GINKGO FOLIAGE FROM THE JURASSIC OF THE CARPATHIAN BASIN

by ZOLTÁN CZIER

ABSTRACT. Mesophytic *Ginkgo* foliage from the Carpathian Basin (Romania and Hungary) is revised using a new statistical method for identification. The genera *Ginkgoites* and *Baiera* are suppressed in favour of *Ginkgo*. New combinations *G. marginata* and *G. skottsbergii* are studied for the first time using scanning electron microscopy. *G. baieraeformis banaticus* subsp. nov. is an Indo-European member of the *Dictyophyllum-Clathropteris* Flora. *G. marginata banatica* subsp. nov. is characteristic of the *Clathropteris meniscioides* Biozone (Hettangian–Sinemurian) of the European Province. *G. polymorpha* is of western origin, later spreading out into Siberia. *G. skottsbergii europeica* subsp. nov. possibly belongs to the *Dictyophyllum-Clathropteris* Flora that originated in the Late Triassic in eastern South-east Asia, spread to Europe in the Early Jurassic and to South America in the Mid Jurassic, where it persisted until the Early Cretaceous.

THE Carpathian Basin yields one of the richest Liassic floras in Europe (Czier 1990, 1994*b*, 1996*a*, in press *b*). However, the only detailed records of *Ginkgo* leaves have been from the lower Liassic of the Transylvanian part of Romania and the Transdanubian part of Hungary (Text-fig. 1). The earliest illustration is of a leaf from Anina figured by Hantken (1878) as *Baiera taeniata* Braun. This locality, now in Romania, was part of Hungary before the First World War and known as Stájerlak or Steierdorf. Other specimens from Anina were described by Humml (1969) as *Ginkgoites taeniata* (Braun) Harris, and by Givulescu (1991) as *Baiera polymorpha* Samylina. Significantly, both papers included details of the cuticles. Mateescu (1958) described specimens from Svinecea Mare as *B. taeniata* but without cuticles. Nagy (1961) described specimens from Komló and Pécsbányatelep (Hungary) as *Ginkgoites marginatus* (Nathorst) Florin, as well as associated fructifications similar to those of living *Ginkgo biloba* Linnaeus.

Other records of Mesophytic *Ginkgo*-type leaves from Romania are in species lists without descriptions or illustrations (Semaka 1961, 1962*a*, 1962*b*, 1963, 1965, 1968, 1970; Oarcea and Semaka 1962; Humml 1963; Semaka *et al.* 1972). They are based mainly on specimens stored in the Institute of Geology and Geophysics in Bucharest, but a request to study these specimens was refused and so nothing is known of their cuticles. As cuticle information is critical, these records are of little value and are not referred to in the rest of this paper.

This paper completely revises all well-documented Liassic *Ginkgo*-like leaves from the Carpathian Basin, including new material from Anina and Şuncuiuş, and may be regarded as a synthesis of Mesophytic *Ginkgo* foliage from this part of Europe. Scanning electron microscopy was used for the first time with such foliage from here, and has yielded results significant for both Carpathian palaeobotany and a wider understanding of the group.

IMPORTANCE OF CUTICLE STUDIES IN THE GENUS *GINKGO*

Cuticles are essential for the identification of *Ginkgo*-type leaves, because biological species show so much morphological variation, as is clearly seen in the extant *Ginkgo biloba*. The limits of this variation are subject to genetic control but climate also has a strong effect. Kimura (*in* Zhao *et al.* 1993, p. 80) demonstrated experimentally that low levels of water supply or natural light would cause seedlings to sprout leaves in May, but they remained abnormally small until leaf-fall in the

[Palaeontology, Vol. 41, Part 2, 1998, pp. 349–381, 4 pls]

TEXT-FIG. 1. Localities yielding *Ginkgo* foliage in the lower Liassic of the Carpathian Basin.

autumn. If such miniature leaves, or the rare outgrowth leaves with multidivided laminae, were preserved as fossil impressions, palaeobotanists would probably recognize them as separate *Ginkgo* species. Significantly, however, the cuticles remained the same.

The wide morphological variation in Mesophytic *Ginkgo*-like leaves, particularly in the early Liassic, was almost certainly influenced largely by climate. Epidermal structure is therefore the only reliable means of distinguishing between *Ginkgo* species. This conclusion has at least four practical implications.

1. Leaf gross morphology must be treated with the greatest caution in *Ginkgo* taxonomy. Macroscopic characters alone cannot define or be used to distinguish fossil species of *Ginkgo*.
2. New species of *Ginkgo* should only be established for fossil leaves where cuticles are known.
3. Fossil *Ginkgo* leaves lacking cuticles should only be assigned with an 'aff.' to a species for which cuticles have been described. If no such comparable species can be found, they should be determined simply as *Ginkgo* sp.
4. It is vital to obtain epidermal evidence for any species of fossil *Ginkgo* leaf diagnosed only on macroscopic characters. If no cuticles are available from the original types, that species should be rejected. No attempt should be made to establish cuticle-bearing neotypes for such species.

The cuticular characters of some of the better studied *Ginkgo* leaves are summarized in the Appendix. However, not all of these characters are of the same taxonomic value. For instance, because the non-stomatal bands correspond mainly to the veins, their width tends to be of very low taxonomic significance. The distinction between the costal and intercostal fields probably depends mainly on the fineness of the venation, and so is again of rather low taxonomic importance. The dimensions, shape and arrangement of the epidermal cells are generally highly variable in a species, sometimes even in the same specimen, and often overlap with the variation in other species. More important are the shape of the cell walls, whether the lamina is hypostomatic or amphistomatic, and the arrangement and orientation of the stomata. The cell ornamentation (papillae and trichomes) and stomatal density and index are also of great taxonomic importance, as well as providing information about the palaeoclimate (Chaloner and Creber 1990). The most important characters are, however, those of the stomatal structure, including the shape and size of the guard cells, the shape, size, number and ornamentation of the subsidiary cells, and the shape of the stomatal pit.

Because of their different taxonomic importance, each character is assigned a Factor of Importance (F), ranging from 1 (least important) to 10 (most important). The Factor of Importance for each of the characters studied is given in the Appendix.

Not all of these cuticular characters are easily observed using light microscopy; details of the stomata can be particularly difficult (e.g. ornamentation, walls and mutual relationships between the guard and subsidiary cells). As such characters are among the most important for *Ginkgo* leaf taxonomy, light microscopy must be supplemented by scanning electron microscopy (SEM). The value of SEM has been clearly demonstrated in the studies of *Ginkgo insolita* Samylina from the Middle Jurassic of western Siberia (Samylina and Markovich 1991) and of *G. manchurica* from the upper Jurassic or lower Cretaceous of Inner Mongolia (Zhao *et al.* 1993).

IDENTIFICATION OF FOSSIL *GINKGO* LEAVES

The following is a new statistical approach to the perennial problem of identifying fragmentary plant fossils. It is used here for *Ginkgo* foliage but could be adapted to any group of plant fossils. The first step is to list all characters on which the identification is to be based and to assign a Factor of Importance (F) to each. Then, for each well-documented species which might be comparable, assign one of four letters to each character: T, if that species is identical to the new material in that character; N, if that species is totally different from the new material in that character; P, if that species partly agrees with the new material in that character; and U, if that character is not known in either that species or the new material. Each occurrence of T, N, P and U is then multiplied by its corresponding Factor of Importance, and then summed over the entire species. This results in four parameters, ΣFT, ΣFN, ΣFP and ΣFU, from which an Affinity Index (A) is calculated.

$$A = \frac{(\Sigma FT - \Sigma FN) \pm (\Sigma FP + \Sigma FU)}{\Sigma F} \times 100.$$

The resulting two values for A reflect the extreme cases whereby all of the P and U values have the same influence as T (i.e. the Highest Affinity Index – A_H) or they all have the opposite influence as T (i.e. the Lowest Affinity Index – A_L).

The next stage depends on whether cuticles are preserved in the new material. If they are, then the following decision tree should be followed through.

1. If $\Sigma FN \neq 0$ for all species, go to 2
   If $\Sigma FN = 0$ for one or more species, go to 3

2. Recalculate ΣFN for cuticular characters only (ΣFN_C)
   If $\Sigma FN_C \neq 0$ for all species, go to 2.1
   If $\Sigma FN_C = 0$ for one species, go to 3; if necessary, emend diagnosis to account for apparent discrepancy in gross morphology
   If $\Sigma FN_c = 0$ for several species, go to 3; where $A_L > 0$ in no species, the assignments should be with 'ex group' rather than 'cf.'

   2.1 If $\Sigma FN < 15$ in one species, assign to that species and emend diagnosis; go to 2.1.1
   If $\Sigma FN < 15$ in several species, select species with lowest ΣFN, assign to that species and emend diagnosis; go to 2.1.1
   If $\Sigma FN < 15$ in no species, select that species with the lowest ΣFN; go to 2.1.2

   2.1.1 If new material is from a quite different geographical area and/or stratigraphical level from the types, create new subspecies
   If new material is from a clearly different population, but the geographical and/or stratigraphical separation is only partly distinct, create new variety

2.1.2 If $A_L > 0$, assign to that species with 'aff.'
If $A_L \leqslant 0$, either continue comparisons with other species or, if all reasonable comparisons have been made, create new species

3. If $A_L > 0$ in no species, assign with 'cf.' to the species with highest A_L; if several species have an equally high A_L, assign with 'cf.' to species with highest A_H
If $A_L > 0$ in only one species, then assign to that species
If $A_L > 0$ in several species, select that species with the highest A_L; if several species have an equally high A_L, assign to species with highest A_H

The limiting value at node 2.1 will vary in different groups of fossils, and reflects those characters which are of low taxonomic value. In the case of *Ginkgo*, it has been given as 15, due to the low F values of the 11 macroscopic characters and of the widths of the stomatal and non-stomatal bands.

If the new material does not have cuticles, the same four parameters ΣFT, ΣFN, ΣFP and ΣFU, and the Affinity Index (A) are calculated on the macroscopic characters alone. A simplified decision tree is then used.

1. If ΣFN = 0 in no species, refer it to *Ginkgo* sp. or *Ginkgo*? sp.
If ΣFN = 0 in one or more species, go to 2.
2. Select species with highest ΣFT values; if only one species has that value, assign there with 'aff.'. If several species have highest ΣFT value, assign it with 'aff.' to that species which is geographically and/or stratigraphically nearest

MATERIAL AND METHODS

The material described in this paper consists of five hand specimens, three slides and two SEM stubs. Two hand specimens were collected by the author in 1987 and 1988, from the lower Liassic of Şuncuiuş, and are now in the Palaeobotanical Collection of the Ţării Crişurilor Museum – Natural Sciences (TCMO-NS. 15364/1 and 16623/4). The other three hand specimens were collected in 1937 from the lower Liassic of Anina (other data not known) and are kept in the Palaeobotanical Collection of the Hungarian Natural History Museum, Budapest (MTM-BP.602241 A–C). The slides (Z.C. 12–14) and SEM stubs (Z.C. 11 SEM, 12 SEM) are currently kept in the Bihor County Museum, Oradea, but are to be deposited in the Hungarian Natural History Museum, Budapest.

Cuticles were prepared by macerating the fossil in Schulze's reagent (HNO_3 plus $KClO_3$) and neutralizing with KOH. The cuticles were mounted in glycerin-jelly for light microscopy, and on a transparent film for SEM study.

SYSTEMATIC PALAEONTOLOGY

Phylum GINKGOPHYTA
Order GINKGOALES
Family GINKGOACEAE

Genus GINKGO Linnaeus, 1771

Type species. Ginkgo biloba Linnaeus, 1771.

Remarks. It has been argued (e.g. Petrescu and Dragastan 1981) that the Ginkgoales belong to the Cordaitopsida (Gymnospermatophyta). However, I follow authors such as Boersma and van Konijnenburg-van Cittert (1991) and use the phylum name Ginkgophyta. I also follow Zhou (1991) in the use of the family name Ginkgoaceae.

Ginkgo was introduced by Linnaeus (1771) for the extant maidenhair tree. Although it has also been used for fossil foliage (e.g. Heer 1876), many palaeobotanists have tended to assign such fossils to *Ginkgoites* Seward, 1919 and *Baiera* Braun, 1843 emend. Florin, 1936. As pointed out by Harris and Millington (1974, p. 4), however, the name *Ginkgoites* has been used in three different ways.

1. Seward (1919) originally proposed it for *Ginkgo*-like fossil leaves for which reproductive organs were unknown; in this sense, *Ginkgoites* has no morphological distinction from *Ginkgo*.

2. Florin (1936) rejected Seward's convention and used *Ginkgoites* for two groups of fossils. Firstly, he used it for species judged to be too different from *Ginkgo* to be included in that genus. This usage is thus based on morphological distinctions, albeit undefined. Secondly, he used it for inadequately known species, especially where cuticles are unknown. Florin's second usage is thus a pure convention, albeit not the same as Seward's.

3. Tralau (1968) gave a clear morphological distinction: *Ginkgo* (and *Ginkgodium* Yokoyama) had leaves 'divided into two or more lobes by shallow notches which never reach the basal part of the lamina'; *Ginkgoites* (and *Baiera*) had leaves 'deeply and symmetrically divided into narrow segments'.

Harris and Millington argued that although the Tralau usage was morphological, it was inapplicable in practice. For instance, at its type locality, the leaves of *Ginkgo huttonii* (Sternberg) Heer were either deeply divided (i.e. *Ginkgoites*-like *sensu* Tralau) or shallowly divided (i.e. *Ginkgo*-like *sensu* Tralau). Even some *G. biloba* trees bear leaves of both morphological type. Harris and Millington therefore proposed to suppress *Ginkgoites*, and I agree. Consequently, all species that have been placed in *Ginkgoites* must be transferred to *Ginkgo*.

I have the same opinion about *Baiera* as it is difficult to distinguish from *Ginkgo* using cuticles (Zhao *et al.* 1993). Harris and Millington (1974) distinguished them on just one macroscopic character, i.e. the segments of *Baiera* have no more than four veins. In my view, this distinction is purely conventional without any scientific logic; it could equally be another number of veins, such as six.

Fossil *Ginkgo*-like foliage is usually fragmentary and represented by only a few specimens, from which the full range of morphological variation cannot be determined. *G. biloba* foliage is by contrast well-known, and the limits of variation can be established on entire populations. This makes *Ginkgo* a much more robust genus than both *Ginkgoites* and *Baiera*. As there is no essential difference between the characters of the fossil and living leaves, and *Ginkgo* has nomenclatural priority, there seems no reason why the name should not also be used for the fossil leaves. *Ginkgoites* and *Baiera* should therefore be suppressed in favour of *Ginkgo*.

Ginkgo baieraeformis (Klipper) Czier comb. nov.

1971 *Ginkgoites baieraeformis* Klipper, p. 92, text-fig. 3; pl. 25, fig. 3; pl. 28, figs 4–6.

Holotype. Specimen JK 702 (hand specimen and microscope slide), Ruhrland Museum, Essen, Germany (Klipper 1971, pl. 25, fig. 3; pl. 28, figs 4–6). Isotype JK 707 (Klipper 1971, text-fig. 3). Origin: Zirab, northern Iran; middle Liassic Shemshak Formation (Assereto 1966; Vozenin-Serra and Taugourdeau-Lantz 1985).

Emended diagnosis. Leaf petiole > 20 mm long, 1–2 mm wide. Basal angle *c.* 60–70°. Lamina divided in to *c.* six or seven segments, *c.* 50–70 mm long. Central division very deep, reaching the top of the petiole. Ultimate segments linear to slightly oblanceolate, their free portion *c.* 30–40 mm long and *c.* 2–9 mm wide. Number of veins in widest part of segments four to fifteen. Leaf hypoamphistomatic. Distinctness of costal and intercostal fields of adaxial epidermis highly variable. Intercostal cells polygonal to slightly elongate, costal cells elongate to polygonal, both of them 20–40 μm in size. Each cell has a faint papilla. Abaxial epidermis with numerous stomata, *c.* 80 per mm^2. Stomatal bands *c.* 200–215 μm wide. Stomata mainly longitudinally oriented, irregularly or more or less regularly arranged, forming even rows. Epidermal cells mainly polygonal, isodiametric to slightly elongate, *c.* 15–20 μm $\times$ 7–15 μm in size, with straight to slightly sinuous

TABLE 1. Statistical analysis of material from Anina figured by Humml (1969) as *Ginkgoites taeniata*.

Species	ΣFT	ΣFN	ΣFN_C	ΣFP	ΣFU	A_L	A_H
G. australis	18	23	23	69	80	−81	+76
G. baieraeformis	26	10	10	31	123	−73	+89
G. cuneifolius	19	19	18	47	105	−80	+80
G. digitata	52	16	14	16	106	−45	+83
G. insolita	46	36	35	36	72	−52	+62
G. iranicus	7	17	17	34	132	−93	+82
G. longifolius	26	14	14	56	94	−73	+85
G. marginata	66	21	21	31	72	−31	+78
G. parasingularis	21	14	14	60	95	−78	+85
G. skottsbergii	47	42	42	29	72	−51	+56
G. taochuanensis	36	28	26	35	91	−62	+71
G. troedssonii	15	51	51	52	72	−84	+46
G. waarrensis	30	24	24	59	77	−68	+75
G. whitbiensis	13	18	17	61	98	−86	+81

walls. Non-stomatal bands *c.* 50–70 μm wide, with cells arranged in longitudinal rows, and with elongate, straight to finely sinuous walls. Papillae present, trichomes absent. Stomatal apparatus cyclocytic, with five to eight subsidiary cells, and guard cells *c.* 40 μm long and *c.* 20 μm wide. Stomatal pit oval, elongate.

Remarks. This diagnosis is partly based on the description given by Klipper (1971), with additional information derived from the specimen described by Humml (1969) as *Ginkgoites taeniata.* Humml's is the only known Mesophytic specimen from the Carpathians that can be assigned to this species. It was subjected to a statistical analysis, as outlined in the earlier part of this paper (Table 1). The parameters ΣFN and ΣFN_C were not zero for any of the species compared, but were less than 15 for *G. baieraeformis.* It is therefore assigned to the latter species, but as a separate subspecies.

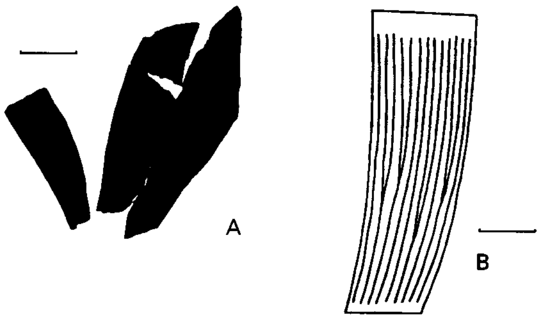
The nearest species appear to be *G. digitata, G. longifolius* and *G. parasingularis.* Both *G. digitata* and *G. parasingularis* have a wider basal angle and shorter segments. *G. digitata* also has much wider segments, more veins per segment, and a hypostomatic lamina with trichomes but not papillae; while *G. parasingularis* has stomata with usually fewer subsidiary cells, and wider non-stomatal bands on the lower cuticle. *G. longifolius* has a longer petiole with few stomata on the abaxial surface and a lower stomatal density on the adaxial surface, much wider stomatal and non-stomatal bands, and an often distinctively stellate stomatal pit.

Ginkgo baieraeformis (Klipper) Czier, comb. nov., subsp. *baieraeformis*

Holotype. As for species.

Diagnosis. Maximum width of free portion of segments no more than 5 mm; no more than six veins in widest part of segment; epidermal cells polygonal; adaxial epidermis with costal and intercostal fields not distinct; abaxial epidermis with irregularly arranged stomata, with no more than seven subsidiary cells.

Distribution. Iran: Zirab, middle Liassic (Klipper 1971).



TEXT-FIG. 2. *Ginkgo baieraeformis* subsp. *banaticus* Czier subsp. nov.; Palaeobotanical Institute, University of Graz; holotype; Anina; lower Liassic (Hettangian–Sinemurian). A, leaf silhouette; scale bar represents 10 mm. B, details of venation; scale bar represents 5 mm. Both based on Humml (1969, pl. 10, fig. 23; text-fig. 9).

Ginkgo baieraeformis subsp. *banaticus* Czier subsp. nov.

Text-figure 2

1969 *Ginkgoites taeniata* (Braun) Harris; Humml (*non* Braun), p. 401, text-fig. 9; pl. 10, fig. 23; pl. 11, figs 24–25.

Derivation of name. From Banat, the type region.

Holotype. Hand specimen and slides (Humml 1969, text-fig. 9; pl. 10, fig. 23; pl. 11, figs 24–25) stored at the Palaeobotanical Institute, University of Graz, Austria. Origin: Anina, Banat region, Romania; Anina Coal Formation, *Clathropteris meniscioides* Biozone (*sensu* Czier in press *a*), lower Liassic (Hettangian–Sinemurian).

Diagnosis. Maximum width of free portion of segments at least 4 mm; adaxial epidermis with distinct costal and intercostal fields; costal cells mainly elongate; on abaxial epidermis, stomata arranged in rows and with at least six subsidiary cells.

Remarks. Humml identified this specimen as *Ginkgoites taeniata* (*Ginkgo taeniata sensu* Sikstel *et al.* 1971), but the nomenclature of this species is very confused and it should probably be rejected. It was first published as a *nomen nudum* (as *Baiera taeniata*) by Braun (1843). The first macroscopic description (Schenk 1867) was based on Early Jurassic material from Germany, but this may not have been conspecific with Braun's original species concept. Antevs (1919) figured cuticles under this name, but Harris (1935) later transferred them to *Ginkgoites hermelinii*, which in turn has been regarded as a synonym of *Ginkgo marginata* (Lundblad 1959). All published records of this species to date are equivocal and there is no firm basis on which to build a coherent taxonomic concept.

Schenk (1867) assigned a specimen from Anina, recorded by Andrae (1855) as *Cyclopteris digitata* (now *Ginkgo digitata*), to *Baiera taeniata*. However, Andrae's specimen has never been described or illustrated and cannot be judged.

Humml (1969, p. 402) stated that his specimen differs from Schenk's (1867) illustrations and so it is difficult to see why he assigned them to *G. taeniata*. The analysis shown in Table 1 indicates that the specimen should rather be assigned to a new geographical subspecies of *G. baieraeformis*, subsp. *banaticus*.

Distribution. Romania: Anina, lower Liassic (Hettangian–Sinemurian, *Clathropteris meniscioides* Zone).

Ginkgo marginata (Nathorst) Czier comb. nov.

1878 *Baiera marginata* Nathorst, p. 51, pl. 8, figs 12(?), 13–14.
1959 *Ginkgoites marginatus* (Nathorst) Florin; Lundblad, p. 10, text-figs 1–4; pl. 1, figs 1–12; pl. 2, figs 1–13.

Holotype. Hand specimen (Nathorst 1878, pl. 8, fig. 13) and cuticles derived from it figured by Lundblad (1959, text-figs 1A, 2A–B; pl. 1, figs 1–8), are stored at the Geological Survey of Sweden, Stockholm. Origin: Hälsingborg, Sweden; lower Liassic.

Emended diagnosis. Leaf fan-shaped. Petiole incompletely known, at least 10 mm long (probably reaching at least 30 mm) and *c*. 3·5 mm wide. Basal angle *c*. 40–145°. Segments 20–80 mm long. Four to eight (typically eight) entire-margined ultimate segments, approximately parallel in middle part of lamina, but converging towards apex and base. Leaf apices rounded to almost obtuse or truncate; free portion of segments up to *c*. 35–40 mm long and 1·5–7·0 mm wide. Veins dichotomous; four to eight veins in widest portion of segments. Distance between veins 0·3–1·8 mm. Leaf hypoamphistomatic; on lower surface, stomatal density *c*. 33–50 per mm^2, stomatal index *c*. 2–7. Upper epidermis consists of bands of cells that are elongated parallel to veins, separating bands of isodiametric, polygonal cells; cell outlines finely sinuous. Cell ornamentation consists of a central thickening, sometimes forming papilla. Lower epidermis consists of alternating stomatal and non-stomatal bands. Non-stomatal bands *c*. 100–150 μm wide, consisting of more or less conspicuous rows of longitudinally oriented, almost smooth-walled, elongated epidermal cells, 25–114 μm long and 13–30 μm wide. Stomatal bands *c*. 300–1800 μm wide, with polygonal to irregularly shaped cells, *c*. 30–48 μm long and *c*. 27–33 μm wide, whose walls are sinuous to almost straight. Stomata uniformly scattered through stomatal bands, irregularly to longitudinally oriented, and not forming distinct rows. Cyclocytic (monocyclic or incompletely amphicyclic) stomatal apparatus. Stomata sunken, oval in shape, with guard cells 36–72 μm long (mean *c*. 54 μm) and *c*. 10–20 μm wide. Each apparatus has three to eight polygonal subsidiary cells with well-developed, distinct to confluent papillae, which may conceal guard cells; stomatal pit oval or variable in shape. Trichomes, if present, exceedingly rare.

Remarks. This diagnosis combines macroscopic details given by Nathorst (1878), and macroscopic and cuticular details given by Lundblad (1959). It also incorporates evidence obtained in the present study, especially from SEM, which had not hitherto been used with this species.

Lundblad (1959, p. 17) showed that a number of the features mentioned in the diagnosis are variable: the size of the leaves; the degree of cutinization of the epidermis; the stomatal density on the upper epidermis; the development of the central cutinized thickenings of the epidermal cells; and the degree of exposure of the guard-cells between the subsidiary cells. The sinuosity of the cell-walls is subject to little variation, but straight-walled cells have been observed in places. Distinct papillae are generally present on each subsidiary cell, but 'atypical' stomata with confluent cutinized thickenings are occasionally present. I agree with all these observations, except that in the Anina material, the thickenings and papillae on subsidiary cells are as a rule confluent and are not 'atypical'.

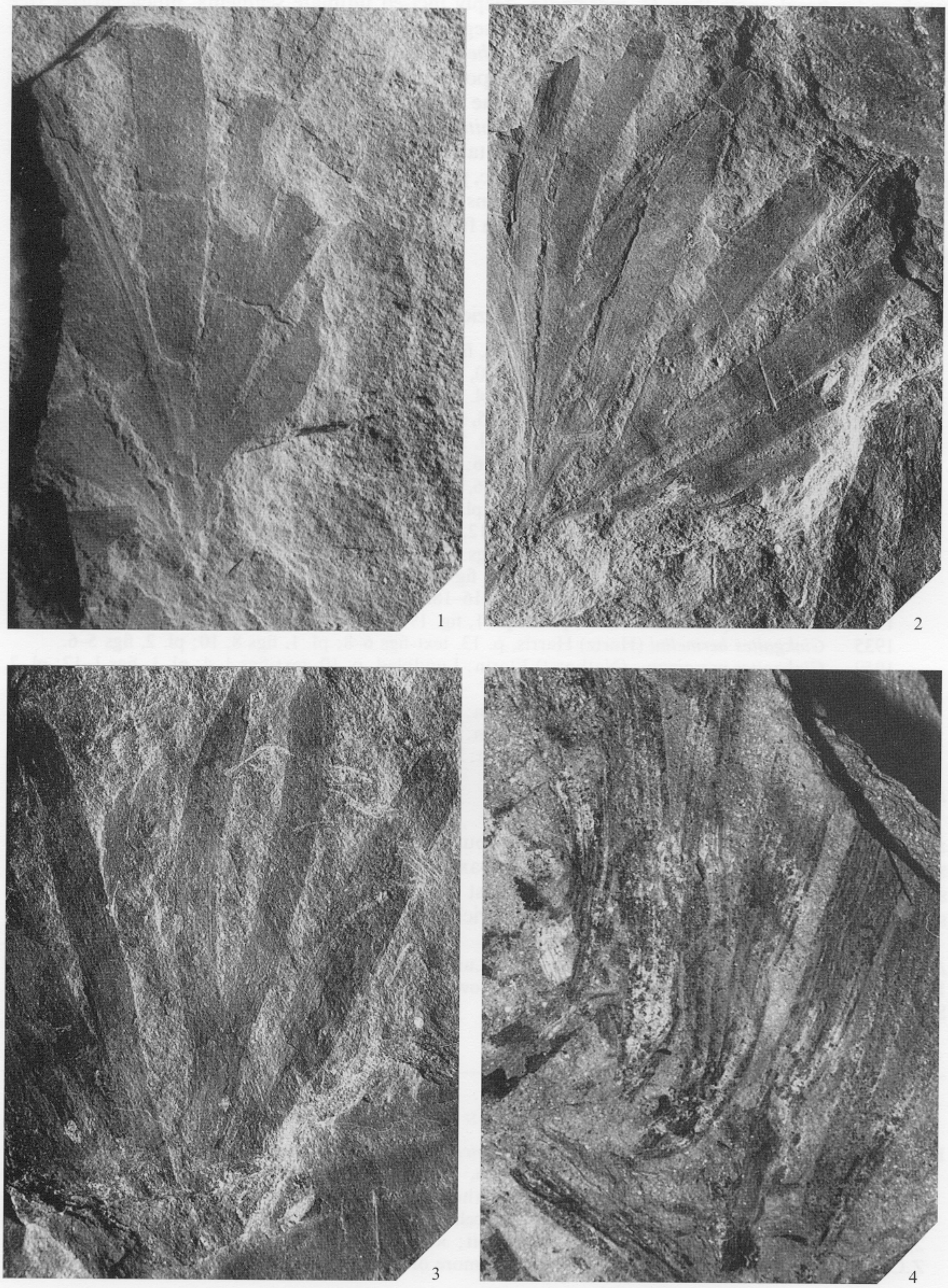
The nearest comparison is with *G. longifolius*, but this has a narrower petiole, ultimate segments that are sometimes incised, an adaxial epidermis with very few stomata, costal and intercostal fields that are poorly distinct, and wider non-stomatal bands on the abaxial epidermis. *G. digitata* has a

EXPLANATION OF PLATE 1

Fig. 1. *Ginkgo marginata* (Nathorst) Czier *banatica* subsp. nov.; MTM-BP.602241C (holotype); Anina, Banat region, Romania; Anina Coal Formation, lower Liassic (Hettangian–Sinemurian); × 2.

Figs 2–3. *Ginkgo skottsbergii* (Lundblad) Czier *europeica* subsp. nov.; Anina, Banat region, Romania; Anina Coal Formation, lower Liassic (Hettangian–Sinemurian). 2, MTM-BP.602241A (holotype); × 1·5. 3, MTM-BP.602241B (paratype); × 1·8.

Fig. 4. *Ginkgo* sp. B.; TCMO-NS. 15364/1; Şuncuiuş, Romania; Şuncuiuş Fireclay Formation, lower Liassic (Hettangian–lower Sinemurian); × 2·4.



CZIER, *Ginkgo*

much wider basal angle than *G. marginata*, deeply incised ultimate segments, much shorter free portions of the segments, and more veins per segment. It also has an hypostomatic lamina, no papillae, and an elongated stomatal pit. *G. skottsbergii* differs in the narrower petiole, segments that are occasionally incised and have a longer free portion, its lower stomatal density and index, the wider non-stomatal bands, the absence of papillae in ordinary epidermal cells, and the rhomboidal to polygonal shape of the stomatal pit. *G. whitbiensis* differs in the narrower petiole, shorter segments, fewer ultimate segments, higher stomatal density, the scarcely recognizable stomatal and non-stomatal bands, the more or less isodiametric, polygonal to rectangular epidermal cells, and the presence of few papillae, restricted to the margins of the stomatal pit.

Based on the analysis in Table 2, one specimen from Anina has been assigned to this species, but as a separate subspecies.

Ginkgo marginata (Nathorst) Czier comb. nov. subsp. *marginata*

1878 *Baiera marginata* Nathorst, p. 51, pl. 8, figs 12(?), 13–14.
1896 *Ginkgo* (*Baiera*) *Hermelini* Hartz, p. 240, pl. 19, fig. 1.
1919 *Baiera taeniata* Braun; Antevs, p. 44, pl. 5, figs 20–24; pl. 6, fig. 43.
1919 Cf. *Ginkgo Geinitzi*; Antevs, p. 43, pl. 5, fig. 18.
1922 *Ginkgo* cf. *sibirica*; Johansson, p. 43, pl. 3, fig. 5; pl. 6, fig. 26; pl. 8, figs 7–9.
1922 *Ginkgo* sp. Johansson, p. 44, pl. 3, fig. 6; pl. 8, fig. 5.
1922 *Baiera taeniata* Braun; Johansson, p. 46, pl. 4, figs 7–8; pl. 8, fig. 12.
1922 *Baiera* cf. *longifolia*; Johansson, p. 45, pl. 3, figs 7–11; pl. 8, figs 3–4.
1922 *Baiera* sp. Johansson, p. 49, pl. 3, fig. 12.
1924 *Ginkgo Hermelini*; Chow, p. 8, pl. 1, figs 13–15.
1924 *Ginkgo* or *Baiera* sp. Chow, p. 9, pl. 1, fig. 20; pl. 2, fig. 7.
1924 *Baiera taeniata*; Chow, p. 9, pl. 1, figs 16–18.
1924 *Baeira* cf. *spectabilis*; Chow, p. 11, pl. 1, fig. 19.
1935 *Ginkgoites hermelini* (Hartz) Harris, p. 13, text-figs 6–8; pl. 1, figs 8, 10; pl. 2, figs 5–6.
1959 *Ginkgoites marginatus* (Nathorst) Florin; Lundblad, p. 10, text-figs 1–4; pl. 1, figs 1–12; pl. 2, figs 1–13.
non 1961 *Ginkgoites marginatus* (Nathorst) Florin; Nagy, p. 629, pl. 16, fig. 2; pl. 17.
? 1970 *Ginkgoites marginatus* (Nathorst) Florin; Semaka, p. 69 [only in list].
? 1993 *Ginkgoites marginatus* (Nathorst) Florin; Zhao *et al.*, p. 89 [cited after lists of Chinese authors].

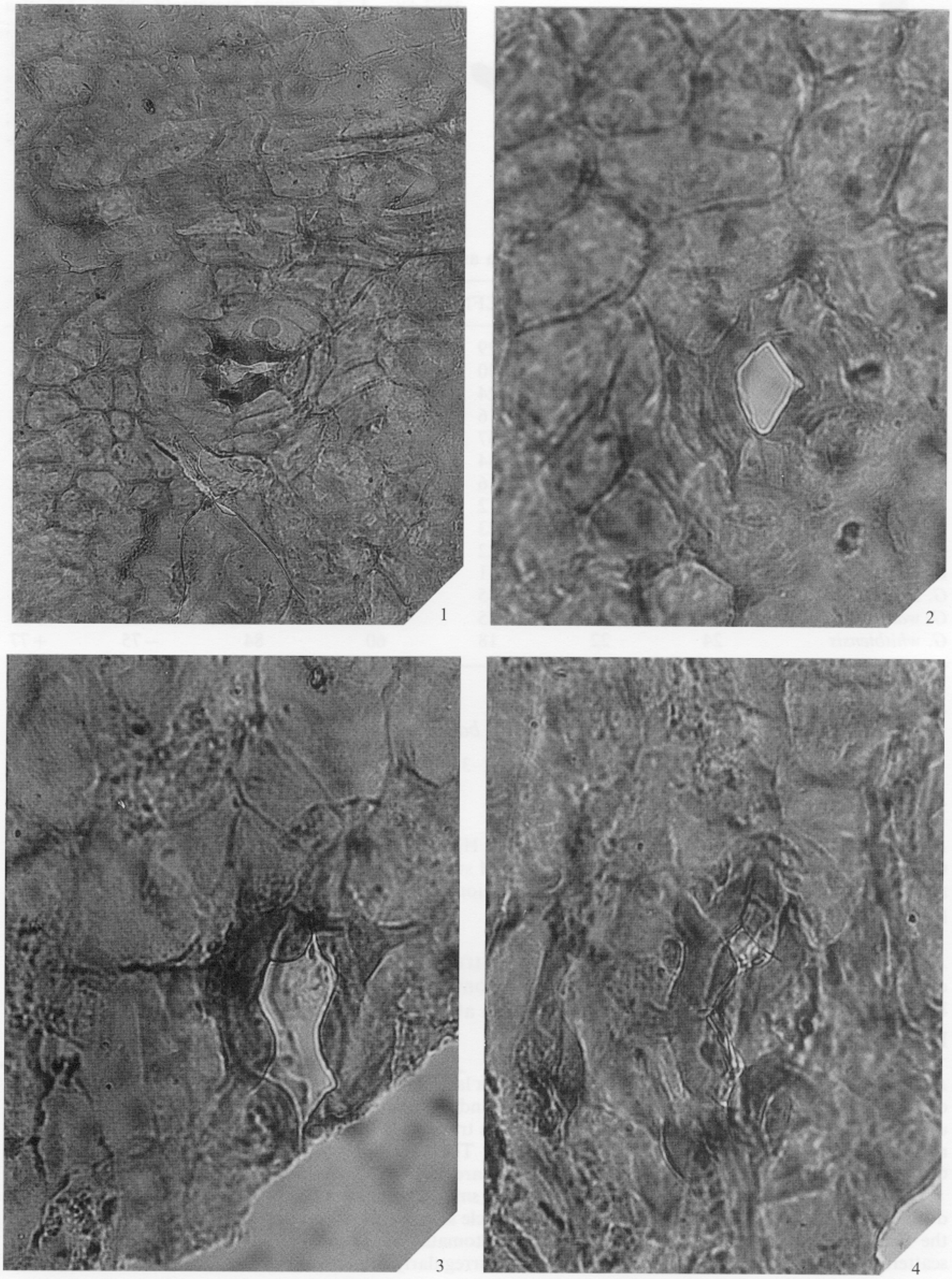
Holotype. As for species.

Diagnosis. Ultimate segments lanceolate with rounded to almost obtuse apex, and no more than seven veins in widest part of segment. On abaxial epidermis, stomatal density *c*. 33 per mm^2, stomatal index *c*. 7, and stomatal bands at least 400 μm wide. Stomata have no more than six subsidiary cells with mainly distinct papillae. Trichomes, if present, exceedingly rare.

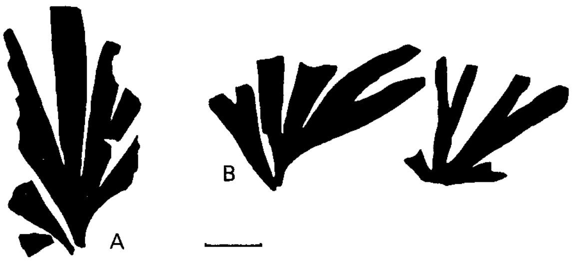
Distribution. Sweden: Hälsingborg (Nathorst 1878; Lundblad 1959), Stabbarp and Skromberga (Johansson 1922), Höör (Antevs 1919), Sofiero and Dompäng (Chow 1924), Billesholm (Lundblad 1959). East Greenland: Scoresby Sound (Hartz 1896; Harris 1935).

EXPLANATION OF PLATE 2

Figs 1–4. *Ginkgo skottsbergii* (Lundblad) Czier *europaeica* subsp. nov.; lower cuticles photographed from outer side, with phase contrast; Anina, Banat region, Romania; Anina Coal Formation, lower Liassic (Hettangian–Sinemurian). 1–2, MTM-BP.602241A (holotype), slide no. Z.C.14. 1, portions of stomatal and non-stomatal bands, the former with polygonal cells and stoma oriented parallel to venation; ×270. 2, stomatal apparatus, with rhomboidal stomatal pit; ×650. 3–4, MTM-BP.602241B (paratype), slide no. Z.C.13; stomata with polygonal stomatal pit, and more or less overlying subsidiary cells; ×650.



CZIER, *Ginkgo*



TEXT-FIG. 3. A, *Ginkgo marginata* subsp. *banatica* Czier subsp. nov.; MTM-BP.602241C, holotype; Anina; lower Liassic (Hettangian–Sinemurian). B, *G.* aff. *marginata* subsp. *banatica* Czier, subsp. nov.; Institute of Geology and Geophysics, Bucharest; based on Mateescu (1958, pl. 3, fig. 2; pl. 9, fig. 1); Svinecea Mare; lower Liassic (Hettangian–Sinemurian). Scale bar represents 10 mm.

TABLE 2. Statistical analysis of specimen from Anina assigned here to *Ginkgo marginata banatica*.

Species	ΣFT	ΣFN	$ΣFN_C$	ΣFP	ΣFU	$\bar{A}_L$	A_H
G. australis	23	33	29	51	83	−76	+65
G. baieraeformis	63	32	30	22	73	−34	+66
G. cuneifolius	23	28	24	23	116	−76	+71
G. digitata	56	21	16	21	92	−41	+78
G. insolita	39	61	57	45	45	−59	+36
G. iranicus	13	37	34	18	122	−86	+61
G. longifolius	33	17	16	61	79	−65	+82
G. marginata	91	14	12	40	45	−4	+85
G. parasingularis	27	27	23	47	89	−72	+72
G. skottsbergii	78	23	22	44	45	−18	+76
G. taochuanensis	35	37	31	29	89	−63	+61
G. troedssonii	63	45	45	37	45	−34	+53
G. waarrensis	30	39	35	54	67	−68	+59
G. whitbiensis	24	22	18	60	84	−75	+77

Ginkgo marginata subsp. *banatica* Czier subsp. nov.

Plate 1, figure 1; Plate 3, figures 1–3; Plate 4, figure 1; Text-figure 3A

Derivation of name. From Banat, the type region.

Holotype. Botanical Department, Hungarian Natural History Museum, Budapest; hand specimen MTM-BP-602241 C (Pl. 1, fig. 1), microscope slide Z.C. 12, SEM stub Z.C. 12 SEM (Pl. 3, figs 1–3; Pl. 4, fig. 1). Origin: Anina, Banat region, Romania; Anina Coal Formation, *Clathropteris meniscioides* Biozone (*sensu* Czier in press *a*), lower Liassic (Hettangian–Sinemurian).

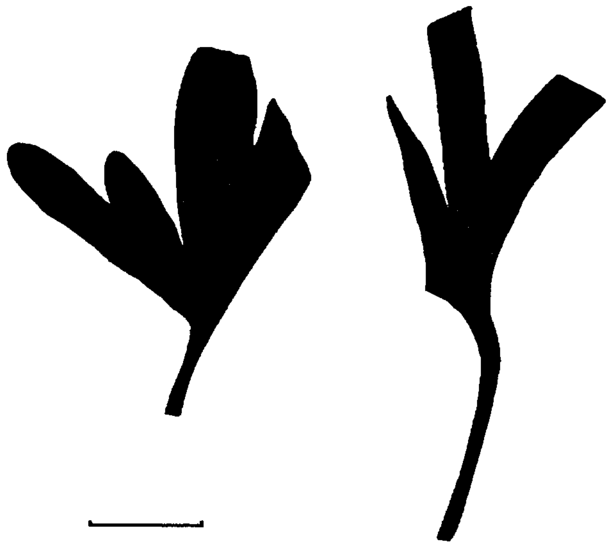
Diagnosis. Ultimate segments oblanceolate with truncate apex, with at least six veins in widest part of segment. Abaxial epidermis with at least 40 stomata per mm^2, Stomatal Index *c.* 2, and stomatal bands no more than 400 μm wide. Stomata with at least six subsidiary cells, which have confluent papillae. Trichomes absent.

Description of new material. The Anina specimen has a lamina with a decurrent base, a basal angle of 90°, and eight segments per leaf. The central two segments are undivided, apparently oblanceolate in shape, 45 mm long and up to 7 mm wide, with margins entire; the apex is truncate (Pl. 1, fig. 1). Other segments are once forked at varying distances (up to 10 mm) from the base. The venation consists of longitudinal veins, forking dichotomously at different positions along leaf. There are six to eight veins in the widest part of each segment.

The upper cuticle is poorly preserved and only very small fragments could be prepared, which showed little detail other than stomata (Pl. 4, fig. 1). The lower cuticle shows alternating stomatal and non-stomatal bands, the latter corresponding to the vein courses. The stomatal bands are 300–400 μm wide, with uniformly scattered stomata. The stomata are longitudinally to irregularly oriented and do not form rows. The normal

TABLE 3. Statistical analysis of material published by Mateescu (1958) as *Baiera taeniata*.

Species	ΣFT	ΣFN	Species	ΣFT	ΣFN
G. australis	5	0	*G. marginata*	5	0
G. baieraeformis	0	1	*G. parasingularis*	4	3
G. cuneifolius	0	1	*G. skottsbergii*	4	0
G. digitata	3	1	*G. taochuanensis*	0	1
G. insolita	4	1	*G. troedssonii*	3	0
G. iranicus	3	1	*G. waarrensis*	2	2
G. longifolius	4	0	*G. whitbiensis*	0	1



TEXT-FIG. 4. *Ginkgo polymorpha* (Samylina) Czier comb. nov. Botanical Museum, 'Babeş – Bolyai' University, Cluj-Napoca; based on Givulescu (1991, text-figs 1–2); Anina; lower Liassic (Hettangian–Sinemurian). Scale bar represents 10 mm.

epidermal cells of the stomatal bands are irregularly shaped and arranged, have slightly sinuous walls, and are about 30 μm in size (Pl. 3, fig. 1). The non-stomatal bands are *c.* 100 μm wide, and consist of more or less conspicuous rows of smooth-walled, elongated epidermal cells, longitudinally oriented and arranged in more or less clear rows; the cells of the non-stomatal bands are 25–100 μm long and 13–20 μm wide. The stomatal density on the lower cuticle is 40–50 per mm^2, with a stomatal index of *c.* 2. The stomatal apparatus is cyclocytic (monocyclic or incompletely amphicyclic) with six to eight polygonal subsidiary cells surrounding each stoma (Pl. 3, fig. 1). Well developed, mainly confluent cutinized thickenings and papillae overarch the stomata. The stomata are sunken (Pl. 3, fig. 2) and oval in shape (Pl. 3, fig. 3), with guard cells *c.* 50 μm long and 20 μm wide; the stomatal pit is usually oval, 25–30 μm long.

Remarks. The table of affinities (Table 2) show very low ΣFN and ΣFN_C values for *G. marginata* and clearly points to its affinities lying there. However, in view of the geographical separation of Anina from Scandinavia, the specimen has been interpreted as a geographical subspecies.

Distribution. Romania: Anina, lower Liassic (Hettangian–Sinemurian, *Clathropteris meniscioides* Zone).

Ginkgo aff. *marginata* subsp. *banatica* Czier

Text-figure 3B

1958 *Baiera taeniata* Braun; Mateescu, p. 12, pl. 3, fig. 2; pl. 9, fig. 1.

Remarks. Mateescu's specimen has not yielded cuticles and so cannot be unequivocally placed in any taxon. The table of affinities worked out for the macroscopic characters (Table 3) suggests that it is best identified as *G.* aff. *marginata banatica.*

Distribution. Romania: Svinecea Mare, lower Liassic (Hettangian–Sinemurian, *Clathropteris meniscioides* Zone).

Ginkgo polymorpha (Samylina) Czier comb. nov.

Text-figure 4

1956 *Baiera polymorpha* Samylina, p. 1523, pl. 1, figs 1–7.
1963 *Baiera polymorpha* Samylina, p. 95, pl. 23, figs 1–3; pl. 24, fig. 1; pl. 25, figs 2–6.
1967 *Baiera polymorpha* Samylina, p. 142, pl. 1, figs 1–2.
1991 *Baiera polymorpha* Samylina; Givulescu, p. 12, text-figs 1–2; pl. 1, figs 1–3.

Holotype. Hand specimen 70-34 (also microscope slides), Palaeobotanical Collection, Botanical Institute of Russia. Origin: lower course of the Aldan River, Siberia; Lower Cretaceous (Samylina 1956).

Remarks. The presence of this species in the Carpathian Mesophytic is based on Givulescu (1991). The Siberian specimens came from the Upper Jurassic and Lower Cretaceous, and are thus significantly younger than Givulescu's material. As pointed out by Givulescu (1991, p. 12), however, the Anina specimens have identical characters to the types from the Aldan River. His determination is therefore fully accepted here and the creation of a geographical subspecies is regarded as unnecessary. *G. polymorpha* may thus be regarded as a long-ranging species (Early Jurassic–Early Cretaceous) and is further evidence that Ginkgoales was (and still is) a slowly evolving group.

Distribution. Siberia: Aldan River, Lower Cretaceous (Samylina 1956, 1963); Kolîma region, Upper Jurassic (Samylina 1967). Romania: Anina, Lower Liassic (Hettangian–Sinemurian, *Clathropteris meniscioides* Zone).

Ginkgo skottsbergii (Lundblad) Czier comb. nov.

1913 *Baiera* cf. *australis* McCoy; Halle, p. 37, pl. 4, figs 23–30; pl. 5, figs 1–6.
1971 *Ginkgoites skottsbergii* Lundblad, p. 237, text-figs 1–11, pl. 1, figs 1–12; pl. 2, figs 1–6.

Holotype. Hand specimen (Halle 1913, pl. 5, fig. 1) and cuticles (Lundblad 1971, text-figs 8–11; pl. 2, figs 1–6) in the Section for Palaeobotany, Swedish Museum of Natural History, Stockholm. Origin: Locality *c* at Rio Fósiles, near Lago San Martin (Santa Cruz), Argentina; Lower Cretaceous, base of division 6, or possibly the transition between divisions 5 and 6, in the section east of Bahia de la Lancha.

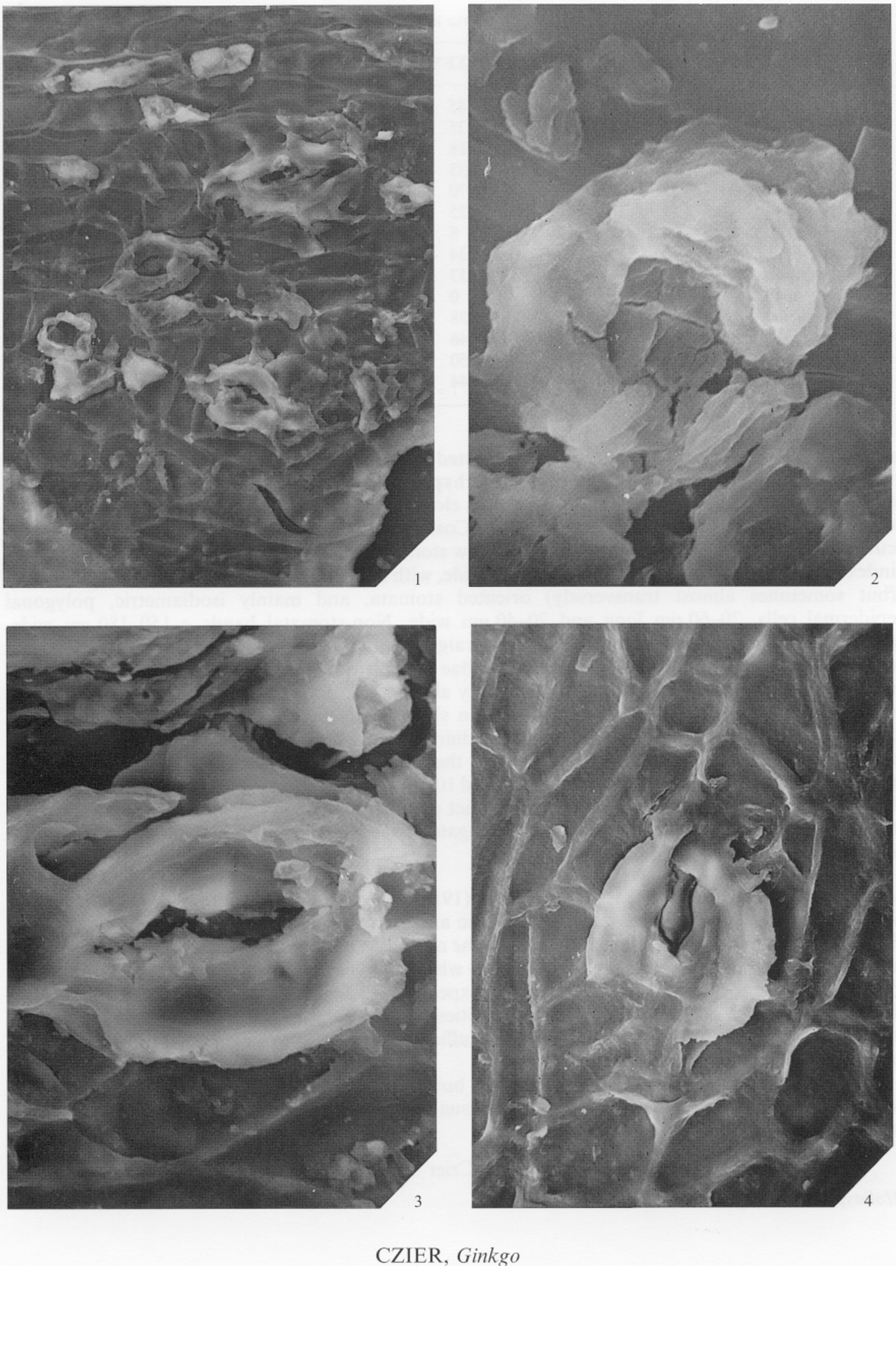
Emended diagnosis. Leaf cuneate to fan-shaped, bipartite and deeply digitate. Petiole up to at least 13 mm long and 0·8–2·0 mm wide. Basal angle 60–220°. Segments 10–60 mm long. Lamina usually divided by repeated dichotomies into six to twelve segments of lanceolate-linear to slightly oblanceolate shape, with rounded to obtuse apices (occasionally irregularly notched). Maximum size of free portion of segments widely variable (10–50 mm long, 2·2–6·0 mm wide). Petiole with two

EXPLANATION OF PLATE 3

Figs 1–3. *Ginkgo marginata* (Nathorst) Czier *banatica* subsp. nov.; SEM views of cuticles; MTM-BP.602241C (holotype), SEM stub no. Z.C.12. 1, inner side of cuticles showing portion of stomatal band between two non-stomatal bands; ×300. 2, stomatal apparatus viewed from outer side; ×1000. 3, stomatal apparatus viewed from inner surface; ×1000.

Fig. 4. *Ginkgo skottsbergii* (Lundblad) Czier *europeica* subsp. nov.; MTM-BP.602241A (holotype), slide no. Z.C.11; SEM view of stomatal apparatus viewed from inner side; ×600.

All from Anina, Banat region, Romania; Anina Coal Formation, lower Liassic (Hettangian–Sinemurian).



CZIER, *Ginkgo*

TABLE 4. Statistical analysis of specimens from Anina assigned here to *Ginkgo skottsbergii europeica*.

Species	ΣFT	ΣFN	ΣFN_C	ΣFP	ΣFU	A_L	A_H
G. australis	24	47	45	52	67	−75	+51
G. baieraeformis	58	35	35	33	64	−39	+63
G. cuneifolius	27	21	18	29	113	−72	+78
G. digitata	34	39	33	33	84	−64	+59
G. insolita	41	73	70	40	36	−57	+23
G. iranicus	11	28	25	38	113	−88	+71
G. longifolius	29	8	8	83	70	−69	+92
G. marginata	76	25	24	53	36	−20	+74
G. parasingularis	22	37	33	59	72	−77	+61
G. skottsbergii	84	2	0	51	53	−12	+98
G. taochuanensis	48	42	38	20	80	−49	+56
G. troedssonii	50	46	46	58	36	−47	+52
G. waarrensis	23	52	50	55	60	−76	+45
G. whitbiensis	35	48	44	32	75	−63	+49

veins that radiate into the segments, and repeatedly dichotomize at all levels; number of veins in widest portion of segments four to nine. Leaf hypoamphistomatic. Upper cuticle slightly thicker than lower one, showing costal zones with cells elongated parallel to the veins, separated by zones of more or less isodiametric, polygonal cells. Costal zones less sharply demarcated in the upper cuticle than the lower one. Lower cuticle with low stomatal density (*c.* 12–26 per mm²) and stomatal index (*c.* 1–2). Stomatal bands *c.* 400–460 μm wide, with irregularly scattered, mainly longitudinally (but sometimes almost transversely) oriented stomata, and mainly isodiametric, polygonal epidermal cells, 20–60 μm long and 20–40 μm wide. Non-stomatal bands *c.* 150–180 μm wide, consisting of rows of longitudinally oriented, straight to finely sinuous-walled, elongate-rectangular cells, 20–158 μm long and 10–45 μm wide. Papillae absent from ordinary epidermal cells. Resin and trichomes only sporadically present and usually absent. Cyclocytic (mostly incompletely dicyclic) stomatal apparatuses. Stomata sunken, oval in shape, with guard cells 46–66 μm long and 15–20 μm wide. Stomatal slit 22–36 μm long. Subsidiary cells partly overarching the stomata, very variable in shape. The number of subsidiary cells in the inner ring varies between six to eight. Stomatal pits rhomboidal to polygonal, 24–53 μm long and 10–24 μm wide, in upper cuticle mostly surrounded by an irregular cutinized rim (rarely with distinct papillae), whilst in lower cuticle the thickenings may carry papillae. Cuticle on petiole with elongated to rectangular cells; stomata present on both sides.

Remarks. This diagnosis is based on Halle's (1913) macroscopic description of what he called *Baiera* cf. *australis*, combined with macroscopic and microscopic data given by Lundblad (1971) following her re-study of Halle's material, and the new SEM data presented in this paper. Lundblad recognized that it represents a new species, which she named after the late Professor Carl Skottsberg, leader of the 1907–1909 Swedish Expedition to South America on which the material had been collected. Although the table of affinities (Table 4) shows the Anina material to be very similar to the South American types, there are sufficient differences to warrant the establishment of a separate geographical subspecies.

G. skottsbergii is very similar to *G. marginata*, but the latter has a usually longer petiole, segments with an irregularly forked to sub-acute apex, usually wider stomatal bands, and papillae on both surfaces.

Ginkgo skottsbergii (Lundblad) Czier comb. nov. subsp. *skottsbergii*

Holotype. As for species.

Diagnosis. Ultimate segments lanceolate-linear, with rounded apex occasionally incised; maximum length of free portion of segment 20 mm. Abaxial epidermis with isodiametric, mainly trapeziform subsidiary cells. Stomatal pit polygonal in shape.

Distribution. Argentina: Lago San Martin, Lower Cretaceous (Lundblad 1971).

Ginkgo skottsbergii subsp. *europeica* Czier, subsp. nov.

Plate 1, figures 2–3; Plate 2, figures 1–4; Plate 3, figure 4; Plate 4, figures 1–3; Text-figure 5A–B

Derivation of name. After Europe, where this subspecies occurs.

Holotype. Botanical Department, Hungarian Natural History Museum, Budapest, hand specimen MTM-BP-602241 A (Pl. 1, fig. 2), microscope slide Z.C. 14 (Pl. 2, figs 1–2), SEM stub Z.C. 11 SEM (Pl. 3, fig. 4). Origin: Anina, Banat region, Romania; Anina Coal Formation, *Clathropteris meniscioides* Biozone (*sensu* Czier in press *a*), lower Liassic (Hettangian–Sinemurian).

Paratype. Hand specimen MTM-BP-602241 B (Pl. 1, fig. 3), microscope slide Z.C. 13 (Pl. 2, figs 3–4).

Diagnosis. Petiole width 2 mm, length of segments at least 50 mm. No more than nine ultimate segments with non-incised apex; free portion of segment at least 20 mm long and 4 mm wide; at least seven veins in widest portion of segment. Abaxial epidermis with straight-walled cells. Subsidiary cells elongated to rounded or polygonal. Trichomes absent.

Description of new material. The Anina material consists of two leaves, with partly preserved petioles. The petioles are 2 mm wide and *c.* 10 mm long (the basal part is missing) and expand distally to form a lamina with a cuneate base (Pl. 1, fig. 2). The basal angle is *c.* 80°. The lamina has straight lateral margins, and is deeply divided usually by three divisions into six to nine, 50–60 mm long segments. The first (central) division is deeper than the others, reaching down to the petiole. The secondary divisions are up to one-sixth of the leaf length, the tertiary divisions up to half the length. Ultimate segments lanceolate-linear to slightly oblanceolate, 4–6 mm wide, with entire margins, and rounded to obtuse apices (Pl. 1, figs 2–3). Tertiary divisions may sometimes be missing (Pl. 1, fig. 3). The petiole has two longitudinal veins that radiate into the segments, and then repeatedly dichotomize at all levels. In the widest portion of the segments, there are seven to nine veins, with *c.* 15 veins per 10 mm.

The upper cuticle is poorly preserved and very fragmentary, showing only a few stomata (Pl. 4, figs 1–3). The lower cuticle is much better preserved, and consists of alternating *c.* 400 μm wide stomatal bands and *c.* 150 μm wide non-stomatal bands. The latter correspond to the costal zones, and are composed of elongated rectangular cells, 20–150 μm long and 10–45 μm wide, arranged in longitudinal rows. The cell walls are straight and thick (up to *c.* 5 μm). Cells of the stomatal bands are 20–60 μm long and 20–40 μm wide, not arranged in rows, isodiametric-polygonal in shape, with smooth walls of the same thickenings as in the non-stomatal bands (Pl. 2, fig. 1). Stomata are irregularly scattered and mainly longitudinally oriented. Stomatal density rather low, 12–26 per mm^2, and the stomatal index is *c.* 1–2. The stomatal apparatuses are cyclocytic, mostly incompletely dicyclic (Pl. 3, fig. 4). The stomata are oval, 48–60 μm long and 30–40 μm wide. The guard cells are sunken. The subsidiary cells vary in shape from elongated to rounded or polygonal. An inner ring of six to eight (most often seven) subsidiary cells surround and may partly overarch the stomata. The stomatal pit is rhomboidal (Pl. 2, fig. 2) to polygonal in shape (Pl. 2, figs 3–4), 24–53 μm long and 10–19 μm wide. Trichomes are absent, but papillae are occasionally present on the inner ring of subsidiary cells.

Remarks. The table of affinities for this newly described Anina material (Table 4) shows it to belong to *G. skottsbergii*, but its stratigraphical and geographical separation from the type material means that it should be regarded as a geographical subspecies.

Distribution. Romania: Anina, lower Liassic (Hettangian–Sinemurian, *Clathropteris meniscioides* Zone).

Ginkgo aff. *skottsbergii* subsp. *europeica* Czier

Text-figures 5C–E, 6

1961 *Ginkgoites marginatus* (Nathorst) Florin; Nagy (*non* Nathorst), p. 629, pl. 16, fig. 2; pl. 17.
1990 *Ginkgoites* ex gr. *lepidus* Heer; Givulescu and Czier, p. 13, pl. 2, fig. 1; tab. 2.
1993 *Ginkgoites* sp. ex gr. *lepida* Czier, p. 174; tab. 1.
1994*a* *Ginkgo* ex gr. *lepida* Heer; Czier, p. 354, tab. 2.
1995 *Ginkgo* ex gr. *lepida* Heer; Czier, p. 50, tab. 1.

Description of new material. The single specimen (TCMO-NS. 16623/4) is an almost entirely preserved impression, without cuticles. The petiole is 1 mm wide, 20 mm long, and apparently complete. The basal angle is 150° and the segments are *c.* 40 mm long. The lamina is symmetrical, being divided into linear-shaped segments. The first-order (i.e. central) division is the deepest, reaching to the petiole. The resulting two primary segments are subdivided into three secondary segments. The middle of these secondary segments is entire, but the outer two are further subdivided into two. There are thus ten ultimate segments of the lamina. The free part of the segments has a maximum length of *c.* 26 mm and a maximum width of *c.* 2·8 mm. The apices of the segments, where preserved complete, show an incision in the middle. The venation is rather poorly preserved, but just shows that there are four to seven longitudinal, sometimes dichotomously forked veins in each ultimate segment.

Remarks. Two groups of material are included here. There are firstly the specimens from Hungary described by Nagy (1961). Secondly, there are specimens that I collected from Şuncuiuş in Romania. The latter have previously been figured by Givulescu and Czier (1990) but the above is the first published description. They were initially identified as *Ginkgoites* ex gr. *lepida.* However, the epidermal structure is unknown in Heer's species and thus needs to be revised before it can be regarded as a useful taxon.

The statistical method for determining affinities was used for both groups of specimens (Table 5). In both groups, ΣFN was zero for *G. skottsbergii.* For the Romanian specimens, it was the only species. For the Hungarian material, ΣFN was also zero for *G. longifolius*, but the ΣFT value was much lower. Consequently, both groups were assigned to the local subspecies *G. skottsbergii europeica*, with an 'aff.'.

Distribution. Hungary: Komló and Pécsbányatelep, lower Liassic (Hettangian, *Clathropteris meniscioides* Zone) (Nagy 1961). Romania: Şuncuiuş, lower Liassic (Hettangian–Lower Sinemurian, *C. meniscioides* Zone) (this paper).

Ginkgo sp. A

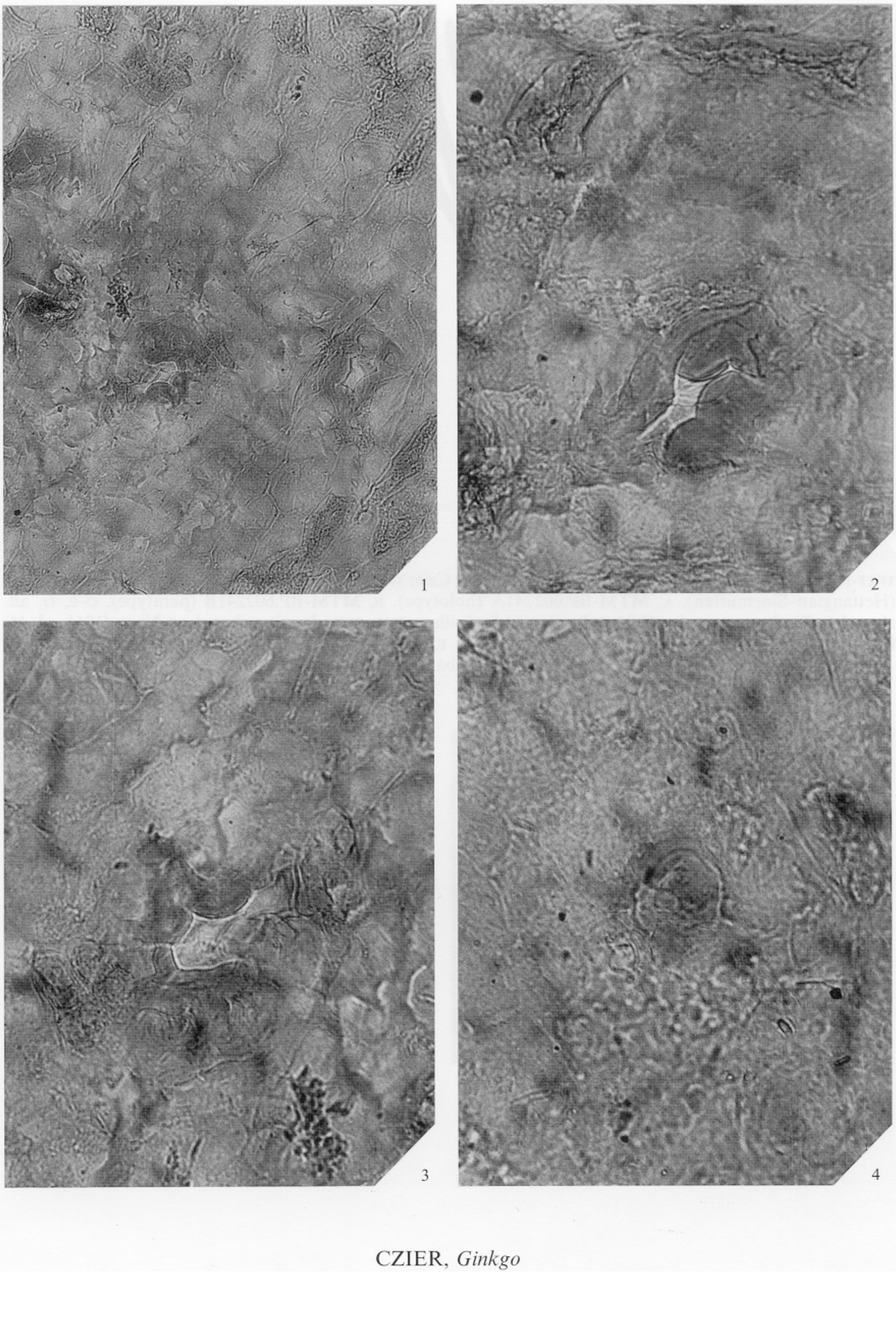
Text-figure 7A

1878 *Baiera taeniata* Braun; Hantken, p. 63, text-fig. 9.

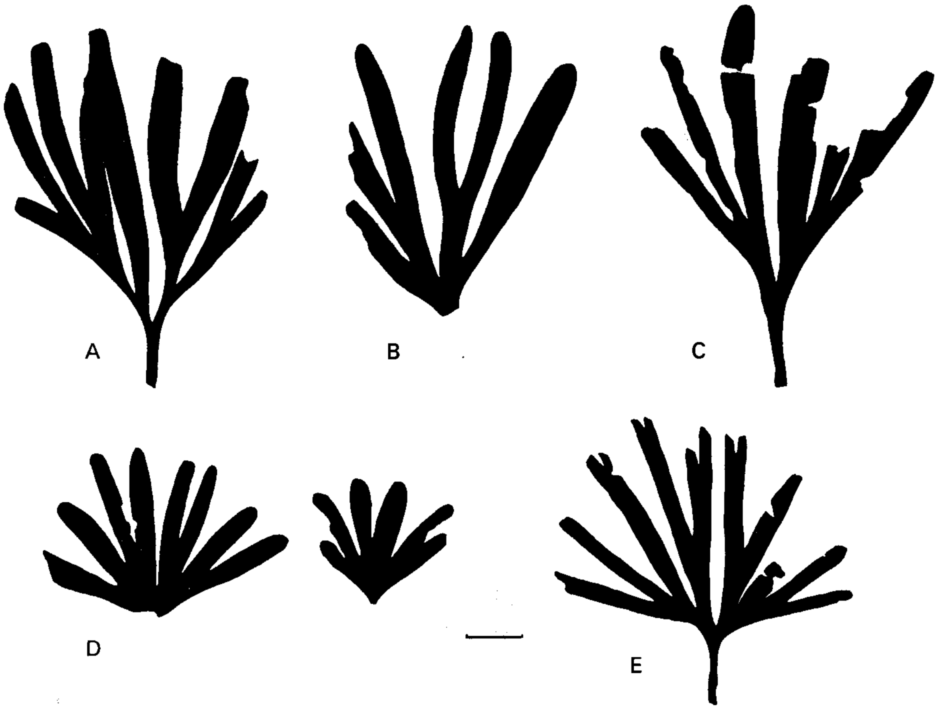
Remarks. Hantken's (1878) specimen originated from the lower Liassic of Anina. It has already been shown in this paper that *Ginkgo taeniata* (Braun) is in need of revision. The analysis of the taxonomic position of this specimen (Table 6) shows that no species gave a zero ΣFN value, and so it is referred to as *Ginkgo* sp. A.

EXPLANATION OF PLATE 4

Figs 1–3. *Ginkgo skottsbergii* (Lundblad) Czier *europeica* subsp. nov. MTM-BP.602241B (paratype), slide no. Z.C.13. 1, epidermal cells with only a few stomata; × 270. 2–3, stomata with polygonal stomatal pits; × 650.
Fig. 4. *Ginkgo marginata* (Nathorst) Czier *banatica* subsp. nov.; MTM-BP.602241C (holotype), slide Z.C.12; stomatal apparatus; × 650.
All show upper cuticles photographed from outer side with phase contrast; Anina, Banat region, Romania; Anina Coal Formation, lower Liassic (Hettangian–Sinemurian).



CZIER, *Ginkgo*



TEXT-FIG. 5. A–B, *Ginkgo skottsbergii* subsp. *europeica* Czier subsp. nov.; leaf silhouettes; Anina; lower Liassic (Hettangian–Sinemurian). A, MTM-BP.602241A (holotype). B, MTM-BP.602241B (paratype). C–E, *G.* aff. *skottsbergii* subsp. *europeica* Czier subsp. nov.; leaf silhouettes. C–D, drawings based on Nagy (1961, pl. 16, fig. 2; pl. 17); Komló or Pécsbányatelep; Hettangian. E, TCMO-NS.16623/4; Şuncuiuş Fireclay Formation, lower Liassic. Scale bar represents 10 mm.

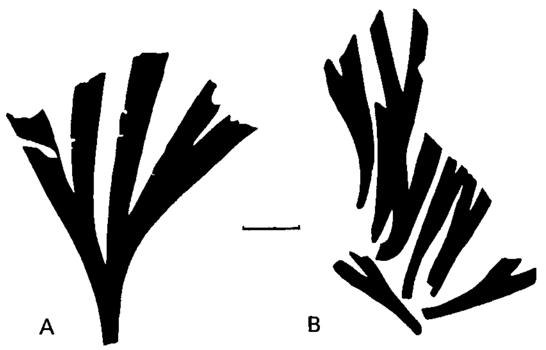
TEXT-FIG. 6. *G.* aff. *skottsbergii* subsp. *europeica* Czier, subsp. nov.; TCMO-NS.16623/4; Şuncuiuş Fireclay Formation, lower Liassic; × 1.

TABLE 5. Statistical analysis of material described by Nagy (1961) as *Ginkgoites marginatus*, and of material figured by Givulescu and Czier (1990) as *Ginkgoites* ex gr. *lepidus*.

	Nagy (1961)		Givulescu and Czier (1990)	
Species	ΣFT	ΣFN	ΣFT	ΣFN
G. australis	2	1	3	3
G. baieraeformis	5	1	4	3
G. cuneifolius	3	5	3	5
G. digitata	2	3	4	4
G. insolita	5	2	3	2
G. iranicus	2	2	4	3
G. longifolius	7	0	4	2
G. marginata	7	2	4	4
G. parasingularis	2	5	4	6
G. skottsbergii	10	0	7	0
G. taochuanensis	0	4	0	5
G. troedssonii	6	1	4	2
G. waarrensis	1	2	1	2
G. whitbiensis	1	5	2	5

TABLE 6. Statistical analysis of material described by Hantken (1878) as *Baiera taeniata*, and of material figured by Givulescu and Czier (1990) as *Baeira muensteriana*.

	Hantken (1878)		Givulescu and Czier (1990)	
Species	ΣFT	ΣFN	ΣFT	ΣFN
G. australis	1	1	1	3
G. baieraeformis	4	1	1	2
G. cuneifolius	1	5	0	3
G. digitata	0	5	0	5
G. insolita	2	3	4	1
G. iranicus	2	3	1	3
G. longifolius	4	1	3	2
G. marginata	3	2	3	2
G. parasingularis	1	3	1	5
G. skottsbergii	3	2	1	2
G. taochuanensis	1	3	0	5
G. troedssonii	3	1	2	2
G. waarrensis	0	2	0	3
G. whitbiensis	2	3	2	3



TEXT-FIG. 7. A, *Ginkgo* sp. A; based on Hantken (1878, text-fig. 9); Anina; lower Liassic (Hettangian–Sinemurian). B, *Ginkgo* sp. B; TCMO-NS.15364/1; Şuncuiuş Fireclay Formation, lower Liassic. Scale bar represents 10 mm.

Ginkgo sp. B

Plate 1, figure 4; Text-figure 7B

1988 *Baiera* sp. Czier and Popescu, p. 609, tab. 1.
1990 *Baiera muensteriana* (Presl *in* Sternberg) Saporta; Givulescu and Czier, p. 13, tab. 2.

Description. Hand specimen TCMO-NS. 15364/1 is from fossiliferous horizon number 2 of the Şuncuiuş Fireclay Formation (Czier 1994*b*), which is Hettangian to lower Sinemurian (*Clathropteris meniscioides* Zone). It shows seven fragmentary leaves without petioles (Pl. 1, fig. 4). The basal angle is very acute, *c*. 20°. The segments are > 40 mm long, but their apices are all missing so must have been longer. There appear to be two oblanceolate ultimate segments. Their free portion is up to 25 mm long and 5 mm wide. The venation consists of well-preserved, longitudinal, sometimes dichotomous veins; in the widest part of the segment are three to six veins. No cuticles are preserved.

Remarks. This specimen has been previously identified as *Baeira muensteriana* but this is the first published description. However, a statistical analysis of its taxonomic position (Table 6) indicates that at best it can be referred to simply as *Ginkgo* sp. B.

DISCUSSION

Czier (in press *a*) has found that the traditional plant biozonation cannot be used in the Carpathian Basin, and instead classified the terrestrial Liassic there into two plant zones: the *Clathropteris meniscioides* Zone in the lower Liassic (Hettangian and Sinemurian) and the *Carpolithes liasinus* Zone in the middle and upper Liassic (Pliensbachian and Toarcian). All of the Mesophytic *Ginkgo* foliage described to date from the Carpathian Basin came from the lower of these zones.

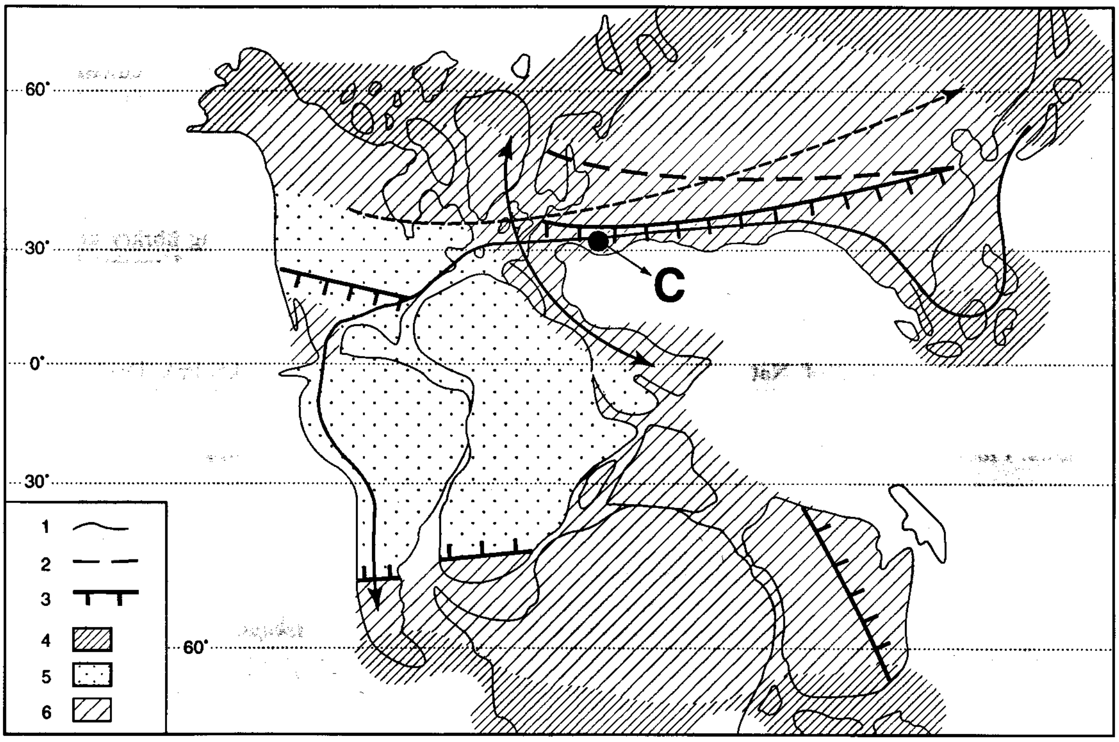
Plant fossils in the lower Liassic of the Carpathians can be classified floristically into three main groups, plus a fourth group for taxa of uncertain floristic affinities (Czier 1996*b*). The *Ginkgo* foliage can be assigned to these groups as follows.

Species only known from the European autochthon

Included here is *Selenocarpus muensterianus* (Presl) Schenk, which I have described in detail in a previous paper (Czier 1994*a*). Of the *Ginkgo* leaves, both subspecies of *G. marginata* belong to this group, having only been reported from the lower Liassic (Hettangian–Sinemurian) of Greenland, Sweden and the Carpathians.

Species of eastern origin

This corresponds essentially to the *Dictyophyllum-Clathropteris* Flora, originally recognized in the uppermost Triassic of China (Sze 1956; Sze and Zhou 1962), and includes species or subspecies mainly characteristic of warm and wet conditions (Text-fig. 8). I have previously argued that it first



TEXT-FIG. 8. Palaeogeographical, palaeofloristic and palaeoclimatic context of the Carpathian Basin in the Early Jurassic. 1, palaeocontinental margins (Smith and Briden 1977). 2, boundary between Indo-European and Siberian floral provinces (Vakhrameev 1964). 3, boundary between warm and temperate regions (Krassilov 1981). 4–6, palaeoclimatic belts (Hallam 1985, 1993); 4, wet; 5, dry; 6, seasonally wet. C, approximate position of Carpathian Basin. Continuous arrowed lines show suggested migration routes for eastern floristic elements, indicating warm, wet palaeoclimate. Dashed arrowed line shows suggested migration route for western floristic elements, indicating temperate, seasonally wet palaeoclimate.

arose in the Late Triassic of eastern South-east Asia (Kimura 1984) and later spread to Europe via the northern margins of the Tethys (Taugourdeau-Lantz and Vozenin-Serra 1987) during the latest Triassic and Liassic. It then migrated further west, spreading to South America by the Mid Jurassic, where it persisted until the Early Cretaceous (Czier 1994*b*). This explains the presence of the same species in the Lower Jurassic of Europe and the Lower Cretaceous of South America.

The two subspecies of *G. baieraeformis* are interpreted as taxa of eastern origin (i.e. members of the *Dictyophyllum-Clathropteris* Flora). This is supported by the fact that both subspecies occur in association with abundant *Clathropteris meniscioides*. *G. skottsbergii* also probably belongs here. Although not yet reported from the Far East, its migration from Europe in the Early Jurassic to South America in the Early Cretaceous seems to support this view.

Species of western origin

This consists of elements mainly characteristic of temperate and seasonally wet environments (Text-fig. 8). They appear first in the Triassic of North America and spread to Europe during the Early Jurassic. They then migrated further north-east, reaching Siberia by the Late Jurassic and Early Cretaceous (Czier 1994*a*). This explains the presence of the same species in the Lower Jurassic of the European palaeofloristic region and the Upper Jurassic and Lower Cretaceous of the Siberia palaeofloristic region.

Ginkgo polymorpha has previously been regarded as characteristic of the Upper Jurassic–Lower Cretaceous of the Siberia palaeofloristic region. However, its presence also in the Lower Jurassic of Europe (this paper) suggests that it was of western origin and only subsequently migrated eastwards to Siberia.

Acknowledgements. I thank Drs Lilla Hably and Maria Barbacka, for allowing me to research material in the Palaeobotanical Collections of the Hungarian Natural History Museum (Budapest). I am also grateful to Dr Gábor Gaál, Director of the Geological Institute of Hungary (Budapest) for providing library and SEM facilities. Special thanks go to Dr J. H. A. van Konijnenburg-van Cittert (State University, Utrecht), Dr C. J. Cleal (National Museums and Galleries of Wales, Cardiff) for comments on the manuscript, and to Prof. Zhou Zhiyan (Institute of Geology and Palaeontology, Nanjing) for translating some Chinese references. I also thank Dr J. G. Douglas (Geological Survey of Victoria, Melbourne), Prof. A. Hallam (University of Birmingham), Prof. T. Kimura (Institute of Natural History, Tokyo), Prof. B. Lundblad (Stockholm), Dr I. Z. Nagy (Budapest), Dr V. A. Samylina (Komorov Botanical Institute, St Petersburg), Dr H. W. J. van Amerom (Geological Survey NRW, Krefeld) and Dr C. Vozenin-Serra (Université Pierre-et-Marie-Curie, Paris) for literature. Finally, I thank the Soros Foundation for an Open Society for financial support.

REFERENCES

ANDRAE, K. J. 1855. Beiträge zur Kenntnis der fossilen Flora Siebenbürgens und des Banates. II: Lias-Flora von Stierdorf im Banate. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt*, **2**, 27–46.

ANTEVS, E. 1919. Die liassische Flora des Hörsandsteins. *Kungliga Svenska Vetenskapsakademiens Handlingar*, **59**, 1–71.

ASSERETO, R. 1966. The Jurassic Shemshak Formation in central Elburz (Iran). *Rivista Italiana di Paleontologia e Stratigrafia*, **72**, 1133–1182.

BOERSMA, M. and KONIJNENBURG-van CITTERT, J. H. A. van 1991. Late Triassic plant megafossils from Aghdarband (NE-Iran). *Abhandlungen der Geologischen Bundesanstalt*, **38**, 223–252.

BRAUN, F. W. 1843. Beiträge zur Urgeschichte der Pflanzen. 1–46. *In* MUNSTER, G. G. (ed.). *Beiträge zur Petrefactenkunde*, *6*. Bayreuth, 100 pp.

BRONGNIART, A. 1828–1838. *Histoire des végétaux fossiles*, *I*. Dufour et d'Ocagne, Paris, 488 pp.

CHALONER, W. G. and CREBER, G. T. 1990. Do fossil plants give a climatic signal? *Journal of the Geological Society, London*, **147**, 343–350.

CHOW, T. C. 1924. The lower Liassic flora of Sofiero and Dompäng in Scania. *Arkiv för Botanik*, **19**, 1–19.

CZIER, Z. 1990. Istoricul cercetărilor paleobotanice în Judeţul Bihor (România). *Crisia*, **20**, 583–601.

—— 1993. Propunere pentru o nauă rezervaţie paleobotanică în Judeţul Bihor. *Nymphaea, Folia naturae Bihariae*, **21**, 173–177.

—— 1994*a*. On a new record of *Solenocarpus muensterianus* (Presl) Schenk from the Fireclay Formation of Şuncuiuş (Romania) and the Lower Liassic age of the flora. *Review of Palaeobotany and Palynology*, **82**, 351–363.

—— 1994*b*. A Körös-vidék és a Bánság liász flórája. Unpublished doctorate thesis, Eötvös Loránd University, Budapest.

—— 1995. Notă preliminară cu privire importanţa ştiinţifică a zăcământului cu plante fosile de la Şuncuiuş (Munţii Pădurea Craiului, România). *Analele Universităţii din Oradea, Geografie*, **3**, 48–53.

—— 1996*a*. Repertoriul punctelor fosilifere cu floră Liasică din România. *Nymphaea, Folia naturae Bihariae*, **22**, 67–70.

—— 1996*b*. *Banatozamites* Czier, gen. nov. (Cycadeoidales) from the lower Liassic. *Review of Palaeobotany and Palynology*, **94**, 345–356.

—— in press *a*. Palaeobotanical biostratigraphy of the terrestrial Liassic of western Romania. *Studia Universitatis Babeş-Bolyai, Geologia-Geographia.*

—— in press *b*. A Körös-vidék és a Bánság liász flóránjának kutatástörténete és szakirodalma. *A Déri Múzeum Évkönyve.*

—— and POPESCU, V. 1988. Cercetări geologice-paleobotanice aspura Liasicului inferior de la Şuncuius – Cariera Principală Recea (Judeţul, Bihor), I. *Crisia*, **18**, 597–626.

DOUGLAS, J. G. 1965. The Mesozoic leaves *Ginkgoites australis* (McCoy) Florin, and *Ginkgoites waarensis* n. sp. *Mining and Geological Journal*, **6**, 20–26.

FLORIN, R. 1936. Die fossilen Ginkgophyten von Franz-Joseph-Land nebst Erörterungen über vermeintliche Cordaitales mesozoischen Alters. 1. Spezieller teil. *Palaeontographica, Abteilung B*, **81**, 71–173.

GIVULESCU, R. 1991. Zwei neue Pflanzen aus dem unteren Lias von Anina, Rumänien: *Baiera polymorpha* Samylina and *Pseudotorellia nordenskjoeldii* (Nathorst) Florin. *Documenta naturae*, **65**, 12–17.

—— and CZIER, Z. 1990. Neue Untersuchungen über die Floren des unteren Lias (Rumänien). *Documenta naturae*, **59**, 8–19.

HALLAM, A. 1985. A review of Mesozoic climates. *Journal of the Geological Society, London*, **142**, 433–445.

—— 1993. Jurassic climates as inferred from the sedimentary and fossil record. *Philosophical Transactions of the Royal Society of London, Series B*, **341**, 287–296.

HALLE, T. G. 1913. Some Mesozoic plant-bearing deposits in Patagonia and Tierra del Poego and their floras. *Kungliga Svenska Vetenskapsakademiens Handlingar*, **51**, 1–58.

HANTKEN, M. P. 1878. *A Magyar Korona országainak széntelepei és szénbányászata*. Légrády Testvérek, Budapest, 331 pp.

HARRIS, T. M. 1926. The Rhaetic flora of Scoresby Sound east Greenland. *Meddeleser om Grønland*, **68**, 44–148.

—— 1935. The fossil flora of Scoresby Sound east Greenland. Part 4, Ginkgoales, Coniferales, Lycopodiales and isolated fructifications. *Meddeleser om Grønland*, **112**, 1–176.

—— 1951. Notes on the Jurassic flora of Yorkshire. Parts 49–51. *Annals and Magazine of Natural History*, **12**, 915–937.

—— and MILLINGTON, W. 1974. *The Yorkshire Jurassic flora. Volume 4, Part 1, Ginkgoales*. British Museum (Natural History), London, 78 pp.

HARTZ, N. 1896. Plateforsteninger fra Cap Stewart i Østgrønland. *Meddeleser om Grønland*, **19**, 217–247.

HEER, O. Beiträge zur Jura-Flora Ostsibiriens und des Amurlandes. *Mémoires de l'Académie Impériale des Sciences de St Petersbourg*, **7**, 1–122.

HUMML, H. 1963. Catalogul florei fosile păstrate în Muzeul Regional al Banatului, Timişoara. *Studii şi Cercetări de Biologie şi Ştiinţe Agricole*, **10**, 185–201.

—— 1969. Contribuţii la flora fosilă a Liasicului inferior de la Steierdorf-Anina. *Studii şi Cercetări de geologie, geofizică, geografie, Seria Geologie*, **14**, 385–404.

JOHANSSON, N. 1922. Die rätische Flora der Kohlengruben bei Strabbarp und Skromberga in Schonen. *Kungliga Svenska Vetenskapsakademiens Handlingar*, **63**, 1–78.

KLIPPER, K. 1964. Über eine Rät/Lias-Flora aus dem Nördlichen Abfall des Alburs-Gebirges in Nord-Iran. Teil 1, Bryophyta und Pteridophyta. *Palaeontographica, Abteilung B*, **114**, 1–78.

—— 1971. Über eine Rät/Lias-Flora aus dem Nördlichen Abfall des Alburs-Gebirges in Nord-Iran. Teil 2, Ginkgophyten-Belaubungen. *Palaeontographica, Abteilung B*, **133**, 89–102.

KIMURA, T. 1984. Mesozoic floras of east and southeast Asia, with a short note on the Cenozoic floras of southeast Asia and China. *Geology and Palaeontology of Southeast Asia*, **25**, 325–350.

KRASSILOV, V. A. 1981. Changes of Mesozoic vegetation and the extinction of dinosaurs. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **34**, 207–224.

LINNAEUS, C. 1771. *Mantissa plantarum 2*. 313 pp.

LUNDBLAD, B. 1959. Studies in the Rhaeto-Liassic floras of Sweden. Volume 2, Part 1, Ginkgophyta from the mining district of NW Scania. *Kungliga Svenska Vetenskapsakademiens Handlingar*, **4**, 1–40.

—— 1971. A restudy of the ginkgoalean leaves of the Mesozoic flora of Lago San Martin, Patagonia. *Journal of the Indian Botanical Society*, **50A**, 236–241.

MATEESCU, I. 1958. Studiul petrografic al căbunilor de la Rudăria (Svinecea Mare). *Anuarul Comitetului Geologic*, **31**, 5–49.

NAGY, I. Z. 1961. Liassic plant remains of the Mecsek Mountains. *Annales Instituti Geologici Publici Hungarici*, **49**, 609–657.

NATHORST, A. G. 1878. Bidrag till Sveriges fossila flora, 2. Floran vid Höganäs och Helsingborg. *Kungliga Svenska Vetenskapsakademiens Handlingar*, **16**, 1–53.

OARCEA, C. and SEMAKA, A. 1962. Flora Liasică din colecţia de la Anina. *Dări de Seamă ale Şedinţelor Comitetului Geologic*, **46**, 239–244.

PETRESCU, I. and DRAGASTAN, O. 1981. *Plantae fosile*. Dacia, Cluj-Napoca, 471 pp.

PHILLIPS, J. 1829. *Illustrations of the geology of Yorkshire*. York, xvi + 192 pp.

SAMYLINA, V. A. 1956. [Two new ginkgoaleans from the lower Cretaceous deposits of the Aldan River.] *Botanicheskiĭ Zhurnal*, **10**, 1525–1526. [In Russian].

—— 1963. [The Mesozoic flora of the lower course of the Aldan River.] *Trudӯ Botanicheskogo Instituta Akademii Nauk SSSR*, **8**, 59–139. [In Russian].

—— 1967. [The Mesozoic flora of the area to the west of the Kolyma River (the Zyrianka coal-basin), 2.] *Palaeobotanika*, **6**, 135–170. [In Russian].

—— and MARKOVICH, E. M. 1991. [On the Jurassic flora of the Nazarovsk Coal Field (the western Siberia).] *Botanicheskiĭ Zhurnal*, **76**, 322–333. [In Russian].

SCHENK, A. 1867. *Die fossile Flora der Grenzschichten des Keupers und Lias Frankens*. C. U. Kreidel, Wiesbaden, 232 pp., 45 pls.

SEMAKA, A. 1961. Über die pflanzenführenden Liasschichten Rumäniens (II. Danubikum). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **8**, 389–394.

—— 1962*a*. Aspura Rheticului de la Bigăr (Banat). *Dări de Seamă ale Şedinţelor Comitetului Geologic*, **45**, 173–176.

—— 1962*b*. Observaţiuni aspura florelor paleomezozoice din danubianul Banatului. *Dări de Seamă ale Şedinţelor Comitetului Geologic*, **47**, 309–321.

—— 1963. Despre vîrsta formaţiunii de Schela. *Comunicări Ştiinţifice, Secţia Stratigrafie (Asociaţia Geologică Carpato-Balanică, Congresul V, Bucureşti)*, **3**, 165–173.

—— 1965. Zur Kenntnis der *Nilssonia orientalis*-Flora in den Südkarpathen. *Acta Palaeobotanica*, **6**, 27–39.

—— 1968. *Williamsonia latecostata* n. sp. aus dem rumänischen Lias. *Argumenta Palaeobotanica*, **2**, 15–17.

—— 1970. Flora Rhaeto-Liasică de la Mehadia. *Dări de Seamă ale Şedinţelor Comitetului Geologic*, **56**, 61–75.

—— HUCIĂ, I. and GEORGESCU, L. 1972. Noi puncte cu plante Liasece în Formaţiunea de Schela (Carpaţii Meridionali). *Studii şi Cercetări de geologie, geofizică, Seria Geologie*, **17**, 435–440.

SEWARD, A. C. 1919. *Fossil plants. Part 4*. University Press, Cambridge, xvi + 534 pp.

SIKSTEL', T. A., KUZICKINA, YU, M., SAVITSKAYA, L. I., KHUDAYBERDYEV, R. and SHVETSOVA, E. M. 1971. [The history of development of ginkgophytes in Central Asia.] 62–116. *In* SIKSTEL', T. A. (ed.). [*Palaeobotany of Uzbekistan, II*.] Instituta Botaniki, Akademiya Nauk USSR, Tashkent. [In Russian].

SMITH, A. G. and BRIDEN, J. C. 1977. *Mesozoic and Cenozoic palaeocontinental maps*. Cambridge University Press, Cambridge, 63 pp.

STIRLING, J. 1892. Reports on Victorian coalfields. *Special Report on Coalfields, Victoria Geological Survey*, **1**, 11–13.

SZE, H. C. 1956. Older Mesozoic plants from the Yenchang Formation, northern Shansi. *Palaeontologica Sinica, New Series, Series A*, **139**, 110–127.

—— and ZHOU ZHIYAN 1962. *Mesozoic continental deposits of China*. Scientific Press, Beijing, 180 pp.

TAUGOURDEAU-LANTZ, J. and VOZENIN-SERRA, C. 1987. Les associations paléofloristiques Nord-Tethysiennes, indices d'un milieu tropical de l'infra-Lias au Dogger. *Mémoires et Travaux de l'Institut de Montpellier*, **17**, 295–313.

TRALAU, H. 1968. Evolutionary trends in the genus *Ginkgo*. *Lethaia*, **1**, 63–101.

VAKHRAMEEV, V. A. 1964. [Jurassic and early Cretaceous floras of Eurasia and the palaeofloristic provinces of this period.] *Trudy̆ Geologo Instituta, Academiya Nauk SSSR*, **102**, 1–263. [In Russian].

VOZENIN-SERRA, C. and TAUGOURDEAU-LANTZ, J. 1985. La flore de la Formation Shemshak (Rhétien à Bajocien, Iran): rapports avec les flores contemporaines, implications paléogéographiques. *Bulletin de la Société de France*, **8**, 663–678.

ZHAO, L. M., OHANA, T. and KIMURA, T. 1993. A fossil population of *Ginkgo* leaves from the Xingyuan Formation, Inner Mongolia. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, **169**, 73–96.

ZHOU ZHIYAN 1984. [Early Liassic plants from southwest Hunan, China.] *Palaeontologica Sinica, New Series, Series A*, **165**, 1–85. [In Chinese].

—— 1991. Phylogeny and evolutionary trends of Mesozoic ginkgoaleans – a preliminary assessment. *Review of Palaeobotany and Palynology*, **68**, 203–216.

ZOLTÁN CZIER

Department of Natural Sciences
Ţării Crişurilor Museum
3700 Oradea, Romania

Typescript received 20 January 1995
Revised typescript received 18 March 1997

APPENDIX

To help with comparing and determining the specimens described in this paper, the key foliar characters of certain *Ginkgo* species have been summarized in Tables 7 and 8. This is not a comprehensive analysis, but concentrates on those species for which cuticular features are well known. The systematic position of the species not described in detail in this paper and the key references are as follows.

Ginkgo australis (McCoy, *in* Stirling) Czier, comb. nov.
Basionym: *Baiera australis* McCoy, *in* Stirling, 1892, p. 12, pl. 1, fig. 2.
Selected reference: Douglas (1965).

Ginkgo cuneifolius (Zhou) Czier, comb. nov.
Basionym *Ginkgoites cuneifolius* Zhou, 1984, p. 41, pl. 12, fig. 3; pl. 23, fig. 5, 5a; pl. 24, figs 1–3.

Ginkgo digitata (Brongniart) Heer, 1876
Basionym: *Cyclopteris digitata* Brongniart, 1830, p. 219, pl. 61 bis, figs 2–3.
Selected reference: Harris and Millington (1974).

Ginkgo insolita Samylina, *in* Samylina and Markovich, 1991, p. 326, text-figs a–iu; pl. 1, figs 1–7; pl. 3, figs 7–9; pl. 4, figs 5–7.

Ginkgo iranicus (Kilpper) Czier, comb. nov.
Basionym: *Ginkgoites iranicus* Kilpper, 1971, p. 93, text-figs 5–6; pl. 25, fig. 4; pl. 28, figs 1–3.

Ginkgo longifolius (Phillips) Harris, *in* Harris and Millington, 1974
Basionym: *Sphenopteris longifolia* Phillips, 1829, p. 148, pl. 7, fig. 17.

Ginkgo parasingularis Kilpper, 1971, p. 90, text-figs 1–2; pl. 25, figs 1–2; pl. 27, figs 2–4.

Ginkgo taochuanensis (Zhou) Czier, comb. nov.
Basionym: *Ginkgoites taochuanensis* Zhou, 1984, p. 42, text-fig. 9; pl. 25, figs 1–5; pl. 34, fig. 6.

Ginkgo troedssonii (Lundblad) Czier, comb. nov.
Basionym: *Ginkgoites troedssonii* Lundblad, 1959, p. 20, text-figs 5–6, 7A–E, 8A–B; pl. 3, figs 4–12; pl. 4, figs 1–7; pl. 6, figs 6–7.

Ginkgo waarrensis (Douglas) Czier, comb. nov.
Basionym: *Ginkgoites waarrensis* Douglas, 1965, p. 23, figs 1–2, 4, 6, 9–10.

Ginkgo whitbiensis Harris, 1951, p. 927, text-figs 3A–K, 4C–G.
Selected reference: Harris and Millington (1974).

TABLE 7. Characters of gross morphology and adaxial cuticle of Mesophytic *Ginkgo* foliage, including the F value (Factor of Importance).

F	Character	*G. australis*	*G. baieraeformis*	*G. cuneifolius*	*G. digitata*	*G. insolita*	*G. iranicus*	*G. longifolius*
	Gross morphology							
1	Maximum petiole length (mm)	*c.* 60	> 20	10 (incomplete)	*c.* 20	> 5	50	40
1	Petiole width (mm)	Slender	1–2	1	–	*c.* 1	1–2	0·5–2
1	Basal angle	≤ 180°	*c.* 60–70°	30°	110° (200°) 260°	*c.* 25–30°	*c.* 200–300°	60° (90°) 120°
1	Length of segments (mm)	< 60	*c.* 50–70	*c.* 50	22 (30) 47	*c.* 23–*c.* 70	*c.* 30–40	< 65
1	Number of ultimate segments	≥ 6	*c.* 6 *or* 7	4	6–9	1–2 (rarely 4)	≤ 16	4 (8) 16
1	Ultimate segment shape	Linear spatulate	Linear to slightly oblanceolate	Elongate	–	Mainly linear-lanceolate	Linear to slightly oblanceolate	Elongate to oblanceolate
1	Ultimate segments incised?	Yes	–	No	Deeply	Sometimes	Slightly in middle	Sometimes
1	Ultimate segment apex	Rounded or bluntly acuminate	–	Obtuse to subacute	Rounded or irregularly truncate	Rounded	Rounded	Rounded to subacute
1	Maximum length of free portion of segment (mm)	60	*c.* 30–40	35	Seldom > 10	Widely variable	*c.* 20	Variable
1	Maximum width of free portion of segment (mm)	*c.* 5	*c.* 2–9	2·5–4	20	3–14	*c.* 5–6	1·5 (3·5) 7
1	Number of veins in widest part of segment	≤ 15	4–15	4–7	*c.* 20	4–9	–	2 (5) 10
	Adaxial epidermis							
7	Stomata	Absent	Present	Present	Absent	*c.* 34 per mm^2	Present	2 or 3 per mm^2 mainly near base of lamina
7	Orientation of stomata	–	–	Mainly random	–	Irregular	Longitudinal	–

3	Costal and intercostal fields distinct?	Poorly	Yes or no	Yes	Poorly	Yes	No	Poorly
5	Intercostal cells	Polygonal to rectangular	Polygonal to slightly elongate	Isodiametric	Isodiametric or slightly elongate	Various, mainly isodiametric	Polygonal	Mainly isodiametric-polygonal
4	Intercostal cell size (μm)	–	20–40	10–25	–	12–110 × 12–55	*c.* 30	–
5	Costal cells	Elongate rectangular	Elongate to polygonal	Rectangular	Elongate	Elongate rectangular to trapezoidal	Polygonal	Slightly elongated
4	Costal cell size (μm)	⩽ 80	20–40	45–55 × 4–7·5	–	50–200 × 15–30	*c.* 30	–
8	Cell ornamentation	Papilla	Faint papillae	Faint papillae	Occasional trichomes	Trichomes, rarely papillae	Papillae	Central thickening, papillae only on subsidiaries

F	Character	*G. marginata*	*G. parasingularis*	*G. skottsbergii*	*G. taochuanensis*	*G. troedssonii*	*G. waarrensis*	*G. whitbiensis*
	Gross morphology							
1	Maximum petiole length (mm)	⩾ 10–30	30	13 (or more)	14 (incomplete)	> 40	–	20
1	Petiole width (mm)	*c.* 3·5	*c.* 1	0·8–2	*c.* 1·5	*c.* 1·5–3	–	2
1	Basal angle	*c.* 40° (90°) 145°	90–170°	60° (80°) 220°	*c.* 50°	90° (150°) 180°	–	*c.* 90°
1	Length of segments (mm)	*c.* 20–80	50–60	10–60	*c.* 30	*c.* 40–50°	> 10	*c.* 10–20
1	Number of ultimate segments	4–8 (typically 8)	Typically 6	6–12	Probably 6	Very variable (often 8)	–	2 or 4
1	Ultimate segment shape	Lanceolate to oblanceolate	Linear	Lanceolate linear to slightly oblanceolate	Elongate	Elongate-linear to oblanceolate	Linear-spatulate	Ligulate
1	Ultimate segments incised?	No	No	Occasionally	No	Occasionally deeply	Sometimes	No
1	Ultimate segment apex	Rounded to almost obtuse or truncate	Rounded	Rounded to obtuse	Rounded	Rounded, occasionally truncate	Rounded	Blunt, rounded slightly lobed

TABLE 7 (*cont.*)

F	Character	*G. marginata*	*G. parasingularis*	*G. skottsbergii*	*G. taochuanensis*	*G. troedssonii**	*G. waarrensis*	*G. whitbiensis*
1	Maximum length of free portion of segment (mm)	*c.* 35–40	*c.* 20–30	*c.* 10–50	Variable	Widely variable	5	–
1	Maximum width of free portion of segment (mm)	1·5–7	7–10	2·2–6	3	2–18	4	2–5
1	Number of veins in widest part of segment	4–8	10–14	4–9	6	6–16	⩽ 7	4–6
	Adaxial epidermis							
7	Stomata	Fewer than abaxial	Rarely	Fewer than abaxial	Fewer than abaxial	36–44 per mm²	Sparse	10–20 per mm²
7	Orientation of stomata	Longitudinal to irregular	Longitudinal	Random	–	Irregular	Usually longitudinal	Irregular
3	Costal and intercostal fields distinct?	Yes	No	Poorly	Yes	Poorly	Yes	Rarely
5	Intercostal cells	Isodiametric polygonal	Polygonal to rectangular	Isodiametric polygonal	Polygonal to rectangular	Mainly polygonal	Polygonal to subrectangular	Elongate rectangular
4	Intercostal cell size (μm)	*c.* 30–42	*c.* 40	35–56	15–80 × 8–55	*c.* 20–50	*c.* 80 × 30	–
5	Costal cells	Elongate	Polygonal to rectangular	Elongate	Elongate	Rectangular	Rectangular to spindle-shaped	Elongate rectangular
4	Costal cell size (μm)	*c.* 69–129 × 12–18	*c.* 40	72–140 × 12–43	25–200 × 5–35	*c.* 20–30	Average 70 × 20	–
8	Cell ornamentation	Sometimes papillae	Papillae	Occasional central thickening	Ridge (?trichome base)	Central thickening	–	Flat unsculptured

* It is uncertain which cuticle is adaxial and which is abaxial in this species.

TABLE 8. Characters of abaxial cuticle of Mesophytic *Ginkgo* foliage, including the F value (Factor of Importance).

F	Character	*G. australis*	*G. baieraeformis*	*G. cuneifolius*	*G. digitata*	*G. insolita*	*G. iranicus**	*G. longifolius*
8	Number of stomata per mm^2	130 (intercostal)	*c.* 80	–	–	*c.* 51	–	50 (70) 85 (intercostal)
8	Stomatal Index	–	–	–	–	5·5	–	–
2	Width of stomatal band (μm)	–	*c.* 200–215	250	–	*c.* 475	–	275 (570) 905
7	Arrangement of stomata	Irregular	In rows to irregular	Irregular	Irregular	Irregular	In rows	Rarely in short rows
7	Orientation of stomata	Longitudinal	Mainly longitudinal	Mainly longitudinal	Irregular, often longitudinal	Irregular	–	Irregular, often longitudinal
9	Guard cell length (μm)	Average 30	*c.* 40	25–28	–	*c.* 35	–	–
9	Guard cell width (μm)	Average 10	*c.* 20	–	–	*c.* 12	–	–
9	Subsidiary cell shape	–	–	–	Rounded or polygonal isodiametric	Mainly isodiametric	–	Various
9	Number of subsidiary cells	5–6	5–8	4–7	*c.* 6–8	4 or 5, rarely 6	4–6	*c.* 6
10	Shape of stomatal pit	Variable	Oval-elongate	–	Elongate	Elongate-narrowed	–	Various, often stellate
5	Arrangement of cells in stomatal band	–	–	–	Not in rows	Sometimes in short rows	Longitudinal	Irregular, rarely in short rows
5	Shape of cells in stomatal band	Subrectangular-polygonal	Polygonal, isodiametric to slightly elongate	Slightly elongate or transversely rectangular	Isodiametric	Various, mainly isodiametric	Rectangular	Isodiametric, polygonal or rectangular
4	Cell size in stomatal band (μm)	–	*c.* 15–20 × 7–15	10–100 × 6–30	–	12–110 × 12–55	*c.* 60 × 15–20	–
6	Cell walls in stomatal band	Often much thickened	Straight to slightly sinuous	–	Straight to finely sinuous	Smooth or slightly sinuous	–	Straight, rarely interrupted
2	Width of non-stomatal band (μm)	–	*c.* 50–70	200	–	*c.* 190	–	105 (180) 275

TABLE 8. (*cont.*)

F	Character	*G. australis*	*G. baieraeformis*	*G. cuneifolius*	*G. digitata*	*G. insolita*	*G. iranicus**	*G. longifolius*
5	Arrangement of cells in non-stomatal band	Longitudinal	Longitudinal rows	Longitudinal rows	More or less clear rows	Longitudinal rows	Longitudinal	More or less clear rows
5	Shape of cells in non-stomatal band	Elongate rectangular to spindle-shaped	Elongate	Elongate rectangular to rhomboidal	Elongate	Elongate rectangular to trapezoidal	Rectangular	Narrow elongated
4	Cell size in non-stomatal band (μm)	< 80	–	30–100 × 7·5–22·5	–	50–200 × 15–30	*c.* 60 × *c.* 15–20	–
6	Cell walls in non-stomatal band	Finely sinuous	Straight to finely sinuous	Thickened with cuticular ridge	More-or-less straight	Smooth or slightly sinuous	–	Prominent
8	Papillae	Present	Present	–	Absent	Rarely on subsidiaries	Absent	Present
8	Trichomes	Absent	Absent	–	Present	Often with wart	Absent	Absent

F	Character	*G. marginata*	*G. parasingularis*	*G. skottsbergii*	*G. taochuanensis*	*G. troedssonii**	*G. waarrensis*	*G. whitbiensis*
8	Number of stomata per mm²	*c.* 33–50	*c.* 108 (intercostal)	12–26	–	*c.* 20	*c.* 40	*c.* 100
8	Stomatal Index	*c.* 2–7	–	*c.* 1–2	–	*c.* 3·8	–	–
2	Width of stomatal band (μm)	300–1800	–	*c.* 400–460	–	*c.* 500–1000	–	–
7	Arrangement of stomata	Uniformly scattered	Poorly defined rows	Irregular	Irregular	Irregular	Poorly defined rows	Mainly evenly scattered
7	Orientation of stomata	Irregular to longitudinal	Longitudinal	Mainly longitudinal	Irregular but mostly oblique	Irregular	Generally longitudinal	Irregular
9	Guard cell length (μm)	36 (54) 72	*c.* 40	46 (54) 66	< 40	32 (65) 81	43–64	–
9	Guard cell width (μm)	*c.* 10–20	*c.* 16	15–20	–	*c.* 10	20–25	–
9	Subsidiary cell shape	Polygonal	Polygonal, forming ring	Very variable	Slightly thickened	Polygonal isodiametric	Mainly rounded with ± sinuous walls	Isodiametric
9	Number of subsidiary cells	3–8	< 6	6–8	3–7 (usually 4–6)	4–6	4–6 (often 6)	*c.* 5 or 6

10	Shape of stomatal pit	Variable, often oval	Variable	Rhomboidal to polygonal	Rectangular, sometimes overarched by papillae	Variable	Variable often elongate	Often round, sometimes narrow
5	Arrangement of cells in stomatal band	Irregular sometimes in short rows	–	Not in rows	Mainly transverse	Mainly longitudinal	Longitudinal	Mainly irregular
5	Shape of cells in stomatal band	Polygonal to irregular	–	Isodiametric polygonal	Short or elongate	Irregular elongate	Sub-rectangular to polygonal	Isodiametric, polygonal
4	Cell size in stomatal band (μm)	*c.* 30–48 × 27–33	–	20–60 × 20–40	15–110 × 10–85	*c.* 20–60 × 15–30	*c.* 80 × 30	–
6	Cell walls in stomatal band	Sinuous or straight	–	Finely sinuous to straight	Straight or slightly sinuous, irregularly thickened or punctate	Straight	Sinuous or very sinuous	Mainly straight
2	Width of non-stomatal band (μm)	*c.* 100–150	*c.* 130	*c.* 150–180	175–200	*c.* 200	–	–
5	Arrangement of cells in non-stomatal band	More or less clear rows	Longitudinal rows	Longitudinal rows	More or less clear rows	More or less clear rows	Longitudinal	Mainly irregular
5	Shape of cells in non-stomatal band	Elongate	Mainly rectangular	Elongate rectangular	Elongate rectangular to polygonal	Rectangular elongate or isodiametric	Rectangular to spindle-shaped	Isodiametric polygonal
4	Cell size in non-stomatal band (μm)	*c.* 25–114 × 13–30	40–60 × *c.* 20	20–158 × 10–45	25–235 × 10–40	*c.* 40–60 × 10–20	Average 70 × 20	–
6	Cell walls in non-stomatal band	Smooth or almost smooth	–	Straight to finely sinuous	Straight or slightly sinuous, irregularly thickened or punctate	Straight	Sinuous to very sinuous	Straight sometimes interrupted
8	Papillae	Well developed, only on subsidiaries	Rare	Only on subsidiaries	Only on subsidiaries	Present on subsidiaries	Absent	Rarely on subsidiaries
8	Trichomes	Very rare	Absent	Usually absent	–	Rare	–	Absent

* It is uncertain which cuticle is adaxial and which is abaxial in this species.