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Greguss's morphogenera of homoxylous fossil woods: a taxonomic and nomenclatural review

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Summary

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Greguss proposed several generic names for homoxylous woods in the 1950s and 1960s. Several are, however, not validly published or fall into synonymy. The present review is based on the re-examination of the original material and protologues. The new combination *Agathoxylon parenchymatosum* is proposed as a consequence of such re-examination.

Introduction

After Gothan and Eckhold, Greguss is perhaps the most prolific author of names of morphogenera for fossil woods. Mainly a neoxylologist, he wrote world-famous books (Greguss, 1955a, 1959, 1967) about both soft- and hardwoods. Neoxylology was always his main subject of research (Gulyás, 1984) but in the 1940s, encouraged by Elemér Vadász of the Hungarian Geological Survey, he began to study fossil woods as well.

Despite the unique value of Greguss's work, his publications are not free of nomenclatural errors and mistaken interpretations. Being unacquainted with the traps of fossilisation, it seems that Greguss was fooled several times by preservational structures in his fossil woods.

Greguss's nomenclatural treatment was avowedly etymological. In one of his papers (Greguss, 1955b, Consp.: 100), he explained his approach as follows: "the writer is applying the rule according to which if a Tertiary wood agrees perfectly in its structure with that of a recent genus, ... it is to be identified by the recent generic name with the suffix 'xylon'". In such cases he seldom used the designation "nov. gen.", even when he was the first author to publish a certain name (e.g., Laricioxylon). Because many of the corresponding genera comprised only one species, described as new, their names have to be accepted as validly published under Art. 42 of the Code. Only when a specimen of fossil wood could not be associated with a non-fossil genus did Greguss choose an entirely new name, and then he always used the designation "nov. gen." (e.g., Pseudagathoxylon). Greguss's "etymological" approach makes his work difficult to interpret, and moreover caused him regularly to violate the rules (see, e.g., Agathoxylon). Furthermore, his approach is often difficult to interpret nomenclaturally as, probably because of supererogatory caution, his phraseology regularly includes indications of doubt (see, e.g., Pteridospermaexylon). The repository of his type material is only rarely indicated. Because in many cases

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there is no indication that more than one specimen was studied and described, the corresponding new species names must nevertheless be accepted as validly published under the *Code* (Art. 37.3).

Although commonly used and quoted, Greguss's generic names have never been reviewed. This paper attempts a reappraisal of the generic names he proposed for homoxylous woods. We found that most of them are either not validly published or fall into synonymy.

Material and methods

At his death, Greguss left a huge collection of slides and a rich library, but he did not succeed in arousing great interest in wood anatomy among the students he supervised. While expecting that the Hungarian National Museum in Budapest or a new museum especially founded for that purpose would eventually receive his collections, Greguss used to keep his original material at home, where the facilities for its methodical arrangement were inadequate (L. Hably, pers. com.). Shortly after his death, the slide collection was moved in great haste to the József Attila University, and apparently some material was lost in the process (M. Kedves, pers. comm.). Also, some of the fossil wood material he studied was returned to diverse institutions during his lifetime, where its safeguard was sometimes neglected. Therefore, some holotypes may have been dispersed, or have lost any indication of their type status.

Through careful examination, we were able to trace some of the original material (Philippe & Barbacka, 1997). The screening of slides for details that were illustrated allowed the secure identification of some holotypes. Some slide sets proved to be composite. Collections were studied from the following institutions: the Hungarian Natural History Museum (HNHM), the József Attila University in Szeged (JAS), and the Hungarian Geological Survey collection in Rakóczitelep (GSR).

All generic names proposed by Greguss or attributed to him were reviewed, whether or not they were validly published, and irrespective of expressions of doubt. Apart from names explicitly stated to represent a "nov. gen.", we consider as new any generic name for which Greguss provided some explanation of why he chose it, without indicating that he knew of its prior existence. Our format follows the *Index nominum genericorum* (Farr & al., 1979, 1986), a work that only lists validly published names and thus omits several of those that are considered here. Some invalid names are listed, however, by Andrews (1970), Blazer (1975), or Watt (1982). On the other hand, Blazer missed several valid names that were published with a "nov. sp." (but without "nov. gen." in the heading).

Names that are not validly published are placed between quotation marks. The abbreviation *ING* refers to the *Index nominum genericorum* (Farr & al., 1979, 1986), *Code* stands for the *International code of botanical nomenclature* (Greuter & al., 1994). The term "morphogenus" is used in preference to "form-genus" following a corresponding decision by the St Louis Congress, in 1999.

Results

Agathoxylon Greguss (1952: 160, 169 [non Hartig 1848]). – Type: A. hungaricum (Andr.) Greguss (Simplicioxylon hungaricum Andr.).

This generic name is listed by *ING* but is absent from Andrews (1970), although this work cites Greguss's (1952) paper.

Greguss restudied material previously described as *Simplicioxylon hungaricum* by Andreánszky (1949). He disagreed with the latter's statement that the secondary wood is of an extremely simple structure (hence the name: *Simplicioxylon*) and, having compared the fossil with *Araucaria* and *Agathis*, concluded that it can be considered as identical with present-day species of *Agathis*, so that the name *Agathoxylon* must be applied.

We found no proof that Greguss was aware in 1952 of Hartig's (1848) work, as he might well have been since he spoke German fluently and had frequent contact with researchers of the Natural History Museum in Berlin (H. Süss, pers. comm.). On the other hand, a map in Greguss (1967: 34, map 1) of the non-fossil and fossil distribution of *Agathis*, besides Cretaceous sites on several continents, shows Mesozoic sites in Hungary only, and none is indicated for the Triassic in Germany (from where the type of Hartig's name originates). To conclude, there is no indication that Greguss was adding a species to Hartig's genus, and *Agathoxylon* should be treated as newly proposed by Greguss.

Agathoxylon Greguss is not only illegitimate as a later homonym (*Code*, Art. 53). As *A. hungaricum* includes all syntypes of *Simplicioxylon hungaricum* Andr. (see Philippe, 1995; Philippe & Barbacka, 1997), the type of *Simplicioxylon* Andr., *Agathoxylon* is also a nomenclaturally superfluous substitute for the latter name.

Baieroxylon Greguss (1961: 142). – Type: B. implexum (Gerda Zimm.) Greguss (Dadoxylon implexum Gerda Zimm.).

Several authors dismiss *Baieroxylon*, either as xylologically not well defined (Süss, 1988) or as of doubtful ginkgoalean affinity (Scott & al., 1962). The description of the single original species, *Dadoxylon implexum*, was based on two samples (syntypes: *Code*, Art. 9.4). However, as Zimmermann bases her specific diagnosis on the sample from Grab, emphasising that its preservation is very good (Zimmermann, 1953: 81), and as she has some reservation as to the specific attribution of the Marbächle sample (op. cit.: 84), we here designate the Grab sample (op. cit.: text-fig. 5 & t. 28, f. 1-6) as lectotype, with G. Zimmermann's approval. The thin-sections of both syntypes are kept at the Institut für spezielle Botanik und Mykologie, University of Tübingen (F. Oberwinkler, pers. comm.). Greguss's material of this species is in JAS.

"Callitroxylon" (Greguss, 1967: 55).

This generic name appears in a heading as "?*Callitroxylon* sp.". It is not associated with any species name, and thus is not validly published (*Code*, Art. 37.1 & 10.1). The identity of the material is stated with doubt: "some kind of *Callitris*, though with no absolute certainty". Greguss's slides are in JAS. The wood preservation is too poor for determination.

"Chamaeparioxylon" (Greguss, 1960: 13).

This name is explicitly proposed for a "nov. gen.". It is based on a "sample L" (Greguss, 1960: text-fig. 4; t. 4, f. 13-16). No species name, however, is proposed for this sample "L". *Chamaeparioxylon* is thus not validly published (*Code*, Art. 37.1 & 10.1). Greguss had some doubt as to the fossil's identity, stating that it resembles *Chamaecyparis* more than it does *Sequoia*. It is peculiar that in this par-

ticular case the designation "nov. gen." is used. Greguss (1967) renamed "sample L" as "*Glyptostroboxylon* sp. n° 3", without mentioning his earlier paper. We did not manage to trace the original material.

"Cryptomerioxylon" (Greguss, 1967: 66).

This generic name appears in a heading as "?Cryptomerioxylon sp.", is not associated with any species name, and thus is not validly published (*Code*, Art. 37.1 & 10.1). The sample's identity, again, is given with some doubt: "So we qualify the fossil with some reservation as *Cryptomerioxylon*." The material is in JAS, but is poorly preserved.

"Dacrydioxylon" (Greguss, 1967: 34).

This name is explicitly proposed for a "nov. gen.", and two species are described. However, Greguss did not designate the type of the generic name, which by consequence is not validly published (*Code*, Art. 37.1).

In fact, the two species are given a different treatment, as Greguss clearly associated the new generic name with *Dacrydioxylon estherae* ("n. gen. et n. sp.") rather than *D. tasnadi-kubacskanum* ("n. sp.").

Laricioxylon Greguss (1967: 97). - Type: L. nogradense Greguss.

Perhaps due to a misprint, Watt (1982) registered this genus as "*Laricioxylon* Greguss 1969", but as a matter of fact correctly cited the page and illustration for this generic name, as published in Greguss (1967).

The case of *Laricioxylon* (with its single named species designated as "n. sp.") illustrates that Greguss in 1967 still followed the same policy as in 1955: "Since the fossil examined is a *Larix* by all certainty, we propose to name it as *Laricioxylon*." Even though Greguss evidently was not aware of having created a new generic name, *Laricioxylon* is validly published under Art. 42 of the *Code*, with the descriptive matter validating *L. nogradense* serving as descriptio generico-specifica.

ING did not take up this generic name because in the same work Greguss mentioned a second, different fossil as "*Laricioxylon* sp.", so that the genus was considered not to be monotypic, and Art. 42 inapplicable. By decision of the Sydney Congress in 1981, the *Code* (Art. 42.2) now defines a "monotypic genus" as one for which a single binomial is validly published, even though the author may indicate that other (unnamed) species belong to the genus. The case of *Laricioxylon* has therefore been reconsidered, and the name will be added to the *ING* database.

We did not manage to trace the holotype of *Laricioxylon nogradense*. According to Greguss it should be in the Hungarian National Museum under No. 6140/1. A thorough search of HNHM only revealed a set of three slides, without name or locality indication, numbered 61.401.1; and a second set of unnumbered slides originating from the holotype locality (Nagradszakall). So far, xylological details of the original illustrations could not been matched on any of these slides, which shows that Greguss's indications of the holotype repository are not always reliable (Philippe & Barbacka, 1997).

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Libocedroxylon Greguss (1967: 56 [non Hudajberdyev, 1964]). - Type: L. gaussenii ('gaussenii') Greguss.

There is nothing in Greguss's treatment that would justify the assumption that he knew that this generic name already existed. In his distribution map (Greguss, 1967: map 6, p. 57) he only indicated the present distribution of *Libocedrus*, along with its Tertiary locality in Hungary. We thus consider *Libocedroxylon* Greguss as a new generic name, validly published under Art. 42 of the *Code*. Penny (1947) had already used the name *Libocedroxylon*, but did not, however, validly publish it: the characters in his descriptive key are based on non-fossil wood of *Libocedrus* and related genera, and he had seen no fossil material. Therefore, Art. 34.1(b) of the *Code* applies: "the name is merely proposed in anticipation of the future acceptance of the group concerned, ..."; in other words, in case fossil wood resembling *Libocedrus* might be found.

We did not manage to trace the holotype of *Libocedroxylon* Greguss. It has not therefore been possible, so far, to decide whether this name can be considered as a junior taxonomic synonym of *Libocedroxylon* Hudajberdyev. As in the case of *Laricioxylon*, Greguss's name is not in the published *ING* but will be included in the *ING* database.

"Metasequoioxylon" (Greguss, 1967: 69).

Greguss was quoted by Watt (1982) as the author of Metasequoioxylon. Greguss (1967) described two specimens as "Metasequoioxylon hungaricum" and "?Metasequoioxylon sp.", respectively. In the context of the first name, while making comparisons, Greguss quoted the binomial "Metasequoioxylon germanicum" as "determined by Schönfeld (1955)" [sic]. In fact, no such binomial was used or mentioned anywhere in the cited work: Schönfeld (1955) described only one species, Taxodioxylon metasequoianum. In the same work, Greguss (1967: 77; also in previous works, e.g. Greguss, 1957: 7) correctly referred to Schönfeld's species under the latter name. His treatment of Schönfeld's name here illustrates Greguss's way of nomenclatural thinking: because the wood agrees perfectly with that of a non-fossil genus, the name of that non-fossil genus with the suffix "-xylon" is to be used for it. Apparently he disliked the combination "Metasequoioxylon metasequoianum", so he coined a new epithet, as if there were no priority rules (he probably did not even realise that "Metasequoioxylon germanicum" was anything new). The serious consequence, however, is that the mention of Schönfeld's species implies that Greguss included two named species under "Metasequoioxylon". As no type was indicated nor a separate generic description given, we must conclude that "Metasequoioxylon" was not validly published (Code, Art. 37.1 & 42).

According to Greguss (1967: 18, footnote), the slides for "Metasequoioxylon hungaricum" are in GSR. However, we did not manage to trace them there.

Palaeocallitroxylon Greguss (1970: 270). - Type: P. limburgense Greguss.

This generic name is typified by a specimen previously identified as *Juniperoxylon silesiacum* (W. Prill) Kräusel by Kräusel & Schönfeld (1924). This specimen, however, belongs to a set of samples which Greguss only partly relates to *P. limburgense*. The "long traces of parenchymatous cells" given as diagnostic by Greguss definitely originate from the mining work of insect larvae (Süss, 1979, 1980). *Pa*- *laeocallitroxylon* cannot be distinguished from *Juniperoxylon* Houlbert except on the basis of traumatic structures, and it is thus a junior synonym of the latter.

Platyspiroxylon Greguss (1961: 136). - Type: P. heteroparenchymatosum Greguss.

Platyspiroxylon has a separate generic diagnosis. Greguss (1967: 47) described a second specimen from Kövágoszöllős (Hungary) as conspecific with the type, plus *P. parenchymatosum* Greguss as a second species of his new genus. The latter has been moved to *Protelicoxylon* M. Philippe (1995) on the basis of the original illustration. A first study of the holotype thin-sections (Bx37 in GSR) appeared to confirm this placement (Philippe & Barbacka, 1997). Subsequent scanning electronic microscopy, however, has clearly shown that the observed spirals are not thickenings but unusually regular furrows due to wood decay, as had already been hypothesised by Jefferson (1987). We therefore formally transfer *P. parenchymatosum* (Greguss) M. Philippe, Zijlstra & Barbacka, comb. nov.

Pseudagathoxylon Greguss (1974: 167). - Type: P. eplenyense Greguss.

Although not mentioned in *ING*, this name was validly published (Philippe, 1993). The diagnosis is written in Hungarian, and an English translation is given in the abstract. After investigation of the original slides in GSR we consider *P. eplenyense* as a taxonomic synonym of *Simplicioxylon hungaricum* Andr. (Philippe & Barbacka, 1997). Investigation of new slide (No. MP928, deposited at the Laboratoire de Paléobotanique of Lyon-1 University, France) prepared from the holotype specimen (a fossil "trunk" stored at the Úrkút Manganese Mine offices in Úrkút, Hungary) fully confirms this opinion.

Pseudotaxodioxylon Greguss (1973: 13). - Type: P. jaehnichenii ('jaehnicheni') Greguss.

The diagnosis of this genus is not purely xylological but includes morphological features as well, viz., scars on the outer side of the wood cylinder. *Pseudotaxodioxylon* is thus not strictly a wood morphogenus. In other words, a piece of isolated secondary xylem cannot be safely placed into this genus unless it shows the morphology of the wood cylinder.

The type material of *Pseudotaxodioxylon jaehnichenii* is in the Natural History Museum of the Humboldt University in Berlin under the inventory No. 1986/240 (formerly No. 3276; H. Süss, pers. comm.).

A set of slides in GSR, No. Bx14, bears the hand-written label "*Pseudotaxodi*oxylon eplenyense Greguss nov. gen. nov. spec.". The sample originates from the Eplény manganese mine and is said to be Liassic in age. Neither the hand-specimen nor the slides have any xylological affinity with the secondary xylem described by Greguss (1973) in his protologue for *Pseudotaxodioxylon*, and we have attributed this unpublished material to *Simplicioxylon hungaricum* (Philippe & Barbacka, 1997).

Pteridospermaexylon Greguss (1952: 171). - Type: P. theresiae Greguss.

This name is not included in *ING*, as it was considered a provisional name and thus not validly published. In the protologue, Greguss indeed wrote: "Vorläufig benenne ich es mit den Namen ...". In our view, this sentence reflects Greguss's

mannered style of writing rather than real hesitation in proposing the names. The second author now agrees that the wording expresses the kind of taxonomic doubt that is permitted under Art. 34 of the *Code*, and the name will therefore be included in the *ING* database. In the protologue there are several discrepancies between text and plate captions; in particular, the name in the latter is given as "*Pteridoxylon*".

The specimen upon which the name *Pteridospermaexylon* is based (Greguss, 1952: t. 13, f. 36, 37, 40) was later reused by Greguss himself (1967: t. 15, f. 3 [enlarged], f. 1 [left-side right] and f. 6 [upside down], respectively) to illustrate his "Araucarioxylon sp. (No. 7)", without any mention of synonymy. The original material has been reinvestigated (Philippe & Barbacka, 1997) and confidently attributed to Agathoxylon Hartig. *Pteridospermaexylon* is thus considered a taxonomic synonym of Agathoxylon. The diagnosis of *Pteridospermaexylon* conflicts with its type in describing the genus as manoxylic whereas the sample is definitely pycnoxylic. As far as we know, no other species has been attributed to this genus.

"Sequoioxylon" (Greguss, 1955b: 275, Consp.: 100 [non Sequoioxylon R. E. Torr., 1923]).

Greguss described a new species, *Sequoioxylon turowense*, in such a way that one is led to believe that at the same time he was creating a new generic name: "the writer is applying the rule according to which if a Tertiary wood agrees perfectly in its structure with that of a recent genus, ... it is to be identified by the recent generic name with the suffix 'xylon'" (Greguss, 1955b, Consp.: 100).

As Greguss (1952) had already quoted Kräusel (1949), where Torrey's work was mentioned, one might well assume that he was aware of the existence of *Sequoi*oxylon R. E. Torr. However, in a later distribution map (Greguss, 1967: 93, map 11) he does not indicate a Cretaceous locality that would correspond to Torrey's *Sequoi*oxylon. Even though *Sequoioxylon* Greguss is not designated as "gen. nov.", it is better treated as a new generic name.

Having compared the fossil wood with that of the two non-fossil species of Sequoia, Greguss concluded that it might belong to one of the known fossil Sequoia species, of which the wood was unknown. "Should it be proved, in the time to come, that the examined lignite cannot be referred to any of the so far identified lignites of Sequoia, the writer proposes to call it Sequoioxylon turowense Greguss n. sp." (Greguss, 1955b, Consp.: 100). We conclude that this binomial is a provisional name, not validly published (Code, Art. 34.1(b)). As there is no generic diagnosis and as Art. 42.2 of the Code does not apply (no validly published binomial exists), the generic name is not validly published either.

Torreyoxylon Greguss (1967: 44). – Type: T. boureaui Greguss.

The original material of *Torreyoxylon boureaui* has been investigated (Philippe & Barbacka, 1997). We consider this name as a taxonomic synonym of *Agathoxylon agathiforme* (Kedves) M. Philippe & Barbacka. The generic diagnosis conflicts with the type (e.g., the tracheid radial pitting of the type is typically araucarian and not abietinean at all) and with the original illustration (e.g. Greguss, 1967: t. 32, f. 4; t. 32, f. 5 is touched up).

Widdringtonioxylon Greguss (1967: 52). - Type: W. raskyae Greguss.

In their revision of the fossil woods related to the *Cupressaceae*, Vaudois & Privé (1971) mention *Widdringtonoxylon* J. S. Penny (1947) and *Widdringtonioxylon* Greguss (1967). Because Penny's generic name is not in use, and its concept is rejected as too wide by Vaudois & Privé (1971), we consider Penny's name as unlikely to be confused with Greguss's almost identically spelled name (*Code*, Art. 53.3).

As for several other new generic names in Greguss (1967), there is nothing in that book to indicate that he intended to create a new name. He quoted Kräusel (1949), who did mention Penny's paper, but nevertheless he was probably unaware of that paper, as in his distribution map (Greguss, 1967: 53, map 5) he failed to indicate any Cretaceous locality that might correspond to *Widdringtonoxylon borealis* J. S. Penny or any other species that, according to Penny, belongs to *Widdringtonoxylon*.

ING does not mention *Widdringtonioxylon* Greguss, considering that it was not validly published under Art. 42 of the *Code* (compare *Laricioxylon* and *Libocedroxylon*). Greguss's name will now be included in the *ING* database.

We found some slides in JAS that might belong to the holotype. We cannot, however, be positive about that, and some material may well be in GSR (see Greguss, 1967: 18, footnote).

Discussion

Among the 17 wood morphogenera proposed by Greguss, only *Baieroxylon*, *Laricioxylon*, *Platyspiroxylon*, and *Widdringtonioxylon* can be used without problem to designate tracheidoxyls (i.e. isolated secondary xylem pieces: Creber, 1972). For all other validly published genera, the type is transferred to an earlier genus (in some of these cases, the type conflicts with the associated diagnosis), or there are earlier homonyms. Fortunately, Art. 55.1 of the *Code* makes it clear that species names published under illegitimate generic names can be used as basionyms of legitimate names. Greguss's type specimen repository indications proved again to be unreliable. His taxonomic and nomenclatural approach is sometimes inconsistent.

Greguss's way of naming fossil wood is not unique but is regularly encountered in fossil wood literature, from its early days (c. 1835) up to the 1950s. Several other authors rarely used the designation "nov. gen.". Andreánszky (1952: 20) validly published "*Ginkgoxylon bihariense* n. sp." for fossil wood that agrees with the wood of non-fossil *Ginkgo biloba;* this was the first validly publication of that generic name, and moreover Andreánszky stated explicitly that fossil *Ginkgo* wood was unknown up to that time. Hofmann (1952: 156) validly published "*Sonneratioxylon prambachense* n. sp." for fossil wood that she believed to belong to *Sonneratia,* also the first time that this generic name appeared in print. As long as for such a "n. sp." a generic or specific description or diagnosis (and after 1911, an illustration) is given, the generic name is to be accepted as validly published under Art. 42 (and Art. 38) of the *Code*.

Greguss unquestionably produced a huge and valuable work on fossil wood. His nomenclatural treatment is, however, to be considered with great care, as several of his other indications. A complete revision of his types, mainly those from the Permian and the Tertiary, is badly needed.

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[Ed. Note: Some of the nomenclatural opinions held by the authors are open to controversy. Most would consider *Widdringtonioxylon* and *Widdringtonoxylon*, two legitimate names referring to closely related if not identical taxa, to be confusingly similar. *Pteridospermaexylon* was stated in the protologue to be "provisionally named" by its author, so why would it not be a *nomen provisorium*, invalid under Art. 34.1(b) of the *Code*?]