Species diversity among agnostoid trilobites

RICHARD A. ROBISON


Most species of the suborder Agnostina are non-intergrading and best fit an allopatric model of speciation. Continued allopatry of some species is indicated by the existence of temporally correlative biofacies. Abrupt introduction of morphologically distinct agnostoid species into many areas suggests that migration often resulted in sympathy of other species. To avoid competitive elimination, sympatric agnostoids probably followed a variety of adaptive pathways. Evidence of two strategies, depth segregation and character displacement with respect to size, is presented. Size displacement apparently increased from the late Early Cambrian until the middle Middle Cambrian, at which time size ratios stabilized at about 1.3. Attainment of apparent optimum size displacement coincides with the beginning of a period of marked increase in agnostoid diversity, which reached a maximum during the late Middle and early Late Cambrian.

R. A. Robison, Department of Geology, University of Kansas, Lawrence, Kansas 66045, 28th September, 1973.

Diversity among agnostoid trilobites reached a maximum during the late Middle and early Late Cambrian when more than 200 species made their appearance. Multiple closely related species commonly are present in a single stratum, and paleoecologic evidence usually indicates that a given agnostoid assemblage lived in the area where the specimens accumulated and were buried. The purposes of this paper are to examine the general nature of speciation among agnostoids, to consider possible adaptive pathways, and to investigate possible techniques by which closely related agnostoid species may have coexisted without competitive elimination.

New or revised descriptions of some of the taxa referred to in this paper are being prepared for separate publication. Several of the agnostoid collections are from the Wheeler Formation of western Utah, and new information requires revision of the concept and biostratigraphy of that formation. Instead of being 94 m (307 feet) thick in the Drum Mountains as previously reported (Robison, 1964:1001), the Wheeler Formation in that area actually is 302 m (990 feet) thick. Depending on the locality in western Utah, the boundary between the Bathyriscus-Elrathina and Bolaspidella Assemblage Zones is located from 27 to 61 m (90 to 200 feet) above the base of the Wheeler Formation.

Because of a major hiatus between the Lower and Middle Cambrian in most of northwestern Europe, in this paper the traditional North American rather than the Scandinavian concept of the Middle Cambrian is used. For purposes of discussion, an informal tripartite subdivision of the Middle Cambrian also is used. The lower Middle Cambrian commences with a mostly undescribed “pre-Albertella” fauna, and it succeeds olenellid-bearing strata. The middle Middle Cambrian commences with the Bathyriscus-Elrathina Zone, and the upper Middle Cambrian commences with the Bolaspidella zone. Occurrences of agnostoids show the boundary between the Bathyriscus-Elrathina and Bolaspidella Zones of North America correlates closely with the boundary between the Ptychagnostus gibbus and Ptychagnostus atavus Zones as defined in Sweden (Westergård, 1946).

AGNOSTOID CHARACTERISTICS

The Agnostina of Moore (1959:172-186) includes relatively small trilobites with a restricted size range. The maximum observed holaspoid or adult length is about 20 mm, but length in most species does not exceed 10 mm. The cephalon and pygidium are similar in outline and nearly equal in size, eyes are absent from the dorsal exoskeleton, the hypostoma and cephalothoracic hinge line are unique among trilobites, and the thorax invariably has only two segments in the
holaspid period (see Fig. 1). Enrollment was an important agnostoid function, which is indicated by a number of specialized exoskeletal structures (Robison, 1972b), and during ontogeny a constant size relationship between the cephalon and pygidium apparently was maintained in response to the method of enrollment.

AGNOSTOID SPECIATION AND COMPETITION

From an extensive study of Middle Cambrian agnostoids in western North America I have found a conspicuous lack of intergradation in species-specific characters, and I also have found little or no change in those characters throughout the observed stratigraphic ranges of most species. This general morphologic stability suggests that substitution or addition of agnostoid species mostly resulted from migration rather than gradual evolution in situ. Such a pattern is consistent with a model of allopatric speciation (Eldredge, 1971; Eldredge & Gould, 1972), which is predicated on the concept that new species arise by relatively rapid development of species-specific characters in peripheral isolates, and that stability of species-specific characters is the norm, except when two species become sympatric for the first time.

When closely related species become sympatric, morphologic differences tend to be accentuated in response to pressures of competition (Brown & Wilson, 1956). Extensive study of competition theory has led to formulation of the Principle of Competitive Exclusion, which states that in equilibrium communities no two species occupy the same niche (Hutchinson, 1965:27). Hundreds of examples of neontological exclusion have been cited, and Mayr (1963:69-88) has reviewed many of them. A few apparent exceptions to the principle have been reported (e.g., Ayala, 1969, 1972), but the great frequency of demonstrable exclusion establishes it as a major factor in evolutionary divergence. Similar patterns of exclusion are shown by Cambrian agnostoid trilobites, and they indicate the operation of competitive exclusion since early in the history of metazoans.

Modern animals have been found to avoid competition by both spatial and nonspatial segregation. Spatial strategies tend to be more conspicuous and mostly involve geographic separation, but among marine faunas they also may involve depth stratification. Non-spatial strategies tend to be more subtle and commonly involve isolating mechanisms such as time, diet, or foraging techniques (e.g., Diamond, 1973:767). Those strategies amenable to analysis in the fossil record are considered here.

SPATIAL SEGREGATION OF AGNOSTOIDS

GEOGRAPHIC.— From several lines of evidence I (Robison, 1972b) have concluded that most agnostoid trilobites probably were pelagic inhabitants of open oceans. Such an inferred mode of
life is supported by the wide geographic distribution of many genera and species. Nevertheless, various types of geographic segregation of some agnostoids can be observed.

Segregation of certain genera occurs on different geographic scales. On an intercontinental scale the condylopigids and phalacromids are common in western Europe and parts of maritime Canada (components of a single early Paleozoic tectonic plate), but are unknown from most of North America. In an opposite pattern, Baltagnostus and Spinagnostus (=Kormagnostus) are common in most of North America, but are absent in western Europe and related maritime Canada. Within North America, Baltagnostus and Spinagnostus normally are found in biofacies shoreward from those with cosmopolitan agnostoids such as Ptychagnostus and Hypagnostus. Similar biofacies patterns have been described for Middle Cambrian agnostoid communities in Tasmania (Jago, 1972). Among modern marine faunas comparable distribution patterns can be found in most pelagic groups.

Some species are further segregated within regional biofacies. For example, 10 agnostoid species have been found in the Ptychagnostus gibbus Zone in Nevada and Utah, and most have similar geographic ranges within the region. However, an observed maximum of six, and usually no more than four species are present in any single stratum, and combinations of species are variable from one stratum to another. The same type of segregation occurs in collections from the same zone in Sweden and Norway.

Partial geographic segregation is displayed by Ptychagnostus gibbus and P. intermedius in Nevada and Utah. Both species are similar in maximum size and commonly are found together in the same stratum, but in any given stratum almost always one species is abundant and the other is rare (e.g., Table 1-D). This suggests the possibility that the respective competitive superiority of the two species may have shifted with environmental conditions or with population densities (cf. Mayr, 1970:49).

The segregation patterns cited for agnostoids are similar to those described for modern animals, and it appears likely that similar adaptive pathways were followed during Cambrian as in modern times. Direct competition for resources probably was more important as a factor in local exclusion, whereas opportunistic adaptation to different resources may have been more significant in segregation on regional and larger scales.

VERTICAL.—Although inconclusive, some evidence suggests the possibility that certain agnostoid species may have achieved habitat segregation by living in different depths of water. In Nevada, Utah, and Sweden; faunas typical of the lower part of the Ptychagnostus gibbus Zone are found in a succession of transgressive marine strata. In these strata Peronopsis fallax consistently makes its first appearance lower in the section than does Ptychagnostus gibbus. However, once Ptychagnostus gibbus appears, the two species commonly are associated in successively higher strata. In a transgressive sequence, such an occurrence pattern would result if Peronopsis fallax lived in shallow depths and Ptychagnostus gibbus lived at greater depths. Also, the same pattern would develop if Peronopsis fallax was adapted for life in additional and more shoreward habitats than those favored by Ptychagnostus gibbus. The fact that the same pattern is found in different rock types and at widely separated localities seems to favor the depth control alternative. Further comment on this pattern is given in the following section.

NON-SPATIAL SEGREGATION OF AGNOSTOIDS

The phenomenon known as character displacement (Brown & Wilson, 1956) develops when the ranges of two or more closely related species overlap geographically. Differences between the species are accentuated in the zone of sympatry, but remain less in the parts of their ranges outside that zone. One of the most common characters displaced is size. From studies of such diverse groups as mammals, birds, and aquatic insects, Hutchinson (1959:152-154, 1965:55-60) has shown that moderate differences in size are sufficient to cause obligate feeding on different sizes of food. Where closely related species are sympatric he found the size ratios of larger to smaller species to range from 1.1 to 1.4 with the mean ratio being 1.28. Several other studies have produced similar observations. For example, in a recent study of New Guinea birds Diamond (1973:767) used body weight as a measure of displacement, and found that among congeners sorted by size

"the ratio between the weights of the larger bird and the smaller bird is on the average 1.90; is never less than 1.33 and never more than 2.73. Species with similar habits and with a weight ratio less than 1.33 are too similar to coexist locally (that is, to share territories) and must segregate spatially."
The cube root of 1.90 equals 1.25, which compares closely with the linear average size ratio of 1.28 calculated by Hutchinson.

Although character displacement with respect to size has been described in many modern faunas, it has received little attention in the study of fossils. A few authors have mentioned the possibility of character displacement in fossils, but usually specific examples have not been cited. Eldredge (1972:93-102) has discussed an apparent case of character displacement in *Phacops rana* and *P. iowensis*, and he states in a recent letter (September, 1973) that the maximum cephalic length ratio for these two species is 1.37. Except for that example, and those mentioned in a preliminary abstract (Robison, 1973) concerning this study, I know of no other specific discussions of size displacement in fossils. From the analysis of several agnostoid trilobite assemblages, I have found that where two or more species occur together they commonly show maximum size ratios remarkably close to the average of 1.28 reported by Hutchinson.

**PROCEDURES.** — Because size displacement has been demonstrated to correlate with differences in size of food, it is desirable to measure the trophic apparatus. In the calcified exoskeleton of agnostoids that apparatus consists only of the hypostoma, which because of its fragile nature is seldom preserved. In fact, only recently have a few such sclerites been discovered and described (Robison, 1972a). Thus, rare and poor preservation make the agnostoid hypostoma an unsuitable subject for biometric analysis.

A second option is cephalic length, which is a measure used by Hutchinson (1959:153) in his study of size displacement in mammals. Again, a problem exists with agnostoids because the exoskeleton commonly is found disarticulated, and in that condition it is difficult to determine the species identity of some cephalas. On the other hand, disarticulated pygidia usually can be identified with ease. Fortunately, because of the special method of enrollment, a constant length ratio is maintained between the cephalon and pygidium during ontogeny. For these reasons, pygidial length (Fig. 1) is the measure selected for size analysis of agnostoid trilobites. The articulating half ring is not included in the measure of pygidal length because it is covered by the posterior thoracic segment of articulated specimens, and not uncommonly is broken on disarticulated specimens.

**AGNOSTOID SIZE DISPLACEMENT.** — From 19 collections analyzed, data from seven are presented in Table 1 to illustrate observed maximum pygidial length (hereafter abbreviated *mpl*) ratios for sympatric agnostoid trilobite species. The collections were selected from different stratigraphic intervals ranging in age from late Early to late Middle Cambrian. An attempt was made to select representative assemblages, as well as to illustrate as many kinds of size patterns as possible. Also, in order to facilitate recognition of possible phyletic trends, the collections (A to G) are ordered in relative stratigraphic position.

Collection A from the upper *Olenellus* Zone of late Early Cambrian age contains the oldest recorded assemblage with multiple species of agnostoid trilobites. The numbers of specimens are from Rasetti & Theokritoff (1967), and I have obtained length measurements from published illustrations. According to Theokritoff (1972, written communication), all specimens of *Peronopsis evansi* and *Eoagnostus acrorhachis* came from a single limestone boulder. The sample of about 13 pygidia is too small to be statistically reliable. However, the observed *mpl* ratio of 1.09 is low, and this may reflect insignificant or only minor displacement of size in the oldest known assemblage of agnostoid trilobites.

Collection B from the lower *Glossopleura* Zone of early Middle Cambrian age contains 26 silicified pygidia of *Peronopsis brighamensis* and *P. bonnerensis*, which were extracted with acid from a single piece of limestone. The *mpl* ratio is 1.15, but again is based on a small sample. Another collection (UU-100) from the same formation and from a similar stratigraphic interval at Wellsville Mountain in northern Utah has yielded 12 pygidia of the same two species. They have an *mpl* ratio of 1.19, which is close to that calculated for the specimens from Idaho, and therefore suggests that the ratios may be meaningful.

Ratios for the three species in collection C have been calculated from maximum pygidial lengths recorded by Westergård (1936), which to my knowledge is the only published study to provide such measurements for multiple agnostoid species from a limited area and from a thin stratigraphic interval. It is not clear from Westergård’s account whether or not the specimens came from a single bed, but they apparently did come from a stratigraphic interval probably no more than five meters thick. Although the statistical validity of the sample is unknown, the ratios of 1.35 and 1.39 suggest that size displacement had evolved to a degree comparable to that observed in modern communities with closely related sympatric species.

Collection D from the upper *Bathyuriscus-Elrathina* Zone of middle Middle Cambrian age
Table 1. Lists of agnostoid trilobite species from selected collections. Data includes total number of specimens of each species in the collection (N), percentage of each species in the collection (%), maximum pygidial length (mpl) measured in mm, and ratios of maximum pygidial length (ratios). University of Utah collections are designated by numbers preceded by the letters UU.

G. Upper Bolaspidella Zone (upper Lejopyge calva Subzone) from top bed of member A, Emigrant Springs Limestone at Patterson Pass, Schell Creek Range, Nevada (UU-154).

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>%</th>
<th>mpl</th>
<th>Ratios</th>
</tr>
</thead>
<tbody>
<tr>
<td>Utagnostus trispinulus</td>
<td>2</td>
<td>&lt;1</td>
<td>2.0</td>
<td>1.25</td>
</tr>
<tr>
<td>Ptychagnostus n. sp.</td>
<td>2</td>
<td>&lt;1</td>
<td>2.5</td>
<td>1.04</td>
</tr>
<tr>
<td>Baltagnostus eurypyx</td>
<td>50</td>
<td>10</td>
<td>2.6</td>
<td>1.35</td>
</tr>
<tr>
<td>Hypagnostus n. sp.</td>
<td>50</td>
<td>10</td>
<td>3.5</td>
<td>1.14</td>
</tr>
<tr>
<td>Lejopyge calva</td>
<td>400</td>
<td>80</td>
<td>4.0</td>
<td></td>
</tr>
</tbody>
</table>

F. Lower Bolaspidella Zone (middle Bathyuriscus fimbriatus Subzone) from 50 feet below top of Wheeler Shale, near Swasey Spring, House Range, Utah (UU-114).

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>%</th>
<th>mpl</th>
<th>Ratios</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ptychagnostus atavus</td>
<td>481</td>
<td>68</td>
<td>2.7</td>
<td>1.04</td>
</tr>
<tr>
<td>Peronopsis fallax ferox</td>
<td>15</td>
<td>2</td>
<td>2.8</td>
<td>1.07</td>
</tr>
<tr>
<td>Hypagnostus parvifrons</td>
<td>9</td>
<td>1</td>
<td>3.0</td>
<td>1.13</td>
</tr>
<tr>
<td>Baltagnostus eurypyx</td>
<td>74</td>
<td>11</td>
<td>3.4</td>
<td>1.29</td>
</tr>
<tr>
<td>Peronopsis interstricta</td>
<td>126</td>
<td>18</td>
<td>4.4</td>
<td></td>
</tr>
</tbody>
</table>

E. Lower Bolaspidella Zone (lower Bathyuriscus fimbriatus Subzone) from 200 feet above base of Wheeler Shale, Drum Mountains, Utah (UU-520).

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>%</th>
<th>mpl</th>
<th>Ratios</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peronopsis? n. sp.</td>
<td>75</td>
<td>48</td>
<td>2.5</td>
<td>1.08</td>
</tr>
<tr>
<td>Ptychagnostus gibbus n. subsp.</td>
<td>9</td>
<td>6</td>
<td>2.7</td>
<td>1.04</td>
</tr>
<tr>
<td>Peronopsis fallax fallax</td>
<td>9</td>
<td>6</td>
<td>2.8</td>
<td>1.18</td>
</tr>
<tr>
<td>Peronopsis segmenta</td>
<td>34</td>
<td>22</td>
<td>3.3</td>
<td>1.30</td>
</tr>
<tr>
<td>Peronopsis interstricta</td>
<td>29</td>
<td>18</td>
<td>4.3</td>
<td></td>
</tr>
</tbody>
</table>

D. Upper Bathyuriscus-Elrathina Zone from 154 feet above base of Wheeler Shale, Drum Mountains, Utah (UU-250).

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>%</th>
<th>mpl</th>
<th>Ratios</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ptychagnostus intermedius (Tullberg)</td>
<td>5</td>
<td>2</td>
<td>2.3</td>
<td>1.13</td>
</tr>
<tr>
<td>Ptychagnostus gibbus n. subsp.</td>
<td>43</td>
<td>17</td>
<td>2.6</td>
<td>1.00</td>
</tr>
<tr>
<td>Peronopsis fallax fallax (Linnarsson)</td>
<td>44</td>
<td>18</td>
<td>2.6</td>
<td>1.27</td>
</tr>
<tr>
<td>Peronopsis interstricta (White)</td>
<td>157</td>
<td>63</td>
<td>3.3</td>
<td></td>
</tr>
</tbody>
</table>
C. Upper *Paradoxides oelandicus* Stage (*P. pinus* Zone), Oland, Sweden (Westergård, 1936).

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>%</th>
<th>mpl</th>
<th>ratios</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Condylopyge carinata</em> Westergård</td>
<td>?</td>
<td>?</td>
<td>3.3</td>
<td></td>
</tr>
<tr>
<td><em>Peronopsis fallax</em> fallax (Linnarsson)</td>
<td>?</td>
<td>?</td>
<td>4.6</td>
<td>1.39</td>
</tr>
<tr>
<td><em>Ptychagnostus praecurrens</em> (Westergård)</td>
<td>?</td>
<td>?</td>
<td>6.2</td>
<td>1.35</td>
</tr>
</tbody>
</table>

B. Lower *Glossopleura* Zone from 50 feet above base of Spence Shale, Two Mile Canyon near Malad, Idaho (UU-142).

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>%</th>
<th>mpl</th>
<th>ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Peronopsis bonnerensis</em> (Resser)</td>
<td>13</td>
<td>45</td>
<td>2.6</td>
<td>1.15</td>
</tr>
<tr>
<td><em>Peronopsis brighamensis</em> (Resser)</td>
<td>16</td>
<td>55</td>
<td>3.0</td>
<td></td>
</tr>
</tbody>
</table>

A. Upper *Olenellus* Zone from Taconic Mountains, New York (Theokritoff locality 58-11; Rasetti & Theokritoff, 1967).

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>%</th>
<th>mpl</th>
<th>ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Peronopsis evansi</em> Rasetti &amp; Theokrit.</td>
<td>3</td>
<td>23±</td>
<td>2.3</td>
<td>1.09</td>
</tr>
<tr>
<td><em>Eoagnostus acrorhachis</em> Rasetti &amp; Theo.</td>
<td>&lt;10</td>
<td>77±</td>
<td>2.5</td>
<td></td>
</tr>
</tbody>
</table>

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**Fig. 2.** Suggested model of inferred depth stratification, relative abundance, and maximum lengths (mpl) of agnostoid trilobites in collection UU-250. *Peronopsis interstricta* is inferred to have lived throughout the water column, whereas *Peronopsis fallax* is inferred to have lived in shallow water, and *Ptychagnostus gibbus* and *Ptychagnostus intermedius* are inferred to have lived in deeper water. *P. intermedius* may have been an immigrant from a peripheral biotope, and not a normal member of this particular agnostoid community.
is only slightly younger than collection C. It includes 249 silicified pygidia, which were extract-
ed with acid from a single piece of limestone, and the sample is large enough to be statistically
reliable. The collection illustrates a different pattern of sizes by having two common species, *Peronopsis fallax* and *Ptychagnostus gibbus*, with the same maximum pygidal lengths. Thus, each of those species has an identical mpl ratio of 1.27 with *Peronopsis interstricta*, which is
the only abundant species in the collection. The same three species also are similarly abundant
and have practically identical mpl ratios in collections UU-251 and 253 from beds one and six
feet higher at the same locality. This stratigraphic repetition indicates an equilibrium in size
displacement and stability in community structure rather than initial sympatric congregation
without size displacement.

It was suggested in the preceding section of this paper that *Peronopsis fallax* probably
lived in a shallow depth zone and *Ptychagnostus gibbus* probably lived in a deeper depth zone.
A suggested model to explain inferred relationships for collection D is illustrated by Figure 2.
In this model *Peronopsis fallax* and *Ptychagnostus gibbus* utilized food resources of the same
size, but avoided direct competition by adapting to different depth zones. *Peronopsis inter-
stricta* was not influenced by depth restrictions and coexisted with both *Peronopsis fallax* and
*Ptychagnostus gibbus*, but avoided competition by utilizing food resources of different size as
indicated by the numerical displacement of maximum exoskeletal size.

*Ptychagnostus intermedius* is a rare component of collection D, and its abundance relative
to that of *P. gibbus* is discussed in a previous section concerning geographic segregation.

Collections E and F exhibit species diversity typical of that observed in several late
Middle Cambrian agnostoid trilobite assemblages, and equilibrium in size displacement appears
to have been achieved among those species that comprise more than about 10 percent of the
specimens in each collection. Collection E contains 156 silicified pygidia that were extracted
with acid from a single piece of limestone. Collection F contains 705 articulated specimens
that came from weathered shale. Three species each comprise more than 10 percent of the
population in both collections, and when arranged according to increasing maximum size, the
mpl ratios all fall within a range from 1.26 to 1.32. The average for those ratios is practically
identical to the average of 1.28 recorded by Hutchinson (1959:152) for modern communities
with closely related sympatric species that take food of different sizes. Therefore, I suggest
that the regular occurrence of similar mpl ratios probably indicates that the common agnostoid
species in collections E and F also avoided competition by taking food of different sizes.
Species comprising less than 10 percent of the agnostoid specimens in collections E and F pos-
sibly filled more restricted niches, or may represent immigrants from more favorable peripheral
biotopes.

Collection G is interpreted here to be an example of mixed agnostoid communities in
which optimum size displacement was not established between some species. The collection is
late Middle Cambrian in age and came from the top bed of member A of the Emigrant Springs
Limestone at Patterson Pass, Nevada. The uppermost beds of member A consist of biosparite,
whereas the lowest beds of member B consist of laminated calcareous mudstone with bio-
micrite lenses. The lithologic change from member A to member B represents an abrupt de-
crease in energy regime, probably as a result of increased water depth. It further represents an
apparent change from outer shelf-edge to basinal marine environments. In the lower 10 feet of
member B the agnostoid fauna also changes from the composition indicated for collection G to
a composition of 95 to 100 percent *Lejopyge calva*. Therefore, I suggest that collection G con-
tains mixed elements of a shallow shelf-edge community and a normally more seaward and
deeper basinal community. These probably correspond to Jago’s (1972:98–120) Tasmanian
agnostoid communities (1) and (2). *Baltagnostus eurylyx* and a new species of *Hypagnostus*
appear to be the dominant species of the adjacent shelf-edge community. They show an mpl
ratio of 1.35, which is near the apparent optimum in size displacement, and I suggest they
avoided competition by that means. On the other hand, *L. calva* appears to be the only com-
mon species in the open ocean community at this particular locality. The mpl ratios between
*L. calva* and associated common agnostoid species in collection G are 1.14 and 1.54, which
are well outside the uniform range of 1.26 to 1.32 observed in collections E and F. In regards
to this interpretation of biofacies, it is notable that *Baltagnostus* as an inferred shelf inhabitant
is known only for North America and questionably from South America, whereas *Lejopyge*
as an inferred inhabitant of open oceans is cosmopolitan.

In conclusion, size displacement among agnostoid trilobites usually is most evident be-
tween those species comprising more than approximately 10 percent of each assemblage, and
in assemblages that are middle Middle Cambrian or younger in age. From the limited number of
collections analyzed, size displacement appears to have been an important technique for the
nonspatial segregation of some agnostoid trilobites, and thereby likely contributed to increased

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diversity. Beginning in the late Early Cambrian, size displacement appears to have been negligible, but increased until the middle Middle Cambrian, at which time ratios tended to stabilize near an apparent optimum of about 1.3. Concomitant with that attainment of apparent optimum size displacement is the beginning of a period of marked increase in diversity in numbers of species per single stratum, as well as increase in total numbers of species per unit time. Prior to the middle Middle Cambrian no more than two agnostoid species have been reported from any single stratum, whereas throughout the upper half of the Middle Cambrian it is not uncommon to find as many as six agnostoid species in a single stratum. Furthermore, a total of not more than a dozen agnostoid species have been described from the interval prior to the middle Middle Cambrian, whereas more than a hundred agnostoid species have been described from the latter half of the Middle Cambrian.

The limited data in Table 1 suggest possible fruitful subjects for further investigation. One such subject involves niche partitioning. Agnostoid trilobites probably arose by neoteny as indicated by the holaspisid retention of juvenile characters such as small size, few thoracic segments, and an isopygous condition. In accord with that probability, figures in Table 1 show that the oldest known agnostoid species were small in relative maximum size. Subsequent niche partitioning usually was achieved by the addition of new species at the upper end of the size scale. In general, this pattern supports the thesis by Stanley (1973) that new taxa tend to arise at small relative body size and niches requiring larger body size tend to be filled subsequently by niche partitioning so that vacant regions of a group’s maximum potential adaptive zone are progressively invaded. Another subject for further investigation involves geographic size difference in the same species. Most cosmopolitan agnostoid species tend to have larger maximum sizes in Scandinavia than they do in western North America. This empirical knowledge is based on direct field investigation as well as study of numerous museum collections, and is exemplified by measurements given for *Peronopsis fallax fallax* in collections C, D, and E. Nevertheless, similar size displacement patterns are developed in both regions. Because marked differences in rock matrices probably reflect significantly different Cambrian environments in Scandinavia and western North America (cf., Robison, 1972b, p. 34–35), I suggest that geographic difference in maximum size for the same species most likely was caused by phenotypic rather than genotypic factors.

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Montreal.


