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THE KRASSER COLLECTION IN THE FACULTY OF SCIENCES, CHARLES UNIVERSITY, PRAGUE – NEW INSIGHTS INTO THE MIDDLE JURASSIC FLORA OF SARDINIA

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Abstract: Revision of part of the Middle Jurassic flora of Sardinia, the Krasser collection, stored in Prague (Lovisato B collection), containing 23 fossil taxa of horsetails, ferns, cycadophytes, ginkgophytes and conifers. The conifers are most diverse, followed by cycadophytes and ferns. The composition of this assemblage differs notably from the Lovisato collection stored in Cagliari, suggesting that it might derive from a different stratigraphic level and/or palaeoenvironment. The palaeodiversity of the Middle Jurassic flora of Sardinia increases to 46 fossil taxa with this revision. *Cycadolepis* sp. *Nilssonia* sp., *Nilssonia* sp. cf. *N. orientalis*, *Pagiophyllum* sp. and *Agathoxylon* sp. are described for the first time from the Middle Jurassic of Sardinia.

Key words: Fridolin Krasser, Italy, historic collections, horsetails, conifers, plant assemblages, biodiversity

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Introduction

Jurassic floras are abundant in Europe, although not all are equally well understood. A recent overview documented 46 Early, Middle and Late Jurassic plant assemblages, with more than 770 taxa (for more details see Barbacka et al. 2014). The fossil sites from Yorkshire in the UK (e.g. Harris 1961, 1964, 1969, 1979, Harris et al. 1974, Van Konijnenburg-van Cittert and Morgans 1999, Cleal et al. 2001, Van Konijnenburg-van Cittert 2008), Franken in Germany (Weber 1968), Scania in Sweden (Pott and McLouglin 2011) and Anina in Romania (Popa and Meller 2009) are among the most famous European Jurassic floras. Italian Jurassic floras include the historical collections from Rotzo (de Zigno 1856–1868, 1873–1885, Grandori 1913a, b, Wesley 1956, 1958, 1966, 1974), Sardinia (Tornquist 1902, 1904a, b, Krasser 1912, 1913, 1920, Edwards 1929, Comaschi Caria 1959, Dieni et al. 1983, Salard-Cheboldaeff and Vozenin-Serra 1984, Scanu et al. 2012, 2015, 2016) and some smaller and less well studied plant assemblages (Sordelli 1896, Praturlon 1965, 1968, Cocozza and Praturlon 1966, Bonci and Vannucci 1986, Bravi 1995, Bravi et al. 2014). The floras of Rotzo, Como/Moltrasio and Monte Palombo are of Early Jurassic age, whereas those of Sardinia, Monti Lepini and Monte Fallano belong to the Middle Jurassic.

The largest assemblage of Sardinian plant fossils is housed in the Geological and Palaeontological Museum "D. Lovisato" of the Cagliari University. It comprises 24 taxa (19 genera) belonging to the horsetails, ferns (*Phlebopteris*, *Hausmannia*, *Coniopteris*, *Todites*, *Cladophlebis*), seed ferns (*Sagenopteris*, *Ptilozamites*), cycadophytes (*Nilssonia*, *Pterophyllum*, *Cycadeospermum*, *Ptilophyllum*, *Williamsonia*, *Weltrichia*), Czekanowskiales (*Czekanowskia*), conifers (*Geinitzia*, *Brachyphyllum*, *Elatocladus*) and plant remains without clear botanical affinity (*Carpolithes*, *Taeniopteris*; Scanu et al. 2012, 2015, 2016). Recently, a second collection (Miccolis collection) of Middle Jurassic plant remains from central Sardinia (Laconi and Nurallao) was discovered at the Natural History Museum of Venice, yielding several additional taxa (e.g. *Marattia*, *Dicksonia*, *Eboracia*). This increases the number to 29 taxa (23 genera), and reveals that the Middle Jurassic flora of Sardinia was more similar to the

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Middle Jurassic flora of Yorkshire than to the Early Jurassic flora of Rotzo (Italy, Scanu et al. 2016). Whether the difference between the two Italian floras (Sardinia and Rotzo) is due to their different depositional/environmental conditions, or reflects the palaeogeographic position of the floras during the Jurassic, remains equivocal (e.g. Bartiromo and Barone Lumaga 2009, Barbacka et al. 2014, Scanu et al. 2016). Moreover, it emphasizes that the Middle Jurassic flora of Sardinia is not yet fully understood, since the discovery of the small Miccolis collection in Venice added a significant number of new taxa to the Sardinian flora.

This study evaluates the composition of the second part of the Lovisato collection, stored in the Faculty of Sciences, Charles University, Prague, and adds new taxon records to the Jurassic flora of Sardinia. All historical collections have now been revised, providing complete available data on the composition of the Jurassic flora of Sardinia; Urbanisation of the area in the last century has impeded further collection of Jurassic plant remains from this area.

Material and methods

Domenico Lovisato (1842–1916), Professor of Mineralogy and Geology, and Director of the Royal Mineralogical and Geological Museum of the University of Cagliari collected the largest Middle Jurassic plant assemblage in Italy. This collection (about 1200 plant fossils), partly studied and described by Tornquist (1902, 1904a, b) and Krasser (1912, 1913), was severely damaged during the World War II. About 500 slabs, housed at the Geological and Palaeontological Museum of the Cagliari University, have been recently revised (Scanu et al. 2012, 2015). A selection of taxa (collected after 1913), was sent to Prague for taxonomical analyses to be carried out by Fridolin Krasser (Krasser 1920, Edwards 1929) were they are still stored.

The plant remains come from the Genna Selole Formation (Costamagna 2015), a siliciclastic to mixed siliciclastic-carbonate succession (Costamagna and Barca 2004). Palynomorphs and molluscs date the formation to the Bajocian – Bathonian (Amadesi et al. 1960, Del Rio 1976, 1984, Dieni et al. 1983, Dieni and Massari 1985). The base is represented by continental sediments (fluvial conglomerates) that grade into transitional and coastal sediments (distal alluvial fan to transitional lagoonal – littoral; see also Scanu et al. 2012 and ref. therein). The top of the formation is characterised by tidally influenced lagoonal sediments (e.g. Amadesi et al. 1960, Dieni et al. 1983, Dieni and Massari 1985).

According to Krasser's numbering, the collection he studied contained at least 190 specimens denoted "Loc. B", thus sent to him after 1913 (Krasser 1920). Only 143 specimens (prefix "JSK") containing almost 200 plant fragments, were found in the collections of the Faculty of Sciences, Charles University, Prague. They are preserved as impressions and compressions in fine-grained sediments (siltstones and marls) typical of the Genna Selole Formation. Photographs were taken with a digital system camera (Panasonic Lumix DMC-LX5). The part of the Lovisato collection described by Krasser (1912) is also numbered, but kept separate (Loc. A of Krasser 1920).

Where possible, cuticles were prepared according to the standard procedures of the Schulze method ($KClO_3$ and 30% HNO_3/neutralization in 5% NH_4OH) as described by Kerp (1990) and Batten (1999).

Plant fossils in the Faculty of Sciences, Charles University, Prague

Sphenophyta

Decorticated stem fragments and diaphragms of horsetails are common in the collection. Based on their dimensions (mostly the diameter of their axes), they can be segregated into two fossil taxa, *Equisetites beanii* (Bunbury) Seward, 1894 and *Equisetites columnaris* (Brongniart) Phillips, 1875. Most fragments belong to *E. columnaris* (Pl. 1, Figs 1–3) characterized by narrower axes, that are generally 40–60 mm wide (Lov. B 2.1–2.3, 4.1–2, 5, 7–10, 12, 18, 22.1–2, 23.1–3, 25, 28.1, 32, 51.1–3, 52–54, 54.1–2, 56, 59–60, 72). External preserved features are impressions of the leaf sheaths (37 × 10 mm) and microphylls (2 mm wide, with pointed apices; Lov. B 3.1, 4.1–4.2, 5, 8). *Equisetites beanii* (Pl. 1, Figs 4–5) was probably a larger plant, with axes reaching up to 100 mm in width (Lov. B 1, 3.1, 6, 11, 16–17, 21, 25). The fossil stem fragments are generally smooth, because leaf sheaths fall off easily. *Equisetites beanii* is a typical Middle Jurassic taxon resembling the Triassic equivalent *Equisetites arenaceus* (Jaeger) Schenk, 1864, whereas *E. columnaris* has been described from both Lower and Middle Jurassic strata (Poland: Jarzynka and Pacyna 2015, England: Harris 1961).

Krasser (1920: 4) listed only one horsetail species (*Equisetites columnaris*), because he considered *E. beanii* to be the thicker stems belonging to *E. columnaris*. In this case, *E. beanii* would represent the older, defoliated stems of *E. columnaris* (Schweitzer et al. 1997: 135–141). If both taxa belong to the same biological species, the specific name *E. columnaris* would have priority. In the Jurassic flora of Yorkshire, both species are present, with *E. columnaris* being more common than *E. beanii*. Both species may occur in the same deposits, but, at some localities, only one species occurs. For example, only *E. columnaris* is known from Hasty Bank, while the cliffs around Scarborough have yielded only *E. beanii*.

One plant fossil (Lov. B 49.1–2; Pl. 1, Figs 10–11) represents a nodal fragment of *Schizoneura* Schimper et Mougeot, 1844 with microphylls, which seem to arise from the same position on the axis and are basally connate. Krasser (1920: 9) indicated that this fragment might represent a badly preserved basal frond fragment of *Dictyophyllum rugosum* Lindley et Hutton, 1834, whereas the label designates it *Equisetites beanii* ("*Asterophyllites* Beblätterung"). Furthermore, Krasser (1920) mentioned that the same specimen contained a fragment of *Sagenopteris goeppertiana* de Zigno, 1865 (on p. 8) and *Nilssonia compta* (Phillips) Brongniart, 1828 (on p. 9), but none of those could be identified on the slab.

Pteridophyta

The fern frond fragments belong to three genera: *Phlebopteris* Brongniart, 1836, *Todites* Seward, 1900 and *Cladophlebis* Brongniart, 1849, all preserved as small fragments. *Phlebopteris* is represented by eight specimens, three of which belong to *Phlebopteris polypodioides* Brongniart, 1836 (Lov. B 17, 25, 95) (Pl. 1, Fig. 8). The fragments are up to 40 mm long and 30 mm wide, with a distinct midrib and reticulate veins in the outer half of the lamina; Lov. B 95 is a fertile fragment, with sori. One fertile fragment (Lov. B 37), bearing circular sori (0.5–1.2 mm diameter) arranged in two rows close to the midrib, could also belong to this species.

Phlebopteris dunkeri (Schenk) Schenk, 1975 (Pl. 1, Figs 6, 7) is represented by small fragments with distinct anastomosing venation and a fusain-like preservation (Lov. B 64, 73.1–2, 78). Other pinna fragments (8 × 4 mm) arising from the frond fragments (up to 45 × 20 mm), are not attributable to any species (Lov. B 77.1–2). Krasser (1920: 8) assigned the *Phlebopteris* (*Laccopteris* Presl, 1838 being a junior synonym of *Phlebopteris* Brongniart, 1828) specimens from the Lovisato B collection to *Laccopteris woodwardii* (Leckenby) Seward, 1910 (Lov. B 87, lost); Harris (1961) questioned this attribution to *P. woodwardii*. Krasser (1920) also mentioned *Laccopteris elegans* Presl in Sternberg, 1838 (Lov. B 37) [which is a synonym of *P. braunii* (Goeppert) Harris, 1980)], *L. polypodioides* (Brongniart) Seward, 1910 (Lov. B 73) and "*L. spectabilis* Stur" (Lov. B 64), the latter being a nomen nudum. According to Krasser (1913: 31) *L. dunkeri* was restricted to the white sandstone and *L. elegans* (= *Phlebopteris braunii*) to the grey marls, but, in the Lovisato B collection, both taxa occur in grey marls. Unfortunately, neither *P. braunii* nor *L. spectabilis* can be confirmed for this collection.

Nine frond fragments belong to *Cladophlebis* or *Todites*. Two samples (Lov. B 16, 43) represent *Todites williamsonii* (Brongniart) Seward, 1900 emend. Harris 1961 (Pl. 1, Fig. 9). The frond fragments are up to 35 mm long and 30 mm wide. Pinnae fragments up to 20 mm long and 10–15 mm wide arise from the 2–2.5 mm wide rachis. The slightly falcate pinnules arise at an acute angle; they are 6–9 mm long and 2–2.5 mm wide. The others (Lov. B 6, 9, 16.4, 28.4, 53, 55, 57.1+2) are too badly preserved for any species determination, and are assigned to *Cladophlebis* sp. Krasser (1913: 31, 1920: 9) listed only *Todites williamsonii* for the Lovisato B collection.

Pteridospermatophyta

The collection yielded four badly preserved leaflets (Lov. B 17, 35.1, 55, 57.1–2) of *Sagenopteris* Presl in Sternberg, 1838 (Pl. 2, Fig. 2). The isolated leaflets are asymmetrically lanceolate, up to 80 mm long and 30 mm wide, with a characteristic net venation. Several of the specimens mentioned by Krasser (1920: 10) as *Sagenopteris goeppertiana* de Zigno, 1885 are lost; the remaining samples are not sufficiently preserved for any species determination. The "sporocarps" identified by Krasser (1920: 8) represent the remains of some branchiopods formerly called *Estheria* (Pl. 3, Figs 4, 6). These aquatic (fresh-water and mainly salt-water) crustaceans occur sporadically in non-marine facies, and are abundant from the Devonian to present (Chen 2008).

Ginkgophyta

A few leaf fragments (Lov. B 66.1, 66.2, 67.2, 94) may belong to the ginkgophyte *Eretmophyllum* Thomas, 1913 (Pl. 2, Figs 5, 7). The fragments are up to 30 mm long and 12 mm wide, with a rounded apex and distinct, parallel veins. Krasser (1920: 14) attributed them to the conifer *Podozamites lanceolatus* (Lindley et Hutton) Braun, 1843. However, Edward's (1929) *E. lovisatoi* Edwards, 1929 from Sardinia (see below) is confirmed by cuticle analyses. Harris et al. (1974) compared it with Yorkshire species of *Eretmophyllum*, considering them different mainly in their cuticular anatomy.

Cycadophyta

The Cycadales (or Nilssoniales) are represented by leaf fragments of *Nilssonia* Bronn, 1835 (Lov. B 16, 35.1, 37). The best-preserved specimen (Lov. B 35.1) is 120 mm long and 40 mm wide, with a 3 mm wide rachis and a 30 mm broad half lamina, with distinct parallel and undivided secondary veins. Krasser (1920) indicated *Nilssonia compta* (Phillips) Brongniart, 1828 for the assemblage, however, the material is not well enough preserved (lacking cuticle) to confirm this attribution. Moreover, both specimens seem to be entire-margined *Nilssonia* leaves, like those of *N. orientalis* Heer, 1878 (see Schweitzer et al. 2000) (Pl. 2, Fig. 1).

Bennettitalean leaves are represented by rare and fragmentary leaves of *Ptilophyllum* Morris in Grant, 1840 (Lov. B 8, 16.1–3, 16.5, 21, 25, 63.1, 65, 92.1). The fragments are up to 45 mm long and 50 mm wide. The lanceolate to slightly falcate segments are 10–25 mm long and 2–3 mm wide, with distinct parallel veins (Pl. 2, Figs 4, 6). The specimens are too fragmentary to determine whether they belong to the previously described species *Ptilophyllum pecten* (Phillips) Seward, 1900 (Krasser 1920), *Ptilophyllum pectinoides* (Phillips) Halle, 1913 or *Ptilophyllum cariae* Scanu et al. 2015 (Scanu et al. 2015). Reproductive organs are represented by fragments of *Williamsonia* Carruthers, 1870 emend. Harris 1969 (Lov. B 16.6, 44.1–2). Krasser (1920: 14) attributed them to *Williamsonia acuminata* (de Zigno) Krasser, 1912 but the material is too badly preserved for a specific determination. The collection also includes isolated linear-lanceolate scales of *Cycadolepis* Saporta, 1875 (Lov. B 44.3–4, xy1).

Coniferophyta

The conifers are among the most abundant groups in this plant assemblage. *Geinitzia divaricata* (Bunbury) Harris, 1979 is one of the most common taxa (Pl. 3, Figs 1, 7). The shoot fragments (Lov. B 3.2, 5, 10, 12, 15, 17, 22.1–2, 28.1–4, 30.1–2, 35.1, 37, 55, 81, 92.1–3, 109) are up to 40 mm long and 30 mm wide, with an axis of 1–2 mm width. Lateral shoots arise alternately at acute angles. Leaves are helically arranged, arch outward at a wide angle (70–90°), and are attached by their entire base. They are falcate, with only one vein and a pointed or slightly rounded apex. They are 2–5 mm long and 0.5–2 mm wide. Krasser (1920: 18) attributed the specimens to *Cheirolepis setosus* (Phillips) Seward, 1900, whereas Edwards (1929) assigned them to *Cryptomerites divaricatus* Bunbury, 1851.

Elatides williamsonii (Lindley et Hutton) Nathorst, 1897 is also common (Pl. 3, Figs 5, 9); it is characterized by elongated leaves of 5–8 mm length and 1–2 mm width, arranged in a loose helix (Lov. B 14.1–2, 17.1–2, 27.1–2, 28.2–3, 29, 51.2, 72.1–3, 78, 90, 94, 107.2, 122.1–3, 127.6, B, C1–5). Krasser (1920: 18) identified this species as *Pagiophyllum williamsonii* (Brongniart) Seward, 1900. Two specimens (Lov B 9, 127.9) with linear leaves are identified as *Elatocladus* sp. Several shoot fragments with broad, leathery leaves are assigned to *Brachyphyllum* sp. (Lov. B 56, 58), and other shoot fragments with very small (< 5 mm long, 1 mm wide) leaves to *Pagiophyllum* sp. (Lov. B 75.1–2, 99, 124, 126, 127.1–2, 127.5, 127.7–9) (Pl. 3, Fig. 8).

The wood fragment (Lov. B 128), labelled as *Dadoxylon* sp. might belong to *Agathoxylon* Greguss, 1952. Krasser (1920: 20) established *Araucarites sardinicus* (Krasser) Krasser, 1920 (formerly *Cycadeospermum sardinicum*) for sub-triangular ovuliferous scales (Lov. B 50, 50.1–2, 55, 56, 57.1–2), each with a large single seed (Pl. 3, Figs 2–3). The scales are 20–25 mm long and 20–22 mm wide, with a central depression or seed of 15–17 × 10–12 mm. The ovuliferous cones (Lov. B 127.8, B) are too fragmentary for determination. Fragments resembling pine-like leaves, with a transversely wrinkled lamina (Lov. B 89, 91) were ascribed by Krasser (1920: 19) to *Pityophyllum nordenskioldii* (Heer) Seward, 1919; unfortunately, no cuticle is preserved to confirm this attribution.

Unknown botanical affinity

Several plant remains of unknown botanical affinity are also preserved in the plant assemblage, such as seeds of *Carpolithes* sp. 1 sensu Scanu et al. (2015; Lov. B 97.2) and *Carpolithes* sp. 2 sensu Scanu et al. (2015; Lov. B 66, 77.1–2) and root fragments (Lov. B 129.1–6). Several rock samples host plant fragments too badly preserved for determination. The collection also includes a single small impression of a narrow stem with sub-rhombic leaf scars, named *Sardoa robitschekii* Krasser, 1920 (Lov. B 46; Pl. 2, Fig. 3). The leaf traces resemble *Bucklandia* Presl, 1825 as figured by Harris (1969: pl. 6, figs 1–5, 8), an attribution to the bennettitales cannot be excluded. However, the leaf traces are too badly preserved for confident identification.

Considerations on plant fossils from the Lovisato collection of Cagliari

In the light of additional and better-preserved plant fossils from the Jurassic of Sardinia, determinations of some plant fossils of the Lovisato collection housed in Cagliari (Scanu et al. 2015) need to be revised. This includes the frond fragment of *Hausmannia* Dunker, 1846 that closely resembles *Hausmannia crenata* (Nathorst) Moeller, 1902, a well-known species from the Late Triassic to Middle Jurassic of Sweden, Denmark (Bornholm), Poland, Russia, Iran and Japan (Schweitzer et al. 2009). The specimen described as *Coniopteris simplex* (Lindley et Hutton) Harris, 1961, might very well be a small fertile fragment of *Coniopteris hymenophylloides* (Brongniart) Seward, 1900. Moreover, some of the specimens attributed to *Todites williamsonii* (Scanu et al. 2015: pl. 2, fig. 1) may represent badly preserved specimens of *Cladophlebis denticulata* (Brongniart) Fontaine, 1889. An unresolved problem is the attribution of *Ptilozamites* sp. cf. *Ptilozamites blasii*. *Ptilozamites* has never been described from the Middle Jurassic, but *Ctenozamites*, a morphologically similar genus, is well known from that interval. A recent discussion suggests that *Ptilozamites* and *Ctenozamites* belong to the same natural genus, based on their resemblance in pinna morphology and cuticle pattern (Popa and McElwain 2009). However, incontrovertible evidence for the synonymy of these genera is missing; thus, we retain them as distinct, but considering the fragmentary nature of the Sardinian remains, we prefer to assign them to *Ctenozamites*. Moreover, the specimens attributed to *Pterophyllum thomasii* Harris, 1969 (Scanu et al. 2015) probably represent badly preserved fragments of *Ptilophyllum hirsutum* Thomas et Bancroft, 1949. Some of the segments might have been attached to the upper side of the rachis, whereas in *Pterophyllum* they are attached laterally.

Overview of the plant groups in the Middle Jurassic flora of Sardinia

Considering all three collections (Lovisato A collection in Cagliari, Lovisato B collection in Prague and Miccolis collection in Venice), the Jurassic flora of Sardinia is represented by more than 660 rock slabs with vegetative shoots and leaves, reproductive organs and dispersed seeds. Plant fossils are preserved as impressions and compressions, in some cases yielding cuticles and in situ spores. At least 46 taxa have been identified belonging to horsetails, ferns, seed ferns, cycadophytes, Czekanowskiales and conifers. Plant remains belonging to lycophytes are absent from the Middle Jurassic flora of Sardinia, but they are represented by dispersed spores (Del Rio 1976, 1984).

Horsetails and ferns are generally poorly and fragmentarily preserved. Horsetail remains in the Cagliari and Venice collections are impressions of stem fragments, with distinct vascular bundles and strobili fragments (Scanu et al. 2015, 2016). Identifiable stem fragments, attributed to *Equisetites columnaris* and *Equisetites beanii* (which might belong to the same biological species) are preserved only in Prague. *Calamites lehmanianus* Goeppert, 1836, indicated by Meneghini (1857), cannot be confirmed for this flora.

Ferns are common and represented by several families. Dicksoniaceae is represented by frond fragments of *Coniopteris* sp. cf. *C. hymenophylloides* (Brongniart) Seward, 1900 emend. Harris 1961, *Dicksonia kendallii* Harris, 1961 and *Eboracia* sp. cf. *Eboracia lobifolia* (Phillips) Thomas, 1911 emend. Harris 1961 (Scanu et al. 2015, 2016). The number of Matoniaceae species described from the Middle Jurassic of Sardinia rises to four (*Phlebopteris polypodioides*, *P. dunkeri, P. muensteri* (Schenk) Hirmer et Hörhammer, 1936 and *P. braunii* (Göppert) Harris, 1980). *Marattia intermedia* (Münster) Kilpper, 1964 is the only representative of Marattiaceae; *Hausmannia crenata* (Nathorst) Moeller, 1902 is the only member of Dipteridaceae. Osmundaceae is represented by *Todites williamsonii* (Brongniart) Seward, 1900 emend. Harris 1961 and *Cladophlebis* sp. cf. *C. denticulata* (Brongniart) Fontaine, 1889 and small fragments attributed to *Cladophlebis* sp. The fern frond taxa *Coniopteris* (= *Kylikipteris*) *arguta* (Lindley et Hutton) Seward, 1900,

Table 1. Overview of all Jurassic plant taxa identified from Sardinia by various researchers. Names are grouped in their major plant groups, but listed alphabetically within each group. Synonymous names are grouped together for better readability (abbreviations: cf. – uncertain determination, n.v. – non vidimus, Ed. – detemination based on figure by Edwards 1929).

TAXA	Meneghini (1857)	De Stefani (1891)	list of Sterzel cited in Tornquist (1904b)	Tornquist (1902, 1904a, b)	Krasser (1912)	Krasser (1913)	Krasser (1920)	Edwards (1929)	Dieni et al. (1983)	Lovisato Cagliari coll. (Scanu et al. 2015)	Miccolis Venice collection. (Scanu et al. 2016)	Prague Krasser coll. (this paper)	**Jurassic flora of Sardinia (this paper)**
Sphenophytes										x	x		
Calamites lehmanianus Goeppert, 1836	x												
Calamites sp.			x										
Equisetites beanii (Bunbury) Seward, 1851												x	**x**
Equisetites columnaris Brongniart, 1828							x	x				x	**x**
Equisetum arenaceum (Jaeger) Schenk, 1864		cf.	x										
Equisetum mougeotii Brongniart, 1828			x										
Schizoneura sp.												cf.	**x**
Pteridophytes													
Caulopteris sp.			x										
Cladophlebis denticulata (Brongniart) Fontaine, 1889						x	x	n.v.					**cf.**
Cladophlebis sp.										x	x	x	**x**
Coniopteris (= *Kylikipteris*) *arguta* (Lindley et Hutton) Seward, 1900				cf.			cf.						
Coniopteris hymenophylloides (Brongniart) Seward emend. Harris 1961						x	x	n.v.		cf.	cf.		**cf.**
Coniopteris simplex (Lindley et Hutton) Harris, 1961										x			
Dicksonia kendallii Harris, 1961											x		**x**
Dictyophyllum rugosum Lindley et Hutton, 1831							x	x					
Eboracia lobifolia (Phillips) Thomas, 1911 emend. Harris 1961											cf.		**cf.**
Hausmannia crenata (Nathorst) Moeller, 1902										sp.			**x**
Klukia exilis (Phillips) Raciborski, 1890						x	x	n.v.					
"*Laccopteris spectabilis* Stur" nom. nudum							x						
Marattia intermedia (Münster) Kilpper, 1964											x		**x**
Phlebopteris (= *Laccopteris*) *dunkeri* (Schenk) Schenk, 1975						x	x					x	**x**
Phlebopteris (= *Laccopteris*) *polypoidioides* Brongniart, 1836								x		x		x	**x**
Phlebopteris (= *Laccopteris*) *woodwardii* Leckenby, 1864							x	x					
Phlebopteris braunii (Goeppert) Harris, 1980 = *Laccopteris elegans* Presl in Sternberg, 1838						x	x				x		**x**
Phlebopteris muensteri (Schenk) Hirmer et Hörhammer, 1936											x		**x**
Todites williamsoni (Brongniart) Seward emend. Harris 1961						x	x	n.v.		cf.		x	**x**
Seed ferns													
Ctenozamites sp. (= *Ptilozamites blasii* (Brauns) Nathorst, 1879)										cf.			**x**
Caytonia sp. = *Gristhorpia nathorstii* Thomas, 1925 = *Laconiella sardinica* Krasser, 1920							x	x					**Ed.**
Sagenopteris goeppertiana de Zigno, 1885						x	x	x					
Sagenopteris phillipsii (Brongniart) Presl in Sternberg, 1838						x	x			x			**x**
Sagenopteris rhoifolia Presl, 1838 var. *elongata* Braun, 1843			x										
Sagenopteris sp.			x									x	
Ginkgophytes													
Baiera phillipsii Nathorst, 1880						x	x	n.v.					
Eretmophyllum lovisatoi Edwards, 1929 = *Podozamites lanceolatus* (Lindley et Hutton) Braun, 1843							x	x				x	**x**
Czekanowskiales													
Czekanowskia furcula Harris et Miller in Harris et al., 1974 = *Czekanowskia murrayana* (Lindley et Hutton) Seward, 1900						x	x	n.v.		cf.			**cf.**
Cycadophytes													
Cycadeospermum lovisatoi Krasser, 1912					x	x	x	x		x			**x**
Cycadeospermum persicum Krasser, 1912					x	x	x	x					
Cycadolepis sp.												x	**x**
Nilssonia compta Brongniart, 1828						x	x	x					
Nilssonia orientalis Heer, 1878									x			cf.	**cf.**
Nilssonia sp.										x			**x**
Otozamites anglica (Seward) Harris, 1949 = *Nageiopsis anglica* Seward, 1900						x	x	n.v.					
Otozamites beanii (Lindley et Hutton) Brongniart,1849				x			x						
Otozamites veronensis de Zigno, 1881 = *Otozamites lovisatoi* Krasser, 1913						x	x	x					**Ed.**
Pterophyllum braunianum Goeppert, 1844			cf.										
Pterophyllum jaegeri Brongniart, 1828			cf.										
Pterophyllum thomasii Harris, 1969										cf.			
Ptilophyllum (= *Williamsonia/Pterophyllum*) *pecten* (Phillips) Morris, 1841				x		x	x	x					
Ptilophyllum cariae Scanu et al., 2015										x			**x**
Ptilophyllum hirsutum Thomas et Bancroft, 1913									x				**cf.**
Ptilophyllum pectinoides (Phillips) Halle, 1913										x			**x**

Table 1. – continued.

TAXA	Meneghini (1857)	De Stefani (1891)	list of Sterzel cited in Tornquist (1904b)	Tornquist (1902, 1904a, b)	Krasser (1912)	Krasser (1913)	Krasser (1920)	Edwards (1929)	Dieni et al. (1983)	Lovisato Cagliari coll. (Scanu et al. 2015)	Miccolis Venice collection. (Scanu et al. 2016)	Prague Krasser coll. (this paper)	**Jurassic flora of Sardinia (this paper)**
Ptilophyllum sp.												x	**x**
Taeniopteris vittata Brongniart, 1831						cf.	x	n.v.					
Weltrichia (= *Williamsonia*) *whitbiensis* (Nathorst) Harris, 1969					x	x					cf		**cf.**
Weltrichia sp.										x			**x**
Williamsonia acuminata (de Zigno) Krasser, 1920						x	x						
Williamsonia hildae Harris, 1969										x			**x**
Williamsonia leckenbyi Nathorst, 1911					x	x	x	x					
Williamsonia sewardii Krasser, 1913							x	x					
Williamsonia sp.												x	
Zamites sp.						x	x	x					
Coniferophytes													
Agathoxylon sp. = *Dadoxylon* sp.								x				x	**x**
Araucarites (= *Cycadeospermum*) *sardinicus* (Krasser) Krasser, 1920					x	x	x	x				x	**x**
Brachyphyllum (= *Thuites*) *expansum* (Presl in Sternberg) Seward, 1919 emend. Kendall 1949						x	x	n.v.		x			**x**
Brachyphyllum mamillare Brongniart, 1828						x	x	x					
Brachyphyllum majus Brongniart, 1828	x												
Brachyphyllum sp.										x		x	**x**
Elatides (= *Pagiophyllum*) *williamsonii* (Brongniart) Harris, 1943							x	x				x	**x**
Elatocladus sp.										x		x	**x**
Geinitzia (= *Cryptomerites*) *divaricata* (Bunbury) Harris, 1979 = *Cheirolepis setosus* (Phillips) Seward, 1900							x	x		x	x	x	**x**
Pagiophyllum sp.												x	**x**
Pityophyllum nordenskioldii (Heer) Seward, 1919							x						
Albertia latifolia Schimper, 1837 or *Albertia braunii* Schimper, 1837			x										
Voltzia sp.		x	x										
Yuccites dubius Schimper et Mougeot, 1844 or *Yuccites vogesiacus* Schimper et Mougeot, 1844			x										
indet.													
Carpolithes sp. 1										x		x	**x**
Carpolithes sp. 2										x	x	x	**x**
Carpolithes sp.							x						
Sardoa robitschekii Krasser, 1920						x	x	x				x	**x**
Taeniopteris sp.						x				x			**x**

Dictyophyllum rugosum Lindley et Hutton, 1831, *Klukia exilis* (Phillips) Raciborski, 1890 and "*Laccopteris spectabilis* Stur" (nom. nudum) were not confirmed for this flora (Tab. 1).

Gymnosperms are more abundant than the remains of spore-producing plants. *Ctenozamites* sp. and *Sagenopteris phillipsii* Presl in Sternberg, 1838 (rather than *Sagenopteris goeppertiana* de Zigno, 1885) are the only seed ferns in the collections of Middle Jurassic plants from Sardinia (Scanu et al. 2015). Unfortunately, *Laconiella sardinica* Krasser, 1920, moved by Edwards (1929) to *Gristhorpia nathorstii* Thomas, 1925, could not be found in the collection. The photographs provided by Edwards (1929: pl. 4, figs 1–2) show a *Caytonia*-type of reproductive organ, which would fit perfectly with the *Sagenopteris* leaves found in the collection (Tab. 1). The specimens, attributed by Krasser (1920: 10) to *Podozamites lanceolatus* (Lindley et Hutton) Braun, 1843, probably belong to the only putative ginkgophyte *Eretmophyllum lovisatoi* Edwards, 1929, whereas *Baiera phillipsii* Nathorst, 1880 could not be confirmed. Czekanowkiales is represented by *Czekanowskia* sp. cf. *Czekanowskia furcula* Harris et Miller in Harris et al., 1974, which might correspond to *Czekanowskia murrayana* (Lindley et Hutton) Seward, 1900 as listed by Krasser (1913, 1920) and Edwards (1929).

The cycadophytes are the most important group, both in species diversity and relative abundance (Scanu et al. 2015). To the Cycadales belong dispersed leaf segments of *Nilssonia* sp., probably *Nilssonia orientalis* Heer, 1878 and the seed type *Cycadeospermum lovisatoi* Krasser, 1912, which could belong to the former (Gothan 1914, Edwards 1929). The bennettitalean leaves are much more diverse, with leaf fragments of *Ptilophyllum pectinoides* (Phillips) Halle, 1913, *Ptilophyllum cariae* Scanu et al. 2015 (Scanu et al. 2015), and perhaps *Ptilophyllum hirsutum* Thomas et Bancroft ex Harris, 1949 (Dieni et al. 1983, Salard-Cheboldaeff and Vozenin-Serra 1984). The reproductive organs *Williamsonia hildae* Harris, 1969 (female) and *Weltrichia* sp. cf. *Weltrichia whitbiensis* (Nathorst) Harris, 1969 (male) together with the leaves *Ptilophyllum pectinoides*, belong to the same natural species (Harris 1969, Scanu et al. 2016). Additional remains are the female reproductive organs *Weltrichia* sp., scales of *Cycadolepis* type, and *Cycadeospermum lovisatoi* Krasser, 1912 seeds

(Tab 1). *Otozamites veronensis* DE ZIGNO, 1881 (Edwards 1929, Comaschia Caria 1959), originally described by Krasser (1913) as *Otozamites lovisatoi* KRASSER, 1913 is missing from the samples in the Prague collection. The illustration does, however, confirm its (former) existence.

Krasser (1920) indicated several additional taxa not confirmed during the revision of the various collections. These include *Nilssonia compta* (PHILLIPS) BRONGNIART, 1828 (Krasser 1920: 11), *Nageiopsis anglica* SEWARD, 1900, *Otozamites beanii* (LINDLEY et HUTTON) BRONGNIART, 1848, *Ptilophyllum pecten* (PHILLIPS) MORRIS, 1841 (Krasser 1920: 12), *Taeniopteris vittata* BRONGNIART, 1831 and *Zamites* sp. (Krasser 1920: 13). Also not confirmed are the reproductive organs *Williamsonia leckenbyi* NATHORST, 1911 (Krasser 1912, 1913), *Williamsonia sewardii* KRASSER, 1913, *Williamsonia acuminata* (DE ZIGNO) KRASSER, 1912 and the seed *Cycadeospermum persicum* KRASSER, 1912 (Tab. 1).

The conifers are among the most abundant groups in this plant assemblage. They are represented by shoots of *Geinitzia divaricata* (BUNBURY) HARRIS, 1979, *Elatides williamsonii* (LINDLEY et HUTTON) NATHORST, 1897, *Elatocladus* sp., *Brachyphyllum expansum* (PRESL in STERNBERG) SEWARD, 1919 emend. Kendall 1949, *Brachyphyllum* sp. and *Pagiophyllum* sp. The wood fragment (Lov. B 128) might belong to *Agathoxylon* HARTIG, 1848, the ovuliferous scales to *Araucarites sardinicus* (KRASSER) KRASSER, 1920. *Brachyphyllum mamillare* BRONGNIART, 1828 and *Pityophyllum nordenskioldii* (HEER) SEWARD, 1919, listed by Krasser (1913, 1920), cannot be confirmed for this flora.

Several seed types with unknown botanical affinity were also recovered from the plant assemblage, such as the seeds *Carpolithes* sp. 1 sensu Scanu et al. (2015) and *Carpolithes* sp. 2 sensu Scanu et al. (2015); Edwards (1929) suggested they might belong to *Williamsonia*. Elongate, entire-margined leaf fragments, with secondary veins perpendicular to the midvein, here attributed to *Taeniopteris* sp. (Tab. 1), are also of ambiguous botanical affinity, but probably belonging to the cycadophytes, whereas the stem fragments named *Sardoa robitschekii* KRASSER, 1920 are probably Bennettitales.

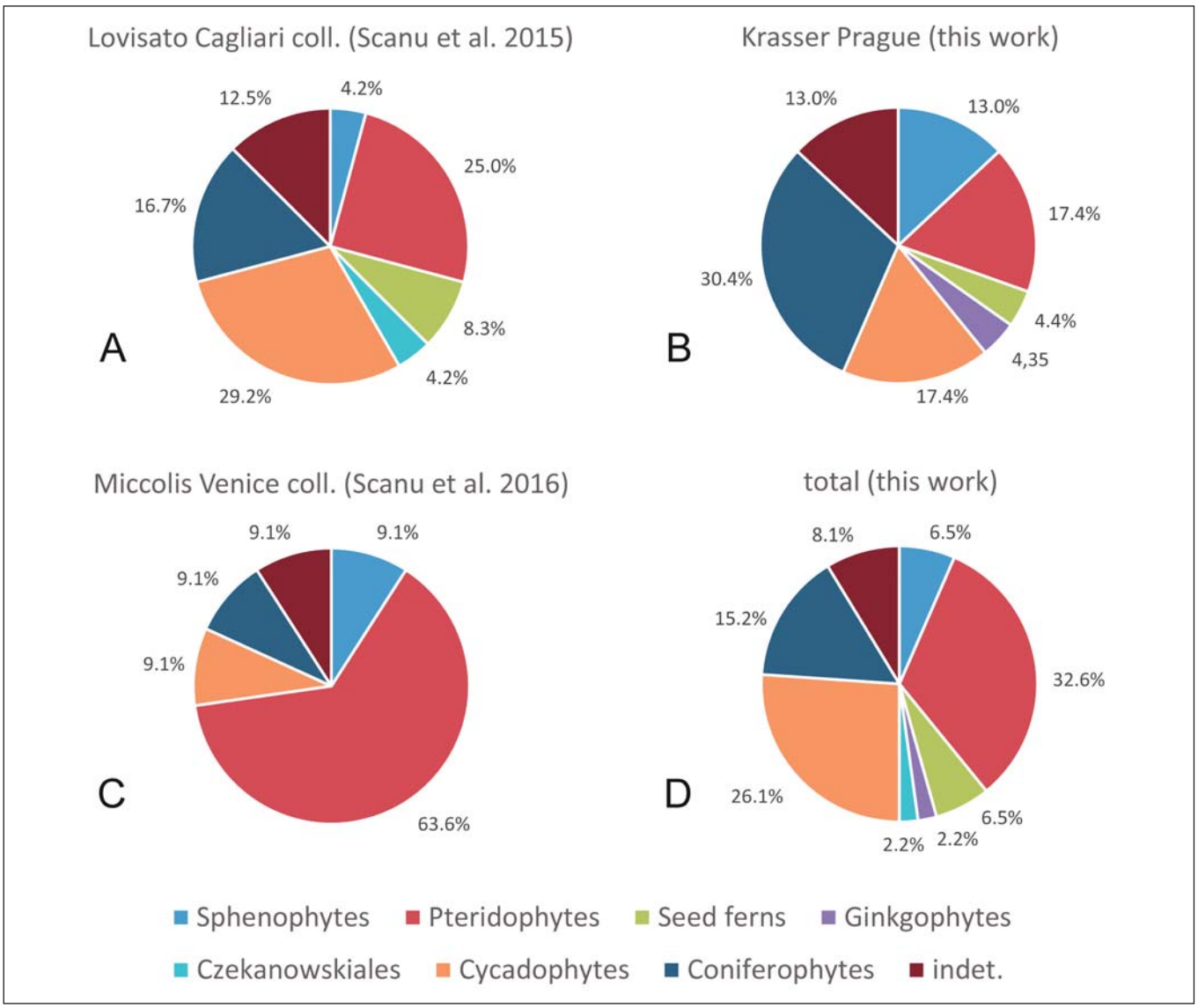
Here we do not consider the typical Triassic taxa taken by Tornquist (1904b), from a list of plant fossils identified by Sterzel, since those attributions were based on an erroneous stratigraphic allocation of the levels yielding plant fossils. This includes the sphenophyte stems *Equisetum arenaceum* (JAEGER) SCHENK, 1864, *Equisetum mougeotii* BRONGNIART, 1828 and *Calamites* sp., the fern stem *Caulopteris* sp., the seed fern leaf *Sagenopteris rhoifolia* PRESL, 1838 var. *elongata* BRAUN in MÜNSTER, 1843, the cycadophytes *Otozamites beanii* (LINDLEY et HUTTON) BRONGNIART, 1849 and *Pterophyllum* sp. cf. *P. braunianum* GOEPPERT, 1844, and the conifers *Voltzia* sp. and *Yuccites vogesiacus* SCHIMPER et MOUGEOT, 1844. Also not considered is the work of Comaschi Caria (1959), which represents a compilation of all historical taxa names through time.

Discussion of the three collections of plant fossils from Sardinia

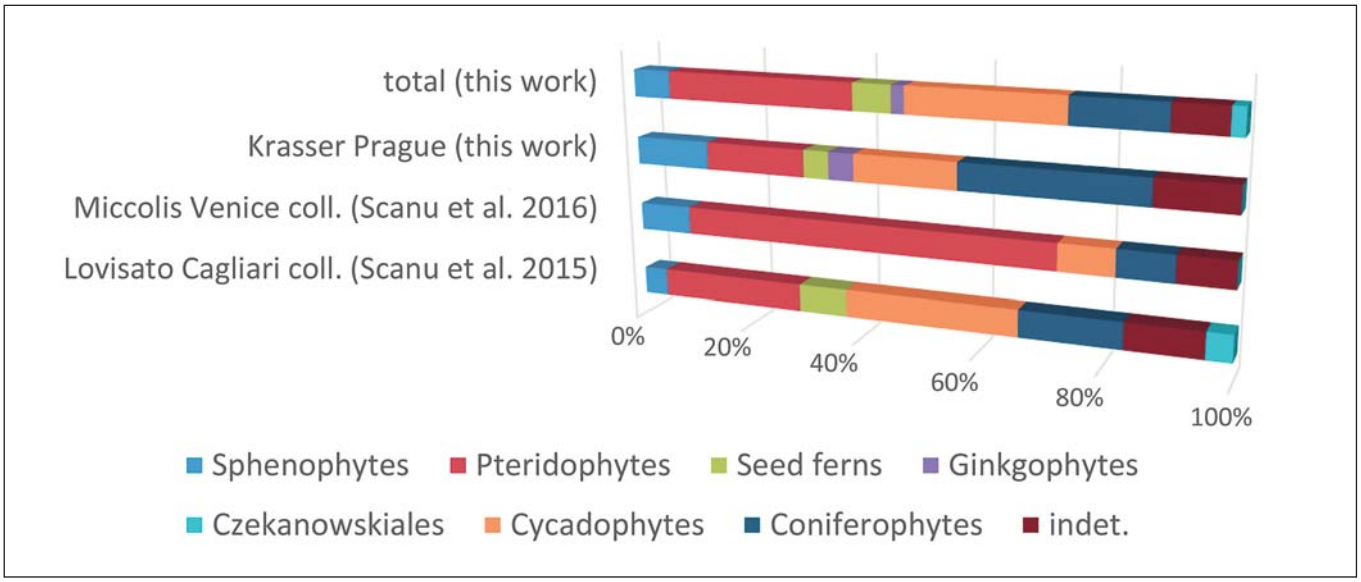
A recent revision (Scanu et al. 2015) of the Lovisato collection stored in Cagliari showed that the plant assemblage was composed of ferns (*Phlebopteris polypodioides*, *Hausmannia* sp., *Coniopteris* sp. cf. *C. hymenophylloides*, *Todites* sp. cf. *T. williamsonii*, *Cladophlebis* sp.), seed ferns (*Sagenopteris phillipsii*, *Ptilozamites* sp. cf. *P. blasii*), cycadophytes (*Nilssonia* sp., *Cycadeospermum lovisatoi*, *Pterophyllum* sp. cf. *P. thomasii*, *Ptilophyllum pectinoides*, *Ptilophyllum cariae*, *Williamsonia hildae*, *Weltrichia* sp., *Taeniopteris* sp.), Czekanowskiales (*Czekanowskia* sp. cf. *C. furcula*), conifers (*Geinitzia divaricata*, *Brachyphyllum expansum*, *Brachyphyllum* sp., *Elatocladus* sp.) and several types of seeds (*Carpolithes* sp. 1, *Carpolithes* sp. 2). The revision of the Domenico Miccolis Collection (Scanu et al. 2016), stored at the Natural History Museum of Venice added several taxa to this list, including the ferns *Dicksonia kendallii*, *Eboracia* sp. cf. *E. lobifolia*, *Marattia intermedia*, *Phlebopteris braunii* and *P. muensteri* and the bennettitalean microsporangiate reproductive organ *Weltrichia* sp. cf. *W. whitbiensis*. This paper, dealing with the second part of the Lovisato collection deposited in the Faculty of Sciences, Charles University, Prague, adds to this list horsetails (*Equisetites beanii*, *Equisetites columnaris*), ferns (*Cladophlebis denticulata*, *Hausmannia crenata*, *Phlebopteris dunkeri*), ginkgophytes (*Eretmophyllum lovisatoi*), cycadophytes (*Nilssonia* sp. cf. *N. orientalis*, *Cycadolepis* sp., *Ptilophyllum* sp. cf. *P. hirsutum*), conifers (*Araucarites sardinicus*, *Agathoxylon* sp., *Pagiophyllum* sp.) and a putative bennettitalean stem (*Sardoa robitschekii*).

The floral composition of the various plant assemblages, considered in terms of the number of fossil taxa (Tab. 1) and not relative abundances is noticeably different. The Lovisato collection in Cagliari (Text-fig. 1a) is the richest in its number of fossil taxa (24). Cycadophytes (29.2%) and ferns (25%) are the two most abundant groups in the Lovisato collection, while conifers are common (16.7%), horsetails and Czekanowskiales are rare (1 fossil taxon each: 4.2%) and ginkgophytes are absent. The Krasser collection (Lovisato B collection; Text-fig. 1b) in Prague is almost as diverse, with 23 fossil taxa (Text-fig. 1b). The three most abundant groups are the same as in the collection of Cagliari, although the conifers are the most diverse plant group (30.4%), followed by cycadophytes and ferns (each represented by four taxa (17.4%)). Horsetails are represented by three fossil taxa and thus common, whereas Czekanowskiales are absent from the Lovisato B collection.

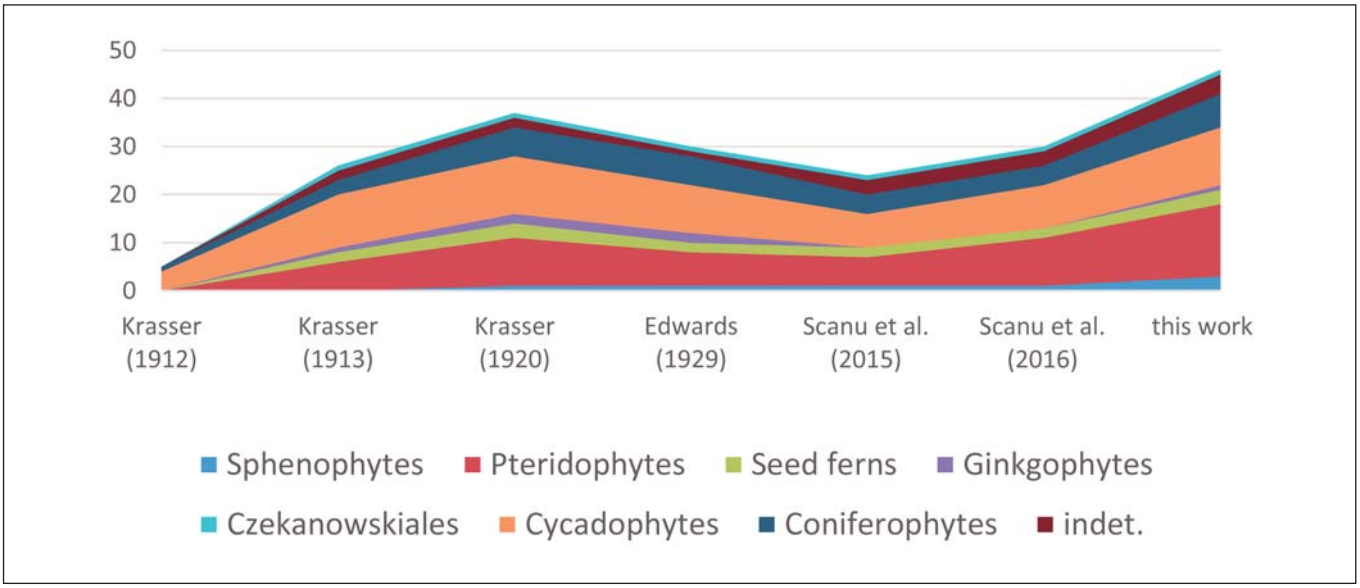
The Miccolis collection (Text-fig. 1c) is the least diverse plant assemblage, with only 11 fossil taxa. The most abundant are the ferns (63.6%), while seed ferns, ginkgophytes and Czekanowskiales are absent. This difference in composition, especially of the Miccolis collection, could be the result of a collecting bias. The specimens of the Miccolis collection are mostly well preserved and beautiful, typical for a fossil collector (Scanu et al. 2016). The two plant assemblages collected by Lovisato apparently come from different stratigraphic levels, and perhaps different geographic locations. Moreover, the Lovisato B collection (Krasser collection in Prague) was sent as an addition to the previously studied Lovisato A collection, and is thus composed mostly of material Lovisato apparently considered different from the A collection. This might explain the contrasting compositions of the three plant assemblages. The total flora (Text-figs 1d, 2), based on the three collections together, is composed mostly of ferns (32.6%), followed by cycadophytes (26.1%) and conifers (15.2%).



Text-fig. 1. Composition in taxa per plant group for different collections: a) composition of Lovisato A collection in Cagliari; b) composition of Lovisato B (Krasser) collection in Prague; c) composition of Miccolis collection in Venice; d) composition of total plant assemblage.



Text-fig. 2. Diagram showing contrast between compositions of the various collections and that of the total flora.



Text-fig. 3. Diagram showing how the composition of the Middle Jurassic flora of Sardinia changed through time, from papers of Krasser to more recent revisions (Krasser 1912, 1913, 1920, Edwards 1929, Scanu et al. 2015, 2016, this paper).

The known biodiversity of the Middle Jurassic flora of Sardinia has increased from 24 fossil taxa (Scanu et al. 2015) to 46 fossil taxa (this paper) just by adding further historical collections to our dataset (the original outcrops are no longer accessible, so no new taxa can be added by further sampling). By considering the papers starting with modern revisions, Text-fig. 3 shows how, from the few taxa described by Krasser (1912), there was a strong increase (from five fossil taxa to 37 fossil taxa) due to Krasser (1913, 1920) having studied more material. Edwards (1929) reduced the number of taxa with his revision of the collection stored in Prague. The study of the three collections carried out in the last few years (Scanu et al. 2015, 2016, this paper) has increased diversity again, up to 46 taxa in this paper. However, the curve still shows a definitive increase through time, indicating that the real biodiversity of the Middle Jurassic flora of Sardinia was somewhat higher (Text-fig. 3).

Conclusions

The Lovisato "collection B", described by Krasser (1920) and Edwards (1929), and preserved in the Faculty of Sciences, Charles University, Prague, differs noticeable from "collection A" described previously by Krasser (1912, 1913), and stored in the Cagliari University. *Cycadolepis* sp., *Nilssonia* sp. and *Nilssonia* sp. cf. *N. orientalis*, *Pagiophyllum* sp. and *Agathoxylon* sp. were previously not known from the Jurassic of Sardinia. On the other hand, *Coniopteris* sp. cf. *C. arguta*, *Dictyophyllum rugosum*, *Klukia exilis*, *Laccopteris elegans* and *Laccopteris spectabilis* (ferns), *Sagenopteris goeppertiana* and *Gristhorpia nathorstii* (seed ferns), *Baiera phillipsii* (ginkgophytes), *Cycadeospermum persicum*, *Nageiopsis* (= *Otozamites*) *anglica*, *Nilssonia compta*, *Otozamites beanii*, *Otozamites veronensis*, *Ptilophyllum pecten*, *Taeniopteris vittata*, *Zamites* sp., *Williamsonia acuminata*, *Williamsonia leckenbyi* and *Williamsonia sewardii* (cycadophytes), *Brachyphyllum mamillare* and *Pityophyllum nordenskioldii* (conifers) could not be confirmed, because they were either missing from the collection or too badly preserved to confirm the determinations. Therefore, the Middle Jurassic flora of Sardinia currently comprises 46 fossil taxa. The three plant fossil collections differ noticeably. Cycadophytes (especially bennettitaleans) dominate the Cagliari collection, ferns the Venice collection, and conifers are the most important group (in diversity and abundance) in the Prague collection. Horsetails are the most abundant plant group in the Krasser collection, although not very diverse. A distinct collecting bias is postulated for the Venice collection, whereas the Cagliari and Prague collections might belong to different stratigraphic levels. Study of the three plant fossil collections indicates a diverse Middle Jurassic flora of Sardinia, although the hidden biodiversity is still very high. This underlines a general problem with allochthonous Palaeozoic and Mesozoic plant assemblages, that they provide a highly fragmented and incomplete picture of the past vegetation.

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Explanations to the plates

PLATE 1

Sphenophytes and ferns
1. *Equisetites columnaris* (Brongniart) Phillips; stem fragment with two leaf sheaths; Lov. B 2.
2. *Equisetites columnaris* (Brongniart) Phillips; nodal fragment with leaf traces; Lov. B 9.
3. *Equisetites columnaris* (Brongniart) Phillips; stem fragment; Lov. B 10.
4. *Equisetites beanii* (Bunbury) Seward; stem fragment; Lov. B 17.
5. *Equisetites beanii* (Bunbury) Seward; stem fragment; Lov. B 17.
6. *Phlebopteris dunkeri* (Schenk) Schenk; frond fragment with partially preserved pinnae; Lov. B 64.
7. *Phlebopteris dunkeri* (Schenk) Schenk; pinna fragment showing reticulate venation; Lov. B 73.
8. *Phlebopteris polypodioides* Brongniart; fertile pinnae fragment indicating position of sori; Lov. B 95.
9. *Todites williamsonii* (Brongniart) Seward; small sterile fragment showing venation; Lov. B 16.4.
10. Sphenophyte nodal fragment with attached microphylls; possibly *Schizoneura* sp.; Lov. B 49.1.
11. Sphenophyte nodal fragment with attached microphylls; possibly *Schizoneura* sp.; Lov. B 49.2.

All scale bars – 10 mm.

PLATE 2

Seed ferns, Cycadophyta, Ginkgophyta and incertae sedis
1. *Nilssonia* sp. cf. *N. orientalis* Heer; leaf fragment with undivided secondary veins; Lov. B 35.
2. *Sagenopteris* sp.; fragment of leaflet, with clear venation; Lov. B 35.
3. *Sardoa robitschekii* Krasser; stem fragment; Lov. B 46.
4. *Ptilophyllum* sp.; leaf fragment with slightly falcate segments; Lov. B 65.
5. *Eretmophyllum lovisatoi* Edwards; partially preserved leaf used for cuticular identification; Lov. B 66.1.
6. *Ptilophyllum* sp.; leaf fragment; Lov. B 63.1.
7. *Eretmophyllum lovisatoi* Edwards; partially preserved leaf, Lov. B 67.

All scale bars – 10 mm.

PLATE 3

Branchiopods and conifers
1. *Geinitzia divaricata* (Bunbury) Harris; large shoot fragment with clear leaf scars; Lov. B 29.
2. *Araucarites sardinicus* (Krasser) Krasser; ovuliferous scale with single, large seed; Lov. B 56.
3. *Araucarites sardinicus* (Krasser) Krasser; ovuliferous scale with single, large seed; Lov. B 50.
4. Branchiopod, formerly called *Estheria*; Lov. B 98.
5. *Elatides williamsonii* (Lindley et Hutton) Nathorst; shoot fragment; Lov. B 72.
6. Branchiopod, formerly called *Estheria*; Lov. B 99.
7. *Geinitzia divaricata* (Bunbury) Harris; shoot fragments with leaves; Lov. B 92.1.
8. *Pagiophyllum* sp., shoot fragment with very small leaves; Lov. B 99.
9. *Elatides williamsonii* (Lindley et Hutton) Nathorst; shoot fragment; Lov. B 122.

All scale bars – 10 mm.

PLATE 1

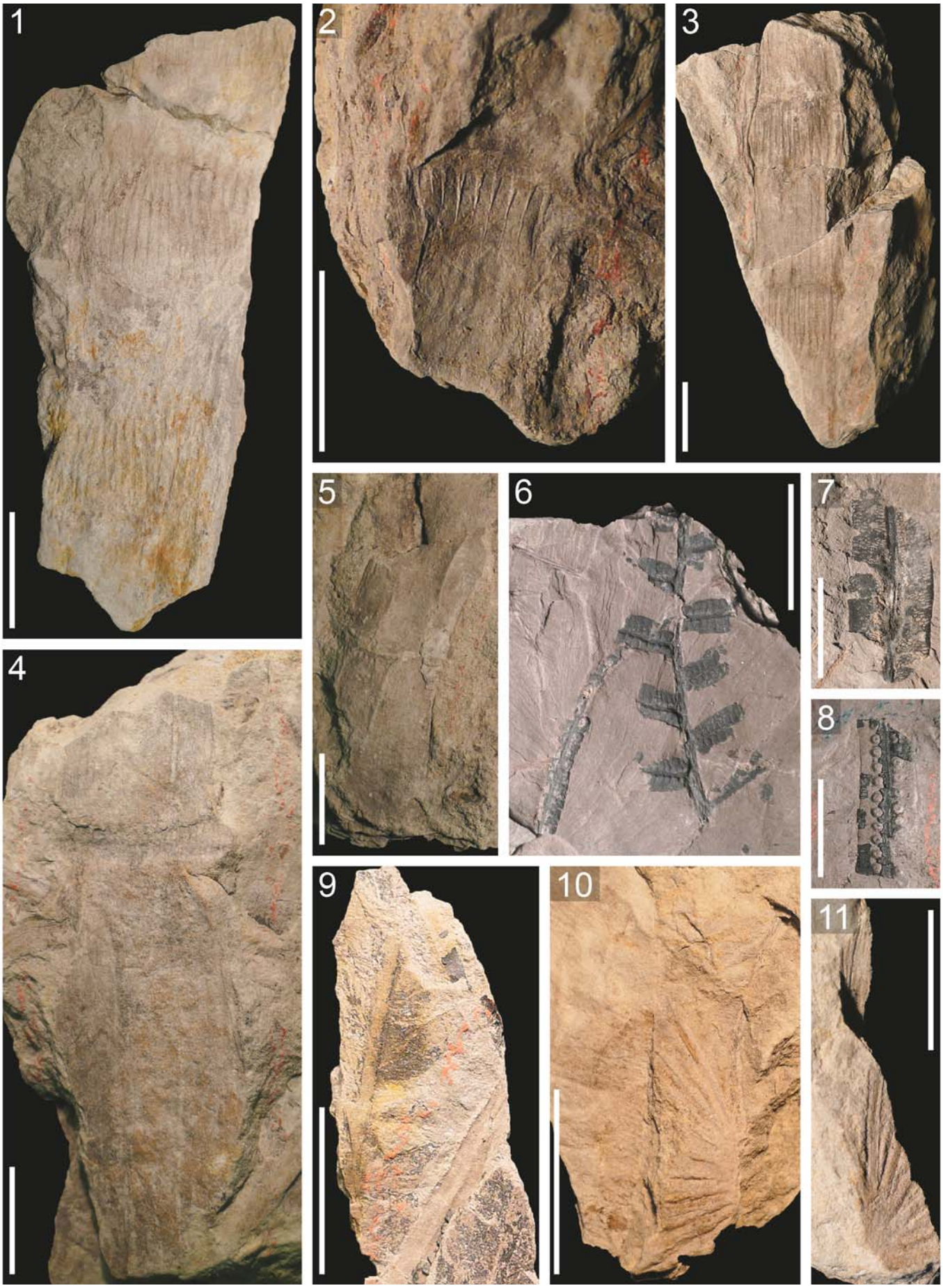

PLATE 2

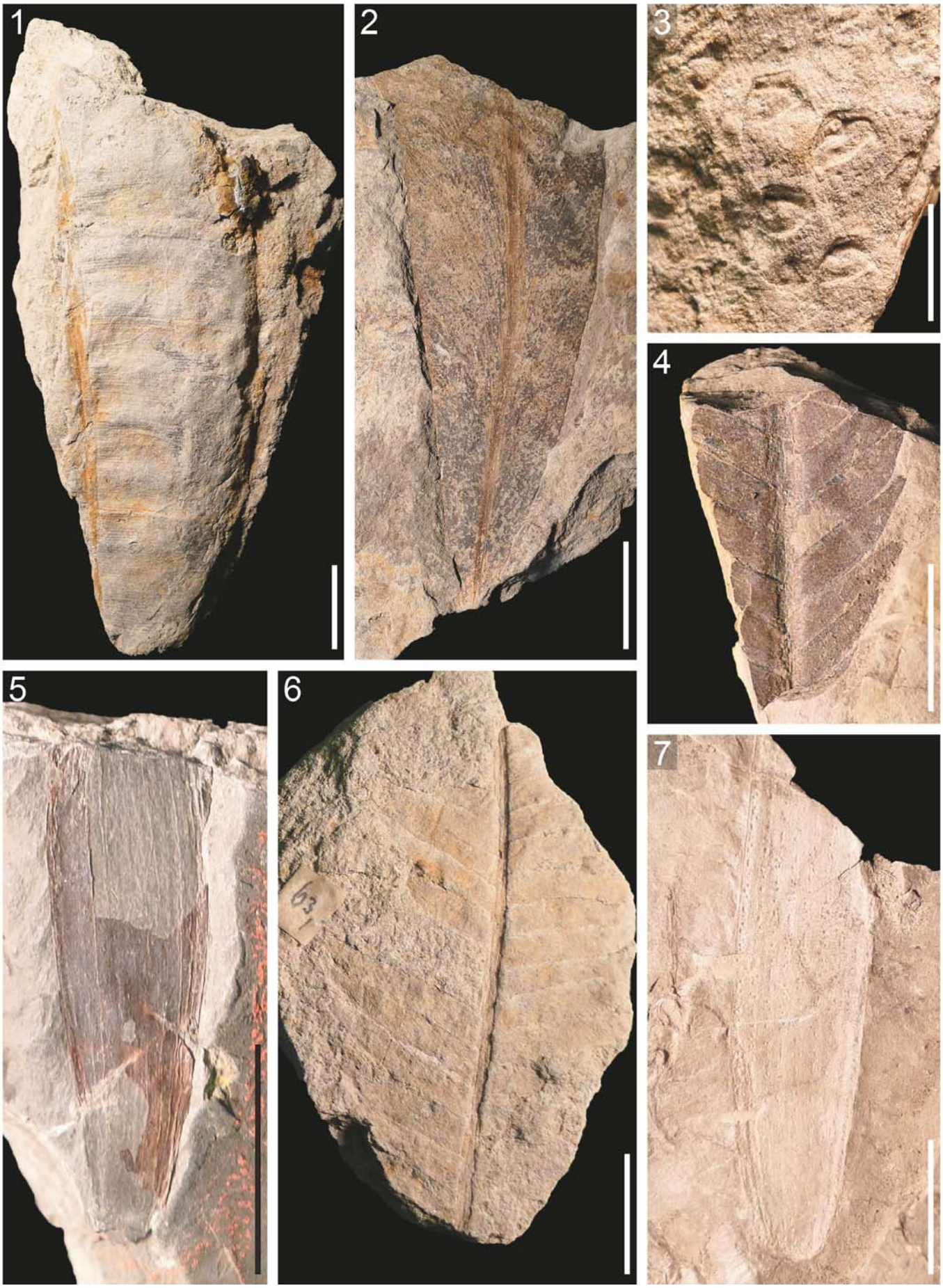

PLATE 3