Acta Botanica Neerlandica **7** (1958) 217—222

ON A MEGASPORE-BEARING LYCOPOD STROBILUS

S. J. DIJKSTRA
(*Geol. Bur., Heerlen*)

(*received February 11th, 1958*)

INTRODUCTION

During the last 30 years many species of Carboniferous megaspores have been described, but until now not much is known with regard to the nature of the fructifications by which they were produced. This may partly be due to the fact that nearly all the megaspores were obtained by macerating lumps of coal, whereas the fructifications are generally derived from the roof of a coal seam. Moreover it is noteworthy that the fructifications rarely contain megaspores; they had apparently shed their spores before they themselves became detached. Some investigators of the past century sometimes found megaspores in the strobili they were studying, but not realizing the importance of their findings, they unfortunately figured them on a very small scale. Their descriptions too are insufficient, so that it is now very difficult or impossible to establish the identity of these spores.

However, during recent years a number of investigators have paid attention to the fructifications as well as to the spores that are included in them. The most important communications on this subject are: ARNOLD (1930), *Lepidostrobus* (?), (1933, '35), *Lepidostrobus* or *Sigillariostrobus*, (1938), *Lepidostrobus* (*Lepidocarpon*?), (1949), *Lepidostrobus;* BOCHENSKI (1936) *Lepidostrobus* (*Lepidocarpon*?), (1939), *Sigillariostrobus;* CHALONER (1952), *Lepidocarpon*, (1953a) *Lepidostrobus* (?), (1953b), *Lepidostrobus*, (1953c), *Sigillariostrobus*, (1954), *Selaginellites*, *Lepidostrobus* (*Lepidocarpon*), (1956), *Sporangiostrobus;* FELIX (1954), *Lepidostrobus*, *Lepidocarpon;* HOSKINS and CROSS (1940, '52), *Lepidostrobus;* LEQLERQ (1938), *Sigillariostrobus* (*Lepidostrobus*?); MATHEW (1940), *Lepidostrobus*; NEMEJC (1931), *Sigillariostrobus* (?); SCHOPF (1938), *Lepidocarpon;* WICHER (1934), *Porostrobus*. A very detailed survey of the American literature can be found in FELIX (1954).

From the list given above, it appears that the identification of several of the fructifications is regarded as doubtful, and this probably applies also to some of the other ones. This is the reason why the assignment of the different species of megaspores to the various strobilus genera often remains uncertain. The same difficulty we have experienced with the fossils described in this paper. It is, on the other hand, as a rule not difficult to refer the megaspores isolated from such strobili to the right spore genus.

DESCRIPTION

Sigillariostrobus cf. *major* (Germar) Zeiller.
Pl. I, Fig. 1; Pl. II, Figs. 4, 5; Pl. III, Fig. 11; Pl. IV, Fig. 12.

Cone cylindrical, at least 9 cm long, 3–4 cm in diameter including the sporophylls. Stalk of the cone unknown. Sporophylls placed in slowly ascending spirals; adaxial part horizontal, rhomboidal, sides slightly concave, 6 mm wide, 5 mm high; sterile part spreading, bent towards the apex of the cone, with the tips nearly vertical, linear, 2.8 mm wide, 17 mm long; margin not ciliate. Axis 4 mm in diam.; from left to right 3–4 leafscars are distinguishable, placed in a spiral which includes an angle of about 27° with the horizon. Distance of the scars in horizontal direction 0.6 mm, distance of the vertical series 2.5 mm. The scar resembles the thumb-nick of a knife, the curvature of which is turned towards the base; it is about 0.5 mm high, 0.7 mm wide. The elliptical sporangia are radially elongated, 2 mm high, 3 mm long.

Fully developed megaspores.
Pl. I, Figs. 2, 3; Pl. II, Figs. 6, 7, 8, 10.

Body of the spore oval-rounded, provided with a neck-like prominence; length body of the spore 600–810 μ (the mean being 702 μ, 10 spec. meas.), length whole spore (the prominence included) 790–1020 μ, (the mean being 909 μ), diameter body of the spore 610–750 μ (the mean being 684 μ). Prominence cylindrical-pyramidal, top rounded, 240–290 μ long, 250–310 μ wide. Triradiate ridges clearly distinguishable, running from tip to arcuate ridges, 30 μ wide and high; distance tip to arcuate ridge 350–570 μ. Arcuate ridges 30–50 μ wide, 10–15 μ high. Wall, the contact faces included, rough by an irregularly spread of hemispherical, red translucent bodies, 5–8 μ in diameter. Wall 20–25 μ thick.

Not-fully developed specimens are 630 μ long; Pl. II, Fig. 9.

Occurrence, discussion and comparison

As Prof. Jongmans informed me, these strobili were found by him and Mr. M. K. Ellias. They were at that time connected with *Sigillaria brardii*, but the discoverers have tried in vain to make a photograph of them in situ. When I found them in the collection of the Geol. Bureau at Heerlen they comprised 8 pieces (parts and counter parts), enclosed in a clayey shale which moreover contains a great number of grass-like leaves; the rests of *Sigillaria brardii* have been lost. They were collected at locality 54, Lawrence Shales, 4 miles W. of Tonganoxio, Ka, the age of which is Stephanian.

The preservation of these fructifications is very good. The axis is partly covered with the imbricate fertile parts of the sporophylls (Pl. IV, Fig. 12), and partly naked, so that a number of sporophyll-scars are clearly distinguishable (Pl. II, Fig. 4). On both sides of the axis complete sporophylls are visible (Pl. I, Fig. 1). The apex of the fructification too is represented (pl. II, Fig. 5). A single megasporangium can be seen (Pl. II, Fig. 4, indicated by the two arrows); another cone, more decayed, is covered with a great number of megaspores (Pl. III, Fig. 11). The spores could easily be removed by means of a needle, and after they had been treated for some hours

S. J. DIJKSTRA: *On a Megaspore-bearing Lycopod Strobilus*

PLATE I

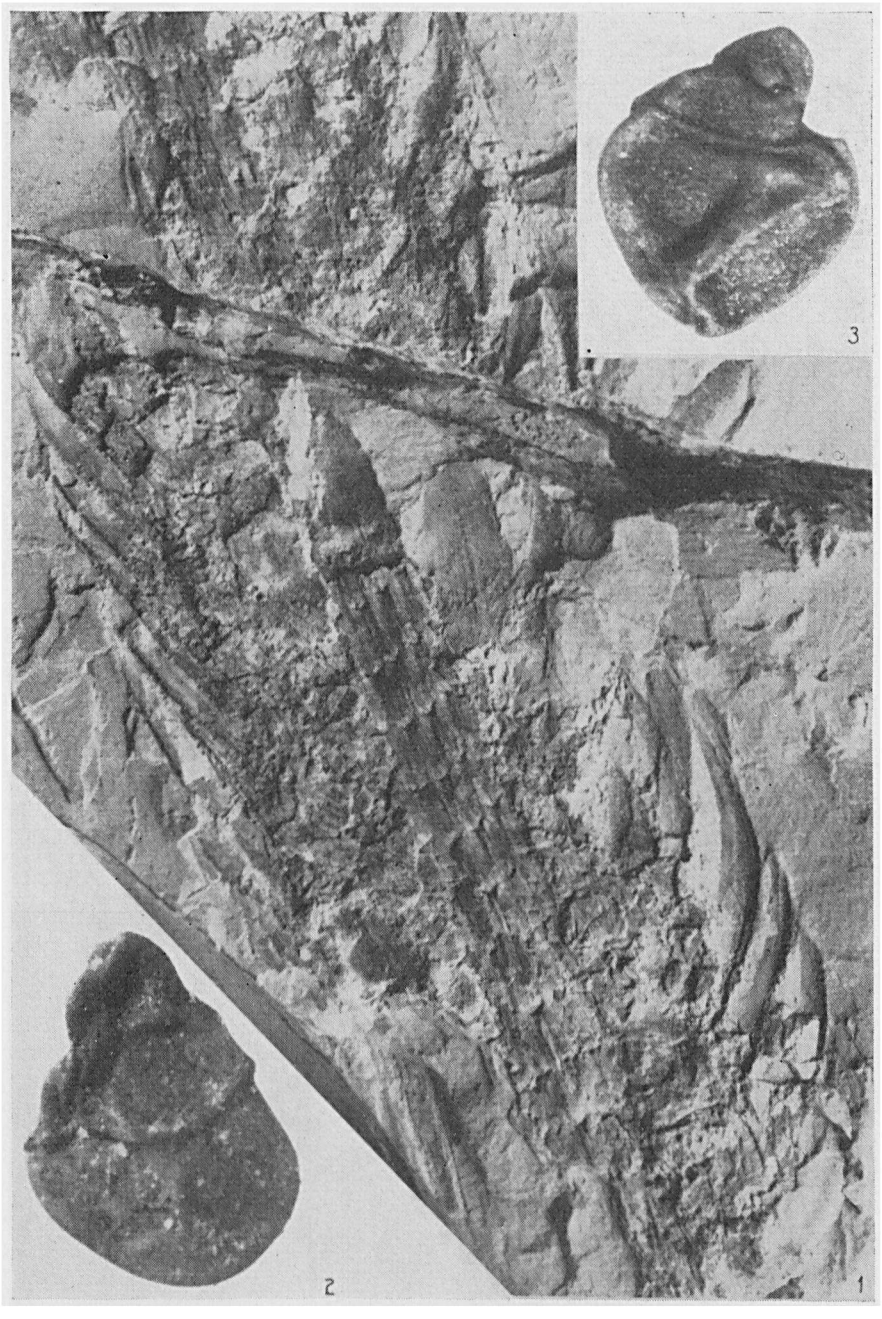
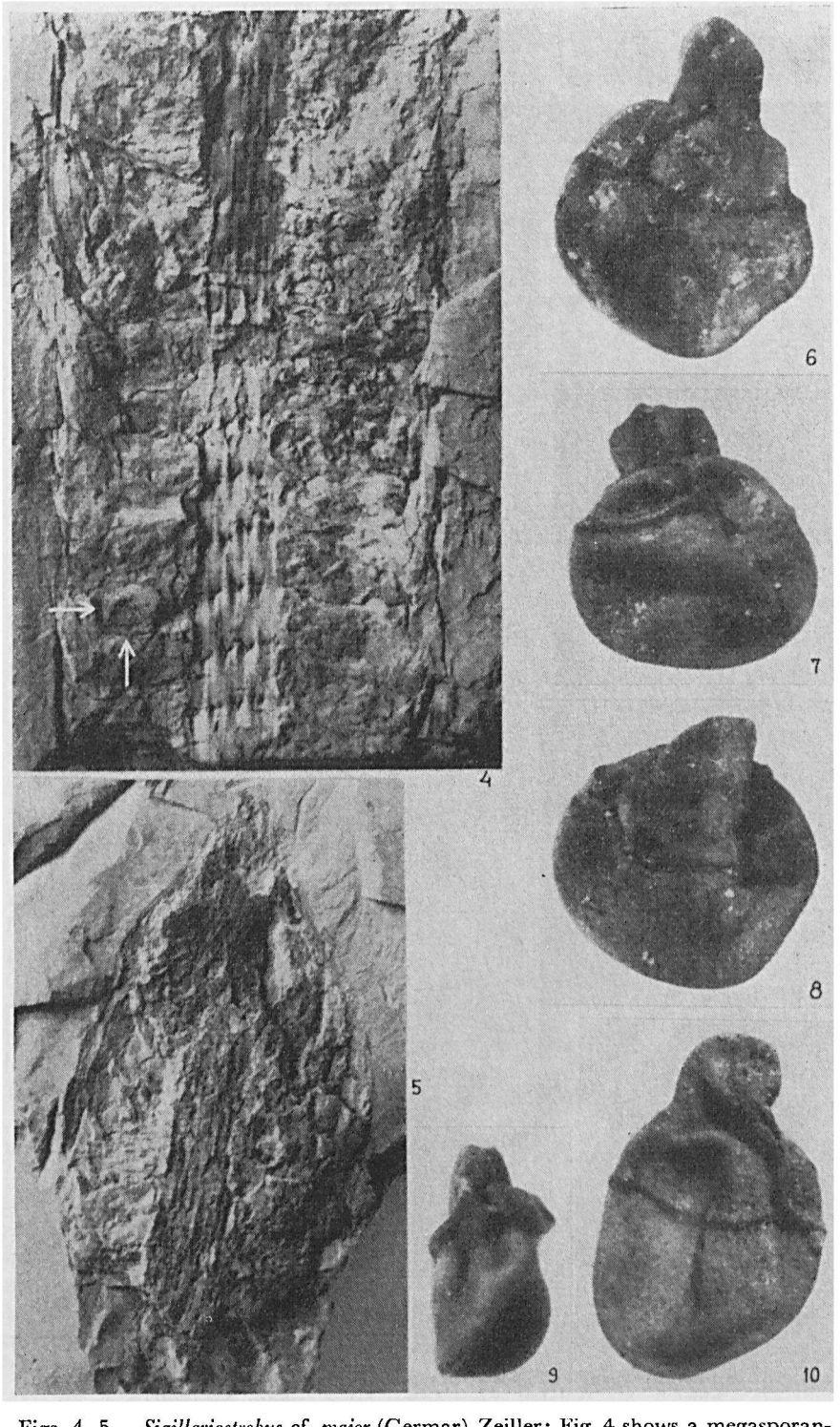


Fig. 1. *Sigillariostrobus* cf. *major* (Germar) Zeiller; 3 ×, photo No. 12274.
Figs. 2, 3. Isolated megaspores; 50 ×, photo No. 5292.



Figs. 4, 5. *Sigillariostrobus* cf. *major* (Germar) Zeiller; Fig. 4 shows a megasporangium (indicated by the two arrows); 3 ×, photo No. 12275.
Figs. 6–10. Isolated megaspores; 50 ×, photo No. 5292.

PLATE III

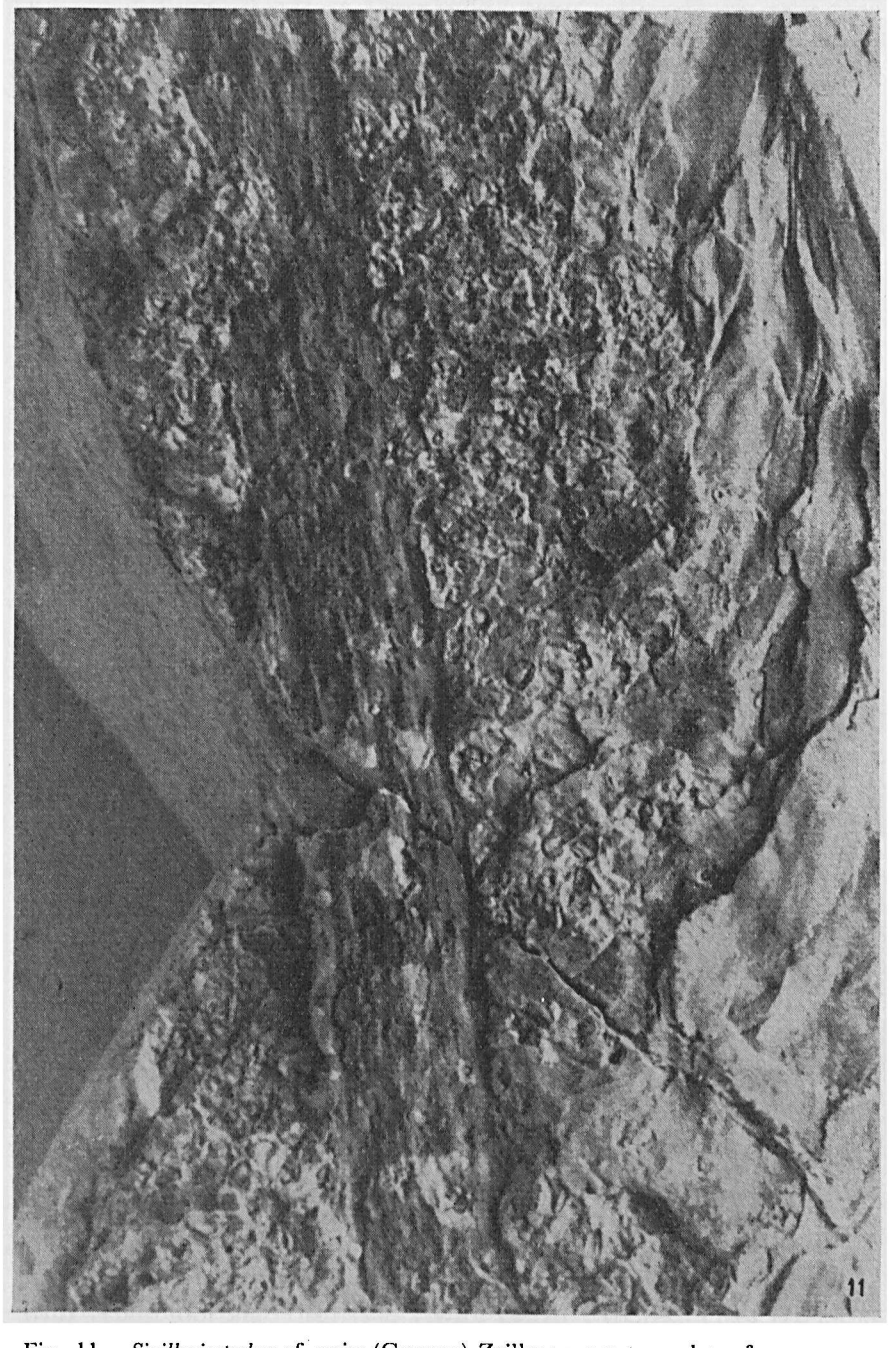


Fig. 11. *Sigillariostrobus* cf. *major* (Germar) Zeiller; a great number of megaspores is distinguishable; 6 ×, photo No. 12276.

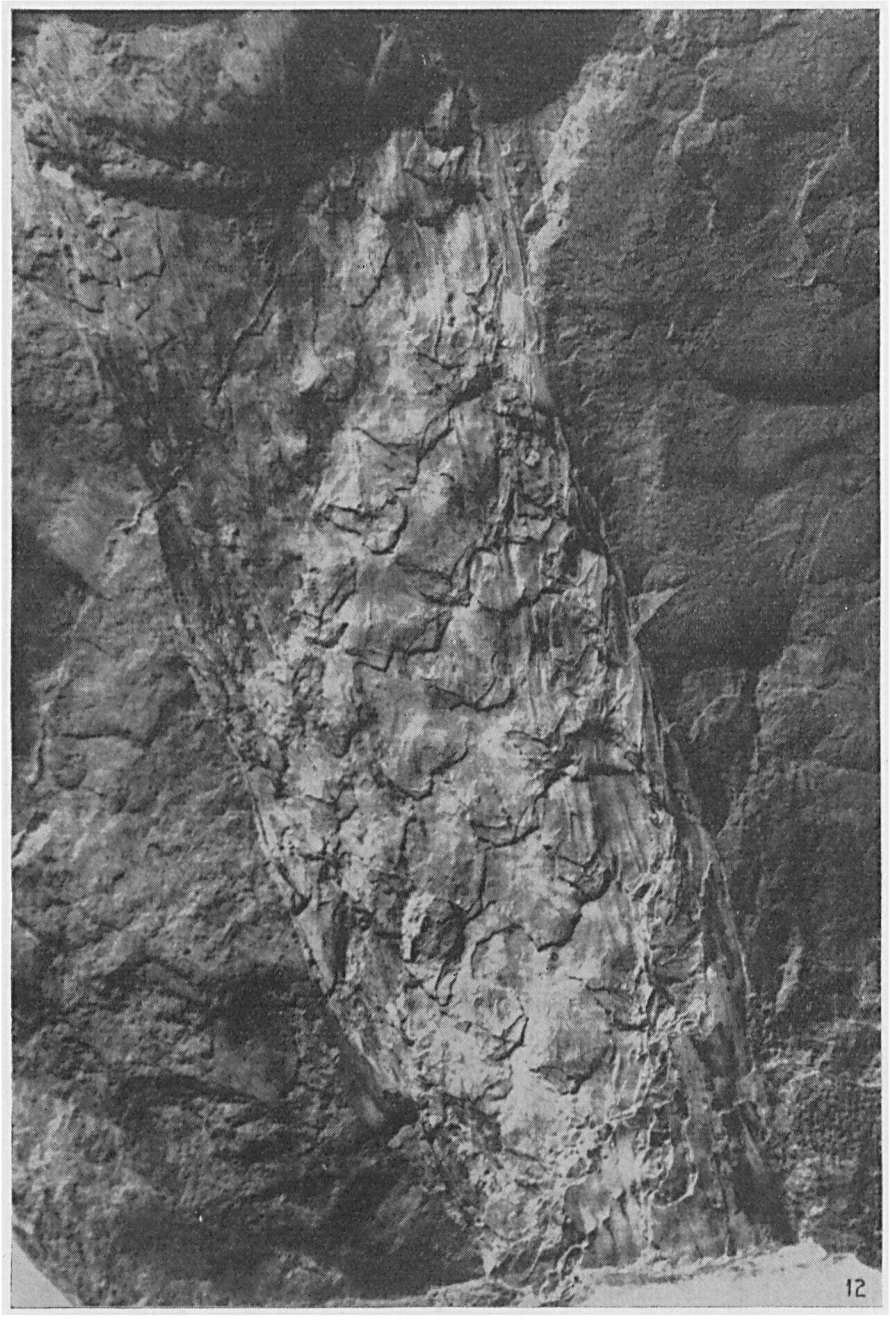


Fig. 12. *Sigillariostrobus* cf. *major* (Germar) Zeiller; 3 ×, photo No. 12271. Photographs by L. R. FUNCKEN

with a 30 % fluoric acid solution, they proved to be sufficiently cleaned (Pl. I, Figs. 2, 3; pl. II, Figs. 6–10). Microspores have not been found. These megaspores belong to the sectio *Lagenicula.*

In the literature two *Sigillariostrobi* are known, to produce megaspores belonging to the sectio *Lagenicula.* They are: *Sigillariostrobus major* Germar and *Sigillariostrobus spectabilis* Renault.

The former was described by ZEILLER (1906), and compared by him with *Sigillodendron frondosum* (Goeppert) Weiss and *Lepidodendron frondosum,* Goeppert and with *Volkmannia major* (Germar), but according to JONGMANS (1932) the specimen of Goeppert is a doubtful rest, and the same can be said of Germar's specimen. The specimen described by Zeiller has a length of 21 cm, and a diameter of 3 cm, the sporophylls included. The curvature of the sporophyll is very similar to that observed in our specimens; its sterile part must be about 1.5 cm long, and about 3 mm wide. It is a pity that Zeiller himself gave but few details with regard to the dimensions of the sporophylls. The megaspores from this fructification typically belong to the sectio *Lagenicula.* The diameter of fully developed specimens is 1–1.5 mm, their wall is smooth; not-fully developed specimens vary from 0.8 to 1.0 mm. The description and the figures of Zeiller's spores are too imperfect for a satisfactory comparison with ours. According to Zeiller it is very probable that *Sigillariostrobus major* is the fructification of *Sigillaria brardii.*

Sigillariostrobus spectabilis Renault (1888) is the other known species that bore lageniculate megaspores. This strobilus is 10.5 cm long, 3 cm in diameter, and on the 4–5 mm wide axis the leaf-scars are placed in an irregular verticil. The adaxial part of the sporophyll is an isosceles triangule, attached by its top. The base of the triangle measures 5.5 mm; the length of the sterile part of the sporophyll is 35 mm. The wall of the megaspores which are 0.8 mm in diameter is minutely granulate. Other specimens belonging, according to RENAULT (1888), to the same species, were found among leaves and branches of *Sigillaria brardii.* ZEILLER (1906) figured and discussed the same species; he rightly recognized the nature of the megaspores. In comparison with our specimens *S. spectabilis* has a larger diameter, the spreading sporophylls included it is 6 cm in diameter; the sterile part of the sporophylls is longer and wider, about 5.5 mm, and they are more spreaded than they are in our specimens. The description and the figures of the megaspores are too incomplete to allow a satisfactory comparison with our spores.

There is still another strobilus, namely *S. strictus* Zeiller which, according to ZEILLER (1884), might be a fructification of *Sigillaria brardii,* and of this strobilus too megaspores are known. However, they belong to the sectio *Aphanozonati.* It is not probable that *S. brardii,* although a very variable "species", may have produced megaspores belonging to different megaspore genera.

Finally we can compare the megaspores from our fructifications with "sporomorphae dispersae", with isolated spores. They resemble *T. brasiliensis* Dijkstra (1955b), but in this species the length of fully

developed specimens varies from about 1180 μ to 1160 μ, their radiate ridges are more robust, their neck-like prominence is more pyramidal than cylindric, and the hemispherical bodies on the wall are generally larger.

Moreover, these spores resemble *T. hispanicus* Dijkstra (1955a). The diameter of the spores of both species is about the same. However *T. hispanicus* is characterized by its rather thin wall which is about 10 μ thick, in consequence of which it is often plicate, and it never bears hemispherical bodies.

A third lageniculate species with which they may be compared, is *T. nudus*, sensu Dijkstra. The dimensions of this species from *S. Limburg* are smaller, it varies from 450 μ to 1025 μ in diameter (the mean being 764 μ for 50 spec.), its neck-like projection is more pyramidal, its wall never bears hemispherical bodies, and its arcuate ridges are not so striking.

Just at the time we were studying these fructifications, Chaloner sent us some spores, and asked our opinion with regard to their affinities. These specimens had been collected by him in Lawrence Shale from Lone Star Lake, near Lawrence Kansas, Stephanian, perhaps Virgil or Monongahela, possibly very top of the Conemaugh. This must be the same, or about the same locality as that at which our specimens had been collected. Chaloner's spores appeared to be identical with ours, and after examining some photographs of our specimens, and hearing further details with regard to them, he agreed with us that these spores must be identical.

Our conclusion is that the spores from these strobili belong to the sectio (or genus) *Lagenicula*, and that they represent a new species. As they were found in a strobilus, they are not provided with a specific name. They are identical with the isolated specimens found by Chaloner. The latter specimens need a specific name.

The fructifications which bore these spores are regarded as comparable with *Sigillariostrobus major* (Germar) Zeiller. This view is mainly based on the shape and size of the spores, which belong to *Lagenicula*, on their joint affinity with *Sigillaria brardii*, and in some respects on the shape of the strobilus. The identity of the fructification is consequently less certain than that of its spores.

Diagnosis of the Genus *Sigillariostrobus*

Before concluding this paper we want to say something concerning the diagnosis of *Sigillariostrobus*. Goldenberg (1855) was the first who referred certain cones to *Sigillariostrobus*. This was done chiefly on account of their supposed association with stems of *Sigillaria*. For these fructifications Schimper (1870) instituted the genus *Sigillariostrobus*. These strobili are pedunculate, elliptical or elongate-cylindrical, and provided with ovate-triangular, suddenly angustilate and lanceolate bracts which are in the middle ribbed. The sporangia are found on the basal part of the sporophyll, on its upper side; mega- (?) and microspores (?) occur. According to Schimper *Sigillariostrobus* should be easily distinguishable from *Lepidostrobus* by the fact that their

bracts are attached with nearly longitudinally instead of transversally extended base.

Later on various investigators have changed or enlarged the diagnosis of *Sigillariostrobus*. We shall regard a number of these added characters. Cone either sessile or pedunculate; peduncle provided with a few leaves, or with leaves reduced to bracts; leaf-scars in longitudinal rows; sporophylls attached either at right angles or more or less oblique; sporophylls either spirally arranged or verticilate, and rhomboidal, lanceolate or acicular in shape; lamina part relatively short, triangular; proximal part rarely detached from the basal part; sporophyll and peduncle deciduous; cones either heterosporous or with one kind of spores only; sporangia developed within the inflated and excarate base of the bract.

The last added character may be correct, but it is of no use in no-petrified cones. The smaller spores mentioned in Schimper's description probably were not fully developed megaspores, and no microspores, as he assumed. Concerning the other amplifications some of them are in conflict with Schimper's diagnosis; most of these variations also occur in *Lepidostrobus*. CROOKALL (1929) stated that: *Lepidostrobus* includes the fructifications belonging to *Lepidodendron*, *Lepidophloios*, *Bothrodendron*, and possibly to some species of *Sigillaria*. The same can probably be said of *Sigillariostrobus*.

We believe that the most valuable character of *Sigillariostrobus* is found in the peduncle (if not broken off), which bears bracts arranged in vertical rows; we should like to add that the sporophylls or their scars are arranged in vertical rows, for this arrangement is the same as that of the leaf-scars of *Sigillaria*. It was the intention of Schimper, Goldenberg, etc. to give a diagnosis of the fructification of *Sigillaria*, which would enable us to distinguish this from the cone of *Lepidodendron*. However, Chaloner drew our attention to the fact that in some *Lepidostrobi* too the sporophylls or their scars are arranged in vertical rows.

Apart from some of the characters mentioned above, SCHOPF (1941), CHALONER (1953bc), and FELIX (1954) place emphasis on the character of the megaspores; those of *Lepidostrobus* which should belong to the *Lageniculae*, those of *Sigillariostrobus* to the *Aphanozonati*. However, according to SCHOPF, p. 32, this does not mean that all cones that have been identified as *Sigillariostrobus*, contain aphanozonate spores.

What is the generic value of the megaspore shape? In order to determine this, let us consider a recent genus related to *Sigillaria*, namely *Isoëtes*. PFEIFFER (1922) in a monographic study of *Isoëtes* gives a short description and photographs of some spores. The spore wall in the various species can be smooth, covered with spines, tubercles, warts, etc., it also can be reticulate. Its shape is generally tetraedric, but the spores of *I. setacea* show something like an equatorial zone, and those of *I. Malivermiana* frequently are provided with a large, compound knob, occurring on the upper face in the angle formed by the triradiate ridges (compare the neck of a lageniculate spore). In some species small and large megaspores occur in the same sporangium

(compare the Carboniferous genus *Cystosporites*). If the spores of *Isoëtes* should have been fossilized, they would have been divided over at least three spore genera, namely: *Aphanozonati*, *Zonales* and *Lagenicula*.

Sigillariostrobi producing lageniculate spores are: *S. major*, *S. spectabilis*, and perhaps *S. crepini*. On the other hand *Lepidostrobus noei* produced aphanazonate spores, see MATHEW (1940), HOSKINS and CROSS (1952), FELIX (1954). These spores are comparable with *T. fulgens* Zerndt (1931, '37), or with *T. subfulgens* Dijkstra (1957).

Our conclusion is that the systematic affinity between cone genera based on the structure of the spores alone, cannot be established with reasonable precision.

ACKNOWLEDGEMENT

The author wishes to express his appreciation of the constructive criticism, and great willingness to help of Dr. W. G. CHALONER, University College, London. He is very much indebted to Dr. C. E. B. BREMEKAMP for correcting the manuscript.

REFERENCES

ARNOLD, C. A. 1930. Amer. Journ. Bot. *17*:1028–1032.
ARNOLD, C. A. 1933. Amer. Journ. Bot. *20*:114–117.
ARNOLD, C. A. 1935. Amer. Journ. Bot. *22*:23–25.
ARNOLD, C. A. 1938. Amer. Midl. Nat. *20*:709–713.
ARNOLD, C. A. 1949. Contr. Mus. Paleont. Univ. Mich. *7*:131–269.
BOCHENSKI, T. 1936. Ann. Soc. Geol. Pol. *12*:193–241.
DIJKSTRA, S. J. 1955a. Estud. Geol., Madrid. *11*:277–354.
DIJKSTRA, S. J. 1955b. Med. Geol. Sticht. Nw Ser. *9*:5–10.
DIJKSTRA, S. J. 1957. Med. Geol. Sticht. Nw Ser. *10*:25–38.
CHALONER, W. G. 1952. Ann. Mag. Nat. Hist. *5*:572–582.
CHALONER, W. G. 1953a. Geol. Mag. *90*:97–110.
CHALONER, W. G. 1953b. Ann. Bot. N.S. *17*:263–293.
CHALONER, W. G. 1953c. Ann. Mag. Nat. Hist. *6*:881–897.
CHALONER, W. G. 1954. Ann. Mag. Nat. Hist. *7*:80–91.
CHALONER, W. G. 1956. Amer. Midl. Nat. *55*:437–442.
CROOKALL, R. 1929. Coal Meas. Plants: 1–80.
FELIX, C. J. 1954. Ann. Miss. Bot. Garden *41*:351–392.
GOLDENBERG, T. 1855. Flora Saraepont. foss. *1*:1–55.
HOSKINS, J. H. et A. T. CROSS. 1940. Am. Midl. Nat. *24*:421–437.
HOSKINS, J. H. et A. T. CROSS. 1952. The Paleobot. *1*:215–238.
JONGMANS, W. 1932. Foss. Catal. Lycop. *4*:992.
LECLERCQ, S. 1938. Ann. Soc. Geol. Belg. *61*:164–170.
MATHEWS, G. B. 1940. Bot. Gaz. *102*:26–49.
NEMEJC, F. 1931. Bull. Inst. Acad. Sci. Boh. *32*:68–80.
PFEIFFER, N. F. 1922. Ann. Miss. Bot. Garden. *9*:79–232.
RENAULT, B. 1888. Bull. Soc. Hist. Nat. Autun. 1177–180.
SCHIMPER, W. P. 1870. Traité de Paléont. Veg. *2*:105.
SCHOPF, J. M. 1938. Rep. Invest. *50*:1–56.
SCHOPF, J. M. 1941. Rep. Invest. *75*:1–40.
WICHER, C. A. 1934. Arb. Inst. Pal. Petrogr. Brennst. *5*:87–95.
ZEILLER, M. R. 1884. Ann. Ac. Nat. Bot. (6), *19*:272.
ZEILLER, M. R. 1906. Blanzy et Creusot: 172–181.
ZERNDT, J. 1931. Bull. Acad. Pol. Sci. Lett. Ser. A: 165–183.
ZERNDT, J. 1937. Acad. Pol. Sci. Lett. Trav. Geol. *3*:1–78.