Genus *Trichomanes* in the European and Bulgarian Cenozoic macroflora

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Abstract. The available finds of *Trichomanes* in the Cenozoic elements on the territory of Europe have been analysed. Some taxa have been revised according to the contemporary nomenclature of the genus, others according to the *status quo* of the fossil species of the genus adopted in this study. The material described by Stefanow & Jordanow (1932) as *Trichomanes* sp. was revised as *Davallia* sp. on the basis of a comparison with recent fern species with similar morphology of the lamina and spore structure.

Key words: Bulgaria, Cenozoic, *Davallia*, Europe, paleomacroflora, *Trichomanes*

Introduction

Genus *Trichomanes* belongs to the family *Hymenophyllaceae*, one of the most interesting families of contemporary ferns. The specificities determining the interest in it lie in the fact that its relationships with other families are uncertain and that it retains a low chromosome number n = 9 and 11, which is regarded as a primitive sign, while the sporangia and anteridia structure clearly indicates an intermediate evolutionary position among the others ferns (Tryon & Tryon 1982).

All species of this family, without exception, are terrestrial plants, but with thin, almost transparent leaves, the tissues of which have underwent a considerable reduction in the process of adaptation to a humid environment. The family representatives are obligate or facultative epiphytes, or growing on rocks or soil.

They usually inhabit the tropical rain forests, reaching the greatest diversity in their mountainous regions. Most of them are attached to the low floors of these forests, growing on the roots, trunks and low branches of trees, usually no higher than 2 m above the soil. There, in close proximity to numerous mosses, they form a green carpet retaining the evaporation and assist the accumulation of moisture on the substrate surface, whether it is a root, tree trunk, dendroid fern, or tree stump, rock or soil (Surova 1978).

A lesser number of the family representatives occur in the subtropics and only single species are spread in the humid regions of the temperate-climate areas.

According to Tryon & Tryon (1982), the family *Hymenophyllaceae* is nearly a worldwide family, consisting of two genera *Hymenophyllum* (seven subgenera) and *Trichomanes* (five subgenera), both genera comprising about 300 species each. The authors have mentioned the earliest paleodata about the family: fossil wood from the Jurassic in Queensland. They also have noted that in general the information about the fossil representatives of the family is scanty.

The ecological requirements of genus *Trichomanes* do not differ from those of the family and this is why the finds of its fossil representatives is so important for the elucidation of ecological parameters during the past geological epochs.

Results

Stefanow & Jordanow (1932) reported a find of a leaf imprint determined by them as *Trichomanes* sp. (Pl. I, Figs 3-4) and isolated *in situ* spores from it, but the presented drawings of recent and fossil spores (Pl. I, Fig. 5) certainly do not correspond either to those of *T. radicans* Sw. (Pl. II, Fig. 10), or to the representatives of that genus (Pl. II, Figs 1-8) and family. Morphologically, the drawings presented by the authors are close to the spores of family *Davalliaceae,* and more specifically to the spores of genus *Davallia* (Pl. III, Figs 1-9, 13). Respectively, they are similar to the spores of *D. haidingeri* Ettingsh. (Pl. III, Fig. 15) described *in situ* by Bozukov & Ivanov (1995), although with a distinct difference in the shape of the leaf lobes and sori between the two fossil finds. Both lobes and sori of the material analysed by Stefanov & Jordanov (1932) are longer than those determined by Bozukov & Ivanov (1995) (Pl. I, Figs 3-4; Pl. III, Fig. 16). Regrettably, owing to the fragmentation of the revised fossil material, it is impossible to say to which order the leaf lobes belong. This makes even more difficult any finding of a precise recent analogue.

Registration of genus *Davallia* itself on the territory of Bulgaria by Bozukov & Ivanov (1959) presumes a possibility that some other representatives of this genus may be present there. The genus is paleotropical and epiphytic and includes about 90 species. Some of these species have been formerly treated in *Humata* Cav., *Pachypleuria* C. Presl, *Parasorus* Alderw. and *Scyphularia* Fée, or *Trogostolon* Copel. (Tryon & Lugardon 1991). Kato (1985) accepted the genus in a more restricted sense, with 40 species, arranged in three sections.

The attachment of representatives of the genera *Trichomanes* and *Davallia* to the highly moist environment determines the similar morphology of their leaf blades, hence the difficulty of their differentiation in fossil state. Proceeding from the similarity of identified *in situ* spores with those of genus *Davallia,* which excludes any possibility that the fossil material analysed by Stefanow & Jordanow (1932) belongs to genus *Trichomanes*, we shall seek resemblance in the leaf morphology with recent species of genus *Davallia.* Closest in this characteristic are the species *D. assamica* (Bedd.) Baker (China) (Pl. III, Fig. 11), *D. trichomanoides* Blume (Japan, Indo-China, Malaysia) (Pl. III, Figs 12, 14) and *D. mariesii* Moore (= *D. bullata* Wall. ex Hook., *D. trichomanoides* var. *trichomanoides*) (China, Japan, Taiwan) (Pl. III, Fig. 10). Against the background of the similar morphology of spores of the entire genus *Davallia,* particularly close are those of *D. falcinella* C. Presl (Philipines) (Pl. III, Fig. 4), *D. mariessii* (Pl. III, Fig. 9) and *D. trichomanoides* (Pl. III, Fig. 13). Considering the fact that the spore structure is more conservative characteristic and leaf morphology is relatively more variable, we could draw the conclusion that the material determined by Stefanow & Jordanow (1932) as *Trichomanes* sp. should be revised as *Davallia* sp. Unfortunately the incompleteness of the fossil material makes impossible any certain inference about its recent analogue.

Discussion

In the contemporary European flora the only representative of genus *Trichomanes* is *T. speciosum* Willd. Its sporophyte has a very limited distribution – only in scattered localities along the Atlantic coast of France and Portugal, also in S Spain (Andalusia), the West Pyrenees, in Ireland and Britain, as well as a single locality in Italy, on its Mediterranean coast close to Toscana. The gametophyte which can grow independently, has larger distribution – is registered in UK, France, Belgium, Luxemburg, Germany, S Spain and the Czech Republic (Prelli 2001). Watson & Dallwitz (2004) reported finds of this species in places with very high humidity – on sheltered, damp rock faces, often near waterfalls, or at cave entrances, very local in Western and Central England, Wales, SW Scotland, and mainly SW Ireland.

It is necessary to specify here that the authors of the paleobotanical literature cited below have compared their fossil finds with one recent species, for which they had used the *Trichomanes radicans* Sw. combination which, according to Derrick & al. (1987) falls among the synonyms of *T. speciosum*. It is the last combination in particular that we use in the present study.

The first data on a fossil find of genus *Trichomanes* for the territory of Europe are provided by Squinabol (1889) (Table 1). The author described the species *T. saccii* Squinab. (Pl. I, Figs 1-2) in the Upper Oligocene sediments from Sant Guistina (Italy).

Chronologically, next came the communication of Stefanow & Jordanow (1932) which was the first for the

Table 1. Geographic and stratigraphic distribution of genus *Trichomanes* in Europe during the Cenozoic and the respective taxonomic revision. The order in the table follows the chronology of publications and the stratigraphic units are according to Gradstein & al. (2004).

Species	Author	Geographic distribution	Stratigraphic distribution	Revision (author)
Trichomanes saccii	Squinabol (1889)	Italy	Upper Oligocene	–
Trichomanes sp.	Stefanow & Jordanow (1932; Stefanoff & Jordanoff 1935)	Bulgaria	Upper Miocene	*Davallia* sp. (Bozukov hoc. loco)
Hymenophyllum fominii	Palibin (1937)	Georgia	Upper Miocene	*T. speciosum* foss. (Bozukov hoc. loco)
Trichomanes cf. *radicans*	Andreanzsky (1949)	Hungary	Lower Miocene	*T. saccii* (Bozukov hoc. loco)
T. radicans foss.	Fataliev (1960)	Azerbaijan	Middle Miocene	*T. saccii* (Palamarev & Petkova 1990)
T. sarmaticum	Fataliev (1961)	Azerbaijan	Middle Miocene	*T. saccii* (Palamarev & Petkova 1990)
Vandenboschia radicans	Takhtajan (1963)	Georgia	Upper Miocene	*T. speciosum* foss. (Bozukov hoc. loco)
T. saccii	Palamarev & Petkova (1990)	Bulgaria	Lower Oligocene	–

territory of Bulgaria. The authors described a fossil imprint of a fragment of a pinnate leaf which, according to them, was completely identical with the recent species *T. speciosum*, but they determined the fossil material as *Trichomanes* sp. The imprint originated from some sediment rocks near Podgoumer village (Sofia district), and their age was determined by Stefanoff & Jordanoff (1935) as late Pontian–early Dacian (or approximately 6–5 million years). On the strength of the above-mentioned reasons we maintain that fossil material should be regarded as a representative of *Davallia*.

From the Upper Oligocene sediments in the Carpathian Basin is known a find determined by Andreánszky (1949) as *Trichomanes* cf. *radicans*, and revised by Takhtajan (1963) as *Vandenboschia radicans* (Sw.) Copel.

Fataliev (1961) described the species *Trichomanes sarmaticum* (Pl. I, Figs 6-7) from some Middle Miocene (Upper Sarmatian) sediments from Mt Katar in Eastern Transcaucasia. The author emphasized the following differences between the fossil material investigated by him and the recent *T. speciosum*, with which he had compared the fossils: smaller size of the fossil, stronger lobing of the blade, stronger adjacent lower and shorter upper segments, distinctly lanceolate and stoup-shaped lobes, reaching seven per segment, thinner tertiary veins.

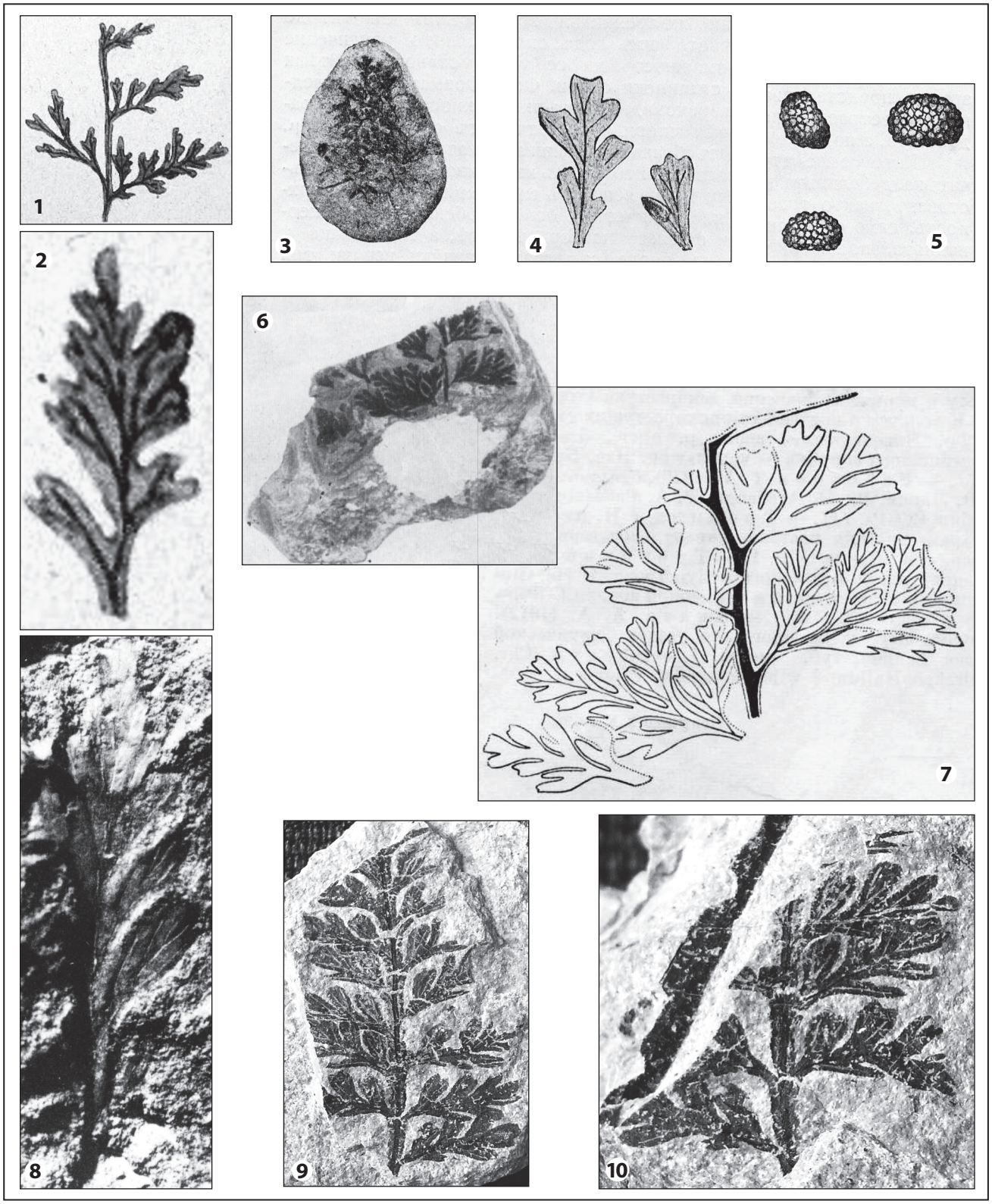
Takhtajan (1963) determined a leaf imprint from the Neogene flora of Goderdzi (Georgia) as *Vandenboschia radicans* (Pl. I, Fig. 8), a combination which, according to Derrick & al. (1987), also belongs to the synonyms of the recent species *T. speciosum*. Takhtajan (1963) also expressed the opinion that to the framework of contemporary species should also belong both Paleogene *T. saccii*, and *Hymenophyllum fominii* Palib., species described by Palibin (1937) and originating from the same location in Georgia.

That idea was rejected by Palamarev & Petkova (1990), who had reported a find of genus *Trichomanes* (Pl. I, Figs 9-10) from Paleogene sediments in Central Rhodopes (S Bulgaria). According to these authors, the material found by them belong to the species *T. saccii*, to which the Middle Miocene fossils from Transcaucasia should be referred too (Fataliev 1960, 1961), owing to the lack of any differences in their morphology with that of the holotype described by Squinabol (1889). The present study adopts the opinion of Palamarev & Petkova (1990) that all finds aged from Oligocene to middle Miocene refer to the species *T. saccii*, while the late Miocene form *Vandenboschia radicans* (Takhtajan 1963) (= *T. speciosum* foss. hoc. loco) is a direct antecedent of the contemporary species *T. speciosum*.

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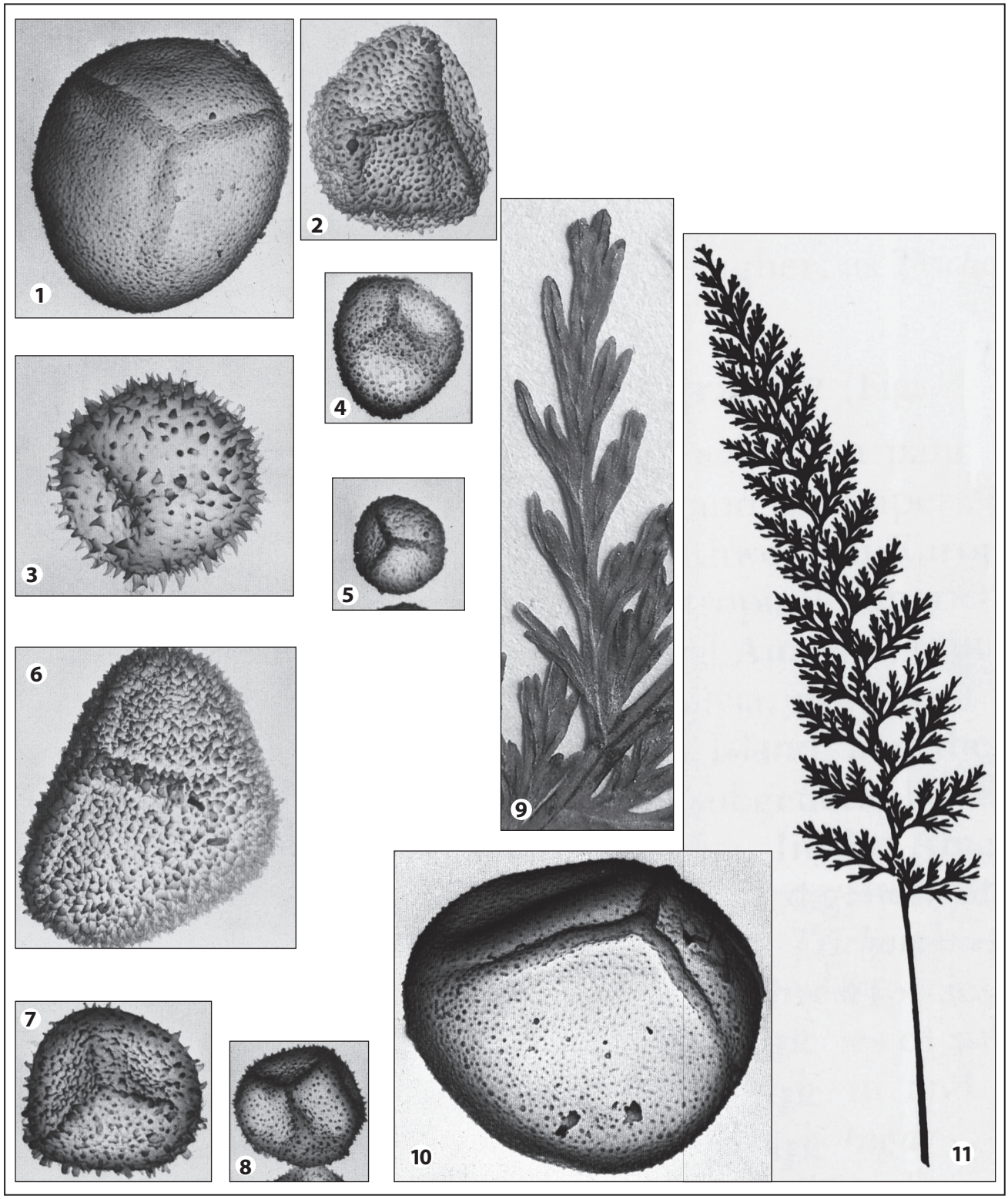
This study is financed by the National Science Fund (Contract B-1525).

Plate I



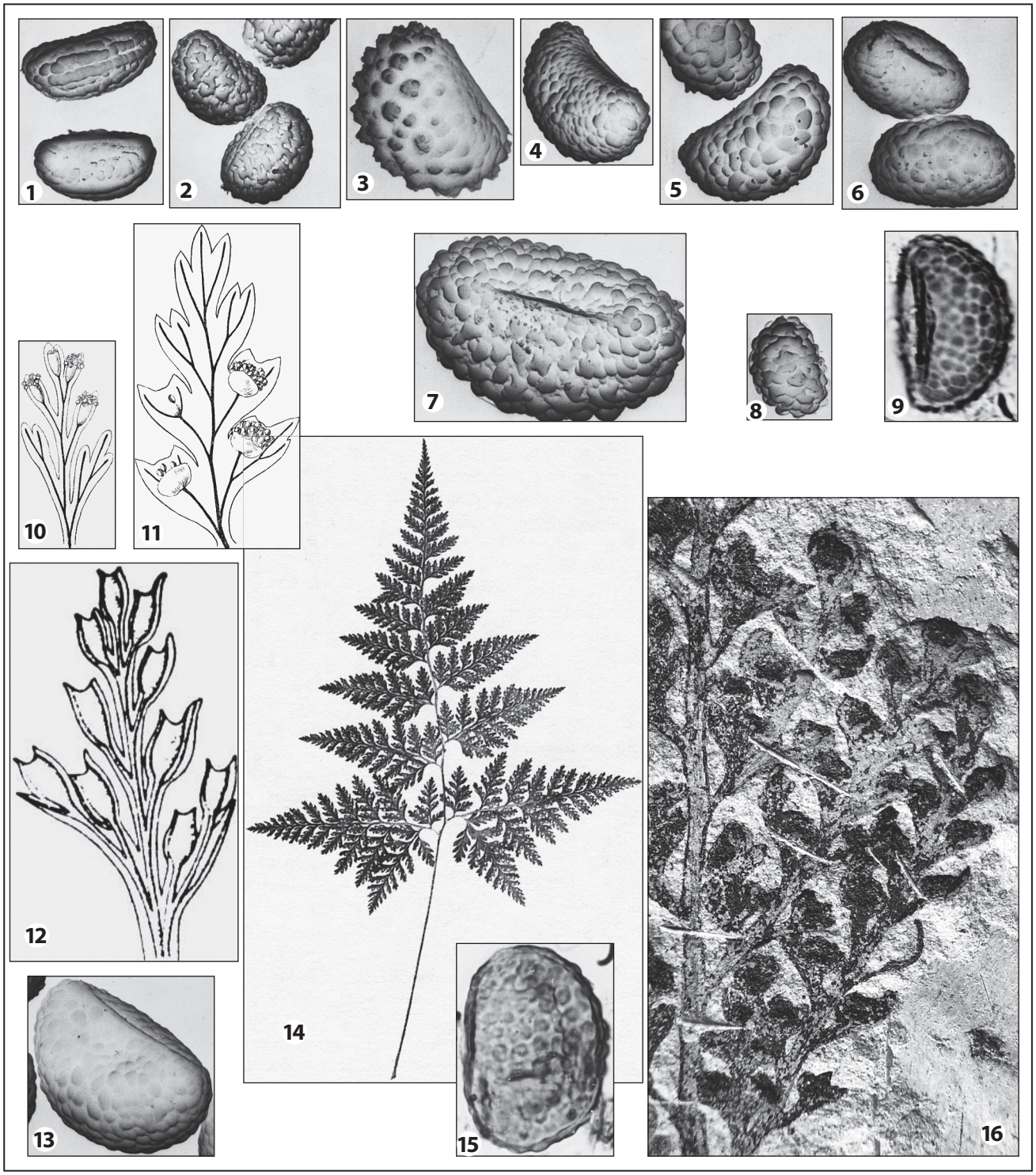
Figs 1–10. Fossil finds of *Trichomanes* and *Vandenboschia*:
1, *T. saccii* (after Squinabol 1889, 1:1); **2,** *T. saccii* – leaf segment (after Squinabol 1889, ×5); **3,** *Trichomanes* sp. (after Stefanow & Jordanow 1932, 1:1); **4,** *Trichomanes* sp. – leaf segment (after Stefanow & Jordanow 1932, ×5); **5,** *Trichomanes* sp. – spores (after Stefanow & Jordanow 1932, ×200); **6,** *T. sarmaticum* (after Fataliev 1961, 1:1); **7,** (after Fataliev 1961, ×5); **8,** *V. radicans* – leaf segment (after Takhtajan 1963, ×5); **9**, *T. saccii* (after Palamarev & Petkova 1990, ×3); **10**, *T. saccii* – leaf segment (after Palamarev & Petkova 1990, ×5).

Plate II



Figs 1–11. Spores and leafs of *Trichomanes*:
1, *T. polypodioides* – spore (after Tryon & Lugardon 1990, ×1000); **2,** *T. pellucens* – spore (after Tryon & Lugardon 1990, ×1000); **3,** *T. arbuscula* – spore (after Tryon & Lugardon 1990, ×1000); **4**, *T. tahitensis* – spore (after Tryon & Lugardon 1990, ×1000); **5,** *T. bimarginatum* – spore (after Tryon & Lugardon 1990, ×1000); **6,** *T. crenatum* – spore (after Tryon & Lugardon 1990, ×1000); **7,** *T. heterophyllum* – spore (after Tryon & Lugardon 1990, ×1000); **8,** *T. membanaceum* – spore (after Tryon & Lugardon 1990, ×1000); **9,** *T. speciosum* – leaf segment (SOM, ×5); **10,** *T. speciosum* – spore (after Tryon & Tryon 1982, ×1000); **11,** *T. speciosum* – leaf (after Tryon & Tryon 1982, ×0.5).

Plate III



Figs 1-16. Spores and leafs of genus *Davallia*:
1, *D. tenuisecta* – spore (after Tryon & Lugardon 1990, ×600); **2,** *D. heterophylla* – spore (after Tryon & Lugardon 1990, ×600); **3,** *D. canariensis* – spore (after Tryon & Lugardon 1990, ×600); **4,** *D. falcinella* – spore (after Tryon & Lugardon 1990, ×600); **5,** *D. solida* – spore (after Tryon & Lugardon 1990, ×600); **6,** *D. chaerophylloides* – spore (after Tryon & Lugardon 1990, ×600); **7,** *D. repens* – spore (after Tryon & Lugardon 1990, ×600); **8,** *D. banksii* – spore (after Tryon & Lugardon 1990, ×600); **9,** *D. mariessii* – spore (palynological collection of the Institute of Botany, BAS., ×600); **10**, *D. mariessii* – leaf segment (after Ching 1935, ×5); **11,** *D. assamica* – leaf segment (after Ching 1935, ×5); **12,** *D. trichomanoides* – leaf segment (after Kramer & Green 1990, ×5); **13,** *D. trichomanoides* – spore (after Tryon & Lugardon 1990, ×600); **14,** *D. trichomanoides* – leaf (after Walters & al. 1986, ×0.4); **15,** *D. haidingeri* – spore (after Bozukov & Ivanov 1995, ×600); **16,** *D. haidingeri* – leaf segment (no. Sat-2421, ×5).

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