. 6, fig.1) as Berenicea polystoma (Römer, 1839), from the Mioaster cortestidunarium Zone (probably Coniacian) of the Chalk at Chatham, Kent, England. It differs in having larger apertures relative to interapertural spacing, smaller length/width ratio of the autozooidal frontal wall and relatively much broader brood chambers than the apparent brood chamber illustrated by Gregory (1899, pl. 5, fig. 5, upper right). Peristomes are long only in parts of colonies that are located in protected recesses; it is unclear whether their shorter size in more exposed areas is due to limited growth or subsequent abrasion of the delicate structures. Irregularly shaped colonies usually are associated with obstructions, substrate irregularities, intergrowths with other encrusters, or with occasional peripheral subcolonies or colony fusions.

In some colonies thickened interzooidal walls extend to the perimeter and there is no projecting flange of basal lamina (Pl. 18, fig. 3). Such colonies are interpreted to have stopped growing in diameter, inasmuch as the thickened walls are indicative of later
ontogenetic stages of autozooids, and the absence of a projecting basal lamina indicates that no further lateral expansion is imminent. This suggests that colonies have determinate growth, as previously inferred for *Actinopora disticha* (von Hagenow) from the *Micraster coranguinum* Zone (Santonian) of England, which produces small, circular encrusting colonies (McKinney & Taylor, 1997).

*Diplosolen Canu, 1918*

*Type species* – *Tubulipora obelia* Johnston, 1838, Recent, British Isles; by original designation.

*Remarks* – This genus is characterised by the presence of nanozooids, polymorphs resembling autozooids skeletally, but of appreciably reduced size. In living colonies of the type species of *Diplosolen*, the nanozooids each have a single tentacle which sweeps the colony surface, possibly clearing it of sediment particles and/or hindering the settlement of larvae of other organisms (Silén & Harmelin, 1974).

*Range* – Turonian - Recent.

*Diplosolen ehrhardi* sp. nov.

*Material* – Holotype: NHM BZ 4796(15), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). Paratypes: NHM BZ 5035(2), BZ 5126, NNM GMR 507 039, details as for holotype.

*Etymology* – Named in honour of Professor Ehrhard Voigt (1905-2004) who first described *Diplosolen* from Maastrichtian rocks.

*Description* – Colony encrusting, thin, multiserial, adnate with marginal, abbreviated, basal budding zone bounded by narrow, peripheral basal lamina. Small colonies usually circular (Pl. 19, fig. 1a), large colonies with irregular outlines and some with regions of self-overgrowth; largest colonies over 10 mm diameter. Protoecium not seen; ancestrula short, aperture about two-thirds diameter of autozooids in zone of astogenetic repetition, primary zone of astogenetic change includes only about two generations of asexually budded autozooids and interspersed nanozooids in which autozooids increase in diameter, colony recurving immediately to cover protoecium and begin spreading radially.

Autozooids and nanozooids usually regularly alternating in longitudinal rows in quincuncial series (Pl. 19, fig. 2), locally disrupted by omission of some nanozooids especially in early parts of colonies. Autozooids narrow, frontal length about four times width, proximal portion adnate, frontal wall flat to moderately convex transversely; peristome of unknown height, some broken at base and sealed by terminal diaphragm. Pseudopores elongate longitudinally, about 5 μm by 8 μm, abundant and uniformly distributed across autozooids and nanozooids. Small transverse rugae cross both autozooids and nanozooids in some colonies.
Nanozooids less than half the length of autozooids, but proportionally wider; peristome as in autozooids, but much smaller, and some apertures also capped by terminal diaphragm just above level of frontal wall.

Gonozooids (Pl. 19, fig. 1b) small, nearly equidimensional, inflated, incorporating bases of peristomes of adjacent autozooids; short ooeciostome with ooeciopore about two-thirds the diameter of autozooidal apertures, located mid-distally on brood chamber.

**Measurements** – FWL 513±62, 405-620 (2, 20); FWW 135±10, 113-151 (2, 20); AD 70±10, 52-90 (4, 40); AS 287±49, 203-390 (4, 40); NWL 216±38, 155-279 (2, 20); NWW 56±10, 60-100 (2, 20); NAD 23±4, 15-31 (2, 20); BCL 345 (1, 1); BCW 377 (1, 1); OD 34 (1, 1).

**Remarks** – Voigt (1929) discriminated and named five Maastrichtian species of *Diplosolen* from Rügen, Germany. Unfortunately, all the collections of the University of Hamburg were destroyed during World War 2, including type specimens of these five species. Voigt (1959, pl. 2, fig. 6) designated a neotype for one of them, *D. pavonius*, which differs from *D. ehrhardi* in having longer autozooids with larger apertural diameters. Among the other species, currently not represented by any type specimens, *D. ehrhardi* most resembles the description (Voigt, 1929) of *D. elliptostomus*, but differs in having smaller, non-elliptical peristomes and apertures. Colonies of the Maastrichtian species *D. ramosus* Voigt, 1962, are organized into encrusting branches 1-2 mm wide rather than being sheet-like as in *D. ehrhardi*. *Diplosolen ehrhardi* differs from the Danian species *D. carinata* Brood, 1972, in having equidimensional and much smaller brood chambers, and lacking the longitudinal wrinkles described as characteristic of *D. carinata* autozooids; from the Danian species *D. scanica* Brood, 1972, in having larger autozooids and autozooidal apertures and smaller, more equidimensional brood chambers; and from the Danian species *D. limhamnia* Brood, 1972, in having much smaller, equidimensional rather than transversely oval brood chambers.

**Diplosolen perexigua** sp. nov.

Pl. 19, fig. 3.

**Material** – Holotype: NHM BZ 5127, Maastrichtian, Ripley Formation, Florence, Quitman County, Georgia (locality GA1). Paratypes: NHM BZ 5128, NNM RGM 507 040-507 041, details as for holotype.

**Etymology** – L., *perexiguus*, very small, in reference to the small autozooids.

**Description** – Colony encrusting, thin, multiserial, adnate sheet with marginal abbreviated basal budding zone bounded by narrow peripheral basal lamina, usually small, up to about 3 mm diameter.

Autozooids regularly alternating in longitudinal rows in quincuncial series, with small nanozooids irregularly distributed between autozooids (Pl. 19, fig. 3b). Frontal wall length of autozooids about three times width, flat to moderately convex transversely; peristome of unknown height, some broken at base and capped by terminal diaphragm.
Nanozooids more than half the length of autozooids, but proportionally narrower; peristome as in autozooids but much smaller. Frontal wall pseudopores of autozooids and nanozooids circular, about 7 μm, abundant and uniformly distributed across autozooids and nanozooids.

Gonozooids elliptical (Pl. 19, fig. 3c), transversely elongate, inflated, incorporating base of peristomes of adjacent autozooids; ooeciostome short, ooeciopore about two-thirds the diameter of autozooidal apertures, located mid-distally on brood chamber; pseudopores about 10 μm diameter and more closely spaced on brood chamber than on autozooids and nanozooids.

Measurements – FWL 313±42, 220-425 (3, 30); FWW 95±20, 62-123 (3, 30); AD 45±7, 34-65 (5, 50); AS 211±29, 161-286 (5, 50); NWL 182±17, 161-208 (2, 11); NWW 45±7, 28-56 (2, 11); NAD 15±4, 10-24 (5, 30); BCL 408±78, 365-546 (3, 5); BCW 650±93, 566-806 (3, 5); OD 32±8 (2, 4).

Remarks – Diplosolen perexigua has much smaller autozooids and autozooidal apertures than D. ehrhardi sp. nov. or any other known Late Cretaceous or Danian species of Diplosolen.

Diplosolen montilaurus sp. nov.

Pl. 20.


Etymology – After its occurrence in the Mount Laurel Formation.

Description – Colony encrusting, thin, multiserial, sometimes caviariform, with marginal abbreviated basal budding zone bounded by narrow peripheral basal lamina. Outline irregular, sometimes becoming multilaminar by self-overgrowth. Zooids at old, abandoned growing edge occasionally sealed by terminal diaphragms. Largest colonies over 15 mm in diameter. Ancestrula and primary zone of astogenetic change not seen.

Autozooids and nanozooids usually regularly alternating in longitudinal rows in quincuncial series (Pl. 20, fig. 1b), locally disrupted by presence of additional nanozooids. Autozooid frontal length about three times width, proximal portion adnate, frontal wall flat to moderately convex transversely, peristome of unknown height, sometimes broken at base and sealed by terminal diaphragm that may have central pore (secondary nanozooid) (Pl. 20, fig. 1c). Pseudopores circular, about 8 μm diameter, abundant and uniformly distributed across autozooids and nanozooids.

Nanozooids less than half the length of autozooids, but relatively wider; peristome as in autozooids, but much smaller (Pl. 20, fig. 1d).

Gonozooids with large, nearly equidimensional brood chambers (Pl. 20, fig. 1e), inflated, incorporating base of peristomes of adjacent autozooids; short ooeciostome with ooeciopore about two-thirds the diameter of autozooidal apertures, located close to centre of brood chamber (Pl. 20, fig. 1f).
Measurements – FWL 435±75, 320-598 (4, 40); FWW 144±26, 107-207 (4, 40); AD 82±8, 64-97 (4, 40); AS 284±38, 196-353 (4, 40); NWL 164±24, 113-218 (4, 40); NWW 72±11, 52-101 (4, 40); NAD 20±3, 13-27 (4, 40); BCL 1224±138, 1127-1322 (1, 2); BCW 1430±209, 1283-1578 (1, 2).

Remarks – Diplosolen montilaurus differs from D. ehrhardi sp. nov. in having shorter, relatively wider autozooids, with larger autozooidal orifices; shorter, relatively broader nanozooids; and larger brood chambers with larger ooeciostomes. It differs from D. perexigua in being larger in all respects except nanozooid length, which is smaller.

Hyporosopora Canu & Bassler, 1929a

Type species – Hyporosopora typica Canu & Bassler, 1929a, Bathonian, France; by original designation.

Remarks – Another genus of the ‘Berenicea’ type, Hyporosopora was originally characterized by Canu & Bassler (1929a) as having transversely elongate gonozooids with autozooidal peristomes restricted to its margins, and with the ooeciostome located between the transverse midline of the gonozooid and its distal border. Taylor & Sequeiros (1982) later noted that in H. typica the gonozooids widen distally, may have distally projecting lateral lobes, and the ooeciostome is small and terminal.

Range – Uncertain, Aalenian? or Bajocian - Maastrichtian.

Hyporosopora praecox sp. nov.

Material – Holotype: NHM BZ 4836(1a), Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5). Paratypes: NHM BZ 4836(1) [additional colonies on same shell as holotype], BZ 5131, BZ 5132, details as for holotype. NHM BZ 5123(2), Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2).

Etymology – L., praecox, for precocious or too early ripe, from the presence of gonozooids in some colonies within the primary astogenetic zone of change.

Description – Colony thin, unilaminar, completely adnate; small; perimeter marked by narrow budding zone composed of one to two generations of autozooids, projecting flange of basal lamina apparently lacking. Colonies rarely discoidal; characterized by fan-shaped primary zone of astogenetic change seldom overlapped by subsequent growth and from which two laterally diverging, commonly recurved, lobes extend (Pl. 21, fig. 1a); recurved lateral lobes seldom meeting. Larger colonies commonly with highly irregular outlines due to peripherally developed subcolonies, potentially larger than the initial colony and/or serially developed. Fine-scaled concentric rugae present on fixed-walled upper surface of well-preserved colonies. Protoecium elongate oval, about 90 μm wide by 110 μm long, ancestrula overall relatively long, giving rise to
astogenetic zone of change about four generations long, in which autozooidal length and apertural diameter gradually increase.

Autozooids small, arranged in well-developed quincuncial pattern; peristomes short, isolated, never connate, highly inclined away from centre of colony. Frontal wall about three times longer than wide, gently convex transversely; autozooidal boundaries clear; pseudopores small, circular.

Gonozooids small (Pl. 21, fig. 1b), commonly developed even in colonies with few autozooidal generations; brood chambers conspicuously inflated, width almost twice the length, crescentic with concave distal side and incorporating peristomial bases of one or two neighbouring autozooids along margins; ooeciopore located on distal edge of brood chamber, circular, smaller than autozooidal apertures, with thickened rim, but no prominent ooeiostome.

Measurements – FWL 297±33, 197-365 (8, 80); FWW 104±15, 66-139 (8, 80); AD 46±9, 30-74 (9, 90); AS 191±29, 143-260 (7, 70); BCW 511±135, 391-821 (7, 14); BCL 280±40, 223-362 (7, 12); OD 32±4, 25-40 (5, 10); GL 446±36, 385-479 (5, 8).

Remarks – Among the three species of *Hyporosopora* from the Faringdon Sponge Gravels (Aptian) of southern England, named and described by Pitt & Taylor (1990), *H. praecox* most closely resembles *H. mantelli*, but differs in having smaller autozooids, smaller autozooidal apertures and smaller brood chambers that are not equidimensional. The concave distal edges of the small gonozooids of *H. praecox* enable it to be distinguished from most congeneric species.

**Mesenteripora de Blainville, 1830**

*Type species* – *Mesenteripora michelini* de Blainville, 1830, Bathonian, Normandy, France; by original designation.

Remarks – This plagioeciid genus has erect colonies with bifoliate branches, generally broad and frondose, but sometimes narrow and strap-like. The Jurassic type species was revised by Walter (1970). Relatively few post-Jurassic taxa have been assigned to the genus, but these do include a few Recent species (Taylor & Gordon, 2001).

Range – Pliensbachian – Recent.

**Mesenteripora lirella** sp. nov.

Pl. 22.

*Material* – Holotype: ANSM 80369, Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1).

*Etymology* – L., *lirella*, diminutive for ridge between two furrows, in reference to the keeled autozooids in this species.

*Description* – Colony with spreading unilaminar encrusting base from which short
multiserial bilaminate sheets arise. Ancestrula and primary zone of astogenetic change not seen.

Autozooids arranged in quincuncial pattern with somewhat variable spacing; autozooidal peristomes isolated, never in fascicles, inclined toward colony margin, preserved length short to about equal to diameter. Most autozooids with prominent median keel along frontal wall and in peristomes (Pl. 22, fig. 1c), although apertures remain essentially circular. Proximal autozooids commonly closed by pseudopore-rich terminal diaphragm. Frontal walls about two to three times longer than wide, convex at proximal end, then with a planar facet on each side sloping down from median keel; autozooidal boundaries generally clear; pseudopores circular, about 10 μm diameter.

Gonozooid with conspicuously inflated brood chamber (Pl. 22, fig. 1d), slightly wider than long, oval to semicircular with linear distal edge and incorporating peristomial bases of neighbouring autozooids; ooeciopore located on distal edge of brood chamber, with proximal and distal wall of outer end of short ooeciostome folded axially, producing transversely elongate ooeciopore approximately 90 μm wide by 50 μm long.

Measurements – FWL 403±63, 328-522 (1, 10); FWW 175±15, 158-196, (1, 10); AD 81±9, 69-95 (1, 10); AS 238±37, 189-301 (1, 10); BCL 997; BCW ~1200; OD (max) 88, OD (min) 52.

Remarks – Mesenteripora lirella differs from M. michelini (de Blainville, 1830), as re-described by Walter (1970), in having frontal walls of less variable length, smaller frontal wall width and smaller autozooidal apertures. It resembles P. carinata (Levinsen, 1925) and P. cristata sp. nov. in having keeled autozooids, but differs in its bilaminate erect growth. It further differs from P. carinata in lacking lateral ridges along autozooidal borders, and from P. cristata in having larger autozooids with larger apertures and more equidimensional brood chambers.

Family Annectocymidae Hayward & Ryland, 1985a

Annectocyma Hayward & Ryland, 1985a

Type species – Alecto major Johnston, 1847, Recent, Britain; by original designation.

Remarks – Annectocyma was established by Hayward & Ryland (1985a) for multiserial, lobate to branched, encrusting cyclostomes that may develop erect cylindrical portions, characterized by dichotomous and lateral branching, autozooidal peristomes frequently fused basally in transverse rows of two to four, and pyriform or elongate oval brood chambers with small, sub-distal, transversely flared ooeciostomes. In the type species a characteristic, lateral adventitious branch develops from the side of the ancestrula, whereas in the new species described here a similar adventitious branch may be present, but it arises from the first budded zooid.

Range – Maastrichtian – Recent.
**Annectocyma cirrita** sp. nov.  
Pls. 23-24.

**Material** – Holotype: BZ 5224, Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). Paratypes: NHM BZ 4802(3), BZ 4808, BZ 5112, BZ 5113, BZ 5132, BZ 5133(1), BZ 5134, BZ 5135, NNM RGM 507 043, 507 044, 507 064, details as for holotype. NHM BZ 5136, BZ 5137, Maastrichtian, Demopolis Chalk, Epes, Sumter County, Alabama (locality AL10). NHM BZ 5138, BZ 5139, Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5). NHM BZ 4960, Maastrichtian, Ripley Formation, Coon Creek Member, Corbula bed, Field Center, Coon Creek, Tennessee (locality TN1).

**Etymology** – *L.*, cirritus, having fine filaments, in reference to the fine, thread-like appearance of the encrusting branches of colonies.

**Description** – Colony encrusting, narrow, variably uniserial to multiserial strap-like branches (Pl. 23, fig. 1a), dividing at various angles both dichotomously and by lateral budding. Laterally budded branches commonly narrow at point of origin, consisting initially of a single autozooid flanked laterally by gradually widening buds. Ancestrula with circular protoecium, about 150 μm in diameter, short with very narrow distal portion, giving rise to single distally budded autozooid from which distal and, in some colonies, laterally budded branches arise (Pl. 23, fig. 2b). Primary zone of astogenetic change includes ancestrula and about three generations of asexually budded autozooids in which length and aperture size increase.

Autozooids highly elongate, those originating medially within branches relatively short, but those originating along branch margins typically much longer with extended, gradually widening proximal portions; peristomes projecting up to at least 200 μm essentially perpendicular to branch surfaces and terminating in circular apertures commonly in transverse groups of two or three. Pseudopores in frontal walls circular to slightly elongated elliptical, approximately 10-12 μm (Pl. 23, fig. 1d; Pl. 24, fig. 1f).

Gonozooids with elongate oval brood chambers (Pl. 23, fig. 1c) where branches widen abruptly, sometimes semi-erect pyriform globular (Pl. 23, fig. 2a), flanked, but not medially perforated, by autozooidal peristomes and with abundant small circular pseudopores. Ooeciopore small, circular, with raised ooeciostomial rim, subterminal, sometimes adnate to a peristome (Pl. 24, fig. 2b).

Kenozooids may be developed as a single row bounding branches laterally.

**Measurements** – FWL 704±121, 470-974 (5, 36); FWW 124±21, 95-172 (5, 35); AD 65±8, 45-80 (5, 35); BVL 531±113.

**Remarks** – The number of autozooids varies unpredictably across branches which are locally constricted to a single autozooid, proliferating to three or four visible rows, and commonly appearing biserial. The number of autozooids present at any one position along a branch is commonly difficult to discern because of the inconspicuous, highly extended, gradually attenuated proximal portions of many autozooids.

*Annectocyma cirrita* differs from *A. major* (Johnston, 1847), as described by Hayward...
& Ryland (1985b), in having narrower branches, much smaller autozooids and autozooidal apertures, and transverse groups of fewer peristomes.

**Family Fascigeridae d’Orbigny, 1853**

*Filifascigera d’Orbigny, 1853*

*Type species* – *Tubulipora megaera* Lonsdale, 1845, Paleocene, Thanetian, Vincentown Formation, New Jersey; by subsequent designation.

*Remarks* – At first sight resembling *Stomatopora*, closer inspection shows that each ‘aperture’ aligned along the bifurcating branches of *Filifascigera* colonies actually consists of a fascicle comprising a cluster of connate apertures. In living species, these fascicles can be moderately tall and the constituent zooids may develop peristomes that split apart from one another, but these are invariably broken-off in fossils, resulting also in the loss of the recognisable parts of the gonozooids.

*Range* – Campanian – Recent.

*Filifascigera cylindrata* sp. nov.

*Material* – Holotype: RU 5627, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2). Paratypes: RU 5525, 5607, details as for holotype.


*Description* – Colony of encrusting, narrow, multiserial strap-like branches with gently convex cross sections, dividing dichotomously at various angles; commonly crossed by distally arcuate growth lines. Branches consist of distally widening internodes that terminate in fascicles of the distal ends of 3-6, usually five, autozooids, orientated perpendicularly to the substrate and extending an unknown distance above the encrusting branch surface (Pl. 25, fig. 1c, d). Ancestrula and primary zone of astogenetic change not seen.

Autozooids within fascicles tightly crowded, most commonly two on the proximal side and three on the distal side of the fascicle. Basally budded autozooids emerge from under each fascicle, in some instances supplemented by 1-2 branch-margin autozooids that pass around the base of the fascicle, initiating the narrow proximal end of the next branch internode and terminating in the fascicle at the end of that internode. Within each gradually widening branch internode, new basally budded autozooids are added, most continuing past the internode-terminating fascicle to initiate the next-distal branch internode, although in some fascicles one or two of the newly budded autozooids may form part of the distal side of the fascicle. Autozooids are all basally budded, very long and narrow with extended lengths of frontal wall between successive fascicles, terminating in irregularly polygonal apertures at outer ends of fascicles; apertures bounded laterally by frontal (fixed-)walls and medially by interior (free-)walls.

Gonozooids not seen.
Measurements – FWL (autozooids exposed along branch surface) 1197±189, 789-1524 (3, 20); FWW (autozooids exposed along branch surface) 98±17, 69-136 (3, 25); AD (min.) 45±10, 30-61 (3, 21); AD (max.) 67±13, 51-94 (3, 21); BRW 372±101, 181-562 (3, 26); FD 240±66, 173-467 (3, 18); FS 1540±308, 914-1924 (3, 13).

Remarks – Filifascigera cylindrata differs from the Thanetian species F. megaera (Lonsdale, 1845) and the Campanian species F. irregularis Hennig, 1894, in having more autozooids per fascicle and in having cylindrical fascicles of autozooids with polygonal cross sections rather than a single row of laterally contiguous autozooids. It differs from the Maastrichtian-Danian species Filifasgera [sic] gracilis Brood, 1972, in having fewer autozooids per fascicle and low clavate rather than cylindrical, uniform-width branch internodes.

The cylindrical autozooidal fascicles are worn in all samples, but none is taller than about 200 µm, which may be close to the maximum length. Where well preserved, autozooids at tops of fascicles in some Recent species of Filifascigera diverge from one another and have individual, delicate peristomes (e.g., Osburn, 1953, pl. 69, figs. 8, 10). The specimens of F. cylindrata available for study were too highly abraded to retain individual peristomes atop fascicles if they were originally present.

Family Cytisidae d’Orbigny, 1854
Osculipora d’Orbigny, 1849

Type species – Retepora truncata Goldfuss, 1827, Maastrichtian, The Netherlands; by original designation.

Remarks – Osculipora includes erect cyclostomes having autozooids grouped into fascicles on a more-or-less well-defined frontal side and with the surface of the colony, other than the fascicles, covered by kenozooids. Desmepora Lonsdale, 1850, putatively differs from Osculipora in lacking kenozooids on the frontal side, but Brood (1972) considered Desmepora to be a junior synonym of Osculipora because of variable development in the extent of between-fascicle kenozooidal cover within populations of pertinent species. In the material from North Carolina studied by us, kenozooidal development typically lags behind the tips of branches or fascicles, which supports Brood’s concept. However, Brood (1972) described the highly elongate autozooids of Osculipora as originating from the reverse sides of branches, for which we see no evidence in our material.

Range – Turonian? – Danian?

Osculipora carolinensis sp. nov.
Pl. 26.

**Etymology** – Named after the State of North Carolina, in which the species was first found.

**Description** – Colony erect, dendroid, highly branched, with poorly defined frontal and reverse sides; branches typically about 0.5 mm in diameter, of variable length, and with no clear distinction between them and local, minimally protruding fascicles of autozooids; fascicles located on ill-defined frontal side, separated by variable distance. Base of attachment thickened into flared cone by radially orientated kenozooids (Pl. 26, fig. 2); ancestrula and primary zone of astogenetic change not seen.

Autozooids opening at subcircular fascicles and branch tips consisting of generally 10-25 completely interior-walled autozooidal apertures surrounded by a cortex of kenozooids; autozooids closely packed, very elongate tubular, parallel with branch/fascicle axis; apertures irregularly polygonal and of variable size due to differing locations of new buds across the fascicle/branch tip.

Gonozooid located on lateral side of branch, interior-walled around perimeter, roof missing, elongate oval (Pl. 26, fig. 3b); placement of ooecestome unknown.

Kenozooids moderately elongate, distally directed, forming single layer around branches above expanded base of attachment; proximal to growing tips of branches, commonly closed by terminal diaphragm of exterior wall with abundant circular pseudopores approximately 5-6 μm in diameter (Pl. 26, fig. 4b)

**Measurements** – BRW 549±77, 446-644 (1, 8); AD 76±10, 56-102 (1, 60).

**Remarks** – *Osculipora carolinensis* differs from *O. iltenensis* (Voigt, 1951) in having much more delicate branches, fewer autozooids per fascicle (10-25 vs 15-150) and no clear organization of fascicles into two well-defined latero-frontal rows. *Osculipora semicylindrica* (Römer, 1840), as characterized by Voigt (1951), differs from *O. carolinensis* in having fewer autozooids per fascicle, which are clearly differentiated from branch dichotomies, and fascicles aligned into two well-defined latero-frontal rows. Stating that the taxonomic limits of *O. truncata* (Goldfuss, 1827) are uncertain, Brood (1972) accepted such wide variation in characteristics and such a long stratigraphic range (Turonian–Danian) that it is impossible to know which morphology actually characterizes Goldfuss’ species and which are different, probably undescribed, species.

An encrusting base of a cytisid cyclostome from the Prairie Bluff Chalk may belong to *O. carolinensis* (NHM BZ 5225). It consists of a radially spreading cone of kenozooids, broken approximately 1 mm above the base of attachment, with the break showing about a dozen polygonal cross sections of autozooids in the centre of the branch.

**Family Theonoidae Busk, 1859**

**Theonoa Lamouroux, 1821**

**Type species** – *Theonoa chlatrata* Lamouroux, 1821, Bathonian, Normandy, France; by monotypy.

**Remarks** – The Jurassic type species of *Theonoa* was revised by Walter (1970).

**Range** – Aalenian – Maastrichtian?
**Theonoa? radiobifurcata** Canu & Bassler, 1926

*Pl. 27.*

1926 *Actinopora radiobifurcata* sp. nov.; Canu & Bassler, p. 38, pl. 7, fig. 8.

In press *Theonoa radiobifurcata* (Canu & Bassler); McKinney & Taylor, pl. 3E.

**Material** – Holotype: USNM 69966, Maastrichtian, Coon Creek Formation, McNairy County, Tennessee (locality TN1).

**Description** – Colony encrusting, multiserial, cateniform (*Pl. 27, fig. 1c*) due to sequential, laterally budded, discoidal daughter subcolonies up to about 6 mm in diameter. Perimeter of each subcolony a steeply inclined, broad, continuous budding zone composed of up to five generations of autozooids that become organized into fascicles with continued growth (*Pl. 27, fig. 1b*). From point of origin of a subcolony, its upper surface organized into radiating fascicles of 2-3 rows of autozooids bounded laterally by exterior wall; new fascicles intercalated between adjacent diverging fascicles. Zooids at budding zones locally closed by terminal diaphragms, marking termination of subcolony growth.

Autozooids within fascicles irregularly polygonal in cross section, those along lateral margins of fascicles mixed free- and fixed-walled, and those isolated from fascicle edge completely free-walled.

Gonozooids not seen.

**Measurements** – AD 107±8, 100-120 (1, 10); ASW 141±17, 120-160 (1, 10); FS 436±55, 360-520 (1, 10); Gap 182±36, 140-240 (1, 10).

**Remarks** – The only colony of this species known to us is the non-fertile holotype. *Theonoa* Lamouroux, 1821, and *Actinopora* d’Orbigny, 1853, have similar a colony habit, with encrusting, multiserial, essentially discoidal colonies in which the autozooids are organized into radiating fascicles bounded laterally and separated by fixed-wall surfaces. The Jurassic species *T. chlatrata* Lamouroux, 1821, type species of *Theonoa*, has distally expanding, subtriangular, essentially equidimensional gonozooids situated between two contiguous fascicles, at the point of origin of a newly intercalated fascicle (Walter, 1970, pl. 20, fig. 1). Gonozooids are not present in the original type specimens of *Actinopora regularis* d’Orbigny, 1853 (see Taylor & Gordon, 2005), nor in the originally illustrated specimen(s) of *Ceriopora stellata* Koch & Dunker, 1837, which Gregory (1909) and subsequent authors considered synonymous with *A. regularis*. Canu & Bassler (1926, pl. 6, fig. 2) published a drawing by Gregory of a fertile colony assigned to *A. stellata* (Koch & Dunker) in which the gonozooid is equidimensional and Voigt (1972, pl. 1, fig. 4) also illustrated an equidimensional gonozooid in a d’Orbigny specimen that he reassigned to *Actinopora*. In contrast, the presence of very broad gonozooids that extend across several fascicles is commonly considered to be a characteristic of *Actinopora* (e.g., McKinney & Taylor, 1997, pl. 3, figs. 1, 3, 4). We have questionably and somewhat arbitrarily transferred *Actinopora radiobifurcata* to *Theonoa* because of the uncertainty of the discrimination of *Actinopora* from *Theonoa* and the more robust fascicles of the Coon Creek species which are closer to those of *T. chlatrata* than *A. stellata*. 
Incertae familiae
‘Berenicea’ sp.
Pl. 28.

**Material** – NHM BZ 5213, Maastrichtian, Prairie Bluff Chalk, Braggs, Lowndes County, Alabama (locality AL3).

**Description** – Colony encrusting, multiserial, unilamellar, maculate(?), up to 25 mm in diameter. Basal lamina extending moderate distance beyond budding zone at growing edge; two generations of new buds usually visible. Early astogeny unknown.

Autozooids large, relatively short, about 500-650 μm long by 200-240 μm wide. Frontal wall gently convex, pseudoporous, zooidal boundaries obscure (Pl. 28, fig. 1c). Apertures longitudinally elliptical, about 140 μm long by 120 μm wide, surrounded by thick bases of broken peristomes, some with terminal diaphragms.

Kenozooids and unequivocal gonozooids not observed.

**Remarks** – A robust sheet-like tubuliporine encrusts some cobbles from the rock-ground at the base of the Prairie Bluff Chalk at Braggs in Alabama. Although this species is clearly different from the other multiserial encrusting tubuliporines described herein, as none of the specimens have unequivocal gonozooids it is impossible to assign it to a family or genus. Therefore, the species is left in open nomenclature as ‘Berenicea’ sp., in accordance with the use of this informal designation advocated by Taylor & Sequeiros (1982).

Most of the specimens of this species are heavily abraded and only one (NHM BZ 5213) is sufficiently well-preserved to warrant description. There is some indication that an erect branch may be developing in this specimen (Pl. 28, fig. 1d), although growth around the base of another bryozoan species cannot be ruled out.

**Suborder Cancellata Gregory, 1896**
**Family Crisinidae d’Orbigny, 1853**

**Polyascosoeciella** Taylor & McKinney, 1996

**Type species** – *Idmonea foraminosa* Reuss, 1851, Miocene, Austria; by original designation.

**Remarks** – Erect, branched cyclostomes in which branches have well-defined reverse surfaces that are occupied entirely by kenozooids, autozooids organized into two bands of transverse fascicles on a strongly curved obverse surface, kenozooids separating each fascicle of autozooids and gonozooids located on the obverse surface, have been grouped into three genera based on wall structure of the gonozooids. *Crisidmonea* Marsson, 1887, has gonozooids roofed by interior wall, *Reteporia* d’Orbigny, 1849, has gonozooids roofed by a ring of interior wall surrounding a central area of exterior wall, and *Polyascosoecia* of authors has gonozooids roofed entirely by exterior wall (see Voigt, 1984; Vávra, 1991; Taylor & McKinney, 1996). However, the type species of *Polyascosoecia* Canu, 1920, is apparently a junior subjective synonym of the type
species of *Crisidmonea* Marsson (Voigt, 1984; Taylor & McKinney, 1996), which led Taylor & McKinney (1996) to propose a new name, *Polyascosoecciella*, to replace *Polyascosoechia* as commonly used (see Zágorsek, 2003, for an alternative viewpoint on this taxonomic problem).

**Range** – Maastrichtian?-Miocene?

*Polyascosoecciella? tripora* (Canu & Bassler, 1926)

Pl. 29.

1926 *Polyascosoechia tripora* sp. nov.; Canu & Bassler, p. 38, pl. 7, figs. 1, 2.

In press *Polyascosoecciella? tripora* (Canu & Bassler); McKinney & Taylor, fig. 4C.

**Material** – Lectotype (here designated): USNM 69963, Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TE1). Paralectotypes, USNM 528383, details as for holotype. Other material: NHM D52246 (3 fragments), BZ 3699, locality as for types. NHM BZ 4816 (sample), BZ 4819, BZ 5140 (2 thin sections), Prairie Bluff Chalk, Braggs, Lowndes County, Alabama (locality AL3). USNM 528384, Maastrichtian, Pee Dee Formation, Neuse River, Lenoir County, North Carolina (locality NC4).

**Description** – Colony erect, unilaminate, consisting of bifurcating branches about 1 mm wide, forming planar branch systems. Obverse surface of branches strongly curved transversely, with autozooids laterally disposed and separated by a median strip of kenozooids. Skeletal organisation interior-(free-)walled throughout.

Autozooids in transverse rows (Pl. 29, fig. 1c) of usually three, locally two, slightly separated circular apertures with somewhat elevated rims; budded in thin-walled endozone initially close to branch reverse side, but in older parts of colony surrounded by thick exozone of prolific kenozooids; no distinct budding lamina. Interzooidal pores present, but diaphragms and other intrazoooidal structures not observed.

Gonozooids not seen.

Kenozooids budded in exozone, constituting vast majority of colony mass and volume, elongated parallel with colony surface rather than with autozooidal axes. Median frontal strip, frontal surface between successive transverse rows of autozooids, and reverse surface occupied by small-diameter tubular kenozooids oriented distally and organized into well- to ill-defined linear longitudinal rows. Spreading base of attachment consisting entirely of radially oriented kenozooids.

**Measurements** – FS 349±34, 280-420 (4, 31); ASW 182±27, 160-240 (1, 10); AD 78±11, 60-96 (4, 40); BrD 942±128, 700-1160 (1, 8).

**Remarks** – No gonozooids are present in any of the available specimens of this species, so its assignment to a genus is uncertain (see ‘Remarks’ for the genus *Polyascosoecciella*, above). It is questionably placed here in *Polyascosoecciella* (the replacement name for *Polyascosoechia* auctt.) because there is no current reason to assign it to any particular genus other than that in which it was first described.
Suborder Cerioporina von Hagenow, 1851
Family Cerioporidae Busk, 1859
Tetrocycloecia Canu, 1917

Type species – Tetrocycloecia dichotoma Canu, 1917 (= Ceriopora dichotoma Goldfuss, 1827, sensu Reuss, 1848), Miocene, Austria; by original designation.

Remarks – Nye (1976) described only the type species in his revision of Tetrocycloecia (often spelt Tretocycloecia). This has dendroid colonies with strongly dimorphic, free-walled zooids. The distinction between Tetrocycloecia and Heteropora Blainville, 1830, requires clarification; some authors (e.g., Walter 1989b) have regarded Tetrocycloecia as a junior subjective synonym of Heteropora. However, zooidal dimorphism is not well-developed in the Cretaceous type species of Heteropora (Nye, 1976). If the two genera are to remain separate then some of the species traditionally assigned to Heteropora, including extant forms, may have to be transferred to Tetrocycloecia. This would have implications for the range of Tetrocycloecia.

Range – Aptian? – Miocene, Recent?

Tetrocycloecia tennesseensis (Canu & Bassler, 1926)
Pl. 30.

1926 Heteropora tennesseensis sp. nov.; Canu & Bassler, p. 38, pl. 7, figs. 3-7.
In press Tetrocycloecia tennesseensis (Canu & Bassler); McKinney & Taylor, fig. 4D.


Description – Colony dendroid, of dichotomously bifurcating cylindrical branches typically 1.5-2.5 mm in diameter; surface uneven, possibly reflecting ill-defined maculae; local, relatively thick self-overgrowths developed and spread from small groups of underlying zooids. Short mural spines common, projecting into zooidal interiors in walls of autozooids, kenozooids and brood chambers (Pl. 30, fig. 5). Ancestrula and primary zone of astogenetic change not seen.

Autozooids elongate, tubular, irregularly polygonal in endozone, originating across entire endozone, curving into thick exozone, where circular cross-section and thick walls are developed, meeting exozone surface at or near 90°. Apertures isolated by kenozooids, arranged in irregular quinuncial pattern; small, circular to commonly elliptical, surrounded by slightly protuberant skeletal rim (Pl. 30, fig. 3).

Gonozooids circular to transversely or longitudinally elongate elliptical, extending across surface of branch among 30 to 40 autozooids, roofed by thin interior wall densely perforated by approximately 5 μm diameter polygonal pseudopores (Pl. 30, fig. 6). Floor of brood chamber formed by occluded apertures of kenozooids (Pl. 30, fig. 5). Ooeciopore not seen.
Kenozooids small, originating within and near base of endozone, parallel with autozooids, forming a continuous or discontinuous ring surrounding each autozooid, some continuing through brood chambers, closely appressed to a central autozooid; apertures rounded to subrounded; locally additional kenozooids present between autozooids.

**Measurements** – AD 65±6, 54-80 (4,40); AS 191±31, 115-262; KAD 35±9, 13-53 (4,40).

**Remarks** – *Tetrocycloecia tennesseensis* occurs around the coastal plain from Tennessee to New Jersey in silts and fine-grained sands that are low in carbonate except for coarse-grained skeletal debris.

*Tetrocycloecia transversa* sp. nov.
Pls. 31, 32.

**Material** – Holotype: NHM BZ 5141, Maastrichtian, Ripley Formation, Florence, Quitman County, Georgia (locality GA1). Paratypes: NHM BZ 5142-9, BZ 5152-4; NNM RGM 507 045-507 046, details as for holotype. RU 5621, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

**Etymology** – Named for the common transverse bands of kenozooids that alternate with bands of mixed autozooids and kenozooids.

**Description** – Colonies dendroid, comprising dichotomously bifurcating cylindrical branches typically 2.0-2.5 mm in diameter. Colony surface organized into transverse bands, 0.5-1.0 mm wide, of mixed autozooids and kenozooids alternating with transverse bands of kenozooids approximately 0.5 mm wide (Pl. 31, fig. 1a; Pl. 32, fig. 1a). Local rejuvenation produced regions of self-overgrowth by thin, radially spreading encrusting sheets (Pl. 32, fig. 2b). Short mural spines common projecting into zooidal interiors in walls of autozooids, kenozooids and brood chambers. Ancestrula and primary zone of astogenetic change not seen.

Autozooids elongate, tubular, irregularly polygonal in endozone, originating across entire endozone, curving into thick exozone where they are circular in cross-section and thick walled, meeting exozone surface at or near 90º (Pl. 31, fig. 2a). Autozooidal apertures arranged in quincuncial pattern, intermediate size, grading to largest apertures adjacent to kenozooidal bands, circular to commonly elliptical, surrounded by slightly protuberant skeletal rim serrated due to approximately 15-20 low spines (Pl. 31, fig. 3a, b). Some autozooids closed by a centripetally calcified terminal diaphragm perforated by a few pseudopores less than 5 μm in diameter.

Gonozooids circular (Pl. 32, fig. 3), spreading across surface of branch among 20 to 40 autozooids, roofed by thin interior wall. Floor of brood chamber formed by occluded apertures of kenozooids, although some kenozooids continue through brood chamber with their contiguous autozooid. Ooeciopore generally central, flaring, slightly larger than autozooidal apertures.

Kenozooids small, polygonal, originating within and near base of endozone, parallel with autozooids, forming a continuous or discontinuous ring surrounding each
autozooid and also massed into transverse bands; more than one row of kenozooids locally present between autozooids. Kenozooids remain open or may be closed by terminal diaphragms with abundant circular pseudopores about 6 μm in diameter.

**Measurements** – AD 84±9, 65-101 (6,60); AS 227±31, 164-320; KAD 36±13, 15-77 (4,40).

**Remarks** – *Tetrocycloecia transversa* differs from *T. tennesseensis* by the branch surface being organized into alternating transverse bands of kenozooids, and mixed autozooids and kenozooids, and by having larger and more widely spaced autozooids.

*Semicrescis d’Orbigny, 1854*

**Type species** – *Semicrescis tubulosa* d’Orbigny, 1854, Senonian (Campanian?), western France; by monotypy.

**Remarks** – D’Orbigny (1854) introduced this genus for *Crescis*-like cyclostomes with tubular colonies. The taxonomic significance of this growth-form character has yet to be evaluated and it is possible that it is due simply to fortuitous growth around soft-bodied cylindrical substrates that subsequently perished. However, Bassler (1953) was mistaken when placing *Semicrescis* in synonymy with *Ditaxia* Hamm, 1881, which has bifoliate colonies.

Skeletal organization in *Semicrescis* is cerioporine, the autozooids and kenozooids being free-walled, but the gonozooids fixed-walled. Unfortunately, the syntypes (MNHN Paris, d’Orbigny Collection 8414; see Pl. 33, fig. 2) of the type species of *Semicrescis* are infertile, but putative conspecific material in the NHM (BZ 524) has subcircular brood chambers roofed by exterior wall pierced and supported by autozooidal peristomes.

**Range** – Campanian.

*Semicrescis implanus* sp. nov.

Pl. 33, fig. 1.

**Material** – Holotype: ANSM 80351, Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1). Paratypes: ANSM 80370, NHM BZ 5150-1, details as for holotype.

**Etymology** – L., *implanus*, meaning uneven, in reference to the hummocky colony surface.

**Description** – Colony tubular (cavariiform) (Pl. 33, fig. 1a), multiserial, uni- or multilaminar, the frontal surface non-planar with irregular ridges and hummocks, some of which are evidently due to overgrowth (bioclaustration) of vermiform fouling organisms. Tube up to 2-3 mm in diameter, lined by transversely-wrinkled, exterior basal lamina. Maculae marked by patches of kenozooids or gonozooids, intermacular areas with mixture of autozooids and kenozooids. Ancestrula and early astogeny unknown.
Autozooids free-walled, with elliptical apertures surrounded by collars up to 150 μm long in protected areas, prolonged in length on sides closest to maculae. Apertures usually non-contiguous and surrounded by kenozooids, average mid-point spacing almost three times their diameter.

Kenozooids free-walled, apertures about two-thirds the diameter of autozooidal apertures, constricted and funnel-like without an upstanding collar; short mural spines (tubercles) visible in some kenozooids.

Gonozooids subcircular in frontal outline, evidently non-septate, but traversed by multiple isolated autozooids supporting the roof (Pl. 33, fig. 1e). Ooeciopore central, circular, slightly more than half autozooidal aperture diameter, with low ooeciostome. Preserved remnants of roof with microstructural fabric obscured by adherent sedimentary grains and coccoliths, but planar morphology and lack of large pores indicative of exterior wall construction.

**Measurements** – AD 94±9, 74-115 (5, 60); AS 258±45, 119-357 (5, 50); KAD 68±13, 30-115 (5, 50); BCL 1509±493, 762-2329(4, 14); BCW 1409±294, 749-1764 (4, 14); OD 58±8, 50-65 (1, 3).

**Remarks** – This new species differs from *Semicrescis tubulosa* d'Orbigny, 1854, in having kenozooids with funnel-like apertures (compare Pl. 33, figs. 1d, 2), autozooids with more prominent collars and a hummocky colony surface. The fragmentary specimens of *S. implanus* known to us do not bifurcate. In *S. tubulosa*, branch bifurcations do occur at intervals and colonies are essentially dendroid.

**Family Densiporidae Borg, 1944**

**Unicavea d'Orbigny, 1853**

*Type species* – *Defrancia vassiacensis* d'Orbigny, 1850, Aptian, Vassy, France; by subsequent designation.

**Remarks** – The fairly numerous low, domal, encrusting colonies that consist of free-walled autozooids interspersed with smaller polymorphs are tentatively assigned to *Unicavea* d'Orbigny. Unfortunately, available material is insufficient to determine the ultimate arrangement and geometry of the autozooidal apertures or the skeletal structure of the brood chamber. The latter is particularly important because colonies of similar form occur in taxa that are logically placed in different suborders on the basis of having brood chambers roofed by exterior wall calcification (Cerioporina) or free-walled calcification (Rectangulata). For example, Gordon & Taylor (2001) reassigned some supposed Recent lichenoporids to the cerioprine genus *Favosipora* MacGillivray, 1885, on this basis. Most Cretaceous 'lichenoporids' (e.g., the species described by Walter, 1989b) have exterior-walled gonozooids and may be more appropriately assigned to the cerioprine family Densiporidae Borg, 1944, as are the two North American species described below.

**Range.** – Aptian?-Maastrichtian?
Unicavea sp. 1
Pl. 34, figs. 1, 2.

Material – ANSM 80772-80774, Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1). RU 5405, 5510, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 and/or NJ2).

Description – Colony encrusting, multiserial, low domal, averaging about 2.5 mm in diameter, with perimeter of calcified basal lamina, and continuous zone of incipient autozooids and smaller polymorphs; less commonly complex colonies of maternal and daughter subcolonies (Pl. 34, fig. 2).

Autozooids obliquely divergent from centre of colony, apparently quincuncially arranged, interspersed with smaller polymorphs (Pl. 34, fig. 1c). Colony centre occupied by small polymorphs, covering proximal portions of oldest divergent autozooids. Gonozooids not seen.

Measurements – Colony diameter 2362±678, 1244-3457 (12); AD 64±9, 45-90 (9, 75); AS 210±46, 127-305 (3, 30).

Remarks – Available material of this species is indifferently preserved and in no colonies are brood chambers developed.

Unicavea sp. 2
Pl. 34, fig. 3.

Material – NHM BZ 4179(3), Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2).

Description - Colonies encrusting, multiserial, discoidal, extending as relatively flat sheet up to about 3 mm in total diameter, with perimeter of calcified basal lamina, and continuous zone of incipient autozooids and smaller polymorphs (Pl. 34, fig. 3b).

Autozooids obliquely divergent from centre of colony, arranged in ill-defined rows interspersed with smaller polymorphs, apertures about 100 μm in diameter. Gonozooid unknown.

Remarks – The few available free-walled, encrusting colonies from the Peedee Formation that consist of autozooids and smaller polymorphs are tentatively determined as Unicavea sp. 2. They appear to differ from specimens of the Mount Laurel and Navesink formations, grouped as Unicavea sp. 1, in having a flatter profile and better defined alignment of autozooids into rows.

Order Cheilostomata Busk, 1852
Suborder Malacostegina Levinsen, 1902
Family Electridae Stach, 1937
Herpetopora Lang, 1914

Type species – Herpetopora anglica Lang, 1914, Upper Chalk, England; by original designation.
Remarks – Although placed in synonymy with Pyripora d’Orbigny, 1849, by Thomas & Larwood (1956, 1960), Herpetopora is here regarded as a separate genus in accordance with Taylor (1988a). It can be distinguished from Pyripora by: having very narrow proximal caudae; the absence of pore chambers; exhibiting extremely steep secondary gradients of astogenetic change; never showing pluriserial growth; and lacking any significant development of pustulose cryptocyst.

Range – Turonian-Maastrichtian. A post-Cretaceous species, Herpetopora danica Lang, 1914, described from the Danish (Paleocene) of Denmark and the Vicksburgian (Oligocene) of Alabama (Canu & Bassler, 1920), lacks the caudate zooids found in true Herpetopora and clearly belongs to another genus. Thomas & Larwood’s (1960, p. 381) observation of ovicells in H. danica place this species outside the malacostegan family Electridae, while other features suggest assignment to the neocheilostome family Calloporidae.

Herpetopora anglica Lang, 1914
Pl. 35.

1914 Herpetopora anglica sp. nov.; Lang, p. 6, pl. 2, figs. 1-3.
1960 Pyripora anglica (Lang); Thomas & Larwood, p. 375, pl. 60, figs. 3, 4, pl. 61, fig. 1, text-fig. 1b, c.
1967 Pyripora sp.; Shaw, p. 1400, pl. 178, fig. 2.
1971 Pyripora shawi sp. nov.; Frey & Larwood, p. 971, pl. 115, figs. 1-3, pl. 116, figs. 1-4.
1988a Herpetopora anglica Lang; Taylor, p. 519, pl. 44, figs. 1, 4, pl. 45, figs. 1, 6.
2002 Herpetopora anglica Lang; Taylor, p. 66, pl. 7, fig. 4, pl. 9, fig. 1.
In press Herpetopora anglica Lang; McKinney & Taylor.

Material – LSUMG-I 8232, 8254, 8257, Santonian, Brownstown Marl, Oklahoma (locality OK1), figured by Shaw (1967, pl. 178, fig. 2); paratypes of Pyripora shawi Frey & Larwood, 1971. NHM BZ 5155(1), Campanian, Demopolis Chalk, Macon, Noxubee County, Mississippi (locality MS1). NHM BZ 5021(1), Maastrichtian, Coon Creek Formation, shelly lens above Corbula bed, upstream of Coon Creek Field Station, McCurtain County, Tennessee (locality TE1; S. Tracey Collection). BZ 5022, same details, but grey, silty, fine-grained sand in stream bed, “Inoceramus” bed aucct.

Description – Colony encrusting, runner-like, uniserial, with new branches arising, singly or in pairs, as distolateral buds and diverging from parent branches at angles of about 60-90°.

Autozooids simple, large though highly variable in size (Pl. 35, fig. 3), elongate, pyriform in shape, with a long, narrow proximal cauda grading into a dilated distal part containing the longitudinally ovate opesia which is 2-3 times longer than wide (Pl. 35, fig. 1c). Pore windows of elliptical shape, paired opposite mid point of opesia and a little proximolaterally of opesia. Calcification entirely gymnocrystal; cryptocyst and spines lacking. Mural rim minutely crenulated. Intramural reparative buds recognizable as concentric mural rims within damaged zooids. Closure plates observed in intramural buds (Pl. 35, fig. 2a). Irregular, tubular kenozooids may link branches. Avicularia and ovicells lacking.

Measurements (from LSUMG-I 8232) – ZL 987±159, 800-1220 (1, 8); ZW 348±32, 300-380 (1, 8); OpL 475±34, 440-520 (1, 4); OpW 180 ± 16, 160-200 (1, 4).
Remarks – European colonies of this species, as well as other North American specimens figured by Frey & Larwood (1971; as Pyripora shawi), show the following additional features: kenozooids with small, subcircular opesiae; autozooids with opesiae covered by closure plates bearing crescent-like scars of the operculum; and strong secondary gradients of astogenetic change along distolateral branches manifested by a progressive increase in caudal length, and narrowing of zooid and opesia width.

Specimens from the Brownstown Marl (Santonian) of Oklahoma originally described by Shaw (1967) as *Pyripora* sp. (but dubbed *Pyripora brownstownensis* on p. 1430 therein) were subsequently included as paratypes of Frey & Larwood’s (1971) new species *Pyripora shawi*. This North American species, with a holotype coming from the Niobrara Chalk (Coniacian) of Kansas, was compared to the European species *Herpetopora anglica* Lang, but considered to differ by lacking a cryptocyst and having less variable dimensions. However, SEM study of *H. anglica* and a second European species (*H. laxata*) show that these, too, lack a cryptocyst. Additionally, all species of *Herpetopora* show great variability in zooidal dimensions, particularly length, mostly due to the extreme astogenetic gradients developed in their colonies. Variability in zooidal length *per se* is therefore not a good character for species discrimination, at least not when dealing with fragmentary material of the sort available in current North American collections. Zooidal dimensions in *P. shawi* fall within the range found in the better known *H. anglica* (see Thomas & Larwood, 1960; Taylor, 1988a), suggesting their synonymy. In Europe, *H. anglica* ranges from late Turonian to early Campanian, and can be distinguished from *H. laxata*, ranging from late Campanian to early Maastrichtian, by having proportionately longer opesia (Thomas & Larwood, 1960) and smooth, non-stepped secondary astogenetic gradients (Taylor, 1988a). The second of these features is impossible to ascertain in the North American material because of its fragmentary condition. However, the opesial (apertural) ratio (2.3-2.9) measured from Oklahoma colonies of *P. shawi* matches the range quoted by Thomas & Larwood (1960) for *H. anglica* (2.2-3.3), but not that of *H. laxata* (1.4-2.4). This permits us to synonymise *P. shawi* with *H. anglica*.

As an inferred malacostegan, *H. anglica* would have had non-brooded, planktotrophic larvae (ovicells for larval brooding are lacking). A geographical range extending from northwest Europe to Kansas is consistent with the wide distributions attained by some species of living malacostegans with such long-lived larvae.

*Herpetopora wightoni* sp. nov.

Pl. 36.

Material – Holotype: NHM BZ 5013, Maastrichtian, Peedee Formation, Rocky Point Quarry, Pender County, North Carolina (locality NC3). Paratypes: NHM BZ 5014, NNM RGM 507 065, Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2). NHM BZ 5156, Maastrichtian, Prairie Bluff Chalk, Emelle, Sumter County, Alabama (locality AL9).

Etymology – Named for Tony Wighton (Department of Mineralogy, NHM) in recognition of his work in preparing the holotype of this new species for SEM and making most of the thin sections employed in this study.
Description – Colony encrusting, uniserial, new branches originating as distolateral buds, usually paired, sometimes single, diverging from parent branch at about 60-90°. Secondary gradients of astogenetic change present, each new branch initiated by an autozooid with a short cauda, caudal length increasing through later generations prior to a transition to long and narrow kenozooids in distalmost parts of branches (Pl. 36, fig. 2a). Ancestrula and early astogeny unknown. Pore chambers absent.

Autozooids pyriform in outline, straight or with a somewhat curved cauda. Caudal length variable, a relatively abrupt transition occurring to the broader distal part of zooid. Gymnocyst immediately proximally of opesia broad and somewhat swollen (Pl. 36, fig. 2b). Cryptocyst narrow, inwardly-sloping, non-pustulose. Opesia elliptical, about 1.5 times longer than wide, the mural rim raised. Intramural buds sometimes present (Pl. 36, fig. 1c). Closure plates not observed. Basal wall uncalcified or very thinly calcified.

Kenozooids of three types: very long kenozooids in distal parts of branches that are dilated slightly at the level of the small subcircular opesia, a little beyond which autozooids forming new branches may arise as distolateral buds; rounded, almost triangular kenozooids with small subcircular opesia formed as distolateral or proximolateral buds; and tubular kenozooids lacking opesia or daughter buds and forming occasional linkages between branches.

No avicularia or ovicells.

Measurements – ZL 404±83, 313-636 (2, 20); ZW 151±14, 133-183 (2, 20); OpL 95±22, 60-124 (2, 20); OpW 62±11, 38-82 (2, 20).

Remarks – This material is sufficiently distinct from existing species of *Herpetopora* to warrant recognition as a new species. The raised mural rim around the opesia (Pl. 36, figs. 1b, 2b) prompts comparison with *Herpetopora filum* Voigt, 1930 (see also Thomas & Larwood, 1960, p. 378), from the Maastrichtian of the type region in The Netherlands. However, the outline shape of the autozooids differs. In *H. filum* there is a gradual increase in width from the proximal cauda to the distal part of the zooid, whereas in *H. wightoni* a more abrupt increase in width results in a moderately larger expanse of gymnocyst between the cauda and proximal edge of the opesia.

‘Footprints’ left on the substrate after detachment of zooids demonstrate both the considerable thickness of the vertical walls (up to about 30 μm) and the lack of pore chambers (Pl. 36, fig. 1a). Growth of diagenetic cement within the interiors of the zooids (i.e., the area bounded by the vertical walls) is similar to that on the unencrusted surface of the substrate around the zooids. This suggests the absence of a calcified basal zooidal wall that might otherwise have impeded or modified cement growth.

*Electra* Lamouroux, 1816

Type species – *Flustra verticillata* Ellis & Solander, 1786 [= *Flustra pilosa* Linnaeus, 1767], Recent, North Atlantic; by subsequent designation.

Remarks – This genus typically has zooids with a well-developed gymnocyst bearing a variable number of spines, generally including a medial spine located on the proximal margin of the opesia. The cryptocyst is slight and pore chambers are well-developed.
Colonies are often loosely multiserial and stellate in outline. The axes of the stars consist of uniserial or oligoserial series of zooids that form the leading edges of colony growth and between which additional zooids are subsequently budded, a colony-form referred to as 'composite multiserial' by Silén (1987). The Recent type species of *Electra* has a gymnocyst deeply pitted from the underside giving the false impression that it is porous when the pits are viewed through the semi-transparent frontal shield. However, this feature is lacking in the majority of species assigned to the genus.

Membraniporimorph anascans, of which *Electra* is the first to be described in this study, are extremely common constituents of Cretaceous bryozoan faunas worldwide, yet their supraspecific taxonomy has received scant attention and is highly problematical. Earlier authors tended to place all such species indiscriminately into *Membranipora*. However, this specialist epiphyte has a weakly-mineralized, aragonitic skeleton and, at best, negligible fossil record. The diagnostic twinned ancestrula possessed by *Membranipora* and other genera of the Membraniporidae (see Taylor & Monks, 1997) has yet to be recorded in the Cretaceous.

A fundamental subdivision of membraniporimorphs is into malacostegans and pseudomalacostegans. Taxa assigned to the malacostegans (e.g., *Membranipora*) constitute a paraphyletic grade of primitive forms. They lack ovicells and seldom have avicularia. Pseudomalacostegans are neocheilostomes which normally possess ovicells, indicating brooding of non-planktotrophic larvae, and very often have avicularia. Since the Cenomanian, malacostegans have been greatly outnumbered by pseudomalacostegans in the fossil record; most Late Cretaceous membraniporimorph cheilostomes are pseudomalacostegans.

**Range** – Maastrichtian-Recent.

*Electra everretti* sp. nov.

**Material** – Holotype: NHM BZ 5015, Upper Maastrichtian, Peedee Formation, Rocky Point Member, Ideal Quarry, Pender County, North Carolina (locality NC2). Paratypes: BZ 5016(1), BZ 5123(3), BZ 5228, details as for holotype. NHM BZ 5029(3), Maastrichtian, Peedee Formation, Rocky Point Quarry, New Hanover County, North Carolina (locality NC3).

**Etymology** – Named for John Everrett (Raleigh, North Carolina) who guided us around quarries in the Wilmington area, leading to the discovery of this new species.

**Description** – Colony encrusting, forming irregular patches, uniserial in early astogeny, becoming multiserial with some uniserial or oligoserial runner-like prolongations (Pl. 37, fig. 2). Autozooids generally not arranged in a regular pattern. Pore chambers present. Ancestrula about 150 μm long, budding distal and proximal daughter zooids. Autozooids elongate and pyriform in frontal outline shape, on average almost twice as long as wide. Opesia occupying most of frontal surface, longitudinally elliptical in shape. Gymnocyst well-developed proximally, narrowing distally, in some zooids bearing a short, spine-like tubercle located along median axis just beneath opesia (Pl.
Cryptocyst variably developed, widest proximally and narrowing distally, sometimes forming a distinct proximal shelf with or without scattered pustules (Pl. 37, fig. 1c). Closure plates present in many zooids from zone of primary astogenetic change and in clusters or rows of zooids within zone of astogenetic repetition; slightly convex, containing a single longitudinally elliptical, bevelled pore, a little distal of which is the scar of the marginal opercular sclerite, deeply incised, crescent-shaped, about 75 μm wide (Pl. 37, fig. 1e). Intramural buds present in some zooids. Basal walls fully calcified.

Kenozooids sporadic, either interzooidal and having an elongate opesia surrounded by cryptocyst (Pl. 37, fig. 1d), or adventitious, overgrowing autozooidal gymnocysts, small, generally subtriangular and poorly-developed with narrow gymnocyst surrounding a wide opesia.

No ovicells or avicularia.

**Measurements** – ZL 353±48, 300-420 (1, 10); ZW 186±28, 120-210 (1, 10); OpL 212±23, 165-240 (1, 10); OpW 134±18, 90-150 (1, 10).

**Remarks** – Assignment of this new species to *Electra* among malacostegans is based on colony growth pattern, the dominantly gymnocystal frontal shield, the sporadic presence of a non-articulated median spine on the proximal edge of the opesia and the lack of articulated mural spine bases. It more closely resembles Recent species such as *E. monostachys* (Busk, 1854) and *E. crustulenta* (Pallas, 1766) than it does *E. verticillata*, the type species.

Early astogeny is poorly preserved in all available specimens of *E. everretti*, but it appears that the ancestrula buds two daughter zooids, one distally and the other proximally. This contrasts with *E. monostachys*, which has a distal and two proximolateral daughter zooids (Poluzzi, 1981), and with *E. pilosa*, which normally has a proximal, a distal and two distolateral daughter zooids (Silén, 1987). The distinctive closure plates, with a single small pore and a conspicuous opercular sclerite scar, the occurrence of occasional zooids with a shelf-like proximal cryptocyst, and the weakly-developed median spine are three features enabling distinction between this new species and previously named species of *Electra*.

Prior to the discovery of *E. everretti* in the Maastrichtian, the oldest known species of *Electra* appears to have been *E. parvimater* which Canu & Bassler (1920) described from the Eocene (Lower Jacksonian) of Mississippi.

**Conopeum Gray, 1848**

*Type species* – *Millepora reticulum* Linnaeus, 1767, Recent, North Atlantic; by monotypy.

**Remarks** – Superficially, the four Cretaceous species here assigned to *Conopeum* resemble *Acanthodesia* Canu & Bassler, 1920 (type species *Flustra savartii* Audouin & Savigny, 1826). However, this post-Cretaceous genus has a twinned ancestrula contrasting with the single ancestrula seen in the type and other species of *Conopeum*. There are similarities between *Conopeum* and two Maastrichtian genera, *Eokotosokum* Taylor & Cuffey, 1992, and *Bullaconopeum* Taylor, 1995. In *Eokotosokum*, however, each zooid has
two large distolateral spine bases, and in *Bullaconopeum* four prominent gymnocystral tubercles are present.

**Range** – Campanian-Recent.

*Conopeum spissamentum* sp. nov.

Pl. 1, fig. 2; Pl. 38.

**Material** – Holotype: NHM BZ 4798, Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). Paratypes: NHM BZ 5062, details as for holotype. NHM BZ 4811, BZ 5158-5159, NNM RGM 507 001-507 002, Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5). NHM BZ 5157, Maastrichtian, Ripley Formation, Florence, Quitman County, Georgia (locality GA1). NHM BZ 5017, Maastrichtian, Prairie Bluff Chalk, Emelle, Sumter County, Alabama (locality AL9). NHM BZ 5018, Maastrichtian, Prairie Bluff Chalk, Braggs, Lowndes County, Alabama (locality AL4). VCSM 13957, Campanian, Demopolis Chalk, Macon, Noxubee County, Mississippi (locality MS2). Other material: RU 5520, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2, R. J. Turner Collection). NHM BZ 5234, Maastrichtian, Ripley Formation, Perote, Bullock County (locality AL2).

**Etymology** – *L.*, *spissamentum*, plug or stopper, in reference to the morphology of zooids containing closure plates.

**Description** – Colony encrusting, multiserial, unilaminar or multilaminar, the autozooids arranged in well-defined longitudinal rows (Pl. 38, fig. 1a) with row divisions at intervals, colonies attaining diameters of up to 60 mm. Kenozooids normally present at the proximolateral corners of the autozooids, the complex formed by the autozooid and its two associated kenozooids subrectangular in outline shape. Pore chambers lacking. Ancestrula single, surrounded by six periancestrular zooids (Pl. 38, fig. 2a, b), the largest of which is proximal, occluded by a closure plate in all scanned examples.

Autozooids broad and elliptical in frontal outline shape, usually about 1.2 times longer than wide, those immediately preceding a row division broadest (Pl. 38, fig. 1b), those immediately succeeding a division narrowest; boundary wall thin, salient. Opesia occupying most of frontal surface, elliptical to rounded rectangular in shape, nearly parallel-sided and equidimensional. Gymnocyst lacking. Cryptocyst slightly pustulose, broad proximally, narrowing and disappearing distally. Ovicells lacking. Closure plates present in autozooids from zone of primary astogenetic change and in clusters of 3-25 autozooids within zones of astogenetic repetition (Pl. 38, fig. 1d); covering entire frontal surface, convex, pitted or perforate, bearing a pair of kidney-shaped indentations distally, about 80-100 μm apart and interpreted as impressions of opercular sclerites.

Avicularia not observed.

Kenozooids typically subtriangular in frontal outline, located at proximolateral corners of autozooids in zones of astogenetic change (Pl. 38, fig. 1c), small, a tiny opesia present at the centre of the cryptocyst. Broader kenozooids quadrate in shape with concave sides, may be associated with the longer of the two autozooids following row bifurcations. Closure plates usually raised and tubercle-like (Pl. 38, fig. 1d).
**Measurements** – ZL 476±27, 450-525 (1, 10); ZW 395±42, 315-435 (1, 10); OpL 342±33, 300-390 (1, 10); OpW 344±35, 285-390 (1, 10).

**Remarks** – This new species is similar to *Conopeum nelsoni* (Canu & Bassler, 1926) and *C. paranelsoni* sp. nov., differing principally in the broader, more quadrate morphology of the autozooids, and the smaller and less prominent cryptocystal tubercles. Further differences of potential taxonomic significance are seen in areas where the zooids have closure plates; autozooidal closure plates in *C. spissamentum* (Pl. 38, fig. 1d) bear paired, kidney-shaped impressions of the opercular sclerites, whereas those of *C. nelsoni* (Pl. 39, fig. 1e) and *C. paranelsoni* (Pl. 40, fig. 1b) have a single, crescent-shaped depression at the distal end of the closure plate. Kenozooids are closed by raised, tubercle-like calcification in *C. spissamentum*, but no equivalent structures have been observed in *C. nelsoni*.

Superficially, colonies of *C. spissamentum* appear to be monomorphic, with rows of subrectangular autozooids each having a small area of proximal gymnocyist. The apparent gymnocyist is usually divided into two triangular patches at the proximolateral corners of the zooid, except for the longer of the two daughter zooids following a row bifurcation where the two patches are united into one. However, SEM examination shows that the apparent gymnocyist is actually a cryptocyst, recognizable by its pustulose surface. In bioimmured specimens exposing the basal colony surface, the triangular patches are seen to be distinct chambers best interpreted as kenozooids. This inference is supported by the tubercle-like calcification of the triangular patches in areas where adjoining autozooids have closure plates; such calcification would not be expected over autozooidal gymnocyist or cryptocyst. A small pore close to the centre of the kenozooids can be interpreted as the reduced opesia. In the type species of *Conopeum* (*C. reticulum*), similar small polymorphs are commonly present and have been termed ‘reticulumzooids’. Like the kenozooids of *C. spissamentum*, reticulumzooids may become closed over by calcification. In culture, the reticulumzooids of *C. reticulum* sometimes contain reduced polypides capable of feeding according to Jebram (1968), but the much smaller opesiae of the kenozooids in *C. spissamentum* makes it very unlikely that these were capable of housing feeding polypides.

Several colonies preserve the ancestrula, which is surrounded by six periancestricular autozooids (Pl. 38, fig. 2a, b). The early budding pattern is uncertain. However, the configuration and relative sizes of the periancestricular zooids suggest that the ancestrula budded one (distal) or perhaps three (distal, left distolateral and right distolateral) daughter zooids, and that the remaining zooids in the circket of six were budded from the other periancestricular zooids. In particular, it seems likely that the proximal zooid of the circket was not budded directly from the ancestrula. In contrast, the ancestrula of *C. reticulum* buds a proximal plus two distolateral daughter zooids (Ryland & Hayward, 1977, fig. 20D).

*Conopeum nelsoni* (Canu & Bassler, 1926)

Pl. 39.

1926  *Alderina nelsoni* sp. nov.; Canu & Bassler, p. 33, pl. 5, fig. 1.
In press  *Conopeum nelsoni* (Canu & Bassler); McKinney & Taylor, fig. 1A.
**Material** – Holotype: USNM 69969, Maastrichtian, Coon Creek Formation, Coon Creek, McNairy County, Tennessee (locality TN1); figured by Canu & Bassler (1926, pl. 5, fig. 1). Other material: NHM BZ 5019, Maastrichtian, Ripley Formation, Coon Creek Member, grey silty fine sands in stream-bed, ‘Inoceramus bed’ auctt., Coon Creek, McNairy County, Tennessee (locality TN1; S. Tracey Collection August 1999).

**Description** – Colony encrusting, multiserial, the autozooids arranged in well-defined longitudinal rows with occasional row divisions. Ancestrula and early astogeny unknown.

Autozooids longitudinally elliptical in frontal outline shape, usually about 1.6 times longer than wide, boundary wall low, crenulated. Opesia occupying most of frontal surface, elliptical in shape. Gymnocyst lacking. Cryptocyst with sparse, but prominent, pustules, broadest proximally, narrowing and disappearing distally (Pl. 39, fig. 1c). Ovicells lacking. Closure plates present in clusters of 3-4 autozooids (Pl. 39, fig. 1d); covering entire frontal surface, convex, densely porous, divided into irregular polygonal sectors each with 1-4 pores (Pl. 39, fig. 1f), a crescent-shaped depressed area at the distal end of the closure plate interpreted as the impression of the operculum (Pl. 39, fig. 1e). Avicularia not observed.

**Measurements** – Holotype: ZL 420±33, 380-500 (1, 10); ZW 262±38, 220-340 (1, 10); OpL 308±21, 260-340 (1, 10); OpW 198±27, 160-240 (1, 10).

**Remarks** – The differences between this species and *C. spissamentum* sp. nov. have already been noted. Only two specimens of *C. nelsoni* are available for study, both encrusting free-living serpulid worm tubes (Pl. 39, fig. 1a).

Closure plates are very well-preserved in the holotype colony (Pl. 39, fig. 1d-f). They are unusual in being subdivided into irregularly polygonal sectors each pierced by 1-4 pores. Nothing similar is known from extant species of *Conopeum*; in *C. seurati*, for example, the closure plates (termed ‘kleistozooids’ by Poluzzi & Sabelli, 1985) are plain, incompletely calcified and have a medial opening.

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**Conopeum paranelsoni** sp. nov.

*Pl. 40.*

**Material** – Holotype: ANSM 80351, Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1). Paratype: ANSM 80352, details as for holotype.

**Etymology** – In reference to its similarity with *Conopeum nelsoni* (Canu & Bassler, 1926).

**Description** – Colony encrusting, multiserial, initially unilaminar, becoming multilaminar through development of irregular overgrowths. Pore chambers present. Ancestrula preserved in paratype; about 300 μm long, occluded by closure plate pierced by at least three pores; mural spine bases present, number unknown. Six periancestrular zooids of which the distal and two distolateral appear to be buds from the ancestrula; all
or most zooids in zone of primary astogenetic change possessing closure plates.

Autozooids rhombic in frontal outline, usually about 1.5 times longer than wide; boundaries marked by conspicuous furrows; basal walls fully calcified. Opesia longitudinally elliptical or oval, occupying most of frontal surface (Pl. 40, fig. 2c). Gymnocyst narrow to moderately developed proximally, tapering distally; oral spines present in at least some zooids, paired, minute, inconspicuous. Cryptocyst pustulose, broadest proximally, narrowing and disappearing distally, inwardly sloping, not forming a distinct shelf; mural rim finely crenulated. Ovicells lacking. Closure plates present in clusters of about 10 autozooids (Pl. 40, fig. 2a); covering entire frontal surface, convex, perforated by up to 15 large, sunken pores; crescent-shaped distal incisions interpreted as impressions of operculum about 110 μm in width (Pl. 40, fig. 1b). Intramural buds infrequent. Avicularia and kenozooids not observed.

Measurements – ZL 491±36, 450-570 (1, 10); ZW 323±40, 255-390 (1, 10); OpL 368±16, 345-390 (1, 10); OpW 212±22, 180-255 (1, 10).

Remarks – The clusters of autozooids with perforated closure plates are reminiscent of *Conopeum nelsoni* (Canu & Bassler, 1926) and, to a lesser extent, *C. spissamentum* sp. nov. However, *C. paranelsoni* differs in having far fewer pores in the closure plates and a much more deeply incised opercular scar. It also lacks the triangular kenozooids present at the corners of the autozooids of the other two species. The presence of minute oral spines is a further distinguishing characteristic and the zooids of the new species are slightly larger than those of *C. nelsoni*. None of the other membraniporimorph species described in this study has clusters of autozooids with closure plates.

Gordon & Taylor (2005) recently revived the genus *Reptoporina* d’Orbigny, 1852 (*in* 1851-1854), an Upper Cretaceous membraniporimorph from Europe characterized by having numerous autozooids occluded by closure plates. Unlike the three North American species described above, however, the closure plates of *Reptoporina* have a longitudinal fissure instead of pores. *Reptoporina* is a calloporid pseudomalacostegan rather than an electrid malacostegan, as colonies are known with ovicells.

*Conopeum rhombica* sp. nov.

Pl. 41.


Etymology – In reference to the rhombic shape of the autozooids.

Description – Colony encrusting, multiserial, often large (>50 mm diameter), the autozooids arranged in well-defined longitudinal rows with occasional row divisions (Pl. 41, fig. 1a). Distal pore chamber visible in some zooids at growing edge, seemingly absent in others (Pl. 41, fig. 1c). Ancestrula and early astogeny unknown. Uncommon eruptive budding resulting locally in multilaminar growth (Pl. 41, fig. 1d).
Autozooids longitudinally rounded rhomboidal in frontal outline shape, small, about 1.3 times longer than wide, attaining maximum width roughly mid-length, zooidal boundaries grooved. Opesia occupying most of frontal surface, longitudinally elliptical to almost pear-shaped, mural rim crenulated. Gymnocyst a very narrow crescent at the proximolateral corners of the zooids. Cryptocyst densely pustulose (Pl. 41, fig. 1d), broad and shelf-like proximally, narrow along lateral edges of opesia and lacking distally. Intramural buds present in some zooids, visible as concentric mural rims. Ovicells lacking. Closure plates not observed.

Polymorphic zooids (kenozooids?, avicularia?) sometimes present as the smaller of the two daughter zooids following row bifurcations, distinguished from autozooids by their significantly reduced size and the presence of a shelf-like distal cryptocyst (Pl. 41, fig. 1b).

**Measurements** – ZL 356±25, 315-405 (1, 10); ZW 276±28, 225-315 (1, 10); OpL 258±22, 225-300 (1, 10); OpW 164±13, 150-180 (1, 10).

**Remarks** – This new species is distinguished from *C. spissamentum*, with which it co-occurs in the Ripley Formation and Prairie Bluff Chalk of Alabama, by the rhombic shape of the autozooids, the cryptocyst being more densely pustulose and broader laterally, the smaller size of the zooids, and the absence of paired kenozooids at the proximolateral corners of the autozooids. An Arabian Maastrichtian species, *Bullaconopeum nodosum* Taylor, 1995, has similarly-shaped autozooids to those of *C. rhombica*, but each zooid possesses four tubercles and has a well-defined area of distal gymnocyst. In another Maastrichtian species, *Eokotosokum bicystosum* (Allan & Sanderson, 1945) from the Western Interior (re-described by Taylor & Cuffey, 1992), the autozooids have a pair of large distolateral spine bases. However, *E. bicystosum* does possess uncommon polymorphic zooids with well-developed distal cryptocysts which resemble the small polymorphs found in *C. rhombica*.

Visible within some of the autozooids of *C. rhombica* are knob-like structures growing proximally from the distal transverse wall at roughly the positions where interzooidal communication pores might be expected to occur (Pl. 41, fig. 1a, lower left). The significance of these enigmatic structures is unknown, but they may be teratological in origin. Indications of disruptions in growth and repair are visible elsewhere in the form of irregularities in zooid distribution and intramural buds.

**Heteroconopeum Voigt, 1983**

*Type species* – *Membranipora janieresiensis* Canu, 1897, Cenomanian-Coniacian, France; by original designation.

**Remarks** – The type species of *Heteroconopeum* occurs in the Cenomanian-Coniacian of Europe and Africa (Voigt, 1983; Taylor & Zaborski, 2002). It is characterised by having erect colonies comprising narrow, cylindrical branches with an axial endozone and peripheral exozone. The endozone is made from the proximal parts of autozooids, polygonal in cross-section, and stacked vertically to form prismatic cylinders. These zooids are bent sharply into the exozone and open on the colony surface, with
the spaces between them being filled by small polymorphs. Multiple laminar overgrowths developed, consisting of zooids arranged exactly parallel with those that they overgrow. Branch thickness may be increased considerably by the addition of such distally oriented overgrowths. The exact mode of origin of the overgrowths is unknown, but it is possible that they were generated at or close to the colony base and grow up the branches. Small, subtriangular kenozooids occur at the corners of the autozooids.

In his original description of *Heteroconopeum*, Voigt (1983) drew comparisons with *Conopeum ovatum* Canu & Bassler, 1926, from the Ripley Formation of Tennessee, but excluded this species from *Heteroconopeum* on account of the presence in *C. ovatum* of polymorphs he regarded as avicularia. However, in spite of these polymorphs, the very close similarities in colony construction and autozooidal morphology between *H. janieresiensis* and *C. ovatum* persuade us to assign the North American species to *Heteroconopeum*. The revised stratigraphical range of *Heteroconopeum* therefore becomes Cenomanian-Maastrichtian. The Argentinean species *Membranipora langana* Canu, 1911, is a possible Danian representative of *Heteroconopeum*, but requires revision before its true generic affinities can be established.

**Range** – Cenomanian-Maastrichtian, Danian?

*Heteroconopeum ovatum* (Canu & Bassler, 1926)

Pls. 42-43.

1926  *Conopeum ovatum* sp. nov.; Canu & Bassler, p. 32, pl. 4, figs. 1-4.
1926  *Conopeum parviporum* sp. nov.; Canu & Bassler, p. 32, pl. 4, figs. 5-6.
1926  *Conopeum wadei* sp. nov.; Canu & Bassler, p. 32, pl. 4, fig. 11.
1962  *Conopeum? ramosum* sp. nov.; Toots & Cutler, p. 84, pl. 18, figs. 1-4.
1962  *Solenophragma ovatum* (Canu & Bassler); Voigt, p. 34, pl. 18, figs. 1-3.
1967  *Solenophragma ovatum* (Canu & Bassler); Shaw, p. 1407, pl. 179, fig. 3.
In press *Heteroconopeum ovatum* (Canu & Bassler); McKinney & Taylor, fig. 1B.

**Material** – Lectotype (here selected): USNM 69964, bifurcating branch figured by Canu & Bassler (1926) as pl. 4, fig. 3 and right-hand branch of pl. 4, fig. 5; Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TE1). Paralectotypes: USNM 528393-528396, details as for lectotype. Other material: USNM 69965 (syntypes of *C. parviporum*), 69953 (holotype of *C. wadei*); details as for lectotype of *C. ovatum*. USNM 526169, Maastrichtian, Peedee Formation, Neuse River, Lenoir County, North Carolina (locality NC4). NHM BZ 4817 (numerous branch fragments probably all from one colony), BZ 4817(a), BZ 4826, BZ 5235 (3 thin sections), Maastrichtian, Ripley Formation, Florence, Quitman County, Georgia (locality GA1). NHM D52249, D53139 (sample), BZ 715, BZ 3115, BZ 5020 (sample), BZ 5028 (sample), NNM RGM 507 003, locality as for lectotype. NHM BZ 5169, Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). NHM BZ 5162-7, Campanian, Cusseta Sand, Lumpkin, Stewart County, Georgia (locality GA2).

**Description** – Colony erect, comprising narrow, cylindrical, bifurcating branches (Pl. 43, fig. 1a) apparently arising from a sheet-like encrusting base (Pl. 42, fig. 4a); distally-
directed laminar overgrowths of zooids in precise alignment with underlying zooids are typically developed. Branch endozone comprising proximal parts of zooids, polygonal in cross-section and with successive zooids stacked vertically so as to form a superficially prismatic cylinder; about 5-10 such cylinders present in the axis of each branch. Longitudinal walls of cylinders contain lines of communication pores, about 15 μm in diameter and spaced 150-300 μm apart, some surrounded by low collars (Pl. 42, fig. 3); transverse walls of cylinders partitioning successive zooids have a crescent of communication pores on their axial sides (Pl. 43, fig. 1f). Zooids bending sharply into exozone. Branch surface occupied by autozooids in longitudinal rows (Pl. 42, fig. 1), along with smaller polymorphs, some avicularium-like.

Autozooids longitudinally elliptical to inverted teardrop-shaped in frontal outline (Pl. 42, fig. 4b, c; Pl. 43, fig. 1c), variable in proportions, ranging from 1.1-1.9 times longer than wide. Opesia occupying most of frontal surface. Gymnocyst lacking. Cryptocyst pustulose, moderately broad proximally and forming a somewhat depressed ledge, narrowing distally and sloping more steeply inwards, mural rim crenulated. Ovicells lacking. Basal walls visible near distal end of opesia contain a variable number of indentations (muscle scars?, basal septulae?), often a median depression flanked by two larger lateral depressions (Pl. 43, fig. 1c). Closure plates and intramural buds not observed.

Polymorphs of variable size and shape infill spaces between autozooids. Largest polymorphs avicularium-like, some almost the same length as neighbouring autozooids (Pl. 42, fig. 2), although narrower, pointed or gothic arch-shaped distally; opesia longitudinally elliptical; proximal cryptocyst broad and long; distal cryptocyst rostrum-like; no calcified pivotal bar (Pl. 43, fig. 1d). Smallest polymorphs irregular in shape, some lacking a clearly-defined cryptocyst (Pl. 43, fig. 1e).

**Measurements** – Syntypes of *C. ovatum*: ZL 426±19, 400-460 (2, 10); ZW 282±18, 260-300 (2, 10); OpL 308±19, 280-340 (2, 10); OpW 204±16, 180-220 (2, 10); AL 364±77, 260-500 (2, 10); AW 156±18, 140-180 (2, 10). Syntype of *C. parviporum*: ZL 370±20, 340-400 (1, 10); ZW 240±16, 220-260 (1, 10); OpL 304±16, 280-320 (1, 10); OpW 198±18, 180-240 (1, 10); AL 338±42, 280-406 (1, 10); AW 142±11, 120-160 (1, 10). Holotype of *C. wadei*: ZL: 488±25, 440-520 (1, 10); ZW: 368±47, 300-480 (1, 10); OpL: 382±24, 340-400 (1, 10); OpW: 270±48, 220-400 (1, 10); AL 270±36, 220-340 (1, 10); AW: 144±13, 120-160 (1, 10); RW: 86±10, 80-100 (1, 10).

**Remarks** – Three species, *Conopeum ovatum*, *C. parviporum* and *C. wadei*, described by Canu & Bassler (1926) from the Ripley Formation of Coon Creek, are here synonymised. Page priority rests with *C. ovatum*. The first two species are based on erect branching specimens, and were distinguished by Canu & Bassler using differences in zooid size and a slight difference in shape, *C. parviporum* having smaller zooids with more rounded ‘termens’. Qualitatively, the two species cannot be separated and it is likely that the specimens selected by Canu & Bassler to define these species represent end-members in a continuum of zooid size range. The third species, *C. ovatum*, is also included in the synonymy. Among Canu & Bassler’s types, this species is represented by a single colony encrusting a small gastropod shell. The morphology of the autozooids and the development of pointed avicularium-like polymorphs between them is
strongly reminiscent of *C. ovatum*, although there are some morphometric differences. However, topotype material in the NHM (BZ 5028) includes examples of encrusting colonies on small gastropods giving rise to erect branches. Similarly expansive encrusting bases have been described in *Heteroconopeum janieresiensis* by Taylor & Zaborski (2002).

An additional nominal species, *Conopeum? ramosum* Toots & Cutler, 1962, can also be placed in subjective synonymy with *Heteroconopeum ovatum*. Toots & Cutler (1962) noted the morphometric similarities between their new species from the Campanian of Wyoming and species previously described by Canu & Bassler (1926) from Tennessee, but used the apparent lack of larger heterozooids in their species as a distinguishing character. As the development and preservation of avicularium-like polymorphs is very variable in *C. ovatum* (e.g., Pl. 42, fig. 2; Pl. 43, fig. 1d, e), this apparent difference may not be taxonomically significant. Comparison of Coon Creek *C. ovatum* with a specimen of *C.? ramosum* from Wyoming in the Voigt Collection (VCSM 10514) supports the synonymy.

The polymorphic zooids of *Heteroconopeum ovatum* are problematical. The larger heterozooids have a well-defined, avicularium-like shape, with an expanded distal cryptocyst that forms a palate-like shelf (Pl. 42, fig. 2). It is reasonable to suppose that they had mandibles closing against this shelf and were avicularia, even though avicularia are uncommon in malacostegan anascans (Taylor, 1987). Those few avicularia that are known among Recent malacostegan species closely resemble autozooids in size and shape, but have an enlarged operculum. At the other end of the spectrum, the smallest polymorphs in *H. ovatum* are little more than interzooecial spaces bounded by minimally calcified walls. Intermediate-sized polymorphs resemble the interzooidal kenozooids found in some anascans.

*Chiplonkarina* Taylor & Badve, 1995

**Type species** – *Ceriopora dimorphopora* Chiplonkar, 1939, Upper Cretaceous, Bagh Beds, Madhya Pradesh, India; by original designation. *Heteropora decipiens* Peron, 1893, from the Turonian of Tunisia is possibly a senior synonym of *C. dimorphopora* on the basis of type material recently found by P.D.T. in the MNHN, Paris.

**Remarks** – Prior to the recognition of *Chiplonkarina* by Taylor & Badve (1995), species assigned to this genus were consistently misidentified as cerioporine cyclostomes with which they are remarkably homeomorphic. The long tubular zooids of *Chiplonkarina*, dendroid branches possessing an axial endozone and peripheral exozone, and subcircular ‘apertures’ opening on the colony surface, are all features more usually associated with cyclostomes than with cheilostomes. However, the true affinity of *Chiplonkarina* is evident from the skeletal microstructure, the compound nature of the interzoooidal walls, which have a corrugated medial suture, and the pustulose cryptocysts defining the apertures.

The type species of this genus occurs in rock-forming abundance in the Bagh Beds of the Narmada Valley in central India. New ammonite evidence (Kennedy *et al.*, 2003) shows the Bagh Beds to be at least partly of Late Turonian age, possibly extending into the Coniacian, and thus younger than their previously suspected Cenomanian age (Taylor & Badve, 1995). This region of peninsular India was situated in the southern hemi-
sphere at the time of deposition of the Bagh Beds. *Chiplonkarina* is also represented by a second species (*C. bretoni* Taylor & Badve, 1995) in the Cenomanian of northern Europe, and by one described (*C. campbelli* Taylor, 1996) and a few undescribed species in the Maastrichtian of New Zealand. Apart from the northern European occurrences, the genus is basically Tethyan or Austral in distribution and, therefore, its discovery in the Maastrichtian of New Jersey was somewhat unexpected.

**Range** – Cenomanian-Maastrichtian, Miocene? An undescribed, questionable species of *Chiplonkarina* occurs in the Lower Miocene of New Zealand (P.D.T. unpublished).

*Chiplonkarina okamurae* sp. nov.

**Pl. 44.**

**Material** – Holotype: RU 5641, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2; R. F. Turner Collection).

**Etymology** – In recognition of the key contributions made to bryozoology by Dr Beth Okamura (University of Reading).

**Description** – Colony erect, dendroid, branches variable in diameter, the single known specimen comprising an irregular, curved branch 5-6 mm in diameter and a lateral branch 2 mm in diameter (Pl. 44, fig. 1a). Zooids irregularly arranged on colony surface, the orientations of autozooids variable and not coincident with branch growth direction. Ancestrula and early astogeny unknown.

Autozooids tubular and horn-shaped in section, frontal outline elliptical, small, on average about 1.2-1.3 times longer than wide. Opesia extensive, occupying most of frontal surface, dumbbell-shaped (Pl. 44, fig. 1e), a minor constriction separating a typically longer and broader portion (proximal?) from a shorter and narrower portion (distal?). Gymnocyst and spines lacking. Cryptocyst wide, not shelf-like, tapering in width towards presumed distal end of zooid, densely pustulose. Closure plates not observed. Possible intramural buds developed in some zooids (Pl. 44, fig. 1d). No ovi-cells or avicularia.

Kenozooids numerous, interspersed between autozooids (Pl. 44, fig. 1c), small, with a variable number of generally concave sides; opesia subcircular; cryptocyst broad, pustulose.

Transversely fractured branches may split along corrugated compound interzooe-clial walls (Pl. 44, fig. 1f), revealing transversely elliptical pores about 25 × 10 μm in diameter.

**Measurements** – ZL 309±27, 270-345 (1, 10); ZW 242±36, 195-300 (1, 10); OpL 171±19, 150-210 (1, 10); OpW 92± 11, 75-105 (1, 10).

**Remarks** – Although represented by only one specimen (in two fragments), this is clearly a new species. It can be distinguished from the formally named species of *Chiplonkarina* (*C. dimorphopora* Chiplonkar, 1939), *C. bretoni* Taylor & Badve, 1995, and *C. campbelli* Taylor, 1996) by the dumbbell-shaped opesiae that contrast with the el-
liptical opesiae present in these three species. The cryptocyst is also noticeably thicker in *C. okamurae*. Mean frontal autozooid size in the new species (309 × 242 μm) is about the same as that in *C. campbelli* (310 μm), larger than that in *C. dimorphopora* (260 × 215 μm), but smaller than *C. bretoni* (390 × 330 μm).

The existence in *C. okamurae* of lateral branches of much smaller diameter than the parent branches is seen also in *C. dimorphopora* (Taylor & Badve, 1995, text-fig. 2A), but is unusual for dendroid bryozoans as a whole where adjacent branches are generally of equal or almost equal diameter. Lateral branches in *Chiplonkarina* are evidently adventitious in origin.

**Basslerinella gen. nov.**

*Type species* – *Conopeum prismaticum* Canu and Bassler, 1926, Maastrichtian, Coon Creek, McNairy County, Tennessee.

*Other species* – *Basslerinella sohli* sp. nov., Maastrichtian, Wilmington, North Carolina.

*Etymology* – In honour of R.S. Bassler, prolific bryozoologist who coauthored the type species.

*Diagnosis* – Colony erect, bifoliate. Autozooids tubular, arranged in well-defined longitudinal rows on colony surface, angular basal walls interlocking with those of back-to-back layer, opesia extensive, longitudinally elliptical, an apertural bar sometimes present overarching opesia distally; gymnocyst normally hidden by kenozooidal overgrowth; cryptocyst inwardly sloping, moderately broad proximally, narrower distally. Kenozooids infilling spaces between autozooidal opesia, concave-sided, triangular or trapezoidal, respectively with one or two opesiae, digitate edges projecting over autozooidal opesia, cryptocyst pustulose. Ovicells and avicularia unknown.

*Remarks* – Two unusual species from the Upper Cretaceous of the eastern U.S.A. are not readily assignable to an existing genus and are here united in the new genus *Basslerinella*. The key characters are the bifoliate colony form, tubular autozooids with gymnocysts which are overgrown and obscured by kenozooids with digitate margins projecting over the autozooidal opesia. In the limited material available, neither ovicells nor avicularia have been found. The affinities of the new genus are therefore uncertain. However, the closest comparison is with *Heteroconopeum*. Both genera have erect growth, long autozooids and smaller polymorphs filling interopesial spaces on the colony surface. Colony-form differs between the two genera, the cylindrical branches of *Heteroconopeum* contrasting with the bifoliate fronds of *Basslerinella*. No equivalent to the delicate apertural bar preserved in two zooids of *B. sohli* has been found in *Heteroconopeum*. Indeed, this enigmatic structure has few analogues among cheilostomes in general. The kenozooids overgrowing the edges of the autozooids in *Basslerinella* are reminiscent of those found in the calloporid *Dactylostega tubigera* (Busk) as figured by Hayward & Cook (1983, fig. 7B).

*Range* – Upper Cretaceous, confirmed Maastrichtian.
**Basslerinella prismatica** (Canu & Bassler, 1926)

Pl. 45, fig. 1.

1926 Conopeum prismaticum sp. nov.; Canu & Bassler, p. 33, pl. 4, figs. 7-10.  
In press “Conopeum” prismaticum (Canu & Bassler); McKinney & Taylor, fig. 1C.

**Material** – Lectotype (chosen here): USNM 69967, specimen figured by Canu & Bassler (1926, pl. 4, fig. 8); Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TE1). Paralectotypes: USNM 644358, details as for lectotype. Other material: NHM BZ 5081-5082, details as for types, W.J. Kennedy Collection 1974.

**Description** – Colony bifoliate, with broad, relatively flat fronds comprising two layers of zooids back-to-back; no median budding lamina. Colony base unilaminar, extensive; early astogeny unknown.

Autozooids elongate, tubular, basal walls angular, interlocking with basal walls of autozooids opening on other side of frond, arranged in well-defined rows (Pl. 45, fig. 1a), periodically bifurcating; zooidal boundaries overgrown by kenozooids. Opesia longitudinally elongate, about twice as long as wide, occupying most of the visible frontal surface, sunken; mural rim sharp. Gymnocyst overgrown by kenozooids, exposed only where these are broken away (Pl. 45, fig. 1b). Cryptocyst pustulose, sloping steeply inwards, broadest proximally. Ovicells lacking. Closure plates and intramural buds not observed.

Kenozooids covering entire colony surface between autozooidal opesiae, usually one per autozooid, trapezoidal in outline shape with concave sides, funnel-like, the walls formed of pustulose cryptocyst. Each kenozooid typically with two opesial openings, one on the left and the other on the right side of midline of the distally neighbouring autozooid. Outer lateral edges of kenozooid fluted or digitate and projecting over the opesia of the autozooid (Pl. 45, fig. 1c).

Possible kenozooid with wide opesia forming one of the daughter zooids following a row bifurcation.

Avicularia not observed.

**Measurements** – USNM 644358 (paralectotype): ZL 460±22, 440-500 (1, 10); ZW 262±18, 240-300 (1, 10); OL: 362±11, 340-380 (1, 10); OW:190±11, 180-200 (1, 10).

**Remarks** – Canu & Bassler (1926) interpreted the kenozooids as interopesial cavities, but it is apparent that they possess their own bounding walls and are consequently zooids rather than spaces between zooids. The fractured proximal part of the lectotype colony (Pl. 45, fig. 1b) is critical in understanding the structure of B. prismatica. Here, the kenozooids have been broken away to expose the relatively long proximal gymnocysts of the underlying autozooids. These walls are usually covered in their entirety by kenozooids, which also grow to a significant height above the level of the autozooidal opesiae. The peculiar fluting around the edges of the opesiae (Pl. 45, fig. 1c) is due not to convolutions in the mural rim of the autozooids as, for example, in *Jellyella* (see Taylor & Monks, 1997), but to the digitate outer edges of the kenozooids which overhang the opesiae of the autozooids.
**Basslerinella sohli sp. nov.**

Pl. 45, fig. 2.

*Material* – Holotype: USNM 526167, Upper Cretaceous, Wilmington Waterworks, New Hanover County, North Carolina (locality NC5).

*Etymology* – After former USGS palaeontologist, the late Norman Sohl, in whose collection was found the only known specimen of this new species as well as material of several other species described here.

*Description* – Colony bifoliate, consisting of folded fronds, each comprising two layers of zooids back-to-back; fronds about 1 mm in depth; no median budding lamina. Overgrowths developed on branch surfaces. Early astogeny, including colony base, unknown.

Autozooids frontally elongate, arranged in well-defined rows (Pl. 45, fig. 2a, b), periodically bifurcating, zooidal boundaries overgrown by kenozooids. Opesia longitudinally elongate, about 1.7 times longer than wide, occupying most of the visible frontal surface, sunken. Gymnocyst not visible, by analogy with *B. prismatica* probably overgrown by kenozooids. Some autozooids with narrow, smooth (gymnocystal?) ‘apertural bar’ overarching opesia about two-thirds of the way along zooidal length (Pl. 45, fig. 2c). Cryptocyst obscured by calcite cement. Ovicells absent. Closure plates and intramural buds not observed.

Kenozooids covering entire colony surface between autozooidal opesiae, usually two kenozooids per autozooid, triangular in outline with concave sides, funnel-like with large opesiae.

Avicularia not observed.

*Measurements* – Holotype: ZL 304±19, 270-330 (1, 10); ZW 179±13, 150-195 (1, 10); OpL 236±12, 225-255 (1, 10); OpW 117±17, 90-135 (1, 10).

*Remarks* – Only one specimen of this species is known, 33 by 25 mm in size, which originally encrusted a gastropod now represented by an external mould on the underside of the bryozoan. Although details of the colony surface are masked by diagenetic calcite cement, several features indicate that it is not conspecific with the closely similar *B. prismatica*. The autozooids of *B. sohli* are appreciably smaller, there appear to be two triangular kenozooids per autozooid rather than one trapezoidal kenozooid and, perhaps most significantly, an apertural bar may overarch the distal autozooidal opesia. This delicate structure is preserved intact in two zooids while broken bases of probable apertural bars are visible in some others. There is no indication of a comparable structure, either intact or broken, in *B. prismatica*, despite the superior quality of preservation of the Coon Creek species.

The age of the holotype of *B. sohli* is given only as Upper Cretaceous, but the appearance of the matrix suggests that it may well have come from the Maastrichtian Peedee Formation.
Suborder Neocheilostomina d’Hondt, 1985
Family Calloporidae Norman, 1903

Pseudoallantopora gen. nov.

Type species – Pseudoallantopora brunswickensis sp nov., Maastrichtian, North Carolina.

Other species – Herpetopora parvicauda Voigt, 1930, Upper Cretaceous, Westfalia, Germany.

Diagnosis – Colony encrusting, uniserial. Autozooids ovoidal to pyriform, gymnocyst well-developed proximally, opesia extensive, occupying most of frontal surface, spines lacking. Ovicells small, ectooecium fully calcified. Avicularia lacking.

Etymology – In reference to its similarity with Allantopora.

Remarks – Although superficially similar to Allantopora Lang, 1914, in having encrusting, uniserial colonies, Pseudoallantopora differs in lacking the articulated spine bases that encircle the opesiae in Allantopora. Other uniserial pseudomalacostegan genera, including Marssonopora Lang, 1914, Allantocallopora d’Hondt & Schopf, 1984, Cymulopora Winston & Hákansson, 1986, Daisylla Gordon, 1989b, Haspidopora Lang, 1917, Pyriporoides Hayward & Thorpe, 1989, and Unidistelopora Ostrovsky & Taylor, 2004, also have spines (see Rosso & Taylor, 2002). Mystriopora Lang, 1915, lacks spines, but has numerous avicularia, thereby differentiating it from Pseudoallantopora. The presence of ovicells distinguishes Pseudoallantopora from uniserial malacostegans such as Pyripora d’Orbigny, 1849, Pyriporopsis Pohowsky, 1973, Rhammatopora Lang, 1915, and Herpetopora Lang, 1914, all of which have been recorded in deposits of Cretaceous age.

A second species assigned to Pseudoallantopora is Herpetopora parvicauda Voigt, 1930, originally described from the Upper Cretaceous of Germany. New material (VCSM 10503, 10504) of this species from the Campanian of Ifö, Sweden, reveals the presence of ovicells, thereby necessitating removal of Voigt’s species from Herpetopora.

Range – Campanian-Maastrichtian.

Pseudoallantopora brunswickensis sp nov.

Pl. 46.

Material – Holotype: USNM 526168, Maastrichtian, Peedee Formation, Mitchells Landing, Brunswick County, North Carolina (locality NC6). This material consists of a cluster of oysters, one of which is encrusted on the interior surface by zooids possibly derived from as many as three original colonies of P. brunswickensis; among these is the holotype colony, depicted in Pl. 46. Paratypes: USNM 528935, same details as holotype, a small fragment, mounted on a stub and gold-coated, comprising three complete autozooids, two with ovicells. USNM 528941, Maastrichtian, Peedee Formation, massive sand unit, Mitchells Landing, Brunswick County, North Carolina (locality NC6), several multizoooid fragments from a broken oyster shell.

Etymology – From the county containing the type locality.
Description – Colony encrusting, uniserial (Pl. 46, fig. 1a), locally pluriserial in areas of zooid crowding. Branches straight or gently curved; new branches originating as distolateral buds, oriented at 45-90° to parent branch, typically at about 60°; distolateral branches formed at a minority of budding sites, usually singly, seldom paired with one on each side of parent zooid; intersecting branches generally abut without overgrowth; secondary gradients of astogenetic change modest. Early astogenetic stages not identifiable.

Autozooids ovoidal or very slightly pyriform, on average 1.6-1.7 times longer than wide; cauda (proximal gymnocyst) short, remainder of gymnocyst narrow and subequal in width; spines lacking. Cryptocyst absent or very reduced; mural rim crenulated. Opesia extensive, ovoidal, averaging 1.8 times longer than wide, attaining maximum width usually somewhat distally of mid-length. Intramural buds present (Pl. 46, fig. 1c), forming a secondary, inner mural rim; closure plates not observed. Pore chambers not observed. Ovicells hyperstomial, small, broader than long (Pl. 46, fig. 1f), the ectooecium completely calcified; ovicellate zooids commonly budded distolaterally and marking ends of branches, the branch terminating with a large, crescent-shaped pore window probably belonging to a distal kenozooid, rarely budding a distal autozooid.

Kenozooids sometimes present in regions of crowding, smaller and more irregularly-shaped than autozooids.

Measurements – Holotype: ZL 600±39, 510-660 (1, 10); ZW 360±22, 320-390 (1, 10); OpL 450±22, 420-480 (1, 10); OpW 250±16, 230-270 (1, 10); OvL 120-140 (1. 5); OvW 200-230 (1, 5).

Remarks – This new species differs from Pseudoallantopora parvicauda (Voigt) principally in the character of the ovicells: whereas the ovicells of P. brunswickensis are appreciably broader than long, those of P. parvicauda are equidimensional. Furthermore, the great majority of ovicellate zooids in P. brunswickensis occur as distolateral branches consisting of the fertile autozooid only (Pl. 46, fig. 1d,e). This is not the case in P. parvicauda, in which ovicellate autozooids are not terminal, but are intercalated among infertile autozooids within long branches.

Unidistelopora krausae (Voigt & Schneemilch, 1986) from the Campanian of Germany is similar in colony form and autozooid shape to P. brunswickensis. However, the German species has about 20-25 small spine bases encircling the opesiae and the ovicells are represented by arcs of about 18-19 spine bases (Ostrovsky & Taylor, 2004).

Wilbertopora Cheetham, 1954

Type species – Wilbertopora mutabilis Cheetham, 1954, Albian-Cenomanian, Texas; by original designation.

Remarks – Pending a comprehensive re-evaluation of membraniporimorph calloporid genera, Wilbertopora is here applied for species showing the following combination of characteristics: spines lacking or oral only and never encircling the opesia; avicularia absent or vicarious/interzooidal, always greatly outnumbered by autozooids, one type only per colony, varying in size and shape, sometimes ‘cryptic’ and differing minimally
from autozooids, but in other cases well-differentiated and spatulate or acuminate; pore chambers present; cryptocyst ledge-like, not forming a distinct shelf proximally; ovicell hyperstomial, the ectooecium fully calcified. Cheetham *et al.* (2006) provide a revision of the type and other species from the mid-Cretaceous of Texas.

A broad range of Cretaceous membraniporimorphs can be accommodated within this definition of Wilbertopora, and there is clearly scope for future phylogenetic studies to unravel their relationships and create a more satisfactory taxonomy. Some of these species, such as *W. inuber* (Shaw, 1967), described below, have previously been placed in Alderina Norman, 1903, but this genus differs from most, if not all, Cretaceous membraniporimorphs in having ovicells with large uncalcified ectooecial windows.

**Range** – Albian-Maastrichtian? While the lower range of Wilbertopora is well established, it will remain unclear whether the genus ranges beyond the Cretaceous until generic concepts in the Calloporidae have been refined and the numerous post-Cretaceous species with similar morphologies have been revised.

*Wilbertopora inuber* (Shaw, 1967)

Pl. 47, fig. 1.

1967 *Alderina inuber* sp. nov.; Shaw, p. 1402, pl. 178, fig. 1.

**Material** – Holotype: LSUMG-I 8234, Campanian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2).

**Description** – Colony encrusting, multiserial, unilaminar. Pore chambers visible at stepped growing edge, each autozooid with one distal pore chamber and two pairs of small, slit-shaped, distolateral pore chambers. Ancestrula and early astogeny unknown.

Autozooids elliptical to rounded rhomboidal in frontal outline, about 1.5 times longer than wide. Gymnocyst narrow, slightly more extensive proximally; spines lacking. Cryptocyst minimally developed, present only as crenulations on the raised mural rim. Opesia occupying most of frontal surface, longitudinally elliptical. Ovicell hyperstomial, small (Pl. 47, fig. 1c), wider than long. Closure plates and intramural reparative buds not observed.

Avicularia not observed.

**Measurements** – Holotype: ZL 724±53, 640-800 (1, 10); ZW 480±34, 440-540 (1, 10); OL 188±18, 160-200 (1, 5); OW 104±9, 100-120(1, 5).

**Remarks** – The holotype is the only available specimen of this morphologically simple species. Although worn (Pl. 47, fig. 1a), it is nonetheless sufficiently different from other North American species of Wilbertopora to justify separate recognition.

*Wilbertopora ovicarinata* sp. nov.

Pl. 47, figs 2-4.

**Material** – Holotype: NHM BZ 5016(2a), Maastrichtian. Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2). Paratypes: NHM BZ
Etymology – Alluding to the carinate appearance of the ovicells.

Description – Colony encrusting, multiserial, unilaminar. Partly calcified zooids often visible at distal growing edges (Pl. 47, fig. 2). Pore chambers present distally and distolaterally, large, ovoidal. Ancestrula about 195 × 135 μm, rounded rhombic with a slight proximal cauda, opesia subcircular, about 90 μm in diameter; surrounded by 5-6 periancestrular zooids, only the distal zooid and sometimes a distolateral zooid budded directly from the ancestrula.

Autozooids rounded rhombic in outline shape, on average 1.4-1.5 times longer than wide, arranged quincuncially. Gymnocyst slight to moderate, broadest proximally, tapering distally; oral spine bases numbering two, moderately large and usually well-separated. Cryptocyst forming an inwardly sloping ledge, broad proximally, tapering and absent at distal end of zooid, finely pustulose, the inner pustules arranged in radial rows; boundary with surrounding gymnocyst indistinct. Opesia occupying majority of frontal surface, longitudinally elongate, pear-shaped, attaining maximum width at or slightly proximally of mid-length. Ovicell large, hyperstomial, rounded quadrate, covering most of proximal gymnocyst of next zooid in series and lapping onto cryptocyst, ectooecium completely calcified with a median carina (Pl. 47, fig. 3); spine bases indenting proximolateral corners of ooecium. Intramural reparative buds present. Closure plates not observed.

Avicularia (Pl. 47, fig. 4) uncommon, not present in all colonies, vicarious, located at row bifurcations and collisions, about same size as autozooids. Gymnocyst broad proximally, narrowing laterally before broadening again in distal half of zooid. Proximal cryptocyst forming an inward-sloping, pustulose crescent. Opesia elongate teardrop-shaped, proximally bulb-like, distally with a pincer-like rostrum tapering to a rounded end. Short, knob-like condyles present at transition from proximal to distal part of avicularium. Palate shallow. Intramurally budded avicularia present in some autozooids.

Measurements – ZL 383±32, 315-420 (1, 10); ZW 261±30, 210-300 (1, 10); OpL 224±24, 195-270 (1, 10); OpW 171±16, 150-195 (1, 10); OvL 122±9, 105-135 (1, 10); OvW 161±16, 120-180 (1, 10); AL 399±32, 315-420 (2, 5); AW 249±20, 225-270 (2, 5); AOL 264±43, 210-315 (2, 5); AOW 132±19, 105-150 (2, 5); ARL 153±36, 120-210 (2, 5); ARW 105±11, 90-120 (2, 5).

Remarks – This new species can be easily distinguished from W. inuber by the much broader cryptocyst and considerably smaller autozooids, and from W. inuber and W. livingstonensis sp. nov. by the larger oovicells that have a median carina and a subquadrate shape. Furthermore, spines and avicularia are unknown in W. inuber, the paired oral spine bases in W. oivicarinata are larger and typically more widely spaced than those
of *W. livingstonensis* sp. nov. (if present at all), and the pore chambers visible at colony growing edges are larger in *W. ovicarinata* than the other two species. None of the eight Albian-Cenomanian species of *Wilbertopora* from Texas and Oklahoma described by Cheetham *et al.* (2006) have such a consistent development of oral spine bases, and all differ in the shape of the avicularia from both *W. ovicarinata* and *W. livingstonensis*.

Making comparisons with the large number of European species of similar morphology is difficult due to the inadequate descriptions and illustrations available for these species. Avicularium and autozooid shape resemble *Callopora acuminella* Berthelsen, 1962, although this Danian species has spines encircling the opesia and may actually belong to *Flustrellaria*. The British Maastrichtian species described by Brydone (1929) as *Membranipora gimensis* shows a strong similarity in autozooid morphology, but the avicularia are not associated with row bifurcations and have a short, rounded distal end.

A peculiar enlarged zooid (Pl. 47, figure 3) is worthy of comment. With an elongated opesia and underdeveloped ovicell, this zooid resembles the cryptic avicularia described from some mid-Cretaceous species of *Wilbertopora* by Cheetham *et al.* (2006). However, unequivocal avicularia of a different morphology occur in *W. ovicarinata* and it seems more likely that the aberrant zooid is a Doppelgänger zooid resulting from the fusion of two autozooids in the same linear series.

**Wilbertopora livingstonensis** sp. nov.

*Pl. 48.*

*Material* – Holotype: NHM BZ 4437(1), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). Paratypes: NHM BZ 4796(14), BZ 5026, BZ 5168(1), BZ 5227, NNM RGM 507 004, details as for holotype.

*Etymology* – From the type locality, Livingston in Alabama.

*Description* – Colony encrusting, multiserial, unilaminar or multilaminar, new layers originating by eruptive budding from intramural reparative zooids. Partly calcified zooids often visible at distal growing edges (Pl. 48, fig. 2d). Pore chambers present, including a large distal pore chamber. Ancestrula (Pl. 48, fig. 2c) about 180 μm in diameter, rounded rhombic, normally surrounded by six periancestrular zooids, the distal and two distolateral zooids probably budded directly from the ancestrula; spine bases variable in number and distribution, sometimes located proximally.

Autozooids rounded rhombic in outline shape, about 1.6 times longer than wide, arranged quincuncially. Gymnocyst slight to moderate, broadest proximally; oral spine bases numbering two, occasionally four, rarely three, or lacking altogether. Cryptocyst forming an inwardly sloping ledge, tapering and absent at distal end of zooid, pustulose, the pustules arranged in radial rows; boundary with surrounding gymnocyst poorly-defined. Opesia occupying majority of frontal surface, longitudinally elliptical, attaining maximum width at or slightly proximally of mid-length. Ovicell small (Pl. 48, fig. 1), hyperstomial, covering most of proximal gymnocyst of next zooid in series, ectoecium completely calcified with a narrow median fissure or suture. Intramural reparative buds common, some raised and forming nucleus of eruptive zooidal budding zooids onto colony surface. Closure plates not observed.
Avicularia uncommon, often wanting, but when present usually in multiples (Pl. 48, fig. 2d), vicarious, located at row bifurcations as close as three generations from ancestrula, almost the same size as autozooids, but a little longer and narrower, subhexagonal in outline shape. Gymnocyst broad proximally and laterally, narrow distally. Cryptocyst proximally pustulose and forming an inward-sloping crescent, laterally wanting, distally forming a short, steeply inwardly-sloping, non-pustulose palate. Opesia elongate teardrop-shaped (Pl. 48, fig. 2e), proximally bulb-like, distally a pincer-shaped rostrum tapering to a rounded end with a short, depressed palate. Short condyles present at transition from proximal to distal part of avicularium. Distal end of avicularium may indent succeeding zooid in series.

Kenozooids uncommon, occasionally present between autozooids and at collisions of colony lobes.

**Measurements** – ZL 512±46, 450-585 (1, 10); ZW 410±39, 345-465 (1, 10); OpL 351±27, 315-390 (1, 10); OpW 230±25, 195-285 (1, 10); OvL 138±16, 120-165 (1, 5); OvW 165±11, 150-165 (1, 5); AL 510±15, 495-525 (1, 5); AW 321±17, 300-345 (1, 5); AOL 363±33, 330-405 (1, 5); AOW 135±15, 120-150 (1, 5); ARL 261±20, 225–270 (1, 5); ARW 117±20, 105-150 (1, 5).

**Remarks** – This species is among the commonest encrusters of mollusc shells in the Maastrichtian of Alabama. It can be easily distinguished from *W. inuber* (Shaw) by the much broader cryptocyst and larger ovicells. Differences from *W. ovicarinata* sp. nov. are noted above. The avicularia are very similar in *W. livingstonensis* and *W. ovicarinata*, suggesting that the two new species are closely related. Among the Texan Albian-Cenomanian species of *Wilbertopora* described by Cheetham *et al.* (2006), the avicularia of these two species most closely resemble in shape those of *W. improcera* Cheetham *et al.*, 2006, but this Texan species lacks the condyles found in the two younger species.

The number of oral spines varies within colonies from one to four. Pore chambers are present in *W. livingstonensis*, but are relatively inconspicuous, even in partially formed zooids at the growing edge, and it is possible that only a distal pore chamber is present, best observed as a wide pore window in slightly more mature zooids.

**Wilbertopora hayesi** sp. nov.

**Pl. 49.**

**Material** – Holotype: NHM BZ 5032, Maastrichtian, Prairie Bluff Chalk, Jefferson, Marengo County, Alabama (locality AL5).

**Etymology** – Named for Nick Hayes of the NHM’s Photographic Unit in gratitude for digitising innumerable photographic SEM negatives used in this work.

**Description** – Colony encrusting multiserial, subcircular, the holotype 6 mm in diameter. Distal pore chamber large, semielliptical (Pl. 49, fig. 1c); distolateral pore chambers absent or very small. Ancestrula 250 × 220 μm, rounded rhombic, normally surrounded by five periancestrular zooids (Pl. 49, fig. 1d), the distal and two distolateral zooids probably budded directly from the ancestrula; spine bases lacking.
Autozooids rounded rhombic in outline shape, about 1.6 times longer than wide, arranged approximately in quincunx. Gymnocyst slight to moderate, broadest proximally, present in zooids from early astogeny, but often not preserved in zooids from zone of astogenetic repetition; oral spine bases numbering four, occasionally two in early astogeny. Cryptocyst forming an inwardly sloping ledge, broadest proximally, pustulose, the pustules arranged in radial rows; mural rim raised. Ovicell occupying majority of frontal surface, longitudinally elliptical. Ovicell hyperstomial, covering most of proximal gymnocyst of succeeding zooid and indenting the mural rim, ectoecium completely calcified with a median suture (Pl. 49, fig. 1e), proximolateral edges with embayments for outer pair of oral spines. Intramural buds and closure plates not observed.

Avicularia (Pl. 49, fig. 1f) abundant, vicarious, located at many (but not all) row bifurcations, variable in size, proportionally narrower than autozooids. Gymnocyst narrow proximally and distally, broad laterally opposite point of maximum constriction of aperture. Cryptocyst proximally narrow, pustulose and forming an inward-sloping crescent, laterally wanting, distally forming a deep palate, about half rostral length and non-pustulose. Ovicell elongate hourglass-shaped, spatulate with a rounded end somewhat depressed. Condyles not visible.

Kenozooids not observed.

Measurements – ZL 549±49, 495-645 (1, 10); ZW 333±30, 285-375 (1, 10); OvL 133±11, 120-150 (1, 6); OvW 183±6, 180-195 (1, 6); AL 567±89, 390-675 (1, 10); AW 224±22, 195-255 (1, 10); AOL 516±47, 420-585 (1, 8); AOW 93±7, 90-105 (1, 5); RL 420±83, 345--510 (1, 7); RW 148±18, 120-165 (1, 9).

Remarks – Although represented by only one mature colony, this species is distinct from the two other species of Wilbertopora described here and also cannot be matched exactly with any European species. The spatulate avicularia of W. hayesi are very different from those of W. livingstonensis sp. nov. and W.ovicarinata sp. nov., which have uniformly tapering rostra. Cheetham et al. (2006) found that avicularium morphology was a powerful means of discriminating between otherwise closely similar species of Wilbertopora in the Washita Group (Albian-Cenomanian) of Texas. Therefore, avicularium morphology alone probably justifies the introduction of W. hayesi. This is supported by the fairly constant occurrence of two pairs of oral spine bases, a feature not seen in the other Campanian-Maastrichtian species described herein, nor for that matter in any of the eight species of Wilbertopora in the Washita Group.

Most of the autozooids in the zone of astogenetic repetition show poor preservation of the proximal gymnocyst, the mural rim often having a ragged appearance. At least two explanations are possible; damage by predators or dissolution in zooids from the zone of astogenetic change of gymnocystal calcification differing slightly in composition (e.g., higher Mg content) from the remainder of the skeleton.

Flustrellaria d’Orbigny, 1853

Type species – Flustrellaria fragilis d’Orbigny, 1853, Cenomanian. Le Mans, France; by subsequent designation (Bassler, 1935).
Remarks – This little-used genus was revived by Gordon & Taylor (1999), who tentatively placed into it a new late Paleocene/early Eocene species - *Flustrellaria australis* - from the Chatham Islands, New Zealand. Canu (1900) described the type species of *Flustrellaria* as having 8-10 spine bases and SEM study of the type specimen (MNHN R61603) confirms the circumopesial distribution of spines in this species. Therefore, the genus *Flustrellaria* is used here for *Wilbertopora*-like species which differ from *Wilbertopora* in having spine bases encircling the opesia, not merely in oral locations. As with so many other membraniporimorph calloporids, the generic concept of *Flustrellaria* requires revision entailing comprehensive monographic research beyond the scope of the current faunal study.

Range – Cenomanian-Eocene? For the same reasons given above for *Wilbertopora*, the younger range limit of this genus is uncertain.

*Flustrellaria anatina* (Canu & Bassler, 1926)  
Pls. 50-51.

1926  
*Callopora anatina* sp. nov.; Canu & Bassler, p. 33, pl. 4, figs. 12-14.

1926  
*Membraniporina crassimargo* sp. nov.; Canu & Bassler, p. 33, pl. 4, fig. 15.

1967  
*Dionella vivistratensis* sp. nov.; Shaw, p. 1408, pl. 179, fig. 1.

In press *Flustrellaria anatina* (Canu & Bassler); McKinney & Taylor, fig. 1D.

Material – Lectotype (chosen here): USNM 69956, colony figured by Canu & Bassler (1926, pl. 4, fig. 12), Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TN1). Paralectotype: USNM 528397, details as for lectotype. Other material: USNM 69972, holotype of *Membraniporina crassimargo* Canu & Bassler, 1926; details as for lectotype. LSUMG-I 8239, holotype of *Dionella vivistratensis* Shaw, 1967 (pl. 179, fig. 1), Campanian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2). VCSM 13956, Maastrichtian, Navesink Formation, Poricy Brook, Monmouth County, New Jersey (locality NJ1; E. Voigt Collection). RU 5515, 5606, 5613, 5628, 5639, Maastrichtian, Navesink Formation, Poricy Brook or Big Brook, New Jersey (locality NJ1 and/or NJ2; R.J. Turner Collection). NHM BZ 5027, Maastrichtian, Coon Creek Member, shelly lenticles in upper part (Corbula bed auctt.), upstream of Coon Creek Field Station, McNairy County, Tennessee (locality TN1; S. Tracey Collection). NNM RGM 507 005, Maastrichtian. Ripley Formation, Coon Creek Member, grey silty fine clays in stream-bed, *Inoceramus* bed auctt., Coon Creek Field Station, McNairy County, Tennessee (locality TN1; S. Tracey Collection). Questionably assigned: VCSM 13960, Campanian, Demopolis Chalk, Macon, Noxubee County, Mississippi (locality MS2).

Description – Colony encrusting, multiserial, unilaminar or multilaminar, often large; autozooids arranged more-or-less quincuncially. Pore chambers absent (Pl. 51, fig. 2) or small and inconspicuous. Ancestrula ovoidal; gymnocyst moderately developed proximally; spine bases estimated to number 8-10, distributed all around opesia; cryptocyst narrow, finely pustulose, steeply sloping; mural rim turned outwards slightly; a distal and two distolateral zooids seemingly budded from ancestrula.

Autozooids rounded rhombic in outline shape, on average 1.5-1.6 times longer than wide, a high proportion of those in zone of astogenetic repetition ovicellate. Gymnocyst
moderately broad proximally, but normally obscured by ovicell of preceding zooid in series or by kenozooids, narrowing laterally; spine bases with an inner concentric ring, indenting the cryptocyst, typically four pairs, the proximolateral pair distant from three closely-spaced distolateral pairs which decrease in diameter distally, some zooids having only two distolateral pairs. Cryptocyst moderately broad, roughly constant in width around perimeter of opesia, inwardly-sloping, finely pustulose, outer pustules evenly spaced, inner pustules aligned in radial rows (Pl. 50, fig. 1c). Mural rim raised. Opesia oval, attaining maximum width proximally of mid-length. Ovicells (Pl. 51, fig. 3c) hyperstomial, variable in length:width proportions, ectooecium fully calcified, often indenting the proximal margin of the succeeding zooid in series. Closure plates and intramural buds not observed.

Avicularia of two types, neither present in all colonies. Vicarious/interzooidal avicularia (Pl. 50, fig. 2b, Pl. 51, fig. 3b) sometimes located at row divisions, about the same length or slightly shorter than autozooids, variously shaped, parallel-sided to slightly spatulate, rounded distally; proximal gymnocyst well-developed; proximal cryptocyst pustulose, separated from non-pustulose distal cryptocyst by a pair of condyles, distal cryptocyst forming an elongate rostrum; palate short or of moderate length. Adventitious avicularia (Pl. 51, fig. 3c) small, variously oriented, often facing obliquely proximally; condyles present; rostrum spatulate, inclined relative to colony surface; budded from pores on proximal gymnocyst of autozooids (Pl. 51, fig. 3d).

Kenozooids may overgrow autozooidal gymnocyst, irregular in shape, often poorly-calcified, open and without cryptocystal or gymnocystal walls, sometimes raised.

**Measurements** – Lectotype and paralectotype: ZL 490±39, 440-560 (1, 10); ZW 318±32, 260-360 (1, 10); OpL 296±42, 260-380 (1, 10); OpW 200±13, 180-220 (1, 10); OvL 116±13, 100-140 (1, 10); OvW 170±22, 140-200 (1, 10); AL 114±17, 90-140 (1, 10) (adventitious); AW 88±11, 80-110 (1, 10) (adventitious); RL 65±11, 50-80 (1, 10) (adventitious); RW 44±15, 20-60 (1, 10) (adventitious); AL 150±22, 120-200 (2, 10) (interzooidal); AW 100±20, 70-120 (2, 10) (interzooidal)

Holotype of *Membraniporina crassimargo*: ZL 500±49, 440-600 (1, 10); ZW 350±31, 310-410 (1, 8); OpL 330±31, 280-360 (1, 8); OpW 200±13, 170-220 (1, 8); OvL 160±18, 150-190 (1, 8); OvW 140±9, 130-150 (1, 8); AL 150±22, 130-190 (1, 8); AW 100±20, 70-120 (1, 8).

**Remarks** – Canu & Bassler (1926) described two nominal species, *Callopora anatina* and *Membraniporina crassimargo*, which are here synonymised. Both appear on the same page of their publication. Although *M. crassimargo* is the first of the two to be described, the type and only specimen is worn, infertile and lacks avicularia. Therefore, strict application of page priority is not followed and *C. anatina* is accepted as the senior synonym. Article 69A.10 of the International Code of Zoological Nomenclature (1999) states that ‘All other things being equal, preference should be given to the nominal species cited first in the work, page or line’. In this instance, however, the type material of the two nominal species cannot be regarded as equal.
Shaw’s (1967) material of *Dionella vivistratensis* is poorly preserved (Pl. 51, fig. 1), but several features demonstrate that this species is a junior synonym of Canu & Bassler’s (1926) species *Callopora anatina*. Morphometrically, the two species overlap, the vicarious avicularia are identical and SEM examination of Shaw’s holotype reveals the typical presence of the four pairs of spine bases which are more clearly seen in the better preserved Coon Creek material. It is likely that the gymnocystal pores mentioned by Shaw represent budding sites of adventitious avicularia and/or kenozooids, like those preserved intact in colonies from Coon Creek. This species is assigned to *Flustrellaria* with some reservation; adventitious kenozooids and even avicularia are well-developed in some parts of colonies, prompting comparison with both *Pyriporella* and *Akatopora* (see below). Vicarious/interzooidal avicularia occur sporadically, but, where present, may show considerable variation, particularly between colonies. They vary in overall size, the shape of the rostrum and the depth of the palate. These differences may eventually be shown to have significance at the species level if further material becomes available and a more detailed study of variance is undertaken.

**Flustrellaria braggsensis** sp. nov.

Pl. 52.

*Material* – Holotype: NHM BZ 4837(1a), Maastrichtian, Prairie Bluff Chalk, Braggs, Lowndes County, Alabama (locality AL3). Paratypes: NHM BZ 4837(1b), BZ 5025, same details as for holotype. BZ 5033 (3 small colonies), Prairie Bluff Chalk, Braggs, Lowndes County, Alabama (locality AL4).

*Etymology* – From the type locality at Braggs in Alabama.

*Description* – Colony encrusting, multiserial, unilaminar, irregularly lobate, autozooids arranged more-or-less quincuncially. Ancestrula known only from a worn example about 200 μm in length; zooids in zone of primary astogenetic change preserved in all three available colonies, exhibiting progressive size increase.

Autozooids rounded rhomboidal in frontal outline (Pl. 52, fig. 1b), broad, on average 1.4 times longer than wide. Gymnocyst broad proximally, moderately wide laterally, tapering distally; spine bases encircling and often indenting opesia (Pl. 52, fig. 1c), usually numbering 11, a single proximal spine base and five paired bases, varying in size, generally the second or third most distal pair being the largest. Cryptocyst narrow to moderately wide, roughly constant in width around perimeter of opesia, inwardly-sloping, pustulose. Mural rim raised. Opesia oval, attaining maximum width proximally of mid-length. Ovicells (Pl. 52, fig. 1c) abundant, hyperstomial, approximately equidimensional, ectooecium fully calcified, a slight median ridge present, occasionally indenting the proximal margin of the succeeding zooid in series. Intramural reparative budding present. Closure plates not observed.

Avicularia of two types, vicarious and adventitious. Vicarious avicularia located at row divisions, the two examples seen probably budded intramurally, one within an autozooid (Pl. 52, fig. 1d), the other within a pre-existing avicularium (Pl. 52, fig. 1e); a
little shorter and distinctly narrower than an autozooid, proximal gymnocyst well-developed, cryptocyst pustulose proximally, rostrum parallel-sided to slightly spatulate, well-rounded. Apparent adventitious avicularia (Pl. 52, fig. 1f) located in grooves between autozooids, elongate, considerably smaller than other zooids, less than 200 μm long.

Measurements – ZL 587±44, 525-660 (1, 10); ZW 422±32, 375-465 (1, 10); OpL 306±26, 255-330 (1, 10); OpW 224±11, 210-240 (1, 10); OvL 167±15, 150-195 (1, 10); OvW 194±18, 165-225 (1, 10); Vicarious AL 600 (1, 1); AW 360 (1, 1); AoL 210 (1, 11); AoW 120 (1, 11); RL 150 (1, 1); RW 120 (1, 1).

Remarks – The most obvious difference between *Flustrellaria braggsensis* and *F. anatina* is the consistently greater number of spines (11 vs 8) in the former species. In addition, there is no indication of overgrowth by kenozooids in *F. braggsensis*.

Most available colonies of this robust species encrust cobbles from the basal Prairie Bluff Chalk. These cobbles were derived from the underlying Ripley Formation. Bryan (1992) has studied the palaeoecology of this horizon and interpreted it as a high energy rockground formed along a rocky shoreline, with the bryozoans showing a tendency to encrust cryptic surfaces.

*Flustrellaria siculifera* sp. nov.

Pl. 53.

*Material* – Holotype: RU 5510, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2). Paratype: RU 5400, same details as holotype.


*Description* – Colony encrusting, multiserial, unilaminar. Pore chambers absent or small and inconspicuous. Ancestrula and early astogeny unknown.

Autozooids rounded rhomboidal in outline shape (Pl. 53, fig. 1e, f), on average 1.4 times longer than wide. Gymnocyst moderately broad proximally, narrowing distally; spine bases numbering 10-12, arranged more or less equidistantly around mural rim, sometimes with a proximal gap. Cryptocyst moderately broad, tapering distally, absent at distalmost end of zooid, finely pustulose or smooth. Mural rim raised, flared outwards at distal end. Opesia oval, attaining maximum width proximally of mid-length. Ovicell (Pl. 53, fig. 1f) hyperstomial, wider than long, about 120 × 190 μm, covering proximal gymnocyst of distal zooid, all known examples broken. Closure plates not observed. Intramural buds present.

Avicularia (Pl. 53, fig. 1c) interzooidal or vicarious, normally comprising one of the two daughter zooids at row bifurcations, slightly shorter and considerably narrower than autozooids. Gymnocyst widest proximally and mediolaterally. Cryptocyst forming a proximal crescent. Proximal opesia small, semielliptical. A pair of short lateral condyles present. Rostrum elongate, accounting for two-thirds or more of opesial length, evenly tapering, distally pointed, generally slightly asymmetrical, bending gently to left or right. Palate short.
Measurements – ZL 460±47, 366-534 (2, 20); ZW 318±33, 253-405 (2, 20); OpL 272±27, 232-332 (2, 20); OpW 174±14, 153-204 (2, 20); AL 379±66, 280-492 (2, 15); AW 188±33, 131-242 (2, 15); AoL 226±32, 160-275 (2, 15); AoW 79±14, 60-110 (2, 15).

Remarks – Although only two colonies of this species were available, the numerous dagger-shaped avicularia are sufficiently different from those of any of the other membraniporimorph species encountered in this study to warrant naming it as a new species. Zooid size is smaller than in the congener described here, F. braggsensis, which has rare, rounded avicularia. Among the numerous species of ‘Membranipora’ illustrated by Brydone (1929) from the British Upper Cretaceous, avicularia of a similar shape are evident in ‘M.’ woodlandi Brydone, 1910c (pl. 8, fig. 16) and ‘M.’ alveolus Brydone, 1929 (pl. 10, fig. 18). However, the first of these species, recently assigned to Wilbertopora by Taylor (2002), has avicularia with fully calcified pivotal bars and the autozooids lack spines, and there is no indication from Brydone’s description or figure that ‘M.’ alveolus has spines either.

Pyriporella Canu, 1911

Type species – Pyriporella ameghinoi Canu, 1911, Danian, Argentina; by original designation.

Remarks – Although accepted in the Treatise on Invertebrate Paleontology (Bassler, 1953, p. G166), Pyriporella has been seldom used since Canu first proposed the genus in 1911. The type species comes from the Danian of Argentina from where Canu described two additional species. He also listed a further six species ranging from Cenomanian to Recent. As interpreted here, and pending a detailed revision of the type species, Pyriporella is used for Wilbertopora-like species budding numerous small adventitious avicularia. The synonymy of Pyriporella with Callopora as proposed by Canu & Bassler (1920, p. 147) is not accepted, most particularly because of the greater spinosity and incomplete ectoecial calcification characteristic seen in Callopora (e.g., Ryland & Hayward, 1977, p. 88).

A species from the British Chalk, Membranipora sagittaria Brydone, has been assigned questionably to Pyriporella (Taylor, 2002), and the genus may be more widespread both geographically and stratigraphically than previously appreciated.

Range – Cenomanian-Recent?

Pyriporella pedunculata (Shaw, 1967)

Pl. 54.

1967 Ramphonotus pedunculatus sp. nov.; Shaw, p. 1405, pl. 178, fig. 4.

Description – Colony encrusting, multiserial, unilaminar. Distal pore chamber large. Ancestrula teardrop-shaped, about 300 × 200 μm, proximal gymnocyst occupying almost half of length, pointed proximally, cryptocyst very narrow, opesia longitudinally elliptical, surrounded by spine bases probably numbering about 16, budding one distal and one (left) distolateral daughter zooids in only available example (holotype).

Autozooids elliptical to rhombic in outline shape, 1.1-1.5 times longer than wide. Gymnocyst moderate to long proximally, narrowing distally; spine bases encircling opesia number about 12-16, but are often obscured by avicularian overgrowths. Cryptocyst narrow, steeply sloping, pustulose, inner pustules aligned in radial rows. Mural rim raised, sharp. Oiges oval, widest proximally of mid-length, occupying approximately half of frontal surface. Ovicell hyperstomial, small, equidimensional, ectooeicum fully calcified, partly overgrown by adventitious avicularia (Pl. 54, fig. 3b). Intramural buds present in some zooids. Closure plates not observed.

Avicularia of two types. Vicarious avicularia parallel-sided, distally well-rounded, with a crescent-shaped palate of non-pustulose cryptocyst; cryptocyst lacking proximally; pivotal bar not observed. Adventitious avicularia columnar, increasing in numbers in later astogeny until occupying almost all colony surface apart from ovcials and opesiae, often four per autozooid overgrowing the proximal gymnocyst and surrounding the ovcials; opesia elliptical, usually elongated tangentially to supporting autozooid, sometimes proximolaterally oriented; complete pivotal bar present in at least some avicularia, positioned slightly more than a third the way along opesia.

Measurements – Holotype (*taken from Shaw, 1967): ZL 380±14, 360-400 (1, 5); ZW 336±26, 300-360 (1, 5); OpL 252±36, 220-300 (1, 5); OpW 204±17, 180-220 (1, 5); OvL 150±4, 140-170 (? , 8)*; OvW 150±10, 140-200 (? , 8)*; AL 260±63, 200-360 (1, 5) (vicarious); AW 136±9, 120-140 (1, 5) (vicarious); AL 106±23, 80-140 (1, 10) (adventitious); AW (adv) 100±16, 80-120 (1, 10) (adventitious).

Remarks – This species is tentatively assigned to Pyriporella on account of the adventitious avicularia. However, it shows some features that raise a question mark over its assignment, notably the presence of vicarious avicularia and of spines encircling the entire circumference of the opesia, neither being characters recorded for the type species of Pyriporella. Another similar genus with columnar adventitious avicularia is Berthelsenia Voigt, 1989a, but this has distinctive pointed ovcials with a median slit.

Shaw (1967) originally assigned this species to Ramphonotus Norman, type species Membranipora minax Busk. However, Ramphonotus is now normally synonymised with Amphiblestrum and the type species, redescribed by Ryland & Hayward (1977, p. 106), is quite unlike Shaw’s species in having a shelf-like cryptocyst and an ovcell with a granular, cryptocystal surface.

Pyriporella lacucarinatensis sp. nov.
Pls. 55, 56.

Material – Holotype: NHM BZ 4810(1), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). Paratypes: NHM BZ 4796(11), BZ 5170-1, NNM RGM 507 030(3), 507 050, details as for holotype.
Etymology – After the type locality, adjacent to Lake (L., lacu) Ridge (L., carinatus) Apartments, Livingston, Alabama.

Description – Colony encrusting, multiserial, unilaminar, autozooids arranged more-or-less in quincunx (Pl. 55, fig. 1a), their gymnocysts overgrown by adventitious avicularia in zone of astogenetic repetition. Distal pore chamber large (Pl. 55, fig. 1e). Ancestrula and earliest astogeny unknown; zooids from zone of astogenetic change small, overgrown (Pl. 56, fig. 1b).

Autozooids elongate rhomboidal in outline shape (Pl. 55, fig. 1b), about 1.6-1.7 times longer than wide. Gymnocyst well-developed proximally, narrowing laterally and absent distally, often obscured by avicularia in later astogeny; spine bases lacking or oral only, small and numbering two to four. Cryptocyst narrow, diminishing in width distally, inwardly sloping, pustulose, inner pustules arranged in radial rows. Mural rim raised, sharp. Opesia oval, widest proximally of mid-length, occupying approximately half of frontal surface area. Ovicells (Pl. 55, fig. 1d, Pl. 56, fig. 1d) hyperstomial, small, approximately equidimensional, sometimes with a median fissure, the ectooecium fully calcified except for a narrow proximal crescent above the opening that exposes entoocium. Closure plates and intramural buds not observed.

Avicularia adventitious, oriented distolaterally or proximolaterally, raised, occurring sporadically in early astogeny, ubiquitous in late astogeny, partially or completely overgrowing autozooidal gymnocysts, often one per autozooid when succeeding a non-ovicellate autozooid or two per autozooid if succeeding an ovicellate zooid and positioned distolaterally on either side of ovicell (Pl. 56, fig. 1d), budded from pores in proximal gymnocyst of autozooid (Pl. 56, fig. 1c). Gymnocyst variable, typically well-developed proximally. Cryptocyst forming a pustulose crescent proximally. Pivotal bar may be completely calcified. Rostrum rounded, parallel-sided or slightly spatulate. Many avicularia incompletely formed and kenozooid-like (Pl. 55, fig. 1d).

Measurements – ZL 524±32, 458-582 (2, 20); ZW 319±49, 242-431 (2, 20); OpL 304±27, 268-359 (2, 20); OpW 187±41, 123-260 (2, 20); OvL 156±16, 130-187 (2, 20); OvW 173±9, 160-193 (2, 20); AL 204±33, 148-264 (2, 20); AW 115±17, 84-151 (2, 20).

Remarks – In early astogeny (Pl. 55, fig. 1b) this new species resembles the co-occurring Wilbertopora livingstonensis sp. nov., but the adventitious avicularia which become increasingly common in later astogeny enable the two species to be distinguished. The avicularia of P. pedunculata are generally more prominent than those of P. lacucarinatensis and the presence of spines bases all around the opesia in P. pedunculata is another important feature enabling the two congeneric species to be distinguished.

Biaviculigera Voigt, 1989b

Type species – Membranipora praecipua Brydone, 1914, Maastrichtian, Norfolk, England; by original designation.

Remarks – Voigt (1989b) assigned nine species of Upper Cretaceous membraniporimorph calloporids to Biaviculigera, stressing the existence of two types of avicularia, large spatulate and small globose.
Range – Cenomanian-Maastrichtian.

*Biaviculigera voigti* sp. nov.

Pl. 57.

**Material** – Holotype: VCSM 13958 (Voigt Photocard 5922(a)), Campanian, Demopolis Chalk, Macon, Noxubee County, Mississippi (locality MS2). Paratype: VCSM 13959 (Voigt Photocard 5922(b)), encrusting same shell as holotype.

**Etymology** – In honour of Professor Ehrhard Voigt (1905-2004), doyen of Cretaceous bryozoology, author of *Biaviculigera* and collector of the type material of this new species.

**Description** – Colony encrusting, multiserial, unilaminar. Pore chambers present, distal pore chamber with a broad window, lateral/distolateral pore chambers numbering up to four pairs with smaller windows (Pl. 57, fig. 1f). Ancestrula present in paratype, obscured by sediment grains, about 300 × 200 μm, proximal gymnocyst moderately long, surrounded by five periancestral zooids, no zooid immediately proximal of ancestrula.

Autozooids large, elongate, pyriform in outline shape, on average almost twice as long as wide. Gymnocyst long proximally, narrowing distally, sometimes with a pore just below opesia; spine bases numbering 12-14, distributed evenly around opesia, slightly indenting mural rim. Cryptocyst steeply sloping, pustulose, of moderate width proximally, tapering and disappearing distally. Opesia elongate elliptical, attaining maximum width about mid-length. Ovicell (Pl. 57, fig. 1c) hyperstomial, ectooecium fully calcified, proximal edge concave. Intramural buds present (Pl. 57, fig. 1e), possessing spine bases. Closure plates not observed.

Avicularia dimorphic. Interzooidal avicularia (Pl. 57, fig. 1d) associated with row divisions, a little smaller than autozooids; gymnocyst broad proximally and laterally, overlapped distally by rostrum; opesia hourglass-shaped, a complete pivotal bar located just proximally of the narrow neck; proximal cryptocyst pustulose, steeply sloping; rostrum spatulate, well-rounded. Adventitious avicularia (Pl. 57, fig. 1b) columnar, prominent, frontally expanded, variable in size, often less than 100 μm in frontal length; located near distolateral corners of fertile autozooids flanking proximolateral edges of ovicells, seldom fully formed or completely preserved, when intact directed laterally and inwards, a complete pivotal bar subdividing the elliptical opesia.

Kenozooids sometimes overgrowing autozooidal gymnocysts, opesia wide.

**Measurements** – ZL 714±77, 615-855 (1, 10); ZW 366±24, 330-405 (1, 10); OpL 329±30, 285-405 (1, 10); OpW 191±12, 180-210 (1, 10); OvL 186±16, 165-225 (1, 10); OvW 198±21, 165-240 (1, 10); AL 645-900 (1, 3); AW 360-390 (1, 3); AoL 405-465 (1, 3); AoW 105-120 (1, 3); RL 315-360 (1, 3); RW 135-150 (1, 3).

**Remarks** – It is with some reservation that we refer this species to *Biaviculigera* in view of the paired small avicularia which have no close equivalents among other species in the genus. These avicularia appear only to be associated with fertile autozooids
where they are located at the two proximolateral corners of the ovicells.

Of the North American Cretaceous species described here, *B. voigti* shares with *Pyriporella pedunculata* (Shaw, 1967) and *Flustrellaria braggsensis* sp. nov. autozooids that have spines around the entire circumference of the opesia and vicarious avicularia with rounded rostra. However, *B. voigti* can be distinguished by the pyriform shape of the autozooids, elongate proximal gymnocyst and the paired columnar avicularia associated with the ovicells.

*Akatopora* Davis, 1934

_Type species_ – *Akatopora clausentina* Davis, 1934, Eocene, Hampshire, England; by original designation.

*Remarks* – This calloporid genus was revised by Gordon (1986), who added three Recent species to the Eocene type species. An additional Late Paleocene/Early Eocene species (*A. chathamica*) was subsequently described by Gordon & Taylor (1999). The key features of *Akatopora* are the encrusting, often multilaminar colony-form, autozooids with large opesia, somewhat immersed ovicells, absence of spines, and the presence of small avicularia and kenozooids between the autozooids. Living species, including *A. circumsaepta* (Uttley, 1951) from New Zealand, often encrust gastropod shells occupied by hermit crabs (Taylor, 1994). However, this is not the case in the Maastrichtian species here referred to *Akatopora* which are usually found encrusting bivalve mollusc shells. A Santonian species, “*Membranipora*” _subwintonensis_ Voigt, 1967, was reassigned to *Akatopora* by Zágorsek & Kroh (2003).

_Password_ – Santonian-Recent.

*Akatopora sulcata* (Canu & Bassler, 1926)

_Pl. 58._

1926 _Callopora sulcata_ sp. nov.; Canu & Bassler, p. 34, pl. 5, fig. 5.
In press _Akatopora sulcata* (Canu & Bassler); McKinney & Taylor, fig. 1E.

*Material* – Holotype: USNM 69951, figured by Canu & Bassler (1926, pl. 5, fig. 5), Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TN1).

*Description* – Colony encrusting, multiserial, unilaminar, the autozooids arranged in quincunx (Pl. 58, fig. 1a) and surrounded by a variety of smaller avicularian and kenozooidal polymorphs. Pore chambers absent.

Autozooids longitudinally elongate, about 1.7 times longer than wide, elliptical or rounded rhomboidal. Opesia occupying most of frontal surface, elongate elliptical, usually somewhat more rounded proximally than distally. Proximal gymnocyst moderately developed, generally hidden by overgrowth of smaller polymorphs, exposed examples sometimes bearing a large pore (possibly budding sites of adventitious polymorphs). Cryptocyst narrow, diminishing in width distally, pustulose, inwardly sloping; mural
rim crenulated. Basal wall with pair of bean-shaped indentations (muscle scars?) visible in distal part of zooid (Pl. 58, fig. 1b). Ovicell (Pl. 58, fig. 1d) hyperstomial, but becoming immersed beneath small polymorphs, longer than wide, ectooecium fully calcified, a subdued median ridge present. Closure plates and intramural buds not observed.

Avicularia numbering about 2-4 per autozooid, variously oriented, some directed distally, some laterally and others proximally (Pl. 58, fig. 1e), shape variable. Gymnocyst well-developed at proximal and/or distal end. Rostrum crescent-shaped, rounded, formed of pustulose cryptocyst which fades and is lacking proximally.

Kenozooids abundant, variable in size and shape (Pl. 58, fig. 1b), the smallest as little as 30 μm in diameter and resembling autozooidal spine bases, the largest 150 μm in diameter. Peripheral gymnocyst generally enclosing area of pustulose cryptocyst. Opesia elliptical.

**Measurements** – Holotype: ZL 460±41, 400-540 (1, 10); ZW 276±21, 240-300 (1, 10); OpL 350±45, 280-420 (1, 10); OpW 194±21, 180-240 (1, 10); OvL 138±8, 120-150 (1, 10); OvW 146±8, 140-160 (1, 10); AL 105±11, 90-120 (1, 10); AW 62±10, 50-80 (1, 10); RW 27±5, 20-30 (1, 10).

**Remarks** – Small polymorphs are more numerous in *A. sulcata* than they are in previously described species of *Akatopora* (see Gordon, 1986). Although some of these polymorphs can be identified confidently as avicularia by the asymmetrical distribution of cryptocyst around the opesia, broadening distally to form the rostrum against which the mandible would have closed in life, others are more equivocal, especially when damaged. The kenozooids are more variable in size and often more irregularly shaped than the avicularia. Some of the kenozooids are very small and resemble autozooidal spine bases, an interpretation which, however, can be discounted because they are located beyond the boundaries of the autozooids.

**Craspedopora Canu & Bassler, 1929b**

**Type species** – *Craspedopora typica* Canu & Bassler, 1929b, Eocene, Belgium; by original designation.

**Remarks** – This genus is used herein very tentatively to accommodate two North American Maastrichtian species that resemble *Akatopora* in having small polymorphs surrounding the autozooids, but in which hyperstomial ovicells have yet to be discovered. Several reasons can be suggested for the apparent absence of ovicells in these two species. They may lack oovicells altogether and be non-brooding malacostegines rather than neocheilostomes. Alternatively, larvae may have been brooded in endoozooidal oovicells with no significant skeletal expression on the colony surface, as in the modern species *Antropora tinctoria* (Hastings, 1930), redescribed by Tilbrook (1998), or internally, as in three anascan cheilostomes described by Ostrovsky et al. (in press).

Unfortunately, the morphology and affinities of the type species of *Craspedopora* are not well understood and a restudy of the type material is called for. Gordon (1986, p. 35) discussed the status of *Craspedopora*, concluding that ‘.. the consistent absence of oovicells from the fossil material may have to continue to serve in distinguishing species of
Craspedopora from those of Akatopora. Davis (1934) was one of relatively few authors subsequently to have used the genus when describing a fauna of British Eocene bryozoans. It has not been recognized previously in the Cretaceous.

Range – Maastrichtian-Lutetian, Recent?

Craspedopora depressa sp. nov.
Pl. 59.


Etymology – From the sunken cryptocyst.

Description – Colony encrusting, multiserial, unilaminar, locally multilaminar, autozooids typically arranged in transverse rows (Pl. 59, fig. 1a). Pore chambers not observed. Ancestrula and early astogeny unknown.

Autozooids small, elliptical to pyriform in shape, about 1.6 times longer than wide. Gymnocyst variably developed, lacking in some zooids, occasionally quite extensive proximally (Pl. 59, fig. 1c). Spines lacking. Cryptocyst sunken (Pl. 59, fig. 2b), smooth or faintly pustulose, broad and shelf-like proximally, narrowing and more steeply dipping distally. Mural rim sharply-defined, forming a conspicuous elliptical border encircling cryptocyst, generally more raised distally. Opesia longitudinally elliptical. Ovicells not observed. Intramural buds comprising autozooids or avicularia. Closure plates lacking.

Avicularia numerous, interzooidal and/or adventitious, together with kenozooids covering much of colony surface between autozooidal opesiae (Pl. 59, fig. 1b), some columnar, others flush, variously oriented, one end (distal?) slightly more pointed and with a deeper cryptocyst than the other end (proximal?). Kenozooids smaller than avicularia, variably developed, the most complete having a pustulose cryptocyst surrounding the subcircular opesia.

Measurements – ZL 446±39, 390-525 (1, 10); ZW 284±24, 225-300 (1, 10); OpL 231±14, 210-255 (1, 10); OpW 188±19, 150-210 (1, 10); AL 174 (1, 5); AW 105 (1, 5).

Remarks – Craspedopora depressa differs from C. scalprata sp. nov. and other species of Craspedopora in showing a strong tendency for the autozooids to be aligned in transverse rows. It is readily distinguished from the co-occurring Pyriporella lacucarinatensis by the deeply sunken and shelf-like cryptocyst. Only two colonies are known of this new species, encrusting the exterior surface of the same heavily bioeroded oyster shell.

Craspedopora scalprata sp. nov.
Pl. 60.

Material – Holotype: NHM BZ 5024(2a), Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2). Paratypes: NHM BZ
Etymology – L., *scalpratus*, having a sharp edge, in reference to the sharp zooidal boundaries.

Description – Colony encrusting, multiserial, unilaminar, larger colonies developing giant buds extending for 3-4 zooid lengths beyond the distalmost complete zooids at the growing edge. Pore chambers lacking. Ancestrula simple, about 225 × 180 μm, surrounded by six periancestular zooids. Autozooids in primary zone of astogenetic change developing broad, outwardly flared cryptocysts (Pl. 60, fig. 1d).

Autozooids elongate rhomboidal or subrectangular, arranged in well defined rows most evident from basal outlines at growing edge, averaging 1.3-1.4 times longer than wide, boundaries sharply raised. Gymnocyst and spines lacking. Cryptocyst sunken, sloping steeply inwards, moderately broad proximally, tapering laterally and absent distally, pustulose, the pustules imparting strong crenulations to inner margin (Pl. 60, fig. 2d). Opesia longitudinally elliptical or ovoidal, occupying most of frontal surface. Ovicells unknown. Intramural buds and closure plates not observed.

Small polymorphs abundant along autozooidal boundaries (Pl. 60, fig. 1b), especially around triple junctions between three autozooids; irregularly arranged, variable in shape and size, some subcircular, others elongate.

Large polymorphs present in some colonies, vicarious, slightly broader than autozooids, the cryptocyst relatively reduced and the opesia large and subcircular.

Measurements – ZL 392±23, 360-435 (1, 10); ZW 287±32, 240-345 (1, 10); OpL 293±19, 270-330 (1, 10); OpW 201±13, 180-225 (1, 10).

Remarks – This new species is moderately common in the Peedee Formation around Wilmington, North Carolina, but has not been found elsewhere. It is readily distinguished by the sharp-edged zooidal boundaries along which tiny polymorphic zooids are aligned and by the lack of a gymnocyst. The fact that the small polymorphs are without obvious polarity, calcified pivotal bars or condyles, suggests that they are kenozooids rather than avicularia. More puzzling are larger polymorphs with almost circular opesiae that are sparsely present in many colonies. Given the apparent absence of ovicells in this species, it is possible that the large polymorphs are gonozooids in which larvae were brooded internally, but this idea is speculative and difficult to test.

*Craspedopora scalprata* differs from *C. depressa* sp. nov. in showing no tendency for the autozooids to be aligned in transverse rows and in lacking a shelf-like proximal cryptocyst. Neither *C. depressa* nor any of the three Eocene species of *Craspedopora* described by Davis (1934) exhibit the large polymorphs found in *C. scalprata*.

**Marginaria Römer, 1840**

Type species – *Cellepora elliptica* von Hagenow, 1839, Lower Maastrichtian, Rügen, Germany (neotype figured by Voigt, 1959, fig. 2); by monotypy.
Remarks – Revised by Voigt (1989b), *Marginaria* is a calloporid characterised by the presence of numerous small, interzooidal avicularia scattered among the autozooids. These avicularia are budded at the growing edge and are consequently unlike the adventitious avicularia of such genera as *Pyriporella* and *Akatopora* which develop later to overgrow autozooidal gymnocysts. Voigt (1989b) assigned ten species to *Marginaria*, all from the Upper Cretaceous of Europe, while Taylor (1988b, p. 53) mentioned the occurrence of an unnamed species from the Albian Red Chalk (Hunstanton Formation) of eastern England (although in this species the interzooidal polymorphs appear to be kenozooids rather than avicularia).

Range – Albian-Maastrichtian.

*Marginaria stipata* (Canu & Bassler, 1926)

Pl. 61.

1926  *Mystriopora? stipata* sp. nov.; Canu & Bassler, p. 35, pl. 4, fig. 18.
1967  *Dionella racemata* sp. nov.; Shaw, p. 1410, pl. 179, fig. 4.
In press  *Marginaria stipata* (Canu & Bassler); McKinney & Taylor, fig. 1F.

Material – Lectotype (selected here): USNM 69955, Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TE1). Paralectotype: USNM 528398, details as for lectotype. Other material: LSUMG-I 8240, holotype of *Dionella racemata* Shaw, 1967 (pl. 179, fig. 4), Campanian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2). NHM BZ 5040-1, NNM RGM 507 010, Maastrichtian. Coon Creek Formation, grey silty fine sands in stream bed. ‘*Inoceramus* bed’ auctt., Coon Creek Field Station, McNairy County, Tennessee (locality TE1; S. Tracey Collection). NHM BZ 4437(2), BZ 5173(1), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).

Description – Colony encrusting, multiserial, unilaminar, with autozooids among which are scattered interzooidal kenozooids, sometimes occurring singly, at other times in clusters. Pore chambers not observed. Ancestrula with oval opesia, surrounded by six periancestrular autozooids, the distal and two distolateral zooids seemingly budded directly from the ancestrula.

Autozooids small, pyriform, about 1.6-1.9 times longer than wide, arranged in longitudinal rows. Gymnocyst elongate proximally, accounting for up to almost half of the length of the zooid, tapering laterally and distally; a spine-like mucro sometimes developed at median proximal edge of opesia (Pl. 61, fig. 1b); no other spine bases present. Mural rim raised, crenulated. Cryptocyst moderately broad, diminishing slightly in width distally, but still present at distal end of zooid, surface smooth, non-pustulose. Opesia oval, attaining maximum width proximally of mid-length. Ovicell (Pl. 61, fig. 2b) hyperstomial, a little longer than wide, a median ridge sometimes developed, occupying most of the proximal gymnocyst of the next zooid in series and often indenting the opesial outline. Closure plates not observed. Intramural buds fairly frequent, consisting of autozooids, avicularia or kenozooids, the latter with a circular opesia.

Avicularia numerous, interzooidal (and intramural), often aligned in longitudinal bands between rows of autozooids (Pl. 61, fig. 1a), orientated distally or almost so,
small, roughly elliptical in outline shape, but very variable; gymnocyst usually well-developed proximally; cryptocyst forming a smooth, narrow crescent proximally; mural rim crenulated, at least proximally; opesia elliptical with a constriction at about mid-length, well-rounded proximally and distally.

**Measurements** – Lectotype: ZL 297±21, 260-320 (1, 10); ZW 188±11, 180-210 (1, 10); OpL 96±11, 80-110 (1, 10); OpW 86±8, 70-100 (1, 10); AL 96±21, 80-140 (1, 10); AW 66±16, 40-100 (1, 10).

**Remarks** – In their original description Canu & Bassler (1926) questionably referred this species to *Mystriopora* Lang, but noted that the small polymorphs (‘zooecules’ of Canu & Bassler, avicularia here) are rarer in *Mystriopora*. Re-study using SEM of the holotype (NHM D21670) of the type species of *Mystriopora*, *M. mockleri*, shows it has a uniserial to pluriserial branching colony form, with occasional small, acuminate avicularia budded distolaterally from the autozooids. This morphology contrasts with the multiserial, sheet-like colonies of *Marginaria stipata* with avicularia widely distributed.

The synonymy of *Dionella racemata* Shaw, 1967, with *M. stipata* is clear based on SEM study of the type material of both nominal species, although the zooids are a little larger in material from Arkansas. Shaw (1967) assigned his species to *Dionella* Medd, 1965 (see below), on the basis of having identified two types of avicularia, interzoooidal and adventitious, but the existence of the second type, which occur in association with ovicells according to Shaw (1967), could not be established during our restudy of the holotype. The 5-8 pairs of mural spines described in this species by Shaw are probably artefacts caused by sediment particles adhering to the colony surface.

*Marginaria guttata* sp. nov.

Pl. 62.

**Etymology** – L., *guttatus*, spotted, alluding to the scattered small avicularia that impart a spotted appearance to early astogenetic stages.

**Material** – Holotype: NHM BZ 5024(3), Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2). Paratypes: NHM BZ 4183(3), BZ 5023(2a, 2b), BZ 5174, NNM RGM 507 007 (several colonies on a shell), same details as for holotype.

**Description** – Colony encrusting, multiserial, unilaminar, delicate. Pore chambers comprising a large elliptical distal chamber and up to three smaller chambers along each distolateral vertical wall (Pl. 62, fig. 1c). Ancestrula longitudinally elliptical, gymnocyst and cryptocyst both narrow, frontal surface dominated by oval-shaped opesia; six mural spine bases, distolateral pair closer to distal pair than they are to proximolateral pair; budding three periancestrular autozooids, distal and two distolateral. Primary zone of astogenetic change containing autozooids and avicularia (Pl. 62, fig. 2c), autozooids close to ancestrula often with one or two pairs of oral spine bases.
Autozooids small and delicate, subrhomboidal in frontal outline, on average about 1.4-1.5 times longer than wide; zooidal boundaries grooved. Gymnocyst moderately broad proximally, tapering distally, occasionally developing a low node near proximal edge of opesia; pores often present on proximal gymnocyst; spines lacking. Cryptocyst narrow, sloping steeply inwards, fading distally, finely pustulose. Opesia oval, occupying most of frontal area. Ovicell (Pl. 62, fig. 1b) hyperstomial, large, globular, ectoecium fully calcified; ovicellate zooids typically surrounded and overlapped by avicularia. Basal wall fully calcified. Closure plates and intramural buds not observed.

Avicularia small, dimorphic. Interzooidal avicularia present from early astogenetic stages onwards, some located immediately distally of an autozooid, others laterally of autozooids, often clustered (Pl. 62, fig. 2b); directed distally. Adventitious avicularia mostly present in later astogenetic stages, variously overgrowing proximal and lateral gymnocysts of autozooids (Pl. 62, fig. 1b); typically directed distally, but some differently oriented. Avicularia small, roughly elliptical in outline shape; gymnocyst moderately developed, especially proximally; cryptocyst a narrow proximal crescent; proximal part of opesia shallower than rostrum, separated from it by a minor constriction; no condyles or calcified pivotal bar; rostrum well rounded.

Measurements – ZL 294±44, 255-375 (1, 10); ZW 203±13, 180-225 (1, 10); OpL 191±17, 165-225 (1, 10); OpW 128±11, 120-150 (1, 10); OvL 95±12, 75-105 (1, 6); OvW 133±11, 120-150 (1, 6).

Remarks – This delicate species of Marginaria differs from M. stipata in having a significantly shorter proximal gymnocyst and autozooids that are more rhomboidal than pyriform in outline shape. In addition, adventitious avicularia are more numerous in M. guttata, while intramural buds have not been observed in the new species.

Co-occurring with M. guttata in the Peedee Formation of the Wilmington region of North Carolina are two other new membraniporimorph species that are superficially similar, Wilbertopora livingstonensis and Marginaria wilsoni. The slightly larger zooids and absence of small avicularia enable the first of these two species to be discriminated, while M. wilsoni differs from its congener in having more robust and longer zooids with four or more large mural spine bases.

Marginaria wilsoni sp. nov.
Pl. 63.

Material – Holotype: BZ 4182(1), Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2). Paratypes: BZ 4174, BZ 4179(1), NNM RGM 507 051, details as for holotype.

Etymology – Named for Mark A. Wilson (Lewis M. and Marian Senter Nixon Professor of the Natural Sciences, College of Wooster, Ohio), together with whom the holotype was collected in 1989.

Description – Colony encrusting, multiserial, typically multilaminar, sometimes
with irregular arrangement of zooids in overgrowths. Pore chambers lacking. Ances-
trula and early astogeny unknown.

Autozooids small, pyriform to subrhomboidal in frontal outline, on average about
1.8-1.9 times longer than wide; zooidal boundaries grooved. Gymnocyst well-devel-
oped proximally, up to one-third of total zooid length, tapering distally; mural spine
bases usually numbering four, comprising proximolateral and mediolateral pairs, oc-
casionally with additional spine bases distally or medioproximally, large, indenting
mural rim. Cryptocyst moderately narrow, not shelf-like, tapering distally, pustulose.
Opesia longitudinally elliptical or oval. Basal wall fully calcified, often with a pair of
distolateral depressions (occlusor muscle scars?). Ovicell (Pl. 63, fig. 1e) hyperstomial,
large, globular, covering entire gymnocyst of distal zooid and indenting or overlapping
mural rim; ectooecium fully calcified, sometimes with a narrow fissure along median
suture. Closure plates and intramural buds not observed.

Avicularia interzooidal, present at row bifurcations and elsewhere, sometimes in
clusters or in discontinuous rows between autozooids (Pl. 63, fig. 1c), small, longitudi-
nally elliptical or pyriform in shape; proximal gymnocyst variably developed; crypto-
cyst a narrow proximal crescent, pustulose (Pl. 63, fig. 1f); opesia dumbbell-shaped,
proximal part of opesia shallower and broader than rostrum; no condyles or calcified
pivotal; rostrum well rounded, raised at hood-like distal end.

**Measurements** – ZL 369±44, 300-420 (1, 10); ZW 200±10, 180-210 (1, 10); OpL 185±7,
180-195 (1, 10); OpW 117±9, 105-135 (1, 10); OvL 128±13, 120-150 (1, 10); OvW 168±12,
150-180 (1, 10); AL 192±31, 135-225 (1, 10); AW 116±14, 90-135 (1, 10); AoL 65±8, 53-75 (1,
10); AoW 45±5, 38-53 (1, 10).

**Remarks** – Marginaria wilsoni can be immediately distinguished from the three other
species of Marginaria described herein by the presence of large mural spine bases in
zooids within zones of astogenetic repetition. Mural spine bases are present in the
French Cenomanian species M. sarthacensis Voigt, 1989b, but these are far more numer-
ous (about 16) and smaller than those of M. wilsoni, which normally has four spine
bases per zooid. The recently redescribed (Zágorsek & Kroh, 2003) species Marginaria
ostioluta Reuss, 1846, from the European Cenomanian-Santonian lacks mural spines and
has pointed avicularia.

This species is much less common than M. guttata sp. nov. in the Peedee Formation
of North Carolina. Some colonies are multilaminar and all are relatively large in size for
membraniporimorphs.

*Marginaria sp.*

Pl. 64, fig. 1.

*Material* – NHM BZ 4818, Maastrichtian, basal Prairie Bluff Chalk, Braggs, Lowndes
County, Alabama (locality AL3).

*Description* – Colony encrusting, multiserial, unilaminar, with interzooidal avicu-
laria scattered among the autozooids. Pore chambers not observed. Ancestralula and
early astogenetic stages not preserved.
Autozooids small, pyriform, or rounded rhomboidal, about 1.7 times longer than wide. Gymnocyst well-developed proximally (Pl. 64, fig. 1b); spines lacking. Cryptocyst moderately broad, pustulose, the pustules tending to be arranged in radial rows. Opesia elliptical. Ovicells hyperstomial, wider than long. Intramural buds consisting of kenozooids with elliptical opesia surrounded by a narrow, sloping cryptocyst.

Avicularia interzoooidal, orientated distally or almost so, longitudinally elongate, variable in outline shape; proximal gymnocyst long, sometimes more than half total avicularium length; cryptocyst moderately broad proximally; opesia longitudinally elliptical, rounded at both ends.

**Measurements** – ZL 405-480 (1, 4); ZW 225-285 (1, 4); OpL 150-195 (1, 4); OpW 120-135 (1, 14).

**Remarks** – The only specimen available of this species is an eroded colony encrusting a cyclostome (Pl. 64, fig. 1a), considered insufficient to justify creation of a new species. In general it resembles *M. guttata*, but has larger zooids, more obviously elliptical rather than oval opesiae and an apparently pustulose cryptocyst.

**Semiflustrella d’Orbigny, 1853**

*Type species* – *Semiflustrella rhomboidalis* d’Orbigny, 1853, ‘Senonian’, Fecamp, France; by subsequent designation.

**Remarks** – Gordon & Taylor (2005) revived this genus after studying material of the type species in the d’Orbigny Collection, MNHN. The frontal wall is poorly-developed and predominantly cryptocystal in *S. rhomboidalis*, spine bases are lacking and the distal avicularium is oriented transversely. The concept of the genus is enlarged somewhat here to include species with moderately developed cryptocysts and obliquely oriented avicularia.

*Semiflustrella* is one of several genera characterised by a distal avicularium which may be informally referred to as ‘ellisinids’. The genus *Ellisina* itself has an extant type species in which the distal avicularium is immersed in a kenozooid, a peculiarity not present in any of the Cretaceous species described here or elsewhere. Another extant genus, *Hincksina* Osburn, 1952, has spinose autozooids, whereas *Cranosina* Canu & Bassler, 1933, possesses maternal zooids with dimorphic orifices, and *Parelolisina* Osburn, 1940, is distinguished by having a kenozooid distal to each avicularium. In *Dionella* Medd, 1965, described below, the avicularium is orientated distally and the frontal shield reduced and predominantly gymnocystal. A new ellisinid genus, *Kristerina*, also described below, has a cryptocystal frontal shield and distally oriented avicularia. Medd (1979) assigned several Cretaceous ‘ellisinids’ to *Peripropopsella* Canu & Bassler, 1917, but the Eocene type species of this genus shows only sporadic development of avicularia.

**Range** – Coniacian-Danian.
Semiflustrella saratogaensis (Shaw, 1967)
Pl. 64, figs. 2, 3.

1967 Ellisia saratogaensis sp. nov.; Shaw, p. 1401, pl. 180, fig. 1.

Material – Holotype: LSUMG-I 8233, figured by Shaw (1967, pl. 180, fig. 1), Campa-
nian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2). Paratype:LSUMG-I 8258, details as for holotype.

Description – Colony encrusting, multiserial, unilaminar, autozooids arranged in quincunx (Pl. 64, fig. 2a), a small interzooidal avicularium positioned distally of each non-ovicellate autozooid. Pore chambers small, irregularly placed along distal and

Autozooids rhomboidal, the proximolateral sides typically longer and more con-
cave than the distolateral sides, broad, on average less than 1.1 times longer than wide. Gymnocyst lacking. No spines. Cryptocyst broad proximally, forming an inclined shelf, diminishing in width and absent in the distal half of the zooid, coarsely pustulose, the inner pustules tending to become aligned in radial rows. Opesia usually broader than
long, the proximal edge convexly curved, with distal and distolateral edges almost
straight. Ovicell (Pl. 64, figs. 2b, 3) hyperstomial, broader than long, ectooecium seem-
ingly fully calcified. Intramural buds and closure plates not observed.

Avicularia (Pl. 64, fig. 2c) interzooidal, located distally of every non-ovicellate auto-
zooid, small, oriented distolaterally, with neighbouring avicularia all usually facing
either left or right, proximally rounded, distally pointed and slightly raised, the ros-
strum forming a long, narrow channel; finer details unclear, possibly with a calcified pivotal bar.

Measurements – Holotype: ZL 476±39, 400-520 (1, 10); ZW 444±35, 400-500 (1, 10); OpL 176±41, 120-220 (1, 9); OpW 232±21, 200-260(1, 9); AL 174±21, 140-200 (1, 10); AW 186±19, 160-220 (1, 10).

Remarks – This distinctive species is known from few specimens, with one possible exception all from the Saratoga Chalk of Arkansas. It is characterised by the broad, rhomboidal autozooids which lack a gymnocyst, but have a shelf-like cryptocyst con-
fined to the proximal third or so of the autozooid, each autozooid being followed dis-
tally either by an ovicell or a small avicularium which is directed distolaterally. Our
only disagreement with Shaw’s comprehensive description concerns the ovicell which
Shaw regarded as endozooecial, but which we feel is more probably hyperstomial.

A specimen (NHM BZ 5038) from the Ripley Formation of Jefferson, Alabama, re-
sembles S. saratogaensis, but has appreciable larger zooids, autozooid length being about
600-750 μm compared with 400-520 μm for type material of the Arkansas species. Until
more material becomes available, this is attributed to S. cf. saratogaensis.

Medd (1979) regarded S. saratogaensis as a synonymy of Ellisina demissa (Brydone,
1910b). However, the specimens illustrated by Medd as E. demissa have longitudinally
elongate opesiae, that contrast with the broad opesiae of S. saratogaensis, and longer proximal cryptocysts.
**Semiflustrrella bifoliata** sp. nov.
Pls. 65, 66.


**Etymology** – From the bifoliate colony-form, comprising two layers of zooids back-to-back, that is developed in most known colonies.

**Description** – Colony erect, bifoliate, broken in all available material and therefore total breadth of fronds unknown, but preserved examples up to 11 mm wide; frond depth about 600 μm. Less common are unifoliate fragments, including tubular, cavariiform pieces, and adnate encrustations. Overgrowths developed locally. Non-ovicellate autozooids typically with associated distal avicularium, occasionally substituted by a kenozooid; ovicellate autozooids lacking avicularia. Ancestrula and early astogenetic stages unknown. Encrusting zooids fringed by multiple embayments at bases of vertical walls resembling pore chambers.

Autozooids large, rhomboidal in frontal outline, on average 1.4 times longer than wide, often separated from laterally adjacent zooids by a slight groove at zooidal boundary, groove lacking between zooids in the same longitudinal row. Gymnocyst and spines absent. Cryptocyst inwardly-sloping, moderately broad proximally, narrowing laterally, tapering until absent at distal end of zooid, densely pustulose, the inner pustules tending to be arranged in radial rows; cavities in cryptocystal calcification sometimes present. Opesia extensive, occupying most of zooid surface, ovoidal, rounded proximally and somewhat squared-off distally. Platforms (occlusor laminae?) may be developed in distolateral corners of opesia (Pl. 66, fig. 1a). Ovicells broken and roofless in all known examples, apparently hyperstomial, wider than long. Ovicellate autozooids with 2-4 knob-like processes projecting inwards from distal and distolateral edges of opesia (Pl. 66, fig. 1d). Closure plates and intramural buds not observed.

Avicularia (Pl. 65, fig. 1d) interzooidal, located immediately distally of most non-ovicellate autozooids, oriented distolaterally, the rostrum aligned along the boundary between the autozooids lateral and distal of the avicularium; in outline elongate diamond-shaped, prolonged distally. Gymnocyst wanting. Proximal cryptocyst an inwardly-sloping crescent, pustules diminishing in density inwardly. Opesia oval, indented by paired condyles. Rostrum long, narrow, concave-sided, with a non-pustulose palate.

Kenozooids occasionally substituting for distal avicularia (Pl. 65, fig. 1e), gymnocyst wanting, cryptocyst funnel-shaped, densely pustulose, opesia small and circular.

**Measurements** – ZL 542±30, 510-600 (1, 10); ZW 387±39, 330-465 (1, 10); OpL 372±28, 315-420 (1, 10); OpW 251±36, 195-315 (1, 10).
Remarks – Medd (1965, 1979), in his descriptions of Cretaceous ellisinids, did not include any erect bifoliate species with which to compare this new species. *Bidenkapia* Osburn, 1950, a little known boreal ellisinid may grow bifoliate branches, but has very thinly-calcified walls unlikely to survive fossilization, transversely oriented avicularia and a proximal gymnocyst. The bifoliate colony-form of most specimens of *S. bifoliata*, plus the large zooids, immediately distinguish it from the other ellisinids described here.

A specimen (ANSM 80365; Pl. 66) from the Mount Laurel Formation of Delaware deserves comment. This colony encrusts a belemnite guard and, despite its large size, shows no evidence of having produced erect fronds. On the other hand, it is the only example of *S. bifoliata* known to have ovicells. These are all broken, but are present in considerable numbers and demonstrate clearly that distal avicularia are lacking in ovicellular autozooids, as is the case for many other ellisinids from the Cretaceous (see Medd, 1979). Another notable feature of the Mount Laurel colony is the occurrence of ingrowths from the distal and distolateral vertical walls of the autozooids beneath the level of the mural rim. In non-ovicellate autozooids these ingrowths consist of a pair of distolateral platforms resembling the oculisor laminae found in the Chaperiidae. Ovicellate autozooids additionally have two to four knob-like ingrowths, a pair along the distal wall and often one or two distolaterally at the ends of the platform seen in non-ovicellate autozooids.

*Semiflustrella brittanica* (Brydone, 1906)

Pl. 67.

1906 *Membranipora brittanica* sp. nov.; Brydone, p. 294, text-fig. 3.
1979 *Ellisina brittanica* (Brydone); Medd, p. 13, pl. 1, figs. 7-10, pl. 2, figs. 2-3, [text-]fig. 3 (for full synonymy see Medd, 1979).

Material – NHM BZ 4804, NNM RGM 507 063, Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).

Description – North American colonies encrusting, multiserial, unilaminar, small, up to 4 mm in maximum diameter, comprising autozooids with small distal avicularia. Ancestrular region obscured by sediment grains (Pl. 67, fig. 1a), but earliest visible generations (periancestrular zooids?) possess avicularia. Pore chambers present, at least distally.

Autozooids rhomboidal to pyriform in outline shape, about 1.5 times longer than wide. Gymnocyst very narrow, slightly wider proximally in pyriform zooids; spines lacking. Cryptocyst moderately broad proximally, narrowing laterally and absent distally, pustulose, the inner pustules tending to be aligned in radial rows. Mural rim raised, crenulated. Opesia extensive, occupying most of autozooidal frontal surface, oval, widest proximally of mid-length. Ovicells, closure plates and intramural buds not seen in North American material.

Avicularia interzooidal, small, positioned distally of each autozooid (Pl. 67, fig. 1d), directed laterally to right or left, neighbouring avicularia typically facing the same way, often curved in parallel with distal edge of the associated autozooid, proximally rounded with a short cryptocyst, distally subpointed, the rostrum a short crescent, pivotal bar calcified.
Measurements – ZL 563±68, 465-660 (1, 10); ZW 366±26, 330-405 (1, 10); OpL 360±34, 300-405 (1, 10); OpW 281±20, 255-315 (1, 10).

Remarks – This species has been described previously from the Campanian, Maastrichtian and Danian of northwest Europe. Brydone’s (1906) type material came from the Campanian Chalk of the Isle of Wight, England. Only two, non-ovicellate colonies are known from North America, but these appear to fit within the revised, comprehensive description of the species published by Medd (1979). The description given above is based entirely on the NHM specimen from the Prairie Bluff Chalk of Alabama, where *S. brittanica* occurs in association with the much commoner ellisinid *Dionella rindsbergi*. The smaller size of the zooids in the NHM Prairie Bluff Chalk colony compared with conspecific colonies from the British Chalk (e.g., NHM D41662) probably reflects the small size of the colony in which all of the zooids are within the zone of primary astogenetic change.

*Dionella Medd, 1965*

*Type species* – *Cellepora trifaria* von Hagenow, 1846, Maastrichtian, Germany; by original designation.

*Remarks* – This genus was established by Medd (1965) for membraniporimorphs with small interzooidal avicularia located distally of the autozooids, hyperstomial ovi-cells and pore chambers.

*Range* – Coniacian-Lutetian.

*Dionella rindsbergi* sp. nov.

Pl. 68.

*Material* – Holotype: NHM BZ 4791(2), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). Paratypes: BZ 4791(1), BZ 4791(3), BZ 4791(6), BZ 5031, BZ 5133(2), BZ 5175-5177, details as for holotype. NNM RGM 507 008, Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5). Questionably assigned: USNM 528938, 528938, Maastrichtian, PeeDee Formation, Neuse River, Lenoir County, North Carolina (locality NC4).

*Etymology* – Named for Dr A. Rindsberg (Geological Survey of Alabama) who drew our attention to the Livingston outcrop, the type locality of this and several other new species described here.

*Description* – Colony encrusting, multiserial, unilaminar, typically small (Pl. 68, fig. 1a); autozooids regularly arranged, each with a distal avicularium. Distal growing edge jagged. One very large distal pore chamber and two large distolateral pore chambers (Pl. 68, figs 1b, 2c). Ancestrula (Pl. 68, fig. 2a) elliptical, proximal gymnocyst variably overgrown by later zooids; spine bases lacking; cryptocyst narrow; opesia oval, widest proximally of mid-length, more pointed distally, lacking an associated avicularium. Six perianestruclar autozooids, all or most with associated avicularia, the distal and two
distolateral zooids apparently budded directly from the ancestrula, perianestruar zooid size increasing from distal to distolateral to proximolateral to proximal positions.

Autozooids usually rounded rhomboidal in frontal outline, about 1.5 times longer than wide, the proximal edges concave and distal edges convex. Gymnocyst narrow, sometimes prolonged proximally; spine bases absent. Cryptocyst inwardly sloping, narrow, absent at distal end of zooid, pustulose, the pustules tending to be arranged in radial rows. Opesia extensive, occupying most of frontal surface of zooid, oval, widest proximally of mid-length, often squared-off distally. Ovicells not identified, possibly cryptic. Intramural reparative buds common (Pl. 68, fig. 2b). Closure plates not observed.

Avicularia oriented distally, interzooidal, located immediately distally of both ovicellate and non-ovicellate autozooids, small, ovoidal with almost straight proximal edge (Pl. 68, fig. 2d), somewhat pointed and arch-like distally; opesia oval; calcified pivotal bar lacking. Budding of avicularia possibly from two small pores visible between distal and distolateral pore chambers in zooids at growing edge.

**Measurements** – ZL 491±24, 450-525 (1, 10); ZW 321±28, 285-375 (1, 10); OpL 345±28, 285-375 (1, 10); OpW 230±22, 195-270 (1, 10).

**Remarks** – Colonies of *D. rindsbergi* are delicate and prone to destruction by weathering. They are characterised by having regularly-arranged autozooids, each followed by a small, distally directed avicularium. There are some similarities between *D. rindsbergi* and the European Maastrichtian-Danian species *Periporosella humililata* (Brydone, 1910a), as redescribed by Medd (1979). The European species, however, has multiple small pore chambers. Unlike *D. trifaria* (von Hagenow) and several other species of *Dionella* described by Medd (1965), *D. rindsbergi* lacks large interzooidal avicularia and mural spines.

**Kristerina gen. nov.**

**Type species** – *Kristerina broodi* sp. nov., Campanian, Delaware.

**Etymology** – Named to honour the contributions to bryozoology of the Swedish palaeontologist Krister Brood (1941-2004).

**Diagnosis** – Colony encrusting. Autozooids with well-developed proximal cryptocyst, shelf-like; gymnocyst lacking or negligible, spines absent; opesia occupying up to half of frontal surface. Ovicells hyperstomial, cryptocystal. Avicularia interzooidal, one located distally of each non-ovicellate autozooid, directed distally; rostrum arched acuminate; pivotal bar uncalcified.

**Remarks** – This new genus is characterised by having relatively large, distally-directed avicularia located distally of each non-ovicellate zooid, a cryptocystal frontal shield and hyperstomial ovicells with cryptocystal roof calcification. It differs from *Dionella* and *Semiflustratella*, described above, in several important respects. Unlike *Dionella* Medd, 1965, the frontal shield is formed by an extensive cryptocyst and the roof of the...
ovicell is similarly constructed. The distally-directed avicularia enable a distinction to be made from *Semiflustra*, which also appears to have more sunken ovicells, although none of the specimens of this latter genus have ovicells completely enough preserved to determine the characteristics of the roof.

The very tentative assignment of *Kristerina* to the Calloporidae is based mainly on the presence of the avicularia distal to the autozooids, an arrangement suggesting an affinity with *Ellisina* and related genera.

**Range** – Campanian.

**Kristerina broodi** sp. nov.

*Pl. 69.*

**Material** – Holotype: ANSM 80357, Campanian, Mount Laurel Formation, Delaware & Chesapeake Canal, New Castle County, Delaware (locality DE1).

**Etymology** – Like the genus, named for the late Krister Brood.

**Description** – Colony encrusting, multiserial, unilaminar, most non-ovicellate autozooids having a distal avicularium (*Pl. 69, fig. 1a*). Pore chambers apparently lacking. Ancestrula unknown, zooids in early astogeny small, avicularia present.

Autozooids slender, on average 2.3 times longer than wide, rounded distally, proximally commonly drawn out to form an elongate cauda-like extension with concave sides. Zooidal boundary a narrow fissure. Gymnocyst lacking; spine bases absent. Cryptocyst extensive, forming a proximal shelf occupying half or more of zooidal length, inwardly sloping around aperture, finely pustulose, the pustules subdued and widely spaced. Aperture longitudinally elliptical to pear-shaped, occupying half or less of frontal surface of zooid. A pair of oval indentations (occlusor muscle scars?) visible at distolateral corners of basal walls of some zooids (*Pl. 69, fig. 1c*). Ovicells hyperstomial, semicircular, wider than long, roof comprising finely pustulose interior wall continuous with proximal cryptocyst of distal zooid (*Pl. 69, fig. 1e*). Intramural reparative buds present. Closure plates not observed.

Avicularia (*Pl. 69, fig. 1f*) orientated distally, interzooidal, located immediately distally of most non-ovicellate autozooids, lacking in ovicellate zooids; small, about one-third or less the length of an autozooid, arch-shaped, proximal edge straight or slightly concave, proximal cryptocyst almost half total length; aperture teardrop-shaped, pointed distally; calcified pivotal bar lacking; rostrum slightly raised, flanked by narrow gymnocyst.

**Measurements** – ZL 702±73, 600-840 (1, 10); ZW 301±21, 255-330 (1, 10); OpL 254±30, 210-300 (1, 10); OpW 201±14, 180-225 (1, 10); OvL 117±13, 105-135 (1, 5); OvW 192±13, 180-210 (1, 5); AL 253±26, 225-300 (1, 8); AW 131±19, 105-165 (1, 8); AoL 106±13, 90-120 (1, 8); AoW 59±10, 45-75 (1, 8).

**Remarks** – Only one specimen of this new species is known, but it is sufficiently distinct from existing species and well-enough preserved to warrant recognition as a new
taxon. There is scarcely a trace of gymnocyst and the ovicells are also composed of cryptocyst calcification. Many of the autozooids are very slender, with cauda-like proximal extensions of cryptocyst. None of the other ellisinid species described herein have such extensive cryptocysts and relatively small apertures. The new species resembles *Semiflustrrella demissa* (Brydone, 1910b), as redescribed by Medd (1979), in its extensive cryptocyst. However, the avicularia are entirely different, being obliquely oriented and having a narrow, parallel-sided rostrum in Brydone’s species, compared with the distal orientation and arched rostrum seen in *K. broodi*. Of the ellisinids described herein, only *Dionella rindsbergi* has distally oriented avicularia, but this is immediately distinguished from *K. broodi* by the autozooids not having shelf-like proximal cryptocysts.

**Aplousina Canu & Bassler, 1927**

*Type species* – *Aplousina gigantea* Canu & Bassler, 1927, Recent, Gulf of Mexico; by original designation.

*Remarks* – *Aplousina* was erected by Canu & Bassler (1927) for Miocene-Recent species characterized by a lack of spines, avicularia and pore chambers, and the presence of entoecial ovicells. The type species is also notable for its greatly reduced frontal calcification, with no appreciable gymnocyst or cryptocyst. The Cretaceous species here assigned to *Aplousina* differs in two respects from the Recent type species, firstly in having pore chambers and secondly in that a small minority of zooids (possibly only from the primary zone of astogenetic change) exhibit moderate development of the cryptocyst. Therefore, its assignment to *Aplousina* is considered to be very tentative.

*Range* – Campanian-Recent.

**Aplousina incompta** sp. nov.

*Pl. 70.*

*Material* – Holotype: NHM BZ 5037, Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). Paratypes: NHM BZ 5035(1), BZ 5036, same details as holotype. NHM BZ 4833-4, NNM RGM 507 014(2), Maastrichtian, Prairie Bluff Chalk, Emelle, Sumter County, Alabama (locality AL9). USNM 526172, Maastrichtian, Peedee Formation, Neuse River, Lenoir County, North Carolina (locality NC4). NHM BZ 4175(5), BZ 4182(3), Maastrichtian, Peedee Formation, Rocky Point Member, Ideal Quarry, New Hanover County, North Carolina (locality NC2). NNM RGM 507 052, Maastrichtian, Peedee Formation, Rocky Point Member, Rocky Point Quarry, Pender County, North Carolina (locality NC3).


*Description* – Colony encrusting, multiserial, unilaminar. Zooids six-sided and regularly arranged, giving the colony a honeycomb-like appearance. Pore chambers present in distal and two distolateral vertical walls; pore windows large, elliptical. Ancestrula
(Pl. 70, fig. 1b) small, about 360 μm long by 255 μm wide, rounded rhomboidal in shape, the proximal end especially well-rounded; spines lacking; gymnocyst well-developed proximally, about half of total zooidal length; mural rim indistinct; cryptocyst forming a pustulose, inwardly sloping, shallow proximal shelf; opesia semielliptical, proximal edge almost straight, distal edge arched, slightly longer than wide, about 90 μm long by 75 μm wide.

Autozooids weakly-mineralized, rhomboidal in frontal outline, slightly elongate, on average 1.5-1.6 times longer than wide, the proximal and distal sides shorter than the proximolateral and distolateral sides; proximal and proximolateral sides slightly concave, the distal and distolateral sides slightly convex. Gymnocyst and spines lacking. Cryptocyst absent except in a very few zooids where there is an inwardly-sloping, coarsely granular, proximal cryptocyst (Pl. 70, fig. 1c). Opesia extensive, normally occupying entire frontal surface within the thin vertical zooidal walls; smaller and pear-shaped in zooids having cryptocyst developed. Ovicells endozooidal, immersed, very inconspicuous, ovicellate zooids being difficult to distinguish from non-ovicellate zooids, the ooecium visible as a narrow crescent of gymnocyst. Closure plates and intramural buds lacking. Basal walls uncalcified.

Avicularia not identified.

Measurements – ZL 561±75, 495-750 (1, 10); ZW 362±36, 315-435 (1, 10).

Remarks – The strongly reduced skeleton of this species gives the impression of heavy abrasion, a deception dispelled by the occurrence of such preservation even in protected hollows on the substrate (Pl. 70, fig. 3). It also provides few taxonomic characters. An un-named species from the Maastrichtian of The Netherlands, designated ‘Membranipora’ (Aplousina) sp. by Voigt (1979, pl. 1, fig. 1), resembles Aplousina incompta and may even be conspecific. Another European Maastrichtian species assigned to Aplousina, A. baltica (Voigt, 1930), shows significantly greater development of cryptocyst and gymnocyst (see Voigt, 1989b, pl. 1, figs. 5, 6). Zooids in the Paleocene A. contunax Canu & Bassler, 1933, from the Vincentown Limesand have less reduced frontal walls than A. incompta. Compared with the Recent type species of the genus, A. gigantea, A. incompta has smaller zooids and possesses pore chambers.

The rare occurrence in A. incompta of autozooids with cryptocysts (Pl. 70, fig. 1c), as well as the gymnocyst-bearing ancestrula (Pl. 70, fig. 1b), prompts a comparison with the unusual species Nudonychocella nuda described by Voigt & Ernst (1985). Most of the zooids in this species from the type Maastrichtian lack frontal calcification, apart from the ancestrula which has a depressed cryptocystal frontal wall and semicircular opesia betraying its onychocellid affinities. A bioimmured specimen of N. nuda (Voigt & Ernst, 1985, fig. 2.1) shows mature zooids with a typically onychocellid appearance. Although bioimmuration in this specimen was interpreted by Voigt & Ernst to mould the unmineralized frontal membranes of the zooids, an alternative interpretation is that it moulds a frontal wall skeleton of aragonite or high-Mg calcite that is normally lost during diagenesis. While the avicularia of N. nuda suggest that it may not be closely related to A. incompta, it is nonetheless possible that the strongly reduced skeleton seen in A. incompta results from the routine dissolution of cryptocystal frontal shields composed of aragonite or high-Mg calcite.
Among the other species described here, *A. incompta* can only be confused with specimens of *Stichomicropora* in which the frontal shield is missing (see below). However, colonies of the latter tend to have somewhat broader zooids and there is usually some remnant of the rim of the orifice.

*Euritina Canu, 1900*

*Type species* – *Eschara eurita* d’Orbigny, 1851 (*in* 1851-1854), Turonian, Ste Maure, France; by original designation.

*Remarks* – Probably the most complete, though still inadequate, description and discussion of this genus is by Canu & Bassler (1920). The type species was figured by Voigt (1981, fig. 5g), along with a second Cretaceous species, *E. welschi* (fig. 5f). Species of *Euritina* are either erect and bifoliate or encrusting and sheet-like. Autozooids have the cryptocyst divided by longitudinal grooves into three facets, a deep proximal facet being flanked by two narrower lateral facets. Interzooidal avicularia are present, generally in association with row bifurcations.

The familial affinities of this genus require future reassessment and for the present it is retained in the Calloporidae as broadly understood.

*Range* – Cenomanian-Recent. Voigt (1981) recorded the type species from the Cenomanian, while Osburn (1950) referred an extant species (*E. arctica*) to the genus.

*Euritina* *metapolymorpha* sp. nov.


*Etymology* – In reference to the change (meta) in polymorph type, from avicularia to autozooids, along the zooidal rows as they slowly increase in width with growth.

*Description* – Colony encrusting, multiserial, unilaminar, occasionally multilaminar. Zooids arranged in well-defined longitudinal rows (Pl. 71, fig. 1a), bifurcation of a row resulting in one daughter row of autozooids and a second daughter row beginning with several generations of avicularia before the first autozooid is budded. Pore chambers lacking.

Autozooids rounded rhomboidal in outline shape, the proximal edge concave, the distal edge convex and the sides bowed; length on average 1.4 times width. Gymnocyst narrow, proximally forming a slight horizontal shelf widening into the proximolateral corners of the zooid, steepening laterally and distally, and forming the outer edge of the raised mural rim. No spines. Cryptocyst densely pustulose, with facets, the proximal facet deep, sloping gently inwards, shelf-like, separated by two slight longitudinal grooves from the left and right lateral facets which slope steeply (Pl. 71, fig.
1d); ill-defined boundary between gymnocyst and proximal cryptocyst; distal cryptocyst wanting. Opesia occupying about half of zooidal frontal surface, longitudinally elongate, rounded rectangular. Ovicells not observed. Closure plates and intramural buds lacking.

Avicularia (Pl. 71, fig. 1f) interzooidal, abundant, constituting the initial five or six zooids in the narrower of the two rows following each bifurcation, elongate rhomboidal or elliptical in outline shape. Gymnocyst expanded proximally, in some zooids containing a large proximally-facing opening, narrowing distally, forming a high arched, somewhat pinched mural rim defining distal edge of avicularium. Cryptocyst pustulose, a deep crescent proximally, lacking distally. Opesia longitudinally elliptical.

Kenozooids (Pl. 71, fig. 1c, d) sometimes substituting for avicularia, rhomboidal, pyriform or more irregular in outline shape, gymnocyst variable in width, cryptocyst pustulose, wide, of subequal breadth around entire circumference of longitudinally elliptical opesia.

**Measurements**

- Holotype: ZL 378±35, 330-435 (1, 10); ZW 270±29, 240-315 (1, 10); OpL 222±26, 180-255 (1, 10); OpW 143±16, 120-165 (1, 10); AL 309±45, 210-375 (1, 10); AW 137±23, 105-165 (1, 10); AOL 101±21, 75-150 (1, 10); AOW 65±7, 60-75 (1, 10).

**Remarks**

- In species of *Euritina*, avicularia are usually the first zooids in one of the two daughter rows following a row bifurcation; however, the second zooid is normally an autozooid. This new species differs from its congeners in having a succession of about five or six avicularia after each row bifurcation. Daughter rows with avicularia expand in width very slowly, matching the ‘delayed’ appearance of autozooids in the row. Slow expansion of rows and retardation in the onset of autozooidal budding may be a geometrical consequence of an unusually large number of row bifurcations being initiated as the encrusting colony grew and its circumference increased.

Among the species described here, there are clear similarities with *Marginaria wilsoni* sp. nov., which has avicularia of similar morphology arranged in rows between the autozooids. However, the frontal shield of *M. wilsoni* is largely gymnocystal and mural spine bases are present, whereas *E. metapolymorpha* has a cryptocystal frontal shield and no spines.

*Euritina bocki* sp. nov.

**Pl. 72.**

**Material**


**Etymology**

- In recognition of the bryozoological work of Dr Phil Bock (Melbourne), especially the invaluable resource provided by his ‘Bryozoa Homepage’ website, <http://www.civgeo.rmit.edu.au/bryozoa/default.html>.
**Description** – Colony encrusting, multiserial, multilaminar, new layers developing through spiral overgrowth around pivot points (Pl. 72, fig. 1a). Zooids arranged in well-defined longitudinal rows, often with alternating rows of autozooids and avicularia. Pore chambers lacking.

Autozooids rounded rhomboidal in outline shape, the proximal edge concave, the distal edge convex and the sides bowed, squat, about 1.2 times longer than width; zooidal boundaries defined by narrow furrows. Gymnocyst and spines lacking. Cryptocyst finely pustulose, broadest proximally, inwardly sloping, deeply incised, variably faceted, with grooves between facets (Pl. 72, fig. 1b). Opesia extensive, occupying most of zooidal frontal surface, sunken, longitudinally elliptical or pear-shaped. Ovicells not observed. Closure plates and intramural buds lacking.

Avicularia (Pl. 72, fig. 2b) interzooidal, numerous, aligned in rows between autozooids or forming one of the two daughter zooids at autozooidal row bifurcations, variable in size, narrower than autozooids and usually shorter, longitudinally elliptical to rounded rhomboidal in outline. Gymnocyst lacking. Cryptocyst pustulose, broad proximally and proximolaterally, tapering distally and absent in distal half to third. Opesia keyhole-shaped, a constriction separating the short proximal part from a longer, broader distal part. Rostrum rounded with a raised, semicircular distal rim.

Kenozooids occasionally present, occupying interzooidal spaces, smaller than avicularia, opesia subcircular.

**Measurements** – Holotype: ZL 236±19, 195-255 (1, 1), ZW 198±23, 165-225 (1, 1); OpL 149±11, 135-165 (1, 1); OpW 99±8, 90-105 (1, 1); AL 219±20, 195-255 (1, 1); AW 135±19, 105-165 (1, 1); AOL 86±7, 75-90 (1, 1); AOW 50±6, 45-60 (1, 1).

**Remarks** – The autozooids in this new species are less elongate and more deeply incised than in *Euritina eurita*, the type species of the genus. Unlike *E. metapolymorpha*, described above, a gymnocyst is totally lacking in *E. bocki* and the opesiae of the avicularia are keyhole-shaped rather than being longitudinally elliptical. In addition, the zooids are substantially smaller in *E. bocki*.

The large, sunken opesia set in an entirely cryptocystal frontal wall, arrangement of avicularia in files between the autozooidal rows and apparent lack of oovicells in *E. bocki* are all characters reminiscent of the Lunulitidae *sensu lato* (see Cook & Chimonides, 1986). The relationship between this new species and the non-lunulitiform genera commonly assigned to the Lunulitidae (e.g., *Volviflustraria*, *Discovibracella*, *Pavolunulites*) certainly deserves future investigation.

**Amphiblestrum** Gray, 1848

**Type species** – *Membranipora flemingii* Busk, 1854, Recent, North Atlantic; see Ryland (1969, p. 214) for a discussion of problems pertaining to the type species.

**Remarks** – This extant genus is characterised by autozooids with extensive, shelf-like proximal cryptocysts, trapezoidal or trifoliate opesiae, oral spines, pore chambers, an oovicell with a frontal area of reduced calcification and adventitious avicularia which are typically located on the proximal gymnocyst (Ryland & Hayward, 1977, p. 103;
Hayward, 1995, p. 76; Rosso, 2002). Cretaceous species assigned to the genus, both in this and previous publications, do not always possess all of these attributes, notably the adventitious avicularia and the ovicell with reduced calcification. It is possible that some may be better placed elsewhere; for example, into Megapora Hincks, 1877, an Amphiblestrum-like genus lacking avicularia (see Ryland & Hayward, 1977, p. 107), or Ramphonotus Norman, 1894, which has a uniformly calcified ovicell, lacking the proximofrontal region of uncalcified ectooecium regarded as typical of Amphiblestrum (Bishop & Hayward, 1989, p. 6). However, pending a monographic revision of these taxa, we provisionally maintain their assignment to Amphiblestrum. Two other genera of similar overall morphology are Floridina Jullien, 1882, and Floridinella Canu & Bassler, 1917 (see below). Both genera, however, have endozooidal ovicells, features not observed in the species described here.

Range – Santonian-Recent. The oldest species that can be attributed to Amphiblestrum appears to be A. hexagonum Voigt, 1930, from the Santonian of Germany.

**Amphiblestrum denticulatum** Canu & Bassler, 1926

Pl. 73.

1926 Amphiblestrum denticulatum sp. nov.; Canu & Bassler, p. 34, pl. 5, figs. 2-4.
In press Amphiblestrum denticulatum Canu & Bassler; McKinney & Taylor, fig. 2B.

Material – Lectotype (chosen here): USNM 69969, the largest syntype colony, probably that figured by Canu & Bassler (1926, pl. 5, fig. 2), Maastrichtian, Ripley Formation, Coon Creek Member, Coon Creek, McNairy County, Tennessee (locality TN1). Paralectotypes: USNM 528399, 528400, two other syntype colonies including that figured by Canu & Bassler (1926, pl. 5, fig. 4); same details as for lectotype. Other material: RU 5600, 5612, 5627, 5638, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 and/or NJ2).

Description – Colony encrusting, multiserial, unilaminar. Ancestrula and early zooids unknown. Lectotype colony exhibits regenerative budding from a fracture, producing bipolar growth (Pl. 73, fig. 1b). Pore chambers large, extending along entire length of zooidal walls (Pl. 73, fig. 2), the distal pore chamber semicircular and larger than the two elliptical distolateral pore chambers.

Autozooids rhomboidal, on average 1.25 times longer than wide, surrounded by distinct furrows. Gymnocyst narrow, usually slightly broader proximally. Oral spine bases usually numbering two, sometimes four, very small, closely-spaced at distal end of zooid. Cryptocyst densely pustulose, single pustules or clusters of pustules around inner edge projecting into the opesia as denticles, proximal cryptocyst broad, shelf-like, sloping gently inwards, width of cryptocyst diminishing distally until lacking at distal end of zooid. Opesia rounded trapezoidal, often somewhat trifoliate, the distal end a semicircle. Ovicell (Pl. 73, figs 1c, 3) hyperstomial, small, ectooecium apparently completely calcified, but sometimes partly or completely overgrown by cryptocyst of distal zooid; oral spines of ovicellate autozooids located near proximolateral corners of ovicell. Intramural buds developed, closure plates not observed.
Avicularia (Pl. 73, fig. 1c, 4) vicarious, occasionally associated with row bifurcations, elongate rhomboidal in outline shape, spatulate, the rostrum expanded and well-rounded. Proximal gymnocyct variably developed, sometimes negligible, narrowing along proximolateral edges before broadening to form steeply-inclined margins of rostrum. Cryptocyst forming a densely pustulose proximal crescent, narrowing and steepening along lateral edges of opesia, shelf-like and non-pustulose at distal end of avicularium. Opesia dumbbell-shaped. Avicularia may host smaller intramurally budded avicularia.

**Measurements** – Syntypes: ZL 416±50, 380-520 (1, 10); ZW 330±32, 280-400 (1, 10); OpL 204±12, 180-220 (1, 10); OpW 178±11, 160-200 (1, 10); OvL 188±10, 180-200 (1, 10); OvW 106±19, 80-140 (1, 10); AL 520±57, 400-600 (3, 10); AW 234±19, 200-260 (3, 10); RL 312±52, 220-360 (3, 10); RW 125±18, 80-140 (3, 10).

**Remarks** – Abraded colonies of this species show very clearly the large pore chambers (Pl. 73, fig. 2). That colonies were routinely damaged during life is evident not only from the occurrence of intramural reparative buds, but also the wholesale regeneration of growth from fractured edges of colonies (Pl. 73, fig. 1b).

*Amphiblestrum parvum* sp. nov.  
Pl. 74.

**Material** – Holotype: NHM BZ 4823, Maastrichtian, Ripley Formation, Florence, Quitman County, Georgia (locality GA1). Paratypes: USNM 526179, 528392, 528940, Maastrichtian, Peedee Formation, Neuse River, Lenoir County, North Carolina (locality NC4). NNM RGM 507 054, Maastrichtian, Peedee Formation, Burgaw, Pender County, North Carolina (locality NC1).

**Etymology** – L., *parvus*, little, referring to the extremely small size of the zooids.

**Description** – Colony encrusting, multiserial, unilaminar, sometimes with minor overgrowths. Pore chambers present; distal pore chamber large, four-sided, broadening distally (Pl. 74, fig. 1d); distolateral pore chambers apparently slit-like, single or paired. Ancestrula in holotype slightly smaller than postancestrular zooids, otherwise identical, surrounded by seven periancestrular zooids (Pl. 74, fig. 1a), the distal and two distolateral of which appear to have been budded from the ancestrula.

Autozooids tiny, rhomboidal in outline shape, about 1.3 times longer than wide, surrounded by grooves. No gymnocyct or spines. Cryptocyst coarsely pustulose (Pl. 74, fig. 1c), forming a proximal shelf accounting for about one-third of zooid length, narrowing distally, and becoming more steeply inclined around the lateral and distal margins of the opesia. Opesia dumbbell-shaped, longer than wide, occupying about half total zooid length, constricted in width at or a little proximally of mid-length, the portion proximal of constriction well-rounded and shorter in length than distal part which may have a somewhat squared-off end. Ovicells not observed. Possible intramural budding indicated by zooid with stepped cryptocyst and smaller opesiae. Closure plates lacking. Avicularia not observed.

Kenozooids rare, small, represented by a single rhomboidal zooid with a longitu-
dinally elliptical opesia and a second, partly overgrown, rounded diamond-shaped zooid with a subcircular opesia, the cryptocyst immediately proximal of which contains a pair of short radial grooves (Pl. 74, fig. 2b, left of centre).

**Measurements** – Holotype: ZL 278±20, 255-315 (1, 10); ZW 218±18, 195-240 (1, 10); OpL 110±10, 90-120 (1, 10); OpW 72±6, 60-75 (1, 10).

**Remarks** – This new species with tiny zooids and small colonies is known only from a few specimens, none with identifiable ovicells. Nevertheless, it is both very distinctive and clearly different from existing species of *Amphiblestrum*. The total lack of gymnocyst readily distinguishes it from *Setosinella meniscacantha* sp. nov. and the absence of oral spines from this species as well as from *A. denticulatum*. The most striking feature of *A. parvum* is the dumbbell-shaped opesia, broad proximally and longer, but narrower distally.

The enigmatic colony origin observed in a paratype (Pl. 74, fig. 2b) contrasts with that seen in the holotype, where a conventional ancestrula can be identified (Pl. 74, fig. 1a). In the paratype, a small zooid, interpreted as a kenozooid, but possibly an autozooid with a closure plate, occurs at the origin of colony growth. This zooid appears to bud left and right distolateral autozooids, each of which has its own daughter bud, completing a circlet of four zooids. The two proximolateral zooids are also part of a group of five zooids that diverge from a point behind (proximally) of the kenozooid in a stellate pattern somewhat reminiscent of the ancestrular complex of the unrelated ascophoran *Reptadeonella* (see Hayward & McKinney, 2002, fig. 19G). It seems possible that this colony, which encrusts the steinkern of a small mollusc, originated by regenerative growth from a kenozooid that remained after destruction of most of an originally larger colony.

### *Setosinella* Canu & Bassler, 1933

**Type species** – *Setosinella prolifica* Canu & Bassler, 1933, Paleocene, New Jersey, U.S.A.; by original designation.

**Remarks** – This genus was founded by Canu & Bassler (1933, p. 41) for a single, rare new species from the Paleocene Vincentown Limesand of New Jersey. Placed in the Family Setosellidae by Canu & Bassler (1933) and later by Bassler (1953) in the bryozoan Treatise, the genus has been reassigned to the Microporidae by D.P. Gordon in his unpublished interim listing of genera for the revised Treatise on Invertebrate Paleontology. However, its similarities to *Amphiblestrum* and lack of opesiules suggest that it belongs in the Calloporidae, at least in the broad current sense of this family.

Canu & Bassler (1933, p. 42) made the enigmatic statement: “We have not observed true perforating opesiules; the place of some of these is, however, sufficiently indicated to prove that they must occur. They must have been very small, which explains their disappearance in fossilization.” Neither Canu & Bassler’s figures of *S. prolifica* nor our SEM studies of *S. meniscacantha* sp. nov. provide any evidence that opesiules are actually present in *Setosinella*.

**Range** – Maastrichtian-Thanetian.
Setosinella meniscacantha sp. nov.
Pls. 75, 76.

Material – Holotype: NHM BZ 4796(1a), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). Paratypes: BZ 4796(1b), BZ 4810(2), BZ 5050(1), BZ 5180, BZ 5181(a), BZ 5181(b), NNM RGM 507 011, details as for holotype. BZ 5042, Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5). BZ 5182, Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2). RU 5640, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

Etymology – Gr. meniskos, crescent, and akantha, thorn, in reference to the prominent crescent of large oral spines.

Description – Colony encrusting, multiserial, unilaminar, usually irregular in outline shape, sometimes with small, fan-like subcolonies (Pl. 75, fig. 1f); growing edge stepped (Pl. 76, fig. 1). Distal pore chamber larger than distolateral pore chambers; pore windows oval. Ancestrula ovoidal, proximal gymnocyst occupying about one-third of total length; cryptocyst forming a proximal shelf; opesia almost circular, an indeterminate number of small oral spine bases present; budding a single periancestrular zooid distally, sometimes becoming overgrown by avicularia. Autozooids in zone of primary astogenetic change transitional in morphology between ancestrula and later autozooids, with pear-shaped mural rim and up to eight oral spine bases.

Autozooids small, rhomboidal, broad, on average 1.2 times longer than wide, separated by deep furrows, arranged in well-defined rows. Gymnocyst narrow, usually broadest proximally. Cryptocyst depressed, forming an extensive, flat proximal shelf, finely and densely pustulose, with pustules immediately proximally of opesia tending to be aligned in weak radial rows. Mural rim salient. Opesia somewhat trifoliate, the larger, distal semielliptical part divided from the shallower proximal part by an indentation in the mural rim. Oral spine bases numbering six or seven, large and closely spaced, forming a prominent crescentic arch around distal rim of opesia (Pl. 75, fig. 1e). Ovicell (Pl. 75, fig. 1c; Pl. 76, fig. 5) hyperstomial, globose, prominent, ectooecium apparently completely calcified, resting on proximal gymnocyst of distal zooid and indented its mural rim; distalmost pair of oral spines hidden by ovicell. Intramural buds observed especially in damaged zooids. Closure plates depressed beneath level of cryptocyst, with a sunken pore located almost centrally.

Avicularia (Pl. 75, fig. 1d) interzooidal or, more commonly, adventitious, originating in furrows between autozooids and budded onto autozooidal gymnocyst, most orientated obliquely distally. Gymnocyst variably developed, more extensive in interzooidal than adventitious avicularia. Cryptocyst pustulose and broadest proximally. Opesia a uniformly-tapered teardrop shape. Rostrum acuminate, longer than wide. Pivotal bar calcified.

Measurements – ZL 361±29, 295-405 (3, 30); ZW 304±33, 243-374 (3, 30); OpL 83±17, 47-123 (3, 30); OpW 98±17, 57-132 (3, 30); OvL 133±21, 78-167 (3, 25); OvW 154±19, 126-191 (3, 24); AL 139±28, 87-183 (3, 12); AW 77±12, 50-90 (3, 12).
Remarks – This is one of the most distinctive species found in the Maastrichtian chalks of Alabama and is especially common encrusting bivalve shells in the Prairie Bluff Chalk of Livingston. The flat cryptocyst bordered by a raised mural rim, trifoliate opesia and crescent of stout oral spine bases are particularly characteristic features. Compared with the Paleocene type species of *Setosinella, S. prolifica*, the new species has more oral spines (6-7 vs 4) and stouter avicularia. Canu & Bassler (1933) also described a small, perforated distal kenozooid surmounting some of the zooids in *S. prolifica*, but no equivalent structure has been seen in *S. meniscacantha*.

Similarities are apparent with some North American Paleogene species referred to *Amphiblestrum* by Canu & Bassler (1920), notably *A. biporosum* and *A. orbiculatum*. However, the first of these species has rounded avicularia and the second has semielliptical opesiae, thereby distinguishing them from *S. meniscacantha*.

A remarkable feature of this species is occurrence of subcolonies at the periphery of some of the larger colonies encrusting a shell from the Prairie Bluff Chalk (Pl. 75, fig. 1f). These fan-shaped expansions begin with the budding of a small ‘pseudoancestrula’ by a zooid at the growing edge of the main colony. The pseudoancestrula has a high, semi-elliptical opesia and inconspicuous oral spine bases. A zone of secondary astogenetic change is initiated through which zooids increase in size and gradually attain the morphology found in astrogenetically mature zooids. Functionally these subcolonies may have a role in spatial competition - several were observed extending towards and in some instances overgrowing adjacent colonies on the same substrate.

**Genus Floridinella Canu & Bassler, 1917**

*Type species* – *Floridinella vicksburgica* Canu & Bassler, 1917, Oligocene, Alabama, U.S.A.; by original designation.

*Remarks* – Canu & Bassler (1917; see also 1920, p. 229) erected this genus for species resembling *Floridina*, but lacking avicularia. Although Canu & Bassler (1920) referred a Maastrichtian species, *Marginaria deshayesi* von Hagenow, 1851, to the genus, *Floridinella* has seldom been used for Cretaceous bryozoan species. However, the new species described below from the Maastrichtian of Georgia and Alabama shows sufficient features in common with the type species of *Floridinella* to allow its assignment to this genus pending a revision of the challenging taxonomy of this difficult group of cheilostomes.

*Range* – Maastrichtian – Miocene.

**Floridinella jeffersoni** sp. nov.

*Pl. 77.*

*Material* – Holotype: NHM BZ 5043(1a), Maastrichtian, Prairie Bluff Chalk, Jefferson, Marengo County, Alabama (locality AL5). Paratypes: NHM BZ 5043(1b), encrusting same shell as holotype. NHM BZ 4825, Maastrichtian, Ripley Formation, Florence, Quitman County, Georgia (locality GA1).

*Etymology* – After Thomas Jefferson who gave his name to the type locality in Marengo County, Alabama.
Description – Colony encrusting, multiserial, unilaminar. Ancestrula unknown. Pore chambers elongate, the distal and two distolateral pore chambers extending along entire length of the zooidal walls containing them.

Autozooids elongate rhomboidal (Pl. 77, figs 1a, 2), on average 1.4-1.5 times longer than wide, surrounded by distinct furrows. Gymnocyst very narrow, lacking a well-defined mural rim separating it from the cryptocyst. Cryptocyst extensive, shelf-like, sloping downwards towards opesia and indented close to proximolateral corners of opesia; evenly and densely pustulose. Opesia higher than wide, rounded trapezoidal with a constriction about mid-length, occupying less than half of frontal zooidal surface. Oral spines lacking. Ovicell (Pl. 77, fig. 1b) hyperstomial(?), the floor depressed a little into the distal zooid; ooeial surface cryptocystal, finely pustulose, resembling and continuous with the cryptocyst of the distal zooid, about 135-150 μm long by 165-180 μm wide. Closure plates (Pl. 77, fig. 1e) cryptocystal, pustulose, bearing deep indentations formed by a marginal opercular sclerite proximal of which is a subcircular or transversely elliptical opening; operculum (as defined by sclerites) about 50 μm high by 60-70 μm wide. Basal walls fully calcified.

Avicularia lacking.

Kenozooids occasionally developed along lateral zooidal boundaries, narrow (Pl. 77, fig. 1b).

Measurements – Holotype: ZL 395±49, 315-480 (1, 10); ZW 269±27, 240-315 (1, 10); OpL 129±10, 120-150 (1, 10); OpW 120±7, 105-135 (1, 10).

Remarks – The Oligocene type species of this genus differs from *F. jeffersoni* in having opesiae with far stronger medial constrictions and proportionally larger oovicells. Another species, *Floridinella deshayesi* (von Hagenow, 1851) from the type Maastrichtian, appears to be very similar to *F. jeffersoni* on the basis of von Hagenow’s small figure (1851, pl. 11, fig. 18). However, the zooids in *F. deshayesi* are depicted as being more diamond-shaped.

Among species described in the current study, *F. jeffersoni* closely resembles *Amphirolestrum denticulatum* from which, however, it is distinguished by lacking avicularia, having relatively smaller opesiae and oovicells with pustulose, cryptocystal (interior-walled) roofs compared to the smooth, gymnocystal (exterior-walled) oovicell roofs of *A. denticulatum*.

Tyloporella Voigt, 1989b

Type species – *Tyloporella reussi* Voigt, 1989b, Cenomanian, Germany; by original designation.

Remarks – This genus was proposed by Voigt (1989b) for a species from the German Cenomanian which had been described as *Membranipora tenuisulca* by Reuss (1872), but was not the same as *Membranipora tenuisulca* Reuss, 1846. Material described by Novak (1877) that was included by Voigt in the synonymy of the type species from the Turonian of the Czech Republic has been studied with K. Zágorsek (National Museum, Prague). The elongate zooids have extensive, depressed cryptocysts and large
opesiae which are semi-elliptical and higher than wide. Small avicularia are present, usually located just distally of the autozooidal opesia and directed distally. Voigt (1989b) noted the presence of 2-3 pairs of oral spines and hyperstomial ovi-cells, although these features are not evident in the scanning electron micrographs of the Czech specimens of the type species.

**Range** – Cenomanian-Thanetian.

*Tyloporella cretacea* (Canu & Bassler, 1926)

Pl. 78.

1926 *Ammatophora cretacea* sp. nov.; Canu & Bassler, p. 35, pl. 4, fig. 17.

In press *Tyloporella cretacea* (Canu & Bassler); McKinney & Taylor, fig. 2A.

**Material** – Lectotype (here designated): USNM 69952, specimen encrusting a small shell figured by Canu & Bassler (1926, pl. 4, fig. 17), Maastrichtian, Ripley Formation, Coon Creek Member, Coon Creek, McNairy County, Tennessee (locality TN1). Paralectotype: USNM 528401, specimen encrusting a larger shell not figured by Canu & Bassler (1926), details as for lectotype. Other material: NHM BZ 5044, Maastrichtian, Ripley Formation, Coon Creek Member, grey silty fine sands in stream bed, ‘*Inoceramus* Bed’ auctt., Coon Creek, McNairy County, Tennessee (locality TN1; S. Tracey Collection). BZ 5045, Maastrichtian, Ripley Formation, Coon Creek Member, shelly lenticles in upper part – *Corbula* bed auctt.; upstream of Coon Creek Field Station, McNairy County, Tennessee (locality TN1; S. Tracey Collection).

**Description** – Colony encrusting, multiserial, unilaminar. Ancestrula and early astogenetic stages unknown. Presence of pore chambers uncertain, possibly lacking.

Autozooids elongate rhombooidal to rounded rectangular, on average about 2.7 times longer than wide, surrounded by distinct furrows. Gymnocyst lacking. Cryptocyst extensive, shelf-like, somewhat depressed immediately proximally of the opesia, finely pustulose, pustules bordering proximal edge of opesia aligned in radial rows. Opesia higher than wide, semi-elliptical, with almost straight proximal margin, occupying about half of frontal zooidal surface. Spines lacking. Ovicell (Pl. 78, figs 1c, 2a, b) hyperstomial, small, but prominent, the roof comprising smooth exterior wall (ecto-oecium), apparently raised into an umbo-like point in at least some examples. Closure plates and intramural buds not observed.

Avicularia (Pl. 78, fig. 1b) present distally of the opesia in some non-ovicellate zooids, small, directed either laterally or proximally, poorly-formed, seemingly without calcified hinge, but with constriction separating broader proximal part from longer distal part with blunt-ended rostrum.

Kenozooids (Pl. 78, fig. 3) budded in place of autozooids at distal edges of NHM BZ 5044 and BZ 5045, extending for at least six longitudinal rows, rhombooidal to rectangular in outline shape, shorter in length than autozooids, with a subcircular, central opesia surrounded by pustulose cryptocyst, pustules becoming smaller and aligned in radial rows on countersunk margins of opesia.
Measurements – Lectotype: ZL 588±100, 500-740 (1, 10); ZW 218±27, 180-260 (1, 10); OpL 216±25, 160-240 (1, 10); OpW 150± 17, 120-180 (1, 10); OvL 122±15, 100-140 (1, 10); OvW: 156±30, 120-200 (1, 10).

Remarks – Canu & Bassler (1926) originally assigned this species to Ammatophora Norman, 1903, a calloporid with a Recent type species, A. nodulosa (Hincks, 1877). According to Ryland & Hayward (1977, p. 108), Ammatophora is characterized by having interzooidal nodes, structures not present in the Cretaceous species. Instead, Canu & Bassler’s Coon Creek species is much more similar to the European Cenomanian-Turonian species Tyloporella reussi Voigt, 1989b, with which it is here regarded as congeneric. The main differences appear to be the transverse orientation of the avicularia in T. cretacea compared with their distal orientation in T. reussi and the proportionally somewhat larger opesia in the North American species.

It seems likely that Tyloporella cretacea is also closely related to Ellisinidra heteropora (Gabb & Horn, 1862) as interpreted by Canu & Bassler (1933). To judge from Canu & Bassler’s illustration (pl. 1, fig. 8), this species, from the Paleocene Vincentown Limestone of New Jersey and Delaware, has autozooids of very similar aspect to those of T. cretacea, with a small transverse or oblique avicularium distally of each autozooid. Whether Canu & Bassler correctly identified Gabb & Horn’s species is not known. However, they included it as the second species in their new genus, Ellisinidra. The type species of Ellisinidra, Membranipora levata Hincks, 1882, is also the type species of Ellisina Norman, 1903 (see Osburn, 1950) and Ellisinidra is, therefore, an objective junior synonym of Ellisina.

Both NHM colonies of this species are fragmentary and comprise mostly or entirely kenozooids (Pl. 78, fig. 3). These kenozooids presumably survived because they are more heavily calcified than the fragile autozooids. Although their function is unclear, there may be parallels with the bizarre sealed zooids budded in bands in the Campanian cheilostome Micropora bedensis (Brydone, 1936) which have been described by Voigt (1975). It seems possible that these zooids are budded as a response to and/or a survival strategy against predators or adverse conditions.

Family Chaperiidae Jullien, 1888

Hagenowinella Canu, 1900

Type species – Cellepora (Marginaria) vaginata von Hagenow, 1851, Maastrichtian, Maastricht, The Netherlands; by original designation.

Remarks – This genus, revised by Gordon (1982), was previously only recorded from the Campanian and Maastrichtian of northwest Europe (Voigt, 1988). It is recognizable among the numerous anascan genera with shelf-like cryptocysts by the presence of occlusor laminae. These ridges or processes projecting into the distolateral part of the opesia would have been points of insertion for the opercular occlusor muscles. Occlusor laminae are an apomorphy of the Family Chaperiidae, a family which is especially diverse in the southern hemisphere at the present day (Gordon, 1982). Vicarious avicularia and endozoooidal ovi cells are present in Hagenowinella, but have yet to be identified in the new species described here.
Range – Campanian-Maastrichtian.

Hagenowinella alabamaensis sp. nov.
Pl. 79, fig. 1.

Material – Holotype: NHM BZ 4815, Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL7).

Etymology – From the type occurrence in Alabama.

Description – Colony encrusting, multiserial, unilaminar. Pore chambers present. Ancestrula unknown, although holotype does preserve some small, proximal zooids evidently from zone of primary astogenetic change.

Autozooids rounded hexagonal in outline shape (Pl. 79, fig. 1b), distal edges convex, slightly upstanding proximal edges concave, broad, on average 1.1 times longer than wide. Gymnocyst lacking or very slightly developed in proximal corners of zooids; spine bases absent. Cryptocyst very extensive, forming a shelf occupying about proximal two-thirds of frontal surface, densely pustulose. Opesia semielliptical, wider than long, the proximal margin straight, distolaterally indented by a pair of processes (occlusor laminae) originating from vertical walls just beneath level of opesia (Pl. 79, fig. 1d). Ovicells unknown. Neither reparative buds nor closure plates present.

Avicularia not observed despite existence of row divisions where they might be expected by comparison with congeneric species.

Kenozooids represented by a single example, the same size as an autozooid, with a cryptocystal frontal shield having a large, longitudinally elliptical, central opening.

Measurements – Holotype: ZL 347±22, 315-390 (1, 10); ZW 309±23, 270-345 (1, 10); OpL 104±9, 90-120 (1, 10); OpW 159±10, 150-180 (1, 10).

Remarks – Compared to the type species of Hagenowinella, H. vaginata (von Hagenow, 1851) (see Gordon, 1982, fig. 6A), this new species has a much deeper proximal cryptocyst and correspondingly smaller opesia. The autozooids of a second European Maastrichtian species, H. dentata (Goldfuss, 1826), have a more extensive proximal cryptocyst than H. vaginata, although this character is still not as well developed as in H. alabamaensis, and there is a median denticle projecting into the distal edge of the opesia. Unfortunately, avicularia (if present) and ovicells have yet to be found in the new species from Alabama.

The knob-like shape of the oculusor laminae and overall morphology of the autozooids recall some Oligocene species that were referred to Floridina by Cheetham & Håkansson (1972), although the cryptocyst is more sunken in these bryozoans from the Rockall Plateau.

Family Onychocellidae Jullien, 1882
Onychocella Jullien, 1882

Type species – Onychocella marioni Jullien, 1882 (= Cellepora angulosa Reuss, 1848), Miocene-Recent, Europe; by original designation.
Remarks – Problems concerning the definition of *Onychocella* were discussed by Gordon & Taylor (1999, pp. 24-25). It is unclear whether the diverse Cretaceous species assigned to this genus, especially those with erect bifoliate colonies, really are congeneric with the Miocene-Recent type species which is an encruster. Several other generic names are available, for example *Semieschara* and *Rhaegasostoma*, but these await revision (see also Schmidt & Bone, 2004).

Range – Cenomanian-Recent.

*Onychocella alveolata* sp. nov.
Pl. 79, fig. 2; Pls. 80, 81.

Material – Holotype: USNM 526180, Maastrichtian, Peedee Formation, Neuse River, Lenoir County, North Carolina (locality NC4). Paratypes: USNM 526181-526184, 526186-526191 (thin sections), details as for holotype. Other material: USNM 526185 (sample), same details.

Etymology – L., *alveus*, cavity, in reference to the cavity within the cryptocyst.

Description – Colony erect, bifoliate, the branches strap-like (Pl. 80, fig. 1a), about 4-6 mm in width, up to 2 mm thick, bifurcating and sometimes anastomosing to give a cribrate structure, occasional new branches originating at right angles to surface of parent branches. Ancestrula unknown. Base somewhat expanded, covered by kenozooids.

Autozooids arranged in rows, boundaries becoming ill defined in older branches, rhomboidal, very slightly longer than wide, the distal and distolateral edges a little convex, proximal and proximolateral slightly concave. Gymnocyst and spines lacking. Cryptocyst well-developed, depressed (except in very old branches), variably pustulose, compound, a primary cryptocyst forming the outermost calcified surface in proximal parts of young zooids becoming overarched by secondary cryptocyst extending proximally from opesial rim (Pl. 80, fig. 1c) enclosing a hollow cavity (Pl. 80, fig. 2); secondary cryptocyst surrounding opesia with weak concentric ornament in young zooids (Pl. 80, fig. 1c). Opesia sunken, occupying up to half frontal surface, in young zooids semieliptical, the proximal edge slightly convex, higher than wide or equidimensional, in old zooids becoming transversely elliptical; often with a narrow, salient rim and occasionally preserving a pair of small, closely-spaced condyles either side of the mid-line on the proximal edge. Ovicells not evident on colony surface (but see below). Closure plates and intramural buds lacking.

Avicularia (Pl. 79, fig. 2a; Pl. 80, fig. 1d) usually associated with row bifurcations, about same length as autozooids, but narrower, opesia longitudinally elliptical, rostrum acuminate, narrow, curved to left or right, accommodated in furrow between autozooids, sometimes becoming enveloped by cryptocyst of adjacent autozooids.

Kenozooids developed around colony base and occasionally elsewhere, polygonal, variable in size, but generally smaller than autozooids, opesia subcircular, reduced, surrounded by funnel-shaped cryptocyst.

Skeletal microstructure cloudy or ‘clotted’ (Pl. 81, figs. 1, 2), fibrous, the fibres oriented at about 45° to wall surface in branch transverse sections. Autozooidal chambers...
in longitudinal sections with a rounded, wedge-shaped proximal part, close to the distal end of which arises a long perpendicular tube, the entire chamber resembling a foot and lower leg (Pl. 81, fig. 5). Tangential sections show thin, non-cloudy zoecial layer around opesia that includes the paired condyles. Possible ovicell visible in longitudinal section of one autozooid, represented by bulge-like enlargement of proximal chamber (Pl. 81, fig. 4).

**Measurements** – Holotype: ZL 330±26, 300-375 (1, 10); ZW 320±20, 300-360 (1, 10); OpL 134±11, 120-150 (1, 10); OpW 146±10, 135-165 (1, 10); AL 311±35, 270-360 (1, 10); AW 188±15, 165-210 (1, 10); AoL 128±13, 105-150 (1, 10); AoW 93±9, 75-105 (1, 10).

**Remarks** – The peculiar cryptocyst of *Onychocella alveolata* warrants further consideration. Young autozooids close to branch growing edges have deeply depressed, pustulose cryptocysts over the proximal third to half of the zooid (Pl. 80, fig. 1b). Distal to this primary cryptocyst, around the opesia, is a secondary cryptocyst with a somewhat ragged proximal edge located slightly above the level (i.e., frontally) of the primary cryptocyst. In older zooids the secondary cryptocyst evidently overgrows the primary cryptocyst, and damaged zooids in which the secondary cryptocyst is broken reveal the presence of a hollow between it and the underlying primary cryptocyst (Pl. 80, fig. 2). It is possible that this hollow within the cryptocyst was originally occupied by diagenetically unstable aragonite or high-Mg calcite. Alternatively, it could have been a coelom-filled cavity. Subsequent growth of the thick secondary cryptocyst walls upwards increases branch depth considerably and results in zooids with long, tubular distal extensions (Pl. 81, fig. 4).

Other Cretaceous onychocellids show similar hollows (‘Cavernen’), notably *Solenonychocella hennigi* Voigt & Williams, 1973, and *Onychocellaria rhombica* (von Hagenow, 1851) (see Voigt, 1979). Unlike *O. alveolata*, however, these two European Maastrichtian species have subterminal opesiae. Other onychocellids resembling *O. alveolata*, including *O. propinqua* (see Voigt, 1979, pl. 5, fig. 1) and *O. regularis* von Hagenow, 1851 (see Voigt, 1959, pl. 7, figs 3-4), lack the cryptocystal hollows seen in the new North American species.

**Cheethamia Shaw, 1967**

**Type species** – *Cheethamia howei* Shaw, 1967, Maastrichtian, Arkansas; by original designation.

**Remarks** – This genus was created by Shaw (1967) for the North American type species plus two European Cretaceous species, *Membranipora nodulifera* Levinsen, 1925, and *Onychocella pinguis* Voigt, 1962. Differences from the related *Onychocella* include the presence of hyperstomial ovicells and generally straight avicularia. Oral spines also occur in *Cheethamia*, but are lacking in the type species of *Onychocella*, *O. angulosa* Reuss, 1848. Indeed oral spines are seldom present in any species of *Onychocella*, *O. propinqua* (von Hagenow, 1851) furnishing a rare exception (see Voigt, 1979, pl. 2, fig. 2).

**Range** – Campanian-Maastrichtian.
Cheethamia howei Shaw, 1967
Pls. 82, 83.

Material – Holotype: LSUMG-I 8237, Campanian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2). Other material: NHM BZ 5049, Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1). NHM BZ 5155(3), Campanian, Demopolis Chalk, Macon, Noxubee County, Mississippi (locality MS1). NHM BZ 5055, Maastrichtian, Ripley Formation, Florence, Quitman County, Georgia (locality GA1). NHM BZ 5226(2), Maastrichtian, Prairie Bluff Chalk, Braggs, Lowndes County, Alabama (locality AL3). NHM BZ 4794(a), BZ 4794(b), BZ 4814, Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5). NHM BZ 4789, BZ 5043(2), Maastrichtian, Prairie Bluff Chalk, Jefferson, Marengo County, Alabama (locality AL5). NHM BZ 4790, BZ 4795(1), BZ 4802(1), BZ 4809, BZ 5050(2), BZ 5178(2), BZ 5183-5, NNM RGM 507 013(2), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). NHM BZ 5052-4, NNM RGM 507 014(1), 507 055, Maastrichtian, Prairie Bluff Chalk, Emelle, Sumter County, Alabama (locality AL9). RU 5525, RU 5633, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 and/or NJ2).

Description – Colony encrusting, multiserial, unilaminar, sometimes becoming multilaminar through eruptive budding (Pl. 83, fig. 3) or spiral overgrowth, often attaining a large size (>25 mm diameter). Ancestrula (Pl. 82, fig. 3) longitudinally ovoidal, about \(340 \times 280 \mu m\), the frontal shield entirely cryptocystal and pustulose, a groove separating a narrow marginal area from the main part of the shield which is gently convex; opesia semieliptical, about \(80 \mu m\) in both length and width, occupying a proportionally smaller frontal area than in later zooids, lacking oral spines; three periancestrular buds, distal and left and right distolateral, later buds derived from the distolateral zooids encircling the proximal side of the ancestrula; zooid size increasing gradually through primary zone of astogenetic repetition encompassing at least six zooidal generations. Growing edge variably stepped or smooth (Pl. 83, fig. 1); pore chambers lacking. Reparative, proximally-directed growth observed from fractured colonies.

Autozooids large, rhomboidal, variably elongate, on average about 1.3 times longer than wide, boundary walls conspicuously raised in most specimens. Gymnocyst lacking. Oral spine bases present in many autozooids, small, paired, closely spaced, located on distal border of opesia (Pl. 82, fig. 2c). Cryptocyst extensive, convex, finely pustulose, the pustules becoming smaller close to opesia. Opesia semieliptical, high arched, proximal edge straight or slightly bowed defining poorly-differentiated opesiules at proximolateral corners, rim slightly salient, especially around distal margin, occupying between one half and a third of zooidal length, a pustulose vestibular arch visible within distal part of opesia of non-ovicellate zooids. Ovicell (Pl. 83, fig. 2c) small, hyperstomial, cap-like, roof cryptocystal, pustulose, continuous with frontal shield of distal zooid; oral spines lacking or obscured; floor sunken into distal zooid, divided from opesia of fertile zooid by an arched ridge. Closure plates and intramural buds not observed. Basal walls calcified.
Avicularia (Pl. 82, fig. 2d; Pl. 83, fig. 2b) interzooidal, usually located at row bifurcations (though not always developed here), absent in primary zone of astogenetic change, variable in size and shape, typically as long as or longer than autozooids, but narrower. Gymnocyst and spines lacking. Cryptocyst convex, pustulose. Distal part of avicularium dagger-shaped. Opesiuule small, circular, possibly confluent with opesia in some examples. Opesia small, longitudinally elliptical. Rostrum with short wings extending outwards at proximal end, main part long and narrow, acuminate, straight or slightly curved, margins raised, usually accommodated in grooves between autozooids, but occasionally lapping onto cryptocyst of an autozooid.

Kenozooids (Pl. 83, fig. 2d) very occasionally found, about the same size as autozooids, frontal surface consisting mainly of convex cryptocyst pierced by a small central pore.

Measurements – ZL 686±47, 630-750 (1, 10); ZW 513±68, 375-585 (1, 10); OpL 161±10, 150-180 (1, 10); OpW 209±17, 180-225 (1, 10); AL 808±98, 615-915 (1, 8); AW 349±32, 300-405 (1, 10).

Remarks – This species is quite common encrusting shells in the Ripley Formation and Prairie Bluff Chalk of Alabama, and is easily distinguished by its large, robust zooids with cryptocystal frontal shields and semielliptical opesia. The small median opesiule of the avicularium is often obscured by sediment grains, probably accounting for the failure of Shaw (1967) to notice it. Examples in which this opesiule is confluent with the opesia may be due to breakage of the intervening cryptocyst.

Shaw (1967) regarded Cheethamia as an age indicator for the Maastrichtian. However, it is now clear that the type species ranges down into the Upper Campanian: the Saratoga Chalk is now considered to be latest Campanian, and the species has also been found in the Upper Campanian Mount Laurel Formation of Delaware.

Cretaceous onychocellids commonly exhibit high degrees of intraspecific zooidal variation (e.g., Voigt, 1975, pl. 1, figs. 1-4) and C. howei is no exception in this respect. Some colonies have highly raised zooidal boundary walls that form prominent features on the frontal surfaces, whereas in others these walls are low and the convex frontal shields of the autozooids provide the main topographical features.

A remarkable triple autozooid was found in a colony from the Ripley Formation (Pl. 82, fig. 2a). This zooid is very broad, spreading out across three zooidal rows. It is likely that the zooid originated from the fusion of three buds, comparable to some of the ‘monster zooids’ described previously in several cheilostome species (Jebram, 1977; Jebram & Voigt, 1977), especially Cryptosula pallasiana (Moll, 1803).

Aechmella Canu & Bassler, 1917

Type species – Aechmella filimargo Canu & Bassler, 1917, Eocene, Alabama; by original designation.

Remarks – This onychocellid has opesular indentations at the proximolateral corners of the broad, but typically low, opesia, an endozooidal ovicell and small lanceolate interzooidal avicularia. Although the type species comes from the Eocene, quite a large
number of Cretaceous (see Voigt, 1930) and Paleocene (see Berthelsen, 1962) species have been assigned to *Aechmella*.


*Aechmella indefessa* sp. nov.

Pl. 84.

**Material** – Holotype: ANSM 80354A, Campanian, Mount Laurel Formation, Chesaapeake & Delaware Canal, New Castle County, Delaware (locality DE1). Paratypes: ANSM 80354B, the other colonies (3?) encrusting the same belemnite guard as the holotype.

**Etymology** – L., *indefessus*, indefatigable, referring to the survival and repair of colonies after damage.

**Description** – Colony encrusting, multiserial, unilaminar, large (holotype >20 mm in maximum diameter), sometimes showing reparative growth after partial destruction of zooids (Pl. 84, fig. 2b). Ancestrula morphology uncertain, possibly represented by a small (260 × 160 μm), heavily damaged zooid at focus of one paratype colony, similar in structure to later autozooids and apparently budding one distal and two distolateral daughter zooids. Pore chambers present, the distal pore chamber elliptical and facing distofrontally, any lateral pore chambers seemingly narrow.

Autozooids small, often in a scale-like arrangement (Pl. 84, fig. 1a) with opesiae aligned in transverse rows, elongate rhomboidal, on average about 1.25 times longer than wide, well-rounded distally and concave proximally; boundary walls raised in most specimens and separated from those of surrounding zooids by a narrow fissure. Gymnocyst and spines lacking. Cryptocyst forming a slightly convex, pustulose, frontal shield occupying most of frontal surface, somewhat depressed proximally of opesia. Opesia semieliptical, low, distal edge rather flattened, proximal edge concave, bowed; opesialues present at proximolateral corners; dimorphic, the opesia of ovicellate zooids larger and more convex distally. Ovicell (Pl. 84, fig. 1b) endozooidal?, partly immersed in next distal zooid, the roof slightly convex, pustulose and not demarcated from the proximal frontal shield of the distal zooid; floor sunken into distal zooid; internally, a ridge-like wall is present between maternal zooid and ovicell. Ovicellate autozooids with slightly larger opesia than non-ovicellate autozooids (mean 75 × 145 μm vs 62 × 134 μm). Closure plates very occasionally present. Intramural buds usually autozooidal, but one example observed of an avicularium budded within an autozooid (Pl. 84, fig. 2b). Basal walls fully calcified.

Avicularia (Pl. 84, fig. 2d) interzooidal, commonly, but not invariably, present at junctions between four autozooids, typically about half the length of an autozooid and substantially narrower, diamond-shaped with concave edges; rostrum of variable length, sometimes long and narrow, infilling space between laterally adjacent autozooids. Gymnocyst and spines lacking. Cryptocyst pustulose, sunken relative to the slightly raised boundary walls and opesial edge. Opesia elongate teardrop-shaped, acuminate, with or without subdued condyles.
Kenozooids developed at obstructions, irregular in shape, the entire frontal surface comprising cryptocyst, with or without an opesial opening.

*Measurements* – Holotype: ZL 417±36, 360-480 (1, 10); ZW 333±38, 285-420 (1, 10); OpL 62±6, 53-75 (1, 10); OpW 134±9, 120-150 (1, 10); AL 258±40, 210-345 (1, 10); AW 111±23, 75-150 (1, 10); AoL 65±10, 45-75 (1, 10); AoW 40±7, 30-45 (1, 10).

*Remarks* – Shaw (1967) named a species *Aechmella ozanensis* from the North American Cretaceous, but this is here reassigned to *Pavolunulites*, leaving the new species *Aechmella indefessa* as the only North American Cretaceous species belonging to this genus. Material of two European species from the Upper Cretaceous Chalk in the NHM collections that were identified by Prof. E. Voigt resemble *A. indefessa* sp. nov. in general features of autozooidal and avicularian morphology. However, as represented by specimen NHM D38923 from the Maastrichtian of northern Germany, *A. anglica* (Brydone, 1909) has autozooids with markedly more convex frontal shields and which are about half as long again as those of *A. indefessa*. German Maastrichtian material (NHM D38925) of a second species, *A. biconvexa* (Brydone, 1909), also differs in its larger, more convex zooids and in having avicularia with extensive palates.

**Reptolunulites** d'Orbigny, 1852

*Type species* – *Reptolunulites angulosa* d'Orbigny, 1852 (*in* 1851-1854), Senonian (Turonian?), Sougé, France; by subsequent designation (Bassler, 1935).

*Remarks* – *Reptolunulites*, despite possessing autozooids that strongly resemble those of *Lunulites*, has encrusting rather than free-living, lunulitiform colonies, and was excluded from the Lunulitidae by Cook & Chimonides (1986). It may, however, be a valid and useful genus within the Onychocellidae. The type species of *Reptolunulites*, *R. angulosa*, was refigured by Voigt (1981, fig. 6a), who gave its horizon as Turonian (cf. d’Orbigny, 1852 (*in* 1851-1854, who gave it as Senonian). Like material of the new species described below, the type specimen of *R. angulosa* encrusts a small pebble, but does not extend beyond the perimeter of the pebble and therefore fails to become effectively free-lying.

*Range* – Turonian-Maastrichtian.

**Reptolunulites zipfi** sp. nov.

Pl. 85.


*Etymology* – This new species is named for Karl Zipf who collected all the known specimens, and kindly made these and material of other bryozoans in his collections freely available for our study.
Description – Colony encrusting (Pl. 85, fig. 1a), multiserial, unilaminar. Ancestrula and early astogeny unknown.

Autozooids rounded rhomboidal in frontal outline, the distal and distolateral edges convex, the proximal and proximolateral edges concave, longitudinally elongate to almost equidimensional, averaging 1.2 times longer than wide; edges of zooids smoothly raised with a fissure at the zooidal boundary. Gymnocyst and spines lacking. Cryptocyst extensive, shelf-like, depressed, pustulose, the pustules densest near perimeter of zooid and surrounding opesia. Opesia occupying slightly less than a half of the frontal area, bell-shaped (Pl. 85, fig. 1c), higher than wide, with opesiular indentations at the proximolateral corners. Ovicell (Pl. 85, fig. 1d) cap-like, small, immersed, roofed by pustulose cryptocyst calcification continuous with that of the distal zooid. Closure plates and intramural buds not observed.

Avicularia (Pl. 85, fig. 1e) interzooidal, common, developed either singly or in pairs between autozooidal rows, smaller or equivalent in length to autozooids, but narrower. Gymnocyst lacking. Cryptocyst concave, pustulose. Opesia elongate, ovoidal, rounded V-shaped proximally, inverted U-shaped distally. Rostrum more than half total avicularium length, usually straight, spatulate, round ended, lapping onto cryptocyst of distal autozooid; palate extensive, bearing pustules.

Measurements – ZL 542±53, 465-645 (1, 10); ZW 452±46, 375-540 (1, 10); OpL 183±14, 165-210 (1, 10); OpW 188±18, 165-225 (1, 10); AL 628±83, 465-705 (1, 6); AW 228±31, 195-270 (1, 6); AoL 245±20, 225-270 (1, 6); AoW 123±11, 105-135 (1, 6).

Remarks – Compared with the two species of Reptolunulites (R. angulosa and R. ovalis) described by d’Orbigny (1852 in 1851-1854), this new species has broader autozooids. The distinct opesiular indentations seen in the proximolateral corners of the opesia of R. zipfi are not evident in R. angulosa which has longitudinally elliptical rather than bell-shaped opesiae. The zooidal boundary walls of R. zipfi are less prominent than those of R. angulosa and the avicularian rostrum is more spatulate.

Among the species here described from eastern North America, R. zipfi most closely resembles Pavolunulites ozanensis (Shaw, 1967). It can be distinguished, however, by its encrusting colony form, opesiular indentations and decreasing pustule density away from the perimeter of the zooids and the opesiae.

Family Bryopastoridae d’Hondt & Gordon, 1999
Pseudothyracella Labracherie, 1975

Type species – Pseudothyracella pulchella Labracherie, 1975; Eocene, Aquitaine Basin, France; by original designation.

Remarks – This genus was established by Labracherie (1975) for narrow-branched, non-bifurcating anascans that probably had articulated, cellariiform colonies during life. The autozooids are simple and arranged in well-defined longitudinal rows. There are occasional vicarious avicularia somewhat larger than the autozooids. Voigt (1987) refigured the type species of Pseudothyracella, P. pulchella from the Lower Eocene, and assigned one new Paleocene species firmly to the genus and two existing species provisionally.
The Maastrichtian species here referred to *Pseudothyracella* possesses avicularia, but these are not generally as large as the autozooids, thereby placing a question mark over its attribution. Although originally described by Shaw (1967) as *Solenophragma elongatum*, it does not belong to *Solenophragma* Marsson, 1887, which lacks avicularia and has prismatic zooids in the branch axis.

**Range** – Maastrichtian-Recent.

*Pseudothyracella elongata* (Shaw, 1967)

Pl. 86, figs. 1-3.

1967 *Solenophragma elongatum* sp. nov.; Shaw, p. 1407, pl. 179, fig. 2.

**Material** – Holotype: LSUMG-I 8236, Maastrichtian, Nacatoch Formation, Arkadelphia, Clark County, Arkansas (locality AR1). Other material: USNM 526192, 526193 (four fragments), Maastrichtian, Peedee Formation, Neuse River, Lenoir County, North Carolina (locality NC1). NHM BZ 5056, NNM RGM 507 015, Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). NHM BZ 5223 (8 fragments), Maastrichtian, Peedee Formation, Burgaw, Pender County, North Carolina (locality NC1).

**Description** – Colony erect, dendroid, comprising narrow, relatively straight branches that taper proximally (Pl. 86, fig. 1a), but do not bifurcate, suggesting that colonies were probably articulated.

Autozooids arranged in well-defined longitudinal rows, up to ten rows around the branch circumference, elongate rhomboidal in frontal outline shape, on average about 1.75 times longer than wide, distal edge convex; zooidal boundary salient. Gymnocyst and spines lacking. Cryptocyst well developed proximally, shelf-like, depressed, not pustulose, a subcircular facet or pore present in some zooids perhaps signifying the position of a rootlet. Opesia large, occupying slightly more than half of frontal surface, generally pear-shaped and widest proximally, but oval and widest distally in NHM BZ 5056. Ovicells unknown. Neither closure plates nor intramural buds seen.

Avicularia (Pl. 86, fig. 3b) present at row bifurcations, slightly smaller than autozooids; opesia oval, slender; rostrum tapering evenly to a well rounded end; palate occupying about one third of opesial length, sloping inwardly.

**Measurements** – ZL 338±41, 285-435 (1, 10); ZW 192±9, 180-210 (1, 10); OpL 176±14, 150-195 (1, 10); OpW 117±6, 105-120 (1, 10); AL 330 (1, 1); AW 135 (1, 1); AoL 135 (1, 1); AoW 90 (1, 1).

**Remarks** – Very limited material is available of this species, but the straight, narrow, non-bifurcating branches suggest that colonies may have been jointed during life, an inference supported by the facets on a few zooids that may have supported a chitinous rootlet of the kind often found in such cellariiform cheilostomes. Some specimens from the Prairie Bluff Chalk of Livingston are provisionally assigned to this species even though the detailed shape of the opesia differs from the type material (compare Pl. 86, figs. 2 and 3a).
The North American species is very similar to a Maastrichtian species from Germany and The Netherlands illustrated by Voigt (1951, pl. 10. figs 1-2) as *Siphonella cylindrica* von Hagenow, 1851 (the genus *Siphonella*, as applied to bryozoans by von Hagenow, is preoccupied).

**Family Lunulitidae Lagaaj, 1952**

*Pavolunulites* d’Orbigny, 1852 *(in 1851-1854)*

**Type species** – *Pavolunulites costata* d’Orbigny, 1852 *(in 1851-1854)*, Senonian, Meudon, France; by subsequent designation (Bassler, 1935).

**Remarks** – This genus, established by d’Orbigny (1852 in 1851-1854) for two French Upper Cretaceous species, is here used for flabellate, non-cemented and apparently free-living cheilostomes that lack the integrated, symmetrical colonies found in *Lunulites* and similar genera (see Cook & Chimonides, 1986). Several northwest European Maastrichtian species of *Pavolunulites* were described by Håkansson & Voigt (1996), but the genus has not previously been recorded in the North American Cretaceous.

**Range** – Coniacian-Danian. Voigt (1981) recorded two species from the Coniacian, probably the oldest examples of this genus.

*Pavolunulites ozanensis* (Shaw, 1967)

Pl. 86, fig. 4.

1967 *Aechmella ozanensis* sp. nov.; Shaw, p. 1415, pl. 180, fig. 2.

**Material** – Holotype: LSUMG-I 8241, Campanian, Upper Ozan Formation, White Cliffs Station, Sevier County, Arkansas (locality AR3). Shaw (1967) also mentioned a paratype (LSUMG-I 8286), but this has not been examined.

**Description** – Colony unilaminar, not attached to a hard substrate, underside comprising basal, exterior(?) walls of zooids with grooves between. Ancestrula and early astogeny unknown.

Autozooids rounded polygonal to scale-like in outline shape, the distal and lateral borders strongly convex, proximal borders strongly concave, length about 1.25 times width on average; edges of zooids smoothly raised with a fissure at the zooidal boundary. Gymnocyst and spines lacking. Cryptocyst extensive, depressed, pustulose over entire surface (Pl. 86, fig. 4b). Opesia occupying between half and a third of frontal area, rounded rectangular to pear-shaped, higher than wide, proximal edge gently convex. Ovicell unknown. Closure plates and intramural buds not observed.

Avicularia (Pl. 86, fig. 4c) located one at the side of each autozooid, elongate, considerably narrower and somewhat shorter than autozooids, lozenge-shaped. Gymnocyst lacking. Cryptocyst pustulose, restricted to a narrow crescent at proximal end of zooid. Opesia longitudinally elliptical. Rostrum accounting for about half total avicularium length, sometimes slightly curved, almost parallel sided, expanding a little distally, round ended, lapping onto cryptocyst of distal autozooid.
Measurements – Taken from Shaw (1967): ZL 430±40, 380-450 (?; 8); ZW 340±38, 280-380 (?; 8); OpL 140±19, 120-150 (?; 7); OpW 130±12, 120-150 (?; 7); AL 340±40, 280-380 (?; 7); AW 120±12, 110-140 (?; 7).

Remarks – As noted by Shaw (1967), the holotype (Pl. 86, fig. 4a) comprises four autozooids, plus three avicularia, representing a tiny fragment of what was undoubtedly a much larger colony. The lack of any bioimmuration of the substrate on the underside suggests that the colony either grew freely or was loosely attached to a soft substrate. The former alternative is favoured and Shaw’s species is thereby transferred from *Aechmella* to the lunulitid genus *Pavolunulites*. Indeed, the colony underside of *P. ozanensis* compares well with that of *P. elegans* d’Orbigny as figured by Voigt (1981, fig. 6c). Features of the frontal surface, including autozooidal and avicularian morphology, also match those of other Cretaceous species of *Pavolunulites*. The type species of *Pavolunulites*, *P. costata* d’Orbigny, has avicularia with shorter rostra than *P. ozanensis*. The avicularia in this species occur at row bifurcations. A similar distribution may characterise *P. ozanensis* although the minute size of the only studied colony makes this impossible to prove.

Family Microporididae Gray, 1848

*Stictostega* Shaw, 1967

Type species – *Stictostega durhami* Shaw, 1967, Campanian, Arkansas, U.S.A.; by original designation.

Remarks – Previously regarded as a hippothoid ascophoran, Taylor & McKinney (2000) showed that *Stictostega* was a microporid anascan and gave a revised diagnosis for the genus. It is characterized by having an extensive, convex, evenly porous cryptocyst and small distal avicularia. The cryptocyst is reminiscent of *Macropora*, but this Cenozoic genus has calcified opercula, very large ovicells and vicarious avicularia. While the type species and the two new species described below are all from North America, it is possible that the genus also occurs in Europe as *Puncturiella tenera* (Voigt, 1924), as interpreted by Berthelsen (1962, p. 156, pl. 17, fig. 3), may perhaps belong to *Stictostega*.

Range – Campanian-Maastrichtian, Danian?

*Stictostega durhami* Shaw, 1967

Pl. 87.

1967 *Stictostega durhami* sp. nov.; Shaw, p. 1423, pl. 182, fig. 6.
2000 *Stictostega durhami* Shaw; Taylor & McKinney, 2000, p. 1, figs. 1, 2.


Description – Colony encrusting, multiserial, unilaminar, growing edge stepped (Pl. 87, fig. 1c). Ancestrula and earliest astogenetic stages missing from both available specimens. Pore chambers not observed.
Autozooids elongate oval to rounded rhomboidal in outline shape, about 1.7 times longer than wide, zooidal boundaries marked by deep grooves. Gymnocyst and spines lacking. Cryptocyst extensive, occupying most of frontal surface, convex, pustulose, porous (Pl. 87, fig. 1b); pustules closely spaced, large, 10-15 μm in diameter; pores numbering up to 50 per zooid, about 15-20 μm in diameter, spaced 40-50 μm apart, evenly distributed over most of the cryptocyst, but lacking in a slightly depressed area with smaller pustules immediately proximal of the opesia. Opesia almost semicircular, wider than high, proximal edge outwardly bowed, the distolateral rim raised. Ovicell (Pl. 87, fig. 1d) small, wider than long, surface pustulose, imperforate, subimmersed, the opening apparently hyperstomial and convex, a longitudinal furrow sometimes present. Closure plates occasionally present, depressed, pustulose. Intramural kenozooids present in autozooids with damaged frontal shields (Pl. 87, fig. 1f).

Avicularia (Pl. 87, fig. 1e) interzooidal, small, located distally of non-ovicellate autozooids only. Opesia obliquely transverse, rostrum acuminate, curved and directed slightly proximally, sometimes with an apparent crossbar.

Kenozooids (Pl. 87, fig. 1a, upper left) sporadic, interzooidal, smaller than autozooids, variable and irregular in shape, surface imperforate, pustulose, with a central, elongate opesia.

**Measurements** – Holotype: ZL* 710±53, 640-770; ZW* 420±34, 370-470; OpL* 120±25, 80-150; OpW* 130±19, 120-150; OvL 240, 220-260; OvW 260, 240-280; AL 70, 60-100; AW 100, 80-120 (*taken from Shaw, 1967).

**Remarks** – The highly convex frontal shield and almost semicircular opesia of *S. durhami* distinguish it from the two new species described below.

**Stictostega turneri sp. nov.**

Pl. 88.

**Material** – Holotype: RU 5535, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2). Paratypes: RU 5530, details as for holotype. NHM BZ 5058, Maastrichtian, Navesink Formation, Poricy Creek, Monmouth County, New Jersey (locality NJ1).

**Etymology** – In honour of Dr Ronald F. Turner, who provided the holotype of this species as well as many other Navesink Formation species used in this study.

**Description** – Colony encrusting, multiserial, unilaminar. Ancestrula unknown. Zooids from primary zone of astogenetic change small, but otherwise similar to later zooids. Pore chambers lacking.

Autozooids rhomboidal in frontal outline, elongate, on average about 1.7 times longer than wide, zooidal boundary walls salient, prominent. Gymnocyst and spines lacking. Cryptocyst extensive, occupying most of frontal surface, moderately convex, sometimes with a few longitudinal ridges and furrows, densely pustulose (Pl. 88, fig. 1b), evenly porous except for imperfect area around opesia, the pores large and numerous (Pl. 88, fig. 2b). Opesia terminal, semielliptical, considerably wider than high,
proximal edge slightly convex, surrounded by a salient, crenulated rim; sometimes plugged by smooth (calcified operculum?) (Pl. 88, fig. 1b) or pustulose (closure plate?) calcification. Ovicell (Pl. 88, figs 1c, 2c) small, hyperstomial, crescent-shaped, low in relief, wider than long, surface cryptocrystalline, pustulose, imperforate or very sparsely porous, merging with cryptocrystalline of distal zooid; ovicell opening higher than opesia and probably not closed by operculum, Intramural buds not observed.

Avicularia (Pl. 88, fig. 1b) very small, located distally of most autozooids, usually longitudinally ovoidal.

Heterozooid (avicularium?, kenozooid?) located distally of opesia in some autozooids, absent in ovicellate autozooids; minute, rounded subtriangular in outline, about 100 μm in maximum dimension, opesia longitudinally elliptical.

Measurements – Holotype: ZL 659±68, 590-803 (1, 10); ZW 396±37, 336-468 (1, 10); OpL 75±9, 60-84 (1, 10); OpW 113±13, 97-136 (1, 10); OvL 123-125 (1, 2); OvW 159-175 (1, 2).

Remarks – This new species is distinguished from S. durhami (Shaw) by its salient boundary walls and relatively wider opesia, and from S. ovicincta sp. nov. by the lack of a smooth transverse rib on the proximal edge of the ovicell. Colonies are very thin and delicate (e.g., Pl. 88, fig. 1), and are easily overlooked or destroyed during weathering. The possible presence of a calcified operculum (Plate 88, fig. 1b) is notable in allying S. turneri with genera such as Macropora and Monoporella.

Stictostega ovicincta sp. nov.

Pl. 89.

In press Stictostega sp. nov.; McKinney & Taylor, fig. 2D.

Material – Holotype: NHM BZ 5949, Maastrichtian, Ripley Formation, Coon Creek Member, ‘Corbula’ bed’ auctt, Coon Creek Field Station, McNairy County, Tennessee (locality TN1; S. Tracey Collection). Paratypes NHM BZ 5059-5060, NNM RGM 507 016, details as for holotype except ‘Inoceramus’ bed’ auctt.

Etymology – L., cinctum, belt, referring to the belt-like structure forming the proximal rim of the ovicell above the opening.

Description – Colony encrusting, multiserial, unilaminar. Ancestrula and early astogenetic stages unknown. Pore chambers lacking. Basal wall incompletely calcified, an elliptical uncalcified window present.

Autozooids rhomboidal in frontal outline, distally well-rounded, elongate, on average about 1.6 times longer than wide, zooidal boundary salient, a fissure normally separating zooids belonging to adjacent rows. Gymnocyst and spines lacking. Cryptocrystalline extensive, occupying most of frontal surface, moderately convex, coarsely pustulose and with large pores distributed everywhere apart from zone immediately proximal of opesia, pores sometimes coalesced around perimeter. Opesia terminal, semieliptical, wider than high, proximal edge slightly convex and crenulated or beaded, small ope-
siular indentations present at corners in some zooids, rim somewhat raised, especially laterally, distal edge of opesia formed by salient zooidal boundary wall. Ovicell (Pl. 89, fig. 2c) small, hyperstomial, crescent-shaped, low in relief, small, wider than long, surface cryptocrystal, pustulose, non-porous, merging with cryptocryst of distal zooid, a transverse, grooved rib of smooth calcification at proximal edge of ooecium; opesia opening higher than opesia and possibly not closed by operculum. Closure plates and intramural buds not observed.

Avicularia (Pl. 89, fig. 3b) present distally of some non-ovicellate autozooids, small, ovoidal, about 90 μm by 70 μm, directed obliquely laterally, aperture dagger-shaped, cryptocryst forming a pustulose crescent, rostrum narrower and longer than opesia, tapering to a subangular point, pivotal bar lacking.

**Measurements** – Holotype: ZL 486±41, 450-570 (1, 10); ZW 314±37, 255-375 (1, 10); OpL 68±7, 60-75 (1, 10); OpW 122±9, 105-135 (1, 10); OvL 98±8, 90-105 (1, 6); OvW 203±8, 195-210 (1, 6).

**Remarks** – The main character distinguishing *S. ovicincta* from both *S. durhami* and *S. turneri* sp. nov. is the smooth rib of calcification around the ovicell opening (compare Pl. 89, fig. 2c with Pl. 88, fig. 1c), the ovicell also being shallower in *S. ovicincta*. Slight opesial indentations are also developed at the corners of the opesiae of some zooids (Pl. 89, fig. 3b), a feature not observed in the other two species of *Stictostega*, and the autozooids are rather shorter.

**Family Monoporellidae Hincks, 1882**

*Stichomicropora* Voigt, 1949

**Type species** – *Stichomicropora sicksi* Voigt, 1949, Campanian, Lägerdorf, Germany; by original designation.

**Remarks** – Revised by Voigt (1989b), *Stichomicropora* has distinctive spinose ovicells formed by the zooid distal of the maternal zooid. In some species the ovicell spines appear to have been articulated at their bases, but in others they were basally fused (Taylor & McKinney, 2002; Ostrovsky & Taylor, 2005). Autozooids have extensive, convex (rarely flat) cryptocrystal frontal shields, pierced by opesiules, and a small, semielliptical orifice/opesia, often with oral spines. Avicularia are known in only one species, *S. bacca* (see below).

**Range** – Cenomanian-Maastrichtian, Danian? *Stichomicropora oceani* (d’Orbigny, 1852 in 1851-1854) from the Lower Cenomanian of Sarthe, France, is the oldest described species of this genus. Several species are known from the Maastrichtian. It is possible that the genus ranges into the Danian if *Micropora convexa* Canu, 1911, from the Roca Formation is correctly assigned to *Stichomicropora*, and if it comes from the Danian and not the Maastrichtian part of the Roca Formation. Voigt (1985, table 2) extended the range of *Stichomicropora* into the Eocene, but is unclear whether Eocene, *Stichomicropora*-like species (e.g., Taylor & McKinney, 2002, fig. 1H) really belong to this genus or to *Monoporella* (see Ostrovsky & Taylor, 2005).
Stichomicropora baccata (Canu & Bassler, 1926)
Pls. 90, 91.

1926 Micropora baccata sp. nov.; Canu & Bassler, p. 36, pl. 6, figs. 4-6.
2002 Stichomicropora baccata (Canu & Bassler); Taylor & McKinney, fig. 1E, F only.
In press Stichomicropora baccata (Canu & Bassler); McKinney & Taylor, fig. 2C.

Material – Lectotype (chosen here): USNM 69954, figured by Canu & Bassler, 1926, pl. 6, fig. 5, Maastrichtian, Ripley Formation, Coon Creek Member, Coon Creek, McNairy County, Tennessee (locality TN1). Paralectotypes: USNM 528402, figured by Canu & Bassler, 1926, pl. 6, fig. 4; USNM 528403, figured by Canu & Bassler, 1926, pl. 6, fig. 6; USNM 528404 (ancestrulate colony on same substrate as 528403), details as for lectotype. Questionably assigned: NHM BZ 5061, Maastrichtian, Ripley Formation, Coon Creek Member, grey silty fine sands in stream bed, “Inoceramus’ bed auctt., Coon Creek, McNairy County, Tennessee (locality TN1; S. Tracey Collection).

Description – Colony encrusting, multiserial, unilaminar, growing edge digitate. Pore chambers present, running along entire length of distal and distolateral walls, opening at growing edge as longitudinally elliptical pore windows about 50 μm broad. Ancestrula (Pl. 90, fig. 3) longitudinally ovoidal, small, about 210 μm long by 140 μm wide; gymnocyst moderately broad proximally, tapering distally, at least one pair of spine bases located on step-like mural rim; cryptocyst extensive, almost heart-shaped, about 100 μm in length and width, convex, pustulose, with paired opesiules located a little distally of mid-length; orifice/opesia semielliptical, about 40 μm long by 50 μm wide, three pairs of oral spines, those at proximolateral corners the largest; one peri-ancestrular zooid, budded distally. Autozooids rhomboidal, proximal and distal edges shorter than proximolateral and distolateral edges, on average about 1.3-1.4 times longer than wide, zooidal boundaries well marked, grooved, sometimes with a distinct boundary wall. Gymnocyst lacking or very narrow; mural rim step-like, crenulated, without mural spines. Cryptocyst very extensive, covering most of frontal surface, densely pustulose, the pustules generally coarser proximally, convex, opesiules usually a single pair located in distal third of cryptocyst just inward from mural rim (Pl. 90, fig. 2a), sometimes a second, more proximal pair; additional holes placed without apparent pattern in some zooids represent either opesiular pores or damage artefacts. Orifice/opesia semielliptical, small, roughly equidi- mensional, with a straight proximal edge (Pl. 90, fig. 2b), set within a slightly raised area of cryptocyst, oral spines 0-4, most commonly 2. Ovicell (Pl. 90, fig. 1b) hyperstomial, spinose, comprising 3-5 basally fused, expanding, laterally juxtaposed, flattened spines forming a trapezoidal canopy significantly broader distally with the sides a little bowed; floor smooth, gymnocrystal, convex (Pl. 90, fig. 1c); secondary orifice defined by ends of ovicell spines higher than primary orifice; operculum probably not closing ovicell opening; lateral foramina opening above deeply facetted cryptocyst of zooids laterally adjacent to ovicell; oral spine bases hidden by ovicell or proximalmost one or two visible. Closure plates and intramural buds not observed. Basal wall fully calcified. Avicularia (Pl. 91, fig. 1a, b) rare, vicarious, proximal parts indistinguishable from autozooids; orifice/opesia pear-shaped, about 130 μm long by 90 μm wide, proximal
edge slightly concave; rostrum long, broad, parallel-sided or mildly spatulate, well-rounded distally, rostral shelf extensive; four oral spine bases near distal extremity.

Kenozooids observed in disrupted areas, small, irregular, cryptocyst depressed, containing one or more small openings.

**Measurements** – Lectotype: ZL 540±16, 520-560 (1, 10); ZW 398±45, 340-480 (1, 10); OpL 78±4, 70-80 (1, 10); OpW 101±6, 90-110 (1, 10); Dis 406±23, 380-460 (1, 10); AL 685±156, 560-900 (1, 4); AW 440±37, 400-480 (1, 4); RL: 285±44, 240-340 (1, 4); RW 190±26, 160-220 (1, 4).

**Remarks** – Following the recognition of *S. ostrovskyi* and *S. senaria* as distinct new species, the only specimens known of unequivocal *S. baccata* are Canu & Bassler’s (1926) syntypes. Canu & Bassler described the ovicells as having 4-6 ‘spinules’ located above them to form a roof-like protection. In fact, as discussed by Taylor & McKinney (2002), the spinules themselves constitute the ovicell roof (Pl. 90, fig. 1b). They originate from the mural rim of the zooid distal of the maternal zooid. The floor of the ovicell is formed by the proximal gymnocyst of this distal zooid. Ovicells constructed thus are interpreted as being primitive among neocheilostomes (see also Ostrovsky & Taylor, 2004). However, the basal fusion and joined edges of the spines represent an advance compared with ovicells in some other species of *Stichomicropora* with basally articulated spines, such as *S. oceani* (d’Orbigny).

Two avicularia only are known in this species, both in paralectotype USNM 528402 (Pl. 91, fig. 1a, b). These are vicarious and differ from autozooids only in the region of the orifice/opesia which is hypertrophied, prolonged distally and has an extensive rostral shelf. Voigt (1989b, pl. 19, fig. 5) illustrated a pair of similar avicularia in the related *Mnoporella exculta* (Marsson) from the type Maastrichtian. One of these avicularia is apparently closed by a calcified operculum, raising the possibility that calcified opercula may also have existed in *S. baccata*, but dropped out of the orifice during fossilization.

An immature colony of *Stichomicropora*, comprising only eight complete zooids, is present in the S. Tracey Collection from Coon Creek (Pl. 91, fig. 2a-d). The ancestrula differs appreciably from that of Canu & Bassler’s material (compare Pl. 90, fig. 3 and Pl. 91, fig. 2c), having two pairs of opesiules penetrating the smoothly calcified cryptocyst which is not depressed and is poorly demarcated from the gymnocyst. Three small mural spine bases are visible proximally of the opesiules. These features place a question mark over the identity of this specimen as *S. baccata*.

**Stichomicropora ostrovskyi** sp. nov.

Pl. 92.

1967 *Micropora*? sp.; Shaw, p. 1412, pl. 180, fig. 3.
2002 *Stichomicropora baccata* (Canu & Bassler); Taylor & McKinney, fig. 1G only.

**Material** – Holotype: NHM BZ 4859(1), Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2). Paratypes: NHM BZ 4178(1), BZ 4184(1), BZ 5066, details as for holotype. NNM RGM 507 017, Maastrichtian, Peedee Formation, Rocky Point Quarry, Pender County, North Carolina (locality NC3).
Etymology – Named for bryozoologist Dr A.N. Ostrovsky (St Petersburg State University) who first drew our attention to the differences between this species and Stichomicropora baccata.

Description – Colony encrusting, multiserial, unilaminar, growing edge digitate. Pore chambers apparently weakly mineralized, pore windows longitudinally elongate. Ancestrula (Pl. 92, fig. 3) ovoidal, small, almost equidimensional, about 220 μm long by 210 μm wide, or slightly longitudinally elongate, the proximal end a little pointed; gymnocyst developed around proximal and lateral margins; cryptocyst extensive, convex, opesiules not observed, probably infilled by cement or sediment grains; orifice/opesia semielliptical, about 40 μm long by 60 μm wide, oral spines not evident. One peri-ancestrular zooid, budded distally from ancestrula.

Autozooids rhomboidal, proximal and distal edges shorter than proximolateral and distolateral edges, on average about 1.25 times longer than wide, zooidal boundaries well marked either by grooves or a salient boundary wall. Gymnocyst and mural spines lacking. Cryptocyst very extensive, covering most of frontal surface, densely pustulose, convex, often compressed or destroyed except for area around orifice/opesia (Pl. 92, fig. 1b); opesiules usually comprising a single pair located in distal third of cryptocyst just inward from mural rim, additional ‘opesiular pores’ numerous, scattered over cryptocyst. Orifice/opesia semielliptical, small, roughly equidimensional, with a straight proximal edge, set within a slightly raised area of cryptocyst, oral spines usually numbering four, sometimes five. Ovicell (Pl. 92, fig. 1c) hyperstomial, spinose, comprising four basally fused, expanding, laterally juxtaposed, flattened spines forming a dumbbell-shaped canopy, the two outermost spines wider and with bowed outer edges; floor smooth, gymnocystal, convex; opening of ovicell defined by ends of ovicell spines at a level above primary orifice; operculum probably not closing ovicell opening; lateral foramina present. Closure plates and intramural buds not observed. Basal walls seemingly uncalcified. Avicularia and kenozooids not observed.

Measurements – Holotype: ZL 488±43, 420-540 (1, 10); ZW 393±42, 315-450 (1, 10); OpL 74±8, 60-90 (1, 10); OpW 92±8, 75-105; OvL 182±19, 165-225 (1, 10); OvW 362±26, 330-405.

Remarks – This new species strongly resembles S. baccata, but differs in the following respects: the existence of numerous opesiular pores which are uncommon in S. baccata; the seemingly unmineralized basal wall and pore chambers; four oral spines normally being present compared with the two typical of S. baccata; and the ovicell which has more of a dumbbell than trapezoidal shape, with strongly convex lateral edges (Pl. 92, fig. 1c). In addition, avicularia have not yet been found in S. ostrovskyi, although they are very rare in S. baccata.
The preservation of the frontal wall deserves comment. In colonies from the Prairie Bluff Chalk of Alabama and the Peedee Formation of North Carolina, most of the autozooidal frontal walls are either crushed or missing, except for the area surrounding the orifice (Pl. 92, fig. 1b). Counterintuitively, the ancestrula and zooids budded during early colony growth are much more likely to preserve intact frontal walls than are mature zooids that formed later in astogeny (Pl. 92, fig. 3). Also surprising in those zooids that have lost their frontal walls is the common preservation of complete ovicells (Pl. 92, figs. 1a, 2), skeletal structures normally among the first to be destroyed during fossilization. Voigt (1989b) illustrated a similar preservational style in *Stichomicropora clathrata* (Reuss) (pl. 18, figs. 1, 2) and *S. cf. clathrata* (pl. 18, fig. 4, pl. 19, figs. 5, 6), the former from the Cenomanian of Germany, and the latter from Maastrichtian of Germany and The Netherlands. The reason for this unusual non-preservation of cryptocyst in at least three different species of *Stichomicropora* coming from several localities is unclear. Two obvious possibilities are that the cryptocyst in these species was composed of diagenetically vulnerable aragonite or high-Mg calcite, or that it was extremely thinly calcified (and porous) and prone to taphonomic destruction. The second hypothesis is tentatively favoured because, compared to *S. baccata*, which does not suffer cryptocystal loss, *S. ostroovskyi* also has non-calcified basal walls and pore chambers, suggesting a more general reduction in the mineralized skeleton.

*Stichomicropora senaria* sp. nov.

Pl. 93.

Material – Holotype: NHM BZ 4186, Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2). Paratypes: NHM BZ 4175(3), BZ 4187, BZ 4188(2), BZ 4189(3), details as for holotype. NHM BZ 5069, Maastrichtian, Peedee Formation, Rocky Point Quarry, Pender County, North Carolina (locality NC3).

Etymology – L., *senarius*, consisting of six, in reference to the six oral spines normally present.

Description – Colony encrusting, multiserial, unilaminar, growing edge digitate (Pl. 93, fig. 1a). Pore chambers numbering three, sausage-shaped with elongate elliptical windows; distal chamber curved, window facing distofrontally; distolateral pore chambers centred midway along distolateral vertical walls. Ancestrula (Pl. 93, fig. 4) longitudinally ovoidal, straight sided, small, about 260 μm long by 190 μm wide, the proximal end well rounded; gymnocyst widest proximally; cryptocyst slightly convex, bounded by U-shaped salient mural rim, opesiules possibly two in number; orifice/opesia semieliptical, about 40 μm long by 60 μm wide, oral spines present. Early budding pattern unknown.

Autozooids rhomboidal, proximal and distal edges shorter than proximolateral and distolateral edges, on average about 1.3 times longer than wide, zooidal boundaries well marked by grooves and/or a salient boundary wall. Gymnocyst and mural spines lacking. Cryptocyst very extensive, covering most of frontal surface, densely pustulose, convex, a low median keel sometimes developed just proximally of orifice/opesia; opesiules (Pl. 93, figs. 1b, 3) usually numbering four, one pair in proximal and a second in
distal part of zooid, up to seven opesiules observed, individual opesiules often set within a shallow subcircular depression in surface of cryptocyst. Orifice/opesia semielliptical, small, roughly equidimensional, with a straight or concave proximal edge, set within a slightly raised area of cryptocyst, oral spines usually numbering six, range 5-7, the outermost often a little larger than the others. Ovicell hyperstomial, costate, none known with intact roofs, apparently large, broad; facets present in frontal shields of laterally adjacent autozooids (Pl. 93, fig. 2b). Closure plates and intramural buds not observed. Regrowth from broken proximal edges of colonies may occur. Basal wall calcified.

Avicularia not observed. A single kenozooid present in BZ 4189(3) is identical to an autozooid, but lacks an orifice and oral spine bases.

**Measurements** – Holotype: ZL 476±39, 435-555 (1, 10); ZW 372±47, 315-465 (1, 10); OpL 78±5, 75-90 (1, 10); OpW 101±6, 90-105.

**Remarks** – With one exception (NHM BZ 5069), all of the material of this new species was collected during March 1989 from a single bedding plane on a large block of Peedee Formation float in the Martin Marietta Ideal Quarry, Wilmington. It differs from *S. ostrovskyi*, collected in abundance from the same locality 11 years later, in having two or more pairs of opesia. *Stichomicropora senaria* can be distinguished from both *S. ostrovskyi* and *S. baccata* by generally having six oral spine bases. All three species of *Stichomicropora* have similarly sized zooids, although there are some slight differences in proportions, with *S. baccata* having the most slender zooids, *S. ostrovskyi* the most equidimensional and *S. senaria* zooids of intermediate proportion.

**Suborder Ascophora Levinsen, 1902**
**Infraorder Acanthostega Levinsen, 1902**
**Superfamily Cribrilinoidea Hincks, 1879**
**Family Cribrilinidae Hincks, 1879**
* Aeolopora Lang, 1916

**Type species** – *Aeolopora distincta* Lang, 1916, Santonian, Berkshire, England; by original designation.

**Remarks** – The most notable feature of *Aeolopora* is the presence of a single boss-like pelmatidium near the distal end of the costae, each pelmatidium positioned so that the entire set defines an oval, slightly depressed central area of the frontal shield. The only costae in which the pelmatidia are essentially at the distal end is the pair that are fused to form the apertural bar. The genus initially included only species in which intercostal bridges were not present. Canu & Bassler (1933) described *Aeolopora grandis* from the Paleocene Vincentown Formation, and their description and untouched portions of photographs (pl. 10, figs. 1-3) suggest the same frontal shield structure as in the type species, although inking of the retouched portions of photographs suggest numerous intercostal connections. The species described below has a robust intercostal connection joining adjacent costae where pelmatidia are located. Therefore, following the emendation of Turner (1973), we accept a broader definition of the genus that accommodates at least a single intercostal bridge between adjacent costae.
Range – Santonian – Maastrichtian; Thanetian?

Aeolopora catillus sp. nov.
Pls. 94, 95.

Material – Holotype: NHM BZ 5216(1a), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). Paratypes: NHM BZ 5216(1b), on same substrate as holotype. RU 5603 and three colonies on RU 5400, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

Etymology – Gr., catillus, small bowl, dish or plate, in reference to the shallow concave area between the pelmatidia.

Description – Colony a multiserial, encrusting, nonmaculate sheet. Six large communication pores (proximal, proximolateral, distolateral, distal) present per autozooid, with prominent salient rim where visible along edge of colony (Pl. 95, fig. 2a). Ancestrula (Pl. 94, fig. 1b) oval, width about two-thirds length, total length slightly over half that of autozooids in astogenetic zone of repetition; frontal shield composed of 14-16 costae, narrower than, but otherwise similar to, costae of autozooids in zone of astogenetic repetition; four(?) spines along distal oral spines. Ancestrula giving rise to intermediate-sized distal bud, which may be followed successively by distolateral and proximolateral buds; proximal bud not seen. Zone of astogenetic change restricted to three, perhaps four generations.

Autozooids small, hexagonal to oval, about 1.5 times longer than wide in zone of astogenetic repetition, deep groove between adjacent autozooids. Frontal shield convex overall, but with central, oval, slightly concave area, in zone of astogenetic repetition comprising 11 to 14, usually twelve, costae with a single intercostal fusion near distal end of costae (Pl. 95, fig. 1c), centred on a single pelmatidium per costa; costae laterally fused (a second intercostal bridge?) at their distal tips, but may or may not be fused across the midline, some zooids with tiny gaps aligned along the zooidal midline; gymnocyrt variably developed, from absent to narrow, broader proximally and distally than laterally where present; pelmatidia at distal ends of distal pair of costae, which are fused into slightly raised apertural bar. Orifice transversely elongate, tending towards D-shaped, with four large orificial spines along distal margin (Pl. 95, fig. 1b). Ovicell (Pl. 94, fig. 1c) hyperstomial, globular, smooth, perforate, approximately equidimensional, with median suture; maternal autozooids developed by 5th astogenetic generation.

Avicularia (Pl. 95, fig. 1b) interzooidal only, abundant, distally oriented; proximal gymnocyrt extensively developed; opesia located in distal half to two-thirds of avicularium, elongate oval, with short condyles slightly closer to proximal than to distal end of opesia, rostral portion generally slightly spatulate.

Kenozooids not seen.

Measurements (Most from Turner, 1973.) – Holotype, one paratype: ZL 410±42, 380-500 (2, 14); ZW 270±33, 230-340 (2, 14); OL 110±25, 80-150 (2, 6); OW 140±14, 120-160 (2, 6); AL 140±24, 100-170 (2, 6); AW 60±8, 50-70 (2, 6); Costae 12±1.2, 10-14 (2, 10); AoL 120±22, 80-164 (2, 13); AoW 53±9, 42-73 (2, 13).
Remarks – As in the other known species of *Aeolopora*, *A. catillus* has a single pelmatidium near the distal end of each costa, with the distance between costal tip and pelmatidium in the costae that originate mid-way along the side of the zooid such that the entire set of pelmatidia defines an oval central space. However, it differs from *A. distincta* Lang, 1916, from the Santonian of England, and *A. nebulosa* Lang, 1921, from the Santonian and Campanian of England and Europe, in the presence of the single intercostal fusion joining adjacent costae at the position of the pelmatidium and in having four rather than six orificial spines.

*Anornithopora* Lang, 1916

_Type species_ – *Anornithopora involucris* Lang, 1916, Campanian, Sussex, England; by original designation.

Remarks – *Anornithopora* is not clearly discriminated from *Castanopora* Lang, 1916. It was characterized by Lang (1916, 1922) as having minute zooids, sparse costae (20 or fewer), without secondary orifice or subsequent skeletal thickening, and few if any avicularia. There are no avicularia in the holotype (NHM D28110) or paratype (NHM D28111) of the type species *Anornithopora involucris* Lang, nor were avicularia present in the other two species included in *Anornithopora* by Lang (1916, 1922).

Larwood (1962) gave an emended diagnosis of *Castanopora*, largely following Lang (1916, 1922), including species in which autozooids have numerous costae that are each linked by several intercostal fusions and small pelmata or pelmatidia, without secondary orifice or subsequent skeletal thickening, and avicularia from absent to up to three interzooidal types per species. There is a confusing range of species across the morphologies encompassed by *Anornithopora* and *Castanopora* as currently defined. An understanding of the relationship between the genera would benefit from phylogenetic analysis.

We use *Anornithopora* here for Upper Cretaceous species from eastern North America that have minute zooids and relatively few costae, and a single type of interzooidal avicularium regardless of their frequency. We also include a species (*A. responsa* sp. nov.) that has on average more than 20 costae per autozooid, because it is obviously congeneric with the other species here considered to belong within *Anornithopora*. None of the species included here have as abundant avicularia as do the Danian specimens assigned by Berthelsen (1962) to *Anornithopora minuta* Voigt, 1925 (which Voigt originally described as having few, sporadically distributed avicularia).

_Range_ – Campanian-Danian.

*Anornithopora spooneri* (Butler & Cheetham, 1958)

Pl. 96.

1958  *Rhiniopora spooneri* sp. nov.; Butler & Cheetham, p. 1154, text-figs. 1, 2.
1962  *Castanopora spooneri* (Butler & Cheetham); Larwood, p. 220.
1967  *Castanopora spooneri* (Butler & Cheetham); Shaw, 1967, p. 1416, pl. 181, fig. 1.

**Material** – Holotype: LSUMG-I 1390, Campanian, Saratoga Chalk equivalent, Rayburns dome, Bienville Parish, Louisiana (locality LA1). Paratype: LSUMG-I 1391, same
Details as holotype. Other material: LSUMG-I 8273, figured by Shaw (1967, pl. 181, fig. 1), Maastrichtian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2). NHM BZ 4437(3), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). NHM BZ 5125(2), Maastrichtian, Prairie Bluff Chalk, Emelle, Sumter County, Alabama (locality AL9). NHM BZ 4436, Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5).

Description – Colony a multiserial, encrusting, nonmaculate sheet. Pore chambers numerous, intermediate in size (Pl. 96, fig. 2). Ancestrula (Pl. 96, fig. 4) tatiform, oval, width about half length, total length approximately half that of autozooids in astogenetic zone of repetition; at least four spines along distal and distolateral margin; six buds surrounding ancestrula, beginning with relatively small distal bud, followed successively by distolateral, proximolateral and proximal buds. Zone of astogenetic change restricted to four generations.

Autozooids small, hexagonal to oval, averaging about 1.3 times longer than wide, deep groove between adjacent autozooids. Frontal shield convex, in zone of astogenetic repetition comprising 7 to 10, usually 8 or 9, pairs of costae with 4 to 6 intercostal fusions producing minute rounded intercostal spaces; several (4 to 6 fide Butler & Cheetham, 1958) pelmatidia per costa; costae fused along zooidal midline without producing median longitudinal bar; distal pair of costae fused into slightly raised apertural bar with central boss. Orifice (Pl. 96, fig. 1c) transversely elongate, tending towards D-shaped, with five orificial spines along distal margin. Ovicell (Pl. 96, fig. 1d) hyperstomial, globular, smooth, non-perforate, longer than wide, with median suture or low keel; maternal autozooids developed by 5th astogenetic generation. Intramural buds sporadically developed (Pl. 96, fig. 3).

Avicularia (Pl. 96, figs. 1b, 2) interzooidal only, widely scattered to abundant and in some colonies very abundant locally and partially encircling autozooids; rostrum commonly slightly overlapping next-distal autozooid; gymnocyst narrow to broad, more extensive proximally; opesia located in distal half to two-thirds of avicularium, elongate oval, lacking condyles, rostral portion generally slightly spatulate, less commonly slightly acute.

Kenozooids not observed.

Measurements – (From Butler & Cheetham, 1958.) Holotype, paratype: ZL 300±26, 260-340 (2, 30); ZW 230±24, 170-270 (2, 30); OL 50±10, 40-70 (2, 26); OW 80±10, 60-90 (2, 26); AL 130±20, 110-150 (2, 8); OvL 130±14, 110-150 (2, 7); Costae 17±1.5, 14-20 (2, 25).

Remarks – The description given here is based on the holotype and paratype from an un-named chalk at Bienville Parish, Louisiana, and additional specimens from the Prairie Bluff Chalk (Maastrichtian) of Alabama. Shaw (1967) recognized the same species from the Saratoga Chalk of Arkansas based on material having slightly different characteristics; slightly larger, more equidimensional autozooids and more equidimensional autozooidal orifices.
Anornithopora oligocostata sp. nov.
Pl. 97.

Material – Holotype: RU 5451, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2). Paratypes: RU 5452, 5613, 5625, 5626, same details as holotype.

Etymology – Gr., oligos, few or scanty, and costae, in reference to the small number of costae.

Description – Colony a multiserial, encrusting, nonmaculate sheet (Pl. 97, fig. 1a). Pore chambers numerous, intermediate in size (Pl. 97, fig. 1b). Ancestrula (Pl. 97, fig. 5b) small, elongate oval, with large opesia and costae represented by minimal lateral crenulations. Zone of astogenetic change restricted to about first five generations of autozooids.

Autozooids small, hexagonal or rhomboidal, averaging about 1.3 times longer than wide, a deep groove between adjacent autozooids. Frontal shield convex, in astogenetic zone of repetition comprising 11 to 15, usually 12 or 13, costae (Pl. 97, fig. 2), with 4 to 6 intercostal fusions producing minute rounded intercostal spaces; inconspicuous pellmatidia present, 4-6 per costa (fide Turner, 1973); costae fused along zooidal midline without producing median longitudinal bar; distal pair of costae fused into slightly raised apertural bar with central boss. Orifice transversely elongate, tending toward D-shaped, with 4 to 6 orificial spines along distal margin (Pl. 97, fig. 3). Ovicell (Pl. 97, fig. 4b) hyperstomial, globular, smooth, non-perforate, approximately equidimensional, with low median keel; maternal zooids have slightly broader orifices than non-fertile zooids, developed by 5th astogenetic generation.

Avicularia interzooidal (Pl. 97, fig. 4b) only, not present in all colonies, few where present; gymnocyst more extensive proximally, opesia located in mid portion of avicularium, elongate oval, with slight condyles, rostral portion generally slightly spatulate. Kenozooids not seen.

Measurements – Holotype and paratypic suite: ZL 364±30,314-432 (5, 50); ZW 282±25, 227-340 (5, 50); OL 46±7, 33-60 (5, 50); OW 64±7, 46-84 (5, 50); AL 144±20, 124-168 (3, 6); AW 93±11, 76-105 (3, 6); OvL 179±27, 138-196 (2, 4); OvW 75±6, 68-82 (2, 4); OOW 75±6, 68-82 (2, 4); Costae 12.3±0.9, 11-15 (5, 50).

Remarks – This species is quite similar to A. spooneri (Butler & Cheetham, 1958), but differs in having slightly larger autozooids, fewer costae and less common avicularia. It differs from A. minuta Voigt, 1925, in having fewer costae and apparently far fewer avicularia (Berthelsen, 1962). Autozooids of A. irrostrata Lang, 1916, have the same general morphological features, but are about 50% larger in both length and width.

Anornithopora? delawarensis sp. nov.
Pl. 98.

**Etymology** – Named after the State of Delaware, from which the holotype and para-types were collected by K. Zipf.

**Description** – Colony a multiserial, encrusting, nonmaculate sheet. Pore chambers numerous, small. Ancestrula and zone of astogenetic change not seen.

Autozooids small, elongate oval, averaging about 1.6 times longer than wide, adjacent autozooids separated by deep groove and interzooidal avicularia (Pl. 98, fig. 1a). Frontal shield convex (Pl. 98, fig. 1b), in zone of astogenetic repetition comprising 10 to 13, usually 12, costae with 1 or 2 intercostal fusions producing small rounded circular to transversely elongate intercostal spaces; pelmatidia absent or not well preserved; costae fused along zooidal midline, producing ill-defined median longitudinal bar; distal pair of costae fused into slightly raised apertural bar with central boss. Orifice transversely elongate, oval, apparently lacking orificial spines. Ovicell (Pl. 98, fig. 1c) hyperstomial, elongate globular, smooth, non-perforate, with low median keel; orifices of maternal zooids similar to those of non-fertile autozooids. Reparative budding generally producing intramural avicularia similar to interzooidal avicularia (Pl. 98, fig. 1d, e).

Avicularia (Pl. 98, fig. 1d) interzooidal only, abundant, commonly encircling or nearly encircling autozooids; gymnocyist more extensive proximally, opesia located in distal portion of avicularium, elongate oval, with small condyles distal of midpoint, rostral portion rounded acuminate, variously but often proximally oriented.

Kenozooids uncommon, essentially flat, irregular in size and shape.

**Measurements** – ZL 310±26, 256-358 (3, 30); ZW 191±16, 153-225 (3, 30); OL 38±4, 28-48 (3, 30); OW 58±6, 45-68 (3, 30); AL 114±25, 70-158 (3, 30); AW 65±8, 50-80 (3, 30); OvL 128±14, 99-152 (3, 30); OvW 128±11, 105-146 (3, 30); Costae 12.0±0.8, 10-13 (3, 22).

**Remarks** – Available specimens of this species are covered by fine syntaxial overgrowths, which may account for the apparent lack of pelmatidia. Many of its characteristics suggest that it belongs in *Pliophloea*, especially the abundant and heterogeneously placed interzooidal avicularia. However, *Pliophloea* is characterized by a row of conspicuous pelmatidia along costal midlines, evidence of which should be retained even through the moderate recrystallization of the available specimens. If subsequent material is found with well-developed pelmatidia, the species perhaps should be transferred to *Pliophloea*. In their absence we tentatively assign it to *Anornithopora*.

This species is quite similar to *A. spooneri* (Butler & Cheetham, 1958) in zooid size, but differs in having fewer costae, fewer intercostal bridges, more frequent avicularia, lack of overlap of avicularia onto next-distal autozooids and an apparent absence of oral spines. It differs from *A. minuta* Voigt, 1925, in having fewer costae and fewer intercostal bridges.

*Anornithopora responsa* sp. nov.

Pl. 99.

**Material** – Holotype: VCSM 13962 (Voigt photocard 5925), Campanian, Demopolis Chalk, Macon, Noxubee County, Mississippi (locality MS2).
Etymology – L., responsus, reply or answer, in reference to the phenotypic variability in autozooid shape and kenozooid production in response to microenvironmental conditions.

Description – Colony a multiserial, encrusting, nonmaculate sheet (Pl. 99, fig. 1a). Each autozooid with 8 or 9 intermediate-sized pore chambers along anterior basal periphery. Ancestrula tatiform, oval, about 1.3 times longer than wide, several small spines distributed around perimeter; length less than one-third that of autozooids in zone of astogenetic repetition; a distal and two proximolateral autozooids budded from ancestrula. Primary zone of astogenetic change occupying approximately eight generations, with gradual increase in size of autozooids and orifices (Pl. 99, fig. 1e).

Autozooids in zone of astogenetic repetition elongate oval to hexagonal, variable in length and shape, on average about 1.4-1.5 times longer than wide, deep groove between adjacent autozooids. Gymnocyst exposed around entire perimeter of most zooids, locally extending as broad skirt just above reverse wall between linear segments of autozooidal border and oval frontal shield. Frontal shield highly convex, comprising 19 to 26 costae (Pl. 99, fig. 1b) with up to 8 intercostal bridges depending on length of adjacent costae; intercostal bridges spaced at approximately 15 μm, producing narrow proximodistally elongated, rounded intercostal spaces; pelmatidia present, probably one at each point of origin of lateral intercostal extension, but not always visible; costae fused along zooidal midline, commonly producing narrow median longitudinal bar; distal pair of costae fused into pronounced apertural bar that may have a small acuminate, possibly bifid median boss. Orifice transversely elongate, D-shaped, with five or less commonly four orificial spines along the distal and lateral margin. Ovicell (Pl. 99, fig. 1d) hyperstomial, small, smooth except for median keel, groove or centrally grooved keel, longer than wide; maternal zooids with slightly broader orifice than non-fertile zooids.

Avicularia (Pl. 99, fig. 1b) of one type, interzooidal, variably placed with respect to adjacent autozooids, lacking crossbar or condyles, but commonly with inflexion midway along length of opesia; opesia oval to fattened figure-eight shaped; orientation ambiguous due to distolateral symmetry.

Kenozooids (Pl. 99, fig. 1c) highly variable in shape and size, developed most commonly at points of crowding, with frontal shield organized as in autozooids, but lacking orifice.

Measurements – Holotype: ZL 516±69, 390-600 (1, 10); ZW 362±51, 300-435 (1, 10); OL 63±5, 60-75 (1, 9); OW 81±6, 75-90 (1, 9); AL 138±47, 90-270 (1, 10); AW 93±22, 60-135 (1, 10); OvL 138±16, 120-150 (1, 10); OvW 140±8, 128-150 (1, 10); Costae 22.9±2.5, 19-26 (1, 10).

Remarks – Anornithopora responsa is very similar to A. spooneri (Butler & Cheetham, 1958), but differs in having more costae in the frontal shield and larger, more elongate autozooids. It resembles Castanopora castanea Lang, 1916, and C. glandulosa Lang, 1916 (both from the Upper Campanian mucronata zone, Rügen, Germany), but differs from the former in having five rather than four apertural spines, and from both in having much smaller autozooids and scattered interzooidal avicularia rather than paired acuminate adventitious avicularia at the autozooidal orifice.
**Castanopora Lang, 1916**

*Type species* – *Castanopora castanea* Lang, 1916, Maastrichtian, Rügen, Germany; by original designation.

*Remarks* – For the concept of *Castanopora* applied here, see discussion above for *Anornithopora*.

*Range* – Santonian – Danian.

**Castanopora lambi** Turner, 1975

Pl. 100.

1975 *Castanopora lambi* sp. nov.; Turner, p. 274, pl. 1, figs. 1-6.

*Material* – Holotype: RU 5405, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

*Description* – Colony a multiserial, encrusting, nonmaculate sheet (Pl. 100, fig. 1a). Size and distribution of pore chambers unknown. Ancestrula not seen, extent of zone of astogenetic change relatively short, but number of generations unknown.

Autozooids (Pl. 100, fig. 1b) hexagonal to oval, approximately 1.5 times longer than wide, deep groove between adjacent autozooids. Frontal shield highly convex, comprising 9 to 11, usually nine, robust pairs of costae with 3 to 5 intercostal fusions producing transversely elongated, rounded intercostal spaces; 3 to 5 pelmatidia per costa, each located at point of origin of lateral intercostal extension; costae fused along zooidal midline without producing median longitudinal bar; distal pair of costae fused into pronounced apertural bar that may have a slight median dilation centred on a visible median suture, otherwise unornamented except for pelmatidia. Orifice transversely elongate, tending towards D-shaped, with four orificial spines along the slightly keeled distal margin. Orifice frequently occupied by D-shaped, calcified operculum (Pl. 100, fig. 1c); calcareous operculum also present in intramural bud (Pl. 100, fig. 1d). Ovicell (Pl. 100, fig. 1e) hyperstomial, smoothly globular without median keel, but with shallow longitudinal grooves suggestive of fusion of spines or costae, longer than wide, finely perforate, perforations evenly distributed; maternal zooids with slightly broader orifice than others.

Avicularia absent.

Kenozooids not seen.

*Measurements* – (From Turner, 1975) Holotype: ZL 685±46, 629-749 (1, 10); ZW 426±23, 391-464 (1, 10); OL 116±18, 96-161 (1, 10); OW 146±18, 108-171 (1, 10); OvL 300±17, 279-315 (1, 4); OvW 284±28, 245-308 (1, 4); OOW 163±15, 140-181 (1, 5); Costae 18.7±1.4, 17-22 (1, 10).

*Remarks* – The ancestrula and first one or two asexually budded generations are overgrown in the only known specimen. All maternal zooids in this colony developed
in a single generation, approximately the 9th generation from the ancestrula.

The single specimen on which this species is based fits uncomfortably within *Castanopora*. It has no avicularia, which is unusual for species of *Castanopora*, and the presence of perforations in the ovicell (Pl. 100, fig. 1e) differs from the non-porous ovi-cells known for several species of *Castanopora*, some of which may have a broad keel (Larwood, 1962). In almost all characteristics it matches *Reginella* Jullien, 1886, including colony habit, large zooid size, fused costae forming the proximal apertural rim, absence of suboral lacunae and ovi-cells formed of modified costae with pores derived from costal pores (Soule et al., 1995), but apertural spines are present and it lacks the diagnostic proximolateral dilations of the orifice that would transform the D-shaped aperture into a bell-shaped aperture. We are uncertain about the correct generic assignment for *C. lambi*, but have retained it in *Castanopora* in the absence of compelling evidence to re-assign it. The presence in *C. lambi* of a calcified operculum (Pl. 100, fig. 1c, d) is unusual, marking the species off from other cribiforms.

*Castanopora dorothyae* sp. nov.

Pl. 101.

**Etymology** – Named in honour of the late Dorothy Soule, accomplished student of cheilostome morphology and taxonomy.


**Description** – Colony a multiserial, encrusting sheet (Pl. 101, fig. 1a). Size and distribution of pore chambers unknown. Ancestrula not seen, extent of zone of astogenetic change relatively short, but number of generations unknown.

Autozooids (Pl. 100, figs 1b, 2a) hexagonal to oval, highly variable in size within zone of astogenetic repetition, approximately twice as long as wide, deep groove between adjacent autozooids. Frontal shield highly convex, comprising 8 to 9 robust pairs of costae with 3 to 5 intercostal fusions producing transversely elongated, rounded intercostal spaces (Pl. 101, fig. 2b); pelmatidia not seen; costae fused along zooidal mid-line without producing median longitudinal bar. Orifice transversely elongate, tending towards D-shaped, no orificial spines, but distal rim of orifice formed of aborted costae. Ovicell (Pl. 101, fig. 1c) hyperstomial, smoothly globular without median keel, finely perforate, slightly wider than long; orifice of maternal zooids same size as non-fertile zooids.

Avicularia absent.

Kenozooids not seen.

**Measurements** – ZL 626±83, 472-779 (3, 30); ZW 358±51, 257-469 (3, 25); OL 91±10, 73-106 (3, 25); OW 127±17, 88-160 (3, 30); OvL 221±26, 174-284 (3, 21); OvW 241±26, 206-309 (3, 21).
Remarks – Castanopora dorothyae differs from C. lambi Turner in lacking calcified opercula and in having slightly fewer costae, more variable and on average more elongate zooids, smaller orifices that are similar in maternal and non-fertile zooids, and smaller ovicells. It differs from Anornothipora responsa sp. nov. in having larger zooids, fewer costae, fewer intercostal bridges, broad rather than elongate ovicells, and few or no kenozooids and avicularia.

**Diacanthopora** Lang, 1916

_Type species_ – Diacanthopora bispinosa Lang, 1916, Danian, Faxe, Denmark; by original designation.

Remarks – Shaw (1967) gave the author of Diacanthopora as Lang (1922), perhaps because there was no description of the genus when the name was first introduced by Lang (1916, p. 100). However, Lang (1916, p. 84) did characterize his subfamily Diacanthoporidae as “Costae stout, with a lateral row of pelmata and a median row of pelmatidia”. Diacanthopora was the only genus included within the subfamily, so by implication the genus was given the same diagnosis as the subfamily, as specifically indicated by Lang in 1922 (p. 230). Eroneously, Bassler (1953) characterized the genus as consisting only of bilaminar species, even though the type species is unilaminar (Lang, 1922).

Range – Campanian – Thanetian.

**Diacanthopora langi** Shaw, 1967

_Pl. 102._

1967 _Diacanthopora langi_ sp. nov.; Shaw, p. 1420.

**Material** – Holotype: LSUMG-I 8244, Campanian, Upper Ozan Formation, White Cliffs Station, Sevier County, Arkansas (locality AR3).

**Description** – Colony an oligoserial, encrusting, nonmaculate sheet (Pl. 102, fig. 1a, b). Pore chambers not clear. Ancestrula absent in single specimen available.

Autozooids (Pl. 102, fig. 1c, d) elongate hexagonal, about 1.5 times longer than wide, separated by deep groove along narrow gymnocystal border, which is broadest proximally. Frontal shield comprising 14 to 16 robust costae without intercostal bridges; elongate intercostal spaces wider than costae at lateral ends, but tapered toward zoidal midline; distal pair of costae forming apertural bridge; costae fused into broad band along median axis of zooid, with moderately deep furrow between contiguous row of pelmata-containing pustules along margins of axial band; corrosion of some autozooids showing thread-like median plane of fusion bordered on both sides by narrow furrow; costae with single lateral pelmata plus single pelmata on pustule visible in best-preserved autozooids. Orifice terminal, circular or D-shaped with short proximal border along apertural bridge; orificial spines present, but number unknown. Ovicell (Pl. 102, fig. 1c) hyperstomial, inflated, broader than long, surface texture unknown.
Avicularia (Pl. 102, fig. 1d) of one type, adventitious, paired adjacent to orifice, oriented distally, placement individually varying from proximal to or distal to orificial mid-point; rostrum rounded to acuminate, with pivot bar possibly present in some.

No kenozooids present in single specimen available.

*Measurements* – (From Shaw, 1967) Holotype: ZL 400±48, 350-450 (1, 5); ZW 250±18, 230-280 (1, 5); OL 110±14. 90-120 (1, 5); OW 90±9, 80-110 (1, 5); AL 70±9, 60-80 (1, 6); AW 50±11, 30-60 (1, 6); OvL 150 (1); OvW 210 (1).

*Remarks* – Only the holotype is known. The specimen is corroded (Pl. 102, fig. 1b), making interpretation of some features ambiguous, for example, number of orificial spines and presence or absence of pivot bar in the avicularia.

The ancestrula is not preserved, but convergence of autozooids in the proximal portion of the colony fragment suggests that it had reached only a small size, since the lateral and distal margins of the specimen have a single row of incompletely formed autozooids. There is no apparent gradient in autozooid size in the preserved portion of the colony, suggesting that the primary zone of astogenetic change was restricted to at most two or three generations.

*Graptoporella* Bassler, 1953

*Type species* – *Graptopora scripta* Lang, 1916; Santonian, France.

*Remarks* – *Graptoporella* was established for unilaminar cribrimorph species with relatively large zooids, few costae that lack pelmata and that fuse along a broad median area, thick interzoecial skeletal deposits (now interpreted as kenozooidal skeleton), and with small avicularia.

*Range* – Santonian – Maastrichtian?

*Graptoporella? angulata* sp. nov.

Pl. 103.

*Material* – Holotype: USNM 528405, Maastrichtian, Peedee Formation, Neuse River, Lenoir County, North Carolina (locality NC4). Paratypes: USNM 528406 (four fragments), details as for holotype.

*Etymology* – The species name refers to the sharply angled bend that the costae make where they meet along the zooecial axis.

*Description* – Colony erect, bifoliate, non-planar, apparently non-maculate (Pl. 103, fig. 1a). Pore chambers and ancestrula not seen.

Autozooids elongate oval, about three times longer than wide, zooidal boundaries overgrown by kenozooids. Gymnocyst reduced, obscured by kenozooids. Frontal shield comprising 7 to 10, usually eight, robust costae without lateral fusions (Pl. 103, fig. 1b);
intercostal spaces wider than costae, ovoidal; distal pair of costae forming raised apertural bar. Costae fused along zooidal midline, bending abruptly and dilating, terminating with an arcuate contact on proximal side of next-distal costa; one pelma per costa, large, located at point of costal dilation (Pl. 103, fig. 1d). Axial lacunae commonly present between dilated portions of costae next proximal to apertural bar, small, circular to oval (Pl. 103, fig. 1c). Primary orifice circular to somewhat transversely elongate; oral spines lacking; secondary orifice slightly larger, D-shaped, defined by apertural bar and peristome. Ovicell (Pl. 103, fig. 1b, c) globular, recumbent on distal zooid, not elevated above general height of zooids, overgrown by a pair of kenozooids meeting to form a sharp ridge along median axis of ovicell.

Avicularia of one type, adventitious, usually paired, located at each end of apertural bar (Pl. 103, fig. 1b), oriented proximo-medially, crossbar complete, rostrum with rounded to pointed tip.

Kenozooids interzooidal, surrounding autozooids, and overgrowing ovicells and edges of frontal shields; elongate, irregular, without cryptocyst or gymnocyst.

**Measurements** – Holotype: ZL 588±40, 523-669 (1, 10); ZW 222±12, 201-239 (1, 10); AL 69±9, 55-81 (1, 10); AD 74±12. 63-100 (1, 10); OL 109±11, 96-128 (1, 10); OW 136±8, 128-151 (1, 10).

**Remarks** – The holotype of *Graptoporella scripta* (Lang) (NHM D 27750) could not be located at the time of writing. Lang’s original drawing suggests that the species has interzooecial avicularia and there is no indication in the description or drawing that pelmata are present. *Graptoporella? angulata* differs from the type species in being bifoliate rather than unilaminate, having smaller zooids, having adventitious rather than interzooecial avicularia and, more importantly, in the presence of conspicuous pelmata in the costae. The latter three differences, especially the presence of pelmata, make us question whether or not *Graptoporella? angulata* belongs within *Graptoporella*, resolution depending on careful restudy of the holotype or additional specimens firmly identified as *G. scripta*.

*Monoceratopora* Lang, 1916

**Type species** – *Monoceratopora unicornis* Lang, 1916, Santonian, Sussex, England; by original designation.

**Remarks** – Lang (1916, 1921) originally included only species with distally placed avicularia and relatively narrow costae in *Monoceratopora*, but we follow Voigt’s (1930) enlarged concept of the genus to include species with broad costae and which places more taxonomic importance on the distal avicularium than on the width of the costae. Turner (1973) first noted that the avicularia in *Monoceratopora* bud from the distal communication pore of the proximal zooid and are, therefore, interzooidal rather than adventitious.

**Range** – Turonian – Danian.
**Monoceratopora mitrifera** sp. nov.

**Pl. 104.**

**Material** – Holotype: NHM BZ 5195, Maastrichtian, Navesink Formation, Poricy Creek, Monmouth County, New Jersey (locality NJ1; P.L. Cook Collection). Paratypes: RU5410, RU5604, RU5609, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 and/or NJ2).

**Etymology** – L., *mitra*, turban, and L., *fero*, to bear or to carry, in reference to the presence of ovicells with bishop’s mitre-shaped outlines.

**Description** – Colony a multiserial, encrusting, nonmaculate sheet (Pl. 104, fig. 1a). Pore chambers lacking. Ancestrula not seen. Zooids from zone of astogenetic change increasing gradually in size (Pl. 104, fig. 1e).

Autozooids elongate hexagonal, about twice as long as wide, zooidal boundaries clear, marked by moderately deep groove. Gymnocyst narrow, generally not seen. Frontal shield comprising 9 to 12 broad, flat, very gently arched costae joined medially into a broad, slightly to slightly concave median strip; costae lack lateral bridges, but 3-6 non-paired marginal serrations (Pl. 104, fig. 1d) may represent incipient or vestigial bridge loci; intercostal spaces narrow and slit-like; distal pair of costae forming a slightly raised apertural bar without median boss. Pelmatidia apparently absent. Proximal margin of orifice covered by apertural bar so that orifice appears D-shaped, slightly broader than wide; lateral and distal orificial edge slightly raised as low acute keel. Ovicell (Pl. 104, fig. 1c) hyperstomial, globular to pentagonal mitre-shaped, recumbent on distal zooid, with pronounced median keel.

Avicularia (Pl. 104, figs 1b, c) of one type, interzooidal, single, small, oval to distally tapered triangular, arising from distal communication pore of non-ovicellate zooids. Kenozooids not seen.

**Measurements** – Two paratypes and (for costae only) holotype: ZL 472±43, 378-524 (2, 12); ZW 261±28, 210-318 (2, 12); OL 74±14, 48-97 (2, 16); OW 86±15, 67-112 (2, 16); AL 106±20, 78-161 (2, 14); AW 66±11, 51-89 (2, 14); OvL 204±21, 180-231 (1, 6); OvW 232±23, 208-270 (1, 6); Costae 10.7±1.1, 9-12 (3, 30).

**Remarks** – This species closely resembles *Monoceratopora hennigi* Voigt, 1930, from the Campanian (Unteres Mukronatensenon) of Germany, but differs in having very slightly smaller zooids, less elongate and smaller orifices, and relatively broader, more pentagonal ovicells.

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**Morphasmopora** Lang, 1916

**Type species** – *Cribrilina jukes-brownei* Brydone, 1906, Campanian, Norfolk, England; by original designation.

**Remarks** – Lang (1922) referred *Morphasmopora* to his subfamily Kelestominae together with *Kelestoma* Marsson and the Recent *Gephyrotes* Norman. In these cribrimorph genera the costae forming the apertural bar are bifid. Costae are fewer (10-12) in *Morph-
asmopora than in Kelestoma (20-30). The North American species described below has an intermediate number of costae, but overall is closer to Morphasmopora.

*Range* – Campanian-Maastrichtian.

**Morphasmopora variostoma** sp. nov.

Pl. 105.

*Material* – Holotype: RU5470, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2). Paratypes, RU5471, RU5629, details as for holotype.

*Etymology* – L., varius, variable, and Gr., stoma, mouth, in reference to the variable construction of the proximal portion of the peristome.

*Description* – Colony a multiserial, encrusting, nonmaculate sheet. Pore chambers and ancestrula not seen.

Autozooids elongate, oval or hexagonal tapered proximally and distally, and with parallel lateral margins, about twice as long as wide. Gymnocyst covered entirely by kenozooids. Planar frontal shield comprising 11 to 16, most commonly 15 or 16, costae graded from robust distally to smaller proximally, each with a near-terminal pelma. Costae broadly fused along midline, lacking intercostal bridges; usually distal pair of costae forming an arched apertural bar (Pl. 105, fig. 1e), the two costae meeting along the zooidal midline, turning outward, and forming a bi-tube extension extending frontally, but slightly inclined distally. Second pair of costae (first pair in some zooids) very robust, bifid, with one of the extensions toward and fusing medially with the underside of the apertural bar or, where apertural bar is lacking, terminating bluntly. Intercostal spaces narrow, inwardly tapering. Primary orifice at base of thick peristome generated by apertural bar, paired lateral adventitious avicularia and extrazooidal skeleton lapping into distal margin of autozooid, around bases of avicularia and commonly along orificial side of apertural bar. Ovicell (Pl. 105, fig. 1f) immersed.

Avicularia (Pl. 105, fig. 1e) of one type, adventitious, paired, located just proximal to midpoint of autozooidal orifice, elevated, visible part smoothly oval with complete pivot bar and rounded mandible directed proximo-medially.

Kenozooids forming complex, irregular serpentine pattern around autozooids, locally concentrated into maze-like areas about equal to autozooids in size (Pl. 105, fig. 1d). Boundaries between autozooids obscured by elongate, complexly dividing kenozooids with thickly calcified margins that lap onto autozooids, commonly around entire perimeters, with intermittent deep groove centred over autozooidal boundary.

*Measurements* – Holotype: ZL 513±51, 460-594 (1, 10); ZW 246±7, 234-259 (1, 10); OW 89±8, 75-102 (1, 10); avicularian OpL 82±6, 73-93 (1, 10); avicularian OpW 56±8, 44-72 (1, 10).

*Remarks* – Morphasmopora variostoma differs from *M. brydonei* Lang, 1916, in the highly salient apertural bar and in having smoothly oval rather than ‘footprint-shaped’ avicularia.
The proximal part of the peristome of this species can be very complex, composed variably of fused costae in an apertural bar, portions of the adventitious avicularia, and a smooth or pleated extension of the kenozooids. Turner (1973) worked out the complex morphology of this species and we differ only with his interpretation of the structure of the bifid costae. He described them as each composed of two longitudinally fused costae that diverge toward the autozooidal midline, with one extending in the same manner as the more proximal costae that comprise the frontal shield and the other extending toward the orifice. We see no evidence that the costae are compound, although the erosional pattern on some bifid and some more proximal costae develops a variably regular longitudinal groove that follows a line of skeletal crystallite boundaries.

**Nannopora Lang, 1916**

*Type species* – *Reptescharella pygmaea* d’Orbigny, 1852 (*in* 1851-1854), Senonian (Coniacian), France; by original designation.

*Remarks* – *Nannopora* was established for species with very small autozooids that lack secondary apertures and in which the distal orifical spines are preserved as narrow spine bases. The frontal shield is composed of laterally linked, transversely rounded costae without pelmata; costae fuse medially to form an unornamented median strip. The apertural bar lacks a median promontory and is rounded transversely in the same manner as the other costae.

*Range* – Coniacian - Eocene (fide Bassler, 1953).

**Nannopora torquata** (Canu & Bassler, 1926)

*Pl. 106.*

1926 *Callopora torquata* sp. nov.; Canu & Bassler, p. 34, pl. 4, fig. 16.

In press *Castanopora? torquata* (Canu & Bassler); McKinney & Taylor, fig. 2E.

*Material* – Holotype: USNM 69962, Maastrichtian, Ripley Formation, Coon Creek Member, Coon Creek, McNairy County, Tennessee (locality TN1). Other material: NHM BZ 5021(2), same details as holotype, but S. Tracey Collection.

*Description* – Colony a multiserial, encrusting, nonmaculate sheet (Pl. 106, fig. 1a). Pore chambers not observed. Ancestrula and primary zone of astogenetic zone of change not seen.

Autozooids elongate hexagonal, about 1.5 times longer than wide. Gymnocyst narrow, visible on short proximal cauda, but not visible along lateral and distal margins. Frontal shield (Pl. 106, fig. 1b, 2c) comprising 11 to 12 robust costae with few intercostal bridges; intercostal spaces roughly equidimensional, varying from circular to irregular in shape, generally narrower than costae; distal pair of costae apparently forming apertural bridge; other costae fused along zooidal midline; pelmata not seen. Orifice oval with somewhat straighter proximal than distal edge to D-shaped, length about two-
thirds width. Opesia large, longitudinally oval, surrounded by narrow cryptocyst, distal margin almost straight, with at least two distal orificial spines. Ovicell (Pl. 106, fig. 1b) hyperstomial, slightly inflated, approximately equidimensional, with smooth surface texture, some with small adventitious avicularia.

In addition to adventitious avicularia on ovicells, two types of interzoooidal avicularia occur. Smaller interzoooidal avicularia variable in size but with uniform-sized elliptical opesia (Pl. 106, fig. 2d). Large interzoooidal avicularium with distally directed spatulate rostrum and overall opesia footprint-shaped (Pl. 106, fig. 2c).

**Measurements** – Holotype: ZL 263±18, 244-293 (1, 10); ZW 173±7, 163-184 (1, 10); OpL 151±19, 125-166 (1, 10); OpW 98±7, 85-109 (1, 10); AL 114 (1, 1); AW 127 (1, 1); avicularian OpL 130 (1, 1); avicularian OpW 60 (1, 1); KL 114±19, 85-137 (1, 7); KW 64±10, 53-73 (11, 7); kenozooidal OpL 80±6, 70-87 (1, 7); kenozooidal OpW 50±4, 41-54 (1, 7).

**Remarks** – The frontal shield is broken in all zooids in the holotype colony (Pl. 106, fig. 2a) and only one zooid preserves more than short stumps of the costae (Pl. 106, fig. 2c). Canu & Bassler (1926, p. 34) interpreted the broken bases of the costae as “small tuberosities” around the mural rim of the zooid, hence their assignment of the species to the non-cribrimorph genus *Callopora*. However, an additional, better-preserved colony (Pl. 106, fig. 1), collected by Steve Tracey, and the single zooid in the holotype that has remnants of intact frontal shield, indicate that the species is characterized by a frontal shield comprised of laterally linked, broad costae.

This species is better placed in *Nannopora* rather than *Callopora* because of the tiny zooidal dimensions, the small orificial spines, the spinocystal construction of the frontal shield and the distribution of interzooecial avicularia. *Nannopora turquata* has fewer costae than any of the three species originally assigned to the genus by Lang (1916, 1921). Its aperture is similar to that of *N. paternensis* Lang, 1916, but transversely rather than longitudinally elongate as are apertures of *N. pygmaea* (d’Orbigny, 1852 in 1851-1854) and *N. lepida* Lang, 1916 (the latter species named on the basis of a single photograph).

**Pelmatopora** Lang, 1916

**Type species** – *Pelmatopora pero* Lang, 1916; Santonian, Surrey, England; by original designation.

**Remarks** – Based on the extensive study of Larwood (1962), *Pelmatopora* is currently accepted as a genus containing species that exhibit highly variable frontal shields in terms of number of costae, with regular to irregularly spaced or no intercostal bridges, and with one terminal or subterminal to multiple pelmata distributed along each costa. A secondary orifice may or may not be present, bordered distally by secondary skeleton, and small avicularia may or may not be present sporadically or paired near the orifice.

**Range** – Coniacian - Danian.
**Pelmatopora irregularis** (Canu & Bassler, 1926)

Pl. 107.

1926 *Membraniporella irregularis* sp. nov.; Canu & Bassler, p. 36, pl. 6, fig. 7.

In press *Pelmatopora irregularis* (Canu & Bassler); McKinney & Taylor, fig. 2F.

**Material** – Lectotype (here designated), USNM 69957, Maastrichtian, Ripley Formation, Coon Creek Member, Coon Creek, McNairy County, Tennessee (locality TN1). Paralectotype, USNM 528407, details as for lectotype.

**Description** – Colony a multiserial, encrusting, nonmaculate sheet (Pl. 107, fig. 1a). Interzoooidal communication via approximately 20 small basal pore chambers forming continuous band around perimeter of each autozooid (Pl. 107, fig. 1c). Ancestrula not seen.

Autozooids small, oval, almost twice as long as wide; partially surrounded by interzoooidal avicularia, but otherwise boundaries partially indefinite due to secondary skeleton (Pl. 107, fig. 2b). Gymnocyst narrow, most extensive proximally, covered by interzoooidal avicularia and secondary skeleton. Frontal shield nearly flat, comprised of 10-12 robust costae separated by narrow slits, the most distal costae very robust due to secondary calcification, but lacking a central boss; costae converge medially, but commonly with a narrow, incised line of contact maintained; proximal ends of costae with broad lateral bulges, commonly merged into a single intercostal bridge just inside the proximal and lateral perimeter of the frontal shield; two pelmata per costa (Pl. 107, fig. 2a), one at the distal tip along the median fused bar, and one centred in the proximal bulge near the frontal shield perimeter. Primary and secondary orifice D-shaped (Pl. 107, fig. 1b), lacking orificial spines, width almost twice length in both maternal and non-maternal autozooids. Ovicell (Pl. 107, fig. 2b) hyperstomial, equidimensional, not strongly inflated, imperforate, covered by nodose secondary skeleton.

Avicularia of one type, interzoooidal, abundant, commonly placed lateral to proximal edge of autozooidal orifice, variable in size, but generally small, some obliquely pedunculate.

Kenozooids not seen.

**Measurements** – Lectotype: ZL 440±25, 400-480 (1, 10); ZW 238±11, 220-260 (1, 10); OL 64±7, 60-80 (1, 10); OW 119±6, 110-130 (1, 10); AL 114±21, 80-140 (1, 10); AW 88±9, 40-60 (1, 10); OvL 136±13, 120-160 (1, 10); OvW 140±16, 120-180 (1, 10).

**Remarks** – Although this species apparently lacks orificial spines, we have re-assigned it to *Pelmatopora* because of the presence of secondary skeleton and the two prominent pelmata on each costa, with the more laterally placed pelmata associated with a septal bridge. The genus *Diacanthopora* is also characterized by two pelmata per costa, one each proximal and distal, but septal bridges are absent.

**Pelmatopora spatulata** sp. nov.

Pl. 108.

**Material** – Holotype: NHM BZ 4832(a), Maastrichtian, Prairie Bluff Chalk, Living-
ston, Sumter County, Alabama (locality AL6). Paratype: NHM BZ 4832(b), on same shell as holotype.

**Etymology** – L., *spatula*, diminutive of *spatha*, meaning a broad flat tool, in reference to the shape of the rostrum of the interzooidal avicularia.

**Description** – Colony a multiserial, encrusting, nonmaculate sheet. Three large pore chambers per autozooid, one distal and two distolateral. Ancestrula (Pl. 108, fig. 2) elongate oval, about two-thirds length and width of autozooids in zone of astogenetic repetition, otherwise similar. Primary zone of astogenetic change restricted to ancestrula and first two to three generations of autozooids.

Autozooids small, oval, averaging 1.45 times longer than wide, autozooidal boundaries distinct, marked by groove and commonly a narrow band of visible gymnocyct, which is most extensive proximally. Frontal shield gently convex, comprised of 10 to 12 robust costae separated by narrow slits, the most distal costae forming an apertural bar slightly more robust than normal costae, with a central boss; costae fused medially along a narrow band; costae with a single intercostal bridge and pelma near the central zone of fusion plus a pelmatidium at the distal tip at the zone of fusion (Pl. 108, fig. 1e).

Primary and secondary orifice D-shaped, with four orificial spines, width almost 1.3 times length in both maternal and non-maternal autozooids. Ovicell (Pl. 108, fig. 1c) hyperstomial, equidimensional, strongly inflated, porous, with six or more pustules each centred on a perforation.

Avicularia of one type, interzooidal, few to abundant (Pl. 108, fig. 1b), intermediate in size, with distally directed spatulate rostrum.

Kenozooids not seen.

**Measurements** – Holotype: ZL 551±63, 450-630 (1, 8); ZW 381±38, 315-450 (1, 8); OL 108±12, 98-135 (1, 7); OW 139±11, 120-150 (1, 7); AL 216±28, 180-255 (1, 8); AW 117±21, 90-150 (1, 7); OvL 243±25, 165-240 (1, 7); OvW 201±19, 180-225 (1, 7); costae 11.4±0.8, 10-12 (1, 7).

**Remarks** – *Pelmatopora spatulata* is most similar to *P. suffulta* (Brydone, 1913), *P. fecampensis* Lang, 1916, and *P. pero* Lang, 1916, in having a D-shaped orifice with four orificial spines and in the character of the costae, with the single pelma and intercostal bridge near the central zone of fusion plus a single pelmatidium at the distal tip. However, it differs from these European species in having fewer costae (10-12 vs 14-22, 16-21 and 13-20, respectively) and in having spatulate rather than acuminate avicularian rostra.

**Phractoporella Lang, 1917**

**Type species** – *Phractopora constrata* Lang, 1916, Maastrichtian, Rügen, Germany; by original designation.

**Remarks** – This genus appears closely related to *Tricephalopora*, but differs in having even more extensively developed tertiary calcification, including a thick tongue extending proximally from the autozooidal peristome and covering much or all of the axial region of the frontal shield.
Range – Campanian – Danian.

Phractoporella daedalus Turner, 1979
Pl. 109.

1979 Phractoporella daedalus sp. nov.; Turner, p. 536, pl. 1, fig. 5.

Material – Holotype: RU 5440, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2). Other material: RU 5632, details as for holotype. USNM 528944, Maastrichtian, Peedee Formation, Neuse River, Lenoir County, North Carolina (locality NC4).

Description – Colony a multiserial, encrusting, nonmaculate sheet radiating from colony origin (Pl. 109, fig. 1a). Pore chambers few, large. Ancestrula surrounded by six autozooids in short (two to three generation) astogenetic zone of change; region of colony origin with very thick secondary skeletal deposits.

Autozooids small, subrounded, almost rhombus-shaped, but with maximum width at orifice, about 1.3 times longer than wide, adjacent autozooids clearly differentiated, but lacking deep groove between. Gymnocyst, and much of the lateral and proximal margins of the frontal shield, buried beneath very thick skeletal deposits, which reach greatest thickness in the vicinity of the orifice. Frontal shield deeply depressed within encompassing skeletal deposits, visible as hollow crescent (Pl. 109, fig. 2c) comprising at minimum 10 to 16 thin costae separated by even more narrow intercostal slits, the most distal costae covered by complex of calcification forming part of the thick peristome; costae converge distally, median area of fusion typically completely covered by thick tongue of skeleton extending proximally from peristome, but not reaching proximal rim of frontal shield in any zooids of the two colonies seen; intercostal bridges not developed; pelmata at inner ends of costae visible in ontogenetically young zooids, but obscured by the thick tongue of skeleton extending proximally from peristome. Primary subcircular orifice deeply buried by peristome; secondary orifice somewhat variable in shape, on average transversely elongate subcircular; oral spines absent. Ovicell (Pl. 109, fig. 1b) hyperstomial, imperforate, broader than long, opening into the peristome.

Avicularia of one type, adventitious, large, paired, placed mid-way alongside orifice; oriented medially to proximally, usually proximo-medially, with broadly acuminate rostrum indenting secondary orifice in some autozooids; short, corroded remnants of condyles or bar present in some avicularia; avicularian chamber rather large, buried within thick skeletal deposits.

Kenozooids apparently absent.

Measurements – (From Turner, 1979) Holotype: ZL 490±49, 380-520 (1, 10); ZW 410±24, 360-440 (1, 10); OL 70±10, 70-100 (1, 10); OW 100±10, 90-130 (1, 10); OvL 130±28, 120-170 (1, 7); OvW 220±32, 180-270 (1, 7); AL 120±14, 100-150 (1, 10); AW 80±10, 60-100 (1, 10).

Remarks – Turner (1979) reported uncommon laterally paired, more rarely a single, medial fenestrae on the proximal side of the peristome, not found by us. In addition to
the holotype, there is a second SEM stub-mounted, metal-coated specimen (RU 5632) of *P. daedalus* in the material studied by Turner, although he did not designate it as a paratype.

**Pliophloea Gabb & Horn, 1862**

*Type species* – *Flustra sagena* Morton, 1834, Thanetian, New Jersey, U.S.A.; by original designation.

*Remarks* – *Pliophloea* contains species in which the costae are broad, relatively flat, closely spaced, joined by multiple intercostal bridges that leave very small intercostal spaces, and with a row of conspicuous pelmatidia along costal midlines, each pelmatidium corresponding with a septal bridge. Abundant interzooidal avicularia of various sizes and placement are characteristic, as is the perforated gymnocyst.

*Range* – Santonian - Thanetian.

**Pliophloea shmoiformis** sp. nov.

Pl. 110.

*Material* – Holotype: RU 5415, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

*Etymology* – Named from the shape of the avicularian opesia, which have the form, as seen in frontal view, of Al Capp’s mid-20th century cartoon creatures, shmoos, and in reference to the large variation in size in this species and uncertain function of all such non-acuminate avicularia, because shmoos could be anything the person looking at them wanted them to be.

*Description* – Colony a multiserial, encrusting, nonmaculate sheet (Pl. 110, fig. 1a). Ancestrula resembling later zooids, but smaller (Pl. 110, fig. 1f); primary zone of astogenetic change at least four generations in length.

Autozooids small, oval, about 1.5 times longer than wide, deep groove between adjacent autozooids. Gymnocyst minimal, commonly visible only proximally. Frontal shield broadly convex, comprising 17-21, usually 19, broad, relatively flat costae with 4-5 intercostal bridges between adjacent costae, at least some of which are accompanied by a very small pelmatidium (Pl. 110, fig. 1e); minute circular to oval intercostal spaces occur between intercostal bridges; costae fused along zooecial midline, producing narrow longitudinal bar; distal pair of costae firmly fused axially, producing robust apertural bar that is part of a broad, low peristome around aperture. Orifice equidimensional, D-shaped, with cardelle-like indentations near straight proximal border so that aperture overall has a very broad keyhole shape (Pl. 110, fig. 1c); oral spines absent or too poorly preserved to be seen. Ovicell unknown.

Avicularia (Pl. 110, fig. 1d) of single type, interzooidal, very abundant, variable in size and shape, proximally oriented; commonly at both distolateral edges of autozooids, as well as other locations; opesia of constant size, located centrally or distal to
broad proximal gymnocyst, broadly keyhole shaped, with short condyles, rostrum discoidal, occupying two-thirds total length of opesia.

Kenozooids not present in holotype.

**Measurements** (Partly from Turner, 1973.) – Holotype: ZL 380±32, 330-420 (1, 12); ZW 260±26, 220-300 (1, 12); OL 80±4, 70-80 (1, 8); OW 80±7, 70-90 (1, 8); AL 100±38, 60-150 (1, 12); AW 90±44, 40-180 (1, 12); Costae 19±1.3, 17-21 (1, 16); AoL 75±3, 72-80 (1, 10); AoW 40±4, 34-47 (1, 10).

**Remarks** – Turner (1973) indicated that there are 4-5 minute pelmatidia per costa, each located adjacent to an intercostal bridge. We concur that tiny pelmatidia do occur adjacent to intercostal bridges, but preservation of the specimen is too poor for us to see pelmatidia at each such point on any of the costae.

Among previously described species, *Pliophloea shmooformis* most closely resembles *P. elegans* Canu & Bassler, 1933, from the Vincentown Formation (Thanetian) of New Jersey, but differs in having smaller autozooids, a more equidimensional and smaller orifice, fewer costae and in lacking a keel along the median strip of costal fusion in the frontal shield.

*Sandalopora* Lang, 1916

*Type species* – *Sandalopora soccata* Lang, 1916, ‘Senonian’, southern England; by original designation.

**Remarks** – Pending a revision of the myriad genera of Cretaceous cribrimorphs created by W.D. Lang, we follow Turner (1973) in provisionally assigning a new North American species to the genus *Sandalopora*. This pelmatoporid genus has the orifice indented proximally by a median projection of the apertural bar. The new species extends the upper range of *Sandalopora* from Santonian to Maastrichtian.

**Range** – Santonian-Maastrichtian.

*Sandalopora luxuria* sp. nov.

Pl. 111.

*Material* – Holotype: RU 5445, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

**Etymology** – L., *luxuria*, profusion, excess or extravagance, in reference to the large number of polymorphs that surround the autozooids.

**Description** – Colony a multiserial, encrusting, nonmaculate sheet (Pl. 111, fig. 1a), multilaminate by self-overgrowth. Pore chambers and ancestrula not seen.

Autozooids small, distally widening oval (Pl. 111, fig. 1b), about twice as long as wide, autozooids commonly separated by interzooidal avicularia and kenozooids.
Gymnocyst not visible. Frontal shield flat, comprising 11-14, usually 12, distally broad to proximally narrow, relatively flat costae (Pl. 111, fig. 1d) with single ringed pelma near lateral ends, but without intercostal bridges; intercostal spaces narrow, slit-like; costae fused along zoeoidal midline, producing broad longitudinal bar; broad apertural bar commonly divided transversely by fissure suggestive of two pairs of fused costae, with pelmata visible either in proximal or distal portion, distal portion commonly with median robust boss (Pl. 111, fig. 1f) extended disto-frontally distal pair of costae; apertural bar continuous with a narrow, but conspicuous, low peristome around aperture; lateral margins of zooids not visible, covered by surrounding polymorphs. Orifice transversely elongate D-shaped to oval; oral spines absent or too poorly preserved to be seen. Ovicell (Pl. 111, fig. 1e) hyperstomial, moderately inflated, lacking median keel, surface smooth and not perforated, broader than long.

Interzoooidal polymorphs very abundant (Pl. 111, fig. 1c), variable in size, shape and orientation, thick, completely surrounding most autozooids and grading from kenozooids to well-developed avicularia with broadly spatulate mandibles.

**Measurements** – Holotype: ZL 293±18, 266-319 (1, 10); ZW 145±12, 131-166 (1, 10); OL 67±6, 61-80 (1, 10); OW 91±7, 79-101 (1, 10); OvL 117±18, 98-134 (1, 3); OvW 151±16, 135-167 (1, 3); AL 98±21, 69-144 (1, 10); AW 83±15, 56-107 (1, 10); Costae 11.8±1.0, 10-14 (1, 10).

**Remarks** – The surface of the holotype is corroded to the extent that the pelmata commonly are difficult to distinguish. Turner (1973) indicated two pelmata per costa, but we saw no costae with more than one, laterally located pelma.

Some of the smaller heterozooids may be adventitious, but the haphazard way in which they are organized, with their margins commonly overtopped by adjacent heterozooids, precludes definitive determination. All heterozooids are closely placed between autozooids, overlapping the edge of the costal shield with a sharp border and seem most reasonably inferred all to have an interzoooidal origin.

**Stichocados Marsson, 1887**

**Type species** – *Stichocados verruculosus* Marsson, 1887, Maastrichtian, Rügen, Germany; by original designation.

**Remarks** – The morphological characterization and taxonomy of *Stichocados* is rather unsettled. Several late Cretaceous and Paleocene species have been placed in the genus, and various authors have re-assigned species into and out of it (Lang, 1922; Voigt, 1930; Canu & Bassler, 1933; Berthelsen, 1962). Unfortunately, the only illustrations for all the species are either stylized drawings or low-magnification photographs.

Pending re-examination and high-magnification illustration of the type species, for now we follow Lang’s (1922, p. 174) characterization of the genus as made of species of “small size, with comparatively few costae (7-14), no or very few aviculoecia [avicularia], and a secondary aperture perforated by fenestrae.”

**Range** – Maastrichtian - Danian, Thanetian?
Stichocados aenigmata sp. nov.
Pl. 112.

Material – Holotype: RU 5455, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

Etymology – L., *aenigma*, obscure, inexplicable or a riddle, in reference to the possible avicularian polymorphs in the holotype colony.

Description – Colony a multiserial, encrusting sheet (Pl. 112, fig. 1a, b). Interzooidal communication via large distolateral and proximolateral pores plus single, smaller distal and proximal pores. Pore chambers not seen. Ancestrula not present in holotype, although the proximal 3-4 generations preserved in the specimen exhibit a size gradient and appear to be part of the primary zone of astogenetic change.

Autozooids oval to hexagonal, about 1.5 times longer than wide, a deep groove between adjacent autozooids. Gymnocyst narrow, visible only at growing edge. Frontal shield (Pl. 112, fig. 1d) nearly flat to highly convex, comprising 9-12, usually nine, tapered costae with 3 to 5 intercostal fusions producing circular to transversely elongated, oval intercostal spaces; no pelmatidia seen; costae convergent on a small suborificial area or point, medially fused without producing median longitudinal bar; distal pair of costae fused into an elevated, thick apertural bar, proximo-distally compressed with a central, low, bipartite boss where costal tips turn up, connected to adjacent pair of costae by about ten pillar-like costal bridges separated by narrow, elongate rectangular intercostal spaces. Primary orifice transversely slightly elongate, tending toward D-shaped. Secondary orifice essentially circular, formed by apertural bar and robust, variably developed curved bars that connect lateral ends of apertural bar and distal orificial margin, apparently leaving lacunae between them and the lateral margins of the primary orifice. Ovicells not developed in material studied.

Avicularia of two types locally present. One type, apparently interzooidal, developed as a small triangular chamber centred on distal pore of the proximal autozooid, with roughly subtriangular, inclined opening on proximal side. The second, apparently larger and adventitious, originating laterally near proximal end of autozooid, extending distally, with inflated chamber about one-third to one-half the width of autozooids, terminating in inclined orifice from one of which an elongate narrow, tapered plate extends, possibly a palate for an acuminate rostrum.

Kenozooids not seen.

Measurements – (From Turner, 1973, except for number of costae) Holotype: ZL 370±65, 230-500 (1, 15); ZW 220±35, 150-280 (1, 15); OL 60±10, 40-70 (1, 10); OW 90±17, 60-120 (1, 10); Costae 11.4±0.8, 10-12 (1, 7).

Remarks – Stichocados aenigmata differs from *S. verruculosus* Marsson as described by Lang (1922) in having smaller autozooids, more costae and fewer costal bridges, and in the presence of apparent avicularia. It differs from *S. subbrachiata* Berthelsen, 1962, in having smaller autozooids, fewer costae that are tapered instead of wide and no intra-zoooidal/kenozooidal skeletal development.
Turner (1973) characterized this species as having 4-5 small pelmatidia per costa, although we could not confirm their presence. He also (1973, p. 165) described the secondary orifice as “tripartite, ... secondarily divided by two large tubular spines that arise proximally from the thickened apertural bar, flatly overarch the primary orifice, and join the subjacent distal oral rim.” The holotype specimen is corroded and we cannot confirm the point of origin of the continuous ring that encircles the secondary orifice, nor are we sure that the subjacent lacunae are original rather than artefacts of weathering.

The high coefficients of variation in linear measurements are probably a reflection of including zooids from the primary zone of astogenetic change as well as those from the zone of astogenetic repetition.

**Tricephalopora Lang, 1916**

*Type species* – *Cribrilina triceps* Marsson, 1887, Maastrichtian, Rügen, Germany; by original designation.

*Remarks* – *Tricephalopora* is a large genus characterised by commonly paired adventitious avicularia located proximolaterally of the autozooidal orifice, often extending across the proximal edge of the orifice and fusing to form a proximal orificial shield or projecting more distally into the orifice to make the secondary orifice keyhole or figure-of-eight shaped; costae lack intercostal bridges, and have a single, commonly near-terminal pelma or pelmatidium; and the frontal shield is visible only medially, and is surrounded by thick skeleton spreading from kenozooids.

*Range* - Coniacian - Thanetian.

**Tricephalopora arkansasensis Shaw, 1967**

*Pl. 113, fig. 1.*

1967 *Tricephalopora arkansasensis* sp. nov.; Shaw, p. 1419, pl. 181, fig. 4.

*Material* – Holotype: LSUMG-I 8243, Maastrichtian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2).

*Description* – Colony a multiserial, encrusting, nonmaculate sheet (Pl. 113, fig. 1a). Pore chambers and ancestrula not observed.

Autozooids elongate oval, over twice longer than wide; smoothly inflated from perimeter to area of maximum elevation at proximal margin of orifice. Gymnocyst not visible. Smooth skeletal deposits over frontal wall cover autozooidal margin and extend over apertural bar; frontal shield comprising 14-20 costae (including pair that form apertural bar) without lateral fusions. Costae turned slightly outward at inner ends, meeting and minimally fused along zooidal midline, resulting in low, broad axial ridge; inner end of each costa perforated by a single small pelma. Intercostal spaces narrow, inwardly tapering. Secondary orifice circular (Pl. 113, fig. 1b), at terminus of prominent peristome composed of tertiary frontal wall. Adjacent autozoocia typically separated by conspicuous groove. Ovicells not seen.
Avicularia of one type, adventitious, single, occasional, situated approximately at level of apertural bar, oriented at variable lateral angle, with highly acuminate tip of rostrum extending into orifice of neighbouring autozoecium.

Kenozooids not seen.

**Measurements** (From Shaw, 1967.) – Holotype: ZL 730±39, 660-800 (1, 10); ZW 300±28, 230-330 (1, 9); OL 140±14, 120-150 (1, 10); OW 140±14, 120-150 (1, 10); AL 130±21, 120-170 (1, 7); AW 90±27, 70-120 (1, 7).

**Remarks** – Shaw (1967) indicated that the primary orifice is circular, but we could not confirm this. The specimen is weathered and many details are obscured by adherent sediment grains; only one frontal shield is sufficiently well preserved for the costal pell mata to be seen confidently.

*Tricephalopora clara* sp. nov.

Pls. 113, figs. 2, 3; Pl. 114.


**Etymology** – *L.*, *clarus*, bright, plain or distinct, in reference to the prominent deep grooves between autozooids and the sharp, pronounced margins of the elongate kenozooids centred along those margins.

**Description** – Colony a multiserial, encrusting, nonmaculate sheet (Pl. 113, fig. 2a). Ten or more large pore chambers around basal perimeter of autozooids. Ancestrula oval, about 1.5 times longer than wide, overall length slightly more than half length of autozooids in zone of astogenetic repetition (Pl. 114, fig. 2), broken in available specimen so that details of frontal wall organization unknown.

Autozooids elongate oval, slightly more than twice as long as wide; smoothly inflated from perimeter to area of maximum elevation at proximal margin of orifice. Gymnocyst restricted to narrow band around perimeter of autozooid, only locally visible where not covered by subsequent skeleton. Narrow band of smooth tertiary frontal wall covers proximal and lateral margin of autozooidal surface, and across distal edge of frontal shield; frontal shield visible in window of variable length from somewhat less to somewhat greater than half the total length of the zooid, with 9-13, most commonly ten, small uniform costae visible; no intercostal fusions. Costae meeting and fused along zooidal midline; distal ends of costae spatulate or turned up axially, containing a single pelma. Likely only one additional pair of distal costae (forming apertural bar) covered by tertiary frontal wall. Intercostal spaces inwardly tapering, at outer ends approximately same width as costae. Primary orifice (Pl. 114, fig. 1c) circular to slightly oval transversely or longitudinally elongate, at base of thick peristome; secondary orifice larger, highly variable in shape, many with lateral indentations where acuminate tips of adventitious avicularia extend into the orifice. Autozooids with two robust distal oral
spines extending from primary orifice partially or completely through peristome (Pl. 114, fig. 1e). Ovicell (Pl. 114, fig. 1a, b, e) initially smoothly inflated and textured, slightly emergent, approximately equidimensional; typically covered by tertiary skeleton spread from adjacent kenozooids.

Avicularia (Pl. 113, fig. 3b; Pl. 114, fig. 1a) of single type, adventitious; paired, single or on some autozooids absent, occurring proximal to midpoint of autozooidal orifice, with acuminate rostrum oriented in any direction, but most commonly pointing toward orifice.

Kenozooids (Pl. 114, fig. 1d) occur between the apparently smoothly oval autozooids, and are clearly defined, elongate, narrow and deep (except where completely filled by skeleton leaving only a single small pit). They produce a narrow band of thickened skeleton around the frontal shield of autozooids and that also surrounds the bases of the adventitious avicularia.

**Measurements** – Holotype and (for costae only) paratype: ZL 569±48, 483-631 (1, 10); ZW 303±36, 251-360 (1, 10); OL 149±19, 120-183 (1, 10); OW 115±9, 97-125 (1, 10); AL 157±15, 136-183 (1, 10); AW 105±13, 76-119 (1, 10); OvL 161±28, 105-190 (1, 10); OvW 157±11, 111-178 (1, 10); Costae 10.2±1.1, 9-13 (2, 20).

**Remarks** – *Tricephalopora clara* generally resembles *T. vibraculata* Turner, 1979, except that the skeletal deposits of the elongate kenozooids in *T. vibraculata* are not as well defined as those of *T. clara*; circular deep interzooidal polymorphs abound in *T. vibraculata*, but are absent in *T. clara*; and *T. vibraculata* has more costae, larger secondary orifices and relatively broader ovicells.

**Tricephalopora lamellaria** (Canu & Bassler, 1926)

Pl. 115.

1926 Gephyrotes lamellaria sp. nov.; Canu & Bassler, p. 37, pl. 6, figs. 8-9.
In press *Tricephalopora lamellaria* (Canu & Bassler); McKinney & Taylor, fig. 3A.

**Material** – Lectotype (here designated): USNM 69968, Maastrichtian, Ripley Formation, Coon Creek Member, Coon Creek, McNairy County, Tennessee (locality TN1). Paralectotypes, USNM 528411, 528412, details as for holotype.

**Description** – Colony a multiserial, encrusting, nonmaculate sheet (Pl. 115, fig. 1a, b). Large pore chambers around distal basal perimeter of autozooidal. Ancestrula not seen.

Autozooids elongate oval to subhexagonal, slightly less than twice as long as wide. Except perhaps at or near growing margin, gymnocyct covered by subsequent skeleton. Frontal shield visible in window of variable length from somewhat less to somewhat greater than half the total length of the zooid, with 5-9 narrow, variably spaced costae visible (Pl. 115, fig. 1c); no intercostal fusions. Costae meeting and fused at zooidal midline along a narrow to broad zone, either produced as a low ridge or marked by a sharp median groove; distal ends of costae narrow or spatulate, containing a single pelma. One or two additional pair(s) of distal costae (those forming apertural bar and in some
cases the next-proximal pair) covered by secondary skeletal deposits joining apertural bar and adventitious avicularia protruding over orifice. Intercostal spaces inwardly tapering, oval or circular, commonly wider than costae. Narrow band of smooth skeleton derived from narrow kenozooids between autozooids covers proximal and lateral margin of autozooidal surface, and extends across distal edge of frontal shield (Pl. 115, fig. 1d), where one or usually two pores reflect former position of intercostal spaces between apertural bar and next-proximal pair of costae. Primary orifice D-shaped, transversely elongate, at base of thick peristome; secondary orifice also D-shaped, defined proximally by acuminate tips of adventitious avicularia and distally by thick secondary skeleton. Ovicell (Pl. 115, fig. 2) initially smoothly inflated and textured, hyperstomial, slightly emergent, width about two-thirds length; typically covered by skeletal deposits from adjacent kenozooids.

Avicularia (Pl. 115, figs. 1c, d, 2) of single type, adventitious, large, paired, located at proximolateral orificial margin, with acuminate rostrum oriented approximately transversely across proximal margin of orifice and forming straight to nearly straight proximal margin of secondary orifice; secondary skeleton forms sloping surface between rostrum and distal portion of frontal shield, bridging across one or two pairs of distal costae and typically with one or two small windows positioned over former intercostal spaces.

Kenozooids clearly defined, elongate, narrow, occurring between autozooids and producing the narrow band of secondary skeleton around the frontal shield of autozooids, that extends to surround the bases of the adventitious avicularia, and to form the lateral and distal portions of the wall of the autozooidal secondary orifice.

**Measurements** – Lectotype: ZL 566±39, 520-640 (1, 10); ZW 267±22, 240-300 (1, 10); OL 126±17, 100-160 (1, 10); OW 151±17, 130-190 (1, 10); AL 192±21, 160-220; AW 96±13, 80-120 (1, 10); OvL 172±11, 160-180 (1, 6); OvW 122±29, 90-160 (1, 6).

**Remarks** – Canu & Bassler (1926) assigned this species to *Gephyrotes*, apparently interpreting the distal costae as bifurcated, but the interior view of the skeleton shows them not to be so, and all attributes of the species fit well within *Tricephalopora*.

*Tricephalopora larwoodi* Shaw, 1967
Pls. 116, 117.

1967 *Tricephalopora larwoodi* sp. nov.; Shaw, p. 1417, pl. 181, fig. 2.
1979 *Tricephalopora larwoodi* Shaw; Turner, p. 522, pl. 1, figs. 1-3.

**Material** – Holotype: LSUMG-I 8242, Maastrichtian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2). Other material: RU 5420, RU 5421, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2). NHM BZ 4810(4), BZ 5035(4), BZ 5111(2), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). NNM RGM 507 058, Maastrichtian, Prairie Bluff Chalk, Emelle, Sumter County, Alabama (locality AL9). NNM RGM 507 059, Maastrichtian, Prairie Bluff Chalk, Braggs, Lowndes County, Alabama (locality AL3).
**Description** – Colony a multiserial, encrusting, nonmaculate sheet (Pl. 116, fig. 1a; Pl. 117, fig. 1a). Approximately 16-20 pore chambers forming continuous ring within basal periphery of autozooids (Pl. 116, fig. 1f; Pl. 117, fig. 1c). Ancestrula (Pl. 117, figs. 2, 3) oval, about 1.5 times longer than wide, overall length about half that of autozooids in zone of astogenetic repetition, small frontal shield comprised of approximately eleven costae, D-shaped primary orifice with orificial spines. In primary zone of astogenetic change full size of orifice developed by second asexually budded generation and full size of zooids with consistent presence of paired oral avicularia developed within four to five generations.

Autozooids elongate oval, slightly less than twice as long as wide, surrounded by deep groove from which kenozooidal skeleton spreads. Gymnocyst visible only in ontogenetically young autozooids along colony margin, covered by skeleton of expanding kenozooids in older zooids. Gymnocyst a moderately broad band around autozooidal perimeter, broadest proximally, usually covered by subsequent skeleton. Frontal shield flat to gently inflated from perimeter to area of maximum elevation at proximal margin of orifice. Smooth, continuous calcification covers proximal and lateral margin of autozooidal surface and crosses distal edge of frontal shield; frontal shield visible in window generally longer than half the total length of the zooid, in which 11 to 14 rounded, slightly tapered costae without lateral fusions may be seen (Pl. 116, fig. 1c). Costae meeting and fused along zooidal midline; inner ends upturned, a single distal pelma present. Distal pair of costae originating along proximal margin of orifice, oriented proximomedially, covered by expanding kenozooids in older zooids. Intercostal spaces about half width of costae, inwardly tapering. Primary orifice subcircular to rounded D-shaped, at base of thick, but relatively narrow peristome; secondary orifice larger, transversely elongated D-shaped or less commonly oval, some key-hole shaped with lateral indentations due to acuminate tips of adventitious avicularia extending into the orifice. Ovicell (Pl. 116, fig. 1d; Pl. 117, fig. 1b) smoothly inflated, slightly emergent, width greater than length, eventually covered over by tertiary wall.

Avicularia (Pl. 116, fig. 1e) of single type, adventitious, paired, located from near proximal margin to midpoint of autozooidal orifice, with complete cross-bar and acuminate rostrum most commonly pointing toward orifice and corresponding with indentation in orificial margin, a few oriented proximomedially.

Kenozooids occur between the apparently smoothly oval autozooids and are elongate, moderately narrow and deep (except where partially filled by skeleton leaving a relatively shallow strip). They produce a narrow band of thickened skeleton around the frontal shield of autozooids (Pl. 116, fig. 1c) and that also surrounds the bases of the adventitious avicularia.

**Measurements** (From Shaw, 1967.) – Holotype: ZL 450±40, 400-540 (1, 10); ZW 250±26, 220-280 (1, 10); OL 90±19, 70-120; OW 110±5, 90-110; AL 120±22, 90-150 (1, 10); AW 110±17, 80-130 (1, 10); OvL 70±22, 950-110 (1, 10); OvW 120±15, 50-150 (1, 10).

**Remarks** – *Tricephalopora larwoodi* is the most widely encountered among the *Tricephalopora* species in the Upper Cretaceous of eastern North America.
**Tricephalopora aff. obducta** Lang, 1916

1979  
*Tricephalopora obducta* Lang; Turner, p. 531, pl. 1, fig. 5.

**Material** — RU5430, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

**Description** — Colony a multiserial, encrusting, nonmaculate sheet with most proximal zooids completely covered by continuous skeletal deposits (Pl. 118, fig. 1a). Pore chambers and ancestrula not seen.

Autozooids moderately elongate oval, about 1.3 times longer than wide; smoothly inflated from perimeter to area of maximum elevation at proximal margin of orifice. Smooth skeletal deposits cover most of autozooidal surface; frontal shield visible only in small window midway between orifice and proximal margin of zooid, in which 11-16 small costae without lateral fusions may be seen (Pl. 118, fig. 1c). Costae meeting and minimally fused along zooidal midline; inner ends upturned, each perforated by a single, small, distal pelma. Additional distal costae, including those forming apertural bar, may be covered by subsequent skeletal deposits. Intercostal spaces narrow, inwardly tapering. Primary orifice circular, at base of thick peristome; secondary orifice (Pl. 118, fig. 1d) circular, approximately same size as primary orifice. Continuous ring of pore chambers around perimeter of zooid, just above base. Ovicells not seen.

Avicularia (Pl. 118, fig. 1b) of single type, adventitious, paired, adjacent or just distal to midpoint of autozooidal orifice, with round-tipped rostrum pointing toward, in some cases slightly extending over, orifice.

A single interzooidal kenozooid fills each gap between contiguous rounded autozooids.

**Measurements** — (From Turner, 1979) RU5430: ZL 480±42, 420-550 (8); ZW 350±22, 310-370 (8); OL 100±30, 70-130 (8); OW 80±14, 80-120; AL 80±10, 60-100 (6); AW 60±10, 50-80 (6).

**Remarks** — Turner (1979) identified this specimen as *T. obducta* Lang, 1916, but we believe the New Jersey population is more likely to be an undescribed species that has affinity with *T. obducta*. As noted by Turner (1979), the New Jersey specimens differ from the type of *T. obducta* in growth habit, in having smaller autozooids and in the presence of conspicuous pore chambers (dietellae). Information on the frontal shield of *T. obducta* is lacking. Turner apparently had access to additional material, but we have seen only one specimen, in which only two autozooids are well preserved and, therefore, we defer from erecting a new species for the New Jersey material.

**Tricephalopora poricyensis** Turner, 1979

1979  
*Tricephalopora poricyensis* sp. nov.; Turner, p. 533, pl. 1, fig. 4.

**Material** — Holotype: RU5435, Maastrichtian, Navesink Formation, Poricy Creek, Monmouth County, New Jersey (locality NJ1).
Description – Colony fragment (Pl. 118, fig. 2) consists of only a few contiguous, encrusting autozooids. Pore chambers and ancestrula not seen. Described by Turner (1979, pp. 533-534) thus: “Tricephalopora with a thick, smooth complete tertiary frontal wall. The frontal shield is visible through a small rimmed oval to reniform fenestra. The costal shield is partly covered by a proximally directed calcareous tongue. The small paired adventitious oral avicularia are directed inward from the lateral peristome. The avicularia are tear-drop shaped and provided with transverse pivotal bars.” Ovicells not seen.

Measurements – (From Turner, 1979) Holotype: ZL 360±47, 300-410 (1, 5); ZW 270±17, 250-300 (1, 5); OL 130±14, 110-150 (1, 5); OW 100±10, 90-110 (1, 5); AL 90±10, 80-100 (1, 4); AW 40±10, 30-50 (1, 4).

Remarks – The specimen here referred to as the holotype was initially termed “figured specimen” by Turner (1979), but the figured specimen was the only one on which the species was based. It has subsequently been misplaced or lost, and we have seen no additional material.

Tricephalopora vibraculata Turner, 1979
Pls. 119-120.

1979 Tricephalopora vibraculata sp. nov.; Turner, p. 528, pl. 1, fig. 7.

Material – Holotype: RU 5425, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2). Other material: RU 5620, details as for holotype. NHM BZ 4437(4), BZ 5230, Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). NNM RGM 507 059, Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5).

Description – Colony a multiserial, encrusting, nonmaculate sheet. Approximately 20 large pore chambers forming continuous ring within basal periphery of autozooids (Pl. 120, fig. 1d). Ancestrula (Pl. 120, fig. 1e) elongate oval, about twice as long as wide, length less than half that of autozooids in zone of astogenetic repetition; ten diminutive costae visible in window exposing frontal shield; secondary orifice D-shaped with six distal oral spines; giving rise directly to one distally budded autozooid, but skeletal deposits covering margins obscure relationships among the other contiguous autozooids. Progressively fewer oral spines (to none in zone of astogenetic repetition), and increase in size of autozooids and autozooidal orifices through primary zone of astogenetic change encompassing approximately 5-6 generations of autozooids (Plate 120, fig. 1a).

Autozooids elongate oval, slightly more than twice as long as wide; smoothly inflated from perimeter to area of maximum elevation at proximal margin of orifice. Narrow peripheral gymnocyct obscured by subsequent skeletal deposits (Pl. 119, fig. 2b). Smooth skeletal deposits cover proximal and lateral margin of autozooidal surface, and cross distal edge of frontal shield (Pl. 119, fig. 2a); frontal shield visible in window somewhat less than half the total length of the zooid, in which 10-14 small costae without
lateral fusions may be seen (Pl. 119, fig. 1c); costae commonly graded from more robust distally to more slender proximally. Costae meeting and fused along zooidal midline; inner ends upturned, a single small distal pelma visible in most. At least one additional pair of distal costae (e.g., those forming apertural bar) covered by subsequent skeletal deposits. Intercostal spaces narrow, inwardly tapering. Primary orifice (Pl. 120, fig. 1b) subcircular, at base of thick peristome; secondary orifice larger, key-hole shaped (Pl. 119, fig. 1d), with lateral indentations most pronounced where acuminate tips of adventitious avicularia extend into the orifice. Ovicells smoothly inflated, slightly emergent, width greater than length.

Avicularia of one type, adventitious, paired, just proximal to midpoint of autozooidal orifice (Pl. 119, fig. 1d), with acuminate mandible oriented in any direction, but most commonly pointing toward orifice and corresponding with indentation in orificial margin that separates larger distal portion from smaller proximal portion.

Kenozooids (Pl. 119, fig. 1b) vertically cylindrical, slightly larger in diameter than length of adventitious avicularia, abundant, but irregularly distributed between autozooids.

Skeletal deposits covering autozooidal margins, around the frontal shield of autozooids, and surrounding bases of adventitious avicularia and cylindrical interzooidal structures, extend from the walls of kenozooids that occur between the apparently smoothly oval autozooids.

**Measurements** – Holotype, topotype: ZL 545±26, 492-582 (2, 20); ZW 254±32, 194-309 (2, 20); OL 235±12, 213-260 (2, 20); OW 143±13, 119-167 (2, 20); AL 162±23, 129-215 (2, 20); AW 106±11, 83-121 (2, 20); OvL 150±22, 131-188 (2, 9); OvW 231±19, 201-264 (2, 9); VD 184±14, 154-207 (2, 16); VO 107±11, 93-134 (2, 16).

**Remarks** – Turner (1979) interpreted the cylindrical kenozooids as basal sockets of large vibracula. However, the structures have similar placement and skeletal organization to elongate kenozooids in other species of *Tricephalopora*. They appear to be derived from the more typical kenozooids. Vibracula are specialized avicularia with setose mandibles, so although the cylindrical kenozooids may have had a particular function, we prefer not to refer to them as vibracula.

**Turnerella gen. nov.**

*Type species – Turnerella periphereia* sp. nov., Maastrichtian, New Jersey, U.S.A.


*Diagnosis* – Cribrimorph with frontal shield comprised of relatively few, broad costae, linked by sparse septal bridges; pelmatidia inconspicuous or absent. Oral spines absent, oval primary orifice outlined by proximal septal bridge of two or more costae and distal oral shield comprised of short costae within a distally complete continuation of costal field. Secondary tissue and avicularia absent in type species.
Range – Lower Maastrichtian.

*Turnerella peripheria* sp. nov.

Pl. 121.

**Material** – Holotype: RU 5633, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2). Paratypes: RU 5465, 5466, 5607, 5611, 5614, details as for holotype.

**Etymology** – Gr., *peripheria*, circumference, in reference to the presence of costae arising from the entire periphery of the zooid, including the distal margin above the orifice.

**Description** – Colony a multiserial, encrusting, nonmaculate sheet (Pl. 121, fig. 1a). Pore chambers and ancestrula not seen.

Autozooids variable in shape and size, typically oval to hexagonal, about 1.5 times longer than wide; deep groove between adjacent autozooids commonly appearing serrated or obscured by interdigitation or overlap of slightly bulbous bases of costae. Gymnocyst not seen. Frontal shield (Pl. 121, fig. 2b) broadly convex, comprising 8 to 13, usually ten, broad, relatively flat costae with 1-2 intercostal bridges between adjacent costae, producing irregularly shaped and sized, generally rounded intercostal spaces; costae apparently lacking pelmatidia, fused along zooidal midline, some with suture visible; gymnocyst rarely and only minimally visible peripherally; distal pair of shield costae fused axially, locally joined on one or both sides by a medioproximally oriented orificial costa. Orifice transversely oval, horizontal to distally downwardly inclined, defined laterally and distally by 4 to 6 short costae connected along oral edge by a thin skeletal band (Pl. 121, fig. 3b). Oral spines absent. Secondary skeletal deposits lacking. Ovicell (Pl. 121, fig. 1b) hyperstomial, moderately inflated, generally wider than long, surface non-perforated and typically smooth, usually with median keel, some with median suture.

Avicularia and kenozooids absent.

**Measurements** – Holotype, four paratypes: ZL 584±66, 464-760 (5, 41); ZW 360±44, 256-486 (5, 41); OL 102±18, 71-138 (5, 44); OW 121±23, 74-152 (5, 44); OvL 214±23, 150-241 (4, 25); OvW 233±22, 172-264 (4, 25); Costae 9.9±1.3, 8-13 (5, 40).

**Remarks** – There are few species with which this remarkably unique species can be compared closely. Following Turner (1973, p. 158), we compare it with *Pelmatopora planaris* Lang, 1916, and *P. quadrivolucris* Lang, 1916, which are superficially similar to *T. peripheria*. However, both these species have prominent pelmata, four oral spines, adventitious avicularia, and meandriform kenozooids covering the autozooidal boundaries and locally overlapped along the distal zooidal edges to define the distal edge of the orifice.

**Ubaghsia Jullien, 1886**

**Type species** – *Steginopora reticulata* Ubaghs, 1865; Maastrichtian, Belgium; by original designation.
Remarks – We have nothing to add to the characterisation of the bizarre genus *Ubaghsia* given by Larwood (1962). In the genus, autozooids have a proximal oral shield comprising a pair of proximolateral oral adventitious avicularia that are raised on stout stalks, medially oriented and uniting above the secondary orifice. There may be an oral spine fused onto the distal side of each oral avicularium. A less well-developed distal oral shield may also be present. Oral spines vary from single to highly branched within the genus. Secondary calcification of the frontal shield may be thick and complex, in some cases leaving rimmed lacunae centred over the intercostal spaces.

Range – Santonian - Maastrichtian, Danian?

*Ubaghsia tragica* sp. nov.

Pl. 122.

Material – Holotype: RU 5460, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

Etymology – L., *tragicus*, because of the resemblance of the orifice to the mask representing tragedy in ancient Greek drama.

Description – Colony a multiserial, encrusting, nonmaculate sheet (Pl. 122, fig. 1a). Pore chambers and ancestrula not seen.

Autozooids variable in size and shape, zooidal boundaries obscured by subsequent skeletal deposits within two generations of growing edge. Gymnocyst narrow, seldom visible. Frontal shield flat to gently convex, comprising about 10-12 costae of variable width, with three intercostal bridges between adjacent costae, generating oval to circular intercostal spaces of variable size; costae thickened by subsequent calcification, transforming frontal shield into a thick continuous shield perforated by lacunae over intercostal spaces that commonly are surrounded by prominent rounded sleeves (Pl. 122, fig. 1e); distal costae fused into apertural bar with a wide median process extending obliquely over proximal portion of orifice; if originally present, pelmatidia obscured by subsequent calcification or by poor preservation. Primary orifice semicircular, at base of broad peristome that incorporates oral avicularia; secondary orifice about same size as primary orifice, but variably circular, D-shaped or squared, with median process of apertural bar falsely giving appearance of lyrula indenting orifice midway along proximal border (Pl. 122, fig. 1f). Ovicell (Pl. 122, fig. 1c) endozooecial, most easily seen distal to maternal zooids along colony margin.

Avicularia of two types, both adventitious; one pair relatively large, located at proximolateral corners of orifice (Pl. 122, fig. 1e), oriented distomedially into orifice, with acuminate rostrum seldom well preserved; one or two additional smaller avicularia located at distolateral corners of orifice (Pl. 122, fig. 1b), oriented proximomedially into orifice.

Measurements (From Turner, 1973.) – Holotype: ZL 480±96, 350-660 (1, 14); ZW 380±79, 280-620 (1, 14); OL 140±33, 120-200 (1, 10); OW 170±39, 120-250 (1, 10); AL 170±17, 150-200 (1, 10); AW140±30, 100-190 (1, 10); OvL 180 (1, 1); OvW 270 (1, 1).
Remarks – Turner (1973, p. 228) indicated that the apertural bar is “provided with a flat robust median process that merged with the overhead bar of the proximal oral shield.” The placement, length and orientation of the median process are consistent with it extending up to the underside of an arched, proximal oral shield that is typical of *Ubaghsia*, but none were visible (possibly because of quality of preservation) in the single specimen available.

*Ubaghsia tragica* most closely resembles *U. crassa* (Lang, 1916) and *U. reticulata* (Ubaghs, 1865), but differs from them in having a median process on the apertural bar and in having paired, symmetrical proximolateral oral avicularia. In addition, *U. tragica* has a greater number of costae and more regular secondary calcification of the frontal shield than *U. crassa*, and a more robust apertural bar than *U. reticulata*.

**Infraorder Umbonulomorpha Gordon, 1989a**

**Superfamily Arachnopusioidea Jullien, 1888**

**Family Arachnopusiidae Jullien, 1888**

*Trichinopolia* Guha & Nathan, 1996

*Type species* – *Trichinopolia crescentica* Guha & Nathan, 1996, Maastrichtian, Tamil Nadu, India; by original designation.

Remarks – Guha & Nathan (1996) erected *Trichinopolia* for arachnopusiid species with autozooids in which moderate to large pores in the frontal wall are rimmed by prominent circular rings of secondary calcification, orifices are transversely elongate oval to crescent-shaped, distal and distolateral dietellae are present, adventitious avicularia are common and located in the proximolateral corners of the orifice, interzooidal avicularia are large, if present, and the ovicells are small and recumbent. The new species described below extends the generic concept to accommodate species with larger ovicells, differently situated dietellae, absence of adventitious avicularia, and with interzooidal avicularia as large as autozooids (i.e., vicarious avicularia).

The genus has previously been reported only from southern India.

Range – Maastrichtian.

*Trichinopolia cassida* sp. nov.

Pl. 123.


Etymology – L., *cassida*, helmet, in reference to the helmet shape of the ovicells, which are so abundant in the holotype as to resemble closely packed files of helmeted warriors.
Description – Colony a multiserial, encrusting, maculate? sheet (Pl. 123, fig. 1a). Several small pore chambers around perimeter of each autozooid. Ancestrula not seen.

Autozooids uniform in size and shape (Pl. 123, fig. 1b), elongate hexagonal, about 1.5 times longer than wide; frontal shield with approximately 20-25 large, circular pores rimmed by thick, conspicuous skeletal ring; orifice oval to D-shaped, commonly slightly elongate transversely, surrounded by a well-defined low peristome, proximal margin of orifice often with two large scallops; non-ovicellate autozooids with five distal oral spines. Ovicell (Pl. 123, fig. 1d) hyperstomial, recumbent, slightly broader than long, non-porous, with low median keel between two relatively flattened or slightly depressed surfaces; present in most autozooids within zone of astogenetic repetition.

Avicularia of two types. Adventitious avicularia (Pl. 123, fig. 1c), up to four per autozooid, two proximolateral to autozooidal orifice and none to two distal of orifice, each with proximally directed spatulate rostra. Vicarious avicularia (Pl. 123, fig. 1e, f) with large opesia occupying half to almost full length, with elongate oval rostrum occupying four-fifths length of opesia and marked proximally by conspicuous short condyles; proximal part of avicularium occupied by frontal shield with rimmed pores similar to those in autozooids.

Measurements – Two paratypes: ZL 364±31, 292-432 (2, 20); ZW 242±24, 191-284 (2, 20); OL 54±9, 40-68 (2, 20); OW 80±14, 60-203 (2, 20); AL 71±9, 55-91 (2, 20); AW 47±7, 33-59 (2, 20); OvL 115±13, 96-138 (2, 20); OvW 130±17, 100-159 (2, 20).


The adventitious avicularia which surround the orifice are commonly subcircular to elliptical in shape and their polarity is difficult to ascertain. Slight constrictions in some of the proximal lateral adventitious avicularia suggest, however, that they are directed distomedially. The vicarious avicularia are moderately regularly spaced at about 3 mm apart in the holotype, possibly interrupting the pattern of water infl ow and serving as centres of maculae in living colonies.

Superfamily Lepralielloidea Vigneaux, 1949
Family Lepraliellidae Vigneaux, 1949
Frurionella Canu & Bassler, 1926

Type species – Frurionella parvipora Canu & Bassler, 1926, Maastrichtian, Tennessee, U.S.A.; by original designation.

Remarks – When establishing Frurionella, Canu & Bassler (1926, p. 35) assigned it to the Anasca, comparing the genus with Foveolaria Busk, but did not attribute it explicitly to a family. Bassler (1953, p. G163) considered Frurionella to belong in the anascan family Calloporidae. However, Shaw (1967) showed the genus to be an ascophoran, placing it in the Porinidae. Gordon (1993) transferred it to the family Lepraliellidae, and later (2002) reassigned to Frurionella several additional Upper Cretaceous and Danian species from Europe that had previously been placed in the genus Pachythecella Bassler, 1934.
Range – Campanian-Danian.

*Frurionella parvipora* Canu & Bassler, 1926
Pl. 124.

1926 *Frurionella parvipora* sp. nov.; Canu & Bassler, 1926, p. 35, pl. 5, figs. 6-18.
1926 *Frurionella grandipora* sp. nov.; Canu & Bassler, 1926, p. 36, pl. 6, figs. 1-3.
1967 *Frurionella parvipora* Canu & Bassler; Shaw, p. 1423, pl. 182, figs. 3, 5.
1988 *Frurionella* sp.; Lauginiger, pl. 1, fig. 6.
1993 *Frurionella parvipora* Canu & Bassler; Gordon, p. 208, figs. 15, 16.
In press *Frurionella parvipora* Canu & Bassler; McKinney & Taylor, fig. 3B.

**Material** – Lectotype (designated here): USNM 69959, specimen figured by Canu & Bassler, 1926, pl. 5, fig. 9, Maastrichtian, Coon Creek Formation, Coon Creek, McNairy County, Tennessee (locality TN1). Paralectotypes (details as for lectotype): USNM 528413, figured by Canu & Bassler, 1926, pl. 5, fig. 11, USNM 528414, figured by Canu & Bassler, 1926, pl. 5, fig. 8, USNM 528415, figured by Canu & Bassler, 1926, pl. 5, fig. 13, USNM 528416, the remaining syntypes. Other material: USNM 69958, holotype of *F. grandipora*, details as above. LSUMG-I 8253, figured by Shaw, 1967, pl. 182, figs 3, 5, Campanian, Saratoga Chalk, Saratoga, Hempstead County, Arkansas (locality AR4). NHM BZ 5218-5222, Maastrichtian, Prairie Bluff Chalk, Emelle, Sumter County, Alabama (locality AL9). RU 5540, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2). NHM D52248 (four fragments), BZ 3117 (five fragments), Maastrichtian, Coon Creek Formation, Coon Creek, McNairy County, Tennessee (locality TN1; collected by E. Voigt). NHM BZ 5070 (two fragments), as above, but W.J. Kennedy Collection. NHM BZ 5071 (sample), Maastrichtian. Coon Creek Formation, shelly lens above Corbula bed, upstream of Coon Creek Field Station, McNairy County, Tennessee (locality TN1; collected by S. Tracey). NHM BZ 5072 (sample), NNM RGM 507 018 (sample), Maastrichtian. Coon Creek Formation, shelly lenticles in upper part - Corbula bed auct., Coon Creek, McNairy County, Tennessee (locality TN1; collected by S. Tracey, August 1999).

**Description** – Colony erect, comprising narrow, bifurcating branches, somewhat flattened (Pl. 124, fig. 1a) and elliptical in cross section, a median budding lamina defining the long axis, about 0.8-1.7 mm wide by 0.9 mm deep. Colony base slightly expanded, comprising apparent kenozooids with small openings. Ancestrula and early astogenetic stages unknown.

Autozooids longitudinally elliptical, indistinctly defined on colony surface, calcification generally continuous across zooidal boundaries (Pl. 124, fig. 1b). Frontal shield umbonuloid, a ring scar visible internally on the underside (Gordon, 1993, fig. 16). Gymnocyst and spines lacking. Cryptocyst extensive, convex, coarsely pustulose, the pustules evenly spaced at edges of zooids, but elongated and aligned to give a concentric fabric around orifice; areolae present in interzooidal furrows, mostly at proximal end of cryptocyst, generally numbering 1-4 per zooid. Secondary orifice large, variable in shape, high-arched to longitudinally elliptical, the proximal edge sometimes almost straight, becoming sunken in older zooids with thickly-calcified frontal shields; orificial rim occasionally developed, narrow. Ovicell (Pl. 124, fig. 2c) immersed, secondary ori-
face of ovicellate zooids elongate pear-shaped, the narrower distal part of opening located over ovicell. Closure plates and intramural buds not observed.

Suboral avicularia (Pl. 124, fig. 2b, d) present beneath secondary orifice of some, but not all, autozooids, variable in size, possibly dimorphic, longitudinally elliptical or egg-shaped, usually directed proximally, but sometimes oriented obliquely or transversely, rostrum more or less parallel sided, well rounded and variably raised distally, pivotal bar complete, ligulate. Interzooidal avicularia (Pl. 124, fig. 3) present along narrow edges of branches, large, hourglass-shaped, directed distally, rostrum spatulate, rounded and slightly raised distally, pivotal bar ligulate, located level with a marked dilation in avicularium width.

Measurements – Syntypes of *Frurionella parvipora*: ZL 510±48, 400-560 (1, 10); ZW 450±24, 420-500 (1, 10); OL (secondary) 167±12, 150-180 (1, 10); OW (secondary) 160±14, 140-180 (1, 10); AL (small suboral) 144±16, 120-160 (3, 10); AW (small suboral) 118±15, 100-140 (3, 10); RL (small suboral) 70±11, 60-80 (3, 10); RW (small suboral) 74±10, 60-80 (3, 10); AL (large suboral) 256±8, 240-260 (6, 10); AW (large suboral) 150±11, 140-160 (6, 10); RL (large suboral) 176±18, 140-200 (6, 10); RW (large suboral) 104±8, 100-120 (6, 10); AL (marginal vicarious) 700±63, 580-780 (3, 10); AW (marginal vicarious) 580±41, 560-640 (1, 5); RL (marginal vicarious) 284±41, 220-340 (3, 10); RW (marginal vicarious) 188±18, 160-200 (1, 5).

Holotype of *Frurionella grandipora*: ZL 520±34, 460-560 (1, 10); ZW 428±29, 380-480 (1, 10); OL (secondary) 188±16, 160-200 (1, 10); OW (secondary) 172±15, 160-200 (1, 10); AL (small suboral) 120 (1, 2); AW (small suboral) 110 (1, 2); RL (small suboral) 70 (1, 2); RW (small suboral) 70 (1, 2); AL (large suboral) 260±27, 240-320 (1, 10); AW (large suboral) 218±15, 200-240 (1, 10); RL (large suboral) 172±14, 160-200 (1, 10); RW (large suboral) 146±19, 120-160 (1, 10); AL (marginal vicarious) 688±64, 580-800 (1, 10); AW (marginal vicarious) 507±35, 480-560 (1, 9); RL (marginal vicarious) 268±43, 200-340 (1, 10); RW (marginal vicarious) 189±20, 160-220 (1, 9).

Remarks – As suggested by Shaw (1967), *Frurionella grandipora* is a junior synonym of *F. parvipora*. Canu & Bassler (1926) distinguished the two species on the basis of slight differences in size, but measurement of the type material of both species shows considerable overlap in ranges. Given the identical type locality, there are no reasonable grounds for maintaining two separate species.

Among Upper Cretaceous bryozoan species from eastern North America, *F. parvipora* is unmistakable. No other species displays such a heavily calcified colony surface, with thick cryptocrystal walls separating the elongate secondary orifices of the autozooids, together with erect colony branches of ovate cross-sectional shape.

**Family Romancheinidae Jullien, 1888**

Remarks – Umbonulomorph ascophorans first became common in the latest Cretaceous. They have been referred in the past to several extant (e.g., *Escharoides*) and extinct (e.g., *Balantiostoma*) genera, and to two families (Romancheinidae and Brydonellidae) in the preliminary listing for the revised bryozoan *Treatise on Invertebrate Paleontology* (D.P. Gordon, unpublished). However, their systematics is problematical. This is
partly because SEM study is mandatory if the morphology of their small zooids is to be adequately elucidated and rather few SEM images of these bryozoans have been published to date. Furthermore, they lack the well-defined primary orifice whose shape is so helpful when identifying lepraliomorph and gymnocystidean ascophorans. Problems are compounded by variability in the development of the avicularia, even within a single colony.

Table 2 summarizes the morphological characters of the principal genera of romancheinids and brydonellids recorded from the Upper Cretaceous as a provisional attempt to clarify generic concepts. Wherever possible, characters are taken from the type species of the genera; note that for Balantiostoma, two other species, B. pusillum von Hagenow, 1851, and B. septentrionalis (Canu & Bassler, 1933), have been used as proxies because the type species is not well-known.

**Balantiostoma Marsson, 1887**

*Type species – Cellepora marsupium* von Hagenow, 1839, Maastrichtian, Rügen, Germany; original designation (monotypy).

*Remarks* – Unfortunately, no modern description exists of the type species of this genus. The genus name is used here, pending taxonomic revision, in a broad sense essentially for romancheinids that cannot be easily accommodated within any of the other Upper Cretaceous genera placed in the family.

In view of the difficulty in recognizing the species of *Balantiostoma* described here, made worse by the small size of the zooids, the following key has been devised as an aid to identification.

1. zooidal boundary walls very prominent; avicularia rare and small ................................................................. *B. erynnos* (Shaw)
   - otherwise .................................................................................................................................................. 2
2. adventitious avicularia borne by a minority of autozooids .............................................................................. 3
   - otherwise .................................................................................................................................................. 4
3. interzooidal avicularia numerous; usually 8 oral spines ...... *B. octospinigera* sp. nov.
   - otherwise .................................................................................................................................................. 5
4. oral spines lacking .......................................................................................................................................... *Balantiostoma* sp.
   - oral spines present .................................................................................................................................. 5
5. usually 6 oral spines ................................................................................................................................. *B. nomas* (Shaw)
   - 2 oral spines; adventitious avicularia constricting secondary orifice ................................................................. *B. powersae* sp. nov.

*Range* - Campanian-Montian. An undescribed *Balantiostoma*-like species occurs in the Pliocene Red Crag of eastern England, but requires further study to establish its true identity.
Balantiostoma danei (Shaw, 1967)  
Pl. 125.

1967    Escharoides? danei sp. nov.; Shaw, p. 1425, pl. 182, fig. 2.

Material – Holotype: LSUMG-I 8246, Campanian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2). Other material: BZ 4439, BZ 5094, Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).

Description – Colony encrusting, multiserial, unilaminar (Pl. 125, fig. 1a). Pore chambers present, including a large distal chamber. Early astogeny unknown.

Autozooids elongate rhomboidal in frontal outline, length averaging about 1.6 times width, boundaries marked by furrows. Frontal shield (Pl. 125, fig. 3a) convex, cryptocrystal, pustulose; areolae present. Primary orifice helmet shaped; oral spine bases either lacking or minute. Secondary orifice semielliptical to pear-shaped, proximal edge straight or slightly convex, thickened and raised to form a distinct rim confluent with the ovicell when present. Ovicell (Pl. 125, figs. 2b, 3b) hyperstomial, non-porous, small, globose, prominent, present in the majority of zooids.

Avicularia of two types. Adventitious avicularia (Pl. 125, fig. 3b) sparsely scattered, located in various sites around periphery of autozooids, small, elliptical. Vicarious avicularia rare, large, opesia elliptical, rostrum rounded, pivotal bar located about one-third way along length.

Measurements – ZL 420±36, 360-480 (1, 10); ZW 260±27, 210-300 (1, 10); OL 104±10, 90-120 (1, 10); OW 110±12, 90-120 (1, 10); OvL 135±15, 120-150 (1, 5); OvW 141±17, 120-165 (1, 5).

Remarks – Shaw (1967) described a mucro and 3-4 oral spines in this species, but these features could not be confirmed during SEM study of the type and other material. Important characters distinguishing B. danei from other species here attributed to Balantiostoma include the sparse, irregularly positioned adventitious avicularia, and the thickened proximal edge and thin lateral walls of the secondary orifice that extend to the ovicell.

Apart from the holotype from the Saratoga Chalk of Arkansas, this species is also recorded from the Prairie Bluff Chalk of Alabama, although it appears to be rarer here than the other species of Balantiostoma.

Balantiostoma erymnos (Shaw, 1967)  
Pl. 126.

1967    Escharoides? erymnos sp. nov.; Shaw, p. 1428, pl. 181, fig. 5.

Material – Holotype: LSUMG-I 8248, Campanian, Ozan Formation, White Cliffs Station, Sevier County, Arkansas (locality AR3). Other material: LSUMG-I 8272, same details, colony encrusting same substrate as the holotype of Stictostega durhami.

Description – Colony encrusting, multiserial, unilaminar (Pl. 126, figs 1a, 2). Pore chambers present distally and distolaterally, elongate. Early astogenetic stages pre-
served in holotype, ancestrula obscured by sediment grains, surrounded by six zooids of varying, but relatively small, size.

Autozooids of moderate size, elongate rhomboidal in frontal outline, length averaging about 1.6 times width; boundary walls prominent, thick and salient (Pl. 126, fig. 1b, c). Frontal shield cryptocrystal, convex, smooth or slightly dimpled (corroded?); areolae impossible to observe in deep, sediment-filled grooves around perimeter. Orifice large, occupying about one third frontal area, variable in shape, often rounded quadrate with an almost straight proximal edge (Pl. 126, fig. 1d), non-mucronate, rim salient; oral spines apparently lacking. Ovicell (Pl. 126, fig. 1e) hyperstomial, seemingly non-porous, small, generally broader than high (cf. Shaw, 1967), slightly overlapping cryptocrystal of distal zooid, details of roof calcification obscure.

Avicularia (Pl. 126, fig. 1c) rare, adventitious, unpaired, located close to and proximolaterally or laterally of autozooidal orifice, elliptical in outline shape, round ended, pivotal bar not observed.

Measurements – (Taken from Shaw, 1967) ZL 450±27, 410-480 (1, 8); ZW 280±22, 260-320 (1, 8); OL 160±12, 150-190 (1, 8); OW 130±9, 120-140 (1, 8); OvL 120±29, 80-130 (1, 3); OvW 150±47, 140-150 (1, 3); AL 110±13, 90-130 (1, 8); AW 80±22, 70-130.

Remarks – Adherent sediment grains obscure some of the details in the only two examples known of this species. For example, it is uncertain whether areolae are present or absent, the orientation of the rare avicularia cannot be ascertained because it is not possible to discern a pivotal bar or condyles, and the surface fabric of the ovicells is not apparent. Shaw (1967) reported a poorly developed mucro, but this is not evident in our scanning electron micrographs.

None of the other species of Balantiostoma described here from the eastern US Late Cretaceous has such pronounced boundary walls or so few avicularia.

Balantiostoma nomas (Shaw, 1967)
Pls. 127-129.

1967 Escharoides? nomas sp. nov.; Shaw, p. 1426, pl. 182, fig. 1.

Material – Holotype: LSUMG-I 8247, Campanian Ozan Formation, McCurtain County, Oklahoma (locality OK1). Other material: NHM BZ 5095A-C, Campanian, Demopolis Chalk, Macon, Noxubee County, Mississippi (locality MS1). VCSM 13961a, b, Campanian, Demopolis Chalk, Macon, Noxubee County, Mississippi (locality MS2). NHM BZ 4437(2), BZ 4438, BZ 4810(4), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). ANSM 80359, 80363, Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1).

Description – Colony encrusting, multiserial, unilaminar, sometimes elliptical in outline when small (Pl. 127, fig. 2a). Pore chambers present, distal chamber large, subtriangular (Pl. 128, fig. 2) with a frontally opening window, distolateral chambers occupying most of wall length, narrow, lens-shaped. Ancestrula seemingly ascophoran, budding distal and two distolateral periancestular zooids. Zooids from zone of primary astogenetic change relatively small, bearing adventitious avicularia.
Autozooids small, elongate rhomboidal in frontal outline, on average about 1.5 times longer than wide, boundary wall variably developed. Frontal shield cryptocystal, smooth in young zooids, ornamented with nodes in older zooids, in weathered zooids showing a pattern of gently curved fissures converging towards middle of proximal edge of orifice (Pl. 128, fig. 1); areolae most apparent in young zooids, usually numbering six, visible near proximal ends of some older zooids. Primary orifice (Pl. 128, fig. 1; Pl. 129, fig. 1c) helmet shaped, a slight constriction separating broad, shallow proximal part of orifice from the main distal part; proximal edge gently curved, distal edge well defined, arch-shaped; oral spine bases (Pl. 128, fig. 1) numbering 4-6, usually six, with a slightly greater median gap than that between other spines bases, the outer (proximal) bases tending to be the largest. Secondary orifice variable in shape, semieliptical to subcircular, proximal edge straight or convex, thickened and raised, usually non-mucronate, very occasionally with a mucro (Pl. 129, fig. 2b). Ovicells (Pl. 127, figs. 1b, 3a, b; Pl. 128, fig. 4a; Pl. 129, figs. 1b, 2a) abundant, hyperstomial, globose, ectooecium apparently uncalcified except for a narrow peripheral rim, entooecium forming mineralized roof; usually only outermost pair of spine bases visible in ovicellate zooids. Intramurally budded avicularia observed within autozooids.

Avicularia of three types. Adventitious avicularia abundant, a pair typically located laterally or proximolaterally of the orifice (Pl. 127, figs. 1b, 3b), directed outwardly, sometimes one positioned slightly more distally than the other, additional more proximal avicularia developed especially in older zooids (Pl. 128, fig. 4b); small, elliptical, rostrum rounded, pivotal bar calcified. Interzooidal avicularia rare (present only in NHM BZ5095; Pl. 127, fig. 3a), quite small, about half autozooid width, rostrum parallel sided, distally rounded, pivotal bar calcified. Vicarious avicularia (Pl. 128, fig. 4b, c; Pl. 129, fig. 2c) sometimes present, solitary or clustered, large, approximately the same size as the autozooids, proximal cryptocyst with areolae, aperture longitudinally elliptical, hinge bar calcified located about one quarter distance along aperture, rostrum parallel sided or slightly spatulate, rounded distally, palate narrow, double mural rim in some examples suggesting origin as intramural buds.

**Measurements** – ZL 417±53, 330-495 (1, 10); ZW 276±13, 255-300 (1, 10); OL 101±14, 90-120 (1, 10); OW 104±10, 90-120 (1, 10); OvL 135±11, 120-150 (1, 5); OvW 168±13, 150-180 (1, 5).

**Remarks** – Shaw’s species from the Campanian Ozan Formation of Oklahoma is also recorded here from the Campanian Demopolis Chalk of Mississippi, the Maastrichtian Prairie Bluff Chalk of Alabama and the Campanian Mount Laurel Formation of Delaware. Specimens from these regions do exhibit some differences, namely the more proximal placement of the paired adventitious avicularia in the holotype from the Ozan Formation, the occurrence of interzooidal and vicarious avicularia in colonies from the Demopolis Chalk, vicarious avicularia in those from the Mount Laurel Formation, which also sometimes have mucronate autozooids, and the tendency for the secondary orifice to have a more convex proximal edge in material from the Prairie Bluff Chalk. These differences are sufficiently minor compared to the overall similarities that we provisionally regard the material from the three regions as conspecific pending a more detailed study. Plates 127-129 serve to illustrate some of the variabil-
ity encompassed within the definition of the species as here employed.

Contrary to the original description, avicularia in the holotype are rounded and not pointed. *Balantiostoma nomas* (Shaw, 1967) can be distinguished from other species of the genus described here by having abundant, well-rounded adventitious avicularia, none of which constrict the autozooidal orifice, and generally six oral spine bases.

*Balantiostoma octospinigera* sp. nov.

Pls. 130, 131.


**Etymology** – Referring to the presence of eight oral spines.

**Description** – Colony encrusting, multiserial, unilaminar, growing edge stepped (Pl. 130, fig. 3; Pl. 131, fig. 1a). Pore chambers elliptical, distal chamber deeper than paired distolateral chambers, its window facing distofrontally. Ancestrula (Pl. 130, fig. 1b; Pl. 131, fig. 3) tatifom, oval, approximately 200 μm long by 160-190 μm wide, spines encircling opesia, about ten in number; gymnocyst well developed proximally, tapering distally; cryptocyst wanting; mural rim salient; opesia oval or longitudinally elliptical, about 100-120 μm long by 90-100 μm wide; containing an ascophoran-grade intramural bud in one example. Periancestrular zooids numbering up to five, including a distal and/or two distolateral zooids budded from ancestrula.

Autozooids very small, slightly elongate rhomboidal in frontal outline, on average 1.55 times longer than wide, boundary wall variably developed, sometimes a narrow gymnocyst developed around perimeter of zooid. Cryptocyst convex, smooth or with low nodes; areolae present, sometimes apparently built upwards into a raised subcircular pore. Primary orifice (Pl. 131, fig. 1b) helmet shaped, a slight constriction separating broad, shallow proximal part from larger distal part; proximal edge gently bowed, distal edge a well defined arch; oral spine bases usually numbering eight (Pl. 131, fig. 1b), less commonly seven (Pl. 130, fig. 4a). Secondary orifice semielliptical to subcircular, proximal edge slightly bowed, sometimes with a subdued, but distinct, mucro (Pl. 130, fig. 2). Ovicell (Pl. 130, fig. 4b; Pl. 131, fig. 2c) hyperstomial, small, globose, non-porous, surface features insufficiently well preserved to identify ectooecial and entooecial calcification; 4-6 oral spines visible in ovicellate zooids.

Avicularia interzooidal and adventitious, abundant (Pl. 131, fig. 2a), increasing in numbers in older parts of colonies, longitudinally ovoidal in shape, usually directed distally, occasionally laterally or proximally, some with a short proximal gymnocyst; rostrum variable in shape, from distally tapering to parallel sided to mildly spatulate, sometimes slightly curved (Pl. 131, fig. 2b), distal end rounded; palate moderately to well developed, in a few avicularia more than half total rostrum length; pivotal bar calcified, located close to proximal end of opesia, often not preserved.
Measurements – ZL 366±28, 330-405 (1, 8); ZW 236±22, 210-270 (1, 8); OL 86±7, 75-90 (1, 8); OW 81±8, 75-90 (1, 8); OvL 110±12, 90-120 (1, 6); OvW 145±20, 120-165 (1, 6).

Remarks – This new species is distinguished by having extremely small zooids, and elongated ovoidal avicularia, usually with a significant palate. Compared with *Balantiostoma nomas* (Shaw, 1967), the autozooids are smaller and oral spines typically number eight rather than six.

*Balantiostoma powersae* sp. nov.

Pl. 132.

Material - Holotype: NHM BZ 5099(1a), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). Paratypes: NHM BZ 5099(1b), BZ 5099(1c), encrusting same bivalve shell as holotype. NHM BZ 5095(2), same details as holotype. NHM BZ 5100, NNM RGM 507 022, Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5).

Etymology – Named for Susan Powers in gratitude for her help during fieldwork in Alabama.

Description – Colony encrusting, multiserial, unilaminar, occasionally multilaminar through spiral overgrowth. Pore chambers present, the distal chamber subtriangular. Ancestrula and early astogeny unknown (abraded or overgrown). Autozooids of moderate size, slightly elongate rhomboidal in frontal outline, on average about 1.3 times longer than wide, boundary wall usually well developed, salient (Pl. 132, fig. 2a). Cryptocyst convex, sloping upwards towards orifice, pustulose; areolae large, numerous, as many as ten per zooid. Primary orifice semielliptical to rounded quadrato (Pl. 132, fig. 1c), facing distofrontally; oral spine bases numbering two, located at the two distolateral corners, becoming obscured in later ontogeny. Secondary orifice semielliptical, the sides often indented by lateral avicularia; mucro usually present, when well preserved anvil-shaped and as high as wide or, alternatively, pointed. Ovicell small, hyperstomial, globose, ectooecium with a small median pore (Pl. 132, fig. 1b).

Avicularia dimorphic. Adventitious avicularia (Pl. 132, fig. 2b) usually paired on each side of orifice, sometimes single or lacking, directed distolaterally and outwards, inclined somewhat distally, elongate elliptical in outline shape, sometimes enclosed by thick rim of calcification (possibly due to intramural budding); rostrum distally tapering, round ended; pivotal bar calcified, positioned about a quarter to a third of the distance along the opening. Vicarious avicularia (Pl. 132, fig. 1d) abundant, about as long as an autozooid, but a little narrower; cryptocystal frontal shield developed proximally, tapering distally; aperture widest proximally, parallel-sided or tapering steadily towards rounded end of rostrum; palate deep, up to half aperture length; mural rim sometimes double (possibly due to intramural budding); pivotal bar located close to proximal end of aperture, thin, somewhat proximally convex.

Measurements – ZL 443±39, 390-510 (1, 10); ZW 332±13, 315-345 (1, 10); OL 108±9, 90-120 (1, 10); OW 107±11, 90-120 (1, 10); OvL 150-165 (1, 3); OvW 165-180 (1, 3).
Remarks – The paired adventitious avicularia that flank and constrict the orifice in the majority of the autozooids are the main feature distinguishing this species of Balantiostoma from the others described herein. The large number of areolae per zooid is also noteworthy. There are only two oral spine bases and these are visible only at the growing edge, in contrast to B. nomas and B. octospinigera which typically have six and eight oral spines, respectively. The mucro of well-preserved zooids is distinctly anvil-shaped, unlike that of other species of Balantiostoma described here.

**Balantiostoma sp.**
Pl. 133.

Material – RU5545, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

Description – Colony encrusting, unilaminar. Early astogeny unknown. Autozooids moderately large, elongate rhomboidal, about 600 μm long by 350 μm wide, boundary walls usually lacking, Cryptocyst convex, pustulose; areolae very large and conspicuous, subcircular (Pl. 133, fig. 1b). Oral spines absent. Secondary orifice semielliptical, a pointed mucro often present on the proximal edge. Ovicell hyperstomial, globular, ectooecium possibly incompletely calcified.

Avicularia of two types. Adventitious avicularia located laterally or proximolaterally of orifice, incompletely formed and without hinge bars in all examples seen. Vicarious avicularia common (Pl. 133, fig. 1a), directed distally, elongate, broadest proximally, pinched in a little at presumed level of hinge, about 500 μm long by 215 μm wide; rostrum slightly spatulate, well rounded; palate deep, about half length of aperture; pivotal bar not seen (uncalcified or broken).

Remarks – Only one fragmentary colony of this species is known. It is mounted on a stub and gold-coated, and, although clearly different from the other species of Balantiostoma described here, the single specimen is deemed insufficient to justify erection of a new species.

**Hoplocheilina Canu, 1911**

Type species – *Eschara osculifera* Reuss, 1872, Paleocene, Vincentown Limesand, New Jersey; by original designation.

Remarks – Voigt (1982) showed that *Hoplocheilina* Canu, 1911, is an objective senior synonym of the more widely-used *Acanthionella* Canu & Bassler, 1917. *Hoplocheilina* was introduced by Canu (1911) with *Eschara osculifera* Reuss, 1872, as the type species, a bryozoan that Reuss mistakenly believed came from the Cenomanian of Germany. In fact, Reuss’s material of *E. osculifera* was from the Paleocene Vincentown Limesand of New Jersey.

Range – Maastrichtian-Priabonian.
Hoplocheilina hagemani sp. nov.
Pl. 134.

**Material** – Holotype: USNM 526195, Maastrichtian, Peedee Formation, Neuse River, Lenoir County, North Carolina (locality NC4). Paratypes: USNM 526196, 526197, same details as holotype.

**Etymology** – Named for Dr S. Hageman (Appalachian State University) in recognition his bryozoan research and his support during our fieldwork in North Carolina.

**Description** – Colony multiserial, bifoliate erect (Pl. 134, fig. 1a), sometimes encrusting unilaminar. Pore chambers not observed. Early astogeny unknown.

Autozooids small, rhomboidal in frontal outline, about 1.2 times longer than wide, boundaries usually indistinct except for patches with salient boundary walls. Frontal shield (Pl. 134, fig. 1c, e) cryptocystal, rugose, bearing nodules and /or pustules; areolae large, varying in number from 2-6 per zooid. Primary orifice semieliptical, deeply immersed in all but the youngest zooids, distal rim with a narrow shelf; oral spine bases numbering four (Pl. 134, fig. 1d), outer pair somewhat larger, distance between inner spine bases slightly greater than between them and outer spines. Secondary orifice with an anvil-shaped mucro (Pl. 134, fig. 1e), sometimes broken-off. Ovicell (Pl. 134, fig. 1f) hyperstomial, seemingly non-porous, becoming enveloped by cryptocyst of neighbouring zooids, only the outer pair of oral spines exposed.

Avicularia of two types. Adventitious avicularia (Pl. 134, fig. 1c) small, oval in shape, suboral, located near proximalateral corners of orifice, unpaired, often wanting, oriented obliquely laterally; rostrum almost two times longer than opesia, well rounded distally, occasionally raised; hinge bar calcified. Interzooidal avicularia sporadic, about half the frontal area of an autozooid, longitudinally elliptical, usually oriented distally; rostrum considerably longer than opesia, parallel-sided, rounded distally, palate well developed, hinge bar calcified.

**Measurements** – ZL 351±29, 300-390 (1, 10); ZW 290±33, 255-345 (1, 10); OL 77±9, 60-90 (1, 10); OW 135±10, 120-150 (1, 10); OvL 129±17, 105-150 (1, 5); OvW 168±13, 150-180 (1, 5).

**Remarks** – This is the oldest known species of Hoplocheilina and the first from the Cretaceous. It resembles the type species of the genus (see Voigt, 1982) from the Paleocene Vincentown Limesand of New Jersey in both the bifoliate colony-form and in zooidal morphology, but the suboral avicularia are single, not paired.

**Family Peedeesellidae fam. nov.**

**Type genus** – Peedeesella gen nov.

**Diagnosis** – As for Peedeesella.

**Remarks** – This family, defined by the characters of the type and only known genus, is erected because of the seemingly unique and very peculiar mode of formation of the
autozooidal frontal shields from adventitious avicularia. This has no close parallel among existing bryozoan families. While of ascophoran grade, it is unclear how the family is related to other ascophoran families. Gordon (2000) discussed various models for the evolution of frontal shields in ascophorans. Most involved an origin from either kenozooids or costae, contrasting with the frontal shields of the Peedeesellidae which are formed by avicularia. An analogy can be made, however, with two chaperiid anascan genera, Scutochaperia Uttley & Bullivant, 1972, and Parmachaperia Uttley & Bullivant, 1972, in which a frontal shield-like structure is formed by one or two avicularia overgrowing the frontal membrane (see Gordon, 1982).

**Peedeesella gen nov.**

*Type species – Peedeesella guhai sp. nov., Maastrichtian, eastern U.S.A.*

*Other species – Bathosella bisinuosa Guha & Nathan, 1996, Maastrichtian, Ariyalur Group, Tamil Nadu, India.*

*Etymology – After the Peedee Formation, which yields common and well preserved examples of the type species of this genus.*

*Diagnosis – Colony encrusting, unilaminar, pore chambers present; autozooid frontal shield formed by one or two adventitious avicularia; primary orifice semieliptical; oral spines present; secondary orifice with proximal edge indented by median lyrula-like tooth when one avicularium is present, otherwise straight and defined by the distal edge of an arch constructed from a pair of inward-facing avicularia joined at their tips, an elongate opening remaining proximally of the arch; ovicell hyperstomial.*

*Remarks – This genus is introduced for a new North American species, *P. guhai*, together with an Indian Maastrichtian species described Guha & Nathan (1996) as Bathosella bisinuosa. The genus Bathosella was founded by Canu & Bassler (1917), with Mucronella aspera Ulrich, 1901, from the Aquia Formation (Paleocene) of Maryland as the type species. Canu & Bassler (1920) redescribed and restudied Bathosella aspera based on type and additional material, quoting verbatim the original description of Ulrich. The proximal edge of the orifice is swollen and avicularia occur scattered in various positions between the autozooids (see also Voigt, 1982). Both species of Peedeesella lack these features and, while SEM study of *B. aspera* will be necessary before it can be fully characterized, there is no indication that it possesses the avicularian characters diagnostic of Peedeesella, particularly the pair of avicularia joining in an arch to form the proximal edge of the secondary orifice, leaving an elongate, spiramen-like opening on its proximal side. Another ascophoran, Bubnolella Voigt, 1959, type species Homalostega suffulta Marsson, 1887, from the Maastrichtian of Rügen, Germany, has a large-chambered, median suboral avicularium resembling that seen in autozooids of Peedeesella with a single avicularium. However, Bubnolella has no oral spines, zooids with paired avicularia are lacking and the presence of spatulate interzooidal avicularia provides an additional distinction from Peedeesella. The contrasting appearance of autozooids bearing one or two avicularia is note-
worthy. While species of several cheilostome genera (e.g., *Microporella*) may have colonies containing both ‘monoaviculariate’ and ‘biaviculariate’ autozooids, differences between the autozooids showing each condition are minor. In *Peedeesella*, however, isolated autozooids of the two sorts could easily be taken as belonging to different families of cheilostomes. Monoaviculariate autozooids (Pl. 136, fig. 3b) have the avicularium opening into the secondary orifice on a lyrula-like median tooth that recalls the organization found in smittinid lepraliomorphs. This is very different from the morphology of biaviculariate autozooids (Pl. 136, fig. 3a) where the two inwardly oriented avicularia are joined at their distal tips to form an arch defining the straight proximal edge of the secondary orifice, with a pore proximal of the arch that presumably opened into the compensation space between the frontal membrane and the underside of the frontal shield. The bridge structure formed by paired avicularia plus the spiramen-like pore recall another lepraliomorph family, the Gigantoporidae. These comparisons with established lepraliomorph families do not necessarily signify phylogenetic relationships, however.

**Range** – Maastrichtian.

*Peedeesella guhai* sp. nov.

Pls. 135, 136.

**Material** – Holotype: NHM BZ 5104(1), Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2). Paratypes: NHM BZ 4183(2), same details as holotype. NHM BZ 4435(a, b), BZ 5102(1), BZ 5103, Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5). NHM BZ 4824, Maastrichtian, Ripley Formation, Florence, Quitman County, Georgia (locality GA1). NHM BZ 5101, Maastrichtian, Coon Creek Formation, Coon Creek, McNairy County, Tennessee (locality TN1; S. Tracey Collection).

**Etymology** – In recognition of the contributions to bryozoology of Indian palaeontologist Dr A.K. Guha (Indian Institute of Technology, Kharagpur).

**Description** – Colony encrusting, multiserial, unilaminar, growing edge irregular (Pl. 135, fig. 1c). Pore chambers present, distal pore chamber large, with transversely elliptical, frontally orientated pore window, distolateral pore windows located near proximal end of distolateral vertical walls, strongly elongated. Ancestrula (Pl. 135, fig. 1f) tataiform, budding three periancestrular zooids in distal, left and right distolateral positions; about 135 μm long and wide; spines numbering at least seven, probably eight, opesia semielliptical, the proximal edge almost straight, about 85 μm long by 90 μm wide. Zooids in primary zone of astogenetic change (Pl. 135, fig. 1e) small, bearing a single suboral avicularium, usually non-ovicellate although ovicells may occur as early as second budded generation of autozooids.

Autozooids small, elongate rhomboidal, length about 1.5 times width, frontal surface convex, zooidal boundaries marked by grooves, occasionally with a narrow, salient boundary wall. Frontal shield non-pustulose, appearing cryptocystal, formed entirely by the adventitious avicularia. Primary orifice (Pl. 135, fig. 1d) semielliptical, facing
frontodistally, sunken; oral spine bases stout, generally four in number. Autozooids of two types according to whether they support one or two suboral adventitious avicularia. Monoaviculariate autozooidal frontal surfaces covered by large, bulbous chamber of single avicularium indenting proximal edge of secondary orifice as a lyrula-like, median, flat-topped tooth (Pl. 136, fig. 3b). Biaviculariate autozooidal frontal surfaces covered by left and right avicularia, chamber bases separated on either side of a slit, rostra joined distally to form an arc with the distal side defining straight proximal edge of secondary orifice, a longitudinally elliptical spiramen-like structure remaining proximal of orifice (Pl. 136, fig. 1a). Early astogenetic stages with monoaviculariate autozooids only (Pl. 135, fig. 1e), later astogenetic stages dominated by biaviculariate autozooids with occasional monoaviculariate autozooids interspersed. Ovicells (Pl. 135, fig. 1b; Pl. 136, figs. 1-3) numerous, found in most mature autozooids within zone of astogenetic repetition, developed in both mono- and biaviculariate autozooids; hyperstomial, globose, positioned well distally of orifice of maternal zooid, ectoecium sometimes apparently with an irregular, uncalcified window near middle of proximal edge; oral spines entirely covered or only outermost pair visible; ridge-like lateral wall of secondary orifice sometimes joining side of ovicell. Viewed from within (Pl. 135, fig. 4), ovicell-bearing biaviculariate autozooids have underside of ovicell of previous zooid occupying most proximal quarter, followed by a transverse arch-shaped band of calcification with a pore at either end, bipartite, a large area of sutured unumbonuloid frontal shield containing a medial elongate opening and the semieliptical primary orifice in the distalmost quarter. Basal walls fully calcified.

Avicularia adventitious (Pl. 136, fig. 3), suboral, single or paired, chambers large, hinge bar calcified, rostrum tapering, subrounded, a small pore opening at proximal end of the frontal wall. Single avicularia pointing proximally, plane of avicularium steeply inclined and facing distally towards orifice of autozooid, proximal edge often a squared-off flange. Paired avicularia directed obliquely laterally towards one another and midline of supporting autozooid, plane of avicularia tilted to face somewhat distally, joined at their distal tips to form an arch.

**Measurements** – ZL 366±26, 330-405 (1, 10); ZW 237±28, 195-285 (1, 10); OL 76±11, 60-90 (1, 10); OW 119±9, 105-135 (1, 10); OvL 114±13, 105-135 (1, 5); OvW 150±11, 135-165 (1, 5).

**Remarks** – This unusual ascophoran can be recognized by the bulbous suboral adventitious avicularia that form the frontal ‘shields’ of the autozooids. When only one avicularium is present this produces a median, lyrula-like indentation along the proximal edge of the secondary orifice. In autozooids with two avicularia the rostral tips are joined to form an arch that defines the straight proximal edge of the secondary orifice and beneath which is situated an elongate opening. The prominent avicularia, along with numerous globose ovicells, contribute to the highly rugose topography of the colony.

**Peedeesella bisinuosa** (Guha & Nathan, 1996) from the Ariyalur Group of Tamil Nadu closely resembles the new North American species. However, ovicells in the Indian species are less prominent and the avicularia are described as having small pores near their proximolateral margins. Although not mentioned in the original description, four oral spines were observed in a scanned specimen of *P. bisinuosa* in the NHM collections, a
character state which is therefore shared with *P. guhai*. Autozooidal dimensions are also smaller in *P. guhai*: in *P. bisinuosa*, ZL = 420-480 μm, ZW = 340-410 μm, OL = 110-130 μm; OW = 150-180 μm.

Zooidal ontogeny can be inferred by comparing zooids at colony growing edges in different stages of development (Pl. 135, fig. 1c, d). The youngest autozooids show calcification of the basal and vertical walls only (Pl. 135, fig. 1c). At a slightly later stage oral spines developed and a narrow mural rim formed around the extensive oval opesia. Proximally of the oral spines the mural rim is a double structure with an inner and an outer rim. Opening between these two rims in the proximal part of the zooid are either one or two small pores which are the loci from which, respectively, one or two adventitious avicularia are subsequently budded (Pl. 135, fig. 1d). The basal walls of these avicularia grew distally over the oval opesia, presumably forming a roof over the frontal membrane of the autozooid. In instances where two avicularia are present, growth occurred from either side of the autozooid obliquely distally towards the mid line, initially leaving a U-shaped embayment in the proximal edge of the developing, semieliptical primary orifice. Closure of this embayment completed the proximal edge of the orifice, leaving a large elliptical opening along the median axis of the zooid. The wall surrounding this opening is turned upwards and outwards. Formation of the uppermost (frontal) wall of the avicularia occurred by centrifugal growth from the upturned wall around the opening, concurrently with centripetal growth from the outer of the two mural rims around the perimeter of the zooid. The two edges of calcification eventually met to complete the upper wall of the avicularium and, hence, the ‘frontal shield’ of the underlying autozooid. In cases where only one avicularium is present, its basal and frontal walls grew sequentially in a distal direction from the small pore located between the mural rims at the proximal end of the autozooid. Because growth proceeded from a single locus, there is no median opening and the proximal edge of the orifice, instead of being an arch formed by avicularia growing from either side of the zooid, is formed by the single avicularium that projects distally as a median denticle.

It remains to be established whether the frontal shield was gymnocystal (i.e., originally covered by cuticle on the upper surface) or umbonuloid with a hypostegal coelom over a cryptocystal upper surface. A small countersunk pore is present at the proximal end of each avicularium constructing the frontal shield. This resembles pores in cryptocystal walls that communicate with the hypostegal coelom. On the other hand, the frontal shield lacks the pustulose surface normally (although not invariably) associated with cryptocystal calcification. A cryptocystal nature is more probable on the balance of this evidence.

**Infraorder Hippothoomorpha Gordon, 1989a**  
**Superfamily Hippothooidea Fischer, 1866**  
**Family Hippothoidae Fischer, 1866**

**Remarks** – Cretaceous taxa belonging to the Hippothoidae were revised by Voigt & Hillmer (1983). They are characterised by having a gymnocystal frontal shield and an orifice with a sinus. Three hippothoids have been found in the Maastrichtian of the Atlantic Coastal Plain: *Boreasina novaehanoverensis* sp. nov., *Boreasina* sp. and *Kronothoa quitmanensis* sp. nov.
Boreasina Voigt & Hillmer, 1983

Type species – Boreasina morrisae Voigt & Hillmer, 1983, Maastrichtian, The Netherlands; by original designation.

Remarks – This genus was introduced by Voigt & Hillmer (1983) for multiserial hippothoids with porous gymnocysts and small avicularia. All known species come from the Upper Cretaceous.

Range – Campanian-Maastrichtian.

Boreasina novaehanoverensis sp. nov.

Material – Holotype: NHM BZ 5016(3), Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2).

Etymology – After the type occurrence in New Hanover County, North Carolina.

Description – Colony encrusting, multiserial, unilaminar (Pl. 137, fig. 1a). Ancestrula and early growth stages unknown.

Autozooids small, elongate, length about 1.9 times longer than width, arranged quite irregularly, boundaries well defined, marked by furrows. Frontal shield gymnocystal, convex, evenly porous, occasional larger pore windows near perimeter, no umbo. Orifice small, slightly longer than wide, sinus U-shaped, about same width as length, anter arch shaped, slight condyles visible in some zooids; oral spines lacking. Ovicell (Pl. 137, fig. 1d) hyperstomial, globose, helmet-shaped, the ectooecium porous.

Avicularia (Pl. 137, fig. 1b, c, e, f) numerous, most arranged in longitudinal lines between autozooids, overlapping autozooidal frontal shields to varying degrees, at least some interzooidal, others possibly adventitious, directed distally, small. Frontal shield gymnocystal, porous with occasional larger pore windows near perimeter, surface area of gymnocyst highly variable between avicularia, small, always less than an autozooid. Orifice with poster broad and shallow, the proximal edge convex, anter narrower and longer, rostrum well rounded.

Polymorphic zooids (Pl. 137, fig. 1c) resembling autozooids sporadically present; orifice large, oval, the more pointed end proximal.

Measurements – ZL 324±32, 285-375 (1, 10); ZW 171±18, 150-210 (1, 10); OL 63±12, 45-75 (1, 10); OW 56±7, 38-60 (1, 10); OvL 78±7, 75-90 (1, 5); OvW 141±13, 120-150 (1, 5).

Remarks – This new species differs significantly from the two European Cretaceous species of Boreasina as described by Voigt & Hillmer (1983). Both B. morrisae Voigt & Hillmer, 1983, and B. carinata (Hennig, 1892) have pointed avicularia that contrast with the rounded avicularia of B. novaehanoverensis. Furthermore, oral spines are lacking in B. novaehanoverensis, but present in B. carinata, while B. morrisae has better developed condyles than the new North American species.
Neither of the European species possess the occasional polymorphs with large orifices found in *B. novaehanoverensis*. The nature of these polymorphs is unknown. Given the enlarged orifice it seems unlikely that they represent androzooids as these male polymorphs have small orifices in the extant hippothoids that do possess them.

**Boreasina sp.**

*Pl. 138, fig. 1.*

*Material* – USNM 526198, Maastrichtian, Peedee Formation, Neuse River, Lenoir County, North Carolina (locality NC4).

*Description* – Colony encrusting, multiserial, unilaminar.

- Autozooids small, about 375 μm long by 235 μm wide. Frontal shield gymnocystal, porous, a prominent umbo developed beneath the orifice. Orifice small, about 65 μm long by 60 μm wide, anter subcircular, sinus wider than deep, rounded, small condyles present. Ovicell (*Pl. 138, fig. 1b*) hyperstomial, large relative to orifice size, about 150 μm long by 175 μm wide, porous, the pores denser around edge.

- Heterozooids (avicularia?, androzooids?) smaller than autozooids, with tiny (<15 μm), narrower orifices (*Pl. 138, fig. 1c*).

*Remarks* – The only specimen known to us of this species is mounted on a stub and gold coated. It is insufficient to warrant the naming of a new species. However, the specimen does appear to differ from *B. novaehanoverensis*, most notably in the larger, more elongate ovicells and the smaller size of the orifice relative to the autozooid as a whole.

**Kronothoa Morris, 1980**

*Type species* – *Hippothoa dissoluta* Voigt, 1930, Upper Campanian, Scania, Sweden; by original designation.

*Remarks* – This uniserial hippothoid, previously represented only from the type species, has avicularia and a porous gymnocyst, permitting it to be distinguished from *Hippothoa*, which lacks both of these characters, and from *Tecatia*, which is also without avicularia. Some of Voigt & Hillmer’s (1983) figures of the Swedish Campanian type species depict irregular colonies with crowding of the uniserial zooids, very like that seen in the new species, *K. quitmanensis*, from the Maastrichtian of Georgia. The short (for a uniserial bryozoan) proportions of the zooids, along with the budding of avicularia between them, accentuate this feature.

*Range* – Campanian-Maastrichtian.

**Kronothoa quitmanensis sp. nov.**

*Pl. 138, fig. 2.*

*Material* – Holotype: NHM BZ 5105, Maastrichtian, Ripley Formation, Florence, Quitman County, Georgia (locality GA1). Paratype: NHM BZ 5106, details as for holotype.
**Etymology** – After the type occurrence in Quitman County, Georgia.

**Description** – Colony encrusting, uniserial, crowded, unilaminar (Pl. 138, fig. 2a). Ancestrula and early growth stages unknown.

Autozooids tiny, about 250 μm long by 120 μm wide, arranged in irregular uniserial series, non-caudate. Frontal shield gymnocystal, convex, evenly porous, the pores having raised, bevelled edges, about 10 μm in diameter and 20-30 μm apart (centre-to-centre spacing); no mucro. Orifice small, longer than wide, about 70 μm long by 55 μm wide, keyhole-shaped (Pl. 138, fig. 2c), sinus broad, wider than long, anter arch shaped; oral spines lacking; closure plates present in some zooids. Ovicell (Pl. 138, fig. 2c) hyperstomial, globose, helmet-shaped, about 80 μm long by 140 μm wide, sparsely porous, the pores less conspicuous than those on frontal shields; opening not closed by operculum.

Avicularia (Pl. 138, fig. 2b) numerous, interzooidal, arranged irregularly often in groups, usually (always?) directed distally. Frontal shield gymnocystal, porous, surface area variable, but always less than that of an autozooid. Orifice considerably smaller than autozooidal orifice; poster shallow, well rounded; anter about three times longer than poster, forming a spatulate rostrum.

**Remarks** – This new species is distinguished from *K. dissoluta* (Voigt, 1930) by having a sinus that is wider than deep, whereas that of *K. dissoluta*, especially as drawn by Morris (1980, text-fig. 7), is substantially deeper than wide. It also lacks any trace of the raised mucro on the proximal edge of the orifice that is developed in *K. dissoluta*.

**Family Dysnoetoporidae Voigt, 1971**

*Dysnoetopora Canu & Bassler, 1926*

**Type species** – *Dysnoetopora celleporoides* Canu & Bassler, 1926, Maastrichtian, Tennessee, U.S.A.; by original designation.

**Remarks** – This genus was originally considered by Canu & Bassler (1926) to be a cyclostome on account of the lack of ovicells, the hollow or vesicular walls visible in cross sections, long, tabulated tubes in the centres of the branches and overall appearance in thin section. Nevertheless, Canu & Bassler did recognise the schizoporellidan, *Cellepora*-like morphology of some of the apertures and the similarity of the heterozooids to cheilostome avicularia. It was left to Voigt (1971) to firmly establish the cheilostome identity of *Dysnoetopora* and to create for the genus a new family, Dysnoetoporidae (note that the family name is given in error as Dysnoetocellidae in the abstract of Voigt’s paper).

Although *Dysnoetopora* superficially resembles dendroid species of some ‘celleporid’ genera such as *Turbicellepora*, *Omalosecosa* and *Celleporaria*, the gymnocystal frontal shields of the zooids suggest strongly that no close phylogenetic relationship exists. Basal encrusting zooids of *D. celleporoides* described below have long, gymnocystal frontal shields containing an ascopore and occasional marginal pores. These zooids are reminiscent of the extant genera *Haplopoma* and *Celleporella*, differing from the former in the absence of evenly distributed frontal pores and from the latter in having an asco-
pore rather than an orificial sinus. Phylogenetic links with the cribromorphs are suggested by the fact that the apertural bar between the ascopore and the orifice comprises two hollow outgrowths fused in the middle. These appear to be costae.

The large avicularia of Dysnoetopora are unusual in having an ascopore-like opening in the gymnocyst (Pl. 140, fig. 2a). This suggests an ascophoran-type soft part organization with a functional ascus and perhaps even a protrusible polypide. In contrast, avicularia in ascophorans usually have an anascan-type organization with a small exposed area of frontal membrane covering the opesia.

Ovicells have yet to be found in this genus. While they may be present, but too delicate for routine preservation, an alternative possibility is that Dysnoetopora brooded its larvae in a different way. Internal brooding has been shown to occur in a wide range of cheilostomes lacking ovicells (see Ström, 1977), while external brooding of embryos was recorded in the genus Aetea by Cook (1977). Thin sections of Dysnoetopora reveal the existence of lacunae frontally of the orifice and gymnocyst in exozonal autozooids (Pl. 141, fig. 1b), These spaces are present because older autozooids are not immediately overgrown by frontal buds which instead appear to grow up around them for a distance, contrary to the usual pattern in multilaminar bryozoans. While the lacunae may be present simply because autozooids continued feeding while new buds were building up around them, they are approximately equivalent in size to ovicells and could possibly represent sites of external brooding. Unfortunately, this idea is difficult to test and must remain speculative.

Range – Campanian-Maastrichtian. The oldest species of the genus is Dysnoetopora demissa (White, 1879), from the Mesaverde Formation of Wyoming, which was revised by Toots & Cutler (1962). As pointed out by Voigt (1971, p. 93), supposed Crimean Danian specimens of D. celleporoides mentioned by him earlier (Voigt, 1962) were incorrectly dated and in reality come from the Maastrichtian.

**Dysnoetopora celleporoides Canu & Bassler, 1926**
Pls. 139-141.

1926  **Dysnoetopora celleporoides** sp. nov.; Canu & Bassler, p. 37, pl. 6, figs. 10-17, pl. 7, figs. 10-12.
1962  **Dysnoetopora celleporoides** Canu & Bassler; Voigt, p. 21, pl. 4, figs. 2-5.
1971  **Dysnoetopora celleporoides** Canu & Bassler; Voigt, p. 79, figs. 1A-D, 2C-E, 3A-E, 4A-D, 8A, 10A-B.
In press  **Dysnoetopora celleporoides** Canu & Bassler; McKinney & Taylor, fig. 3C-D.

**Material** – Lectotype (designated here): USNM 69960, specimen figured by Canu & Bassler, 1926, pl. 6, fig. 12, Maastrichtian, Coon Creek Formation, Coon Creek, McNairy County, Tennessee (locality TN1). Paralectotypes: USNM 528934, the remaining syntypes, details as for lectotype. Other material: NHM BZ 3118, BZ 3698, details as for lectotype, but E. Voigt Collection. NHM BZ 5231-5233, Maastrichtian, PeeDee Formation, Burches Ferry, Florence County, South Carolina (locality SC1). NHM BZ 5073, Maastrichtian, PeeDee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2). NHM BZ 5074. BZ 5075, BZ 5076, BZ 5077 (sample), NNM RGM 507 019 (sample), Maastrichtian, Coon Creek Formation, shell lenticles in upper part, Corbula Bed auctt; Coon Creek, McNairy County, Tennessee (locality TN1; S. Tracey Collection). NHM BZ
5078 (sample), Maastrichtian, Coon Creek Formation, shelly lens above Corbula Bed; upstream of Coon Creek Field Station, McNairy County, Tennessee (locality TN1; S. Tracey Collection). NHM BZ 5079, Maastrichtian, Coon Creek Formation, grey silty fine sands in streambed, Coon Creek, McNairy County, Tennessee (locality TN1; S. Tracey Collection). NHM BZ 5080 (sample), Maastrichtian, Coon Creek Formation, Coon Creek, McNairy County, Tennessee (locality TN1; W.J. Kennedy Collection). NHM D34481-D32284, Maastrichtian, Ripley Formation, Oktibbeha County, Mississippi (locality MS3). USNM 526194, Maastrichtian, Peede Formation, Neuse River, Lenoir County, North Carolina (locality NC4). NHM BZ 5083-5085, Maastrichtian, Ripley Formation, Eufaula, Barbour County, Alabama (locality AL1). NHM BZ 5086, BZ 5210-2 (thin sections), Maastrichtian, Ripley Formation, Florence, Quitman County, Georgia (locality GA1). NHM BZ 5087(6), Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5). NHM BZ 5088, Maastrichtian, Prairie Bluff Chalk, Jefferson, Marengo County, Alabama (locality AL5). NHM BZ 5089 (sample), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). NHM BZ 5090-5091, Maastrichtian, Prairie Bluff Chalk, Emelle, Sumter County, Alabama (locality AL9). NHM BZ 5092, Maastrichtian, Prairie Bluff Chalk, Braggs, Lowndes County, Alabama (locality AL4). NHM BZ 5093 (eight fragments), Maastrichtian, Prairie Bluff Chalk, Braggs, Lowndes County, Alabama (locality AL3). ANSM 80356, Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1).

**Description** – Colony erect, dendroid, branches subcylindrical (Pl. 139, fig. 1a), bifurcating, thick, up to 9 mm in diameter, but more commonly 2-5 mm, endozone formed of an axial grouping of long, prismatic, tabulated zooids (Pl. 140, fig. 3a), exozone comprising piles of smaller, frontally-budded zooids meeting colony surface at 70-90°; growing tips conical. Ancestrula unknown. Encrusting colony base (Pl. 139, fig. 2) moderately extensive, multiserial with fan-shaped subcolonies at growing edge (Pl. 139, fig. 2c), multilaminar; autozooids in basal layer elongate, subpyriform, about 200 μm long by 100 μm wide, tending to be arranged in ill-defined transverse rows, frontal shield entirely gymnocystal, convex, ornamented with growth checks and transverse undulations, pore windows sporadically developed near perimeter, orifice terminal, semi-elliptical, proximal edge straight, ascopore transversely elliptical, located close to orifice on side of low umbone, facing distally (Pl. 139, fig. 2d). Pore chambers lacking.

Autozooids on colony surface longitudinally elliptical, surrounded and partly enveloped by basal walls of frontal buds. Proximal frontal surface comprising a small area of gymnocystal frontal shield (Pl. 140, fig. 2b), usually overgrown. Distally raised with a transversely elliptical ascopore proximal of a semielliptical orifice, proximal edge straight, sometimes with tiny condyles (Pl. 140, fig. 1b), formed of an apertural bar comprising a pair of costae fused along mid-line (Pl. 140, fig. 3b); distally a slight oral ledge may be visible. Endozenal zooids very long (Pl. 140, fig. 3a), proximally parallel to branch axis with thin walls having uniporous and multiporous septulae, distally bending outwards towards branch surface. Exozenal zooids having an elongated, cyst-like appearance in branch longitudinal sections, 3-4 times longer than wide, the gymnocystal frontal shield resembling an inferior hemiseptum. Orientation of autozooidal orifices on colony surface variable (Pl. 140, fig. 1a), usually directed distally almost parallel to branch axis, sometimes laterally or obliquely proximally. Ovicells unknown.
Avicularia (Pl. 139, fig. 1c; Pl. 140, fig. 2a) moderately common, scattered, vicarious, large, occupying surface area of about two autozooids, elongate, proximal frontal shield gymnocystal, comprising about one third of total avicularium length, an apparent ascopore present, rostrum varying in shape from spatulate to distally tapering, always with a rounded end, hinge line sometimes preserving a low, medial boss flanked by two small condyles.

Measurements – OL 77±6, 68-90 (4, 20); OW 79±7, 68-90 (4, 20); RL 324±26, 300-380 (3, 10); RW 158±21, 140-200 (3, 10).

Remarks – The surface features of Dysnoetopora celleporoides colonies can appear very confusing and difficult to interpret; delineating individual zooids and identifying their orifices among the numerous holes of varying size that cover branch surfaces is by no means straightforward. This is partly because the thin calcification of the skeletal walls results in frequent breakage, but is also because frontal budding of new zooids across branch exteriors means that these surfaces are dynamic growth zones covered by zooids in varying stages of skeletal development, including many new buds. Furthermore, the surface details of specimens from chalky facies are often masked by adherent sediment grains, in which case the distinctive appearance of the fractured ends of branches provide the best clue to the identity of material as D. celleporoides.

Dysnoetopora celleporoides is unique among the common bryozoans of the Upper Cretaceous of eastern North America in forming dendroid colonies with robust branches of highly variable diameter. It is likely to be confused only with the far less common cyclostome Tetrocycloecia (see above), but this genus lacks the axial grouping of large zooids visible in branch cross sections of D. celleporoides.

Differences in avicularian morphology exist between the type material of this species from the Coon Creek Formation of Tennessee and specimens from the Peedee Formation of South Carolina; the former have spatulate avicularia, the latter distally tapering avicularia which are also smaller. This variation is regarded provisionally as intraspecific, but warrants further investigation.

Acknowledgements

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References


Gohn, G.A. 1826-1833. *Bryozoa: Gymnolaemata (Cheilostomida Anasca) from the Western South Island continental shelf and slope.*


Table 1. Species listing with known regional occurrences.

<table>
<thead>
<tr>
<th>Species</th>
<th>Europe</th>
<th>New Jersey and Delaware</th>
<th>Carolinas</th>
<th>Tennessee</th>
<th>Alabama (Georgia, Mississippi and Louisiana)</th>
<th>Arkansas (Oklahoma)</th>
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<tbody>
<tr>
<td>Voigtopora maconensis sp. nov.</td>
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<td>Voigtopora thurni sp. nov.</td>
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<td>cf. Spiropora verticillata (Goldfuss, 1826)</td>
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<td>Amphiblestrum parvum sp. nov.</td>
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<td>Cheethamia howei Shaw, 1967</td>
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<td>Stictostega durhami Shaw, 1967</td>
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<td>Stictostega turneri sp. nov.</td>
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Europe, New Jersey and Delaware, Carolinas, Tennessee, Alabama (Georgia, Mississippi and Louisiana), Arkansas (Oklahoma)
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<th>Species Name</th>
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<td>Stictostega ovicincta sp. nov.</td>
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<td>Stichomicropora baccata (Canu &amp; Bassler, 1926)</td>
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<td>Stichomicropora ostrovskyi sp. nov.</td>
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<td>Aeolopora catillus sp. nov.</td>
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<td>Anorthipora spooneri (Butler &amp; Cheetham, 1958)</td>
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<td>Castanopora lambi Turner, 1975</td>
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<td>Castanopora dorothyae sp. nov.</td>
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<td>Monoceratopora mitrifera sp. nov.</td>
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<td>Morphasmpora variostoma sp. nov.</td>
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<td>Nannopora lonquata (Canu &amp; Bassler, 1926)</td>
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<td>Pelmatoopora irregularis (Canu &amp; Bassler, 1926)</td>
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<td>Pliophloea shmoiformis sp. nov.</td>
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<td>Stichocados aenigmata sp. nov.</td>
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<td>Tricephalopora aff. obducta Lang, 1916</td>
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<td>Tricephalopora vibraculata Turner, 1979</td>
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<td>Turnerella periphercia sp. nov.</td>
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<td>Ubaghsia tragica sp. nov.</td>
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<td>Frurionella parvipora Canu &amp; Bassler, 1926</td>
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<td>Balantiostoma danei (Shaw, 1967)</td>
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<td>Balantiostoma nomas (Shaw, 1967)</td>
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<td>Balantiostoma octospinigera sp. nov.</td>
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<td>Balantiostoma poversae sp. nov.</td>
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<td>Hoplocheilina hagemani sp. nov.</td>
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<td>Peedeesella guhai sp. nov.</td>
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<td>Kronothoa quitanensis sp. nov.</td>
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<td>Boreasina novaehanoverensis sp. nov.</td>
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<td>Boreasina sp.</td>
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<td>Dysnoetopora celleporoides Canu &amp; Bassler, 1926</td>
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Table 2. Type species and morphological characters of the principal genera of romancheinid and brydonellid ascophoran cheilostomes recorded from the Cretaceous.

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<th>Genus and range</th>
<th>Type species</th>
<th>Characters</th>
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<td>Balantiostoma</td>
<td><em>Cellepora marsupium</em> von Hagenow, 1839</td>
<td>Colony encrusting; orifice mucronate, with oral spines; areolae small; avicularia adventitious, paired on either side of orifice, directed distally, pointe?</td>
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<td>Marsson, 1887</td>
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<td>Bathosella</td>
<td><em>Mucronella aspera</em> Ulrich, 1901</td>
<td>Colony encrusting; orifice without mucro or oral spines; areolae rare; avicularia irregularly distributed, rounded</td>
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<tr>
<td>Canu &amp; Bassler, 1917</td>
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<td>Biporochella</td>
<td><em>B. regularis</em> Guha &amp; Nathan, 1996</td>
<td>Colony encrusting; orifice without mucro or oral spines; areolae regularly arranged around entire margin of zooid; avicularia adventitious, paired on either side of orifice, rounded</td>
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<td>Guha &amp; Nathan, 1996</td>
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<td>Brydonella</td>
<td><em>Homalostega vulcani</em> Brydone, 1913</td>
<td>Colony encrusting or erect bifoliate; frontal shield derived from overgrowing kenozooids; orifice with oral spines, without mucro; avicularia adventitious, small, scattered around orifice, rounded, and interzooidal, large, rounded</td>
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<td>Berthelsen, 1962</td>
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<tr>
<td>Bubnoffiella</td>
<td><em>Homalostega suffulta</em> Marsson, 1887</td>
<td>Colony encrusting; orifice without mucro or oral spines; areolae lacking; avicularia adventitious, median suboral, large chambered, proximally? directed, and interzooidal, large, rounded</td>
</tr>
<tr>
<td>Voigt, 1959</td>
<td></td>
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<tr>
<td>Escharoides</td>
<td><em>Cellepora coccinea</em> Abildgaard, 1806</td>
<td>Colony encrusting; orifice mucronate, with oral spines; areolae present; avicularia adventitious, paired on either side of orifice, directed distolaterally, pointed</td>
</tr>
<tr>
<td>Milne Edwards, 1836</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hoplocheilina</td>
<td><em>Eschara osculifera</em> Reuss, 1872</td>
<td>Colony erect bifoliate; orifice mucronate, with oral spines; areolae present; avicularia interzooidal, rounded, large or small, and adventitious, suboral, paired, directed distolaterally, rounded</td>
</tr>
<tr>
<td>Canu, 1911</td>
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Plate 1
Bryozoan-encrusted oyster shells from the Maastrichtian of the eastern U.S.A.
Figs. 1, 2. Encrusted internal surfaces of right valves of Pycnodonte from the Prairie Bluff Chalk, near Lake Ridge Apartments, Livingston, Sumter County, Alabama. Fig. 1. NHM BZ 4796, with a diverse assemblage of 15 different bryozoan species, including the holotype of Wilbertopora livingstonensis sp. nov.; × 1. Fig. 2. NHM BZ 5062, with the shell substrate dominated by a single colony of Conopeum spissamentum sp. nov.; × 0.85.

Figs. 3, 4. Encrusted external surfaces of Flemingostrea from the Peedee Formation, Ideal Quarry, New Hanover County, North Carolina. Fig. 3. NHM BZ 5063, complete valve with numerous sheet-like colonies belonging to several species concentrated along left side; × 0.6. Fig. 4. NHM BZ 5064, shell fragment with dense bryozoan coverage; × 1.
Voigtopora maconensis sp. nov.
Campanian, Demopolis Chalk, near Macon, Noxubee County, Mississippi (locality MS1).
Fig. 1. Holotype, NHM BZ 5107(1). a, subparallel branches; × 20. b, general view of colony with multiple lateral branches; × 8. c, founding autozooid of a lateral branch; × 65. d, short ancestrula with circular, but not quite hemispherical, protoecium, giving rise to a distal and two lateroproximal autozooids, each establishing a primary branch of the colony; × 40.
Voigtopora thurni sp. nov.
Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).

Fig. 1. Holotype, NHM BZ 5111(1a). a, dichotomous branch bifurcations; × 25. b, two colonies, holotype encircling smaller paratype preserving ancestrula with both dichotomous and adventitious branching; × 14.

Fig. 2. Paratype, NHM BZ 4803(4). Dichotomous and adventitious branching growing around encrusting foraminiferan; × 30.

Fig. 3. Paratype, NHM BZ 5111(1b). a, branch termination with median autozooidal chamber flanked on both sides by proximal ends of distal autozooids; × 50. b, pseudoporous frontal wall; × 60. c, ancestrula giving rise distally to single, curved branch, with adventitious bud emerging from its left side; × 50.

Fig. 4. Paratype, NHM BZ 4805(1). Short ancestrula with complete protoecium, giving rise distally to two diverging autozooids; × 40.
Plate 4
Oncousoecia? nonomogolabili sp. nov.
Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).
Fig. 1. Holotype, RU 5600. a, typical colony surface; × 20. b, general view of colony; × 12. c, irregularly
distributed autozooidal apertures across colony surface; × 50. d, growing margin of colony (top), with
ontogenetic gradient of autozooids (increasing age towards bottom right); × 35. e, circular pseudopores
on exterior wall of autozooid; × 240.
Plate 5
Microeciella livingstoni sp. nov.
Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).
Fig. 1. Paratype, NNM RGM 507 030(a). a, general view of colony; × 20. b, gonozooid; × 125.
Fig. 2. Holotype, NHM BZ 4796(7). a, fertile colony with very narrow perimeter beyond development of frontal exterior wall; × 45. b, gonozooid (left) with ooeiopore about two-thirds diameter of an autozooidal aperture; × 100.
Plate 6
Idmonca sp.
Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 and/or NJ2).
Fig. 1. RU 5500. a, partially overgrown colony; × 20. b, narrow budding zone at tip of branch (top) and slightly oblique transverse rows of autozooids; × 55.
Fig. 2. RU 5631. a, ancestrula (bottom) and widening primary astogenetic zone of change to well-developed, slightly oblique transverse rows (top); × 65. b, robust circular pseudopores in frontal wall; × 500. c, autozooid and branch-margin kenozooids; × 200.
Mecynoecia? exterogemma sp. nov.
Figs 1-7. Maastrichtian, Peedee Formation, Neuse River, North Carolina (locality NC4).
Fig. 1. Holotype, USNM 526199. a, general view of branch segment; × 20. b, pseudopores; × 150.
Fig. 2. Paratype, USNM 526200. Bifurcating branch segment; × 17.
Fig. 3. Paratype, USNM 526201. Branch segment broken so that a single autozooid with origin along the branch perimeter extends proximally beyond the primary transverse break; × 12.
Fig. 4. Paratype, USNM 526202. Branch transverse section; × 25.
Fig. 5. Paratype, USNM 526203. Branch longitudinal section; × 10.
Fig. 6. Paratype, USNM 526204. Branch segment with coronet-shaped autozooidal peristome (right centre) and fused distal tip of another branch (bottom right); × 13.
Fig. 7. Paratype, USNM 526205. Traces of elongate autozooids separated by narrow grooves; × 40.
Fig. 8. Paratype, NHM BZ 4831, Maastrichtian, Ripley Formation, Florence, Georgia (locality GA1). Encrusting base of colony with broken erect branch origin in lower right corner; × 12.
Plate 8

*Platonea adnata* sp. nov.

Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2).

Fig. 1. Holotype, NHM BZ 4189(1a). a, branch tip with brood chamber extending between fascicles of autozooidal peristomes; × 20. b, general view of colony; × 4. c, fascicles of connate peristomes of autozooids and adnate thin kenozooids (right); × 40. d, transversely elongate ooeic pore elevated on ooeiciostome located between two fascicles of autozooidal peristomes; × 40.

Fig. 2. Paratype, NHM BZ 4188(1). Pseudopores in frontal wall of autozooids; × 190.

Fig. 3. Paratype, NHM BZ 4175(4a). Young colony with hemispherical, broken protoecium; × 75.
Platonea catenula sp. nov.

Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).

Fig. 1. Holotype, NHM BZ 5099(2a). a, branch segment with brood chamber occupying broadest point; × 20. b, two successive brood chambers with distal ooeciopores (centre, top centre) slightly smaller in diameter than autozooidal orifices; × 33. c, ooeciopore on short ooeciostome, located between three short autozooidal peristomes; × 175. d, growing tip; × 60.

Fig. 2. Paratype, NNM RGM 507 031. Branch from which two adventitious branches (top left, bottom right) originate at right angles; × 20.

Fig. 3. Paratypes, NHM BZ 5114(1). Two small colonies, touching and deflected, not fused; × 17.
Plate 10

*Platonea mississippiensis* sp. nov.

Campanian, Demopolis Chalk, near Macon, Noxubee County, Mississippi (locality MS1).

Fig. 1. Holotype, NHM BZ 5107(2a). a, parent branch with transverse fascicles of connate autozooidal peristomes where branch is relatively wide, and laterally budded branch with isolated autozooidal peristomes; × 20. b, general view of colony; × 10. c, autozooids; × 85. d, crushed brood chamber at distal tip of parent branch in (b); × 40. e, pseudopores in frontal wall of autozooids; × 210. f, pseudopores in frontal wall of brood chamber; × 160.
Plate 11
Idmidronea traceyi sp. nov.
Maastrichtian, Ripley Formation, Coon Creek Member, above Corbula bed upstream from Field Center, Coon Creek, Tennessee (locality TN1).
Fig. 1. Holotype, NHM BZ 5115. a, anastomosing branches; × 21. b, kenozooidal overgrowth spreading onto frontal surface of branch; × 43.
Fig. 2. Paratype, NHM BZ 5116. Lateral view of branch showing rows of autozooidal apertures (top) and kenozooids on branch reverse (bottom); × 46.
Fig. 3. Paratype, NHM BZ 5117. a, broken gonozooid on lateral edge of branch; × 40. b, detail showing fluted collar of ooeiostome within brood chamber; × 230.
Fig. 4. Paratype, NHM BZ 5118. Colony base covered by kenozooids; × 32.
Plate 12

cf. Spiropora verticillata (Goldfuss, 1826)
Maastrichtian, Navesink Formation, Poricy Creek, Linford, Monmouth County, New Jersey (locality NJ1).

Fig. 1. NHM BZ 5120. a, branch originating from trifurcation; × 20. b, transversely broken branch with annular rings of autozooids around central budding axis; × 35.

Fig. 2. NNM RGM 507 034. Ring of corroded autozooidal apertures just below growing tip of branch; bored frontal walls of autozooids with narrow, clear borders; × 40.

Fig. 3. NNM RGM 507 035. Encrusting base of colony giving rise to multiple branches of variable diameter; × 18.
**Plagioecia cristata** sp. nov.

Fig. 1. Holotype, NHM BZ 5121(a), Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5). a, typical colony surface; × 20. b, general view of fertile colony; × 11. c, keeled exterior walls of autozooids with large round pseudopores; × 150.

Fig. 2. Paratype, NHM BZ 4791(4), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). Brood chamber with distal ooeciopore about two-thirds diameter of autozooidal apertures; × 50.

Fig. 3. Paratype, BZ 5122, Maastrichtian, Prairie Bluff Chalk, Jefferson, Marengo County, Alabama (locality AL5). a, general view of parent colony and two generations of daughter colonies; × 11. b, second generation daughter colony originating from pseudoancestrula; × 35.
Plate 14

*Plagioecia koinos* sp. nov.
Maastrichtian, Prairie Bluff Chalk, Lake Ridge Apartments, Livingston, Sumter County, Alabama (locality AL6).

Fig. 1. Holotype, NHM BZ 4803(1). a, colony with several gonozooids; × 2.7. b, growing edge and two gonozooids; × 14. c, gonozooid with ooeciopore just above centre; × 35.

Fig. 2. Paratype, NHM BZ 5099(3). a, autozooids, two with terminal diaphragms; × 55. b, subcolony at margin of large colony; × 25. c, lobate colony margin; × 30.
Plate 15

Plagioecia maculata sp. nov.
Maastrichtian, Peedee Formation, Rocky Point Member, Ideal Quarry, North Carolina (locality NC2).
Fig. 1. Holotype, NHM BZ 5124(1a). a, typical colony surface with well developed maculae; × 20. b, autozooidal aperture closed by terminal diaphragm in middle of macula (upper left of (a)), × 140.
Fig. 2. Paratype, NHM BZ 5104(3a). a, general view of colony with well developed brood chambers; × 9. b, growing edge of colony and fully formed autozooids; × 40. c, ooeciostome about two-thirds distance from proximal to distal edge of brood chamber; × 25. d, proximally tilted, long ooeciostome; × 70.
Fig. 3. Paratype, NHM BZ 4175. Young colony with hemispherical, broken protoecium (left); × 45.
Plate 16

*Plagioecia* spp.

Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1).

Fig. 1. *Plagioecia amplimaculata* sp. nov. Holotype, ANSM 80364. a, general view of part of the variably preserved colony; × 16. b, autozooids with macula devoid of apertures just left of centre; × 27. c, thickened growing edge suggestive of incipient erect growth; × 19. d, autozooids with rugose frontal walls and, in most cases, apertures closed by terminal diaphragms; × 64.

Fig. 2. *Plagioecia?* sp. ANSM 80363. a, lobate colony; × 13. b, two broken gonozooids; × 29.
Plate 17

Plagioecia kryptos sp. nov.
Maastrichtian, Prairie Bluff Chalk, Emelle, Sumter County, Alabama (locality AL9).
Fig. 1. Holotype, NHM BZ 5214. a, subcolony (top) overgrowing parental colony; × 21. b, autozooids close to growing edge (top left); × 42. c, gonozooid; × 56.
Fig. 2. Paratype, NNM RGM 507 062. Keeled autozooids and growing edge (top); × 42.
Plate 18

*Mesonopora patane* sp. nov.

Fig. 1. Holotype, NHM BZ 5125, Maastrichtian, Prairie Bluff Chalk, Emelle, Alabama (locality AL9). a, entire fertile colony; × 20. b, brood chamber, with distal ooeiciopore about half diameter of an autozooidal aperture; × 55. c, edge of colony with basal thin-walled endozone; × 75.

Fig. 2. Paratype, NHM BZ 4813, Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5). Ovicell with roof removed and distal ooeiciopore partially preserved; × 65.

Fig. 3. Paratype, NNM RGM 507 037, Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). Edge of colony in which growth apparently stopped, with thick-walled exozone extending to peripheral base of colony; × 95.

Fig. 4. Paratype, NHM BZ 5114(2), Maastrichtian, Prairie Bluff Chalk, Jefferson, Marengo County, Alabama (locality AL5). Corroded surface of ancestrula (centre) and earliest-budded autozooids of colony; × 70.
Plate 19

*Diplosolen ehrhardi* sp. nov.
Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).
Fig. 1. Holotype, NHM BZ 4796(15). a, small complete colony; × 20. b, growing edge of colony and (lower left) crushed, slightly elongate brood chamber with ooeciostome just beyond midpoint; × 60.
Fig. 2. Paratype, NHM BZ 5035(2). Autozooids and typically alternating nanozooids; × 60.

*Diplosolen perexigua* sp. nov.
Maastrichtian, Ripley Formation, Florence, Quitman County, Georgia (locality GA1).
Fig. 3. Holotype, NHM BZ 5127. a, general view of colony; × 20. b, autozooids and interspersed nanozooids; x60. c, transversely elongate brood chamber with ooeciostome at distal margin; × 60.
Diplosolen montilaurus sp. nov.
Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1).

Fig. 1. Holotype, ANSM 80366. a, part of the large colony showing sealed, abandoned growing edge (running left to right across centre of image) and caviariiform upgrowth (top right); × 16. b, undulose colony surface with autozooids, nanozooids and some secondary nanozooids; × 35. c, secondary nanozooid (arrowed), two nanozooids, two autozooids with open apertures and an autozooid with an aperture closed by a complete terminal diaphragm (lower right); × 95. d, aperture of autozooid and smaller aperture of distal nanozooid; × 180. e, gonozooid; × 25. f, ooeciopore (centre) and autozooidal peristomes penetrating the brood chamber roof; × 65.
Plate 21

_Hyporosopora praecox_ sp. nov.
Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5).

Fig. 1. NHM BZ 4836(1). a, holotype (left) and a paratype, both fertile; × 20. b, brood chamber in paratype; × 70. c, holotype (upper centre) and several of the surrounding paratypes; × 10. d, paratype with brood chamber in subcolony; × 35.
Plate 22

*Mesenteripora lirella* sp. nov.
Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1).

Fig. 1. Holotype, ANSM 80369. a, frondose colony with broken-off bilaminate branch (extending from lower centre about halfway towards top left corner of image); × 12. b, growing edge of convoluted frond showing mixture of autozooids with open apertures and apertures with terminal diaphragms; × 22. c, autozooids with apertures closed by terminal diaphragms; × 45. d, gonozooid; × 29.
Plate 23
Annnectocyma cirrita sp. nov.
Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).
Fig. 1. Holotype, NHM BZ 5224. a, bifurcate branch; × 20. b, autozooids at growing tip of branch; × 60. c, elongate, inflated brood chamber at branch bifurcation, with ooeicopore near distal end; × 60. d, branch bifurcation; × 330.
Fig. 2. Paratype, NHM BZ 5113. a, general view of colony with both adventitious and bifurcating branches; × 20. b, ancestrula with discoidal protoecium, giving rise to single autozooid from which a second branch originated adventitiously; × 80.
**Plate 24**

*Annectocyma cirrita* sp. nov.

Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).

Fig. 1. Paratype, NHM BZ 5112. a, bifurcate branch segment; × 20. b, bifurcate branch segment with brood chamber at bifurcation; × 20. c, broken brood chamber at branch bifurcation point; × 50. d, brood chamber at branch bifurcation point; × 40. e, detail of brood chamber in Fig. 1d; × 70. f, pseudopores in exterior frontal wall partially closed by centripetal platelets; × 540.

Fig. 2. Paratype, NHM BZ 5113. a, globular, semi-erect brood chamber at branch bifurcation; × 40. b, ooeiopore and peristomes of contiguous autozooids; × 95.
Filifascigera cylindrata sp. nov.
Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).
Fig. 1. Holotype, RU 5627. a, cluster of autozooidal apertures separated by barren stretches of frontal exterior wall; both adventitious (bottom centre) and dichotomous (lower right) branching, and branch approaching from right terminating upon contact with central branch; × 25. b, typical branch segments; × 20. c, branch with unusually elevated base of group of autozooidal apertures; × 25. d, detail of group of autozooidal apertures shown in (c); × 100. e, minimally diverging branches (lower right) and adventitious branch originating from single autozooidal aperture (upper left); × 40. f, complex branch divergence; × 40.
Plate 26

Osculipora carolinensis sp. nov.
Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 and/or NJ2).
Fig. 1. Holotype, USNM 528377. Dichotomously divided branches with several fascicules; ×13.
Fig. 2. Paratype, USNM 528378. Base of small colony; × 18.
Fig. 3. Paratype, USNM 528379. a, colony with brood chamber; × 18. b, detail of roofless brood chamber; × 90.
Fig. 4. Paratype, USNM 528380. a, edge of overgrowth comprising free-walled zooids; × 180. b, fasciclebounding exterior wall; × 115.
Plate 27

*Theonoa? radiobifurcata* Canu & Bassler, 1926

Maastrichtian, Coon Creek Formation, Coon Creek, McNairy County, Tennessee (locality TN1).

Fig. 1. Holotype, USNM 69966. a, daughter subcolony; × 20. b, distal edges of fascicles along colony margin, bounded by narrow band of buds closed by terminal diaphragms; × 50. c, three successive subcolonies, added from left (proximal) to right (distal); × 12.
Plate 28

‘Berenicea’ sp.
Maastrichtian, Prairie Bluff Chalk, Braggs, Lowndes County, Alabama (locality AL3).
Fig. 1. NHM BZ 5213. a, part of damaged colony growing on a cobble, with growing edge visible at top; × 14. b, relatively well preserved zooids in a hollow on the substrate; × 22. c, detail of some autozooids, × 55. d, base of erect branch or growth around erect colony of a different species; × 18.
Plate 29

*Polyascosociella? tripora* (Canu & Bassler, 1926)

Fig. 1. Lectotype, USNM 69963, Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TN1). a, obverse side of branches; × 20. b, highly branched colony with expanded base on right, and reverse side of colony (paralectotype, USNM 528383); × 5. c, broken end of branch with central endozone, and obverse surface; × 42.

Fig. 2. USNM 528384, Maastrichtian, PeeDee Formation, Neuse River, Lenoir County, North Carolina (locality NC4). a, obverse surface; × 9. b, distal branch with ontogenetic gradient from oblique autozooids on right to mixture of autozooids and exozonally budded kenozooids on left; × 50.

Fig. 3. NHM BZ 5140, Prairie Bluff Chalk, Braggs, Lowndes County, Alabama (locality AL3). a, transverse section; × 28. b, longitudinal section with reverse-side on left; × 28.
Plate 30

*Tetrocycloecia tennesseensis* (Canu & Bassler, 1926)
Maastrichtian, Coon Creek Formation, Coon Creek, McNairy County, Tennessee (locality TN1).
Fig. 1. Lectotype, USNM 69971. Branch with de-roofed brood chamber at lower left; × 20.
Fig. 2. Paralectotype, USNM 528385. Branch with large, de-roofed brood chamber (top centre); × 13.
Fig. 3. Paralectotype, USNM 528386. Autozooidal apertures with short peristomes surrounded by ill-defined of kenozooids; × 40.
Fig. 5. Paralectotype, USNM 528387. Margin of de-roofed brood chamber with spinose inner wall penetrated by numerous broken autozooids; × 75.
Fig. 6. NHM BZ 3700. Small fragment of pseudopore-rich brood chamber roof; × 120.

Maastrichtian, Peedee Formation, Neuse River, Lenoir County, North Carolina (locality NC4).
Fig. 4. USNM 528389. a, longitudinal section through terminal overgrowth; × 28. b, transverse section; × 28. c, tangential section; × 28.
Plate 31

*Tetrocycloecia transversa* sp. nov.

Maastrichtian, Ripley Formation, Florence, Quitman County, Georgia (locality GA1).

Fig. 1. Paratype, NHM BZ 5153. a, general colony surface with alternating transverse bands of kenozooids and intermixed kenozooids and autozooids; × 25. b, detail of intermixed autozooidal apertures and open kenozooids; × 65.

Fig. 2. Paratype, NHM BZ 5149. a, longitudinal section; × 28. b, transverse section; × 28. c, tangential section; × 28. d, longitudinal section through region with self-overgrowth; × 28.

Fig. 3. Paratype, NHM BZ 5152. a, autozooid with row of pustules on crest of low peristome and autozooidal aperture as well as kenozooids closed by terminal diaphragms; × 140. b, detail of autozooidal aperture closed by centripetally grown terminal diaphragm penetrated by several pseudopores; × 310.
Plate 32
*Tetrocycloecia transversa* sp. nov.
Maastrichtian, Ripley Formation, Florence, Quitman County, Georgia (locality GA1).
Fig. 1. Holotype, NHM BZ 5141. a, general view of typical branch; × 9. b, transverse band of kenozooids, all closed by terminal diaphragm; × 65.
Fig. 2. Paratype, NHM BZ 5229. a, distal end of branch with multiple centres of overgrowths; × 14. b, edge of laterally spreading overgrowth, growing from bottom to top of figure; × 100.
Fig. 3. Paratype, NHM BZ 5142. Brood chamber; × 40.
Plate 33

*Semicrescis implanus* sp. nov.
Campanian; Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1).
Fig. 1. Holotype, ANSM 80351. a, oblique view of interior of hollow colony; × 12. b, colony surface, some details obscured by adherent sediment grains; × 20. c, edge of colony showing autozooids and kenozooids; × 50. d, detail of autozooidal and smaller, funnel-like kenozooidal apertures; × 105. e, gonozooid with broken roof; × 31.

*Semicrescis tubulosa* d’Orbigny, 1854
Fig. 2. Syntype, MNHN d’Orbigny Collection 8414, Senonian, Néhou, France. Autozooids and kenozooids; × 58.
Plate 34

*Unicavea* sp. 1
Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1).
Fig. 1. ANSM 80774. a, general view of colony; × 18. b, growing edge; × 55. c, large, elongate autozooidal apertures surrounded by smaller polymorphs; × 60.
Fig. 2. ANSM 80773, abraded colony with parent colony at left and multiple daughter colonies; × 17.

*Unicavea* sp. 2
Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2).
Fig. 3. NHM BZ 4179(3). a, part of large colony; × 15. b, growing edge; × 55.
Plate 35

*Herpetopora anglica* Lang, 1914

Fig. 1. LSUMG-I 8254, paratype colony of *Pyripora shawi* Frey & Larwood, 1971, Santonian, Brownstown Formation, McCurtain County, Oklahoma (locality OK1). a, group of zooids growing around a borehole; × 11. b, three autozooids and the damaged remains of several others; × 40. c, elongate opesia of an autozooid with a tubular kenozooid connecting into the left lateral pore window; × 70.

Fig. 2. NHM BZ 5155(1), Campanian, Demopolis Chalk, Macon, Noxubee County, Mississippi (locality MS1). a, intramural bud with closure plate occupying an autozooid; × 65. b, autozooid (lower right) and its distolaterally budded daughter autozooid (upper left); × 50.

Fig. 3. NHM BZ 5022, Maastrichtian, Ripley Formation, Coon Creek Member, Coon Creek Field Station, McNairy County, Tennessee (locality TN1). Two caudate autozooids with small opesiae and three other autozooids with larger opesiae; × 55.
Plate 36

_Herpetopora wightoni_ sp. nov.

Fig. 1. Holotype, NHM BZ 5013, Maastrichtian, Peedee Formation, Rocky Point Quarry, Pender County, North Carolina (locality NC3). a, densely-packed uniserial branches; × 35. b, detail of an autozooid; ×185. c, autozooids with intramural buds; × 125. d, autozooids and a small kenozooid (centre); × 110.

Fig. 2. Paratype, NHM BZ 5156, Maastrichtian, Prairie Bluff Chalk, Emelle, Sumter County, Alabama (locality AL9). a, branch (growing bottom right to top left) comprising an autozooid and two elongate kenozooids budding distolateral daughter branches; × 31. b, autozooid with prominent mural rim; × 125.
Plate 37

Electra everetti sp. nov.
Maastrichtian, PeeDee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2).
Fig. 1. Holotype, NHM BZ 5015. a, irregularly-arranged zoooids, some with intramural buds; × 48. b, autozooids and adventitious kenozooids; × 80. c, autozooids with pustulose proximal cryptocytes; × 110. d, autozooid with a median tubercle close to the proximal mural rim and an interzooidal kenozooid (left); × 125. e, two autozooids with closure plates bearing scars of the opercular sclerite; × 120.
Fig. 2. Paratype, NHM BZ 5016(1). Uniserial and biserial branches; × 35.
Plate 38
Conopeum spissamentum sp. nov.
Fig. 1. Holotype, NHM BZ 4798, Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). a, group of zooids; × 25. b, zooidal size variation according to position relative to row bifurcation; × 48. c, autozooid with subtriangular kenozooids at the corners; × 80. d, zooids with closure plates; × 48.
Fig. 2. Paratypes, NHM BZ 4811, Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5). a, colony origin showing early zooids with closure plates; × 44. b, small colony showing budding pattern from tiny ancestrula (centre) with closure plate; × 55.
Plate 39
Conopeum nelsoni (Canu & Bassler, 1926)
Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TN1).
Fig. 1. Holotype, USNM 69969. a, colony encrusting a free serpulid tube; × 18. b, group of zooids; × 50.
  c. detail of zooids showing pustulose cryptocysts; × 115. d, several zooids, some with closure plates; × 48.
  e, zooid with porous closure plate; × 115. f, detail of closure plate surface showing polygonal sectors containing 2-4 pores; × 460.
Conopeum paranelsoni sp. nov.
Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1).
Fig. 1. Holotype, ANSM 80351. a, group of zooids, some with closure plates; × 26. b, closure plate with crescentic opercular scar and sparse, large pores; × 75. c, open zooids; × 25.
Fig. 2. Paratype, ANSM 80352. a, closed zooids in early astogeny; × 25. b, zooids with and without closure plates; × 25. c, zooid showing pustulose cryptocyst narrowing distally; × 95.
Conopeum rhombica sp. nov.

Fig. 1. Holotype, NHM BZ 4799, Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). a, group of zooids in area of colony with row bifurcations; × 42. b, small polymorph and knob-like growths into autozooidal chambers (lower left and lower right); × 115. c, abraded growing edge; × 37. d, eruptive frontal overgrowth and intramural buds near colony edge; × 35.

Fig. 2. Paratype, BZ 4812, Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5). a, group of autozooids; × 40. b, two autozooids showing pustulose cryptocysts; × 115.
Plate 42

*Heteroconopeum ovatum* (Canu & Bassler, 1926)
Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TN1).
Fig. 1. Paralectotype, USNM 528393. Autozooids in longitudinal series with intercalated smaller polymorphs; × 35.
Fig. 2. Lectotype, USNM 69964. Avicularium; × 105.
Fig. 3. Paralectotype, USNM 528394. Branch fractured longitudinally along the endozone showing prismatic, porous wall of zooids; × 65.
Fig. 4. USNM 69953, holotype of *Conopeum wadei* Canu & Bassler, 1926. a, colony encrusting gastropod; × 22. b, autozooids and intercalated smaller polymorphs; × 42. c, two autozooids with small polymorphs at their corners; × 80.
Plate 43
*Heterocomeum ovatum* (Canu & Bassler, 1926)
Maastrichtian, PeeDee Formation, Neuse River, Lenoir County, North Carolina (locality NC4).
Fig. 1. USNM 526169. a, bifurcate branch; × 6.4. b, branch surface showing autozooids and smaller polymorphs; × 38. c, autozooid with pits in the basal wall; × 125. d, avicularium-like polymorph; × 200. e, cluster of small polymorphs, probably mostly kenozooids; × 150. f, transversely fractured distal end of branch; × 37.
Plate 44
Chiplonkarina okamurae sp. nov.
Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).
Fig. 1. Holotype, RU 5641. a, narrow lateral branch; × 12. b, zooids on main branch; × 34. c, three autozooids and several kenozooids from lateral branch; × 65. d, slightly oblique view of zooids on main branch showing multilayered pustulose cryptocysts suggestive of intramural budding; × 95. e, autozooid on main branch with dumbbell-shaped opesia; × 190. f, fractured end of main branch exposing corrugated interzooecial walls; × 50.
**Plate 45**

*Basslerinella prismaticum* (Canu & Bassler, 1926)
Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TN1).

Fig. 1. Lectotype, USNM 69967. a, group of zooids; × 32. b, proximal zooids in broken frond with exposed gymnocysts; × 45. c, detail of autozooids and kenozooids; × 105.

*Basslerinella sohli* sp. nov.
Upper Cretaceous, Wilmington Waterworks, North Carolina (locality NC5).

Fig. 2. Holotype, USNM 526167. a, group of zooids; × 36. b, detail of autozooids with small kenozooids at their corners; × 90. c, several autozooids including two in the row right of centre preserving narrow apertural bars; × 85.
Plate 46
Pseudoallantopora brunswickensis sp nov.
Maastrichtian, Pee Dee Formation, Mitchells Landing, Brunswick County, North Carolina (locality NC6).
Fig. 1. Holotype, USNM 526168. a, uniserial branch; × 18. b, cruciate branching pattern; × 22. c, autozooid with distolateral daughter autozooid containing an intramural bud; × 60. d, autozooids with abraded and intact ovicells; × 45. e, ovicellate autozooids, one exceptionally with a distal bud; × 50. f, ovicell with crescent-shaped distal pore chamber window; × 165.
Wilbertopora inuber (Shaw, 1967)
Fig. 1. Campanian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2). Holotype, LSUMG-I 8234. a. preserved colony; × 10. b. autozooids close to growing edge; × 30. c. ovicellate autozooid; × 85.

Wilbertopora ovicarinata sp. nov.
Maastrichtian. Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2).
Fig. 2. Paratype, NHM BZ 5023(1); growing edge showing large distal and distolateral pore chambers, oral spine bases and ovicells; × 60.
Fig. 3. Holotype, BZ 5016(2); aberrant enlarged zooid surrounded by ovicellate autozooids; × 50.
Fig. 4. Paratype, BZ 4183; avicularium with small condyles; × 115.
Wilbertopora livingstonensis sp. nov.
Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).
Fig. 1. Holotype, NHM BZ 4437(1); zooids with broken ovicells; \( \times 32 \).
Fig. 2. Paratype, NHM BZ 4796(14). a, early astogeny; \( \times 34 \). b, autozooid hosting intramural bud; \( \times 105 \).
c, ancestrula; \( \times 195 \). d, growing edge with incompletely calcified autozooids and three avicularia; \( \times 37 \).
e, avicularium; \( \times 98 \).
Plate 49
Wilbertopora hayesi sp. nov.
Maastrichtian, Prairie Bluff Chalk, Jefferson, Marengo County, Alabama (locality AL5).
Fig. 1. Holotype, NHM BZ 5032. a, general view of colony with ancestrula on right and growing edge on left; × 11. b, zooids in transitional area between zones of astogenetic change (bottom) and repetition (top); × 25. c, growing edge showing distal pore windows; × 34. d, ancestrula (centre) and early buds; × 43. e, ovicell with median suture; × 190. f. avicularium; note also presence of four oral spine bases in autozooid lower left; × 63.
Plate 50

**Flustrellaria anatina** (Canu & Bassler, 1926)

Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TN1).

Fig. 1. Lectotype, USNM 69956. a, colony encrusting bivalve shell; × 6. b, early astogeny; × 36. c, autozoooid; × 140.

Fig. 2. Paralectotype, USNM 528397. a, ovicellate autozooids and an avicularium; × 40. b, avicularium; × 110.

Fig. 3. USNM 69972, holotype of *Membraniporina crassimargo* Canu & Bassler, 1926; abraded autozooids showing clearly the spine bases; × 50.
Flustrellaria anatina (Canu & Bassler, 1926)

Fig. 1. LSUMG-I 8239, holotype of Dionella vivistratensis Shaw, 1967, Campanian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2); worn, ovicellate zooids; × 47.

Fig. 2. VCSM 13956, Maastrichtian, Navesink Formation, Poricy Brook, Monmouth County, New Jersey (locality NJ1); growing edge; × 33.

Fig. 3. RU 5515, Maastrichtian, Navesink Formation, Poricy Brook or Big Brook, New Jersey (locality NJ1 or NJ2). a, ovicellate colony with well-developed adventitious avicularia; × 16. b, interzooidal avicularium; × 65. c, ovicell and adventitious avicularia; × 51. d, autozooids with pores in gymnocyist representing sites for budding of adventitious avicularia; × 38.
Flustrellaria braggsensis sp. nov.
Maastrichtian, Prairie Bluff Chalk, Braggs, Lowndes County, Alabama (locality AL3).
Fig. 1. Holotype, NHM BZ 4837(1a). a, irregular growth of colony on cobble; × 12. b, group of zooids close to growing edge; × 35. c, autozooid with broken ovicell; × 70. d, intramural bud (upper left) and vicarious avicularium apparently intramurally budded within a heavily damaged autozooid; × 75. e, vicarious avicularium with intramural bud; × 100. f, apparent adventitious avicularium; × 145.
Plate 53

*Flustrellaria siculifera* sp. nov.

Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

Fig. 1. Holotype, RU 5510. a, general view; × 21. b, autozooids and avicularia associated with row bifurcations; × 38. c, avicularium; × 110. d, autozooids showing spine bases and an intramural bud in the ovicellate zooid on the right; × 63. e, autozooids and avicularia; × 47. f, autozooid with broken ovice; × 69.
Plate 54

*Pyriporella pedunculata* (Shaw, 1967)

Fig. 1. Holotype, LSUMG-I 8235, Campanian?, Ozan Formation?, White Cliffs Station, Sevier County, Arkansas (locality AR3); entire preserved colony; × 22.

Fig. 2. LSUMG-I 8261, Campanian?, Saratoga Chalk?, Saratoga?, Howard County, Arkansas (locality AR2?); early astogeny; × 51.

Fig. 3. LSUMG-I 8263, same details as Fig. 2. a, autozooids and small avicularia; × 43. b, ovicellate autozooid with adventitious avicularia; × 78.

Fig. 4. ANSM 80352, Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1); growing edge; × 30.

Fig. 5. ANSM 80353, same details as Fig. 4; avicularia in varying stages of development; × 50.
**Plate 55**

*Pyriporella lacucarinatensis* sp. nov.

Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).

Fig. 1. Holotype, NHM BZ 4810(1). a, colony showing adventitious avicularia presence in later growth stages (top right), but lacking during early astogeny (lower centre); × 16. b, early astogeny; × 45. c, well-developed, exposed gymnocysts in earliest preserved zooids; × 110. d, ovicellate autozooids and adventitious avicularia in various stages of development; × 37. e, growing edge; × 50.
Plate 56
*Pyriporella lacucarinatensis* sp. nov.
Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).
Fig. 1. Paratype, NNM RGM 507 030(3). a, edge of colony (upper left) overgrowing colony of *Dionella rindsbergi* sp. nov. (lower right); × 16. b, early astogeny, the ancestrula probably overgrown; × 45. c, growing edge showing large distal pore chamber (upper left) and a pair of pores (arrowed) representing budding loci of adventitious avicularia on either side of an ovicell; × 85. d, complete ovicell flanked by a pair of adventitious avicularia; × 140.
Plate 57
Biavicularigera voigti sp. nov.
Campanian, Demopolis Chalk, Macon, Noxubee County, Mississippi (locality MS2).
Fig. 1. Holotype, VCSM 13958, a. autozooids and avicularia; × 23. b. adventitious avicularia and ovicellate autozooids; × 38. c. autozooid with intact ovicell; × 59. d. interzooidal avicularium; × 115. e. growing edge and two intramural buds (centre left); × 43. f. autozooid at edge of colony showing pore windows; × 73.
Plate 58
*Akatopora sulcata* (Canu & Bassler, 1926)
Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TN1).
Fig. 1. Holotype, USNM 69951. a, variably preserved zooids; × 25. b, abraded autozooids, with pair of depressions (muscle scars?) in distal part of basal wall, separated by kenozooids; × 105. c, ovicellate autozooids and smaller polymorphs; × 64. d, ovicell penetrated by microendolith borings; × 235. e, avicularium; × 400. f, various types of zooids at collision between colony lobes; × 47.
Plate 59

*Craspedopora depressa* sp. nov.
Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).

Fig. 1. Holotype, NHM BZ 4807(1). a, group of zooids; × 33. b, autozooids in transverse rows and avicularia; × 60. c, autozooid from edge of colony showing exposed proximal gymnocyst; × 100. d, growing edge; × 46.

Fig. 2. Paratype, NHM BZ 4807(2). a, group of zooids; × 32. b, autozooids with sunken cryptocysts and small polymorphs along zooidal margins; × 73.
Crasedopora scalprata sp. nov.

Fig. 1. Holotype, NHM BZ 5024(2a), Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2). a, colony with growing edge at top; × 24. b, autozooids with small polymorphs developed along raised boundaries; × 60. c, early astogeny; × 28. d, zooids from early astogeny showing pustulose cryptocysts; × 73.

Fig. 2. Paratype, NHM BZ 5124(2), Maastrichtian, Peedee Formation, Rocky Point Member, Rocky Point Quarry, Pender County, North Carolina (locality NC3). a, group of zooids; × 69. b, autozooids and small polymorphs; × 115.
**Plate 61**

*Marginaria stipata* (Canu & Bassler, 1926)

Fig. 1. Lectotype, USNM 69955, Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TE1). a, colony lobe growing downwards; × 43. b, detail of autozooids and avicularia from same lobe; × 95. c, early astogenetic stages partly overgrown by a small oyster; × 47.

Fig. 2. LSUMG-I 8240, holotype of *Dionella racemata* Shaw, 1967, Campanian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2). a, early astogeny; × 42. b, ovicellate autozooids; × 67. c, growing edge with autozooids, small avicularia and an intramural bud (centre); × 57.
Plate 62

*MARGINARIA GUTTATA* sp. nov.

Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2).

Fig. 1. Holotype, NHM BZ 5024(3). a, early astogeny; × 31. b, ovicellate autozooids and adventitious avicularia; × 39. c, growing edge illustrating pore chambers; × 58.

Fig. 2. Paratype, NHM BZ 5174. a, group of zooids showing variably distributed avicularia, mostly interzooidal; × 40. b, autozooids and avicularia; × 70. c, ancestrula and periancestrular zooids; × 87.
Plate 63

*Marginaria wilsoni* sp. nov.
Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2).

Fig. 1. Holotype, BZ 4182(1). a, colony lobe; × 17. b, group of zooids with two borings; × 33. c, autozooids and avicularia; × 83. d, ovicellate autozooids and avicularia; × 49. e, ovicells; × 75. f, avicularium; × 205.
Plate 64
Marginaria sp.
Maastrichtian, Prairie Bluff Chalk, Braggs, Lowndes County, Alabama (locality AL3).
Fig. 1. NHM BZ 4818. a, worn colony encrusting a cyclostome; × 39. b, autozooids and avicularia; × 82.

Semiflistrella saratogaensis Shaw, 1967
Campanian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2).
Fig. 2. Holotype, LSUMG-I 8233. a, autozooids with distal avicularia; × 30. b, autozooids with broken ovicells; × 43. c, avicularium; × 165.
Fig. 3. Paratype, LSUMG-I 8258; autozooids, some ovicellate, and avicularia; × 43.
Plate 65

*Semiflustrella bifoliata* sp. nov.

Fig. 1. Holotype, USNM 526170, Maastrichtian, Peedee Formation, Neuse River, Lenoir County, North Carolina (locality NC8). a, bifoliate frond fragment; × 10. b, autozooids and avicularia; × 32. c, autozooids with and without (centre) distal avicularia; × 56. d, avicularium; × 135. e, kenozooid; × 120.

Fig. 2. Paratype, NHM BZ 5034, Maastrichtian, Prairie Bluff Chalk, Braggs, Lowndes County, Alabama (locality AL3). Colony fragment; × 11.
Plate 66
Semiflustrella bifoliata sp. nov.
Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1).
Fig. 1. Paratype, ANSM 80365, encrusting colony on a belemnite guard. a, autozooids and avicularia; × 27. b, abraded edge of colony viewed obliquely; × 34. c, autozooids with broken ovicells and a pair of avicularia (lower edge); × 41. d, close-up of avicularia and ingrowths (platforms and knobs) around the distal edge of the opesia of ovicellate autozooids; × 75.
Plate 67

*Semiflustrrella brittanica* (Brydone, 1906)
Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).
Fig. 1. NHM BZ 4804, a, early astogeny, partly obscured by sediment grains; × 27. b, autozooids and avicularia; × 50. c, zoooids at growing edge; × 55. d, avicularium; × 230.
Plate 68

*Dionella rindsbergi* sp. nov.
Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).
Fig. 1. Paratype, NHM BZ 4791(1). a, small colony; × 20. b, growing edge showing distolateral pore windows and large distal pore chamber from which the distal avicularium evidently originates; × 72.
Fig. 2. Holotype, NHM BZ 4791(2). a, early astogeny with ancestrula at centre; × 54. b, autozooids (two with intramural buds) and avicularia; × 50. c, incomplete zooid at growing edge showing pore chambers; × 80. d, avicularium; × 345.
Plate 69

*Kristerina broodi* sp. nov.
Cenomanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1).

Fig. 1. Holotype, ANSM 80357. a, general view showing autozooids and avicularia; × 19. b, autozooids, some with ovicells, and avicularia; × 45. c, distal end of autozooid with oval depressions at distolateral corners which may be oculisor muscle scars; × 110. d, ovicellate autozooid and several avicularia; × 56. e, ovicell; × 180. f, avicularium, × 123.
Plate 70

*Aplopusina incompta* sp. nov.

Fig. 1. Holotype, NHM BZ 5037, Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). a, early astogeny with ancestrula at lower left; × 34. b, ancestrula; × 125. c, zooids from zone of astogenetic repetition, one with proximal cryptocyst moderately developed; × 48.

Fig. 2. Paratype, NHM BZ 4833, Maastrichtian, Prairie Bluff Chalk, Emelle, Sumter County, Alabama (locality AL9); slightly oblique view of several zooids; × 43.

Fig. 3. Paratype, NHM BZ 4182(3), Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2); colony growing in a protected hollow; × 13.

Fig. 4. Paratype, USNM 526172, Maastrichtian, Peedee Formation, Neuse River, Lenoir County, North Carolina (locality NC4); note development of cryptocyst in zooid near bottom left; × 40.
Plate 71
*Euritina metapolymorpha* sp. nov.
Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).
Fig. 1. Holotype, NHM BZ 4797. a, zooids in well-defined longitudinal rows; × 27. b, rows of avicularia between autozooids; × 50. c, autozooids, avicularia and a kenozooid (bottom centre); × 55. d, faceted autozooidal cryptocysts; × 72. e, growing edge; × 55. f, avicularium; × 190.
Plate 72

*Euritina bocki* sp. nov.

Maasriachtian, PeeDee Formation, Neuse River, Lenoir County, North Carolina (locality NC4).

Fig. 1. USNM 526174. a, view of colony centred above pivot point of spiral overgrowth; × 34. b, oblique view of faceted autozooids; × 110. c, edge of overgrowth; × 59. d, two autozooids and a small polymorph; × 125.

Fig. 2. Holotype, USNM 526173. a, oblique view showing rows of avicularia between autozooids; × 46. f, autozooids and avicularia; × 74.
*Amphiblestrum denticulatum* Canu & Bassler, 1926

Fig. 1. Lectotype, USNM 69969, Maastrichtian, Ripley Formation, Coon Creek, Tennessee. a, group of zooids; \(\times 43\). b, bipolar growth caused by regeneration after damage; \(\times 36\). c, ovicellate autozooids and avicularium (bottom centre); \(\times 47\).

Fig. 2. Paralectotype, USNM 528399, details as for Fig. 1; abraded colony edge showing large pore chambers; \(\times 57\).

Fig. 3. RU 5600, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2); autozooids, some having ovicells (centre); \(\times 51\).

Fig. 4. RU 5627, details as for Fig. 2; avicularium with opesia obscured by sediment grains; \(\times 55\).
Plate 74
Amphiblestrum parvum sp. nov.

Fig. 1. Holotype, NHM BZ4823, Maastrichtian, Ripley Formation, Florence, Quitman County, Georgia (locality GA1). a, early astogeny with ancestrula at centre; × 71. b, group of autozooids; × 64. c, incomplete and damaged zooids at growing edge; × 115. d, worn zooid showing distal pore chamber (upper left); × 185.

Fig. 2. Paratype, USNM 528940, Maastrichtian, Peedee Formation, Neuse River, Lenoir County, North Carolina (locality NC4). a, zooids near colony edge; × 80. b, colony origin; × 67.
Plate 75
Setosinella meniscacantha sp. nov.
Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).
Fig. 1. Holotype, NHM BZ 4796(1a). a, early astogeny; × 29. b, detail showing overgrowth of some early zooids at centre; × 59. c, ovicellate and non-ovicellate autozooids; × 71. d, two avicularia; × 135. e, opesia, with centrally perforated closure plate and six orificial spine bases; × 330. f, peripheral subcolony growing from parent colony at top left; × 44.
Plate 76

*Setosinella meniscacantha* sp. nov.

Fig. 1. Holotype, NHM BZ 4796(1a), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). a, growing edge with intramural kenozoid occupying one of the incompletely-formed buds; × 43. b, growing edge with oviceellate autozooids and avicularia; × 56.

Fig. 2. Paratype, NHM BZ 4796(1b); small colony encrusting same shell as holotype; × 28.

Fig. 3. Paratype, NHM BZ4810(2), Details as Figure 1; colony with diagonal band of destroyed zooids; × 40.

Fig. 4. Paratype, NHM BZ 5042, Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5); edge of colony with pore windows visible along left margin; × 47.

Fig. 5. Paratype, NHM BZ 5182, Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2); autozooids, oviceells, avicularia and intramural bud (top centre); × 72.
Floradinella jeffersoni sp. nov.

Fig. 1. Holotype, NHM BZ 5043(1a), Maastrichtian, Prairie Bluff Chalk, Jefferson, Marengo County, Alabama (locality AL5). a, zooids in varying states of preservation; × 40. b, group of autozooids, mostly ovicellate, and a narrow kenozooid (just right of and beneath centre); × 72. c, well-preserved autozooid showing pustulose cryptocystal frontal shield; × 135. d, disrupted growth pattern in damaged area; × 45. e, zooids with closure plates bearing impressions of the opercular sclerites; × 125.

Fig. 2. Paratype, NHM BZ 4825, Maastrichtian, Ripley Formation, Florence, Quitman County, Georgia (locality GA1); damaged autozooids; × 90.
Plate 78

*Tyloporella cretacea* (Canu & Bassler, 1926)
Maastrichtian, Ripley Formation, Coon Creek Member, Coon Creek, McNairy County, Tennessee (locality TN1).

Fig. 1. Lectotype, USNM 69952. a, fragmentary colony encrusting interior of bivalve shell; × 30. b, oblique view of autozooids with ovicells or distal avicularia; × 69. c, opesia and proximal cryptocyst; × 145.

Fig. 2. Paralectotype, USNM 528401. a, oblique view of ovicellate autozooids; × 78. b, detail of ovicell with endolith traces; × 240.

Fig. 3. NHM BZ 5044; kenozoooids; × 40.
Plate 79

*Hagenowinella alabamaensis* sp. nov.
Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL7).
Fig. 1. Holotype, NHM BZ 4815. a, earliest preserved zooids; $\times$ 23. b, group of zooids; $\times$ 47. c, detail of autozooids showing pustulose cryptocystal frontal shields; $\times$ 88. d, opesia with occlusor lamina processes; $\times$ 225.

*Onychocella alveolata* sp. nov.
Maastrichtian, PeeDee Formation, Neuse River, Lenoir County, North Carolina (locality NC4).
Fig. 2. Holotype, USNM 526180. a, autozooids and an avicularium; note holes in cryptocysts; $\times$ 56. b, detail of an autozooid with small condyles visible in opesia; $\times$ 118.
Onychocella aleolata sp. nov.
Maastrichtian, Peedee Formation, Neuse River, Lenoir County, North Carolina (locality NC4).
Fig. 1. Paratype, USNM 526181. a, distal edge of branch; × 17. b, autozooids and an avicularium (left); × 52. c, detail of an autozooid showing frontal shield with cavity; × 116. d, avicularium; × 87.
Fig. 2. Holotype, USNM 526180; oblique view of autozooids with broken or partly-formed secondary cryptocysts; × 54.
Fig. 3. Paratype, USNM 526183; surface of old branch; × 52.
Onychocella alveolata sp. nov.
Maastrichtian, PeeDee Formation, Neuse River, Lenoir County, North Carolina (locality NC4).
Fig. 1. Paratype, USNM 526186; part of transverse thin section showing thick calcification of zooidal walls; × 35.
Fig. 2. Paratype, USNM 526188; transverse thin section of entire narrow branch; × 22.
Fig. 3. Paratype, USNM 526189; shallow tangential section. a, longitudinal files of autozooids showing subcircular opesia alternating with crescent-shaped proximal zooidal chambers; × 18. b, detail with avicularium (centre left); × 50.
Fig. 4. Paratype, USNM 526190; longitudinal section of autozooid showing small chamber (left of centre, with bubble) that may be an ovi-cell; × 55.
Fig. 5. Paratype, USNM 526191; two zooids and median lamina in longitudinal section; × 60.
Plate 82

*Cheethamia howei* Shaw, 1967

Fig. 1. Holotype, LSUMG-I 8237, Campanian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2); × 25.

Fig. 2. NHM BZ 4794(a), Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5). a, enlarged zooid (centre) surrounded by autozooids and avicularia; × 27. b, group of autozooids; × 56. c, autozooidal opesia with pair of oral spine bases at distal end; × 205. d, avicularium; × 90.

Fig. 3. NHM BZ 4794(b), details as for Figure 2; ancestrula and three daughter zooids; × 70.
Plate 83

*Cheethamia howei* Shaw, 1967

Fig. 1. BZ 4795(1), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6); growing edge; × 17.

Fig. 2. NHM BZ 4789, Maastrichtian, Prairie Bluff Chalk, Jefferson, Marengo County, Alabama (locality AL5). a, ovicellate autozooids and an avicularium; × 28. b, detail showing avicularium between two ovicellate autozooids; × 50. c, ovicell and opesia; × 105. d, kenozooid (centre) surrounded by autozooids; × 35.

Fig. 3. BZ 4790, details as for Figure 1; overgrowth origin; × 17.
Plate 84

Aechmella indefessa sp. nov.
Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1).
Fig. 1. Holotype, ANSM 80354A. a, part of large colony; × 20. b, ovicell; × 115.
Fig. 2. Paratype, ANSM 80354B. a, autozooids and avicularia; × 44. b, avicularium budded intramurally within an autozooid (right of centre); × 70. c, collision between colonies; × 32. d, avicularium with particularly long rostrum; × 105.
Reptolunulites zipfi sp. nov.
Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1).
Fig. 1. Holotype, NHM BZ 5057. a, damaged colony encrusting a small pebble; × 17. b, autozooids and an avicularium; × 37. c, autozooid opesia; × 115. d, autozooid with broken ovicell; × 90. e, avicularium; × 67.
Fig. 2. Paratype, ANSM 80355; autozooids and avicularia; × 40.
Plate 86

*Pseudothyracella elongata* (Shaw, 1967)

Fig. 1. Holotype, LSUMG-I 8236, Maastrichtian, Nacatoch Formation, Arkadelphia, Clark County, Arkansas (locality AR1). a, entire preserved branch; × 20. b, detail of autozooids; × 48.

Fig. 2. NHM BZ 5056, Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6); autozooid showing opesia and depressed proximal cryptocyst; × 105.

Fig. 3. USNM 526192, Maastrichtian, Peedee Formation, Neuse River, Lenoir County, North Carolina (locality NC4). a, autozooids; × 60. b, avicularium; × 180.

*Pavolunulites ozanensis* (Shaw, 1967)

Fig. 4. Campanian, Upper Ozan Formation, White Cliffs Station, Sevier County, Arkansas (locality AR3). Holotype, LSUMG-I 8241. a, specimen; × 32. b, two autozooids and avicularium; × 85. c, avicularium; × 125.
Plate 87

*Stictostega durhami* Shaw, 1967

Campanian, Upper Ozan Formation, White Cliffs Station, Sevier County, Arkansas (locality AR3).

Fig. 1. Holotype, LSUMG-I 8245. a, group of zooids; × 30. b, two autozooids; × 60. c, growing edge; × 32. d, ovicellate autozooids; × 65. e, autozooid opesia and small distal avicularium; × 190. f, kenozooid budded intramurally within a severely damaged autozooid; × 80.
Plate 88

*Stictostega turneri* sp. nov.

Fig. 1. Paratype, NHM BZ 5058, Maastrichtian, Navesink Formation, Poricy Creek, Monmouth County, New Jersey (locality NJ1). a, group of compressed zooids; × 38. b, autozooid opesia, with remnants of possible calcified operculum, and poorly-preserved distal avicularium, × 150. c, ovicell; × 150.

Fig. 2. Holotype, RU 5535, Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2). a, group of zooids, some ovicellate; × 30. b, autozooid with tiny distal avicularium (left) and another autozooid with an ovicell (right); × 70. c, ovicell; × 145.
**Plate 89**

*Stictostega oxicincta* sp. nov.
Maastrichtian, Ripley Formation, Coon Creek Member, Coon Creek, McNairy County, Tennessee, (locality TN1).

Fig. 1. Holotype, NHM BZ 5949; ovicellate zooids; × 45.
Fig. 2. Paratype, NHM BZ 5059. a, group of zooids from damaged colony; × 34. b, ovicellate zooids; × 73. c, opesia and ovice; × 215.
Fig. 3. Paratype, NHM BZ 5060. a, zooids in a concavity; × 67. b, opesia of non-ovicellate autozooid with distal avicularium; × 210.
Plate 90

*Stichomicropora baccata* (Canu & Bassler, 1926)

Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TN1).

Fig. 1. Lectotype, USNM 69954. a, group of zooids, two with ovicells; × 37. b, ovicell with intact roof of spines; ×120. c, ovicell with broken roof, exposing gymnocystal floor; × 115.

Fig. 2. Paralectotype, USNM 528403. a, non-ovicellate autozooids with some opesiules visible in the frontal shields; × 70. b, opesia with three oral spine bases; × 190.

Fig. 3. Paralectotype, USNM 528404. Ancestrula; × 220.
Stichomicropora baccata (Canu & Bassler, 1926)
Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TN1).
Fig. 1. Paralectotype, USNM 528402. a, autozooids and one avicularium; × 37. b, avicularium; × 140.

Stichomicropora cf. baccata (Canu & Bassler, 1926)
Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TN1).
Fig. 2. NHM BZ 5061. a, small colony; × 37. b, ancestrula and first budded zooid; × 105. c, detail of ancestrula showing spine bases and opesiules; × 235. d, later zooids; × 67.
Plate 92

*Stichomicropora ostrovskyi* sp. nov.

Fig. 1. Holotype, NHM BZ 4859(1), Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2). a, group of zooids, most with oicells; × 32. b, zooids close to the growing edge; note pore windows and loss of most of frontal shield; × 58. c, oicell; × 125.

Fig. 2. NHM BZ 5067(2), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6); typical preservation of zooids and two broken oicells; × 36.

Fig. 3. NHM BZ 4796(12), locality as for Figure 2; early astogeny with ancestrula at bottom left; × 38.

Fig. 4. LSUMG-I 8251, Campanian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2); specimen figured as *Micropora?* sp. by Shaw (1967, pl. 180, fig. 3); × 33.
Plate 93

Stichomicropora senaria sp. nov.
Maastrichtian, PeeDee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2).
Fig. 1. Paratype, NHM BZ 4189(3). a, zooids close to the growing edge; × 42. b, two zooids showing opesiae, opesiules and oral spine bases; × 105.
Fig. 2. Holotype, NHM BZ 4186. a, zooids and growing edge; × 37. b, remnants of ovicell lacking spinose root; × 115.
Fig. 3. Paratype, NHM BZ 4188(2); slightly corroded zooid; × 115.
Fig. 4. Paratype, NHM BZ 4187; early astogeny with ancestrula at lower right; × 50.
Plate 94

*Aeolopora catillus* sp. nov.

Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).

Fig. 1. Holotype, NHM BZ 5216(1a). a, early astogeny of colony in which some zooids have become detached from the substrate; associated bryozoans are *Balantiostoma octospinigera* sp. nov. (bottom left) and *B. nomas* (Shaw, 1967) (right); × 16. b, ancestrula; × 90. c, autozooids showing frontal shield, oral spine bases and an ovicell; × 63.

Fig. 2. Paratype, NHM BZ 5216(1b). Small, ancestrulate colony on same shell as holotype; × 40.
Plate 95

_Aeolopora catillus_ sp. nov.

Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

Fig. 1. Paratype, RU 5400. a, general view of colony; × 30. b, autozooid with four oral spines and three interzooidal avicularia with slightly spatulate rostra; × 110. c, detail of central portion of frontal shield of autozooid, with single septal bridge and one pelmatidium per costa; × 280.

Fig. 2. Paratype, RU 5400. a, autozooid at margin of small colony, with four oral spines, and a distal and a pair of distolateral communication pores; × 120. b, fragment of small colony with anomalously small autozooid with constricted orifice (upper centre); × 55.
Anornithopora spooneri (Butler & Cheetham, 1958)

Fig. 1. Holotype, LSUMG-I 1390, Campanian, Saratoga Chalk equivalent, Rayburns Dome, Bienville Parish, Louisiana (locality LA1). a, general view of portion of colony; × 45. b, group of autozooids with interzooidal avicularia and three ovicellate zooids; × 65. c, autozooid with orifical spines; × 240. d, ovicell flanked by two orifical spines of the maternal zooid; × 180.

Fig. 2. NHM BZ 4436, Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6); growing edge with interzooidal avicularium distal to autozooid with five orifical spines; marginal zooid to right of avicularium may be a maternal zooid; × 80.

Fig. 3. NHM BZ 4437, Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6); damaged autozooid with smaller autozooid reparatively budded within it; × 80.

Fig. 4. NHM BZ 5125(2), Maastrichtian, Prairie Bluff Chalk, Emelle, Sumter County, Alabama (locality AL9); ancestrula, first-budded autozooid and adjacent autozooids; × 77.
Plate 97
Anornithopora oligocostata sp. nov.
Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 and/or NJ2).
Fig. 1. Holotype, RU 5451. a, general view of colony; × 25. b, autozooid at colony margin with multiple pore chambers visible around distal margin; × 100.
Fig. 2. Paratype, RU 5625; typical autozooid; × 135.
Fig. 3. Paratype, RU 5613; secondary orifice of autozooid, with six robust orificial spines; × 250.
Fig. 4. Paratype, RU 5626. a, group of autozooids, maternal zooid (lower right) and interzooidal avicularium (left centre); × 55. b, two ovicells and a single interzooecial avicularium; × 90.
Fig. 5. Paratype, RU 5452. a, ancestrula (a) and early zooids, including kenozooid (k); × 45. b, ancestrula (a) and first generation autozooid (f); × 120.
Anornithopora? delawarensis sp. nov.
Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1).
Fig. 1. Holotype, ANSM 80361. a, general view of colony; × 50. b, autozooid at colony margin with large interzooidal pore visible in left distal margin; × 135. c, fertile autozooid with distal oviceell; × 135. d, marginal area of colony with clustered interzooidal avicularia, intrazooidal budding of an avicularium within a partially formed marginal autozooid (upper right), and damaged autozooid with calcified plate filling opesia and base of distal left costa (bottom right of figure); × 100. e, damaged autozooid with reparative budding consisting of two avicularia; × 90.
Plate 99
Anornithopora responsa sp. nov.
Campanian, Demopolis Chalk, Macon, Noxubee County, Mississippi (locality MS2).
Fig. 1. Holotype, VCSM 13962. a, central portion of colony; × 17. b, interzooidal avicularium, autozooid with four orificial spines, and ovicell; c. × 110. c, two large kenozooids surrounded by avicularia and autozooids; × 72. d, maternal zooid with four visible orificial spines and associated ovicell with median crest; × 170. e, primary zone of astogenetic change, centred on ancestrula (just left of centre) and first-budded autozooid (top centre); × 75.
**Plate 100**

_Castanopora lambi_ Turner, 1975

Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

Fig. 1. Holotype, RU 5405. _a_, general view of colony; × 20. _b_, group of autozooids including three ovicells, × 40. _c_, autozooid with calcified operculum; × 150. _d_, intramurally budded autozooid with calcified operculum; × 225. _e_, ovicellate zooid in which pelmatidia and two orificial spines are clear, with abundantly perforated ovicell; × 120.
Plate 101

Castanopora dorothyae sp. nov.

Fig. 1. Holotype, NHM BZ 5187(1), Maastrichtian, Prairie Bluff Chalk, Jefferson, Marengo County, Alabama (locality AL5). a, group of autozooids, most with ovicells; × 25. b, ovicellate autozooids; × 45. c, detail of ovicell, frontal shields and orifices; × 83. d, damaged growing edge showing large distal pore chambers; × 35.

Fig. 2. Paratype, NHM BZ 5191, Maastrichtian, Prairie Bluff Chalk, Braggs, Lowndes County, Alabama (locality AL3). a, group of autozooids about half of which have ovicells; × 33. b, damaged zooids with intercostal spaces conspicuous; × 33.
Plate 102
*Diacanthopora langi* Shaw, 1967
Campanian, Upper Ozan Formation, White Cliffs Station, Sevier County, Arkansas (locality AR3).
Fig. 1. Holotype, LSUMG-I 8244. a, general view of colony surface; × 20. b, group of autozooids and ovicellate zooids proximal to single row of incompletely zooids along colony margin; × 40. c, ovicellate zooid with eccentrically placed ovicell; × 160. d, autozooid with paired adventitious avicularia adjacent to orifice; × 130.
Graptoporella? angulata sp. nov.
Maastrichtian, Peedee Formation, Neuse River, North Carolina (locality NC4).
Fig. 1. Holotype, USNM 528405. a, general view of colony surface; × 20. b, ovicellate zooid; × 140. c, distal end of ovicellate zooid showing bifurcated costae with the distally directed fused portions joining the undersurface of the apertural bar, and extensions of secondary skeleton onto ovicell; × 260. d, single ringed pelma at inner ends of medially joined costae; × 430.
Plate 104
Monoceratopora mitrifera sp. nov.
Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 and/or NJ2).
Fig. 1. Holotype, NHM BZ 5195, Poricy Creek (locality NJ1). a, general view; × 21. b, autozooids and avicularia close to the growing edge; × 47. c, ovicell (lower left) and an autozooid with distal avicularium (upper right); × 105. d, costae with incipient? or vestigial? bridges; × 330. e, damaged early astogenetic stages; × 33.
Fig. 2. Paratype, RU 5604. Autozooid with distal acuminate interzooidal avicularium; × 75.
Plate 105

*Morphasmopora variostoma* sp. nov.
Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

Fig. 1. Holotype, RU5470. a, general view of colony; × 20. b, group of autozooids with continuous thick ribbon of kenozooidal skeleton overlapping their margins; × 50. c, two ovicellate zooids (centre and left) and non-fertile autozooid (right), with thick ribbon of kenozooidal skeleton along zooidal margins and extending onto ovicells; × 70. d, maze-like area of kenozooids with thick skeleton (upper right); × 70. e, bifurcated costae with the distally directed fused portions joining the undersurface of the apertural bar, which has adventitious avicularia at either end; × 165. f, largely immersed ovicell partially covered by secondary calcification; × 165.
Nannopora torquata (Canu & Bassler, 1926)
Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TN1).
Fig. 1. NHM BZ 5021(2). a, damaged autozooids and avicularia; × 44. b, ovoidal autozooids and avicularia; × 75.
Fig. 2. Holotype, USNM 69962. a, general view of colony; × 60. b, group of autozooids and interzooidal avicularia; × 115. c, autozooid with remnant of frontal shield preserved; × 195. d, autozooids with proximal gymnecyst and interspersed interzooidal avicularia; × 150.
Plate 107
*Pelmatopora irregularis* (Canu & Bassler, 1926)
Maastrichtian, Ripley Formation, Coon Creek Member, Coon Creek, McNairy County, Tennessee (locality TN1).

Fig. 1. Lectotype, USNM 69957. a, general view of colony; × 20. b, group of autozooids, ovicellate zooids and small interzooidal avicularia; × 70. c, autozooids from which frontal shield has been broken, with pore chambers visible; × 70.

Fig. 2. Paralectotype, USNM 528407. a, frontal shield of autozooids with proximal and distal pelmata visible on costae, and several interzooidal avicularia; × 230. b, maternal zooid and associated pustulose-textured ovicell, with transverse ‘figure-8’ kenozooid proximal to zooid and curved pedunculate interzooidal avicularium distal to ovicell; × 160.
Plate 108

Pelmatopora spatulata sp. nov.
Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).
Fig. 1. Holotype, NHM BZ 4832(a). a, colony; × 20. b, fertile colony with abundant interzooidal avicularia; × 40. c, maternal zooid with associated pustulose ovicell and adjacent interzooidal avicularia; × 115. d, autozooid with four orificial spines and adjacent interzooidal avicularia; × 105. e, frontal shield of ovicellate zooid with conspicuous single pelma on each costa at point of intercostal bridge; × 160.
Fig. 2. Paratype, NHM BZ 4832(b). Ancestrula (bottom centre) and earliest-formed autozooids; × 70.
Plate 109

*Phractoporella daedalus* Turner, 1979

Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

Fig. 1. Holotype, RU 5440. a, general view of colony; × 20. b, growing edge of colony, with autozooidal pore chambers visible (top edge), and complete ovicell and orificial avicularia on autozooid one generation from edge (bottom centre); × 70. c, autozooids and, by left edge, ovicellate zooid; × 75.

Fig. 2. RU 5632. a, group of autozooids, showing extensive secondary skeletal development; × 55. b, autozooid with extensive secondary skeleton, including median strip extending proximally from apertural bar; × 95. c, secondary skeleton encroaching on frontal shield of autozooid from perimeter and along median strip, with fenestra-like indentations near both ends of apertural bar; × 240.
Pliophloea shmooformis sp. nov.
Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).
Fig. 1. Holotype, RU 5415. a, general view of colony; × 20. b, group of autozooids with locally varying concentration of interzooidal avicularia; × 80. c, autozooid at edge of colony, with slightly inflected D-shaped orifice; × 120. d, interzooidal avicularium, showing ‘shmoo-shaped’ opesia; × 270. e, proximal portion of autozooidal frontal shield, with single pelmatidium near proximal end of each costa; × 270. f, ancestrula (lower right) and short primary zone of astogenetic change; × 65.
Plate 111

*Sandalopora luxuria* sp. nov.
Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

Fig. 1. Holotype, RU 5445. a, general view of colony; × 28. b, group of autozooids and ovicellate zooid (top right); × 60. c, autozooid, interzooidal spatulate avicularium (bottom right) and smaller kenozooids or interzooidal avicularia; × 140. d, costae of autozooidal frontal shield, with single pelmata near lateral end of each costa; × 300. e, ovicellate zooid; × 140. f, secondary orifice of autozooid, with part of primary orifice visible within, and proximal apertural bar with low median boss; × 220. g, numerous kenozooids or interzooidal avicularia of variable size; × 130.
Stichocados aenigmata sp. nov.
Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2). Fig. 1. Holotype, RU 5455. a, general view of colony; × 30. b, group of autozooids; × 55. c, oblique view of distal end of autozooid, showing robust apertural bar and curved spines that form distal edge of secondary orifice; × 210. d, autozooid with small distal (interzooidal?) avicularium and acuminate rostrum (upper right) of larger, ill-defined adventitious avicularium; × 130.
Tricephalopora arkansasensis Shaw, 1967

Fig. 1. Maastrichtian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2). Holotype, LSUMG-I 8243. a, general view of colony; × 15. b, group of autozooids; × 56.

Tricephalopora clara sp. nov.

Maastrichtian, Pee Dee Formation, Neuse River, Lenoir County, North Carolina (locality NC4).

Fig. 2. Holotype, USNM 528408. a, general view of colony; × 20. b, group of autozooids, most of which have associated ovicells; autozooidal orifice in lower right has four orificial spines; × 50.

Fig. 3. Paratype, USNM 528409. a, basal portion of colony with thicker secondary calcification than in holotype; × 60. b, detail of distal end of autozooid with margins of adventitious avicularia immersed in secondary skeleton; × 150.

Plate 113

Tricephalopora arkansasensis Shaw, 1967

Fig. 1. Maastrichtian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2). Holotype, LSUMG-I 8243. a, general view of colony; × 15. b, group of autozooids; × 56.

Tricephalopora clara sp. nov.

Maastrichtian, Pee Dee Formation, Neuse River, Lenoir County, North Carolina (locality NC4).

Fig. 2. Holotype, USNM 528408. a, general view of colony; × 20. b, group of autozooids, most of which have associated ovicells; autozooidal orifice in lower right has four orificial spines; × 50.

Fig. 3. Paratype, USNM 528409. a, basal portion of colony with thicker secondary calcification than in holotype; × 60. b, detail of distal end of autozooid with margins of adventitious avicularia immersed in secondary skeleton; × 150.
Tricephalopora clara sp. nov.
Maastrichtian, Peedee Formation, Neuse River, Lenoir County, North Carolina (locality NC4).
Fig. 1. Holotype, USNM 528408. a, ovicellate autozooids and elongate kenozooids in zone of astogenetic repetition; × 75. b, autozooid proximal to the zone in which all zooids have ovicells; × 95. c, primary orifice of ovicellate zooid visible at base of peristome, with partial interior of hyperstomial ovicell visible at top of figure; × 200. d, ovicell covered laterally and distally by secondary skeleton; × 160. e, autozooid in primary astogenetic zone of change, with three orificial spines extending from primary orifice through peristome; × 140.
Fig. 2. Paratype, USNM 528410. Juvenile colony with ancestrula (bottom, just right of centre) broken or corroded away; × 60.
Plate 115

*Tricephalopora lamellaria* (Canu & Bassler, 1926)

Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TN1).

Fig. 1. Lectotype, USNM 69968. a, general view of colony; × 20. b, group of autozooids and maternal zooids, with thick secondary calcification developed in narrow kenozooids between autozooids; × 35. c, autozooid (left) and ovicellate zooid (centre), both with single adventitious avicularium; × 85. d, secondary orifice of autozooid flanked by paired adventitious avicularia, with apron of secondary calcification proximal to orifice and avicularia, covering distalmost costae of frontal shield; × 155.

Fig. 2. Paralectotype, USNM 528411. Secondary orifice of ovicellate zooid flanked by paired adventitious avicularia, and ovicell with thin secondary calcification; × 120.

Fig. 3. Paralectotype, USNM 528412. View of undersurface of zooidal frontal shields and proximal partially submerged ovicells; × 50.
Plate 116

*Tricephalopora larwoodi* Shaw, 1967

Maastrichtian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2).

Fig. 1. Holotype, LSUMG-I 8242. a, general view of colony; × 20. b, adventitious avicularia-bearing autozooids; × 80. c, autozooid in primary zone of astogenetic change, bounded laterally by kenozooids; × 120. d, ovicellate zooids; × 80. e, adventitious avicularium with complete crossbar; × 300. f, partially developed autozooid at colony margin, with continuous row of pore chambers around distal perimeter; × 110.
Plate 117

Tricephalopora larwoodi Shaw, 1967
Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).
Fig. 1. NHM BZ 4810(4). a. complete small colony; × 13. b, group of autozooids partially separated by elongate kenozooids; × 40. c, ontogenetically young zooids at edge of colony; × 40. d, autozooid, possibly ovicellate (note chamber distal to well-defined primary orifice) at edge of colony; × 85.
Fig. 2. NHM BZ 5035(4). Immature colony consisting of ancestrula (bottom centre) with six orificial spines, plus initial four autozooids in various stages of development; × 80.
Fig. 3. NHM BZ 5111(2). Immature colony with ancestrula (lower left) plus initial six autozooids, some of which have completely developed adventitious avicularia; ca × 45.
Plate 118

*Tricephalopora aff. obducta* Lang, 1916
Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).
Fig. 1. RU 5430. a, general view of colony, with lower right portion extensively draped by secondary skeleton; × 20. b, autozooids at growing edge of colony; × 95. c, small window in extensive secondary skeleton on lower right autozooid of Figure 1b, exposing centre of frontal shield; × 330. d, region proximal to growing edge of colony, with secondary skeleton covering frontal shield window of autozooid on left; × 105.

*Tricephalopora poricyensis* Turner, 1979
Maastrichtian, Navesink Formation, Poricy Creek, Monmouth County, New Jersey (locality NJ1).
Fig. 2. Holotype, RU 5435. Four, incompletely preserved zooids; × 110.
Plate 119
*Tricephalopora vibraculata* Turner, 1979
Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

Fig. 1. Holotype, RU 5425. a, general view of portion of colony; × 28. b, group of ovicellate zooids and cylindrical kenozooids; × 57. c, secondary skeleton with incipient axial tongue encircling window onto frontal shield of zooid; × 260. d, paired avicularia projecting into secondary aperture of ovicellate zooid, resulting in figure-eight shape of orifice; × 75.

Fig. 2. RU 5620. a, secondary calcification surrounding frontal shield of zooid, including long tongue extending proximally along zooidal midline from apertural bar; × 105. b, secondary calcification completely covering frontal shield of zooid in centre of figure; × 60.
Plate 120

Tricephalopora vibraculata Turner, 1979
Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6).
Fig. 1. NHM BZ 5230. a, general view of small colony; × 19. b, autozooids and cylindrical kenozooids along growing edge of colony; × 40. c, cylindrical kenozooid (bottom centre) and autozooids with incomplete chambers of adventitious avicularia at growing edge of colony; × 70. d, autozooid with two orificial spines (lower left), orifice (bottom right) of first-budded autozooid in colony with six orificial spines and incomplete autozooid (top) at colony margin with multiple pore chambers; × 95. e, ancestrula with six orificial spines; × 100.
Turnerella peripheria sp. nov.
Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).
Fig. 1. Holotype, RU 5633. a, general view of colony; × 26. b, ovicellate zooid; × 85.
Fig. 2. Paratype, RU 5465. a, group of autozooids; × 55. b, newly completed autozooid at colony margin; × 75.
Fig. 3. Paratype, RU 5607. a, oblique view of autozooids showing curvature of costae forming distal margin of orifice; × 65. b, autozooidal orifice bounded proximally by fused costae of apertural bar and distally of shorter costae linked along their outermost margins; × 210.
Ubaghsia tragica sp. nov.
Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

Fig. 1. Holotype, RU 5460. a, general view of colony; × 24. b, group of autozooids; × 65. c, autozooid (right) and two ocellate zooids (left and bottom centre); × 70. d, well preserved surface of frontal shield with extensive secondary calcification generating prominent sleeves around pores derived from intercostal spaces; × 130. e, recumbent, tubular adventitious avicularia flanking lateral margins of frontal shield and terminating in essentially circular orifices flanking the autozooidal orifice; × 230. f, severely corroded surface typical of the colony, with plane of fusion between costae deeply etched into basal part of the central flat process of the apertural bar; × 330.
Plate 123

_Trichinopolya cassida_ sp. nov.
Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5).

Fig. 1. Holotype, NHM BZ 4835. a, general view of colony; × 20. b, autozooids, ovicellate zooids and a vicarious avicularium (left); × 40. c, autozooid with four apparent adventitious avicularia around orifice; × 120. d, orifice of ovicellate zooid; × 260. e, zooids, including vicarious avicularium (centre), adjacent to growing edge of colony; × 70. f, more equidimensional vicarious avicularium (top centre) than that depicted in Figure 1e; × 100.
Frurionella parvipora Canu & Bassler, 1926
Maastrichtian, Coon Creek Formation, Coon Creek, McNairy County, Tennessee (locality TN1).
Fig. 1. Paralectotype, USNM 528415. a, bifurcating branch (centre) mounted on a card with other syn-
types; × 8. b, autozooids and avicularia; × 42.
Fig. 2. Lectotype, USNM 69959. a, edge of branch; × 21. b, autozooids with (top) and without (lower left) suboral avicularia; × 74. c, elongate secondary orifices of ovicellate autozooids; × 65. d, orifice and subo-
ral avicularium; × 145.
Fig. 3. Paralectotype, USNM 528413; interzooidal avicularium; × 120.
Fig. 4. USNM 69958, holotype of *F. grandipora* Canu & Bassler, 1926; × 44.
Plate 125

*Balantiostoma danei* (Shaw, 1967)

Figs 1. NHM BZ 5094, Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). a, colony edge; × 21. b, autozooids and ovicells; × 60.

Fig. 2. Holotype, LSUMG-I 8246, Campanian, Saratoga Chalk, Saratoga, Howard County, Arkansas (locality AR2). a, ovicellate autozooids, poorly-preserved and partly obscured by sediment grains; × 58. b, orifice and ovicell; × 122.

Fig. 3. NHM BZ 4439, Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). a, ovicellate autozooids; × 64. b, orifices and ovicells of two autozooids, that in the upper left having a small adventitious avicularium (centre); × 95.
Plate 126

*Balantiostoma erymos* (Shaw, 1967)
Campanian, Ozan Formation, White Cliffs Station, Sevier County, Arkansas (locality AR3).

Fig. 1. Holotype, LSUMG-I 8248. a, general view; × 14. b, autozooids with salient boundary walls; × 62. c, autozooids and scattered avicularia; × 55. d, avicularium (lower left) and autozooidal orifice; × 167. e, ovicell and orifice; × 190.

Fig. 2. LSUMG-I 8272; small colony; × 22.
Plate 127

*Balantiostoma nonas* (Shaw, 1967)

Fig. 1. Holotype, LSUMG-I 8247, Campanian Ozan Formation, McCurtain County, Oklahoma (locality OK1). a, group of zooids; × 41. b, ovicellate autozooid and several small adventitious avicularia; × 92.

Fig. 2. NHM BZ 5095a, Campanian, Demopolis Chalk, Macon, Noxubee County, Mississippi (locality MS1). a, small transversely elongated colony; × 14. b, zooids at growing edge; ×39.

Fig. 3. NHM BZ 5095b, details as for Figure 2. a, ovicellate autozooids, adventitious avicularia and a larger interzooidal avicularium (lower edge, right of centre); × 70. b, ovicell, orifice and paired avicularia with cross-bars; × 170.
Plate 128

Balantiostoma nomas (Shaw, 1967)

Fig. 1. NHM BZ 4437(2), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). Primary orifice and oral spine bases in zoolid at growing edge; × 120.

Fig. 2. NHM BZ 4810(4), details as Figure 1. Growing edge; primary orifice and oral spine bases of one zoolid (left), and large distal pore chamber in another incompletely-formed zooid (lower right); × 88.

Fig. 3. NHM BZ 4438, details as Figure 1. Autozooids and adventitious avicularia; × 88.

Fig. 4. VCSM 13961a, Campanian, Demopolis Chalk, Macon, Noxubee County, Mississippi (locality MS2). a, oviocellate zooids and adventitious avicularia; × 75. b, area with abundant avicularia; × 37. c, collision zone between two lobes with several interzoooidal avicularia; × 43.
Plate 129

*Balantiostoma nomas* (Shaw, 1967)

Campanian, Mount Laurel Formation, Chesapeake & Delaware Canal, New Castle County, Delaware (locality DE1).

Fig. 1, ANSM 80363. a, colony margin; × 24. b, ovicellate autozooids and an interzooidal avicularium (right); × 36. c, growing edge showing large distal pore chambers and oral spines; × 80.

Fig. 2, ANSM 80359. a, colony surface showing ovicellate autozooids, small adventitious avicularia and a few larger, interzooidal avicularia (top left, bottom left, lower centre); × 40. b, mucronate autozooids with broken ovicells; × 78. c, interzooidal avicularium preserving pivotal bar; × 100.
Plate 130

*Balantiostoma octospinigera* sp. nov.

Fig. 1. Paratype, NHM BZ 4803(3), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). a, small colony; × 35. b, ancestrula and two distolateral buds; × 110.

Fig. 2. Holotype, NHM BZ 4810(5), details as for Figure 1. Zooids at growing edge showing primary orifice, oral spine bases and an avicularium (right); × 112.

Fig. 3. Paratype, NHM BZ 4810(6), details as for Figure 1. Edge of colony showing new buds; × 52.

Fig. 4. Paratype, NHM BZ 4436(1), Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5). a, avicularium (left), complete autozooids with 7 or 8 oral spine bases and a new bud at the growing edge; × 117. b, ovicellate autozooids; × 95.
Plate 131

*Balantiostoma octospinigera* sp. nov.

Maastrichtian, Ripley Formation (Fig. 1) or Prairie Bluff Chalk (Figs 2-3), Jefferson, Marengo County, Alabama (locality AL5).

Fig. 1. Paratype, NHM BZ 5096. a, zooids near growing edge; × 40. b, primary orifice and oral spine bases; × 220.

Fig. 2. Paratype, NHM BZ 5097. a, area of colony with numerous avicularia; × 42. b, avicularium (left) and mucronate autozooid with incomplete ovicell; × 120. c, oovicell; × 162.

Fig. 3. Paratype, NHM BZ 5098. Poorly-preserved ancestrula, possibly accommodating an intramural bud; × 143.
Balantiostoma powersae sp. nov.

Fig. 1. Paratype, NHM BZ 5100, Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5). a, group of ovicellate autozooids and avicularia; × 40. b, adventitious avicularia on either side of the orifice of a mucronate autozooid with an ovicel having a small pore; × 120. c, autozooids at the growing edge with oral spine bases visible at the distolateral corners of the orifice on the right; × 90. d, interzooidal avicularium; × 75.

Fig. 2. Holotype, NHM BZ 5099(1a), Maastrichtian, Prairie Bluff Chalk, Livingston, Sumter County, Alabama (locality AL6). a, autozooids, small adventitious avicularia and a large interzooidal avicularium (centre); × 44. b, two ovicellate autozooids with paired adventitious avicularia constricting the orifices; × 85.
Plate 133

*Balantiostoma* sp.

Maastrichtian, Navesink Formation, Monmouth County, New Jersey (locality NJ1 or NJ2).

Fig. 1. RU 5545. a, autozooids and avicularia; × 25. b, autozooids near colony edge with large areolae; × 46.
Hoplocheilina hagemani sp. nov.
Maastrichtian, Peedee Formation, Neuse River, Lenoir County, North Carolina (locality NC4).
Fig. 1. Holotype, USNM 526195. a, entire fragmentary colony; × 17. b, zooids at the growing edge; × 42.
c, autozooids, two avicularia and conspicuous areolae; × 102. d, autozooid with broken ovicell showing
oral spine bases; × 172. e, mucronate autozooids with ovicells; × 77. f, ovicell and secondary orifice; × 180.
Plate 135

Peedeesella guhai sp. nov.
Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2).

Fig. 1. Holotype, BZ 5104(1). a, general view; × 25. b, group of zooids in area of row bifurcations, each intercalated row beginning with a monoaviculariate autozooid contrasting with the biaviculariate autozooids developed elsewhere; × 70. c, growing edge showing new buds and pore chambers; × 48. d, zooids at growing edge showing oral spine bases and development of the frontal shield in a biaviculariate (left) and monoaviculariate (upper right) autozooid; × 93. e, early astogeny with monoaviculariate autozooids predominating; × 51. f, ancestrula; × 245.
Plate 136

Peedeesella guhai sp. nov.

Fig. 1. Paratype, NHM BZ 4183(2), Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2). Group of autozooids, mostly ovicellate, some having single and others twin avicularia; × 55.

Fig. 2. Paratype, NHM BZ 4824, Maastrichtian, Ripley Formation, Florence, Quitman County, Georgia (locality GA1). Two ovicellate autozooids with frontal shields formed of single avicularia; note pore at proximal end of frontal shield of autozooid in top right; × 150.

Fig. 3. Paratype, NHM BZ 4435(a), Maastrichtian, Ripley Formation, Jefferson, Marengo County, Alabama (locality AL5). a, ovicellate, biaviculariate autozooid with two avicularia forming frontal shield; × 155. b, ovicellate, monoaviculariate autozooid with one avicularium forming frontal shield; × 165.

Fig. 4. Paratype, NHM BZ 5101, Maastrichtian, Coon Creek Formation, Coon Creek, McNairy County, Tennessee (locality TN1). a, colony with basal wall stripped showing zooids from the underside; × 60. b, detail showing spiramen-like structure between the two avicularia forming the frontal shield, orifice and position of ovicell; × 115.
Boreasina novaehanoverensis sp. nov.
Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2).
Fig. 1. Holotype, NHM BZ 5016(3). a, general view of colony encrusting oyster shell with two boreholes (Entobia); × 23. b, avicularia; × 250. c, autozooids, avicularia and two polymorphic zooids with large orifices (just left and right of centre); × 63. d, autozooid orifice and ovicell; × 235. e, autozooids and sparse avicularia; × 80. f, autozooids and abundant avicularia; × 110.
Boreasina sp.

Fig. 1. USNM 526198, Maastrichtian, Pee Dee Formation, Neuse River, Lenoir County, North Carolina (locality NC4). a, group of zooids; × 62. b, autozooid orifice and ovicell; × 185. c, avicularium; × 290.

Kronothoa quitmanensis sp. nov.

Fig. 2. Holotype, NHM BZ 5105, Maastrichtian, Ripley Formation, Florence, Quitman County, Georgia (locality GA1). a, irregularly-arranged, densely-packed uniserial zooids; × 43. b, autozooid surrounded by avicularia; × 158. c, autozooid showing primary orifice and slightly broken ovicell; × 228.
Plate 139

*Dysnoetopora celleporoides* Canu & Bassler, 1926

Fig. 1. Lectotype, USNM 69960, Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TN1). a, branch fragment mounted on card; × 3.9. b, autozooid; × 230. c, avicularium; × 80.

Fig. 2. NHM BZ 5073, colony base, Maastrichtian, Peedee Formation, Ideal Quarry, New Hanover County, North Carolina (locality NC2). a, incipient erect growth; × 24. b, transitional region with frontal buds beginning to develop above older zooids at lower left; × 38. c, fan-like growth at outer edge of colony base; × 25. d, basal zooids with extensive gymnocysts; × 120.
Plate 140

*Dysnoetopora celleporoides* Canu & Bassler, 1926

Maastrichtian, Ripley Formation, Coon Creek, McNairy County, Tennessee (locality TN1).

Fig. 1, NHM BZ 5076. a, typically chaotic arrangement of zooids on branch surface; × 34. b, autozooid showing orifice, condyles, ascopore and partly overgrown frontal shield; × 200.

Fig. 2, NHM BZ 5074. a, autozooids and avicularium (left); × 105. b, two autozooids, that on the right having the frontal shield not yet overgrown; × 170.

Fig. 3, NHM BZ 5075, longitudinally fractured branch. a, endozone with zooidal tubes arranged parallel to growth direction, flanked by exozone with tubes at right angles; × 25. b, orificial region of endozoneal autozooid viewed from within to show the hollow, costate apertural bar between orifice and ascopore; × 245.
Plate 141

*Dysnoetopora celleporoides* Canu & Bassler, 1926
Maastrichtian, Ripley Formation, Florence, Quitman County, Georgia (locality GA1).

Fig. 1. NHM BZ 5210, transverse thin section. a, exozone; × 16. b, detail of exozone; × 38. c, damaged endozone; × 46.

Fig. 2. NHM BZ 5211, tangential thin section. a, zooids varying in size and maturity; × 26. b, detail showing some autozooids sectioned in plane of orifice and ascopore; × 55. c, autozooids and avicularium (lower right); × 63.