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MIDDLE TRIASSIC (ANISIAN) FERNS FROM KÜHWIESENKOPF (MONTE PRÁ DELLA VACCA), DOLOMITES, NORTHERN ITALY

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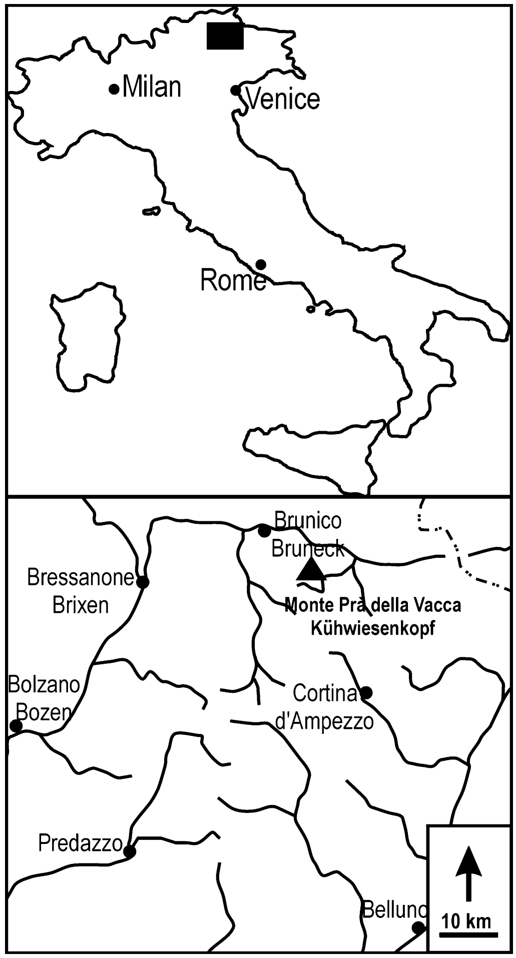
Abstract: This papers deals with the description of the ferns found in the recently discovered Anisian locality of Kühwiesenkopf (Monte Prà della Vacca). A revision of the genera and species involved has been undertaken where necessary. Because of transitional material found at Kühwiesenkopf, the number of *Neuropteridium* species found in the European Middle Triassic floras is reduced from five to three: *N. voltzii* (Brongniart) Schimper, *N. elegans* (Brongniart) Schimper and *N. grandifolium* (Schimper et Mougeot) Compter. The fertile material attributed to this genus is transferred from the illegitimately published genus *Crematopteris* Schimper and Mougeot to the genus *Scolopendrites* Goeppert, in two species: *S. scolopendrioides* (Brongniart) comb. nov. and *S. grauvogelii* sp. nov. *Anomopteris mougeotii* Brongniart is unequivocally recorded for the first time from Italy. *Gordonopteris lorigae* gen. et sp. nov. is described for tripinnate fern fronds without the aphlebiae typical for the bipinnate genus *Anomopteris* but in which both sterile and fertile pinnule resemble closely those from that genus. Two probable marattialean ferns are described and recorded for the first time from the Middle Triassic of Italy: *Marattiopsis* sp. and *Marantoidea* sp. The nomenclature of the latter genus is discussed. Some ferns attributed to morphogenera are also described, namely: *Sphenopteris schoenleiniana* (Brongniart) Presl, *Cladophlebis remota* (Presl) comb. nov. and *Cladophlebis* sp. Moreover, two specimens from Kühwiesenkopf are described under gen. et sp. indet. as we are unsure if they are ferns or seed ferns. Similar material has been described from the Scythian of China as *Neuropteridium curvinerve* Wang and Wang.

Key words: fossil ferns, Dolomites, Italy, Middle Triassic, Anisian.

LOWER Triassic to lower Middle Triassic floras from the German Basin have long been known (e.g. from France: see Schimper *et al*. 1844; Fliche and Berger-Levrault 1910; Grauvogel-Stamm 1978; from Germany: see Blanckenhorn 1886; Schimper 1869; Frentzen 1914; Mägdefrau 1931; Gothan 1937; Fuchs *et al*. 1991) but contemporary floras from the Alpine Basin are rare. Apart from the flora of Recoaro (de Zigno 1862; Schenk 1868) only younger Triassic floras have been described, such as the Ladinian flora from the Dolomites (e.g. Leonardi 1953; Wachtler and van Konijnenburg-van Cittert 2000; Kustatscher *et al*. 2004) and Carnian floras from Austria (e.g. the wel-known Lunz flora: see, e.g. Dobruskina 1994, 1998), Switzerland (e.g. Neue Welt: Leuthardt 1903–04; Kräusel 1955, 1959; Kräusel and Schaarschmidt 1966) and Italy (e.g. Raibl: Stur 1885; Monte Pora: Passoni and van Konijnenburg-van Cittert 2003).

In 1999, a rich stratiform plant level was discovered by one of us (MW) in the Anisian (lower Middle Triassic) succession of Kühwiesenkopf (= Monte Prà della Vacca in Italian; the area is bilingual) in the Pragser (= Braies in Italian) Dolomites, northern Italy (in the rest of the manuscript we refer simply to Kühwiesenkopf and Prags). It is contained in the Dont Formation, a hemipelagic carbonate-terrigenous succession of a marginal basin environment, and traditionally dated as Pelsonian–Illyrian (Delfrati *et al*. 2000, and references therein). Biostratigraphical analyses, based on foraminifers, palynomorphs, brachiopods and ammonoids, indicate a Pelsonian age for the bed (1 m thick) in which fossils are concentrated in several cm-thick layers (Broglio Loriga *et al.* 2002). The fossil assemblage contains a terrestrial biota, with very abundant plant remains and a single reptile, as well as a marine biota (fishes, bivalves, brachiopods and ammonoids).

The first report on the macroflora (Broglio Loriga *et al.* 2002) provided a preliminary list of macrofloral remains. The current paper deals in detail with the ferns from the locality. The ferns comprise approximately 25 per cent of the fossil plant assemblage, a percentage that is roughly the same for conifers and cycadophytes as well; the remainder of the assemblage consists of about 10 per cent lycophytes and about 10 per cent seedferns, while horsetails occur but are rare (< 2 per cent); some unidentified taxa also occur in small quantities. Some of the ferns are common in the assemblage (e.g. two *Neuropteridium* species with their fertile fronds named *Scolopendrites*, *Anomopteris mougeotii* and *Gordonopteris lorigae*), some are more scarce (e.g. the *Sphenopteris* and *Cladophlebis* species) and some are very rare (e.g. ?*Marattiopsis* sp. and *Marantoidea*). We have had to deal with a number of nomenclatorial problems, mainly related to some of the old publications that appeared almost at the same time. With the help of the IAPT (International Association of Plant Taxonomists), we have tried to solve these problems and apply the correct names to all the species.



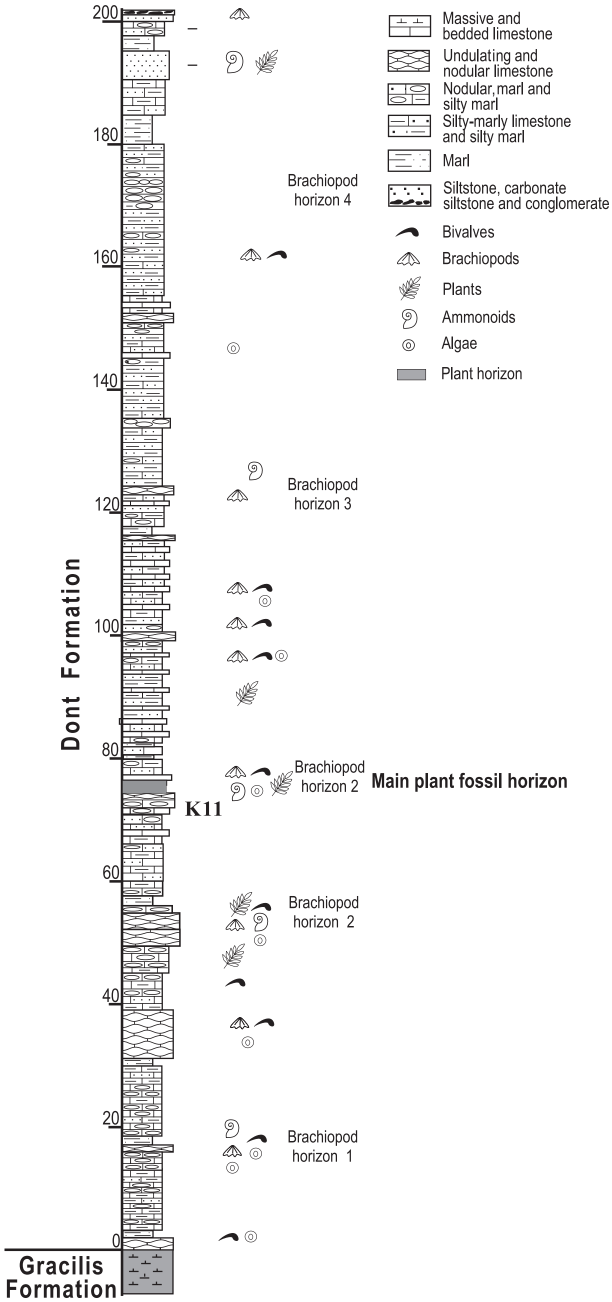
TEXT-FIG. 1. Map indicating the location of the Kühwiesenkopf locality.

MATERIAL AND METHODS

The plant horizon crops out for several hundred metres along steep gullies furrowing the western slope of Kühwiesenkopf mountain, inside the Natural Park of Prags (Text-fig. 1). Stratigraphically it is located in the lower part of the Anisian basinal succession (Text-fig. 2), nowadays called the Dont Formation (for details, see Broglio Loriga *et al.* 2002). The Dont Formation of the Dolomites is traditionally considered to be Pelsonian–Illyrian in age (Delfrati *et al.* 2000, and references therein). In this section, studied in detail by Bechstädt and Brandner (1970), the Dont Formation is more than 200 m thick, and the plant-bearing beds are about 75 m above a massive carbonate platform previously known as 'Algenwellenkalk' (Bechstädt and Brandner 1970), and now assigned to the Gracilis Formation (De Zanche *et al.* 1992; Gianolla *et al.* 1998). According to De Zanche *et al.* (1993), the lower part of the Dont Formation is equivalent to the Voltago Conglomerate of the Dolomites and to the *Voltzia* beds of Recoaro.

The plant horizon is about 1 m thick and situated just above bed K11 of Bechstädt and Brandner (1970) (Text-fig. 2). Plants are concentrated in several cm-thick layers of siltstone, marly siltstone and carbonate siltstone, which are lens-shaped, and change in number and thickness laterally. They alternate with silty and marly limestone layers, in which only sparse terrestrial plant remains occur. Marine biota (e.g. bivalves, brachiopods, ammonoids and fishes) are present, though not abundant, throughout the horizon (Broglio Loriga *et al.* 2002).

The specimens have been studied with the aid of a dissecting microscope, and when possible, *in situ* spore preparations were made. For this purpose, single sporangia or clusters of sporangia were macerated in Schulze's reagent ($KClO_3$ and 30 per cent HNO_3) and neutralized with 5 per cent ammonium hydroxide. The sporangia were then separated into single or groups of spores (depending on the maturity of the spores) with the aid of needles. The spores were mounted in glycerine jelly and sealed with paraplast. Some of the sporangia and spores were examined under a scanning electron microscope (SEM) at the University of Utrecht.



TEXT-FIG. 2. Stratigraphic column of the section (modified from Broglio Loriga *et al.* 2002). The main plant horizon occurs just above bed K11 of Bechstädt and Brandner (1970). Plant debris is also present in several other layers in the section and their location is indicated in the stratigraphic column.

The majority of the macrofossil plant collection from Kühwiesenkopf, including all figured specimens, and the palynological preparations, are stored at the Natural History Museum in Bolzano (Italy). They all have the specimen code KÜH followed by a number. The remainder of the collection is in Wachtler's Museum Dolomythos at Innichen (San Candido, Italy).

SYSTEMATIC PALAEONTOLOGY

Order FILICALES Bower, 1899

Family?OSMUNDACEAE Bercht. and Presl, 1820

Genus NEUROPTERIDIUM Schimper, 1879

Remarks. Brongniart (1828*a*–*c*) attributed two species from the famous Triassic Grès bigarré in the Vosges to the genus *Nevropteris*, namely *N. elegans* and *N. voltzii*. In 1844, Schimper and Mougeot described three new species from this flora, changing the genus name to *Neuropteris*: *N. grandifolia*, *N. imbricata* and *N. intermedia*, and included all these *Neuropteris* species in the subgenus *Neuropteridium* to distinguish them from the Carboniferous *Neuropteris* species, which are characterized by bipinnate fronds. Later, Schimper (in Schimper and Schenk 1879) raised the subgenus *Neuropteridium* to the rank of a genus without indicating a type species (Farr *et al.* 1979). In most of the literature (see Andrews 1970), *N. grandifolium* is indicated as the type species; however, Grauvogel-Stamm (1978) considered *Neuropteridium voltzii* (Brongniart) Schimper (the species first described by Brongniart 1828) to be the type species.

Neuropteridium is characterized by a globular–ovoid rhizome with simply pinnate fronds; the pinnules, which show typical neuropterid venation, arise more or less perpendicularly from the rachis, and are usually contracted at their base or have an auriculate base. Of the five species mentioned above, *N. grandifolium* is distinguished by its large, obtuse pinnules (average length around 5 cm, width 2·5 cm); the upper basal angle of the pinnules is auriculate while the lower one is decurrent; veins dichotomise up to four times. We have not encountered similar forms in the Anisian flora from Kühwiesenkopf, but intend to maintain the species as it seems to be different in size and shape from all the other material.

Neuropteridium voltzii has long fronds reaching a length of almost 1 m (according to Blanckenhorn 1886) with a broad rachis (up to 1 cm wide) and pinnules that can be even longer (perhaps up to 8 cm but usually 4–5 cm long) but their width is usually only 1 cm; pinnules are attached almost by their whole base and are only slightly auriculate; their apex is rounded-acute and the venation is characterized by a distinct midrib and a large number of secondary veins that fork several times. In 1886 Blanckenhorn described *N. bergense* from the Buntsandstein of the neighbourhood of Floisdorf (Germany). This species consists of fronds that are 30–45 cm long and have a rachis *c.* 5 mm wide; the imbricate (overlapping) pinnules are around 3 cm long and 5–6 mm wide with an obtusely acute apex. They are much longer than wide (4–6 times). The pinnules, which are slightly constricted at their base, are somewhat auriculate, especially at the lower angle. The midrib is often slightly decurrent and the dense secondary veins fork up to three times. In our opinion, *N. voltzii* and *N. bergense* are conspecific (the latter being simply an imbricate form of the first). Previously, Blanckenhorn (1886, p. 129) stated that the two species (and indeed also *N. intermedium*) are difficult to distinguish. Both forms also occur in the Anisian flora of Kühwiesenkopf. As *N. voltzii* (Brongniart) Schimper has priority over *N. bergense*, the latter species becomes a junior synonym.

Neuropteridium intermedium (Schimper and Mougeot) Schimper has (according to Blanckenhorn 1886) fronds *c.* 65 cm long with a thinner rachis than the two species mentioned above (maximum width *c.* 6 mm, usually narrower), and obtuse pinnules that are up to 2·5 cm long and 6–8 mm wide, and slightly contracted at their base. The length of the pinnules may reach 1–3 times their width. The pinnules are usually crowded and therefore it is quite possible that *N. imbricatum* (Schimper and Mougeot) Schimper (1844, p. 77, pl. 36, figs 2–5), just differing in overlapping pinnules, is only the middle part of a frond of *N. intermedium*. This view is strengthened by the fact that there are only two fragments of *N. imbricatum* known, while *N. intermedium* is quite common. *N. elegans* (Brongniart) Schimper has small fronds (up to 15 cm long according to Schimper and Mougeot 1844) with a narrow rachis (*c.* 2 mm wide) and densely placed obtuse pinnules. Schimper and Mougeot (1844, p. 81) mentioned that this species is very like *N. intermedium*, differing only in the smaller size of both fronds and pinnules, and by the fact that the pinnules almost always either overlap or lack any space between them. As the two forms occur together, not only in the Vosges (e.g. Schimper and Mougeot 1844; Grauvogel-Stamm 1978), but also in the Buntsandstein flora of Germany (Blanckenhorn 1886, pls 18–19) and in the Anisian flora of Kühwiesenkopf, we believe that they are conspecific, *N. elegans* being young fronds of *N. intermedium*. As *N. elegans* (Brongniart, 1828) Schimper, 1879 has priority over *N. intermedium* (Schimper and Mougeot, 1844) Schimper, 1879, the latter becomes a junior synonym. It is the same for *N. imbricatum* (Schimper and Mougeot, 1844) Schimper, 1879, as discussed above.

The original figures of *N. elegans* in Brongniart (1828*b*; pl. 74, figs 1–2) show pinnules that are intermediate in size between *N. elegans* and *N. intermedium* in Schimper and Mougeot (1844, pls 39 and 38, respectively). In particular Brongniart's plate 74, figure 1 shows a frond fragment that is over 12 cm long without any trace of the base or apex. Therefore, the frond must have been longer than the 15 cm given by Schimper and Mougeot (1844) in their diagnosis of *N. elegans*.

In conclusion, we think that we are dealing with only two *Neuropteridium* species in the flora from Kühwiesenkopf, *N. elegans* and *N. voltzii*, differing from one another in the width of the rachis (much thicker in *N. voltzii* than in *N. elegans*) and the shape of the pinnules, including the length/width ratio.

Not many other species have been correctly assigned to *Neuropteridium*. Most come from Carboniferous–Permian sediments and could be better placed in *Neuropteris* or *Botrychiopsis*, also because no fertile foliage of the *Scolopendrites*-type has been found associated with it (see below). These plants are almost certainly not ferns but seed-ferns (see Archangelsky and Arrondo 1971). From Scythian and Anisian layers (Early and Middle Triassic) in China definite *Neuropteridium* material has been described: *N. voltzii* with *Crematopteris* (= *Scolopendrites*) sp. (Meng 2000), *Neuropteridium* sp. associated with *Crematopteris* sp. (Wang and Wang 1990), and *N. curvinerve* Wang and Wang, 1990, which we discuss in a later section of this paper as its assignment to *Neuropteridium* is equivocal. Zhou and Li (1979) described *Neuropteridium marginatum* from the Scythian flora of Hainan Island, China. This species differs from all other *Neuropteridium* species in having pinnules with a thick texture and a narrow thin marginal zone.

Neuropteridium elegans (Brongniart, 1828) Schimper, 1879
Plate 1, figures 1–2, 8; Text-figure 5A

Selected synonymy

1828*a* *Nevropteris elegans* Brongniart, p. 54 (name only).
1828*b* *Nevropteris elegans* Brongniart, p. 247, pl. 74, figs 1–2.
1828*c* *Nevropteris elegans* Brongniart, p. 441.

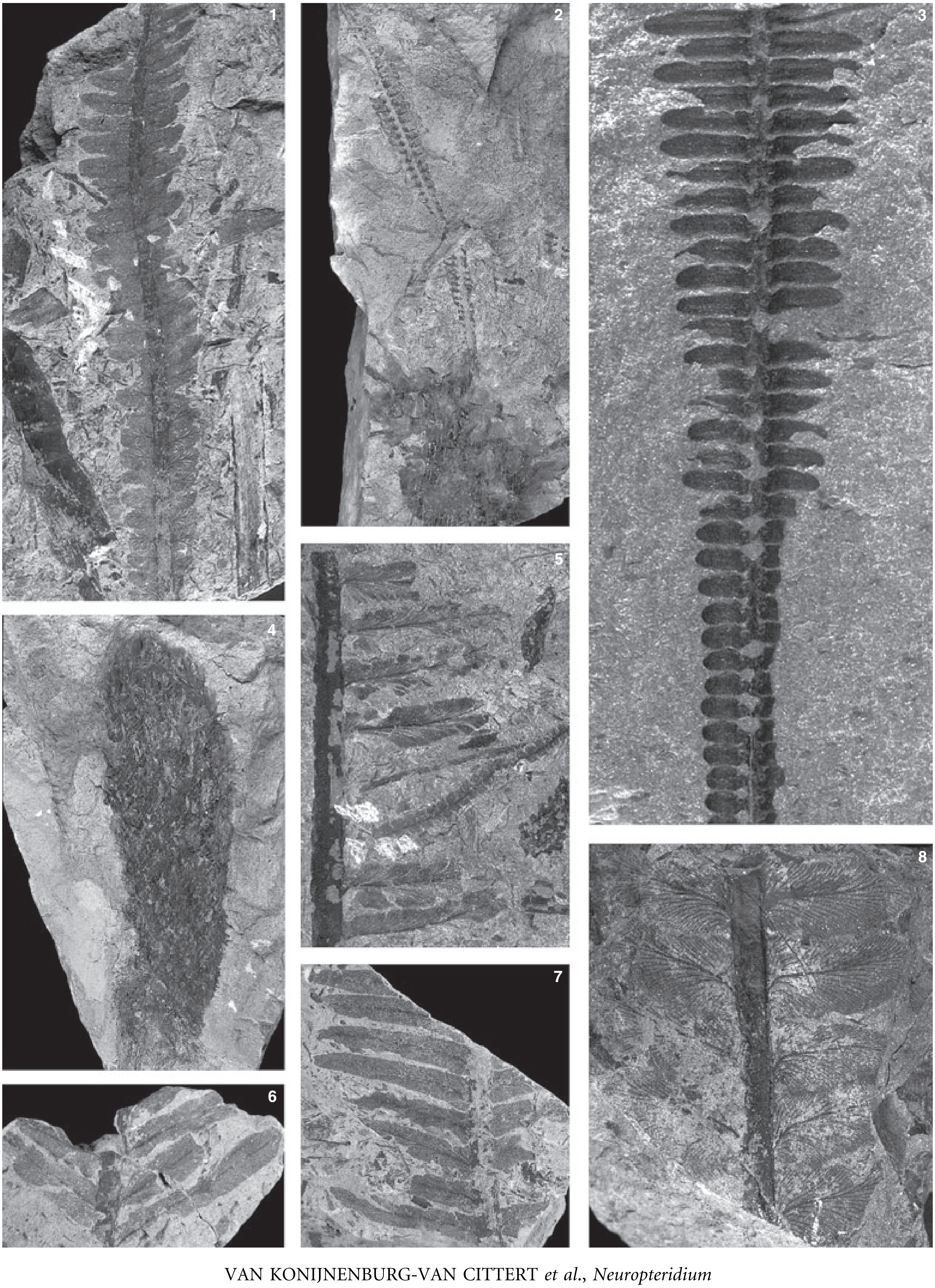
EXPLANATION OF PLATE 1

Figs 1–2, 8. *Neuropteridium elegans* (Brongniart) Schimper and Mougeot. 1, frond fragment showing the transition between the *elegans* and the *intermedium* form, KÜH970; × 1. 2, fronds attached to a rhizome fragment, KÜH220; × 0·5. 8, detail of venation, KÜH557; × 1·5.

Figs 3, 5–7. *Neuropteridium voltzii* (Brongniart) Schimper. 3, frond fragment, KÜH973; × 1. 5, poorly preserved fragment resembling *Asplenites palmetta* (Brongniart) Goeppert, KÜH516; × 1. 6, detail of venation, KÜH522; × 1. 7, frond fragment with detail of venation, KÜH818; × 1.

Fig. 4. Ovoid rhizome of *Neuropteridium* sp., KÜH244; × 0·5.

PLATE 1



VAN KONIJNENBURG-VAN CITTERT *et al.*, *Neuropteridium*

1844 *Neuropteris imbricata* Schimper et Mougeot subgenus *Neuropteridium* Schimper; Schimper and Mougeot, p. 77, pl. 36, figs 2–5.
1844 *Neuropteris intermedia* Schimper et Mougeot subgenus *Neuropteridium* Schimper; Schimper and Mougeot, p. 79, pl. 38.
1844 *Neuropteris elegans* Brongniart subgenus *Neuropteridium* Schimper; Schimper and Mougeot, p. 80, pl. 39.
1869 *Neuropteris elegans* Brongniart subgenus *Neuropteridium* Schimper; Schimper, p. 449.
1879 *Neuropteridium elegans* (Brongniart) Schimper; Schimper and Schenk, p. 117.
1886 *Neuropteridium intermedium* Schimper et Mougeot; Blanckenhorn, p. 127, pl. 17, figs 3–6; pls 18–19.
1890 *Neuropteridium elegans* (Brongniart) Schimper; Schimper and Schenk, p. 117.
1910 *Neuropteridium intermedium* Schimper; Fliche, p. 99.
1910 *Neuropteridium elegans* Schimper; Fliche, p. 100.
1910 *Neuropteridium intermedium* Schimper; Seward, p. 521, fig. 349.
1928 *Neuropteridium intermedium* Schimper; Schmidt, p. 70, fig. 77.
1928 *Neuropteridium elegans* Schimper; Schmidt, p. 70, fig. 78.
1928 *Neuropteridium imbricatum* Schimper; Schmidt, p. 70, fig. 79.
1931 *Neuropteridium elegans* Schimper; Mägdefrau, p. 301.
1937 *Neuropteridium elegans* Schimper; Gothan, p. 355, pl. 31, fig. 4.
1956 *Neuropteridium intermedium* Schimper; Mägdefrau, p. 214, fig. 200.
1956 *Neuropteridium imbricatum* Schimper; Mägdefrau, p. 217, fig. 204b.
1978 *Neuropteridium elegans* (Brongniart) Schimper et Mougeot; Grauvogel-Stamm, p. 26, pl. 2, fig. 3.
1978 *Neuropteridium* cf. *intermedium* Schimper et Mougeot; Grauvogel-Stamm, p. 26, pl. 2, fig. 4.
1994 *Neuropteridium intermedium*; Sander and Gee, p. 120, fig. 12.6.
2002 *Neuropteridium elegans* (Brongniart) Schimper et Mougeot; Broglio Loriga *et al.*, p. 385.
2004 *Neuropteridium elegans* (Brongniart) Schimper; Kustatscher, p. 134, pl. 3, fig. 1.

Description. *Neuropteridium elegans* is a relatively common fossil in the flora of Kühwiesenkopf (over 100 specimens), occurring usually as small frond fragments (up to 10 cm long), but several specimens show (round to ovoid) rhizomes with frond fragments attached (e.g. KÜH050, 219, 220, 243, 684), and several other specimens demonstrate longer fronds, often with the transition between the *N. elegans* and *N. intermedium* form (e.g. KÜH223, 505, 532, 771, 970).

Rhizomes with attached frond fragments (Pl. 1, fig. 2) are more or less global in shape with a diameter of around 5–6 cm, although some of the rhizomes found are ovoid (Pl. 1, fig. 4). The number of petioles or frond fragments attached to the rhizomes is usually small. Petioles are usually not much wider than the rachis in the lower part of the frond (3–5 mm). The rachis in the middle part of the frond is *c.* 3 mm thick while it decreases to 1 mm towards the apex. However, no complete frond was found. The petiole is usually *c.* 2–3 cm long before pinnules begin to arise. Basal pinnules are small (*c.* 4 × 2–3 mm; see Pl. 1, fig. 1); pinnule size increases rapidly up to *c.* 15–20 × 6–7 mm but decreases again towards the apex. The venation is typically neuropterid with a clear midrib that extends about one-half to two-thirds of the pinnule length and the secondary veins that diverge and fork up to three times (Pl. 1, fig. 8; Text-fig. 5A).

Discussion. As mentioned in the discussion of *Neuropteridium*, and according to our observations on the *Neuropteridium* material from Kühwiesenkopf, we believe that the three species, *N. elegans*, *N. intermedium* and *N. imbricatum*, as described by Schimper and Mougeot (1844) from the Anisian of the Vosges fall within the natural variability of one species, and should therefore be merged into *N. elegans*, which has nomenclatural priority. In fact several specimens in our collection demonstrate the transition from the *elegans* form to the *intermedium* form (Pl. 1, fig. 1).

Apart from the Vosges (from where Brongniart's type material also originated) the species has been recorded from Buntsandstein floras at various localities in Germany. For example, Blanckenhorn (1886) described *N. intermedium* from the region around Kommern in the text of his paper but some of his figures (e.g. pl. 17, figs 3–6) resemble the *elegans* form closely. Gothan (1937) described a small fragment of *N. elegans* from Üdingen, and discussed the possibility that *N. elegans* and *N. intermedium* are conspecific, but he could not demonstrate this with his own material.

Blanckenhorn (1886) described and figured in his plate 18 a large specimen with a small (diameter *c.* 6 cm) globose rhizome with at least five fronds attached to it. Sander and Gee (1994) refigured the specimen, as did Seward (1910) and Mägdefrau (1956). We never found more than three fronds attached to a rhizome but this may be owing to lack of preservation. Grauvogel-Stamm (1978, p. 27, pl. 2, fig. 4) indicated that several entire plants have been found with a rhizome. Her plate 2, figure 4 is the counterpart of a specimen showing a trunk with 10–12 fronds (Grauvogel-Stamm, pers. comm. 2003).

It is not clear if the more ovoid rhizomes encountered at Kühwiesenkopf (e.g. KÜH241, 244; Pl. 1, fig. 4) also belong to this species or may have belonged to *N. voltzii* or to another plant.

Neuropteridium voltzii (Brongniart, 1828) Schimper, 1879
Plate 1, figures 3, 5–7

Selected synonymy

1828*a* *Nevropteris voltzii* Brongniart, p. 54 (name only).
1828*b* ?*Sphenopteris palmetta* Brongniart, p. 211, pl. 55, fig. 1.
1828*b* *Nevropteris voltzii* Brongniart, p. 232, pl. 67, figs 1–2.
1828*c* *Neuropteris voltzii* Brongniart, p. 440.
1836 ?*Asplenites palmetta* (Brongniart) Goeppert, p. 283, pl. 15, fig. 6.
1844 *Crematopteris typica* Schimper et Mougeot; Schimper and Mougeot, pl. 35, figs 1–2.
1844 *Neuropteris voltzii* Brongniart subgenus *Neuropteridium* Schimper; Schimper and Mougeot, p. 78, pl. 37.
1869 *Neuropteris voltzii* Brongniart subgenus *Neuropteridium* Schimper; Schimper, p. 448.
1886 *Neuropteridium voltzii* Brongniart; Blanckenhorn, p. 125, pl. 15; pl. 16, figs 1–3; pl. 17, figs 1–2a.
1886 ?*Neuropteridium voltzii* var. *latifolium*; Blanckenhorn, p. 127, pl. 16, fig. 4.
1886 *Neuropteridium bergense* Blanckenhorn, p. 129, pl. 20, figs 1–6.
1910 *Neuropteridium voltzii* Brongniart; Fliche, p. 96, pl. 9, fig. 2.
1928 *Neuropteridium voltzii* Brongniart; Schmidt, p. 69, fig. 75.
1928 *Neuropteridium bergense* Blanckenhorn; Schmidt, p. 70, fig. 80.
1978 *Neuropteridium bergense* Blanckenhorn; Grauvogel-Stamm, p. 26.
1978 *Neuropteridium voltzii* (Brongniart) Schimper; Grauvogel-Stamm, p. 26.
2002 *Neuropteridium voltzii* (Brongniart) Schimper; Broglio Loriga *et al.*, p. 385, pl. 1, fig. 4.
2004 *Neuropteridium voltzii* (Brongniart) Schimper; Kustatscher, p. 136, pl. 3, fig. 2.

Description. Although this species is less common than *N. elegans* in the Kühwiesenkopf flora, we still have about 35 specimens, all consisting only of frond fragments. Some of the best ones are KÜH522, 816, 818 and 973. None of these is attached to a rhizome and most fragments are only between 5 and 10 cm long (Pl. 1, fig. 3). The rachis of the fronds is usually broader than in *N. elegans*, with a width of 3–6 mm in the frond fragments. Pinnules are longer (up to *c.* 5 cm) than in *N. elegans* with more or less the same width (4–9 mm), resulting in a much greater length/width ratio (Pl. 1, fig. 6). The pinnule base is slightly contracted; the apex is roundly acute. The venation is neuropterid, with a clear midrib extending about two-thirds of the pinnule length. Secondary veins are numerous and fork 2–3 times (Pl. 1, figs 6–7).

Discussion. Brongniart's holotype (Brongniart 1828*b*, pl. 67, fig. 1) from the Vosges is a frond fragment over 20 cm long with a rachis *c.* 5 mm wide and pinnules that arise more or less perpendicularly. The pinnules are 4–5 cm long and 8–10 mm wide with a constricted base and a pointed apex. Schimper and Mougeot (1844) figured a frond fragment *c.* 25 cm long that includes the apical region. The width of the rachis decreases from 8 mm basally to 3 mm apically, and the apical pinnules arise at a smaller angle and also diminish in size. This material originates from the Upper Buntsandstein of the Vosges. Blanckenhorn (1886) also described and figured material from the surroundings of Floisdorf (Berg) near Kommern that consists of long frond fragments (up to 1 m long according to Blanckenhorn) with a rachis varying from 1 cm in width at the base to 2 mm at the apex. The pinnules are usually 4–5 cm long and 8–12 mm wide. The venation is in all cases the same as in our material. Blanckenhorn also described and figured one broad pinnule fragment (his pl. 16, fig. 4) as *N. voltzii* var. *latifolium*. This fragment is too small to be sure of its identification. As discussed above, Blanckenhorn created the species *N. bergense* from the same locality, which is characterized by shorter fronds (30–45 cm long), a rachis 5 mm wide, and pinnules 28 × 5–6 mm with an obtusely acute apex. Earlier he stated that the species were difficult to distinguish and we believe that *N. bergense* is actually a smaller variety of *N. voltzii*. We have both forms in our collection as well.

Brongniart (1828*b*) described and figured the species *Sphenopteris palmetta* based on a specimen from the same beds in the Vosges as *N. voltzii*, stating that the pinnules resemble those of *N. voltzii* that were dissected during preservation, but that he thought these incisions were so regular that it was probably a different species. Goeppert (1836) transferred the species to his new genus *Asplenites*. Schimper (1869, p. 449) considered that *Sphenopteris palmetta* was based on a poorly preserved *Neuropteris intermedia* frond. Fliche (1910), p. 90) decided that the specimen would be better placed in the genus *Acrostichites* and that it was probably a poorly preserved specimen of *A. densifolius* Fontaine. However, we agree with Schimper (1869) that it is quite possible that the specimen is indeed a poorly preserved specimen of *N. voltzii*. A specimen of this type is illustrated here in Plate 1, figure 5.

Genus SCOLOPENDRITES Goeppert, 1836

Remarks. The nomenclatural history of this fertile fern genus, characterized by hanging pinnules on which the lower surface is completely covered with sporangia, is rather complicated. Brongniart (1828*b*, *c*) described material from the Vosges in the general fern genus *Filicites* Schlotheim, 1820 under the name *Filicites scolopendrioides*. Goeppert (1836, p. 276) created the generic name *Scolopendrites* for this material, but with the new epithet

S. jussieui (Brongniart) Goeppert, which is nomenclaturally illegitimate (Greuter *et al*. 2000; International Code of Botanical Nomenclature, art. 11.4). Presl in Sternberg (1838, p. 125), without having seen Goeppert's work, transferred the same material to the genus *Reussia*, with the correct epithet, *Reussia scolopendrioides* (Brongniart) Presl. However, this new generic name is not valid as it was published after Goeppert's. Therefore, the legitimate name is *Scolopendrites scolopendrioides* (Brongniart) comb. nov.

Schimper and Mougeot (1844, p. 73) created the generic name *Crematopteris* with the epithet *typica* for the same material, but this new taxon is also illegitimate (see above). Nevertheless, all subsequent authors (e.g. Blanckenhorn 1886; Fliche 1910; Frentzen 1914; Grauvogel-Stamm 1978) used the name *Crematopteris typica* for this type of fertile fern. Indeed, Schimper and Mougeot (1844, p. 73) stated that the name *Scolopendrites* was inappropriate as the fossils are not related to the living fern genus *Scolopendrium* as Brongniart (1828*b*) and Goeppert (1836) had thought. However, this is no reason to create a new genus (Greuter *et al*. 2000; International Code of Botanical Nomenclature, art. 51.1), and the generic name *Scolopendrites* Goeppert has priority.

Moreover, close examination of the fertile *Scolopendrites* material in the Anisian flora from Kühwiesenkopf demonstrated that we are dealing with two species of this genus (*S. scolopendrioides* and *S. grauvogelii* sp. nov.) that are difficult to distinguish. The main difference lies in the shape and size of the sporangia (see below), and the width of the rachis to which the fertile pinnules are attached.

The connection between *Scolopendrites* and *Neuropteridium* was not recognized until Schimper and Schenk (1879, 1890) stated that the former might be the fertile part of *Neuropteridium imbricatum* (a junior synonym of *N. elegans*; see above). Since then the general opinion has been that *Scolopendrites* material represents fertile fronds of *Neuropteridium* Schimper. However, it is difficult to understand why Schimper and Mougeot (1844, pl. 35, fig. 2) did not recognize earlier the relationship between *Scolopendrites* and *Neuropteridium* since they figured a specimen (named *Crematopteris typica*) split in two parts that shows several fronds in organic connection, two of which bear basally *Scolopendrites scolopendrioides* and apically *Neuropteridium* pinnules. Moreover, we believe that this sterile foliage corresponds to *N. voltzii* whereas Schimper and Schenk (1879, 1890) suggested that it represented *N. imbricatum*. Grauvogel-Stamm (1978, pl. 2, fig. 2) figured a specimen that shows *N. elegans* and *Scolopendrites* sp. nov. on one slab and according to her (pers. comm. 2002) they were once organically connected but preparation work destroyed this connection. In our collection there is a specimen (KÜH222) that also shows basal *Scolopendrites grauvogelii* sp. nov. pinnules in connection with apical *Neuropteridium elegans* pinnules (Pl. 2, fig. 9).

Therefore, we believe that *Scolopendrites scolopendrioides* is the fertile foliage of *Neuropteridium voltzii* (as proved in Schimper and Mougeot 1844, pl. 35, fig. 2) and *Scolopendrites grauvogelii* sp. nov. that of *Neuropteridium elegans* (proof in KÜH222). The two *Scolopendrites* species are difficult to distinguish, especially in small fragments and when well-preserved sporangia are not present. Indeed, the main difference lies in the shape and size of the sporangia (oval and twice as large in *S. scolopendrioides* as in *S. grauvogelii* sp. nov. where they are circular). The second difference is in the width of the rachis, which is narrower in *S. grauvogelii* (usually 1–3 mm wide) than in *S. scolopendrioides* (usually 4–6 mm); and thirdly, the pinnules in *S. grauvogelii* are usually somewhat shorter than in *S. scolopendrioides*. Therefore, we propose to use *Scolopendrites* sp. for all those frond fragments that are not absolutely unequivocal in their characters. Moreover, when the fertile and sterile material is in organic connection, we believe that we can call the whole plants *Neuropteridium voltzii* or *N. elegans*, respectively.

On the basis that the whole lower surface of the fertile pinnules is covered with sporangia, we may attribute the genus *Scolopendrites* probably to the family Osmundaceae.

Scolopendrites scolopendrioides (Brongniart, 1828) comb. nov.
Plate 2, figures 1–3, 5–6

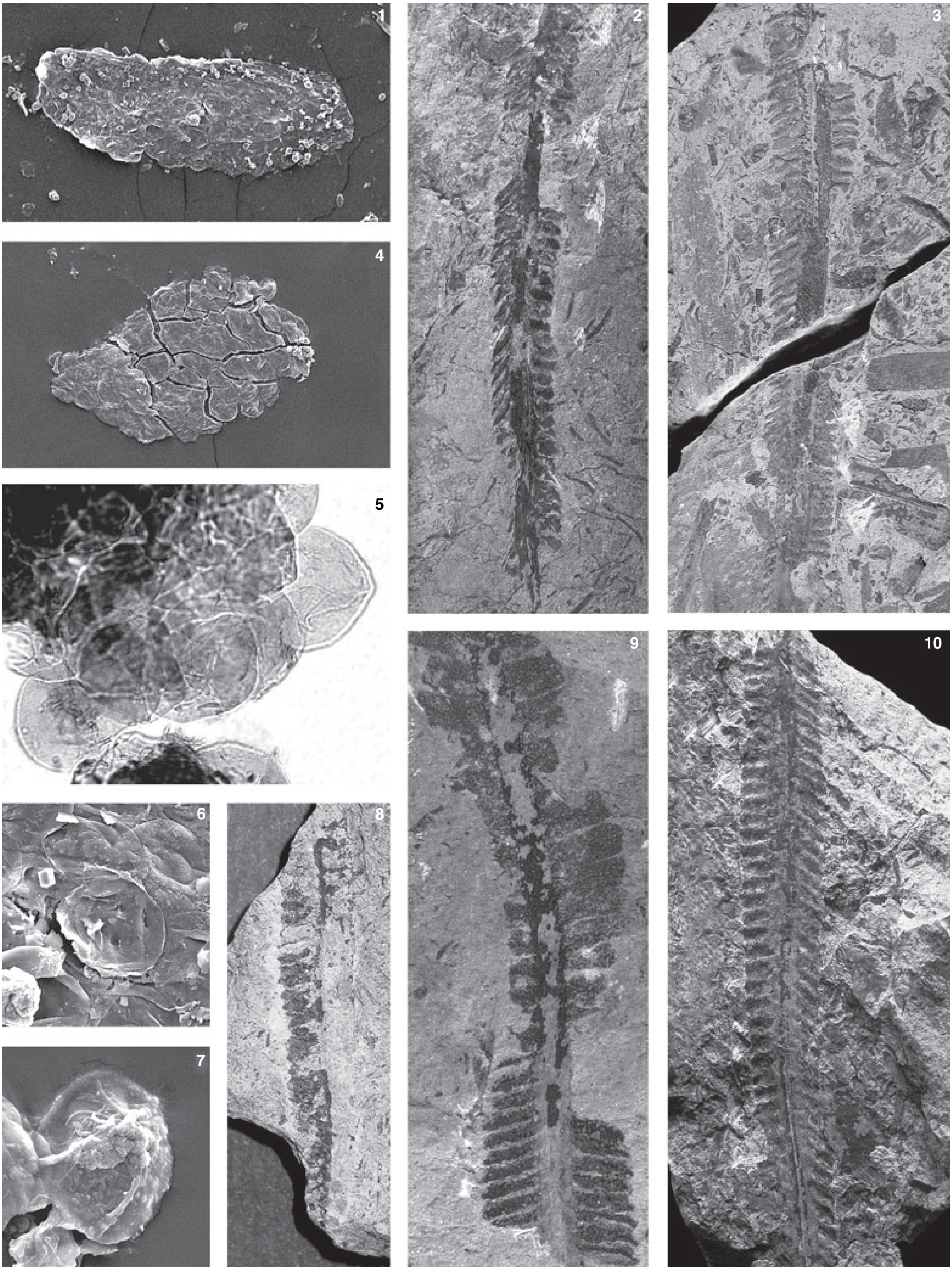
1828*a* *Filicites scolopendrioides* Brongniart, p. 190 (name only).

EXPLANATION OF PLATE 2

Figs 1–3, 5–6. *Scolopendrites scolopendrioides* (Brongniart) comb. nov. 1, single sporangium SEM, KÜH216; × 100. 2, KÜH810; × 1. 3, KÜH356; × 1. 5, a few almost isolated spores, KÜH216; × 500. 6, detail of sporangium showing some spores with trilete mark, SEM, KÜH216; × 500.

Figs 4, 7–9. *Scolopendrites grauvogelii* sp. nov. 4, single sporangium, SEM, KÜH201; × 100. 7, one almost isolated spore, KÜH201; × 800. 8, paratype, KÜH201; × 2·5 9, holotype, KÜH222; × 1·5.

Fig. 10. *Scolopendrites* sp., frond fragment, KÜH010; × 1.



VAN KONIJNENBURG-VAN CITTERT *et al.*, *Scolopendrites*

1828*b* *Filicites scolopendrioides* Brongniart, p. 388, pl. 137, figs 2–3.
1828*c* *Filicites scolopendrioides* Brongniart, p. 443, pl. 18, fig. 2.
1836 *Scolopendrites jussieui* Goeppert, p. 276.
1838 *Reussia scolopendrioides* Presl *in* Sternberg, p. 125.
1844 *Crematopteris typica* Schimper et Mougeot, p. 74, pl. 35, figs 1–2, in organic connection with *N. voltzii*.
1879 *Crematopteris typica* Schimper; Schimper and Schenk, p. 129.
1886 ?*Crematopteris typica* Schimper et Mougeot; Blanckenhorn, p. 129, pl. 21, figs 1–7 (associated with *Neuropteridium voltzii*).
1890 *Crematopteris typica* Schimper; Schimper and Schenk, p. 129.
1910 ?*Crematopteris typica* Schimper et Mougeot; Fliche, p. 103.
1915 ?*Crematopteris typica* Schimper et Mougeot; Frentzen, p. 24, pl. 13, figs 4–5.
2002 *Crematopteris typica* Schimper et Mougeot; Broglio Loriga *et al.*, p. 385.
2004 *Crematopteris scolopendrioides* (Brongniart) nov. comb.; Kustatscher, p. 137, pl. 4, figs 1–3.

Description. As explained above, unequivocal specimens of *Scolopendrites scolopendrioides* are rare in most floras. In our flora we have many *Scolopendrites* specimens (just under 100) that can only be classified as *Scolopendrites* sp. Only KÜH205, 208, 216, 810, 812, 912 and 936 have yielded the typical oval sporangia of this species (length 500–600 μm, width 200 μm). Various other specimens (e.g. KÜH356, 359, 412, 425, 587, 1020) might belong to the species on the basis of their rachis, which is over 4 mm wide, but this cannot be proven.

Most specimens are frond fragments *c.* 10 cm long with a broad rachis (at least 4 mm wide, often 5–6 mm, e.g. in Brongniart 1828*b*, pl. 137, fig. 3) and hanging pinnules with the whole lower side covered with sporangia. That the pinnules hung down was not recognized by Brongniart (1828*b*, *c*), who figured them standing up in his type specimen (1828*b*, pl. 137, fig. 2; 1828*c*, pl. 18, fig. 2). Schimper and Mougeot (1844, pl. 35, figs 1–2) were the first to demonstrate this feature. In some specimens the pinnules are occasionally folded together giving the impression that they are quite narrow (Pl. 2, figs 2–3). Specimens in which the complete lower side of the pinnules is visible are relatively rare (e.g. Blanckenhorn 1886, pl. 21, figs 3–4). Sporangia are oval, *c.* 600×200 μm (Pl. 2, fig. 1), and cover the whole lower surface of the pinnules. Spores are trilete, circular in equatorial outline, with a diameter of 35–45 μm and the exospore is scabrate to granulate (Pl. 2, figs 5–6).

Discussion. As stated earlier, many specimens can only be classified as *Scolopendrites* sp. (Pl. 2, fig. 10). Blanckenhorn's (1886) specimens probably belong to *S. scolopendrioides* as only *Neuropteridium voltzii* has been recorded from the assemblage. Fliche (1910) discussed several specimens of *Crematopteris* described in the literature and their relationship with *Neuropteridium* but he did not figure any of them. The two specimens figured by Frentzen (1914) are so small and fragmentary that it is not possible to attribute them to either *Scolopendrites* or *Neuropteridium*.

Scolopendrites grauvogelii sp. nov.
Plate 2, figures 4, 7–9; Text-figure 3

1928 *Crematopteris typica* Schimper et Mougeot, fertile part of *Neuropteridium imbricatum*; Schmidt, p. 70, fig. 79b.
2002 *Crematopteris* sp.; Broglio Loriga *et al.*, p. 385, pl. 1, fig. 3.
2004 *Scolopendrites* sp. nov.; Kustatscher, p. 138, pl. 3, figs 3–4, pl. 4, fig. 4.

Derivation of name. In honour of Dr Lea Grauvogel-Stamm for all the work she has done on the Anisian flora of the Vosges.

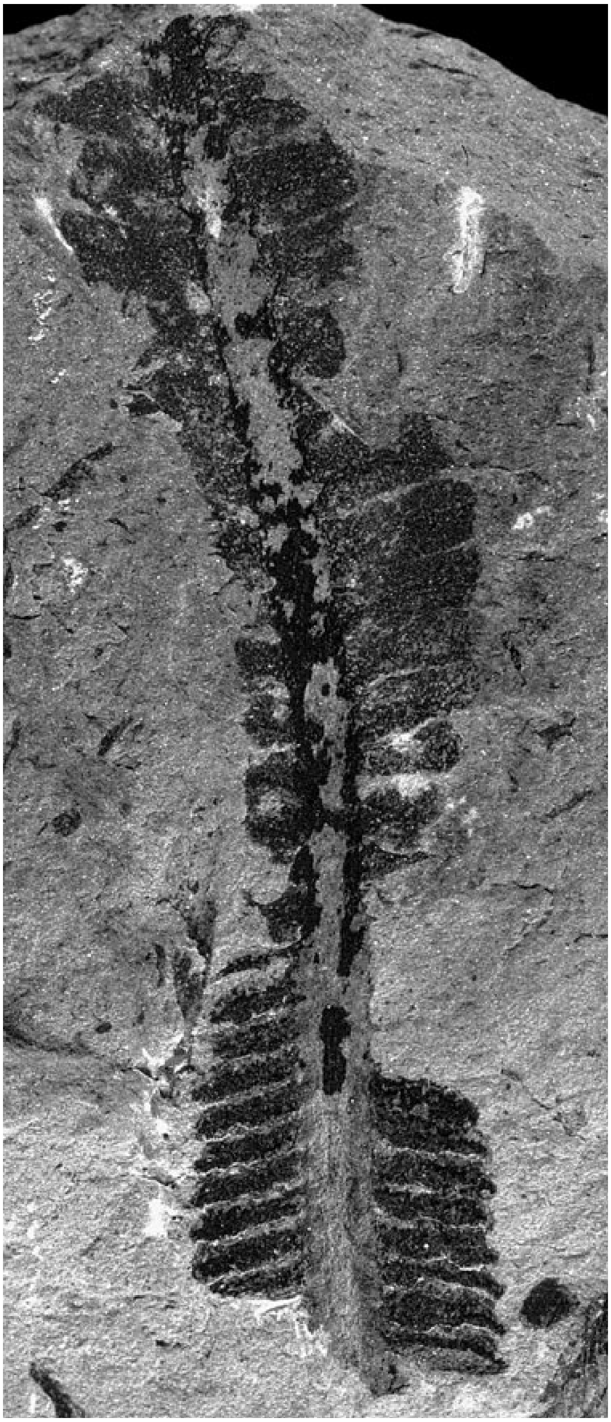
Holotype. KÜH222 (Pl. 2, fig. 9), because of the organic connection with *Neuropteridium elegans*.

Paratype. KÜH201 (Pl. 2, fig. 8), because of the details of sporangia and spores.

Material. Many specimens (*c.* 50) probably belong to this species. Because of the globular shape of the sporangia the following are unequivocal: KÜH50, 200, 203, 217, 221, 238, 410, 414, 688, 800, 980, 1022, 1116, 1121.

Diagnosis. Simply pinnate, fertile fern fronds arising from a rhizome; fronds with relatively narrow rachis and hanging pinnules. Complete lower side of pinnules covered with globular sporangia *c.* 300 μm in diameter. Spores trilete, circular in equatorial outline, *c.* 35–45 μm in diameter, exospore scabrate to granulate.

Description. The holotype (KÜH222; Pl. 2, fig. 9; Text-fig. 3) shows a frond fragment 7·5 cm long with a basal *Scolopendrites* part and an apical *Neuropteridium elegans* part. This specimen proves that the two belong to one natural species. However, no sporangia and spores were obtained from this specimen and therefore KÜH201 was chosen as paratype (Pl. 2, fig. 8). This specimen has only a small *S. grauvogelii* fragment (33 mm long) but shows all the other details of the species. In all specimens the rachis is generally narrow (0·6–3·0 mm) and the pinnules are hanging, as in *S. scolopendrioides*. They are usually slightly smaller than in *S. scolopendrioides*, with a mean length of 4–8 mm (8–11 in *S. scolopendrioides*), and a mean width of 2–3 mm as in *S. scolopendrioides*. The sporangia are more or less circular in outline, with a diameter around 300–400 μm, whereas in *S. scolopendrioides* they are oval and *c.* 600×200 μm. Just as in *S. scolopendrioides*, the spores are trilete, circular in equatorial



TEXT-FIG. 3. *Scolopendrites grauvogelii* sp. nov., holotype, KÜH222; ×2.

outline, with a diameter of 35–45 μm, and the exospore is scabrate to granulate (Pl. 2, fig. 7).

Discussion. S. grauvogelii is macromorphologically difficult to distinguish from *S. scolopendrioides*, as the main distinguishing character in this respect is the thickness of the rachis (narrower than in *S. scolopendrioides*). The pinnules also are smaller than in *S. scolopendrioides*, but there is an overlap in length. When sporangia are present, the difference is easy to observe, as the sporangia in *S. grauvogelii* are circular (Pl. 2, fig. 4) and those in *S. scolopendrioides* are oval and twice as large (Pl. 2, fig. 1). Spores of the two species are indistinguishable.

Most *Scolopendrites* specimens that have been figured in the literature (as *Crematopteris*) can only be determined as *Scolopendrites* sp. if they are either not organically connected with *Neuropteridium* remains or not closely associated with them. Neither sporangia nor spores have been described or figured from any of the specimens in the literature concerning French and German assemblages (Brongniart 1828*b*, *c*; Schimper and Mougeot 1844; Blanckenhorn 1886; Fliche 1910; Frentzen 1914; Schmidt 1928; Grauvogel-Stamm 1978).

Wang Zi-qiang (1996) figured *Crematopteris brevipinnata* from Scythian (Lower Triassic) sediments in China, using data in Wang and Wang (1990) for the description. The latter paper, however, contains figures of only a few fragments of *Crematopteris* cf. *typica* and *Crematopteris* sp., and these cannot be identified above the level of *Scolopendrites* sp. In the same beds some *Neuropteridium* fragments occur that are comparable with *N. elegans*. Wang and Wang (1990) also described a new *Neuropteridium* species, *N. curvinervis*, but this will be discussed later. Meng (2000) discussed Middle Triassic plants from the Yangtze Valley in China, and mentioned the presence of *Scolopendrites* (*Crematopteris*) sp. and *Neuropteridium voltzii* in Anisian assemblages from that area.

Distribution. Anisian (lower Middle Triassic).

Order FILICALES Bower, 1899
Family unknown, possibly OSMUNDACEAE Bercht. and Presl, 1820

Genus ANOMOPTERIS Brongniart 1828

Remarks. Brongniart (1828*a*–*c*) created the genus *Anomopteris* from the Anisian flora of the Vosges with the type species *A. mougeotii*. The frond is bipinnate, with a broad rachis and long, linear and crowded pinnae. The short pinnules are perpendicularly attached to the pinna rachis; in the basal part of the pinnae they are sterile, in the more distal part usually fertile. In their revision of *Anomopteris*, Grauvogel-Stamm and Grauvogel (1980) emended the generic diagnosis to include a very important and unusual character of the genus, the presence of an aphlebia at the base of each pinna. They also demonstrated that *Pecopteris sulziana* Brongniart, 1828*b* from the same layers is the juvenile form of *Anomopteris mougeotii*.

Anomopteris mougeotii Brongniart, 1828
Plate 4, figures 1, 3

Selected synonymy

1828*a* *Anomopteris mougeotii* Brongniart, p. 60, 190 (name only).
1828*b* *Anomopteris mougeotii* Brongniart, p. 258, pls 79–81.
1828*b* *Pecopteris sulziana* Brongniart, p. 325, pl. 105, fig. 4 (juvenile form).
1828*c* *Anomopteris mougeotii* Brongniart, p. 439.
1844 *Anomopteris mougeotii* Brongniart; Schimper and Mougeot, p. 71, pl. 34.
1844 *Pecopteris sulziana* Brongniart; Schimper and Mougeot, p. 82, pl. 40.
1869 *Anomopteris mougeotii* Brongniart; Schimper, p. 598.
1871 *Anomopteris mougeotii* Brongniart; Weiss, p. 363, text-figs 1–3.
1891 *Anomopteris mougeotii* Brongniart; Schimper and Schenk, p. 125.
1910 *Anomopteris mougeotii* Brongniart; Fliche, p. 93, pl. 6, fig. 4.
1915 *Anomopteris mougeotii* Brongniart; Frentzen, p. 22, pl. 13, figs 1–3.
1928 *Anomopteris mougeotii* Brongniart; Schmidt, p. 67, fig. 68.
1953 *Pecopteris sulziana* Brongniart; Mägdefrau, p. 211, fig. 179.
1978 *Anomopteris mougeotii* Brongniart; Grauvogel-Stamm, p. 25, pl. 2, fig. 5.
1978 *Pecopteris sulziana* Brongniart; Grauvogel-Stamm, p. 26, pl. 2, fig. 1.
?1978 cf. *Anomopteris mougeotii* Brongniart; Wang, Xie and Wang, p. 210, pl. 4, figs 1–2.
1980 *Anomopteris mougeotii* Brongniart; Grauvogel-Stamm and Grauvogel, p. 55, pls 1–6, text-figs 1–2.
1991 *Anomopteris mougeotii* Brongniart; Fuchs, Grauvogel-Stamm and Mader, p. 99, pl. 8, figs 4–7.
1999 *Anomopteris mougeotii* Brongniart; Gall and Grauvogel-Stamm, p. 293, fig. 22.
2002 *Anomopteris mougeotii* Brongniart; Broglio Loriga *et al.*, p. 385.
2004 *Anomopteris mougeotii* Brongniart; Kustatscher, p. 133, pl. 2, fig. 3.

Description. Just over 30 specimens of *Anomopteris mougeotii* have been found at Kühwiesenkopf, especially in the upper layers of the plant beds. Most are frond fragments showing a thick rachis (*c.* 5–10 mm) with long, almost perpendicular pinnae (Pl. 4, fig. 1). In some specimens (e.g. KÜH1159, 1197) aphlebia are visible, which are characteristic for the genus and species (Pl. 4, fig. 3). The largest frond fragment is KÜH1197, which is 33·7 cm long with a main rachis 9 mm wide. The pinnae are incomplete, but at least 11·5 cm long and 5 mm wide. They are closely spaced but never in contact; their rachis is *c.* 1 mm wide. The pinnules arise perpendicularly and vary in size between $1{\cdot}5 \times 2$ mm and 2×3 mm. Sterile pinnules often have a basal lobe. The venation is usually difficult to observe; the midrib forks in the apical part of the pinnule. Secondary veins arise at an angle of 60–90 degrees and usually fork only once, but the basal ones may fork twice. In only a few specimens are the distal pinnules fertile (lower surface covered with sporangia); the basal part of the pinnae is always sterile (as described by Grauvogel-Stamm and Grauvogel 1980). This may be one of the reasons why we have so little fertile material, since only the frond rachis with the sterile basal parts of the pinnae are usually preserved. None of our specimens yielded spores, but Grauvogel-Stamm and Grauvogel (1980) described them: spores circular, trilete, 25–40 μm in diameter with a punctate exospore.

Discussion. Our material is indistinguishable from that recorded from the Vosges (see Grauvogel-Stamm and Grauvogel 1980 for detailed descriptions). Apart from the Vosges, *Anomopteris mougeotii* has been described from various other Lower and Middle Triassic localities in France (see Fliche 1910; Grauvogel-Stamm and Grauvogel 1980), Germany (Frentzen 1915; Mader 1990) and as *Anomopteris* cf. *mougeotii* from the Lower Triassic of China (Wang *et al.* 1978). Wachtler and van Konijnenburg-van Cittert (2000) recorded pinna fragments from the Ladinian flora of the Dolomites, but as these are only small fragments without the main rachis and the typical aphlebiae, we believe that this determination may not be correct, although one of the fragments (their pl. 1, fig. 4) shows a pinna fragment with pinnules that have a venation that is typical of the juvenile form of *A. mougeotii* (formerly recorded as *Pecopteris sulziana* by Grauvogel-Stamm and Grauvogel 1980). These fern fragments are better considered as *incertae sedis*.

None of the fronds from Kühwiesenkopf is attached to a rhizome. However, several large rhizomes (about 1 m long and 20 cm wide) have been found in the Triassic of the Vosges, on one side of which several frond rachises depart. These rhizomes very likely belong to *A. mougeotii* (Grauvogel-Stamm, pers. comm. 2003). Similar rhizomes have so far not been encountered in our material.

The botanical affinity of *Anomopteris* is not clear. The fertile pinnules including the spores have all the characters of the Osmundaceae, but an aphlebia at the base of each pinna, a terminal sporangial annulus and a W-shaped frond trace have never been recorded from the Osmundaceae. Therefore, we only attribute *A. mougeotii* provisionally to this family.

Very few other species of *Anomopteris* have been recorded. Fuchs *et al.* (1991) described an *Anomopteris* sp. from the Lower Triassic of Lammersdorf in the Eifel (Germany) with fronds that are much smaller than those of *A. mougeotii*. Most are isolated fragments but some are attached to globose rhizomes. Complete fronds of this *Anomopteris* sp. are bipinnate and are only 15–30 cm long (those of *A. mougeotii* may reach a length of 1–2 m) and 3–6 cm wide (*A. mougeotii* fronds can be 30–50 cm wide). Each pinna has an aphlebia at its base, and the pinnae arise at an angle of *c.* 60–80 degrees. Pinnules are small and the venation is invisible. Because of the poor preservation of the material, the authors did not give the species a name. Similar material was described by Wang and Wang (1990) as *Anomopteris minima* from Scythian (Olenekian) beds in North China. According to these authors, this species (refigured in Wang 1996) differs from *A. mougeotii* in having much smaller mono- to bipinnate pinnae. Complete fronds have an estimated length of only 15 cm and a width of 3·5 cm. This material may, however, be conspecific with the material described by Fuchs *et al.* (1991) as *Anomopteris* sp. from Germany.

Order FILICALES Bower, 1899
Family unknown, possibly OSMUNDACEAE Bercht. and Presl, 1820

Genus GORDONOPTERIS gen. nov.

Diagnosis. At least tripinnate fern frond. Aphlebia absent from the bases of the pinnae of the first and second order. Pinnules relatively small, attached with their whole base, rounded in outline with a short midrib and forking secondary veins (neuropterid venation). Fertile pinnules with a reduced, completely rounded lamina, sporangia on the lower side, circular. Spores circular, trilete, with a punctate exospore.

Derivation of name. After Dr Marie Ogilvie Gordon who was one of the pioneers of Triassic palaeobotany in the Dolomites.

Type species. *Gordonopteris lorigae* sp. nov. (see below).

Remarks. As mentioned above, Wachtler and van Konijnenburg-van Cittert (2000) described fragments from the Ladinian assemblage in the Dolomites as *Anomopteris mougeotii* based on venation (their pl. 1, fig. 4) or pinnule shape (their pl. 1, fig. 5). However, in the Anisian assemblage at Kühwiesenkopf numerous specimens of the same nature as that shown in their plate 1, figure 5 were encountered but they are much larger. Fertile material was also found at Kühwiesenkopf. In none of these specimens could aphlebia typical for *Anomopteris* be demonstrated. Another difference from *A. mougeotii* is that the frond is at least tripinnate and not bipinnate, and that the pinnae of the last order do not arise almost perpendicularly as is the case in *A. mougeotii* but at much smaller angles (usually 45–60 degrees). They are also much shorter than in *Anomopteris*. Fertile pinnules have the same morphology as in *Anomopteris*. Therefore, we have created *Gordonopteris*, which is probably related to *Anomopteris*, for this material.

Gordonopteris lorigae sp. nov.
Plate 3; Text-figures 4, 5D

?2000 *Anomopteris mougeotii* Brongniart; Wachtler and van Konijnenburg-van Cittert, p. 108. pl. 1, fig. 5.
2002 *Anomopteris* nov. sp.?; Broglio Loriga *et al.*, p. 385, pl. 1, fig. 5.
2004 Filicales indet.; Kustatscher, p. 140, pl. 5, fig. 2.

Derivation of name. After the late Prof. Dr Carmela Loriga Broglio, who stimulated research on the fossil flora of Kühwiesenkopf and was the leader of the project on the fossil fauna and flora from this locality.

Holotype. KÜH633 (Text-fig. 4; Pl. 3, fig. 3).

Material. This fern is one of the common elements in the flora. About 170 sterile and fertile specimens have been encountered so far.

Diagnosis. At least tripinnate fern frond. Rachis of first order broad, smooth. First-order pinnae arising alternately to suboppositely at angles of 45–60 degrees, relatively long, neighbouring pinnae in close contact, but never overlapping. Rachis of second order *c.* 2 mm wide, smooth; second-order pinnae arising at 60–90 degrees, relatively short (longest 4·5 cm), in close contact, but never overlapping. Pinnules relatively small (*c.* 2–3 × 2–3 mm), attached with whole base, rounded in outline, containing a short midrib and forking secondary veins (neuropterid venation). Fertile pinnules with a reduced, completely rounded lamina, sporangia on lower side. Spores globose, trilete, around 45–60 μm in diameter, exospore finely punctate.

Description. The holotype (KÜH633; Text-fig. 4) is a large fragment of a fern frond (base and apex are missing), dimensions 46 × 37 cm. The rachis tapers from a width of 10 mm basally to 5 mm apically and is smooth. The pinnae of the first order arise alternately to suboppositely at angles of 45–60 degrees. The pinnae are long, none is complete but even then they vary in length between 18 and 25 cm. The distance between neighbouring pinnae is between 3 and 5 cm on the rachis. The rachis of the second order is *c.* 2 mm wide, and also smooth; the pinnae of the second order arise usually suboppositely at 60–90 degrees, and are relatively short (20–45 mm long and 4–5 mm wide) (Pl. 3, fig. 4). The pinnules are small (usually *c.* 2–3 × 2–3 mm), attached with their whole base, rounded in outline with a neuropterid venation (Text-fig. 5D). Fertile pinnules have an even more reduced, completely rounded lamina with more or less circular sporangia (annulus unknown) on the lower side (Pl. 3, fig. 4). Three specimens (KÜH102, 483 and 1073) yielded many sporangia with good (almost) mature spores. The spores are globose, trilete, 43–62 μm in diameter, with a finely punctate exospore (Pl. 3, figs 1–2).

Discussion. This fern is one of the more common elements in the Anisian flora of Kühwiesenkopf. Most of the material consists of fragments of pinnae of the first order but there are quite a few larger, more complete specimens (Pl. 3, fig. 3). As mentioned above, the Ladinian fossil figured by Wachtler and van Konijnenburg-van Cittert (2000, p. 108. pl. 1, fig. 5) also belongs to *Gordonopteris*.

So far, similar fern material has not been found in Early and Middle Triassic floras from other areas, with the exception of a specimen described and figured by Kelber and Hansch (1995) as *Phlebopteris* sp. from a lower Keuper (probably Ladinian) locality near Kreuzthal in Franken (Germany). That specimen is certainly not a *Phlebopteris*. It shows a frond fragment with a rachis and pinnae that are 2–3 cm long and around 4 mm wide, and arise almost perpendicularly, exactly like the secondary pinnae of *Gordonopteris lorigae*. The pinnules are small and attached with their whole base as in *Gordonopteris*, but the venation is not visible. Kelber and Hansch compared it with *A. mougeotii*, stating that, although the specimen has a similar gross morphology, it cannot be attributed to that species because of the absence of aphlebiae.

An assignment at family level can only be provisionally suggested since there is no information on the rhizome and sporangia of the genus. Because of its resemblance, especially of the fertile pinnules, to *Anomopteris mougeotii*, including the arrangement of the sporangia on the lower surface of the fertile pinnules, we think that a relationship with the Osmundaceae is possible.

Distribution. Anisian and Ladinian (Middle Triassic).

Order MARATTIALES Prantl, 1874
Family MARATTIACEAE Bercht. and Presl, 1820

Genus MARATTIOPSIS Schimper (1869)

Marattiopsis sp.
Plate 5, figures 1–2

2002 ?*Marattiopsis* sp.; Broglio Loriga *et al.*, p. 384.
2004 ?*Marattiopsis* sp.; Kustatscher, p. 141, pl. 5, fig. 1.

Description. There are a few specimens that may represent pinna fragments of *Marattiopsis*. KÜH215 especially resembles this genus. It is an apical pinnae fragment 5·8 cm long and 0·6 cm wide basally, tapering towards the apex. The midrib is distinct, *c.* 1 mm wide at the base. Secondary veins arise at an angle of about 60 degrees, then curve outwards and fork once in the middle part of the lamina. The secondary veins reach the margin almost perpendicularly except in the apical area where the angle is smaller (Pl. 5, figs 1–2).

Discussion. Although the other pinna fragments in the collection are even shorter than KÜH215, they are attributed to *Marattiopsis* sp. because of their similar venation. The shape of the pinna of KÜH215 and its venation resembles closely that of other Late Triassic and Jurassic *Marattiopsis* (or *Marattia*) species such as *M. intermedia* (Muenster) Kilpper and *M. asiatica* Kawasaki, but the present material is narrower and as fertile material has not been found so far, we can only compare our specimens to *Marattiopsis*.

Genus MARANTOIDEA Jaeger, 1827

Marantoidea sp.
Plate 4, figures 2, 4

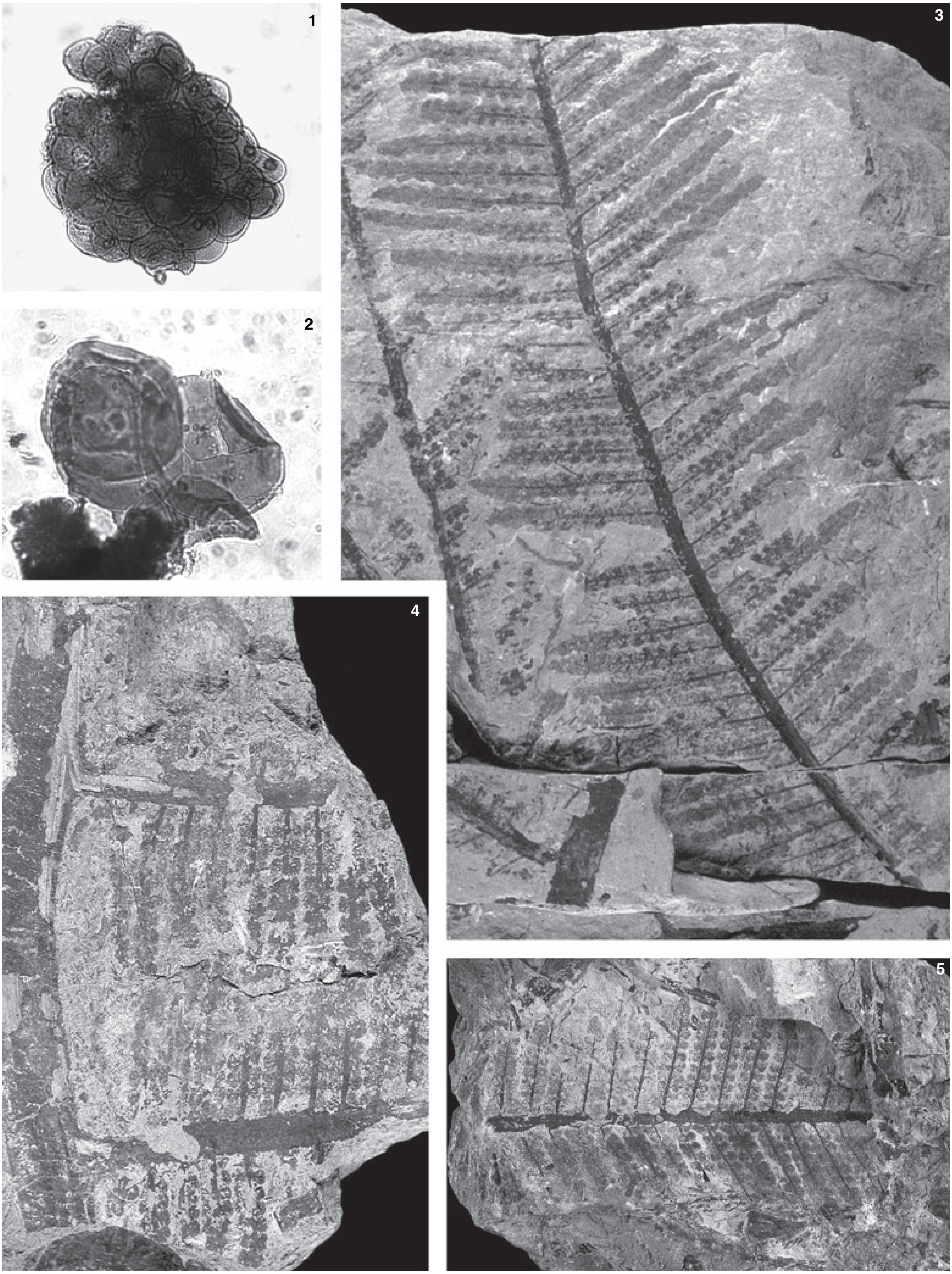
2004 *Marantoidea* sp.; Kustatscher, p. 141, pl. 5, fig. 3.

Description. Just over ten fragments of fern leaves that can be attributed to this genus were found in the Kühwiesenkopf assemblage. There are only relatively small fragments of pinnules, none of which is complete; more and better material has been found at another, slightly younger, locality in the Dolomites (Furkelpass) that will be described later. The largest fragment (KÜH907A, B) reaches a length of 11·5 cm but the venation is badly preserved. It is better in KÜH555 (length of the fragment 8 cm, width 2·5 cm) where secondary veins arise from a broad midrib (2·5–4 mm wide) at an angle of *c.* 70 degrees, then bend downwards and fork, usually once, near the midrib (Pl. 4, fig. 2). Sometimes the veins fork more in the middle part of the lamina. They reach the margin more or less perpendicularly at a concentration that varies in the specimens from between 8 and 12 cm.

Discussion. Marattialean fern fragments like those described above have usually been attributed to the genus *Danaeopsis* Presl, 1838 (often as *D. marantacea* or *D. arenacea*; see Kelber and Hansch 1995). However, Presl

EXPLANATION OF PLATE 3

Figs 1–5. *Gordonopteris lorigae* sp. nov. 1, sporangium with spores, KÜH102; ×200. 2, spores, KÜH102; ×500. 3, detail of holotype, KÜH633; ×1. 4, fertile leaf fragment, KÜH483; ×1·5. 5, frond fragment, KÜH089; ×1.



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TEXT-FIG. 4. *Gordonopteris lorigae* sp. nov., holotype, KÜH633; ×0·4.

(1838) created this genus illegitimately for material that had previously been described as *Marantoidea arenacea* by Jaeger (1827), as Webb (2001) rightly pointed out (it is the type species of the genus *Marantoidea* and originates from the Middle Triassic of Germany). Therefore, following Webb, we also attribute our material to the valid genus *Marantoidea*.

We cannot attribute our specimens to any species of *Marantoidea* because they are too fragmentary, and none is fertile. They resemble specimens of *M. arenacea* in venation, but differ in being of slightly narrower width.

Mojsisovics (1879) mentioned that material identified as *Danaeopsis marantacea* by Stur was found in the Wengener Schichten from Corvara (Ladinian). However, descriptions and illustrations are lacking, and because the specimens were not found during an extensive search by one of us (EK) of various museum collections, we cannot compare our material with that from the Ladinian of the Dolomites. It is the only other record of *Marantoidea* material in northern Italy.

PTERIDOPHYTA *incertae sedis*

Genus SPHENOPTERIS Sternberg, 1825

Sphenopteris schoenleiniana (Brongniart, 1835) Presl, 1838
Plate 5, figures 3–4, 7

1835 *Pecopteris schoenleiniana* Brongniart, p. 364, pl. 126, fig. 6.
1838 *Sphenopteris schoenleiniana* (Brongniart) Presl in Sternberg, p. 132.
1850 *Sphenopteris schoenleiniana* (Brongniart) Presl; Unger, p. 125
1864 *Sphenopteris schoenleiniana* (Brongniart) Presl; Schenk, p. 80, pl. 2, figs 2, 2*a*.
1922*a* *Sphenopteris schoenleiniana* (Brongniart) Presl; Frentzen, pp. 7, 10.
1922*b* *Sphenopteris schoenleiniana* (Brongniart) Presl; Frentzen, p. 30, pl. 3, fig. 3.
1928 *Pecopteris schoenleiniana* Brongniart; Schmidt, p. 65, fig. 63.
1990 *Sphenopteris schoenleiniana* (Brongniart) Presl; Kelber, p. 40, fig. 72.
1995 *Sphenopteris schoenleiniana* (Brongniart) Presl; Kelber and Hansch, p. 58, figs 123, 125–126.
2004 *Sphenopteris schoenleiniana* (Brongniart) Presl; Kustatscher, p. 142, pl. 5, fig. 5.

Description. There are *c.* 15 specimens of this relatively rare, tripinnate fern species, most of which are only pinna fragments. KÜH668 shows part of a rachis (2–3 mm wide) and several pinna fragments, and KÜH1171 demonstrates the remains of five parallel pinnae, although the rachis has not been preserved (Pl. 5, fig. 4). The longest specimen is KÜH524 (Pl. 5, fig. 3), which is an apical fragment *c.* 15 cm long with several pinnae attached to the 1–2-mm-wide rachis. Pinnae usually vary in length between 5 and 7 cm, and have a width of *c.* 1 cm. Pinnules (usually 1 cm long and 3 mm wide) are usually attached with only part of their base at an angle of 30–60 degrees, and are sometimes slightly falcate, giving an undulating margin. The venation consists of a midrib that does not reach the apex, and once forking secondary veins arising at *c.* 60 degrees.

Three fertile specimens of this species have been found for the first time (KÜH1083, 1084 and 1085; Pl. 5, fig. 7). Of these, KÜH1085 is the largest, showing a rachis 3 mm wide with three parallel pinna fragments. However, details of the sporangia are indistinct. Although only a small pinna fragment, KÜH1083 shows the fertile pinnules; the *c.* 1-cm-long, undulating pinnules have sporangial attachment areas at the end of the secondary veins. Since the sporangia themselves have not been preserved, no attribution to a fern family can be made.

Discussion. Until now *Sphenopteris schoenleiniana* has only been recorded as a rare element in Europe from the 'Lettenkohle' (Ladinian) and 'Schilfsandstein' (Carnian) from Germany (Schenk 1864; Frentzen 1922*a*, *b*; Schmidt 1928; Kelber and Hansch 1995) and never from Anisian assemblages. Nevertheless, our material resembles that species so much that we have to attribute it to *S. schoenleiniana*, which was first described by Brongniart (1835) as a species of *Pecopteris*. Indeed several specimens in the literature demonstrate a pinnule attachment with a more or less complete base and an almost straight pinnule margin as in that genus (e.g. Kelber 1990, fig. 72; Kelber and Hansch 1995, figs 125–126). Other specimens (Schenk 1864, pl. 2, figs 2–2*a*; Schmidt 1928, fig. 63; Kelber and Hansch 1995, fig. 123, and the present material) show a sphenopterid type of pinnule attachment and an undulating pinnule margin. Frentzen (1922*b*) stated that both pinnule types occur and might represent sun and shade fronds. The 'pecopterid' form resembles *Cladophlebis ruetimeyeri* rather closely. Often both species occur in the same localities, as is also the case with our material, but as long as they have never been found in one frond or attached to one rhizome, we maintain them as separate species (see below).

Genus CLADOPHLEBIS Brongniart, 1849

Remarks. Cladophlebis-type ferns are relatively rare in the Kühwiesenkopf flora, and indeed in general in Middle and early Late Triassic floras in Europe. Most of the material has been described under the name *Cladophlebis distans* (Presl, 1838) Frentzen, 1922, or *Anotopteris distans* (Presl, 1838) Schimper, 1869 (see e.g. Schmidt 1928, p. 63, fig. 58; Kelber 1990, p. 40, figs 23*b*, 70–71, 78; Kelber and Hansch 1995, p. 66, figs 136–139). However, the original basionym *Neuropteris distans* Presl, *in* Sternberg 1820 (part 1, p. 17) refers to a specimen from 'the mines in Eschweiler, Germany' and is almost certainly Carboniferous in age, and may indeed be a *Neuropteris* rather than *Cladophlebis* (see also Brongniart 1828*b*, p. 250). However, Presl (in Sternberg 1838, part 8, p. 136, pl. 40, fig. 4), discussed *Neuropteris distans* from the Triassic (Keuper) of Germany, and on p. 220 in the same volume he wrote (apparently seeing his mistake in nomenclature) that one should read *Neuropteris remota* for the Triassic material instead of *Neuropteris distans*. Schimper (1869, p. 470, pl. 33) took this latter

Neuropteris distans Presl as a basionym, and stated that the material came from the Upper Triassic of Stuttgart, Sinsheim, Estenfeld and Erlach near Würzburg and possibly Kronungen near Schweinfurt. Indeed some of our specimens (e.g. KÜH493, 579–581, 1072) resemble especially the specimen in his plate 33, figure 2. Schimper takes into his synonymy of *Anotopteris distans* material described and figured by Schenk (1864, p. 75, pl. 1; pl. 2, fig. 3), stating that they are without doubt identical. The latter author combined the Triassic *Neuropteris distans* Presl with *Neuropteris remota* Presl in Sternberg (1838, p. 220), naming the species correctly as *Neuropteris remota*, and figuring material from the surroundings of Würzburg, although without indicating the exact localities or age. He stated that the specimen in his plate 2, figure 3 was 'the original specimen', and that *Neuropteris ruetimeyeri* Heer from the Keuper flora of Neue Welt, Basel differed only in the direction in which the pinnules pointed, but that he knew it only from the original illustration of Heer (1865, pl. 2, fig. 6) who figured only an apical pinna fragment. Matters are further complicated because Fontaine (1889, p. 77, pl. 13, figs 4–5) described a species as *Cladophlebis distans*, which is generally used for Cretaceous *Cladophlebis* material.

Frentzen (1922*b*, p. 22, pl. 1, figs 4, 6) described and discussed *Anotopteris* (*Cladophlebis*) *distans* in detail, stating that Schenk's *Neuropteris distans* and *N. remota* are indeed one species, and that *N. schoenleiniana* as described by Schenk (1864, p. 74) from Germany is conspecific as well. He also stated that *Pecopteris ruetimeyeri* (Heer) Heer, 1877 is a different species, although it resembles *Anotopteris distans* closely. According to Frentzen the differences are narrower pinnules, a more acute pinnule apex and sometimes a slightly contracted pinnule base in *P. ruetimeyeri*. Compter (1918, p. 440, figs 2–5) described three different *Pecopteris* species from the Keuper flora of Apolda, Germany that might be partly or entirely conspecific: first, his new species *P. parvifolia*, then *P. ruetimeyeri* (Heer) Heer and finally *P. augusta* Heer. In the last of these, the pinnules are adnate up to about half of their length, so this species might indeed be different (see also Schmidt 1928, p. 66, fig. 66). The other two occur on the same slab and might well belong to the same species, in which case *P. parvifolia* is the basal part of pinnae from *P. ruetimeyeri*. *Cladophlebis ruetimeyeri* (Heer) Leonardi, 1953 has been recorded from Ladinian strata in the Dolomites (Leonardi 1953, p. 10, pl. 1, figs 1, 15; pl. 3, fig. 6).

Stur (1885) created the genus *Speirocarpus* for this type of pecopterid fossil of Triassic age. In it he included *P. ruetimeyeri* (Heer) Heer and six new species from the Late Triassic flora of Lunz, which Krasser (1909) later revised. The Lunz species do not bear any resemblance to the Anisian material from Kühwiesenkopf described here and is therefore not discussed further. The genus *Speirocarpus* is not in common use, and we prefer to use the general morphogenus *Cladophlebis* until fertile material has been discovered that can lead to a definite taxonomic attribution of this material. We believe that *Cladophlebis ruetimeyeri* might be conspecific with *Cladophlebis* (*Neuropteris*) *remota*, but the material is so fragmentary that we cannot be absolutely sure. Therefore, all references to *Cladophlebis* (*Pecopteris*) *ruetimeyeri* in the synonymy are accompanied by a question mark.

It is clear that the specific name *Cladophlebis distans* cannot be used for Triassic material of this type as the basionym *Neuropteris distans* Presl, *in* Sternberg (1820, p. 17) was first used for a Carboniferous fossil, and Presl (1838, p. 220) himself corrected his second, invalid (Greuter *et al.* 2000; ICBN art. 34) submergence of *N. distans* (for Triassic material, p. 136) into *N. remota*. In other words, *Neuropteris distans* Presl, 1838 does not exist. For the same reason *Anotopteris distans* (Presl, 1838) Schimper, 1869 cannot be used. Frentzen (1922*b*) used a heading *Anotopteris* (*Cladophlebis*) *distans* Schimper in his paper, but in the text he simply used Schimper's illegitimate (ICBN art. 52.1) name *Anotopteris distans*. In other words, he did not recognize the combination *Cladophlebis distans*. Since about 1910 no author has used the epithet *remota*, but this appears to be the correct epithet and we formally propose the new combination *Cladophlebis remota* here.

From the Triassic of France, a number of *Cladophlebis* species have been described (see Fliche 1910), most of which are based on poorly preserved material and are, therefore, indeterminable (see Grauvogel-Stamm 1978, p. 38). Some of these might resemble our material, but the figures in Fliche (1910) are of insufficient quality to permit sensible comparison.

Cladophlebis remota (Presl) comb. nov.
Plate 5, figures 5–6; Plate 6, figure 4; Text-figure 5B

Selected synonymy

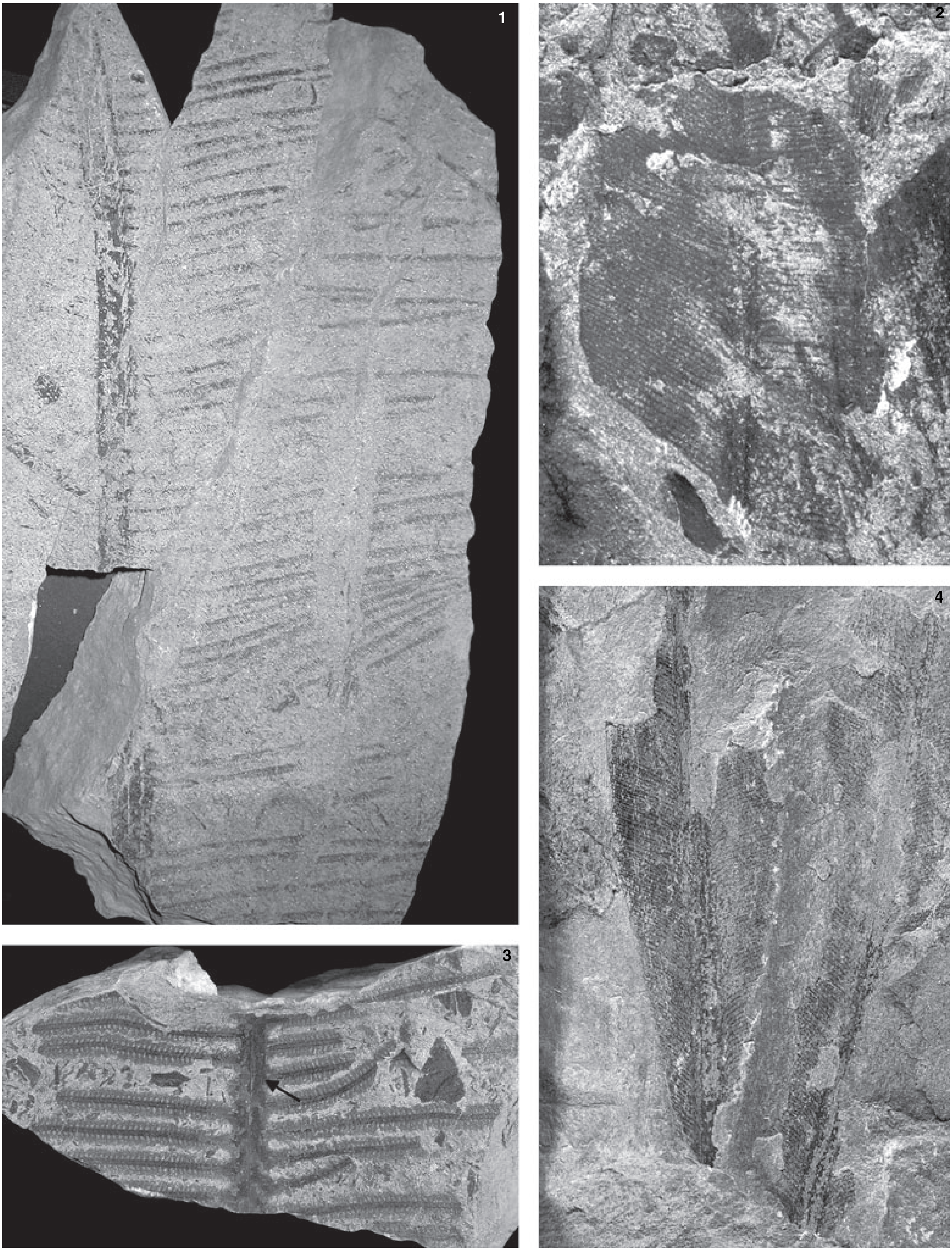
non 1820 *Neuropteris distans* Presl, *in* Sternberg, p. 17.

EXPLANATION OF PLATE 4

Figs 1, 3. *Anomopteris mougeotii* Brongniart. 1, frond fragment, KÜH1197; ×1. 3, frond fragment with aphlebia (see arrow), KÜH1159; ×1.

Figs 2, 4. *Marantoidea* sp. 2, frond fragment showing in detail the venation, KÜH555; ×2. 4, two frond fragments, KÜH575; ×1·5.

PLATE 4



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1838 *Neuropteris distans* Presl, *in* Sternberg, p. 136, pl. 40, fig. 4, nom. inval. (ICBN art. 34).
1838 *Neuropteris remota* Presl, *in* Sternberg, p. 220.
1864 *Neuropteris remota* Presl = *Neuropteris distans* Presl; Schenk 1864, p. 75, pl. 1; pl. 2, fig. 3.
?1865 *Neuropteris ruetimeyeri* Heer, p. 53, pl. 2, fig. 6.
1869 *Anotopteris distans* (Presl) Schimper, p. 470, pl. 33, nom. illeg. (ICBN art. 52.1).
1874 *Neuropteris remota* Presl; Compter, p. 6.
?1877 *Pecopteris ruetimeyeri* (Heer) Heer, p. 70, pl. 25, figs 10–12.
1918 *Pecopteris parvifolia* Compter, p. 440, figs 2a, 3.
?1918 *Pecopteris ruetimeyeri* (Heer) Heer; Compter, p. 442, figs 2b, 4.
1922b *Anotopteris* (*Cladophlebis*) *distans* (Presl) Frentzen, p. 22, pl. 1, figs 4, 6.
?1928 *Cladophlebis ruetimeyeri* Heer; Schmidt, p. 58, fig. 41.
1928 *Anotopteris distans* Presl; Schmidt, p. 63, fig. 58.
?1953 *Cladophlebis ruetimeyeri* (Heer) Leonardi; p.10, pl. 1, fig. 15; pl. 3, fig. 6.
?1968 *Cladophlebis ruetimeyeri* (Heer) Leonardi, p. 176, pl. 28, fig. 6.
?1968 *Cladophlebis* cfr. *denticulata* Brongniart, p. 176, pl. 28, fig. 7.
1990 *Cladophlebis distans*; Kelber, p. 40, figs 23b, 70–71, 78.
1995 *Cladophlebis distans*; Kelber and Hansch, p. 66, figs 136–139.
2004 *Cladophlebis* sp. 1; Kustatscher, p. 139, pl. 2, fig. 4.

Description. There are *c.* 25 specimens of this relatively rare, at least bipinnate fern species, most of which are only small pinna fragments under 10 cm long. KÜH574 (Pl. 5, fig. 5) is by far the largest specimen; it is an apical frond fragment *c.* 20 cm long. The rachis is narrow (2–3 mm wide) and pinnae arise alternately at an angle of 45 degrees or even less near the apex. The longest complete pinna is *c.* 10 cm long and basally it is just under 2 cm wide. The rachis is 1·5 mm wide and the pinnules arise alternately. They are attached with their whole base but are not adnate, and they measure 3–16 × 2–8 mm. Venation (Text-fig. 5B) is obscure but tends to be intermediate between a typical pecopterid venation with a clear midrib and secondary veins, and a more neuropterid one in which the midrib extends to *c.* two-thirds of the pinnule length. The secondary veins fork twice in the basal part of the pinnules, and only once more apically. In some specimens (e.g. KÜH580) the pinnules tend to have a more acute apex, and a midrib that extends to almost three-quarters of the pinnule length.

There are a few small *Cladophlebis* fragments that appear to be fertile (e.g. KÜH732, 1155; Pl. 6, fig. 4) but it is not clear that they belong to *C. remota*. No details of sporangia can be seen and no *in situ* spores could be obtained.

Discussion. It is clear that this type of Triassic fern foliage is difficult to classify. It has been attributed to genera such as *Pecopteris*, *Neuropteris* and *Cladophlebis*, and even new genera have been made (e.g. *Anotopteris*, *Speirocarpus*). We think that it is best attributed to the Mesozoic morphogenus *Cladophlebis* until its fertile frond is well known. This attribution is based mainly on the morphology of the slightly falcate pinnules and the venation, which is more or less intermediate between a pecopterid and a neuropterid type. The nomenclatural problems concerning this taxon were discussed in the introductory paragraph on *Cladophlebis*. We believe our sterile material might be conspecific with *C. ruetimeyeri* from the Neue Welt flora near Basel, but the material is so fragmentary that we cannot be absolutely sure.

The fertile specimens resemble material that has been described as *Pecopteris latepinnata* Leuthardt, 1904 from the Keuper flora of Basel (see e.g. Schmidt 1928, p. 65, fig. 64), but we cannot definitely attribute these fertile specimens to the same species as our sterile material.

Cladophlebis sp.
Plate 6, figures 1, 3, 5; Text-figure 5C

2004 *Cladophlebis* sp. 2; Kustatscher, p. 139, pl. 2, fig. 5.

Description. There are about eight specimens of a pecopterid type of fern foliage, demonstrating at least bipinnate frond fragments with a relatively thick rachis (2–4 mm wide) from which pinnae arise perpendicularly. In KÜH1147 16 pinnae arise from one side of the rachis (distances between them 6–8 mm); the longest of these is *c.* 7 cm, but it is incomplete, and only 5 mm wide. The pinna rachis is 1–1·5 mm wide and small, triangular-like pinnules (2–4 × 1·5–2·5 mm) arise perpendicularly from it. The venation consists of only a midrib; no secondary veins can be seen (Pl. 6, fig. 1; Text-fig. 5C). KÜH1075 is the most complete specimen. It is a 3-cm-long rachis fragment with six attached pinna fragments, and eight more parallel pinna fragments continuing but without the presence of a rachis. There are parts of 11 more or less parallel pinna fragments oblique to

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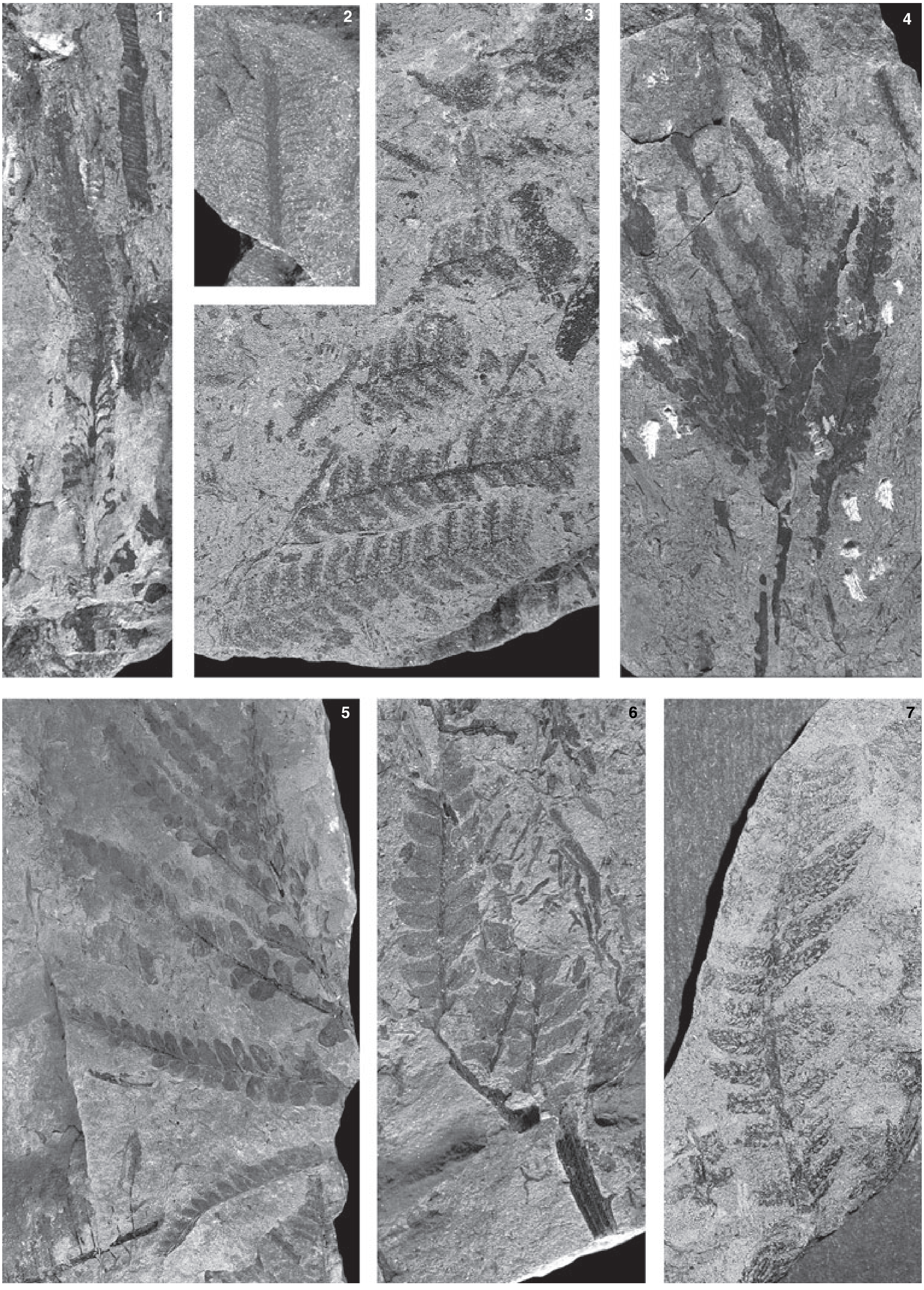
EXPLANATION OF PLATE 5

Figs 1–2. *Marattiopsis* sp. 1, pinnule, KÜH215; ×1. 2, venation, KÜH1242; ×1.

Figs 3–4, 7. *Sphenopteris schoenleiniana* (Brongniart) Presl. 3, apical frond fragment, KÜH1171; ×1. 4, frond fragment, KÜH524; ×1. 7, fertile frond fragment, KÜH1083; ×2.

Figs 5–6. *Cladophlebis remota* (Presl) comb. nov. 5, apical frond fragment, KÜH574; ×0·5. 6, frond fragment with pinnules showing an acute apex, KÜH874; ×1.



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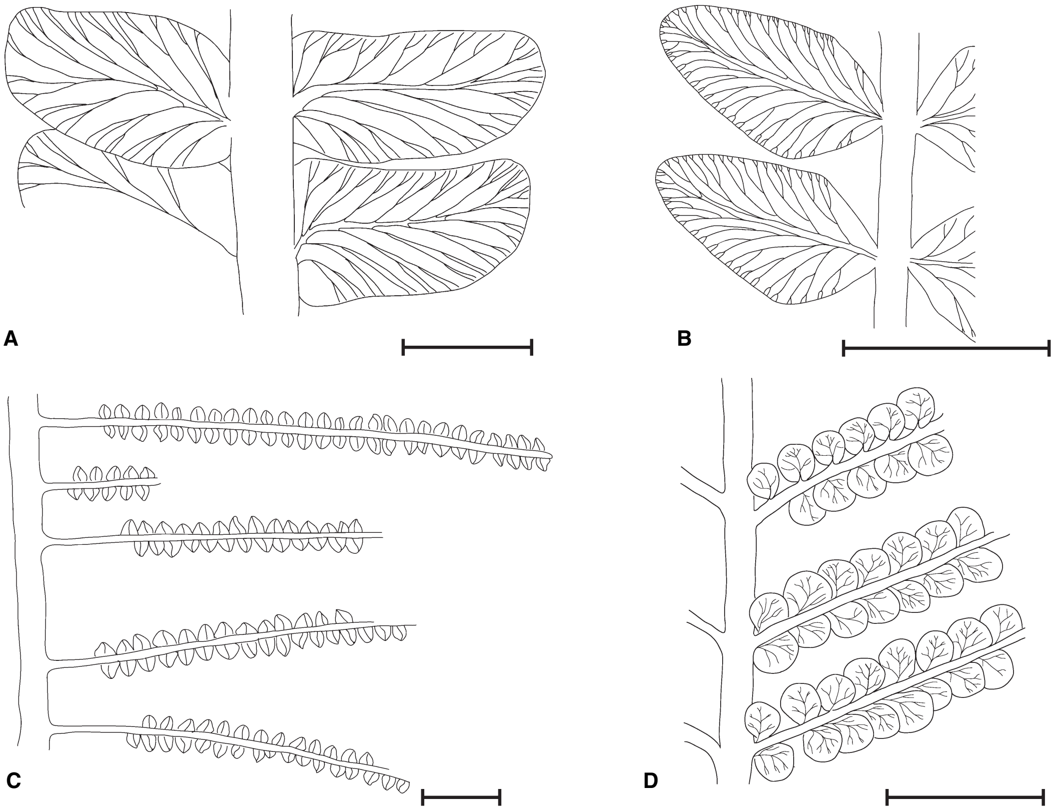

TEXT-FIG. 5. Line drawings of venation in the pinnules of some of the fern species. A, *Neuropteridium elegans* (Brongniart) Schimper and Mougeot. B, *Cladophlebis remota* (Presl) comb. nov. C, *Cladophlebis* sp. D, *Gordonopteris lorigae* sp. nov. Scale bars represent 1 cm.

this frond fragment. All of these fragments may have belonged to one large bipinnate frond (Pl. 6, fig. 3).

Two specimens (KÜH1155 and 1269) show similar pinna fragments with apparently fertile pinnules attached to them. However, because of poor preservation these fragments do not show any details of the sporangia (Pl. 6, fig. 5).

Discussion. This type of fern frond also superficially resembles *Anomopteris mougeotii* fronds because of the relatively broad rachis and perpendicularly arranged pinnae. However, the triangular pinnule shape is different from the more rounded one in *Anomopteris*, and no aphlebia have been found at the base of the pinnae. Because the preservation of all the material is rather poor, we attribute these fragments here to the morphogenus *Cladophlebis* as *Cladophlebis* sp. We have not seen any records of comparable Middle Triassic fern foliage in the literature.

PTERIDOPHYTA *incertae sedis*

Gen. et sp. indet.
Plate 6, figure 2

?1990 *Neuropteridium curvinerve* Wang and Wang, p. 121, pl. 20, figs 9–13; pl. 22, fig. 9; pl. 23, figs 1–3.
?1996 *Neuropteridium curvinerve* Wang and Wang; Wang, pl. 3, figs 1–3.
2004 ?Pteridophyta gen. et sp. indet.; Kustatscher, p. 143, pl. 5, fig. 4.

Description. Two specimens (KÜH444 and 583) in the collection show small fragments of a fern-like plant with rhomboid pinnules. The best specimen (KÜH444; Pl. 6, fig. 2) is 8·3 cm long and 3·3 cm wide. In it the rachis is *c.* 3 mm wide and bears rhomboid pinnules varying in size from 17 × 14 mm to 20 × 16 mm. The venation arises from the lower basal angle

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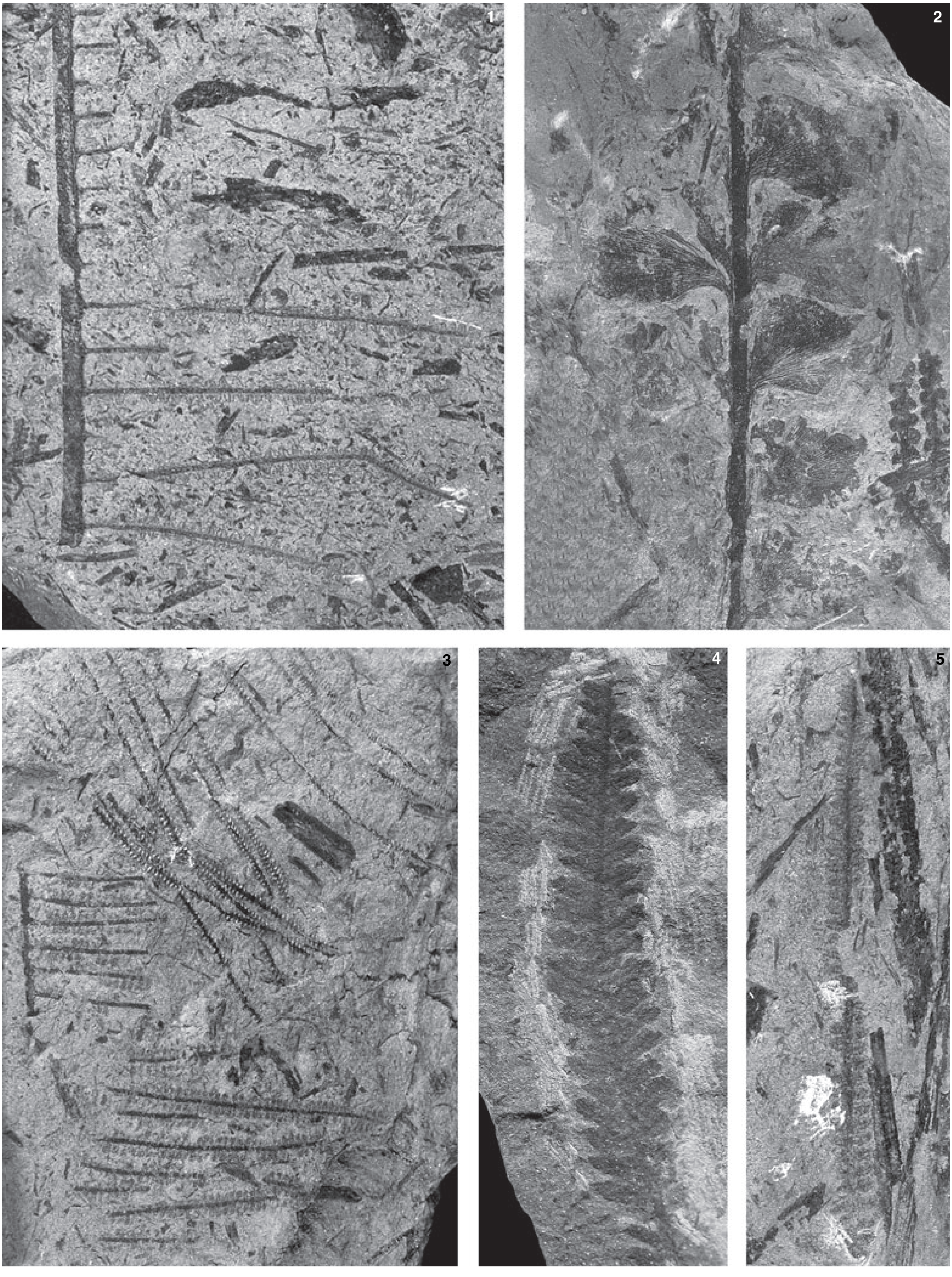
EXPLANATION OF PLATE 6

Figs 1, 3, 5. *Cladophlebis* sp. 1, frond fragment, KÜH1147; ×1. 3, frond fragment, KÜH1075; ×1. 5, fertile pinna, KÜH1269; × 1·5.
Fig. 2. Pteridophyta gen. indet. sp. indet., frond fragment, KÜH444; ×1·5.
Fig. 4. *Cladophlebis remota* (Presl) comb. nov., fertile frond fragment, KÜH732; ×3.



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of the pinnules as an undeveloped midvein that forks several times, and some veins below this 'midvein' arise directly from the rachis. The secondary veins end near the margin. The apex of the pinnules is relatively acute.

Discussion. This is the rarest fern-like foliage in the whole assemblage. We are not even sure if the specimens belong to ferns or seedferns. Maceration of the coaly substance that was preserved did not yield any cuticle. Therefore, although it is possible that we are dealing with a fern, the type of venation is more like that found in seedferns.

In the literature on Early and Middle Triassic floras, only *Neuropteridium curvinerve* described by Wang and Wang (1990) from Scythian sediments in China is similar to the present fossils. Their material obviously consists of more specimens (?seven) than ours. Wang and Wang described the pinnules as triangular (as is illustrated in their pl. 20, figs 9–13) with an obtusely pointed apex and wide base. Not all of their specimens are similar to our material but especially those on their plate 22, figure 9 and plate 23, figures 1–3 (partly re-figured in Wang 1996) show more or less rhomboidal pinnules with basically the same venation as in our specimens. Wang and Wang (1990) stated that this species is easily distinguished from the Early Triassic *Neuropteridium* species from Europe by its decurrent pinna base, pointed apex and venation. Since this is indeed the case, we hesitate to assign our material and the Chinese material to *Neuropteridium*, which is for probable osmundaceous ferns with a totally different pinnule morphology. As the material is very limited, we hesitate to create a new genus and/or species for it.

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