

EVOLUTION, TAXONOMY AND RELATIONSHIPS OF THE SILURIAN CONODONT *PTEROSPATHODUS*

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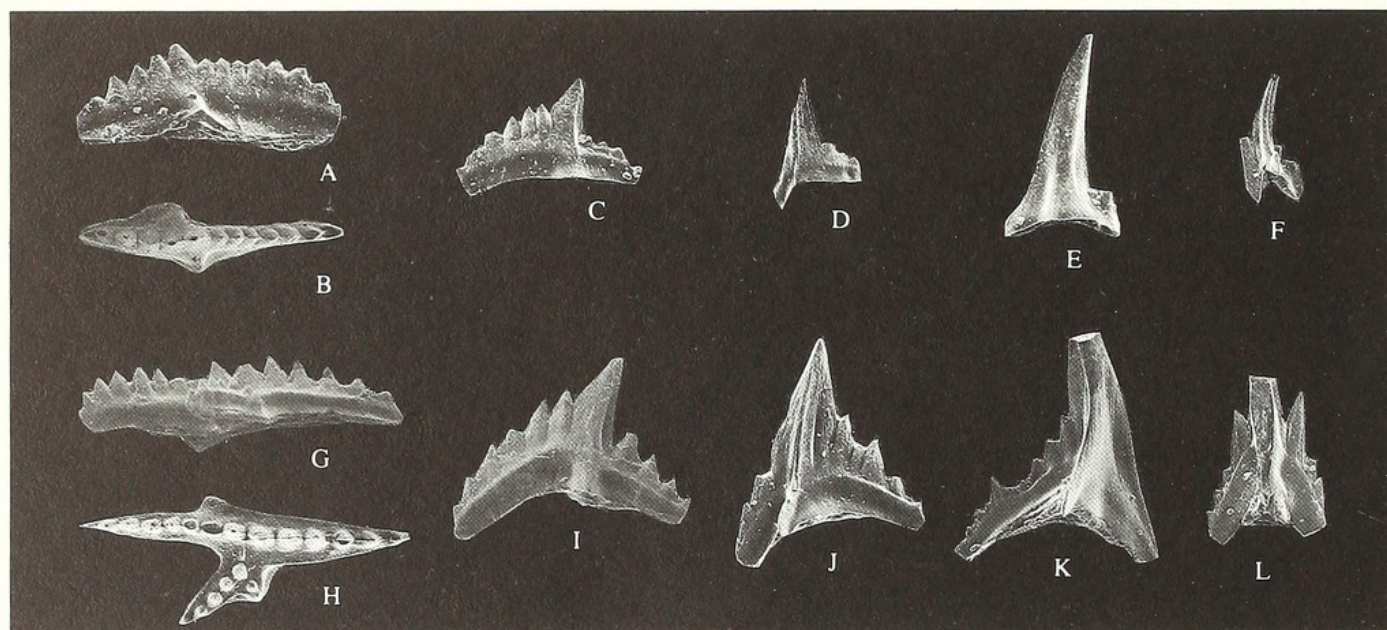
ABSTRACT. The apparatus of *Pterospathodus* species comprises Pa, Pb, Pc, M and Sa/Sb elements. A more complete first symmetry transition series of Sa-Sc elements occurs in some related species, which are assigned to a new genus, *Pranognathus*. A sequence through the *celloni* and *amorphognathoides* biozones of Estonia has been sampled in detail, allowing documentation of sequential changes shown by *Pterospathodus* populations. The least conservative element is the Pa, in which gradual trends of increasing size, lateral process development and platform development prevail. Morphological differences between sinistral and dextral specimens in the *celloni* Biozone include a preferential development of pennate lateral processes on dextral elements; pennate and non-pennate forms previously included in the separate taxa *Pterospathodus celloni*, *P. pennatus* and *P. angulatus* are conspecific and all are assigned to *P. celloni* (Walliser). *Pterospathodus* species of the *amorphognathoides* Biozone: *P. amorphognathoides* Walliser, *P. procerus* (Walliser) and *P. rhodesi* Savage, are distinguished from *P. celloni* by the presence of platform ledges. There are no major differences between sinistral and dextral elements within any of these species.

SPECIES of the genus *Pterospathodus* are characteristic and biostratigraphically important constituents of upper Llandovery and lowermost Wenlock conodont faunas worldwide. They were first described from the Silurian sequence exposed at Mount Cellon in the Carnic Alps of Austria by Walliser (1964), who applied the generic name to a single species, *Pterospathodus amorphognathoides*. Other taxa that Walliser assigned initially to *Spathognathodus* (*S. celloni*, *S. pennatus angulatus*, *S. pennatus pennatus*, *S. pennatus procerus*) and then to a new genus, *Llandoverygnathus* (Walliser 1972), were subsequently confirmed to be close relatives of *P. amorphognathoides* and transferred to *Pterospathodus* (Klapper and Murphy 1974). The three subspecies of *P. pennatus* were given specific status by Bischoff (1986). The stratigraphic value of this group of species was emphasized by Walliser (1964), who included successive *celloni* and *amorphognathoides* biozones in his pioneer conodont zonal scheme for the Silurian System. These two zones have been recognized over a wide geographical area (see e.g. Jeppsson 1987) in strata of early Telychian to earliest Sheinwoodian age, with the range of *P. amorphognathoides* particularly important in bracketing and aiding correlation of the base of the Wenlock Series (Mabillard and Aldridge 1985). There have been suggestions that morphological changes between sequential populations of the *Pterospathodus* species may provide a basis for subdivision of the zones and hence for more refined correlation (e.g. Brazauskas 1983, Aldridge and Schönlaub 1989).

Walliser (1964) applied the name *Pterospathodus* to only the platform element of the species *amorphognathoides*, but realized that other elements must have been associated with this in a multi-element apparatus. In particular, he recognized a consistent association with specimens he called *Ozarkodina gaertneri* and combined the two in his 'Conodonten-apparat C', also noting that '*Spathognathodus*' *pennatus procerus* could have occupied the platform position in a similar apparatus. Likewise, '*Spathognathodus*' *celloni*, '*S.*' *pennatus angulatus* and '*S.*' *pennatus pennatus* were alternative platform elements in an apparatus ('Conodonten-apparat B') that also contained specimens of *Ozarkodina adiutricis*. Additional elements of both apparatuses were subsequently identified by Barrick and Klapper (1976), who applied a locational notation to the different element types to indicate their probable relative positions in the apparatus structure (see Sweet 1981). The multi-element reconstructions given by Barrick and Klapper (1976) are as follows:

- a. *Pterospathodus amorphognathoides* Walliser: *P. amorphognathoides* Walliser (Pa element), *O. gaertneri* Walliser (Pb element), *Neoprioniodus triangularis triangularis* Walliser (M element), *N. costatus costatus* Walliser (S element);
- b. *Pterospathodus celloni* Walliser: *P. celloni* (Walliser) (Pa element), *O. adiutricis* Walliser (Pb element), *N. triangularis tenuirameus* (M element), *N. costatus paucidentatus* (S element).

A fifth element in both apparatuses is represented by specimens referred to *Roundya brevialata* Walliser, occupying an Sa/Sb position (Jeppsson 1979; Mabillard and Aldridge 1983); few specimens of this element show true bilateral symmetry. The quinquemembrate reconstructions for the two species are shown in text-fig. 1. The 'S' element of Barrick and Klapper (1976) does not appear to be associated in a transition series with the Sa/Sb element, but is linked with the Pa, Pb and M elements in a 'second transition series' in the sense of Barnes *et al.* (1979). Aldridge (1985) referred to this element as a Pb/M intermediate, but to indicate that it is a distinct element within the apparatus we propose to employ the designation 'Pc'. This element has morphological similarities to elements that have been termed 'Pb' in some genera (e.g. *Icriodella*).



TEXT-FIG. 1. The quinquemembrate apparatuses of *Pterospathodus celloni* and *P. amorphognathoides*, all specimens $\times 40$. A–F, *P. celloni* (Walliser) from horizon 10J, Cellon Section, Carnic Alps, Austria (see Walliser 1964, pl. 1); A, B, lateral and upper views of Pa element, specimen $\times 1066$; C, lateral view of Pb element, specimen $\times 1067$; D, lateral view of Pc element, specimen $\times 1068$; E, lateral view of M element, specimen $\times 1069$; F, posterior view of Sa/Sb element, specimen $\times 1070$. G–L, *P. amorphognathoides* Walliser from sample 127/5, Wych Formation, Birches Farm Lane, West Malvern, England, NGR SO 7603 4685; G, H, lateral and upper views of Pa element, specimen $\times 1071$; I, lateral view of Pb element, specimen $\times 1072$; J, lateral view of Pc element, specimen $\times 1073$; K, lateral view of M element, specimen $\times 1074$; L, posterior view of Sa/Sb element, specimen $\times 1075$. Repository of specimens: British Museum (Natural History), London.

There have been suggestions that other elements were also included in the *Pterospathodus* apparatus. In particular, Jeppsson (1979) considered the plexus of elements normally referred to multi-element *Carniodus carnulus* Walliser to be additional components. There are strong reasons for this suggestion: *Carniodus* and *Pterospathodus* are consistent associates, especially in the *amorphognathoides* Biozone, and morphological developments in the two genera were also sometimes concurrent. For example, the acquisition of ledges beneath the denticle rows of the Pa and Pb elements is one character that separates *Pterospathodus* taxa of the *amorphognathoides* Biozone from those of the preceding *celloni* Biozone; some associated *Carniodus* elements show a contemporaneous development of similar ledges. However, the evidence of association is less compelling for *Pterospathodus* species of the *celloni* Biozone, where *Carniodus* is often only

represented by very small numbers of specimens. For example, Walliser (1964, table 2) recorded only sporadic *Carniodus* elements in the *celloni* Biozone of the Carnic Alps, whereas they are present in all samples from the *amorphognathoides* Biozone. Other comparable records include those of Aldridge (1972, tables I–IV), who found only 13 *Carniodus* elements in samples with 223 Pa specimens of *P. celloni* and *P. pennatus*, and of Barrick and Klapper (1976, table 1), whose sample with 61 Pa elements of *P. celloni* contained only one *Carniodus* specimen. Klapper and Murphy (1974, p. 28) considered the possibility that *Carniodus* elements should be included in the *P. celloni* apparatus, but concluded that such a speculation was not supported by their material from Nevada. The available evidence thus suggests that the apparatus of *Carniodus* is separate from that of *Pterospathodus*.

However, more recently Bischoff (1986) has suggested that one of the elements normally referred to the *Carniodus* apparatus, *Neoprioniodus subcarnus* Walliser, is in fact the M element of *P. celloni*. This conclusion is based on his assignment to a similar element of the M position of a presumed direct ancestor of *P. celloni*, *P. cadiaensis* Bischoff. The distributional evidence from the Carnic Alps, Britain and Oklahoma, cited above, is inconsistent with this proposal, as are the strong morphological similarities between '*N. subcarnus*' and the other elements of the *Carniodus* apparatus (see Walliser 1964; Barrick and Klapper 1976). It is pertinent to note that Bischoff (1986) retained M elements of the '*Neoprioniodus triangularis*' type in the apparatuses of *P. pennatus* and *P. amorphognathoides*. If '*N. subcarnus*' should be shown to be an element of *Pterospathodus*, it is more likely to have occupied an Sc than an M position.

The *P. celloni*/*P. pennatus* group has long been considered to be directly ancestral to *P. amorphognathoides* (e.g. by Walliser 1964), but the evolutionary transition has never been fully documented. Rich new collections from continuous upper Llandovery and lower Wenlock sequences are now available from Estonia, allowing description and re-evaluation of the changes displayed by *Pterospathodus* populations through this interval.

STRATIGRAPHIC SEQUENCES WITH *PTEROSPATHODUS* FAUNAS

Estonia

Specimens of the types previously referred to the three taxa *P. celloni*, *P. pennatus* and *P. amorphognathoides* are common in Estonia. They occur in the Velise Formation of the Adavere Stage (upper Llandovery) and the lowermost beds of the Jaani Stage (lower Wenlock). This stratigraphic interval represents a major marine transgression, during which open-shelf grey-green marlstones with rare carbonate nodules and muddy marlstones were deposited. Occasional carbonate interbeds occur in the lower part of the Velise Formation (text-fig. 2). Abundant conodont elements have been recovered from all lithologies.

The most complete sequence of samples is from the Jõhve borehole in western Estonia. Here, the *celloni* Biozone spans 25 m (85.0–60.0 m) and the *amorphognathoides* Biozone 13 m (60.0–47.0 m). Thirty-one samples have been examined from this section (text-fig. 2). The dip is close to horizontal, so the borehole thicknesses represent true sediment thicknesses. Beneath the lowest occurrence of *P. celloni*, conodont specimens are fragmentary and sparse, but above the last *P. amorphognathoides* conodonts continue to occur in abundance. Small specimens of *O. sagitta rhenana* (Walliser), a stratigraphically important lower Wenlock subspecies (see Aldridge and Schönlaub 1989), are found sporadically from 40.2 m upwards.

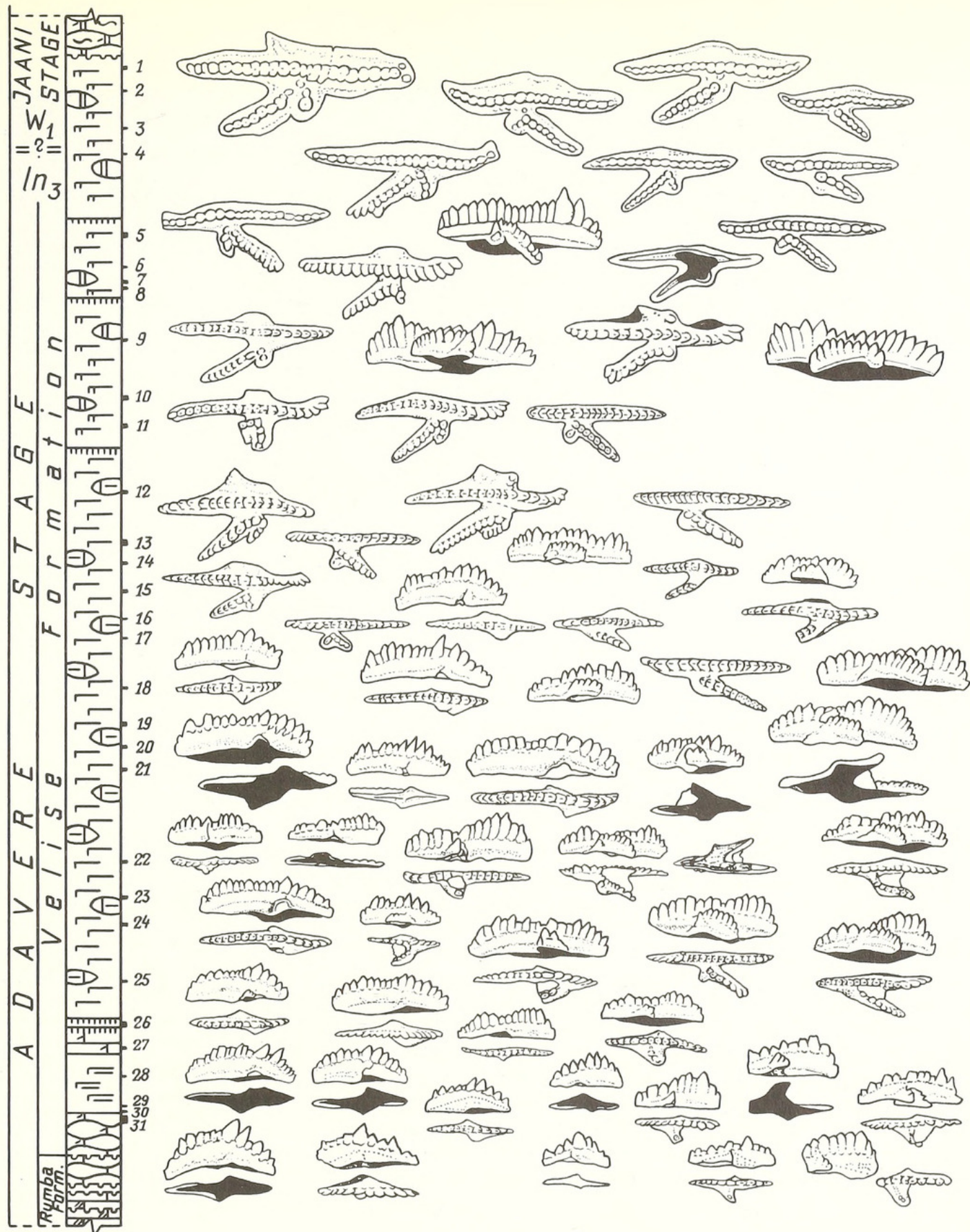
The greatest morphological variation in the *Pterospathodus* types is shown by the Pa elements. These may be broadly categorized as of '*celloni*', '*angulatus*', '*pennatus*', '*procerus*' or '*amorphognathoides*' morphology. The '*celloni*' forms lack denticulate lateral processes, the pennate ('*angulatus*', '*pennatus*' and '*procerus*') forms have a single or double branched lateral process, and the '*amorphognathoides*' forms have a double branched process (text-fig. 3). We follow Barrick and Klapper (1976) in regarding the side bearing the process as the outer side. Where two branches are present, the posterolateral one is always much the shorter. In typical specimens

of *P. amorphognathoides* and of those referred to *P. pennatus procerus*, a ledge-like platform is developed beneath the denticle row on the blade and on the lateral process; in *P. pennatus procerus* the process has only one branch. There is some difficulty in distinguishing between specimens of 'celloni' and 'pennatus' in which the lateral flare or process has been damaged or lost, but otherwise most specimens can be readily categorized. The numbers of each type in each of the thirty-one borehole samples are given in Table 1.

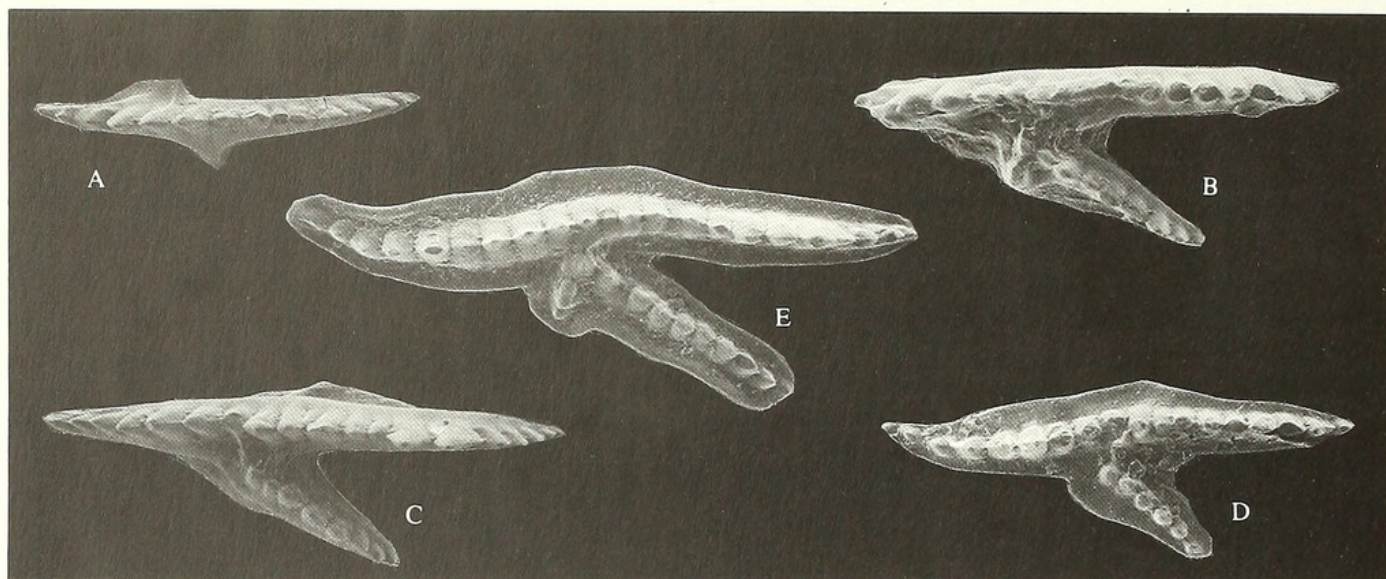
TABLE 1. Numbers of sinistral and dextral specimens of the 'celloni', pennate and 'amorphognathoides' morphotypes of *Pterospathodus* in the Jöhve borehole sequence

Sample	Depth (m)	celloni		pennate		amorphognathoides	
		sinistral	dextral	sinistral	dextral	sinistral	dextral
1	47.05-47.15					5	9
2	47.90-48.00				2	12	12
3	49.25-49.35			1	1	9	2
4	50.15-50.25			4	1	35	47
5	53.00-53.20					19	24
6	54.20-54.30				1	14	21
7	54.70-54.85					22	23
8	54.90-55.05			5		16	16
9	56.80-56.90					2	11
10	58.80-59.00					3	1
11	59.80-59.95					4	8
12	62.25-62.35	?		6	8		
13	64.00-64.20	1		1	1		
14	64.80-64.90	22	6	1	9		
15	65.80-65.90	4	2		3		
16	66.80-66.90	20	10	4	12		
17	67.50-67.60	5	3	1	5		
18	69.30-69.40	24	10	1	17		
19	70.55-70.70	10	4		3		
20	71.40-71.50	17	5		9		
21	72.20-72.30	30	16	2	23		
22	75.50-75.60	32	9	2	9		
23	76.80-76.90	52	14	6	38		
24	77.80-77.90	19	8	3	22		
25	79.80-79.90	44	9	14	32		
26	81.30-81.50	82	28		32		
27	82.20-82.30	152	102		41		
28	83.25-83.30	1					
29	84.30-84.40	8	6		2		
30	84.50-84.60	8	4		7		
31	84.70-85.00	5	2		6		

Representative specimens of *Pterospathodus* Pa elements through the Jöhve borehole are shown in text-fig. 2. Some general trends are apparent: primarily an increase in size, in lateral process development and in platform development up the sequence. Pennate elements occur throughout the *celloni* Biozone, but are represented predominantly by 'angulatus' morphotypes in the lower part and 'pennatus' morphotypes towards the top. Some of the higher 'pennatus' specimens display an incipient second branch to the lateral process in the form of a small lobe bearing a single nodose denticle. In the uppermost beds a characteristic pennate morphotype is present with wider, broader lips to the basal cavity and a double branched outer lateral process in which both the longer and shorter branches are directed somewhat anteriorly.



TEXT-FIG. 2. Sample horizons in the Jõhve borehole, west-central Estonia, and examples of the Pa elements of *Pterospathodus* through the sequence; scale 1 cm = 2 m. Lithological key: 1, clayey marl; 2, calcitic marl with nodules of argillaceous mudstone; 3, dolomitic mudstone with dolomite nodules; 4, fine bioclastic nodular limestone with trace fossils; 5, fine bioclastic nodular limestone; 6, nodular limestone; 7, fine to coarse bioclastic limestone; 8A, discontinuity surface; 8B, metabentonite; 9, sample horizon.



TEXT-FIG. 3. Morphotypes of *Pterospathodus* Pa elements represented in the Jõhve borehole, all upper views $\times 50$. A, 'celloni', specimen Cn 5052, 82.2–82.3 m; B, 'angulatus', specimen Cn 5053, 77.8–77.9 m; C, 'pennatus', specimen Cn 5054, 77.8–77.9 m; D, 'procerus', specimen Cn 5055, 47.9–48.0 mm; E, 'amorphognathoides', specimen Cn 5056, 47.9–48.0 m. Repository of specimens: Institute of Geology, Tallinn.

The Pa elements in individual apparatuses of the 'celloni'/'pennatus' types did not form mirror-image pairs. In sinistral elements the blade is characteristically arc-shaped in lateral view, with the higher denticles towards the posterior end. Some specimens have well-developed cusps. In the upper part of the *celloni* Biozone, where the specimens are larger, the denticles are somewhat lower in the middle of the blade and higher at each end. Many of the sinistral specimens are broken, but it is nevertheless apparent that pennate forms are relatively rare. Dextral elements differ from the sinistral forms in that the higher denticles are at the anterior end of the blade. The denticle row is lowest at the point of junction with the outer lateral lobe or process. The inner lateral lobe is less prominent than in sinistral forms and is lacking in some specimens. Although again several specimens are broken, it is noteworthy that the majority of elements with a well-developed and preserved pennate process are of the dextral form. This pattern is evident throughout the *celloni* Biozone (Table 1), with pennate morphologies being represented by only dextral specimens in the lower part.

Dextral specimens broadly resembling the Pa element of *P. amorphognathoides* occur as low as sample 25 and become more common from sample 16 upwards. The first true *P. amorphognathoides* Pa elements, with clearly-developed though very narrow platform ledges, are found in sample 11, showing that the base of the *amorphognathoides* Biozone should be placed between samples 11 and 12. Throughout the *amorphognathoides* Biozone there are sporadic occurrences of single branched specimens of the 'procerus' morphotype. Elements of both types show an increase in maximum size and a gradual widening of the platform ledges through the biozone. A similar sequence has been reported from Lithuania by Brazauskas (1983), who referred the stratigraphically lower, smaller 'amorphognathoides' forms with narrow platforms to *P. amorphognathoides lithuanicus* Brazauskas, and the stratigraphically higher, larger and broader forms to *P. amorphognathoides amorphognathoides* Walliser. In the Jõhve borehole, the highest specimens are very large, with broad platforms and incipient inner lateral processes. The disappearance of *Pterospathodus* in the sequence is very abrupt and no specimens occur above 47 m. Elsewhere in Estonia, and in Lithuania, especially where the sediments indicate a deeper water environment, the highest broad platforms are succeeded for a short interval by small pennate specimens with narrow platforms, before final disappearance of the *Pterospathodus* lineage.

In contrast to the elements of the *celloni* Biozone, there is no clear disparity in the development

of lateral processes on sinistral and dextral *amorphognathoides* Biozone specimens. In *P. amorphognathoides* both sinistral and dextral forms have relatively high denticles at the anterior end of the blade, although these tend to be more prominent on the dextral member.

Mount Cellon, Carnic Alps, Austria

The type specimens of all the *Pterospathodus* taxa named by Walliser (1964) are from the Silurian sequence exposed on Mount Cellon in the Carnic Alps. Here, the *celloni* Biozone is represented by just 2.4 m of strata and the *amorphognathoides* Biozone is only 1.2 m thick (Walliser 1964). It is possible that the lowest samples with *P. celloni* do not represent the bottom of the stratigraphic range of the species, as they overlie a hiatus in the succession (Schönlaub 1971). However, the tables presented by Walliser (1964) record *P. celloni* specimens only in the upper 1.5 m (samples 10–10J) of the zone. Within this interval, the lowest beds contain 'celloni' morphotypes and, in a single sample (10B), pennate specimens of the 'angulatus' morphotypes. Walliser (1964, p. 79) recovered 22 pennate specimens from this level, but did not give relative numbers of sinistral and dextral forms. His illustrations (Walliser 1964, pl. 14, figs. 19–22) show two sinistral and two dextral specimens. The 'celloni' morphotypes illustrated by Walliser (1964, pl. 14, figs. 3–16) and present in samples from Cellon collected by one of us (R.J.A.) show the same clear distinctions in blade morphology between sinistral and dextral specimens as recognized in the Estonian populations. Higher in the *celloni* Biozone (samples 10C/D–10H/J) the 'celloni' morphotype is accompanied by pennate specimens of the 'pennatus' morphotype, but again there is no record of relative sinistral/dextral numbers.

The base of the *amorphognathoides* Biozone at Cellon is sharp, with the lowest Pa specimens of *P. amorphognathoides* showing quite well-developed platform ledges. There is, however, a gradual increase in size up the biozone, accompanied by a broadening of the platform ledges and an increase in the lengths of both branches of the outer lateral process. The upper boundary of the biozone is also sharp. Pennate specimens of the 'procerus' morphotype occur sporadically throughout the biozone, with a single specimen from the topmost sample (12A) showing, in addition to the outer lateral process, a short denticulate inner lateral process directed perpendicularly from the blade (Walliser 1964, pl. 15, fig. 7).

Britain

No complete sequences covering the stratigraphic range of *Pterospathodus* have been recorded from Britain. Scattered samples containing *P. celloni*, mostly in association with pennate morphotypes, have been collected from the upper Llandovery (Telychian) of the Welsh Borderland (Aldridge 1972, 1975). The largest collection is from the Wych Formation of Gullet Quarry in the Malvern Hills (sample Gullet 4 of Aldridge 1972), with a total of 193 well-preserved specimens of the Pa element. Of these, 92 are of the sinistral member, only three of which show any development of an outer lateral process. Of the 101 dextral specimens, 47 have well-developed processes and on a further 5 there is an incipient process. Thus, as in the Estonian material, it appears that some individuals in the *celloni* population must have possessed a pennate dextral Pa element and a non-pennate sinistral element. In the Gullet sample, the pennate forms are close to the 'angulatus' morphotype and the sample is probably from low in the *celloni* Biozone. Differences in blade profile between dextral and sinistral forms are less marked than in the Estonian material, although some dextral specimens do have high denticles at the anterior end.

The boundary between the *celloni* and *amorphognathoides* Biozones is exposed at the international stratotype section for the base of the Wenlock Series at Leasows, Shropshire (Mabillard and Aldridge 1985). Of the *celloni* Biozone, only the uppermost part is represented and Pa elements of the *P. celloni*/*P. pennatus* plexus are relatively scarce and largely broken. However, the pennate forms include a morphotype in which a bifurcating process is separated from the blade by a low, unornamented area (*P. pennatus* subsp. nov. of Aldridge 1985, p. 81, pl. 3.1, fig. 28). Similar specimens were reported by Aldridge (1972, pl. 3, fig. 18) from beds of similar age at the nearby locality of Ticklerton; these were originally identified as *P. amorphognathoides*, but lack the

development of platform ledges diagnostic of that species. A few specimens from Ticklerton have a bifurcating process in which the shorter branch curves to become subparallel to the longer branch, as is also apparent in some specimens from the top of the *celloni* Biozone in Estonia (text-fig. 2, sample 12). Most Ticklerton specimens with well-developed pennate processes are dextral; in sinistral elements lateral processes are lacking or short.

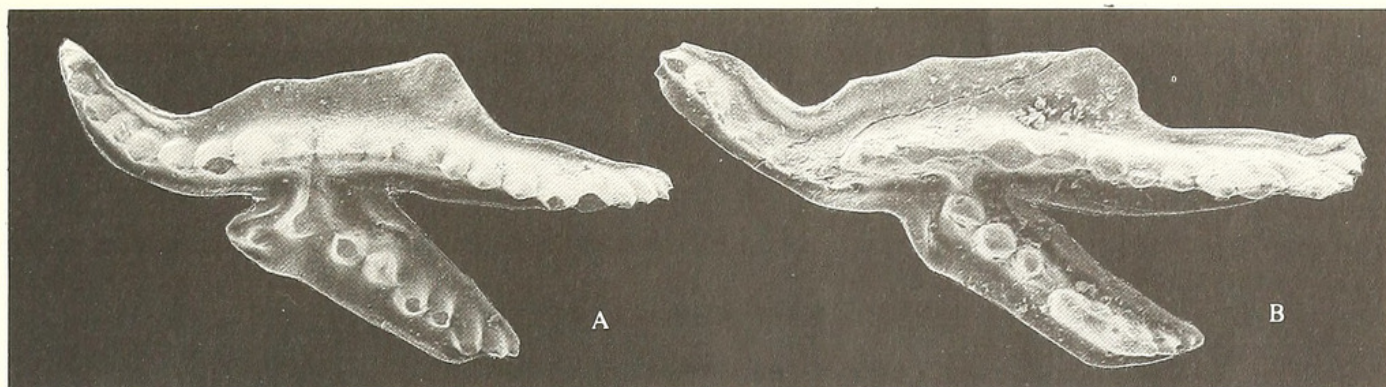
In the Leasows section, Pa elements of *P. amorphognathoides* appear abruptly 70 cm below the top of the Llandovery (Mabillard and Aldridge 1985). The lowest specimens have broad platform ledges and there is little evidence of size increase up-section. The highest specimens of *Pterospathodus* in the sequence, just before the final disappearance of the genus, are all diminutive, as in some Estonian sections. A similar occurrence of small specimens at the top of the range of *P. amorphognathoides* is apparent in collections from the Malvern Hills.

Other areas

Although *Pterospathodus* species of the *celloni* and *amorphognathoides* biozones have been very widely recorded, there are no other successions that have been collected or reported in sufficient detail to determine if the sequence of events documented above is repeated elsewhere. Some records, however, do corroborate parts of the story. For example, Klapper and Murphy (1974) recorded *P. angulatus* in their lowest samples from the *celloni* Biozone of Nevada, and Jeppsson (1979) found small *Pterospathodus* specimens at the top of the range of the genus in Gotland. In contrast, Nakrem (1986) reported specimens of '*P. pennatus angulatus*' in association with *P. amorphognathoides* in the Vik Formation of the Oslo Region, Norway; the *angulatus* specimens were not illustrated and the record needs to be confirmed. Recent work has also revealed the occurrence of at least one additional species of *Pterospathodus*, first reported as *P. n. sp. A* by Stouge and Bagnoli Stouge (1984) from Hall Land, North Greenland. Other records are from southeastern Alaska (*P. amorphognathoides rhodesi* of Savage 1985), the Northwest Territories, Canada (Over and Chatterton 1987), and New South Wales, Australia (*P. latus* of Bischoff 1986). The Pa element is readily distinguishable from that of *P. amorphognathoides*, with a single-branched outer lateral process, a lobelike, normally adenticulate, inner lateral process, and a very wide platform ledge with upturned margins in mature specimens. Although this morphotype co-occurs with *P. amorphognathoides* and *P. procerus* in Australia and Canada, and with the latter in Alaska and Greenland, it clearly represents a distinct population. The correct name is *Pterospathodus rhodesi* Savage, 1985. The remainder of the apparatus, as reconstructed by the cited authors, is comparable with that of *P. amorphognathoides*. This is confirmed by additional material we have examined from Greenland, where a single sample (GGU 275048 from Valdemar Gluckstadt Land, processed and brought to our attention by Dr H. A. Armstrong) contains bifurcate as well as pennate morphotypes of the Pa element in the population (text-fig. 4).

EVOLUTIONARY IMPLICATIONS

Most of the evolutionary changes shown by the sequence of *Pterospathodus* populations appear to have been gradual. This is shown particularly by the Pa element, the least conservative of those in the apparatus. Upwards through the *celloni* Biozone the relative number of pennate elements increases steadily, with the denticulate process being first developed preferentially by dextral elements. This change is accompanied by a gradual size increase. Pennate specimens with bifurcating outer lateral processes occur in populations of the highest *celloni* Biozone, with the onset of very narrow platform ledges marking the first true populations of *P. amorphognathoides*. Above this, a gradual trend of size increase is again apparent, accompanied by increasing platform ledge development. It is clear throughout that the morphological elaborations are not simply size-dependent, as equivalent specimens from different parts of the sections also reveal the gradual sequence. One probable punctuational event is the appearance in some areas of *P. rhodesi*, which has much broader platform ledges than other coeval morphotypes. The distribution and origins of this taxon are as yet uncertain, but it is unlikely to be very widely spread, as it is unknown from many



TEXT-FIG. 4. Specimens of the Pa element of *Pterospathodus rhodesi* Savage, from sample GGU 275048, Valdemar Gluckstadt Land, North Greenland; both upper views $\times 50$. A, dextral specimen with bifurcate outer lateral process, MGUH 18982; B, dextral specimen with single-branched, pennate outer lateral process, MGUH 18983. Repository of specimens: Geologisk Museum, Copenhagen.

of the areas where *P. amorphognathoides* is common. However, its occurrence on the cratonic margins of Australia and Greenland is of potential importance, as these are regarded as having been of wide longitudinal separation in the early Palaeozoic (Smith *et al.* 1973).

The detailed sequence of populations in Estonia refutes the phyletic relationships within *Pterospathodus* postulated by Bischoff (1986). He proposed that *P. celloni* and *P. pennatus* were members of two separate lineages, the former giving rise to *P. procerus* and the latter to *P. rhodesi* (= *P. latus*). However, we have demonstrated that 'celloni' and 'pennatus' morphotypes occurred as sinistral and dextral elements in the same individuals, and the differing apparatus structures proposed by Bischoff (1986) for these two are not sustainable.

TAXONOMIC AND NOMENCLATURAL IMPLICATIONS

It is clear from our collections that *Pterospathodus angulatus*, *P. celloni* and *P. pennatus* are not separate taxa. We therefore recommend that the species name *celloni* be applied to all *celloni* Biozone populations. It may well be possible to subdivide this species into chronological subspecies, but this should be postponed until the sequence we have recognized has been more widely established and firm criteria for the division documented. We would point out, however, that there are nomenclatural restrictions on the names available for any subspecies: the holotype of *P. pennatus* is from the same sample as that of *P. celloni* (C10J of Walliser 1964) and *pennatus* is evidently a subjective junior synonym of *celloni* at species and subspecies levels. The holotype of *P. angulatus* is from horizon C10B (Walliser 1964), so the subspecies name *angulatus* may be appropriate for low *celloni* Biozone populations containing angulate specimens. Pending a complete taxonomic revision, we recommend that features of *P. celloni* populations are recorded by reference to 'celloni', 'angulatus' and 'pennatus' morphotypes, together with any appropriate terms for additional morphotypes. This may not be an ideal solution, but there are always problems in subdividing lineages that are demonstrably gradual (see e.g. Sheldon 1987, p. 563).

The relationship between *P. amorphognathoides* and *P. procerus* is less obvious. They may genuinely represent separate species or may be different morphotypes in single populations. There is currently no evidence that the two morphotypes coexisted in any single individual, so for the present it is preferable that both names are retained.

The possession of distinct dextral and sinistral Pa elements in *P. celloni* may be considered of sufficient significance for the species to be allotted to a separate genus. However, the evolutionary continuity with *P. amorphognathoides* and the overall similarity of apparatus composition between the two show that *P. celloni* is correctly accommodated in *Pterospathodus*.

BIOSTRATIGRAPHIC IMPLICATIONS

The *celloni* and *amorphognathoides* conodont biozones are among the most widely recognized in the Silurian. Their usefulness can be enhanced by subdivision based on the sequential changes documented here. Thus the *celloni* Biozone comprises a lower part, with 'celloni' and 'angulatus' morphotypes, and an upper part, in which 'celloni' and 'pennatus' morphotypes are joined by various forms with bifurcating outer processes but not platform ledges. The boundaries are gradational and cannot be precisely defined, so we recommend that these subdivisions be used informally.

The base of the *amorphognathoides* Biozone is determined by the first appearance of specimens with platform ledges. This is an important morphological development, both for taxonomy and biostratigraphy. Some authors have considered the development of a bifurcate process to be a more important feature (e.g. Bischoff 1986), but occasional pennate specimens throughout the *celloni* Biozone have a denticle or two on the postero-lateral outer lobe (e.g. the 'angulatus' specimen figured by Walliser 1964, pl 14, fig. 21). By restricting the diagnosis of *P. amorphognathoides* to specimens with ledges, the concept of an *amorphognathoides* Biozone as defined by Walliser (1964) is retained, and there is no need to define new biozones incorporating other taxa (e.g. the *Pterospathodus amorphognathoides* - *P. latus* Assemblage Zone of Bischoff 1986).

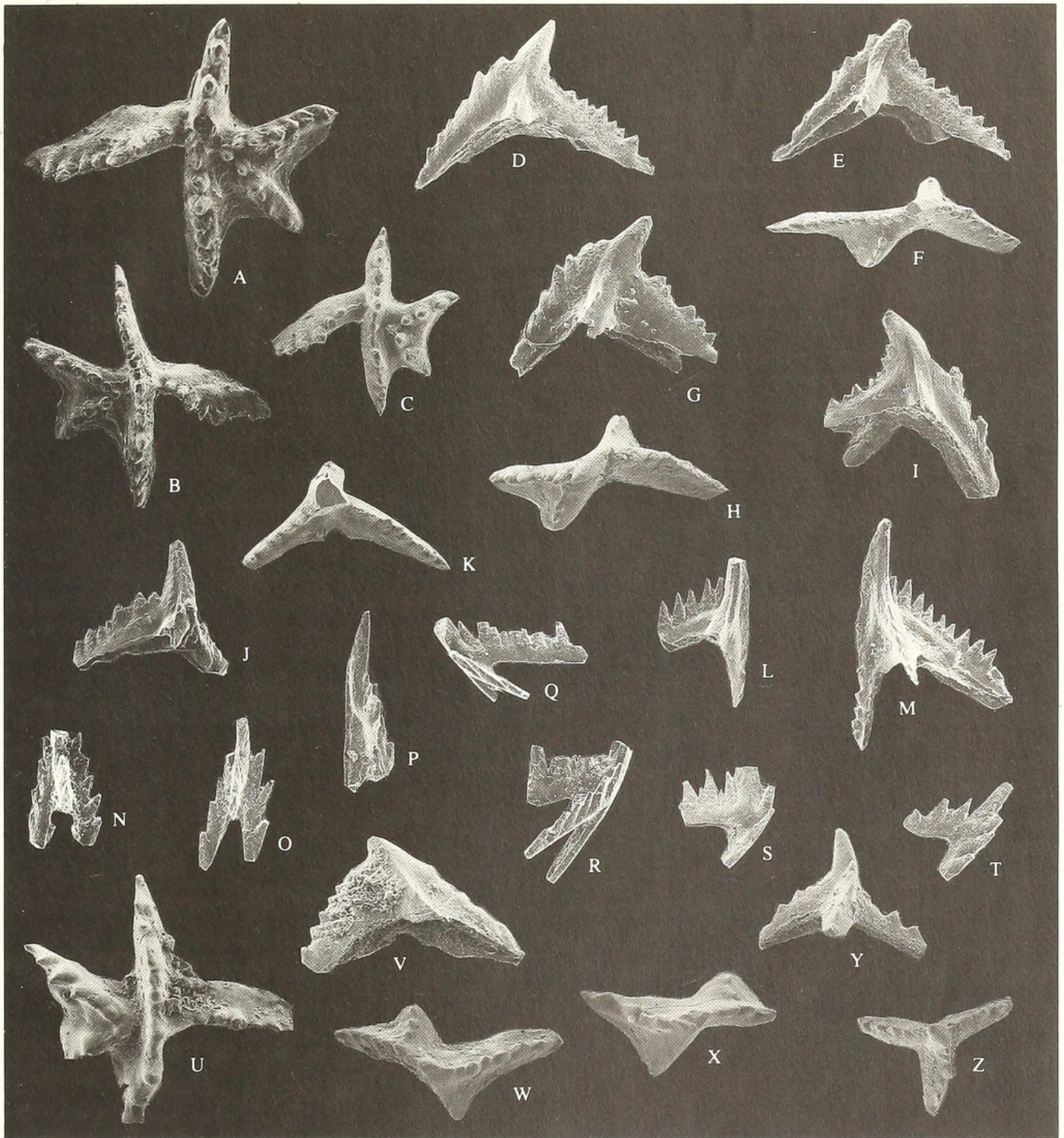
Within the *amorphognathoides* Biozone, the degree of development of platform ledges in mature forms generally increases upwards, and can be used to recognize relative position within the biozone. It may appear possible to use the subspecies proposed by Brazauskas (1983) to define a lower, *lithuanicus*, subzone and an upper, *amorphognathoides*, subzone, but the division between the two is arbitrary and cannot provide a consistently recognizable boundary. The top of the *Pterospathodus* range can often be identified by the occurrence of diminutive specimens. This last population, if widely recognized, may merit separate taxonomic status and may provide the basis for a useful biozone or subzone.

ORIGINS AND RELATIONSHIPS OF *PTEROSPATHODUS*

Several Llandovery species that precede the appearance of *P. celloni* have been assigned by some authors to the genus *Pterospathodus*. Among these, *P. cadiaensis* Bischoff was regarded by Bischoff (1986) as a direct ancestor of *P. celloni*. The Pa element of *P. cadiaensis* (Bischoff 1986, pl. 28, figs. 13, 17-25) has a similar lateral profile to specimens of *P. celloni* and comparable offset lateral lobes, but differs in the larger size and smaller number of denticles and in the more extensive basal cavity. A close relationship is possible, although the remainder of the elements assigned to the *P. cadiaensis* apparatus by Bischoff do not distinctly resemble their counterparts in *P. celloni*.

A further group of species comprises those originally designated *Aphelognathus siluricus* by Pollock *et al.* (1970), *Amorphognathus tenuis* by Aldridge (1972) and *Pterospathodus posteritenuis* by Uyeno and Barnes (1983). Partial apparatus reconstructions have been published for all these taxa, the most complete being that of *P. posteritenuis* by Uyeno and Barnes (1983, pl. 2, figs. 1-11, 14-18). The apparatus of *A. tenuis* is illustrated in text-fig. 5, from rich and well-preserved collections from Severnaya Zemlya and Britain. The three species differ principally in the development of lateral processes on the Pa element, and it is probable that the complete apparatuses of them all were comparable. The Pa, Pb, Pc and M elements can be readily homologized with those of *P. amorphognathoides*, but show several differences, one being the development of deep, broad cavities in the Pa and Pb elements. A further departure from *P. amorphognathoides* is the presence of an entire first symmetry transition series of Sa-Sc elements. Uyeno and Barnes (1983, p. 25) noted that for *P. posteritenuis* this series is remarkably complete, and we recognize a closely comparable suite of elements in *P. tenuis*. These observations contrast with the severely reduced first series in *P. celloni* and *P. amorphognathoides*, where only an Sa/Sb element has been identified.

Although an ancestor of *P. celloni* may exist within this group, the three species share characteristics of element morphology and apparatus composition that set them apart from true



TEXT-FIG. 5. *Pranognathus tenuis* (Aldridge), all $\times 50$. A–T from sample 159–2 from the lower part of the Vodopadnaya Formation exposed in the Spokoinaya River, October Revolution Island, Severnaya Zemlya; A–C, upper views of Pa element, specimens Cn 5057, Cn 5058, Cn 5059; D, lateral view of Pb element, specimen Cn 5060; E, F, lateral and upper views of Pb element, specimen Cn 5061; G, H, lateral and upper views of Pb element, specimen Cn 5062; I, lateral view of Pb element, specimen Cn 5063; J, lateral view of Pc element, specimen Cn 5064; K, upper view of Pc element, specimen Cn 5065; L, M, inner lateral views of M element, specimens Cn 5066, Cn 5067; N, O, posterior views of Sa element, specimens Cn 5068, Cn 5069; P, posterior view of Sb element, specimen Cn 5070; Q, R, lateral views of Pb element, specimens Cn 5071, Cn 5072; S, lateral view of Sc₂ element, specimen Cn 5073; T, lateral view of Sc₁ element, specimen Cn 5074. U–Z from sample 40/3, lower Pentamerus Beds of New House Farm, Marshbrook, near Church Stretton, Shropshire, England, NGR SO 4341 8982; U, upper view of Pa element, specimen $\times 1076$; V, W, lateral and upper views of Pb element, specimen $\times 1077$; X, upper view of Pb element, specimen $\times 1078$; Y, Z, lateral and upper views of Pc element, specimen $\times 1079$. Repositories of specimens: Institute of Geology, Tallinn (A–T); British Museum (Natural History), London (U–Z).

Pterospathodus. We propose that they be allocated to a separate genus, *Pranognathus*, with a type species of *Amorphognathus tenuis* Aldridge.

Another species that shares common features with *Pterospathodus* and *Pranognathus* is *Icriodella? sandersi* Mabillard and Aldridge (1983, p. 33, pl. 2, figs. 1–10). The apparatus structure is closer to that of *Pterospathodus*, but a distinct Pb (as against Pc) element is lacking, as in other species of *Icriodella*, such as the Ordovician *I. superba* Rhodes as reconstructed by Bergström and Sweet (1966, p. 337, pl. 29, figs. 1–11). Similarities between the apparatuses of *Pterospathodus* and *Icriodella* were pointed out by Mabillard and Aldridge (1983), and Cooper (1977) suggested that *Icriodella* was ancestral to *Pterospathodus*, but it is impossible to demonstrate a direct link between the two.

An alternative Ordovician ancestor of *Pterospathodus* is *Amorphognathus*. Jeppsson (1979) drew comparisons between the two genera, emphasizing similarities in the Pa elements. He also noted that in *Amorphognathus* the Pa element pairs do not form mirror images, an interesting point in the light of our observations on *P. celloni*. However, there are considerable differences in the remainder of the apparatus, *Amorphognathus* having a complete four-element Sa-Sd first transition series, but only a three-element second transition series (see Bergström 1971). Greater similarity is shown by the late Ordovician *Gamachignathus* (McCracken *et al.* 1980), which has a three-element first transition series and a four element second series, the latter differing from *Pranognathus* in having two types of M element and no Pc (or no Pb) element. In this respect, the *Gamachignathus* apparatus possibly compares with that of early Silurian species of *Icriodella*, for example *I. discreta* Pollock *et al.* (see Aldridge and Mohamed 1982, pl. 1, figs. 11–15).

It is evident that *Pterospathodus*, *Pranognathus* and, possibly, Silurian species of *Icriodella* shared a common ancestor, but in the absence of an Ordovician species with homologous Pa, Pb, Pc and M elements this ancestry remains cryptic. The same is true of other early Silurian genera that have been included in the family Pterospathodontidae: *Astropentagnathus*, *Aulacognathus* and *Apsidognathus* (Cooper 1977; Klapper 1981). Complete apparatus reconstructions of *Astropentagnathus* and *Aulacognathus* have yet to be published, while the internal relationships of the elements of *Apsidognathus* are uncertain.

SYSTEMATIC PALAEOLOGY

Genus PRANOGNATHUS gen. nov.

Derivation of name. From the initial letters of Pollock, Rexroad and Nicoll, the authors who first described elements of this genus.

Type species. *Amorphognathus tenuis* Aldridge, 1972, from the Pentamerus Beds (Aeronian Stage, Llandovery Series) of south Shropshire, England.

Diagnosis. Apparatus octomembrate, with Pa, Pb, Pc, M, Sa, Sb, Sc₁ and Sc₂ elements. Pa, Pb and Pc elements with broad, deep basal cavities and low cusps; Pa with lateral lobes that may be developed into denticulate processes; Pb pastinate, Pc pyramidal with a triangular base. M element with a prominent cusp and long, denticulate posterior process, S elements with short processes.

Discussion. The first description of elements here referred to *Pranognathus* was by Pollock *et al.* (1970), who described *Aphelognathus siluricus* and *Ambalodus anapetus* from the northern Michigan and Ontario area. A partial reconstruction was provided by Cooper (1977, p. 1064), who recognized Pa, Pb, 'M' (= Pc) and 'S' (= Sa) elements, which he assigned to *Llandoverygnathus siluricus* (Pollock *et al.*). Uyeno and Barnes (1983) recognized the true M element of this species, but the apparatus is probably as yet not completely known. As a complete first symmetry transition series of Sa-Sc elements has yet to be demonstrated, there is possible doubt that *Pranognathus siluricus* conforms fully to the diagnosis above. Therefore, we have chosen to designate *A. tenuis* as the type species.

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