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ASPECTS OF PERMIAN PALAEOBOTANY AND PALYNOLOGY. VI. TOWARDS A FLEXIBLE SYSTEM OF NAMING PALAEOZOIC CONIFERS

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SUMMARY

A natural classification of extinct conifers requires the recognition of natural taxa. In conifers reproductive organs provide the most successful characters for delimiting natural genera and families. Based on assembled species, a genus should at least be diagnosed in terms of overall morphology of leafy shoots in combination with the organization of ovuliferous organs. In addition, detailed statements about the epidermal structure are of great practical value.

However, most taxa of fossil conifer remains are artificial by implication. Most genera are form-genera, established for all kinds of isolated organs. They have a highly variable degree of artificiality, ranging from taxa comprising fragments which only supposedly belong to conifers, to taxa which can be attributed to a natural family.

Fossil conifer taxonomy should recognize the variable status of the taxa to which plant fragments may be assigned. Within a framework of natural genera and varied form-genera, it is possible to integrate taxonomic progress through a "promotion" of taxa. If better preserved material permits a more thorough analysis, species may be transferred to more precisely defined form-genera or even to a natural genus. Some form-genera may gain a natural status through adequate redefinition.

Such a flexible procedure is introduced as a possibility to rationalize Late Carboniferous – Permian conifer taxonomy. Within the Walchiaceae one may recognize the three natural genera *Walchia* Sternberg, *Ernestiodendron* Florin and *Ortiseia* Florin. Form-genera explicitly related to this family are *Culmitzschia* Ullrich (foliage with preserved epidermal structure), *Walchiostrobus* Florin (ovuliferous organs) and *Walchianthus* (polliniferous organs).

The present state of species assignment is reviewed. The new form-genus, *Hermitia* Kerp et Clement-Westerhof is established in order to accommodate part of the many species, formerly assigned to *Walchia*, which can only be diagnosed in terms of overall leaf morphology; the included species are not explicitely related to the Walchiaceae. The following new combinations are introduced (Kerp et Clement-Westerhof): *Culmitzschia parvifolia, Hermitia arnhardtii, H. bertrandii, H. carpentieri, H. dawsonii, H. gallica, H. geinitzii, H. germanica, H. imbricatula, H. minuta, H. rigidula, H. schlotheimii, H. schneideri, H. stephanensis,* and *H. whitei.*

1. INTRODUCTION

In his essay on the problem of naming fossil conifer remains, HARRIS (1969, p. 245) puts the current practice of fossil conifer taxonomy clearly into words: "a medley of compromises between a thorough-going though rough artificial system and attemps at a natural one ranging from very insecure to very good".

A natural classification constitutes, of course, the most rewarding goal of the taxonomic study of fossil conifers. Such a classification asks for natural

taxa whose components are thought to be phylogenetically related. Unfortunately, the possibility of recognizing natural taxa among conifer remains is restricted due to the dispersed nature of the material available for investigation. Being established on the basis of comparative studies of isolated plant parts, most taxa of conifer remains are artificial by implication.

Most genera of conifer remains are explicitly or implicitly form-genera in the sense of Article 3,2 of the International Code of Botanical Nomenclature (I.C.B.N.). Form-genera have been established for all kinds of conifer remains, such as isolated leaves and leafy shoots (with or without preserved epidermal structure), wood, ovuliferous and polliniferous organs and parts thereof (ovuliferous dwarf shoots, bracts, seeds, microsporophylls, pollen or prepollen). It should be noted that a limited but important category of genera based on individual parts of conifers still corresponds to the concept of organ-genera of pre-1978 editions of the I.C.B.N.

Palaeobotanical studies aimed at characterizing extinct conifers as complete biological entities should provide the necessary evidence for a more natural delimitation of taxa. Fortuitous discoveries of organs in organic connection and, especially, sophisticated analyses of suitable collections of dispersed material may enable the establishment of a fairly accurate concept of a more or less completely assembled and/or reconstructed plant. However, even when the fossil material thus permits an association of different remains within a single natural genus, a number of authors (e.g., MEYEN 1984a) presently propagate the inclusion of the individual organs of an assembled conifer in separate artificial genera.

We feel that such a rigid artificial approach to whole plant taxonomy of extinct conifers is neither realistic nor practical. It conceals the potential of the fossil record as a primary tool in unravelling the phylogeny of conifers. On the other hand, in the practice of palaeobotanical research, well-defined form-genera will always remain taxonomic units of primary importance. Inspired by the philosophy of HARRIS (1969), therefore, we try to follow a more flexible procedure with regard to the taxonomic interpretation of Palaeozoic conifer remains.

This procedure has already successfully been applied in the recent re-evaluation of the Walchiaceae by CLEMENT-WESTERHOF (1984). In the present paper our approach is more specifically outlined. In addition, as a sequel to the revision of the genus *Walchia* Sternberg 1825, a number of taxonomic and nomenclatural consequences are treated. These include the presentation of emended diagnoses of the form-genera *Walchiostrobus* Florin 1940 and *Walchianthus* Florin 1940 as well as the establishment of the form-genus *Hermitia* Kerp et Clement-Westerhof, nov. gen. Establishment of the latter taxon is necessary in order to accommodate a large number of species which had to be excluded from *Walchia.*

It should be noted that the present paper is a progress report rather than a final synthesis in which all problems related to the classification of Palaeozoic conifer remains have been adequately treated. We believe, however, that the method we have chosen may considerably help in setting up order in the chaos currently characterizing the taxonomy of fossil conifers. Of course, mutatis mutandis, our approach may also be applied to other groups of gymnosperms.

2. TAXONOMIC PROCEDURE

The minimum requirements for a realistic concept of natural taxa of fossil conifers are conditioned by the combination of taxonomic characters used for diagnosing comparable taxa of extant conifers. In addition, however, palaeobotanical research has become highly dependent on the evaluation of characters which are not (yet) commonly applied in taxonomic studies of living conifers. It is certain that in conifers some characters more accurately reflect natural relationships than others:

(1) Although the four main leaf types as well as the different kinds of phyllotaxy may have a certain value in phylogenetic considerations (DE LAUBENFELS 1953), overall leaf morphology alone rarely provides accurate criteria for recognizing natural coniferous genera and families. Yet external morphological characters should never be neglected since we are faced with the fact that leafy shoots are among the most frequently occurring conifer remains to be classified.

(2) In conifers the epidermal structure may vary according to family, genus and species (FLORIN 1931, 1950) and hence proves to be of great potential in natural classification. Moreover, in absence of organic connection, detailed epidermal studies provide the most reliable alternative for correlating vegetative foliage and reproductive organs of fossil conifers.

(3) Wood anatomy is also known to be a source of valuable taxonomic information. Unfortunately, however, evidence from fossil conifer wood can only rarely be correlated with characters derived from other organs.

(4) Reproductive organs are generally accepted to provide the most successful characters for delimiting natural genera and families of conifers. Especially morphological and anatomical features of the ovuliferous organs are of the foremost importance in phylogenetic considerations. Information on polliniferous organs seems to be less accurate, but the possibilities and limitations still need further exploration. Pollen (or prepollen), when studied according to advanced pollenmorphological methods, is certainly of taxonomic importance, notably at a generic level.

Considering this character weighting, a natural genus of fossil conifers and its included species should at least be diagnosed in terms of the overall morphology of leafy shoots in combination with the organization of the ovuliferous organ. If leafy shoots and ovuliferous organs are not found in organic connection, a diagnosis should preferably include a detailed statement about the epidermal structure. Such a statement is also required in order to reach the optimum applicability of the taxon as a practical identification unit for various kinds of fragments. Statements about the organization of polliniferous organs, including detailed pollenmorphological information, as well as wood-anatomical data may considerably corroborate the natural status of the taxon concerned.

Natural genera should be the basis for the establishment of families of extinct conifers. Such families ought to be carefully constructed since they represent the most likely categories to be used in future phylogenetic classification schemes of conifers. In order to become valuable units in natural plant classification,

families and any other formally recognized suprageneric categories should never be groupings of form-genera alone.

If material does not permit an interpretation in terms of a natural genus, dispersed organs should necessarily be included in form-genera. These form-genera logically have a highly variable degree of artificiality, ranging from taxa comprising fragments which only supposedly belong to conifers, to well-defined taxa enabling the attribution of the included organs to a single family (the organ-genus of pre-1978 editions of the I.C.B.N.).

Within this framework of more or less clearly defined form-genera, the most practical way of integrating taxonomic progess may be the "promotion" of taxa. If better preserved material permits a more thorough analysis, species should be transferred to more precisely defined form-genera or even to a natural genus. But also a diagnosis of a form-genus may be emended by adding more information, based on a re-evaluation of its type-species. Some form-genera may thus gain a natural status.

If material permits the recognition of assembled conifer species, these may well be directly assigned to a natural genus. It is here considered that (additional) formal classification of the individual organs of assembled species in separate (form- or "organ"-)genera is frequently a superfluous procedure. Pollen grains, however, may form an exception. Palynological systematics is highly independent of the remainder of palaeobotanical systematics. Palynological species, newly established or revised on the basis of in situ pollen or prepollen of conifers could well contribute to a more rational palynological taxonomy.

Nomenclatural consequences of taxonomic procedures within a flexible framework of varied form-genera and natural genera should preferably remain in accordance with the rules of the I.C.B.N. Unfortunately this is not always possible. Since, for example, the concept of the organ-genus has been rejected, we are forced to recognize a category of form-genera which can be assigned to a family. Such a procedure is against the rules. We feel, however, that the rules in some respect hardly recognize the specific problems related to palaeobotanical systematics. In this case we believe that palaeobotanical practice, rather than the I.C.B.N. should dictate the status of a form-genus.

3. THE WALCHIACEAE

A flexible taxonomic procedure has recently been followed with regard to the re-evaluation of the Late Carboniferous – Early Permian Walchiaceae (CLEMENT-WESTERHOF 1984); as a result of this study the following revised concepts are presented:

(1) *Ortiseia* Florin 1964, originally established as a form-genus by implication (leafy shoots with epidermal structure) is given an emended diagnosis to constitute an natural genus. The emendation has been based on the detailed analysis of the vegetative and reproductive organs of three assembled species. The genus is proved to be closely related to the genera *Walchia* Sternberg 1825 and *Ernestiondendron* Florin 1934.

(2) *Walchia* Sternberg 1825, orginally established as a form-genus by implication (leafy shoots) and explicitly treated as a form-genus by FLORIN (1939c), is given an emended diagnosis to constitute a natural genus. The emendation has been based on the diagnosis of the natural genus *Lebachia* Florin 1938, together with a new interpretation of the ovuliferous organs. The name *Lebachia* is shown to be illegitimate.

(3) *Ernestiodendron* Florin 1934, originally established as a natural genus, is given an emended diagnosis on the basis of a new interpretation of the ovuliferous organs.

(4)Walchiaceae (Göppert 1865) Schimper 1870, originally established as a taxon of family rank by implication, is given an emended diagnosis to constitute a natural family of conifers which include the natural genera *Walchia, Ernestiodendron* and *Ortiseia.* The name Walchiaceae replaces the illigitimate name Lebachiaceae Florin 1945.

(5) *Culmitzschia* Ullrich 1964, originally established as a form-genus by implication (leafy shoots with epidermal structure) is given an emended diagnosis to constitute a form-genus for leafy shoots, showing the epidermal structure which is thought to be characteristic of the Walchiaceae. It should be noted that *Culmitzschia* in effect constitutes an organ-genus in the sense of earlier editions of the I.C.B.N. Although not necessarily representing natural units, the characteristics of the included species may well reveal their walchiaceous nature.

As a next logical step it is here considered that also form-genera have to be recognized to accommodate reproductive organs, not (yet) assignable to natural genera but clearly showing walchiaceous affinities. In the present paper, therefore, the form-genera *Walchiostrobus* Florin 1940 and *Walchianthus* Florin 1940 are re-diagnosed in order to accommodate walchiaceous ovuliferous and polliniferous cones, respectively.

4. THE FORM-GENUS WALCHIOSTROBUS

To retain *Walchiostrobus* within the Walchiaceae as a form-genus for ovuliferous cones and dispersed fertile dwarf shoots, the original diagnosis has to be radically changed. Considering the diagnosis of the Walchiaceae (CLEMENT-WESTERHOF 1984) only specimens showing a single ovuliferous scale per dwarf shoot can be taken into account. Furthermore it should be realized that the ovules described by FLORIN (1940) probably represent ovuliferous scales (see also CLEMENT-WESTERHOF 1984, fig. 16).

DIJKSTRA (1975, P. 1068) suggested a relationship between *Walchiostrobus* and *Curionia* Sordelli 1896. We agree with FLORIN (1940, p. 261) that the organization of *Curionia* is insufficiently known, so that this form-genus cannot be regarded as a practical taxon for classifying ovuliferous cones.

Florin did not indicate a type-species for *Walchiostrobus.* We therefore selected *Walchiostrobus gothanii,* representing the only of Florin's species characterized by the presence of a single ovuliferous scale per dwarf shoot. Considering the unique organization of the ovuliferous cones within the Walchiaceae, we

are of the opinion that epidermal features are not strictly necessary to recognize species of *Walchiostrobus*.

Form-genus *Walchiostrobus* Florin 1940, *emend.* Clement-Westerhof et Kerp
Type-species: *Walchiostrobus gothanii* Florin 1940
Holotype of the type-species: the specimen figured and described by FLORIN (1940, plate CLI/CLII, 47; p. 262)
Emended diagnosis: Compound ovuliferous cones; cone axis bearing spirally arranged bracts with ovuliferous dwarf shoots, freely arising in their axils. Ovuliferous dwarf shoots composed of a number of sterile scales and a single ovuliferous scale, emerging on the adaxial side. Ovuliferous scale bearing a single inverted ovule on its abaxial surface.
Status: Form-genus for ovuliferous cones and fertile dwarf shoots of the Walchiaceae.
Species recognized: *Walchiostrobus gothanii* Florin 1940 (type-species). A possible transfer of *Molyostrobus texanum* Miller et Brown 1973 to *Walchiostrobus* needs further investigation.
Species excludendae: The following species, showing more than one ovuliferous scale per dwarf shoot (compare MEYEN 1983, 1984b), or showing an unclear organization have to be excluded:
W. elongatus Florin 1940
W. fasciculatus Florin 1940
W. germanicus (Florin 1939) Němejc 1968
W. lodevensis Florin 1940

5. THE FORM-GENUS WALCHIANTHUS

Walchianthus was explicitely established by FLORIN (1940) as a form-genus for coniferous cones of walchiaceous affinity. However, Florin's diagnosis has to be emended and completed with a description of the epidermal structure. Since the general organization of walchiaceous polliniferous cones is by no means unique, cones with unknown epidermal structure cannot be exclusively related to the Walchiaceae. The three species of *Walchianthus* recognized by FLORIN (1940) have been correctly diagnosed. Because Florin did not indicate a type-species we have selected *Walchianthus cylindraceus* Florin 1940, being the most extensively described and figured species.

Form-genus *Walchianthus* Florin 1940, *emend.* Clement-Westerhof et Kerp
Type-species: *Walchianthus cylindraceus* Florin 1940
Holotype of type-species: The specimen figured and described by FLORIN (1940, plate CLV/CLVI, 11; p. 269)
Emended diagnosis: Simple polliniferous cone; cone-axis bearing spirally arranged subpeltate microsporophylls. Proximal part of microsporophyll arising at an angle of approximately 90°. Distal part narrow-subtriangular, basally rounded, apex acute, parallel to the cone-axis or slightly divergent. Epidermal

structure showing stomata-free median and often apical zones, especially on abaxial surface of distal part where stomata may sometimes be totally absent. Stomata arranged in longitudinal bands or rows; stomatal complexes mono- to dicyclic, 4–8 subsidiary cells, sometimes bearing papillae. Hair bases present. Papillae on epidermal cells may occur.

Status: Form-genus for polliniferous cones of the Walchiaceae.

Species recognized:

W. crassus Florin 1940

W. cylindraceus Florin 1940 (type-species)

W. papillosus Florin 1940

6. THE POSITION OF SPECIES FORMERLY ASSIGNED TO WALCHIA OR LEBACHIA

Since the establishment of the generic name *Walchia* Sternberg 1825 (type species *Walchia piniformis,* designated by MILLER 1889), a great variety of leafy conifer remains has been included in a large number of species assigned to this genus. These species also comprise a number of combinations related to the illegitimate concept of *Walchia* Florin 1939. To a lesser extent material was assigned to the illegitimate genus *Lebachia* Florin 1938 and to *Ernestiodendron* Florin 1934. As a direct consequence of the work of CLEMENT-WESTERHOF (1984) the potential of *Walchia* in accommodating coniferous leaf remains has become drastically diminuished. In the following paragraphs it is attempted to recognize a number of categories among the many species formerly assigned to *Walchia* and/or *Lebachia.* For additional references and information on the various species one is referred to the work of FLORIN (1938–1945), DIJKSTRA (1975, p. 1045–1062), BOERSMA & BROEKMEYER (1979, p. 105; 1981, p. 68) and CLEMENT-WESTERHOF (1984).

Species assigned to *Walchia*

Following the natural concept of *Walchia* (emended diagnosis of CLEMENT-WESTERHOF 1984), only a limited number of species is sufficiently well-known to justify an inclusion in the genus. The species concerned are:

W. garnettensis (Florin 1939) Clement-Westerhof 1984

W. goeppertiana (Florin 1939) Clement-Westerhof 1984

W. hypnoides (Brongniart 1828) Brongniart 1849

W. piniformis Sternberg 1825 (type-species)

A possible transfer of the recently described species *Lebachia lockardii* Mapes et Rothwell 1984 to *Walchia* needs further investigation.

Species assigned to *Ernestiodendron*

Within the natural genus *Ernestiodendron* Florin 1934, only one species can so far be recognized, viz. *Ernestiodendron filiciforme* (Sternberg 1825) Florin 1934.

Nomina nuda

A considerable number of species names related to *Walchia* ought to be regarded as nomina nuda. These include:

W. cutassaeformis Brongniart 1849
W. eutassaeformis Brongniart 1849
W. gravenhorstii (Brongniart 1928) Brongniart 1838
W. grandeuryi Saporta 1885
W. hoeninghausii (Brongniart 1828) Brongniart 1838
W. patens (Brongniart 1824) Brongniart 1838
W. polyphyllus (Brongniart 1828) Göppert 1848
W. sillimannii (Brongniart 1828) Brongniart 1838
W. sternbergii Brongniart 1838

Illegitimate homonyms

The following two names are illegitimate homonyms:

W. gracilis Dawson 1871 non Emmons 1857
W. longifolia Göppert 1864–65 non Emmons 1857

Species assigned to *Culmitzschia*

On the basis of preserved epidermal structure, another category of species, formerly assigned to *Walchia* or *Lebachia*, can confidently be assigned to the walchiaceous form-genus *Culmitzschia* Ullrich 1964 emend. Clement-Westerhof 1984:

C. americana (Florin 1939) Clement-Westerhof 1984
C. angustifolia (Florin 1939) Clement-Westerhof 1984
C. florinii Ullrich 1964 (type-species)
C. frondosa (Renault 1885) Clement-Westerhof 1984
C. hirmeri (Florin 1939) Clement-Westerhof 1984
C. intermedia (Florin 1939) Clement-Westerhof 1984
C. laxifolia (Florin 1939) Clement-Westerhof 1984
C. mitis (Florin 1939) Clement-Westerhof 1984
C. mucronata (Florin 1939) Clement-Westerhof 1984
C. parvifolia (Florin 1939) Kerp et Clement-Westerhof, *nov. comb.*
Basionym: *Lebachia parvifolia* Florin 1939a, p. 64.
Holotype: the specimen figured by FLORIN (1939a, plate XXXI/XXXII, 1–2).
C. speciosa (Florin 1939) Clement-Westerhof 1984

Synonyms

According to the taxonomic interpretations of Florin, one might recognize a number of synonyms in relation to some of the here accepted species of *Walchia, Ernestiodendron* and *Culmitzschia*. These synonyms would include the following names:

W. affinis Sternberg 1825
W. fertilis Renault 1896
W. flaccida Göppert 1864–65

W. gracillima White 1929
W. imbricata Schimper 1870
W. linearifolia Göppert 1864–65
W. pinnata (Bronn 1834) Gutbier 1849
W. robusta Dawson 1871

With the exception of *W. affinis*, a name now generally accepted as a synonym of *Ernestiodendron filiciforme* (compare GÖPPERT 1864–65, p. 241; FLORIN 1938, p. 9–10; 1939c, p. 178; CLEMENT-WESTERHOF 1984, p. 100); in the present paper we refrain from any formal statement about synonomy. A number of the species listed are in fact heterogeneous and should be carefully lectotypified before they can be nomenclaturally treated. Some of the names, if acceptable as synonyms, will have priority over accepted names. The problem of synonomy is presently under investigation.

Species already assigned to other taxa

A considerable number of species, originally accommodated in *Walchia*, was based on Mesozoic conifer remains:

W. angustifolia Emmons 1857
W. brevifolia Emmons 1857
W. diffusus Emmons 1857
W. gracile Emmons 1857
W. longifolius Emmons 1857
W. variabilis Emmons 1857
W. williamsonis (Brongniart 1828 ex Lindley et Hutton 1833) Brongniart 1838

The species were already treated by FONTAINE (1883, 1900), who considered an attribution of the plant fragments concerned to the coniferous form-genera *Cheirolepis* and *Palissya*.

The combination *Walchia valdajolensis* (Mougeot 1852) Seward 1919 was changed by FLORIN (1940, p. 277) into *Walchiopremnon valdajolense* (Mougeot 1852) Florin 1940.

The material described under *Walchia antecedens* Stur 1875 could well belong to *Lepidodendron* (WHITE 1934 p. 77; FLORIN 1940, p. 327).

Species to be transferred to a new form-genus

In addition to the species listed in the previous paragraphs, there remains a category of species which, as a consequence of the newly established natural concept of *Walchia*, need to be placed within form-genera accommodating leafy shoots without preserved epidermal structure. The greater part of this category is composed by the following species, originally described from the Upper Palaeozoic of Western and Central Europe, North America and North Africa:

W. arnhardtii Florin 1939
W. bertrandii Florin 1939
W. carpentieri Florin 1939
W. dawsonii White 1929
W. gallica Florin 1939

W. geinitzii Florin 1939
W. germanica Florin 1939
W. imbricatula Dawson 1885
W. minuta Florin 1939
W. rigidula Florin 1939
W. schlotheimii Brongniart 1849 ex Renault 1885
W. schneideri Zeiller 1906
W. stephanensis Florin 1939
W. whitei Florin 1939

A formal transfer of these species to the form-genus *Hermitia* Kerp et Clement-Westerhof *nov.gen.* is presented hereafter.

7. THE FORM-GENUS HERMITIA

A considerable number of species, formerly assigned to *Walchia* Sternberg 1825 or *Walchia* Florin 1939 can not be transferred to any available form-genus established to accommodate coniferous foliage preserved as compression/impression fossils without epidermal structure and without sufficient knowledge of correlated ovuliferous organs. HARRIS (1969) suggested that leafy shoots corresponding to *Walchia* should be placed in *Geinitzia* Endlicher. This might be a realistic solution, but in the practice of Jurassic palaeobotanical research *Geinitzia* became subsequently accepted as a form-genus for the classification of foliage with preserved epidermal structure (HARRIS 1979).

Many of the species concerned are adequately described and figured in FLORIN's (1938–1945) monograph. Moreover, some them play an important role in the practice of latest Carboniferous and/or Early Permian biostratigraphy, phytogeography and palaeo-ecology. In order to accommodate these species, the new form-genus *Hermitia* is here proposed.

It should be noted that *Hermitia* should not be applied to the classification of foliage of known walchiaceous affinity. It is likely that, in time, some of the Palaeozoic species may turn out to belong to the Walchiaceae. In that case, however, a species can easily be transferred to a more precisely defined form-genus, such as *Culmitzschia,* or even to a natural genus, such as *Walchia, Ernestiodendron* or *Ortiseia.* Moreover, it should be realized that *Hermitia* is not necessarily an exclusively Palaeozoic form-genus; the name may be equally well applied in the classification of younger material.

Form-genus *Hermitia* Kerp et Clement-Westerhof, *nov.gen.*
Type-species: *Hermitia dawsonii* (White 1929) Kerp et Clement-Westerhof, *nov.comb.*
Lectotype of the type-species: the specimen selected by FLORIN (1939c, p. 226: "Typus"), figured by DAWSON (1866, plate 4, 16), refigured by FLORIN (1939, plate CXXXVII/CXXXVIII, 1–2)
Diagnosis: Pinnately branched lateral shoot systems, consisting of a (leafy) penultimate branch with two lateral series of parallel leafy ultimate branches.

Bifacial leaves spirally disposed.

Status: Form-genus to accommodate coniferous foliage without preserved epidermal structure; uncertain affinity at the family level.

Derivatio nominis: Named after the Hermit Shale, Grand Canyon, Arizona, U.S.A., the formation where the type species of the form-genus was first recognized as an individual taxon (WHITE 1929).

Species recognized: The following new combinations are formally proposed:

Hermitia arnhardtii (Florin 1939) Kerp et Clement-Westerhof, *nov.comb.*
Basionym: *Walchia* (*Ernestiodendron?*) *arnhardtii* Florin 1939c, p. 230–231.
Holotype: The specimen figured by FLORIN (1939c, plate CXLI/CXLII, 3–5).

Hermitia bertrandii (Florin 1939) Kerp et Clement-Westerhof, *nov.comb.*
Basionym: *Walchia* (*Lebachia?*) *bertrandii* Florin 1939c, p. 212.
Holotype: The specimen figured by FLORIN (1939c, plate CXXXV/CXXXVI, 1–3).

Hermitia carpentieri (Florin 1939) Kerp et Clement-Westerhof, *nov. comb.*
Basionym: *Walchia* (*Lebachia?*) *carpentieri* Florin 1939c, p. 223.
Holotype: the specimen figured by CARPENTIER (1930, plate X, 1–2), refigured by FLORIN (1939c, plate CXXXVII/CXXXVIII, 3–5).

Hermitia dawsonii (White 1929) Kerp et Clement-Westerhof, *nov.comb.*
Basionym: *Walchia dawsonii* White 1929, p. 99.
Lectotype: The specimen selected by FLORIN (1939c, p. 226: "Typus"), figured by DAWSON (1866, plate 6, 14), refigured by FLORIN (1939c, plate CXXXVII/CXXXVIII, 1–2.

Hermitia gallica (Florin 1939) Kerp et Clement-Westerhof, *nov.comb.*
Basionym: *Walchia* (*Lebachia?*) *gallica* Florin 1939c, p. 210.
Holotype: The specimen figured by FLORIN (1939c, plate CXXXI/CXXXII, 6–9).

Hermitia geinitzii (Florin 1939) Kerp et Clement-Westerhof, *nov.comb.*
Basionym: *Walchia* (*Lebachia?*) *geinitzii* Florin 1939c, p. 221.
Holotype: the specimen figured by FLORIN (1939c, plate CXXXIII/CXXXIV, 7–9).

Hermitia germanica (Florin 1939) Kerp et Clement-Westerhof, *nov.comb.*
Basionym: *Walchia* (*Ernestiodendron?*) *germanica* Florin 1939c, p. 237.
Holotype: the specimen figured by FLORIN (1939c, plate CXLVII/CXLVIII, 2–3).

Hermitia imbricatula (Dawson 1885) Kerp et Clement-Westerhof, *nov.comb.*
Basionym: *Walchia imbricatula* Dawson in Bain and Dawson 1885, p. 161.
Holotype: the specimen figured by BAIN & DAWSON (1885, fig. 2).

Hermitia minuta (Florin 1939) Kerp et Clement-Westerhof, *nov.comb.*
Basionym: *Walchia* (*Lebachia?*) *minuta* Florin 1939c, p. 222.
Holotype: The specimen figured by CARPENTIER (1930, plate XII, 3) as *Walchia* aff. *hypnoides*, refigured by FLORIN (1939c, plate CXXXV/CXXXVI, 6–10).

Hermitia rigidula (Florin 1939) Kerp et Clement-Westerhof, *nov.comb.*
Basionym: *Walchia* (*Ernestiodendron?*) *rigidula* Florin 1939c, p. 229.
Holotype: The specimen figured by FLORIN (1939c, plate CXLI/CXLII, 1–2).

Hermitia schlotheimii (Brongniart 1849 ex Renault 1885) Kerp et Clement-Westerhof, *nov.comb.*
Basionym: *Walchia schlotheimii* Brongniart 1849, p. 100, validated by RENAULT 1885, p. 86.
Lectotype: The specimen selected and figured by FLORIN (1939c, plate CXXIX/CXXX, 3–5).

Hermitia schneideri (Zeiller 1906) Kerp et Clement-Westerhof, *nov.comb.*
Basionym: *Walchia schneideri* Zeiller 1906, p. 206.
Lectotype: The specimen designated by FLORIN (1939c, p. 216), figured by ZEILLER (1906, plate 48, 5).

Hermitia stephanensis (Florin 1939) Kerp et Clement-Westerhof, *nov.comb.*
Basionym: *Walchia* (*Lebachia?*) *stephanensis* Florin 1939c, p. 214.
Holotype: The specimen figured by FLORIN (1939c, plate CXXXVII/CXXXVII, 10).

Hermitia whitei (Florin 1939) Kerp et Clement-Westerhof, *nov.comb.*
Basionym: *Walchia* (*Lebachia?*) *whitei* Florin 1939c, p. 219.
Holotype: The specimen figured by FLORIN (1939c, plate CXXXIX/CXL, 1–2).

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