Biogeography, evolutionary relationships, and biostratigraphic significance of Ordovician platform conodonts

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FOSSILS AND STRATA

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Fewer than 15 of the nearly 100 currently recognized Ordovician conodont genera have platform elements in the apparatus, but these are of special interest because they represent the oldest such types known and they include some types of platform developments not known in younger strata. Eight of these genera have their origin and main occurrence in the North Atlantic Province, three in the Midcontinent Province, and three are present in both provinces. The data at hand suggest that especially during Middle Ordovician time, some North Atlantic Province platform taxa invaded parts of the Midcontinent Province, but there is much less evidence of such migrations in the opposite direction. Five evolutionary lineages are recognized and discussed (those of Amorphognathus, Cahabagnathus nom. nov., Eoplacognathus, Icriodella, and Pygodus) and other genera (Complexodus, Nericodus, Polonodus, Prattognathus n. gen., Rhodesognathus, Sagittdontina, Scyphiodus, and Serratognathus) are dealt with in less detail. Species of Amorphognathus, Cahabagnathus, Eoplacognathus, and Pygodus are of major biostratigraphic significance but most other taxa are either too long-ranging or too restricted in their distribution to be useful biostratigraphically.

Two new generic designations (Cahabagnathus chayensis, C. earnesi, Pygodus anilis) are proposed. Conodonts, platform conodonts, biostratigraphy, biogeography, evolution, Ordovician.

A decade ago, at the 1971 Marburg Symposium on Conodont Taxonomy, I reviewed some new data bearing on the morphology and phylogenetic relationships of Middle and Upper Ordovician platform conodonts (Bergström 1971c). For various reasons, especially the need to get additional supportive materials, most of that information has remained unpublished, and on the basis of additional collections and other data now at hand, some of my 1971 interpretations have been modified. The purpose of the present study is to summarize data that bear on the biogeography, evolution, mutual relationships, and biostratigraphic significance of Ordovician platform conodonts. It may be particularly appropriate to attempt such a summary at this time because the recently published revised conodont volume of the Treatise on Invertebrate Paleontology (Clark et al. 1981) does not address most of the matters to be discussed below.

Different authors have given a somewhat different scope to the admittedly somewhat vague term ‘platform conodont’. ‘Platform’ was recently (Sweet 1981) defined as a ‘laterally produced shell-like structure flanking a process . . .’, and in the present contribution, I use the term ‘platform conodont’ in a rather broad sense for conodonts having platformlike elements; thus I include both Nericodus Lindström 1955 (which has no distinct processes) and Serratognathus Lee 1970 (which is based on alate ramiform elements with platformlike lateral processes) among the platform conodonts. On the other hand, I do not regard Prioniodus (Baltoniodus) Lindström 1971 as a platform conodont genus although it includes some species (e.g. P. (B.) gerdensis Bergström 1971) in which one element has a platformlike posterior process. All in all, I here recognize 12 previously named genera of Ordovician platform conodonts, namely Amorphognathus Branson & Mehl 1933, Complexodus Dzik 1976, Eoplacognathus Hamar 1966, Icriodella Rhodes 1953, Nericodus Lindström 1955, Polonodus Dzik 1976, Polyplacognathus Stauffer 1935, Pygodus Lamont & Lindström 1957, Rhodesognathus Bergström & Sweet 1966, Sagittdontina Knüfer 1967, Scyphiodus Stauffer 1935, and Serratognathus Lee 1970. In addition, I am aware of the existence of several other types of platform conodonts that appear distinctive enough to merit generic recognition, and two of these, Cahabagnathus nom. nov. and Prattognathus n. gen., are named in this contribution.

One problem confronting everyone who is carrying out studies related to the vertical distribution of Ordovician fossils on a world-wide scale is the current uncertainty of the precise chronostratigraphic relations between units in the successions on different continents. Although considerable progress has been made in recent years in establishing long-distance correlations of Ordovician rocks, alternate interpretations are still being proposed, especially in the case of the lower half of the system, and it may take years before conclusive evidence becomes available to settle some of these problems. In the present contribution, I have followed the graptolite–conodont biostratigraphy set forth in a recent paper (Bergström 1983),
and I use the terms Lower, Middle, and Upper Ordovician in the sense of the Baltoscandic Oelandian, Viruan, and Harjuan Series. For convenience, the British series designations have been employed; the base of the Middle Ordovician is taken to be in the middle Llanvirnian, and that of the Upper Ordovician in the upper Caradocian.

Scope of study

Extensive studies during the last three decades have made Ordovician conodonts reasonably well known in North America and northwestern Europe, but Asian, Australian, and South American forms have received far less study. However, the data at hand do not suggest that there are numerous undescribed Ordovician platform conodonts. The interpretations and descriptions presented below are based largely on specimens in my own collections, which have been assembled since 1958 from a considerable number of localities in Europe and North America, and a few in North Africa and The People’s Republic of China. I have also had full access to large collections of Ordovician conodonts from North America kept at the Department of Geology and Mineralogy at the Ohio State University, and I have examined most type collections containing Ordovician platform conodonts in Europe and North America. Unfortunately, I have not had the opportunity to study specimens of a few Siberian platform conodonts dealt with by Moskalenko (1970, 1977) as well as those in other collections in the USSR, and the currently available descriptions and illustrations are insufficient for a proper evaluation of some of these forms, most of which appear to be unrelated to the taxa dealt with herein. Although the oldest platform conodonts known are from strata as old as the Tremadocian (Lindström 1955, 1964), this type of conodont became common and diversified only in the Llanvirnian and younger parts of the Ordovician. Because of this, and the fact that the available collections of Tremadocian and Arenigian platform conodonts are small and not very informative, my discussion will center on post-Arenigian forms.

Provincial differentiation

The vast majority of the currently known Ordovician platform conodonts were originally described from Europe, particularly from the Baltoscandic–Polish region, and this area appears to have a greater diversity of such conodonts than any other region with Ordovician deposits. In terms of the two commonly recognized Ordovician conodont faunal provinces (Sweet & Bergström 1974), North American Midcontinent Province and the North Atlantic Ordovician Province, the Ordovician platform conodont genera are strikingly unequally distributed. That is, Ambalodus, Complexodus, Eoplacognathus, Neriodus, Polonodus, Pretognathus, Pygodus, and Sagittodontina are virtually restricted to the North Atlantic Ordovician Province, whereas only Sophiodus, Serratognathus, and Polyplacognathus are Midcontinent Province genera. Amorphognathus, Icriodella, and Rhodesognathus are known from numerous localities in both provinces, and are almost cosmopolitan in their distribution; however, Amorphognathus and Icriodella are most diversified, and have their evolutionary origin, in the North Atlantic Province and may be considered more typical of the latter province than of the Midcontinent Province. Thus, there is no question that at the generic level, the North Atlantic Province has the greatest diversity of platform conodonts. That this diversity trend is even more evident at the species level is illustrated by the fact that more than 30 platform conodont species are known from the North Atlantic Province and fewer than five are restricted to the other province. The reasons for this difference are obscure and may be very complex. The Midcontinent Province appears to have included primarily, but not exclusively, shallow-water environments in the tropical zone whereas the North Atlantic Province seems to have occupied mainly temperate and arctic latitudes where its conodont biotas became preserved in rocks representing a very wide range of depth environments. Interestingly, the greatest diversity of platform conodonts in the latter province was in off-shore subtidal environments, in many cases on continental-shelf margins, and these environments are also characterized by a high diversity of platform conodonts in some other geologic periods, for instance, the Devonian. Quite clearly, the data at hand support the idea that the Ordovician platform-condont distribution pattern is a conspicuous exception to the well-known rule that tropical faunas generally are characterized by a considerably higher species diversity than the temperate–arctic ones.

Migration patterns

A discussion of the distribution of Ordovician platform conodonts in time and space should clearly address the question of distribution centers and patterns of migration at both the species and genus levels. Regrettably, the current lack of a reliable base map of the Ordovician regional paleogeography prevents proper illustration of these matters but pertinent data are discussed below.

As noted above, the stratigraphically oldest known platform conodont, Ambalodus n. sp. of Lindström (1955) from the upper Tremadocian of Sweden, is similar to an element of Eoplacognathus and it may well be interpreted as an ancestor of the latter genus. Be this as it may, the data at hand suggest that the center of diversification of Eoplacognathus was in the Baltoscandic area, where at least seven species appeared during Llanvirnian through Llandeiloan time, and representatives of these are regularly, and in many cases quite commonly, represented in most lower Middle Ordovician samples. The only known other area with an early (Arenigian–Llanvirnian) diversification of Eoplacognathus comparable to that of the Baltoscandic region is Hubei Province in The People’s Republic of China (Sheng 1980; An 1981). Unfortunately, the Chinese taxa are not yet known in enough detail to permit firm conclusions regarding their precise relations to the Baltoscandic forms. Clearly, however, they are very similar to and occur with many other conodont species characteristic of Baltoscandic faunas. Outside these areas, occurrences of representatives of Eoplacognathus are far more scattered but some species exhibit a very wide, in some cases almost cosmopolitan, distribution. For instance, E. suecicus is known from Nevada (Harris et al. 1979) and forms similar to both E.
folicaeus and *E. reclinatus* have been found, however in most cases only rarely, in Tennessee (Bergström 1971a; Bergström & Carnes 1976), central Nevada, eastern New York and Oklahoma (Harris *et al.* 1979), and Alabama (Bergström 1971a; listed as *E. folicaeus*). Similar forms are also known from south-central China (Sheng 1980; An 1981; Ni 1981) and the Canning Basin of Western Australia (McTavish & Legg 1976). In contrast, representatives of *E. robustus*, although found locally in Tennessee (Bergström 1973) and possibly in northeastern Newfoundland (Bergström *et al.* 1974; Fähraeus & Hunter 1981), are very rare outside the Baltoscandic–Polish region. A far wider distribution is exhibited by *E. lindstroemi*, and especially by *E. elongatus*; in addition to its many occurrences in Baltoscandia, the latter species is known from Wales (Bergström 1981a), many localities in the Appalachians (Bergström 1971a; Bergström & Carnes 1976; Nowlan 1981), Oklahoma, Arkansas (Repetski & Ethington 1977), central Nevada (Harris *et al.* 1979), Poland (Dzik 1978), and western USSR (Drygant 1974). This species may possibly be the most widespread of all those currently referred to *Eoplacognathus* suggesting a maximum dispersal of the genus just before its extinction.

Although the ancestor of *Cahabagnathus* has not been identified with certainty, it appears that the genus had a center of evolution in southeastern and southern USA, where it is common in the lower Middle Ordovician and all known forms are present. Representatives of the stratigraphically next oldest species, *C. friendsvillensis*, occur also outside this area in North America, for instance in New York and Quebec (Roseoe 1973), Northwest Territories in western Canada (Tipnis *et al.* 1978), and central Nevada (Harris *et al.* 1979). As far as I know, this form is still unknown in Europe but a closely similar species was recently reported from The People’s Republic of China (An 1981). The geographically most widespread species of *Cahabagnathus* is likely to be *C. sweeti*, which is known not only from localities in much of the Appalachians but also from Texas (Bergström 1978), Arkansas (Repetski & Ethington 1977), southwestern Scotland (Bergström 1971a), and, from rare specimens in a very limited interval, in Norway and Sweden (Bergström 1971a) as well as in Volyn in western USSR (Drygant 1974), and Siberia (Moskalenko 1977). This distribution pattern clearly shows a considerable expansion of the range of the genus in Llandeilian time. The stratigraphically youngest species of the *Cahabagnathus* lineage (*C. carnesi*) has not as yet been found outside Tennessee, and the genus might have had a very restricted geographic range before becoming extinct.

The presence in the Baltoscandic region of not only its apparent ancestors but also primitive species of *Pygodus* may be taken as an indication that this area was a center of diversification of that important genus. The virtually cosmopolitan distribution of *P. serra* and *P. anserinus*, especially in geosynclinal regions in North America (Sweet & Bergström 1974), Scotland (Bergström 1971a), Wales (Bergström 1981a), the Ursals (Nasedkina & Pushkov 1979), The People’s Republic of China (Sheng 1980; An 1981; Ni 1981), New Zealand (Simes 1980), and Australia (Nicoll 1980) shows power of dispersal over huge regions. In view of this distribution, and the common occurrence of forms of *Pygodus* also in black shale facies, the suggestion recently put forward by Fähraeus & Hunter (1981) that these conodonts were benthic, seems rather improbable. Interestingly, it appears that the stratigraphically youngest species of the *Pygodus* lineage had a wider geographic distribution than any other species of the genus.

Another area of origin is apparently represented by *Icriodella*, the oldest representatives of which are known from the British Isles and Brittany in strata of latest Llandeiliian age (Lindström *et al.* 1974). This genus is not known from the Baltoscandic region in strata older than the late Caradocian, and the genus is only rarely represented in the Ashgillian there. In North America, the stratigraphically oldest species is *I. superba*, which appears in Rocklandian strata (Schopf 1966; Roscoe 1973), that is, in beds coeval with a portion of the lower Caradocian. This species migrated into the North American Midcontinent, where it is quite widespread, during middle to late Caradocian time and it persisted there to the late Ashgillian (Richmondian). I am aware of only one reported occurrence of Ordovician representatives of *Icriodella* outside Europe and North America, namely in The People’s Republic of China (Sheng 1980), but it would not be surprising if occurrences were also found in other parts of Asia and in Australia.

From available evidence (see pp. 38–40), it appears that the evolutionary origin of *Amorphognathus* was in the Baltoscandic area, where there are some Arenigian–Llanvirnian species not known with certainty elsewhere. However, An (1981) has recently reported primitive forms from the People’s Republic of China that are associated with conodonts of Baltoscandic type. Unfortunately, those platform conodonts are still not known in enough detail to permit close comparison with Baltoscandic forms. The same applies to some forms from the Ursals described by Nasedkina & Pushkov (1979). The Llandeiliian species *A. inaequalis* is currently best known from Wales (Rhodes 1953; Bergström 1964) and Brittany (Lindström *et al.* 1974) but has also been recorded from Poland (Dzik 1976). It may also be present in Baltoscandia but most middle Middle Ordovician specimens there are clearly *A. tvaerensis*. The Siberian form referred to as *A. inaequalis* by Moskalenko (1977, Pl. 8:14, 15) is clearly not conspecific, and may not even be congeneral, with Rhodes’ species. Unlike *A. inaequalis*, representatives of *A. tvaerensis* are widely distributed also in North America where the species has been recorded in the Appalachians (Bergström 1971a; Bergström & Carnes 1976; Nowlan 1981), Oklahoma, central Nevada (Harris *et al.* 1979), New York State and the Midcontinent (Sweet & Bergström 1971). The stratigraphically younger species *A. superbus* and *A. ordoxicus* have an even wider distribution in North America and Europe, and the latter species may be regarded as essentially cosmopolitan. From distribution data now available, it seems that *Amorphognathus* gradually expanded its geographic range during late Middle and Late Ordovician time.

Most of the other Ordovician platform genera have a very limited geographic range and exhibit no very clear migration patterns. Yet, representatives of *Complexodus* are known from Wales (Bergström 1981a), the Baltoscandic–Polish–Volyn region (Dzik 1976), and The People’s Republic of China (An 1981) but all these occurrences are in a narrow stratigraphic interval in the *Pygodus anserinus* to lower *Amorphognathus*
taerensis Zone. Representatives of Rhodesognathus first appear in the lower Caradocian of the British Isles (Bergström 1971a) and in equivalent strata in New York State and Vermont (Schopf 1966; Roscoe 1973), and the genus expanded its range into much of the North American Midcontinent and the Baltoscandian region (Bergström, J. et al. 1968) during middle to late Caradocian time. At least in North America, it exhibits a distribution pattern similar to that of Icriodella superba. Also, representatives of Rhodesognathus almost invariably occur with specimens of Amorphognathus, which is far more widespread than Rhodesognathus but also exhibits a striking progressive evolution in several features that has no counterpart in the morphologically stable and conservative representatives of Rhodesognathus.

Summarizing the above observations, it appears that Amorphognathus, Eoplacognathus, and Pygodus had their evolutionary origin in Baltoscandia in Early and early Middle Ordovician time, and subsequent spread from that region into particularly the British Isles and marginal areas of North America. Whereas the last two genera became extinct in the early Caradocian, Amorphognathus later expanded its range and in the Late Ordovician became essentially cosmopolitan. The distribution of these three genera in time and space also suggests close faunal interchange between Baltoscandia and The People’s Republic of China and, possibly, New Zealand and the Canning Basin of Western Australia. Icriodella and Rhodesognathus may have originated in the British Isles – Brittany region, and representatives of these genera subsequently migrated into large areas of the North American plate. These genera are comparatively poorly represented in Baltoscandia where most occurrences are in a limited interval in the middle to upper Caradocian. Interestingly, many of these occurrences are associated with the invasion of North American megafossils discussed by Jaanusson & Bergström (1980:92–93), and it seems appropriate to regard both Icriodella and Rhodesognathus as exotic elements in the Baltic conodont faunas. Cahabognathus seems to have had a center of evolution in eastern North America and it never became common or widespread outside the North American plate although rare specimens of one species (C. sweeti) have been found in Scotland, Baltoscandia, Volyn in western USSR, and Siberia. Again, it is of interest to note that in Baltoscandia this species occurs in an interval that also has representatives of the unusual but widespread genus Complexodus and the Midcontinent Province genus Phragmodus (Bergström 1971a:106), which suggests a brief period of long-distance faunal exchange. Another, and markedly stronger contemporaneous expression of this may be the ‘flood’ of North Atlantic Province elements, including Pygodus and Prioniodus (Baltiodius), which in early Middle Ordovician time invaded the continental-plate margins in several parts of the world, especially around North America.

Evolutionary lineages

Based on their vertical occurrence and evolutionary relationships, one can distinguish three groups of Ordovician platform-conodont genera. One includes Nericodus, Prattognathus, and Serratognathus, each of which appears suddenly in the succession without any obvious ancestral forms. Another, which comprises Complexodus, Icriodella, Polyplacognathus, Rhodesognathus, Sagittodontina, and Scaphiodus, differs from the first in that its genera show at least some similarity to other forms and an evolutionary origin can be proposed. With the exception of Icriodella, and possibly Polyplacognathus, these genera currently include only one species each. A third group of genera includes Amorphognathus, Cahabognathus, Eoplacognathus, Polonodus, and Pygodus. Each of these genera contains more than one species, and these species are parts of rapidly evolving evolutionary lineages, the ancestor of which is known in at least some cases. Compared to the two other groups mentioned, this group has a far wider geographic distribution in that in some cases it is virtually cosmopolitan, and the genera of this group include many biostatigraphically important species. It is the evolution and evolutionary relationships of these taxa that are of major concern in the present study. For convenience, I will first discuss each of these lineages and will then deal with the other platform conodont genera in a separate section.

The Amorphognathus lineage (Fig. 1)

The upper Middle and Upper Ordovician part of this lineage, which includes A. taerensis Bergström 1962, A. superbus Rhodes 1953, and A. ordovicicus Branson & Mehl 1933, was discussed in some detail by Bergström (1971a), who described the composition of the Amorphognathus apparatus and used the species mentioned as zonal indices in the North Atlantic Province conodont-zone succession. Subsequent work has confirmed the apparatus reconstruction and the biostatigraphic significance of these species, but it has also added important data on the early phylogeny of Amorphognathus (Sweet & Bergström 1972; Lindström 1977; Dzik 1976).

The idea that Amorphognathus taerensis evolved from A. inaequalis Rhodes 1953 (Bergström 1971a) is supported by new data from Poland (Dzik 1976) and Great Britain (Bergström coll.) and the ancestor of the latter species is now also clear. Forms with an array of elements similar to that of A. ordovicicus are known from rocks as old as Early Ordovician. Holodontiform (M) elements, which are very characteristic of the Amorphognathus apparatus, are represented by the type of Lenodus Sergeeva from the Arenigian of the Baltic region, and this genus has generally been interpreted as a junior synonym of Amorphognathus (Bergström 1971a, 1981b; Dzik 1976; Lindström 1977). The occurrence of this type of element in the Lower Ordovician is important because it gives a clue to the origin of Amorphognathus; that is, this evidence suggests (Lindström 1964, 1970, 1977; Bergström 1971a; Dzik 1976) that Amorphognathus evolved from the Prioniodus (Baltiodius) stock in the middle Arenigian (Fig. 5). Lindström (1977) indicated that the non-holodontiform elements of primitive species of Amorphognathus such as A. falodiformis (Sergeeva) may be closely similar to those of Prioniodus (Baltiodius) nasi Lindström but the morphological differences, if any, have not yet been described. At any rate, only minor morphological modification is needed to derive the holodontiform (M) element of the former species from the oistodontiform element of the latter, and there is little doubt that the ancestor of Amorphognathus is in the Prioniodus (Baltiodius) stock.

Although known in its main features, the pattern of
**Fig. 1.** Suggested evolutionary relationships and known stratigraphic ranges of taxa of the Amorphognathus and Icriodella lineages and of Sagittodontina, Complexodus, Rhodesognathus, Scyphiodus, and Polyplacognathus. Only key elements in the apparatuses are illustrated. The zonal framework is that of Bergström (1971a) and Löffgren (1978) with minor modifications. As in the other diagrams, horizontal lines from boxes mark the approximate stratigraphic position of the illustrated specimen(s). Abbreviations of subzonal designations are as follows: va-jl, A. variabilis-M. jlabellum; va-o.:; A. variabilis-M. o.:;arkodella; su-gr, E. suecicus-S. gracilis; su-su, E. suecicus-P. sulcatus; fo, E. foliaceus; re, E. reclinatus; ro, E. robustus; li, E. lindstroemi; ki, A. kielcensis; in, A. inaequalis; va, P. (B.) variabilis; ge, P. (B.) gerdae; al, P. (B.) alobatus.

Evolution exhibited by *Amorphognathus* in the Llanvirnian and Llandoillian is still not safely established in all details. For instance, Löffgren (1978) records observations in support of the interpretation that a Swedish form identified as *A. variabilis* Sergeeva has an apparatus composed of only two types of platform elements and, accordingly, is closely similar to that of *Eoplacognathus* (cf. p. 41). A different opinion is expressed by Dzik (1976) and Lindström (1977) who include seven types of elements in the apparatus of *A. variabilis* and, with justification, regard this as a typical *Amorphognathus* appara-
tus. This view is supported by the fact that platform conodont elements strikingly similar to the types of Sergeeva's *A. variabilis* occur with holodontiform (M) elements in Hubei Province, The People's Republic of China (Bergström coll.). However, it appears that the only way to definitely establish the nature of the *A. variabilis* apparatus is to reinvestigate Sergeeva's type collection and, preferably, also topotype material. Nevertheless, it is of interest to note that regardless of the outcome of such a study, there is evidence that there was at least one platform conodont species, that referred to as *A. variabilis* by Dzik (1976), in the late Arenigian — early Llanvirnian that had an array of elements similar to that in advanced species of *Amorphognathus*.

From this form Dzik (1978, Fig. 1) derived a stratigraphically slightly younger species, *A. kielcensis* Dzik 1976, which differs from the former species in minor details in the pastinscaphe (P) and holodontiform (M) elements. This species, which is widely distributed geographically in the Baltic area but somewhat erratic in its occurrence, ranges from strata at least as old as about the base of the *E. foliaceus* Subzone in Sweden. With its ancestor, it shares the character of having a postero-lateral process nearly as long as the posterior process and also the tendency of developing, in mature amorphognathiform elements, lateral expansions of especially the posterolateral ridges, nodes, and denticles.

An extreme case of the latter tendency, in the same position on the pastinscaphe element, is exhibited by *Complexodus pugionifer* (Dryvant 1974), type species of *Complexodus* Dzik 1976. This species has a distinct anterior lobe on the postero-lateral process that in adult specimens tends to have an irregular denticulation (Dzik 1978, Fig. 1:20, Pl. 13:6). In other respects, the pastinscaphe element of *C. pugionifer*, the only type of element currently known in its apparatus, is so reminiscent of that of *A. kielcensis* that it seems justified to suggest that the latter species is the ancestor of *Complexodus* (Fig. 1).

A group of closely related species, including *Amorphognathus inaequalis*, *A. tooarenis*, *A. superbis*, and *A. ordovicicus*, forms a lineage that extends from the upper Middle Ordovician to near the top of the Upper Ordovician. To this group belong also *A. complicatus* Rhodes 1953 and some other, but still incompletely known, forms such as *A. lindstroemi* (Serpagli 1967). As noted by Bergström (1971a) and Dzik (1976, 1978), the oldest species of this group, *A. inaequalis*, apparently evolved into the stratigraphically next younger species, *A. tooarenis*. Morphological differences between these species are minor but recognizable in the platform as well as the holodontiform (M) elements (Lindström 1977; Dzik 1976). I share the opinion of Dzik (1976, 1978) that *A. inaequalis* is closely related to the *A. variabilis* of Dzik — *A. kielcensis* stock and there seems to be evidence supporting the view that it evolved directly from the latter species. Likewise, there is very little doubt that *A. tooarenis* evolved from *A. inaequalis* as suggested by Bergström (1971a).

Representatives of *Amorphognathus tooarenis*, *A. superbis*, and *A. ordovicicus* show considerable intraspecific variation and the currently used morphologic concept of these species is relatively broad. Both *A. tooarenis* and *A. superbis*, and *A. superbis* and *A. ordovicicus*, are connected by morphological transitions, and relations between these species appear to be rather clear. The characteristic species *A. complicatus* is interpreted as an offshoot from *A. superbis*; apart from the simple posterolateral process in the pastinscaphe elements of the former species these species are closely similar to each other. Contrary to a recent statement by me (Bergström 1981b), *Amorphognathus* seems to be restricted to the Ordovician because a recent taxonomic and stratigraphic reevaluation of some reported Silurian occurrences of the genus failed to establish a single reliable record in that system. Also, among the Silurian platform-conodont genera, none has been identified as a likely descendant of *Amorphognathus* and the lineage might have become extinct in latest Ordovician time.

The *Icriodella* lineage (Fig. 1)
The type, and probably most common species, of *Icriodella* is *I. superbis* Rhodes 1953. Since this species, and the genus, were defined in terms of multielement taxonomy (Bergström & Sweet 1966; Webers 1966), only a rather limited amount of basic new data has been published on Ordovician forms whereas Silurian species have been discussed much more extensively. Although *I. superbis* is widespread geographically in North America and Europe and shows a certain degree of morphological variation that has led to taxonomic splitting (Rhodes 1953; Orchard 1980), the collections studied have not permitted the recognition of distinct evolving morphological trends in this species.

The stratigraphically oldest representatives of *Icriodella superbis* known are from the Harnagian of the Welsh Borderland (Bergström 1971a) and Rocklandian strata in New York State (Schopf 1966) and Vermont (Roscoe 1973). Slightly older (Costonian and possibly latest Llandeilian) strata in the Welsh Borderland contain a distinct species (Fig. 6 A–H) that may be conspecific with *I. praecox* Lindström, Racheboeuf & Henry 1974, which was originally described from the Middle Ordovician of Brittany. This form is characterized particularly by the fact that it has a single, rather than double row of denticles on the anterior process of the platform element although the other elements of its apparatus are quite similar to those of *I. superbis*. The suggestion of Lindström, Racheboeuf & Henry (1974) that *I. praecox* is the ancestor of *I. superbis* appears to be fully supported by the evidence at hand, and the latter species is likely to have evolved from the former in late Costonian or early Harnagian time in northwestern Europe (Fig. 1).

The ancestor of *Icriodella praecox* has not yet been identified. However, the platform element of this species shows some similarity in the development of its anterolateral process to *Amorphognathus* and *Prioniodus* (Baltoniodus) although its rami-form elements differ from those of the latter genera not only in the denticulation and other morphological details but also, and probably more significantly, in the absence of a tetrapri ­niodontiform element. Bearing in mind the very close similarity between the two *Icriodella* species, I reject Dzik’s (1976:411) proposal that *I. praecox* should be referred to *Prioniodus* rather than to *Icriodella* because of its lack of a double denticle row. In my opinion, following that suggestion would lead to a highly artificial taxonomy. Nevertheless, the suggestion that *Icriodella* initially evolved from a prioniodontidean ancestor appears
as likely today as when it was proposed more than ten years ago (Lindström 1970; Sweet & Bergström 1972, Fig. 3).

Because the youngest reported occurrence of *Icriodella superba* is in the Upper Ordovician (Richmondian) of the North American Midcontinent (Sweet & Bergström 1976), it is evident that the species has a rather long vertical range. However, as noted above, the species exhibits no very obvious morphological trends through its range although it cannot be ruled out that such trends may be masked by the considerable intraspecific variation and by the fact that the platform elements are susceptible to breakage and complete specimens are uncommon. Orchard (1980) described *I. prominens* from the lower to middle Ashgillian of Great Britain. Although the morphological features of that species are not entirely clear from the original description and illustrations, it may be conspecific with a previously unreported, but quite distinctive, species from strata of the same age in Sweden (Bergström coll.).

No representative of *Icriodella* is currently known from the uppermost Ordovician and it is unclear if the lowermost Silurian (Lower Llandoveryan) species of the genus reported from North America (Pollock, Rexroad, & Nicoll 1970; McCracken & Barnes 1981; Nowlan 1981), as well as possibly slightly stratigraphically younger forms from Great Britain (Aldridge 1972), were derived from *I. superba*, *I. prominens*, or both. At any rate, the Early Silurian species are so similar to the Ordovician ones that there can be no doubt that they belong in the same genus. Aldridge (1972) described the vertical distribution and phylogenetic relationships of the *Icriodella* species in the British Llandoveryan and a closely similar stratigraphic distribution pattern has recently been found in eastern Canada (Nowlan 1981).

As currently known, *Icriodella* does not range above the Wenlockian and the later history of the *Icriodella* lineage is somewhat unclear because of the poor record of this type of conodonts in much of the Wenlockian and the Ludlovian. However, the Upper Silurian *Pedanis* Klapper & Philip 1971, *Peleksygnathus* Thomas 1949, and *Icriodus* Branson & Mehl 1938 exhibit so many morphological similarities to *Icriodella* that it seems justified to assume that these three genera are descendants of the *Icriodella* lineage. Particularly striking are the morphological changes in the ramiform elements, which by loss of the processes have attained a coniform shape. It is also of interest to note that *Icriodus* in the Devonian exhibits a taxonomic diversity far greater than that of any portion of the *Icriodella* lineage.

**The Cahabagnathus lineage (Fig. 2)**

The platform conodonts herein referred to *Cahabagnathus* nom. nov. have been included in *Polyplacognathus* Stauffer 1935 by all previous authors except Drygant (1974), who proposed the preoccupied generic designation *Petalognathus* for this group of conodonts. *Petalognathus bergstrromi* Drygant 1974; type species of Drygant’s genus, is clearly a junior synonym of *Cahabagnathus sweeti* (Bergström 1971), here designated type species of *Cahabagnathus*. The Middle Ordovician conodonts referred to this genus are interpreted to represent a lineage separate from those of other genera, and the introduction of a generic designation appears justified, especially as these conodont elements have a characteristic appearance and a wide distribution. For a generic diagnosis of *Cahabagnathus*, see p 51.

Although reported from Scotland (Bergström 1971a), Scandinavia (Hamar 1966; Bergström 1971a), the USSR (Drygant 1974; Moskalenko 1977), and The People’s Republic of China (An 1981), representatives of *Cahabagnathus* are currently known primarily from North America, where they are widespread in the lower Middle Ordovician, especially in the Appalachians.

As shown by collections from eastern Tennessee, Virginia, and Oklahoma, five distinct species of *Cahabagnathus* occur in stratigraphic order and form an evolutionary lineage of intergrading successive morphotypes (Fig. 2). Illustrations of the four youngest of these species and their ranges were given by Bergström (1973, Fig. 4) and Bergström & Carnes (1976, Fig. 2) but the oldest species in the lineage, *Cahabagnathus* n. sp. A (Fig. 6 Q, R), which is currently known only from Oklahoma, has not been illustrated previously. Two of these species, *C. friendsvillensis* and *C. sweeti*, were named by Bergström (1971a), and for two others, *C. chazyensis* (= *Polyplacognathus friendsvillensis–sweeti* transition of Bergström 1978; Fig. 6 M–P) and *C. carnesi* (= *P. sweeti*, late form of Bergström & Carnes 1976; Fig. 6 K–L), specific names are formally proposed in the present paper.

The apparatus of *Cahabagnathus* n. sp. A and other species of the genus is composed of two types of paired platform elements which are stelliplanate and pastiniplanate, respectively. As described in the systematic part of the present paper, morphologic evolution in the *Cahabagnathus* lineage can be recognized in both of these element types, and is expressed primarily in the following features (Fig. 2): (1) Gradually decreasing size, and ultimate disappearance, of the anterior lobe of the anterolateral process in the stelliplanate element; (2) widening of the posterior process of the pastiniplanate elements in adult specimens, which is well displayed in the transition of *C. friendsvillensis* into *C. chazyensis*; and (3) a progressive change in the appearance of the main denticle row at the junction of the posterior and anterior processes in the pastiniplanate element as illustrated in Fig. 2. It is of interest to note that three of the *Cahabagnathus* species exhibiting these changes have been found in successive order in the same formation at three localities, and the development of the most advanced species, *C. carnesi*, from its ancestor, *C. sweeti*, is documented in two sections. Furthermore, where representatives of the *Cahabagnathus* lineage have been found at other localities in North America and elsewhere, the order of succession of species is always the same.

When searching for an ancestor of the *Cahabagnathus* lineage, it is perhaps natural to turn first to the *Eoplacognathus* lineage, the other common and widespread group of early Middle Ordovician platform conodonts. In basic morphology, the two types of elements of the oldest known species of *Cahabagnathus*, *C. n. sp. A*, are not very unlike two of the four types of elements in the apparatus of species of *Eoplacognathus* such as *E. foliaceus* and *E. reclinatus* (Fig. 2). The *Cahabagnathus* elements differ, however, in occurring in mirror-image pairs and in having a distinct node and ridge ornamentation lateral to the central denticate row on the upper surface of the processes. It is my conclusion that these differences are more significant than they may appear at first sight and they occur in all growth stages. Although it cannot be ruled out completely...
In the present state of our knowledge that the ancestor of *Cahabagnathus* may belong to the *Eoplacognathus* lineage, no truly intermediate form has been found to support this idea. A potential ancestor is the *E. foliaceus* → *E. reclinatus* transition of Harris et al. (1979, Fig. 16), which occurs with, as well as stratigraphically below, primitive forms of the *Cahabagnathus* lineage in several North American sections. However, even though elements of this species are reminiscent in some respects of those of a species of *Cahabagnathus*, its apparatus has four types of platform elements that do not occur in mirror-images, and thus, this form is referable to *Eoplacognathus*. It should also be noted that early species of *Cahabagnathus* are unknown in Europe, which appears to have been a center of morphological diversification of *Eoplacognathus*. Furthermore, there are undescribed, and still poorly known, platform conodont elements with a surface ornamentation quite similar to that of representatives of *Cahabagnathus* in the early Middle Ordovician of North America, for instance, *Gen. et sp. nov.* of Bergström (1978, Pl. 79:17). It is quite conceivable that the ancestor of *Cahabagnathus*, although not identified at the present time, may be found among that complex of species, which occurs lower stratigraphically than *Cahabagnathus* n. sp. A. Clearly, additional studies are needed to clarify the origin of the *Cahabagnathus* lineage.

In the successions studied so far, the youngest species of the *Cahabagnathus* lineage, *C. carnesii*, disappears without any
obvious descendant. Representatives of *Polyplacognathus ramosus* Stauffer 1935 have two types of platform elements that occur in mirror-images, and have a surface ornamentation similar to that in species of *Cahabagnathus*. However, *P. ramosus* has a different, and more complex, process arrangement in the stelliplanate element, and the pastimplanate element also differs conspicuously from that of *Cahabagnathus*. Further, in view of the fact that evolutionary trends in the *Cahabagnathus* lineage are in some respects opposite to what one would expect if it were the progenitor of *Polyplacognathus*, I consider it unlikely that the latter genus has its roots in the *Cahabagnathus* lineage. Other interpretations are discussed below (p. 45).

**The *Eoplacognathus* lineage (Fig. 2)**

This lineage, which includes more species than any other Ordovician platform conodont lineage, was recognized by Bergström (1971a), who described six of its species on a multielement basis, namely *Eoplacognathus suecicus* Bergström 1971, *E. foliaceus* (Färhræus 1966), *E. reclinatus* (Färhræus 1966), *E. robustus* Bergström 1971, *E. lindstroemi* (Hammar 1962), and *E. elongatus* (Bergström 1962). Viira (1972) discussed the symmetry of elements of this type, and Bergström (1973) illustrated the range, and the four types of elements in the apparatus, of each of five species in this lineage. Good schematic illustrations of some element types were given by Dzik (1976, 1978) who also discussed the evolutionary trends briefly. He included *E. pseudoplanus* (Viira 1974) and *E. zierzenisis* Dzik 1976, which occur in strata older than those dealt with by Bergström (1971a), in the lineage and agreed with Bergström (1971a) that the ancestor of the primitive *Eoplacognathus* species is likely to be *Amorphognathus variabilis* Sergeeva 1963 or a closely related form. Löfgren (1978), in a detailed discussion, considered *E. pseudoplanus* a questionable junior synonym of *E. suecicus*, and expressed the opinion that true *A. variabilis* is likely to have lacked ramiform elements in the apparatus, and also in other respects to have been more similar to *Eoplacognathus* than to *Amorphognathus*. In accordance with this, she referred the latter species with question to *Eoplacognathus* and considered it to be the oldest species in the *Eoplacognathus* lineage.

A review of collections at hand and of available data from the literature suggests that it is possible to recognize two groups of species within the *Eoplacognathus* lineage. The oldest of these, which includes *E. suecicus, E. pseudoplanus*, and related forms and which is here referred to as the *E. suecicus* – *E. pseudoplanus* species complex, is characterized by the fact that processes of pastimplanate elements are of subequal length and the dextral and sinistral stelliplanate elements are in many cases closely similar to each other. The various species within this complex have been separated mainly on the basis of minor differences in the mutual length of the processes and their angles with each other.

As noted by Löfgren (1978), there is considerable intraspecific variation in both fully developed elements and between growth stages in this species complex, and there appears to be a virtually continuous series of transitional forms between its morphological end members. This makes separation into well defined taxa difficult, and the introduction of several species on the basis of very small collections with little, if any, consideration of intraspecific variation has led to taxonomic problems, some of which have been discussed by Löfgren (1978).

Bergström (1971a) and Dzik (1976) suggested that the ancestor of early species of *Eoplacognathus* may be *Amorphognathus variabilis* or a closely similar form. As noted above, there is still some uncertainty regarding the apparatus of the latter species although now-available data appear to indicate that it has a full set of ramiform elements and is a true *Amorphognathus*. Evolution of a typical *Eoplacognathus* from *A. variabilis* would have involved loss of the ramiform elements but otherwise no drastic morphological changes, and this ancestry for *Eoplacognathus* remains a distinct possibility. Alternatively, *Eoplacognathus* might have evolved from an as-yet-unknown ancestor without ramiform elements in the apparatus.

In discussing the origin of *Eoplacognathus*, it is also appropriate to draw attention to the fact that Lindström (1955, 1964, Fig. 3D) described a platform conodont quite similar to the pastimplanate element of *Eoplacognathus* from lowermost Ordovician (upper Tremadocian) strata in south-central Sweden (Fig. 2). Unfortunately, only a few specimens are known and most of them are incomplete. Although there are undescribed platform conodonts in early and middle Arenigian strata in Europe and North America (Bergström coll.), none of those collected thus far represents this particular type, and relations between the Tremadocian form and *Eoplacognathus* remain obscure. Lindström (1964) interpreted it as a homeomorph of *Eoplacognathus*, but in the present state of our knowledge it cannot be ruled out that it may be the evolutionary ancestor of the *Eoplacognathus* lineage.

The post-*Eoplacognathus suecicus* portion of the *Eoplacognathus* lineage includes a series of species connected by morphological intermediates. I refer to this group of species as the *E. foliaceus* – *E. elongatus* species complex. Morphological evolution within this complex is expressed mainly in changes in the mutual length, direction, and number of processes of the platform elements (for illustrations, see Bergström 1971a, 1973; Bergström & Carnes 1976; Dzik 1976, 1978). All of these species have four types of morphologically different platform elements that do not occur in mirror-images, and they are also characterized by the very long anterior process of the pastimplanate elements (Fig. 2).

Typical specimens of *Eoplacognathus foliaceus* appear abruptly in my sections and I have not seen any actual specimens, or illustrations, of elements truly transitional between this species and *E. suecicus*. Although there is a distinct morphological gap between the species mentioned, *E. foliaceus* can be derived rather readily from *E. suecicus*, which is likely to be its ancestor. An interesting separate lineage in the *E. foliaceus* – *E. elongatus* species complex is represented by the still incompletely known *Eoplacognathus* n. sp. A of Bergström (1971a) which occurs in strata close to the *Pygodus serra* – *P. anserinus* zonal boundary in Baltoscandia (Bergström 1971a), Poland (Dzik 1978, Fig. 1: 13 – listed as *E. l. robustus*) and The People’s Republic of China (Bergström coll.; Ni 1981). I interpret this form as a descendant of *E. foliaceus*, or a closely related species, and it seems to have considerable stratigraphic significance.

The youngest known species of the *Eoplacognathus foliaceus* – *E. elongatus* complex, *E. elongatus*, disappeared in the early Caradocian without leaving any obvious descendants. The idea that *Polyplacognathus* Stauffer evolved from *Eoplacognathus*,
put forward without supporting evidence by Barnes & Fähræus (1975), is not unreasonable on morphological grounds but as noted below (p. 45), there are also other possible ancestors of *Polyplacognathus*. It is interesting that elements of some post-Ordovician platform conodonts have the basic morphology of elements of *Eoplacognathus*. This applies to the Early Silurian *Astropentagnathus* Mostler 1967 and the Late Silurian *Ancoradella* Walliser 1964 which are similar to stiltiplanate elements of *Eoplacognathus* in terms of process organization and other morphological features. Although different in surface ornamentation, the Devonian *Anycryognathus* Branson & Mehl 1934 and the Mississippian *Doliognathus* Branson & Mehl 1941 are reminiscent in basic morphological plan to the pastiniplanate elements of *Eoplacognathus*. The appearance of the apparatus is still incompletely known in some of these genera but information currently available (Schönlau 1971; Klapper & Philip 1971) suggests that in each case, it differs markedly from that of *Eoplacognathus*. Accordingly, it seems very likely that the similarities mentioned are cases of homeomorphy rather than characters implying phylogenetic relationship, and that the *Eoplacognathus* lineage became extinct in Middle Ordovician time.

The *Pygodus* lineage (Fig. 3)

One of the morphologically most distinct, and biostratigraphically most useful, of the Ordovician platform genera is *Pygodus* Lamont & Lindström 1957. Representatives of *P. serrae* (Hadding 1913) and *P. anserinus* Lamont & Lindström 1957 are present not only in an unusually wide range of facies but they are also among the most widespread geographically of all compound Ordovician conodonts.

*Pygodus* was discussed in some detail, and defined in terms of multielement taxonomy, by Bergström (1971a). Shortly afterward, at the *Marburg Symposium on Conodont Taxonomy* in 1971, I described the morphological evolution of the *Pygodus* lineage and discussed its origin but my conclusions and illustrations have not been published. On the basis of Swedish collections very similar to mine, Löfgren (1978) arrived at conclusions that agree closely with those I presented orally in Marburg. Some additional data supporting this interpretation have become available subsequently but, as noted below, some points are still unclear even if the general evolutionary scheme appears rather safely established.

Information now at hand strongly suggests that the origin of the stratigraphically oldest well-known species of *Pygodus*, *P. serrae*, can be traced back via two primitive species, here referred to as *P. anitae* n. sp. and *P.?* n. sp. (Fig. 3), to forms that have been referred to *Polonodus* Dzik 1976 in the recent literature. The origin of *Polonodus* is still uncertain but it should be noted that fragments of primitive platform conodont elements similar in surface sculpture and in development of the basal cavity are not uncommon in Baltic strata as old as the *Megistaspis planilimbata* Limestone (early Arenigian) (Bergström coll.). Unfortunately, affinities of these fragments are obscure because no specimen complete enough to reveal the architecture of the platform elements of this species has been found thus far. At any rate, in cannot be ruled out that the *Polonodus* lineage might extend far down in the Lower Ordovician.

As presently understood, *Polonodus* includes a group of early Llanvirnian platform conodonts of complex architecture among which only one species, *P. cliouensis* (Viira 1974), has been named formally. Although specimens of *Polonodus* have been collected in Estonia, Sweden, Poland, Newfoundland, New York State, and Nevada, the total number of elements recovered to date is small, and most of the specimens are fragmentary. This has made it difficult to evaluate the intraspecific variation in species of the genus, and the taxonomy of *Polonodus* is still poorly understood. Nevertheless, the evolution of *Polonodus* into *Pygodus* can readily be traced in the pygodontiform elements, although there are also rather striking morphological changes in the other elements of the apparatus. As noted by Löfgren (1978), perhaps the most characteristic feature in this evolution is the gradual reduction and, ultimately, the virtual disappearance of the posterior processes in the pygodontiform element. This morphological change is associated with a simplification in the branching of
the anterior processes, which ultimately merge into a subtriangular platform.

Early forms of Polonodus, such as those illustrated as *P. elionus* (Vira) by Lögren (1978, Pl. 16:12A, 12B), have two posterior processes that are platform-like and distinctly shorter than the lateral and anterior ones (Fig. 3). Stratigraphically slightly younger forms have relatively shorter posterior processes and two anterior processes with double denticle rows (Fig. 3). Such elements have been referred to as *Pygodus?* sp. B by Lögren (1978, Pl. 16:2, 3) and they are herein referred to as *Pygodus?* n. sp. Still higher stratigraphically, there are specimens with the posterior processes reduced to just a short simple lobe posterior to the cusp. The anterior part of these elements consists of two confluent lobes that bear, in most specimens, double rows of denticles (Fig. 3). I regard these specimens as representatives of the earliest known typical species of *Pygodus*, herein named *Pygodus anitae* n. sp. (Fig. 6V–Z). Specimens of this type were illustrated as *Pygodus* sp. C by Lögren (1978, Pl. 16:5, 6). Representatives of the next younger well-defined form, *P. serra*, have only three denticle rows on the anterior platform, and this species is connected with *P. anitae* via morphological intermediates (*P. serra* early) in Fig. 3. As noted by Bergström (1971a), *P. serra* evolved into *Anserinus*. The latter two species, as well as *P. anitae*, and, probably, the *Polonodus* species have at least three types of elements in the apparatus in addition to the pygodontiform elements (Fig. 3). These elements also underwent a rather conspicuous evolution in the early Middle Ordovician but it was not as rapid, and is not as easily defined morphologically, as that of the pygodontiform elements. Evolutionary changes in elements of these types are illustrated schematically in Fig. 3.

*Pygodus anserinus*, the youngest known species of the *Pygodus* lineage, apparently became extinct in the early Caradocian in view of the fact that the stratigraphically youngest specimens found (Bergström 1971a) are from the *Prioniodus* (B.) *gerdae* Subzone of the *Amorphognathus toverensis* Zone. There are no other conodonts even remotely similar to *Pygodus* in younger Ordovician strata, and it appears that this lineage left no descendants. The two species from the Llandoveryan of the Carnic Alps described by Walliser (1964) as P.? lenticularis and *P. lyra* in all probability are not related to *Pygodus* at even the family level. The latter species was based on elements now interpreted (Walliser 1972) as part of the apparatus of *Apisognathus tuberculatus* Walliser 1964, the type species of *Apisognathus*, the apparatus of which is very different from that of *Pygodus* (Klapper 1981). *Pygodus? lenticularis* is based on a single specimen that is morphologically rather different from *Pygodus* and it can clearly be rejected as a representative of the latter genus. Accordingly, it appears fully justified to consider these Silurian elements as, at the most, only homeomorphs of the pygodontiform element of *Pygodus*.

Other platform conodonts

Several Ordovician platform conodont genera are monospecific and show little, if any, phylogenetic evolution through the stratigraphical intervals where they are present. Such genera include *Prattognathus*, *Rhodesognathus*, and *Scyphiodus*. To this group should probably also be added *Nericodus* and *Sagittodontina* but, as indicated below, these genera are currently so poorly known in terms of their morphology, and they have such a restricted distribution, that there is little basis for an evaluation of possible morphological trends. It is also possible that *Polyplacognathus* and *Serratognathus* should be included in this group although several species have been referred to each of these genera; however, the information at hand is insufficient to evaluate the evolution within these genera, and in the case of *Polyplacognathus*, the generic reference of some species is questionable (cf. p. 41).

Species of some of the genera mentioned have a relatively wide geographic and stratigraphic range; such species are *Rhodesognathus elegans* (Rhodes 1953) and *Polyplacognathus ramosus* Stauffer 1935. The other genera are represented by species with far more restricted ranges. Clearly, this decreases the possibilities of postulating evolutionary relationships at the generic level.

*Nericodus* is one of the oldest platform conodonts known in the geologic record but only a few specimens of its type species, *N. capillamentum* Lindström 1955, have been found thus far and the genus is very poorly understood. The specimens available are all fragmentary and even basic features of their morphology and morphological variation are uncertain. Miller (1980, 1981) has recently restudied the type and other specimens, and his suggestion that the early Arenigian (*Paroistodus proteus Zone*) *Nericodus* is related at the family level to the Tremadocian *Clashoamalus* Furnish 1938 and *Hirsutodontus* Miller 1969 is not unreasonable on morphological grounds. Likewise, it is possible that *Nericodus* may be related to the Tremadocian *Ambalodus* n. sp. Lindström 1955. Indeed, it cannot now be ruled out that one, or both, of the latter taxa may represent a lineage leading to *Polonodus*, but supporting evidence through much of the Arenigian is needed to prove the correctness of this idea.

By contrast, rich collections have been assembled of *Polyplacognathus ramosus* (Fig. 1), the type of *Polyplacognathus*, and this species is widespread in faunas of North American Midcontinent type through much of the upper Middle Ordovician [Faunas 6 through 10 of Sweet et al. (1971); cf. Sweet & Bergström 1976]. Compared to many other Ordovician platform conodonts, this species exhibits a great morphological stability throughout its range, and evolving morphological features suitable for further taxonomic discrimination have not been recognized. Characteristically, the apparatus includes one type of paired stelioplane elements and dextral and sinistral pastioplane elements that are closely similar to each other. Apparently, the apparatus lacked ramiform elements.

In terms of element types and surface ornamentation, *Polyplacognathus* is similar to *Cahabognathus*. However, data at hand do not support the idea that the former evolved from the latter. It is also possible to derive *Polyplacognathus ramosus* morphologically from advanced representatives of *Eoplacognathus* such as *E. elongatus* by modification of the processes and development of a complex and irregular surface ornamentation. Yet, no transitional forms are known and I consider a direct ancestor–descendant relationship between these genera as unlikely even if it cannot be completely ruled out at the present time (Fig. 5). Another, and perhaps more likely, ancestor of *Polyplacognathus ramosus* might be present in the complex of early Middle Ordovician platform conodonts from
Si beria described as *P. petaloides*, *P. sp.*, and *P. lingualis* by Moskalenko (1970, Pl. 14:2, 3a, 3b, 4, 5). Although her illustrated specimens are all fragmentary and not easily interpreted in terms of, for instance, number and mutual length of the processes, it is clear that the type of basal cavity and the general appearance and arrangement of the processes are reminiscent of those of *P. ramosus*. Furthermore, Moskalenko’s specimens are associated with typical North American Midcontinent Province conodonts and occur in strata that have been correlated with the Llandeilian (Chuageva 1976:286–287), that is, an interval older than the earliest known occurrences of *P. ramosus*, which are likely to be of early Caradocian age. The stratigraphically youngest occurrences of *P. ramosus* reported thus far are in the lower part of the Amorphognathus superbus Zone (Sweet & Bergström 1971, 1976) and the species apparently became extinct in the late Middle Ordovician without leaving any descendants.

Representatives of *Prattognathus* are currently known only from Alabama, Tennessee, and Nevada, and all occurrences are in a rather narrow stratigraphic interval, namely the upper part of the Pygodus serra Zone and the lower part of the *P. anserinus* Zone. As interpreted herein, the apparatus of *Prattognathus* includes two types of paired platform elements (Figs. 2, 6S–U), and no additional elements are recognized as probable, or possible, parts of its apparatus. Although different in details, one of the two types of platform elements, up to now known as Polyplacognathus stelliformis Sweet & Bergström 1962 is so similar in overall appearance to the stelliplanate element in the apparatuses of Eoplacognathus, Polyplacognathus and, in particular, Cahabagnathus that it is quite natural to regard it as corresponding to that type of element in the apparatus. The other type of platform element in the apparatus of *Prattognathus*, originally described as Polyplacognathus rutiliformis Sweet & Bergström 1962 is also a stelliplanate element but it is here interpreted as corresponding to the pastiplanate element in species of Cahabagnathus. Although specimens of the multielement species *P. rutiliformis* have been found in association with representatives of Cahabagnathus friendszillensis, the type of stelliplanate element just mentioned is more similar to that of advanced species of Cahabagnathus, such as the specimen of *C. chayzensis* illustrated by Bergström (1978, Pl. 79:15), than to that of *C. friendszillensis*.

Available specimens of *Prattognathus rutiliformis* are all quite distinct morphologically, and no forms have been found that are transitional with a species of Cahabagnathus or any other early Middle Ordovician platform genus. Accordingly, the origin of *Prattognathus* is enigmatic. However, based on morphology, and its stratigraphic and geographic occurrence, one may perhaps suggest that the ancestor of *Prattognathus* may be present among some poorly known platform taxa in the Whiteockian of North America, for instance, *Polyplacognathus* n. sp. A of Fähraeus (1970) (cf. Bergström 1980, Fig. 2M) and/or *Polonodus* newfoundlandensis of Stouge (1980, Pl. 13:14–16). Both these species occur in an interval that is considerably older than that in which *P. rutiliformis* occurs.

The peculiar appearance of the second type of stelliplanate element in *Prattognathus rutiliformis* is not at all what one would expect in the ancestor of Polyplacognathus ramosus, and the relationships between *Prattognathus* and Polyplacognathus are unclear. However, regardless of the precise nature of their relationship, it seems both natural and justified to group these two genera, along with Cahabagnathus and Eoplacognathus, in Polyplacognathidae Bergström 1981.

The type of *Rhodesognathus*, *R. elegans*, has been recorded from upper Middle Ordovician strata at many localities in the North American Midcontinent and from a few in the Appalachians and northwestern Europe. As noted by Roscoe (1973) and Bergström (1981b), its apparatus contains a set of ramiform elements that are currently indistinguishable from corresponding elements of the apparatus of Amorphognathus species, which commonly occur together with representatives of *R. elegans*. The form described by Dzik (1976) as *R. elegans polonicus* apparently lacks ramiform elements and it differs also in other respects from typical *R. elegans* to the extent that it seems justified to regard it as a separate species; indeed, I hesitate to refer this form without question to *Rhodesognathus*. Likewise, the form described from the Middle Ordovician of Brittany by Lindström, Racheboef & Henry (1974) as *Priionodus* (Rhodesognathus)? n. sp. aff. *Priionodus variabilis* Bergström 1962 and *Priionodus gerdae* Bergström 1971 seems more similar to *Priionodus* (Baltonioides) than to *Rhodesognathus*, particularly in that the edge of the lateral process continues into the anterior edge of the cusp rather than into the denticule anterior to the cusp as is characteristic of *Rhodesognathus* (Bergström & Sweet 1966:392).

As currently known, *Rhodesognathus* ranges from the lower Caradocian to a level well up in the Ashgillian (Sweet & Bergström 1976). The striking similarity between the ramiform elements of *Rhodesognathus* and *Amorphognathus* suggests close relationship, but no transitional specimens have been described. However, based on the admittedly incomplete data at hand it seems reasonable to suggest that *Rhodesognathus* evolved from *Amorphognathus* in the early Middle Ordovician (Fig. 1). The genus apparently became extinct in Late Ordovician time without leaving any descendants.

Up to now, the concept of *Sagittodontina* has been based solely on the fragmentary original specimens from the Upper Ordovician of Thuringia described by Knüpf (1967). As shown by Bergström & Massa (in preparation), the type species of *Sagittodontina*, *S. bifurcata* Knüpf 1967, has an apparatus of paired pastiniscapate and pastinate elements and an array of ramiform elements of the same general types as in species of *Amorphognathus* (Fig. 4). In the appearance of both the platform and the ramiform elements, *Sagittodontina* is clearly different from *Amorphognathus* and other Ordovician platform genera, and its relationships are not clear. The architecture of its apparatus suggests that *Sagittodontina* might have its origin in the *Amorphognathus* lineage (Figs. 1, 5) but there is no direct evidence to support this idea. An alternative interpretation is that *Sagittodontina* represents a separate evolutionary lineage from a prioniodontacean ancestor parallel to that of *Amorphognathus*. Additional material is clearly needed to show, which, if either, of these interpretations is correct.

Representatives of *Scyphiodus* (Figs. 1, 5), the only Middle Ordovician platform conodont genus that appears to be indigenous to the North American Midcontinent, are relatively common in several formations there (see, for instance, Webers 1966 and Sweet 1982) but attempts to reconstruct the apparatus of *S. primus* Stauffer 1935, the type and only known
species of the genus, have thus far been unsuccessful. The fact that no ramiform elements have been identified as regular associates of the platform elements led Webers (1966), Sweet & Bergström (1972), Sweet (1982), and Bergström (1981b) to suggest that the apparatus might have been unimembrate and might have included only paired platform elements. These authors also noted that apart from the platform-development of the anterior process, Scyphiodus elements are remarkably similar to blade-like elements in the apparatus of Bryantodina and Plectodina, which are present in the same stratigraphic interval.

If Scyphiodus is closely related to one, or both, of these genera, it is, of course, to be expected that its ramiform elements, if present, would be similar to those of the genera mentioned, and there is a possibility that their true relationship has not been recognized. This possibility should be kept in mind in future studies of Scyphiodus-bearing samples as an alternative to the interpretation of Scyphiodus as having a unimembrate apparatus. Regardless of whether or not Scyphiodus had a more complex apparatus than is apparent now, it appears likely that this genus evolved in the Middle Ordovician from a stock such as Plectodina rather than from another platform conodont lineage such as Amorphognathus, Icriodella, or Polyplacognathus to which Scyphiodus is probably not closely related.

Patterns of evolution

It is beyond the scope of the present paper to discuss in detail the speciation processes in Ordovician platform conodonts. However, some of the taxa studied appear to show an interesting pattern of evolution that warrants some brief comments.

As shown by the summary diagram of my interpretation of the relations between Ordovician platform conodont taxa (Fig. 5), at least five lineages can be recognized, each apparently quite independent of the others, namely those of Amorphognathus, Cubahagnathus, Eoplacognathus, Icriodella, and Pygodus. In terms of evolutionary processes, these long-ranging lineages are of particular interest. Each includes series of successive species showing little overlap in their individual vertical ranges (Fig. 1–3). In most cases, these species are distinguished from each other on characters in the platform elements showing rapid evolution. Also the nonplatform elements in the apparatuses of Amorphognathus and Pygodus exhibit evolutionary changes, and such changes in the holo­dontiform (M) elements of Amorphognathus have been used for separating taxa at the species level. The rate of evolution varied greatly between different types of elements; some morphologically conservative elements, such as the ramiform S elements, may be so similar in several species that they are virtually indistinguishable whereas the platform and M elements show rapid morphological change.

These conodont species lineages have a low species diversity at virtually every level in the Middle and Upper Ordovician; indeed, as shown in Fig. 5, each lineage is, as a rule, represented by only a single species at a particular time plane. It could perhaps be argued that this low diversity is a taxonomic artifact caused by the use of a very broad species concept. However, the concept employed does not differ appreciably from that used in the classification of other conodonts, and study of collections from areas widely separated geographically suggests that representatives of a particular genus show surprisingly little regional variation. For instance, platform elements of the genera listed above from East Asia and North America are, as a rule, indistinguishable from those of Baltoscandia.

In these lineages, the common type of speciation, as expressed by changes in morphology of the skeletal elements, is characterized by periods of rather slow to almost imperceptible morphological change, which are interrupted by relatively short episodes of accelerated evolution that is, in some cases, almost explosive. In a series of samples through a section representing such an episode, it is in many instances possible
EVOLUTIONARY RELATIONSHIPS OF ORDOVICIAN PLATFORM CONODONTS

ASHGILLIAN
A. orдовicus
Rhodesognathus
elegans
A. complicatus
Amorphognathus
superbus

CARADOCIAN
A. superbus
Rhodesognathus
elegans
A. complicatus
Amorphognathus
superbus

LLANDEILIAN
P. aenseni
Amorphognathus
inaequalis

LLANVIRNIAN
Pygodus
Pygodus
P. serrae
re
fo

ARENGIAN
A. variabilis
Amorphognathus
varibalis
Amorphognathus
suecicus

British Series
CONODONT
ZONES

RHODESOGNATHUS

SAGITTO-
DONTINA

ICRIODELLA

POLYPLACOGNATHUS

SCPHIODUS

COMPLEXODUS

AMORPHOGNATHUS

EOPLACOGNATHUS

PRATTO-
GNATHUS

CAHABA-
GNATHUS

PYGODUS

POLONODUS

Arenigian ancestor in the
Prionodus (Beltonodus) complex

Ancestor in the Tremadocian or in
the Arenigian A. variabilis complex?
(for instance, the transition from *Pygodus serrus* to *P. anserinus*) to trace the gradual, but rapid, development of one species into another through transitional morphotypes. Such a speciation event appears to be of the same type as those described recently in Permian and Triassic conodonts (Carr 1982; Wardlaw 1982). Because it seems to have occurred in the same time interval over a large region, and its geological record is preserved in a very narrow stratigraphic interval, such an event represents an excellent datum for regional biostratigraphic correlation. In fact, such levels have been used as zonal boundaries in the North Atlantic Province Middle and Upper Ordovician conodont zone succession since its introduction (Bergström 1971a).

Obviously, we have no way of knowing if the conodont 'species' we recognize in these lineages on the basis of combinations of certain morphological characters in the skeletal elements correspond to 'biologic' species but this is a problem conodonts share with other fossil groups. Assuming that our conodont taxonomy at the species level is indeed comparable to that in extant organisms, it appears that the much-publicized model involving a tree- or bushlike pattern of evolution does not describe the evolutionary scheme I envision for Ordovician platform conodonts very well. This scheme seems to combine features of both of the two contrasting concepts of speciation, phyletic gradualism and punctuated equilibria, as they were described by Eldredge & Gould (1972). However, further studies are needed to establish the detailed nature of this scheme as well as its occurrence among other types of conodonts. Because they show rapid evolution and can be obtained in large numbers from closely spaced samples, conodonts are well suited for studies of speciation processes, and further investigations of these matters are likely to yield results applicable not only to conodonts but also to other types of organisms.

**Biostratigraphical remarks**

The zonal scheme introduced by Bergström (1971a) for the Middle and Upper Ordovician of the North Atlantic Province was based largely on taxa of *Amorphagnostus*, *Eoplagagnostus* and *Pygodus*, and has proved to be applicable widely in Europe and North America as well as to successions in Asia and Australia. Since 1971, many new data have become available that bear on the biostratigraphic use of Ordovician platform conodonts, and some of this information is briefly discussed below.

**Tremadocian and Arenigian**

Although An (1981) recognized a *Seragnostus diversus* Zone and a *S. bilobatus* Zone in the upper Tremadocian–lower Arenigian of the People's Republic of China, platform conodonts have thus far been used very little in the Lower Ordovician conodont biostratigraphy. Some of the reasons for this are that they are uncommon, not very diversified morphologically, and still poorly known. The appearance in the upper Arenigian of the first major platform conodont lineage, that of *Amorphagnostus*, is of major biostratigraphic significance. Taxa in the oldest part of this lineage (*A. faladoformis*, etc.) clearly have potential as zonal indices but they are still too poorly known both in terms of morphology and stratigraphic range to be useful biostratigraphically. Until recently, the oldest unit based on *Amorphagnostus* was the *A. variabilis* Zone. However, on the basis of a new species said to be present in an interval just below that of *A. variabilis*, An (1981) introduced an *A. antivariabilis* Zone. An's zonal index is incompletely known and the characteristics he used to separate it from *A. variabilis* need further evaluation. However, if this species proves to be distinct, it may be the direct ancestor of *A. variabilis*. Although *A. antivariabilis* was said to be present below the interval of *A. variabilis*, An (1981, Fig. 3) correlated the base of his *A. antivariabilis* Zone with a level well above the base of the North Atlantic *A. variabilis* Zone. No reason was given for this somewhat surprising correlation.

**Llanvirnian**

Several different schemes of Llanvirnian conodont zones have been proposed (Sergeeva 1966 a, b; Lindström 1971; Bergström 1971a; Viura 1974; Dzik 1976, 1978; Löfgren 1978) but because of both taxonomic and biostratigraphic problems, the zonal classification has not yet been stabilized, especially in the lower Llanvirnian where the problems center round the *A. variabilis* Zone. Lindström (1971), Dzik (1978), and Löfgren (1978) have each given a different scope to this unit, and even identification of the zonal index remains problematic (for discussion, see Löfgren 1978:58). In Dzik's (1978) scheme, the *A. variabilis* Zone is overlain by the *Eoplagagnostus pseudoplanus* Zone and the zonal boundary is placed at the level of transition of *E. zgierzensis* Dzik into *E. pseudoplanus*. Regrettably, there is some uncertainty regarding the morphological characteristics of *E. zgierzensis* because Dzik's one-sentence original description is too vague to permit definite assessment of the differences in morphology between it and *E. pseudoplanus*, and the illustrated holotype, which is from an erratic boulder of indeterminable stratigraphic origin, is just a fragment that is unworthy to serve as a morphological reference for the species (cf. Löfgren 1978). Potential confusion is also introduced by the fact that Dzik's (1976, Fig. 7) drawing of reconstructed complete specimens of *E. pseudoplanus* is mislabeled and should instead be *E. zgierzensis* (Dzik pers. comm. 1982). Löfgren (1978) discussed in some detail several of the problems related to the conodont biostratigraphy of this interval. She recognized an *A. variabilis* (*Eoplagagnostus? variabilis* in Löfgren 1978) Zone and an *E. suecicus* Zone, each of which was subdivided into two subzones. My Swedish collections suggest that the top of Dzik's (1978) *E. pseudoplanus* Zone corresponds to a level in the middle part of the *E. suecicus–P. sulcatus* Subzone of Löfgren (1978). Because the top of the *E. suecicus* Zone was defined in the same way by Löfgren (1978) and Dzik (1978), the scope of Dzik's (1978) *E. suecicus* Zone is markedly smaller than that employed by Löfgren (1978). As noted by Dzik (1978:52–53), the precise scope of his *A. variabilis* and *E. pseudoplanus* zones is uncertain in terms of Baltoscandic standard units, and my attempts to pin down the boundary between these zones in the Swedish sections studied have been unsuccessful. Accordingly, for the purpose of the

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Fig. 5. Summary diagram showing suggested interpretation of evolutionary relationships of Middle and Upper Ordovician platform conodonts. Only key elements of some apparatus are illustrated. For explanation of subzonal abbreviations, see Fig. 1.
present paper, I prefer to follow Løfgren’s (1978) zonal scheme, which is firmly based on the faunal succession in specific Swedish successions.

The upper Llanvirnian *E. foliaceus* and *E. reclinatus* subzones are well established and noncontroversial. As noted by Bergström (1971b), a primitive form of *Pygodus serra* (Fig. 3) appears very near the base of the *E. foliaceus* Subzone in Baltoscandia, and it seems justified to follow Løfgren (1978) in defining the base of the *P. serra* Zone as coinciding with the base of the *E. foliaceus* Subzone. Interestingly, the stratigraphically oldest specimens of *Amorphognathus kielcensis* Dzik 1976 known to me are from strata very close to the base of the *P. serra* Zone, so the appearance of that characteristic species may also be a useful guide to the zonal boundary level in the absence of specimens of *Pygodus* or *Eoplacognathus*.

In a detailed study of the very condensed Middle Ordovician Mójca sequence in the Holy Cross Mountains, Poland, Dzik (1978) dropped the *Pygodus serra* Zone and elevated its subzones to zones. He has subsequently used the same terminology when dealing with collections from other areas (Dzik 1980, 1981). Because the subzonal indices are far less widespread geographically than *P. serra*, abandonment of the *P. serra* Zone seems unjustified and may be considered a step backward in the process of developing a regionally useful Middle Ordovician conodont biostratigraphy.

**Llanvirnian**

The base of the succeeding *Pygodus anserinus* Zone was originally defined (Bergström 1971a:97) as the level of appearance of *P. anserinus*. The latter species clearly developed from *P. serra*, which is present locally in the lowermost part of the *P. anserinus* Zone as pointed out long ago (Bergström 1971a:150). This fact was apparently overlooked or misunderstood by Fähraeus & Hunter (1981) in their recent study of a Newfoundland succession that ranges across the zonal boundary. If those authors had followed the original definition of the *P. anserinus* Zone, they would have had no difficulty to pick its base and that level would have been very close to the one established by Bergström et al. (1974) in the same sections, but based on much smaller collections.

Bergström (1971a) subdivided the *P. anserinus* Zone into a Lower and Upper Subzone with the subzonal boundary marked by the evolutionary transition of *Prioniodus (B.) previariabilis* into *P. (B.) variabilis*. Dzik (1978) suggested that the evolutionary transition of *Amorphognathus kielcensis* into *A. inaequalis* also takes place near that level. I know of no confirmed record of the latter species in the Baltoscandian region, but support for Dzik’s suggestion is given by the succession in the Smedsby gård drilling core, south-central Sweden (Bergström unpubl.) in which specimens of *A. kielcensis* occur up to a level less than 1 m below the base of the Upper Subzone. Also the distribution of other conodont taxa (especially *Complexodus*) in that core and in other sections in Sweden suggests that the subzonal boundary and the level of the *A. kielcensis* - *A. inaequalis* transition are likely to be so close to each other stratigraphically that for all practical purposes, these levels can be considered to represent the same horizon. These subzones are in need of formal designations and I here propose that the Upper Subzone be renamed the *A. inaequalis* Subzone. It includes the interval of co-occurrence of *P. anserinus* and *A. inaequalis* up to the level of appearance of *A. tvaerensis*, a direct descendant of *A. inaequalis*. Likewise, the Lower Subzone is renamed the *A. kielcensis* Subzone and defined as the interval of co-occurrence of *P. anserinus* and *A. kielcensis* up to the level of appearance of *A. inaequalis*, which is apparently a direct descendant of *A. kielcensis*. Because the latter species ranges through the *P. serra* Zone, presence of both *P. anserinus* and the subzonal index is needed for certain identification of the *A. kielcensis* Subzone. In the absence of these species, the subzonal boundary can be recognized, as previously, as the level of transition of *Prioniodus (B.) previariabilis* into *P. (B.) variabilis*. Because Dzik (1978) elected to use the level of appearance of *A. inaequalis* as the top of his *P. anserinus* Zone, his scope of the latter zone is the same as the *A. kielcensis* Subzone as defined herein.

In this connection it is of interest to note that specimens of *A. inaequalis* are now known (Bergström coll.) from the conglomerate unit in the very uppermost part of the Ffairfach Group below the base of the key section of the Llandeilian near Afon Cennen on Llandilo. This proves that the base of the type Llandeilian is coeval with a level somewhere within the *A. inaequalis* Subzone and not with the base of the *P. anserinus* Zone as was tentatively suggested by Bergström (1971a). This new evidence is in excellent agreement with that from the megafossil (Addison & Williams et al. 1972) and confirms that the much cited correlation of the Llandeilian with the *Glyptograptus reticulatus* Zone is erroneous. As noted by Bergström et al. (1974:1653) and Jaanusson (1979:1A4–1A45), if one follows the traditional practise of defining the top of the Llanvirnian as the top of the *Didymograptus murchisoni* Zone, and if one accepts the conodont evidence of the age of the strata immediately below the base of the Llandeilian in its type area, then one will have to conclude that there is a post-Llanvirnian, pre-Llandeilian interval which has no series designation in the British succession and which corresponds to most of, if not the entire, *Glyptograptus reticulatus* Zone. Obviously, the new conodont data presented above increase the magnitude of this interval in terms of biostratigraphic units, and it would be most welcome if the proper authorities soon addressed the problems of the Llanvirnian–Llandeilian boundary and proposed a workable solution.

Although additional work is needed to establish their precise ranges in terms of the North Atlantic conodont zonal succession, species of *Cahabagnathus* are clearly useful index fossils in the upper Llanvirnian and the Llandeilian. As shown in Fig. 2, the known range of *C.riendsvillensis* approximates that of the *P. serra* Zone; *C. chazyensis* and *C. sweeti* occur in the *P. anserinus* Zone; and *C. carci* in the latter zone and in the lowermost *A. tvaerensis* Zone.

**Caradocian**

The next younger conodont zone, the *Amorphognathus tvaerensis* Zone, has been recognized widely in Europe and North America, as have the lower two of its three subzones, the *Prioniodus (B.) variabilis* and *P. (B.) gorda* subzones. The uppermost subzone, the *P. (B.) alobatus* Subzone, although widely recognized in Baltoscandia, has been recorded from only a single locality in North America (Kennedy et al. 1979). Bergström (1971a), Dzik (1978), and Kennedy et al. (1979) have all commented on the similarity between *P. (B.) variabilis*...
and P. (B.) alobat us, and it may well be that these species have an ancestor–descendant relationship. This is supported by the fact that a few specimens approaching the appearance of P. (B.) alobat us have been found in the P. (B.) variabilis Subzone in Sweden (Bergström unpubl.). Nevertheless, the three subzones are readily distinguishable in the Baltoscandic sections studied.

The precise position of the Llandeillian–Caradocian boundary in the North Atlantic conodont zone succession remains somewhat uncertain. The occurrence of specimens resembling A. tvaerensis in the upper Llandeillian of the type area (Bergström 1971b:184), and of A. tvaerensis and Eoplacognathus elongatus in basalmost Caradocian (Costonian) strata in the Narberth area to the west of Llandilo (cf. Addison in Williams et al. 1972:36), together with the fact that the type Llandeillian is directly overlain by graptolitic shales of the Nemagraptus gracilis Zone (Williams 1953), suggest that the top of the type Llandeillian in all probability is coeval with a level in the Primipodus (B.) variabilis Subzone (Fig. 5).

Also the next younger zone, the Amorphognathus superbus Zone, has been recognized at many localities in Europe and North America. The zonal index is a direct descendant of A. tvaerensis, and the principal difference between these species has been taken to be the appearance of the dextral pastiniscaphate element (Bergström 1962, 1971a:136). Dzik (1978:55) proposed a different circumscription of A. tvaerensis and A. superbus based on the holodontiform element and in accordance with this, a downward adjustment of the base of the A. superbus Zone. However, from my experience with large collections of A. tvaerensis and A. superbus, it is my definite impression that the gradual reduction and ultimate disappearance of the ‘extra’ posterolateral process in the dextral pastiniscaphate element is a more useful feature for separating these taxa within the interval of morphological intergradation than minor changes in the morphologically rather variable holodontiform element, which, furthermore, is only sparsely represented in most collections. Accordingly, I prefer to retain the traditional morphological scope of these species.

No formal subzones have been proposed within the A. superbus Zone. At least in the Baltoscandic region, the upper part of the zone is characterized by the appearance of A. complicatus and Hamarodus europaeus. It is still not known if this distribution pattern also pertains to other regions, so it is probably premature to introduce a subzonal subdivision for this zone at the present time.

Ashgillian

The base of the next younger zone, the A. ordovicicus Zone, is marked by the evolutionary transition of A. superbus into A. ordovicicus (Bergström 1971a), and this level has been recognized both in Europe and North America in strata of early Ashgillian age. Based on his investigation of several Ashgillian faunas from Great Britain, Orchard (1980) suggested that the zonal boundary is in the lower Cauleyean Stage of the Ashgillian. I have had the opportunity to examine his collections at Cambridge University and in my opinion, the conodont evidence for a Cauleyean age of this zonal boundary is inconclusive. It appears that this boundary could as well be in the (upper) Pugziallian. Clearly, additional work is needed in the British sections to solve this problem. No formally defined subzones have as yet been proposed within the A. ordovicicus Zone but as noted by Bergström (1971a) and Orchard (1980), there are indications that subdivision of the zone may ultimately be possible although the appreciable differences in the local ranges of several potentially useful taxa have thus far prevented the establishment of regionally useful subzones.

Systematic paleontology

Lack of space prevents a full description of the many platform conodont taxa dealt with above. However, in order to validate new generic and specific names, I furnish descriptions of a few selected taxa. The morphologic terminology follows, where appropriate, that employed in the recent conodont volume of the Treatise on Invertebrate Paleontology (Clark et al. 1981).

Cahabagnathus nom. nov.


Derivation of name. – Referring to Cahaba Valley, Alabama, where representatives of the genus were first found in North America.

Type species. – Polyplacognathus sweetti Bergström 1971.

Diagnosis of the genus. – A genus of conodonts with an apparatus having one type of stelliplanate and one type of pastinoplanate elements, both occurring in mirror-images; no ramiform elements are known to belong to this apparatus. Stelliplanate elements with unbranched platformed posterior and posterolateral processes, an unbranched or bifid platformed antero-lateral process, and a platformed or bladelike unbranched anterior process. Pastinoplanate elements with a broad, unbranched platformed lateral process, and a considerably longer, almost bladelike to platformed, anterior process that makes an angle of about 90° with the posterior process. All elements with a central denticile row on all processes, and lateral to this row a conspicuous but irregular ornamentation of transverse ridges and nodes; there is no distinct cusp in either type of element. Basal cavity shallow, restricted, with central pit, and wide recessive margin.

Remarks. – In order to conform with the orientation used in Eoplacognathus, and at the suggestion of Dr. J. Dzik, orientation of the pastinoplanate element is changed 90° from that adopted previously (Bergström 1971a, Fig. 14, 1975, Fig. 1, 1978, Pl. 79:13, 15; Bergström & Carnes 1976, Fig. 2) but the process designations are the same. In this new orientation, the anterior process is directed downward and the posterior one horizontally.

Only two other Ordovician conodont genera exhibit an even superficial similarity to Cahabagnathus, namely Eoplacognathus and Polyplacognathus. Cahabagnathus is distinguished from Eoplacognathus by having two types of elements, both of which are present in mirror-image pairs, rather than four types of elements that do not occur in mirror-image pairs, and by having a well-developed ornamentation over the entire upper platform surface rather than only a central denticile row. It differs from Polyplacognathus in the outline of both types of elements, especially the pastinoplanate one. As noted above (p. 41), it is possible that Cahabagnathus might have its
ancestor in the *Eoplacognathus* lineage (Fig. 2) but other evolutionary relationships are also conceivable. It seems unlikely that *Polyplacognathus* evolved from the *Cahabagnathus* lineage.

Detailed descriptions of two (*C. friendsvillensis*, *C. sweeti*) of the five species currently included in the genus were given by Bergström (1971a:142–144) and there is no need to redescribe these species here, especially as I plan to deal with the morphology and ontogenetic development of these species in a separate study. Below, I describe two stratigraphically important, but previously unnamed, species.

**CAHABAGNATHUS CARNESI n. sp.**

*Fig. 6K, L*

**Synonymy.** — □1975. *Polyplacognathus sweeti* Bergström (late form) — Carnes, p. 197–202, Pl. 8:10, 13, 15 (only). □1976 *Polyplacognathus sweeti* Bergström (late form) — Bergström & Carnes, Fig. 2:6.

**Derivation of name.** — In honor of Dr. John B. Carnes, the discoverer of the present species.

**Type locality.** — Cuba, Hawkins County, Tennessee (Carnes 1975:62–69).

**Type stratum.** — Holston Formation, sample 73CC2-16 of Carnes (1975); *Prioniodus* (*B.*) variabilis Subzone.

**Holotype.** — OSU 37186 (Fig. 6K).

**Diagnosis.** — A *Cahabagnathus* species similar to *C. sweeti* (Bergström 1971) but distinguished from the latter by the fact that in the pastioplanate element the main denticle row is not straight but makes a distinct bend toward the anterior process at the junction of the posterior and anterior processes.

**Description.** — In all essential features, the stelliplanate element of the present species is closely similar to that of *C. sweeti*. Although there may be some minor differences in the outline of the processes (Fig. 2), they are hardly distinctive enough to separate these elements from the corresponding ones of *C. sweeti*, particularly in view of the rather considerable variation of these features in the collections at hand. Also the pastiplanate elements are similar to those of *C. sweeti* but they can be readily distinguished by the difference in the appearance of the main denticle row mentioned in the diagnosis.

**Remarks.** — The morphological features used to separate this species from *C. sweeti* may appear to be rather insignificant at first sight but they seem to be quite constant in collections of hundreds of specimens from a limited stratigraphic interval at several localities. As described by Carnes (1975), specimens of *C. carnesi* first appear rather rarely in large populations of *C. sweeti* but in stratigraphically slightly younger samples, the former species becomes completely dominant and only very rare elements of *C. sweeti* are present. Some morphological intermediates connect *C. carnesi* with *C. sweeti*, and there is no doubt that the latter species is its ancestor. Being characteristic of a narrow stratigraphic interval above that characterized by rich occurrences of *C. sweeti*, the present species has the potential to be a useful guide fossil. The vertical ranges of these species show some overlap (Fig. 2) but also this overlap has potential correlative usefulness.

**Known occurrences.** — Tennessee, Hawkins County, Cuba, Holston Formation (Carnes 1975); and Grainger County, Thorn Hill, Holston Formation (Carnes 1975). In addition, according to Dr. T. W. Broadhead (personal communication, 1975a, 13 km SE of Shrewsbury, Welsh Borderland, sample W66–13.

**Fig. 6.** Elements of important platform conodont species discussed in the text. □A. *Iriscidella cf. I. praecox* Lindström et al. 1974, pastinate pectiniform Pa element, OSU 37180, lateral view, ×84. ‘Narberth Group’, Llandeilo–Carnian transition beds, Bryn-banc quarries, 3 km E of Narberth, Wales, sample 79B40-1. □B. Same specimen as A, upper view (note single row of denticles on anterior process). □C. Same species as A, pastinate pectiniform Pa element, OSU 38181, lateral view, ×22. Costonian beds, Evenwood quarry (Bergström 1971a), 13 km SE of Shrewsbury, Welsh Borderland, sample W66–13.

□D. Same specimen as C, upper view, ×22. GE. Same species, locality, and sample as A, one of two types of tertiopedate S elements, OSU 37182, lateral view, ×84. EF. Same species, locality, and sample as A, bipennate element, OSU 37183, lateral view, ×84. □G. Same species, locality, and sample as A, tertiopedate Pb element, OSU 37184, lateral view, ×70. □H. Same species, locality, and sample as A, one of two types of tertiopedate S elements, OSU 37185, posterior view, ×84. □I. *Cahabagnathus sweeti* (Bergström 1971), pastioplanate element, VPIL 4597, upper view, ×35. 6 m above base of Elfna Limestone in section along railroad at Montgomery Lime Production Company, Ellett Valley, Montgomery County, Virginia. Coll. J. M. Wilson. □J. Same species, locality, and sample as I, stelliplanate element, VPIL 4597, upper view, ×35. Coll. J. M. Wilson. □K. *Cahabagnathus carnesi* n. sp. (holotype), pastioplanate element, OSU 37186, upper view, ×78. Holston Formation, sample 73CC2-16 of Carnes (1975), Cuba, Hawkins County, Tennessee. □L. Same species, locality, and sample as K, stelliplanate element, OSU 37187, upper view, ×78. □M. *Cahabagnathus chazensis* n. sp. (syntype), pastioplanate element, VPIL 4578A, upper view, ×68. 8.6 m above base of Lincolnshire Limestone, section at Montgomery Lime Production Company quarry, Ellett Valley, Montgomery County, Virginia. Coll. J. M. Wilson. □N. Same specimen as M, lower view, ×68. □O. Same species, locality, and sample as M (syntype), stelliplanate element, VPIL 4578A, upper view, ×62. Coll. J. M. Wilson. □P. Same specimen as O, upper–lateral view, ×62. □Q. *Cahabagnathus* n. sp. A, pastioplanate element, OSU 37188, upper view, ×48. 106 m above base of McElsh Formation in section on west side of U.S. highway 77, north of Ardmore, Carter County, Oklahoma, sample 72SE-416 of Sweet & Bergström. □R. Same species, locality, and sample as Q, stelliplanate element, OSU 37189, upper view, ×48. □S. *Prtognathus nutriiformis* (Sweet & Bergström 1962), one of two types of stelliplanate element, OSU 36373, upper view, ×53. 36 m above base of section of Little Oak Limestone at quarry 3 km north of Pelham, Shelby County, Alabama (sample 80MS-72 of Schmidt 1982). □T. Same specimen as S, under side (note appearance of basal cavity), ×53. □U. Same species, locality, and sample as S, other type of stelliplanate element, OSU 37190, upper view, ×53. 32 m above base of section (sample 80MS-70 of Schmidt 1982). □V. *Pygodus anita* n. sp., quadriramate element, LO 5624, lateral view, ×84. Top 0.5 m of Segerstad Limestone (sample J65–11), Lunne quarry, Brunflo, Jemtland, Sweden. □W. Same species, locality, and sample as V, tertiopedate element, LO 5622, lateral view, ×84. □X. Same species, locality, and sample as V, stelliscaphate element, LO 5623T (holotype), lateral view, ×84. □Y. Same specimen as X, upper view, ×84. □Z. Same species, locality, and sample as V, tertiopedate element, LO 5624, lateral view, ×84. Abbreviations of repositories of figured specimens are as follows: OSU, Department of Geology & Mineralogy, Orton Geological Museum, The Ohio State University, Columbus, Ohio, USA; VPIL, Department of Geological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA; and LG, Institute of Palaeontology, University of Lund, Sweden.
1982), elements of the present species have been found at other localities in the western thrust belts of eastern Tennessee.

Material. — More than 500 elements. It appears as if the ratio between pastininplanate and stelliplanate elements is 1:1.

CAHABAGNATHUS CHAZYENSIS n. sp.
Fig. 6M-P


Comments to the synonymy list. — The references of Read & Tillman (1977) and Markello, Tillman, & Read (1979) include no formal descriptions or illustrations of the present species and the synonymy is based on my own study of their collections. Inclusion in the synonymy list was deemed appropriate because of the biostratigraphic importance of their papers, as well as the fact that the late C. G. Tillman assembled the finest collection of this species in existence.

Derivation of name. — From the Middle Ordovician Chazy Group, Champlain Valley, New York and Vermont in which the species is the dominant platform conodont and where specimens were first collected by Raring (1972).


Type stratum. — Lincolnshire Limestone, 26 feet above base, Pygodus anserinus Zone (sample VPIL 4578).

Syntypes. — VPIL 4578A (Fig. 6M–P).

Diagnosis. — A Cahabagnathus species characterized by the stelliplanate element with a bifid anterolateral process and a relatively broad, crudely square, posterolateral process; and pastininplanate elements with a broad posterior process with an almost straight main denticle row extending to near the platform margin in the proximal part of the process.

Description. — A good description of both element types of this species was given by Raring (1972) on the basis of specimens from the Chazy Group, but because that description is not readily accessible, the critical features are dealt with herein.

The pastininplanate elements show close similarity to those of C. friendsvillensis in most important respects, including the presence of a bifid anterolateral process, but in most instances, those of the present species may be distinguished by their broader and less pointed, in many cases crudely square, posterolateral process with markedly bent, rather than slightly evenly curved, anterior margin. The pastininplanate element is closer morphologically to that of C. sweeti than to that of C. friendsvillensis in that it has a much wider posterior process, and a different appearance of the denticule row proximally in the posterior process, compared to the latter species (Fig. 2).

Remarks. — Although elements of C. chazyensis are morphologically intermediate between those of C. friendsvillensis and C. sweeti, the present species is quite distinct and easily recognizable when both types of elements are present. It is of interest to note that Wilson (1977) found unmixed populations of this species through more than 80 m of strata in Ellett Valley, where there is a very minor overlap with the range of C. sweeti in the topmost part of the interval of C. chazyensis. Likewise, at its known occurrences in Texas, Tennessee, and Champlain Valley, C. chazyensis is the only Cahabagnathus species present through an interval ranging in thickness from several tens of meters to more than 100 m. There is no doubt that the present species is a descendant of C. friendsvillensis, and morphological intermediates connect it with C. sweeti at the top of its range.

Known occurrences. — Tennessee, Blount County, Friendsville, Lenoir Limestone (Bergström coll.) and Hawkins County, St. Clair, Lenoir Limestone (Bergström coll.); Virginia, Montgomery County, Ellett Valley, New Market and Lincolnshire formations (Wilson 1977); Texas, Brewster County, Marathon area, Woods Hollow Shale (Bergström 1978); New York and Vermont, Champlain Valley, Chazy Group, upper Crown Point and lower Valcour formations (Raring 1972). All known occurrences are apparently in the lower part of the Pygodus anserinus Zone but it is possible that the species might be present in the uppermost part of the P. serru Zone.


PRTTGNATHUS n. gen.

Derivation of name. — Named for the Pratt family, long-time residents at Pratt Ferry, Alabama, the type locality of P. rutiformis.

Type species. — Polyplocognathus rutiformis Sweet & Bergström 1962 (Fig. 6S-U). [The specific designation rutiformis has been used in a multielement sense for this species by Bergström (1973), Bergström & Carnes (1976) and Harris et al. (1979)].

Diagnosis of genus. — A genus of conodonts with apparatus having two types of asymmetrical albid platformed elements, both stelliplanate and occurring in mirror-image pairs; no ramiform elements known in the apparatus. One of these types with five, short, more or less bladelike processes that branch out from a common point in the middle of the unit. The other type with four processes, three of which are platformed and one bladelike, all branching from a central point. All processes in both types of elements with central row of denticles, and marginal to that an irregular ornamentation of low ridges and scattered nodes. Basal cavity broad but shallow beneath platformed processes, slitlike beneath bladelike processes.
Remarks. — In their study of the conodonts from the Pratt Ferry beds of Alabama, Sweet & Bergström (1962) described in some detail the elements herein referred to the multielement species *P. rutiformis* as *Polyplacognathus rutiformis* and *P. stelliformis*. Subsequently, these types of elements have been found at several other localities in Alabama (Schmidt 1982), eastern Tennessee (Bergström 1973; Bergström & Carnes 1976), and Nevada (Harris et al. 1979). Although no occurrence of abundant specimens of these elements is known, they are associated so constantly with each other that it seems very likely that they belong to one and the same apparatus. Furthermore, because this apparatus differs appreciably in several important respects from those of previously named conodont genera, it is appropriate to introduce a new generic name.

*Prattognathus* is distinguished from *Eoplacognathus* by having two types of elements, present in mirror-image pairs, rather than four types of elements that do not occur in mirror-image pairs. In addition to the central denticule row, these elements have an irregular pattern of ridges and nodes on the upper surface. The genus can be separated from *Cahabagnathus* and *Polyplacognathus* by the process arrangement and the outline of the elements, especially the one with dominantly platformed processes. It differs from *Polonodus* in the number and arrangement of the processes, and the appearance of the basal cavity, but, as noted above, it cannot be ruled out that *Prattognathus* may have its ancestor among forms similar to those referred to *Polonodus* by some authors.

**Polonodus* Lamont & Lindström 1957**

*Pygodus* anitae n. sp.

Type species. — *Pygodus anitae* Lamont & Lindström 1957

**Pygodus** Lamont & Lindström 1957

**Pygodus** anitae n. sp.

Fig. 6V-Z

**Prattognathus** is closely similar to corresponding elements in *Pygodus* rutiformis and *P. serra*, but they tend to be wider basally and less extended longitudinally, and have less strongly and less regularly denticulated processes.

Remarks. — The present species is a morphological intermediate between *Pygodus?* n. sp. and *P. serra*, and specimens transitional to the latter are present in the upper part of the *Eoplacognathus fusiulus* Subzone (*P. serra* (early)) in Fig. 3; also cf. Löfgren 1978, Fig. 32D-F. However, both the pygodonticiform and haddingodontiform elements differ appreciably from those of typical specimens of *P. serra* and the two species are readily separable.

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*Pygodus* anitae n. sp.

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