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## NATURAL ASSEMBLAGES OF *PALMATOLEPIS* FROM THE UPPER DEVONIAN OF THE NORTHERN URALS

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Two bedding-plane assemblages from the Upper Devonian (lower Famennian, Upper *triangularis* Zone) of the Evtropiny Noski section on the Unya River in the northern Urals are of extraordinary significance for the controversial question of the structure of the *Palmatolepis* apparatus. The assemblages indicate that some species of *Palmatolepis* were characterized by nothognathellan (Pb), palmatodeltan (M), smithiform (Sc), falcodontan (Sb), and asymmetrical (Sb) and symmetrical (Sa) scutulan elements, in addition to the platform (Pa) element. Thus, earlier views based on fused clusters and statistical analysis are reinforced by the discovery and description of the Unya River specimens. *Palmatolepis* is used as the generic name, because *Palmatodella* is a *nomen dubium*.

**Key words:** conodonts, apparatus reconstruction, Devonian.

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### INTRODUCTION

Knowledge of the elemental composition of Devonian conodont apparatuses can still be regarded as in a relatively early stage. Although a number of reconstructions based on isolated specimens from Devonian carbonate residues have been postulated (e.g. Ferrigno 1968; Klapper and Philip 1971, 1972; Ziegler 1972; Klapper and Murphy 1975; Philip and McDonald 1975; Sandberg 1976; Boogaard and Kuhry 1979; Sparling 1980; Nicoll 1980; Pickett 1980; Klapper and Murphy 1980), such reconstructions should be viewed as hypotheses that must be tested against the evidence of fused clusters and especially bedding-plane assemblages. Several fused clusters of Devonian conodonts have been described by Lange (1968),

among which is a cluster composed of ramiform elements and a pair of the platform element, *Palmatolepis* Ulrich and Bassler. Nevertheless, such clusters are subject to various interpretations. Some (e.g. Lange 1968; Klapper and Philip 1972: 100) have accepted the cluster containing the *Palmatolepis* pair as representative of the apparatus of the genus, even though a coprolitic origin for the cluster was acknowledged. Others (e.g. Ziegler 1972: 92), however, have suggested that the coprolitic nature of the cluster need indicate only that the *Palmatolepis* animal was a victim of the same predator that trapped the animal containing the other elements. Thus, fused clusters may perhaps be of equivocal interpretation.

Bedding-plane assemblages would seem therefore to provide the best confirmation of apparatus reconstructions. Hundreds of specimens of the *Idiognathodus* (= *Scottognathus*) apparatus have been found on the bedding planes of black shale in the Upper Carboniferous (Pennsylvanian, Missourian Stage) at Bailey Falls, near LaSalle, Illinois (Collinson *et al.* 1972) and these provide a model for reconstructions of closely similar Carboniferous genera. In the Devonian, however, only two bedding-plane assemblages have been described previously. A Lower Devonian *Ozarkodina* apparatus, probably close to *O. remscheidensis*, was described and illustrated by Mashkova (1972), and *Hibbardella angulata* (as *Oulodus angulatus*) was described from an Upper Devonian nodule that also showed a single element of *Icriodus* prior to dissolution (Nicoll 1977: fig. 4). Consequently, the discovery of two bedding-plane assemblages containing the dominant Upper Devonian platform element, *Palmatolepis*, is of extraordinary taxonomic significance. The description and implications of these specimens from the northern Urals are the subject of the present paper.

The extremely refined conodont zonation of the Upper Devonian, comprising 27 zones, is largely based on evolution in the genus *Palmatolepis*, the species of which define and characterize the majority of the zones. At present about 40 form species (and numerous form subspecies) of *Palmatolepis* are recognized in a taxonomic concept based on morphologic changes in the platform (Pa) element. Some taxonomists consider this element to have been the only component of a unielemental apparatus (e.g. Ziegler 1972; Sandberg and Ziegler 1979), a concept apparently strengthened by the excessive dominance of the palmatolepan element in some insoluble residues from the Upper Devonian. It should be emphasized, however, that a shift to a multielement concept of *Palmatolepis* will not necessarily alter the present taxonomy at the specific and infraspecific levels. This is so because morphologic changes in the most rapidly evolving element of the apparatus should be expressed in a purposeful taxonomy that reflects the phenomenon of mosaic evolution in conodonts. Thus multielement taxonomy, if it emphasizes evolution of the Pa element for infrageneric taxonomy, can parallel the previous form-species concept of *Palmatolepis*.

## LOCALITY AND STRATIGRAPHY

Upper Devonian (Lower Famennian, Upper *triangularis* Zone) bedding-plane assemblages of the conodont genus *Palmatolepis* were collected by V. N. Puchkov in 1972 from the western limb of the Evtropiny Noski section (Puchkov 1979: 45—48), situated on the right bank of the Unya River, approximately 200 m downstream from the mouth of Evtropina Creek. The Unya River is a tributary of the upper reaches of the Pechora River on the western slope of the northern Urals (fig. 1). The Upper Devonian strata of the Evtropiny Noski section are within the Malopechora facies zone and were assigned to the Evtropina Formation (or Svita) and interpreted as a relatively deep-water, bathyal sequence by Puchkov (1974).

The Evtropiny Noski outcrop (Puchkov 1979; fig. 3) is about 330 m in length and is formed by a simple, wide syncline, the eastern limb of which is faulted just to the east of the synclinal axis. The sequence in the western limb of the syncline extends from the *gigas* Zone (Frasnian) to the *rhomboidea* Zone (early Famennian), according to Puchkov (1979), and contains the natural assemblage specimens 0.5 m above the base of unit 7. The stratigraphy of both limbs of the syncline has been described previously (Puchkov 1979: 45—50), but it seems necessary here to give an English version of the description of the western limb only. The section is described going stratigraphically upwards to the east, in an upstream direction (fig. 1). The conodont identifications are by Puchkov (1979) and those of other fossils are by specialists cited in the following text. All conodont identifications are based on platform (Pa) elements.

1. Unit 1 consists of grey, dark grey, bluish, pinkish, and brownish banded, platy cherts divided by thin interlayers of clay material. The bedding planes commonly are uneven and knobby. There are abundant radiolarians. Unit thickness is 8 m. At 1 m above the base, the following conodonts were found: *Palmatolepis* sp. cf. *P. provera* Ziegler, *Ancyrodella* sp., and *Polygnathus* sp.

2. 6 m unexposed.

3. Unit 3 consists of banded, platy cherts like those of unit 1. The color of the upper 1 m acquires a slightly greenish-grey tint. Thickness is 9.5 m. At 3 m below the top, the following conodonts were found: *Palmatolepis subrecta* Miller and Youngquist and *P. hassi* Müller and Müller.

4. 17 m unexposed.

5. Unit 5 consists of thin and thick, banded, platy cherts and phthanites. The cherts are light and dark grey, greyish green, and green, with thin (up to 2—3 cm thick) intercalations of argillite. On the even bedding surfaces conodonts may be seen as well as relatively well-preserved radiolarians. Unit thickness is 19 m. At 6 m above the base, the following conodonts occur: *Palmatolepis subrecta*, *P. hassi*, *P. sp. cf. P. foliacea* Youngquist, and *Ancyrodella nodosa* Ulrich and Bassler. In the top bed there are: *Palmatolepis gigas* Miller and Youngquist, *P. subrecta*, *P. hassi*, *P. sp. cf. P. foliacea*, and *Ancyrognathus* sp. aff. *A. inequalis* (Holmes), and the radiolarians: *Entactinia* sp. and *Entactinisphaera* sp. aff. *E. cancellicula* (Foreman) (the work on radiolarians of this sections has been done by B. B. Nazarov, GIN Acad. Sci., USSR).

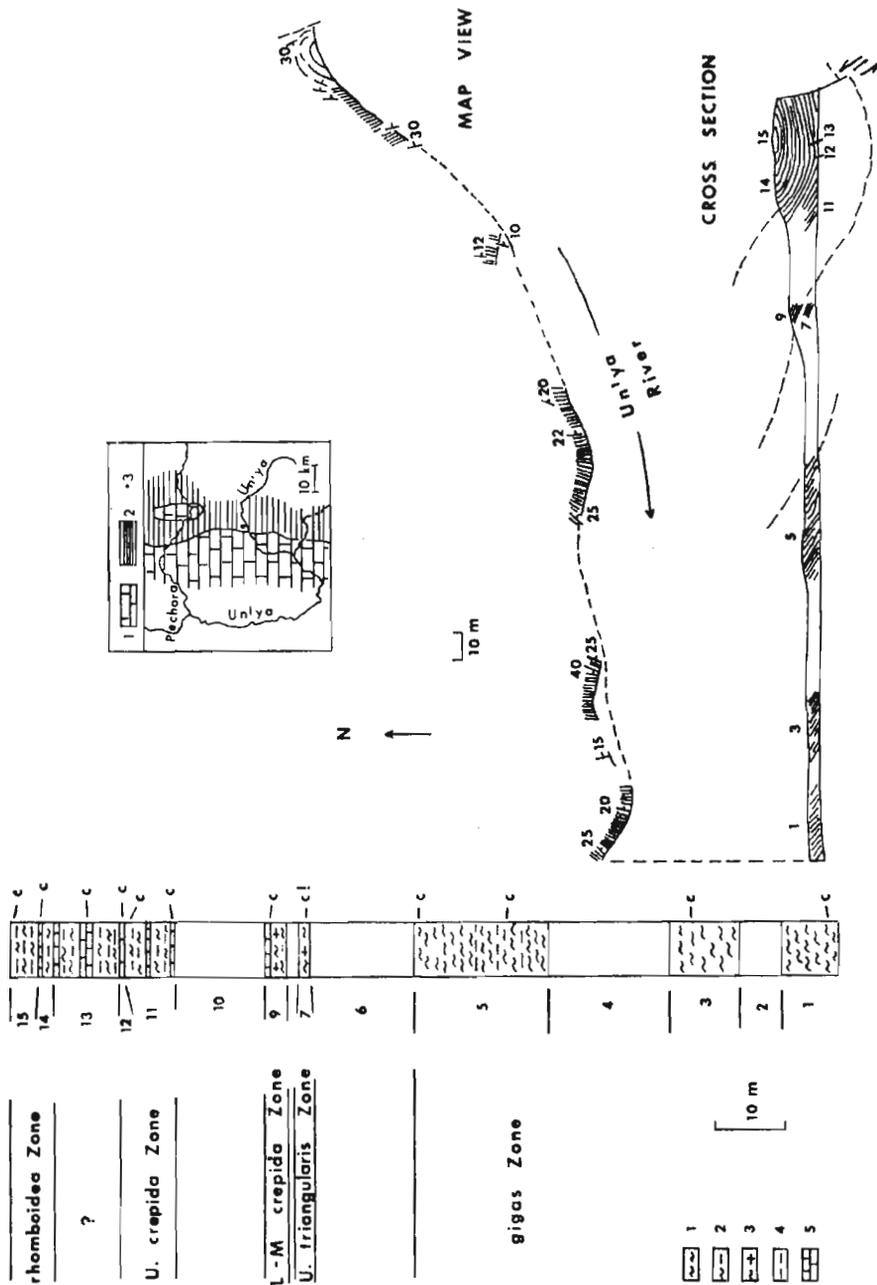


Fig. 1. Western limb of syncline of the Evtropilny Noski section, Unya River, northern Urals. Small map at top shows location of section (3) on Unya, a tributary of the upper reaches of the Pechora River; symbol (1) indicates distribution of Upper Devonian carbonate-terrigenous neritic facies, (2) the distribution of chert-clay-carbonate bathyal facies. The western limb of the syncline is shown in both cross section (below) and map view (with dip readings indicated, degrees omitted); the eastern limb was described and illustrated by Puchkov (1979). Unit numbers on left of columnar diagram are also shown on cross section. Generalized lithologic symbols are as follows: 1) thick, platy cherts, with thin layers of argillite; 2) thin, platy cherts and cherty shales, with thin layers of argillite; 3) fine alternations of cherts, shales, and thin limestones; 4) argillite; 5) foraminiferal limestones. Conodont zones to left and position of conodont faunas discussed in text, indicated to right of column. Assemblages from unit 7 are the subject of the present paper. Drawings modified after Puchkov (1979: fig. 3).

Units 1—5, with a total thickness of 60 m, contain associations of conodonts characteristic of the *gigas* Zone (Ziegler 1971) of the Frasnian Stage or Mendym (Lyayol) Horizon of the Volgo-Uralian region (Ovnatanova 1972), according to Puchkov (1979: 47).

6. 15 m unexposed.

7. Unit 7 comprises green argillaceous and cherty shales and platy cherts, alternating with thin intercalations of green cherts and white limestones (thickness of chert layers: 1—1.5 cm; thickness of limestones — a few millimeters). Total thickness of unit 7 is 1.5 m. At 0.5 m above the base the following conodonts were found: *Palmatolepis triangularis* Sannemann, *P. tenuipunctata* Sannemann, *P. minuta minuta* Branson and Mehl, *P. sp. cf. P. regularis* Cooper, and *Ancyrognathus* sp., as well as the two natural assemblages of *Palmatolepis* described in this paper. All the conodonts were found at approximately the same level on surfaces of the argillaceous, cherty shales and cherts. The association is that of the Upper *triangularis* Zone (Ziegler 1962) of the Lower Famennian (Bouckaert and Ziegler 1965; Ziegler 1971).

8. 2 m unexposed.

9. Unit 9 consists of dark green, greyish or brownish green argillaceous, cherty shales, thin intercalations of green cherts and white limestones, and some layers of black foraminiferal limestones. The latter are up to 15 cm thick and are commonly nodular, somewhat argillaceous, fine crystalline, and contain 30—40% tests of simple unilocular Foraminifera. Unit 9 is 3 m thick. At 80 cm below the top an association of conodonts has been obtained from a limestone layer: *Palmatolepis triangularis*, *P. quadrantinodosalobata* Sannemann, *P. perlobata* Ulrich and Bassler, *P. tenuipunctata*, *P. minuta minuta*, *P. crepida* Sannemann, *Polygnathus* ex gr. *P. glaber* Ulrich and Bassler, and *Icriodus alternatus* Branson and Mehl, a fauna that indicates the Lower to Middle *crepida* Zone. The Foraminifera from the same level are: *Parathurammia paulis* Bykova, *P. elegans* Poyarkov, and *P. subvasta* Bykova (the Foraminifera of this section have been studied by V. A. Cheremnykh, Institute of Geology, Komi Branch of the Acad. Sci., USSR). At 40 cm below the top on bedding-plane surfaces of shale, the following conodonts were found: *Palmatolepis minuta minuta*, *P. tenuipunctata*, *P. subperlobata* Branson and Mehl, and *P. crepida*. The same layer contains the radiolarian *Entactinia* ex. gr. *E. grandis* Nazarov.

10. 13 m unexposed.

11. Unit 11 includes dark grey to black, dark green, greyish green, argillaceous, cherty shales and platy cherts with layers of foraminiferal limestones, which are fine crystalline, somewhat cherty, and about 20—30 cm in average thickness. Unit 11 is 7 m thick. From a limestone at the base the following conodonts were obtained: *Palmatolepis quadrantinodosalobata*, *P. perlobata perlobata*, *P. tenuipunctata*, *P. sp. cf. P. crepida*, *P. glabra prima* Ziegler and Huddle, *P. subperlobata*, *Polygnathus* ex gr. *P. glaber*, and *Icriodus* sp., indicating the Upper *crepida* Zone. The same layer also contains Foraminifera: *Parathurammia dagmarae* Suleimanov, *P. paracushmani* Reitlinger, *P. crassithec*a (Antropov), and *P. regularis* Chuvashov.

At the top of unit 11 a layer of green shale contains: *Palmatolepis perlobata schindewolfi* Müller, *P. subperlobata*, *P. tenuipunctata*, *P. minuta minuta*, and *P. sp. cf. P. glabra* Ulrich and Bassler. The same layer contains radiolarians: *Spongoentactiinae?* gen. et sp. indet., *Entactinia* sp., *Entactinosphaera* sp. cf. *E. aitpaensis* Nazarov, *Polyentactinia* sp. (*P. ex gr. P. craticulata* Foreman).

12. Unit 12 is a bed of foraminiferal limestone, which is nodular to conglomeratic. The thickness varies, ranging up to 0.6 to 0.7 m. The limestone contains the conodonts: *Palmatolepis quadrantinodosalobata*, *P. perlobata*, *P. tenuipunctata*, *P. minuta minuta*, *P. crepida*, *P. glabra prima*, *P. subperlobata*, *P. sp. cf. P. regularis*, *P.*

*subgracilis* Bischoff, *Polygnathus* ex. gr. *P. glaber*, *P. sp.*, *Icriodus costatus* (Thomas), and *Pelekysgnathus?* sp. The bed also contains the Foraminifera: *Evolutina elementa* Antropov, *Parathurammina paracushmani*, and *Tikhinella* sp.

The conodonts obtained from the intervals 9—12 (totaling 24 m) are characteristic of the *crepida* Zone, those from unit 9 are within the Lower to Middle *crepida* Zone and those from units 11 and 12 are within the Upper *crepida* Zone. The *crepida* Zone corresponds to part of the lower part of the *Cheiloceras* Stufe of the ammonoid scale (II  $\alpha$ , see Ziegler, in Klapper and Ziegler 1979: fig. 7; also Ziegler 1962, 1971; Kononova 1975).

Upward in the section, in the core of the syncline exposed in the steep rock wall are observed:

13. Unit 13 consists of dark grey and brown, argillaceous, cherty shales and phthanites, calcareous argillites, and layers of foraminiferal limestones that in some instances are very cherty. Unit thickness is 9.5 m. At 4 m above the base of unit 13 from a layer of limestone, there were obtained a few conodonts: *Palmatolepis subperlobata*, *P. minuta minuta*, and *P. sp.* cf. *P. glabra?* This association is not precisely zonable.

14. Unit 14 consists of greenish and bluish grey argillaceous, cherty shales with a layer of dense calcareous argillite. At the top of the shales there is a bed of medium crystalline limestone of conglomerate-like nodular structure, 0.3 m thick. The total thickness of unit 14 is 1.8 m. From the limestone bed a conodont fauna was obtained: *Palmatolepis subperlobata*, *P. minuta minuta*, *P. tenuipunctata*, *P. rhomboidea* Sannemann, *P. quadrantinodosalobata*, *P. sp.* cf. *P. regularis*, *P. glabra prima*, and *P. sp.*

15. Unit 15 consists of greyish green argillaceous, cherty shales and cherts. Thickness is 4 m. At the top of the unit are found the conodonts: *Palmatolepis* sp. cf. *P. rhomboidea*, *P. glabra prima*, *P. glabra lepta* Ziegler and Huddle, and *P. ex gr. P. quadrantinodosa* Branson and Mehl. The faunas of units 14 and 15 are characteristic of the *rhomboidea* Zone (which corresponds to part of the upper part of the *Cheiloceras* Stufe, II  $\beta$ , of the ammonoid scale; Ziegler 1971; Kononova 1975).

Upward along the slope there are no outcrops and the detritus of red argillaceous cherty shale and loose slabs of chert suggests an upward continuation of the sequence.

#### TERMINOLOGY

The symbolic notation for conodont skeletal elements introduced by Sweet and Schönlaub (1975: 42—43; Cooper 1975) and based on a discussion by Sweet (which is the basis for the system used in the revised volume on conodonts in the *Treatise on Invertebrate Paleontology*), is used here. The advantage of this system of notation is that each symbol provides "a means of identifying and [informally] naming homologous, or supposedly homologous, positions within the apparatus" (Sweet 1981), without simultaneously attempting to give a description of the elements. This dual function is a disadvantage of other systems (e.g. the other two shown in table 1), because the descriptive content inherent in the symbols, tied originally as they were to certain form genera, limits their widespread usage for a maximum number of apparatuses.

Table 1

Symbolic notations for conodont apparatuses proposed by several authors

Sweet 1981	Jeppsson 1971	Klapper and Philip 1971	
		Type 1	Type 2
Pa	sp	P	P
Pb	oz	01	02
M	ne	N	N
Sc	hi	A1	B1
Sb	pl	A2	B2
Sa	tr	A3	B3

### HISTORICAL REVIEW

Lange (1968: 40—41) was the first to reconstruct the apparatus of *Palmatolepis*, on the basis of eleven fused clusters from the Upper Devonian upper Kelwasserkalk at Schmidt quarry in the Kellerwald (Rhenish Slate Mountains, West Germany). The best preserved and most complete of the clusters contains palmatolepan (Pa), nothognathellan (Pb), palmatodellan (M), smithiform (Sc; "*Prioniodina smithi*"), falcodontan (Sb), and scutulan (Sb and Sa) elements (Lange 1968: 40—41, pl. 1, 2; Klapper and Philip 1972: 100; Boogaard and Kuhry 1979: 2). At the time this cluster was illustrated, the pair of palmatolepan elements was still attached to the rami-form elements, but by December, 1970, when one of us (GK) studied these specimens the palmatolepan pair had become separated. Although Lange identified the Pa element as *Palmatolepis triangularis* Sannemann, it appears to be *P. subrecta* Miller and Youngquist, on evidence especially of the platform outline.

Klapper and Philip (1972: 100) interpreted the *Palmatolepis* (or *Palmatodella* in their terms) apparatus primarily in the light of Lange's cluster containing *Palmatolepis*, but also cited the occurrences of the same kinds of elements in insoluble residues that were described by Glenister and Klapper (1966) from the Upper Devonian of Western Australia. Klapper and Philip (*op. cit.*) reidentified some of the elements in the cluster of Lange (1968). In the same symposium, Ziegler (1972: 92, 94) interpreted *Palmatolepis* as a unielemental apparatus and the *Palmatolepis* pair as out of place in Lange's cluster and taxonomically unrelated to the other elements.

Further work on Upper Devonian residues from some of the same formations in Western Australia, as well as a sample from slightly below the lower Kelwasserkalk at Schmidt quarry, led Philip and McDonald (1975) to reinterpret the constituency of the *Palmatolepis* (or *Palmatodella* in their terms) apparatus. Their reconstruction of *Palmatolepis hassi* (*op. cit.*: fig. 6) replaced the palmatodellan element with a lippertiform element (name based on "*Enantiognathus lipperti*") in the M position and

shifted the palmatodellan element to the Pb position, thereby removing the nothognathellan element from the apparatus. The next younger species dealt with by Philip and McDonald (1975: fig. 8, 11), *P. triangularis*, was reconstructed similarly to *P. hassi*, but with the position of the M element vacant. According to these authors, two younger species, *P. minuta* and *P. glabra*, also lack an M element and a tripodellan element was reconstructed in the Sa position of *P. glabra* (Philip and McDonald 1975: 104, fig. 10). They further stated (*op. cit.*: 102—103) that the nothognathellan element is not part of the generalized *Palmatolepis* apparatus, but did not comment on the generic allocation of this element.

On evidence of statistical analysis of 58 samples mainly from a variety of European localities, Boogaard and Kuhry (1979) interpreted the *Palmatolepis* apparatus in a closely similar reconstruction to that of Klapper and Philip (1972). In early species such as *Palmatolepis subrecta* (belonging to the multielement subgenus *Manticolepis* in the concept of Boogaard and Kuhry) the reconstruction is the same in terms of kinds of elements present, the only difference being the inferences about homologies with better known apparatuses. Boogaard and Kuhry (1979: 25—26) interpreted the smithiform as a second M element, the falcodontan element as the Sc, the asymmetrical scutulan as the Sb, and the symmetrical scutulan element as the Sa. In contrast, Klapper and Philip (1972: 100) had interpreted the smithiform as the Sc, the falcodontan as the Sb, and the two scutulan elements as intergrading variants of the Sa. More importantly, the statistical reconstruction of *Palmatolepis subrecta* by Boogaard and Kuhry (1979: fig. 1) is identical element for element to that of Lange's (1968: pl. 1, 2) cluster.

In some later species of *Palmatolepis* such as *P. gracilis* and *P. minuta* (belonging to the subgenus *Tripodellus* in the concept of Boogaard and Kuhry), a tripodellan element replaces the nothognathellan element in the Pb position in the reconstruction of Boogaard and Kuhry (1979: 26, 39). Note however that according to these authors a tripodellan element is not part of the apparatus of species of the *P. glabra* group, which instead has a nothognathellan Pb element. This contrasts with the interpretation of Philip and McDonald (1975) cited earlier (Boogaard and Kuhry did not have a copy of Philip and McDonald's paper available to them at the time of writing of their paper; M. van den Boogaard, August 4, 1980: oral communication).

If *P. gracilis* and *P. gonioclymeniae* (and related species) had a tripodellan instead of a nothognathellan Pb element, as indicated by the data of Boogaard and Kuhry (1979: tables 2, 4—6) this at least partly if not entirely explains the observation of Sandberg and Ziegler (1979: 177) on the extreme scarcity of nothognathellan elements in the late Famennian (*styriacus* and *costatus* Zones) part of the Upper Devonian.

Boogaard and Kuhry (1979: 16—19) discussed the problem of the ex-

cessive number of Pa elements *versus* the comparatively low frequency of the other elements in the *Palmatolepis* apparatus reconstructed from their samples. The ratios differ drastically from expectations based on Lange's cluster or on a general model derived from Carboniferous bedding-plane assemblages. Nevertheless, a point raised by Boogaard and Kuhry (1979: 17) should be emphasized in a slightly different form; viz. that there is also generally an excess of platform elements (*Idiognathodus*) in residues of the same age as the "Scottognathus" bedding-plane assemblages (see Merrill and Powell 1980). Yet, as briefly mentioned in the introductory section of the present paper, there is substantial evidence for the *Idiognathodus* reconstruction (independently arrived at by von Bitter 1972, and Baesemann 1973), as confirmed by the hundreds of specimens of "Scottognathus." Merrill and Powell's (1980) hypothesis involving loss of the non-platform elements during ontogeny would explain the over-representation of the platform elements in many Carboniferous residues.

Two questions arising from this summary of previous attempts to interpret the *Palmatolepis* apparatus, are the following: 1) was *Palmatolepis* a multielemental, as opposed to a unielemental genus? and 2) did nothognathellan elements occupy the Pb position in the *Palmatolepis* apparatus, excluding the subgenus *Tripodellus sensu* Boogaard and Kuhry from the discussion? It is our opinion that the specimens found in the northern Urals reinforce an affirmative answer to both questions.

#### DESCRIPTION OF UNYA RIVER ASSEMBLAGES

Two assemblages from 0.5 m above the base of unit 7 on the western limb of the Evtropiny Noski section (Puchkov 1979: 45—48) provide critical evidence on the structure of the *Palmatolepis* apparatus. The first assemblage (pl. 25: 1) contains a symmetrical pair (Class II symmetry of Lane 1968: 1259) of palmatolepan (Pa) elements, a pair of nothognathellan (Pb) elements, and a single fragmentary specimen of the symmetry transition series (Sc-Sa). The Pa elements are identifiable as the form-species *Palmatolepis triangularis* Sannemann and the Pb elements compare only in lateral aspect with *Nothognathella typicalis* Branson and Mehl (1934: pl. 13: 7, 8; other form species of these authors, *N. reversa*, pl. 13: 9, 10, and *N. incurva*, pl. 13: 13, 14, most probably should be considered as junior synonyms of *N. typicalis*). It is uncertain if the inner platform development below the apex of the arch is as broad as that described for *N. typicalis*, because there appears to be a line of breakage along the point of contact of the platform and blade in the Unya River specimens. The element of the symmetry series is possibly scutulan, although the identification is uncertain. This assemblage is represented by a part and counterpart and, as in the instance of the second assemblage, is best viewed immersed in glycerine or a comparable liquid. The assemblage mea-

tures about 4.5 mm from the Pb element on the left to the edge of the outer lobe of the Pa element on the right (as oriented in pl. 25: 1), and it is 5 mm from there to the edge of the piece of shale.

The second assemblage contains a single palmatolepan (Pa) element exposed in lower view, a pair of nothognathellan (Pb) elements, a single palmatodellan (M) element, a pair of smithiform (Sc) elements, a pair of falcodontan (Sb) elements, a third Sb element that is either falcodontan or scutulan, and two indeterminate elements (fig. 2; pl. 25: 2). In the outline of the platform, length of free blade, and configuration of the keel, the Pa element conforms most closely to *Palmatolepis delicatula delicatula*

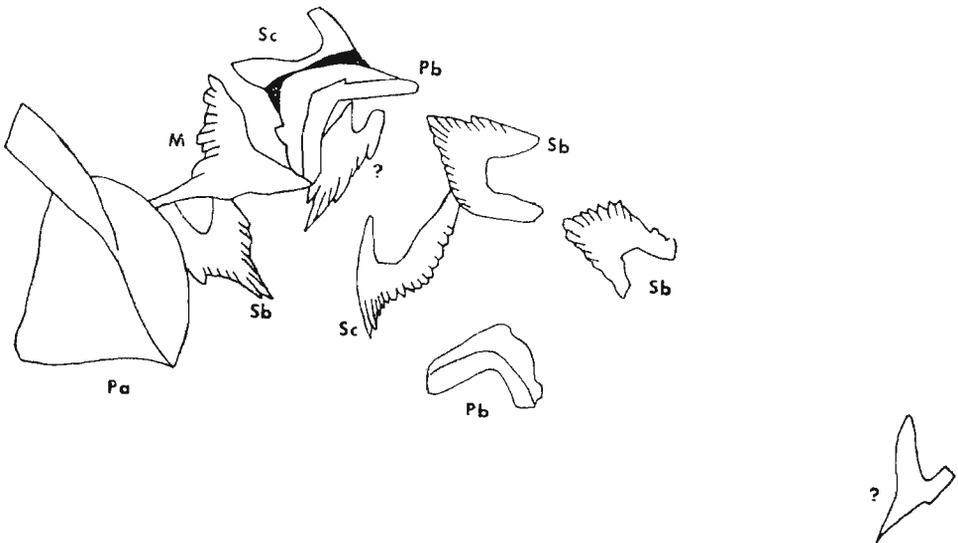


Fig. 2. *Palmatolepis delicatula delicatula* Branson and Mehl. Drawing of same assemblage as in pl. 25: 2, but with symbolic notation for elements indicated (see Terminology). Dark area between Sc and Pb elements is obscured by matrix. Questionable element just below Pb may be a scutulan (Sa or Sb) element. Magnification approximately 50.

Branson and Mehl (1934: pl. 18: 4, 10; see e.g. Ziegler 1962: pl. 2: 13—19; Bouckaert and Ziegler 1965: pl. 2: 9, footnote; Glenister and Klapper, 1966: pl. 95: 17). The nothognathellan element compares with *Nothognathella abnormis* Branson and Mehl, especially the morphotype illustrated by Boogaard and Kuhry (1979: fig. 1, 4, the Pb element with *P. subrecta* and *P. gigas*), although it differs in lacking such a well-developed shelf-like platform. Instead of a platform the Unya River Pb element has a narrow but conspicuous ridge like that of the form illustrated by Boogaard and Kuhry (1979: fig. 5, the Pb element with *P. triangularis*), from which it differs, however, in a number of other respects including details of denticulation. The M element is easily identifiable as *Palmatodella delicatula*, the Sc elements as "*Prioniodina*" *smithi* Stauffer (Glenister and Klapper

1966: 833, pl. 96: 7—9), and the pair of falcodontan Sb elements are extremely close to *Falcodus variabilis* Sannemann (1955: pl. 4: 1—4). The third Sb element is either another falcodontan close to *F. variabilis* or it is an asymmetrical scutulan element (*Scutula venusta* of form taxonomy). As noted in the literature (Sannemann 1955: 155; Lindström 1964: 89, Boogaard and Kuhry 1979: 28) these two forms intergrade and are closely similar in inner lateral aspect, the chief difference being the addition of an outer lateral process in *S. venusta*. Because of possible breakage parallel to the bedding surface of the shale, it cannot be stated confidently that an outer process was not present.

Of the two elements that cannot be allocated to a position of homology indicated by the notational system of Sweet and Schönlaub (1975), identification of the one that is partially obscured below the nothognathellan element cannot be suggested with much certainty. The thin and high, needle-like cusp suggests a scutulan element as a possibility. The affinities of the second specimen, which is off to the side of the assemblage (pl. 25: 2) and more deeply covered by the shale matrix than the others, are unclear. The assemblage measures about 2.5 mm from the free blade of the Pa element to the second indeterminate element, which itself is less than 1 mm from the edge of the piece of shale. The specimens are on one piece of shale that lacks a counterpart. The color of the matrix is green and the conodonts are relatively dark, about 4 in the conodont alteration index (Epstein *et al.* 1977).

#### NOTE ON PRESERVATION AND PHOTOGRAPHY

The specimens described under the second assemblage (pl. 25:2) present a difficult photographic problem. These specimens do not stand up in relief from the surrounding matrix. In fact, they are covered by a thin film of shale, which precludes effective coating either for optical or SEM photography. Furthermore, viewing the specimens in air is unrewarding. The only way that these specimens show to advantage is through immersion in a liquid such as glycerine. Even so, there is so little difference in contrast between the specimens and the matrix in terms of black and white images that an extremely long exposure was required (about 5 minutes, Leitz Aristophot, 50 mm Milar lens). The result (pl. 25) is less than adequate. Therefore, a drawing of the assemblage was prepared (fig. 2) with the outlines taken from the photograph and the denticles drawn from microscopic observation of the specimens.

X-ray radiographs were attempted with the help of Bertram Woodland of the Field Museum of National History, Chicago, but there appears to be so little density contrast between the specimens and matrix that images of the specimens were not produced even under very long exposure.

## IMPLICATIONS OF UNYA RIVER SPECIMENS

A logical interpretation of the *Palmatolepis* apparatus that follows from the evidence of the Unya River bedding-plane assemblages is that the *Palmatolepis* apparatus was multielemental and that nothognathellan elements were constituents in the Pb position of the skeletal structure of *P. triangularis* and *P. delicatula delicatula*. The specimen of *P. delicatula delicatula* reinforces the reconstructions of Lange (1968), Klapper and Philip (1972), and Boogaard and Kuhry (1979). These conclusions appear to apply to at least some stages in the ontogeny (cf. Merrill and Powell 1980). Of course, it may be possible still to suppose that these reconstructions are incorrect and that they derive from a coincidental ecologic association of a unielemental *Palmatolepis* apparatus with the other elements. To focus on just one aspect of the multielement *Palmatolepis* apparatus, however, is it indicative of coincidence of something more fundamental that the fine details of ornament on the platform of many of the nothognathellan elements are so closely similar if not identical to those of the respective palmatolepan elements? Is this nearly perfect parallel evolution in separate genera or, to the contrary, an indication of generic identity? Considering another aspect, are the stratigraphic ranges of the palmatolepan Pa element (plus the Pa of *Mesotaxis* Klapper and Philip 1972: 100, an apparatus that apparently shared some of the same elements with *Palmatolepis*), the nothognathellan plus tripodellan Pb elements, the palmatodellan M, the smithiform Sc, the falcodontan Sb, and the scutulan Sb and Sa elements a coincidence? If there were no generic relationship of these elements, why do not at least some of them extend either above or below the Upper Devonian? We think that the answer to these questions is generic identity rather than ecologic coincidence.

## HOMOLOGIES

If we assume that the proposed multielemental reconstructions of the *Palmatolepis* apparatus supported in this paper are essentially correct, then some comments on homology with other conodont apparatuses are appropriate. The symmetry series appears to consist of at least four kinds of elements: smithiform (Sc), falcodontan (Sb), asymmetrical scutulan (Sb), and symmetrical scutulan (Sa). Such a number is not uncommon, as the symmetry series of species of *Aethotaxis*, *Hindeodus*, and *Idiognathodus* in the Upper Carboniferous (Baesemann 1973) and species of *Prioniodus*, *Amorphognathus* (Dzik 1976), *Aphelognathus* (Sweet 1979), and *Plectrodina* (Sweet and Bergström 1972) in the Ordovician have been recognized to comprise four elements. Furthermore, according to unpublished data, at least some of the species of *Polygnathus* and *Pandorinellina* in the Devonian appear to have a four-element symmetry series, either with two

kinds of Sc elements (as in the Carboniferous examples of Baesemann 1973) or two Sb (angulodontan and plectospathodontan) elements. Thus, more than three elements in the symmetry series have been recognized for some time (*contra* Nicoll 1980: 135).

It seems clear that the nothognathellan (Pb) element is comparable in basic morphology to the ozarkodinan element of *Ozarkodina*, *Pandorinellina*, and *Polygnathus* among Devonian genera, with the difference being the addition of the platform-like ledge developed especially on the inner side in the former. Of course, the nothognathellan element is morphologically identical with the Pb element of *Mesotaxis*, as originally reconstructed (Klapper and Philip 1972). A homology temporally far removed is with the ambalodontan element of *Prioniodus* and *Amorphognathus*, the fundamental morphologic difference being the extra process in the latter. The nothognathellan element is also homologous with the ozarkodinan element of *Gondolella* in the Upper Carboniferous (von Bitter 1976) and Triassic (Dzik and Trammer 1980), as well as other genera of similar age.

The palmatodellan (M) element of *Palmatolepis*, as represented by characteristic examples of the form-species *Palmatodella delicatula*, is not particularly close morphologically to other Devonian M elements, because the lower margin of the posterior process inclines upward. The range of variation of *Palmatodella delicatula*, however, extends to forms (e.g. Sannemann 1955: pl. 4: 13; Helms 1959: pl. 1: 11) in which the same margin inclines downward as in other "pick-shaped" Devonian M elements (e.g. in the palmatodellan element of *Mesotaxis asymmetrica asymmetrica*, in the reconstruction of Klapper and Philip 1972, but not that of Philip and McDonald 1975). Nevertheless, the characteristic form of the M element of *Palmatolepis*, in which the lower margin of the posterior process inclines upward, bears a striking resemblance to that of the falodontan (or oistodontan) M element of *Prioniodus* (Bergström 1971; Dzik 1976). These lines of evidence suggest that the palmatodellan element is indeed the M and not the Pb element of *Palmatolepis* (*contra* Philip and McDonald 1975).

There is some question about the homology of the smithiform element, because Boogaard and Kuhry (1979: 28, fig. 1) interpreted it as a second M element. Representative smithiform specimens have the fine, alternating denticulation that is characteristic of the other elements of the symmetry series, as opposed to the uniform denticulation of the palmatodellan (M) element. Thus, it is more closely allied with the falcodontan and scutulan elements in style of denticulation. Furthermore, the resemblance to the cordylodontan element of *Prioniodus* (Dzik 1976: fig. 5) is striking, as it was in the previous comparison of the M elements of the two genera.

Of the two Sb elements, the falcodontan homologizes with the angulodontan element of other apparatuses (e.g. that of *Polygnathus*). The asy-

mmetrical scutulan element seems to resemble the keislogathan element of early species of *Prioniodus* (Dzik 1976: fig. 5) only in the number of processes developed. The symmetrical scutulan (Sa) element has two anterior and two posterior processes and thus the only close comparison is with the form genus *Avignathus* Lys and Serre (cf. Ziegler 1972: 94), which may represent the Sa element in some Frasnian species of *Palmatolepis*.

Our present understanding of the *Palmatolepis* apparatus does not support the inclusion of the lippertiform element as the M element in Frasnian species (*contra* Philip and McDonald 1975).

In the light of the above comparisons of some of the elements of the *Palmatolepis* apparatus with those of *Prioniodus*, comparisons which at first thought may seem somewhat strained, it is interesting to recall that Lindström (1964: 101) commented on the similarity of morphologic plan of the Pa elements. We do not suggest, however, anything more than homology of some of the elements of the two apparatuses and are not implying a close evolutionary relationship. *Palmatolepis* possibly evolved from *Mesotaxis* (see discussion in Klapper and Philip 1972: 98).

#### NOMENCLATURAL CONSEQUENCES

There is a slight nomenclatural problem surrounding the generic name of the species whose apparatus is discussed in this paper. *Palmatodella* Bassler (1925: 219, type species is *P. delicatula*) and *Palmatolepis* Ulrich and Bassler (1926, type species = *P. perlobata*) were based on isolated M and Pa elements, respectively, that are now considered to be skeletal parts of a single generic apparatus. Although introduced in an abstract, the name *Palmatodella* dates from 1925, and not from the study of Ulrich and Bassler (1926), because of the rules for names published before 1931 (ICZN, 1961, Art. 12, 16vi). Nonetheless, in multielement taxonomy there is serious doubt about the specific identity of *Palmatodella delicatula*, which was a stable element during the evolution of the apparatus and apparently occurred with most if not all of the Pa and Pb elements of *Palmatolepis*. The type specimen of *Palmatodella delicatula* is from the Gassaway Member of the Chattanooga Shale at Quicks Mill on Flint River near New Market, Alabama (Ulrich and Bassler 1926: 41; Huddle 1968: 5), which has yielded a fauna including at least two species of *Palmatolepis* (*P. perlobata* and *P. glabra*, including several subspecies), according to data in Holmes (1928), Huddle (1968), and Ziegler (1977: 349). Thus, we agree with Boogaard and Kuhry's (1979: 26) statement that "it does not appear to be possible to reconstruct the apparatus corresponding to the type specimen of '*Palmatodella delicatula*.'" If the specific identity of the type species is in serious doubt then the generic name rests on an insecure foundation and should be regarded as a *nomen dubium*. Thus we

follow Boogaard and Kurhy in using *Palmatolepis* as the valid multielement name, and not the practice of Klapper and Philip (1972) and Philip and McDonald (1975) who used *Palmatodella*.

*Scutula* Sannemann (1955) is a junior synonym of multielement *Palmatolepis*.

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NATURALNE GÓRNODEWOŃSKIE ZESPOŁY *PALMATOLEPIS*  
Z PÓŁNOCNEGO URALU

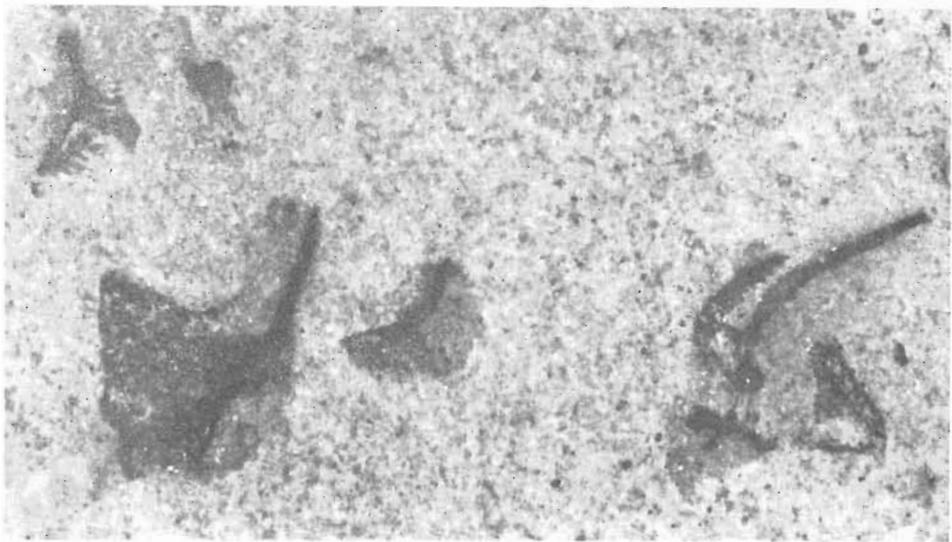
*Streszczenie*

W niniejszej pracy opisano dwa naturalne zespoły konodontowe. Występują one na powierzchni ławicy w utworach dolnego famenu (górną Zoną *triangularis*) profilu Evtropiny Noski nad rzeką Unja, na północnym Uralu. Zespoły te mają duże znaczenie dla rozstrzygnięcia kontrowersyjnego problemu budowy aparatu w rodzaju *Palmatolepis*. Wykazały one, iż pewne gatunki *Palmatolepis* charakteryzowały się, w uzupełnieniu do elementów platformowych (Pa), obecnością elementów notognatolowych (Pb), palmatodelowych (M), smitifformowych (Sc), falkodontowych (Sb), asymetrycznych (Sb) i symetrycznych (Sa) skutulowych. Opisane tu okazy z nad rzeki Unja potwierdzają wcześniejsze poglądy na temat budowy aparatów *Palmatolepis*, które opierały się na znanych połączonych zespołach i na analizie statystycznej. W niniejszej pracy użyto nazwy rodzajowej *Palmatolepis*, gdyż nazwa *Palmatodella* stanowi *nomen dubium*.

EXPLANATION OF THE PLATE 25

Plate 25

1. *Palmatolepis triangularis* Sannemann, Upper Devonian (lower Famennian, Upper *triangularis* Zone), 0.5 m above base of unit 7, Evtropiny Noski section, Unya River, northern Urals; pair of Pa elements in upper view (bottom left and right corners), pair of Pb elements in lateral view (upper left corner and between the Pa elements), and a specimen of the symmetry series (Sc-Sa) just to the right of the Pb element in the left corner. Slab immersed in glycerine; magnification approximately  $\times 30$ . SUI 47280.
2. *Palmatolepis delicatula delicatula* Branson and Mehl, same horizon and locality as that of 1; for identification of elements see fig. 2 in the text. Pa element is in lower view. Slab immersed in glycerine; magnification approximately  $\times 50$ . SUI 47281.



1



2