



Sueria laxinervis, a new fossil species of Cycadales from the Upper Cretaceous Quiriquina Formation in Cocholgüe, Biobío Region, Chile

TOSHIHIRO YAMADA^{1,*}, TAKAE F. YAMADA², KAZUO TERADA³, TAKESHI A. OHSAWA⁴, ATSUSHI YABE⁵, JULIEN LEGRAND⁶, KAZUHIKO UEMURA⁵, MARCELO LEPPE⁷, LUIS FELIPE HINOJOSA⁸, PATRICIO LÓPEZ-SEPÚLVEDA⁹ & HARUFUMI NISHIDA⁶

¹Botanical Gardens, Faculty of Science, Osaka City University, Kisaichi, Katano, Osaka 576-0004, Japan

²School of Natural System, College of Science and Technology, Kanazawa University, Kanazawa 920-1192, Japan

³Fukui Prefectural Dinosaur Museum, Katsuyama, Fukui 911-8601, Japan

⁴Graduate School of Science, Chiba University, Chiba 263-8522, Japan

⁵Department of Geology and Paleontology, National Museum of Nature and Science, Tsukuba, Ibaraki 305-0005, Japan

⁶Department of Biological Sciences, Faculty of Science and Engineering, Chuo University, Tokyo 112-8551, Japan

⁷Instituto Antártico Chileno, Plaza Muñoz Gamero 1055, Punta Arenas, Chile

⁸Laboratorio de Paleocología, Facultad de Ciencias, Universidad de Chile, Instituto de Ecología y Biodiversidad, Las Palmeras 3425, Ñuñoa, Santiago CP 780-0024, Chile

⁹Departamento de Botánica, Universidad de Concepción, Casilla 160-C, Concepción, Chile

*Corresponding author. e-mail address: ptilo@mb.infoweb.ne.jp

Abstract

A new fossil cycad species, *Sueria laxinervis*, is described from the Upper Cretaceous (Maastrichtian) Quiriquina Formation in Cocholgüe, Biobío Region, Chile. The generic assignment is supported by the taeniopterid-type leaf with haplocheilic stomata and sinuate anticlinal walls of leaf epidermal cells, while *S. laxinervis* clearly differs from the other two described *Sueria* species in its sparse veins and large epidermal cells. The vascular bundles of the midrib are arranged in an inverted-omega shape, supporting the placement of *Sueria* in Cycadales.

Keywords: Cycads, Maastrichtian, Mesozoic, taeniopterid-type leaf

Introduction

Cycadales is a small order consisting of only ten extant genera, which are classified into two families: Cycadaceae and Zamiaceae (Christenhusz *et al.* 2011). This order was much more diverse during the Mesozoic, especially in the Southern Hemisphere (Artabe & Stevenson 1991, Martínez *et al.* 2012). *Sueria* Menéndez emend. Baldoni (1977: 301) is an extinct genus that might be related to Cycadales and was established based on taeniopterid-type simple leaves from the Lower Cretaceous (Aptian) of Argentina (Menéndez 1965). The genus is characterized by haplocheilic stomata and sinuate anticlinal walls of the leaf epidermal cells (Menéndez 1965, Baldoni 1977, Villar de Seoane 1997). Little is known about the spatiotemporal distribution of the genus since only two species have been reported so far, both from the Lower Cretaceous of the Santa Cruz Region of Argentina: *S. rectinervis* Menéndez emend. Baldoni (1977: 301) and *S. elegans* Villar de Seoane (1997: 136).

The external morphology of the leaves of Cycadales is quite similar to that of Bennettitales, making it difficult to distinguish their affinities based only on macro-morphology. Therefore, haplocheilic stomata have been used to distinguish cycad leaves from bennettitalean ones, characterized by syndetocheilic stomata (*e.g.*, Harris 1964, 1969). Based on this criterion, *Sueria* is considered to belong to the Cycadales (Menéndez 1965, Baldoni 1977, Artabe & Stevenson 1991). However, leaf epidermal cells with sinuate anticlinal walls are unusual in cycadaleans, while these are common in bennettitaleans (*e.g.*, Harris 1964, 1969). Haplocheilic stomata are also found in other gymnosperm groups, such as Ginkgoales and conifers (*e.g.*, Harris 1964). Since taeniopterid-type leaves are found in groups other than cycads, such as pteridosperms (Axsmith *et al.* 2003), the affinity of *Sueria* to cycads should be tested using other anatomical characters.

Here, we describe a new fossil species, *Sueria laxinervis*, from the Upper Cretaceous (Maastrichtian) Quiriquina Formation in Caleta Cocholgüe, near Concepción, Chile. We describe the anatomy of the leaf midrib of the new fossil species to validate its affinity to the Cycadales.

Materials & methods

Two fossil leaves were collected from calcareous concretions formed in the fine sandstone of a Quiriquina Formation outcrop at Caleta Cocholgüe, Tomé, BíoBío Region, Chile. The Quiriquina Formation comprises shallow marine deposits consisting mainly of sandstone and yields many Mollusca. Its estimated age is Late Cretaceous (Maastrichtian) based on coexisting ammonoids (Salazar *et al.* 2010).

Serial anatomical sections were made using the peel technique (Joy *et al.* 1956). The epidermal features of lamina were observed in paradermal sections of the holotype specimen, while midrib features were seen in cross-sections of the paratype specimen.

Systematic palaeontology

Sueria laxinervis T.Yamada & H.Nishida, *sp. nov.* (Fig. 1)

Diagnosis—Veins of lamina set sparsely at ca. 10–15 per cm. Epidermal cells of lamina more than 60 µm in maximum diameter on both the adaxial and abaxial sides.

Holotype—CHILE. BíoBío Region: Caleta Cocholgüe, Tomé. 36°59'38"S, 72°98'13"W, 8 February 2014. SGO. PB 1571, Museo Nacional de Historia Natural, Santiago (Figs. 1A, B, D, E).

Paratype—CHILE. BíoBío Region: Caleta Cocholgüe, Tomé. 36°59'38"S, 72°98'13"W, 8 Feb. 2014. NSM PP-9291, National Museum of Nature and Science, Tokyo (Figs. 1C, F, G).

Type Strata—The Quiriquina Formation (Maastrichtian).

Description—Leaves are linear with an undulate margin, > 5.8 × 2.5 cm (Figs. 1A, B). No specimens with the leaf apex or base have been found. Midrib is 1.1–3.0 mm wide and gives off veins at 45–90 degrees to the midrib (Figs. 1A–C). Veins often bifurcate at the base, run parallel to each other and reach the margin (Figs. 1A–C). The vein density is ca. 10–15 per cm (Figs. 1A–C). Leaves are hypostomatic. Anticlinal walls of epidermal cells are sinuate (Figs. 1D, E). Epidermal cells are 60–70 × 30–40 µm on the abaxial side (Fig. 1D) and 80–90 × 30–60 µm on the adaxial side (Fig. 1E). Stomata are haplocheilic with 6–7 subsidiary cells encircling guard cells and are 80–100 µm in diameter (Fig. 1D). Guard cells are 35–45 × 15–20 µm (Fig. 1D). Midrib is rectangular in cross-section and ca. 1 mm thick (Figs. 1F, G). Epidermal cells are papillate on the adaxial side and smooth on the abaxial side (Figs. 1F, G). Hypodermis is composed of parenchymatous cells, 4–6 cells thick on the adaxial side and 1 or 2 cells thick on the abaxial side (Figs. 1F, G). Planner masses of sclerenchymatous cells are present below the hypodermis on both the adaxial and abaxial sides (shaded in Fig. 1G); layers are 2 or 3 cells thick (Fig. 1F). In the midrib of the paratype specimen, 14 vascular bundles are recognized, which are arranged in an inverted omega shape (Figs. 1F, G).

Etymology—The specific epithet refers to the leaf character in which veins are sparsely set, from Latin *laxus*, wide or loose, and *nervus*, sinew.

Discussion

Our specimens were identified as a species in the genus *Sueria* based on the following characters (Menéndez 1965, Baldoni 1977, Villar de Seoane 1997): linear leaf with stout midrib, parallel veins that sometimes bifurcate at the base, epidermal cells with sinuate anticlinal walls and haplocheilic stomata (Fig. 1). Two species in this genus have been reported, but both were from the Lower Cretaceous (Aptian) of Argentina (Menéndez 1965, Villar de Seoane 1997). Our finding extends the fossil range of the genus to the Late Cretaceous (Maastrichtian). This is also the first report of the genus outside Argentina.

Sueria rectinervis and *S. elegans* have veins at a density of 20–25 per cm (Menéndez 1965) and 20 per cm (Villar de Seoane 1997), respectively, while the vein density is 15 per cm in *S. laxinervis*. In addition, *S. laxinervis* has larger

epidermal cells than the other two species, i.e., 60–90 μm vs. < 60 μm in the maximum diameter (Menéndez 1965, Villar de Seoane 1997). Therefore, *S. laxinervis* is clearly distinguished from *S. rectinervis* and *S. elegans*.

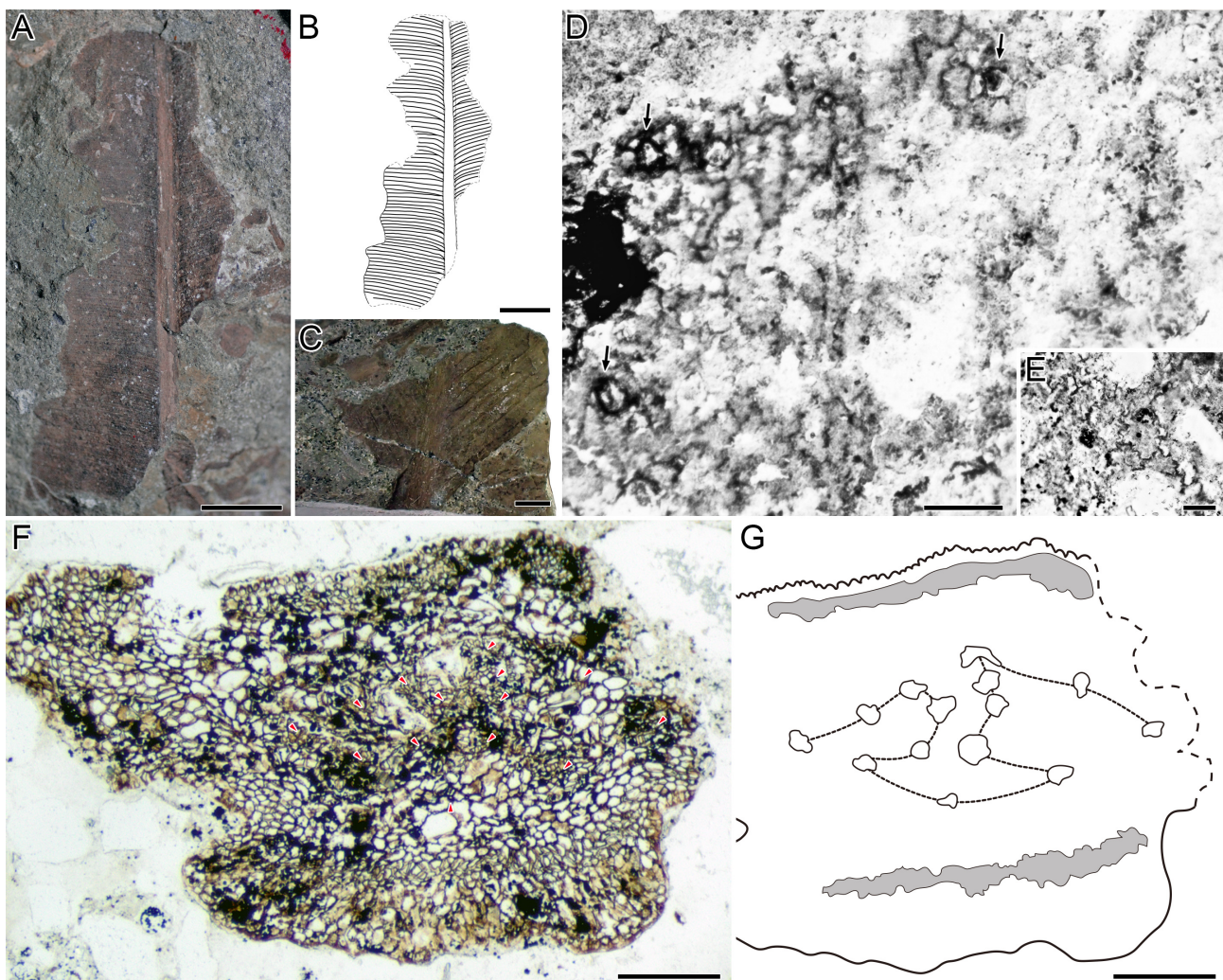


FIGURE 1. *Sueria laxinervis* T.Yamada & H.Nishida. Holotype (A, B, D, E) and paratype (C, F, G). A, C. External views. B. Line drawing of A. D. Abaxial epidermis. Arrows indicate stomata. E. Adaxial epidermis. F. Midrib cross-section. Red arrowheads indicate vascular bundles. G. Camera-lucida illustration of F. The dashed line shows the arrangement of the vascular bundles (white circles). Sclerenchymatous plates are shaded. Scale bars: 1 cm (A, B), 2.5 mm (C), 100 μm (D), 50 μm (E), 250 μm (F, G). Illustrations and photographs by T. Yamada.

In the extant cycads, which comprise Cycadaceae and Zamiaceae (Christenhusz *et al.* 2011), the vascular bundles are arranged in an inverted-omega shape, except for *Bowenia* Hooker (1863: ad t. 5398), *Encephalartos* Lehmann (1834: 3) and *Stangeria* Moore (1853: 228) species in which the inverted-omega shape is modified by elaboration of traces to pinnae (Yoshida 2000, Hermsen *et al.* 2007). *Sueria laxinervis* also has vascular bundles arranged in the inverted-omega shape, providing another line of evidence that the genus *Sueria* belongs in Cycadales. This arrangement is markedly different from that in the midrib of the bennettitalean species *Nilssoniopteris oishii* Yamada *et al.* (2009: 411), which has a taeniopterid-type leaf and vascular bundles arranged in a circle (Yamada *et al.* 2009), as in the other bennettitalean species (Dower *et al.* 2004, Yamada 2009).

It has been hypothesized that the pinnate leaves found in fossil and extant cycads evolved from a simple taeniopterid-type leaf through progressive dissection of the leaf lamina (Mamay 1976). Under this hypothesis, the midrib of a taeniopterid-type leaf should be comparable to the rachis of pinnate leaves, but this has not been tested in light of leaf anatomy. The omega-shaped vascular arrangement in the midrib of *Sueria* provides the first anatomical evidence supporting the homology between the midribs of taeniopterid-type and other cycad leaves. Although it is not clear if the Permian taeniopterid-type leaves represent the ancestral cycad leaf (Axsmith *et al.* 2003), our results suggest that transition(s) between pinnate and simple states would be possible in principle during the evolution of cycad leaves.

Acknowledgments

We thank the Consejo de Monumentos Nacionales de Chile for allowing us to collect fossil materials. This study was supported by KAKENHI (Grant-in-Aid for Scientific Research) from the Ministry of Education, Culture, Sports, Science and Technology to HN (14255007, 18405013 and 24570112) and TY (15H05233).

References

- Artabe, A.E. & Stevenson, D.W. (1999) Fossil Cycadales of Argentina. *Botanical Review* 65 (3): 219–238.
<https://doi.org/10.1007/BF02857630>
- Axsmith, B.J., Serbet, R., Krings, M., Taylor, T.N., Taylor, E.L. & Mamay, S.H. (2003) The enigmatic Paleozoic plants *Spermopteris* and *Phasmatocycas* reconsidered. *American Journal of Botany* 90: 1585–1595.
<https://doi.org/10.3732/ajb.90.11.1585>
- Baldoni, A. (1977) Nota sobre *Sueria rectinervis* Menéndez del Cretácico inferior de la Formación Baqueró, Provincia de Santa Cruz. *Ameghiniana* 14 (1): 301–304.
- Christenhusz, M.J.M., Reveal, J.L., Farjon, A., Gardner, M.F., Mill, R.P. & Chase, M.W. (2011) A new classification and linear sequence of extant gymnosperms. *Phytotaxa* 19: 55–70.
<https://doi.org/10.11646/phytotaxa.19.1.3>
- Dower, B.L., Bateman, R.M. & Stevenson, D.W. (2004) Systematics, ontogeny, and phylogenetic implications of exceptional anatomically preserved cycadophyte leaves from the Middle Jurassic of Bearerraig Bay, Skye, Northwest Scotland. *Botanical Review* 70: 105–120.
[https://doi.org/10.1663/0006-8101\(2004\)070\[0105:SOAPIO\]2.0.CO;2](https://doi.org/10.1663/0006-8101(2004)070[0105:SOAPIO]2.0.CO;2)
- Harris, T.M. (1964) *The Yorkshire Jurassic flora II. Caytoniales, Cycadales and Pteridosperms*. British Museum (Natural History), London, 191 pp.
- Harris, T.M. (1969) *The Yorkshire Jurassic flora III. Bennettitales*. British Museum (Natural History), London, 186 pp.
- Hermesen, E., Taylor, T.N., Taylor, E.L. & Stevenson, D.W. (2007) Cycads from the Triassic of Antarctica: permineralized cycad leaves. *International Journal of Plant Sciences* 168 (7): 1099–1112.
<https://doi.org/10.1086/518840>
- Hooker, W.J. (1863) *Curtis's Botanical Magazine, comprising the plants of the Royal Gardens of Kew and of other botanical establishments in Great Britain with suitable descriptions* 89, London, t. 5354–5419.
- Joy, K.W., Willis, A.J. & Lacey, W.S. (1956) A rapid cellulose peel technique in palaeobotany. *Annals of Botany* 20: 635–637.
<https://doi.org/10.1093/oxfordjournals.aob.a083546>
- Lehmann, J.G.C. (1834) *Novarum et minus cognitarum stirpium pugillus VI addita enumeratione plantarum omnium in his pugillis descriptorum*. Meissner, Hamburg, 66 pp.
- Mamay, S.H. (1976) Paleozoic origin of the cycads. *U.S. Geological Survey Professional Paper* 934: 1–48.
<https://doi.org/10.3133/pp934>
- Martínez, L.C.A., Artabe, A.E.E. & Bodnar, J. (2012) A new cycad stem from the Cretaceous in Argentina and its phylogenetic relationships with other Cycadales. *Botanical Journal of the Linnean Society* 170: 436–458.
<https://doi.org/10.1111/j.1095-8339.2012.01300.x>
- Menéndez, C.A. (1965) *Sueria rectinervis* n. gen. et sp. de la Flora fósil de Ticó, provincia de Santa Cruz. *Ameghiniana* 4 (3): 75–83.
- Moore, T. (1853) List of Mr. Plant's Natal ferns. In: Hooker, W.J. (Ed.) *Hooker's Journal of Botany and Kew Garden Miscellany* 5. London, pp. 225–229.
- Salazar, C., Stinnesbeck, W. & Quinzio-Sinn, L.A. (2010) Ammonites from the Maastrichtian (Upper Cretaceous) Quiriquina Formation in central Chile. *Neues Jahrbuch für Geologie und Paläontologie* 257: 181–236.
<https://doi.org/10.1127/0077-7749/2010/0072>
- Villar de Seoane, L. (1997) Estudio cuticular comparado de nuevas Cycadales de la Formación Baqueró (Cretácico Inferior), provincia de Santa Cruz, Argentina. *Revista Española de Paleontología* 12 (1): 129–140.
- Yamada, T. (2009) Structurally preserved *Zamites bayeri* Kvaček from the Coniacian Kashima Formation (Yezo Group) of Hokkaido, Japan. *Cretaceous Research* 30: 1301–1306.
<https://doi.org/10.1016/j.cretres.2009.07.007>

- Yamada, T., Legrand, J. & Nishida, H. (2009) Structurally preserved *Nilssoniopteris* from the Arida Formation (Barremian, Lower Cretaceous) of southwest Japan. *Review of Palaeobotany and Palynology* 156: 410–417.
<https://doi.org/10.1016/j.revpalbo.2009.04.006>
- Yoshida, A. (2000) Histological study on the petioles of extant cycads. *Science report of the Research Institute of Evolutionary Biology* 9: 49–71.