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CLADISTIC ANALYSIS OF THE PALEOZOIC BRYOZOAN FAMILIES MONTICULIPORIDAE AND MESOTRYPIDAE

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ABSTRACT—A set of 127 binary and multistate characters, weighted by the number of derived character states, degree of covariation, and level of homoplasy, was used in a cladistic analysis of type species representing 12 genera previously assigned to families Monticuliporidae and Mesotrypidae. The most parsimonious tree consisted of a 10-genus monophyletic crown group with the remaining two genera forming a basal paraphyletic stem group. The composition of the monticuliporid crown group is broadly similar to two earlier classifications while stem group membership matches the family Mesotrypidae. Phenetic groupings, based on overall morphological similarity, have memberships that are similar to those of clades but provide no means of determining the polarity of evolutionary relationships either within or between them. Finally, only the observed stratigraphic ranges of the type species of genera provide a statistically significant match with cladistic branching sequence, perhaps because current composite generic ranges reflect the mixing of species belonging to different genera. Based on cladogram topology, we propose the placement of all 12 genera into a single family Monticuliporidae.

INTRODUCTION

THE MONTICULIPORIDAE and Mesotrypidae are currently recognized families of Ordovician and Silurian stenolaemate trepostome bryozoans (Class Stenolaemata, Order Trepostomata). The twelve genera currently assigned to these families (Table 1) contain species that typically form slender or massive cylindrically-branching colonies (stem diameters 4–8 mm) having maximum sizes ranging between a few millimeters to several centimeters. The validity of current family definitions has been questioned (Anstey and Perry, 1970; Boardman, 1983), but family-level revisions have been few (Anstey and Perry, 1970; Anstey, 1990; Anstey and Pachut, 1995). Although morphological studies (e.g., Boardman and Utgaard, 1966; Bork and Perry, 1967, 1968; Pachut and Anstey, 2002) have provided a foundation for a taxonomic revision, re-descriptions of some constituent genera have resulted in cases of synonymy (Boardman and Utgaard, 1966; Astrova, 1978; Boardman, 1983; Brown and Daly, 1985; Hickey, 1988), underscoring the need for a reanalysis.

Historically, conventional taxonomic classifications of bryozoans have been phenetic (e.g., Anstey and Perry, 1973; Pachut and Horowitz, 1987). Measurements or codings of morphologic characteristics were analyzed, typically using cluster analysis, resulting in groupings of taxa based on overall morphological similarity. In contrast, cladistic techniques attempt to determine patterns of relatedness using only shared-derived, or synapomorphic (i.e., advanced), characters rather than using all attributes, some of which might be shared-primitive, or symplesiomorphic, features. Morphological attributes, or continuous measurements of them, are coded as discrete character states that are compared with those of an outgroup taxon (presumed to be related to ingroup taxa) to evaluate genealogical relationships. Cladistic characters can be reweighted to reduce the effects of homoplasy, or convergent evolution, using objectively determined measures of character independence. Comparisons between cladistic branching patterns and phenetic cluster membership can add support to genealogical groupings and/or document patterns of convergent evolution.

This study evaluates cladistic relationships among 12 Ordovician bryozoan genera previously assigned to the families Monticuliporidae or Mesotrypidae (Table 1, Figs. 1–6), using a set of 127 morphologic characters. The goals are to compare cladistic results to existing taxonomic assignments, to determine whether support exists for two distinct monophyletic families, and to compare cladistic branching pattern to the stratigraphic distributions of genera. Results indicate the presence of a single monophyletic family Monticuliporidae, with two genera forming a basal paraphyletic grouping and 10 genera comprising a derived monophyletic clade. A statistically significant match occurs between the stratigraphic distributions of the type species of genera and cladistic branching pattern.

HISTORICAL REVIEW

Establishment of the families.—Nicholson (1881) created the family Monticuliporidae that included the genera *Monticulipora*, *Fistulipora*, *Constellaria*, and *Dekayia*. Three of these genera have subsequently been reassigned either to another trepostome family (*Dekayia* to the Heterotrypidae) or to families of cystoporate bryozoans (*Fistulipora* to the Fistuliporidae, *Constellaria* to the Constellariidae). *Monticulipora* was divided into five sub-genera: *Heterotrypa*, *Diplotrypa*, *Monotrypa*, *Prasopora*, and *Peronopora* (Nicholson, 1881). *Heterotrypa* and *Monotrypa* have been reassigned to the Heterotrypidae and Amplexoporidae, respectively, *Diplotrypa* was reassigned to the Mesotrypidae (Astrova, 1978; Table 1), and *Prasopora* and *Peronopora* are now considered genera of monticuliporids (Table 1). In his informal listing of generic assignments, Bock (2010) included *Acantholaminatus* (Marintsch, 1998), *Gortanipora* (Vinassa de Regny, 1921), and *Aspidopora* (Ulrich, 1882) in the Monticuliporidae. The most recent review of the Monticuliporidae defined the family using a single cystiphragm character (i.e., it is monothetically defined; Boardman, 1983).

Astrova (1965) established the family Mesotrypidae to include the genera *Mesotrypa* and *Diazipora* that were of uncertain taxonomic status but appeared to be allied with genera assigned to families Monticuliporidae and Halloporidae. The possession of thin walls and a lack of blister-like cystiphragms separated

TABLE *1*—History of generic assignments to the Monticuliporidae and Mesotrypidae. Dashes indicate genera not classified by an author. Astrova considered *Aspidopora* and *Prasoporina* to be synonyms of *Prasopora*, and *Homotrypella* a synonym of *Homotrypa*; Marintsch considered *Homotrypella* to be synonymous with *Peronopora. Gortanipora** was included in the Monticuliporidae in Bock's (2010) informal compilation.

Genus	Ulrich 1890	Astrova 1978	Marintsch 1998
Acantholaminatus	–	–	Monticuliporidae
Atactoporella	Monticuliporidae	Monticuliporidae	–
Aspidopora	–	Monticuliporidae	–
Diazipora	–	Mesotrypidae	–
*Gortanipora**	–	–	–
Homotrypa	Monticuliporidae	Monticuliporidae	Monticuliporidae
Homotrypella	Monticuliporidae	Monticuliporidae	Monticuliporidae
Mesotrypa	–	Mesotrypidae	Monticuliporidae
Monticulipora	Monticuliporidae	Monticuliporidae	Monticuliporidae
Peronopora	–	Monticuliporidae	Monticuliporidae
Prasopora	Monticuliporidae	Monticuliporidae	Monticuliporidae
Prasoporina	–	Monticuliporidae	–

mesotrypids from monticuliporids. Later, Astrova (1978) provided an overview of monticuliporid evolution, viewing the family as displaying the following temporal trends: decreasing autozooecial sizes, increasing numbers of acanthostyles, and a shift from polygonal to round and/or petaloid apertures, the latter produced by abundant inflecting acanthostyles. Additionally, she suggested that *Mesotrypa* might be ancestral to the genus *Prasopora*, considered to be a monticuliporid because it possessed cystiphragms. *Monticulipora* was inferred to have given rise to *Homotrypa* based on a shared colony growth form and compressed autozooecial apertural shapes. A second group of monticuliporids included *Peronopora* and *Atactoporella*, distinguished by their abundant mesozooecia and numerous large acanthostyles (Astrova, 1978, p. 47–50).

Table 1 summarizes the history of generic assignments to the Monticuliporidae and Mesotrypidae. The two most recent analyses either placed eight genera in the Monticuliporidae and two in the Mesotrypidae (Astrova, 1978) or only assigned seven genera to the Monticuliporidae (mesotrypids were not considered; Marintsch, 1998)). Marintsch's concept of the Monticuliporidae removed three of Astrova's genera—*Atactoporella*, *Aspidopora*, and *Prasoporina*—and added the genus *Acantholaminatus* to the family. These differences of opinion underscore the need for a reanalysis of these families using cladistic methods.

Taxonomic revisions.—Boardman and Utgaard (1966, p. 1097) revised the generic concept of *Peronopora* to include species sharing similar autozooecial characteristics and hooked, offset, or segmented acanthostyles. This resulted in the grouping of species with bifoliate (two-layered, back-to-back) colony growth forms, like that of the type species, with those having non-bifoliate growth habits. Specifically, species formerly assigned to *Atactoporella*, *Aspidopora*, *Homotrypella*, *Monticulipora*, and *Prasopora* were transferred into *Peronopora* (Boardman and Utgaard, 1966; Astrova, 1978; Brown and Daly, 1985).

This transfer prompted Hickey (1988) to reinvestigate generic and familial concepts in monticuliporids through a cladistic analysis. Using a set of 57 characters, the resulting clades supported a monophyletic grouping of bifoliate species of *Peronopora*. Conversely, the removal of median lamina characters resulted in a non-monophyletic clade containing bifoliate species. This result indicates that bifoliate and unilaminate species share some convergent (i.e., homoplastic) autozooecial characters and could be considered congeneric if median lamina characters are considered to be taxonomically unimportant. Hickey concluded that a discontinuous median lamina in *Peronopora* was characteristic of the morphology and development of bifoliate forms and represented a heritable trait. Including non-bifoliate species within the genus was unwarranted, negating Boardman and Utgaard's (1966) concept of *Peronopora*. Additional observations in bifoliate species of *Peronopora* supported this claim. They include a unique pattern of astogeny (colony development), a restricted paleogeographic distribution, and the inconsistent occurrence of hooked acanthostyles in other genera. Pachut and Anstey (2002) supported Hickey's (1988) restriction of bifoliate species to *Peronopora*.

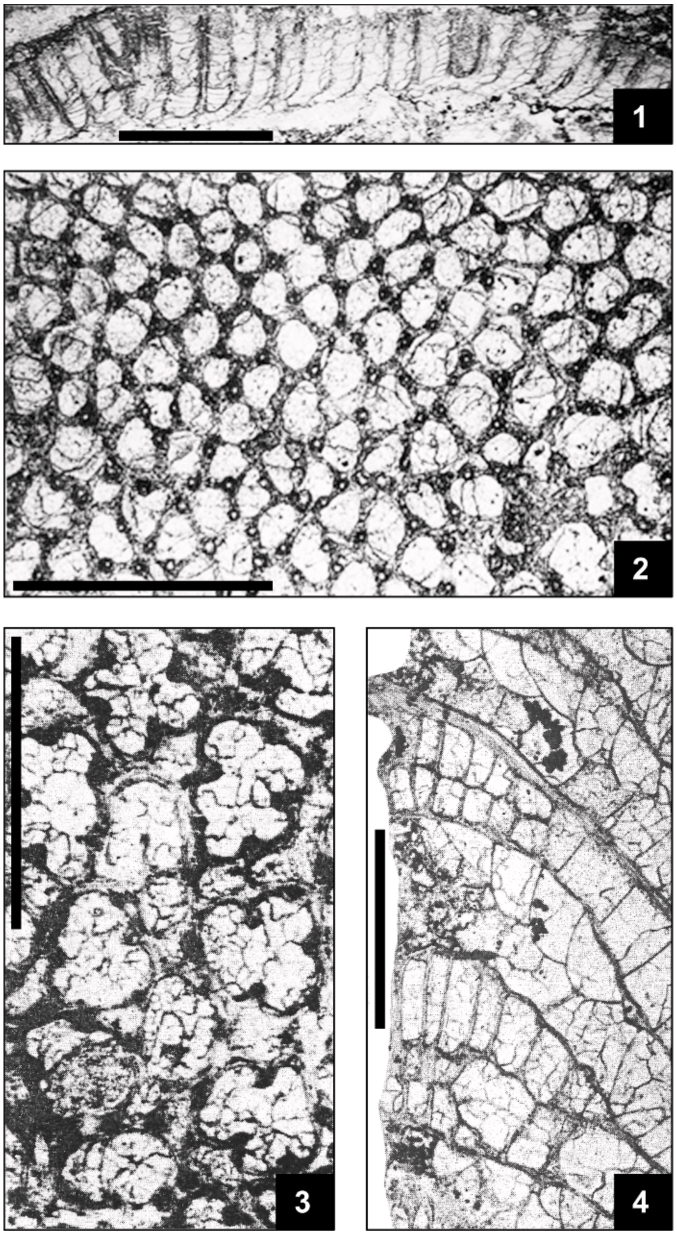

FIGURE *1*—*Acantholaminatus typicus* Marintsch, 1998, and *Atactoporella typicalis* Ulrich, 1883. *1, 2*, *Acantholaminatus typicus* (holotype, USNM 431850), from Marintsch (1998), plate 4, figures 1a and 1c, respectively: *1*, longitudinal section illustrating autozooecia containing planar diaphragms, cystiphragms, and acanthostyles; *2*, tangential section displaying normal-sized autozooecia containing cystopores, a macula (lower right) with megazooecia, and acanthostyles with hollow cores; *3, 4*, *Atactoporella typicalis*, holotype USNM 43863-2 and syntype USNM 43625-2, respectively, from Astrova (1978) plate XV, figures 2a and 2b, respectively: *3*, tangential section in which inflecting acanthostyles produce petaloid autozooecial cross sections; *4*, longitudinal section with autozooecia containing planar diaphragms, curved cystiphragms, and small-diameter mesozooecia. USNM=US National Museum (Smithsonian Institution); all scale bars=1 mm except for *3*=0.05 mm.

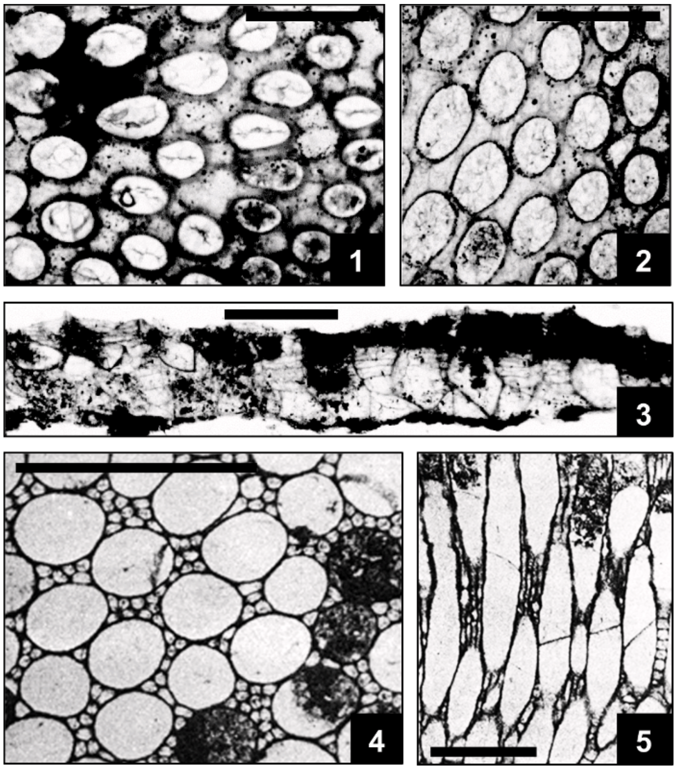

FIGURE 2—*Aspidopora areolata* Ulrich, 1882 and *Diazipora milleporacea* (Bassler, 1911). *1–3*, *Aspidopora areolata*, photos courtesy of the USNM: *1, 2*, tangential sections of USNM 43632, with ovate autozooecia, large polygonal mesozooecia, and a macula (upper left, in *1*); *3*, longitudinal section of USNM 460389 (43632-2) illustrating larger autozooecia and smaller, interspersed, mesozooecia arising from the encrusting surface of the colony; *4, 5*, *Diazipora milleporacea* (IGE B-3120), from Astrova (1978), plate XVI, figures 2a and 2b, respectively: *4*, tangential section with numerous, small, mesozooecia between large, circular, autozooecia; *5*, longitudinal section oriented obliquely to the direction of colony growth; autozooecia, containing planar and curved diaphragms, and mesozooecia remain recognizable. IGE=Geological Institute of Estonia; all scale bars=1 mm.

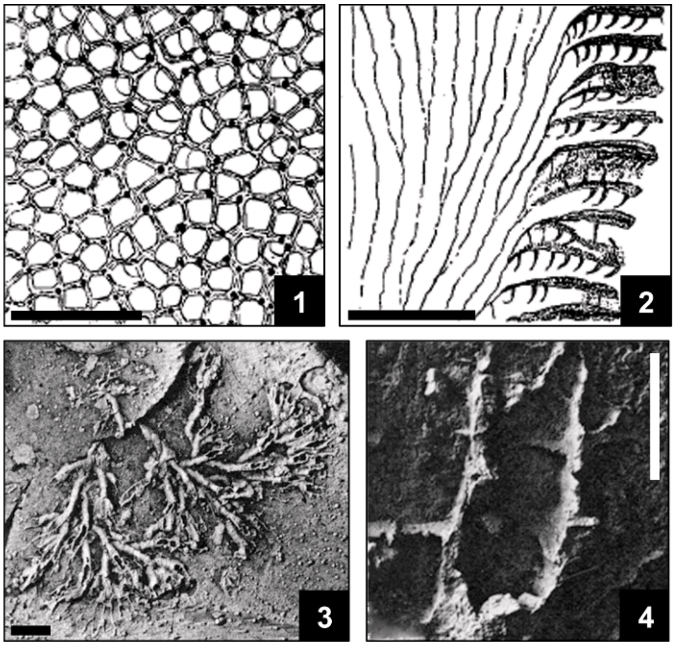

FIGURE 3—*Gortanipora bassleri* (Nickles, 1902) and *Goryunovia hemiseptata* Taylor and Rozhnov, 1996. *1, 2*, *Gortanipora bassleri* (USNM 96584) from Nickles (1902), figures 3 and 4, respectively: *1*, longitudinal section with autozooecia containing curved, hook-like, partial diaphragms or incomplete cystiphragms; *2*, tangential section with abundant acanthostyles and autozooecial apertures containing cystiphragms; *3, 4*, *Goryunovia hemiseptata* (PIN 4565/1) from Taylor and Rozhnov (1996), figures 3 and 5, respectively: *3*, colony growth habit; *4*, broken zooid containing two partial diaphragms (hemisepta). PIN=Paleontological Institute, Russian Academy of Sciences; all scale bars=1 mm except *4*=0.25 mm.

As indicated above, Marintsch (1998) redescribed five of the genera included in this study (*Peronopora*, *Prasopora*, *Mesotrypa*, *Homotrypa, Monticulipora*) and established a new genus, *Acantholaminatus*, placing all of them in family Monticuliporidae. He disagreed with Hickey's restriction of bifoliate forms to *Peronopora* and adopted Boardman and Utgaard's (1966, p. 1097) generic concept. That decision made *Homotrypella* a subjective junior synonym of *Peronopora* (Marintsch, 1998).

This overview of the history of monticuliporid systematics illustrates how the combination of morphological uncertainties and inadequate generic descriptions has resulted in a number of reassignments of both species and genera. Historically, most of the genera in our study have been considered to belong to the Monticuliporidae (Ulrich, 1890; Astrova, 1978; Anstey, 1987; Pachut et al., 1994; Marintsch, 1998; Pachut and Anstey, 2002; and others) leaving the Mesotrypidae with the two genera (*Diazipora* and *Mesotrypa*) that Astrova (1965) originally assigned to that family.

Previous cladistic studies of bryozoans.—Anstey (1987, p. 33) analyzed the role of astogeny in Paleozoic bryozoan evolution, illustrating a previously unpublished genus-level phylogenetic tree for the Monticuliporidae developed by D. Hickey. The tree was generated using 67 characters and Dollo parsimony which minimizes the probability of character state gains in favor of character state losses. *Mesotrypa* and *Diazipora* were sister genera that, in turn, represented a sister group of *Prasopora*. All three genera represented a sister clade to one that included *Homotrypa*, *Gortanipora*, *Homotrypella*, *Peronopora*, *Atactoporella*, and *Monticulipora. Aspidopora* preceded both clades in the branching sequence. Clades in this tree were moderately to highly congruent with generic clusters produced by phenetic methods (Anstey and Perry, 1973; Pachut and Anstey, 1984).

A cladistic study by Key (1990) resulted in the recognition of a new trepostome genus, *Bimuropora*. Characters involving wall structure, colony growth patterns, and autozooecial ontogeny controlled the location of taxa within the cladogram. Specifically, four species assigned to *Bimuropora* shared a common ancestor with four species assigned to *Champlainopora*, resulting in the establishment of family Bimuroporidae. However, the analysis produced 19 equally parsimonious trees and a consensus cladogram that contained two large unresolved polytomies.

Anstey (1990) performed a cladistic analysis of Paleozoic bryozoan classes and orders, using 54 two- and multistate characters. Each of the following formed separate monophyletic, derived, clades: Class Stenolaemata, Paleozoic free-walled stenolaemates, Order Trepostomata, and Order Cheilostomata. Conversely, Class Gymnolaemata, and Orders Ctenostomata, Tubuliporata, Cryptostomata, and Cystoporata were paraphyletic taxa. Anstey concluded that extant groups of bryozoans were more plesiomorphous (primitive) than extinct free-walled stenolaemates. However, the low consistency index (CI) of 0.438 and the large number of character reversals and homoplasies suggested that the tree's topology might change if new characters were included in the analysis.

Anstey and Pachut (1995) analyzed phylogenetic relationships among 60 families of stenolaemate bryozoans using 54 characters. Initially 11 stenolaemate suborders were analyzed

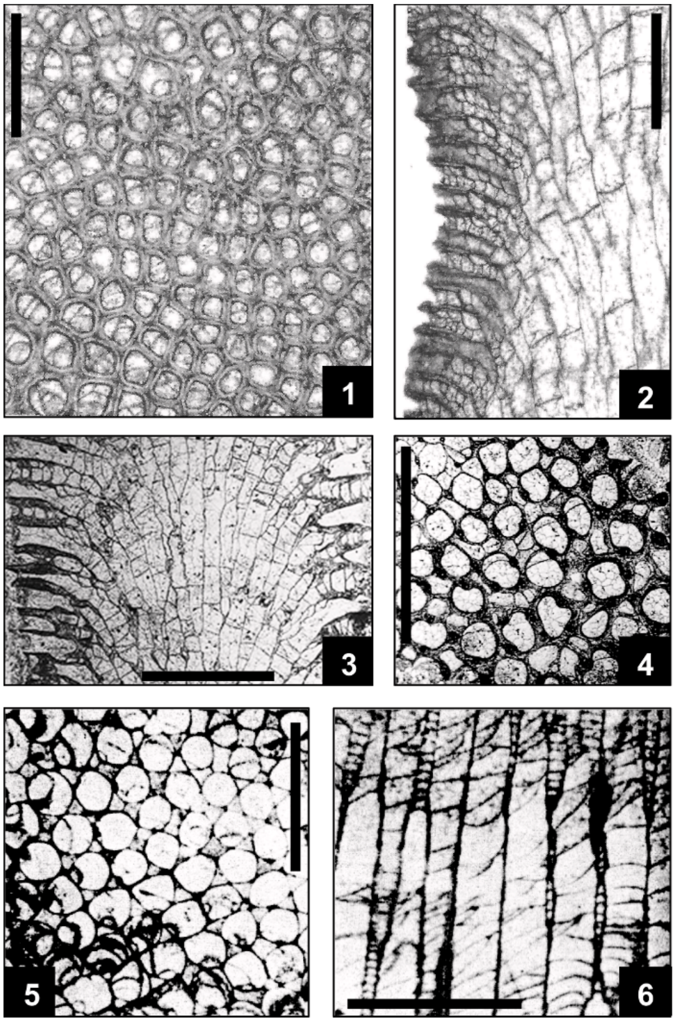

FIGURE 4—*Homotrypa curvata* Ulrich 1882, *Peronopora mundula* (Ulrich, 1893) and *Mesotrypa infida* Ulrich, 1886. *1, 2*, *Homotrypa curvata* (plesiotype, IU 16531-018-31) from Brown and Daly (1985), plate 7, figures 7 and 8, respectively: *1*, tangential section with thick autozooecial walls, a median line, and acanthostyles; *2*, longitudinal section with a short exozone containing an overlapping series of cystiphragms; *3, 4*, *Peronopora mundula* (Ulrich, 1893) (for *Homotrypella instabilis* Ulrich, 1886, now *Peronopora instabilis*), hypotype USNM 431803 [NL IV 50(85)A-14-B], from Marintsch (1998), plate 2, figures 2a and 2c, respectively: *3*, longitudinal section with endozonal diaphragms that become rare or absent in the exozone, common overlapping cystiphragms, and mesozooecia with thicker diaphragms than in autozooecia; *4*, tangential section with subpolygonal autozooecial apertures and thick autozooecial walls with inflecting and offset acanthostyles in shallower portion of the section (upper right); deeper portion of section (lower left) has subrounded thin-walled autozooecia, angular mesozooecia, and smaller acanthostyles; *5, 6*, *Mesotrypa infida* Ulrich, 1886 (syntype, USNM 43542) from Astrova (1978) plate XVI, figure 1: *5*, tangential section illustrating 3–5 mesozooecia associated with each large circular autozooecial aperture; *6*, longitudinal section in which autozooecia have oblique and convex diaphragms and transform into mesozooecia. IU=Indiana University Department of Geological Sciences; all scale bars=1 mm.

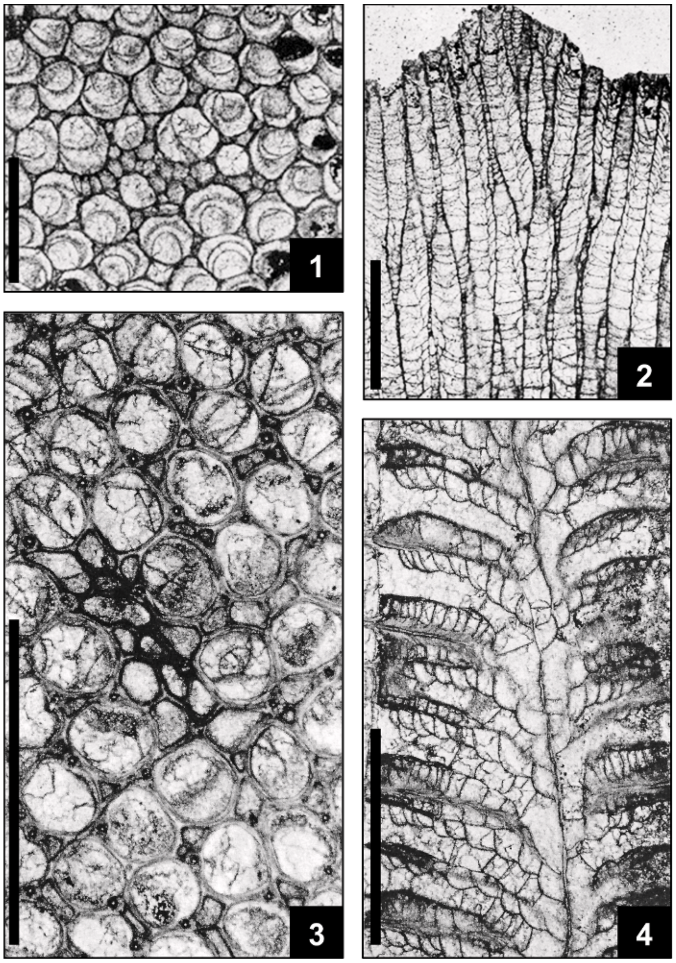

FIGURE 5—*Monticulipora mammulata* d'Orbigny, 1850 and *Peronopora decipiens* (Rominger 1866). *1, 2*, *Monticulipora mammulata*, from Boardman and Utgaard (1966), plate 133, figures 1a and 1b, respectively: *1*, tangential section of massive topotype with abundant mesozooecia in central macula and common cystiphragms (USNM 146486); *2*, longitudinal section of same zoarium (USNM topotype suite 43829) illustrating a monticule at the top of the image; vertical, attenuated, mesozooecia bend out of the plane of the section; *3, 4*, *Peronopora decipiens* (lectotype, UMMP 6676-3), from Boardman and Utgaard (1966), plate 135, figures 1c, 1f, respectively: *3*, tangential section illustrating a monticule and mesozooecia; *4*, longitudinal section showing a break in median lamina (broken vertical line), making it discontinuous, and autozooecia budding from its left and right sides; overlapping series of cystiphragms are common within autozooecia;. UMMP=University of Michigan Museum of Paleontology; all scale bars=1 mm except for *1*=0.5 mm.

by coding the most frequently displayed trait in a subset of 26 characters. The Branch and Bound algorithm of PAUP (Swofford, 2007) produced two trees with a CI of 0.556. Trepostomes and cystoporates were sister groups, and the three major stenolaemate orders (i.e., Cystoporata, Trepostomata, and Cryptostomata) were monophyletic. A second family-level analysis utilized character codings for the oldest known genus within each family and reproduced the subordinal branching patterns of the first analysis. They concluded (fig. 8.2, p. 245) that both the Halloporina and the Trepostomata, minus the Esthonioporina, form ordinal-level clades. Interestingly, the Monticuliporidae and Mesotrypidae were not closely related. This might have resulted from the use of the oldest genus within each family that lacked the synapomorphies that define conventional groupings (Anstey and Pachut, 1995, p. 243). When representative or typical genera were used, the Monticuliporidae and Mesotrypidae were closely related sister clades, as were the Families Halloporidae, Trematoporidae, Heterotrypidae, and Dittoporidae (Anstey and Pachut, 1995, fig. 8.3, p. 246).

More recently, Pachut and Anstey (2002) applied cladistic techniques to a data set consisting of 202 specimens, recognizing eight species of the Middle and Upper Ordovician bryozoan genus *Peronopora*. A subsequent paper (Anstey and Pachut, 2004) extended the earlier analysis by comparing cladistically-defined species to those recognized using phenetic methods. Eight

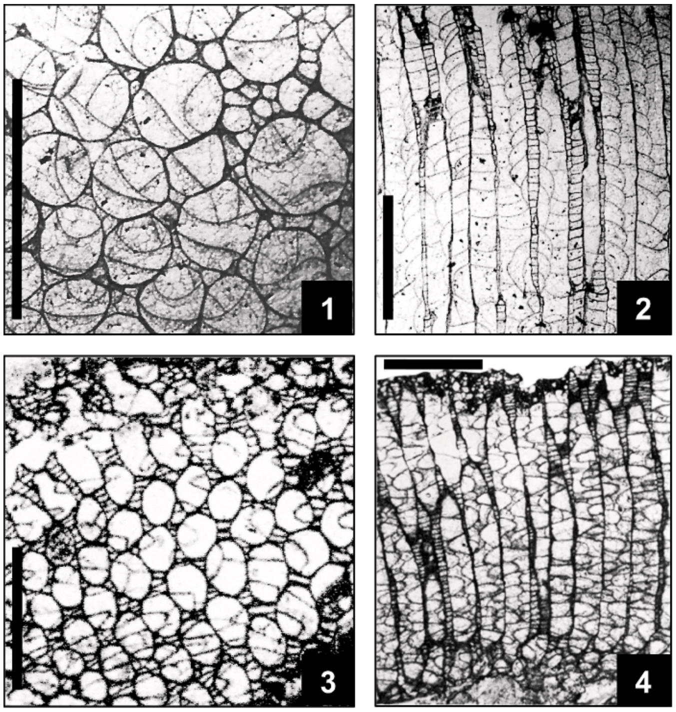

FIGURE 6—*Prasopora falsei* (James, 1884) (for *Prasopora grayae*) and *Prasoporina selwynii* (Nicholson, 1881). *1, 2*, *Prasopora falsei* (hypotype, USNM 431732 [CB 145B-5-A]): *1*, tangential section with rounded to subrounded autozooecial apertures, small polygonal to subrounded mesozooecia associated with, and sometimes isolating, megazooecia in maculae, small acanthostyles, and large cystiphragms that wrap around two-thirds to three-fourths of autozooecial apertures, from Marintsch (1998), plate 1, figures 2a and 2c, respectively: *2*, longitudinal section containing autozooecia with planar and curved diaphragms, overlapping series of cystiphragms, and smaller-diameter, closely tabulated, mesozooecia; *3, 4*, *Prasoporina selwynii*, from Ross (1967), plate 48, figure 1 and plate 49, figure 8, respectively: *3*, oblique tangential section (Loc. 8-27-A; YPM 25198) illustrating small, crescentic, cystiphragms within ovate autozooecia that are separated by small mesozooecia; *4*, longitudinal section (YPM 25214) with large, cystiphragm containing, autozooecia and smaller, closely tabulated, mesozooecia passing into and out of the plane of the thin section. YPM=Peabody Museum, Yale University; all scale bars=1 mm.

monophyletic species and eight paraphyletic metaspecies were identified.

METHODS

Morphologic characters.—The character set was developed, in part, from those used in earlier studies of Paleozoic stenolaemate bryozoans including Anstey and Perry (1970, 1973), Corneliussen and Perry (1973), McKinney (1977, 2000), Anstey (1978), Prezbindowski and Anstey (1978), Pachut and Anstey (1984), Blake and Snyder (1987), Hickey (1988), Anstey (1990), Key (1990), Cuffey and Blake (1991), Hageman (1991), Pachut, Anstey, and Horowitz (1994), Anstey and Pachut (1995), Spearing (1998), Tang and Cuffey (1998), and Taylor and Weedon (2000). Characters from these analyses were merged into a comprehensive listing of 317 characters having a total of 701 derived states (Paquette, 2008; online Supplemental file 1). An initial subset of 267 characters was appropriate for coding the genera of this study. Lacking reasons to exclude characters, based on previous cladistic or phenetic studies, all characters were initially retained for analysis.

Character state codings (online Supplemental file 2) were determined from published photographs of thin sections, SEM photomicrographs, line drawings, and from systematic descriptions of the type species of ten of twelve genera from Anstey and Perry (1973), Astrova (1978), Boardman and Utgaard (1966), Bork and Perry (1968), Brown and Daly (1985), Marintsch (1998), Nickles (1902), Taylor and Rozhnov (1996), Ross (1967), Utgaard and Perry (1964). Descriptions and illustrations of the type species of *Prasopora* (*P. grayae*) and *Homotrypella* (*H. instabilis*) were inadequate; two closely related species, *Prasopora falesi* and *Peronopora mundula*, were used to complete character codings.

The analytical ingroup includes 10 genera currently assigned to the Monticuliporidae and two to the Mesotrypidae (Table 1; Figs. 1–6). *Goryunovia* (Taylor and Rozhnov, 1996) was selected as the outgroup genus for cladistic analysis. It is older, stratigraphically, and possesses abundant plesiomorphic character states compared to the 12 ingroup genera. Cladistic analysis employed a subset of 127 of the original 267 characters, each of which shared a character state with at least one other ingroup genus and also possessed at least one character state coding not shared with *Goryunovia*.

Cladistic analysis.—Cladistic analysis was performed using PAUP (Phylogenetic Analysis Using Parsimony; Swofford, 2007) employing both exhaustive (branch and bound) and heuristic search strategies. Exhaustive searches begin with an initial tree consisting of three taxa. As taxa are added, the search backtracks one node, evaluates all possible trees created by that addition, and continues this procedure until all possible trees have been evaluated. The initial exhaustive search was followed by a bootstrapped version that holds taxa constant while character states are replicated, with replacement, building a series of replicate trees equal in size to the original tree. Each replicate is searched, using the branch and bound algorithm, resulting in a series of trees from which a majority rule consensus tree is generated. The frequencies (percentages) of clade occurrences within the set of replicates are indicted at each node, providing measures of confidence associated with branching points in the cladogram.

Heuristic searches employ a trial-and-error method rather than performing a comprehensive search. However, searches are faster (require fewer computer resources) and can analyze larger data sets than exhaustive searches. Heuristic searches are hill-climbing methods that begin with a three-taxon tree to which the remaining taxa are added (several methods are available). After each addition, all possible combinations of taxa are evaluated and the shortest tree is retained. Genera in this study were added randomly (RANDOM option) followed by tree bisection and reconnection (TBR) branch swapping. TBR bisects a tree along a branch and then reconnects the resulting subtrees in every way possible. Trees are evaluated using parsimony, retaining those that required the fewest character state changes. The steepest descent option was used to ensure that a search path was evaluated along its entire length rather than being abandoned when a shorter tree was found. Character state reconstruction at internal (ancestral) nodes was accomplished by character state optimization, minimizing the amount of change required by a single character for any particular tree. In cases where character state changes could be placed at multiple nodes, the accelerated transformation criterion (ACCTRAN) placed them closer to the root of the tree rather than closer to branch tips. Searches used the heuristic search algorithm, the TBR option, and Fitch optimization (unordered character state changes); the latter does not penalize (i.e., increase tree length) character state reversals or the skipping of sequential character states.

Several quantitative indices were calculated during each analysis for the entire tree (ensemble index) and for individual characters (individual index). The consistency index, CI (Kluge and Farris, 1969), measures the fit of a character (or all

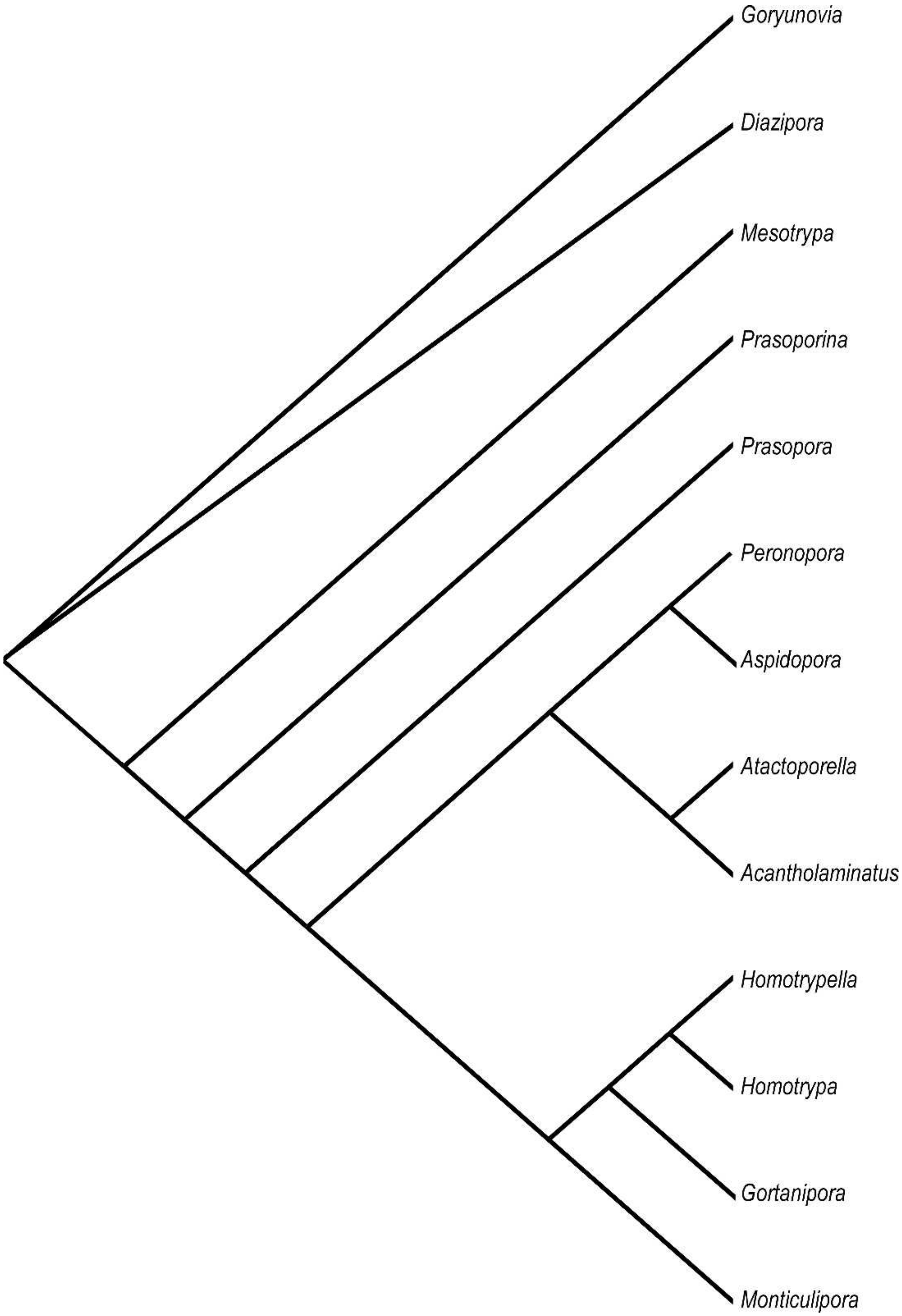

FIGURE 7—Cladogram resulting from a heuristic search that was reweighted using values of the rescaled consistency index (RC) and rerun using PAUP. Tree length=118, consistency index (CI)=0.6924, and homoplasy index (HI)=0.3076. Lengths and indices for alternative trees are listed in Table 3. The initial search weighted characters by the number of derived states and degree of covariation.

characters) to the tree. Values range from a lower bound based on the number of possible character states to an upper bound of one, indicative of the best possible character fit. The retention index, RI (Archie, 1989; Farris, 1989), is a function of the maximum, minimum, and actual amount of change in a character. RI equals zero when a character fits the tree as poorly as possible. The rescaled consistency index, RC (Farris, 1989), is the product of RI and CI. With a lower bound of zero (no fit) and an upper bound of one (perfect fit), it provides a proportional indicator of a character's fit to the tree. Homoplasy is morphological similarity

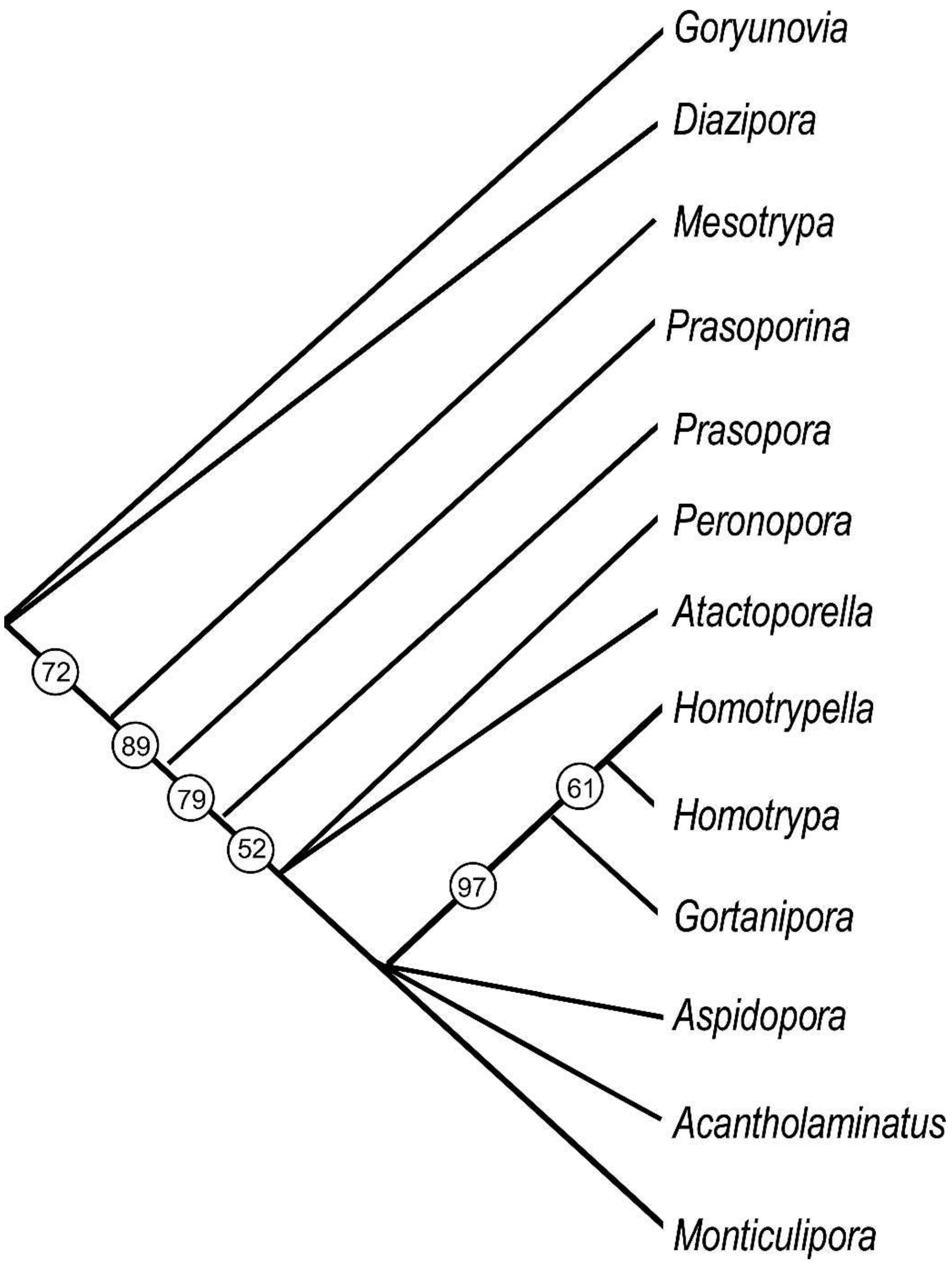

FIGURE *8*—Majority-rule (50%) consensus tree resulting from a bootstrapped heuristic search. The tree represents a consensus of 100 replicate trees; circled numbers equal the percentages of replicated trees in which a subclade appeared. For example, the *Homotrypella–Gortanipora* subclade occurred in 97 percent of replicated trees.

resulting from convergent evolution, not from genealogical descent. It is measured by the homoplasy index, HI (Sang, 1995), equaling 1-CI. Finally, the stratigraphic congruence index, SCI, (Huelsenbeck, 1994) measures the fit of proposed cladistic relationships to observed stratigraphic positions of taxa. Stratigraphic consistency indices (Table 2) were calculated using PAST (Hammer et al., 2001) based on first and last appearance datums (FADs and LADs, respectively). Separate analyses were performed using composite (entire) generic ranges and the ranges of the type species of each genus. Stratigraphic data were obtained from original publications with positions located within the temporal stratigraphic framework of Ogg (2009).

Unweighted characters were used in initial cladistic analyses. Secondary heuristic searches permitted character reweighting using the maximum (individual character) value of the RI, CI, or RC, calculated during the initial run. Reweighting reduces the importance of homoplastic characters in establishing cladistic relationships, removing the need to assign weights a priori when justification for those weights (e.g., from previous studies) is lacking.

Phenetic clustering.—Two separate cluster analyses were performed, permitting comparisons between groupings based on overall morphologic similarity and those based on inferred genealogical relationships. In the first, Euclidean Distance was used along with the unweighted pair-group average linkage

TABLE 2—Stratigraphic distributions of monticuliporid and mesotrypid genera. First and last appearance datums (FAD and LAD, respectively) represent reported ranges for type species (S) and composite ranges of constituent species for genera (G). Stages and durations are from the International Stratigraphic Chart (Ogg, 2009) based on dates from Gradstein et al. (2004) and Ogg et al. (2008). Epoch abbreviations: Ordov=Ordovician; Silur=Silurian; L=Lower, M=Middle, U=Upper.

Genus	Epoch (G)	FAD (G)	LAD (S)	FAD (S)	LAD
Monticulipora	U. Ordov–U. Silur	460.5	418.7	460.5	449.5
Gortanipora	U. Ordov	460.5	443.7	460.5	443.7
Peronopora	U. Ordov–L. Silur	460.5	428.2	460.5	443.7
Aspidopora	U. Ordov–L. Silur	455.8	428.2	452.5	443.7
Acantholaminatus	U. Ordov	455.8	445.6	455.8	445.6
Homotrypa	U. Ordov–U. Silur	460.9	418.7	460.5	449.5
Prasopora	U. Ordov–U. Silur	460.9	418.7	460.5	449.0
Prasoporina	U. Ordov–U. Silur	460.9	418.7	460.5	449.0
Diazipora	U. Ordov	472.0	445.6	472.0	460.5
Mesotrypa	M. Ordov–U. Silur	471.8	418.7	460.5	449.0
Atactoporella	M. Ordov–L. Silur	471.8	422.9	452.5	443.7
Homotrypella	M. Ordov–U. Ordov	471.8	443.7	460.5	449.0
Goryunovia	L. Ordov	479.0	466.0	479.0	466.0

TABLE 3—Indices for branch and bound and heuristic cladistic searches. Included are the consistency index (CI), rescaled consistency index (RC), retention index (RI), homoplasy index (HI), and stratigraphic consistency index (SCI); all indices are described in the text. A branch and bound search resulted in two trees having identical statistics. Heuristic tree two had the best summary indices and was reweighted using CI, RC, and RI; RC reweighting produced the most parsimonious tree having the best summary indices.

Search	Tree Length	CI	RC	RI	HI
Branch and Bound					
Standard	442	0.5249	0.2317	0.4415	0.4751
Bootstrapped	232	0.5667	0.2675	0.4720	0.2675
Heuristic Search					
1	442	0.6949	0.4832	0.6954	0.3051
2	442	0.7042	0.4989	0.7085	0.2958
3	442	0.6890	0.4732	0.6868	0.3110
4	442	0.6845	0.4656	0.6802	0.3155
5	442	0.6912	0.4769	0.6900	0.3088
Reweighted Tree Number 2					
CI	242	0.5910	0.3152	0.5333	0.4176
RC	118	0.6924	0.4892	0.7066	0.3076
RI	181	0.6180	0.3882	0.6281	0.3820
Bootstrapped	486	0.4774	0.1549	0.3245	0.5226

method. The Dice similarity coefficient was matched with the neighbor joining algorithm in the other. Both analyses employed 100 bootstrap replicates that permit the calculation of occurrence frequencies for each cluster, providing quantitative measures of the phenetic stability of the resulting groupings (PAST; Hammer et al., 2001).

RESULTS

Exhaustive, branch and bound, searches generated two equally parsimonious trees (EPTs) each with a length of 442 (Table 3). Both trees had a consistency index (CI) of 0.5249, a retention index (RI) of 0.4415, a rescaled consistency index (RC) of 0.2317 and a homoplasy index (HI) of 0.4751 (i.e., 48% homoplasy).

The heuristic search also found five EPTs each with a length of 442. However, these trees had higher quantitative indices than corresponding trees found by the exhaustive search, indicative a better fit of taxa to heuristically-determined trees (Table 3). CI values ranged between 0.6845 and 0.7085 (30% to 35% higher), RIs between 0.6802 and 0.7085 (54% to 60% higher), and RC values between 0.4656 and 0.4989 (100% to 115% higher). Mean homoplasy across trees was 31 percent, 17 percent lower than for the exhaustive search. Tree number two had the best suite of ensemble index values.

Reweighted heuristic searches (using CI, RI, and RC; Table 3) produced single, shorter, trees that match the topology of one of the two most common trees found by unweighted heuristic searches. They also produced the same branching pattern found in one tree from the exhaustive search but with reduced levels of homoplasy. In both heuristic and branch and bound searches, *Peronopora* is a basal taxon of a clade that also includes *Atactoporella, Aspidopora*, and *Acantholaminatus*. In the other exhaustive search that clade consists of two sister-group pairs: *Peronopora–Aspidopora* and *Atactoporella–Acantholaminatus*. The repeated appearance of one tree topology, irrespective of the algorithm or analytical options used to generate it, suggests that it represents the most accurate pattern of cladistic relationships among genera, based on our set of character data (Fig. 7). Reweighting in heuristic searches appears to be responsible for reducing the effects of homoplastic (convergent) characters and producing shorter trees than unweighted exhaustive searches.

A bootstrapped heuristic (BH) search resulted in high occurrence frequencies at each clade-defining node (Fig. 8), increasing confidence in the topology displayed by the most commonly occurring tree. For example, the *Homotrypa–Homotrypella* clade occurred in 61 percent while the *Gortanipora–Homotrypa–Homotrypella* clade occurred in 97 percent of bootstrap-replicates. Similar percentages occurred in the bootstrapped branch and bound (BB) search. However, the BH search partially resolved a polytomy in the bootstrapped BB tree, separating *Prasopora* from *Peronopora* and *Atactoporella*.

Table 4 lists clade-defining apomorphies that are also plotted on the optimal most parsimonious tree (Fig. 9). A complete listing of character state changes associated with each node in the tree can be found in online Supplemental file 3. Synapomorphic character states evolved only once if they have consistency indexes (CIs) equaling one. These characters display no homoplasy (no convergence) and potentially provide the most reliable traits for characterizing clades. Specifically, all genera except *Mesotrypa* and *Diazipora* share monticule and cystiphragm characters, a result consistent with Astrova's (1965) phenetic definition of the Mesotrypidae as a family whose members lack monticules and cystiphragms. The possession of acanthostyles of different sizes and diaphragms having variable orientations within autozooecia separates *Prasopora* and all remaining taxa from *Prasoporina*. The *Gortanipora–Homotrypa–Homotrypella* clade is defined by colony growth form, autozooecial wall structure, and budding patterns; it has very strong bootstrap support and is recognizable in several phenetic groupings. Basal keel and sinus structures make *Aspidopora* a sister taxon to *Peronopora*.

At the genus-level, most parsimonious tree 1 had the highest stratigraphic consistency index (SCI) of 0.4545 providing the closest match (at 45%) between observed stratigraphic distributions and cladistic branching pattern. However, this value is not statistically significant at $p \leq 0.05$. This might result from compiling stratigraphic range data for species currently assigned to these genera for which cladistic support does not exist. In other words, the poor match between stratigraphic distribution and cladistic branching pattern could result from composite FADs and LADs that reflect the mixing of range data for species belonging to different genera. Conversely, when composite ranges were replaced by the observed ranges of the type species of each genus, a highly significant ($p \leq 0.01$) SCI of 0.9091 (91% match) was obtained. Until species-level cladistic analyses have been completed, we might expect poor matches between

TABLE 4—Clade-defining characters that are free of homoplasy (consistency indices=1.0). All characters are described, coded states listed, and apomorphies tabulated in online Supplemental files 1–3.

Character number	Type	Description
6	Zoarial Form	Cross-section shape, cylindrical to polygonal
7	Zoarial Form	Cross-section shape, type of branching
9	Zoarial Form	Diameter of branches
10	Zoarial Form	Cross-section shape, uniform to variable diameter
70	Zooecia	Zooecial bend, rounded to abrupt
71	Endozone	Wall type, curving or linear
81	Budding	Axial endozone, presence of growing tips
84	Budding	Axial bud arrangement
87	Budding	Axial bundle, not present to well-defined
88	Budding	Axial endozone without/with spiral budding
89	Budding	Axial endozone, non-radial to strongly radial
90	Budding	Axial zooecial arrangement
91	Budding	Axial endozone, medial rows of zooids
94	Basal Zooecia	Keel
95	Basal Zooecia	Sinus
107	Endozone	Regular to corrugated walls
155	Monticules	Size
184	Acanthostyles	Unimodal or discrete sizes
205	Diaphragms	orientation relative to zooecial wall
209	Cystiphragms	abundance
211	Cystiphragms	present in zoarium, or only in exozone
213	Cystiphragms	degree of curvature
215	Cystiphragms	presence/absence of proximal fringe
219	Cystiphragms	single and large or small and numerous

evolutionary branching patterns and sampled stratigraphic positions for studies conducted at and above the genus level. For example, a cladistic analysis of the bryozoan genus *Peronopora* (Pachut and Anstey, 2007) indicated that stratigraphic sampling was incomplete. Cladistic relationships were used to adjust sampled stratigraphic ranges. In spite of obtaining a significant correlation (SCI) between observed stratigraphic positions and cladistic branching patterns, the stratigraphic first appearances of 11 of 16 species and metaspecies of *Peronopora* were too young by estimated time spans ranging up to 3.9 myr.

In contrast to the use of synapomorphic characters in cladistics, phenetic methods use overall morphologic similarity to group taxa; the status of attributes, as either plesiomorphic or apomorphic, is ignored. For the genera of this study, phenetic cluster membership is similar to that of clades (Figs. 10 and 7, respectively) when based on the Dice coefficient and either the unweighted pair-group average linkage method or neighbor joining (PAST; Hammer et al., 2001). Neighbor joining does not require branches from the same internal node to have identical lengths (Hammer et al., 2001) a modification appropriate for data sets including taxa that might possess characteristics that evolved at different rates. The phenograms include strong bootstrap support for a basal *Diazipora–Mesotrypa* cluster. That cluster is followed by an *Aspidopora–Atactoporella–Acantholaminatus* and a *Gortanipora–Homotrypella–Homotrypa* cluster, both of which have weaker bootstrap support. *Monticulipora* is more closely (and strongly) associated with *Peronopora* rather than with *Gortanipora, Homotrypella, and Homotrypa* (GHH) in Figure 10.1, but neighbor joining places *Monticulipora* at the base of the GHH cluster, although with weak bootstrap support (Fig. 10.2). Therefore, clades are recognizable phenetically, although other combinations of similarity measures and linkage methods (not illustrated) produced phenetic groups with membership that diverged from that of clades. This volatility makes phenetic analyses easy to manipulate and the interpretation of both intra- and inter-group relationships subjective. We suggest that it is impossible to confirm purported evolutionary relationships depicted by phenetic groupings without having prior knowledge of cladistic relationships.

DISCUSSION

Crown and stem groups.—Jefferies (1979) defined a crown group as a living monophyletic taxon that includes extinct members that possess (or have secondarily lost) all of the diagnostic characteristics of that taxon. Therefore, a crown group contains the latest common ancestor of a taxon and all of its descendants. In contrast, a total group includes all extinct members that possess one or more diagnostic characteristics of the taxon (Smith, 1994). Removal of the crown group from the total group results in a paraphyletic stem group (stem lineage of Ax [1987]). This distinction was introduced to accommodate fossil taxa within living taxa without unnecessarily inflating the taxonomic hierarchy (Smith, 1994). Jefferies (1979) thought that the task of paleontologists was to place fossils in their proper stem groups and then establish sister group relationships among them. In such a system, the name and Linnaean rank of the crown group is extended to its associated stem group (i.e., applies to the total group; Smith, 1994). When a group included both living and fossil members, fossils were indicated separately as plesions and taxonomic rank was used only to denote relative inclusiveness. Our data set consists only of fossilized specimens from extinct bryozoan genera. We have extended the concept of crown and stem groups to our analysis of monticuliporid genera based on the topological structure of our cladogram, an approach applied earlier by Anstey and Pachut (2004) in defining species and metaspecies of the Ordovician bryozoan genus *Peronopora*.

Family Monticuliporidae (Fig. 7) is represented by a crown group that includes *Prasoporina, Prasopora, Peronopora, Aspidopora, Atactoporella*, *Acantholaminatus*, *Homotrypella*, *Homotrypa*, *Gortanipora*, and *Monticulipora*. The stem group consists only of *Diazipora* and *Mesotrypa,* equivalent to Astrova's (1965) family Mesotrypidae. The placement of *Prasoporina* and *Prasopora* within the crown group is somewhat arbitrary, based on the possession of mesozooecial and diaphragm synapomorphies that display varying levels of homoplasy (i.e., CI values <1.0).

Key apomorphic characters.—Synapomorphic character states, important in defining clades, are listed in Table 4 and corresponding character numbers have been placed at appropriate nodes on the cladogram (Fig. 9). Once again, character state changes having consistency indexes (CI) equaling 1.0 evolved only once, making them the most useful attributes with which to define taxa. Starting at the base of the cladogram, node 18 (e.g., listed in online Supplemental file 3 as node 17→node 18) is defined by a single character having a CI of 0.2, indicating the strong presence of homeomorphy. Character 100 differentiates *Diazipora* from *Goryunovia* by the shape of the living chamber (was equidimensional, became elongate).

Several key synapomorphic character states occur at Node 19, but none of them have a CI of 1.0. Characters (in parentheses) with the highest CI of 0.667 include the presence of a constant or distally decreasing number of mesozooecia (124) and the presence of monticules within which autozooecial diameters decrease imperceptibly into intermonticular regions (134). Character 206, the presence of oblique diaphragms attached to proximal walls of zooids, has a CI of 0.6.

Characters that define the base of the crown-group at node 20 (occurred in 79% of bootstrapped trees; Fig. 8) include the presence of abundant cystiphragms throughout the zoarium (character 209; CI=1.0), large cystiphragms (220) present throughout the zoarium (211) that lack a proximal fringe (215), monticules that are flat or depressed (150), have a central macula

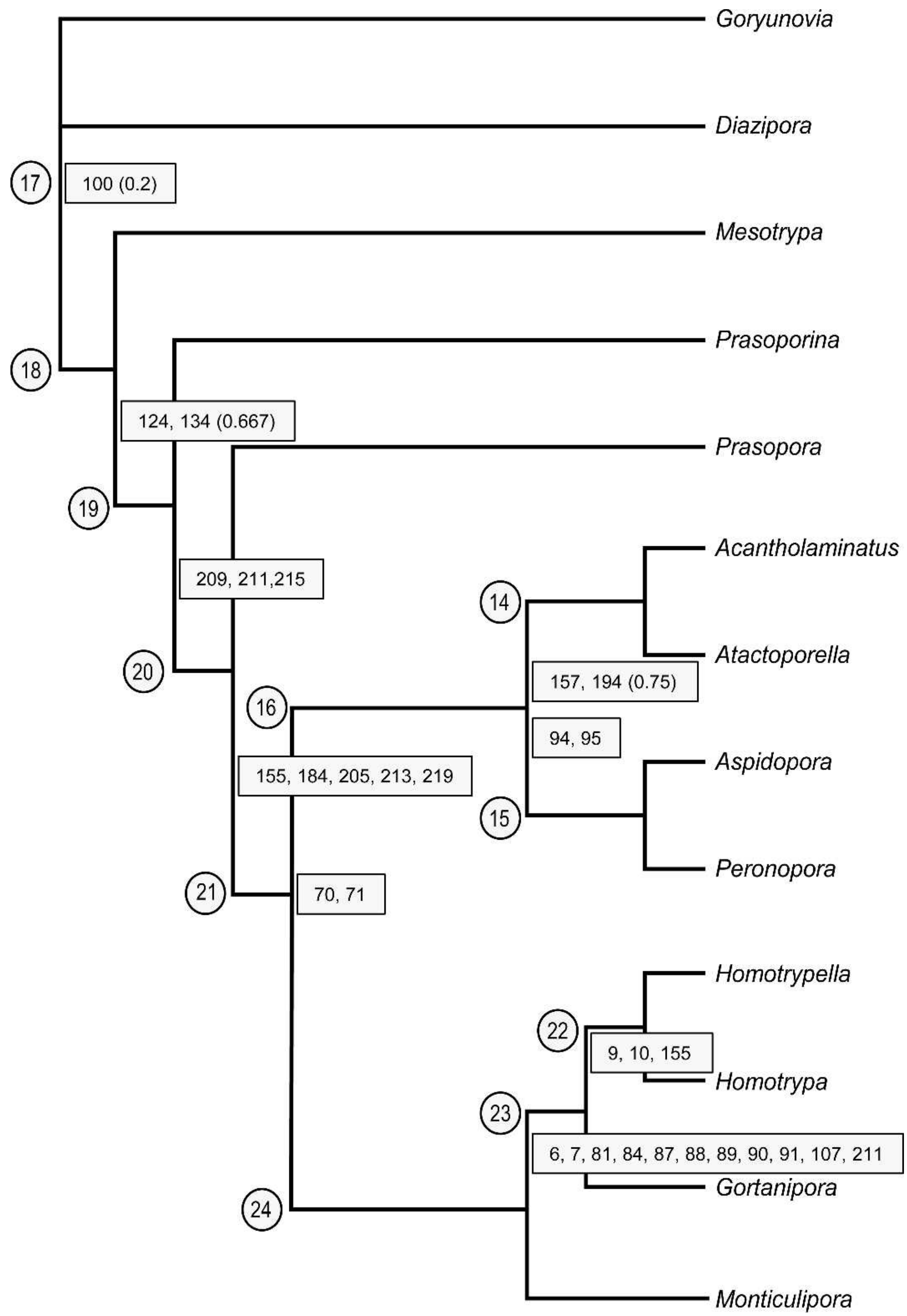

FIGURE 9—Cladogram with synapomorphic characters indicated at selected nodes. Tree is ladderized for easier readability. Node numbers are circled; characters displaying key apomorphies are listed inside rectangles. Characters are described, codings tabulated, and apomorphic character state changes listed in online Supplemental files 1–3.

(152) that is smaller than one autozooecial diameter (153) and are regularly spaced (154), have megazooecia in the monticules (146), and diaphragms that revert from convexly curved to concave or absent (203). The latter seven characters include varying degrees of homoplasy (CIs between 0.25 and 0.75).

Beginning at node 21, the rest of the crown group is defined by synapomorphies that are free of homoplasy (CI=1.0) that include small (<1.5 mm) monticules (155), acanthostyles with a unimodal size distribution (184), the presence of normally-curved cystiphragms (213), and large cystiphragms in each autozooecium

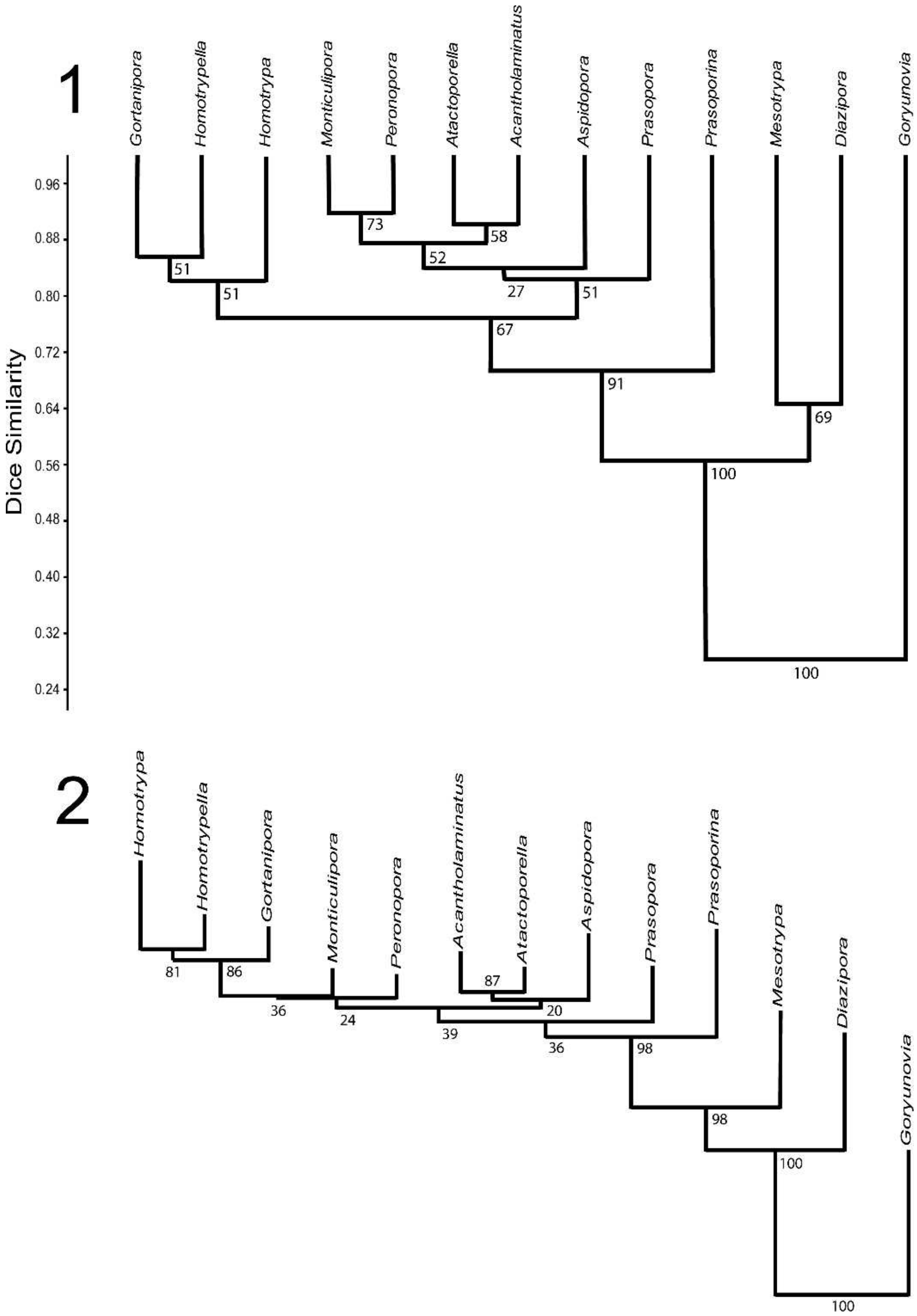

FIGURE *10*—Cluster analyses of genera using the Dice similarity coefficient. *1,* phenetic grouping using pair-group linkage; *2*, groupings based on neighbor joining linkage. Numbers indicate bootstrap frequencies of each hierarchical cluster. Phenetic groupings are recognizable in cladograms, with departures involving the placements of *Peronopora* and *Monticulipora*. Other clustering methods produced results that were less concordant with cladistic patterns.

(219). Obliquely oriented diaphragms undergo a character state reversion, becoming perpendicular to autozooecial walls (205), acanthostyles occur at autozooecial junctions (194), cystiphragms are abutted by half-diaphragms (214), and single cystiphragms are present in autozooecial apertures (221). This clade occurred in 52 percent of bootstrapped trees, a percentage reflecting topological variety related to the presence of polytomies in many of the replicated trees (Fig. 8).

Two synapomorphies at node 24 display no homoplasy: the presence of a gently rounded autozooecial bend (70) and the existence of a distinct endozone (71). Additional synapomorphies include abundant acanthostyles (183) that have a clear core and include laminations (189). All of synapomorphies that defined the *Monticulipora* subclade are also shared at node 16, the base of the *Acantholaminatus* subclade, along with completely laminated wall structure (161), acanthostyles along the autozooecial walls

(192), and more than four diaphragms or cystiphragms in the endozone (197).

Numerous synapomorphies support a very well-supported subclade (97% of bootstrapped trees; Fig. 8) at node 23. Genera include branching colonies (7) that have cylindrical cross sectional shapes (6); earlier genera were predominantly massive. They possess an axial endozone (81) containing irregularly polygonal or rounded buds (84), a well-defined axial bundle (87) lacking a radial budding pattern (88), and medial rows of autozooecia (91). Finally, endozones have wavy walls (107) while cystiphragms occur only in the exozone (211).

Homotrypa and *Homotrypella* branch at node 22 (bootstrap frequency=61%; Figs. 8, 9), and display synapomorphies with a CI of 1.0 involving branch diameter (9) and its variability (10). Other synapomorphies (CIs between 0.40 and 0.75) include lateral branching (8), a high autozooecial reorientation angle (75), subpolygonal autozooecial apertures (41; a reversion), and non-localized budding (79).

The *Acantholaminatus* subclade, at node 16, is characterized by the same synapomorphies as those at node 24 (the *Monticulipora* subclade), the strongest of which are the presence of a gently rounded autozooecial bend (70) and a distinct endozone (71). Additional synapomorphies include a gradual change in wall thickness between the endozone and exozone (69), short overlap of recumbent zones (98) limited to the base of the zoarium (97), the presence of subcircular megazooecia (148), larger acanthostyles in monticules (158), and acanthostyles that predominantly inflect autozooecial apertures (191). This subclade also has a number of synapomorphies reflecting character state reversals. Among them are restricted budding reverting to non-localized budding in the exozone (79), elongate living chambers reverting to equant (100), planar mesozooecial tabulae reverting to concave (122), less than four diaphragms in the innermost exozone becoming absent or rare (198), and large cystiphragms returning to intermediate sizes (220).

Acantholaminatus and *Atactoporella* (node 14) share synapomorphies displaying levels of homoplasy (CIs) between 0.333 and 0.750. They include intermediate length endozonal portions of autozooecia (74), mesozooecia that are closed at the zoarial surface (115), four to seven acanthostyles per autozooecium in monticular areas (157), five to seven acanthostyles per autozooecium outside of the monticules (193), and the presence of diaphragms/cystiphragms in the endozone (197). The loss of a central macula in monticules (152, 153) and non-clustered mesozooecia in monticules (117) represent character state reversals.

The association of *Aspidopora* and *Peronopora* at node 15 is defined by the presence of keel (94) and sinus (95) structures in the endozone (CIs=1.0). Additional synapomorphies (CIs between 0.500 and 0.667) involve budding pattern and basal zooecia characteristics (33, 93, 255), whereas the loss of diaphragms or cystiphragms in the exozone (201) reflects a character state reversal.

Stratigraphic consistency.—Based on observed first appearance datums (FADs; Fig. 11) most crown group genera appeared nearly synchronously in the stratigraphic record. *Acantholaminatus*, *Atactoporella*, and *Aspidopora* are exceptions, appearing approximately 5 my later. This pattern is broadly consistent with the cladogram because the latter three genera, along with *Peronopora*, share a more recent common ancestor separating them from the other crown group genera. Similarly, *Diazipora* and *Mesotrypa* are basal stem genera that appear early, and consecutively, in the stratigraphic record. The statistically significant (p≤0.01) stratigraphic consistency index (SCI) of 0.91, calculated using the temporal ranges of the type species of genera, confirms the close correspondence between stratigraphy and cladistic branching. Conversely, a statistically significant SCI was not calculated using composite generic ranges based on all species currently assigned to these genera. This might reflect the mixing of valid and incorrectly assigned species to genera, but an evaluation of this possibility requires an analysis at the species-level.

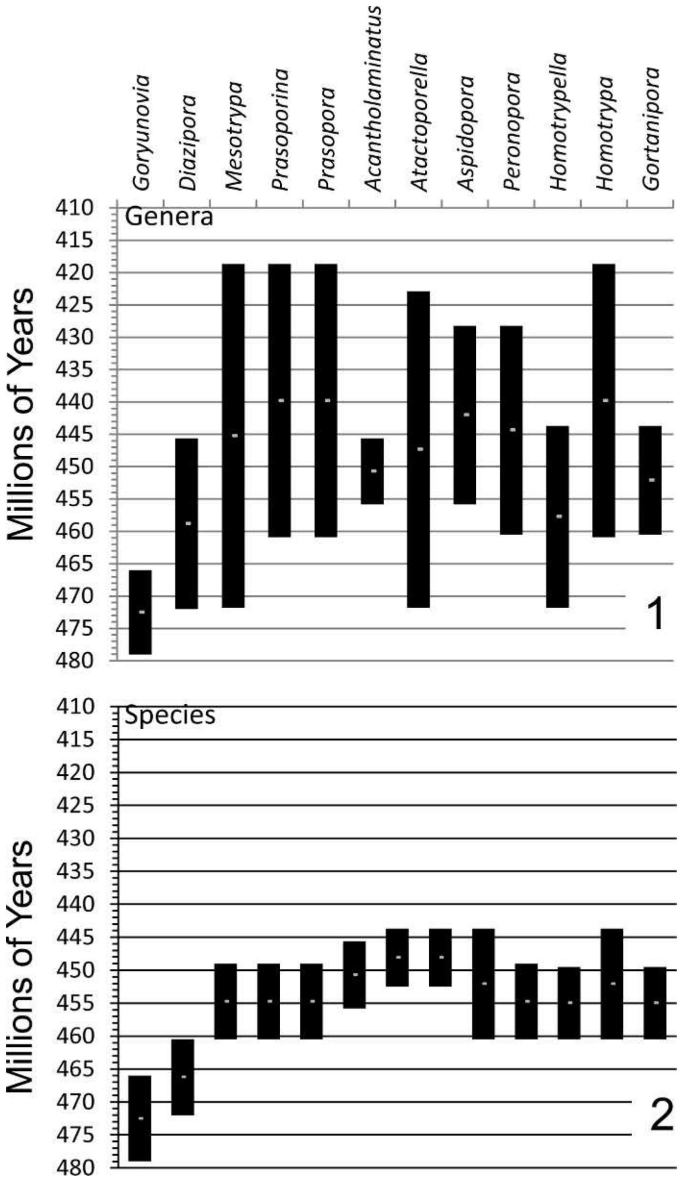

FIGURE *11*—Stratigraphic ranges of genera assigned to the Mesotrypidae and Monticuliporidae. *1*, composite ranges based on first (FADs) and last appearance datums (LADs) of each genus; *2*, ranges based only on the FADs and LADs of the type species of each genus. FADs and LADs are listed in Table 2.

Comparisons with previous classifications.—Earlier classifications (Table 1) defined the difference between monticuliporids and mesotrypids monothetically, based on the presence or absence of cystiphragms, respectively. Applying that definition to our cladistic results places *Prasoporina* within the monophyletic crown group of family Monticuliporidae leaving *Diazipora* and *Mesotrypa* as a basal paraphyletic stem group of the family. This cladistic result agrees with Astrova's (1965) original assertion of a close association between *Diazipora* and *Mesotrypa* and her inferred ancestor-descendent relationship between

Mesotrypa and *Prasopora* (Astrova, 1978; Fig. 7); she considered *Prasoporina* to be a synonym of *Prasopora. Monticulipora* was viewed as ancestral to *Homotrypa*, based on zoarial form and the possession of compressed autozooecia, and *Peronopora* and *Atactoporella* were proposed as a second lineage. Genera in each of these pairs are sister taxa in two separate crown group subclades (Fig. 7).

Similarities also exist between relationships depicted in our cladogram and the one published by Anstey (1987, fig. 7; p. 33, developed by Hickey but unpublished). In our analysis, *Mesotrypa* and *Diazipora* are sister taxa representing two basal branches in the cladogram. They are followed in the branching sequence by *Prasopora* and *Prasoporina* which are, in turn, are at the base of a terminal clade that, like Anstey's, includes *Homotrypella*, *Homotrypa*, *Gortanipora*, and *Monticulipora*. Our cladogram differs from Anstey's by placing *Acantholaminatus* (not considered by Hickey), *Atactoporella*, *Aspidopora*, and *Peronopora* in a separate, more basal, sister clade rather than in a single terminal one and has *Aspidopora* in a much more derived location. The latter genus was at the base of Hickey's cladogram.

SYSTEMATIC PALEONTOLOGY

Phylum Bryozoa Ehrenberg, 1831
Class Stenolaemata Borg, 1926
Order Trepostomata Ulrich, 1882
Family Monticuliporidae Nicholson, 1881

Type species.—*Monticulipora mammullata* d'Orbigny, 1850, p. 25.

Remarks.—Zoarial form includes encrusting, discoidal, hemispherical-massive, branching, and occasionally frondescent or bilaminate, typically displaying regularly-spaced monticules. Autozooecial apertures may be polygonal, subrounded to circular, and sometimes petaloid. Walls in most genera thin, longitudinally-fibrous or granular, partly separated, and with zones of thickenings in a few genera; fused walls obliquely- and transversely-laminated. Cystiphragms typically numerous, occurring as separate blisters or stacked in an overlapping series, and developed either throughout the colony or restricted to the exozone; absent in *Mesotrypa* and *Diazipora*. Diaphragms straight, oblique, and curved, varying in abundance. Mesozooecia rare to numerous, usually containing abundant horizontal diaphragms. Acanthostyles small, rare to numerous, and occasionally large and inflecting autozooecial apertures, making them petaloid, in a few genera.

The family-level cladogram of Anstey and Pachut (1995, fig. 8.3, p. 245) indicated that the Monticuliporidae are most closely related to families Halloporidae and Trematoporidae. Halloporids differ from monticuliporids by have ramose growth forms and virtually lacking acanthostyles. Trematoporids differ by having a broader range and variety of internal structures, including wall microstructures, the presence of hemiphragms, cystose vesicles separating autozooecia in some genera, and an absence of cystiphragms.

Important studies that have described family-level concepts for the Monticuliporidae include the following: Nicholson (1881), Ulrich, (1882, 1890, 1893), Foerste (1887), Simpson (1887,), Waagen and Wentzel (1887), Simpson (1897), Nickles and Bassler (1900), Ulrich and Bassler (1904), Bassler (1906, 1911), Hennig (1908,), Vinassa de Regny (1911, 1921), Coryell (1921), Dreyfuss (1948), Modzalevskaya (1953), Astrova (1959, 1960, 1965, 1978), Yaroshinskaya (1960), Ross (1961, 1963, 1970), and Marintsch (1998).

Family includes *Monticulipora* d'Orbigny 1850, *Prasopora* Nicholson and Etheridge 1877*, Peronopora* Nicholson 1881*, Aspidopora* Ulrich 1882*, Homotrypa* Ulrich 1882*, Atactoporella* Ulrich 1883*, Homotrypella* Ulrich 1886*, Mesotrypa* Ulrich 1893*, Diazipora* Vinassa de Regny 1921*, Gortanipora* Vinassa de Regny 1921*, Prasoporina* Bassler 1952, and *Acantholaminatus* Marintsch 1998.

CONCLUSIONS

Earlier classifications assigned either seven or eight of the 12 genera of this study to the Monticuliporidae, placed *Mesotrypa* and *Diazipora* in a separate family Mesotrypidae, or did not consider the latter two genera at all. A cladistic analysis of these genera used a set of 127 binary and multistate characters each of which were initially weighed by both the number of derived character states and levels of character covariation across genera. The most parsimonious tree resulted from reanalyzing the results of an initial heuristic search after reweighting characters using values of the rescaled consistency index, calculated during the original search, to reduce the effects of homoplasy. Unweighted exhaustive searches and alternate heuristic searches produced the same tree topology, but with greater lengths, by employing different weighting strategies. Cladistic results indicate that all 12 genera should be merged into a single family Monticuliporidae. Ten genera constitute a monophyletic crown group while *Diazipora* and *Mesotrypa* form a basal, paraphyletic, stem group.

The stratigraphic ranges of the type species of each genus were significantly ($p \leq 0.01$) correlated with cladistic branching pattern. A similar, statistically significant, correlation between branching pattern and composite generic ranges was not found, perhaps because current generic concepts mix species from different genera.

Cladistic results support a close association between *Diazipora* and *Mesotrypa,* an inferred ancestor-descendent relationship between *Mesotrypa* and *Prasopora*, *Monticulipora* as possibly ancestral to *Homotrypa*, and the existence of a *Peronopora*-*Atactoporella* lineage initially recognized by Astrova (1965, 1978). Similarities also exist between our cladogram and that of Anstey (1987), including the basal location of *Diazipora* and *Mesotrypa* and the presence of a monophyletic crown group. While the overall compositions of crown groups in both cladograms are similar, each displays a different internal branching sequence.

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ACCESSIBILITY OF SUPPLEMENTAL DATA

Supplemental data deposited in Dryad repository: http://dx.doi.org/10.5061/dryad.72vq2.

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