ON THE PALAEOZOIC PTERIDOPHYLLS

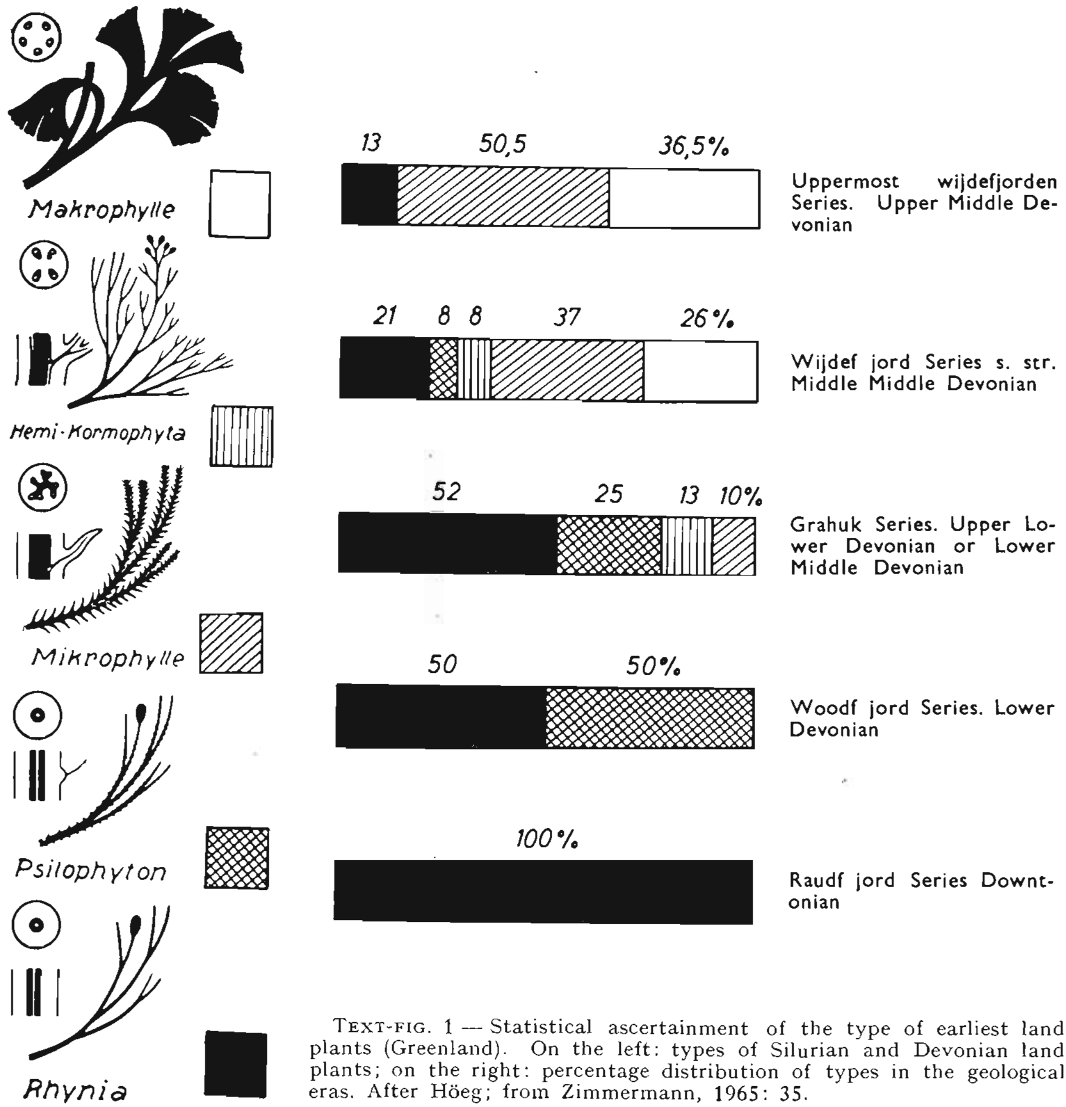
WALTER ZIMMERMANN
Institut für angewandte Botanik, Universität Tübingen

ABSTRACT

The Palaeozoic pteridophylls hold an excellent intermediate position in their entity as well as in their individual characteristics between the oldest (silurian and early devonian) plants and the land-plants of today. This is also illustrated by the genera as they were named by Brogniart as follows: *Archaeopteris, Sphenopteris, Pecopteris, Neuropteris, Linopteris, Alethopteris, Callipteris.*

These genera demonstrate how the phylogenetic development was carried out by few elementary processes, still isolated and restrained to primitive stages. The same elementary processes also formed the structure of palaeozoic stems in their primitive stages.

The mesozoic pteridophylls are a further step of phylogenetic changes towards present day leaf-forms.



TEXT-FIG. 1 — Statistical ascertainment of the type of earliest land plants (Greenland). On the left: types of Silurian and Devonian land plants; on the right: percentage distribution of types in the geological eras. After Höeg; from Zimmermann, 1965: 35.

THE Palaeozoic pteridophylls are connecting links between the earliest land plants and the pteridophylls of the Mesozoic and Cenozoic eras. They hold an obvious intermediate position between the oldest land plants (Silurian and early Devonian) and the plants of today. This intermediate position exists in morphology and anatomy as well as in the geological era. As a result, we find an uninterrupted morphological line: Devonian *Rhyniales* (*Rhynia*-type, TEXT-FIG. 1) → late Devonian *Protopteridiales* (*Hemicormophytic*-type, TEXT-FIG. 1) → the bulk of the mentioned Palaeozoic pteridophylls (especially Carboniferous Pteridophylls) → Mesozoic Pteridophylls → recent Pteridophylls. We are able to understand this continuous line of phylogenetical development only if we take into consideration the phylogenetical elementary processes, according to the Telome Theory. This means, the Cormophytic type results from the metamorphosis of the Thallophytic *Rhyniales* type by means of five phylogenetical processes (TEXT-FIG. 2).

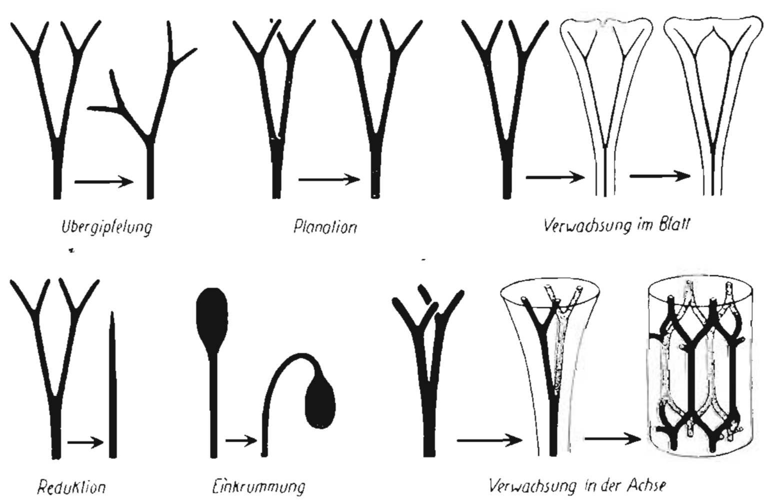
1. Overtopping = Übergipfelung
2. planation = Planation
3. fusion (webbing) = Verwachsung
4. incurvation = Inkurvation
5. reduction = Reduktion

These five elementary processes are combined also with other elementary processes which are already completed in the archisyntelomes, especially with the polar differentiation. Therefore, reduction, overtopping and fusion are active in a different manner in the base and in the top of the leaves and their parts.

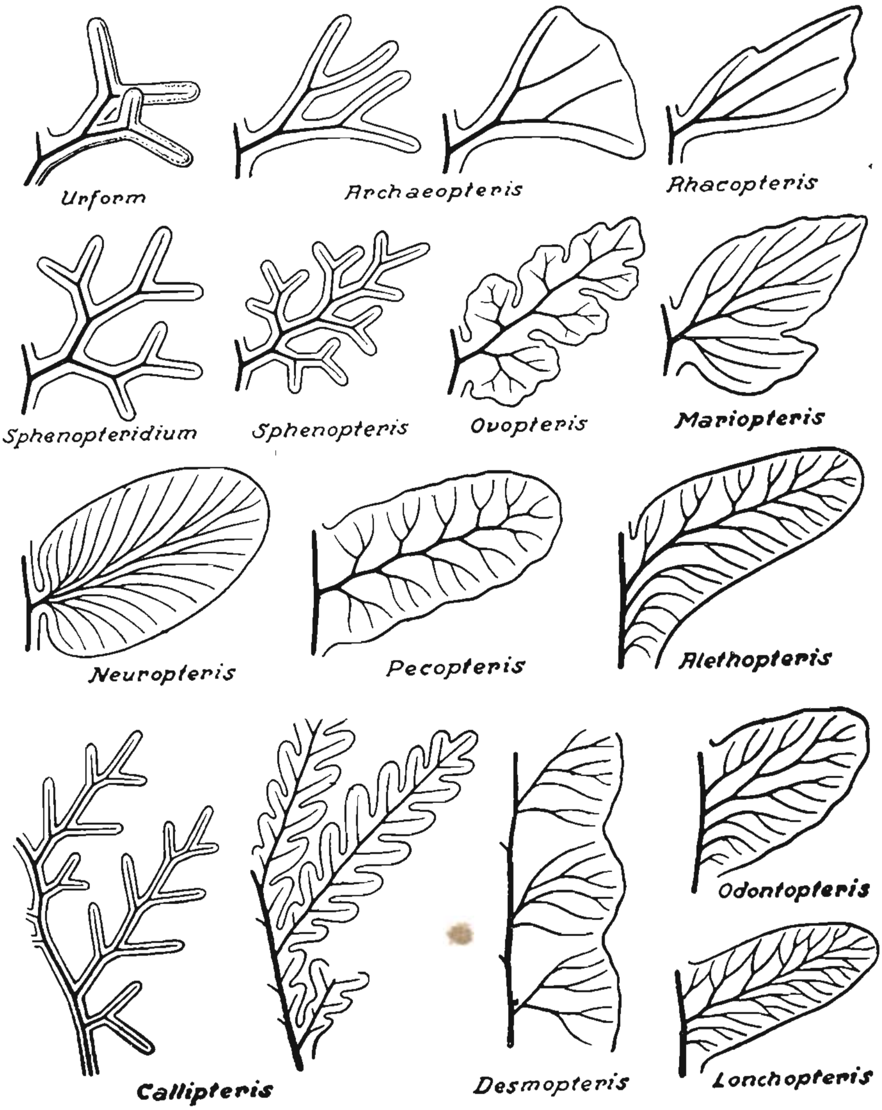
Already, in 1828, the famous palaeobotanist, A. Brongniart, has seen these characteristics of the elementary processes. His magnificent illustrations of Palaeozoic and recent pteridophylls testify this knowledge very clearly. Since 1895, another excellent palaeobotanist, H. Potonié, had demonstrated very clearly the independence of some elementary processes, especially the overtopping.

It is a characteristic feature of the elementary processes that they vary independently from one another. This is important for the knowledge of the physiology of the elementary processes and for the ability to measure the degree of phylogenetical progress. In our case, we can measure the phylogenetical position of the Palaeozoic pteridophylls on the developmental scale.

For this purpose, we assign the " variability degrees " of the above mentioned five elementary processes numerical values from 0 to 5 (0: the primitive stage; 5: the most



TEXT-FIG. 2 — The five elementary processes in the course of development from early land-plants to " typical " *Cormophyta*; from Zimmermann, 1959: 50.

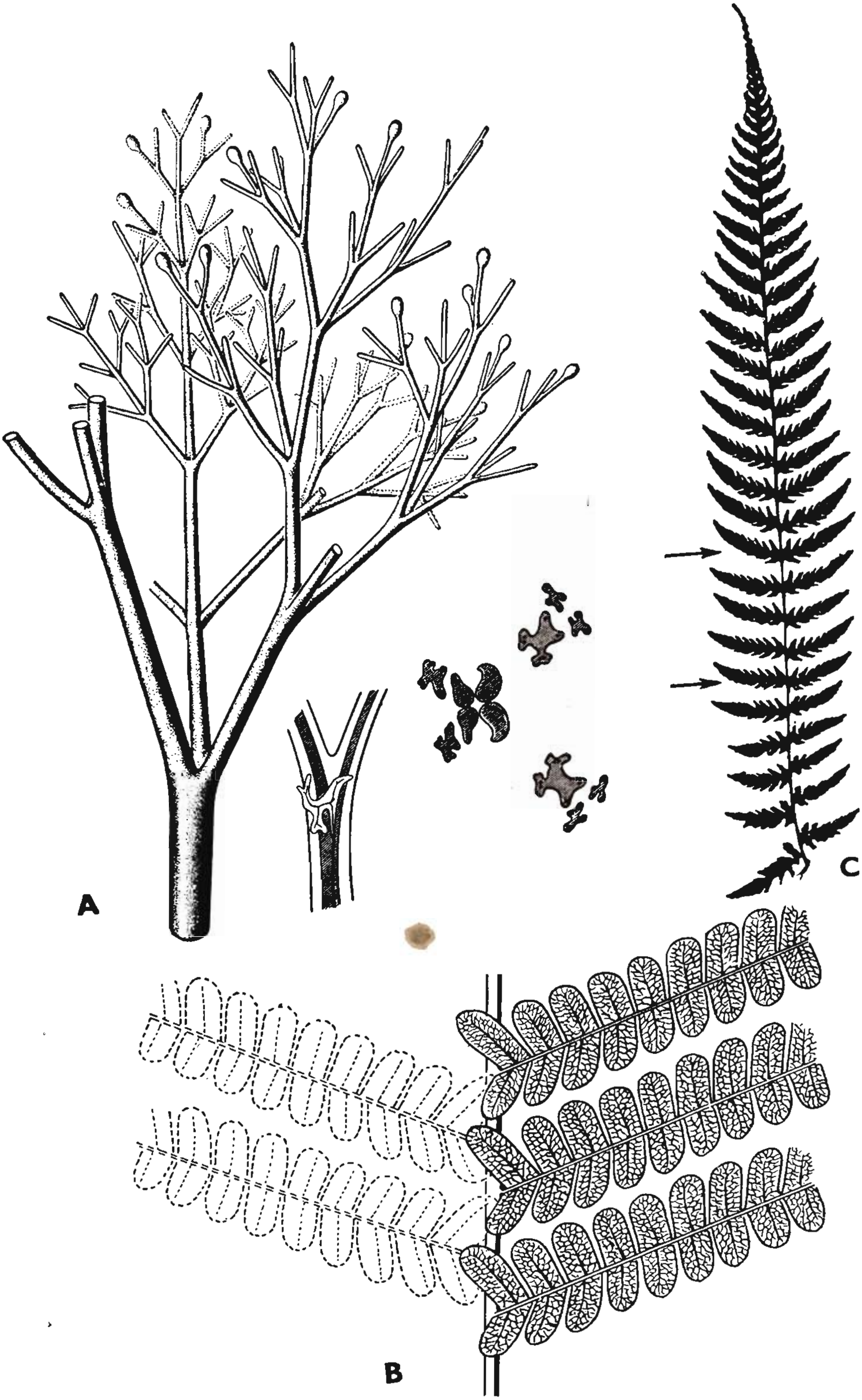


TEXT-FIG. 3 — Pinnule types of Palaeozoic pteridophylls (From Zimmermann, 1959: 278).

advanced stage). The variability of a genus (primitive/advanced) is expressed in two ways: (i) the various species vary on the whole during the elementary processes of development; (ii) the individual parts of one leaf vary also in their stages of development. These two variabilities are combined in one number in Table 1, which quantitatively demonstrates the intermediate position of the Palaeozoic pteridophylls between the *Rhyniales*-type and the recent pteridophylls.

Degree		%	
0	=	< 10	(advanced species and parts of the leaf)
1	=	10-30	,, ,,
2	=	31-50	,, ,,
3	=	51-70	,, ,,
4	=	71-90	,, ,,
5	=	> 90	,, ,,

1) The technique for obtaining this combined number shall be explained later.



TEXT-FIG. 4 — Pteridophylls — (A) *Stauropteris oldhamia* Binney; Upper Carboniferous reconstruction longitudinal and transverse section; from Zimmermann, 1959: 258. (B) *Weichselia* sp.: Lower cretaceous; from Zimmermann, 1959: 321. Shifting of pinnules to opposite position; reticulate pattern in pinnules. (C) *Athyrium filix-Femina*. Pinna 1 order; shifting of pinnules, the arrows indicate opposite position of pinnules and the Upper side of the pinna.

ELEMENTARY PROCESSES / GENERA	PLANATION	OVERTOPPING	SHIFTING OF PINNULES	FUSION (PARENCHYMA)	FUSION (BUNDLES)	PRODUCTION	SUMME-INDEX	PREVALENT GEOLOGICAL TIME
Rhynia	0	0	0	0	0	0	0	Early Devonian
Archaeopteris	4,0	3,1	0	2,5	0	0	7,1	Upper ,,
Stauropteris	0	2,0	0	0	0	0	2,0	Carboniferous
Sphenopteris (incl. *Sphenopteridium* + *Rhodeopteridium*)	4,5	4,2	0	1,1	0	1,8	11,6	,,
Mariopteris	5,0	3,8	0	1,8	0	2,0	12,6	,,
Pecopteris	4,8	4,6	0	2,5	0	2,5	14,4	,,
Neuropteris	5,0	4,0	0	2,8	0	2,9	15,9	,,
Alethopteris	5,0	5,0	0	3,3	0	3,0	16,3	,,
Lonchopteris	5,0	5,0	0	3,5	2,2	3,0	18,7	,,
Glossopteris	4,6	4,5	0	4,8	0,8	4,0	18,7	Permocarboniferous
Clathropteris	5,0	5,0	4,8	5,0	3,1	5,0	22,9	Rhaeto-Jurassic
Phyllitis	5,0	5,0	0,8	5,0	0	4,3	20,1	Recent
Athyrium	5,0	5,0	5,0	2,0	0	5,0	22,0	,,

The " summe index " indicates only the great line of phylogenetic differentiation. In some cases here are deviations. They results from the complex way of phylogenetical connections (parallel and reversible variations of elementary processes). For instance *Stauropteris* has a very low index. Evidently *Stauropteris* is developed in quite a different way, parallel to the other pteridophylls. The relative low indices of recent pteridophylls contrary to Mesozoic pteridophylls, like *Clathropteris*, are the result of our technique for obtaining these indices.

But all things considered, the numerical indices of elementary processes indicate that the Palaeozoic pteridophylls are the intermediates between the earliest land plants and the pteridophylls of later eras.

Characteristic of certain types of pinnules (incl. archetype = urform)
(Text-fig. 3)

Devonian
- *Rhynia*: Almost all phylogenetical processes in primitive stage, small degree of irregular overtopping.
- *Archaeopteris*: Characterized by dichotomous bi-forked pinnules or dichotomous bi-veined pinnules; planes of pinnules not the same as those of the frond.

Carboniferous
- *Stauropteris*: Most of the elementary processes in primitive stages; stele of axes by basipetal shifting of pairs of traces with 4 or 6 protoxylem traces.
- *Pecopteris*: Brongniart, 1828, characterizes this type by the dichotomy of overtopped veins and the basal reduction fusion with the supporting mesome.
- *Sphenopteris* s.l.: Distinct types of pinnules; in certain species, sometimes designated as *Sphenopteridium* or *Rhodeopteridium* (Pl. 1, Fig. 1) the pinnules are archisyntelomes scarcely modified by overtopping. Other species (Pl. 2, Fig. 6) differ by parenchymatous fusion of telomes.
- *Pecopteris*: Brongniart, 1928, characterizes this type by dichotomy of overtopped veins and the parenchymatous fusion of pinnules with the supporting mesomes (Brongniart uses the words axes or archis) in connection with the basal reduction, the outlines of pinnules are parallel.
- *Neuropteris*: The pinnules-incontrast to *Pecopteris* — are not parenchymatously fused with the supporting mesome. In many species of *Neuropteris* the overtopping of veins is also wanting. The patterns of these pinnules have more resemblance to the dichotomous type (Text-fig. 2) than the *Pecopteris* type.
- *Alethopteris*: The base of pinnules (including the basal veins) are fused with the supporting mesome.
- *Callipteris*: (mostly permian): Fusion of segments of the pinnules with the supporting mesome.
- *Odontopteris* (Text-fig. 3): Low degree of overtopping; basal parts of the pinnules fused largely with the supporting mesome.

Permo-Carboniferous
- *Glossopteris*: Fusion of all telomes in one frond, symmetrical overtopping (symmetrische Dachübergipfelung).
- *Gigantopteris*-Group (Permian, Pl. 1, Fig. 2). demonstrates evident line of increasing fusion.

Trias
- *Clathropteris*: Reticulate venation (Venatio Drynariae) a result of the fused veins.
- *Weichselia* (Cretaceous: shifting (Text-fig. 4) of pinnules to opposite position. Fusion of veins. (12 and 13 as representative of mesozoic pinnules)

Recent
- *Phyllitis scolopendrium*: Characterized by intensive parenchymatous fusion of overtopped dichotomous veins.
- *Athyrium filix femina*: Characterized by intensive shifting of pinnules, low degree of parenchymatous fusion. All the Palaeozoic peridophylls (4-10) have katadrome patterns of venation.

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EXPLANATION OF PLATES

PLATE 1

1. Four carboniferous pinnules: (A) *Rhodeopteridium* sp. Lower Carboniferous Schlesien. 5/2x; From Zimmermann 1965: 122.

2. *Bicoemplectopteris hallei* Asama (= *Gigantopteris nicotianaefolia* Halle). Permicarboniferous. Upper Shihhotes Series, Taiyuan, Shansi, N. China. × 4.

3. *Pecopteris lamurensis* var. . . . , Westfalian D. Allaggeny: Kittaning group, Mazon Creek. Illinois.

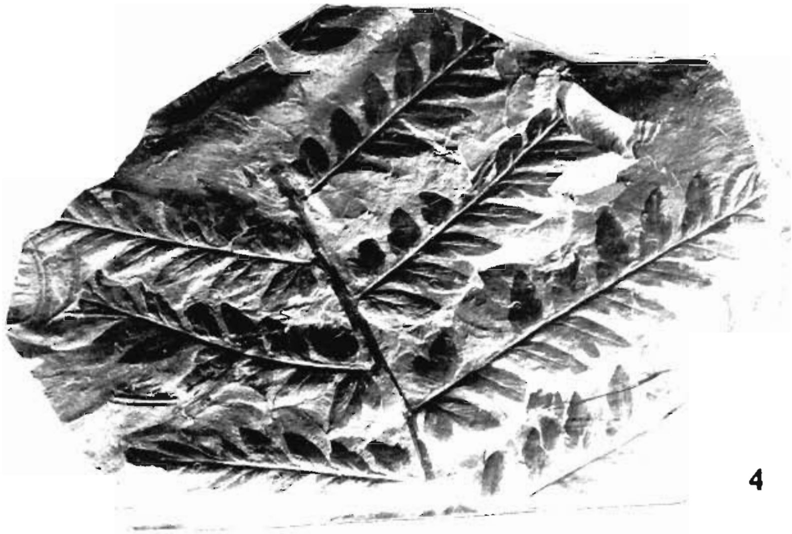
4. *Mariopteris* cf. *muricata* Schloth. Upper Westfalien. Anna deposite, Emil Emscher mine.

PLATE 2

5. Pteridophylls representing the fusion of veins to a reticulate pattern. (A) *Gigantonoclea lagrelii* Koidzumi (= *Gigantopteris lagrellii*) Halle. × 3. *Permocarboniferous* Lower Shihhotes Series, Taiyuan, Shansi, N. China. After Asama, 1959, Pl. 11.

6. *Sphenopteris* cf. *dentaefolia* (sic !) Danzé; Westfalien Ruhrgebiet; Inst. f. Spez. Bot., Tübingen. Unusual reduction of basiscopic part of pinnule) (acrotony).

7. *Clathropteris meniscoides* Schloth. Rhaeto-Jurassic, Baden-Württemberg; from Zimmermann, 1965: 73.



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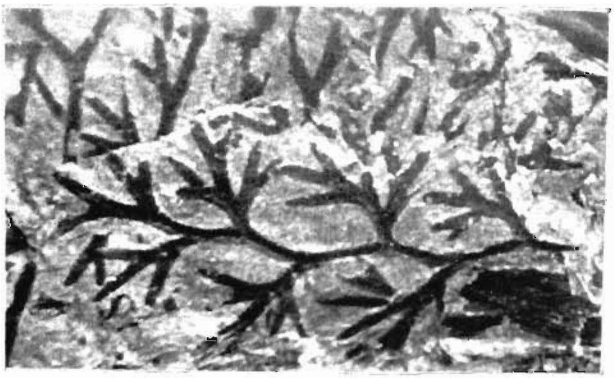

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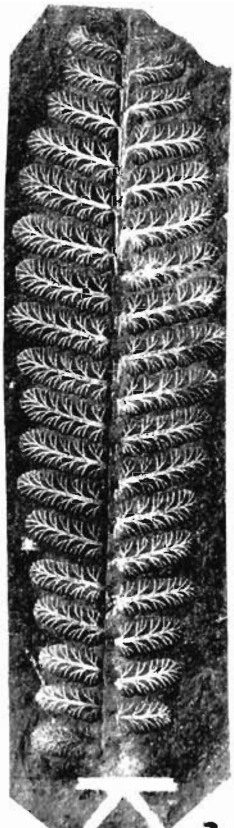

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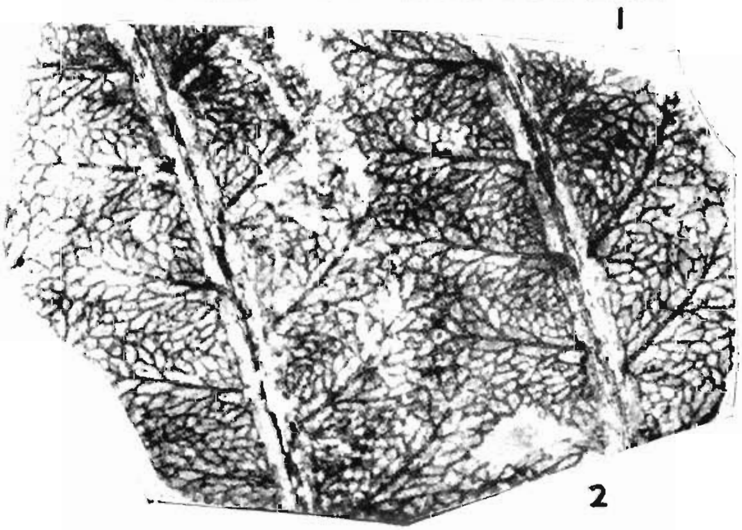

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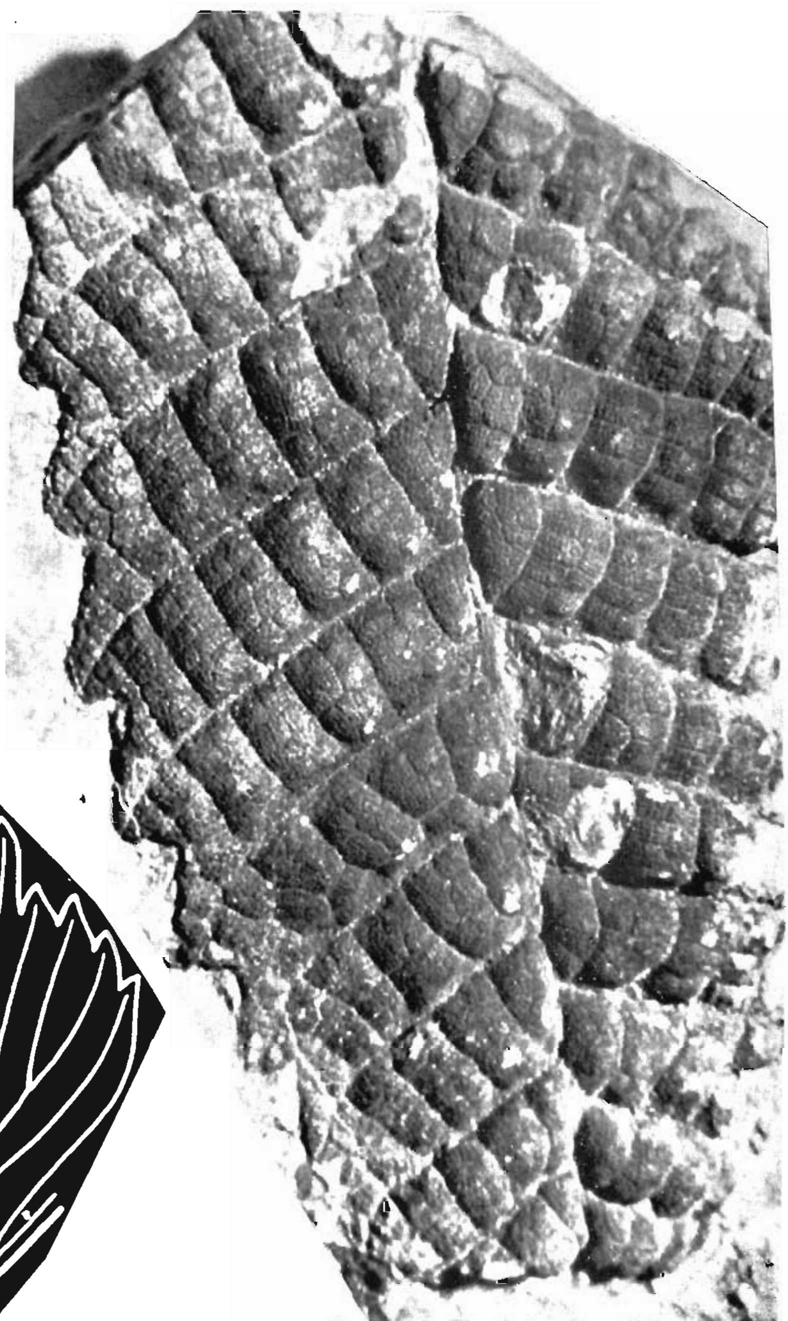

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