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Additional data on *Todites* (Osmundaceae) from the Lower Jurassic with special references to the paleogeographical and stratigraphical distributions in China

Considérations sur la distribution paléogéographique et stratigraphique du genre *Todites* (Filicales Osmundaceae) en Chine sur la base de nouvelles données du Jurassique inférieur

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Abstract

Additional material of *Todites* (Osmundaceae) from the Lower Jurassic Xiangshan Group in Jiangsu and Anhui Provinces, Eastern China is investigated. Five species of *Todites* are described based on collections (including sterile and fertile pinnae) from eight localities along the Yangtze River, including *Todites denticulatus* (Brongniart) Krasser, *Todites* cf. *goeppertianus* (Muenster) Krasser, *Todites nanjingensis* sp. nov., *Todites princeps* (Presl) Gothan and *Todites* sp. Material of *T. denticulatus* and *T. nanjingensis* sp. nov. contains further data of the fertile pinnae. The stratigraphical ranges and the geographical distribution of the genus *Todites* in China are discussed and reviewed. Available data show that *Todites* mostly occurs in the Late Triassic to Middle Jurassic of China. The genus was widely distributed in both the Northern and Southern Floristic Provinces of China, and especially abundant and diverse in the Southern Floristic Province.

Résumé

De nouveaux matériels du genre *Todites* (Osmundaceae) provenant du Jurassique inférieur de l'Est de la Chine sont étudiés. Cinq espèces de *Todites* sont décrites à partir des collections des provinces de Jiangsu et Anhui. Elles comprennent à la fois les pennes stériles et fertiles. Il s'agit de *Todites denticulatus* (Brongniart) Krasser, *Todites* cf. *goeppertianus* (Muenster) Krasser, *Todites princeps* (Presl) Gothan, *Todites nanjingensis* nov. sp. et *Todites* sp. Nous proposons une discussion et une révision de la distribution phytogéographique du genre *Todites* en Chine. Le genre *Todites* est distribué du Trias supérieur au Jurassique moyen. Ce genre est largement représenté dans les deux Provinces floristiques chinoises (nord et sud). Il est particulièrement abondant et diversifié dans la Province floristique du sud. © 2005 Elsevier SAS. All rights reserved.

Keywords: Osmundaceae; Todites; Paleogeographical distribution; Early Jurassic; China

Mots clés : Osmundaceae ; Todites ; Distribution paléogéographique ; Jurassique inférieur ; Chine

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1. Introduction

The family Osmundaceae is among the most primitive ferns of the Filicales, and consists of three extant genera (Osmunda, Todea and Leptopteris) and over 20 species (Hewitson, 1962). The family is regarded as intermediate between the more primitive eusporangiate ferns and the derived leptosporangiate ferns, and is therefore of particular interest in terms of evolutionary significance. This family has an extensive fossil record that can be traced from the Late Paleozoic (Permian), and over 150 fossil species have been documented (Tidwell and Ash, 1994). Most of them are based on compressed foliage, about 20 are represented by sporangia and spores (Miller, 1971; Van Konijnenburg-Van Cittert and Morgans, 1999; Van Konijnenburg-Van Cittert, 2002), and approximately 50 or more are known from permineralized stems (Miller, 1971; Tidwell and Ash, 1994; Collinson, 1996). During the Mesozoic, fossils of Osmundaceae are recorded in both the Northern and Southern Hemispheres with the foliage represented by three genera, Todites, Osmundopsis (fertile foliage) and partly Cladophlebis (sterile foliage).

Osmundaceous ferns are very abundant during the Mesozoic of China, including the common foliage genera *Todites*, *Osmundopsis* and *Cladophlebis* as well as fossil rhizomes (e.g. *Osmundacaulis* and *Millerocaulis*). Among them, *Todites* is one of the most widespread. So far, about 17 species of *Todites* have been recorded in the Mesozoic deposits of China. The lack of evidence from fertile material for many of these, however, means that the identification of some species is still open to question. The purpose of this article is to describe additional material of *Todites* based on collections from the Lower Jurassic Xiangshan Group in Anhui and Jiangsu Provinces, eastern China. Furthermore, the stratigraphical range and the geographical distribution of *Todites* in China are reviewed and discussed in detail.

2. The Lower Jurassic Xiangshan Flora and the fossil diversity

The Early and Middle Jurassic deposits along the Yangtze River in Jiangsu and Anhui Provinces, eastern China are named the "Xiangshan Group". This group is well known for rich plant fossils that are preserved in the lower part, i.e. the "Xiangshan Flora", one of the important Early Jurassic floras in Southern China phytoprovince.

According to previous investigations (Cao, 1982, 1998, 2000; Huang, 1983, 1988) and our collections, the Early Jurassic Xiangshan Flora in Jiangsu and Anhui Provinces is composed of over 70 species of about 30 genera, representing the Equisetales, Filicales, Cycadales, Bennettitales, Ginkgoales and Coniferales. This flora is dominated by Cycadophytes (Cycadaleans and Bennettitaleans: *Nilssoniopteris, Ptilophyllum, Otozamites, Tyrmia, Nilssonia* and *Pterophyllum*). Ginkgoales and ferns rank second in abundance; the former including *Sphenobaiera, Baiera, Ginkgoites* and *Desmiophyllum*.

Equisetales are not abundant and are represented by *Equisetites* and *Neocalamites* only. Conifers are rare, including *Pityophyllum, Podozamites, Elatocladus* and *Swedenborgia. Pachypteris* is the only Pteridosperm element of this flora.

Ferns are one of the important and diverse groups of the Xiangshan Flora, and are represented by members of the Marattiaceae, Osmundaceae, Matoniaceae, Dipteridaceae and Dicksoniaceae. Nine genera have been documented: *Marattia, Todites, ?Osmundopsis, Phlebopteris, Coniopteris, Dictyophyllum, Clathropteris, Thaumatopteris* and *Cladophlebis*. In composition, the present Xiangshan Flora is generally consistent with the Early Jurassic Hsiangchi Flora well developed along the Yangtze River in western Hubei, one of the most famous early Mesozoic floras in China (Sze, 1949; Wu et al., 1980; see also Wang, 1999, 2002). According to Cao (1982, 1998, 2000) and Huang (1983), the geological age of the Xiangshan Flora is middle–late Early Jurassic.

Detailed investigations on the Xiangshan Flora are still scarce, only some taxa were briefly described and illustrated based on limited materials (Sze, 1931; Cao, 1982; Wang et al., 1982; Huang, 1983, 1988). In recent years, Cao (1998, 2000) studied the cuticular structures of gymnospermous material, including the cycadalean *Nilssonia*, the bennettitaleans *Nilssoniopteris*, *Otozamites*, *Tyrmia*, *Ptilophyllum*, *Pterophyllum* and *Anomozamites*, and the ginkgoalean *Baiera*.

3. Biostratigraphy

The Xiangshan Group is widely distributed along the Yangtze River in Anhui Province (including Susong, Taihu, Huaining, Zongyang, Tongcheng, Lujiang, Wuwei, Caoxian, Hanshan, Tongling, Wuhu and Dangtu Counties) and Jiangsu Province (including Nanjing, Zhenjiang, Changzhou, Yangzhou and Jiangdu Cities) (Fig. 1). The name "Xiangshan Group" was derived from the "Xiangshan Bed" that was originally used for the Jurassic strata in Nanjing area, Jiangsu Province (Li et al., 1935). In this area, the group was divided into two parts based on lithological characters: the lower part, the "coal bearing strata" is named as the "Nanxiangshan Formation"; the upper part, consisting of "variegated sandstones and shales", is called the "Beixiangshan Formation" (Ju, 1987) (Table 1). They have been considered to be Early Jurassic and Middle Jurassic in age, respectively.

The Early and Middle Jurassic strata that crop out along the Yangtze River in the An-Qing area of southern Anhui Province are lithologically similar to those from the adjacent Nanjing area with a separate subdivision scheme, i.e. the Moshan Formation for the lower part of the Group and the Luoling Formation for the upper part, respectively (Wan, 1981, 1987). The subdivision and correlation of the Xiangshan Group in Jiangsu and Anhui Provinces are summarized in Table 1.

The biota in the upper part of the Xiangshan Group are mainly represented by fauna of fluviolacustrine origin. According to Wan (1987), fossil conchostraca are found in the Luoling Formation in Huaining of Anhui Province, includ-



Fig. 1. Sketch map showing the distribution of the Early–Middle Jurassic Xiangshan Group and the localities of fossil *Todites* along the Yangtze River in Aanhui and Jiangsu Provinces, Eastern China. 1. Maoling of Susong, Anhui; 2. Xincang of Taihu, Anhui; 3. Shuangdian of Tongcheng, Anhui; 4. Lintou of Hanshan, Anhui; 5. Huashan of Dangtu, Anhui; 6. Cangbomen of Nanjing, Jiangsu; 7. Shifoan of Nanjing, Jiangsu; 8. Zhuanqiao of Jiangdu, Jiangsu. Fig. 1. Carte de répartition des gisements du Jurassique inférieur et du Jurassique moyen du Groupement Xiangshan et localités à *Todites* le long de la rivière Yangtze dans les provinces du Aanhui et du Jiangsu. 1. Maoling de Susong, Anhui ; 2. Xincang de Taihu, Anhui ; 3. Shuangdian de Tongcheng, Anhui ; 4. Lintou de Hanshan, Anhui ; 5. Huashan de Dangtu, Anhui ; 6. Cangbomen de Nanjing, Jiangsu ; 7. Shifoan de Nanjing, Jiangsu ; 8. Zhuanqiao de Jiangdu, Jiangsu.

ing *Psilunio sinensis*, *Lamprotula cremeri*, *Cuneopsis sichuanensis* and *Undulatula* sp., which are index fossils of the Middle Jurassic in northern and southern China. Fossil assemblages of ostracoda (*Darwinella*), charophytes (*Euaclistachara*) and gastropods (*Amniala*) from this formation also indicate a Middle Jurassic age. Furthermore, fossil pollen and spores were recently reported from the dark purple red silty shales of the upper part of the Xiangshan Group, i.e. the Beixiangshan Formation, in Nanjing area (Huang, 2001). The assemblage of 77 species and 37 genera of pollen and spores suggest a Middle Jurassic age for this formation.

The lower part of the Xiangshan Group contains the characteristic Early Jurassic plants, i.e. the Xiangshan Flora, whereas fossil fauna are very rare. This part of the strata is characterized by limnetic deposits with coal measures. In the An-Qing area of Anhui Province, the Moshan Formation attains a thickness of 649.3 m. Taking this section as an example, the lower member of the Moshan Formation is com-

Table 1

The subdivision and correlation of the Early-Middle Jurassic Xiangshan Group in Jiangsu and Anhui Provinces, eastern China Subdivision et corrélation du Jurassique inférieur et moyen du Groupement Xiangshan dans les Provinces du Jiangsu et du Anhui, Chine de l'Est.

Group	Ages	Lithology	Jiangsu Province	Anhui Province	Fossils		
			(Nanjing and its vicinity)	(An-Qing region)			
Lower-	Middle	Upper part: variegated	Beixiangshan Fm.	Luoling Fm.	Fossil conchostraca, ostracoda,		
Middle Jurassic	Jurassic	sandstone and shales	(= former "Xishansi Fm".)	(= former "Ziliujing Fm".)	gastropods and charophytes; pollen and spores		
Xiangshan	Early	Lower part:	Nanxiangshan Fm.	Moshan Fm.	Plants (i.e. the Xiangshan Flora)		
Group	Jurassic	coal-bearing strata	=former "Lingyuan Fm" and	(= former "Wuchang Fm".)			
			"Zixiadong Fm".				



Fig. 2. Lithostratigraphy and fossiliferous horizons of the Lower Jurassic Moshan Formation (the lower part of the Xiangshan Group) in Huaining, Anhui Province (Drawn based on data of Wan, 1987). **1**. Mudstones; **2**. Dark colored shales; **3**. Coal seams; **4**. Muddy siltstones; **5**. Siltstones; **6**. Fine grained sandstones; **7**. Sandstones; **8**. Conglomerates or conglomeratic sandstones; **9**. Mudstone lenticels; **10**. Plant fossil horizon; **11**. Fossil fauna horizon.

Fig. 2. Lithostratigraphie et horizons fossilifères de la Formation Moshan du Jurassique inférieur (partie inférieure du Groupe de Xiangshan) à Huaining, Province d'Anhui (dessin d'après des données de Wan, 1987).
Province d'Anhui (dessin d'après des données de Wan, 1987).
Mudstones;
Shales de couleur sombre;
Veine de charbon;
Silstones boueux;
Silstones;
Sandstones à grains fins;
Sandstones;
Bonglomératiques;
Lentilles de mudstones;
Horizons à plantes fossile;

posed of quartzose sandstones with intercalations of carbonaceous shales and siltstones. The upper member of the formation is dominated by sandy shales and siltstones, with little quartzose sandstones, yielding several layers of thin coal seams (Fig. 2). Abundant fossil plants occur in this horizon of the Moshan Formation in Anhui and the equivalent Nanxiangshan Formation in Jiangsu Province.

4. Material, localities and occurrence

About 20 specimens of *Todites* were collected from the Jurassic Xiangshan Group in eight localities. They came from the Lower Jurassic Moshan Formation in Maoling of Susong County, Xincang of Taihu County, Shuandian of Tongcheng County, Lintou of Hanshan County and Huashan of Dangtu County in Anhui Province, as well as the Nanxiangshan Formation in Canbomen and Shifoan of Nanjing City, and Zhuanqiao of Jiangdu City in Jiangsu Province (Fig. 1).

Almost all specimens were collected from outcrops; only one specimen of *Todites princeps* came from a borehole. Specimens are preserved as impressions on the grayish black and yellowish white shale or siltstone matrix. In some specimens of *Todites denticulatus*, bipinnate fronds are preserved on both the front and back faces of a slab. Most of the specimens are preserved as bipinnate fronds bearing main rachis and pinnae that are essential for identification and comparison. The venation of the pinnule is well preserved and distinct. In some specimens, fertile or both fertile and sterile fronds are preserved (e.g. *T. denticulatus* and *T. nanjingensis* sp. nov.). Specimens described and figured in this paper are housed in the Paleobotany Collection, Nanjing Institute of Geology and Paleontology, CAS, Nanjing, China with registration numbers from PB19795 to PB19809.

5. Descriptions of the material

Order FILICALES.

Family OSMUNDACEAE.

Genus Todites Seward, 1900, emended Harris, 1961.

Todites denticulatus (Brongniart) Krasser.

Figs. 3(1–7); 4(A–F) and 5(1).

Selected references:

1828. *Pecopteris denticulata* - Brongniart, p. 301, Pl. 28, Fig. 3.

1900. *Cladophlebis denticulata* - Seward, p. 134, Pl. 14, Figs. 1,3,4.

1911. *Cladophlebis denticulata* var. *punctata* - Thomas, p. 64.

1961. *T. denticulatus, Cladophlebis denticulata* - Harris, p. 78, Text-figs. 25–27.

1963. Cladophlebis punctata - Sze et al., p. 106.

Description: There are 10 specimens in our collection belonging to *T. denticulatus* (Brongniart) Krasser. Both sterile and fertile leaves are preserved. They are generally of similar size and shape, but pinnules are dimorphic. In most cases, specimens are preserved as part of a bipinnate frond (e.g. Figs. 3(1, 2, 4) and 4(A-F)). In Fig. 3(4), two frond fragments are preserved together in a slab, one is sterile and the other one is fertile. Two sterile frond fragments also occur in a specimen (Fig. 5(1)), and the pinnae are irregularly curved due to the compression during the fossilization.

The sterile leaf is at least bipinnate. The lamina as a whole is lanceolate, gradually narrow towards apex. The main rachis is thick, up to 5.5 mm wide, bearing on the surface many fine longitudinal striations or irregular raised pitting (Fig. 3(1-3)and 4(F)), which are probably the impressions of bristles or spines. Pinnae are lanceolate, arising from the main rachis at intervals of about 2 cm, forming a wide angle, occasionally 45° to the main rachis (Fig. 3(1, 2, 4); 4(F) and 5(1)). Pinnae rachis is thin, attaining a width of 0.5–1.0 mm, with fine raised longitudinal ridges and small raised pitting on surface. Pinnae are alternate or almost subopposite. Pinnules are falcate and slightly larger on the lower side of the pinna than on the



Fig. 3. *Todites denticulatus* (Brongniart) Krasser. 1, 2. Partly preserved sterile fronds showing pinnae, pinnules and thick main rachises. 1. PB19795, from Xincang of Taihu, Anhui Province. Scale bar = 1 cm. 2. PB19796, from Maoling of Susong, Anhui Province. Note the fine longitudinal striations on the main rachis surface. Scale bar = 1 cm. 3. Detail of 2, showing the shape and size of pinnules, specialized basiscopic pinnules and the dentate margins of pinnules (arrows). Scale bar = 0.5 cm. 4. A sterile frond (A) and a fertile frond (B) preserved in the same slab. PB19797. Scale bar = 1 cm. 5. Detail of 4, showing the



Fig. 4. Sterile fronds of *Todites denticulatus* and venation (Scale bars = 1 cm). A. A specimen representing the upper part of a pinna. PB19800; B. A small specimen representing the upper part of a pinna. PB19801; C. A partly preserved frond with two pinnae. PB19802; D. Detail of B showing the midrib and the bifurcating of lateral veins. E. A small specimen with rachis and the pinnules with marginal teeth. PB19803; F. A specimen representing the lower part of a frond. Note the longitudinal striations on the main rachis. The reverse side of PB19797 in figure 3(4).

Fig. 4. Frondes stériles et nervation des pinnules de Todites denticulatus (Échelle = 1 cm). A. Spécimen représentatif d'une partie apicale de pinne. PB19800. B. Petit échantillon de la partie supérieure d'une penne. PB19801. C. Fronde préservée partiellement avec deux pennes. PB19802. D. Détail de B visualisant la nervure principale et les nervures latérales bifurquées. E. Petit échantillon avec rachis et pinnules à bordures marginales dentées. PB19803. F. Échantillon de la partie basale d'une fronde. Remarquez le rachis principal longitudinalement strié. Face opposée de PB19797 figure 3(4).

upper one. The first pinnule is specialized. It arises at a right angle from the pinna rachis on the basiscopic side (catadromic), and is close to the main rachis (Fig. 3(1-3)). The basal lower part of the pinnule is contracted, whereas the upper side is expanded. The apex is rather narrow, acute and usu-

ally has a dentate margin (Fig. 3(3)). Ultimate pinnules are alternate to opposite, arising at an angle of 60° – 70° from the pinna rachis. In the upper part of leaf, pinnules are smaller and relatively shorter, and are more forward-pointing. Basal pinnules on the basiscopic side are somewhat specialized, aris-

fertile pinnae, shape and size of fertile pinnules. Note that the surface of pinnules is waved. Scale bar = 0.5 cm. 6. Several fertile pinnae preserved in a slab. These pinnae may represent the middle to upper part of a frond. PB19798. Scale bar = 1 cm. 7. Detail of a pinna in 6 (left side, A) showing the size, shape and marginal teeth (arrows) of fertile pinnules. Scale bar = 1 cm.

Fig. 3. *Todites denticulatus* (Brongniart) Krasser. **1**, **2**. Fronde stérile en partie préservée montrant un rachis principal épais et deux pennes portant les pinnules. **1**. PB19795, Xincang de Taihu, Province de Anhui. Échelle = 1 cm. **2**. PB19796, Maoling de Susong, Province de Anhui. Remarquez la fine striation longitudinale à la surface du rachis principal. Échelle = 1 cm. **3**. Détail de l'illustration 2 montrant la forme et la taille des pinnules, les pinnules basiscopiques spécialisées et la marge dentées (flèches) des pinnules. Échelle = 0,5 cm. **4**. Fronde stérile (A) et fronde fertile (B) préservées sur le même échantillon. PB19797. Échelle = 1 cm. **5**. Détail de l'illustration 4, montrant une penne fertile avec la taille et la forme des pinnules fertiles. La surface des pinnules est ondulée. Échelle = 0,5 cm. **6**. Nombreuses pennes fertiles préservées. Ces pennes représentent la partie médiane et apicale de la fronde. PB19798. Échelle = 1 cm. **7**. Détail d'une penne de l'illustration 6 (partie gauche) montrant en détail la taille, la forme et les dents marginales (flèches, A) d'une pinnule fertile. Échelle = 1 cm.



Fig. 5. *Todites denticulatus* (Brongniart) Krasser, *Todites* cf. *goeppertianus* (Muenster) Krasser and *T. nanjingensis* sp. nov. 1. Two sterile fronds of *Todites denticulatus*. Note that the pinna becomes irregularly curved due to the compression during the fossilization. PB19799. Scale bar = 1 cm. 2, 3. *Todites* cf. *goeppertianus*. 2. A small but well preserved specimens showing two sterile pinnae. PB19804. Scale bar = 1 cm. from Daijiaku of Nanjing, Jiangsu Province. 3. Detailed of 2 showing the shape, size and venations of pinnules. Scale bar = 0.5 cm. 4-7. *T. nanjingensis* sp. nov. 4. A sterile leaf showing opposite to subopposite pinnae. PB19805. Scale bar = 1 cm. 5. A small fertile pinnae. PB19806. Scale bar = 1 cm. 6. A typical frond fragment showing the sterile pinnae (the upper part) and the attached three fertile pinnae (the right lower side). Type specimen. PB19807. Scale bar = 1 cm. 7. Detail of 6, showing the main rachis, sterile pinnae, the shape and size of pinnules as well as pinnule venation. Scale bar = 0.5 cm. Specimens of 4 and 5 from Daijiaku of Nanjing, type specimen (6) from Shifo'an of Nanjing, Jiangsu Province.

Fig. 5. *Todites denticulatus* (Brongniart) Krasser, *Todites* cf. *goeppertianus* (Muenster) Krasser and *T. nanjingensis* sp. nov. 1. Deux fronds stériles de *Todites denticulatus*. Les pennes deviennent irrégulièrement incurvées suite à la compression durant la fossilisation. PB19799. Échelle = 1 cm. 2, 3. *Todites* cf. *goeppertianus*. 2. Deux pennes stériles petites mais bien préservées. PB19804. Échelle = 1 cm. Provenant de Daijaku, Nankin, Province de Jiangsu. 3. Détail de l'illustration 2 montrant la forme, la taille et la nervation des pinnules. Échelle = 0,5 cm. 4–7. *T. nanjingensis* sp. nov. 4. Fronde stérile portant des pennes en position opposées à sub-opposées. PB19805. Échelle = 1 cm. 5. Petite penne fertile. PB19806. Échelle = 1 cm. 6. Fragment de fronde typique portant des pennes stériles (dans la partie supérieure) et trois pennes fertiles (droite de la partie basale de la fronde). Type PB19807. Échelle = 1 cm. 7. Détail de l'illustration 6, figurant le rachis principal, les pennes stériles, la forme et la taille des pinnules ainsi que leur nervation. Échelle = 0,5 cm. Échantillons 4 et 5 provenant de Daijiaku, Nankin; échantillon type (6) provenant de Shifo'an, Nankin, Province de Jiangsu.

ing at a right angle from the pinna rachis. Teeth on pinnule margin are often sharp and forward-pointing (Figs. 3(3) and 4(E)). The veins are thin. The midrib is distinct and slighter thicker than the lateral veins. It gives off its first lateral branch on the basiscopic side (catadromic). Lateral veins generally fork once, arising at an acute angle to the midrib, nearly straight, persisting almost to the apex (Figs. 3(4A); 4(D) and 5(1)).

Pinnules of the fertile leaf are generally similar to those of the sterile one, but are often smaller, arising at 75° -80° from the main rachis. Margins of pinnules are dentate with rounded teeth (Fig. 3(7)), but teeth become smaller and hardly developed in smaller pinnules (Fig. 3(5)). Pinnules are often falcate; the apex of is blunt and the base is slightly expanded on acroscopic side but contracted on the basiscopic side. Substance of lamina is fairly thick, usually irregularly wrinkled. The upper surface is often transversely waved and margins are slightly depressed (Fig. 3(5)). The midrib is distinct. The lateral veins are simple and generally forked only once (Fig. 3(7)) or do not fork (Fig. 3(5)), sometimes they are inconspicuous. Sporangia are distributed on the under surface. Because our specimens are preserved as ventral impressions, the details of sporangia are unknown.

Discussion: Our specimens closely resemble those described by Harris (1961) as *T. denticulatus* from the Middle Jurassic of Yorkshire, in both sterile and, crucially, in fertile leaves. Previous descriptions of this species in China were based on incomplete sterile specimens. The present material from Jiangsu and Anhui, China, represents the first record of fertile leaves of *T. denticulatus* in this country. However, further work is needed to study the fertile structure and in situ spores of this species in China.

It is noteworthy that *Cladophlebis denticulata* (Brongniart) var. *punctata* was instituted by Thomas (1911: p. 64, Pl. 2, Figs. 13, 13a) from the Kamenka region of the former USSR. Chow and Yeh (in Sze et al., 1963: p. 106) considered this to be a distinct species and renamed it *Cladophlebis punctata* (Thomas) Chow and Yeh. It is characterized by the fine striae and lots of raised pitting on the rachis. According to Harris (1961), all well preserved sterile pinnae of *T. denticulatus* show a pitted surface. This feature is also present in our specimens, e.g. in Fig. 3(1–3). The numerous fine striae and pits are conspicuous on the rachis under higher magnification and are even present on the veins. It is therefore reasonable to treat both *Cladophlebis denticulata* var. *punctata* and *Cladophlebis punctata* as synonyms of *T. denticulatus*.

If preserved only as sterile pinnae, *T. denticulatus* is often indistinguishable from *T. scoresbyensis* from the Rhaetic-Liassic of eastern Greenland (Harris, 1931). According to Harris (1961), a small difference is that in *T. scoresbyensis* in the lower part of the leaf the first basiscopic pinnule does not tend to lie over the rachis, and in the upper part the first pinnule is less rounded in shape. The fertile leaf differs considerably in its incurved pinnule margin. Two other species of Greenland, *T. hartzi* and *T. recurvatus* are also similar to *T. denticulatus*, but differ considerably in having relatively shorter sterile pinnules and in their less lobed fertile ones. In addition, *T. recurvatus* has more crowded veins (Harris, 1931). According to a recent investigation (Van Konijnenburg-Van Cittert, 1996), specimens of *Todites* (*Cladophlebis*) types are also closely associated with *Osmundopsis* fertile foliages. *Osmundopsis sturii* and *O. hillii* from Yorkshire might be fertile foliages of *Cladophlebis denticulata* and *C. harrisii*, respectively.

Material: PB19795, PB19796, PB19797, PB19798, PB19799, PB19800, PB19801, PB19802, PB19803.

Localities and horizons: Xincang of Taihu County, Maoling of Susong County, Shuangdian of Tongcheng County and Lintou of Hanshan County, Anhui Province, the Lower Jurassic Moshan Formation; Daijiaku of Nanjing, Jiangsu Province, the Lower Jurassic Nanxiangshan Formation.

Todites cf. goeppertianus (Muenster) Krasser.

Fig. 5(2, 3).

Selected references:

1846. *Neuropteris goeppertianus* - Muenster in Goeppert, p. 104, Pls. 8, 9, Figs. 9,10.

1922. *Todites goeppertianus* (Muenster) - Krasser, p. 355. 1931. *Todites goeppertianus* (Muenster) Krasser - Harris, p. 31, Pl. 11, Figs. 3 and 8; Text Figs. 6 and 7.

Description: Only a fragmentary specimen of a sterile frond is found in our collection (Fig. 5(2)). Frond is at least bipinnate. The pinna rachis is about 1 mm thick. Pinnules arise at an angle of about 40° from the rachis. Typical pinnules attain 10×5.5 mm in size. Adjacent pinnules are usually closely set and the margins may also overlap or separate up to 1 mm (Fig. 5(3)). Typical pinnule is falcate, ovate-lanceolate and forward bending. The pinnule also has a broad base, an entire margin and a pointed apex. Pinnules have *Neuropteris*-like venation. Veins are conspicuous, lateral veins are crowded (concentration of veins at the margin is about 15 per cm) and nearly straight. The lower lateral veins arise from its base or from the pinna rachis, bifurcating twice to three times; upper ones form a very small angle to the midrib and generally divide once (Fig. 5(3)).

Discussion: Though the present specimen is incompletely preserved, it shows the major distinguishing characters of T. goeppertianus, e.g. the shape and size of the pinnules, the neuropterid venation, and the crowded veins. This Chinese specimen bears a close resemblance to the sterile leaf of T. goeppertianus (Muenster) Krasser from the Rhaetic and Liassic of Eastern Greenland (Harris, 1931; Fig. 6B-D and possibly F). It is also similar to some specimens of T. williamsonii with smaller pinnules from the Middle Jurassic of Yorkshire (Harris, 1961), but the T. williamsonii differs in having basally contracted pinnules rather than the basally expanded ones. Harris (1931) once believed that T. williamsonii in Yorkshire has two types, one with the larger pinnules and one with smaller pinnules than T. goeppertianus. Subsequently, Harris (1961) suggested to sort these two types into the extreme forms of T. williamsonii based upon extensive material of Yorkshire. As we have only one fragmentary ster-



Fig. 6. Sterile and fertile pinnae of *T. nanjingensis* sp. nov. 1. Detail of type specimen in figure 5(6), showing the main rachis and the catadromic pinnules. Note the impression of bristles (hairs) (arrows) and the pitted surface on the rachis. Scale bar = 2 mm. 2. Detail of a fertile pinna in figure 5(6). Scale bar = 0.5 cm. 3. Detail of a fertile pinna in figure 5(5), showing the arrangement of the pinnules. Note that the pinnules are covered by crowded sporangia. Scale bar = 0.5 cm. Fig. 6. Pennes stériles et fertiles de *T. nanjingensis* sp. nov. 1. Détail de l'échantillon type figure 5(6), montrant le rachis principal ainsi que les pinnules catadromes. Observez les empreintes en « brosses » (poils) (flèches) et les perforations en surface du rachis. Échelle = 2 mm. 2. Détail d'une penne fertile (Fig. 5(6)). Échelle = 0.5 cm. 5(6)). Échelle = 0.5 cm. 5(6)). Échelle = 0.5 cm.

ile specimen of *T. goeppertianus*, we cannot determine the variation of pinnule size and their sporangia characters, and therefore prefer to identify the present Chinese specimen as *T.* cf. *goeppertianus*.

Material: PB19804.

Localities and horizon: Daijiaku of Nanjing, Jiangsu Province; the Lower Jurassic Nanxiangshan Formation.

Todites nanjingensis sp. nov.

Figs. 5(4–7); 6(1–3) and 7(A–C).

Diagnosis: Frond at least bipinnate. Main rachis straight and strong, about 1.5–2 mm wide, bearing a wing with striking ridge on surface. Pinnae subopposite to alternate, arising at a wide angle from the rachis. Ultimate pinnules small, ca. 3 mm long and 2 mm wide, *Pecopteris*-like, arising at a right angle from the pinna rachis. Pinnules closely set, margins entire without lobes, catadromic. Basal pair of the lower side pinnules enlarged. Venation delicate but distinct; midrib slightly decurrent, bifurcating and almost disappearing near the apex. Lateral veins fine and distinct, anadromic branching straight or slightly arching, bifurcating once to twice. Fertile pinnae linear to lanceolate, more or less resembling sterile, but more slender. Venation indistinct, secondary veins bifurcating twice. Sporangia closely covering the dorsal surface of pinnules, rounded to oval in shape, about 150–180 μ m in diameter.

Description: There are three specimens in our collection, including both sterile and fertile pinnae, which are in a good state of preservation. The specimen in Fig. 5(6) is interesting. It bears about 16 pinnae of differing degrees of development. The three basal pinnae are fertile, whereas the others are sterile. The specimen probably represents the middle part of a larger bipinnate frond. The specimen in Fig. 5(4) is a sterile frond with at least 12 attached pinnae, representing part of a sterile frond. Fig. 5(5) shows a fertile pinna found in association with other sterile and fertile specimens.

The sterile frond is at least bipinnate. The main rachis is strong and straight, up to 1.5-2 mm wide, tapering gradually towards the upper part of frond. The rachis bears lateral "wings" with a broad and striking median ridge on its surface (Fig. 7(A)). The impressions of bristles are present on the main rachis and pinna rachis (Fig. 6(1)). Pinnae are lanceolate, subopposite (to alternate), arising at a wide angle (60–70°) from the rachis, about 8 mm broad and 4.5–5 cm long, gradually narrowing from the base to the apex. The pinna rachis is straight, about 0.6 mm in thickness, arising from the main rachis at an angle of about 60°. Pinnae arise from the main rachis at an interval of 8–10 mm from each other. Pin-



Fig. 7. Sterile and fertile leaves of *T. nanjingensis* sp. nov. **A.** Detail of the basal part of frond in figure 5(6) showing thick main rachis, a broad and striking median ridge and the lateral "wings" of the rachis. Scale bar = 0.5 cm; **B.** Detail of sterile part of figure 5(6) showing the thick rachis, pinnae, pinnules and venations. Note the first basiscopic pinnule of the basal pinnae is especially developed and catadromic; the venations of pinnule is anadromic (simplified drawing from Fig. 5(7)). Scale bar = 0.5 cm. **C.** Detail of a fertile pinnule, showing the closely distributed sporangia. Scale bar = 0.6 mm. Fig. 7. Frondes stériles et fertiles de *T. nanjingensis* sp. nov. **A.** Détail de la partie basale de la fronde (Fig. 5(6)) montrant l'épais rachis principal, une crête large et dégagée et les « ailes » latérale du rachis. Échelle = 0.5 cm; **B**. Détail de la partie stérile de la figure 5(6) illustrant le large rachis, les pinnules et leur nervation. Remarquez que la première pinnules basiscopique des pennes basales est catadrome et particulièrement développée ; la nervation de la pinnule

est anadrome (dessin simplifié de la Fig. 5(7)). Échelle = 0,5 cm. C. Détail d'une pinnule fertile montrant la distribution compacte des sporanges. Échelle = 0,6 mm.

nules are small, about 3 mm long and 2 mm wide, pecopteridlike, rhomboidal with a generally obtuse apex, or the upper part of pinnule bending forward, falcate, with blunt or slightly acute (sub-acute) apex (Fig. 5(4, 6, 7)). Pinnules are closely set. Their margins are entire and without lobes. They arise at a right angle from the rachis, with its whole base attached to the rachis. The first basiscopic pinnule of the pinnae is catadromic and developed, partly covering the pinnule rachis (Fig. 5(6, 7) and Fig. 7(A, B)). Other pinnules on the distal portion of pinna vary from opposite to alternate. Venations are delicate and distinct. The midrib is slightly decurrent, then bifurcating and dissolving almost to the apex. Lateral veins are finer than the midrib, but are very distinct, straight or slightly arching. Branching of lateral veins is anadromic. They typically divide twice at the proximal side of the pinnules and divide once in the distal part of the pinnules the lateral veins (Fig. 5(7) and Fig. 7(B)).

The fertile pinnae are more slender than the sterile ones. They are linear to lanceolate, arising from the main rachis at an angle of about 45° , attaining a maximum width of 5 mm

and a length of about 4.5 cm. The pinna rachis is slender, usually bending forward, about 0.2 mm wide in the lower part, generally narrowing towards the apex (Figs. 5(6) and 6(2, 3)). Pinnules are very small, up to 2 mm wide and 4.5 mm long. They are alternate to subopposite, forming an angle of about 70°–80° with the rachis, loosely set with an entire unlobed margin and almost obtuse or sub-acute apex (Fig. 6(2, 3)). Veins are bifurcating, generally indistinct, often dividing once to twice. Sporangia closely distributed on the dorsal surface of the pinnule. Judging from the impression, the sporangia are more or less rounded to oval in shape, generally attaining a diameter of about 150–180 µm (Figs. 6(3) and 7(C)). Because our specimens are preserved as impressions, the spores are unknown.

Comparison and discussion: The present specimens bear some characters of *Todites princeps* (Presl) Gothan, such as the straight rachis with bristles, pinnae arising almost at a right angle from the rachis, pinnules small and asymmetrical and the anadromic venations. But the present new species is characterized by the catadromic pinnule branching with



Fig. 8. *Todites princeps* (Presl) Gothan and *Todites* sp. 1, 2. *Todites* sp. 1. A partly preserved sterile specimen with five pinnae. PB19809, from the borehole in Jiangdu of Jiangsu Province. Scale bar = 1 cm. 2. Detail of 1 showing the pinna and the sphenopterid-like pinnules. Scale bar = 0.5 cm. 3. *Todites princeps* (Presl) Gothan. The specimen shows the arrangement of pinnae. PB19808, from Dahengshan of Tongcheng, Anhui Province. Scale bar = 1 cm. Fig. 8. *Todites princeps* (Presl) Gothan and *Todites* sp. 1, 2. *Todites* sp. 1. Spécimen partiellement préservé avec cinq pennes stériles. PB19809, provenant de la mine de Jiangdu, Province de Jiangsu. Échelle = 1 cm. 2. Détail de l'illustration 1 montrant une penne à pinnules de type sphénoptéridienne. Échelle = 0,5 cm. 3. *Todites princeps* (Presl) Gothan. L'échantillon montre l'arrangement des pennes. PB19808 provenant de Dahengshan, Tongcheng, Province de Anhui. Échelle = 1 cm.

anadromic venation; the pinnule margins of *T. nanjingensis* are entire and unlobed. Therefore this Chinese species shows distinct characters from *T. princeps*. A fragmentary specimen recently figured by Q.S. Huang (2001) as *T. princeps* from the Early Jurassic of Sichuan, China, bears some similarities to those of the sterile pinna of *T. nanjingensis* sp. nov. Due to the poor preservation of Sichuan specimen, it is diffi-

cult to make a further and detailed comparison with our specimens of *T. nanjingensis*.

With regard to the pinna and pinnule forms and venation features, some of the specimens described as *T. williamsonii* (Brongniart) Seward from Yorkshire (Harris, 1961; Figs. 28-A, C and 29-N, O) closely resemble the present Chinese specimens. However, the former are catadromic both in the basal



Fig. 9. Sketch map showing the stratigraphical ranges and geographical distribution of the genus *Todites* in the Mesozoic of China. Fig. 9. Carte de répartition géographique et stratigraphique du genre *Todites* du Mésozoïque de Chine.

pinnules and lateral veins, the veins fork more often, and the basal pinnules are not specialized. Sometimes fertile pinnae show no variation in form and size. In general, *T. nanjingensis* and *T. williamsonii* are easily distinguished from each other.

Holotype: PB19807; Fig. 5(6).

Additional material: PB19805, PB19806; Fig. 5(4, 5).

Etymology: "*nanjingensis*" refers the type locality of Nanjing, Jiangsu Province, China.

Locality and horizon: Daijiaku of Cangbomen and Shifo'an, Nanjing, Jiangsu Province; the Lower Jurassic Nanxiangshan Formation.

Todites princeps (Presl) Gothan.

Fig. 8(3).

Selected references:

1914. *Todites princeps* Presl - Gothan, p. 95, Pl. 17, Figs. 3 and 4.

1931. *Todites princeps* (Presl) Gothan - Harris, Pl. 11, Fig. 1 and Text-Figs. 8 and 9; p. 35.

1961. *Todites princeps* (Presl) Gothan - Harris, pp. 93–98, Text-figs. 30, 31.

Description: This species is represented by one specimen in our collection. This large specimen in Fig. 8(3) shows a partly preserved frond of over 16 cm long and about 9 cm wide. Frond is at least bipinnate. Main rachis is thin, about 1-2 mm thick. Pinnae on the middle part of frond are alternate to subopposite, arising almost at right angles (80°–90°) from the rachis, linear or elongated triangular in form with thin lamina. The typical pinnae on the middle portion of the frond are about 5 cm long and 2–3 cm wide, and are usually closely set with 13–14 mm intervals to one another. Pinnules are sphenopterid-like. The pinnule apex is subrounded or obtuse pointed. The margin is lobed or petal-like. The first pinnule arises on the upper side of the pinna followed by the lower side, i.e. anadromic (Fig. 8(3)). Midrib of the pinnules arises from the rachis at a wide angle, penetrating adaxially into the pinnules; the lateral veins are anadromic, but are not always conspicuous.

Discussion: T. princeps is characterized by its small pinnules and the rectangular insertion of the pinnae on the rachis as well as by the anadromic branching of the pinnules and the lateral veins. The present Chinese specimens are identical in these aspects to those of T. princeps from the Rhaetic-Liassic of Greenland (Harris, 1931, especially his plate XI, Fig. 1 and Text-Figs. 8 and 9); and also agree with the Middle Jurassic specimens from the Yorkshire described by Seward (1900: Pl. XVI, Fig. 2) and Harris (1961: Figs. 30 and 31). The present specimens are similar to T. princeps from the Nariwa flora of Japan (Oishi, 1932, 1940). In addition, our specimen is indistinguishable from those described as Sphenopteris modesta Leckenby from the Early Jurassic Hsiangchi Flora in western Hubei, China (Sze, 1949) and subsequent descriptions from the Late Triassic Hsuchiaho Flora in Kwangyuan, Sichuan, China (Li, 1964).

Material: PB19809.

Localities and horizons: Dahengshan of Tongcheng, Anhui Province, the Lower Jurassic Moshan Formation.

			T. asianus	T. yanbianensis	T. subtilis	T. recurvatus	T. microphylla	T. kwangynanensis	T. shensiensis	T. crenatum	T. scoresbyensis	T. goeppertianus	T. princeps	T. williamsonii	T. denticulatus	T. leei	T. nanjingensis	T. cf. thomasi	T. major	
(a	Cretaceous	lower																	1?	1
	man	Upper													1				1	2
ern Chiı	lurassic	Middle												5	6			L Eastern		12
Northe	<u>ں</u>	Lower												5			Eastern	L Eastern		11
	sic	Upper							2	5 Eastern	1	1		5	3					13
	Trias	Middle ¹							3											3
Southern China Triassic		Upper				,														
	urassic	Middle											1	1	1			Eastern		4
	J	Lower										4	4	3	3	1	Eastern	1 Eastern		17
	ssic	Upper	1	1	1	1	1	1	11	3	5	6	6	2	5					44
	Tria	Middle																		

Fig. 10. Stratigraphical ranges of genus *Todites* in Northern and Southern China. Each number represents the number of formation that yields fossils. Fig. 10. Répartition stratigraphique du genre *Todites* dans le Nord et le Sud de la Chine. Les nombres représentent les occurrences du genre.

Todites sp.

Fig. 8(1, 2).

Discussion: There is only one fragmentary specimen in our collection (Fig. 8(1)). It was collected from a borehole rock sample, but with well preserved lamina and pinnae. Frond is at least bipinnate. It is very similar in gross morphology to *T. princeps* that is figured in Fig. 8(3), but the present specimen differs from *T. princeps* in having acute lobes in the pinnules (Fig. 8(2)). This specimen is also comparable with that of *T. crenatum* from the Early Jurassic of Iran (Barnard, 1965), but *T. crenatum* has a somewhat waved pinna rachis, and the pinnules arise at a smaller angle from the rachis; the veins are

also more divided and crowded in *T. crenatum*. Because the Chinese specimen is fragmentary, we therefore identify it as *Todites* sp.

Material: PB19808.

Localities and horizon: Jiangdu of Jiangsu Province, the Lower Jurassic Nanxiangshan Formation.

6. General discussion

The genus *Todites* was named for its resemblance to modern *Todea* by Seward (1900) and was emended by Harris (1961). The species of *Todites* were divided into three groups: (1) Those with purely pecopterid venations, include T. denticulatus, T. thomasii, T. scoresbyensis and T. recurvatus. (2) Those with more or less neuropterid venation in larger pinnules include T. goeppertianus and T. williamsonii. and (3) Those with sphenopterid venations represented by T. princeps (Harris, 1961). Among five Todites species described in this paper, T. denticulatus and T. nanjingensis can be assigned into group (1), T. cf. goeppertianus and T. princeps are apparently attributed to groups (2) and (3), respectively. According to sterile and fertile features, T. denticulatus agrees with T. thomasii in venation and denticulate margin. Spores of these two species are also very much alike (Van Konijnenburg-van Cittert, 1978; Van Konijnenburg-Van Cittert and Morgans, 1999). The main difference between them is that T. thomasii has a strongly contracted pinnule base while it is expanded in T. denticulatus. T. goeppertianus (Muenster) Krasser is very like T. williamsonii in all features, the main difference is that in T. goeppertianus the pinnules are normally basically expanded, while they are basally contracted in T. williamsonii. Some authors, like Harris (1961); Kilpper (1964) tended to regard them as among the two extreme forms of a single species. Further investigation of in situ spores indicated that the spores differ in size by 10 µm and in thickness of exine (1.5–2.5 µm in T. williamsonii and 1–1.5 µm in T. goeppertianus). Therefore, regarding to the spores, T. goeppertianus and T. williamsonii are two different but closely allied species (Van Konijnenburg-van Cittert, 1978). T. princeps differs from other species by the anadromic order of lateral veins and pinnules, while in all other species it is catadromic. The spores also differ slightly from those of the other species by relatively smaller size and a very thin exine (Van Konijnenburg-van Cittert, 1978; Van Konijnenburg-Van Cittert and Morgans, 1999). Therefore T. princeps is unique in its anadromic branching of the pinnules and veins. It is so far the only osmundaceous (living and fossil) species that shows this feature. T. nanjingensis sp. nov. from eastern China shows some similarities to T. princeps, but it differs from having unlobbed pinnules and catadromic pinnules.

Specimens of *Todites* described in this paper show incomplete fronds. The related fern rhizomes are not found in our collection. The larger specimen of *T. princeps* (Fig. 8(3)) is over 16 cm long and probably 10 cm broad. According to Harris (1961), specimens of *T. princeps* from the Middle Jurassic of Yorkshire have a larger size frond as almost 100×15 cm, and only a fragmentary rhizome was found in the fossiliferous bed. This *Todites* fern was suggested to be probably an epiphyte: the whole plant could rather easily fall and be swept by water into the pools where preservation occurred (Harris, 1961). The most complete reconstruction of *T. princeps* was presented by Schweitzer (1978) based on very well preserved material from the Rhaetian to Jurassic in Iran and Afghanistan.

7. Stratigraphical range and geographical distribution of *Todites* in China

The earliest fossil record of *Todites* in China is dated to the Middle Triassic and is found in North China with the spe-

cies Todites shensiensis (P'an) Sze. It is one of the most common Todites species in China (Table 2). This species was initially described as *Cladophlebis shensiensis* from the Upper Triassic of Yen' chang Formation (Group) of northern Shaanxi (P'an, 1936). It was subsequently transferred as Todites shensiensis based upon well preserved fertile material (Sze, 1956; Sze et al., 1963). Afterwards, this species was described and figured from the Middle Triassic Ermaying Formation in Wuziwan of Zhungerqi, Inner Mongolia as well as the Middle Triassic Tonghcuan Formation in northern Shaanxi (Zhang, 1976; Huang and Zhou, 1980). A couple of fragmentary specimens were also described as T. cf. shensiensis from the Middle Triassic Linjia Formation in Benxi, Liaoning Province (Zhang et al., 1983). This represents, however, the earliest recorded occurrence of the genus Todites in China. In addition, this species was also recorded in Late Triassic deposits of Sichuan, Hubei, Yunnan, Tibet (Xizang) of southwestern China, Jiangsu and Zhejiang Provinces, eastern China as well as Guangdong of South China (Table 2).

There is only one possible record of *Todites* that occurs later than Late Jurassic. Todites major Sun and Zheng was recently described and illustrated from the lower part of the Yixian Formation in western Liaoning (Sun et al., 2001). It is necessary to mention that the age of the Yixian Formation is uncertain. It might range from Late Jurassic to Early Cretaceous. Therefore, if the identification of T. major is accepted, this species may represent the latest fossil record of Todites in China. Unfortunately, this species was described based upon one sterile impression fossil only, and the size of the complete frond and the fertile features of it are still unknown. It is therefore possible, that it might be a species of Cladophlebis. Further collection and detailed investigations are necessary to confirm the generic attribution of this species. At present, T. denticulatus is the latest unequivocal fossil record of Todites in China.

Besides T. shensiensis, the other most frequently distributed species in China include: T. denticulatus, T. williamsonii, T. goeppertianus, T. princeps and T. scoresbyensis (Table 2). T. denticulatus is recorded from the Upper Triassic to Middle Jurassic in northwestern (Shannxi and Gansu) (Liu, 1982), northern (Beijing and Hebei) (Chen et al., 1984) and northeastern China (Liaoning, Jilin and Heilongjiang) (Mi et al., 1993, 1996; Zheng and Zhang, 1982; Zhang and Zheng, 1987; Yang and Sun, 1982, 1985). It is also distributed in the Upper Triassic of Sichuan Province, southwestern China and Late Triassic to Middle Jurassic in Hunan, Anhui, Jiangsu and Zhejiang Provinces, southern and eastern China (Li, 1964; Li and Wu, 1982; Chen, 1986; Chen et al., 1987; Huang and Qi, 1991; Zhang, 1985; Hsü et al., 1979; this paper). T. williamsonii has almost the same stratigraphic range (Upper Triassic to Middle Jurassic) and distribution area as T. denticulatus. It has been mainly recorded in northern part of China, including Shaanxi, Gansu, Qinghai, Beijing, Hebai, Liaoning, Jilin, and Heilongjiang Provinces (Liu, 1982; Huang and Zhou, 1980; Li et al., 1988; Chen et al., 1984; Mi et al., 1993, 1996; Zhang and Zheng, 1984; Zheng and Zhang, 1990; Sun

Table 2 Stratigraphical record and geographical distribution of *Todites* in China Distribution géographique et stratigraphique du genre *Todites* en Chine

Species	Ages	Localities, horizons and references
T. denticulatus	Late Triassic (T ₂) to	Northwestern: Zhenba, Shaanxi (Hsuchiaho Fm., T., Baitianba Fm J.,). Wudu Gansu (Lon-
(Brongniart) Krasser	Middle Jurassic (J ₂)	gjiagou Fm., J ₂) (Liu, 1982). Northern: Western Hils, Beijing (J ₁₋₂) (Chen et al., 1984); Northeastern: Wangqing, Jilin (Malugou Fm., T ₃), Chengde, Hebei (Xingshikou Fm., T ₃) (Mi et al., 1993); Beipiao, Liaoning (Beipiao Fm., J ₁) (Mi et al., 1996); Baoqing and Mishan, Heilongjiang (Dongsheng Fm., J ₂ and Chaoyangtun Fm., J ₂₋₃) (Zheng and Zhang, 1982); Beipiao, Liaoning (Lanqi Fm., J ₂) (Zhang and Zheng, 1987); Dahingaling (Hongqi Fm., J ₁) (Yang and Sun, 1982, 1985); Southwestern: Qinghe, Sichuan (Hongguo Fm., T ₃) (Chen et al., 1987); Guangyuan, Sichuan (Hsuchiaho Fm., T ₃) (Li, 1964); Baoding, Sichuan (Daqing Fm., T ₃) (Hsü et al., 1979); Dege, Sichuan (Lamaya Fm., T ₃) (Li and Wu, 1982); Southern and Southeastern: Quxian, Zhejiang (Chayuanli Fm., T ₃) (Chen, 1986); Lanxi, Zhejiang (Majian Fm., J ₁₋₂) (Huang and Qi, 1991); Eastern Hunan (Shikang, Tanglong and Gaojiaba Fms., J ₁) (Zhang, 1985); Anhui and Jiangsu (lower part of the Xiangshuan Group, J ₁) (this paper)
T. goeppertianus	Late Triassic (T ₃) to	Northeastern: Jinlingsi-Yangshan Basin, Liaoning (Laohugou Fm., T ₃) (Zhang and Zheng,
(Münster) Krasser	Early Jurassic (J ₁)	1984) (No description and illustration); Southwestern: Daocheng, Western Sichuan (Lamaya Fm., T_3) (Li and Wu, 1982); Lufeng, Yunnan (Yipinglang Fm., T_3) (Li et al., 1976); Nanzhang, Hubei (Jiuligang Fm., T_3) (Meng, 1987); Southern and Southeastern: Qiyang, Hunan (Paijiachong Fm., J_1) (Zhou, 1984); Hengyang,Hunan (Shaqiao Fm., T_3) (Zhou, 1989); Qiyang, Hunan (Guanyingtan Fm., J_1) (Zhou, 1984); Eastern Hunan (Shikang Fm., T_3) (Zhang, 1985); Hengnan, Hunan (Zaoshang Fm., J_1) and Qujiang, Guangdong (T_3) (He and Shen, 1980); Nanjing, Jiangsu (Nanxiangshan Fm., J_1) (This paper)
T. princeps (Presl)	Late Triassic (T_3) to	Southwestern: Eastern Sichuan (Zhengzhuchong Fm., J ₁) (Ye et al., 1986); Qinghe, Sichuan
Gothan	Middle Jurassic (J ₂)	(Hongguo Fm., T ₃) (Chen et al., 1987); Guangyuan, Sichuan (Hsuchiaho Fm., T ₃) (Li, 1964); Yuan'an, Hubei (Wanglongtan Fm., T ₃) and Dangyang, Hubei (Hsiangchi Fm., J ₁) (Feng et al., 1977; Meng, 1987); Zigui, Hubei (Hsiangchi Fm., J ₁) (Wu et al., 1980; Wu, 1991; Wang, 2002); Southeastern and Eastern: Lanxi, Zhejiang (Majian Fm., J ₁₋₂) (Huang and Qi, 1991); Liuyang, Hunan (Sanqiutian Fm., T ₃) (He and Shen, 1980); Taihu, Susong, Tongcheng and Hanshan, Anhui (Moshan Fm., J ₁) (This paper); Nanjing, Jiangsu (Nanxiangshan Fm., J ₁) (This paper)
T. shensiensis (P'an)	Middle Triassic (T_2) to	Northwestern and Northern: Northern Shaanxi (Yanchang Group, Yanchang Fm., T ₃) (P'an,
Sze	Late Triassic (T ₃)	1936; Sze, 1956; Sze et al., 1963); Ordos Basin, Shaanxi (Yanchang Fm., T_3) (Liu, 1982); Ton- gchuan and Shenmu, Shaanxi (Tongchuan Fm., T_2) and Wuziwan, Zhungerqi, Inner Mongolia (Ermaying Fm., T_2) (Zhang, 1976; Huang and Zhou, 1980); T. cf. shensiensis: Benxi, Liaoning (Linjia Fm., T_2) (Zhang et al., 1983); Southwestern: Dazhu, Sichuan (Hsuchiaho Fm., T_3) (Ye et al., 1986); Qinghe, Sichuan (Hongguo Fm., T_3) (Chen et al., 1987); Yanbian, Sichuan (Hon- gni Fm., T_3) (Chen and Duan, 1981); Baoding, Sichuan (Daqiaodi and Daqing Fms., T_3) (Hsü et al., 1979); Lufeng, Yunnan (Yipinglang Fm., T_3) (Li et al., 1976); Gongjue and Chaya, Tibet (Bagong Fm., T_3) (Wu, 1982b); Nanzhang, Hubei (Jiuligang Fm., T_3) (Meng, 1987); cf. T. shensiensis: Xiangcheng, western Sichuan (Lamaya Fm., T_3) (Li and Wu, 1982); Southern : Gaoming, Guangdong (Xiaoping Fm., T_3) (Feng et al., 1977); Eastern: Nanjing, Jiangsu (Fan- jiachang Fm., T_3) (Ju et al., 1983); Quxian, Zhejiang (Chayuanli Fm., T_3) (Chen, 1986)
<i>T. williamsonii</i> (Brongniart) Seward	Late Triassic (T_3) to Middle Jurassic (J_2)	Northwestern: Northern Shaanxi and central Gansu (J_{1-2}) (Liu, 1982; Huang and Zhou, 1980); Dameigou, Qinghai (Xiaomeigou Fm., J_1) (Li et al., 1988);
		Northern: Western Hills, Beijing (Xiayaopo, Shangyaopo and Longmen Fms., J ₁₋₂) (Chen et al., 1984) Northeastern: Wangqing, Jilin (Malugou FM., T ₃), Shuanyang, Jilin, (Dajianggang Fm., T ₃) and Beipiao, Liaoning (Yangcaogou Fm., T ₃) (Mi et al., 1993); Beipiao, Liaoning (Beipiao Fm., J ₁) and Haifanggou Liaoning (Haifanggou Fm., J ₂); Funing, Hebei (Beipiao Fm., J ₁) (Mi et al., 1996); Jinlingsi-Yangshan, Liaoning (Laohugou Fm., T ₃) (Zhang and Zheng, 1984);
		Tianshitu ot Benxi, Liaoning (Dabao Fm., J_2) (Zheng and Zhang, 1990); Mishan, Heilongjiang (Peide Fm., J_2) (Zheng and Zhang, 1982); Shuangyang, Jilin (Dajianggang Fm., T_3) (Sun et al., 1983); Southwestern : Qinghe, Sichuan (Hongguo Fm., T_3) (Chen et al., 1987); Guangyuan, Sichuan (Hsuchiaho Fm., T_3) (Li, 1964); Zigui, Hubei (Hsiangchi Fm., J_1) (Wu, 1991); Southern and Southeastern : Lanxi, Zhejiang (Majian Fm., J_{1-2}) (Huang and Qi, 1991); Eas- tern Hunan (Tanglong and Gaojiatian Fms., J_1) (Zhang, 1985)
<i>Todites asianus</i> Wu <i>Todites crenatum</i> Barnard	Late Triassic (T ₃) Late Triassic (T ₃)	Southwestern: Huili, Sichuan (Baiguowan Fm., T ₃) (Wu, 1999) Eastern and Southwestern: Jiangxi and Hunan (Anyuan Fm., T ₃) (Zhang, 1982); Hengyang, Hunan (Shaqiao Fm., T ₃) (Zhou, 1989); cf. T. crenatum: Amdo, Tibet (Tumaingela Fm., T ₃)
T. kwangyuanensis	Late Triassic (T ₃)	(Wu, 1982) Southwestern: Guangyuan, Kaijiang, Daxian and Xuanhan, Eastern Sichuan (Hsuchiaho Fm., T.) (Li 1964; Va et al. 1986):
T. leei Wu	Early Jurassic (J ₁)	Southwestern: Zigui, Hubei (Hsiangchi Fm., J_1) (Wu, 1991; Wang, 2002)
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(continued on next page)

Table 2 (continued)

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Species	Ages	Localities, horizons and references				
<i>T. microphylla</i> (Fontaine) Li Late Triassic (T_3)		Southwestern: Lufeng, Yunnan (Yipinglang Fm., T ₃) (Li et al., 1976)				
T. major	Late Jurassic (J ₃)/)	Northeastern: Beipiao, western Liaoning (Jianshangou Fm. = the lower part of the Yixian Fm.,				
Sun and Zheng	Early Cretaceous (K1	J_3/K_1) (Sun et al., 2001)				
T. nanjingensis sp. nov.	Early Jurassic (J ₁)	Eastern: Nanjing, Jiangsu (Nanxiangshan Fm., J1) (This paper)				
T. recurvatus Harris	Late Triassic (T ₃)	Southwestern: Yidun, western Sichuan (Lamaya Fm., T ₃) (Li and Wu, 1982)				
T. scoresbyensis Harris	Late Triassic (T ₃)	Northern: T. cf. scoresbyensis: Western Hills, Beijing (Xingshikou Fm., T ₃) (Mi et al., 1993); Southwestern: Qinghe, Sichuan (Hongguo Fm., T ₃) (Chen et al., 1987); Guangyuan, Sichuan (Hsuchiaho Fm., T ₃) (Li, 1964); Lufeng, Yunnan (Yipinglang Fm., T ₃) (Li et al., 1976); Southern: Puxin, Hubei (Wuchang Group, T ₃) (Feng et al., 1977); Liuyang, Hunan (Sanqiutian Fm., T ₃) (He and Shen, 1980)				
T. subtilis Duan and Chen	Late Triassic (T ₃)	Southwestern: Yanbian, Sichuan (Hongni Fm., T ₃) (Chen et al., 1979; Chen and Duan, 1981)				
T. cf. thomasi Harris	Early to Middle Jurassic (J ₁₋₂)	Eastern: Lanxi, Zhejiang (Majian Fm., J ₁₋₂) (Huang and Qi, 1991)				
<i>T. yanbianensis</i> Duan and Chen	Late Triassic (T ₃)	Southwestern: Yanbian of Sichuan (Hongni Fm., T ₃) (Chen et al., 1979; Chen and Duan, 1981)				

et al., 1983). In southern China, it has been found in Sichuan, Hubei, Hunan and Zhejiang Provinces (Li, 1964; Chen et al., 1987; Wu, 1991; Zhang, 1985; Huang and Qi, 1991). Another three species, T. goeppertianus, T. princeps and T. scoresbyensis are mainly recorded in southern China. The former one is distributed in the Upper Triassic of Sichuan, Yunnan, Hubei, Guangdong (Li et al., 1976; Li and Wu, 1982; Meng, 1987; He and Shen, 1980; this paper), and the Upper Triassic to Lower Jurassic in Hunan and Jiangsu (Zhou, 1984, 1989; Zhang, 1985; He and Shen, 1980). There is only one possible record of T. goeppertianus in northern part, i.e. from the Upper Triassic of western Liaoning (Zhang and Zheng, 1984). The authors, however, provided no illustration and descriptions in their report with only the citation of the species name. T. princeps has only been recorded so far in the Late Triassic to the Middle Jurassic deposits of southern China, including Sichuan, Hubei, Hunan, Zhejiang, Anhui and Jiangsu Provinces (Li, 1964; Ye et al., 1986; Chen et al., 1987; Wu et al., 1980; Meng, 1987; Feng et al., 1977; Huang and Qi, 1991; He and Shen, 1980; this paper). There is no record of this species in northern part of China. T. scoresbyensis is mainly documented from the Upper Triassic of southern region, including Sichuan, Yunnan, Hubei and Hunan Provinces (Li, 1964; Li et al., 1976; Chen et al., 1987; Feng et al., 1977; He and Shen, 1980). Only a fragmentary specimen that might be comparable to this species was figured as T. cf. scoresbyensis from the Upper Triassic in Western Hills of Beijing (Mi et al., 1993).

Besides those species mentioned above, another 10 species of *Todites* documented in China so far only occur in the southern part of China (Table 2), and are limited in their spatial distribution. *T. crenatum* Barnard was described from the Upper Triassic of Jiangxi and Hunan Provinces (Zhang, 1982; Zhou, 1989). It might also occur in the Upper Triassic of eastern Tibet based upon two fragmentary specimens figured as "cf. *T. crenatum*" (Wu, 1982). Another two species, *T. recurvatus* Harris (from Greenland) and *T. thomasii* Harris (from Yorkshire) were found only in Upper Triassic of Sichuan and Early to Middle Jurassic of Zhejiang, respectively (Li and Wu, 1982; Huang and Qi, 1991). There is no other record of these species being reported elsewhere in China. It is note-worthy that specimens from Sichuan and Zhejiang are fragmentary and sterile, with no associated fertile pinnae. Furthermore, according to the authors, a slight difference exists in between *T. thomasii* from Yorkshire and specimen from Zhejiang (Huang and Qi, 1991).

An interesting phenomenon is that, about six endemic species of *Todites* have been described based on Chinese material, and they are distributed only in southern China. Among them, *T. kwuanguanensis* (Li) Ye and Chen, *T. subtilis* Duan and Chen, *T. yanbianensis* Duan and Chen and *T. asianus* Wu are restricted to the Upper Triassic in Sichuan Province (Li, 1964; Li et al., 1976; Ye et al., 1986; Chen et al., 1979; Wu, 1999); whereas *T. leei* Wu and *T. nanjingensis* sp. nov. are, respectively, documented from the Early Jurassic in Hubei (Wu, 1991), Jiangsu and Anhui Provinces as well (this paper).

During the Early Mesozoic, there are two phytogeographical provinces in China: Southern Floristic Province and Northern Floristic Province, which are bordered by the westerneastern ranges of the Kunlun, Qingling and Dabie Mountains. Available data indicate that, during the Late Triassic to Middle Jurassic, Todites is distributed both in Northern and Southern Floristic Provinces (Fig. 9), represented mainly by T. denticulatus, T. shensiensis, T. williamsonii and T. goeppertianus. Further analysis shows that, Todites is especially abundant and highly diverse in the Southern Floristic Province. Throughout the Triassic and Jurassic, the distribution of Todites differed between South and North China. Sixteen different species have been described in South China compared to only nine in the North. The geological formations containing the genus Todites are much more numerous in the South than in North China (65 against 42; Fig. 10).

Even if the first remains of *Todites* occurred in North China during the Middle Triassic, the maximum development of this genus has been in South China during the Upper Triassic. The lack of Middle Triassic terrestrial outcrops in South China may be a factor in this discrepancy. During the Early and Middle Jurassic, the number of geological formations containing the genus *Todites* decreased in South China and at the same time increased in the northern part. We also observe a "migration" of *Todites* species from South to North during the Early Jurassic (Fig. 10). A proposal to explain these observations could be the environment and especially the climatic changes during this time.

According to Sze (1956); Wu et al., (1980); Zhou (1984), the floral elements of Southern Floristic Province are characterized by *Dictyophyllum-Clathropteris* flora in the Late Triassic and *Ptilophyllum-Coniopteris* flora in the Early to Middle Jurassic, indicating subtropical to tropical climate conditions; whereas the coeval Northern Province is warm and moderate to subtropical climate conditions. This could explain the fact that *Todites* is more abundant and diverse in Southern Floristic Province of China during the Early Mesozoic era. At the end of the Jurassic and the beginning of the Cretaceous, the *Todites* species of China disappeared as more arid climatic conditions became established in South and North China.

It is necessary to remark that most of the Chinese specimens described as Todites are impressions and are mainly sterile leaves. Fertile leaves are not often preserved because they are generally less numerous than sterile ones and have a short existence in the life cycle. Presently, only a few species are found with fertile pinnae. The most well documented species is T. shensiensis, which has specialized fertile pinnules. Specimens of *T. denticulatus* described in this paper are the first fertile pinnules of this species known from China. T. nanjingensis is also interesting because it bears fertile pinnae and pinnules. T. leei and T. williamsonii from the Early Jurassic in Western Hubei and T. crenatum Barnard from the Upper Triassic of Hunan were also reported bearing fertile pinnules (Wu, 1991; Zhou, 1989). Due to the preservation of specimens, the fine structure of sporangia and in situ spores of Chinese Todites material are still not well documented. Morework (including further collection) is needed to further our knowledge of these features.

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