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Diversification of atypical Paleozoic echinoderms: a quantitative survey of patterns of stylophoran disparity, diversity, and geography

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Abstract.—The analysis of morphological disparity and of morphospace occupation through the macroevolutionary history of clades is now a major research program in paleobiology, and increasingly so in organismal and comparative biology. Most studies have focused on the relationship between taxonomic diversity and morphological disparity, and on ecological or developmental controls. However, the geographic context of diversification has remained understudied. Here we address geography quantitatively. Diversity, disparity, and paleogeographic dispersion are used to describe the evolutionary history of an extinct echinoderm clade, the class Stylophora (cornutes, mitrates), from the Middle Cambrian to the Middle Devonian (about 128 Myr subdivided into 12 stratigraphic intervals). Taxonomic diversity is estimated from a representative sample including 73.3% of described species and 92.4% of described genera. Stylophoran morphology is quantified on the basis of seven morphometric parameters derived from image analysis of homologous skeletal regions. Three separate principal coordinates analyses (PCO) are performed for thecal outlines, plates from the lower thecal surface, and plates from the upper thecal surface, respectively. PCO scores from these three separate analyses are then used as variables for a single, global, meta-PCO. For each time interval, disparity is calculated as the sum of variance in the multidimensional morphospace defined by the meta-PCO axes. For each time interval, a semiquantitative index of paleogeographic dispersion is calculated, reflecting both global (continental) and local (regional) aspects of dispersion.

Morphospace occupation of cornutes and mitrates is partly overlapping, suggesting some morphologic convergences between the two main stylophoran clades, probably correlated to similar modes of life (e.g., symmetrical cornutes and primitive mitrocystitids). Hierarchical clustering allowed the identification of three main morphological sets (subdivided into 11 subsets) within the global stylophoran morphospace. These morphological sets are used to analyze the spatiotemporal variations of disparity. The initial radiation of stylophorans is characterized by a low diversity and a rapid increase in disparity (Middle Cambrian–Tremadocian). The subsequent diversification involved filling and little expansion of morphospace (Arenig–Middle Ordovician). Finally, both stylophoran diversity and disparity decreased relatively steadily from the Late Ordovician to the Middle Devonian, with the exception of a second (lower) peak in the Early Devonian. Such a pattern is comparable to that of other Paleozoic marine invertebrates such as blastozoans and orthid brachiopods. During the Lower to Middle Ordovician, the most dramatic diversification of stylophorans took place with a paleogeographic dispersion essentially limited to the periphery of Gondwana. In the Late Ordovician, stylophorans steadily extended toward lower paleolatitudes, and new environmental conditions, where some of them radiated, and finally survived the end-Ordovician mass extinction (e.g., anomalocystitids). This pattern of paleobiogeographic dispersion is comparable to that of other examples of Paleozoic groups of marine invertebrates, such as bivalve mollusks.

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Introduction

The early Paleozoic radiations continue to galvanize debates concerning the tempo and mode of macroevolution. Such debates, as well as attendant empirical, theoretical, and methodological issues, have in turn matured in several respects. The Cambrian explosion can now be placed in the broader context of both the late Precambrian and the Ordovician fossil record, as it involved the origin not only of most animal phyla, but also of most classes and orders. The Cambrian explosion has come to be seen less as a single event and more as

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an ensemble of Cambro-Ordovician events and processes relatively clustered in time and manifested as an unprecedented period of major morphological innovation in the history of animal life. Furthermore, it is realized that the Cambro-Ordovician radiations are only meaningful in contrast to what happened or did not take place afterward, both in the Paleozoic and post-Paleozoic. Ecological and developmental explanations involving differential flexibility and enhanced innovation during the early Paleozoic in particular, and during evolutionary radiations in general, have served as contrasting hypotheses for many studies, and have been complemented by renewed attention to the influence of the context of abiotic environmental change (Valentine 2004).

Against this backdrop, the quantification of morphological disparity and of morphospace occupation emerged as a major research program in evolutionary paleobiology (e.g., Foote 1991, 1997; Gould 1991; Briggs et al. 1992; Wills et al. 1994; Conway Morris 1998; Valentine 2004). This alternative view of macroevolution effectively revitalized the practice of evolutionary paleobiology, and represented a new ''way of seeing'' large-scale evolution, complementary to and enriching of more classical taxonomic diversity descriptors of macroevolutionary patterns and processes. The study of disparity and morphospaces was mainly stimulated by the prospect of more objectively characterizing morphological signatures of diversification. In this context, patterns of morphological disparity and taxonomic diversity are often discordant and for this very reason highly informative (e.g., Foote 1993a).

Despite its scope, this research program is still a relatively young enterprise, and most studies have focused on the relationship between taxonomic diversity and morphological disparity through time, and on the ecological or developmental meaning of morphological and taxonomic signatures of evolutionary radiations and diversification in general. A variety of groups (arthropods, echinoderms, mollusks, and brachiopods) have been studied in this manner and, inductively, a few tentative generalizations have emerged (see Foote 1996, 1997; Valentine 2004).

On the other hand, although disparity is now recognized as an appropriately rigorous measure to test hypotheses of differential constraint over time and to address its causes, geographic correlates of diversification have rarely been incorporated into disparity studies. Theoretically and empirically, the geographic context of morphological diversification presents itself as potentially important in terms of both correlation and causation, and is eminently tractable given the paleogeographic data available. As is already the case with taxonomic diversity (Jablonski 1986, 1987, 1993, 1998; Jablonski and Bottjer 1991), the possibility of meaningful geographic correlates of disparity dynamics could be conducive to a better and broader understanding of the spatial context of morphological diversification. In this paper, we explicitly address geography along with diversity and disparity, and attempt to develop a quantitative index to facilitate comparisons.

In the arena of quantification of morphology itself, Gould's (1991) compelling case for ''why we must strive to quantify morphospace'' motivated the rigorous characterization of morphospaces and of the dynamics of morphological disparity, understood as a distinct and relatively objective aspect of biodiversity. However, a real challenge persists: making objects and variables commensurate.

The problem of quantification of data is a perennial one, having already been recognized as fundamental 60 years ago, with Woodger's (1945) critique of D'Arcy Thompson's transformation grids and its limits. More recently, Bookstein (1994: p. 220) provided this assessment regarding morphometric studies on macroevolutionary scales: ''No important evolutionary change can be captured persuasively in the language of morphometrics.'' Later, referring to ''the incoherence of any legible geometric metaphor for ''morphospace'' above the species level,'' he states: ''The fundamental analogy between a morphospace . . . and a vector space of shape descriptors quickly becomes untenable as the relevant range of shapes broadens'' (Bookstein 1994). Perhaps the survival of disparity and mor-

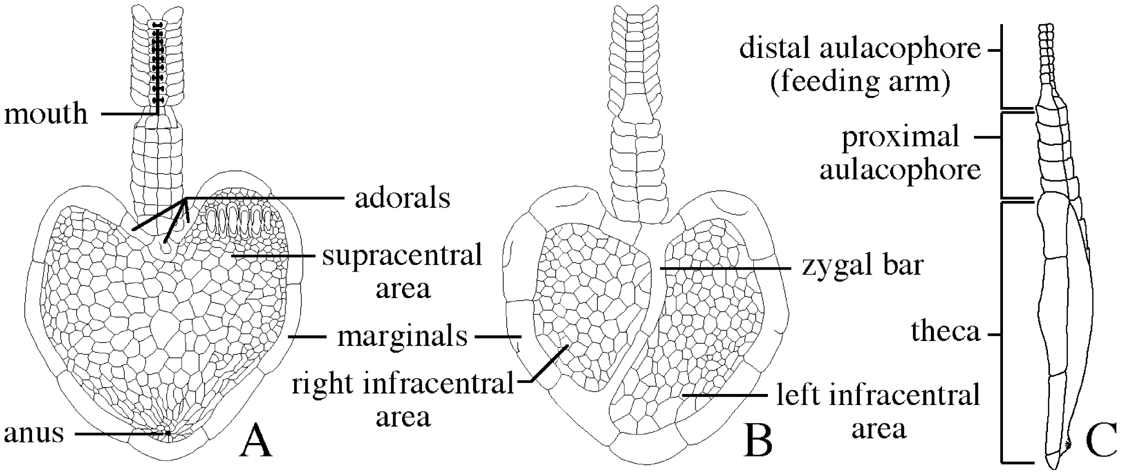

FIGURE 1. Stylophoran morphology: *Phyllocystis blayaci* (Cornuta), Early Ordovician, Montagne Noire (France), about ×2.2 (redrawn and modified after Ubaghs 1970). A, Upper view. B, Lower view. C, Left lateral aspect.

phospace studies lies in the multiple meanings of "shape," a nontrivial issue. In any case, Gould himself also voiced some doubts (1991: p. 421): "I do confess some fears that, in toto, the question of morphospace may be logically intractable, not merely difficult."

In other words, a variety of groups with puzzling morphologies discourage quantification and do not immediately lend themselves to a morphometric study with prescribed methods. Often, even within a higher taxon, interspecific variation appears difficult to quantify and interpret, given the various scales of morphological organization and homology. Is there a solution? Perhaps, if one is willing to consider a pluralistic approach in which several techniques are combined and pragmatically explored. We argue that one can, and must be willing, to abandon the hope of uniformly applying one's favored technique in some instances, whether traditional, outline-based, or landmark-based. Instead, we must strive to be pluralistic and flexible in the methods we apply. Exactly how to do so remains an open question, and there may be several answers. Here we provide an empirical case study to address the issue in a macroevolutionary context.

In this paper, the class Stylophora has been chosen as a model to document the initial diversification of the phylum Echinodermata. Stylophorans are one of four classes formerly included in the subphylum "Homalozoa" (David et al. 2000). Stylophorans are an extinct class of echinoderms (about 120 species and 66 genera) that offers the possibility to illustrate the complete evolutionary history of an echinoderm clade, from their initial radiation in the Middle Cambrian to their decline and final disappearance in the late Carboniferous.

Stylophorans are a major component of Late Cambrian to Early Ordovician echinoderm faunas (Guensburg and Sprinkle 2000; Lefebvre and Fatka 2003). They have been recorded from all around the world, with the exception of Antarctica. A relatively good phylogenetic framework is available for the class, which is usually subdivided into the two monophyletic orders Cornuta and Mitrata (Ubaghs 1968; Parsley 1988; Lefebvre 2001; Sprinkle and Guensburg 2004). All stylophorans share the same basic anatomical organization, with their body consisting of two well-defined regions: the aulacophore and the theca (Fig. 1) (Ubaghs 1961, 1981; Chauvel 1981; Parsley 1988; Lefebvre 2001). The aulacophore is a delicate, flexible, tripartite appendage. It is a functional, composite structure comprising a feeding arm (distal regions), and an exothecal extraxial extension (proximal portion; David et al. 2000). The mouth is located at the base of the feeding arm (Ubaghs 1961; Nichols 1972; David et al. 2000). The theca is a massive, flattened, asymmetrical extraxial calcite box, which enclosed most organs in life. This anatomical interpretation of stylophorans is root-ed in the Extraxial Axial Theory (Mooi et al. 1994; Bergström et al. 1998; David and Mooi 1999; David et al. 2000). However, the results of this paper are not conditioned on this theory, and the only prerequisite is that Stylophora corresponds to a monophyletic group, which is now widely accepted (e.g., Peterson 1995; Parsley 1997; Sumrall 1997; Ruta 1999a). Number, morphology, and arrangement of thecal skeletal elements (plates) are constant and diagnostic of a given species of stylophoran (Lefebvre 2001). A solid, well-established model of homologies has been proposed to identify equivalent skeletal elements among stylophorans (Lefebvre et al. 1998; Lefebvre and Vizcaïno 1999; Lefebvre 2000a,b, 2001). Such a model of plate homologies allows direct interspecific comparisons and the use of a variety of morphometric methods to quantify disparity. Although disparity could be quantified in terms of total change with phylogenetic measures (Smith 1994; Wills et al. 1994; Wagner 1995; Eble 2000), no morphospace would be made explicit, and its differential exploration would be difficult to evaluate in terms of phylogeny alone. In contrast, disparity as net change (Foote 1995, 1996) emphasizes both actual and possible locations of taxa in a multidimensional space of traits. Thus, morphospace itself is made explicit in discourse, analysis, representation, and interpretation. The patterns documented by using this approach are independent of any given phylogeny and of the phylogenetic position of the Stylophora as a group, whether within or outside the echinoderms.

Material and Methods

Sampling.—Data were collected at the species level, based on a comprehensive, nearly complete sample of stylophoran taxa. This choice was motivated by the small number of species described so far in the class (about 120), by the presence of great morphological variation within some genera (e.g., in *Scotiaecystis*), and so as to avoid problems related to the definition of genera, given that there is more consensus about the identity of species than of genera. For example, all workers distinguish the four species *P. africana*, *P. buretti*, *P. flemingi*, and *P. garratti*, included here in the genus *Placocystella* (following Lefebvre 2001), even though they were traditionally considered as belonging to four different genera (Caster 1983; Parsley 1991, 1997; Ruta 1999b; Ruta and Jell 1999e). In this context, stylophoran disparity has been estimated from the largest possible sample of well-preserved forms, including 88 species and 61 genera, and corresponding, respectively, to 73.3% and 92.4% of all forms described to date. This sample includes the two most primitive known stylophoran species (genus *Ceratocystis*) and representatives of the two monophyletic orders Cornuta and Mitrata. Here we consider cornutes and mitrates as clades, following phylogenetic analyses by Lefebvre and Vizcaïno (1999) and Lefebvre (2001). The identification of plate homologies within stylophorans strongly supports the view that the ''ankyroids'' of Parsley (1997) are a polyphyletic assemblage based on superficial similarities (Lefebvre 2001). In our analysis, 38 of 49 species (77.5%), and 27 of 30 genera of cornutes (90%), and 48 of 69 species (69.6%), and 33 of 35 genera of mitrates (94.3%) have been considered (see supplementary materials online at http://dx.doi.org/10.1666/05044.s1).

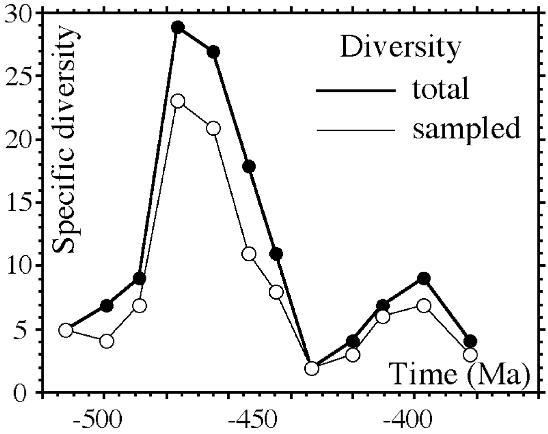

FIGURE 2. Stylophoran taxonomic diversity: comparison of sampled and total number of described species.

Thirty-two species (five genera) were excluded from the analysis. However, this did not affect the pattern of stylophoran diversity through time (Fig. 2). Taxa were excluded for the following reasons: (1) they are known only from isolated skeletal elements (e.g., the cornute *Babinocystis dilabidus*, most kirkocystid mitrates); (2) they were described from a single, incomplete specimen (e.g., the cornutes *Hanusia obtusa*, *Thoralicystis zagoraensis*, *Trigonocarpus singularis*); (3) their morphology is too poorly known, owing to disarticulation, poor preservation, and/or difficulty in discerning plate boundaries (e.g., the cornute *Acuticarpus delticus*, the mitrates *Dalejocystis casteri* and *Mongolocarpos minzhini*); (4) there is no reconstruction of their morphology available in the literature (e.g., the mitrates *Enoploura balanoides*, and ?*Mitrocystites styloideus*); (5) they possibly represent junior synonyms of taxa included in the analysis (e.g., *Anomalocystites disparilis* is a possible junior synonym of *A. cornutus*, after Parsley 1991). Furthermore, the exclusion of about 26.7% of stylophoran taxa for mostly preservational reasons appears to be unbiased with respect to the two major stylophoran groups, as comparable proportions of cornutes (22.5%) and mitrates (30.4%) were not sampled. However, a closer examination of excluded taxa suggests that the occurrence of poorly preserved species is not completely random within subgroups: for example, 66.7% of peltocystid mitrates have been excluded from the analysis, as most of their species were described on the basis of isolated skeletal elements (e.g., most species of the genus *Anatifopsis*). It should be stressed, however, that the small number of peltocystids included in the analysis is not expected to alter the overall pattern of stylophoran disparity, as morphologies are very conservative in this group of mitrates. For example, the morphologies of excluded taxa such as *Anatifopsis balclatchiensis* (Upper Ordovician) and ?*Mitrocystites styloideus* (Early Devonian) look very similar to that of the included species *A. trapeziiformis* (Early Ordovician).

Whenever complete specimens were not available, we relied on composite reconstructions, which are widely accepted. This was necessary because fossil remains of stylophorans are almost always found more or less disarticulated, distorted, and/or incomplete, so that reconstruction of their morphology is frequently based on several individuals. This was possible because intraspecific morphological variation, when documented in stylophorans, is in most cases very limited and can be neglected in comparison with interspecific variation (Chauvel 1941; Ubaghs 1968, 1979; Jefferies 1984; Ruta 1998; Lefebvre 1999; Ruta and Jell 1999d). Similarly, ontogenetic variation was not considered because it is very limited, with isometric growth being characteristic of most stylophorans. Reconstructions of stylophorans used in this analysis have been extracted from the relevant literature (see supplementary materials).

Choice of Anatomical Scheme.—The stylophoran theca (Fig. 1) is an extraxial ''box'' with a stable plate pattern, made of a reduced number of plates but still having the potential for local variation (extraxial regions are relatively free of constructional limitations as compared to regions associated with the axial component [Mooi and David 1998; David and Mooi 1999]). This stability allows the identification of homologous skeletal thecal elements in all stylophorans (Lefebvre et al. 1998), thus permitting the comparison of the wide array of thecal morphologies exhibited by cornutes and mitrates. Here, we classically treat the flat surface of the theca as homologous in cornutes and mitrates (Ubaghs 1968, 1981; Chauvel 1981; Parsley 1988, 1997; Lefebvre 2000a, 2001; but see Jefferies 1968, 1999). The aulacophore has been discarded from the study for two main reasons: (1) it is the most delicate and brittle portion of the organism, and it is thus seldom preserved (Lefebvre et al. 1998; Ruta 1999a)—the precise length and morphology of the distalmost portion of the aulacophore has been only rarely documented (Ubaghs and Robison 1988; Ruta and Bartels 1998; Sumrall and Sprinkle 1999); (2) its morphology, and especially that of its distal portion (arm), is partly composed of axial skeleton and thus is much less variable than the extraxial theca; the morphology of the appendage is accordingly very conservative and uniform across all stylophorans (Ubaghs 1968, 1981; Lefebvre 2001).

Plate Homologies.—Three main systems of plate homologies have been proposed for stylophorans: the ''calcichordate'' (Jefferies and Prokop 1972; Jefferies 1986; Cripps and Daley 1994), the ''ankyroid'' (Parsley 1997; Ruta 1999a), and the ''*Ceratocystis*'' models (Lefebvre and Vizcaïno 1999; Lefebvre 2000b, 2001). The calcichordate system of plate homologies

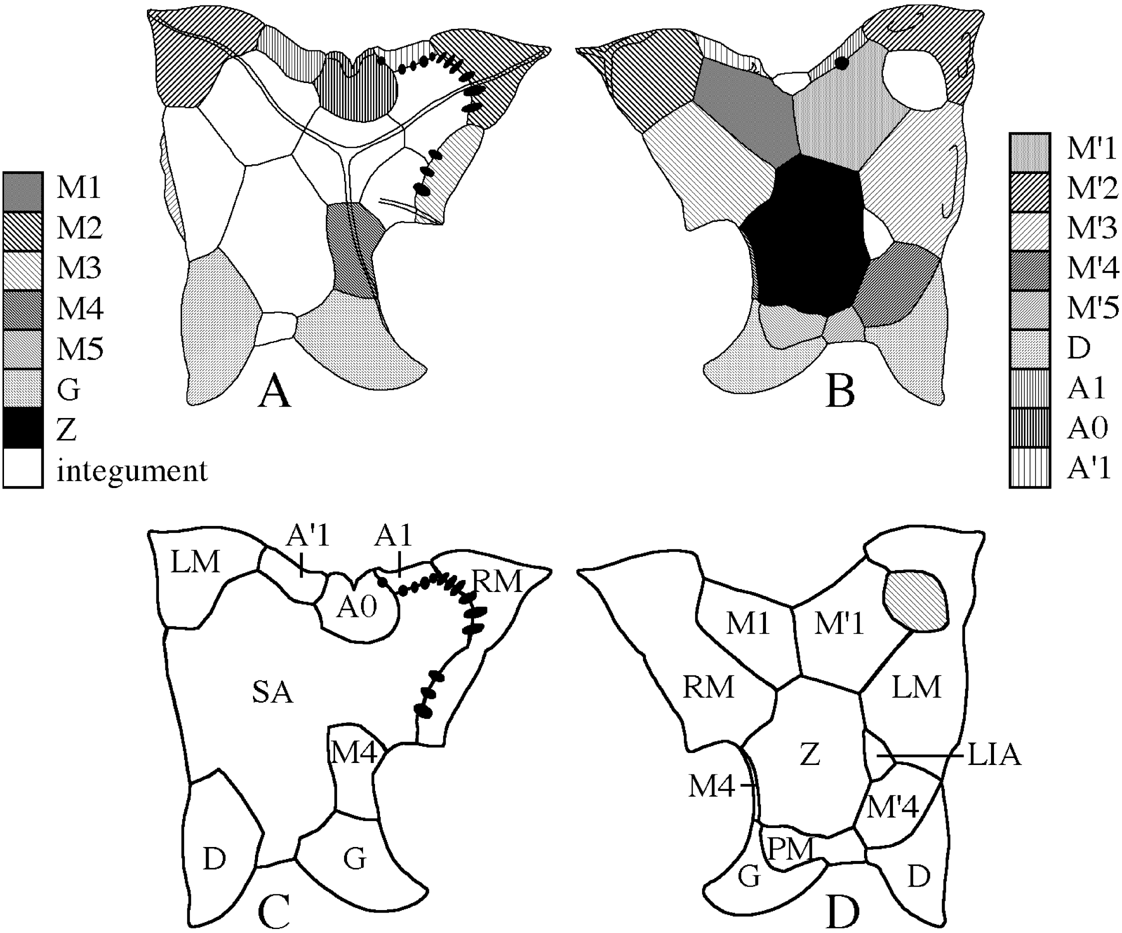

FIGURE 3. Theca of the primitive stylophoran *Ceratocystis perneri*, Middle Cambrian, Bohemia (Czech Republic), about ×1.5 (redrawn and modified after Ubaghs 1968). A, B, Identification of plate homologies. A, Upper surface. B, Lower surface. C, D, Surfaces used for morphometric analysis. C, Upper surface. D, Lower surface. See text for abbreviations.

is well suited for recognizing homologies within each stylophoran order, but it fails in identifying equivalent skeletal structures in cornutes and mitrates (Ubaghs 1981; Ruta 1999a; Lefebvre 2000a; Marti-Mus 2002). In turn, the identification of homologous elements is sometimes ambiguous in the ankyroid system because of superficial similarities in shape and/or position (Lefebvre 2001). In contrast, the *Ceratocystis* system suggests that the identification of homologies can be deduced in all stylophorans from a comparison of their morphology with that of the most primitive known member of the class, *Ceratocystis* (Fig. 3A,B). This system, which is adopted below, consistently allows the identification of homologous skeletal elements in both cornutes and mitrates, whatever their number of plates and the shape of their theca (e.g., boot-shaped, heart-shaped). The *Ceratocystis* model of plate homologies uses the plate terminology first applied to mitrates by Jaekel (1901) and later extended to cornutes (Ubaghs 1963). In this terminology, the insertion of the aulacophore is considered as a reference point, such that all marginals (M) and adorals (A) to the right of it are designated Mn and An, and those to the left of it, M′n and A′n (with n as a number indicating the position of the plate away from the insertion of the aulacophore; n = 0 in the case of a plate in central position). However, this terminology was adjusted (following Lefebvre and Vizcaïno 1999) so that putatively homologous plates are given the same name.

Number, morphology, and arrangement of thecal plates are constant and diagnostic for any given species of stylophoran, but highly variable from one species to another. A stylophoran theca basically comprises two infracentral areas (left and right), one supracentral area, and 16 major plates, consisting of five pairs of left and right marginals, three adorals, one posterior zygal plate (Z), and two posterior elements (glossal and digital). However, additional plates are sometimes present: cothurnocystid marginal (Mc) in some cornutes, and posterior plates (PP_1, PP_2) in some mitrocystitid mitrates. Consequently, the theca of some stylophorans comprises more than 16 major plates (e.g., 17 in the primitive cornute *Cothurnocystis fellinensis*). Moreover, the right infracentral area and/or several major skeletal elements are frequently lost in derived forms, typically characterized by a theca consisting of a reduced number of elements (e.g., only ten major plates in the cornute *Lyricocarpus*, and in kirkocystid mitrates). The number of plates seems to be particularly reduced in the most recent stylophoran, *Jaekelocarpus oklahomaensis*, with only nine major plates and a single integumentary area (Kolata et al. 1991; Domínguez et al. 2002).

To perform the analysis of stylophoran disparity optimally, it was necessary to group some plates, so as (1) to minimize the effect of large variation in the number of major skeletal elements and integumentary areas in cornutes and mitrates, and (2) to reduce the uncertainty associated with the identification of some thecal plates. Whatever the adopted model of plate homologies (''calcichordate,'' ''ankyroid,'' or ''*Ceratocystis*''), several thecal elements (e.g., M1, M′1, adorals) are considered as equivalent by most authors (see Marti-Mus 2002: Fig. 9 for an overview of unambiguous plate homologies within cornutes). In this study, each region of ''problematic'' thecal elements was treated as if it constituted a single thecal plate: for example, the left portion of the marginal frame delimited by M′1, the left infracentral area, and M′4 was treated as a single morphological unit (''left marginals'' or ''LM''), whatever its number of elementary plates and their putative identification. Consequently, not only do such groupings of thecal elements follow the homology of subsets of plates, but they also dramatically reduce the sensitivity of the analysis to the adoption of one particular model of plate homologies.

All in all, 17 surfaces have been retained for the analysis (see Fig. 3C,D): (1) thecal outline, TH; (2) M_1; (3) M'_1; (4) right marginals, RM ($M_2 + M_3 + Mc$); (5) left marginals, LM ($M'_2 + M'_3$); (6) M_4; (7) M'_4; (8) glossal, G; (9) digital, D; (10) posterior zygal plate, Z; (11) posterior marginals, PM ($M_5 + M'_5 + PP_1 + PP_2$); (12) plates of the right infracentral area, RIA; (13) plates of the left infracentral area, LIA; (14) right adoral A_1; (15) median adoral, A_0; (16) left adoral, A'_1; and (17) plates of the supracentral area, SA. The central marginal M_0 of *Ceratocystis* has not been considered in the study because it is an autapomorphy of this genus.

The profile of the theca is sufficiently low so that it is possible to consider that projections (drawings) of the plate patterns are without distortion. Portions of plates or groups of plates shared by both the lower and the upper thecal surfaces were considered as independent elements in each case and treated separately. This is justified because in most cases their extension is different on the lower and upper thecal surfaces. The only example of surfaces showing similar extensions in upper and lower views are the glossal (G) and digital (D), where these skeletal elements occur in the form of exothecal processes, articulated to the posterior end of theca (e.g., in the cornute *Cothurnocystis*, and in most anomalocystitid mitrates). The three adorals (A_1, A'_1, A_0), and the supracentral area (SA) are restricted to the upper thecal side in almost all stylophorans. However, A_1 and A'_1 can extend onto the lower side (e.g., *Ceratocystis*), and sometimes overlap the lateral edges of the underlying marginals (e.g., *Anatifopsis*, *Balanocystites*). Extension of supracentrals onto the lower side occurs in the mitrate *Lagynocystis*. Consequently, so as to avoid redundancy and autocorrelation related to the extension of surfaces from the upper side toward the lower side of the theca (e.g., overlap of marginal elements), no portions of A_1, A'_1, and SA located on the lower side of the theca have been considered in the analysis.

Quantification of Form.—Stylophoran morphology has been quantified with morphometric parameters derived from image analysis of homologous skeletal regions: plates, on the one hand, and outlines of the theca, on the other. The aim is to use the geometry of both the whole theca and its individual plates as morphological descriptors to measure stylophoran disparity. This combined approach also makes it possible to compare global and local aspects of stylophoran shape. Stylophorans constitute an appropriate model for the application of such morphometric methods, as they are a relatively small group with clearly identified plate homologies, and with all species sharing a standard organization. Consequently, given the aim of the study and the intrinsic characteristics of stylophoran morphology, it appears that morphometric methods based on the geometry of both thecal outlines and homologous individual plates constitute a good compromise approach to quantify disparity in the group. However, other descriptors of shape could have been used. Procrustes methods based on landmarks, for example, would have allowed us to estimate morphological variety among stylophorans by comparing actual architectural relationships between sets of plates, rather than on plate-by-plate geometry per se. However, Procrustes methods would not have permitted a comparison between thecal and plate geometries. Fourier methods are another powerful tool allowing precise description of outlines of surfaces such as the theca or individual plates, but such precision is achieved at a cost of biological interpretability; this is particularly true in the present situation, where the number of distinct surfaces is considerable, and the too numerous Fourier coefficients would have been almost impossible to relate to morphological differences. In addition, the presence of distorted specimens inevitably leads to imprecise reconstructions with uncertain reliability of the fine details that Fourier analyses are supposed to capture. Therefore, we preferred to use variables that convey information more roughly, but are also more reliable at the level of the whole organism.

Morphometric variables were measured using the software OPTIMAS (version 6). The measurements chosen were a subsample of the total number available, and the choice was carefully made in light of the stylophoran body plan. Finally, seven parameters (out of about 40) were specifically chosen for their ability to characterize all surfaces concerned. Together, they capture distinct yet complementary aspects of plate and thecal morphology. Special emphasis was placed on variables considered the most pertinent for describing the large array of plate outlines in stylophorans (e.g., sub-circular to elliptical, sub-quadrate to polygonal, rodlike, Y-, T-, or C-shaped). Redundant, uninformative, and/or uninterpretable (from a biological point of view) parameters were discarded. Of the seven retained parameters, four (1 to 4 below) were applied to all 17 areas, two (5 and 6 below) only to the 16 plates and groups of plates, and one (7 below) only to the whole theca. Definitions for these variables are as follows: (1) Circularity (C) expresses the ratio of the square perimeter divided by the area. Circularity is minimum for a circle ($C = 12.57$), which represents the smallest perimeter for a given area. Low circularity values correspond to rounded, massive surfaces, and high values to long, narrow, and/or digitated surfaces. (2) Rectangularity (R) corresponds to the ratio of the surface area divided by the area of the square box (parameterized by the major and minor axes) including it. (3) Relative length major axis (RLMA) is the ratio of the surface area divided by the square length of the major axis of the corresponding surface. (4) Coefficient of variation of Feret diameters (CVFD) represents the standard deviation as a proportion of the mean of 16 successive diameters measured every 11.5° around the surface. (5) Relative area (RA) expresses the ratio of a given surface area divided by the area of the whole theca. (6) Relative perimeter (RP) corresponds to the ratio of a given surface perimeter divided by the thecal perimeter. (7) Scaled area (SA) is expressed in mm^2 (chosen size estimate of the whole theca).

These variables were used to produce three separate raw data matrices: (1) for the whole theca, comprising 88 species and five morphometric variables (C, R, RMAL, CVFD, SA); (2) for plates and groups of plates of the lower surface, including 88 species and 72 morphometric variables (six variables measured for each of the 12 plates or groups of plates: C, R, RMAL, CVFD, RA, RP); and (3) for plates and groups of plates of the upper surface, including 88 species and 84 variables (six variables measured for each of 14 plates or groups of plates).

Missing plates occasionally reflect imperfect preservation of posterior thecal region (D and G), but in most cases they reflect true absences. Coding in such situations proceeded as follows. When due to imperfect preservation, entries were coded as missing values. When due to true plate absence, entries were coded as zero when logically interpretable (RLMA, CVFD, RA, RP), or as a missing value when this was mathematically impossible (C and R).

It was not necessary to take into account measurement error given that, at the scale of this study, observed interspecific differences are several orders of magnitude larger than those induced by drawing error in the reconstruction of plate architecture.

To evaluate the persistence of correlations among the variables considered in the three modules, we calculated Van Valen's measure of dimensionality or non-redundancy (Van Valen 1974) for all pairwise comparisons between variables pertinent to each of the three modules. Figure 4 illustrates the result for the upper surface only, but the degree of non-independence is highly significant for the three modules, although weaker for the theca.

Data Analyses.—Gower's coefficient of similarity (Gower 1971) and principal coordinates analysis (PCO; Gower 1966) were used to analyze the data. Although all variables were continuous, Gower's coefficient and PCO are appropriate here so as to allow every species to be considered regardless of missing values. In addition, given that the variables are not all strictly commensurate, PCO is the technique of choice. PCO axes were used to project the original, raw multidimensional space onto a smaller, more informative number of dimensions. In this PCO space, species are naturally ordinated in proportion to morphological distance. Here, we treat PCO ordinations as providing a useful graphical representation of the general patterns of empirical morphospace occupation.

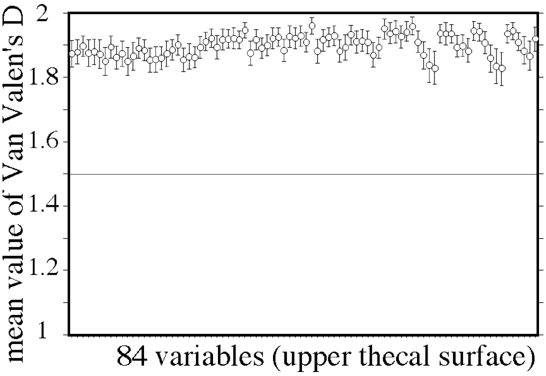

FIGURE 4. Diagram illustrating the degree of pairwise independence between the 84 variables of the upper surface using Van Valen's (1974) measure of dimensionality (D). Mean value of D is shown for each variable, as well as the 95% confidence interval. The degree of non-independence is highly significant ($p < 0.0001$, sign test with expected null value of 1.5).

A separate PCO analysis (using Gower's distance-transformed coefficient for quantitative characters) was performed on each of the three data matrices referred to above. These include (1) whole theca, (2) plates of lower thecal surface, and (3) plates of upper thecal surface. Given that our purpose was to consider all taxa and all three morphological contexts together in a single, comprehensive analysis, we performed a ''meta-PCO'' (similar to that proposed by Klingenberg [1996] for ''meta-PC'') based on the PCO axes (treated as new variables) retained from each of the three analyses above. A meta-PCO allows for a balance between the three anatomic modules considered (whole theca, upper surface, lower surface), although they are each depicted by very different numbers of variables (5, 84, and 72 respectively). The number of PCO axes retained was based on the decay of the eigenvalues. The quality of the reduced space representation (analogous to the cumulative proportion of variance in principal components analysis) was estimated as the ratio of the sum of the eigenvalues of the retained axes to the total sum of the eigenvalues. Because of neg-

TABLE 1. Timescale, total number of stylophoran genera and species, and sample sizes. Age at base of intervals in millions years before present (Ma), and durations in millions of years (Myr) based on data from the International Stratigraphic Chart (Gradstein et al. 2004), and the new Ordovician stratigraphic chart (Webby et al. 2004a). Abbreviations in parentheses are also used in the figures and the online appendix.

Stratigraphic interval	Age at base (Ma)	Duration (Myr)	No. of genera		No. of species	
			Total	Sampled	Total	Sampled
Pennsylvanian (Pe)	318.1	19.1	1	1	1	1
Middle Devonian (MD)	397.5	12.2	4	3	4	3
Emsian (Em)	407.0	9.5	7	6	9	7
earliest Devonian (eD)	416.0	9	6	6	7	6
late Silurian (lS)	422.9	6.9	4	3	4	3
early Silurian (eS)	443.7	20.8	2	2	2	2
Ashgill (As)	449	5.3	8	8	11	8
Caradoc (Ca)	460.9	11.9	10	9	18	11
Middle Ordovician (MO)	471.8	10.9	19	19	27	21
Arenig p.p. (Ar)	478.6	6.8	21	19	29	23
Tremadocian (Tr)	488.3	9.7	7	7	9	7
Late Cambrian (LC)	501.0	12.7	6	4	7	4
Middle Cambrian (MC)	513.0	12	4	4	5	5

ative eigenvalues resulting from imbalance in the distance matrices due to missing values and non-Euclidean property of the resulting distance, these sums were corrected according to the absolute value of the largest negative eigenvalues (see Legendre and Legendre 1998). Approximately 70% of the cumulative variance corresponded to most of the structure in all three analyses. Therefore, using this criterion, five PCO axes were retained for the whole theca, eight for the lower surface, and 8 for the upper surface, yielding 21 ''meta-variables'' for the meta-PCO. In this way, a global morphospace projection reflecting different aspects and scales of stylophoran variation was possible. All retained axes have larger values than the absolute value of the largest negative eigenvalues. Therefore, the Euclidean approximation of the reduced space is meaningful (Legendre and Legendre 1998).

In addition, cluster analysis was used to identify morphological clusters. This analysis was performed using Euclidean distances and unweighted pair-group method using arithmetic averages as aggregation rule. A threshold was identified according to the importance of steps on the aggregation graph, and the fine-scale structure of the dendrogram was not kept. The resulting 11 morphological groups are hierarchically clustered into three main sets (I to III), and were used in turn as morphological units in further analyses.

Stratigraphic Intervals and Resolution.—The time frame of the analysis (about 215 Myr) encompasses the entire evolutionary history of the class Stylophora, from the Middle Cambrian (*Archaeocothurnus*, *Ceratocystis*, *Ponticulocarpus*, *Protocystites*), to the Pennsylvanian (*Jaekelocarpus*). It is worth pointing out that the recent discovery of *Jaekelocarpus* has considerably extended the stratigraphic range of the class from the Middle Devonian to the late Carboniferous (Kolata et al. 1991; Domínguez et al. 2002). However, the presence of a single species more than 65 million years after the Middle Devonian is uninformative. Thus, for the purposes of reconstructing disparity history, this interval was discarded from the study. Even so, the species was retained for its contribution to the total empirical morphospace. The 12 stratigraphic intervals used in the analysis represent a compromise between sample size and time resolution (Table 1). Ages and durations of time intervals were based on the IUGS timescale produced by Gradstein et al. (2004), and the revised Ordovician stratigraphic chart of Webby et al. (2004a). The duration of intervals is between 5.3 and 20.8 Myr, with a mean value of 10.7 Myr, and duration of 9–13 Myr for 8 of 12 of them. The duration of intervals and the number of taxa per interval (total number and/or number of sampled taxa) are clearly not correlated ($r^2 = 0.198$, $p = 0.128$; Table 1).

Quantification of Geographic Space Occupation.—The aim was to define a semiquantitative index that could be used to draw curves of paleo(bio)geographic dispersion through time, comparable to curves of taxonomic and morphological diversity. Specifically, our goal was to use a biogeographic index that both is relevant for large-scale studies and displays the same degree of generality with which diversity and disparity changes were documented (only 12 stratigraphic intervals between the Middle Cambrian and the Middle Devonian). Therefore, such an index differs from most ''traditional'' paleogeographic indices, usually designed for comparison of faunal compositions and/or quantification of biogeographic affinities between regions. Geographic space occupation was quantified on both a global and a regional scale.

The global scale reflects overall colonization and dispersion patterns around continental margins, with high precision but low resolution, given the relatively small number of sampling units (continents). Estimation of global-scale dispersion is based on available data concerning the absence/presence of stylophorans around paleocontinents (as defined on paleoreconstructions; e.g., Scotese and McKerrow 1990; Scotese 2001), which reflect general dispersion events. In contrast, the local scale expresses the number of distinct regional occurrences around the same paleocontinent. Although the local approach is more precise, and conveys more information than the global one, the signal is more influenced by preservational biases: the presence of stylophorans in a regional entity is partly correlated to outcrop area (volume and accessibility of rock strata), number of echinoderm Lagerstätten, and effort of sampling (see Smith 1988). Several weighting combinations between continental and regional entities have been explored. All combinations are strongly correlated to each other ($r^2 \geq 0.90$) and lead to very similar ''paleogeographic curves.'' For the purpose of this paper, a ''mixed'' paleogeographic index [Bi] was calculated for each time interval, as the sum of both relative global dispersion (number of distinct ''continental'' occurrences [Co] divided by total number of paleocontinents [NC] ever colonized) and relative local dispersion (number of distinct regional occurrences [Ro] divided by total number of regions ever occupied [NR]). Therefore, $Bi = Co/NC + Ro/NR$.

All stylophorans included in this study were collected on the continental margins of three paleocontinents: Baltica (Russia, Scandinavia), Gondwana (Africa, South America, Australia, southwestern Europe, Korea), and Laurentia (North America, northern Ireland, Scotland). However, by late Silurian times, Baltica and Laurentia had collided (Scandian orogeny) to form a single paleocontinent, Laurussia. The estimate of stylophoran global dispersion is not affected by the reduction in the number of major continental masses after the Silurian, as only one Laurussian species is considered (*Anomalocystites cornutus*). During the Ordovician, Avalonia (Belgium, England, most of Nova Scotia and New Brunswick, Wales) formed a fourth, separate, short-lived paleocontinent, which split off from the northwestern margin of Gondwana (Early Ordovician), drifted northward, and finally collided with Baltica (Ashgill to early Silurian; Cocks et al. 1997; Nance et al. 2002; Verniers et al. 2002). Consequently, Avalonian faunas exhibit strong Gondwanan affinities in the Early Ordovician, and increasing Baltic influences in the Late Ordovician (Cocks and Fortey 1990; Cocks et al. 1997). In this study, Avalonian stylophorans were considered as ''Gondwanan'' from the Middle Cambrian to the Darriwilian, and as ''Baltic'' from the Caradoc to the Middle Devonian. A fifth paleocontinent, Siberia, was not considered because the single known stylophoran reported so far from this region was too poorly preserved to be included (*Mongolocarpos minzhini*).

Seventeen distinct regional entities were considered: (1) eastern North America (Illinois, Indiana, Kentucky, Maryland, Missouri, New York State, Ohio, Oklahoma, Ontario, Quebec, Pennsylvania, Tennessee, Virginia, Wisconsin); (2) western North America (Nevada, Utah); (3) Argentina; (4) Australia (Victoria); (5) Bohemia; (6) Brazil (Paraná Basin); (7) England (Shropshire and Worcestershire) and Wales; (8) Germany; (9) Ibero-Armorica (western France, Spain, Portugal); (10) Korea; (11) Montagne Noire (southern France); (12) Morocco (Anti-Atlas); (13) New Zealand; (14)

Norway; (15) Scotland and Northern Ireland; (16) South Africa; (17) Tasmania.

Results and Discussion

Morphospace Ordination.—Principal coordinate analysis of the 21 ''meta-variables'' reveals considerable structure in the data, with about 27.5% of the variation expressed in the first three ''meta-axes.'' At face value, the amount of information conveyed in this compound analysis is smaller than that obtained in each of the three ''source'' analyses performed independently on the theca (63% of the variance in the first three axes), the lower surface (51.5% of the variance in the first three axes), and the upper surface (48.2% of the variance in the first three axes). Nevertheless, despite an unavoidable loss of resolution, the meta-PCO analysis has the advantage of constituting an integrative and heuristic approach allowing representation and visualization, however obliquely and partially, of a ''global'' morphospace that takes simultaneously into account three different aspects of stylophoran morphology. These three aspects are here viewed as the relevant organizational and variational modular regions of the phenotype (Eble 2004, 2005), and each modular region in turn can be expressed in terms of a partial morphospace. Combining partial morphospaces allows the portrayal of all sampled species in a single global morphospace, which is not the case for the source PCO analyses of the lower surface (six missing species) and of the upper surface (12 missing species; see supplementary materials). The meta-axes of the global PCO analysis reflect a multidimensional space in which ordination is possible for all sampled stylophorans, including partially preserved forms.

The projection of this multidimensional space in the plane defined by the first two meta-axes, i.e., meta-PCO1 (10.5% of the variance) and meta-PCO2 (9.5% of the variance), allows a partial yet still heuristically informative and practical visualization of broad morphospace occupation among stylophorans (Fig. 5). Occupation in general is not homogeneous, with several ''clouds'' or groupings situated at the periphery of an almost empty central ''zone,'' occupied only by a primitive form, *Ceratocystis vizcainoi*. The partitioning of the two main clades of stylophorans in this morphospace is relatively clear: cornutes show great variability along meta-PCO1 but reduced dispersion along meta-PCO2 (with almost exclusively positive values), whereas mitrates are characterized by great variability along the metaPCO2, and to a lesser extent also along meta-PCO1 (Fig. 5). As plotted, the two groups are relatively distinct, although there is a large zone of overlap representing convergent morphologies among certain mitrocystitid mitrates (e.g., *Ovocarpus*, *Vizcainocarpus*) and various derived cornutes (e.g., *Amygdalotheca*, *Lyricocarpus*). It is interesting to point out that the two primitive forms of the genus *Ceratocystis* appear in a position roughly intermediate between the clouds of points corresponding to cornutes and to mitrates. The partitioning of cornutes and mitrates in this global reference morphospace reflects quite well the preliminary results previously obtained by principal components analyses of the thecal outlines and of the lower surface (Lefebvre et al. 2003). In fact, those results suggested that although the distinction between cornutes and mitrates was very clear with respect to the morphology of plates in the lower surface, these two groups could not be distinguished on the basis of their thecal outlines. This indicates that very similar thecal outlines were independently achieved by the

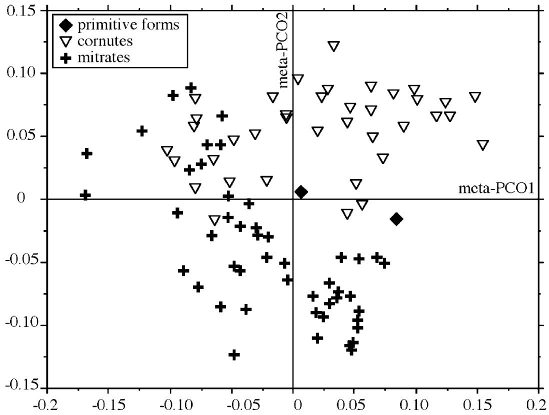

FIGURE 5. Plot of the global morphospace of the 88 sampled stylophoran species on the first two principal coordinates axes of the meta-PCO, with distinction between primitive forms, and representatives of the two main clades, cornutes and mitrates.

two clades, but with plates having different morphologies (Lefebvre et al. 2003). Similarly, the existence of a region of overlap between cornutes and mitrates in the global morphospace defined by the meta-PCO axes can be explained by the fact that variables describing thecal outline and variables describing plate morphology were both taken into account. In any case, the present study seems to confirm the existence of form convergences between the two groups (see Lefebvre 2001).

In order to minimize a priori taxonomic assumptions, and so as to better characterize the heterogeneities in occupation of stylophoran morphospace (the existence of a large zone of superposition between its two component groups suggesting that the classical distinction between cornutes and mitrates is not necessarily the most pertinent for describing disparity), several morphological subgroups of stylophorans were identified a posteriori, on the basis of hierarchical clustering of all pairwise distances. The application of this clustering procedure yielded a dendrogram of distances among different stylophoran species in the multidimensional space defined by the axes of the meta-PCO (Fig. 6). Eleven morphological subgroups (understood as operational subsets) were revealed. These 11 subsets can themselves be grouped into three main sets (I, II, and III), containing five (Ia–Ie), four (IIa–IId), and two subsets (IIIa, IIIb), respectively. Seven subsets comprise at least six species, but four subsets are small and contain only one (IIc, IId), two (Id), or three (Ie) taxa.

The first axis of the meta-PCO is mainly influenced by the general morphology of thecal contours (Fig. 7). This axis discriminates clearly stylophorans belonging to sets II and III, characterized by very asymmetrical and digitated thecal contours (thecal outgrowths, such as digital, glossal, and spinal; positive values of scores in meta-PCO1), from those in set I, which have symmetrical and massive thecae, without outgrowths (negative values in meta-PCO1). The second axis of the meta-PCO appears to reflect more the relative importance of integumentary areas (especially infracentral; Fig. 7). Meta-PCO2 thus separates quite clearly forms with large integumentary surfaces and, consequently, with a relatively large thecal width (set III, subsets Ia, Ic–Ie, and IIb), from forms with reduced or absent integumentary surfaces and with a narrower and more elongated theca (subsets Ib, and IIa, IIc, IId). The third axis of the meta-PCO is more difficult to interpret, but it shows a distinction between two ensembles of subsets: in one case, Ia, Ib, and IIIa (positive values), and in the other case, Ic–Ie, IIb, and IIIb (negative values); the remainder subset, IIa, is spread all along meta-PCO3 (taking both positive and negative values).

Set I comprises 36 stylophorans (10 cornutes and 26 mitrates), all characterized by massive thecae, symmetrical and without outgrowths, and with integumentary areas at times reduced (subset Ib), but more often relatively large (subsets Ia, Ic–Ie). The second set comprises 38 stylophorans (two primitive forms, 14 cornutes, and 22 mitrates) with an asymmetrical theca, sometimes with extensive outgrowths and infracentral areas (subset IIb), but more often reduced (subsets IIa, IIc, IId). Finally, set III comprises 14 cornutes that are very strongly asymmetric (boot-shaped theca), characterized by large integumentary areas (subset IIIa) and by large exothecal outgrowths (subset IIIb).

It is interesting to note that the general aspect of the dendrogram produced by hierarchical clustering for purely operational reasons resembles the general aspect of the cladogram produced by Parsley (1997, 1998). In effect, sets I and II bring together the ''ankyroid'' stylophorans (mitrates and symmetrical cornutes), whereas set III corresponds to cornutes with a boot-shaped theca. These observations suggest that the phylogenetic tree produced by Parsley (1997, 1998), which takes into account numerous characters based on the general morphology and the asymmetry of the theca, may be more similar in structure to a dendrogram than to a cladogram (see Lefebvre 2001).

The existence of convergent morphologies among cornutes and mitrates, for example between mitrocystitids and symmetrical cornutes (set I) or between asymmetrical cornutes and mitrates with posterior processes (set II), brings to the fore the issue of a possible relation between morphology and mode of life.

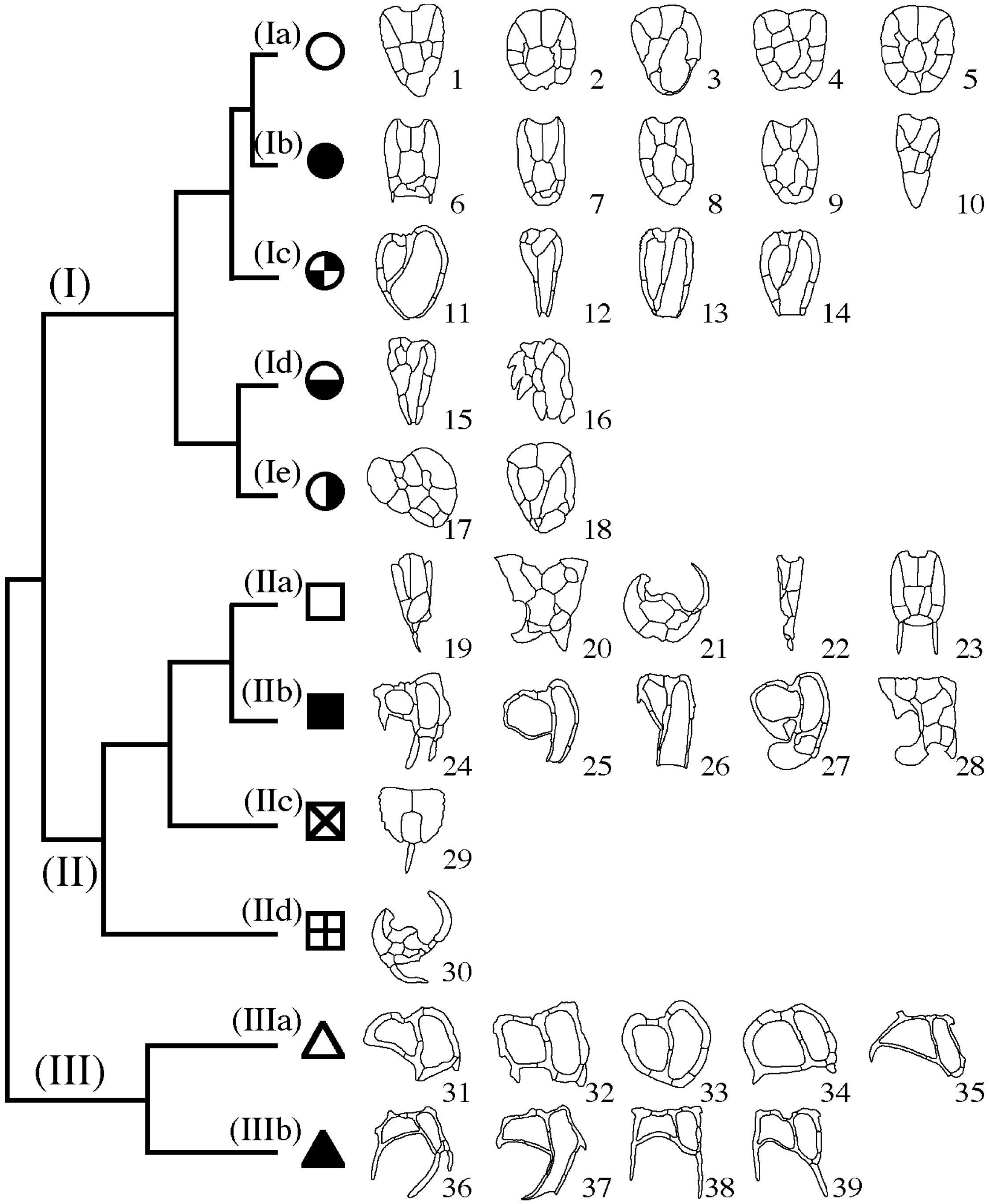

FIGURE 6. Dendrogram resulting from the hierarchical clustering of the global stylophoran morphospace (see Fig. 5), and showing the disconnection into three well-defined main morphological sets (I, II, and III), consisting of five (Ia–Ie), four (IIa–IId), and two (IIIa, IIIb) subsets, respectively. Morphologies included in each subset are illustrated by some significant taxa (all thecae illustrated in lower view, and showing surfaces used for morphometric analysis): 1, *Adoketocarpus acheronticus*; 2, *Aspidocarpus bohemicus*; 3, *Chinianocarpos thorali*; 4, *Mitrocystites mitra*; 5, *Ovocarpus moncereti*; 6, *Ateleocystites guttenbergensis*; 7, *Barrandeocarpus jaekeli*; 8, *Eumitrocystella savilli*; 9, *Mitrocystella incipiens*; 10, *Yachalicystis triangularis*; 11, *Amygdalotheca griffei*; 12, *Lyricocarpus courtessolei*; 13, *Nanocarpus milnerorum*; 14, *Reticulocarpos hanusi*; 15, *Ampelocarpus landeyranensis*; 16, *Prochauvelicystis semispinosa*; 17, *Lobocarpus vizcainoi*; 18, *Vizcainocarpus dentiger*; 19, *Balanocystites primus*; 20, *Ceratocystis perneri*; 21, *Diamphidiocystis drepanon*; 22, *Lagynocystis pyramidalis*; 23, *Placocystella africana*; 24, *Arauricystis primaeva*; 25, *Chauvelicystis spinosa*; 26, *Hanusia prilepensis*; 27, *Ponticulocarpus robisoni*; 28, *Protocystites menevensis*; 29, *Jaekelocarpus oklahomaensis*; 30, *Diamphidiocystis* sp.; 31, *Arauricystis occitana*; 32, *Cothurnocystis fellinensis*; 33, *Phyllocystis blayaci*; 34, *Scotiaecystis jefferiesi*; 35, *Thoralicystis griffei*; 36, *Cothurnocystis elizae*; 37, *Galliaecystis ubaghsi*; 38, *Scotiaecystis collapsa*; 39, *Scotiaecystis curvata*.

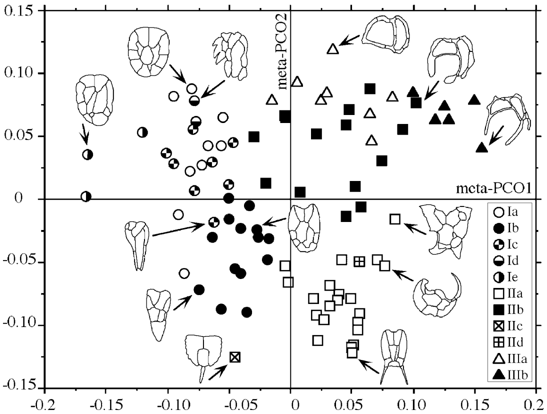

FIGURE 7. Plot of the global morphospace of the 88 sampled stylophoran species on the first two principal coordinate axes of the meta-PCO, with distinction between the 11 morphological subsets identified by hierarchical clustering (see Fig. 6).

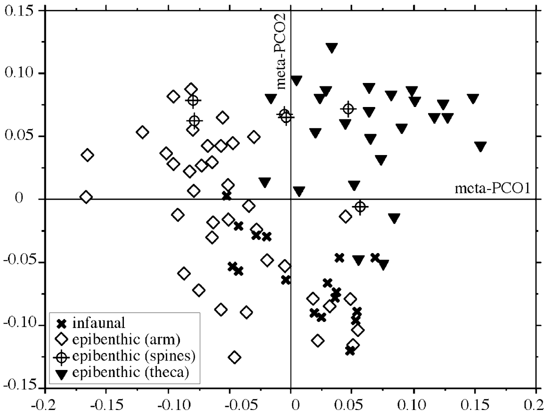

FIGURE 8. Plot of the global morphospace of the 88 sampled stylophoran species on the first two principal coordinate axes of the meta-PCO, with distinction between infaunal and various epibenthic forms.

Four major modes of life among stylophorans have been identified (Lefebvre 2003): one is endobenthic (theca buried under the substrate), and three are epibenthic, with the animal attaching itself to the substrate by means of thecal protuberances, spines arranged on the perimeter of the theca, or the arm. A general relationship seems to exist between morphology and mode of life (Fig. 8). In fact, meta-PCO1 discriminates quite well the epibenthic forms anchored with the arm (and having a rather symmetric theca; left of diagram) from the endobenthic and epibenthic forms clinging to the sediment by means of the theca (asymmetric forms and/or forms having exothecal outgrowths; right of the diagram). Similarly, meta-PCO2 separates quite well, on the right portion of the diagram, the epibenthic forms anchored by means of the theca or of spines (large integumentary areas, thecae staggered transversally; positive values on meta-PCO2) from the endobenthic forms (reduced integumentary areas, thecae staggered anteroposteriorly; negative values on metaPCO2). Therefore, it is probable that very similar morphologies, independently evolved in some cornutes and mitrates, show very similar modes of life, as exemplified in set I (epibenthic mode of life with anchoring by the arm). On the other hand, in set II the presence of exothecal outgrowths corresponds to two very distinct modes of life: epibenthic with anchoring by the theca (IIb in cornutes and IId in mitrates), or else endobenthic (only mitrates, IIa). A certain correspondence between thecal morphology and mode of life could be expected, given that the latter was partly deduced from the general aspect of the theca (Lefebvre 2003). However, there is no direct correspondence between thecal morphology and presumed mode of life, as the latter was also largely deduced from the morphology of the appendage (Lefebvre 2003), which is not considered herein. Moreover, several aspects of stylophoran thecal morphology are not correlated with functional morphology (e.g., asymmetry of lower thecal surface, with the zygal bar), but possibly reflect constructional constraints.

It is also interesting to note that certain morphological types were never developed in mitrates (e.g., set I), perhaps because such types are associated with a mode of life inherently uncommon in this clade (epibenthic with anchoring by the theca; e.g., *Diamphidiocystis*). Likewise, neither of the two main morphological types characteristic of burrowing forms was adopted by cornutes (subsets Ib and IIa). This suggests the existence, in each of the two clades, of functional limits and/or structural constraints intrinsic to their body plans, and impervious to convergent evolution. Thus, although convergence is relatively common, it is conditioned on the degrees of freedom established in the history of the clade.

Spatiotemporal Pattern of Stylophoran Diversification in Morphospace.—The spatiotemporal evolution of taxonomic and morphologic diversity may be followed in simplified fashion, by representing, for each of the 12 stratigraphic intervals considered (representing about 128 Myr from the base of the Middle Cambrian to the end of the Givetian), the distribution of various forms in the projection of the global morphospace and the corresponding paleogeographic dispersion. Thus, inspection of the temporal sequence of 12 morphospace projections on the meta-PCO1–metaPCO2 plane beside 12 associated ''snapshots'' of paleogeographic partitioning allows a generalized but heuristic assessment of the broad evolutionary dynamics of this class of echinoderms. A succession of five main phases is apparent and explained below.

Initially, from the Middle Cambrian to the Tremadocian (Fig. 9), stylophorans underwent an apparent increase in disparity, in spite of the relatively small sample sizes. Although members of only one main morphological set (II) were represented in the Middle Cambrian (subsets IIa and IIb), they were followed by two (I and II) in the Late Cambrian (subsets Ic, Ie, and IIb), and finally three (I, II, and III) in the Tremadocian (subsets Ic, Id, Ie, IIa, IIb, and IIIa). Therefore, in less than 35 Myr, stylophorans occupied all three distinct zones in morphospace; no other main morphological set would appear in the ensuing 180 Myr. This expansion in morphospace was accompanied by an even greater paleogeographic dispersion during the Cambrian, but it must be emphasized that disparity remained low within each of the three zones considered. Conversely, in the Tremadocian, disparity increased strongly, while paleogeographic dispersion was extremely low (restricted to the northern-Gondwanan margin).

During the early and middle Arenig (Fig. 9), stylophorans displayed a marked increase in taxonomic diversity, yet disparity remained comparable to that of the Tremadocian, despite the appearance of two additional morphological subsets (Ia and IIIb). This interval seems to correspond to a simple filling of morphospace previously partitioned in the Tremadocian. This important Arenigian phase of taxonomic diversification occurred exclusively on the north-Gondwanan margin, i.e., the same paleogeographic region as in the Tremadocian.

Stylophoran taxonomic diversity steadily decreased from the Middle Ordovician to the end of the Ashgill (Fig. 10). Nevertheless, morphological disparity was maintained, with the persistence of the three main morphological sets even as the number of subsets represented regularly declined (eight in the Middle Ordovician, four in the Caradoc, and three in the Ashgill) and intermediate forms among the three sets disappeared. In the Ashgill, these three sets were represented only by extreme morphologies, such as those of the strongly asymmetric cornutes *Cothurnocystis elizae* or *Scotiaecystis curvata*. In parallel with the decline in taxonomic diversity and the evacuation of morphospace, stylophorans showed an increase in paleogeographic dispersion from the Middle Ordovician to the Ashgill, with expansion into Avalonia, then Laurentia, and finally Baltica and the east-Gondwanan margin). This paleogeographic expansion was accompanied by a decrease in disparity within the region of origin (the north-Gondwanan margin) and by a relatively low disparity within each of the different zones occupied at the end of the Ordovician. It is also apparent that one of the three main morphologies remaining in the Ashgill (IIa, anomalocystitids) exhibited a vast paleogeographic distribution at lower paleolatitudes, on both sides of the equator. This type of stylophoran dispersion seems very different from that of the Early and Middle Ordovician, almost exclusively limited to high paleolatitudes. The paleogeographic expansion toward low paleolatitudes, observed from the Middle Ordovician, might conceivably correspond to the adaptation of certain forms to new environmental conditions.

The early Silurian (Fig. 10) was characterized by a profound reduction not only of taxonomic diversity, but also of disparity, as there remained only one morphological type (II), represented by a single subset (IIa). Through this time interval, by far the longest in this

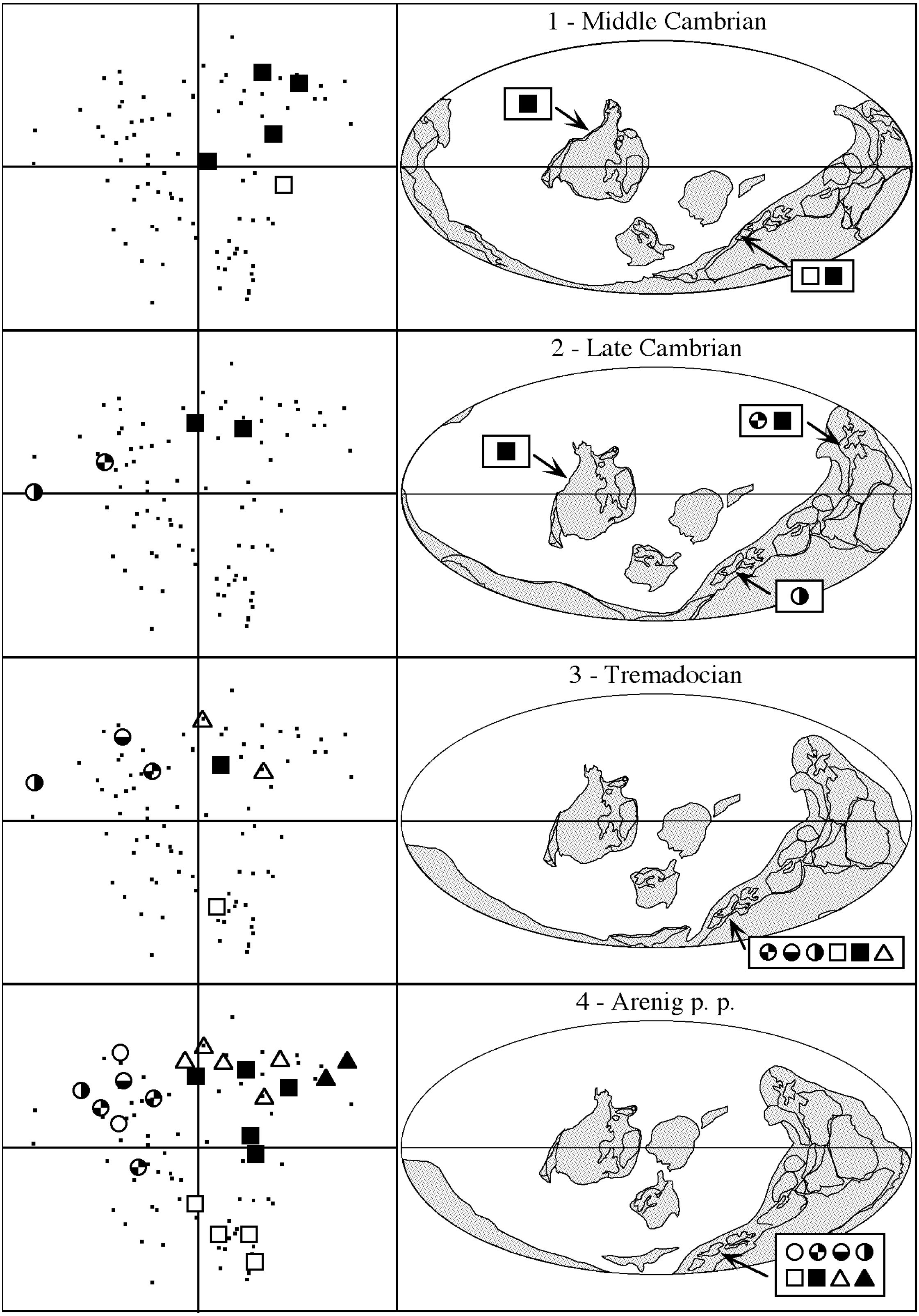

FIGURE 9. Evolution of stylophoran morphospace occupation and paleogeographic dispersion from the Middle Cambrian to the end of the Early Ordovician.

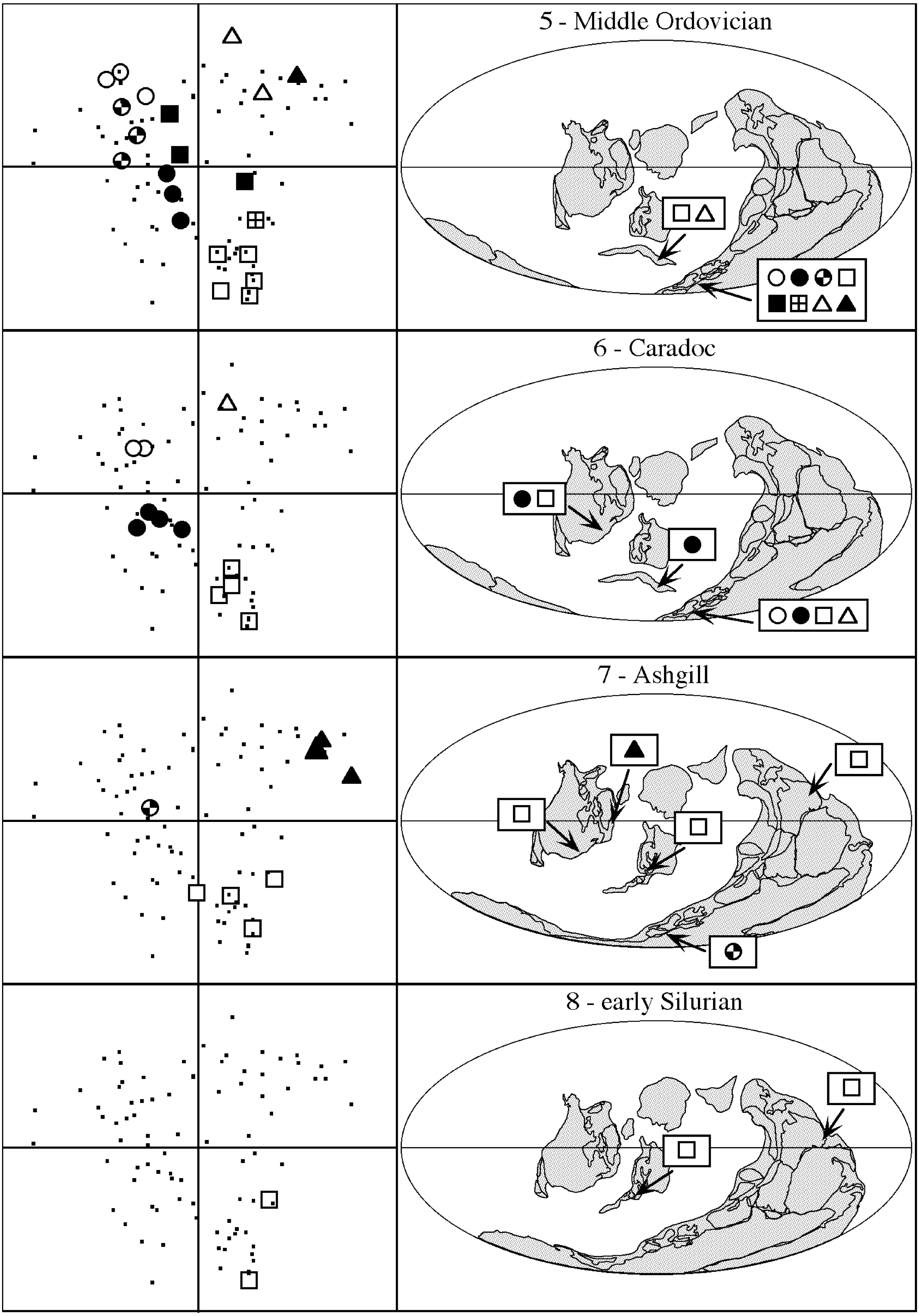

FIGURE 10. Evolution of stylophoran morphospace occupation and paleogeographic dispersion from the Middle Ordovician to the early Silurian (Llandovery–Wenlock).

study (20.8 Myr), paleogeographic distribution was also strongly reduced, with one species from the Llandovery of Tasmania (*Placocystella buretti*) and one species from the Wenlock of England (*Placocystites forbesianus*). These two anomalocystitid mitrates are from regions then situated at very low paleolatitudes and they belong to the same morphological type (IIa) as that of Ashgillian stylophorans present in those regions. This was also the first time since the Middle Cambrian that stylophorans were absent from the various regions of the northern-Gondwanan margin. In fact, in the early Silurian these regions were characterized by extensive deposits of black shale, indicating the existence (and persistence) of anoxic oceanic conditions following the major climatic perturbations of the end-Ordovician (Cocks and Fortey 1990; Paris and Le Hérissé 1992; Storch et al. 1993). It is therefore possible that the presence of a single stylophoran morphological type in the early Silurian signaled not only the disappearance of types I and III from high paleolatitudes, by virtue of unfavorable environmental conditions (anoxia), but also the persistence of type II only at low paleolatitudes, given that paleoenvironmental conditions were more favorable (Cocks and Fortey 1990; Robardet et al. 1990), and given that this type became established in the end-Ordovician. Curiously, the only morphological type that survived the biological crisis at the end of the Ordovician (set II) was precisely the same that was initially present in the Middle Cambrian.

Finally, from the late Silurian to the Middle Devonian (Fig. 11), stylophorans underwent a second phase of diversification, which corresponded to an increase in disparity with the reappearance of the type I morphology. Consequently, in contrast to the Cambro-Tremadocian radiation, no fundamentally new forms evolved during the Siluro-Devonian diversification—as if somehow mitrates were limited in their evolution and could only produce morphologies of types I and II. This second phase was characterized by a peak of diversity and disparity (two morphological types, represented by three subsets, Ia, Ib, and IIa) in the Early Devonian (Lochkovian to Emsian), as well as by an increase in paleogeographic dispersion. This phase was followed by a slight decrease in diversity and disparity (two morphological types each represented by only one subset) and reduced paleogeographic dispersion in the Middle Devonian. Also, a second important difference from the Cambro-Tremadocian radiation concerns the paleogeographic context of the Siluro-Devonian diversification: whereas the former occurred essentially in a single region (the northern-Gondwanan margin), the latter was characterized by strong paleogeographic dispersion.

Spatiotemporal Pattern of Stylophoran Diversification: Comparison of Quantitative Indices.—The three main aspects of the stylophoran diversification of interest in this study, i.e., taxonomic diversity, morphological disparity, and paleogeographic dispersion, can be analyzed in a more rigorous manner by means of comparisons through time of quantitative indices summarizing the general signal conveyed by each of these aspects. The taxonomic diversity curve expresses temporal variations in number of species. The morphological disparity curve indicates, for each interval considered, the sum of the variances of the principal coordinates scores as calculated by the software MDA (Navarro 2003). Other relevant disparity measures, such as the total range, were explored, but the results did not differ much, or else demanded the use of rarefaction with a baseline sample size too small to allow meaningful interpretation, owing to the large error bars. The sum of the variances was therefore chosen as the reference disparity measure because it is relatively insensitive to sample size differences, and more directly comparable and interpretable with a number of other studies of disparity in the literature. Error bars for disparity values were estimated by bootstrapping (Efron and Tibshirani 1993). For each stratigraphic interval, species coordinates on PCO axes were resampled with replacement and the sum of variance was calculated. This procedure was repeated 500 times, and the mean and standard deviation were calculated. Standard deviation of the bootstrap samples provides an estimate of the standard error, which, in paleobiological studies, essentially reflects an estimate of analytical error (Foote 1993b). Finally, the curve sum-

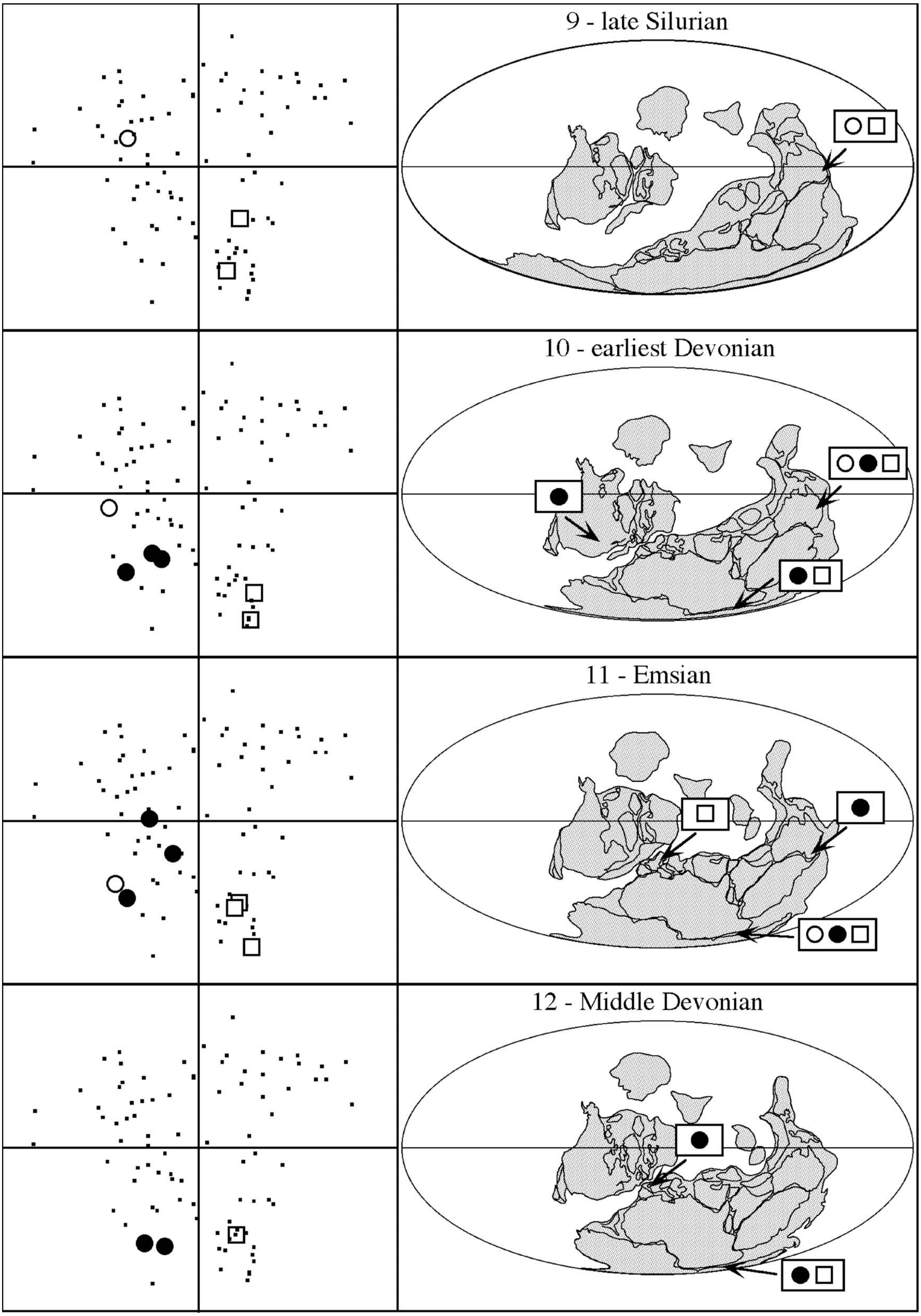

FIGURE 11. Evolution of stylophoran morphospace occupation and paleogeographic dispersion from the late Silurian (Ludlow–Pridoli) to the Middle Devonian.

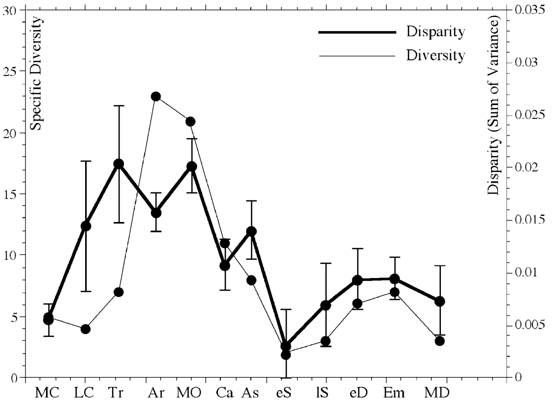

FIGURE 12. Patterns of stylophoran disparity (thick line) and taxonomic diversity (thin line) from the Middle Cambrian to the Middle Devonian. Disparity is measured as the sum of variances. Diversity is the number of sampled species. Errors bars on disparity were estimated by bootstrap (500 replications). MC, Middle Cambrian. LC, Late Cambrian. Tr, Tremadocian. Ar, Arenig pro parte. MO, Middle Ordovician. Ca, Caradoc. As, Ashgill. eS, early Silurian. lS, late Silurian. eD, earliest Devonian. Em, Emsian. MD, Middle Devonian.

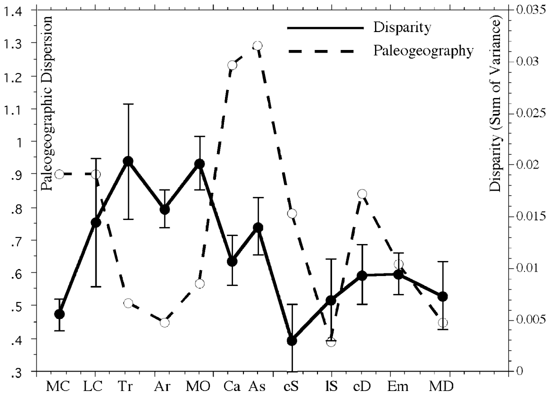

FIGURE 13. Patterns of stylophoran disparity (thick line) and paleogeographic dispersion (dotted line) from the Middle Cambrian to the Middle Devonian. Disparity is measured as the sum of variances. Paleogeographic dispersion measured as indicated in the text. Errors bars on disparity were estimated by bootstrap (500 replications). Abbreviations as in Figure 12.

marizing general paleogeographic dispersion through time was constructed by calculating for each stratigraphical interval an index of dispersion reflecting the distribution of both global (paleocontinents) and local (regions) samples (see above).

The comparison of diversity and disparity curves (Fig. 12) quantitatively confirms the various patterns revealed by the qualitative examination of the details of morphospace occupation in the metaPCO1-metaPCO2 projection (Figs. 9–11). A very clear discordance existed between disparity and diversity in the first half of stylophoran history, although it was manifested in several ways. During the initial radiation phase (Cambro-Tremadocian), disparity greatly increased while diversity remained relatively low. From the earliest Arenig to the Middle Ordovician, disparity remained elevated and relatively constant, while diversity strongly increased and reached its peak (Fig. 12). Finally, from the Late Ordovician (Caradoc) to the Middle Devonian disparity and diversity show relatively good concordance, with both decreasing monotonously, despite a second peak in the Early Devonian (though much smaller than the Early to the Middle Ordovician).

The comparison between the signals of disparity and paleogeographic dispersion reveals two distinct diversification phases (Fig. 13). During the first phase, which corresponds to the principal radiation (Middle Cambrian to Middle Ordovician), the signals of disparity and paleogeographic dispersion appear inversely related: dispersion was maximal when disparity was lowest (Cambrian) and, conversely, dispersion was minimal when disparity was highest (Early to Middle Ordovician). During the second phase (Late Ordovician to Middle Devonian), the relationship between the two signals was reversed.

Conclusions

The disjunction between the peaks of disparity and diversity during the initial radiation of stylophorans is in itself an interesting result, given that a similar pattern characterizes a number of other marine invertebrate clades, including arthropods (Gould 1989; Briggs et al. 1992; Foote and Gould 1992; Wills et al. 1994), brachiopods (Carlson 1992; McGhee 1995), gastropods (Wagner 1995), blastozoans (Foote 1992, 1993a), and crinoids (Foote 1994, 1995, 1999). Nevertheless, the opposite pattern has also been described, for example in trilobites whose Cambrian diversity peak clearly preceded the Ordovician disparity peak (Foote 1991, 1993a). In the case of stylophorans, it seems that diversification was characterized by a relatively rapid saturation of morphospace, with initially few species in the Cambro-Tremadocian occupying rapidly but sparsely the main morphospace regions, later followed, in the Arenig-Middle Ordovician, by an important phase of diversification that nonetheless only filled in an already occupied morphospace.

The macroevolutionary pattern of stylophorans is quite similar to that documented for several other marine invertebrate groups, which began to diversify comparatively slowly during the Cambrian, achieving a diversity peak in the Ordovician, and then declined in relatively consistent manner until their disappearance during the late Paleozoic (Carboniferous–Permian), but still displayed a second disparity peak in the Early Devonian. This is the case of blastozoans (Foote 1992, 1993a) and orthid brachiopods (Harper and Tychsen 2004). The similarity in macroevolutionary patterns might have involved common causes (e.g., paleoenvironmental) to particular fluctuations and/or reflect more general macroevolutionary trends, of intrinsic (increase in constraint through time) or extrinsic character (replacement of the Paleozoic fauna by the modern fauna). Preservational and sampling biases cannot be completely excluded, notably with respect to the strong decline in both taxonomic and morphological diversity in the Silurian and to the diversity peak in the Early Devonian. Indeed, as with stylophorans, a number of echinoderm groups relatively common in the Ordovician were virtually absent in the Silurian, only to reappear in Lazarus-like fashion in the Early Devonian. This was the case, for example, of solutes and of pleurocystitid rhombiferans. Thus, the rarity of certain echinoderm groups in the Silurian may be tied to the lack of preservation (or underrepresentation) of certain types of environments or Lagerstätten. Finally, stylophorans differ from other groups with an otherwise similar pattern by the fact that their diversity clearly peaked earlier: earliest Arenig (''unnamed stage 2'' [Sprinkle and Guensburg 2004]) instead of Middle to Late Ordovician (Foote 1992; Harper and Tychsen 2004).

The apparent inverse relationship between paleogeographic dispersion and diversity (both taxonomic and morphologic) during the initial history of stylophorans runs conversely to the hypothesis of diffusion on a global scale, which entails an expectation of positive correlation between the two signals. This relationship suggests that the colonization of new geographic areas, and putatively of new environments, is not necessary for speciation and morphological differentiation. The stylophoran pattern is reminiscent of other groups of marine invertebrates, in particular bivalve mollusks. Bivalves apparently radiated in the Cambrian, diversified extensively in the Early and Middle Ordovician, but remained extremely restricted paleogeographically (Babin 1993; Cope and Babin 1999; Cope 2004). From the Caradoc onward, bivalves extended their range toward lower paleolatitudes, where a second major diversification occurred, though they became rarer and less diverse in the region of origin (notably the northern-Gondwanan margin). The similarity of the stylophoran and bivalve macroevolutionary patterns suggests perhaps the influence of common paleoenvironmental controls of the paleogeographic dispersion of these two groups.

More generally, results of the threefold approach (diversity, disparity, geography) pursued in this study suggest that the relationships among the three signals can be complex and at times too idiosyncratic for simple interpretation. Still, the explicit consideration of the geographic context of taxonomic and morphological diversification has enhanced our understanding of the macroevolutionary dynamics of stylophorans by providing an important additional perspective for the characterization and interpretation of biodiversity. Biodiversity is inherently complex, having multiple aspects, measures, and contexts. Accordingly, different patterns are likely to be collectively informative in novel and valuable ways, complementing the rich body of knowledge stemming from generally accepted studies focusing on a particular aspect, measure, and context.

Although comparisons of diversity and disparity have yielded important insights about macroevolution, more work is needed because generalizations have emerged mostly in an inductive fashion, and many groups still await study. An eventual theory of biodiversity dynamics cast in terms of diversity and disparity remains possible, but would remain inevitably partial given the heterogeneity of biodiversity. It may well be that some components of biodiversity are less informative and of limited interest or applicability in paleobiology, yet factors such as biogeography are well established in their empirical and theoretical value for understanding diversification and its controls.

Biogeography should be more widely considered in studies of diversity and disparity, and a threefold approach is almost self-evidently appealing, notwithstanding that (1) data resolution and the relevance of various biases would hardly be equivalent among the three given the very nature of the signals and their estimation; (2) as a consequence the signal-to-noise the ratio will be uneven for different patterns, thus limiting the types of comparison possible as well as the content of generalizations; (3) the array of possible discordances or concordances among signals may not be equally likely, because different signals are not completely independent and have different degrees of freedom. In any case, comparisons of multiple signals of biodiversity can be informative provided that the issues listed above are taken into account. In the case of biogeography, a richer characterization of macroevolutionary pattern was possible here, facilitating the inference of mechanisms and causes. However, additional case studies will be needed to produce generalizations about the paleoecological trinity that is diversity-disparity-geography.

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Appendix

List of species included in the analysis, with corresponding taxonomic group, stratigraphic ranges, illustration sources for reconstructions used in morphometric analysis, and studied areas. MC = Middle Cambrian; LC = Late Cambrian; Tr = Tremadocian; Ar = Arenig *pro parte* (Early Ordovician, stage 2 of Webby et al. 2004); MO = Middle Ordovician (stages 3 and 4); Ca = Caradoc; As = Ashgill; eS = early Silurian (Llandovery and Wenlock); lS = late Silurian (Ludlow and Pridoli); eD = early Devonian (Lochkovian and Praguian); Em = Emsian; MD = Middle Devonian (Eifelian and Givetian); Pe = Pennsylvanian. Abbreviations for bibliographic references are: 1 = Beisswenger (1994); 2 = Chauvel (1966); 3 = Craske and Jefferies (1989); 4 = Cripps (1988); 5 = Cripps (1989a); 6 = Cripps (1989b); 7 = Cripps (1990); 8 = Cripps and Daley (1994); 9 = Daley (1992); 10 = Gil Cid et al. (1996); 11 = Haude (1995); 12 = Jefferies (1968); 13 = Jefferies (1986); 14 = Jefferies and Lewis (1978); 15 = Jefferies and Prokop (1972); 16 = Jefferies et al. (1987); 17 = Kolata and Guensburg (1979); 18 = Kolata and Jollie (1982); 19 = Kolata et al. (1991); 20 = Lee et al. (2005); 21 = Lefebvre (1999); 22 = Lefebvre (2000b); 23 = Lefebvre (2000c); 24 = Lefebvre and Gutiérrez-Marco (2003); 25 = Lefebvre and Vizcaïno (1999); 26 = Marti Mus (2002); 27 = Parsley (1991); 28 = Ruta (1997); 29 = Ruta (1999a); 30 = Ruta (1999b); 31 = Ruta and Bartels (1998); 32 = Ruta and Jell (1999a); 33 = Ruta and Jell (1999b); 34 = Ruta and Jell (1999c); 35 = Ruta and Jell (1999e); 36 = Ruta and Theron (1997); 37 = Smith and Jell (1999); 38 = Sumrall and Sprinkle (1999); 39 = Ubaghs (1963); 40 = Ubaghs (1968); 41 = Ubaghs (1970); 42 = Ubaghs (1979); 43 = Ubaghs (1983); 44 = Ubaghs (1987); 45 = Ubaghs (1991); 46 = Ubaghs (1994); 47 = Ubaghs and Robison (1988); 48 = Woods and Jefferies (1992). These references are listed in the Literature Cited section. Abbreviations for studied surfaces: TH = Theca; LTS = Lower Thecal Surface; UTS = Upper Thecal Surface.

Species	Order	Range	Refs.	Studied areas
Adoketocarpus acheronticus	mitrate	lS	33	TH, LTS, UTS
Adoketocarpus janeae	mitrate	eD	33	TH, LTS
Ampelocarpus landeyranensis	cornute	Ar	25	TH, LTS, UTS
Amygdalotheca griffei	cornute	Tr–Ar	41	TH, LTS
Anatifopsis barrandei	mitrate	MO–Ca	21	TH, LTS, UTS
Anatifopsis minuta	mitrate	MO	23	TH, UTS
Anatifopsis trapeziiformis	mitrate	Tr–MO	21	TH, LTS, UTS
Anomalocystites cornutus	mitrate	eD	27	TH, LTS, UTS
Arauricystis occitana	cornute	Ar	46	TH, LTS, UTS
Arauricystis primaeva	cornute	Ar	41	TH, LTS
Archaeocothurnus bifida	cornute	MC	47	TH, LTS, UTS
Aspidocarpus bohemicus	mitrate	Ca	42	TH, LTS, UTS
Aspidocarpus discoidalis	mitrate	MO	7	TH, LTS, UTS
Aspidocarpus riadanensis	mitrate	Ca	22	TH, LTS
Ateleocystites guttenbergensis	mitrate	Ca	18	TH, LTS, UTS
Ateleocystites huxleyi	mitrate	Ca	40	TH, LTS
Balanocystites primus	mitrate	Ar–MO	23	TH, LTS, UTS
Barrandeocarpus jaekeli	mitrate	Ca	42	TH, LTS, UTS
Barrandeocarpus norvegicus	mitrate	As	3	TH, LTS, UTS
Beryllia miranda	cornute	MO	8	TH, LTS, UTS
Bokkeveldia oosthuizeni	mitrate	Em	36	TH, UTS
Ceratocystis perneri	primitive	MC	40	TH, LTS, UTS
Ceratocystis vizcainoi	primitive	MC	44	TH, UTS
Chauvelicystis spinosa	cornute	Ar	41	TH, LTS, UTS
Chauvelicystis ubaghsi	cornute	Ar	2	TH, LTS, UTS
Chauvelicystis vizcainoi	cornute	Ar	9	TH, LTS
Chinianocarpos thorali	mitrate	Ar	13	TH, LTS, UTS
Cothurnocystis courtessolei	cornute	Ar	41	TH, LTS, UTS
Cothurnocystis elizae	cornute	As	40	TH, LTS, UTS
Cothurnocystis fellinensis	cornute	Tr–Ar	41	TH, LTS, UTS
Diamphidiocystis drepanon	mitrate	As	17	TH, LTS, UTS
Diamphidiocystis sp.	mitrate	MO	23	TH, LTSa
Domfrontia pissotensis	cornute	MO	8	TH, LTS, UTS
Drepanocarpos australis	cornute	LC	37	TH, LTS, UTS
Enoploura popei	mitrate	Ca–As	27	TH, LTS, UTS
Eumitrocystella savilli	mitrate	MO	1	TH, LTS, UTS
Flabellicarpus rushtoni	cornute	Tr	26	TH, LYS, UTS
Galliaecystis ubaghsi	cornute	Ar	41	TH, LTS, UTS
Hanusia prilepensis	cornute	MO	6	TH, LTS, UTS
Jaekelocarpus oklahomaensis	mitrate	Pe	19	TH, LTS, UTS
Kierocystis inserta	mitrate	Ca	27	TH, UTS
Kopficystis kirkfieldi	mitrate	Ca	27	TH, UTS
Lagynocystis pyramidalis	mitrate	Ar–MO	40	TH, LTS, UTS
Lobocarpus vizcainoi	mitrate	LC	22	TH, LTS
Lyricocarpus courtessolei	cornute	Ar	25	TH, LTS, UTS

Appendix. Continued.

Species	Order	Range	Refs.	Studied areas
Milonicystis kerfornei	cornute	MO	8	TH, LTS, UTS
Mitrocystella incipiens	mitrate	MO	12	TH, LTS, UTS
Mitrocystites mitra	mitrate	MO	40	TH, LTS, UTS
Nanocarpus dolambii	cornute	Ar	45	TH, LTS, UTS
Nanocarpus milnerorum	cornute	As	29	TH, LTS, UTS
Nevadaecystis americana	cornute	LC	39	TH, LTS, UTS
Occultocystis koeneni	mitrate	eD–Em	11	TH, UTS
Ovocarpus moncereti	mitrate	Ar–MO	24	TH, LTS, UTS
Paranacystis petrii	mitrate	Em	40	TH, LTS, UTS
Paranacystis simoneae	mitrate	MD	21	TH, LTS
Peltocystis cornuta	mitrate	Ar	41	TH, LTS, UTS
Phyllocystis blayaci	cornute	Ar	41	TH, LTS, UTS
Phyllocystis crassimarginata	cornute	Tr–Ar	41	TH, LTS, UTS
Placocystella africana	mitrate	Em–MD	36	TH, LTS, UTS
Placocystella buretti	mitrate	eS	30,35	TH, LTS, UTS
Placocystella flemingi	mitrate	Em	30,35	TH, LTS, UTS
Placocystella garratti	mitrate	lS	30,35	TH, LTS, UTS
Placocystites forbesianus	mitrate	eS	14	TH, LTS, UTS
Ponticulocarpus robisoni	cornute	MC	38	TH, LTS, UTS
Prochauvelicystis semispinosa	cornute	Tr	9	TH, LTS, UTS
Procothurnocystis owensi	cornute	MO	48	TH, LTS, UTS
Prokopicystis mergli	cornute	MO	5	TH, LTS, UTS
Promitrocystites barrandei	mitrate	MO	40	TH, LTS, UTS
Proscotiaecystis melchiori	cornute	Ar	43	TH, LTS
Protocystites menevensis	cornute	MC	16	TH, LTS, UTS
Protocytidium elliotae	mitrate	As	32	TH, LTS, UTS
Pseudovictoriacystis problematica	mitrate	eD	34	TH, LTS, UTS
Reticulocarpos hanusi	cornute	MO	15	TH, LTS, UTS
Rhenocystis latipedunculata	mitrate	Em	31	TH, LTS, UTS
Scotiaecystis collapsa	cornute	As	4	TH, LTS, UTS
Scotiaecystis curvata	cornute	As	12	TH, LTS, UTS
Scotiaecystis guilloui	cornute	MO	25	TH, LTS, UTS
Scotiaecystis jefferiesi	cornute	Ca	10	TH, LTS, UTS
Sokkaejaecystis serrata	cornute	LC	20	TH, LTS, UTS
Thoralicystis bouceki	cornute	MO	40	TH, LTS, UTS
Thoralicystis griffei	cornute	Ar	41	TH, LTS, UTS
Victoriacystis hulmesorum	mitrate	eD	34	TH, LTS, UTS
Victoriacystis wilkinsi	mitrate	lS	28	TH, LTS, UTS
Vizcainocarpus dentiger	mitrate	Ar	22	TH, LTS, UTS
Vizcainocarpus rutai	mitrate	Tr	22	TH, LTS
Willmanocystis denticulata	mitrate	Ca	18	TH, LTS, UTS
Yachalicystis triangularis	mitrate	eD–Em	11	TH, LTS, UTS
Yachalicystis sp.	mitrate	MD	21	TH, LTS