

Epigondolella populations and their phylogeny and zonation in the Upper Triassic

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Eight distinctive populations of the conodont *Epigondolella* occur in the Norian (Upper Triassic) of British Columbia. Each is associated with rich ammonoid faunas. Intercalibration of the faunal succession through a remarkably complete Norian sequence is documented. The range of morphological variety within each conodont population is presented, a central morphotype is selected, and its growth series described. The problems arising from an inadequate appreciation of growth stages and of homomorphy are stressed. New criteria for species determination are outlined, including the nature of microreticulation. The following succession is recognized: *E. primitia* – restricted to the *S. kerri* Zone; *E. abneptis* subsp. A – upper *S. kerri* and lower *M. dawsoni* Zones; *E. abneptis* subsp. B – upper *M. dawsoni* and *J. magnus* Zones; *E. multidentata* – *D. rutherfordi* Zone; *E. n. sp. C* – lower lower *M. columbianus* Zone; *E. postera* – upper lower *M. columbianus* Zone; *E. n. sp. D* – lower upper *M. columbianus* Zone; and *E. bidentata* – *G. cordilleranus* and *C. amoenum* Zones. □*Conodonta, Epigondolella, biostratigraphy, evolution, Triassic, British Columbia.*

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The Pardonet Formation (McLearn 1960) of northeastern British Columbia in western Canada is a thin (maximum of about 135 m) but remarkably complete succession of Norian (Upper Triassic) strata deposited near the edge of the Cordilleran miogeosyncline. Now exposed in the Rocky Mountain foothills, particularly in the area of Peace River, the formation consists of dark calcareous siltstones and shales with subordinate coquinoid limestones (see Gibson 1971:22–3 for details) of relatively deep-water origin that contrast markedly with the Carnian dolomites of the underlying Baldonnel Formation.

The Pardonet Formation contains rich ammonoid faunas that have been central to the development of a biochronological standard for late Triassic time (Tozer 1967). New exposures of the formation, resulting from damming of the Peace River, have been studied and sampled in collaboration with E.T. Tozer, who has recognized sequences of ammonoid faunas embracing the zones of *Stikinoceras kerri*, *Malayites dawsoni*, *Juvavites magnus* (Lower Norian), *Drepaniceras rutherfordi*, *Mesohimavatites columbianus* (Middle Norian) and *Gnomohalorites cordilleranus* (Upper Norian). Abundant conodont faunules have been recovered from all of these zones. Elsewhere in western Canada, rare conodonts have also been found in strata assigned to the *Cochloceras amoenum* Zone (Upper Norian).

This paper outlines the succession of *Epigondolella* species, establishes criteria for recognizing and distinguishing eight principle species-complexes, and presents their relationship with each other and with the ammonoid standard.

Illustrated specimens are deposited with the Geological Survey of Canada in Ottawa.

Epigondolella populations

Conodont faunules from the Pardonet Formation include abundant representatives of the discrete platform element of *Epigondolella*. Eight successive *Epigondolella* populations covering the Norian ammonoid zones of *S. kerri* through *C. amoenum* (Fig. 1) are recognized. Within each population examples of the diverse array of morphotypes, including representatives of different growth stages, have been chosen for illustration (Figs. 2, 4, 6, 8, 10, 11, 13, 14). Of these, the most common element type has been selected as a *central morphotype* (shown shaded in the figs.).

Each population comprises specimens in addition to the central morphotype that have characteristic features in common with it, yet in some respects appear markedly different, particularly if considered in isolation. To a large extent individual conodont elements form points in a broad morphological continuum that I have attempted to illustrate and describe below (see also Fig. 14). Many individual morphotypes of a population can be hypothetically derived from different growth stages (frequently the earlier ones) of the central morphotype by the retention of certain characteristics or the exaggeration of certain trends. Most members of a population may be linked as shown in Fig. 14, which shows these relationships within *Epigondolella bidentata*, the youngest and structurally least complex of the epigondolellids. In this way, stratigraphically restricted, but less common morphotypes are generated in each population in addition to the central morphotype. These specimens are often homeomorphic with structurally comparable morphotypes of a different age.

	Ammonoid Zones (Tozer 1967, 1979, 1981)	Conodont Zones (Orchard, this paper)
UPPER	C RICKMAYI	?
	A M O E N U M	
	C O R D I L L E R A N U S	E. bidentata
MIDDLE	C O L U M B I A N U S	4 ? E. n. sp. D. E. postera E. n. sp. C.
	R U T H E R F O R D I	E. multidentata
LOWER	M A G N U S	E. obneptis subsp. B
	D A W S O N I	E. obneptis subsp. A.
	K E R R I	E. primitia

Fig. 1. Zonation of the Norian based on ammonoids and conodonts.

In some species of *Epigondolella*, early growth stages are quite different from later ones, but may resemble later growth stages of other species. This phenomenon of neoteny, recognized in *Epigondolella* by Mosher (1970:740), demands that an accurate determination of growth stages be made, which requires a full appreciation of scale. This work attempts to define the growth series of each *Epigondolella* species as exemplified by its central morphotype. Put into this perspective, it becomes clear that many *Epigondolella* species, and their stratigraphic range, have been misinterpreted.

There follows an outline of the eight *Epigondolella* species-complexes recognized herein, and their age. New systematics, numerical and stratigraphic detail will be presented in a future paper.

The *Epigondolella primitia* population

Figs. 2, 3 A, B, F, 7 A, L, X, 15 A, B, C

Epigondolella primitia was originally described by Mosher (1970). The type material was recovered from the matrix of *S. kerri* Zone ammonoids from Brown Hill on Peace River. Abundant collections from the type locality and elsewhere demonstrate the extent of variation within populations of the species. This is shown in Fig. 2, and described below.

Platform shapes.—Generally elongate, length to breadth ratio of between 2:1 and 3:1, commonly 5:2. Small specimens have a characteristic mid-platform constriction (Fig. 2 R, J). Late

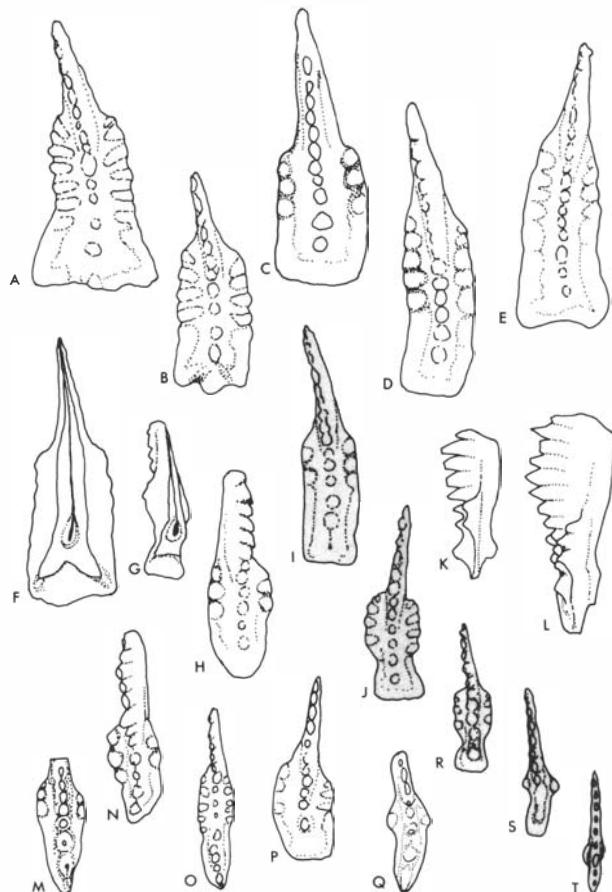


Fig. 2. Central morphotype growth series (shaded specimens) and morphological variation in *Epigondolella primitia* populations. The scale bar is 1 mm long.

growth stages may have either subparallel margins (Fig. 2 B, C, D, I) or wedge-shaped posterior platforms (Fig. 2 A). Some specimens are tapered to a narrowly rounded posterior termination (Fig. 2 H), which is pointed in rare specimens (Fig. 2 M, N, O). Generally, the posterior margin is squared-off; rarely it is irregular due to undulations of the platform margins (Fig. 2 B). Specimens sometimes have a linguiform posterior when one postero-lateral margin is more strongly developed and the axis of the conodont is flexed: this condition occurs in younger epigondolellids too.

Platform ornament.—Almost entirely restricted to the anterior platform margin. Three to five, round to transversely elongate nodes occur on each side, except in the earliest growth stages, and in rare larger specimens, in which there is only one (Fig. 2 Q). Nodes are generally subequal in size, well differentiated and discrete (Fig. 2 A, B) but may be subdued and coalescing (Fig. 2 E); rarely, they are only feebly developed. Posterior platforms are characteristically free of relief; occasionally they may be marginally undulose, but they are never serrate.

Carina.—Nearly always subterminal. Small specimens display a prominent subterminal cusp (Fig. 2 K), which becomes subdued with additional platform growth. Uncommon morphotypes (Fig. 2 M, O) have a posteriorly continuous carina as

well as a narrow, pointed platform. Large specimens may develop secondary carinae.

Free blade. – Between one-third and one-half total unit length, decreasing with growth, arcuate in profile and becoming progressively lower onto the platform.

Lower-side morphology. – A pit with a distinct lip is situated posterior of the platform midlength. The basal attachment area may be bifurcate in those large specimens with marked postero-lateral growth (Fig. 2 F).

Microreticulae. – Present over the whole of the platform except for the carina and an area surrounding it on all sides. This is manifest as a distinct marginal band that contrasts sharply with a smooth adcarinal area. The reticulae consist of closely-shaped, equidimensional pits that have a diameter of about 10 µm (Fig. 3 A, B, F).

Central morphotype growth series. – Growth proceeds through an early bidentate condition (Fig. 2 S) by increase in the size of the anterior platform and in the number of marginal nodes. The posterior platform expands laterally less quickly, but the medial part shows least growth initially so that a mid-platform constriction arises. Thereafter, subparallel platform margins are developed by medial filling-in (Fig. 2 I): this is the condition of the holotype. Later growth may be uniform (Fig. 2 D) or the posterior platform may outstrip anterior growth to produce wedge-shaped outlines (Fig. 2 A).

Comparisons. – Uncommon specimens that are relatively short (Fig. 2 C, P) mimic *E. abneptis* but may be distinguished by the relatively low anterior nodes, which are also more numerous, and the rounded postero-lateral platform margins. Further, microreticulae are more uniformly developed marginally, including over the nodes. Specimens that have a posterior carina (Fig. 2 M, N, O) vaguely resemble *E. multidentata* but both the carina and anterior nodes of the latter species are much more prominent and the microreticulae are totally different, as is the case also with bidentate (one denticle on each side of the carina) specimens (Fig. 2 Q) that resemble *E. bidentata* (see below).

Age. – The *E. primitia* population described above appears at the base of the Norian and occurs throughout its range with *S. kerri* Zone ammonoids. Late Carnian *E. primitia?* occurs within faunules dominated by gondolellids of the *Paragondolella polygnathiformis* – *Metapolygnathus nodosa* group but its morphological variation within those faunules has yet to be assessed.

The *Epigondolella abneptis* subsp. A population

Figs. 3 D, E, G, 4, 7 B, M, N, Y, 9 A, 15 D, E, F

Epigondolella abneptis was originally described by Huckriede (1958) from the Hallstatt Limestone at Sommersaukogel, Austria. The type material was recovered from strata containing an ammonoid association referred to the *Cyrtopleurites bicrenatus* Zone. Krystyn (1980:90) elucidated the faunal

succession at Sommersaukogel and demonstrated that the *C. bicrenatus*-Fauna proper is more restricted than originally thought. The precise stratigraphic origin of the type of *E. abneptis* is therefore in doubt.

The species is the most generalised of the epigondolellids. All previous authors have regarded it as ranging throughout most of the Norian as well as the late Carnian. Previous attempts to subdivide it have not substantially improved its stratigraphic utility. I recognize three distinct *abneptis*-like homeomorphs, of Late Carnian, Early Norian and Middle Norian age. Each arose independently from non-'*abneptid*' predecessors. Additional species also occur that might fall within the existing, rather broad concept of the species and this has undoubtedly led to the long range attributed to *E. abneptis*.

Pending a study of the type material and a rationalized taxonomy, I retain the name *E. abneptis* for the early Norian species (e.g. Mosher 1973). Two broad groups may be distinguished, based on the morphology of the posterior platform. In addition, several distinct morphotypes of stratigraphic value are recognized. Variability within *E. abneptis* subsp. A populations is illustrated in Fig. 4.

Platform shapes. – Relatively squat elements with an average platform length to breadth ratio of about 3:2. This contrasts markedly with *E. primitia* populations as shown graphically in Fig. 5. Posterior margins are generally quadrate, although the 'linguiform condition' distorts this symmetry (Fig. 4 O, Q). Some forms become increasingly wedge-shaped posteriorly, and this reaches an extreme in specimens that have sharp, strongly extended, postero-lateral corners (Fig. 4 F). Other specimens, generally more elongate, have rounded posterior terminations (Fig. 4 K, L).

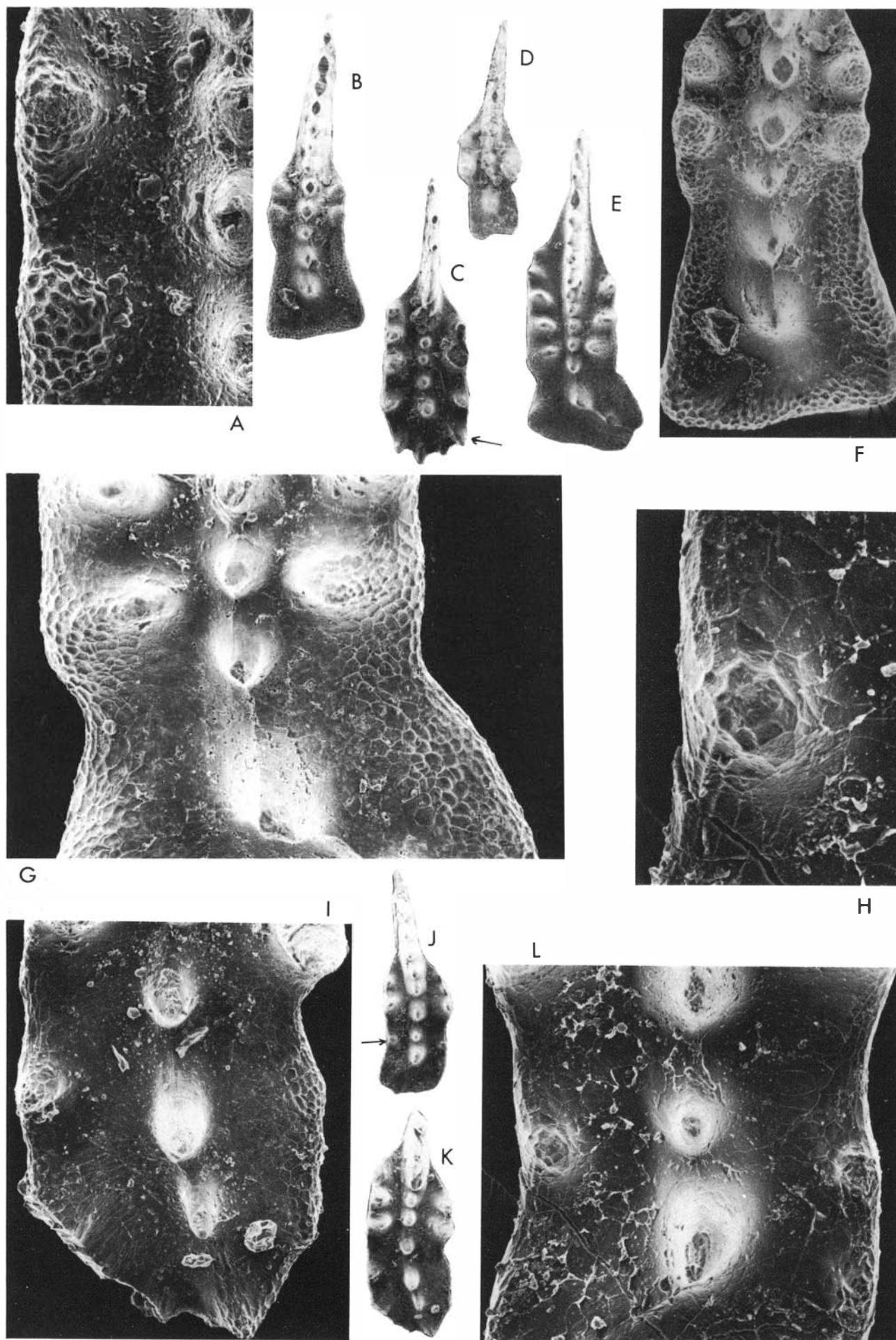
Platform ornament. – Nodes or denticles are generally restricted to the anterior but are fewer in number (usually two or three) and have greater relief than those of *E. primitia*. The posterior platform is generally smooth or has incipient nodes developed marginally, particularly at the postero-lateral corners or at the posterior border in line with the carina (Fig. 4 E, F), or as secondary carinae (Fig. 4 B). Specimens with distinct posterior ornament are rare and never have nodes as strongly developed as those anteriorly.

Carina. – Always subterminal, even in early growth stages. Rare specimens with crenulated posterior margins may have a marginal node aligned with the carina and in some late growth stages, one or both secondary carinae may extend to near the postero-lateral corner.

Free blade. – Generally one-third unit length, with convex profile.

Lower-side morphology. – A pit with a distinct lip is situated at or slightly posterior of platform midlength. A bifurcate keel is common.

Microreticulae. – Present over much of the platform but receding from the more prominent anterior nodes. For the most part comparable to that in *E. primitia* but showing elongation, enlargement and decreasing relief toward the carina (Fig. 3 D,



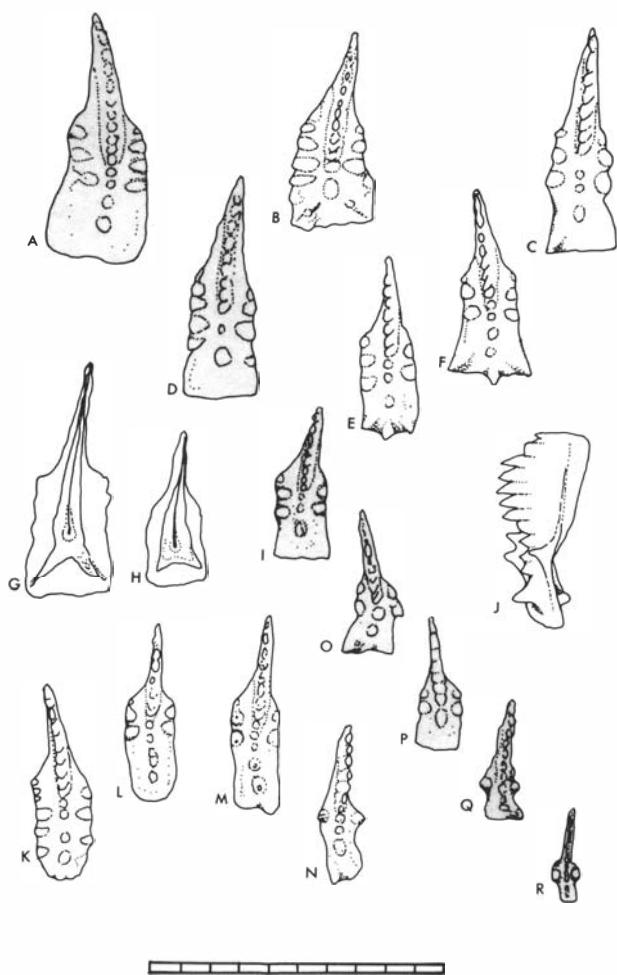


Fig. 4. Central morphotype growth series (shaded specimens) and morphological variation in *Epigondolella abneptis* subsp. A populations. The scale bar is 1 mm long.

E, G). This is an initial stage in the development of the more subdued, open reticulae that characterize Middle Norian epigondolellids.

Central morphotype growth series. — Growth proceeds uniformly from an early stage that strongly resembles later stages except that they have fewer anterior nodes (Fig. 4 R, Q, P, O, I, D, A).

Comparisons. — See *E. primitia* and *E. abneptis* subsp. B.

Fig. 3. Microreticulation on the platforms of Lower Norian epigondolellids. Arrows indicate positions of illustrated detail. □A, B, F. *E. primitia*. Note uniform, compact reticulation. □A. GSC 68846 (= Fig. 15 B) from Pardonet Hill, GSC Loc. No. O-98514. $\times 500$. □B, F. GSC 68869 from Brown Hill, GSC Loc. No. C-87908. $\times 80$, $\times 210$. □C. *E. abneptis* subsp. B, late form. GSC 68870 (= Fig. 9 I) from McLay Spur, GSC Loc. No. O-98537. $\times 80$. □D, E, G. *E. abneptis* subsp. A. □D. GSC 68871 (= Fig. 9 A) from McLay Spur, GSC Loc. No. O-98538. $\times 80$. □E, G. GSC 68872 from Pardonet Hill, GSC Loc. No. O-98509. $\times 80$, $\times 350$. Note more open, finer reticulae toward carina. □H, I, J, K, L. *E. abneptis* subsp. B, early forms. Note that compact reticulae are confined to nodes whereas open form characterizes platform. □H, J, L. GSC 68873 from Brown Hill, GSC Loc. No. C-87912. $\times 1200$, $\times 80$, $\times 500$. □I, K. GSC 68874 from Brown Hill, GSC Loc. No. C-87913. $\times 300$, $\times 80$.

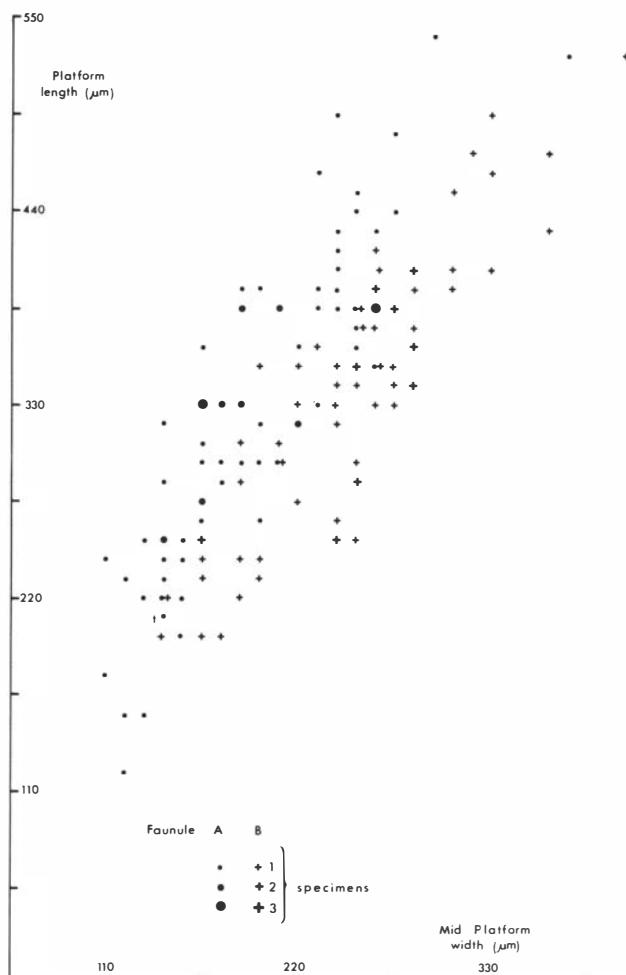


Fig. 5. Graphical illustration of the change in platform proportions between faunule A = *E. primitia* from GSC Loc. No. C-87908, and faunule B = *E. abneptis* subsp. A from GSC Loc. C-87909. The collections, from Brown Hill, were made 1.5 m apart.

Age. — *E. abneptis* subsp. A appears abruptly within the late *S. kerri* Zone. At Pardonet Hill, its appearance corresponds to a distinctive *Aulacoceras* belemnite–ammonoid bed. *Epigondolella* faunules from low in the *M. dawsoni* Zone are not abundant but are probably referable to *E. abneptis* subsp. A. Thereafter, representatives of this complex, if present, are strongly subordinate to *E. abneptis* subsp. B. Rare specimens resembling the central morphotype persist throughout the remainder of the Lower Norian, but not beyond it.

The *E. abneptis* subsp. B population

Figs. 3 C, H, I, J, K, L, 6, 7 C, O, P, Q, R, Z, 9 I, 15 G, H, I

The upper half of the Lower Norian is dominated by strongly ornate epigondolellids. Although similar in relative dimensions to *E. abneptis* subsp. A, the species-complex is characterized by a distinctive growth series and by morphotypes that allow further subdivision of the interval. Morphological variation is illustrated in Fig. 6.

Platform shapes. — Relatively squat elements with a length to breadth ratio comparable to *E. a.* subsp. A, but with fewer

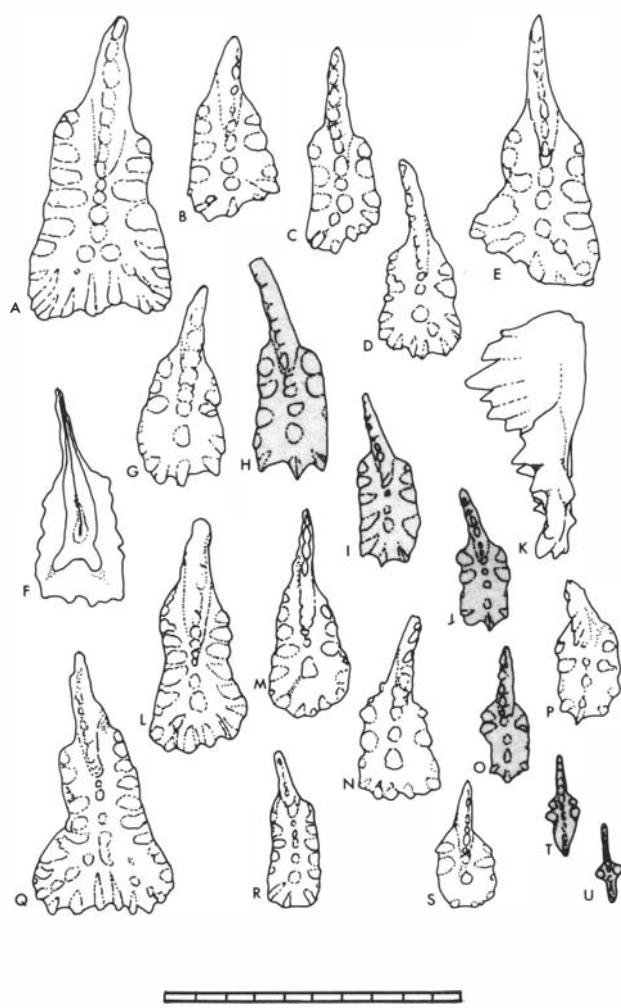


Fig. 6. Central morphotype growth series (shaded specimens) and morphological variation in *Epigondolella abneptis* subsp. B populations. The scale bar is 1 mm long.

elongate morphotypes, and including elements with virtually equidimensional platforms. Most are subquadrate apart from the early growth stages, which are narrow and pointed. Irregular outlines are produced by strong marginal ornament. Elements with round posterior margins, present throughout the Lower Norian, become progressively more expanded laterally producing flask-shaped outlines (Fig. 7 L–P). This trend appears to have stratigraphic utility, as does a further trend toward increasing asymmetry of the posterior platform whereby one postero-lateral lobe is developed more strongly posteriorward (Fig. 6 B, D, E). In the upper *J. magnus* Zone, rare elongate elements with one posterior lobe suppressed (Fig. 6 C) appear; these are similar to some Middle Norian epigondolellids.

Platform ornament. – All but the smallest growth stages bear strong marginal nodes around their entire perimeter. At first, the anterior denticles are stronger but subsequent growth introduces and enlarges the posterior nodes until they too are very prominent. As observed by Mosher (1973:159), these tend to radiate from the terminal node of the carina, a feature exaggerated by additional nodes introduced as secondary carinae.

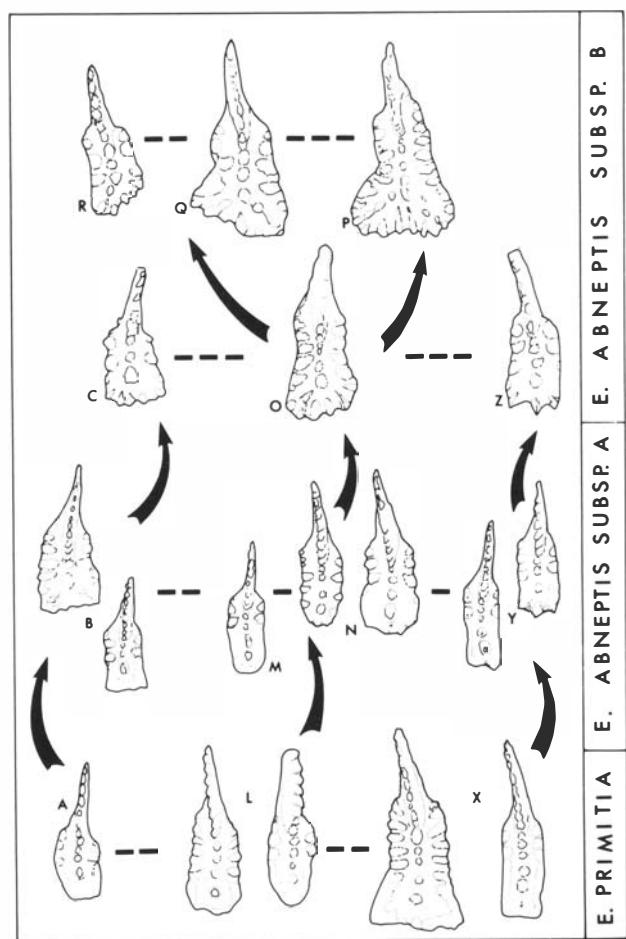


Fig. 7. Some intraspecific morphological variability (horizontal links) and phylogenetic trends (vertical arrows) in some Lower Norian epigondolellids. □A, B, C. Relatively squat morphotypes. □L, M, N. Morphotypes with rounded posterior platforms. □O, P. Morphotypes with increasing latero-posterior growth. □Q, R. Morphotypes with asymmetric posterior growth. □X, Y, Z. Relatively elongate morphotypes.

Carina. – In small specimens, the carina persists to the posterior tip (Fig. 6 T, U) but with continued growth the terminal platform node and the carina become separated (Fig. 6 O) although rare specimens retain the continuity into later growth stages (Fig. 6 P). Secondary carinae are common and in the stratigraphically youngest representatives of the group (see above) the central (terminal) node of the primary carina may be connected to the tip of the enlarged posterior lobe (Fig. 6 C).

Free blade. – Between one-quarter and one-third unit length, with a strongly convex profile.

Lower-surface morphology. – A pit with a strong lip is situated at or slightly anterior of platform midlength. Bifurcate keels are common.

Microreticulae. – Less common on the strongly ornate specimens. When present they are marginally developed and generally restricted to the posterior platform. For the most part they are of the open, irregular type (see *E. multidentata*), but the compact style is often preserved on denticle ridges and platform edges (Fig. 3 C, H, I, J, K, L).

Central morphotype growth series. – The smallest elements are bidentate (Fig. 6 U). Initially, nodes are added anteriorly with only a minor increase in posterior platform width (Fig. 6 T). Subsequently, nodes are added in postero-lateral positions giving the elements their characteristic subquadrate outline, and thereafter marginally as the elements grow more uniformly (Fig. 6 O, J, I, H).

Comparisons. – Their strongly ornate character separates *E. abneptis* subsp. B from other Lower Norian conodonts. Similar elements occur in the Middle Norian but they are characterized by one or more of the following features: a continuous carina, a more elongate form, more asymmetrically disposed nodes, a longer free blade, a more anteriorly situated slit-like pit without a distinct lip and/or a style of microreticulae that does not include the close-packed form.

Age. – *E. abneptis* subsp. B ranges from within the *M. dawsoni* Zone through the *J. magnus* Zone, up to the Lower/Middle Norian boundary.

The *Epigondolella multidentata* population

Figs. 8, 9 E, H, 12 A, B, L, X, Y, 15 J, K, L

The type of *E. multidentata* Mosher 1970 was recovered from the *D. rutherfordi* Zone at the Crying Girl locality of the Pardonet Formation. Rich collections from that zone at the type locality and along the Peace River demonstrate a range of variation illustrated in Fig. 8.

Platform shapes. – Six, partly intergradational morphological categories are recognized. The central morphotype (e.g. Fig. 8 I) is the most common and compares closely to the holotype. It is characteristically elongate having a length to breadth ratio of about 3:1. The platform generally has subparallel anterior margins and thereafter tapers, often sinuously (the linguiform condition), to a posterior point, although there is frequently a node adjacent to the posterior tip, which produces a narrow, squared-off termination: this is the case in the holotype. An extension of the latter trend produces specimens that bear relatively broad posterior outlines (Fig. 8 D). A further, less common morphotype is relatively short, and is characterized by rounded posterior platform margin (Fig. 8 M to O). A rare morphotype is plano-convex in upper view (Fig. 8 C). Two additional morphotypes (Fig. 8 E, H) are distinguished on the basis of platform ornament but have platform proportions similar to the central morphotype.

Platform ornament. – The majority of specimens that occur in faunules in the lower half of the *D. rutherfordi* Zone are characterized by strong anterior denticles numbering between two and four. Rare morphotypes have only a single denticle on one margin (Fig. 8 H), a morphology that becomes very common in the upper Middle Norian. The posterior platform is typically smooth although one marginal node may occur, particularly on the posterior border. In the upper part of the *D. rutherfordi* Zone, specimens with strong marginal

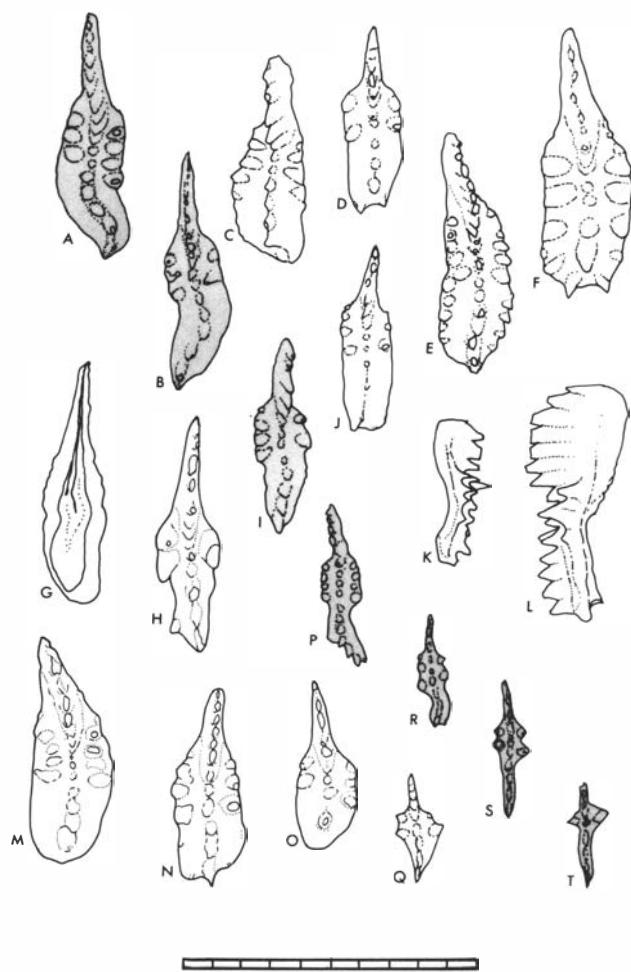
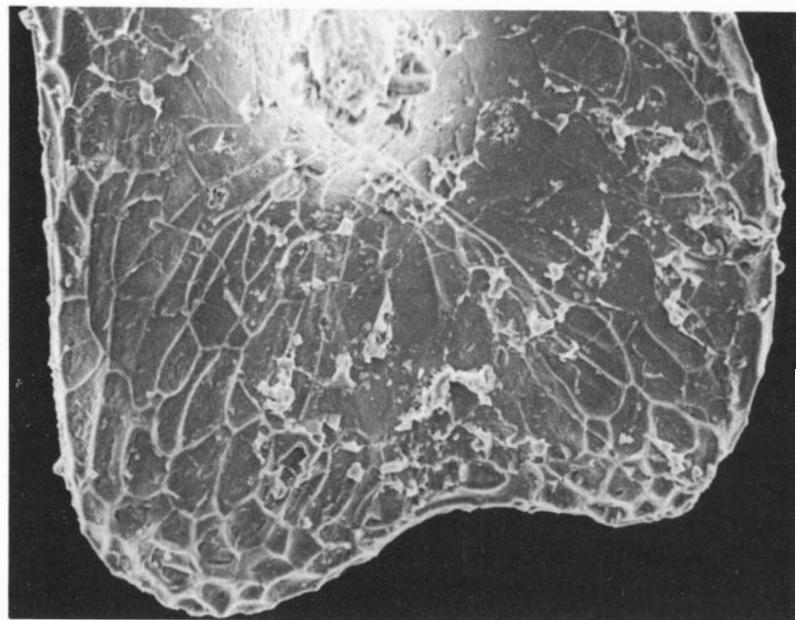


Fig. 8. Central morphotype growth series (shaded specimens) and morphological variation in *Epigondolella multidentata* populations. The scale bar is 1 mm long.

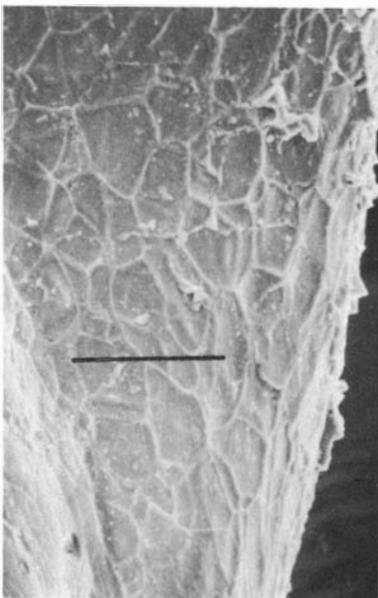
ornament throughout their length (Fig. 8 E), which are uncommon earlier, become dominant whilst the predominantly smooth morphotypes give way to forms with an increasing number of marginal nodes, usually on one side. This imparts a strong asymmetry to the elements, and represents a trend that culminates in *Epigondolella* n. sp. C (Fig. 12 A to C).

Carina. – From the beginning of Middle Norian time, epigondolellids are characterized by a prominent carina that extends, and generally rises, to the posterior tip of the elements (Fig. 8 L). In a few elements the continuity is not complete (Fig. 8 D, F) but the carina is nevertheless prominent. This morphology appears suddenly and is most evident in the early *D. rutherfordi* Zone. Subsequently, the carina becomes less prominent in *E. n. sp. C* but most other Middle and Upper Norian epigondolellids are characterized by a posteriorly extended carina, and thus differ from most of those in the Lower Norian.

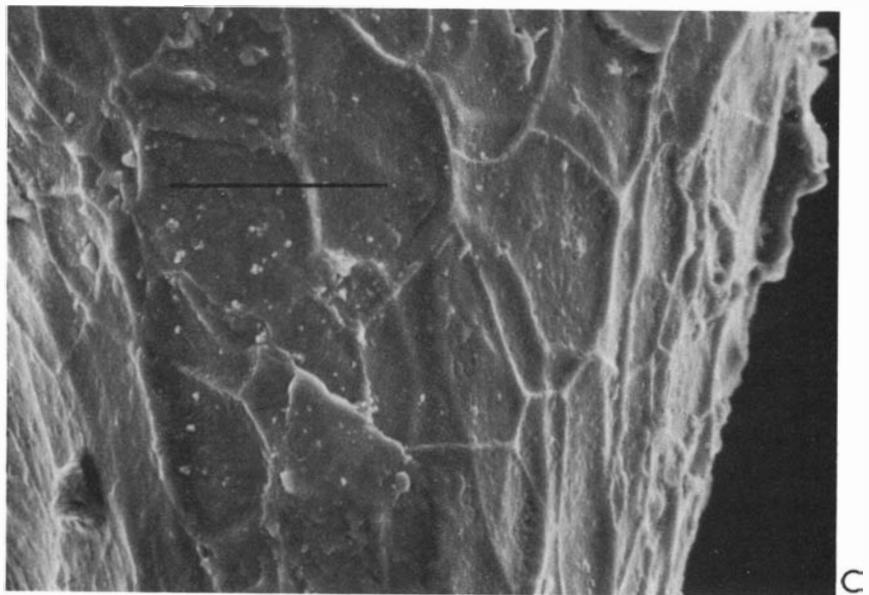
Free blade. – This is between one-quarter and one-third unit length and has an arcuate profile. Some younger representatives develop a shorter blade than is typical of the central morphotype.



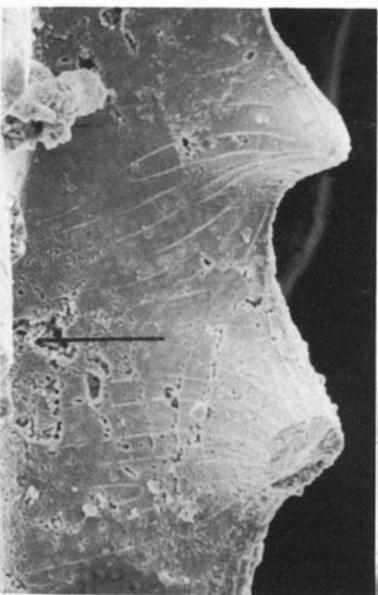
A



B



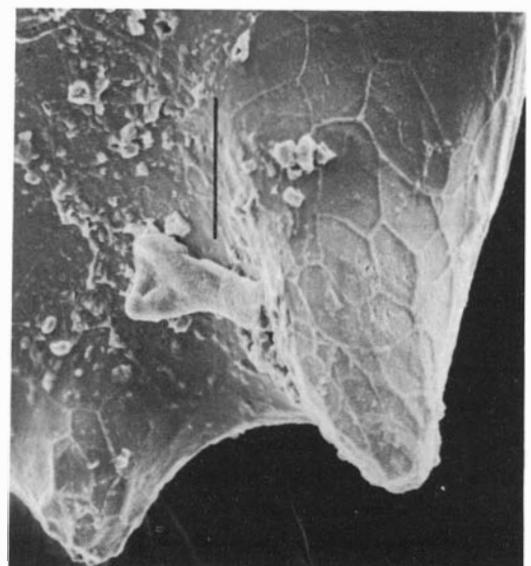
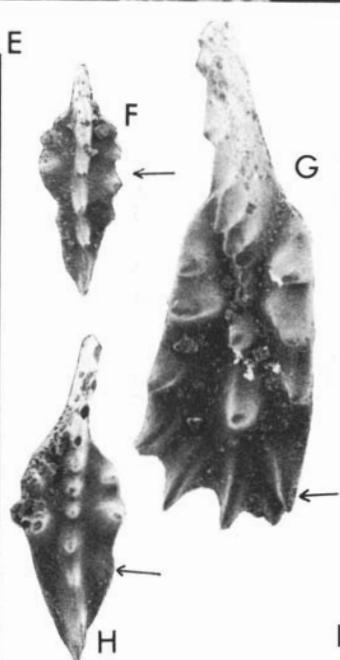
C



D



E



I

Lower-side morphology. – The pit is slit-like and is not surrounded by a prominent lip. The basal attachment scar is elongate and extends far posterior of the pit, which is situated anterior of the platform midlength.

Microreticulae. – The development of micro-ornament in post-Lower Norian epigondolellids continues the trend that began with the development of *E. abneptis*. *E. multidentata* is characterized by a total absence of compact reticulae. Instead, platform margins may be covered (they are not always present) by a relatively faint, very irregular anastomosing network in which subdued ridges are commonly up to 20 µm apart (Fig. 9 E, H). This style of reticulae has completely replaced the compact form.

Central morphotype growth series. – As exemplified in Fig. 8 T, S, R, P, I, B, A, growth begins with a very elongate form. Anterior nodes are added prior to the enlargement of the posterior platform.

Comparisons. – The prominent carina and elongate form separates these specimens from all others. Rare squat forms with rounded margins (Fig. 8 O) resemble elements of *E. postera* but the anterior denticles are more numerous and the whole element is more robust. See also *E. n. sp. D*.

Age. – *E. multidentata* ranges through the *D. rutherfordi* Zone, but the ornate morphotypes replace the central morphotype in the upper part of that zone (and allow subdivision of it), and typical specimens are not found later. Elements resembling early growth stages of the central morphotype do occur in late Middle Norian faunas but they are referred to *E. n. sp. D*.

The *Epigondolella* n. sp. C population

Figs. 9 B, C, G, 10, 12 C, D, Z, 15 M, N, O

At the beginning of *M. columbianus* Zone time, conodont faunas become dominated by *Epigondolella* n. sp. C, a homeomorph of *E. abneptis* subsp. B. At the moment, there is uncertainty as to which species should bear the name *E. abneptis*, but they are clearly different and I do not regard the younger as having developed directly from the older. Rather, *E. n. sp. C* developed from the central morphotype of *E. multidentata* by way of a general reduction in length and in posterior carina prominence and an increase in posterior ornamentation

Fig. 9. Microreticulation of some Lower and Middle Norian epigondolellids. Arrows indicate positions of illustrated detail. Bar = 20 µm, except C = 10 µm. □A. *E. abneptis* subsp. A. GSC 68871 (= Fig. 3 D) from McLay Spur, GSC Loc. No. O-98538. ×910. Note marginal compact reticulae passing into subdued irregular reticulae toward carinae. □B, C, G. *E. n. sp. C*. GSC 68876 from Crying Girl, GSC Loc. No. O-83835. ×1000, ×2700, ×80. Note superimposition of two generations of subdued, irregular reticulae. □D, F. *E. n. sp. D*. GSC 68875 from Black Bear Ridge, GSC Loc. No. O-98548. ×800, ×80. Note irregular, discontinuous striae replacing reticulae. □E, H. *E. multidentata*. GSC 68877 from Brown Hill, GSC Loc. No. C-87921. ×810, ×80. Note subdued, irregular reticulae covering platform margin. □I. *E. abneptis* subsp. B. GSC 68870 (= Fig. 3 C) from McLay Spur, GSC Loc. No. O-98537. ×900.

coupled with an asymmetric development of the postero-lateral margins. Fig. 10 illustrates morphological variation within the population.

Platform shapes. – Compared with the platform element of *E. multidentata*, that of *E. n. sp. C* is relatively squat and some elements have rectangular platforms (Fig. 10 S, T). A more common shape is distinctly asymmetric with one margin laterally expanded at midlength and then incurved to meet the posteriormost point of the element on the opposite margin (Fig. 10 J). Many of the elements have very irregular outlines due to the outgrowth of strong marginal nodes. Some specimens have symmetrical, subparallel or weakly convex margins and squared-off posterior borders (Fig. 10 F, G, M), others have rounded posterior outlines (Fig. 10 N, R).

Platform ornament. – As in all Middle Norian epigondolellids, anterior denticles are strongly developed. These number between one and three, relatively fewer on average than in *E. multidentata*; two nodes on one side and one on the other, a condition seen only rarely in populations of the latter, is more common. Posteriorly, early growth stages and rare large specimens are smooth (Fig. 10 N, R) whereas other sub-symmetrical elements have either completely nodose posterior margins (Fig. 10 F), or one lateral margin that is ornate (Fig. 10 G), or bears nodes only on the posterior border (Fig. 10 M). To an extent, all of these specimens intergrade with the central morphotype in which nodes are developed initially, and thereafter more strongly, on one postero-lateral margin, whereas the opposite, less expanded, margin carries fewer or sometimes no nodes. The postero-lateral corner of the expanded margin bears the strongest node, which is ultimately responsible for the subquadrate outline of some platforms (e.g. Fig. 10 O). In such specimens it is common for the anteriormost platform nodes to be unpaired.

Carina. – Carina development is variable in this group of conodonts. In many elements it extends to the posterior end, but it is not especially prominent. In the central morphotype, the carina tends to become progressively retarded through growth in conjunction with the increased development of one postero-lateral corner. Ultimately, the terminal node of the carina becomes indistinguishable from adjacent marginal nodes, while anteriorly the carina is represented by discrete, often large nodes occupying a central position on the platform (Fig. 10 S, T).

Free blade. – Rather variable. In some specimens relatively long, like that of *E. multidentata*, in others shorter, like that of *E. postera* (see below).

Lower-surface morphology. – A slit-like pit is situated anterior, sometimes far anterior of platform midlength. There is no distinct protuberance surrounding it. The basal scar may be bifurcate but secondary branches are developed laterally from the principal scar rather than arising from its division, as may be envisaged in *E. abneptis*.

Microreticulae. – Often difficult to detect on the strongly ornate elements but present marginally and on the sides of platform

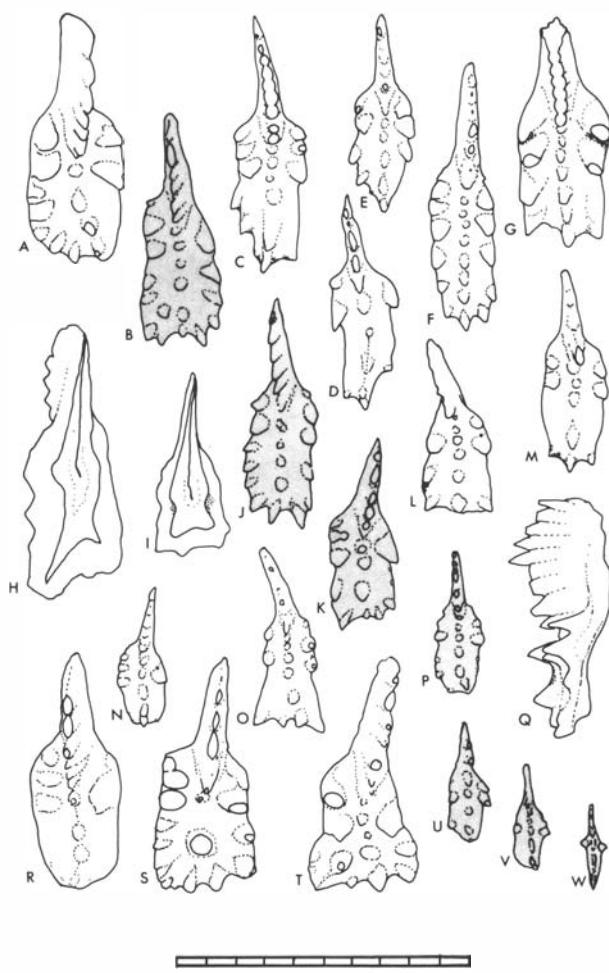


Fig. 10. Central morphotype growth series (shaded specimens) and morphological variation in *Epigondolella* n. sp. C populations. The scale bar is 1 mm long.

denticles. It is of the subdued, irregular-network type, like that of all post-Lower Norian epigondolellids. The phenomenon of superimposed reticulae was first observed in a specimen of *E. n. sp. C*, although I have subsequently recognized it in other species that bear the irregular style of reticulae. In these specimens, the latest reticulae development appears to be superimposed completely randomly over an earlier set that, although faint, can still be seen at high magnification. It is possible that the greater relief of the early Norian compact reticulae arises from the superimposition of later sets exactly over earlier ones, whereas the pattern that characterized younger species remains subdued because it is never duplicated.

Central morphotype growth series. — Asymmetry of the posterior platform arises at an early stage in the growth of *E. n. sp. C* (Fig. 10 V). This morphology is essentially that retained by the next younger species *E. postera*. Growth proceeds with the addition of postero-lateral nodes on the expanded margin as well as generally even growth elsewhere (Fig. 10 U, P). Later growth tends to emphasize the earlier asymmetry as one postero-lateral margin expands to rival the posterior carina in position and development (Fig. 10 K, J, B). This is often accompanied by a posterior shifting of the anterior denticles on the expanded side producing anterior asymmetry as posterior symmetry increases (Fig. 10 S, T).

Comparisons. — Specimens of *E. n. sp. C* that develop posterior symmetry strongly resemble *E. abneptis* subsp. B but specimens of the latter are generally more symmetrically developed anteriorly. In young *E. abneptis* subsp. B populations, in which posterior asymmetry develops, one postero-lateral lobe is developed in a relatively medial position. In general, *E. abneptis* bears nodes that have a stronger vertical component of growth than *E. n. sp. C*. Hence, in upper view, elements of *E. abneptis* subsp. B are not as marginally serrate. Other criteria that may be used in distinguishing the two species are the relative blade lengths (compare Figs. 6 K, 10 Q), the frequent suggestion of posterior carina continuity in *E. n. sp. C*, the position and shape of the pit and its surrounding area, and the presence of 'residual' compact reticulae in *E. abneptis* subsp. B. Morphological variability within populations of the two species are quite different too.

Age. — *E. n. sp. C* characterizes the lowermost division of the *M. columbianus* Zone of the Middle Norian. It is replaced toward the top of that interval (*M. columbianus* 1) and especially in the zone of *M. columbianus* 2, by *E. postera*.

The *Epigondolella postera* population

Figs. 11, 12 M, N, O, P, Q, R, S, T, 15 P, Q, R

The type of *E. postera* (Kozur & Mostler 1971) came from the Middle Norian of Sommersaukogel, Austria. Available illustrations of this specimen correspond closely to elements that dominate collections from the *M. columbianus* 2 Zone in NE British Columbia. Fig. 11 illustrates representative morphologies of the *E. postera* population.

Platform shapes. — The platform elements of *E. postera* are smaller than those of older species of *Epigondolella* and mark the beginning of a general diminution in size of the genus that continued until its extinction. This trend is evident even within the range of *E. postera* and provides the means to subdivide the interval. The oldest faunules are characterized by relatively elongate specimens (Fig. 11 D, I, cf. Fig. 10 C, D) that often gradually taper to a point, although the margins may be very irregular due to node development. Rather squat elements, often with lobate outlines like the holotype, characterize the younger faunules. They may taper to a point (Fig. 11 U) but are frequently posteriorly rounded (Fig. 11 V) or, with node development, squared-off. The abruptly terminated morphotypes (Fig. 11 G, M) in association with bidentate elements (see below) characterize the youngest faunules.

Platform ornament. — The common anterior morphology of *E. postera* comprises three prominent denticles: two on one platform margin and one on the other. Less commonly, there are as many as three on one margin, but unequal development of the two margins is normal. In the upper part of the range, bidentate morphotypes appear (Fig. 11 P, T, Y, Z, AA). The posterior platform is commonly unornamented but single nodes may be developed on one lateral margin (Fig. 11 D, F, Y), on one postero-lateral margin (Fig. 11 K, L, M, T), or on both sides of the posterior carina (Fig. 11 H, G). Less common

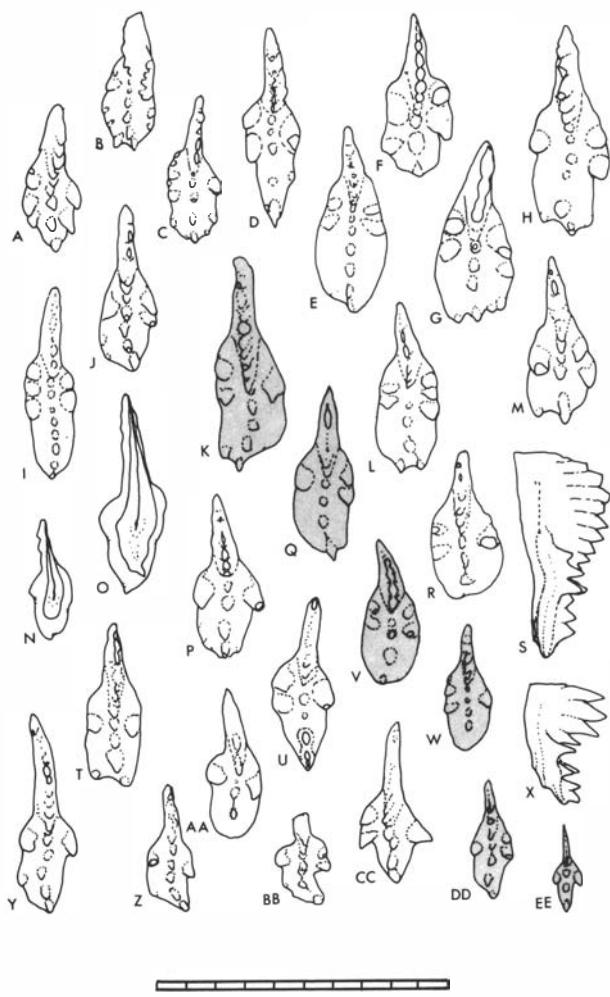


Fig. 11. Central morphotype growth series (shaded specimens) and morphological variation in *Epigondolella postera* populations. The scale bar is 1 mm long.

specimens bear multiple nodes on one (Fig. 11J) or both (Fig. 11A, B, C) margins.

Carina. — Generally continuous to the posterior tip but sometimes terminating in front of this point (Fig. 11R, W, AA). It is often prominent posteriorly (Fig. 11X), especially in small specimens, but with platform growth it may become relatively submerged (Fig. 11S).

Free blade. — Many specimens of *E. postera* have a short high blade with relatively few stout denticles (Fig. 11X). This type of blade is characteristic of this and all younger representatives of the genus whereas a longer blade is more common in *D. rutherfordi* and basal *M. columbianus* Zone faunas. Some specimens (Fig. 11S, Y) still retain a long blade, but they are rare.

Lower-side morphology. — A slit-like pit without a lip is situated anterior of platform midlength.

Micoreticulae. — Not frequently observed but when present are marginal, subdued and irregular.

Central morphotype growth series. — As with most if not all epigondolellids, small specimens of *E. postera* are bidentate. General enlargement of the platform is accompanied by the

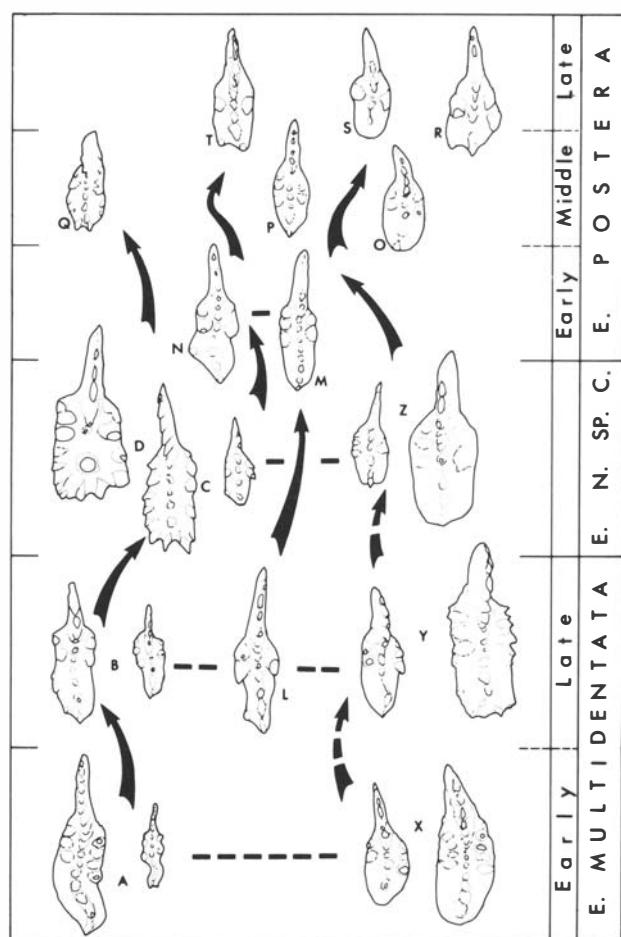


Fig. 12. Some intraspecific morphological variability (horizontal links) and phylogenetic trends (vertical arrows) in some Middle Norian epigondolellids. □A, B, C. Development of *E. n. sp. C* from *E. multidentata* via an intermediate morphology. □X, Y, Z. Uncommon morphotypes in successive faunules characterized by an *E. postera*-like morphology. □L. Elongate, 'tridentate' element with *E. postera*-like morphology. □M, N, O, P, Q. *E. postera* morphotypes showing possible derivation by retention of 'juvenile' characteristics (N) of *E. n. sp. C*, and/or development from *E. postera*-like variants L, X, Y, Z. Specimen Q shows a 'dwarfed' development of 'mature' *E. n. sp. C* morphology. □R, S, T. Late stage *E. postera* morphotypes with abruptly terminated posterior platforms, and development of 'bidentate' morphology.

formation of an additional node on one anterior margin. This general morphology is retained thereafter as the specimen simply enlarges in size, commonly developing one postero-lateral margin more strongly than the other.

Comparisons. — Small specimens of other species may resemble *E. postera* but the rather lobate posterior outline is distinctive. Such an outline characterizes early growth stages of *E. n. sp. C* but that species quickly developed postero-lateral nodes and attained a larger size. Rare specimens in older Middle Norian faunules mimic *E. postera* in possessing smooth, rounded posterior platforms but their anterior nodes are characteristically more numerous and they do not exhibit the same lobate outline (Fig. 12 X, Y, Z): isolated specimens may be difficult to determine, however. Large bidentate specimens (Fig. 11 P, T, Y, Z, AA) retain the anterior morphology developed at an early growth stage (Fig. 11 EE) but have broad platforms that are identical to that of the central morphotype of *E. postera*, and

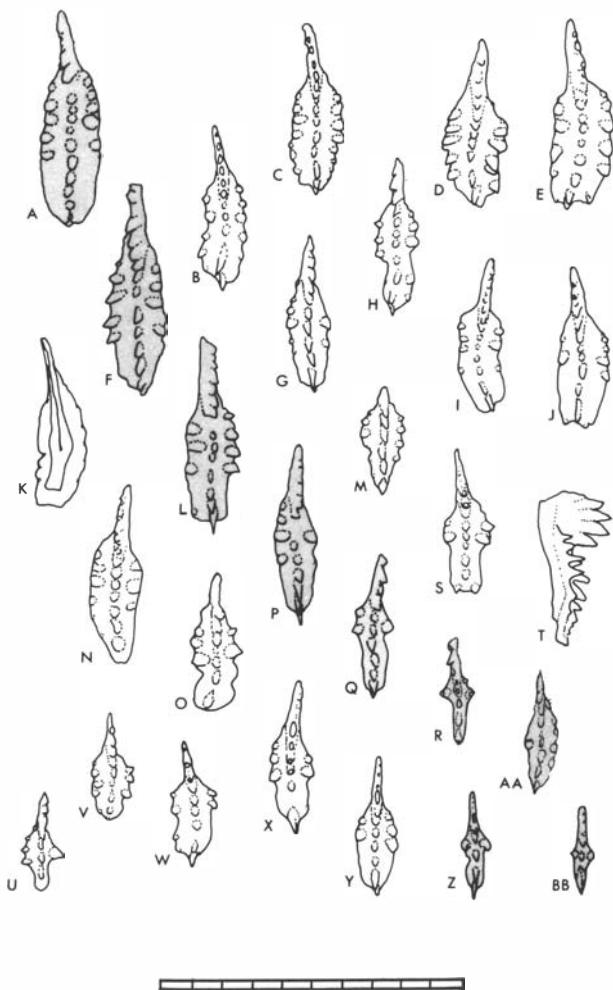


Fig. 13. Central morphotype growth series (shaded specimens) and morphological variation in *Epigondolella* n. sp. D populations. The scale bar is 1 mm long.

thus differ from *E. bidentata*, which is a narrow, relatively elongate species.

Age. – The central morphotype of *E. postera* is characteristic of the *M. columbianus* 2 Zone. Rare morphotypes (e.g. Fig. 12 L) that appear within the *D. rutherfordi* Zone and continue into the *M. columbianus* Zone have much in common with *E. postera* but are for the present regarded as extremes within the *E. multidentata* and *E. n. sp. C* populations. Elongate morphotypes dominate faunules in the upper *M. columbianus* 1 Zone, whereas bidentate and abruptly terminated specimens characterize the upper part of the *M. columbianus* 2 Zone.

The *Epigondolella* n. sp. D population

Figs. 9 D, F, 13, 15 S, T, U

Epigondolellids from *M. columbianus* 3 Zone are markedly different from the preceding *E. postera* populations. They resemble those of *E. multidentata* but are noticeably smaller and more delicate. Fig. 13 illustrates the variety of form.

Platform shapes. – Generally elongate, average length to breadth ratio of 5: 2. Margins are often subparallel for much of

their length, although some specimens have a medial constriction (Fig. 13 H, O), and others taper markedly in their posterior half (Fig. 13 M, N). Anterior platform terminations are often less abrupt than in older species, the margins meeting the blade in an even curve (Fig. 13 F). Posterior terminations are pointed to narrowly square depending on posteriormost ornamentation; a few specimens have round, lobate posteriors (Fig. 13 O, U, V).

Platform ornament. – Rather variable but commonly smooth posteriorly. Anterior nodes are relatively numerous, small and spike-like. They increase to a maximum of five in the largest specimens available, although the development may be noticeably unequal on the two margins (Fig. 13 P, AA). As in other Middle Norian species, posterior ornament may be present on one margin (Fig. 13 H), both margins (Fig. 13 C, E) or only terminally (Fig. 13 J, S).

Carina. – Usually continuous to the posterior tip of the elements and often projecting beyond it as strong spike-like extension (Fig. 13 L, P). Less commonly terminating short, as is the case in posteriorly lobate specimens (Fig. 13 O, U, V).

Free blade. – Distinctive cockscomb-like, much shorter than lower Middle Norian epigondolellids. Commonly one-quarter or one-fifth unit length.

Lower-side morphology. – Slit-like pit on featureless attachment scar is medial or anterior of the medial point.

Microreticulae. – When present, marginal, subdued and irregular, sometimes extending onto denticles as striations.

Central morphotype growth series. – Initially bidentate, becoming tridentate and enlarging platform progressively in all directions, particularly antero-posteriorly, with the irregular introduction of additional nodes.

Comparisons. – The small size yet highly ornate character of *E. n. sp. D* populations is distinctive. The short blade and the spike-like nature of the ornament differ from that in *E. multidentata*. The posteriorly lobate forms and those with medial constrictions are unknown in older Middle Norian faunules but bear some resemblance to *E. primitia* which generally has relatively subdued nodes, a short carina, longer blade and totally different microreticulae.

Age. – Restricted to the *M. columbianus* 3 Zone. Only sparse conodont faunules have been recovered from the *M. columbianus* 4 Zone, so it is uncertain whether *E. n. sp. D* extends nearer to the top of the Middle Norian.

The *Epigondolella bidentata* population

Figs. 14, 15 V, W, X

E. bidentata Mosher 1968 is based on Upper Norian material from the Hallstatt Limestone at Steinbergkogel by Hallstatt Salzberg, Austria. It is recognized that all platform elements of

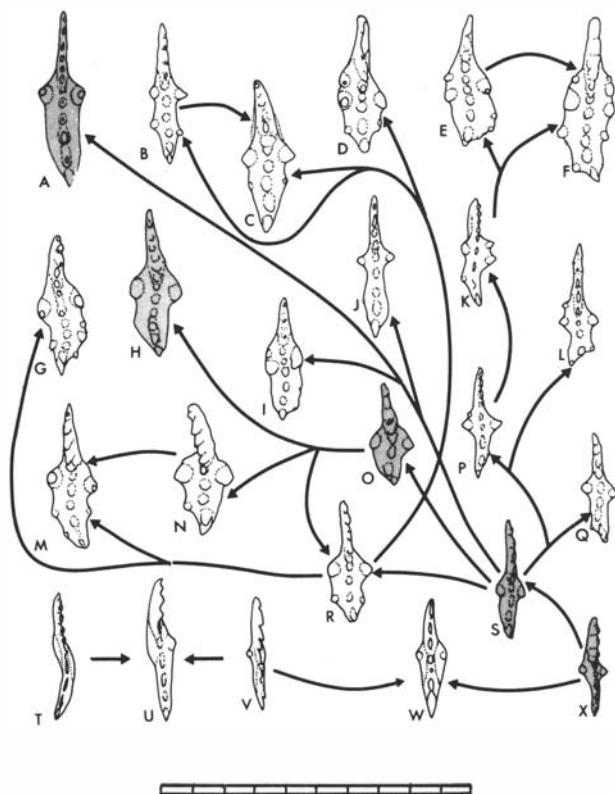


Fig. 14. Central morphotype growth series (shaded specimens) and morphological variation in *Epigondolella bidentata* populations. The arrowed lines link morphotypes that could be theoretically derived through growth. This illustrates the complex relationships typical of an *Epigondolella* population. The scale bar is 1 mm long.

Epigondolella pass through a 'bidentate' morphology early in their growth but most do not retain it. Large bidentate specimens are known, however, within the Lower and Middle Norian too, so it is important to examine bidentate forms closely. Small isolated growth stages may be difficult to determine. Fig. 14 illustrates the variety of platform elements within the Lower Upper Norian *E. bidentata* faunules.

Platform shapes. — Always small, generally slender, occasionally almost totally reduced to a blade-like condition (Fig. 14 T, U, V). Platforms may be subparallel, biconvex, plano-convex, sagittate or spindle-shaped in outline. Posterior terminations generally pointed, occasionally squared-off by node development.

Platform ornament. — A single strong node on either side of the anterior platform is typical, but these may be supplemented by an additional, generally smaller denticle anterior of one of these (Fig. 14 D, E, I, K, L, P); specimens with additional anterior nodes (Fig. 14 F) are rare. The posterior platform is smooth in the holotype, but incipient nodes (as occur in the type of *E. mosheri* Kozur & Mostler 1971) or distinct nodes may be developed symmetrically (Fig. 14 B, C, D, R) or asymmetrically (Fig. 14 E, F, G, K, L, M, N). In the younger *E. bidentata* populations, specimens with one or no platform denticles occur (Fig. 14 T, U, V), and their size demonstrates that they are not simply early growth stages of the bidentate forms.

Carina. — Extends to posterior tip of elements and is often very prominent at the posterior end (Fig. 14 W).

Free blade. — Identical to that of *E. n. sp. D.*

Lower-surface morphology. — Slit-like pit situated within narrow attachment area beneath or slightly posterior of principal anterior nodes, that is anterior of platform midlength.

Microreticulae. — Often absent.

Central morphotype growth series. — The bidentate condition is introduced at an early stage and persists with uniform or slightly asymmetrical platform enlargement.

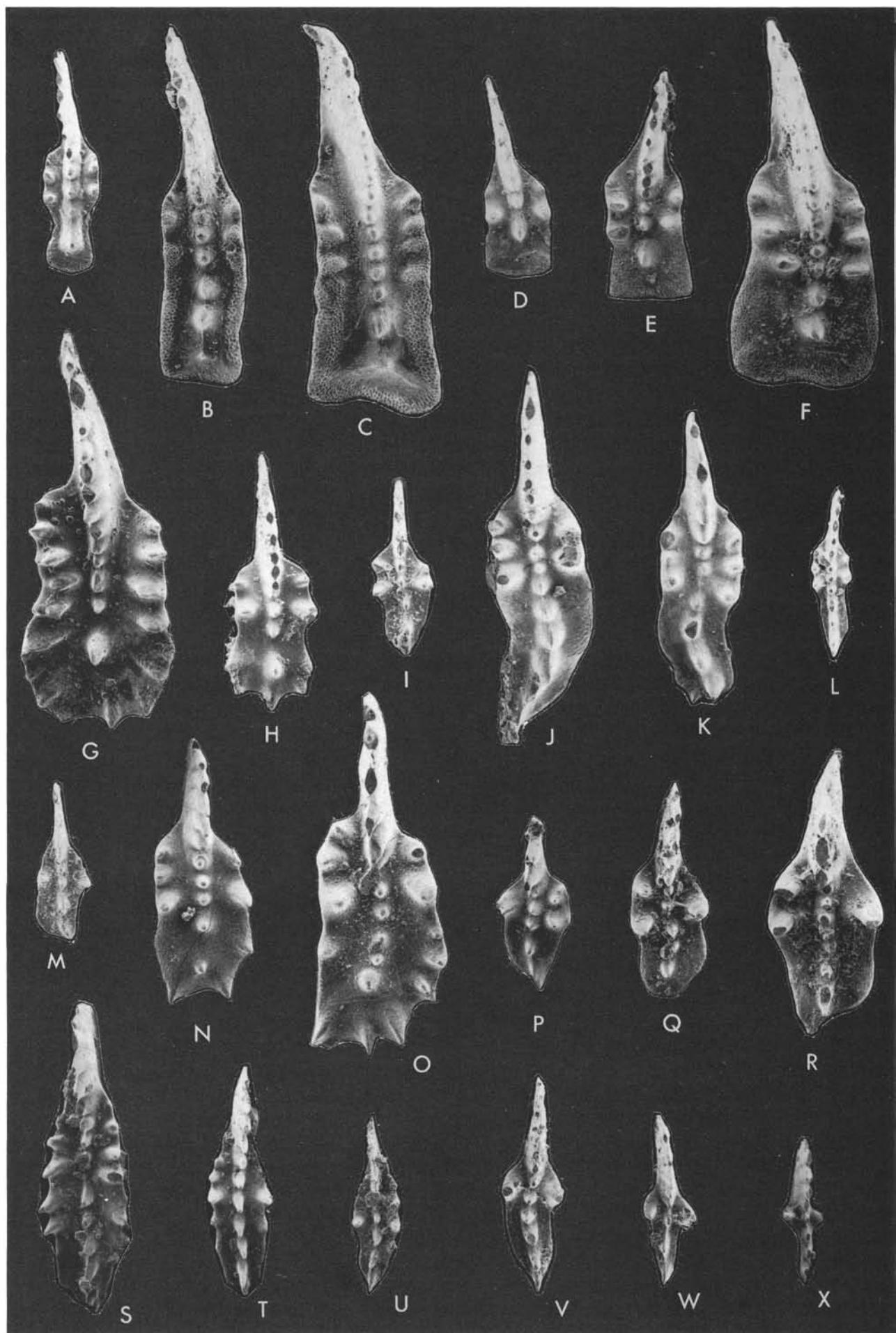
Comparisons. — The holotype of *E. bidentata* is about 570 µm in length, which is about the size of the largest specimen in my collection (Fig. 14 A). Comparable morphology is known up to about 250 µm in *E. abneptis* subsp. B, up to about 300 µm in *E. n. sp. C*, and up to about 350 µm in *E. n. sp. D*. This suggests a progressively longer retention of the bidentate condition through time. On the other hand, bidentate morphotypes in both the *E. primitia* (Fig. 2 Q) and *E. postera* (Fig. 11 Y) populations attain a size greater than found in *E. bidentata*. The Lower Norian specimens can be readily distinguished on the basis of microreticulation, whilst *E. postera* is generally broader. Other isolated post-Lower Norian specimens should be regarded as specifically indeterminate unless they attain a length of greater than 350 µm. Alternatively, '*E. bidentata*' would have to be regarded as ranging through much of the Middle and Upper Norian.

Age. — The *E. bidentata* population characterizes the *G. cordilleranus* Zone and at least part of the *C. amoenum* Zone. It is possible that the species appears first in the zone of *M. columbianus* 4. Higher *G. cordilleranus* Zone and younger collections may be characterized by a greater number of morphotypes with strongly reduced platforms.

A summary of *Epigondolella* phylogeny

Eight *Epigondolella* populations are recognized in the Norian. They follow one upon the other with only one sparsely productive interval of uncertain content, that is the uppermost Middle Norian (*M. columbianus* 4). Each of the species complexes is bounded by a faunal break of varying abruptness. The most profound of these occurs at the Lower-Middle Norian boundary between the *J. magnus* and *D. rutherfordi* Zones, and within the late Middle Norian between the Zones of *M. columbianus* 2 and 3. The change that occurs near the top of the Lower Norian *S. kerri* Zone is also abrupt, but the derivation of *E. abneptis* subsp. A from *E. primitia* appears straightforward. The evolutionary event is more significant, however, because the microreticulation of the platform began to change at that point. This criterion may be useful in separating the two species at the generic level since '*E. primitia*' is characterized by what might be regarded as a *Metapolygnathus* microreticulation (Orchard, in preparation).

Morphological changes between the *E. abneptis* subspp. populations, between the *E. multidentata*, *E. n. sp. C* and *E. postera* faunas, and between those characterized by *E. n. sp. D* and *E. bidentata* are also marked, but rare morphotypes within



the ancestor populations predict the changes that find common expression in the descendant faunas. In the case of both *E. postera* and *E. bidentata*, the central morphotypes show a retention of 'juvenile' characteristics (neoteny).

Upper Lower Norian faunules of *E. abneptis* subsp. B include strongly asymmetric elements that become less squat and more elongate as one postero-lateral lobe (and secondary carina) is extended and the other is suppressed. This development is the continuation of a trend that begins with the bifurcation of the basal attachment scar in some large early Norian epigondolellids. The morphological change at the Lower-Middle Norian boundary appears to have consisted of a shift of emphasis from dual lobe development to posterior carina growth. Hence the derivation of the uni-lobed, strongly carinate *E. multidentata* from the bi-lobed, weakly carinate *E. abneptis*. The functional advantages of postero-lateral enlargement were presumably great, however, because *E. n. sp. C* evolved by a secondary outgrowth of one platform margin (Fig. 12A, B, C). This development of homeomorphic characteristics in the mid Middle Norian was superseded by a general diminution both in overall size and in the degree of platform development, particularly of the anterior denticles. *E. postera* thus became posteriorly attenuated and anteriorly bidentate (one denticle on each side of the carina) prior to disappearing in the upper Middle Norian (Fig. 12R, S, T). The appearance of *E. n. sp. D* marked a second major shift, this time away from broad platforms and a few large denticles to relatively elongate elements with more numerous but more delicate denticles. The general diminution continued into the Upper Norian as *E. bidentata* emerged as the last remnant of platform conodont development.

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Fig. 15. Norian epigondolellids, exemplified by representative growth stages of the central morphotype. All figures $\times 80$. □A, B, G. *E. primitia*. Respectively, GSC 68845, 68846, 68847 from Pardonet Hill, GSC Loc. No. O-98514. □D, E, F. *E. abneptis* subsp. A. Respectively, GSC 68848 from Brown Hill, GSC Loc. No. C-87909, GSC 68849 and 68850 from Pardonet Hill, GSC Loc. No. O-98509. □G, H, I. *E. abneptis* subsp. B. Respectively, GSC 68851 from McLay Spur, GSC Loc. No. O-98538, GSC 68852 and 68853 from Brown Hill, GSC Loc. No. C-87915. □J, K, L. *E. multidentata*. Respectively, GSC 68854, 68855, 68856 all from Brown Hill, GSC Loc. Nos. C-87921, O-97538, O-97533. □M, N, O. *E. n. sp. C*. Respectively, GSC 68857 from Crying Girl, GSC Loc. No. O-83835, GSC 68858 and 68859 from McLay Spur, GSC Loc. No. O-98878. □P, Q, R. *E. postera*. Respectively, GSC 68860 from McLay Spur, GSC Loc. No. O-98541, GSC 68861 and GSC 68862 from Black Bear Ridge, GSC Loc. Nos. O-98552 and O-98549. □S, T, U. *E. n. sp. D*. Respectively, GSC 68863, 68864, 68865 from Black Bear Ridge, GSC Loc. No. O-98548. □V, W, X. *E. bidentata*. Respectively, GSC 68866, 68867, 68868 from Ne-Parle-Pas Rapids, GSC Loc. No. O-98504.

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Appendix

The following GSC Locality Numbers refer to conodont collections from the Pardonet Formation (P.F.). All lie within the Halfway River Map Area (Sheet 94 B, 1: 250,000 National Topographic Series), British Columbia. Numbers prefixed by O- are from beds containing ammonoid faunas.

Brown Hill

53°06'05"N, 122°53'00"W.

- C-87908 6 m above exposed base of P.F. Bracketed by *S. kerri* Zone ammonoids.
 C-87909 8 m above base P.F. *S. kerri* Zone ammonoids 2 m below, *M. dawsoni* Zone ammonoids 2.5 m above.
 C-87912 19 m above base P.F. Bracketed by *M. dawsoni* Zone ammonoids.
 C-87913 22 m above base P.F. Bracketed by *M. dawsoni* Zone ammonoids.
 C-87915 24 m above base P.F. Bracketed by *M. dawsoni* Zone ammonoids.
 O-97538 33.0 m above base of P.F. Occurring with *D. rutherfordi* Zone ammonoids.
 C-87921 34.5 m above base P.F. Bracketed by *D. rutherfordi* Zone ammonoids.
 O-97533 38.5 m above base of P.F. Occurring with *D. rutherfordi* Zone ammonoids.

Black Bear Ridge

56°05'10"N, 123°02'25"W. This locality lies immediately to the east of Black Bear Ridge shown on topographic maps.

- O-98552 48.5 m below top of P.F. Occurring with *M. columbianus* 2 Zone ammonoids.
 O-98549 41 m below top of P.F. Occurring with *M. columbianus* 2 Zone ammonoids.
 O-98548 36.5 m below top of P.F. Occurring with *M. columbianus* 3 Zone ammonoids.

Crying Girl Prairie Creek

- 56°28'N, 122°54'W (White Creek; upper reaches of Graham River).
 O-83835 Occurring with *M. columbianus* 1 Zone ammonoids.

McLay Spur

56°06'16"N, 122°43'00"W (east of Childerhose Coulee).

- O-98538 About 18.5 m above base of P.F. Occurring with *M. dawsoni* Zone ammonoids.
- O-98537 About 48 m above base of P.F. Occurring with *J. magnus* Zone ammonoids.
- O-98878 About 54 m above base of P.F. Occurring with *M. columbianus* 1 Zone ammonoids.
- O-98541 About 58 m above base of P.F. Occurring with *M. columbianus* 2 Zone ammonoids.

Ne-Parle-Pas Rapids

56°00'53"N, 123°05'05"W (new exposure on south side of Williston Lake).

- O-98504 About 25 m below top of Monotis Beds. Occurring with *G. cordilleranus* Zone ammonoids.

Pardonet Hill

56°04'N, 123°02'W.

- O-98514 0.5 m above exposed base of P.F., within *Juvavites* Cove. Occurring with *S. kerri* Zone ammonoids.
- O-98509 About 30 m above exposed base of P.F. Occurring with belemnites and *S. kerri* Zone ammonoids.