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INTERSPECIFIC MORPHOLOGICAL RELATIONS WITHIN THE « *QUADRANTINODOSA*-STOCK » (BRANSON & MEHL, 1934) (*MARGINIFERA*-ZONE, UPPER DEVONIAN) (*)

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(5 figures dans le texte, 1 planche, 1 hors-texte)

RÉSUMÉ

Le but de la présente note consiste en une révision systématique du « groupe de *quadrantinodosa* BRANSON & MEHL », auquel appartiennent différents guides importants pour la Zone à *Palmatolepis marginifera* HELMS.

La totalité des différents subgroupes de ce stock morphologique et leur formes de transition, caractérisent en Belgique la partie inférieure de la Zone. La partie supérieure de cette Zone ne contient aucun conodonte significatif et est considérée comme Zone d'interval. *Palmatolepis marginifera* HELMS est subdivisée en 4 sous-espèces, dont 2 nouvelles formes; leur importance stratigraphique est discutée.

ABSTRACT

The purpose of this paper is to give a short systematic review of the so-called « *quandrantinodosa*-stock », to which some important conodont guide-markers of the *marginifera*-Zone belong.

The different subgroups of this stock and their transitional forms may, as a whole, characterise the lower part of the *marginifera*-Zone in Belgium. The Upper *marginifera*-Zone is less characteristic, and must be regarded as an interval-Zone.

A further subdivision of *Palmatolepis marginifera* HELMS is given : two new subspecies are described and the stratigraphic value of the different subspecies of *P. marginifera* HELMS is discussed.

ACKNOWLEDGEMENTS

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I. *Interspecific morphological relations within the* « quadrantinodosa-*stock* »

The Lower *marginifera*-Zone (ZIEGLER, 1962, 1970; SANDBERG & ZIEGLER, 1973) is characterised by the association of *P. inflexa* MULLER, *P. inflexoidea* ZIEGLER *P. marginifera* HELMS, *P. quadrantinodosa* BRANSON & MEHL and *P. stoppeli* SAND-

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BERG & ZIEGLER; these are the different members of the socalled « *quadrantinodosa*-group », after the form species *Palmatolepis quadrantinodosa* first described by BRANSON & MEHL (1934) from the Grassy Creek Shale of Missouri (USA).

The definition of a new species, *Palmatolepis inflexa* by MULLER (1956), in which the author included morphologically widely divergent forms, led to a certain confusion in the interpretation of this stock.

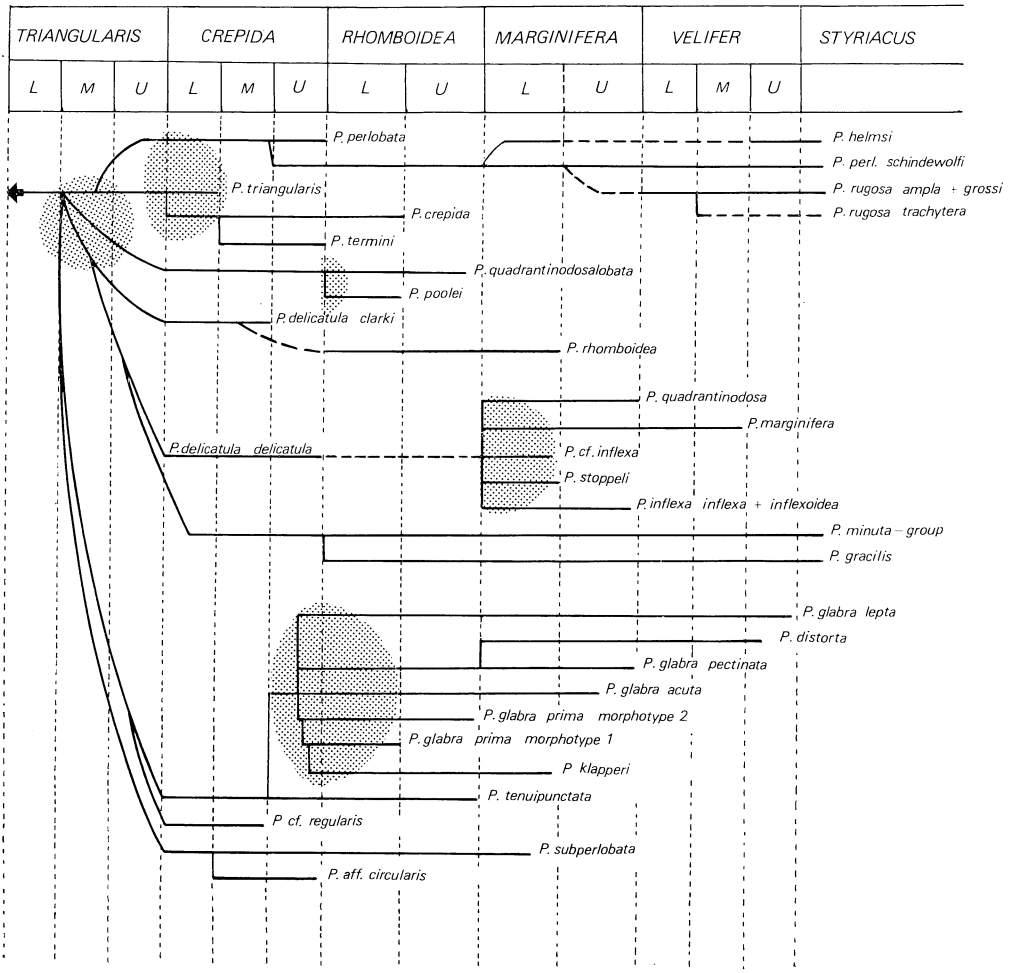


Fig. 1 : « Phylomorphogeny » of Palmatolepis during the Famennian stage.
Shaded areas = fields of transition,
Dotted lines = not observed evolutionary lines within Belgian faunas.
L = lower, M = middle, U = upper.

Palmatolepis inflexa MULLER (1956) has been introduced by its author as the European morphological counterpart of the American form species *Palmatolepis quadrantinodosa* BRANSON & MEHL (« vikarierende Arten von *Palmatolepis* »); but at the present time, most authors accept the world wide conodont distribution during the Upper-Devonian, and MULLER's interpretation is abandoned. Consequently,

P. inflexa MULLER is regarded by ZIEGLER (1960, 1962) and most of the later authors, such as GLENISTER & KLAPPER (1966), as a subspecies of *P. quadrantinodosa* Br. & M.; at the same time ZIEGLER (1960) defined 2 new subspecies : *P. quadrantinodosa marginifera* and *P. quadrantinodosa inflexoidea*, which originally fell within the morphological variation pattern of one and the same form species *P. inflexa* MULLER (see MULLER, 1956, Pl. V, fig. 1-11). Except for ZIEGLER (1962), most authors illustrated specimens of *P. quadrantinodosa inflexa*, which differed considerably from the original holotype of *P. inflexa* MULLER (1956, Pl. V, fig. 10). Further, this holotype does not conform to the original description of *P. quadrantinodosa* by BRANSON & MEHL (1934, p. 235). Therefore, *P. inflexa* MULLER has been restricted to the description of the holotype and has been raised to species level; *P. inflexoidea* ZIEGLER has been treated in the same way (DREESEN & DUSAR, 1974, p. 24-25). SANDBERG & ZIEGLER (1973) no longer considered *P. marginifera* HELMS as a subspecies of *P. quadrantinodosa* Br. & M., but they raised it to species level, and introduced a new subspecies *P. marginifera duplicata*.

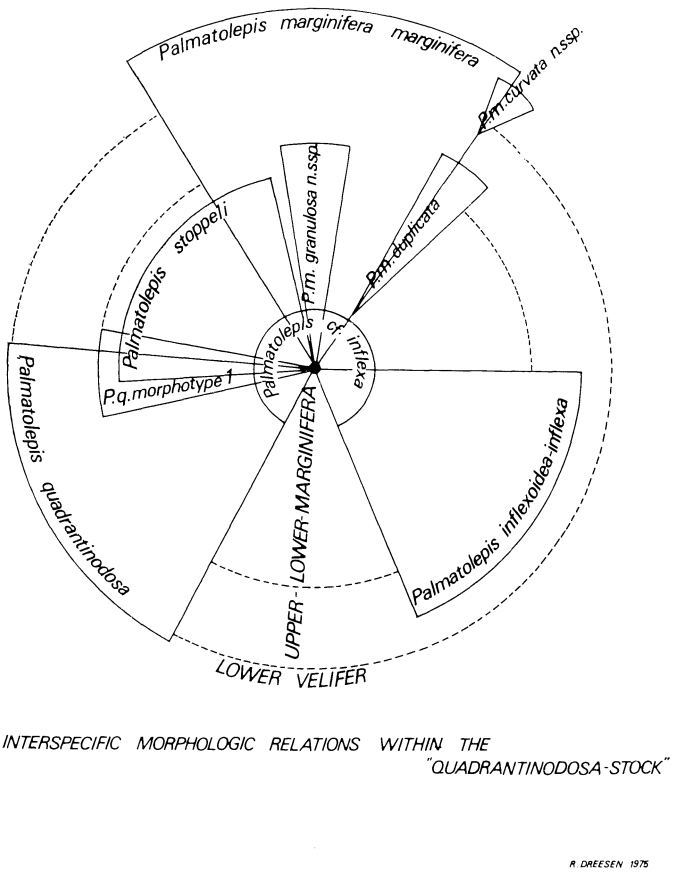


Fig. 2

Within this form species *P. marginifera* HELMS, it is possible to distinguish 2 new subspecies, with different stratigraphic ranges : *P. marginifera granulosa*

n. subsp. and *P. marginifera curvata* n. subsp. The small form species *P. cf. inflexa* MULLER (see DREESEN & DUSAR, 1974, p. 22) may be considered as the primitive form of the whole « *quadrantinodosa*-stock ». From this conodont form, distinguished from *P. inflexa* MULLER by its platform outline and margins, developed three important form groups : the *quadrantinodosa-*, the *marginifera-* and the *inflexa*-group (see Pl. I; Fig. 2). The transitional forms between these three form groups, and between each of them and *P.* cf. *inflexa* MULLER, are frequent throughout the whole Lower *marginifera*-Zone.

Consideration of this morphological subdivision, gives rise to some important remarks :

— The morphological relation between the *quadrantinodosa* and *marginifera* form groups is more pronounced than between the *inflexa* form group and each of the former groups. This relation, moreover, is characterised by the intermediate form group of *P. stoppeli* SANDBERG & ZIEGLER, 1973.

— *P. quadrantinodosa* Br. & M. morphotype 1 (DREESEN & DUSAR, 1974) an early ontogenetic stage of *P. quadrantinodosa* Br. & M., is a transitional form between the latter and *P. stoppeli*.

— *P. marginifera* HELMS evolved from *P.* cf. *inflexa* MULLER ; many transitional forms with *P. stoppeli* S. & Z. can also be recognized, by their elongation, and the progressive incurving of the platform, and by the elongation, narrowing, and heightening of the « bulge » to a « parapet ».

P. quadrantinodosa Br. & M. evolved from *P.* cf. *inflexa* MULLER through *P. quadrantinodosa* morphotype 1, by a progressive development of rows of nodes, on the anterior part of the inner platform, parallel to the blade-carina.

— The *inflexa-inflexoidea* form group is more or less isolated, with respect to the other form groups, since there are no typical transitional forms. Nevertheless, it is still possible to find some morphological relation with some elongated juvenile specimens of *P. marginifera marginifera* HELMS.

P. inflexoidea ZIEGLER and *P. inflexa* MULLER represent **2 different stages within the morphological evolution of one and the same form species,** since there is a complete transition series between them, by progressive invurving of the blade and widening of the platform. (see Pl. 1). We therefore propose to consider them as two subspecies : *P. inflexa inflexa* MULLER and *P. inflexa inflexoidea* ZIEGLER, instead of as two distinct form species.

A final peculiarity concerns the morphological relation between *P. marginifera duplicata* S. & Z. and *P. klapperi* S. & Z. (proposed by their authors, 1973, p. 105), which are in fact 2 different form species, evolved from 2 different morphological stocks : *P. marginifera duplicata* originated from the « *quadrantinodosa*-stock », *P. klapperi* from the « *glabra*-stock ».

II. *Biozonation*

The association of the different members of the « *quadrantinodosa*-stock » (*P. marginifera* HELMS, *P. stoppeli* SANDBERG & ZIEGLER, *P. quadrantinodosa* BRANSON & MEHL, and *P. inflexa* MULLER) and their numerous transitional forms, may, as a whole, characterise the Lower part of the *marginifera*-Zone. These transitional forms range throughout the whole Lower *marginifera*-Zone (in Belgium, especially at the top of this zone, in quite rich conodont faunas). The base of the

marginifera-Zone corresponds to the first occurrence of *P. marginifera marginifera* HELMS; because fo the relative scarcity of this form species at this stratigraphic level, the first occurrence of any other member « *quadrantinodosa*-association » may also be used.

An interesting additional guide marker for delimiting the *rhomboidea/marginifera*-Zones boundary, is *Palmatolepis* cf. *helmsi* ZIEGLER (Plate II, fig. 3), in different sections of the eastern part of the Dinant Basin (see DREESEN & DUSAR, 1974, p. 29-30; 1975, p. 64). This form species evolved from the *P. perlobata*-stock (ZIEGLER, 1962). The Lower/Upper *marginifera*-Zones boundary is classically based on the extinction of *P. quadrantinodosa, quadrantinodosa P. quadrantinodosa inflexa* and *P. quadrantinodosa inflexoidea*. The first occurrence of *P. rugosa ampla* and *P. rugosa grossi* is also proposed (ZIEGLER, 1962, Table II; 1971, Chart 6). These boundary criteria are not useful within Belgian conodont populations. Some members of the «*quarandtinodosa*stock» (such as *P. stoppeli, P. quadrantinodosa* morphotype 1) disappear earlier within the *marginifera*-Zone, but their extinction is not always simultaneous; most probably it is the result of a sudden change of facies.

Other form species of this stock, such as *P. inflexa inflexa* and *P. inflexa inflexoidea*, persist longer and may reach the top of the *marginifera*-Zone (see fig. 3). *P. quadrantinodosa* even ranges into the basal layers of the Lower *velifer*-Zone (see DREESEN & DUSAR, 1974, p. 33).

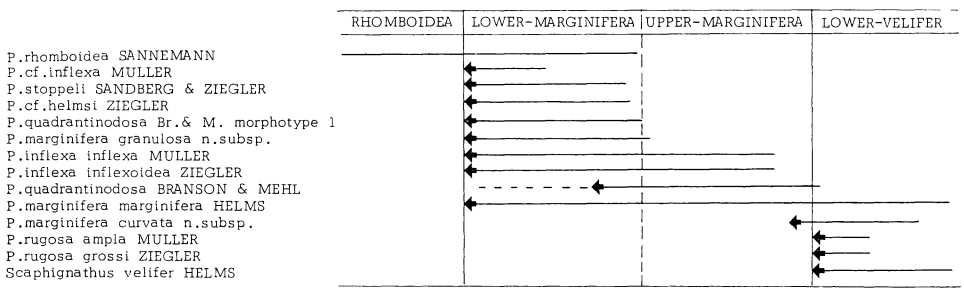


Fig.3: Range chart of significant Belgian conodonts delimiting the marginifera-Zone (modified after DREESEN & DUSAR, 1974)

On the other hand, the first occurrence of *P. rugosa ampla* and *P. rugosa grossi* falls within rich conodont faunas at the base of the Lower *velifer*-Zone.

In this way, the classic Lower/Upper *marginifera*-Zones boundary (ZIEGLER, 1962, 1971) must be abandoned.

In Belgium, the following criterium is used and has proved successful within the Dinant- and Vesdre Basins : the extinction of *P. stoppeli, P. quadrantinodosa* morphotype I and the different transitional forms of the « *quadrantinodosa*-group ». Nevertheless, it is not internationally valuable, since it is based upon the facies controlled extinction of conodont forms, and chronologically it has no significance.

The extinction of an important and frequent conodont form, *Palmatolepis rhomboidea* SANNEMANN, has also proved to be a successful additional criterium for delimiting the Lower-Upper *marginifera*-Zones boundary (see DREESEN & DUSAR, 1974, 1975).

The association of *P. marginifera marginifera* and *P. rhomboidea* below the *rhomboidea/quadrantinodosa*-Zones boundary (see ZIEGLER, 1962 + 1971), formerly

considered as a transition zone between the *rhomboidea*- and *quadrantinodosa*-Zone (see BOUCKAERT & ZIEGLER, 1965; BOUCKAERT, STREEL & THOREZ, 1968, Horstexte II), in fact characterises the Lower part of the *marginifera*-Zone.

Because of the lack of important conodont guide markers, the Upper part of the *marginifera*-Zone, must be regarded as an **interval-zone** between the characteristic Lower *marginifera*-Zone and the well-defined Lower *velifer*-Zone, which is based upon the first occurrence of *Scaphignathus velifer* HELMS (ZIEGLER, 1962 + 1971), (Plate II, fig. 6-7).

The extinctions that mark the Lower/Upper *marginifera*-Zones « boundary » more or less coincide with the establishment of a new lithofacies, the so-called « Souverain-Pré »-formation (lower part of the Upper-Famennian); this seems to indicate a certain **facies control** of the conodont associations (see also DREESEN, 1975).

Palmatolepis marginifera HELMS is now subdivided into 4 subspecies, including **2 new conodont forms,** with different ranges :

P.marginifera granulosa n. subsp. (Pl. I, fig. 24-25) is restricted to the upper part of the Lower *marginifera*-Zone; *P. marginifera curvata* n. subsp. (Pl. I, fig. 40-41) starts in the basal layers of the Lower *velifer*-Zone, but transitional forms with the nominate species are already found in the uppermost *marginifera*-Zone (see DREESEN & DUSAR, 1974, p. 28).

No specimens of *P. marginifera duplicata* SANDBERG & ZIEGLER have yet been found in Belgian strata; according to SANDBERG & ZIEGLER (1973) this subspecies appears within the Lower *marginifera*-Zone.

A few specimens of *P. marginifera duplicata* S. & Z. have recently been found (DREESEN, unpublished) in an isolated sample from the *Cheiloceras*-limestone of Erfoud in Morocco, associated with specimens of *P. stoppeli*, *P. marginifera marginifera*, *P. quadrantinodosa* morphotype 1, *P.* cf. *inflexa*, and many transitional forms.

III. *Systematic outline*

Genus Palmatolepis ULRICH & BASSLER, 1926

Palmatolepis cf. *inflexa* MULLER, 1956

Synonymy :

— 1961 — *P. inflexa* (MULLER)-FREYER, p. 64, Pl. IV, fig. 84.

— 1967 — *P. quadrantinodosa inflexa* MULLER-FREYER & ZAKOWA, p. 118, Pl. II, fig. 5.

— 1974 — *P.* cf. *inflexa* MULLER-DREESEN & DUSAR, p. 22, Pl. V, fig. 15-20, Textfig. 14.

Description :

P. cf. *inflexa* is a small species of *Palmatolepis* with an oval or circular shagreen platform. The inner part of the platform begins about half-way between the anterior tip of the blade and the central node. It generally has a marginal rim, often nodose or a small rounded bulge, not extending posterior to the central node. The outer platform begins at the anterior end of the blade. Its margin is concave anteriorly

and convex posteriorly. The carina posterior to the central node is weak to absent; it consists of small fused denticles. The blade-carina is sigmoidal.

Remarks :

P. cf. *inflexa* is the primitive form of the « *quadrantinodosa*-stock » (see SANDBERG & ZIEGLER, 1973; DREESEN & DUSAR, 1974).

Transitional forms to *P. inflexa* occur by elongation of the platform and tapering of the posterior tip; to *P. stoppeli* by thickening of the platform and expansion of the bulge; to *P. quadrantinodosa* morphotype 1 by development of nodes on the inner platform; and to *P. marginifera* by the formation of a parapet and increase in convexity of the outer platform margin. *P.* cf. *inflexa* differs from *P. rhomboidea* by the absence of a free blade.

Range :

P. cf. *inflexa* is restricted to the Lower *marginifera*-Zone.

Palmatolepis inflexa inflexoidea ZIEGLER, 1962

Synonymy :

— 1962 — *Palmatolepis quadrantinodosa inflexoidea* n. subsp.-ZIEGLER, p. 74-75, Pl. V, fig. 14-18.

— 1962 — *Palmatolepis* (*Pand.*) *elegans* HELMS in MULLER, p. W89, t.fig. 47, fig. 58 (nomen nudum).

— 1963 — *P.* (*Pand.*) *inflexoidea* (ZIEGLER)-HELMS, t.fig. 2, fig. 58, Pl. III, fig. 5, 7, 9, 11.

— 1966 — *P. quadrantinodosa inflexoidea* ZIEGLER-GLENISTER & KLAPPER, p. 820, Pl. XCIII, fig. 11, 12.

— 1969 — *P. quadrantinodosa inflexoidea* ZIEGLER-OLIVIERI, Pl. XIX, fig. 4, 6.

— 1973 — *P. quadrantinodosa inflexoidea* ZIEGLER-SANDBERG & ZIEGLER, p. 105, Pl. êV, fig. 1-3.

— 1974 — *P. inflexoidea* ZIEGLER-DREESEN & DUSAR, p. 24-25, Pl. VI, fig. 1-6, t.fig. 15-16.

— 1975 — *P. inflexoidea* ZIEGLER-DREESEN & DUSAR, Pl. XXIV, fig. 25-28.

Diagnosis :

P. inflexa inflexoidea represents the early stage of the *P. inflexoidea-inflexa* transition series; it is characterised by an elongate and flat shagreen platform, without an inner margin parapet. The outer part of the platform has no lobe and begins at the anterior end of the blade. The carina posterior to the central node is very weak to absent.

Description :

Juvenile specimens have a narrow elongate platform without much variation in its width. The inner and outer platform margins are subparallel, except for a tapering and inward curved posterior tip. The blade-carina is only slightly sigmoidal. The carina posterior to the central node is usually absent. On mature specimens, a bulge can be formed on the anterior part of the inner platform, which is otherwise smooth. The outer platform margin is strongly curved halfway between the anterior

and posterior tips. Strongest curvature of the blade-carina just anterior of the central node.

Remarks :

P. inflexa inflexoidea is no longer considered as a subspecies of *P. quadrantinodosa* (see DREESEN & DUSAR, 1974, p. 25) because of its deviation from the original description of the species (BRANSON & MEHL, 1934, p. 235). There is a complete transition series (fig. 1) between the typical « *inflexoidea* » and « *inflexa* » forms, by progressive incurving of the blade and widening of the platform. Therefore we consider *P. inflexoidea* as a subspecies of the first described form, *P. inflexa* MULLER. *P. inflexa inflexoidea* differs from the typical *P. inflexa inflexa*, by its elongate narrower platform and only a minor or weak incurving of the blade.

Range :

From the Lower *marginifera*-Zone into the Upper *marginifera*-Zone.

Palmatolepis inflexa inflexa MULLER, 1956

Synonymy :

— 1956 — *Palmatolepis* (*Pand.*) *inflexa* n.sp. — MULLER, p. 30-31, Pl. X, fig. 5.
— 1962 — *P. quadrantinodosa inflexa* MULLER-ZIEGLER, p. 73-74, Pl. VII, fig. 1-5.
— 1974 — *P. inflexa* MULLER-DREESEN & DUSAR, Pl. VI, fig. 11.
— 1975 — *P. inflexa* MULLER-DREESEN, Pl. I, fig. 2.

Diagnose :

The nominate sunspecies of *P. inflexa* MULLER and final stage of the *inflexoidea-inflexa* transition series. It is characterized by a large and wide suboval shagreen platform and a strongly curved blade-carina.

Description :

The strongest curvature of the carina lies just anterior to the azygous node. The posterior platform (posterior to this node) is about half the size of the anterior part. There is only a minor variation in the width of the platform, anterior or posterior to the central node. The outer platform margin is anteriorly strongly concave, posteriorly strongly convex. The carina posterior to the central node is absent or very weak and lies in a longitudinal depression.

In the practice, only those forms which strongly ressemble the original holotype of *P. inflexa* MULLER (Pl. X, fig. 5a + b), are considered as *P. inflexa inflexa*. These specimens are rather large and they represent the final stage of the *inflexoidea-inflexa* transition series.

Range :

Sporadically recorded from the Lower and Upper *marginifera*-Zone.

Palmatolepis marginifera HELMS, 1959

Diagnosis :

A species of *Palmatolepis*, characterized by the presence of a typical sharp-crested rim, the parapet, on the inner platform margin, and by the absence of a

lateral lobe. This parapet may be nodose or smooth and extends from the anterior platform tip to beyond the central node. In advanced forms this parapet may reach the posterior platformtip. The carina posterior to the central node is absent or very weak and lies in a longitudinal depression. The blade-carina is strongly curved anterior to the central node; posterior to this node the reduced carina continues rectilineally. The platform outline varies from round or ovalshaped to slender, oblong.

Remarks :

P. marginifera is morphologically subdivided into 4 subspecies; 3 of them were already figured by HELMS (1963), under open nomenclature, in his classical phylomorphogenetical sketch of the Genus *Palmatolepis*. (Textfig. 2).

Palmatolepis marginifera marginifera HELMS, 1959

Synonymy :

— 1959 — *Palmatolepis quadrantinodosa marginifera* ZIEGLER-HELMS, p. 649, Pl. V, fig. 22-23.
— 1960 — *P. quadrantinodosa marginifera* ZIEGLER-ZIEGLER, Pl. II, fig. 7a-c (holotype).
— 1962 — *P. quadrantinodosa marginifera* ZIEGLER-ZIEGLER, Pl. VII, fig. 6-8.
— 1963 — *P. quadr. marginifera* (ZIEGLER)-HELMS, Abb. 2, fig. 61-62.
— 1965 — *P. quadr. marginifera* HELMS-BOUCKAERT & ZIEGLER, Pl. III, fig. 9.
— 1966 — *P. quadr. marginifera* HELMS-GLENISTER & KLAPPER, Pl. XCI, fig. 7, 11, 13, 14.
— 1967 — *P. quadr. marginifera* HELMS-WOLSKA, Pl. IX, fig. 10-13; t.fig. 15.
— 1967 — *P. quadr. marginifera* HELMS-CLARK & ETHINGTON, Pl. V, fig. 5.
— 1969 — *P. quadr. marginifera* HELMS-OLIVIERI, Pl. XIX, fig. 1-3.
— 1972 — *P. quadr. marginifera* HELMS-MATYJA, Pl. IV, fig. 13.
— 1973 — *P. marginifera marginifera* HELMS-SANDBERG & ZIEGLER, p. 104-105, Pl. III, fig. 13-14.
— 1973 — *P. quadr. marginifera* ZIEGLER-SCULCZEWSKI, Pl. I, fig. 2.
— 1974 — *P. marginifera marginifera* HELMS-DREESEN & DUSAR, Pl. V, fig. 26-28.
— 1975 — *P. marginifera marginifera* HELMS-DREESEN, Pl. I, fig. 1.

Description :

P. marginifera marginifera, the nominate subspecies, is characterized by an oval to elongate shagreen platform. The parapet, parallel to the blade-carina, extends beyond the central node; in some specimens it may reach the posterior platform end. A deep adcarinal through may exist between carina and parapet. The outer platform is essentially flat; its margin is anteriorly slightly concave, posteriorly strongly convex. In juvenile specimens the inner platform is completely occupied by the parapet.

Remarks :

P. marginifera marginifera evolved from *P.* cf. *inflexa*, together with *P. stoppeli* and *P. quadrantinodosa* morphotype 1, trough different transitional forms. These forms, marked by a round to oval platform, with short parapet, are frequent within the basal *marginifera*-Zone. The typical parapet developed by narrowing heighening

and extending of the ramp or bulge in *P. stoppeli* and *P. quadrantinodosa* morphotype 1 (DREESEN & DUSAR, 1974).

Range :

The first occurrence of *P. marginifera marginifera* marks the base of the *marginifera*-Zone; it ranges into the Middle *velifer*-Zone (DREESEN & DUSAR, 1974).

Palmatolepis marginifera granulosa n. subsp.

Synonymy :

— 1959 — *Palmatolepis quadrantinodosa marginifera* (ZIEGLER) n. subsp. b-HELMS, Abb.2, fig. 60.

— 1966 — *P. quadrantinodosa marginifera* HELMS ex ZIEGLER-GLENISTER & KLAPPER, Pl. XCI, fig. 6 + 8.

— 1967 — *P. quadr. marginifera* HELMS-WOLSKA, p. 403c, fig. 15, (first row, right specimen).

— 1973 — *P. marginifera marginifera* n. subsp. SANDBERG & ZIEGLER, p. 104, Pl. III, fig. 20 + 26.

— 1974 — *P.* cf. *inflexa* MULLER → *P. marginifera marginifera* HELMS-DREESEN & DUSAR, Pl. VI, fig. 7 (juvenile form) + 8.

— *P. marginifera marginifera* HELMS — ibidem, Pl. VI, fig. 9.

— *P.* cf. *inflexa* MULLER → *P. inflexoidea* ZIEGLER — ibidem, Pl. VI, fig. 10 (juvenile form).

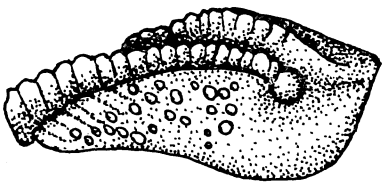
Derivatio nominis : « granulosa » : because of the typical coarselygranulated anterior part of the outer platform.

Holotype : C1398; see DREESEN & DUSAR (1976, in press) Plate I, fig. 1. This paper, textfig. 1.

Locus typicus : Theux 93, Franchimont Castle.

Stratum typicum : nodular limestones of the Souverain-Pré formation.

Material : about 10 specimens.



Text fig. 1. — *Palm. marginifera granulosa* n. subsp. Holotype (× 75).

Diagnosis :

A subspecies of *P. marginifera* HELMS, characterized by an extremely reduced or even missing inner platform, a parapet which extends to the posterior platform tip, and a series of nodes on the anterior part of the outer platform.

Description :

The inner platform margin is slightly indicated or missing; it is completely

occupied by a sigmoidal smooth or nodose parapet. The anterior part of the outer platform, (anterior to the central node) bears a series of rows of nodes, obliquely oriented to the blade; in a further stage they run parallel to it.

In juvenile specimens, these nodes are weakly developed and coincide with the growth-lines of the conodont. The carina posterior to the central node is absent or very weak and ends in a longitudinal depression. The oval or elongate platform tapers and is slightly inwards-oriented.

Remarks :

SANDBERG & ZIEGLER (1973, Pl. III, fig. 26) illustrated a rather atypical or an extreme form of the subspecies. *P. marginifera granulosa* most probabley evolved from *P.* cf. *inflexa* MULLER.

Range :

According to SANDBERG & ZIEGLER (1973), distinctly above the base of the *marginifera*-Zone. In the Australian material it is associated with *P. rhomboidea* and *P. inflexoidea* (Lower *marginifera*-Zone). In Belgium in the Lower *marginifera*-Zone.

Palmatolepis marginifera curvata n. subsp.

Synonymy :

— 1959 — *Palmatolepis quadrantinodosa marginifera* (ZIEGLER) n. subsp. b — HELMS, Abb. 2, fig. 60.

— 1973 — *Palmatolepis quadrantinodosa marginifera* HELMS-SCULCZEWSKI, Pl. I, fig. 1.

— 1974 — *Palmatolepis marginifera* n. subsp. a — DREESEN & DUSAR, p. 28, Pl. V, fig. 29-32.

Derivatio nominis : « curvata » after the strongly incurved blade-carina.

Holotype : C1068 (see DREESEN & DUSAR, 1974, Pl. V, fig. 29). This paper, textfig. 2.

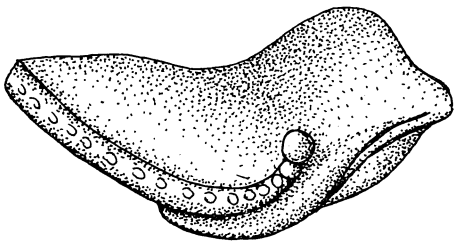
Stratum typicum : HNS 26.

Locus typicus : Hamoir-Néblon supérieur.

Material : 15 specimens.

Diagnosis :

A subspecies of *P. marginifera* HELMS, with a strongly sigmoidally incurved platform and a strongly arched central platform.



Text fig. 2. — *Palm. marginifera curvata* n. subsp. Holotype (× 75).

Description :

The blade-carina is strongly sigmoidally incurved. The carina posterior to the azygous node is weakly developed and is cut by the smooth or nodose parapet, which continues in its direction and extend to the posterior platform tip. The outer platform margin is anteriorly strongly concave, posteriorly extremely convex. The central part of the conodont is strongly arched or elevated; its surface dips to the margins interrupted on the inner side by a parapet. Because of this arching of the central platform and the strong development of a parapet, which extends to the posterior tip, some specimens may show a concave kink in the outer platform margin (see Pl. I, fig. 41).

Range :

Characteristic forms occur in basal layers of the *velifer*-Zone, but transitional forms with the nominate subspecies are already found in the Upper *marginifera*-Zone. (DREESEN & DUSAR, 1974). According to HELMS' scheme, it represents the youngest form within the *P marginifera*-group (1963, Abb. 2).

Palmatolepis marginifera duplicata SANDBERG & ZIEGLER, 1973

Synonymy :

— 1973 — *Palmatolepis marginifera duplicata* n. subsp. — SANDBERG & ZIEGLER, p. 105, Pl. III, fig. 15-19; fig. 21-25; Pl. V, fig. 15.

Diagnosis :

A subspecies of *P. marginifera* with a elongate shagreen platform; on the outer part it is occupied by an elongated bulge, or a second parapet, parallel to the carina. The platform outline is anteriorly strongly concave, posteriorly strongly convex. The carina posterior to the central node is mostly absent.

Remarks :

According to SANDBERG & KLAPPER (1973), this subspecies evolved from *P. klapperi* by narrowing and heighening of the ramp to a parapet, reducing of the posterior carina, and by the posteriorly migration of the azygous node.

This new subspecies is not yet recorded from Belgian strata.

Range :

According to its authors, *P. marginifera duplicata* occurs in the Lower and possibly the Upper *marginifera*-Zones.

Recently (DREESEN, unpublished) a few specimens were discovered from the *Cheiloceras*-Limestone at Erfoud (Morocco), associated with many specimens of *P. quadrantinodosa* morphotype 1, *P.* cf. *inflexa*, *P. stoppeli*, *P. marginifera marginifera*, and different transitional forms.

Palmatolepis quadrantinodosa BRANSON & MEHL, 1934

Synonymy :

— 1934 — *Palmatolepis quadrantinodosa* n. sp. — BRANSON & MEHL, p. 235, Pl. XVIII, fig. 17, 20.

— 1956 — *P. quadrantinodosa* BRANSON & MEHL-HASS, Pl. III, fig. 11.

— 1956 — *P.* (*Palm*) *inflexa* n. sp. — MULLER, p. 30, Pl. X, fig. 7.
— 1957 — *P. quadrantinodosa* Br. & M. — CLOUD, BARNES & HASS, Pl. IV, fig. 8.
— 1960 — *P. quadrantinodosa quadrantinodosa* Br. & M. — ZIEGLER, Pl. VII, fig. 10-11.
— 1963 — *P.* (*Pand.*) *quadrantinodosa* Br. & M. — HELMS, t.-fig. 2, fig. 57.
— 1967 — *P. quadrantinodosa quadrantinodosa* Br. & M. — WOLSKA, p. 402, Pl. IX, fig. 7.
— 1972 — *P. quadrantinodosa quadrantinodosa* Br. & M. — MATYJA, Pl. IV, fig. 7, 11.
— 1973 — *P. quadrantinodosa quadrantinodosa* Br. & M. — SANDBERG & ZIEGLER, p. 105, Pl. III, fig. 27-30.
— 1974 — *P. quadrantinodosa* Br. & M. — DREESEN & DUSAR, p. 21.

Description :

The platform is suboval in outline and weakly arched. The inner platform margin begins about halfway the anterior platform tip and the central node, then it becomes widened and reaches in an equal convex bow the rounded or tapering end. The most characteristic feature consists in 2 or 3 closely spaced rows of nodes, parallel to the blade, on the anterior part of the inner platform margin.

Remarks :

Palmatolepis quadrantinodosa Br. & M. is no longer subdivided into subspecies (which are raised to species level) but is restricted to the type species, as illustrated by BRANSON & MEHL (1934, Pl. XVIII, fig. 17, 20); as a matter of fact ZIEGLER (1960) designated this specimen as nominate subspecies.

Characteristic Belgian forms are rather scarce; they show a bulge on the inner anterior platform, with 2 or 3 rows of nodes, parallel to the carina, or short transverse ridges of fused paires of nodes.

Range :

P. quadrantinodosa evolved from *P.* cf. *inflexa* trough the intermediate form *P. quadrantinodosa* morphotype 1, which is restricted to the Lower *marginifera*-Zone; *P. quadrantinodosa* it self ranges from the Lower *marginifera*-Zone into the base of the *velifer*-Zone.

Palmatolepis quadrantinodosa BRANSON & MEHL morphotype 1

Synonymy :

— 1974 — *Palmatolepis quadrantinodosa* morphotype 1 — DREESEN & DUSAR, p. 27, Pl. V, fig. 9-14; textfig. 18.

Description :

P. quadrantinodosa morphotype 1 has a rounded, arched shagreen platform. The posterior half of the platform is sometimes slightly elongated and upturned. The inner platform bears anteriorly a short secondary row of nodes, parallel to the carina, often located on a small bulge. The inner platform margin may contain 2 or 3 complementary rows of nodes. These nodes are not restricted to this bulge, but extend to the central node. All the nodes can stand isolated or in part fused and

ridgelike. The carina posterior to the central node is absent or weak, but does not reach the platform tip.

Remarks :

P. quadrantinodosa morphotype 1 is an intermediate form between *P.* cf. *inflexa* and *P. quadrantinodosa*, which is characterized by a further development of nodes in rows parallel to the carina, or short transverse ridges. *P. quadrantinodosa* morphotype 1 is similar to *P, stoppeli* in platform outline, which shows however more variability than in the latter form species.

Range :

Lower *marginifera*-Zone into the lowermost part of the Upper *marginifera*-Zone.

Palmatolepis stoppeli SANDBERG & ZIEGLER, 1973

Synonymy :

— 1973 — *Palmatolepis stoppeli* n. sp. — SANDBERG & ZIEGLER, p. 106-107, Pl. III, fig. 1-11, Pl. V, fig. 13.

— 1974 — *Palmatolepis stoppeli* SANDBERG & ZIEGLER-DREESEN & DUSAR, Pl. V, fig. 1-7; t.fig. 17.

— 1975 — *Palmatolepis stoppeli* S. & Z. — ZIEGLER in Catalogue of Conodonts, Vol. II, p. 249-250, Palm. Plate, fig. 5-7.

— 1975 — *Palmatolepis stoppeli* S. & Z. — DREESEN, Pl. I, fig. 4-5.

Description :

Palmatolepis stoppeli is characterized by a rounded or even circular and thickened shagreen platform, The outer platform half has no lobe and starts at the anterior end of the blade. The inner platform margin begins at a point, 1/3 to halfway between the anterior platform tip and the central node. The inner platform margin is occupied by a high ramp, beginning at its anterior margin and ending at a point between the central node and the posterior tip. This ramp is mostly flattopped and gently dipping, equally in both directions.

Usually the ramp converges to the central node, in which case it has a sharp edge towards the blade-carina. The carina posterior to the central node is generally absent or only weak developed, but does not extends to the posterior tip.

Remarks :

This form species evolved from *P.* cf. *inflexa* by thickening of the platform and upward bulging of the inner platform margin to form a ramp.

Morphologically, this form is intermediate between *P. marginifera* and *P, quadrantinodosa* morphotype 1; transitional forms with both types are frequent in the Lower *marginifera*-Zone.

Range :

In Belgium *P. stoppeli* is restricted to the Lower *marginifera*-Zone.

EXPLANATION OF PLATE I

P. cf. *inflexa* MULLER

Fig. 1 : Haversin 6 (C1119)

P. quadrantinodosa Br. & M. morphotype 1

Fig. 2 : Louveigné 6 — Fig. 3 : Erfoud 5/46 — Fig. 4 : HNS 2 (C1120) — Fig. 5 : Silenrieux, Bois des Violettes — Fig. 6 : Haversin 8 — Fig. 7 : Silenrieux, déversoir 2.

P. quadrantinodosa Br. & M.

Fig. 8 + 9 : Steinbruch Schmidt — C (Mi).

P. stoppeli SANDBERG & ZIEGLER → *P. quadrantinodosa* Br. & M. morphotype 1

Fig. 10 : Erfoud 5/46

P. stoppeli SANDBERG & ZIEGLER → *P. marginifera* HELMS

Fig. 11 : Erfoud 5/46 — Fig. 20 : Aeketal Quarry, Bank 6 — Fig. 21 : HNS 4 (C1066) — Fig. 22 : Aeketal Quarry, Bank 6.

P. stoppeli SANDBERG & ZIEGLER

Fig. 12 : Aeketal 16/6 (Mi) — Fig. 13 : HNS 2 — Fig. 14 : Walcourt SVP 5 — Fig. 15 : Sil. Chap. St. Anne Belvédère 2 — Fig. 16 : Dison 1 (C1058) — Fig. 17 : Dison 1 (C1233) — Fig. 18 : Louveigné 6 — Fig. 19 : Esneux SVP 20.

P. marginifera marginifera HELMS

Fig. 23 : Aeketal Quarry, Bank 6 — Fig. 26 : Haversin 5 — Fig. 27 : Haversin 2 — Fig. 28 : Haversin 1 — Fig. 29 : Haversin 10 — Fig. 30 : Erfoud 5/46 — Fig. 31 : Haversin 3 — Fig. 32 : Haversin 1 — Fig. 33 : Ham. MD. 72.3′.

Fig. 34 : Haversin 5 — Fig. 35 : Erfoud 5/46 — Fig. 36 : Erfoud 5/46 — Fig. 37 : Dison 8 (C1075) — Fig. 38 : Aeketal Quarry, Bank 6 — Fig. 39 : Badon 4.

P. marginifera granulosa n. subsp.

Fig. 24 : Theux 93, C1398 (holotype) — Fig. 25 : Theux 93, C1399.

P. marginifera curvata n. subsp.

Fig. 40 : HNS 26 (C1068) (holotype) — Fig. 41 : Walcourt SVP 5.

P. marginifera duplicata SANDBERG & ZIEGLER

Fig. 42, 43 + 44 : Erfoud 5/46.

P. inflexa inflexoidea ZIEGLER

Fig. 45 : Haversin 5 — Fig. 46 : Ham. MD. 72.11 — Fig. 47 : Ham. MD. 72.11. — Fig. 48 : Haversin 10 — Fig. 49 : Haversin 8.

P. inflexa inflexoidea ZIEGLER → *P. inflexa inflexa* MULLER

Fig. 50 : Haversin 3 — Fig. 51 : Haversin 4.

P. inflexa inflexa MULLER

Fig. 52 : Dison 3 (C1061) — Fig. 53 : Haversin 4.

EXPLANATION OF PLATE II

Fig. 1 : *P. rugosa grossi* ZIEGLER : HNS 26 (C1048).
Fig. 2 : *P. rugosa ampla* MULLER : HNS 26 (C1217).
Fig. 3 : *P.* cf. *helmsi* ZIEGLER : Ham. MD. 18-9.
Fig. 4 : *P. rhomboidea* SANNEMANN : Haversin N-35.
Fig. 5 : *P. klapperi* SANDBERG & ZIEGLER : Ry de Mosbeux 49.
Fig. 6 : *Scaphignathus velifer* HELMS : Falemprise 2.
Fig. 7 : *Scaphignathus velifer* HELMS : Badon 5.

PLATE 1

Interspecific morphological relations within the «quadrantinodosa – stock»

R. DREESEN 1975

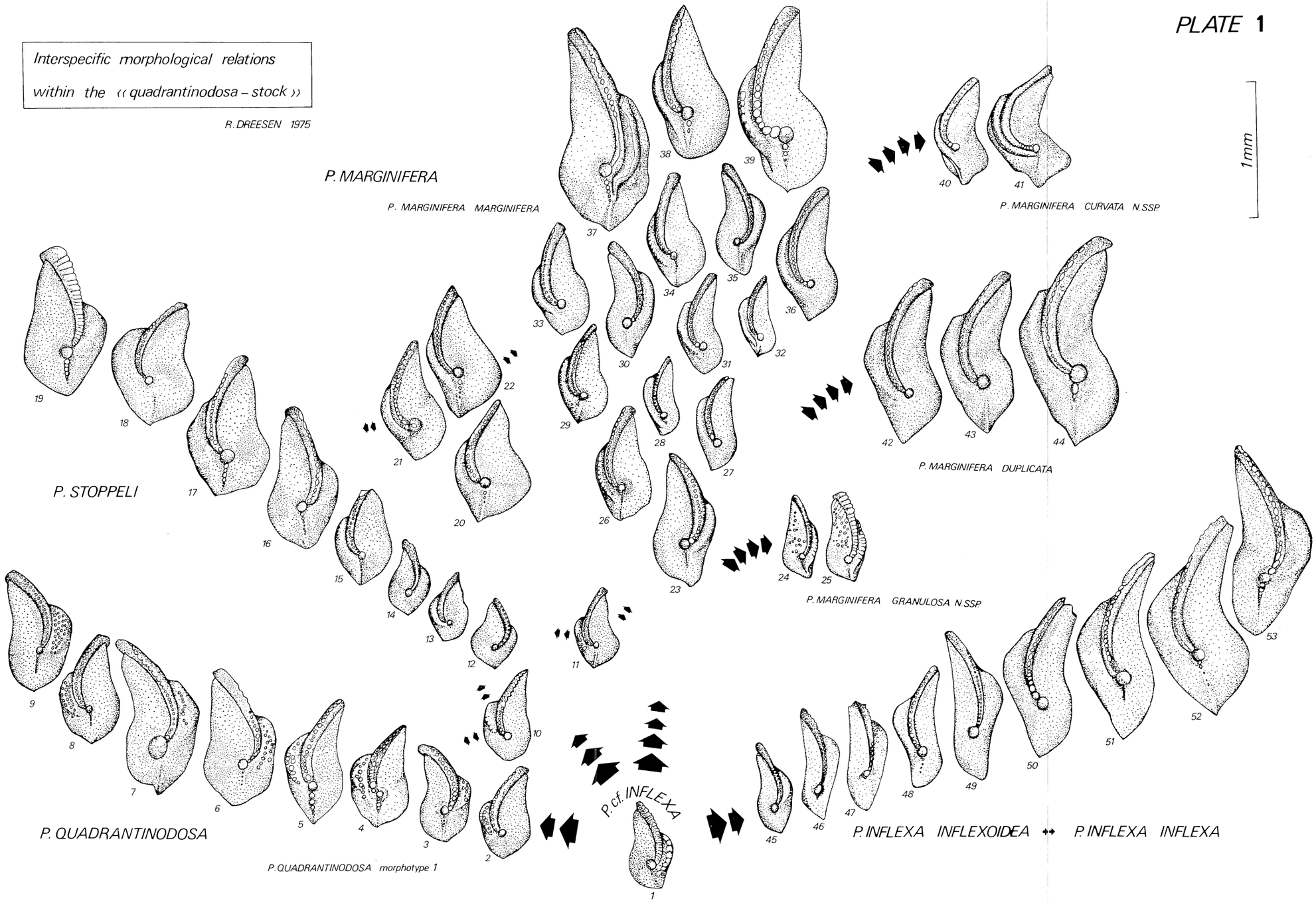
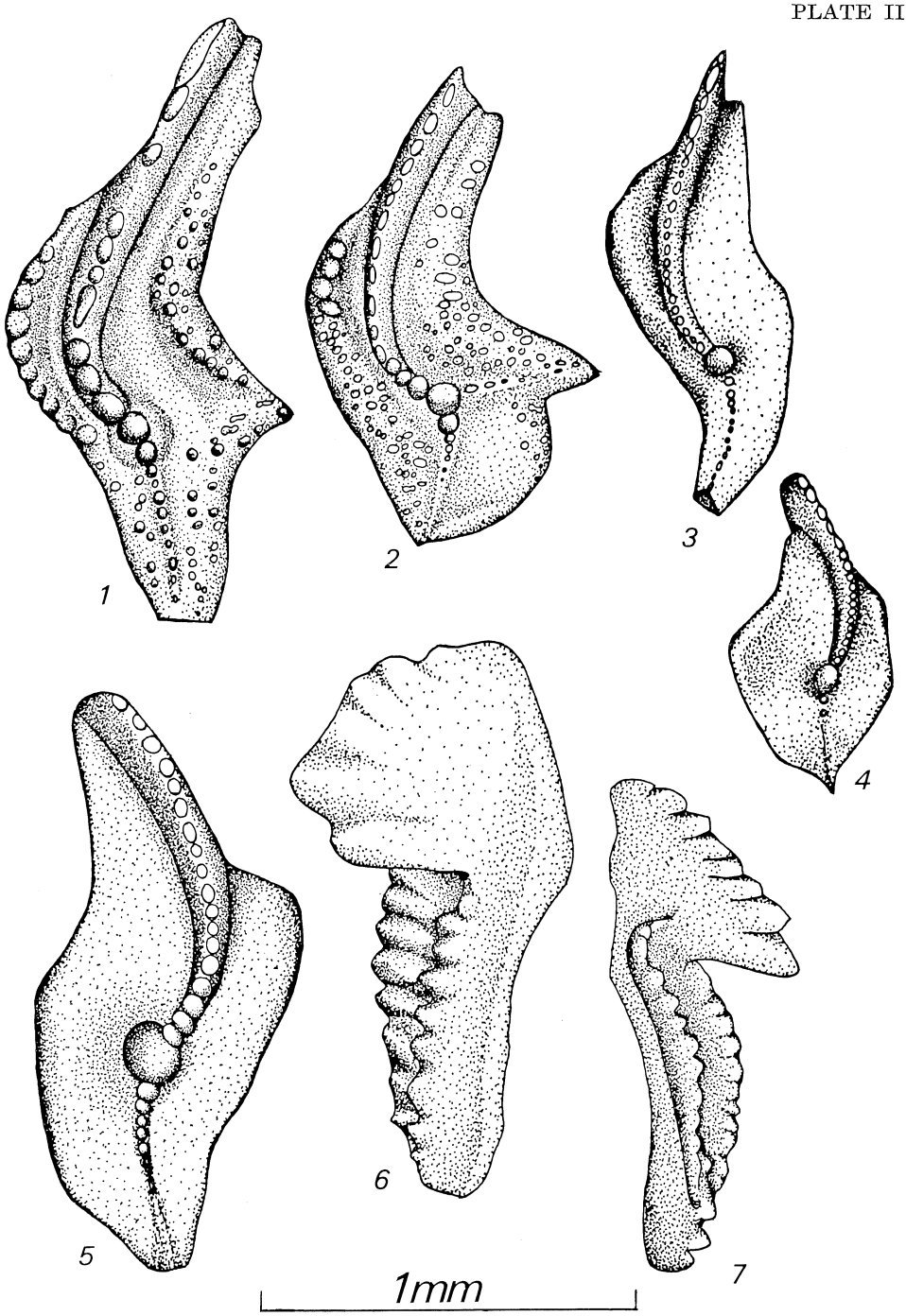


PLATE II



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