Early Cretaceous *Athyrium* Roth from Northeastern China

Fen Chen, Shenghui Deng & Keqin Sun

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Four species of the Early Cretaceous genus *Athyrium, viz., A. cretaceum* Chen et Meng, *A. fuxinense* Chen et Meng, *A. huluntanum* Chen, Ren et Deng and *A. hailaerianum* Deng et Chen from Northeastern China have been systematically studied by scanning electron microscope. The palaeoecology of the Early Cretaceous *Athyrium* has also been discussed in detail in this paper.

Key-words — Pteridophytes, *Athyrium*, Fern, Early Cretaceous, Northeastern China.

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सारांश

उत्तर चीन से प्रारम्भिक क्रीटेश्यस कालीन *एथाइरियम* रोथ

फेन चेन, शेंघुई देंग एवं केकिन सन

उत्तर-पूर्वी चीन से प्रारम्भिक क्रीटेश्यस कालीन *एथाइरियम* प्रजाति की चार जातियों—*ए. क्रीटेश्यम* चेन व मेंग, *ए. फक्सिनेन्से* चेन व मेंग, *ए. हुलुनिआनम* चेन, रेन व देंग तथा *ए. हेलारियानम्* देंग व चेन का क्रमवीक्षण सूक्ष्मदर्शी द्वारा अध्ययन किया गया है। इसी शोध-पत्र में प्रारम्भिक क्रीटेश्यस कालीन *एथाइरियम* की पुरापारिस्थितिकीय विवेचना भी की गई है।

ATHYRIUM is a large genus of more than 200 species distributed in the temperate zone and mountain woodlands in the subtropics, especially in Himalayas, China and Japan. Of them, more than 100 species occur in China and form a centre of distribution in mountain woodlands of southeastern China (Wu et Ching, 1991). Only a few species are found in Europe and North America (Hsieh, 1986).

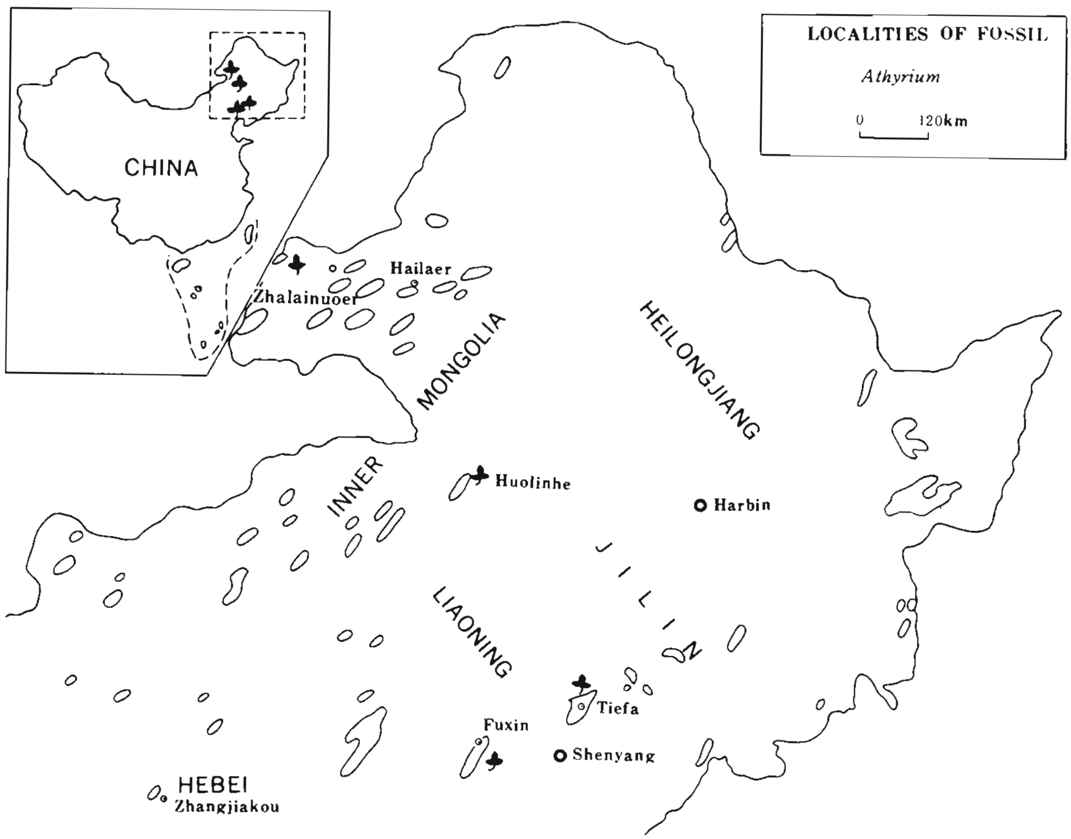
Very few fossils of *Athyrium* have been recorded in literature. *Athyrium crossii,* as an example, was described from the Tertiary of Denver Formation, North America. A poorly preserved pinna was described as *A. gracilium* Pabst (Pabst, 1968) from the sediments of the latest Cretaceous to Early Tertiary of America. Based upon some fertile material, two Early Cretaceous species *Athyrium cretaceum* and *A. fuxinense* and a possible one *Cladophlebis (Athyrium?) asymmetrica* were reported from Fuxin Basin, Liaoning, Northeast China (Chen *et al.*, 1988). These species were also found from the adjacent areas of Fuxin Basin (Deng, 1991a, 1991b, 1992). Recently, two new species: *A. hulunianum* and *A. hailaerianum* have been preliminarily described from Zhalainuoer Basin, Inner Mongolia by the authors (Chen *et al.*, 1993).

This paper is the result of systematic study of the material including a number of specimens collected recently. The main work has been focussed on the microstructures of reproductive organs *in situ.* The fossil specimens have been compared with the extant species of living *Athyrium*— *Athyrium filix-femina.* The palaeoecological characters of the Early Cretaceous *Athyrium* have been discussed in the present paper as well.

STRATIGRAPHY, MATERIAL AND METHODS

The material studied in this paper was collected from Fuxin Basin, Tiefa Basin, Liaoning Province and Huolinhe Basin, Zhalainuoer Basin, Inner Mongolia (Text-figure 1). The correlation between these four Mesozoic basins is shown in Table 1. The fossil bearing sediments belong to the Early Cretaceous.

1. Fuxin Basin— The Late Mesozoic strata in Fuxin Basin are represented by the Yixian, Jiufotang, Shahai, Fuxin and Sunjiawan Formations, in



Text-figure 1— Map showing the fossil localities.

upward sequence (Table 1). The Yixian Formation is characterized by thick volcanics. Jiufotang Formation is a series of fresh water lacustrine deposits, and both of the Shahai and Fuxin Formations are represented by coal-bearing units. The Sunjiawan Formation is composed of varicoloured sandstones and conglomerates which indicate arid or semiarid climatic conditions during deposition. The Fuxin Formation is rich in plant fossils including *Athyrium cretaceum* and *A. fuxinense*.

2. Tiefa Basin — The palaeogeographic environment of this basin as well as its geological age and the features of Late Mesozoic strata are

Table 1— Correlation of the Late Mesozoic Formations in Inner Mongolia and Liaoning Province, Northeast China

	Inner Mongolia			Liaoning	
	Zhalainuoer	Huolinhe		Fuxin	Tiefa
Albian	Qinglonggang Formation			Sunjiawan Formation	Sunjiawan Formation
Aptian	Yimin Formation	Huolinhe Formation	Upper member	Fuxin Formation	Xiaominga-nbei Formation
Neocomian	Damoguaihe Formation		Lower member	Shahai Formation	
Late Jurassic	Xinganling Group	Xinganling Group		Jiufotang Formation	Baijiagou Formation
				Yixian Formation	Datai Formation

PLATE 1

All specimens are housed in China University of Geosciences (Beijing). All figures are in natural size except where indicated. Scanning electron microscope pictures are marked with "SEM"

1-8. *Athyrium cretaceum* Chen et Meng

1. Fertile pinnae. Fuxin Formation, Fuxin Basin, Liaoning.

3-5, 8. Fertile pinnae; 3a, showing the sori. Xiaominganbei Formation, Tiefa Basin, Liaoning.

2, 6-7 Sterile pinnae. Xiaominganbei Formation, Tiefa Basin, Liaoning.

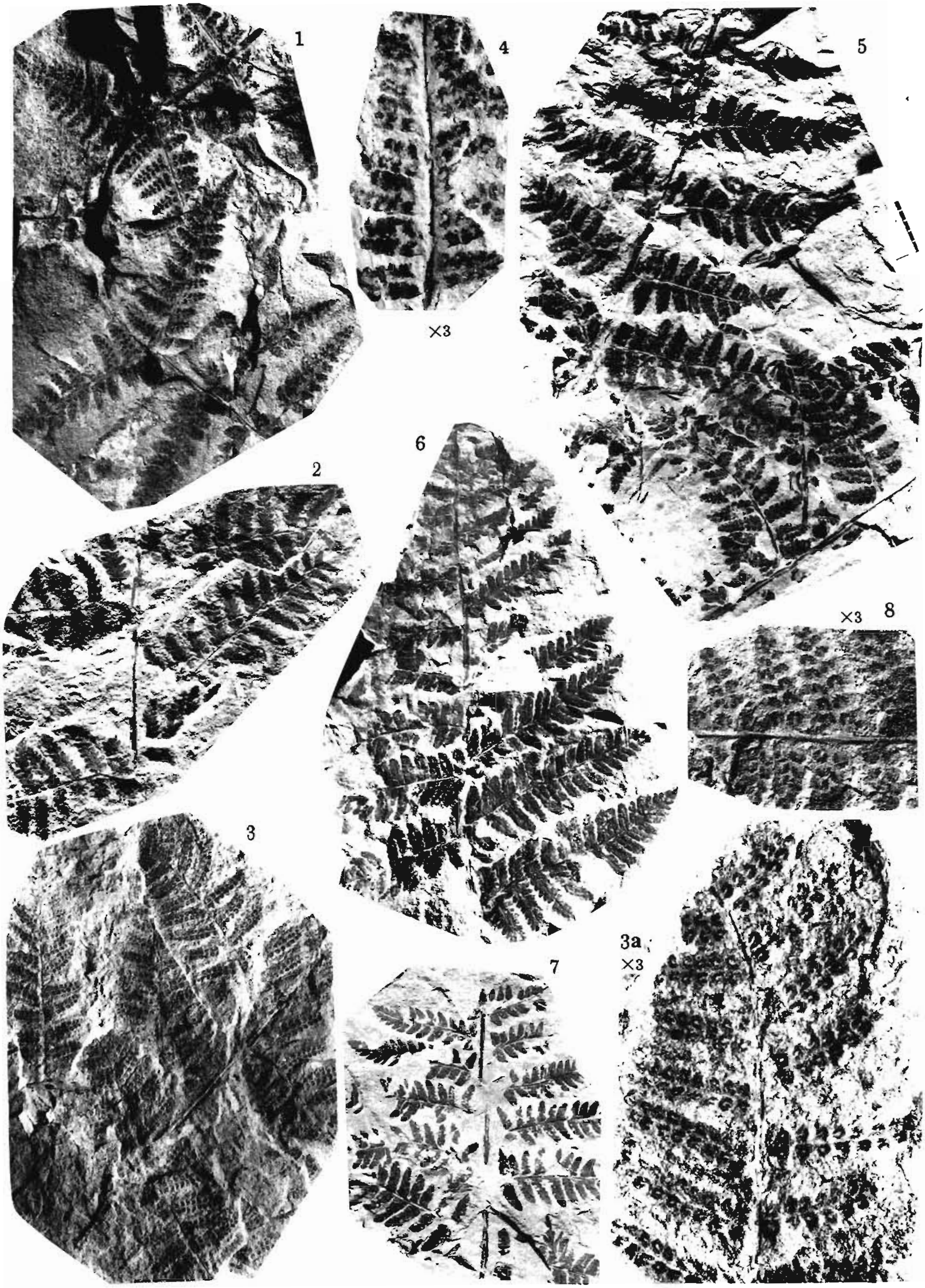
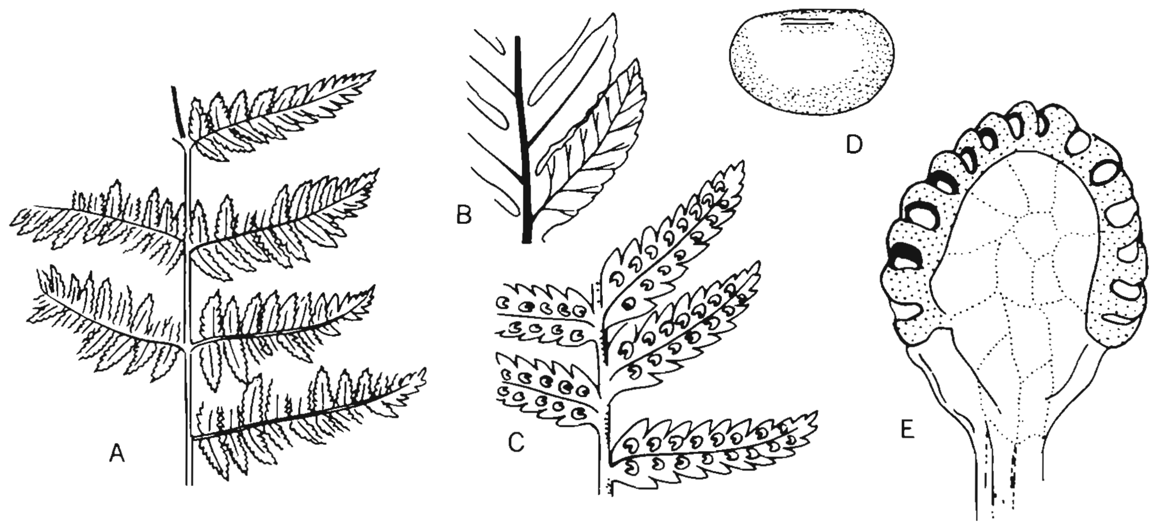


PLATE 1



Text-figure 2—*Athyrium cretaceum* Chen & Meng ; **A**, frond x 1; **B**, sterile pinnules showing the venation x 4; **C**, fertile pinnules showing the sori x 4; **D**, spore x 600; and **E**, sporangium x 264.

similar to those of Fuxin Basin. The coal-bearing Xiaominganbei Formation, yielding *Athyrium cretaceum*, is equal to the Shahai and Fuxin Formations of Fuxin Basin (Table 1).

3. Zhalainuoer Basin — This basin lies in eastern Inner Mongolia (Text-figure 1). The Early Cretaceous coal-bearing strata of Damoguaihe and Yimin Formations are very abundant in plant fossils (Ren, 1986). *Athyrium huluniianum* and *A. hailaerianum* were discovered from the Yimin Formation.

4. Huolinhe Basin — The Huolinhe Formation, unconformably overlying the Late Jurassic volcanic rocks, is divided into lower and upper coal members. The lower member which contains *Athyrium cretaceum* and other plant fossils is regarded to early Early Cretaceous (Deng, 1991a).

All the specimens are well preserved compressions. Most of them are fertile fronds with carbonaceous remains which contain numerous sori and sporangia. Firstly, the specimens were observed under a stereomicroscope and then the *in situ* sori and sporangia removed from the matrix by bulk maceration of rock with hydrofluoric acid or directly transferred from the matrix with a needle. The black sori or sporangia were treated with Schulz's solution or sodium hypochlorite until they become brown and then examined under a light microscope. The sporangia then were treated with ammonium hydroxide or sodium hydroxide solution to get the spores released. In order to count the spores output accurately, some sporangia were isolated and moved to an acuvette (1-2 mm in diameter) carefully, and then broken with a needle. Some of the spores, sporangia and sori were studied under scanning electron microscope.

The specimens of the extant *Athyrium* were provided by Dr Zhang of the Institute of Botany, Academia Sinica.

PLATE 2

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All specimens are housed in China University of Geosciences (Beijing). All figures are in natural size except where indicated. Scanning electron microscope pictures are marked with "SEM"

1-11. *Athyrium cretaceum* Chen et Meng. 1-7 Sporangia. 1, sporangium with a stalk, x 264, 2-3, x 132, 4 (SEM), x 270; 5 (SEM), x 300; 5a (SEM), x 1080, enlargement of fig. 5, showing the stalk; 6 (SEM), x 400; 7 (SEM), x 400; 7a (SEM), x 1000, enlargement of fig. 7 showing the thickened cells of the annulus.

8-9. Spores. 8, x 660; 9 (SEM), x 400; 9a. (SEM), x 1000.

10. Enlargement of Pl. 1, fig. 10 x 30 showing the sori.

11. Fertile pinnae, Huolinhe Formation, Huolinhe Basin, Inner Mongolia.

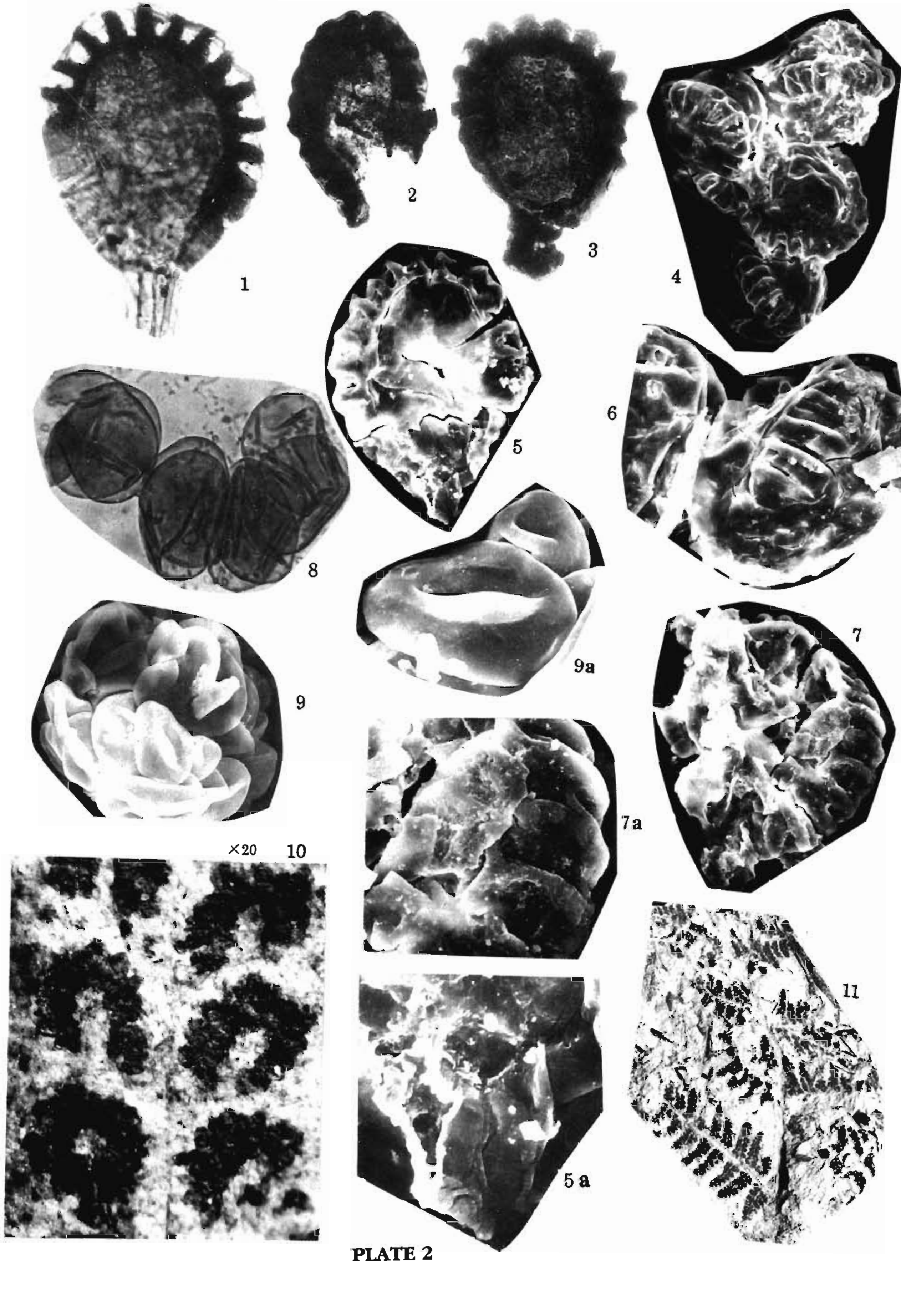


PLATE 2

DESCRIPTION

Family—Athyriaceae

Athyrium cretaceum Chen et Meng

Pl.1, figs 1-8; Pl. 2, figs 1-11; Text-figure 2

1988 *Athyrium cretaceum* Chen *et al.,* p. 42, pl.13, figs 5-9; pl.14, figs1-11; Text-fig. 14b.

1991 *Athyrium cretaceum* Deng, pl. 1, figs 1-2.

1992 *Athyrium cretaceum* Deng, pl. 4, figs 1-4.

Fronds — Medium size, over 15 cm long and 10 cm wide, bipinnate, triangular, elongated triangular or lanceolate in outlines.

Stipes and rachis — Stipes up to 6 cm long and 2 mm wide; smooth, with a longitudinal groove on the adaxial surface. Rachis smooth, 1-2 mm thick, weak, curved very often (Pl. 1, figs 3, 5), with a shallow and longitudinal groove on the upper side.

Pinnae and pinnules— Ultimate pinnae lanceolate, usually 2-5 cm long, 0.7-1.5 cm broad at the base, oppositely to alternately arranged, arising at right angles, with intervals of 0.8-2 cm between the adjacent pinnae. A pair of pinnae at the base of the frond usually asymmetrical and the pinnules on the basiscopic sides of these pinnae typically longer and larger than those on the acroscopic sides.

Pinnules typically lanceolate or triangular, 0.6-1.5 cm long and 0.3-0.5 cm wide at the base; apices acute; margins dentate with 6-9 pairs of triangular teeth. Pinnules in opposite or slightly katadromic at the bases and usually after 4-5 pinnules upwards turned into anadromic order (Pl. 1, figs 1, 5-6). The pinnules on the basiscopic side generally larger and arranged less crowded than those on the acroscopic side.

Venation — Pinnate, midvein slightly decurrent at the base and reaches up to the apex of the pinnule; lateral veins slender, simple or forked once or twice (Text-figure 2B).

Fertile pinnules and sori — Fertile pinnules are similar to the sterile ones. Sori attached to the lateral veins or their anterior branches, arranged in a single row on each side of midvein (Pl. 1, figs 1, 3-4, 8; Text-figure 2 C). One sorus in each tooth, 4-7 pairs or even 9 pairs in each pinnule. Sori typically hook or hoof-like, those at the bases of the pinnules usually semicircular, 0.3-0.6 x 0.5-0.8 mm in diameter, with about 45^0 to the midvein (Pl. 1, figs 3a, 8; Pl. 2, fig. 10), indusium present occasionally.

Sporangia and spores — Sporangia spherical or elliptic, 90-100x130-150 μm in size, stalk more than 200 μm long and about 30 μm in diameter (Pl. 1, fig. 7; Pl. 11, figs 4,6). Thin-walled cells of the sporangium polygonal, 40-50 μm in diameter. Annulus vertical, incomplete, composed of 13 to 15 thickened cells. Stomium dehisces transverse (Pl. 2, figs 1-7; Text-figure 2E). Spores bilateral, elliptic in polar view and kidney-like in equatorial view (Pl. 2, figs 8-9; Text-figure 2 D), 64 spores per sporangium. In mature spores, equatorial axis 30-45 μm long and polar axis 20-30 μm long, the ratio of two axes about 1.5. Some spores very small, less than 13 x 20 μm in size, supposed to be immature ones. Monolete, laesura usually 10-20 μm long, about half of the equatorial axis. Exine smooth, wrinkled.

Horizon and localities — Fuxin Formation, Fuxin Basin; Xiaominganbei Formation, Tiefa Basin; Lower member of the Huolinhe Formation, Huolinhe Basin.

Athyrium fuxinense Chen et Meng

Pl. 3, figs 1-10; Text-figure 3

1988 *Athyrium fuxinense* Chen *et al.,* p. 43, pl. 14, figs 12-13; pl. 15, figs 1-5; text-figure 14a.

Frond— Medium size, up to 20 cm long, 8-10 cm wide, tripinnate at the lower region and bipinnate at the upper region, elongated triangular or lanceolate in outline.

PLATE 3 ⟶

All specimens are housed in China University of Geosciences (Beijing). All figures are in natural size except where indicated. Scanning electron microscope pictures are marked with "SEM"

(All the specimens are from Fuxin Formation, Fuxin Basin, Liaoning)

1-10. *Athyrium fuxinense* Chen et Meng

1-3. Sterile pinnae, arrow in fig. 1 showing the stipes.

4-5. Fertile pinnae, 4a, 4b; 5, enlargement of fig. 4, showing the fertile pinnules and sorus.

6. Spores in a sorus (SEM), x 600.

7-8. Sporangia (SEM), x 120.

9. Showing the thickened cells of the annulus (SEM), x 1000.

10. Spores, x 800.

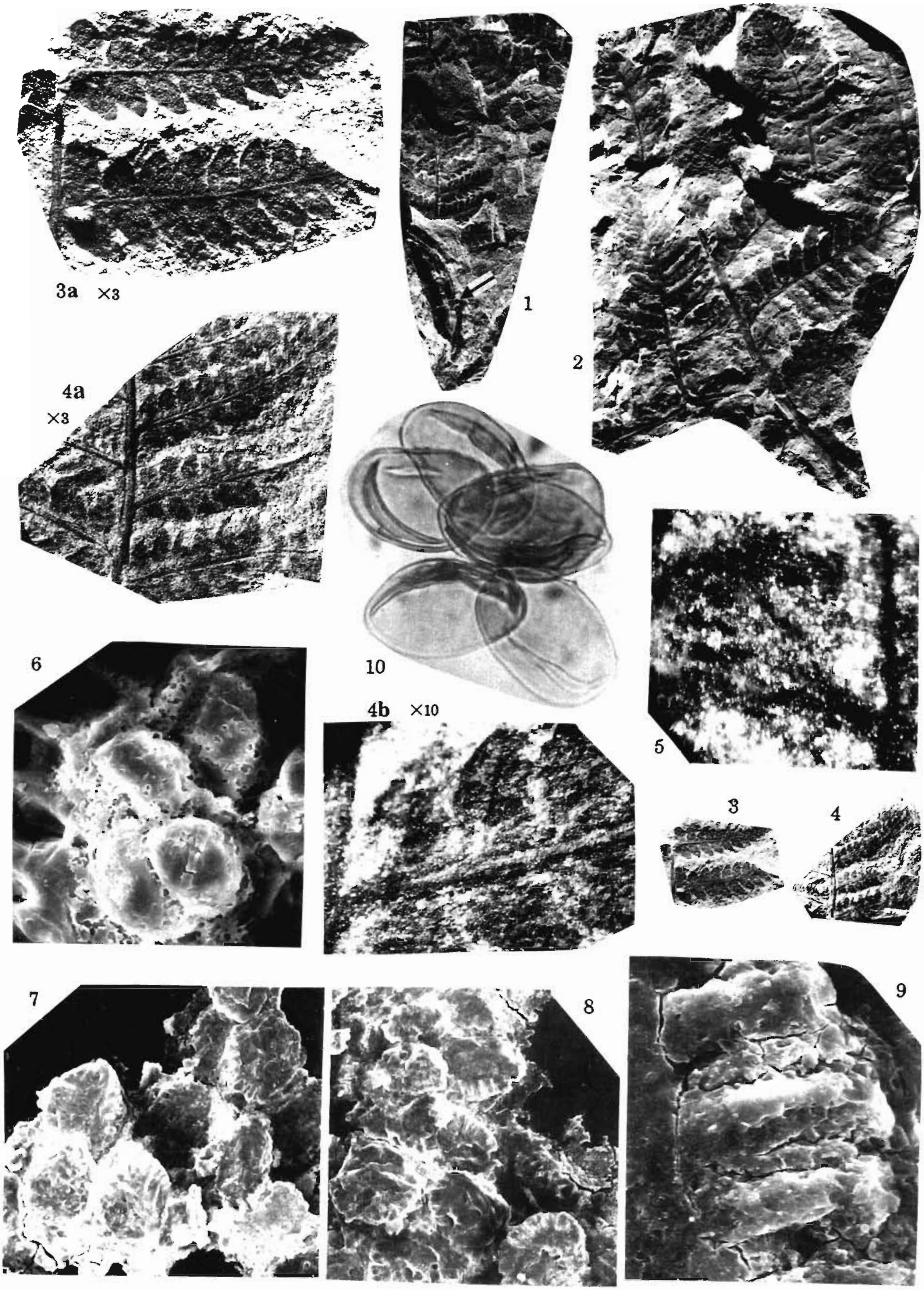
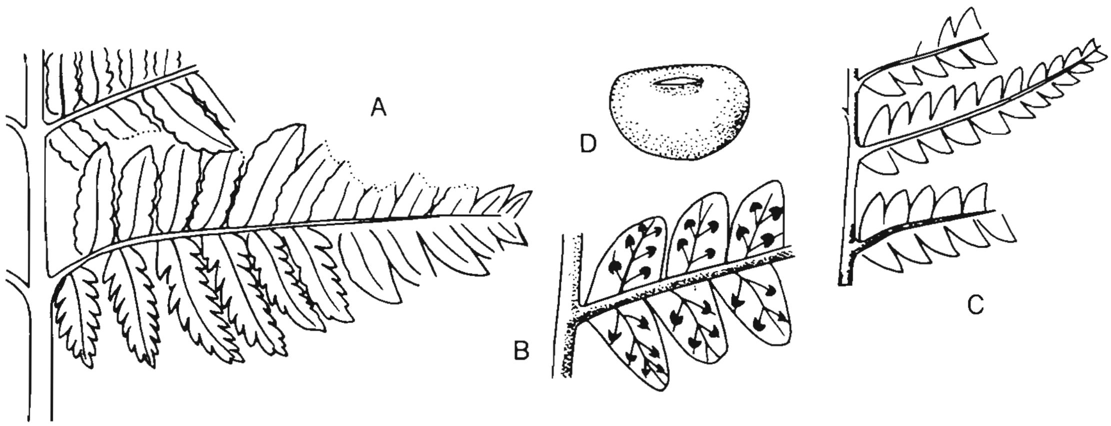


PLATE 3



Text-figure 3 — *Athyrium fuxinense* Chen & Meng; **A**, lower part of a frond x 1; **B**, fertile pinnules showing the sori x 6; **C**, fertile pinna x 3, and **D**, spore x 600.

Stipes and rachis — Stipes clustered (Pl. 3, fig. 1), over 4 cm long, 3 mm wide, slightly curved, smooth, convex on the lower side with a longitudinal groove on the upper side. Ultimate rachis 0.2-0.3 mm wide, upper surface concave, lower surface rounded (Pl. 3, figs 3a, 4a).

Pinnae and pinnules — Penultimate pinnae arising at angles of 80^0, opposite to subopposite, quite crowdedly arranged. A basal pair of penultimate pinnae 8-10 cm long and 4-5 cm broad. The upper part of the frond tending bipinnate. Ultimate pinnae lanceolate, acute, 2-3 cm in length and 0.7-1.5 cm in breadth, arranged in slightly opposite to katadromic order. Pinnules triangular, falcated or ligulate, 0.5-0.8 cm long and 0.3-0.4 cm wide, margins entire or lobed into teeth; apices pointed, acute or obtuse (Pl. 3, figs 1-3); slightly katadromic at the base and anadromic after 3-5 pinnules upwards (Pl. 3, figs 2-3; Text-figure 3 A).

Venation — Pinnate, quite fine, midvein reaches to two thirds of the pinnules, lateral veins simple or forked once.

Fertile parts and sori — Fertile pinnae reduced (Pl. 3, figs 4-4b), typically 1.5 cm long and 0.4 cm wide. Fertile pinnules ligulate or falcated, 2-3 mm long and 1.5-2.5 mm wide, apices obtuse, margins slightly lobed into 3-4 pairs of teeth. Sori rounded or hood-shaped, about 0.5 mm high, 0.5 mm wide, marking 60^0-70^0 angle to the midvein, situated at the lateral veins or the anterior branches of the lateral veins (Pl. 3, figs 4b, 5; Text-figure 3 B); usually 2-3 pairs in each pinnule; arranged in two rows. Sorus consisting of about 20 sporangia.

Sporangia and spores — Sporangia elliptic in lateral view, 100-150 μm in diameter with stalks. Annulus vertical, incomplete, composed of 13 thickened cells (Pl. 3, figs 7-9), output 60-64 spores per sporangium. Spores bilateral, elliptic in polar view and kidney-shaped in equatorial view. Equatorial axis 25-35 μm long and polar axis 20-30 μm long. The ratio of the two axes about 1.4. Monolete, laesura 15-18 μm long. Exine smooth, slightly wrinkled.

Horizon and locality — Fuxin Formation, Fuxin Basin.

Athyrium hulunianum Chen, Ren et Deng

PLATE 4 ⟶

All specimens are housed in China University of Geosciences (Beijing). All figures are in natural size except where indicated. Scanning electron microscope pictures are marked with "SEM"

(All the specimens are from Yimin Formation, Zhalainuoer Basin, Inner Mongolia)

1-7. *Athyrium hulunianum* Chen, Ren et Deng

1. Fertile pinnae. 1a, enlargement of fig. 1.

2. Sterile pinnae. 2a, showing the rachis; 2b, showing the pinnule and venation.

3-5. Sori 3-4 x 20; 5, x 30.

6-7. Spores. x 280; x 1300.

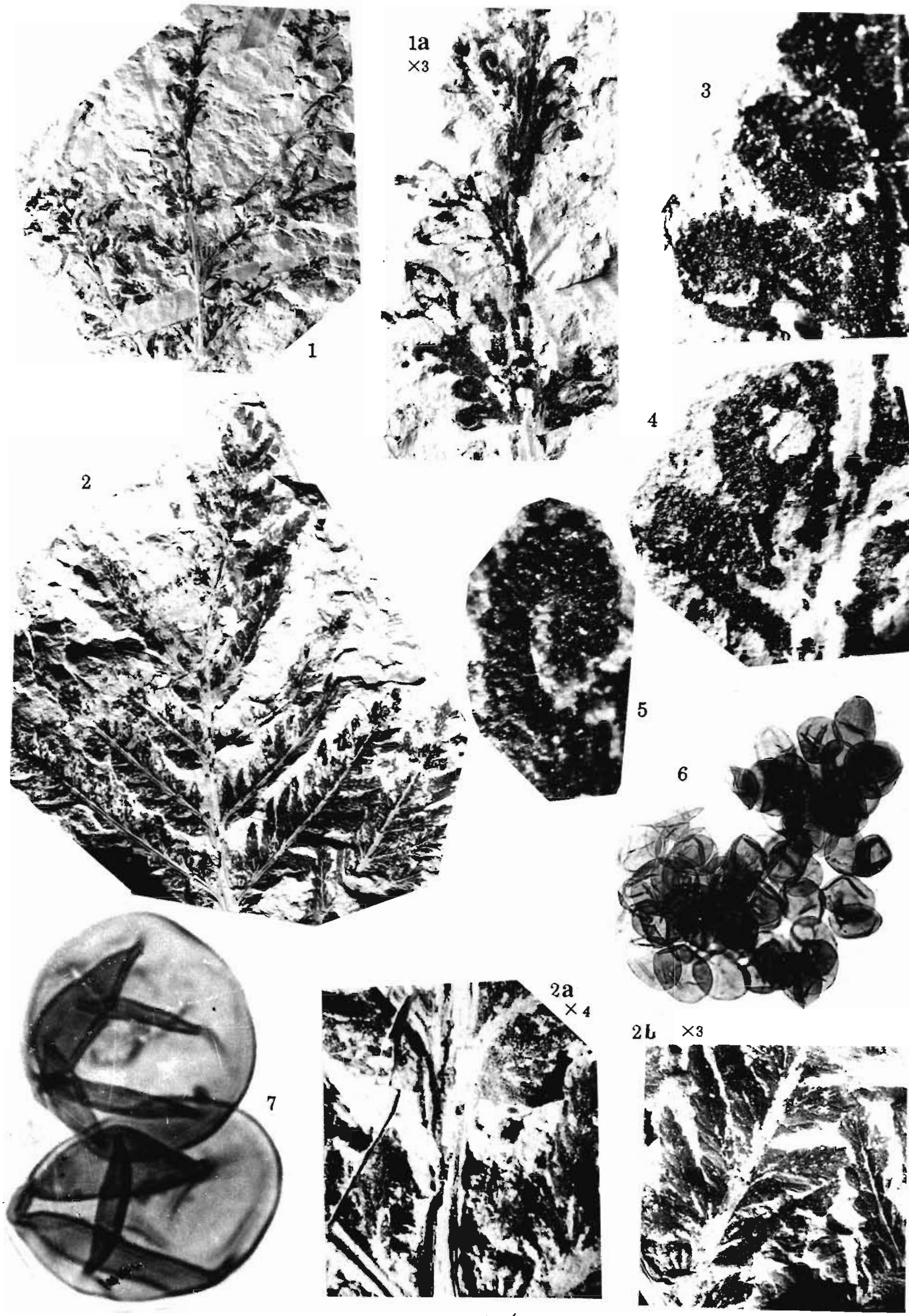


PLATE 4

Pl. figs 1-7; Pl. 5, figs 1-5; Text-figure 4

1993 *Athyrium huluntanum* Chen *et al.*, p. 562, pl. 1, figs 1-4, 9-11.

Frond — Medium size, triangular in outline, bipinnate at least, up to 8 cm long and 7 cm broad.

Rachis— Penultimate rachis quite strong, about 2-3 mm wide with a longitudinal ridge on the lower side; the ridge occupying one third of the rachis and expanded to about half of the rachis at the position where ultimate rachis arising (Pl. 4, fig. 2a); ultimate rachis 0.8 mm thick, abaxial side rounded, arising at acute angle, slightly decurrent at the base and curved forwards.

Pinnae and pinnules — Ultimate pinnae lanceolate, up to 3-5 cm long, 1-1.5 cm wide, apices acute, arising at angles of about 50^0, quite crowdedly arranged in opposite order (Pl. 4, fig. 2). Pinnules falcated, triangular or lanceolate, 1.0-1.2 cm long, 0.4 cm wide, widest at the base, slightly decurrent, apices tapering downwards, tip margins lobed into 6-8 pairs of teeth with acute apices. Pinnules attached at an angle of about 45^0 to the ultimate rachis, arranged in slightly katadromic order at the bases and anadromic after 4-5 pinnules upwards (Pl. 4, fig. 2). The first basiscopic pinnule decurrent, attached to the base of the pinna, close to its insertion.

Venation — Pinnate, midvein rather strong at the base, slender forwards and the apex usually flexuous. Lateral veins very slender, simple or forked once (Pl. 4, fig. 2b). The distal parts of the lateral veins usually thickened.

Fertile frond and sori — Fertile pinnae and pinnules are similar to the sterile ones. Sori borne on the abaxial surface of the pinnule, situated at the lateral veins or the anterior branches, 4-5 in a row on each side of the midvein, one in each tooth excluding the base ones which usually bear two. Sori on the lower part of the pinnule especially those at the base typically hoof or hook-shaped. The hoof-shaped ones symmetrical, 1.5-2.0 mm high and 1-1.5 mm wide. Of the hook-shaped ones, the side closer to the midvein parallel to the midvein and usually longer than the other part. Sori on the mid-upper region of a pinnule usually hook-like and those on the apices typically crescent-shaped or rectangular, 1-1.5 mm in length (Pl. 4, figs 1, 3-5; Text-figure 4 C). Sori with more than 60-80 sporangia.

Sporangia and spores — Sporangia typically rounded, a few elliptic in lateral view, about 180 μm in diameter or 150-180x180-200 μm in size, with long but thin stalks consisting of 3 files of cells (Pl. 5, figs 2, 4, 4a). Annuli incomplete, vertical, composed of about 13 thickened cells; stomium transverse (Pl. 5, figs 1-4; Text-figure 4E).

Spores bilateral, typically rounded or elliptic in polar view; equatorial axis 30-40 μm long and polar axis 25-35 μm long, the ratio of equatorial axis to polar axis 1.00-1.30, average 1.24; monolete, laesura 16-25 μm in length, exine smooth, usually with wrinkles on the surface (Pl. 4, figs 6-7; Pl. 5, fig. 5; Text-figure 4F).

Horizon and locality—Yimin Formation, Zhalainuoer Basin.

Athyrium hailaerianum Deng et Chen

Pl. 5, figs 8-9; Pl. 6, figs 1-6; Pl. 7, figs 1-11; Text-figure 5

1993 *Athyrium hailaterianum* Chen *et al.*, p. 563, pl. 1, figs 5-8, 12-13.

Frond— Small size, bipinnate, elongated triangular in outline, up to 4 cm long and 3 cm broad.

Rachis — Penultimate rachis quite slender, less than 1 mm thick, with a longitudinal groove on the upper side, two sides of the groove with sharp edges.

PLATE 5 ⟶

All specimens are housed in China University of Geosciences (Beijing). All figures are in natural size except where indicated. Scanning electron microscope pictures are marked with "SEM"

1-5. *Athyrium huluntanum* Chen, Ren et Deng

1-4. Sporangia. 1, (SEM), x 400; 2, sporangium with a stalk (SEM), x 330; 3, x 264; 4, sporangium with a stalk, 264; 4a, enlargement of fig. 4, showing the stalk, x 660.

5. Spores (SEM), x 1000.

6-7,10. *Athyrium filix-femina* (L) Roth.

6. Sporangium with a stalk, x 264.

7. Granulate spore (SEM). x 1200.

10. Sori, x 30.(Specimen of fig. 10 from Yunnan, Southeast China)

Athyrium hailaerianum Deng et Chen

8. Sterile pinna.

9. Sori. x 20 (Specimens of figs 8 and 9 are from Yimin Formation, Zhalainuoer Basin, Inner Mongolia).

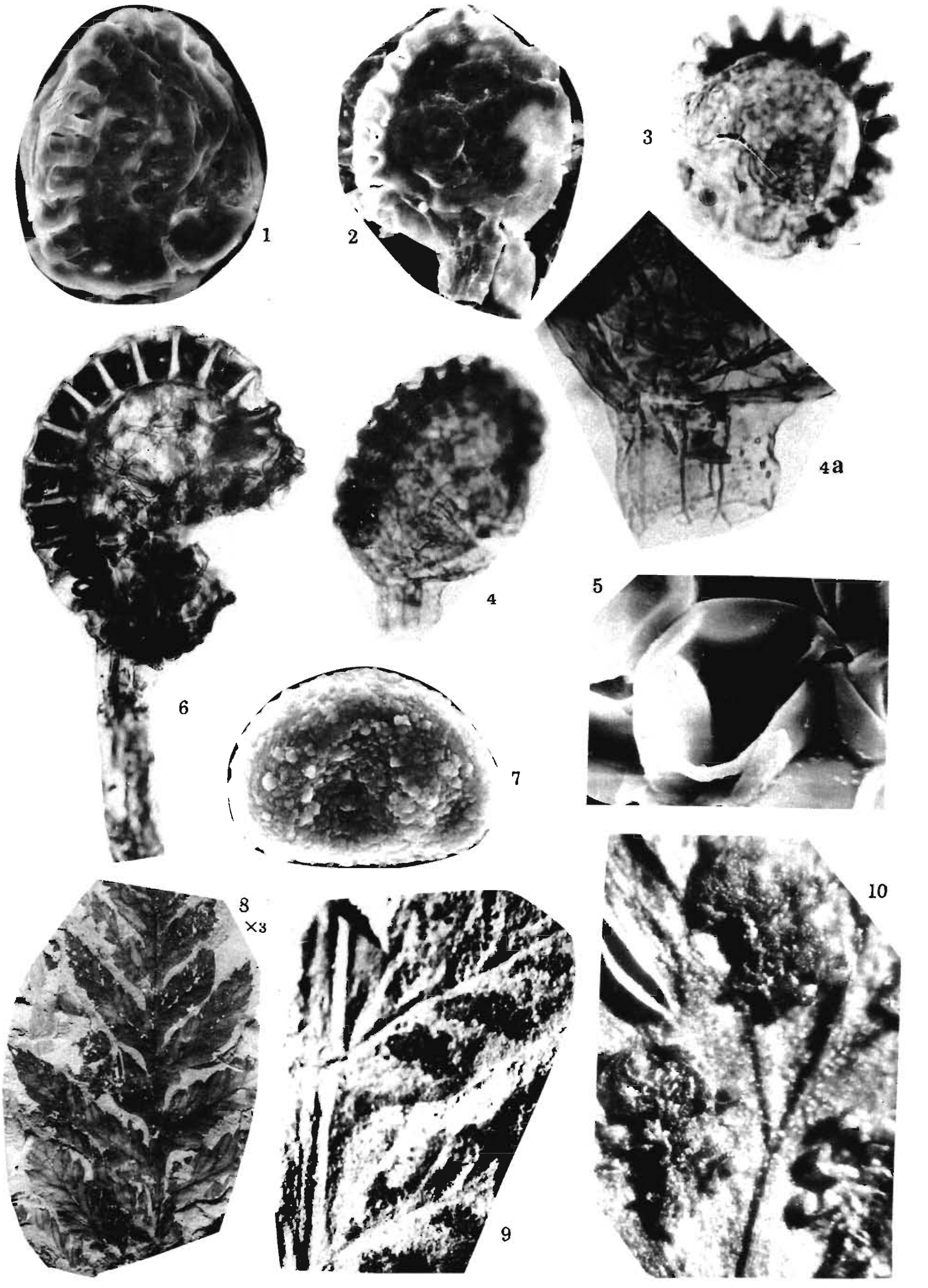
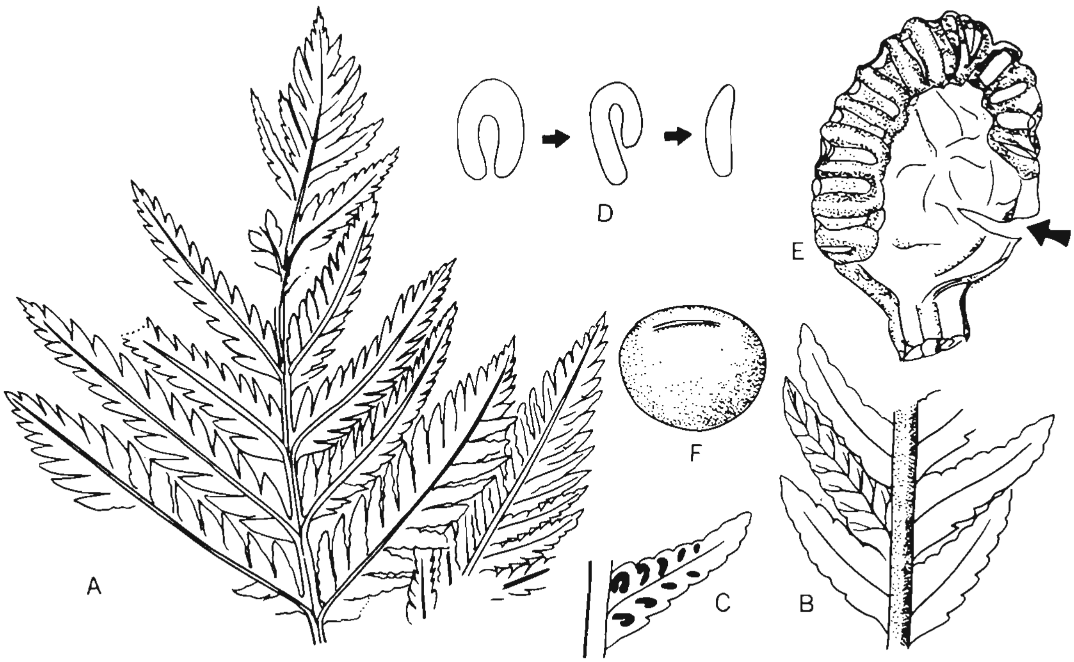


PLATE 5



Text-figure 4—*Athyrium hulunianum* Chen, Ren & Deng; **A**, sterile pinnae x 1; **B**, sterile pinnules showing venation x 3; **C**, fertile pinnule showing sori x 3; **D**, showing sorus x 15; **E**, sporangium showing annulus, the arrow shows stomium x 264; and **F**, spore x 600.

A fine longitudinal ridge of 0.2 mm broad on the lower side of the penultimate rachis. Ultimate rachis 0.2-0.5 mm thick, lower side convex with a fine ridge.

Pinnae and pinnules — Ultimate pinnae lanceolate, up to 5-6 cm long, 1.0-1.2 cm broad, alternately arranged, arising at angles of 40°-45° to the penultimate rachis, mid-upper part curved forward. Those on the apex of the frond slightly linear, usually 1-1.5 cm long and 0.2-0.3 cm broad, margins dissected into teeth with acute apices, alternately arising at angles of 30°, rather crowdedly arranged. Pinnules lanceolate, apices acute, 0.4-1.0 cm in length and 0.2-0.4 cm in width, widest at the base, margins dissected into lobes with acute apices, making acute angle to the ultimate rachis, arranged in katadromic order at the bases of pinna and anadromic order after 4-5 pinnules upwards.

Venation—Venation pinnate. Midvein very slender, flexuous, reaching to the apices of pinnules. Lateral veins simple, forked once or twice.

Fertile frond and sori—Fertile frond is similar to the sterile ones. Sori borne abaxially, situated at the lateral veins, arranged in two rows, half way to the margins, oblique to the midvein at angles of 30°-40°. Commonly 4-9 sori in a row (Pl. 6, figs 3-4), one in each tooth except some developed ones usually with two sori at the base of pinnules. Sori varies in shape. Generally, at the lower region of a pinnule, the sori usually rounded or hoof-shaped, about 1 mm in diameter (Pl. 7, fig. 4); at the mid-upper region, sori usually very curved as hoof or hook-shaped (Pl. 7, fig. 2); and those at the top of a pinnule rectangular, crescent or banana-like (Pl. 7, fig. 2). Therefore, from the base to the apex of a pinnule, the forms of sori

PLATE 6 →

All specimens are housed in China University of Geosciences (Beijing). All figures are in natural size except where indicated. Scanning electron microscope pictures are marked with "SEM"

(All the specimens in this Plate are from Yimin Formation, Zhalainuoer Basin, Inner Mongolia)

1-6. *Athyrium hailaerianum* Deng et Chen

1-2. Sterile pinnae.

3-4. Fertile pinnae. 3a enlargement of fig. 3 showing the sori.

5. Spores (SEM). x 1200.

6. Sporangia in one sorus (SEM). x 260.

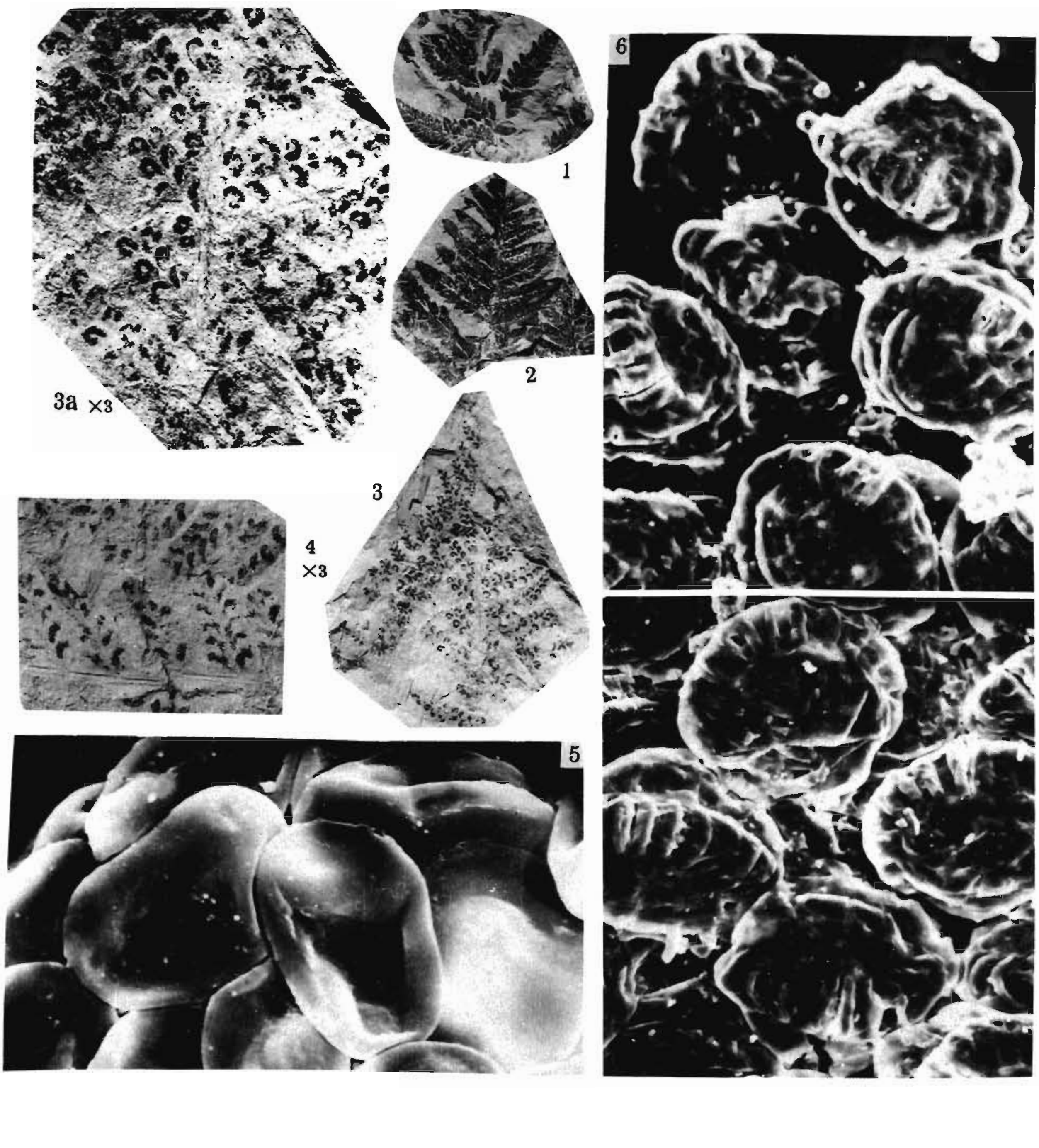


PLATE 6

changing gradually (Text-figure 5D) from rounded to crescent shape. In the upper region of a frond, sori usually crescent-shaped. One sorus comprises more than 80 sporangia (Pl. 7, fig. 1).

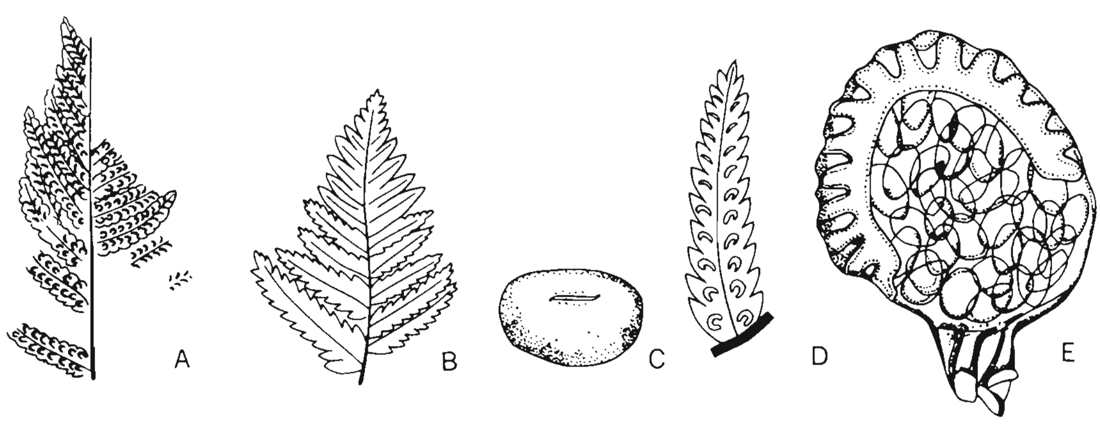
Sporangia and spores — Sporangia rounded or elliptic in lateral view, size about 120x180x200 μm, stalks about 20x40 μm in diameter, composed of 3 files of cells (Pl. 7, figs 7, 9; Text-figure 5E). Annulus vertical, incomplete, composed of 13-17 thickened cells. Stomium transverse (Text-figure 5E). Each sporangium comprises about 64 spores. Spores monolete, typically elliptic in polar view except a few rounded ones. The polar axis 22-25 μm (average 22.6 μm) long and the equatorial axis 30-35 μm (average 30.6 μm) long. The ratio of two axes 1.35. Laesura 13-20 μm long. Exine smooth, wrinkled (Pl. 7, figs 5, 10; Text-figure 5C).

Horizon and locality—Yimin Formation, Zhalainuoer Basin.

DISCUSSION

Four species described above can be distinguished from each other. *Athyrium hulunianum* is characterized by its strong rachis and oppositely arranged pinnae, and especially its large, hoof and hook-shaped sori. *A. hailaerianum* is distinct in its smaller size, slender rachis and a large number of sori which are gradually variable in forms from lower to upper regions of a pinna or a pinnule. *A. fuxinense* is the only one whose fertile pinnules are smaller than sterile ones. It can also be identified by its ligulate fertile pinnules and rounded or hook-like sori which are fewer in number and smaller in size. *A. cretaceum* is characterized by smaller size, triangular pinnules and regular hoof-like sori.

These four species show a similar pinnule arrangement of katadromic order at the base of a pinna and anadromic after 4-5 pinnules upwards. The sporangia of these species show similarity with each other. But those of *A. hulunianum* are relatively globular or rounded in lateral view and a little larger than that of the others. The annuli of all these species are vertical and composed of 13-17 thickened cells, commonly 13. The sporangia possess long but slender stalks which are composed of 3 tier of cells as shown in *A. hulunianum* and *A. hailaerianum* (Pl. 5, fig. 4; Pl. 7, fig. 9). It seems that



Text-figure 5 —*Athyrium hailaerianum* Deng & Chon; **A**, fertile frond x 1; **B**, sterile frond x 1; C, spore x 1; **D**, fertile pinnule showing the sori x 3; and **E**, sporangium showing the annulus, stalk and spores in the sporangium x 264.

PLATE 7 ⟶

All specimens are housed in China University of Geosciences (Beijing). All figures are in natural size except where indicated. Scanning electron microscope pictures are marked with "SEM"

1-11. *Athyrium hailaerianum* Deng et Chen

1. Sporangia in one sorus. x 110

2-4. Sporangia at different positions of a pinnule. x 30.

5,10. Spores (SEM). x 600; x 1500.

6-9, 11. Sporangia. 6-7 (SEM), x 450; 7a (SEM), showing the stalk, x 600; 8-9, x 264; 9a, showing the stalk, x 800, 11 (SEM), x 450.

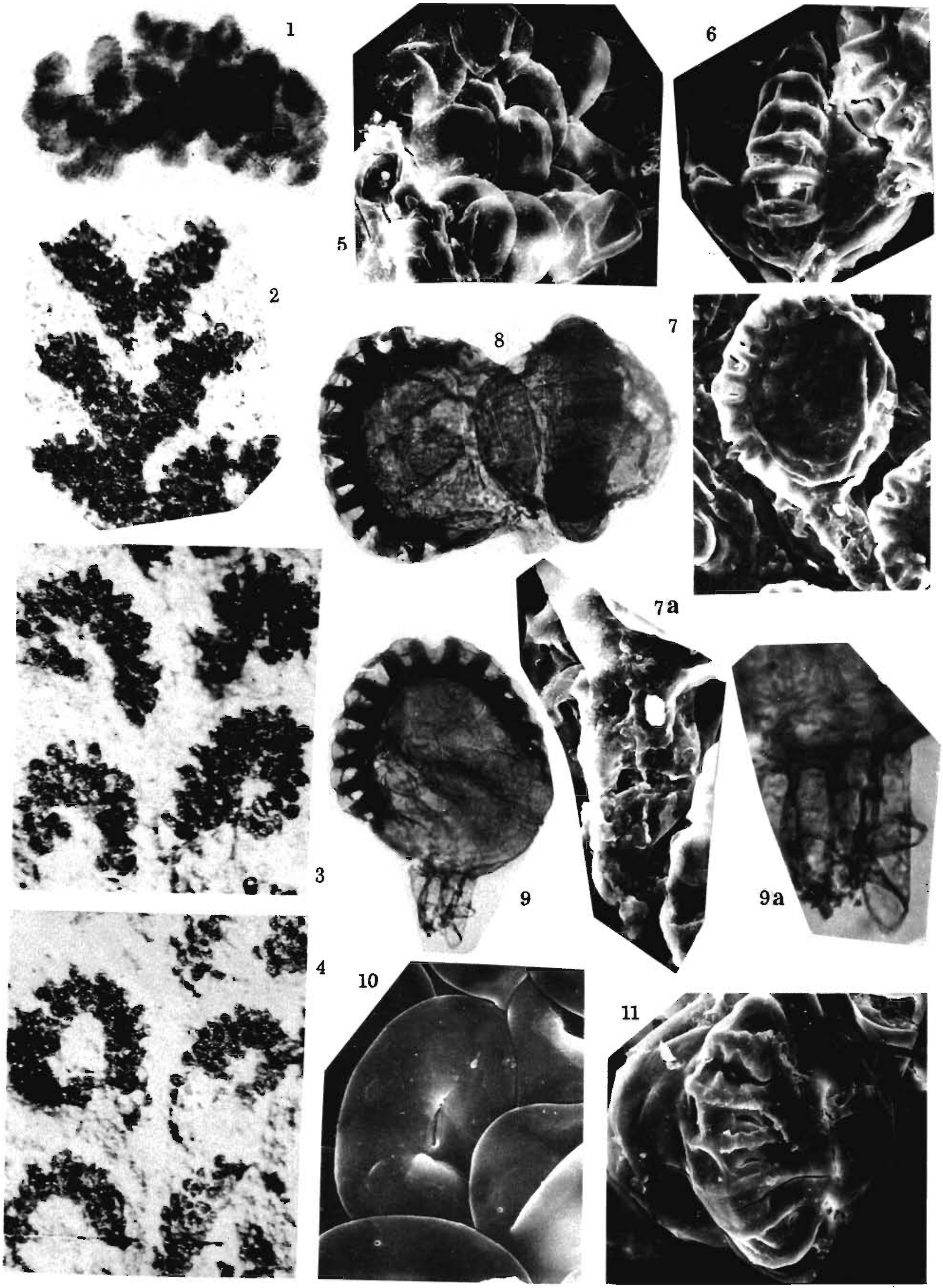


PLATE 7

a single sporangium bears 64 spores, although in some cases it is determined to be less than this number. Spores of the four species are quite similar in shape excluding those of *A. huluntanum* which are rather rounded (Pl. 4, fig. 7; Pl. 5, fig. 5).

The present fossils can be closely compared with the extant *Athyrium* especially in the sori, indusia, sporangia, annuli and spores. Although the sori and indusia of the extant *Athyrium* are variable in forms, they are typically hook or hoof-shaped, occasionally linear or crescent-shaped as well as that of the fossils. The indusia of the extant *Athyrium* are usually broken or dispersed on the maturity of sori. Additionally, the morphology of sterile portions of the fossils shows closeness to some species of extant *Athyrium*.

Of the living *Athyrium*, *A. filix-femina* (L) Roth, *A. sinense* Rupr. and *A. brevifrons* Nakai can be compared most closely with the fossil species. *A. filix-femina*, the generic type, widely distributed over Europe, North America and Asia, is close to *A. cretaceum* on the outlines of its fronds and pinnules. The pinnules of *A. filix-femina* are characterized by their triangular-lanceolate forms, acute apices, slightly contracted bases and dissected margins. Usually, a single developed pinnule of *A. filix-femina* has 5-8 pairs of sori, generally one sorus in each tooth. The shapes of the sori change gradually from the lower to upper regions of a pinnule as from hoof or hook to crescent or strip-shaped as well as that of *A. hailaerianum*. *A. sinense* and *A. brevifrons* which have limited geographic distribution in Northeast China are also similar to the fossils in the outlines of the pinna, the pinnules and the sori, especially the variance of sori. The pinnules of these living species are arranged in katadromic order at the base of pinnae and in anadromic order after 4-5 pinnules upwards as in present fossils. In *A. filix-femina*, the pinnule arrangement is shown on several specimens from the United States, Sweden, Poland, Switzerland and China. The sporangia of the living *Athyrium* are elliptic or globular, about 200 μm in diameter (Pl. 7, fig. 6), with stalks of 180-200 μm long. The stalks consist of 3 files of cells. The annuli are vertical type and composed of 13-16 thickened cells. But the annulus of *A. filix-femina* extends up to the stalk (Pl. 7, fig. 2). The spores are monolete as that of the fossils but their exine or perine are usually sculptured with granules (Pl. 7, fig. 5).

Dryopteris, a monolete spore fern, is close to the present fossils on the basis of morphology of frond, pinnae and somewhat pinnules, but its sori and indusia are typically circular or rounded-kidney shaped. The kidney-shaped indusium is usually with a sinus on its back. Moreover, the exine or perine of spores are commonly sculptured with rugulae (Zhang *et al.*, 1976; Wu & Ching, 1991).

In *Asplenium*, the sori are typically elongate or crescent-shaped and therefore can be distinguished from *Athyrium*.

A specimen of an ultimate pinna from the latest Cretaceous-Early Tertiary deposits of Northeastern Washington, America, was described as *Athyrium gracilium* Pabst (Pabst, 1968). Its pinnules are much larger than that of the present specimens. The specimen differs greatly from the extant *Athyrium* in having elongate sori. *Polypodites polysorus* Prynada from the Omusukchan, Russia (Samylina, 1976; pl. 12, figs 1-3) possesses crescent or hook-shaped or elongate sori as those of *A. hailariaenum*. An Early Cretaceous fossil from south Primorie, Russia identified as *Asplenium samylina* Krassil. (Krassilov, 1967; pl. 21, figs 1-7) is characterized by its rounded hook or crescent-shaped sori as well as those of *Athyrium hailariaenum*. The specimens both from Omusukchan and South Primorie probably belong to *Athyrium*.

Eogymnocarpium sinense Lee et Yhe (Li *et al.*, 1986) referred to Athyriaceae has similarities with the presen specimens on the outline of leaves, but differs from *Athyrium* in its rounded or elliptic sori, oblique annuli and a wide range of spores (48-128 in number). Moreover, its pinnules are larger than that of the present specimen.

PALAEOECOLOGY

The studied specimens mainly belong to the flood-plain or lacustrine facies sediments, such as mudstone and muddy siltstone. Most of them were preserved as single leaf and in very few cases several leaves preserved together.

The fossils are usually found in association with fern like *Acanthopteris gothanii* Sze, *Coniopteris concinna* (Heer) Chen *et al.*, *Cladophlebis* spp. and gymnosperms such as *Pterophyllum liaoningense* Meng et Chen, *Nilssonia* spp. and *Ginkgo manchurica* (Yabe et Oishi) Meng et Chen. This indicates that the remains of *Athyrium* were not preserved in the original place where they were growing. But since the fossils are well preserved, they had not been tansported for a long distance before being fossilized. As the pinnae are typically arranged at quite wide intervals, the basal pinnae are usually asymmetrical and the fronds commonly in triangular shape. *Athyrium* is possibly a shade loving fern probably living in woodlands.

According to the palaeomagnetic study, the Early Cretaceous *Athyrium* has only been discovered in Northeastern China and Russia. Northeastern China is close to the present area in latitude in the Early Cretaceous (Fan, 1990) and belongs to the temperate phytogeographical province and in the temperate zone (Chen *et al.*, 1988; Chen, 1990). The vegetation is dominated by Ginkgoales and long leaf Coniferales. Meanwhile, *Athyrium* has also not been found in lower latitude areas, such as North China and South China which represent semiarid or hot-dry palaeoclimate in Early Cretaceous. According to the palynological information, the distribution of dispersed monolete spores from the Lower Cretaceous was controlled by temperate-humid climate in time and space (Deng, 1995). They were mainly distributed in Northeast China. Consequently, the Early Cretaceous *Athyrium* is possibly a thermophilic and hygrophilous fern.

The extant *Athyrium*, having more than 200 species, are typical temperate ferns distributed in the temperate zone and high mountains in the subtropics. Most of them live in woodlands in the Himalayan area, China and Japan, especially the mountain areas of Yunnan, Southwest China. The type species *A. filix-femina* is widespread especially in moist woodlands, along stream banks and in rainy region extending to a considerable altitude on mountains (Page, 1982). The ecological characters of early *Athyrium* are similar to the living genus.

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