Statistical reconstruction of the *Palmatolepis* apparatus (Late Devonian conodontophorids) at the generic, subgeneric, and specific level

M. van den Boogaard and B. Kuhry

Boogaard, M. van den & B. Kuhry. Statistical reconstruction of the *Palmatolepis* apparatus (Late Devonian conodontophorids) at the generic, subgeneric and specific level. – Scripta Geol., 49: 1 - 57, 4 diagrams, 28 figs., Leiden, April 1979.

Extensive frequency data are used for a reconstruction of Devonian conodont apparatuses. Correspondence analysis and a related clustering method are selected as statistical tools, and are used as informal methods for testing a priori hypotheses rather than as search mechanisms.

In our view, the *Palmatolepis* apparatus consists of palmatolepan P elements, tripodellan or nothognathellan O elements, palmatodellan and smithiform N elements, and a symmetry transition consisting of falcodontan A_1 elements, asymmetrical scutulan A_2 elements, and symmetrical scutulan A_3 elements.

A peculiar phenomenon, already described by other authors, is the numerical dominance of the P elements, which are on the average 15 times as frequent as corresponding O and N elements. It is argued that this phenomenon is not due to post-mortem processes. Several biological explanations are considered.

The O elements corresponding to various palmatolepan elements are identified, and this result allows a critical reappraisal of phylogenetical views based on the P elements alone. Results broadly support current views. We recognize five subgenera: *Manticolepis, Tripodellus (= Deflectolepis), Palmatolepis, Panderolepis,* and *Conditolepis* (new subgenus).

Our most important result with respect to other apparatuses is the strong evidence that '*Icriodus*' and simple cones, contrary to the prevailing opinion, did not belong to a common apparatus.

M. van den Boogaard and B. Kuhry, Rijksmuseum van Geologie en Mineralogie,
Hooglandse Kerkgracht 17, 2312 HS Leiden, The Netherlands.

Introduction

Of prime importance for the reconstruction of the *Palmatolepis* apparatus is the description of a cluster of conodonts found in a bituminous pellet (Lange, 1968), which presumably represents a completely or partly preserved apparatus. The following elements are listed by Lange: one pair of *'Palmatolepis triangularis'*, one pair of *'Ozarkodina regularis'*, one pair of *'Prioniodina* cf. *prona'*, two pairs of *'Prioniodina smithi'*, one pair of *'Falcodus variabilis'*, and single specimens of *'?Falcodus conflexus'*, *'Scutula venusta'*, and *'Scutula sinepennata'*.

As suggested by Ziegler (1972) and Klapper & Philip (1972), these determinations need some revision. Lange's *'Ozarkodina regularis'* can be identified as a nothognathellan element with reduced platforms (a variety of *'N. abnormis'*), his *'Prioniodina* cf. *prona'* as *'Palmatodella delicatula'*, while we interpret *'?Falcodus conflexus'* and *'Scutula sinepennata'* as incomplete specimens of *'Scutula venusta'* and *'Scutula bipennata'*.

On the basis of Lange's observations, by assuming analogies with reconstructed apparatuses of Silurian and Carboniferous age, and by using information from samples characterized by a low diversity of form taxa, Klapper & Philip (1971, 1972) reconstructed a large number of Devonian conodont apparatuses. In their view, *'Palmatolepis'*, *'Polygnathus'*, *and 'Spathognathodus'* would represent the platform elements in complex conodont apparatuses consisting of six types of elements: platform (P) elements, ozarkodinoid (O) elements, neopriodinoid (N) elements, and three elements forming a symmetry transition (A_1-A_3). In their view, the *Palmatolepis* apparatus would consist of palmatolepan P elements, nothognathellan O elements, palmatodellan N elements, smithiform A_1 elements, falcodontan A_2 elements, and A_3 elements intergrading between asymmetrical and symmetrical *'Scutula'*.

A quite different view is held by Ziegler (1972), who noted an extreme surplus of palmatolepan and polygnathan platform conodonts with respect to ramiform conodonts. He suggested that these platform conodonts may have belonged to mono-element apparatuses, which would have been derived from more complex apparatuses by phylogenetic reduction. The coprolitic assemblage of Lange is interpreted by Ziegler as an aggregate of an apparatus lacking P elements and an unrelated pair of platform conodonts.

Part of the data analysed in this paper has already been presented by van den Boogaard (1963) and van den Boogaard & Schermerhorn (1975). The latter study confirmed the surplus of platform elements observed by Ziegler, but an analysis of correlation coefficients based on frequency data for form taxa supported the hypothesis of Klapper and Philip on the composition of the *Palmatolepis* apparatus to some extent. However, the apparatus was found to contain *'Tripodellus robustus'* rather than a nothognathellan O element. Though its scope has been extended later on, our study initially aimed at a clarification of these controversies by using frequency data of a larger number of samples from a broader stratigraphical interval and by applying more appropriate statistical techniques.

Nomenclature

Like other authors we faced considerable nomenclatorial problems in dealing with conodont apparatuses. As long as the composition of apparatuses is under discussion, it is hardly possible nor desirable to avoid Linnean terminology for the separate elements. We have adopted the custom of putting Linnean terms referring to separate elements between quotation marks. When referring to form genera, we will also use vernacularized generic names following Klapper & Philip (1972) and others.

Acknowledgements

Thanks are due to Dr M. Freudenthal, Prof. Dr H. J. Mac Gillavry, Prof. Dr R. A. Reyment, and Dr C. F. Winkler Prins for critically reading the manuscript and valuable suggestions. Thanks are also due to Prof. Dr S. P. Ellison Jr for providing us with the samples from Holt's Summit and Dr U. Dornsiepen for the sample from Meggen. Furthermore we want to express our gratitude to Messrs E. de Stoppelaar and W. A. M. Devilé for assistance in preparing the scanning electron micrographs, and Mr J. Timmers for drawing the diagrams.

Methodological considerations

Form taxa representing the elements of conodont apparatuses may be expected to show a consistent numerical association over a series of samples. From a methodological point of view, the problem is related to that of quantitative geochemical, petrographical and ecological studies which all deal with the distribution of components over samples. However, there are certain significant differences. In the latter three fields, associations among components as well as among samples tend to be of interest. Many ecological studies, for example, aim at a classification of samples in a number of biofacies characterized by different assemblages of taxa. Useful results may be obtained by focusing on relationships among samples rather than taxa (e.g. applications of principal components analysis and principal coordinates analysis in ecological studies). In a study dealing with a reconstruction of conodont apparatuses, however, relationships among (form) taxa are obviously the prime object.

A fundamental problem leading to considerable difficulties in using numerical techniques as a search mechanism for the reconstruction of conodont apparatuses is the evidently 'mosaic' evolution pattern of conodontophorids, separate elements being characterized by unequal rates of morphological evolution and diversification. Thus one form species may have belonged to apparatuses of different composition in a single sample. Also, partial overlaps in stratigraphical range may occur for form species which in the interval of overlap have been part of the apparatus of one and the same biological species. If mozaic evolution plays a major part in the group of interest, the best result to be expected from a numerical analysis at the form specific level is a partial reconstruction of apparatuses.

Therefore the strategy should be to lump form species representing rapidly evolving elements in order to obtain taxonomical categories showing a consistent numerical association with form species representing more stable elements. Decisions in the lumping process may be based on a priori hypotheses, morphological arguments, or on a preliminary analysis of the data. The prospects for developing a numerical method which adequately deals with this complex situation and which may replace subjective decisions are rather dim. Instead emphasis is given to the use of numerical methods for testing a priori hypotheses on the composition of apparatuses.

Separate parts of a skeleton or dentition may be expected to occur in fixed numerical proportions within a restricted taxonomic group. The chi-square test of independence can be used as a test for constant numerical proportions of taxa in sampled populations. However, as will be seen below, almost all chi-square tests aplied to our conodont data lead to a rejection of the underlying hypotheses. Rather than concluding that all these hypotheses are in error, we suspect that secondary distortions of original numerical proportions are partly responsible for the negative test results. Causes for deviations of numerical proportions in fossil populations from the original proportions in the life community may include: sedimentary sorting, differential preservation and post-depositional fragmentation. As disturbing factors one should also take into account problems of identification and sampling.

As an alternative for rigorous chi-square tests, factor analysis or cluster analysis may be used as informal test procedures for hypotheses. If a specific hypothesis on the composition of apparatuses and the delimitation of taxa are more or less correct, the form taxa should join a well-defined cluster in factor plots or dendrograms. The validity of this approach is based on the assumption that distributional differences between elements of different groups of conodont apparatuses are sufficiently large to dominate over disturbing effects such as secondary distortions of proportions.

Although frequency data are listed in quite a number of publications on conodonts, formal numerical analyses sofar mainly have been based on presence/absence data (e.g. Kohut, 1969; von Bitter, 1972; Druce, Rhodes & Austin, 1972; Babcock, 1976). Presence/absence methods do not require a time-consuming counting procedure. On the other hand, there are sound arguments in favour of an analysis based on frequency data. First, unless relative frequencies are drastically distorted by secondary processes, much valuable information is lost in presence/absence studies. Secondly, many of our form taxa occur in all or nearly all samples. Thirdly, numerical proportions of elements in conodont apparatuses are in themselves of considerable interest.

A disturbing aspect of factor and cluster analysis is the wide scala of available methods, which occasionally may lead to drastically different results. Methods differ in the selection of a measure of association as well as in the way in which complex patterns of association are reduced to easily interpretable diagrams. In the framework of this paper, it is not feasible to discuss statistical methods in detail, and for a general introduction readers are referred to appropriate text-books such as Jöreskog, Klovan & Reyment (1976) for factor analysis and Sneath & Sokal (1973) for cluster analysis.

Winder (1974) and van den Boogaard & Schermerhorn (1975) have analysed associations among conodont form taxa on the basis of a visual inspection of a correlation matrix. Their approach involved a rather dubious sample-wise restandardization of frequencies to numbers of individuals per weight unit of rock. A more serious shortcoming of this approach is that a perfect correlation between two taxa need not at all imply constant mutual proportions.

Inverse applications of the principal components or principal coordinates method aiming at an ordination of taxa rather than samples would lead to useful results, provided that data are subjected to a taxon-wise rescaling to proportions. However, of the standard methods available, correspondence analysis (e.g. Benzecri, 1973; Jöreskog et al., 1976; David, Dagbert & Beauchemin, 1977) is definitely to be preferred, since this method involves an appropriate chi-square weighting of frequency data, and since it allows a simultaneous and interpretable ordination of samples and taxa.

Factor plots tend to offer a more reliable and interpretable representation of complex relationships among objects than clustering techniques, but suffer from the drawback that only a factor space of limited dimensions can be taken into account. Therefore, we decided to add single-linkage dendrograms based on distances of objects in correspondence factor space. If we would refrain from reduction of dimensions, inter-object distances would equal the so-called chi-square distances. However, the contribution of lower order factors tends to blur the picture considerably, not only because these largely represent sampling error and distortions of proportions due to secondary processes, but also because these factors may contribute disproportionally to inter-object distances due to a secondary rescaling procedure in correspondence analysis. Unfortunately, there does not seem to be a sound criterion for elimination of factors since chi-square significance must be rejected in our context as too rigorous a criterion. We selected the rather arbitrary criterion of retaining the smallest set of higher order factors which together contribute at least 95% to total chi-square.

Although results are not equivalent to those obtained when data are added prior to the analysis, it is possible and instructive to compute the position of additional taxa and samples in factor plots after the analysis is performed. In our application of correspondence analysis, this approach is extremely useful, since it allows an appreciation of the effects of lumping and splitting taxa in a single analysis. Especially for the purpose of lumping the computation involved is very simple, since the coordinates of the lump taxon are a weighted average of the coordinates of the separate taxa:

$$c^* = \Sigma (N_k . c_k)/\Sigma N_k$$

Here, c^* represents the coordinate of the lump taxon, while c_k represents the coordinate and N_k the marginal frequency of the k-th taxon.

Table 1. Localities and conodont zones of the samples used in this study.

Sample		Locality	Conodont Zone
Our serial no.	Field no.		
1	16-9-22	Hönnetal railway cut, Germany	Upper *Bispathodus costatus* Zone
2	65 Tr 18	Triollo area, Spain	M. - U. *Bispathodus costatus* Zone
3	C 66	Nerva, Spain	M. - U. *Bispathodus costatus* Zone
4	65 Tr 16	Triollo area, Spain	M. - U. *Bispathodus costatus* Zone
5	Wp Boh. nr. 9	Hostenice, Czechoslovakia	M. - U. *Bispathodus costatus* Zone
6	Prof. 1, lr. 2	Groszer Pal, Austria	M. - U. *Bispathodus costatus* Zone
7	65Ca/545	Castells, Prov. Lerida, Spain	M. - U. *Bispathodus costatus* Zone
8	65Ca/650	Castells, Prov. Lerida, Spain	M. - U. *Bispathodus costatus* Zone
9	Prof. 1, lr. 5	Groszer Pal, Austria	Middle *Bispathodus costatus* Zone
10	65Ca/745	Castells, Prov. Lerida, Spain	L. - M. *Bispathodus costatus* Zone
11	GZn 51/1	Velez Rubio area, Spain	Lower *Bispathodus costatus* Zone
12	C.d.P.	Cabezas del Pasto, Spain	M. - U. *Polygnathus styriacus* Zone
13	62 Tr 7	Triollo area, Spain	*Polygnathus styriacus* Zone
14	151	Pomarao region, Portugal	*Polygnathus styriacus* Zone
15	634	Pomarao region, Portugal	*Polygnathus styriacus* Zone
16	660	Pomarao region, Portugal	*Polygnathus styriacus* Zone
17	1187	Pomarao region, Portugal	*Polygnathus styriacus* Zone
18	1345/1	Pomarao region, Portugal	Middle *Polygnathus styriacus* Zone
19	1345/2	Pomarao region, Portugal	Middle *Polygnathus styriacus* Zone
20	1362/b	Pomarao region, Portugal	Middle *Polygnathus styriacus* Zone
21	1362	Pomarao region, Portugal	Middle *Polygnathus styriacus* Zone
22	1362/1	Pomarao region, Portugal	Middle *Polygnathus styriacus* Zone
23	1366	Pomarao region, Portugal	Middle *Polygnathus styriacus* Zone
24	1386	Pomarao region, Portugal	Middle *Polygnathus styriacus* Zone
25	G 1465	Velez Rubio area, Spain	Middle *Polygnathus styriacus* Zone
26	1278	Pomarao region, Portugal	L. - M. *Polygnathus styriacus* Zone
27	1114	Pomarao region, Portugal	L. - M. *Polygnathus styriacus* Zone
28	1154	Pomarao region, Portugal	L. - M. *Polygnathus styriacus* Zone
29	1272	Pomarao region, Portugal	L. - M. *Polygnathus styriacus* Zone
30	GZn 51/2	Velez Rubio area, Spain	L. - M. *Polygnathus styriacus* Zone

31	19-9-26	Ballberg near Balve, Germany	M. - U. *Scaphignathus velifer* Zone
32	60	Pomarao region, Portugal	Middle *Scaphignathus velifer* Zone
33	Prof. 3, lr. 4	Groszer Pal, Austria	Upper *Palmatolepis marginifera* Zone
34	Prof. 3, lr. 7	Groszer Pal, Austria	Upper *Palmatolepis marginifera* Zone
35	Ell. 6890	Holt's Summit, Missouri, U.S.A.	Upper *Palmatolepis marginifera* Zone
36	41/71	Aeketal, Hartz, Germany	Upper *Palmatolepis marginifera* Zone
37	73/209	La Lastra – Santibanez de Resoba, Spain	Upper *Palmatolepis marginifera* Zone
38	G 1643	Velez Rubio area, Spain	Upper *Palmatolepis marginifera* Zone
39	0.8623	Messinghausen near Brillon, Germany	Upper *Palmatolepis marginifera* Zone
40	Villasalto	Villasalto, Gerrei Basin, Sardinia	Lower *Palmatolepis marginifera* Zone
41	43/71	Aeketal, Hartz, Germany	Top *Palmatolepis rhomboidea* Zone
42	L. 8798	Messinghausen near Brillon, Germany	Lower *Palmatolepis rhomboidea* Zone
43	Vries 773	Velez Rubio area, Spain	Top *Palmatolepis crepida* Zone
44	15-9-16	Martenberg near Adorf, Germany	Middle *Palmatolepis crepida* Zone
45	15-9-8	Steinbruch Schmidt, Wildungen, Germany	L. - M. *Palmatolepis crepida* Zone
46	15-9-7	Steinbruch Schmidt, Wildungen, Germany	base Middle *Palmatolepis triangularis* Zone
47	15-9-6	Steinbruch Schmidt, Wildungen, Germany	Uppermost *Palmatolepis gigas* Zone
48	15-9-13	Martenberg near Adorf, Germany	Upper *Palmatolepis gigas* Zone
49	15-9-5	Steinbruch Schmidt, Wildungen, Germany	Upper *Palmatolepis gigas* Zone
50	15-9-4	Steinbruch Schmidt, Wildungen, Germany	Upper *Palmatolepis gigas* Zone
51	G 67/49	near Marbella, Spain	Upper *Palmatolepis gigas* Zone
52	15-9-3	Steinbruch Schmidt, Wildungen, Germany	Lower *Palmatolepis gigas* Zone
53	F 3082	Löhnberg, Germany	Lower *Palmatolepis gigas* Zone
54	17-9-36	near Ballersbach, Germany	Lower *Palmatolepis gigas* Zone
55	M 1038	Grottenberg near Bredelar, Germany	Upper *Ancyrognathus triangularis* Zone
56	15-9-14	Martenberg near Adorf, Germany	*Ancyrognathus triangularis* Zone
57	AB 3/16	Northeast Leon, Spain	*Ancyrognathus triangularis* Zone
58	44/71	Lautenthal, Hartz, Germany	Lower *Ancyrognathus triangularis* Zone
—	Dorn FB 22	Meggen, Germany	*Polygnathus asymmetricus* Zone
—	Ell. 6890-2	Holt's Summit, Missouri, U.S.A.	Upper *Palmatolepis marginifera* Zone

---

* The samples 60, 660, 1114, 1154, and 1272 are stored in the Geological Institute of the University of Amsterdam, registration numbers PA 2844 - PA 3087. All other samples are stored in the Netherlands National Museum of Geology and Mineralogy, Leiden, registration numbers RGM 172 802 - 172 885, 172 945 - 172 965, 172 995 - 173 064, 173 208 - 173 522, 173 583 - 173 711, 173 948 - 174 390, 174 455 - 174 917.

Table 2. Frequency distribution of conodont form taxa.

Serial number of sample	*Palmatolepis* minus *Deflectolepis*	*Deflectolepis*	*Palmatodella*	*Prioniodina smithi*	*Tripodellus*	*Nothognathella*	*Scutula venusta*	*Scutula bipennata*	*Falcodus*	*Polygnathus*	*Bispathodus stabilis*	*Bispathodus* minus *B. stabilis*	*Spathognathodus*	*Ozarkodina*	Simple cone	*Belodella*	Prioniodinan element	*Pseudopolygnathus*	*Scaphignathus*	*Icriodus*	*Ancyrodella*	*Ancyrognathus*	*Pelekysgnathus*
1	—	324	53	51	50	—	15	7	19	40	—	769	535	173	55	—	86	15	—	—	—	—	—
2	—	48	5	6	4	—	2	6	4	162	—	95	94	17	—	—	27	53	—	—	—	—	—
3	—	426	50	47	52	—	18	11	16	324	—	2062	193	202	50	—	128	68	—	—	—	—	—
4	—	47	7	10	7	—	3	—	7	59	8	29	14	12	—	—	7	—	—	—	—	—	—
5	—	28	6	7	2	—	2	—	—	34	22	81	27	18	18	—	14	—	—	—	—	—	—
6	—	232	34	17	26	—	7	3	6	2	—	312	544	98	11	—	38	55	—	—	—	—	—
7	—	45	11	17	15	—	9	2	6	121	88	450	155	136	82	—	123	—	—	—	—	—	—
8	—	78	20	22	23	—	7	6	12	212	75	296	165	106	92	—	79	38	—	—	—	—	—
9	—	664	153	172	145p	—	75	51	138	274	107	337	851	275	34	—	156	145	—	—	—	—	—
10	—	52	16	17	12	—	4	—	5	196	94	253	59	47	27	—	30	—	—	—	—	—	—
11	—	33	4	2	2	—	—	2	1	23	6	2	13	1	1	—	3	—	—	—	—	—	—
12	280	1439	180	108	154	15	45	26	74	279	233	—	359	75	55	—	57	48	—	2	—	—	—
13	9	55	5	7	9	2	4	—	4	1	63	—	8	4	2	—	7	—	—	—	—	—	—
14	37	87	6	5	10	1	1	1	2	4	4	—	10	5	—	—	1	2	—	2	—	—	—
15	124	536	39	32	43	7	12	5	24	42	86	—	277	23	19	—	14	5	—	—	—	—	—
16	65	229	17	19	30	2	12	5	11	25	41	—	39	6	1	—	4	—	—	—	—	—	—
17	10	204	12	20	12	2	4	2	5	39	20	—	56	10	13	—	4	1	—	—	—	—	—
18	65	943	51	57	85	3	36	14	43	138	64	—	776	50	44	—	19	1	—	—	—	—	—
19	12	63	7	9	8	1	8	1	6	42	58	—	—	6	2	—	8	—	—	20	—	—	—
20	3	46	4	3	2	—	3	—	1	4	50	—	3	10	1	—	3	3	—	—	—	—	—
21	11	51	9	5	8	—	—	1	7	4	21	—	15	7	1	—	4	3	—	—	—	—	—
22	55	135	7	10	10	5	7	2	7	55	65	—	95	15	7	—	17	5	—	—	—	—	—
23	63	145	8	13	9	2	10	2	7	10	15	—	69	12	10	—	2	—	—	—	—	—	—
24	3	76	13	10	6	—	3	3	6	37	7	—	42	9	7	—	7	—	—	—	—	—	—

25	19	125	27	18	15	1	13	7	8	6	129	2	91	100	11	—	39	14	—	—	—	—	—
26	30	254	5	5	13	7	9	3	8	199	58	—	56	17	19	—	6	—	—	6	—	—	—
27	194	820	65	60	80	20	11	14	22	111	117	28	87	14	41	—	13	3	—	—	—	—	—
28	276	760	86	90	96	20	16	21	50	198	136	1	104	22	57	—	32	—	—	—	—	—	—
29	60	700	63	70	74	4	17	9	27	2	279	5	154	49	6	—	37	61	—	—	—	—	—
30	16	11	1	1	1	2	—	2	3	—	—	—	43	9	3	—	5	—	—	—	—	—	—
31	143	52	5	5	9	5	3	3	6	41	2	—	18	5	12	—	3	—	4	—	—	—	—
32	150	134	6	8	11	9	7	4	2	13	2	—	—	8	8	—	5	—	53	—	—	—	—
33	280	78	15	7	7	8	14	3	23	13	—	—	132	35	11	—	28	—	—	—	—	—	—
34	124	31	5	8	4	4	3	1	10	16	—	—	61	20	3	—	14	—	—	—	—	—	—
35	173	1	7	2	—	18	2	—	—	43	—	—	27	16	36	—	16	—	—	—	—	—	—
36	621	122	44	31	10	31	12	9	12	183	—	—	214	49	7	—	31	—	—	—	—	—	—
37	40	2	1	3	—	1	1	—	—	12	—	—	45	34	—	—	26	—	—	—	—	—	—
38	1164	452	125	121	61	41	91	50	108	179	—	—	374	254	24	—	109	—	—	—	—	—	—
39	189	65	9	7	4	8	1	2	6	36	—	—	29	21	31	—	11	—	—	—	—	—	—
40	2387	690	113	93	23	78	32	10	66	208	—	—	52	95	20	—	65	—	—	26	—	—	—
41	822	344	64	54	25	67	21	8	36	95	—	—	43	109	37	—	89	—	—	18	—	—	—
42	745	155	48	44	6	61	15	8	23	55	—	—	21	61	56	—	50	—	—	8	—	—	43
43	26	16	4	3	—	1	—	3	4	7	—	—	—	2	—	—	2	—	—	3	—	—	—
44	1485	742	89	58	20[f]	131	45	38	68	30	—	—	2	220	9	—	93	—	—	16	—	—	113
45	2600	773	267	218	17[f]	224	95	54	272	110	—	—	8	190	39	—	168	—	—	12	—	5	120
46	76	—	4	6	—	5	—	2	—	8	—	—	9	6	—	—	4	—	—	34	—	—	—
47	1158	—	55	51	—	49	23	17	26	110	—	—	10	93	—	5	44	—	—	3	94	10	—
48	426	—	28	19	—	24	5	2	15	197	—	—	5	65	—	—	36	—	—	38	11	5	—
49	1702	—	121	116	—	124	55	21	49	635	—	—	6	148	—	9	74	—	—	56	31	30	—
50	1371	—	62	44	—	60	33	12	44	227	—	—	3	102	—	12	67	—	—	61	29	8	4
51	853	—	41	19	—	34	12	1	10	449	—	—	8	81	—	—	29	—	—	32	16	5	—
52	329	—	25	27	—	21	20	1	15	66	—	—	2	22	—	38	34	—	—	97	24	3	—
53	230	—	7	4	—	9	—	1	3	94	—	—	4	15	—	6	21	—	—	15	2	—	—
54	63	—	6	2	—	7	—	—	1	17	—	—	—	6	—	1	6	—	—	3	2	3	—
55	289	—	23	17	—	15	8	2	7	5	—	—	49	20	—	21	18	—	—	—	—	—	—
56	1025	—	106	87	—	120	35	16	46	202	—	—	—	86	—	3	86	—	—	86	74	17	—
57	10	—	3	1	—	5	—	—	—	548	—	—	3	96	—	—	91	—	—	199	37	10	7
58	855	—	49	39	—	85	17	3	19	525	—	—	11	116	—	30	105	—	—	17	23	11	—
Total	20665	12313	2296	2004	1200	1323	903	477	1400	6767	1850	4776	6091	3503	962	125	2295	520	57	754	343	107	287

---

[p] Including 2 "pseudo-nothognathellan" tripodellans

[f] '*Tripodellus flexuosus*'

Preliminary investigation of data

Our study is based on 70 959 individual conodonts derived from 58 samples of Late Devonian age. Geographic derivation and biostratigraphic position of these samples are listed in Table 1. In the bottom lines of the table, a few samples have been added which are mentioned in the text, but which have not been incorporated in the statistical analysis. Frequency data are listed in Table 2. As a rule, form species have been lumped at the generic or subgeneric level. Data include all platform conodonts in the faunas as well as all O and N elements. From the conodonts commonly ascribed to the transition series, only those are considered which according to Klapper and Philip (1972) are incorporated in the *Palmatolepis* apparatus.

Fragmentation of conodonts is a quite common feature in our samples and appears to be mainly due to cleavage. Obviously multiple counts of a single fragmented individual should be avoided, and for this reason only fragments showing some unique feature (e.g. basal cavity or main cusp) have been considered. As a rule we have only considered well- or reasonably well-preserved samples.

For most samples, the sieve fraction below 0.10 mm has been disregarded since identification of juvenile specimens and small fragments in this fraction was found to be quite difficult. Although the eliminated size interval is small with respect to the size range encountered in our material, a considerable percentage of individuals may thus be disregarded. This approach will generally lead to a systematic misrepresentation of original proportions and in evaluating results we will have to take this disturbing factor into account.

According to Klapper & Philip (1972), asymmetrical '*Scutula venusta*' and symmetrical '*Scutula bipennata*' would represent intergrading variants of the A_3 element. However, a preliminary inspection of the material showed that both forms occur throughout the entire range of the form genus. In our view, it is more likely that these long-ranging co-existent forms represent different elements of the apparatus. In order to test this assumption, symmetrical and asymmetrical scutulan conodonts have been treated separately in our study.

As discussed in the introduction, results of Klapper & Philip (1972) and van den Boogaard & Schermerhorn (1975) differed with respect to the identity of the O element of the *Palmatolepis* apparatus. According to the former authors this would be nothognathellan, while the latter authors hardly encountered nothognathellan conodonts in their samples. Instead, they noted a consistent association between other elements of the *Palmatolepis* apparatus and the form species '*Tripodellus robustus*'. An inspection of our material indicates that both views may be correct: '*Tripodellus*' appears to be associated with the subgenus '*Palmatolepis (Deflectolepis)*', and '*Nothognathella*' with the other representatives of '*Palmatolepis*'. In order to test this hypothesis, '*Deflectolepis*' has been treated separately.

There has also been some feed-back from preliminary results to the determination process. Such a feed-back is somewhat dubious from a methodological point of view, but it can also be considered an important result of the quantitative approach. The most important examples concern the form-species '*Nothognathella abnormis*' and '*Nothognathella palmatoformis*'. In an early stage of the study representatives of these rather aberrant species had not been recognized as nothognathellan elements. Upon noticing strongly disagreeing frequencies for the O element and ramiform elements of the hypothetical *Palmatolepis* apparatus in certain samples, we began to look for misclassified nothognathellan elements. It appeared that '*N. abnormis*' originally was classified as '*Ozarkodina?* sp. aff. *regularis*' and '*N. palmatoformis*' as a platform conodont of dubious affinity. Similar problems occurred with respect to '*N. falcata*' and '*N.* sp. cf. *polygnathoidea*'.

For technical reasons, the form genus '*Scaphignathus*' has not been incorporated in the analysis. This form genus is almost exclusively restricted to sample 32 in which it is fairly abundant. As a result of the association measure used in correspondence analysis, this taxon, which is otherwise irrelevant to the purpose of our analysis, would obtain a disproportionate weight.

Analysis at the generic level

The analysis is based on the frequency data presented in Table 2. Calculations have been performed using a FORTRAN programme developed by one of the authors (B. Kuhry). Listings of this programme are available upon request.

Total chi-square for the 58 x 22 contingency table is 89 937. Contributions of the first three factors are respectively 39.7, 23.6 and 11.9% of total chi-square. In Diagrams 1 and 2, factor plots are given for the first and second, respectively second and third factors.

Diagram 1 displays a rather vague curvilinear arrangement of points. Such so-called 'horse-shoe' plots are rather common in correspondence analysis. In this curvilinear arrangement, samples are roughly ordered according to their biostratigraphic position and taxa according to the gravity point of their stratigraphic distribution. More essential is the information on associations of form taxa which will be discussed below.

As shown by Diagram 2, the third axis mainly contrasts '*Icriodus*' and a sample exceedingly rich in this form taxon (no. 57) with all other samples and taxa. In view of current hypotheses on conodont biofacies, in which '*Icriodus*' is thought to be characteristic for shallow water faunas, the third axis to some extent might represent ecological influences. The lack of differentiation along this axis is presumably due to the fact that almost all our samples consist of an assemblage typical for the *Palmatolepis* biofacies. The most important contribution of Diagram 2 to the over-all picture is that it breaks up some of the clusters recognizable in the first diagram.

In Diagram 3 a single-linkage dendrogram is given based on partial chi-square distances computed from the coordinates of taxa on the first nine factors, which together contribute 95.5 percent of total chi-square. Form taxa for which the partial chi-square distance to the nearest other taxon exceeds 2.0 have been omitted. Two different cases are represented in a single figure. In this case, the information on lump taxa (dotted lines) should be disregarded. In general, there is a close agreement between the relationships indicated by the dendrogram and the configuration in the factor plots.

Four different clusters of taxa can be recognized, while a fifth is more controversial:

I. *'Palmatolepis'* s.s. and *'Nothognathella'*. This cluster confirms the hypothesis that most palmatolepan platform conodonts are associated with a nothognathellan O element.

II. *'Prioniodina? smithi'*, *'Palmatodella'*, *'Falcodus'*, *'Scutula venusta'*, and *'Scutula bipennata'*. This cluster consists of all ramiform elements of the hypothetical *Palmatolepis* apparatus. More in particular, the hypothesis is supported that asymmetrical *'S. venusta'* and symmetrical *'S. bipennata'* are separate elements of the apparatus.

III. *'Deflectolepis'* and *'Tripodellus'*. This cluster confirms the hypothesis that palmatolepan conodonts belonging to the form subgenus *'Deflectolepis'* are associated with a tripodellan rather than a nothognathellan element. Although the over-all association between these two form taxa is rather pronounced, a marked difference occurs between their coordinates on the first axis. This is related to a stratigraphical decrease of the ratio *'Deflectolepis'/'Tripodellus'*.

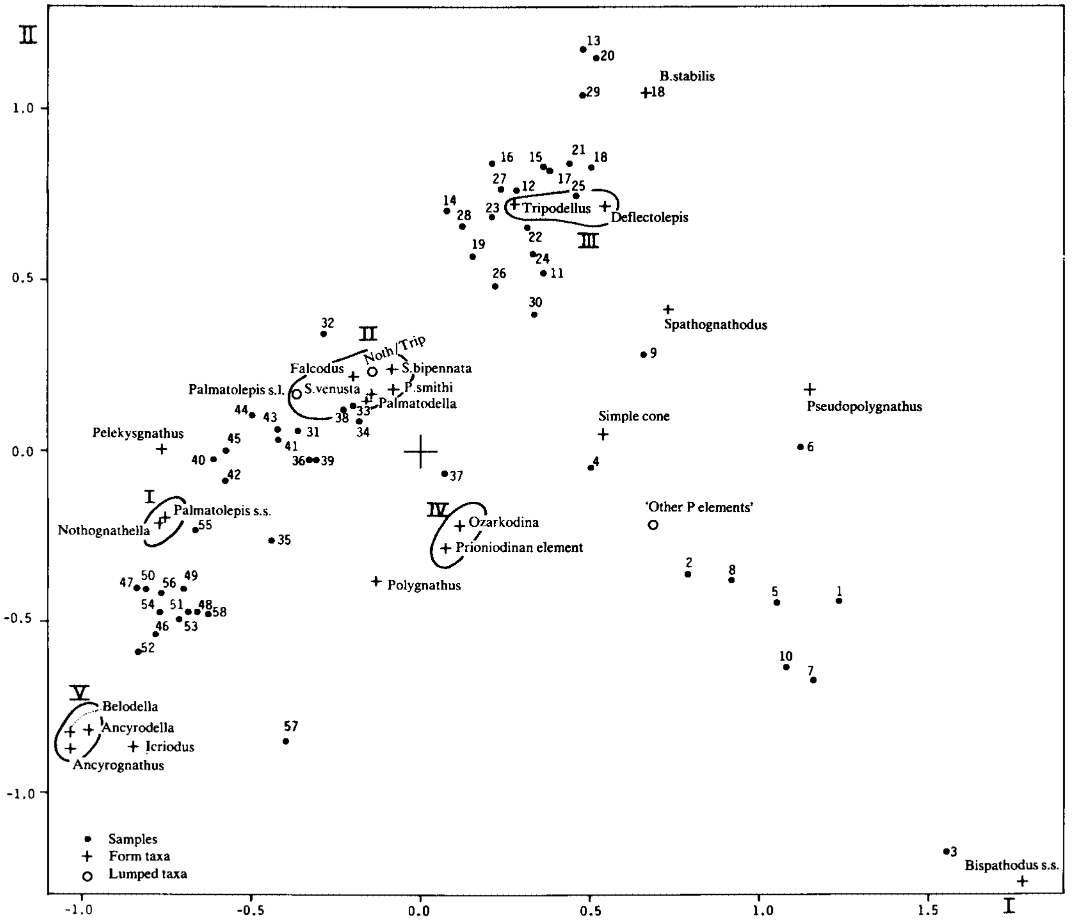

Diagram 1. Scattergram showing projections of points representing taxa and samples on the plane defined by the first two factors.

IV. *'Ozarkodina'* and prioniodinan elements. These presumably represent the O and N elements of other apparatuses in the samples. Conodont form taxa which according to current hypotheses would represent the elements of the transition series of these apparatuses have not been considered in this study.

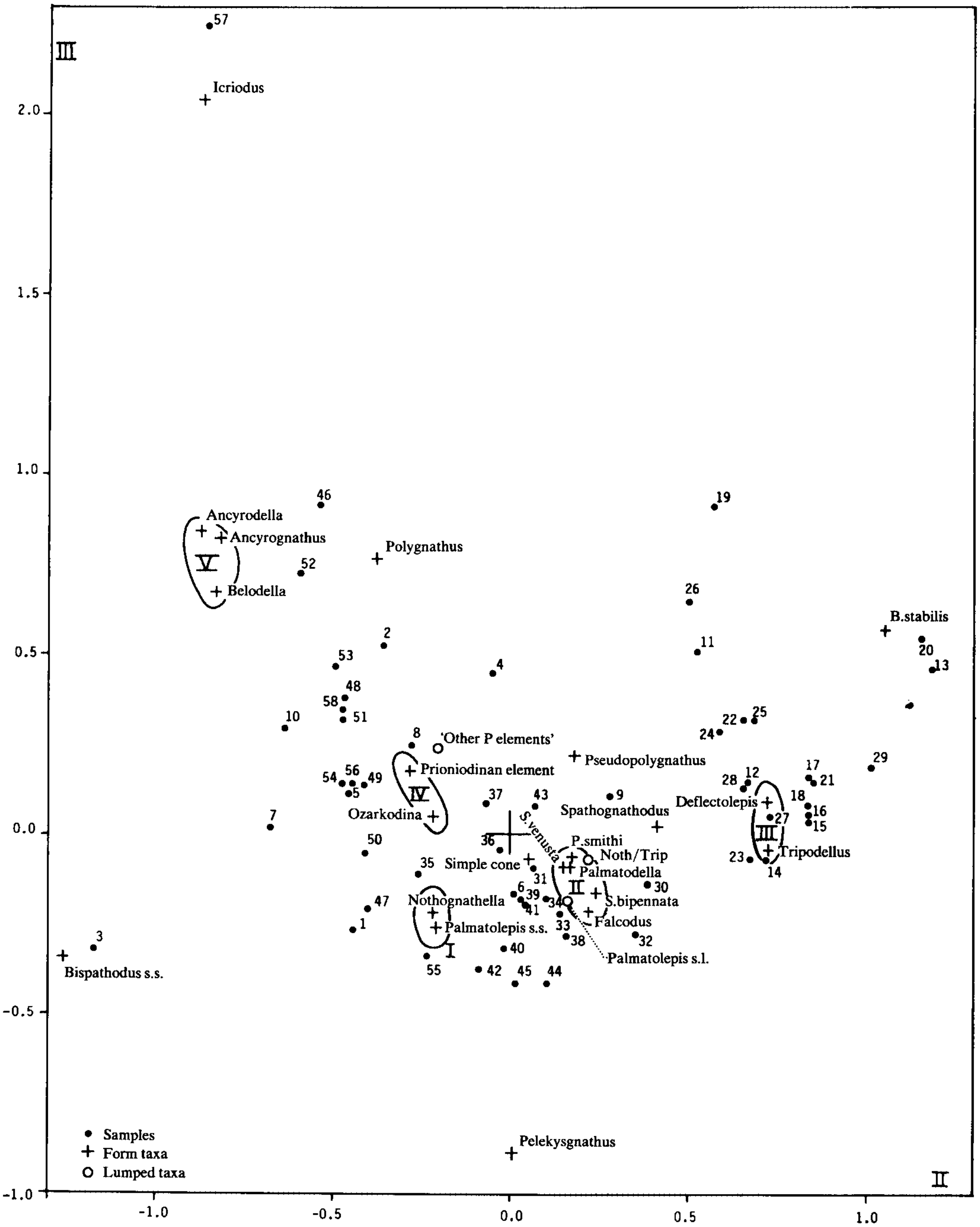

Diagram 2. Scattergram showing projections of points representing taxa and samples on the plane defined by the second and third factor.

V. *'Ancyrodella'*, *'Ancyrognathus'* and *'Belodella'*. While the factor plots indicate a close association between these form genera, this relationship is not at all confirmed by the dendrogram. Ziegler (1972) proposed an apparatus composed of *'Ancyrodella'* and *'Ancyrognathus'*. Although there is a marked stratigraphical association between these form taxa, we do not believe that these formed part of a common apparatus in view of the quite erratic numerical proportions.

Results indicate that *'Nothognathella'* and *'Tripodellus'* do not show a consistent numerical association with the ramiform elements of the hypothetical

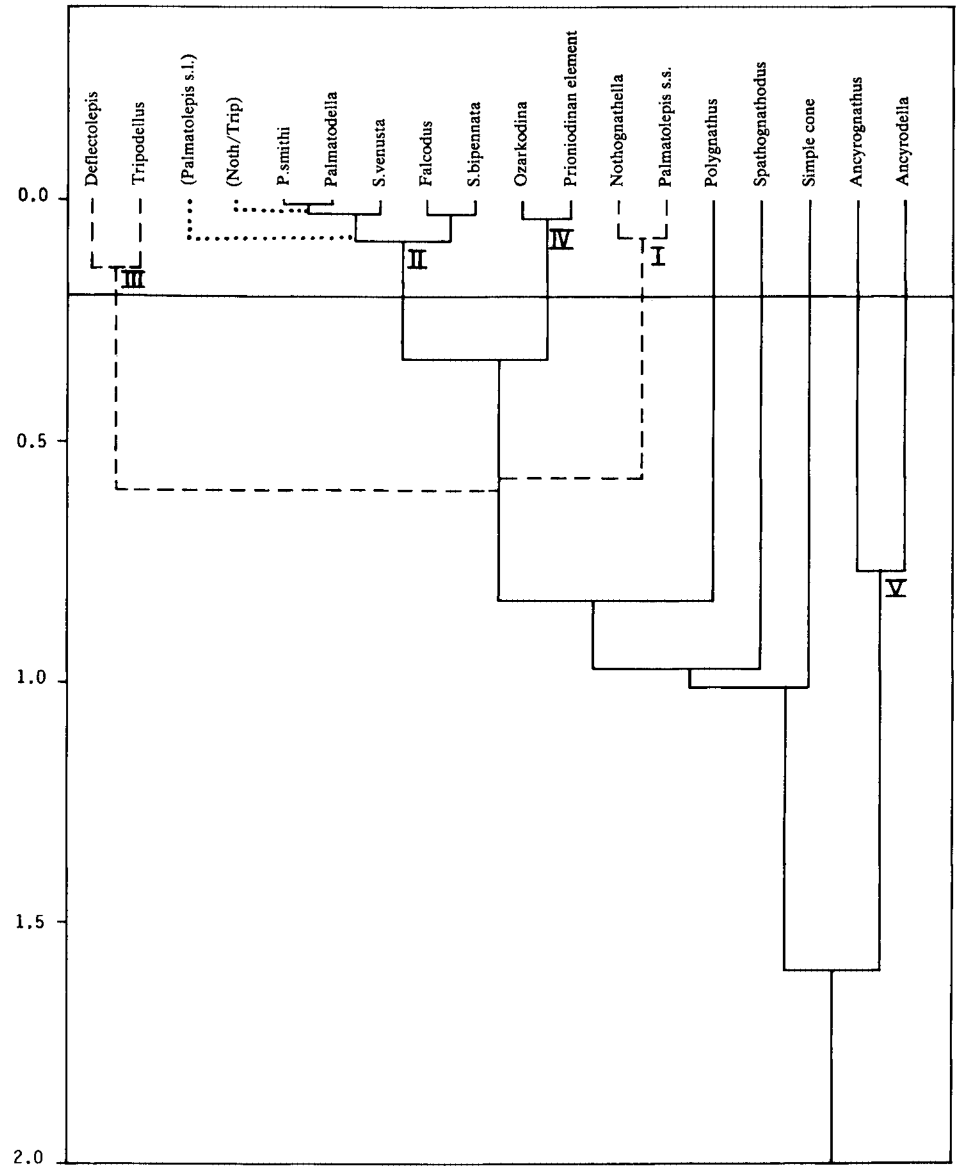

Diagram 3. Single linkage dendrogram based on partial chi-square distances among conodont form taxa.

Palmatolepis apparatus. Moreover, the bipartition of the form genus *'Palmatolepis'* precludes an evaluation of the complete apparatus. Therefore, we have calculated the position of the lump categories *'Palmatolepis'* s.l. and *'Nothognathella'*/ *'Tripodellus'* by means of the algorithm of weighted averages given on p. 5. Calculated positions are given on Diagrams 1 and 2, and indicate a close numerical association of these lump taxa with the ramiform elements of cluster II. By using the same algorithm, partial chi-square distances between these lump taxa and other form taxa can be calculated. The shortest links are indicated by dotted lines in Diagram 3. As a matter of fact, we have carried out a separate analysis based on a priori lumping of P and O elements of this apparatus. The resulting factor plots gave essentially the same information as those in Diagrams 1 and 2 and the dendrogram was similar to Diagram 3 when dashed lines are disregarded.

The results indicate that the *Palmatolepis* apparatus consists of palmatolepan; tripodellan or nothognathellan, palmatodellan, smithiform, falcodontan, as well as asymmetrical and symmetrical scutulan elements. Thus, our preliminary hypothesis on the apparatus is confirmed.

Lange (1968) described a coprolitic assemblage consisting of *'Icriodus'* and simple cones. The evidence that this assemblage corresponds to a natural apparatus is not very strong since no pairwise arrangement of simple cones could be demonstrated. For various reasons, an apparatus consisting of these elements is assumed by Klapper & Philip (1971, 1972), Ziegler (1972), Klapper & Ziegler (1975), and Nicoll (1977). Bultynck (1972) opposed this view, since he only encountered simple cones in 20 out of 450 *'Icriodus'*-bearing samples of Middle Devonian age. Carls (1977) reports extreme variations (roughly between 40 and 0.04) in the frequency ratio *'Icriodus'*/simple cones and gives sound arguments that this variation is not due to agents such as sedimentary sorting. In our material, simple cones are encountered in 40 samples and *'Icriodus'* in 22 samples, but these forms occur together in only 9 samples. Although it is probable that simple cones as a result of their slender form are systematically underrepresented in our samples due to the elimination of the finest sieve fraction, we do not see how this effect or any other disturbing agent could be responsible for this complete lack of association. With Bultynck (1972), we conclude that it is extremely unlikely that these forms belonged to a common apparatus.

None of the remaining platform genera plots close to the cluster formed by *'Ozarkodina'* and prioniodinan elements. In fact, no lump category consisting of two or more of the remaining platform genera can be found which plots close to this cluster. As an example, a point is indicated in Diagrams 1 and 2 which is labeled 'other platforms' and which represents the lump category consisting of *'Spathognathodus'*, *'Bispathodus'* s.s., *'B. stabilis'*, *'Polygnathus'*, and *'Pseudopolygnathus'*. This lack of numerical association could imply that these platform conodonts or a majority of them formed part of mono-element apparatuses in agreement with the opinion of Ziegler (1972). Alternatively, one could also assume that these platform conodonts formed part of type 1 apparatuses sensu Klapper & Philip (1971, 1972) and that the lack of numerical association between P and other elements is due to the occurrence of apparatuses consisting of O and ramiform elements but lacking P elements (type 3 apparatuses of Klapper & Philip, type c apparatuses of Ziegler). Obviously, a thorough taxonomical study of the ozarkodinan and ramiform conodonts would be required in order to clarify this point.

Relative frequencies of elements

If the elements of apparatuses would have occurred in fixed mutual proportions in living conodontophorids, and if original proportions would not have been distorted by post-mortem processes, results of chi-square tests for constant relative frequencies should be non-significant for elements belonging to a single type of apparatus. Moreover, marginal frequencies (added frequencies over all samples) would represent an unbiased estimate of original proportions in the apparatus. However, almost all pertinent chi-square tests lead to a rejection of the underlying hypothesis.

A huge chi-square value of 2612 is obtained for the 58 x 7 contingency table listing the frequency distribution of the hypothetical elements of the *Palmatolepis* apparatus. If the platform element is omitted, a considerably lower, but still highly significant, value is obtained (chi-square 713 with 285 degrees of freedom). With exception of the pair '*P. smithi*' and '*P. delicatula*' (chi-square 64.0 with 57 degrees of freedom), all chi-square tests dealing with pairwise combinations of elements of the *Palmatolepis* apparatus lead to a rejection of the hypothesis of constant mutual proportions.

Marginal frequencies for '*Palmatolepis*' s.l., the lump taxon '*Tripodellus*'/ '*Nothognathella*', '*Palmatodella*', '*P. smithi*', '*Falcodus*, '*S. venusta*', and '*S. bipennata*' are 32978, 2539, 2296, 2004, 1400, 903, and 477, respectively. The simplest ratio for which chi-square is accepted (3.40 with 6 degrees of freedom) is 144 : 11 : 10 : 9 : 6 : 4 : 2. However, the value of this estimate is doubtful in view of the large fluctuations of proportions from sample to sample and the possibility of systematic errors due to a variety of causes. The coprolitic *Palmatolepis* assemblage of Lange (1968) is interpreted by us as representing a 2 : 2 : 2 : 4 : 2 : 2 : 1 ratio. With respect to this standard, our material shows an outrageous surplus in P elements and notable differences in relative frequencies of other elements.

A surplus of P elements is not only observed for the *Palmatolepis* apparatus, but also for '*Spathognathodus*', '*Bispathodus*', and '*Polygnathus*' with respect to '*Ozarkodina*' and prioniodinan elements, in particular in younger samples (1 to 32). In older samples, the deficit in '*Ozarkodina*' is less drastic, and in a few samples (44 and 45) a surplus of the latter element is found.

Ziegler (1972) and Ziegler & Lindström (1975) interpreted the surplus of palmatolepan and polygnathan conodonts with respect to ramiform conodonts as an indication that these did not belong to a common apparatus. They suggested that these platform conodonts occurred in mono-element apparatuses, which would have been derived from more complex apparatuses by phylogenetical reduction. In the framework of this model, Ziegler has to consider Lange's *Palmatolepis* assemblage as a mixture of an apparatus consisting of nothognathellan and ramiform elements (his apparatus e) and a pair of platform conodonts. However, the results of our multivariate analysis indicate a consistent numerical association of '*Palmatolepis*' with the other elements encountered in Lange's assemblage. Moreover, as will be demonstrated in the next chapter, stocks of '*Palmatolepis*' are associated with characteristic nothognathellan and tripodellan O elements. Therefore, we reject the hypothesis of Ziegler concerning the *Palmatolepis* apparatus.

An excess of P elements has been observed by many other authors e.g. Carls (1977) for Late Silurian and Devonian faunas; Rexroad (1969), Rhodes, Austin & Druce (1969), Koike (1971), von Bitter (1972), and Austin & Hill (1973) for Carboniferous faunas; van den Boogaard & Simon (1973) and Ramovš (1978) for Triassic faunas. Apparently, a predominance of P elements is characteristic for most Devonian and Carboniferous faunas, including those rich in *Lewistonella* and *Scottognathus* (von Bitter, 1972). On the other hand, classical natural assemblages such as *Lochriea, Lewistonella, Illinella,* and *Scottognathus,* the assemblage containing '*Spathognathodus steinhornensis*' described by Mashkova (1972), and the coprolitic '*Palmatolepis*'- and '*Spathognathodus*'-bearing assemblages of Lange (1968) rarely contain more than one pair of platform conodonts. In fact there are, as far as we know, no records of a pronounced surplus of P elements in descriptions of natural assemblages.

Although samples supposedly have been subjected to distortions of original proportions due to a variety of causes, we are convinced with Carls (1977) that such processes in general cannot account for the drastic overrepresentation of P elements. Our samples are derived from fine-grained sediments which do not show evidence of sedimentary sorting and tend to contain individuals in all ontogenetic stages. A strong influence of post-depositional solution processes is unlikely, since conodonts consist of resistant calcium phosphate and since we did not observe evidence for partial solution in our samples. If sedimentary sorting played a major part, one would expect to find as many samples with a deficiency as samples with a surplus of P elements, but the former category is extremely rare (see also Ziegler, 1972). In our material, frequencies of O elements are of the same magnitude as those of ramiform elements. Among these O elements are robust nothognathellan conodonts such as '*N. brevidonta*', '*N. palmatoformis*', and '*N. typicalis*', which cannot be expected to behave essentially similar as ramiform elements in response to post-mortem processes which drastically affect the relative frequencies of P elements. Extensive arguments of this type are presented by Carls (1977).

Numerical tests can be devised allowing an appreciation of the influence of several disturbing factors.

For reasons discussed above, the sieve fraction below 0.10 mm has been eliminated from most of our samples. Unsieved samples are mainly derived from the *Polygnathus styriacus* Zone in the Iberian peninsula. Marginal totals for the elements of the *Palmatolepis* apparatus in these samples have been compared with those of a control group of samples from which the finest sieve fraction has been eliminated. Data are summarized in Table 3a and do not give an indication of a strong influence of sieving on the mutual proportions of elements in the *Palmatolepis* apparatus. In fact, chi-square is only 14.1 (6 degrees of freedom), which is significant at a 95%, but not at a 99% level.

A prominent feature in our samples is fragmentation, which appears to be mainly due to cleavage. This process might affect ramiform elements more than solid platforms, and in addition might lead to identification problems affecting certain elements more than others. In order to test the influence of fragmentation, we have divided samples in two groups on the basis of a visual estimation of the degree of fragmentation. Marginal subtotals for the two categories are given in Table 3b. In this case, chi-square is highly significant (116 with 6 degrees of freedom). More intensively fragmented samples are characterized by lower relative frequencies of N and A elements with respect

Table 3a. Influence of elimination of the fraction < 0.10 mm on proportions of elements of the *Palmatolepis* apparatus.

	P	O	N_1	N_2	A_1	A_2	A_3
Sieved (1)	3864	339	298	230	161	113	52
Unsieved (2)	4056	406	301	304	147	94	64

(1) Samples 12, 15, 18, 22 - 24. (2) Samples 14, 16, 17, 19 - 21, 25 - 29.

Table 3b. Influence of fragmentation on proportions of elements of the *Palmatolepis* apparatus.

	P	O	N_1	N_2	A_1	A_2	A_3
Well-preserved (1)	14620	1176	1138	1002	760	465	250
Moderately fragmented (2)	18358	1363	1158	1002	640	438	227

(1) Samples 1, 4 - 9, 13, 25, 39, 42, 44 - 47, 49, 50, 52 - 56. (2) All other samples.

to P and O elements. However, degree of fragmentation hardly affects the ratio of P and O elements, and as such cannot account for the surplus of P elements.

A general test for the influence of post-mortem processes including sedimentary sorting and differential preservation can be based on a comparison of the ratio of P and other elements in different groups of apparatuses. If the excess of P elements would mainly be due to post-mortem processes, one would expect a positive correlation of these ratios over a series of samples. We have computed the frequency ratios '*Deflectolepis*'/'*Tripodellus*' and '*Palmatolepis*' s.s./'*Nothognathella*' for the 28 samples in which these four form taxa co-occur. Spearman's rank correlation coefficient for these ratios is -0.29, a negative value close to the 95% significance boundary. We consider this result as a strong indication, that the surplus of P elements is not due to post-mortem processes.

We have considered the possibility that platform elements might have been distributed over other parts of the organism than ramiform elements which would diminish the chance that all elements would be preserved together or be recognized as constituents of a single individual. However, if this model were correct, one would expect a larger number of incomplete assemblages consisting of ramiform elements only than recorded in literature. Moreover, extreme fluctuations in mutual proportions of elements at the intraspecific level as documented by Carls can hardly be explained by a model involving the assumption that sample compositions essentially reflect the composition of individuals.

It is possible, even likely, that discrete variation occurred with respect to the composition of apparatuses both on the intra- and interspecific level. This may explain moderate deviations of mutual proportions of ramiform elements with respect to expected or feasible ratios: Carls' observation of a deficit in A_3 elements, the curious 6 : 4 : 2 ratio for the marginal frequencies of A elements in our *Palmatolepis* material which may be due to a mixture of apparatuses characterized by a 4 : 2 : 1 and a 2 : 2 : 1 ratio, and similar discrepancies. We have considered the possibility that the surplus of P elements might be caused by a dimorphism involving the presence or absence of ramiform elements. Since this dimorphism would be a consistent feature over a broad taxonomic group, we might be dealing with sexual dimorphism in combination with a pronounced unbalance of the sexes. In this connection Denham's (1944) interpretation of conodonts as copulatory structures may be mentioned. However, this explanation does not appear to be compatible with the composition of some of Carls' samples consisting of dominant P elements, common O elements and rare ramiform elements.

Carls (1977) developed a model in which the excess of P elements and the more moderate surplus of O elements is explained by repeated loss and regeneration of these elements. He arrived primarily at this solution by elimination of other alternatives, and took pains to show that it is compatible with other information. Nevertheless, no strong positive arguments are given in favour of this hypothesis involving a curious loss and rapid replacement of apparently undamaged hard parts up to twenty times during the lifetime of the average individual. According to this model, the rather large fluctuations in mutual proportions of P and O elements on the one hand and ramiform elements on the other in Carls' material could possibly be explained by assuming a more extensive post-mortal transport of decaying remains in comparison to drop-out elements. Such a mechanism differs from post-mortem agencies working on the separate elements, which above have been rejected as a main cause for the surplus in P elements. Actually, Carls' data agree rather well with an average initial ratio of 2 : 2 : 9 for P, O, and cumulated ramiform elements, and a corresponding average replacement ratio of 15 : 5 : 0.

Though we are of the opinion that further corroboration of Carls' hypothesis remains highly desirable, we fail to see any alternative for Carls' solution.

Analysis at the subgeneric and specific level

The form genus *'Palmatolepis'* is characterized by a rapid morphological evolution and diversification. The O element of the apparatus, which was represented by the form genera *'Nothognathella'* and *'Tripodellus'*, also underwent considerable morphological changes. In contrast, the other five elements of the apparatus have remained quite stable.

A distribution chart for species belonging to the form genus *'Palmatolepis'* is given in Table 4, while corresponding data for the form genera *'Tripodellus'* and *'Nothognathella'* are listed in Table 5. Since species of *'Palmatolepis'* are rarely consistently associated with a single species of *'Tripodellus'* or *'Nothognathella'*, standard numerical techniques are of rather restricted use as a search mechanism. Instead, we have used a type of reasoning similar to that of Klapper & Philip (1971) involving the following types of argumentation:

1) evidence from samples containing a single P and/or O element
2) elimination of known combinations of P and O elements from more complex samples
3) morphological relationships among P or O elements
4) evaluation of frequency numbers

The association between *'T. robustus'* and *'P. gracilis'* is obvious in samples 1 to 11 and confirmed in samples 12 to 30. In several older samples, in particular 41 and 42, *'T. robustus'* is not accompanied by *'P. gracilis'*. In these samples,

Table 4. Frequency distribution of form species of *Palmatolepis*.

Serial number of sample	*P. gracilis*	*P. glabra* group	*P. subrecta* group	*P. schindewolfi* group	*P. minuta*	*P. distorta*	*P. quadrantinodosalobata*	*P.* cf. *regularis*	*P. gigas*	*P. rugosa*	*P. marginifera*	*P. rhomboidea*	*P. triangularis*	*P. crepida*	*P. termini*	*P. tenuipunctata*	*P. gonioclymeniae*	*P. manca*	*P. linguiformis*
1	324	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2	48	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3	426	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
4	47	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5	28	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6	232	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7	45	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8	78	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9	633	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	31	—	—
10	52	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
11	33	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12	1439	—	—	268	—	—	—	—	—	12	—	—	—	—	—	—	—	—	—
13	55	—	—	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
14	87	—	—	37	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
15	528	—	—	124	—	—	—	—	—	—	—	—	—	—	—	—	—	8	—
16	229	—	—	62	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—
17	204	—	—	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
18	910	—	—	65	—	—	—	—	—	—	—	—	—	—	—	—	—	33	—
19	63	—	—	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
20	46	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
21	51	—	—	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
22	135	—	—	43	—	—	—	—	—	12	—	—	—	—	—	—	—	—	—
23	145	—	—	63	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
24	76	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
25	125	—	—	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
26	254	—	—	30	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
27	820	16	—	168	—	—	—	—	—	10	—	—	—	—	—	—	—	—	—
28	760	58	—	212	—	—	—	—	—	6	—	—	—	—	—	—	—	—	—
29	700	5	—	54	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
30	11	7	—	8	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
31	27	15	—	112	25	—	—	—	—	16	—	—	—	—	—	—	—	—	—
32	134	80	—	62	—	1	—	—	—	7	—	—	—	—	—	—	—	—	—
33	70	83	—	5	8	122	—	—	—	—	70	—	—	—	—	—	—	—	—
34	—	47	—	1	31	62	—	—	—	—	14	—	—	—	—	—	—	—	—
35	—	53	—	—	1	89	—	—	—	—	31	—	—	—	—	—	—	—	—
36	101	240	—	11	21	237	—	—	—	16	117	—	—	—	—	—	—	—	—
37	—	3	—	—	2	30	—	—	—	2	5	—	—	—	—	—	—	—	—
38	333	476	—	54	119	469	—	—	—	10	155	—	—	—	—	—	—	—	—
39	47	121	—	5	18	—	—	—	—	4	59	—	—	—	—	—	—	—	—
40	690[m]	2187	—	95	—[m]	—	—	—	—	—	105	—	—	—	—	—	—	—	—
41	—	593	—	6	344	—	5	—	—	3	70	145	—	—	—	—	—	—	—
42	—	548	—	—	155	—	129	55	—	—	8[i]	—	—	—	—	5	—	—	—
43	—	16	—	—	16	—	5	—	—	—	—	—	—	—	—	5[s]	—	—	—
44	—	—	—	—	742	—	247	159	—	—	—	25[d]	—	134	268	652	—	—	—
45	—	—	—	—	773	—	454	7	—	—	—	—	—	197	147	1795	—	—	—
46	—	—	—	—	—	—	—	—	—	—	—	—	76	—	—	—	—	—	—
47	—	—	1090	—	—	—	—	—	36	—	—	—	—	—	—	—	—	—	32
48	—	—	134	—	—	—	—	—	285	—	—	—	—	—	—	—	—	—	7
49	—	—	1674	—	—	—	—	—	28	—	—	—	—	—	—	—	—	—	—
50	—	—	1189	—	—	—	—	—	182	—	—	—	—	—	—	—	—	—	—
51	—	—	853	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
52	—	—	329	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
53	—	—	226	—	—	—	—	—	4	—	—	—	—	—	—	—	—	—	—
54	—	—	61	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—
55	—	—	289	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
56	—	—	1025	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
57	—	—	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
58	—	—	855	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

[m] = total of *P. gracilis* and *P. minuta* in *gracilis* column

[i] = *Palmatolepis quadrantinodosa inflexa*

[d] = *Palmatolepis delicatula protorhomboidea*

[s] = *Palmatolepis subperlobata*

Table 5. Frequency distribution of form species of *Nothognathella*.

Serial number of sample	*N. typicalis*	*N. ziegleri*	*N. falcata*	*N. palmatoformis*	*N. condita*	*N. abnormis* var. d	*N. abnormis* var. c	*N. iowaensis*	*N. sublaevis*	*N.* aff. *sublaevis*	*N. brevidonta* - *N. abnormis* var. a	"pseudo *N. sublaevis*"	*N.* cf. *polygnathoidea*
12	—	15	—	—	—	—	—	—	—	—	—	—	—
13	—	2	—	—	—	—	—	—	—	—	—	—	—
14	1	—	—	—	—	—	—	—	—	—	—	—	—
15	—	7	—	—	—	—	—	—	—	—	—	—	—
16	—	2	—	—	—	—	—	—	—	—	—	—	—
17	—	2	—	—	—	—	—	—	—	—	—	—	—
18	—	3	—	—	—	—	—	—	—	—	—	—	—
19	1	—	—	—	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—	—	—	—	—
21	—	—	—	—	—	—	—	—	—	—	—	—	—
22	2	3	—	—	—	—	—	—	—	—	—	—	—
23	—	2	—	—	—	—	—	—	—	—	—	—	—
24	—	—	—	—	—	—	—	—	—	—	—	—	—
25	1	—	—	—	—	—	—	—	—	—	—	—	—
26	4	3	—	—	—	—	—	—	—	—	—	—	—
27	3	17	—	—	—	—	—	—	—	—	—	—	—
28	8	10	2	—	—	—	—	—	—	—	—	—	—
29	—	4	—	—	—	—	—	—	—	—	—	—	—
30	2	—	—	—	—	—	—	—	—	—	—	—	—
31	5	—	—	—	—	—	—	—	—	—	—	—	—
32	4	2	3	—	—	—	—	—	—	—	—	—	—
33	—	—	—	2	2	—	—	—	—	—	—	—	4
34	—	—	—	2	—	—	—	—	—	—	—	—	2
35	—	—	—	7	2	—	—	—	—	—	—	—	9
36	1	—	13	9	4	—	—	—	—	—	—	—	4
37	—	—	—	—	—	—	—	—	—	—	—	—	1
38	3	—	11	14	2	—	—	—	—	—	—	—	11
39	1	—	1	5	1	—	—	—	—	—	—	—	—
40	10	—	47	13	8	—	—	—	—	—	—	—	—
41	—	—	2	61	4	—	—	—	—	—	—	—	—
42	—	—	—	51	1	7	—	2	—	—	—	—	—
43	—	—	—	1	—	—	—	—	—	—	—	—	—
44	—	—	—	—	2	12	47	27	30	13	—	—	—
45	—	—	—	—	—	46	138	1	24	15	—	—	—
46	—	—	—	—	—	—	—	—	—	—	5[t]	—	—
47	—	—	—	—	—	—	—	—	—	—	48	1	—
48	—	—	—	—	—	—	—	—	—	—	23	1	—
49	—	—	—	—	—	—	—	—	—	—	124	—	—
50	—	—	—	—	—	—	—	—	—	—	60	—	—
51	—	—	—	—	—	—	—	—	—	—	34	—	—
52	—	—	—	—	—	—	—	—	—	—	21	—	—
53	—	—	—	—	—	—	—	—	—	—	9	—	—
54	—	—	—	—	—	—	—	—	—	—	7	—	—
55	—	—	—	—	—	—	—	—	—	—	15	—	—
56	—	—	—	—	—	—	—	—	—	—	120	—	—
57	—	—	—	—	—	—	—	—	—	—	5	—	—
58	—	—	—	—	—	—	—	—	—	—	85	—	—

[t] *abnormis*-like O element of *P. triangularis*

'T. robustus' is presumably associated with *'P. minuta'*, a form which is morphologically quite similar to *'P. gracilis'*. In samples 44 and 45 on the other hand, *'P. minuta'* is not accompanied by *'T. robustus'*. Instead, representatives of *'T. flexuosus'* are encountered. In view of the morphological similarity between both representatives of the form genus *'Tripodellus'*, it is likely that *'P. minuta'* is associated with *'T. flexuosus'* in spite of the rather low relative frequency of the latter form. *'P. manca'* is too rare in our material to allow any definite conclusion on the corresponding O element. The O element corresponding to *'P. gonioclymeniae'* is rather similar to *'N. falcata'* at first view. However, a careful study of its morphology reveals characteristic features of *'Tripodellus'* (see systematical section).

In addition to *'P. gracilis'* and *'T. robustus'* as dominant P and O elements, samples 12 to 31 contain representatives of the *'P. schindewolfi'* group as well as *'N. ziegleri'* and *'N. typicalis'*. The latter forms are quite similar and may be intergrading variants in the samples in which they co-occur. *'N. typicalis'* and the *'P. schindewolfi'* group occur in subordinate numbers down to the level of sample 41. Both in range and frequency numbers, the correspondence between these groups of P and O elements is quite striking. In some of these samples, representatives of the *'P. rugosa'* group occur in subordinate numbers. This group is generally considered a close relative of the *'P. schindewolfi'* group. Although the *'P. rugosa'* group is relatively rare, it occurs in sufficient numbers to expect the presence of corresponding O elements. Since no other potential candidates are found, this group must also be associated with an O element resembling *'N. typicalis'*.

More complications arose with respect to the identification of O elements corresponding to the *'P. glabra'* stock (samples 27 to 43), of which representatives include *'P. lepta'*, *'P. pectinata'*, *'P. prima'*, and *'P. distorta'*. Since problems have been encountered in identifying juveniles, the former three form species have been lumped to a *'P. glabra'* group. In some of the younger samples (28, 32), *'P. lepta'* is obviously associated with *'N. falcata'*, while *'P. prima'* is clearly associated with *'N. palmatoformis'* in the oldest samples (41 and 42). At first view, slender *'N. falcata'* seems to be totally unrelated to sturdy *'N. palmatoformis'*. However, a phylogenetical relationship is made more plausible by the discovery of transitional forms (see the systematical section). The numerical association and agreement in range between the *'P. glabra'* group and the lump category *'N. falcata'*/*'N. palmatoformis'* is satisfactory. We encountered severe problems in identifying the O element corresponding to *'P. distorta'*, and have considered the possibilities that this form species corresponded to *'T. robustus'* or formed part of an apparatus in which the O element was lacking. Only at a very late stage of the study, while studying a sample which has not been included in the counts (see the systematical section), we identified the O element as *'N.* cf. *polygnathoidea'*, a form hitherto misclassified under various headings. The phylogenetical derivation of this element is not clear. *P. distorta* is provisionally included in *Panderolepis* because of the similarity of the P element to *'P. pectinata'*.

The association of *'P. marginifera'* and *'N. condita'* is rather obvious in samples 33 to 41. In samples 42 and 44, *'N. condita'* is apparently associated with *'P. inflexa'* and *'P. delicatula protorhomboidea'*, respectively. The identity of the O element corresponding to *'P. rhomboidea'* is more controversial (sample 41). Frequency data support an association with *'N. palmatoformis'* rather than with *'N. condita'*, while platform morphology supports an affiliation with its supposed ancestor '*P. delicatula protorhomboidea*' rather than with the '*P. glabra*' stock. Additional material is required before a definite conclusion can be drawn.

Our material includes only five samples from the *P. crepida* and *P. rhomboidea* Zone (41 to 45), the level at which the form genus '*Palmatolepis*' displays its maximal diversification. Fortunately, two of our largest samples are derived from this level (44 and 45), and we can heavily draw on numerical evidence in unraveling relationships of P and O elements. Data give a strong indication for an association of '*P. tenuipunctata*' with '*N. abnormis*' var. c, '*P. quadrantinodosalobata* with '*N. abnormis*' var. d, and '*P. regularis*' with '*N. iowaensis*'. Frequency data moreover support an association of the remaining form-species '*P. crepida*' and '*P. termini*' with the two varieties of '*N. sublaevis*'.

Samples 47 tot 58 contain platform conodonts of the '*P. subrecta*' group and nothognathellan forms ranging between '*N. brevidonta*' and a morphologically rather similar variety of '*N. abnormis*' (var. a). '*P. subrecta*' is the dominant form, but in several samples forms identifiable as '*P. hassi*', '*P. unicornis*' and '*P. proversa*' are encountered. The latter form occurs in a sample which contains typical '*N. brevidonta*' as only nothognathellan element. Younger samples contain '*P. gigas*', which is apparently associated with '*N. abnormis*' var. a (sample 48). '*P. linguiformis*' appears to be associated with a nothognathellan form bearing some resemblance to '*N. sublaevis*'. Sample 46 contains individuals of '*P. triangularis*' together with a smooth variety of '*N. abnormis*' (var. b).

In order to identify matching pairs of P and O elements, an informal evaluation has been made of frequency data. The subgeneric scheme proposed in the systematical section of this paper leads to a lumping of P elements on the one hand and O elements on the other in such a way that a consistent numerical association may be expected. Hence, the validity of the matchings of P and O elements underlying this scheme may be tested by a correspondence analysis based on the frequency data for P and O elements regrouped to subgeneric units (Table 6). The number of conodonts involved is 35 517 and total chi-square for the 58 x 10 contingency table is 53 848. The first three factors represent 94.5% of total information. In Diagram 4, a scattergram is given for the coordinates of taxa on the second and third factor. In geometrical terms, the first factor is mainly effective in elevating P and O elements of *Manticolepis* and samples 44 to 58 two units in a direction perpendicular to the page. The figure shows that the assumptions on relationships between P and O elements as reflected in the subgeneric scheme are in broad lines consistent with numerical data.

The frequency ratio of P over O elements is 10.3 for *Tripodellus,* 14.0 for *Palmatolepis,* 14.2 for *Manticolepis,* 17.7 for *Panderolepis,* and 30.9 for *Conditolepis.* For the latter subgenus, marginal frequencies are rather low and as a result, the ratio estimate may be unreliable. We interpret the rather small differences of the P/O ratio for the other subgenera as additional support for our subgeneric reconstruction.

Table 6. Frequency data for P and O elements regrouped to subgeneric units.

Serial number of sample	*P. (Manticolepis)*		*P. (Palmatolepis)*		*P. (Panderolepis)*		*P. (Conditolepis)*		*P. (Tripodellus)*	
	P element	O element	P element	O element	P element	O element	P element	O element	P element	O element
1	—	—	—	—	—	—	—	—	324	50
2	—	—	—	—	—	—	—	—	48	4
3	—	—	—	—	—	—	—	—	426	52
4	—	—	—	—	—	—	—	—	47	7
5	—	—	—	—	—	—	—	—	28	2
6	—	—	—	—	—	—	—	—	232	26
7	—	—	—	—	—	—	—	—	45	15
8	—	—	—	—	—	—	—	—	78	23
9	—	—	—	—	—	—	—	—	664	145
10	—	—	—	—	—	—	—	—	52	12
11	—	—	—	—	—	—	—	—	33	2
12	—	—	280	15	—	—	—	—	1439	154
13	—	—	6	2	—	—	—	—	55	9
14	—	—	37	1	—	—	—	—	87	10
15	—	—	124	7	—	—	—	—	536	43
16	—	—	65	2	—	—	—	—	229	30
17	—	—	10	2	—	—	—	—	204	12
18	—	—	65	3	—	—	—	—	943	85
19	—	—	12	1	—	—	—	—	63	8
20	—	—	3	—	—	—	—	—	46	2
21	—	—	11	—	—	—	—	—	51	8
22	—	—	55	5	—	—	—	—	135	10
23	—	—	63	2	—	—	—	—	145	9
24	—	—	3	—	—	—	—	—	76	6
25	—	—	19	1	—	—	—	—	125	15
26	—	—	30	7	—	—	—	—	254	13
27	—	—	178	20	16	—	—	—	820	80
28	—	—	218	18	58	2	—	—	760	96
29	—	—	55	4	5	—	—	—	700	74
30	—	—	8	2	8	—	—	—	11	1
31	—	—	128	5	15	—	—	—	52	9
32	—	—	69	6	81	3	—	—	134	11
33	—	—	5	—	205	6	70	22	78	7
34	—	—	1	—	109	4	14	—	31	4
35	—	—	—	—	142	16	31	2	1	—
36	—	—	27	1	477	26	117	4	122	10
37	—	—	2	—	33	1	5	—	2	—
38	—	—	64	3	945	36	155	2	452	61
39	—	—	9	1	121	6	59	1	65	4
40	—	—	95	10	2187	60	105	8	690	23
41	5	—	9	—	593	63	215	4	344	25
42	189	9	—	—	548	51	8	1	155	6
43	10	—	—	—	16	1	—	—	16	—
44	1058	86	—	—	402	43	25	2	742	20
45	2256	185	—	—	344	39	—	—	773	17
46	76	5	—	—	—	—	—	—	—	—
47	1158	49	—	—	—	—	—	—	—	—
48	426	24	—	—	—	—	—	—	—	—
49	1702	124	—	—	—	—	—	—	—	—
50	1371	60	—	—	—	—	—	—	—	—
51	853	34	—	—	—	—	—	—	—	—
52	329	21	—	—	—	—	—	—	—	—
53	230	9	—	—	—	—	—	—	—	—
54	63	7	—	—	—	—	—	—	—	—
55	289	15	—	—	—	—	—	—	—	—
56	1025	120	—	—	—	—	—	—	—	—
57	10	5	—	—	—	—	—	—	—	—
58	855	85	—	—	—	—	—	—	—	—

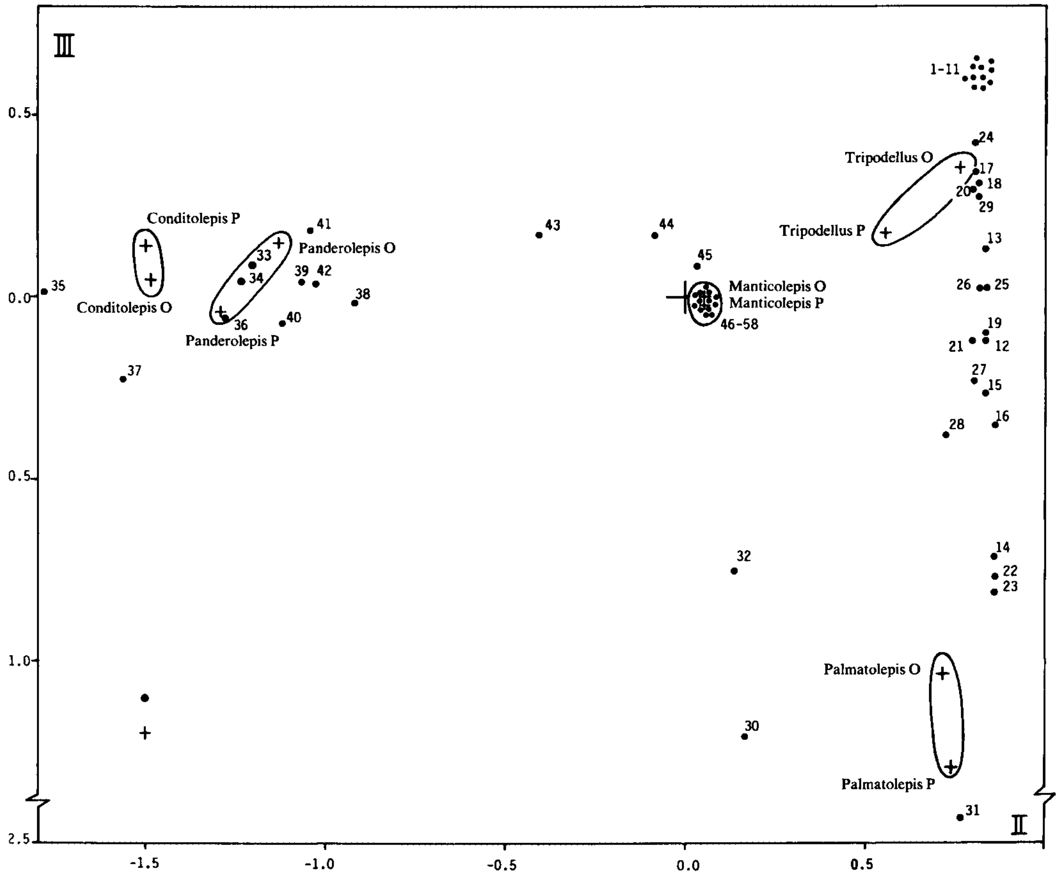

Diagram 4. Scattergram showing projections of points representing samples and P and O elements of subgenera of *Palmatolepis* on the plane defined by the second and third factor.

Systematics

Genus *Palmatolepis* Ulrich & Bassler, 1926

1972 *Palmatodella* Bassler, 1925 — Klapper & Philip, p. 100.

Type species — *Palmatolepis perlobata* Ulrich & Bassler, 1926.

Diagnosis (emend.) — P O N_1 N_2 A_1 A_2 A_3.

Type 1 apparatus in the sense of Klapper and Philip, 1972, of which the P (platform) element is palmatolepan, the O (ozarkodinoid) element is nothognathellan or tripodellan, the N (neoprioniodoid) elements are palmatodellan and smithiform, and the elements of the symmetry transition are falcodontan (A_1), asymmetrical scutulan (A_2) and symmetrical scutulan (A_3).

Discussion — Our reconstruction differs from that of Klapper and Philip in that seven rather than six elements are recognized. Our data indicate that asymmetrical and symmetrical scutulan conodonts must be interpreted as separate elements rather than as intergrading variants of the A_3 element. Consequently, the falcodontan element must be considered as A_1 element. The smithiform element cannot be included in the symmetry transition because of its morphology, and is interpreted as a second N element. Data moreover indicate that the nothognathellan element in certain species is replaced by a tripodellan element.

Klapper and Philip (1972) consider the genus name *Palmatolepis* as a junior synonym of *Palmatodella*. However, the type species of the latter genus (*Palmatodella delicatula* Bassler, 1925) is a morphologically stable element that forms part of a large number of apparatus species characterized by different P and O elements. It does not appear to be possible to reconstruct the apparatus corresponding to the type specimen of '*Palmatodella delicatula*'. In agreement with Walliser's proposal in Marburg 1971 (see Ziegler & Lindström, 1975, p. 579 - 580) we consider the name *Palmatodella* as a nomen dubium. The name *Palmatolepis* should be preserved as the appropriate name for the natural genus not only because the apparatus corresponding to the type specimen can be reconstructed with reasonable confidence, but also because the palmatolepan element is the most characteristic and variable element in this genus.

The P element of *Palmatolepis* underwent during the Late Devonian a rapid development into numerous species and subspecies. Phylogenetic relationships have been discussed by i.a. Müller (1956), Ziegler (1962a), Helms (1963), and Sandberg & Ziegler (1973). According to these authors, several well-defined lineages can be recognized and Helms (1963) has proposed a corresponding subgeneric classification for '*Palmatolepis*'. Although this latter approach has sofar not gained wide support, we think that it is good taxonomical practice to express the existence of clusters of morphologically and phylogenetically related species in formal nomenclature and will therefore follow the approach of Helms. Narrow morphological and presumed phylogenetical relationships between taxa can also be expressed by applying subspecific nomenclature. However, current use of the subspecies category by conodont workers is not always in agreement with the zoological concept which demands that subspecies should be geographically (or chronologically) separated (Mayr, 1969).

Morphological and phylogenetical relationships established among the platform elements are, of course, also valid for the apparatuses containing these platform elements. However, identification of the O elements corresponding to form species of '*Palmatolepis*' yields independent evidence for phylogenetical relationships among representatives of the apparatus genus *Palmatolepis* and allows a critical reappraisal of earlier results. On the whole, our results support existing views on phylogenetic and morphological relationships to a remarkable extent. On the basis of the considerations in the previous paragraph, five subgenera may be recognized: *Palmatolepis (Manticolepis), P. (Tripodellus), P. (Panderolepis), P. (Conditolepis),* and *P. (Palmatolepis).*

The subgenus *Palmatolepis (Manticolepis)* Müller, 1956 is in addition to the typical development of the P elements, also characterized by nothognathellan O elements ranging from '*Nothognathella brevidonta*' in the older species to '*N. abnormis*' in the younger species.

The transition of '*N. brevidonta*' to '*N. abnormis*' has been noted by Druce (1975, p. 129). However, because of the primitive character of '*N. abnormis*' he thought this to be the older form although he had found that it appeared later in the geological column than *'N. brevidonta'*. He believed that the general phylogenetic tendency of the nothognathellid group is to develop an increasingly large platform. This is only part of the picture. Platform development of an originally ozarkodinan form will have resulted in the O element *'Nothognathella klapperi'* of *Mesotaxis*. From *'N. klapperi'* the lineage evolved along *'N. brevidonta'* by platform reduction to *'N. abnormis'* and *'N. abnormis'* – like forms with no platform or almost no platform in the species *Palmatolepis triangularis* and *P. tenuipunctata*. The nothognathellan elements of the younger subgenera *Palmatolepis, Panderolepis* and *Conditolepis* show well developed platforms except for the 'end' forms *'N. falcata'* and *'N. ziegleri'* which again show considerable reduction of platform. The common opinion that these younger subgenera have evolved from *P. triangularis* and in the case of the *glabra* group (= *Panderolepis)* through *P. tenuipunctata,* would imply that the platform-bearing nothognathellan elements of the younger species of *Palmatolepis* have evolved from a nothognathellan element with almost no platform. The phylogenetic tendency thus would be *'Ozarkodina'* – *'Nothognathella'* with large platform - *'Nothognathella'* with almost no platform - *'Nothognathella'* with large platform - *'Nothognathella'* with almost no platform. It is more likely that the younger nothognathellids with platform directly evolved from the older type with platform and that the 'intermediate' stage with almost no platform is nothing but a side lineage. This splitting up of the lineage would have happened somewhere in the *Palmatolepis gigas* Zone and implies that for instance *P. tenuipunctata* is not ancestral to the *P. glabra* group.

The subgenus *Palmatolepis (Palmatolepis)* Ulrich & Bassler in the sense of Helms, 1963 (the *perlobata* lineage of Ziegler, 1962a) does have as typical O element *'Nothognathella typicalis'* which later on develops into *'N. ziegleri'*.

The subgenus *Palmatolepis (Tripodellus)* Sannemann, 1955, is characterized by P elements of the form subgenus *'Deflectolepis'* Müller, 1956, and O elements of the form genus *'Tripodellus'* Sannemann, 1955. *Deflectolepis* is here considered as a junior synonym of *Tripodellus* (see discussion on p. 40).

We considered the possibility of raising this subgenus to the rank of genus because of the occurrence of a different O element. However, the N as well as the A elements cannot be distinguished from those of the other species of the genus *Palmatolepis*. In our opinion all species with these N and A elements should belong to one taxonomic unit at the generic level in order to avoid the problem to what genus one should ascribe isolated palmatodellan, smithiform, falcodontan, and scutulan elements.

The subgenus *Palmatolepis (Panderolepis)* Helms, 1963, has been divided by him into two groups, one around *Palmatolepis glabra* and another which he named the *marginifera* group. Ziegler 1962a recognized a *subperlobata-glabra* lineage and a *crepida-rhomboidea-quadrantinodosa* group. We propose to split this subgenus into two subgenera.

1. *Palmatolepis (Panderolepis)* comprising the species around *Palmatolepis glabra,* characterized by O elements of the lineage *'Nothognathella sublaevis'*, *'N. palmatoformis'* and morphologically closely associated forms which evolve into *'N. falcata'*.
2. *Palmatolepis (Conditolepis)* n. subgen. comprising the *marginifera* group of Helms — the *rhomboidea-quadrantinodosa* group of Ziegler — characterized by the name giving O element *'Nothognathella condita'*.

A rather isolated position is taken by *Palmatolepis* cf. *regularis* which has as an O element *'Nothognathella iowaensis'*. Ziegler as well as Helms placed *P. regularis* in a side-branch.

N elements — The N skeletal elements are palmatodellan and smithiform. We chose to classify the palmatodellan element as N_1 and the smithiform element as N_2 mainly because in Lange's apparatus (1968, pl. 1) the palmatodellan element occurs more to the exterior.

The palmatodellan element encountered in the investigated faunas is predominantly identical or almost identical to the form species *'Palmatodella delicatula'* Bassler, 1925. This form may have undergone some change during evolution. This could not be proven because so many specimens have incomplete bars. However, we got the impression that in younger forms the posterior bar is less fan-like, in other words has denticles that tend to be more equal-sized. In some samples *'Palmatodella unca'* Sannemann, 1955 occurs in minor amounts. It is not impossible that this form is restricted to the apparatus of one of the subgenera or species in particular. However, such a connection could not be established because of lack of sufficient material.

The smithiform element of the *Palmatolepis* apparatus is the form species *'Prioniodina ? smithi'* (Stauffer, 1938). This element is nearly identical in all faunas. We got the impression that during evolution the anterior bar has increased in length but could not prove this because of the great number of incomplete bars. Klapper & Philip (1972) classified the smithiform element as A_1 in a symmetry transition series with *'Falcodus'* (A_2) and *'Scutula venusta'* and *'S. bipennata'* (both as A_3). We believe that the smithiform element does not belong to this transition series but represents a second N element.

A elements — The A_1 element is falcodontan and must have evolved from the A_1 element of *Mesotaxis* Klapper & Philip, 1972, which is also falcodontan. *'Falcodus variabilis'* Sannemann, 1955 is the common form. *'Falcodus aculeatus'* Sannemann, 1955 is present in some samples. Whether there is any relation between the latter form and any palmatolepan species in particular could not be established.

The A_2 and A_3 elements are the form species *'Scutula venusta'* Sannemann, 1955, and *'Scutula bipennata'* Sannemann, 1955, respectively. As already described by Sannemann *'Falcodus variabilis'* grades into *'Scutula venusta'* by the addition of a lateral branch. By the development of a further branch on the outer side of the posterior process of *'S. venusta'* *'S. bipennata'* could arise (Lindström, 1964). We could not establish any essential difference in scutulan elements of older faunas compared to those of younger faunas possibly because so many scutulan elements are incomplete.

Palmatolepis has evolved from *Mesotaxis* Klapper & Philip, 1972. It has been generally accepted that the form species *'Polygnathus asymmetricus asymmetricus'* — the P element of *Mesotaxis* — is the ancestor of the form genus *'Palmatolepis'*, the P element of the natural genus *Palmatolepis*. The O element *'Nothognathella klapperi'* Uyeno, 1967 of Mesotaxis (according to Uyeno, 1974) is the ancestor of *'Nothognathella* cf. *brevidonta'*, the O element of the oldest species of *Palmatolepis*. The N element of *Mesotaxis* — *'Palmatodella? paridens'* Huddle, 1934 (according to Uyeno, 1974) — clearly is a predecessor of *'Palmatodella delicatula'*, the N_1 element of *Palmatolepis*. Klapper & Philip did not recognize a N_2 element in *Mesotaxis*. However, in this respect it should be mentioned that Klapper & Philip (1972) as well as Uyeno (1974) report that the N element is palmatodellan or synprioniodinan. We do not know whether they investigated the possibility that both forms could occur together in the *Mesotaxis* apparatus. As already said above the A_1 element of *Palmatolepis* — '*Falcodus variabilis*' — has evolved from the A_1 element of *Mesotaxis,* which is the form species '*Falcodus*? cf. *F.*? *tortus*' Huddle, 1934 according to Uyeno (1974). The relation between the A_2 as well as the A_3 elements of *Mesotaxis* and *Palmatolepis* is less clear. The data given by Klapper & Philip (1972) and Uyeno (1974) are rather scanty and, since we have no *Mesotaxis* faunas at our disposal we refrain from giving an opinion upon the relation between the A_2 and the A_3 elements of *Mesotaxis* and *Palmatolepis.*

Subgenus *Palmatolepis (Manticolepis)* Müller, 1956

Type species — *Palmatolepis subrecta* Miller & Youngquist, 1947.

Discussion — In our material the species *Palmatolepis gigas, P. hassi, P. unicornis, P. subrecta,* and *P. proversa* belong to Müller's subgenus *Manticolepis.* Apart from the typical development of their P element (see Müller, 1956), they are characterized by an O skeletal element of the '*Nothognathella brevidonta*'-'*N. abnormis*' lineage. In the lower part of the *Ancyrognathus triangularis* Zone the O element is the form species '*Nothognathella brevidonta*'. In the upper part of the *Ancyrognathus triangularis* Zone transitions to the form species '*Nothognathella abnormis*' appear together with forms which still are '*brevidonta*'-like and others that already resemble genuine '*abnormis*'. In the uppermost *P. gigas* Zone '*N. brevidonta*' has dissappeared, only '*N. abnormis*' is present. In our material are several faunas with *brevidonta*-type as well as *abnormis*-type nothognathellans and transitional forms. But for some exceptions, it has not been possible to ascribe one particular form to one of the palmatolepan species present in these faunas. It is possible that subsequent investigation will establish which palmatolepan elements corresponded to the holotypes of '*Nothognathella brevidonta*' Youngquist, 1947 and '*N. abnormis*' Branson & Mehl, 1934. In that case these names applying to O elements may have nomenclatorial priority over names based on P elements. Since we could not establish such a correspondence, we have only used specific names based on P elements for natural species of *Manticolepis.*

The O element '*Nothognathella brevidonta*' has evolved from the O element '*N. klapperi*' Uyeno, 1967 of the *Mesotaxis* apparatus by increase of the size of the platform and reduction in height of the denticles of the anterior part of the carina thereby loosing the saddle-shaped profile.

Pollock (1968) described conodont faunas from Alberta ranging from Lower *Polygnathus asymmetricus* Zone to Upper *Palmatolepis gigas* Zone in which he found '*Polygnathus asymmetricus asymmetricus*', '*Polygnathus asymmetricus ovalis*' and a number of palmatolepan species belonging to the subgenus *Manticolepis.* Furthermore he described and pictured a number of nothognathellan elements which in our opinion represent '*Nothognathella klapperi*', '*N. brevidonta*' and transitional forms* towards '*N. abnormis*'. If the '*Ozarkodina regularis*' he

---

*Note: The form '*Palmatolepis? ziegleri*' Clark & Ethington, 1967 was moved by Pollock (1968) into the genus '*Nothognathella*'. The species name *ziegleri,* however, had already been used by Helms (1959) for a quite different form of '*Nothognathella*'. This '*Nothognathella ziegleri*' (Clark & Ethington) is closely related to '*N. brevidonta*'.

mentioned — but did not figure — is a *'Nothognathella abnormis'* than all nothognathellan elements are present that we would expect to occur if our conception of the apparatuses of *Mesotaxis* and the subgenus *Palmatolepis (Manticolepis)* is correct.

The species *Palmatolepis quadrantinodosalobata* and *Palmatolepis tenuipunctata* no longer show the primitive platform development of the P element characteristic for the subgenus *Manticolepis*. On the other hand their O elements are still *abnormis*-like forms, closely related to the O element of *Palmatolepis triangularis*. We are inclined to consider *P. quadrantinodosalobata* and *P. tenuipunctata* as last representatives of the subgenus *Manticolepis* because of this development of the O element.

The species *Palmatolepis* cf. *regularis* and *P. linguiformis* still have the 'manticolepan' platform development of the P element. Their O elements, however, although apparently evolved from the O elements of *Manticolepis*, are no longer typical for the subgenus. Therefore these two species are only provisionally assigned to this subgenus.

Palmatolepis (Manticolepis) subrecta Miller & Youngquist, 1947
Figs. 1 - 2.

Diagnosis — P element is the form species *'Palmatolepis subrecta'*. O element in the older forms is similar to the form species *'Nothognathella brevidonta'*, in the youngest forms the O element approaches the form species *'N. abnormis'* var. a. In fact we are dealing with two rather than one (sub)species. However, we do not know to which of those the lectotype of *'Palmatolepis subrecta'* corresponds, and it would be difficult to make this distinction in taxonomical practice. Therefore we have refrained from recognizing two formal taxa.

Description — For a description of the P element see Miller & Youngquist (1947) and Ziegler (1958). In the lower part of the *Ancyrognathus triangularis* Zone the O element (Fig. 2) largely conforms to the description of *'Nothognathella brevidonta'* Youngquist, 1947, as given by Druce, 1975: An arched nothognathellid with a conspicuous platform on the inner side. The arching varies from as little as 30° to near 90°. The platform is well developed, especially on the inner side, where it stretches from end to end, it is widest in the middle and narrows gradually. The ornamentation consists of isolated nodes and transverse ridges at the platform edge. The carina consists of a sequence of up to 28 low nodose denticles fused at their bases but with free tips. The denticle at the flexure point is occasionally somewhat stouter than the others. The denticles of the posterior limb are smaller than those of the anterior limb. The unit is deflected through about 70° and arched. Sometimes the carina is sinuous. The outer platform is extremely narrow, widest at the flexure point of the unit. In aboral view the unit is keeled. At about the platform midpoint the keel bifurcates for a short distance, forming a small, shallow pit.

The O element of the younger forms is transitional to *'Nothognathella abnormis'* or occasionally already almost identical to *'N. abnormis.'* The pictured element (Fig. 1) from the Uppermost *P. gigas* Zone may be considered a transitional form. The unit is arched and bowed. It has a well-developed platform on the inner side of the posterior bar, widest at midpoint and stretching in anterior direction as a very narrow ledge. On the outer side the platform development is confined to the posterior part or only the central part. The denticles of the carina are fused at their bases. Those of the anterior bar are subequal. Those of the posterior bar are smaller and outwardly inclined. The posterior bar is deflected inward through 30° - 70°. Sometimes the carina is sinuous. In some other specimens the platform is only a tumescence at about mid-bar height or

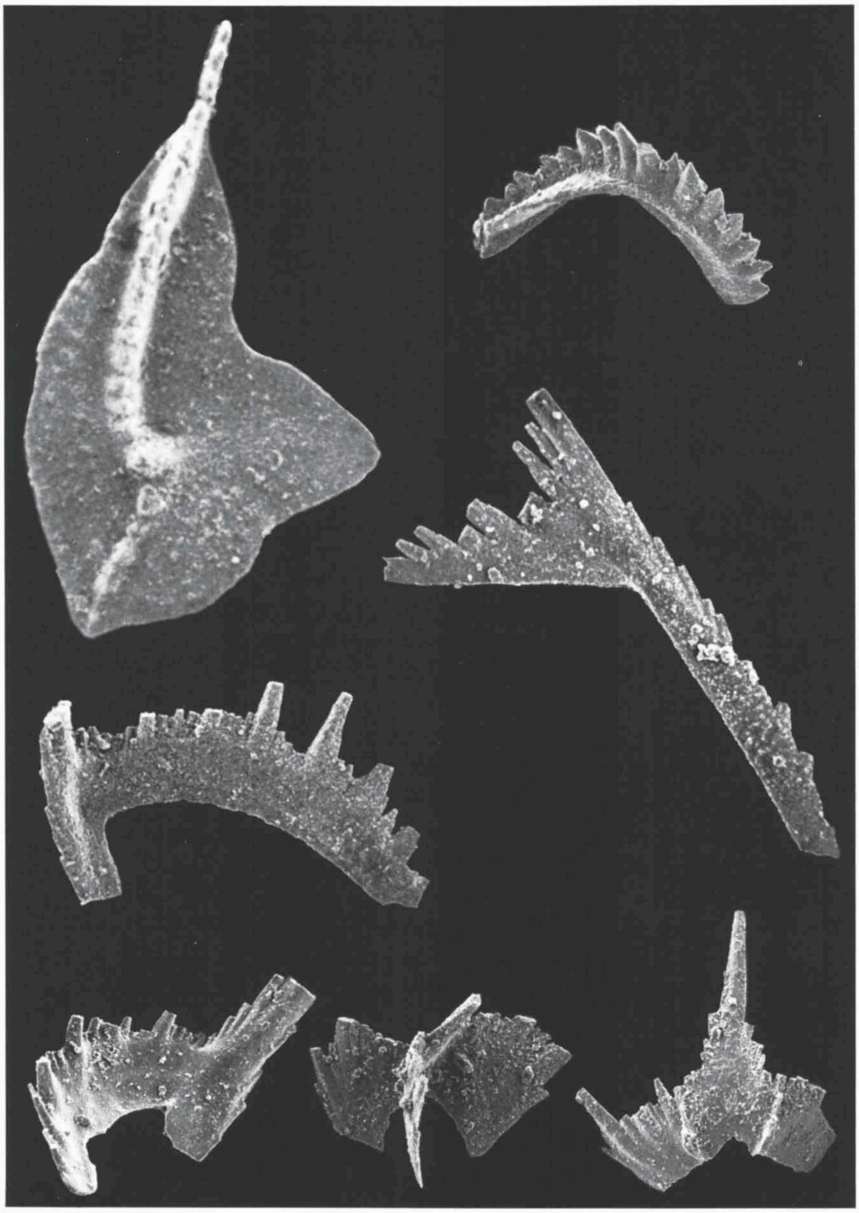

Fig. 1. *Palmatolepis (Manticolepis) subrecta* from the Uppermost *Palmatolepis gigas* Zone (sample 15-9-6). P element (above left), O element (above right), N_1 element (middle right), N_2 element (middle left), A_1 element (below left), A_2 element (below middle), A_3 element (below right); × 66, RGM 295 291.

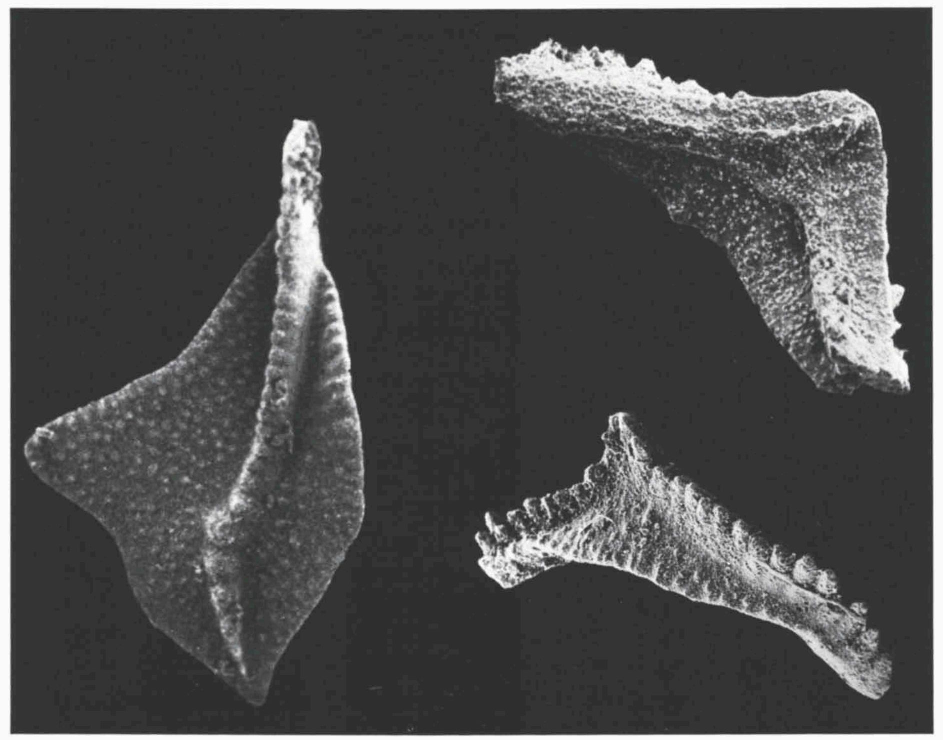

Fig. 2. *Palmatolepis (Manticolepis) subrecta* from the Lower *Ancyrognathus triangularis* Zone (sample 44/71). P element × 54 (left) RGM 295 292, O element, aboral side × 125 (above right), oral side × 60 (below right) RGM 295 286.

a small platform on the inner side at about midpoint. The elements are keeled and have a minute basal cavity.

The nothognathellids of these younger faunas have an inner platform that is considerably smaller than that of '*N. brevidonta*'. In most cases the platform is still somewhat larger than that of the types of '*N. abnormis*' pictured by Branson & Mehl, 1934.

Palmatolepis (Manticolepis) proversa Ziegler, 1958
Fig. 3.

Diagnosis — P skeletal element is the form species '*Palmatolepis proversa*' Ziegler, O skeletal element is nothognathellan.

Remarks — For description of the P element see Ziegler, 1958. The nothognathellan O element is closely related to '*N. brevidonta*' as described by Druce, 1975. The inner platform may even be somewhat wider, the denticles of the carina are somewhat longer and fused with free tips.

These P and O elements of *P. proversa* occurred in a fauna from Meggen (Germany) donated to one of the authors (M. v. d. B.) by Dr U. Dornsiepen. This fauna could not be included in the countings due to the fact that it had been picked for stratigraphical reasons only and consequently all prioniodinan and scutulan elements had been left in the residue which later on was lost.

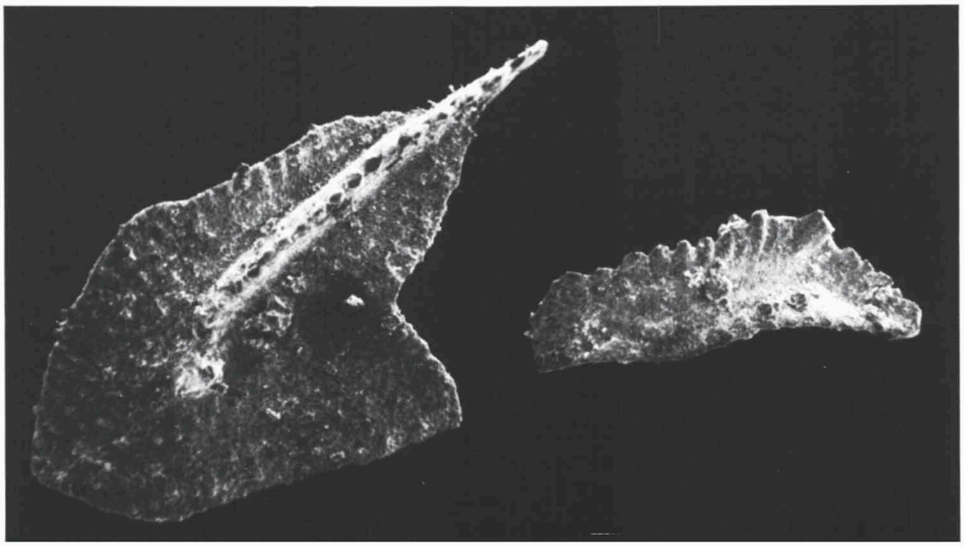

Fig. 3. *Palmatolepis (Manticolepis) proversa* from the *Polygnathus asymmetricus* Zone (sample Dorn FB 22). P element (left), O element (right) × 74, RGM 295 298.

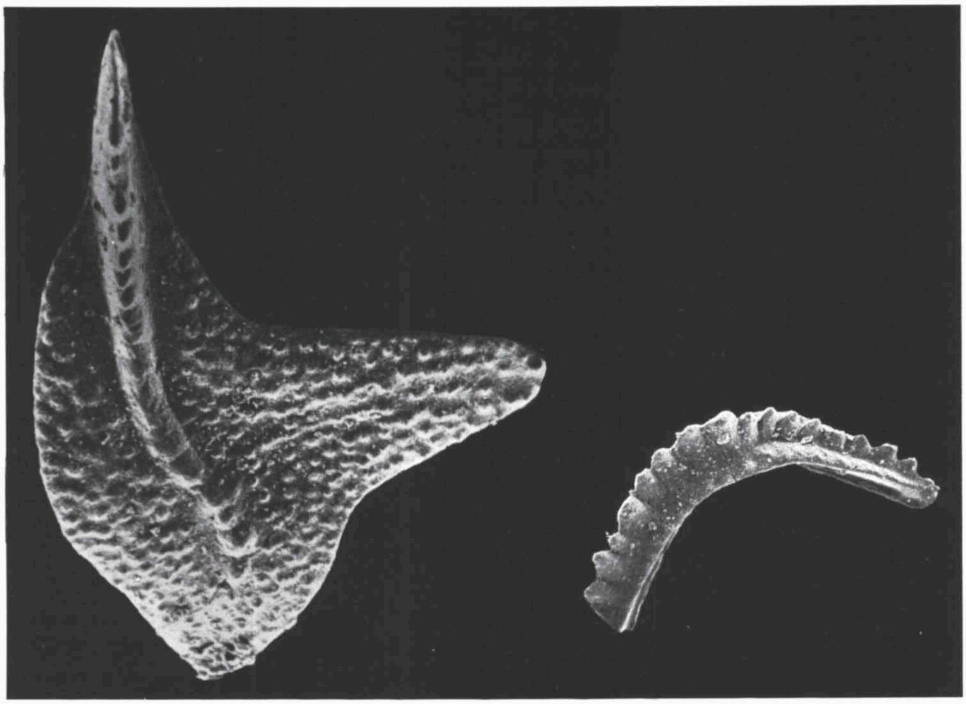

Fig. 4. *Palmatolepis (Manticolepis) gigas* from the Upper *Palmatolepis gigas* Zone (sample 15-9-4). P element × 61 (left) RGM 295 284, O element × 55 (right) RGM 295 294.

Palmatolepis (Manticolepis) gigas Miller & Youngquist, 1947
Fig. 4.

Diagnosis — P skeletal element is the form species '*Palmatolepis gigas*' Miller & Youngquist. O skeletal element is an *abnormis*-like nothognathellan element ('*N. abnormis* var. a').

Description — The O element is arched and bowed. Both inner and outer platforms are rather narrow, widest in the central part of the element and stretching along the inner side of the posterior bar. Occasionally the platform extends also along the outer side of the posterior bar. Denticles fused at their bases, sharp edged. Those of the anterior bar are higher and less discrete than those of the posterior bar.

Palmatolepis (Manticolepis) triangularis Sannemann, 1955
Fig. 5.

Diagnosis — P skeletal element is the form species '*Palmatolepis triangularis*' Sannemann, 1955; O skeletal element resembles '*Nothognathella abnormis*' (var. b).

Description — For a description of the P element see Sannemann (1955a) and the Catalogue of Conodonts, vol. I. The O element is a nothognathellid with a reduced platform. The element is arched and bowed. The denticles of the anterior bar are fused over somewhat more than half their length and gradually increase in size towards the flexure point. The denticles of the posterior bar are lower and less fused, occasionally isolated and outwardly inclined. The posterior bar

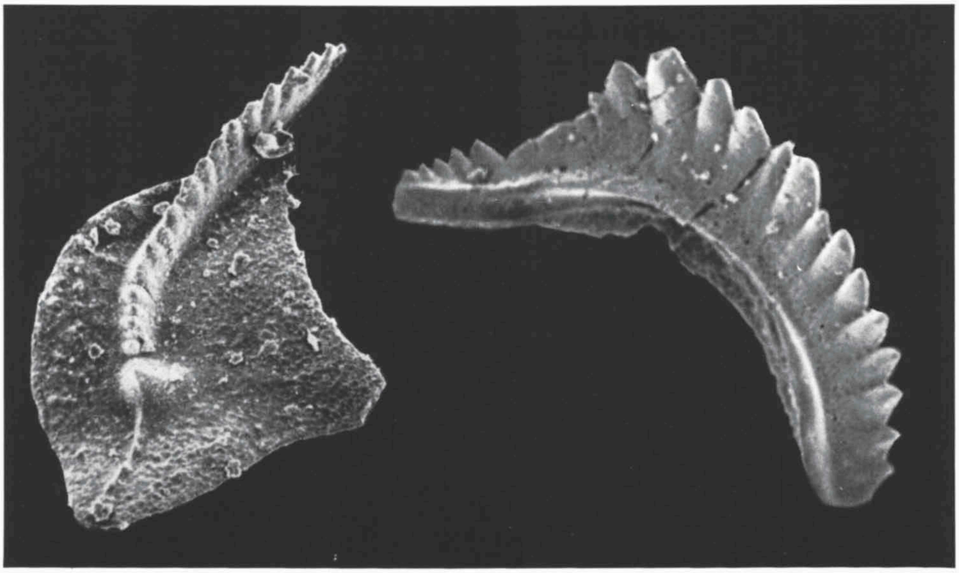

Fig. 5. *Palmatolepis (Manticolepis) triangularis* from the *Palmatolepis triangularis* Zone (sample 15-9-7). P element (left) RGM 295 290, O element (right) RGM 295 292; × 100.

is deflected inward through 45° - 70°. In some specimens the platform is only a tumescence of the inner side at about mid-bar height. This tumescence expands into a genuine platform, especially from about midpoint towards the posterior end. On the outer side no platform has been developed. The element is keeled and has a minute cavity.

The O element differs from the O element of *P. (M.) subrecta* in having no platform development on the outer side and in the gradual increase in size of the denticles of the anterior bar.

Palmatolepis (Manticolepis) quadrantinodosalobata Sannemann, 1955
Fig. 6.

Diagnosis — P skeletal element is the form species '*Palmatolepis quadrantinodosalobata*' Sannemann, 1955; O skeletal element resembles '*Nothognathella abnormis*' (var. d in Table 5).

Description — For a description of the P element see Sannemann (1955a) and Catalogue of Conodonts, vol. I, p. 295. The O element is nothognathellan and referred to as '*N. abnormis*' var. d in Table 5. The element is arched and bowed. A narrow platform exists along the inner side of the posterior bar and extends

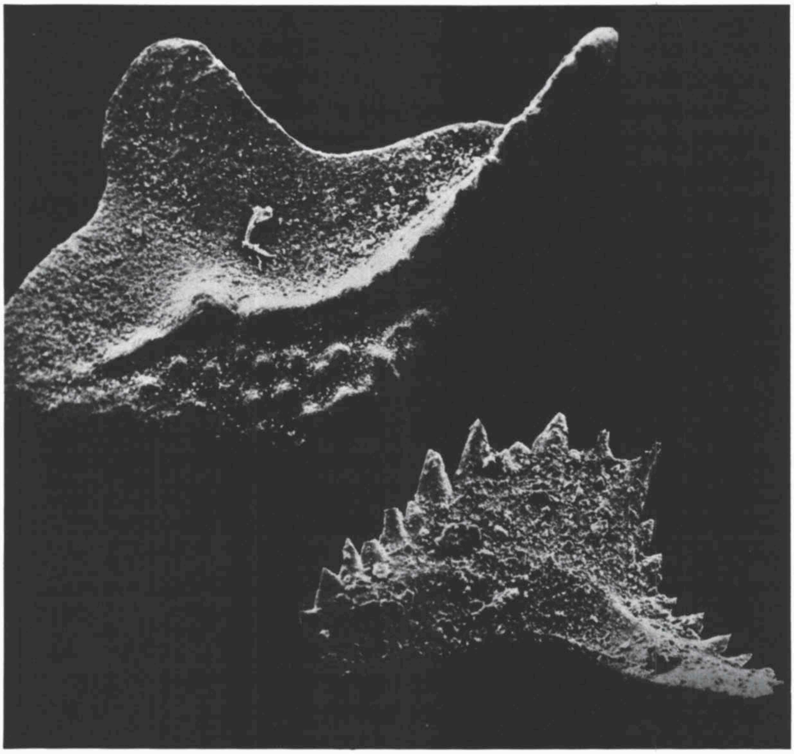

Fig. 6. ***Palmatolepis (Manticolepis) quadrantinodosalobata*** **from the Middle** ***Palmatolepis crepida*** **Zone (sample 15-9-16). P element (left) RGM 295 287, O element (right) RGM 295 288; × 100.**

as a ridge or swelling along part of the inner side of the anterior bar. The anterior bar is high; its denticles regularly increase in length towards the flexure point. They are fused with free chevron tips. The posterior bar is deflected inward through 45° - 70°; its denticles are lower, less fused, almost isolated, and strongly inclined outwards to such an extent that they parallel the base of the anterior bar. The element is keeled and has a minute cavity at the point of flexure with a small lip-like extension on the outer side. The element is shorter and higher than the nothognathellan elements of *P. tenuipunctata, P. subrecta* and *P. triangularis.* It also has a much narrower platform than the latter two.

P. quadrantinodosalobata evolved from *P. triangularis* (see i.a. Ziegler, 1962a). This relationship is confirmed by the development of the O element which must have been derived from an O element like that of *P. triangularis.*

Palmatolepis (Manticolepis) tenuipunctata Sannemann, 1955
Fig. 7, 8.

Diagnosis — P skeletal element is the form species '*Palmatolepis tenuipunctata*' Sannemann, 1955b. O skeletal element resembles '*Nothognathella abnormis*' (var. c in Table 5).

Description — For description of the P element see Sannemann (1955b) and Ziegler (1962a). The O element is arched and has a strongly inward deflected posterior termination. Its platform is reduced to a very narrow ledge along the inner side of the posterior bar, or not present at all. The denticles of the anterior bar gradually increase in length towards the flexure point. Those of the posterior bar gradually decrease in length towards the posterior termination. Behind the 3 or 4 foremost denticles, which are still in the same plane as those

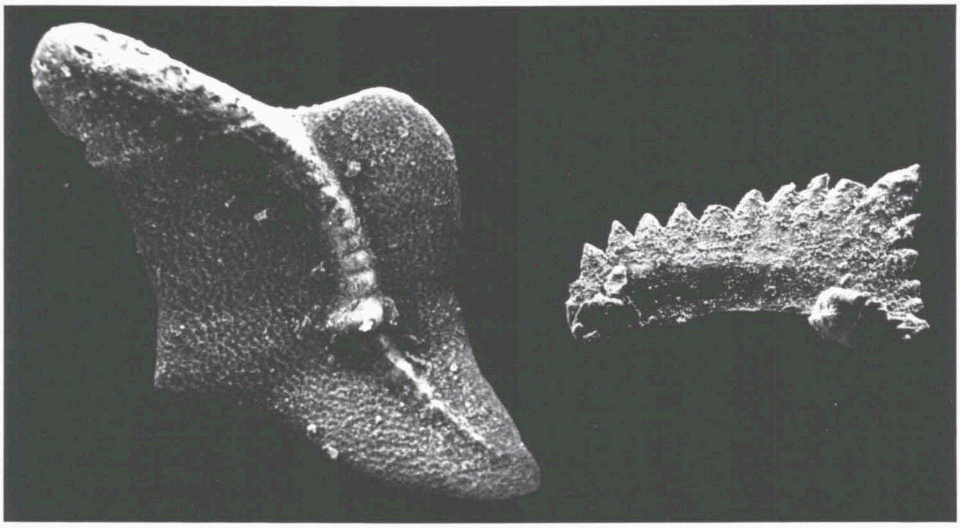

Fig. 7. *Palmatolepis (Manticolepis) tenuipunctata* **from the Lower - Middle *Palmatolepis crepida*** **Zone (sample 15-9-8). P element (left) RGM 295 292, O element (right) RGM 295 289; × 77.**

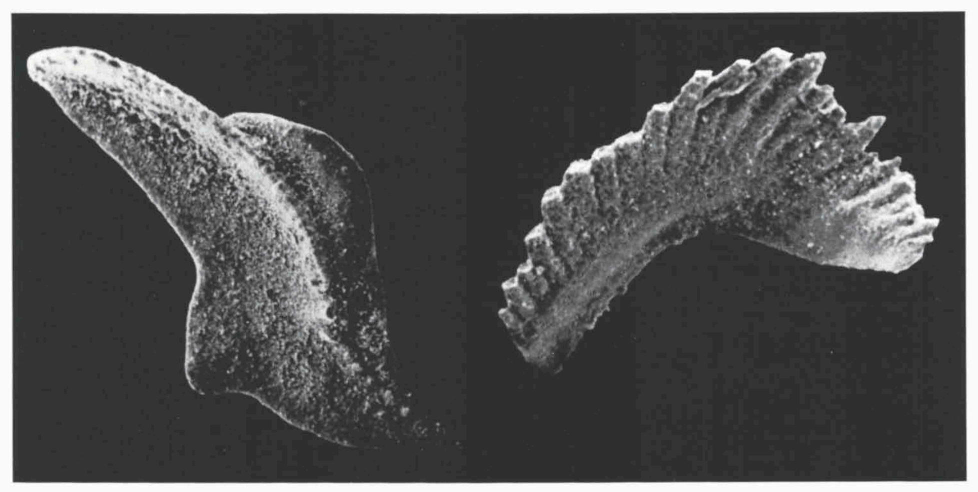

Fig. 8. *Palmatolepis (Manticolepis) tenuipunctata* from the Middle *Palmatolepis crepida* Zone (sample 15-9-16). P element × 60 (left) RGM 295 285, O element × 105 (right) RGM 295 293.

of the anterior bar, the posterior bar is abruptly deflected and its denticles stand in a plane at right angles to the anterior bar and are outwardly inclined to such an extent that they almost parallel the base of the anterior bar. The element is keeled and has a minute basal cavity with a small outer lip at the point of flexure.

Remarks — The O element is distinguished from that of *P. quadrantinodosalobata* by the lenght of the bars, by the small variability in length of the denticles and by the extent of fusion of the denticles of the posterior bar. The differences with the O element of *P. triangularis* are the stronger fusion of the denticles and the nearly complete reduction of the platform.

The characteristics of the O element which is still so closely related to that of *P. triangularis* confirms that *P. tenuipunctata* has evolved from a stock which has its origin in *P. triangularis*. The current opinion that *P. tenuipunctata* belongs to the subgenus *Panderolepis* (Helms, 1963) or *subperlobata-glabra* stock (Ziegler, 1962a) is not confirmed by the nature of the O element.

Palmatolepis (Manticolepis ?) cf. *regularis* Cooper, 1931
Fig. 9.

Diagnosis — P skeletal element is the form species *'Palmatolepis* cf. *regularis'* Cooper, O skeletal element resembles the form species *'Nothognathella iowaensis'* Youngquist, 1945.

Description — For description of the P element see Ziegler (1962a, p. 75 - 77). The O element is a nothognathellid with a platform virtually restricted to the inner posterior portion of the element. The carina is composed of up to 25 laterally compressed, fused denticles with free chevron tips. The anterior half consists of rather tall denticles and is gently curved. The posterior part consists of somewhat lower denticles and is occasionally slightly curved in opposite direction, producing a sigmoidal carina. The platform has a smooth edge and bears extremely minute

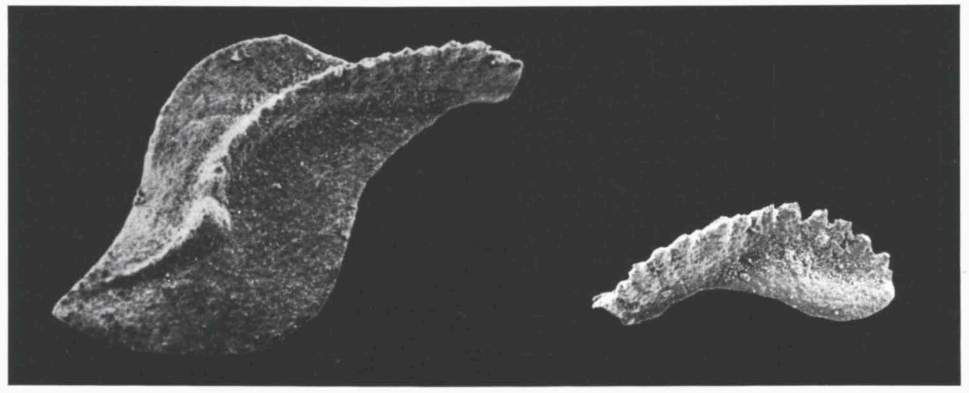

Fig. 9. *Palmatolepis (Manticolepis ?) regularis* from the Middle *Palmatolepis crepida* Zone (sample 15-9-16). P element × 62 (left) RGM 295 285, O element × 55 (right) RGM 295 294.

tubercles. On the outer side exists a very narrow platform in the central portion of the element. The element is keeled and has a minute cavity at the point of flexure.

Remarks — This O element must have evolved from '*Nothognathella brevidonta*' by reduction of the platform, especially in the anterior portion. Because of the primitive platform development of the P element we incorporate this species provisionally in the subgenus *Manticolepis*.

Palmatolepis (Manticolepis ?) linguiformis Müller, 1956
Fig. 10.

Diagnosis — P skeletal element is the form species '*Palmatolepis linguiformis*' Müller. O skeletal element is nothognathellan.

Description — For description of the P element see Müller (1956) and Catalogue of Conodonts, vol I, pp. 283-285. The O element has a sigmoidal carina. The denticles are slightly fused, almost discrete. Those of the anterior limb are nearly equidimensional. The denticles of the posterior limb are somewhat shorter but also have about equal length. The inner platform is widest in mid portion of the element. It narrows rather rapidly in anterior direction but only slowly posteriorly and reaches the posterior end. The outer platform is as wide as the inner one in the central part of the unit. It also narrows rapidly anteriorly and slowly posteriorly but does not extend to the posterior tip. The upper surface of the platforms is shagreenlike. This form probably originated from a nothognathellan element in the '*brevidonta*' - '*abnormis*' lineage by developing a wider outer platform. This is in agreement with the opinion that *Palmatolepis linguiformis* is an offspring of the group of the older, wide-plated *Palmatolepis* species (Ziegler, 1973). Nothognathellan elements of the '*brevidonta-abnormis*' lineage are characteristic for that group.

The platform development of the O element shows some resemblance to that of '*N.* cf. *sublaevis*' (the O element of *Palmatolepis crepida)* and therefore was counted as "pseudo *N. sublaevis*" (see Table 5). However, the development

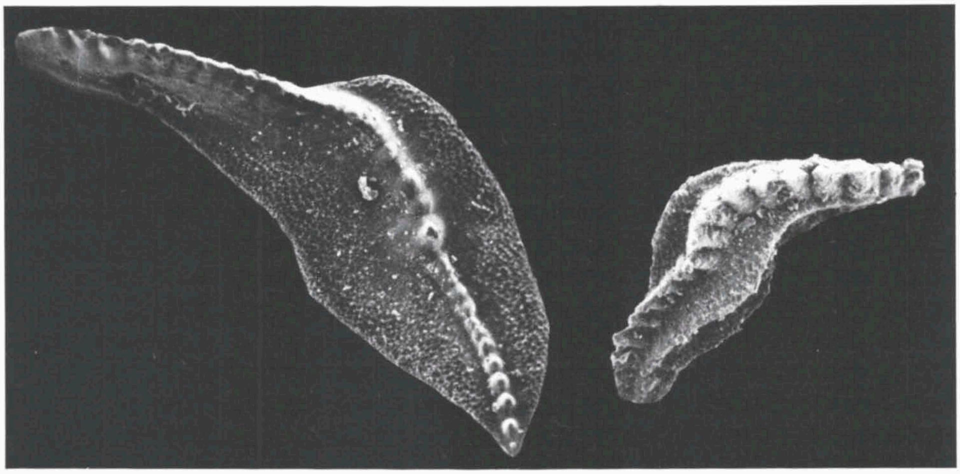

Fig. 10. *Palmatolepis (Manticolepis ?) linguiformis* from the Uppermost *Palmatolepis gigas* Zone (sample 15-9-6). P element (left), O element (right); × 70, RGM 295 294.

of the carina is different and still resembles the carina of '*Nothognathella brevidonta*'. Nevertheless it is rather striking that the similarity of the P. elements of *Palmatolepis linguiformis* and *P. crepida,* which originally led Ziegler (1958) to consider *P. linguiformis* as a subspecies of *P. crepida,* is matched by a similarity of the O elements.

Subgenus *Palmatolepis (Tripodellus)* Sannemann, 1955

Type species — *Palmatolepis (Tripodellus) minuta flexuosa* Sannemann, 1955b.

Discussion — Of the species encountered in our faunas the following belong to this subgenus: *Palmatolepis (Tripodellus) gracilis* Branson & Mehl, 1934, *P. (Tripodellus) sigmoidalis* Ziegler, 1962, *P. (Tripodellus) gonioclymeniae* Müller, 1956, *P. (Tripodellus) minuta flexuosa* Sannemann, 1955, and *P. (Tripodellus) minuta minuta* Branson & Mehl, 1934. Apart from the typical development of the P elements this subgenus is characterized by an O skeletal element which is tripodellan instead of nothognathellan. The N and A skeletal elements do not differ from those of the other subgenera.

Palmatolepis (Tripodellus) minuta flexuosa in our samples 15-9-8 and 15-9-16 from the *Palmatolepis crepida* Zone has as an O element '*Tripodellus flexuosus*' Sannemann, 1955b. The O element of *P. (Tripodellus) minuta minuta* in younger strata is a transitional form towards '*Tripodellus robustus*' Bischoff, 1957. Genuine '*Tripodellus robustus*' occurs in the apparatuses of *Palmatolepis (Tripodellus) gracilis* and *P. (Tripodellus) sigmoidalis. P. (Tripodellus) manca* ascribed by Sandberg & Ziegler (in Catalogue of Conodonts, vol. III, p. 321) to the '*gracilis*' stock occurred in rather small numbers together with great numbers of *P. (Trip.) gracilis* and therefore we could not establish whether its O element is also '*Tripodellus robustus*' or absent from the faunas. *Palmatolepis (Tripodellus) gonioclymeniae* differs from the other species of the subgenus in not having a tripodellan but a "pseudo-nothognathellan" O element.

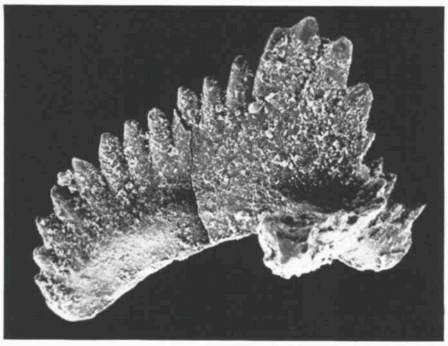

Fig. 11. O element cf. the form species *'Nothognathella abnormis'* with extra (outer) posterior bar (view of outer side) from the Lower - Middle *Palmatolepis crepida* Zone (sample 15-9-8); × 77, RGM 295 288.

The name *'Deflectolepis'* given by Müller (1956) to the P elements of this subgenus must be considered a junior synonym of the name for the characteristic O element *'Tripodellus'* Sannemann, 1955. The type species of this latter genus, *'Tripodellus flexuosus'* Sannemann, belongs to the same apparatus as platform elements identifiable as *'Palmatolepis minuta'* Branson & Mehl, 1934. Both skeletal elements occur in samples from the *P. crepida* Zone. However, in younger samples the platform element *'P. minuta'* is found together with a form of *'Tripodellus'* intermediate between *'T. flexuosus'* and *'T. robustus'*. It is not clear which O element corresponds to the lectotype of *'P. minuta'* designated by Müller, 1956. Nor is it clear from which stratigraphical level the lectotype derives, which would give an indirect clue to the nature of the corresponding O element. From Helms' range-chart (1963) we deduce that this author assumes that the lectotype of *'P. minuta'* can be identified as a relatively young representative of this stock. On the basis of the other palmatolepan species described by Branson & Mehl (1934) one would also conclude that most of their material derives from relatively young strata. In view of the wide-spread use of the name *P. minuta* and in view of the fact that stratigraphically oriented conodont workers, who tend to focus on platform conodonts, probably will continue to use this name, we refrain from rejecting *P. minuta* as a nomen dubium. Instead, we recognize two subspecies, *Palmatolepis (Tripodellus) minuta minuta,* characterized by an O element intermediate between *'T. flexuosa'* and *'T. robustus',* and *Palmatolepis (Tripodellus) minuta flexuosa,* characterized by the O element *'Tripodellus flexuosus'*.

The tripodellan element must have evolved from *'Nothognathella abnormis'* by the addition of an extra (outer) posterior bar. Sannemann (1955b, pl. 6, fig. 17) pictured a *'Nothognathella abnormis'* with what he supposed to be a small pathological branch which extends from the outer side of the flexure point more or less backwards. This specimen occurred in Do IIα strata from Bernstein in Germany. We have found a similar specimen in a sample of the same age, Lower to Middle *Palmatolepis crepida* Zone from Wildungen, Germany (Fig. 11). Whether this form is intermediate towards *'Tripodellus'* or just pathological could not be established but it possibly shows how easy *'Tripodellus'* could evolve from *'Nothognathella abnormis'*. This intermediate form occurs in faunas in which *'Tripodellus flexuosus'* also is found. It is curious that *'T. flexuosus'* is more distinct from *'N. abnormis'* than the younger forms transitional towards *'T. robustus'*.

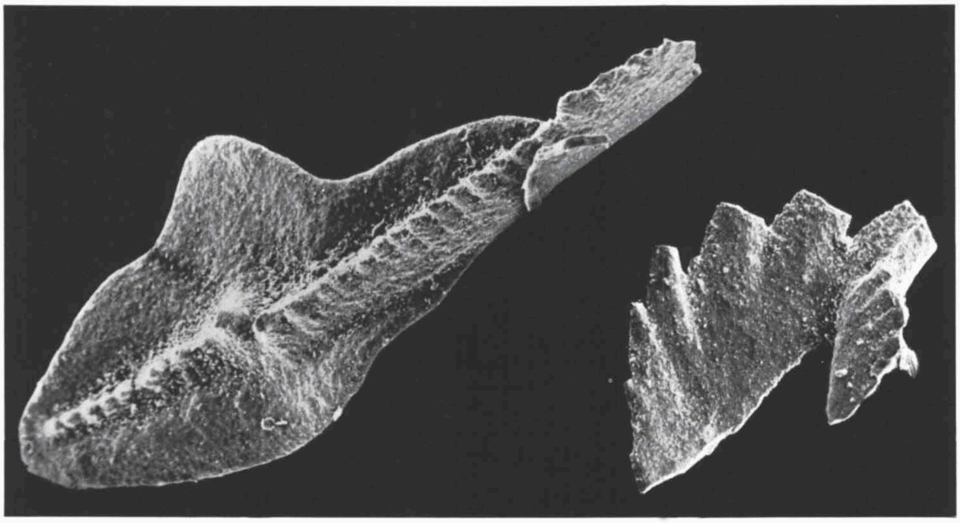

Fig. 12. *Palmatolepis (Tripodellus) minuta flexuosa* from the Middle *Palmatolepis crepida* Zone (sample 15-9-16). P element × 93 (left) RGM 295 287, O element × 100 (right) RGM 295 283.

Palmatolepis (Tripodellus) minuta flexuosa (Sannemann, 1955)
Fig. 12.

Diagnosis — P skeletal element is the form species described by Sannemann (1955b) as '*Palmatolepis minuta*' Branson & Mehl, 1934. O skeletal element is the form species '*Tripodellus flexuosus*' Sannemann, 1955b.

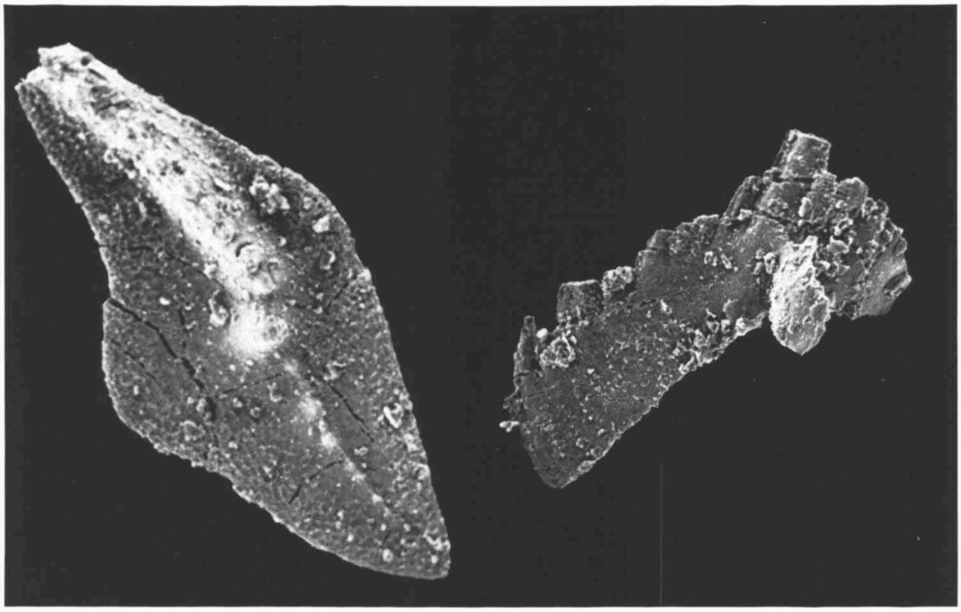

Fig. 13. *Palmatolepis (Tripodellus) minuta minuta* from the top of the *Palmatolepis rhomboidea* Zone (sample 43/71). P element (left), O element (right); × 105, RGM 295 293.

Remarks — For description of both elements see Sannemann (1955b).

Palmatolepis (Tripodellus) minuta minuta Branson & Mehl, 1934
Fig. 13.

Diagnosis — P skeletal element is the form species '*Palmatolepis minuta*' Branson & Mehl, 1934. The O skeletal element is tripodellan.

Remarks — The O element probably is a transitional form between '*T. flexuosus*' and '*T. robustus*', similar to the specimen in Fig. 13. This element is less arched and has more but smaller denticles than '*T. flexuosus*' except for the main denticle.

Fig. 14. ***Palmatolepis (Tripodellus) gracilis*** **from the Middle - Upper** ***Polygnathus styriacus*** **Zone (sample C.d.P.). P element (top left) RGM 295 296, O element (top right) RGM 295 299, N_1 element (bottom left) RGM 173 701, N_2 element (upper middle) RGM 173 703, A_1 element (lower middle) RGM 173 691, A_2 element (middle right) RGM 173 695, A_3 element (bottom right) RGM 173 696; × 67.**

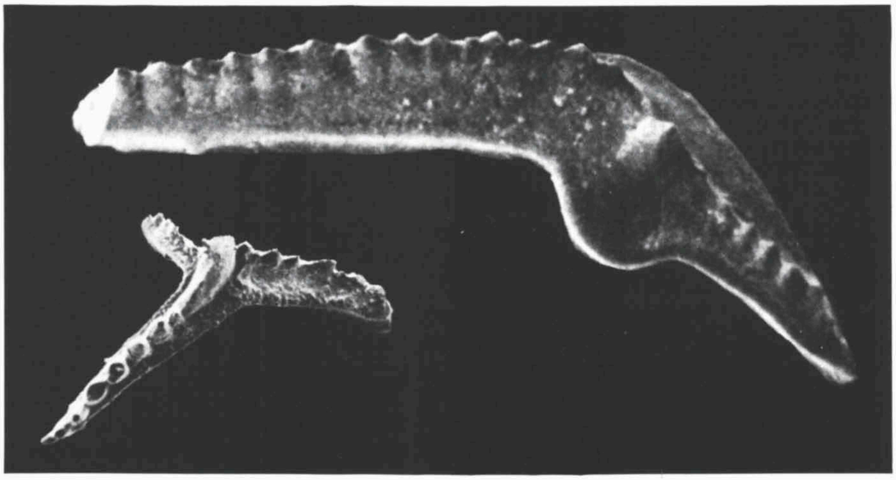

Fig. 15. *Palmatolepis (Tripodellus) gracilis* from the Middle *Bispathodus costatus* Zone (sample Prof. 1, lr. 5). P element (right), O element (left); × 83, RGM 295 295.

Palmatolepis (Tripodellus) gracilis Branson & Mehl, 1934
Figs. 14, 15.

Diagnosis — P skeletal element is the form species '*Palmatolepis gracilis*'. The O skeletal element is the form species '*Tripodellus robustus*' Bischoff, 1957. N_1 and N_2 are the form species '*Palmatodella delicatula*' and '*Prioniodina smithi*', A_1, A_2 and A_3 are the form species '*Falcodus variabilis*', '*Scutula venusta*' and '*Scutula bipennata*'.

Remarks — For description of the P element see Branson & Mehl (1934) and Catalogue of Conodonts, vol. III, p. 313 - 317. For description of the O element see Bischoff (1957, p. 58) and Helms (1959, p. 659).

Palmatolepis (Tripodellus) gonioclymeniae Müller, 1956
Fig. 16.

Diagnosis — The P skeletal element is the form species '*Palmatolepis gonioclymeniae*' Müller, the O element is "pseudo-nothognathellan".

Description — For description of the P element see Müller (1956) and Catalogue of Conodonts, vol. I, p. 279 and vol. III, p. 319. The O skeletal element resembles '*Nothognathella falcata*'. However, it is less abruptly deflected and has a rather expanded flattened base at the point of flexure and thus differs from the real '*falcata*' form. The inner rim of the base extends as a keel below the posterior bar, the outer rim terminates as a ridge on the outer side of the posterior bar (Fig. 16).

Remarks — In the past, views have differed on the affiliation of '*P. gonioclymeniae*', which has been considered as a relative of either '*P. gracilis*' or of

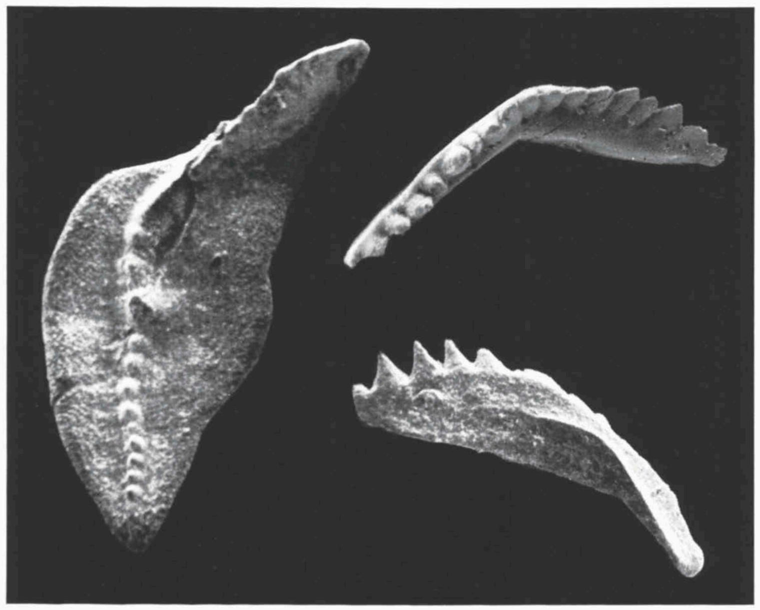

Fig. 16. *Palmatolepis (Tripodellus) gonioclymeniae* from the Middle *Bispathodus costatus* Zone (sample Prof. 1, Ir. 5). P element × 53 (left) RGM 295 295, O element, oral view × 70 (upper right) RGM 295 294, aboral view × 70 (lower right) RGM 295 297.

the *'P. glabra'* group (Catalogue of Conodonts, vol. III, p. 319). One would assume that this controversy might be settled as soon as the corresponding O element is identified. If this would resemble *'N. falcata'*, *'P. gonioclymeniae'* would be a relative of the *glabra* group and if it is tripodellan, it would be a relative of *'P. gracilis'*. Unfortunately, this element bears a similarity to both types of O elements. In our opinion, the morphology of the base of the O element suggests a development from *'Tripodellus robustus'* by complete reduction of the shorter (outer) posterior bar and reduction of the main denticle. We therefore agree with Sandberg and Ziegler (Catalogue of Conodonts, vol. III, p. 319) that *P. gonioclymeniae* must have evolved from the *Palmatolepis (Tripodellus)* lineage.

Subgenus *Palmatolepis (Panderolepis)* Helms, 1963

Type species — *Palmatolepis glabra* Ulrich & Bassler, 1926.

Discussion — The O skeletal elements of *Palmatolepis termini, P. crepida* and *P. glabra* are so closely related that they must have evolved from the same stock. The origin of this stock must be sought for in the *P. subrecta* group. We surmise that the nothognathellan O element of *Panderolepis* has developed from a nothognathellan form of the *'N. brevidonta'*-*'N. abnormis'* transition series and not from the *abnormis*-like O element of *P. tenuipunctata,* which latter in our opinion represents an end stage of an *'abnormis'* lineage (see p. 27). Some additional support for this supposition is the fact observed by Druce (1975) as well as by us that some *'N. brevidonta'* like forms do have a shagreen platform ornamentation. Shagreen ornament of the platform could be observed on all nothognathellan elements of the subgenus *Panderolepis,* except in the case of *'Nothognathella falcata'* where the platform is reduced to nil.

Owing to insufficient data it was impossible to relate all the *glabra*-group species with a particular form of *'Nothognathella'*. However, it seems that *P. (Panderolepis) prima* has *'N. palmatoformis'* as O element and *P. (Panderolepis) lepta 'N. falcata'* as O element.

Palmatolepis (Panderolepis) termini Sannemann, 1955
Fig. 17.

Diagnosis — P skeletal element is the form species *Palmatolepis termini* Sannemann, O skeletal element is the form species *'Nothognathella sublaevis'* Sannemann, 1955b.

Description — For description of the P element see Sannemann (1955b) and Catalogue of Conodonts, vol. I, p. 307. The O element is arched and bowed, the carina highest in the anterior part. The denticles are fused with free chevron tips. The inner platform is developed in the posterior half of the unit. Its margin extends in a convex bend from the posterior termination towards the middle of the unit where it continues in a concave bend towards the middle of the anterior part of the carina. The outer platform has almost the same shape as the inner but is developed somewhat more anteriorly. Both platform halves do have a shagreen-like upper surface. The element is keeled. There is no basal cavity. This nothognathellan element is identical to the holotype of *'N. sublaevis'* Sannemann (1955b, pl. 3, fig. 10).

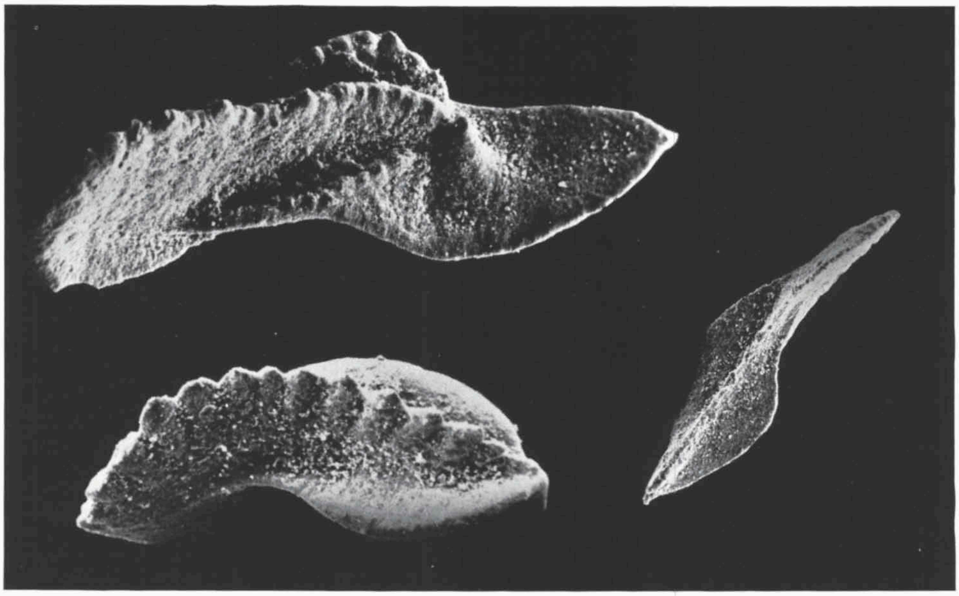

Fig. 17. *Palmatolepis (Panderolepis) termini* **from the Middle *Palmatolepis crepida* Zone (sample 15-9-16). P element (above left) RGM 295 287, O element, oral view (below left), aboral view (below right) RGM 295 285; × 110.**

Fig. 18. *Palmatolepis (Panderolepis) crepida* from the Middle *Palmatolepis crepida* Zone (sample 15-9-16). P element (left) RGM 295 287, O element (right) RGM 295 289; × 62.

Remarks — '*Nothognathella sublaevis*' as well as '*Palmatolepis termini*' have both been described as new form species by Sannemann (1955b). In that paper '*N. sublaevis*' has precedence of position. The present authors, however, believe that stability of nomenclature is best ensured by selecting the specific name *termini* for this natural species.

Palmatolepis (Panderolepis) crepida Sannemann, 1955
Fig. 18.

Diagnosis — P. skeletal element is the form species '*Palmatolepis crepida*' Sannemann, 1955b, O skeletal element resembles the form species '*Nothognathella sublaevis*' Sannemann, 1955b.

Description — For description of the P element see Sannemann, 1955b and Catalogue of Conodonts, vol. I, p. 263. The O element is nothognathellan and resembles the O element of *Palmatolepis termini* but for the position of the outer platform. This outer platform has moved towards the posterior termination. Inner and outer platform together form an almost symmetrical platform divided in equal halves by the carina. This form is identical to the specimen pictured by Sannemann 1955b in pl. 3, fig. 12 which was considered by him as a variant of the form species '*N. sublaevis*'. The close relation supposed to exist between *Palmatolepis crepida* and *P. termini* (Catalogue of Conodonts, vol. I, p. 263, 307) is thus confirmed by the strong resemblance of their O elements.

Palmatolepis (Panderolepis) glabra group
Figs. 19, 20, 21.

Diagnosis — P skeletal elements are the form species (subspecies) of '*Palmatolepis glabra*' Ulrich & Bassler, 1926. The O skeletal elements are nothognathellan and vary from forms with a well developed platform bearing shagreen ornamentation — '*N. palmatoformis*' — to forms with almost no platform — '*N. falcata*'.

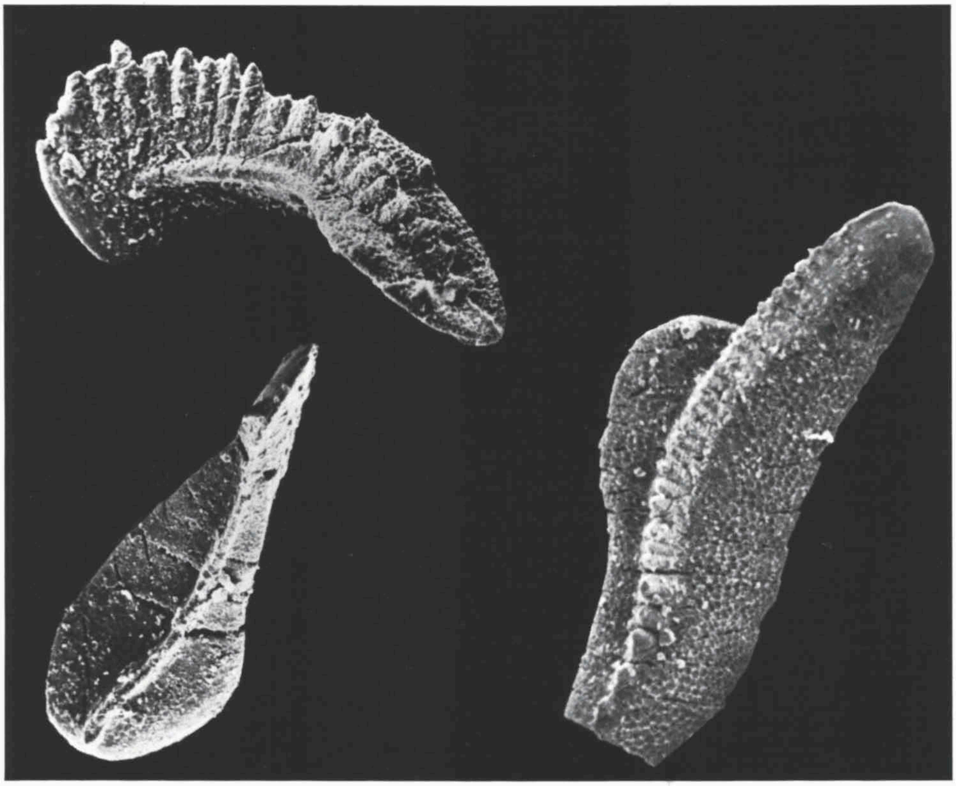

Fig. 19. *Palmatolepis (Panderolepis) glabra prima* from the *Palmatolepis rhomboidea* Zone (sample 43/71). P element × 105 (right) RGM 295 292, O element, oral view × 130 (upper left), aboral view × 125 (lower left) RGM 295 283.

Remarks — In a fauna from the *Palmatolepis rhomboidea* Zone *Palmatolepis (Panderolepis) glabra prima* Ziegler & Huddle, 1969 has an O element, which is a typical '*Nothognathella palmatoformis*' Druce, 1975 (see Fig. 19). The element has a well developed platform on both sides of the carina. The outer platform

Fig. 20. O element belonging to the apparatus of some species of the *Palmatolepis (Panderolepis) glabra* group from the Upper *Palmatolepis marginifera* Zone (sample G. 1643); × 160, RGM 295 284.

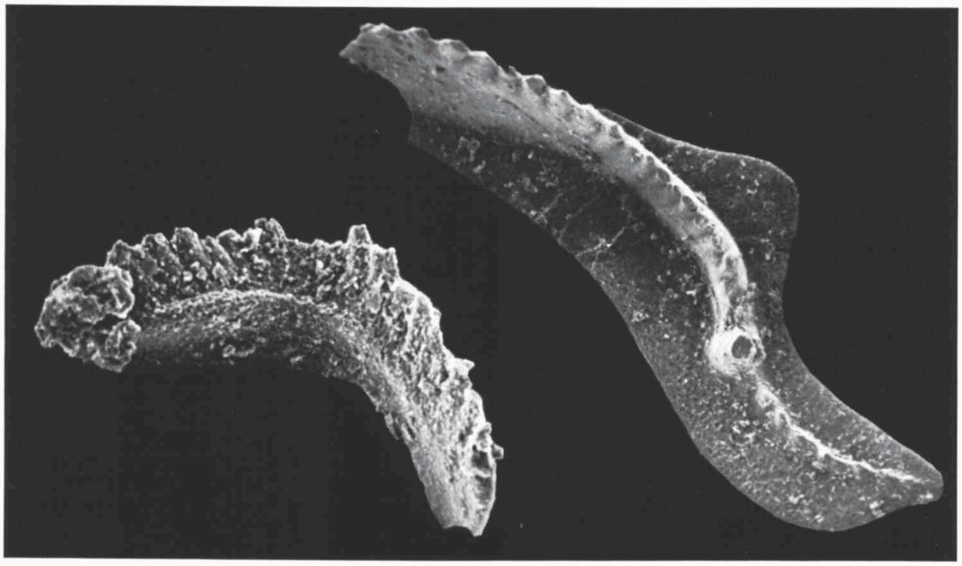

Fig. 21. *Palmatolepis (Panderolepis) falcata* from the Upper *Palmatolepis marginifera* Zone (sample 41/71). P element × 77 (right), O element × 155 (left); RGM 295 292.

has a convex outer edge and is subparallel to the convex carina. The inner platform is wide and has a well developed notch just anterior to the midpoint. Both platforms have shagreen-like ornamentation. The carina is tallest in the anterior half and extends anteriorly as a short free blade. The posterior half is shorter and on some specimens barely reaches the posterior termination. In aboral view the unit is keeled and lacks a basal cavity. In specimens where the carina does not reach the spatulate posterior termination the keel also terminates before reaching the margin. This O element can be distinguished from the O elements of *Palmatolepis termini ('Nothognathella sublaevis')* and *P. crepida ('N.* cf. *sublaevis')* by the greater platform development, especially of the outer platform.

In faunas from the *Palmatolepis marginifera* Zone containing the platform elements '*Palmatolepis glabra prima*', '*P. pectinata*', and '*P. lepta*' the corresponding nothognathellan elements are a slender form with platforms (Fig. 20) as well as a form with almost no platforms, '*Nothognathella falcata*' (Fig. 21). In these faunas we could not establish a correspondence between palmatolepan and nothognathellan elements belonging to *Panderolepis.*

The nothognathellan element with platforms (Fig. 20) is highly flexed, up to 90°. The platforms extend along both sides of the carina. They are about as wide as the base of the carina or slightly wider. They have a shagreen-like ornamentation. The denticles of the carina are rather low, inclined posteriorly and behind the point of flexure often also outwardly inclined. This form differs from the nothognathellan element '*N. palmatoformis*' in having a narrower platform and in being strongly deflected.

The O element '*Nothognathella falcata*' Helms, 1959 is slightly arched. The posterior bar is deflected through 90°. Both bars are tumid. Extremely narrow platforms extend along both sides of the carina, or are reduced to small ones near the point of flexure or completely missing. The carina is composed of low, fused denticles with free tips. The denticles are inclined posteriorly and behind the flexure point also outwardly. The element is keeled, but no basal cavity is obvious. This O element differs from the one described above in having almost no platform.

Close inspection of Helms' 1959 paper shows that the P element '*Palmatolepis glabra lepta*' (cited as '*P. glabra elongata*') is the only representant of the *glabra* group that occurs together with the type material of '*Nothognathella falcata*'. Also in our material from the *Scaphignathus velifer* Zone '*P. lepta*' is the only '*P. glabra*' group species occurring together with '*N. falcata*'. Therefore we must assume that both elements belong to one apparatus. Because of the priority of the name *falcata* the valid name for this apparatus will be *Palmatolepis (Panderolepis) falcata* (Helms, 1959). It cannot be excluded that forms similar to '*N. falcata*' also occur associated with other platforms of the '*Palmatolepis glabra*' group.

Palmatolepis (Panderolepis ?) distorta Branson & Mehl, 1934
Fig. 22.

Diagnosis — The P skeletal element is the form species '*Palmatolepis distorta*' Branson & Mehl, 1934. The O skeletal element is a nothognathellan element which has many of the characteristics of the form species '*Nothognathella polygnathoidea*' Branson & Mehl, 1934.

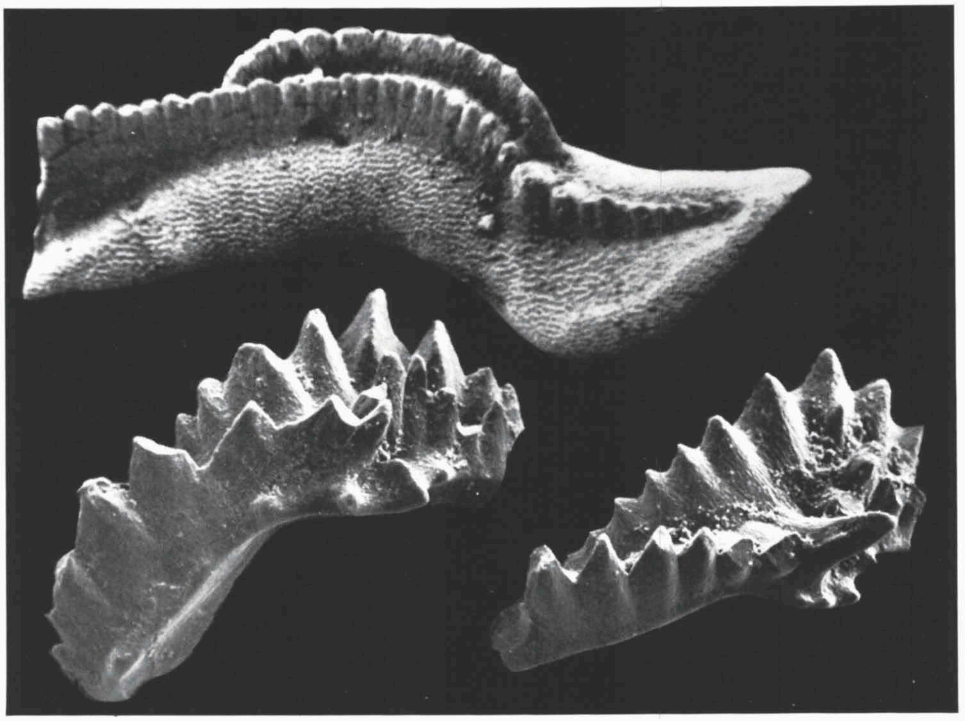

Fig. 22. *Palmatolepis (Panderolepis ?) distorta* from the *Palmatolepis marginifera* Zone. P element × 80 (above) sample G. 1643 RGM 295 290, O element × 80 (below) two specimens from Holt's Summit RGM 295 301; lateral view (left), upper view (right).

Description — For a description of the P element see Branson & Mehl, 1934 and Catalogue of Conodonts, vol. III, p. 297 - 300. The O element is a nothognathellid with a very well developed platform. Arch of the base is low, broadly rounded, with the aboral edge sharp on the anterior limb, differentiated into a low sharp keel on a comparatively flat surface on the posterior limb. The apical pit of the aboral surface is small but distinct. Length of the anterior and posterior limbs is about equal; the anterior limb is laterally straight, slightly curved down in the vertical plane; the carina on the posterior limb is curved sinuously. The outer platform is recognizable as a ridge nearly to the ends of the limbs and is markedly extended laterally for about one-fourth its length on the posterior limb near the apex of the arch. The inner platform is wide at the apex of the arch, narrows rapidly anteriorly and gradually posteriorly, and extends to the ends of the limbs. The oral surface is sometimes nodose, but more generally adorned with sharp transverse ridges. The oral denticles are not sharply set off into anterior and posterior series and their number varies from fourteen to twenty. In general they are larger on the anterior limb. All are more or less peg-like and closely approximated.

Remarks — We do not know from which nothognathellan element this rather aberrant form has developed. However, the shape of the carina and the absence of a conspicuous apical denticle reminds us of the carina of *'Nothognathella sublaevis'*. Because of this and because of the similarities between the P element of *P. distorta* and those of species of *P. (Panderolepis)* we provisionally incorporate *P. distorta* in the subgenus *Panderolepis.*

In the counted samples 33 - 38 these *polygnathoidea*-like nothognathellan elements occur in small numbers and are not very well preserved. To confirm our idea about the nothognathellan element of *Palmatolepis distorta* a second sample from Holt's Summit was preliminary studied (only the sieve fraction > 0.25 mm). In this sample containing thousands of conodonts *'P. distorta'* is the dominant palmatolepan element (> 60% of the total of palmatolepids) and the nothognathellan element described above is the dominant *'Nothognathella'* (also more than 60%). Because this fauna contained well preserved specimens the photographed specimens were taken from it.

Subgenus Palmatolepis (Conditolepis) n. subgen.

Type species — *Palmatolepis marginifera* Helms, 1959.

Discussion — This subgenus is characterized by the occurrence of nothognathellan O elements which have the characteristics of the form species *'Nothognathella condita'* Branson & Mehl, 1934. These are arched elements with the denticles of the anterior limb much higher than those of the posterior limb, the denticle at the apex being exceptionally high. The carina divides the posterior limb into two nearly equal areas. These nothognathellan elements show some resemblance to the nothognathellan elements *'N. typicalis'* and *'N. ziegleri'* of the nominate subgenus *Palmatolepis*. *'N. condita'* differs from *'N. typicalis'* in having a much more pronounced denticle at the apex, less denticles on the anterior limb, and in the form of the platform which is mainly restricted to the posterior limb and divided into two equal parts by the carina. In *'N. typicalis'* the platform is widest in the central part especially on the inner side. *'N. ziegleri'* has a very pronounced apical denticle but differs from *'N. condita'* by its very narrow platform and the presence of the apical lobe.

The following species present in our faunas belong to this subgenus: *Palmatolepis (Conditolepis) delicatula protorhomboidea* Sandberg & Ziegler, 1973, *P. (C.) quadrantinodosa inflexa* Müller, 1956, *P. (C.) rhomboidea* Sannemann, 1955, and *P. (C.) marginifera* Helms, 1959. All these forms belong to the group named: *marginifera* group by Helms (1963), *rhomboidea-quadrantinodosa* group by Ziegler (1962a), *Palmatolepis delicatula* stock by Sandberg & Ziegler (1973).

'Nothognathella condita' was first described by Branson & Mehl (1934, p. 230). In the same paper on p. 235 they described *'Palmatolepis quadrantinodosa'* and on p. 237 *'Palmatolepis delicatula'*. These two form species of *'Palmatolepis'* represent P elements of two different natural species of *Palmatolepis* both of which in our opinion, have had an O element similar to *'Nothognathella condita'*. However, which of these two species corresponds to the holotype of *'N. condita'* is not known.

Palmatolepis (Conditolepis) delicatula protorhomboidea Sandberg & Ziegler, 1973
Fig. 23.

Diagnosis — P skeletal element is the form species *'Palmatolepis delicatula protorhomboidea'*, O skeletal element is a nothognathellan form closely related to the form species *'N. condita'* Branson & Mehl, 1934.

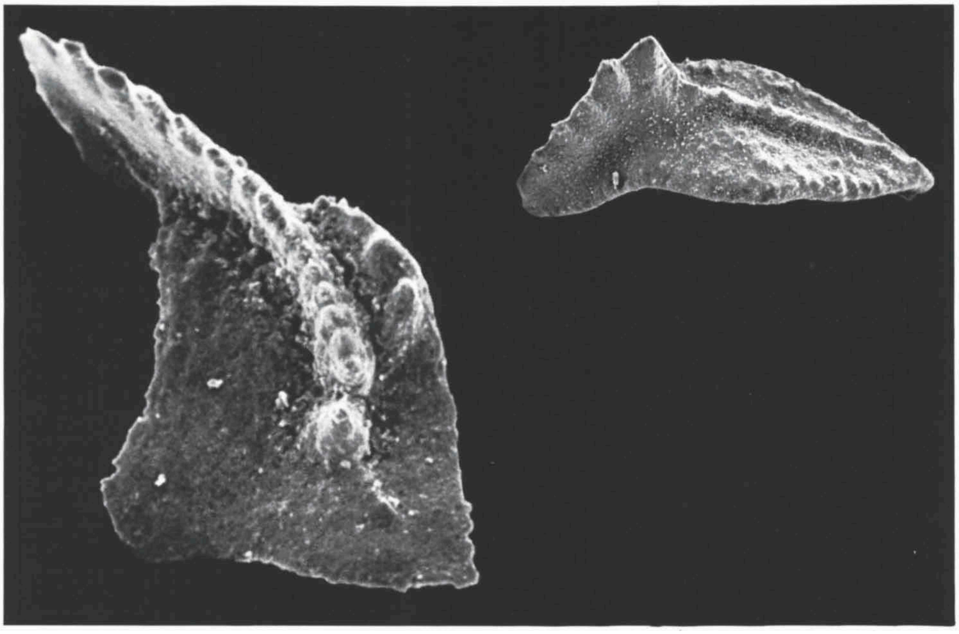

Fig. 23. *Palmatolepis (Conditolepis) delicatula protorhomboidea* from the Middle *Palmatolepis crepida* Zone (sample 15-9-16). P element (left), O element (right); × 210, RGM 295 293.

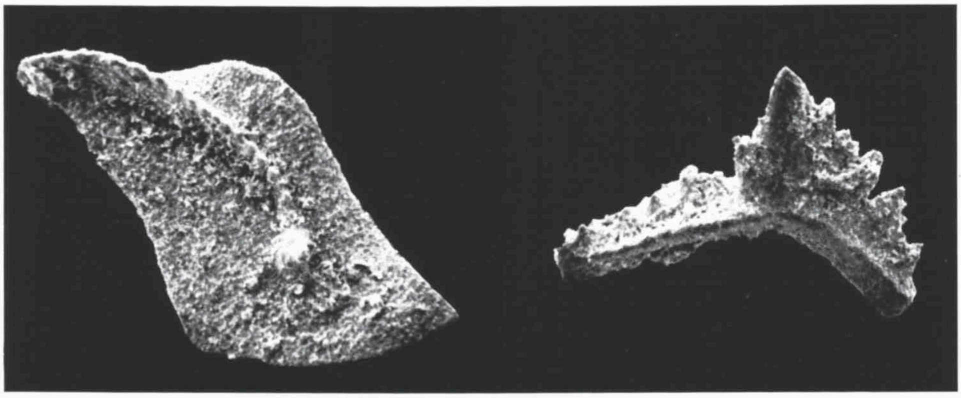

Fig. 24. *Palmatolepis (Conditolepis) quadrantinodosa inflexa* from the Lower *Palmatolepis rhomboidea* Zone (sample L. 8798). P element (left), O element (right); × 88, RGM 295 297.

Description — For description of the P element see Sandberg & Ziegler (1973, p. 103). The O element is arched and has nearly straight limbs of about equal length. The posterior limb is slightly curved inward and expanded regularly from the sharp aboral edge to the oral surface which is flat transversely and tilted inward. The edge of this oral surface is marked by low coarse nodes. The carina is low, consists of fused nodes and divides the oral surface into two nearly equal areas. The inner platform is continued along the anterior limb and wedges out towards the anterior termination. The platform surface between carina and nodose edge bears irregularly placed low nodes. The five to seven denticles of the anterior limb are fused. The sharp upper edge increases in height toward the apex of the arch. The apical denticle is the highest and thickest of the series. The aboral side is keeled and has a small pit.

Palmatolepis (Conditolepis) quadrantinodosa inflexa Müller, 1956
Fig. 24.

Diagnosis — P skeletal element is the form subspecies *'Palmatolepis quadrantinodosa inflexa'* Müller, O skeletal element is a nothognathellan form closely related to the form species *'N. condita'* Branson & Mehl, 1934.

Remarks — For description of the P element see Müller (1956), and Catalogue of Conodonts, vol. III, p. 377 - 379. The platform of the O element is much less wide than that of the O element of *P. delicatula protorhomboidea.* The posterior part is divided in equal areas by the carina which consists of low nodes. The anterior limb bears high denticles, only partly fused with free tips. The apical denticle is the highest and thickest of the series. The element is keeled and has a small pit.

Palmatolepis (Conditolepis) rhomboidea Sannemann, 1955
Fig. 25.

Diagnosis — P skeletal element is the form species *'Palmatolepis rhomboidea'*,

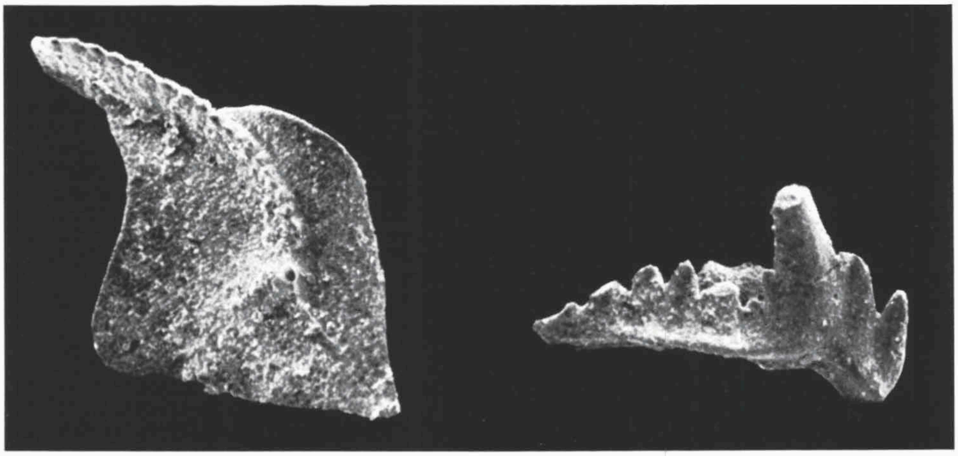

Fig. 25. *Palmatolepis (Conditolepis) rhomboidea* from the *Palmatolepis rhomboidea* Zone (sample 43/71). P element (left), O element (right); × 95, RGM 295 296.

O skeletal element is a nothognathellan form closely related to the form species '*N. condita*'.

Remarks — For description of the P element see Sannemann, 1955a, and Catalogue of Conodonts, vol. I, p. 299 - 301. The O element is very similar to that of *P. quadrantinodosa inflexa*. The denticles of the posterior limb are somewhat higher. The difference in height and thickness of the apical denticle compared to the other denticles of the anterior limb is more pronounced. The element is keeled and has a small pit.

Palmatolepis (Conditolepis) marginifera Helms, 1959
Fig. 26.

Diagnosis — P skeletal element is the form species '*Palmatolepis marginifera marginifera*' Helms, O skeletal element resembles the form species '*Nothognathella condita*' Branson & Mehl, 1934.

Description — For description of the P element see Ziegler (1962b) and

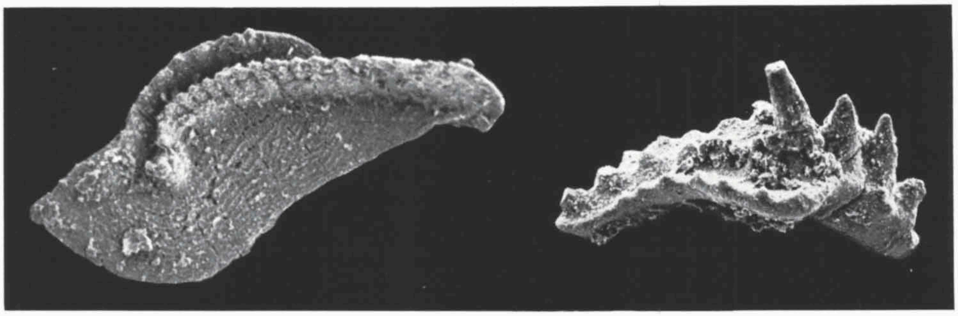

Fig. 26. *Palmatolepis (Conditolepis) marginifera* from the Upper *Palmatolepis marginifera* Zone (sample 41/71). P element × 79 (left) RGM 295 292, O element × 94 (right) RGM 295 286.

Catalogue of Conodonts, vol. III, p. 327 - 330. The O element is arched, slightly flexed and has limbs of about equal length. The anterior limb has four to five discrete denticles, the one at the apex being the highest. The denticles of the posterior limb are low and only partly fused. The platforms on both sides of the carina are of nearly equal size. The platform edges are nodose. The outer platform ends in a convex bend on the anterior limb anterior of the apical denticle. The edge of the inner platform is continued along the anterior limb and wedges out towards the anterior termination. The platform is slightly concave. The aboral side is keeled and has a small pit.

Remarks — This form differs from the O element of *P. delicatula protorhomboidea* by having a more slender platform and less fused denticles. In comparing it to the O element of *P. rhomboidea* one notes that the denticles of the anterior limb are more discrete and that the apical denticle is somewhat less pronounced.

Subgenus *Palmatolepis (Palmatolepis)* Ulrich & Bassler, 1926

Type species — *Palmatolepis perlobata* Ulrich & Bassler, 1926.

Discussion — Several species belonging to this subgenus are present in our material: *Palmatolepis (Palmatolepis) perlobata schindewolfi* Müller; *P. (P.) grossi* Ziegler, 1960; and *P. (P.) maxima* Müller, 1956, grouped in Table 4 as *P.* gr. *schindewolfi.* And furthermore *P. (P.) rugosa trachytera* Ziegler, 1960; and *P. (P.) ampla* Müller, 1956, grouped in Table 4 as *P.* gr. *rugosa.* Of these species only the P elements of the first species occur in large quantities. Those of the other species of the *schindewolfi* group and those of the *rugosa* group occur in rather small numbers.

The O skeletal elements corresponding to this subgenus are the form species '*Nothognathella typicalis*' Branson & Mehl, 1934, and '*N. ziegleri*' Helms, 1959. In older samples '*N. typicalis*' is the only nothognathellan element corresponding to this subgenus, while younger samples contain '*N. ziegleri*' or both

Fig. 27. *Palmatolepis (Palmatolepis) perlobata schindewolfi* s.l. from the *Polygnathus styriacus* Zone (sample 634). P element (left), O element (right); × 56, RGM 295 296.

forms. These two nothognathellan forms are narrowly related and *'N. ziegleri'* must derive from *'N. typicalis'*. In samples where both forms co-occur they may represent intergrading variants. Although numbers of form species other than *'P. schindewolfi'* are too small in individual samples to permit any conclusion as to the presence or absence of other nothognathellan forms, the combined information from all samples leads us to the conclusion that the other form species of *'Palmatolepis'* must also have been associated with an O element resembling *'N. typicalis'*.

According to Helms (1959), *'N. typicalis'* is already encountered at the stratigraphical level at which *'P. triangularis'* occurs. According to Ziegler (1962a) *'P. perlobata'* also appears in the *P. triangularis* Zone. We surmise that the O element corresponding to the type species *P. (P.) perlobata perlobata* was a form resembling *'N. typicalis'*, but due to the lack of material containing the type species no definite proof for this assumption can be given.

Palmatolepis (Palmatolepis) perlobata schindewolfi Müller, 1956
Figs. 27, 28.

Discussion — According to Ziegler (Catalogue of Conodonts, vol. III) the concept of the form species *'P. schindewolfi'* is very broad and includes several different morphotypes which possibly may be recognized as distinct subspecies. Judging from our data at least two different species or subspecies with a P element resembling *'P. schindewolfi'* are to be recognized, one characterized by the O element *'N. ziegleri'* (Fig. 27) and another one characterized by the O element *'N. typicalis'* (Fig. 28). The former would derive from the latter, and apparatuses characterized by intermediary O elements could be interpreted as transitional forms. We have not been able to find conspicuous differences between older and younger platform elements, and do not know whether the holotype corresponds to *'N. ziegleri'*, *'N. typicalis'* or to an intermediate form. Investigation of the fauna that contained Müller's holotype might clarify this matter. For the moment, we will rank the different morphotypes under one species.

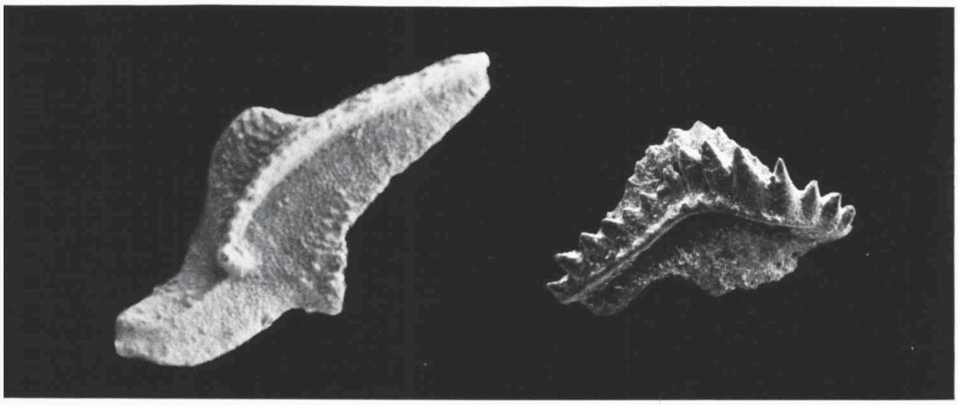

Fig. 28. *Palmatolepis (Palmatolepis) perlobata schindewolfi* s.l. from the Upper *Palmatolepis marginifera* Zone (sample G 1643). P element (left), O element with basal plate (right); × 55, RGM 295 297.

REFERENCES

Austin, R. L. & P. J. Hill, 1973. A Lower Avonian (K-Zone) Conodont Fauna from near Tintern, Monmouthshire,-Wales. — Geol. Palaeont., 7: 123 - 134.

Babcock, L. C., 1976. Conodont paleoecology of the Lamar Limestone (Permian), Delaware Basin, West Texas. — Geol. Assoc. Canada, Spec. pap. 15: 279 - 294.

Benzecri, J. P., 1973. L'analyse des données. 2. L'analyse des Correspondances. — Dunod, Paris.

Bischoff, G., 1957. Die Conodonten des rhenoherzynischen Unterkarbons mit Berücksichtigung der Wocklumeria-Stufe und der Devon/Karbon-Grenze. — Abh. hess. L.-Amt Bodenforsch., 19: 1 - 64.

Bitter, P. H. von, 1972. Environmental control of conodont distribution in the Shawnee Group (Upper Pennsylvanian) of eastern Kansas. — Univ. Kansas Paleont. Contr., 59: 1 - 105.

Boogaard, M. van den, 1963. Conodonts of Upper Devonian and Lower Carboniferous age from Southern Portugal. — Geol. Mijnbouw, 42: 248 - 259.

Boogaard, M. van den, & L. J. G. Schermerhorn, 1975. Conodont faunas from Portugal and southwestern Spain, part 2. A Famennian conodont fauna at Cabezas del Pasto. — Scripta Geol., 28: 1 - 36.

Boogaard, M. van den & O. Simon, 1973. *Pseudofurnishius* (Conodonta) in the Triassic of the Betic Cordilleras, SE Spain, — Scripta Geol., 16: 1 - 23.

Branson, E. B. & M. G. Mehl, 1934. Conodonts from the Grassy Creek shale of Missouri. — Univ. Missouri Studies, 8: 171 - 259.

Bultynck, P., 1972. Middle Devonian Icriodus Assemblages (Conodonta). — Geol. Palaeont., 6: 71 - 86.

Carls, P., 1977. Could Conodonts be lost and replaced? — N.Jb. Geol. Paläontol. Abh., 155: 18 - 64.

Catalogue of Conodonts, vol. I, 1973. Edited by W. Ziegler. — Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Catalogue of Conodonts, vol. III, 1977. Edited by W. Ziegler. — Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Cooper, C. L., 1931. New Conodonts from the Woodford formation of Oklahoma. — Jour. Paleont., 5: 230 - 243.

David, M., M. Dagbert & Y. Beauchemin, 1977. Statistical analysis in Geology: correspondence analysis method. — Quart. Colorado School Mines, 72, 1: 1 - 60.

Denham, R. L., 1944. Conodonts. — Jour. Paleont., 18: 216 - 218.

Druce, E. C., 1975. Conodont biostratigraphy of the Upper Devonian reef complexes of the Canning Basin, Western Australia. — Bureau Mineral Resources Geol. Geophys., Bull. 158, 1: 1 - 303; 158, 2: pls. 1 - 97.

Druce, E. C., F. H. T. Rhodes & R. L. Austin, 1972. Statistical analysis of British Carboniferous conodont faunas. — Jour. Geol. Soc., 128: 53 - 70.

Glenister, B. F. & G. Klapper, 1966. Upper Devonian conodonts from the Canning Basin, Western Australia. — Jour. Paleont., 40: 777 - 842.

Helms, J., 1959. Conodonten aus dem Saalfelder Oberdevon (Thüringen). — Geologie, 8: 634 - 678.

Helms, J., 1963. Zur 'Phylogenese' und Taxionomie von *Palmatolepis* (Conodontida, Oberdevon). — Geologie, 12: 449 - 485.

Jöreskog, K. G., J. E. Klovan & R. A. Reyment, 1976. Geological Factor Analysis. — Elsevier Sci. Publ. Comp.

Klapper, G. & G. M. Philip, 1971. Devonian conodont apparatuses and their vicarious skeletal elements. — Lethaia, 4: 429 - 452.

Klapper, G. & G. M. Philip, 1972. Familial Classification of reconstructed Devonian Conodont Apparatuses. — Geol. Palaeont., SB 1: 97 - 114.

Klapper, G. & W. Ziegler, 1975. In: Catalogue of Conodonts, vol. II. Edited by W. Ziegler. — Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Kohut, J. J., 1969. Determination, statistical analysis, and interpretation of recurrent conodont groups in the Middle and Upper Ordovician strata of the Cincinnati region (Ohio, Kentucky, and Indiana). — Jour. Paleont., 43, 2: 392 - 412.

Koike, T., 1971. A Carboniferous Succession of Conodont Faunas from the Atetsu Limestone in Southwest Japan (Studies of Asiatic Conodonts, part VI). — Sci. Rep. Tokyo Kyoiku Daigaku, sect. C, Geol. Min. & Geogr., 9 (91 - 93): 279 - 318.

Lange, F. G., 1968. Conodonten-Gruppenfunde aus Kalken des tieferen Oberdevon. — Geol. Palaeont., 2: 37 - 57.

Lindström, M., 1964. Conodonts. — Elsevier Publ. Comp., Amsterdam: 196 pp.

Mashkova, T. V., 1972. Ozarkodina steinhornensis (Ziegler) apparatus, its conodonts and biozone. — Geol. Palaeont., SB 1: 81 - 90.

Mayr, E., 1969. Principles of Systematic Zoology. — McGraw Hill.

Miller, A. K. & W. L. Youngquist, 1947. Conodonts from the type section of the Sweetland Creek shale, Iowa. — Jour. Paleont., 21: 501 - 517.

Müller, K. J., 1956. Zur Kenntnis der Conodonten-Fauna des europäischen Devons, 1. Die Gattung *Palmatolepis*. — Abh. Senckenb. naturf. Ges., 494: 1 - 70.

Nicoll, R. S., 1977. Conodont apparatuses in an Upper Devonian palaeoniscoid fish from the Canning Basin, Western Australia — BMR Jour. Australian Geol. Geophys., 2: 217 - 228.

Pollock, C. A., 1968. Lower Upper Devonian conodonts from Alberta, Canada. — Jour. Paleont., 42: 415 - 443.

Ramovs, A., 1978. Mitteltriassische Conodont clusters in Slovenien. — Paläont. Z., 52: 129 - 137.

Rexroad, C. B., 1969. Conodonts from the Jacobs Chapel Bed (Mississippian) of the New Albany Shale in Southern Indiana. — Ind. Geol. Surv., Bull. 41: 1 - 55.

Rhodes, F. H. T., R. L. Austin & E. C. Druce, 1969. British Avonian (Carboniferous) conodont faunas, and their value in local and intercontinental correlation. — Bull. Brit. Mus. (Nat. Hist.), Geology, suppl. 5: 1 - 313.

Sandberg, C. A. & W. Ziegler, 1973. Refinement of Standard Upper Devonian Conodont zonation based on sections in Nevada and West Germany. — Geol. Palaeont., 7: 97 - 122.

Sannemann, D., 1955a. Beitrag zur Untergliederung des Oberdevons nach Conodonten. — Neues Jb. Geol. Paläont., Abh. 100: 324 - 331.

Sannemann, D., 1955b. Oberdevonische Conodonten (to IIα). — Senckenb. Lethaea, 36: 123 - 156.

Sneath, P. H. A. & R. R. Sokal, 1973. Numerical Taxonomy. The Principles and Practice of numerical classification. — W. H. Freeman & Co, San Francisco — London.

Ulrich, E. O. & R. S. Bassler, 1926. A classification of the toothlike fossils, conodonts, with descriptions of American Devonian and Mississippian species. — Proc. U. S. Nat. Mus., 68, 12: 1 - 63.

Uyeno, T. T., 1967. Conodont zonation, Waterways Formation (Upper Devonian), Northeastern and Central Alberta. — Geol. Surv. Canada, paper 67-30: 1 - 21.

Uyeno, T. T., 1974. Conodonts of the Waterways Formation (Upper Devonian) of Northeastern and Central Alberta. — Geol. Surv. Canada, Bull. 232: 1 - 93.

Winder, C. G., 1974. Recognizing the Conodont Assemblage *Amorphognathus* by Correlation Coefficient. — Geology, 2, 6: 299 - 300.

Youngquist, W. L., 1945. Upper Devonian conodonts from the Independence shale (?) of Iowa. — Jour. Paleont., 19: 355 - 367.

Youngquist, W. L., 1947. A new Upper Devonian conodont fauna from Iowa. — Jour. Paleont., 21: 95 - 112.

Ziegler, W., 1958. Conodontenfeinstratigraphische Untersuchungen an der Grenze Mitteldevon/Oberdevon und in der Adorfstufe. — Notizbl. hess. L.-Amt Bodenforsch., 87: 7 - 77.

Ziegler, W., 1962a. Taxionomie und Phylogenie Oberdevonischer Conodonten und ihre stratigraphische Bedeutung. — Abh. hess. L.-Amt Bodenforsch., 38: 1 - 166.

Ziegler, W., 1962b. Die Conodonten aus den Geröllen des Zechsteinkonglomerates von Rossenray. — Fortschr. Geol. Rheinl. Westf., 6: 391 - 406.

Ziegler, W., 1972. Über devonische Conodonten-Apparate. — Geol. Palaeont., SB 1: 91 - 96.

Ziegler, W., 1973. In Catalogue of Conodonts, vol. I, edited by W. Ziegler. — Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Ziegler, W. & J. W. Huddle, 1969. Die *Palmatolepis glabra* — Gruppe (Conodonta) nach der Revision der Typen von Ulrich & Bassler durch J. W. Huddle. — Fortschr. Geol. Rheinl. Westf., 16: 377 - 386.

Ziegler, W. & M. Lindström, 1975. Fortschrittsbericht Conodonten. — Paläont. Z., 49: 565 - 598.

Manuscript received 7 December 1978.