Acta Bot. Neerl. 31(5/6), November 1982, p. 417–427.

ASPECTS OF PERMIAN PALAEOBOTANY AND PALYNOLOGY
II. ON THE PRESENCE OF THE OVULIFEROUS ORGAN AUTUNIA MILLERYENSIS (RENAULT) KRASSER (PELTASPERMACEAE) IN THE LOWER PERMIAN OF THE NAHE AREA (F.G.R.) AND ITS RELATIONSHIP TO CALLIPTERIS CONFERTA (STERNBERG) BRONGNIART

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SUMMARY

New material of *Autunia milleryensis* (Renault) Krasser, an Early Permian representative of the pteridospermous family Peltaspermaceae, is described from the Lower Permian of the Nahe area, F.G.R. *Sandrewia texana* Mamay appears to be a synonym of *Autunia milleryensis*. The new combinations *Autunia thomasii* and *A. dzungarica* are introduced. *Callipteris conferta* (Sternberg) Brongniart is the sterile foliage attributed to *Autunia milleryensis*.

1. INTRODUCTION

Since some years the author is involved in investigations on Early Permian fossil floras from the Saar-Nahe Basin, F.G.R. Special attention is given to the problems related to the pteridospermous form genus *Callipteris* Brongniart. This genus was conventionally considered to be of extreme importance for Late Palaeozoic stratigraphy. On the second Congress on Carboniferous Stratigraphy, Heerlen 1935, it was selected as a valuable index fossil for the Carboniferous-Permian boundary (JONGMANS & GOTHAN 1937). However, some recent discoveries of *Callipteris* in the Upper Carboniferous (see, e.g., KOZUR 1978; DOUBINGER et al. 1979) gave reasons to question the value of *Callipteris* as a macrofloristic marker for the Carboniferous-Permian boundary. Therefore more information on the morphology/taxonomy, palaeo-oecology and biostratigraphy of the genus is needed.

Some years ago some specimens of a peculiar fossil plant were collected in a brick-pit at Sobernheim. Initially the material was identified as *Sandrewia texana* Mamay (Kerp, in press). Subsequently, more material was collected, not only at Sobernheim but also in some other localities in the vicinity. The material was further investigated and the discovery of ovules attached to the lower surfaces of the fan-shaped leaf-like structures in some of the Sobernheim specimens considerably contributed towards a better understanding of this problematical

fossil plant. It clearly demonstrated the fertile nature of *Sandrewia*, and necessitated a comparison with other ovuliferous pteridospermous organs. It is demonstrated that *Sandrewia texana* appears to be identical with *Autunia* (al. *Cycadospadix milleryensis* (Renault) Krasser, long since known from the Lower Permian of Europe.

In this preliminary note some of the new material from the Nahe area is described and figured. A revised concept of the genus *Peltaspermum* Harris and an emendation of the genus *Autunia* Krasser appeared to be necessary. The classification of *Autunia* within the Peltaspermaceae and its relationship to *Callipteris* are discussed.

2. source strata and material

The material under investigation forms part of the macrofloras collected from several lithostratigraphical units in the Nahe area (table 1). The age of the fossiliferous beds is considered to be Autunian (Late Carboniferous? – Early Permian).

The material is preserved as compressions/impressions, sometimes with cuticle (*table 1*). The largest specimens have been collected in the brick-pit of "Ziegelei Eimer" at Sobernheim. More fragmentary material was collected in the other localities. Especially the material from Langenthal is very well preserved with excellent cuticle.

The material described and figured is stored in the following collections: (1) Private collection of Mr. K. Baum, Sobernheim, F.G.R., (2) Collection of the Laboratory of Palaeobotany and Palynology, Utrecht, The Netherlands, and (3) Palaeobotanical collection of the "Forschungsinstitut Senckenberg", Frankfurt am Main, F.G.R.

3. OBSERVATIONS

Some of the material from the Nahe area is described below.

Specimen A (Collection Baum, Sobernheim) – Ziegelei Eimer, Sobernheim (*figs. 1, 2*).

Compressions of 15 leaf-like structures, up to 1.8 cm wide. Their original length could not be measured, because petioles are lacking. The fan-shaped, cupped leaf-like structures with strongly convex outer sides show a prominent ribbing, Ribs diverging from the petioles, sometimes dichotomising. The ribs are ending in lobes on the anterior margin.

Specimen B (Collection Baum, Sobernheim) – Ziegelei Eimer, Sobernheim (*fig. 4*).

This specimen consists of a stout axis, 4 mm wide, with fan-shaped leaf-like appendages spirally attached. The specimen is 16.5 cm long and the width measures about 2.5 cm including the appendages. The axis shows a distinct longitudinal striation. Appendages with stout petioles gradually passing into the leaf-like

Table 1. Localities in the Nahe area from which *Autunia milleryensis* (Renault) Krasser has been collected. The scheme shows the approximate stratigraphical positions of the fossiliferous beds, the composition of the flora and the occurrences of *A. milleryensis* with their state of preservation.

Localities	Stratigraphy	Composition of the macroflora	Occurrences of *Autunia milleryensis* and preservation of the material
Sobernheim	Waderner Gruppe	The *Autunia*-bearing horizons are dominated by conifers and *Callipteris conferta*.	Large specimens, showing the organization of the fructification: axes with ovuliferous peltate heads organized in frond-like systems; axes with ovuliferous peltate heads; isolated peltate heads. Compressions/impressions.
Staudernheim	Tholeyer Gruppe	Flora completely dominated by *Callipteris conferta* (about 80%), with additional sphenopsids and pecopterids.	Small isolated peltate heads. Compressions/impressions, incidently with cuticle.
Rehborn	Lebacher Gruppe	Qualitatively poor and restricted flora dominated by conifers. *Callipteris* and *Odontopteris* are the most common pteridophylla.	Small isolated peltate heads. Compressions/impressions.
Langenthal	Lebacher Gruppe	Mainly conifers; among the limited number of pteridophylla *Callipteris conferta* is dominant.	Axes with peltate heads, isolated peltate heads and seeds. Fragmentary specimens with excellent cuticle.

structures without any abrupt transition. Petioles of the appendages are directed apically near the attachment to the axis, but most of the leaf-like structures are curved sidewards or hanging downwards. Leaf-like structures with a convex upper side. Especially on their upper surfaces they show a strong ribbing, radiating from the petioles. In most of the leaf-like appendages the anterior margin is damaged, but otherwise it appears to be slightly crenulate. Sometimes only the prominent ribs are preserved and the intervening lamina has disappeared.

Specimen C (Collection Baum, Sobernheim) – Ziegelei Eimer, Sobernheim (*figs. 3, 5*).

Part of an axis, 7.4 cm long, with spirally attached approximately 20 leaf-like appendages. Axis stout, 4 mm wide, longitudinally striated, partly obscured by overlying appendages. These appendages are bilaterally symmetrical, broadly flabelliform with convex upper sides. Stout petioles are gradually passing into the leaf-like structures without any abrupt transition. Near the axis the petioles

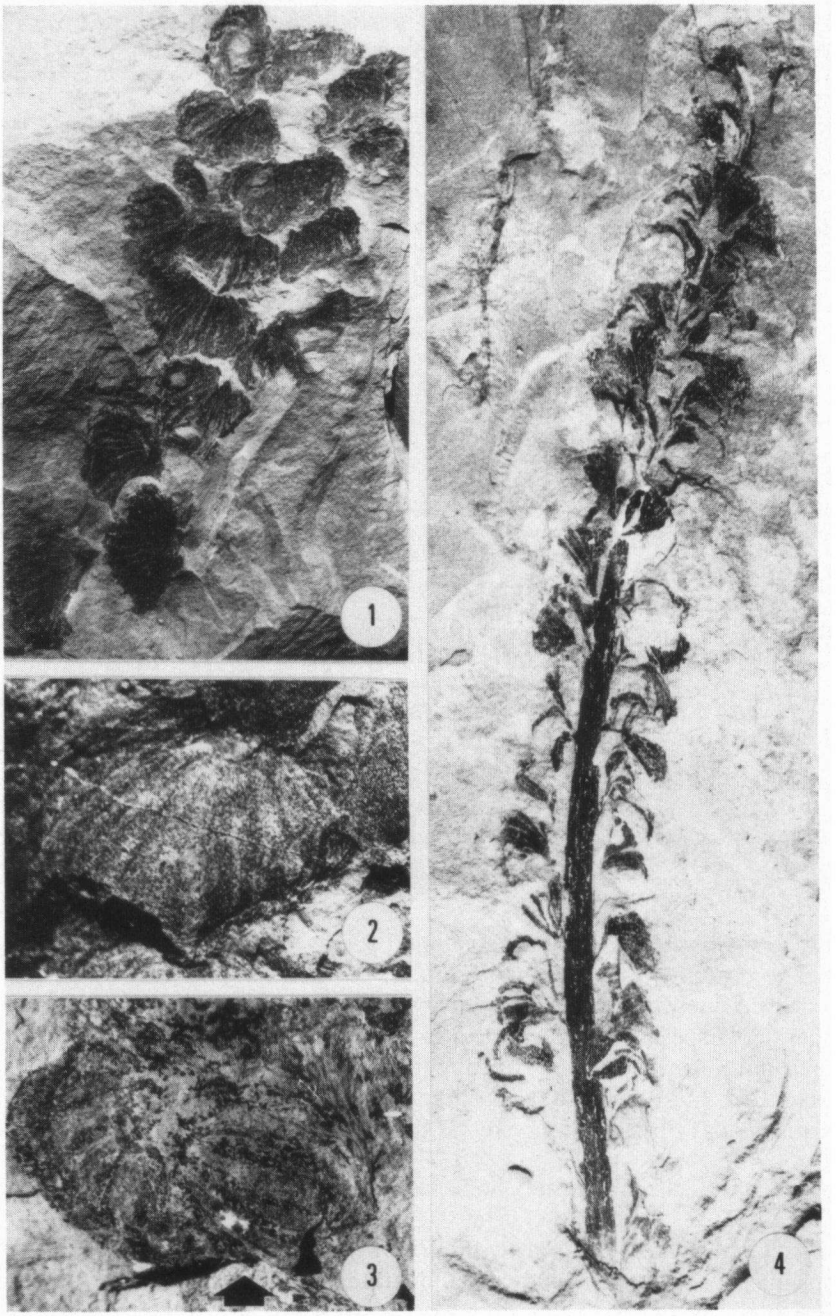

Fig. 1–4. *Autunia milleryensis* (Renault) Krasser.
Fig 1. Specimen A, × 1. Fig. 2. Specimen A, detail, × 3. Fig. 3. Specimen C; abaxial side of a peltate head with attached ovule (arrow), × 4. Fig. 4. Specimen B, × 1 (all specimens Collection Baum, Sobernheim).

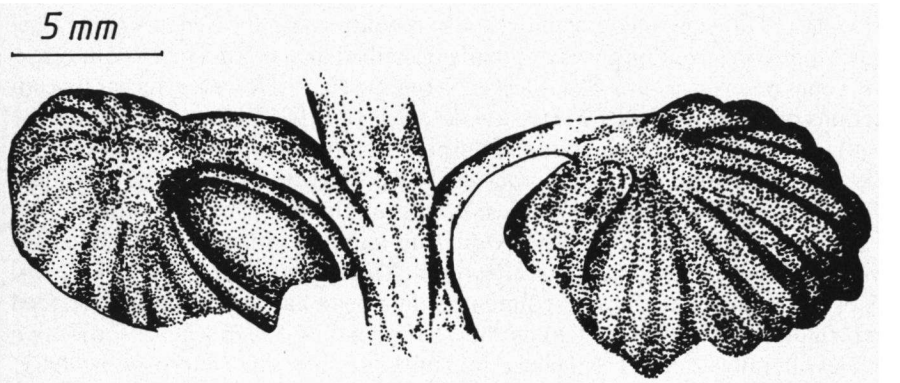

Fig. 5. *Autunia milleryensis* (Renault) Krasser. Axis with two peltate heads; the left one corresponds to *fig. 3.*

are directed apically, but the leaf-like structures themselves are curved downwards. Prominent ribs are radiating from the petiole towards the lateral and anterior margins which are slightly crenulate. To some of the appendages, showing the abaxial side, ovules are attached. On some of the other appendages vague molds of seeds are to be observed. The best preserved ovule-bearing appendage is figured on *fig. 3, 5.* Its abaxial surface clearly shows the radiating ribs. The ovules are incompletely preserved, ovoid, differentiated into an inner body and an outer layer, at least 7 mm long and 4.5 mm wide. Ovules apparently attached with their narrowest side to the appendages. To the appendage figured on *fig. 3, 5* a single ovule is attached, lateral to the insertion of the petiole.

Apart from this material several other specimens have been collected in the last years. A recently discovered specimen from Sobernheim is very interesting. It shows several axes with ovule-bearing appendages, organized in a frond-like system. The cuticle of one of the Langenthal specimens shows that there were two ovules attached to the abaxial side of each appendage. The ovules were situated laterally to the insertion of the petiole.

4. DISCUSSION

4.1. Interpretation of the described material and comparisons to other plants

Especially specimen A shows remarkable similarities to the holotype of *Sandrewia texana* (MAMAY 1975). Dr. S. H. Mamay (Washington) kindly identified the here described specimens A and B as *Sandrewia texana* (written communication, 1981). From direct observation of both specimens it appears that the holotype of *Sandrewia texana* is figured upside down.

Sandrewia Mamay is a problematical form genus of fan-shaped foliage, originally described from the Lower Permian of Texas and Kansas (MAMAY 1975).

MAMAY (1978) suggested a vojnovskyalean relationship for *Sandrewia*. The genus *Vojnovskya* Neuburg was originally described as a gymnosperm with bisexual cones and *Nephropsis*-like foliage (NEUBURG 1955). However, recent investigations on Vojnovskyales (MAHESHWARI & MEYEN 1975; KRASSILOV & BURAGO 1981) have shown that Neuburg's interpretation of *Vojnovskya*, on which Mamay's comparisons with *Sandrewia* were based, is wrong. Therefore a classification of *Sandrewia* within the Vojnovskyales can no longer be maintained.

The present recognition of the ovuliferous habit considerably contributes towards a better understanding of *Sandrewia*. The appendages can be interpreted as ovuliferous peltate heads. A similar peltate head has already been described and figured by MAMAY (1978) as the "strobilus" of *Sandrewia*. It shows two ovules laterally attached to the insertion of the petiole. The "microsporophylls" of Mamay's "strobilus" obviously represent the prominent ribs, whereas the intervening lamina has disappeared as in some of the appendages of our specimen B.

The recognition of the fertile nature of *Sandrewia* facilitates comparison with other plants. *Sandrewia texana* appears to be very similar to *Autunia milleryensis* (Renault) Krasser. This fructification can be characterized as a 8–16 cm long axis, with spirally arranged fan-shaped appendages. The appendages are 8–10 mm long, and attached to the axis with slender petioles. The appendages show a prominent venation, especially on the convex adaxial sides; veins diverging from the petiole and subsequently dichotomising. According to RENAULT (1896) the anterior margins of the appendages are denticulated. Two seeds are said to be attached to the abaxial side of each appendage.

The only difference between *Sandrewia texana* and *Autunia milleryensis* appears to be the shape of the anterior margin. However, some badly preserved material from the Nahe area also suggests a denticulation of the anterior margin, because only the prominent ribs have been fossilized. On the other hand some of the appendages figured by RENAULT (1893) strongly suggest the presence of an entire, rounded or slightly crenulate anterior margin. Because both types of shape of the anterior margin can be attributed to the preservation of the material, *Sandrewia texana* and *Autunia milleryensis* are considered to be identical. The name *Sandrewia texana* is a synonym, because *Autunia milleryensis* has priority as it was published earlier (KRASSER 1919).

4.2. The systematical position of the genus *Autunia* and a revised concept of the genus *Peltaspermum* Harris

Since a long time the systematical position of the genus *Autunia* has been the subject of controversies in palaeobotanical literature. DOUBINGER (1961) briefly summarized the different opinions on the classification of this genus, for which cycadalean, cordaitalean and pteridospermous affinities were suggested. However, it is here considered that comparisons with *Peltaspermum thomasii* Harris leave no doubt that *Autunia* has to be classified within the Peltaspermaceae, a family which apart from sterile foliage and polliniferous organs includes only a single genus of ovuliferous organs, viz. the genus *Peltaspermum*, established

by HARRIS (1937) to include certain female fructifications attributed to *Lepidopteris* foliage. The type species, *P. rotula* Harris, from the Rhaetian (Upper Triassic) of East Greenland, was initially described as the seed-bearing cupulate disc of *Lepidopteris ottonis* (Goeppert) Schimper (HARRIS 1932). It can be characterized as a radially symmetrical cupulate disc, with up to 20 seeds, attached to the abaxial side, in a ring around the insertion of the stalk.

In its basic organization *Autunia* is very similar to *Peltaspermum thomasii* Harris. *P. thomasii,* from the Middle Triassic of South Africa, was originally described as the ovuliferous organ of *Lepidopteris natalensis* Thomas (THOMAS 1933). It consists of an axis with helically arranged, bilaterally symmetrical peltate seed-bearing heads. HARRIS (1937) included this fructification in *Peltaspermum.* Reinvestigations of *P. thomasii* (TOWNROW 1960) have shown that there were only two seeds attached to the abaxial side, instead of the "less than ten seeds" mentioned by HARRIS (1937).

However, there are some striking differences between *P. rotula* and *P. thomasii. P. rotula* has radially symmetrical cupulate seed-bearing discs and *P. thomasii* has bilaterally symmetrical peltate seed-bearing heads. The discrepancies between both species were already noticed by TOWNROW (1960), but nevertheless they were left in one genus, because they were considered to be similarly organized. The recognition of *Autunia* as a true peltasperm and the discovery of several ovuliferous organs from the Permian and Triassic of the U.S.S.R. (STANISLAVSKY 1976; SALMENOVA 1979; GOMANKOV & MEYEN 1979; DURANTE 1980 and DOBUSKINA 1980) strongly favour the subdivision of peltaspermaceous ovule-bearing organs into two genera.

The species with bilaterally symmetrical peltate heads have to be separated from *Peltaspermum* Harris. *Peltaspermum* has to be restricted to include radially symmetrical cupulate discs, with ovules attached to the abaxial side in a ring around the insertion of the stalk, which is in accordance with the original diagnosis. Because the generic name *Autunia* has already been established for peltaspermaceous fructifications with bilaterally symmetrical heads, two species have to be transferred to *Autunia,* viz. *Peltaspermum thomasii* Harris and *Peltaspermum dzungaricum* Salmenova.

Autunia Krasser emend. Kerp
type species: Autunia milleryensis (Renault) Krasser
generic diagnosis: KRASSER 1919, p. 20
emended diagnosis: Ovuliferous organs consisting of axes with helically arranged, bilaterally symmetrical peltate ovule-bearing heads, with convex adaxial sides. Axes may be organized in frond-like systems. Petiolate heads broadly flabelliform with ribs radiating from the petiole; ribs sparsely dichotomising. Petioles attached marginally to the heads or gradually passing into the heads. Anterior margins of peltate heads rounded or crenulate. Two ovules borne on the abaxial sides of the heads, lateral to the insertion of the petiole.

Autunia milleryensis (Renault) Krasser
basionym: Cycadospadix milleryensis Renault
synonyms: Strobilites milleryensis (Renault) Seward (1917, p. 141)
Sandrewia texana Mamay (1975, p. 81)
lectotype here selected: the specimen figured by RENAULT (1893) on Plate LXXIII, fig. 2.
paratypes: the specimens figured by RENAULT (1893) on Plate LXXIII, fig. 1, 3, 4.
diagnosis: RENAULT (1896, p. 329–330).

Autunia thomasii (Thomas) Kerp nov. comb.
basionym: Peltaspermum thomasii Harris 1937, Medd. Grønland, 112(2), p. 35
holotype: the specimen figured and described as *Lepidopteris natalensis* by THOMAS (1933), text-figure 55, p. 254.
diagnosis: HARRIS (1937, p. 35).
emended diagnosis: TOWNROW (1960, p. 356).

Autunia dzungarica (Salmenova) Kerp nov. comb.
basionym: Peltaspermum dzungaricum Salmenova 1979, Palaeontological Journal, 1979(4), p. 126.
holotype: the specimen figured by SALMENOVA (1979) on Plate VIII, fig. 11.
diagnosis: SALMENOVA (1979, p. 126).

Relationship of *Autunia milleryensis* to sterile foliage

Sterile foliage attributed to *Peltaspermum* is known as *Lepidopteris* Schimper (HARRIS 1932, TOWNROW 1960; STANISLAVSKY 1976) and *Tatarina* Meyen (GOMANKOV & MEYEN 1979). The sterile foliage attributed to *Autunia thomasii* (Harris) Kerp nov. comb. is known as *Lepidopteris natalensis* Thomas (THOMAS 1933; TOWNROW 1960). A certain number of facts and interpretations have contributed to the belief that *Callipteris conferta* (Sternberg) Brongniart, the well known type of foliage conventionally considered to characterize the Euramerian Early Permian floras (*figs. 6–8*) can be attributed to *Autunia milleryensis*:

1. *Callipteris conferta* and *Autunia milleryensis* are always found in close association (compare *table 1*). At Sobernheim both forms occur together in an association, remarkably poor in species, which is presumed to represent an autochtonous flora. At Staudernheim *Autunia milleryensis* is to be found in an association which consists for about 80% of callipterids. At Millery, the type locality of *A. milleryensis*, the seeds of *A. milleryensis* were found in association with *Callipteris* leaves (RENAULT 1896; SEWARD 1917). The Belle Plains Formation (Leonardian, Lower Permian) exposed at Baylor County, Texas (the type locality of *Sandrewia texana*) contains abundant callipterids (READ & MAMAY 1964; MAMAY 1975). *Callipteris conferta* also occurs in the Vale Formation (Leonardian, Lower Permian) from which additional material has been reported (READ & MAMAY 1964; MAMAY 1975).
2. The cuticles of *Callipteris conferta* and *Autunia milleryensis* show very close resemblances (Kerp, in prep.).

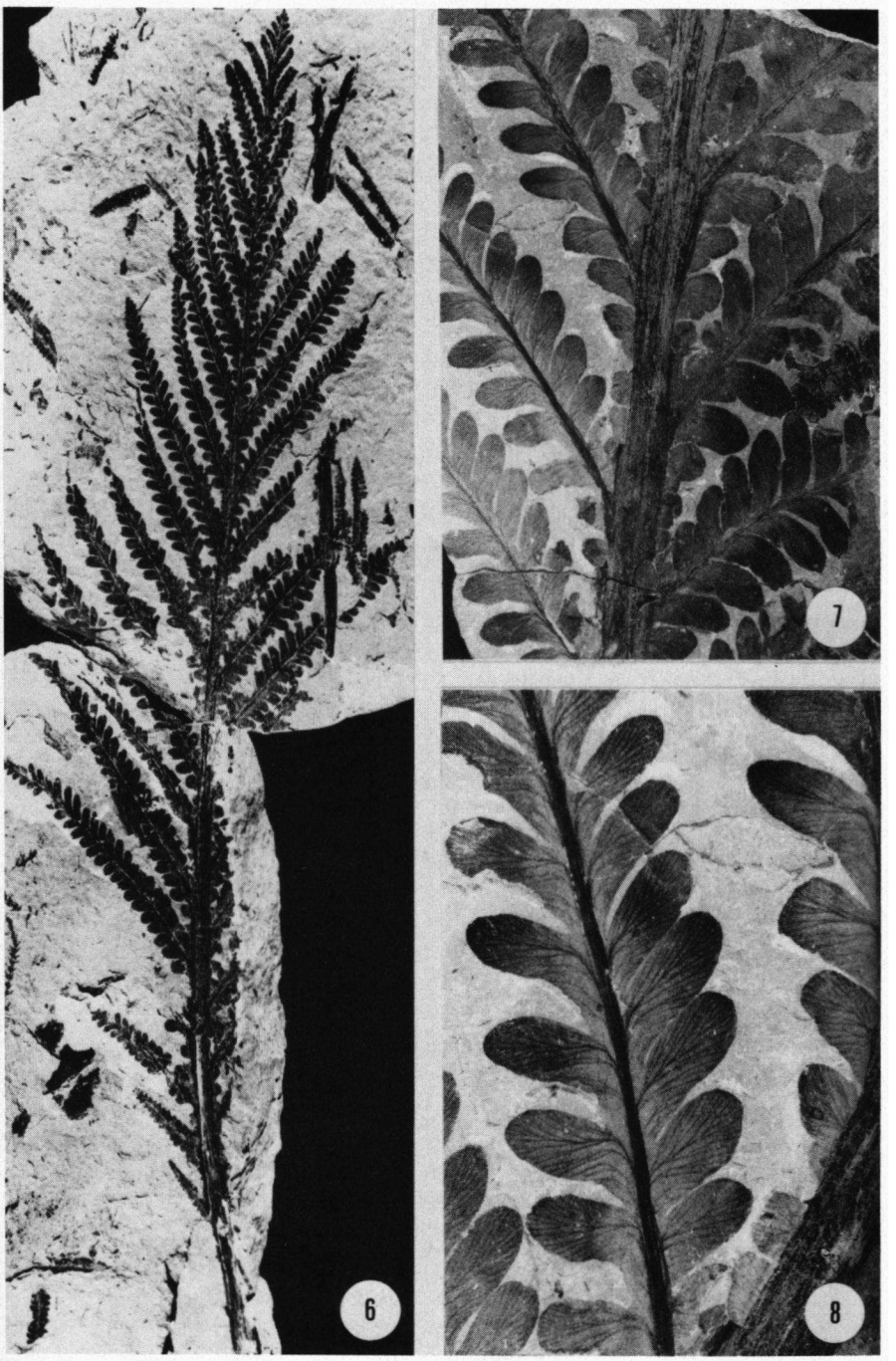

Fig. 6–8. Examples of *Callipteris conferta* (Sternberg) Brongniart from Sobernheim, the sterile foliage attributed to *Autunia milleryensis*.
Fig. 6. An almost complete leaf, × 0.35 (Collection Senckenberg, Frankfurt, B 13476 AB). Fig. 7. Part of a leaf, × 1 (Collection Laboratory of Palaeobotany and Palynology, Utrecht, 8434 A). Fig. 8. Detail of *fig. 7*, showing pinnules with venation, × 2.

3. The axes of *Callipteris conferta* and *Autunia milleryensis* are very similar. They show the same longitudinal striation. The compound system of *Autunia* axes from Sobernheim is strongly reminiscent of the rachial system of a *Callipteris* leaf.
4. A peltaspermaceous relationship was already suggested by ROSELT (1962) in his paper on *Callipterianthus arnhardtii* Roselt, a polliniferous organ of *Callipteris*.
5. On the basis of epidermal anatomy of the leaf of *Callipteris conferta*, BARTHEL & HAUBOLD (1980) suggested a peltaspermaceous relationship for this species.
6. Fertile specimens of *Callipteris naumannii* (Gutbier) Sterzel, showing ovules attached to the abaxial sides of modified pinnules, were described and figured by BARTHEL & KOZUR (1981). They consider *Callipteris naumannii*, a species closely related to *C. conferta*, to be a peltasperm.
7. *Callipteris* leaves show a remarkable similarly to the leaves of *Lepidopteris*. On the basis of epidermal characters TOWNROW (1960) included *Callipteris martinsii* (Kurtze) Zeiller, a Late Permian representative, in *Lepidopteris*. Of this species ovuliferous peltaspermaceous organs have been recently recognized (Clement-Westerhof & Kerp, in prep.).

ACKNOWLEDGEMENTS

In the first place the author wishes to thank Mr. H. Eimer (Sobernheim) for providing the collecting facilities and Mr. K. Baum (Sobernheim) for the loan of his specimens; without their help this study would have been inpossible. Prof. Dr. H. Visscher needs to be acknowledged for his valuable comments on the manuscript. Thanks are due to Dr. S. H. Mamay (Washington)and Dr. S. V. Meyen (Moscow) for their information on *Sandrewia* and on the Vojnovskyales. The author is indebted to Dr. F. Schaarschmidt (Frankfort) for his permission to publish the specimen of Fig. 6. Grateful acknowledgement is extended to Mr. H. A. Elsendoorn for preparing the photographs. The investigations were supported by the Netherlands Foundation for Earth Science Research (AWON) with financial aid from the Netherlands Organization for the Advancement for Pure Research (Z.W.O.).

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