

EQUISETITES FROM THE EARLY PERMIAN OF NORTH-CENTRAL TEXASWILLIAM A. DIMICHELE¹, JOHANNA H.A. VAN KONIJNENBURG-VAN CITTERT^{2,3}, CYNTHIA V. LOOY¹,
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Abstract—*Equisetites* is a genus of fossil plants allied with, if not identical to, modern *Equisetum*, which is the only extant genus of the ancient lineage Sphenopsida. This class-level group of lower vascular plants is characterized by whorled vegetative and reproductive appendages, distinctive nodal and internodal morphologies, and unique “sporangiophores,” specialized reproductive organs of uncertain homology on which the sporangia are borne. Described, heretofore, from rocks ranging in age from Middle Permian through Pleistocene, *Equisetites* is primarily a genus of the post-Paleozoic. Fossils similar to isolated leaf sheaths of this genus have been found in a single deposit of Early Permian age in north-central Texas. Five specimens are known, each composed of up to 10 basally fused and apically free leaves that are straight-sided but taper sharply to an acute tip. Leaves have a single midvein. Attribution to *Equisetites* must remain tentative in the absence of any other organs of the plant, including stems. However, it is common in some species of extant *Equisetum* for leaf sheaths to fall away from the main stem as they die and dry, so such isolation is not entirely unexpected.

INTRODUCTION

Equisetites is a genus of fossil plants with similar gross morphology and anatomy to modern *Equisetum*. In addition to the general sphenopsid characteristics of whorled appendages and sporangiophores, these genera are characterized by small leaves fused into a leaf sheath, and strobili that lack bracts. The fossils are placed in a separate genus primarily because of their state of preservation, not because they share some distinguishable derived characteristics that unite them as a group while at the same time separating them from *Equisetum*. *Equisetites* is reported to have a range of mid-Permian through the Pleistocene (Stewart and Rothwell, 1993, p. 207). Most of the reported Paleozoic occurrences have proven to be cases of mistaken identity, however, a consequence of the vagaries of natural processes that alter the appearances of living organs and continue to modify them during the process of fossilization. For example, *E. contractus* Göppert (1864) is likely a calamitean stem (Schimper, 1869); *E. lingulatus* Germar (1845) (= *E. priscus* Geinitz) is possibly an *Annularia*, although at least one of the illustrations appears to show an *Equisetites*-like leaf sheath (Germar, 1845, plate X, fig. 5); *E. rugosus* Schimper (1869) is very large with connected leaves and appears to be a *Phyllothecca*; *E. zaeiformis* (Schlotheim) Andrae (Schlotheim, 1820) has very broad leaves with large teeth and may be a torn *Cordaites*.

Possible candidates for Paleozoic occurrences include *Equisetites vaujolyi* Zeiller (1895) from the Permian of France, which has large leaves, up to 6 cm long and 6 mm wide, with a single vein per leaf (Doubinger, 1956). However, this species is quite different in appearance from better known Mesozoic forms. The bractless *Equisetites hemingwayi* is in appearance very much like strobili of modern *Equisetum* and, thus, could belong to this lineage. Based on specimens in the British Museum (Kidston, 1901), strobili were apparently sessile and borne at the nodes on stems that are very *Equisetum*-like in appearance. This species was described from what is now referred to as the Middle Pennsylvanian, or Westphalian, from the Yorkshire coal measures in Great Britain, which would make this most certainly the earliest, if uncorroborated, occurrence of this branch of the Sphenopsid family tree. Seward (1898) who previously had examined Kidston’s specimen determined that the strobili, although *Equisetum*-like in construction, are lateral instead of terminally attached, and stems show no evidence of leaf sheaths; Seward thought the leaves to be *Asterophyllites*-like, putting the generic affinities of this species in question, as well.

Specimens very similar to *Equisetites* leaf sheaths have been

found in rocks of Early Permian age from north-central Texas. The specimens are not found in attachment to stems or in association with identifiably sphenopsid reproductive organs. Consequently, the identification remains tentative. Nonetheless, the Early Permian precocious occurrence of plants typical of the Late Permian and Mesozoic has been reported elsewhere in north-central Texas for cycad and conifer taxa (DiMichele et al., 2001a), and scraps of conifers are known to occur millions of years before the appearance of good specimens within a macrofloral context (Lyons and Darrah, 1989). Such occurrences suggest the existence of many vascular-plant evolutionary lineages well before their appearance in the fossil record.

GEOLOGIC SETTING

The *Equisetites* fossils are part of a larger plant collection made in 1993 and 1994 under USNM collection numbers 40050, 40053 and 40648 and informally named “Harmel Quarry.” The exposure is in the Lake Kemp 7 ½’ Quadrangle, in a small road metal quarry operated on a private ranch north of the town of Seymour, Baylor County, Texas. The plant fossils occur in a sandstone channel, in the lower two meters of the Clear Fork Formation. The actual contact with the underlying Lueders Formation is obscured by recent soil cover. These rocks are Leonardian (Early Permian) in age (Nelson et al., 2001).

The 2-m thick, fine-grained, gray sandstone is exposed for approximately 100 m along strike. The sandstone consists of a series of scours filled with fining upward sand and clay interbeds. The laminations are frequently contorted within any individual scour-and-fill sequence. At a larger scale, the deposit consists of a series of larger scale “cut and fill” sandbodies, probably representing channel bars. These deposits appear to represent a complex of actively migrating bars in a sinuous channel that experienced significant waning and waxing of flow.

FLORA

Plant fossils from this deposit are sporadic in occurrence, varying from large stems, branches and leaves, to finely comminuted plant material. The best preserved specimens occurred within the fill of one of the small scale scour troughs. For the most part, the plants occur in the sandstone itself, not in the clay interbeds. Thus, from actualistic models, such as that of Scheihing and Pfefferkorn (1984) or Burnham (1989), it is likely that the flora was growing close to the channel margins. The flora associated with the *Equisetites* specimens is moder-

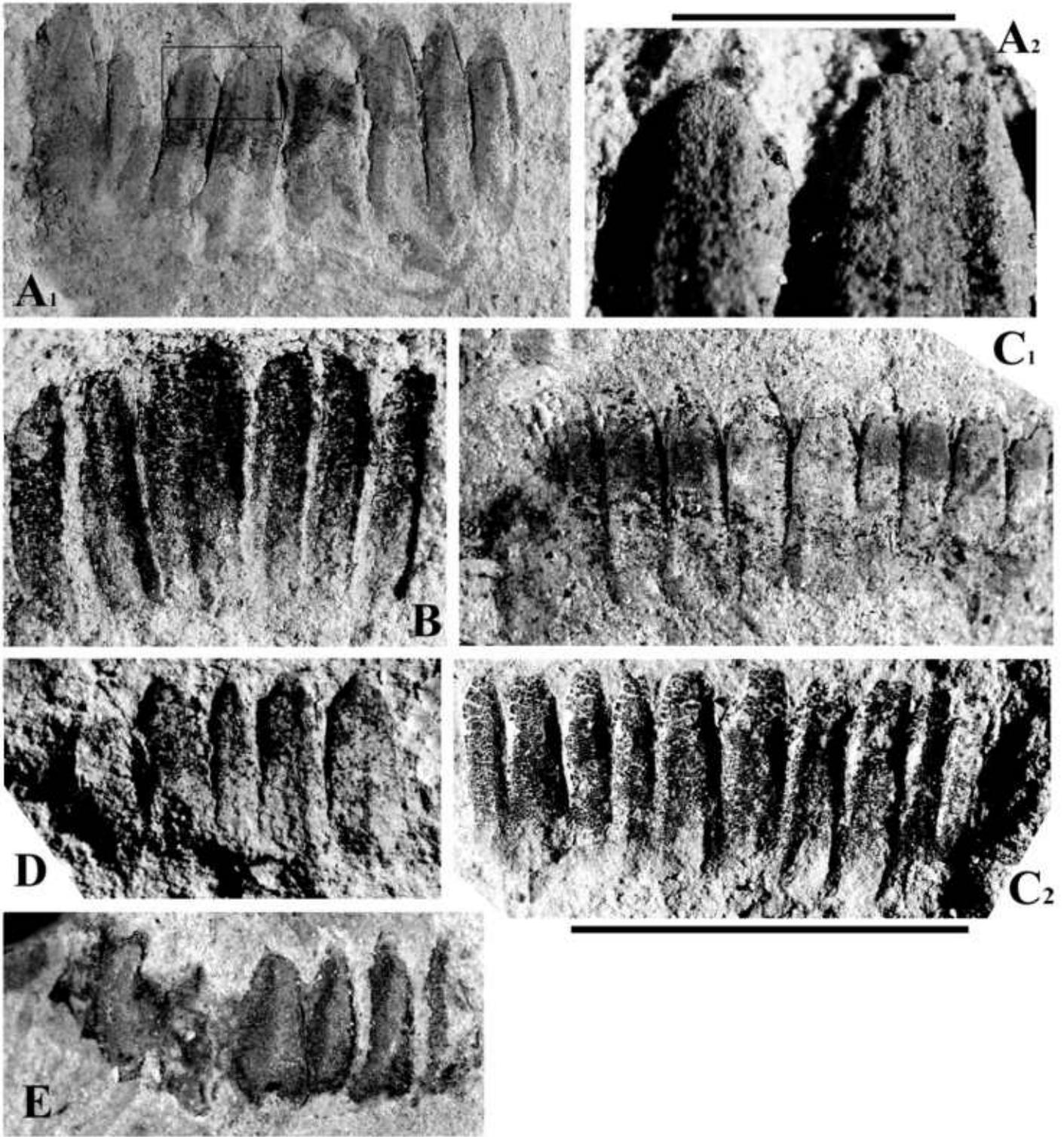


FIGURE 1. *Equisetites* sp., leaf sheaths. A) USNM 528507: A₁, X 7. A₂, Enlargement of specimen figured in A₁ to show leaf tips and groove in leaves representing the median veins, scale bar = 0.2 cm. B) USNM 528508. C) USNM 528505, C₁ Part. C₂ Counterpart. D) USNM 528504. E) USNM 528506, scale bar = 0.5 cm. Scale bar for A₁, B, C₁ and C₂, and D below C₂ = 1 cm.

ately diverse compared to other floras from the Clear Fork Group. It consists of the peltasperms *Comia* sp., *Autunia* cf. *A. conferta*, *Peltaspermum* sp., and *Cathaysiopteris yochelsonii*, the conifers cf. *Culmitzschia speciosa* and *Walchia hypnoides*, cordaitalean leaves, the pteridosperm *Neuropteris* sp., the indeterminate seed plant *Taeniopteris*

sp., rare and questionable calamitean stems, marattialean tree foliage *Pecopteris* sp., and small fern or pteridosperm foliage of indeterminate affinities.

The dominant element of the flora, based on the number of specimen occurrences, is *Comia*. *Autunia* cf. *A. conferta* also is quite com-

mon. *Culmitzschia speciosa* and *Taeniopteris* sp. are present but not notably abundant. All other elements are rare, occurring as just a few or single specimens.

EQUISETITES FOSSILS

Five specimens were collected that can be attributed to cf. *Equisetites*. All consist of straight-sided leaves with pointed, acutely tapered apices. Free for almost their entire length, the leaves are fused at the base into a sheath. They appear to have been part of a leaf whorl, all inserting on the stem at the same level. Although somewhat obscure in most specimens, where visible, the leaves appear to have a single, median vein that runs from the base of the leaf all the way to the apex (Figure A₂).

Most of the leaves are approximately 0.5 cm in length, with a maximum of 0.75 cm (USNM 528508 Figure 1B) and a minimum of 0.25 cm (USNM 528506 Figure 1E). The maximum number of leaves preserved in any one sheath is 10 (USNM 528505 Figure 1C₁ and C₂). Variations in length within a single sheath are most likely preservational, given that such variations are minor.

The base of each of the leaf sheaths is obscure. It appears that the sheaths were torn from their attachment points leaving an irregular lower margin (note especially Figure 1C₁ and C₂).

In the absence of corroborative evidence, such as stems with attached leaf whorls or equisetalean reproductive structures, it seems best not to describe these specimens as representative of new species. Rather, their presence is noted in order to document the occurrence of this evolutionary lineage of sphenopsids at this time and place.

DISCUSSION

The Sphenopsida consist of three main evolutionary lineages, the Calamitales, the Equisetales, and the Sphenophyllales. The Calamitales and Equisetales are so similar in form that they often are treated as synonymous and lumped together into the Equisetales. These two groups differ in that the wholly extinct calamites were woody, had free leaves that were supposedly photosynthetically active throughout their lifespans, and bracts or leaves subtending the sporangiophores in the strobili. In contrast, the leaves of the Equisetales are scale-like, are not photosynthetically significant throughout most of their lives, and are fused into sheaths at the nodes. Equisetalean strobili are disposed terminally, either on the main axis or on small side branches (Kelber and van Konijnenburg-van Cittert, 1998), and lack bracts subtending the sporangiophores. Equisetalean stems are non-woody. In both groups the leaves are single veined, sporangiophores are stalked peltate structures, and stems are upright in growth architecture. The sphenophylls are a markedly different group with broad, multiveined leaves (see Batenburg, 1981), complexly branched sporangiophores, stems with trailing habit, and distinctive triangular shaped steles with limited wood.

The calamiteans and sphenophylls were common elements in Carboniferous tropical landscapes. They are well known from coal-ball and adpression preservation. Derivative forms were common in both north and south temperate floras as well (e.g., Rayner, 1992, Naugolnykh, 2002). Thus, these lineages were clearly established early in the vascular plant radiation that took place during the later Devonian and earliest Carboniferous (DiMichele et al., 2001b). Documented members of the Equisetales, on the other hand, are not known till much later and have been presumed to be derived from the calamites by the loss of certain developmental capabilities (e.g., wood production, leaf elaboration, bracts within the strobili). Naugolnykh (2004) noted developmental irregularities in the position and morphology of strobili in

modern *Equisetum*, which resulted in plants very similar to Permian and Triassic members of the Angaran sphenopsid family Tchernoviaceae, which have leaf sheaths “virtually identical to those of *Equisetum*” (p. 340), thus potentially identifying these late Permian plants as clear members of the equisetalean clade.

The appearance of the equisetalean remains described here in association with xeric floras opens the possibility that the early evolution of this latter group took place in “extrabasinal” areas (sensu Pfefferkorn, 1980), remote from basinal lowlands, only moving into the lowlands as regional climates became seasonally dry. Given the morphological and anatomical differences between the Calamitales and the Equisetales, it should be considered that all three of the sphenopsid lineages are quite ancient, of deep Paleozoic origin. Although all evidence strongly supports a sister group relationship between the calamiteans and the equisetaleans s.s., the evolution of equisetalean-like plants may have occurred in areas where detection of the earliest evolutionary stages of would not have been detectable given the preservational biases of the terrestrial fossil record.

Parallel precocious Early Permian or later Carboniferous appearances of a number of groups previously known only from Late Permian or Mesozoic rocks (Kerp, 1983; DiMichele et al., 2001a), and the early appearance of groups as scrappy fossils prior to their “full blown” appearances (e.g., conifers, Lyons and Darrah, 1989) assuredly indicate that a great deal of evolution was happening outside the window of basinal wetland depositional systems, appearing initially in these lowlands only under unusual circumstances. In the case of early conifers, it seems that bits of material arrived by long-distance transport from adjacent upland areas. In the case of precocious Mesozoic and Late Permian plants, it seems that whole assemblages were brought into lowland basins by short-term climatic anomalies. This pattern seems to apply, in detail, to the sphenopsids as well, indicated by sporadic findings such as that of the typically Mesozoic *Neocalamites* in the Late Permian of Japan (Kon’no, 1973).

The lycopsids offer a parallel to this sphenopsid pattern. It was long thought that the Isoetales evolved from the lepidodendrids, often narrowed down to the Sigillariales, via a “reduction series” in which the overall size of the plant, its shoot and root systems, were progressively diminished. This “trend” supposedly turned a Paleozoic tree ancestor with a stigmarian rooting system into a Mesozoic descendent of small monopole habit with a reduced cormose root base. Ample evidence now shows that monopoles with cormose bases occurred in the Late Devonian (e.g. Chitaley and Pigg, 1996). In other words, the rhizomorphic (stigmarian) lycopsids (sensu DiMichele and Bateman, 1996) and the cormose based Isoetales are probably equally ancient groups, or perhaps the rhizomorphic forms are even the descendents of the cormose-based forms, a reversal of previous thinking.

Although speculative, we suggest that fortuitous collecting may one day turn up a very early equisetalean and prove that this group also underwent its basic radiation rapidly and not through a long-delayed or extended evolutionary transition.

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REFERENCES

Batenburg, L.H., 1981, Vegetative anatomy and ecology of *Sphenophyllum zwickaviense*, *S. emarginatum*, and other “compression species” of

Sphenophyllum compared: *Review of Paleobotany and Palynology*, v. 32, p. 275-313.

- Burnham, R.J., 1989, Relationships between standing vegetation and leaf litter in a paratropical forest: implications for paleobotany: *Review of Palaeobotany and Palynology*, v. 58, p. 5-32.
- Chitaley, S. and Pigg, K.B., 1996, *Clevelandodendron ohioensis*, gen. et sp. nov., a slender upright lycopsid from the Late Devonian Cleveland Shale of Ohio: *American Journal of Botany*, v. 83, p. 781-789.
- DiMichele, W.A. and Bateman, R.M., 1996, The rhizomorphic lycopsids: a case-study in paleobotanical classification: *Systematic Botany*, v. 21, p. 535-552.
- DiMichele, W.A., Mamay, S.H., Chaney, D.S., Hook, R.W., and Nelson, W.J., 2001a, An Early Permian flora with Late Permian and Mesozoic affinities from North-Central Texas: *Journal of Paleontology*, v. 75, p. 449-460.
- DiMichele, W.A., Pfefferkorn, H.W., and Gastaldo, R.A., 2001b, Response of Late Carboniferous and Early Permian Plant communities to climate change: *Annual Review of Earth and Planetary Sciences*, v. 29, p. 461-487.
- Doubinger, J., 1956, Contribution à l'étude des flores autuno-stéphaniennes: *Mémoires de la Société Géologique de France*, v. 35(1/2), *Mémoire* 75, p. 1-180.
- Germar, E.F., 1845, *Die Versteinerungen des Steinkohlengebirges von Wettin und Löbejün im Saalkreise*. Vol. 2, Halle: T.A. Schwetschke und Sohn. 28 pp.
- Göppert, H.R., 1864, Die fossile Flora der Permischen Formation: *Palaeontographica*, v. 12, p. 1-224.
- Kelber, K.-P. and van Konijnenburg-van Cittert, J.H.A., 1998, *Equisetites arenaceus* from the Upper Triassic of Germany with evidence for reproductive strategies: *Review of Palaeobotany and Palynology*, v. 100, p. 1-26.
- Kerp, J. H. F., 1983, Aspects of Permian Paleobotany and Palynology, I, *Sobernheimia jonkeri* nov. gen., nov. sp., a new fossil plant of cycadalean affinity from the Waderner Gruppe of Sobernheim: *Review of Palaeobotany and Palynology*, v. 38, p. 173-183.
- Kidston, R., 1901, The flora of the Carboniferous period: *Proceedings of the Yorkshire Geological and Polytechnic Society*, v. 14, p. 189-230.
- Kon'no, E., 1973, New species of *Pleuromeia* and *Neocalamites* from the Upper Scythian Bed in the Kitakami Massif, Japan – with a brief note on some Equisetacean plants from the Upper Permian Bed in the Kitakami Massif: *Tohoku University Science Reports*, 2nd Series (Geology), v. 43, p. 99-115.
- Lyons, P.C. and Darrach, W.C., 1989, Earliest conifers in North America; upland and/or paleoclimatic indicators? *Palaios*, v. 4, p. 480-486.
- Naugolnykh, S.V. 2002, *Paracalamitina striata*—a newly reconstructed equisetophyte from the Permian of Angaraland: *Journal of Paleontology*, v. 76, p. 377-385.
- Naugolnykh, S.V. 2004, On some aberrations of extant horsetails (*Equisetum* L.) and the origin of the family Equisetaceae: *Paleontological Journal*, v. 38, p. 335-342.
- Nelson, W.J., Hook, R.W. and Tabor, N., 2001, Clear Fork Group (Leonardian, Lower Permian) of North-Central Texas: *Oklahoma Geological Survey Circular*, v. 104, p. 167-169.
- Pfefferkorn, H.W., 1980, A note on the term "upland flora": *Review of Palaeobotany and Palynology*, v. 30, p. 157-158.
- Rayner, R.J., 1992, *Phyllothea*: The pastures of the Late Permian: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 92, p. 31-40.
- Seward, A.C., 1898, *Fossil Plants: for Students of Botany and Geology*. Vol. 1. Cambridge: Cambridge University Press. 452 pp.
- Scheihing, M.H. and Pfefferkorn, H.W., 1984, The taphonomy of land plants in the Orinoco Delta: A model for the incorporation of plant parts in clastic sediments of Late Carboniferous age of Euramerica: *Review of Palaeobotany and Palynology*, v. 41, p. 205-240.
- Schimper, W. P., 1869, *Traité de Paléontologie végétale ou la flore du monde primitif dans ses rapports avec les formations géologiques et la flore du monde actuel*. I. J. B. Baillière et Fils éd., Paris, 738 pp.
- Schlotheim, E.F von, 1820, *Die Petrefakten-Kunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinertes und fossiler Ueberreste des their- und Pflanzenreichs der Vorwelt erlaeutert*. Gotha, 437 pp.
- Stewart, W.N. and Rothwell, G.W., 1993, *Paleobotany and the evolution of plants*. Cambridge: Cambridge University Press, pp. 198-211.
- Zeiller, R., 1895, Notes sur la flore des gisements houillers de la Rhune et d'Ibantelly (Basses-Pyrénées): *Bulletin de la Société Géologique de France*, v. 3 (23), p. 482.