



Systematic palaeontology (Palaeobotany)

## *Annalepis*, a pioneering lycopsid genus in the recovery of the Triassic land flora in South China

*Annalepis*, un genre de lycopside pionnier dans la reconstitution d'une flore terrestre triasique en Chine du Sud

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### ABSTRACT

Fossil plants are scarce in the Earliest Triassic marine deposits of western Guizhou and eastern Yunnan. Only *Annularia shirakii*, *Lobatannularia* sp., *Paracalamites stenocostatus*, *Gigantopteris* sp., *Pecopteris* sp. were reported from the base of the Kayitou Formation dated as Early Induan by marine fauna. Recently, we discovered numerous representatives of the genus *Annalepis* in the same Lowermost Triassic beds: *A. latiloba*, *A. brevicystis*, *A. angusta*, *Annalepis* spp. occur associated with a basal Triassic marine fauna. This discovery fills the biostratigraphic gap between the Late Permian “*Gigantonoclea guizhouensis*–*Ullmannia* cf. *bronnii*–*Annularia pingloensis*” and the late Lower Triassic “*Neuropteridium*–*Albertia*–*Voltzia*” assemblages reported from South China. It represents an important datum dealing with the very beginning of a new terrestrial flora installation after the Permian flora disappearance following the Permian–Triassic boundary mass extinction. This “starting point” of a new vegetal cover in South China is to be taken into account in reconstructing through space and time the settlement process of the Mesozoic floristic provinces.

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### R É S U M É

Les plantes fossiles sont rares dans le Trias basal marin du Guizhou occidental et du Yunnan oriental. Ont été identifiées *Annularia shirakii*, *Lobatannularia* sp., *Paracalamites stenocostatus*, *Gigantopteris* sp., *Pecopteris* sp. à la base de la Formation Kayitou, datée Induen par sa faune marine. Récemment, nous avons découvert de nombreux spécimens du genre *Annalepis* dans les mêmes strates du Trias basal. Ont été identifiées : *A. latiloba*, *A. brevicystis*, *A. angusta*, *Annalepis* spp. Elles sont associées avec une faune marine du Trias basal et les rares éléments permien de la « flore à Gigantoptérides » ayant persisté dans le Trias inférieur. La découverte de cette nouvelle paléoflore comble le hiatus floristique entre les associations « *Gigantonoclea guizhouensis*–*Ullmannia* cf. *bronnii*–*Annularia pingloensis* » (Permien supérieur) et « *Neuropteridium*–*Albertia*–*Voltzia* » (sommet du Trias inférieur) de Chine du Sud. Cela constitue une donnée importante sur le début de réinstallation d'une flore terrestre au Trias basal après la disparition de la flore permienne, liée à la

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crise d'extinction biologique de la limite Permien–Trias. Ce « point de départ » d'un couvert végétal en Chine du Sud devra être pris en compte dans la reconstitution spatiotemporelle des processus de mise en place des diverses provinces floristiques mésozoïques.

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## 1. Introduction

It is well known that most of South China was located in a vast ocean during the Lower–Middle Triassic and that, therefore, the fossil plants are quite rare in these marine deposits. Indeed, in studying the floras of this area, one is always struck by the almost entire absence of fossil plants in the Lower Triassic deposits. However, in the recent years, palaeobotanists regularly reported the presence of fossil plants from the late Lower and Middle Triassic series of the Yangtze River region and the Hainan Island (Liu et al., 2004; Meng, 1996, 1998; Meng and Li, 2002; Ye, 1979; Zhou and Li, 1979). A flora characterized by Lycopsidea, consisting of especially spectacular *Pleuromeia* and *Annalepis* specimens, has been found from the Middle Triassic (Anisian and Ladinian) in the Yangtze Gorge area (Meng, 1995, 1999). Similarly Zhou and Li (1979) described fossil plants from the Early Triassic Lingwen group exposed along the Jiuqu River in Hainan Island and indicated that this taphoflora can be compared with that of the “Buntsandstein” flora of Europe. It is worth noting that in western Europe, where the “Buntsandstein” flora has been originally described, its age is regarded as late Early Triassic, i.e. Olenekian, to early Middle Triassic, i.e. Early Anisian (Grauvogel-Stamm, 1978; Grauvogel-Stamm and Ash, 2005a, 2005b; Mader, 1990).

The genus *Annalepis* (Fliche) was reported for the first time in the Middle Triassic of Lorraine, France (Fliche, 1910). Later it has been emended (Grauvogel-Stamm and Düringer, 1983; Ye, 1979). Indeed, although it is one of the most important lycopsids of the Triassic, besides *Pleuromeia*, it passed unnoticed for a long time because of a misunderstanding of its structure and therefore of its affinities. As a matter of fact, originally the genus *Annalepis* was thought to have gymnospermous (*Araucarites*-like) affinities (Fliche, 1910). In contrast, Schuster (1931) suggested that it belongs to the Cycadaceae but finally he abolished it. However, Ye (1979) described some *A. zeilleri* specimens within a Middle Triassic flora in Hubei and Sichuan Provinces, South China, and suggested that this taxon belongs in fact to the Lepidodendrales rather than to the Gymnosperms. Grauvogel-Stamm and Düringer (1983) similarly described *A. zeilleri* from the Ladinian of eastern France, and showed that they are sporophylls of lycopsids containing microspores of the *Aratrisporites* type. These authors also concluded that *A. zeilleri* belongs to the Lepidodendrales. Meng (1998) definitely indicated that *Annalepis* resembles the living plant *Isoetes* in many aspects, such as its herbaceous habit with a corm, its more or less clustering sporophylls, the presence of a ligule, its monolet microspores of the *Aratrisporites*-type and its trilete megas-

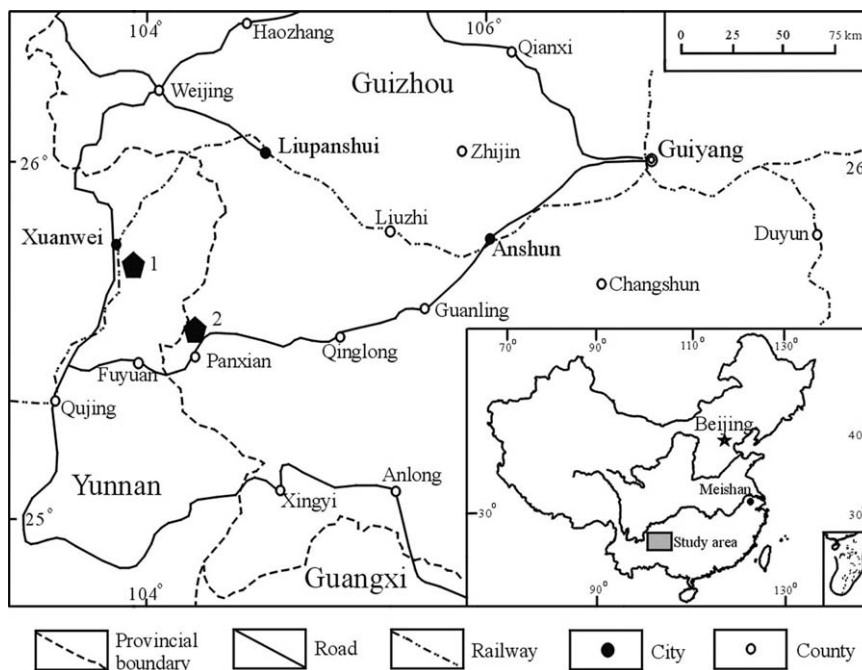
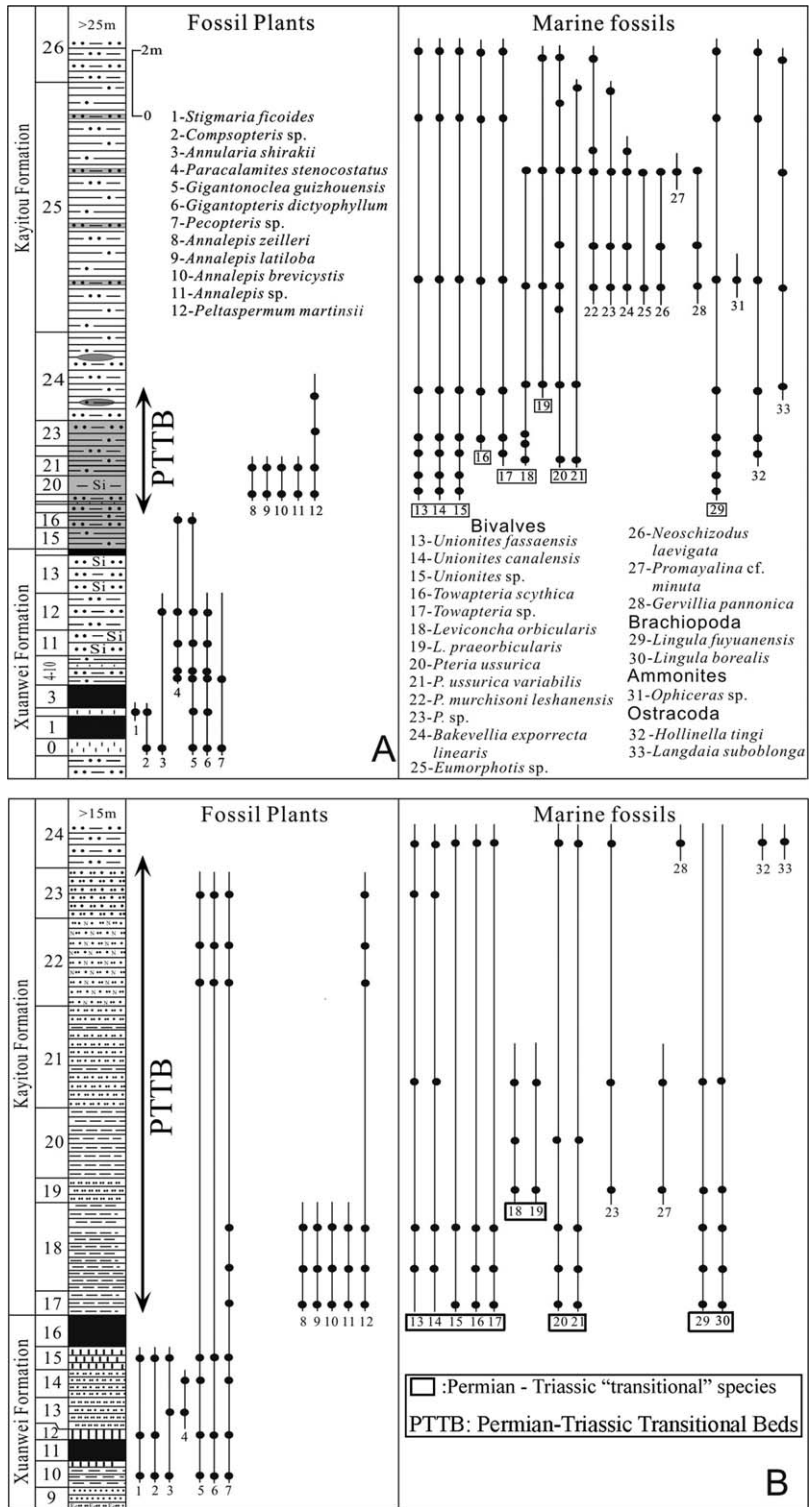


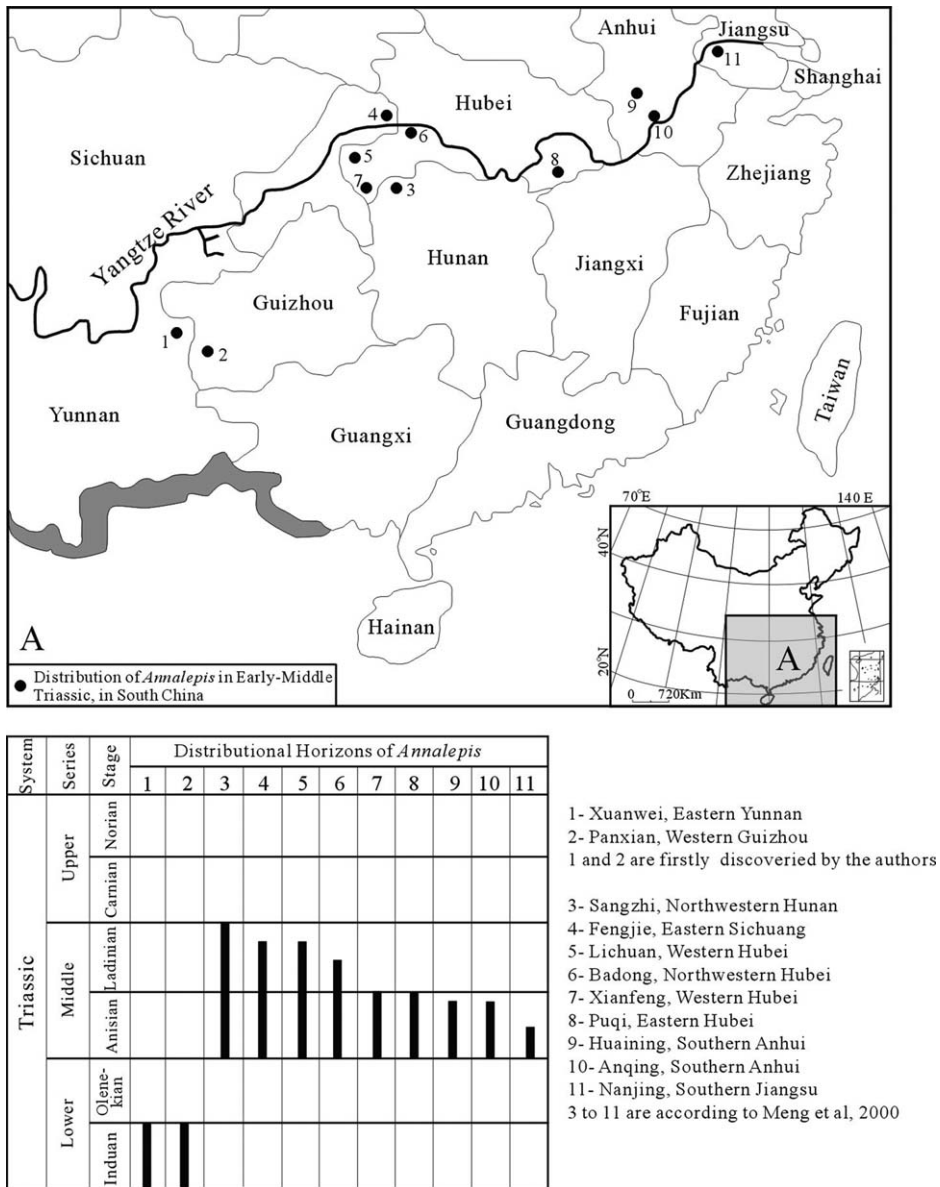
Fig. 1. Geographic location of the studied areas: western Guizhou (2 - Tucheng Section) and eastern Yunnan (1 - Mide Section).

Fig. 1. Localisation géographique du secteur d'étude : Guizhou occidentale (2 : section de Tucheng) et Yunnan oriental (1 : section de Mide).



**Fig. 2.** Stratigraphical distribution of the plant and marine fossils during the Permian-Triassic transition, i.e. in the Upper Permian Xuanwei Formation and in the Lower Triassic Kayitou Formation of the Mide (A) and Tucheng (B) sections.

**Fig. 2.** Distribution stratigraphique des plantes et des fossiles marins au passage Permien-Trias, au sommet du Permien supérieur de la Formation Xuanwei au Trias inférieur de la Formation Kayitou dans les sections de Mide (A) et Tucheng (B).



**Fig. 3.** Geographical and stratigraphical distributions of *Annalepis* in South China.  
**Fig. 3.** Distribution géographique et stratigraphique d'*Annalepis* en Chine du Sud.

pores (Fig. 5, 14). Ultrastructural studies of its microspores have shown that they have characteristic isoetalean features (Grauvogel-Stamm and Lugardon, 2001).

*Annalepis* was considered as important for identifying deposits of the late Early and Middle Triassic age. It was also shown to extend into the Carnian (Meng et al., 2000). However, as demonstrated in the present article, in fact this genus appeared in the Early Induan Kayitou Formation (Liu and Yao, 2002) in western Guizhou and eastern Yunnan. Moreover, as all the specimens attributed to this genus in the past, the new ones consist of isolated sporophylls (Fig. 5, 1–12). It is worth noting that this genus is more widely distributed than *Pleuromeia* in South

China and that the first appearance of the latter is dated from the Anisian whereas in western Europe this genus is characteristic of the Olenekian (Grauvogel-Stamm, 1999; Grauvogel-Stamm and Ash, 2005a). Until now, the genus *Annalepis* was reported in South China only from the Middle Triassic in eastern Sichuan, western Hubei, northwestern Hunan, eastern Anhui and western Jiangsu (Meng, 1994; Meng et al., 2000) (Fig. 3). Its discovery in the basal deposits of the Kayitou Formation of western Guizhou and eastern Yunnan shows now that, in fact, it was already present in the earliest Triassic (Figs. 2, 4). *Annalepis* often grew in inland swamps near the coast or lived in shallow water and wet soil, like modern *Isoetes* (Wang, 1991).

Taxa	Permian		Triassic		
	Late Permian		Early Triassic		Middle-Late Triassic
	Wuchia-pingian	Changhsingian	Induan	Olenekian	
<b>Bivalves</b>					
<i>Unionites fassaensis</i>		--			
<i>Unionites canalensis</i>		--			
<i>Towapteria scythica</i>					
<i>Leviconcha orbicularis</i>		--			
<i>L. praeorbicularis</i>		--			
<i>Pteria ussurica</i>		--			
<i>P. ussurica variabilis</i>		--			
<i>P. murchisoni leshanensis</i>		--			
<i>Bakevellia exporrecta linearis</i>					
<i>Eumorphotis</i> sp.					
<i>Neoschizodus laevigata</i>					
<i>Promyalina vetusta minuta</i>					
<i>Gervillia pannonica</i>					
<b>Brachiopoda</b>					
<i>Lingula fuyuanensis</i>					
<i>L. borealis</i>					
<b>Ammonites</b>					
<i>Ophiceras</i> sp.					
<b>Ostracoda</b>					
<i>Hollinella tingi</i>					
<i>Langdaia suboblunga</i>					

According to Rong and Fang, 2004, -- stands for Permian-Triassic boundary beds

Fig. 4. Stratigraphical range of the marine fossils during the Late Permian–Triassic transition in South China (after Rong and Fang, 2004).

Fig. 4. Extension stratigraphique des fossiles marins du Permien supérieur au Trias en Chine du Sud (d'après Rong and Fang, 2004).

## 2. Materials and methods

The numerous dispersed and well preserved *Annalepis* specimens described in the present paper have been collected in the lower part of the Kayitou Formation at the Mide section, within Xuanwei City of the Yunnan Province and at the Tucheng section, Panxian County, Guizhou Province (Fig. 1). These sections include the Upper Permian Xuanwei Formation and the lower part of the Kayitou Formation. The Xuanwei Formation consists of terrestrial clastics sediments (sandstones and siltstones), interbedded with coal beds and/or seams. It is conformably overlain by the Kayitou Formation, mainly composed of siltstones and mudstones interbedded with sandstone.

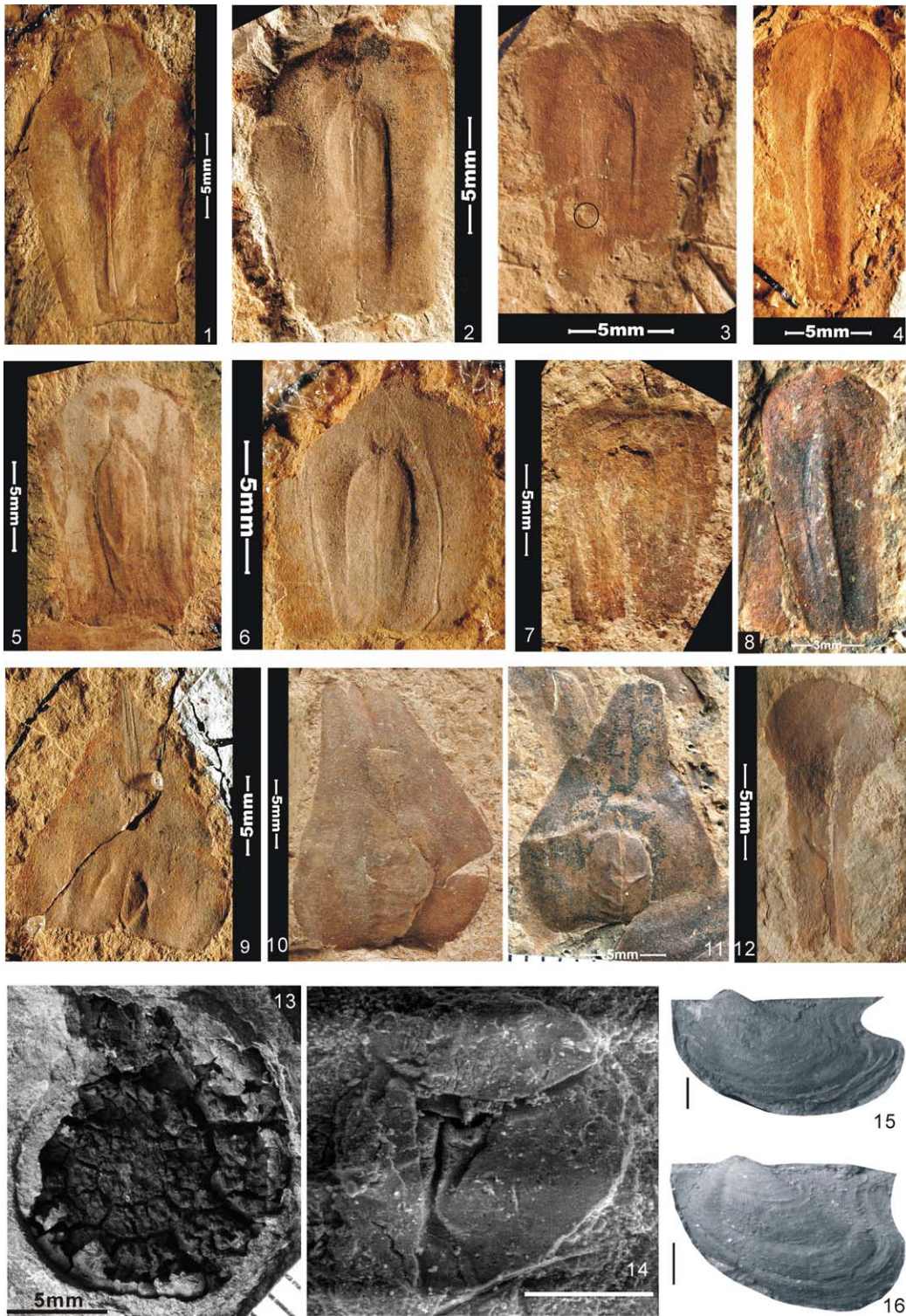
The elements of the *Gigantopteris*-flora, such as *Stigmara*, *Lepidodendron*, *Paracalamites*, *Gigantopteris*, *Gigantonoclea* and *Pecopteris* which are relics, come from the Kayitou Formation in the Mide and Tucheng sections. *Annalepis*, *Stigmara*, *Pecopteris* and *Lepidopteris* (al. *Calopteris*) *martinsii*-like foliage associated with *Peltaspermum* radially symmetrical peltate ovuliferous discs have been found in the Beds 19 and 21 of the Mide section and in Beds 17 and 18 of the Tucheng section (Fig. 2) (Yu, 2008) where they are associated with Early Triassic marine bivalves<sup>1</sup> such as *Unionites*, *Pteria*, etc. and the brachiopod *Lingula*. Many Early Triassic marine bivalves (*Leviconcha*, *Pteria*, *Towapteria*, *Unionites*, etc.), brachiopods (*Lingula*), ammonites (*Ophiceras*) and ostracods (*Langdaia*, *Hollinella*)

have been found in the overlying Beds 22–25 of the Kayitou Formation. The Tucheng section has yielded the same fossil assemblage as the Mide Section (see Fig. 2). The specimens of *Annalepis* which have been collected consist of isolated sporophylls, some of which still show the insertion site of their ligule.

## 3. Updated Nomenclatural aspects

Very recently (Kustatscher et al., 2010), studying an outstanding Triassic material from the Dolomites, considered “the two genera *Annalepis* and *Lepacyclotes* to be identical” following the emendation proposed by Retallack (1997). We do not follow, at the moment in the framework of this paper, this treatment. The emended diagnosis given by Retallack for the genus *Lepacyclotes* Emmons 1856, making *Annalepis* Fliche 1910 falling down as a junior synonym, is mainly based on the cormus organisation. He postulated that: “separation of *Annalepis* from *Lepacyclotes* can no longer be supported, considering that the latter probably: (!) also has microspores of *Aratrisporites*”. Kustatscher et al. are, without any doubt, right to put their fossil remains into *Lepacyclotes* as this material is complete enough to do so. Furthermore, it appears that their new species *Lepacyclotes bechstaedtii* would had been a better new type species for this genus than the Retallack’s emendation of *Lepacyclotes circularis* Emmons, insofar as the ICBN would allow it. In our present work, we are dealing only with disarticulated sporophylls, undoubted related to quillworts but unable to provide enough comparative characters to be definitely reported to *Lepacyclotes*. In our mind the naming *Annalepis* is to be considered here only as a form genus to accommodate isolated sporophylls of still uncertain generic affinity (as initially stated besides). By the way, it is clearly out of

<sup>1</sup> Some of those marine species are now considered as to appear in the Latest Permian and to extend into the Triassic since the new PTB based on conodonts has been accepted (i.e. “transitional forms”) (Rong and Fang, 2004).



**Fig. 5.** Fossils of the Kayitou Formation (Lower Triassic) in the Mide and Tucheng Sections (YXM - Yunnan, Xuanwei, Mide; GPT - Guizhou, Panxian, Tucheng). 1-12: Lycophyte sporophylls assigned to several species of the genus *Annalepis* (Fliche). 1-3, 5-7. *Annalepis latiloba* Meng, 1998; black circle on the Fig. 3 = megaspore (cf. Fig. 14); Locality: Mide section; Sample Numbers: 1: YXM-21-27; 2: YXM-21-2; 3: YXM-21-11; 5: YXM-21-29; 6- YXM-19-2; 7: YXM-21-37. 4, 8, 12. *Annalepis angusta* Meng, 1995. Locality: Mide section; Sample Numbers: 4: YXM-21-5; 8: YXM-21-1; 12: YXM-19-11. 9-11. *Annalepis brevicystis* Meng, 1995. Locality: Mide section; Sample Numbers: 9: YXM-21-7; 10: YXM-21-18; 11: YXM-21-63. 13. *Ophiceras* sp.; Locality: Mide section; Sample Number: 13: YXM-25-5. Detail of the in situ megaspore of *A. latiloba* shown in Fig. 3 (black circle). Note its smooth surface and its trilete mark. Scale bar = 0.5 mm. 15-16. *Pteris ussurica variabilis* Chen et Lan, 1956; Localities: Mide and Tucheng sections; Sample Numbers: 14: YXM-21-68; 15: GPT-17-15; Scale bar = 1 mm.

the scope of this paper to perform an extensive revision of the numerous fossil remains named as *Annalepis* to attribute each to one or another genus within the complex *Lepacyclotes–Annalepis–Tomioistrobus–Skillioistrobus Isoetites*... being clear, besides, that we still need to discover which kind of cornus were bearing it, especially for the Chinese remains.

#### 4. Biostratigraphic and biogeographic discussions

From the distribution pattern in time and space of the *Annalepis*-type fossils (Fig. 3) and the related genera (Grauvogel-Stamm and Lugardon, 2001) coupled with the extant *Isoetes* (Hoot and Taylor, 2001; Liu et al., 2004), it has been inferred that the *Annalepis*-type sporophylls originated almost simultaneously from the Early Triassic in the Russian South-East Siberia, where they were named as *Tomioistrobus* by Neuburg (1936) and in Australia, named there as *Cylostrobus* by Helby and Martin (1965) and *Skil-liostrobus* by Ash (1979). Moreover some authors suggested that they have migrated along the northern and the southern coasts of the Tethys, and spread to China (*Annalepis*), Germany (*Annalepis*) and France (*Annalepis*) on the northern coast of the Tethys during the Middle Triassic (Liu et al., 2004). Similarly, they suggested that the Middle Triassic *Annalepis* of China might have derived from the *Annalepis*-type *Cylostrobus* of the Early Triassic of Australia. However, since *Annalepis* is now known to have appeared in the Induan Kayitou Formation (such as the Mide and Tucheng sections) in South China, it seems that this taxon may also have derived from South China. Moreover, according to the distribution characteristics of the *Annalepis* horizon-bearing in the Yangtze River valley (Meng et al., 2000), it seems that the taxon *Annalepis* extended to this region during the Early Anisian (early Middle Triassic) and that its distribution gradually shrunk during the Middle Anisian-Ladinian (middle-late Middle Triassic), in response to the marine regression that occurred from east to west on the Yangtze Platform during that period (Meng, 1998; Meng et al., 2000).

It is very significant that in eastern Yunnan and western Guizhou border the genus *Annalepis* occurred in marine sediments together with typical Induan bivalves, ostracods, brachiopods and ammonites (Fig. 4). These observations indicate that the first occurrence of *Annalepis* is Early Induan in southwestern China, thus much earlier than in the Yangtze River area (Fig. 3). During the late Early and Middle Triassic, they might have migrated to the north and widely spread over the middle and lower reaches of the Yangtze River, in relation to the marine regression and transgression.

Zhou and Li (1979) were the first to describe Olenekian plants in South China, and to report that the fossil plants of the Lingwen Formation from the Qionghai District, Hainan Island, though fragmentary, are rich in individuals, comprising more than 20 species belonging to 18 genera. Later, Li (1995) added 38 species belonging to 28 genera, among which *Equisetites*, *Phyllothea*, *Neocalamites*, *Neuropteridium*, *Albertia*, *Voltzia*, *Glyptolepis* etc. The fossil plants of the Lingwen Formation are not only very similar to those of the “Buntsandstein” flora of western Europe, but also the plant-bearing beds of this formation are very similar to it in lithology. Thus, the *Neuropteridium–Albertia–Voltzia* assemblage present in the Lingwen Formation undoubtedly also belongs to the late Early Triassic, i.e. the Olenekian, in China.

Yao et al. (1980) indicated that the fossil fauna (including the bivalves *Towapteria* aff. *scythica*, *Leptochondris bittneki*, *Neoschizodus ovata*, *Unionites fassaensis*, *Pteria ussurica variabilis*; the brachiopod: *Lingula borealis*; the insect *Tomia*) and the fossil plants (Permian relics *Paracalamites stenocostatus*, *Annularia shirakii*, *Lobatannularia multifolia*, *Pecopteris* sp., *Gigantopteris* sp., and now *Annalepis* which was not yet reported) appeared simultaneously in the lowest part of the Kayitou Formation along the Yunnan and Guizhou border (Yao et al., 1980). This stratum corresponds to the *Claraia wongi* zone of the lowest part of the Feixianguan Formation, which is Induan in age (Fig. 4) (Zhou and Li, 1979). These elements of the Late Permian *Gigantopteris*-flora should have survived into the early Early Triassic (Wang, 1991; Yu et al., 2007). Our study indicates that the fossils showed in Fig. 2 from the Mide and the Tucheng sections are consistent with the above-mentioned fossils, except that *Annalepis* spp. were not recorded in Yao et al. (1980) paper. Thus we demonstrate that the relics of the former Late Permian *Gigantopteris*-flora and the Early Triassic *Annalepis* representatives co-formed the floral assemblage of the Early Triassic in South China. This assemblage is undoubtedly older than the *Neuropteridium–Albertia–Voltzia* assemblage recorded from the Lingwen Formation. Therefore, the Induan age of this floral assemblage fills the biostratigraphic gap between the *Changhsingian Gigantonoclea guizhouensis–Ullmannia* cf. *bronnii–Annularia pingloensis* assemblage defined by Li et al. (1995) and the Olenekian Triassic *Neuropteridium–Albertia–Voltzia* assemblage reported by Zhou and Li (1979).

#### 5. Conclusion

Until now the occurrence of the genus *Annalepis* was considered as a good biomarker for dating the late Early to Middle Triassic period. Therefore, it is highly relevant

**Fig. 5.** Fossiles de la Formation Kayitou (Trias inférieur) dans les sections de Mide et Tucheng (Mide: YXM - Yunnan, Xuanwei; Tucheng: GPT - Guizhou, Panxian.). 1–12: Sporophylles de Lycophyte attribuées à diverses espèces du genre *Annalepis* (Fliche). 1–3, 5–7. *Annalepis latiloba* Meng, 1998; cercle noir sur la Fig. 3 = mégaspore (cf. Fig. 14); Localité: section de Mide; Numéros d'échantillons - 1: YXM-21-27; 2: YXM-21-2; 3: YXM-21-11; 5: YXM-21-29; 6: YXM-19-2; 7: YXM-21-37. 4, 8, 12. *Annalepis angusta* Meng, 1995; Localité: section de Mide; Numéros d'échantillons - 4: YXM-21-5; 8: YXM-21-1; 12: YXM-19-11. *Annalepis brevicystis* Meng, 1995; Localité: section de Mide; Numéros d'échantillons-9: YXM-21-7; 10: YXM-21-18; 11: YXM-21-63. 13. *Ophiceras* sp.; Localité: section de Mide; Numéro d'échantillon-13: YXM-25-5. Détail de la mégaspore in situ d'*A. latiloba* de la Fig. 3 (cercle noir). Noter sa surface lisse et sa marque trilète. 1 barre d'échelle = 0.5 mm. 15–16. *Pteria ussurica variabilis* Chen et Lan, 1956; Localités: sections de Mide et Tucheng; Numéros d'échantillons - 14: YXM-21-68; 15: GPT-17-15; Barre d'échelle = 1 mm.

that in eastern Yunnan and western Guizhou, this genus occurred associated with typical Induan bivalves, ostracods, brachiopods and ammonites in the marine basal deposits of the Kayitou Fm (Fig. 5). This indicates that the First Appearance Datum (F.A.D.) of the “pioneering lycopsid genus” *Annalepis* is in fact Early Triassic (Induan) in southwestern China, where it newly occurred associated with surviving Permian plants, thus much earlier than in the Yangtze River domain and any other area in South-East Asia. It is now to be considered as marking the very beginning of Triassic deposition for the western Guizhou and eastern Yunnan domain. During the Early and Middle Triassic, it might have migrated to the north and spread widely over the other areas of South-East Asia.

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