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Faunal invasions as a source of morphological constraints and innovations? The diversification of the early Cardioceratidae (Ammonoidea; Middle Jurassic)

Nicolas Navarro, Pascal Neige, and Didier Marchand

Abstract.—Multivariate analysis of shell characters and quantification of morphological diversity (morphospace occupation and disparity) are used here to investigate the modes of morphological diversification of ammonites. We define five events in early cardioceratid history that connect geographical changes causing emigration or immigration phases with biodiversity dynamics: (1) the initial colonization of the Arctic Basin by the Cardioceratidae at the end of the Bajocian, Middle Jurassic; (2) the first appearance of the Kosmoceratidae clade in the Boreal Realm during the Bathonian; (3) the ensuing expansion phase of this clade in the Boreal Realm; (4) the first phase of migration of the Cardioceratidae (early Callovian) through Eastern Europe, Western Britain and the Yukon corridor; and (5) the second unrelated migration phase in the Western Interior only. Analysis of spatial occupation shows that acquisition of this field occurs essentially by replacement or subdivision of preexisting peaks of occupation. These replacements seem to follow different patterns: progressive trend, saturation, iteration, and apparent preferential extinction. We describe these patterns and suggest different factors that may have shaped them, including a morphological differentiation that has been interpreted by various authors as sexual dimorphism. Another factor that could cause disparity modification is fluctuations in the ammonites' proximal environment. The effect of immigrating faunas is a third (and preponderant) factor that is prominent in the studied example: immigration phases of the Cardioceratidae lead to increased morphological diversity, whereas the spread of nonindigenous species reduces it and is contemporaneous with a morphological shift in the native clade. We thus demonstrate here that geographical constraints play a significant role in the expression of innovation and may be seen as a major factor in macroevolutionary dynamics.

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Introduction

Global climate change, biodiversity, and their interaction are fundamental scientific topics. Climate change may remove or reposition geographical barriers, allowing faunal exchanges between adjacent areas. Expansion of geographic species ranges may or may not lead to species invasions in adjacent regions. Invasion is successful when a spreading phase of nonindigenous species occurs, and it is related to various factors during the preceding establishment stage (e.g., competition with native species). Where invasion is successful, the integration of the invasive species may bring about many changes in ecology and biodiversity such as niche shifts or extinction (Moyle and Light 1996). Even in the present-day ecosystem, many aspects of the tempo and mode of biological invasions are not yet understood. Rapid phenotypic changes are expected to occur in invasive species in response to new environmental conditions (Hänfling and Kollmann 2002). However, long-term patterns (i.e., those found in the fossil record) of response of native and invasive species, especially in terms of morphology, are largely unknown. This paper is a pilot study of ammonite biodiversity and its fluctuations in a context of species emigration and immigration.

The Jurassic Boreal Realm was a complex set of epeiric basins that were episodically isolated from adjacent provinces. Episodic landlocking was a primary factor in the evolutionary isolation of its life forms and in their differentiation from Tethyan faunas (Pozaryska and Brochwicz-Lewinski 1975; see Enay and Cariou 1997 for a synthesis). This geo-

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graphical control compounded the effects of other environmental factors (Enay and Cariou 1997) such as the incidence of solar radiation, seasonal fluctuations of illumination (Reid 1973), and the cooling of surface seawater by restricted exchange and heat transfer between water masses (Imlay 1965; Hallam 1985). The incidence of solar radiation and seasonal fluctuations of illumination affect the stability of trophic resources (Valentine 1971) and seem to control the structure of the ecosystem (Enay and Cariou 1997). Thus, the configuration of the Arctic Basin was a major factor in creating and maintaining specific environmental conditions suitable for Boreal taxa (Enay and Cariou 1997). As a result Boreal ammonite faunas display low taxonomic diversity throughout the Jurassic (Enay and Cariou 1997), although considerable morphological variation occurs within species (cf., for Triassic, Dagys and Weitschat 1993). The Arctic Region became landlocked in Jurassic times largely as a result of North Sea doming. This regional tectonic event (Underhill and Partington 1993) formed a physical barrier preventing any communication between the Boreal Realm and the northwest European province from Aalenian times onward. Similarly nonmarine detrital facies on the Russian shelf prevented communication with the Tethyan region. The Arctic Basin was less effectively sealed off, however, in North America and northern Siberia. The Cardioceratidae lineage is one of the best-studied faunas of the Boreal Realm. The first forms appeared in this previously ammonite-free area at the onset of the late Bajocian: the last reported faunas in the area before the advent of the Cardioceratidae are dated to the early Toarcian in Greenland (Dam and Surlyck 1998; Surlyck and Noe-Nygaard 2000) and to the early Bajocian in the Arctic area of North America and Siberia (Poulton et al. 1992; Sey et al. 1992).

A conceptual and methodological framework of disparity (morphological component of biodiversity) developed over the last decade provides a fresh view of biodiversity and the way it is structured over time. Disparity has proved to be a useful tool when exploring large-scale (i.e., in both temporal and taxonomic senses) evolutionary dynamics (e.g., Saunders and Swan 1984; Foote 1991a,b, 1995, 1999; Wills et al. 1994; Dommergues et al. 1996; Wagner 1997; Eble 2000a). A few studies have also applied this tool to other fields, e.g., phenotypic variation (Smith 1998), short time intervals with high time resolution (Neige et al. 2001), or developmental disparity (Eble 2002). However, examples of empirical studies combining a small taxonomic scale with high stratigraphic resolution (i.e., biozone-scale) are still lacking. The wealth of data collected over the last 100 years (see Appendix) makes ammonites prime examples for an empirical study of this type.

It is in this context that the present study, by quantifying the morphological component of biodiversity, sets out (1) to monitor morphological modifications in the initial (strictly boreal) phase of the Cardioceratidae, (2) to evaluate the consequences of their first ingressions into peripheral faunal provinces, and (3) to evaluate the impact on cardioceratid diversification of competing immigrant ammonites in the Boreal Realm (i.e., the Kosmoceratidae clade).

Early Cardioceratid History

To explore biodiversity dynamics, we define here five separate events in early cardioceratid history associated with geographical changes that gave rise to phases of emigration or immigration (see Figs. 1, 2). The rootstock species of the Cardioceratidae family is *Cranocephalites borealis* (Callomon 1985, 1993; Marchand *in* Dommergues et al. 1989). This species derived from sphaeroceratids, closely related to *Chondroceras oblatum*, found in the lower Bajocian (Oblatum zone) of the northeast Pacific terranes and Canadian Western Interior (Poulton et al. 1992). The first event considered here is the initial colonization of the Arctic Basin by the Cardioceratidae (E1) at the beginning of the Borealis zone (end of the Bajocian, Middle Jurassic). The Bering region seems to have been colonized first probably via the Yukon strait (Fig. 1) (Callomon 1985). The rootstock species then spread throughout the Arctic (Callomon 1985, 1993; Marchand *in* Dommergues et al. 1989). The Cardioceratidae were virtually the only ammonites in the Boreal area, to which they were confined. The

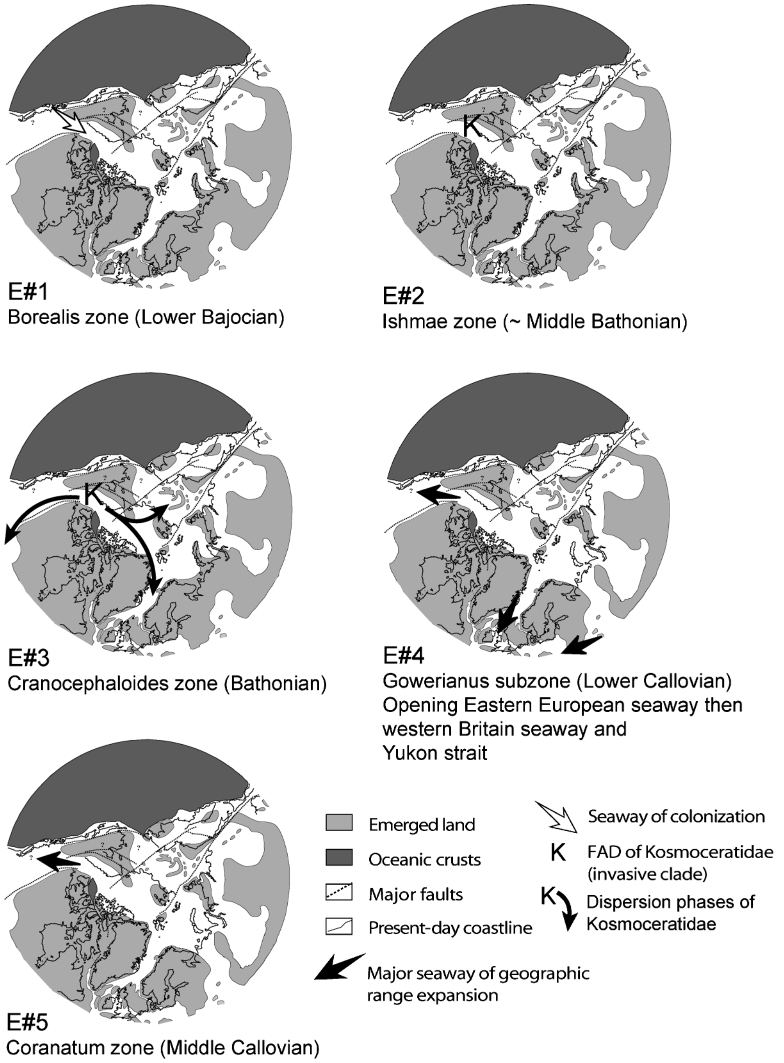

FIGURE 1. Major events of early Cardioceratidae history. Position of present-day coastline, tectonic faults and oceanic crusts are taken from the Bajocian map of Owen (1983); the simplified outline of emerged land is drawn after Vinogradov (1968), Poulton (1987), and Ziegler (1988).

second event (E2) was the FAD of the Kosmoceratidae clade in the Boreal Realm (earliest record is in the Yukon), at the beginning of Ishmae zone, during the Bathonian (Poulton, 1987). After this first sporadic record, this clade came to form the second major ammonite stock in the Boreal Realm. The third event (E3) was the expansion phase of this clade in the Boreal Realm, beginning in the Cranocephaloides zone. From this time on, these ammonites were a major component of ammonite biodiversity and presumably in competition with the Cardioceratidae. The onset of the Callovian saw the first sporadic connections between the Arctic Basin and adjacent regions. However, the Cardioceratidae remained confined to the Arctic Basin until the Koenigi zone (early Callovian) when permanent seaways opened up between the Boreal Realm and Eastern Europe, Western Britain and Yukon (see Fig. 1). At this time (Gowerianus subzone, Fig. 2), the Cardioceratidae migrated through these corridors, giving rise to new taxa (*Cadochamoussetia* and *Chamoussetia*). These migration phases were the fourth event (E4). A second independent migration phase occurred during the Coronatum zone (Fig. 2) but in the Western Interior only (see Fig. 1),

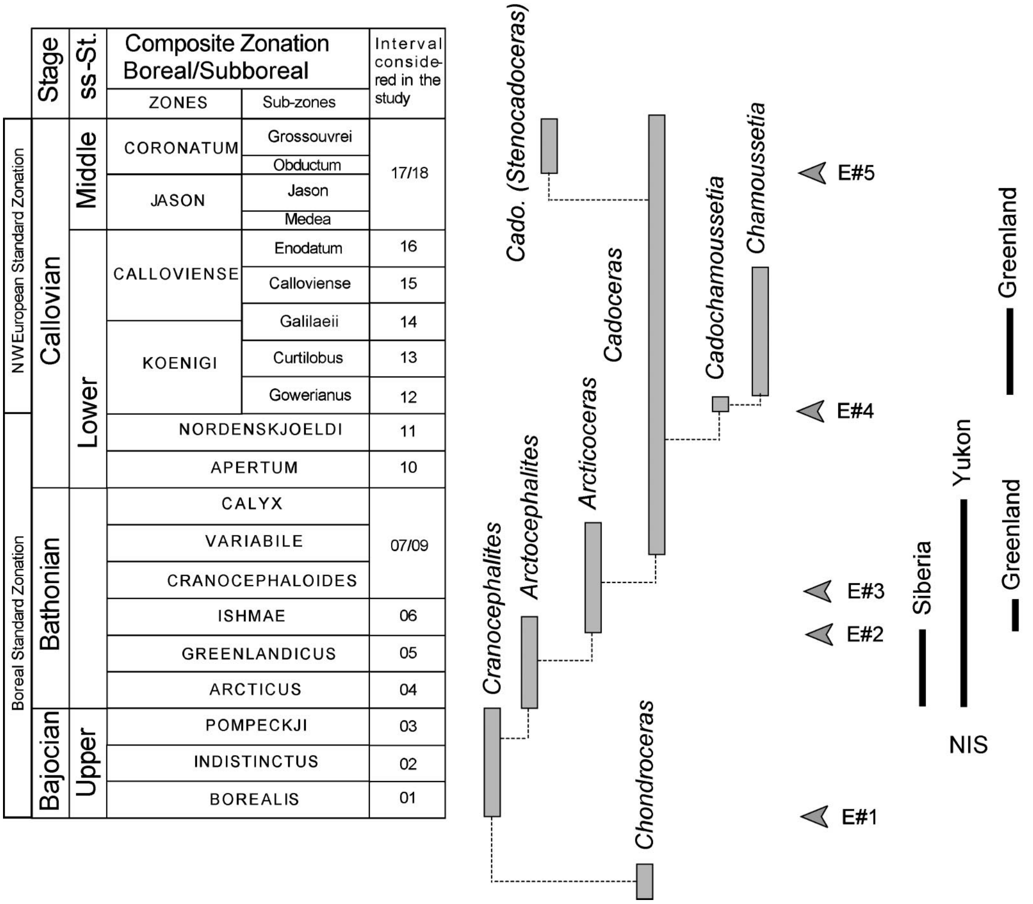

FIGURE 2. Composite zonation used in this study, major events, and stratigraphic range of the non indigenous species (NIS). Subboreal zonation is after Callomon et al. (1988); Thierry et al. (1997). Boreal zonation is after Callomon (1993). Numbers from 1 to 18 show time divisions considered in this study (see text for explanations of zonal grouping or subdivisions).

giving rise to *Stenocadoceras*. It was the fifth event (E5).

A second phase of southward expansion (not studied here) began in the late Callovian, peaking in the early Oxfordian (Cariou et al. 1997; Taylor et al. 1984). Then, the final episode extended from the mid-Oxfordian to late Kimmeridgian, when the Cardioceratidae resumed a more northerly distribution. The family died out without descendants in the late Kimmeridgian at the base of Autissiodorensis zone (Callomon 1985). In all, the Cardioceratidae, a monophyletic family (following Callomon 1985; Donovan et al. 1981), occupied the Boreal Realm for 21 Myr without interruption (after ages of Gradstein et al. 1994, 1995 and assuming constant duration of zones), spreading sporadically into other regions. In most cases, this phenomenon of southward expansion went along with pronounced morphological modifications (as with *Chamoussetia*, *Longaeviceras*, and the Cardioceratinae).

Materials and Methods

Sampling.—In most studies of disparity, the sampling method involves studying just one specimen per genus. However, this technique is effective only when comparing high-level taxa. Ammonite species exhibit widely differing morphologies (e.g., sexual dimorphism [Makowski 1963; Callomon 1963]; developmental polymorphism sensu Matyja [1986, 1994], and marked intraspecific variability [e.g., Dagys and Weitschat 1993]). In addition, our study focuses on a single lineage with little taxonomic diversity. Accordingly, one specimen per morph (sexual, thick/compressed or others) was sampled regardless of the taxonomic interpretation of the authors, and 163 specimens were used in all. Three forms of *Chondroceras oblatum* were included to allow for the initial morphological differentiation between the early Cardioceratidae and their putative ancestor (Callomon 1985; Marchand *in* Dommergues et al. 1989). Nineteen specimens of nonindigenous species (i.e., non-Boreal species collected from locations near the boundary between the Boreal and other regions), and nine specimens of Kosmoceratidae are also included. The kosmoceratid specimens correspond to Cranocephaloid forms from the Calyx zone. Just a single specimen is available for the Ishmae zone displaying a typical morphology (Poulton 1987). Thus, we expanded the stratigraphic range of the nine sampled kosmoceratid specimens to the Ishmae zone. All are described from illustrations in various monographs or publications about the Arctic regions or about the Cardioceratidae lineage (see Appendix).

Stratigraphic Resolution.—The Boreal Realm in mid-Jurassic times displayed a clear tendency to provincialism and at times to complete endemism. The Boreal ammonites were first figured by Keyserlying (1846) for the Petshora Basin, by Newton (*in* Newton and Teall 1897) and then Whitfield (1907) for the islands of Franz Joseph Land, by Madsen (1904) and then Spath (1932) for the Jameson Land Basin (eastern Greenland), and by Salfeld and Frebold (1924) for New Zembla. Since then, work in the Jameson Land Basin (see essentially studies by Callomon from 1959 to 1993) has led to the development of a biostratigraphic standard for the Arctic area. This succession for the period considered here (late Bajocian to mid-Callovian) is based on the identification of 37 faunal horizons grouped into 14 zones, 11 of which are strictly Boreal (Callomon 1993). Studies of other Arctic areas (North Sea [Callomon 1975, 1979] and Svalbard [Rawson 1982]) for the same period show similar faunas to Greenland. In North America (Callomon 1984; Poulton 1987; and for synthesis see Poulton et al. 1992) and Siberia (Meledina 1973, 1977; for synthesis see Sey et al. 1992), faunas were initially similar to those of Greenland but then became distinct, and so regional scales have been constructed for these two areas. Correlations between these different regions of the Boreal Realm and between this realm and non-Arctic regions of North America (''Western Interior,'' Terranes) are based on studies by Callomon (1984, 1993), Poulton (1987), and Hillebrandt et al. (1992). Correlations between the northwest European province and the Boreal Realm are based on the work of Dietl and Callomon (1988), Callomon and Wright (1989), and Callomon (1993).

To make our reference scale both homogeneous and operational several established biozones have been grouped or split and a composite zonation constructed (Fig. 2): the early part corresponds to zonation for Greenland (from Borealis to Nordenskjoeldi: late Bajocian to early Callovian) whereas the late part corresponds to the northwest European standard zonation (from Koenigi to Coronatum: early Callovian to mid-Callovian). This latter zonation is that of Great Britain (Callomon et al. 1988; see also synthesis of Thierry et al. 1997). Time divisions are based on the biozone scale. The study period (late Bajocian–mid-Callovian) covers some 11.5 Myr (according to the data of Gradstein et al. 1994, 1995, adjusted assuming constant duration of zones).

Morphospace Definition.—Currently, disparity is mainly quantified from empirical morphospaces (i.e., from ordination of actual forms). This approach has been vigorously criticized by McGhee (1999) as its sample dependence induces non-comparability and instability of empirical morphospaces. Eble (2000b) reviewed these various points, emphasizing bias and contributions from these two approaches and suggested a possible combined approach (Eble 2002).

Since Raup's characterization (1966, 1967) of coiled shell shapes, there has been a tendency to produce increasingly complex theoretical models (e.g., Bayer 1978; Okamoto 1988; Ackerly 1989; Savazzi 1990; Schindel 1990; see McGhee 1999 for a review). However, such models have become barely serviceable as morphometric descriptors of actual forms. As with theoretical models, the empirical quan-

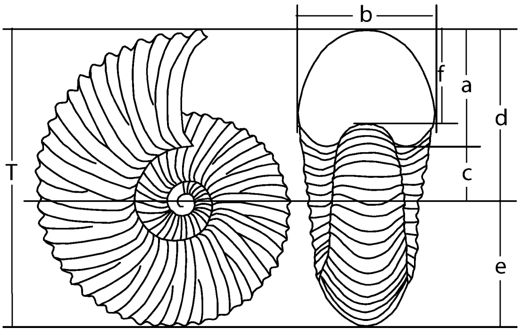

FIGURE 3. Morphometric measurements of shell shape. The derived shape ratios used in this study are: D = c/d; S = b/a; RH = a/T; W = (d/e); RW = b/T and AH = f/a.

tification of ammonite shape has tended to use increasing numbers of descriptors. This trend is also marked by the increasing use of discrete characters (Saunders and Swan 1984; Dommergues et al. 1996; Neige et al. 2001). One so far unresolved problem is that these discrete characters, although allowing morphologies to be more exhaustively described, may involve redundancy and misunderstood covariation.

The present study is based on six parameters (Fig. 3): three from Raup (1967: D, W and S; T = 0 in the Cardioceratidae) and three indices (RW, RH, and AH). Measurements are made at the end of the adult phragmocone thereby ensuring homologous measurements between specimens and so obviating ontogenetic effects.

The Cardioceratidae morphospace was obtained by normalized principal component analysis (PCA) of the six tube parameters using the 163 specimens strictly belonging to the cardioceratids. Other taxa have been plotted on the morphospace as additional data not involved in the computation of the new axes. Because some shape ratios contain similar measurement variables, a direct algorithmic relationship may exist between them. In order to obtain a better representation of shape ratio on PCs, a Varimax transformation was performed. A density analysis was performed on the overall morphospace. This procedure was first used by Raup (1967) and has been adopted in various morphological studies of cephalopod shells (Ward 1980; Chamberlain 1981; Saunders and Swan 1984). Under the original procedure, density was calculated by counting points per cell. We quantified morphospace density by a binned approximation to the 2D kernel density estimate (Wand 1994; Wand and Jones 1995). This analysis was performed with the bkde2D function of the KernSmooth package vs. 2.22–4 (B. Ripley) under R freeware (Ihake and Gentleman 1996). Observed differences in morphospace density may reflect various factors such as historical contingency, historical constraints, distribution of biomechanical optima, developmental constraints (Eble 2000b, 2002), and clusters observed may result from complex interactions among these factors.

Quantification of Disparity.—Consideration of the factorial plane as a morphospace implies that coordinates on an axis can be understood as quantifying a complex morphology. Thus each axis can be seen as a composite morphological character combining the covariant part of the initial morphometric parameters. Under this hypothesis, the dispersion and position parameters of distribution on any axis can be viewed as a simple morphological character. These two types of metric (dispersion and position) are used here to quantify the modification of morphological diversity.

Numerous methods have been proposed for quantifying morphospace occupation: various pairwise distances or between specimen and centroid (e.g., Foote 1991a, 1993, 1994a, 1995, 1996, 1999), morphospace occupation counted as cells occupied in subspace (Foote 1992; Dommergues at al. 1996), sums or products of variances or ranges (e.g., Foote 1991b; Wills et al. 1994; Eble 2000a), hypersphere or hyperellipsoid volume (Wills et al. 1994; Foote 1999), convex hull volume (Foote 1999) and, for discrete characters, character-state combinations (Foote 1995, 1999). Here, dissimilarity between forms at each stratigraphic interval was measured as the mean Euclidean pairwise distance and the area of a bidimensional convex hull is used to quantify the amount of morphospace occupation.

Spatial Modifications in Morphospace Occupation.—Most recent works on changes in morphological diversity over time concentrate on quantifying variations in dispersion. In these studies, changes in distribution within a morphospace over time have received little attention (Foote 1994a,b, 1995). In this perspective, Dommergues et al. (1996) proposed to trace changes of position using cumulative Euclidean distances between successive centroids of subspace over time. However, such measurement gives only an indication of the magnitude of displacement; the directional dimension of the change is totally lost.

Alternatively, various distributional parameters (mean, median, skews, minimum and maximum) have been used to detect and distinguish long-term trends in the evolutionary history of clades (McShea 1994; Wagner 1996). Modes too have been used to study body-size patterns (Roy et al. 2000). These different parameters are able to reveal patterns relative to central trends: i.e., stasis, unidirectional trends within the same or different overall morphospace occupation, or shifts in optimal shape. However, morphospace occupation is not always continuous. Thus mean and sometimes median shapes may lie in unoccupied morphospace zones and so model a non-existent morphology for the time interval considered. Conversely, minima and maxima quantify the extreme peaks of morphospace occupation. Accordingly, they reveal expansion or contraction of space occupation and so correspond to morphological innovations in relation to the appearance of new species or loss of shape resulting from the extinction of species. In this study, the latter two parameters (minimum and maximum) are used to model the spatial occupation of univariate components of the morphospace.

Correction of Indices.—The crude value of indices is sample-dependent and is biased by the experimental procedure. An estimator and the associated standard error may be computed by the bootstrap procedure (Efron 1979; Efron and Tibshirani 1993): data are resampled randomly with replacement, and the mean and standard deviation then calculated. Standard deviation then provides an estimate of standard error, which, in paleobiological studies, essentially reflects an estimate of analytical error (Foote 1993; Eble 2000a). Moreover, both convex hull area and maximum and minimum are sensitive to sample size. The rarefaction procedure was used to correct sample size dependence for these indices at each time interval (see Foote 1991b, 1992). The rarefaction procedure was carried out by resampling of k individuals ($k < n$) with replacement (Foote 1992; Eble 2000a). The bootstrapping procedure used for rarefaction yields the same statistical structure of error for all indices whether rarefied or not (Eble 2000a). Five hundred replicates were used for various indices whether rarefied or not. Because bootstrap sample statistics are normally distributed, z-tests are computed here (and see Foote 1993; Eble 2000a) to test for differences associated with critical events (E2 to E5).

TABLE 1. Loadings of the two first rotated principal components of the cardioceratid dataset.

	PC 1	PC 2
% Variance explained	48.3	32.7
D	−0.21	0.95
W	0.60	−0.12
S	−0.91	0.30
RW	−0.91	−0.04
RH	0.37	−0.90
AH	0.54	0.73

These procedures were performed using the MDA package (Navarro 2003) running on MATLAB software and available at http://www.u-bourgogne.fr/BIOGEOSCIENCE/NNavarro/MDA_prgm.html.

Morphospace through Time

Overall Morphospace.—Principal component analysis (PCA) of the six shape parameters describing the shell tube summarizes 81% of the total variance on the first two axes alone (Table 1, Fig. 4A). In order to clearly illustrate which shapes the morphospace includes, we have added some theoretical ammonite shapes (see crosses on Fig. 4A) corresponding to the main morphological peak as defined by Westermann (1996). This will help later (see Discussion) when interpreting shape changes in terms of habitat changes. PC 1 (48.3% of variance, Table 1) essentially reflects variation in the shape of the whorl section (S), the relative width (RW), and to a lesser extent variation of the whorl expansion rate (W). PC 2 (32.7% of variance) essentially reflects variation in the distance of the generative curve (D), relative

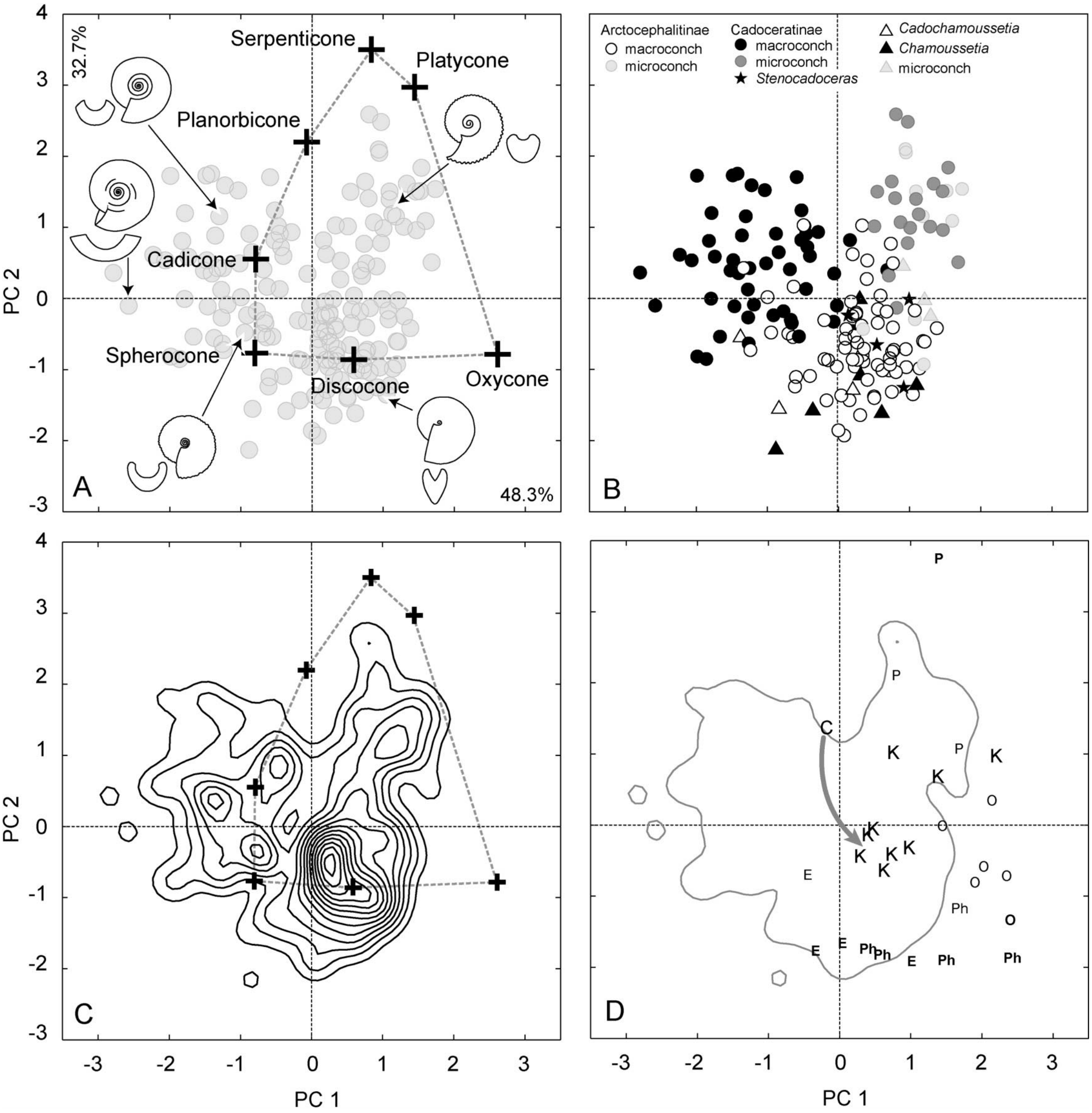

FIGURE 4. Morphospace structure for the Cardioceratidae. Ordination is based on principal component analysis with Varimax rotation. The first factorial plane represents 81% of total variance. A. Cardioceratid morphospace with addition of Westermann's shape triangle (Westermann 1996: Fig. 1). B. Taxonomic information. White and light grey dots for the Arctocephalitinae (respectively to macro- and microconchs); black and dark grey dots for the Cadoceratinae; white, black and grey triangles correspond respectively to *Cadochamoussetia*, *Chamoussetia* and their microconchs; black stars correspond to the *Stenocadoceras* subgenus. C. Structure of the cardioceratid morphospace. Contour plot is based on binned approximation to the 2D kernel density estimate. D. Cardioceratid spectrum with non indigenous species (NIS) and invasive clade (Kosmoceratidae). E: Eurycephalitinae; P: Perisphinctidae; C: Cadomites; K: Kosmoceratidae; Ph: Phylloceratidae; O: Oppelidae. The gray arrow represents the phylogenetic relationship between *Cadomites* and the kosmoceratids. The more positive group of kosmoceratids corresponds to the microconch morphs.

height (RH), and aperture overlap (AH). Axis polarization (from negative to positive peak) exhibits on PC 1 a decrease in shell thickness (S, RW) with its negative covariation with whorl expansion (W) from extreme cadicone to oxycone forms. PC 2 shows a decrease in shell involution with its negative or positive covariation with relative height (RH) and respectively with apertural height (AH) from discocone to serpenticone forms.

Morphological dispersion seems to be distributed into three subgroups (Fig. 4B). The first is situated on positive values (near zero) of PC1 and on negative values (also near the zero value) of PC 2. This peak clusters the Arctocephalitinae pars (the primitive family) and the genera *Cadochamoussetia* (in part), *Chamoussetia* and *Stenocadoceras* (derived genera). The second subgroup forms an uninterrupted cluster with the first group but has its peak density at high positive values of PC 1 and PC 2. This group comprises microconch morphologies of *Articoceras* and *Cadoceras*. The final, less structured, group is localized on negative values of PC 1 and corresponds essentially to Cadoceratinae macroconchs with a few thick Arctocephalitinae macroconchs. Thus the Cardioceratidae morphospace has a multipolar style of preferential occupation. These zones of preferential occupation correspond either to a particular morph (case of microconchs) or to a particular genus (*Cadoceras*) associated with certain specific forms (thick morphs). The first peak is the most heterogeneous taxonomically as it includes primitive forms (Arctocephalitinae) as well as several derived forms (*Cadochamoussetia* in part, *Chamoussetia* and *Stenocadoceras*).

Morphospace through Time.—After an initial contraction (Indistinctus zone), the pattern of morphospace occupation (Fig. 5) exhibits a progressive increase in occupation followed by individualization of new morphological peaks: two with the differentiation of microconchs up to the Gowerianus subzone (#12), then three with the appearance of *Cadochamoussetia* and *Chamoussetia* (E4) up to the Enodatum subzone (#16) and the extinction of *Chamoussetia*. The appearance of *Stenocadoceras* (E5) in the mid-Callovian (#17/18) leads to recolonization of positive values of PC 1 whereas the most negative value on PC 1 disappears. The appearance of the clade and the colonization of the Boreal Realm (E1) did not result in any marked morphological differentiation from the hypothesized ancestor (*Chondroceras oblatum*). Morphospace occupation seems unmodified between the Greelandicus zone (#05) and the Ishmae zone (#06), whereas this period corresponds to the appearance of the kosmoceratids in the Yukon region (E2). Conversely, a large morphological shift toward the cadicone morphs occurred parallel to the geographic clade-range expansion of the kosmoceratids (E3). The geographic clade-range expansion of the cardioceratids in the European area (E4) and North Eastern Pacific (E5) seems to have allowed the recolonization of unoccupied morphospace by species origination.

A broken-down picture of this temporal occupation can be assessed using location indices. Maximum values on PC 1 (Fig. 6A) increase progressively from the Borealis (#1) to Ishmae (#6) zones (late Bajocian to mid-Bathonian), reflecting a trend toward more compressed forms. Subsequently the maximum decreases markedly corresponding to the extinction of compressed forms of *Arcticoceras* (survivors exhibit a thicker morphology), contemporaneous with Event 3. Immediately after that values recover, rising to the previous maximum, and then remain stable. This recovery and stabilization is due to microconchs occupying a morphological peak. From the Pompeckji zone (#03) to the Gowerianus subzone (#12) and after an initial contraction of variability, minimum values (corresponding to thicker forms) display a marked tendency to decrease until a minimum in the Gowerianus subzone. However, we note a slight increase in the Ishmae zone followed by a decrease immediately after. The origination of the first *Cadoceras* (cadicone morphology) in the Variabile zone (here associated with the Cranocephaloides and Calyx zones; #07–09) is encompassed in this pattern of decrease. Thereafter the minimum rises progressively (i.e., less extreme cadicone morphs), with a more marked shift at the beginning of the Late Callovian (Jason and Coronatum zones, #17–18), contemporaneous with Event 5.

Initially the position of the PC 2 maximum is near zero (Fig. 6B). During a first phase (Borealis to Greenlandicus zone: late Bajocian to mid-Bathonian; #01–05), minimum and maximum follow a similar pattern, shifting toward more positive values and then decreasing. Subsequently the two parameters are more or less independent. In the Ishmae zone, the maximum shifts markedly toward high positive values (corresponding to platycone

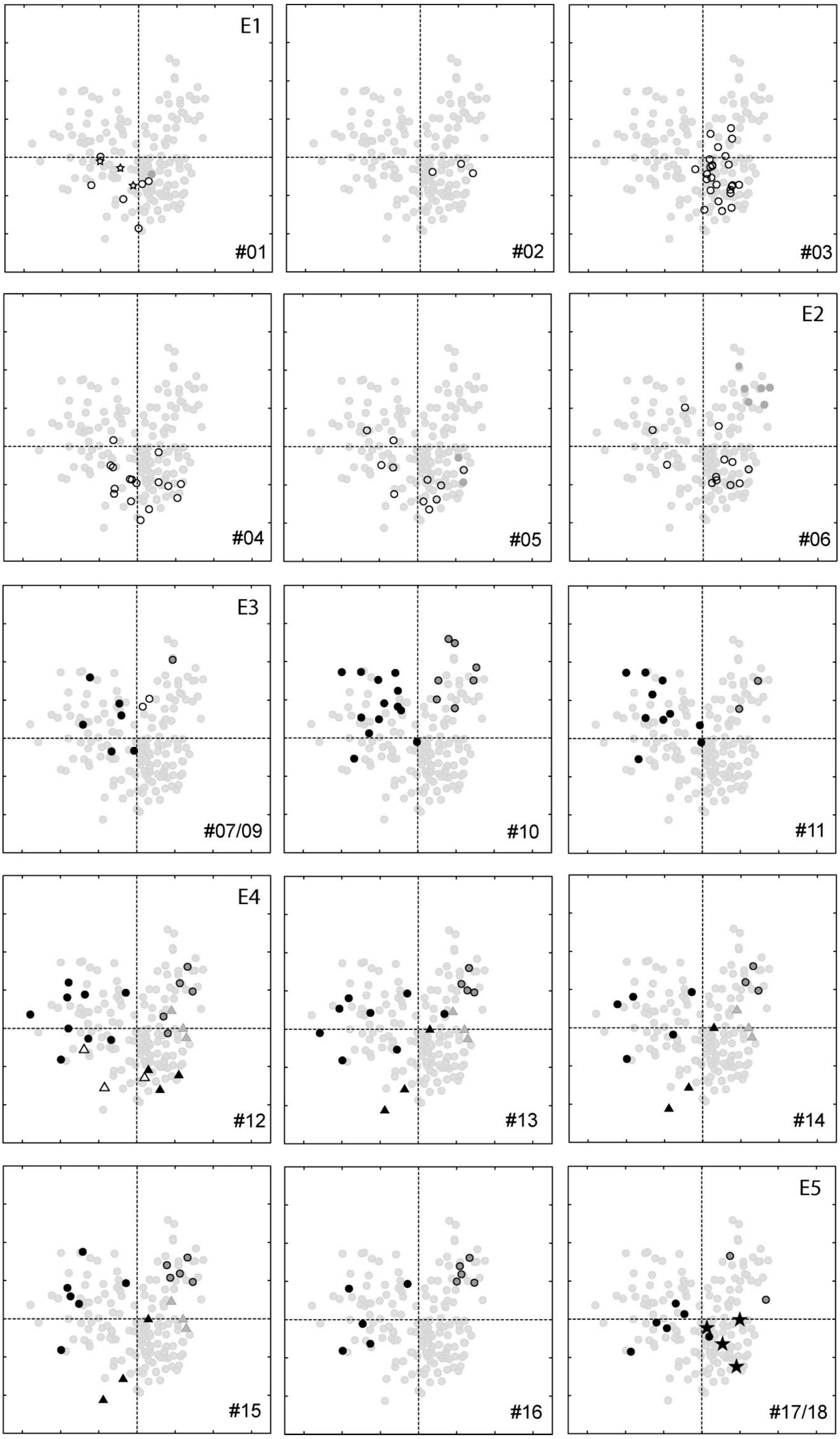

FIGURE 5. Pattern of morphospace occupation in the Cardioceratidae from the late Bajocian to mid-Callovian (11.5 m.y.). Same convention as in Figure 4. See Fig. 2 for key to zone numbers.

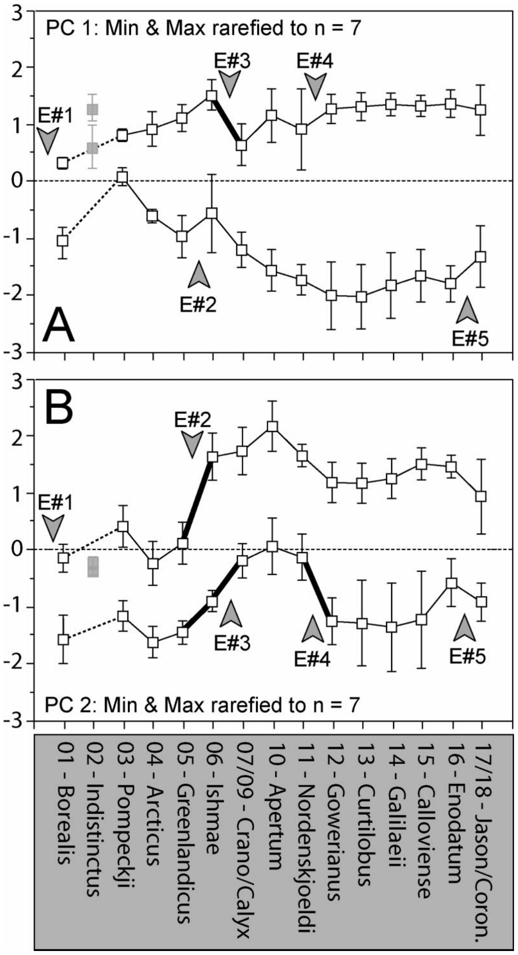

FIGURE 6. Patterns of spatial occupation from the late Bajocian to mid-Callovian. Spatial occupation is measured by minimum and maximum values of coordinates on principal components. Error bars were generated by bootstrapping (500 replicates) and samples are rarefied to $n = 7$. Values for the Indistinctus zone are for information only (poor sample with $n = 3$). Thick lines indicate significant difference at 5% (tested only for events 2 to 5).

morphology) and then becomes relatively stable, although a decrease is clearly marked from the Apertum to Gowerianus zones. This new morphological peak corresponds to the differentiation of microconchs appearing in the Ishmae zone and remaining present thereafter. Thus PC 2 reflects rapid saturation of this maximum value by differentiation of microconchs. After this event, drastic modification of morphospace occupation is only possible by modification of minimum values. The minimum shows a clear increase from the Greenlandicus to Cranocephaloides zone (#05–07), corresponding to the loss of discocone morphology and contemporaneous with Events 2 and 3. Minimum values recover in the Gowerianus subzone (#12) with the origination of *Cadochamoussetia* and *Chamoussetia* (Event 4) and the re-occupation of the discocone morphology. Subsequently, the minimum remains constant up to the extinction of Chamoussetia in the Enodatum subzone (#16).

Patterns of Disparity.—Temporal sequences of analyzed disparity indices (rarefied area of convex hull and mean pairwise distance, Fig. 7) exhibit quite similar patterns: they are different only at the end of the period under study (Enodatum subzone (#15), end of early Callovian). We observe a progressive and sustained increase until the Ishmae zone (#06; mid-Bathonian) which can be attributed to (1) the progressive recovery of thick forms (trend of the minimum values on PC 1) and (2) the individualization of microconchs inducing a major increase in morphospace occupation. Next, the two metrics exhibit, contemporaneous with Event 3, a decrease (but not statistically significant, see Fig. 7) corresponding to the extinction of compressed forms of *Arcticoceras*. Earlier values are restored in the Apertum zone. Thus, it seems that disparity reaches a first plateau from the Ishmae to Nordenskjoeldi zones reflecting a disparity level based on two morphological peaks of occupation. This plateau is modified in the Gowerianus subzone (#12), where a major increase occurs. A second plateau is reached and maintained until the Calloviense subzone (#15). This arrangement is based on three occupational peaks and corresponds to the origination of *Cadochamoussetia* and *Chamoussetia* (Event 4), which recovered morphological niches lost. Thereafter the two metrics follow different patterns. The amount of morphospace occupation decreases markedly before stabilizing at values comparable with those of the Nordenskjoeldi subzone (#11), while the mean dissimilarity between species declines progressively to values comparable with those found for the Nordenskjoeldi subzone. The separation of these two parameters reflects the extinction of *Chamoussetia* which was a pe-

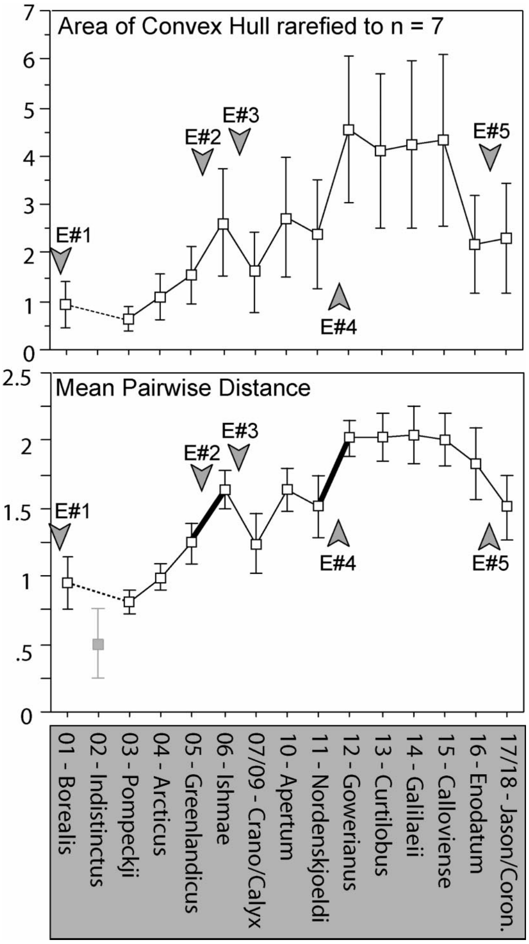

FIGURE 7. Patterns of morphological disparity from the late Bajocian to mid-Callovian. Disparity is measured by mean pairwise distance. An alternative metric is the area of convex hull that quantifies the amount of morphospace occupied. Error bars were generated by bootstrapping (500 replicates) and for convex hull area samples were rarefied to $n = 7$. Values for the Indistinctus zone are for information only (poor sample with $n = 3$). Thick lines indicate significant difference at 5% (tested only for events 2 to 5).

ripheral form and so preferentially affected the amount of occupation rather than the dissimilarity. The origination of *Stenocadoceras* in the mid-Callovian is not expressed here as it is masked by the extinction of extreme cadicone forms (negative values of PC 1) offsetting the potential increase that origination would have caused. Recovery of values similar to those preceding the Gowerianus subzone (#12) reflects a return to the initial plateau and so a return to a morphospace structured around two occupational peaks.

Discussion

The conceptual and methodological framework of disparity, although developed in relation to major evolutionary radiations, has proved a transposable approach with great potential for the study of biodiversity in various contexts: geographic patterns, geographic range expansion, taxon sorting, evolutionary dynamics, extinction events, and scale effects. However, in developing this new methodology, the spatial component of morphospace occupation has been largely overlooked. Alongside the quantification of dispersion, the use of indices based on the position of the minimum and maximum values on each axis (to decipher the extreme peaks of space occupied) is highly informative (1) for quantifying temporal sequences of occupied morphospace and not just simply observing this occupation and (2) for understanding the various components of changes in disparity. In contrast to the approach involving tests of extreme modifications, such as that used by Foote (1994a,b, 1995), our approach provides temporal sequences that can be compared directly with temporal sequences of indices based on dispersion of shapes in the morphospace. However, this method is a non-synthetic one (each axis is treated separately). Moreover, for the minor factorial axis, the covariant part of characters becomes less intuitive and noise becomes more important. However, it may be suggested that only major axes need be observed since they summarize the essential part of dispersion and so display the more interesting patterns. On the other hand, indices based on dispersion possess a synthetic quality. However, using dispersion without control of position would make it difficult to interpret events involving disparity. The method used here, involving analysis of position and dispersion using similar metrics, allows us (1) to compensate the detachment of disparity indices with group centroids; (2) to interpret disparity modifications in morphological terms; and (3) to detect significant variations (i.e., trend, saturation of morphological peak, location of extinction or origination) in terms of morphology and not just of dispersion.

Cardioceratidae shells occupied a large morphological field similar to that of all planispiral ammonites. Differential filling shows that their morphospace is structured around three peaks corresponding to specific groups. One corresponds to derived microconchs. The other two correspond essentially to macroconchs: one combining the majority of the primitive subfamily and several derived genera; the second corresponding to Cadoceratinae and some thick forms of the primitive subfamily. Analysis of spatial occupation shows that acquisition of this field occurs essentially by the replacement or subdivision of preexisting peaks of occupation. These replacements seem to be produced by different patterns:—progressive trend: (1) progressive increase in thickness from the Pompeckji (#03; late Bajocian) to Nordenskjoeldi zones (#11; early Callovian) and then a decrease through the second part of early and mid-Callovian;—saturation: acquisition of platycone morphology by microconchs in the Ishmae zone (#06; mid-Bathonian) and its subsequent conservation;—iteration: re-acquisition of the discocone morphology presents from Indistinctus to Ishmae zone (#02–06), then in the early Callovian (*Chamoussetia*: northwest European platform and Russian platform; #12–15) and in the mid-Callovian (*Stenocadoceras*: North America; #18);—apparent preferential extinction: (1) extinction of compressed forms (late Bathonian; #07); (2) extinction of discocone morphology at the end of the early Callovian (#16); (3) extinction of extreme cadicone morphology in the mid-Callovian (#17).

After observing these patterns, we can suggest different factors that may have shaped them. One of these factors corresponds to a morphological differentiation that has been interpreted by various authors as sexual dimorphism. After its acquisition, the microconch morphological peak shows a ''regional morphologic stasis'' (McGhee 1999). This substantial morphological differentiation between microconchs and macroconchs is thought to reflect sexual segregation in mode of life.

Another factor that could cause disparity modification is fluctuations in ammonites' proximal environments. Such relationships between morphology and environment are frequently observed in ammonites (Batt 1989, 1993; Bayer and McGhee 1984; Jacobs 1992; Jacobs et al. 1994; Tintant et al. 1982; Westermann 1996). For example, changes in shell shape are related to sea-level changes (e.g., Dommergues et al. 1996; Neige et al. 1997). This is because the shell is the hydrostatic apparatus of the ammonite. This apparatus was in direct contact with the physical conditions of the environment and the initial assumption is that the two may be related. However, such correlations may be misleading because a correlation between environmental and morphological curves does not necessarily reflect a true connection between them and such correlations may just be random features (McKinney 1990; Alroy et al. 2000). Nonetheless ammonite shells potentially harbor information about environment and mode of life. The study of shell distribution initiated by Ziegler (1967) and the study of hydrostatic properties of shells such as aperture orientation (Trueman 1941; Saunders and Shapiro 1986) have allowed habitat and mode of life models to be developed (see synthesis of Westermann 1996). However, there are many exceptions to these major trends (Elmi 1993), and thus models have to be seen as very general guidelines of ammonites' habitats. Moreover, the hypothesis about body extension outside the body chamber (Chamberlain 1980; Jacobs and Landman 1993) challenges relationships between body chamber length and aperture orientation. This capability would permit total control over orientation. The study by Elmi (1993) of hydrodynamic properties (e.g., drag) shows that the relationship between shell and fluid can be more complex. Parameters such as shape of ventral area or shape of umbilicus play a preponderant role. Ornament can make up for an unfavorable general morphology. Thus it appears that (1) shells contain information about ammonite mode of life although that information remains difficult to extract by modeling except for general features; (2) understanding the mode of life for a group involves, above all, collecting facts about faunal distribution. In our case, a particular pattern may be interpreted in the light of such shape/environment relationships. It concerns the initial and progressive increase in disparity from the Indistinctus zone to Greenlandicus zone. This phenomenon is due to a modification of morphospace occupation toward negative values on PC 1 (see Fig. 5), and reflects a faunal assemblage modification: initially strictly composed of discocone shapes then progressively composed of discocone but associated with cadicone shapes (see Fig. 4). Following Westermann's model (1996: Fig. 1), this suggests a modification from nektonic ammonites only to nektonic and planktonic ammonites. Boreal signals of relative sea level exist but they are derived from tectonically controlled basins. Due to this local control, curves present numerous discrepancies, and thus are not, a regional (Boreal Realm) proxy of environmental modifications. Thus, unfortunately, our signals of regional morphological diversification cannot be compared with these local curves.

A third preponderant factor is related to geographical modifications and potentially illuminated by the previous considerations. In a theoretical perspective (see Neige 2003 for a draft model), geographical modifications may affect disparity (1) when the modifications offer the possibility of emigration events for a clade, the so-called faunal transgressions, leading to an expansion of geographic clade-range and (2) in turn when these modifications offer the possibility of immigration events for another clade. This latter may display a diversification in its new geographic range and thus compete with native clades. Emigration events can be driven by adult emigration or by juvenile dispersal. Adult morphology can be a key to emigration or on the contrary emigration can yield morphological changes (e.g., Hellberg et al. 2001). In our example, emigration of Cardioceratidae from the Boreal Realm over the Russian and northwest European platforms (Event 4), inducing the origination of *Cadochamoussetia* and *Chamoussetia*, led to the colonization of a new part of the morphospace (i.e., a new peak) in coexistence with the initial one causing increased disparity. This marked morphological differentiation at the time of faunal transgressions is thought to reflect acquisition of a new ecological niche, much as Marchand *in* Dommergues et al. (1989) interpreted the origination of *Chamoussetia* by acquisition of a nectobenthic mode of life. On the contrary, a similar emigration event, the origination of *Stenocadoceras* associated with the colonization of the Western Interior in the mid-Callovian (Event 5), is not related here with increased disparity. However, as explained before, this is mainly because its effect (see Fig. 5, stars in diagram #17/18) is masked by the extinction of extreme cadicone forms.

The effect of immigrating faunas is also clearly marked in the studied example. The Kosmoceratidae first arrived in the Ishmae zone (Event 2), but clearly expanded their geographical range and invaded the Boreal Realm just after in the Cranocephaloides zone (Event 3). This diversification is clearly apparent in the decreased disparity of the Cardioceratidae clade (see Fig. 7). Early kosmoceratids (Kepplerites) have discocone morphology and thus present a large morphological differentiation from their putative ancestor from the *Cadomites* genus, which has cadicone morphology. When plotting kosmoceratid morphologies as additional points, this clade lies within the cardioceratid morphospace (Fig. 4D). Other nonindigenous species occurred episodically in one border region (Yukon, Siberia, Greenland) but unlike the kosmoceratids did not invade the entire Boreal Realm. In this case, all species are located in the peripheral region of the cardioceratid morphospace (Fig. 4D). It can be noted that the only clade to have invaded the Boreal Realm is also the only one to occur within the cardioceratid morphospace. Moreover, when the Kosmoceratidae originated in the Ishmae zone (#06) their morphospace location (discocone peak) was at the same time occupied by the Cardioceratidae (Fig. 8). Immediately after, in the Cranocephaloides zone (#07), Cardioceratidae underwent a large morphological shift from discocone to cadicone morphology, giving rise to the *Cadoceras* genus. However, whereas the two clades have the same shell morphology, their costal patterns are very different. Early kosmoceratid species have numerous thin ribs whereas cardioceratids have only a few flat, rough ribs. Considering the hydrodynamic models, a similar shell shape implies similar

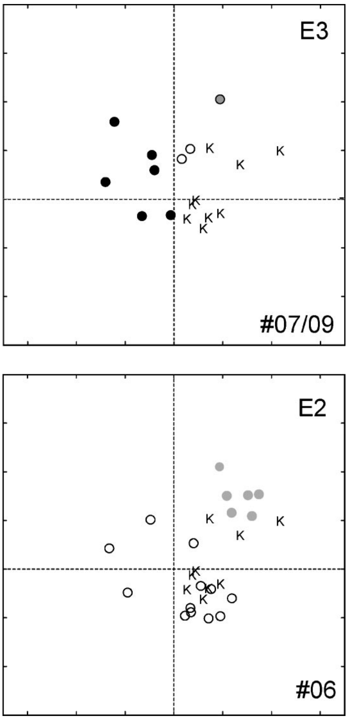

FIGURE 8. Patterns of morphospace occupation for the Cardioceratidae compared with the location of the Kosmoceratidae (top: Cranocephaloides to Calyx zones, bottom: Ishmae zone). Kosmoceratidae (labeled K) are added as additional points and are not included in the factor analysis process. White and light gray dots for Arcticocephalitinae (respectively macro- and microconchs) and black and dark gray dots for Cadoceratinae (respectively macro- and microconchs). Kosmoceratid forms of the Ishmae zone are considered to be the same as in the latter zone (see text for additional discussion).

hydrodynamic capabilities. However, costal patterns and umbilical shape could vastly improve these capacities (Elmi 1993). It may be that their costal pattern favored Kosmoceratidae by improving their hydrodynamic capacities. Consequently, when the two clades occupied what was probably the same ecological niche, the Kosmoceratidae temporally excluded the native clade of the discocone peak and induced the morphological shift of Cardioceratidae to the cadicone peak. The discocone peak was recovered only when some cardioceratid species immigrated to adjacent regions.

The overall type of disparity pattern can thus be described as follows: first, an increase (maybe due to environmental change and subsequent ammonite adaptations to a near planktonic mode of life) toward a plateau; then once this plateau was reached, fluctuations occurred around it corresponding to extinction and origination events. These events may be seen as second order ones as they do not drastically modify disparity. The plateau corresponds to a specific structure of the morphospace (e.g., number of distinct morphological peaks). To actually modify this plateau and not merely generate minor fluctuations around it requires a drastic reorganization of the morphospace. A new morphospace structure is obtained either by destruction of the initial arrangement (e.g., extinction of some peak), or by modification of the initial arrangement by acquisition of a new peak and its superimposition on the former one (e.g., origination of a new peak). At the very onset of the early Callovian, expansion of the geographic area by ingression into new provinces entailed a reorganization of the morphospace with the origination of a new peak in association with the two existing ones. This reorganization allowed a new disparity plateau to be reached. Similarly, a diversification phase of an immigrant clade (Kosmoceratidae) during the Bathonian also caused a reorganization (see suppression of shapes of the positive PC 1—negative PC 2 corner on Fig. 5) of the morphospace. Geographic constraints thus played a preponderant role in maintaining or modifying the state of disparity. Removal of those constraints allowed faunas to encounter new environmental conditions (e.g., Russian and European platforms) while retaining their initial Boreal niche. Finally, just a few branching events entail substantial increases in disparity. These events coincide with faunal transgressions to other provinces and their confrontation with different environmental conditions (Russian and northwest European platforms). Nevertheless, the Cardioceratidae acquired a large morphological field equal to the near complete field of major morphological types among planispiral ammonites (Raup 1967, Ward 1980). This spectrum was obtained by progressive shifting of the whole clade over time (so without any marked increase in disparity). In fact, while they were exclusively or nearly exclusively confined to the Boreal Realm, the Cardioceratidae never displayed genuine diversification and only the opening of the Arctic trap permitted diversification with marked morphological differentiation: expansion of the geographic clade-range allowed confrontation with a new environmental niche while conserving the existing one and so, a new morphological peak was acquired without the initial peak being lost, inducing major increases in Cardioceratidae disparity. On the other hand, the invasion of the Boreal Realm by another clade induced a major morphological shift and probably the loss of an initial ecological niche.

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Appendix

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