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Plant remains from the Early Cretaceous deposits of Qubsang, Doilungdeqen, northwestern Lhasa of Tibet, China

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ABSTRACT

New fossil plants are reported from the lower part of the Linbuzong Formation at Qubsang, Doilungdeqen, Lhasa, Tibet. The assemblage comprises *Neocalamites* sp., *Ptilozamites tibetica* Yang, *Ptilozamites* sp., ?*Ptilozamites* sp., *Zamites* sp. 1, *Zamites* sp. 2, ?*Zamites* (?*Otozamites*) sp. 1, ?*Zamites* sp. 2., *Ptilophyllum* sp. 1, *Ptilophyllum* sp. 2, *Ptilophyllum* sp. 3, *Geinitzia* sp. and *Elatocladus* (?*Torreyites*) sp. Among these plants at least two of them, *Ptilozamites tibetica* and *Elatocladus* (?*Torreyites*) sp. are firstly discovered in this area, and the others occured frequently in the Mesozoic flora in Tibet. Associated miospores suggests an Early Cretaceous age for the assemblage. The abundance of *Ptilophyllum* and conifer *Geinitzia* sp. and the absence of Ginkgoales might indicate a palaeoenvironment with both a low latitude and high temperatures, and a tropical arid to semi-arid climate predominating in this coastal area. The Qubsang assemblage, composed mainly of Bennettitales and Coniferopsida, does not resemble any contemporaneous ones known from Gondwanaland or Eurasia. Although the flora lacks characteristic Wealden ferns, such as *Weichselia*, the plant assemblage shows a general relation to Tethyan floras of the area and might roughly correspond in age to the Wealden floras of Western Europe.

1. Introduction

In Tibet, Upper Mesozoic deposits are well developed in an east–west belt from Nujiang, Lhasa, Gaize to Ritu (Fig. 1); Early Cretaceous fossil plants in Tibet are mainly discovered from coal-bearing strata in this belt (Li, 1982; Tuan et al., 1977; Chen and Yang, 1983; Wu, 1985; Zhou and Liu, 1987; Li and Wu, 1991; Liu et al., 2007). All of these floras are considered similar to those of palaeo-coastal regions of southeast China and Wealden floras of Europe. In 1994, an Upper Gondwana plant flora dated as Early Cretaceous was discovered from the Puna Formation, southern Tibet, which indicated that the northern limits of Gondwanaland extended further into southern Tibet (Zhou and Wu, 1994).

In 2016, a new fossil pteridosperm with an unusual bipinnate forked frond, *Ptilozamites tibetica* Yang, was reported from the Lower Cretaceous Linbuzong Formation in Qubsang, Doilungdeqen, Lhasa, Tibet (Yang and Li, 2016). This genus was known to occur throughout the Northern Hemisphere from Early Triassic to Middle Jurassic but *P. tibetica* occurs in the Early Cretaceous on the Tibetan Plateau. In the present paper, all fossil plants associated with *P. tibetica* are described and the whole plant assemblage is compared with other floras from coeval deposits, especially those of the Tibet Plateau in Tibet, China.

2. Stratigraphy of the plant-bearing formations

The Qubsang section is located in the south of the Lhasa Block, some 50 km north-west to Lhasa City (Fig. 1). It comprises the Upper Jurassic Duodigou Formation, the Lower Cretaceous Linbuzong and Chumulong formations in ascending order (Fig. 2). The Duodigou Formation is composed of grey medium- to thick-bedded limestone with greyish-black shale interbeds. The Lower Cretaceous Linbuzong Formation, where the present plant fossils were collected, is underlain by the Duodigou Formation possibly separated by a fault, and consists of black shale intercalated with siltstone and sandstone. Coal seams are also developed in this formation. A total thickness of 148 m has been measured for this formation. Besides plant macrofossils, ammonites, bivalves and miospores have also been found (Wang et al., 1983; Zhou, 1994). Overlying this formation is the Lower Cretaceous Chumulong Formation which comprises grey or bright, medium- to thick-bedded quartz sandstone intercalated with sandy conglomerate and thin-bedded black shale. Coal seams occur occasionally.

3. Description of the fossil plants

All fossil plants described in this paper were collected from the outcrop of the Lower Cretaceous Linbuzong Formation in Qubsang. Due

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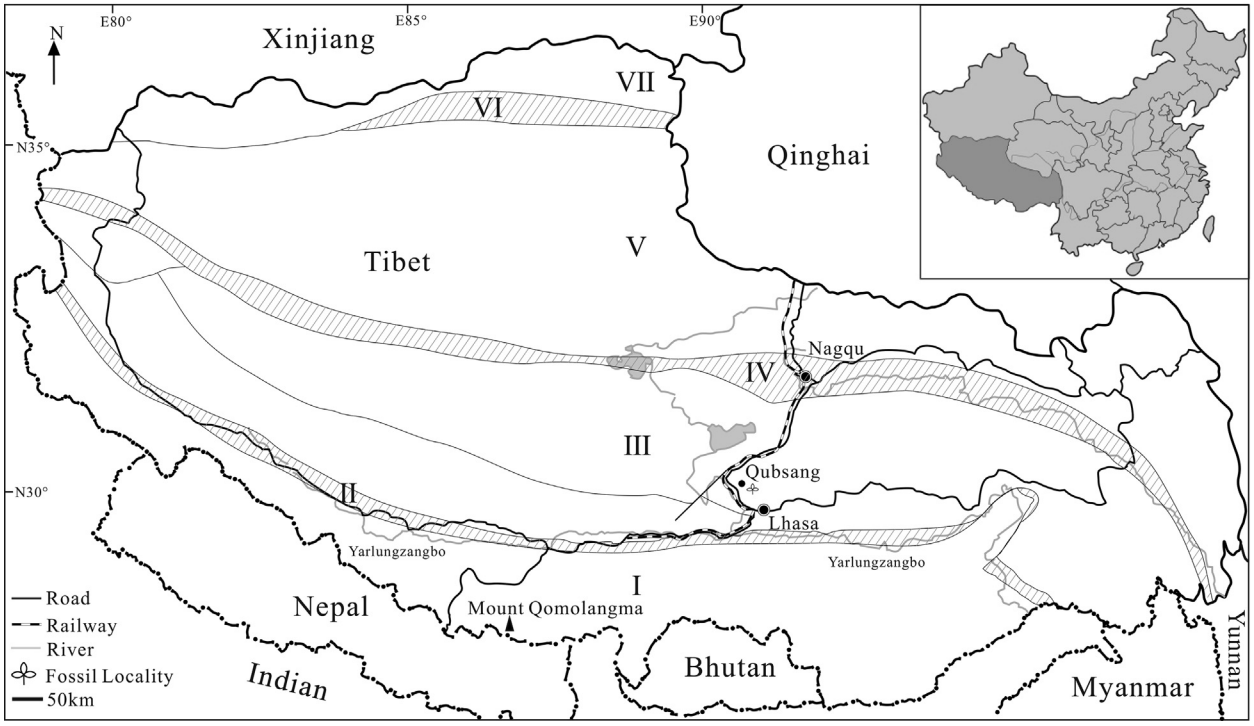

Fig. 1. Tecto-sedimentary division map of Xizang, western China; the fossil locality Qubsang is indicated by ⚘. I, Himalaya Block; II, Yarlung Zangbo suture; III, Gandise–Lhasa Block; IV, Bangong–Nujiang suture; V. Qiangtang Block; VI, Jinsha suture; VII, Bayan Har (Sangpan-Ganzi) Block. Modified after Bureau of Geology and Mineral Resources of the Xizang Autonomous Region (1993).

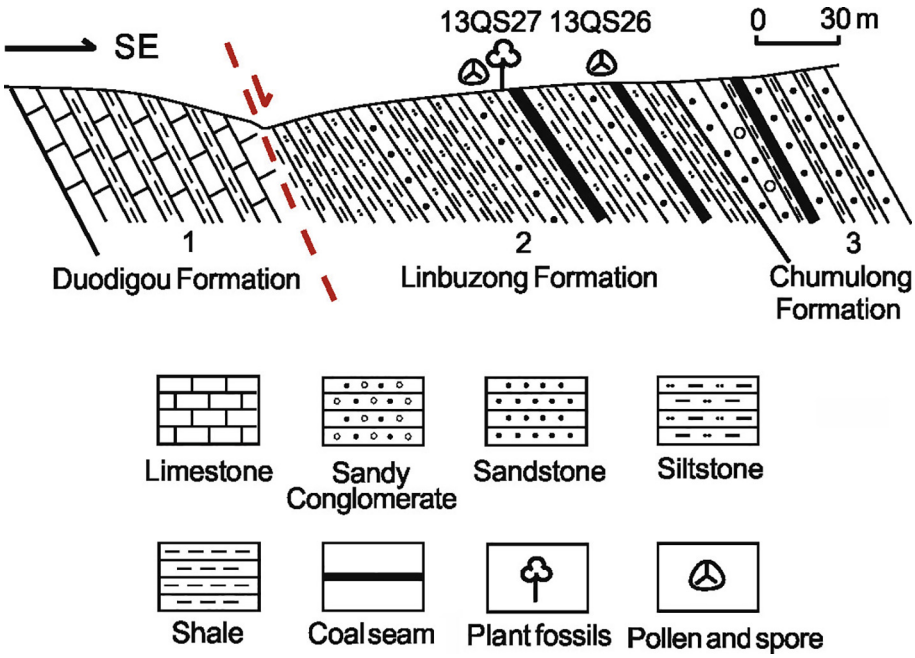

Fig. 2. Stratigraphical section of the Libuzong Formation in Qubsang, Lhasa, Tibet, showing the fossil-bearing horizons.

to regional orogenic movement, the plant-bearing bed in the study area is metamorphic. Most of the plant remains are incompletely preserved, making it difficult to identify to species level. Although coaly substance sometimes present on some specimens, there are no useful cuticles so far obtained by maceration.

Equisetaceae

Genus *Neocalamites* Halle

***Neocalamites* sp.** (Fig. 3a)

Material: specimen number PB22682

Deposition: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Description: The specimens are a few pieces of incomplete stem. The stems are straight, up to 9 cm long and to 4.5 cm wide. The internode is more than 7 cm long. Nodes are indistinct and scarcely discernible, two successive internode bundles at node seems opposite to subopposite. Leaves are not preserved, and leaf scars not visible. The surface of the internode, is marked with densely (ca. 14–16 per cm) longitudinal ridges and furrows (impressions of vascular bundles).

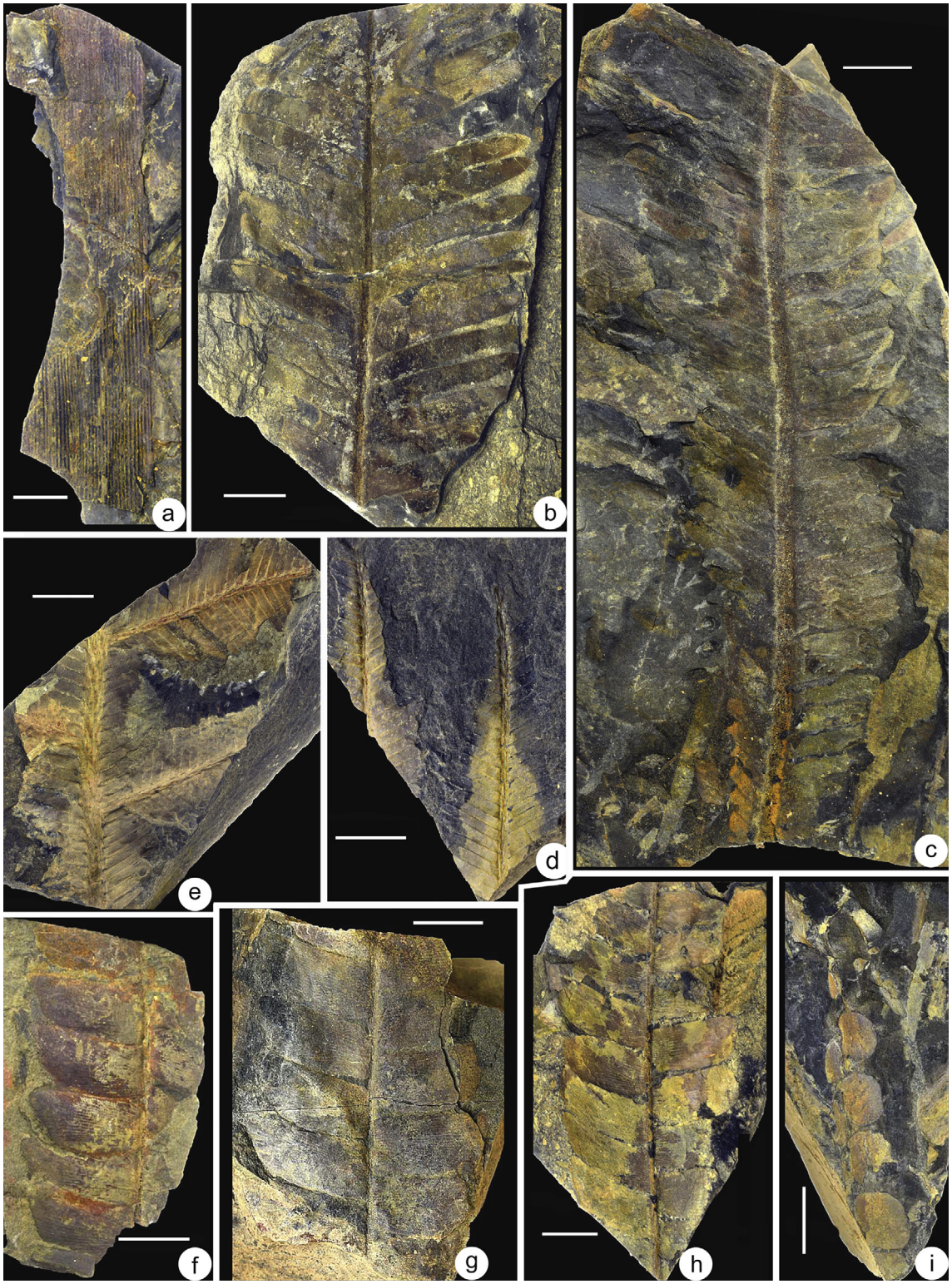

Fig. 3. All specimens deposited in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. a. *Neocalamites* sp., PB22682 b–c. ?*Ptilozamites* sp., PB22686, PB22687 d–e. *Ptilozamites tibetica* Yang, PB22271, PB22272 f–h. *Ptilozamites* sp., PB22683, PB22684, PB22685 i. ?*Zamites* sp 2., PB22691, scale bar: 1 cm.

Remarks: *Neocalamites* is a Mesozoic morphogenus with *Calamites*-like stems and leafy shoots, usually recorded from the Triassic (Taylor et al., 2009); it became rarer after the Lias in China (Sze et al., 1963; Zhou, 1995). All specimens described here are very fragmentary and difficult to compare with any known species of the genus. In the scarcely discernible nodes and distinct longitudinal ridges, the present specimens are somewhat similar to *Neocalamites* cf. *carrerei* (Zeiller) Halle from the Late Triassic to Middle Jurassic of the South and West of China (Sze et al., 1963), and some specimens of *Neocalamites suberosus* (Artabe & Zamuner) from the Triassic of East Antarctica (Bomfleur et al., 2013). It is noted that at node level two successive internode bundles are opposite and occasionally alternate in *N. suberosus*

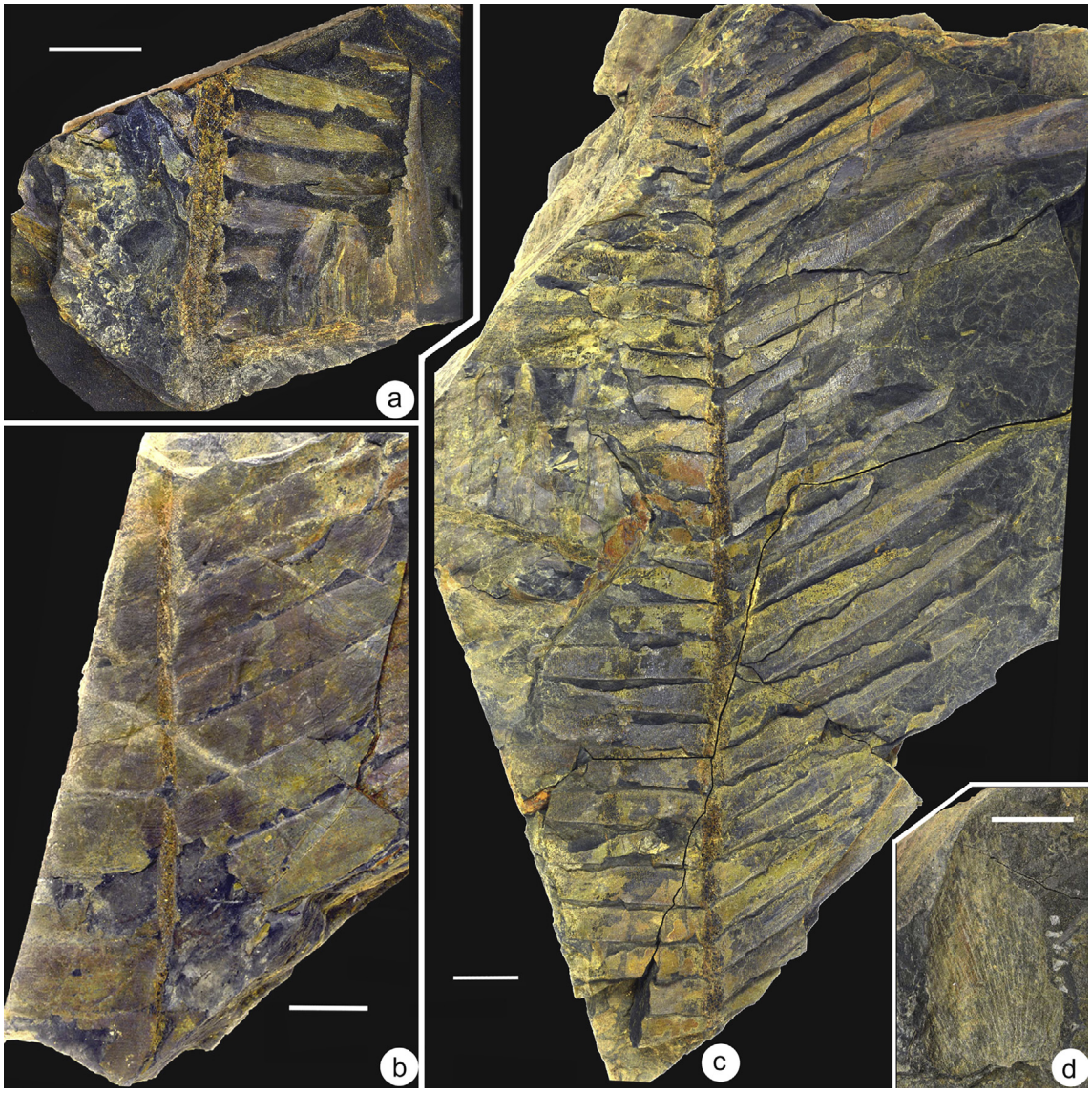

Fig. 4. All specimens deposited in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. a. *Zamites* sp. 1, PB22688 b. *Zamites* sp. 2, PB22689 c. *Ptilophyllum* sp. 1, PB22692 d. ?*Zamites* (? *Otozamites*) sp 1., PB22690, scale bar: 1 cm.

(Bomfleur et al., 2013, Fig. 1D). The present discovery might be the latest record of *Neocalamites* in the Northern Hemisphere.

Pteridospermae

Genus *Ptilozamites* Nathorst

***Ptilozamites tibetica* Yang (Fig. 3d-e)**

2016: *Ptilozamites tibetica* Yang, Yang and Li, p. 472, Fig. 2A–E

Material: specimen numbers PB22271, PB22272

Deposition: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Description: The leaves are bipinnate with a stout penultimate rachis and inflated strumae longitudinally arranged; the ultimate rachis has oblique short ridges. The pinnae are lanceolate, arising alternately on the penultimate rachis at intervals of about 15 mm. The pinnules are narrowly lanceolate to linear, arising alternately to oppositely, especially there are pinnules also arising alternately on the penultimate rachis. Pinnules with an entire margin are arranged closely, and are completely attached laterally to the rachis. Veins arising from the rachis are parallel and indistinct.

Remarks: *Ptilozamites tibetica* Yang (Yang and Li, 2016; p. 472, Fig. 2A–E) is a

Ptilozamites was initially considered a typical genus for the Rhaeto–Liassic (Late Triassic–Early Jurassic) of Sweden (Nathorst, 1878). It has been reported from the Lower Triassic to the Middle Jurassic throughout the Northern Hemisphere (Kustatscher and Van Konijnenburg Van Cittert, 2007). *Ptilozamites tibetica* has bipinnate leaves, unlike typical species of the genus characterized by forked or dichotomous branching leaves, with pinnae arranged closely and alternately on the penultimate rachis as on the ultimate rachis. This taxon might represent a much younger member of *Ptilozamites* extending into the Early Cretaceous on the Tibetan Plateau (Yang and Li, 2016).

***Ptilozamites* sp. (Fig. 3f-h)**

Material: specimen numbers PB22683, PB22684, PB22685

Deposition: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Description: The pinna leaf is incomplete, at least 7.5 cm long and 3.5 cm wide, with the petiole not preserved. The rachis is about 0.7–1 mm in width, and straight. Pinnae are attached entirely on the upper side of the rachis, and alternate; adjacent pinnae are usually contiguous but not overlapped, 15–17 mm long and 7–9 mm wide. The pinnae are elongated and broadly falcate in shape, contracted slightly at base, with an acroscopic margin almost straight and the basiscopic margin also straight but usually curved upward near the top of the

pinnae, the apex obtuse. The veins are parallel and slightly divergent, bifurcating at the base or in the lower part and reaching the lateral margin.

Remarks: These specimens can be attributed to *Ptilozamites*. All of them are incomplete, with neither the upper nor the basal parts of leaves preserved. The present specimens could be compared morphologically with *Ctenozamites* sp. 1 from the Lower Cretaceous Duoni Formation of Baxoi in East Tibet in having a slender rachis with pinnae attached entirely and alternatively on the upper side of the rachis, but the specimen from the Duoni Formation is more incomplete (Liu et al., 2007). As *Ctenozamites* is a synonym of *Ptilozamites* (Popa and McElwain, 2009), the present specimens were described as *Ptilozamites* sp.

? *Ptilozamites* sp. (Fig. 3**b-c)**

Material: specimen numbers PB22686, PB22687

Deposition: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Description: There are two incomplete pinnae, at least 13 cm long and 4.6 cm wide. The rachis are 2–2.8 mm in width. The pinnae are 2–3 cm long and 3–4.5 mm wide, arranged closely, alternative to opposite; adjacent pinnae are always contiguous. The veins are parallel.

Remarks: The characters of the specimens are preserved poorly. The outline and shape are somewhat similar to the pinnae of *Ptilozamites tibetica*: the pinnae closely arranged, alternately or to opposite, adjacent pinnae always contiguous, and veins parallel. However, the size of the present specimens is much bigger than that of *P. tibetica*, and the characteristic of the rachis unclear.

Bennettitales

Genus *Zamites* Brongniart

***Zamites* sp. 1** (Fig. 4**a)**

Material: specimen number PB22688

Deposition: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Description: The specimen is incompletely preserved. The pinna is at least 3.4 cm long and 2.7 cm wide. The rachis is 4 mm in width or wider. The pinnae are distant arising from the rachis at right angles, alternately to opposite with pinna bases strongly and symmetrically contracted. Veins are distinct, radiating and dichotomizing from the base and then parallel to the apex.

Remarks: In having a thick rachis, the present specimen might represent the basal part of a leaf. As the pinna base is contracted symmetrically it could be attributed to *Zamites*. In gross morphology, it somewhat resembles a leaf described by Sze as *Zamites hoheneggeri* (Schenk) Li from the Middle Jurassic at Hechuan of Chongqing, southwestern China (Sze et al., 1963). The present specimen is a fragment with no cuticle preserved, and so it is difficult to compare it with other species of *Zamites*.

***Zamites* sp. 2** (Fig. 4**b)**

Material: specimen number PB22689

Deposition: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Description: A fragment of a leaf with pinnae arranged closely, at least 3 cm long and 1.1 cm wide. The rachis is 2 mm in width. The pinnae alternate, arising at a wide angle from the upper surface of the rachis, with bases slightly and symmetrically contracted. The vein is obscure, radiating slightly at the base and then parallel.

Remarks: The present specimen has broad pinnae with a symmetrical base, similar in part to *Zamites gigas* (L. & H.) Harris from the Middle Jurassic of Yorkshire (Harris, 1969). However, the leaf is preserved incompletely, the shape and size of the pinna unknown and with no cuticle, and so cannot be compared to *Z. gigas*.

?*Zamites* (? *Otozamites*) **sp. 1** (Fig. 4**d)**

Material: specimen number PB22690

Deposition: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Description: This fossil is only a piece of oval pinna, at least 3 cm long and 1.7 cm wide in its middle–lower part. The veins are distinct, radiating and dichotomizing from the base and middle, parallel then gradually tapering to the apex.

Remarks: The present specimen is similar to *Zamites* because the pinna base seems contracted symmetrically, but the base part attached to rachis is not preserved and it is possible forming an auricle as in *Otozamites*. Although very fragmentary, it may be compared with some pinna of *Zamites notokenensis* Watson and Sincock (1992; text fig. 50A–D) or *Zamites manoniae* Watson and Sincock (1992; text fig. 30C).

?*Zamites* sp. 2 (Fig. 3**i)**

Material: specimen number PB22691

Deposition: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Description: A piece of a fragment of leaf, with pinna about as wide as long. The pinnae are arranged closely, rounded square in shape, and bases contracted. The veins are obscure.

Remarks: The specimen seems to be compressed obliquely and deformed. It is difficult to identify how the pinnae are attached on the rachis and the pattern of the veins. The real size and shape of the pinna remain unclear. It is tentatively attributed to ? *Zamites*.

Genus *Ptilophyllum* Morris

***Ptilophyllum* sp. 1** (Fig. 4**c)**

Material: specimen number PB22692

Deposition: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Description: The leaf is incomplete, at least 17 cm long and 11 cm wide with a rachis 2.4–3 mm wide. The pinnae are arranged regularly and closely, sometimes contiguous, opposite, and attached to the upper surface of the rachis; they are linear, with entire and parallel margins, arising at an angle of 70° or more from the rachis, 5–6 mm in width and 50–55 mm or more in length; the upper basal angle is rounded, and the lower basal angle slightly decurrent. The veins are obscure.

Remarks: This leaf is preserved incompletely, without the upper and basal parts, and the lengths and widths unknown. The basal angles of the pinnae are somewhat obscure. Since the pinnae are attached to the upper surface and their acroscopic basal angles are rounded and basiscopic parts are slightly decurrent, the present leaf is attributed to *Ptilophyllum*.

***Ptilophyllum* sp. 2** (Fig. 5**a–b)**

Material: specimen number PB22693

Deposition: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Description: The length of a leaf is unknown but at least 10 cm long, up to 9.6 cm wide in the middle part, narrowing slightly and gradually towards the top. The rachis is 2–2.5 mm wide. The pinnae are arranged regularly and close together, with adjacent pinnae always contiguous and overlapping, opposite or subopposite, linear, with entire and parallel margins, arising at an angle of 80–90° from the rachis, 2–3 mm wide and 45–48 mm long, the apex obtuse or obtuse rounded; the lower base is slightly decurrent. The veins are dense and distinct, 10–13 in number, parallel and occasionally dichotomizing.

Remarks: In respect of the regularly arranged contiguous and overlapping pinnae, and the mosaic at the base on the upper surface of rachis, the present specimens should be attributed to genus *Ptilophyllum*. The present specimen is not similar to any described species of *Ptilophyllum* and so might be a new species.

***Ptilophyllum* sp. 3** (Fig. 5**c-d)**

Material: specimen numbers PB22694, PB22695

Deposition: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Description: Fragmentary leaves are 7 cm long and up to 7 cm wide. The rachis is 2–3 mm wide. The pinnae of one side are attached to the rachis at almost right angles whereas the pinnae on the opposite side are attached to the rachis at an angle of 70° or less. The pinnae are arranged contiguously with adjacent pinnae always in contact, opposite or subopposite, 2.8–4.2 cm long and 2–4 mm wide, and probably

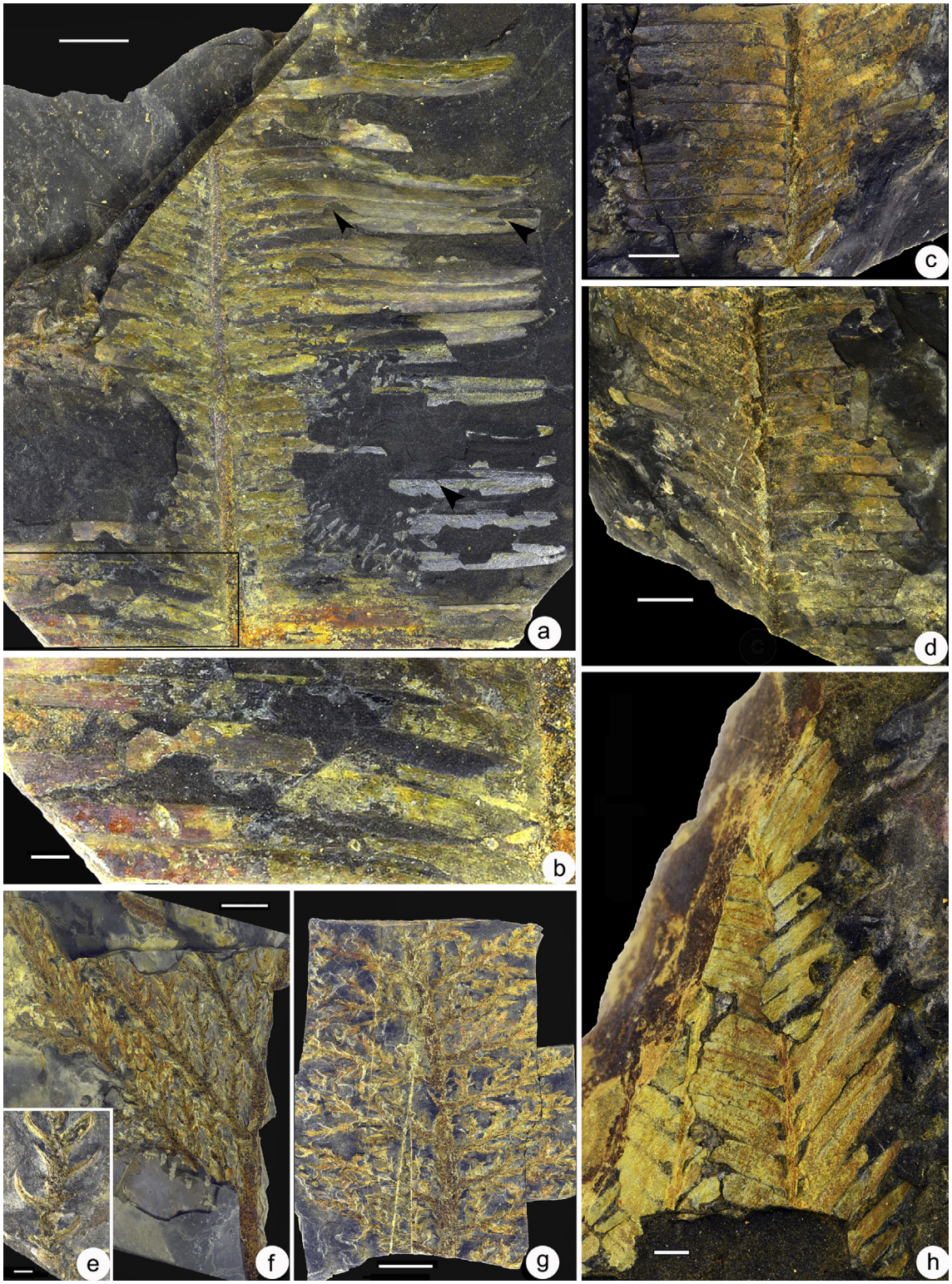

Fig. 5. All specimens deposited in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. a, b. *Ptilophyllum* sp. 2, note the contiguous and overlapped pinnae (arrow), b is an enlargement from the lower-left part of a, showing the overlap of pinnae. PB22693 c, d. *Ptilophyllum* sp., PB22694, PB22695 3. e–g. *Geinitzia* sp., note the subulate leaves (e). PB22696, PB22697, PB22698 h. *Elatocladus* (? *Torreyites*) sp., note the twisted petiole and two possible stomatal grooves on the leaf. PB22699, scale bar: 1 cm (a, c, d, f, g) and 2 mm (b, e, h).

attached to the upper surface of the rachis. The veins are dense and distinct, parallel and occasionally dichotomizing.

Remarks: All specimens belonging to this taxon are incomplete, neither their upper or lower parts preserved, and the base of the pinnae are not clearly shown. It is difficult to identify how the pinnae are attached to the rachis, which is important for bennettitalean taxonomy. All specimens have the pinnae attached to the rachis with different angles on two side of the rachis, which might indicate that the pinnae expanded obliquely from the rachis.

Cupressaceae *sensu lato*

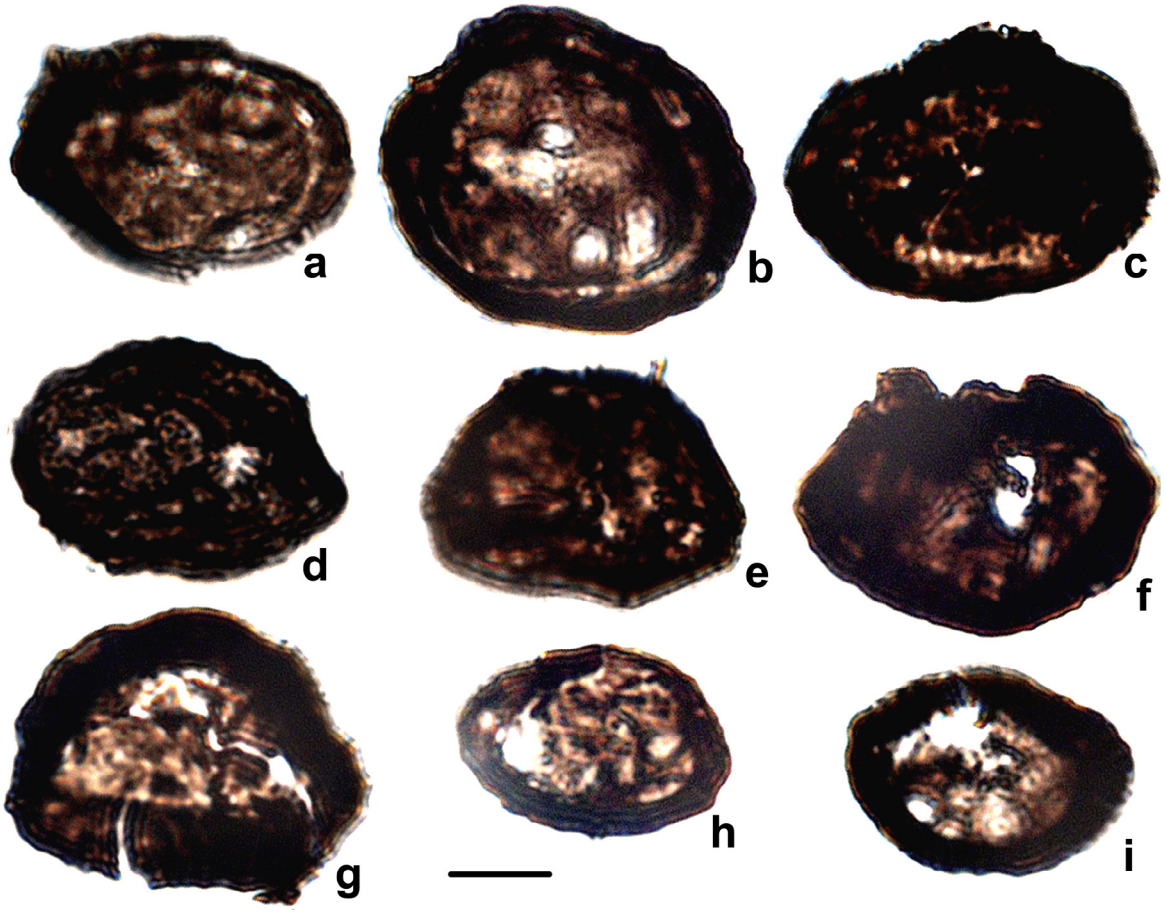

Fig. 6. Representative pollen and spores from the Linbuzong Formation at the Qubsang section. All specimens are from sample 13QS26. Scale bar: 10 μm. A. *Classopollis classoides* (Pflug) Pocock et Jansonius; B. *Classopollis annulatus* (Verbitzkaya) Li; C. *Classopollis* sp.; D. *Zlivisporites* sp.; E. *Foraminisporis wonthaggiensis* (Cookson et Dettmann 1958) Dettmann; F, G. *Cooksonites variabilis* Pocock; H, I. *Cooksonites* spp.

Genus *Geinitzia* Endlicher

Geinitzia sp. (Fig. 5**e–g)**

Material: specimen numbers PB22696, PB22697, PB22698

Deposition: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Description: The main shoot branches in one plane, and leaf twigs branch less regularly but also in one plane. The axis is thick usually up to 4 mm, whereas the smallest one less than 1 mm. Leaves are borne helically and divergent radially, each arising from a decurrent cushion and with the free part strongly falcate; the cross section of the leaf is isodiametric or rhomboidal in shape. They are up to 6 mm long, 0.8 mm wide in the middle part and 1.5 mm wide at the base, tapering to an acute apex (Fig. 5e).

Remarks: In the present collection, vegetative leafy-shoots attributed to *Geinitzia* sp. are abundant. They are thickly massed and appressed on the bedding planes. The shoot systems are richly branched, monopodially or irregularly. Some material similar to the present specimens has been recorded but is not as abundant as at the present locality from the Early Cretaceous in Tibet and all of them were described as *Elatides curvifolia* (Tuan et al., 1977; Li, 1982; Liu et al., 2007). Wherever the shoots are common there are no male or female cones discovered, and so the specimens are described as *Geinitzia* sp.

Taxaceae

Genus *Elatocladus* Halle

Elatocladus (?*Torreyites*) sp. (Fig. 5**h)**

Material: specimen number PB22699

Deposition: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Description: A piece of shoot are about 3.3 cm long and 1.1 cm wide. The axis is slender, about 0.5 mm thick, with spirally disposed but laterally flatted leaves. The leaves are borne closely in almost opposite pairs; the petioles are short and twisted, attached to the uppermost part of the decurrent leaf bases, forming narrow cushions on the axis surface. The leaves are straight or curved slightly, commonly 1.9 cm long and 1.8 mm wide, linear or lanceolate. The lamina is of uniform width in the middle region, in upper part gradually tapering towards the apex, at the base contracted rapidly to a short petiole, usually diverging at an angle of 70° or less; the apex is usually obtuse, and the margins entire. The surface of the leaf is flat, with no obvious midrib present. Between the middle and the edges of the lamina there are two parallel grooves, which suggest stomatal bands.

Remarks: The present specimen was attributed to conifer form genus *Elatocladus* for having no cuticles and reproductive structures. Although the cuticle of the single specimen is not preserved, in general morphology of the shoot and leaves, it exhibits a close agreement with modern species of the genus *Torreya* Arnott, especially in the presence of two well-marked stomatal grooves on the lower surface, and the absence of a prominent midrib. Except for *Torreyites detriti* Watson et al. (2001), most Mesozoic species with *Torreya*-like leaves have been attributed to the modern genus: *Torreya arctica* Bose and Manum (1990), *Torreya borealis* Meng (Chen et al., 1988), *Torreya bureica* Krassilov (1973), *Torreya fangshanensis* Xiao (Xiao et al., 1994), *Torreya gracilis* Florin emend. Harris (1979), *Torreya longifolia* Gomolitzky (1964), *Torreya moelleri* Florin (1958), *Torreya nicanica* Krassilov (1967) and *Torreya valida* Florin (1958). The genus *Torreyites* was erected by Seward (1919) applying it to the type species *Torreyites carolinanum*

(Berry) Seward, but this genus name has been little used. We agree with Watson et al. (2001) that *Torreyites* is a useful and more appropriate form-generic name for fragmentary material lacking reproductive structures. The *Torreya*-like shoot from the Early Cretaceous of Lhasa might belong to *Torreyites*.

4. The miospore assemblage

From the outcrop of the Linbuzong Formation in Qubsang, pollen and spores were recovered from two samples, i.e. 13QS26 and 13QS27; the latter sample was collected from a black shale bed about 30 m below the bed containing 13QS26. The two samples are similar in composition. Trilete spores are low in number and diversity. No bisaccate pollen is encountered in the assemblage. Both samples are dominated by *Classopollis*, with subordinately common *Cooksonites*, *Spheripollenites* and *Foraminisporis*. The miospore assemblage from the Qubsang section is composed of *Classopollis classoides* (Pflug) Pocock et Jansonius, *Classopollis annulatus* (Verbitzkaya) Li, *Classopollis* sp., *Zlivisporites* sp., *Foraminisporis wonthaggiensis* (Cookson et Dettmann) Dettmann, *Cooksonites variabilis* Pocock and *Cooksonites* spp. (Fig. 6).

The co-existence of *Cooksonites* and *Foraminisporis* suggests an Early Cretaceous age for the assemblage. The abundant occurrence of *Classopollis*, which has an affinity to the Cheirolepidaceae, together with the relatively low abundance of pteridophyte spores indicates a hot and arid climate during the deposition of this formation.

5. Discussion on botanical characters and geological age of the plant assemblage

A total of 13 plant species belonging to six genera is identified in this study. The assemblage consists of *Neocalamites* sp., *Ptilozamites tibetica* Yang, *Ptilozamites* sp., ?*Ptilozamites* sp., *Zamites* sp. 1, *Zamites* sp. 2, ?*Zamites* (?*Otozamites*) sp. 1, ?*Zamites* sp. 2, *Ptilophyllum* sp. 1, *Ptilophyllum* sp. 2, *Ptilophyllum* sp. 3, *Geinitzia* sp. and *Elatocladus* (?*Torreyites*) sp. Among these, *Ptilozamites* and *Elatocladus* (? *Torreyites*). are discovered in Tibet for the first time. In this assemblage, the Bennettitales are the most dominant components, especially *Ptilophyllum*. Pteridosperms and presumed cycadophytes, such as *Ptilozamites* rank second. Two conifers are found in the assemblage: *Geinitzia* sp. is very abundant in specimens; the presence of *Elatocladus* (? *Torreyites*) sp. is firstly recorded in this area. The occurrence of such older Mesozoic elements as *Ptilozamites* and *Neocalamites* in the assemblage, is noteworthy. So far, *Ptilozamties tibetica* is the only species reported from the Early Cretaceous (Yang and Li, 2016). *Neocalamites* had declined since the late Middle Jurassic and taxa of this genus are very rarely reported from the late Mesozoic (Taylor et al., 2009).

Up to now, several late Mesozoic assemblages have been studied in Tibet. The assemblages from the Chuanba Formation in Gerze (Li and Wu, 1991), the Risong Group in Shiquanhe (Chen and Yang, 1983), and the assemblages of northeastern Lhasa (Tuan et al., 1977), as well as the rich assemblage of the Tuoni and Lagongtang formations in Changdu (Li, 1982; Liu et al., 2007; Zhou and Liu, 1987), are all from coal-bearing strata characterized by having *Klukia*, *Gleichenites*, *Cladophlebis*, *Onychiopsis*, *Ptilophyllum*, *Nilssonia*, *Pterophyllum*, *Zamiophyllum*, *Frenelopsis* and *Brachyphyllum*, and absence of ginkgoaleans, czekanowskialeans and podozamitaleans. The present assemblage is in general agreement with these assemblages in having dominant tropical and semi-tropical elements such as Bennettitales and conifers and a lack of temperate elements such as ginkgoaleans, czekanowskialeans and podozamitaleans. The former are all Lower Cretaceous assemblages of northern Tethys and Pangea. The Qubsang plant assemblage likely represents an early Early Cretaceous age.

The small assemblage collected from the Lower Cretaceous Puna Formation in Tingri, southern Tibet consisting of *Cladophlebis* sp., *Pachypteris specifica* Feistmantel, *Ptilophyllum acutifolium* Morris, *Araucarites minutus* Bose et Maheshwari, *Elatocladus tenerrimus* (Feistmantel) Sahni, *Brachyphyllum* (*Allocladus*?) sp., *Coniferocaulon rajmabalense* Gupta and *Coniferocaulon* sp. (Zhou and Wu, 1994) appears to be very different from the present assemblage. Although they are no great differences in botanical composition, the Puna assemblage is marked by a “Gondwana Aspect”. All identified taxa are typical of the Upper Gondwana flora and the assemblage should belong to Assemblage Zone 9 in India (Sukh-Dev, 1988).

The spore-pollen assemblage from the Linbuzong Formation in the Qubsang section is composed of *Classopollis classoides* (Pflug) Pocock et Jansonius, *Classopollis annulatus* (Verbitzkaya) Li, *Classopollis* sp., *Zlivisporites* sp., *Foraminisporis wonthaggiensis* (Cookson et Dettmann) Dettmann, *Cooksonites variabilis* Pocock and *Cooksonites* spp., which also suggests an Early Cretaceous age for the plant-bearing bed. It is different from the previous studied spore-pollen assemblage from the Linbuzong Formation in Maizhokunggar County, East Lhasa (Zhou, 1994), which contains more pteridophyte spores including *Leiotriletes* sp., *Lygodiumsporites subsimplex* (Bolch.) Gao et Zhao, *Verrucosisporites* sp., *Biretisporites* sp., *Concavissimisporite* sp., *Schizaeoisporites* sp., *Pterisisporites* sp., *Cicatricosisporites pseudotripartites* (Bolch.) Dettmann, *Cicatricosisporites dorogensis* (Potonié et Gennetich) Couper, *Murospora* sp., *Classopollis muralis* Bai and *Classopollis annulatus* (Verb.) Li and less numerous *Classopollis* than the Qubsang palynoassemblage, suggesting a younger Early Cretaceous age (Zhou, 1994). Ammonites *Lytoceras* sp. and bivalves *Cuspidaria* sp., *Astarte*? sp., *Exogyra* sp., *Caestocorbula* sp., *Inoceramus* sp. and *Parallelodon* sp. recorded from the Linbuzong Formation were also considered as Early Cretaceous (Wang et al., 1983).

Thus, the geological age of the Qubsang plant-bearing bed is proposed as Early Cretaceous.

6. Palaeoenviromental implications

Fossil plants are important indicators of palaeoenvironment and palaeoclimate. Although most of plant remains from Qubsang are incompletely preserved, making it difficult to identify them at the species level, the genera of the assemblage exhibit that most fossil plants of Qubsang lived in tropical and subtropical, and arid or semi-arid climates. Representative is the order Bennettitales, and perhaps the genus *Elatocladus* (? *Torreyites*) sp. (?family Taxaceae). The extinct group Bennettitales flourished with many species, and represents a major component of the assemblage. Study of the English Wealden floras has shown that many leaves of Bennettitales bear xeromorphic characters, such as stomatal pits overhung by papillae, stomata confined to narrow grooves, numerous trichomes, and the likelihood of a large amount of cuticular wax on the upper cuticle (Sincock and Watson, 1988; Watson and Sincock, 1992). The absence of Ginkgoales in the assemblage supports such an inference. *Ginkgo*-like leaves usually were widely distributed at high latitudes in the Mesozoic (Zhou, 2009), and the absence in the Qubsang assemblage might indicate both a low latitude and high temperatures. It is likely that for much of the period of deposition of the Qubsang sedimentary succession, the climate was characterized by dry seasons of varying length.

It is noteworthy that ferns are absolutely absent in this assemblage, similar to what is seen in the Hastings Beds of the English flora (Watson and Alvin, 1996). It was interpreted that periods of aridity then were probably severe, combined with high temperatures and probably accompanied occasionally by vegetation fires (Watson and Alvin, 1996). So, the Qubsang environment was likely similar to that of the Hastings Beds, as a variable salinity coastal mudplain with lagoons and sandy watercourses with variable river-flow producing sometimes coalescent alluvial fans (Allen, 1976); the assemblage is preserved in what was near-coastal mudplain deposits.

As mentioned above, the plant assemblage of the Linbuzong Formation differs from other coeval assemblages of coal-bearing formations in Tibet in its relative lack of ferns and predominance of bennettitaleans and conifers. The miospore assemblage, containing abundant *Classopollis* (Cheirolepidiaceae) and a few fern spores points

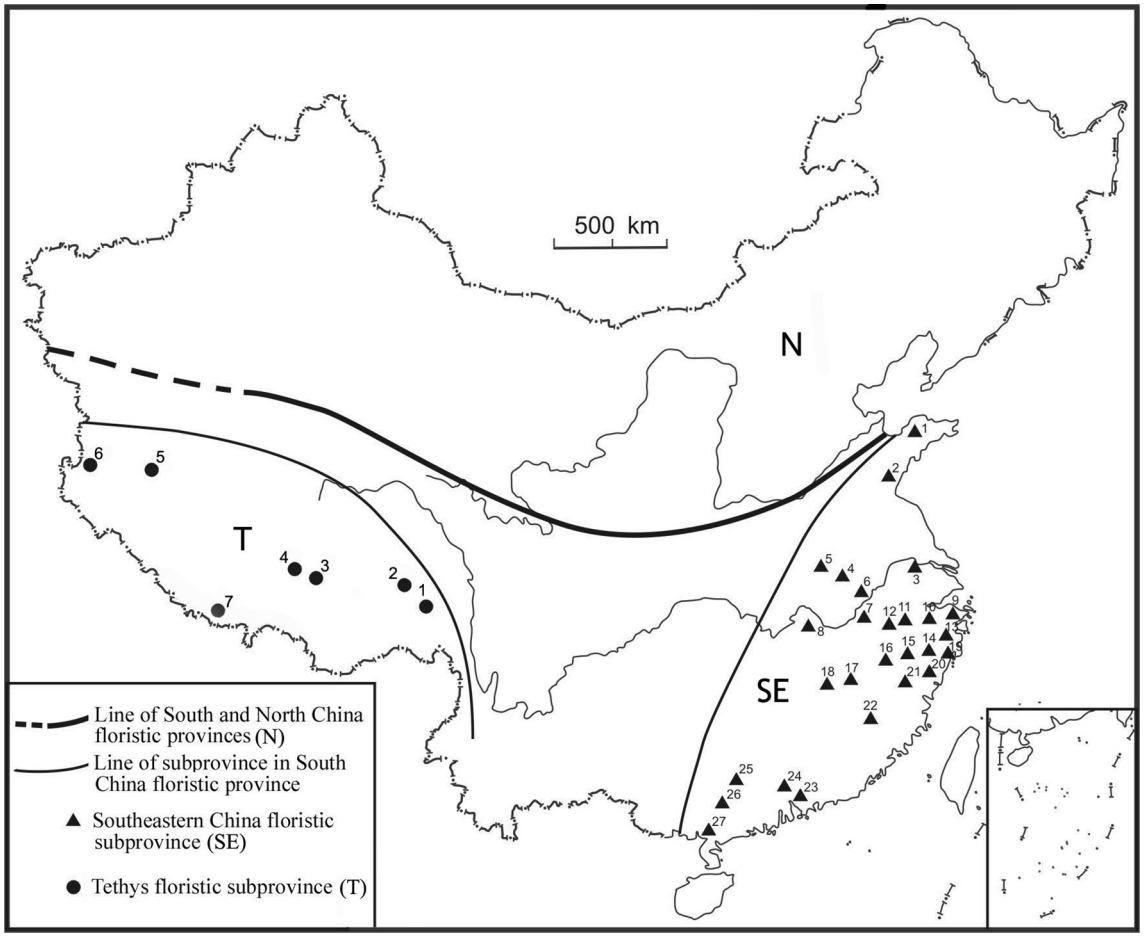

Fig. 7. Distribution and division of the southern China floristic province in the Early Cretaceous. ▲ Fossil plant sites in the southeastern China floristic subprovince: 1. Laiyang, Shandong; 2. Zhucheng, Shandong; 3. Qixiashan, Jiangsu; 4. Liu'an, Anhui; 5. Lujiang, Anhui; 6. Congyang, Anhui; 7. Shangcheng, Henan; 8. Lingxiang, Hubei; 9. Ningbo, Zhejiang; 10. Shengzhou, Zhejiang; 11. Jinhua, Zhejiang; 12. Shouchang, Zhejiang; 13. Linhai, Zhejiang; 14. Lishui, Zhejiang; 15. Jiangshan, Zhejiang; 16. Shangrao, Jiangxi; 17. Linchuan, Jiangxi; 18. Fengcheng, Jiangxi; 19. Wenling, Zhejiang; 20. Taishun, Zhejiang; 21. Zhenghe, Fujian; 22. Yong'an, Fujian; 23. Bao'an, Guangdong; 24. Guangzhou, Guangdong; 25. Tengxian, Guangxi; 26. Rongxian, Guangxi; 27. Bobai, Guangzi. ● Fossil plant sites in the Tethys floristic subprovince 1. Baxoi; 2. Lhorong; 3. Linzhou; 4. Duilongdeqing; 5. Shiquanhe; 6. Gerze; 7. Tingri.

to a similar composition of the vegetation. It seems, therefore, that the absence of ferns might not be the result of transport and depositional factors, but was caused by the constitutional disparities of the plant communities. The richly branched conifer *Geinitzia* sp. dominated in the assemblage and is usually well-preserved and sometimes forms thick masses. It indicates that such specimens did not suffer high-energy transportation or transport over long distance. The well-preserved leaves of *Ptilozamites* also support this deduction.

The abundance of cheirolepidiaceous conifers and bennettitaleans, especially *Ptilophyllum* characteristic of mangrove-like vegetation (Vakhrameev, 1991), suggests that the assemblage represents a lowland and seashore salt marsh-mangrove forest not far from the site of deposition.

The Qubsang plant assemblage shows a relationship to the Early Cretaceous floras of the Tethys area, belonging to the Indo-European Realm or Euro-Sinian Realm of Vakhrameev (1991), and to the *Ruffordia–Onychiopsis* flora by Sze and Chow (1962). Zhou and Li (1980) proposed the term *Weichselia–Ptilophyllum boreale* assemblage to refer to the Late Mesozoic floras of southern China. Up to now there are at least seven plant assemblages that have been discovered from the Early Cretaceous in Tibet. In general aspect, except for the Puna assemblage from southern Tibet, all other plants from coal-bearing beds closely resemble the Wealden flora of Western Europe, and are quite different in floristic composition from those in the southeastern China, such as at Shandong (Liu, 1990), Zhejiang (Cao, 1982, 1999), Fujian (Wang et al.,1982), Anhui and Guangdong provinces (Wang et al.,1982). In the southeastern Chinese floras, there is no authentic record of *Weichselia* characteristic of the European and Tethys floras. On the contrary, *Dictyozamites*, one of the most important elements of the Inner Zone of Japan, which exists also in Shandong, Zhejiang and Fujian, is entirely absent from the Tibet flora. Based on these differences, the southern China floristic province in the Late Mesozoic may, therefore, be further divided into two subprovinces: the southeastern China floristic subprovince characterized by the *Dictyozamites–Ptilophyllum boreale* assemblage and the Tethys floristic subprovince characterized by the *Weichselia–Ptilophyllum boreale* assemblage (Fig. 7).

7. Conclusions

The small assemblage collected from the Lower Cretaceous Linbuzong Formation of Qubsang, Doilungdeqen, Lhasa, Tibet, comprises *Neocalamites* sp., *Ptilozamites tibetica* Yang, *Ptilozamites* sp., ?*Ptilozamites* sp., *Zamites* sp. 1, *Zamites* sp. 2, ?*Zamites* (? *Otozamites*) sp. 1, ?*Zamites* sp. 2, *Ptilophyllum* sp. 1, *Ptilophyllum* sp. 2, *Ptilophyllum* sp. 3, *Geinitzia* sp. and *Elatocladus* (? *Torreyites*) sp. Among these plants *Ptilozamites tibetica* and *Elatocladus* (? *Torreyites*) sp. are discovered for the first time in this area, and the others frequently occur in the Mesozoic flora in Tibet. In this assemblage, the Bennettitales are the predominant components, especially *Ptilophyllum*, while *Geinitzia* sp. is very abundant in number of specimens. The occurrence of *Ptilozamites*

and *Neocalamites* in the assemblage is noteworthy, for both genera had declined since the late Middle Jurassic and are very rarely reported from later Mesozoic. The Qubsang plant assemblage likely represents an early Early Cretaceous age, older than other assemblages of floras in Tibet. The co-existence of miospores also suggests an Early Cretaceous age for the assemblage. The abundance of *Ptilophyllum* and conifer *Geinitzia* sp. and the absent of Ginkgoales might indicate both a low latitude and high temperatures, and that a tropical arid to semi-arid climate dominated this area in a coastal environment. The characteristics of this assemblage, in accordance with the miospores, suggest that the assemblage represents a lowlands and seashore salt marsh–mangrove forest not far from the site of deposition.

The Qubsong assemblage, composed mainly of Bennettitales and Coniferopsida, does not resemble any contemporaneous ones known from Gondwanaland or Eurasia but shows a general relationship to floras of the Tethys area. It might roughly correspond in age to the Wealden floras of Western Europe.

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