SOME FOSSIL WOODS FROM THE UPPER TRIASSIC NARIWA AND MINÉ GROUPS, THE INNER ZONE OF SOUTHWEST JAPAN

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Abstract The Mesozoic transitional conifers have been reported and described as a group named the Protopinaceae which show a specific combination of araucarian and abietineous characters. Any living genus of the Coniferales no longer presents the combination. In this paper, the latest knowledge concerning the Protopinaceae, especially the widely known form-genera *Xenoxylon* GOTHAN and *Protocedroxylon* GOTHAN, is commented and some problems with regard to the classification of the Protopinaceae, especially about the treatment of pitting on radial walls of tracheids, are discussed, and furthermore the Triassic woods of the Protopinaceae from Japan are described. All of them have been reported and described from the Upper Triassic Nariwa and Miné Groups distributed in the Inner Zone of Southwest Japan, containing *Protocedroxylon triassicum* YAMAZAKI et TSUNADA, *Araucariopitys japonica* YAMAZAKI et TSUNADA, *Xenoxylon nariwaense* YAMAZAKI et TSUNADA, *X. cf. japonicum* VOGELLEHNER by YAMAZAKI & TSUNADA, *X. sp. A* YAMAZAKI et TSUNADA and *X. sp. B* YAMAZAKI et TSUNADA.

Introduction

The numerous fossil coniferous woods which show "araucarian" characters, *e.g.*, araucarioid pitting on radial walls of tracheids, together with "abietineous" characters, *e.g.*, abietineous pits on tangential and horizontal walls of ray cells, have been widely reported and described from the Mesozoic strata. Such a combination of anatomical characters as araucarian and abietineous ones is not observed in any living genus of the Coniferales, so that those "transitional" fossil woods occupy a very important place in paleobotany also from a phylogenetic point of view.

Once there was a hot controversy concerning the derivation of the Coniferales among the German and American authors: they insisted on the development of the Abietaceae from the Araucariaceae (*e.g.*, GOTHAN, 1910; KRÄUSEL, 1919; ECKHOLD, 1922) or the development of the Araucariaceae from the

Abietaceae (*e.g.*, JEFFREY, 1912; HOLDEN, 1914; TORREY, 1923). Later, some authors, *e.g.*, GRAMBAST (1952) and VOGELLEHNER (1967), criticized this "barren" controversy and showed a different point of view in which the polyphyletic evolution of transitional coniferous woods was considered.

From the records of fossils, it is sure that the Araucariaceae belong to the primitive type in the Coniferales, but the detailed phylogenetic position of the family is still unknown. The key to give a light on the problem exists, first of all, in multiplying the specimens from the Mesozoic strata, especially from the Triassic when the principal differentiation of the Coniferales would begin.

In this paper, the data of fossil coniferous woods, recently described by YAMAZAKI *et al.* (1980) and YAMAZAKI & TSUNADA (1981a) from the main plant-bearing strata of the Triassic distributed in Japan, *i.e.*, the Nariwa and Miné Groups, are compiled and next, the latest knowledge concerning the Mesozoic transitional conifers, especially the form-genera *Xenoxylon* GOTHAN and *Protocedroxylon* GOTHAN, is commented.

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Table 1. The Protopinaceae described from the Triassic in Japan.

Genus, species	Locality			
	Nariwa G.		Miné G.	
	Hinabata F.		Momonoki F.	
			*1	*2
1. <i>Protocedroxylon triassicum</i> Yamazaki et Tsunada 1980	+		+	
2. <i>Araucariopitys japonica</i> Yamazaki et Tsunada 1980	+			
3. <i>Xenoxylon nariwaense</i> Yamazaki et Tsunada 1980	+			
4. <i>X. cf. japonicum</i> Vogellehner 1968	+			
5. <i>X. sp. A</i> Yamazaki et Tsunada 1981				+
6. <i>X. sp. B</i> Yamazaki et Tsunada 1981				+

*1 : the Mugikawa Coal-bearing member, *2 : the Ominé Coal-bearing member.

Triassic Protopinaceae in Japan

In Japan, the Triassic land flora is represented by the *Dictyophyllum* Series (Triassic-early Jurassic), which occurs abundantly in the Middle and Upper Triassic in the Inner Zone of Southwest Japan, especially in the Nariwa and Miné Groups. This flora is characterized by the Dipteridaceae and Marattiaceae, and resembles the Rhaeto-Liassic type flora in Europe and Greenland.

According to YAMAZAKI *et al.* (1980) and YAMAZAKI & TSUNADA (1981a), the Protopinaceae described from the Nariwa and Miné Groups are six species belonging to three genera, as shown in Table 1.

Description

Protocedroxylon GOTHAN

1910 : *Protocedroxylon* GOTHAN, Kun. Svenska Vetensk.-Akad. Handl., N. F., **45**, p. 27.

1913 : *Metacedroxylon* HOLDEN, Ann. Bot., **27**, p. 538.

1916 : *Planoxylon* STOPES, Ann. Bot., **30**, p. 111.

1949 : *Araucariopitys* JEFFREY, Palaeontogr., B, **89**, p. 179, (excl. Type).

1970 : *Embergerixylon* LEMOIGNE, Bull. Soc. Géol. de France, 7, **12**, p. 398, (in part).

Generic type : *P. araucarioides* GOTHAN, l. c., p. 27, Pl. 5, Figs. 3—5, 7—11; Pl. 6, Fig. 1.

Diagnosis : Radial tracheidal pitting araucarioid and/or protopinoid. Horizontal and tangential walls of ray parenchyma cells pitted (abietineous pitting). Resin canals absent in normal wood.

Age and distribution : Triassic to Cretaceous. Ca. 25 species. The Arctic, Europe, Central & East Asia, North America, Africa, Australia.

Remarks : KRÄUSEL (1949) assigned the fossil wood characterized by the above combination of anatomical features to the genus *Araucariopitys* JEFFREY. This genus was described by JEFFREY (1907) as monotypic with the species *Araucariopitys americana* JEFFREY. In effect, the diagnostic characteristics of the secondary wood of the genus coincide with those of *Protocedroxylon* GOTHAN, while the former preserves the pith and primary xylem furthermore. VOGELLEHNER (1967) insisted that the specimen which consisted of secondary wood only should not be identified with *Araucariopitys* JEFFREY, and separated *Protocedroxylon* GOTHAN from *Araucariopitys* JEFFREY.

SHILKINA & KHUDAIBERDYEV (1971) agreed with VOGELLEHNER (1967), but they pointed out that the difference between the two genera lay not only in presence or absence of pith but also in the anatomical features of secondary wood itself.

STOPES (1916) noted that both Gothan's *Cedroxylon transiens* [= *Protocedroxylon transiens* (GOTHAN) ECKHOLD] and *Protocedroxylon araucarioides* should be included in her genus *Planoxylon*, while ECKHOLD (1922) put *Planoxylon* STOPES (in part) under the genus *Protocedroxylon* GOTHAN, giving priority to the latter. VOGELLEHNER (1967) included *Planoxylon* STOPES in *Protocedroxylon* GOTHAN because of difficulty in discerning araucarioid pitting on radial tracheidal walls clearly from protopinoid one, while SHILKINA & KHUDAIBERDYEV (1971) disagreed with VOGELLEHNER (1967) in this point.

LEMOIGNE (1968) established a new genus *Embergerixylon*, and LEMOIGNE (1970) included *Protocedroxylon* GOTHAN (in part) in *Embergerixylon* LEMOIGNE together with his two species of *Dadoxylon* (LEMOIGNE, 1966; LEMOIGNE & DEMARCO, 1967). The generic definition seems to be too rough to distinguish and classify fossil woods.

Protocedroxylon triassicum

YAMAZAKI et TSUNADA

1980 : *Protocedroxylon triassicum* YAMAZAKI et TSUNADA, Mem. Sch. Sci. Engin. Waseda Univ., No. 44, p. 100, Pl. V, Figs. 1—5; Pl. VI, Figs. 1—6; Pl. VII, Figs. 1—7; Text-fig. 4.

1981 : *Protocedroxylon triassicum* YAMAZAKI et TSUNADA, Bull. Sci. Engin. Res. Lab. Waseda Univ., No. 97, p. 2, Pl. I, Figs. 1—2; Pl. II, Figs. 1—5; Pl. III, Figs. 1—7; Pl. IV, Figs. 1—5; Pl. V, Figs. 1—5; Text-fig. 2.

Original material : YAMAZAKI

et al. (1980, l. c.),

YAMAZAKI & TSUNADA
(1981, l. c.)

Diagnosis : Radial tracheidal pitting uni- to biseriate; uniseriate pits compressed by mutual contact, oval in outline, sometimes separate and round, biseriate pits arranged alternately, rarely oppositely. Cross field pits half-bordered in part and podocarpoid-type,

relatively large, 1—3, very rarely up to 4, mostly 1—2 per field. Ray parenchyma uni- or sometimes biseriate in part, (2—) 8—22 (—50) cells high; tangential and horizontal walls of the cells with abietineous pits. Tangential tracheidal pits present, restricted to late wood, small, round in outline, contiguous or separate, arranged in uni- or biseriate & alternately. Wood parenchyma present, not so numerous, scattered throughout the growth rings; horizontal walls thickened and pitted. Tylosis-like structure prominent in the lumina of tracheids. Resin canals absent in normal wood.

Formation : The Hinabata Formation, the Nariwa Group, Okayama Pref.; the Momonoki Formation, the Miné Group, Yamaguchi Pref., Southwest Japan.

Araucariopitys JEFFREY

1907 : *Araucariopitys* JEFFREY, Bot. Gaz., 44, p. 435.

1922 : *Protocedroxylon* GOTHAN, Jb. Preuß. Geol. Landesanst., 42, p. 491, (in part).

1949 : *Araucariopitys* JEFFREY, Palaeontogr., B, 89, p. 179, (Type).

Generic type : *A. americana* JEFFREY, l. c., p. 435, Pl. XXVIII, Figs. 1—5; Pl. XXIX, Figs. 6—11; Pl. XXX, Figs. 12—17.

Diagnosis : Radial tracheidal pitting araucarioid and/or protopinoid. Horizontal and tangential walls of ray parenchyma cells pitted (abietineous pitting). Resin canals present but in traumatic wood. Short shoots present, the axillating leaf deciduous. Pith consists of parenchymatous cells and diaphragms of sclerenchymatous cells.

Age and distribution : Triassic, Cretaceous. 2 species. North America, East Asia (Japan).

Remarks : According to JEFFREY (1907), radial tracheidal pitting of *Araucariopitys americana* is mostly uniseriate, and biseriate & alternate or opposite one may occasionally observed, while generic type of *Protocedroxylon* GOTHAN, i.e., *P. araucarioides*, shows araucarioid-predominating pitting of uni- to triseriate. KRÄUSEL (1949) regarded this difference of radial tracheidal pitting as that of species from the phylogenetic point of view, and set *Protocedroxylon* GOTHAN under *Arau-*

Fig. 1. *Protocedroxylon triassicum* YAMAZAKI et TSUNADA.

Transverse (A), Radial (B) and Tangential (C) sections. wp : wood parenchyma, ap : abietineous pits on the walls of ray cells, pp : podocarpoid-type pit in a cross field, s : septum. (after YAMAZAKI *et al.*, 1980)

cariopitys JEFFREY, giving priority to the latter.

VOGELLEHNER (1968) established a new genus *Yorkoxylon* VOGELLEHNER whose generic diagnosis is as follows; "Mark, Primär- und Sekundärholz strukturbietend erhalten. Mark wenig mächtig, parenchymatish, aus mehr oder minder gleichartigen Zellen aufgebaut, ohne Sklerenchym. Protoxylem endarch, sämtliches Holz somit zentrifugal. Sekundärholz vom Bautyp *Protocedroxylon*." Therefore, fossil woods which show *Protocedroxylon*-type characters in the secondary wood are classified into three genera, *i.e.*, *Araucariopitys* JEFFREY, *Yorkoxylon* VOGELLEHNER and *Protocedroxylon* GOTHAN, and the first two are distinguished each other mainly by whether sclereids are present in the pith or not.

Some authors, *e.g.*, VOGELLEHNER (1965) and LEPEKHINA (1972), place great importance on presence of pith and primary xylem and try to classify the Paleozoic and Mesozoic pycnoxylic gymnospermous woods. This way

of classification is supported by the fact that not only in the Paleozoic pycnoxylic gymnospermous woods but also in the Protopinaceae, the same type of secondary woods can be accompanied by the different types of pith and primary xylem, and *vice versa*. Though a possibility of double nomenclature for one woody plant cannot be denied, these artificial classifications of fossil woods are needed as long as form-genera are treated.

Araucariopitys japonica

YAMAZAKI et TSUNADA

1980 : *Araucariopitys japonica* YAMAZAKI et TSUNADA, Mem. Sch. Sci. Engin. Waseda Univ., No. 44, p. 105, Pl. I, Figs. 2—3; Pl. VIII, Figs. 1—4; Pl. IX, Figs. 1—7; Pl. X, Figs. 1—6; Text-fig. 5.

Original material : YAMAZAKI *et al.* (1980, *l. c.*)

Diagnosis : Radial tracheidal pitting uni- to biseriate; uniseriate pits compressed by mutual contact and oval in outline, sometimes

Fig. 2. *Araucariopitys japonica* YAMAZAKI et TSUNADA.

Radial (A) and Tangential (B) sections. ap: abietineous pits on the walls of ray cells, s: septum. (after YAMAZAKI *et al.*, 1980)

separate and round, biseriate pits arranged alternately, rarely oppositely. Cross field pits half-bordered like, 1—3, usually 2 per field. Ray parenchyma uni- or sometimes biseriate in part, (2—) 10—30 (—45) cells high; tangential and horizontal walls of the cells with abietineous pits. Tangential pits present, restricted to late wood, small, circular in outline, contiguous or separate, arranged in uni- or biseriate & alternately. Wood parenchyma absent. Tylosis-like structure prominent in the lumina of tracheids. Vertical resin canals present but in traumatic wood, horizontal ones absent in both normal and traumatic woods. Short shoots present, but the detailed structure indistinct. Development of primary wood endarch, tracheary elements of protoxylem with spiral thickenings. Pith star-shaped, consists of parenchymatous cells and grouped sclerenchymatous cells.

Formation: The Hinabata Formation, the Nariwa Group, Okayama Pref., Southwest Japan.

Xenoxylon GOTHAN

1905: *Xenoxylon* GOTHAN, Abh. Kön. Preuß. Geol. Landesanst., N. F., 44, p. 38.

Generic type: *X. latiporosum* (CRAMER) GOTHAN, *l. c.*, p. 38.

Diagnosis: Radial tracheidal pitting uni- or biseriate; uniseriate pits strongly flattened by mutual contact, rarely separate and oval or round in outline, biseriate pits arranged alternately or oppositely. Cross field pits large, simple, oval or round in outline; mostly one and occupying almost whole field, rarely two, per field. Horizontal and tangential walls of ray parenchyma cells unpitted. Wood parenchyma sometimes present, resin canals absent.

Age and distribution: Triassic to Cretaceous. Ca. 10 species. The Arctic, Europe, Siberia, Caucasia, Central & East Asia, North America.

Remarks: Since GOTHAN (1905) established the genus *Xenoxylon* and moreover GOTHAN (1910) gave it the detailed generic diagnosis, many authors, *e.g.*, FLICHE (1910), HOLDEN (1913), CHANG (1929), GOTHAN & SZE (1933), SHIMAKURA (1936), OGURA (1944), BOUREAU (1950), HSÜ (1950), OGURA *et al.* (1951), ARNOLD (1952), GRAMBAST (1954), MAEDA (1959), WATARI (1960), VOGELLEHNER

Fig. 3. *Xenoxylon nariwaense* YAMAZAKI et TSUNADA.

Radial (A) and Tangential (B) sections. l: late wood, e: early wood, s: septum. (after YAMAZAKI et al., 1980)

(1965), SHILKINA (1967), NEMATULAEV & KHUDAIBERDYEV (1968), SHILKINA & KHUDAIBERDYEV (1971), KHUDAIBERDYEV et al. (1971), MEDLYN & TIDWELL (1975), YAMAZAKI et al. (1980) and YAMAZAKI & TSUNADA (1981a, b), reported the occurrence of *Xenoxylon*, and it has been proved that *Xenoxylon* has a wide geographical distribution in the Northern Hemisphere.

Xenoxylon canoasense (RAU) KRÄUSEL was the only representative of the genus from the Southern Hemisphere but it was put under the genus *Protopolyporoxylon* VOGELLEHNER by VOGELLEHNER (1968) together with *Xenoxylon jurassicum* (ECKHOLD) KRÄUSEL, while SHILKINA & KHUDAIBERDYEV (1971) insisted that the both might be involved in the genus *Podocarpoxylon* GOTHAN.

Such anatomical characters as tangential pits on late wood tracheids and relatively high rays are generally accepted as the diagnostic ones for the species of *Xenoxylon*, whereas some authors, e.g., SHILKINA & KHUDAIBERDYEV (1971), regard that those characters cannot be used for a specific clas-

sification. We think that a large difference of ray height in cells or presence of tangential tracheidal pits should be treated as the characters indicating the independent species of the genus.

Xenoxylon nariwaense

YAMAZAKI et TSUNADA

1980: *Xenoxylon nariwaense* YAMAZAKI et TSUNADA, Mem. Sch. Sci. Engin. Waseda Univ., No. 44, p. 93, Pl. I, Fig. 1; Pl. II, Figs. 1—2; Pl. III, Figs. 1—6; Text-fig. 2.

Original material: YAMAZAKI et al., (1980, l. c.)

Diagnosis: Radial tracheidal pitting mostly uniseriate and rarely biseriate; uniseriate pits strongly compressed by mutual contact, often in groups of 2—16 ones, pit diameter varies from 15 μ m in late wood to 50 μ m in early wood, biseriate pits arranged alternately or oppositely. Cross field pits large and simple, one, rarely two per field in early wood; lenticular and obliquely elongated, always one per field in late wood. Ray parenchyma uni- or rarely partly or fully biseriate, (1—) 2—6 (—12) cells high; tan-

Fig. 4. *Xenoxylon* cf. *japonicum*
VOGELLEHNER.

Radial (A) and Tangential
(B) sections. s : septum.
(after YAMAZAKI *et al.*, 1980)

gential and horizontal walls of the cells thin and smooth. Tangential tracheidal pits present, restricted to late wood, small, contiguous and slightly flattened, sometimes separate and round, arranged in uni- to triseriate. Tylosis-like structure prominent in the lumina of tracheids. Wood parenchyma and resin canals absent.

Formation: The Hinabata Formation, the Nariwa Group, Okayama Pref., Southwest Japan.

Xenoxylon* cf. *japonicum
VOGELLEHNER

1868 : *Pinites latiporosus* CRAMER, in HEER's Fl. Foss. Arct., 1, p. 176, Pl. XL, Figs. 1—8.

1905 : *Xenoxylon latiporosum* (CRAMER) GOTHAN, Abh. Kön. Preuß. Geol. Landesanst., N. F., 44, p. 38.

1936 : *Xenoxylon latiporosum* (CRAMER) GOTHAN, Sci. Rep. Tōhoku Imp. Univ., Ser. 2 (Geol.), 18, p. 278, Pl. XIV, Figs. 7—8; Pl. XV, Figs. 1—8; Pl. XVI, Figs. 1—3; Pl. XVII, Figs. 6—7; Text-fig. 4.

1968 : *Xenoxylon japonicum* VOGELLEHNER, Palaeontogr., B, 124, p. 145.

1980 : *Xenoxylon* cf. *japonicum* VOGELLEHNER, Mem. Sch. Sci. Engin. Waseda Univ., No. 44, p. 97, Pl. IV, Figs. 1—5; Text-fig. 3.

Original material : SHIMAKURA (1936, *l. c.*), YAMAZAKI *et al.* (1980, *l. c.*)

Diagnostic characteristics: Radial tracheidal pitting mostly uniseriate and rarely biseriate; uniseriate pits contiguous, strongly compressed by mutual contact, pit diameter varies from 15 μ m in late wood to 30—40 μ m in early wood, biseriate pits arranged alternately. Cross field pits large and simple, one, rarely two per field in early wood; lenticular and obliquely elongated, always one per field in late wood. Ray parenchyma uni- or rarely biseriate in part, (1—) 10—20 (—35) cells high; tangential and horizontal walls of the cells thin and smooth. Tangential bordered pits present, restricted to late wood, small, contiguous or separate, arranged in uni- or rarely biseriate. Tylosis-like structure prominent in the lumina of tracheids. Wood parenchyma and resin canals absent.

Formation: The Hinabata Formation, the Nariwa Group, Okayama Pref., South-

west Japan.

Xenoxylon sp. A

YAMAZAKI et TSUNADA

1981 : *Xenoxylon* sp. A YAMAZAKI et TSUNADA, Bull. Sci. Engin. Res. Lab. Waseda Univ., No. 97, p. 6, Pl. VI, Figs. 1—5.

Original material : YAMAZAKI & TSUNADA (1981, *l. c.*)

Diagnostic characteristics : Radial tracheidal pitting uniseriate; pits strongly compressed by mutual contact. Cross field pits large and simple, oval or oblong in outline, one or rarely two per field. Ray parenchyma uniseriate, 1—7 cells high. Tylosis-like structure present in the lumina of tracheids. Wood parenchyma and resin canals absent.

Formation : The Momonoki Formation, the Miné Group, Yamaguchi Pref., Southwest Japan.

Xenoxylon sp. B

YAMAZAKI et TSUNADA

1981 : *Xenoxylon* sp. B YAMAZAKI et TSUNADA, Bull. Sci. Engin. Res. Lab. Waseda Univ., No. 97, p. 7, Pl. VII, Figs. 1—4; Pl. VIII, Figs. 1—4.

Original material : YAMAZAKI & TSUNADA (1981, *l. c.*)

Diagnostic characteristics : Radial tracheidal pitting uniseriate; pits contiguous, strongly compressed by mutual contact. Cross field pits large and simple, one or rarely two per field. Ray parenchyma uniseriate, 1—7 cells high. Tylosis-like structure prominent in the lumina of tracheids. Wood parenchyma and resin canals absent. Tracheary elements of protoxylem have spiral thickenings; metaxylem consists of centrifugal tracheids. Pith consists of parenchymatous cells and grouped sclerenchymatous cells; sclereids with thick and lamellated cell walls.

Formation : The Momonoki Formation, the Miné Group, Yamaguchi Pref., Southwest Japan.

Discussion

1 History of the Protopinaceae

All the form-genera described in the present paper, *i.e.*, *Protocedroxylon* GOTHAN, *Araucariopitys* JEFFREY and *Xenoxylon* GOTHAN, belong to the so-called Protopinaceae proposed

by KRÄUSEL (1917). The Protopinaceae have been reported as a group of Mesozoic coniferous woods which show an admixture of “araucarian” and “abietineous” anatomical characters.

BLANCKENHORN (1886) considered that the fossil woods possessing abietoid pitting on radial tracheidal walls had developed from those possessing araucarioid one on radial tracheidal walls on the basis of the fossil woods obtained from the Triassic of Westfalen. GOTHAN (1907a) described *Cedroxylon transiens* [= *Protocedroxylon transiens* (GOTHAN) ECKHOLD] and *Protopiceoxylon extinctum* GOTHAN from the Lower Cretaceous of Spitzbergen, both showing “abietineous” characters, *e.g.*, abietineous pits on ray cell walls and/or normal resin canals in the secondary wood together with “araucarian” characters, *e.g.*, strictly araucarioid pitting on radial tracheidal walls in part. GOTHAN (1907a) pointed out that the above two genera situated phylogenetically between araucarian-type and abietineous-type woods, and that the latter developed from the former. GOTHAN (1907b) studied more in detail concerning the phylogenetic relations between araucarioid and abietoid tracheidal pitting, and concluded anew that the above two genera represented an intermediate stage of evolution in the Coniferales. KRÄUSEL (1919) recognized that the Protopinaceae were in accord with Gothan’s intermediate-type woods.

On the other hand, JEFFREY (1912) insisted that the Araucariaceae evolved from the Abietaceae on the basis of some living and fossil genera of the Araucariaceae and his two fossil genera of the Araucariopityae, *i.e.*, *Araucariopitys* JEFFREY and *Woodworthia* JEFFREY, from the Cretaceous of New York and the Triassic of Arizona, respectively (JEFFREY, 1907, 1910).

GOTHAN and his followers, *e.g.*, KRÄUSEL and ECKHOLD, interpreted the abietineous characters observed in the Protopinaceae, retaining the “old” araucarian characters yet, as the evidence that the Protopinaceae were the ancestors of the Pinaceae, whereas JEFFREY and his followers, *e.g.*, HOLDEN and TORREY, recognized the araucarian characters in the Protopinaceae, retaining the “old”

Table 2. The generic classification of the Protopinaceae.

Genus	Tracheidal pitting on radial walls	Abietineous pits on ray cell walls	Pits in cross fields	Resin canals	
				normal	traumatic
1. <i>Protopodocarporylon</i> Eckhold 1922	M	-	C podocarpoid or simple	-	-
2. <i>Protophyllocladorylon</i> Kräusel 1939	A(M)	-	C phyllocladoid	-	-
3. <i>Araucariopitys</i> Jeffrey 1907	M	+	C	-	+
4. <i>Planorylon</i> Stopes 1916	A(M)	+	C	-	+
5. <i>Palaeopiceorylon</i> Kräusel 1949	M	+	C	+ V. & H.	+ V. (& H.)
6. <i>Pinorylon</i> Knowlton 1900	M	+	C	+ V. only	+ V. (& H.)
7. <i>Protopinuxylon</i> Eckhold 1922	M	+(-)	C simple and large	+ V. only	+ V. (& H.)
8. <i>Protoeupressinorylon</i> Eckhold 1922	M	-	C partly cupressoid	-	-
9. <i>Protojuniperorylon</i> Eckhold 1922	M	+ juniperoid	C partly cupressoid	-	-
10. <i>Arctorylon</i> Kräusel 1949	M	-	C	-	+ H.: fusiform
11. <i>Brachyorylon</i> Hollick et Jeffrey 1909	A(M)	-	A	-	+
12. <i>Xenorylon</i> Gothan 1905	A xenoxylloid	-	C simple and large	-	-

A : araucarian, M : mixed-type, C : modern coniferous, v : vertical, h : horizontal, () : a rare occurrence. (after YAMAZAKI *et al.*, 1980)

abietineous characters yet, as the evidence that they were the ancestors of the Araucariaceae. In other words, the former considered the evolution from the Araucariaceae to the Pinaceae, whereas the latter considered the evolution from the Pinaceae to the Araucariaceae.

VOGELLEHNER (1967) criticized the "either-or" attitude, or their treatment of the Protopinaceae as "missing links" between the araucarian and abietineous conifers. He remarked the parallel evolution and convergent adaptation of each anatomical character, and considered that the Protopinaceae, characterized by "heterobathmie" of tissues, represented a certain polyphyletic group. According to him, some of the Protopinaceae developed from *Dadoxylon*-type woods and some, by any chance, from the Permocarbiniferous gymnospermous woods, e.g., *Abietopitys* KRÄUSEL and *Phyllocladopitys* KRÄUSEL.

Twelve form-genera of the Protopinaceae settled by KRÄUSEL (1949) are put in order in Table 2 with some of their diagnostic characteristics. In practice, the works by VOGELLEHNER (1967, 1968) and KRÄUSEL (1949) are fundamental for the classification of the Mesozoic transitional coniferous woods, i.e., the Protopinaceae.

2 Protopinoid pitting on radial walls of tracheids

HENES (1959) studied the phylogeny of tracheidal pitting of the Paleozoic woody plants, and indicated the evolution from spiral and/or ring thickenings on tracheidal walls of the Psilophyta to scalariform or bordered pits as observed in *Protopytis*, *Lyginopteris*, *Callixylon* and *Dadoxylon* for example. Protopinoid pitting on radial tracheidal walls represents a transitional stage from araucarioid ("dadoxyl-oid") to abietoid one, but the definition is very difficult as araucarioid pitting itself has the variety. For example, *Araucarioxylon balachonskiense* LEPECHINA from the Middle-Upper Carboniferous of the Kuznetsk Basin, *Dadoxylon keuperianum* (UNGER) ENDLICHER from the Keuper of Franken and some Indian species of *Dadoxylon* from the Permian do not show, in the strict sense, araucarioid pitting on radial tracheidal walls. In effect, it is

very difficult to draw a line of demarcation between araucarioid and protopinoid pitting, and it seems quite natural also from the phylogenetic point of view for most of early Mesozoic coniferous woods and some of late Paleozoic ones to show the mixed-type pitting on radial walls of tracheids.

In spite of the difficulty, it is still required to define the protopinoid pitting, and VOGELLEHNER (1967) expressed it as follows; "Radiale Tracheidenhoftüpfel ein- bis zwei-, selten dreireihig, bei Einreihigkeit sich teilweise berührende, oben und unten abgeplattete, aber auch (nicht nur ausnahmsweise) freie, runde, über eine Tüpfelhöhe voneinander entfernte Tüpfel vorkommend. Bei Zwei- und Dreireihigkeit alternierende und zum Teil auch deutlich opponierte Tüpfel."

BAILEY (1933) insisted that *Protocedroxylon* GOTHAN, *Araucariopitys* JEFFREY, *Meatacupressinoxylon* TORREY, etc., should be included in *Cedroxylon* KRAUS, and that they fell within the range of structural variability of the living some genera of the Abietaceae on the basis of his observation of araucarioid/protopinoid pitting on radial walls of tracheids in some living genera belonging to the Abietaceae, e.g., *Cedrus deodara* (ROXBURGH) LOUDON. KRÄUSEL (1949) built up a counterargument to him, and emphasized that the mixed-type pitting was never so prominent as to be regarded as a general tendency in the living non-araucarian representatives of the Coniferae although araucarioid or mixed-type pitting were certainly observed in the quite restricted part. As GRAMBAST (1960) pointed out, mixed-type, or protopinoid pitting may represent a certain evolutionary stage which all genera of the Coniferales have not necessarily passed through in Mesozoic Era.

When the Mesozoic coniferous woods are anatomically observed, it is necessary to take notice especially of which pitting is more predominant, araucarioid, protopinoid or abietoid one.

3 *Xenoxylon* GOTHAN and *Protocedroxylon* GOTHAN

It is noteworthy that *Xenoxylon* GOTHAN and *Protocedroxylon* GOTHAN have the tendency to coexist in the same horizon, especially in that

of the Nariwa Group from which several tens of petrified woods were collected and the ratio of occurrence between *Xenoxylon* and *Protocedroxylon* was about fifty-fifty (YAMAZAKI *et al.*, 1980). This tendency is also reported in the Mesozoic strata distributed in the Arctic, Central Asia and Caucasia (SHILKINA, 1967; SHILKINA & KHUDAIBERDYEV, 1971). Accordingly, both may have grown under the rather similar circumstance, while the anatomical characters of the two are quite different each other.

The most peculiar character of *Xenoxylon* is the strongly elongated bordered pits on radial tracheidal walls, observed especially in *X. latiporosum* (CRAMER) GOTHAN. This feature shows that the phylogenetic "starting point" of the genus cannot be sought in *Dadoxylon*-type woods occurred abundantly in the late Paleozoic strata. SEWARD (1919) pointed out that *Xenoxylon* resembled the Paleozoic species *Dadoxylon protopityoides* FELIX and the living non-pored woods of the Dicotyledoneae in the form of the pits on the tracheids, and HENES (1959) indicated the development of *X. latiporosum*-type pitting from scalariform one. VOGELLEHNER (1968) noted that the structural similarity with *X. latiporosum* concerning pits on radial tracheidal walls was also recognized in the woods of cycadophytes, *e.g.*, *Sahnioxylon* BOSE *et* SAH, *Paradoxoxylon* KRÄUSEL and *Scalaroxylon* VOGELLEHNER. As the structure of pith of *Xenoxylon* (*X. sp. B* YAMAZAKI *et* TSUNADA) is the conifer-type one (also see OGURA, 1954), the direct affinity of the genus with the above cycadophytes-type forms is not possible to be supposed. *X. latiporosum*-type pitting should be understood as the relatively primitive character to have been retained still in Mesozoic Era. VOGELLEHNER (1967) proposed the evolutionary line of *X. barberi*-type pitting from *X. latiporosum*-type one, but there is a possibility for the genus *Xenoxylon* itself to include the species which had passed through the independent evolutionary line one another.

The cross field pits of *Xenoxylon*, *i.e.*, one or rarely two large simple pits per field, are not so uncommon to the woods occurred in the Mesozoic strata, but the very combination

with xenoxylloid pitting on radial tracheidal walls is characteristic. This type of cross field pits are also observed in some other fossil genera, *e.g.*, *Circoporoxylon* KRÄUSEL or *Protocircoporoxylon* VOGELLEHNER, and in some living genera, *e.g.*, *Dacridium* of the Podocarpaceae and *Sciadopitys* of the Sciadopityaceae.

NATHORST (1897) suggested a possible relationship between *Cedroxylon pauciporosum* (CRAMER) SCHENK [= *Xenoxylon latiporosum* (CRAMER) GOTHAN] and araucarian *Elatides* HEER (GOTHAN & WEYLAND, 1964), while some authors, *e.g.*, OGURA *et al.* (1951), ARNOLD (1952) and WATARI (1960), reported that *Podozamites* BRAUN was abundant where *Xenoxylon* occurred. MEDLYN & TIDWELL (1975) situated *Xenoxylon* in the Podocarpaceae, while some Russian authors, *e.g.*, NEMATULAEV & KHUDAIBERDYEV (1968), placed it in the Sciadopityaceae. Thus, the systematic position of *Xenoxylon* is still uncertain, and the following interpretation by ARNOLD (1952) seems to be the most appropriate one at the present time; "*Xenoxylon* is an example of a fossil conifer that cannot be placed with positiveness in any modern family, and an arbitrary disposition of such woods only causes confusion."

The species of *Xenoxylon* ever described from the Mesozoic strata are shown in Table 3 with some of their diagnostic characteristics. The species of *Xenoxylon* are divided into two large groups by the arrangement of pits on radial walls of tracheids; one is *X. latiporosum*-type group and the other is *X. barberi*-type one. The latter group has a possibility to include some of other "cricoporoid-type" woods, *e.g.*, *Protocircoporoxylon* VOGELLEHNER.

Xenoxylon morrisonense MEDLYN *et* TIDWELL shows abietineous pits on ray cell walls, which in the case of living conifers are unquestionably of taxonomic importance. Accordingly, this specimen is more suitable to be put under the different genus, *e.g.*, *Protocedroxylon* GOTHAN. Both wood parenchyma and crassulae described in *Xenoxylon hopeiense* CHANG are not so clearly ascertained characters, and in that case, this species becomes to have the close affinity with *X. barberi* (SEWARD) KRÄUSEL, but the former is still distinguished

Table 3. The species of *Xenoxylon* GOTHAN described from the Mesozoic strata.

Species	Geologic age	Radial tracheidal pitting	Cross field pits		Ray parenchyma		Tangential tracheidal pits	Wood parenchyma
			number	form	width in cells	height in cells		
1. <i>X. conchyliform</i> Fliche 1910	T Muschelkalk	L (B)	1	round to elliptical	1	(1-)5-10(-12)	-	-
2. <i>X. parvipunctatum</i> Vogellehner 1965	T Keuper	B grouped	1	ditto	1	(1-)2-8(-11)	-	-
3. <i>X. narivaense</i> Yamazaki et Tsunada 1980	T Norian	B grouped	1(2)	ditto	1(2)	(1-)2-6(-12)	+	1-3 rows
4. <i>X. cf. japonicum</i> Vogellehner Yamazaki et Tsunada 1980	T Norian	L	1(2)	ditto	1(2)	(1-)10-20(-35)	+	1-2 rows
5. <i>X. latiporosum</i> (Cramer) Gothan 1905	T-C	L	1(2)	ditto	1(2)	1-15-20	-	-
6. <i>X. japonicum</i> Vogellehner 1968	T-C	L	1(2)	ditto	1(2)	1-40(-50-)	+	1-2 rows
7. <i>X. barberi</i> (Seward) Kräusel 1949	J-C	B	1(2)	ditto	1(2)	1-10(-20)	-	-
8. <i>X. hopeiense</i> Chang 1929	J Upper	B	1(2)	ditto	1(2)	(1-)10-20(-65)	+	+
9. <i>X. ellipticum</i> Schultze-Motel 1960	J Lias	B	1(2)	elliptical & inclined in part	1(2)	2-34	-	-
10. <i>X. suljuctense</i> Shilkina et Chudajberdyev 1971	J	L (2 rows)	1	round to elliptical	1	(1-)5-6(-10)	+	-
11. <i>X. cf. suljuctense</i> Shilkina et Chudajb. Yamazaki et Tsunada 1981	J Lower	L (2 rows)	1(2)	ditto	1(2)	(1-)3-8(-20)	+	1-3 rows
12. <i>X. pseudo-ellipticum</i> Yamazaki et Tsunada 1981	J Lower	B	1(2)	elliptical & inclined in part	1(2)	(1-)3-12(-20)	+	-
13. <i>X. morrisonense</i> Medlyn et Tidwell 1975	J Upper	B	1-2	podocarpoid in part	1(2)	(2-)10-15(-35)	-	+

T : Triassic, J : Jurassic, C : Cretaceous, L : *X. latiporosum*-type, B : *X. barberi*-type, () : a rare occurrence. (after YAMAZAKI & TSUNADA, 1981b)

Table 4. The species of *Protocedroxylon* GOTHAN described from the Triassic and Jurassic.

Species	Geologic age	Pit's rows on radial tracheidal walls	Cross field pits		Ray parenchyma		Wood parenchyma	Tangential tracheidal pits
			number	form	width in cells	height in cells		
1. <i>P. brianense</i> (Sahni) Vogellehner 1967	T	1	frequently 3-4	bordered	1	up to 15	-	+
2. <i>P. dibneri</i> (Shilkina) Shilkina et Chudajb. 1971	T Upper	1-3	2-3	simple	1(2)	1-19	+	+
3. <i>P. gregussi</i> (Shilkina) Shilkina et Chudajb. 1971	T Upper	1-2	1-2(-4)	cupressoid	1(2)	(1-)5-12(-19)	+	+
4. <i>P. triassicum</i> Yamazaki et Tsunada 1980	T Upper	1-2	1-2(-4)	podocarpoid	1(2)	(2-)8-22(-40)	+	+
5. <i>P. araucarioides</i> Gothan 1910	J	1-2	1-3	simple	1	1-10 ?	-	+
6. <i>P. latiporosum</i> (Holden) Eckhold 1922	J	1: xenoxylloid, 2: opposite	1-2 ?	? small	1 ?	low	-	?
7. <i>P. scoticum</i> (Holden) Seward 1919	J Malm	1	1(2)	bordered	1-2	(2-)8-12(-20)	-	-
8. <i>P. haraulachicum</i> (Shilkina) Vogellehner 1968	J lower	1-2	2-5	simple	1	(1-)2-4(-8)	-	-
9. <i>P. lindicianum</i> (Khan) Vogellehner 1968	J Lias	1(2)	1-3	simple	1	4-8-15	-	-
10. <i>P. bebenhusanum</i> (Khan) Vogellehner 1968	J Lias	1(2)	1-3	simple	1(2)	(1-)4-5(-10)	+	-
11. <i>P. liassicum</i> (Khan) Vogellehner 1968	J Lias	1(2)	1-3	simple	1	2-12	+	+
12. <i>P. lacunosum</i> (Salard) nov. comb.	T ?	1-2	2-8	simple	1	(1-)2-7(-30)	-	+
13. <i>P. neocaledonicum</i> (Salard) nov. comb.	T ?	1(2)	2-6	simple	1-3(-4)	1-20-35	(+)	?

T: Triassic, J: Jurassic, () : a rare occurrence.

from the latter by the presence of tangential tracheidal pits although they are observed only in the radial section. Both *Xenoxylon jurassicum* (ECKHOLD) KRÄUSEL and *X. canoasense* (RAU) KRÄUSEL are put under *Protopolyxylon* VOGELLEHNER on the basis of their characteristic pits on lateral walls of ray cells (VOGELLEHNER, 1968).

It is noteworthy that the species from Central Asia (10), North China (8) and the Inner Zone of Southwest Japan (3, 4, 11, 12) have pits on tangential walls of late wood tracheids instead of lacking in them in European and the Arctic species (cf. Table 3). This may reflect the difference of paleofloristic areas where they had grown at that time.

In Table 4, the species of *Protocedroxylon* GOTHAN ever described from the Triassic and Jurassic are put in order. The species of *Protocedroxylon* are also divided into two large groups by presence or absence of wood parenchyma. TORREY (1923) proposed a new genus *Metacupressinoxylon* TORREY, characterized by scattered wood parenchyma and *Protocedroxylon*-type secondary wood, for *Paracupressinoxylon cedroides* HOLDEN described from the Jurassic of Yorkshire, whereas ECKHOLD (1922) regarded it as one of the species belonging to *Protocedroxylon* GOTHAN. KRÄUSEL (1949) did not adopt the generic name *Metacupressinoxylon* and set Holden's species under the genus *Araucariopitys* JEFFREY, while SEWARD (1919) previously noted that *Paracupressinoxylon cedroides* closely allied to the Abietaceae though abietineous pits on ray cell walls were also observed in some living *Juniperus* or the extinct genus *Protocedroxylon* GOTHAN.

Whether wood parenchyma is present or not is an important point for the specific classification of the genus *Protocedroxylon*, so that the cells should be carefully distinguished from other elements, e.g., strand tracheids or tracheids with tyloses. For example, *Protocedroxylon triassicum* has many septa of tyloses origin in the lumina of tracheids, which are rarely arranged at regular intervals like the arrangement of end walls of wood parenchyma cells or those of strand tracheids. The pit-pairs between the cells of wood parenchyma and tracheids are half-bordered, whereas tra-

cheids with tyloses or strand tracheids show the strictly same bordered pits as normal tracheids. Furthermore, the pits between axial wood parenchyma cells and transverse ray parenchyma ones in radial section can be easily distinguished from the true cross field pits, i.e., those between ray parenchyma cells and tracheids or strand tracheids, and the difference of diameter of those cells is another point to be distinguished each other.

Scattered wood parenchyma is surely one of the important diagnostic characters of most genera belonging to the Cupressaceae, whereas abietineous pits on ray cell walls are not common to them. Furthermore, wood parenchyma is observed rather irrespectively of the families of the Coniferales. Therefore, we think that the combination of araucarioid/protopinoid pitting on radial walls of tracheids and abietineous pits on ray cell walls, for which *Protocedroxylon* was proposed, should be emphasized first of all, and that wood parenchyma should be used in the specific classification. In that case, some species of *Metacupressinoxylon* which show abietoid pitting on radial walls of tracheids become to be a problem systematically. The genus *Metacupressinoxylon* TORREY em. NISHIDA will be discussed with reference to the genus *Juniperoxylon* HOULBERT em. KRÄUSEL.

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西南日本内帯に分布する上部三畳系成羽・美祢両層群産材化石

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(要 旨)

中生界産出の材化石の多くは、いわゆる *Protopinaceae* と呼ばれる1つの大きなグループに属し、それらは放射組織細胞壁に見られるモミ型壁孔や二次木部内に見られる樹脂道というようなアラウカリア的でない解剖学的特徴とともに、アラウカリア型もしくは移行型の仮道管放射壁壁孔を持つことによって特徴づけられる。このような組織構造の組み合わせは現生属にはもはや認められないので、球果目の系統を考察するうえにも *Protopinaceae* の研究は重要である。本論文では、今までに記載された日本の三畳系産出の *Protopinaceae* をまとめた。それらは全て、西南日本内帯に分布する上部

三畳系成羽、美祢両層群から産したものである。また、*Protopinaceae* の重要な構成員である *Xenoxylon* 属と *Protocedroxylon* 属についての最新の知見を、表にして示した。本論文で記載した材化石は、以下の通りである。*Protocedroxylon triassicum* YAMAZAKI et TSUNADA, *Araucariopitys japonica* YAMAZAKI et TSUNADA, *Xenoxylon nariwaense* YAMAZAKI et TSUNADA, *X. cf. japonicum* VOGELLEHNER by YAMAZAKI & TSUNADA, *X. sp. A* YAMAZAKI et TSUNADA, *X. sp. B* YAMAZAKI et TSUNADA.