Middle Triassic lycopsid flora of South China and its palaeoecological significance

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In recent years, a flora characterized by Lycopsida has been found from the Middle Triassic Badong Formation in Yangtze Gorge area, China, and may be subdivided into two plant assemblages, i.e., Anisian *Pleuromeia marginulata-Annalepis sangzhiensis* assemblage and Ladinian *Annalepis latiloba-Scytophyllum* assemblage. Of them, the former assemblage, containing 18 genera and 30 species, is one of the typical floras of the tidal flat in the world during Anisian. In addition, the character and ecology of the Anisian plant assemblage are emphaically discussed in this paper.

Key-words— Plant megafossils, Lycopsida Middle Triassic.

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सारांश

दक्षिण चीन का मध्य ट्राएँसिक वनस्पतिजात तथा इसकी पुरापारिस्थितिकी

मेंग फानसोंग

अभी हाल ही के वर्षों में चीन में यॉंग्जे गोर्ज क्षेत्र में मध्य ट्राएँसिक बाडोंग शैल-समूह से लाइकोंप्सिड पौधों से युक्त वनस्पतिजात प्राप्त हुआ है। इसे दो पादप समुच्चयों–एनीसियन *प्ल्यूरोमिआ मार्जिनुलाटा–ऍनालेपिस साँघझियेन्सिस* समुच्चय तथा लेडिनियन *एनालेपिस लेटिलोबा–साइटोफिल्लम* समुच्चय में विभक्त किया जा सकता है। इनमें से पहली समुच्चय जिसमें 18 प्रजातियाँ एवं 30 जातियाँ हैं, विश्व के एनीसियन सामान्य वनस्पतिजातों से सम्बन्ध व्यक्त करती है। इसके साथ-साथ एनीसियन कालीन पादप समुच्चय के लक्षण और पारिस्थितिकी की भी इस शोध-पत्र में विवेचना की गई है।

THE most part of South China was in a vast expanse of ocean during Early-Middle Triassic due to which the fossil plants are quite rare there. Besides, the Middle Triassic plants are also very scarce. In recent years, however, a flora characterized by Lycopsida, especially spectacular *Pleuromeia* and *Annalepis*, has been found from the Middle Triassic Badong Formation in the Yangtze Gorge area, China (Text-

PLATE 1 →

1-3. *Pleuromeia marginulata* Meng. Locality : Dawoshang, Fengjie County, Sichuan. Horizon: Member 2 of the Badong Formation.
1. Most of a plant body, terminating in a quite large strobilus at the top of stem, X 3/5.
2, 3. Two isolated sporophylls, showing a sporangium and a ligular scar on upper surface of each sporophyll, all X 1.
4-10. *Pleuromeia sanxiaensis* Meng. Locality and Horizon: just the same above.
4. A sporophyll, showing some longitudinal striations on the upper surface of sporangium, X 2.
5. A megaspore, X 102.
6. A sporophyll with a sporangium, X 1.
7. Middle-upper part of a plant, X 1.
8. A rhizophore, showing appendixes and appendixnarbes, X 1.
9. A complete plant, X 2.
10. A rhizophore with appendixes, X 1.
11-13. *Pleuromeia hunanensis* Meng. Locality: Hongjiaguan, Sangzhi County, Hunan. Horizon: Member 2 of the Badong Formation.
11. A small sporophyll, noticing the "V"-shape base of sporophyll, X1.
12. A large sporophyll, X 1.
13. A leaf, X 1.

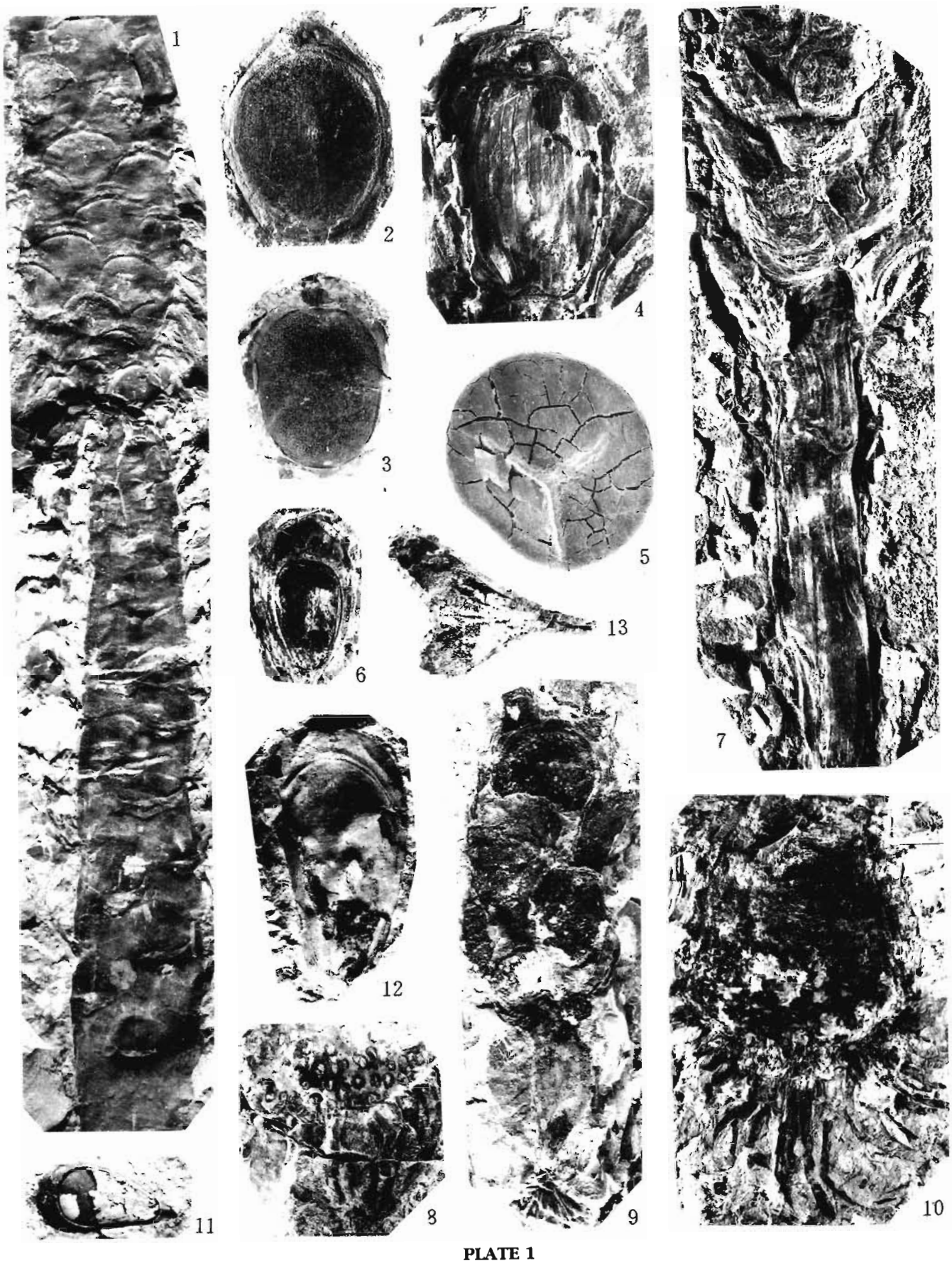
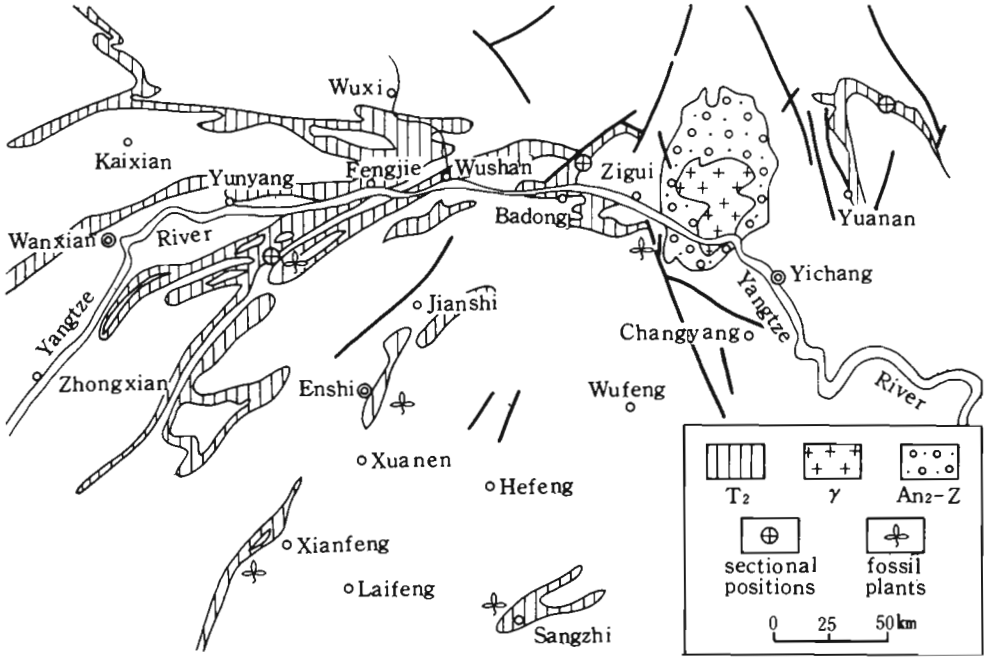


PLATE 1



Text-figure 1—Distribution of the Middle Triassic Badong Formation and fossil plants in the Yangtze Gorge area.

figure 1). The discovery of this flora, therefore, not only fills the gap of Middle Triassic plant assemblage in South China, but also significant in the evolution of Triassic flora, the palaeobotanical and geographical regionalization and in the correlation of global Middle Triassic floras.

The Badong Formation, consisting chiefly of a set of purple clastic deposits intercalated with carbonate rock in the middle part, is widespread in the Yangtze Gorge area, with a total thickness of about 1000 m. This formation may be subdivided into 5 lithologic members. Members 1, 3 and 5 consist mainly of grey limestone, argillaceous limestone and limy mudstone, respectively being about 50 m, 250 m and 20 m thick; whereas Members 2 and 4 are composed of purple siltstone and silty mudstone, respectively being about 400 m and 500 m thick. According to the marine bivalves, such as *Eumorphotis (Asoella) subillyria* (Hsü), *Myophoria (Costatoria) goldfussi mansuyi* Hsü, *Plagiostoma striatum* (Schlothein), etc., and the ammonoids *Progonoceratites* of Members 1-3 and the bivalves *Costatoria goldfussi* (Alberti),

PLATE 2

1-2. *Calamites shanxiensis* (Wang). Locality: Dawoshang, Fengjie County, Sichuan. Horizon: Member 2 of the Badong Formation

1. A stem with long internodes, X 1.
2. A stem with a node, X 1.

3-5. *Annalepis sangzhiensis* Meng. Locality: Hongjiaguan, Sangzhi County, Hunan. Horizon: Member 2 of the Badong Formation.

3. Two strobili, showing a corm at the centre of each strobilus, X 1.
4. A strobilus, X 1.
5. Two sporophylls, showing a ligular scar and a leaf-tip at the top of each sporophyll, X 2.

6-8. *Neuropteridium voltzii* Brongniart. Locality: Furongqiao, Sangzhi County, Hunan. Horizon: Member 2 of the Badong Formation.

6. Middle part of a frond, X 1.
7. Lower part of a frond, X 1.
8. Middle-upper part of a frond, X 1.

9-10. *Annalepis angusta* Meng. The obverse and reverse of a strobilus fragment, X 1. Locality: Hongjiaguan, Sangzhi County, Hunan. Horizon: Member 2 of the Badong Formation.

11-14 *Annalepis breviсystis* Meng.

11. A few isolated sporophylls, X 1. Locality: Dawoshang, Fengjie County, Sichuan. Horizon: Member 2 of the Badong Formation.
12-13. The obverse and reverse of a sporophyll, all X 1. Locality: Meiping, Xianfeng County, Hubei. Horizon : Member 2 of the Badong Formation.
14. A tip of a sporophyll, X 3.
15. *Cladophlebis* sp., lower-middle part of an ultimate pinna, X 2. Locality: Dawoshang, Fengjie County, Sichuan. Horizon: Member 2 of the Badong Formation.
16. *Equisetites arenaceus* (Jaeger) Brongniart. A part of stem with 2 nodes, showing the leaf sheath with long teeth, X 1. Locality: Hongjiaguan, Sangzhi County, Hunan. Horizon: Member 4 of the Badong Formation.

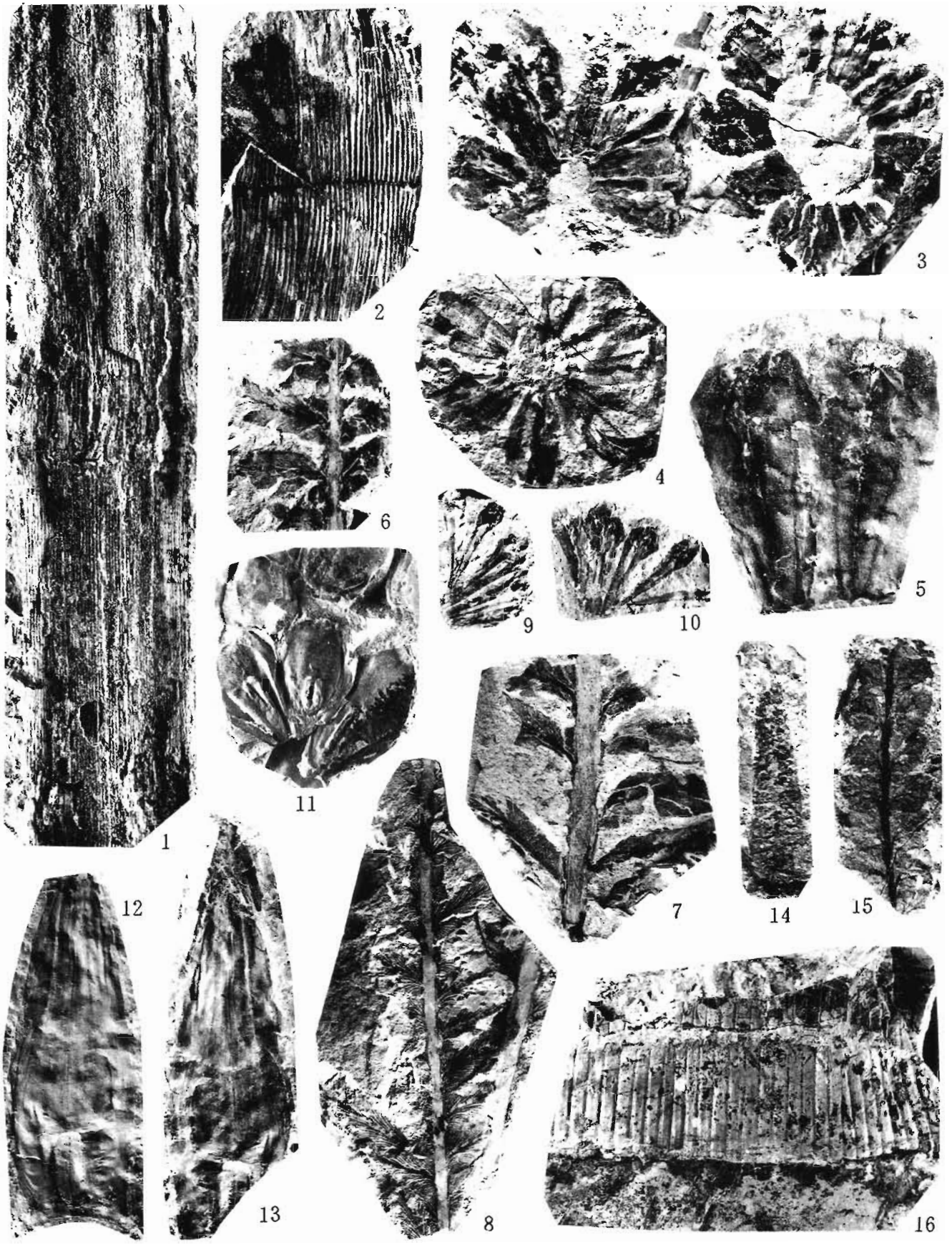


PLATE 2

Modiolus cf. *quiyangensis* Chen, etc. of Members 4 and 5, most workers incline to put Members 1-3 into Anisian, and Members 4-5 into Ladinian at present. The fossil plants were mainly found in the gray-greenish argillaceous siltstones or the siltstone lens in Member 2, whereas a few of specimens were collected from the sandy mudstone in Member 4.

Member 2 of the Badong Formation is considered a shore deposit of the tidal flat, with a lot of similar depositional rhythms ranging from coarse to fine. The sandy deposit with ripples and flattened beddings is mainly present in the lower part (lower tidal flat) in each rhythm, the argillaceous deposit without bedding is in the upper part (upper tidal flat). Both mixed deposits are in the middle transitional zone (middle tidal flat), which is rich in fossil plants, estherids and trace fossils in some localities. Field investigations show that the fossil plants occur in the depressions of the middle tidal flat of Member 2.

PLANT ASSEMBLAGES OF THE BADONG FORMATION

In accordance with the changes in time and space, the fossil plants of the Badong Formation may be subdivided into the following two assemblages in ascending order :

Pleuromeia marginulata-Annalepis sangzhiensis assemblage

The assemblage is represented by the fossil plants from Members 1-2 of the Badong Formation, belonging to 18 genera and 30 species, of which the main elements are : *Pleuromeia marginulata* Meng, *P. sanxiaensis* Meng, *Annalepis sangzhiensis* Meng, *A. brevicystis* Meng, *Calamites shanxiensis* (Wang), *Equisetites* cf. *gracilis* (Nathorst), *Crematopteris* sp., *Neuropteridium voltzii* Brongniart, *Cladophlebis* sp., *Peltaspermum multicostatum* Zhang et Shen, *P. miracarinatum* Meng, *Scytophyllum hunanense* Meng, *?Thinnfeldia nordenskiöldi* Nathorst, *Nilssonia costanervis* Meng, *Yuccites anastomosis* Wang Z.Q. et Wang L.X., *Y. vogesiacus* Schimper et Mougeot, *Voltzia heterophylla* Brongniart, *V. curtifolia* Meng, *Willsiostrobus* cf. *cordiformis* (Grauvogel-Stamm), *Pagiophyllum* sp., etc. It is obvious that the assemblage is predominated by Lycopsida, especially *Pleuromeia* of Pleuromeiales and *Annalepis* of Isoetales. Since *Pleuromeia* was first reported in Germany in the middle of the last century, it has been considered the most typical plant for the Early-Middle Triassic in the world. This genus is widespread in Eurasia, with stable horizon, like marine faunal fossils. Hence, it has attracted the attention of workers in stratigraphic correlation. *Pleuromeia* was discovered in South China for the first time and it is widely distributed in eastern Sichuan, western Hubei and northwestern Hunan. It is more abundant and well preserved in this area than that reported at home and abroad before. *Annalepis* is a rare genus in the Northern Hemisphere and has important significance for the identification of the Middle Triassic age. All the specimens attributed to this genus in the past are isolated sporophylls and sporangia. This genus is more extensive than

PLATE 3 →

1. *Scytophyllum* sp. 1. Upper-apical part of a pinna, X1. Locality : Furongqiao, Sangzhi County, Hunan. Horizon: Member 2 of the Badong Formation
2-3. *Peltaspermum multicostatum* Zhang et Shen. Locality: Hongjiaguan, Sangzhi County, Hunan. Horizon : Member 2 of the Badong Formation.
2. An orbiculate sporophyll, X 2.
3. An orbiculate sporophyll showing many radiate ridges on the upper surface, X 1.
4-5. *Peltaspermum miracarinatum* Meng. Both the obverse and reverse of a sporophyll; peltate disc bearing 16 seeds on the under surface, all X3. Locality and Horizon: the same as above.
6-8. *Scytophyllum hunanense* Meng. Locality: Furongqiao, Sangzhi County, Hunan. Horizon: Member 2 of the Badong Formation.
6. Middle part of a pinna, X 1.7.
7. Part of a pinna, X 1.
8. A single pinnule, X 1.
9-10. *Annalepis latiloba* Meng (MS). Locality : Hongjiaguan, Sangzhi County, Hunan. Horizon: Member 4 of the Badong Formation.
9. A sporophyll, X 1.
10. The same specimen as shown in fig. 9, X 2.
11-12. *Nilssonia costanervis* Meng. Locality : Furongqiao, Sangzhi County, Hunan. Horizon: Member 4 of the Badong Formation.
11. Part of a leaf, X 1.
12. Lower-middle part of a leaf, X 1.
13. *Sphenozamites* sp., part of a pinna fragment, X 1. Locality: Hongjiaguan, Sangzhi County, Hunan. Horizon: Member 4 of the Badong Formation.
14. *?Thinnfeldia nordenskioldi* Nathorst. A single pinna, X 1. Locality: Furongqiao, Sangzhi County, Hunan. Horizon: Member 2 of the Badong Formation.
15. *Nilssonia* sp.—Middle-upper part of a pinna, X 1. Locality and Horizon: the same as above.

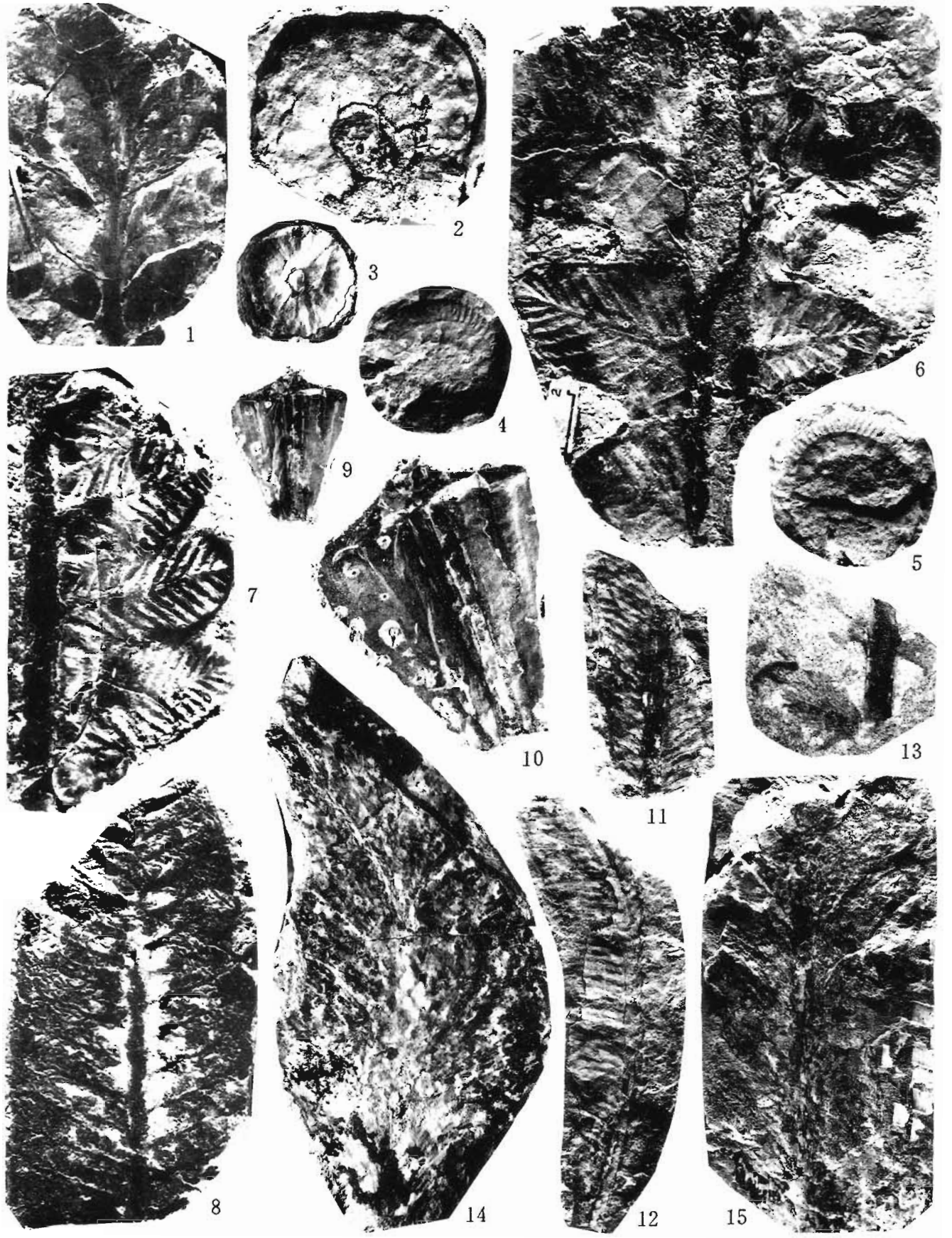


PLATE 3

Pleuromeia in distribution of South China and was found in Member 2 of the Badong Formation in eastern Sichuan, western Hubei and northwestern Hunan. Most specimens are complete cones, which are very valuable for studying the morphology of *Annalepis*. Pteridosperms, comprising 3 genera and 7 species, are also rather abundant in the assemblage, with large leaves and peculiar nerves except *Peltaspermum*. Among them the genus *Scytophyllum* is a leading element of the Scytophyllum flora in Eurasia (Dobruskina, 1982), while others may be originated from the Palaeozoic pteridosperms. Sphenopsida and conifers occupy a certain proportion. The former is represented by species with a thick stem and long internode, while the latter is characterized by shoots and cones of *Voltzia heterophylla*; Filices and cycadophytes only have individual genera and species. In addition, there is also *Yuccites* of Cordaitales in this assemblage. This genus is characterized by large leaves, and might be clustered on the ground. Judging from the compositions, the present assemblage could be comparable with those floras from the Muschelkalk of Germany (Blanckenhorn, 1886), the Lettenkohlen of France (Fliche, 1910) and the bottom of the Ermaying Formation of North China (Wang *et al.*, 1990). The characteristic elements, such as *Pleuromeia, Annalepis, Neuropteridium, Yuccites, Voltzia heterophylla*, etc., occur in all these floras. On the ground that it occurs in association with the Middle Triassic marine bivalves: *Costatoria goldfussi mansuyi*(Hsü), *Bakevellia mytiloides ornata* (Chen), *Mytilus eduliformis praecusor* Frech, *Unionites gregaria* Quenstedt, *Eumorphotis (Asoella) illyrica* (Bittner) and the overlying strata yield the latest Anisian ammonoids *Progonoceratites*, this assemblage undoubtedly belongs to early Middle Triassic or Anisian in age.

Annalepis latiloba-Scytophyllum assemblage

The assemblage represented by the fossil plants from Members 4-5 of the Badong Formation chiefly includes *Annalepis latiloba* Meng (MS), *Equisetites arenaceus* (Jaeger), *Neocalamites* sp., *Scytophyllum* sp., *Sphenozamites* sp., *Sinoctenis pulcella* Ye, *Voltzia* sp., *Taeniopteris* sp., etc. Although the genera and species are not rich in this assemblage, it is obviously different from above assemblage. The present assemblage has no *Pleuromeia* of Members 1-2, whereas *Scytophyllum* evidently increases in amount and *Sphenozamites* and *Sinoctenis* which are commonly found from the Late Triassic in South China. Since this assemblage contains some Late Triassic plant members and lies over the stratum with the latest Anisian ammonoids *Progonoceratites*, it is undoubtedly younger than the assemblage of Members 1-2 of the Badong Formation, belonging roughly to late Middle Triassic or Ladinian in age. This assemblage is similar to that from the upper part of the Ermaying Formation in North China in general aspect.

PALAEOECOLOGY OF ANISIAN PLANT ASSEMBLAGE

It is well known that the plant is bound up with the surrounding environment and both have interaction. The variability and plasticity of plant structures were changeable with different ecological conditions. Based on the palaeobotanical data obtained from the Badong Formation within this area, it is possible to trace the ecological environment of floras and to reconstruct the vegetational landscape then. The fossil plants of the Badong Formation were mainly found from Member 2. Now the plant assemblage of this member is taken as an example, whose ecological environments are interpreted as follows :

PLATE 4

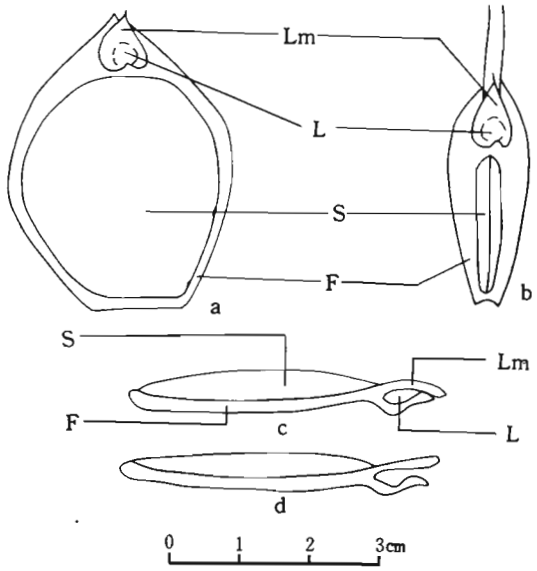
1-4. *Voltzia heterophylla* Brongniart. Locality: Furongqiao, Sangzhi County, Hunan. Horizon: Member 2 of the Badong Formation.
1. Part of an ultimate shoot fragment, with long leaves, X 1.
2. Part of a penultimate shoot, X 1.
3. A cone-scale, X 1.
4. An ultimate shoot, X 1.
5. *Voltzia* sp. —Middle-upper part of an ultimate shoot, X 1. Locality and Horizon : same as above.
6. *Cladophlebis* sp.—Part of an ultimate pinna, X 2. Locality and Horizon: the same as above.
7. *Willsiostrobus* cf. *cordiformis* (Grauvogel-Stamm). A male strobilus, X 3. Locality and Horizon : the same as above.
8. *Yuccites anastomosis* Wang Z.Q. et Wang L.X. A leaf, X 1. Locality and Horizon : the same as above.
9. *Voltzia curtifolia* Meng. An ultimate shoot, terminating in a strobilus at the top, X 1. Locality and Horizon : the same as above.
10. *Scytophyllum* sp. 2. A single pinnule, X 1. Locality: Hongjiaguan, Sangzhi County, Hunan. Horizon : Member 4 of the Badong Formation.
11. *Yuccites vogesiacus* Schimper et Mougeot. A single leaf, noticing morphology of the leaf base, X 1. Locality: Furongqiao, Sangzhi County, Hunan. Horizon: Member 2 of the Badong Formation.

PLATE 4

Based on the field observations, the plants from Member 2 of the Badong Formation are different from one another in their burial states in the same horizon. The genus *Pleuromeia* is generally well-preserved with a complete plant body which includes stem, strobilus, appendixes and rhizophores. Some stems are almost vertically preserved in the sediments, and appendixes show a growing state almost perpendicular to the bedding plane. The phenomena mentioned above indicate that it may be autochthonous taphocoenose. The genus *Annalepis* has both isolated sporophylls and rather perfect cones, with some sporophylls retaining the leaf-tip. Presumably, it had ever been transported for a short distance at that time, but basically is suballochthonous taphocoenose. Sphenopsida and *Yuccites* are also well-preserved. The former is mostly stem pith cast, while the latter shows a large and complete leaf and distinct nerves. It seems that as if they could be transported for a distance, but are also suballochthonous taphocoenose. All other plants are preserved as fragments without the cuticle, and with indistinct nerves. Even if conifers are only scattered branches, and their cones are separate from the branches. These plants might have been transported for a long distance under the strong waterpower conditions.

As to the ecology of *Pleuromeia*, it was briefly discussed by some authors before. It was generally considered to be a kind of xerophyte because it has short and thick succulent stem without branches. Since it is often associated with marine faunas, some authors (Mägdefrau, 1931; Kon'no, 1973; Krassilov et Zakharov, 1975) thought that it was a kind of tidal flat plant, and possesses the "mangrove bush" ecotype in the modern tropical shore seas. *Annalepis* often grew in land swamp near the coast or lived in shallow water and wet soil, like modern *Isoetes* (Wang Ziqiang, 1991).

The genus *Pleuromeia* of the Yangtze Gorge area consists of 3 species of dwarf bushes, representing a monogenetic association. These plants are generally not very high, most of which are about 50 cm in height, whereas the minority, such as *P. marginulata*, may be more than 1 m high. It might grow in a relatively flat shoreline area, frequently influenced by waves and tides, or it was distributed in the flat coastal area without lashing by the stormy



Text-figure 2—Morphology of sporophylls and ligular texture of *Pleuromeia* and *Annalepis*: **a**. *Pleuromeia*, **b**. *Annalepis*, **c-d**. longitudinal sections of the ligule of *Pleuromeia* (c. closed labellum; d. opened labellum), **F**. sporophyll, **L**. ligule, **Lm**. labellum, **S**. sporangium.

waves and on the sludgy shallow of the bay. When the tide was coming in, the plants might be submerged partly or totally, resulting in a nearshore lagoon there; and while the tide was going out, they emerged again, creating a dried lagoon environment there. In such an ecological environment, those plants have formed a lot of special ecological structures (Text-figure 2).

The sporangia of *Pleuromeia* take the shape of a plate, with a concave upper surface and a convex lower surface, and attach closely to the ventral surface of sporophylls posteriorly. Most of the sporangia were still attached to the sporophylls when they dropped. The sporophylls generally are ovate in outline, with a smooth lower surface and an upturned surrounding margin. All the features show that the sporangia possess a function for drift in water. It is more important that a ligule and special labellum are present at the anterior part of the sporophylls. The ligule could be analogous to an air cavity, while the labellum to a lid of the air cavity, which could open and close automatically. Presumably, the ecological function of both structures could be related to the plant respiration and hydathodal roles. As soon as the plant was submerged by tide, the labellum closed automatically. Then the plant made use of the air in

the ligule to breathe (Text-figure 2 c). As soon as the plant was emerged by ebb, the labellum opened automatically. In that case, the plant continually spat water (Text-figure 2 d). In addition, the macrospores of *Pleuromeia* are relatively durable and with smooth surfaces, and its specific gravity is larger than that of other plants. These features are advantageous to the precipitation of the macrospores and the development of new plants in the coastal environment. It is necessary for *Pleuromeia* to adapt the seashore living environment.

The genus *Annalepis*, including 3 species, has also a monogenetic association, and it likely grew in the marginal area of nearshore with *Pleuromeia*'s shrub or in the swamps of land marginal area along the coast. The sporophylls of this genus are lanceolate, with acute apex, truncate base and smooth lower surface, resembling a small boat in shape. The sporangia are slender stick-shaped and attached closely to the central part of the ventral surface of the sporophyll, with a warped anterior apex of the sporophyll formed in water possibly because of its weight. The sporangium is attached to sporophyll when it dropped. All the features show that *Annalepis* also possesses drifted ecological characters in water. In addition, there are also a ligule and a labellum on the sporophyll, whose ecological functions are basically identical with the *Pleuromeia*. As soon as the plant was influenced by the breaker, they were advantageous to air and spitting water.

The Sphenopsida and *Yuccites*, occurring in coassociation, might grow in swamps along the coast or in the margin of lake, and formed the shrubberies of the coastal margin together. Since the gametic fertilization of the former required to have the aid of water, and the latter characterized by tall body and large leaves possessed rather violent transpiration, only by growing near water banks could they maintain normal life. Other plants, such as filices, pteridosperms, etc., might grow under the shrubberies near water banks, consisting of the lower bedded textures of the vegetation.

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