instrument before and after the Uranus encounter, may also provide evidence for or against the disk-dynamo interaction model. This model predicts (*4*) that the nightside aurora, if any, should be dimmer than the dayside aurora, and that the morphology of the dayside auroral emission region should depend on the orientation of the magnetic dipole moment relative to the solar wind, forming a bright circular ring at the polar cap boundary if the north magnetic pole faces the sun or a diffuse glow filling the center of the polar cap if the south magnetic pole faces the sun. No such predictions are available for an Earth-like interaction model within the expected pole-on geometry.

If the observations of bright Lyα radiation from Uranus are being interpreted correctly as indicating a polar aurora (*1–3*), the aurora is a powerful one. According to either of the theoretical models described herein, the inferred auroral emission output of at least 6×10^9 W (*14*) implies a large magnetosphere, which in turn implies a large planetary magnetic moment. It is apparent that remote sensing of auroral emissions does not provide a precise determination of a planetary magnetic moment because of the uncertainties in the various mechanisms involved and their efficiencies. However, reasonable lower limits can already be established that indicate that Uranus has a significant dipole moment.

If we accept the present interpretation of the IUE observations of Uranus (*1–3*), then the surface magnetic field of Uranus must have a value of at least 0.6 G, making it the second strongest magnetic field of any of the planets. At this lower limit the magnetosphere, operating at maximum efficiency, is just large enough to collect enough power from the solar wind to drive the aurora. The most probable value of the surface magnetic field, again based on the IUE results, is ~4 G according to the disk-dynamo model and ~13 G according to the Earth-like model. The upper limits range from 20 to 300 G and are hardly to be taken seriously. During the next few months Voyager approach observations should allow us to sharpen our estimates; in early 1986 Voyager will test our theoretical understanding by direct measurements in situ.

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Margin to Craton Expansion of Late Ordovician Benthic Marine Invertebrates

Abstract. *A biostratigraphic survey of 57 Late Ordovician marine shelly invertebrates from the* Climacograptus manitoulinensis *zone of eastern Canada supports suggestions that throughout the Early Phanerozoic benthic marine speciations occurred preferentially in marginal marine environments. The species subsequently spread onto the craton. There is no obvious positive correlation between the times of first appearance of new associations or novel communities along the continental margin and the first appearance on the craton of the species making up these communities. Taxonomic similarities between marine communities that occupied both marginal and cratonic regimes may reflect a more static local ecology than the evolutionary dynamics of a piecemeal species-by-species reassembly.*

The suggestion that many Paleozoic benthic marine invertebrates expanded from nearshore marginal marine environments into the cratonic offshore seas is the subject of this investigation. Eldredge (*1*) especially recognized the implications of such movement with regard to modes of speciation. Allopatric speciation was more likely to have taken place along the more spatially heterogeneous marginal environments. In many studies of faunal migrations the offshore, as compared to the marginal nearshore, environments usually have referred to bathymetrically deeper waters. Reconstructed shelf profiles then often resemble the present, passive Atlantic margin (*2*). Eldredge, however, defined the offshore as the epicontinental or epeiric sea regimes—that is, those marine environments that covered the continents during much of the Paleozoic and that seemingly lacked the degree of spatial heterogeneity characteristic of more marginal habitats.

The details of multispecies expansion have been clouded by biostratigraphic imprecision especially in correlation between localities in different geological provinces (*3*). Correlations often must be carried out through the use of temporally persistent species, and although accurate, faunal zones can span millions of years. In the case of the Ordovician the most reliable zones used to correlate

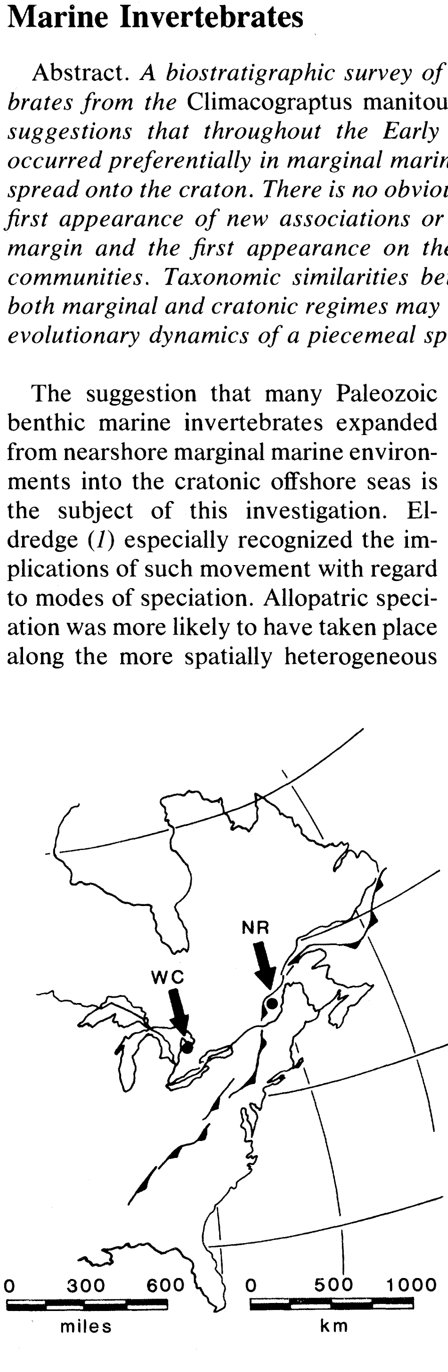

Fig. 1. Locality map of eastern North America showing the location of the Workman's Creek (WC), which is also known as the East Meaford Creek, and the Nicolet River (NR) exposure (*8*). The heavier barbed line indicates the edge of the thrust belt or highly folded strata.

from marginal to cratonic sections have been defined through the use of conodonts or graptolites (*4*).

We have correlated two stratigraphically continuous, but geographically isolated, Late Ordovician exposures (Maysvillian Stage) from eastern Canada (Fig. 1) (*5*) by using the well-preserved and in situ shelly benthic marine macroinvertebrates and a graphical technique first introduced by Shaw (*6*). These correlations were drawn within the upper two-thirds of the 3-million-year *Climacograptus manitoulinensis* zone, as defined by Riva (*7*). Detailed stratigraphic collections permitted us to identify 112 invertebrate species from the Nicolet River mudstones and 71 species from the Workman's Creek (also known as East Meaford Creek) mudstones (*8*). Fifty-seven species are common to both sections, perhaps a surprisingly high percentage since a 250-foot (76.25-m) thick portion of the Workman's Creek section turned out to be equivalent to about a 1000-foot (305-m) thick interval along the Nicolet River.

In Shaw's technique each exposure is considered a single axis in a two variable *xy* coordinate system. Bases and tops of species ranges (that is, the first appearances and last occurrences) are plotted as points on this *xy* graph. As explained by Shaw and a number of subsequent investigators (*6*), the points that tend to fall along a straight line represent points of equivalent time for both sections. A regression line can be drawn through these points—Shaw called it a "line of correlation." Once this line has been established, any discrete points falling away from it represent events with a reasonably high probability of having occurred earlier or later in one local section than in the other one.

Biostratigraphers who have used Shaw's line-of-correlation technique rarely have addressed the ecological or evolutionary significance of the discrepant points; these were dismissed, and often quite logically, as representing only a portion of the species range and one that had resulted from the effects of the local environment. Before attempting to establish a line of correlation, we eliminated all those species (21 of the 57) whose first introductions were within the lowermost 20 feet or whose last occurrences were in the uppermost 20 feet (6.1 m) of the Workman's Creek section, as well as last occurrences that were beyond the 2250-foot (686.25-m) level at Nicolet River. By doing this, we were attempting to avoid a very basic sampling bias wherein the first appearance or the last occurrence of any given species was a result of the availability of the exposure and not reflective of its actual stratigraphic distribution.

Rather than a single regression analysis of the first appearances and last occurrences of the remaining 36 species (*9*), three separate reduced major axis analyses were carried out so that the most precisely defined line of correlation could be determined. An analysis of last occurrences ($n = 20$) provided a much more reliable line of correlation ($r^2 = 0.667$) than analyses of all the data points for the 36 species ($n = 43$; $r^2 = 0.108$) or only those of first appearances ($n = 23$; $r^2 = 0.027$). Thus it appears that the benthic species within these Late Ordovician marine environments may have been going extinct in a manner similar to Cenozoic planktonic Foraminifera recently documented by Emiliani (*10*), who emphasized the occurrence of geographically widespread synchronous extinctions of individual species.

The reduced major axis line of correlation for the last occurrences of 20 species common to both sections is shown in Fig. 2A, and 2B incorporates this line of correlation on a graph showing the first appearances of 23 species common to both sections. Although no first appearances are recorded for the first 20 feet (6.1 m) of the Workman's Creek section, for again these appearances could be based simply on the availability of exposure, it is obvious that the overwhelming majority of the first appearances have occurred initially within the marginal Nicolet River section—that is, they are well below the line of correlation. From this relation we can draw five conclusions.

1) The hypothesis of some kind of preferential expansion of species from marginal environments onto the craton appears to have been supported by the analyses of these Late Ordovician data.

2) Species appear to have spread across the craton at variable rates; there were some species whose movement was geologically instantaneous and hence almost migrational on an ecological time scale [for example, the modiomorphoid and palaeotaxodont bivalve mollusks (species 52, 55, and 56)]; whereas the spreading rate of gastropods, whether bellerophontid (20), pleur-

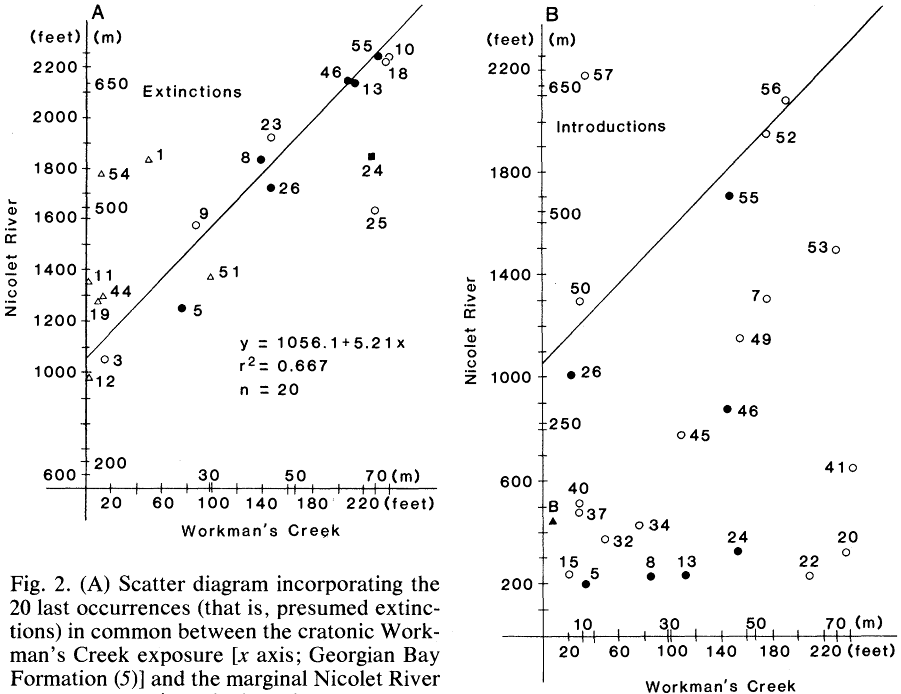

Fig. 2. (A) Scatter diagram incorporating the 20 last occurrences (that is, presumed extinctions) in common between the cratonic Workman's Creek exposure [*x* axis; Georgian Bay Formation (*5*)] and the marginal Nicolet River exposure [*y* axis; Nicolet River Formation (*7*)]. A reduced major axis "line of correlation" has been drawn through the points of last occurrence for these 20 species (*9*). The darkened points are those species for which first appearances are recorded in (B). Seven of the 20 last occurrences are represented by only a single sample (open triangles). One taxon, the pleurotomariid gastropod, *Lophospira* cf. *L. ventricosta* (Hall) (species 24, solid square) is a taxonomic enigma for it probably represents more than one species. (B) Scatter diagram of first appearances of 23 species. The solid circles are species for which last occurrences were plotted (A). The open circles are species that have been found throughout both stratigraphic sections and in the stratigraphically highest samples and, hence, presumably have not undergone extinction during the lower two-thirds of the *Climacograptus manitoulinensis* zone. Point B (solid triangle) records the first appearance of the trepostome bryozoan *Bythopora dendrina*.

otomariid (24 and 41) or murchisoniid (13), across the craton, was relatively slow.

3) This pattern of movement of these benthic marine invertebrates across the craton may be positively correlated with the physical effects of the retreat of the Late Ordovician seas from the North American craton. Thus as the epeiric seas became shallower, those species that had previously occupied shallow-water marginal regimes were able to colonize the craton. However, even when a number of species appeared almost geologically instantaneously (that is, a new or novel community) along the continental margin (such as the cluster of species near the 200-foot or 61-m Nicolet River horizon), this marginal community seems not to have spread intact onto the craton; rather, the first appearances of individual species are staggered throughout the entire cratonic section.

Zinsmeister and Feldmann (*11*) documented examples of speciation in Cenozoic marine invertebrates in the extremely seasonal high latitudes. Movement of these species into lower latitudes was very variable, and differences in the rates of spreading have given rise to heterochronic stratigraphic relationships that are based on first appearances. These heterochronic relationships may have resulted from the combined effects of the variable expansion of the physical habitat within which speciation had occurred and the possibility that some species may have undergone adaptational migrations—that is, physiological adaptations, rather than just a simple tracking of a single initially preferable habitat. For whatever reasons, in our example, colonization of the craton usually did not occur until well after the initial speciation events had taken place somewhere along the margin.

4) During the Late Ordovician, movement from the craton toward the continental margin was a very rare event, with the only obvious candidate being the thick-walled ramose trepostome bryozoan *Bythopora* cf. *B. delicatula* (Nicholson) (species 57). Specimens of the genus *Bythopora* are common in both sections, yet the first appearance of a significantly thinner walled, presumably ancestral, *Bythopora* [cf. *B. dendrina* (James)] does take place along the margin (point B, Fig. 2B). *Bythopora dendrina* continues throughout both sections, but *B. delicatula* appeared first on the craton, indeed well before it was recorded along the eastern margin. Explanations for this apparent reversal in migration are obscure, but from Pachut's (*12*) study of trepostome phenotypic variance within and among colonies, it could be that some different modes of speciation affected colonial populations on the stable craton.

5) Jablonski *et al.* (*2*) have outlined a model of benthic community migrations from shallow to deeper water regimes. Implied within this model is that biologically "innovative" speciations have occurred in the shallow-water regimes, and it was there that some community-level integrative structure was formed. These "innovative" communities then migrated progressively through time as a whole.

The results of our study do not address the "innovative" versus a more "mundane" aspect of speciation, nor do we take issue with the notion of large-scale geographic movements of most species; rather we call into question evolutionary explanations that require these geographic movements to have been undertaken by integrated communities of species. It seems as if a more static ecological analysis has masked the evolutionary dynamics of the piecemeal, species-by-species reassembly of the cratonic communities from the original marginal parts.

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9. The following species were used in the regression analyses and the numbers appear in Fig. 2, A and B, and Table 1 below. (E, extinction; I, introduction; and I/E, both recorded): 1. *Leptaena moniquensis* Foerste (1924) (E), 3. *Cryptolithus bellulus* (Ulrich) (E), 5. *Nuculites postvolutus* (Foerste) (I/E), 7. *Nuculites praevolutus* (Foerste) (I), 8. *Similodonta astarteformis?* (Salter) (I/E), 9. *Eoplectodonta* sp. A (E), 10. *Onniella meeki?* (Miller) (E), 11. *Obolus? hyacinthensis* (Foerste) (E), 12. *Triarthus eatoni* (Hall) (E), 13. *Hormotoma gracilis?* (Hall) (I/E), 15. *Colpomya pusilla?* Foerste (1914) (I), 18. *Cyclocoelia crassiplicata?* Foerste (1910) (E), 19. *Temnodiscus? parvus* (Ulrich) (E), 20. *Bucania* sp. A (I), 22. *Pterinea demissa?* (Conrad) (I), 23. *Sinuites cancellatus?* (Hall) (E), 24. *Lophospira* cf. *L. ventricosta* (Hall) (I/E), 25. *Lepidocoleus jamesi* (Hall and Whitfield) (E), 26. *Heterotrypa* sp. A (I/E), 32. *Craniops subtruncata* (Hall) (I), 34. *Cymatonota parallela?* (Hall) (I), 37. *Dekayia* sp. A (I), 40. *Stictopora* sp. A (I), 41. *Clathrospira conica?* Ulrich and Scofield (1897) (I), 44. *?Ceraurinus* sp. A (E), 45. *Orthodesma* cf. *O. approximatum* Foerste (1914) (I), 46. *Hebertella occidentalis* (Hall) (I/E), 49. *Deceptrix levata* (Hall) (I), 50. *Coeloclema* cf. *C. alternatum* (James) (I), 51. *Modiolopsis meafordensis?* Foerste (1924) (E), 52. *Modiolopsis* cf. *M. modiolaris* (Conrad) (I), 53. *Strophomena planumbona?* (Hall) (I), 54. *Pterotheca* cf. *P. pentagona* Foerste (1914) (E), 55. *Ctenodonta? pulchella* (Hall) (I/E), 56. *Pholadomorpha pholadiformis* (Hall) (I), and 57. *Bythopora* cf. *B. delicatula* (Nicholson) (I).

Table 1. Stratigraphic horizons (in feet) of first appearances (originations) and last occurrences (extinction). NR, Nicolet River; WC, Workman's Creek.

Species	Originations		Extinctions	
	NR	WC	NR	WC
1			1832	50.5
3			1047	16
5	170	33	1249	76.5
7	1274	174.5		
8	195	84	1832	140
9			1575	89.5
10			2223	239.5
11			1352	5
12			972	5
13	198	119	2140	213.5
15	198	19.5		
18			2223	239.5
19			1285	12
20	287	236.5		
22	198	228		
23			1924	149.5
24	301	151	1853	227
25			1635	229.5
26	978	20	1727	147
32	340	48		
34	405	74		
37	447	26.5		
40	481	26.5		
41	627	241		
44			1295	14
45	753	106.5		
46	850	143.5	2140	208.5
49	1127	153.5		
50	1260	26.5		
51			1374	99
52	1925	172		
53	1470	227.5		
54			1774	12
55	1674	143	2250	239
56	2055	188		
57	2151	29		

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